THE PHYLUM TARDIGRADA

Third Edition

by

G. Ramazzotti and W. Maucci

English Translation by

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This translation is dedicated to Barbara,

who has tolerated the obvious priority

that the tardigrades demand.

Ma quando immediatamente riposava sopra l'arena aveva moto regolare, e progressivo, lento però a segno che a riscontro del Rotifero sembrava una testuggine, che si trascinasse; onde per segnarlo con qualche nome io non avrò difficoltà di chiamarlo il TARDIGRADO.

(da Lazzaro Spallanzani, 1776)

This selection was in the 1962 edition of "Il Phylum Tardigrada", but was not included in later editions.

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PREFACE TO THE TRANSLATION

This work began through translations of keys and species descriptions which were needed at various times. After the 1985 4th International Symposium on the Tardigrada in Modena, Italy, Sandra McInnes and Deedee Kathman traded translated sections with me. It was not the initial intent or hope to complete the total monograph, but it eventually became evident that it was feasible.

This is not a polished translation, for which I apologize, but I find some comfort in two quotations. The first is in the introduction of Pearl S. Buck's translation of *All Men Are Brothers*: "... it is inevitable that so long a book should be uneven in quality." The second is from Michael Crichton's *Eaters of the Dead*: "... it is in the nature of languages that a pretty translation is not accurate, and an accurate translation finds its own beauty without help."

The original pagination has been retained, as much as possible, to aid in comparison with the original text. The authors used many dashes, semicolons, and colons, and these were usually left as used. An occasional error was corrected, but it remains essentially as it was originally printed. No effort was made to include species described since the publication of the monograph.

The worker should be cautious at all times. Some species descriptions are based upon a single specimen. The species descriptions should be used in conjunction with the keys, and even then it will sometimes be very difficult and subjective. The descriptions of the species, characteristics used in the keys, and the illustrations are not always in agreement. Usually this is due to variation within the species, but it can be quite confusing to a beginner. My greatest fear is that some critical word like "not" might have been omitted, completely changing a statement. It is inevitable that some errors exist in this work, but hopefully not this type.

Permission to publish the English translation of this monograph was granted by Dr. Riccardo de Bernardi, director of the *Istituto Italiano di Idrobiologia*. Recognition is given to the following people for their contributions: Anne Engel and Robert P. Higgins for the translation of the first 145 pages of the second edition, which was used in translation of the third edition; Deedee Kathman for the key to genera, and species descriptions of *Hypsibius runae*, *Macrobiotus beotiae*, *M. dentatus*, and *M. occidentalis*; Sandra McInnes for "Observations" and key to *Macrobiotus*, and species descriptions *Dactylobiotus ambiguus*, *Hypsibius antarcticus*, *H. arcticus*, *Macrobiotus polaris*, and *M. meridionalis*. The support and friendship of Sandra McInnes and Deedee Kathman is gratefully acknowledged -- they are two of the nicest deuterostomes I know.

I close with a quote from Howard Ensign Evans' *Wasp Farm* which expresses many people's awe of tardigrades:

> TARDIGRADES: there is a frontier for you. Have you ever seen one? I may not know where to find the distributor in my car; I may stumble over the laws of thermodynamics; but I have seen a tardigrade!

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PREFACE TO THE THIRD EDITION

Already during 1979 I was persuaded that the monograph *The Phylum Tardigrada* was by this time old, as seven years had lapsed since its first edition. In fact lots of new studies were everywhere on tardigrades, there were numerous descriptions of new genera and new species, either in scientific publications, or in relation to three international symposia on tardigradology (Pallanza, 1974; Cracow, 1977; Johnson City, 1980). It made necessary then a new amplified edition and in large part redone, especially with regard to the systematics.

Joined with this point of my consideration, I was persuaded that I could not succeed this with only my effort: I had by this time surpassed eighty years and I did not feel absolutely free to face a work of such mass. I thought then to turn to a collaboration and preferred then Professor Walter Maucci, both because he has excellent knowledge of the tardigrades, and because of my friendship with him of several decades, and finally because of the nearness of his residence to Milano, that which facilitated our meetings, during the drafting of the work.

It is therefore that this new edition of *The Phylum Tardigrada* is owed in large part to Maucci, to whom we are extremely grateful and with whom I share in full the possible defects and the possible errors in the text, because of any doubt or uncertainty we have always discussed in length between us, or with direct meeting, or by telephone.

I wish also to thank, for the constant affectionate support, my very dear old friend Livia Tonolli of the Italian Institute of Hydrobiology of Pallanza.

PREFACE TO THE FIRST EDITION

The aim of this volume is to present an up-to-date picture of the Tardigrada of the world -- as complete as possible, but always in a simple and clear way -- especially from the systematic point of view; accordingly, the book -- at least in the author's intentions -- should become a useful and modern instrument for research-workers, but it makes no pretense of being a substitute for other basic works, amongst which I will mention only Marcus' monumental 1929 treatise.

A group of initial chapters summarize -- in brief synthesis -- the extent of our present knowledge concerning the morphology, physiology, and ecology of the Tardigrada; after a few brief indications on methods of collecting and studying the animals, comes an account on classification, different keys for the identification of the genera and the species with the individual genera, accompanied by numerous practical observations on their habits, and finally descriptions of the different species. In this last part of the work, I adopted a criterium for grouping the species which differs considerably from classical schemes and which will no doubt be criticized by those who favour pure systematic formalism: by this I mean that the species are listed in alphabetical order, regardless of the order, sub-order, family, genus, or subgenus to which they may belong.

This method of grouping allows easy and quick reference to the desired species, as one might look up a word in a dictionary. I hope that -- in practice -- the advantages will supersede the drawbacks, which in fact seem minor to me, as it is always possible to obtain the systematic order of the species by consulting the chapter which deals with the taxonomic subdivision of the Tardigrada: the chapter in question contains a complete classification scheme and also refers, in accordance with every genus or subgenus, to the list of species which are part of it (drawn up in alphabetical order). The identification keys for species in individual genera are also set up in alphabetical order (by genus).

In compiling these determining keys, and in describing the species, my main aim was to facilitate, as much as possible, recognition of the species themselves, and distinction from the other species which resemble them most; the sketches which are not original were for the most part redrawn by me for technical reasons; in the appendix are listed the few species not included in the identification keys or the text, either because they have been discovered so recently, or for other reasons.

The bibliography -- excepting a few pre-1936 works I hold as being fundamental -- only contains works published later than 1936, as all those of preceding years are already listed in Marcus' 1929 and 1936 treatises: in spite of the care which went into the bibliographical research, there are probably certain omissions, especially regarding eastern publications, for which I should like to apologize right now.

I hope that this work -- by providing less painful initiation -- may induce some young people to study Tardigrada, which present us with such numerous, interesting and yet unsolved biological and ecological problems; the problems at hand are not always, I admit, very easy, but for this very reason, tackling and solving them, or merely contributing to their solution, could be a source of deep satisfaction to the scholar.

Finally, I should like to thank my friends Professor Vittorio Tonolli, Director of the Italian Institute of Hydrobiology, and Professor Dr. Livia Tonolli Pirocchi for their helpful and affectionate support, always shown in the most pleasant way.

Pallanza, Italian Institute of Hydrobiology, January 1962.

I.

NOTES ON THE MORPHOLOGY AND PHYSIOLOGY OF TARDIGRADES

GENERAL REMARKS.

Tardigrades are small animals, almost always invisible to the naked eye, provided with 4 pairs of locomotor appendages (legs), generally ending with claws of varying numbers and shapes (cf. Fig. 1).

A single genus (*Hexapodibius* Pilato, 1969) has the 4th pair of legs very reduced, or absent. (Maucci, 1974, has also observed a teratological example of *Itaquascon* sp. completely lacking the 4th pair of legs.)

The body, bilaterally symmetrical, is of varying lengths, flat on the ventral side and more or less convex on the dorsal side; it is covered with an epidermis which in some cases is smooth, in others rough, warty, tuberous, or grooved over the whole surface or only certain parts. The epidermis is often thicker on the dorsal surface (sometimes also ventrally) to the point that it forms a proper plate, subdivided into sections (Fig. 2).

The total length, excluding the 4th pair of locomotor appendages (which are lateroventral like the others, but extend considerably further than the posterior of the body) varies between a minimum of about 50μ for *Bryodelphax parvulus* when it has just hatched, and a maximum of about 1,200μ for exceptionally large members of *Adorybiotus coronifer* and *Milnesium tardigradum*; the average measurements vary from 250-300μ for members of the family Echiniscidae and from 350-500μ for members of the family Macrobiotidae. These average lengths refer to adult specimens which have completed their full growth. As a rule, the marine species are ordinarily smaller.

Tardigrades are often colorless or greyish and more or less transparent; at other times they are brownish, yellow, orange, pink, or red, through pigmentation of the epidermis or accumulation of reserve matter floating in the coelomic fluid; a few very rare species (almost all included in the *Echiniscus viridis* group) are partially or totally colored in various shades of green.

Some tardigrades live in the ocean, others in freshwater, still others in soil and in the leafy deposits inland, or else they form a part of the biocoenosis characteristic of sands washed by fresh- or salt-water, distinguished by the name of psammon or interstitial fauna; but the greatest number of known species live in moss, liverworts, lichen, and also

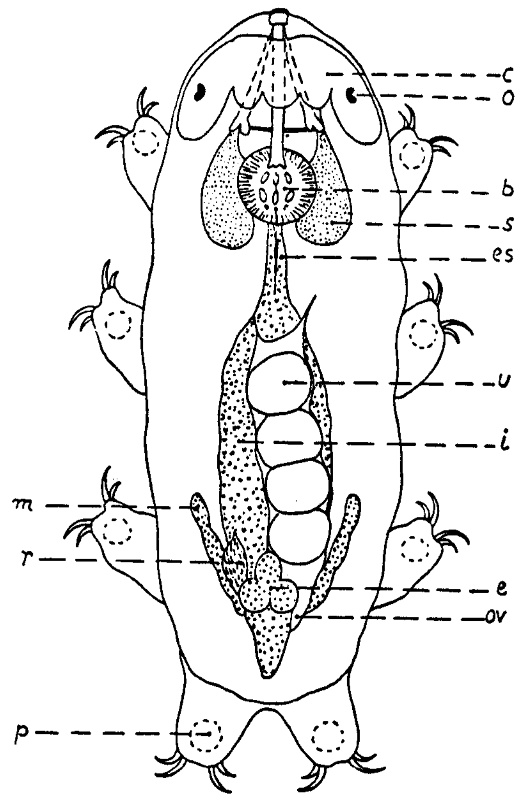


Fig. 1 - Dorsal, semi-schematic view of *Macrobiotus*; b, pharynx; c, brain; e, dorsal excretory gland; es, esophagus; i, intestine; m, lateral excretory gland (vasa Malpighii); o, eyespot; ov, oviduct; p, pedal gland (or claw gland); r, seminal receptacle; s, buccal (or salivary) gland; u, fully developed egg (after Pennak, modified).

certain flowering plants (*Silene*, *Saxifraga*, *Androsace*, etc.), which in their growth assume the shape of small pads (pulvini). However, tardigrades must be considered as definitely aquatic animals, even when they do inhabit environments which can be termed terrestrial (like moss, lichen, soil, etc.) as they are able to lead an active life only in presence of water, which moistens their environment and surrounds their bodies with a liquid layer of varying thickness.

The moss-inhabiting tardigrades, on which most information has been collected, are widespread throughout the world and are found wherever there is a moss or lichen vegetation, especially in temperate and cold zones, whereas tropical mosses seem to have a smaller fauna even taking into account numerous exceptions. Various species are cosmopoli-

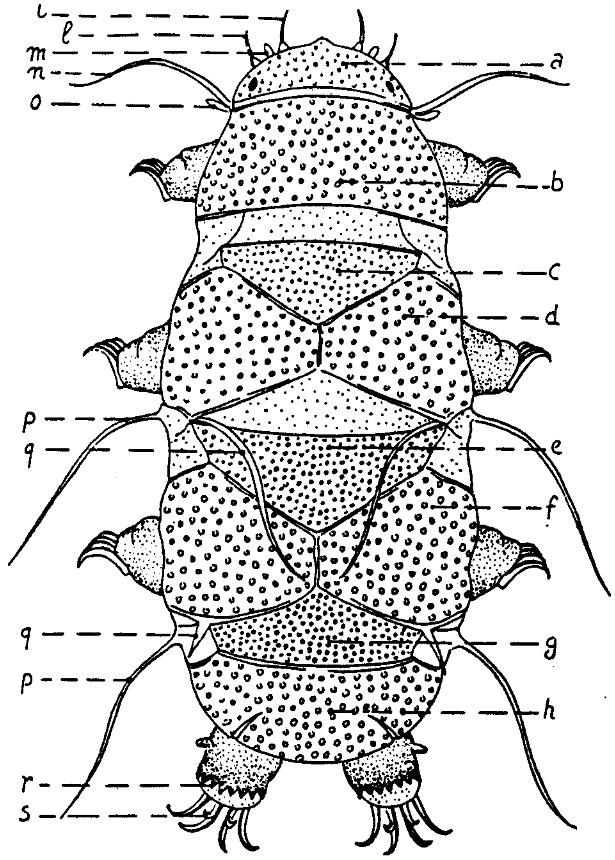


Fig. 2 - Dorsal view of an *Echiniscus*. a, frontal plate; b, scapular plate; c, first median plate; d, first paired plates; e, second median plate; f, second paired plates; g, third median plate; h, terminal plate; i, internal buccal cirrus; l, external buccal cirrus; m, cephalic papilla; n, lateral cirrus (cirrus A); o, clava; p, lateral appendices (filaments); q, dorsal appendices (filaments and spines); r, dentate collar on the 4th pair of legs; s, spur on the internal claws.

tan, for example *Macrobiotus hufelandi*, *Hypsibius oberhaeuseri*, *Milnesium tardigradum*, etc., which have been observed almost everywhere, from the Arctic to the Antarctic; other species are far rarer and were discovered only in a few areas -- or even in a single locality. Observations carried out to date are still too scarce to permit the compilation of a sound account on the geographic distribution of various species of tardigrades; not only the moss-inhabiting species, but especially the marine and freshwater psammon and various terrestrial types.

Especially with regard to the marine species, however, the knowledge has greatly increased since the publication of the second edition of this work.

The tardigrade's body is separated into 5 segments, somewhat indistinct from the outside: a first cephalic segment, 3 segments corresponding to the first 3 pairs of legs, and 1 terminal segment, corresponding to the last pair of legs. This is covered by a cuticle which often has sculpture, or processes in the form of spines or filaments, very important in precise taxonomy; the cuticle invaginates to line the anterior intestine and the rectum.

The general body cavity contains a colorless liquid, in which float large grayish, yellowish, or orangish spheroid cells, or sometimes (e.g., in many Echiniscidae) several reddish granulations, which owe their color to the presence of carotene. According to some authors this is a kind of separate adipose tissue, but these spheroid cells (or body cavity cells) do constitute reserve matter. These cells, when the animal is in motion, continually move about inside the body, swept by the flow of the coelomic fluid and as there is no circulatory system, circulation occurs in the simple way just described.

Respiration is carried out through the epidermis, which is permeable, as the swift dehydration of the tardigrade indicates. These animals are hypersensitive to any reduction of oxygen content in the water surrounding them, which causes them to immediately fall into a special state (asphyxial state), which is not always reversible and, prolonged even for a few days, leads to death.

The mouth opens in an anterio-ventral position and is followed by the buccal tube which leads to the pharyngeal bulb (pharynx, bulb), which has a sucking function; on the sides of the buccal tube are arranged, one on each side, 2 pointed teeth, of varying shape and size (stylets), which can be pushed forward or retracted. The pharynx is followed by a short esophagus, the midgut, and the rectum (Fig. 1). A ventral anus, which can alternatively be terminal in position, lies between the last pair of legs: this can represent the orifice of a cloaca or be distinct from the genital opening.

Many tardigrades feed on the chlorophyll content of cells, perforating the membranes with their stylets, or they can feed on algae, fungi, or detritus; some species are occasionally or exclusively carnivorous. Rarely one can find cases of parasitism and ectocommensalism.

The musculature is made up of bundles of smooth muscle fiber, the tips of which are fused into small internal protuberances in the epidermis; muscle contraction produces only adductive motion, while the antagonistic action is generally produced by the pressure of the internal body fluids and the elasticity of the epidermis. However for the buccal stylets there are retracting and protracting muscles.

The nervous system (Fig. 23) is made up of a supraesophageal (cerebral) ganglion, joined by a circumesophageal ring to a subesophageal ganglion, and also by a ventral chain of 4 simple ganglia, which are more or less bilobed. Since the first ventral ganglion is also linked by 2 strands to the subesophageal ganglion and by 2 other strands to the supraesophageal ganglion, there are in fact 2 circumesophageal rings present. Then there are a few other small peripheral ganglia. There may or may not be eye spots on the lateral lobes of the brain.

The gonad (Fig. 1) is single, secondarily uneven, and is made up of a sack, fixed in a dorsal position by its anterior end, and held by filiform ligaments. In the male there are 2 deferens ducts, while the female has only 1 duct on the right or left of the intestine, which can lead either to a ventral or preanal gonopore, or into the rectum. Sometimes the females have a seminal receptacle, which opens ventrally into the rectum, besides the oviduct.

Some species deposit free eggs, singly or in small groups, while other species deposit their eggs in the old discarded epidermis, abandoned while molting.

Fertilization can take place in two ways: internally, through the cloaca (probably when the female is molting), in the species which deposit free eggs, and externally in other species, which abandon the eggs in the old cuticle. The sexes are separate[1], but the males are sometimes very rare (e.g., in *Milnesium tardigradum*) or -- in some cases -- still unknown.

One of the moss- or lichen-inhabiting tardigrades' most interesting characteristics is their ability to fall into a state of latent life (cryptobiosis or anabiosis) when the environment in which they live becomes dehydrated. Tardigrades of distinctly aquatic species do not have this ability to enter into cryptobiosis.

Another way of overcoming periods of unfavorable atmospheric conditions is the formation of cysts, however, little is known about the causes of this phenomenon, common mainly in freshwater and terrestrial species, less among the moss-inhabiting species.

[1]Recently Bertolani (1979) verified hermaphroditism in Isohypsibius granulifer baicalensis.

The tardigrade's position in the zoological system is rather difficult to determine and different authors still disagree. We shall come back to this further on, but at this point I shall say only that, according to the more modern view, the tardigrade is to be considered as a Phylum.

FIRST OBSERVATIONS OF THE TARDIGRADES

It seems very likely that tardigrades were studied for the first time, by different naturalists, during the years 1773 to 1776; the first to write about them was almost certainly J. A. E. Goeze, parish priest to Quedlinburg (Harz), who described a freshwater tardigrade, calling it a "Kleiner Wasser Bär" (little water bear) and made a sketch of it. Because Goeze states that the animal has three claws on every leg, Marcus (1929) believed that the type described is a member of the genus *Hypsibius*, in which the secondary branch of the smaller doubleclaw is often hard to distinguish, thus it is understandable that this author should have spoken of three claws, rather than four (in fact there are really two doubleclaws).

In 1774 the Italian abbot Bonaventura Corti, professor of physics at the college of Reggio Emilia published a brief work in Lucca, "*Osservazioni microscopiche sulla Tremella e sulla circolazione del fluido in una pianta acquaiola*," which entailed the author's acquaintance with tardigrades which he called *Brucolini* (little caterpillar) and a few annotations on his part on their ability to come back to life. He writes on page 97: "When I poured water onto the sand in the gutter, I saw not only the Rotifera, but also some tiny animals, which I have called gutter-sand-worms because of their resemblance with caterpillars, come back to life; it even seemed to me that they revived faster than the rotifers themselves." Corti carries this perceptive and extremely important observation even further: "This then is the condition for reviving the little animals, and the Tremellae, that they dry up slowly, which condition can be obtained when they move about it wet sand, or dirt, ... etc."

J. C. Eichorn follows in 1775, saying that in June 1767 he observed a "Wasser-Bar" (tardigrade) among freshwater algae.

We have now reached the year 1776 when the abbot Lazzaro Spallanzani, professor of Natural History at Pavia University, published the second volume of his "*Osservazioni e Sperienze intorno ad alcuni prodigiosi Animali, che è in balìa dell'Osservatore il farli tornare de morte a vita*," and more specifically in Section II, the author describes admirably "a little animal of a sort of dirty yellow color," which he had often seen "moving crookedly and with difficulty at the bottom of the water, it was hardly able to move at all, and it turned over so many times with its legs upwards and trying to continue on its way repeated its efforts to return to its natural position, but mostly without avail ... ." Then he goes on: "But a more continuous and deeper examination indicates to me it is a truly aquatic animal, which dragged itself along in what I would term a very awkward manner, in that it could not remain upright because of the smoothness of the small watch glass on which I had put it to study it. But as soon as it stood on sand it moved regularly and made smooth progress, slow in its track, and when compared with the Rotifera it looked like a small tortoise crawling along, so that when it came to distinguish it by some name, I thought it suitable to call it Tardigrade."

So it was Spallanzani who first gave the name of tardigrade to the animals with which we are dealing, and who first conducted an admirable experimental investigation into the phenomenon of cryptobiosis and anabiosis (to use the modern terms) which occur in certain rotifers, tardigrades, and nematodes.

In fact, Spallanzani, describing his tardigrade and illustrating it in 3 sketches, made a mistake by giving it 6 legs, instead of 8; but this is understandable in view of the lesser mobility of the tardigrade's 4th pair of legs, which often drag behind and can be mistaken for a caudal appendage, especially if one takes into account the imperfections in the optical equipment in those days. Spallanzani, referring precisely to this 4th pair of legs, says: "... the front part (of the animal) is rounded, and the back part ends in 4 filaments which have hooked ends, that are used for holding on wherever it wishes."

It is now impossible to establish, on the basis of his descriptions and sketches, which species the tardigrades studied by Spallanzani belonged to. A note on page 443 of the 1935 edition of "Opere complete di Lazzaro Spallanzani" (Ed. U. Hoepli, Milano) states that the species concerned is *Macrobiotus Oberhaeuseri*, Doyère. Apart from the fact that the exact term today is *Hypsibius oberhaeuseri*, I would tend to deny that this was the species in question, for an observer, as perceptive and precise as Spallanzani doubtless was, would not have passed by the characteristic brownish-purple longitudinal stripes of *H. oberhaeuseri*, easily visible even under weak magnification and with imperfect optical equipment, and he would not have spoken of "a little animal of a sort of dirty yellow color." I would agree more readily with Doyère (1840) and Marcus (1929) in holding that this particular animal is a *Milnesium tardigradum*.

However it is clear that despite attempts to identify the species seen by the first researchers, due to the inevitable inadequacy of the descriptions, remain highly questionable.

It is certain that Spallanzani was able to observe a good number of tardigrades (and thus perhaps different species) and that he experienced difficulties in breeding them as he writes: "In comparison with rotifers, tardigrades are very rare, so you could call yourself lucky if, for every twenty rotifers, you met three or four tardigrades. All have the same outline, however much they may differ in size. I have isolated several, shutting them up alone in bell jars, then putting them on their native sand, and then leaving them in pure water. The aim was to see how they propagate. But instead of propagating they inevitably died, some sooner than others. All however were dead within six days."

He described vividly how the tardigrade contracts at the beginning of anabiosis (assuming that characteristic shape often called "barrel" by more modern authors): "The phenomenon of death, in the absence of water, and revival, when water is replaced, occur in the same way in the tardigrades as they do in the rotifers; movement gradually lessens, the legs are retracted and disappear completely into the body, which shrinks a great deal, dries out completely and takes on a globose shape. And the opposite of what has just been related occurs when reviving the tardigrade with a new dose of water. And just as in rotifers the number of revivals is limited, so it is in the tardigrades."

Spallanzani, just as Bonaventura Corti had done before him, also understood the importance of slow dehydration, in order that the animal might enter into a cryptobiotic state. However, he held that this was a real death, followed by a resurrection, and in fact (confirming this concept, often expressed in the text quoted above) he continues about rotifers, tardigrades, and nematodes: "And these are the three species which dwell in the sands on roofs, to whom resurrection after death has been granted by nature, ..." We shall return to this topic, and the lengthy controversy ensuing from it, in the chapter on cryptobiosis.

Succeeding Spallanzani, in 1785, O. F. Muller published a work on tardigrades in Zurich, and spoke of *Acarus ursellus*, the description of which (according to Marcus) can be adapted to any species of *Hypsibius*. In 1795 Senebier observed "Das Faultierchen" ("the little lazy animal," which is a tardigrade, but also "the little putrefying animal"). In 1803 Schrank spoke of *Arctiscon tardigradum*, of which however no sketch is provided and whose identity accordingly remains very uncertain, as in the case of all tardigrades studied by previous scholars, although there is some probability that the type concerned is *Milnesium tardigradum*.

Thus we reach the beginning of the 1800's and the initiation of more precise observations on the part of different naturalists, especially Schultze (1834, 1840) who defined the genera *Macrobiotus* and *Echiniscus*, and Doyère (1840) the genus *Milnesium*. Whoever is interested in the history of scientific research in this field in the following years, until the first decades of the 1900's should consult the relevant chapter in Marcus (1929), where the subject is treated in considerable depth or also Ramazzotti and Maucci (1982).

SHAPE, COLORATION, AND SIZE

Fundamentally, the shape of a tardigrade can be considered that of a cylinder, more or less modified, to the point of assuming an elliptical outline, and always convex on the dorsal side and flat on the ventral side; study of the sketches will help better than any description to show a typical aspect of the members of different species.

From a practical point of view, one can divide tardigrades into two large groups: one, to which belongs the species possessing a distinct carapace composed of individual plates, which can be called the "armored" type containing the families Stygarctidae (with 5 marine genera: *Stygarctus*, *Mesostygarctus*, *Parastygarctus*, and *Megastygarctides*) and Echiniscidae (with 8 moss-dwelling genera: *Echiniscus*, *Bryochoerus*, *Bryodelphax*, *Hypechiniscus*, *Parechiniscus*, *Pseudechiniscus*, *Mopsechiniscus*, and *Cornechiniscus*).

The other group can be termed "naked" tardigrades and includes the members of all the remaining families and genera.

Usually tardigrades are widest around the middle of the body, or a little further forward with the width decreasing at the head and tail ends. The width/length and length/thickness ratios differ widely, for example: the order Eutardigrada has a length/width ratio of 3.5/1 to 5/1 and a length/thickness ratio of 5/1; the suborder Echiniscoidea has a length/width ratio of 2/1 to 3/1 and a length/thickness ratio of about 3/1; on the other hand the parasitic *Tetrakentron synaptae* is far wider and flatter.

As far as the tardigrade's apparent coloring is concerned, one must keep in mind that it can have different sources, and these are:

1. Coloration due to intestinal content:

   This is easily visible, especially in transparent tardigrades and careful examination is enough to avoid being misled. This coloring naturally depends on food intake and the digestive process and generally ranges from different shades of yellow and green to brown and blackish; in exceptional cases a bluish color is seen, either in the intestinal content, or in the intestinal cells themselves (Marcus observed it in *Macrobiotus islandicus*, *Hypsibius dujardini*, *Hypsibius arcticus*, and *Doryphoribius evelinae*).

2. Coloration due to body cavity cells and granules:

   Certain species in the genus *Macrobiotus* (e.g., *M. furcatus*, *M. islandicus*, *M. occidentalis*, etc.) exhibit a bright yellow to orange coloring caused by pigment granules enclosed inside the body cavity cells: these appear colored, in the species listed above, while the greatest part of the other tardigrades of the same genus are colorless. Nearly all Echiniscidae (of the genera *Echiniscus*, *Pseudechiniscus*, and *Mopsechiniscus*) owe their red or reddish coloring to free granulations (spherical or oval in shape) which are not contained within the cells but float in the body cavity liquid.

3. Coloration of the epidermis and cuticle:

Examples of this type of coloring are the green specimens of armored tardigrades in the *Echiniscus viridis* group, the longitudinal, brownish stripes of the naked tardigrade *Hypsibius oberhaeuseri*, and the uniform pink, yellow, or brown color of the naked tardigrade *Milnesium tardigradum*; when these last two species are treated with a dilute solution of KOH (potassium hydroxide) the pigment dissolves and turns to a bright shade of purple.

If we set aside the tardigrade's pseudocoloration due to intestinal content, only two other types of coloring remains; the first of these, that is the type due to pigment granules contained in the body cavity cells or else free, owes its coloring to carotene.

In the case of the genus *Echiniscus* Massonneau and May (1950) showed that the pigment is enclosed within small lipid bodies (orange, yellow, and red spherical cells) free inside the body cavity liquid. The cells' dimensions are no more than 5μ (in about 23% of the cases no more than 2μ, in 75% between 2 and 3μ, in 2% between 3 and 5μ) and their chemical reactions, including an intense blue coloring when in contact with sulfuric acid, are those of carotene.

Nevertheless, according to the authors named above, the depth of color does not change during cryptobiosis and seems to increase when *Echiniscus* is placed on a lichen rich in carotene, such as *Xanthoria parietina* Acharius. Thus it appears that this kind of pigment has alimentary origins, especially since the specimens of a deep red color are those with intestines swollen by greenish or brown substances, originating from plant food intake, while the less strongly colored specimens have normal intestines with a low, or nonexistent, food content.

Different depths and shades of red in various specimens are also due to the fact that pigment cells in a single animal can have an uneven color, partly yellow and partly orange or red: the total coloring of the tardigrade depends on the predominance of one or another tone in the pigment cells present.

This difference in the coloring of individual pigment cells in the same specimen, also shows that the pigment does not remain in a constant state, but undergoes continual transformation, partly being worn down through oxidation (through the permeable cuticle) and partly being reshaped: this mainly applies to adults, as young specimens are barely colored at all.

Massonneau and May put forward the hypothesis that carotene, through its characteristic ability to absorb the solar spectrum's shorter wavelength radiations, also has a protective function for the intestine and its cells, which produce enzymes, and which are in turn ultrasensitive to ultraviolet radiation.

Carotene also exists in the orange and reddish eggs of the Echiniscidae but in this case the pigment appears to be diffused and to impregnate them completely, instead of being confined to cells.

According to Mihelčič (1950), who does however admit the carotene's alimentary origin, the pigment of *Echiniscus* and *Pseudechiniscus* also migrates in the epidermis and plays an important part in the formation of the new carapace during molting, but it must be noted that there are completely colorless, armored tardigrades (for example, in the species *Bryodelphax parvulus* and *Parechiniscus chitinoides*) which are able to form a new carapace in the absence of pigments. Furthermore it is easy to observe, by pressing the brightly colored adult *Echiniscus* between two slides under a microscope, that the cuticle and the epidermis underneath often come out totally colorless and transparent. This would lead one to conclude that pigment is mostly absent from the epidermis.

Mihelčič believes that the carotenes, together with the small, oily cavity drops, constitute an important food reserve, and he also observed that in *Echiniscus*, which have been starved, the small oily globules containing pigment are the first to be consumed, decreasing in number and size, and then the pigment granules, no longer enclosed in the oily droplets but floating free in the cavity liquid are consumed. However, not all the pigment cells are consumed (since *Echiniscus* never completely lose their color), but a portion of them are retained to rebuild the carapace, in Mihelčič's view, at the time of molting.

This author also holds that carotene, which is yellow or red in Echiniscidae, is colorless in the genera *Macrobiotus* and *Hypsibius*, but this statement most certainly demands deeper study before it can be accepted without reservation.

Mihelčič adds that armored tardigrades of a deeper red tone are those from sunny environments where the evaporation of water is swifter, and where the atmospheric acidity is slight; but in shady environments, where evaporation is slower and the atmosphere more acid, the coloring is paler. Based upon our observations, we are not completely willing to agree with this point of view, which appears only sometimes valid. We have observed, for example, in populations of *Echiniscus* of the *blumi* group, a coloration clearly darker in shady environments, and light colored, even yellow, in very sunny environments (for example, on the plateau of Anatolia).

On the other hand Eutardigrada exposed to a high intensity solar radiation (as, for instance, those in glacier fusion pockets, or *Kryonitlocher*) are certainly of a dark brown or black color.

We are left with the last type of coloring: that of the epidermis and cuticle, but information on the subject is scarce. Nothing is known about the green coloring of *Echiniscus viridis*, a rather rare species: the usual red body cavity granules (probably carotene) are found here, but the cuticle, claws and cirri are brightly colored green or olive-green.

In *Hypsibius oberhaeuseri* and *Milnesium tardigradum* (and in a few other species) the epidermal pigments turn bright purple in the presence of alkali: according to May (1948) the pigment seems very like the yellow or orange coloring substance (parietina or chrysophoric acid) contained in *Xanthoria* and in a few other lichens.

In addition to all the colorings we have dealt with in the preceding passage, there is often in tardigrades an epidermal pigmentation which increases with age. Quite frequently, if one observes larger and older specimens under transmitted light, especially of the genera *Macrobiotus* and *Hypsibius*, they show uniformly diffuse black or brownish pigmentation, which can alternatively be gathered into longitudinal or transverse stripes or small granular spots. These are most likely to be metabolic waste products (Marcus, 1929) and also occur, through aging, in species which in youth were completely colorless or grayish. This type of "old age" pigmentation does however acquire a whitish tinge under reflected light and differs in this way from the original colors, which hardly change at all (except for slight variations in the nuances of color) under either transmitted or reflected light.

As far as dimensions are concerned, we have already provided some brief indications on the subject in the chapter "General Remarks." We will only add that the greatest average lengths are found in the families Macrobiotidae and Milnesiidae, with exceptional maxima at around 1,200μ, while the measurements of members of other families remain much lower, ranging in general from 120 to 750μ, whatever their habitat.

It is important to keep in mind that a tardigrade's length must always be measured from head to tail, *excluding the last pair of legs*, and with the animal stretched out.

THE EPIDERMIS.

The epidermis, which secretes the cuticle, is made up of large, flat cells, containing large nuclei and numerous vacuoles. As far as one has been able to make out until now, it seems that the number of cells (not, however their size) remains constant in both young and old specimens of the same genus, and that the differences between one genus and another are slight.

Figure 3 shows the cell layout on the dorsal and ventral sides of *Milnesium tardigradum*, and the conspicuous differences in their shape and size in various zones of the body.

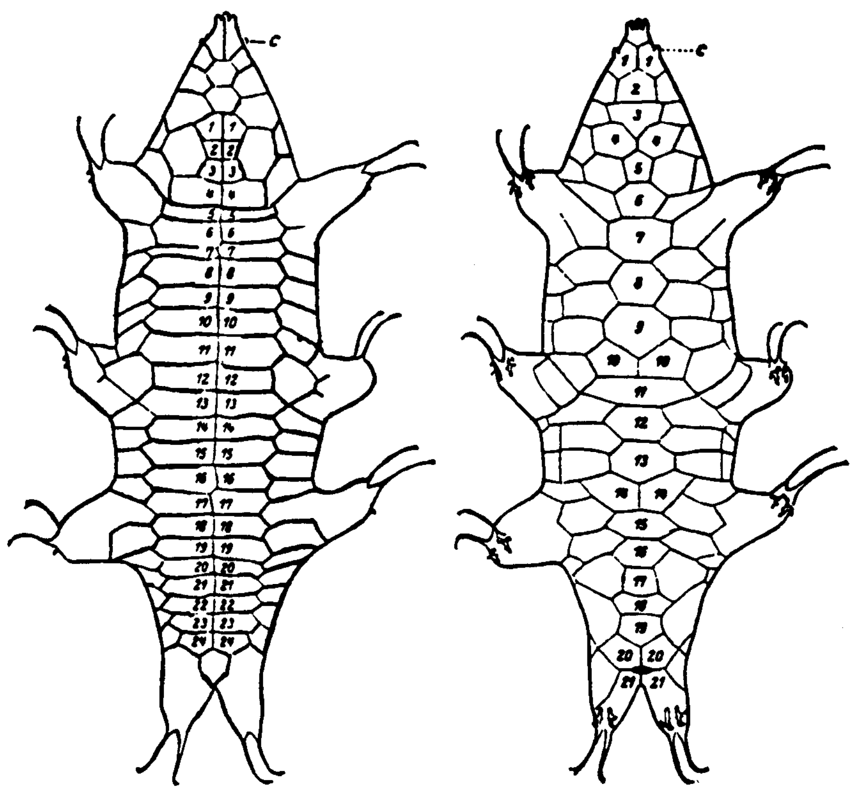


Fig. 3 - Dorsal and ventral views of *Milnesium tardigradum*, after impregnation in silver, of the outline of the epidermal cells (from Marcus).

From the works of Baumann (1922) and Marcus (1927, 1928, 1929) stems the knowledge that the epidermis, apart from secreting the cuticle, has two other functions:

1. It stores metabolic waste products, as has been verified in experiments through the use of vital stains; such excretions sometimes produce those stripes or zones of pigmentation of which we spoke in the previous chapter and which acquire a darker color with growing age.

2. It stores reserve foodstuffs, which cannot be distinguished morphologically from the excretory granules mentioned above, but which differ from them through their disappearance in tardigrades which have been deprived of food, which accordingly become highly transparent; the excretory granules on the other hand remain unchanged, even in these conditions. It must, however, be noted that the function of the epidermis as storage space for food reserves has not yet been quite clarified and that its importance, in this respect, is far less than that of the body cavity cells.

At the distal extremity of the tardigrade's motor appendages (legs), the epidermis thickens and forms a sort of bulb (claw gland, cf. Fig. 4), which secretes the new claws at the time of molting and which will be mentioned again further on.

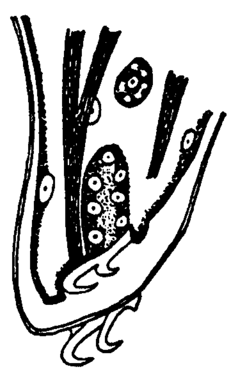


Fig. 4 - Fourth leg of *Macrobiotus hufelandi* before molting, with claw gland (from Cuénot, redrawn).

THE CUTICLE AND ITS PROCESSES.

The cuticle, more or less transparent, covers the epidermis, and has a rather complex structure, which recent research by use of the electron microscope has illustrated for some species either of Hetero- or Eutardigrada. The results of such research does not yet allow conclusions to be made. However it appears that it might acknowledge the existence of an internal layer (procuticle) and an external (epicuticle) both subsequently subdivided. The total thickness is about 1μ (for example, in *Macrobiotus hufelandi*), with a lesser amount for various marine species, while in the armored Heterotardigrada (Echiniscidae) it reaches thickness up to 2μ (*Echiniscus testudo*, according to Crowe) and even 2.9μ (*Echiniscus viridis*, according to Crowe et al.).

According to Marcus and other authors, the cuticle is composed of protein and not of chitin. So for example Baccetti and Rosati (1971) and Crowe et al. (1971) were not able to establish the presence of chitin. On the contrary, Cuénot, May, and more recently Bussers and Jeuniaw (1973) have obtained reaction of chitin, in Eutardigrada, and in the Heterotardigrada *Echiniscus merokensis*. We have to think that the procuticle is chitinous, while the epicuticle is not chitinous. Further research is still necessary.

The cuticle covers the body and lines both the stomodeum and the proctodeum.

With regard to systematics, the external aspect of the cuticle and its processes are very important; these processes can take the shape of granulations, bumps, plates, spines, filaments, papillae, etc. Thus a thorough knowledge of these different characteristics is necessary for the use of the keys, drawn up further on. We therefore think it advisable to dwell at length on the description and illustration of the cuticular processes of the tardigrades.

We have already said that (see page 25) from the practical point of view (not taxonomic) we have to distinguish armored tardigrades and "nude" tardigrades. The first includes the family Stygarctidae (marine) and Echiniscidae (terrestrial). All the other families have species not armored.

The "nude" tardigrades have smooth cuticle, or variously sculptured. They may have pores (which Cuénot called "pearls"), which show in optical section as small dots, circular or oval refractory, variously scattered, more abundant and larger on the dorsum, especially on the caudal part of the body. At times (as in *Macrobiotus intermedius*, *Macrobiotus spallanzani* and several others) these pores are very visible (with diameters up to 2-2.2μ, and even as much as 6-7μ, in *Macrobiotus pustulatus*). In other species (*M. areolatus*, *M. richtersi*) the pores are absent.

The sculpture of the cuticle in the "nude" tardigrades may consist of a fine granulation (on all the dorsum, or on some part of it) or of plates, of papillae, and of reinforced cuticle which has a reticular network design more or less marked. In many species (almost all included in the genus *Isohypsibius*) the dorsum has gibbosities, in various number and arrangement (associated or not with other types of sculpture).

In the armored tardigrades, the cuticle on the dorsum (and sometimes also on the venter) has plates, of which the number and arrangement constitutes important taxonomic characteristics.

In the family Stygarctidae the dorsum has five plates, aligned in a cranio-caudal sense, and to be exact: a cephalic plate, three somatic plates, and a caudal plate.

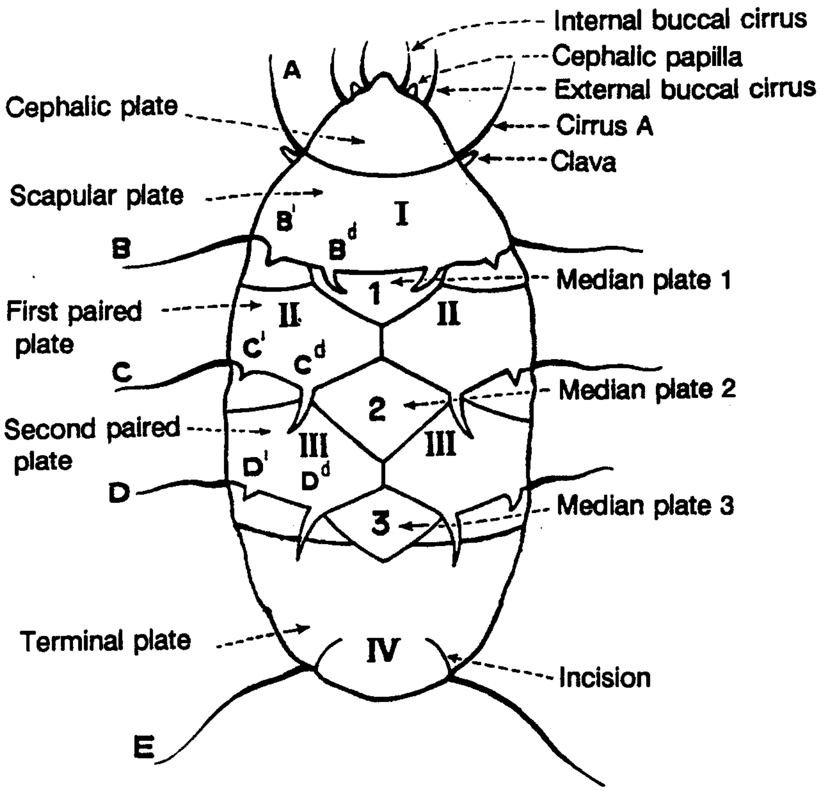


Fig. 5 - Plan of the arrangement of the plates and appendages in an *Echiniscus*.

For the Echiniscidae the plan of the armor may be based on the genus *Echiniscus* (which is illustrated, in outline, in Figures 2 and 5). Such armor is composed as follows:

- A cephalic or frontal plate which covers the cephalic region.

- A scapular (I) plate, unpaired and very wide.

- A first median, or intersegmental, plate (1), unpaired, which does not reach the sides of the body.

- A first paired plate (II), which is in fact made of two plates, divided by a longitudinal line in the middle; this division can be more or less clear.

- A second median, or intersegmental, plate (2), similar to 1.

- A second paired plate (III), similar to II.

- A third median, or intersegmental, plate (3), which can be at times hard to see or even lacking.

- A terminal plate (IV) which, near the posterior end, shows two notches or incisions which are missing only in exceptionally rare cases; the terminal plate can be more or less deeply faceted.

This scheme undergoes modification in the other genera of the family (some of these were for a long time considered as subgenera, but now almost all of the specialists are agreed in their elevation to genus rank).

In the genus *Bryochoerus*, all the median plates 1, 2, and 3, are divided transversely into a rostral and a caudal part, so that it looks like six median unpaired plates; the terminal plate does not have an incision.

In the genus *Bryodelphax* the median plates 1 and 2 are divided transversely, while plate 3 is undivided, so that it looks like 5 median plates; lacking the incision of the terminal plate.

In the genus *Hypechiniscus* the plates are subdivided as in the preceding genus *Bryodelphax*, however the terminal plate has an incision (Fig. 6).

Finally in the genera *Pseudechiniscus*, *Mopsechiniscus*, and *Cornechiniscus* (Fig. 7) besides these plates, of which already spoken, there is an additional plate, the so-called pseudosegmental plate (subIII) inserted between the III and the IV, and which is undivided (unpaired), or else divided along a longitudinal median line (paired). They can have various appendages, lateral, dorsolateral, and dorsal, which are designated with the letters used for the genus *Echiniscus*.

The subdivision of the armor of the Echiniscidae into single plates, giving reciprocal mobility, gives the tardigrade armor which allows -- within limits -- bending of the body according to the arc of a circle, with venter turned toward the center of the circle; this makes it possible for them to proceed smoothly enough within the intanglement of mosses, lichens, and liverworts, adapting their body to the roughness of the path. And the same value for the Stygarctidae, which is part of the marine interstitial fauna.

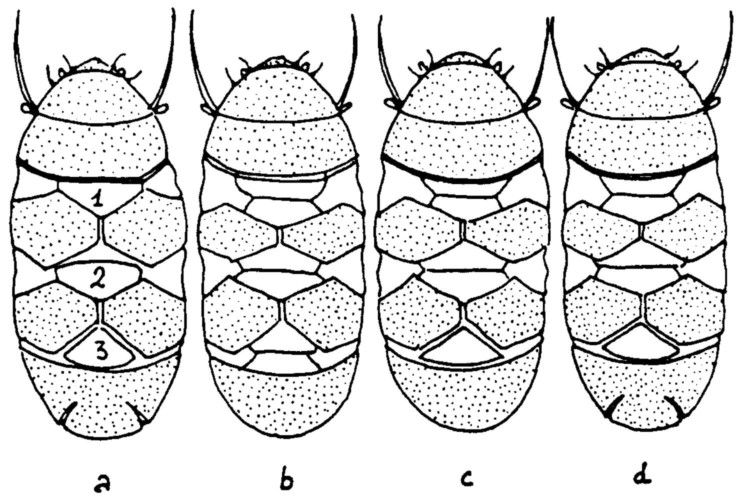


Fig. 6 - Arrangement of the plates in the genera: a, *Echiniscus*; b, *Bryochoerus*; c, *Bryodelphax*; d, *Hypechiniscus*.

The plates of the armor have generally a sculpture which is characteristic for each species (with rare exception) and of which we will speak more abundantly about shortly, and then in the species descriptions; such sculpture has to be composed of small tubercles or of small cavities, circular or polygonal in outline, of uniform granulation or not, of reticular design, variously formed, etc.; the sculpture may continue sometimes even beyond the plates, on the thin and pliable cuticle found between them, or in definite zones on the flanks and legs. To decide if a definite type of sculpture is composed of from example small tubercles or small cavities, it may be necessary to put the tardigrade on its side, in order to observe laterally and in profile -- with high magnification -- the detailed structure of the sculpture, that is the single relief, or socket, which composes it.

In the Heterotardigrada and the Mesotardigrada, there is cuticular enlargement, which sometimes has the appearance of enlarged thin expansion (as in the marine genera *Actynarctus* and *Florarctus*).

More frequently the cuticular appendages have the form of slender filaments, papillae, or spines.

Such appendages are considered in the following groups: cephalic appendages, lateral appendages, dorsal appendages, dorsolateral appendages, and caudal appendages (this last is present in a few marine species, for example the genus *Batillipes*).

The cephalic appendages are the following:

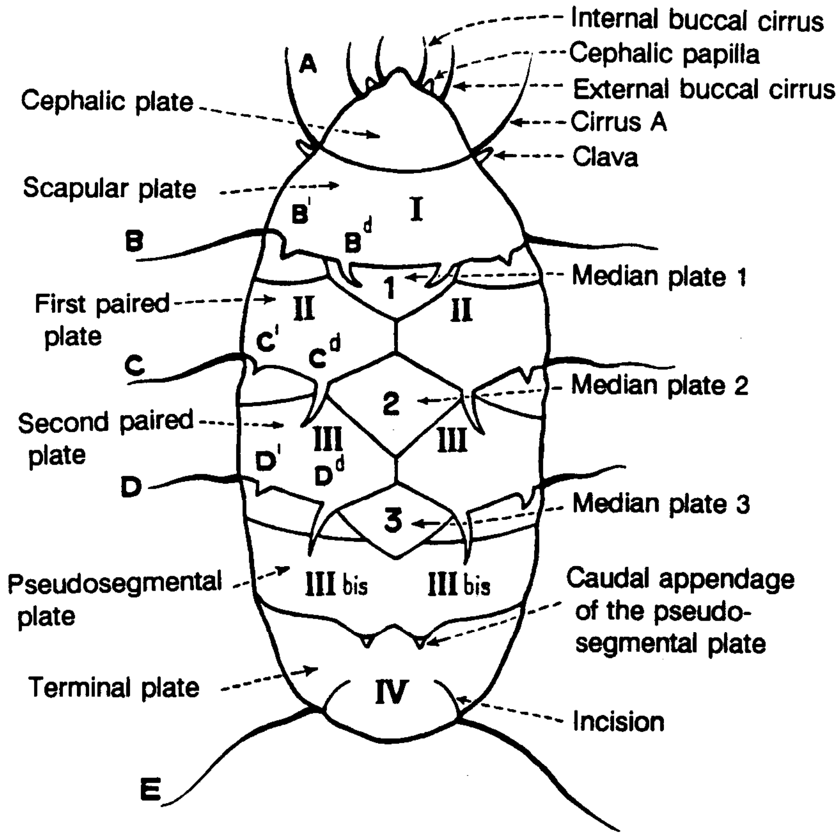


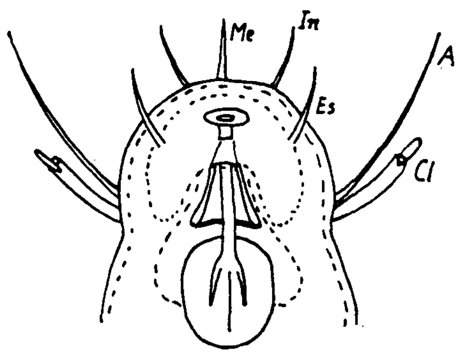
Fig. 7 - Arrangement of the plates and the appendages in a *Pseudechiniscus* (schematic).

- A median or rostral cirrus (median cirrus), present only in certain marine species (Fig. 8) and in a very rare freshwater species (*Echinursellus longiunguis*).
- On each side of the mouth opening, 2 buccal cirri (internal median cirrus and external median cirrus), between which there is usually a papilla (cephalic papilla) of varying length.
- Two lateral cirri A (lateral cirri) placed one on each side and inserted laterally, between the frontal and scapular plates; at the base of these cirri there is nearly always a papilla, generally a fairly long one, called the clava.

- In some marine species there is anterior to cirrus A, an anterior clava. In still other marine species, the cirrus A may be very reduced while the clava is instead very long.

These cephalic appendages are all present only in marine tardigrades. The Echiniscidae are always lacking the median cirrus. In the genus *Cornechiniscus* the cirrus A has the form of a spine, slightly curved, conical, with a restraining basal collar.

Fig. 8 - Scheme of the arrangement of the cephalic appendages in *Styraconyx sargassi* (A, lateral cirrus; Cl, clava; Es, external buccal cirrus; In, Me, median cirrus).



In the genus *Thermozodium* (Mesotardigrada) the cephalic appendages are limited to only cirrus A, while the genus *Mopsechiniscus* lacks the buccal cirri and the cephalic papillae, while there is present cirrus A and the clava.

The lateral and dorsal appendages have considerable taxonomic importance, in particular for the Echiniscidae. They may be in the form of more or less slender filaments, or else in the form of spines, reduced sometimes to small teeth. Such appendages (which may be totally lacking, or only in some positions) are the following (see Fig. 5):

- Cirrus A (once cited as between the cephalic appendages) inserted at the boundary between the cephalic plate and the scapular,
- lateral appendage B, inserted on the posterio-lateral angle of the scapular plate,
- appendage C, inserted at the posterio-lateral angle of the first paired plate (plate II),
- appendage D, inserted at the posterio-lateral angle of the second paired plate (plate III),
- appendage E, inserted on the terminal plate at the beginning of the incision.

In the genera *Pseudechiniscus*, *Cornechiniscus*, and *Mopsechiniscus*, there may also be appendages inserted at the posterio-lateral angles of the pseudosegmental plate.

The dorsal appendages are the following:

- Dorsal appendage B (B^d) inserted on the posterior margin of the scapular plate (they are somewhat rare, and present in a few species of *Echiniscus* and *Cornechiniscus*),
- dorsal appendage C (C^d) inserted on the posterior angle of the first paired plate (plate II), or else a little medially of it,
- dorsal appendage D (D^d) inserted at the posterior angles of the second paired plate (plate III).

In the genera *Pseudechiniscus*, *Cornechiniscus*, and *Mopsechiniscus* there may also be appendages on the posterior margin of the pseudosegmental plate (spines, or else lobes or small teeth).

In position B' (scapular plate), C' (paired plate II), and D' (paired plate III) there may be dorsolateral teeth.

In the genus *Hypechiniscus* there may be a single unpaired dorsal appendage, inserted on the rostral margin of the second paired plate (plate III).

All the body appendages (spines and filaments) vary greatly, not only in size, but sometimes also in their presence or absence. This is easily verified by studying a certain number of tardigrades, e.g., of *Echiniscus testudo*, from a single population. Putting aside the young specimens (which lack a few appendages, to appear later with advancing age and repeated molting) and studying only the adult specimens, appreciable differences will still be observed in the length of the lateral filaments, the shape and size of the dorsal spines D^d, sometimes even in the unilateral or bilateral absence of presence of certain lateral or dorsal appendages.

These observations lead one to use the greatest caution when classifying armored tardigrades (the same in fact for the naked ones) and especially when establishing new species; one must always study a good number of specimens, and not merely one individual to account for variations within a single species and not run the risk of reaching too hasty a conclusion.

As Maucci (1954) correctly pointed out, the characteristics of the cuticle and its appendages present degrees of variability in the genus *Echiniscus*, which can be summed up as follows:

1. These characters appear to be unchanging, in single species: the type of raised pattern, the presence of a spur on the 2 internal claws of the 4th pair of legs, the characteristics of cirrus A, the presence or absence of the median plates, but there are exceptions concerning the constancy of the latter characteristics.
2. These traits vary only slightly: the occasional spur at the base of the external claws of the 4th pair of legs, the dentate collar on these same legs, the filament E if it is present.

3. The following are somewhat more variable: the dorsal appendages (the D^d more so than the C^d), the spine E.
4. The most changeable details are those concerning the lateral appendages, in the following order: B, D, C, A.

An interesting statistical study on the variability of dorsal and lateral appendages of *E. merokensis* was published in 1964 by T. Franceschi and A. Lattes. In this species they observed that the length of the lateral filaments seemed to follow more or less fixed patterns between them. The same thing did not apply to C^d and D^d dorsal appendages, the presence of which was independent of any other body element. If however C^d is present, it also seems to follow certain ratios with the other filaments, whereas it seems that D^d is a trait totally disassociated from other characteristics, but the latter conclusion is not certain, given the small number of animals studied in which D^d was present.

THE SCULPTURE OF THE PLATES IN THE ECHINISCIDAE.

Recently, the cuticle sculpture has been studied closely by different authors, especially in armored tardigrades (of the family Echiniscidae): Franceschi and Lattes (1964) have observed by applying statistical methods that in *E. merokensis* the density of the ornamentation increases with the size of the animal (or with age). Mihelčič, in all his more recent systematic works, also judged the ornamentation to be an element of fundamental importance when identifying species, and described several new species on the basis of the ornamentation alone.

Our point of view is the following: Mihelčič describes the ornamentation as it appears at different levels of focus under a microscope (up to four different planes of observation, with the objective at four different distances). This method is difficult to apply in practice and risks being somewhat too subjective, in other words giving the observer the possibility of a personal interpretation of the shape and layout of the individual elements in the ornamentation itself. We do not think it feasible that different researchers will always agree on the identification of a given species, merely on the basis of ornamentation, as defined by Mihelčič.

But, apart from these practical problems (and the difficulty of introducing such complex observation methods into the keys, which should be as simple and easy to consult as possible) there is another consideration of a far more general nature. I am referring to our very minimal knowledge on the variability of the ornamentation and we have no firm information on variations which occur with age, sex, environmental conditions, etc.

In conclusion: It is highly likely that the type of ornamentation is of really great importance in systematics and perhaps also in relation to phylogenetics, however it seems premature at this point to make it the basis for new systematics, more so since many of the old descriptions are so imprecise or incomplete concerning the ornamentation of the different species (the prepared specimens of which are often lost or no longer usable), that one would run the risk of increasing the already considerable confusion of tardigrade systematics.

It is therefore to be hoped that the attention of researchers in Mihelčič's footsteps will turn more frequently than in the past to the fine details of the ornamentation, with a future goal in mind, so that we shall be in position eventually of having enough fully valid information.

LEGS AND CLAWS.

There are four pairs of legs (with the sole exception of *Hexapodibius*, which possesses only three pair of legs) which are placed in a lateroventral position. The first three pairs, directed somewhat forward, are those which contribute most to locomotion, while the fourth pair, the middle part of which forms an angle of about 45μ with the sagittal part of the body, always seems to be dragging behind, and (though they may be used to help push the animal along) their main role seems to be to help the animal keep upright, grasping various projections of the substratum (stalks and foliage of moss, vegetable and mineral detritus, etc.).

The shape of the legs (which are not articulated) is somewhat cylindrical, generally rounded towards the distal extremity, which in the greatest number of cases finishes in claws of varying shapes and sizes, are also important in classification. However, in several marine species of the suborder Arthrotardigrada, the distal extremity of the legs is digitate (Figs. 32, 44) and the individual projections (called digits for short) can bear these claws, an adhesive disk (genus *Batillipes*, Fig. 61), or else have a peg-like shape (genus *Orzeliscus*, Fig. 570).

As we will describe the claws of the marine species in greater detail (and those of the single species in the order Mesotardigrada) when we actually deal with them, we will now provide more information on the claws of the tardigrades belonging to the family Echiniscidae and to the order Eutardigrada in which are included the greatest number of the known species and varieties.

All adult Echiniscidae have four more or less rounded claws, symmetrically placed around the axis of the leg. Sometimes all four claws are smooth, more often the two internal, or central claws have a ventral spur, placed at different distances from the base and the shape of which can range from that of a very slender spine, visible only under high magnification with careful observation, to that of a thick, straight or curved prong (Fig. 9, B and C).

Exceptionally there are one or more spurs, close together, on the two external claws but in this case the spurs are always very close to the base of the claw (Fig. 9, C). The younger specimens of the family Echiniscidae (commonly called larvae) have two single claws, often with spurs, which correspond to the two internal (central) claws in adults.

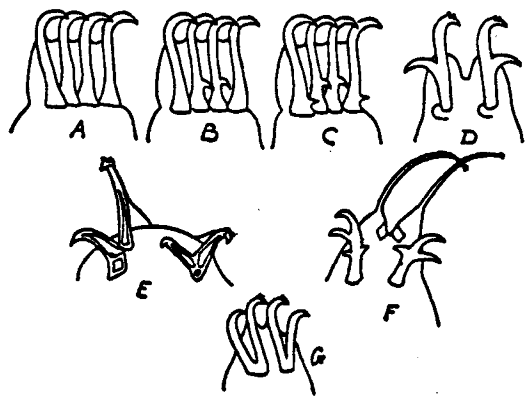


Fig. 9 - Various types of claws: A, B, C, from Echiniscidae; D, G, from *Macrobiotus*; E, from *Hypsibius*; F, from *Milnesium* (see text).

In the suborder Echiniscoidea, to which the family Echiniscidae also belongs, the claws are individually fixed to the distal extremity of the legs with a papilla; according to Marcus and other authors these papillae are homologous to the digits of the Arthrotardigrada.

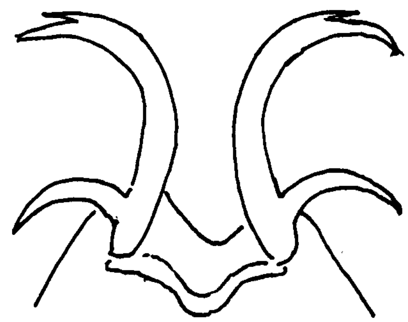
The tardigrades contained in the order Eutardigrada can be taken as having four claws for each leg, although these are joined two by two, to form a so-called doubleclaw.

Each doubleclaw is made up of a primary branch (or ramus) consisting of the section which is the longer and closer to the midline, bearing two small teeth at the tip (Fig. 9, D, G), usually called accessory points, and of a secondary branch (or ramus) which is further out and has no accessory points.

Because the claws of the Eutardigrada constitute a very important taxonomic character not only at the species level but also at that of the genus, we shall describe here the principal types of claws.

"*Dactylobiotus* type" claws: the two doubleclaws of each leg are symmetrical with respect to the median plane of the leg, that is to say the spatial succession of the principal (1) and secondary (2) branches is 2-1-1-2. The secondary branch is much shorter than the principal (at times it is reduced almost to a spur, at least on the first three pairs of legs) and is inserted very near to the base, for which the common basal branch is very short; the two doubleclaws of each leg are connected together medially by a sclerified band (Fig. 10).

Fig. 10 - Doubleclaws of the "*Dactylobiotus* type"



"*Macrobiotus* type" claws: the spatial succession of the branches of each leg is also here of the 2-1-1-2 type, but the secondary branch is not much shorter than the principal, and the bases of the doubleclaws are not connected.

Within the bounds of this type of claw, some authors prefer to further discriminate between "*hufelandi* type" claws (in which the principal branch and the secondary are united for a more or less long distance, to form a common basal branch) (see Fig. 9, D) and "*echinogenitus* type" claws (in which the two branches diverge from each other close to the base or almost (Fig. 9, G).

We think however that this distinction has very poor taxonomic value (*Macrobiotus echinogenitus* has, in general, "*hufelandi* type" claws), also since in many cases there is a difference between young individuals and fully developed individuals.

"*Calohypsibius* type" claws: as in the two preceding cases, the two branches of the claws are rigidly connected together, but the spatial succession of the branches is 2-1-2-1, that is to say the doubleclaws of each leg are asymmetrical with respect to the median plane of the leg; the doubleclaws of each leg (as in the two preceding types) are equal or almost equal to each other in shape and size (Fig. 11, a).

"*Hypsibius* type" claws: the spatial succession is here also 2-1-2-1; the common basal branch (more or less long) is directly continuous to the secondary branch, while the principal branch, often longer, always more slender, is inserted on the basal branch by means of a flexible junction; the two doubleclaws of each leg are normally of considerable difference in shape and size, having the posterior, or external, doubleclaws longer and often more slender than the anterior or internal (Fig. 11, c and 12).

"*Isohypsibius* type" claws: the succession of the branches is also 2-1-2-1, the principal branch is inserted on the basal branch (directly continuous to the secondary branch) by means of a flexible junction, the two doubleclaws of each leg are often (but not always) fairly similar to each other in shape and size (Fig. 11, b).

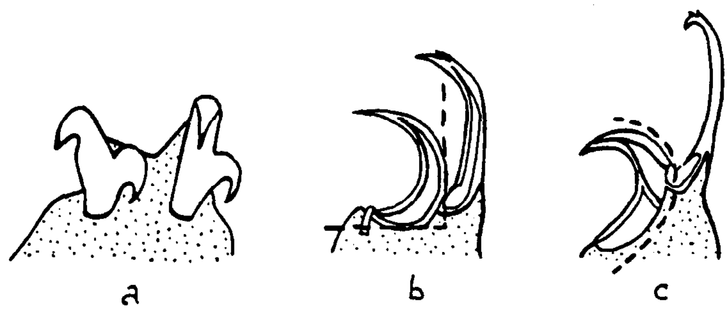
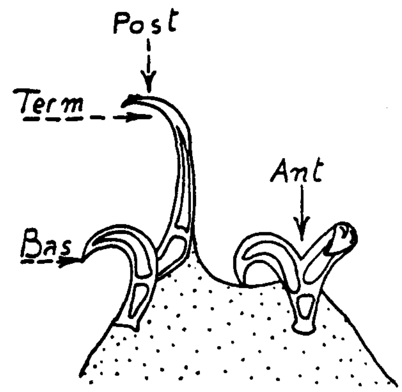


Fig. 11 - Types of claws: a, *Calohypsibius*; b, *Isohypsibius*; c, *Hypsibius*.

Fig. 12 - Claws of the 4th pair of legs of the genera *Hypsibius*, *Diphascon*, and *Itaquascon*. Post., posterior or external doubleclaw; Ant., anterior or internal doubleclaw; Bas., basal claw; Term., terminal claw, or principal branch.



The difference between *Isohypsibius* and *Hypsibius* type claws is not very important and sometimes rather difficult to determine (for which an experienced eye can hardly be mistaken); therefore, to make this obvious, the tardigrade has to be placed under a microscope in such a way that one posterior (external) doubleclaw, preferably from one of the first three pairs of legs, shows its secondary branch (basal claw) exactly in profile. Then, if the secondary branch just about forms a right angle with its own basal section, as the dotted line in Fig. 11b shows, the doubleclaw is of the *Isohypsibius* type. If, on the other hand, the secondary branch and its basal section run in a continuous curve, without forming an angle between them, as the dotted line in Fig. 11c shows, the doubleclaw is of the *Hypsibius* type.

In the genus *Milnesium*, the claws have the shape shown in Fig. 9, F; here also there are two doubleclaws for each leg, but with widely spaced, clearly distinguishable branches. The main branch of each doubleclaw is long and thin, with the usual accessory points at the tip, while the secondary branch is thicker, and bears 2, 3, or 4 curved spurs.

At the base of each doubleclaw the cuticle may have an impression almost circular, which may be smooth, crenate, or dentate, of large or small size, the so-called lunule.

The legs of the Arthrotardigrada (marine) often have one or more folds in the cuticle, so that by muscle contraction the middle part of the leg can be pulled back into the proximal part (Fig. 290); the Mesotardigrada and sometimes the Heterotardigrada also have this ability if within more restricted limits to make a middle portion of their leg retract into the proximal. In many Echiniscidae the posterior legs have a dentate collar (Fig. 13), broken on the ventral side of the leg and in about the same position as the cuticular fold of the Arthrotardigrada. We shall not describe the different spines, papillae, etc., which can in addition be present on the legs, but we shall mention them from time to time when necessary.

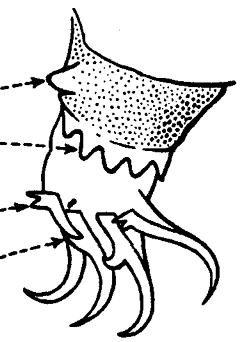


Fig. 13- Leg of the 4th pair of *Echiniscus*.

We have already alluded to the so-called pedal glands, which carry out the function of forming new claws at the time of molting and which are to be found on the distal extremity of the leg (Fig. 4); without entering into great detail, it suffices to say that one or two vacuoles are produced inside the gland, in which one can observe the gradual differentiation of the claws, in which one can observe the gradual differentiation of the claws, through secretion by the surrounding glandular cells. When the new claws are completely formed, the vacuole changes into a sort of distally opened pouch, while the claws fix themselves to the tardigrade's new cuticle, which has been formed meanwhile under the old one.

Right after molting the gland returns to its smaller size, having reached its maximum slightly before the formation of the open pouch and precisely accompanying the so-called simplex stage which as we will see more clearly further on, takes place a few days before molting and during which the tardigrade's buccal apparatus is rejected. During the simplex stage there is, therefore, no possible intake of food.

CONNECTIVE TISSUE.

B. Baccetti and F. Rosati's research (1969) using histochemical methods and an electron microscope noted the presence of a connective tissue in tardigrades (the species being studied was *Macrobiotus hufelandi*). The main characteristics of this tissue, say the authors, are: presence of a basic substance made up of collagen fibers immersed in a cementing polysaccharide, not a classical type of basal membrane. The traits of the fiber (580 A period with 9 subbands) are similar to those of annelids and many classes of arthropods.

RESPIRATION, CIRCULATING LIQUIDS, RESERVE MATERIAL.

Tardigrades, during periods of active life (not those of anabiosis or cryptobiosis) are extremely sensitive to any decrease in oxygen in the atmosphere. One must keep in mind that tardigrades, not only those living in fresh or sea water, but also the so-called "terrestrial" species which inhabit moss, lichen, soil, etc., are distinctly aquatic animals which can lead an active life only if surrounded by a film of water, thin as it may be.

There are no special respiratory organs as respiration most probably goes on through the whole surface of the cuticle and epidermis in naked tardigrades, while it is thought that in armored species it occurs mainly in the areas where the cuticle is thinner, or in between two plates, and through the lateral and ventral integument.

In a series of highly interesting works Pigon and Weglarska (1953, 1954, 1957) reached the conclusion that during active life oxygen consumption is of about 1×10^{-3} microliters per hour for either the moss-inhabiting tardigrade *Macrobiotus hufelandi* or for the freshwater species *Dactylobiotus dispar*.

In the exchange of oxygen between the animal and its environment, the coelomic liquid no doubt plays an important part as it circulates continually within the general body cavity through the animal's movements, and without the intervention of any special circulatory organ; floating inside this liquid there are numerous spheroid cells, the cavity globules, bearing a nucleus which in turn contains one to three nucleoli, chromatin granules, a chondrisome with many mitochondria, and an abundance of reserve material.

The majority of authors today hold correctly that the body cavity cells have the function of food reserve and can be considered a kind of separate adipose tissue, as Plate wrote of it at the end of 1889. The alternative hypothesis, put forward by Richters (1926) has been given up completely. According to him, the body cavity cells might be able to absorb any matter which was damaging to the organism and which had been rejected by it, "loading" itself with poison, until, at saturation point it caused the tardigrade's death.

The body cavity cells are surrounded by an elastic membrane so that their shape can change while moving from organ to organ inside the general body cavity. They vary in number and size according to the tardigrade's state of nutrition, as a prolonged lack of food can not only reduce their size but also cause their reabsorption.

The size of the body cavity cells in the Eutardigrada, in normal feeding conditions, vary in different species, but on the average range from 10 to 15μ, with a minimum of five and maximum of about 25μ. In the Heterotardigrada they are of a smaller size.

The reserve matter is mainly made up of fats and polysaccharides. While the fats, in the form of droplets, are for the most part contained within the body cavity cells, the polysaccharides (glycogen) are found mainly in the body cavity liquid, at least during the animals' periods of active life, and gather in the body cavity cells only under certain conditions, slightly before ecdysis (Weglarska, 1957) as we shall see later.

At the end of an interesting study, using an electron microscope, F. Rosati (1968) writes: "The ultrastructure and histochemical study of 'cavity globules' in *Macrobiotus hufelandi* has shown that these cells are used to accumulate and transport reserve matter. The most important characteristics of these cells are: the evolution of protein substances collected inside large vacuoles together with lipid inclusions; the presence of other reserve matter like glycogen and polysaccharides; the possibility of passive motion inside the body cavity and lack of a collagen covering; absorption of material from the coelomic liquid, especially near the intestine by pinocytosis and phagocytosis; transport of reserve matter to the epidermis and other organs in the animal. Any excretory function is excluded."

We have already spoken of the pigments enclosed in the body cavity cells or floating in the coelomic liquid, functioning purely as a food reserve, in the chapter on the coloring of tardigrades and we will not deal with the subject any further.

CONSTANT CELL NUMBER.

Martini (1908) has demonstrated that some small Metazoa (Rotifera, Nematoda) are composed of a constant number of cells, which precociously differentiate losing all capacity to multiply; it follows that all of the organs of their body are composed of permanent tissue lacking regenerative capacity. Among these animals are in general also counted the Tardigrada, according to the observations of several authors (Plate, Basse, Baumann). Marcus however also confirmed the cellular constancy in many organs, ascertained numerical oscillation of the cells in the pedal gland and the cavity globules, affirming then that the constancy is only partial.

Recently R. Bertolani (1970) has observed somatic mitosis in various organs of *Macrobiotus hufelandi*, *M. areolatus*, and *M. richtersi*, deduced that the Tardigrada do not have constant cell number, and that many of their tissues are composed of cells of limited life cycle.

FEEDING.

In general, tardigrades feed on vegetable matter, even if occasionally some of them (e.g., *Macrobiotus richtersi*, *M. hufelandi*, etc.) can take in animal food. *Milnesium tardigradum* is perhaps the only species which is normally, though not exclusively, carnivorous and one can fairly frequently observe specimens belonging to this species whose intestines contain mastax from bdelloid rotifers: I actually saw three in one tardigrade found in Austria.

The Echiniscidae (armored) feed exclusively on chlorophyll cells in moss, whose contents they suck after having perforated the cellular membrane with their pointed stylets. Naked moss-inhabiting tardigrades usually do the same for they also often feed on algae, fungi, and in rare instances on rhizopods, rotifers, and on other tardigrades.

According to Mihelčič's (1953) observations, 2000 tardigrades he studied which lived in one patch of moss consumed around 750 leaflets in two days, which means that, on an average, one leaflet provided a day's food for five tardigrades. Marcus (1927) said a *Macrobiotus furciger* 360μ long emptied ten cells of a leaflet of *Hypnum* in a maximum of 24 hours (but more likely in less time than that). Thus such a specimen, weighing around 0.003 mg consumed about 0.00001 mg of food in less than 24 hours. It is fairly easy, under a microscope, to discern the traces left by the tardigrades' feeding on the leaflets of moss, which show empty cells, sometimes gathered in groups, at other times isolated.

However, Baumann (1966) does not exclude the possibility that mosses might constitute only the tardigrade's habitat and puts forward the conclusion that its food is mainly provided by algae, which is present in abundance in moss and lichen. Protozoa are also often assumed to be the food of certain species of tardigrades.

Terrestrial tardigrades feed differently, mainly on plant detritus, fungi, algae, and perhaps also on small animals (protozoa, rotifers, etc.). I have had the chance to observe, in the intestine of certain *Diphascon bullatum* gathered from a field in Pallanza, numerous green algae (of the genus *Scenedesmus*). It is likely that a similar sort of food is consumed by tardigrades dwelling in lichen, in cushion-like flowering plants (phanerogams), and perhaps even in moss, where algae, fungi, and organic detritus are present in abundance.

As we shall see more clearly in the next chapter dealing with the buccal apparatus, there is in tardigrades no mastication process for the food ingested. Therefore, it often occurs, especially in the Eutardigrada with their wide buccal tube, that whole plant and animal organisms are ingested.

The often mentioned *Milnesium tardigradum* (family Milnesiidae, Fig. 560) is typified by its short, wide buccal tube (with a diameter greater than 25μ) through which it can suck in diatoms and rotifers; but numerous species of the family Macrobiotidae are also able to ingest more or less voluminous organisms and sometimes even ones of remarkable dimensions. I myself observed a whole nematode in the intestine of a moss-inhabiting *Macrobiotus richtersi*, the buccal tube of which had a diameter of about 12μ, and I have also often seen mastax from rotifers in other tardigrades of the same species.

Tardigrades, during stages of active life, are capable of undergoing fairly long periods deprived of food. Marcus observed that specimens gathered from good feeding conditions were observed to survive without food for five weeks. During the period of their privation, the animals consumed all their reserve matter, several body cavity cells were reabsorbed along with the ovigerous females, the content of the ovary, or most probably the deuteroplasm. My observations have led to similar results.

There is not much information on the feeding of marine or freshwater tardigrades or those which are part of the interstitial fauna (the latter group of genera and species are clearly aquatic). It is most likely that algae, protozoa, and organic detritus play an important part in their diet, as do underwater mosses, at least for the freshwater species of certain habitats.

Cases of ectoparasitism and commensalism are very rare and observed only in marine species up to now. *Tetrakentron synaptae* is the only species usually considered parasitic, but in fact this is far from being a certainty. The tardigrade in question is flat and fairly small (around 100 to 200μ), observed on the prinnate peribuccal tentacles of the holothurian *Lepto-*

synapta galliennei, where in fact there is usually a rotifer, *Dicopus synaptae*. In general there are two or three *Tetrakentron* on each holothurian, moving about slowly, keeping a tight grasp on their host with their claws. It must be noted that they dwell only on the tentacles and never on other parts of the *Leptosynapta* body.

Pleocola limnoriae lives on the pleotelson and base of pleopods of *Limnoria lignorum* and its commensal to these isopods (but it was also recently found free-living). Three specimens of *Echiniscoides sigismundi* were gathered by Green (1950) on the mantle of *Mytilis edulis*, but this species normally inhabits algae and it is impossible to say whether Green's report is exceptional or not. *Actinarctus doryphorus* can, according to Marcus (1936) be an optional parasite of the echinoid *Echinocyamus pusillus*, but Grell (1937) denies this.

FEEDING APPARATUS, EXCRETION.

The digestive tract is divided into three parts: the anterior part, including the buccal orifice, the pharynx, and esophagus; the middle part, in which the digestion of food occurs; and the posterior, or rectal, part. The anterior and posterior parts have an ectodermal origin, while that of the middle part is endodermal.

The position of the mouth can be terminal (e.g., in *Milnesium* and the greatest number of the *Macrobiotus* species) or else slightly ventral (nearly always in *Hypsibius*) or even distinctly ventral, as in some of the marine tardigrades.

There can be peribuccal structures, like elongated papillae (genus *Milnesium*), or else flattened papillae or lobes.

The buccal cavity opens with a cuticular ring, which may or may not bear a crown of buccal lamellae (which allows the mouth to be applied like a sucker on the body which constitutes the food of the tardigrade).

In *Milnesium* the mouth may appear enclosed in 6 lobes; in the species belonging to the family Echiniscidae (armored) the small mouth opening is often surrounded by cuticular folds in the form of a rosette.

On each side of the mouth is a piercing organ, the stylet, made up partly of cuticular substances, with a calcified central zone (Marcus, 1927) and operated by several retracting and protracting muscles. When they are at rest, their tips are protected by a short case (stylet sheath, Figs. 14 and 15) made up of a small tube, through which they can penetrate into the buccal tube and project some of their length outwards. The stylets can have different shapes, sometimes straight, sometimes curved, and of varying thickness: these characteristics have a certain taxonomic importance.

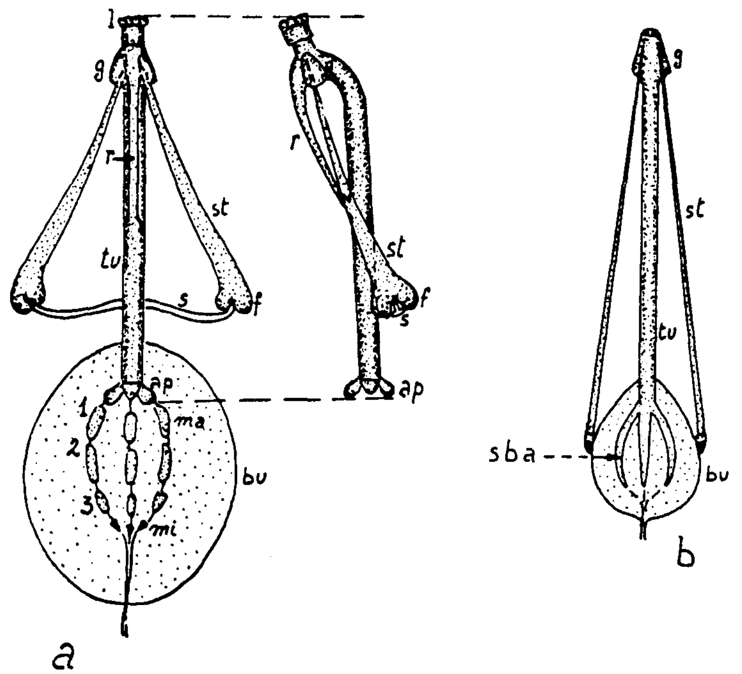


Fig. 14 - Sketch of the buccal apparatus of the Eutardigrada (a) and the Heterotardigrada (b) (ap, apophyses; bu, pharynx; f, furca; sh, stylet sheath; l, peribuccal lamella; ma, macroplacoid; mi, microplacoid; r, reinforcement rod; s, stylet support; sba, pharyngeal rod of the Heterotardigrada; st, stylet; tu, buccal tube; 1, 2, 3, first, second, and third macroplacoids).

In the order Eutardigrada the stylets look like daggers, being thicker at the base and often bifurcated, composing the so-called furca, which is attached to the stylet supports (Fig. 14, a). These are usually small cuticular rods of an elastic, flexible nature, straight or curved, articulating with the hollow end of the furca and fixed to the buccal tube at the other end.

In the order Heterotardigrada the stylet supports can be present or absent. In the family Echiniscidae they are sometimes present, but they are very delicate and placed in such a way that they are often difficult to see; frequently the stylets are very long and thin and joined directly to the pharynx by a muscular band (Fig. 14, b), so that the stylet supports are missing.

(Recent observations using a scanning microscope (Schuster, in litt.) shows that in reality the so-called stylet sheath is present only in the genus *Milnesium*: in the other genera the stylets enter the tube through a simple opening.)

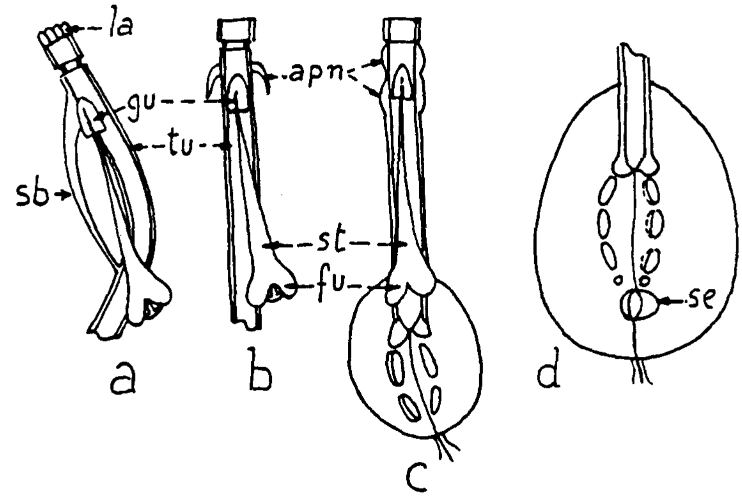


Fig. 15 - Sketches of buccal apparatus of: a, *Macrobiotus*; b, *Hypsibius*; c, *Isohypsibius*; c, pharynx and placoids of *Diphascon*; apn, insertion appendages for the stylet muscles (in b "hook-shaped", in c "crest-shaped"); fu, furca; gu, stylet sheath; la, peribuccal lamellae; sb, reinforcement bar; se, septulum; st, stylet; tu, buccal tube.

The buccal cavity has as a rule a wide mouth, and then narrows to form a truncated cone. In its interior there is often cuticular support, present normally as an anterior band of teeth, a posterior band of teeth followed by three transverse ventral crests and three dorsal. Pilato, in numerous works, has emphasized the taxonomic importance of this buccal reinforcement (for this we refer especially to Pilato, 1972).

After the buccal cavity follows the buccal tube, more or less wide (of about 1μ for some species of *Diphascon*, up to more than 25μ in *Milnesium*), which extends into the pharynx penetrating for a distance.

The buccal tube in its anterior part has, ventrally and dorsally, insertion appendages for the muscles of the stylets which are normally in the shape of a hook (genus *Hypsibius*) or a crest. In the genus *Macrobiotus*, and in others, there is ventrally a reinforcement bar (Fig. 14a, 15a).

The musculature of the buccal apparatus is schematically illustrated in Fig. 16; without going into detail (for which we refer back to Marcus, 1929), we shall merely say that movement of the stylets is governed by a rather complex muscle system. There are two protracting muscles (one for each stylet) which operate any forward movement by the stylets extending from the furca and attached towards the rostral extremity of the buccal tube. There are four pairs (one dorsal and one ventral for each stylet) of retracting muscles acting in opposition, which extend from the furca and are fixed externally to the pharynx.

There are also three muscle bands (compressor dorsalis, ventralis, and obliquus), which extend from the furca of one stylet to that of the other, joining them and preventing the stylets from slipping from their support, making their movement forward and backward awkward.

This last section applies to *Macrobiotus hufelandi* in particular, as it was studied especially with this aspect in mind, but it is most likely that in all tardigrades there is a similar muscle arrangement, with some variation.

The buccal tube penetrates the pharynx, or bulb, penetrating it some way, ending there, often (in the family Macrobiotidae) expanding into a flange-like structure bearing three equal cuticular thickenings, the apophyses, which probably function as valves, serving the purpose of preventing ingested food from rising up into the buccal tube from the pharynx. Sometimes instead of apophyses there are other attachments with the same function, as for instance the cuticular folds placed between the end of the buccal tube and the pharynx in the genus *Milnesium*.

Sometimes the buccal tube, rather than being rigid for all its length, may be composed of a rigid part between its rostral end and the stylet supports, and a flexible part more or less long (up to more than two times the length of the pharynx), between the stylet supports and the pharynx (Fig. 613); the rigid part is usually called buccal tube (in the strictest sense), while the flexible part is called more appropriately pharyngeal tube. The latter has a characteristic structure of the wall of cuticular reinforcement arranged in a very tight spiral. This type of tube is found in the genera *Diphascon*, *Pseudodiphascon*, and *Itaquascon*.

The pharynx functions as a sucking organ and is generally ovoid in shape; a longitudinal section of it can have a nearly circular outline, or that of more or less elongated ellipse (the longitudinal axis can have a certain heteropolarity). Figure 17 shows a transverse section of it, with the small cavity, connected to the buccal tube, consisting of three very narrow cavities, placed at about 120μ to each other. These cavities can tighten up or loosen variously, and can even close up completely, thus preventing, together with the valve action of the apophyses, food which has been taken in from returning to the buccal tube.

There are in the family Macrobiotidae a series of cuticular swellings (placoids) corresponding to the above mentioned cavities, set up in three double rows and alternating in position with the apophyses. In general they look like granules, or small clubs (macroplacoids), which are sometimes followed by a small or very small granule for each row

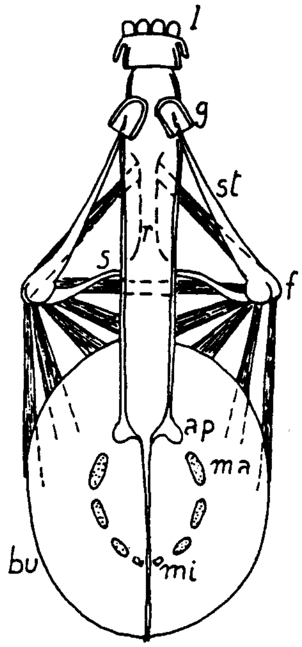


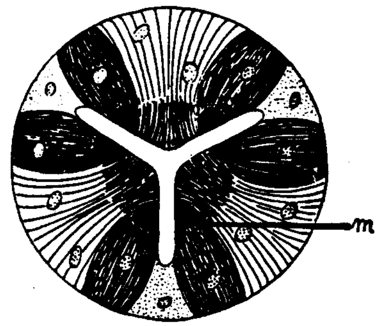
Fig. 16 - Buccal apparatus and its musculature in a *Macrobiotus* (schematic), dorsal view (from Pennak, modified) (ap, apophyses; bu, pharynx; f, furca; g, stylet sheath; l, peribuccal lamellae; ma, macroplacoid; mi, microplacoid; r, reinforcement bar; s, stylet support; st, stylet).

(microplacoid or comma) whose function is probably that of mechanical reinforcement, not for mastication. When one observes one of these tardigrades under the microscope, one can perceive three rows each of two (or three) single macroplacoids which are sometimes followed by a microplacoid (Fig. 14); but in fact, each placoid is double, or rather made up of a pair, in each center of which lies one of the three cavities at 120μ to each other, shown clearly in transverse section (Fig. 17). In tardigrades which have been prepared for the microscope, tightly pressed between two slides, one can often see the three rows of placoids separated into two parts (Fig. 18).

The shape, number, and layout of the placoids are very important items for the classification of the family Macrobiotidae. It is usually said that a tardigrade has two or three macroplacoids, when there are in fact two or three macroplacoids *in each row*, respectively; the first macroplacoid is taken to be anterior, while the second and third (not always present) are those which follow caudally (Fig. 14, a). Similarly it is generally stated that tardigrades have, or lack, a microplacoid rather than microplacoids always referring to a single row of placoids.

In the genus *Diphascon* there are sometimes (in an immediately caudal position in relation to the macroplacoids) three tiny plates, or blades (septula, Fig. 15, d); it is likely that each of the septulae, like the apophyses, is paired, that is they separate into two separate small blades.

Fig. 17 - Transverse section of the pharynx of *Macrobiotus* (semischematic); m, macroplacoid.



The septulae, like the apophyses, are placed in alternating positions with the placoids and only appear in certain species of *Diphascon*.

It must be noted that the relative shape and size of the placoids present a certain individual variability (which has been taken into account in the keys, in addition to far more noticeable variations in relation to the animal's age: accordingly, one should always chose adult specimens when classification of a tardigrade is to be carried out, so as not to be grossly misled).

Among the Eutardigrada, all the species have placoids inside the pharynx, with scarcely exception. The genus *Milnesium* (family Milnesiidae) with one species and two varieties and the genus *Itaquascon* (family Macrobiotidae) with too few species known as yet, have a pharynx containing no placoids.

However in *Itaquascon* the placoids are often replaced by a thin continuous cuticular lining.

In the class Mesotardigrada (a single Japanese species, observed only once in thermal waters) there are placoids present, while in the class Heterotardigrada there are none, these being substituted by three hard continuous cuticular bars (Fig. 14, b), which can be called pharyngeal rods.

The mass of the pharynx, in the Eutardigrada, is made up of three longitudinal bundles of epithelial cells corresponding with the corners of the cavities, alternating with epitheliomuscular cells, with fibers laid out in a radial direction (Cuénot, 1932). According to Marcus (1928) the number of cells in the pharynx is constant in all Heterotardigrada and Eutardigrada, and amounts to exactly 51, out of which there are 27 epithelial cells and 24 muscle cells. The only exception is the genus *Milnesium* in which there are 24 epithelial cells and 39 muscle cells.

The epithelial cells fill the role of producing the placoids, when they exist, also the covering of the pharynx at the appearance of the molt, while the muscle cells permit the pharynx the movement necessary to suck in food and send it into the midgut.

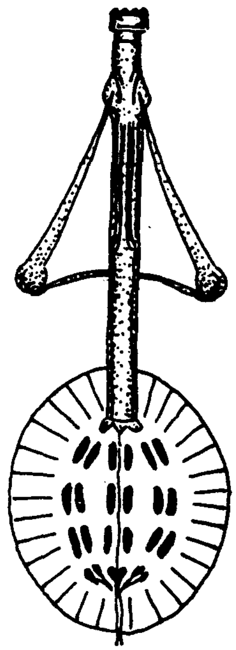


Fig. 18 - Sketch of the buccal apparatus of *Macrobiotus*, flattened during preparation, which shows the separation of the placoids.

Lateral to the buccal tube and bulb, there are large rostral glands (or *salivary glands*, see Fig. 1, s): these have the additional function, at molting time, when the whole buccal apparatus is discarded, of producing certain new cuticular parts of the buccal apparatus itself, which are: the buccal cavity wall, the stylets, the stylet supports, and the buccal bulb. The epithelial bulb cells in fact also contribute to the formation of the last part mentioned, just as they reconstitute the placoids as well. In the genus *Diphascon*, the flexible part of the buccal tube, between the stylet supports and the bulb (*pharyngeal tube*), is, on the other hand, rebuilt by the surrounding tissues.

It must be noted that the salivary glands, which are normally found lateral to the bulb, move backwards after the expulsion of the buccal apparatus, so as to proceed to its re-formation; one must also keep in mind that the musculature of the stylets is not discarded during molting, but remains in place and is used again.

Tardigrades, in the period between the discarding and re-forming of the buccal apparatus, are said to be in a *stadio simplex*. We shall mention this again, when dealing with molting.

According to the majority of authors, the salivary glands also have excretory functions: Cuénot (1932) observes that these glands, during the interval between two molts contain large vacuoles with a weak acid reaction (Ph between 6.5 and 6.8) while they take on their original compact shape again after the stylets have been expelled, so as to form new ones. However, it has not been confirmed whether the salivary glands secrete the digestive juices or not.

The bulb is followed by a short esophagus, and then a more or less lobed midgut, where intercellular digestion of foods takes place. The order Heterotardigrada has five or six lateral diverticula (Fig. 19), which are not

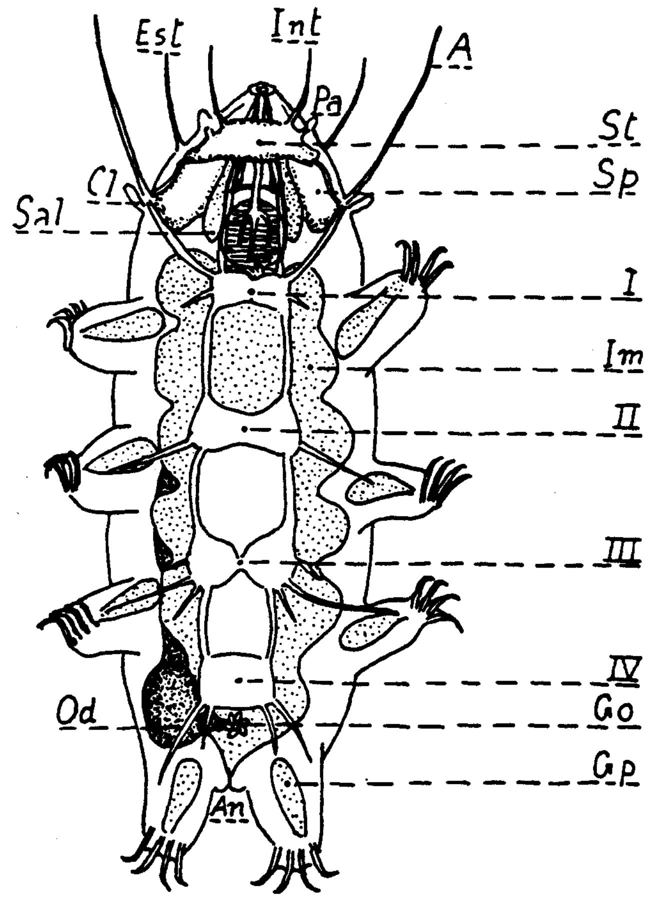


Fig. 19 - Ventral view of *Bryodelphax parvulus* male (from Marcus, redrawn). (A, cirrus A; An, anus; Cl, clava; Est, external buccal cirrus; Go, gonopore; Gp, claw gland; Mg, midgut; Int, internal buccal cirrus; Od, oviduct; Pa, cephalic papilla; Sal, salivary gland; Sp, supraesophageal ganglion; Sb, subesophageal ganglion; I, II, III, IV, ventral ganglia 1-4).

normally visible in the Eutardigrada, but which according to Marcus (1929) also appear clearly in that class and are placed metamerically when the midgut is very full. Personally I was never able to observe intestinal diverticula in the Eutardigrada.

According to the same author, the pH assumes (during digestion) the following amounts: between 4.4 and 5.5 in the foregut, between 6.5 and 6.8 in the salivary gland vacuoles and between 8.4 and 8.7 in the midgut. It is likely that the strong acidity in the foregut is due to the presence of secretions, which may have their source in the salivary glands.

In tardigrades which feed predominantly on vegetable matter, as for instance the majority of the moss-inhabiting species, the intestinal content is of a yellow or green color if the meal has just been consumed, and becomes gradually more brown as time goes on, until it turns very dark just before defecation. This applies to naked tardigrades (Eutardigrada), as Heterotardigrada only defecate at molting time, abandoning the feces in the old cuticle.

If the tardigrade has a transparent intestinal content, this means that the specimen concerned has not eaten for a period of time, and in such a case the midgut has reduced dimensions, and is not swollen like a sack, as in well fed animals. The predatory tardigrades (*Milnesium tardigradum* in particular) also have transparent intestinal contents.

The midgut is followed by the rectum and the anus. In the Heterotardigrada there is a pre-anal gonopore, while in the Eutardigrada the anus is in fact the orifice of a cloaca, since the genital ducts also lead into the rectum.

In the Eutardigrada -- but not the Heterotardigrada -- there are also three large glands present, one dorsal and two lateral Malpighian tubules, whose openings into the intestine are placed exactly where the midgut ends and the rectum begins (Figure 20). These glands (identical in both sexes) are basically of two different types, which, along with Marcus, we will call the short type and the long type, the difference consisting of the varying length of the two lateral glands, as the dorsal (middle) one is always short. In Figure 20 the short type is shown, the length of which can range from about 24 to 64μ, (15 to 32μ in width), in specimens from different species about 190 to 545μ in length. The long type of lateral gland has much larger dimensions, for instance 128μ (16μ in width) for a *Macrobiotus hufelandi* of 585μ.

The malpighian tubules can show other morphological differences in different species. For instance, the lateral glands sometimes take on a trilobed shape, like a clover leaf, or else all divisions in it can disappear so it appears bean-like. The individual types do not change when they reach sexual maturity, or indeed at any specific age. However, in tardigrades

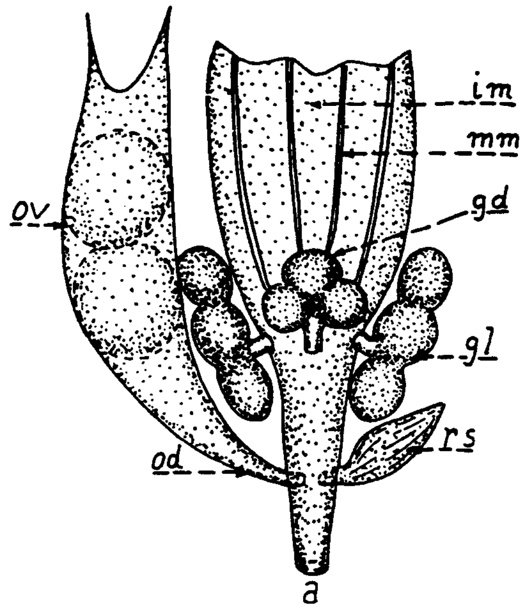


Fig. 20 - Schematic dorsal view of the midgut and hindgut of the excretory glands and of the genital apparatus in the *Hypsibius* female (from Marcus, modified). (a, anus; gd, dorsal excretory gland; gl, lateral excretory gland; im, midgut; mm, longitudinal muscles in the midgut; od, oviduct; ov, ovary; rs, seminal receptacle).

which have been deprived of food, the lateral glands shrink, especially in length (for instance from 128 to 60μ) or rather are reabsorbed length (e.g., from 128 to 60μ) or rather are reabsorbed as we saw happen in the body cavity cells and the ovarian content.

After the work of Marcus (1929) there should no longer be any doubt as to the excretory function of these three glands. The first stage of excretion is characterized by the appearance of a fine granulation inside the glands, whose particles subsequently increase in size, joining together in the central part of the gland itself to form filaments, which come together in a ball. At the same time, vacuoles appear in the marginal zones of the glands and the "ball" of excretions turns into more or less spiral-shaped filaments which move through the opening ducts into the rectum.

It is interesting to observe that the Heterotardigrada, which have no Malpighian tubules, have a considerable amount of mid-gut surface through which excretory processes could take place. In the Eutardigrada on the other hand, it seems that excretion is carried out only through the Malpighian tubules, if these are of the long type, and partially through the intestinal wall as well, if they are of the short type (Marcus, 1929).

To sum up present knowledge, it is probable that tardigrade excretion occurs in four different ways: 1) through the action of the salivary glands (at molting time, when the buccal apparatus is discarded); 2) through the epidermis in which the excretions are gathered in the shape of granules; 3) through the wall of the mid-gut; 4) through the Malpighian tubules when they are present. We are still not yet absolutely sure that excretion really takes place in these ways, and in these ways only.

MUSCULAR SYSTEM.

Tardigrade musculature has been studied in detail only in a relatively small number of species, and even in these, there are still doubts as to certain details.

We shall provide only basic information of a general nature at this point as anyone who is seeking a deeper knowledge of the subject can consult the specialized studies (the summary of Marcus (1929) in particular).

The musculature shows a distinct segmentation and consists, according to the species and excluding the musculature of the buccal apparatus, of 40 to 140 single muscles, and possibly more. Doyère (1840) states that *Milnesium tardigradum* has 165 trunk muscles and 126 limb muscles, but such figures are held to be excessive by more modern authors and probably refer to muscle cells, not to muscles. In fact, each muscle can be made up of one single uninuclear cell, or of several cells joined together in a chain.

Figure 21 schematically shows the musculature of an *Echiniscus*. As in all other tardigrades, the number of ventral muscles is greater than that of dorsal muscles. In *Echiniscus* (and in the Heterotardigrada in general) there are only two longitudinal dorsal muscles, while there are four in the Eutardigrada, which have greater dorsal flexibility so that they can bend their head and the anterior part of their trunk backwards.

Whereas these longitudinal dorsal muscles, in conjunction with the longitudinal ventral muscles, permit the contracting and bending of the body, the movement of the motor appendages is controlled by a series of muscles inserted near the distal extremity of the legs and at the other end to the ventral or dorsal cuticle. A group of muscles in the caudal zone acts in egg deposition and defecation.

The complex musculature of the buccal apparatus (stylet movements) has already been described briefly in the preceding chapter. We will only

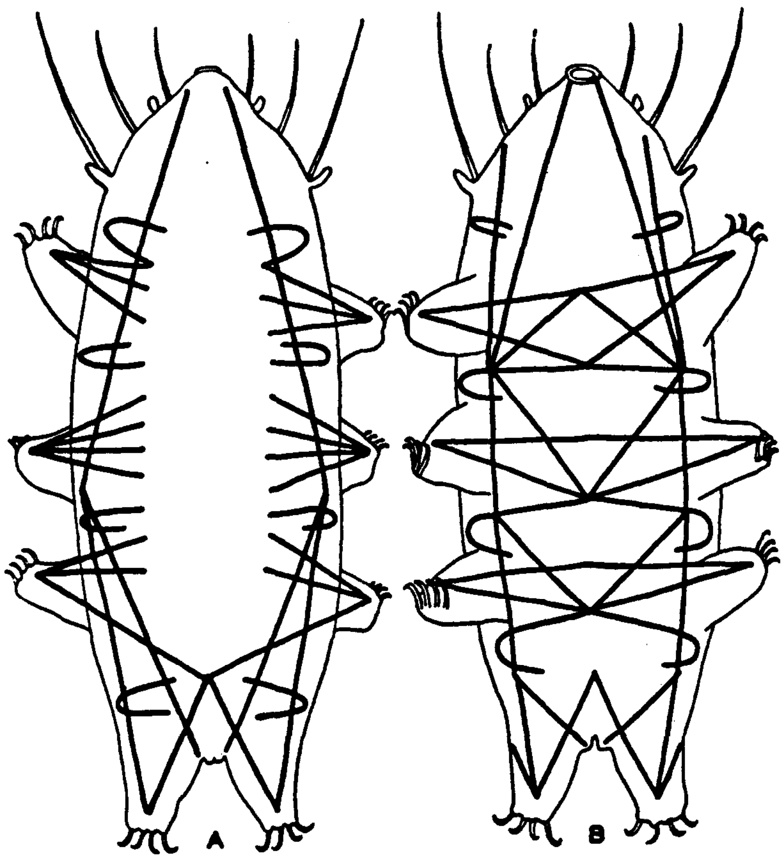


Fig. 21 - Trunk and leg musculature in an *Echiniscus*, semischematic. A, dorsal view; B, ventral view (from Pennak).

add that in certain genera there are also longitudinal muscles in the mid-gut consisting of eight muscle cells placed around the intestine, beginning at the esophagus and ending just posterior to the opening of the Malpighian tubules into the intestine (Figs. 20 and 25). The presence of this musculature is confirmed in the genera *Macrobiotus*, *Hypsibius*, and *Milnesium*, while it is uncertain in *Echiniscus* and *Pseudechiniscus*; it does not exist in *Echiniscoides*, nor probably in *Batillipes* and *Tetrakon*. Nothing precise is known regarding other genera.

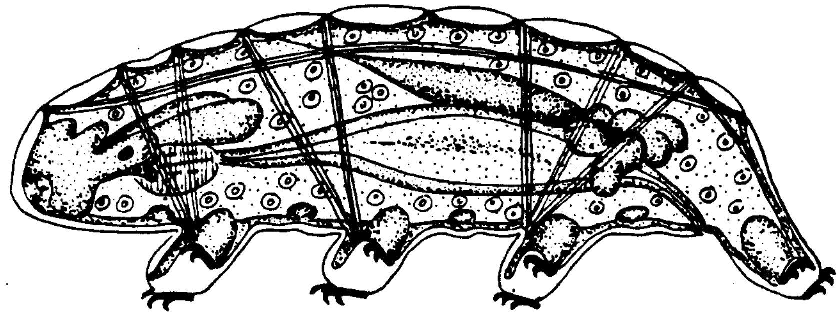


Fig. 22 - Schematic section of a *Macrobiotus* during the stage preceding molting, the points of attachment of the muscles to the cuticle and the claw glands which have formed the new claws are clearly visible. Observe, from left to right: the brain, with the cerebral lobes and eye; salivary glands above the pharynx; esophagus; midgut with gonad above it; Malpighian tubules; rectum; the body cavity cells can be seen inside the general body cavity and, ventrally, the ganglion chain (from Marcus, modified).

The attachment of muscles to the cuticle are on cuticular protrusions, which cross through the epidermis (Fig. 22) and are reformed at each molt. This close connection between muscle cells and cuticle also explains the movements which have at times been noticed in the cuticular extensions of the Echiniscidae (bristles and filaments) and which must be considered entirely passive, as none of these possess their own musculature.

All the muscle fibers are smooth and only permit adductive motion. There is no circular musculature, but the antagonistic action is generally produced by the pressure of the liquids contained in the body, and by the elasticity of the cuticle.

The movements of the claws, which occur constantly in tardigrades, are not governed by muscles, but are simply passive. The contractions of the leg muscles, which are attached a little behind the base of the claw, raise the claws which fall back down again due to the elasticity of the cuticle.

NERVOUS SYSTEM AND SENSE ORGANS.

The nervous system is of a type similar to that of the Arthropoda and consists of a supraesophageal or cerebral ganglion, of a subesophageal ganglion and a ventral chain of four slightly bilobed ganglia, in addition to other small peripheral ganglia (Fig. 23).

The supraesophageal ganglion (Fig. 24) has, in all tardigrades four lobes directed backwards. In the Eutardigrada the external lobes are much

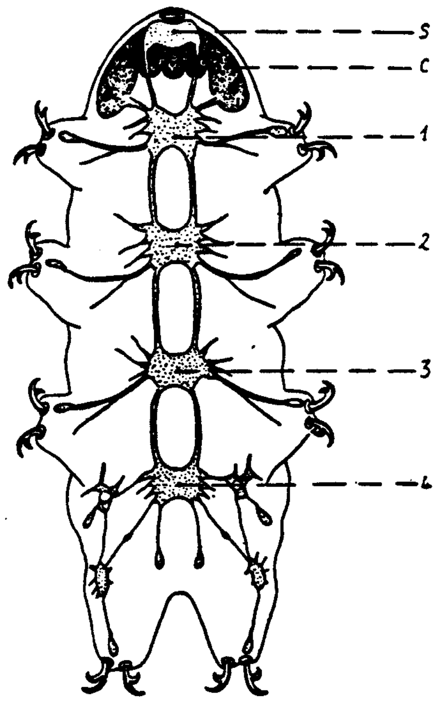


Fig. 23 - Nervous system of a *Macrobiotus* (semi-schematic, ventral view); b, brain; s, subesophageal ganglion; 1, 2, 3, 4, 1st, 2nd, 3rd, 4th ventral ganglia (from Pennak, modified).

longer than the internal lobes and there is, in addition to these, a middle lobe inserted between them, so that in fact the brain appears to be composed of five lobes (Fig. 24, e, f). There are no morphological differences between the brains of the genera *Macrobiotus* and the *Hypsibius*. Nerves spread out from the supraesophageal ganglion, leading to the longitudinal dorsal musculature and the cephalic appendages (middle cirrus, internal and external buccal cirri, lateral cirrus "A", clava); in the Macrobiotidae, which have no cephalic appendages, these nerves lead to the anterior zone of the head.

Our knowledge concerning the number and layout of the nerves, which start from the brain, is somewhat limited and has numerous gaps, caused mainly by the technical difficulties of preparation and observation. For instance, we know nothing of the course of the nerve bundle to the musculature of the buccal apparatus. According to Thulin (1928) and Marcus (1929), there are supposedly 19 nerves in the cephalic zone of the tardigrade, even in the type lacking cephalic appendages.

The brain (supraesophageal ganglion) is linked by a periesophageal ring to the subesophageal ganglion, in turn connected to the ventral chain of four ganglia, corresponding to the legs. The first ventral ganglion, in addition to the subesophageal ganglion, is also joined to the external lobes

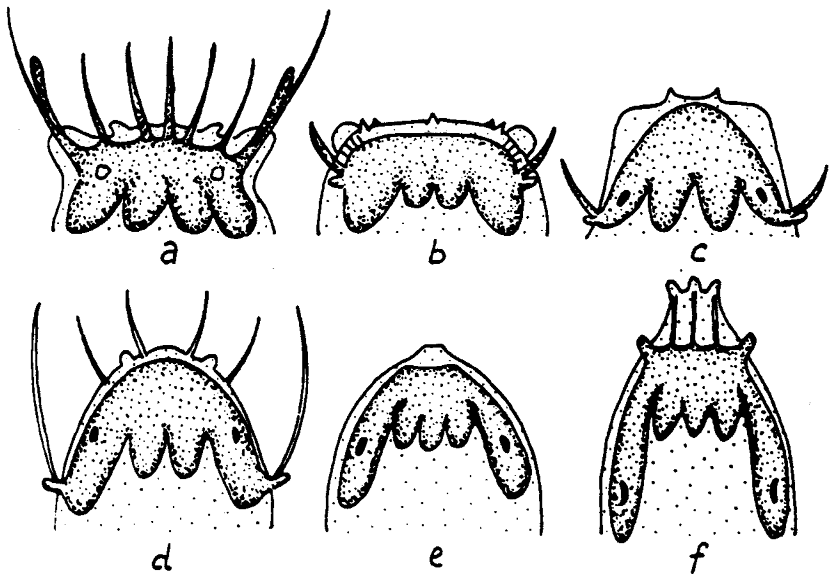


Fig. 24 - Schematic dorsal view of the brain in: a, *Batillipes mirus*; b, *Tetrakon synaptae*; c, *Echiniscoides sigismundi*; d, *Echiniscus (Bryodelphax) parvulus*; e, *Macrobiotus hufelandi*; f, *Milnesium tardigradum* (from Marcus, redrawn).

of the brain, so that one can consider that there are in fact two periesophageal rings present.

Counting the brain cells can be technically very difficult. On the basis of the number of nuclei observed in one section, which included the lateral lobes and the periesophageal ring, Marcus (1928, 1929) concluded (in a highly approximate manner) that there were about 300 to 400 cells in the supraesophageal ganglion in Macrobiotus.

The peripheral nerves extending from the ventral ganglia have been observed only in the Eutardigrada and even then only incompletely. There are also small peripheral ganglia, especially corresponding to the distal part of each leg, in the caudal zone and near the anus.

The sense organs are most likely represented by the cephalic appendages in the Heterotardigrada, and the papilla of the fourth pair of legs and the rostral papillae in *Milnesium*. However, if one touches these appendages with a fine needle, there does not seem to be any reaction. The external lobes of the brain in several tardigrades are provided with two photosensitive spots (eyes, for short), which are black in the Eutardigrada, nearly always red (occasionally black) in the Echiniscidae. The eye consists of a cup-shaped pigmented cell, open towards the front, and containing a single photosensitive cell, which differs from the other cerebral cells through its greater transparency. The centripetal fibers of the photosensitive cell can be followed only a short distance into the brain, as there are not yet any methods of selective staining available.

Sometimes the eyes can be present or absent in the same species, and cases have also been recorded in which there was an eye spot only on one side of the animal; other species usually have no eyes. In the Eutardigrada the eye spots are normally situated in a caudal position, on the external lobes of the brain (the so-called posterior eyes) but in a few cases (e.g., in *Macrobiotus fuciger*) they can be found further forward and placed near the anterior margin of the brain, though still in a lateral position (anterior eyes).

Little can be said about phototropism in tardigrades as the few experiments carried out have given contradictory results. This can most likely be attributed mainly to experimental conditions, very different from those existing in the tardigrade's normal environment, but on the other hand, it is not possible to study them in their natural surroundings -- moss or lichen, for instance, where among other things -- the animals very quickly become invisible. However, in certain cases tardigrades have shown positive phototropism (Von Etlanger, 1895, for *Hypsibius dujardini*) in others it was positive under diffuse lighting and negative under intense lighting (Von Wenck, 1914, for *Pseudobiotus augusti*), and in others still, they seemed indifferent to lighting effects. In a very well conducted experiment on *Dactylobiotus dispar*, Marcus (1928) was able to note that, in experimental conditions, there was a distinct, and nearly immediate, negative phototropism.

Baumann (1961) observed that young *H. convergens*, when they have just come out of their shells, show positive phototropism, which does however disappear after the second molt.

In the genus *Batillipes*, which lives in an interstitial environment, one can detect a thigmotropism when the animal moves between the granules of sand, and a rheotropism when reacting to strong movement.

REPRODUCTIVE APPARATUS.

The sexes are continually separated. The unpaired gonad, placed in a dorsal position, above the intestine, is sack-shaped, with very thin walls, and is held up, in adult Eutardigrada, by two anterior ligaments, fixed to the dorsal body wall (Figs. 1, 22, 25). The younger specimens of *Hypsibius* and *Milnesium* (also members of the order Eutardigrada) have two supplementary supporting filaments which later disappear with age, and which are placed beside the rostral ligaments. In the Heterotardigrada, on the other hand, the gonad is supported by a single middle and anterior ligament.

The dimensions of the gonad vary in both sexes with age and sexual activity. In sexually mature females, approaching egg-laying time, the swollen sack-shaped gonad covers the whole mid-gut and the rectum, whereas at earlier stages in life its length and diameter are reduced. In *Milnesium tardigradum* the male gonad (testis) is not sack-shaped, but spheroidal and flattened, and it is also very small and only covers dorsally the posterior part of the excretory glands (Malpighian tubules). Other morphological variations in the gonads exist in single species, especially the marine species.

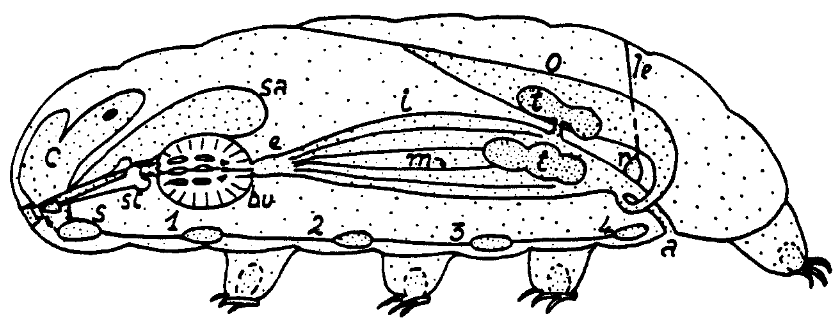


Fig. 25 - Schematic lateral view of a *Macrobiotus*. a, anus; bu, pharynx; c, brain; e, esophagus; l, midgut; le, ligament of the seminal receptacle; m, longitudinal muscles of the midgut; o, ovary; r, seminal receptacle; s, subesophageal ganglion; sa, salivary gland; st, stylet; t, Malpighian tubules; 1, 2, 3, 4, ventral ganglia.

The male has two more or less curved sperm ducts, which (in the Eutardigrada) open into the rectum. One can frequently observe mature males, in which sperm ducts are full of spermatozoa, easily rendered more visible by staining with acetic carmine.

The female however has only one oviduct, sometimes on the right, sometimes to the left of the ovary, and these variations can even occur within the same species.

Whereas (as has been stated frequently) the sperm ducts and oviducts of the Eutardigrada open into the rectum, those of the Heterotardigrada end in a ventral, preanally situated gonopore, often surrounded by rosette-shaped cuticular folds.

In females of the genera *Macrobiotus* and *Hypsibius* a seminal receptacle has been observed at times (during the autumn and winter) placed on the right or left of the rectum, but it is not known whether this exists in all species of the above mentioned genera, or only in some of them (Marcus, 1928). The seminal receptacle (Figs. 1 and 20) looks like a small sack, pointed at the distal extremity, and containing immobile apparently agglutinated spermatozoa, is about 30 to 40μ long and 10 to 15μ wide and opens ventrally into the rectum, next to the oviduct opening. A thin supporting ligament joins the pointed end of the seminal receptacle to the dorsal epidermis (Fig. 25).

The tardigrade's spermatozoa have been described only in a few species. Those of *Hypsibius dujardini* (Marcus, 1929) are very thin, 80 to 90μ long, with a spirally-shaped head (7 to 8 coils) about 11 to 12μ long, or occasionally even 16μ; the haploid chromosome number is 5. The spermatozoa of *Macrobiotus hufelandi* are of the same type (Baumann, 1920) whereas in the gonad of a male *Tetrakentron synaptae* 105μ long, spermatozoa 35μ long were seen with heads twisted towards the gonopore and the tails of which nearly reached the anterior extremity of the testis (Marcus, 1928); this same author observed spermatozoa in *Isohypsibius nodosus* about 80μ long.

Tardigrade eggs, which take on a great importance in recognizing the species, especially in the genus *Macrobiotus*, are sometimes smooth, with a thin shell, and are deposited in the exuvia in numbers ranging from 2 to 60, at the time of molting (genera *Parechiniscus*, *Echiniscus*, *Pseudechiniscus* and nearly all *Hypsibius* and *Milnesium*); At other times the eggs, with stronger and variously ornamented shells (protuberances or extensions) are deposited freely, isolated or in small groups, in numbers up to about 15 (genera *Macrobiotus*, with rare exceptions, *Echiniscoides* and *Batillipes*). Nothing is known about the egg laying methods of numerous genera, especially marine genera.

Only in a very few cases has it been possible to observe tardigrades mating and the fertilization of the eggs so that the details regarding these processes are not fully known. In *Hypsibius dujardini* and *Pseudobiotus augusti*, which deposit the eggs in the old cuticle, one or more males gather around a female about to deposit her eggs (Von Wenck, 1914) and, while she undergoes the molting process and deposits the eggs in the discarded cuticle, they sprinkle the eggs with their spermatozoa. According to Henneke (1911) the males supposedly pierce the old cuticle with their stylets, introducing the spermatozoa in this way, but according to Von Erlanger (1895) the spermatozoa are inserted through the cloaca of the old cuticle, whose hypothesis would seem more probable.

In *Isohypsibius nodosus* Marcus (1929), observed an actual mating process, independently from the egg-laying. A male of this species clambered onto a female, which was larger than it, and undergoing a molt, and injected the spermatozoa through its cloaca into the anal aperture of the female's old cuticle, which was already partly detached from it. Ten minutes later there were very few spermatozoa (about 80μ long) left in the old cuticle, while many of them had passed into the female's ovary. Twenty-four hours later the female had completed the molt and left behind the old cuticle, without however leaving any eggs in it.

As for *H. convergens*, Baumann (1961) observed "games" (courting?) on the part of the male, before mating.

Spermatozoa have often been noticed inside the ovary of the females even in other species and sometimes even when the oocytes were still at the first stages of development. Of course the studies carried out until now in artificial breeding conditions are too unsubstantiated for one to draw any general conclusions. For instance, it is not known whether the spermatozoa remain in the ovary and in the seminal receptacle, or whether they penetrate into the oocytes immediately, whether mating always coincides with molting and whether or not in *Pseudechiniscus*, *Echiniscus* and other species, in which the males are rare or unknown, there is parthenogenetic reproduction in addition to sexual reproduction. It is very difficult to answer these questions, as it has not yet been possible to breed tardigrades, belonging to the family Echiniscidae, for long periods of time.

The secondary sexual characteristics of tardigrades are few and rarely apparent:

In several Heterotardigrada the sexes can be distinguished by the position and appearance of the gonopore: the females have a rosette gonopore, positioned about in the middle of the ventral surface, between the 3rd and the 4th pair of legs, while the males have a protruding aperture, less distant from the anus.

In the genus *Halechiniscus* and others the males have a club, as long or longer than cirrus A, while in the females it is considerably shorter.

With regard to the Eutardigrada, one can cite the modification of the claws of the first pair of legs in the males of *Milnesium tardigradum* (Fig. 26) and of *Pseudobiotus augusti* and *megalonyx*.

The male of *Hypsibius oberhaeuseri* has a concealed gibbosity on the external side of the fourth pair of legs; it may be that some other species have small differences in the claws, usually the first pair of legs.

Even the sizes of the adult individuals are not usable for the sure distinction of the sexes, because in the same population may be males smaller than the females, but also of equal size; one should always keep in mind that the sexual maturity is in general attained in the two sexes, and in all the tardigrades, before the maximum size is attained; therefore it is easy to observe egg-bearing exuvia of *Echiniscus* half the length, or even less, of the adult females living in the same moss. In *Milnesium tardi-*

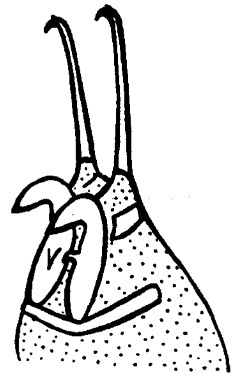


Fig. 26 - Modified doubleclaw on the first pair of legs of a *Milnesium tardigradum* male.

gradum it appears that the males can often be smaller than the females, and this can probably be verified also in some species of *Macrobiotus*, however with reservation and without wanting to give a general rule.

SEXUAL REPRODUCTION AND PARTHENOGENESIS.

In the tardigrades have been observed parthenogenetic populations, which are sexual.

Parthenogenesis was experimentally verified by Ammermann (1962) for *Hypsibius dujardini* and by Baumann (1964) for *Milnesium tardigradum*.

The hydrophilic and hygrophilic species *H. dujardini* was raised successfully by Ammermann, and as a substratum he used a mixture of sessile algae, belonging to the order Chlorococcales, probably the genus *Chlorella*. The culture liquid he used was a diluted soil decoction (described by Hammerling) and the temperature was maintained at between 21° C and 23° C.

Without going into any great detail (I refer the reader to the original for that), Ammermann observed that *H. dujardini*, in culture conditions, presents obligatory parthenogenesis: males never appeared (the culture lasted six years, when these results were given in 1967).

The first meiotic division reduces the number of chromosomes, and the chromosomes ($2n=10$) split up between a polar body and the egg nucleus. Before the second division, the dyads split thus reconstituting the diploid number. After the egg nucleus has moved toward the center of the egg, segmentation begins. During the second meiosis and the first division of segmentation, the chromosomes can develop into "large chromosomes" which presumably consist mainly of RNA. No "large chromosomes" were observed after the seventh cellular division. During the first division, the chromosomes are always "small".

It is very strange, and unexpected, that a *obligatory parthenogenesis* (diploid) was observed in this batch of *H. dujardini*, a species among which there are males in nature, varying in percentage according to the number of females.

Parthenogenesis was also confirmed in the case of *Milnesium tardigradum* (Baumann, 1964) and of *Dactylobiotus dispar* (Ammermann, unpublished, but quoted by the author in his 1967 publication). It was excluded however, in the case of *H. convergens* (Baumann, 1961).

However, while in interbreeding sexual populations of tardigrades (as, e.g., the marine species, but also many terrestrial) the sex ratio is normal, that is to say 1:1, in the Echiniscidae (except in two species, *Pseudechiniscus pseudoconifer* and *P. hannae*) males have not been observed until recently, and also in the Eutardigrada were observed populations in which the males are rare or absent. These populations evidentally result parthenogenetically. On the other hand, parthenogenesis and interbreeding sex sometimes appear in the same species, Bertolani even established that parthenogenetic and interbreeding sexual "biotypes" can coexist in the same habitat. These biotypes may constitute sibling species, distinguished exclusively on the basis of their reproduction and chromosomal characteristics.

Thus, for *Macrobiotus hufelandi* and *M. richtersi* have been noted diploid bisexual biotypes ($2n=12$) and triploid parthenogenetic biotypes ($3n=18$).

In *Hypsibius oberhaeuseri* there are three biotypes, one diploid bisexual ($2n=12$) and two parthenogenetic, one triploid ($3n=18$), the other tetraploid ($4n=24$).

Also diploid populations may be parthenogenetic, like *Hypsibius dujardini* ($2n=10$) and *Dactylobiotus dispar* ($2n=10$).

DEVELOPMENT AND EGGS.

The development of the embryo in certain species of tardigrade has been studied in depth and described by Marcus (1929), to whom we refer anyone wishing to acquire more information on the subject, since we will only sum it up here according to Cuènot's (1932) treatment.

Total and equal cleavage leads to the formation of a blastula, with a very small central cavity (blastocoele), which is sometimes invisible, the walls of which consist of cells with peripheral nuclei.

The endoderm is formed through cleavage and the endodermal cells divide, filling up the blastocoele. When there are 50 to 60 cells inside, a cavity appears in the center, surrounded by the cellular coating, which takes on the aspect of an epithelium, delimiting the cavity of the primitive intestine. The embryo curls up, and a proctodeal hollow forms on the ventral side, and soon connects up with the archenteron. Endodermal cells of a particular type begin to appear, which are the primordial ova. Then the embryo curls up even more and (still on the ventral side) the stomodeal hollow is formed. Different coelomic pouches appear which are only temporary and later disappear, except for two of them, whose walls disintegrate and form the large spheroidal cells, floating in the coelomic fluid (body cavity cells), and also form the muscle cells. The two pouches, which have not disappeared and on the ventral walls of which are attached the ova, move closer together on the dorsal side and then unite to form the single gonad. The oviduct or the sperm ducts then originate ventrally.

The brain and the ventral ganglia first appear as thick swellings in the ectodermal wall. The stomach, which is connected to the midgut differentiates into an anterior part, which then forms the buccal tube with the large lateral stylet glands (salivary glands), into a middle part which becomes the pharynx, and into a terminal section which turns into the short esophagus. Where the midgut ends and the proctodeum begins, the malpighian tubules, whose origin is ectodermal, are formed.

Baumann (1966) observed that *H. oberhaeuseri* females lay eggs within the 48 hours following mating.

The time span between the deposition of eggs and hatching of young tardigrades varies a great deal, not only according to species, but also according to atmospheric conditions. If the deposition of eggs in moss on a rainy day, for instance, is followed by a long rainy period, the moss will stay moist and the tardigrades will hatch long before they would have if the egg laying had been followed by several days of dry weather delaying development. Apart from the degree of humidity in the atmosphere, certain other factors also play a part, first of all the temperature (from which stems a seasonal variation in the duration of development), and perhaps also the chemiophysical conditions of the habitat, solar radiation, etc.

Taking as a basis, the observations of several authors and researchers, it is not possible to indicate exactly what time is needed for the egg to develop, from deposition to hatching; a period which (even with no change in temperature) can vary within the same species. Perhaps (but this is far from being certain knowledge) eggs with thin shells, deposited in the old cuticle, develop more swiftly than those with thicker shells, bearing ornamentations.

One can only say that the minimum development time, observed in tardigrades, reared at a temperature of 18°C, was five days for *Hypsibius convergens* (average time for 100 eggs taken from 10 old cuticles (Marcus, 1929), whereas the maximum was about 30 to 40 days for eggs from several species of *Macrobiotus* and *Hypsibius oberhaeuseri*. Experiments on the period required for the development of eggs of *Milnesium tardigradum* at different temperatures (Marcus, 1929) gave the following results: 21 days at 8° to 10°C, 13 days at 18°C, 10 days at 24°C.

Baumann (1964) observed shorter development periods for *Milnesium tardigradum*: from a minimum of seven days to a maximum of twelve days (but the temperature was not kept constant). Baumann also observed (1966) that development of *H. oberhaeuseri* took place within eight to twenty days.

In a natural environment things probably occur quite differently, especially for moss and soil inhabiting species, which are subject to atmospheric conditions very difficult to reproduce in an experiment. It has been observed that in mosses and lichens, eggs can be found at any time of the year, and the same applies to soil inhabiting species where, however, the eggs are perhaps more numerous in winter (Ramazzotti, 1959). For freshwater and psammon tardigrades observations have been too few for any conclusions yet to be drawn.

Some freshwater species (*Isohypsibius annulatus*, *Pseudobiotus augusti*, and *P. megalonyx*) carry -- but not always -- for a certain time (up to the time of the opening of the eggs) the egg-bearing exuvium attached to the head (*I. annulatus*) or to the 4th pair of legs (the two species of *Pseudobiotus*). The same happens also, often, in the marine species *Echiniscoides sigismundi*. Other species abandon the exuvium with the eggs after molting, while in many others the eggs are deposited free.

When development is completed, the young tardigrade comes out of its shell, sometimes perforating it with its stylets, at other times tearing it apart with its hind legs, and increasing its volume rapidly and noticeably because of the absorption of water. With regards to eggs deposited in the old exuvium it often occurs that the tardigrade explores the discarded cuticle for a long time without finding an exit, until it meets the tear through which its mother discarded the old cuticle, thus managing to set itself free. However, I have seen in a few exceptional cases, young tardigrades die inside the discarded cuticle because they could not get out.

Young specimens of the family Macrobiotidae are exactly like the adults, except in size, the state of the gonads and certain characteristics of the claws and the placoids. On the other hand, the young (larvae) of the family Echiniscidae have a still incomplete dentate collar, two claws for each leg (corresponding to the adult's two central claws) instead of four, and a lesser number of occasional bristle and spine extensions in comparison with the adults: they will take on their final shape through successive molts.

The increase in the size of the body does not occur through cellular division, but through growth of the individual cells.

Not much is known about the young of marine tardigrades: McGinty and Higgins (1968) observed that *Ba. mirus* has only four digits in early stages (instead of six); *Ec. sigismundi* has five claws in youth, while the adults have nine to eleven (Marcus, 1927).

We must now return to the eggs in greater detail, especially their morphological aspect, given their enormous taxonomic importance, particularly in the genus *Macrobiotus*.

The eggs, spherical or oval, develop in the ovary which (during the period immediately preceding egg-laying) is so swollen that it almost completely compresses the midgut. In many cases (nearly always in the genus *Macrobiotus*) the eggs are covered with various ornaments and protuberances (appendages) which may be used to stop external agents from making them slip off their substratum (moss, lichen, etc.). These ornamentations usually become visible only after deposition of the eggs, since inside the ovary the eggs and their extensions are flattened, due to pressure on both sides.

We have already mentioned the existence of two different types of egg. We can subdivide the eggs particularly of non-marine tardigrades (since the marine ones are so little known) in the following way:

1. Smooth eggs, with a thin shell, always deposited in the old cuticle during molting and usually ovoid in shape. Among these are included the generally colorless, whitish or grayish, eggs of nearly all *Hypsibius*, *Milnesium*, and two species of *Macrobiotus* (*M. rubens* and *M. artipharyngis*) and the yellowish, reddish, or more rarely colorless species of *Parechiniscus*, *Echiniscus*, and *Pseudechiniscus*.

2. Smooth eggs, with a thin shell, deposited freely, belonging to a single very rare species, *Hypsibius antarcticus*, which can however also deposit them in the old cuticle.

3. Eggs with various ornamentation (appendages), deposited free. Belonging to this category of eggs almost all the *Macrobiotus*, the *Dactylobiotus* (except *D. macronyx*), the *Amphibolus* and some species of *Hypsibius* (which sometimes however abandon the eggs also in the exuvium).

In the scope of classification, the most interesting eggs are those of the third type, particularly those of *Macrobiotus*; in this genus the exact identification of species with smooth cuticle is almost always impossible if there are no eggs present, whereas it is often possible to identify the species by examining the eggs, in the absence of tardigrades.

The dimensions of eggs can vary within fairly wide limits. The smallest usually are those deposited in the old cuticle during molting, and these range from a minimum of about 42 by 30μ for *Hypsibius indicus*, and 42 by 36μ for *Bryodelphax parvulus*, to a maximum of about 135 by 90μ for *Milnesium tardigradum* (the numbers correspond to the smallest and largest diameter of the rotation of an ellipse which the shape of the egg is closest to). On the other hand, the freely deposited eggs of *Macrobiotus* are larger, more often round than ovoid and their diameter (extensions included) range from a minimum of about 40μ in *M. intermedius*, to a maximum of greater than 210μ in *M. spertii* and 235μ in *M. conifer*. It must be remembered that the size of the eggs is subject to considerable variations, not only among different groups, but even within the limits of a single population.

In many cases the shape of the ornamentation of the egg (that is, those of the above third example) take on considerable taxonomic importance.

The variety of shapes of ornamentations on the eggs can take on is huge. We will not attempt to list them all, but we will come back to them from time to time, when necessary. We do however hold it useful, so as to facilitate subsequent use of the keys, to assemble them into a few basic groups at this point and to describe the main modifications which occur in the different species of *Macrobiotus*.

The ornamentations (protuberances or appendices) on the shell can accordingly be divided roughly according to their shape into the following groups (see Fig. 27):

1) Extensions Protruding Freely from the Shell.

a. Hemispherical (Fig. 27 A, 1). Varieties of this type are hemispherical, flattened, mammary protuberances, illustrated under numbers 2 and 3 of the same figure. Generally these are rather small extensions, a few microns long, which can be separate from each other or have united bases.

b. Conical. Pyriform or shaped like onion bulbs (Fig. 27 B); usually these ornamentations are fairly large and can be 12 to 32μ long. The sketch shows only a few types, but there can be a very wide range of variations, for instance in the height/width ratio, in the presence of more or less complex veins, in the circular or polygonal bases (which may or may not be touching), in the rounded, pointed, or broken off distal extremities, which may also bear a vesicular swelling, etc.

c. Small tubercle shaped (Fig. 27 C). In general these protuberances are tiny, with simple distal extremities (No. 9, 10, 11 of the same figure) or

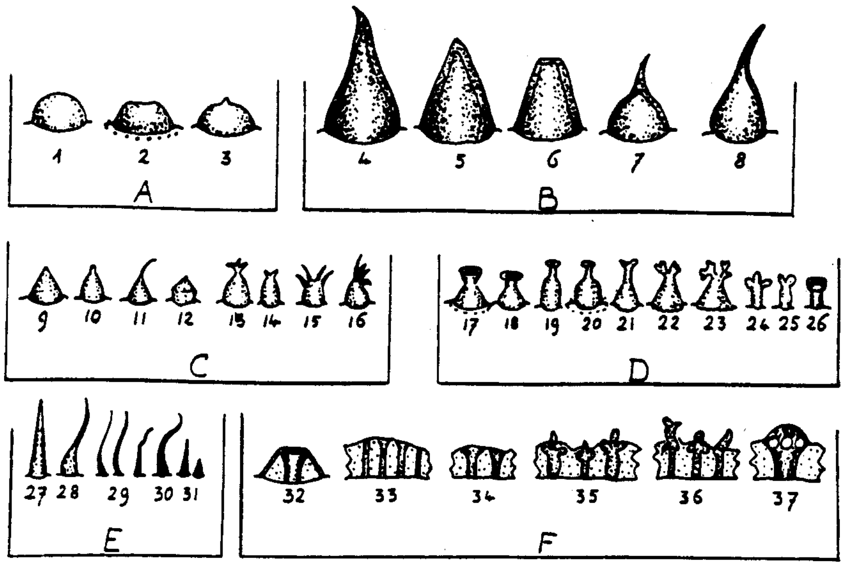


Fig. 27 - A few aspects of the ornamentations on *Macrobiotus* eggs. A, hemispherical; B, conical and pyriform; C, tubercles; D, various shapes; E, spines; F, ornamentations immersed in a transparent layer on the shell (see text for greater detail).

variously subdivided or ramified (13, 14, 15, and 16).

d. In the shape of different objects (Fig. 27 D), for instance "inverted egg cups" (17, 18), "bottles" (19, 20, 21), roots (22, 23, 24, and 25), bottlenecks (26), funnels, etc. In general they are a few microns long and occasionally reach 12 to 13μ.

e. Thorn-shaped (Fig. 27 E) with a base of varying widths, flexible or rigid, straight or curved, rough (27, 28) or smooth (29, 30, 31), only a few microns long, reaching about 20μ and sometimes distally subdivided.

2). Extensions Totally or Partially Immersed in a Transparent Zone, Which Covers the Shell.

f. Bottleneck-shaped (32), small cylinders (33), heraldic fleur-de-li's (35, 36), various (37). The thickness of the shell's transparent zone ranges from a few microns to about 22μ, depending on the species.

The egg shell, in between the protuberances, may be smooth, spotted or granulated, or else appear divided into polygonal areas, of varying size and regularity (so-called "plating" or "aerolation" to the Germans). In addition, the ornamentations are often surrounded at their bases by a small crown of spots, tiny circles or rectangles sculptured in the shell.

It is most likely that the eggs of certain species of *Macrobiotus* (*M. hufelandi*, for instance) have a sticky surface as groups of two to eight eggs can often be seen glued together, and also single eggs attached to blades of moss or mineral detritus, and which oppose a certain amount of resistance to being detached with a needle.

The tendency of certain aquatic species of tardigrade (*M. pullari*, *M. hastatus*, etc., for instance) to deposit the eggs, usually in groups, inside hollow objects, like the shells of Cladocera and Ostracoda, or old insect shells is most interesting. Therefore, when searching for freshwater *Macrobiotus* eggs at the bottom of lakes and ponds (always a very tedious, and often unsuccessful enterprise) one should carefully examine all old shells, but in particular those of Cladocera.

Sometimes it happens that the identification of a species of *Macrobiotus* is impossible because of a complete lack of eggs. If however, live females are present, containing in their ovary eggs in an advanced stage of development, one can attempt to obtain eggs in either of the following two ways:

--with a delicate and careful compression of the female it is not difficult to expel the eggs, but one must be extremely careful when identifying species through the study of eggs obtained in this way, as the form of the ornamentation often ends up modified, and different from the usual pattern. This method does not apply to fixed material, but requires fresh specimens.

--or else one can put the females under bell jars with a little water, to be changed daily, and a few strands of moss, waiting for the eggs to be deposited. This method is particularly adapted to freshwater species, but even with these, it is not always successful.

MOLTING, LIFE SPAN.

Molting, considering all the processes it involves, probably takes five to ten days. First, the components of the buccal apparatus are ejected, more specifically, the buccal tube, the pharyngeal tube (or the flexible part of the buccal tube, characteristic of the genus *Diphascon*) when there is one, the stylets, the stylet supports (which fold over during molting, allowing the stylets to stretch out inside the buccal tube), the external bulb

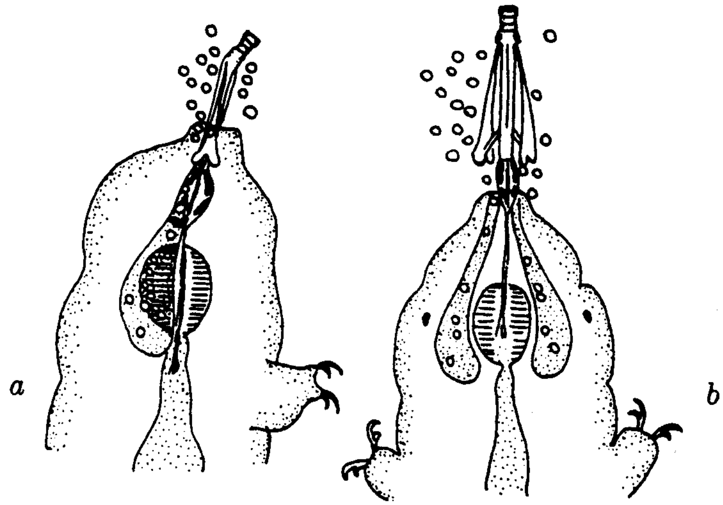


Fig. 28 - Expulsion of the buccal apparatus, and simultaneous expulsion of the pigment cells, from the salivary glands of *Macrobiotus hufelandi*; a, initial stage; b, more advanced stage (from Marcus, redrawn).

coating, and also the internal esophageal wall (Fig. 28). The buccal opening, which had previously widened considerably to permit the expulsion of the buccal organs, closes up. Thus the tardigrade finds itself in the so-called *stadio simplex*, recognizable precisely because of the absence of the buccal apparatus, and it is unable to take in food until all the discarded buccal parts are regenerated.

We have already said, when dealing with the digestive system, that the musculature of the buccal apparatus is not expelled. It remains in place and is completely surrounded by the salivary glands, which have moved forward at the expulsion of the buccal parts, ready to fix themselves onto the new stylets and corresponding supports after these have been regenerated.

The salivary glands provide for the reconstitution of the buccal tube, the pharyngeal tube (if applicable), the stylets, and stylet supports; the epithelial cells of the bulb regenerate the placoids (macroplacoids and microplacoids) and the external coating of the bulb itself; while the cells of the esophagus wall regenerate the internal cuticular coating itself.

The complete reconstitution of the buccal apparatus is followed, within a few days, by molting of the body cuticle and that lining the rectum, and also the molting of the claws which were being replaced by the claw glands in the meantime (see preceding chapter "Legs and Claws").

The duration of various phases in the molting process probably varies, depending on the species and atmospheric factors. With captive specimens of *M. hufelandi*, *D. dispar*, and *H. oberhaeuseri* Marcus (1929) recorded the following times:

--Expulsion of the buccal parts: about 6 days before molting.
--Period of absence of buccal parts: from 1 to 3 days.
--Duration of the reconstruction of the buccal apparatus: from 2 to 4 days.
--Period following, up to molting: from 0 to 2 days.
--Time needed to shed the old cuticle: 0 to 3 days.

So that, in the above mentioned artificial rearing of the three species concerned, a period of 3 to 9 days is needed for the complete molting process, to which a period of 0 to 3 days for shedding the old cuticle must be added. This last phase is probably much swifter in a natural environment than in a culture where it is difficult to set up the right conditions for anchorage (and perhaps partial compression of the old cuticle) which helps the animal to climb out.

Molting is made possible through an increase in the surface area of the cuticle to be abandoned, due either to the disappearance of the different folds, permitting a complete spreading of the cuticle itself, or to an intake of water. The surface of the tardigrade decreases simultaneously, occurring in different ways: 1) through a decrease in volume due to defecation (Heterotardigrada, *Hypsibius*, etc.); 2) through a change in shape, due to muscular contraction (*Macrobiotus*, etc.). Both of these methods of decreasing the surface can coexist.

It is noted that during molting and right up to its last stages, the old cuticle does not detach itself completely from the old, but contact zones remain, corresponding to the insertion points of the major body and leg muscles. This allows the molting animal to preserve its mobility.

At each molt the tardigrade's dimensions increase proportionally but much more during the first molts than the last. In exceptional cases, through lack of food, for instance, it can happen that there is a decrease in size after molting.

Baumann (1961) observed that specimens of *H. convergens* which had hatched out of their eggs during rearing had their first molt after three to six days, their second after about nine days, and their third after about 17 days. For *H. oberhaeuseri*, the first molt (Baumann, 1966) occurs as early as within the first four days following hatching.

The Echiniscidae, which as adults possess a determinate number of cuticular extensions (lateral, dorsolateral, dorsal filaments or spines, etc.), when they are young have only some of these, not only in the two-claw stages, but also the following, first four-claw stages. Accordingly when carrying out species identifications one must always choose fully-developed specimens, as in certain species the young can have extensions which are identical in size and layout to those of adults of other species. It must also be remembered that tardigrades are often sexually mature before having reached their full growth. Baumann (1961) was able to establish that well fed *H. convergens* females laid their eggs as early as after their second molt. The same occurs with *H. oberhaeuseri* (Baumann, 1966).

It is therefore possible to observe in Echiniscidae discarded cuticles which are smaller than the normal ones and already contain eggs, although they have fewer cuticular extensions than are characteristic of the species they belong to. All these variations collected at the time are, as far as possible, taken into account, either in the body of the keys or in the description of each species, but only a careful study of all the characteristics of several specimens, and above all a great deal of experience, can prevent mistakes.

The number of molts through which tardigrades go during the course of their lives is a problem which in my opinion, has not yet been completely solved. According to various authors, there are supposedly six molts in many species. Marcus (1929) notes a figure around twelve for *M. hufelandi*, *D. dispar*, and *H. oberhaeuseri*, an estimate based on different considerations, partly confirmed through results in breeding, which, however, took place as is usual and unavoidable, in artificial conditions.

Higgins (1959), studying the frequency distribution of types of body length and buccal apparatus in a group of about 800 *Macrobiotus islandicus* in Colorado (U.S.A.) came to the conclusion that there were seven molts. Observations of Ramazzotti of 1959 and 1960, on over 1000 *Macrobiotus areolatus*, inhabiting moss in Pallanza, on which measurements of the length of the body, the buccal tube, the chains of macroplacoids, and the diameter of the buccal tube were taken, while they did not lead to any certain results, could however give the impression that *M. areolatus* molts more frequently than *M. islandicus* (according to Higgins) and that their number is close to twelve, just as Marcus (1929) wrote of the species observed by him, as did Baumann (1961) of *H. convergens*.

A publication by Franceschi-Crippa and Lattes (1967) informs us that *M. hufelandi* also most likely has twelve molts.

It must however be noted that the causes of error inherent in this method, which seeks to establish the number of molts on the basis of the frequency of size categories in a population, are many and by no means negligible. Thus, for example, results vary greatly with the variation of the assumed size classes, without having any valid reason (at least within certain limits) for adopting one size rather than another. Then one must also take into account the eventual presence, within the same population, of distinct races of the same species, this being suggested (not a certainty) by the bimodality of a frequency curve for the diameter of the eggs, or the length or diameter of the buccal tube, when there are distinct differences in animals included in the same class of body lengths. But this last difference could represent a secondary sexual characteristic, and thus the necessity arises of measuring a great number of males and females separately (distinguishing them is not always easy). There must also be separate measurement of both sexes of variation of maximum and minimum because the range of body length can be different in the male and female. Accordingly, to reach a correct interpretation of the results, one must take this into account.

We have dwelt at some length on this subject and listed possible causes of error (though not all) so as to stress that one must always take great care before drawing hasty conclusions in this type of study, in which there are all too many, often very well concealed, pitfalls.

To sum up our present knowledge on the number of molts during the tardigrade's life, one can say that it is probably somewhere between six and twelve in certain species of *Macrobiotus* and *Hypsibius*; but we know very little about other species, not even whether the number of molts can vary within a single species, in relation to different atmospheric conditions, or to possible different physiological races.

Since it is not only the number of molts but also the time between one molt and the next which is uncertain, it follows that the tardigrade's life span is equally uncertain; of course, we are now dealing with *active life*, excluding the cryptobiotic (anabiotic) periods, which can be very long (certain high altitude alpine mosses come to mind, for instance, which are covered in snow and ice six to eight months of the year); on the other hand, by *total life*, the complete period from the hatching of the egg to death, is understood, and therefore includes the periods spent in cryptobiosis.

The problem might seem simpler for aquatic tardigrades, for which the period of active life corresponds to that of total life since there is no cryptobiosis. But in fact it is not possible to follow the continuous growth of aquatic tardigrades in their natural habitat, while various attempts at rearing from eggs have often failed before the animals had reached their complete development.

Nevertheless, it has been possible to establish roughly the active life span for some species, partly on the basis of experiments (breeding, marking tardigrades in their moss habitat) and partly on theoretical considerations. Marcus (1929 and 1936) reached the conclusion that active life (in *M. harmsworthi* and *H. convergens*) ranges over 18 to 30 months and that total life can last up to 67 years. This last figure seems exaggerated, even basing one's calculations on the longest apparent active life span (30 months) when one considers the few following examples in which it is acknowledged that the periods of active life correspond only to rainy days:

- with about 73 rainy days yearly (as occurs for instance in certain parts of Sicily) the total life span supposedly comes to about 12 years.
- with snow and ice for 6 to 7 months and 42 days of rain in the rest of the year (as happens with high altitude alpine mosses) the total life span would be about 22 years.
- with about 110 days of rain a year (as in many parts of northern Italy, for example) there would be a total life span of about 8 years.

Of course these deductions must only be taken as rough approximations. A relationship between days of rain and the active life span has been implied, but this may not play any part as mosses often remain humid long after the rain has stopped, or they can become moist in other ways. It has also been taken for granted that tardigrades can pass from cryptobiosis to active life and vice versa an unlimited number of times, whereas nothing is known about this except that in experimental conditions, which are in no way comparable to those in nature, tardigrades are able to survive a maximum of 14 desiccations. The number of cryptobiotic periods a tardigrade can undergo without suffering damage has been considered unrelated to time span between one cryptobiosis and the next. So, in fact, these and other factors have been disregarded, though they may be of great importance.

Then one must take into account the great variety of conditions which one animal may experience. For example, considering only moss and its level of humidity, one can go from those of high altitude, with about 40 days of rain in the warmer season, to those from a very humid area, with an abundance of dew, in which the moss is immersed in water nearly every day, at least for a few hours. In this latter habitat, it seems that tardigrades must undergo continual and swift changes from cryptobiosis to active life, while in the former there would be a long cryptobiotic winter period (six to seven months) followed by very short alternating periods of cryptobiosis and active life during the summer. Furthermore one can imagine the not unlikely condition of high altitude moss or lichen, set back in cracks or small rocky cavities, reached by rain only when the wind blew in certain directions so that it could become wet only a few times, ten for instance, during the warmer season. In such cases the total life span of the tardigrade inhabiting the moss would reach (with all the reservations listed above) more than 90 years; but, of course, such specimens (admitting the possibility of their existence) would be exceptions. One can conclude by saying that:

1. For a few freshwater species of the genus *Macrobiotus* and *Hypsibius* it seems that active life (also corresponding to total life) has a span of 12 to 24 months (although L. W. Pollock proposed a life span of 3-4 months, based on the publications of Francheschi and collaborators of 1962-63).
2. For certain moss inhabiting species of the same genera, if one agrees to an active life span of about 15 to 30 months, the total life span in average conditions could vary from 4 to 12 years, without however excluding the fact that it can decrease by a few years in extreme conditions or extend beyond 20 to 25 years.
3. For all other marine, moss and soil inhabiting species (by far the largest group) there is no reliable information on which to base conclusions, however one tends to think that the active life spans do not differ too widely from those guessed at in paragraph 2 above, at least for moss inhabiting species.

It is still necessary to stress the fact that all hypotheses (including the one just expounded) concerning the life span of tardigrades are purely theoretical and not at all reliable at the present stage of our knowledge.

ASPHYXIAL STATE.

When atmospheric conditions become unfavorable, tardigrades invariably tend, through muscular contraction, to take on their characteristic "barrel" shape (Fig. 29), which is peculiar to the cryptobiotic state, as we shall see more clearly in the next chapter. If however the water of the environment (the liquid which immerses the moss, for the moss inhabiting species, the atmospheric liquid for the freshwater species, etc.) is lacking in oxygen, the tardigrades are unable to reach their "barrel" state, but stretch out completely, taking on a longer shape, with their legs stiff and extended, become quite transparent and stop moving completely. This is the so-called "asphyxial state" or "asphyxia".

This asphyxial state is easily brought on by putting the tardigrade in a drop of water on a slide, covered by a coverglass. The time needed for the asphyxial state to appear can vary from a few hours to a few days and is an inverse function of temperature, and if boiled water is used, the asphyxia occurs, logically enough, with greater speed.

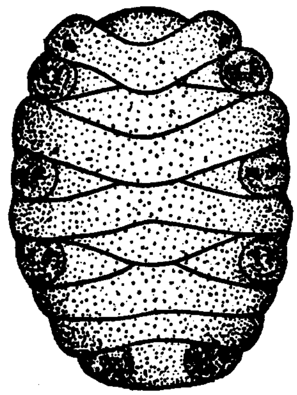


Fig. 29 - "Barrel" stage of *Macrobiotus*.

Tardigrades in an asphyxial state, because of their high degree of transparency, lend themselves very well to the study of their internal structure (muscles, digestive system, Malpighian tubules, etc.), which appear best in these conditions of visibility; Doyère (1840) and Greeff (1865) made use of tardigrades in an asphyxial state to study their anatomy.

If the asphyxial period lasts less than four to five days, a return to active life is often possible, by providing water with oxygen (stirring in contact with atmospheric air, changing the water itself, etc.), otherwise the animal dies.

It seems that strictly aquatic tardigrades are able to resist asphyxia for less time (from a few hours to three days), but observations on the subject are scarce. One can only state that generally the asphyxial state is not always reversible and that it should most probably be regarded as a pathological manifestation, rather than as an effective way of overcoming unfavorable conditions where oxygen is lacking. However, it cannot be excluded that sometimes, in the water which moistens the deepest part of the moss, there are short periods of oxygen shortage, during which the moss-inhabiting species go into an asphyxial state.

The process of asphyxia is probably due to imperfect osmotic control, as in the asphyxial state the tardigrade's body appears swollen by the excess os water it contains, which is precisely what produces its complete extension and the disappearance of any cuticular folds; just as dead or damaged tardigrades frequently appear when there is no longer any osmoregulation possible.

The marine tardigrade *Echiniscoides sigismundi*, transferred to freshwater, goes into an asphyxial state swelling up considerably, and can stay like that for three days without dying. Transferred back into salt water, it immediately returns to active life, whereas it takes a few hours in normal conditions, if the asphyxia has been brought on by distilled or boiled water, instead of natural fresh water (Marcus, 1929); these experiments also help to prove that the asphyxial state has its origins in osmotic phenomena and in the consequent passage of external water into the denser fluids, contained within the tardigrades's body.

CRYPTOBIOSIS (OR ANABIOSIS).

All tardigrades must be regarded as aquatic animals. Even those dwelling in moss, lichen, liverwort and in soil, etc., can lead an active life only if a film of water at least as thick as their body, covers the environment in which they live. It follows that so-called "terrestrial" tardigrades have limited periods of active life, coinciding with rainfalls, heavy dew, melting ice or snow, or else with high degrees of humidity.

When their environment dries up, the majority of tardigrades (excluding nearly all marine and fresh-water species) can pass into a special state of latent life, called anabiosis or, more recently, cryptobiosis, returning to active life once more when placed in contact with water.

Cryptobiosis is not characteristic of tardigrades alone, but exists in many other animals, for instance in protozoa, rotifers, nematodes, etc., and in numerous eggs (of rotifers, tardigrades, turbellarians, crustacea, acarina, etc.) as well as in plants (seeds, spores, bulbs, etc.).

The phenomenon of cryptobiosis is so interesting and has given rise to so many controversies in the past, that it seems opportune to provide some historical information at least, summing it up very briefly, and referring anyone with a desire to know more on the subject to Keilin (1959), Marcus (1929), and May (1948).

The Dutchman Leeuwenhoek was probably the first to observe the resistance of bdelloid rotifers to desiccation, and to carry out relevant experiments (1701); he thought that life went on, although in a latent manner, after the disappearance of the water around them, and that their desiccation was not complete, due to the presence of the cuticle. In 1743 and in 1753 respectively, Needham and Baker observed nematodes coming back to life, after a desiccation which, contrary to Leeuwenhoek, they considered complete. Many other scholars dealt with the subject reaching differing conclusions, though they were generally negative, on the ability of certain animals, which had dried up, to return to active life. Opinions also differed regarding the question whether the period spent in that state, which we now call cryptobiosis, was to be regarded as suspended life or not.

Then in 1776 Lazzaro Spallanzani published his extremely perceptive observations on the revival of tardigrades, rotifers and nematodes, which we already partly dealt with in the chapter "First Observers of the Tardigrade". His experiments were carried out on a very wide scale and took place at various temperatures, in different humidity ratios, in a vacuum and at atmospheric pressures, and in the presence of different substances, various gases and vapors. Two things are to be noted in Spallanzani's work: firstly, he proves that the presence of sand around the animal during desiccation is indispensable for reviving tardigrades and rotifers, thus explaining the sometimes negative results obtained by previous observers; secondly, that he interpreted the return to active life, after desiccation, as an actual "resurrection".

Spallanzani's admirable observations should have erased any doubts concerning the ability of certain animal groups to withstand desiccation, instead, the greatest proportion of naturalists, even the best known ones (except Lamarck and a few others) continued to deny the existence of this phenomenon for decades. This state of affairs continued until 1842, when Doyère, in a series of experiments on Tardigrades, was able to demonstrate this return to life, which he however thought of as a resurrection, of animals which had quite definitely dried up, as he had left them in dry air for eight days, and then for 17 days in a desiccator with sulfuric acid, and after that in a vacuum inside a barometric tube in the presence of calcium chloride.

In the following years a new controversy arose between the supporters of the two opposing doctrines regarding cryptobiosis. One group, headed by Doyère, maintained, in accordance once more with Spallanzani's opinion, that the revival was really a resurrection, the other, led by Pouchet and upholding Leeuwenhoek's concepts, declared that the phenomenon of life was a continuous one, and that, therefore, during cryptobiosis, life itself did not cease, but continued in a latent state; this last group also believed that the revival itself showed an incomplete desiccation.

The supporters of both theories discussed the matter in Paris in 1859, at the *Societé de Biologie*, which set up a commission composed of Balbiani, Berthelot, Broca, Brown-Sequard, Dareste, Guillemin, and Robin. Without going into detail about the very active work of this commission, which met about 42 times and ended in a report over 60,000 words long, it is enough to say that the factual basis of the revival phenomenon in tardigrades and rotifers was reconfirmed, and that the desiccation of these animals in experiments was deemed to be the most complete obtainable "at the present stage of science and in experimental conditions" (82 days in dry vacuum at atmospheric temperature, then 30 minutes at 100°C under atmospheric pressure). As far as the continuation of life, or its suspension, is concerned, no definite judgement was arrived at.

Concluding this brief historical digression, we now turn to examine in greater detail the process of the phenomenon of cryptobiosis, the experiments which have been carried out, and the more modern scholars' opinions on the subject.

Let us, for the present, consider only the moss-inhabiting species of naked (Eutardigrada) and armored (Echiniscidae) tardigrades. When their environment starts drying up, and the film of water which usually surrounds them becomes thinner than their body thickness, all these species contract, gradually retracting their head and legs, until they cease moving completely, and take on the characteristic "barrel" shape which shows up most typically in the Eutardigrade (Fig. 29). To give an idea of its dimensions, we shall take as an example *H. oberhaeuseri* (average of 10 specimens) from Marcus (1929): during active life its length was 290μ, its width 90μ and its thickness (dorsoventral 75μ; the "barrel' shrinks to a length of 90μ, a width of 80μ and a thickness of 40μ. In the Echiniscidae (armored) in a cryptobiotic state, the "barrel" shape is less distinct, as the animals, having drawn in their legs in the same way, are curved longitudinally and transversely.

Among marine Heterotardigrada, *Echiniscoides sigismundi*, which lives on the intercotyledonal part of *Enteromorpha*, can withstand limited periods of desiccation: after about ten days 42% of the population is still alive, but within four weeks, death is complete. Very little is known about other marine species but it has been recorded that *Batillipes mirus* cannot survive desiccation (Marcus, 1927) and *Styraconyx haploceros* is perhaps able to withstand short periods of desiccation.

With regard to freshwater tardigrades (belonging to the order Eutardigrada) it must first be remembered that it is very difficult to distinguish clearly between the moss-inhabiting and freshwater species, as there are eurytopic species, which dwell in both habitats (for instance *H. dujardini*, *M. hufelandi*, etc.) whereas many other hygrophiles and hydrophiles live in almost permanently moist or immersed moss, from where they can pass into the water around.

In spite of the fact observations are scarce and therefore no general conclusions can be drawn, it may however be stated that distinctly aquatic species, that is to say, those found only in lakes and ponds which do not dry up (stenokous species according to Marcus (1929), polystenokous according to Mihelčič (1954)), are unable to withstand desiccation, or rather do not undergo periods of cryptobiosis (for instance *D. dispar*, *D. ambiguus*, etc.). On the other hand it is possible that other eurytopic species which inhabit moist moss and water (Mihelčič's 1954 mesostenokous species *H. dujardini* for instance) or dry moss, humid moss and water

(Mihelčič's 1954 eu-eurokous species of which *M. hufelandi* is perhaps the only example) can behave in different ways in the various habitats. In other words, it must not be excluded that there may be different physiological races formed by selection so that the same species may be unable to withstand desiccation, if it is adapted to a distinctly aquatic life, while it might survive desiccation, if permanently inhabiting moss, removed from water and not always moist, or in ponds which dry up. A definite answer on this matter can only be provided through further observation, which does not, however, promise to be very easy, technically speaking.

To return to species which do undergo periods of cryptobiosis, it must be noted how important the *slow desiccation* of tardigrades is, failing which the animals very often do not return to life, when they are moistened again, explaining why many scholars failed in the past to obtain revival.

We have said that Spallanzani had already noticed the need for sand, surrounding tardigrades about to undergo desiccation, so that they might return to active life with the addition of water. The sand in fact has the function of making the animal's desiccation slower and more uniform as occurs in nature, in moss, where the evaporation of water takes place slowly, thus allowing the tardigrades to desiccate gradually. For experimental purposes, tardigrades may also be placed on moist absorbent or filter paper which delays the drying up process and allows one to follow the different stages of cryptobiosis with a binocular microscope.

If on the other hand the tardigrades dry up quickly when put on a watch glass, for instance, they contract in an irregular and asymmetrical manner and are often completely flattened onto the lens under the surface tension of the drop of water which is evaporating. Certain damage is done to the animal's delicate structure, thereby and very often it does not revert to active life with a later addition of water because instead of going into a cryptobiotic state, the animal has died.

During cryptobiosis the tardigrade's resistance to external agents reaches quite exceptional proportions. We shall not report the observations of different authors here, but only sum up the results of the experiments carried out by Rahm in the years between 1921 and 1927. Three hundred tardigrade "barrels" were placed in a dry environment for six months and were then kept at liquid air temperature (between -190° and -200°C) for 22 months; when they were moistened once more, the following percentage of return to active life was obtained, in samplings collected successively:

- after 1-3 months: nearly the whole number had survived.
- after 5-20 months: 80%
- after 21 months: 60%
- after 22 months: zero

It is interesting to note that after 20 months the moistened tardigrades returned to active life at the same speed as other tardigrades from the same patch of moss, which had been kept, for comparison reason at ambient temperature, however the percentage of mortality was higher than that shown in tardigrades kept at liquid air temperature, perhaps because of predatory bacteria or mites. The sharp increase in mortality (from 40% to 100%) which took place between the 21st and the 22nd month, could not be satisfactorily explained.

In other experiments, Rahm put tardigrades in a cryptobiotic state in liquid hydrogen (-253°C) for 26 hours, then into liquid helium for a further 8 hours (about -272°C), or made them go through strong changes in temperature (more than 340°C), by cooling them in moss at -190°C for 5 hours (having first desiccated the moss in air for a month) and raising the temperature suddenly, within 15 minutes, to 151°C. In each case the tardigrades survived the tests and, having been moistened again, reverted to active life.

The "barrels" also withstood an atmosphere of CO_2, H_2S, illuminating gas (Baumann, 1922), but not of SO_2 (Lance, 1896); they can tolerate strong acid solutions, osmic acid, alcohol and sublimate at 0.1% (Rahm, 1921) and an hour's radiation under ultraviolet rays, but when moss, containing active tardigrades, was placed 5 to 10 millimeters away from a quartz lamp condenser, which was equipped with suitable mechanisms for cooling the beam of light, the tardigrades die after having been exposed for 10 minutes (Rahm, 1921). We shall not mention any other experiments regarding the effect of differently colored lights during cryptobiosis, as they are not sufficiently reliable.

More recently May, Maria and Guimard (1964) published the results of their radiation experiments with ultraviolet rays of *M. areolatus* in both cryptobiotic and active states, demonstrating the high degree of resistance of this species of tardigrade to such radiation.

The revival from the cryptobiotic state, due to the return of water is first evident when the cuticle starts swelling, activated by the water penetrating through it into the animal's body: this was demonstrated by using a neutral red solution. Usually the extension of the body and movement of the limbs begins caudally and continues upwards anteriorly, but there can be exceptions to this.

The time span between the moistening of the animal and the first signs of movement probably varies from species to species, but it is generally proportional to the duration of cryptobiosis, and decreases with higher water temperatures (not over about 30°C). So, whereas animals having been in a cryptobiotic state for a few days or weeks need only a few minutes, animals which have been in a "barrel" state for years take from three to four hours. However, even in the same species, at the same temperature, having spent the same amount of time in a cryptobiotic state, one can observe considerable differences in the time needed for the first signs of movement to appear. It does seem, though, that this time is greater in armored and adult tardigrades than in naked and young ones.

Crowe and Higgins, in a 1967 publication observe that the time needed for return to active life and the survival from cryptobiosis is a function of pH, dissolved oxygen, and the temperature (the two latter factors being the most important).

Many authors (Cuénot, Heinis, Rahm, etc.) hold that an alternation between active life and cryptobiosis in necessary to tardigrades, but this, even though it is possible and even probable, has not been proven by experiments. It is however an established fact that the desiccation of their habitat, and their subsequent cryptobiotic state definitely constitute critical moments in the tardigrades' life. Mortality always increases by a certain amount, and is in any case higher than that among animals kept constantly in active life during the same period of time (we are dealing here with experimental results, of fairly short duration).

The maximum duration of cryptobiosis in nature has not yet been definitely confirmed. According to Baumann (1927) certain *Macrobiotus* returned to active life after seven and a half years of desiccation while according to Richters (1906) *Adorybiotus coronifer* failed to revive after two and one half years; Franceschi (1948) on the other hand, moistened moss (*Funaria hygrometrica*) which had been kept dry for 120 years, observed a movement of extension, followed by a retraction, in the first pair of legs of one of the tardigrades present, probably of the *Macrobiotus* genus.

We have already said, when dealing with the life span of a tardigrade that it is entirely unknown how many times a tardigrade can undergo cryptobiosis. Results of experiments tell us very little, being carried out in conditions very remote from the natural environment, and according to which tardigrades can withstand no more than 14 desiccations.

During cryptobiosis, as has been clearly demonstrated by May (1948), considerable cytological changes occur, especially in the body cavity cells, which lend themselves best to observation. The chromatin of their nuclei moves toward the nuclear membrane and takes on an annular appearance or else agglomerates in one spot, on the periphery or, more often, at the center of the nucleus. The nucleolus is no longer visible, the chondriosome disappears and the cytoplasm becomes clear, sometimes decreasing in volume and being with or without scattered granulations. Only the fatty reserve matter in the cytoplasm in granule form, remains unchanged, compared with the body cavity cells of tardigrade in active life.

According to May, who carried out his observations on tardigrades and nematodes, the changes in cell structure caused by slow dehydration are completely reversible, when the cells are once again put in contact with water, and in so swift a manner that one is reminded of the rate of a chemical reaction. The return of the cytoplasm to acidophilic (it was conspicuously basophilic during cryptobiosis), the reconstitution of a normal nucleus, and the reappearance of the mitochondria, all take place in a few seconds. May compares the reviving cell of a tardigrade to an embryonic cell in other animal forms, in which the different embryonic stages succeed one another very rapidly and therefore considers it a "transient embryonic cell".

May concludes by saying that, if one accepts the hypothesis that a metabolism, even though slowed down, exists during cryptobiosis in spite of the great changes which have taken place in the cells, it must be admitted that the metabolism which is present when the cellular structure is normal, could also exist with a completely different cell structure. He therefore believes it to be likely that, during cryptobiosis, there is not only a slowing-down of the metabolism, but it is perhaps also completely transformed.

More recently, Pigón and Weglarska (1953 and 1957) demonstrated, using refined, experimental techniques, that the metabolism continues during cryptobiosis, even if only at a reduced rate. The average O_2 consumption of a *Macrobiotus hufelandi* in a cryptobiotic state, and at a temperature of 24° C, in fact ranges from about $4 \cdot 10^{-7}$ to $1 \cdot 10^{-3}$ microliters/hour according to the degree of humidity in the atmosphere in which the specimen is placed. Under more humid conditions the consumption increases, according to two exponential equations of the type

$$y = ae^{bx}$$

one of which applies to under, and the other to over 93% humidity (y is the consumption of O_2; e is the base of natural logarithms; a, b are two constants; x is the degree of humidity). A consumption of about $1 \cdot 10^{-3}$ microliters/hour is obtained when the tardigrade is immersed in water and thus corresponds to that of the animals during active life.

In 1959 Keilin concluded his highly interesting work on anabiosis with these words:

"In a living organism the state of a good number of its constituents is the result of a dynamic equilibrium between the reactions involved in their constant degenerative and regenerative processes. The organism continually has to supply the energy needed for the upkeep of its complex structure, which has a tendency to collapse. The stability of such an organism is of a dynamic nature.

"During anabiosis no energy can be provided by the organism for the maintenance of its complex structure, which nonetheless remains intact. This is nor surprising, since the reactions involved in the degeneration of the structure demand water, heat and oxygen.

"The stability of such an organism is of a purely static nature ... ; and as long as the structure of these organisms remain intact, they retain the ability to return to a normal active life.

"The concept of life, as applied to an organism in an anabiotic (or cryptobiotic) state, becomes synonymous with that of structure, which supports all the components of its catalytic system. Only when the structure is damaged or destroyed, can the organism pass from a state of anabiosis, or latent life, to that of death."

An obvious result of May's (1948) words and even clearer consequence of Keilin's (1959) text reported above is how far removed the modern idea of metabolism is from the classical view. The modern trend according to Keilin is that during cryptobiosis metabolism can be completely absent. The problem is certainly fascinating and has had most interesting developments, but we do not think one can at present say that it has been wholly solved.

Since at different times we have used the terms "anabiosis", "cryptobiosis" and "latent life", we should now like to throw more light on their meaning according to Keilin. The term "anabiosis" was used by Preyer (1872, 1891) to distinguish the two possible states of an organism, which are: (1) deprived of life, but able to return to life = *anabiotic*; (2) deprived of life, and unable to return to life = *dead*; the term "cryptobiosis" was introduced by Keilin (1959) to indicate the state of "latent life" that is to say "that the state in an organism, in which it does not show any visible signs of life and when its metabolic activity becomes very difficult to detect, or comes to cease all together." As for the expression "latent life", which also has its flaws, but is a convenient one, it was defined by Claude Bernard (1878) as a state of absolute chemical inactivity, characterized by the suspension of any relationship between the organisms and their environment, and in fact that very state which takes over in many animals and plants, among which we find the tardigrade, during cryptobiosis (although, in tardigrades, it seems that the metabolism does not cease completely).

Keilin advises us to abolish the old and unsuitable term "anabiosis" and to put in its place that of "cryptobiosis"; this is what we have done in this work, in which the word "anabiosis" has however been used at times, only with regard to tradition.

Before closing the chapter on cryptobiosis we will add that, whereas the "barrels" show an enormous resistance to external agents, in active life tardigrades most likely die at temperatures approaching 50°C (except perhaps a few thermal water species or physiological races); they do not withstand swift freezing, because of the damage caused to the organism by the sudden formation of ice; and they are hypersensitive to various solutions, even very dilute chemicals (for example methylene blue).

The eggs of moss and soil-inhabiting tardigrades can also withstand very long periods of desiccation, subsequently developing swiftly when the environment has once again recovered its water. Little is known about the eggs of distinctly aquatic tardigrades, but it is likely that in certain species or races, they are able to remain in a dry atmosphere for some time without incurring any damage. Among marine tardigrades it is known that the eggs of *Echiniscoides sigismundi* have developed, after having remained in a dry atmosphere for four days on *Enteromorpha*.

ENCYSTMENT.

In certain conditions, which are not yet fully known and which we will come back to later on, tardigrades have the ability to turn into cysts and go through different periods of time in this quiescent cyst state.

Encystment (first observed by Lauterborn in 1906) begins in a similar way to molting, meaning that the tardigrade, having already rejected its buccal apparatus, contracts inside the cuticle and takes on an ovoid shape, pulling in its legs tightly. In contrast to what occurs in the molting process, the tardigrade does not subsequently come out of its old skin, but its movement slowly decreases, until it is reduced to complete immobility.

The cuticle (second cuticle) of the animal thickens and becomes harder as the days and weeks go by, while the old cuticle (first cuticle) sloughs off and generally is destroyed (Fig. 30). In this way the animal becomes an actual and proper cyst, with strong walls, which are sometimes encrusted with detritus of various types, and usually, though not in all cases, completely opaque. Its color can range from lemon yellow to greyish and dark brown; only the legs remain as small flattened protuberances, but the claws nearly always stay visible on the outside of the cyst, or folded up inside it. Later, when the tardigrade emerges from the cyst, it is covered by a third cuticle (Fig. 31).

The dimensions of the cyst are far smaller than that of the tardigrade before cyst formation, its length, especially, decreasing considerably from about 20% to 50%. Younger specimens can also become cysts.

Cysts are not able to withstand high temperatures, as can tardigrades in a cryptobiotic ("barrel") state. In fact, encysted animals die at 60°C (Rahm, 1925) an occurrence most likely due to their high water content.

Fig. 30 - *Isohypsibius nodosus* encysted (from Marcus, redrawn).

Certain authors state that, at a certain moment, inside the cyst, a complete histolysis of the animal takes place. Murray (1907) confirmed this for *Dactylobiotus dispar* and Heinis (1910) for *Adorybiotus coronifer*; other authors (Richters, 1919; Von Wenck, 1914; Nederstrom, 1919; Reukauf, 1924; Rahm, 1925; Thulin, 1911, 1926) deny the occurrence of histolysis, though admitting the possibility of regressive organ transformations.

Until very recently the causes for this cyst formation remained unknown. Von Wenck (1914) attributed it to the scarcity of food available and held that the exit from the cyst was induced by the exhaustion of reserve matter, accumulated in the body cavity cells; Marcus (1929, 1936) seems at least partially to agree with these views, but he adds that cyst formation may also be caused by a rise in temperature.

In 1957 Weglarska published the results of a very interesting and exhaustive study of hers, on the encystment of a freshwater tardigrade *Dactylobiotus dispar* during which she followed large numbers of specimens for about a year. This study has thrown light on many obscure aspects of the cyst formation process, which in the species mentioned, takes place in the manner we are about to describe.

Before encysting the tardigrade takes in great quantities of food (which excludes the lack of food as the cause of cyst formation) accumulating considerable reserves in the body cavity cells. It then rejects its buccal apparatus, and enters in to the *simplex* state, and proceeds to empty its gut through defecation. Then a process not unlike that of molting takes place, without the old cuticle being torn however, and within about 12 hours the first cyst membrane is formed, which at first is wrinkled and whitish, but gradually becomes smooth and darker until, after 96 hours, it is completely black.

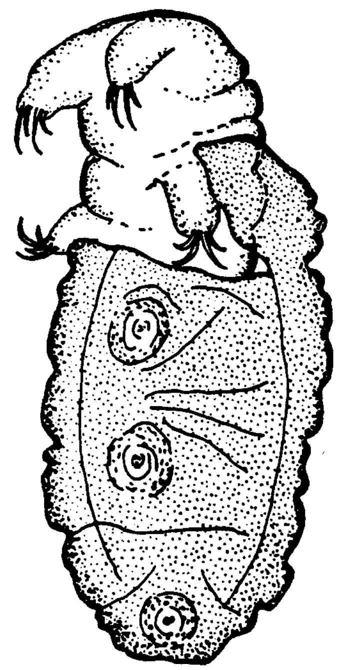


Fig. 31 - *Dactylobiotus dispar*, covered by the third cuticle, while coming out of the cyst made of the second cuticle (from Marcus, redrawn).

Six days after the formation of the cyst membrane, the epithelial cells within the space between the membrane and the epithelium, produce another membrane, which is thinner and less colored, and does not show any folds or protuberances corresponding to the legs. If the cyst is broken at this stage, one finds the animal in a *simplex* state, covered with a delicate cuticle; the legs bear only the new claws, in the process of being formed, visible inside the claw glands and the contracted, completely differentiated tardigrade, will remain inside the membranes until it emerges from the cyst. After about 12 days brown granules can be seen in the midgut, probably excretory products.

So as to decide definitely whether or not histolysis took place during encystment, for nine months Weglarska prepared microscopic preparations of cyst sections, taken from the group every six days during the first two months, and every 15 days for the following seven months. All the internal organs remained clearly visible the whole time, so that it can be said, in opposition to Murray's views, that no histolysis takes place inside the cysts of *D. dispar*.

The quantity of food taken in before the formation of the cyst, increases the fat content considerably, which in the shape of large drops, almost completely fill the body cavity cells. For a few weeks or months of encystment the fat shows no visible sign of decreasing but after eight months a considerable reduction occurs. In addition to fats, tardigrades also accumulate glycogen which occupies, in animals approaching encystment, the whole space between the drops of fat within the body cells, whereas in tardigrades in active life, it is found only on the surface of these same body cavity cells. After having been in a cyst for three months, the quantity of this particular polysaccharide has already decreased considerably, these decrease occurring frequently, in accordance with lack of food, until gradually all reserve matter is used up in the following order: saccharides, fats, proteins.

In rearing conditions, at 20 to 25°C, encysted tardigrades survive for about ten weeks, while tardigrades in active life, kept in the same conditions, and deprived of food, die within four to five weeks. In nature, however, the cyst state can most likely last more than a year.

Among the most important results, obtained by Weglarska in the course of her research, one must mention that of having firmly established at least one of the causes of the formation of cysts. In her rearing of *D. dispar* duly encysted regularly within 12 hours, if placed in water containing many cyanophyceae or decomposing leaves, whereas this did not occur in frequently changed water (in which they lived for more than nine months, even laying eggs in November and February) or by depriving them of food for four weeks in tap water. From these and other experiments, Weglarska concluded that the cyst formation is caused by a *gradual* worsening of atmospheric conditions. If on the other hand this worsening is swift, *D. dispar* does not enter the cyst state, or pass into asphyxial state. Consequently she believes that encystment is not an obligatory stage in the course of a tardigrade's life.

Regarding the emergence of the animal from the cyst, a probing series of experiments, which we shall not relate here, proved that Von Wenck's view (1914) could not be upheld, since he believed it was due to the exhaustion of reserve matter in the body cavity cells; nor that of Marcus (1928), who thought it likely that emergence was induced by a reappearance of abundant food in the environment. However it now seems certain that *D. dispar* emerge from their cysts (in 6-48 hours) when the reasons for the cyst formation have vanished (in the experiments mentioned above this occurred when the cysts, after having remained in water with cyanophyceae for nine months, were placed back in tap water).

It must be noted that the emergence of the animals from the cyst was not hindered, and also took place in the same time as the control tardigrades, kept in normal conditions, by putting small dishes with the cysts in a desiccator from which the air was expelled with a Bunsen pump and substituted with a nitrogen atmosphere, which most certainly changed the oxygen conditions in the water. Even with a water temperature of about 6°C, the tardigrades came out of their cysts.

We still do not know whether the results obtained by Weglarska for the aquatic *D. dispar*, and above all the conclusion that cyst formation is due to a gradual worsening of the environment, can be generalized and applied to moss and soil inhabiting tardigrades. The cause made known by this skillful scholar is certainly a possible one, but perhaps not the only one. In fact, during a study of tardigrades in a meadow habitat in Pallanza (Ramazzotti, 1959) Ramazzotti often observed cysts, and tardigrades which were not in a cyst state, coexisting, within a small cylinder of earth of about 3 cm^3. Thus one would have to concede that in certain parts of the soil conditions had gradually worsened, while they stayed the same in other parts, only a few millimeters away. This could possibly happen, however it is improbable, but the cause of encystment of tardigrades cannot therefore be attributed immediately in this case, to a gradual deterioration of the surrounding conditions.

The same applies to moss-inhabiting tardigrades, in which cysts are very rare, but do exist: they are rarer still among Echiniscidae, though it is possible to see certain *Echiniscus* cysts also coexisting with tardigrades which are not encysted.

During research on soil inhabiting tardigrades Ramazzotti (1959) was able to examine and open up dozens of cysts from *Diphascon bullatus* and *Isohypsibius tuberculatus* without ever discovering histolysis. Only in two cysts, among those examined, was there still some doubt, as it was not possible to perceive any differentiation in them, but this must probably be attributed to a deterioration in the animal, or to partial compression, which had occurred during the delicate operation of opening the cyst. Thus we agree, for the two above mentioned species as well, with the view expressed by Weglarska for *D. dispar*, and that no histolysis takes place during encystment. What the additional reasons are which induce the emergence of the soil-inhabiting tardigrades from the cysts, still remains to be established.

Pigón and Weglarska (1957) also demonstrated that the consumption of O_2 by an encysted *D. dispar* is 2.4×10^{-4} microliters/hour, while it is of 1×10^{-3} microliters/hour for an individual of the same species in active life. Comparing these figures with those related, in the preceding section, for cryptobiosis, one can conclude that there is a vast difference between cryptobiosis and encystment as regards metabolism.

II.

BIOLOGICAL NOTES ON THE TARDIGRADES

HABITATS.

Tardigrades live in widely differing environments, which can be grouped briefly in the following way:

1. Marine and brackish waters
2. Sands immersed in the above (Marine *psammon* biocoenosis)
3. Fresh (and thermal) waters
4. Sands immersed in the above (Freshwater *psammon* biocoenosis)
5. Mossy environments (included in these, apart from moss, are lichen, liverworts, phanerogams [flowering plants] which assume the form of a "cushion": as for instance *Silene*, *Saxifraga* and *Androsace*, etc.
6. Terrestrial environments of various types
7. Leaf litter beneath forests

We shall not examine each single habitat in detail, referring the reader to more specialized publications (i.e., Bartoš, 1940, 1941; Mihelčič, 1949, 1950, 1952, 1953, 1954, 1955, 1957, 1958; Pennak, 1939, 1940, 1941; Ramazzotti, 1958, 1959; Renaud-Debyser, 1956, 1959, etc.) and will keep to a few essential data.

Purely as a means of making our text simpler and clearer, we shall speak of "aquatic" tardigrades (those dwelling in habitats 1 to 4 in the list above) and "terrestrial" tardigrades (those living in environments 5 to 7 of the same list); but we must once again stress that, in fact, all tardigrades must be considered aquatic animals.

Having said that, and leaving aside the distinctly aquatic species for a while, we will state immediately that the habitats of "terrestrial" tardigrades have the three following characteristics in common:

1) a structure which allows sufficient aeration: tardigrades are hypersensitive to lack of oxygen, which, as we have seen, makes them go into an asphyxial state, often followed by death, if conditions fail to change rapidly;

2) the ability to undergo alternate periods of wetting and desiccation, mainly through solar radiation and wind;

3) suitable and sufficient food.

From these basic requirements for tardigrades, one can deduce several facts confirmed by observations. Thus, for instance, the need for sufficient oxygen immediately indicates that highly compact, or thicker mosses constitute an unsuitable environment, at least in the deeper layers. It also indicates that soil, so as to be a favorable habitat, must have a certain degree of porosity (in fact, soil-inhabiting tardigrades live in the more porous superficial strata, only a few centimeters below the surface, with the greatest number living within the first centimeter where porosity and the presence of oxygen are greater and where the interstices and convolutions facilitate their movements).

The second condition, the necessity for alternate wet and dry periods, indicates that one would be very unlikely to find large colonies of tardigrades in moss, or permanently wet ground, with an impermeable clayey substratum, in a shady forest, and which was never exposed to the sun or wind.

Lastly, the third condition, the need for sufficient and suitable food, explains the reason why in certain large mosses (i.e., *Polytrichum*) there are no tardigrades. In such cases, they are probably unable to perforate the hard walls of the plant cells with their weak stylets, so as to suck in their content, as is usually done by most moss-dwelling species, or alternatively, because there is a lack of algae, protozoa, etc., which can also constitute a welcome food for many species of tardigrade.

We shall now review the main habitats of tardigrades:

1. MARINE AND BRACKISH WATERS.

Of the marine tardigrades, so far only four species are known belonging to the class Eutardigrada: *Isohypsibius appellofi*, *I. geddesi*, *I. itoi*, and *I. stenostomus*. All the other marine species belong to the class Heterotardigrada, either in the order Arthrotardigrada, or in the order Echiniscoidea. Exclusively marine are the genera indicated in the following summary:

A. Order Arthrotardigrada Marcus 1927
- a). Family Coronarctidae Renaud-Mornant 1974
  - 1). Genus *Coronarctus* Renaud-Mornant 1974
- b). Family Halechiniscidae Puglia 1959
  - 1). Genus *Halechiniscus* Richters 1908
  - 2). Genus *Pleocola* Cantacuzene 1951
  - 3). Genus *Actinarctus* Schultz 1935
  - 4). Genus *Euclavarctus* Renaud-Mornant 1975
  - 5). Genus *Tetrakentron* Cuenot 1893
  - 6). Genus *Styraconyx* Thulin 1942

7). Genus *Bathyechiniscus* Steiner 1926
8). Genus *Florarctus* Delam. Debout. & Ren.-Morn. 1965
9). Genus *Tanarctus* Renaud-Debyser 1959
10). Genus *Angursa* Pollock 1979
11). Genus *Orzeliscus* Du Bois-Reymond Marcus 1952
c). Family Batillipedidae Ramazzotti 1962
1). Genus *Batillipes* Richters 1909
d). Family Stygarctidae Schulz 1951
1). Genus *Stygarctus* Schulz 1951
2). Genus *Mesostygarctus* Renaud-Mornant 1979
3). Genus *Parastygarctus* Renaud-Mornant 1965
4). Genus *Pseudostygarctus* McKirdi et al. 1976
5). Genus *Megastygarctides* McKirdi et al. 1976
e). Family Archechiniscidae Binda 1978
1). Genus *Archechiniscus* Schultz 1953

B. Order Echiniscoidea Marcus 1927
a). Family Echiniscoididae Kristensen & Hallas 1980
1). Genus *Echiniscoides* Plate 1889
2). Genus *Anisonyches* Pollock 1975

(Among the other families and genera of the Echiniscoidea no marine species are known.)

Ecological information concerning marine species was very scarce up until a few years ago, therefore we were able to provide only a few very general indications. For instance, the genus *Batillipes*, which feeds on diatoms and other algae, seems to prefer sandy environments and to belong more to the interstitial fauna but Hay (1917) was able to observe *B. mirus* on the brown algae *Dictyota*; *Echiniscoides sigismundi* is often to be found in the intercotyledal zone on *Enteromorpha*, although it was also discovered in the mantle of *Mytilus edulis* (Green, 1950); *Styraconyx sargassi* lives on *Sargassum*; *Tetrakentron synaptae*, which we have already mentioned, was found only on the peribuccal tentacles of an holothuroidian (*Leptosynapta galliennei*); *Actinarctus doryphorus* has been gathered on the echinoderm *Echinocyamus pusillus*, of which it is possibly a facultative parasite (although Grell, 1937, denies this); *Plecola* was observed on the pleotelson of the isopoda *Limnoria lignorum*, but also free in the interstitial environment. Very little was known about the other species, because of the fact that the specimens found were rare and sometimes even confined to a single individual. Today we are better informed, thanks to a wider study of marine shores, as we shall soon relate.

2. SANDS IMMERSED IN MARINE WATERS (MARINE PSAMMON).

The study of tardigrades living in this habitat (typical of psammon or interstitial fauna) had hardly begun, when the first fragmentary information appeared: Renaud-Debyser (1959) was able to establish five different species, three of which belong to the same genus (*Batillipes littoralis*, *B. phreaticus*, *B. pennaki*, *Stygarctus bradypus*, and *Halechiniscus remanei*) and although they live in the same environment, have different ecological requirements. This means that the above-mentioned species are variously distributed on the same beach and are established at different levels, ranging from the surface to a depth of 1.50 meters, at which they find conditions most suitable, especially as regards the presence of oxygen, available food, the salinity of the water and temperature. It is not yet known whether the marine interstitial fauna species migrate to other types of habitat.

At this point, our knowledge has increased greatly, thanks to the interesting work of many researchers, who have studied various aspects of the marine psammon: seasonal frequencies, the influence of the particle size of the sand, migrations, successive development stages, etc. These results cannot be related here, since a simple summary would require a large number of pages. We therefore refer the reader who wishes to pursue the matter to the original publications, especially to the following: De Zio and Grimaldi (1966), McGinty and Higgins (1968), Renaud-Debyser (1965), Renaud-Mornant (1966), Pollock (1970).

The genera *Coronarctus*, *Euclavarctus*, and *Bathyechiniscus* are found in the abyssal environment.

3. FRESH (AND THERMAL) WATERS

Certain species, which, to reach an understanding, we have called "distinctly aquatic" live only in fresh water and have never been found in any other habitat: these are the *hydrophilous* species (*polystenokous* of Mihelčič, 1954), confined nearly exclusively to naked tardigrades (Eutardigrada). To this category belongs all the species of the genera *Dactylobiotus* and *Pseudobiotus*, and also some species of *Isohypsibius* (*I. baldii*, *I. granulifer*, etc.) We know also only two species of Heterotardigrada from fresh water: *Echinursellus longiunguis* and *Carphania fluviatilis*.

In water, hygophilous species can be found, which can also inhabit moist moss (Mihelčič's *mesostenokous* species, 1954) as for instance *H. dujardini*, *H. convergens*, etc., or else eurytopic species, able to live in any type of moss, from those which dehydrate to those which are constantly wet and ever underwater: the two most widespread and common tardigrades in this category are *Macrobiotus hufelandi* and *Milnesium tardigradum* (Mihelčič's *polyeurokous* and *eu-eurokous* species, 1954; he did however consider *M. tardigradum* a *mesoeurokous* species and only *M. hufelandi eu-eurokous*).

These species generally live fairly near the surface, at the bottom of ponds, along the shore line of lakes, in streams, and sometimes in wet, floating, or submerged mosses. Sporadically they have been found at considerable depths, for instance *M. tardigradum* at 40 to 150 meters in Lake Geneva (Forel, 1901, and others), *D. macronyx* at depths of up to 100 meters in small mountain lakes at high altitudes (Zschokke, 1900), *M. hufelandi* in Loch Ness (Scotland), at 100 meters (Murray, 1905), etc.

The food of aquatic tardigrades is probably made up of a large proportion of algae, of protozoa, but also of organic detritus, apart from the cell contents of submerged mosses. It must however be admitted that the information regarding their diet is slight, in the same way that little is known about optimum living conditions for aquatic tardigrades.

Among Japanese thermal water algae, at a temperature of about 39° - 42°C, lives *Thermozodium esakii*, the only species known to date in the order Mesotardigrada. Very little is known about tardigrades which may inhabit this type of environment especially those observed in mosses infused with steam at a temperature of about 40°C (mainly *H. oberhaeuseri*), at the thermal springs of Abano (Padua) at 81°C (Ramazzotti, 1942).

4. SANDS IMMERSED IN FRESHWATER (FRESHWATER PSAMMON)

The study of the interstitial fauna (psammon) only just began in the last decades and tardigrades have frequently been observed in the sands on the shores of lakes, or along river banks, at various distances from the shore and different depths. The data at hand are not yet sufficient to permit the presentation of a precise picture of their life cycle, the distribution of the different species, etc.

The facts do however recur constantly:

1) the majority of the species present are "aquatic" (*D. dispar*, *P. augusti*, *I. granulifer*, etc.) or hygrophilous (*H. dujardini*, *H. convergens*, etc.) joined in rare cases by eurytopic species (*M. hufelandi*, *D. alpinus*, etc.);

2) there is a distinct "seasonality" in the population density of tardigrades, peak periods being at different times of the year, perhaps mainly in winter and spring.

At this point, the reason for the nearly complete disappearance of tardigrades during certain months of the year is completely unknown. One might however reasonably conclude that this is due to a migration perhaps to free waters, or else to cyst formation.

5. MOSS ENVIRONMENT

We shall deal with this habitat at greater length as it is inhabited by the greatest number of tardigrade species and the material on the subject, the result of countless observations, is so rich.

It must be kept in mind from the start that, however much the tardigrade's living conditions may vary from one moss to another, there are still characteristics common to all mosses, which suffice to distinguish this particular environment from many others.

It may be said in a general sense and with reference to tardigrades and the microfauna as a whole that this "moss environment" has a very limited spatial extension and great variability in time. In other words, every moss, or group of mosses, constitutes a kind of "island", or separate habitat, the hygrometric conditions of which are most important as regards the settling in of specific tardigrade species and vary continuously, in an irregular way.

For practical purposes, still with reference to the different species inhabiting them, mosses can be divided into three groups, containing five categories (Bartoš, 1940, 1941; Ramazzotti, 1958), as follows:

1. Group "A" (Wet mosses)
   - Category I: Submerged or floating mosses, meaning those which are constantly soaked in water.
   - Category II: Mosses which never dehydrate completely, those on the banks of waterways, lakes, ponds, etc., or else in the immediate vicinity of waterfalls, or frequently submerged by floods.

2. Group "B" (Moist mosses)
   - Category III: Mosses on the ground, on tree trunks, rocks, etc., inside thick forests, or in shady valleys; or else mosses which, although they grow in very humid environment and never receive any direct sunlight, can sometimes desiccate within varying lengths of time, which distinguishes them from Category II.

3. Group "C" (Dry mosses)

Category IV: Mosses which are exposed to sunlight daily for short periods, i.e., those growing on tree trunks, rocks and soil in thinner forests or at their edge.

Category V: Mosses which are exposed to the sun for a great part of the day and which are, accordingly, subject to swift and complete desiccation; this includes mosses growing on open ground, rocks, walls, roofs, sometimes also on isolated trees, exposed to sun and wind. These mosses desiccate very rapidly, passing swiftly from a very high to a very low degree of humidity and with long periods corresponding to the minimum humidity.

Thus the mosses in the first 2 categories never dehydrate completely, whereas those of the following 3 categories can reach total desiccation, the duration of which is, fairly logically relative to atmospheric precipitations and their frequency.

Therefore, after an abundant rainfall, which soaks the moss, complete desiccation can occur, for instance, within 15 to 20 days for mosses of Category III, 4 to 5 days for those of Category IV, and 1 to 2 days for those of Category V. It is obvious that, if the time span separating successive downpours is less than that needed for complete dehydration, the moss will still stay moist. It is also obvious that, dealing with the IIIrd, IVth, and Vth categories, the duration of the periods of desiccation will be increasingly greater compared with the periods of humidity.

The mosses of the IIIrd category constitute a stepping stone between wet and dry mosses, although they have more in common with the last as regards microfauna (not just that of tardigrades).

We shall see, further on, which are the most common species of tardigrade inhabiting these various categories of moss, making do with a rather empirical sort of enumeration, that will be based purely on the result of numerous discoveries, as many elements, which might throw some light on the points which are still obscure, have unfortunately not yet been clarified. For example, we know very little about the oxygen content of the water which drenches mosses in the different conditions under which they grow and in the different phases of their desiccation; the same goes for all substances which eventually dissolve, pH, temperature, and so on.

Let us examine morphologically -- I should perhaps say topographically -- the way in which moss appears internally, this being the usual habitat of a great number of tardigrade species. In order to get a clear idea one needs only to examine a fragment of moss under a binocular microscope, magnified 20 to 30 times, especially if the moss has been moistened some time before, in order that the hygroscopic cellular membranes may absorb water and give the leaflets their original freshness. The species of moss does not matter, since their general aspect is very similar, apart from differences in details, if submerged mosses are excluded, as well as those from very humid places, Sphagnum for instance.

A very dense tangle of leaflets and stalks, thickening progressively toward the center, especially at the pulvini will be observed. The complexity of this green labyrinth is increased even further by the presence of antheridia, archegonia, and differently positioned paraphyses and in addition, if the season is right, the sporangium capsules protrude, often oddly terminated by their caps. A thin film of water covers the more external leaves and the tips of the stalks and gathers in larger quantities in the deeper parts or in the hollows of the leaves or between these and the twigs, where it forms tiny pools.

This is how moss appears after a rainfall, even in nature, and it is precisely in these internal small pools of water, mentioned previously, due mainly to a mechanical attraction of the water, running downwards, that the greatest concentration of tardigrades is to be found. If, however, the degree of humidity is high enough, and such that a film of water covers the twigs and leaves surrounding these microscopic internal lakes, through capillarity, then tardigrades can be seen moving about everywhere.

It is interesting to see how tardigrades behave, when the outer-most leaves start drying up. On several occasions I have seen specimens of the genus *Macrobiotus* come out of the film of water and move towards the tips of leaves which were already in the process of dehydrating. The tardigrade advanced with its body surrounded by a drop of water, which stuck to it as it came out of the film of water, but it soon realized that it was proceeding along a dry substratum and turned back quickly, slipping back into the film of water, indispensable to its needs in active life.

Do not, however, take it for granted that the tardigrades all gather inside these tiny pools we have just dealt with. They often inhabit the deeper layers, at the base of the twigs and in the tangle of rhizoids, where plant detritus is to be found in abundance. Down in these parts, tardigrades manage to move about swiftly with surprising agility along narrow passages, between the plant walls holding them up on each side, helping themselves along with their eight sharply clawed legs.

This vital activity goes on as long as the moss retains enough water, which can be for many days or several weeks, during the rainy season or when the snow melts. Then there is enough time for egg-laying, or generally for the reproduction of the species, and for molting, etc.

When meteorological conditions change, and the weather becomes sunny again, or when the wind blows and the temperature rises, the mosses begin to desiccate. As the cellular membranes of many species of moss are highly permeable, considerable changes often occur in the shape of the leaves during desiccation, due to variations in cellular turgescence and in membrane hygroscopic tension. Sometimes the leaves curl around the stems, or else the leaves themselves curl up, or their edges fold inward so that they look grooved, and so on.

Along with the desiccation process of mosses, the tardigrades tend to move downwards into the deeper moister parts, so obviously many specimens go into a cryptobiotic state in the internal moss zones. Regarding this, Ramazzotti sometimes observed that, in alpine "cushion" mosses, gathered during the hard frost period in winter, the tardigrades in a cryptobiotic state and their ovigerous cuticles were to be found in great numbers in the deepest regions closest to the ground, under gelatinous looking mucilage, which was obviously of plant origin.

In many places, where there is a high degree of humidity, depending on the season, dew is abundant enough to moisten the moss to the point where the tardigrades are able to come back to life. In such cases, there can be daily periods of cryptobiosis, alternating with periods of active life at night, or in the early hours of the morning. Hence the impossibility of establishing the relationship between the time spent in a cryptobiotic state and in active life, since this is a function of meteorological conditions in the different places and also of chemical and physical changes in the water remaining in the moss, about which we know nothing. In fact, we must not exclude the possibility that tardigrades may enter into a cryptobiotic state when the moss is still moist, or rather when the conditions might seem to us to be suited to the continuation of life.

The time moss takes to desiccate varies within fairly wide limits, from the moment the influx of water from outside ceases (this may be in the form of rain, melted snow or ice, or dew), depending mainly on the place in which the moss grows. This is the criterion which was applied to subdivide mosses into 5 categories in the 3 groups "A", "B", and "C".

Since the majority of tardigrades remain in active life as long as the moss stays moist, it would be interesting to learn how the oxygen present in the water varies according to the changes in the degree of humidity, given the animals' hypersensitivity to lack of oxygen.

Unfortunately we know hardly anything at all on the subject except that the photosynthetic function is generally localized in the stem cells. We may reasonably assume that the water in which the moss is immersed is provided with oxygen, in addition to the daily photosynthetic process, by movements in the atmosphere with which it is in contact. The fact that a greater number of tardigrades are found in mosses in open and wind-swept spots, as opposed to the more shady and sheltered mosses, should most likely be attributed to these facts.

It must be remembered that the uppermost stratum of a submerged moss is always saturated with oxygen and that therefore tardigrades can move towards the surface, when there is an oxygen deficiency deeper down. Thus one might be led to think of this in terms of a vertical migration, a view which could only be completely confirmed through a series of observations which have not hitherto been carried out. On the other hand, certain authors (Dobers, Mihelčič) noted that there are species of tardigrades and rotifers which populate the more superficial parts of moss, while others inhabit the depths, and others still seem to have no preference either way. This could be attributed to the different requirements of each species are regards oxygen, although, of course, the possibility of other important unknown factors is not excluded. One must consider the above factors in order to find the origin of the distinctly "insular" distribution of tardigrades within one patch of moss, or a dense, or nonexistent population in small zones, which may even be close together, of the same patch of moss.

A great deal of what has been said until now about mosses, can be applied to liverworts, lichens, "cushion-like" phanerogams, but it is probable that the food of tardigrades, especially in the last two habitats mentioned, is mainly made up of algae or organic plant detritus, rather than cellular juices (and perhaps also, for certain species of protozoa).

Some interesting ecological research on moss-inhabiting *M. hufelandi* populations, carried out over about two years, with weekly samplings based on quantitative criteria, was undertaken by Francheschi, Loi, and Pierantoni (1962-63). They observed qualitative and quantitative variations, etc., and demonstrated the close correlation between the quantitative variations in the populations and meteorological factors (relative humidity, showers, temperature), which mark the situation for the 10-20 days preceding the removal of the tardigrades for study. They were able to note the swift development of the populations and the prevalence of younger individuals in the spring, as opposed to the winter.

An analogous increase of young, in summer, compared to winter, was noted by Ramazzotti (1977) for the species *M. areolatus* during research on a large moss-dwelling population in Pallanza.

6. VARIOUS TYPES OF SOIL
7. LEAF LITTER

We have thought it useful to put these two habitats together, as they are often very close, although they differ in certain aspects. It should suffice to mention all the points of contact existing between the two types, where the leafy layer becomes thinner to give way to the soil, or where soil is mixed in with leaves. Since the study of these environments only began recently, existing information does not allow any rational classification of different soils and leaf litter based on their characteristics and relation to the different species of tardigrades inhabiting them.

Tardigrades and their eggs were already sporadically found in soil many years ago (i.e., Heinis, 1916), but it was thought that these were exceptional discoveries, due to passive transportation (Marcus, 1929). Only in fairly recent times, did various authors show that soil and leaf litter constitute a usual habitat for tardigrades (i.e., Delamare-Deboutteville, 1954; Franz, 1952; Lüdi, 1948; Ramazzotti, 1959; but above all Mihelčič with his research during the decade 1948-1958).

Subsequent works of Mihelčič's (1963 and 1967) brought to light other interesting characteristics of soil-inhabiting tardigrades. For instance, their ecological worth (i.e., their tolerance of different environmental factors) referring to cryptobiosis, egg and cyst frequency, the establishment of so called "nests" (zones where the density of population increases, thus making room for the well-known "insularity", or "insular distribution" of tardigrades) of various species.

As regards feeding, Mihelčič confirms that soil inhabiting tardigrades feed on algae in particular (diatoms, Desmidiaceae, Protococcoceae, etc.), fungi, bacteria, and organic waste.

Tardigrades are not evenly distributed in soil (Mihelčič, 1952), but are found in certain densely populated zones for reasons which we are not yet fully acquainted and which must not be attributed only to the presence, or absence, of plants and their roots (Ramazzotti, 1959). This "insularity" is typical of distribution of the terrestrial tardigrades, and probably for the reasons that have been verified also in the moss: it depends certainly on many factors (aeration, light, chemicals, food, deposition of the eggs, manner of distribution, etc.) but probably one of the principal causes of the irregular distribution to be considered is the different degrees of cold of the soil, which may vary from one point to another; in fact to a large extent coldness corresponds to a less penetration of oxygen and a smaller volume of the interstitial cavity, within which the animals displace (Ramazzotti, 1959); this is as yet a hypothesis, that can however be confirmed by further study.

The larger density of populations seems to be in the more superficial layers of the soil; maximum in the first centimeter, or centimeters, it then decreases -- until depleted -- from 5 to 10 cm depth.

Concerning the various leaf litter, or the needles of conifers, Mihelčič (from 1948 to 1958) has put light on how they constitute often an environment adapted to establish an abundant colony of tardigrades, which occupies the shallower layers, up to a maximum depth of 3-5 cm; in order for the tardigrades to be present it seems necessary that the deposit of leaves be permanent, or at least maintained for a couple of years; conclusive facts are also a suitable humidity value, the sun and the wind, but -- as usual -- our knowledge in this regard is indeed scarce: it is hoped that a large number of studies will confront the many and interesting problems, all now unsolved, that the tardigrades present in this area.

POPULATION DENSITY.

Because one specific species can be installed in a definite habitat it is evidently necessary that it finds there at least all the minimum conditions necessary to life; but its greater or lesser development in time, that is to say the density of the population reaches, depending on many factors which -- with regard to tardigrades -- are not easily analyzed and understood but certainly the quantity and the type of food available, sufficient presence of oxygen, competition with other animals (including tardigrades of different species and predators), temperature, chemicals (and therefore pH, the absence of noxious substances, etc.), which should increase, for the non-aquatic tardigrades, humidity, insolation, ventilation and the cycle of the desiccation period of their environment. It is possible that other factors intervene, but are not now determined.

We can not therefore establish "a priori" if, for example, in certain moss or in a certain zone of the shallow lake we might encounter many, few, or no tardigrades, exactly because we still do not know what are the optimal conditions for tardigrades, or -- if some are known -- they have not been recognized and measured in the environment. It is the experience of us who -- as the writers -- after working for years on tardigrades, may happen to collect moss which does not contain even one, having had the certain confidence of achieving a perfect choice and of expecting very richly inhabited moss.

We will be limited then to furnish few facts, of purely orientation purpose, indicating also population density, observed in different habitats.

-- Marine water and beach sand

Marcus (1929) refers encountering, for *Echiniscoides sigismundi*, a maximum of 60 individuals in a cubic centimeter of water with *Enteromorpha*; Renaud-Debyser (1959) collected, in the sand of the beach of Eyrac (Arcachon) up to 350 tardigrades in 75 cc of sand (the animals belonged for the most part to the species *Stygarctus bradypus* with some *Batillipes mirus* and *Ba. pennaki*).

McGinty and Higgins (1968) observed a sample of 100 cc of sand at Sandy Point (Virginia, U.S.A.) which contained about 3,000 tardigrades of the species *Ba. mirus*, during the month of April; however samples collected simultaneously at other points of the same locality, contained less than 6 individuals. The density of populations is then "topographically" variable: one does certainly find the maximum density in spring and fall.

-- Fresh water and sand saturated with it

Sometimes the tardigrades of fresh water reach high density of population during their maximum development, often in the spring. Marcus (1929) cites a number of 100-150 individuals in a cubic centimeter of water with algae from Wannsee near Berlin. On the bottom of some alpine and subalpine lakes, which Ramazzotti has examined, the tardigrades can not be considered rare, but has not observed particularly high densities.

In the littoral *psammon* of fresh water of lakes of Wisconsin, Pennak (1940) collected up to 675 individuals in 80 cc of sand (that is a cylinder with a base of 10 sq cm, taken between the surface and 8 cm of depth), with horizontal distribution and seasonal variability, of which as yet we can not give a satisfactory explanation. Tardigrades are present in the sand of the beach up to a distance of more than 1.50 meters from the edge of the water.

-- Moss environment

In moss of Austrian Tirolo Mihelčič has observed numbers of tardigrades from a minimum of 1,000-5,000 to a maximum of 5,000-20,000 individuals per square decimeter of surface. Our examination of moss from various sources leads to analogous results, with the only reservation that the maximum of Mihelčič may be considered exceptional, while more common values correspond to the minimums cited by this author; naturally it can happen that the moss can still be scarcely inhabited and it is not rare for there to be a complete absence of tardigrades; the usual moss can be considered rich if it contains 10 to 20 specimens per square centimeter.

Marcus (1929) mentions a maximum of 660 tardigrades in a moss, the dry weight of which (after washing and removal of its microfauna) was 0.0286 grams, that is 22,000 tardigrades in one dry weight gram of moss.

Lichens, at our latitudes, and "cushion" plants, are usually less densely populated and the number of specimens per square decimeter rarely reaches more than three figures. I have however had the chance of examining lichen from northern regions (i.e., Lapland) in which tardigrades were present in very high numbers, probably above 1-3 x 10^3 per dm^2.

Different species can be mixed inside the same habitat, generally two to six being found together, but occasionally one can observe 10 or more of them in the same moss or lichen.

-- Soil and leaf litter

The little information at hand, about the population density of tardigrades in soil, varies within very wide limits. Franz indicates that there are about 300,000 specimens per square meter, Mihelčič indicates that there are about 500 to 2,000 specimens per square decimeter (figures not too far removed from those of Franz), and Ludi notes that there are from 20 to 5,000 per kg of soil, which corresponds (taking into account the method of collection) to an equal number of tardigrades per decimeter and in the first 10 cm under the soil surface.

In 2 cm^3 (surface 1 cm^2, depth 2 cm) of field soil in Pallanza (1959) Ramazzotti was able to count a maximum of 40 tardigrades, 1 cyst, and 58 discarded shells, containing 368 eggs, that is 4,000 tardigrades, 100 cysts, and 36,800 eggs for every dm^2 of soil, if one can deduce the population density of a larger sample from a small one. But this cannot be done, as the distribution of tardigrades in soil, instead of being uniform, is typically "insular", thus, there can be strips between two densely populated zones of grass, placed a few centimeters apart, containing hardly any tardigrades at all.

However, 6 samples from the same soil in Pallanza (pH ranging between 6.8 and 7.1) each 1 cm^2 in surface area, examined thoroughly in depth down to 5 cm, provided an average of about 40 tardigrades, 1.5 cysts, and 120 eggs per cm^2, which represents figures fairly close to the maximum mentioned above.

Cysts were often very numerous in this type of field soil and at times there were more than 40 per sq cm, this being the number of tardigrades present in the same surface unit.

With regard to the leaf litter and conifer needles in a woodland habitat, there are at present no quantitative data to be had on the subject, although it is known that tardigrades can be found in abundance in these locations.

THE RELATIONSHIP BETWEEN ENVIRONMENTAL CONDITIONS AND SPECIES PRESENT.

We have seen how incomplete is our knowledge of the living conditions of marine, freshwater, interstitial, soil, and leaf litter tardigrades. For these groups we shall have to limit ourselves to a little information of a very general nature, whereas it is possible to say somewhat more about tardigrades from a moss habitat where about 80% of all known species and varieties are found.

In the section "Habitats" we already gave a list of the exclusively marine genera that is the Suborder Arthrotardigrada containing only marine genera and species (with the sole exception of *Echinursellus longiunguis*). There are also two marine genera of the 12 in the Suborder Echiniscoidea, and in the Order Eutardigrada four species. There is nothing to add to the little information given in the previous pages on tardigrades from marine environments, as some species were studied only a few times, or even once,and then mainly from the morphological and systematic points of view.

With regard to the freshwater tardigrades it might be useful at this stage to group them with moss inhabiting species in order to get a better overall picture of the ecological requirements of this large group of tardigrades, which we can call "non-marine". This procedure is all the more necessary in that it is often very difficult to make a clear distinction between some species of moist mosses and aquatic species, although there are a few which can be considered truly and exclusively aquatic (cf. "Habitats" section).

First of all, let us note that different species of moss do not seem to have a specific influence on the species of tardigrade present and if there does at times seem to be some relationship, it is probably a secondary effect. Thus, for instance, the fact that in sphagnum one can often observe certain species of tardigrades, can be attributed to the distinctly hygrophilous nature of such species, whose presence in sphagnum is therefore wholly logical, since these plants only grow in very humid soil and atmospheric conditions. Similarly, the scarcity, or complete lack, of tardigrades in a moss of the genus *Polytrichum* should perhaps be attributed, as we have already said, to a mechanical reason in that the considerable thickness of the cellular membrane prevents the delicate buccal apparatus stylets from perforating and absorbing food.

One factor, which no doubt plays a very important part (even though it may not be the sole agent) in determining the presence or absence of different species, is the degree of humidity in the moss, as many authors, Bartoš and Mihelčič in particular, have made obvious. This is the one reason why mosses were divided into 3 groups and 5 categories in the "Habitat" section.

An initial classification of tardigrade species, in relation to the environment in which they live, can accordingly be made on the basis of their degree of *hygrophilia* and for the sake of maximum clarity and simplicity, the species can be divided into the 4 following groups (the Roman numerals in brackets indicate the categories of mosses in which they find favorable environmental conditions):

1. *xerophilous*: typical in dry mosses (IV and V);
2. *eurytopic*: can be found in every kind of moss (from I to V, although sometimes not in the first);
3. *hygrophilous*: characteristic in moist mosses (II and often III);
4. *hydrophilous*: in wet mosses (I) and also in water.

Obviously, it is not possible to draw up a list of all known tardigrades here, indicating for each species the group to which it belongs, since many species have only been studied once, or a few times, and it would be hazardous to assign these to one group, rather than another. We shall therefore only mention the more common species:

1. Xerophilous species:
   - the majority of the *Echiniscus*, and in particular *E. testudo*, *E. blumi*, *E. trisetosus*, *E. granulatus*.
   - *Parechiniscus chitonides*.
   - all the *Cornechiniscus*.
   - *Adorybiotus coronifer*.
   - *Macrobiotus islandicus*, *M. occidentalis*.
   - *Hypsibius oberhaeuseri*.
   - *Milnesium tardigradum*.

2. Eurytopic species:
   - *Macrobiotus areolatus*, *M. echinogenitus*, *M. furcatus*, *M. harmsworthi*, *M. hufelandi*, *M. richtersi*.
   - *Isohypsibius prosostomus*.
   - *Echiniscus merokensis*.
   - *Bryodelphax parvulus*, *B. tatrenis*.

- *Pseudechiniscus suillus*.

3. Hygrophilous species:
   - *Macrobiotus hibernicus*, *M. intermedius*.
   - *Hypsibius pallidus*, *H. convergens*, *H. microps*, *H. dujardini*.
   - *Isohypsibius tetradactyloides*.
   - the majority of *Diphascon*.

4. Hydrophilous species:
   - all the *Dactylobiotus*.
   - all the *Pseudobiotus*.
   - *Isohypsibius granulifer*, and some others.

It must be remembered that the various species in this list have been subdivided among the four categories on the basis of the frequency with which they appear in the different environments; the criterion of such a classification is, therefore, somewhat uncertain, and eventual discrepancies between the entries in the list and discoveries in nature are bound to occur. Further, it must always be remembered that there probably exists different physiological races in the same species, which, although they are identical morphologically, can inhabit different habitats.

Statistical research on this subject was published by Maucci (1980).

Naturally the degree of humidity in moss, however important, is not the only factor which is entailed in the subdivision of tardigrades in different types of moss. There are tardigrades which prefer more or less sunshine and others which have different reactions to a relative deficiency of oxygen and so on. On these grounds, Mihelčič (1954) proposed a highly complex classification of tardigrades, which however -- precisely because of its complexity -- seems premature and more theoretical than practical. In fact our present limited knowledge of the ecological requirements of individual species, due to still too few and incomplete observations in the field, do not allow for so clear a subdivision of each species.

Nevertheless, we shall sum up Mihelčič's classification briefly (it is derived from that of Strenzke, 1952, for mites), not because it is of any immediate use, but because it may be that with the right modifications, it could constitute a good basis for a more advanced stage in these studies. First of all, the species are considered in relation to their *plasticity* factor, in other words the possibility of living with great or slight changes in all the environmental factors involved:

1) *stenoplastic* species, which can withstand only limited changes in the different factors;
2) *euryplastic* species, which can withstand a wide range of changes;

3) *eu-euryplastic* species, which, like the previous group, can withstand a wide range of changes, but which do not show any *optimum* correlation with any of the factors involved;

Mihelčič then subdivides categories 1 and 2 respectively into *oligo-*, *meso-*, *poly-stenoplastic* species and into *oligo-*, *meso-*, *poly-euryplastic* species, with the usual meaning of these prefixes ("small", "average", and "very" respectively).

He then considers the *humidity* factor. From this point of view, the three groups of species, first subdivided on the basis of their plasticity in the general sense, become:

1) *stenokous* species:
   a) *oligostenokous*; b) *mesostenokous*; c) polystenokous.
2) eurokous species:
   a) *oligoeurokous*; b) *mesoeurokous*; c) *polystenokous*.
3) *eu-eurokous* species.

Regarding sunlight (*heliophilia*) Mihelčič only considers three groupings of species, applying to Echiniscidae, which are: *mesostenoheliophilous* - *polystenoheliophilous* - *mesoeuryheliophilous*.

As for oxygen requirements, the groups of species are as follows:

1) *stenaerobic* species:
   a) --- ; b) *mesostenaerobic*; c) *polystenaerobic*;
2) *euryaerobic* species:
   a) --- ; b) *mesoeuryaerobic*; c) *polyeuryaerobic*.

Then other subdivisions are dealt with, which we shall not include here, based on *feeding*, *geophilia*, etc.; Mihelčič, in his publications of 1954, 1955, 1957, shows different species of tardigrades as belonging to one or other of these groups or subgroups in his classification. Here, on the other hand no name of species is mentioned, because in actual fact we think that to do so now with so few data at hand would not only be premature, but also a probable source of mistakes. In fact, some of Mihelčič's examples, in the assignation of certain species to specific categories, do not coincide with observations of other authors, including us.

Awaiting some progress in our knowledge, it is perhaps preferable to keep to the previous subdivision of species into *hydrophilous*, *hygrophilous*, *eurytopic*, and *xerophilous* groups. Along general lines, this method is useful and simple, even if, at times, it may give rise to uncertainty.

In a very general sense, it can be said that mosses which are well exposed to sunlight in open places, especially those which grow in thin and even very thin strata, are often very rich in tardigrades, and quite frequently, one can find large colonies of Echiniscidae (armored) there. In mosses growing in shady and somewhat moist places, on the other hand, we find an abundance of Eutardigrada (naked) whereas species of Echiniscidae are few, that is *Bryodelphax parvulus* and *Pseudechiniscus suillus*, are often absent.

Moss-inhabiting tardigrades have no competitors in their search for food, as they feed mainly on algae or on the cellular content of mosses, whereas the other members of the moss-inhabiting microfauna (rotifers, nematodes, thecamoebae, etc.) have a different diet. In addition, the food offered to the tardigrade by moss does not seem to constitute a limiting factor to population density as food is always there in excess (Ramazzotti, 1959) even in the case of the most numerous colonies ever observed, of about 20,000 specimens per dm^2, which are also extremely rare.

We are not yet well enough acquainted with the feeding habits of tardigrades to be able to decide if the presence, or absence, of certain species can be attributed to the availability or lack of a certain type of food in the moss. There are certainly, especially among the Eutardigrada, species which feed on algae, fungi, bacteria, and organic detritus in addition to cell contents, and thus it cannot be ruled out that the existence of certain species in a moss may be linked with the possibility of finding a favorite food there in sufficient quantity. The same goes for predatory tardigrades, *Milnesium tardigradum* in particular, for which the presence of their usual prey is required (nematodes, rotifers, other tardigrades, etc.).

It may also be that an excess of organic detritus is damaging to tardigrades, and perhaps more so for certain species than for others. It this were true, it could be one of the causes which limit or prevent the growth of the particular population.

The presence of predators (nematodes and other predatory tardigrades, perhaps amoebae, mites, spiders, insect larvae) or parasites (sporozoa, fungi, among which Baumann (1961) observed the phycomycete *Macrobiotophtora vimareusis* Reukauf, etc.) are other factors which might influence the selection of species existing in a moss. In this sense certain causes, which are even more difficult to investigate, may be involved, which we shall illustrate by the numerical relationship between tardigrades and rotifers dwelling in a moss. Mihelčič (1953) thinks that there are close links between these two groups of animals in as much as if one cut down the number of tardigrades in a moss, or increased it, on the other hand, the rotifers would suffer from this, in that they would show signs of degeneration, would grow more slowly, and would not reach sexual maturity. The same would occur with the tardigrades, perhaps to a different extent according to each species, if the rotifers disappeared. We must not therefore exclude a relationship not only between tardigrades and rotifers (which could be useful in the sense of avoiding any excessive or damaging accumulation of organic detritus) but perhaps also between tardigrades and other moss-inhabiting animals, like thecamoebae, nematodes, etc.

In soil and leaf litter we find different species in relation, above all, to the degree of humidity and the oxygen available. Among the more common are:

- *Macrobiotus harmsworthi, M. hufelandi, M. richtersi*
- *Hypsibius convergens, H. dujardini, H. oberhaeuseri, H. pallidus*
- *Isohypsibius franzi, I. prosostomus, I. tuberculatus*
- *Diphascon bullatus, D. scoticum*
- *Echiniscus granulatus, E. trisetosus* (both not very frequent)
- *Pseudechiniscus suillus*
- *Milnesium tardigradum*

The only species which have been observed in soil only until now are *Macrobiotus terricola* and *Isohypsibius tuberculoides*. It is perhaps somewhat premature to term them *eu-edaphon*.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTION.

There are many cosmopolitan tardigrade species, although others may be rare, or very difficult to find, with the result that they have been observed in very few places, or in a single location. Therefore, it is not possible to hazard any judgement on the geographic distribution of the rare species, a judgement which is excluded by the very scarcity of finds. Accordingly we hold it quite useless to devote any more space to the subject, which can be taken up again only when the amount of data available increases.

The information at hand, even though it is not very extensive, tends to show significant differences in the altitudinal distributions of tardigrades. For instance, in the alpine and subalpine zones, out of 109 known species and varieties (in 1956), the 36 following species can probably be considered "alpine" (Ramazzotti, 1956):

- *Echiniscus arctomys, E. heterospinosus, E. jagodici, E. lapponicus, E. oihonnae, E. phocae, E. rosaliae, E. wendti.*
- *Pseudechiniscus novaezeelandiae marinae, P. islandicus, P. scortecci, P. victor.*
- *Oreella mollis* (its discovery in the Alps is uncertain).
- *Adorybiotus coronifer*

- *Macrobiotus kolleri, M. rollei, M. striatus.*
- *Hypsibius arcticus, H. calcaratus, H. microps.*
- *Isohypsibius annulatus minor, I. cyrilli, I. hadzi, I. montanus, I. papillifer, I. schaudinni, I. undulatus.*
- *Calohypsibius ornatus, C. verrucosus.*
- *Diphascon angustatum, D. clavatum, D. gerdae, D. mariae, D. nonbullatum, D. pingue, D. recamieri.*

This list will no doubt increase with time, and probably also be modified, as studies multiply. Species found at altitudes of more than 500 to 1,000 meters, and especially at lower altitudes, were considered "alpine" species, not omitting the occasional find in arctic zones, and this is based either on personal observations, or on information of various authors.

Then, based on personal evidence in the Alps, Ramazzotti added still the following species:

- *Echiniscus capillatus*
- *Pseudechiniscus facettalis* (there are however several reports at lower altitudes)
- *Macrobiotus pustulatus*

In an investigation conducted with statistical methods, on more than 2,000 samples of mosses, Maucci (1980) recognized as montane the following species (the numbers between parentheses indicates the percentage of presence, according to four bands of increasing altitude):

- *Echiniscus testudo* (2.7, 8.9, 16.3, 18.3), *E. granulatus* (2.4, 8.9, 16.3, 24.1)
- *Macrobiotus harmsworthi* (5.4, 9.3, 17.7, 17.8)
- *Adorybiotus coronifer* (0.7, 2.1, 9.5, 9.9)

On the contrary, always according to the same research, the following species tend to avoid the higher elevations (between parentheses always the percentage of presence in bands of increasing altitude):

- *Bryodelphax tatrensis* (5.2, 2.5, 0, 0)
- *Macrobiotus hufelandi* (53.1, 41.9, 37.4, 24.1), *M. intermedius* (9.8, 6.3, 4.7, 0)
- *Diphascon alpinum* (9.9, 8.9, 3.4, 0)

From unpublished observations from Ramazzotti on 482 Italian mosses seems to infer that the genus *Hypsibius* may be more copious above 2,000 meters: results in fact that in the altitudinal band between 2,000 and 3,000 meters for every 100 mosses collected the genus *Hypsibius* was found 98 times, *Macrobiotus* 86, *Echiniscus* 57, *Pseudechiniscus* 17, and *Milnesium* 2; in the band between 3,000 and 4,000 meters *Hypsibius* appears 100 times, *Echiniscus* 50, *Macrobiotus* 10, and the other genera are absent. These results are reported only as indicative proof, because the number of mosses examined (59 in the 2,000-3,000 meter band and 10 in the 3,000-4,000 meter band) is too small -- if however not negligible -- to be able to generalize the calculated percentages and the relative conclusions.

The brief statistical analysis of Maucci, with references to the genera, result considerable different (the percentages refer to the presence in the bands of altitude: 0-500, 500-1,000, 1,000-2,000, more than 2,000):

Bryodelphax (7.8, 4.6, 3.4, 0)
Echiniscus (15.6, 30.9, 48.3, 51.7)
Pseudechiniscus (8.8, 11, 19.7, 0)
Macrobiotus (86.1, 86.8, 77.5, 65.5)
Hypsibius (20.3, 27.5, 18.3, 17.2)
Isohypsibius (13, 18.2, 18.3, 17.2)
Diphascon (13.8, 11.4, 9.5, 0)

The contradictory results (in part) demonstrates how one must use caution, on this topic, at least until there is much more numerous data.

Tardigrades have been observed at an altitude of about 6,600 m in the Himalayas (*E. arctomys* and *spec. dub. et inquir. M. eminens*, perhaps a synonym of *M. hufelandi*; Ehrenberg, 1859) and in Europe at about 4,300 m in the Mount Blanc group (*P. suillus* and *H. oberhaeuseri*; Menzel, 1914). The high altitude mosses in our Alps, between 2,000 and 4,000 m, frequently contain tardigrades and it happens fairly frequently that one meets uncommon species there. It may be however, that these are not "rare" species in all cases, since they are "alpine" and seem rare only because high altitude mosses, searched for tardigrades, are fairly small in number.

ACTIVE AND PASSIVE DISSEMINATION.

During cryptobiosis tardigrades take on a "barrel" shape and thus their normal dimensions are reduced, losing weight at the same time through dehydration. Accordingly, when the moss is desiccated, tardigrades which have been surprised by cryptobiosis before succeeding in descending into the deeper and more protected zones, are easily carried off by wind, the same occurring with eggs and cysts, or at least for a certain percentage.

Indeed, the greatest influence on the dispersal of moss-inhabiting tardigrades must be attributed to the wind. It would not otherwise be possible to explain Heinis' observations (1910 and 1928) on a moss population of a stone monument, erected in 1904. These observations led to the recognition of the settlement of two tardigrade species in 1906, remaining at two in 1908, but going up to five in 1927.

On dry and windy days it is thus possible that quiescent forms and eggs of tardigrades may be carried through the air. A methodical and quantitative study of the subject would certainly be interesting, since we have until now reached only an inferential stage and have no data, even of an approximate nature, on the number and species of animals transported per unit time over unit surface, in specific conditions of place and wind velocity.

Nonetheless, one can make a few reasonable suppositions: take for instance a moss, growing alone on a block in the open and which contains only two species of tardigrade, one lighter than the other, each with an equal number of specimens. Assume, in addition, that all other mosses around are completely devoid of tardigrades, but are suitable for them and allow their development.

When an isolated moss like this is in a dehydrated state and is swept by wind, it becomes a real radiation center for diffusion of the two species present. All other conditions being equal, among which is included the equal resistance which the two species present when being torn from the moss, and the surface open to the wind, the specimens of the lighter species would on an average be carried further, whereas those of the heavier species would land at a lesser distance from the moss of origin. The diffusion zone would be about circular if the wind blew as long and with the same speed from every direction (a purely theoretical case), or would cover a more or less elongated zone, corresponding in its direction and shape to those of the wind, if its orientation never altered.

It follows that, after a certain period of time, the mosses nearest to that of origin will be more populated by the heavier species and the mosses further away populated by the lighter species. But each of these newly populated mosses will in turn, under the action of the wind, become a radiation center.

The process will go on by the same diffusion methods, and, if the wind direction never changes, the lighter species will always be ahead in their diffusion. That is at a specific instant fairly close to the beginning dispersal, the mosses farthest away from that of origin will have a population made up exclusively, or prevalently, of the lighter species (even though it may be less dense compared with the heavier species, if the dissemination surface is larger and the initial number of specimens of both species is taken to be equal).

Of course, in this hypothetical example, things have been simplified to the extreme and numerous factors disregarded, including the fact that the young and certain eggs from the heavier specie can be lighter than the adults, and can be lighter than certain eggs from the lighter species. But, apart from this, events proceed very differently in nature and in a far more complex way. One need only think of the wide range of moss inhabiting tardigrade species, of their different requirements for life, of the probably different reproductive pace (and thus of the different density of population of the different species, with which it is partly correlated), of the continual changes in the wind direction and speed, and so on.

An extremely complex picture results from which one can deduce only that with the passing of very long periods of time, a certain tendency towards uniformity of population in all mosses should manifest itself, meaning of course those mosses which offer equal living conditions. This tendency towards uniformity can, however, be hindered by occasional inability to adapt on the part of single species and by causes of genetic origin, particularly arising from molting.

Just as we explained by using the simplified example of a moss with two different species only, this can also explain the frequent presence of an identical species in mosses of the same zone, in other words in mosses placed close together. That this greatly depends on the direction and path of the dominant winds, is also proved by the following fact. In 1954, Ramazzotti thoroughly examined an abundant moss vegetation on the trunks of four lime trees, placed fairly close together in a straight line. On the first lime tree in the row, there was an abundance of *Echiniscus trisetosus* which were absent from the three remaining trees, on which, however, were found two other species of tardigrades (also present on the first lime tree). In 1960 he reexamined the same mosses and the situation was unchanged, which means that within a period of six years, the *E. trisetosus* were still only to be found in the moss on the first lime tree and had not passed on to the others, although they were very close by. This is most likely due to the dominant winds in good weather (and dry moss), the directions of which just about coincide with that of the row of four trees, but the strength of which was directed from the fourth to the first lime tree, thus hindering the transportation of *E. trisetosus* onto the other trees in the row.

Therefore, wind is the predominant factor in the dispersal on moss inhabiting tardigrades, but there are also other dispersal methods. Firstly, rain and flood waters, melting snow, etc., can carry along living specimens, those in a cyst, those in a cryptobiotic state and their eggs, especially over steep surfaces, i.e., tree trunks and sloping rocks.

The drag effect of water is considerable in certain conditions, when for instance there is an unexpected downpour of rain onto mosses which are already desiccated, then the tardigrades are caught in a cryptobiotic state, with its characteristic "barrel" shape, and can be carried off more easily by the water current, together with encysted specimens and eggs (if however these are not fixed to the mosses by adhesive secretions, which, it seems to me, occurs in numerous cases, e.g., for those of *M. hufelandi*).

When, on the other hand, the mosses are already moist, due to previous light rainfalls, or for other reasons, the tardigrades are found in active life and cannot easily be dislodged from their environment by water, this is perhaps due to the presence of filaments, bristles, and well-developed claws. This can be verified by collecting the water pouring down from a moss covered roof, during a heavy rainfall. There are very rarely any tardigrades to be found, even if these mosses are rich in them. Thus the same happens with rain as with wind, which can produce a maximum effect on the dispersal of tardigrades when it acts on highly dehydrated mosses, whereas its action is practically nil on wet or moist mosses.

Another means of dispersal, far more important than it may seem at first glance, consists of the animals which occasionally visit mosses, like birds, snails, myriapods, Acarina, Apteryogota, Coleoptera, etc. Heinis (1910) carried out numerous studies on some of these animals, taking them from moss and ridding them of every plant particle with forceps, then washing them in distilled water with the help of a brush, and studying what was left. In this way he was able to detect on several snails (of the genera *Fruticicola*, *Helicigona*, etc.) up to a maximum of four thecamoebae, two rotifers, one tardigrade, three nematodes, in addition to rotifer and tardigrade eggs. In myriapods of the genus *Julus* Ramazzotti observed on a single specimen, up to three thecamoebae, two rotifers, one tardigrade and one egg. He also obtained results comparable to these by examining isopods of the genus *Oniscus* (soil piglets) and Coleoptera of the genera *Carabus*, *Staphylinus*, etc.

Man can also, though in a minimal way, contribute to the dispersal of moss-inhabiting tardigrades, through the transportation of moss covered timber for instance, and of moss itself, which is widely used by florists to decorate plants, etc.

These are the main passive diffusion methods. Active diffusion is of little importance and can only occur in special conditions of humidity and cover very brief distances. Ramazzotti was able to see when looking at tree trunks during a rainfall through a lens, which magnified 40 times, a few tardigrades moving about on the bark, passing in this way from one patch of moss to another. On the basis of his observations the speed with which they progress is about 12.6 cm/hr for *Hypsibius oberhaeuseri* and 17.7 cm/hr for *M. hufelandi*. During these experiments on velocity measurement the tardigrades were proceeding over a film of agar gelatin, which offered their appendages a good grip.

The arrival of new species, due mainly to passive dispersal, causes the association of the species themselves to vary in time, according to methods which remain completely unknown and which depend on different factors, among which one can probably include the age of the moss, the composition of the moss biocoenosis (and not of tardigrades alone), the occasional variation in the degree of humidity or of exposure to the sun (i.e., through shade thrown by trees growing nearby), etc.

Mihelčič (1951) kept mosses from straw roofs under observation for nearly three years noting a regular alternation between *Echiniscus blumi* (peak in summer) and *E. trisetosus* (peak in winter), but in this case the phenomenon is probably due to the fact that these two species belong to the well known *Echiniscus blumi* - *Echiniscus canadensis* series, which includes species which are very close which may also be able to reproduce at a stage of incomplete development (neoteny?).

Experiments, carried out at intervals over a period of several years (up to a maximum of 19) on certain mosses from the Bellunese and Pallanza, always provided me with the same species of tardigrade, be it from moss on walls or stone, or that from tree trunks. Inasmuch as the number of experiments is too low to draw any reliable conclusions, one can however reasonably suppose that it is not very easy for a new species to settle in a moss where there are already long standing colonies of tardigrades. The phenomenon is bound to be far more complex than it seems at a glance, and is to be attributed to the same group of causes, of which a great part is unknown, to which the "insular" distribution is due, either in different or the same moss.

A typical example among many, is given by *Cornechiniscus lobatus* which has been seen occupying three different places a few hundred kilometers apart, the moss in a small zone (a few square meters) and not in the surrounding moss which apparently was of an identical species, soil and exposure. To explain this fact, three hypotheses can be presented:

1. that these rare tardigrades, localized in tiny areas, have numerous special needs, that they therefore avoid great areas (and are therefore *stenoplastic*) and can live and reproduce only in certain mosses and conditions;

2. that these are rare species in the region in question, and that they have arrived there recently (wind, transportation by

birds, etc.); local diffusion would thus be just beginning and would not have reached the surrounding mosses;

3. that the factors of point 1 and 2 above act together, meaning that the species are stenoplastic and of recent arrival.

The third hypothesis is probably closest to the truth, in addition to which there could be a possible recent segregation of the species due to molting. However, we are dealing only with suppositions, which no experimental data can back up or deny to date.

The dispersal from one lot of water to another by distinctly aquatic species, which in many cases do not undergo cryptobiosis, can rarely be assisted by wind, except perhaps only, or mainly, with the transportation of eggs (which resist dehydration) and cysts (?). Other methods of dispersal are probably more effective, such as transportation along the river system during floods, and also the intervention of birds and other animals, through mud which can contain tardigrade eggs sticking to their legs.

The present information is so slight, that very little can be said about aquatic and soil tardigrades. For both these groups it must not, however, be excluded that highly plastic species, of a moss inhabiting origin can, with the right means, be carried by wind or other methods and pass into a new environment and prosper there. Normally moss inhabiting tardigrades can fairly often be observed in water (i.e., *M. hufelandi*, *M. tardigradum*, etc.).

III

NOTES ON METHODS OF COLLECTING AND STUDYING

COLLECTION.

a) Marine and freshwater tardigrades

These tardigrades (except for a few marine species which are ectoparasitic or commensal with other animals) live exclusively on the bottom particularly in the littoral zone because tardigrades are unable to swim and therefore need some sort of substratum, on which they can rest.

Collecting methods -- which we shall not describe -- are the same as those used for the other members of the benthic microfauna: dragging finely woven nets across the bottom; use of dredges or grabs; washing and occasional scraping from macrophytes, algae and immersed mosses, etc.

For tardigrades belonging to the interstitial fauna, one usually merely withdraws -- or sucks up artificially -- specific quantities from a hollow dug in the sand. This method probably has the advantage of producing a selective effect on the tardigrades gathered, as for instance the younger and smaller ones are dragged out of the water more easily than the larger tardigrades, which can grasp hold of individual mineral granules more easily and have more trouble in passing through the gaps and narrow passages. But on the other hand the examination in depth of a constant volume of sand, of large enough dimensions to be significant, would demand an enormous amount of time, such that it is really out of the question.

It is advisable to study marine, freshwater, and interstitial tardigrades immediately, when they are fresh, as this makes their identification much easier but if this is not possible, one should fix them with formalin, and if necessary carry out preliminary sorting by decanting part of the water collected, if its quantity is excessive. The addition of formalin must be such that the total volume of the liquid has a 5 to 10% concentration (using sufficient 40% formalin with about a quarter, or a fifth, of the volume of water being dealt with).

Formalin, of course, is not an ideal fixative, but is easy, cheap and still better than alcohol, or other compounds. It is advisable to use *neutralized* formalin which is easily obtained by leaving magnesium carbonate at the bottom of the container in which it stands (to prevent the calciferous parts of the stylets from dissolving).

Puglia (1959) writes of having obtained good results using -- either as fixative, or as preservative -- Bouin's solution, diluted 1 to 4.

b) Moss inhabiting tardigrades

The collection of dry mosses, lichens, etc., is very easy, as all that is needed is to detach them from their support, if necessary using a blade, and to put them in envelopes of small bags, or even simply wrap them up in paper, in which they can be kept at length without damage.

The use of impermeable polyethylene bags or such like is not advised, as there may still be some trace of water on the moss, and preventing this from evaporating encourages the appearance of mold or fermentation. Paper or cloth, due to their porosity, rarely cause this kind of inconvenience.

When the moss is very wet it may be wrapped in a large amount of newspaper, taking care to let it dry in the open as soon as possible, before putting it back in envelopes or small bags, for longer preservation when it is not to be examined immediately.

The things we have just mentioned refer to mosses of categories III, IV, and V. The collecting method for mosses of categories I and II is different, these being mosses growing or submerged in water, which can thus contain tardigrades lacking the ability to go into a cryptobiotic state. These mosses must therefore be gathered in tubes or jars, together with the water in which they are found, and examined as soon as possible.

If immediate observation is not possible, the moss should be squeezed out completely, as if it were a sponge, and then washed several times and squeezed out again (only for quantitative studies is it necessary to carry out a microscope control, to make sure there are no tardigrades in the residue). Then the liquid should be fixed with neutralized formalin or diluted Bouin's, as we have said previously, concerning aquatic tardigrades.

For each moss, one must note the date and place of collection, the altitude, whether the moss in question was found on a rock, wall, tree trunk, etc., adding any other useful information. This is of great importance for any consequent studies, and it has often occurred that I had to complain about the insufficiency of the notes taken down on the first collection.

Which mosses are to be chosen for study naturally depends on one's aims. If it is the study of tardigrades in a specific zone, one should collect a fair number of samples taking care that all categories of moss present are represented, from I to V; if however one simply wishes to gather tardigrades, it is useful to keep in mind that they are usually most numerous and richest in species, in mosses which are exposed to sunlight (categories IV and V), especially those growing in thinner layers, in open places. There are few, or none, to be found in muddy or powdery mosses, in towns, industrial zones, or along roads with heavy traffic.

There is a point to be noted, observed by us and others, namely that in powdery mosses, or those exposed to industrial and automobile fumes, there are often only two species to be found, which are: *Milnesium tardigradum* and *Echiniscus testudo*, which obviously resist this type of interference best.

c) Tardigrades in soil and leaf litter

No special care is needed for needle-like or other leaf litter of which one should gather the uppermost layers, down to a depth of 5 to 10 cm. One should examine the material as soon as possible, and, if this is not possible, the leaves should be transported in a container with water, leaving them there for a few hours and stirring frequently, then adding formalin to the water in the way we have already mentioned.

As for soil, it is advisable to collect numerous samples, which may then be mixed together, that is, if the aim of the study is not to show an eventual distribution in space; collecting methods are numerous and easy to think of, but a particularly practical one is to sink a small circular metal tube with a sharp edge into the ground (a tube similar to boring tubes used in chemistry laboratories). The cylinder of soil, contained in the metal tube, is then pushed out with a small rod with a rubber or plastic tip, the external diameter of which is nearly the same as the tube's internal diameter.

If the metallic tube has the right diameter (about 11.3 mm) the resulting section is about 1 cm^2 and the cm^3 thus corresponds to the depth in cm the instrument has penetrated the ground. This is most useful for quantitative studies.

If one is unable to examine the soil immediately, it should be preserved in paper bags, so that it stays dry or one should let it dry in the open, before storing.

QUALITATIVE STUDY

We shall now provide some information dealing particularly with recently gathered or preserved moss, but which can, for the most part, be extended to tardigrades from sea or freshwater, soil, or those already fixed in formalin, etc.

One of the most useful processes, among the different alternatives, is to put a piece of moss (with a surface of a few cm^2) into a small crystallizing dish with water, and to leave it there for a few hours. The amount of water must be such that some of it still remains at the bottom after the period of time mentioned has gone by.

Then the moss should be squeezed into the same crystallizing dish and, after a few minutes, the greatest part of the remaining liquid should be carefully poured off. All the tardigrades are in the sediment at the bottom, of which a few samples are taken with a pipette, for examination under a stereoscopic microscope prepared to magnify 30 to 60 times, with abundant light. According to each case and species, transmitted or reflected light can be used, the last usually being better against a dark background.

Still using the pipette, the interesting samples should be transferred to another slide to look at them under a compound microscope, in their living state, with the usual technique. Simple methods for obtaining permanent preparations will be given later.

One can also forego the use of the preparatory stereoscopic microscope completely and use only the compound microscope, by proceeding with the examination of a drop of water placed, uncovered on a slide. It is then necessary to adopt an objective with enough working distance and fairly weak magnification (30 to 60 times, together with the eyepiece) and one must also be able to carry out different accurate manipulations (using needles, pipettes, etc.) in spite of the inverted image. This is not too difficult, after a short training period, and presents considerable advantages later on.

It can sometimes be of use, for anatomical observations in particular, to make the tardigrades go into an asphyxial state, so that they stretch out completely and become quite transparent. All one needs to do is place the specimens, with a lot of water, into the small hollow of a cavity slide (the type used for drop examination), and then to cover it with a cover slip and seal. The tardigrades are generally in an asphyxial state within 48 hours, after having gone through a more or less complete "barrel" stage. If one wishes to obtain stretched and transparent specimens right away -- for systematic purposes only -- one can add a drop of 10% KOH (caustic potash) or 3 to 5% acetic acid which does however destroy a large portion potash) or 3 to 5% acetic acid which does however destroy a large portion of the stylets.

Maucci uses to maintain the moist moss, rather than a crystallization dish, plastic glasses, squeezing then the water which is absorbed in a Petri dish for search under the binocular: the glass, because of its depth results in less oxygen, and the tardigrades are found very often in asphyxiated state, very convenient either for anatomical observations, or for obtaining more permanent preparation of the well extended animal, even without the treatment of KOH. For the Heterotardigrada, and in particular for the armored tardigrades of the genera *Echiniscus*, *Pseudechiniscus*, etc., the treatment with KOH is however recommended.

The prescribed procedure for examining tardigrades not living in moss is similar. Those from water, leaf deposits, and soil should be found with a stereoscopic microscope after having left them in frequently mixed water for a few hours with the submerged moss, algae, various sediments, leaves, etc., so as to obtain a thorough washing. Soil must be softened in water and examined in small quantities, to make the search easier (watch out for eggs and cysts especially, as these can easily be missed!). If needed, one can proceed to filter through a loosely woven gauze, to eliminate the rougher particles.

It is rather more difficult to examine tardigrades which have been kept for a time in alcohol, formalin, or such, as they are often completely opaque, stiff, deformed and difficult to identify. In such cases it is almost always necessary to make permanent preparations (see further on) and reexamine the tardigrades a few days later after the mounting medium has had time to act and make the animals more transparent, thus allowing examination of the placoids, the cuticular ornamentation, etc. This procedure does however produce the inconvenience of immobilizing the tardigrades in a fixed position, which is often not ideal for observation. Before making permanent preparations one can try to add to the water on the slide a drop of 10% KOH allowing it to act for a time, following its effects with a microscope, and then washing with a lot of water.

Always keep in mind, when examining fresh or formalin preserved tardigrades, that one should note immediately whether they have eye spots or not, as the medium used in the permanent preparation of specimens, caustic potash, etc., often cause them to disappear.

We can only give the reader some completely elementary though important advice and suggestions at this point, and indeed throughout. Only a considerable period of time spent on personal practice can enable the reader to carry out every operation in the best possible way.

QUANTITATIVE STUDY.

If one wishes to acquire a fairly precise knowledge of the number of tardigrades, eggs and cysts present per surface unit (or per unit volume or weight) in moss, the bottom of lakes, or in soil, etc., the most exact method would no doubt be to carry out an actual count under a microscope, using a magnification of 30 to 60 times.

Unfortunately this procedure is practically applicable only to moss which is not too muddy, to lichen, liverworts and "cushion" flowering plants. But when one has to examine marine or freshwater sediment, sand, soil and similar environments, observation becomes extremely laborious and requires an enormous amount of time, in addition to which some of the tardigrades which have just hatched may be overlooked in the count, as they are very small and highly transparent, and similarly for a good proportion of the cysts, which are easily confused with small particles of detritus.

To give an example of the time required for quantitative research into soil inhabiting tardigrades, we shall say that the thorough examination of 5 cm^3 cylinder took four days of uninterrupted work on average, even with a great deal of practice and a well trained eye. This means that if one wanted to examine 1 dm^3 of soil thoroughly, one would need more than two years.

One can therefore easily see why the procedure involved in a complete examination is applicable only to small samples and with special aims, while in the majority of cases it is necessary to be content with statistical sampling. We shall give some brief suggestion of the subject leaving the reader to study the many possible variants, in relation to individual needs. Practice, common sense and some knowledge of the principles and methods of statistics will still be the best guides.

For moss and similar environments where a complete examination is possible, one should proceed in the following way. Moss of a definite area, preferably no more than a few cm^2 should be left in a small crystallizing dish with water for a few hours, then squeezed thoroughly, washed and squeezed again, so that no tardigrades remain inside. It is advisable to continue washing and wringing until a microscopic examination shows there are hardly any specimens, cysts or eggs left in the liquid that is squeezed out.

One should then allow the water collected to settle for a few minutes and remove almost all the supernatant with a pipette, taking care that it is sucked up slowly, so as to avoid removing any part of the deposit at the bottom. It is advisable to carry out a microscopic inspection of the liquid which has been removed so as to check that there are no tardigrades.

The remaining deposit should then be thoroughly examined and the count taken written down. It is preferable to observe live specimens, in the way we mentioned, as it is easier to find the smaller and more transparent specimens, because of their motion.

For other tardigrade habitats, the problem of collecting samples representative of the environment in question, is added to that of counting specimens, and one often has to be content with approximate results. Thus, for instance, small cylinders of 3 to 5 cm^3 each should be taken from the ground at various points in the zone in question with the metal tube process we just described. From the bottom of lakes considerable areas and depths of sediment should be dug up with buckets for that purpose, keeping in mind the many imprecisions this method entails which can often be quite important. As for leaf litter, one should choose a certain area and establish a depth, but here again mistakes are far from negligible, especially where depth is concerned.

At this point we have material which already contains quantitative imprecisions in its dimensions (surface, volume, or weight) due to the collecting method itself, the first cause for error.

Then water should be added to the material, stirred, softened, and washed. Possibly there are still tardigrades, eggs or cysts left on the leaves (which will later be eliminated through filtering through loosely woven gauze) just as they may have been left on the roots, etc., contained in the soil, or on the coarser detritus in lake sediment. This is a second cause for error.

We now have a mixture of liquid and various plant and mineral particles (the aspect of which varies according to their origin: soil, lake sediment, etc.) which, when left standing for a while, deposits a thick layer of detritus, above which there remains fairly clear water. The quantity of material is nearly always too large to be able to examine it thoroughly and it is therefore necessary to have recourse to approximate sampling methods.

To get results, one should proceed, with occasional variations, as follows: the volume of material at hand should be measured (a volume we know contains just about all the specimens from a certain area, volume or weight) and then shaken vigorously, in order to produce the most complete mixing possible of the liquid and its deposit, then a small fixed quantity should be withdrawn by a narrow pipette (1 to 2 cm^3). The container should then be shaken again and replicate samples taken from different parts of the container, it being agreed, of course, that this way we get a smaller quantity of material, in which however the "density" of tardigrades (meaning their quantity per unit volume) is equal to the density in the material as a whole when perfectly mixed. Do not forget, though, that a third cause for error has been introduced here.

One can now count the specimens, eggs, etc., which were contained in all the small pipette samples under a microscope. The number of specimens, etc., present in the material as a whole, corresponds to the number counted, multiplied by the difference between the total volume of the original liquid and the volume of the liquid taken out and examined. During the count, it is most likely, as we have already said, that a few very young specimens may be overlooked, as well as some of the eggs and cysts, a fourth cause of error.

The last three types of mistakes (tardigrades left on the coarser filtered material, imprecisions in the pipette procedure, counting errors) are all "oversights", which means they tend to give a smaller number of specimens, eggs, etc., than the real one. The first type of error, on the other hand, (choice of a certain area, volume or weight) can be one of under rating, or else over rating, and this is probably the one which contributes most to the results' imprecision. We shall not go into further detail, as all we want to do is throw light on the most frequent causes for error, so that the reader is able to render them minimal, by using the technique best suited to each case. Also, in the study of population density, subject to so many causes for variation and error, all one generally seeks is an approximate figure, which is more than satisfactory in this case (consider, for instance, the high degree of imprecision connected with area determination, and volume choice, compared with which even considerable mistakes in counting become negligible, since the count is carried out under far stronger magnification than that under which the areas or volumes are measured).

While one is counting, one also needs to separate the different species of tardigrades, eggs, and cysts, so as to go on and identify them subsequently. Practice and personal preference should indicate the best method. Very often, especially with material that has been fixed with alcohol, formalin or the like, or if the species present are numerous, one in unfortunately bound to make permanent preparations of all the tardigrades, eggs and cysts that have been counted, as identification can be carried out only a few days later, when the animals transparency is sufficient to allow detailed examination.

Sometimes the aim is not to find out the number of specimens present per unit area (volume or weight) in each habitat, but simply to know the percentage of each species in relation to all the tardigrades present. In this case, another procedure may be applied, which -- if correctly carried out -- allows one to obtain fairly satisfactory results. This method consists of choosing a few samples (3 for instance) from different points on the moss, soil or sediment, etc., which are then examined, without taking into account the area, weight or volume in question. These samples should then be treated in various ways, according to each case: squeezed and washed in the case of moss, mixed with water and stirred in that of soil or sediment, etc., allowing it to settle and then gathering the deposit on the bottom of a crystallizing dish a few cm in diameter, keeping it horizontal without removing any supernatant.

With a narrow micropipette (a simple mark on the pipette glass is sufficient, so that the quantity sucked out is always the same) one then takes 5 to 10 samples from different, regularly placed points on the deposit on the bottom.

Each of these samples should be examined under a microscope, and the number of individuals from each species noted down. The relation between the total number of individuals from each species, from all the samples and the total number of individuals of all species will thus provide the average percentage of each species, in relation to all the species present.

Of course, the methods which have just been mentioned can, as we have said, undergo variations. It must be granted that for certain habitats (i.e., soil, sand, and sediment) the difficulties to be overcome are far from slight, and the first among these is due to the recognition and counting of the specimens, eggs and cysts, which requires very hard work, the highest level of concentration and an enormous amount of time. Therefore, let us hope for some perfecting of collecting and study methods, to make them more satisfactory than those which are in use at present, especially for interstitial and sediment tardigrades, and which, even when one is only taking statistical samples, can lead to timesaving, without entailing too many mistakes, which might distort the results obtained.

STAINING, PERMANENT PREPARATIONS.

Since the nature of this work is mainly systematic, we shall not describe the far from simple techniques for making thin sections, or the staining methods proposed (the effectiveness of which is often doubtful and which are in any case superfluous as far as taxonomy is concerned) and we shall only give limited information on a few vital and *in toto* stains.

Among vital stains, neutral red can be used to mark tardigrades inside moss, and methylene blue (which gives a non-selective coloring of the muscles and nerve fibers) should be used carefully in very diluted forms, as it is often harmful to tardigrades.

Aceto-carmine lends itself well to *in toto* staining but its effect must be followed under a microscope, so as to avoid too intense a color. It has the disadvantage of destroying a large part of the stylets, etc., the advantage of showing up the spermatozoa, chromosomes and such clearly and may be used without fixing the animals or eggs previously.

We shall deal a little more lengthily with the Del Rio Hortega method, according to the technique used by May (1948), as it produces excellent selective staining, ranging from yellow to brown and black, of various organs and cells, especially in the nerve centers. First of all a solution of silver ammonium carbonate is prepared by proceeding as follows: into 50 ml of 10% silver nitrate is poured, a little at a time, stirring continuously, 150 ml of 5% sodium carbonate. The precipitate is then redissolved by adding the necessary quantity of ammonia drop by drop, and no more, then the solution should be kept away from light, in a tightly stoppered bottle.

Then the tardigrades are treated with 2% acetic acid to obtain a thorough extension, washed with water and put in 10% neutralized formalin for 24 hours. After this, the tardigrades should be washed rapidly and immersed in a solution made of 5 parts of distilled water and 1 part of the above mentioned solution of silver ammonium carbonate and placing them for 1 to 2 minutes in an oven at 60 to 65°C. Small variations in this period of time allow a selective coloring of different organs and cells.

The animals are then washed and put in 10% neutralized formalin and the final mounting is carried out in fresh neutralized formalin, using one of the different current methods for preparing a slide and cementing the cover slip.

Concerning the setting up of permanent preparations as far as we are concerned, there are two simple and practical methods to obtain satisfactory results, these being the use of Faure's solution and of polyvinyl lactophenol -- long-standing experience has shown me that, on the whole, the preparations made up with Faure's keep perfectly except for a small percentage, which, after a certain period, showed ramifying crystallization and empty zones, which can induce severe damage. It is however possible to recover the specimens inside, by taking off the cover slip under a microscope, having previously soaked it at length in hot water, then diluting it with fresh water and placing the specimens on another slide with a micropipette which obviously needs practice and concentration.

We have not yet been able to identify the causes resulting in the disadvantage we just complained of, however rarely it may occur, but it seems to us that too small a quantity of Faure's may sometimes play a part in this, as well, perhaps, as a lack of proper sealing. Faure's also has the advantage of preserving aceto-carmine colorings well, which is often useful (though indispensable as far as systematics are concerned) to avoid excessive fading of Eutardigrada as time passes.

Polyvinyl lactophenol (to which one usually adds chlorazol black so that the chitinous parts show up more clearly, especially in microscopic crustaceans), has come to be used fairly recently and it is therefore too early to make any statements about its reactions over a period of time. We can only say, on the basis of our own personal experience, that it has an advantage over Faure's in that it produces an excellent extension of the animal and that it preserves the cuticular ornamentations in the Eutardigrada very well, i.e., the convexities on *Isohypsibius* in the "*tuberculatus* group", which often disappear completely in preparations made with Faure's. It does however have a serious disadvantage, in that a certain number of prepared specimens, after having kept perfectly for a few months, begin to show blank areas as well as irreparable damage to the enclosed tardigrades, which, as opposed to what occurs in the case of Faure's, cannot be salvaged. We do have prepared specimens in polyvinyl lactophenol however, which have been preserved for more than 18 years since their preparation and do not show the slightest alteration.

We cannot state for certain what are the factors which produce this disadvantage, but we would tend to think it is due to too small a quantity of polyvinyl lactophenol and to the presence of an excessive amount of water around the tardigrade, at the moment when it is placed on the slide.

If there is to be a choice between Faure's and polyvinyl lactophenol, the first should be opted for, if that is, one wishes to obtain long preservation, and if the animals in question are not ornamented or bumpy Eutardigrada, for this last type, polyvinyl lactophenol should be used, in abundant quantity, after having eliminated the water around the tardigrade (by sucking it out with a micropipette, with a paper filter, etc., using a microscope).

Here are the formulae for the two mounting media:

<u>Faure's Solution:</u>

Distilled water	50 cm^3
Chloral hydrate	50 gm
Glycerine	20 cm^3
Gum arabic	30 gm

The chloral hydrate should be dissolved at a low temperature, the glycerine added and at the same time the gum arabic is suspended in the liquid inside a gauze bag. One should avoid any filtering if possible, so as to prevent the liquid from going brown when in contact with the air. This is to be kept in a tightly shut container.

Polyvinyl lactophenol with chlorazol black:

Dissolve a dot of chlorazol black on the end of a spatula in absolute alcohol (solubility in alcohol 0.1%) and mix into this solution enough polyvinyl lactophenol to obtain a fairly dark brown coloring. Then add, drop by drop, a solution of concentrated KOH, until a grey-blue coloring is reached (the reagents may be obtained from the firm E. Gurr in London). Keep in a tightly shut container away from light. For tardigrades one can use polyvinyl lactophenol without adding chlorazol black, the staining effect of which is not very obvious.

These two solutions do not require any fixative and are used in the same way, which is:

a) Place a drop of water, with the specimen (or specimens) to be mounted inside it, on a slide; then take away as much of the water around the tardigrade as possible, in the aforesaid manner.

b) Add the desired mounting medium with a pipette or a glass tube, taking care that there is too much rather than too little.

c) Observing with a microscope, push the specimens into the center with the usual needles, taking care that the tardigrades are well immersed in the medium and do not float; sometimes it may be useful to add a fragment of glass or hair to the liquid, to avoid excessive squashing, but this is rarely necessary, especially when using Faure's.

d) Lay the cover slip down gently, in the center of which a certain amount of the same liquid has been previously placed, in order to avoid the formation of air bubbles and to stop the enclosed objects from moving towards the edge of the slide.

e) Place the tardigrade in the best position, by moving the cover slip gently with a rigid needle to bring about slight changes in position; this is more easily done with a single specimen. Follow the operation with a microscope and during the first hours of drying check to make sure the tardigrade has not moved, and if necessary use the needle again, before the mounting medium hardens completely.

f) Let the prepared specimen dry (about 5 or 6 days in an oven at 60°C, or in the open for about 20 days) keeping it in a horizontal position the whole time.

g) When the specimen is quite dry, clean off any excessive liquid from the slide with a moist cloth, and seal it with a good transparent or colored nitrocellulose, varnish; it is best to wait for a few months before sealing the specimen.

It must be kept in mind that, when using Faure's, the tardigrade often shrivel up, but they usually return to their normal state within an hour or more. Both Faure's solution and polyvinyl lactophenol tend to make the immersed animals fade a great deal as time passes, thus it is advisable to note down their position as soon as possible, for instance by a circle traced in ink on the cover slip, which is easily done under a microscope, as soon as the specimen is dry.

Another mounting medium for permanent preparations, which has provided us with excellent results, and which is used like the preceding, is "Turtox CMC-10 mounting medium" product of CCM General Biological, Inc., at 8200 South Hoyne Avenue, Chicago, Illinois 60620 (U.S.A.) [no longer in business].

In observing older, highly transparent specimens, phase contrast is very useful, as it brings out structural detail which is often hard to see under normal lighting.

When observing permanent preparations under a microscope, a magnification of 600 to 700 is usually sufficient. However, as far as systematics are concerned, one is often forced to use an oil immersion objective, especially in critical cases (i.e., for distinguishing certain types of ornamentation on the plates of *Echiniscus*, for observing the detail of claws, etc.).

There are of course innumerable other methods for making permanent mounts of tardigrades, among which we will mention the immersion of the animal in 10% neutralized formalin (animals in an asphyxial state, or killed with 2% acetic acid, to avoid contraction) or in a mixture made up of 90 parts of 70% alcohol, 8 parts of glycerin, and 2 parts of acetic acid (after fixing with neutralized formalin); but these different processes are rather laborious, as they require the preparation of a cavity slide, perfect sealing, and in the end the results obtained are no better than those with Faure's and polyvinyl lactophenol. The same may be said for Canada balsam, or different resins, which are complex to use and require too much time, because of the need to carry out a series of progressive dehydrations.

CULTURING.

Many authors, including us, have tried to culture tardigrades, but these attempts have ended unsatisfactorily. The major difficulty resides in the impossibility of raising the animals in their natural environment (i.e., in moss, sand, sediment, soil, etc.), for the simple reason that the tardigrades quickly disappear and cannot be found by eye, inside the tangle of the leaflets and stems of the moss, or among the heap of mineral or plant detritus, or algae, etc., in the other habitats. In addition, culturing in different artificial environments leads to unfavorable conditions, to which the failures up to the present time must probably be attributed.

For moss and freshwater tardigrades, attempts have been made at culturing them in belljars containing a little water and a stalk of moss the tardigrade came from, or of algae or aquatic macrophytes, etc., in other habitats. To prevent evaporation, the belljars may be placed in a basin in which there is another receptacle containing water, and covering it with a glass top, but not completely, to permit adequate aeration.

It is advisable to place a certain amount of detritus at the bottom of the belljars (or in a petri dish) so as to allow the tardigrades more freedom of movement, without compromising visibility, or else the bottom may be covered with a slightly rough varnish, or gelatins of different kinds. When beginning to culture tardigrades, it is better to use the water squeezed out of the moss in which they lived, after having made sure there are no other animals present. Subsequently, ordinary water, or better (?) rainwater may be used, changing it every day, to avoid excessive saline concentration, due to evaporation. A fairly low temperature seems most favorable, between 3° and 10°C.

However, the environmental conditions in culturing are too different from those existing in nature to provide any really positive results: and what is more, if one manages to keep a certain percentage of tardigrades alive for a few weeks, months or even more than 16 months (*M. harmsworthi*), one cannot prevent the more or less swift death of the young, after the eggs have hatched, probably due to the insufficient number of leaflets placed in the water, compared with those in the moss of origin, or to other causes, which evade us completely.

Attempts made by various authors and the writers to culture the tardigrades on agar and the like, using algae as food (of the genus *Chlorella*) in addition to the usual leaflets of moss, have been negative, due to the excessive development of the algae which in no time obstructed visibility.

It must not be forgotten, that in nature mosses go through alternate periods of wetness and desiccation and are subject to the influence of sun, rain, and wind, conditions which are probably all of great importance in the development of tardigrades and cannot easily be reproduced in culture conditions. The groups being cultured, artificially, are also continually being disturbed by the continual removal of specimens necessary in the changing of water and leaves, to their study, etc.

In conclusion, it is, of course, still worthwhile to go on with culturing experiments, trying new methods, but the problem is certainly neither easily nor rapidly solved especially for armored tardigrades. Until a few years ago success in witnessing the eggs being laid and hatching was limited to naked tardigrades, but it was possible to keep the young alive until they in turn laid their eggs.

It is only recently that certain authors have found a way of culturing tardigrades over long periods of time. Baumann (1961) for one, cultured *H. convergens* for a few months in small crucibles, containing a variety of algae *Chlorella pyrenoidosa*, which has the characteristic of developing like a carpet at the bottom of the container, instead of floating in the water. These algae were originally gathered from moss on a tree trunk.

Baumann, again (1964), was able to culture *Milnesium tardigradum* for three months, using a culture medium, in petri dishes, composed of the following: a plant nutrient solution (as prescribed by Kolkwitz) 1 cm deep, *Chlorella pyrenoidosa*, a small piece ($4mm^3$) of *Brassica rapa*, rotifers as a supplementary food, and a control of the presence of a sufficient quantity of bacteria.

Ammerman (1962, 1967) managed to raise *H. dujardini* successfully for more than six years, using as a substrate a mixture of sessile algae of the order Chlorococcales (probably the genus *Chlorella*); as a culture liquid he used a diluted soil decoction (as prescribed by Hammerling). Higgins (personal communication) was also able to culture Eutardigrada, feeding them on nematodes.

As far as we are concerned, we have not yet succeeded in culturing "armored" (Echiniscidae) tardigrades, which no doubt have more environmental requirements, unfortunately unknown to us.

Perhaps it might be promising to culture armored tardigrades on lichens, especially the foliose type, by using pieces of the same lichen on which the specimens were found. Small crucibles could be used in the open and in a similar environment -- in light and temperature -- to the place they were found. It would be necessary to reproduce artificially the moisture and drying conditions existing in nature, studying the most suitable alternation of these.

This type of culturing was attempted by Ramazzotti and, although it gave no really satisfactory results, did however allow him to keep *Echiniscus* alive longer than under belljars with moss leaves, allowing access then to some hope.

IV.

SYSTEMATICS OF THE TARDIGRADA

POSITION OF THE TARDIGRADA IN ZOOLOGICAL SYSTEMATICS.

Tardigrades, starting from Voigt (1843) who took them to be Infusoria, have in the past been though, at different times, to resemble gastrotrichs, rotifers, nematodes, annelids, Onychophora, Linguatulida, arthropods (and among these acarina, crustaceans, insect larvae).

Even today, in many zoological treatises, they are classified among arthropods and are included in the heterogeneous group of Malacopods, which includes animals with primitive characteristics (classes Onychophora, Tardigrada, and Linguatulida).

According to Cuénot (1932) tardigrades "logically fit in between the aquatic para-arthropodic branch (now no more, but which is continued in the Onychophora, adapted to terrestrial life) and the aquatic pro-arthropodic branch, from which the real arthropods derive, with striated muscle and articulated appendages, like arachnids, crustaceans, insects and so on."

Marcus (1936) thinks that tardigrades belong to the articulated Protostomia (Annelida + Arthropoda) and to Arthropoda more specifically, where they should be classified among Protracheata (Onychophora) and Eutracheata (Myriapoda + Hexapoda).

The more modern tendency, which we have adopted here, as it seems very logical, is to call the tardigrade a Phylum on its own, separate even from the Phylum Onycophora which differ from tardigrades in many ways, among which for instance are the presence of mandibles, trachea, a circular musculature, cilia in the gonoducts, the absence of molting, etc.

Tardigrades are probably very close to the Onychophora and should be fitted into general zoological systematics between Myriapoda and Onychophora. In as much as they share characteristics with annelids and especially the arthropods (locomotor appendages with terminal claws, absence of cilia, malpighian tubules, and nervous system perhaps a similar type, etc.) the many and considerable differences justify the opinion that they are not considered to be arthropods (unarticulated appendages, smooth instead of striated muscle, no mandibles, etc.).

In their recent work, J. H. Crowe and collaborators (1970), examining the cuticle and its sections of *E. viridis*, both with normal and scanning electron microscope, observed that the dorsal cuticle has different structure from the ventral. In fact, the dorsal cuticle is composed of two distinct laminated layers, each provided with small canals similar to the pore canals of the Insecta. The ventral cuticle is instead composed of a striped layer, of an electron transparent layer traversed by dense small rods, and of a basal fiber layer.

Since the above described structure of the ventral cuticle is similar to that -- very characteristic -- of some Nematoda, the authors tend toward a phylogenetic affinity of the Tardigrada with Nematoda (which have also analogous pharynx structure) and with other members of the group of Aschelminthes.

SYSTEMATIC SUBDIVISION OF THE PHYLUM TARDIGRADA.

After the publication of the previous edition of this "Phylum Tardigrada", work of different authors (and also of our own) proposed different systematic innovations, which restored the old classification (Marcus, Thulin) somewhat surpassed. There were described some new genera (especially marine), other old genera were subdivided, subgenera were elevated to the rank of genera, and innovations were proposed also to taxonomic levels above genus. Therefore we have deemed now, for this edition, a considerably different classification from that of the previous edition, to conform with the prevalent opinion today among the specialists.

In order to conserve a certain continuity, we begin with an account of the classification given in the previous editions (1962, 1972), repeating also some observations (in these observations, reported here fully, the first person singular naturally refers to Ramazzotti):

"It is not my intention to search thoroughly here the study of the systematics of the Tardigrada: I can not however hold back my opinion that -- even leaving out the marine tardigrades, for whose condition is, as said, still very fluid -- it will be sooner or later necessary to originate a systematic reorganization of the species. There are in fact at present numerous species -- or subspecies, or varieties -- of uncertain determination (for example the species of *Hypsibius* with gibbosities of the *H.* (*I.*) *tuberculatus* group, those of the *H.* (*H.*) *pallidus-microps* group, or *H.* (*D.*) *scoticus-arduifrons-prorsirostris*, etc.); some species show a great variability in their morphology, or exhibit the limits between one and another (for example those of the *E.* (*E.*) *blumi-E.* (*E.*) *canadensis* series, those of the *E.* (*E.*) *spitsbergensis* group, many species of *Pseudechiniscus*, etc.).

Also Mihelčič (*in litt.*, 1961) is of my same opinion and our views can be therefore summarized:

Subdivision of the Phylum Tardigrada

ORDER	SUBORDER	FAMILY	GENUS	SUBGENUS
I HETEROTARDIGRADA Marcus, 1927	1. ARTHROTARDIGRADA Marcus, 1927	1. Halechiniscidae Puglia, 1959	1. *Halechiniscus*	—
			2. *Pleocola*	—
			3. *Actinarctus*	—
			4. *Echinursellus*	—
			5. *Tetrakentron*	—
			6. *Styraconyx*	—
			7. *Bathyechiniscus*	—
			8. *Florarctus*	—
			9. *Tanarctus*	—
		2. Batillipedidae Ramazzotti, 1962	1. *Batillipes*	—
			2. *Orzeliscus*	—
		3. Stygarctidae Schulz, 1951	1. *Stygarctus*	—
			2. *Parastygarctus*	—
	2. ECHINISCOIDEA Marcus, 1927	1. Oreellidae Puglia, 1959	1. *Oreella*	—
			2. *Echiniscoides*	—
			3. *Archechiniscus*	—
		2. Echiniscidae Thulin, 1928	1. *Echiniscus*	1. *Echiniscus*
				2. *Bryochoerus*
				3. *Bryodelphax*
				4. *Hypechiniscus*
			2. *Parechiniscus*	—
			3. *Pseudechiniscus*	—
			4. *Mopsechiniscus*	—
II MESOTARDIGRADA Rahm, 1937		1. Thermozodiidae Rahm, 1937	1. *Thermozodium*	—
III EUTARDIGRADA Marcus, 1927		1. Macrobiotidae Thulin, 1928	1. *Macrobiotus*	—
			2. *Haplomacrobiotus*	—
			3. *Hypsibius*	1. *Hypsibius*
				2. *Calohypsibius*
				3. *Isohypsibius*
				4. *Diphascon*
			4. *Itaquascon*	—
			5. *Hexapodibius*	—
		1. Milnesiidae Ramazzotti, 1962	1. *Milnesium*	—

1) a general revision is necessary, and particularly for the genus *Hypsibius*, in which perhaps should be elevated to the rank of genera the subgenera *Hypsibius*, *Calohypsibius*, *Isohypsibius*, and *Diphascon*;
2) it is then advisable to enlarge the diagnosis for the new genera formed, and especially for the species;
3) in the "*tuberculatus* group" the number and shape of the gibbosities and of the tubercles are less important than their position and their development (from young to adult);
4) the differences should be better explained between species and "ecological races" (as for example for *H.* (*I.*) *tuberculatus-franzi-nodosus*, etc., but not only for these species).

"However being in large part in agreement with Mihelčič -- while recognizing however the difficult matter of a revision of this genus -- it seems to me that our knowledge is still too incomplete for so extensive a reform of the systematics of the Tardigrada; I think that we should proceed by degrees and that only with time we may reach a more satisfactory scheme, more simple and -- above all -- less artificial.

"Moreover -- unlike Mihelčič -- I am not personally of the opinion to elevate to rank of genera the subgenera *Hypsibius* and *Isohypsibius* (on account of the frequent difficulty dealing with distinguishing between them), while it seems to me more logical to elevate to genus the subgenus *Diphascon*, which has very particular characteristics. However, in this volume, I have preferred to still consider *Diphascon* as subgenus, in expectation of a more expanded and logical reform of the systematics."

A new classification, based on an interesting phylogenetic hypothesis, was proposed by Pilato (1969), regarding the Eutardigrada:

ORDER	FAMILY	SUBFAMILY	GENUS
EUTARDIGRADA	Macrobiotidae		*Macrobiotus* *Pseudodiphascon*
	Calohypsibiidae		*Haplomacrobiotus* *Parhexapodibius* *Hexapodibius* *Calohypsibius*
	Hypsibiidae	Hypsibiinae	*Isohypsibius* *Doryphoribius* *Hypsibius*
		Diphasconinae	*Diphascon* *Itaquascon*
	Milnesiidae		*Milnesium*

More recently, Schuster *et al.* (1980) has proposed a revision of the systematics of the Eutardigrada, somewhat radical, according to the following scheme:

CLASS	ORDER	FAMILY	GENUS
Eutardigrada	Parachela	Macrobiotidae	*Macrobiotus*
			Pseudodiphascon
			Dactylobiotus
			Minibiotus
			Haplomacrobiotus
			Parhexapodibius
			Hexapodibius
			Doryphoribius
		Hypsibiidae	*Pseudobiotus*
			Calohypsibius
			Isohypsibius
			Hypsibius
			Diphascon
			Itaquascon
			Necopinatum
	Apochela	Milnesiidae	*Milnesium*
			Limmenius

The principle innovation of this classification, consisting of the differentiation of the families Macrobiotidae and Hypsibiidae, no longer based on the sequence of the branches of the claws, rather based on the presence or absence of the reinforcement bar of the buccal tube.

For the systematics we now consider in this work, we have based it on the following criteria:

1. We think acceptable the proposal of Schuster *et al.* to elevate to rank of class the orders Heterotardigrada, Mesotardigrada, and Eutardigrada.
2. To keep, for the Heterotardigrada, the two orders (previously suborders) Arthrotardigrada and Echiniscoidea.
3. To accept, for the Eutardigrada, the two orders proposed by Schuster *et al.*: Parachela and Apochela. (We are not very convinced of the appropriateness of this subdivision, but having it formally proposed, we do not see any valid reason for rejection.)
4. For the Arthrotardigrada, we accept all the families (and subfamilies) proposed by the various authors.
5. With regard to the Eutardigrada, we subscribe in principle to the proposal of Pilato. However provisionally (in expectation that further observations will make clear the systematic position) we think to insert the

genus *Necopinatum*, in a new family Necopinatidae.

6. We do not in any way comply with the proposal of Schuster *et al.*, to distinguish Macrobiotidae and Hypsibiidae based on the support bar of the buccal tube, disregarding the characters of the claws: such systematics seems to us absolutely artificial, and so makes worse and not whatsoever reduce taxonomic confusion.

7. We accept all the genera so far proposed by the various authors, excluding only *Minibiotus* Schuster *et al.*, for the reasons that we shall state, in the systematic section, with regard to *Macrobiotus intermedius*.

8. We think timely to elevate to rank of genera all the subgenera so far proposed, as has by now become practice on the part of numerous authors.

9. We think timely (as already suggested by Schuster, and as proposed by Maucci, 1981) to unite, under the name *Hexapodibius*, the two genera *Hexapodibius* and *Parahexapodibius*.

In conclusion, the classification presented here comes to be that stated in the following table:

Class Heterotardigrada

ORDER	FAMILY	SUBFAMILY	GENUS
Arthrotardigrada	Coronarctidae		*Coronarctus*
	Halechiniscidae	Halechiniscinae	*Halechiniscus*
			Pleocola
			Euclavarctus
			Echinursellus
			Tetrakentron
			Styraconyx
			Bathyechiniscus
			Florarctus
			Angursa
			Orzeliscus
		Tanarctinae	*Actinarctus*
			Tanarctus
	Batillipedidae		*Batillipes*
	Stygarctidae		*Stygarctus*
			Mesostygarctus
			Parastygarctus
			Megastigarctides
	Archechiniscidae		*Archechiniscus*

Echiniscoidea	Oreellidae	*Echiniscoides* *Oreella* *Anisonyches* *Carphania*
	Echiniscidae	*Echiniscus* *Bryochoerus* *Bryodelphax* *Hypechiniscus* *Parechiniscus* *Pseudechiniscus* *Cornechiniscus* *Mopsechiniscus*

Class Mesotardigrada

ORDER	FAMILY	GENUS
Thermozodia	Thermozodiidae	*Thermozodium*

Class Eutardigrada

ORDER	FAMILY	GENUS
Parachela	Macrobiotidae	*Macrobiotus* *Pseudodiphascon* *Dactylobiotus* *Adorybiotus* *Haplomacrobiotus*
	Calohypsibiidae	*Calohypsibius* *Hexapodibius* *Microhypsibius* *Eohypsibius*
	Hypsibiidae	*Hypsibius* *Doryphoribius* *Isohypsibius* *Pseudobiotus* *Itaquascon* *Diphascon*
	Amphibolidae	*Amphibolus*
	Necopinatidae	*Necopinatum*
Apochela	Milnesiidae	*Milnesium* *Limmenius*

FOSSIL TARDIGRADA.

Kenneth W. Cooper, in his 1964 publication, recorded finding a fossil tardigrade (in Canadian amber from Cretaceous) about 300μ long, looking very much like a *Hypsibius*. Cooper created the new genus *Beorn* for it (and the species *leggi*), because of a spine on the first pair of legs and the fact that the longest main branch on the claws belongs to the internal double claw, and not the external one, as occurs in *Hypsibius*; also *Beorn* has "telescopic" legs.

In the same amber, he also saw another specimen, belonging to Heterotardigrada (perhaps Echiniscidae), but which was not identifiable, due to its poor state of preservation.

Durante and Maucci (1972) cited two fossil eggs of *Macrobiotus hufelandi*, found in Quaternary travertine, in which the presence of pollen of *Tsuga pattoniana*, indicated a pre-Rissian age. [Editor's note: Riss is a European glacial period.]

SYSTEMATICS OF THE TARDIGRADA.

I. Class HETEROTARDIGRADA Marcus, 1927

Cephalic appendages -- lateral cirri A included -- present; no separate placoids in pharynx distinct from one another, but with pharyngeal stripes (continuous cuticular bands, which are uninterrupted).

1. Order ARTHROTARDIGRADA Marcus, 1927

Median cirri usually present, rarely absent; extremities of the legs digitate; or not digitate, but in such cases the claws fixed directly onto ends of legs and not on papillae.

1) Family Coronarctidae Renaud-Mornant, 1974

Marine tardigrades, with median cephalic cirri, claws with basal spurs; not armored.

1. Genus *Coronarctus* Renaud-Mornant, 1974

Same characteristics as for the family.
Genus type: *C. tenellus* Renaud-Mornant, 1974
1 species: *tenellus*.

2) Family Halechiniscidae Ramazzotti, 1962

Marine tardigrades; legs with 4 digits, each terminated with a claw or with an enlargement in the shape of a peg.
Genus type: *Halechiniscus* Richters, 1908

a) Subfamily Halechiniscinae Renaud-Mornant, 1980

Genus type: *Halechiniscus* Richters, 1908

1. Genus *Halechiniscus* Richters, 1908

Each leg with 4 digits ending in 1 simple claw, without spurs; median cirri present, clava highly developed.
Genus type: *Hal. guiteli* Richters, 1908
7 species: *greveni*, *guiteli*, *intermedius*, *perfectus*, *remanei*, *subterraneus*, *tuleari*.

2. Genus *Pleocola* Cantacuzene, 1951

Digits with simple claws, without spurs; median cirri is 1 short bristle; 2 dorsal cirri, near the caudal end.
Type species: *Pl. limnoriae* Cantacuzene, 1951
2 species: *conifera*, *limnoriae*

3. Genus *Euclavarctus* Renaud-Mornant, 1975

Cephalic cirri composed of a cirriform in a funnel, a basal sheath, a large principal part, and a slender distal part; two pair of clava, claws lacking spurs.
Type species: *Eu. thieli* Renaud-Mornant, 1975
1 species: *thieli*

4. Genus *Echinursellus* Iharos, 1968

Freshwater. Tubular processes and spines present laterally, dorsally and ventrally.
Type species: *Echin. longiunguis* Iharos, 1968
1 species: *longiunguis*

5. Genus *Tetrakentron* Cuénot, 1893

Digits end in 1 claw with 2 spurs: animal flattened dorsoventrally; cephalic appendages short, including median cirri, which is short spine.
Type species: *Tetr. synaptae* Cuénot, 1893
1 species: *synaptae*

6. Genus *Styraconyx* Thulin, 1942

Digits end in claws with 2 spurs, median cirri short and thin, clava present or absent.
Type species: *Sty. haploceros* Thulin, 1942
4 species: *hallasi*, *haploceros*, *paulae*, *sargassii*.

7. Genus *Bathyechiniscus* Steiner, 1926

Digits end in claws with 2 spurs, median cirri long.
Type species: *Bath. tetronyx* Steiner, 1926
1 species: *tetronyx*

8. Genus *Florarctus* Delam. Debout. & Renaud-Mornant, 1965

Large wing-shaped lobate, lateral and posterior expansions, more or less covering legs; legs have 4 digits with bifid claws.
Type species: *Fl. heimi* Delam. Debout. & Renaud- Mornant, 1965
5 species: *antillensis*, *cinctus*, *heimi*, *hulingsi*, *salvati*

9. Genus *Angursa* Pollock, 1979

Body slender; legs digitate, with four digits and terminated with two bent points.
Type species: *Ang. bicuspis* Pollock, 1979
1 species: *bicuspis*

10. Genus *Orzeliscus* Du Bois-Reymond Marcus, 1952

Legs with 4 equal peg-shaped digits.
Type species: *Orz. belopus* Du Bois-Reymond Marcus, 1952
2 species: *belopus*, *septentrionalis*

b) Subfamily Tanarctinae Renaud-Mornant, 1980

Type Genus: *Tanarctus* Renaud-Debyser, 1959

1. Genus *Actinarctus* Schulz, 1935

Digits with simple claws, without spurs; gelatinous external membrane, in which lateral and dorsal tubular processes immersed; long internal median cirri, linked to base of membrane, median cirri present.
Type species: *Act. doryphorus* Schulz, 1935
2 species: *doryphorus*, *lyrophorus*

2. Genus *Tanarctus* Renaud-Debyser, 1959

Extremely long clava and extremely long caudal filaments; legs digitate.
Type species: *Tan. tauricus* Renaud-Debyser, 1959
7 species: *arborspinosus*, *gracilis*, *dendriticus*, *heterodactylus*, *ramazzottii*, *tauricus*, *velatus*

3) Family Batillipedidae Ramazzotti, 1962

Legs end in 6 digits of equal or differing lengths, each digit expanded distally into adhesive disk; actual, proper claws never present.
Type genus: *Batillipes* Richters, 1909

1. Genus *Batillipes* Richters, 1909

Legs with 6 digits sometimes reduced or missing; distal ends of digits expanded and variously shaped as spoon-like or ball-shaped.
Type species: *B. mirus* Richters, 1909
16 species: *acaudatus*, *adriaticus*, *annulatus*, *bullocaudatus*, *camonensis*, *dicrocercus*, *fraufi*, *gilmartini*, *mirus*, *noerrevangi*, *pennaki*, *phreaticus*, *littoralis*, *roscoffensis*, *similis*, *tubernatis*

4) Family Stygarctidae Schulz, 1951

Legs without digits but with claws fixed directly onto legs and not onto tiny papillae. Dorsum armored with plates.

1. Genus *Stygarctus* Schulz, 1951

Median cirri present; cephalic papillae well developed and curved; 4 claws without spurs, the two internal with a long filament.
Type species: *Styg. bradypus* Schulz, 1951

3 species: *abornatus*, *bradypus*, *granulatus*

2. Genus *Mesostygarctus* Renaud-Mornant, 1979

There exists a cephalic plate, composed of two parts, three plates on the trunk and a caudal plate without posterior expansion; anterior clava rudimentary; legs with 4 claws, without bristle, the internal two with distal spurs.
Type species: *Mes. intermedius* Renaud-Mornant, 1979
1 species: *intermedius*

3. Genus *Parastygarctus* Renaud-Mornant, 1965

Head is subdivided transversely into 2 parts: anterior part with buccal cirri, posterior part with 4 marginal expansions, bearing other cephalic appendages.
Type species: *Par. higginsi* Renaud-Debyser, 1965
2 species: *higginsi*, *sterreri*

4. Genus *Pseudostygarctus* McKirdi, Schmidt & McGinty- Bayli, 1976

Cephalic plate, three dorsal plates and a terminal plate furnished with caudal spiniform processes; anterior clava semiglobular; all the legs with three claws, supplied with accessory points.
Type species: *Pseud. triungulatus* McKirdi *et al.*, 1976
1 species: *triungulatus*

5. Genus *Megastygarctus* KcKirdi, Schmidt & McGinty- Bayli, 1976

Between the dorsal plates is inserted accessory plates arising from folds of the dorsal cuticle. The first three pair of legs bear 4 claws, the fourth pair only 2.
Type species: *Meg. orbicularis* McKirdi *et al.*, 1976
1 species: *orbicularis*

5) Family Archechiniscidae Binda, 1978

Without armor; median cirri absent; legs provided with only two digits, bearing claws.
Type genus: *Archechiniscus* Schulz, 1953

1. Genus *Archechiniscus* Schulz, 1953

Characteristics of the family.
Type species: *Arch. marci* Schulz, 1953
1 species: *marci*.

2. Order ECHINISCOIDEA Marcus, 1927

The claws are inserted on minuscule papillae positioned at the end of the legs, which are not digitate; median cirrus absent.

1) Family Echiniscoididae Kristensen & Hallas, 1980.

Marine species, nor armored. Cephalic papillae dome-shaped or indistinct; the cephalic appendices are reduced; cirri A and E similar to each other.
Type genus: *Echiniscoides* Plate, 1889

1. Genus *Echiniscoides* Plate, 1889

Legs with 5-11 claws.
Type Species: *Ech. sigismundi* Plate, 1889
3 species: *hoepneri*, *sigismundi* (with subspp.), *travei*

2. Genus *Anisonyches* Pollock, 1975

Four claws on each leg of the first three pair of legs, three claws on the fourth pair; the claws bear basal spurs.
Type species: *An. diakidius* Pollock, 1975
1 species: *diskidius*

2) Family Oreellidae Ramazzotti, 1962

Cuticle lacking armature.
Type genus: *Oreella* Murray, 1910

1. Genus *Oreella* Murray, 1910

Legs with 4 claws each; a short caudal projection is present.
Type species: *O. mollis* Murray, 1910
3 species: *minor*, *mollis*, *vilucensis*

2. Genus *Carphania* Binda, 1978

Freshwater; two claws on each leg of the first three pair of legs, one the fourth pair; the claws have basal spurs.
Type species: *C. fluviatilis* Binda, 1978
1 species: *fluviatilis*

3) Family Echiniscidae Thulin, 1928

A dorsal armor exists, formed of plates; legs with 4 claws.
Type genus: *Echiniscus* Schultze, 1840

1. Genus *Echiniscus* Schultze, 1840

Armor composed of cephalic plate, scapular plate, first median plate, first paired plate, second median plate, second paired plate, third median plate (which may be lacking), terminal plate.
Type species: *E. testudo* (Doyère, 1840)
116 species: *africanus*, *angolensis*, *apuanus*, *arcangelii*, *arctomys*, *baius*, *baloghi*, *bartramiae*, *becki*, *bigranulatus*, *bisetosus*, *blumi*, *calcaratus*, *calvus*, *canadensis*, *canedoi*, *capillatus*, *carsicus*, *carusoi*, *cavagnaroi*, *cervicornis*, *clavisetosus*, *columinis*, *crassispinosus*, *dearmatus*, *dikenli*, *diploglyptus*, *divergens*, *dreyfusi*, *duboisi*, *egnatiae*, *elegans*, *evelinae*, *filamentosus*, *fischeri*, (?)*glaber*, *granulatus*, *heterospinosus*, *horningi*, *inocellatus*, *insuetus*, *jagodici*, *japonicus*, *kerguelensis*, *knowltoni*, *kofordi*, *lapponicus*, *laterospinosus*, *limai*, *longispinosus*, *loxophthalmus*, *manuelae*, *marinellae*, *markezi*, *mauccii*, *mediantus*, *melanophthalmus*, *menzeli*, *meridionalis*, *merokensis*, *migiurtinus*, *mihelcici*, *militaris*, *molluscorum*, *moniliatus*, *multispinosus*, *murrayi*, *nepalensis*, *nigripustulus*, *nobilis*, *oihonnae*, *osellai*, *pajstunensis*, *perarmatus*, *perviridis*, *phocae*, *pooensis*, *parabrus*, *postojnensis*, *pusae*, *quadrispinosus*,

ramazzottii, ranzii, reticulatus, reymondi, robertsi, rosaliae, rufoviridis, rugospinosus, siegristi, simba, speciosus, spiculifer(?), spiniger, spinuloides, spinulosus, spitsbergensis, storkani, sylvanus, tardus, tenuis, tesselatus, testudo, trisetosus, trojanus, tympanista, velaminis, zetotrymus, virginicus, viridis, viridissimus, weisseri, wendti, vinculus.

2. Genus *Bryochoerus* Marcus, 1936

Median plates 1, 2, 3 divided transversely, so that total of 6 median plates visible.
Type species: *B. intermedius* Marcus, 1936
1 species: *intermedius.*

3. Genus *Bryodelphax* Thulin, 1928

The median plates 1 and 2 are divided, not 3, so that there are visible in total 5 median plates; lacking the notches on the terminal plate.
Type species: *B. parvulus* Thulin, 1928
7 species: *alzirae, amphoterus, ortholineatus, parvulus, sinensis, tatrensis, weglarskae.*

4. Genus *Hypechiniscus* Thulin, 1928

There are visible inclusively 5 median plates; there exists the notches on the terminal plate.
Type species: *Hyp. gladiator* (Murray, 1905)
2 species: *gladiator, papillifer.*

5. Genus *Parechiniscus* Cuénot, 1926

The plates are not well defined in the rostral part of the dorsum, better defined in the caudal part.
Type species: *Par. chitonides* Cuénot, 1926
2 species: *armadilloides, chitonides.*

6. Genus *Pseudechiniscus* Thulin, 1911

After the second paired plate, or after the third median plate if present, follows a pseudosegmental plate, paired or unpaired, and then the terminal plate; buccal cirri present; cirri A of filament shape.
Type species: *Pseud. suillus* (Ehrenberg, 1853)
25 species: *bartkei, bidenticulatus, bispinosus, clavatus, conifer, dicrani, distinctus, goedeni, hannae, islandicus, jiroveci, juanitae, lateromammillatus, megacephalus, novaezeelandiae, occultus, pseudoconifer, pulcher, quadrilobatus, ramazzottii, raneyi, scorteccii, suillus, transylvanicus, victor.*

7. Genus *Cornechiniscus* Maucci and Ramazzotti, 1981

The plates are as in *Pseudechiniscus*; cirri A of conical shape, wide at the base, curved, internally hollow, with "saber blade" appearance.
Type species: *Corn. cornutus* (Richters, 1906)
7 species: *ceratophorus, cornutus, holmeni, lobatus, schrammi, subcornutus, tibetanus.*

8. Genus *Mopsechiniscus* Du Bois-Reymond Marcus, 1944

The plates are as in *Pseudechiniscus*; the internal and external buccal cirri are absent.
Type species: *Mops. imberbis* (Richters, 1907)
2 species: *granulosus*, *imberbis*.

II. Class MESOTARDIGRADA Rahm, 1937

Pharynx with placoids; claws similar to each other, not differentiated into principal branch and secondary branch; cirri A present.

1. Order THERMOZODIA nov. ord.

The characteristics are those of the class.

1) Family Thermozodiidae Rahm, 1937

The characteristics are those of the class.

1. Genus *Thermozodium* Rahm, 1937

Type species: *Th. esakii* Rahm, 1937
1 species: *esakii*.

III. Class EUTARDIGRADA Marcus, 1927

Lacking the cephalic appendices and therefore also cirri A; not armored; doubleclaws differentiated into a principal claw and a secondary.

1. Order PARACHELA Schuster, Nelson, Grigarick, & Christenberry, 1980

Lacking cephalic papillae; the principal branch and the secondary of the claws are united to form a doubleclaw.

1. Family Macrobiotidae Thulin, 1928

The two doubleclaws of each leg are approximately of equal size, similar to each other and symmetrical with respect to the median plane of the same leg (sequence 2112).
Type genus: *Macrobiotus* Schultze, 1834

1. Genus *Macrobiotus* Schultze, 1834

The buccal tube is rigid all of its length and there is a reinforcement bar; lunule present, at least on the fourth pair of legs; claws "*hufelandi* type" or "*echinogenitus* type" (see page 41).
Type species: *M. hufelandi* Schultze, 1834
92 species: *acontiscus*, *aculeatus*, *adelges*, *allani*, *andersoni*, *annae*, *areolatus*, *arguei*, *ariekammensis*, *artipharyngis*, *ascensionis*, *australis*, *aviglianae*, *beotiae*, *bisoctus*, *brevipes*, *carsicus*, *crassidens*, *csotiensis*, *chieregoi*, *dentatus*, *dianae*, *echinogenitus*, *evelinae*, *furcatus*, *furciger*, *gemmatus*, *granatai*, *gildae*, *grandis*, *harmsworthi*, *hastatus*, *hibernicus*, *hibiscus*, *hufelandi*, *hufelandioides*,

hystricogenitus, *insignis*, *intermedius*, *islandicus*, *julietae*, *kolleri*, *komareki*, *lissostomus*, *liviae*, *longipes*, *mahunkai*, *marcusi*, *mauccii*, *meridionalis*, *montanus*, *nocentinii*, *norvegicus*, *nuragicus*, *occidentalis*, *orcadensis*, *ovidii*, *ovovillosus*, *pallarii*, *papillosus*, *persimilis*, *polaris*, *polyopus*, *porteri*, *potockii*, *primitivae*, *psephus*, *pseudohufelandi*, *pseudofurcatus*, *pullari*, *pustulatus*, *rawsoni*, *recens*, *richtersi*, *rollei*(?), *rubens*, *santorois*, *spallanzanii*, *spectabilis*, *spertii*, *stellaris*, *striatus*, *subintermedius*, *subjulietae*, *submorulatus*, *tenuis*, *terricola*, *tonollii*, *topali*, *virgatus*, *wauensis*, *willardi*.

2. Genus *Pseudodiphascon* Ramazzotti, 1964

Buccal tube flexible and undulating.
Type species: *Ps. inflexus* (Arcidiacono, 1964)
3 species: *bindae*, *diphasconoide*, *inflexum*.

3. Genus *Dactylobiotus* Schuster, Nelson, Grigarick, Christenberry, 1980

Claws very large, with principal branch strongly curved, and secondary branch inserted very near to the base, short or extremely short; the base of the claws are structurally connected to each other; lunule absent. Freshwater species.
Type species: *Dact. grandipes* (Schuster, Toftner & Grigarick, 1977)
6 species: *ambiguus*, *ampullaceus*, *dispar*, *grandipes*, *haplonyx*, *macronyx*(?).

4. Genus *Adorybiotus* Maucci and Ramazzotti, 1981

The buccal tube has, dorsally and ventrally, laminae of muscle insertion, unpaired, with undulating border, of which the ventral may or may not be united to the median tube reinforcement bar; lunule large, strongly dentate.
Type species: *Ad. granulatus* (Richters, 1903)
2 species: *coronifer*, *granulatus*.

5. Genus *Haplomacrobiotus* May, 1948

The secondary branch of the claws is absent on the first three pair of legs, and is extremely reduced (spur) on the fourth pair.
Type species: *Hapl. hermosillensis* May, 1948
1 species: *hermosillensis*.

2) Family Calohypsibiidae Pilato, 1969

Sequence of the claws 2121. Principal branch and secondary branch rigidly connected.
Type genus: *Calohypsibius* Thulin, 1928

1. Genus *Calohypsibius* Thulin, 1928

Buccal tube lacking reinforcement bar; the claws of all the legs have approximately equal size; sculptured cuticle with spines and plates.
Type species: *Cal. ornatus* (Richters, 1900)
3 species: *ornatus*, *placophorus*, *verrucosus*.

2. Genus *Microhypsibius* Thulin, 1928

Claws like *Calohypsibius*; reinforcement bar present or absent; cuticle smooth.

Type species: *Micr. truncatus* Thulin, 1928

3 species: *bertolanii*, *minimus*, *truncatus*.

3. Genus *Hexapodibius* Pilato, 1969, Maucci, 1981, amend.

Buccal tube with reinforcement bar; claws like *Calohypsibius*; the fourth pair of legs, or the claws of them, reduced or even absent.

Type species: *Hex. micronyx* Pilato, 1969

6 species: *castrii*, *lagrecai*, *micronyx*, *pilatoi*, *pseudomicronyx*, *xerophilus*.

4. Genus *Eohypsibius* Kristensen, 1981

Buccal tube composed of a rigid and a flexible part with spiral structure; peribuccal lamellae present; claws like *Calohypsibius*; lunule present.

Type species: *Eo. nadiae* Kristensen, 1981

1 species: *nadiae*.

3) Family Amphibolidae Bertolani, 1981

The claws are composed of three clearly distinct part.

Type genus: *Amphibolus* Bertolani, 1981

3 species: *smreczinskii*, *volubilis*, *weglarskae*.

4) Family Hypsibiidae Pilato, 1969

The two doubleclaws of each leg are asymmetrically arranged with respect to the median plane of the same leg (sequence 2121).

Type genus: *Hypsibius* Thulin, 1928

1. Genus *Hypsibius* Thulin, 1928

The claws of each leg are more or less different from each other; the basal branch + secondary branch form a rounded curve, as a sickle, on which is inserted the secondary branch, with flexible junction; lunule always absent; mouth without lamellae, buccal tube rigid, with appendices of muscle insertion of hook shape; reinforcement bar absent.

Type species: *H. oberhaeuseri* (Doyère, 1840)

28 species: *allisoni*, *anomalus*, *antarcticus*, *arcticus*, *baumanni*, *biscuitiformis*, *calcaratus*, *camelopardalis*, *cataphractus*, *conifer*, *convergens*, *dujardini*, *furmanni*(?), *giusepperamazzottii*, *hypostomus*, *iharosi*, *janetscheki*, *klebelsgergi*, *maculatus*, *microps*, *novemcinctus*(?), *oberhaeuseri*, *pallidus*, *runae*, *scabropygus*, *simoizumii*, *thulini*(?), *zetlandicus*.

2. Genus *Isohypsibius* Thulin, 1928

Buccal tube rigid, without reinforcement bar; the basal branch + secondary branch of the doubleclaws is strongly turned so as to form almost a right angle, at the vertex of which is inserted, with flexible attachment, the principal branch; the appendices of muscle insertion of the stylets are crest shaped.

Type species: *I. prosostomus* Thulin, 1928
85 species: *alicatai*, *annulatus*, *appelloefi*, *asper*, *austriacus*, *bakonyiensis*, *baldii*, *bartosi*, *basalovoi*, *belliformis*, *bellus*, *brevispinosus*, *brulloi*, *bulbifer*, *cameruni*, *canadensis*, *costatus*, *cyrilli*, *deconincki*, *deflexus*, *dudichi*, *duranteae*, *effusus*, *elegans*, *epleynensis*, *flavus*, *franzi*, *fuscus*, *glaber*, *geddesi*, *gracilis*, *granulifer*, *gyulai*, *hadzii*, *helenae*, *hypostomoides*, *indicus*, *itoi*, *josephi*, *latiunguis*, *leithaicus*, *lineatus*, *lunulatus*, *macrodactylus*, *mammillosus*, *marcellinoi*, *mihelcici*, *montanus*, *myrops*, *neoundulatus*, *nipponicus*, *nodosus*, *novaeguineae*, *papillifer*, *pappi*, *pauper*, *pilatoi*, *pratensis*, *prosostomus*, *pseudoundulatus*, *pulcher*, *renaudi*, *reticulatus*, *roncisvallei*, *rudescui*, *saltursus*, *saracenus*, *schaudinni*, *sculptus*, *sellnicki*, *septentrionalis*, *silvicola*, *sismicus*, *solidus*, *stenostomus*, *tetradactyloides*, *theresiae*, *torulosus*, *trunconum*, *tuberculatus*, *tuberculoides*, *undulatus*, *vejdovskyi*, *vietnamensis*, *wilsoni*.

3. Genus *Doryphoribius* Pilato, 1969

Buccal tube rigid, with reinforcement bar; claws like *Isohypsibius*.
Type species: *D. doryphorus* (Binda & Pilato, 1969)
6 species: *citrinus*, *doryphorus*, *evelinae*, *pilatoi*, *zappalai*, *zyxiglobus*.

4. Genus *Pseudobiotus* Schuster, Grigarick, Nelson and Christenberry, 1980

Buccal tube rigid, without reinforcement bar, and with muscle insertion as crests; thirty peribuccal lamellae; claws like *Isohypsibius*, very large, those of each leg little different from each other; lunule absent; freshwater species.
Type species: *Ps. augusti* (Murray, 1907)
4 species: *augusti*, *matici*, *megalonyx*, *stephaniae*.

5. Genus *Itaquascon* Barros, 1939

Claws like *Hypsibius*; the buccal tube consists of a rigid part and a flexible of spiral structure; pharynx without placoids, which are substituted for by cuticular thickenings, not interrupted.
Type species: *It. umbellinae* Barros, 1939
9 species: *bartosi*, *enckelli*, *pawlowskii*, *placophorum*, *ramazzottii*, *simplex*(?), *tamaensis*, *trinacriae*, *umbellinae*.

6. Genus *Diphascon* Plate, 1889

Claws *Hypsibius* type; buccal tube divided into a rigid part and a flexible part of spiral structure; in the pharynx exists placoids.
Type species: *Diph. chilenense* (Plate, 1888)
45 species: *aculeatum*, *affine*, *alpinum*, *angustatum*, *arduifrons*, *belgicae*, *bisbullatum*, *brevipes*, *bullatum*, *carolae*, *chilenense*, *clavatum*, *coniferens*, *conjugens*, *elongatum*, *gerdae*, *granifer*, *halapiense*, *higginsi*, *iltisi*, *itaquasconide*, *latipes*, *marcusi*, *marcuzzii*, *mariae*, *montigenum*, *nobilei*, *nodulosum*, *nonbullatum*, *oculatum*, *ongulense*, *patanei*, *pingue*, *prorsirostre*, *punctatum*, *ramazzottii*, *recamieri*, *rugocaudatum*, *rugosum*, *scoticum*, *speciosum*, *spitzbergense*, *stappersi*, *tenue*, *trachydorsatum*.

3) Family Necopinatidae nov. fam.

Lacking claws of the second, third, and fourth pair of legs; the first pair possesses two sclerified pieces inserted on the median plane of the leg and form forceps, which may be lacking.

1. Genus *Necopinatum* Pilato, 1971

Characters of the family.
Type species: *N. mirabile* Pilato, 1971
1 species: *mirabile*.

2. Order APOCHELA Schuster, Nelson, Grigarick, and Christenberry, 1980

Cephalic papillae present; the principal branch and the secondary branch of the claws are completely divided, the second is bifid or tripartite; pharynx without placoids.

1. Family Milnesiidae Ramazzotti, 1962

Characters of the order.

1. Genus *Milnesium* Doyére, 1840

Six peribuccal papillae are present and six buccal lamellae form an operculum; buccal tube short and wide.
Type species: *Miln. tardigradum* Doyére, 1840
1 species: *tardigradum*.

2. Genus *Limmenius* Horning, Schuster & Grigarick, 1978

Four buccal lamellae; buccal tube composed of a short and wide anterior part and a slender posterior part, very elongated, flexible.
Type species: *L. porcellus* Horning, Schuster & Grigarick, 1978
1 species: *porcellus*.

Total number of species:

The cataloged species are 531 inclusively, thus subdivided (in parentheses we indicate some of the genera richer in species):

Order Arthrotardigrada	60	(*Batillipes*: 116)
Order Echiniscoidea	170	(*Echiniscus*: 116; *Pseudechiniscus*: 25)
Class Mesotardigrada	1	
Class Eutardigrada	300	(*Macrobiotus*: 92; *Hypsibius*: 28; *Isohypsibius*: 85; *Diphascon*: 45)

IDENTIFICATION OF TARDIGRADA AND NOTES ON THE USE OF THE RELATED KEYS.

The identification of tardigrades is not always easy, even for someone who knows them and has been studying them for a long time. This explains the relative complexity of the following keys for certain species, in spite of efforts to obtain maximum clarity and simplicity, by considering, when possible, only the most obvious characteristics.

Until a certain stage of knowledge is reached, so that species can be distinguished from each other at a glance, it would be advisable to start out each identification by consulting the key for genera, which will then allow one to establish what genus the specimen in question belongs to. If one is not dealing with marine tardigrades, the 18 genera of the suborder Arthrotardigrada can be disregarded forthwith, as one is highly unlikely to meet the single freshwater species *Echinursellus longiungus*, found only once in Chile.

At a more advanced stage of study, it will nearly always be superfluous to use the above mentioned key and one can pass straight into the keys for the species in each genus, which leads directly to the species. If the species is exclusively or prevalently "aquatic" the keys indicate this.

Naturally it is essential that one considers the various characteristics of the armor, filamentous or spinous appendices, buccal apparatus, claws, etc., used in systematics. In the first attempts at identification it is therefore necessary to read attentively what has been said on the subject on the preceding pages.

Remember not to establish the competence of a given species on the basis of a single specimen (apart from truly *exceptional* cases and after long practice). One should always examine as many tardigrades as possible, remembering that their morphological characteristics, useful for their identification, often vary considerably and are distributed more or less according to a Gaussian curve. This applies particularly to measurements (i.e., length and diameter of the buccal tube, length of the macroplacoids and of the lateral and dorsal appendices, etc.). One must keep in mind that the dimensions of the buccal apparatus vary at each molt and that its components often vary in their relative sizes, just as the relation between claw and body length changes, and that between placoid row and bulb length, etc. All one needs to do to realize this is to measure a few hundred specimens of the same species and the same population.

It is for this reason that we have not used the two symbols *cph* and *ms* in the keys. These symbols were put forth by Thulin for the comparison of the buccal apparatus and claws of different species and we shall give a brief explanation of their meaning as they are sometimes used by certain authors:

cph: is the percentage of the length of the pharynx (i.e., if the external diameter of the buccal tube is 2μ and the length of the pharynx is 40μ one may say that the diameter of the buccal tube is 5 cph, because 2:40 = 0.05 = 5%)

ms: is the part per thousand of the length of the body (i.e., if the buccal tube is 50μ long and the animal 250μ it may be said that the length of the buccal tube is 200 ms). Analogous for the claws.

Often it is necessary to make permanent preparations in Faure's solution or polyvinyl lactophenol in order to carry out species identification. One has to wait until the tardigrade is transparent enough and to avoid mistakes, do not hurry when undertaking this type of work but decide that a specimen belongs to a particular species only after repeated observation, with intervals of a few days. Sometimes it takes a week or more in the mounting medium to bring out the more delicate details, like the dorsolateral appendices for instance, shaped like small teeth, or the ornamentation on the plates in certain Echiniscidae, or the micro- and macroplacoids in the Eutardigrada, especially if they have been kept in alcohol or formalin for a long period.

One must also always take care to observe the tardigrade in question in a fresh state, inside a drop of water, before making a permanent preparation as mounting media nearly always makes the eyespots disappear and dissolves the rostral part of the stylets. It is therefore necessary to note these important characteristics previously, the first especially.

One can never stress too often that great care should be taken in describing new species, particularly during the initial stages in the study of tardigrades. In addition to longstanding experience and a practiced eye, one may also need abundant material, permitting one to take into account its variability.

We will give one example concerning the latter proposition. In two places far apart (Appennine and Pallanza) and in different years, Ramazzotti collected 4 examples (2 in each place) of an *Echiniscus* with spines on its scapular plate, in a position where appendices are rare, and met within a few rare species, which do however differ from this *Echiniscus* in other characteristics. Under superficial observation, one would not have hesitated to create a new species. Yet this *Echiniscus*, apart from the spines on the scapular plate, showed an absolute conformity with the species *E. merokensis*, present in abundance in the moss in both places, and was to be found only in a very limited number (on average one specimen to every 150 to 200 *E. merokensis*, in Pallanza or the Appennines). This made him think that this animal was derived from *E. merokensis* and not a member of a well defined new species (Ramazzotti, 1958).

It is probable that an analogous case is represented by the species *Echiniscus oihonnae* and *E. multispinosus*, that are differentiated from each other only by the presence, in the second, of the dorsal spines B. Maucci has however observed an abundant population referable to as *E. oihonnae* (northern Norway), in which, among ten of the examples, seven were found that possessed the dorsal appendices B, two of which had B of only one part.

If one does observe bifid appendices in tardigrades, or the absence of appendices on one side, or any peculiarity of this kind, one should not draw any hurried conclusions, but examine several other specimens in the same population. In this way alone can one reach practical certainty (not theoretical) of the consistency of a particular feature.

Lastly, remember that:

1. the sketches, provided further on to illustrate each species, are often somewhat schematic and mainly serve to facilitate recognition; therefore, certain features have at times been exaggerated (length and diameter of the spines or filaments, dimensions of the placoids, or the granules which make up the ornamentation on the cuticle and plates, etc.). The exact dimensions are given in the text, when necessary, but remember that the figures given are approximate in relation to individual variability and the tardigrade's age;

2. when a genus contains one species only, the key for identification of genera refers to the species itself, in addition to the genus;

3. in the keys for identification of species in each genus, we give other information and advice, *which must be taken into account*; the genera and subgenera, for the reader's convenience, are referred to with the following abbreviations (in alphabetical order):

A.	= *Actinarctus*	*Hyp.*	= *Hypechiniscus*
Ad.	= *Adorybiotus*	*H.*	= *Hypsibius*
Am.	= *Amphibolus*	*I.*	= *Isohypsibius*
Ang.	= *Angursa*	*It.*	= *Itaquascon*
Ani.	= *Anisonyches*	*L.*	= *Limmenius*
Arch.	= *Archechiniscus*	*M.*	= *Macrobiotus*
B.	= *Bryodelphax*	*Meg.*	= *Megastygarctides*
Ba.	= *Batillipes*	*Mes.*	= *Mesostygarctus*
Bath.	= *Bathyechiniscus*	*Mi.*	= *Microhypsibius*
Br.	= *Bryochoerus*	*Mil.*	= *Milnesium*
C.	= *Calohypsibius*	*Mops.*	= *Mopsechiniscus*
Car.	= *Carphania*	*N.*	= *Necopinatum*
Co.	= *Cornechiniscus*	*O.*	= *Oreella*
Cor.	= *Coronarctus*	*Orz.*	= *Orzeliscus*
D.	= *Diphascon*	*P.*	= *Pseudechiniscus*
Da.	= *Dactylobiotus*	*Par.*	= *Parechiniscus*
Dor.	= *Doryphoribius*	*Pl.*	= *Pleocola*
E.	= *Echiniscus*	*Psb.*	= *Pseudobiotus*
Ec.	= *Echiniscoides*	*Psd.*	= *Pseudodiphascon*
Ech.	= *Echinursellus*	*Pss.*	= *Pseudostygarctus*
Eo.	= *Eohypsibius*	*Pst.*	= *Parastygarctus*
Eu.	= *Euclavarctus*	*S.*	= *Stygarctus*
F.	= *Florarctus*	*Styr.*	= *Styraconys*
Hal.	= *Halechiniscus*	*T.*	= *Tetrakentron*
Hapl.	= *Haplomacrobiotus*	*Tan.*	= *Tanarctus*
Hex.	= *Hexapodibius*	*Th.*	= *Thermozodium*

4. after having established to which species the tardigrade in question belongs, through the use of the keys, the accuracy of the identification just made should be checked, by reading the description of the species carefully; relevant illustrations may also be of use at times. Note that each species is described in alphabetical order, within the genus, the genera being in turn listed alphabetically, which makes finding them a great deal easier.

The identification keys for each genus are reported at the beginning of that same genus, according to alphabetical order.

KEY FOR THE DETERMINATION OF THE GENERA OF THE PHYLUM TARDIGRADA

Observations.

1. In the use of the key it is naturally indispensable to have good evidence of the various morphological characters used in the subtle systematics; in the first attempts at determination it will therefore be necessary to attentatively reread as much as disclosed in the preceding pages.

2. The first 22 genera of the key are all marine (except the freshwater *Thermozodium*, *Echinursellus*, and *Carphania*).

3. In the distinction of the genera of the Eutardigrada, the fundamental characters are those relating to the buccal apparatus and the locomotion apparatus (legs and claws): it seems premature, actually, to try to give greater relevance to one rather than the other.

4. The distinction between the genera *Hypsibius* and *Isohypsibius* can be sometimes difficult, even to an experienced eye, and can be mistaken.

1. Lateral cirrus A present 2
Lateral cirrus A absent 33

2 (1). Pharynx with distinct placoids, with separation between them . *Thermozodium*
Within the pharynx the placoids are not distinct and separate, but rather a thin bar, namely a continuous cuticle 3

3 (2). Legs digitate 4
Legs not digitate 16

4 (3). Claws absent; last toe with blades or wide, flat disks 5
Claws present 6

5 (4). Expansion of the toe elongated, to form a spatula, longer than wide, 4th toe equal on each leg, 4th pair of legs with papilla with spine-like apex (which may be lacking) but not a spine . . . . *Orzeliscus*
Terminal expansion of the toe is more or less wide, rounded, squarish, or heart-shaped; 4th toe more unequal on each leg; 4th pair of legs with a spine . . . . *Batillipes*

6 (4).	Two toes on each leg; median cirrus absent	*Archechiniscus*
	Four toes on each leg; median cirrus present or absent	7
7 (6).	Lateral and posterior cuticular expansions in the form of wings that border the body	8
	No wing-like expansions around the body	9
8 (7).	Dorsally the cuticle is covered with a gelatinous layer in which there is immersed small tube formations; besides the clava near the lateral cirrus A, is appendix A'	*Actinarctus*
	The dorsal cuticle is smooth, or else with large papillae, but no gelatinous layer; no appendix A'	*Florarctus*
9 (7).	The claw is doubled at the apex into 2 hooked ends, nearly equal in size	*Angursa*
	The claw has a single bent apex with or without spurs	10
10 (9).	Claws with spurs	11
	Claws without spurs	13
11 (10).	Body flattened dorsoventrally; median cirrus present	*Tetrakentron*
	Body not flattened	12
12 (11).	The median claws of each leg bearing 4 points in the shape of teeth	*Bathyechiniscus*
	The median claws with 3 points, that is to say the apex and 2 spurs	*Styraconyx*
13 (10).	Two pairs of clavae; the cephalic cirri are composed of a funnel-shaped cirriphore, a basal sheath, a principal part, and a sharp slender distal part	*Euclavarctus*
	One pair of clava; different cephalic cirri	14
14 (13).	At the base of the 4th pair of legs is an extremely long flexible spine that is widely branched or else bears a membranous expansion	*Tanarctus*
	At the base of the 4th pair of legs is a papilla or a short flexible spine (shorter than the leg	15
15 (14).	Clava much shorter than lateral cirrus A	*Pleocola*
	Clava as long or longer than lateral cirrus A	*Halechiniscus*
16 (3).	Median cirrus present	17
	Median cirrus absent	22

17 (16). Not armored; a single clava per side 18
Armored; 2 clavae per side 19

18 (17). The ventral and dorsal surface is covered with a
gelatinous layer in which there are immersed small
tube-shaped processes; freshwater .... *Echinurselllus*
The body surface without a gelatinous layer .... *Coronarctus*

19 (17). Each leg with 4 claws; anterior clava
shaped like a mallet (cane), erect or folded 19a
Each leg with less than 4 claws, with or
without setae; anterior clava rounded 21

19a (19). The 2 internal claws with a long flexible seta 20
Internal claws without setae .... *Mesostygarctus*

20 (19a). The cephalic plate is nearly twice as wide as long .... *Stygarctus*
The cephalic plate is about 3 times as wide as long .... *Parastygarctus*

21 (19). On each leg are 3 claws without setae; cephalic
plate 2 times wider than long .... *Pseudostygarctus*
On the 4th pair of legs are 2 claws with setae;
the width of the cephalic plate is equal to
the length .... *Megastygarctides*

22 (16). The legs have 5 or more claws; or else the
first pair bears 4 and the last, 3; or else
the first 3 pairs have 2 claws and the
last, 1; not armored 23
All the legs with 4 claws; armored or not 25

23 (22). Each leg with 5 to 11 claws .... *Echiniscoides*
All the legs with less than 5 claws 24

24 (23). The first 3 pairs of legs with 4 claws, the
last pair with 3 claws .... *Anisonyches*
The first 3 pairs of legs with 2 claws, the
last pair with only 1; freshwater .... *Carphania*

25 (22). Not armored .... *Oreella*
Armored 26

26 (25). The armor is not well defined in the rostral
part of the body, it is best in the caudal
part; the terminal plate is distinctly
defined .... *Parechiniscus*

The armor is well developed, divided into distinct plates, and it extends over the entire dorsal surface 27

27 (26). At the 2nd paired plate (II) or at the 3rd median plate (3) there immediately follows a terminal plate 28
At the 2nd paired plate or at the 3rd median plate there follows a pseudosegmental plate, paired or not, and then the terminal plate 31

28 (27). The median plates 1, 2, and 3 are plain, so that there is visible in total 3 median plates (3rd plate may be lacking) . . . . *Echiniscus*
The median plates 1 and 2, and sometimes even the 3rd, are transversely divided, so that there is visible in total 5 or 6 median plates 29

29 (28). The median plates 1, 2, and 3 are divided transversely, so that there is visible in total 6 median plates; without the notching of the terminal plate . . . . *Bryochoerus*
The median plates 1 and 2 are divided, not on contrary the 3rd, which is one; therefore there are 5 median plates visible in total 30

30 (29). Without the notching on the terminal plate; no lateral or dorsal appendices (except cirrus A) . . . . *Bryodelphax*
Notching present on terminal plate; usually there is present an uneven median dorsal appendix . . . . *Hypechiniscus*

31 (27). Internal and external buccal cirri absent . . . . *Mopsechiniscus*
Buccal cirri present 32

32 (31). The lateral cirrus A has the normal filament form . . . . *Pseudechiniscus*
The lateral cirrus A is short, thick, inwardly curved, hollow, with the aspect of a saber blade . . . . *Cornechiniscus*

33 (1). The principal and secondary branches of the doubleclaw are distinctly separate; the principal is slender, long, and straight, the secondary short, divided into 2 or 3 parts; pharynx without placoids 34

The legs have doubleclaws; the secondary
branch is not divided 35

34 (33). There are 6 peribuccal papillae and another
2 smaller papillae behind; 6 buccal lamellae
forming a kind of operculum on the buccal
aperture . . . . *Milnesium*
No peribuccal papillae; the opening on the buccal
aperture has 4 round lamellae . . . . *Limmenius*

35 (33). The claws lacking, except sometimes on the 1st pair
of legs, where there is substituted 2 sclerotized
pieces, both inserted at the median plane of
the legs and forming a kind of pincer . . . . *Necopinatum*
The legs, except sometimes the 4th pair, with
doubleclaws 36

36 (35). The claws of the 1st 3 pairs of legs are simple,
that is without the 2nd branch; the claw of
the 4th pair has a small basal spur . . . . *Haplomacrobiotus*
The doubleclaws of legs I, II, and III are
normally developed 37

37 (36). The 2 doubleclaws of each leg have equal size
and shape, and have symmetry with respect to
the median plane of the leg, sequence 2-1-1-2 38
The doubleclaws of each leg are more or less
dissimilar, and always asymmetrical with respect
to the median plane of the leg, sequence 2-1-2-1 41

38 (37). The buccal tube is flexible between the
stylet support and the pharynx . . . . *Pseudodiphascon*
The buccal tube is rigid in its entire length 39

39 (38). Doubleclaws very large and strongly recurved,
with the secondary branch short or very short,
inserted near the base; the base of each claw
has connected between them a cuticular
structure; lunule absent; freshwater . . . . *Dactylobiotus*
The branch of the secondary claw is inserted
at about the middle of the primary branch or
else, if inserted near the base, the 2
branches are about equally long; lunule
present (at least on the 4th pair of legs) 40

40 (39). No crest at the insertion of the stylet muscle; but there is, on the ventral side of the buccal tube, a reinforced bar (ventral tube support) . . . . *Macrobiotus*
On the ventral and dorsal sides of the buccal tube there is an unpaired crest with wavy margins; from the ventral crest it may, or may not, become separated by a very slender bar connected to the same tube; lunule very large and largely dentate . . . . *Adorybiotus*

41 (37). The buccal tube is rigid and provided with a reinforced bar (ventral tube support) 42
The buccal tube is rigid or flexible, but does not have a ventral tube support 45

42 (41). The 4th pair of legs are reduced or absent, without claws, or with claws very small compared to those of the other legs, or else with a single doubleclaw rather than two; the branches of the claw have rigid connections between them (claw of *Calohypsibius* type, shown on p. 41) . . . . *Hexapodibius*
The 4th pair of legs and their claws are not less developed than the others, or else, if they are, the claw is not of the *Calohypsibius* type 43

43 (42). Claw of the *Calohypsibius* type 44
Claw different 46

44 (43). Buccal tube divided into a rigid part and a flexible part, the latter with a spiral structure; lunule present; peribuccal lamellae present . . . . *Eohypsibius*
Buccal tube rigid all its length 45

45 (44). Cuticle strongly sculptured; two macroplacoids . . . . *Calohypsibius*
Cuticle smooth; 3 macroplacoids . . . . *Microhypsibius*

46 (43). The buccal tube rigid, with no spiral structure 47
The buccal tube is divided into a rigid rostral part (buccal tube) and a flexible part (pharyngeal tube); the latter part has a spiral structure on the internal wall (attention: at times the spiral structure is difficult to distinguish) 51

47 (46). The branches of the claws have rigid connection and each claw is formed of 3 distinct sections; peribuccal lamellae present; eggs deposited free, with ornamentation .... *Amphibolus*
The primary branch is connected to the basal branch plus secondary branch by means of a flexible junction 48

48 (47). The claws of each leg are somewhat different from each other; the external doubleclaw is differentiated into a basal branch + secondary branch, on which is inserted the primary branch; the basal + secondary branch is recurved, sickle-shaped (claw of *Hypsibius* type, p. 41); lunule absent; buccal opening without lamellae; insertion of the stylet muscles in the shape of a hook .... *Hypsibius*
The claws of each leg have a little difference from each other; the basal branch + secondary branch form a marked angle between them, almost right (claw of *Isohypsibius* type, p. 42) 49

49 (48). Reinforced (support) bar of buccal tube present .... *Doryphoribius*
Without the reinforced support bar; stylet muscle insertion of crest shape 50

50 (49). The claw is very large, with very diverted branches; lunule absent; peribuccal lamellae present; freshwater .... *Pseudobiotus*
Claw of normal size, sometimes with lunule; peribuccal lamellae usually absent, rarely present; cuticle often sculptured with granulations and/or gibbosities (humps) .... *Isohypsibius*

51 (46). Pharynx with macroplacoids, with or without microplacoid and/or septula .... *Diphascon*
Pharynx without placoids there may be substituted a slender, sclerotized border, not interrupted .... *Itaquascon*

V.

IDENTIFICATION KEYS AND DESCRIPTIONS FOR THE SPECIES OF THE GENERA

Genus *ACTINARCTUS* Schulz, 1935.

Diagnosis: Halechiniscidae with digits with simple claws, without spurs; the animal has an external gelatinous membrane, in which are immersed dorsal and lateral tubular processes; internal buccal cirri long and connected at the bases by a membrane; median cirrus present.

KEY TO THE SPECIES

1. Caudal cirri bifid, of lyre shape, with small spinous projections .... *A. doryphorus*
   Caudal cirri not bifid 2

2. None, or at maximum 2, eye spots .... *A. doryphorus doryphorus*
   From 7 to 10 pigmented cephalic spots, of reddish-brown color .... *A. doryphorus ocellatus*

ACTINARCTUS DORYPHORUS Schulz, 1935 (Figs. 32, 33).

Marine tardigrade, colorless and transparent, lacking ocular pigment, but with a hyaline spherical structure at the base of the clava, which may perhaps represent a photosensitive organ. Length about 125-140μ and 70μ width excluding the cylindrical tubes and the cuticular extension between them (as the fabric of an umbrella between the ribs), while -- included in the measurements -- reaches a length of about 185μ and a width of 170μ, so that the animal has almost a circular outline. The dorsal region of the body is covered with an extended cuticle, very differentiated, more transparent and membranous at the margin, almost gelatinous in the central region, reinforced by numerous processes of tubular shape according to Schulz (1935), but this structure is on the contrary clear according to Grell (1936). Such processes are in extremely variable number and differently arranged in the dorsal gelatinous zone of

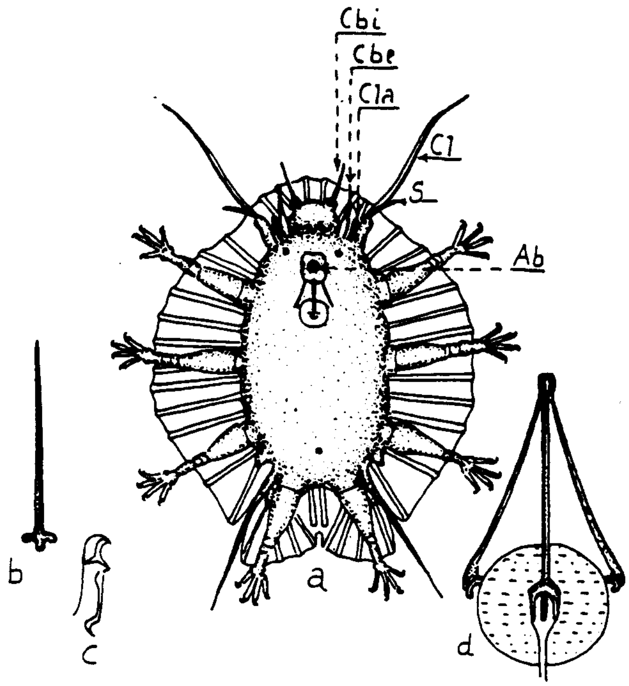


Fig. 32 - *A. doryphorus* Schulz. a, ventral view; b, stylet; c, claw; d, buccal apparatus; Ab, buccal aperture; Cbe, external buccal cirrus; Cbi, internal buccal cirrus; Cl, lateral cirrus A; Cla, clava; S, bristle A' of the lateral cirrus (from Grell, redrawn).

the cuticle (almost vertical at the center), but their number -- according to Grell -- is almost constant in the marginal zone and equals about 48 (10 rostral; on each side 13 lateral and 5 laterocaudal; 2 caudal; see Fig. 33).

The cephalic appendices are: median cirri (unpaired), without bases, relatively short, spiniform and distally somewhat curved toward the top; around it the dorsal gelatinous layer leaves a free space; internal median cirrus (paired) and external median cirrus (paired), shorter than the preceding: both arise from a long cylindrical base; lateral cirrus A (paired), which originates from a wide conical base, positioned near the external medial cirri; from this same base arises a short and delicate bristle, which is named A', difficult to see (Grell does not think it is homologous -- in spite of the corresponding position -- with the clava, which *A. doryphorus* has in the typical form); clava (paired), with usual appearance of enlarged club at the distal end and slightly curved, positioned ventral to the common base of cirrus A and the bristle A'.

The only appendices of the body are the caudal cirri (one per side), implanted on cylindrical bases, and the dorsal cirri (also one per side) about which the gelatinous layer leaves a free zone, as in the case of the median cirrus. The long legs are conical and their terminal part may be telescopically retracted into the proximal; at the distal end of the legs exists the so-called terminal organ, which bears 4 digits, the central 2 longer and more slender, the lateral 2 shorter and more robust, each with a claw provided with spur.

The buccal apparatus is composed of the ventral buccal aperture (positioned on a slight conical projection, directed somewhat rostroventrally), the buccal tube, two weakly curved stylets, and the pharynx, with three pharyngeal bars; stylet supports are present.

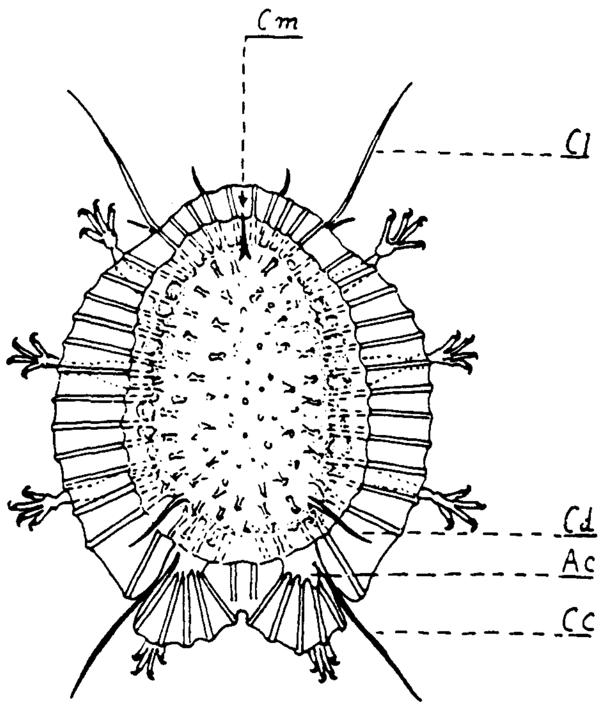


Fig. 33 - *A. doryphorus* Schulz, dorsal view. Ac, caudal appendix; Cc, caudal cirrus; Cd, dorsal cirrus; Cl, lateral cirrus; Cm, median cirrus (from Grell, redrawn).

Grell observed 4 individuals in stadium simplex, in which the buccal apparatus had been expelled, and 5 individuals which -- in his opinion -- represented a stage of cyst, in which had disappeared completely the dorsal gelatinous layer and its membranous marginal layer "umbrella", with the related reinforcement cylindrical processes.

A. doryphorus was collected with reasonable abundance in the shallow layers of marine sediment (the so-called *Polygordius Bruschschill* of the Germans), near the dunes of Helgoland, and probably feeds on diatoms. According to Grell it is excluded from a obligate, or facultative, parasitism and the discovery on the part of Schulz of an individual on *Echinocyamus pusillus* should be considered purely accidental.

A subspecies has also been described:

Actinarctus doryphorus ocellatus Renaud-Mornant, 1971 (Fig. 34).

This subspecies differs from the species especially by the presence of numerous pigmented nodules, being analogous with eye spots; they are in number from 7 to 10, situated on the head, of reddish-brown color, slightly translucent, subspherical or oval (diameter 6-7μ), and form a frontal semicircle. Often is observed one of these spots at the center of the head, isolated and a little posterior to the median cirrus. Their arrangement more frequently is the following: two frontal nodules, which form a semicircle with a pair of lateral anteriors, a lateral pair on each side, in proximity with the dorsal cephalic expansion, which bears cirrus A and the clava. Sometimes exists a supplementary pair, in a still more posterior position.

Besides the great development of the sensory organs (clavae and caudal cirri) others exist: a bristle on each of the first three pair of legs, positioned on the proximal part (non-retractile) of the same legs; they may be 18μ long on the 1st pair of legs and 14-16μ on the 2nd and 3rd pairs, but difficult to see, because of their fineness; these bristles were not noted by the previous author for the species *doryphorus*.

For the rest, the subspecies *ocellatus* is similar to the typical species; the radiating covering is all equal: only -- in the larger individuals of *ocellatus* -- the ventral surface of the cuticle is entirely composed of small pointed outgrowths, with appearance of a granulation in relief; these outgrowths increase laterally in size, toward the insertion of the legs, by being transformed into small rods (4-5μ), which give a "combed" appearance to such zones of the body.

The subspecies was collected at sea, out from Brest, at depths between 130 and 170 m, on the continental platform.

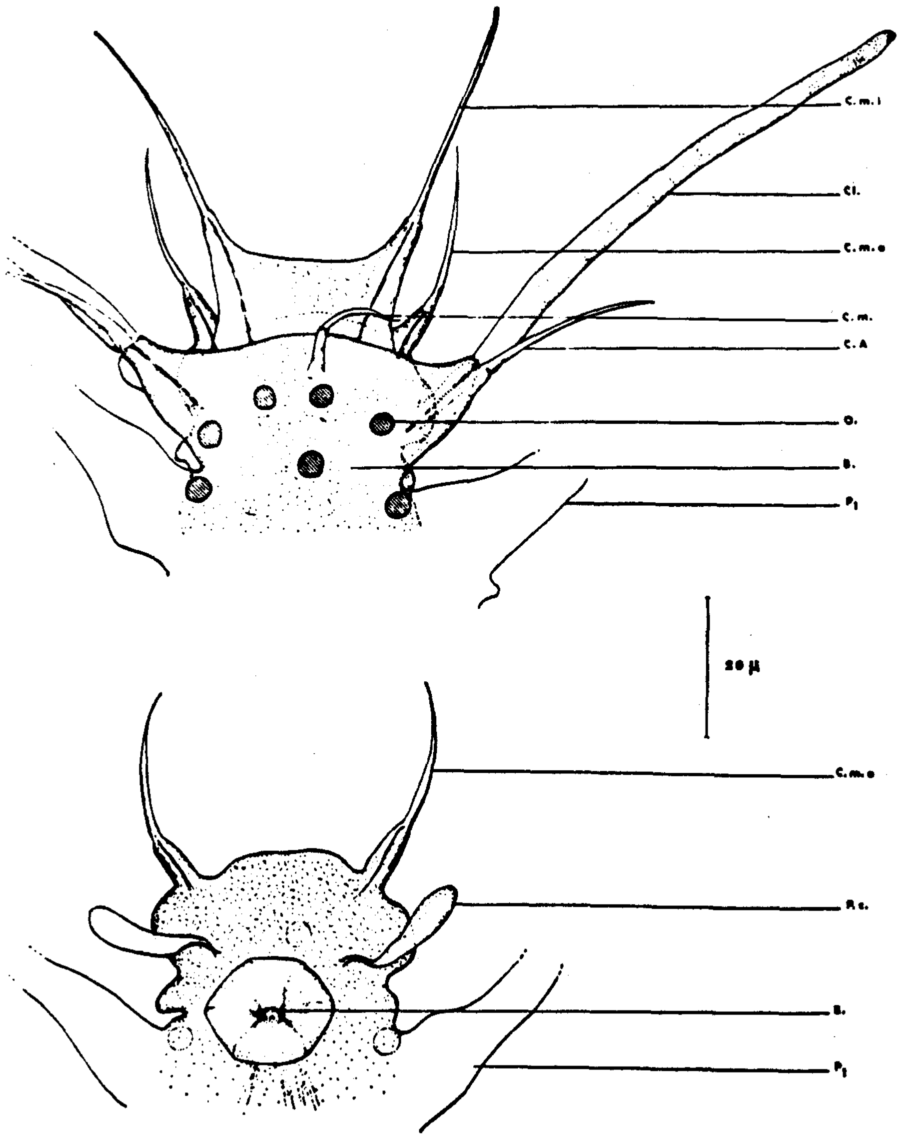


Fig. 34 - Head of *Actinarctus doryphorus ocellatus*, dorsal view; below, ventral view (not showing the cuticular rods). B, mouth; C.A., cirrus A; Cl, clava; C.m.i., internal medial cirrus; C.m.e., external medial cirrus; O., pigmented spot; P_1, first leg; P.c., cephalic papilla (from Renaud-Mornant).

ACTINARCTUS LYROPHORUS Renaud-Mornant, 1979 (Fig. 35).

Length 120μ, width 60μ (in the holotype), a little bigger for the female. The body is oval, and its volume is considerably increased dorsally, by the covering of rods which support a hemispherical cuticular veil; this latter originates at the level of the unpaired median cirrus, and extends dorsally to the legs, on all the surface of the body. The rods which support it are of tubular shape, with expanded bases, straight half way, and apex then expanded, to support the cuticular veil. These rods are 35μ long on the flank of the animal, and are reduced to 8-10μ on the central and anterior parts of the animal. On the ventral side, near to the base of the legs and at the base of the cone on which are inserted cirrus A and the clava exists much smaller rods, which are reduced as far as to form a simple punctation.

The cephalic cirri, with pointed apices, are borne on a base; there exists an unpaired median cirrus (18μ), internal median cirri (30μ), external median cirri in ventral position (20μ), cirrus A (20μ), and a very long clava (120μ); lacking ventral secondary clavae.

The caudal lobes are well developed. These bear dorsally, at the level of the 4th pair of legs, a filament E, 35μ long, as well as caudal cirri formed of an expanded base and prolonged into two filaments, which bear small spinous projections, in the shape of a lyre, 115μ long.

The legs are very similar to those of *A. doryphorus* and to those of the species of the genus *Tanarctus*. The first proximal third of legs 1, 2, and 3 possess a rather long filament (respectively 18, 29, and 30μ). The digits are elongated, pointed, the median digits longer than the externals; the claws of the internal digits bear a spur, the externals are smooth.

A. lyrophorus has been collected at Tuléar, on the western coast of Madagascar.

Genus *ADORYBIOTUS* Maucci and Ramazzotti, 1981.

Diagnosis: Macrobiotidae, in which the buccal tube presents, dorsally and ventrally, from the crests of muscle insertion, unpaired and median robust laminae, with undulated border, of which the ventral may or may not unite to the tube by means of a short and slender reinforcement bar; lunules large and strongly dentate.

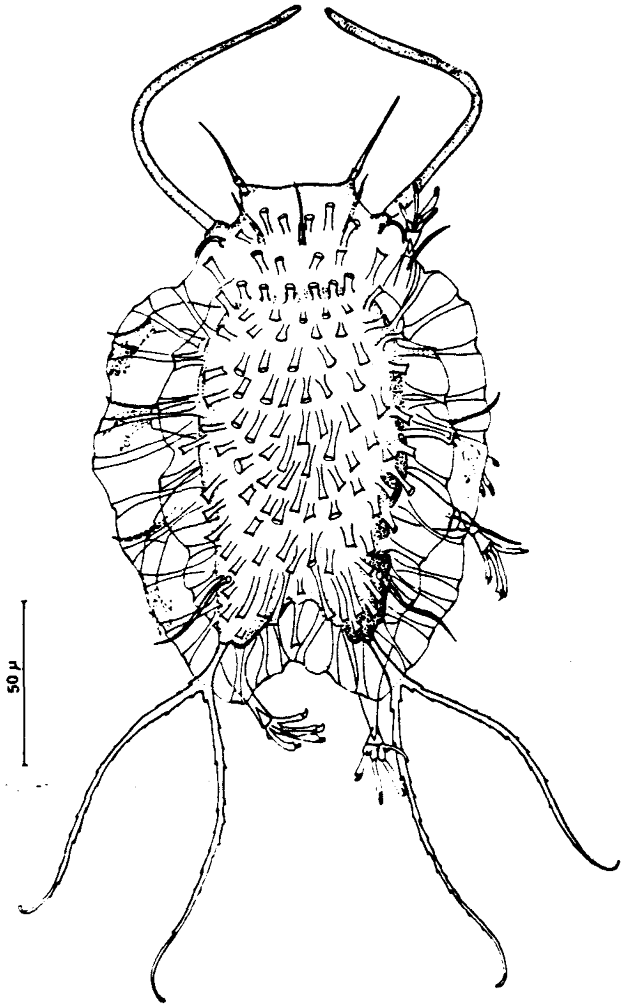


Fig. 35 - *A. lyrophorus*, dorsal view of male.

KEY TO THE SPECIES

1. There is a thin reinforced bar; the cuticle has pores, but not granules .... *Ad. coronifer*
   There is no reinforcement bar; the cuticle has pores and, on the legs, a dense and regular granulation .... *Ad. granulatus*

ADORYBIOTUS CORONIFER (Richters, 1903) (Fig. 36)
= *Macrobiotus coronifer* Richters, 1903, and others

Large size, up to more than 1,000μ prepared. Usually yellow or orange, very rarely colorless; the cuticle is smooth and has numerous, clearly evident pores ("pearls").

Buccal tube rather wide, but sometimes narrow, probably in respect to the age (e.g., 3-4μ diameter for individuals of 450-550μ); the buccal tube has the appendices for the stylet muscles insertion of hook shape. Pharynx slightly oval with 2 short and wide macroplacoids, almost square, but with rounded corners, of which the first has larger size than the second; microplacoid absent.

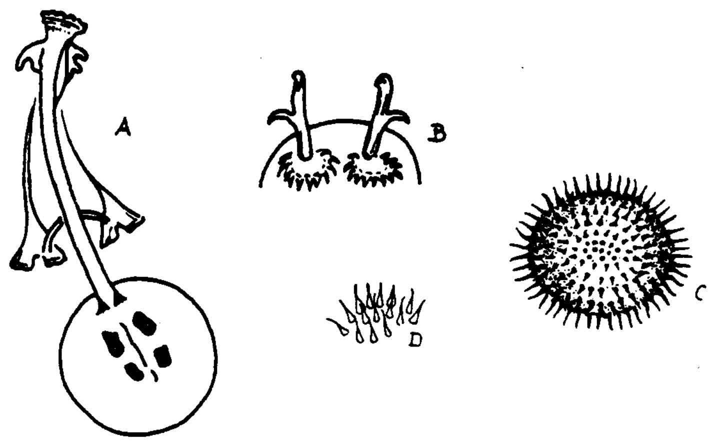


Fig. 36 - *Ad. coronifer.* A, buccal apparatus; B, doubleclaws of the 4th legs; C, egg; D, detail of the spines of the egg.

The median crest of muscle insertion on the buccal tube has a strongly corrugated margin, which both dorsally and ventrally forms an obvious rounded hook, the ventral one markedly larger.

Doubleclaw of the *hufelandi* type: the primary branch has 2 strong accessory points and is longer than the secondary; characteristic of the species is the enormous dentate lunule, which exists at the base of each doubleclaw and which bears 10-18 teeth; the lunule of the 4th pair of legs is more developed.

Eggs deposited free, yellowish or yellow, ovoid or round and of large size, with a maximum diameter of 235μ (Greenland); in Swiss material were found smaller round eggs (diameter 78μ) and also observed -- in the same alpine moss of other altitudes -- round eggs with a diameter of about 124μ, together with ovoid eggs 100 x 126μ; the ornamentations of the eggs are rough thorns, more or less pliable, length up to 22μ.

The distinction of the eggs of *Ad. coronifer* from those of *Macrobiotus islandicus* can be difficult: nevertheless, the spines of the eggs of *coronifer* are wrinkled (rough) from the base to the apex and are up to 22μ long, while those of the eggs of *islandicus* are shorter, a maximum of 11-12μ, smooth towards the base and wrinkled only distally. *Ad. coronifer* is a fairly common species, and was found in many European localities (also in Italy), in South America (Colombia), in the Arctic, and in Turkey. Type loc.: Norway and Spitsbergen Island.

ADORYBIOTUS GRANULATUS (Richters, 1903) (Fig. 37)
= *Macrobiotus granulatus* Richters, 1903, and others

Large size (up to 825μ), eyespots present. The young examples are colorless, the adults have, as a rule, a gray-brown pigmentation, often oriented according to transverse bands. The cuticle has numerous elliptical pores, of variable size and spread irregularly, clearly larger and more pronounced than the "pearls" that one sees in other species. These pores are present also on the legs, where they are also accompanied by (especially on the 4th pair) a dense and regular granulation. The cephalic end has a steep "forehead", with an anterio-ventral mouth, namely similar to those of the genus *Hypsibius*. The mouth is surrounded by lamellae, and the buccal cavity (that has neither a crest nor teeth) is very wide at its aperture, rapidly narrowing to a very long and especially narrow buccal tube (the width exceeds by a little 3% of the length).

The sagittal crest of muscular insertion at the buccal tube has corrugated margins, without hooks; the ventral, larger, does not unite at the tube by means of a reinforcement bar.

The pharynx is very slightly oval, and contains apophyses and 2 macroplacoids in the shape of stubby rods, length about double that of the width, almost equal, or else the first slightly longer than the second; the microplacoid is present, large, round, very close to the second macroplacoid.

The claws are large and a little thin, of the *hufelandi* type, with accessory points on the primary branches. Lunule very large and considerably dentate (about like that of *Ad. coronifer*).

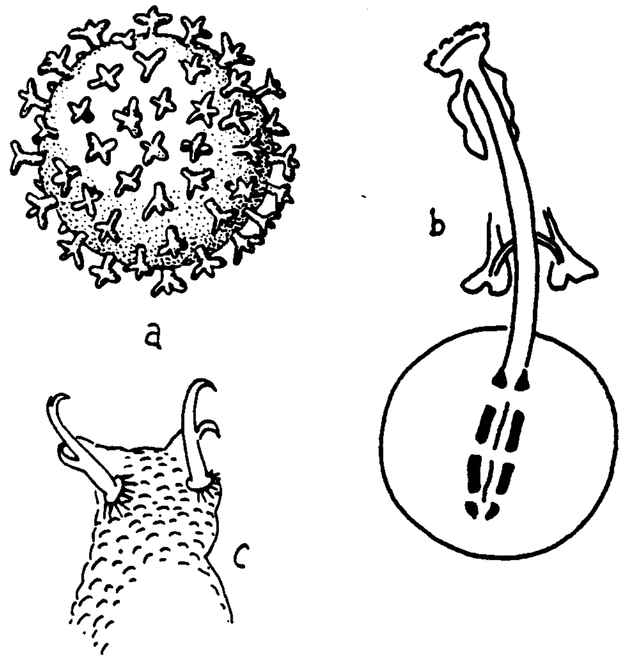


Fig. 37 - *Ad. granulatus*. a, egg; b, buccal apparatus; c, doubleclaws of the 4th pair of legs (a and b from Richters, redrawn).

The eggs are round and their diameter varies between 152 and 182μ, including the characteristic projections, length about 20μ, made up of a basal part weakly conical or almost cylindrical, subdivided at the apices into 2-4 branches; in some cases one or more of these branches can at times be subdivided into 2-3 thin branches; in the Greenland material (Petersen) there was visible about 18 projections in the optical section and their surface appeared rough.

Ad. granulatus, which seems to have a northern transatlantic distribution, is known from diverse localities from Norway and from Greenland. The present redescription was based on the observations of abundant Norwegian material collected by Maucci. Typ. loc.: Merok (Norway).

Genus *AMPHIBOLUS* Bertolani, 1981

Diagnosis: the doubleclaw of each leg appears distinctly subdivided into 3 sections, distinct from each other: a basal section, a section of the secondary branch, and a section of the primary branch separate from the secondary branch; this subdivision into 3 sections of the claw is apparent in neither *Hypsibius* nor in *Isohypsibius*. In addition, in the internal doubleclaw (a little smaller than the external) the secondary branch forms a right angle with the basal section (as in *Isohypsibius*), while in the external doubleclaw the secondary branch forms an obtuse angle with the basal section (as in *Hypsibius*). Cuticle with pores; eyespots present and 14 peribuccal lamellae; a crest is found on the buccal tube for the insertion of the stylet muscles, eggs with ornamentation, deposited free.

KEY TO THE SPECIES

1. There are two macroplacoids .... *Am. volubilis*
   There are three macroplacoids 2

2. Length up to as much as 900μ; macroplacoids long and slender; eggs with conical or bulbous projections .... *Am. smreczynskii*
   Length up to 540μ; macroplacoids short and squat; eggs enveloped in a hyaline layer .... *Am. weglarskae*

AMPHIBOLUS SMRECZYNSKII (Weglarska, 1970) (Fig. 38)
= *Isohypsibius smreczynskii* Weglarska, 1970
= *Hypsibius (Doryphoribius) smreczynskii* Ramazzotti, 1974

Aquatic, large, length up to 960μ. Cuticle smooth, olive-green color (in reflected light). Eye spots black, in anterior position; peribuccal lamellae present. Buccal tube straight, 60μ long, with 12μ diameter. The stylets are slightly curved, with well developed furcae. Stylet supports 18μ long. Apophyses projecting; at the level of the apophyses are visible two slender oblique cuticular bars, very clear at 100 magnification. Pharynx oval with 3 macroplacoids, the 1st of 12μ, the 2nd of 15, and the 3rd of 18μ length. Microplacoid absent.

Claws large, but rather slender, with smooth lunules on the 4th pair of legs and with accessory points on the principal branches.

The eggs are spherical, with diameter of 115μ with ornamentation; these are 36-40μ high and resemble those of *Macrobiotus echinogenitus*; they have conical or bulbous shape, and have a reticular sculpture, with mesh wider at the base.

The species was collected in Lake Crusoe (Land of Axel Heiberg, northern Canada), among algae and moss. Some eggs, among which were

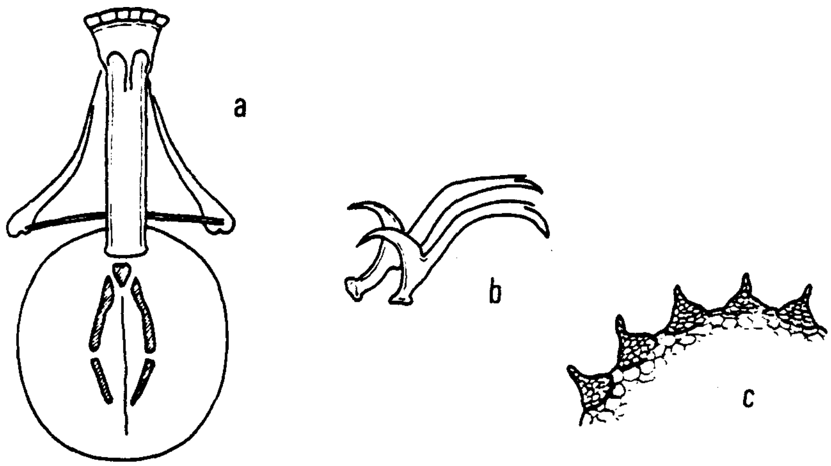


Fig. 38 - *Am. smreczinskii* (Weglarska). A, buccal apparatus; B, doubleclaws of the 1st pair of legs; C, ornamentation of the egg.

two embryonated, were later found near Hammerfest, Norway.
In addition exists a subsequent report from Spitsbergen Island.

AMPHIBOLUS VOLUBILIS (Durante Pasa and Maucci, 1975) (Fig. 39).
= *Hypsibius (Isohypsibius) volubilis* Durante Pasa & Maucci, 1975

Species of large size (850μ maximum, average included between 650 and 750μ). Color sepia brown to blackish, sometimes hyaline yellow. Eyes present, constituted of small irregularly sparse spots. Cuticle smooth, with small oval pores or of drop shape aligned in dorso-lateral position.

Mouth surrounded by lamellae, large, with the apices striped longitudinally. Buccal cavity short and very wide. The buccal armature has anteriorly, at the base of the lamellae, a fine punctation, which follows three slender rough transverse crests. Posteriorly, a medio-dorsal semilunar crest, and two square dorso-lateral teeth, flanked by two transverse teeth of comma shape and anteriorly to this formation, numerous elongated teeth, arranged in more irregular rows.

The buccal tube is short and wide; length (including the mouth cavity) 82μ in the holotype (800μ long); width (in the holotype) 10μ. The anterior half of the tube is slightly wider than the posterior (12μ) and has a ventral thickening and the appendices of muscle insertion of the stylets, of robust crest shape. Stylets robust, with large furcae and strong supports.

Pharynx oval (72 by 60μ, in an individual of 600μ), with large triangular apophyses and two macroplacoids of slender rod-shape; the first (28μ, in the holotype) has the anterior end pointed and has a constriction about half its length, preceded by a median swelling, the second (18μ) is unbroken and has rounded end. Microplacoid absent.

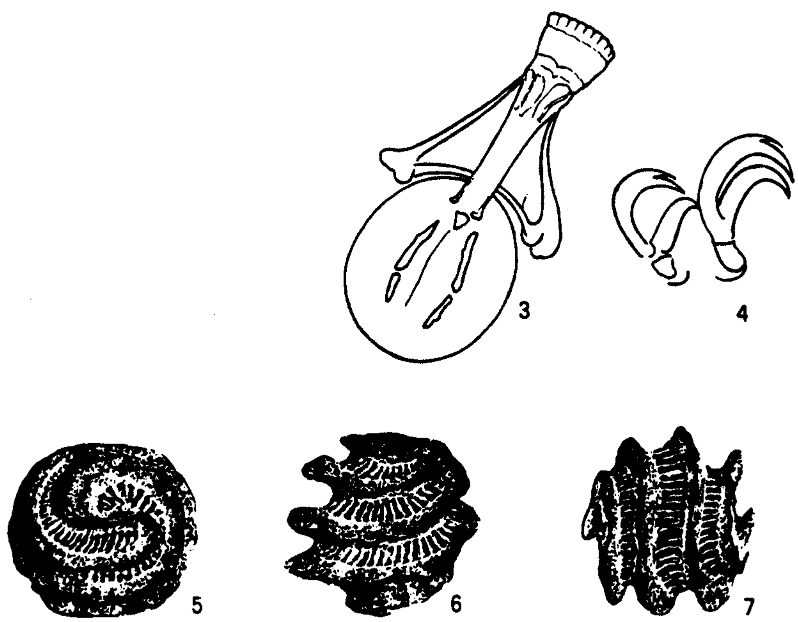


Fig. 39 - *Am. volubilis* (Durante and Maucci). 3, buccal apparatus; 4, doubleclaws; 5, 6, 7, eggs viewed at different angles (from Durante and Maucci).

The claws have a rather variable appearance according to the angle of view. The claws of each pair of legs are almost equal. Common basal branch very short, principal branch and secondary branch little different, robust, strongly curved. The principal branch has strong accessory points. At the base of the claws exists a small cuticular thickening, similar to a lunule.

The eggs are deposited free, spherical, with size included between 80 and 120μ, color red-violet or grayish. The egg is enclosed in an envelope of transparent tissue, of alveolar structure, with reticular appearance, which constitutes a double spiral crest, which starts from the poles and extends about the egg in two spirals, stopping at the opposite pole. The furrow between the two crests has on its bottom numerous transverse scaffolding of the same alveolar tissue, which connects the crests to each other, and which leaves free small elongated windows, in correspondence with those seen on the surface of the egg, which is completely smooth. Including the subdivided covering, the diameter results between 118 and 155μ.

The species was collected in the vicinity of Bodö, at Forsa, and near Narvik (northern Norway).

Other reports from the island of Crete and from some Italian localities.

AMPHIBOLUS WEGLARSKAE (Dastych, 1972) (Fig. 40).
= *Isohypsibius weglarskae* Dastych, 1972.

Length 540μ, massive body, color yellow-brown. Eye spots present. Mouth cavity wide, surrounded by buccal lamellae. Buccal tube straight, 49μ long, 6 wide; appendices of muscle insertion of the stylets of robust crest shape. Pharynx oval, with apophyses and three macroplacoids; they are of almost equal length (the first a little longer than the second), the third is more distant and longer. Microplacoid absent.

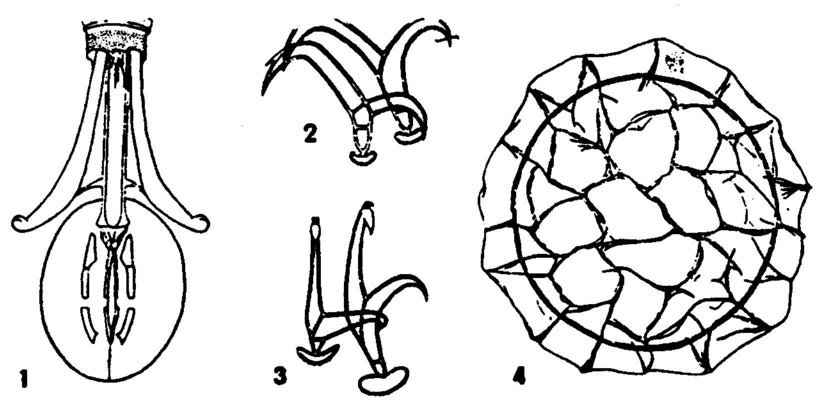


Fig. 40 - *Am. weglarskae* (Dastych). 1, buccal apparatus; 2, doubleclaws of the 2nd pair of legs; 3, doubleclaws of the 3rd pair of legs; 4, egg (from Dastych).

Claws large, of *Isohypsibius* type, of increasing size from 1st to 4th pair. The claws are not very massive, and the principal branch bears accessory points. At the base of the claws there is a lunule, which is small on the first three pair of legs, very large, however slender on the 4th pair.

Eggs deposited free, yellow-brown color. The diameter of the eggs is

75-85μ, without projections; they are enveloped in a hyaline layer, of characteristic appearance, producing on the surface an irregular reticular design, with wide mesh.

Am. weglarskae was found in damp moss, on the Tatra Mountains (typ. loc.) and in some Italian localities (also in water).

Genus *ANGURSA* Pollock, 1979.

Diagnosis: Halechiniscidae with slender body; on each toe of every leg there are claws ending with two apices turned opposite.

ANGURSA BICUSPIS Pollock, 1979 (Fig. 41).

Body slender, 5-6 times longer than wide; length 163μ. Head moderately rounded. Cephalic cirri slender and short; the median cirrus seems absent. Clavae large, with slender bases, 12μ long, positioned a little posterior to the lateral cirri, which are 5μ long.

Cuticle transparent. Cirri E (14μ) positioned between the legs of the 4th pair, that is, more posterior than usual in the Heterotardigrada.

Legs slender, terminally telescopic; the 4th legs are longer than the other pairs. On the first pair of legs a short spine (8μ), on the other legs neither papillae nor spines. The legs end with four digits, the external shorter than the internal. Claws small, terminated with two apices curved in lateral position between them, of about equal size.

Of this species have been found so far only two examples, one in a beach of Massachusetts (Crene's Beach) in intertidal environment, the other at 400 meter depth, in front of North Carolina.

Genus *ANISONYCHES* Pollock, 1975.

Diagnosis: Echiniscoididae with cuticle not armor-plated; four claws on each of the first three pair of legs, three claws on the 4th pair; the claws bear basal spurs.

ANISONYCHES DIAKIDIUS Pollock, 1975 (Fig. 42).

Length 177μ. Cephalic cirri short, 3μ long, with a basal swelling.

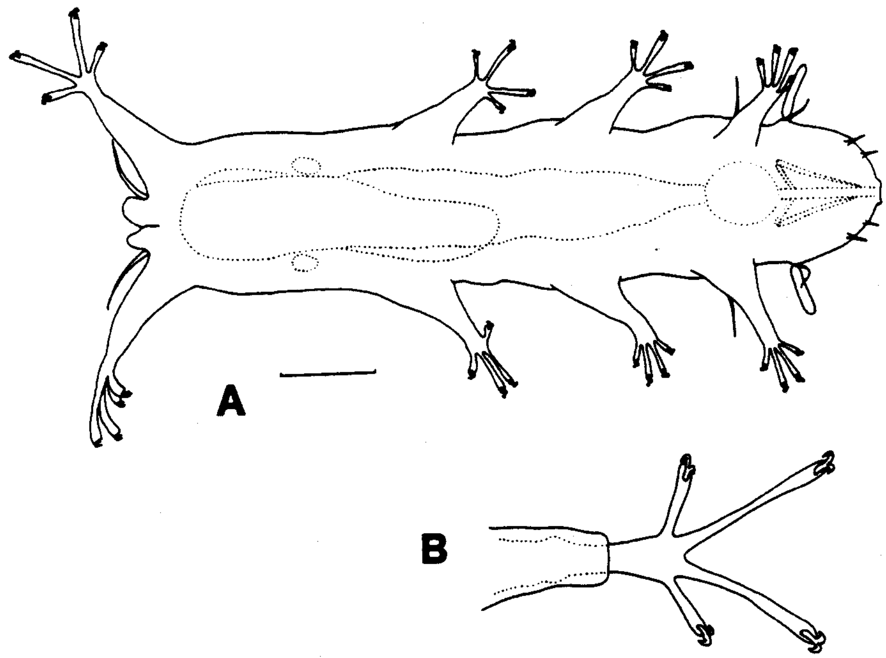


Fig. 41 - *Ang. bicuspis* Pollock. A, habitus; B, leg of the 4th pair (from Pollock).

Median cirrus absent. Clavae small, ovoid, lateral cirri only 4μ long. Eye spots present. Mouth subterminal; small round pharynx, sometimes pear-shaped; stylet supports absent. The placoids, 6μ long, are fused at the anterior end, as in many other Heterotardigrada.

Cuticle smooth, without plates or granulations or other sculpture. Cirri are present in position E, 9μ long. Gonopore a rosette, with six small cuticular plates.

Legs of equal length, without digits. Claws terminal, slightly curved at the apices, each bearing two spurs, near the base, arranged at right angles to each other. The claws of each leg are progressively longer from the internal to the external; a membrane connects each claw to the leg. The first three pair of legs bear four claws, the fourth pair only three. On the fourth pair of legs there is a papilla, which is lacking however on the first three pair.

The species is near to *Echiniscoides sigismundi*, from which it differs by the number of claws and by the presence of two spurs on each claw.

Ani. diakidius was found in interstitial environment (medium and fine sand, 0-20 cm depth), in different stations of the Galapagos Islands.

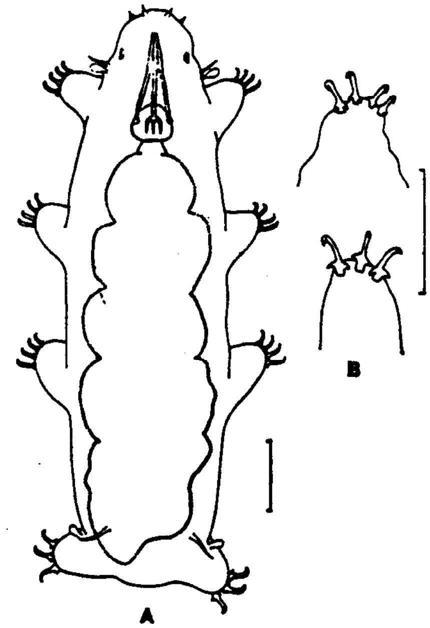


Fig. 42 - *Ani. diakidius* Pollock. A, habitus; B, leg and claws of the 1st (above) and 4th (below) pair of legs (from Pollock).

Genus *ARCHECHINISCUS* Schulz, 1953.

Diagnosis: Archechiniscidae with four claws, of which the internal two are inserted on digits and the external two directly on the distal end of the leg, by means of a papilla; body indistinctly subdivided into nine segments.

ARCHECHINISCUS MARCI Schulz, 1953 (Figs. 43 and 44).

Length 198μ, body conically tapered toward the rostral end, rounded at the caudal end, with maximum width (92μ) between the 3rd and 4th pairs of legs. The cuticle is smooth, but with strong magnification it appears subdivided into 9 regions by transverse lines; line 1 delimits a rostral cephalic zone; between lines 2 and 3 exist ventrally the 1st pair of legs, the 2nd is positioned between lines 3 and 5, the 3rd between lines 5 and 7, the 4th pair of legs approximately under line 8. The author has noted that dorsally *Archechiniscus* is subdivided into 9 regions, while in the genus *Oreella* only 8 are present. The median cirrus is absent, while there are other cephalic appendices, which are: internal buccal cirrus (paired, 3.8μ long) a little above the subterminal buccal aperture; somewhat back, and more toward the external, a projection from each side -- probably in the shape of an oval ring -- which the author believes to be the cephalic the shape of an oval ring -- which the author believes to be the cephalic papilla (paired); under the preceding projection, the external buccal cirrus (paired, 4.5μ long); lateral cirrus A (6.4μ) and clava of typical shape (4.5μ), both paired, close together and inserted laterally. About the level of these last two appendices -- at a distance of 29μ from the buccal aperture -- there are two eye spots, of dark red color.

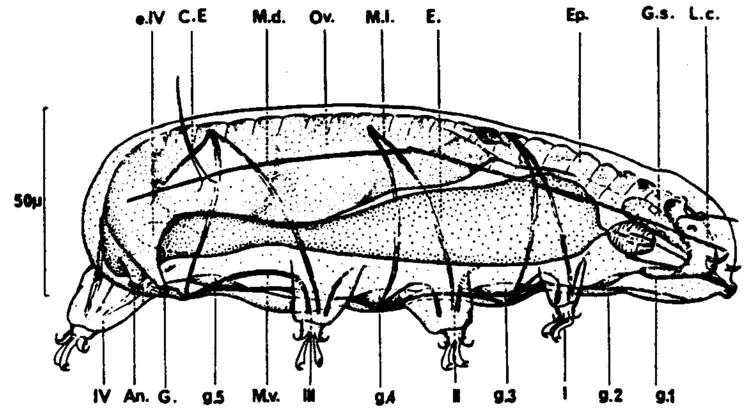


Fig. 43 - *Arch. marci* Shulz. Profile view. An, anus; CE, appendix E; E, intestine; Ep, epidermis; eIV, position of the 4th leg, not drawn; G, gonopore; Gs, salivary gland; g1, g2, g3, g4, g5, nervous ganglia of the ventral chain; Lc, cerebral lobe; Md, dorsal muscle; Ml, latero-ventral muscle; Mv, ventral muscle; Ov, ovary; I, II, III, IV, legs (from Renaud-Mornant).

The buccal apparatus inclusively measures 44μ in length, but it was not possible clearly to examine its morphology on the single specimen collected; the pharynx is oval (diameter 13μ) and seems to contain 3 pharyngeal bars and apophyses; the buccal tube is 32μ long, the stylets measure 17μ and have thickened bases. The only cuticular appendices observed on the body are two spines, approximately 6.5μ long and positioned one on each side, over the 4th pair of legs, approximately in the position where exists -- in the genus *Echiniscus* -- the appendices E.

The four pair of legs are terminated in characteristic manner and all different, with regard to the other genera of tardigrades; each leg ends, that is, with four claws, of which the two external (about 7μ long and with basal spurs) are inserted directly on it by means of a papilla, while the internal two (about 6.5μ long and smooth) are implanted on two distinct digits. In other words, the external claws are connected to the leg as in the suborder Echiniscoidea, those internal as in the suborder Arthrotardigrada; the two internal digits measure 15.6μ, claw included.

The description up to now is that original of Schulz, based on the single example he collected; we shall now relate the variation described by Renaud-Mornant, which is based on examination of abundant material from New Caledonia (Saint-Vincent Bay).

And here now the differences -- with respect to the description of Schulz -- noted by Dr. J. Renaud-Mornant, in numerous examples of her study (1967). The cuticle is not smooth, rather dorsally punctated. As for the subdivision into "regions" of the cuticle, Renaud-Mornant writes that cuticular folds are formed when one observes the animal dorsally, compressed between slide and coverslip; but observed in profile, the cuticle appears extended, without any folds, and as far as occurs underneath the epidermis, well visible with its rectangular cells, in close contact (6-7μ).

About the cephalic cirri: the external buccal are ventral and do not seem to be flanked by a papilla, but only by a fold of the cuticle. Clava and lateral cirrus A arise close together, from a small cuticular outgrowth. The stylets have the shape indicated by Schulz, but after dissection and observation with strong magnification, one sees that they are formed of sliding lamellae, a little curved anteriorly. The pharynx contains 3 rods.

The anus is not a slit, more or less complex, as occurs in the Halechiniscidae and the Stygarctidae, but is instead composed of numerous cuticular folds, which close around the orifice. The genital aperture does not have rosette shape, but consists of a longitudinal slit, with a cuticular fold at the posterior margin. The spine, positioned in correspondence with appendix E of the *Echiniscus*, measures 26μ, rather than 6.5μ (as occurred in the single example studied by Schulz). The claws are supported by a membrane-formed sheath and which leaves free only the extreme point of the claw. For other details on the claws, the musculature and the nervous system, we refer the reader to the work of Renaud-Mornant (1967).

Of this species, after the only example, coming from the washing of Cirripedia (Crustacea), collected -- together with detritus -- on the coastal reef of El Salvador (Central America), numerous examples were found in Saint-Vincent Bay (New Caledonia), in a sandy bottom, at 18 meters depth. It was collected also at the Bahamas Islands, and an example (Schuster and Grigarick, 1966) at the Galapagos Islands.

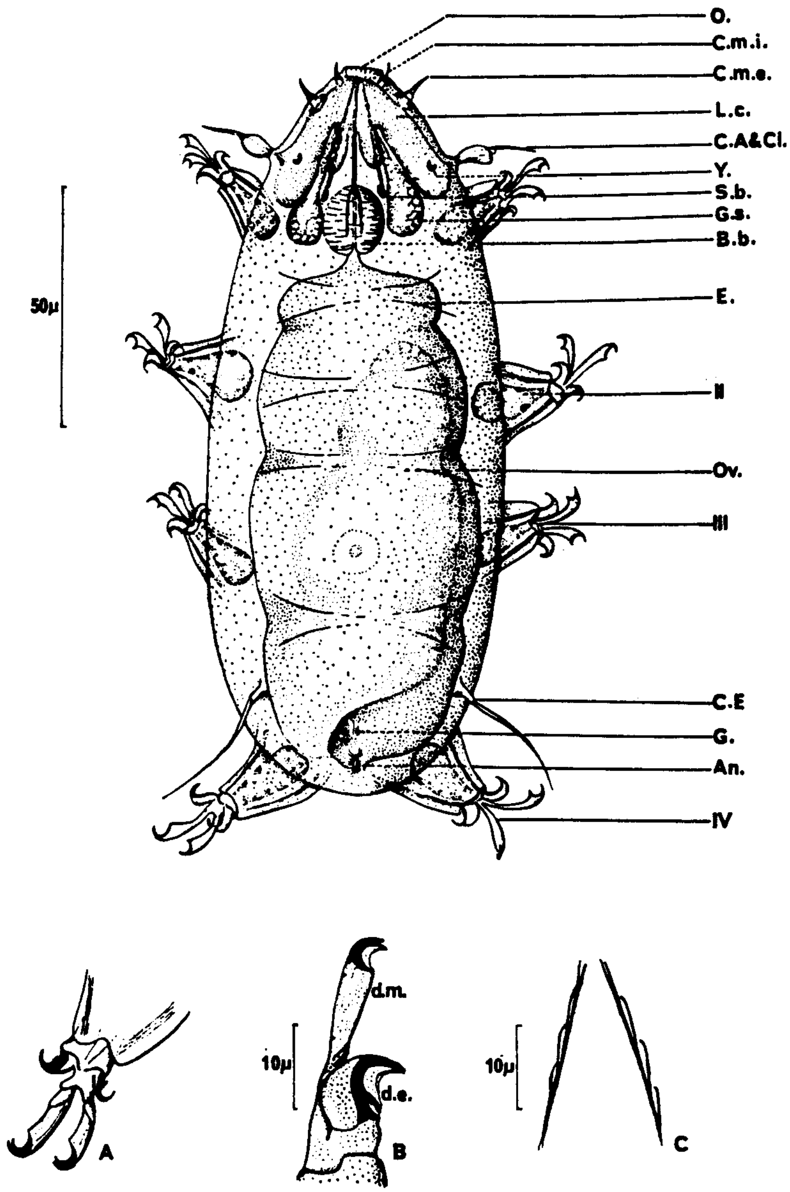


Fig. 44 - Above: *Arch. marci* Schulz, 1953. General view. An, anus; Bb, pharynx; CA and Cl, cirrus A and clava; CE, appendix E; Cme, external buccal cirrus; Cmi, internal buccal cirrus; E, intestine; G, gonopore; Gs, salivary gland; LC, cerebral lobe; O, buccal aperture; Ov, ovary; Sb, stylet; Y, eye; I, II, III, IV, legs. Below: A, detail of the end of the 4th leg; B, detail of the two digits; dm, median digit; de, external digit; C, detail of the structure of the stylet (from Renaud-Mornant).

Genus *BATHYECHINISCUS* Steiner, 1926.

Diagnosis: Halechiniscidae with digits terminated by claws with two spurs; long median cirrus.

BATHYECHINISCUS TETRONYX Steiner, 1926 (Fig. 45).

Length 119μ, maximum width 33-34μ, body approximately cylindrical, cuticle smooth, eye spots absent. The median cirrus is a long bristle and the medial cirri are also bristles, of which those external (12-13μ) are inserted somewhat ventrally and those internal rather dorsally, with respect to the rostral cephalic margin. Clava of lancet shape, lateral cirrus (29-30μ) more than twice as long as the clava. Buccal apparatus not well known; it is known only that the ventral buccal aperture is found on a conical rounded projection and that the pharynx is almost spherical. The first three pairs of legs bear dorsally -- on their proximal part -- a rather long spine, while the legs of the fourth pair have -- in position where inserted on the body -- a long spine and, more caudally, a papilla with swollen and rounded base, which ends with a slender point. Probably the terminal part of the legs is telescopically retractable into the proximal; the

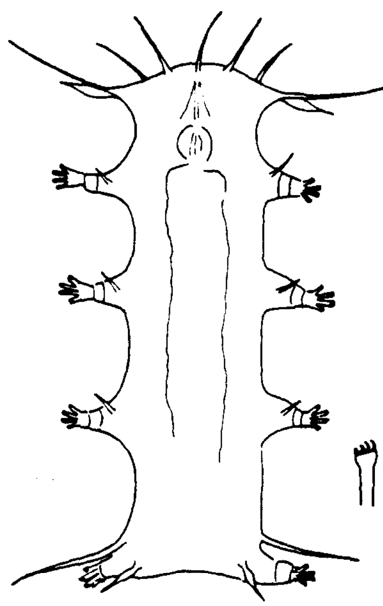


Fig. 45 - ***Bath. tetronyx*** **Steiner (from Steiner, redrawn).**

legs have distally four digits, on each of them there is a transverse border, which bears four short claws, of tooth shape. Eggs unknown.

The only sure report is relative to a single individual, fished from the Antarctic (Gauss station) at 385 m depth; the animal found had probably sunk to the bottom and was already dead. The other reports cited for *Bath. tetronyx* (coast of Spain, of Majorca, of Texas, and of California) are referring almost certainly to *Styraconyx sargassi*; also the species illustrated and described by Marcus (1936) as *Bath. tetronyx* (from the Sargassum Sea) is instead *Styr. sargassi* (see Thulin, 1942, and Du Bois-Reymond Marcus, 1952).

Genus *BATILLIPES* Richters, 1909

Diagnosis: Batillipedidae with legs terminating with six digits, somewhat reduced or absent; all digits end with a dilated distal end, variously adapted into disk, spoon, shovel.

KEY TO THE SPECIES

1. Without any caudal appendix 2
   With caudal appendices 5

2(1). Terminal caudal margin swollen, cephalic appendices long ..... *Ba. tubernatis*
   Caudal margin relatively plain 3

3(2). Cuticle smooth, or with sparse pores 4
   Cuticle has a coarse sculpture, formed of dots not symmetrical .... *Ba. roscoffensis*

4(3). Spines on the legs turned distally; squat and short (6.6μ) .... *Ba. acaudatus*
   Spines on the legs turned toward the base of the leg, slender and long (12-16μ) .... *Ba. noerrevangi*

5(1). The caudal appendix is a single spine (Figs. 46, C, D, E, F, G) 6
   The caudal appendices are more than one (Figs. 46, J, K, L, M) 13

6(5). The caudal appendix ends in a membranous bulb
(Fig. 46, C) . . . . *Ba. bullacaudatus*
The caudal appendix does not end in a bulb 7

7(6). The caudal spine has blunt point (Figs. 46, D,E) 8
The caudal spine has sharp point (Figs. 46, F,G,H,I) 9

8(7). The caudal spine departs from a bilobed base
(Fig. 46, D); clavae with constriction . . . . *Ba. gilmartini*
The caudal spine departs from a smooth
base (Fig. 46, E); clavae without constriction . . . . *Ba. similis*

9(7). Clavae with one or more constriction 10
Clavae without constriction 11

10(9). Clavae with a constriction; caudal
appendix, see Fig. 46, F . . . . *Ba. pennaki*
Clavae with more of a constriction; caudal
appendix, see Fig. 46, G . . . . *Ba. annulatus*

11(9). Caudal spine short, inserted directly on the body . . . . *Ba. mirus*
Caudal spine long, inserted on a base 12

12(11). Cuticle with light stripes . . . . *Ba. camonensis*
Cuticle supplied with mammillary tubercles . . . . *Ba. adriaticus*

13(5). Caudally there are two spines 14
Caudally there are three or more spines 15

14(13). Anterior to the 4th pair of legs, the
lateral margin of the body has two
prominent and sharp projections . . . . *Ba. dicrocercus*
The projections are lacking or else have
little relief and are blunt . . . . *Ba. noerrevangi*

15(13). Between the 3rd and 4th pair of legs
there is on each side a minuscule papilla . . . . *Ba. friaufi*
There are no lateral minuscule papillae 16

16(15). Caudally there are three spines 17
Caudally there are more than three spines . . . . *Ba. phreaticus*

17(16). The three spines have about equal length (Fig. 46, L) . . . . *Ba. littoralis*
The central spine is longest, the two lateral
are minuscule, turned toward the internal,
and barely visible . . . . *Ba. littoralis submersus*

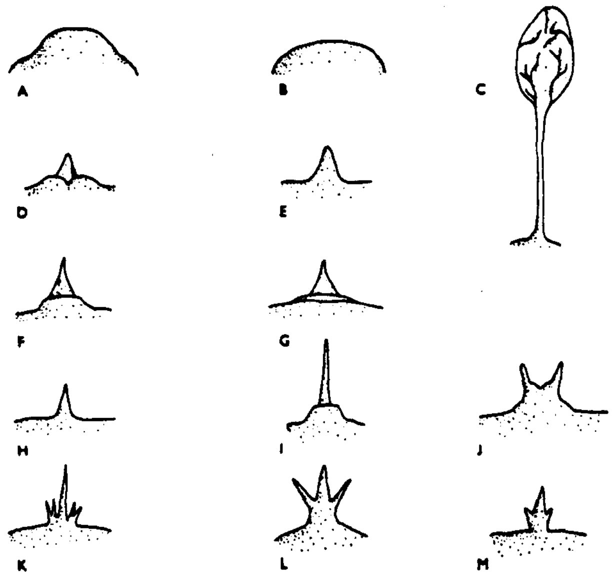


Fig. 46 - *Batillipes*, caudal appendages:

A. *Ba. tubernatis*	F. *Ba. pennaki*	K. *Ba. phreaticus*
B. *Ba. acaudatus*	G. *Ba. annulatus*	L. *Ba. littoralis*
C. *Ba. bullacaudatus*	H. *Ba. minus*	M. *Ba. friaufi*
D. *Ba. gilmartini*	I. *Ba. camonensis*	
E. *Ba. similis*	J. *Ba. dicrocerus*	(from Pollock).

BATILLIPES ACAUDATUS Pollock, 1971 (Fig. 47).

The caudal region of this species is smoothly curved, without any appendix (nor spines, nor structure of other type); the lateral projections of the body are reduced; cephalic appendices short; legs digitate.

Length of the holotype, from the base of the cephalic appendices to the end of the body: 187.8μ; width of the body, between the bases of the lateral cirri A: 48.6μ. Median dorsal cirrus of 12μ, departing from a small base; internal buccal cirri of 16.6μ on minuscule base; external buccal cirri: 10.4μ; clavae, 8.8μ; lateral cirri A: 17.2μ from the base, which is common with the clava.

Cuticle transparent, with projecting and uniformly distributed pores; pharynx oval, from 22.1 x 17.7μ. Outline of the smooth body with slight projections between the 1st and the 2nd, as well as between the 2nd and 3rd pairs of legs. The lateral projections between the 3rd and 4th pairs of legs are very reduced, or else totally lacking. There is a cirrus E, 17.7μ long, over the 4th pair of legs.

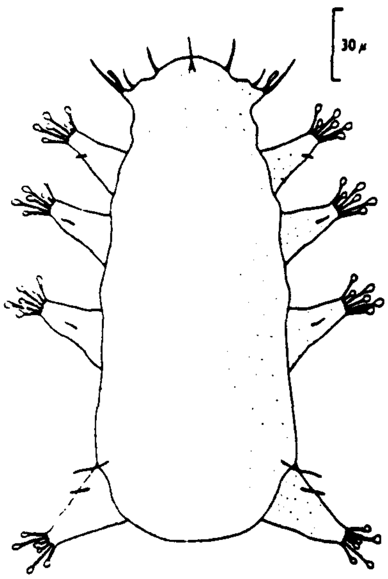


Fig. 47 - *Ba. acaudatus*, dorsal view (from Pollock).

Short robust spine on all the legs, 6.6μ long on the 4th pair; legs distally somewhat telescopic; 6 digits on each leg, similar to those of *Ba. mirus*.

The species was collected in sand (marine interstitial fauna), with granules of 280μ average, near to the surface of the sediment, generally in the deeper quarter of the intertidal region in the vicinity of Whitlog (Stoupe Beck Beach, Yorkshire, England).

BATILLIPES ADRIATICUS Grimaldi De Zio, Morone De Luca, D'Addabbo Gallo, and Grimaldi, 1979 (Fig. 48).

The more remarkable characteristics of this species are the showy cuticular ornamentation and the conical shape of the large lateral processes. The cuticle has in the dorsal region mammillary tubercles which have a diameter between 2 and 3μ and an arrangement such, by which each one is surrounded by six others. Such projections extend as far as the bases of all the appendices. In the ventral region and along the lateral margins, the granulation attenuates giving way to punctation common to the other species belonging to the genus *Batillipes* as *Ba. annulatus*, *Ba. tuberatis*, *Ba. pennaki*, etc. The punctation of the cuticle becomes extremely rare in correspondence with the anus and gonopore.

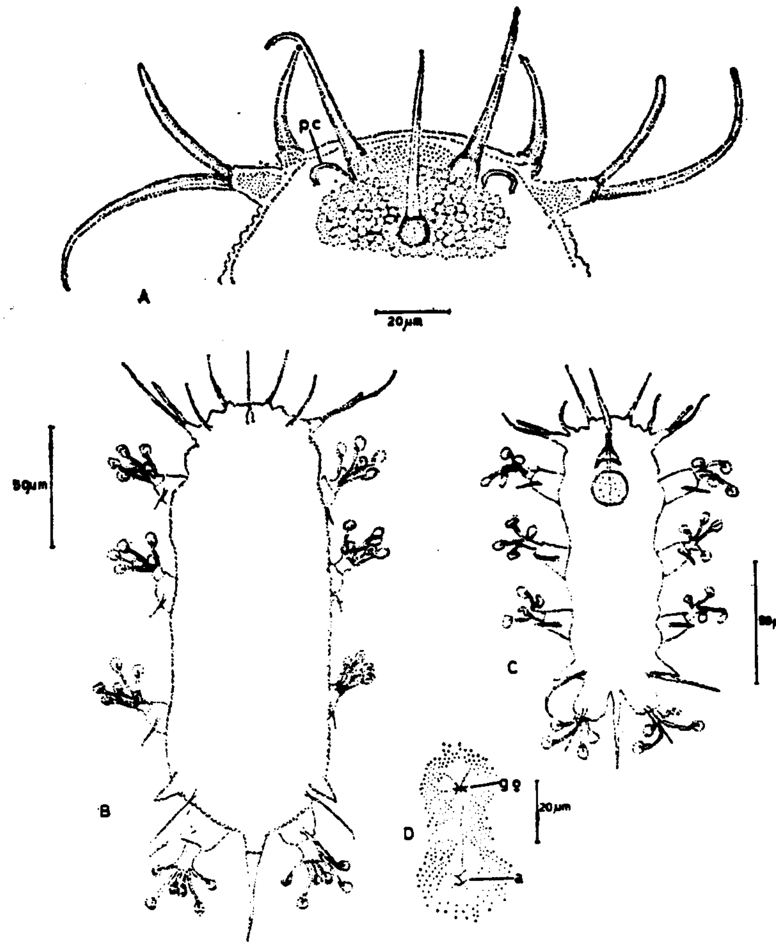


Fig. 48 - ***Ba. adriaticus*** **Grimaldi de Zio et al. A, cephalic region; B, adult; C, larva with four digits; D, female anus-gonopore region; pc, cephalic papilla; g, gonopore; a, anus.**

The body of the adult is about 200μ long from frontal margin to the base of the tail, with the tail about 250μ. The diameter of the body is rather uniform, tending to increase only in the posterior third, at the level of the lateral process and cirrus E. The lateral cirri are of length equal to the cephalic diameter, while the clavae, smooth as in *Ba. mirus* and *Ba. tubernatis*, are about half that of the lateral cirri; there is no difference between males and females. The median cirri, internal and external, are of degrading size. All the cephalic appendices end with the point enlarged as a spatula. On the front margin, between the internal and external cirri, there are two cephalic papillae. Underneath the common base of the lateral cirrus and clava there is a hemispherical protuberance rendered still more evident by the projecting design of the tuberosity of the cuticle. Lacking eyes. The legs are of the A1 type (Pollock, 1970), the first three with the second digit sessile and all the others stalked, the fourth with the two central sessile. On each of the first three pair of legs there is a short spine while on the fourth pair of legs the spine is twice the length of the others (20μ).

The cirrus E, in the few examples in which it was possible to be measured, is much longer in the females than in the males, but because of the scantiness of the data, we do not think it wise to speak of sexual dimorphism at this time. Laterally and anteriorly to the cirrus E, that is between the third and the fourth pairs of legs, there are two large lateral processes which in this species have a very characteristic appearance. They are in fact conical, 15μ long, contrasting from the coarse punctation which characterizes all the dorsal region. The tail is a long flagellum which is inserted on a cylindrical protuberance from the posterior region. The flagellum does not have the cuticular punctation which instead exists on the base. The tail, base included, corresponds to about 20% of the total length of the body. Individuals have also been found with bifid tail or with accessory points at the base of the flagellum. The same variability had been already noted for *Ba. pennaki* (Grimaldi de Zio and D'Addabbo Gallo, 1975).

Ba. adriaticus was found on the native coast in Masseria Morello River locality (Torre Canne, Brindisi), in the zone of the middle coastline, at minimum level of low tide, to a depth between 15 and 20 cm.

BATILLIPES ANNULATUS De Zio, 1963 (Fig. 49).

Length of the body 150-300μ, colorless and transparent, cuticle with extremely light granulation. Lateral margins slightly undulating; between the 3rd and the 4th pairs of legs there are two dorsolateral hook-shaped conical processes (one per side), much resembling those of *Ba. similis*. With regard to *Ba. pennaki*, rather squat, the body is more slender and slim and is terminated caudally by a spine and wide base, whose length may reach 25μ.

Buccal apparatus similar to that of *Ba. pennaki*, with a "knob" thickening at the bases of the three pharyngeal bars. The cephalic appendices, with conical bases as in *pennaki*, are:

-- unpaired median cirrus (15μ), longer than in *pennaki*;
-- paired medial internal cirri (20μ);
-- paired medial external cirri (15μ);
-- paired clavae, with 4 annular constrictions, of which the last (apical) is not very pronounced; the clavae assume then a segmented appearance (6 segments);
-- paired lateral cirri A (40μ).

All the legs have a spine, of which those of the fourth is longer. On the first three pairs of legs the second digit is sessile, lacking a peduncle, as in *Ba. pennaki*; a difference however exists in that species, the second and third digits of the 4th pair of legs are instead pedunculate.

The species was collected in Italy, in sand of an Apulian beach, near the mouth of Aloisa River (Manfredonia) and on the beach of Siponto.

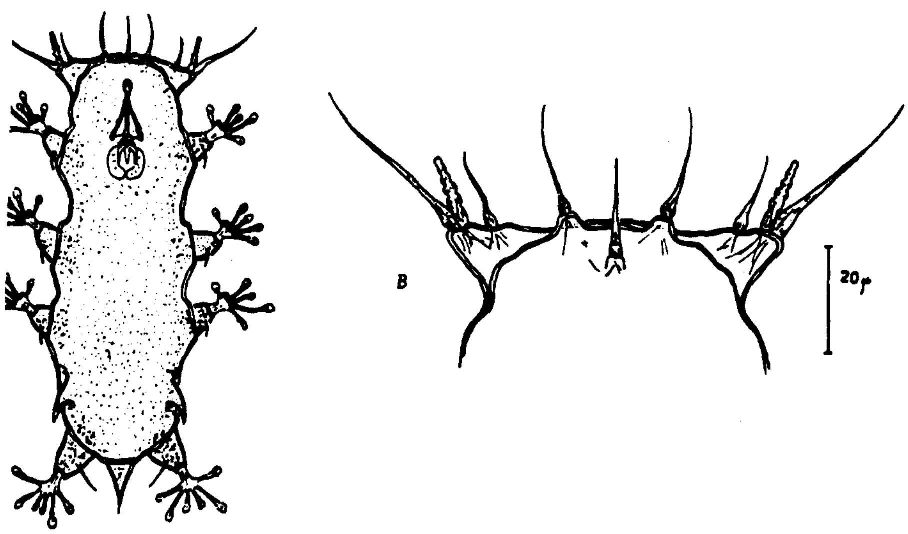


Fig. 49 - *Ba. annulatus* De Zio. A, dorsal view; B, details of the cephalic appendices (from De Zio).

BATILLIPES BULLACAUDATUS McGinty and Higgins, 1968 (Fig. 50).

Length 126μ; median cirrus (20μ) lacking base, internal buccal cirri (20μ) with base; external buccal cirri (14μ), inserted on the cephalic papillae; clavae (13μ); lateral cirri (28μ) originating from a base common with the clavae. The median cirrus, the internal buccal, and those lateral

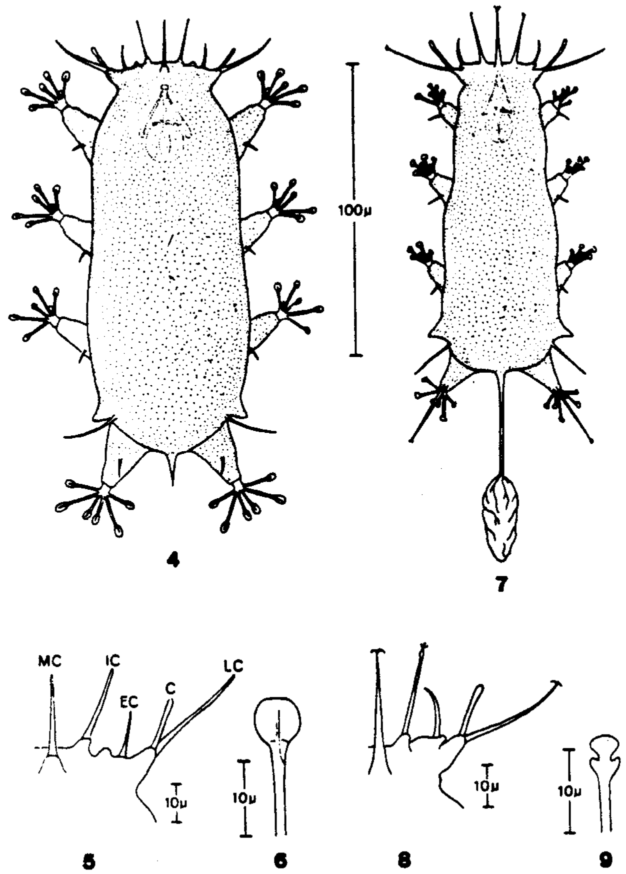


Fig. 50 - From 4 to 6: *Ba. mirus* Richters. 4, dorsal view of the adult; 5, right half of the cephalic zone of the adult (MC, median cirrus; IC, internal buccal cirrus; EC, external buccal cirrus; C, clava; LC, lateral cirrus); 6, digit; - From 7 to 9: *Ba. bullacaudatus* McGinty & Higgins. 7, dorsal view of the adult (holotype); 8, right half of the cephalic zone of the adult, dorsal view; 9, digit (from McGinty and Higgins).

are notched at the distal end (often trifid). Cuticle transparent, with uniformly arranged pores. Mouth ventral, buccal tube straight and narrow; pharynx subspherical. Eyes absent.

The cephalic region is bound by a constriction, posterior to the lateral cirri. The width of the body is caudally increased; two lateral conical and pointed projections, anterior to the 4th pair of legs; a long flexible spine (22μ) on each side, in posterio-lateral position with respect to the conical projections.

Short spine on the first three pair of legs, a long spine (28μ) on the 4th pair, extending over the extremity of the leg and distally notched; legs telescopic; adults with 6 digits of various length, terminated in a disk.

Caudal spine obvious, distally bearing a conspicuous bulbous hollow structure, characteristic, and of a type until now unknown among the tardigrades. Such appendage makes the determination of the species easy, which has a certain variability (individuals with a lateral "V" extension in the region of the neck, variation in the curvature and in the distal notching of the cirri and of the spines, in the size, in the shape of the 4th pair of legs at the base, in the presence or absence of the lateral spines and of those on the legs).

The species was discovered in a beach of coarse sand and sea shells, at a depth of 0-20 cm, at Sandy Point (Indian Field Creek, York River, Virginia) in the U.S.A., as well as Woods Hole, Massachusetts, and in addition in North Carolina, Florida, and also in Scotland.

BATILLIPES CARNONENSIS Fize, 1957 (Fig. 51).

Length up to 220μ, eyes absent. The lateral margin of the animal presents slight undulations, barely visible in living material, better in the preparations under coverslip: the first undulation, corresponding to the first pair of legs, is more developed than the others. The cuticle shows light streaks, particularly evident at the height of the legs and on the frontal (rostral) margin, which is rounded and does not possess cephalic papillae.

The median cirrus, dorsally inserted and not actually on the anterior margin, is slender and directed almost vertical; the internal buccal cirri, inserted on a base, are not different from those of *Ba. minus*, while the external buccal cirri are curved in constant and characteristic manner toward the internals and permit an easy identification of the species. Cirrus A and clavae without particular peculiarities, first three pair of legs provided with spine, while the legs of the 4th pair bear a very robust spine, curved toward the internal, so long as to reach the distal end of the digits.

Caudally, there is a long and slender median spine, inserted a little anterior to the caudal margin, which is prolonged into a kind of cone; the caudal spine reaches in length the distal end of the digits.

Above the 4th pair of legs there is a tooth-shaped lateral process: under it there is a slender bristle, however often absent, perhaps because subject to breakage, because of its fragility. The legs of the first three pairs bear six terminal digits, of which one is not pedunculate, two have longer

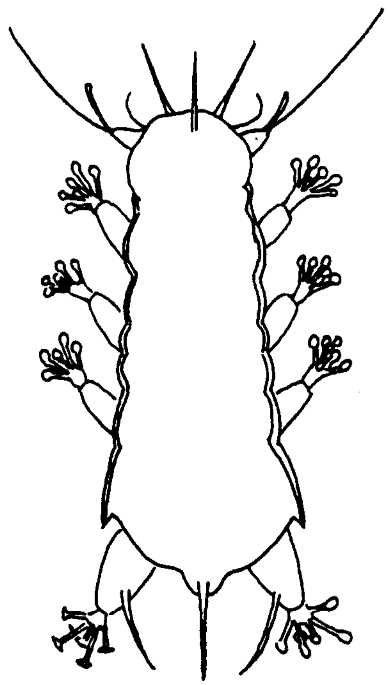


Fig. 51 - *Ba. carnonensis* Fize
(from Fize, redrawn).

peduncles, and three shorter peduncles; the legs of the 4th pair have six digits, all pedunculate, but of which two possess a shorter peduncle.

The species was taken from a depth of 0.5-1 m in the sand from the beach of Carnon (France).

BATILLIPES DICROCERCUS Pollock, 1970 (Fig. 52).

Description of the holotype: length from the base of the cephalic appendices to the base of the caudal process, 139.9μ; width of the head, between the bases of the lateral cirri A, 52.2μ; median dorsal cirrus, 16.3μ, including the base; external buccal cirri, 14.7μ, with base; clavae, 14.7μ; lateral cirri A, 26μ (on base common to the clava).

Cuticle transparent, with prominent and uniformly distributed pores, of about 1.5μ diameter. Pharynx subspherical of 15 x 13μ; eyes absent. The head is delimited by a posterior constriction at the lateral cirri; the width of the body increases in rostro-caudal sense. Anterior to the 4th pair of legs, the lateral margin of the body shows two prominent and sharp projections; lateral to these there are two spines E, 16.3μ long.

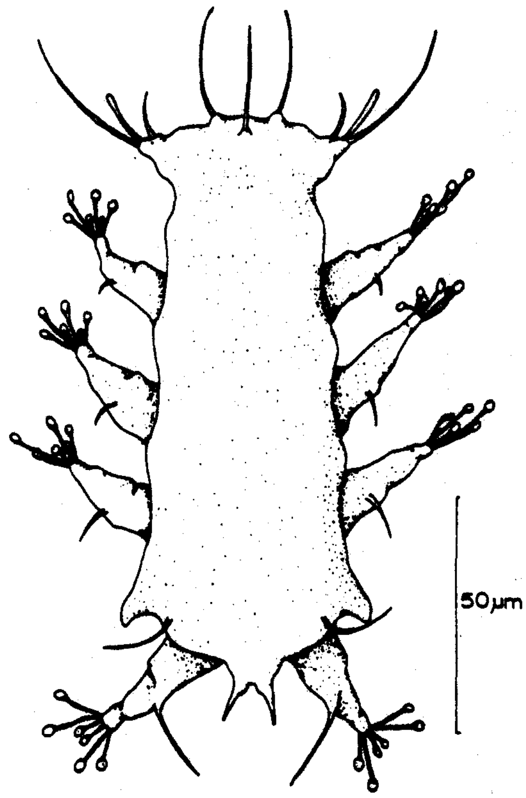


Fig. 52 - *Ba. dicrocercus* Pollock. Dorsal view (from Pollock).

Legs with spines, which increase in length from 3rd to 4th pair of legs: on the latter, the spines measure 21.1μ. Legs distally somewhat telescopic; 6 digits terminated in a disk, as described for *Ba. bullacaudatus*.

The species was collected in sand, of the 1st quarter of the average level of low tide, at a depth of 5-25 cm, at Woods Hole, Massachusetts, and at Santa Rosa Island, Florida (U.S.A.).

A report of Rodriguez-Roda (1947), on the Catalonian coast (Spain), cited as *Ba. mirus*, probably belongs to this species.

BATILLIPES FRIAUFI Riggin, 1962 (Fig. 53).

Length of the only two individuals observed, 200 and 208μ, eyes absent, cuticle smooth and colorless. The lateral margin of the body has only slight undulation, not counting a masked constriction posterior to the lateral cirri A. Between the 3rd and the 4th pairs of legs there are laterally two minuscule papillae (one per side) and dorsolaterally two long spines, turned backward. At the caudal end there is a spinous trifurcated process.

The buccal aperture is ventral and the buccal tube straight and narrow; stylets also straight, enlarged in a bulb at the caudal end; stylet supports present. Pharynx subspherical, 17.6-20.8μ long and 17.6-19.2μ wide. The cephalic appendices present are:

-- unpaired median cirrus, relatively short, very robust;
-- paired internal medial cirri, curved and with bulbose base;
-- paired cephalic papillae, rather small and laterally directed;
-- paired external medial cirri, departing from a bulbose base, curved and much shorter than the internal medial cirri;

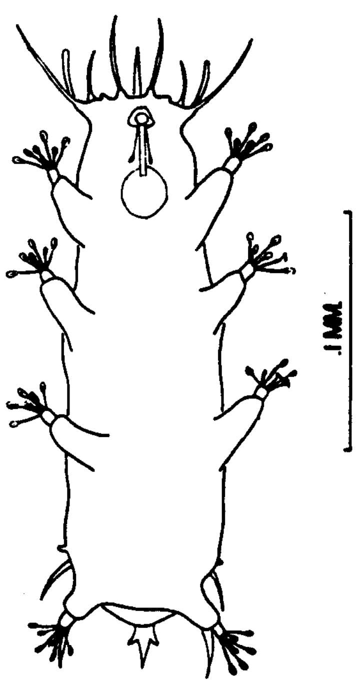


Fig. 53 - *Ba. friaufi* Riggin. Ventral view (from Riggin).

-- paired clavae, of club shape and which originate near cirri A from a common bulbous process of the cephalic region;
-- paired lateral cirri A, rather slender, a little longer than the internal medial cirri.

Legs of the fourth pair with a long dorsal spine, turned caudally; legs of the first three pair without spines. Six digits on each leg, terminated in a disk; the 2nd and the 4th digits are shorter than the others on all the legs. Locality of collection of the species: Alligator Harbor, Florida (U.S.A.).

BATILLIPES GILMARTINI McGinty, 1969 (Fig. 54).

Length 185μ; median cirrus (10μ) inserted on a base; internal buccal cirri (14μ) also on a base; external buccal cirri (14μ) ventral; clavae (11μ) with constriction at half its length; lateral cirri (39μ) rising from a common base with the clavae. Posterior lateral spine of about 16μ.

Cuticle transparent, with pores. Mouth ventral, buccal tube straight

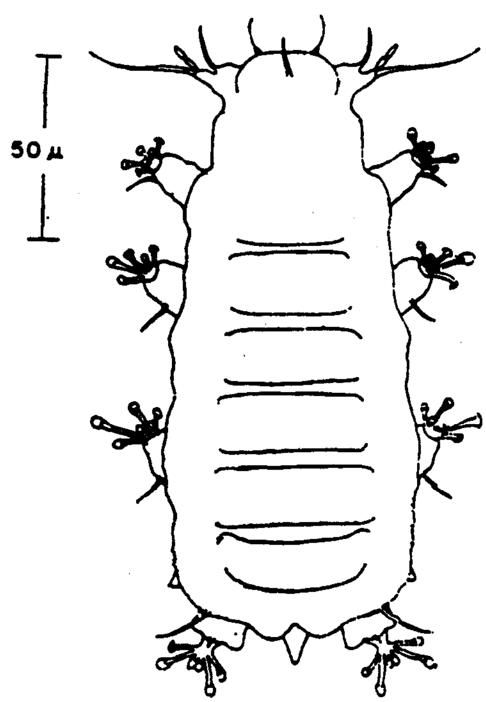


Fig. 54 - *Ba. gilmartini* McGinty. Dorsal view (from McGinty.

and slightly curved; pharynx spherical. Eyes absent.

Body incompletely subdivided into segments, with plates visible on the dorsum; width of the body slightly increasing in rostro-caudal sense. Slender lateral projections between the 3rd and the 4th pairs of legs. Digits terminate in spatulas, considerably developed and inserted on short legs, of which the first three bear a short straight spine. Median caudal spine blunt, without base, projecting between two caudal projections (gibbosities) of the body. On the 4th pair of legs a spine, with a small apical narrowing and terminated with a minuscule bulbous structure, visible only with immersion objective and phase contrast, but perhaps produced secondarily by the preservation technique.

Ba. gilmartini resembles *Ba. pennaki* by many characters, however distinguished by the two caudal projections at the sides of the median caudal spine, by the dorsal plates (a cephalic, indistinct, and 5 dorsal plates, often not well delimited). The species was collected in a sandy beach (granules of the sand of medium size), near Hopkins Marine Station, Pacific Grove, California (U.S.A.), at a depth of 0-20 cm.

BATILLIPES LITTORALIS Renaud-Debyser, 1959 (Fig. 55).

Length 180-200μ, width 70-80μ, exclusive of appendices, eyes absent. The cuticle is finely striated and has very pronounced lateral projections between the various legs and between the 1st pair of legs and the cephalic region. The median cirrus is inserted back with respect to the anterior margin of the head, and is dorsal, directed ventrally and 17μ long; the internal buccal cirri (paired) measures about 20μ. The external buccal cirri, the lateral cirri A, and the clavae (all paired) are implanted on a common base, but are not inserted on the same peduncle; the external buccal cirri measure 12μ and are inserted on a peduncle 5-6μ long; the common peduncle to lateral cirri A and the clavae is 9-10μ long, the clavae 17-18μ, and the lateral cirri 30-35μ. Cephalic papillae absent.

Buccal apparatus as in *Ba. mirus*. The legs all bear a very slender spine, longer (20-25μ) on the 4th pair of legs, which possesses also a robust chitinous spur, basal and external; at the distal end the legs have 6 digits, of varied length, terminated by an oval concave shovel. There are two dorsolateral flexible spines (25-30μ) at about where the appendices E are in the genus *Echiniscus*. The caudal end of the body is composed of a process of tripartite spine shape, much more obvious than those of *Ba. mirus* and *Ba. similis*. The morphological characters of *Ba. littoralis* are such that is makes it easy to distinguish from other species of the genus.

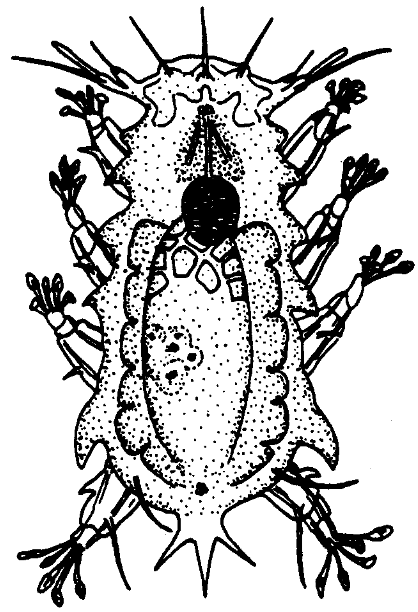


Fig. 55 - *Ba. littoralis* Renaud-Debyser. (from Renaud-Debyser, redrawn).

The species belongs to the interstitial fauna of the Arcachon Basin (Gulf of Guascogna) and was collected from the surface of the beach down to a depth of 80 cm; the maximum density of population (from 15 to 17 individuals per 75 cm^3 of sand) was found at depths between 20 and 50 cm.

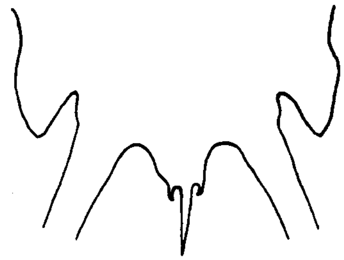
A subspecies has also been described:

Batillipes littoralis submersus D'Hondt, 1970 (Fig. 56).

Morphology identical to those of the species; the only difference of this variety is in the caudal trifurcate spine: such spine -- in the typical species -- is composed of three long points, rather fine and sharpened, departing from a common base; in the variety *submersus* instead, only the central spine in normally developed, while the two lateral points are reduced to minuscule spines, slightly bent toward the interior and barely visible.

The subspecies was collected in immersed marine sand at Roscoff.

Fig. 56 - Caudal appendix of *Ba. littoralis submersus* (from d'Hondt).



BATILLIPES MIRUS Richters, 1909 (Figs. 50 and 57).

Length up to 720μ, but in general 400-600μ; young individuals even 100μ and less; without eye pigment, however sometimes with small drops of fat, of variable size, on the external lobes of the supraesophageal (cerebral) ganglion; colorless, smooth cuticle, with weakly developed cuticular folds and barely visible external segmentation. Buccal aperture ventral; the cephalic appendages positioned dorsally with respect to the buccal aperture are: median cirrus (unpaired), internal and external medial cirri (both paired) slightly longer than the median cirrus; the internal medial cirri are positioned a little above, and the internals a little below the rostral margin of the tardigrade; between them there is the cephalic papillae (paired); the cirrus A (paired) is a long bristle, the clava is long, robust, slightly curved and has the characteristic clavate shaped point. All these appendices are inserted on a cuticular projection, or base, which in the case of cirrus A and of the clava is common to both and barely developed. Pharynx short oval, with three pharyngeal bars; stylet supports present. The appendices of the body are two robust lateral bristles, between the third and the fourth pair of legs, but closer to the latter, and a caudal median cirrus, a little shorter than the rostral median cirrus; there is also a small lateral marginal spine, not far from the base of the lateral bristle, but which may be present on only one side, or else totally lacking.

The median part of the legs is telescopically retractile into the wider proximal part, each with a basal and external spine; the legs are terminated with 6 digits, all always very obvious on the 4th pair, and in general also on the 1st pair and especially on the 2nd pair, a digit is almost always very short, to such an extent as to easily escape observation. The four central digits are arranged in two rows and have different length: the two internal, shorter, are inserted somewhat ventrally, and the two external, longer, somewhat dorsally. Each digit is terminated with a cuticular expansion in the shape of a shovel, reinforced by a median longitudinal thickening. Eggs probably deposited free.

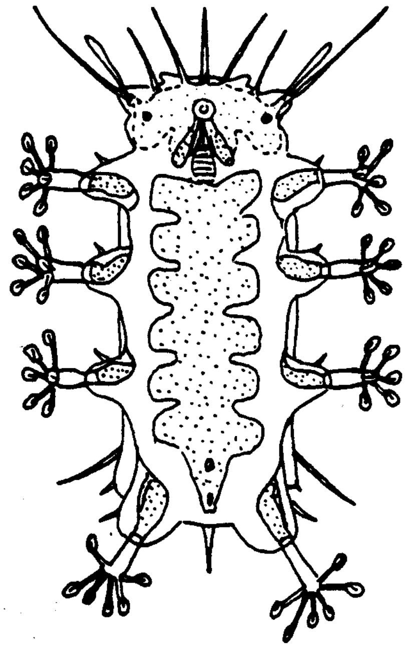


Fig. 57 - *Ba. mirus* Richters (from Marcus, redrawn).

McGinty and Higgins, in their extremely interesting publication (1968), give ample information on an abundant population collected at Sandy Point (Virginia, U.S.A.), of which they examined at least 5,600 individuals. The length of the *Ba. mirus* observed was less than that indicated above and varied between a minimum of 64μ and a maximum of 373μ. The cited authors divided the specimens collected into 5 arbitrary groups, according to the size and stage of development: they noted various morphological differences (for which refer to the original work) in different stages; in particular the young of the first two groups (that is to say those included between 64 and 120μ length) always have legs with 4 digits, rather than 6, as occurs in the adults.

The species belongs to the interstitial fauna of the marine coast and is collected, at depths varying from 0.30 m to 6 m, in sand of many beaches of Europe (French and Spanish coast of the Atlantic, Gulf of Leone, Italian Coast of Tirreno between Castiglioncello and Quercianella in Livorno Province, coast of the Black Sea, etc.); in the U.S.A. it has been collected near Beaufort, North Carolina, at Sandy Point, Virginia, and at Woods Hole, Massachusetts.

The species seems to be more frequent in stations of the temperate zone; it has been found however also at the Bahamas, in Florida, in Malaya, and in Madagascar.

Typ. loc.: Kieler Föhrde (Germany).

BATILLIPES NOERREVANGI Kristensen, 1978 (Fig. 58).

Body vermiform, not boxy (as *Ba. mirus*) or triangular (as *Ba. dicrocercus*). Length from 163 to 217μ. Head clearly delimited, even in adult animals. There are three lateral projections, as in *Ba. similis*, which however may also be lacking in part. The median cirrus and the internal cirri have a basal base, which is lacking for the external cirri. The clava is slightly S-curved, the lateral cirrus is relatively large. The legs bear long

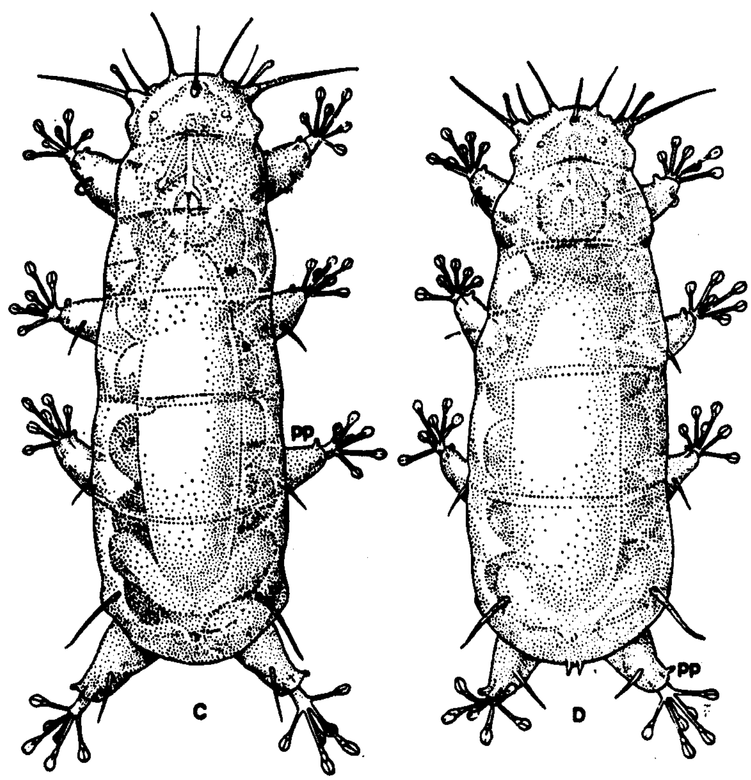


Fig. 58 - *Ba. noerrevangi* Kristensen. C, adult male without caudal appendices; D, mature male with two small caudal spines; pp, pseudopapilla (from Kristensen).

spines, of which those of the 1st pair are wrapped around those legs and are very long (13-16μ). Disks of the digits small, circular. Digits very long. The caudal spine is composed of two points, which may often be lacking (it is not ever a single spine). Eyes always present.

Ba. noerrevangi has been found in three localities of the Danish coast, in shallow water.

Typ. loc.: Niva Bay.

BATILLIPES PENNAKI Marcus, 1946 (Fig. 59).

Length of the adult 200μ, transparent, eye spots absent, cuticle with fine and dense granulation, intestinal contents of variable color. The lateral margin, between the 3rd and the 4th pair of legs, has a large projecting lobe (o in Fig. 59); the mouth is ventral; all the cephalic appendices are inserted dorsally, with respect to the buccal aperture. The pharynx is a short oval and the three pharyngeal bars have a knob enlargement at their bases (k); stylet supports present. The cephalic appendices -- all with conical base -- are the following:

-- very short median cirrus (unpaired);
-- medial internal cirrus (paired), longer than the median cirrus;
-- medial external cirrus (paired), longer than the median cirrus;
-- clava (paired), with basal part wider and distal part more slender, the two parts separated by a constriction;
-- lateral cirrus A (paired), in the shape of a long bristle, which arises together with the clava from a common base.

It is noted that the cephalic papilla is absent and that the medial internal cirri are inserted above the frontal margin, while the medial external cirri are on that margin.

The cuticular appendices of the body are two robust dorso-caudal spines (d) -- one per side -- positioned over the 4th pair of legs and somewhat posterior to the lateral lobes (o), as well as a large and sharp median caudal spine (s), twice as long as the cephalic median cirrus and arising from a wide cylindrical base. All the legs near their base bear a short spine; on the first three pair of legs the second digit is lacking the peduncle, while on the 4th pair it is lacking on the two central digits.

The species was collected in the United States (Massachusetts, Florida), at Bermuda, in Brazil (near Rio de Janeiro and near Santos), in different localities from France. In Italy it was found on the Apulian coast.

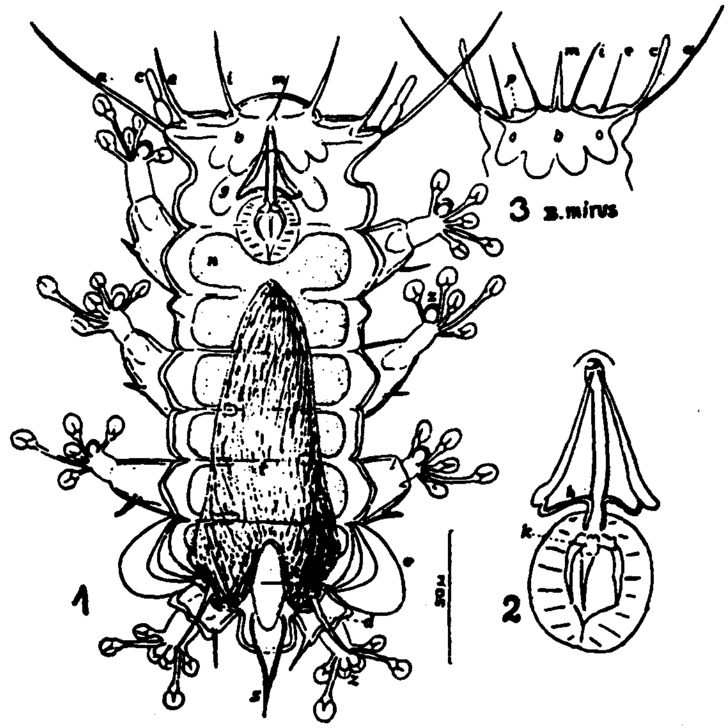


Fig. 59 - *Ba. pennaki* Marcus. 1, dorsal view: a, lateral cirrus; b, cerebrum; c, clava; d, spine; e, external medial cirrus; g, salivary gland; i, internal medial cirrus; m, median cirrus; n, intestine; o, marginal lobe; s, caudal spine; t, testes; z, nonpedunculate digit. 2, pharynx: h, stylet supports; k, knob thickening of the pharyngeal bars. 3, cephalic region of *Ba. mirus*, for comparison: p, cephalic papilla; the other letters as in 1 (from Marcus).

BATILLIPES PHREATICUS Renaud-Debyser, 1959 (Fig. 60).

Length 170-180μ, width 75μ, excluding the appendices; cuticle, even on the legs, very finely striated. The lateral margin of the animal, in the caudal zone, has a very accentuated projection, exactly over the 4th pair of legs. The head is more massive than in *Ba. littoralis* and bears appendices, inserted on a short base of 2-3μ height; there is a papilla (pa), slightly projecting, between the internal (medial) and external buccal cirri. The median cirrus, 15μ long, is inserted back with respect to the anterior margin of the head, and is vertically erect. The internal buccal cirri are

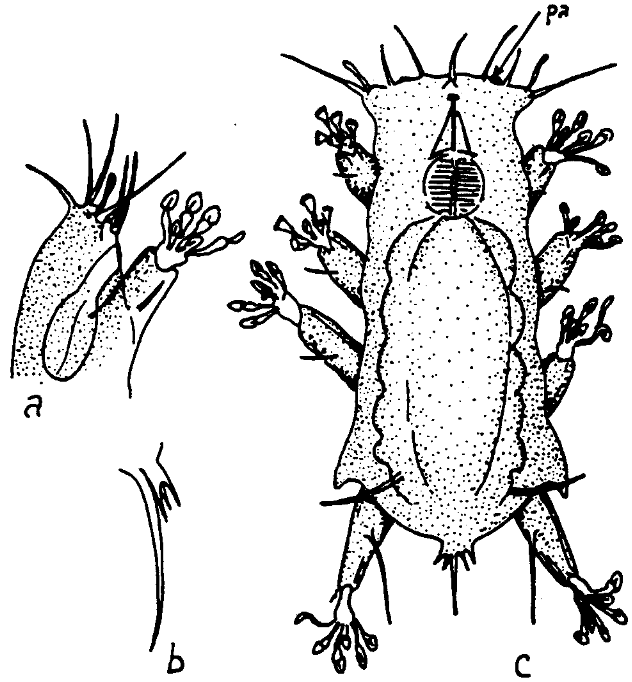


Fig. 60 - *Ba. phreaticus* Renaud-Debyser. a, lateral view of the cephalic region; b, lateral view of the caudal spine; c, habitus; pa, cephalic papilla (from Renaud-Debyser, redrawn).

22μ long and the externals about 15μ. Clava very characteristic, very refringent, speckled with brilliant black dots, 13-14μ long and distally curved toward the interior. Lateral cirri A about 30-32μ.

Buccal apparatus as in *Ba. minus*; the first three pair of legs with a fine bristle, the last pair with a bristle clearly longer (25μ); digits as in *Ba. littoralis*. Above the 4th pair of legs and in latero-dorsal position (approximately where appendices E are in the genus *Echiniscus*) there are two bristles (or slender spines) of 25-28μ, one on each side. Caudally there is -- in median position -- a long straight spine of 20-25μ, which bears at its base a variable number of smaller spines (from 2 to 4): with the increase in number of these secondary spines increases also the width of the common base, on which they are inserted, which varies from 5 to 10μ.

The species was observed in France, at Arcachon (Guascogna Gulf); it was collected only on the surface of the beach, in proximity to the phreatic layer, with a density of 28 individuals per 75 cm^3 of sand.

BATILLIPES ROSCOFFENSIS Kristensen, 1978 (Fig. 61).

Length from 230 to 250μ. Head well delimited. Body robust as in *Ba. mirus*, with three lateral prominences, of which the third has wing shape. The cuticle has a coarse granulation, composed of large dots disorderly arranged, similar to smallpox pustules. Lacking the terminal caudal spine, substituted by a furrow. The cirrus E is slender, not sculptured. The cephalic appendices are very long; the lateral cirrus measures up to 100μ.

The spines on the legs are turned caudally and dorsally: those of the 1st pair are shorter (or equally short) than those of the 2nd and 3rd; the spine of the 4th pair is short and robust. The terminal disk of the digits is wide and almost elliptical, with blunt apices.

The species, which is distinguished from other *Batillipes*, especially by the characteristic sculpture, was found only at D'aber de Roscoff.

BATILLIPES SIMILIS Schulz, 1955 (Fig. 62).

The denomination *similis* is due to a certain resemblance which the author noted with *Halechiniscus remanei*. According to Schulz, the 13 examples he observed can -- with regard to size -- be subdivided into two groups, one including individuals 105-130μ long and the other individuals of 145-170μ, morphologically indistinguishable; Swedmark (1956) has however found individuals even 200μ long.

The cephalic appendices are those usual of the Arthrotardigrada (median cirrus, internal and external medial cirri, lateral cirrus A, cylindrical and long clava, but shorter than the lateral cirrus; lacking the cephalic papilla). The author has observed that -- examining the animal dorsally -- one does not at once see the external median cirri, because they are covered by the common conical base of cirrus A and the clava; the median cirrus is obvious and at least as long as the internal median cirri and even more. Buccal aperture ventral; pharynx oval, with length:width ratio of about 1.2:1.

The characteristic more evident of the species is its conical lateral processes; even in *Ba. pennaki* (not in *Ba. mirus*) there are analogous processes between the 2nd and 3rd pairs of legs; but in the aforesaid two species there is no large process, curved in a hook, which *Ba. similis* possesses between the 3rd and the 4th pairs of legs. The body has also a obvious conical median caudal appendix, 18-20μ long, and two spines, one per side, in the position in which there are -- in the Echiniscidae -- appendices E. At the end of the proximal and wider region of the 4th pair

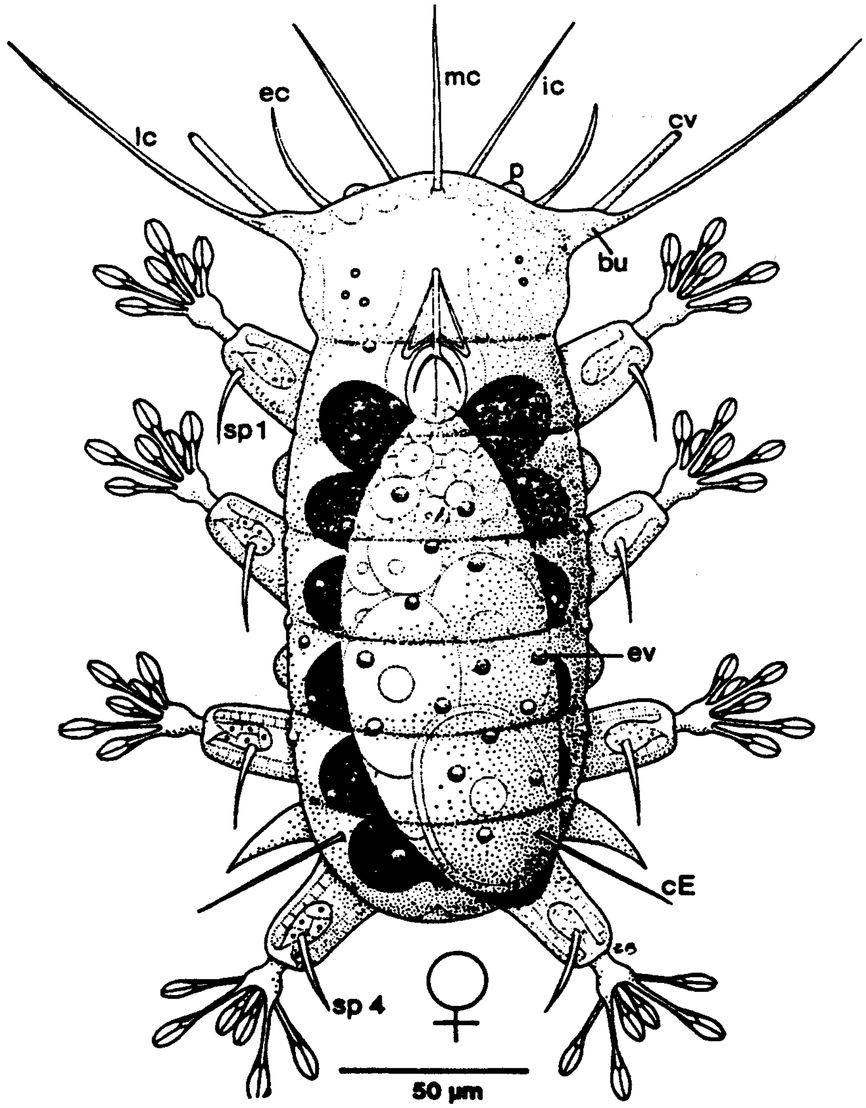


Fig. 61 - *Ba. roscoffensis* Kristensen (from Kristensen).

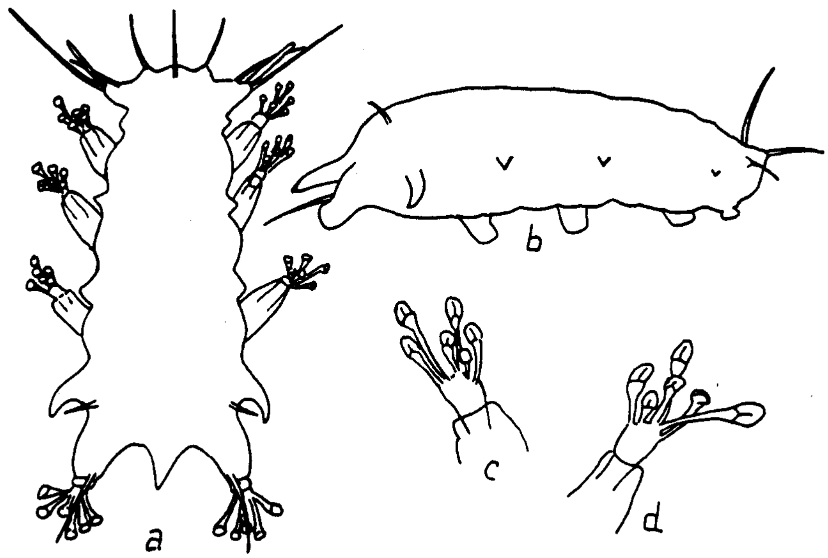


Fig. 62 - *Ba. similis* Schulz. a, dorsal view; b, lateral view: not drawn are the lateral cirrus, clava, and the distal end of the legs; c, distal end of a leg of the first pair (left); d, *idem*, of a leg of the third pair (right) (from Schulz, redrawn).

of legs, there is a long spine, which reaches the distal end of the digits; these are 6 in number and are terminated by a cuticular expansion in the shape of a shovel, typical for the genus *Batillipes*.

The species, which is part of the marine interstitial fauna, was collected in Italy (sand near Baia, in the Gulf of Napoli) and in France (sand of the beach near Marsiglia).

BATILLIPES TUBERNATIS Pollock, 1971 (Fig. 63).

Description of the holotype: length between the base of the appendices and the end of the body, 190μ. Width of the head, between the bases of the lateral cirri A, 44.2μ. Dorsal median cirrus, on base, 17.7μ. Internal buccal cirri, on base, 22.1μ. External buccal cirri, 14.4μ. Clavae, 11.7μ. Lateral cirri A, 25.4μ, from the common base with the clava.

Cuticle transparent, with pores in relief uniformly distributed; pharynx spherical, diameter 19μ. A slight lateral projection, between the head and the 1st pair of legs; elsewhere the contour of the body is smooth and the body does not become wider caudally. In position E (of the *Echiniscus*)

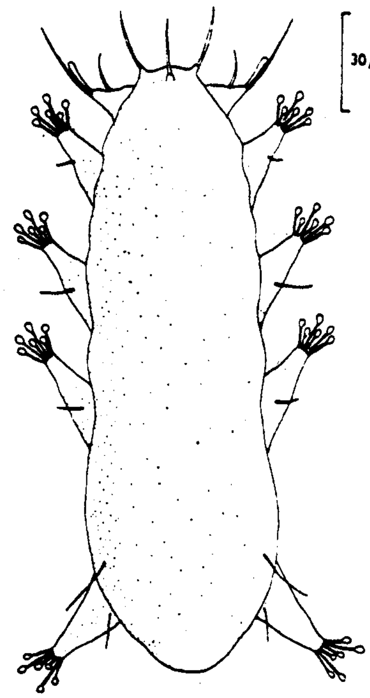


Fig. 63 - *Ba. tubernatis* dorsal view; (from Pollock).

there is a slender cirrus of 18.3μ, positioned dorsally and a little rostral with respect to the 4th pair of legs. Caudal profile of the body swollen and rounded (in the shape of rounded protuberance).

Robust spines on the legs; longest (12μ) are on the 2nd pair, shorter on the 1st, 3rd, and 4th pairs, of about 6.5μ in length. Legs distally somewhat telescopic and with 6 digits each.

The species was collected in Firemore Bay, on the western coast of Scotland (England), at depth of 5-12 cm, in sand (granules of 220μ average), just above the level of the low tide (typ. loc.).

Also, in England (Yorkshire), in Germany (Elba estuary), and in numerous localities of Florida.

Genus *BRYOCHOERUS* Marcus, 1936.

Diagnosis: Echiniscidae, median plates 1, 2, and 3 divided transversely, so that there are visible in total six median plates; lacking the incisions on the terminal plate.

KEY TO THE SPECIES

1.	Terminal plate not facetted	2
	Terminal plate facetted	*Br. intermedius* forma *hawaiica*
2.	Caudal part of the median plates 1 and 2 sculptured with more or less reticular design, while the caudal part of plate 3 is smooth, not sculptured	*Br. intermedius*
	Caudal part of the median plates 1, 2, and 3 smooth, not sculptured	*Br. intermedius* forma *laevis*

BRYOCHOERUS INTERMEDIUS (Murray, 1910) (Fig. 64).

Length about 109-150μ, colorless, or yellowish, or else greenish-yellow; eyes present and red (Australia), or absent (Brazil); the sculpture of the Australian material is composed of an assemblage of wide and flat depressions (5-6μ diameter), whose margins form a reticular design of hexagonal elements, without leaving free and smooth transverse bands on

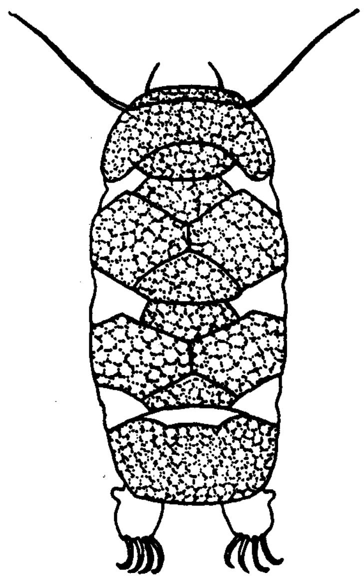


Fig. 64 - *Br. intermedius* (Murray). (from Murray, redrawn).

the paired plates. The three median plates of the genus *Echiniscus* are here transversely subdivided in two, as is characteristic for the genus *Bryochoerus*, and should be considered 6 distinct plates; they are however sculptured, with exception of the caudal portion of median plate 3 (or posterior segment of the median plate 3), which is smooth. There are no dorsal appendices; the only lateral appendix is cirrus A, of about 40μ in animals 150μ long. Papilla on the 4th pair of legs, which are provided with dentate collar; internal and external claws without spurs. The only individual (length 109μ, with cirrus A of 26μ), collected by Barros in Brazil, is somewhat different: the sculpture is an extremely fine punctation, spread on all the plates -- including the caudal part of the median plate 3 -- which leaves however free and smooth a transverse band on the paired plates (as in *Br. intermedius laevis*); there are also two tiny and short spines (teeth) on the anterior margin of the caudal part of median plate 3; the terminal plate has three facets, one dorsal and two lateral, while lacking the two notches, always absent in the genus *Bryochoerus*.

The species appears to be very rare, and is known only from Australia (typ. loc.) and a single example from Brazil, although regarded as the nominate subspecies.

There have been described two forms:

Br. intermedius forma *hawaiica* (Thulin, 1929) (Fig. 65).

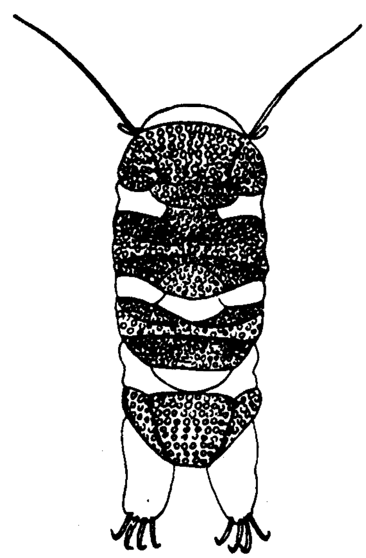


Fig. 65 - ***Br. intermedius*** **forma** ***hawaiica*** **Thulin (from Murray, redrawn).**

Length 190-220μ, sculpture similar to that of *Br. intermedius*, to which the reader is referred, although the median plate is present; the sculpture covers the rostral and the caudal part of the median plate 1, while it is limited to the rostral part -- leaving free and smooth the caudal -- on the median plates 2 and 3. The median plate 3 is separated from the terminal only by a slender line; the paired plates bear transverse grooves. The terminal plate has three facets, a dorsal and two lateral, and does not have notches. The only appendices of the body are the cirri A, relatively long (about 70μ ?); absent are the papilla and the dentate collar of the 4th pair of legs; claws without spurs. Eggs oval (about 32 x 50μ), deposited in the exuvium.

Br. intermedius forma *hawaiica* was collected only on the Hawaiian Islands (Oahu).

Br. intermedius forma *laevis* (Marcus, 1936) (Fig. 66).

Small size, length about 150μ, stylet supports present. The sculpture is a fine punctation, which leaves free and smooth a transverse band on the paired plates and which is lacking on the caudal part of the median plates 1, 2, and 3, as well as a small caudal zone on the rostral part of the median plates 2 and 3. Terminal plate not facetted. The only appendices of the body are the cirri A; on the 4th pair of legs there is a papilla and a weak

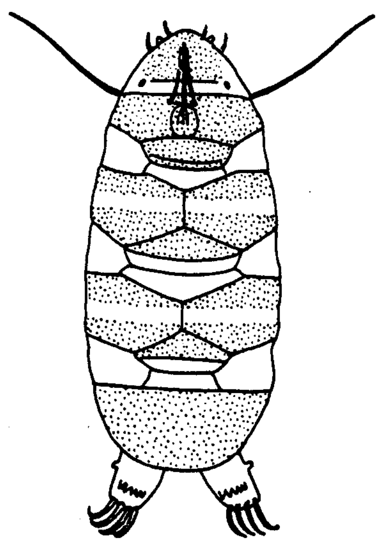


Fig. 66 - *Br. intermedius* forma *laevis* (Marcus) (from Marcus, redrawn).

dentate collar, composed of 5 sharp teeth, in contact with each other at the bases.

Br. intermedius forma *laevis* was collected only one time in Germany (Turingia).

Genus *BRYODELPHAX* Thulin, 1928.

Diagnosis: Echiniscidae with median plates 1 and 2 divided transversely, while the 3rd is single; there are then visible in total 5 median plates; lacking the notches on the terminal plate.

KEY TO THE SPECIES

1. Terminal plate clearly facetted; no supplementary lateral plates 2
   Terminal plate indistinctly facetted; small supplementary lateral plates; dentate collar with 12 teeth .... *B. alzirae*

2. Dentate collar on the 4th pair of legs absent 3
   Dentate collar present 5

3. There is a ventral sculpture composed of 6 rows of sclerified surfaces .... *B. sinensis*
   There is no ventral sculpture 4

4. Cirri A longer, from a quarter to a third of the length of the animal; on the terminal plate the facetting defines a median (central) facet, whose angles run straight and originates about the anterior margin of the same terminal plate ...... *B. parvulus*
   Cirri A very short, length only a fifth of the length of the animal; on the terminal plate the facetting does not extend to all the plate but begins only a certain distance from its anterior margin .... *B. ortholineatus*

5. There is a ventral sculpture composed of 8 rows of sclerified surfaces; cirri A bifid .... *B. weglarskae*
   There is no ventral sculpture 6

6. The sculpture is composed of an extremely fine granulation, evident only with strong magnification (better with oil immersion and phase contrast); dentate collar with 4-6 teeth .... *B. tatrensis*
   The sculpture is composed of a coarser granulation, evident already at approximately 300X magnification; dentate collar with 3-8 teeth .... *B. amphoterus*

BRYODELPHAX ALZIRAE (Du Bois-Reymond Marcus, 1944) (Fig. 67)
= *Echiniscus* (*B.*) *alzirae* Du Bois-Reymond Marcus, 1944

Small size, length from 140 to 160μ, color brick red, eye spots red, sculpture composed of red, irregularly arranged granules. The species has no lateral or dorsal cuticular processes, with exception of the usual cephalic appendices and cirri A, about 25μ long; the median plates 1 and 2 are transversely divided, while plate 3 is undivided; on each side of these three plates, there is a small median supplementary plate (6 then in total), especially visible observing the tardigrade laterally. The terminal plate is indistinctly facetted and not notched, or incised. Legs of the 4th pair with papilla and dentate collar, bearing 12 minuscule teeth.

The species is very similar to *B. parvulus* and *B. tatrensis*: it differs however from the first by the presence of the lateral plates and the dentate collar and from the second by the same lateral plates and because the dentate collar of *tatrensis* has at maximum 6 teeth.

B. alzirae has so far been observed only in Brazil (Bertioga, State of Sao Paulo).

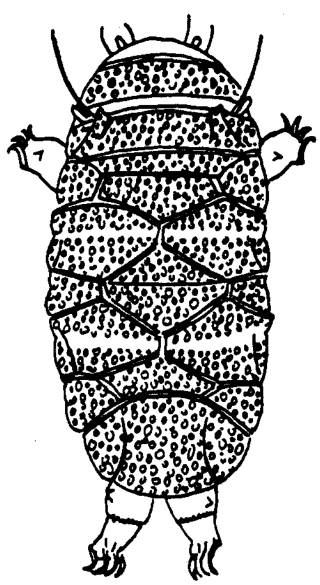
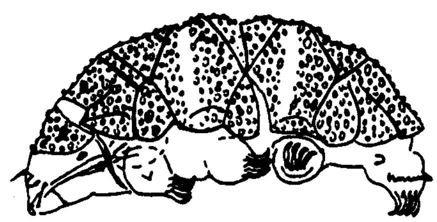


Fig. 67 - *B. alzirae* du Bois-Reymond Marcus (from du Bois-Reymond Marcus, redrawn).



BRYODELPHAX AMPHOTERUS (Durante and Maucci, 1975) (Fig. 68).
= *Echiniscus (B.) amphoterus* Durante & Maucci, 1975.

Size up to 190μ, colorless or very slightly rose, eyes small, black, sometimes lacking.

The sculpture is a regular punctation, formed of equidistant granules, of slightly stellate shape; this granulation is very evident and marked (more than in *Br. parvulus*) on the rostral half of the cephalic plate, on all the scapular, on the caudal half of the paired plates, and on all the terminal plate; the other portions of the plates have a sculpture with analogous character, but decisively finer. Some granules, much larger, strongly refringent, are found irregularly sparse, especially at the margins of the scapular and the terminal plates, and at the sides of the paired plates. The cuticle between the plates is smooth on the sides, and has an extremely fine regular granulation on the ventral surface. The terminal plate does not have notches and is facetted in the majority of the examples

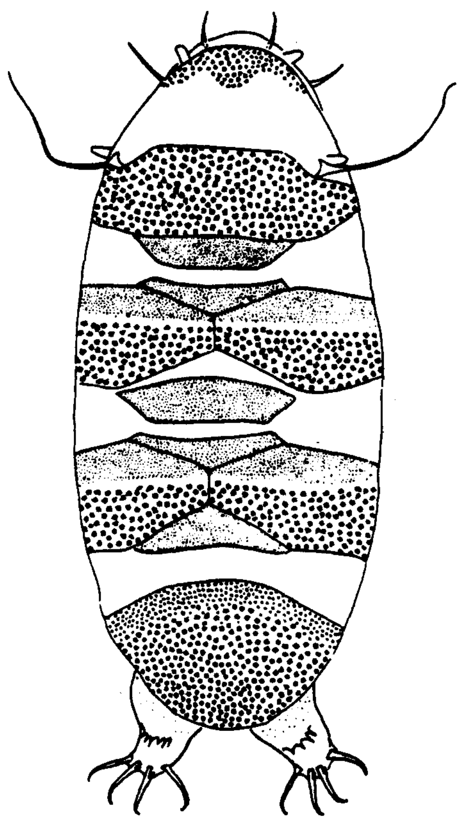


Fig. 68 - *B. amphoterus* (Durante and Marcus) (from Durante and Marcus).

observed: the facetting seems absent in about 25% of the examples.

The lateral cirrus is from 40 to 50μ long.

The 4th pair of legs has a dentate collar with from 3 to 8 teeth, usually long and sharp, sometimes however short and stumpy. The internal claws of all the legs have a large spur, slender, very curved; the external claws have an extremely small spur, very difficult to observe, extremely near the base.

This species has been found in different localities from Carso Yugoslavia (Istria, Postumiese, Bainsizza). Typ. loc.: Ucka (Mt. Maggiore, Istria).

BRYODELPHAX ORTHOLINEATUS (Bartos, 1963) (Fig. 69).
= *Echiniscus* (*B.*) *ortholineatus* Bartos, 1963.

Length about 110μ, colorless and transparent, small, eyes of clear red color, often indistinct. Lateral cirri A very short (about 22μ). Rostral portion of the median plates 1 and 2 very large, pentagonal, having size considerably bigger than the caudal part, that is, small and triangular. Median plate 3 triangular, large, with longer side narrowly in contact with the anterior margin of the terminal plate; the latter very developed, with

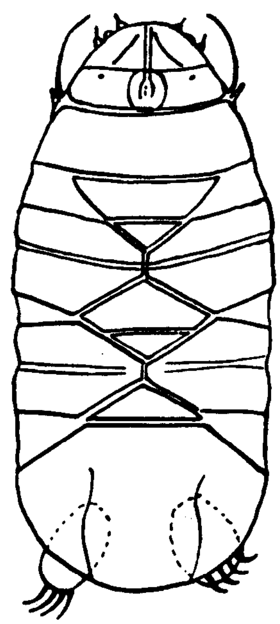


Fig. 69 - *B. ortholineatus* Bartos (from Bartos).

anterior margin straight in its median portion, and folded backwards laterally. The notches and facetting lacking does not apply to the entire terminal plate, rather only to approximately the last two-thirds of its length. The median (central) facet, defined from the facetting of the plate, has the lateral edges which run rather sinuous, and not straight as in *B. parvulus*.

Claws supplied with spurs; the author has not been able to observe if the spine on the first pair of legs and the papilla on the fourth pair are present or absent: this is because the examples examined had the legs almost completely retracted. Eggs unknown.

This species differs from *B. parvulus* especially by the small length of cirri A, by the shape of the median plates 1, 2, 3, and by the different facetting of the terminal plate. Because the observation of the median plates -- and especially of 3 -- is often difficult in *Bryodelphax*, it is always advisable to treat the tardigrade with a KOH solution, in order to obtain a complete extension of the animal, legs included.

The species was collected in moss at Puntjak Pass, between Bogoe and Bandung, in Java (typ. loc.) and on the Andamana Islands.

BRYODELPHAX PARVULUS Thulin, 1928 (Fig. 70).
= *Echiniscus* (*B.*) *parvulus* Auct.

Length 150-175μ, colorless, or greyish, or with reddish granulation; eye spots red color in the living animal. Sculpture of the plates coarse and regularly arranged, with exception of the scapular (I) and terminal (IV)

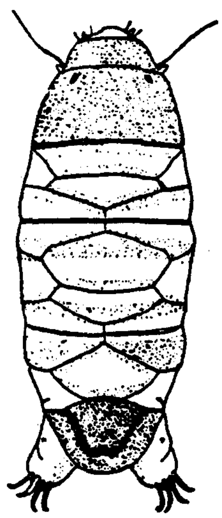


Fig. 70 - *B. parvulus* (Thulin).

plates, on which it is possible to distinguish -- with strong magnification -- an extremely fine, dense and uniform granulation; in some individuals there is a transverse band almost devoid of sculpture on the paired plates (II and III). The median plate 3 is well developed and has a characteristic shape (semi-circle surmounted by a triangle), which is rendered visible when the animal is completely extended, for example after treatment with KOH; the median plates 1 and 2 are divided transversely in two, as always in the genus *Bryodelphax*; the terminal plate is strongly facetted and does not have notches. The stylets are short, slender and straight, and there are stylet supports.

First pair of legs with a slender spine and fourth pair with a blunt papilla, not always present; the dentate collar is absent. Internal claws generally with small spurs, which -- according to Marcus -- may sometimes be lacking. Eggs ovoid, colorless or yellowish, deposited in the exuvium and having the greater dimension of about 45-46μ. The larvae with two claws measures from 50 to 85μ.

The species, widespread, is known from numerous localities from Europe (also common in Italy), from Brazil, Canada (Vancouver Island), Sumatra, Vietnam, and Angola.

It is however probable that many old reports of this species refer instead to *Br. tatrensis* or to other species of the genus. Type loc.: Lapland.

BRYODELPHAX SINENSIS (Pilato, 1974) (Fig. 71).

Length up to 120μ, colorless, eyes red. The cephalic plate and the scapular have a mid-dorsal fold and some transverse folds; the terminal plate is strongly facetted, and has an anterior facet elongated transversely and three posterior facets elongated longitudinally. The plates have a very fine and uniform sculpture (as in *Br. tatrensis*) and larger dots irregularly sparse. The posterior half of the unpaired plates and a transverse band on the paired plates are devoid of sculpture.

On the ventral surface sclerified surfaces are present in the form of platelets distributed in six transverse rows: the caudal row includes three plates, one of these is situated posterior to the anal aperture, and two at the side of it; in correspondence with the third pair of legs there are two sclerified elliptical surfaces; there follows two circular areas and, still more forward two other elliptical, two circular, and finally then two elliptical.

Cirrus A up to 27μ long. On the fourth pair of legs there is no dentate collar. On all the legs the internal claws have well developed spurs.

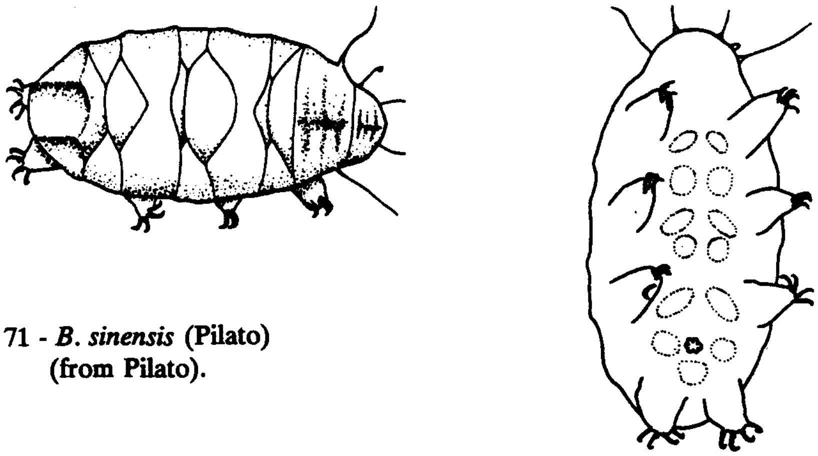


Fig. 71 - *B. sinensis* (Pilato)
(from Pilato).

The species was collected in moss on tree bark in China (near Canton).

BRYODELPHAX TATRENSIS (Weglarska, 1959) (Fig. 72).
= *Echiniscus* (*B.*) *tatrensis* Weglarska, 1959

Length up to 176μ, in general 150μ. The tardigrade, with superficial examination, does not differ from *B. parvulus* (to which description refer), but more detailed observation shows various differences. Colorless, or greenish gray; eye spots red-orange. Plates well delineated, covered with an extremely fine granulation, which is rendered evident only at strong magnification (better using immersion objective and phase contrast) and not -- as in *parvulus* -- already at about 300 magnification. Besides this extremely fine, there is, irregularly sparse on all the surface of the plates, larger granules, similar to those that one observes at the margin of the cephalic and terminal plates of *parvulus*. Cephalic papilla large and flattened (length 5μ, width 3.7μ in an individual of 153μ); lateral cirrus A straight (32-33μ). Papilla on the 1st and the 4th pair of legs: the latter bears the dentate collar, characteristic of the species (absent in *parvulus*), composed of 4-6 (usually 5) sharp teeth, very long and slender. Claws of the 4th pair of legs longer (10μ) than those of the first three pair of legs (7.5μ). In its description, Weglarska does not speak of spurs on the internal claws, which perhaps -- as in *parvulus* -- may be present or absent; in an individual of *tatrensis*, collected in Austria, I seem to perceive a minuscule spur, very near to the base, on the internal claws of the 4th pair of legs.

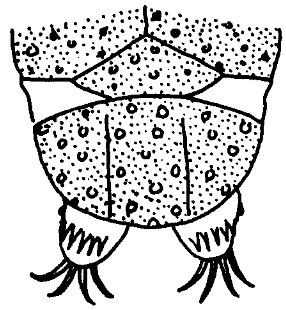


Fig. 72 - *B. tatrensis* (Weglarska). Caudal region and 4th pair of legs.

Marcus (1929) had already observed -- in material from Germany and from Indonesia -- in *parvulus* a dentate collar, thinking however that such character fell within the limits of variation of the species; however the very different sculpture, the size of the cephalic papilla, and the presence of the collar sufficiently justify -- in our opinion -- the separation of *B. tatrensis* from *B. parvulus*.

The species was collected in Germany, Poland, Austria, and Indomalaysia; recently it was found also in Sicily, on the Apuane Alps, Istria, and Carso, in Verona, and in Yugoslavia.

BRYODELPHAX WEGLARSKAE (Pilato, 1972) (Fig. 73).
= *Echiniscus* (*B.*) *weglarskai* Pilato, 1972

Maximum length 111μ, eyes red. Terminal plate with two longitudinal folds which seem to have facetting, and without incisions. Shape and sculpture very similar to *B. tatrensis*, from which it is distinguished by the sculpture of the ventral surface: this, in fact, has sclerified areas (similar to platelets) in constant number and position; it has double sculpture (uniform fine granulation and large irregularly distributed dots), while between the sclerified areas the cuticle has only a uniform and extremely fine granulation. The ventral sclerites are in 8 transverse rows, thus arranged: 2 under the head, only one and ample approximately between the anterior legs, then 5 (of which the central 3 are arranged in a triangle), 4 immediately behind the 2nd pair of legs, then two rows of 2 sclerites each (the second between the 3rd pair), finally a caudal row of 3 sclerites, of which the central is posterior to the anal aperture.

Cirri A, 25μ, are bifurcated at the ends. The internal and external buccal cirri are also bifurcated.

Fourth pair of legs with papilla and dentate collar of few teeth, but well developed. Claws of the legs of the fourth pair about 8.1μ. Internal claws with slender spurs.

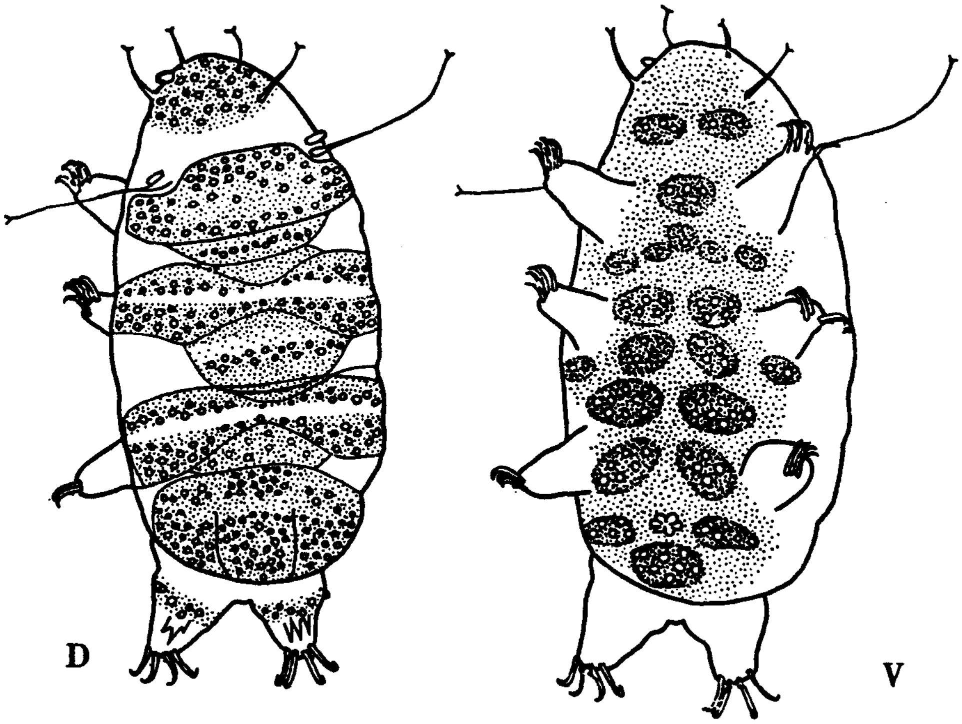


Fig. 73 - *B. weglarskae* (Pilato). D, dorsal view; V, ventral view (from Pilato).

In the 1st and 2nd paired plates and in the first two unpaired plates there is a transverse band devoid of sculpture, with indistinct margin. The cuticle between the plates is smooth.

The species was collected from moss from Marettimo (Cala Rossa, Egadi Islands).

Genus *CALOHYPSIBIUS* Thulin, 1928

Diagnosis: Calohypsibiidae with rigid buccal tube, not spiral, without reinforcement bar; mouth without lamellae; the two doubleclaws of each leg are similar in shape and size, with 2121 sequence; both the doubleclaws have the branches rigidly connected; sculptured cuticle.

KEY TO THE SPECIES

1. The cuticle has spines more or less long, arranged in transverse rows .... *Cal. ornatus*
   The cuticle has granules, tubercles, or plates 2

2. There are rounded, or slightly truncate conical tubercles, arranged in transverse rows, but united to form plates .... *Cal. ornatus caelatus*
   The cuticle has small irregularly dispersed granules, which form a prominent transverse ridge, or else are intermingled with larger plates 3

3. There are no plates present, but the granulation is grouped to form protuberances or prominent transverse ridges; or else there are also flattened plates, only on part of the dorsal surface (usually in the median zone) .... *Cal. verrucosus*
   There are flattened plates on all the dorsum, symmetrical with respect to the median line, arranged in about 6-7 transverse rows, and between these there are often smaller plates, together with a granular sculpture .... *Cal. placophorus*

CALOHYPSIBIUS ORNATUS (Richters, 1900) (Figs. 74, 75, 76 & 77).

= *Macrobiotus ornatus* var. *spinifer* Richters, 1900
= *Hypsibius* (*Calohypsibius*) *ornatus* + var. *spinosissima* Marcus, 1936
= *Hypsibius* (*Cal.*) *ornatus typicus* + *H.* (*Cal.*) *ornatus carpaticus* Bartos, 1940
= *Hypsibius* (*Cal.*) *armatus* Bartos
= *Hypsibius* (*Cal.*) *intermedius* Mihelčič, 1939

This is an extremely variable species, which often is as in Fig. 74 -- rather schematic -- but which may appear morphologically very diverse; with 32 known varieties, all assembled in Fig. 77. Bartos (1940) has completed a very thorough study of the variability of *ornatus*: before explaining -- in brief summary -- his conclusions, we think however advisable to describe the more common appearance of the species.

Length up to about 180μ, eye spots absent: in the position which they occupy, there are instead two papillae. On the dorsum and on a good portion of the lateral surface are present 8 transverse rows of cuticular spines or thorns (from 8 to 12 per row); the first transverse row is situated

Fig. 74 - *C. ornatus* (Richters) (from Richters, redrawn).

in correspondence with the first pair of legs, the last in correspondence with the fourth pair and has particularly long spines. The cephalic region bears rounded papillae, similar to small knobs, and these papillae are also found dorsally and laterally, between the rows of spines. Buccal tube very narrow, pharynx oval with apophyses and 2 macroplacoids (rounded granules); lacking microplacoid; doubleclaws of each leg of about equal size and *Calohypsibius* type appearance.

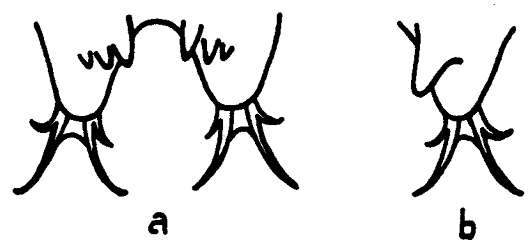


Fig. 75 - *C. ornatus* (Richters) *carpaticus* Bartos. a, fourth pair of legs; b, right leg of the fourth pair of the variety *δ-transgrediens* with a single tubercle (from Bartos, redrawn).

With regard to the 32 varieties of *ornatus*, we shall now -- because of space -- limit ourselves to mention very few, referring those interested to the cited work of Bartos. This author distinguished then two forms -- or better, subspecies -- of *ornatus* and specifically *H.* (*C.*) *ornatus typicus* and *H.* (*C.*) *ornatus carpaticus*: the latter is especially characterized by the presence of 1-3 conical tubercles on the dorsolateral internal surface of each leg of the 4th pair (Fig. 75), which is lacking in *ornatus typicus*. Each of the two subspecies is subdivided in turn into two ecological races, one stenohygrophilic, the other euryhygrophilic, which is designated with numbers 1-13 for the varieties of *ornatus typicus* and with numbers 14-32 those -- more numerous -- of *ornatus carpaticus*; the stenohygrophilic race of *ornatus typicus* (race α of Bartos) includes numbers 1-6 (first horizontal row); those euryhygrophilic (race β), numbers 7-13 (second horizontal row); the stenohygrophilic race of *ornatus carpaticus* (race γ) includes numbers 14-19 (third horizontal row) and those euryhygophilic (race δ and ε); the second of the forma *septemcinctus*, the third of the forma *heterospinosus*, the fourth of the forma *laterospinosus*, the fifth of the forma *costatus*, the sixth of the forma *glaber*, the seventh of the forma *transgrediens* and the eighth of the forma *finalis*. As we see from the figures, only one race (the δ) has the entire series of the forms.

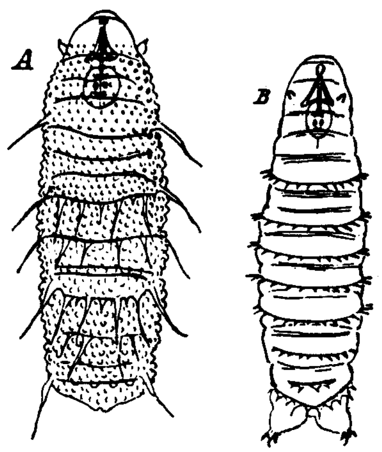


Fig. 76 - *Cal. ornatus* (Richters) *spinosissimus* Richters. A, form with long, irregularly arranged spines; B, form with shorter spines, regularly arranged (from Marcus).

A better explanation with regard to this opinion, we cite three examples of nomenclature: in Fig. 77 the No. 6 is *ornatus typicus α-glaber*, No. 16 is *ornatus carpaticus γ-heterospinosus*, No. 27 is *ornatus carpaticus δ-finalis*.

The variations considered interesting are those of the sculpture of the cuticle: in the stenohygrophilic races (α, γ), from individuals with long spines, amongst spines always shorter, to animals completely, or almost, devoid of sculpture; in the euryhygrophilic (β, δ), from individuals with long spines to instead to animals with the cuticle partly with spines and partly with granules, or little knobs ("pearls" according to Bartos) or papillae, or nipples, or else various combinations of all these cuticular appendices, as shown in Fig. 77.

According to Bartos, included in the series of variations of *ornatus typicus* and *ornatus carpaticus* is: *H.* (*C.*) *armatus* Bartos, *H.* (?) *indicus* (Murray), *H.* (*C.*) *ornatus caelatus* Marcus (Fig. 78), *H.* (*C.*) *ornatus*

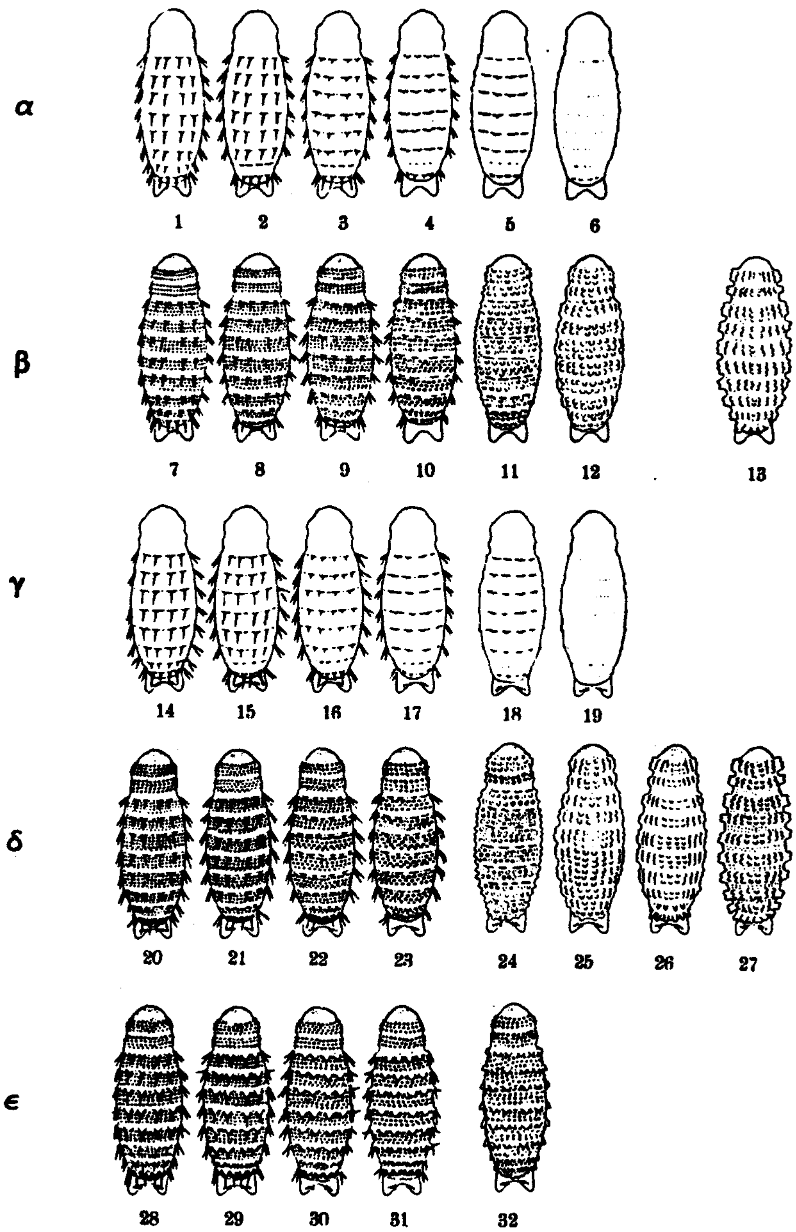


Fig. 77 - Varieties of *C. ornatus* (Richters). 1-6, race α (stenohygrophilic); 7-13, race β (euryhygophilic); 14-19, race γ (stenohygophilic); 20-27, race δ (euryhygophilic); 28-32, race ϵ (euryhygophilic). From 1 to 13 are included in the variety *ornatus typicus*; from 14 to 32, the variety *ornatus carpaticus*. The first figure of each row represents the 5 "initial" forms of each race (α - ϵ), the second ones are the variety *septemcinctus*, the third ones the variety *heterospinosus*, the fourth ones the variety *laterospinosus*, the fifth ones the variety *costatus*, the sixth ones the variety *glaber*, the seventh ones the variety *transgrediens*, the eighth ones the variety *finalis* (from Bartos).

oligospinosus Bartos, *H.* (*C.*) *ornatus spinosissimus* Richters (Fig. 75) and, partially, *H.* (*C.*) *verrucosus* (Richters). As a matter of principle we are agreed with this opinion of Bartos, except for *H.* (?) *indicus*, whose belonging to the genus *Calohypsibius* does not seem definitely certain (see the description of *indicus*); we wish then to add that included certainly among the variation of *ornatus carpaticus* also the species described in 1939 by Mihelčič with the name *H.* (*C.*) *intermedius* (treated probably as *H.* (*C.*) *ornatus carpaticus δ-finalis*).

The work of Bartos is naturally very interesting since it is the most complete work on the problem of intraspecific variability in the Tardigrada. We do have however some reservations on the ecological value of the described forms, which perhaps have need of more numerous observations. On the other hand it is evident that the names suggested by Bartos, according to the International Code of Zoological Nomenclature, do not have taxonomic status. For this reason, we prefer to keep the classic taxonomy, for which the forms supplied with spines arranged in transverse rows (which are long or short) represent the nominal species *Cal. ornatus*, while the following is considered a subspecies:

Cal. ornatus caelatus (Marcus, 1928) (Fig. 78). Length up to about 175μ, eyes absent; the cuticle is covered with small, rounded tubercles, arranged in transverse rows, while there is a reduction of the spines, which -- typically -- are totally lacking; sometimes reaching a total disappearance of the tubercles, so that the cuticle is completely (?) smooth. The buccal tube is -- in some cases -- somewhat longer than normal (Fig. 78C), as however may happen in all the varieties of *ornatus*; placoids and doubleclaws as in *Cal. ornatus*.

Cal. ornatus, with all its varieties, is very common in mountain localities, usually (but not always) at altitudes higher than 800-1,000 meters. There are numerous reports from Europe (Italy included), South America (Colombia), New Zealand, and Greenland. Typ. loc.: Taunus.

Cal. ornatus caelatus is cited by Marcus for Scotland and Ireland (typ. loc.), by Bartos for Switzerland, and by Marcus for Scandinavia: it is probable that this variety often accompanies the nominate subspecies in many damp localities.

CALOHYPSIBIUS PLACOPHORUS (Da Cunha, 1943) (Fig. 79).
= *Hypsibius* (*Cal.*) *placophorus* Da Cunha, 1943

Length up to 220μ, short, eye spots present; colorless, or slight yellowish. Buccal tube very narrow, pharynx spherical with apophyses and

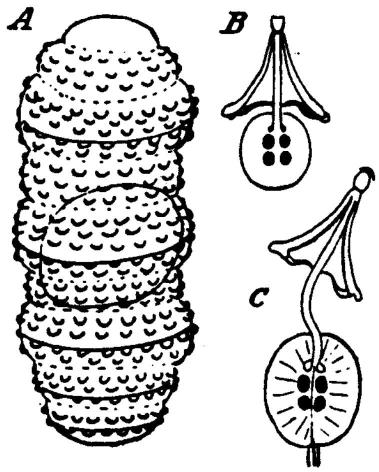


Fig. 78 - *Cal. ornatus* (Richters) *caelatus* Marcus. A, dorsal view; B, typical buccal apparatus and pharynx; C, buccal apparatus with longer buccal tube and pharynx (from Marcus).

and 2 macroplacoids of round granular shape, of about equal size; microplacoid absent. The cuticle is granulated and covered with extremely numerous papillae (granules) and plates of various size; also on the legs there are many small tubercles. The plates have -- for the most part -- small size and irregular shape, but also are arranged on the dorsum with a certain symmetry, with respect to the median line, and calls to mind a little the plates of the Echiniscidae. Also in the young (of 140μ) there is already a pair of dorsal plates in correspondence with each pair of legs, and another pair in the region between the pairs of legs. The anterior plates -- or rather those of the first four rostral pairs -- are more regular and constant; in the caudal region there is a tendency toward the fusion of the single plates, and even toward the formation of supplementary plates. There are then other plates -- sufficiently developed and symmetrically arranged -- in dorsolateral position; Fig. 79 is an example. The doubleclaws, short and robust, are of the *Calohypsibius* type, with accessory points on the principal branches. Eggs unknown.

Cal. placophorus is certainly a very near species to *Cal. verrucosus*; we think however that it should be kept distinct from the latter, because of considerable development of the plates and of their symmetrical development.

The species was collected in moss and lichen on rocks from a single locality from Portugal (Cabril do Ceira, near Coimbra).

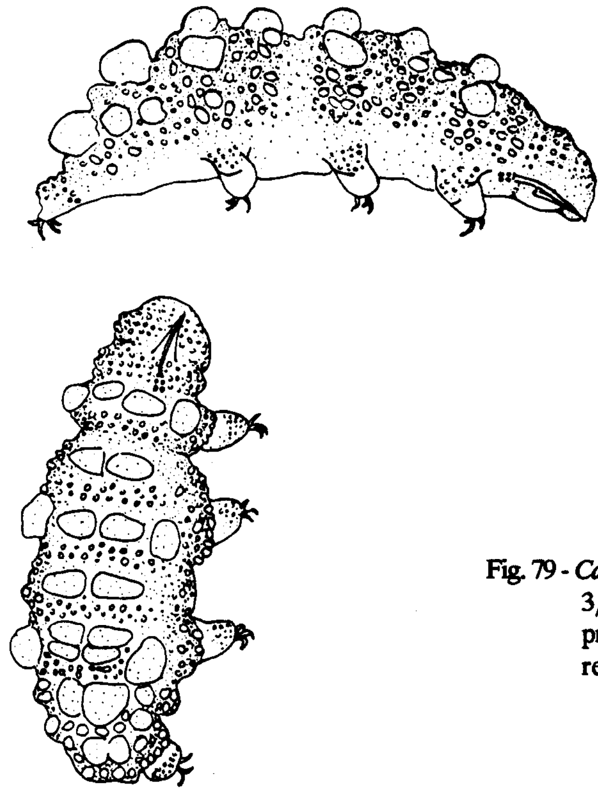


Fig. 79 - *Cal. placophorus* Cunha. 3/4 dorsal view and in profile (from da Cunha, redrawn).

CALOHYPSIBIUS VERRUCOSUS (Richters, 1900) (Fig. 80).
= *Calohypsibius scabrosus* Thulin, 1928

Length up to about 250μ, eyes in general present, body rather massive and short. The cuticle is covered with numerous minuscule tubercles, of different size and often angular, that may unite in mass. These tubercles are found on all the surface of the body, including the legs (where they are smaller), with exception sometimes of some dorsal inconstant transverse zones and of the rostral caudal region. There is a certain bilateral symmetry in the arrangement of the tubercles: they are united to form on the dorsum very protruding transverse bands, especially visible in profile; other times there are instead small dorsal plates, more common between the third and fourth pairs of legs. Buccal tube very narrow (1μ diameter),

Fig. 80 - *Cal. verrucosus* (Richters) (from Marcus and Cuènot, redrawn).

curved at the entrance into the pharynx; stylets small; pharynx spherical, with apophyses and 2 macroplacoids (granules), a little longer than wide; lacking the microplacoid. Doubleclaws large and wide, with secondary branch considerably robust; the principal branch bearing accessory points. Only one egg is known, oval (larger diameter 64μ), deposited in the exuvium.

It is possible -- as rightly thought Bartos (1940) -- that a part of *verrucosus* of the author should instead be considered belonging to the extremely variable species *Cal. ornatus*; we do not go into more detail, limited to say that here are considered as *verrucosus* the *Calohypsibius* (Fig. 80) which have dorsal platelets, or else in which the tubercles combine to form on the dorsum very protruding transverse bands; in fact such appearance does not ever occur in *ornatus* and its varieties. Individuals with larger dorsal plates, symmetrically arranged -- especially in the rostral region -- so much so that it calls to mind the plates of the Echiniscidae, belong to the species *Cal. placophorus*, certainly very near to *verrucosus*.

Of *verrucosus* are known reports in various European localities, Italy included, in Brazil, and in Vietnam. Typ. loc.: Taunus (Germany).

Genus *CARPHANIA* Binda, 1978.

Diagnosis: Oreellidae with total appearance of the Eutardigrada, without armor, legs not digitate. Two claws on the first three legs, a single on the fourth pair.

CARPHANIA FLUVIATILIS Binda, 1978 (Fig. 81).

The body, colorless, appears very slender and in the four examples found has a length between 186μ and 290μ; such measurements do

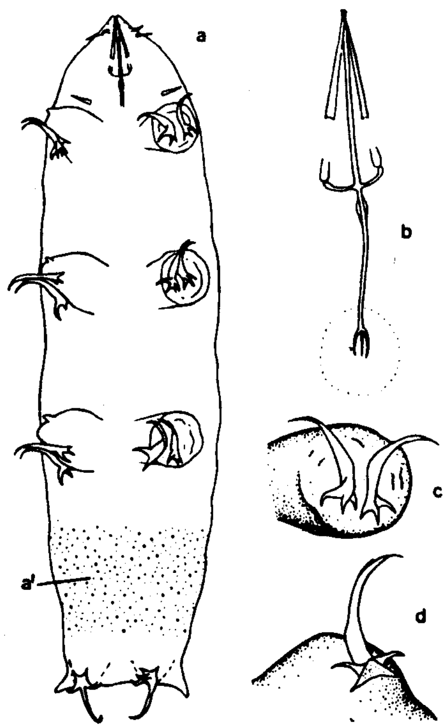


Fig. 81 - *Car. fluviatilis* Binda. a, habitus; a', details of the sculpture of the body; c, claws of the first three pair of legs; d, claw of the fourth pair of legs.

exclude those which can be treated as young individuals. Caudally the body ends with two obvious conical protuberances which extend dorsally to the posterior legs. The eyes are absent and the cuticle, both dorsally and ventrally, is uniformly strewn with small granules.

The cephalic appendices are rather short: the buccal cirri are situated in more dorsal position and appear shorter but more robust than the laterals. In an example 220μ long the median cirri are about 4μ long and the laterals about 5μ. Even the cirrus A is rather short, measuring 8.5μ in the larger examples. Such cirri are turned dorsally so that, given their shortness, they may escape a superficial observation. The cephalic papilla and the clava seem to be absent in all the examples. The mouth is subterminal. The buccal tube, from the mouth to the beginning of the pharyngeal bars, is 41μ long in the larger examples, and less than 1μ wide. The stylet supports are slender and short. Posteriorly to the stylet supports the external wall of the buccal tube appears, for a brief distance, thickened without the diameter of the lumen of the tube being reduced. The pharyngeal bulb contains the typical pharyngeal bars of the Heterotardigrada.

The legs appear short and are not digitate. On the first three pair is present a conical papilla with blunt apex which measures 5.3μ on the first pair of legs of an example 290μ long. On the 4th pair of legs no papilla seems to be present.

The claws, well developed, are two on the first three pair of legs and only one on the fourth pair. Each claw is composed of a single piece differentiated into a more ample basal portion and a long and slender branch bearing two slender accessory points (the latter structures have not as yet ever been pointed out in the Oreellidae). The basal portion of the claws is not plain but bent at a dihedron angle and its four angles are each prolonged into a robust spur: two constitute in practice the base of installation of the claws of the leg, the other two are instead turned laterally and toward the apex of the claw. By way of the particular conformation of the basal portion, the two basal spurs, thus as the two superior, are not opposite but form between them an angle. The total length of the claw, in an example 220μ, is 12μ on the first pair and about 16μ on the fourth pair of legs.

Cal. fluviatilis was found in the Saracena stream, near Raudazzo (Catania, Sicily).

Genus *CORNECHINISCUS* Maucci and Ramazzotti, 1981

Diagnosis: Echiniscidae; besides the paired plates I and II, there is a pseudosegmental plate, paired or unpaired; body level ventrally and convex dorsally; cirrus A of conical shape, wide at the base, curved, hollow, with "a dagger blade" appearance; the sculpture bears a W design on the scapular plate; claws without spurs.

KEY TO THE SPECIES

1. Besides cirri A, other obvious dorsal and lateral appendices ..... *Co. holmeni*
   Besides cirri A, there are no appendices (except possibly on the pseudosegmental plate), or else there are only small or extremely small spines 2

2. There are neither spines nor dentate collar on the fourth pair of legs 3
   On the fourth pair of legs there is a dentate collar formed of one or more teeth 4

3. The posterior margin of the pseudosegmental plate is straight or slightly sinuous; there are no spines, neither lateral nor dorsal .... *Co. cornutus*
The posterior margin of the pseudosegmental plate has from 1 to 3 extremely small spines; there are also extremely small spines dorsally at D and laterally at C and D .... *Co. schrammi*

4. The posterior margin of the pseudosegmental plate bears two triangular spines, short and blunt; cirrus A is very short (equal or less than the external buccal cirrus) 5
The posterior margin of the pseudosegmental plate bears an obvious lobing, paired or unpaired, sometimes supplied with one or more apical teeth 6

5. Size up to over 700μ; folds and bands not sculptured on the plates simulating supplementary plates; squat, short lateral spines C and D and strong spine E; dentate collar formed of 2 teeth .... *Co. tibetanus*
Size not above 330μ; extremely small lateral spines C and D (which may also be lacking); a single tooth on the 4th pair of legs; the external claws have a small spine near the base .... *Co. subcornutus*

6. Besides the lobing of the pseudosegmental there are no other dorsal appendices; extremely small lateral teeth C and D (at times absent); on the 4th pair of legs a robust tooth, at the place of the dentate collar .... *Co. lobatus*
Besides the lobing of the pseudosegmental, there are dorsal teeth B, C, and D, and dorsolateral C' and D'; also lateral teeth B, C, and D (all these teeth may be lacking in some positions); on the 4th pair of legs a dentate collar of 3-7 teeth .... *Co. ceratophorus*

CORNECHINISCUS CERATOPHORUS (Maucci, 1972) (Figs. 82 & 89).
= *Pseudechiniscus ceratophorus* Maucci, 1972

Large size, as much as 540μ; body massive, with dorsal arched and ventral side flat; eye spots black, elliptical, very small, often absent. The sculpture is a coarse granulation: the granules are regular, sub-round, rather uniformly distributed; between them exists smaller granules, dot-

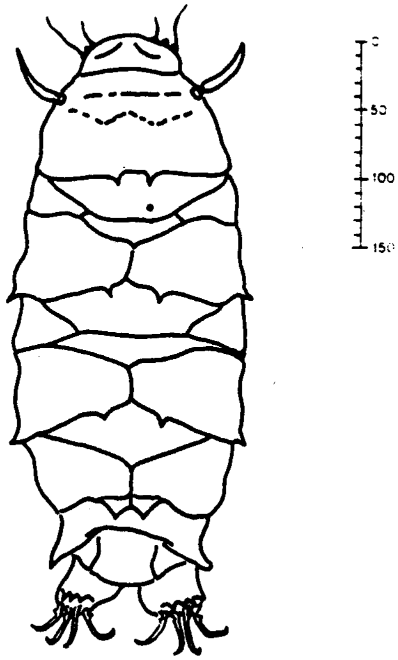


Fig. 82 - *Co. ceratophorus* (Maucci) (from Maucci).

shaped. Such sculpture is present also on the cuticle between the plates.

Cephalic plate strongly facetted; the scapular has a W design, showing a fold and a band void of sculpture; rostrally to the W exists another transverse fold. Intersegmental plates 1 and 2 divided transversely, 3 undivided. Pseudosegmental plate divided (paired) with a caudal lobing, composed of two triangular points, projecting up. Terminal plate clearly facetted, with distinct notching, connected by a transverse fold, which simulates the limits of a supplementary plate; in position E the corner of the faceting is projecting and forms two pointed structures, sometimes divergent, similar to robust spines.

Internal buccal cirrus short, with wide and conical bases; external buccal cirrus slender and very long. Lateral cirrus A short, wide, 20μ long, width at the base 4; it is a little wider than the cirrus A of *Co. holmeni* and a little less than that of *Co. lobatus*. At the base, cirrus A has a constricting collar. Laterally there are short and squat triangular spines B, C, D; dorsally small spines B, C, and D, whose position and development varies greatly; often they are very near to the median line, sometimes more displaced laterally; the spines B^d are longer (about 6μ); in about half the examples there exists also extremely small dorsolateral spines C' and D'.

Shorter legs than usual (for this genus), sculpture on the proximal half;

the first pair with strong spine, the fourth with large papilla on the interior side; dentate collar with 3-4 large, sharp teeth (rarely 2 or 7), somewhat distant at the bases. Claws without spurs.

Exuvia have been observed with 4-5 yellowish, subspherical eggs.

Numerous examples of this species were collected in different samples from three localities from southern Turkey, in moss in full sun and very dirty.

CORNECHINISCUS CORNUTUS (Richters, 1906) (Figs. 83 & 89).
= *Echiniscus cornutus* Richters, 1906
= *Pseudechiniscus cornutus* Thulin, 1911, and Auct.
= *Pseudechiniscus intermedius* Mihelčič

Maximum length up to 460μ, but usually less. Body ventrally flat and dorsally arched. Color red-orange. Eye spots large, black, elliptical. The plates of the carapace have few distinct margins, sometimes confusing. The cephalic plate is strongly facetted. The scapular plate has a band devoid of sculpture in the shape of a W, which follows a hollowed transverse band, with very fine sculpture. The unpaired 1, 2, and 3, are undivided. The paired I and II sometimes have a transverse fold, barely marked. The pseudosegmental is paired, with straight caudal margin, sometimes slightly sinuous: there are neither lobes nor spines. The terminal, not facetted, has extremely small notches.

The internal buccal cirri are very short, conical, those external are rather sword-shaped.

The appendices A are short, rather curved: they arise from a low conical base, which follows a restraining collar. The "sword shaped" appearance is from the fact that this appendix is conical, internally hollow.

The sculpture is composed of granules of rounded outline, between which exists, sparsely, other granules much smaller. On the ventral side there is a granulated zone, not delimited as plates.

Besides cirrus A there are no other appendices. Only a few examples show a very small spine in position E. In extremely few examples may be two small dorsal spines B.

The legs are relatively short and squat, and have the basal part sculptured. On the first pair of legs the usual spine is lacking, which is present in a few examples. The fourth pair has neither dentate collar nor isolated spines. The claws are rather short, without spurs.

This description is based on numerous examples found in Turkey and Greece, which have made possible a redescription of this species.

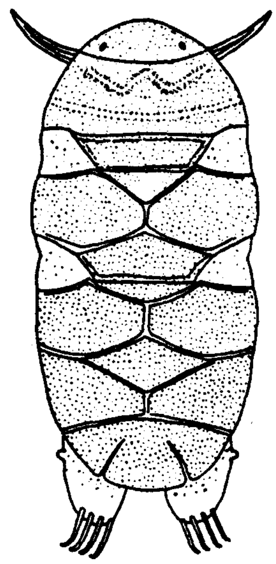


Fig. 83 - *Co. cornutus* (Richters)
(from Richters, modified).

In material from Hindukush, collected by Dastych, was found a little different characters; the unpaired plates 1 and 2 were divided transversely.

The species is cited for central Europe, Bulgaria, Rumania, northern Italy, Greece, Turkey, and Cyrenaica. Typ. loc.: Palalinato (Germany).

CORNECHINISCUS HOLMENI (Petersen, 1951) (Figs. 84 & 89).
= *Pseudechiniscus holmeni* Petersen, 1951

Length from 460 to 670μ, body rather elongated and slender, brownish red color, eyes in general present (in about 75% of the population studied by Petersen) and black. The sculpture is a fine and regular granulation, less intense on the cuticle between the plates; the median plates have transverse bands of finer sculpture. The cephalic plate is strongly facetted, and the scapular bears a design in the shape of a W and three depressions, one median and two lateral, as well as a transverse line; the paired plates have well delineated transverse folds; the two incisions of the terminal plate appear almost connected to each other by a curved line, with the convexity turned rostrally. The cephalic appendices (paired) are characteristic: internal medial cirrus very short, cephalic papilla slightly projecting and hemispherical, external medial cirrus of usual type, but short in relation to the size of the tardigrade, clava extremely small and visible with difficulty.

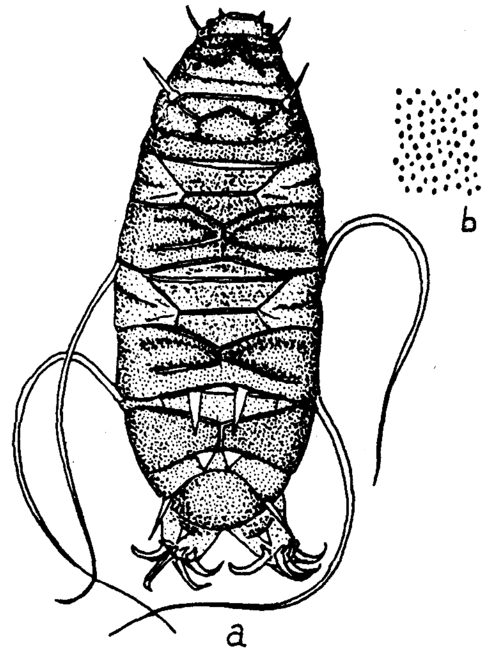


Fig. 84 - *Co. holmeni* (Petersen). a, dorsal view; b, detail of the sculpture of the plates (from Petersen, redrawn).

The cirrus A is very short (28-40μ), with sword-shaped appearance, similar to those of *Co. cornutus* (however in proportion considerably shorter).

The lateral appendices, besides cirrus A, are: long filaments C (260-400μ), D (240-370μ), and spines E (22-40μ). Dorsally there are robust spines D^d (10-33μ) and two large teeth (length 8-17μ) on the posterior margins of the pseudosegmental plate, near the median line. Legs robust: those of the 1st pair bear a spine of 15μ on the external side and those of the 4th pair have a spine completely similar rather than the dentate collar. Claws rather short (30-38μ) on the first three pair of legs, longer on the fourth pair (38-54μ) without spurs. Oval eggs (105 x 90μ) deposited in the exuvium; the larvae of 2 claws observed measured from 290 to 320μ.

Co. holmeni was described for the first time from Greenland. A second report, by Weglarska, from the island Axel Heiberg (Canada).

CORNECHINISCUS LOBATUS (Ramazzotti, 1943) (Figs. 85, 86, & 89).
= *Pseudechiniscus cornutus* forma *lobata* Ramazzotti, 1943
= *Pseudechiniscus cornutus lobatus* Ramazzotti, 1962 & 1972

= *Pseudechiniscus cornutus* Mihelčič, 1966; Dastych, 1972, et al.
(not Richters, 1906)

Length up to 640μ, reddish color, eyes black, oval, and voluminous. The median plates 1 and 2 are clearly transversely divided into two parts; the median plate 3 is undivided. The sculpture of the plates is a coarse granulation, which is extended even on part of the external surface of the legs and on the cuticle between the plates. On the scapular plate is observed a design in the shape of a W, in slight relief, smooth, without sculpture: behind it is a transverse smooth line, which however is not always present. Cephalic papilla barely projecting, internal and external medial cirri and lateral cirri A as in *Co. cornutus*.

The pseudosegmental plate III is longitudinally divided into two (paired) in the individuals of all Italian and Austrian localities, while it is undivided (unpaired) in those of Switzerland, collected by Bartos (1950). At the posterior margin of the pseudosegmental plate there are two lobes, more or less pronounced, of shape slightly different from one individual to

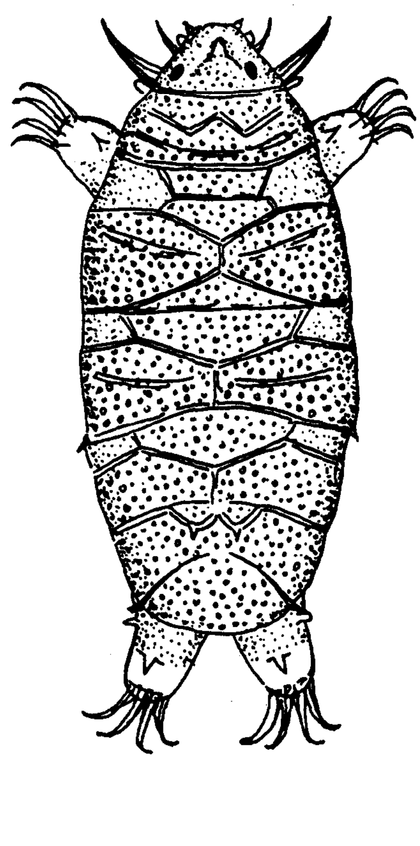
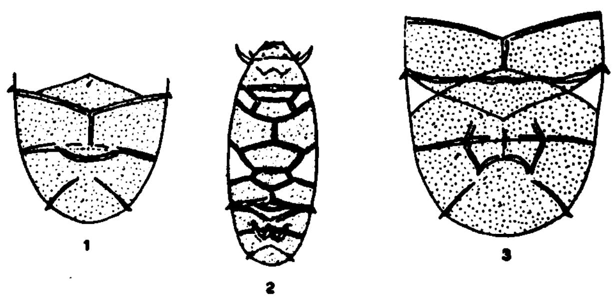


Fig. 85 - *Co. lobatus* (Ramazzotti).

another; sometimes each lobe bears an extremely small tooth, sometimes two, or else one lobe has two teeth and the other, one; rarely there aren't any teeth visible.

Some examples have the pseudosegmental plate caudally prolonged into an appendix composed of a single lobe, rather than of two, and such lobe may be provided with teeth, or else having two, symmetrical with respect to the median line of the dorsum. The appendices of the pseudosegmental plate, characteristic of this variety, are posteriorly turned up, so that in profile the animal appears as in Fig. 86-5; also the posterior margin of the second paired plate (III) has a smaller appendix (Fig. 86-3, 5, 6), however bent up and which in extremely rare cases may bear one or two extremely small teeth. In the larvae of two claws the special conformation of plate III is already well defined (Fig. 86-7). The terminal plate has the two notches.

Laterally there are minuscule teeth D and E, so slight that they easily escape observation. The legs of the first pair bear a spine, those of the 4th



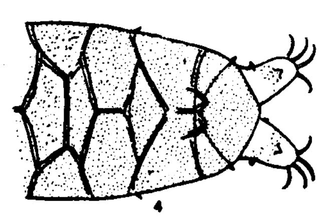
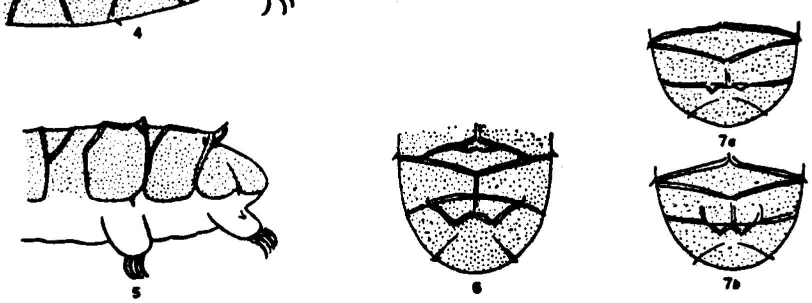


Fig. 86 - *Co. lobatus* (Ramazzotti). Variability in the appendices of the pseudosegmental plate, already well defined in larvae of two claws (7a), schematic representations.



pair the usual papilla and a wide triangular process (tooth shaped) at the position of the dentate collar, which is absent. The eggs (2-3), of yellowish-red color, are deposited in the exuvium.

Co. lobatus is the species most common of all the genus *Cornechiniscus*. Found the first time at Abano Terme (Padova, Italy), it was later found in various other Italian localities, in Austria, Switzerland, Rumania, Yugoslavia, Spain, Turkey, Iran, China, Afghanistan, and Saudi Arabia.

CORNECHINISCUS SCHRAMMI (Dastych, 1979) (Fig. 87).
= *Pseudechiniscus schrammi* Dastych, 1979

Length between 362 and 520μ. Color red or yellowish, eyes black. The sculpture is a regular and minute granulation (size of the granules as much as 1μ) similar to that of *Co. lobatus*; such sculpture is more distinct and larger on the terminal plate. Internal buccal cirri conical (length 10μ, width at the base 5μ), external filamentous, 23μ long. The appendices A have the shape of a robust spine and a little curved (length 24-40μ, width at the base 6-8μ). In some examples there are laterally slender and minuscule spines C and D lateral, sometimes only on one side, often absent. Cephalic plate facetted, scapular plate with a design of a W, not sculptured. The paired plates I and II present transverse folds. The unpaired plates 1 and 2 are double. The terminal plate presents two deep incisions and small spines E, sometimes absent. On the posterior margins of the paired plate II exists from 1 to 8 small spines, often difficult to observe, rarely absent. On the posterior margins of the pseudosegmental plate exists from 1 to 3 spines, slightly larger, but always not easily distinguishable; also these spines may sometimes be lacking. The 4th pair of legs without spines or dentate collar. Eggs deposited in the exuvium, in numbers from 2 to 7.

This species is very similar to *Co. cornutus*, from which it is differentiated by the sculpture, somewhat finer, by the folds of the paired plates, and by the small lateral and dorsal spines.

Co. schrammi was collected in Afghanistan, in moss on rock, on mountains of northern Badakshan.

CORNECHINISCUS SUBCORNUTUS Maucci & Ramazzotti, 1981 (Fig. 88).

Maximum length 330μ. Color red, eye spots present, black, or irregular

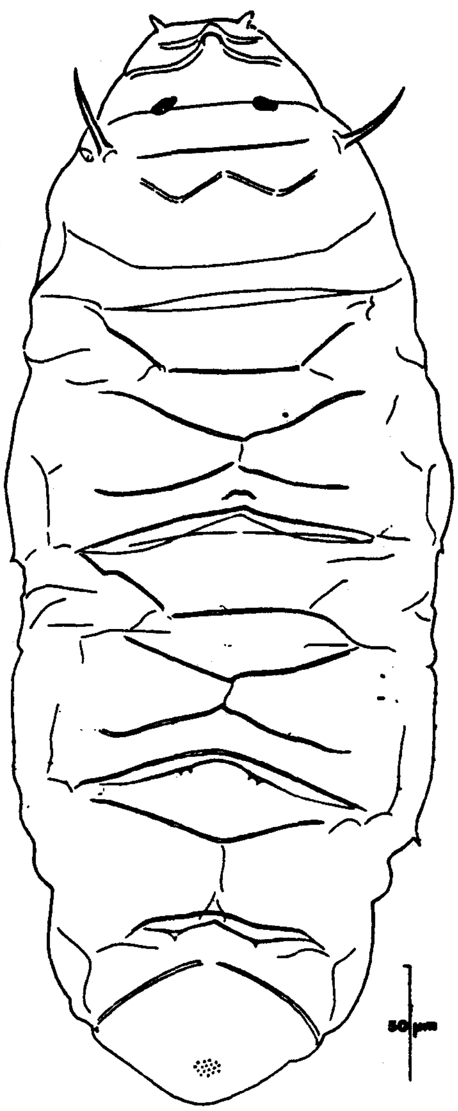


Fig. 87 - *Co. schrammi* (Dastych) (from Dastych).

shape. The sculpture is a regular, uniform granulation, a little more marked than that of *Co. lobatus*. On the scapular plate a zone devoid of sculpture and marked of a fold form a design of the shape of a very open W, more or less accentuated.

The cephalic plate and the terminal plate are facetted, at times in a not very evident manner. On the terminal plate there are deep incisions, connected to each other by one angle of the facetting.

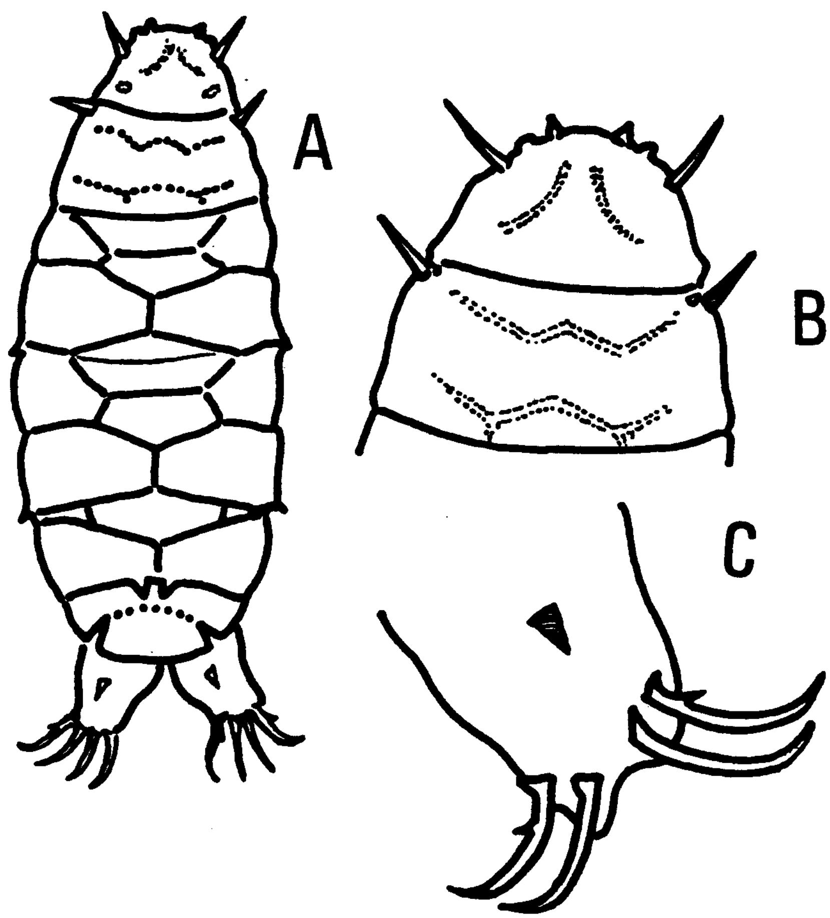


Fig. 88 - *Co. subcornutus* (Maucci and Ramazzotti). A, habitus; B, cephalic end; C, fourth leg and claws.

The internal buccal cirri have a bulbous base and a filiform extension, the externals have "sword shape" from similar to the shape and length of the appendices A, although more slender.

The appendices A have the characteristic squat conical shape of the genus, and are very short, that is equal to or shorter than the external buccal cirri. These appendices A, different from other species of the genus, depart from a plain base, and do not have any constricting collar.

There are no other lateral or dorsal appendices, except possibly extremely short and barely visible lateral spines at C and D, which however may be lacking.

The pseudosegmental plate is paired. Its posterior margin may have a pair of short and obtuse triangular teeth, which may be very reduced or almost absent.

Legs slender and long; the first pair has a spine, the fourth has, in place of the dentate collar, a large triangular tooth. Claws slender and long (proportionally more than those of *Co. ceratophorus*, and less than those of *Co. tibetanus*). On the 4th pair of legs the external claws have a type of small spur, in the shape of a straight spine, while the internals are smooth.

Co. subcornutus has been found in Spain, near Huesca (Pyrenees).

CORNECHINISCUS TIBETANUS (Maucci, 1979) (Fig. 89).
= *Pseudechiniscus tibetanus* Maucci, 1979

This is a larger than general species: the larger examples are 740μ long, with an average of the population of 556μ. Color intense red. Body slender, flat ventrally and dorsally arched. Eyes black, usually elliptical, small or extremely small. Cephalic plate strongly facetted: on its posterior margin sometimes exists some furrows devoid of sculpture which separates a series of transverse facets. Bands devoid of sculpture describe a W near the anterior margin of the scapular plate, and two Y's lying laterally. The unpaired plates 1 and 2 are transversely divided, the 3rd is undivided. The paired plates have deep transverse folds. The pseudo- segmental is paired. The terminal is not facetted, and has deep incisions, connected transversely by a marked fold. All the plates have folds and bands not sculptured, which give the impression of an exceptionally high number of plates, with numerous supplementary plates.

The sculpture is a coarse granulation, with rather fine granules, of polygonal outline, very close to each other, and connected by rays of extremely fine lines. Ventrally there are two paired, sculptured zones, well defined, but not conforming to plates, immediately behind the mouth.

The internal buccal cirri have a large bulbous base and thin, sharpened apices, rather long. The external buccal cirri have however a short bulbous base, and a somewhat saber shape, similar to those of cirri A.

Cirrus A, although with saber-shaped appearance, is rather short (a little longer, at times equal to, the external buccal cirrus).

Laterally exists short triangular spines in positions C and D, and strong spine E, sometimes bifid. The posterior margin of the pseudosegmental has two strong triangular spines. There are no other dorsal spines.

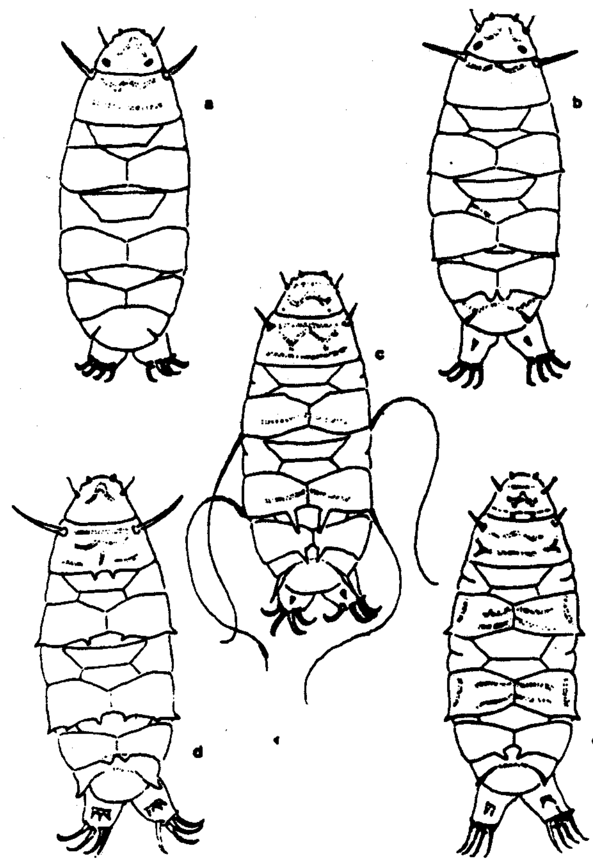


Fig. 89 - a, *Co. cornutus* (Richters); b, *Co. lobatus* (Ramazzotti); c, *Co. holmeni* (Petersen); d, *Co. ceratophorus* (Maucci); e, *Co. tibetanus* (Maucci) (from Maucci).

The legs are long, slender. On the first pair a short blunt spine, on the 4th a dentate collar formed of two robust sharp teeth. The claws are very long, slender, slightly curved, with expanded bases and without spurs or spines.

Some exuvia contained 4 eggs, orange, elliptical.

This species has been collected only at Ladak-Dras (Kashmir, India) at 3,300 elevation.

Genus *CORONARCTUS* Renaud-Mornant, 1974.

Diagnosis: Coronarctidae, with median cephalic cirri, body elongated, anteriorly attenuated; legs short with four curved claws, with basal spurs.

CORONARCTUS TENELLUS Renaud-Mornant, 1974 (Fig. 90).

Length from 330 to 350μ, for the females, and from 350 to 370 for the males. The head is narrow, and medially divided by a depression into an anterior conical part, covered with two frontal plates which outline the unpaired median cirrus and the mouth, and a posterior part which bears the cirri A and the clavae.

The cephalic cirri are short and not articulated. The internal median cirri (5μ) are apical, near the mouth, the externals (6μ) are ventral. The cirri A and the clavae are inserted on the basal part of the head. The cirri A are 10μ long, the clavae have subspherical mammillary shape with 5μ diameter.

The trunk is smooth and has a slight constriction between the pairs of legs. There are short lateral filaments, posterior to the 1st and 2nd legs and anterior to the 4th legs: the length of these filaments is respectively 19, 25, and 30μ.

The legs are short, retractile but not telescopic. Each leg has 4 claws of unequal length, of which those of the 4th pair are clearly longer. The claws are curved, supplied with basal spurs and are connected to the leg by a membrane. The internal claws are always longer than the externals (20 and 16μ, for the 1st, 2nd, and 3rd; 55-60 and 35μ, for the 4th legs) and bear a distal accessory point.

The mouth is apical; the buccal tube is narrow, stylets present, pharynx oval.

Cor. tenellus belongs to the abyssal meiobenthos, and has been collected in diverse stations in the Indian Ocean and the Atlantic Ocean (both African and American sides) at depths between 400 and 3,694 m.

Genus *DACTYLOBIOTUS* Schuster, Nelson, Grigarick & Christenberry, 1980.

Diagnosis: Aquatic Macrobiotidae; large claws, with short or extremely short secondary branches and bases connected to each other; lunules absent.

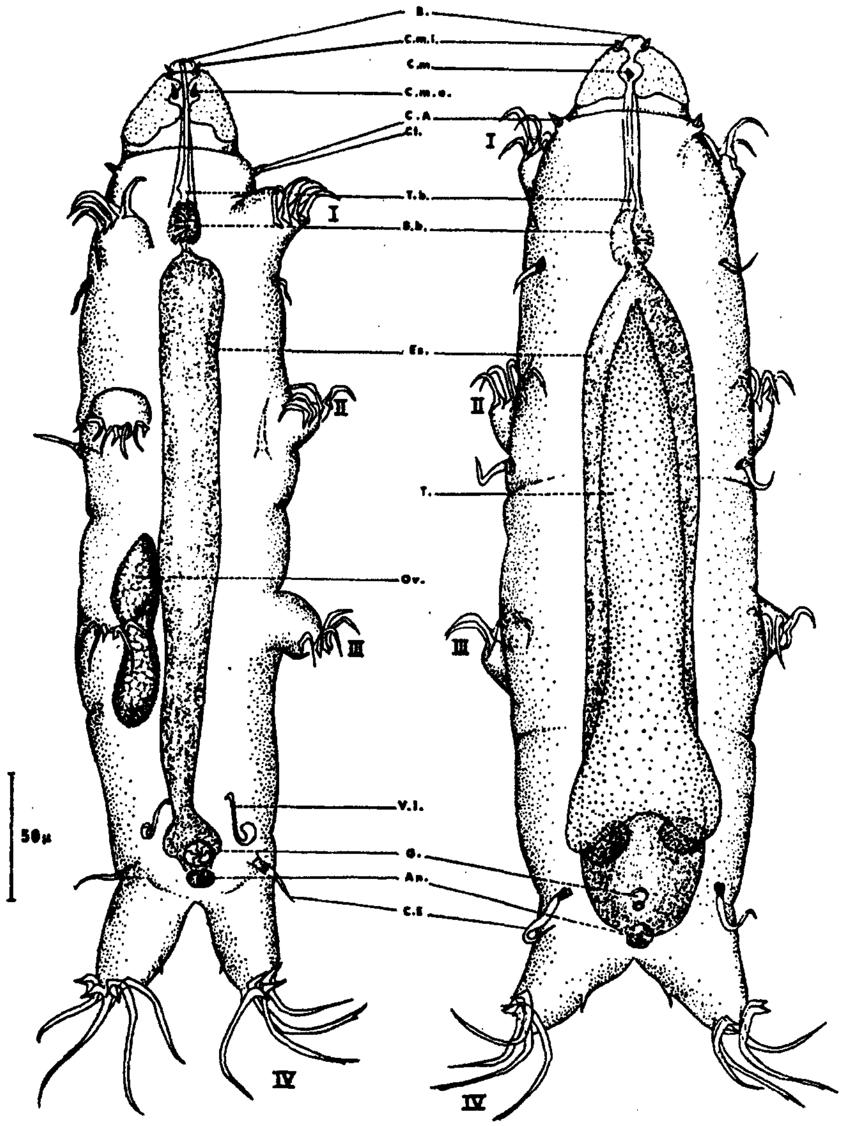


Fig. 90 - *Cor. tenellus* Renaud-Mornant. At left, female ventral view; at right, male dorsal view; An, anus; B, mouth; B.b., pharynx; C.A., cirrus A; C.E., cirrus E; C.m., median cirrus; C.m.e., external median cirrus; C.m.i., internal median cirrus; Cl, clava; Es, stomach; G, gonopore; Ov, ovary; T, testis; T.b., buccal tube; V.l., lateral vesicle; I, II, III, IV, legs (from Renaud-Mornant).

KEY TO THE SPECIES

1. There are two conical appendices dorsolaterally, between the 3rd and 4th pairs of legs 2
   There are no conical appendices 3

2 (1). Buccal tube narrow (less than 10% of the length); stylet supports joined to the buccal tube at a distance near the mouth equal to the diameter of the tube .... *Da. dispar*
   Buccal tube wide (11-12% of the length); stylet supports joined to the buccal tube at a distance near the mouth equal to double the diameter of the tube .... *Da. grandipes*

Posterior opening, not mouth

3 (1). Buccal tube wide (more than 20% of the length); secondary branch of the 1st-3rd doubleclaws very short, reduced almost to a spur 4
   Buccal tube rather narrow (less than 10% of the length); secondary branch of the doubleclaws not reduced 5

4 (3). Eggs smooth, deposited in exuvium .... *Da. macronyx*
   Eggs with ornamentation, probably deposited free .... *Da. haplonyx*

5 (3). The projections of the eggs make contact at their bases 6
   Between the projections of the egg remains a free zone of the shell .... *Da. dispar*

6 (5). Eggs of 115-130μ; claws long and graceful, with principal branch moderately curved; macroplacoids moderately slender rods .... *Da. ambiguus*
   Eggs of about 90μ; claws rather short, with large principal branch and strongly curved; macroplacoids rods, very slender .... *Da. ampullaceus*

DACTYLOBIOTUS AMBIGUUS (Murray, 1907) (Fig. 91).
= *Macrobiotus ambiguus* Murray, 1907

The species is capable of reaching large size, up to 900μ in length, but it does not often exceed 500-700μ. The cuticle is smooth and the animal

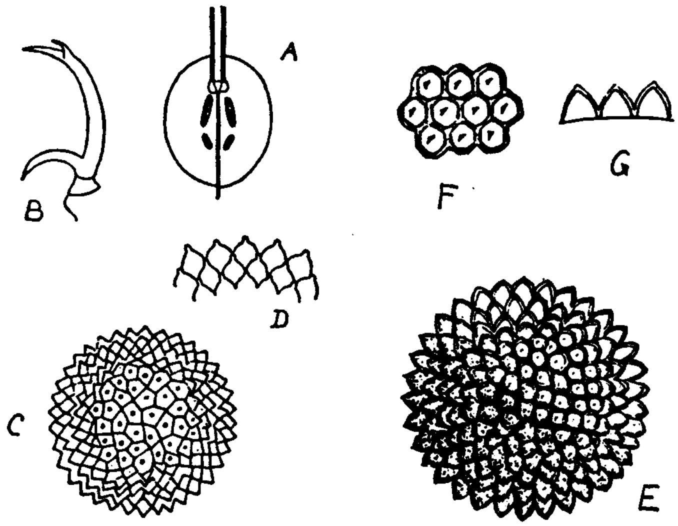


Fig. 91 - *Da. ambiguus* (Murray). A, pharynx; B, doubleclaw of the 4th leg; C, egg; D, alternate form of ornamentation (projections) of the egg; E, alternate type of egg; F, projections viewed straight on; G, the same viewed from the side.

is usually colorless or yellow, but may be pigmented brown with advanced age. Eyes posterior; buccal aperture encircled by lamellae; buccal tube moderately wide; stylets with very large furca; pharynx large with well developed apophyses, and two macroplacoids, of which the first is longer than the second (up to twice) and sometimes appears divided into two by a narrow constriction; microplacoid absent. The doubleclaws are of the *macronyx* type.

Eggs deposited free, are spherical and have projections in the form of pointed tubercles, with contacting polygonal bases, and have a total diameter (including ornamentation) of 115-150μ. The projections were described by Murray as assuming mammary form and by Richters as like an onion bulb.

This species, in the absence of eggs, can not be distinguished from specimens of *dispar* which lack the dorsolateral conical gibbosity between the third and fourth legs. The eggs are however very different and permit an easy separation from *dispar*; and also from *ampullaceus* (whose individuals are of smaller size, the macroplacoids thinner, and the claws much smaller in comparison to *Da. ambiguus*).

Da. ambiguus is probably cosmopolitan and is also present in Italy.

DACTYLOBIOTUS AMPULLACEUS (Thulin, 1911) (Fig. 92).
= *Macrobiotus ampullaceus* Thulin, 1911

The species is usually aquatic, however has been also collected in moss subject to desiccation; Cuénot considers it a mutant of *Da. ambiguus* and Marcus subscribes to the same opinion: certainly the two species are very close.

The length may reach 530μ, the cuticle is smooth, eye spots present. Pharynx rather elongated oval, with two slender macroplacoids; microplacoid absent. The doubleclaws are short and rather small, of *macronyx* type, with large principal branch, very curved and bears two accessory points, while the secondary branch is minuscule and slender on the first three pair of legs, more developed on the fourth pair.

Eggs deposited free, diameter about 90μ including the projections and about 68μ without them; the ornamentations of the egg have diameter between 14 and 23μ, while the height is about 10-12μ; they arise from a base more or less hexagonal, remaining laterally in contact with each other for a certain distance and ending distally in a cone, or else with a superficial hemisphere.

The species, in absence of eggs, may not always be distinct from *ambiguus* and *dispar* (for more details in this regard, see the description of *Da. ambiguus*).

Da ampullaceus has been observed only in Hungary and in Lapland.

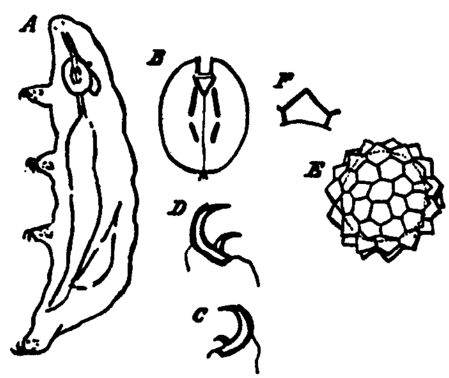


Fig. 92 - *Da. ampullaceus*(Thulin). A, lateral view; B, pharynx; C, claw of the 1st pair of legs; D, claw of the 4th pair of legs; E, egg; F, one projection of the egg (from Marcus).

DACTYLOBIOTUS DISPAR (Murray, 1907) (Fig. 93).
= *Macrobiotus dispar* Murray, 1907 et Auct.

Aquatic, of large size (up to 1,000μ, but usually less), with long legs; colorless (white in reflected light), yellowish, grayish, or brown; eyes

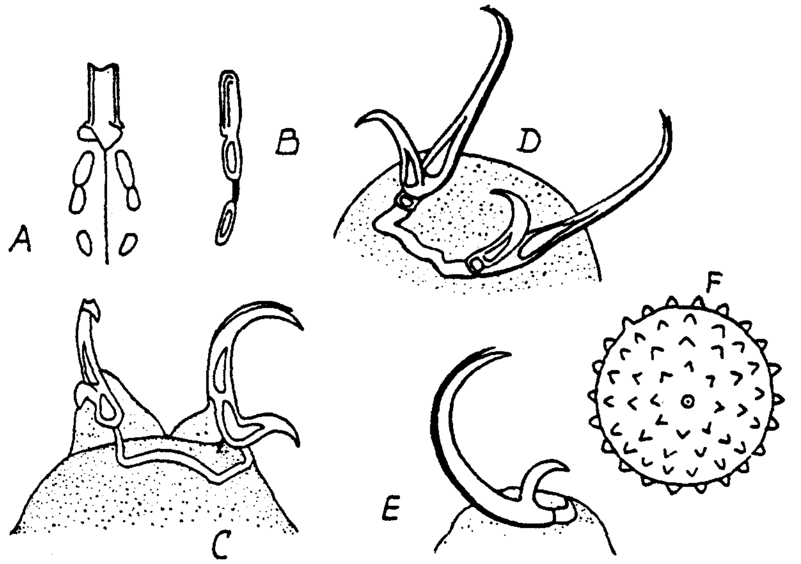


Fig. 93 - *Da. dispar* (Murray). A, B, placoids; C, D, doubleclaws of the 4th pair of legs; E, doubleclaw of the 3rd leg; F, egg.

present. Cuticle in general smooth, but sometimes finely granulated: two dorsal gibbosities -- or else dorsolateral -- between the 3rd and 4th pair of legs, nearer however to the latter, and having conical shape with rounded ends; such processes may also be lacking. There are peribuccal lamellae, the buccal tube is medium wide (less than 10% of the length), the pharynx large, ovoid, with apophyses and two macroplacoids, of which the first appears interrupted and is twice as long as the second; often the junction between the 1st and 2nd macroplacoids is very visible, as described by Cuénot; microplacoid absent.

The macroplacoids are usually long and slender rods, rarely short.

Doubleclaws very large (those of the 4th pair may measure 50-55μ in an animal of about 500μ) and of the *macronyx* type; the principal branch, robust, bears two very long and straight accessory points, while the secondary branch is short and weak on the first three pair of legs, more developed on the fourth pair. The two doubleclaws of each leg are connected by a sort of chitinous bar, very visible especially on the 4th pair of legs. Eggs deposited free, up to 19 per time, spherical, with diameter of about 90μ, including the projections, which are small distant cones.

When the two conical dorsolateral processes are not present, *Da. dispar* -- in absence of eggs -- may not be distinct from *Da. ambiguus* which however is an aquatic species; if instead the eggs are present, the distinction is easy; *ambiguus* deposits much larger free eggs and with ornamentation of different appearance.

Da. dispar is probably cosmopolitan: there are numerous reports known in Europe (also in Italy, for example Lake Maggiore, down to depths of over 50 m), as well as in South America, Africa, Asia, Australia, New Zealand, and the Arctic. It was always observed in aquatic or interstitial environment.

DACTYLOBIOTUS GRANDIPES (Schuster, Toftner, and Grigarick, 1977) (Fig. 94).
= *Macrobiotus grandipes* Schuster et al., 1977

Length up to 714μ; cuticle wrinkled, without pores; a small dorsolateral spine is present, between the third and the fourth pairs of legs. Mouth surrounded by 10 lamellae. The buccal tube is 86μ long (in the holotype) and 10 wide. Small apophyses are present and two macroplacoids (the first 26μ, the second 17) of slender rod shape; the first has a constriction. Microplacoid absent. Claws large, of *macronyx* type. Eggs similar to those of *Da. dispar.*

The species, which is aquatic, was collected in over a thousand examples at Pope Beach, Lake Tahoe, California (typ. loc.), and in numerous other localities of California.

Da. grandipes is distinguished from *Da. dispar*, among others by the stylet supports inserted on the buccal tube at a distance from the posterior

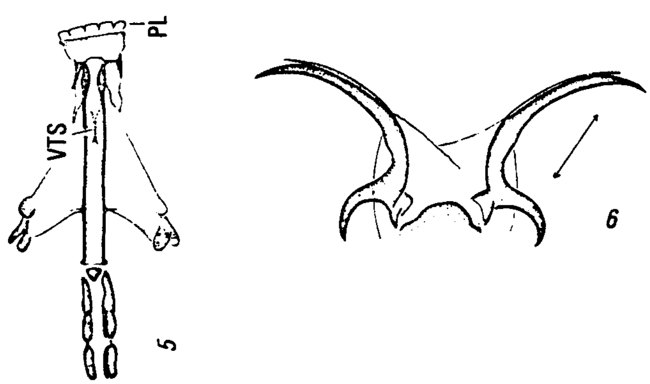


Fig. 94 - *Da. grandipes* (Schuster et al.). Buccal apparatus and claws (from Schuster et al.).

opening of it equal to twice the diameter of the tube (in *Da. dispar*, such distance does not surpass the diameter of the tube).

According to the author, the species may correspond to those which were originally described as *Macrobiotus macronyx* (see however the description of *Da. macronyx*).

DACTYLOBIOTUS HAPLONYX Maucci, 1980 (Fig. 95).

Size up to 440μ, rather squat shape, with short legs. Eye spots present, obvious, composed of pigmented granules, very dense. Cuticle smooth, without pores.

The mouth opening is surrounded by 10 buccal lamellae. The buccal tube is rather short and very wide (about 18% of the length). The stylet supports are fused to the tube at a distance from the opening to it, a little greater than the diameter of the tube.

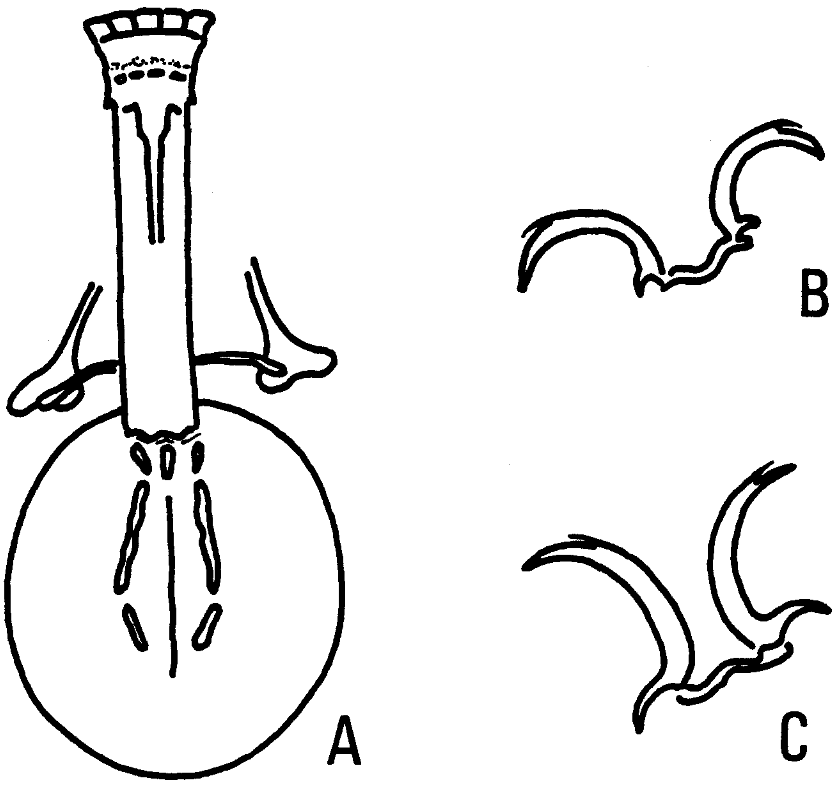


Fig. 95 - *Da. haplonyx* Maucci. A, buccal apparatus; B, claws of the 1st pair of legs; C, claws of the 3rd pair of legs (from Maucci).

The pharynx is oval, slightly elongated. The apophyses are slender and elongated; there are two macroplacoids of very slender rod shape, the first of 12, the second of 6μ; both the placoids, but especially the first has irregular thickness, with projections and constrictions, and the first has besides a deep constriction, which seems almost to divide it in two. Microplacoid absent.

The claws are very large. Lacking the lunules, but the claws of each leg are connected to each other at the bases by means of a sclerified band. The principal branch, strongly arched, has accessory points. The secondary branch is inserted very near to the base of the claw, and on the first three pair of legs is very short, extremely slender, reduced almost to a spur. On the fourth pair of legs, the secondary pair -- always considerably shorter than the principal -- has a normal development.

Eggs have not been found, but two females contained respectively 5 and 10 eggs almost mature, strongly supplied with ornamentation, which seems to be slightly rounded cones, wide and low, distant from each other. It may be that such eggs are deposited free.

Da. haplonyx has been found in different stations from Adige (near Verona), Piave, and Oglio.

DACTYLOBIOTUS MACRONYX (Dujardin, 1851) (Fig. 96).
= *Macrobiotus macronyx* Dujardin, 1951, et Auct.

It is a freshwater species, of large size; length is generally about 500μ, but may reach 1,000μ; colorless; eyes present or lacking. Buccal tube wide; pharynx oval to short oval, containing 2 macroplacoids of rod shape, sometimes of equal size, sometimes different: in this case the longer may

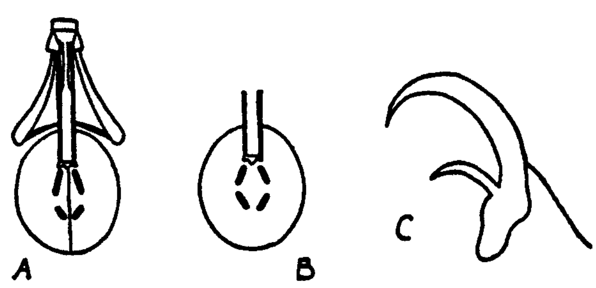


Fig. 96 - *Da. macronyx* (Dujardin). A, buccal apparatus; B, pharynx; C, a claw of the fourth leg.

be the first, or else the second. Microplacoid absent. The two doubleclaws of each leg are equal to each other, very characteristic (*macronyx* type): the secondary branch, much shorter than the principal, and which articulates near the base of this, is positioned almost at a right angle with the principal branch, especially on the first three pair of legs. Deposited in the exuvia are smooth oval eggs -- with diameter about 60μ -- in numbers of 15-17: this distinguishes this species from *Da. ambiguus* and *Da. dispar*, which deposit instead free eggs with conical projections; when however one does not find eggs, it is impossible to decide if one is working with *macronyx*, *ambiguus*, or *dispar*, except that the individuals of *dispar* have dorsolateral gibbosities (not always present).

Although the species is very frequently cited for freshwater, especially by the nonspecialist, there is some doubt concerning the actual existence of *Da. macronyx* as a standing species, which deposits smooth eggs in the exuvia; it may be that *macronyx* and *dispar* are synonyms and that the exuvia with smooth eggs, observed by various authors, belong to other coexistent species; such is the opinion of Cuénot (1932) and Marcus (1936), to which the reader is referred for more detail (especially the latter).

We, in numerous samples of material from freshwater and also interstitial, have often seen *Da. dispar* and also (less often) *Da. ambiguus*, but have not ever come across examples of *Da. macronyx*, and we know no recent and trustworthy reports of this species, which we therefore have come to consider as dubious.

Genus *DIPHASCON* Plate, 1889.

Diagnosis: Hypsibiidae with claw sequence of 2121, with *Hypsibius* type claws; the rigid buccal tube is extended into a flexible pharyngeal tube with spiral structure.

Observations:

1. In the text of the key the expression "buccal tube" refers only to the rigid part, while "pharyngeal tube" refers only to the flexible part.
2. It can sometimes be difficult, without experience, to distinguish the microplacoids from septula. We have noted that the microplacoids are arranged on the axis of the macroplacoids while the septula are in other positions.
3. Pilato (1975) has indicated the taxonomic importance of the "drop" formation stage of the joint between the buccal tube and the pharyngeal

tube. In the key this when the presence or absence of it is known. We note that for many species of older description and not recently redescribed this character is not known.

4. It's the same for the presence or absence of the cuticular bar, on 1st-3rd pairs of legs, near the base of the claws.

5. The species *D. enckelli* and *D. scoticum simplex* are not included here because we consider that they are included in *Itaquascon*. The species *D. bicorne* (*D. scoticum bicorne*) is here considered as a species by itself. Likewise for *D. aculeatum* (*D. bullatum aculeatum*).

KEY TO THE SPECIES

1. Cuticle sculptured or with gibbosities 2
Cuticle smooth 24

2 (1). The cuticle is only sculptured, without gibbosities 3
There are also gibbosities or tubercles 14

3 (2). There is a granulation only on the caudal end 4
The granulation is extended over all the dorsum 6

4 (3). There are three rod-shaped macroplacoids (the third ends in a knob), without microplacoid or septula; eyes absent . . . . *D. clavatum*
There are two macroplacoids; eyes present 5

5 (4). The pharyngeal tube is very long (about twice that of the pharynx); septula present . . . . *D. oculatum*
The pharyngeal tube is a little longer than the pharynx; microplacoids present . . . . *D. rugocaudatum*

6 (3). Three macroplacoids are present 7
Two macroplacoids are present 8

7 (6). The macroplacoids are short rods (the length of the line of placoids is less than the length of the buccal tube); lacking microplacoids and septula; granulation in transverse rows . . . . *D. speciosum*
The macroplacoids are long rods (the length of the line is greater than the length of the buccal tube); microplacoids and septula present; sculpture of polygonal network; two pointed lobes at the sides of the mouth . . . . *D. bicorne*

8 (6). The macroplacoids are slender rods;
microplacoid and septula absent .... *D. punctatum*
Microplacoid and/or septula present 9

9 (8). Microplacoid present 10
Septula present 12

10 (9). Eyes absent; the sculpture is a fine granulation;
there is a gibbosity on each leg .... *D. latipes*
Eyes present 11

11 (10). The sculpture is a fine granulation; the claws
of each leg are of different size, slender .... *D. rugosum*
Sculpture of polygonal network; claws
short, little difference in size .... *D. iltisi*

12 (9). Eyes absent; there are "drops" on the buccal
tube; there are no bars on legs .... *D. granifer*
Eyes present 13

13 (12). The sculpture is a fine granulation; the
macroplacoids are short rods; there are
"drops"; bars on the legs .... *D. ramazzottii*
The sculpture is composed of rounded granules,
projecting, increasing anterior to
posterior; macroplacoids are short granules .... *D. nodulosum*

14 (2). Gibbosities or tubercles are present only on the
caudal end 15
There are gibbosities on all the dorsum 17

15 (14). There is a single transverse line of
4 gibbosities .... *D. halapiense*
There are gibbosities or tubercles caudally
in more rows 16

16 (15). There are 4 or 5 transverse rows of conical
tubercles .... *D. coniferens*
There are 2 caudal rows, or sometimes more, of
rounded gibbosities, arranged two by two .... *D. bullatum*

17 (14). Besides gibbosities there is a sculpture of
plates which form - with proper focusing -
a polygonal pattern; there are 7 pairs of
dorsal gibbosities plus an eighth pair
caudally, dorsolaterally .... *D. patanei*
Besides the gibbosities there is a more
or less fine granulation 18

18 (17). There are 8 pairs of gibbosities; the last two pairs bear a spine . . . . . . *D. aculeatum*
There are only gibbosities without spines 19

19 (18). There are 8 pairs of gibbosities; the claws have lunules . . . . . . *D. trachydorsatum*
Lunules are not present 20

20 (19). There are 6 pairs of gibbosities; lacking septula and microplacoid . . . . . . *D. nonbullatum*
Microplacoid or septula present 21

21 (20). Microplacoid present 22
Septula present 23

22 (21). The gibbosities are arranged in 7 rows of 4 gibbosities each, of which the center two are larger; doubleclaws of approximately equal size . . . . . . *D. gerdae*
The gibbosities are arranged in 6 rows of 2 gibbosities; doubleclaws are of different size . . . . . . *D. elongatum*

23 (21). There are 9 pairs of gibbosities (at times less, even reduced to 2 pairs more caudally) . . . . . . *D. bullatum*
There are 8 pairs of larger gibbosities, separated by 11 transverse rows of smaller gibbosities . . . . . . *D. bisbullatum*

24 (1). Buccal tube and pharyngeal tube somewhat short and wide: the width is greater than 10% of the total length; there are 2 slender or extremely slender placoids 25
The tube is very long and slender: the width is much less than 10% of the length 28

25 (24). The buccal + pharyngeal tube is very short and wide (width about 14% of the length); there are 2 long, extremely slender placoids . . . . . . *D. itaquasconoide*
The buccal tube is wide, about 10% of the total length 26

26 (25). There are 2 slender macroplacoids (the first about half of the 2nd); microplacoid present . . . . . . *D. spitzbergense*
Lacking microplacoid and septula 27

27 (26). Body anteriorly attenuated . . . . . . *D. angustatum*
Body not anteriorly attenuated . . . . . . *D. affine*

28 (24). There are 3 macroplacoids 29
There are 2 macroplacoids 43

29 (28). There is neither microplacoid nor septula 30
There is microplacoid and/or septula 33

30 (29). The width of the tube is about 3-4% of the total length 31
The width of the tube is at maximum little more than 2% of the total length 32

31 (30). Mouth anterio-ventral, forehead bulging; claws small, of almost equal size .... *D. arduifrons*
Mouth terminal; slender claws of different size .... *D. prorsirostre*

32 (30). "Drop" formation present; macroplacoids rather long, in the shape of slender rods .... *D. tenue*
"Drop" absent; oval, granular macroplacoids .... *D. montigenum*

33 (29). Microplacoid and septula present 34
Microplacoid or septula present 39

34 (33). The macroplacoids are slender, long rods; the length of the row is greater than the length of the buccal tube (rigid part); "drop" absent 35
The macroplacoids are short rods: the length of the row is less than the buccal tube; "drop" present; bar in legs absent 37

35 (34). Claws have an expanded, dentate base .... *D. higginsi*
Base of the claws may or may not be expanded, but it is not dentate 36

36 (35). Claws small, with base not expanded; there is no bar in the legs .... *D. carolae*
Claws large, very different, with expanded base; there is a bar in the legs .... *D. scoticum*

37 (34). Macroplacoids have equal length; claws of little difference in size .... *D. chilenense*
Macroplacoids have increasing length from first to third; claws of different size 38

38 (37). The macroplacoids are very short; the complete row surpasses by a little the middle of the length of the buccal tube (rigid part) .... *D. alpinum*
The macroplacoids are not as short; the complete row almost reaches 65% of the length of the buccal tube .... *D. pingue*

39 (33). Microplacoid present, septula absent 40
Septula present, microplacoid absent .... *D. ongulense*

40 (39). Aquatic species; macroplacoids slender, of increasing length; principal branch of external claws long and strongly curved, without accessory points .... *D. marcuzzii*
Different 41

41 (40). Macroplacoids are short or very short rods; eyes present .... *D. stappersi*
Macroplacoids slender, long rods, of increasing length; the row is longer than the length of the buccal tube (rigid) 42

42 (41). Eyes present; claws large, with massive and dentate base .... *D. nobilei*
Eyes absent; claws slender, with non-dentate base .... *D. marcusi*

43 (28). Macroplacoids short granules; microplacoid and septula absent; pharyngeal tube short .... *D. conjungens*
Microplacoid and/or septula present 44

44 (43). Microplacoid and septula present; there is a "drop" formation and bar in the legs; eyes present .... *D. brevipes*
Microplacoid or septula present 45

45 (44). Microplacoid absent, septula present; eyes present; macroplacoids short rods, almost granules; there is a "drop", and bar in the legs is absent .... *D. oculatum*
Microplacoid present, septula absent 46

46 (45). Macroplacoids slender, very long; their row is greater than the length of the rigid buccal tube; the 1st macroplacoid is half as long as the 2nd; there is not a "drop" and there is a bar in the legs .... *D. belgicae*

Macroplacoids short rods, the 1st longer than the 2nd 47

47 (46). Eyes absent; the 1st macroplacoid double the 2nd; claws almost equal .... *D. mariae*
Eyes present; the 1st macroplacoid about one and a half times the 2nd; claws of different size .... *D. recamieri*

DIPHASCON ACULEATUM (Maucci, 1951-52) (Fig. 97).
= *Hypsibius* (*D.*) *bullatus aculeatus* Maucci, 1951-52.

Small size (length 185μ), colorless, eye spots present. The cuticle has a sculpture composed of a regular, extremely fine granulation (recognizable only with immersion objective, phase contrast). Also present are hemispherical gibbosities, arranged in eight rows of two gibbosities each: in the first seven rows the gibbosities are in dorsal position, in the last row, the position is dorsolateral. The gibbosities of the last two rows (seventh and eighth) have a short triangular pliable spine.

The buccal tube, rigid, is 17μ long, and bears at its end a "drop" formation; the pharyngeal tube, very flexible, is 23μ long; the tube is very narrow (1.6μ, that is 4% of the total length of the tube). Pharynx short oval, with apophyses and two macroplacoids in the shape of short rods, the first twice as long as the second, and clearly constricted at the middle. There are present microplacoids and septula.

The legs are short and squat. The claws, rather small: the two doubleclaws of each leg are of almost equal shape, and of little different size. The basal branch however is very short, the two branches are squat and robust; there are no accessory points. Near to the claws of the first three pair of legs there is a cuticular bar, little more than the external claws, with sinuous course.

Of this species has been collected so far a single example in fully shaded moss, on Capri Island (Napoli). This report here is a redescription based on a re-examination of the holotype.

Initially this species was considered as a variety of *D. bullatum*. The re-examination allows to consider *D. aculeatum* as a good species, especially by the clear difference in the type of sculpture.

DIPHASCON AFFINE (Mihelčič, 1951) (Fig. 98).
= *Hypsibius* (*D.*) *affinis* Mihelčič, 1951.

Large size (up to 600μ), slender with cephalic region rostrally reduced, almost pointed; observing from the dorsum, the length of the body appears

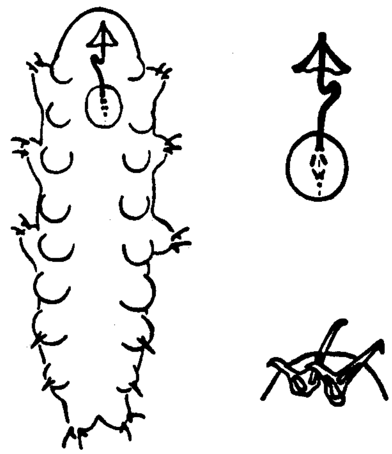


Fig. 97 - *D. aculeatum* (Maucci) (from Maucci).

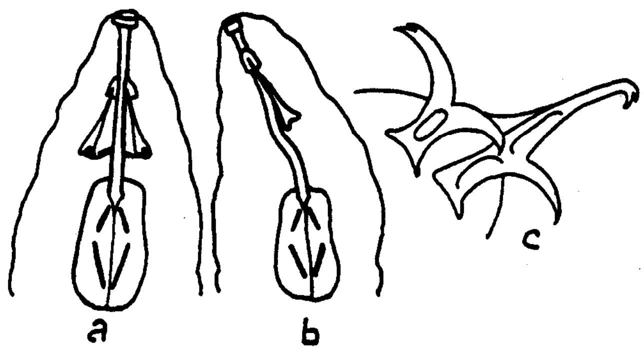


Fig. 98 - *D. affine* (Mihelčič). a, cephalic zone, dorsal view; b, cephalic zone, lateral view; c, doubleclaws of the 4th pair of legs (from Mihelčič, redrawn).

unvaried from the 1st to the 4th pair of legs, while in profile the maximum thickness is between the 3rd and 4th pair of legs. Cuticle smooth, eyes absent, buccal aperture subterminal. Pharyngeal tube wide, as long as the pharynx: this is approximately cylindrical, however wider caudally than rostrally, and is twice as long as its width. The macroplacoids are two long, slender rods, of which the second is almost twice the first. The claws are robust and large.

This species does not seem too well defined, particularly in comparison to *D. angustatum*, which differs by the shape of the enlarged pharynx.

D. affine was found a single time, in a sample of soil from Swedish Lapland, near Abisko.

DIPHASCON ALPINUM Murray, 1906 (Figs. 99 and 100).
= *Hypsibius* (*D.*) *alpinus* Marcus, 1936.

Size small or medium (length up to 400μ, often 200-250μ); the body is rather narrow and elongated, colorless or whitish, with smooth cuticle; eyes absent. The buccal tube is very narrow (about 1μ entire diameter), rigid in the anterior part, up to an thickening in which is inserted the muscles of the stylets, then flexible up to the pharynx (pharyngeal tube): in the flexible part designs a noose or of undulation.

Between the rigid part and the flexible part of the buccal tube, there is a cuticular "drop" formation.

The pharynx is oval, but has great variation in the shape: in it -- besides the apophyses -- is contained 3 macroplacoids (elongated granules, or else rods), of length and width increasing from first to third, microplacoid and septula. Sometimes may be lacking the microplacoid and only the septula, according to Marcus, in some cases are present only the macroplacoids, but we have not ever observed individuals thus conformed.

The two doubleclaws of each leg are, in general, rather small and very different from each other: the internal (anterior) is short and large and on its principal branch has accessory points more robust than those which are found on the principal branch of the external (posterior) doubleclaw.

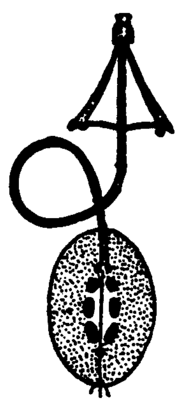


Fig. 99 - *D. alpinum* Murray.
Buccal apparatus.

The eggs are deposited in the old cuticle, in numbers of 2 to 8, and have 39-52μ diameter.

The following characteristics -- according to Marcus (1936) -- distinguishes the three species *D. chilenense*, *D. stappersi*, *D. tenue* from *D. alpinum*:

- *chilenense* has macroplacoids of equal length and short oval pharynx (it does not seem however that this character can be determined) and claws little different from each other.
- *stappersi* is eyed and has shorter pharynx (as in the preceding species; we are not however inclined to accord importance to the size of the pharynx, whose length to width ratio is extremely variable in *alpinum*).
- *tenue* has more slender macroplacoids and all three of about equal width; besides the length of each row of placoids is shorter than half the length of the pharynx (in *alpinum* is longer); finally always lacking microplacoid and apophyses.

The species (common also in Italy) is cosmopolitan and habitat of preference -- but not always -- moss of shady location; *D. alpinum* is the more common and more wide spread species of all the genus *Diphascon*. Typ. loc.: Scotland.

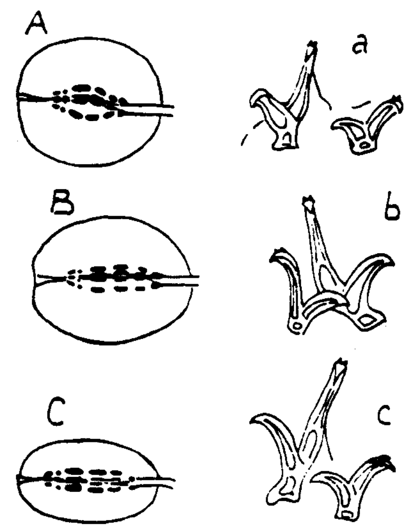


Fig. 100 - *D. alpinum* Murray. A, B, C, different types of pharynx and placoids; a, b, c, corresponding claws of the 4th pair of legs (from Petersen, redrawn).

DIPHASCON ANGUSTATUM Murray, 1905 (Fig. 101).
= *Hypsibius* (*D.*) *angustatus* Marcus, 1936

Length included between 350 and 490μ, transparent, with smooth cuticle, not eyed. The body has its maximum width (observed from dorsum) in correspondence with the 3rd pair of legs, then reducing progressively toward the rostral end, becoming almost conical in the cephalic region. Pharyngeal tube short and wide, with typical annular sculpture, sometimes visible only at strong magnification.

Between the buccal tube proper (rigid) and the pharyngeal tube there is no "drop" formation present as in most *Diphascon*.

Stylets slender, straight, almost parallel to the buccal tube, little divergent caudally; pharynx cylindrical, about twice the length of its width, with two slender macroplacoids, the second of twice the length of the first, sometimes less; microplacoid absent. Eggs unknown.

It may be sometimes rather difficult to distinguish *angustatum* from *affine*: see under the description of this last species other information in this regard; *D. spitzbergense* has the microplacoid.

The species was collected in many localities from Europe (also in Italy), the Arctic, and Canada. Typ. loc.: Scotland.

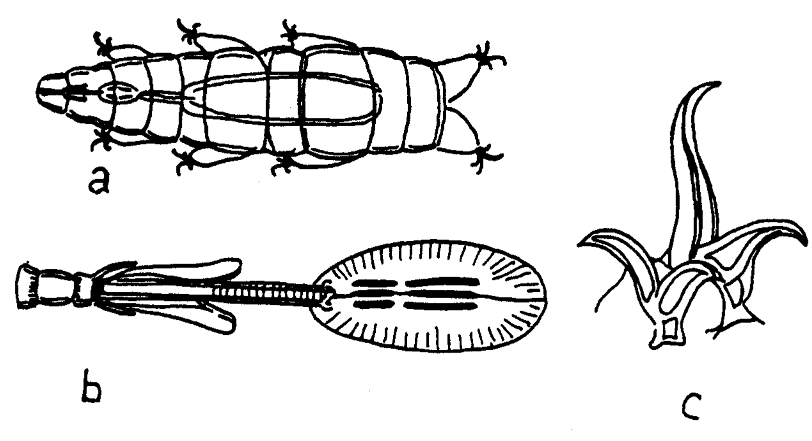


Fig. 101 - *D. angustatum* Murray. a, dorsal view; b, buccal apparatus; c, doubleclaws of the 2nd pair of legs (a, from Murray; b, c, from Petersen, redrawn).

DIPHASCON ARDUIFRONS (Thulin, 1928) (Fig. 102).

Small size (length about 285μ); cuticle smooth; eyes absent. Body posteriorly wide, which becomes thinner rostrally starting at the second pair of legs. The buccal aperture is turned obliquely down (subventral) and the forehead -- observing the tardigrade in profile -- appears high and upright, almost as if the animal was anteriorly truncated.

Buccal tube very narrow (less than 1.5μ in an individual 284μ long), pharyngeal tube (flexible) approximately as long as the pharynx, which is large and of elongated oval shape (length to width ratio = 1.8:1).

Apophyses visible and these macroplacoids, with appearance of slender rods, of increasing length from first to third; microplacoid absent; length of the individual row of three macroplacoids slightly longer than half the length of the pharynx.

D. arduifrons is a species very close to *D. prorsirostre*, so that -- in agreement with Cuénot and Marcus -- we have many doubts that these two species ought to be held distinct, or rather should not be grouped together in a single species; the fact remains that -- in a population of the very same moss from Val Martello -- we have been able to observe some individuals with position of the buccal aperture and shape of *prorsirostre* and others of *arduifrons* (see also the description of *D. scoticum*).

The species has so far been observed in moss of relatively few localities in Bohemia, Italy, Lapland, Austria, and Siberia.

Typ. loc.: Telezki Lake (Altai, Siberia).

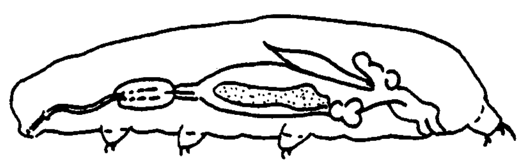


Fig. 102 - *D. arduifron* Thulin (from Thulin, redrawn).

DIPHASCON BELGICAE Richters, 1911 (Fig. 103).

Large size, up to almost 500μ, cuticle smooth, eye spots absent. The buccal and pharyngeal tube is very narrow (diameter about 2.5μ) and very long. Between the buccal tube and the pharyngeal tube there is no "drop" formation. The pharynx is oval-cylindrical, of greater length than twice the

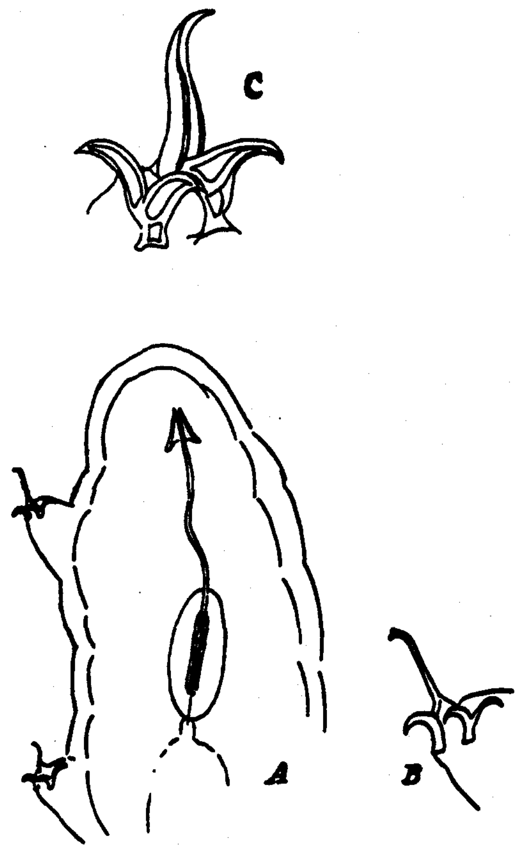


Fig. 103 - *D. belgicae* Richters. A, rostral region, with pharynx; B, doubleclaws (from Marcus).

width, with two very slender and long macroplacoids (thickness about 1μ), of which the first is about half the second.

The legs present massive claws, remarkably different in size. Near the claws exists a cuticular bar, on the first three pair of legs. Eggs unknown.

The species, not common, is known from the Spitsbergen Archipelago, Orsi Island, Berlin, Bohemia, Bulgaria, Norway, and Austria. Typ. loc.: Spitsbergen.

DIPHASCON BICORNE (Mihelčič, 1971) (Fig. 104).
= *Hypsibius* (*D.*) *scoticus bicornis* Mihelčič, 1971.

The original description is extremely summary, and perhaps insufficient. From it can be extracted the following.

Medium size (perhaps up to about 400μ, but probably less); eye spots absent. The cuticle presents a sculpture of polygonal mesh. At the sides of the head there exists two pointed lobes, dentiform. The buccal tube is narrow, with internal diameter of perhaps 1.5μ; the pharyngeal tube is about as long as the pharynx. The pharynx is very elongated, that is to say about two times longer than wide, with small apophyses and three macroplacoids in the shape of slender rods, of length little different from each other; microplacoid and septula are present.

The two doubleclaws of each leg are very different from each other.

The author had considered this form as subspecies of *D. scoticum* (based for this purpose reconstructed of the aforesaid description), of which may differ only by the reticular sculpture of the cuticle, and by the two lobes at the sides of the head. It is not possible to interpret the significance of these lobes, however the sculpture of the cuticle seems sufficient to specifically separate *bicorne* from *scoticum*.

D. bicorne was found only in the vicinity of Ampach, near Lienz (Tirolo, Austria).

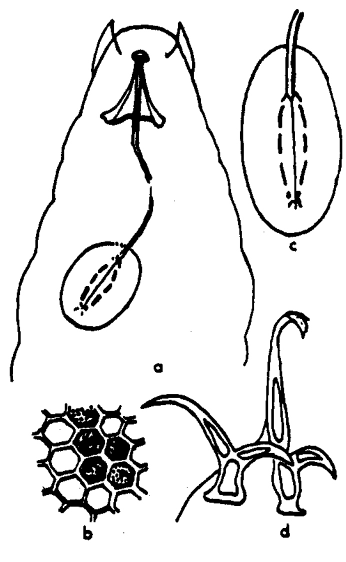


Fig. 104 - *D. bicorne* (Mihelčič). a, cephalic region; b, sculpture; c, pharynx; d, claws (from Mihelčič).

DIPHASCON BISBULLATUM (Iharos, 1964) (Fig. 105).
= *Hypsibius* (*D.*) *bisbullatus* Iharos, 1946.

Length 160-190μ, colorless, eye spots absent. Dorsally exists large and small gibbosities: the large are arranged in 8 transverse rows, the small in 11 transverse rows; the height of the larger gibbosities is 5.5-7μ, of the smaller 2.7-3μ. The cuticle presents also a fine granulation.

Buccal and pharyngeal tube narrow. The pharyngeal tube is long and curved; the oval pharynx contains the apophyses, 2 macroplacoids in the shape of rods, and septula. Doubleclaws very small: the anterior 4.6μ long, the posterior 6μ (on the 4th pair of legs). Eggs unknown.

D. bisbullatum was observed in leaf litter in the Pilikan forest (Mount Keszthelyer, Hungary).

Some few examples, among them an exuvium containing 7 embryonated eggs, found by Maucci near Vrsar (western Istria) belongs perhaps to this species.

Fig. 105 - *D. bisbullatum* (Iharos). Lateral view and doubleclaws of the 4th pair of legs (from Iharos).

DIPHASCON BREVIPES (Marcus, 1936) (Fig. 106).
= *Hypsibius* (*D.*) *brevipes* Marcus, 1936.

Length about 350μ, colorless, smooth cuticle, eye spots present; the maximum width of the body is in correspondence with the 3rd pair of legs; legs short. Buccal tube narrow (external diameter about 2μ); pharyngeal tube as long as the length of the pharynx. Between the buccal tube (rigid) and the pharyngeal tube, exists the "drop" formation.

Pharynx oval (length:width = 1.5:1).

There is present apophyses and 2 macroplacoids of which the first is longer than the second: there exists the septula. Doubleclaws of each leg of size and shape little different and rather small (about 10μ the principal branch of the caudal doubleclaw of the 4th pair of legs).

Near the claws, the first three pair of legs bear a short cuticular bar. Eggs unknown.

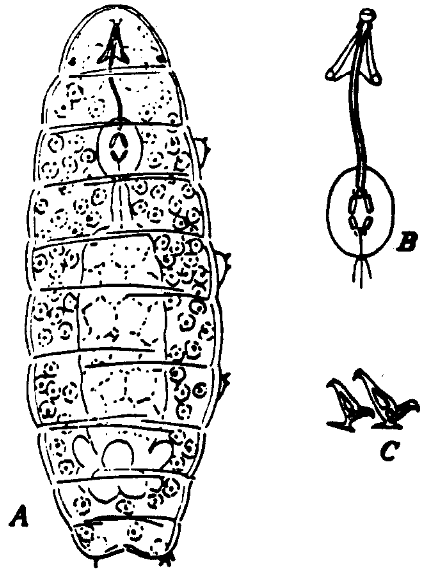


Fig. 106 - *D. brevipes* (Marcus). A, dorsal view; B, buccal apparatus and pharynx; C, double-claws (from Marcus).

D. brevipes has been collected in Hungary, Romania, Sicily, Trieste Carso, U.S.A. (Illinois), and also near Verona in interstitial environment. Typ. loc.: Hungary.

DIPHASCON BULLATUM Murray, 1905 (Fig. 107).
= *Hypsibius* (*D.*) *bullatus* Marcus, 1936.

Length up to 400μ, maximum width of the body in correspondence with the 3rd pair of legs; eye spots present or absent, legs rather short. The cuticle bears a sculpture composed of rounded granules, especially in the dorso-caudal region; there exists dorsally up to 9 transverse rows of two gibbosities each, which however maybe reduced to only the last two caudal rows (that is to say the gibbosities may be inclusively only four); the pair of gibbosities of the first (rostral) row are sometimes in contact on the dorsal median line, while more often distant apart proceeding in a rostro-caudal sense: the caudal gibbosities are largest.

Pharyngeal tube narrow, with external diameter of about 2μ, rather longer than the oval pharynx (length:width ratio included between 1.8:1 and 1.3:1); the "drop" formation is present on the buccal tube. In the pharynx are present apophyses, two macroplacoids in the shape of rods, and septula; the macroplacoids may have approximately the same length, or else often the first is longer than the second and with a constriction little more back from the middle, or else finally both have a constriction.

The two doubleclaws of each leg have length little different and are rather small. Near to them, the first three pair of legs bear a short cuticular bar.

The eggs are deposited in the exuvium in numbers from 3 to 14 (more frequently 5-7).

Rather more difficult to arrive at the distinction between *D. bullatum* and *D. trachydorsatum*, and it is not excluded that this last species is included within the limits of variability of *bullatum*, in which however the last two caudal gibbosities are often widely divergent. It is not sufficiently distinctive character, neither the presence of eyes in *trachydorsatum* (for example almost all the *bullatum* of the soil at Pallanza were eyed), nor the length of the macroplacoids, extremely variable also in *bullatum*; there remains as only characteristic of *trachydorsatum* the dorsal "swelling" on the legs, particularly very visible on those of the first pair (Bartos, 1937). It is not easy even to separate *bullatum* from *D. elongatum*, which differs only by the characteristics stated in the key to determination of the species of the genus *Diphascon* (see also the description of *D. elongatum*).

D. bullatum is known from various European localities: in Italy it was found in the vicinity of Trieste, on the Veronese Lessini, and in meadow soil of Pallanza (Maggiore Lake). Typ. loc.: Scotland.

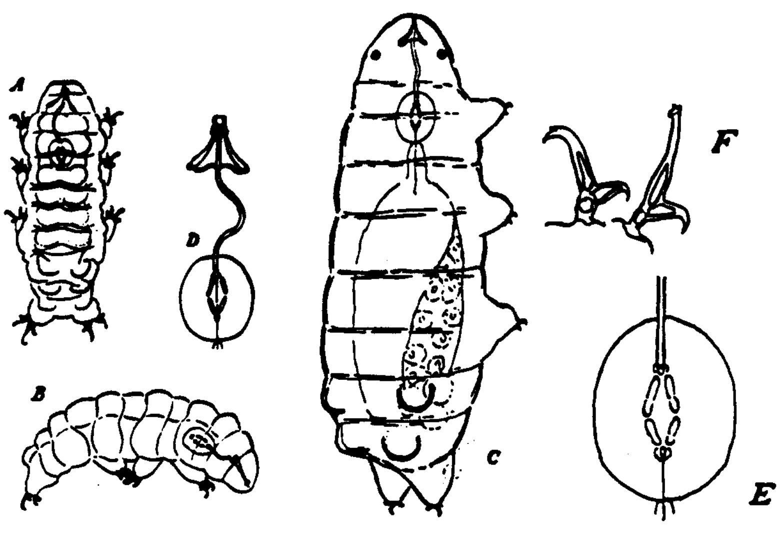


Fig. 107 - *D. bullatum* Murray. A, B, dorsal and lateral view; C, individual with reduced number of gibbosities; D, E, pharynx and placoids; F, doubleclaws (from Marcus).

DIPHASCON CAROLAE Binda & Pilato, 1969 (Fig. 108).

The two specimens collected measured 161μ, the eyes are absent and the anterior portion of the body is clearly narrowed; cuticle smooth. Buccal tube with insertion appendices of the stylet muscles in the shape of crests; pharyngeal tube (flexible) very narrow (diameter about 1μ), about 1.5 times as long as the pharynx and with the usual twisting spiral of its wall. There is no "drop" formation on the buccal tube.

Pharynx of very elongated shape, with length:width ratio equal to 2.1-2.2:1 (about 21-22μ x 10μ). Very small apophyses and 3 macroplacoids (rods), the first two of almost equal length (respectively 2.3 and 2.5μ), the third clearly longer (about 6μ); microplacoid and septula absent. The length of the row of 3 placoids is about 14μ and therefore greater than half the length of the pharynx.

Doubleclaws of *Hypsibius* type and the two of each leg are somewhat different from each other in shape and size; small accessory points, either on the principal branch of the external doubleclaw (7.8μ long), or of the internal doubleclaws (6μ long). Since the principal branch is inserted on the basal claw at about a third of its length, the basal portion of the claws appears not particularly short.

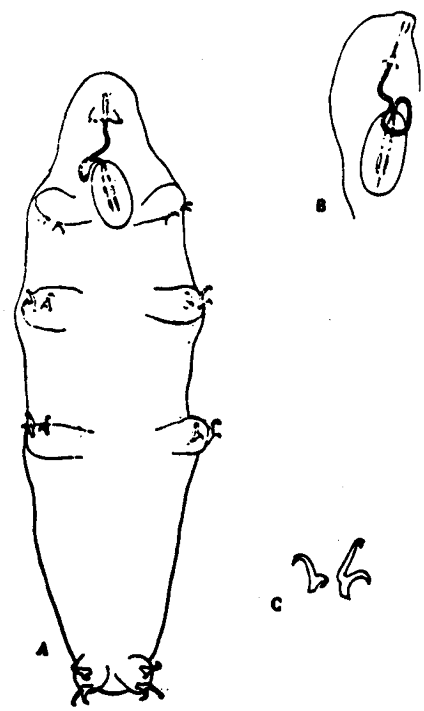


Fig. 108 - *D. carolae* Binda & Pilato. A, ventral view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs (from Binda & Pilato).

D. carolae is distinguished from *D. tenue* (the species which it closest resembles) by having the rostral part of the body slender, by the presence of small apophyses (lacking in *tenue*), by the considerable length of the row of the placoids (larger than half the length of the pharynx, while in *tenue* is less), by having the basal portion of the claws not particularly short, while in *tenue* it is short, by the posterior legs of normal length and not short like *tenue*.

The species was collected in beech soil at Portella Mandrazzi in Peloritani (Sicily).

DIPHASCON CHILENENSE Plate, 1888 (Fig. 109).
= *Hypsibius* (*D.*) *chilenensis* Marcus, 1936

Length up to 272μ, rather squat and wide. Eye spots absent. Buccal and pharyngeal tube long and narrow (width little more than 1μ). Between the buccal tube and the pharyngeal tube exists the "drop" formation.

The pharyngeal tube is about one and a half times as long as the length of the pharynx which is small, in optical section almost round, or else oval (length:width ratio = 1.5:1 or less). Apophyses well developed, or else reduced; 3 macroplacoids in the shape of short rounded rods or of oval granules, of about equal length and often almost in contact with each other, microplacoid and septula.

The doubleclaws are slender and rather short, without considerable difference between the anterior doubleclaws and the posterior, because the principal branch of the latter is not very long. The smooth eggs are deposited in the exuvium in numbers from 1 to 3.

For the distinction of *D. chilenense* from *D. alpinum*, from *D. stappersi*, and from *D. tenue* we refer the reader to what is said in the description of *D. alpinum*.

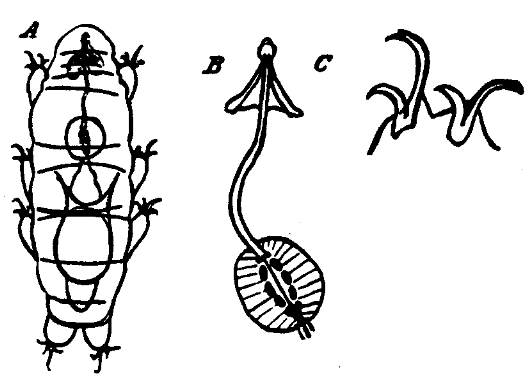


Fig. 109 - *D. chilenense* Plate. A, dorsal view; B, buccal apparatus and pharynx; C, doubleclaws (from Marcus).

The species is cosmopolitan and was collected in Europe (also in Italy), Asia, North and South America, Australia, New Zealand, Arctic and Antarctic. Typ. loc.: Chile.

There was also described as "forma", the following subspecies:

D. chilenense langhovdense Sudzuki, 1946 (Fig. 110).

Length 122-180μ, eyes absent, cuticle smooth; other characters approximately as in *D. chilenense*; the variety *langhovdense* differs from the typical particularly by:

- the absence of the septula;
- the length:width ratio of the body (about 3.2 in *chilenense*; from 3.6 to 4 in the variety);
- the ratio between length of the pharyngeal tube and of the pharynx, which is somewhat larger in *langhovdense*.

This variety was collected in moss at Langhovde (Antarctic continent).

DIPHASCON CLAVATUM (Bartos, 1935) (Fig. 111).
= *Hypsibius* (*D.*) *clavatus* Bartos, 1935

Length 203-211μ, eyes absent, legs short. The cuticle is everywhere smooth, with exception of a small zone of the caudal end of the dorsum and of the external surface of the 4th pair of legs, which are covered with a dense and regular granulation, composed of polygonal granules.

The buccal opening is in terminal position; buccal and pharyngeal tube narrow (about 1.4μ); without the "drop" formation.

The pharyngeal tube (20μ) is slightly shorter in length than the pharynx, which has length about twice of the width (20 x 11μ) and contains very visible apophyses and 3 macroplacoids, the first and the second of about equal length, the third longer and caudally enlarged in the shape of a club. Microplacoid absent. Doubleclaws large, those internal smaller than the external, with principal and secondary branch very curved; the principal branch has accessory points. Eggs unknown.

The species is easily distinguished -- on the basis of characters stated in the identification key -- from others of the genus *Diphascon* having caudally granulated cuticle (*nodulosum*, *oculatum*, *rugocaudatum*) or everywhere (*latipes*, *rugosum*).

D. clavatum was collected in moss in sun, at 880 m altitude in Czechoslovakia, and later in Rumania.

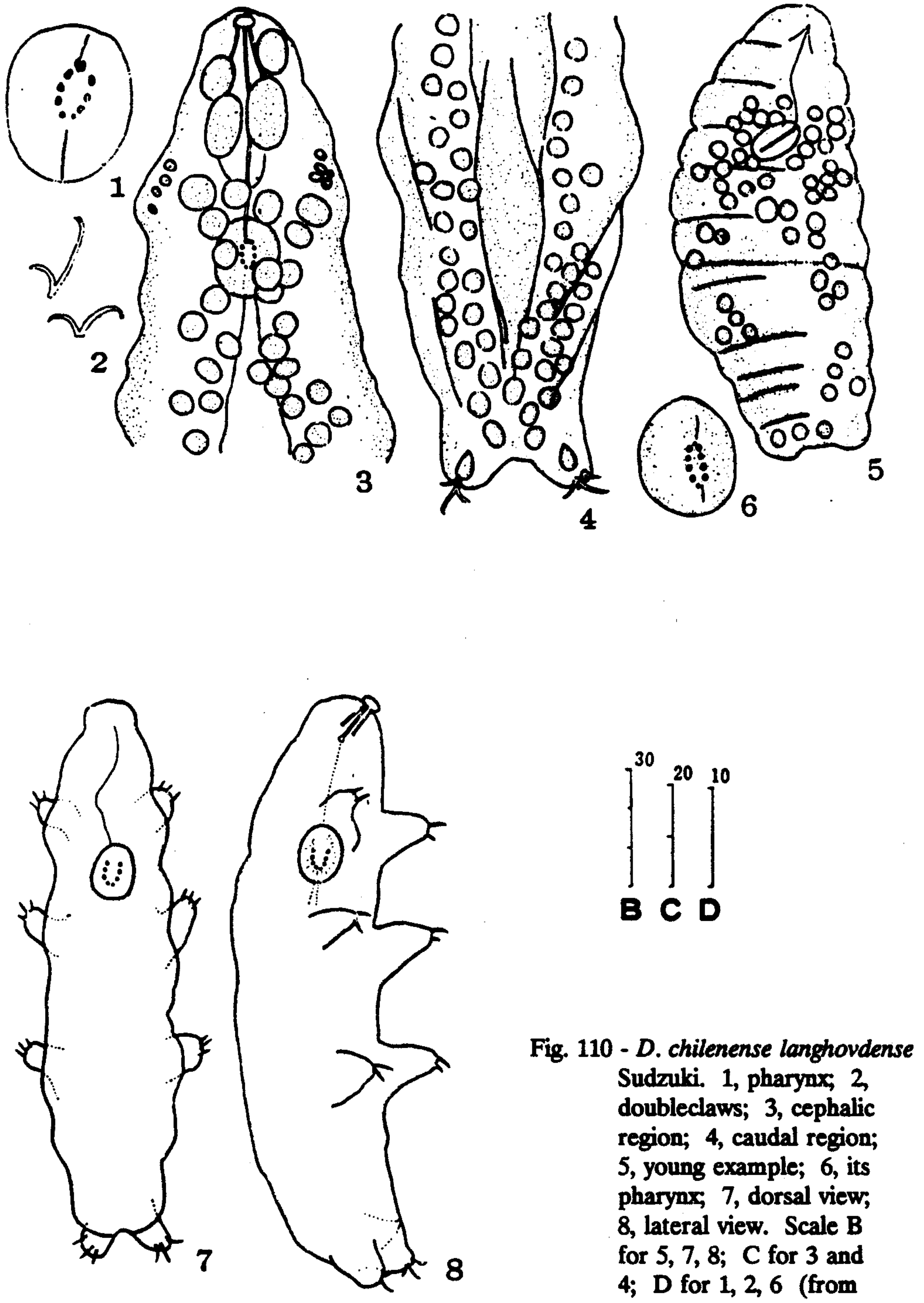
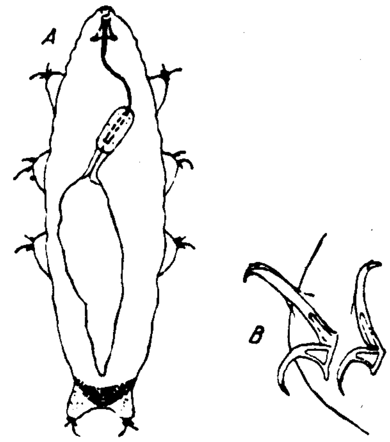


Fig. 110 - *D. chilenense langhovdense* Sudzuki. 1, pharynx; 2, doubleclaws; 3, cephalic region; 4, caudal region; 5, young example; 6, its pharynx; 7, dorsal view; 8, lateral view. Scale B for 5, 7, 8; C for 3 and 4; D for 1, 2, 6 (from Sudzuki).

Fig. 111 - *D. clavatum* (Bartos). A, dorsal view; B; doubleclaws of the 4th pair of legs (from Marcus).



DIPHASCON CONIFERENS (Bartos, 1960) (Fig. 112).
= *Hypsibius* (*D.*) *coniferens* Bartos, 1960

Length up to 260μ, slender, not eyed. The cuticle of the dorsum is smooth on the rostral end as far as the third pair of legs, while caudal to them shows 4-5 transverse rows of small tubercles (7-9 per each row), turned backward and having obtuse conical shape, or almost hemispherical; also three tubercles exists on the dorsal surface of each leg of the fourth pair.

The buccal tube and the pharyngeal tube are narrow (external diameter about 1.4μ), the pharynx is elongated oval (23 x 16μ), with apophyses, 3 macroplacoids of rod shape, of increasing length rostro-caudally, and well-developed microplacoid. The two doubleclaws of each leg are not very different from each other and are robust. The eggs are unknown.

The species was cited only for one locality in Bohemia and collected in dry moss on soil.

DIPHASCON CONJUNGENS (Thulin, 1911) (Fig. 113).
= *Hypsibius conjungens* Thulin, 1911
= *Macrobiotus conjungens* Rahm, 1928
= *Hypsibius* (*H.*) *conjungens* Marcus, 1936

Length up to 265μ, colorless, or yellowish. Eyes present. The old individuals often have brownish transverse bands, or spots of pigment. The body is narrow and elongated, the legs small.

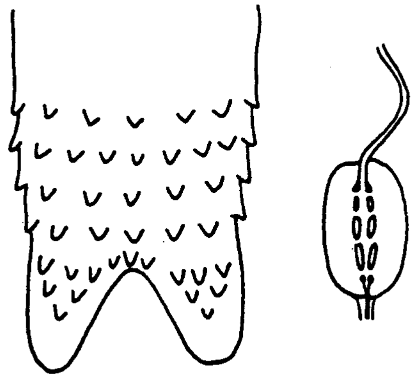


Fig. 112 - *D. coniferens* (Bartos, 1960). Caudal zone and pharynx with placoids (from Bartos, redrawn).

The buccal tube is slender, the pharyngeal tube is not much longer than to barely surpass half the length of the pharynx; the spiral-shaped structure of the wall of the pharyngeal tube appears barely evident.

The very narrow buccal tube possesses the two appendices for muscle insertion of hook shape and may often be slightly undulating between the stylet supports and the pharynx. Pharynx with two macroplacoids (granules), of which the first is sometimes a little larger than the second; microplacoid absent.

The two doubleclaws of each leg are short and stumpy and the principal branches of each bear accessory points. A unique example os the genus *Diphascon*, the eggs are deposited free and have ornamentation: they are oval (26-30μ x 57μ), covered with slightly dense and slightly rigid thorns, with conical bases and with apices often bent; Cuénot observed one time, exceptionally, an egg deposited in the exuvium.

The species was initially considered as belonging to the genus *Hypsibius*, however at the limits between *Hypsibius* and *Diphascon*. Robotti (1972), emphasizing the spiral structure of the pharyngeal tube, has proposed the transferring of the species to the genus *Diphascon*.

D. conjungens was found everywhere in Europe (including Italy), as well as North America (Maryland, U.S.A.) and Greenland. Typ. loc.: northern Sweden.

DIPHASCON ELONGATUM (Mihelčič, 1959) (Fig. 114).
= *Hypsibius* (*D.*) *elongatum* Mihelčič, 1959

Length 280-300μ, colorless or transparent, slender, with length:width ratio = 4:1. Eye spots absent; between the first and the 4th pair of legs the width of the body -- in dorsal view -- remains constant. The cuticle is

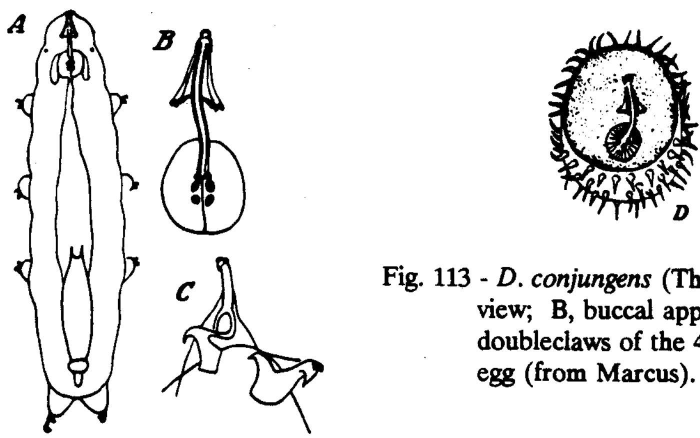


Fig. 113 - *D. conjungens* (Thulin). A, dorsal view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs; D, egg (from Marcus).

granulated and there are also 6 transverse dorsal rows of two gibbosities each. The pharynx is elongated oval, has length about twice of the width and contains 2 macroplacoids of rod shape -- of which the first is longer -- and the microplacoid; the pharyngeal tube is a little shorter than the entire length of the pharynx, and is narrow as in *D. bullatum*. Legs short and large; doubleclaws of each leg very different in size and shape.

The species is undoubtedly very close to *D. trachydorsatum* and *D. bullatum*; it differs from the latter by the small size (300μ rather than 400μ, but this is certainly not a sufficient distinctive character) and by other characteristics -- in reality not very important; we refer the reader to what is said in the description of *D. bullatum* adding that only the examination of abundant material may establish if *elongatum* and *trachydorsatum* are really species themselves, or if rather not included in the limits of variability of *bullatum*.

D. elongatum was collected only in moss on rock from the Austrian Alps.

DIPHASCON GERDAE (Mihelčič, 1951) (Fig. 115).
= *Hypsibius* (*D.*) *gerdae* Mihelčič, 1951.

Medium size (the author has not published the length in μ), body slender, eye spots absent. The cuticle shows a regular and extremely fine granulation: there exists also 7 dorsal transverse rows of two large gibbosities each, at its sides -- one per side -- there are two other smaller hemispherical gibbosities (in other words: each of the 7 transverse rows is composed of 4 gibbosities, the central two larger and the two lateral

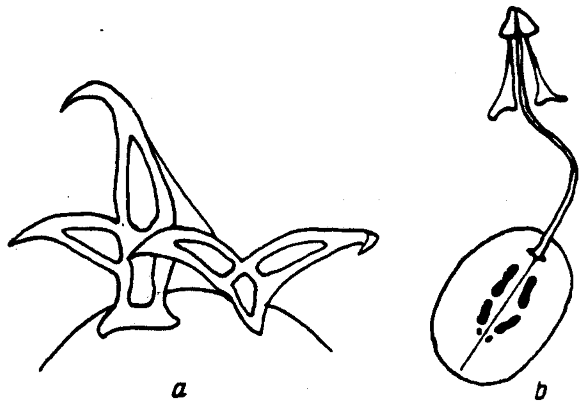


Fig. 114 - *D. elongatum* Mihelčič. a, doubleclaws of the 4th pair of legs; b, buccal apparatus and pharynx (from Mihelčič).

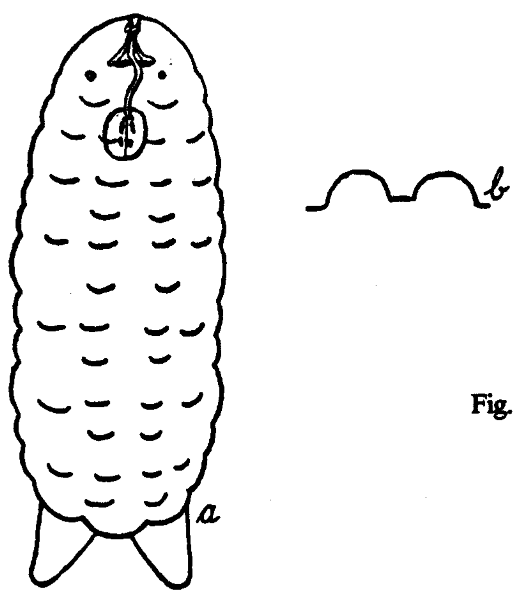


Fig. 115 - *D. gerdae* (Mihelčič). a, dorsal view; b, profile of the gibbosities (from Mihelčič).

smaller). Also smaller gibbosities exist between the aforesaid 7 transverse rows, and still others (in two rows) on the cephalic region; the rows of larger gibbosities start in correspondence with the first pair of legs.

Pharynx almost spherical, with 2 macroplacoids (rods), of which the first is longer than the second, and microplacoid; legs short; external and internal doubleclaws of almost equal size.

The species is known only from a locality in the Austrian Alps (eastern Tyrol) and was observed in conifer leaf litter.

DIPHASCON GRANIFER Greven, 1972 (Fig. 116).

Length from 164 to 210μ; pharyngeal tube long and slender (little longer than the pharynx); between the buccal tube and the pharyngeal tube exists the "drop" formation.

Apophyses very obvious, 2 macroplacoids in the shape of wide rods (the 1st with clear constriction) and septula. The cuticle is uniformly granulated on the dorsum, from the cephalic end as far as the caudal; the granulation brings to mind that of *H. oberhaeuseri*. It deposits 4 smooth eggs (diameter about 45μ) in the old cuticle.

This species seems to be rather close to *D. ramazzottii* and *D. nodulosum*. However a comparison performed on typical examples resulted that *D. ramazzottii* has a much finer sculpture, the more slender buccal tube is longer, and it possesses on the first three pair of legs a cuticular bar which is lacking in *D. granifer*; also the eyes are present, while they are instead absent in *granifer*.

D. nodulosum has however eyes present, buccal tube more slender and narrow, macroplacoids shorter, almost granular; also the sculpture is composed of larger plates, increasing in the direction of the caudal end.

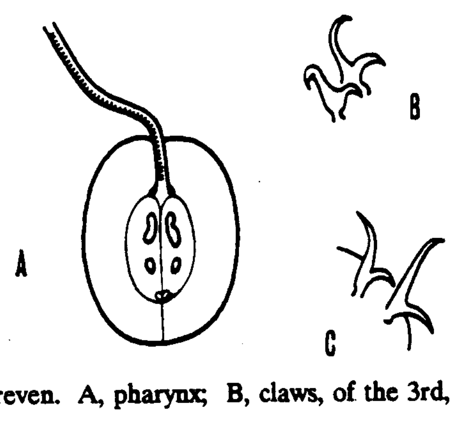


Fig. 116 - *D. granifer* Greven. A, pharynx; B, claws, of the 3rd, C, of the 4th pair of legs (from Greven).

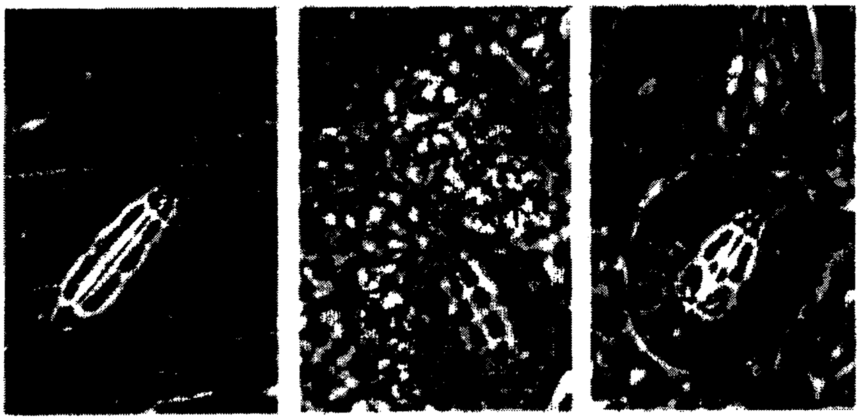


Fig. 117 - Buccal apparatus in *Diphascon*. A, *scoticum*; B, *alpinum*; C, *granifer* (from Greven).

D. granifer was collected in moss on trunks and on stones in the vicinity of Volkringhausen (Sauerland, Germany).

DIPHASCON HALAPIENSE (Iharos, 1964) (Fig. 118).
= *Hypsibius* (*D.*) *halapiense* Iharos, 1964.

Length 110-195μ, colorless, eye spots absent. Dorsally the cuticle is smooth and there exists only 4 hemispherical gibbosities in the caudal region, arranged in a transverse row, just above the 4th pair of legs.

Buccal and pharyngeal tube narrow: the latter is about twice as long as the pharynx, which is practically spherical (from 17 x 17μ to 22 x 24μ). Three macroplacoids, of which the first two are short rounded rods and the third is somewhat longer. Microplacoid present. Anterior doubleclaws of the 4th pair of legs 3.5-6μ long, posterior 6-10.3μ. Eggs unknown.

D. halapiense was collected in moss on soil at Zalahalap, Weinberg (Hungary).

DIPHASCON HIGGINSI Binda, 1971 (Fig. 119, 144, 145).

Maximum length 427μ. Without eyes; cuticle smooth. Rigid part of the buccal tube, which is prolonged a little further than the attachment of the stylet supports and without the small enlargement of "drop" shape.

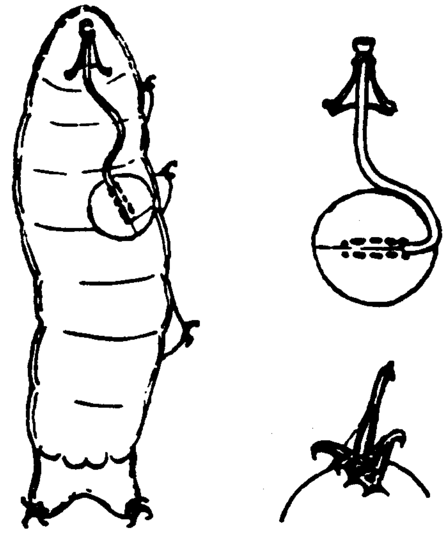


Fig. 118 - *D. halapiense* (Iharos). Dorsal view, detail of the buccal apparatus and doubleclaws of the 4th pair of legs (from Iharos).

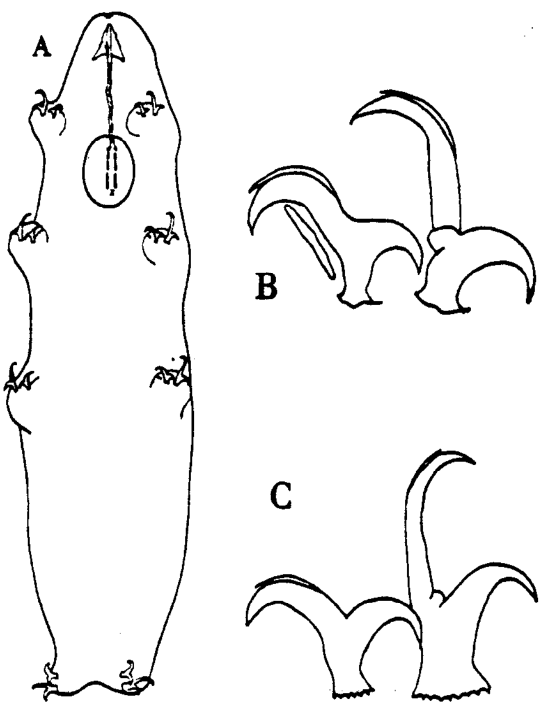


Fig. 119 - *D. higginsi* Binda. A, habitus; B, claws of 2nd pair of legs; C, claws of the 4th pair of legs (from Binda).

Pharyngeal tube almost as long as the pharynx or scarcely longer and very narrow (about 2μ). Pharynx elongated oval, with length:width ratio of 1.6:1, containing apophyses, 3 macroplacoids, microplacoid, and septula. The 1st and the 2nd macroplacoids are equally long and the 3rd is longer, or else the 3 macroplacoids increase in length from the 1st to the 3rd (in an animal 427μ long, they measure from 1st to 3rd: 3.7, 5.8, 8.4μ). Bases of the claws expanded, with basal margins enlarged and dentate on the 4th pair, while they are slightly notched or smooth on the first three pair. On the first three pair of legs exists a cuticular bar at the base of the claws.

The principal difference of this species from *nobilei* consists of: septula present -- pharyngeal tube as long as or a little more than the pharynx -- lacking the "drop" and the eyes -- less development of the claws.

D. higginsi, which is probably an aquatic species, was collected in damp moss at Oukaimeden (Mariakeeh at 2,500 m altitude, Atlante Peak, North Africa).

DIPHASCON ILTISI (Schuster & Grigarick, 1965) (Fig. 120).
= *Hypsibius* (*D.*) *iltisi* Schuster & Grigarick, 1965.

Length 335μ, cuticle of the dorsum and of the legs with polygonal sculpture; the polygons have a diameter of 3-4μ medially and of 1-1.5μ laterally; cuticle of the ventral surface apparently smooth. Eyes present. Rigid part of the buccal tube 25μ long, with stylet supports inserted in the posterior third: at the end of the buccal tube exists a "drop" formation. Flexible part (pharyngeal tube) 42μ long, with diameter of about 2μ. Apophyses large; two macroplacoids: the first 7μ long, divided transversely at the middle, and the second of 5μ, sometimes divided before the posterior fourth; microplacoid of about 3μ.

The authors consider the species near to *D. latipes* and *D. rugosum*, but both of these species have very fine granulation (which posteriorly becomes a little less fine in *rugosum*). *D. latipes* presents also a smooth gibbosity on each leg. The granulation of *iltisi* is large and the size of the granules do not increase caudally (as occurs instead in *nodulosum*); the legs do not have a gibbosity and the macroplacoids are large. The authors note that the dorsum of two examples -- among those observed -- exhibits regular swellings, so much so as to suspect the presence of weak gibbosities: if in any case there were really such gibbosities, the individuals may be mistaken for *D. nonbullatum*, given that the placoids of this species correspond to those of *iltisi*: however *iltisi* appears always easily recognizable by the polygonal sculpture of the cuticle.

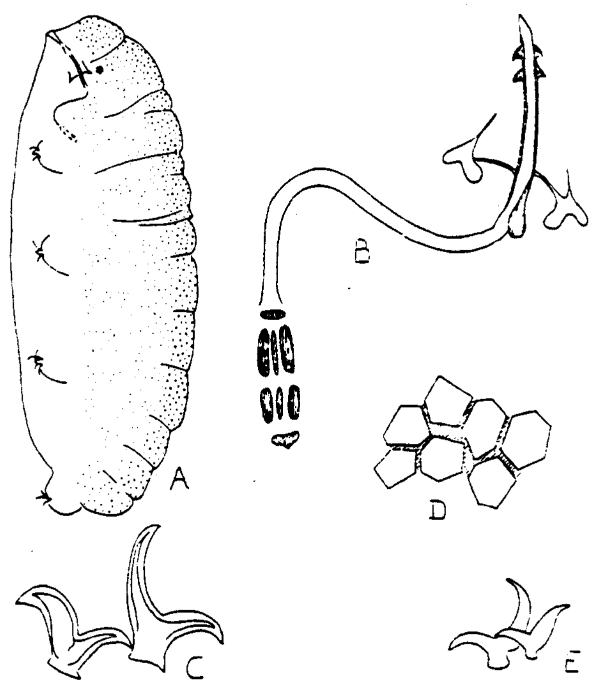


Fig. 120 - *D. iltisi* (Schuster & Grigarick). A, lateral view; B, buccal apparatus; C, E, doubleclaws of the 4th pair of legs; D, detail of the sculpture of the cuticle (from Schuster & Grigarick, redrawn).

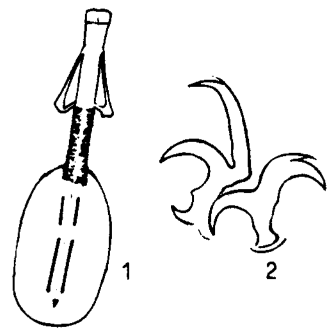
The eggs, deposited in the old cuticle, are spheroidal and have a diameter of 50-60μ.

The species was collected in various localities from California, in moss and also in a decomposing cone of *Pseudotsuga menziesii*.

DIPHASCON ITAQUASCONOIDE Durante & Maucci, 1975 (Fig. 121).

Species of moderate size (holotype, 550μ), of white color, with eye spots absent. The cuticle is smooth except for an extremely fine granulation on the external side of the legs, somewhat more extended on the 4th pair. Body squat, with short legs and snout clearly rounded. Buccal aperture terminal (like *D. prorsirostre* Thulin). The buccal tube is very short and wide: length 58μ, half of which is the rigid buccal tube, and

Fig. 121 - *D. itaquasconoide* Durante & Maucci. 1, buccal apparatus; 2, claws of the 4th pair of legs (from Durante and Maucci).



half (29μ) the pharyngeal tube, which does not appear very flexible; width 8μ. The index "width, expressed in % of the length" is then equal to almost 14, that is absolutely unusual for a *Diphascon*, and much higher than that of any other species of the same genus. The pharyngeal tube presents in very evident manner the spiral structure, characteristic of the genus, while the rigid part (buccal tube, in strict sense) presents scarcely an incomplete and extremely vague trace. Stylets straight, very near to the tube, with medium large furcae. Stylet supports short and robust. The pharynx is very elongated, almost cylindrical (64μ by 35μ). There are present two extremely slender macroplacoids, with thickness a little irregular and appearance slightly knobby, however less than 1μ in thickness: the first is 8μ long, the second (very close to the first, and almost in contact with it) 22μ; the entire row barely surpasses 30μ. Microplacoid present, large, elongated; septula absent.

The claws are very large and strong, with considerable resemblance to those of *Itaquascon*. The larger (external) claws present the common basal branch and the secondary branch of about equal length (10μ), sickle-shaped, very robust, while the principal branch, inserted laterally (18μ long) presents a slender insertion, which follows a nodular enlargement, then continues straight terminating with a sharp hooked curvature, with strong and evident accessory points. The basal common branch of the 4th pair of legs presents a type of small spur, at half of its length. The small claw (internal) has the basal common branch and the secondary branch almost equal to the external claw, the principal branch markedly more massive and shorter, and also it is with large accessory points. Both the claws present a dilated base, which, on the internal claw possesses a light dentation, which brings to mind somewhat that of *D. nobilei* Binda.

D. itaquasconoide was found in moss on granitic rock in full sun, east of Norrköping (Sweden).

DIPHASCON LATIPES (Mihelčič, 1955) (Fig. 122).
= *Hypsibius* (*D.*) *latipes* Mihelčič, 1955.

Length 280-340μ, with width of about 85μ in correspondence with the 1st pair of legs and of 110-115μ between the 2nd and 3rd pair; the legs of the 4th pair are widely divergent toward the external. Eye spots absent, body transparent or colorless, cuticle covered with a fine granulation, but without gibbosities or projections, with exception of a gibbosity positioned anteriorly on each leg. Pharyngeal tube longer than the length of the pharynx (about 1.5-1.7:1, according to the author), very narrow (1.2μ); the pharynx is short oval (length:width ratio = about 1.3:1) and contains 2 macroplacoids in the shape of smooth rods, of which the first is longer than the second; microplacoid present, septulum absent. Legs short and wide, with characteristic anterior gibbosity; doubleclaws of each leg of similar shape and of little different size.

D. latipes is distinguished from *D. rugosum* -- which also possesses cuticle covered with a fine granulation and 2 macroplacoids -- by having the gibbosities on the legs, the pharyngeal tube 1.5-1.7 times as long as the pharynx, and external and internal doubleclaws of almost equal length, while in *rugosum* there are not gibbosities on the legs, the pharyngeal tube is little longer than the pharynx, and the doubleclaws of each leg have very different size.

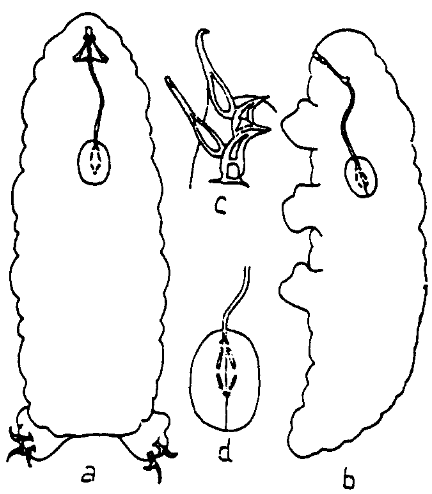


Fig. 122 - *D. latipes* (Mihelčič). a, dorsal view; b, lateral view; c, claws; d, pharynx (from Mihelčič, redrawn).

The species was collected in Austria (Carinzia) in moss exposed on a wall.

DIPHASCON MARCUSI (Rudescu, 1964) (Fig. 123).
= *Hypsibius* (*D.*) *spec. 16* Marcus, 1936.
= *Hypsibius* (*D.*) *marcusi* Rudescu, 1964.

This species was described as *H.* (*D.*) *spec. 16* by Marcus, who did not wish to ascribe any name, because he observed a single example; Rudescu found it in moist moss, named it *marcusi.*

The individuals are small (220-250μ), colorless, with smooth cuticle; eye spots absent; legs long. Buccal and pharyngeal tubes narrow (2μ); length of the pharyngeal tube approximately equal to that of the pharynx. Pharynx very elongated, 3 times longer than wide (about 13 x 38-39μ); three macroplacoids, in general of increasing length from 1st to 3rd (respectively 6, 7.5, 10.5μ): sometimes the 1st and the 2nd macroplacoids have equal length. Microplacoid present and septulum absent.

The two doubleclaws of all legs have different size and the principal branch of the external doubleclaws is much longer than the secondary (on the 4th pair of legs the length of the principal branch is of about 13μ). Eggs oval, colorless, from 40-48μ, deposited in the exuvium. The species, probably hygrophilic, was observed in Poland and in Rumania.

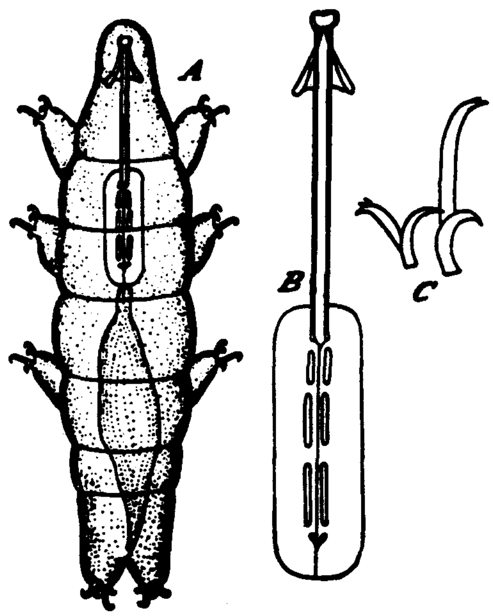


Fig. 123 - *D. marcusi* (Rudescu). A, dorsal view; B, buccal apparatus, C, detail of the doubleclaws (from Rudescu).

DIPHASCON MARCUZZII (Mihelčič, 1971) (Fig. 124).
= *Hypsibius* (*D.*) *marcuzzii* Mihelčič, 1971.

Length about 320μ, cuticle smooth. Pharyngeal tube with two curvatures (the rostral weak, the caudal clear); the last portion of it enters straight in the pharynx and perhaps is more rigid. Pharynx elongated oval, with length:width ratio equal to about 1.6:1. The apophyses are robust, the 3 macroplacoids are slender rods: the 1st is shortest, the 2nd is twice the first, the 3rd is two-thirds longer than the second; that is the macroplacoids increase in length in rostro-caudal sense. Microplacoid present, septulum absent. Legs short, doubleclaws *Hypsibius* type, with principal branch of the external claw strongly curved and elongated point; lacking the accessory points. Eggs smooth, deposited in the exuvium.

The species was collected in a pool near Pietra Rossa (Trieste): the author considers it an aquatic species, but perhaps the single report is not sufficient for affirmation, and it should be treated simply as a hygrophilic species. Other species of *Diphascon* have also been found casually in water or in interstitial environment, but as yet no species of this genus has been shown with confidence to be aquatic.

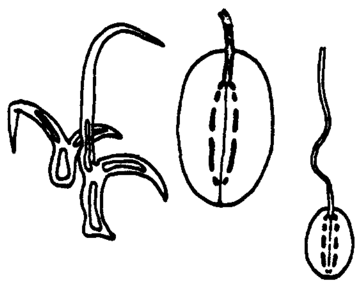


Fig. 124 - *D. marcuzzii* (Mihelčič). Doubleclaws, pharynx, and pharyngeal tube (from Mihelčič).

DIPHASCON MARIAE (Mihelčič, 1949) (Fig. 125).
= *Hypsibius* (*D.*) *mariae* Mihelčič, 1949.

Length 380-500μ, body rostrally and caudally rounded, not very thin in the cephalic region, almost cylindrical in its totality; eye spots absent; cuticle smooth. Buccal and pharyngeal tube narrow; the pharyngeal tube

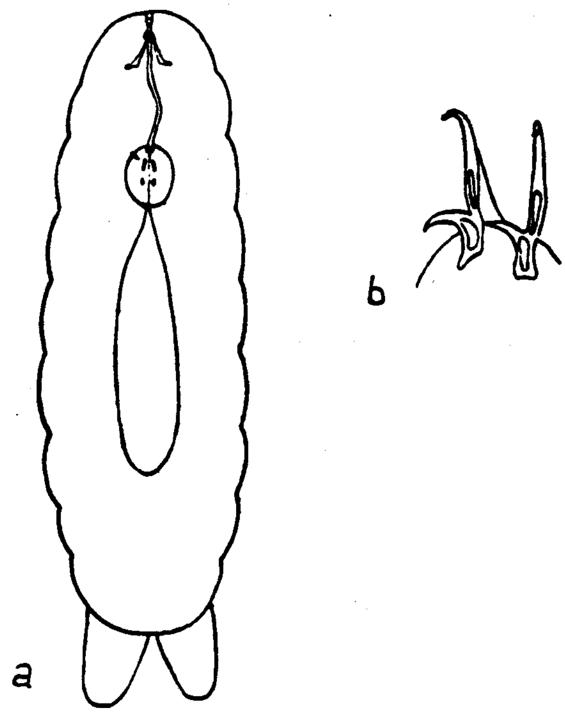


Fig. 125 - *D. marie* (Mihelčič). a, dorsal view; b, doubleclaws (from Mihelčič).

is a little longer than the short oval pharynx; stylets caudally divergent. The pharynx contains little developed apophyses and 2 wide macroplacoids (rods), of which the first presents a constriction and is about twice as long as the second; microplacoid present, septulum absent. Legs short, doubleclaws of all legs little different from each other, with principal branch longer than the secondary and inserted almost at the base of the claw. Eggs unknown.

The species differs from *D. recamieri* especially by the absence of the eyes, the pharyngeal tube shorter (in *recamieri* it is twice as long as the length of the pharynx), and by the two doubleclaws of each leg not very dissimilar in size.

D. mariae is known only for some localities in Austria and was collected in moss, in leaf litter, and in soil of forest floor: it seems to prefer shady and dry habitat.

DIPHASCON MONTIGENUM Pilato & Dastych, 1974 (Fig. 126).

Length from 240 to 260μ. Colorless, body slender and anteriorly attenuated. Cuticle smooth, eyes absent. The buccal tube and the flexible part of the pharyngeal tube are narrow (1.2μ) with a length of 56.4μ. The flexible part alone is 33.4μ long. Lacking the "drop" formation between the buccal tube the pharyngeal tube. Pharynx oval (19 by 16μ), with well developed apophyses and three macroplacoids in the shape of oval granules of increasing length from first to third. Lacking both microplacoid and septula.

Legs short. Claws small, with basal part very short. The two claws of each leg are clearly different from each other, in shape and size. Near the claws there are no cuticular bars. The species appears rather similar to *D. tenue* Thulin, from which it is distinguished by the shorter macroplacoids and by the presence of apophyses which are instead absent in *D. tenue*.

D. montigenum was found in moss on granite, at 1,950 elevation, in the Tatra Mountains (Poland).

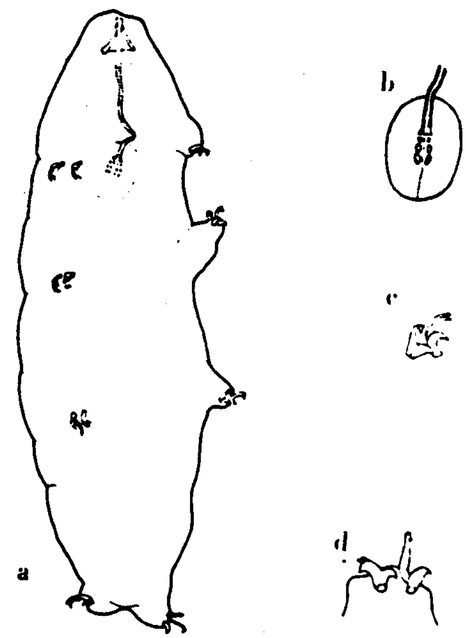


Fig. 126 - *D. montigenum* Pilato & Dastych. a, ventral view; b, pharynx; c, claws of the 3rd pair of legs; d, claws of the 4th pair (from Pilato and Dastych).

DIPHASCON NOBILEI (Binda, 1969) (Fig. 127, 144, 145).
= *Hypsibius* (*D.*) *nobilei* Binda, 1969.

Length 188-390μ, colorless, cuticle smooth, eye spots present. The buccal tube presents the "drop" formation, while the flexible pharyngeal tube is a little shorter than the pharynx, slender, with diameter about 2μ.

Pharynx elongated, with length:width ratio of 1.8:1, containing the apophyses and 3 macroplacoids (rods), of which the 2nd is shorter and the 3rd longest (caudally terminated in a swelling). Microplacoid present.

Legs short, with doubleclaws of different shape and size: the external doubleclaw, robust, has the principal branch inserted about the middle of the basal claw; the internal doubleclaw, also robust, is smaller and the two branches form between them a greater angle than in the external doubleclaw. The basal part of the doubleclaw -- especially on the 4th pair of legs -- is robust, considerably expanded in the proximal part and presents robust teeth: they are, these, unusual characteristics in *Diphascon*, which renders the species then easily identifiable. The principal branches of all

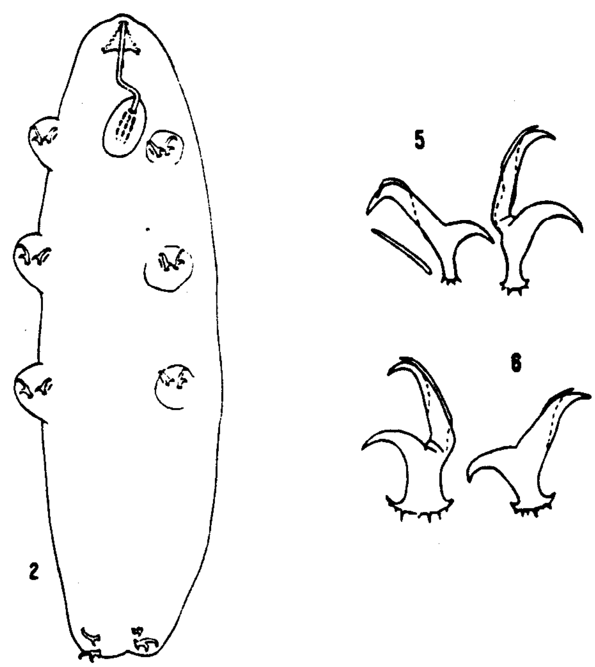


Fig. 127 - *D. nobilei* (Binda). 2, ventral view; 5 and 6, claws of the 3rd and 4th pair of legs (from Binda).

the doubleclaws bear obvious accessory points; also close to the base of the internal doubleclaws exists -- on the first three pair of legs -- a smooth cuticular bar, about 6μ long.

D. nobilei was observed in moss from coastal dunes of Gela (Sicily) and of Pietra Cannone (region of Etna, Sicily).

DIPHASCON NODULOSUM (Ramazzotti, 1957) (Fig. 128).
= *Hypsibius* (*D.*) *nodulosus* Ramazzotti, 1957.

Maximum length about 260μ, colorless, eye spots present. The sculpture of the cuticle is composed of tubercles of irregular rounded shape, very large in the dorsal caudal region, where often flattened distally (perhaps because of the coverslip?), assuming sometimes the appearance of small irregular polygonal plates, with diameter up to about 5-6μ. These tubercles project considerably at the lateral margins, especially at the caudal end; the size of them becomes smaller going toward the rostral end of the tardigrade: from the middle of the animal forward the sculpture is reduced to a simple granulation, always less distinct, as far as reaching the cephalic region, which seems to be completely smooth, even observed with strong magnification.

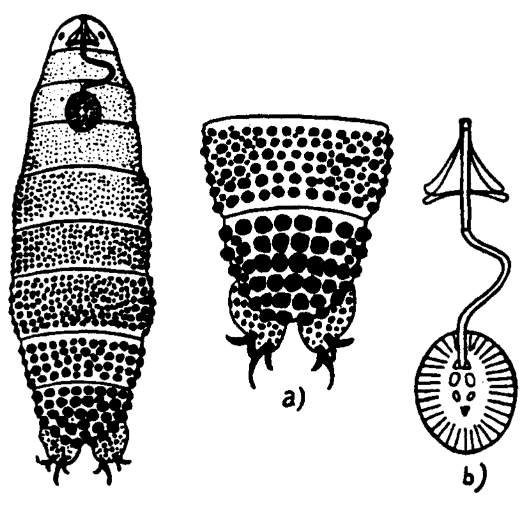


Fig. 128 - *D. nodulosum* (Ramazzotti). a, caudal region; b, buccal apparatus. At left, schematic appearance, with phase contrast.

Pharynx tube very narrow (diameter less than 2μ), longer than the length of the pharynx.

Between the buccal tube and the pharyngeal tube exists the "drop" formation. The pharynx is short oval (29 x 24μ in an animal of 230μ) with very visible apophyses, 2 macroplacoids (granules), of which the first is a little longer and larger than the second, and septula (or microplacoid?). The legs of the 4th pair are also covered with small tubercles, which become smaller on the 2nd and 3rd pairs, while those on the 1st pair seem to be smooth, or almost; doubleclaws of very different size from each other, especially on the 4th pair of legs, where the principal branch of the external doubleclaw, very slender (as in *H. oberhaeuseri*), reaches a total length -- from base to apex -- of about 17μ.

The species may be near to *D. rugocaudatum*, which presents however only granulation in a restricted caudal zone. For the difference from *D. granifer* and *D. ramazzottii* we refer the reader to the observation with regard to *D. granifer*.

D. nodulosum was collected in Wisconsin (in moss on conifer trunks) as well as California, Virginia (U.S.A.), and in Canada.

DIPHASCON NONBULLATUM (Mihelčič, 1951) (Fig. 129).
= *Hypsibius* (*D.*) *nonbullatum* Mihelčič, 1951.

Length 180-320μ, eyed, body rather squat and equally wide -- in dorsal view -- between the 1st and the 4th pair of legs. The cuticle is everywhere

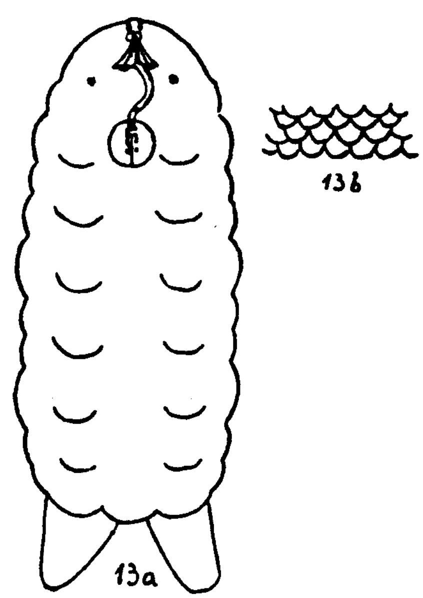


Fig. 129 - *D. nonbullatum* (Mihelčič). 13a, dorsal view; 13b, detail of the sculpture (from Mihelčič).

covered, especially on the gibbosities, but even on the legs, with a granulation of which the single elements have different size: according tothe focal setting of the objective, appears a reticular design, or else becoming evident as granulation. The dorsal gibbosities are arranged in 6 transverse rows of two gibbosities each: the first row is found in correspondence with the first pair of legs, the last row between the 3rd and the 4th pair of legs. Stylets straight and not very divergent, pharyngeal tube (the author has not made note of the diameter) approximately as long as the pharynx: the latter shortly oval, almost spherical, with 2 macroplacoids of about equal size and of which the first appears constricted or interrupted. The two doubleclaws of each leg are robust and of considerably different size from each other.

The species is very near to *D. bullatum*, *trachydorsatum*, and *elongatum* and perhaps included within the limits of variability of *bullatum*: different however by the lack of the pair of caudal gibbosities -- or laterocaudal -- positioned near the bases of the 4th pair of legs, which are typical of the aforesaid three species.

D. nonbullatum is known only for a few localities from Austria (eastern Tyrol) and was collected either in moss, or in needle leaf litter of conifers.

DIPHASCON OCULATUM Murray, 1906 (Fig. 130).
= *D. canadense* Murray, 1910.
= *Hypsibius vancouverensis* Thulin, 1911.

Length up to or over 350μ, colorless, eyes present (sometimes much reduced). Cuticle in general smooth, but in some cases densely and finely granulated in the caudal region. Stylets strongly curved; flexible portion of the buccal tube (pharyngeal tube) very narrow, with internal diameter of about 1μ or a little more and very long (about 2 times the length of the pharynx), describing a noose or undulating before entering the pharynx.

Between the rigid portion, buccal, and the flexible portion, pharyngeal, exists a "drop" formation.

Pharynx short oval (length:width ratio of about 1.3:1), more narrow anteriorly than posteriorly, containing apophyses, 2 macroplacoids and septula; microplacoid absent. The macroplacoids are short rounded rods, or else granules, sometimes of equal length, sometimes the first -- which may be constricted in the middle -- longer, or twice that of the second. The two doubleclaws of each leg are very different from each other, robust and with accessory points on both the principal branches; on the external doubleclaws the principal branch is long and straight. It deposits up to 5

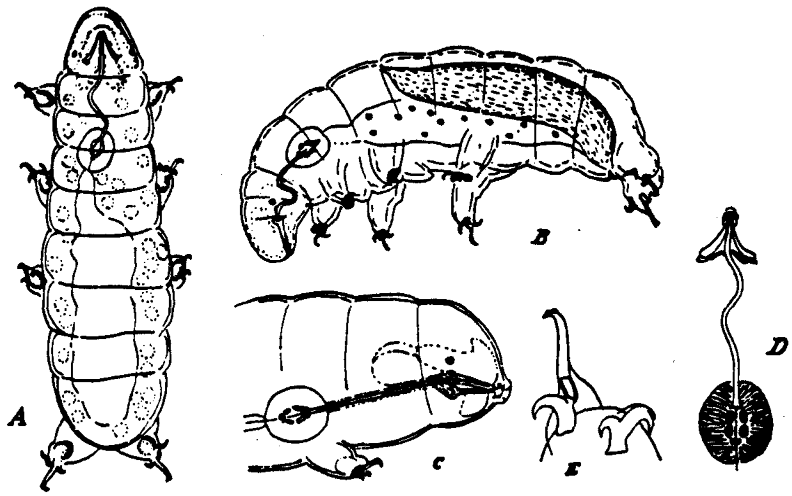


Fig. 130 - *D. oculatum* Murray. A, dorsal view (Lapland); B, lateral view (Harz); C, anterior part of the body, in profile; D, pharynx (Scotland); E, doubleclaws of the 4th pair of legs (from Marcus).

eggs (about 63 x 51μ) in the exuvium.

For distinction of this species from *D. rugocaudatum*, see what is said in the description of this latter species.

D. oculatum is known for many localities of Europe (Italy included) and North America. Typ. loc.: Scotland.

There have been described two varieties, to which we give here the rank of subspecies, in provisional way, for the purpose of simplifying the taxonomy with a trinominal nomenclature. The taxonomic value of such subspecies however still remains to be verified.

D. oculatum alpium (Mihelčič, 1964) (Fig. 131).

Length 280-320μ, width 60-78μ. The animals, very slender and elongated (length:width ratio from 4.8 to 5.4), have smooth cuticle as far as the 3rd pair of legs, while the segments of the caudal zone -- posterior, that is, to the 3rd pair of legs -- have a fine granulation, even very visible at low magnification. At higher magnification (270) the granules appear as clear rings, with a dark circle at their center. In some individuals (among the 25 observed) the author saw 4 dark tubercles on the last segment: the two caudal close together, the two rostral more widely

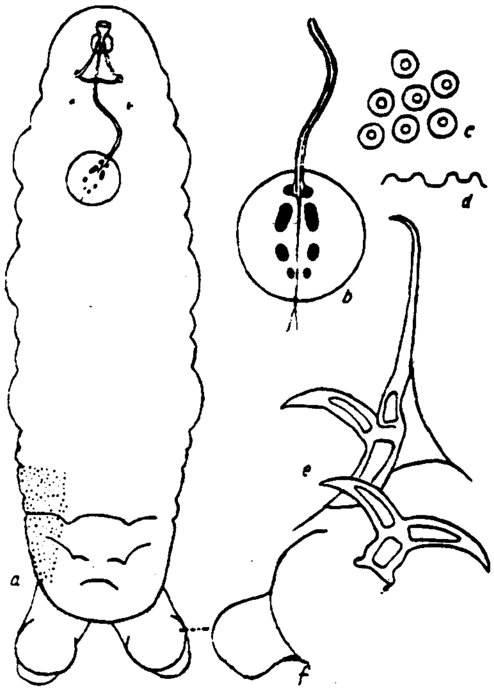


Fig. 131 - *D. oculatum* (Mihelčič). a, dorsal view; b, pharynx with a part of the pharyngeal tube; c, granulation from high focus; d, granulation in profile; e, claws of the fourth pair of legs; f, a part of the last segment with one of its legs (claws not drawn) (from Mihelčič).

separated. The size of the body is approximately constant between the first and the fourth pair of legs.

Eye spots present, in posterior position, situated caudally to the stylets; the buccal and pharyngeal tube is very narrow (about 1μ). The ratio between the length of the pharyngeal tube (48μ) and the length of the pharynx (32μ) is equal to 1.5 (such data partially different from that published in *Zool. Anz.*, 1964, was confirmed by letter from the author). The pharynx is approximately spherical and contains robust apophyses, 2 macroplacoids, and a large microplacoid. The first macroplacoid is a wide rounded rod, about one and a half times longer than the second, which has a granular shape.

The legs of the fourth pair dorsally bears a gibbosity, which covers (in dorsal observation) the doubleclaws. The size of the doubleclaws of each leg is very different: the internal doubleclaw has both robust branches and about equal to each other; the external has the principal branch slender, graceful, straight in lateral view and slightly curved in oblique view, while the secondary branch is robust and is disposed at a right angle with its basal portion.

D. oculatum alpium differs from *D. oculatum* principally by the position of the eyes (posterior rather than anterior), by the shorter pharyngeal tube, by the type of granulation, and by the more slender principal branch of the external doubleclaw. It differs from *D. oculatum vancouverense* by the presence of the eyes, by the shorter pharyngeal tube, by the more robust secondary branch of the external doubleclaw. There is not precise information about the presence or absence -- in *vancouverense* -- of sculpture on the caudal zone.

D. oculatum alpium was collected on Lienz Mountain (Zettersfeld, Austria) in lichen on a roof of wood exposed to full sun; the discovery in a single locality recommends caution in judgement, it is possible that the variety *alpium* may be xerophilic, unlike the typical species *oculatum* which seems to be hygrophilic.

Diphascon oculatum vancouverense (Thulin, 1911) (Fig. 132).

Described by Thulin as a species in itself, it was then considered by Marcus (1936) as "forma" of *H.* (*D.*) *oculatum*.

Length 230-250μ, eye spots absent; body narrow and elongated; pharyngeal tube narrow -- little more than 1μ in diameter -- about twice as long as the length of the pharynx: this last approximately spherical, containing the apophyses, 2 macroplacoids, and a microplacoid (or septulum?); the first macroplacoid is two times longer than its width and a constriction may be present, the second is as long as wide. The external doubleclaw (of larger size) has very slender principal branch (12-15μ) and large secondary branch; the internal doubleclaw is instead more slender than the external, a difference which occurs in *D. oculatum*, where both the doubleclaws of each leg have about equal size; also the claw and the base of the internal doubleclaw are united near their bases, while in *oculatum* there is a base in common. However Ramazzotti observed individuals

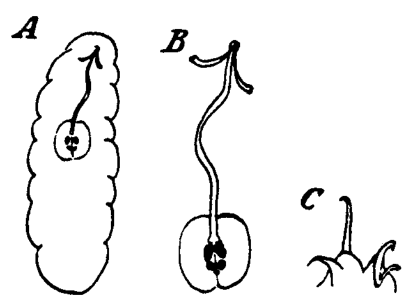


Fig. 132 - *D. oculatum vancouverense* (Thulin). A, dorsal view; B, pharynx; C, doubleclaws (from Marcus).

from U.S.A. (Mount Palomar), lacking eye spots like *oculatum vancouverense*, but otherwise identical to *oculatum*; it may not then be excluded that *oculatum vancouverense* may be included -- at least partially -- within the limits of variability of *oculatum*.

There are reports known from the Carpathians, Canada (Vancouver Island, typ. loc.), and the U.S.A. (California).

DIPHASCON ONGULENSE (Morikawa, 1962) (Fig. 133).
= *Hypsibius* (*D.*) *ongulense* Morikawa, 1962.

Length about 240μ, width 66μ; cuticle smooth, eye spots absent, body slender and transparent. Mouth subventral; pharyngeal tube curved and narrow (0.9μ), about as long as the pharynx. The pharynx is oval (29 x 23μ) and contains 3 macroplacoids of rod shape, which increase in length from the first to third (2.0, 3.3, 4.3μ); septula present. The doubleclaws,

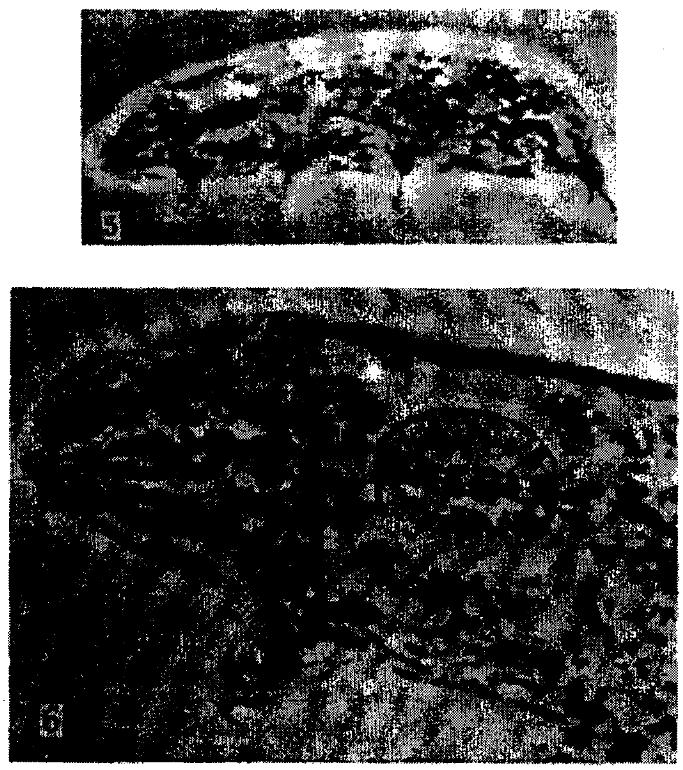


Fig. 133 - *D. ongulense* (Morikawa). 5, general view; 6, buccal apparatus (from Morikawa).

on which the author furnishes some detail, do not have particular characteristics and are not different from those of many other species of *Diphascon*. Legs long (about 38μ). Eggs have not been observed.

The species, according to the author, resembles *D. pingue* and *D. alpinum* but *ongulense* is distinguished from *pingue* because it does not possess microplacoid, has narrower buccal tube, body more slender, and legs longer; from *alpinum* it is distinguished by the smaller length of the pharyngeal tube.

D. ongulense was collected among cyanophyta, chlorophyta, and diatoms, in a pool on East Ongul Island (Antarctica).

DIPHASCON PATANEI Binda & Pilato, 1971 (Fig. 134).

Maximum length about 230μ, eyed. Cuticle sculptured with 8 transverse rows of hemispherical gibbosities (2 per row); cuticle with characteristic polygonal sculpture: the polygons are larger rostrally (1.5-2μ). The gibbosities are dorsal in the first 7 rows, dorsolateral in the last.

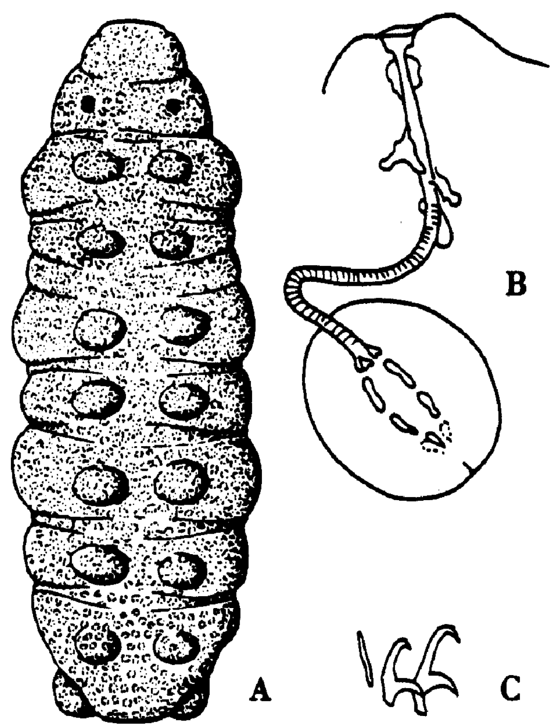


Fig. 134 - *D. patanei* Binda & Pilato. A, habitus; B, buccal apparatus; C, claws of the 3rd pair of legs (from Binda & Pilato).

The first row (rostral) corresponds to the first pair of legs. Buccal tube (rigid) which is prolonged a short way beyond the stylet supports and presents a thickening in the shape of a "drop" near its connection to the flexible pharyngeal tube, which is a little longer than the pharynx (26μ opposed to 22μ). Pharynx short oval (20-22μ x 18-16μ), with length:width ratio equal to 1.21-1.25:1, containing apophyses, 2 macroplacoids, and septula, without microplacoid. The first macroplacoid (3.7μ) is longer than the second (3μ). Cuticular bar on the first three pair of legs. Eggs unknown.

The principal differences between *bullatum* and *elongatum* are: the polygonal sculpture and not punctation of the cuticle, with polygons of about 1.5-2μ. The species is near to *iltisi*, but this does not have gibbosities and the claws are different.

The species was observed on Eolie Islands (Stromboli and Salina), in Sicily, Istria, and Trieste Carso.

DIPHASCON PINGUE (Marcus, 1936) (Fig. 135).
= *Hypsibius* (*D.*) *pinguis* Marcus, 1936.

Length about 240μ, wide, squat, with short legs, colorless, eye spots absent; buccal aperture subterminal. Buccal tube (diameter 1.8μ) and pharyngeal tube narrow: the latter is approximately as long as the pharynx; the stylets are very near -- almost against -- the buccal tube and the stylet supports are strongly curved backwards.

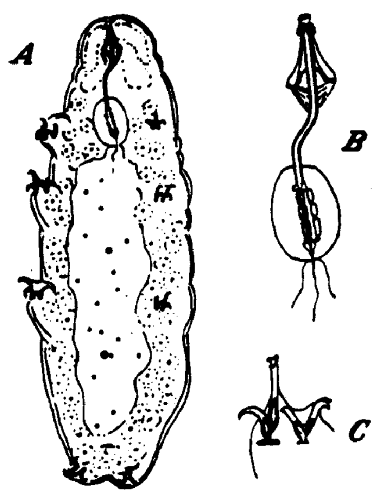


Fig. 135 - *D. pingue* (Marcus). A, dorsal view; B, buccal apparatus and pharynx; C, doubleclaws of the 4th pair of legs (from Marcus).

There exists the "drop" formation between the buccal tube and the pharyngeal tube.

Pharynx oval (length:width ratio = 1.2-1.3:1), containing apophyses, 3 macroplacoids of rod shape -- of about equal width and of increasing length in rostro-caudal sense -- microplacoid and septulum. The width of the macroplacoids about 1.5μ and their length, from first to third is, for example, respectively 2.8, 3, 3.6μ. The two doubleclaws of all legs are of different length, while often the principal (with accessory points) and secondary branches are approximately equal in both the doubleclaws. Eggs unknown.

D. pingue is distinguished from *D. arduifrons*, from *D. prorsirostre*, and from *D. scoticum* -- species very close to each other -- especially by the less elongated pharynx (in the three species cited the length:width ratio of the pharynx is included between 2:1 and 1.6:1); also *arduifrons* and *prorsirostre* lacks the microplacoid and septula.

The species was observed in Germany (Harz, typ. loc.), Switzerland (near Zermatt, at about 2,000 m altitude), the Carpathians, Bulgaria, Brazil, U.S.A., India, and in Vietnam, at Bali.

With the name *D. pingue brunsvicense*, Argue (1972) distinguished his examples from Canada, which appeared collectively more slender and elongated than the typical variety. Also examples from Wisconsin examined by Maucci, may belong to this last variety, whose subspecific value however does not seem to be certain.

DIPHASCON PRORSIROSTRE Thulin, 1928 (Fig. 136, 144, 145).

Length 245-325μ, body slender, buccal aperture terminal as in the genus *Macrobiotus*, so that the "forehead" becomes receding and all the cephalic region, viewed in profile, assumes an appearance more of *Macrobiotus* than of *Hypsibius*. Eyes absent, cuticle smooth. Buccal tube and pharyngeal tube rather narrow, without the "drop" formation. The pharyngeal tube is about as long as the pharynx, which is of elongated oval shape, with length:width ratio of 1.6-1.7:1; in the pharynx there are apophyses and 3 macroplacoids (slender rods) of increasing length in rostro-caudal sense; microplacoid absent. The length of the individual row of 3 macroplacoids is about equal to half the length of the pharynx. Doubleclaws of all the legs of different size and similar to those of *D. scoticum*. Eggs unknown.

D. prorsirostre is a species very near to *D. scoticum* from which it differs by the absence of microplacoids and septulum) and from *D. arduifrons*, so

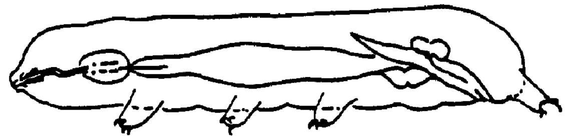


Fig. 136 - *D. prorsirostre* Thulin (from Thulin, redrawn).

that Cuénot had serious doubt of keeping distinct -- or not -- the three species, and we are in accord with him: in particular manner, the difference between *prorsirostre* and *arduifrons* is limited to the different position of the buccal aperture, but we have been able to observe -- in the same moss -- some individuals with buccal aperture and shape of the "forehead" of *prorsirostre* and other *arduifrons*. The ratio between the length of the row of macroplacoids and length of the pharynx does not seem -- at least within certain limits -- a sufficiently valid distinct character, because subject to too great variability, as in general all the ratios between the different components of the buccal apparatus (this statement is however based on measurements of Ramazzotti performed on over 1,000 individuals of another species of tardigrade, *Macrobiotus areolatus*). For further information, see the description of *D. scoticum*.

D. prorsirostre is fairly common, and is cited from different European localities (Italy, Carpathians, Poland, Spain, Germany, Scotland, Sweden, Austria, Yugoslavia, Finland, Norway, Pyrenees) and also from Tierra del Fuego, Chile, and Canada. Typ. loc.: Sweden, Scotland, Mecklenburg.

DIPHASCON PUNCTATUM (Iharos, 1962) (Fig. 137).
= *Hypsibius (D.) punctatus* Iharos, 1962.

Length 340-380μ, yellowish color, eyes absent. The cuticle of the body and of the legs is covered by a fine and dense granulation: the granules have about the same size and are arranged more or less irregularly.

Stylets small and slender; buccal and pharyngeal tube narrow (diameter about 2μ) and about 56μ long (completely?). The pharynx is very elongated oval, of about 32 x 12μ, and containing 2 macroplacoids in the shape of rods, of which the first (6μ) is shorter than the second (14μ); microplacoid and septulum absent.

The two doubleclaws of each leg have different size: the principal branch of both the doubleclaws is robust, strongly bent in a hook at the

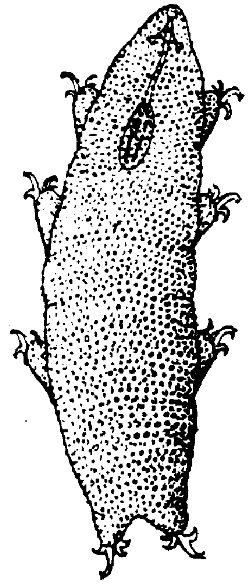
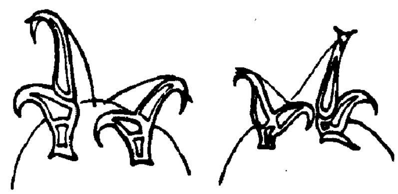


Fig. 137 - *D. punctuatum* (Iharos). A, dorsal view; B, doubleclaws of the 1st pair of legs; C, doubleclaws of the 4th pair of legs (from Iharos).



distal end, and bearing two accessory points. Smooth eggs deposited in the exuvium.

D. punctatum was collected in leaf litter near a stream in the Magyarüröga (Mecsek Mountains -- southern Hungary).

DIPHASCON RAMAZZOTTII (Robotti, 1970) (Fig. 138).
= *Hypsibius* (*D.*) *ramazzottii* Robotti, 1970.

Maximum length 435μ, more often 350μ, colorless, eyed. Cuticle with extremely fine granulation, more evident caudally. Pharyngeal tube very narrow (internal diameter 1.23μ), about 1.3 times as long as the pharynx. Between the buccal tube and the pharyngeal tube exists the "drop" formation.

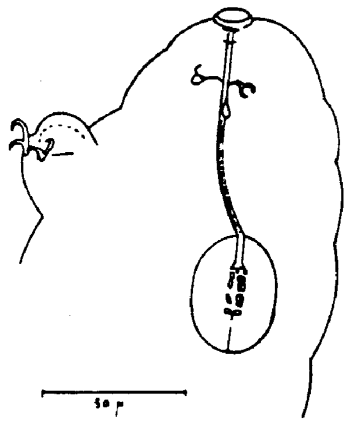
Pharynx oval, with length:width ratio equal to 1.5:1; large apophyses, 2 macroplacoids and septula; lacking the microplacoid. The first macroplacoid is almost 1.5 times as long as the second and bears a type of little button at the caudal end. Each leg has a large gibbosity, rendered bilobe by a longitudinal depression: on the 4th pair, in dorsal observation, the gibbosity covers the doubleclaw.

On the first three pair of legs exists, near to the claws a cuticular bar, lacking the accessory points on the principal branches of the claws. Eggs (3-4, of 60 x 80μ) deposited in the exuvium.

The species was collected in very muddy moss, on a small wall, at Avigliana (Piemonte).

For the distinction of this species from *D. granifer* and from *D. nodulosum*, see what is said in the description of *D. granifer*.

Fig. 138 - *D. ramazzottii* (Robotti). Cephalic region and buccal apparatus.



DIPHASCON RECAMIERI Richters, 1911 (Fig. 139).
= *Hypsibius* (*D.*) *recamieri* Marcus, 1936 and *Auct.*

Length 290-416μ, colorless, body slim and elongated, cuticle smooth. Eye spots present, in anterior position. Buccal tube narrow, or medium narrow (diameter 1.8-2.2μ); the pharyngeal tube (diameter 2-2.5μ), which is very long, is almost double the length of the pharynx.

There exists the "drop" formation.

The pharynx has a length:width ratio of about 1.6:1, that is to say it is rather elongated, and contains apophyses, 2 macroplacoids, and the microplacoid; the first macroplacoid -- about 1.5 times as long as the second -- may be undivided, or else presents a constriction, which sometimes is so deep as to divide it almost into two distinct placoids. According to Weglarska (1959) in some individuals exists also septula.

The two doubleclaws of each leg have very different size, but similar shape, because even the internal (anterior) doubleclaws possesses the principal branch much longer than the secondary and with two robust accessory points; part of the doubleclaw -- that is to say the common part to the principal and secondary branches -- very short; more precisely (for the terminology see Fig. 12): the claw end of the external doubleclaw and of the interior is inserted on the claw base of the first third of the latter.

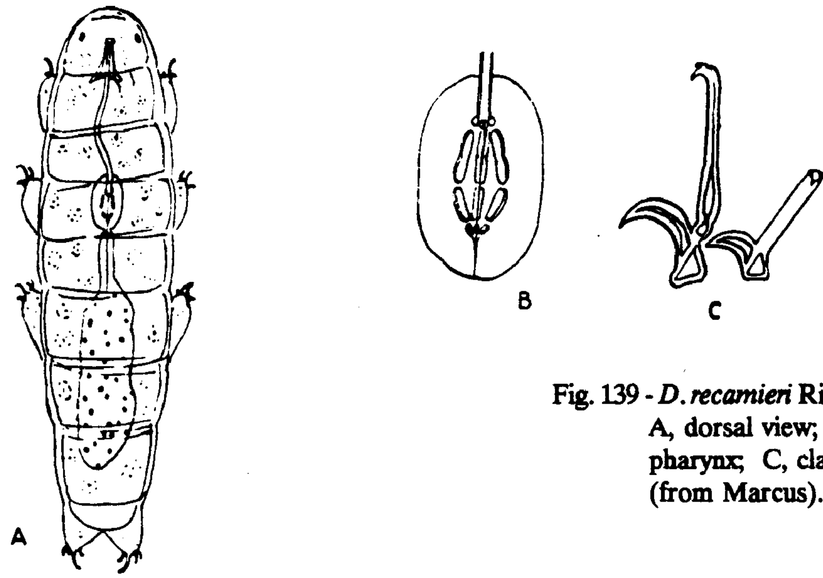


Fig. 139 - *D. recamieri* Richters. A, dorsal view; B, pharynx; C, claws (from Marcus).

The species, which is easily distinguished from *D. oculatum* by the more elongated pharynx and by the structure of the internal doubleclaws, was cited for Switzerland (at 2,700 m altitude), Austria, Hungary, Czechoslovakia, Poland, Spitsbergen Archipelago (typ. loc.), Sweden, Finland, Istria. In Italy, it was collected in Sicily. Outside Europe reports are cited for Greenland and Argentina.

DIPHASCON RUGOCAUDATUM (Rodriguez Roda, 1952) (Fig. 140).
= *Hypsibius* (*D.*) *rugocaudatus* Rodriguez Roda, 1952.

Length 281-302μ; eye spots black, frequently composed of few granules of pigment. Buccal and pharyngeal tube narrow, of about 1.5μ diameter; there exists the "drop" formation; the pharyngeal tube is somewhat longer than the pharynx (from 20-30%): this latter short oval, sometimes almost spherical, containing apophyses, 2 macroplacoids, and the microplacoid (or septulum?); the first macroplacoid is longer than the second, and often has a constriction. The cuticle, in the caudal region of the dorsum is granulated and the larger granules formed of minuscule rounded platelets: the granulated zone does not ever reach to the level of the 3rd pair of legs, but covers only the last caudal 30-45μ of the dorsum. Doubleclaws of each leg of different size. Eggs unknown.

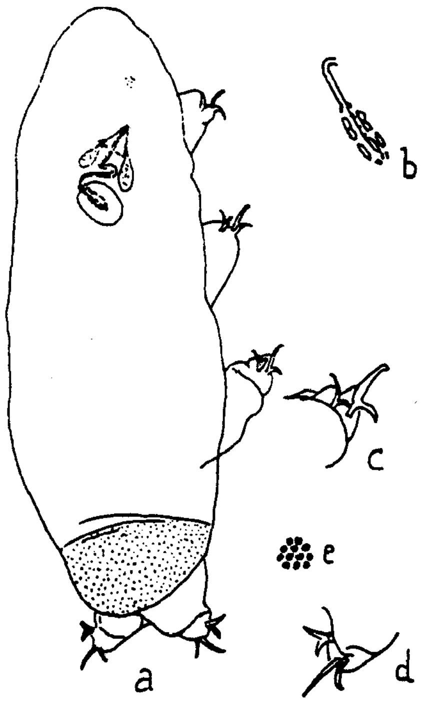


Fig. 140 - *D. rugocaudatum* (Rodriguez-Roda). a, dorsal view; b, placoids; c, d, doubleclaws; e, detail of the caudal sculpture (from Rodriguez-Roda, redrawn).

The species may be distinguished from others similar in basis by the following differences:

- *D. oculatum* which also has 2 macroplacoids and sometimes a granulated caudal zone, has longer pharyngeal tube (about twice that of the pharynx); it is probably a specie very near to *rugocaudatum*.
- *D. clavatum* has 3 macroplacoids.
- *D. nodulosum* (2 macroplacoids) has platelets of the caudal region much larger (diameter 4-6μ) and also the granulation extends on all the dorsum, leaving free and smooth only the cephalic region.

D. rugocaudatum is known for Spain (Pyrenees) and Finland.

DIPHASCON RUGOSUM (Bartos, 1935) (Fig. 141).
= *Hypsibius* (*D.*) *rugosus* Bartos, 1935.

Length 157-311μ, colorless; eyes composed of 6-8 small granules of pigment, or else absent; maximum width of the body between the 2nd and the 3rd pair of legs. The cuticle is covered with an extremely fine granulation, composed of regularly arranged granules, which become

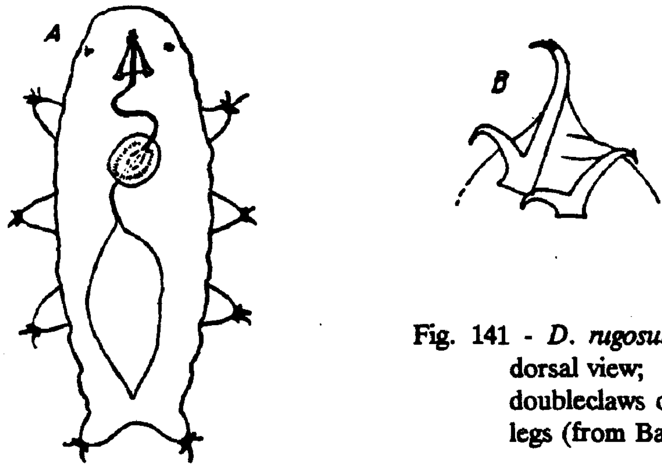


Fig. 141 - *D. rugosum* (Bartos). A, dorsal view; B, doubleclaws of the 4th pair of legs (from Bartos).

somewhat larger and more distinct in the caudal region of the dorsum, posterior to the 3rd pair of legs. Buccal tube very narrow (internal diameter 1μ); pharyngeal tube little longer than the pharynx; this last (length:width ratio of about 1.1-1.2:1) containing the apophyses, 2 slender macroplacoids -- of which the first is twice as long as the second -- and a very distinct microplacoid. Doubleclaws of each leg of different size: principal branch with accessory points. It deposits 2-5 oval eggs in the exuvium.

D. rugosum is distinguished from *D. latipes* -- which however possesses cuticle covered with a fine granulation and 2 macroplacoids -- by having pharyngeal tube little longer than the pharynx and internal and external doubleclaws of different size, while in *latipes* (which possesses besides a gibbosity anterior on each leg) the pharyngeal tube is 1.5-1.7 times as long as the pharynx and the doubleclaws have size very little different. *D. nodulosum* has much larger granulation, especially on the caudal region, where the individual granules are transformed into platelets of 4.6μ in diameter; *D. oculatum* has pharyngeal tube twice as long as the pharynx and -- just as occurs in *D. rugocaudatum* -- granulation limited to the caudal zone.

The species is known from Spain, Austria, Hungary, and the region of the Carpathians. Typ. loc.: Karlik, near Mosovce (Czechoslovakia).

DIPHASCON SCOTICUM Murray, 1905 (Fig. 142, 144, 145).
= *D. crozetense* Richters, 1907
= *Hypsibius* (*D.*) *scoticus* Marcus, 1936

Length up to 462μ, however in general 215-370μ. Body very slender, not narrowing anteriorly, eye spots absent, colorless (however in Scandinavian examples Maucci has sometimes observed a brownish color), cuticle smooth. The buccal tube is narrow, but less than in other species (internal diameter up to 2.7μ, equal to about 2.6% of the total length of the tube); there is no "drop" formation; the pharyngeal tube is about as long as the pharynx. This latter is very elongated (about two times longer than wide), sometimes rather pear-shaped. There are small apophyses, and three macroplacoids in the shape of slender elongated rods of increasing length, or else the first and the second equal and the third longer, less frequently all three of equal length. Present are microplacoid and septula (Cuénot has described individuals with microplacoid, but lacking septula).

On the first three pair of legs exists cuticular bars. The two doubleclaws of each leg are very different from each other in size, but not in shape: the common basal part is expanded, stumpy with smooth margin, sometimes laterally prolonged in the shape of a spine, the principal branch is long slender, with accessory points.

D. scoticum has not been often confused with other close species, such as *D. nobilei*, *D. higginsi*, *D. prorsirostre*, and *D. arduifrons*. On the contrary Cuénot and Marcus think possible that the last two might have been identified with *D. scoticum*. To us it seems that the distinction between *prorsirostre* and *arduifrons* is certainly somewhat artificial (see what was said in the description of *D. arduifrons*); there is instead no doubt on the separation of *D. scoticum* from all the species cited. Thus *nobilei* and *higginsi* have the base of the posterior claws expanded, with dentate margin, and the first is distinguished also by the presence of the eyes and of the

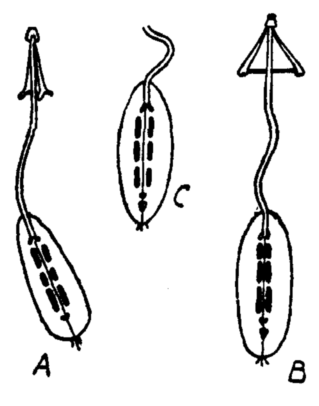


Fig. 142 - *D. scoticum* Murray. Three views of the buccal apparatus.

"drop" formation. *Arduifrons* and *prorsirostre* do not have the cuticular bar on the first three pair of legs and have neither microplacoid nor septula.

Mihelčič, 1971, has described as variety of *D. scoticum* two forms. One, *D. scoticum bicorne*, is here considered as a species itself, especially by the existence of a sculptured cuticle of polygonal sculpture (see *D. bicorne*). The other, *D. scoticum simplex*, can be characterized by the absence of placoids, substituted by two slender cuticular thickenings: the description is certainly not thorough, however the absence of placoids causes one to think this form of Mihelčič belongs to the genus *Itaquascon*.

Valid instead seems to be the subspecies *D. scoticum ommatophorum* Thulin, 1911 (Fig. 143).

Length up to 318μ, with eye spots; buccal apparatus as in *D. scoticum*. The principal branch of the external doubleclaws is yet longer than in *scoticum* and the same doubleclaws may present differences, which here are not reported, because too subject to variation. It is possible that *scoticum ommatophorum* is included within the limits of variability of *scoticum* and may then be united with this species, because in the same population of eyed individuals is found some with doubleclaws of all identical to those of

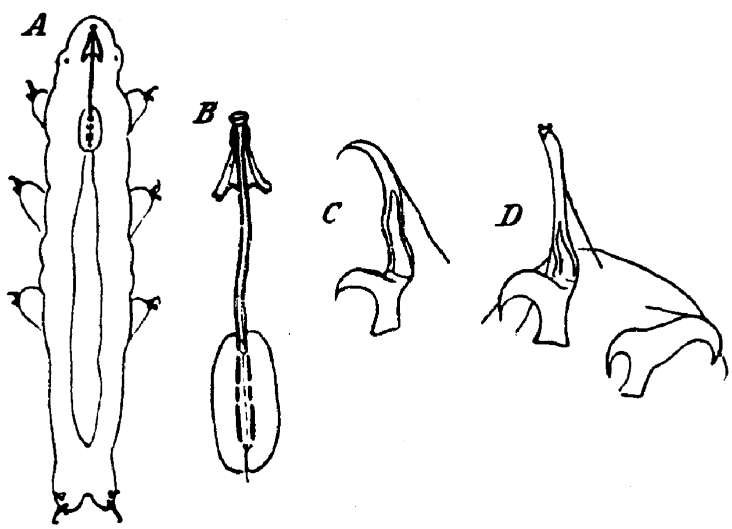


Fig. 143 - *D. scoticum ommatophorum* Thulin. A, dorsal view; B, buccal apparatus and pharynx; C, posterior doubleclaws; D, doubleclaws of the 4th pair of legs (from Marcus).

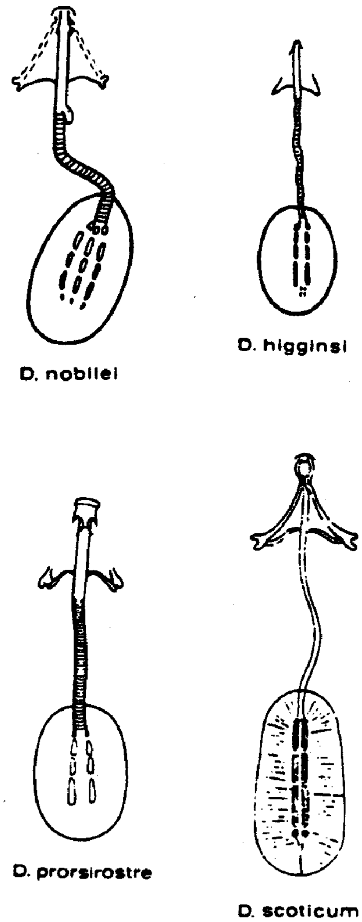


Fig. 144 - Buccal apparatus of four species of *Diphascon*: *D. nobilei*, *D. higginsi*, *D. prorsirostre*, *D. scoticum* (from Pilato).

scoticum, there remains as the only character -- perhaps insufficient for the separation of the two species -- the presence of the eyes.

D. scoticum is a species with wide distribution, cited from many European localities (Italy included), from North and South America, Africa, India, Afghanistan, Australia, New Zealand, the Arctic and Antarctic (typ. loc.: Scotland). The subspecies *ommatophorum* has been cited from Poland, Switzerland, Lapland, Greenland, Fernando Poo Island. Typ. loc.: Swedish Lapland.

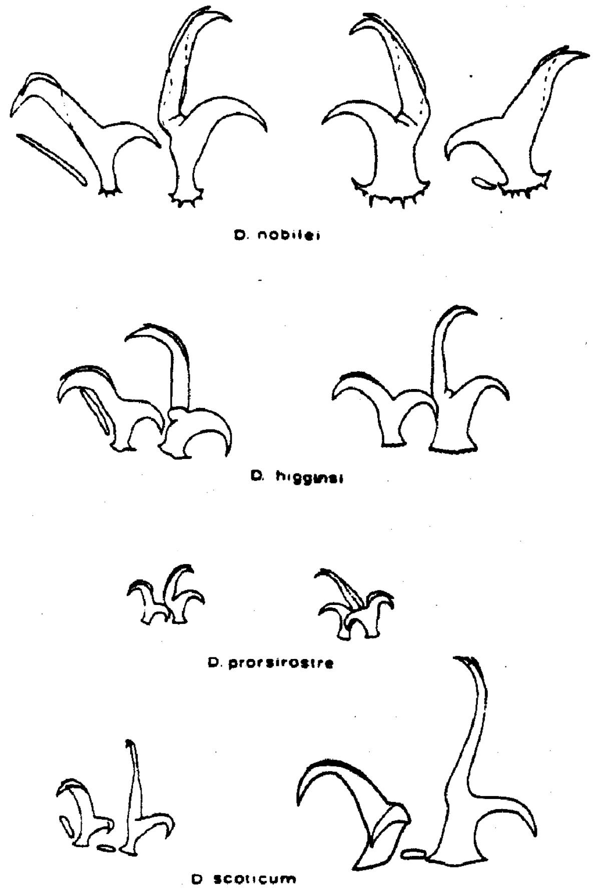


Fig. 145 - Doubleclaws of four species of *Diphascon*: *D. nobilei*, *D. higginsi*, *D. prorsirostre*, *D. scoticum*. At left the claws of the second or third pair of legs, at right those of the 4th pair (from Pilato).

DIPHASCON SPECIOSUM (Mihelčič, 1971) (Fig. 146).
= *Hypsibius* (*D.*) *speciosus* Mihelčič, 1971

Length not indicated by the author; cuticle sculptured with fine granules, in transverse rows. Pharyngeal tube visibly longer than the narrow pharynx of unequal width (more narrow anteriorly than posteriorly and truncated both rostrally and caudally); length:width ratio of the pharynx equal to about 1.7:1. Three macroplacoids, of increasing length

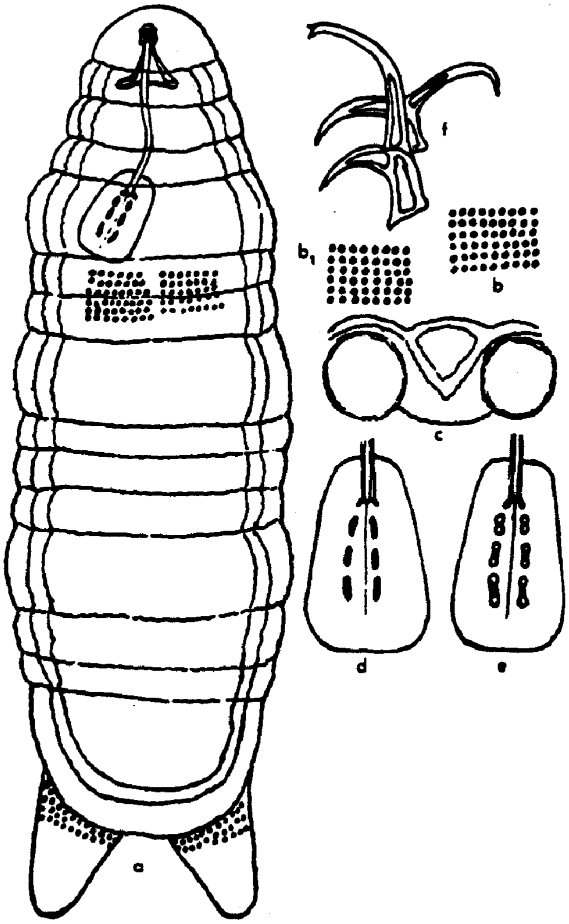


Fig. 146 - *D. speciosum* (Mihelčič). a, habitus; b, sculpture with microscope tube high; b_1, sculpture with tube low; c, anal zone, surrounded by sculptured lines (formed by granules); d, pharynx and macroplacoids in dorsal view; e, idem, in lateral view (from Mihelčič).

from front to back: viewed from the side, each appears double and is composed of two granules, united in a line.

The species was observed in moss and lichen near Amlach (in the vicinity of Lienz, South Tyrol, Austria).

DIPHASCON SPITZBERGENSE Richters, 1903 (Fig. 147).
= *Hypsibius* (*D.*) *spitzbergense* Marcus, 1936 and *Auct.*

Length up to 450μ, but often 240-260μ, colorless, eyes absent, cuticle smooth. The body is slender and elongated, the buccal tube wide (4-5μ in an animal 250-260μ long), pharyngeal tube as long as the pharynx, or else a little more, or a little less.

There does not exist the "drop" formation between the rigid part and the flexible part.

Pharynx very elongated oval, with length:width ratio of about 2:1, containing two slender macroplacoids of rod shape, of which the second is two to three times as long as the first, and the microplacoid. There are no apophyses, but the pharyngeal tube ends in the pharynx with a thickened ring (flange).

Doubleclaws robust. There exists no cuticular thickenings near the claws.

It deposits smooth and oval eggs (78 x 60μ) in the exuvium.

It is not to be excluded that *D. emmautinum* (Rahm, 1936), a species insufficiently described and therefore not included in the identification key,

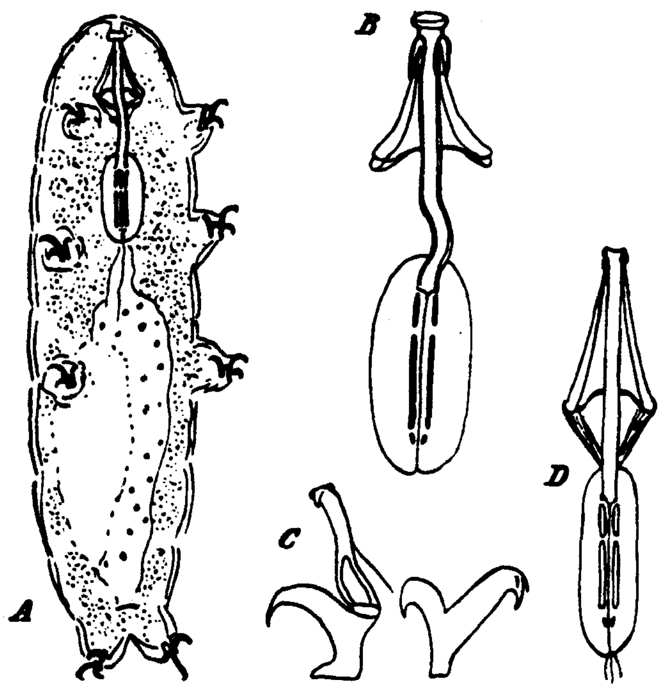


Fig. 147 - *D. spitzbergense* Richters. A, ventral view; B, D, buccal apparatus; C, doubleclaws (from Marcus).

may be a variety of *spitzbergense*; the microplacoid is lacking in *D. affine* and in *D. angustatum*.

D. spitzbergense was collected in many localities in Europe (including Italy), the U.S.A., Canada, and the Arctic. Typ. loc.: Spitsbergen.

DIPHASCON STAPPERSI Richters, 1911 (Fig. 148).

Length up to 225μ, eyes present, cuticle smooth. The buccal and the pharyngeal tube are very narrow (diameter about 1μ). Pharynx oval, with length:width ratio of 1.3-1.4:1, but sometimes almost spherical, containing obvious apophyses, 3 macroplacoids of granular shape or even of short rounded rods, increasing in length from 1st to 3rd, and small microplacoid.

Exuvia have been observed with one egg.

For distinction from *D. alpinum* (very uncertain), from *D. chilenense*, and from *D. tenue* we refer the reader to that said under the description of *D. alpinum*.

D. stappersi has been found only on the Spitsbergen Islands and on Orsi Island.

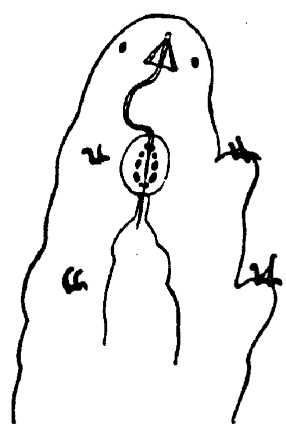


Fig. 148 - *D. stappersi* Richters (from Marcus).

DIPHASCON TENUE Thulin, 1928 (Fig. 149).

Length up to 231μ, eyes absent, cuticle smooth. Body slender, slightly tapered anteriorly, with legs -- especially those of the 4th pair, very short.

Buccal aperture subventral, buccal tube very narrow (the diameter, little more than 1μ, represents about 2.3% of the length of the entire tube). Between the rigid buccal tube, and the flexible pharyngeal tube, exists the "drop" formation. The pharyngeal tube is 1.6-1.7 times the length of the pharynx: this last is oval, with length:width ratio equal to about 1.4-1.5:1, and containing 3 macroplacoids (slender rods), of which the third is the longest, and the first slightly shorter than the second.

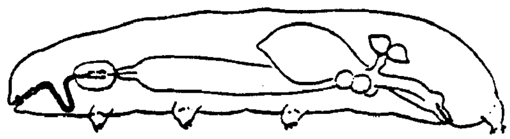


Fig. 149 - *D. tenue* Thulin. Lateral view (from Thulin).

Lacking apophyses (distinguishing character with regard to *D. montigenum*), microplacoid, and septula (distinguishing character with regard to *alpinum*, *chilenense*, and *stappersi*.

Doubleclaws small, with basal part short and branches slender. No cuticular thickening on the legs near the claws.

The species has been found in the region of the Carpathians, on the Faroe Islands (typ. loc.), in Sweden, and in Norway.

DIPHASCON TRACHYDORSATUM (Bartos, 1937) (Fig. 150).
= *Hypsibius (D.) trachydorsatus* Bartos, 1937

Length 190-305}, colorless or yellowish, eye spots in general present. The cuticle is covered -- dorsally and on the flanks -- with a dense sculpture of small hemispherical granules, while the ventral surface is smooth; the granules increase in size in rostro-caudal sense. There also exists dorsally 8 transverse rows of 2 large gibbosities each, of which the anterior are smaller, somewhat flattened, and very near to the dorsal median line, while the last 2 pair (rows) of gibbosities -- higher and almost spherical -- are in somewhat lateral rather than dorsal position; the last caudal pair is positioned almost at the bases of the legs of the 4th pair, so that the gibbosities follow the movement of those legs. All the legs bear a dorsal swelling, especially visible on the first pair.

Buccal aperture subterminal; stylets short and robust; buccal tube narrow (about 2μ), which follows the flexible pharyngeal tube (27μ), a little shorter than the pharynx and which describes one or two loops. The

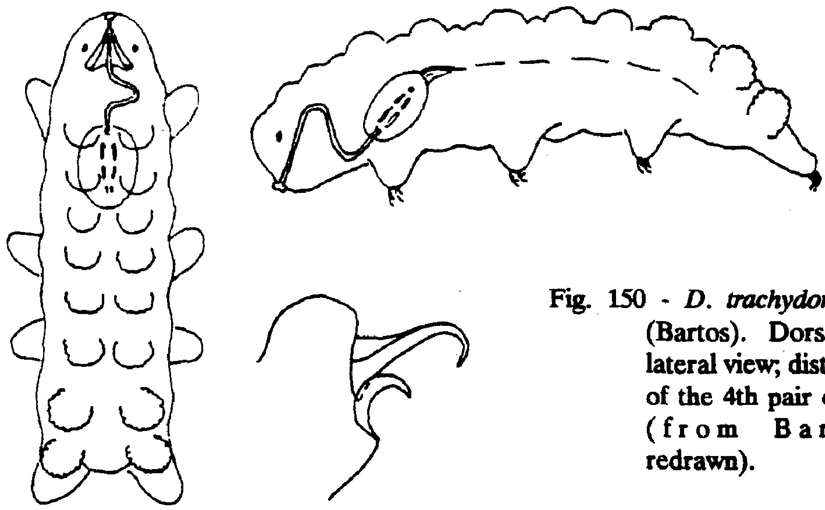


Fig. 150 - *D. trachydorsatum* (Bartos). Dorsal and lateral view; distal end of the 4th pair of legs (from Bartos, redrawn).

pharynx is short oval (30 x 23μ) and contains robust apophyses, 2 macroplacoids (rods) and an obvious microplacoid (1μ); the first macroplacoid (5.4μ) is longer than the second (4μ). Doubleclaws large, very curved, with principal branch longer than the secondary. The author cites large lunules at the base of all the claws, this fact rather unusual and which needs to be confirmed, because usually the genus *Diphascon* does not possess lunules.

It is not easy to distinguish *trachydorsatum* from *D. bullatum* in which however the last two caudal gibbosities are often widely divergent; it is not sufficient distinctive character, neither the presence of eyes in *trachydorsatum* (however not constant), nor the length of the macroplacoid: the only character for the separation remains the "swelling" on the legs and especially the lunules. It is not then excluded that *trachydorsatum* is included within the limits of variability of *bullatum*. It is however difficult to distinguish from *D. elongatum* (see also what is said in the description of *D. bullatum* and *D. elongatum*).

The species is known from the Carpathian region, Hungary and Poland. Typ. loc.: Pribram (Bohemia).

Genus *DORYPHORIBIUS* Pilato, 1969.

Diagnosis: Hypsibiidae with *Isohypsibius* type claws; there is present the reinforcement bar of the buccal tube.

KEY TO THE SPECIES

1. Aquatic species 2
   Terrestrial species 3

2 (1). There are 2 macroplacoids; the legs have a gibbosity formed of fused tubercles .... *Dor. evelinae*
   There are 3 macroplacoids; the legs do not have a gibbosity .... *Dor. zappalai*

3 (1). The claws of the last pair of legs, extremely reduced, are much smaller than those of the other legs .... *Dor. pilatoi*
   Last pair of legs have normally developed claws 4

4 (3). Cuticle is sculptured, or there is a gibbosity 5
   Cuticle is smooth, and there is no gibbosity (except possibly a gibbosity on each leg) 6

5 (4). Yellow color; cuticular sculpture with a reticulated pattern .... *Dor. citrinus*
   Colorless; cuticle with gibbosities arranged in 8 transverse rows .... *Dor. zyxiglobus*

6 (4). Legs with gibbosity composed of fused, small tubercles .... *Dor. evelinae*
   Legs with neither gibbosity nor small tubercles .... *Dor. doryphorus*

DORYPHORIBIUS CITRINUS (Maucci, 1972) (Fig. 151).
= *Hypsibius* (*Dor.*) *citrinus* Maucci, 1972

Species of large size (more than 600μ). Rather squat shape, with short and fat legs. Cavity globules intensely yellow. Eyes present.

The cuticle is sculptured in a protruding crest which outlines areolated polygons somewhat dense and regular. Such sculpture is extended on the dorsum and the flanks, for all the length of the body, and is extended, weaker and with more marked areolation, on a limited area of the external side of the legs. The sculpture is absent on the anterior end, on the ventral side, and on the legs. The cuticle also has ten transverse grooves of various lengths. All the legs have, on the external side, a blunt gibbosity, in correspondence of which exists a band composed of a fine punctation.

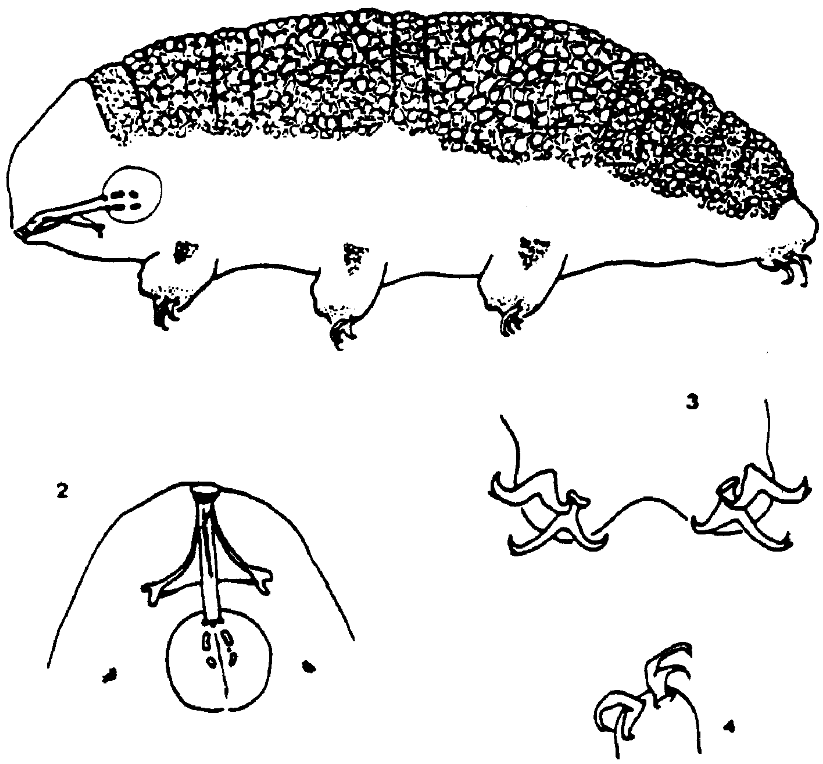


Fig. 151 - *Dor. citrinus* (Maucci). 1, habitus; 2, buccal apparatus; 3, claws of the 4th pair of legs; 4, claws of the 1st pair of legs (from Maucci).

The mouth is in an anterio-ventral position, and the forehead is bulging. The buccal tube is medium wide. The reinforcement bar, characteristic of the genus, is joined to the buccal tube at about 2/3 of its length. Buccal aperture without lamellae. Stylets markedly curved, with large but slender furcae. Pharynx subcircular. Robust apophyses. Two macroplacoids in the form of stumpy rods, the first one and a half times longer than the second, and strongly constricted at the middle. Microplacoid absent.

Claws very robust. The two doubleclaws of each leg little different from each other. The basal part is large and short. The external claws (larger) have enlarged lunuliform bases. The principal branch bears two robust accessory points.

The eggs are deposited in the exuvium; exuvia have been observed with 2 to 7 spherical eggs, yellow.

The species, described for the first time from the locality of Gracisce (near Pisino, Istria), and discovered also on Carso Triestino, in Turkey, China, and Spain.

By various characters *Dor. citrinus* appears somewhat similar to *Isohypsibius flavus* Iharos, and also to *Isohypsibius reticulatus* Pilato, however these last two species, not having the reinforcement bar on the buccal tube, are not included in the genus *Doryphoribius*.

DORYPHORIBIUS DORYPHORUS (Binda and Pilato, 1969) (Fig. 152).
= *Hypsibius* (*H.*) *doryphorus* Binda & Pilato, 1969

Small, with maximum size of 200μ, colorless, smooth cuticle and eyes in posterior position. Ventral mouth, without peribuccal lamellae; forehead sloped. Buccal tube with reinforcement bar, 25μ long, and about 2.3μ wide, in specimens of 107μ. The buccal tube, observing the animal in profile, is curved (see Fig. 152, B); slender stylets, furcae sufficiently

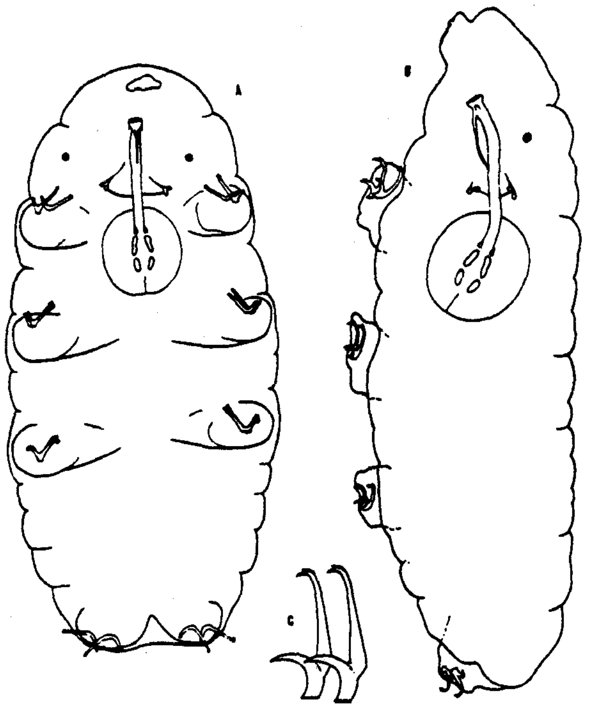


Fig. 152 - *Dor. doryphorus* (Binda & Pilato). A, ventral view; B, lateral view; C, doubleclaws (from Binda & Pilato).

developed. Pharynx oval, with length to width ratio equal to about 1.2-1.3:1. Apophyses well developed and 2 macroplacoids (wide rods); the 1st is almost twice as long as the 2nd and has a slight central constriction (in a 107μ specimen the 1st placoid measures 4.6μ, the 2nd about 2.4μ).

Isohypsibius type slender doubleclaws, but relatively large size, with respect to that of the body; principal branch with two thin accessory points; the doubleclaws of each leg not very different in shape and size: the external is scarcely a little larger than the internal. Eggs are unknown.

The species was collected from Ustica Island (Sicily), and later in Istria.

DORYPHORIBIUS EVELINAE (Marcus, 1928) (Fig. 153).
= *Hypsibius* (*H.*) *evelinae* Marcus, 1928

Hydrophilic and hygrophilic tardigrade; length up to 500μ, eyed, colorless, or with yellow or reddish cavity globules; short legs. Smooth cuticle on the body, but not on the legs, which bear -- on the dorsum, above the claws -- a gibbosity, composed in general of an assembly of 2-12 small tubercles in the form of nail heads: this process is particularly developed on the 4th pair of legs; sometimes it lacks the individual small tubercles and the gibbosity on the legs appears then completely smooth.

Buccal tube rather wide (5μ), curved, with dorsal convexity and supplied of reinforcement bar, small curved stylets, with large furcae. Pharynx oval (length:width ratio = 1.5:1), with apophyses and 2 macroplacoids in the form of short, wide rods, of which the first is almost twice the length of the second and has a constriction; microplacoid absent. The two doubleclaws of all legs are relatively small, slender, and do not show great difference in their size: the principal branch of the internal and external doubleclaws measure respectively 15 and 11μ and both have accessory points.

The original assignment of the species to the subgenus *Hypsibius* was because (however not explicitly mentioned) the claws are of the *Hypsibius* type; however the design, despite the fact that all the species so far belonging to the genus *Doryphoribius* have claws of *Isohypsibius* type, leaves open doubt on the real type of claws. (However even for *Dor. doryphorus* the original description indicates *Hypsibius* claws, and only further observations, and the evidence of other examples, have permitted to definitely verify the claws as *Isohypsibius* type).

In a Mexican example, collected by Dr. Schuster, we have been able in fact to observe (however not with absolute certainty) that the claws are of the *Isohypsibius* type.

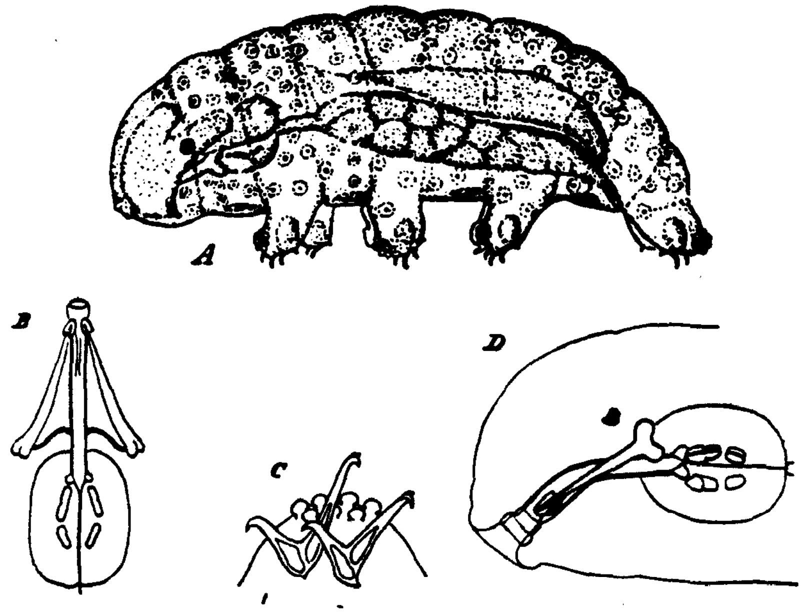


Fig. 153 - *Dor. evelinae* (Marcus). A, lateral view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs; D, cephalic region (from Marcus).

The eggs, oval and smooth, are deposited in the exuvium, in maximum number of 16.

Dor. evelinae was collected in Germany, Poland, Romania, Mexico, and Brazil, either within terrestrial moss, or within submerged moss, and in algae from a small lake.

Type loc.: Schlachtensee (Berlin).

DORYPHORIBIUS PILATOI Bertolani, 1983.

This species, of which we have observed the holotype, was illustrated in a communication at the 3rd International Symposium on the Tardigrada (Johnson City, 1980). Being still unpublished, we have not given the description so as to not prejudice the priority.

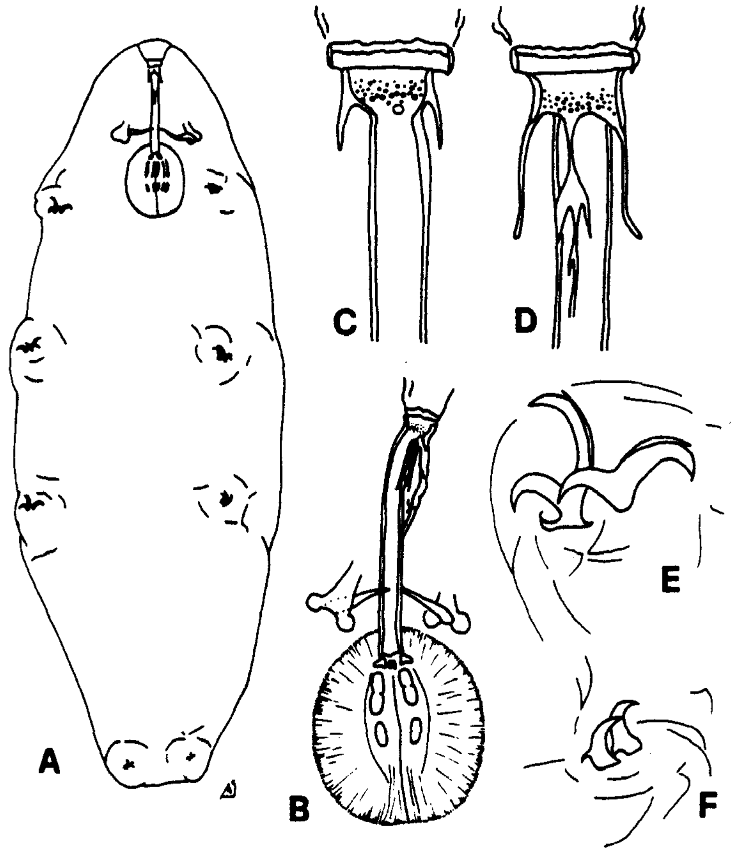


Fig. 154 - *Dor. pilatoi* Bertolani. A, habitus; B, buccopharyngeal apparatus; C, dorsal buccal armature; D, ventral buccal armature; E, claws of the third pair of legs; F, claws of the fourth pair of legs (same enlargement as E) (from Bertolani).

DORYPHORIBIUS ZAPPALAI Pilato, 1971 (Figs. 155 and 156).

Length up to 500μ, but often 400μ or less, eyed, reddish-yellow color, tending to brown caudally. Buccal apparatus small, with respect to the size of the animal. Buccal tube 37μ long, with diameter of almost 4μ in specimens 400μ long. Pharynx short oval, sometimes almost spherical, containing well-developed apophyses and 3 macroplacoids in the shape of small rods with rounded corners, of which the 3rd is always the longest. Microplacoid absent.

Claws *Isohypsibius* type, well developed; the two doubleclaws of all legs are not very different in shape and size. The principal branch is slender and in the external doubleclaw a little longer than in the internal. At the base of the claws there is a lunule.

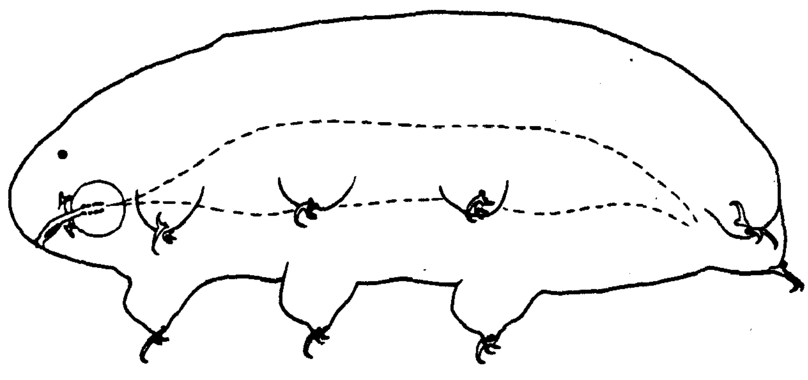


Fig. 155 - *Dor. zappalai* Pilato (from Pilato).

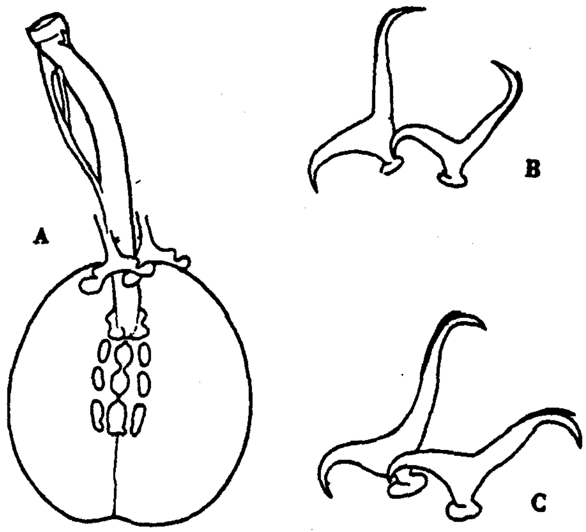


Fig. 156 - *Dor. zappalai* Pilato. A, buccal apparatus; B, claws of the 1st pair of legs; C, claws of the 4th pair (from Pilato).

Eggs smooth, oval, deposited in the exuvia in numbers up to 7.

This species, which is aquatic, was collected in a marginal pool of water of the Alcantara River (northwest Sicily).

DORYPHORIBIUS ZYXIGLOBUS (Horning, Schuster, & Grigarick, 1978) (Fig. 157).
= *Macrobiotus zyxiglobus* Horning, Schuster & Grigarick, 1978

Length from 170 to 444μ, eyes present or absent. The dorsum has gibbosities arranged in eight transverse rows, composed (from the anterior end) respectively of 6, 4, 6, 4, 6, 4, 4, and 2 gibbosities. Between the gibbosities and on them there are fine tubercles.

Buccal tube medium wide (width about 10% of the length); the pharynx contains small apophyses and two macroplacoids, of which the first is twice as long as the second; microplacoid absent.

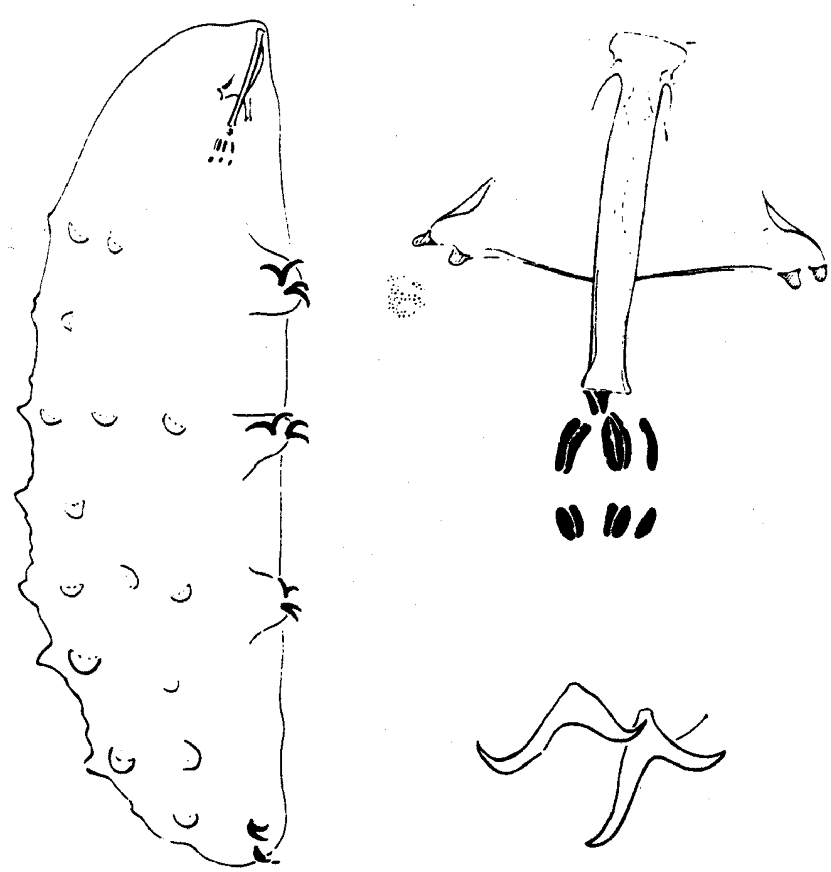


Fig. 157 - *Dor. zyxiglobus* (Horning et al.). Habitus, buccal apparatus, and claws of the 4th pair of legs (from Horning et al.).

Claws of *Isohypsibius* type, with usual very short basal branch. The doubleclaws of each leg are almost equal. Lacking lunule and accessory points.

This species is assigned by the authors to the genus *Macrobiotus*, in spite of the typical claws, owing to the presence of the reinforcement bar of the buccal tube. We think it advisable, for uniform systematics, to include it in the genus *Doryphoribius*.

The species is known from two localities from New Zealand.

Genus *ECHINISCOIDES* Plate, 1889.

Diagnosis: Echiniscoididae with cephalic appendices (cirrus A and clava) reduced; each leg bears more than 4 claws (from 5 to 11), devoid of spurs.

KEY TO THE SPECIES

1. Buccal tube and stylets very long: they extend beyond the level of the first pair of legs .... *Ec. hoepneri*
   Buccal tube and stylets do not reach the level of the first pair of legs 2

2. The caudal end has on the dorsal side a sclerified plate, slightly carinate .... *Ec. travei*
   There is no caudal plate 3
   (*Ec. sigismundi, sensu lato*)

3 (2). Cuticle smooth 4
   Cuticle regularly sculptured 5

4 (3). 8-10 claws on 1st-3rd legs .... *Ec. s. sigismundi*
   10-12 claws on the 1st-3rd legs .... *Ec. s. mediterraneus*

5 (3). The central legs are turned at right angles and are considerably larger than the lateral claws .... *Ec. s. polynesiensis*
   The claws of each leg are all equal and have a normal curvature 6

6 (5). The 1st and 2nd legs bear a small papilla .... *Ec. s. groenlandicus*
   There is no papilla on the 1st and 2nd legs 7

7 (6). Sculpture composed of small circular tiled plates .... *Ec. s. hispaniensis*
The plates of the sculpture are not tiled .... *Ec. s. galliensis*

ECHINISCOIDES HOEPNERI Kristensen & Hallas, 1980 (Fig. 158).

Body torpedo shaped. The paired cephalic papillae are positioned between the internal and external cirri. The median cirrus is absent (in one example -- among several hundred -- a short median cirrus is present). Clava ovoid, with a pore at the apex. Eyes present, black. The buccal tube, considerably long, ends with a bulbous dilation, before its opening in the pharynx. The stylets have a rigid median swelling.

Cuticle smooth. On the 2nd-4th legs there are appendices present: a slender seta on the 4th legs. The 1st - 3rd bear 7-9 claws, the 4th legs bear 6-8.

Ec. hoepneri has been found on the barnacle *Balanus balanoides*, at 10 cm below the average level of the sea, in three localities of Greenland.

Typ. loc.: Godhavn (Disko Island, Greenland).

ECHINISCOIDES SIGISMUNDI (Schultze, 1965) (Figs. 159, 160, 161)
= *Echiniscus sigismundi* Schultze, 1965

Length up to 310-340μ, average 200μ; the young measure 100μ or less. Transparent, colorless or rosy; cuticle smooth and delicate, with dorsal transverse fold. Large black eye spots. Buccal aperture subterminal, buccal tube rather long, stylets with truncate bases. Pharynx oval, a little wider posteriorly. There is neither median cirrus nor cephalic papillae; the cephalic appendices are composed of very short lateral cirrus A and in the shape of sharp spines, accompanied by a small clava (papilla) and minuscule internal and external buccal cirri: the first, positioned more dorsally, the second more ventrally with respect to the anterior cephalic margin. In the position of the appendices E in the Echiniscidae (that is to say, between the 3rd and 4th pairs of legs) there is a spine, longest cuticular appendices of the animal; at the point of insertion of the fourth legs -- but on them -- exists a papilla, and the third legs bear a spine. There is a characteristic dome-shaped projection on each side of the head.

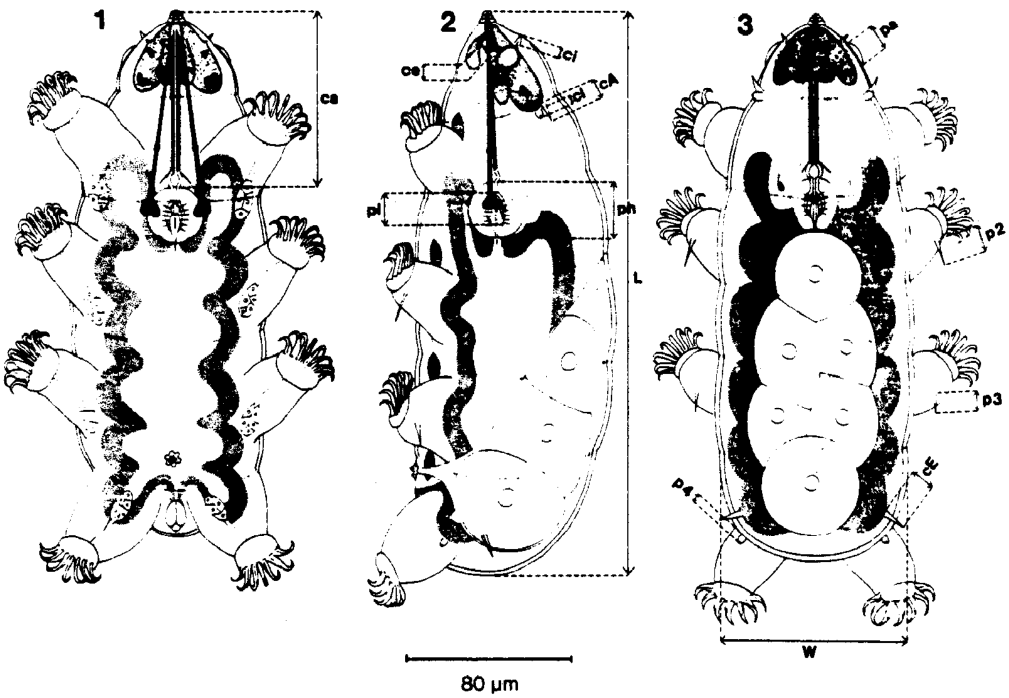


Fig. 158 - *Ec. hoepneri* Kristensen and Hallas. 1, ventral view; 2, lateral view; 3, ventral view (from Kristensen and Hallas).

The claws are smooth, without spurs, of equal length and of numbers varying from 5 to 11 (usually 5-9) per leg, a function of age. The eggs, oval (41 x 22μ) or almost spherical, smooth, colorless or else rosy, are deposited singularly or in small clutches (up to 9); in the ovary of the female have been observed also 12 mature eggs for deposition (Marcus).

Typ. loc.: Helgoland (North Sea).

This description refers to *Ec. sigismundi, sensu lato*.

Recently have been described numerous subspecies.

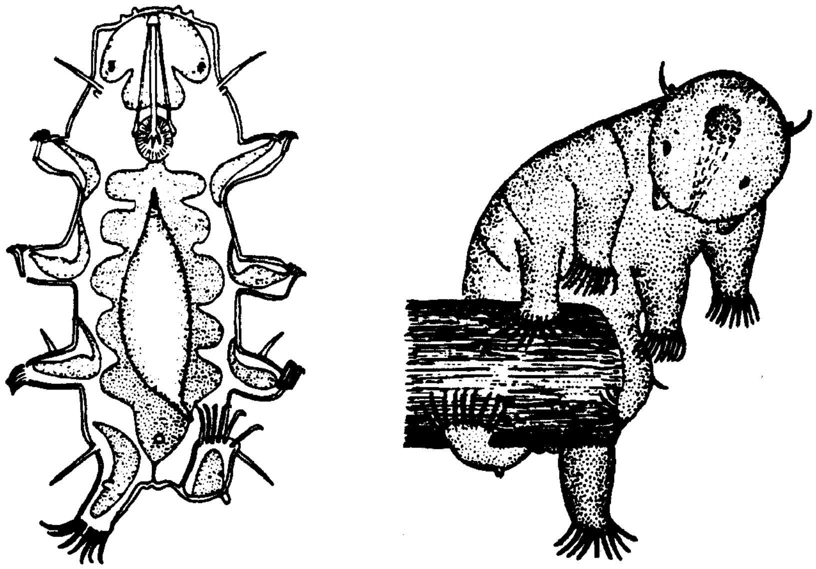


Fig. 159 - *Ec. sigismundi* (Schultze). At left from Cuénot, at right from Marcus.

Echiniscoides sigismundi sigismundi (Schultze, 1865) (Fig. 161).

Medium size. Cuticle smooth. At the sides of the head exists two large lateral prominences, having a flat or indistinct cephalic papilla. Appendices on the 1st and 2nd legs present or absent. There are 8-10 claws present on each leg.

Neotype: Julebaek Beach (Denmark).

According to Kristensen and Hallas (1980) this nominate subspecies is spread along the European coast from Norway and Sweden as far as northern France. There is however also a report from Tenerife Island.

Ec. s. s. belongs to the intertidal fauna, and has been found in Enteromorph algae, but also as commensals of Cirripedia.

Echiniscoides sigismundi groenlandicus Kristensen & Hallas, 1980.

Very large size. The cuticle has a variable granulation. The 1st and 2nd legs have a small papilla, the 3rd pair a normal seta. There are 8-10 claws on the 1st-3rd legs and 7-9 claws on the 4th legs.

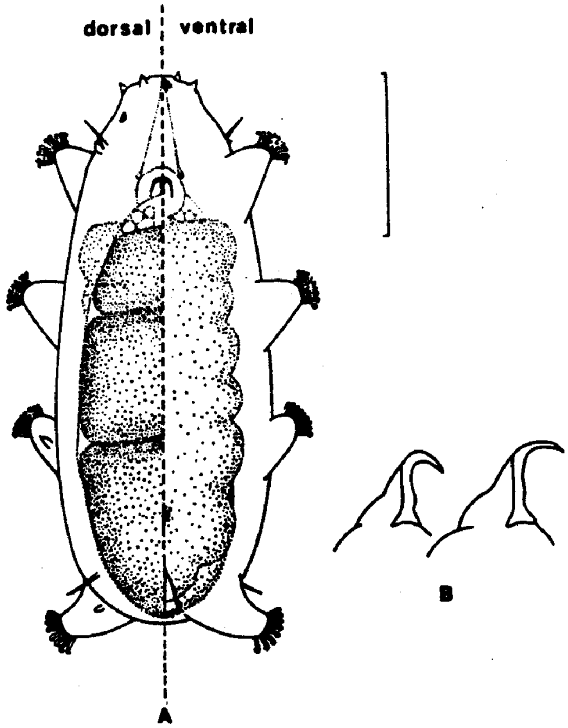


Fig. 160 - *Ec. sigismundi* (Schultze). Composite: at left dorsal view, at right ventral view; B, claws, at left internal claw, at right external claw (from Renaud-Mornant).

Typ. loc.: Godhavn (Disko Island, Greenland).

This subspecies was collected on the coast of the United States, western Greenland, and northern Norway.

Echiniscoides sigismundi galliensis Kristensen & Hallas, 1980 (Fig. 161).

Small size. The lateral prominences of the head are small or absent. The cuticle is strongly sculptured, and presents circular figures, in which one sees a small circle of discontinuous lines. The 1st and 2nd legs do not bear appendices. 9-10 claws on the 1st-3rd legs, 8-9 on the 4th legs.

Typ. loc.: St. Pol de Leon (northern France), on the cirripedia *Chtamalus stellatus*. An example collected by Thulin at S. Malo belongs to the same subspecies.

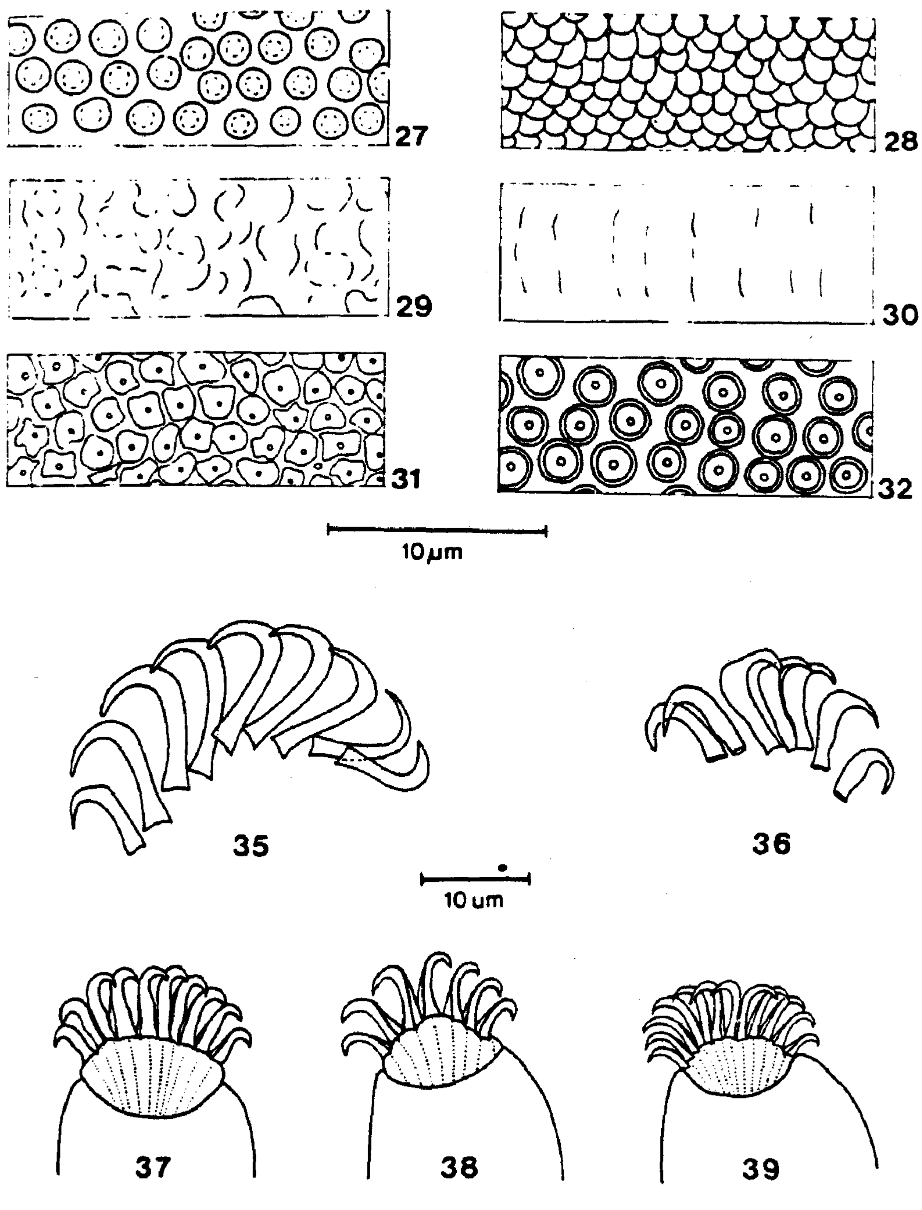


Fig. 161 - Sculpture (above) and claws (below) of each subspecies of *Echiniscoides*: 27 & 37, *Ec. sigismundi galliensis*; 28 & 38, *Ec. sigismundi hispaniensis*; 29 & 39, *Ec. sigismundi mediterraneus*; 30 & 35, *Ec. sigismundi sigismundi*; 31 & 36, *Ec. sigismundi polynesiensis*; 32, *Ec. sigismundi polynesiensis* specimen from Melbourne (from Kristensen and Hallas).

Echiniscoides sigismundi hispaniensis Kristensen & Hallas, 1980 (Fig. 161).

Very small size. Lateral prominences of the head indistinct. Cuticle strongly sculptured, with cuticular elements with tiled disposition. The 1st and 2nd legs have no appendices. There are 7-9 claws on the 1st-3rd legs, 6-8 claws on the 4th legs.

Typ. loc.: Sada, near La Coruna (Spain), on Cirripedia.

Echiniscoides sigismundi mediterraneus Kristensen & Hallas, 1980 (Fig. 161).

Medium size. Lateral prominences of the head and cephalic papilla barely accentuated. Cuticle smooth, or with slender crests. First and second legs without appendices. 10-12 claws on the 1st-3rd legs, 9-11 on the 4th legs.

Typ. loc.: Tarragona (Spain).

Echiniscoides sigismundi polynesiensis Renaud-Mornant, 1976 (Fig. 161).

Medium size. Cirrus A has an annulated base. Cephalic prominences distinct. Cuticle sculptured, with mammillary circles. On the first legs the appendices are present or absent, on the second legs there is a small hemispherical papilla, as likewise on the third and fourth legs. The claws are 8-10 for each leg. The claws are pointed and the central ones abruptly bent at the end.

Typ. loc.: Tiahura Island (Pacific Ocean). Other examples came from Melbourne (Australia).

ECHINISCOIDES TRAVEI Bellido and Bertrand, 1981.

Size from 150 to 420μ. Cuticle smooth. There is a sclerified plate on the caudal end. There are lateral cephalic lobes, which are attached to the anterior part of the body at the level of a very marked integumental fold. Cephalic cirri very small, flattened, with leaf appearance. There is a short appendix in position E. There are no appendices on the first legs, while papillae are present on the 2nd-4th legs. On each leg there are 8-11 claws.

Ec. t. differs from *Ec. sigismundi* by the larger size, by the spine on the third legs reduced to a papilla, by the presence of the cutaneous fold over the mouth.

The species was found on Kerguelen Island.

The authors think that *Ec. sigismundi polynesiensis* Renaud-Mornant is nearer to *Ec. travei* than to *Ec. sigismundi.*

Genus *ECHINISCUS* Schultze, 1840

Diagnosis: Echiniscidae with armor consisting of: cephalic plate, scapular plate (I), first median plate (1), first paired plates (II), second median plate (2), second paired plates (III), third median plate (3) which is often lacking, terminal plate (IV).

Observations:

1. We have taken this opportunity to abandon the "groups of species" proposed by Marcus and adopted in the preceding edition, based on the lateral appendages. Such groupings, while convenient, are totally artificial.

2. It has been taken into careful consideration the type of sculpture, which is taxonomically important. In the key of determination these are considered, for simplicity, of three fundamental types of sculpture:

a). Granular sculpture; it appears, with proper focusing, like granules (which are in reality pores), rounded, with irregular size and distribution, clearly darker at the base (example: *E. testudo*);

b). Polygonal sculpture; with proper focusing the sculpture appears composed of polygons more or less narrowly in contact between them (example: *E. granulatus*).

c). Double sculpture; two sculptures superimposed, one composed of larger granules and one of smaller granules; when focused on one sculpture it appears light, while the other appears dark.

It holds that in species of older description, the details of the sculpture are seldom stated, overlooked by the authors, who say in a very general way "granulation" or "punctation".

3. The species of the "*arctomys* group" can be distinguished from others by studying the difference in the sculpture, often somewhat subdued. It is not possible to include them in this key; where needed, it will be necessary to resort to the descriptions of the individual species.

4. The following species, included in the preceding edition, are now eliminated: *E. bellus* (synonym of *E. canadensis*), *E. fischeri* (it is not even certain that it is an *Echiniscus*), *E. iharosi* (synonym of *E. merokensis*, *E. macronyx* (insufficient description), *E. muscicola* (the description is very

contradictory, and it probably refers to more than one species), *E. punctulatus* (synonym of *E. canadensis*), *E. roseus* (synonym of *E. speciosus*), *E. scrofa* (synonym of *E. quadrispinosus*), *E. spiculifer* (very doubtful species, insufficient description; if it happens to be rediscovered, it should probably be put in a new genus).

We have also considered as species: *E. dearmatus* (*E. wendti dearmatus*) and *E. glaber* (*E. testudo glaber*).

KEY TO THE SPECIES

1. Other than cirrus A, there are no other appendages, dorsal or lateral 2
   Besides cirrus A there are other appendages 7

2 (1). Red, reddish-brown, or orange color 3
   Green color, at least partially 4

3 (2). In the positions C or D there are hemispherical or slightly conical projections . . . . . . *E. maucci*
   There are no lateral hemispherical projections . . . . . . *arctomys* group (*arctomys*, *bigranulatus*, *calvus*, *capillatus*, *carsicus*, *dearmatus*, *elegans*, *insuetus*, *japonicus*, *kerguelensis*, *kofordi*, *limai*, *markezi*, *mihelcic*, *moniliatus*, *nigripustulus*, *nobilis*, *phocae*, *ranzii*, *reticulatus*, *robertsi*, *speciosus*, *sylvanus*, *tardus*, *tenuis*, *tesselatus*, *vinculus*, *wendti*)

4 (2). Green color only in the caudal part; cavity globules red . . . . . . *E. rufoviridis*
   The color is entirely green 5

5 (4). Cirrus A is very long (150-170μ) . . . . . . *E. perviridis*
   Cirrus A is short, or of medium length (from 30 to 80μ) 6

6 (5). The plates exhibit whitish or black spots; internal claws without spurs . . . . . . *E. viridissimus*
   Color olive green, with dark green spots; internal claws with little spurs . . . . . . *E. viridis*

7 (1). There are no dorsal appendages 8
There are dorsal appendages 12

8 (7). The lateral appendages are all filaments 9
Other than cirrus A, the lateral appendages are spines 10

9 (8). The sculpture is of the polygonal type; there are spurs on all the claws of the 4th pair .... *E. becki*
The sculpture is "double"; internal claws with spurs, externals with a small spine .... *E. postojnensis*

10 (8). There is a spine at E 11
There is not any appendage at E .... *E. robertsi*

11 (10). There is a lateral spine C; "double" sculpture .... *E. cavagnaroi*
There is not a lateral spine C; granular sculpture .... *E. baius*

12 (7). Besides cirrus A, there are no other lateral appendages 13
Besides cirrus A, there are other lateral appendages 17

13 (12). Dorsal appendages are present at C and D 14
Dorsal appendages are present in a single position (at B or D) 16

14 (13). Dorsal appendages at C and D are both spines .... *E. murrayi*
Dorsal appendages C are filaments, D are spines 15

15 (14). The sculpture is a fine granulation .... *E. punctulatus*
The sculpture is of the polygonal type .... *E. canadensis*

16 (13). There are very small spines at dorsal B and dorsolateral C; spurs are present on all the claws of the 4th pair .... *E. molluscorum*
There are dorsal spines D; spurs are present only on the internal claws .... *E. migiurtinus*

17 (12). Appendage E is present 18
Appendage E is not present (attention! The small spines that are sometimes found at E are *not* considered appendages) 74

18 (17). All the lateral and dorsal appendages, including E, are distally enlarged, like a drum stick .... *E. tympanista*
The appendages, dorsal and lateral, are small teeth, spines, or filaments 19

19 (18). The appendage E is a spine 20
The appendage E is a filament 48

20 (19). Lateral appendages are present only at A and E; "double" sculpture 21
Lateral appendages are present also in other positions 22

21 (20). Dorsally there are only filaments in position C .... *E. carusoi*
Dorsally there are spines C and D .... *E. angolensis*

22 (20). Except for cirrus A, all the lateral appendages are spines 23
There are also lateral filaments 43

23 (22). Besides cirrus A, there are lateral spines in all the positions (B, C, D, E) 24
There are not lateral appendages in all the positions 36

24 (23). Dorsally there is only filament C; "double" sculpture .... *E. carusoi*
The dorsal appendages are spines 25

25 (24). Dorsal spines are present on the scapular plates, that is at B 26
Dorsal spines do not exist at B 27

26 (25). Dorsal spines exist at B, C, and D .... *E. arcangelii*
Dorsally there are 6 spines on the scapular plate, that is at B, 2 spines at C, and 2 spines at D .... *E. africanus*

27 (25). Dorsally there are only spines D 28
Dorsally there are spines C and D 30

28 (27). Lateral B, C, and D, and dorsal D spines are very short and difficult to observe; the sculpture is "double" .... *E. perarmatus*
Lateral and dorsal spines D are normally developed and evident; sculpture is granular 29

29 (28). The internal and external claws of the
4th pair are without spurs .... *E. dreyfusi*
The internal claws of the 4th pair bear
large and robust spurs .... *E. virginicus*

30 (27). The dorsal and lateral spines are dentate;
"double" sculpture .... *E. duboisi*
Spines not dentate 31

31 (30). Green color .... *E. pooensis*
Red or orange color 32

32 (31). The lateral spines are very short .... *E. spinulosus*
The lateral spines are normally developed, or else long 33

33 (32). The sculpture is polygonal .... *E. pusae*
The sculpture is different 34

34 (33). There are dorsal spines C and dorsal teeth
D; the sculpture is a fine granulation
as a string of pearls .... *E. laterospinosus*
Different 35

35 (34). There are dorsal spines D, robust, strongly
divergent; indistinct sculpture .... *E. divergens*
There are dorsal spines C and D of equal length,
not divergent; granular sculpture .... *E. spiniger*

36 (23). Other than cirrus A and spine E, there is a spine at C or D 37
Besides cirrus A and spine E, there are spines C and D 39

37 (36). There is a lateral spine at C; dorsally
there are short spines C and D; claws
without spurs .... *E. calcaratus*
Different; "double" sculpture 38

38 (37). There are lateral spines C or D; dorsally
there is filament C .... *E. carusoi*
There is lateral spine C; dorsally spine D,
that is often lacking .... *E. cavagnaroi*

39 (36). Dorsally there are spines C and D, notched;
sculpture with scattered pores .... *E. manuelae*
The dorsal appendages are only at C or D 40

40 (39). Dorsally exists only spine C 41
Dorsally exists filament C or spine D;
"double" sculpture 42

41 (40). All the spines are rough; dorsolateral
tooth C present; "double" sculpture .... *E. reymondi*
The sculpture is a dense granulation;
there are no dorsolateral teeth; spurs
are present on all claws of the 4th pair of legs .... *E. virginicus*

42 (40). Dorsal filament C present .... *E. carusoi*
Dorsal spine D present .... *E. crassispinosus*

43 (22). Except for spine E, all the other lateral
appendages are filaments; polygonal sculpture 44
Besides E there are other lateral spines; granular sculpture 46

44 (43). The lateral appendages are filaments A, B,
C, and D, and spine E; dorsal appendages
are present at B, C, and D .... *E. militaris*
In the dorsal positions there are appendages at C and D, not B 45

45 (44). The lateral appendages are filaments A, C,
and D, and spine E; dorsally filament C
and spine D .... *E. trojanus*
The lateral appendages are filaments A,
B, C, and D, and very short spine E;
dorsally robust spine C and short
divergent spine D .... *E. heterospinosus*

46 (43). The lateral appendages are spines or filaments A,
B, C, D, E; dorsally there are long spines
C and short triangular teeth D .... *E. laterospinosus*
Different 47

47 (46). The lateral appendages are short filaments,
flanked by a small spine at C, D, and E;
dorsally there is a short filament C, and
a filament or spine D; near this last,
some small teeth .... *E. baloghi*
The lateral appendages are filaments A and C,
spines D and E; dorsally only spines C .... *E. simba*

48 (19). Laterally there are only filaments A and E 49
There are also other lateral appendages 51

49 (48). Filament E has a short bifurcation;
dorsally there are filaments C and very
short teeth D; there are also dorsolateral
appendages C' .... *E. cervicornis*
The filament E is not bifurcated; dorsally
there are only appendages D 50

50 (49). The plates are deprived of sculpture . . . . *E. glaber*
There is "double" sculpture present . . . . *E. evelinae*

51 (48). All the lateral appendages are filaments 52
Laterally spines are also present 66

52 (51). There are lateral filaments in all the positions (A, B, C, D, E) 53
Lateral filaments are not present in all the positions 58

53 (52). There are dorsolateral appendages B', C', D', E'; dorsal appendages at B, C, and D . . . . *E. multispinosus*
There are no dorsolateral appendages 54

54 (53). "Double" sculpture; dorsal spines C and D . . . . *E. quadrispinosus*
Granular sculpture 55

55 (54). Dorsally there are filaments C and short teeth or spines D; moreover, at C and D, spines very converged at the median plane, arranged like scissors, which may also be lacking . . . . *E. lapponicus*
Different 56

56 (55). The dorsal spines C and D are rough and coarse; there are no spurs on the claws of the 4th pair of legs . . . . *E. rugospinosus*
Different 57

57 (56). The dorsal appendages C (spines or filaments) are situated at the posterior angles of plate II, or only slightly displaced toward the median line . . . . *E. merokensis*
The dorsal appendages C are considerably displaced toward the median line . . . . *E. columinis*

58 (52). Lacking the lateral appendages D 59
Lateral appendages D present 61

59 (58). There are lateral filaments A, C, E; dorsal filament C; polygonal sculpture . . . . *E. nepalensis*
Different 60

60 (59). There are lateral filaments A, C, E, sometimes also B; granular sculpture . . . . *E. testudo*
There are lateral filaments A, B, C, E; dorsally two spines C on each side, and spine D . . . . *E. filamentosus*

61 (58). Dorsally there are only spines C; granular sculpture 62
Dorsally there are filaments or spines C and D 63

62 (61). Laterally there are filaments A, C, D, E .... *E. iharosi*
Laterally there are filaments A, D, E .... *E. jagodici*

63 (61). "Double" sculpture; dorsally spines C and D .... *E. quadrispinosus*
Granular sculpture; dorsally spine or filament C and D 64

64 (63). Granular sculpture, dense and fine on all
the plates, very coarse and sparse on the
terminal; dorsal filaments C and D, laterals
A, C, D, E; near D a spine .... *E. velaminis*
Granular sculpture uniform on all the plates 65

65 (64). Dorsally long "rigid filaments" C and D .... *E. bartramiae*
Dorsally filaments C, and spines or
teeth D, which may be lacking .... *E. merokensis*

66 (51). There are lateral appendages in all
the positions (A, B, C, D, E) 67
Lateral appendages are not present in all the positions 71

67 (66). Except for filaments A and E, all the
lateral appendages are spines; there
are no dorsolateral appendages 68
Besides A and E, all other lateral
appendages are filaments; there
are dorsolateral appendages 69

68 (67). Dorsally there are spines B, C, and D;
claws of the 4th pair without spurs .... *E. weisseri*
Dorsally there are spines C and D;
there are spurs on the claws of the 4th pair .... *E. dikenli*

69 (67). Dorsally there are spines B, C, and D;
laterally there are appendages A, B,
C, D, E, of which B and D have a
curved spine .... *E. multispinosus*
There are no appendages B dorsally 70

70 (69). There are lateral filaments A, B, C, E,
and a lateral spine D; the dorsal
appendages are a filament C and a
spine D .... *E. oihonnae*
The lateral appendages A, C, E are spines
or filaments; B, D are spines; dorsally
spines C and D .... *E. horningi*

71 (66). Lateral appendages B present 72
Lateral appendages B lacking 73

72 (71). Lateral appendages D present; dorsally
spines C present .... *E. siegristi*
Lacking lateral appendages D; dorsally
spines D present .... *E. testudo*

73 (71). A short lateral spine D is present;
dorsally there are filaments C and
spines D .... *E. meridionalis*
Lacking lateral appendages D; dorsally
there are spines D .... *E. testudo*

74 (17). There are present lateral appendages
A, B, C, and D 75
Besides E, lacking any other lateral
appendages 82

75 (74). All the lateral appendages are filaments;
there are dorsolateral appendages;
polygonal sculpture 76
Lacking dorsolateral appendages 79

76 (75). Dorsolateral appendages B' present 77
Dorsolateral appendages B' not present 78

77 (76). There are short dorsolateral spines
B', C', and D' .... *E. spinuloides*
Only dorsolateral filament B' .... *E. ramazzotti*

78 (77). There are dorsolateral appendages
C' and D' .... *E. melanophtalmus*
Only dorsolateral appendages D' .... *E. spitsbergensis*

79 (75). The lateral appendages terminate
distally in a club; ventral
armor present .... *E. clavisetosus*
The lateral appendages are not terminated
in a club; lacking ventral armor 80

80 (79). All the lateral appendages are filaments;
dorsal appendages C and D present 81
Lateral A, C, and D are filaments; lateral
B is a spine; dorsally there is a spine
B, filaments C, and teeth D .... *E. apuanus*

81 (80). The dorsal appendages C and D are robust spines of almost equal length; internal claws of the 4th pair with spurs, externals smooth .... *E. granulatus*
The dorsal appendages are filaments C and spines D; the internal claws of the 4th pair with spurs, the externals with 1, 2, or 3 spines .... *E. blumi*

82 (74). There are lateral appendages A, C, and D 83
There are less than three lateral appendages 95

83 (82). All the lateral appendages are filaments 84
The lateral appendages C and D are spines 92

84 (83). Dorsolateral appendages present; polygonal sculpture 85
Dorsolateral appendages not present 87

85 (84). There are dorsolateral appendages C' and D'; dorsally small teeth C and D .... *E. marinellae*
There are dorsolateral appendages D'; the dorsal appendages are filaments c and spines or teeth D 86

86 (85). Red eyespots; internal claws of the 4th pair with spurs, externals smooth .... *E. menzeli*
Black eyespots; all the claws of the 4th pair with spurs .... *E. rosaliae*

87 (84). Dorsally there are only small teeth C .... *E. loxophthalmus*
Dorsally there are appendages C and D 88

88 (87). The dorsal appendages C are filaments 89
Dorsal appendages C and D are both spines 90

89 (88). The dorsal appendage C is a filament, D is a spine; polygonal sculpture; the internal claws of the 4th pair have a spur, the externals one or more spines .... *E. trisetosus*
The dorsal appendages C and D are both filaments; granular sculpture; all the claws without spurs .... *E. longispinosus*

90 (88). The dorsal appendages C and D are both spines; polygonal sculpture; internal claws with spurs, externals smooth .... *E. granulatus*
Granular sculpture; spurs on all four claws of the 4th pair 91

91 (90). Eyes present; dentate collar with 9-12
indistinctly separate teeth .... *E. knowltoni*
Eyes absent; dentate collar with 5-6
teeth, very distinct .... *E. inocellatus*

92 (83). The dorsal appendages are spines C and D 93
Dorsally there are spines D, and possibly also filaments C 94

93 (92). Polygonal sculpture .... *E. osellai*
Granular sculpture .... *E. egnatiae*

94 (92). The dorsal appendages are filament C and
spine D; laterally there are long spines .... *E. storkani*
Dorsally there are only spines D;
the lateral spines are short .... *E. canedoi*

95 (82). Lateral appendages A and D are present; polygonal sculpture 96
Lateral appendages A and C are present 97

96 (95). The lateral appendages A and D are filaments;
dorsal appendages C and D are spines .... *E. pajstunensis*
The lateral appendage D is a spine; the dorsal
appendage C is a filament, D a spine .... *E. bisetosus*

97 (95). Lateral appendage C is a spine; dorsally
there is a filament C and spine D;
polygonal sculpture .... *E. bisetosus*
Lateral appendages A and C are filaments 98

98 (97). Dorsally there are filaments C
and spines D; polygonal sculpture .... *E. mediantus*
Dorsally there are only spines D;
sculpture is not polygonal, and
has different on the cephalic and
terminal plates, compared to the other plates ...... *E. diploglyptus*

ECHINISCUS AFRICANUS Murray, 1907 (Fig. 162).

Rather small size (length up to 200μ); the sculpture is composed of a regular granulation; the paired plates appear almost subdivided into three parts, because on each there are two transverse lines lightly incised; median plate 1 sculptured to the caudal margin, median plate 2 subdivided in two by a slender vertical median line deprived of sculpture, median plate 3 present; terminal plate with the usual notch.

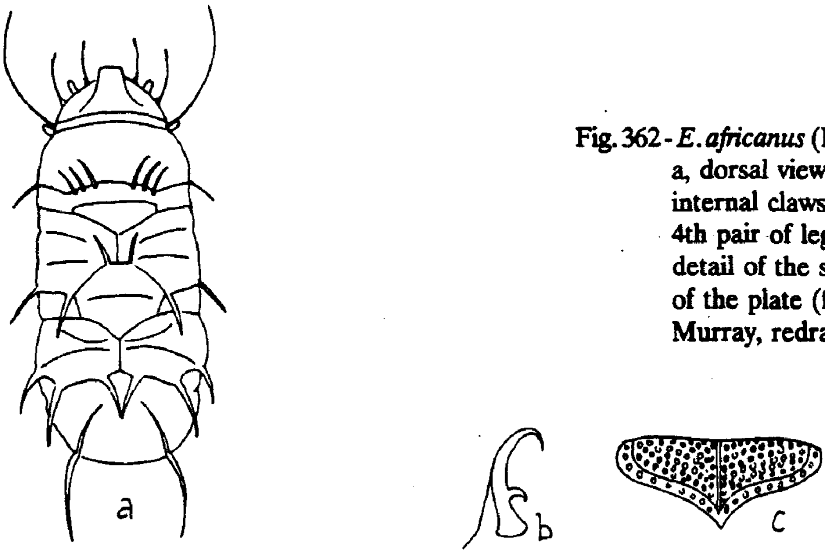


Fig. 362 - *E. africanus* (Murray). a, dorsal view; b, internal claws of the 4th pair of legs; c, detail of the sculpture of the plate (from Murray, redrawn).

Cirrus A of medium length; laterally curved spines B, C, D, E (B is more slender than the others and may be lacking); dorsally 6 slender and pointed curved spines (three per side), found between the caudal margin of the scapular plate and the rostral margin of the first median plate two short and pointed spines on the first and second paired plates, positioned one per side near the median line, and often crossed as scissors. Also a pair of spines at the posterior angle of the first and second paired plates.

Dentate collar on the 4th pair of legs with pointed teeth; internal claws with small spurs near the bases.

The species was found in North Transvaal, in South Africa (typ. loc.), Vietnam, and Angola.

ECHINISCUS ANGOLENSIS da Cunha & Ribeiro, 1964 (Fig. 163).

Maximum length 183μ. Rose eyes. Sculpture composed of a fine punctation and another larger and irregular punctation. Median plate 3 present, but small in size. Dorsally short appendages C^d and D^d. Cirrus A 38μ. Short filament or short spine E, with irregular surface (rough).

The description of the species, as written by the author, is not very clear: in fact it does not discuss the presence of a lateral spine C, which is however shown in the figure, and there is a dorsal appendage C, which is not shown in the drawing (see Fig. 163).

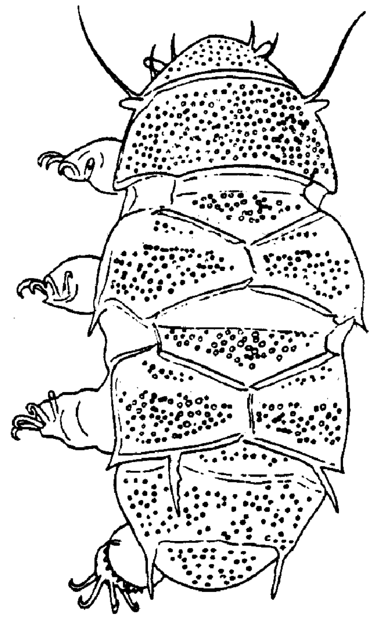


Fig. 163 - *E. angolensis* da Cunha and do Nascimento Ribeiro. Dorsolateral view (from da Cunha and do Nascimento Ribeiro).

According to the author, *E. angolensis* is set apart from *spinulosus* group, having certain resemblances to *E. crassispinosus*, from which it differs by the size and the configuration of the appendices and by the presence of median plate 3.

The discovery of *E. angolensis* was in lichen from Boca da Humpata, Sà da Bandeira (Angola). The species was later found by Maucci at Bugenjuzi (Burundi).

ECHINISCUS APUANUS M. Bertolani, 1946 (Fig. 164).

Size rather small, length about 200μ, rose color, eyes present. The cuticle has polygonal sculpture. The dorsal appendices are: a slender spine B^d, a short filament C^d, a short tooth D^d; laterally, besides cirrus A, are present: a slender spine B, a short filament C, a long filament D.

Fourth pair of legs with the usual papilla and with dentate collar bearing 6 rather large teeth, spacing between them.

This is one of the six rare species of *Echiniscus* with dorsal appendices on the scapular plate (the others are *africanus*, *arcangelii*, *militaris*, with its subspecies *multispinosus* and *weisseri*, if leaving out the rare individuals of *merokensis* with spines on the scapular plate).

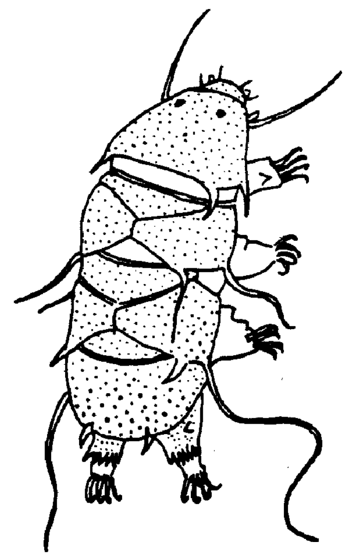


Fig. 164 - *E. apuanus* M. Bertolani
(from M. Bertolani, redrawn).

E. apuanus was collected only one time, in Italy, in the Apuane Alps.

ECHINISCUS ARCANGELII Maucci, 1973-74 (Fig. 165).

Length 250μ, rose color, eyes absent. The sculpture is composed of a regular granulation, very dense: the granules (which are in reality small depressions) are separated by a distance less than their diameter (1.15-2μ), and are joined by slender radial streaks. Such sculpture is less dense on the anterior margin of the paired plates and on the 3rd unpaired, which is present. The cuticle between the plates has a fine and rare punctation, which is present also on the proximal half of the legs. The terminal plate is clearly facetted, with strong incision.

The external and internal buccal cirri begin with a base enlarged into a bulb, the buccal papilla is elongated oval.

Cirrus A slender, 80μ long, with straight conical clava. The lateral appendices are all spines: B, C, and D, robust spines, very short, slightly increasing in anterio-posterior sense; E is curved spine, 40μ long, similar to those of *E. militaris*. The dorsal appendices are likewise spines, short and robust at B and C, long, straight, very spread out in D. There exists also 6 small triangular teeth, bent forward, at the anterior margin of the scapular plate.

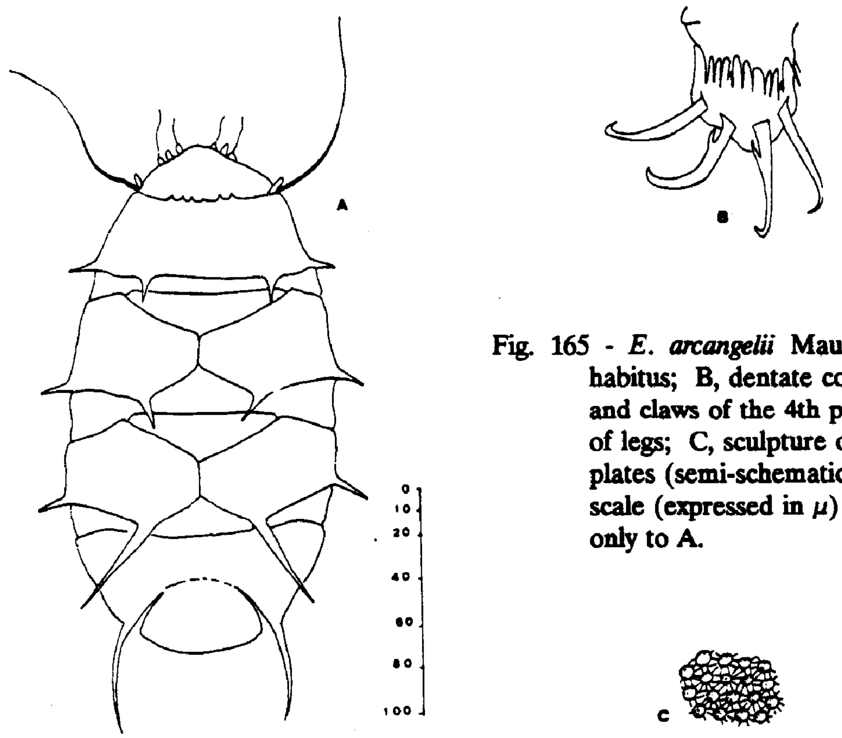


Fig. 165 - *E. arcangelii* Maucci. A, habitus; B, dentate collar and claws of the 4th pair of legs; C, sculpture of the plates (semi-schematic). The scale (expressed in μ) refers only to A.

First pair of legs with spine, 4th pair with papilla and dentate collar, formed of 11 spiniform teeth, long (10μ) and sharp. Internal claws with slender and long spurs, external smooth.

The species, which calls to mind *E. militaris* by the presence of the dorsal appendix B, by the appearance of the appendix E, and by the dentate collar, is nevertheless clearly separated by the type of sculpture, which excludes any relationship between the species.

E. arcangelii was collected only one time, in Italy, on Carso Triestino.

ECHINISCUS ARCTOMYS Ehrbg., 1853 (Fig. 166).

Length varies between 230 and 330μ, eyes reddish. The sculpture of the plates is composed of a dense and uniform punctation: the distance between the dots (which are true projecting granules not depressions) is less than their diameter, and does not resolve into small dots, even using phase contrast immersion.

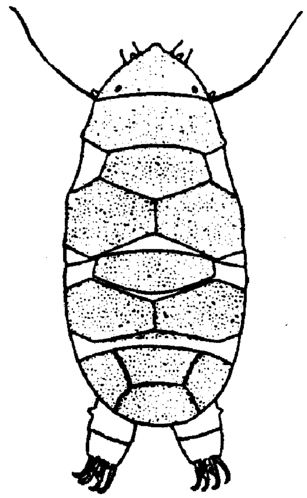


Fig. 166 - *E. arctomys* Ehrbg.

Sometimes the paired plates (II and III) have an anterior zone finely punctated. Lacking the 3rd median plate and there is only a narrow punctated zone, immediately behind the paired plate III. The faceting of the terminal plate is variously clear in different individuals: there is always the notch, or incision. Outside of cirrus A (50μ or less) and the usual cephalic appendices, there are no other lateral or dorsal appendices. There is the spine on the first pair of legs and the papilla on the fourth, which bears a dentate collar, composed of many sharp teeth, irregularly arranged; internal claws with very large curved spurs. It deposits few eggs (2-4) in the exuvium.

E. arctomys belongs to a group of *Echiniscus*, characterized by the absence of dorsal and lateral appendices (except cirrus A): it includes 28 good species (including *arctomys*). The differences consist especially of the type of sculpture, which should therefore be examined with great care every time you find one of these species. Unfortunately the descriptions of the older species remain sometimes too vague in the description of the sculpture, while for certain other species (for example *tardus*, *speciosus*, *nobilis*, *mihelcic*, *markezi*, *carsicus*) the description is too detailed, so as to be difficult to use.

E. arctomys is cosmopolitan, but seems to be more frequent at higher altitudes: in Italy it has not been collected under 1500 meters altitude.

Typ. loc.: Rosa Mountain (Italy).

ECHINISCUS BAIUS Marcus, 1928 (Fig. 167).

Small size: length 100-155μ for the adults with 4 claws, 90-125μ for the larva with 2 claws; color rose; eyes present and red. The sculpture is composed of an irregular punctation not too dense, that leaves free and smooth a transverse band on each of the paired plates. The median plates 1 and 2 are smooth in the rostral zone, sculptured in the caudal. The median plate 3 is present, clearly visible and covers the entire space included between the second paired plate and the terminal plate: this last is not faceted and has the usual notch or incision.

Besides the lateral cirrus A of 20μ, the only appendices are the spine E, length at maximum 14μ, sometimes bifurcated: only in an individual Marcus observed a dorsal spine D^d of 6μ. Dentate collar of the fourth pair of legs with short sharp teeth; internal claws with spurs.

The species was collected in Korea, at Giava and Lombock.

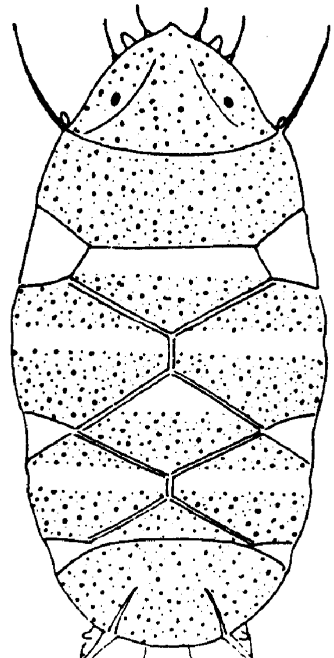


Fig. 167 - *E. baius* Marcus (from Marcus, redrawn).

ECHINISCUS BALOGHI Iharos, 1973 (Fig. 168).

Length 110-160μ, color of red orange to cherry red, eyes red; cephalic papilla long and large, lateral cirrus from 32-46μ long. Sculpture composed of different sized granules, larger on the dorsal plates and smaller on the median plates, but those of largest size are on the terminal plate; cuticle "rough". The granules of the sculpture appear as small black dots, when the microscope tube is in high position; lowering the tube, they have instead appearance of equal size, of clear color, rounded and uniformly distributed: lowering further the tube brings out a black dot at the center of all granules.

The median plate 2 is transversely subdivided, the median 3 is absent or sometimes weakly emphasized; on the terminal plate there is present the usual incision, while the faceting may be more or less evident or even lacking completely.

The number of lateral appendices varies in the young and in the adults. A typical adult has: a small short spine B; rather short filaments D, C, E; also a small lateral spine at the margin of the paired plates and one at E, above the filament. Even the dorsal appendices are variable: typically there is a filament C^d and one D^d, or else this last may change into a small spine. At the caudal margin of the second paired plate there are 2 or 3 small teeth at both the sides.

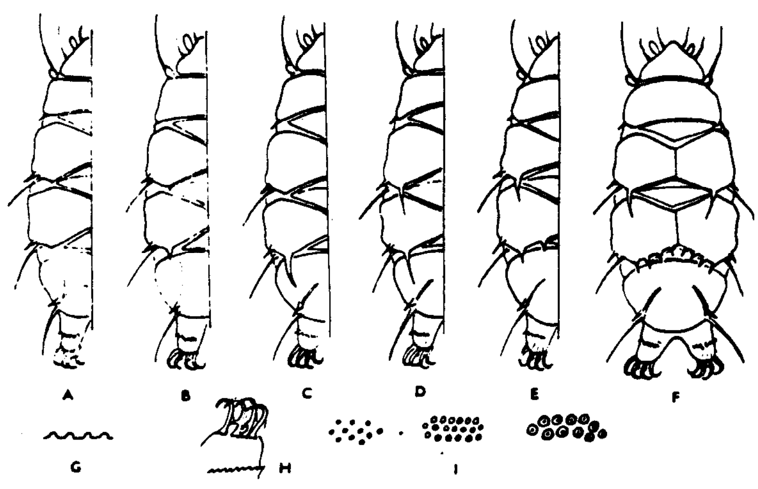


Fig. 168 - *E. baloghi* Iharos. A-F, different conformations of the appendices (F, animal of full development); G, section of the cuticle; H, claws of the 4th pair; I, sculpture of the cuticle, with different planes of focus (from Iharos).

Dentate collar with 8-10 small teeth, very close to each other; claws 8-9μ long, the internal with spurs turned basally.

Large reddish eggs deposited in the exuvium in numbers of three.

According to the author the species belongs to the "*spinulosus* group" because of the lateral appendices. We are not of this opinion, because laterally there are also filaments or bristles (*Borste* in German), and because the sculpture seems to be of different type.

The species was collected in New Guinea.

ECHINISCUS BARTRAMIAE Iharos, 1936 (Fig. 169).

Length up to 321μ, color red-brown. The sculpture of the cuticle is composed of a regular punctation; it is present on the third median plate (principal difference with regard to *E. simba*).

The lateral appendages, besides cirrus A of about 96μ, are filaments C, D, E, of which E is the longest (about 100μ) and D the shortest (about 71μ). Dorsally there are "rigid filaments" (thus declares the author) C^d and D^d, which may reach 50μ in length.

The species has been collected only in two different localities in Hungary.

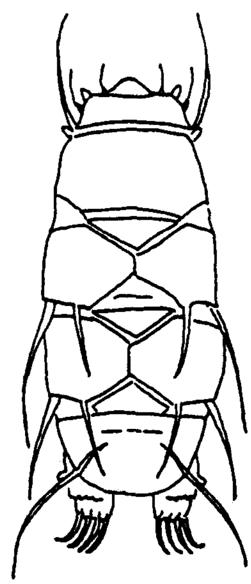


Fig. 169 - *E. bartramiae* Iharos. (from Iharos, redrawn).

ECHINISCUS BECKI Schuster and Grigarick, 1966 (Fig. 170).

Length 290-420μ. Eye spots present, showy, of dark red color. Sculpture of the dorsal plates (immersion objective!) composed of compact polygons, tenuously connected: each polygon has at its external perimeter 4, 5, or 6 marginal pores (see figure). Such pores are absent in the anterior half of the first and second paired plates and from median plate 2: in this position the polygons are not connected together. Sculpture of the legs weak, more evident on the 4th pair. Cephalic plate divided in two distinct halves, with an anterior platelet and an extremely reduced posterior. Median plates not subdivided transversely, however -- as said -- the sculpture on the anterior part of the median plate 2 is different from that of the posterior part.

Internal (6-7μ) and external (17μ) buccal cirri shortly bifurcated at the distal end, or sometimes terminated in a small disk, and lateral cirri A distinctly expanded or bifurcated at the distal end. Lateral filament C (115μ in individuals of 400μ) and D (100μ) slender and sharpened. Lacking the dorsal appendices and spine E.

Legs of the 1st and 4th pairs with basal papilla; dentate collar with 8-14 teeth. Internal claws of the first three pair of legs smooth, according

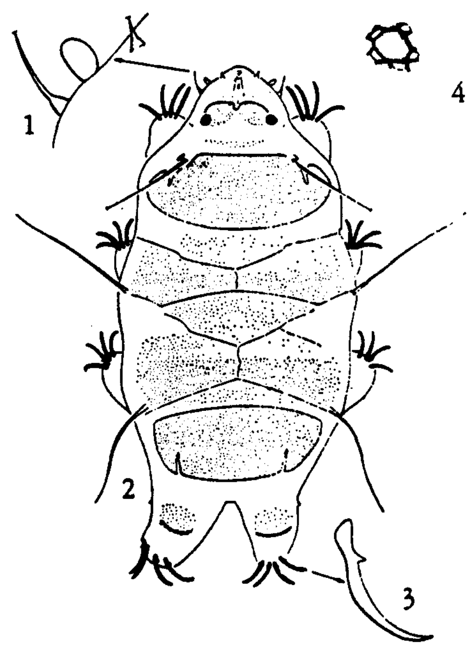


Fig. 170 - *E. becki* Schuster & Grigarick. 1, details of the buccal cirri and the papilla; 2, dorsal aspect; 3, external claws of the 4th pair of legs; 4, details of a polygonal element of the sculpture and of the marginal pores (on the perimeter of the polygon) (from Schuster & Grigarick).

to the authors: however in 3 of the 4 examples of the Ramazzotti collection, such claws have a small spur. Internal claws of the 4th pair of legs with spurs, which exist -- apically straight -- on the external claws.

The species was collected in moss on rocks, near Mountaineer Mine, Riverside Mountains, in California (U.S.A.).

ECHINISCUS BIGRANULATUS Richters, 1907 (Fig. 171).

The description of Marcus (1936) may be thus summarized: "modest size, length up to 208μ, lateral cirrus of about 60μ. The sculpture of the robust plates is double, that is to say it appears composed of a dense fine and regular punctation, on which is superimposed larger granulation and much less dense; with a fixed setting of the objective focus, the sculpture of one type appears dark and the other light; there are sometimes transverse bands lacking sculpture on the paired plates. The third median plate is present and the terminal plate has the usual incision and has weaker sculpturing. Dentate collar on the fourth pair of legs, claws short (12μ), without spurs."

However the numerous examples of *E. bigranulatus* coming from Cerro El Roble (Chile, at about 1,900 m) and from our examination differs from the preceding description by the following characters:

- large size (exceptionally up to 290-300μ, in complete extension;

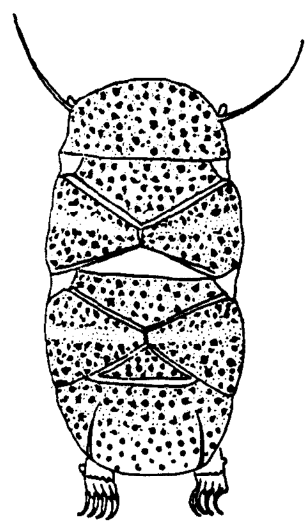


Fig. 171 - *E. bigranulatus* Richters. (from Heinis, modified).

- presence of a small spur, in the shape of a sharp spine, on the internal claws; it is very near to the base of the claws and turned toward them (probably the minute spur will be missed at first observation);
- clear faceting of the terminal plate.

The species much resembles -- at a quick glance -- *E. ranzii*: the numerous differentiating characters, permitting however identification without excessive difficulty, are stated in the description of *E. ranzii*, to which therefore we refer the interested.

The species is known from south Africa, South America (Chile, Colombia, Paraguay, Tierra del Fuego) and Krakatoa; it is not known however from Italy and a report of 1945 for Val Bognanco peak was found in error.

Typ. loc.: Tierra del Fuego.

ECHINISCUS BISETOSUS Heinis, 1908 (Fig. 172 and 174).

This species is part of the "*blumi-canadensis*" series, of which we treat more extensively in the description of *E. blumi*, to which we refer for more information.

Size variable from 214 to 300μ and more. The sculpture of the plates may be polygonal, similar to that of *E. blumi* or else have the appearance of a dense regular granulation, which sometimes becomes less dense along transverse bands on the paired plates. The median plate 3 is absent, however there is a sculptured zone and laterally delimited between the second paired plate and the terminal plate: this last has the usual incision.

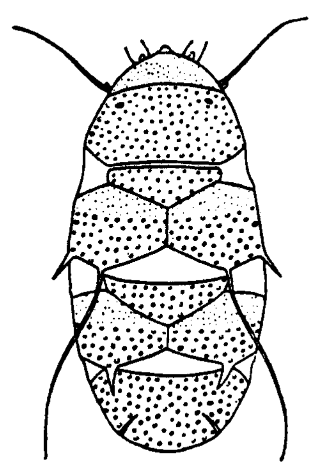


Fig. 172 - *E. bisetosus* Heinis, and detail of the claws of the 4th pair of legs.

Laterally besides cirrus A, there are only short spines C ("*bisetosus* C" of Cuénot), or else only short spines D ("*bisetosus* D" of Cuénot); such processes may exist on only one side, or else assume the shape of double spines (spine at whose base is inserted an extra shorter spine). Dorsally there are filaments C^d, longer than cirrus A, and short spine D^d. Dentate collar and papilla on the fourth pair of legs, whose external claws often bear -- but not always -- one or two straight teeth, very near to the base; internal claws with short and curved spurs.

The eggs of red-brown color (diameter 60-68μ) are deposited in numbers of 4-5 in the exuvium.

The species was collected from numerous localities in Europe (also Italy), North America, and Turkey.

In almost all the cited reports, however, the species is accompanied by other species of the "*blumi-canadensis*" series, for which is reason to have some doubt on the goodness specifically of the individuals described as *bisetosus*. To our knowledge are only two pure populations of *E. bisetosus*: one coming from Schabs, near Bressanone (Alto Adige) and one from Alpedrinha, near Fundao (Portugal). Typ. loc.: Swiss Jura.

ECHINISCUS BLUMI Richters, 1903 (Figs. 173 and 174).

Length from 300 to 450μ, more often around 325μ; eyes red. Polygonal sculpture of the plates, that is the single dots of the granulation seem to be contained in pentagons, or in a hexagon: with a determined focal setting of the objective, one sees clear circles not touching, on darker bottoms; at another setting of the focus appears clear polygons, rather regular, touching or not, and with dark spots at the center (in Fig. 173A is represented the appearance of the sculpture with a focal setting intermediate between the two described). Sometimes the paired plates II and III bear one or more transverse bands lacking sculpture: even the second median plate may have a transverse smooth band. Median plate 3 is present; the terminal plate is not facetted and has the usual two notches.

Normally the lateral appendices are A, B, C, D, all filaments; often there is a small spicule E, which may also be lacking. The dorsal appendix C^d is a filament more or less long, while D^d is a spine of medium length, or else short, or extremely short. The legs are partially sculptured: the first pair bears a small spine, the fourth pair the usual papilla and a dentate collar with 6-10 points. Internal claws with curved spurs; those external on the 4th pair of legs have always -- near the base -- from one to

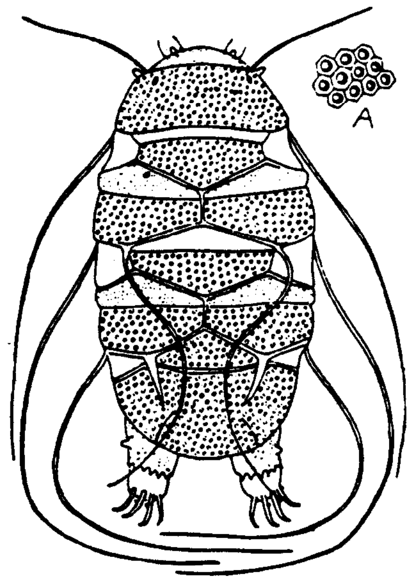


Fig. 173 - *E. blumi* Richters. A, details of the sculpture of the plates.

three straight spurs; often but not always they have a similar spur also on the external claws of the 3rd pair of legs.

We have observed young with 4 claws (length 215-345μ) yet lacking filament B; on the other hand larvae with 2 claws (length 120-160μ) may already have all the appendices, B included. The reddish eggs are deposited in the exuvium (3-5).

From *E. blumi* begins an interesting series, studied especially by Cuénot and Marcus, which -- by successive loss of lateral appendices -- leads to *E. canadensis*, through to *E. trisetosus-bisetosus-mediantus* (see Fig. 174). Between *blumi* (with maximum number of lateral appendices) and *canadensis* (in which is lost all the lateral appendices) exists all the intermediate expressions in passing: however the species of this series are considered distinct, because there have been observed eggs deposited in the exuvium, having all the varieties of characteristic appendices of the individual species. On the other hand it is necessary to note the young *Echiniscus*, with smaller size than the maximum reaches -- and hence sometimes with less number of appendices -- may indeed deposit eggs: cases of the genus have been seen by various authors and, often, also by us, also Mihelčič observed regular seasonal alternation, in one moss, of *trisetosus* and *blumi* (see p. 113).

This last consideration -- and others which are omitted here -- may seem to recommend the grouping of these species, or of at least part of them: but we think that may be premature, at the present state of our knowledge, the more that there are contrasting observations; so, for

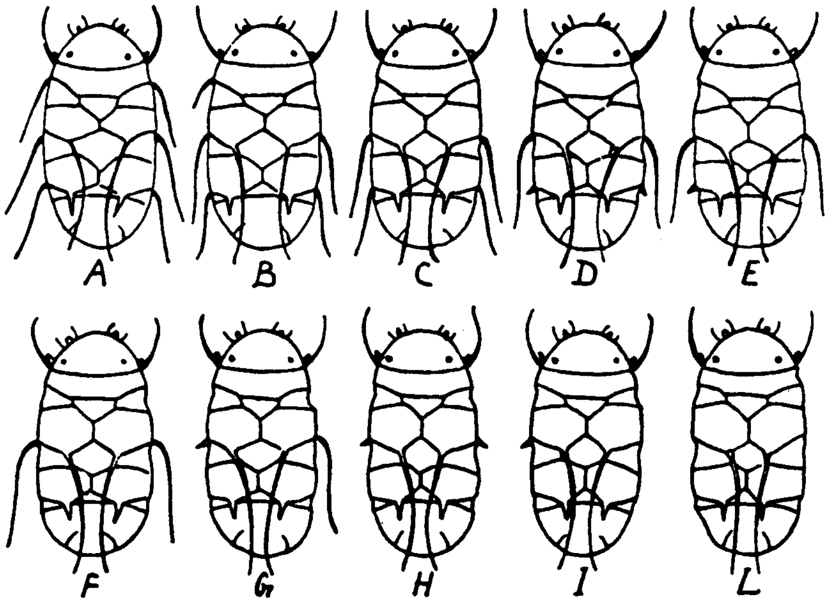


Fig. 174 - Series of *E. blumi* to *E. canadensis*. A, typical *blumi* Richters; B, *trisetosus* Cuénot with filament B on one side; C, typical *trisetosus* Cuénot; D, E, *mediantus* Marcus having respectively on two sides and on only one side extremely small appendix D; F, typical *mediantus* Marcus; G, *bisetosus* Heinis with a filament C; H, typical *bisetosus* Heinis; I, *canadensis* Murray with spine C on only one side; L, typical *canadensis* Murray (from Marcus, modified).

example, if it is true that Ramazzotti has been able to collect in an Italian moss near Lake Maggiore the series of *blumi* to *canadensis* (*blumi* - *trisetosus* - *trisetosus* with extremely reduced C - *trisetosus* with D on a single side - *bisetosus* D with only left C - *mediantus* - *canadensis* with extremely reduced D on a single side - *canadensis*) it is as much true that we have observed from moss, in which exists only *trisetosus* and forms with smaller number of appendices, without which ever not even in successive years, did they appear as *blumi* (present in other mosses of the area).

So it may however be observed that, given that we are inclined to accept the concept of "orthogenetic series", it may not be interpreted in the sense of Cuénot, that is of a progressive *reduction* of the number of appendices (and therefore from *blumi* to *canadensis*), rather in the sense of Marcus, that is of a progressive *acquisition* of appendices (and therefore from *canadensis* to *blumi*): this is affirmed by the ontogenesis of all the species of the series.

At the present state of the knowledge it is not possible to attribute some precise specific value to a single individual: they happen to be considered in the limit of their population. And under this point of view it is possible to verify the existence of the following types of populations.

a) Pure populations. They are not rare for *trisetosus* and for *canadensis*, while happen less frequent for *blumi*, and rarely however for *bisetosus* and for *mediatus*.

b) Populations in which the acquisition of the appendices represents a ontogenetic progression, in which the successive forms correspond -- as a rule -- to an increase in the individual size. The complete series *canadensis* - *bisetosus* - *mediantus* - *trisetosus* - *blumi* may happen rather rare. More frequently the series *canadensis* - *trisetosus*, with or without the intermediary expressions, and sometimes with extremely few or few individuals of full development (over 400μ) in *blumi* phase. There are not lacking however cases in which the *canadensis* phase is practically absent, being limited to only larvae with 2 claws.

c) Mixed populations, in which the diverse forms are distributed without precise correlation with the size of the individuals. In these cases (however not frequent) one often happens to find anomalus examples, with asymmetry in the appendices.

However -- as rightly written by Marcus (1936) -- experiments on rearing of eggs, found in an exuvium with appendices of a definite species (e.g., *bisetosus*), furnished adult individuals with the appendices of another species of the series, yet proceeded to the grouping of the species (or of a part of them), considered the species as *blumi* -- described first in order of time -- and all the others with form of *blumi*, that have not attained complete development.

E. blumi is a very widespread species, collected almost everywhere in Europe (also in Italy), in Turkey, Greenland, North and South America, Australia, and New Zealand.

Typ. loc.: Spitsbergen and Norway.

E. blumi forma *schizofilus* Bartos, 1941, (Fig. 175) is a variety that has the same characteristics as *blumi*, but the lateral appendices -- and sometimes also the dorsal -- are variously split and subdivided, as shown in the figure.

Naturally entire populations were observed -- and in different mosses -- which presented such peculiarities we can not talk of *schizofilus* whenever we treat for example a single individual with double split appendices, etc., within a population of normal *blumi*. The forma *schizofilus* is known only from the Carpathians.

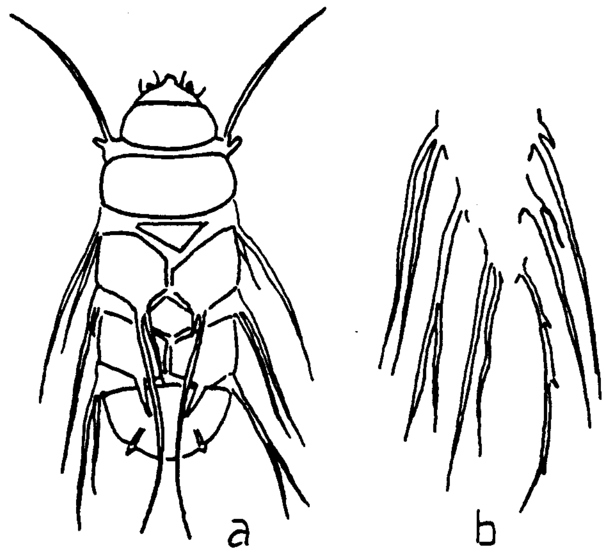


Fig. 175 - *E. blumi* Richters *schizofilus* Bartos. a, dorsal view; b, splits of various types of the filaments (from Bartos, redrawn).

ECHINISCUS CALCARATUS Richters, 1908 (Fig. 176).

Length 192μ; the granulation of the plates is coarse and not very dense; lacking the third median plate and the terminal plate has the usual notch.

Laterally besides cirrus A, there are short spines C and E; dorsally short spines C^d and a little longer spine D^d. Dentate collar of the 4th pair of legs with about 8 teeth; claws without spurs.

The species was observed only from Ascension Island.

ECHINISCUS CALVUS Marcus, 1931 (Fig. 177).

Length 230μ, reddish color composed of a fine punctation; the paired plates exhibit -- on the first rostral third -- a transverse band very weakly sculptured. Median plates 1 and 2 sculptured only on the caudal half; median plate 3 is present which is in large part smooth and has a weak sculpture uniquely in one small median zone, near the terminal plate.

Particularly characteristic of this species are the remarkably long cephalic papillae and the extremely short lateral cirri A, whose length is only one and a half times that of the clava, or else about equal to the

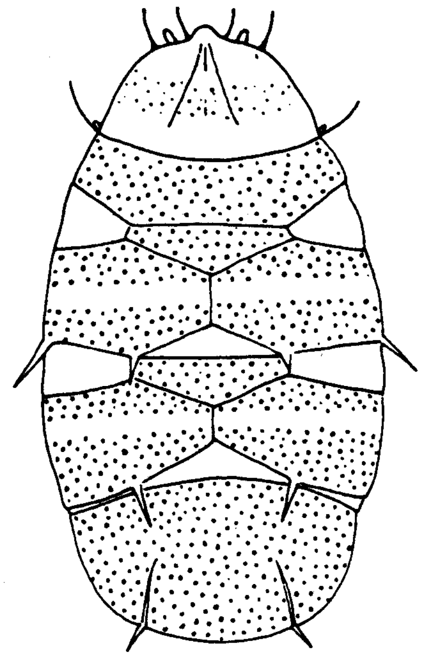


Fig. 176 - *E. calcaratus* Richters. (from Richters, modified).

length of the median cirri. There are no other lateral or dorsal appendices.

Legs robust, those of the 4th pair with an obtuse papilla and granular as far as the dentate collar, which is composed of extremely small pointed teeth, with irregular distance between them. First pair of legs with a minute spine. All the claws are very long (about 25μ) and the internal have a short and slender spur.

The species was collected only in Sumatra.

ECHINISCUS CANADENSIS Murray, 1910 (Fig. 178).
= *E. punctulatus* Mihelčič, 1955.
= *E. bellus* Mihelčič, 1967.

Length up to over 300μ, reddish color, sometimes orange; the sculpture of the plates is composed of small hexagons or of circles with central dots, that is similar to those of *E. blumi*; sometimes the paired plates II and III are crossed by a band with weaker sculpture.

The only lateral appendix is cirrus A (75μ long in an animal of 300μ) sometimes also a small spine C on a single side; there may also be present

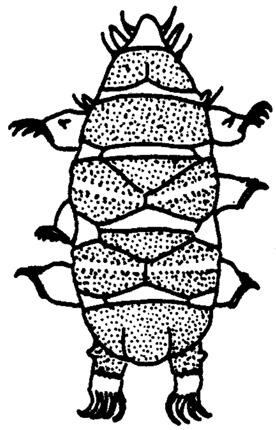


Fig. 177 - *E. calvus* Marcus (from Marcus, redrawn).

-- or lacking -- small spine E on the notch of the terminal plate. Dorsally C^d (filament) and D^d (more or less short spine); so C^d, as D^d, may become extremely short and D^d reduced to such a degree that it is barely visible.

Dentate collar and papilla on the 4th pair of legs; the internal claws bear a curved spur; those external -- of the 3rd and 4th pair of legs -- have often two short spines near the base. The eggs (1-4) of orange color and slightly ovoid, are deposited in the exuvium.

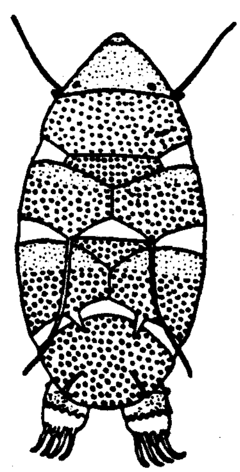


Fig. 178 - *E. canadensis* Murray.

E. canadensis belongs to the *canadensis-blumi* series of which we have spoken with regard to *E. blumi*. It is often found in mixed populations with the other species of the series; there are however also pure populations.

The species has been collected in numerous European localities (also in Italy), Turkey, Korea, Afghanistan, and North America (Vancouver Island and Illinois).

Typ. loc.: Vancouver (British Columbia, Canada).

ECHINISCUS CANEDOI da Cunhà & do Nascimento Ribeiro, 1962 (Fig. 179).

Length of the single collected specimen 196μ; brownish red color; eyes red. The sculpture is composed of coarse dots (depressions), not uniformly distributed on the surface of all the plates.

Cirri A of 31μ; laterally there are short spines C of 10μ and D, this last reduced to little more than a tooth; dorsally there is only spines D^d of 17μ.

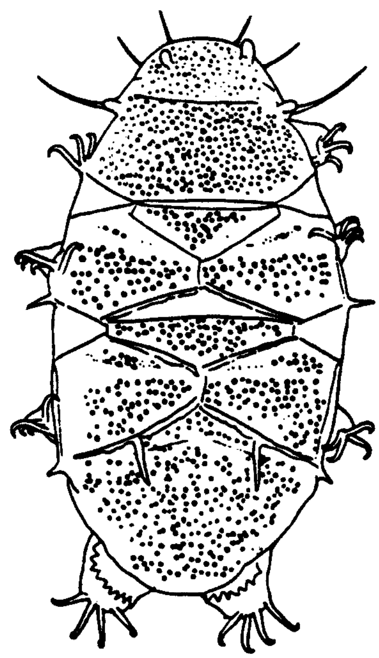


Fig. 179 - *E. canedoi* da Cunha & do Nascimento Ribeiro. Dorsal view (from X. da Cunha & F. do Nascimento Riberro).

Median plate 3 absent; terminal plate not facetted, with the usual notch; dentate collar, composed of 9 teeth, on the fourth pair of legs. The authors gave no sign of the presence, or absence, of spurs on the claws, of spine of the 1st pair of legs and of papilla on the 4th pair.

The species was collected on Madera Island, Camacha locality, in lichens.

ECHINISCUS CAPILLATUS Ramazzotti, 1956 (Fig. 180).

Length 300-325μ, reddish color. The species is easily recognized at first glance by the enormous development of the lateral cirri, length up to one and a half times the length of the tardigrade (and therefore much longer than in *E. wendti* and *E. reticulatus*, where they do not ever surpass 70-80% of the body length); in the larva of two claws of *capillatus* cirri A may be even longer.

The sculpture is a rather fine punctation, diffuse on all the plates, including the intersegmental (median) and that continues even on the 4th pair of legs, as far as the dentate collar: this last is composed of few teeth (9-10), irregularly distributed, larger than those in *wendti.* The third median plate is present; the terminal is not facetted.

The claws are very long, up to about 31μ; the internal has near the base a small spur in the form of a spine, turned downward (toward the base), while the external claws of the 4th pair of legs have a spur turned

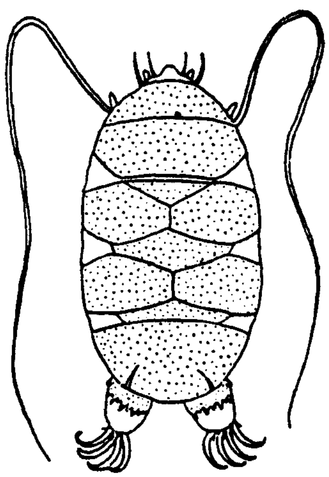


Fig. 180 - *E. capillatus* Ramazzotti.

upwards (or toward the distal extremity of the claws), also very near to the base and similar to a spine. Eggs unknown.

The species was collected only in one moss at 2,400 m altitude in the Dolomites of S. Martino of Castrozza (Italy).

ECHINISCUS CARSICUS Mihelčič, 1966 (Fig. 181).

Length 280-380μ. Color red, eye spots red. Cirrus A of about 60μ; cephalic plate not well developed and its sculpture reaches the scapular plate.

Sculpture complex, which appears different according to the level of "focal setting" of the microscope and different even on the various plates: on the scapular and terminal are seen -- with high microscope tube -- small, irregular, clear polygons, which include a dark interior (Fig. 181, 1c). With tube lower they appear however "granules" of oval shape, but irregular: they are not true granules, because they do not project from the cuticle, but small plates (Fig. 181, 1b), which form a polygon figure.

The first and the second paired plates have equal sculpture; with tube high they are perceived as regular granules, larger in the anterior region of the plate, small in the posterior. In the folds of the plates small irregular polygons are seen, or else clear granules, tied together by extremely fine extensions. The two paired plates have caudally a band not sculptured.

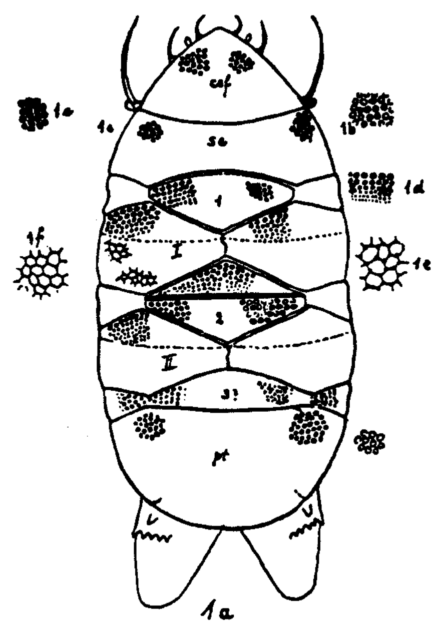


Fig. 181 - *E. carsicus* Mihelčič. 1a, dorsal view; 1b, scapular and terminal plate sculpture; 1c, aspects of the same sculpture with a lower focal plane; 1d, sculpture of the median plates 1 and 2; 1e, f, sculpture of the posterior zone of the paired plates; the sculpture of the anterior zones of these plates is identical to 1d; cef, cephalic plate; sc, scapular plate; 1, 2, first and second median plates; 3?, position of the third median plate, missing; pt, terminal plate (from Mihelčič).

The sculpture of the median plate is as follows: on median 1, with tube high, they appear anteriorly regular granules, which diminish posteriorly in size; with tube lower brilliant polygons are seen, which includes dark. On the median plate 2, with tube high, anteriorly is perceived a sculpture equal to that of the median 1; in the posterior of the plate there are instead depressions, surrounded by brilliant polygons; with tube low the design appears instead inverse.

Median plate 3 absent, however the corresponding area has sculpture equal to that of median 1. Dentate collar of the 4th pair of legs with 6-10 teeth; papilla distant from the collar; internal claws with small spurs.

We have fully reported the description of the sculpture data by Mihelčič, but we can not hide the difficulty of individuals of this species and of separation from others of the "*arctomys* group" described by the same author and by others. This is all the more so, for the meticulous descriptions of the various aspects of the sculpture do not mention neither magnification used for observation, nor the use of phase contrast.

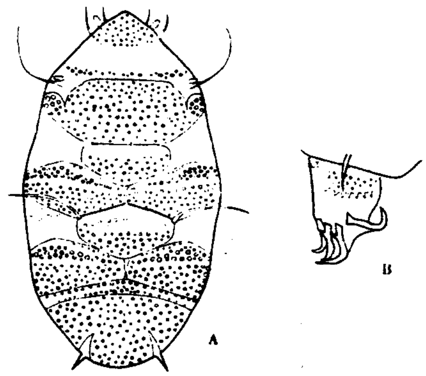
The species is cited for Carso of Doberdò and near Miramare (Trieste). It should be treated as a very rare species, because our observations, over several years in the vicinity of Trieste, it has not been ever found again.

ECHINISCUS CARUSOI Pilato, 1972 (Fig. 182).

Maximum length 314μ, more often 220-270μ; larvae of two claws of about 120μ. The eyes -- to judge from the figures -- seem to be absent. On 85 examples observed there is a certain variability in the lateral and dorsal appendices, but a perfect uniformity of the sculpture and of the other characters. The characteristic appearance of the species is -- according to the author -- that with lateral appendices A (24μ long) and E (long spine up to 20μ), and with dorsal appendices C (filament of 57μ). Such appendices are always present; exceptionally there have been also lateral appendices B, C, D.

The sculpture of the plates and the proximal zone of the legs may seem similar -- with superficial examination -- to that of *E. merokensis*, that is composed of irregularly distributed dimples: with a more thorough examination it is noted that the dimples are circular (in *merokensis* they are not of sparse ellipses), smaller and more numerous, and that between them is noted (as in *E. quadrispinosus*, however finer) an extremely fine, dense regular granulation.

Fig. 182 - *E. carusoi* Pilato (A) and details of one of its posterior legs (B).



The intersegmental plate 1 is anteriorly deprived of sculpture, the 2nd is sculptured also anteriorly, but in less evident manner; the paired plates I and II have a transverse band not sculptured. The unpaired plate 3 is absent, but the relative area is sculptured and displays instead a transverse band devoid of sculpture. At the sides of the plates 1 and 2 the cuticle has a less evident punctation, while the ventral surface has an extremely fine granulation.

Fourth pair of legs with dentate collar of 4-11 teeth (usually 5-7) and papilla; claws of 22.6μ in the larger examples, with curved spurs on only the internal claws; claws of the other legs of about 19.3μ; spine on the anterior legs.

The species was collected at Favignano and Marettimo (Egadi Islands) and near Catania (Sicily).

ECHINISCUS CAVAGNAROI Schuster and Grigarick, 1966 (Fig. 183).

Length 160-220μ; eye spots absent. The paired dorsal plates have -- on their anterior region -- a slender transverse band devoid of sculpture. Internal buccal cirri shorter than the external, which measures about 15μ. Cephalic papilla of about 7μ; lateral cirri A of about 50μ and clava of 5μ. Laterally short spines C and E of about 8μ (all the measured data refers of an individual 220μ long). The spine E is sometimes bifurcated; there are sometimes (not always) spines D^d.

Median plate 3 present. The sculpture of the plates consists of a punctation, composed of larger pores (diameter about 3μ) irregularly sparse and of much smaller pores (0.5-1μ). Fourth pair of legs with dentate collar (8-12 sharp teeth); internal claws of all the legs with small spurs, directed basally.

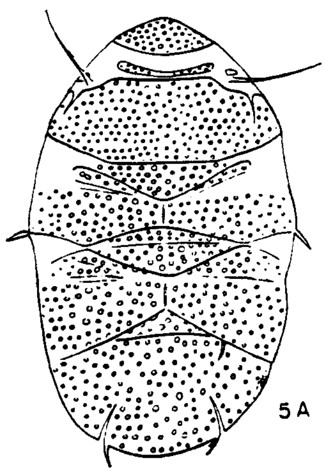


Fig. 183 - *E. cavagnaroi* Schuster and Grigarick. 5A, dorsal view; 5B, photomicrograph of the sculpture (from Schuster & Grigarick).

The species has some resemblance to *E. calcaratus*, but is distinguished by the absence of C^d, the presence of median plate 3 and spurs on the internal claws.

E. cavagnaroi was collected in lichen and liverworts on Santa Cruz Island (Galapagos) (Typ. loc.) and in the United States (Alabama).

ECHINISCUS CERVICORNIS Murray, 1906 (Fig. 184).

According to Marcus (1936) it is treated as a *spec. inquir.*, because it is based on the discovery of a single exuvium, from which only a few characters could be deduced. Medium size, sculpture composed of a fine granulation; third median plate present, terminal plate facetted, with hint of a division in two medially from its caudal part.

The cirri A were not very recognizable on the exuvium; lateral filaments E very long, which bear, at about half their length, extremely short filiform appendices, which calls to mind the bifurcation of a horn of the stag. Dorsally filaments C^d, near which exists, in dorsolateral position, an extremely small tooth; also extremely short teeth D^d, with sufficiently wide base.

The exuvium mentioned above was observed on the Orcadi Islands, Australia.

ECHINISCUS CLAVISETOSUS Mihelčič, 1957 (Fig. 185).

Length up to 340-350μ, brownish red color; lateral cirri long, distally swollen; clava normal. Laterally there are filaments B, C, D, terminated

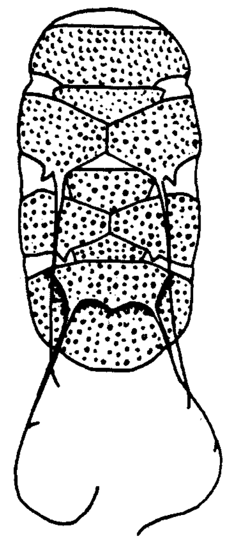


Fig. 184 - *E. cervicornis* Murray (from Murray, redrawn).

distally in a club, with exception of B, which can be, or less, clubbed and which can also be absent (Mihelčič, *in litt.*). The posterior lateral angles of the paired plates are pronounced and assume tooth-shape; also on the terminal there are two lateral teeth, in the position of the beginning -- in most *Echiniscus* -- of the notch, or incision. Dorsally there are filaments C^d, however with distal end clubbed, while lacking appendices D^d.

The sculpture is similar to that of *E. blumi*, that is to say it is composed of small hexagons with circular centers, and leaves free a rostral transverse band on the paired plates and on the medians. Median plates 1 and 2 are present, while 3 is absent. The cephalic plate is facetted and the terminal is strongly curved downward in its caudal zone. The legs of the 4th pair are sculptured from the bases up to the dentate collar, which bears 4-6 teeth (the longest can reach 8μ); the internal claws have a spur.

There is also a ventral armor, composed of distinct plates (more or less evident), arranged as follows:

- anterior to the first pair of legs 2 adjacent quadrangular plates, finely granulated (*jugular plates*);
- between the first and second pairs of legs the cuticle is thickened and shows some lines;
- immediately before the second pair of legs, and almost between them, there is a triangular plate (*sternal plate*);
- following, successively, between the second and third pair of legs, two smooth trapezoidal plates, medially separate, then two granulated plates, medially in contact, and finally two granulated plates and

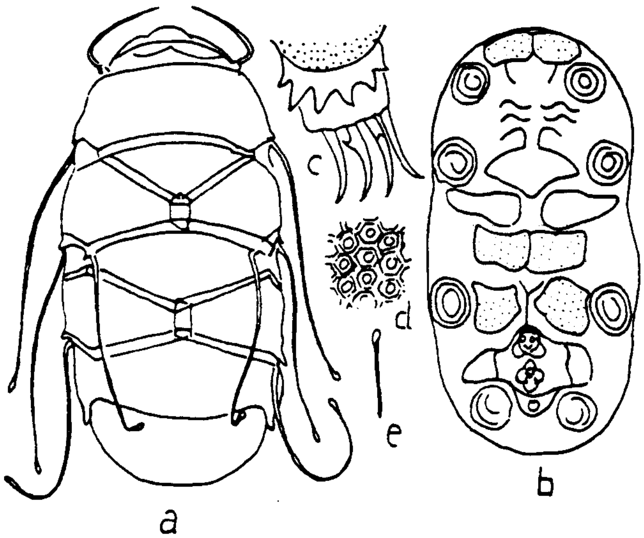


Fig. 185 - *E. clavisetosus* Mihelčič. a, dorsal view; b, ventral view; c, leg of the 4th pair; d, sketch of the sculpture; e, distal end of the filaments (from Mihelčič, redrawn and slightly modified).

medially separate, positioned between the legs of the third pair. These three pair of plates constitute the *ventral plates*;

- between the third and the fourth pair of legs there is the *genito-anal plate*, which has rostrally a conical shoe, on which there are two circular structures and one in the shape of S (disks, as for example in the Hydracarina); a structure in the shape of a rosette follows, which surrounds the genital pore, and finally a rounded caudal appendix (plate) with the anal aperture.

Dastych (1973) has established the presence of a similar ventral armor in examples of *E. spitsbergensis*, coming from the Tatra Mountains, from Iran, and from Canada, reaching the conclusion that the difference between *E. clavisetosus* and *E. spitsbergensis* includes the limits of the variability of this last species. Therefore *E. clavisetosus* may be considered as a synonym of *E. spitsbergensis*.

In material from Val Pusteria (Italy), from Norway, and from Axel Heiberg Island (mixed population of *E. spinuloides*, with related species) we have established the constant presence of the plates which Mihelčič named "jugular plates", clearly sculptured, and the frequent presence (sometimes barely distinct) of other ventral plates very weakly sculptured (never however the clubbed appendices). He nevertheless thinks the synonymy proposed by Dastych as valid. We prefer however to preserve here the species of Mihelčič, as much as the whole problem of the "*spinuloides* group" (see p. 466) should, sooner or later, be re-examined in depth.

E. clavisetosus has as yet been observed only in moss on rock in the shade in the woods of the Austrian Alps (Carinthia).

ECHINISCUS COLUMINIS Murray, 1911 (Fig. 186).

Length about 200μ, red. Sculpture similar to that of *E. merokensis*, that is, constituted of small isolated dots, that sometimes have the appearance of depressions, but they seem to be granules. Lacking the third median plate, terminal plate in general not facetted, but which may sometimes be.

The lateral appendices are A, B, C, D, E, all filaments, of which E is the longest. Dorsally there are long filaments C^d (about 80μ), not inserted at the posterior angles of the first paired plates, rather somewhat more

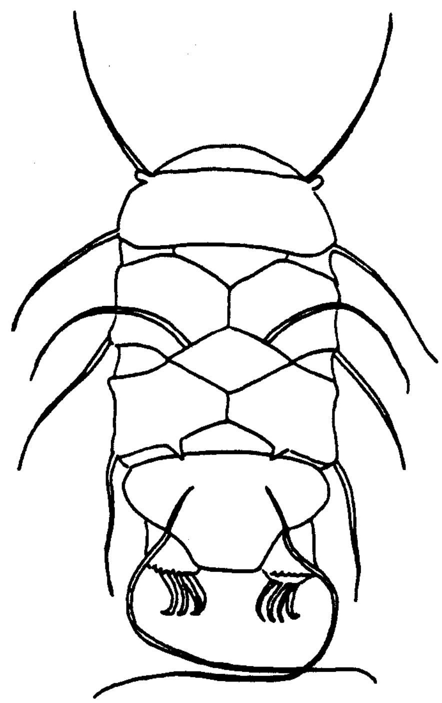


Fig. 186 - *E. columinis* Murray, redrawn).

medially; also are present short spines D^d. Dentate collar with small triangular teeth, internal claws with spurs.

Besides the typical form, here described and figured, Marcus (1936) cited also three modified forms, having the following characteristics:

1) absence of filament B;
2) absence of B, extremely short spines C^d rather than filaments, and lateral appendices C, D, E, with base enlarged;
3) absence of filaments B and E, and C^d constituted of a robust spine of medium size.

Forms 1 and 2 -- when the terminal plate is facetted -- can not at first glance be distinguished from *E. merokensis* and from its doubtful variety *suecica*, which demonstrates also frequently a displacement toward the median line of appendices C^d and a remarkable basal enlargement of the lateral filaments.

On the other hand the considerable individual variability of *E. merokensis* seems able to include in its limits all the possible forms of *E. columinis*; neither the presence or the absence of the median plate 3 seems to be a character of certain specific separation. An established doubt comes up therefore on the specific goodness of *E. columinis*, which can probably be nothing other than synonymy with *E. merokensis*.

Of *E. columinis* are known reports from Ireland (Typ. loc.), Poland, and Turkey.

ECHINISCUS CRASSISPINOSUS Murray, 1907 (Fig. 187).

Length 260μ, red. The sculpture of the plates is a punctation, composed of single dots of two different types, one larger, more distant, irregularly arranged, and the other smaller, more densely and regularly distributed between the preceding. Median plates 1 and 2 are present, while 3 is absent; terminal plate not facetted, with the usual two notches.

Laterally, besides very long cirri A, there are short spines C, D, E; dorsally spines D^d, wide and flat. Fourth pair of legs with papilla and dentate collar, composed of obtuse teeth, a difference from *crassispinosus fasciatus*, which are sharp; the internal claws bear a very small and curved spur.

The species has been collected only in South Africa (Cape Colony).

A subspecies is also known (initially described as a "forma"):

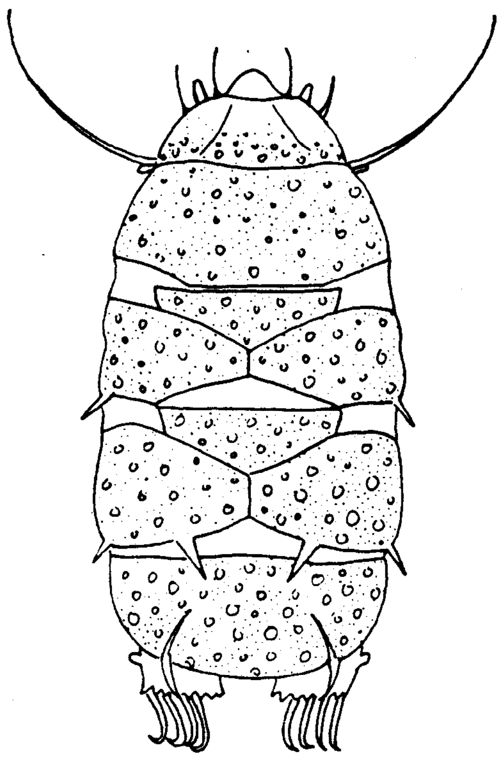


Fig. 187 - *E. crassispinosus* Murray. (from Murray, redrawn).

E. crassispinosus fasciatus Marcus, 1928 (Fig. 188).

Length 152-260μ; sculpture as in the nominate subspecies composed of a double punctation, which however leaves free and smooth -- in large or small extent -- two transverse bands on the paired plates II and III. Sometimes a spine B is present. Median plates 1 and 2 present; 3 is absent. The dentate collar has sharp teeth, and this is perhaps clearer difference with respect to *crassispinosus*, which has instead obtuse.

It has been observed in eastern Africa (typ. loc.) and in Brazil: however the Brazilian individuals (De Barros, 1942) had a single band devoid of sculpture -- rather than two -- on the paired plates and was considered by the author *crassispinosus fasciatus* solely by the sharp teeth of the dentate collar.

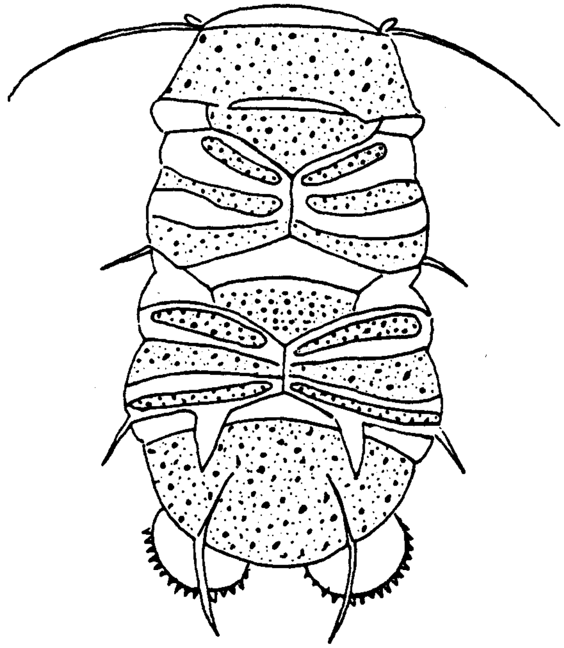


Fig. 188 - *E. crassispinosus fasciatus* Marcus (from Marcus, redrawn).

ECHINISCUS DEARMATUS Bartos, 1935 (Fig. 189).
= *E. wendti* forma *dearmata* Marcus, 1936
= *E. wendti dearmatus* Ramazzotti, 1962 & 1972
= ? *E. bellus* Mihelčič, 1967
= *E. szaboi* Iharos, 1973.

Length 200-220μ, eye spots red; the sculpture is a rather coarse but regular granulation; the median plates 1 and 2 are large, the median plate 3 is absent. Terminal plate not facetted, with the usual two notches. Internal and external medial cirri with enlarged base; cephalic papilla well developed; the lateral cirri A are long (90μ) and slender; clava long; there are no other lateral or dorsal appendices. First pair of legs with small spine; fourth pair with papilla and dentate collar, composed of about 15 long and sharp teeth, distant between them; internal claws with large curved spurs on the first basal third; external claws with straight and slender spurs. Eggs (2-3) deposited in the exuvium.

In the original description Bartos refers to having found his examples in moss in which there was present also *E. trisetosus*, *bisetosus*, and *canadensis*. This author thinks therefore that *E. dearmatus* can be near *canadensis*, distinguished from it by the lack of dorsal appendices.

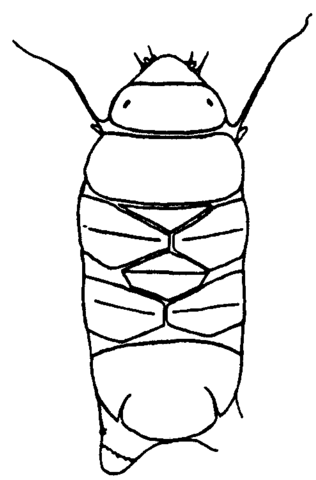
Marcus however thinks it a variety of *E. wendti*, different only by the presence of spurs on the external claws.

We have noted that the sculpture, so summarily described by the author does not seem to correspond to those of the "*canadensis-trisetosus* group", and much less to that of *E. wendti*.

E. bellus, described by Mihelčič initially as a good species, was then, by the same author (*in litteris*) considered as synonymous with *canadensis*, with the following description.

Length 190-220μ, red color, eye spots dark red. Lateral cirri A rather short, which surpasses a little the rostral cephalic end. Sculpture of different appearance 3 successive levels of "focal setting" of the microscope: with tube high (Position 1) dark spots are seen, surrounded by clear polygons; with tube a little lower (Pos. 2) from the clear small disks are seen polygonal outlines with central dark dots; with tube still lower (Pos. 3) round granules are perceived, clear, bright, similar to pearls, on dark background. Lowering the tube further, the visibility of the sculpture disappears completely. Median plate 3 absent, however the corresponding area is sculptured. The 4th pair of legs has dentate collar (6-10 teeth) and the internal claws have a spur turned basally, while those external have one turned apically.

Fig. 189 - *E. dearmatus* Bartos (from Bartos).



The species was collected in moss on tree trunks of the Andes (Argentina).

On the other hand, numerous reports by us and other authors have not ever established -- not even irregularly -- the complete absence of dorsal appendices in *canadensis*, neither in any of the species of the "*canadensis-trisetosus -blumi*" group. We consider therefore justified to consider *E. dearmatus* as a species in itself, and as such Bartos as much as Mihelčič consider their species as near to *canadensis*, appears reasonable to believe that they should be treated as the same species.

As for *E. szaboi*, the description -- and especially the drawing -- of the sculpture suggests it is also synonymous here proposed.

The species is cited for the Carpathians (*dearmatus*), for the Argentine Alps (*bellus*), and for Canada (*szaboi*).

ECHINISCUS DIKENLI Maucci, 1972 (Fig. 190).

Length up to 252μ, red color, eye spots present, red. The sculpture is composed of round pores, distributed with irregular density; the sculpture is absent along the caudal margin of the cephalic plate and the anterior end of median plate 2; between the pores the cuticle is smooth. This sculpture is therefore very near to that *p.e.* of *E. merokensis* and *E. testudo*. The median plates 1 and 2 occupy the entire space between the paired plates; the median plate 3 is absent; the terminal plate has the usual notch and is not facetted.

The internal and external buccal cirri are long and slender and starts with a cylindrical base. Cirri A up to 115μ long. Laterally there are spines B, C, D, short and robust, as well as filament D (from 42 to 90μ). Dorsally there are robust spines C and D (20-34μ), of which the C^d are a little longer than D^d.

First pair of legs with spine, 4th pair with basal papilla and sculptured in the proximal zone, as far as the dentate collar, which is formed of 7 triangular teeth, sharp, with wide base, rather distant. Internal claws with large spurs, external with extremely small spurs near the base, hardly a hint and barely visible.

The species (*dikenli*, Turkish for "thorny") was collected in moss at Dinar (Turkey) at an altitude of 1,100 m.

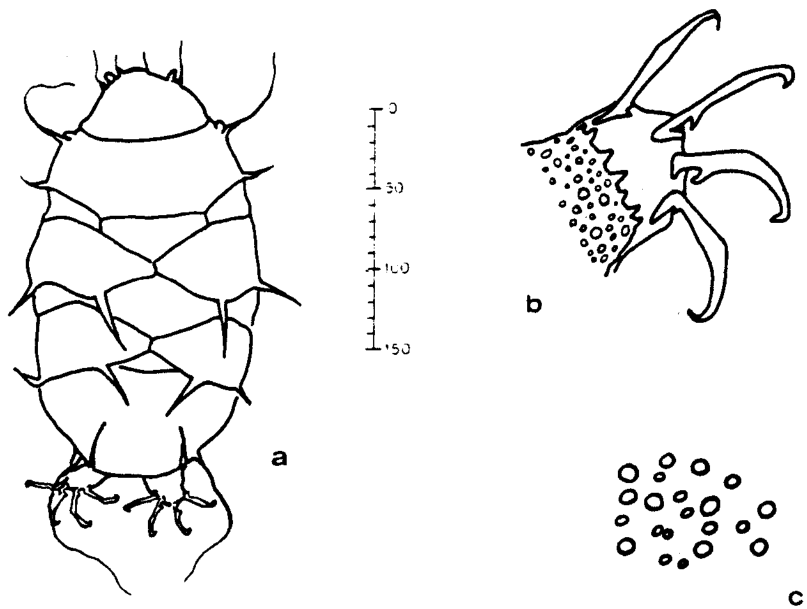


Fig. 190 - *E. dikenli* Maucci. a, habitus; b, claws of the 4th pair of legs; c, details of the sculpture of the plates (from Maucci).

ECHINISCUS DIPLOGLYPTUS Durante Pasa & Maucci, 1975 (Fig. 191).

Length 280μ. Color brick red, eyes small, red. The sculpture is of two clearly distinct types. On the cephalic plate, on the scapular, and on the terminal there are numerous small round or elliptical depressions, irregularly sparse, on a regular background and extremely finely punctated (sculpture of the "*merokensis*" type). The paired plates and unpaired 1 and 2 have instead large round granules, of star shape, with dark lines connecting them, delimited thus from rings of small depressions (sculpture of the "*elegans*" type, that is found also in *E. arcangelii*). The unpaired plate 3 is absent; the cuticle between the plates is smooth.

The internal buccal cirri are considerably shorter than the external. The lateral appendices are cirri A (50μ long) and filaments C (60μ). The dorsals are only short spine D (15μ).

The legs have a finely granulated proximal part. First pair of legs

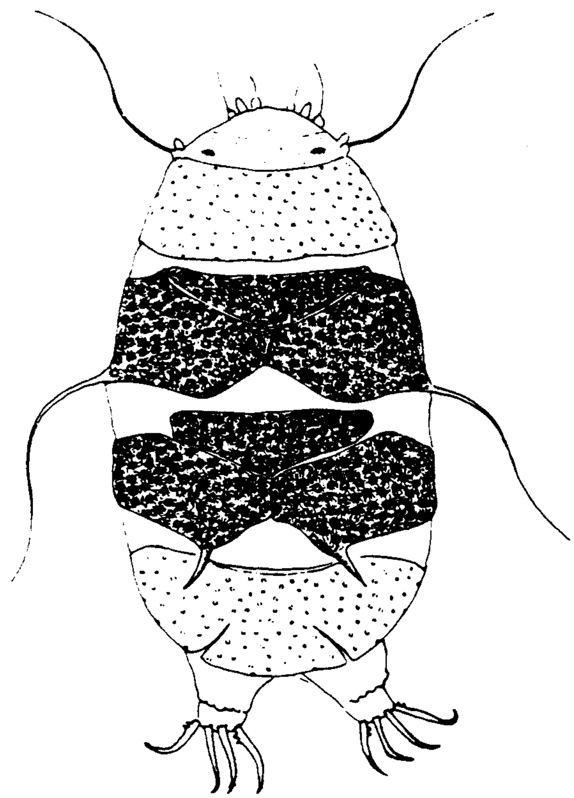


Fig. 191 - *E diploglyptus* Durante & Maucci. Dorsal view (from Durante and Maucci).

without spine. The external claws of the first three pairs of legs may have a small straight spur, near to the base, while on the 4th pair the spurs of the external claws are two, straight, slightly divergent. The internal claws of all the legs are smooth, without a trace of spurs. Lacking also a true dentate collar, substituted by a crenated crest.

The species has been found in a single locality, at Kanfarnar (Istria).

ECHINISCUS DIVERGENS Marcus, 1936 (Fig. 192).

Size not indicated by the author (Murray, 1913, which he named *Echiniscus spec.*), red, with indistinct sculpture. Median plate 3 present.

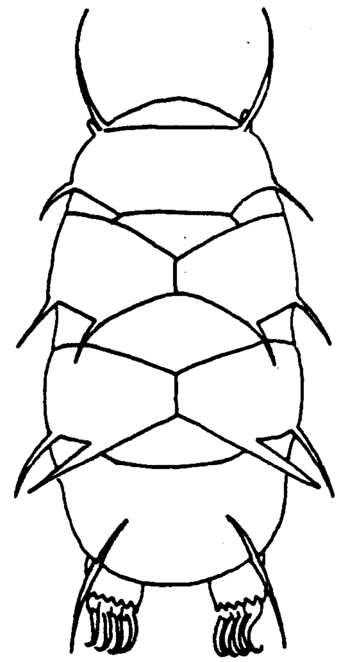


Fig. 192 - *E. divergens* Marcus (from Marcus, redrawn).

Laterally, besides cirrus A, there are spines B, C, D, E, all curved, of which the first two have medium length and the last two are longer; dorsally curved spines C^d, of medium length, and wide spine D^d, much longer, strongly divergent toward the exterior. Fourth pair of legs with dentate collar.

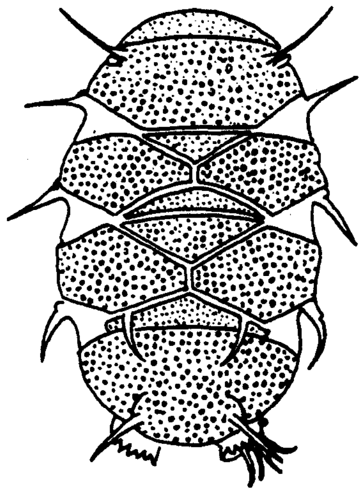
E. divergens was collected in Peru, or else Bolivia (without greater specifications).

ECHINISCUS DREYFUSI de Barros, 1942 (Fig. 193).

Length about 150μ, color orange, eye spots red. The sculpture is a regular granulation, finer on the median plate 3 (present), on the rostral part of 2, and on caudal part of the terminal plate; it is instead coarser on the remaining plates, where -- however the remaining regularly distributed -- the sculpture is composed of granules of different size. The terminal plate is not facetted and has the two usual laterocaudal incisions.

The lateral appendices, besides cirrus A, are spines B, C, D, E, with bulbous bases; dorsally there are only short spines D^d, having smaller size

Fig. 193 - *E. dreyfusi* Barros. (from de Barros, redrawn).



than those lateral. Internal claws without spurs, the 4th pair of legs with dentate collar, composed of about 7 sharp teeth.

The species is known only from Brazil (State of Sao Paulo).

ECHINISCUS DUBOISI Richters, 1902 (Fig. 194).

Length up to 250μ, red or orange; the sculpture of the plates is a dense punctation, composed of dots of different size, between which some are also very large, having the appearance of small depressions. The median plate 3 is present, or at least there is a sculptured zone, posteriorly to the second paired plates; the paired plates may be entirely sculptured, or else have smooth transverse bands; the terminal plate is not facetted and has the usual two notches.

The lateral appendices -- besides cirrus A of 80μ (in animal of 250μ) and elongated clava of about 15μ -- are spines B, C, D, E, of which B is in general straight, shorter, and may even be lacking, while C, D, E have greater length, however very variable; the dorsal appendices are spines C^d and D^d, positioned between the posterior angles of the paired plates and the median line, of equal or different size (for example, $C^d = 12\mu$; $D^d = 50\mu$). All these spines are very characteristic, because clearly dentate, sometimes with small notching, sometimes instead with 3-4 large thorns; however the dorsal spines may even -- all or in part -- be smooth.

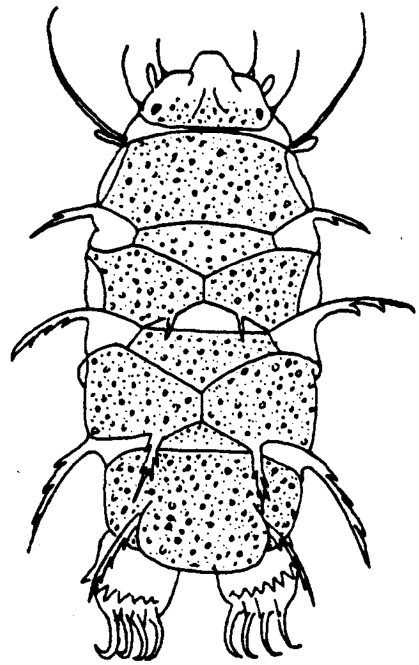


Fig. 194 - *E. duboisi* Richters (from Murray, redrawn).

Internal claws with, or without, spurs; fourth pair of legs with dentate collar, composed of long and slender sharp teeth (e.g., 15), basally separated between them. The oval eggs are deposited in the exuvium.

The species was collected in Australia (Blue Mountains and Queensland), Java (up to 3,000 altitude), Krakatoa, South America (Brazil, State of Sao Paulo), Galapagos Islands, New Guinea, and South Africa (Territory del Capo). Typ. loc.: Java.

ECHINISCUS EGNATIAE Durante Pasa and Maucci, (Fig. 195).

Length up to 470μ, usually about 400μ. Color yellow- orange, sometimes colorless. Eye spots absent. The sculpture is very regular, composed of small, very close depressions, in outline irregular stars, between which appears small round dots, very sparsely scattered. The sculpture is more coarse on the terminal plate, which is facetted. The unpaired 3 is absent.

Buccal cirri filiform, with bulbous base, the external longer than the internal. Cirri A rather short (60μ). The lateral appendices are long spines C and D (38 and 30μ in the holotype), slightly curved: the length

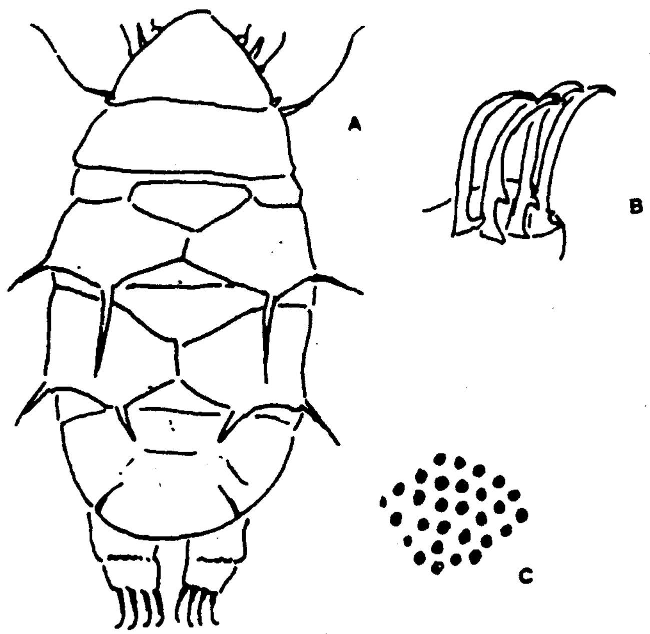


Fig. 195 - *E. egnatiae* Durante Pasa and Maucci. A, habitus; B, claws of the 4th pair; C, details of the sculpture (from Durante and Maucci).

is somewhat variable and there is sometimes some asymmetry. The dorsal appendices are robust spines C (similar to those of *E. granulatus*, but sometimes rather slender), 80 to 100μ long, and short, obtuse, robust spines D, 15-45μ long. There is no spine E.

The first pair of legs has a short, triangular spine. The 4th pair has a papilla and a dentate collar of 9 obtuse teeth, very short and irregular. The internal claws have a large, robust spur; the externals a slender straight spine, always present on the 4th pair, present or absent on the other legs.

The species has been found, with a very abundant population, in Greek Thrace, at Mesti (in the neighborhood of ancient Egnatia road).

ECHINISCUS ELEGANS Richters, 1906 (Fig. 196).

Length about 182μ, eyed. The sculpturing is spread over not only all the plates, but also on the cuticle between them, and is composed of densely distributed granules (less dense on the scapular plate), connected

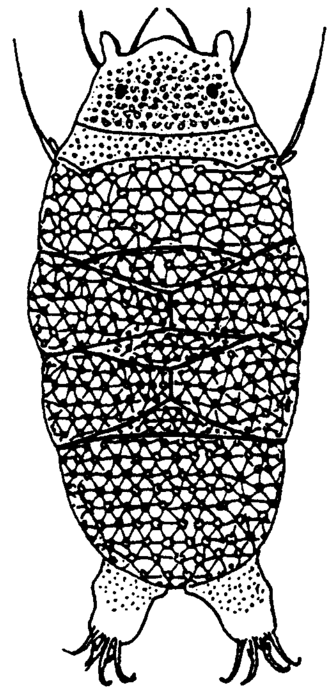


Fig. 196 - *E. elegans* Richters (from Richters, redrawn).

by lines so as to form a hexagonal design, which resembles a small wheel with six spokes and which also calls to mind the "network of points" of embroidery.

The sculpture of the cephalic zone is different: in the rostral zone there is a coarse granulation, followed caudally by a slender smooth transverse band and then another transverse band with fine punctation. Median plate 3 absent, but there is sculpture in that area. The two incisions of the terminal plate are poorly developed.

Cephalic papillae rather long (6μ); the only lateral appendages are cirri A. The fourth pair of legs are finely granulated and do not have dentate collars; the internal claws have a short curved spur.

A single example of this species was collected in southern Japan, near Nagasaki.

ECHINISCUS EVELINAE Barros, 1942 (Fig. 197).

Size 185--200μ, color red or orange, eyes red. The sculpture is a dense granulation, with granules of two different types -- larger and smaller -- variously distributed, which leaves free and smooth a transverse band on the paired plates II and III; also the cuticle between the plates is sculptured. Median plate 3 absent. The terminal plate, besides the two usual notches, bears two other furrows, totally unusual in the genus *Echiniscus*: these supplementary furrows are positioned -- one per side -- between the notch and the lateral margin.

Cephalic papilla large, cirri A normal; the only lateral appendices are the long filaments E (98-220μ); dorsally small teeth C^d and short spines D^d, which may however be lacking in both the positions. The 4th pair of legs have dentate collars (6-8 sharp teeth) and papilla, and has the external claws furnished with a small spine at the base; on the internal claws of all the legs there is one curved spur.

The species is known from different localities in Brazil.

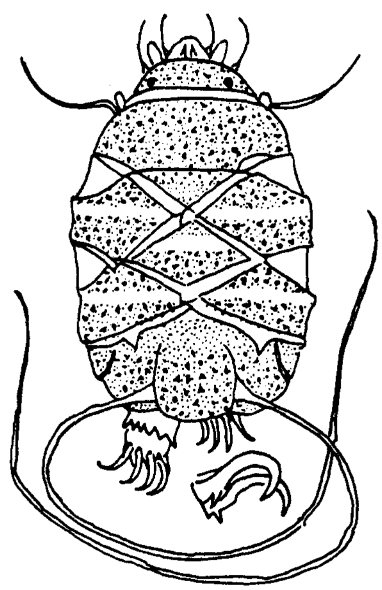


Fig. 197 - *E. evelinae* Barros (from du Boys-Reymond Marcus, redrawn).

ECHINISCUS FILAMENTOSUS Plate, 1888.

Length about 226μ; the lateral appendices, beside cirri A, are filaments B, C, E; dorsally there are two spines C^d *on each side* of the plate II, that is 4 in total, and spines D^d. Probably the notches are present on the terminal plate; a drawing of *filamentosus* has never been published and even the original description is incomplete.

The species -- easily recognized by the double number, compared to the usual, of spines C^d -- was collected in Switzerland, Germany, and Sweden. Typ. loc.: Marburg.

Iharos (1973) described, from Mongolia, a subspecies *E. f. mongoliensis*, and a "forma", *E. f.* forma *aspinosa*. Since these two forms do not have the double spines C^d, which are the principal -- if not only -- determining characteristic for the species, we think that *E. f. mongoliensis* can not in any way be distinct from *E. testudo*, and is therefore synonym of this last species which we here consider (see p. 475).

ECHINISCUS GLABER Bartos, 1937 (Fig. 198).
= *E. testudo* forma *glaber* Bartos, 1937.
= *E. testudo glaber* Ramazzotti, 1962 & 1972.

Length 250-270μ, color brownish-red, eye spots red. The plates are completely smooth, destitute of sculpture; the median plate 3 is present, but narrow and of reduced size. The only lateral appendices are the cirri A (40μ) and the long filaments E (81μ); dorsally there are spines (teeth) D^d. Claws large, without spurs; dentate collar on the fourth pair of legs, composed of fine obtuse teeth. Up to 4 oval eggs (24-26μ x 19-20μ) are deposited in the exuvium.

This species was considered by the author as a "forma" of *E. testudo*. The cuticle devoid of sculpture (this character very unusual in *Echiniscus*) seems to advise whatsoever against subspecific subordination.

E. glaber is cited only from Romania (Dobrugia) and from Bulgaria (Capo Caliacra).

ECHINISCUS GRANULATUS (Doyére, 1840) (Fig. 199).
= *Emydium granulatum* + *granulosum* Doyére, 1840.
= *E. crassus* Richters, 1904 et al.
= *E. fortis* Bartos, 1935.
= *E. abanti* Maucci, 1972.

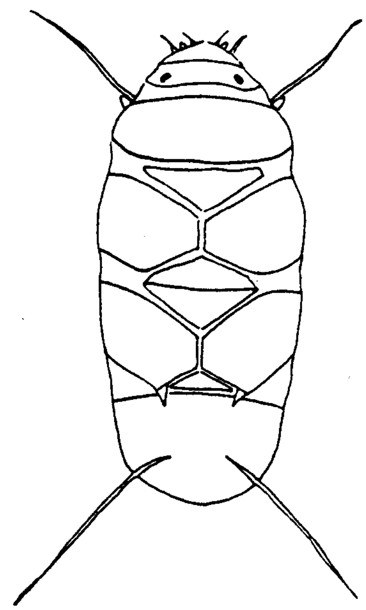


Fig. 198 - *E. glaber* Bartos
(from Bartos, redrawn).

Length 258-416μ, of red color, or brownish red, with red eye spots. Sculpture of the plates polygonal, that is apparently composed of granules enclosed in small polygonal areas, similar to that of *E. blumi*. Median plate 3 present. The lateral appendices -- besides cirri A of about 80μ -- are B, C, D, all filaments, of which the longest is C, or else D: there is always a small spine E, not always easy to see, in the notch of the terminal plate; the lateral filaments B are very often absent. The dorsal appendices C^d and D^d are usually long curved spines of about equal length, at times very robust, sword-shaped, other times more slender. Individuals in which the spines are of length and coarseness somewhat different were described as *E. abanti*. Exceptionally D^d may be absent, or else C^d may be filaments. The terminal plate, in general, is not facetted in the adults, while it is sometimes in the young.

Fourth pair of legs with dentate collar (12-14 teeth); internal claws with spurs, external smooth: individuals which have spurs on the external claws certainly do not belong to the species *granulatus*, as they do not belong to the subspecies *E. granulatus inocellatus*, with spurs on the external claws and dentate collar of 5 teeth, described by Mihelčič in 1938.

E. granulatus deposits in the exuvium from 3 to 5 eggs, oval or spherical, of red brown color and diameter of 55-62μ. The larvae of two claws, as soon as exiting the egg, measure 112μ and have only filaments

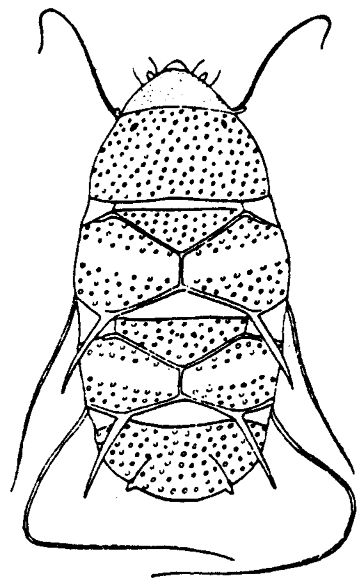


Fig. 199 - *E. granulatus* (Doyére).

A, D, and the small spines E, while C^d and D^d are very short: I have also observed larvae of 2 claws with A, D, and D^d, but with C^d not visible; the young of 4 claws may lack C, which appears as completely developed.

The species was collected in a great many localities from Europe (and common also in Italy), Turkey, and North America (U.S.A.: Colorado): but this last report is very doubtful and was almost certainly *E. blumi*, because spurs were described at the base of the external claws and dorsal appendices of different length (Higgins, 1959).

Typ. loc.: Paris.

ECHINISCUS HETEROSPINOSUS Maucci, 1954 (Fig. 200).

Length 144-304μ, dark red color. The sculpture is composed of pores of irregular polygonal outline not in contact between them: altogether, this type of sculpture calls to mind that of *E. blumi* or, better still, that of *E. spinuloides*. The cephalic plate is smooth in the rostral region and in the caudal, or else only in the last; the paired plates have a transverse median band not sculptured. Median plate 3 is absent. The terminal plate is very strongly sculptured and has two deep notches.

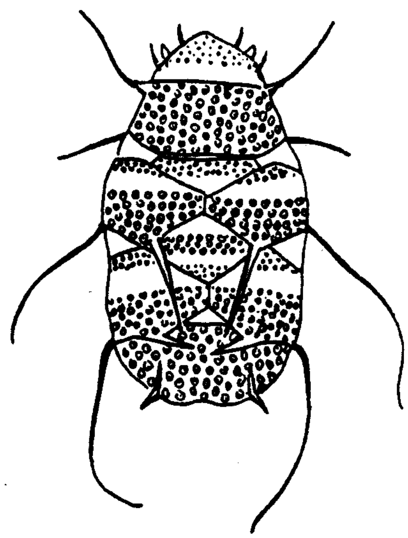


Fig. 200 - *E. heterospinosus* Maucci (from Maucci, slightly modified).

Laterally, besides cirri A, there are filaments B, C, D, of which the longest is usually D (from 54 to 131μ) and the shortest B (from 13 to 58μ). Cirrus A is enlarged at the base, in the shape of a bulb. In E there is always a robust spine. The dorsal appendices are robust spines C, similar to those of *E. granulatus*, and robust spines but very short D; these last are arranged in convergent manner toward the medial plane.

First pair of legs with spine, 4th pair with papilla and dentate collar of 8 teeth. The internal claws have a spur, the external are smooth.

E. heterospinosus is known from few localities in northern Italy, from Austria, and Carso Yugoslavia.

Typ. loc.: Collina (Forni Avoltri, Carnia).

ECHINISCUS HORNINGI Schuster & Grigarick, 1971 (Fig. 201).

Length of the holotype 250μ, width 125μ; eyes present. Dorsal plates as in Fig. 201. The sculpture is composed of polygons (diameter 1-1.7μ) with pores having diameter of about 1μ, irregularly distributed: it is a sculpture that is near to that of *E. becki*. On the other hand, internal buccal cirri of 28μ, external of 34μ, and cephalic papilla 10μ long and 6 wide.

The lateral appendices are filaments A, B, C, D, and E: the filaments D and E are clearly "barbed". The dorsal appendices are spines C and short spines D, similar to *E. heterospinosus*. There are also extremely small

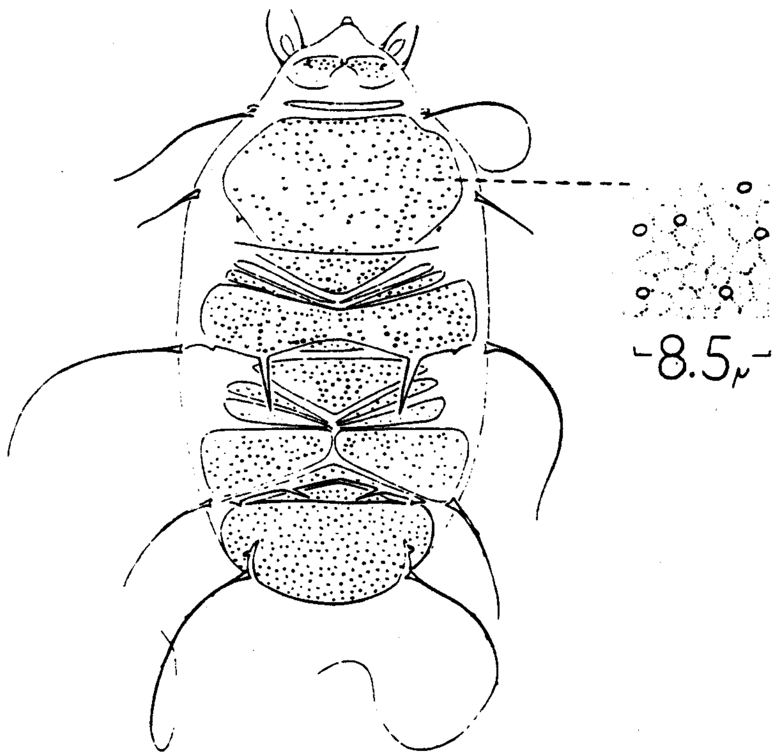


Fig. 201 - *E. horningi* Schuster and Grigarick. Dorsal view and detail of the sculpture (from Schuster and Grigarick).

dorsolateral teeth B', C', D', and E'.

The legs of the 1st and the 4th pairs have a papilla, and those of the 4th pair a dentate collar with 13 teeth. The internal claws have a spur, the external are smooth.

The species is known only from the United States (Oregon, California, Tennessee).

ECHINISCUS INOCELLATUS Mihelčič, 1964 (Fig. 202).

Length 480-530μ, color usually dark red, but sometimes bright red, eyes constantly absent. The sculpture is a regular granulation: the individual granules are rounded and do *not* have polygonal shape, present for example in *E. trisetosus*. Cirri A rather short; external and internal buccal cirri short and robust, cephalic papilla elongated, clava normal.

Laterally there are filaments C and D, of about equal length; dorsally spines C^d and D^d, in general of equal length, of which however the right or left may sometimes be shorter, as much as reduced to a tooth. Spine E very visible. The fourth pair of legs have a dentate collar with 5-6 distant teeth and the external claws have slender spurs at their bases; the internal claws have instead a more robust spur and more distant from the base. Eggs unknown.

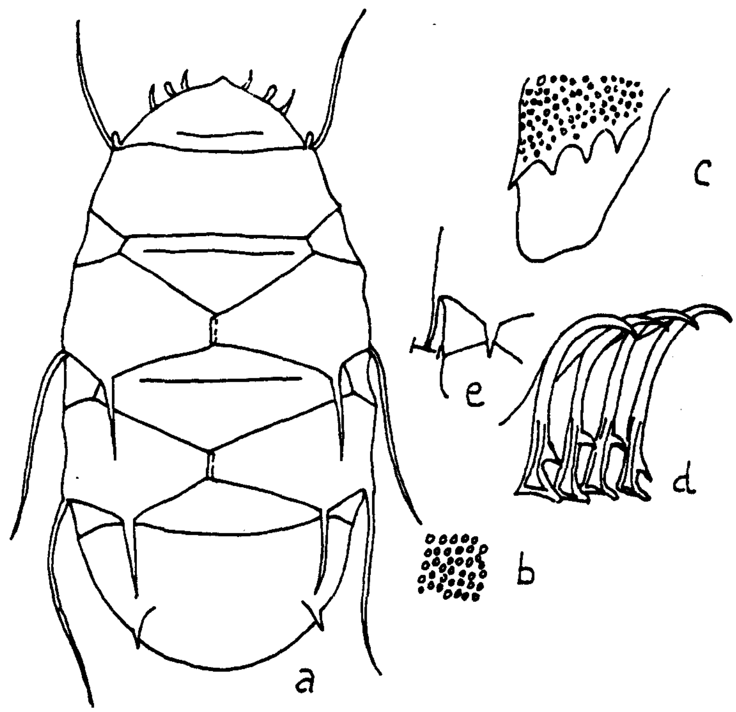


Fig. 202 - *E. inocellatus* Mihelčič. a, dorsal view; b, detail of the granulation; c, dentate collar; d, claws of the 4th pair of legs; e, variation in the length of the left appendix (from Mihelčič, redrawn).

At a quick examination the species may be mistaken for *E. granulatus*, owing to the equal length of the dorsal appendices C^d and D^d, but is different because:

- the granules of the sculpture are round and not polygonal;
- the eyes are always absent;
- the dentate collars have few teeth;
- the external claws of the 4th pair of legs have spurs.

E. inocellatus is cited from various localities of the Yugoslavia Carso and in the vicinity of Trieste, always in moss subject to strong desiccation, on calcareous rock.

It should be treated however as a rather rare species since our prolonged research, with the examination of thousands of samples from Trieste and Yugoslavia Carso, have not ever found *E. inocellatus*.

ECHINISCUS INSUETUS Mihelčič, 1967 (Fig. 203).

Length from 270 to 320μ; color red-brown, eye spots red. The sculpture is composed of granules and of depressions and is uniformly distributed on the plates, which does not have bands with sculpture more scarce or lacking. The median plate 1 is smooth, 2 is not really subdivided in two, but has a strong transverse fold, which does not however reach the extreme sides of the plate. Median plate 3 is present. The two notches of the terminal plate are little developed. The figure shows as present the sculpture with varied height of the tube of the microscope, or rather with observation at different focal planes.

Cirrus A of about 90μ, distally very slender and filamentous; 4th pair of legs with dentate collar (6-12 teeth); all the claws smooth, without spurs.

The species, which resembles *E. speciosus*, belongs to the "*arctomys* group", of which recently was described many new species -- in particular by Mihelčič -- but which (according to our opinion) are very difficult to distinguish from each other and from others of the group, because their separation is only based on differences, not always evident, nor easily observed, in the sculpture.

E. insuetus was collected in lichen on tree trunks and on rocks, in the Andes (Argentina).

ECHINISCUS JAGODICI Mihelčič 1951 (Fig. 204).

Length up to 200μ, color red, eyes present and black. The sculpture consists of a fine and regular granulation, which extends even on the median plates and on the margins of the paired plates; the median plate 3 is present; the terminal is facetted, but does not possess the two notches. Laterally, besides cirri A (length so as to reach the cephalic rostral margin), there are filaments D (70-80μ) and E (about 70μ); dorsally there are only spines C^d (25-30μ). Claws slender and long, internals with spurs.

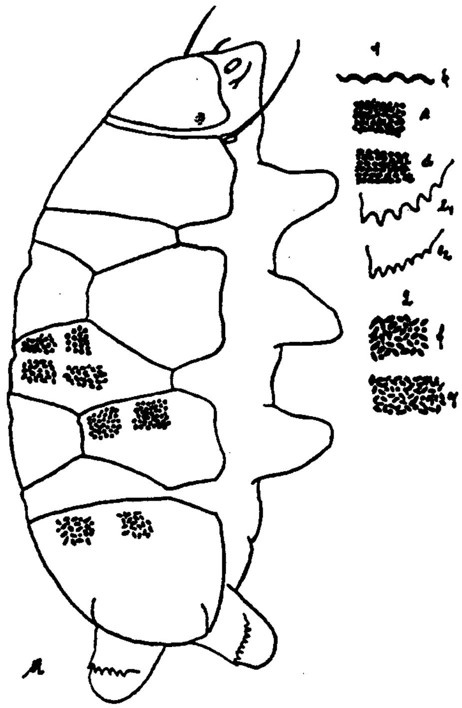


Fig. 203 - *E. insuetus* Mihelčič. a, lateral view; 1b, sculpture from high: surface of the cuticle; 1c, sculpture, with tube low, on the dorsal plates and on the median plate 2; 2, sculpture on the cephalic region, on the scapular plate, on the median 1 and on the posterior part of the median 2; 2f, with tube low; 2g, with tube high; e_1, e_2, two types of dentate collar dentation of the 4th pair of legs (from Mihelčič).

This species is known from a single report in Austria (eastern Tirolo), at about 2,100 m altitude, in moss on rock.

We think that there may exist strong doubt on the validity of this species, which probably is synonymous with *E. merokensis*.

ECHINISCUS JAPONICUS Morikawa, 1951 (Fig. 205).

Length about 220-240μ. Cirri A of about 92μ in an individual of 220μ and of about 80μ in another individual of 240μ. The sculpture is similar to that of *E. reticulatus*, that is composed of small depressions, with circular or hexagonal margins; the internal circular zone is finely punctated; the individual circles or hexagons have however larger size than in *reticulatus* (the size does not however seem specific). Terminal plate facetted and with the two usual notches. Legs of the 1st pair with spine similar to that of *reticulatus* and legs of the 4th pair with papilla; all the internal claws have an extremely small spur, visible only with immersion objective.

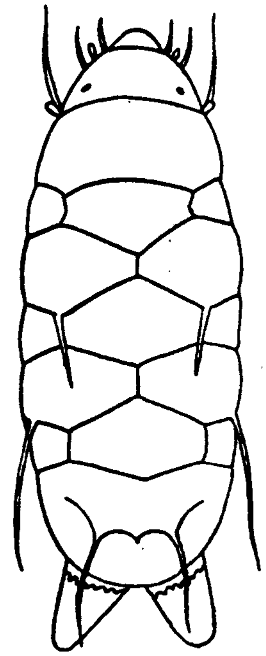


Fig. 204 - *E. jagodici* Mihelčič (from Mihelčič).

The eggs are deposited in the exuvium (usually two) and the larvae -- according to the author -- have 4 claws (?).

Unfortunately the original description does not furnish other details (for example absence or presence of the median plate 3, size of the elements of the sculpture, etc.) therefore the distinction of *E. reticulatus* remains based only on the smaller length of the lateral cirri A and on the larger size of the individual elements of the sculpture in *E. japonicus*. It is probably therefore timely to consider for the present the species as *spec. dubia*; it was found in moss on Mt. Ishizuchi, Ehime Prefecture (Japan) at 2,800 m altitude.

ECHINISCUS KERGUELENSIS Richters, 1904 (Fig. 206).

Length up to 270μ, red, eye spots red; the sculpture may be a granulation, or else a punctation, more or less fine and regular; the individual dots always have appearance of pores. The two paired plates may have -- or not -- a transverse smooth band, not sculptured; median plate 3 absent; terminal plate not facetted, with notches. Lateral cirri A of about 50-80μ, that is much shorter than in *E. wendti*. Fourth pair of legs

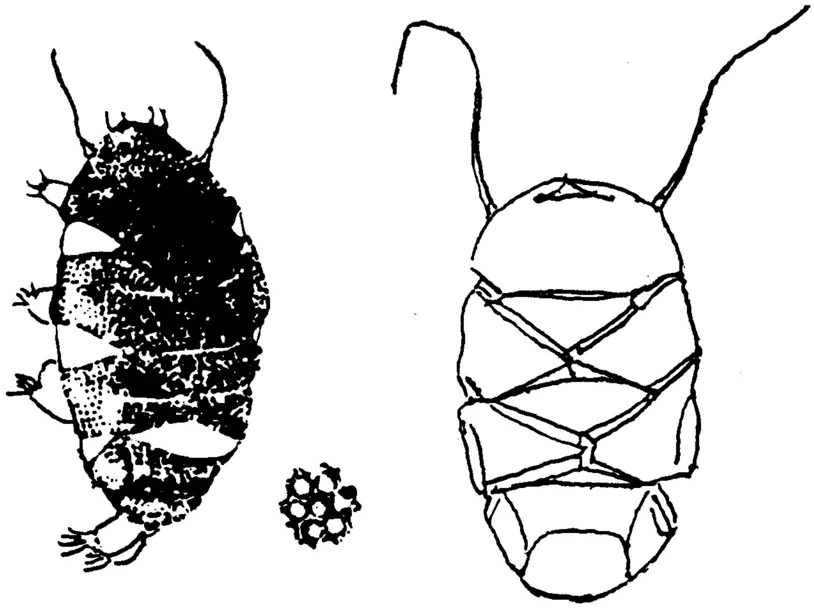


Fig. 205 - *E. japonicus* Morikawa.

with papilla and dentate collar, composed of slender sharp isolated teeth; claws of about 18μ, internal with curved spur. Eggs deposited in the exuvium.

The species belongs to the "*arctomys* group", but easily distinguished in as much as it is the only one of the group to have sculpture composed of sparse and distant pores. An example found in Istria, agrees to validify that this sculpture may be definitely of the "*testudo*" type.

E. kerguelensis was cited from Scotland, South-West Africa (1,600 m altitude), Australia (1,700-2,000 m), Desolacion Island (Kerguelen) (Typ. loc.), Greenland, Istria, and -- perhaps -- various localities in U.S.A.

ECHINISCUS KNOWLTONI Schuster and Grigarick, 1971 (Fig. 207).

Holotype 255μ long, 120μ wide, eyes present. The cuticle is sculptured with pores of diameter less than 1μ, irregularly distributed; between the pores the cuticle is smooth. Internal buccal cirri 9μ long, external 17, cephalic papilla 6μ long and 5 wide.

The scapular plate has two transverse stripes and three longitudinal with sculpture more dense. The terminal plate with 4 longitudinal stripes,

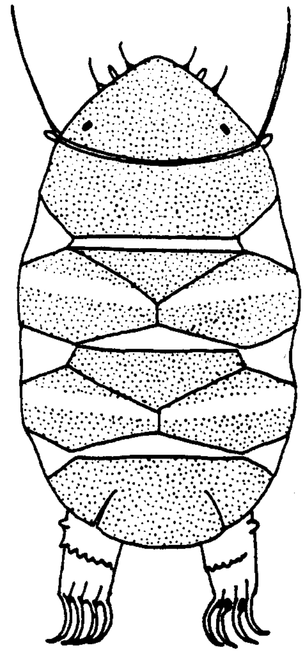


Fig. 206 - *E. kerguelensis* Richters (from Marcus, redrawn).

one very visible transverse stripe on the first anterior third and a dark stripe on the terminal third. The anterior surface of the plates II and III, of the median plate 2, and all the surface of the median plate 3 has irregular sculpture.

There are lateral filaments A, rather short, C and D about 120μ long; dorsally there are spines C^d and D^d of about 30μ.

Legs of the 1st and 4th pair with papilla; those of the 4th pair with dentate collar plain and narrow, with 9-12 teeth indistinctly separate; internal claws with large curved spurs and external claws with straight spurs.

The species was collected in the United States (Utah and Idaho).

ECHINISCUS KOFORDI Schuster and Grigarick, 1966 (Fig. 208).

Length 190μ; eye spots absent. Dorsal paired plates with indistinct transverse division. Median plates 1, 2, 3 present: there is indistinct transverse division of plate 2 (clearly visible only in some examples). Scapular and terminal plates with protruding bands, which intersect. First and second paired plates with an analogous longitudinal lateral band.

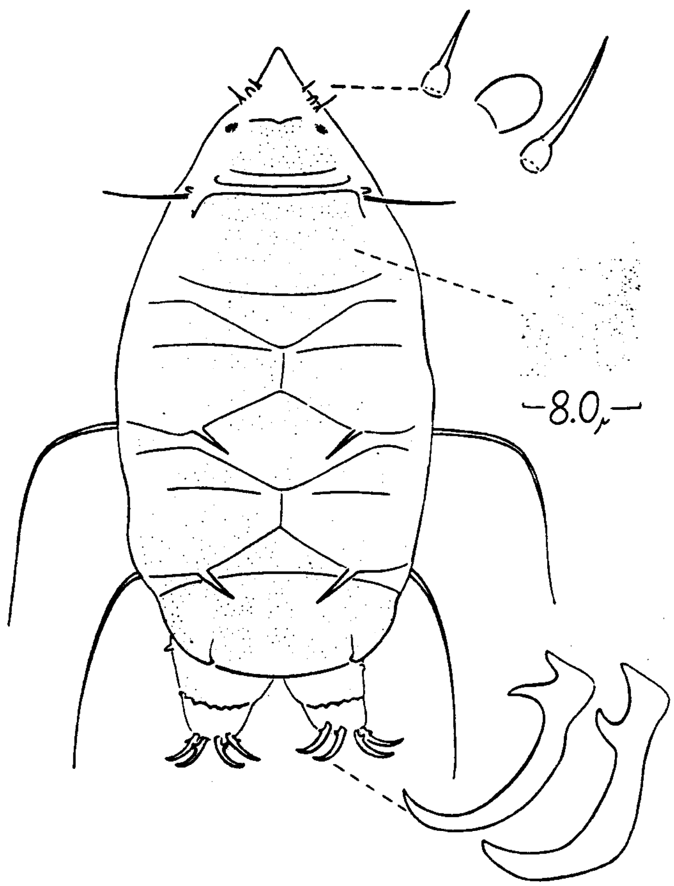
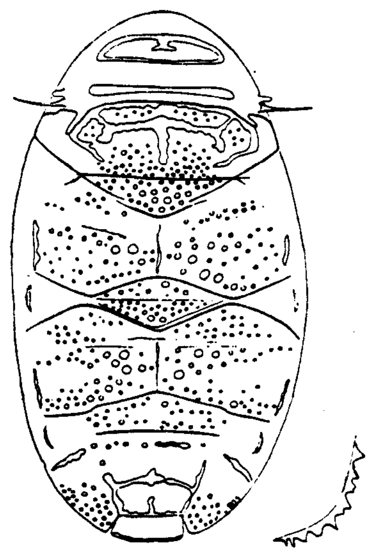


Fig. 207 - *E. knowltoni* Schuster & Grigarick. With details (from Schuster and Grigarick).

Notches of the terminal plate very weak. Internal buccal cirri 10μ, cephalic papilla 7μ, external buccal cirri 12μ. Cirri A of 22μ (or very short), clava of 5μ. There are no other lateral or dorsal appendices. The sculpture of the plates is composed of large granules, arranged irregularly and with diameter up to 2.5μ. Legs of the 4th pair with dentate collar (about 12 teeth) and internal claws with small spurs, directed basally.

The species differs from *E. tesselatus* by the subdivision of the scapular and terminal plates and by the much shorter lateral cirri A: it was collected in lichen on Santa Cruz Island (Galapagos) and, later, in Alabama (U.S.A.) and on the Andamane Islands.



6C

6A 6B

Fig. 208 - *E. kofordi* Schuster & Grigarick. 6A, dorsal view; 6B, dentate collar of the 4th pair of legs; 6C, photomicrograph of the cuticular sculpture (from Schuster & Grigarick).

ECHINISCUS LAPPONICUS Thulin, 1911 (Fig. 209).

Length up to 192μ; red, rarely colorless; the sculpture is a regular punctation, fine or very fine; sometimes the sculpture is more coarse and the individual dots, of larger size, appear composed of smaller dots. The two paired plates have a smooth transverse band, not sculptured; the median plate 3 is absent, however hinted at by a punctation of the cuticle, in the position which it would occupy; elsewhere the cuticle between the plates is not sculptured. Terminal plate facetted, with the usual two notches.

Laterally, besides cirri A, there are filaments B, C, D, E (the longer appendices are A and C; B may be lacking). Dorsally there are spines C^d and D^d of medium length, very near to the median line, often crossed like scissors; either in C^d, or in D^d, the spines may sometimes be 4 (2 per side), rather than only 2, this fact unusual in the genus *Echiniscus*. In dorsolateral position, at the posterior angles of the paired plates, there are filaments C' of medium length and short triangular teeth D'. First pair of legs with small spine, fourth pair with papilla and dentate collar, composed

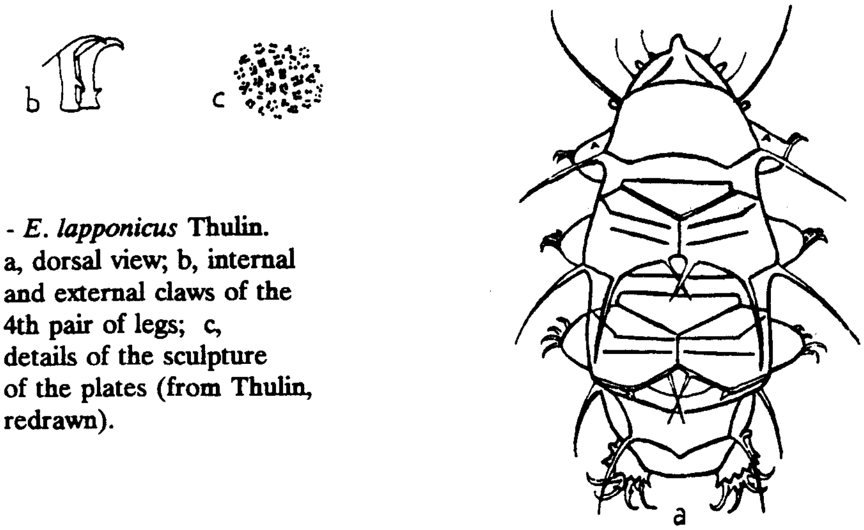


Fig. 209 - *E. lapponicus* Thulin. a, dorsal view; b, internal and external claws of the 4th pair of legs; c, details of the sculpture of the plates (from Thulin, redrawn).

of 5-6 triangular teeth; internal claws with spurs, external claws of the 4th pair of legs with minuscule straight spine. Eggs unknown; larvae with 2 claws of 95μ with only appendices A and E (filaments) and sometimes C^d, or else D^d.

The species was collected in Lapland (typ. loc.), in Switzerland, and in the Carpathians.

Examples lacking the lateral appendices B and the dorsal spines crossed like scissors, and having in D' long spines, were collected by Bartos in the Capathians, intermingled with the typical form, and described as *E. lapponicus* forma *carpatica*.

We should take up however as whether erroneous to homologate to the dorsal appendices C and D the small crossed spines of the nominate form, and to consider as dorso-lateral the spines positioned at the angles of the plates. In reality these last are true dorsal appendices, while the dorso-median spines are supernumerary.

ECHINISCUS LATEROSPINOSUS Rudescu, 1964 (Fig. 210).

This species was described as *E. spec.* by Murray in 1905 and named *E. spec. 10* by Marcus in 1928. The individuals measured about 250μ in length; the sculpture varies from one individual to another and is

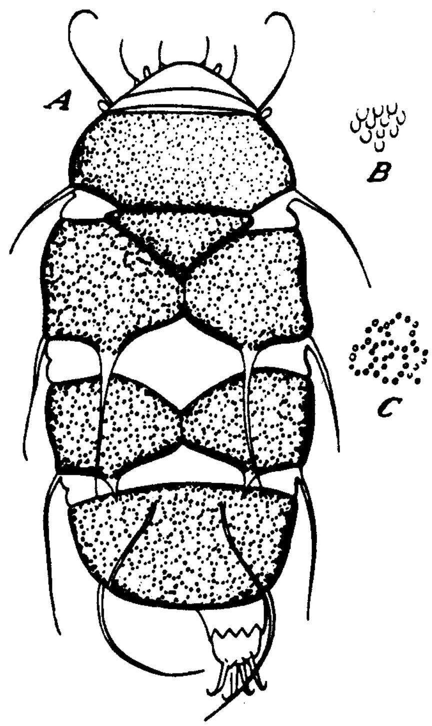


Fig. 210 - *E. laterospinosus* Rudescu. A, dorsal view; B, detail of the "fine" sculpture; C, detail of the "necklace of pearls" sculpture (from Rudescu).

sometimes composed of small granules arranged as a necklace of pearls (see *P. islandicus*), while other times consists of a fine punctation. Laterally there are appendices B, C, D, E (spines or filaments) with enlarged bases; dorsally long spines C^d, likewise with enlarged bases, and triangular teeth D^d (or else short spines with wide bases). Median plate 3 absent; terminal plate not facetted, with the usual notches. Oval eggs deposited in the exuvium.

The type of sculpture is generally one of the characters more constant in the genus *Echiniscus*: the fact that in this species the sculpture may be instead very variable from one individual to another induces us to consider for the present *laterospinosus* as *spec. inquir.*; it is in fact possible that the population observed was composed of two different species. It may be perhaps advisable to consider as "*laterospinosus*" only the individuals with the "necklace of pearls" sculpture, because the individuals with "punctation" sculpture can be distinguished from *E. columinis* only by some characteristics of secondary importance, for example the shorter cirri A (1/4 of the length of the body, rather than 1/3), the constant presence of the lateral appendices B, the terminal plate not facetted. But also in *E. columinis* (species very confusedly described) these characters are subject to variation, so that the only valid criteria for the distinction of the two species may sometimes be the diversity of the sculpture.

E. laterospinosus was collected in moss in sun in Scotland and in Romania.

ECHINISCUS LIMAI da Cunha & do Nascimento Ribeiro, 1964 (Fig. 211).

Small, maximum length 142μ; eye spots red. Plates very thick and with sculpture composed of a more or less regular punctation. Cirri A very short (14-15μ). Lacking median plate 3. Fourth pair of legs with dentate collar and papilla. Characteristic of the species -- besides the short cirri A -- is that the cephalic plate, the scapular, and the terminal are carinate and facetted.

The species was observed in lichen at Mahondo, Uige (Angola).

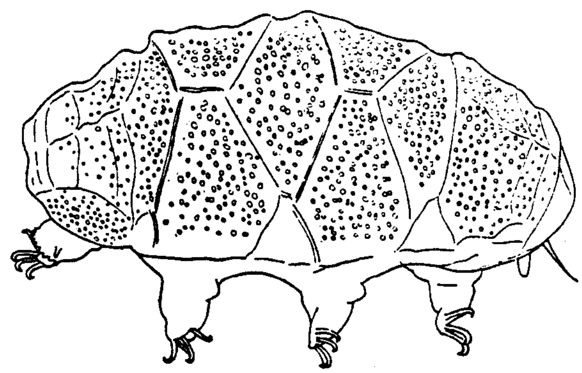


Fig. 211 - *E. limai* da Cunha and do Nascimento Ribeiro. Dorso-lateral view (from da Cunha and do Nascimento Ribeiro).

ECHINISCUS LONGISPINOSUS Murray, 1907 (Fig. 212).

Length about 200μ, eye spots red. The sculpture is a coarse and irregular punctation, composed of individual dots of different size, often distant between them and which have the appearance of depressions, or of impressions. Median plate 3 absent; terminal plate with notches and facetted: the caudal facet is medially subdivided in two.

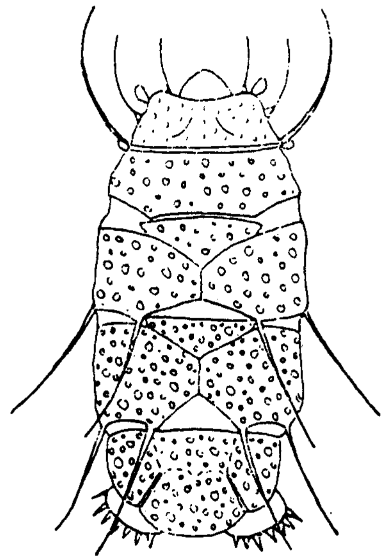


Fig. 212 - *E. longispinosus* Murray (from Murray, redrawn).

Cephalic papilla well developed, median (buccal) cirri long. Laterally there are slender and long filaments A (lateral cirri), C, D; dorsally filaments C^d and D^d, of about equal length, positioned usually at the posterior angles of the paired plates. Fourth pair of legs with dentate collar, composed of long transparent teeth, separated from one another; internal and external claws without spurs.

The species is known only from South Africa (Cape Colony).

ECHINISCUS LOXOPHTHALMUS Richters, 1911 (Fig. 213).

This is a *spec. inquir.*; length up to 336μ, eye spots black, not rounded as in the other *Echiniscus*, rather composed of two straight and elongated stripes of pigment (9μ length), between them rostrally convergent. The sculpture is a dense punctation not too fine (Richters) or a double granulation, composed of larger rounded granules, between which often exists smaller (Mihelčič). Median plate 3 absent; the two notches of the terminal plate are present, which is not facetted. Laterally, besides cirri A, there are filaments C and D of medium length; minuscule spine ("point") E, barely visible. Dorsally small teeth C^d. Legs of the 4th pair provided with dentate collar (about 4 teeth); internal claws with spurs and external with small basal spine; the claws are rather long (30μ in an animal of 336μ). Eggs unknown.

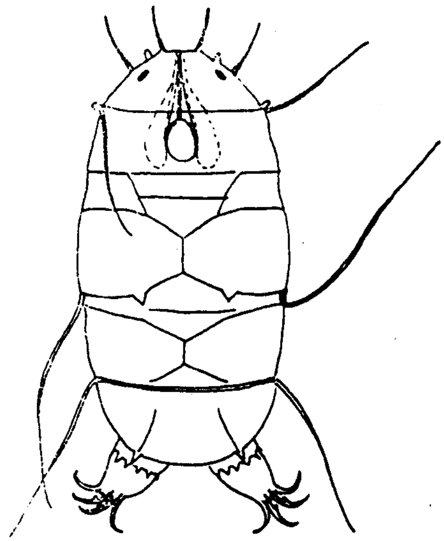


Fig. 213 - *E. loxophthalmus* Richters (from Marcus, redrawn).

This species was considered by Marcus (1936) as *spec. inquir.*; Mihelčič (1939) thought he found *loxophthalmus* in Yugoslavia (near the Postumia grotto) and gave an ample description.

More recently (1967) Mihelčič published the description of *E. postojnensis* -- informing -- following the study of new Austrian material -- that the species of his description of 1939 as *E. loxophthalmus* was instead the new species *E. postojnensis*.

E. loxophthalmus was cited only for northern Norway (typ. loc.) and South America.

ECHINISCUS MANUELAE da Cunha & do Nascimento Ribeiro 1962 (Fig. 214).

Length about 223μ, brown or reddish brown color, eyes red. The sculpture is composed of large dots (depressions) not very numerous.

Cirri A short, 23-27μ in the adults and 12-17μ in the larvae of two claws (87-102μ long); laterally there are spines C (10-16μ), D (10-15μ), and E (12-22μ); the spines E are rough or dentate, sometimes bifid on a single side. Dorsally there are spines C^d (10-21μ) and D^d (21-26μ), both dentate and notched on the margin. The larvae observed had C^d and D^d respectively of 3 and 7μ, or else only D^d of 5μ, while they do not show any

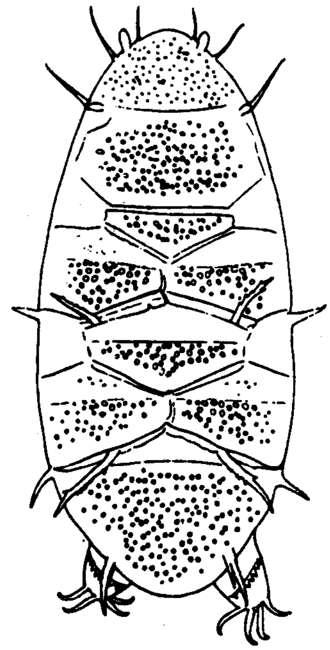


Fig. 214 - *E. manuelae* da Cunha & do Nascimento Ribeiro.

lateral appendices, or only E of 5μ.

Median plate 3 absent; terminal plate carinate. Fourth pair of legs with dentate collar, composed of robust triangular teeth, and papilla; small spine on the first pair of legs. The authors did not hint at the presence, or absence, of spurs on the claws.

The species was observed on Madera Island, in Canico locality, in lichen on the trunk of *Quercus*.

ECHINISCUS MARKEZI Mihelčič, 1971-72 (Fig. 215).

It is one of the larger species of *Echiniscus*: fully developed examples reach 320-450μ. Color dark red, eyes present, black.

The cirri A is long (as in *E. wendti*). The plates, either paired or unpaired, appear smooth, with high position of the tube. Lowering the tube, they appear as clear granules, sparse, orderly arranged; each granule is divided into three thickenings of the cuticle in the shape of leaves, arranged in rays, which in their total effect form a reticular design. On the

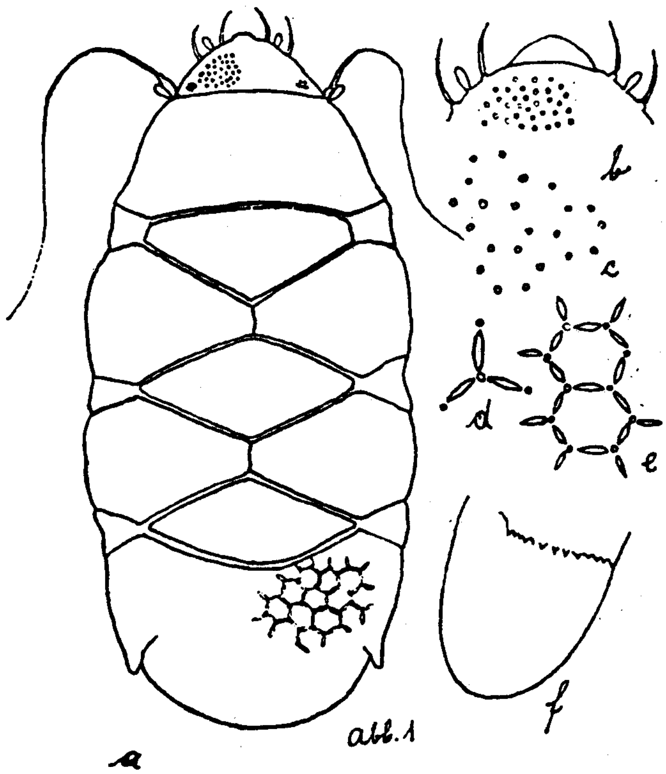


Fig. 215 - *E. markezi* Mihelčič. a, habitus; b, cephalic end; c, granulation of the plates; d, e, detail of the sculpture; f, legs of the 4th pair (from Mihelčič).

cephalic plate the sculpture is represented only by a light granulation.

Besides the cephalic appendices, there are no other appendices, neither dorsal nor lateral.

The unpaired plate 3 is present in the adult examples; in the young exists only a granulated space.

Legs medium long. Internal claws with spurs, external smooth. The dentate collar composed of numerous small subequal teeth, which may be continuous, or else here and there interrupted.

The species (which belongs to the "*arctomys* group") has been found in moss and lichen on rock and on tree trunks, exclusively in Argentina.

ECHINISCUS MARINELLAE Bartos, 1935 (Fig. 216).

Length up to 216μ, color brownish-red, eye spots black. The sculpture is a rather coarse granulation, composed of granules of polygonal outline, as in *E. blumi* or in *E. spinuloides*. Median plate 1 small, median plate 2 large and pentagonal, median plate 3 absent. The scapular plate has two teeth at its posterior angles; terminal plate with two notches, in each of which is found 2-3 teeth ("points"), facetted in characteristic manner, that is with two lateral facets and three median facets between the notches.

Buccal cirri normal, cephalic papilla pointed; laterally besides cirri A (46μ), there are filaments C and D (respectfully about 60 and 70μ); dorsally there are teeth C^d and D^d, also smaller teeth C' and D' in dorsolateral position. Minuscule spine on the first pair of legs and papilla on the 4th pair, which bears also a robust dentate collar, composed of 4 long teeth (5-9.5μ) with wide bases and somewhat distant between them; the length of the teeth may vary: the two internal are more developed, the two lateral smaller. Internal claws with showy spurs at about half of their length. Eggs reddish-brown, deposited in the exuvium; the larvae of two claws of 162μ have only A, D', and the "point" E; larvae of 190μ have also short filaments D and short teeth C^d.

The species seems to be very near to *E. spinuloides*, which usually has red eyes, but of which however I have seen populations with black eyes (analogous observations were made also by Petersen); it is distinguished however by the shorter dorsal appendices and by the lacking of B: this last

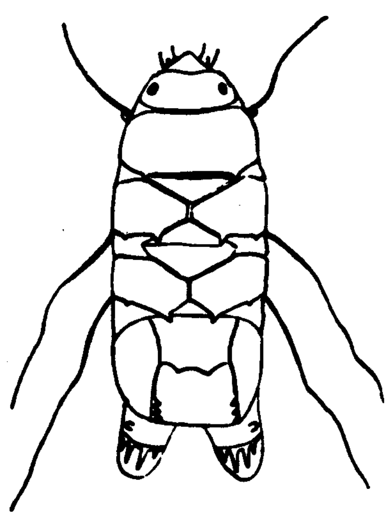


Fig. 216 - *E. marinellae* Bartos (from Bartos).

characteristic has not however great importance, because often B may be present or absent in *Echiniscus*. It remains in doubt -- pointed out by Peterson -- that the individuals examined by Bartos may not have been adults and may not have had then the completely developed appendices: in such case *marinellae* would be identified as *spinuloides*; this argument is spoken to again in the description of *E. spitsbergensis*, to which we refer the reader. From *E. loxophthalmus*, with granular sculpture or with punctation, *marinellae* is distinguished principally by having appendices D^d and terminal plate facetted.

The species was collected in Czechoslovakia at about 1,600 m altitude.

ECHINISCUS MAUCCII Ramazzotti, 1956 (Fig. 217).

Maximum length about 250μ, reddish color; the sculpture is a very coarse and irregular granulation, finer in the anterior part of the paired plates, where it is also partially lacking: it is also absent on a good part of the cephalic plate, with exclusion of a small rostral zone. The scapular plate possess very pronounced and protruding posterior external angles; the median plate 3 is absent; the terminal is clearly facetted and bears the usual notches. Cephalic appendices without special peculiarity: cephalic papilla large and elongated; lateral cirri A fairly long (about 90μ in an individual of 190μ), but much shorter than in *E. wendti*, clava well developed. Laterally there are two pair of characteristic cuticular projections, in hemispherical shape or slightly conical, positioned respectively between the first and second paired plates, and between the second paired plate and the terminal (they are therefore approximately from appendices C and D). These typical lateral projections -- which sometimes seem turned up at the external posterior angles of the paired plates -- may be more or less developed; Fig. 217 shows an individual mounted in Faure's solution, where it at once has a slight swelling: but they are however always very visible, even in the living animal, and are constantly present in the numerous individuals observed. There are no other lateral or dorsal appendices.

Internal claws of the fourth pair of legs with extremely small sharp spurs, similar to spines, positioned about a quarter of the length of the claws on the 4th pair of legs -- which bears the usual papilla and dentate collar -- and yet nearer to the base of the first three pair; the dentate collar is composed of 7-12 irregular teeth, of different size between them, often distant to the bases; the legs of the first pair have a small triangular spine.

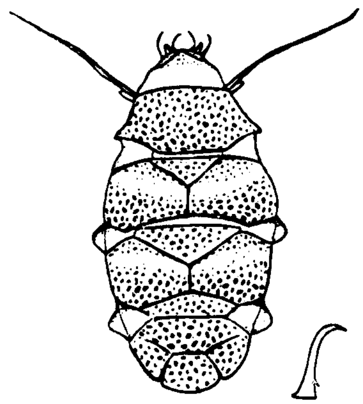


Fig. 217 - *E. mauccii* Ramazzotti. Dorsal view and detail of the internal claws.

The species is easily recognized by the two pair of typical lateral projections and by the external posterior angles of the scapular plate strongly accentuated; it was collected in moss and lichen on conifers in Wisconsin (U.S.A.) (typ. loc.) and later in Canada and in Tennessee.

ECHINISCUS MEDIANTUS Marcus, 1930 (Fig. 218).

Length about 320μ, color red or orange, eye spots red. The sculpture of the plates is a granulation more or less fine, at times also of "polygonal" or "hexagonal" type -- as for example in *E. blumi* -- sometimes weaker according to a transverse band on the paired plates II and III. The median plate 3 lacking, although there may be a zone of sculptured cuticle and well delineated at the sides, between the paired plate III and the terminal (IV). Laterally, other than cirri A, there are only filaments C, a little longer than cirri A (while in *E. bisetosus C* the lateral appendices C are spines and not filaments); there may be an extremely little spine and a short filament D, at one or both sides. There are present C^d (filaments) and D^d (short and wide spines). The first pair of legs has the usual spine and the fourth pair the normal papilla and dentate collar; internal claws with spurs; the straight spine, at the base of the external claws of the 4th pair of legs, may be present or absent. Eggs spherical or oval, brown-red color, deposited in the exuvium in numbers of 3-5.

The species belongs to the *canadensis-blumi* series, of which we have spoken in the description of *E. blumi*, to which we refer the reader.

Because of the ontogenesis on *E. trisetosus* (the more frequent species in the series) the lateral appendices D appear before the C, and as a rule more developed, examples furnished only with lateral filaments D have

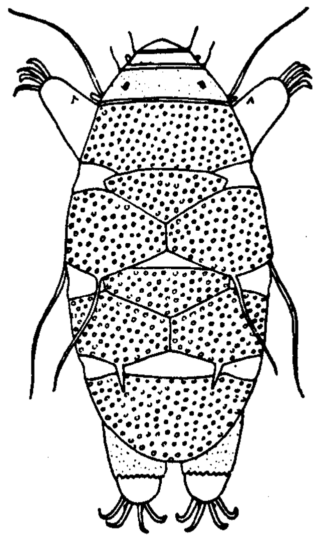


Fig. 218 - *E. mediantus* Marcus.

been considered as *trisetosus*. On the contrary we think they should be referred to as *E. mediantus* examples with lateral filaments C and D, when the C are markedly longer than D.

E. mediantus, which sometimes accompanies other species of the "*canadensis* series", is known from some localities in Italy, Scotland, Spain, Switzerland, Hungary, Greece, Turkey, and Portugal. In the Portuguese station the species was sometimes found in pure populations.

ECHINISCUS MELANOPHTHALMUS Bartos, 1936 (Fig. 219).

Length up to 432μ, in general however around 300μ; reddish-brown color, eye spots black. The sculpture is of the "polygonal" type, that is to say such that -- by a definite focal setting of the objective -- it appears composed of minuscule hexagons, contained within a circle. Median plate 3 absent; cephalic plate facetted and terminal plate with two deep notches, in which there is a minuscule tooth ("point") E. The lateral appendices are filaments A, B, C, D, of increasing length from A (70μ, in an individual of 270μ) to D (220μ, id.); dorsally filaments C^d (135μ) and D^d (80-120μ); dorsolateral teeth C' and D', very near to the base of the lateral filaments C and D.

First pair of legs with spine of 7μ, fourth pair of legs with papilla rather long and dentate collar composed of 4 sharp teeth and distant between

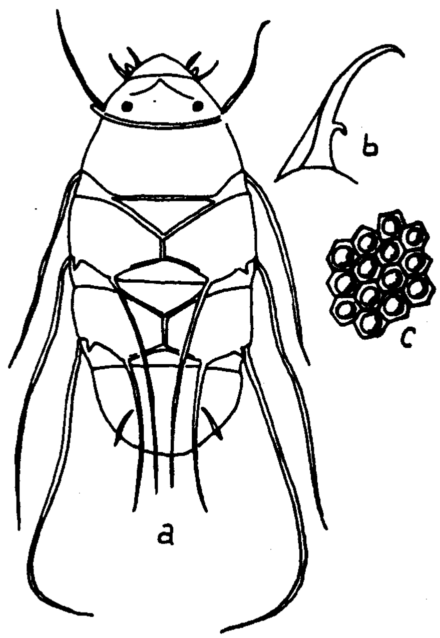


Fig. 219 - *E. melanophthalmus* Bartos. a, dorsal view; b, internal claws of the 4th pair of legs; c, detail of the sculpture of the plates (from Bartos, redrawn).

them, the external two of 8μ, the internal two of 11μ. Claws large, those internal with small curved spurs, positioned in the first proximal quarter, those external with small spine near to the base; the length of the claws is $20\text{-}22\mu$. Eggs reddish-brown, oval ($97 \times 76\mu$), deposited in numbers of 1 to 4 in the exuvium.

Take note of the great variability in the cuticular appendices of *melanophthalmus*: therefore the long filaments D^d may be substitute for wide and short teeth, the lateral filaments D may be lacking, it is not rare to be present asymmetry or double dorsolateral appendices.

The species is described here as current, but probably should instead be placed in synonymy with *E. spinuloides*: it differs especially by the black eye spots, rather than red, a character which does not seem however definite. For greater details of determination, see the above-mentioned in the description of *E. spitsbergenesis*.

E. melanophthalmus was observed in the Carpathians, in Romania and Istria.

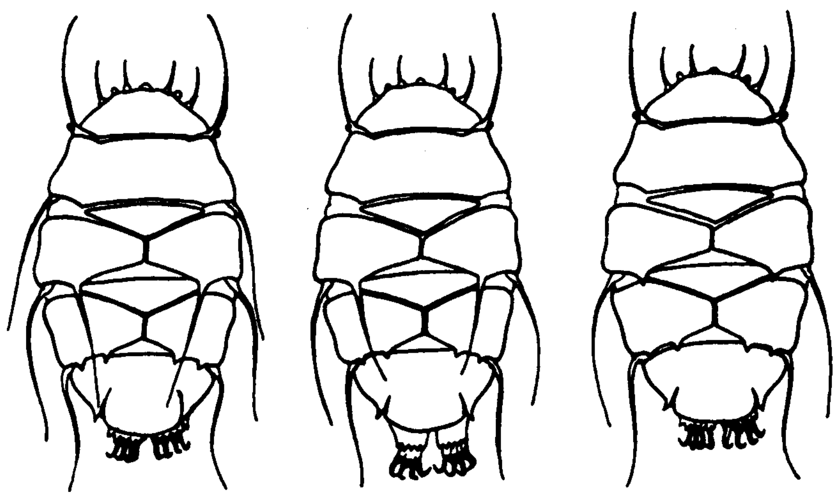
ECHINISCUS MENZELI Heinis, 1917 (Fig. 220).

Length about 260μ, eyes absent, sculpture of the plates "polygonal" type, as described for example for *E. spinuloides*; median plate 3 absent, but the cuticular zone, which it occupies, is in part sculptured.

Laterally there are filaments A, B, C, D, all of about equal length, and extremely short spine E ("point") in the notches of the terminal plate. Dorsally there are long filaments C^d, which may be lacking, and triangular teeth D^d with wide bases; in dorsolateral position smaller teeth D'. First pair of legs with spine; fourth pair with dentate collar, internal claws with curved spurs, positioned about at the middle of the claws, however somewhat distal.

It is not excluded that *E. menzeli* (species belonging to the "*spitsbergensis*" group) may be a variety of *E. spinuloides*: for a more complete discussion on the subject, we refer the reader to that subject in the description of *E. spitsbergensis*.

The species was cited for Italy (in the vicinity of Trieste, Carso, and Val Pusteria), for Hungary, Romania, and Yugoslavia (Istria).



a b c

Fig. 220 - *E. menzeli* Heinis. a, completely developed adults; b, c, stages of development (from Iharos).

ECHINISCUS MERIDIONALIS Murray, 1906 (Fig. 221).

Length 136-200μ, yellowish, sculpture of the plates very weak. Lateral cirri A have an "enlargement" (?) at the base, besides the usual clava. Median plate 3 present; terminal plate facetted and with notches, as in *E. merokensis*. Laterally there are cirri A and filaments C of medium length, extremely short spines D, which may be easily missed in observation, and finally long filaments E. Dorsally there are filaments C^d -- in general, length of twice that of the lateral C, but sometimes of about equal length -- and short spines D^d. On the first pair of legs is seen an obtuse tooth, while on the fourth pair is observed only the dentate collar, composed of few (usually 5) very wide teeth, which however may be lacking in the young individuals; internal claws with small spurs, curved toward the base. Eggs unknown.

ECHINISCUS MEROKENSIS Richters, 1904 (Fig. 222).

Length 205-230μ, red, rarely colorless or yellowish, eye spots red. Sculpture of the plates coarse, composed of points of various size and shape, the coarser with appearance of depressions or pores; between the elements and the other of the sculpture, that is between the single dots or pores, the plates appear practically smooth, even observed with the

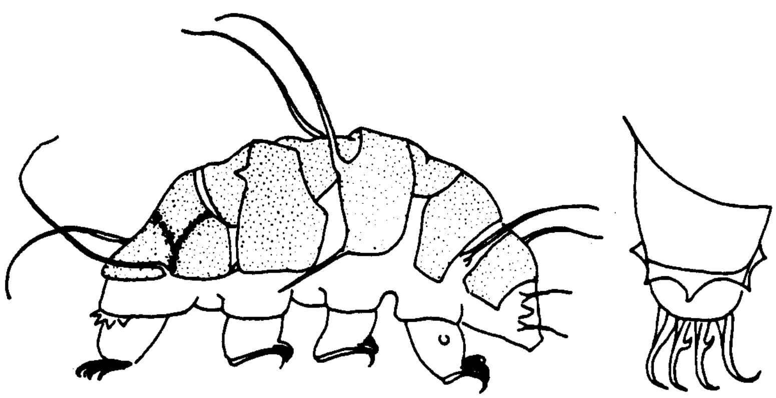


Fig. 221 - *E. meridionalis* Murray and detail of a leg of the 4th pair (from Marcus, redrawn).

immersion objective: only rare times, in *merokensis* of some localities, is noted an extremely fine and almost indistinct punctation, but may not be a clear granulation. Careful examination of the sculpture is then necessary to distinguish *merokensis* from *E. quadrispinosus cribrosus* lacking appendices B, which most often resembles, but in which between the pores, or depressions, of the sculpture resembles, but in which between the pores, or depressions, of the sculpture (which are -- according to records -- of different size) there is a uniform granulation (see Fig. 247A) very evident especially with phase contrast.

The median plate 3 is present and well developed; the paired plates II and III sometimes have a transverse band less sculptured and longitudinal fold at the anterior margin. The terminal plate is always facetted, sometimes clearly, sometimes in manner less visible; often the scapular plate (I) has a transverse band -- at times also three longitudinal bands -- smooth, without sculpture; analogous design may be on the terminal plate (IV). The lateral appendices are filaments A, C, D, E; the dorsal appendices C^d may be filaments, or else a short spine, and so likewise D^d, which may become even an extremely short triangular tooth. It should be treated then as a species endowed with great variability, particularly in regard to the dorsal appendices: as other authors, we have seen individuals in which the spines C^d were long, short, or absolutely absent; as much happens to spines D^d, which can have length much greater than normal and equal to that of spine C^d, or else reduced in all

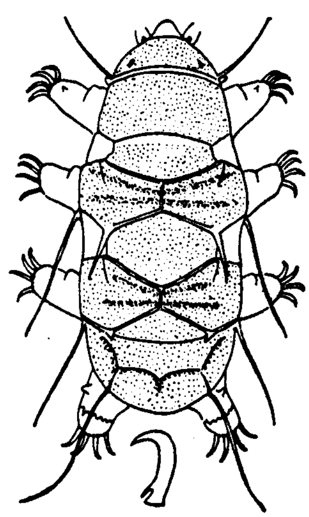


Fig. 222 - *E. merokensis* (Richters).

reports, as much as their total disappearance; there finally may be rare cases of asymmetry between the right and left dorsal spines. In the *merokensis suecicus* variety, for the purpose perhaps of reuniting with *merokensis* (see the relative description), Ramazzotti observed also spines B^d on the scapular plate (I).

First pair of legs with small spine, fourth pair with papilla and dentate collar, composed of 8-12 teeth; internal claws provided with curved spurs, external claws smooth. The eggs, reddish and oval (larger diameter 56μ), are deposited in the exuvium; the larvae of 2 claws $83\text{-}132\mu$ in general do not have dorsal appendices and have laterally only A and E, or else A, D, E.

Because it is treated as a greatly variable species, we always advise examining the largest number possible of individuals: we refer the reader also to the description of *E. merokensis suecicus* with regard to the distinction of this somewhat doubtful variety.

E. merokensis is wide spread and has been cited for numerous localities from Europe (including Italy), northern Africa, U.S.A., Spitsbergen Archipelago, and Turkey. Typ. loc.: Merok (Norway).

In the Carpathians was found examples identical to all the characteristics of the typical form (with which they were intermingled), however lacking every dorsal and lateral appendices (except cirri A). These examples (which included also egg-bearing exuvia) were considered by Bartos as a "forma" of the species: *E. merokensis* forma *inermis*.

Another form was described:

E. merokensis forma *suecica* Thulin, 1911 (Fig. 223).

Length up to 245μ. This variety is identical to the variety *merokensis* by the shape, the sculpture, the disposition of the plates, the appendices, etc.; it is only differentiated by the presence of lateral filaments B and by the size, sometimes a little bigger; perhaps also because appendices C^d are not inserted exactly at the posterior angles of the first paired plates (II), but a little more interior, that is, displaced toward the median line. During its growth and later molting, *E. merokensis suecicus* passes through a stage (lacking B), which is absolutely identical and indistinguishable from typical *E. merokensis*: it seems logical then to consider *suecicus* only as the last stage of *merokensis*, corresponding to its complete development (for greater details see Peterson, 1951, which reports also some data from Thulin, 1911, Bartos, 1941, Cunha, 1944). At the present time it is however perhaps premature to group as a single species typical *merokensis* and *merokensis suecicus*: in fact the insufficient number of observations, lack of observations, lack of significant statistics, does not agree to attain a definite decision in one sense or another. That is, for example, in 38 Italian mosses Ramazzotti has encountered 27 times typical *merokensis* in pure colonies, 2 times *merokensis suecicus*, likewise in pure colonies, and 9 times a mixture of the two forms; but the number of individuals examined in each sample was in general too insufficient to make a sure conclusion about the true existence of pure colonies of the forma *suecica*. Maucci has only found two times pure populations of the forma *suecica* (Turkey and Norway).

Also *merokensis* forma *suecica* shows an extremely great variability in the appendices especially dorsal, and it may be repeated what is said in the description of *merokensis*; Ramazzotti (1958) has observed, in two different Italian localities and in an abundant population of *merokensis*, 4 individuals with spines B^d on the scapular plate (Fig. 223 b), which certainly are *merokensis suecicus*, but which -- examined outside their populations -- no scholar of tardigrades would recognize as such (see, for this purpose, as stated in the section "Determination of the Tardigrada and Notes on the Use of the Keys"). We think timely to add that -- in rare cases of very abundant populations -- there may always be a mixture of *merokensis* and of *merokensis suecicus*: this leads one to think probably indicates the hypothesis that *merokensis suecicus* is actually the stage of complete

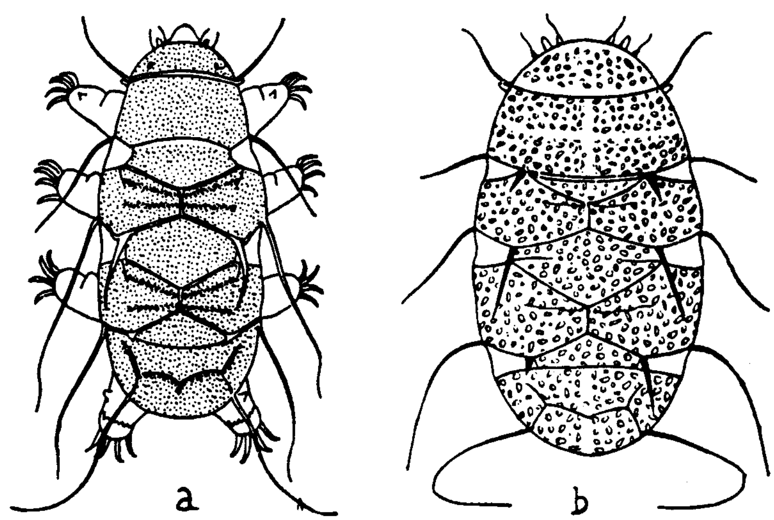


Fig. 223 - *E. merokensis* Richters forma *suecica* Thulin; a, typical; b, extremely rare anomalous form with spines on the scapular plate.

development of *merokensis*. About the distinction of *E. quadrispinosus cribrosus*, based on the type of sculpture, we refer the reader to the description of *E. merokensis* (see also Franceschi and Lattes, 1964).

E. merokensis suecicus was cited from numerous European localities (also from Italy), Greenland, and Angola, and Turkey. Typ. loc.: Sweden.

ECHINISCUS MIGIURTINUS Franceschi, 1957 (Fig. 224).

Length 140-230μ, colorless, eyes absent; sculpture rather coarse, composed of dots or of small depressions of different size and shape, of the type of that of *E. merokensis*; the sculpture is absent in some zones of the frontal plate, of the first paired plate (II), of median 2 and of the second paired plate (III). Median plate 3 absent, substituted by a granulation of the cuticle. On the terminal plate (IV), which has the two usual notches, the sculpture determines often a particular design, formed by the crossing of two horizontal lines with one vertical. Unique cuticular appendices present, besides cirri A, are the spines D^d. Fourth pair of legs with dentate collar, composed of small teeth of different size, arranged in irregular manner. The external claws are smooth, while internals bear near the base

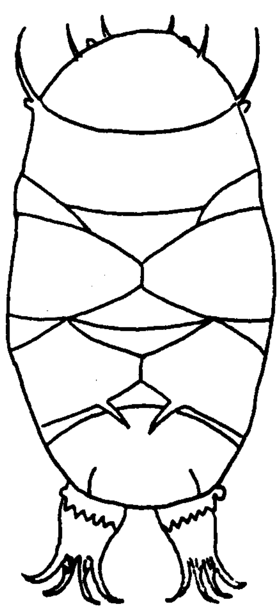


Fig. 224 - *E. migiurtinus* Franceschi (from Franceschi, redrawn).

an extremely small spur and difficultly visible, with appearance of an extremely slender and straight spine, turned downwards, that is toward the base of the claws.

Of this species are so far known only 19 individuals, collected in eastern Africa in lichen, at about 2,000 m altitude (Somalia, mountainous group of the Uar Medo).

ECHINISCUS MIHELCICI Iharos, 1973 (Fig. 225).

Size small or medium (122-382μ), color red orange, eyes absent. Sculpture weakly developed, composed of elements of equal size, regularly distributed, separated between them by free space, more or less rounded, or else slightly angular. With microscope tube in high position one sees clear circles with darker interior, in whose center is a clear dot; lowering the tube one sees clear granules, circular, distributed regularly and not in contact with each other.

Lateral cirri A of variable length, from 36 to 145μ; no other lateral or dorsal appendices; median plate 3 is weakly developed. The median plates are wide, the dorsal plates also show laterally a weak and interrupted border. Rostral margin of the terminal plate a little folded

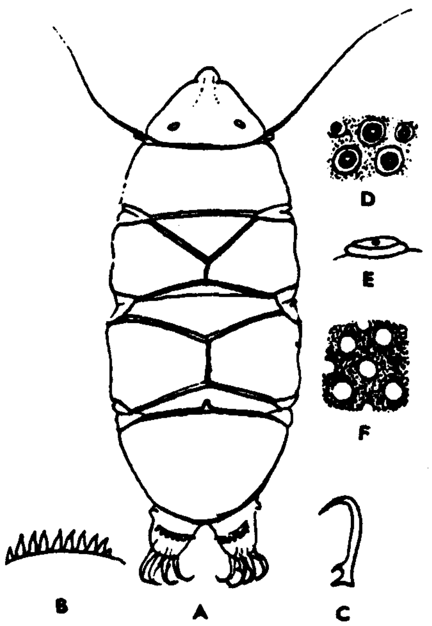


Fig. 225 - *E. mihelcici* Iharos. A, habitus; B, dentate collar; C, internal claws of the 4th pair of legs; D, E, F, particulars of the sculpture at different focal levels (from Iharos).

toward the forward, or interrupted at its middle; the terminal plate is not facetted and does not have notches. Legs rather short, dentate collar with numerous slender conical teeth (from 7 to 9). The 4th pair of legs has a small lateral papilla; claws of 22-30μ, without basal spines, those internal with curved spurs.

Three oval eggs deposited in the exuvium.

This species joins the numerous others of the "*arctomys* group"; the author writes that this species was examined also by Mihelčič, to which he submitted to vision.

E. mihelcici was observed in moss on trees, on Mount Pakjon (Korea) at 2,300 m altitude.

ECHINISCUS MILITARIS Murray, 1911 (Figs. 226, 227, & 228).

Maximum length 200μ, color red, sculpture composed of regular rows of granules or of small circular depressions, almost in contact with each other, which leave free and smooth from the straits transverse bands on the paired plates. Median plate 3 lacking; terminal plate with the usual notches, indistinctly facetted. Laterally, besides cirri A of about 50μ, there are very slender filaments B (50μ), filaments C, D (respectively 100 and 150μ), with wide bases and apices growing thin, and finally short, obtuse

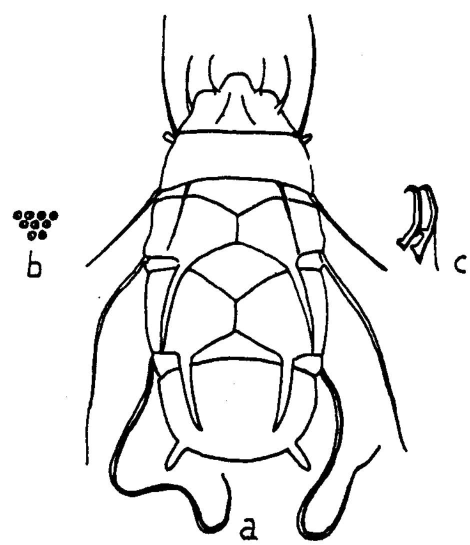


Fig. 226 - *E. militaris* Murray. a, dorsal view; b, detail of the sculpture of the plates; c, external and internal claws of the 4th pair of legs (from Murray, redrawn).

cylindrical spines E, sometimes a little swollen in the middle, with the appearance of a bolt or peg. Dorsally there are extremely slender filaments B^d on the posterior margin of the scapular plate and robust spines C^d and D^d, straight or barely curved, about 50μ long and in section nearly circular. Dentate collar of the 4th pair of legs composed of numerous sharp teeth, very long; large claws (about 25μ of length), the external smooth, those internal with small spurs. Eggs (2) deposited in the exuvium.

The aforesaid description refers to the *E. militaris* of the report in Ireland (Fig. 226), remaining the only for some ten years.

A second report given by Ramazzotti in 1955, in a moss at 2,400 m altitude in the western Dolomites (south cliff of Rosetta Peak) presents examples that differ slightly from the type, by the following characteristics:

- appendices E are not short and obtuse, rather they are robust spines of 26μ;
- the length of the animals is about 160μ, rather than 200μ.

In spite of these differences it does not seem likely to establish a new variety of *militaris*, having well noted the great variability of the genus *Echiniscus*, either by the lateral appendices, or by the size; we confine ourselves to furnish some specifics on *militaris* observations:

a) the sculpture is sufficiently similar to that of *E. spinuloides*; in Fig. 113 it is schematic, because the circles (or rather the polygons with

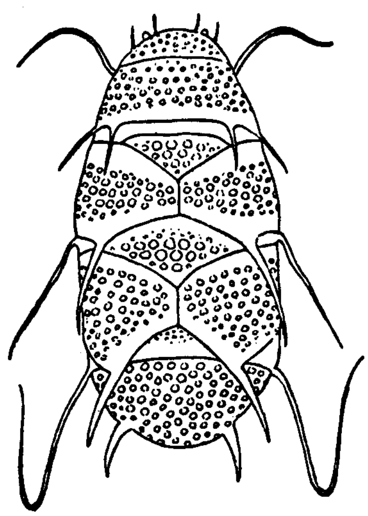


Fig. 227 - *E. militaris* Murray. Example from the Dolomites.

rounded angles) are almost in contact with each other; the largest diameter of the individual circles is observed on the median plates 1 and 2 and on the terminal plate IV, but reaches the maximum on the median plate 2;

b) in the position which maybe occupied by the median plate 3 (absent) there is a rostral zone sculptured;

c) spines D^d are extremely robust and very wide (from 4 to 6μ at the bases), of flattened section, rather than round; the average length in microns of the various appendices are the following: A, 60; B, 21; C, 58;

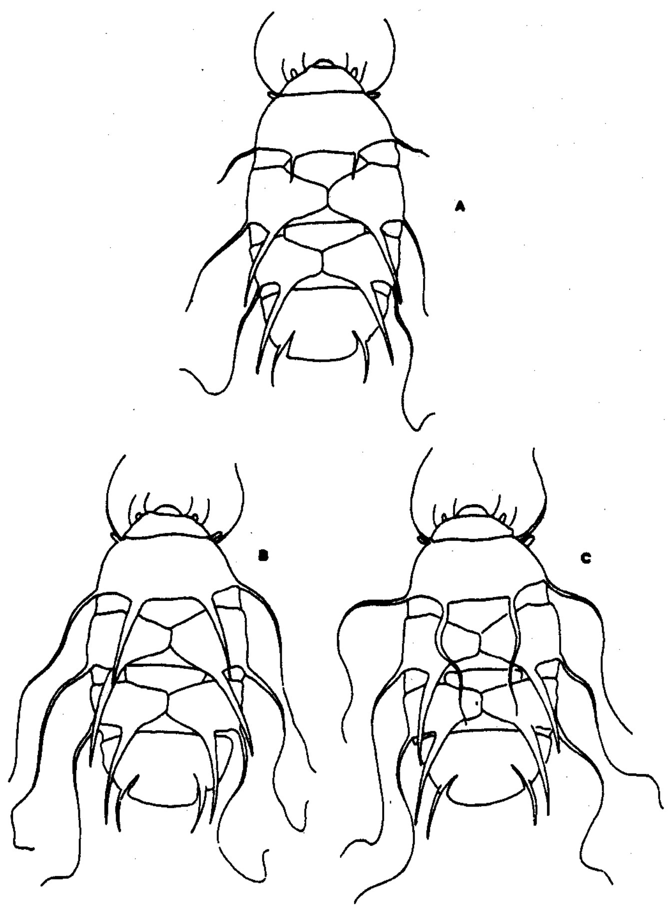


Fig. 228 - Varieties of *E. militaris*. A, *E. militaris militaris* Murray; B, *E. m. hexacanthus* Maucci; C, *E. m. hystrix* Maucci (from Maucci).

D, 105; E, 26; B^d, 14; C^d, 43; D^d, 34. The claws of the 4th pair of legs measures about 15-19μ; dentate collar is composed of 7-8 sharp teeth. The exuvium contains 3 eggs.

Numerous subsequent reports by Maucci, agrees at present to distinguish some subspecies, clearly differentiated:

E. militaris militaris Murray, 1911 (Fig. 228).

Modest size (from 140 to 200μ). Lateral appendices B are very short and dorsal filaments B are extremely slender and much shorter than the strong saber-shaped dorsal spines C and D. To this subspecies belongs the typical material of Murray and the three examples of Ramazzotti, as well as a numerous population of Bodo (Norway).

E. militaris hexacanthus Maucci, 1972 (Fig. 228).

Once described as *E. hexacanthus*. Size up to 300μ. Lateral appendices B are up to 140μ long (in an example of 270μ). Dorsal appendices B are robust, saber-shaped spines equal to length and robustness to C^d and D^d.

Of this subspecies was described different populations in Istria (typ. loc.), in Trieste and Yugoslavia Carso.

E. militaris hystrix Maucci, 1973-74 (Fig. 228).

Size up to 300μ. Lateral appendices B are longer than in the other subspecies (up to 170μ). Dorsal appendices B are robust, large filaments, considerably longer than spines C^d and D^d.

This subspecies appears in some populations of the Trieste Carso.[1]

[1] There was also described *E. militaris* forma *quadrispinosa* M. Bertolani, 1946: characterized by the absence of dorsal appendices B. The description is however very superficial, lacking any design, and Prof. Bertolani, interpolating, has communicated that his examples have been lost. In expectation of further reports this form should therefore be considered a *nomen nudum*.

ECHINISCUS MOLLUSCORUM Fox and Garcia-Moll, 1962 (Fig. 229).

Length 185-196μ, color orange or red, eye spots present or absent. The sculpture is a dense and strong granulation and the individual granules are larger and prominent in the central zone of the various plates, and especially on the terminal.

The lateral cirri A are very short (about 19μ) and its length is always less than double that of the buccal cirri (internal buccal cirri about 11μ, external 14μ). There are no other lateral appendices; dorsally exists minuscule spicules B^d on the scapular plate, visible with much difficulty; in dorsolateral position, on the first paired plate, are present spicules C', just as minuscule.

Median plate 3 is probably absent, because we can not perceive its lateral limits: however the space between the second paired plate and the terminal is strongly sculptured. The terminal plate is not facetted and the usual two notches are present, even if not always very evident. Fourth pair of legs with papilla and dentate collar, composed of teeth of irregular shape: the claws of this pair of legs are 14 to 19μ long and all four have at the bases a spur, which may however be lacking. The larvae of two claws measure about 98μ.

E. molluscorum was at first observed in the feces of the terrestrial gastropod *Bulimulus exilis*, collected in different localities in San Juan (Puerto Rico, U.S.A.). Over 886 snails examined, coming from 18 different localities, the author observed tardigrades in the feces of 2.1% of them.

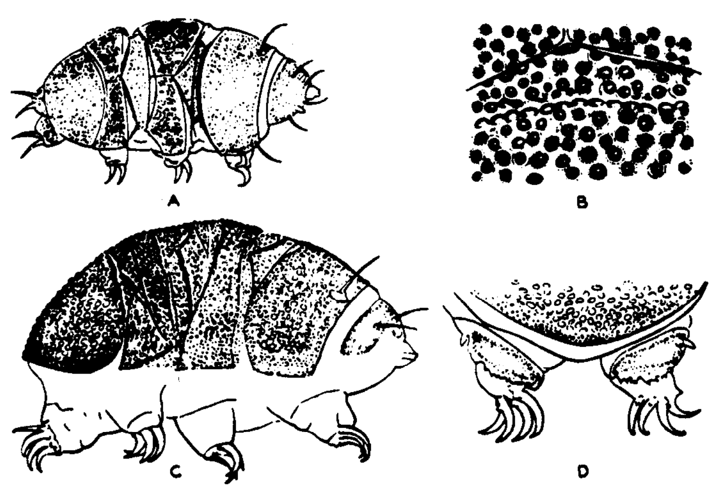


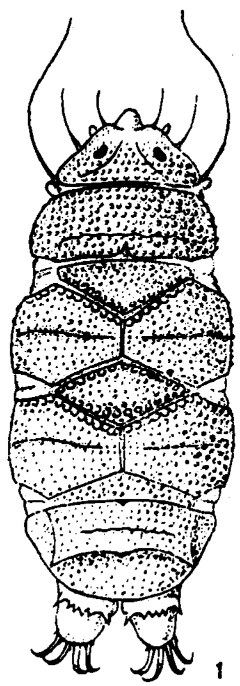
Fig. 229 - *E. molluscorum* Fox & Garcia-Moll. A, larva in dorsal view; B, cuticle between the second dorsal plate and the terminal plate; C, adult in lateral view; D, detail of the 4th pair of legs (from Fox and Garcia-Moll).

It was noted that the tardigrades remained active for two and a half days in the feces of the snails, placed on a microscope slide and covered with a cover slip.

Then (1964) *E. molluscorum* was also observed, with rather high density, on a garden concrete wall support, on Cacique Street in San Juan (Puerto Rico); more precisely in correspondence with a particularly humid zone of that same wall, which was manifest with appearance of blackish spots and accomplished by simply scraping the surface of the wall and gathering the concrete rubble, which was then placed in water for microscopic examination.

ECHINISCUS MONILIATUS Iharos, 1967 (Fig. 230).

Length 150-180μ; color clear yellow-orange; eye spots present. The sculpture is composed of granules of different size: on the cephalic and scapular plates the granules are coarser, and are on the contrary



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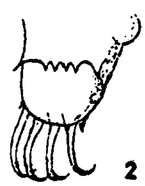

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Fig. 230 - *E. moniliatus* Iharos. 1, dorsal view; 2, dentate collar of the 4th pair of legs and tubercle (from Iharos).

smaller on the two paired plates and on the median plates 1 and 2. At the posterior margin of the median plate 1, therefore like the anterior margin of the two paired plates and of the median plate 2 there are large granules, in contact with each other and with pearl-shaped appearance.

The paired plate appears divided in two by a transverse line; the median plate 3 is indistinct and not well delimited. Lateral cirri A slender, filiform, 65-73μ long. Fourth pair of legs with small tubercles at the interior margin and dentate collar (6 teeth, of which the two at the lateral ends longer than the others). All the claws without spurs. Exuvia were observed with 3 eggs.

The species has been collected in moss on tree trunks of Mt. Kaindi (New Guinea).

ECHINISCUS MULTISPINOSUS da Cunha, 1944 (Fig. 231).

Length up to 190μ, eye spots red, color brown or reddish-brown.

The sculpture appears as a fine and regular net, of isometric polygonal spots, some of which, irregularly sparse, have a definitely more pronounced outline.

Median plate 3 absent, terminal plate carinate. Laterally, besides cirri A (36-62μ), there are filaments B, C, D, E; sometimes B and D are shorter, or even transformed into curved spines (C and E vary between 22 and 114μ, and E is always longer; B and D vary between 14 and 44μ, and

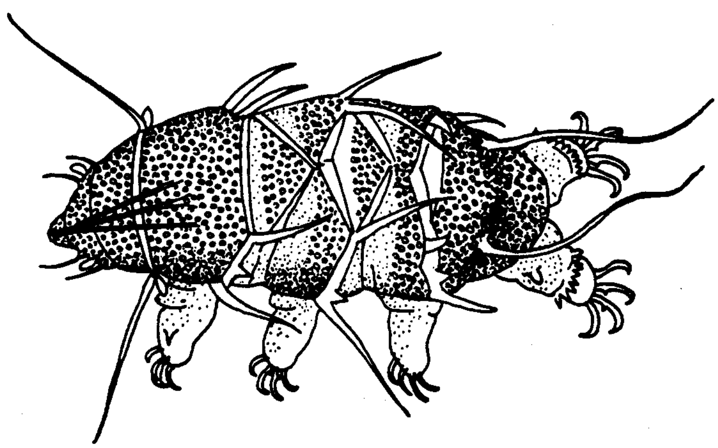


Fig. 231 - *E. multispinosus* da Cunha (from da Cunha, redrawn).

B is always longer). There are then small dorsolateral teeth B', C', D', E', positioned very near to the bases of the lateral appendices, as well as dorsal filaments B^d (4-30μ), C^d (20-52μ) and short, robust spines D^d (4-12μ). First pair of legs with minuscule spine and fourth pair with papilla and dentate collar, composed of numerous triangular teeth; claws long, those internal with spurs. Eggs and larvae unknown: smallest individual observed (130μ) already had 4 claws.

The species, which much resembles *E. oihonnae* -- but which is distinguished from this by the presence of the spines B^d on the scapular plate -- is known for Portugal, for California and Oregon (U.S.A.).

Maucci has also collected some examples at Forsa (northern Norway), in a moss containing also an abundant population of typical *E. oihonnae*. It is certainly possible that *E. multispinosus* may in reality be included in the limits of the variability of *oihonnae*, of which it may therefore be a synonym, or else a variety.

Typ. loc.: Viseu (Portugal).

ECHINISCUS MURRAYI Iharos, 1969 (Fig. 232).

Length 230μ, color orange-yellow. The sculpture is composed of rounded granules, of equal size and uniformly arranged. Lacking the median plate 3; terminal plate with the usual notches. Lateral cirri A of 55μ; all other lateral appendices absent. C^d (40μ) and D^d (30μ) present,

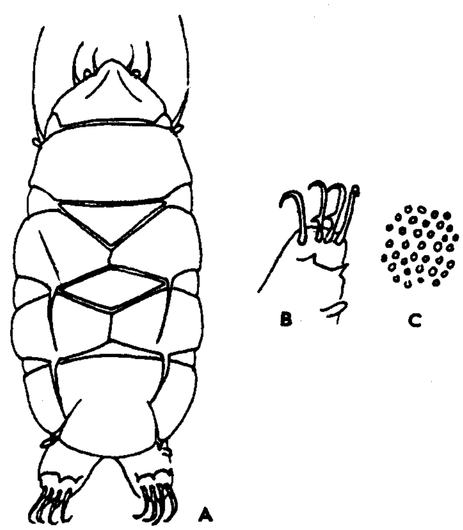


Fig. 232 - *E. murrayi* Iharos. A, dorsal view; B, claws of the 4th pair of legs; C, sculpture of the plates (from Iharos).

in the form of strong spinose filaments, slightly curved. Fourth pair of legs with dentate collar (4-5 teeth, distant between them) and papilla; internal claws with spurs, external smooth. Eggs have not been observed.

The author thinks that this species may be the same described in 1913 by J. Murray as *E. spec. 3*, collected in a single example in South Africa, of which however there is no drawing and which Marcus considers as *spec. dubia et inquir.*

E. murrayi was observed in leaf litter at 4,800 m altitude at La Cotacotani Lagoon (South America - Chile?).

ECHINISCUS NEPALENSIS Dastych, 1975 (Fig. 233).

Length 155-210μ. Eyes red. The cuticle has small granules (about 1μ) distributed irregularly, which become larger (1.5-2μ) on the terminal plate. There is also a larger granulation, composed of polygons bearing in the interior a dark ring: such sculpture corresponds to that of *E. blumi* and of *E. osellai*. Lacking median plate 3. Terminal plate with incisions, not facetted.

Internal buccal cirri 16μ, external 20μ. The cirri A are 30 to 47μ long. There are also lateral filaments C (20-70μ), and E (55-85μ). In addition dorsal filaments C (30-65μ).

First pair of legs with a small basal spine, 4th pair with a papilla and dentate collar formed of spines at times long (4μ) and few (6-7), at times shorter and more numerous (8-9): the internal claws have a spur curved toward the base, the external are smooth.

The author thinks this species near to *E. meridionalis*.

The species was found in the Lang Tang Valley (Nepal).

ECHINISCUS NIGRIPUSTULUS Horning, Schuster & Grigarick, 1978 (Fig. 234).

Length 150-170μ. Buccal cirri pointed, the internal 10μ long, the external 11. Eyes absent. The sculpture is composed of a weak polygonal design on the scapular plate; the other plates have pores irregular in size and spacing; and some large (3μ) opaque granules, also irregularly distributed.

First and 4th pair of legs with papilla; dentate collar with 10 teeth; internal claws with basal spurs.

The species belongs to the *arctomys* group, and is distinguished by the

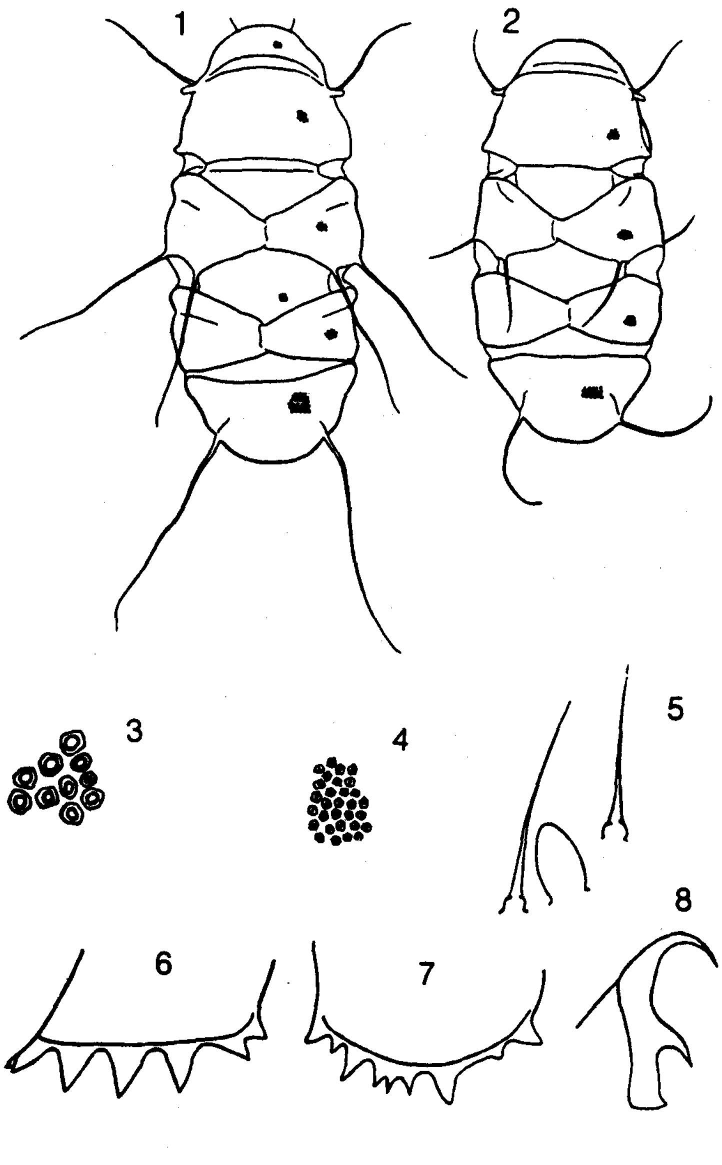


Fig. 233 - *E. nepalensis* Dastych. 1, adult; 2, juvenile; 3-4, dorsal sculpture; 5, cephalic appendices; 6-7, dentate collar; 8, internal claws of the 4th pair of legs (from Dastych).

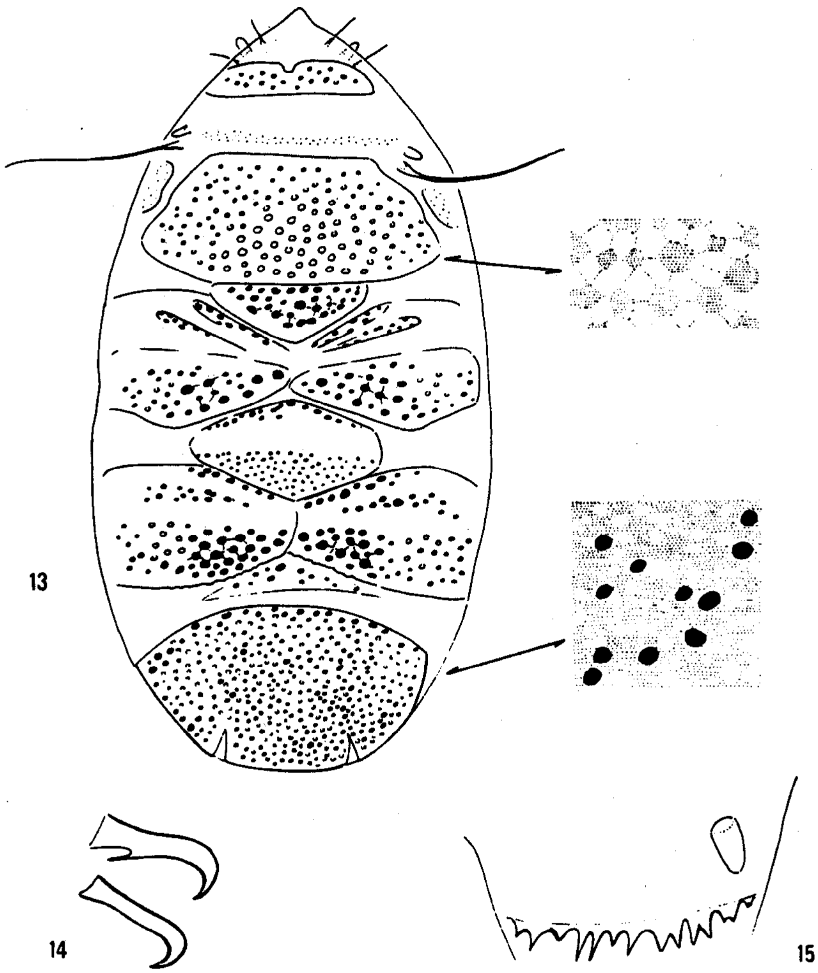


Fig. 234 - *E. nigripustulus* Horning et. al. 13, dorsal view and detail of the sculpture; 14, claws of the 4th pair of legs; 15, dentate collar (from Horning, Schuster and Grigarick).

irregular opaque granulation of the dorsal plates.

E. nigripustulus has been collected in some localities of New Zealand.

ECHINISCUS NOBILIS Mihelčič, 1967 (Fig. 235).

Length 280-320μ, color red-brown, eye spots red. Buccal cirri short, that is to say little longer than the cephalic papilla. Cirri A very long (202μ in an animal of 300μ). There is not a true cephalic plate, but it is substituted by a sculptured zone, which does not reach as far as the anterior margin of the scapular plate, but remains separated by a small space. Plates with margins not strongly developed, so that on the scapular plate -- all and regular sculptured -- the sculpture extends laterally beyond that plate, reaching the cuticle (without however forming a supplementary lateral platelet). The paired plates are sculptured on the first and the last third, while anteriorly and posteriorly are smooth.

There are only the median plates 1 and 2, while 3 is absent: the corresponding zone is very narrow and sculptured. The 1 has a transverse fold caudally on its first third; the 2 lacking the fold and is smooth. The sculpture of the median plates is finer (individual elements smaller), with respect to those of the dorsal plates. The terminal plate does not have true notches, but -- in their place -- only slender smooth space.

Characteristic of the sculpture, which shows different appearance according to the level of focal setting of the microscope; in general it is the same type on all the plates, but more marked on the terminal. With high position of the tube clear granules are seen, connected by slender clear spaces; it is derived from a mesh design, whose angles are composed of coarse and round granules; the interior is dark (dimples). In many zones the design appears regular, in many other irregular. Especially in the posterior part of the terminal plate the dark links are curved. With low position of the tube they appear, at first, as clear granules, round or elongated shape, irregularly arranged; at closer observation it is noted that the clear granules on dark background form polygonal figures, of which the same granules constitute the sides of the polygons, more or less regular.

The legs are strongly sculptured at the bases, with the same type of sculpture, especially on the 4th pair; these have a dentate collar with 5-6 teeth, often double (with 2 points) and less distant than their width. The external claws of the 4th pair have a sharp spur; the internal are smooth, with spurs.

According to the author, the species differs from *E. reticulatus* and *E. kerguelensis*: from *reticulatus* by the cephalic plate not clear, by the lack of facetting, of median plate 3, and of the notches of the terminal, as well as

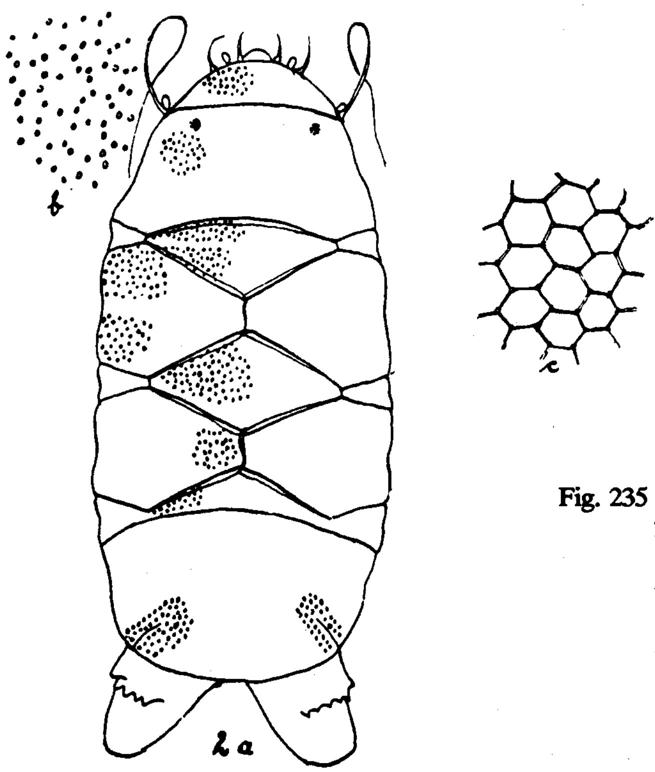


Fig. 235 - *E. nobilis* Mihelčič. 2a, dorsal view; b, aspect of the sculpture with tube high; c, aspect of the sculpture with tube low (from Mihelčič).

by the different sculpture; from *kerguelensis* by the longer cirri A, by the entire median plate 2, the different sculpture and the lack of the notches.

Also in this species -- as in others of the "*arctomys* group" described by Mihelčič -- and determined by the identification by an accurate examination of the sculpture, accomplished by different focal planes: it is feared that this is not always easy and that perhaps gives too suggestive interpretation.

E. nobilis was collected in material either from Yugoslavia Carso (Deinice) or from Italian Carso (Trieste, Doberdò), in very dry environment.

It should be treated as a rather rare species, in that systematic research conducted by Maucci on the Trieste and Yugoslavia Carso, with examination of thousands of samples, has not allowed discovery.

ECHINISCUS OIHONNAE Richters, 1903 (Fig. 236).

Length up to 270μ, color of red to dark brown.

The sculpture is presented as a regular fine reticulum, of polygonal mesh, isodiametric, some of which, irregularly distributed present the sides

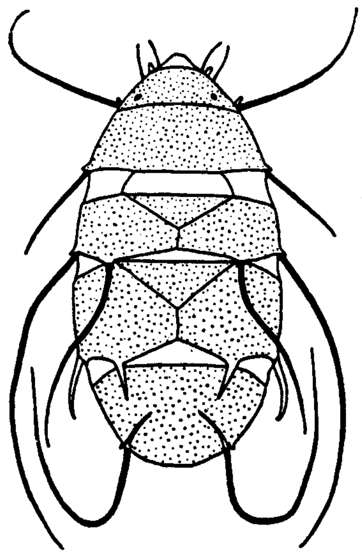


Fig. 236 - *E. oihonnae* Richters.

markedly more often. This sculpture is particularly developed on the scapular plate. On the paired plates the sculpture may be limited to the caudal zone; median plate 3 absent, terminal plate with the usual two notches, smooth or else more or less distinctly facetted. Stylet supports present (Marcus). Laterally, besides cirri A, exists filaments B, C, E, and curved spines D: with this arrangement of the appendices the longer are C and E, the shorter B and D. There are however some variants: B may be lacking, or else be a long spine, or else all the lateral appendices are filaments and B is absent. Characteristic of the species are the dorsolateral teeth B', C', D', E' (or even only some of them), in the shape of a triangular hook, of very regular appearance and robust.

Dorsally there may be long and slender spines C^d and short spines D^d, often wide, triangular and curved toward the median line, or else long filaments C^d, long spines D^d, and spines, or dorsolateral teeth -- besides that at D' -- positioned between this last and D^d.

Dentate collar on the 4th pair of legs, composed of sharp triangular teeth. External claws usually smooth, but sometimes also (Scottish material, Marcus, 1936) with straight spines near the bases; internal claws of all the legs with spurs on the first basal third, which is particularly robust on the 4th pair of legs. Eggs (up to 5) deposited in the exuvia.

The species is certainly very near to *E. multispinosus* (refer to that description).

In an abundant population found in Norway (Forsa), Maucci has found some examples furnished with robust dorsal spines B (in one of these this spine was present only on the left): such examples had been identified as *E. multispinosus*, but should be treated very probably as a variety of *oihonnae*.

E. oihonnae was collected in Switzerland (up to 4,000 m altitude), in Portugal and in various localities in northern Europe (not in Italy), in the Arctic (Spitsbergen, Novaja Zemlja, Islands of Orsi), in the U.S.A. (Wisconsin and California), in Canada (Vancouver Island), and in Australia.

Typ. loc.: Merok (Norway).

ECHINISCUS OSELLAI Maucci, 1975 (Fig. 237).

Large size: up to 400μ. Color yellowish-red. Eye spots absent. The sculpture is composed of round dimples surrounded by a dense granulation arranged in the shape of polygons almost in contact with each other: between the polygons the cuticle is smooth, save for extremely small dot-shaped granules, very sparse and irregularly scattered. Such

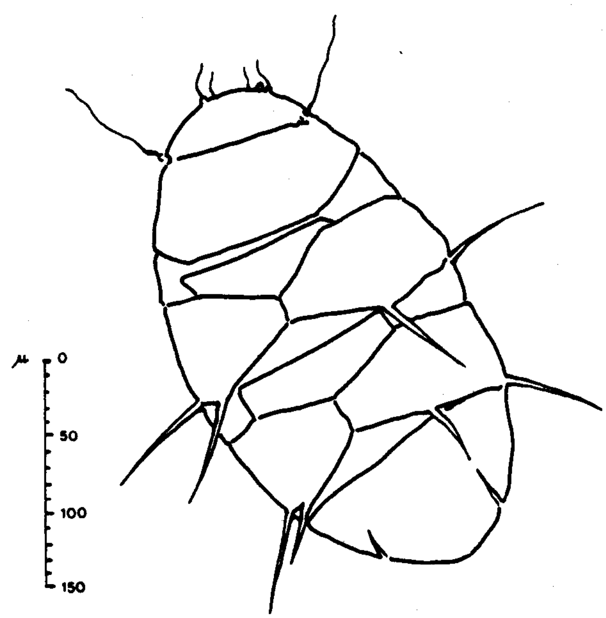


Fig. 237 - *E. osellai* Maucci (from Maucci).

sculpture is included in the "polygonal" type, as in *E. blumi*. The sculpture is a little more fine on the cephalic plate (where left free are two smooth transverse bands), on the scapular and on the unpaired, and is larger on the terminal. The paired plates have a slender transverse band. A sculpture of the same type, but much finer is found also on the cuticle between the plates, and on the proximal half of the legs. The median plate 3 is absent; the terminal plate is not facetted and presents the usual notches, in correspondence with these exists an extremely small spicule E.

The lateral appendices are the cirri A, of medium length, or short (from 60 to 80μ), and long and slender spines C and D (70 and 60μ respectively), somewhat flexible, sometimes transferred almost to a filament a little rigid. Dorsally exists long spines C and D (this last a little shorter than the first). There were observed some asymmetry in the appendices, at times present on a single side, on else bifid. One example lacked all the dorsal appendices.

First pair of legs with basal spine, 4th pair with dentate collar, composed of 8-10 (usually 9) teeth, wide, rather distant. Internal claws with robust spurs, external smooth on the first three pair of legs, with one or two small straight spines, near to the bases, on the 4th pair. In young examples the external claws may be smooth even on the 4th pair.

One exuvium was observed with four eggs.

The species, certainly near to the "*canadensis-blumi*" series, was observed on Bey Daglari, at about 1,400 s.m., in Turkey.

ECHINISCUS PAJSTUNENSIS Bartos, 1941 (Fig. 238).

Length 180-240μ, color brownish-red, eye spots red; sculpture of the plates composed of large polygonal granules. The median plate 1 is very developed in length, the 2 is transversely divided in two parts, a rostral triangle and a caudal pentagon; the median plate 3 is present. Laterally, besides cirri A of about 43μ, exists filament D (48μ); dorsally there are spines C^d (20μ) and D^d (16μ); the D^d are very divergent from each other and not turned caudally, rather obliquely toward the external. Terminal plate not facetted, with the two usual notches, each provided with a long tooth ("point" E). The fourth pair of legs possess a dentate collar, composed of 3-4 large obtuse teeth; internal claws of all the legs with a long curved spur; external claws smooth. The eggs, of reddish-brown color, are deposited in the exuvium in numbers of 2-4.

The species was collected only in the Carpathians (Pajstún, near Bratislava), in moss in the sun.

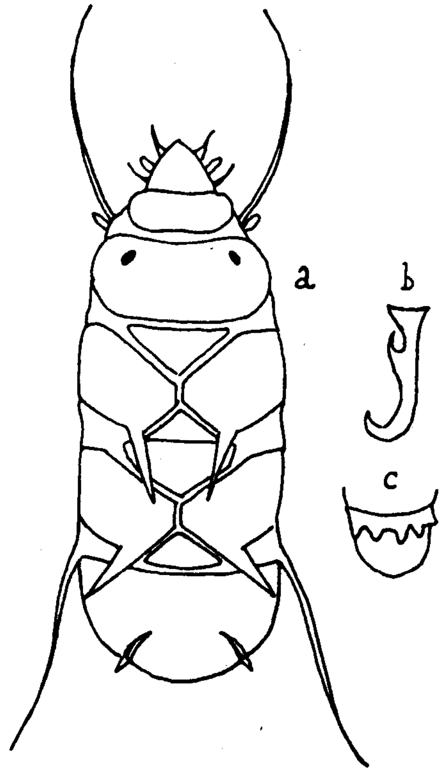


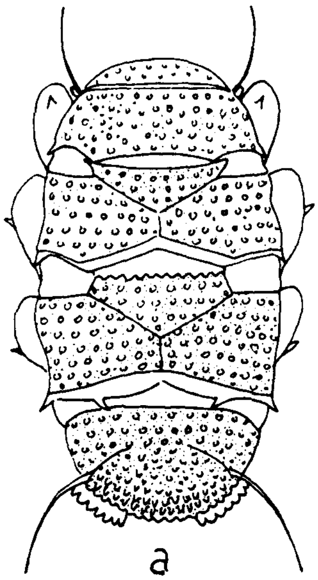
Fig. 238 - *E. pajstunensis* Bartos. a, dorsal view; b, internal claws of the 4th pair of legs; c, dentate collar (from Bartos, redrawn).

ECHINISCUS PERARMATUS Murray, 1907 (Fig. 239).

Length about 260μ; the sculpture is double, composed that is of an extremely fine and uniform granulation, to which is superimposed with much larger dots, regularly distributed. Median plate 3 absent; terminal plate with the usual two notches. At the posterior margins of the paired plates (II and III) exists a wide band devoid of sculpture, all smooth. Laterally, besides the short cirri A, there are small teeth B, C, D, and curved spines E, longer than cirri A; dorsally are present extremely short spines D^d.

The lateral teeth B, C, and D are at times very small, to such an extent as to require very careful attention, and may even be lacking in some or in all the positions.

All the legs of the first three pairs (and not only those of the first pair, as often in *Echiniscus*) bears a minuscule spine; legs of the fourth pair with dentate collar, composed of rather long teeth, with obtuse apices;



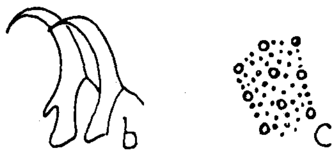


Fig. 239 - *E. perarmatus* Murray. a, dorsal view; b, internal and external claws of the 4th pair of legs; c, detail of the sculpture of the plates (from Murray, redrawn).

internal claws with small spurs.

The eggs (2-3) are deposited in the exuvium, are red and oval, with largest axis of about 66μ; larvae of two claws of 96μ with all the appendices of the adults, but with E shorter.

The species was collected in South Africa (Cape Colony); for one other report on Hawaii Islands (Oahu), the identification of the species is not certain.

Recently it was found also in Florida.

ECHINISCUS PERVIRIDIS Ramazzotti, 1959 (Fig. 240).

Maximum length 285μ, average 220-260μ, smallest of the young of 4 claws observed 185μ. In reflected light the tardigrade appears dorsally of very dark brownish-green color, almost black, while ventrally the color is yellowish in the young and brick-red in the adults; in transmitted light it appears instead an olive-green coloration and of this color are the dorsal and median plates, the cirri A, the claws and the proximal region of the 4th pair of legs, including the dentate collar (6-9 teeth, often multiple), while the other parts of the cuticle, the buccal cirri, the elongated cephalic papilla and the clava are extremely light greenish, almost colorless. The interior of the body contains the usual red granulation, typical of the *Echiniscus*.

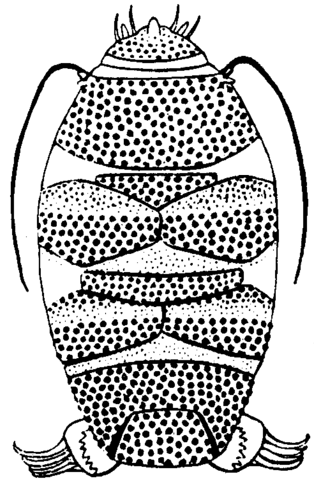


Fig. 240 - *E. perviridis* Ramazzotti.

The sculpture of the plates -- especially observed with phase contrast -- calls to mind that of *E. wendti* and especially of *E. phocae*; however it is composed of projecting granules, which appear clearly in the profile of the tardigrade, where it is seen in optical section; the granules are larger on the scapular, terminal, median 1, and in the caudal zone of the first and second paired plates (II, III) and of median 2; smaller in the rostral zone of these last plates and in the regions included between the second paired plate (III) and the terminal, where the cuticle is strongly thickened and sculptured (as far as the flanks of the animal), so much that one may perhaps consider the presence of median plate 3, in spite of the absence of a clear lateral delineation. Other than the larger sculpture cited, there is also -- on all the plates -- a dense extremely fine regular granulation visible only with strong magnification. The plates -- as occurs in *E. viridis* -- has greater relief than of the other *Echiniscus*, probably because of greater thickness. The claws of the 4th pair of legs are long (up to 26μ) and those internal bear -- on their basal part -- an extremely slender spur, very difficult to see. Exuvia observed with 3 eggs (72 x 65μ).

Characteristic of the species is the great length of the lateral cirri A, which in general varies from 150 to 170μ for the larger individuals, while in the other three species of the "*viridis* group" the cirri A are short, or extremely short (about 30-40μ for *E. viridis* and *E. rufoviridis*, about 80μ for *E. viridissimus*); it is noted that the length of cirri A is one of the more constant characteristics of the *Echiniscus*, presenting a rather narrow variation.

E. perviridis has been collected in Italy (Pallanza, Lake Maggiore), in moss on a wall slightly exposed to the sun.

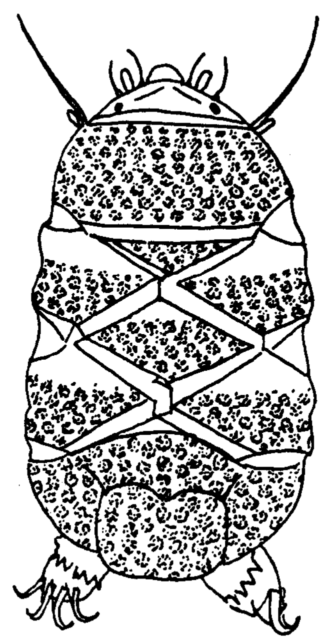
A subsequent report came from Johnson City (Tennessee, U.S.A.).

ECHINISCUS PHOCAE Du Bois-Reymond Marcus, 1944 (Fig. 241).

Length 230-275μ, color red, eyes present and red. The sculpture of the plates is composed of groups of minuscule dots, assembled together in an areola of circular outline: between them one and the other of these round areolas the plate is smooth, not sculptured. Such characteristic sculpture, which shows the aspect of "seal skin", is really very visible at high magnification with normal lighting, but extremely evident with immersion objective and phase contrast.

In the Italian individuals which we examined, the circular punctations of the sculpture have a maximum diameter of 4μ on the terminal plate and are formed of a variable number of extremely small dots (from 6 to 20); for the Brazilian individuals du Bois-Reymond Marcus wrote that the circles of the sculpture have 5μ diameter on the terminal plate and 4μ on the others, and that also the cephalic plate and the rostral part of the median plate 2 and of the paired plates II and III is lacking sculpture; the

Fig. 241 - *E. phocae* du Bois-Reymond Marcus (from du Bois-Reymond Marcus, redrawn).



Italian examples show the aforesaid zone smooth, not sculptured, only in the young; the adults, however, have a partially sculptured cephalic plate, plate 2 smooth in the rostral zone and plate II and III completely sculptured, save for a transverse band more or less wide. Also the terminal plate, with the usual two incisions, is not often -- or indistinctly -- facetted, while it is always facetted in the Brazilian individuals.

Median plate 3 absent; the only lateral appendices are cirri A (from 53 to 90μ, this last length for an individual of 275μ). Small spine on the first pair of legs; fourth pair with papilla and dentate collar, composed of about 9 teeth; such teeth are sharp, irregular, and often two teeth are united together, that is to say have common base. Internal claws with robust curved spur, positioned at about half their length.

It is interesting to note that, in other Italian mosses of high elevation (Dolomites), Ramazzotti has found boundary crossings between *E. phocae* and *E. arctomys*: the circular punctations of the sculpture that is decreased in diameter, sometimes reduced to a simple granulation; however the characteristic sculpture of *phocae* always persists, at least in some zones of the plates, which does not occur in the typical *arctomys*.

The species was collected only in Brazil and in Italy.

ECHINISCUS PORABRUS Horning, Schuster & Grigarick, 1978 (Fig. 242).

Length 160μ, width 92μ. Buccal cirri pointed, the internal 15μ long, the external 17. Eyes absent. The sculpture is composed of polygon sculpture, drawn close, dense, between which is noted small rounded pores, irregularly arranged. Laterally, besides cirri A there are only appendices E (the original description cited a "spine" E, but the associated drawing rather resembled a filament). Dorsally there are long and slender spines C and extremely small teeth D.

The first pair of legs present a spine, the fourth pair a stumpy papilla and a dentate collar formed of 12-14 small teeth. The internal claws bear a large basal spur, curved, the externals are smooth.

The species was found in New Zealand (South Island, Arthurs Pass National Park).

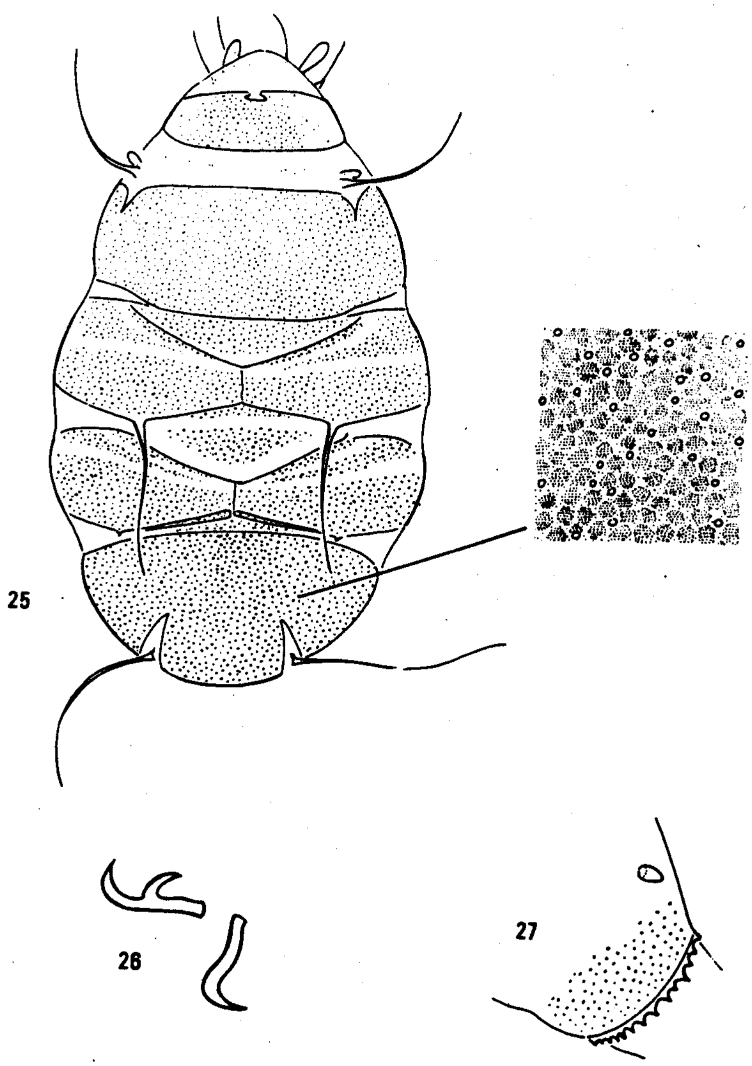


Fig. 242 - *E. porabrus* Horning *et al.* 25, dorsal view and detail of the terminal plate; 26, claws of the 4th pair of legs; 27, dentate collar (from Horning, Schuster, and Grigarick).

ECHINISCUS POOENSIS Rodriguez-Roda, 1948 (Fig. 243).

Length 175μ, color dark green: it is consequently one of the extremely rare species of green *Echiniscus* (the others belong to the "*viridis* group" and are provided with lateral and dorsal appendices). The sculpture is composed of a fine granulation, which leaves free and smooth the posterior margin of the cephalic plate, median 1 and median 2, as well as a transverse band on the paired plates II and III. The median plate 2 is divided in two parts: a rostral, smaller, and the other, caudal, of larger size; median plate 3 is present; terminal plate with notches. There are laterally -- besides cirri A of 30μ -- short spines B, C, D, E (respectively 22, 28, 24, 22μ long); in a single individual -- of three collected -- that the author has examined, D was present on only one side. Dorsally there are spines C^d and D^d, both of 20μ, and D^d terminated in a dagger point. Fourth pair of legs with papilla and dentate collar of 11 irregular teeth, in contact with each other at the base; internal claws with small basal spur. Eggs unknown.

The species was cited only for Fernando Póo Island (western Africa), where it was collected in moss and hepatics, at 2,500 m altitude (Pico Basilé).

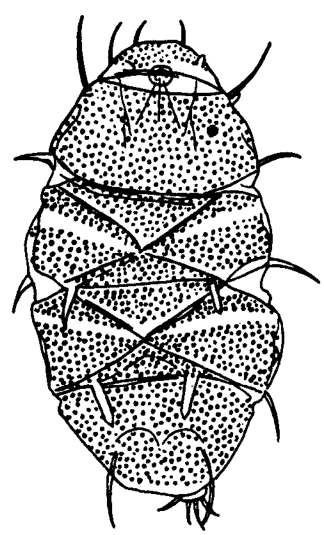


Fig. 243 - *E. pooensis* Rodriguez-Roda (from Rodriguez-Roda, redrawn).

ECHINISCUS POSTOJNENSIS Mihlecic, 1967 (Fig. 244).
= *E. loxophthalmus* Mihelčič, 1939 (not Richters, 1911)

In 1939 Mihelčič described as *E. loxophthalmus* (*sp. inquir.*) the *Echiniscus* he collected near Postojna (Yugoslavia); following deeper study of the material of Postojna and especially in consequence of new Austrian material, the author was persuaded that the aforesaid tardigrade belongs instead to this new species *E. postojnensis*, which he later described in 1967. Here are the characteristics.

Cephalic plate facetted; median plate 1 triangular, robust, not subdivided and sculptured in uniform manner. Median plate 2 subdivided by a wide transverse band. The sculpture is composed of granules of different size (larger on the rostral and caudal zones of the tardigrade). Focusing the microscope one sees -- with tube in high position -- a double sculpture, that is a deep finer background granulation, over which is superimposed larger granules, positioned at uniform distance from each

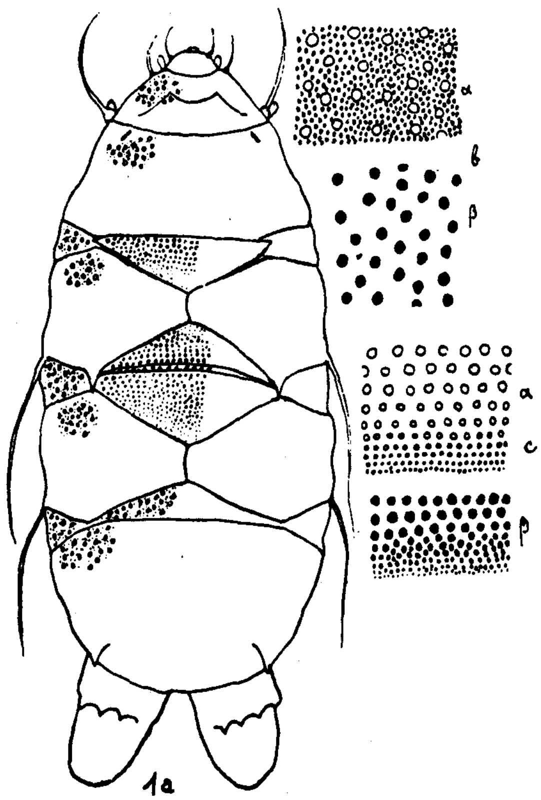


Fig. 244 - *E. postojnensis* Mihelčič. 1a, dorsal view; b, sculpture of the paired plates, cephalic, scapular, and terminal plates, as well as on the cuticle between the second paired plate and the terminal plate (a, with tube high; b, with tube low); c, sculpture on the median plates 1 and 2 (a, with tube high; b, with tube low) (from Mihelčič).

other. With lower position of the microscope tube, in place of the granules which appear clear with tube high, they are perceived now as dark spots, surrounded by clear circles, more or less regular.

On the median plates the sculpture is distributed in different manner: on plate 1 the granules are larger anteriorly and smaller posteriorly, while on plate 2 the larger granules are found in the central zone. The cuticle of the flanks of the animal, as likewise the zone corresponding to the missing median plate 3 and the basal part of the legs are strongly sculptured.

The species was collected the first time -- as said -- at Postojna (Yugoslavia), but later in Stiria and Carinzia (Austria) in moss on tree trunks.

ECHINISCUS PUSAE Marcus, 1928 (Fig. 245).

Length 120-150μ, color yellow or orange; the sculpture is composed of a dense punctation, or better of small cavities, the outlines of which are indistinctly polygonal and in contact with each other, with honeycomb

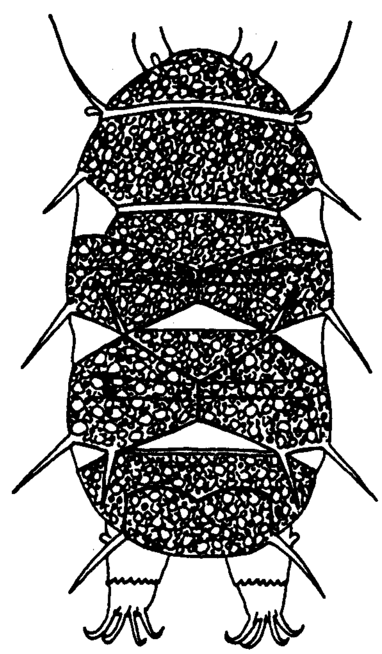


Fig. 245 - *E. pusae* Marcus (from Marcus, redrawn).

appearance, or also of seal skin. Median plates 1 and 2 divided transversely, having the rostral part not well delineated, lacking sculpture and smooth; median plate 3 is absent. Terminal plate (IV) facetted, with the usual notches. Besides cirri A, laterally exists short spines B, C, D, E, but often B may be lacking; dorsally there are spines C^d and D^d. The fourth pair of legs bear a dentate collar, composed of wide and short sharp teeth, in contact with each other at the bases; internal claws with spur.

The species was cited for South Africa (Cape Colony) and for Indomalaya (Lombok Island, at 1,600 m altitude).

ECHINISCUS QUADRISPINOSUS Richters, 1902 (Fig. 246).
= *E. scrofa* Richters, 1902

Length up to 280μ, color dark red, eyes present and red. The sculpture of the plates, at medium enlargement, appears composed of depressions (pores) of irregular size, arranged without any order, but at high magnification, with the use of immersion objective -- in normal light and better still with the use of immersion objective -- it is observed that, besides this sculpture, there is another extremely fine, which covers with great regularity all the plates (different from *E. merokensis*). There is a uniform granulation, of which Fig. 247A provides a representation -- in phase contrast -- and which may be even coarser under the sculpture (in the figure, for greater clarity, this sculpture was not drawn under the depressions of the coarser sculpture). Median plate 3 present; on the

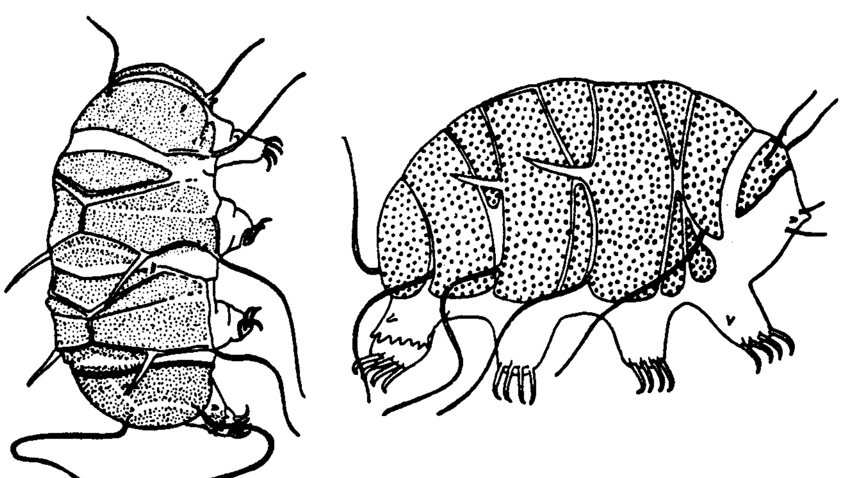


Fig. 246 - *E. quadrispinosus* Richters.

terminal plate IV there are the usual two notches, which appear connected by a slender band lacking sculpture, smooth. Besides the paired plates II and III, there are small supplementary plates, in rostral and lateral position with respect to them, and precisely -- of each side -- two or three small accessory plates between the scapular plate I and II and one between the plates II and III. Very often, more than well distributed plates, one finds a subdivision of the paired plates into individual plates, or sculptured areas, parted by smooth bands, deprived of sculpture.

The lateral appendices A, B, C, D, E are all filaments -- sometimes rather rigid -- which increase in length from A to E, or else of varied length; the dorsal appendices C^d and D^d are spines, usually of equal length, however C^d may become short or extremely short up to being scarcely visible. Small spine on the first pair of legs, papilla on the fourth pair, which is provided with dentate collar with 8-9 irregular teeth. Internal claws with straight spurs toward downwards, external claws of the 4th pair of legs in general smooth, sometimes with a short and straight spur near the base; rarely such spurs exist on the external claws of all the legs. Eggs oval, red-brown, (up to 5) deposited in the exuvium; larvae with 2 claws of 84μ and young of 4 claws of 147μ already have appendices C^d and D^d, but laterally have only A and E; in the young the appendices C and D may be short spines rather than filaments.

The lateral appendices B appear late, after various changes; sometimes are found adult individuals lacking B and unprovided with small accessory plates -- always the type of sculpture of which described above -- these should not be treated as *quadrispinosus*, rather one of its varieties *cribosus* or *fissispinosus*; if the sculpture is simple, not double (that is it does not present uniform granulation, extremely fine and regularly distributed) it is treated as *E. merokensis* or *merokensis suecicus*, which in general has however also terminal plate facetted.

E. quadrispinosus is probably cosmopolitan; it was cited for numerous localities from Europe (Italy included), for the Canaries, Africa, North and South America, Spitsbergen Archipelago, Galapagos Islands, and Vietnam.

Typ. loc.: Germany.

It was cited recently also for New Zealand; however this material does not seem to have the double sculpture, nor the subdivision of the paired plates into supplementary plates.

We think (at least provisionally) the rank of subspecies should be given to the following varieties:

E. quadrispinosus cribrosus Murray, 1907 (Fig. 247).

Length up to 280μ, sculpture of the plates double, as described for typical *quadrispinosus*, that leaves free on the scapular plate a median longitudinal band or two, or three, transverse bands; also on the terminal plate there are two smooth bands, without sculpture, one longitudinal and the other transverse. Median plate 3 always present; the paired plates II and III are not subdivided into smaller plates (that is to say there are no supplementary plates), as occurs instead in the typical species. All the lateral appendices may be short, or else may be only short C, or finally B may be lacking; even the dorsal appendices may be completely lacking, or else D^d reduced to small triangular spines; or else the lateral and dorsal appendices corresponds to those of the typical *quadrispinosus*.

E. quadrispinosus cribrosus may sometimes easily be confused with *E. merokensis* and *merokensis suecicus*, but these last two have simple sculpture, not double, and in general their terminal plates are facetted (for more details about the sculpture, see the description of *merokensis* and *quadrispinosus*).

Internal claws with spur, dentate collar on the 4th pair of legs. Eggs oval (60 x 45μ) deposited in the exuvium in numbers of 2-4; the larvae of two claws measure up to 150μ.

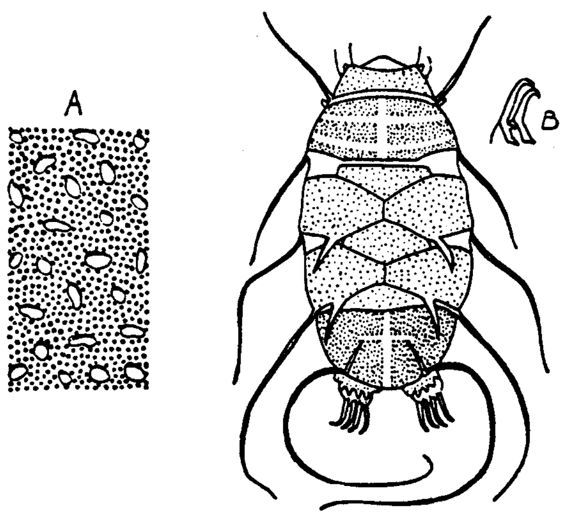


Fig. 247 - *E. quadrispinosus cribrosus* Murray. A, detail of the sculpture of the plates; B, internal and external claws of the 4th pair of legs.

Reports are known from various localities in Europe (also in Italy), Greenland, and -- with some doubt -- the Himalayas.

Typ. loc.: Shetland Islands.

E. quadrispinosus fissispinosus Murray, 1907 (Fig. 248).

Length up to 280μ; sculpture and other characteristics as in *quadrispinosus cribrosus*, to whose description one should refer. The paired plates are not, not even here, subdivided in manner to form supplementary plates; the lateral appendices D are however bifid on one or both the sides, while B may be lacking and C is robust and curved. Sometimes the dorsal appendices are completely lacking; other times spines D^d may be reduced to small triangular teeth, while C^d maintains the usual appearance. Fourth pair of legs with dentate collar; internal claws with spur.

Reports have been cited for Scotland, Shetland Islands (typ. loc.), France, and in the Carpathian region.

On the contrary, only the rank of variety may be attributed to *E. quadrispinosus* forma *brachyspinosa* Bartos, 1930:

Length 176-189μ. Characteristics as in typical *E. quadrispinosus*, with the difference that the lateral appendices, rather than being filaments are wide and short spines. Since the individuals examined were part of a population of typical *quadrispinosus*, it was not excluded that they may be young *quadrispinosus*, which often -- as already noted by Cuénot -- have appendices C and D in the form of spines; the small size of the tardigrades, collected by Bartos, seems to strengthen this hypothesis.

This variety is cited for the Carpathians, Vietnam, and the United States (Tennessee). A recent citation from New Zealand does not mention the double sculpture and indicates the lateral appendices as short filaments.

ECHINISCUS RAMAZZOTTII Binda and Pilato, 1969 (Fig. 249).

Length of the two individuals collected 308 and 342μ. The sculpture is characteristic: resembling at first glance -- with illumination by normal light -- to that of *E. blumi*, but a closer observation (especially with phase contrast) shows that the single elements have different shapes; in fact they are less clear polygons in comparison to *blumi* and tend to be almost circular.

The sculpture on the scapular plate is uniform, but the single elements (dots) are smaller on the terminal plate. The median plate 1 has a caudal zone clearly punctated and a rostral zone with finer and barely visible sculpture.

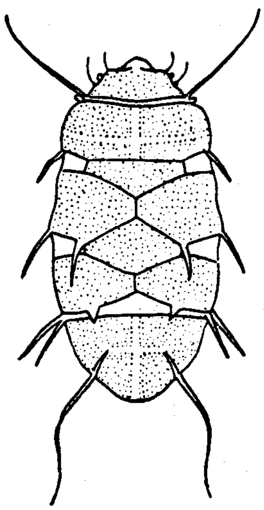


Fig. 248 - *E. quadrispinosus fissispinosus* Murray.

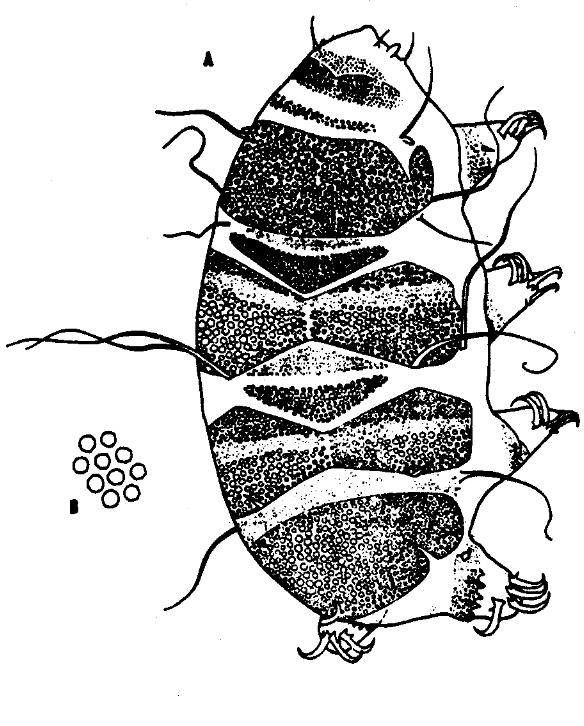


Fig. 249 - *E. ramazzotti* Binda and Pilato. A, dorsal view; B, particulars of the sculpture of the plates (from Binda and Pilato).

The median plate 2 has 2 analogous zones of sculpture, separated by a smooth band, lacking sculpture. The median plate 3 is not laterally delineated (and may perhaps then be considered absent), but the corresponding zone is sculptured as far as the bases of the lateral filaments D. The dorsal paired plates have an ample caudal zone with showy punctation and a rostral zone with smaller dots. The two zones are separated by a transverse band with scarce sculpture, or else completely smooth. Terminal plate uniformly sculptured, with the usual two notches.

The appendices present are: laterally filaments A, B, C, D (A, 55μ in both the examples; B, 73μ in the smaller individual and 83μ in the larger; C, 98 and 116μ respectively; D, 86 and 92μ). Dorsally: long dorsolateral filaments B' on the scapular plate (it is the first time that filaments are observed in such position in the genus *Echiniscus*): they are over 43μ long in the individual of larger size, while in the smaller individual B' is present only on one side and measures 23μ.

Legs with a proximal zone sculptured; all the internal claws with robust spur curved toward the base. The 4th pair of legs has the external claws with straight spur, less developed on the external claws of the 3rd pair; also dentate collar (7-8 unequal teeth) and papilla).

The species was collected in moss on Salina Island (Eolie or Lipari Islands - Sicily).

ECHINISCUS RANZII Ramazzotti, 1964 (Figs. 250 and 251).

Because of the absence of all lateral appendices, the species belongs to *Echiniscus* of the *arctomys* group; it is also lacking dorsal appendices. Reddish color, maximum length 320μ, but in general somewhat smaller; the larvae of 2 claws measure from 124 to 164μ, however there are individuals with 4 claws of that length and of 130μ that is less than those of some larvae. Eye spots red, small and often barely visible. External buccal cirri much longer than the internal, and precisely by two or three times longer. Lateral cirri A well developed, of length variable between 128 and 200μ, correlated of course to the body length; measurements performed on 15 individuals have furnished a value included between 0.50 and 0.90 for the "length of cirri A:length of the animal" ratio, with average of 0.66 ± 0.03.

Median plate 3 present in the adults and always very visible, also sometimes incomplete and limited at the rostral part, that is to say at the more proximal zone of the second paired plate. Terminal plate facetted, with the usual two notches. Sculpture on the plates double, composed of

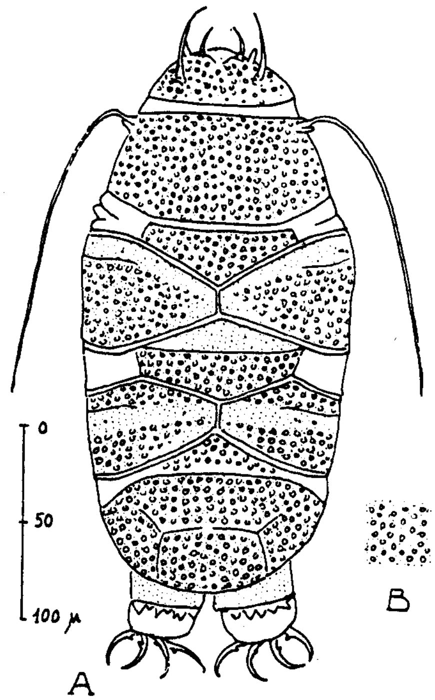


Fig. 250 - *E. ranzii* Ramazzotti
A, dorsal view; B, detail of the sculpture.

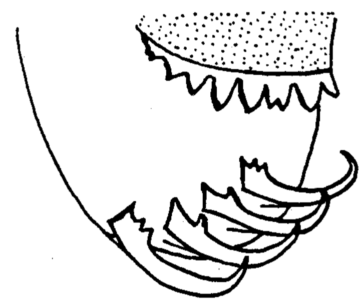
a fine background punctation, which is superimposed on a coarse punctation, as in *E. bigranulatus*; but in *E. ranzii* the coarse granulation is denser and arranged in more regular pattern.

The internal claws and those external of the 4th pair of legs bear a spur, near to their base; often the spur of the external claws is double and sometimes the spurs -- of the internal and external claws -- exist also on part of the other pairs of legs, or else on all. Small spine on the first pair of legs, papilla and dentate collar (4-9 teeth) on the fourth pair. Oval eggs (about 83 x 74μ), color orange, deposited in the exuvium.

At a first hasty examination *E. ranzii* may be mistaken for *E. bigranulatus*; with a more attentive observation the difference however appears considerable and may thus be summarized:

1) cirri A of *ranzii* are much longer; the "length of cirri A:length of the animal" ratio is equal to 0.50-0.94 (average 0.66 ± 0.03 on 15 individuals); in *bigranulatus* however such ratio is from 0.22-0.44 (average 0.25 ± 0.02 on 17 individuals).

Fig. 251 - *E. ranzii* Ramazzotti. Detail of the 4th pair of legs.



2) The external buccal cirri of *ranzii* are 2 to 3 times longer than the internal, while in *bigranulatus* the external and internal buccal cirri have equal length, or else the external are a little longer than the internal.

3) The external claws of *ranzii* always bear -- at least on the 4th pair of legs -- one or two spurs, constantly absent in *bigranulatus*.

4) In both the species the sculpture of the armor is of the "double" type, but the density of the larger granules is very different in the two species. In fact the performed calculations on the central region of the median plates, which better gives the scope -- because less convex -- results that:

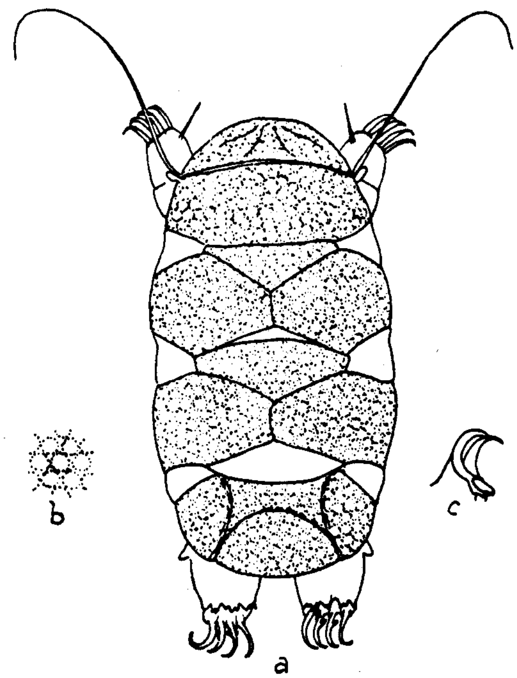
- in *ranzii* and for 17 observed individuals, within a square of about 9.5 x 9.5μ are included from 14 to 31 larger granules with an average of 23.23 ± 1.17;
- in *bigranulatus* and for 22 observed individuals, the larger granules, contained in a square of the same size, varies from 9 to 13 with an average of 9.88 ± 0.28.

E. ranzii was collected in lichen on rock, at Cerro del Pajonal (Chile), at an altitude of about 4,600 m, and was the only species of tardigrade present.

ECHINISCUS RETICULATUS Murray, 1905 (Fig. 252).

Length up to 214μ, color bright red. The sculpture of the plates is composed of small flattened depressions, whose margins -- circular or hexagonal -- are in contact with each other, outlining thus a reticular design. Median plate 3 present, however barely sculptured and often fused with the terminal plate which is facetted. Cirri A very long (142μ in an exuvium of 214μ); spine on the first pair of legs very long and papilla

Fig. 252 - *E. reticulatus* Murray. a, dorsal view; b, detail of the sculpture of the plates; c, internal and external claws of the 4th pair of legs (from Murray, redrawn).



on the fourth pair; this last with dentate collar, composed of dentation of one or two points; internal claws with spur. Eggs (1-4) deposited in the exuvium.

Difficult to distinguish from *E. japonicus* Morikava, which differs from *reticulatus* only by a larger size of the single elements of the sculpture and by the shorter cirri A.

The species is distinguished however from *E. wendti* -- which however has very long cirri A -- by the presence of median plate 3 and by the different sculpture; it was cited from Scotland (in submerged moss), the Himalayas at 2,700 m altitude, and the Carpathians.

ECHINISCUS REYMONDI Marcus, 1928 (Fig. 253).

Treated as *E. spec.* Murray, 1910, which Marcus gave the identification indicated above. Length 212μ; sculpture composed of small dots, of which one part has the appearance of pores, so that in microscopic vision the larger appear dark and the smaller clear. Median plate 3 absent; terminal plate with the usual two incisions. Laterally exist cirri A of 70μ and wide

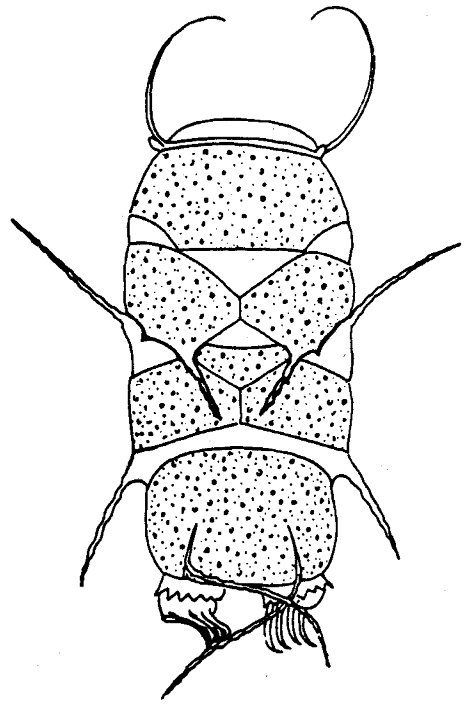


Fig. 253 - *E. reymondi* Marcus (from Marcus, redrawn).

spines C, D, E, respectively of 50, 50, 80μ length; dorsally there are flattened spines C^d of 40μ and dorsolaterally small triangular teeth C', on the caudal margin of plate II. All the spines -- either those lateral, or those dorsal -- are rough, rather than smooth as usual. Dentate collar of the fourth pair of legs composed of obtuse teeth; there is no published information about the existence, or absence, of spurs on the internal and external claws.

Of this characteristic species was collected a single individual at Victoria, on Vancouver Island (Canada).

ECHINISCUS ROBERTSI Schuster and Grigarick, 1965 (Fig. 254).

Length 148-200μ; sculpture of the plates consists of well defined and separate polygons. Cephalic plate subdivided into a small anterior section and a large posterior. Scapular plate normal, but with two indistinctly separate lateral zones. Median plate 1 single and sculptured. First and second paired plates subdivided medially and apparently subdivided also in transverse sense, owing to two more weakly sculptured bands. Median

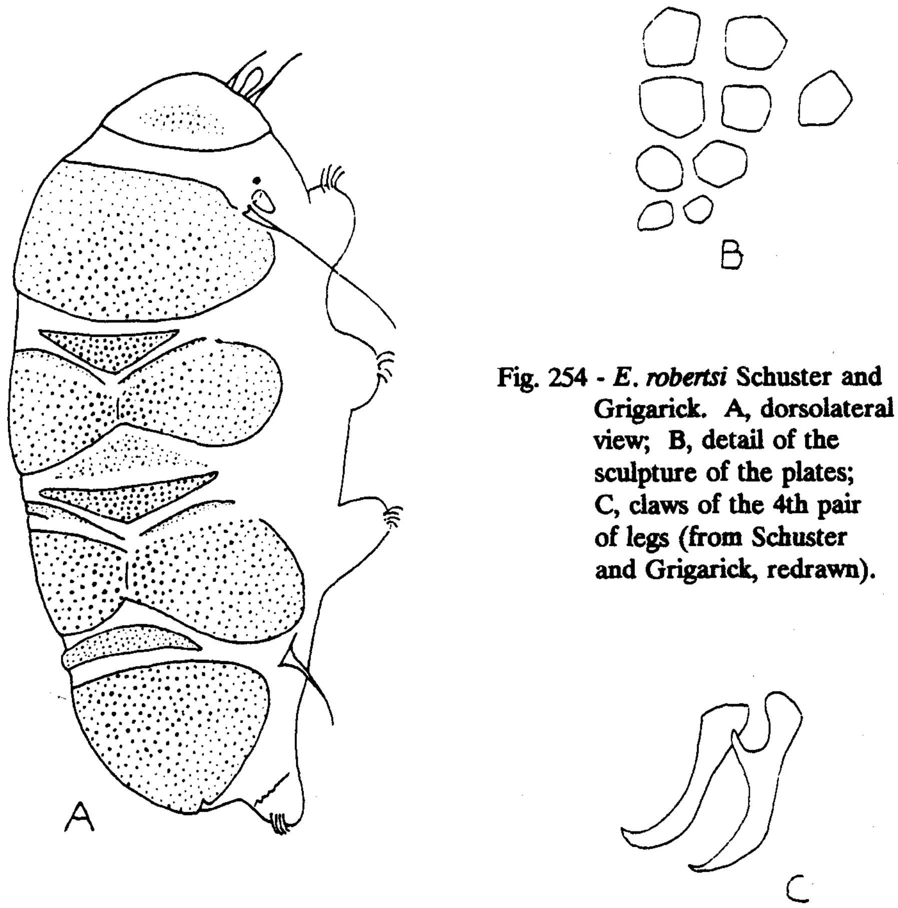


Fig. 254 - *E. robertsi* Schuster and Grigarick. A, dorsolateral view; B, detail of the sculpture of the plates; C, claws of the 4th pair of legs (from Schuster and Grigarick, redrawn).

plate 2 indistinctly sculptured in the anterior zone and strongly in the posterior (projecting granules). Median plate 3 present. Terminal plate with weak notches, without spines E. The sculpture is more pronounced and larger in the posterior half of the of the scapular plate, in the central zone of the first and second paired plates, in the median plates 1 and 2, and in the anterior part of the terminal plate.

Cirri A of 42μ and spines D of 25μ; dorsal appendices absent. First pair of legs with small conical appendices, fourth pair with large rounded papilla and dentate collar of 5-6 teeth; internal claws of the first three pair of legs with large spur directed basally; internal claws of the 4th pair with curved spur, external claws without spurs.

Eggs unknown. The species is characterized by the presence of only lateral appendices A and D.

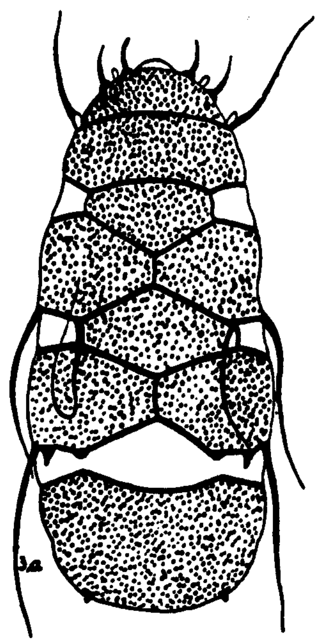
E. robertsi was collected in a mixture of various cryptogams not better specified, in a marsh at Saint Point, Popof Island (Alaska).

ECHINISCUS ROSALIAE Mihelčič, 1951 (Fig. 255).

Length of 275 to 350μ, reddish or dark red, with black eye spots. The sculpture -- fine and regular -- is composed of minuscule circles with a clear spot at the center, which seems however to be small depressions.

It should be in practice considered the type of sculpture which is characteristic of different species, those of the "*blumi* group" and those of the "*spitsbergensis* group".

Laterally, besides cirri A, there are long filaments C and D, this last longer; present is a small tooth ("point") E in the notches of the terminal plate. Dorsally exists long filaments C^d and short triangular spines



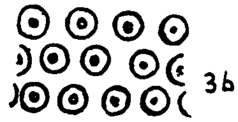


Fig. 255 - *E. rosaliae* Mihelčič. 3a, dorsal view; 3b, detail of the sculpture (from Mihelčič).

D^d; in dorsolateral position teeth D'. Median plate 3 absent. Dentate collar of the 4th pair of legs composed of 5-7 sharp teeth; claws large, those internal with curved spur, those external also with spur, however more proximal to the base.

In our opinion we can not exclude that this species belongs to the "*spitsbergensis* group" (for more detail see the description of *E. spitsbergensis*); in fact it differs from *E. menzeli* only by the black eye spots, rather than red, and by the absence of filaments B, characteristics both that do not seem to be sufficient for the separation of the two species; also the type of sculpture, according to the description published by the author, does not appear very different.

Of *E. rosaliae* are known only a few reports in Austria, at about 3,200 m altitude, in Hungary, and in Romania.

ECHINISCUS RUFOVIRIDIS du Bois-Reymond Marcus, 1944 (Fig. 256).

Length about 190μ, eye spots red. In the caudal region of the body the cuticle is green, with exception of the individuals that have recently molted, in which the cuticle is still colorless; the cavity granules are red, as in the majority of *Echiniscus*. The sculpture is double, that is to say is composed of a fine, dense, and uniform punctation, which is superimposed over small

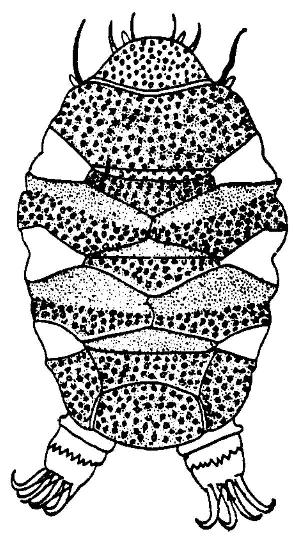


Fig. 256 - *E. rufoviridis* du Bois-Reymond Marcus (from du Bois-Reymond Marcus).

depressions (pores) of irregular shape and of larger size. The larger sculpture lacking on the rostral half of the paired plates and of the median plate 2, and on the entire median plate 3. The terminal plate is facetted and has the two usual incisions. Cirri A short, of about 30μ; there are no other lateral or dorsal appendices. The fourth pair of legs bear a dentate collar composed of 10 sharp unequal teeth; internal and external claws without spurs, 22μ long on the 4th pair of legs and 18μ on the other legs. Exuvia have been observed containing 4 eggs of bright red color.

The species is characterized by the short cirri A, by the green color in the posterior region, by the double sculpture, by the long claws, and by the facetting of the terminal plate; it is known only from Brazil (State of Sao Paulo) and was often collected in moss on tree trunks.

ECHINISCUS RUGOSPINOSUS Marcus, 1928 (Fig. 257).

Treated as *E. spec.* Murray, 1913, which Marcus gives the above identification. Length 200μ, red. The sculpture is composed of small clear dots, regularly arranged, which seem to be minuscule flattened papillae, or granules. Lacking median plate 3; the terminal plate has the usual two

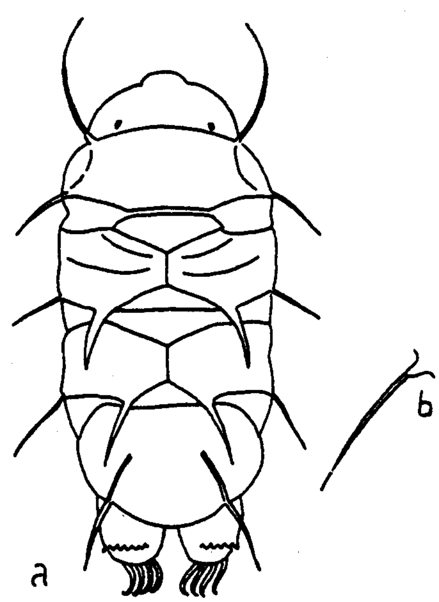


Fig. 257 - *E. rugospinosus* Marcus. a, dorsal view; b, lateral filament (from Murray, redrawn).

notches. Laterally there are -- besides rather longer cirri A -- short and slender filaments B, C, D, E, which arise from small papillae; dorsally there are spines C^d and D^d, characterized by being coarse and rough. Fourth pair of legs with dentate collar, provided with short teeth; internal and external claws without spurs.

There was cited a single report of the species in tropical eastern Africa, without better precision.

The species seems to be very near to *E. spiniger*, from which it differs by the rough dorsal appendices (it is however doubtful that systematic value may be attributed to this particular) and by the claws without spurs.

ECHINISCUS SIEGRISTI Heinis, 1911 (Fig. 258).

Length 180-220μ; the sculpture of the plates is composed of an irregular granulation and not very dense. The plate 3 is absent and not even visible is the space it usually occupies in the genus *Echiniscus*, so that the second paired plate (III) results in immediate contact with the terminal

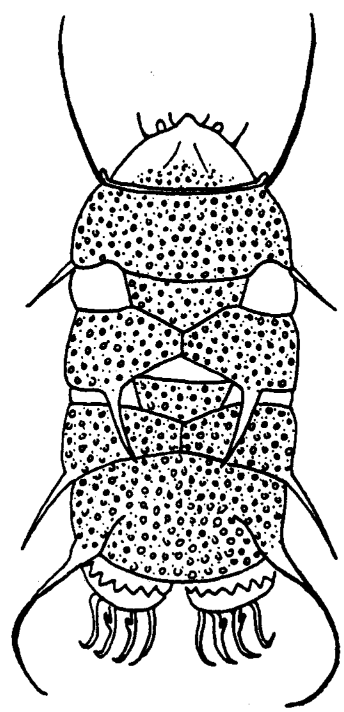


Fig. 258 - *E. siegristi* Heinis (from Heinis, redrawn).

plate (IV); this last is not facetted and with the usual two normal incisions. Laterally, besides cirri A of 50μ, there are spines B of medium size, extremely robust spines D, and filaments E; dorsally there are only spines C^d. The fourth pair of legs bears a dentate collar, furnished with sharp teeth; internal claws with curved spur, positioned at an undetermined distance from the base; external claws smooth. Eggs unknown.

It was cited a single time in southern Mexico.

ECHINISCUS SIMBA Marcus, 1928 (Fig. 259).

Length up to 235μ, color red, eye spots red. Sculpture composed of a rather irregular granulation dense and irregularly arranged, visible especially on the caudal half of the plates. Terminal plate not facetted, with two notches; lacking median plate 3. Present are lateral appendices A, B, C, D, E (all spines, with exception of A and C, which are filaments) and those dorsal C^d (12-20μ) and D^d (8μ); the lateral appendices B and the dorsal D^d are however almost always absent. The filaments A (lateral cirri) and C are of about equal length (23-46μ); the spines E (15-34μ) are a little longer than D (11-30μ); often the spines D and E are visibly enlarged at the base. Small spine on the first pair of legs and papilla on the fourth pair, which bears a dentate collar, composed of sharp teeth of unequal size, positioned at irregular distance; the internal claws have a weak spur.

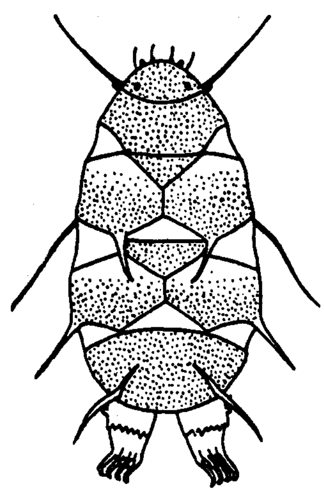


Fig. 259 - *E. simba* Marcus.

Already individuals 120μ long present all the appendices; there has not been found either eggs, or larvae of two claws.

Reports are cited from Italy (Sardinia and Trieste Carso), from Austria, Poland, regions of the Carpathians, and Romania.

ECHINISCUS SPECIOSUS Mihelčič, 1967 (Fig. 260).

Length 190-220μ, color rosy-red, eye spots dark red (almost black). As usual -- as in other species of the "*arctomys* group" described by Mihelčič -- determining character for the identification of the species is the sculpture: this consists of "dimples" which, during the focal setting with microscope tube in higher position (position 1) appears as small dark circular elements, surrounded by a clear polygonal perimeter, determining thus a reticular design. With position of the tube a little lower (position 2) no polygonal mesh is seen, rather a dark background scattered with minuscule brilliant dots (of clear color) similar to granules; lowering the microscope tube still slightly more (position 3), we see in place of the bright granules dark dots (dimples) of equal size, circumscribed by slender irregular polygons in contact with each other. Further lowering the tube (position 4) we see larger clear "granules", distant one from another and dispersed.

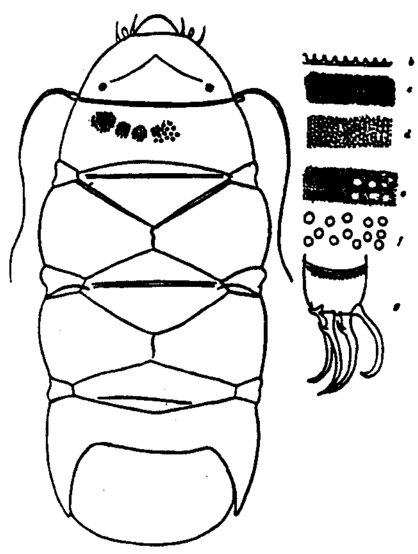


Fig. 260 - *E. speciosus* Mihelčič. a, dorsal view; b, surface of the cuticle in profile; c, sculpture with tube high (post. 1); d, sculpture with tube lower (post. 3); f, sculpture with tube in lowest position of all (post. 4); g, leg of the 4th pair and dentate collar (from Mihelčič).

Cirri A of about 195μ; cephalic plate with a facetting; also the terminal plate is strongly facetted and has two very developed notches. Dentate collar composed of a ribbon-like thickened band, with small conical teeth, near each other, of equal shape and size and very short (about 12-15 teeth). Internal claws with robust spur, curved toward the base; external claws smooth.

It is noted, from the complete description of the sculpture, it is not easy to identify the species and separate from others of the "*arctomys* group", of which often we do not know in detail the type of sculpture, that which renders practically impossible to establish comparison.

E. speciosus was collected in lichen on trees and on rock, in the Argentine Andes.

E. roseus, which is here considered as a synonym of this species, was described by the same author, and its sculpture is described as follows (Fig. 261).

The sculpture of the plates appear as a granulation, which an attentive examination shows to be composed of "dimples" (and not granules in relief). The appearance is different according to the focal setting of the microscope; with tube in high position we see dark spots (dimples) surrounded by irregular polygons; lowering the tube of the microscope we

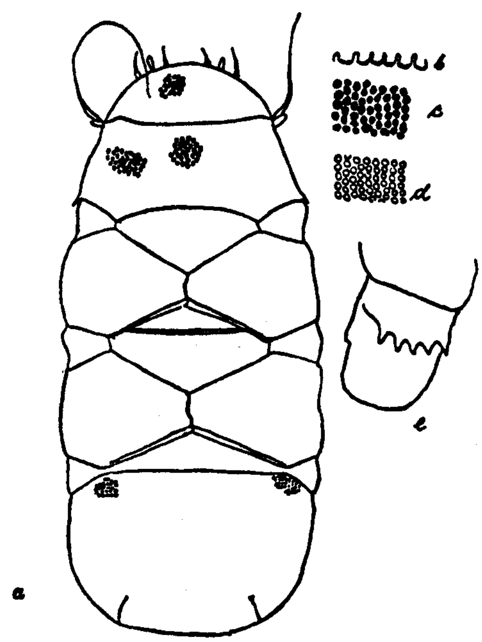


Fig. 261 - *E. roseus* = *E. speciosus* Mihelčič. a, dorsal view; b, surface of the cuticle, lateral view; c, sculpture with tube high; d, sculpture with tube low; e, dentate collar of the 4th pair of legs (from Mihelčič).

see instead clear "granules", of irregular shape, but rather rounded.

It seems that this description, however meticulous, may not bring out such elements to be able to clearly differentiate the two species. Also *E. roseus* comes from Argentina.

ECHINISCUS SPINIGER Richters, 1904 (Fig. 262).

Length up to 350μ; the sculpture is composed of small rounded depressions, arranged in irregular manner, rather spaced out ("*merokensis* type" sculpture). New Zealand example (one of them observed by us, kindly donated by D. Nelson) presents pores considerably larger, clearly round, closer and with regular distribution. Median plate 3 absent and terminal plate facetted, with the usual two notches. The lateral appendices -- besides cirri A of about 55μ in an individual of 350μ -- are spines B, C, D, E of about equal length (30-36μ); Marcus has however noted that sometimes B is shorter (8-10μ), which in material from Sumatra lacks B and which finally, in individuals collected in Sardinia, all the lateral spines were only 15μ long. The dorsal appendices C^d and D^d present a great variability; they may be completely lacking, or else C^d are filaments of 51μ and D^d curved spines of 48μ, or even C^d and D^d are equally long spines (from 10 to 35μ). Fourth pair of legs with dentate collar, composed of

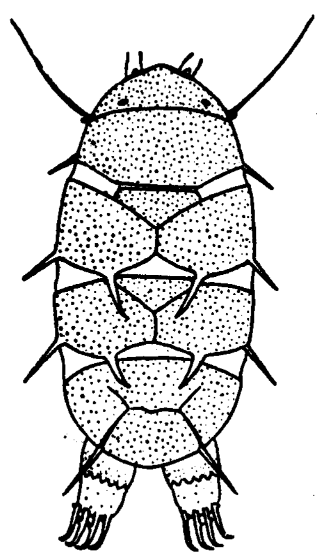


Fig. 262 - *E. spiniger* Richters.

obtuse teeth, and internal claws supplied with very robust curved spur and positioned a larger distance than usual from the base of the claw. Eggs unknown.

Cuénot, 1932 (in which he noted the individuals of *E. spinulosus* with lateral spines D and E longer than normal and which approaches then *E. spiniger*), proposed to include *spiniger* in the species *spinulosus*; Marcus, 1936, seemed to think the two species distinct, however not as far as the individuals found with longer spines C in populations of *spinulosus*, or individuals with shorter spines C in populations of *spiniger*.

Also we think (in the present state of our knowledge) valid the specific separation of *spiniger* and *spinulosus*.

E. spiniger was found in Sweden, Switzerland, Italy (Sardinia, Trieste Carso, and Verona), in Istria, Romania, Sumatra, Australia, South America, and New Zealand.

Typ. loc.: southern Sweden.

ECHINISCUS SPINULOIDES Murray, 1907 (Figs. 263 and 266).

Length up to 500μ, eye spots in general red, but sometimes black, as we have had occasion to observe in entire populations; also Petersen (1951) found not rarely individuals with black eyes in the "*spitsbergensis* group", to which *spinuloides* belongs. Sculpture of the polygonal type which -- by a determined focal setting of the objective -- appears composed of

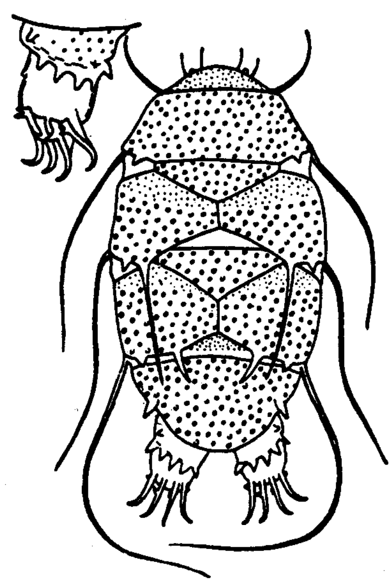


Fig. 263 - *E. spinuloides* Murray. Habitus and detail of the 4th leg.

minuscule polygons, usually hexagons or pentagons, often rounded angles, containing a circle or a dot; this apparent granulation (in reality small depressions) is composed of larger elements on the scapular and terminal plates and of smaller elements on the cephalic plate. The median plate 3 is absent, but in its position exists a zone more or less triangular, covered with granulation.

Laterally there are filaments A, B, C, D, of increasing length from A (about 50μ) to D (about 250μ); from 1 to 6 small spicules E ("points") in each of the two notches of the terminal plate; dorsally long filaments C^d (very rarely we have seen also spine C^d) and filaments with enlarged bases -- often curved -- or else short spines or triangular teeth D^d; in dorsolateral position triangular teeth B', C', D', more or less robust. Fourth pair of legs with papilla and dentate collar, composed of about 5 triangular teeth of different size, distant from each other; internal claws with spur, external claws with one or more straight spines (teeth) near the base. The oval eggs (larger diameter about 72μ), reddish, are deposited in the exuvium in numbers from 1 to 5; larvae of two claws, of about 165μ, present cirri A, points E, dorsolateral teeth C' and D'; the young of four claws still lack the lateral filaments B and dorsolateral teeth B'.

Almost certainly two other species have been included in the species *E. spinuloides*, as yet considered distinct, that is to say *E. spitsbergensis* and *E. melanophthalmus*; it is not even excluded that also *E. menzeli*, *E. marinellae*, and *E. rosaliae* may be synonyms of *spinuloides*: for a more complete discussion on this topic, we refer the reader to the account in the description of *E. spitsbergensis*.

The species was collected in Austria, Bulgaria, France, Italy, Poland, Norway, Yugoslavia, Scotland, Hungary, Romania, Greenland, and in various Arctic localities.

Typ. loc.: Scotland and Novaja Semlja.

ECHINISCUS SPINULOSUS (Doyére, 1840) (Fig. 264).

Length up to 350μ, but more often around 250μ. Sculpture composed of an irregularly arranged and rather coarse punctation; the individual dots may have different size. The cephalic plate is often sculptured only toward the center and smooth at the margins; the paired plates II and III have a slender transverse smooth band and the sculpture is limited to a reduced rostral zone and to a larger caudal zone. Lacking the median plate 3, but the space between the plate III and the terminal (IV) presents a small punctated zone; analogous punctated zone exists also posteriorly to the

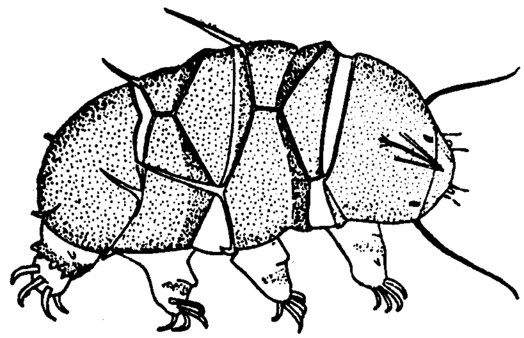


Fig. 264 - *E. spinulosus* (Doyére).

first paired plate. The terminal platepossesses the usual two incisions and presents a more or less evident facetting, which may also be lacking (observations of Cuénot and us). Laterally, besides rather short cirri A (but we have seen them approaching 86μ in an individuals of 180μ), there are short or extremely short spines, as far as becoming teeth, B, C, D, E; of these there may be lacking B (often), or else C, or else D. Dorsally there exists appendices C^d and D^d, of very variable appearance: of extremely short spines (teeth), of short, long, or very long spines; C^d may be lacking, or -- to the contrary -- become a long filament, however D^d remaining a short spine (Cuénot, 1932, also say various times individuals with spine E covered with roughness, as in *E. duboisi*).

On the fourth pair of legs exists the papilla and dentate collar provided with sharp triangular teeth; spine on the first pair of legs. The two internal claws bear a curved spur at about a quarter of their length, measured from the base: such spur is especially robust on the claws of the fourth leg; external claws smooth, although Cuénot has collected an individual in which they have a spur. Eggs oval, deposited in the exuvium (3-4).

Cuénot deemed to unite into a single species *E. crassispinosus*, *E. spiniger*, and *E. spinulosus*, but *crassispinosus* should be considered distinct -- as was likewise noted by Marcus -- by the different sculpture: in fact it is "double", that is composed of more scarce larger dots and more abundant and uniformly distributed fine dots; with regard to *spiniger* we refer the reader to that which is said in the relative description.

E. spinulosus was observed in France, Switzerland, Italy, Austria, Greece, Hungary, Poland, Spitzbergen Archipelago, Hawaii Islands, and Vietnam.

Typ. loc.: Paris.

ECHINISCUS SPITSBERGENSIS Scourfield, 1897 (Figs. 265 & 266).

Length 250-300μ; sculpture of the plates presents an assemblage of minuscule grains of polygonal base -- in general pentagons or hexagons -- which are actually small depressions: it is the same type of sculpture possessed for example by *E. spinuloides* or by *E. blumi*. Median plate 3 lacking; the lateral appendices A, B, C, D are all filaments and increase in length from A to D: the original author did not cite "points" E in the notches of the terminal plate IV. The typical dorsal appendices include long spines C^d, short curved spines D^d, small dorsolateral spines (teeth) D'; sometimes C^d is transformed into a filament, D^d becomes a long spine, D' may be lacking (?). Dentate collar on the 4th pair of legs, with teeth very close together at the bases (Murray, 1911), internal claws with curved spur, positioned on the first proximal third of their length. Eggs reddish, or orange color, deposited in the exuvium (from 1 to 6).

According to the description reported here, *E. spitsbergensis* is distinguished from *E. menzeli* by the absence of small spines ("points") E in the notches of the terminal plate and from *E. spinuloides* by the same characteristic and besides by having dorsolateral teeth or spines only at D', rather than at B', C', and D'. It may be however a very artificial distinction, because *spitsbergensis* is a species endowed with great variability -- often difficult to separate from others of its group -- so that previously Cuénot (1932) proposed uniting into a single species *spitsbergensis*, *menzeli*, and *spinuloides*. It is then advisable to examine all the species included in the so-called "*spitsbergensis* group", of which is included *E. spitsbergensis* Scourfield, *E. spinuloides* Murray, *E. menzeli* Heinis, *E. marinellae* Bartos, *E. melanophthalmus* Bartos, and what they have in common (Petersen, 1951):

1) The polygonal sculpture of the plates;

2) the presence of lateral appendices A, B, C, D (B may be lacking, as not rare in *Echiniscus*) and of 1-4 teeth E in the notches of the terminal plate (with exception of *E. spitsbergensis*, but it is possible that these, very minuscule, may have escaped the observation of the original author);

3) the presence of dorsal appendices C^d and D^d;

4) the presence of dorsolateral appendices in various numbers in the different species (D' in *spitsbergensis* and *menzeli*; C', D' in *melanophthalmus*; B', C', D' in *spinuloides* and *marinellae*; this last species possesses the dorsolateral teeth, particularly B', in more dorsal position than in *spinuloides*);

5) the absence of the median plate 3;

6) the dentate collar of the 4th pair of legs well developed,

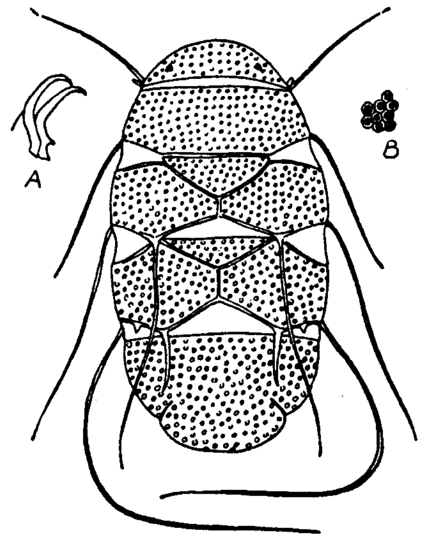


Fig. 265 - *E. spitsbergensis* Scourfield. A, internal and external claws; B, detail of the sculpture of the plates.

composed of large teeth (from 4 to 9, but in general 4-5, not in contact with each other at the bases);

7) presence of spurs, in various positions, on the internal claws and of slender spines at the base of the external claws;

8) eye spots red, brownish, and black, or absent (*menzeli*).

In the abundant Greenland material, studied by Petersen, in also Hungarian and Bulgarian, examined by G. Iharos (Fig. 266) and finally in material of various sources, which we have had an occasion to observe individuals or entire populations in which the characters may be considered as overlaps between one and another of the 5 species of the "*spitsbergensis* group"; it is not possible -- especially for reason of space -- to go into here in great detail, for which the reader is referred to the work of G. Iharos (1961) and particularly of Petersen (1951), but we restrict ourselves to summarize the more interesting points and to add some personal consideration:

a) It is probable that *spinuloides* constitutes the adult stage of *spitsbergensis*. G. Iharos (1961) is however of different opinion, because in moss, which contains the two species together, it is possible to collect series of individuals -- from larva of two claws to adult -- all without spines E (*spitsbergensis*), or all with spines E (*spinuloides*), as shown in Fig. 266. It seems however that the conclusion which the author reached, that such two species may then be considered distinct, may not be accepted at once; in fact they have not been reared from the eggs, while it is always possible -- from a numerous population of a very variable species -- to pick out series of individuals which simulates the development of two or more distinct

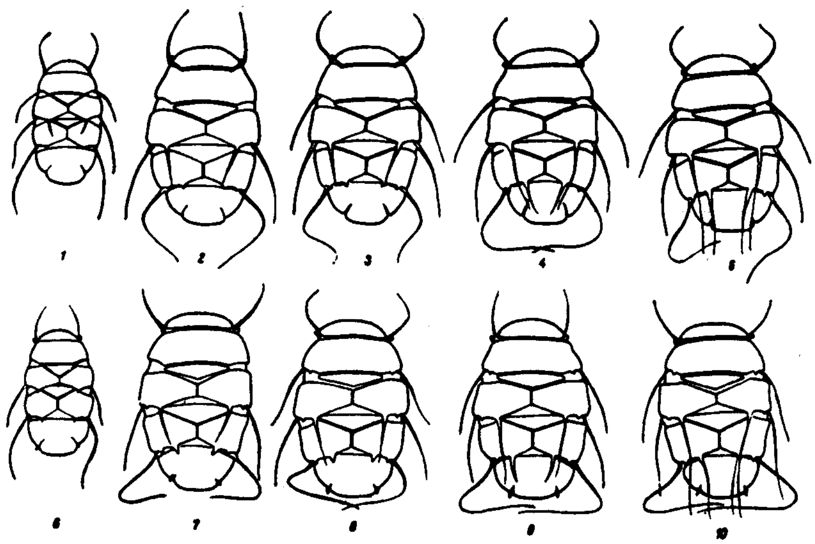


Fig. 266 - From 1 to 5: stages of development of *E. spitsbergensis*: 1, larvae of two claws; 2, juvenile stage with 4 claws; 3, 4, adult stages; 5, typical adult. From 6 to 10: stages of development of *E. spinuloides*: 6, larvae of two claws; 7, juvenile stage of 4 claws; 8, 9, adult stages; 10, typical adult (from G. Iharos).

species; it is added that we have seen -- if however rare -- larvae of two claws without spines E in populations of *spinuloides*. It is noted finally that the adults, considered as *spitsbergensis* by Iharos, measures 300μ maximum, while those considered as *spinuloides* measures 500μ; that, on the one hand the different size of the two distinct species may be significant, while on the other it may instead indicate an incomplete development in the individuals of 300μ and their possible transformation into *spinuloides* in successive molts.

b) It is possible that *menzeli* may be a synonym of *spitsbergensis* (or rather *spinuloides*), that they should be treated as a single species.

c) *E. melanophthalmus* is very similar to *spitsbergensis* and to *spinuloides* and constitutes an overlapping of the limits between these two species, having the dorsolateral appendices C' and D'. It does not seem that the color of the eyes may be determining: there have been observed *spitsbergensis* and *spinuloides* with reddish-brown or blackish eyes by De Coninck, by Petersen, and by us.

d) *E. marinellae* seems to be the species, which more clearly stands out from the others of the "*spitsbergensis* group", not so much by the lacking of B (common in the *Echiniscus*), as much as by the particular facetting of the terminal plate; however Petersen has observed some Greenland *spitsbergensis* with the facetting characteristics of *marinellae* (2 lateral facets and 3 medio-caudal facets between the notches). It should not however be excluded that *marinellae* may be young individuals of *spinuloides* for which Bartos has found egg-bearing exuvia with the appendices described for the species: but it is noted that the *Echiniscus* may deposit eggs before reaching complete development.

e) Fairly often the dorsolateral teeth are reduced to such an extent in size, it may not be decided with confidence of its existence or absence: in rare cases they are certainly absent.

f) We think finally very probable that also *E. rosaliae*, described by Mihelčič in 1951, may be only a variety of *spinuloides* with black eyes, which is very near to *menzeli*, because the only dorsolateral appendices present are D' and there is a small tooth in the notches of the terminal plate.

In conclusion, when abundant material is examined, only few individuals have the considered typical characteristics of one of the three species *spitsbergensis*, *spinuloides*, *melanophthalmus*, while more numerous are the tardigrades considered as overlapping limits between one species and the other (always leaving out of consideration the color of the eye spots); also the facetting of the cephalic and terminal plates presents considerable variation; it is then probable that the species may be only one, and that is *spitsbergensis*, endowed with extreme variability. *E. menzeli* is very near to *spitsbergensis*, and therefore to *spinuloides*, and may perhaps be considered only a variety of this last: it is noted however that Petersen haws not observed any individuals identified as *menzeli*, in his abundant Greenland material. With regard to *marinellae* it is possible -- but not certain -- that it is incompletely developed *spinuloides*. As we see, there are many good reasons (but perhaps not sufficient) to unite in a single species *spitsbergensis*, *spinuloides*, and *melanophthalmus*, while there are less for including *marinellae*, *menzeli*, and *rosaliae*: we have uncertainly preferred to still consider distinct the six species, however thinking very probable that the first three may be all included in *spitsbergensis*.

E. spitsbergensis is cited from many localities in Scotland, Germany, Switzerland, Hungary, Bulgaria, Rumania, Afghanistan, Greenland, and the Arctic, and has been found also in Italy (Pusteria Valley and Aosta Valley).

Typ. loc.: Spitzbergen Island.

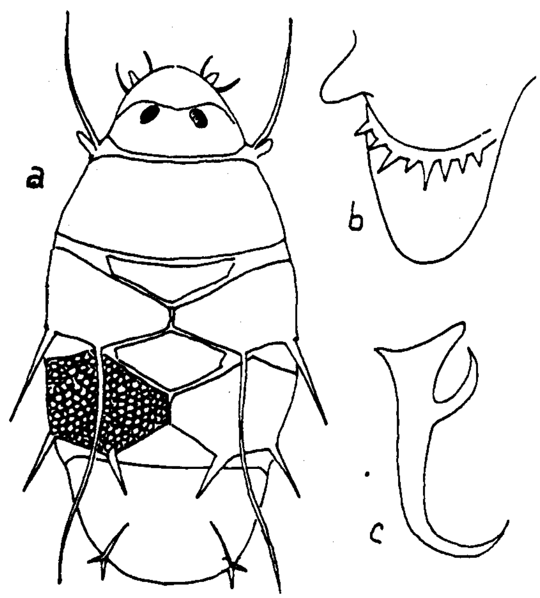
ECHINISCUS STORKANI Bartos, 1940 (Fig. 267).

Length 160-265μ, of brownish-red color, with large eye spots. The sculpture is a regular granulation, composed of single granules of about equal size. Median plate 3 absent. The lateral appendices, besides cirri A (32-41μ), are long spines C (19-38μ), sometimes absent, D (16-22μ), and short spines E, simple or double; dorsally exists filaments C^d (41-81μ) and short spines D^d (5-8μ). First pair of legs with spine; the fourth pair bears the usual papilla and the dentate collar, composed of 7-8 sharp teeth, rather distant from each other; internal claws with long spur curved toward the base. Deposited are 2-3 eggs in the exuvium; the larvae of 2 claws measure 108-120μ, are sometimes provided with spines C and D and spicules E.

The species, which belongs to the "*spinulosus* group", is distinguished from *E. trisetosus* by the absence of the median plate 3 and because the lateral appendices C and D are spines, not filaments.

E. storkani was collected only in Czechoslovakia and Rumania.

Fig. 267 - *E. storkani* Bartos. a, dorsal view; b, dentate collar; c, internal claws of the 4th pair of legs (from Bartos, modified).



ECHINISCUS SYLVANUS Murray, 1910 (Fig. 268).

Length 275μ, color yellow; the sculpture of the plates is composed of dots of different size, positioned at different distance between each other, with appearance of pores or of small depressions. The paired plates (II and III) present -- near the rostral margin and parallel to it -- a slender projecting band, which is extended to the sides. Median plate 1 widely separated from the scapular plate; median plate 2 subdivided, with a smooth transverse band, in two distinct sculptured parts; median plate 3 absent. The terminal plate is facetted, with 3 facets, of which the median caudal is indistinctly subdivided into two; there exists the usual notches. Cephalic papillae well developed, internal and external buccal cirri short; the lateral cirri A, of about 50μ, are much larger and wider than in the other *Echiniscus*, are not sharp at the ends, but with distal ends truncate and scarcely rounded; clava large and triangular. Fourth pair of legs provided with dentate collar (8-10 sharp teeth very close together, but not in contact); claws large (about 25μ): the internal bear -- near the base -- a small curved spur.

The species was cited only from Canada (Ontario).

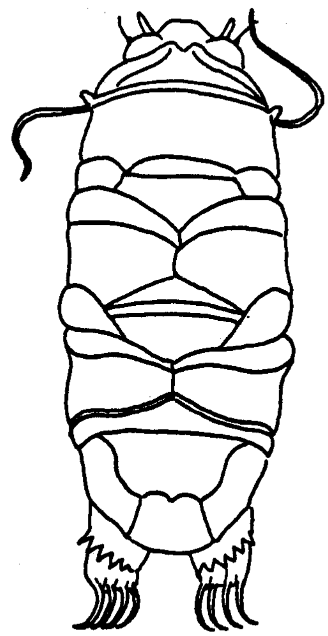


Fig. 268 - *E. sylvanus* Murray (from Murray, redrawn).

ECHINISCUS TARDUS Mihelčič, 1951 (Fig. 269).

Length up to 250μ, color dark red; eye spots absent, but in place of each of them exists a small cuticular projection. The sculpture is composed of a dense and uniform granulation and the individual granules assume -- by a determined focal setting of the objective -- the appearance of hexagons with slender sides; such sculpture is extended on all the plates, including those median. Besides the usual cephalic appendices, the only cuticular appendices present are the lateral cirri A, up to 80μ long (filaments); the clava is minuscule. The separation line between the dorsal plates and the medians are slender and not very evident. The median plate 3 is absent; the terminal plate is not facetted and has the two usual notches, which however are not drawn in the figure. Legs long and robust: those of the 4th pair bear a dentate collar (9 teeth); claws large, sickle-shaped: the internals with spur turned toward the base.

The species is distinguished from others of the "*arctomys* group" by the presence of papillae, rather than eyes, and by the characteristic type of sculpture.

The author named this *Echiniscus* as *tardus* because of the particular slowness of its movement; it was collected a few times in Austria, in moss on the trunk of a tree, and always in scarce numbers of individuals.

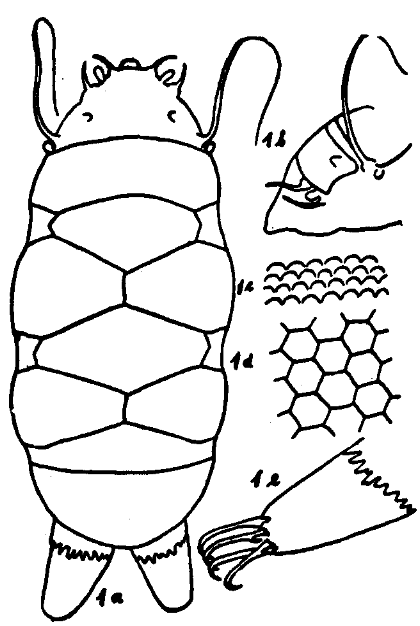


Fig. 269 - *E. tardus* Mihelčič. 1a, dorsal view; 1b, cephalic region, lateral view; 1c, 1d, detail of the sculpture; 1e, claws (from Mihelčič).

ECHINISCUS TENUIS Marcus, 1928 (Fig. 270).

Length 140-190μ, colorless or yellowish, eye spots black. All the plates are everywhere smooth, not sculptured: only if the tardigrade is completely dried is a regular and extremely fine punctation rendered visible; plates slender, delimited only by cuticular folds. Median plate 3 absent; paired plates II and III with longitudinal folds, which leave the anterior margins and runs obliquely until it reaches to about the middle of each plate. Terminal plate with lateral facets and with two very short notches, which may easily escape observation; in its general appearance, this plate reminds one of the terminal of *B. parvulus*. Cephalic appendices normal: there are no other cuticular appendices except for lateral cirri A, about 25μ long: however the posterior angles of the paired plates are shortly pointed. There is no dentate collar on the 4th pair of legs; the claws, about 8μ long, are smooth, all lacking spurs.

The species was cited for Indonesia (Lombok Island) at about 1,600 m altitude and for Brazil (State of San Paolo).

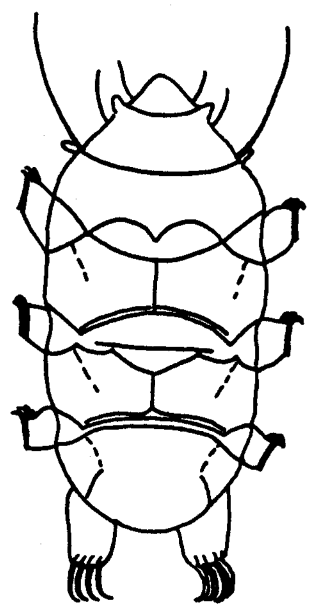


Fig. 270 - *E. tenuis* Marcus (from Marcus, redrawn).

ECHINISCUS TESSELATUS Murray, 1910 (Fig. 271).

Length about 200μ, color yellow, lateral cirri A very long. The sculpture on the plates is composed of very large papillae, with granular appearance, or of hemispherical knobs. The plates are variously subdivided by smooth bands, in the following characteristic manner:

- scapular plate subdivided into 10 individual platelets
- paired plates II and III, each subdivided into 3 parts by 2 transverse lines
- terminal plate subdivided in 6 individual facets.

The lateroventral margins of the two paired plates project laterally as far as the edge and are smooth, deprived of sculpture, the terminal plate has the usual notches. The fourth pair of legs with dentate collars, internal and external claws smooth, without spurs. In the exuvium are deposited 1-2 eggs.

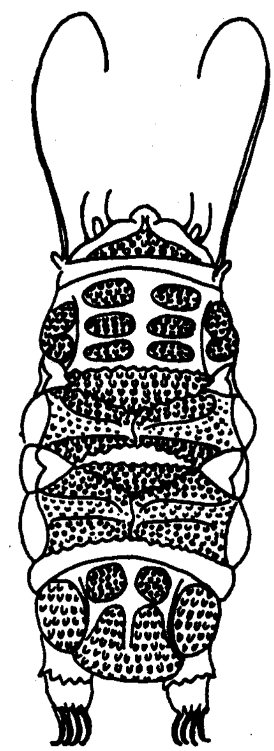


Fig. 271 - *E. tesselatus* Murray (from Murray, redrawn).

E. tesselatus is distinguished from *E. kofordi* by the different subdivisions of the scapular and terminal plates and by the cirri A of *tesselatus*, much longer.

The species was collected only in Australia (Queensland).

ECHINISCUS TESTUDO (Doyére, 1840) (Figs. 272 and 273).

= *Emydium testudo* Doyére, 1940
= *Echiniscus bellermanni* Schultze, 1840
= *E. inermis* Richters, 1902
= *E. trifilis* Rahm, 1921
= *E. filamentous mongoliensis* Iharos, 1973
(not *E. filamentosus* Plate, 1888)

Length up to 360μ, color brownish-red, brick red, or yellowish, eyes red. The sculpture is composed of rounded pores, of a little irregular size, variously sparse and fairly distant from each other (*merokensis* type sculpture).

The median plate 3 is not always present: when it is lacking there is however a punctated zone between the plate III and the terminal, which is not facetted. In the variety *quadrifilis* of Cuénot are present the lateral appendices A, B, C, E, all filaments; in the variety *trifilis* of Rahm are present only A, C, E. On the dorsum exists only the spines D^d, of medium length, or short. The species often has anomalies in the appendices.

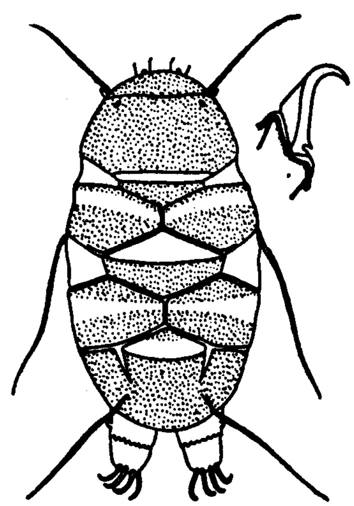


Fig. 272 - *E. testudo* (Doyére). Forma *trifilis*, and internal claws of the 4th pair of legs.

Usually A is the shortest appendices, E the longest, while B and C have about equal length. Fourth pair of legs with dentate collar; internal claws with minuscule spur, difficult to see; external claws smooth, however we have observed various times individuals with a clear and straight spine, at a certain distance from the base (Rahm had already described South American examples with small spine on the external claws). Up to 7 eggs deposited in the exuvium; the larvae of two claws, from 110 to 148μ long, have only A and E and sometimes, but not always, D^d; the young of 4 claws (160-180μ) have already filaments C, while B appears later.

Cuénot observed that the *trifilis* variety may be in pure colonies, while *quadrifilis* is always intermingled with *trifilis*; to give an idea of the numerical proportion between the two varieties in the same moss, we report some data: Marcus observed 10 *quadrifilis* and 29 *trifilis*; Ramazzotti reports in material from Pallanza 1 *quadrifilis* opposed to 20 *trifilis* and, in material from Bergamo, 8 *quadrifilis* opposed to 36 *trifilis*.

Observations completed by Maucci on abundant Turkish material have instead resulted in the existence of populations in which the ratio between *trifilis* forma and *quadrifilis* forma appears reversed, and even pure populations of *quadrifilis*. In general we have observed that in the mixed populations of the two forms, the *quadrifilis* presents examples of larger size, and therefore more complete development.

According to Maucci, in standard individuals, *trifilis* forma, or *quadrifilis* forma may not have any taxonomic value. In standard populations instead there may be considered two types of populations, which is possible to attribute perhaps to subspecies value:

E. testudo testudo (Doyére): populations in which the acquisition of the appendices B is the rule, by which the *quadrifilis* forma reaches, more or less precociously of all or almost all the individuals; *E. testudo trifilis* Rahm: populations in which the *quadrifilis* forma is not reached by any individuals, or only by extremely few individuals at full development.

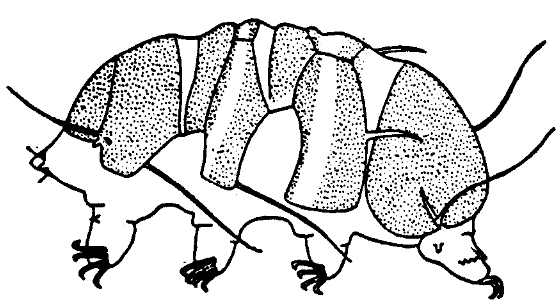


Fig. 273 - *E. testudo* (Doyére), "*quadrifilis*".

The nominal subspecies has been as yet noted only from diverse localities in Turkey. The subspecies *trifilis* appears instead very frequently, and has been cited for a great many European localities (Italy included), for South America, Spitsbergen Islands, India, Turkey, Afghanistan.

The species seems to prefer strongly insolated moss, with long periods of desiccation, and appears not rare even in very muddy moss.

Typ. loc.: Paris. For *E. bellermanni*, typ. loc.: Greifswald (Pomerania, Germany).

ECHINISCUS TRISETOSUS Cuénot, 1932 (Fig. 274).

Length up to 375μ, but also less, eye spots red. The sculpture of the plates is similar to that of *E. blumi*: with a determined focal setting of the objective is seen clear circles not touching, on dark background; at another focal setting, there appears clear polygons, rather regular (often hexagons), touching or not, and with dark spots at the center; the sculpture may however also be reduced and a regular and dense granulation. The paired plates II and III often show a smooth transverse band, lacking sculpture; the median plate 3 is present, sometimes very visible, sometimes instead only more or less distinctly delimited at the sides, with sculpture scarce or almost absent, little more thick than the surrounding cuticle. Terminal plate (IV) not facetted, with the two usual notches. Cephalic appendices normal, cephalic papilla elongated.

The lateral appendices -- all filaments -- are: cirri A (44-78μ) with enlarged base, C (51-155μ), D (50-125μ); there may be -- or not -- a

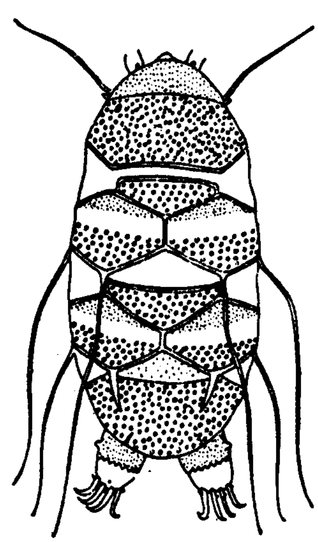


Fig. 274 - *E. trisetosus* Cuénot.

spicule ("point") E in the notches of the terminal plate, general extremely short, rarely fairly long. Dorsally there are long filaments C^d (82-130μ) and short spines D^d (11-27μ) which may however be reduced to simple triangular teeth. The measurements furnished for the appendices are only indicative, because there is considerable variability even in the appearance of the same appendices: therefore, for example, C, D, C^d may be spines, rather than filaments; D^d may be lacking, some appendices may become bifid, or else asymmetrical, that is exist on a single side, etc.

Legs short and large, basally sculptured: fourth pair of legs with papilla and dentate collar (6-8 teeth); the internal claws of all the legs bear a spur; the external of the 4th and sometimes of the 3rd pair of legs have one, two, or three straight spurs, of which the basal is longest. It deposits up to 5 eggs in the exuvium; the larvae of two claws of 160-178μ length -- and sometimes even young of 4 claws of 190-207μ, already provided with spur on the external claws of the 4th pair of legs -- may still be lacking C: however larvae of two claws have been observed of 130μ, which already possess all the appendices (A, C, D, C^d, D^d).

E. trisetosus belongs to the series of *blumi- canadensis* species, and is certainly the most frequent. There have been found both pure populations, and mixed populations. For more details, we refer the reader to the description of *E. blumi.*

The species is cited for many localities in Europe, North America, and Turkey. It was even collected -- however rarely -- in sandy soil.

ECHINISCUS TROJANUS Maucci, 1972 (Fig. 275).

Length 230-300μ. Color yellow-orange or greenish- yellow. The sculpture is formed of large pores, round, surrounded by a ring of coarse dots, very near each other; between the pores the cuticle is finely punctated and presents a thin reticular design. At lower magnification the sculpture has the appearance of adjacent polygons, similar to that of *E. blumi*, and becoming finer and more dense at the caudal margins of the plates. Sometimes the paired plates I and II present a transverse band devoid of sculpture. The cuticle between the plates is finely punctate, except in the zone where the unpaired plate 3 should be found -- which is absent -- where the granulation is more marked.

The animal is very squat and massive, and the plates of the armor are very robust; the posterior angles of the scapular plate project markedly to the outside, almost simulating two spines; the terminal plate is not facetted.

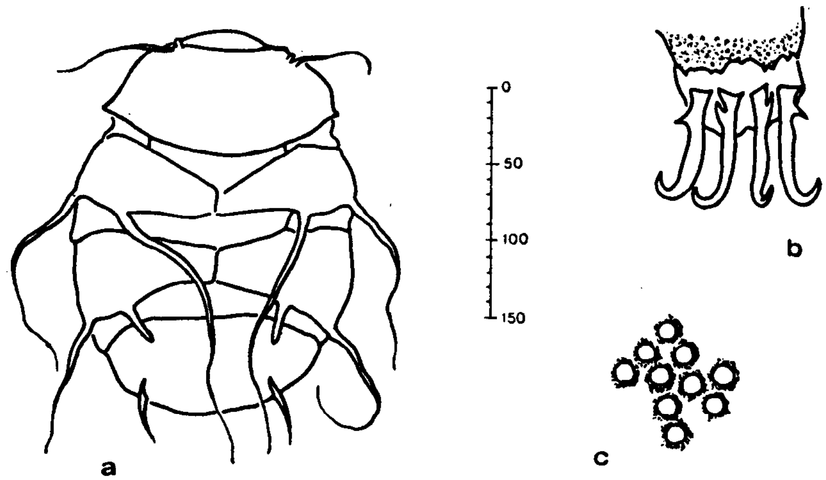


Fig. 275 - *E. trojanus* Maucci. a, habitus; b, claws of the 4th pair of legs; c, detail of the sculpture (from Maucci).

Laterally exists filaments C, D, and spines E, of variable length (C from 70 to 130μ, D from 60 to 160); the spines E are slightly curved, short or extremely short. The lateral filaments are very robust, with swollen bases, and are suddenly attenuated, at about half their length. Dorsally there are robust and long filaments C and short and stumpy spines D. Asymmetry of the appendices is not rare.

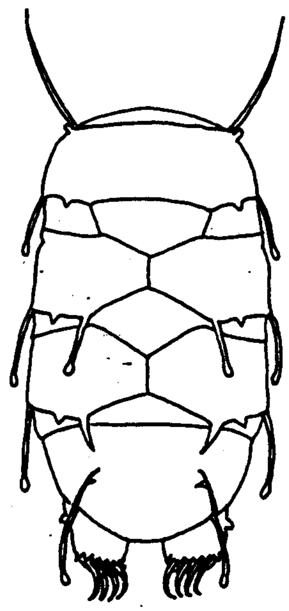
First pair of legs with a large and robust spine, about 8μ long; fourth pair with dentate collar (8-10 irregular teeth). Internal claws with small spur, but very visible, external claws with a straight spine.

The species was collected only in Turkey, near to the ruins of Troy (Truva), and on Boz Dag (to the east of Smyrna).

ECHINISCUS TYMPANISTA Murray, 1911 (Fig. 276).

Length 240μ, red; the sculpture is a dense, regular punctation, composed for the greatest part of small dots and in small measure of other dots, somewhat larger and with the appearance of pores, distributed here and there between the first. Median plate 3 absent, terminal plate with two notches. Laterally, besides cirri A, there are appendices B, C, D, E, in the shape of cylindrical rods, 35-45μ long, enlarged and rounded at the apices, whose appearance brings to mind a drum stick; dorsally exists appendices C^d, also in the shape of drum sticks, and short spines D^d with

Fig. 276 - *E. tympanista* Murray
(from Murray, redrawn).



wide bases; in the dorsolateral position are present minuscule teeth B', C', D', E'. Fourth pair of legs with papilla and dentate collar; internal claws provided with spur. Eggs unknown.

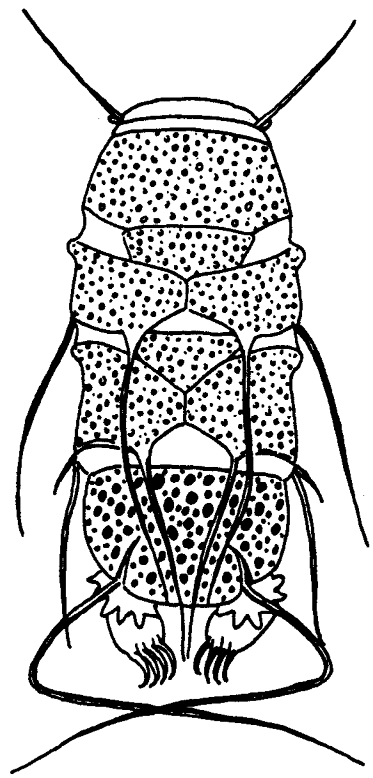
The species has been cited only from Scotland.

ECHINISCUS VELAMINIS Murray, 1910 (Fig. 277).

Length up to 245μ, sculpture composed of small depressions of different size, with appearance of pores irregularly arranged; the sculpture is very dense and fine on all the plates -- including the medians 1 and 2 -- while it is very coarse and less dense on the terminal plate (IV), which possesses the usual two notches. Median plate 3 absent. The lateral appendices -- besides cirri A of 75μ -- are filaments C (125μ), D (80μ), and E, the longest of all (250μ); often there is also a short curved spine, inserted near to the base of filaments D. Dorsally exists long filaments C^d and D^d. Fourth pair of legs with papilla and dentate collar, composed of 5-6 teeth strongly obtuse and large; internal and external claws smooth, without spur. Eggs unknown.

The species has been collected only in New Zealand.

Fig. 277 - *E. velaminis* Murray
(from Murray, redrawn).



ECHINISCUS VINCULUS Horning, Schuster & Grigarick, 1978 (Fig. 278).

Length from 150 to 260μ, with an average of 200μ. Internal buccal cirri 10μ long, external 14μ. Eyes absent. The sculpture consists of pores or irregular granules, with interposed wide smooth areas on the scapular and terminal plates. The only appendices present are cirri A, rather short.

The first pair of legs present a small papilla, the fourth a rounded papilla and a dentate collar of 11-15 teeth. The internal claws of all the legs have a small spur, near to the base.

The species belongs to the *arctomys* group, and is near to *E. kofordi*, from which it is distinguished by the sculpture.

E. vinculus has been found in different localities from New Zealand.

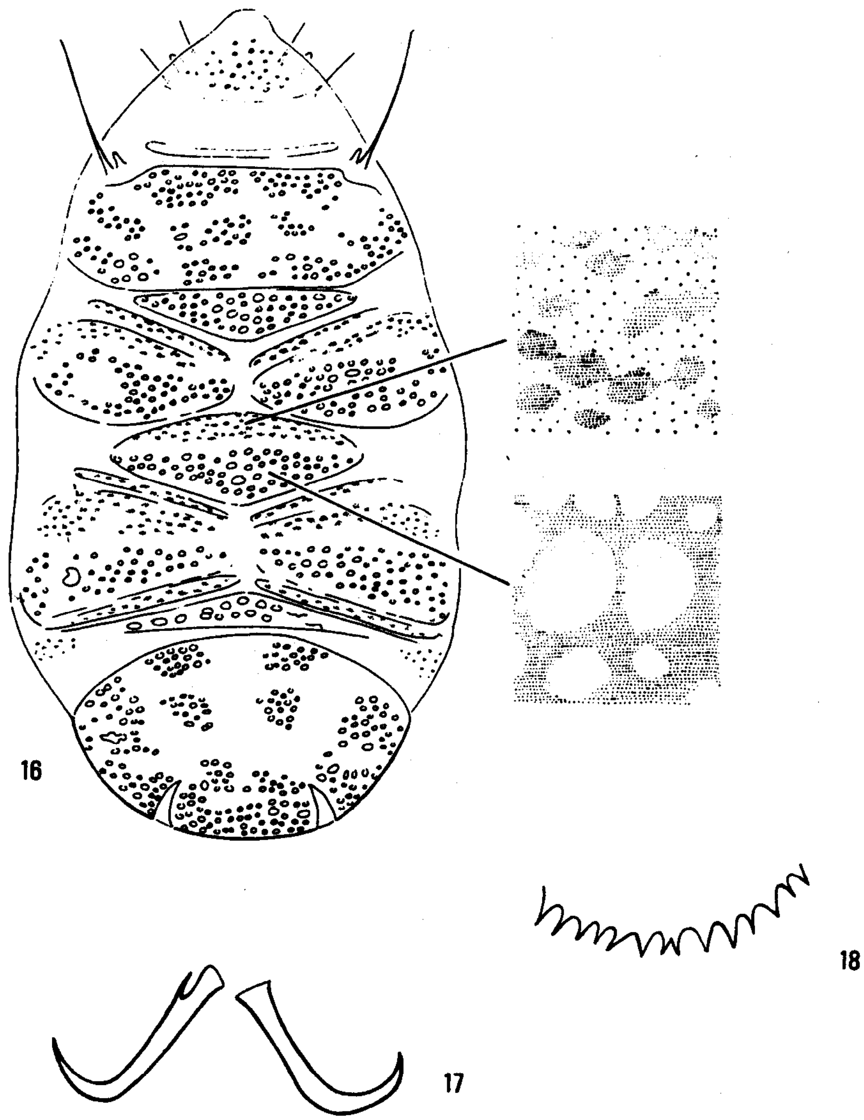


Fig. 278 - *E. vinculus* Horning et al. 16, dorsal view, with detail of the sculpture; 17, claws of the fourth pair of legs; 18, dentate collar (from Horning, Schuster and Grigarick).

ECHINISCUS VIRGINICUS Riggin, 1962 (Fig. 279).

Length up to 183μ, sculpture composed of a dense granulation. Presence or absence of eye spots and coloration of the tardigrade not indicated by the author. The internal and external buccal cirri are slender filaments, the cephalic papilla is well developed.

The lateral appendices are spines C, D, E (respectively 18-22μ, 12-21.6μ, 21.6-25μ long) with enlarged bases; dorsally, exists short, robust spines C^d (7μ) and D^d (10,8-14.4μ).

Median plate 3 present, terminal plate not facetted, with the usual two notches. Dentate collar with 9 teeth on the fourth pair of legs; internal claws of all the legs with strong spur curved in proximal direction, positioned at considerable distance from the base of the claw. The description of the author does not cite the presence of papilla on the 4th pair of legs and of the spine on the 1st pair, which on the other hand are not figured even on the drawing and which should then be considered absent.

E. virginicus was collected in three different localities from Virginia (U.S.A.) and precisely: Mountain Lake, Giles County; Johns Creek Valley, Craig County; Johns Creek Mountain, Craig County.

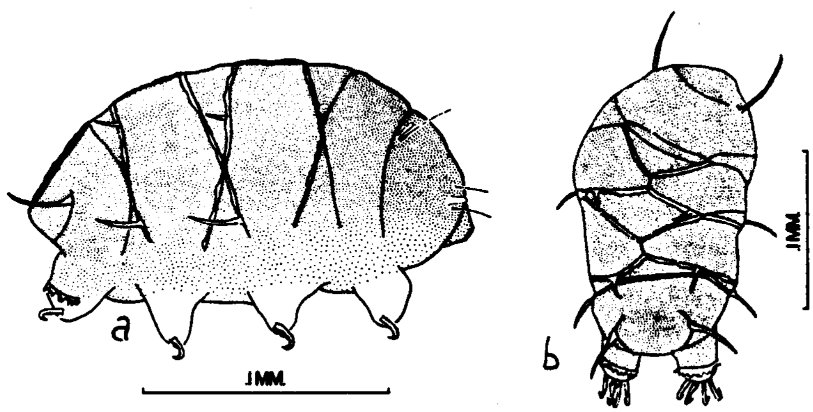
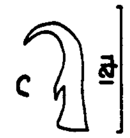


Fig. 279 - *E. virginicus* Riggin. a, lateral view; b, dorsal view; c, internal claws of the 4th pair of legs (from Riggin).



In the 1972 edition of the present monograph, *E. virginicus* was considered as *spec. dubia*, very near to *E. quadrispinosus brachyspinosus*. The discovery of new material in Florida has made it possible, thanks to the courtesy of Dr. Christenberry, to examine some specimens, recognizing the character of good species.

The sculpture is in fact clearly different from that of *E. quadrispinosus*, and consists of rounded or polygonal pores, small, very dense and regularly distributed.

The lateral appendices are filaments A and robust spines B, C, D, and E. Dorsally there are very short spines C, at times hardly a hint or even absent, and spines D which may even become considerably long and robust.

The spine on the first pair of legs, and the papilla on the fourth (not mentioned in the first description) are in reality absent.

The new examples were collected in Walton Co., Florida, in lichens and hepatics.

ECHINISCUS VIRIDIS Murray, 1910 (Fig. 280).

Length up to 250μ, legs large and robust, body wide and massive; lateral cirri very short (30-40μ), inserted on a conical base. The description of Marcus (1936) says:

"The color of the plates is olive-green, with spots of a darker green and not with small depressions or tubercles (projections); the median spots have larger size, those lateral smaller. The coloration of the plates is extended to the fourth pair of legs as far as the dentate collar, but not on the cuticle between the plates; the interior of the body is red, as is the majority of the *Echiniscus* and *Pseudechiniscus*. The delineation of the plates is very clear, with exception of the median plate 3, which is reduced only to a zone badly defined and spotted, positioned immediately behind the second paired plate. The paired plates, each with three transverse bands, the anterior and the posterior darker and the median lighter, with smaller spots."

From the description it should then be deduced that it is lacking all types of sculpture, but that are present only green spots or varied size and intensity; on the other hand Ramazzotti had occasion to examine numerous green *Echiniscus* -- coming from moss at Rio de Janeiro -- which showed on the plates, rather than spots, regularly arranged tubercles; however even du Bois-Reymond Marcus (1944) says the "sculpture" of the plates, which may be extended to the base of the first pair of legs (also that of the fourth).

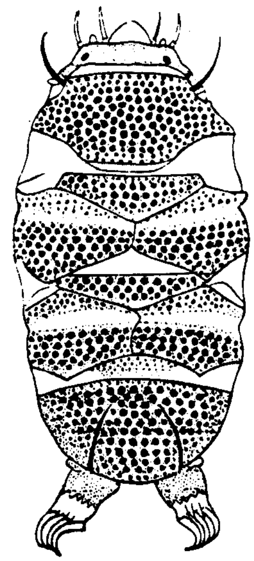


Fig. 280 - *E. viridis* Murray (from du Bois-Reymond Marcus, redrawn).

We think therefore advisable to amplify the description of *viridis* and to consider as belonging to this species also the individuals with green plates uniformly granulated and with darker spots present or absent.

The median plate 1 is sometimes -- but not always -- rather far away from the scapular plate (I) and in contact with the first paired plate (II); the terminal plate is not facetted and has the usual two notches. First pair of legs with small spine, fourth pair with papilla and dentate collar; long claws (25μ), those internal with slender and short spur, sometimes very difficultly visible. Eggs unknown; Ramazzotti observed larvae with two claws which measured 84μ in length.

The distinction between *viridis* and the remaining three species of the "*viridis* group" (to which belongs *Echiniscus* of green color, without other appendices except the cephalic and cirri A) may be based on the following characteristics:

- *perviridis* has cirri A much longer (150-170μ);
- *rufoviridis* is of green color only caudally, with short cirri A (30-40μ);
- *viridissimus* has on the plates whitish and also black spots, cirri A measures about 80μ, lacking spurs on the internal claws.

It is noted that, besides the preceding, this is another *Echiniscus* of green color. *E. pooensis*, which is however easily recognizable by the presence of lateral and dorsal appendices (and by such cause does not belong therefore to the "*viridis* group"). We add that the green *Echiniscus*, described by Ramazzotti (1944) as *E. viridis* is certainly different from the four species of the "*viridis* group", considered here; we do not think however to make a new species since, having collected a single individual and not having succeeded in finding others, in spite of repeated and accurate research on the mosses of the same locality.

E. viridis was cited for Scotland, Brazil, Hawaiian Islands, Galapagos, and different localities in the United States.

ECHINISCUS VIRIDISSIMUS Péterfi, 1956 (Fig. 281).

Length 180μ; color olive green, not only of the plates, but of all the cuticle of the body, including the ventral surface, the legs, the claws, and the appendices: the plates, the claws, and the dentate collars of the 4th pair of legs are however of more intense green color. The plates present small white spots, irregularly arranged; the paired plates (II and III) have a rostral zone of apparently black circles, but which are actually small depressions, arranged near to each other and separated by clear protruding in profile, which outlines a reticular design; posteriorly to this rostral zone, the paired plates bear a whitish and brilliant transverse band, which follows a caudal zone with small white spots, of which is as said above. Besides this sculpture, there is another, composed of a very fine and regular granulation, which is extended to the cuticle between the plates and on the legs. The third median plate (3) is absent, but the cuticle, which occupies its position, is strongly covered by the same type of sculpture, existing in

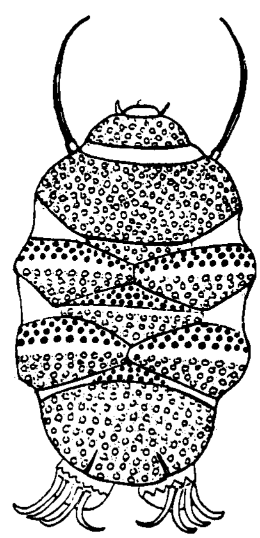


Fig. 281 - *E. viridissimus* Péterfi (from Péterfi, redrawn).

the rostral zone of the paired plates (black circles). Terminal plate not facetted, with the usual two notches. All the plates -- as is characteristic for the species of the "*viridis* group" -- appears more clearly delineated than in the other *Echiniscus*.

Cephalic appendices normal, cirri A about 80μ long, clava elongated; there are no other lateral or dorsal appendices. The legs of the first pair bear a small spine, those of the 4th pair a basal papilla and a dentate collar, composed of large triangular teeth. Claws simple, without spurs (thus wrote the author, but it is noted that -- in the "*viridis* group" -- the spurs are often extremely slender and visible only with immersion objective and phase contrast); the claws have basal part straight, which are hook-shaped at the apices: their length is about 20μ on the 4th pair of legs and about 16μ on the other legs. Eggs unknown.

For the distinction of *viridissimus* from the other three species of the "*viridis* group" (*perviridis*, *rufoviridis*, *viridis*), we refer the reader to what is said in the description of *E. viridis*.

The species was observed in Rumania (near Gilau) in moss very exposed to the sun. Recently it was found at Johnson City (Tennessee, U.S.A.).

ECHINISCUS WEISSERI Maucci, 1978 (Fig. 282).

Length 230μ. Color dark red. The sculpture of the plates is composed of polygonal pores or irregularly covered with stars, very close to each other, so that the distance is less than their diameter. On the cephalic plate, on the scapular, and on the dorsal anterior of the paired plates the sculpture appears less marked, with slightly smaller pores. The cuticle between the plates is not sculptured, except that in the position usually occupied by the unpaired plate 3, which is absent. The terminal plate is not facetted, and the notches are not present.

The internal buccal cirri are rather long (16μ) with a bulbous base. Longer (22μ) external buccal cirri, whose base is enlarged, but not bulbous.

The appendices A are filaments, 45μ long. The lateral appendices are spines, rather rough, 20μ long in B, 25μ in C and in D, while the appendices E are filaments 80μ long. Dorsally exists spines in B (20μ), C (20μ), and D (25μ, strongly bent toward the external).

The first pair of legs carries the usual spine. On the 4th pair exists a dentate collar, composed of four irregular, large, squat teeth, and rather distant from each other. The claws are very long, those of the last pair (longer than the others) measures at least 30μ. Spurs do not exist.

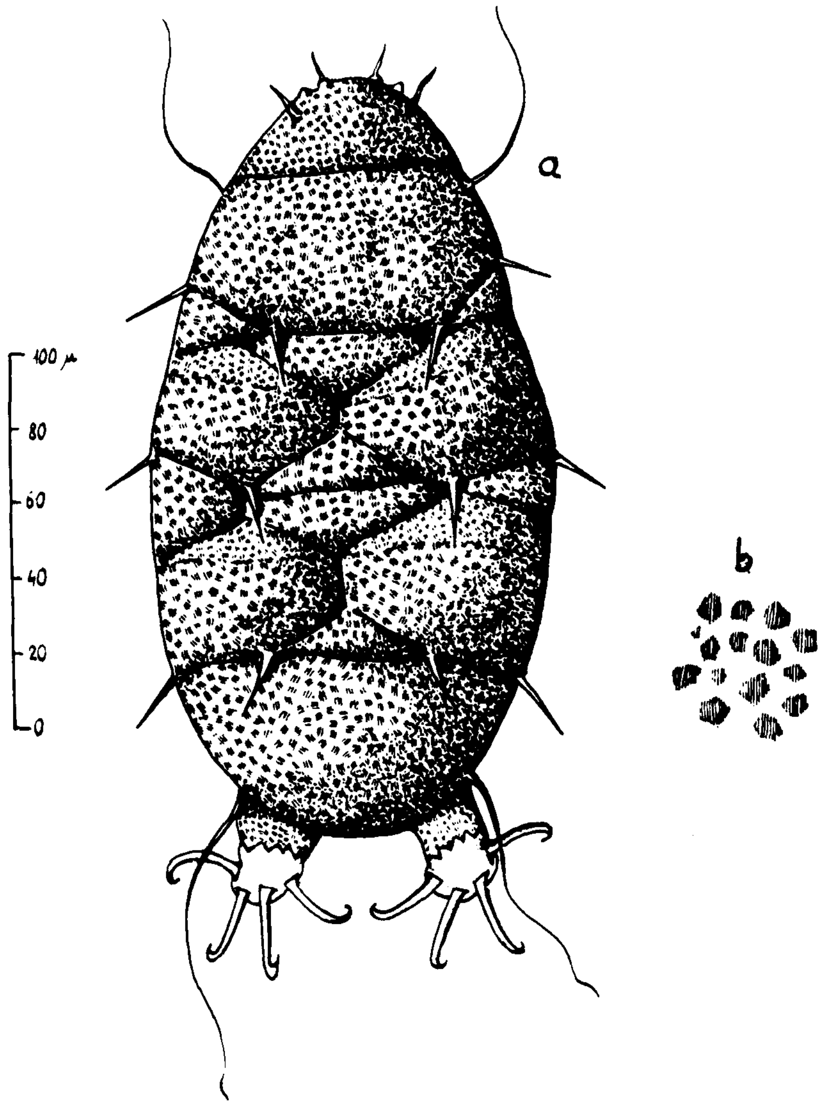


Fig. 282 - *E. weisseri* Maucci. a, habitus; b, sculpture (from Maucci).

A single example has been found at Astana in the Pandjir Valley, at the foot of the Hindukush highlands, in Afghanistan.

ECHINISCUS WENDTI Richters, 1903 (Fig. 283).

Length up to 300μ, color red or even lemon yellow (in examples from Lapland, examined by Ramazzotti), eye spots red. The sculpture -- although variable, especially in the size of the individual elements -- is composed of granules which assume different appearance according to the focal setting of the objective and in Fig. 283c is reproduced a somewhat schematic likeness (with phase contrast): when however the objective is in the more elevated position, there appears small round punctated areas, whose circumference is subdivided into dashes, therefore appears connected by small lines: when instead the objective is in lower position, groups of circular dots are seen, which calls to mind the sculpture of *E. phocae*; the maximum diameter of the circles is included between 2 and 3μ. The paired plates (II and III) show a smooth rostral transverse band, devoid of sculpture; lacking the median plate 3; on the median plates 1 and 2 the individual elements of the granulation often have larger size.

The more evident characteristic of the species is the large length of the lateral cirri A, which may reach 55-70% of the length of the body (for example 148μ in an animal 212μ long). There are no other lateral or dorsal appendices, with the exception of the usual cephalic appendices. Terminal plate in general not facetted: however the individuals of Lapland show a clear indication of facetting; the two notches are present. Legs short and large; the first pair with a small spine, the fourth with basal papilla and dentate collar, composed of many slender teeth; the external claws are smooth, the internal have a curved spur, positioned about half

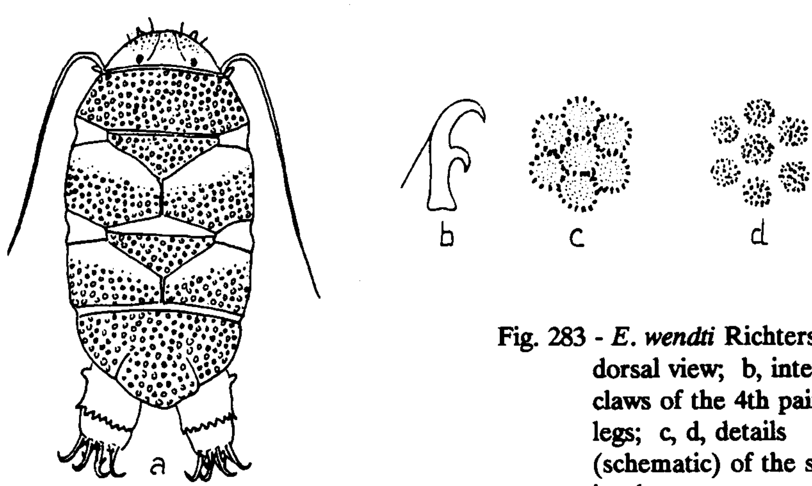


Fig. 283 - *E. wendti* Richters. a, dorsal view; b, internal claws of the 4th pair of legs; c, d, details (schematic) of the sculpture in phase contrast.

their length, particularly robust on the claws of the 4th pair of legs (Fig. 283b). Eggs oval (up to four) deposited in the exuvium; the larvae of two claws, 140-150μ, have more pale color and cirri A of 80μ.

Cuénot (1932) and Richters (1911) were of the opinion that *E. arctomys* and *E. wendti* should be united into a single species; Marcus (1936) is not of this opinion, because *arctomys* possesses -- different from *wendti* -- the terminal plate facetted; we tend to not give great importance -- at least in this case -- to this character, because we have seen *arctomys* with facetting absent, or almost, and *wendti* with clear indication of a facetting. There seems however that the great length of the cirri A and the type of sculpture are sufficiently characteristic for the distinction of *wendti* from *arctomys*: the sculpture of the latter species (which is perhaps still insufficiently studied) is in general, a regular granulation and lateral cirri A are much shorter (50μ or less). *E. kerguelensis* is especially recognized by its poriform sculpture and has short cirri A (50-80μ). *E. capillatus* is distinguished by the presence of median plate 3 and by the lateral cirri A still longer (up to one and a half times the length of the animal), also by the well developed claws (31μ).

E. wendti is known from many European localities (especially from high elevations and including Italy), from North and South America, India, the Arctic, and the Antarctic. Typ. loc.: Spitsbergen and Merok (Norway).

ECHINISCUS ZETOTRYMUS Horning, Schuster & Grigarick, 1978 (Fig. 284).

Length between 235 and 300μ. Eyes absent. Internal buccal cirri 17μ long, external 22μ. The sculpture is composed of irregularly distributed and rather distant pores. The lateral appendices are long filaments A, B, C, and D; the dorsal appendices are sometimes long filaments C. First pair of legs with spine, fourth pair with papilla and dentate collar composed of 11-12 small teeth. The internal claws of the 4th pair have a large spur, while the internal claws of the other legs present a smaller one.

The species has been collected in only one locality in New Zealand.

Genus *ECHINURSELLUS* Iharos, 1968.

Diagnosis: It is the only Arthrotardigrada so far known from fresh water. There exists tubular and spinose processes, laterally, dorsally, and ventrally.

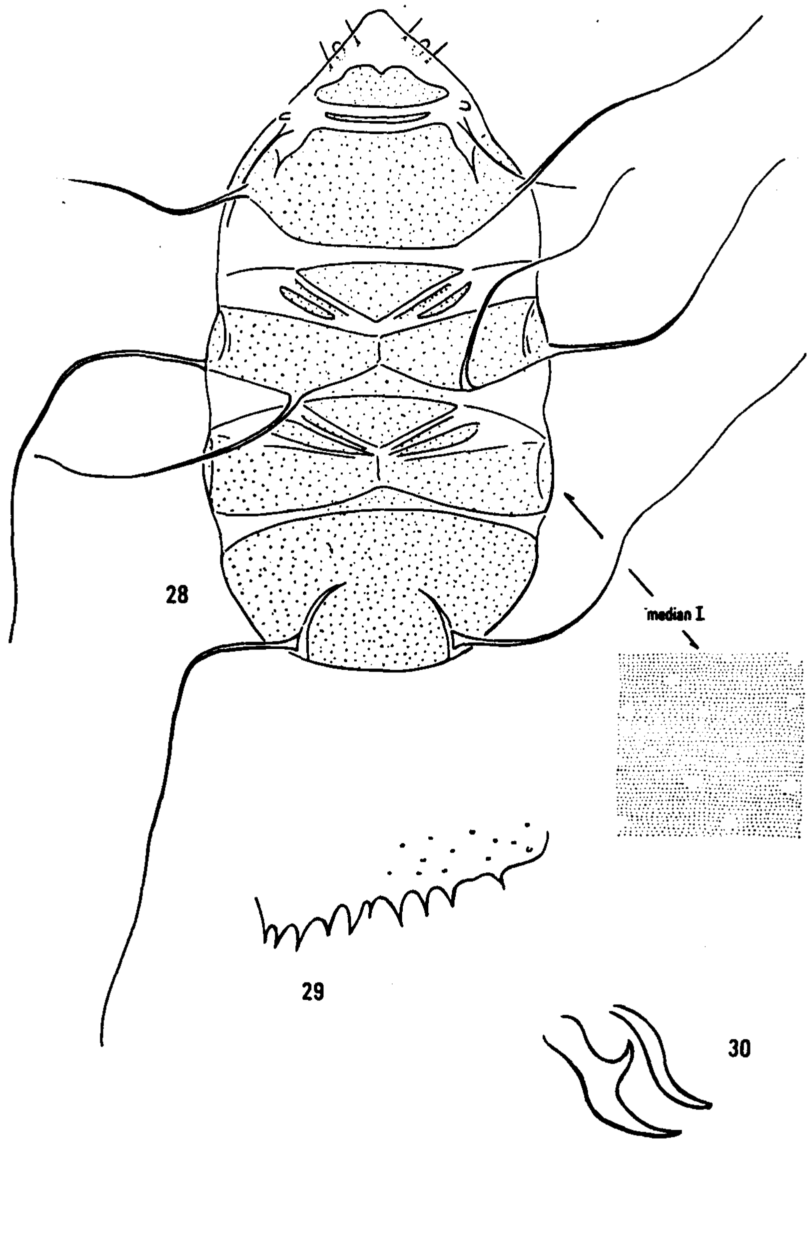


Fig. 284 - *E. zetotrymus* Horning et al. 28, dorsal view and detail of sculpture; 29, dentate collar; 30, claws of the 4th pair of legs (from Horning, Schuster, and Grigarick).

ECHINURSELLUS LONGIUNGUIS Iharos, 1968 (Figs. 285 and 286).

Length without appendices 140-190μ, with appendices up to 230μ; width 65-97μ. Probably colorless, while the cysts are yellowish-brown. At the position of the eyes one sees, on each side, two black triangular spots (perhaps -- writes the author -- small conical projections?); on the ventral surface there are black oval spots. The dorsal and ventral surfaces of the body are covered by slender tubes, in the shape of rods or spines, but not as densely arranged as in *Actinarctus doryphorus*; these cuticular appendices are shorter in the median zone of the dorsum and on the ventral surface, longer on the flanks (10-12μ) and on the caudal part of the body (18-20μ): on the cephalic region they reach maximum length (22-27μ); such measurements refer to an individual of 190μ.

The entire body is surrounded by a gelatinous envelop. The cephalic appendices are: median cirrus, rather short, spine shaped; buccal (or medial) cirri, short and with setous appearance, connected to each other by a gelatinous membrane; lateral cirri A large, bristle-like, distally curved, considerably shorter than in *A. doryphorus*; clava, of shape exactly of clava

Fig. 285 - *Ech. longiunguis* Iharos. Dorsal view (from Iharos).

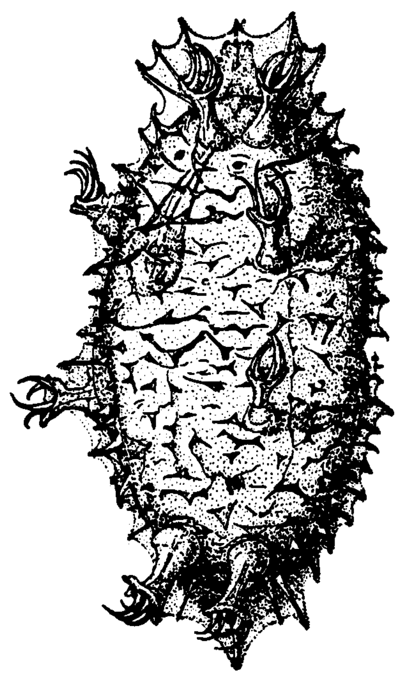
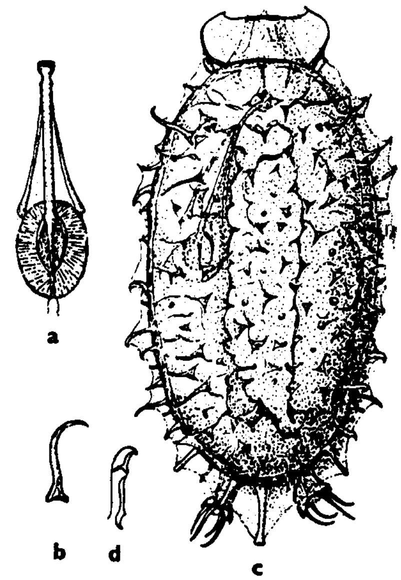


Fig. 286 - *Ech. longiunguis* Iharos. a, pharynx; b, claw; c, dorsal view of the tardigrade; d, a digit of *Actinarctus doryphorus* (from Iharos).



and small. All the cephalic appendices are not on conical base. Buccal aperture ventral, buccal tube 40μ long and 2.4μ wide; pharynx elongated oval (30 x 18μ). Stylets slender and curved.

Legs telescopically withdrawn, with distal end enlarged into a cup; digits lacking, claws slender, very curved, 16μ long. On the legs there are no long bristles. At the caudal end of the body the gelatinous envelop is homogeneous; no specific anal lobes whatsoever over the 4th pair of legs.

This species (of which we have been able to examine an example, kindly loaned by Dr. Gyula Iharos) is particularly interesting because it is the only freshwater representative of the Arthrotardigrada (typically marine). *Ech. longiunguis* was collected in damp soil, under bushes, on the beach of Lake Chungara (Tarapaca Province, north Chile) at about 4,500 m altitude.

Genus *EOHYPSIBIUS* Kristensen, 1982.

Diagnosis: Calohypsibiidae with extremely slender body with legs and claws reduced; mouth with lamellae; buccal tube with wall of spiral structure; claws of *Calohypsibius* type, with lunules.

EOHYPSIBIUS NADJAE Kristensen, 1982 (Fig. 287).

Length up to 208μ. Eyes absent. Cuticle smooth. The mouth is surrounded by 14-16 small peribuccal lamellae. The buccal tube is 32μ long and 6 wide (in the holotype, 195μ long). There is no reinforcement bar, rather there are two wing-shaped crests, dorsal and ventral. From the insertion of the stylet supports to the pharynx, the wall of the buccal tube has an annular, spiral structure. Pharynx short oval or round. Apophyses small. Three macroplacoids, of which the first two of equal length (1.95μ), the third longer (2.60μ), and a large microplacoid (1.3μ).

Legs reduced. The claws are small, those of the first three pairs of legs are almost equal in shape and size, those of the 4th pair are somewhat larger. There are lunules on the claws of the first three pairs of legs as well as on the external claw of the 4th pair. The principal branch bears accessory points. On the 1st-3rd legs, near the claws, there is a cuticular bar.

Eggs have not been found, but a mature female contained an egg which had small ornamentation.

The species is aquatic, and was found in a homothermic spring (12μ), in two localities from Disko Island (Greenland).

Genus *EUCLAVARCTUS* Renaud-Mornant, 1975.

Diagnosis: Halechiniscidae with cephalic cirri composed and supplied with basal cirrophorus; two unequal clavae per side; legs supplied with digits which bear claws lacking spurs.

EUCLAVARCTUS THIELI Renaud-Mornant, 1975 (Fig. 288).

Length from 220 to 280μ, for the females, 285 for the males. Body squat, which enlarges in the caudal portion. Cuticle smooth, without cuticular processes or plates.

The cephalic cirri have a peculiar structure. The internal and median cirri have a funnel cirrophorus, followed by a sheath from which extends a leaf-like part ending with a simple distal process; the external median cirri do not have a sheath (or one has not been seen); there exists then cirri A (15μ) and two clavae per side, one anterior subspherical (with 6μ diameter) and another posterior oblong (18 by 16μ).

The mouth is terminal and is found at the apex of a conical process, through which may pass the stylets. The buccal tube ends with a subspherical pharynx, which contains apophyses and a placoid-shaped, internal undivided cutaneous thickening. Stylet supports absent.

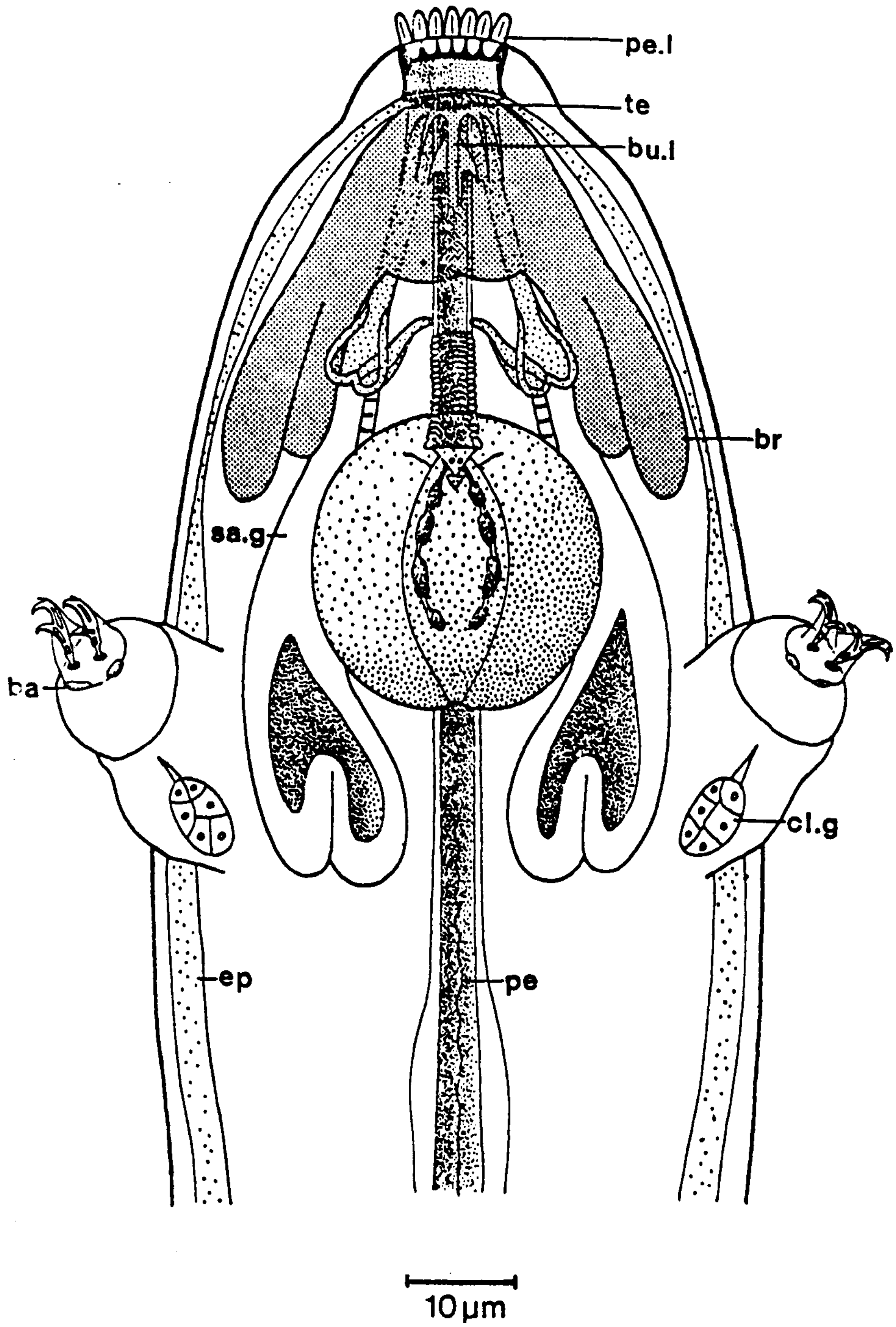


Fig. 287 - *Eo. nadjae* Kristensen. Ventral view of the holotype. (from Kristensen).

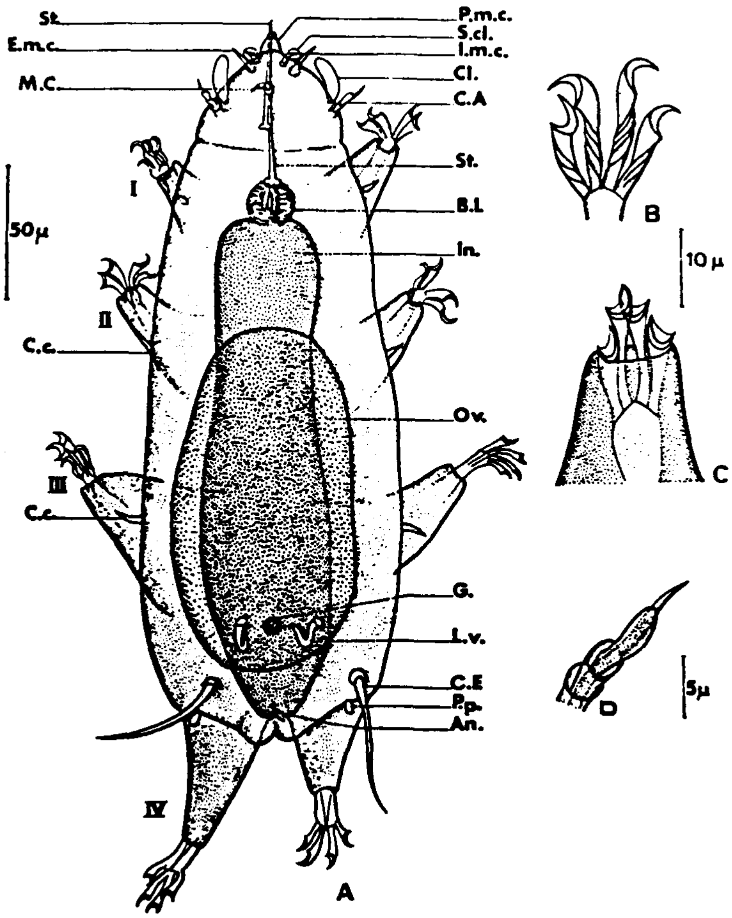


Fig. 288 - *Eu. thieli* Renaud-Mornant. A, dorsal view of the female; B, digits of the 4th leg, extended; C, the same retracted; D, dorsal cirrus (from Renaud-Mornant).

On the dorsal side there are short lateral spines, at the level of the insertion of the 1st, 2nd, and 3rd legs (respectively 10, 11, and 12μ long); above the 4th pair of legs exists cirrus E, 45-47μ long, and a papilla of 6-7μ.

The telescopic legs have four digits inserted on the tarsus, the median digits longer than the laterals. Claws simple, curved, retractile.

Eu. thieli is part of the abyssal meiobenthos, and has been collected in two stations from the Indian Ocean at a depth of 2,600-2,650 meters.

Genus *FLORARCTUS* Delamare Deboutteville & Renaud-Mornant, 1965.

Diagnosis: Halechiniscidae with large wing-shaped expansions around the body; legs with 4 digits, supplied with bifid claws.

KEY TO THE SPECIES

1. On the 4th pair of legs there is a papilla; there are in total five wing expansions, those lateral divided into two wings per side 2
   On the 4th pair of legs there is a spine; the lateral wing expansions may be divided or undivided, so that the wings may be in total 3 or 5 3

2. The dorsum has a mammillary appearance, because of the presence of numerous dot-shaped papillae . . . . *F. cinctus*
   The dorsum is smooth, without papillae . . . . *F. hulingsi*

3. There are in all 3 expansion wings, since the lateral wings are undivided . . . . *F. salvati*
   There are in all 5 expansion wings, since the lateral wings are divided in two on each side 4

4. The caudal wing expansion has a slightly lobed margin . . . . *F. antillensis*
   The caudal expansion wing is deeply notched . . . . *F. heimi*

FLORARCTUS ANTILLENSIS Van der Land, 1968 (Figs. 289, 290, and 291).

The two examples collected measure about 300μ in length, with a maximum width of about 200μ. The cephalic region bears the usual appendices of the Arthrotardigrada, each composed of 3 parts: a bulbous base (cirrophorus) which -- as we shall see -- may be common to more appendices; an intermediate trumpet-shaped piece (scapus), and a terminal filamentous part (flagellum). The cephalic appendices are: median cirrus (scapus 15μ, flagellum 35μ); buccal, or medial, internal cirri (scapus 25μ, flagellum 45μ); buccal, or medial, external cirri (scapus 13μ, flagellum 20μ). The large clava (length 130μ) and the lateral cirri A (scapus 15μ, flagellum 40μ) have a common ample base; in this cirrophorus is present a refringent structure and an analogous structure is visible in the scapus of the internal buccal cirrus. The rostral (cephalic) wing-shaped expansion (ala) is united to the internal buccal cirri as far as the middle of the scapus; each anterio-lateral wing is united to the internal buccal cirrus and to the lateral cirrophorus. The buccal cone is positioned scarcely anterior to the level of the 1st pair of legs. The structure of the buccal apparatus has not been studied by the author in detail; the subspherical pharynx has a diameter of about 30μ.

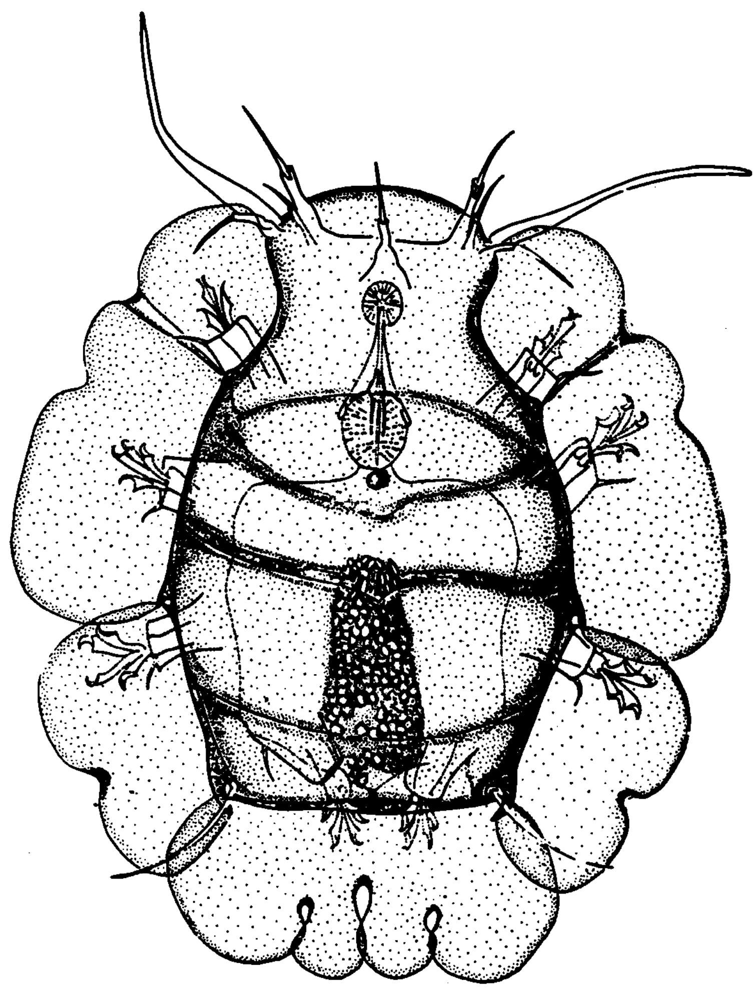


Fig. 289 - *F. antillensis* Van der Land. Adult male, dorsal view (from Renaud-Mornant).

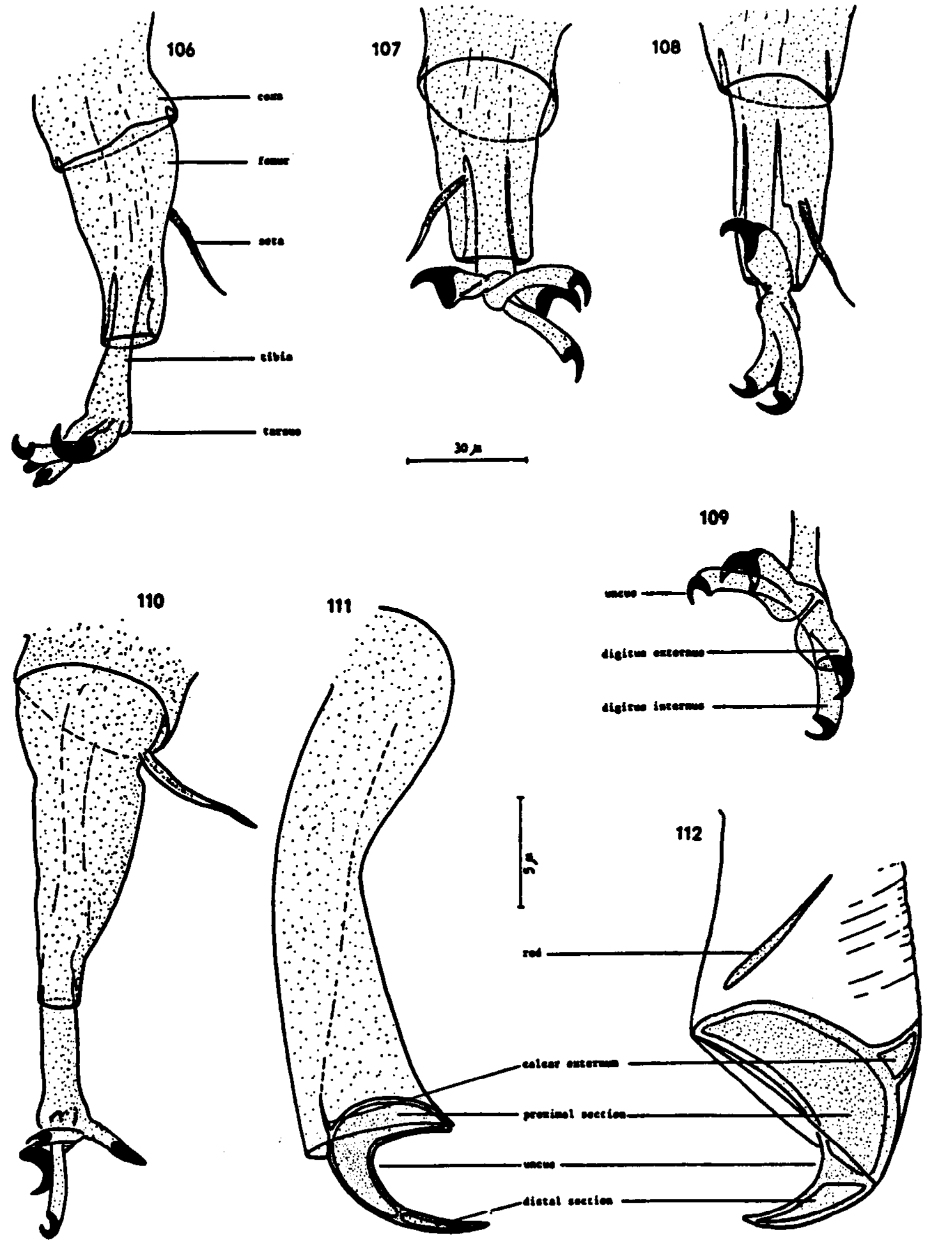


Fig. 290 - *F. antillensis* Van der Land. 106, 1st leg; 107, 2nd leg; 108, 3rd leg; 109, tarsus of 3rd leg; 110, 4th leg; 111, internal digit of 2nd leg; 112, external digit of 2nd leg (from Van der Land).

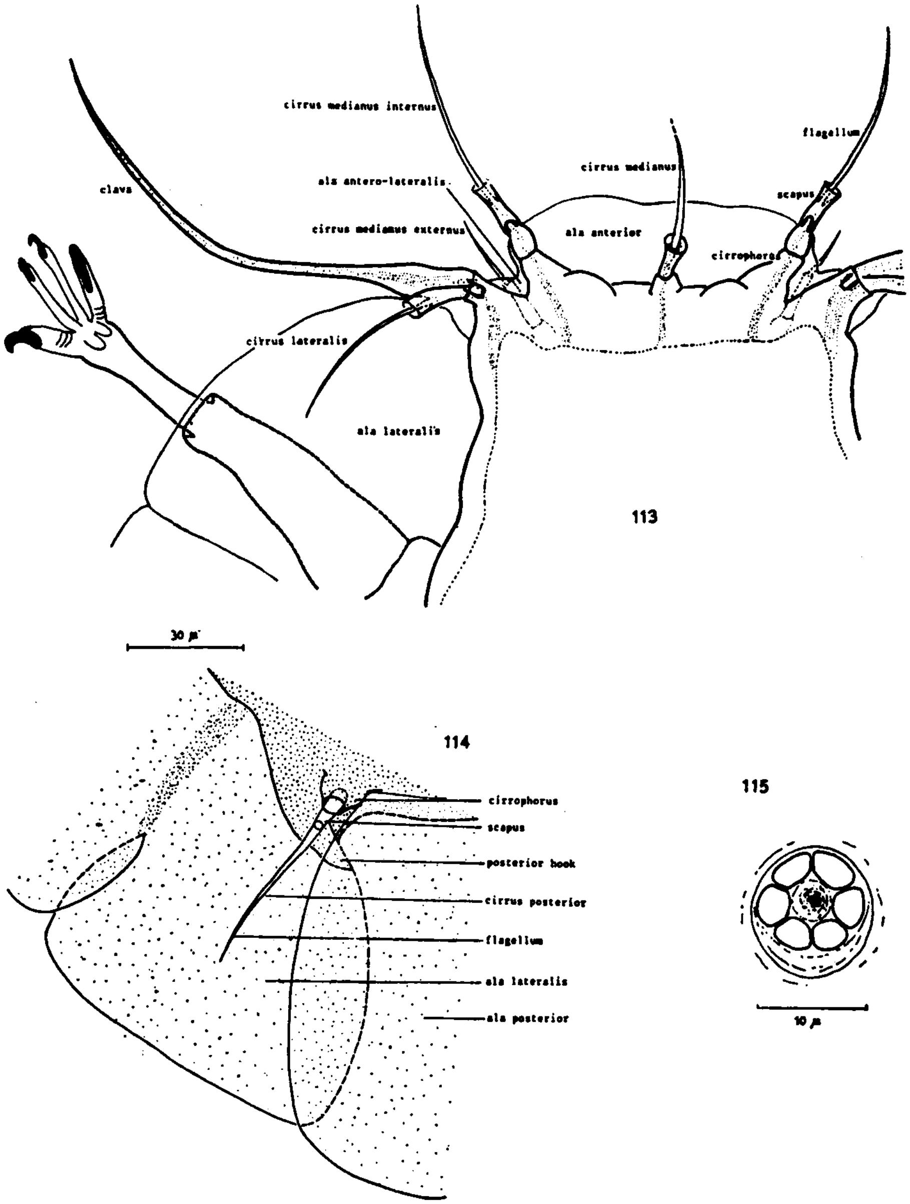


Fig. 291 - *F. antillensis* Van der Land. 113, cephalic region in dorsal view; 114, left portion of the caudal region in dorsal view; 115, gonopore (from Van der Land).

The body is ventrally flat and dorsally arched: its height (often) is much less than the width; it bears two latero-caudal curved teeth as well as two latero-caudal filaments and reaches the lesser width in the zone immediately posterior to the cephalic region and the greater width a little anterior to the 3rd pair of legs. The anus is positioned between the legs of the 4th pair. The wing-shaped extensions (alae) are transparent, but appear finely punctated with a closer observation. The lateral alae are up to 70μ wide, the posterior (caudal) up to 100μ. The two pairs of lateral alae correspond each to two segments of the body. On the alae of the first pair may be distinguished 5 sectors, one smaller and the other 4 larger. The bilobed alae of the 2nd pair copy in part those of the 1st pair and are united to the two latero-caudal teeth of the body; the quadrilobed caudal alae rises a little on the dorsum, between the 2 latero-caudal filaments, which do not differ from the lateral cirri A, except for the much smaller scapus and because the principal articulation is between scapus and cirrophorus.

Each leg consists of a short and wide coxa (length up to 20μ), a femur (up to 25μ in extended position), a slender tibia (as long as 35μ) which may be all telescopically retracted into the femur, and a tarsus. Each femur has a slender spine of bristle appearance: the spines of the 4th pair of legs, positioned near the coxa, are 35μ long and about 3μ wide; those of the 1st-3rd legs are a little smaller (30μ long and about 2μ wide) and appear wrinkled, at least basally. The internal digits are slender, up to 30μ long, and bear a small claw with maximum length of 8μ. The claw has at its base and *dorsally* a minuscule spur (calcar externum). The external digits are not as long (up to 20μ) however are wider and have a well developed claw (maximum length about 12μ); the dorsal spur of the claw (calcar externum) is obvious. In the digits exists a small rod formation, about 7μ long.

For the cirri and the legs we have used the same nomenclature adopted by the author, who has noted that *Florarctus* really has Arthropoda legs and even the cirri are segmental in structure.

The species was found in coralline sand at Curaçao, Piscadera, Baai, Boca, at depths of 3 meters, and in numerous stations at Tuléar, on the western coast of Madagascar.

FLORARCTUS CINCTUS Renaud-Mornant, 1976 (Fig. 292).

Length up to 187μ in the female, and up to 120μ in the male. Width, respectively, 112 and 65μ. The dorsal cuticle is covered with a punctation

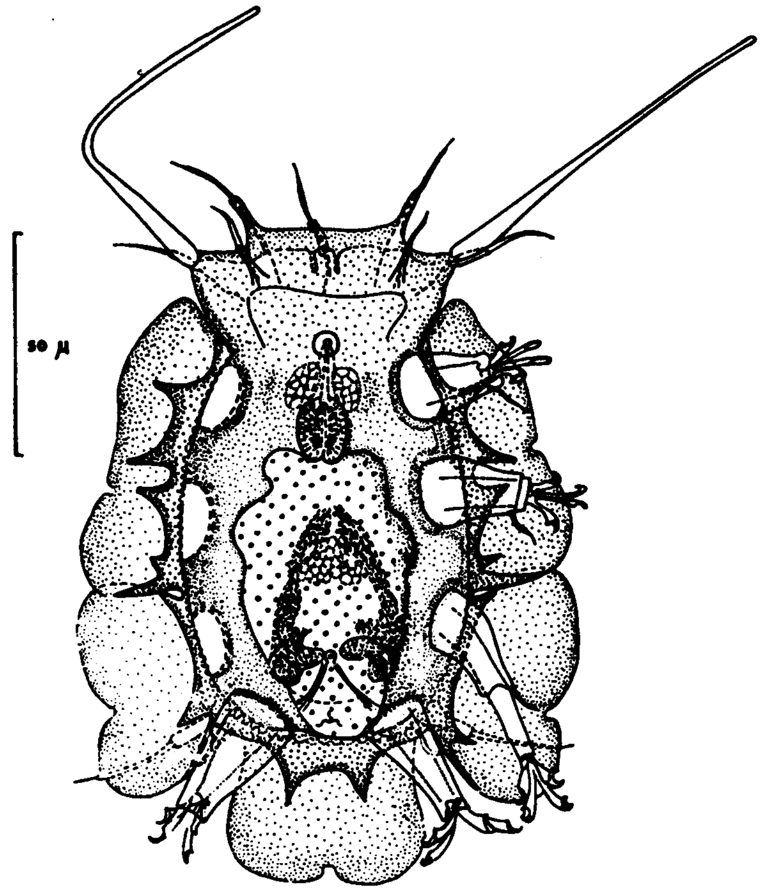


Fig. 292 - *F. cinctus* Renaud-Mornant. Male, ventral view (from Renaud-Mornant).

bearing a mammillary structure. The alar expansions are six: unpaired frontal and caudal, two large expansions (extended as far as the insertion of the 3rd legs) and two lateral posterior expansions, between the 3rd and 4th legs: the lateral and caudal expansions are supported at the base by a cuticular belt which is supported by pointed lateral apophyses laterally and posteriorly. The wing-shaped expansions are very finely punctated.

The cephalic cirri are borne on a cirrophorus, and include, as in all species of *Florarctus*, a proximal part and a more slender, pointed, distal flagellum.

The measurements are the following: unpaired median cirrus 28μ, internal median cirrus 40, external median cirrus 27, cirrus A 26, and clava

40. The cirrus E is also inserted on a cirrophorus, and is 32μ long, the setae on the 1st, 2nd, and 3rd legs are respectively 15, 17, and 17μ long; on the 4th legs is found an elongated papilla, inserted on a narrow and refringent base.

The legs bear four digits with claws typical of the genus. The internal digits are slightly longer, and their claws bear a distal spur and a basal point. The external claws are larger and more robust.

The mouth, ventral, opens at the level of the median cirrus, the buccal tube ends in a pharynx, with three apophyses; there are no stylet supports.

This species is distinguished from the others of the genus by the ornamentation of the cuticle and by the belt of strong apophyses which outlines the trunk.

F. cinctus has been found, as a single example, in coarse infralitoral sand, northwest of the Gulf of Napoli, at a depth of 11.5 meters. Later almost 200 examples were found at different stations at Tuléar, on the coast of Madagascar.

FLORARCTUS HEIMI Delamare Deboutteville & Renaud-Mornant, 1965 (Fig. 293A).

Length about 400μ, including the caudal lobe; the head is massive and bears the following appendices: median cirrus, unpaired (35μ); internal buccal cirrus, paired (20μ); external buccal cirrus, paired (50μ); lateral cirrus A, paired, rather short (25μ); clava, paired, very long (up to 180μ). All these cirri are contained at their bases in a cylindrical peduncle, with appearance of a sheath.

Buccal aperture ventral and very distant from the rostral margin of the tardigrade, that is to say very removed backwards.

The wing-shaped expansions of the cuticle are extremely developed and their total surface area is larger than that os the body. The lateral expansions are subdivided on each side into 4 lobes, while the caudal expansion is subdivided into 2 lobes by a deep median incision. Each of the two lobes of the caudal expansion bears 2 long spines (200μ) and 3 secondary lobes ending in a point or a spine.

Dorsally, above the caudal expansion (and approximately in position corresponding to the E of the *Echiniscus*) there are two gibbosities, from which departs the post-dorsal cirri (40μ).

Anus in posterior position; gonopore ventral, positioned more anterior than the anus and surrounded by 6 cuticular folds.

Legs telescopically retractile by about half their length, each with a

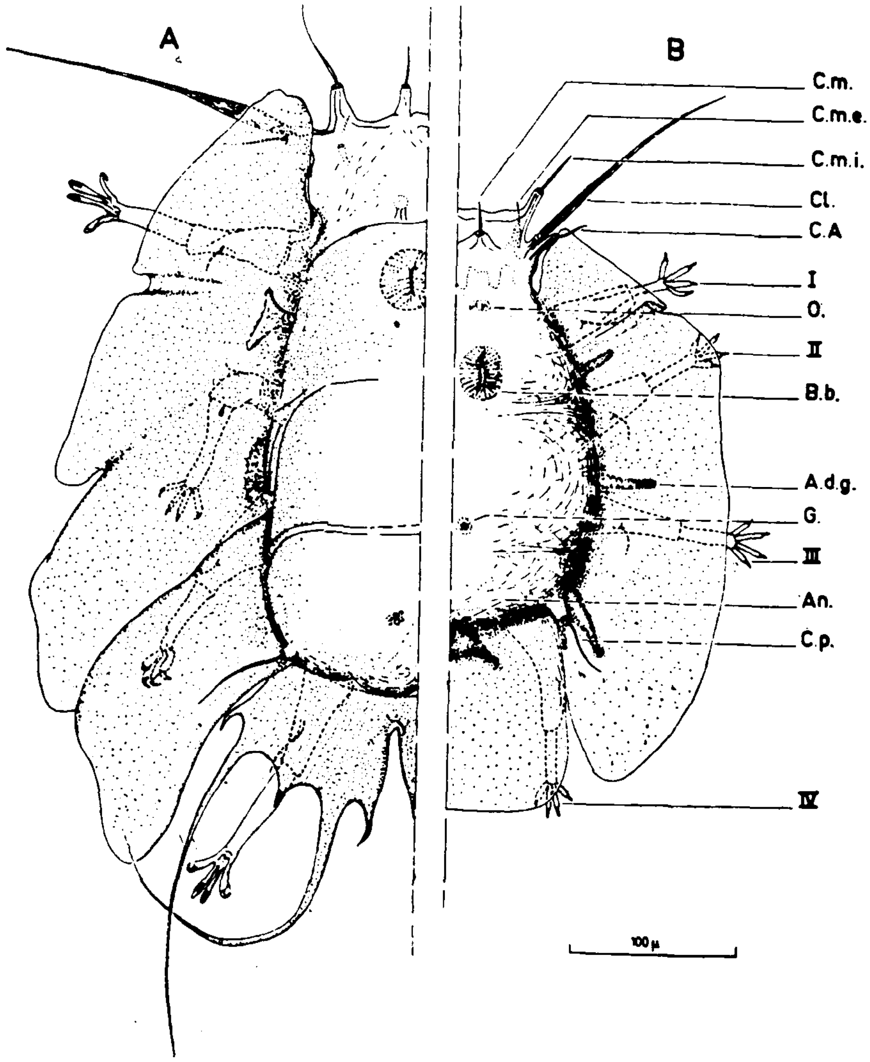


Fig. 293 - A, *F. heimi* Delam. Debout. and Ren.-Morn. B, *F. salvati* Delam. Debout. and Ren.-Morn.. C.m., median cirrus; C.m.e., external medial cirrus; C.m.i., internal medial cirrus; Cl., clava; C.A., cirrus A; I, II, III, IV, legs; O., buccal aperture; B.b., pharynx; A.d.g., "glove finger" appendix (thickening on the ventral surface of the lateral wing expansion); G., gonopore; An., anus; C.p., caudal cirrus (from Delamare Deboutteville and Renaud-Mornant).

small spine, positioned on the portion notretractile. Digits of unequal length: the externals are shorter and wider than the internals. All the claws have a median spur, which is inserted on the digit. The claws of the external digits are different from those of the internal digits and are as follows:

-- Claws of the two internal digits:

On the first pair of legs the claws (7μ) are bifid in their distal part and bears two teeth of equal size; on the 2nd and 3rd pairs of legs one of the teeth is smaller than the other, while on the 4th pair of legs they are reduced and a very slender spine.

-- Claws of the two external digits:

They are much more robust and massive: there exists median spurs and also the distal end of the claw is constituted of an article which is closed on one point, with appearance of very imperfect pincers (chelae) ($10\text{-}12\mu$).

The species *Florarctus heimi* was collected in coralline sand on the coast of New Caledonia.

FLORARCTUS HULINGSI Renaud-Mornant, 1976 (Figs. 294, 295).

Length up to 132μ (the females; the males are smaller, 122μ maximum), width 75μ. The dorsal cuticle is not punctated. The expansion wings are in total five, two anterior pairs extending as far as the insertion of the 3rd pair of legs, two lateral pairs between the 3rd and 4th legs and a caudal expansion between the 4th legs. The expansion wings are directly attached to the body, without basal cuticular thickening: the trunk forms ventrally two small paired lobes under the lateral wings and an unpaired lobe under the caudal wing, but the cuticle is not thickened at their level.

The morphology of the cephalic cirri corresponds to that of the other species of *Florarctus*. They are borne on the cirrophorus and include a basal part and a pointed distal flagellum. The measurements are the following: unpaired median cirrus 18μ, internal median cirri 30, external median cirri 15, cirrus A 19, clava 40 (in the males the clava is much longer, as much as 120μ). Cirrus E, also inserted on the cirrophorus, is 20μ long; the setae on the 1st-3rd legs are respectively 12, 5, and 4μ long; on the 4th legs there is an elongated papilla.

The legs bear four digits, of which the medians are longer, and their claws have a distal spur, while the lateral digits, shorter, have larger claws, with less accented curved, and a distal part in the shape of pincers.

This species is the only one of the genus which does not have cuticular thickenings which accompany the expansion wings.

F. hulingsi has been collected in numerous littoral stations of the Mediterranean. The type locality is Kelibia, in Tunisia.

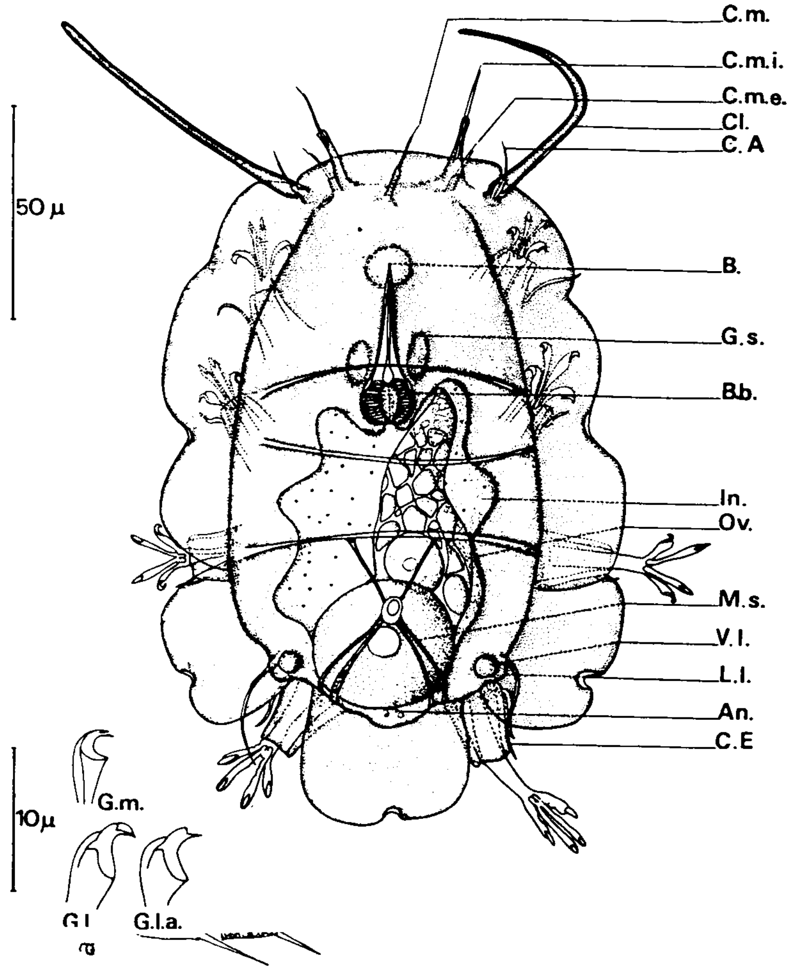


Fig. 294 - *F. hulingsi* Renaud-Mornant, adult female, dorsal side. An., anus; B., mouth; B.b., pharynx; C.A. cirrus A; C.E., cirrus E; C.m.i., internal median cirrus; G.l., external claw; G.l.a., external claw which has lost the superior unit; G.m., lateral lobe claw; M.s., supporter muscle of the ovary; Ov., ovary; V.l., lateral vesicle (from Renaud-Mornant).

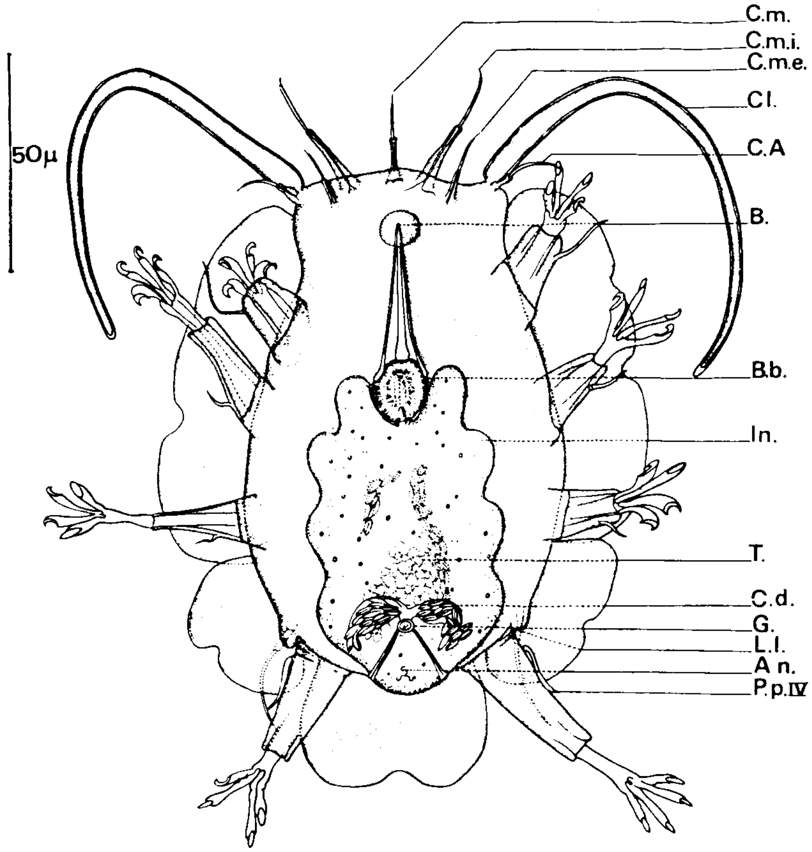


Fig. 295 - *F. hulingsi* Renaud-Mornant (adult male, ventral side). An, anus; B, mouth; B.b., pharynx; C.A., cirrus A; C.d., vas deferens; Cl, clava; C.m., median cirrus; G, gonopore; In, intestine; L.l., lateral lobe; P.p.IV, papilla of 4th leg; T, testis (from Renaud-Mornant).

FLORARCTUS SALVATI Delamare Deboutteville & Renaud-Mornant, 1965 (Fig. 293 B).

The characteristics are very similar to those of the above described *Florarctus heimi*, from which it differs especially by the following details:

- Smaller size (250μ).
- Number and shape of the wing expansions (see figure).

- Unpaired caudal wing expansion, completely lacking lobing and spines.

Also *F. salvati* as *F. heimi* was collected in coralline sand on the coast of New Caledonia, and later at Tuléar, on the west coast of Madagascar.

Genus *HALECHINISCUS* Richters, 1908.

Diagnosis: Halechiniscidae with legs with four digits, terminating with a sickle-shaped claw, with or without distal spurs; head flattened, with lateral expanded lobes.

KEY TO THE SPECIES

1. Along the flanks and at the caudal end exists cuticular wing-shaped expansions .... *Hal. intermedius*
   There are no cuticular wing-shaped expansions 2

2. There is a caudal appendix in the shape of a short obtuse spine .... *Hal. remanei*
   There is no caudal appendix 3

3. On the 4th pair of legs exists a papilla, ending or not with an apical spine; claws with or without spurs 4
   On the 4th pair of legs exists a spine, not inserted on a papilla; claws without spurs 6

4. Claws without spurs; the papilla on the 4th pair of legs bears an apical spine .... *Hal. perfectus*
   Claws with spurs; the papilla on the 4th pair of legs has no apical spine 5

5. Median cirrus present .... *Hal. subterraneus*
   Median cirrus absent .... *Hal. guiteli*

6. There are lateral expansions, in the shape of large conical spines, over the first three pair of legs .... *Hal. tuleari*
   There are no lateral conical expansions .... *Hal. greveni*

HALECHINISCUS GREVENI Renaud-Mornant & Deroux, 1976 (Fig. 296).

Length 125μ for the female, 78μ for the male. There is neither lateral nor caudal expansions. The head, rounded on the front part, is elongated into two lateral conical lobes. The cephalic cirri are inserted on mammillary bases; such cirri are formed of a widened proximal part, of

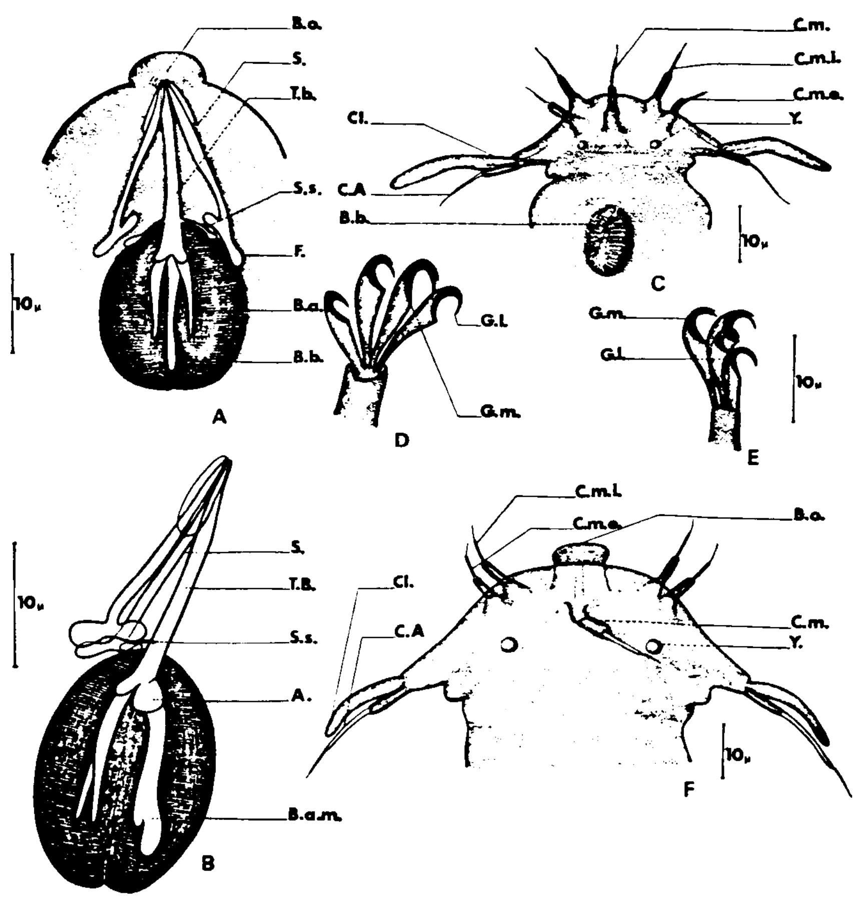


Fig. 296 - *Hal. greveni* Renaud-Mornant & Deroux. A, buccal apparatus and pharynx, ventral view; B, buccal apparatus and pharynx, profile view; C, dorsal view of the head of the male; D, digits and claws of the 3rd leg; E, digits and claws, in profile; F, dorsal view of the head of the female (from Renaud-Mornant & Deroux).

sheath shape, a middle part and a sharpened distal part. The unpaired median cirrus, set back with respect to the front border is 12μ long; the internal cephalic cirri are 15μ long, the external, in ventral position, 11μ. Cirri A and the clavae are inserted on the lateral cephalic cones: cirri A 25μ, clava 19μ. The eyes, in the form of refringent spheres, are situated behind the insertion of the internal cirri. There are also cirri, with enlarged bases, on the 1st, 2nd, and 3rd legs, with increasing length from 1st to 3rd (9, 12, and 20μ, respectively). Above the 4th legs is found cirrus E of 30μ, inserted on a conical base. The 4th legs bear an elongated papilla, with pointed apex.

The telescopic legs have four digits supplied with sickle-shaped claws; the median digits are slightly longer than the lateral digits; the internal claws have a distal spur, the externals are simple.

The mouth is clearly ventral. There are stylets and stylet supports, the pharynx has apophyses but not placoids.

Sexual dimorphism has been noted regarding the clavae, which are longer than cirrus A, in the male.

Hal. greveni has been collected, in large numbers of examples, immediately under the intertidal zone (on vesicular *Fucus*) at Roscoff (Bretagna).

HALECHINISCUS GUITELI Richters, 1908 (Fig. 297).

Length 100-200μ, transparent, eyes absent; cuticle wrinkled, or granular. The buccal aperture is positioned ventrally, on a widely rounded conical projection. Stylet supports probably present, buccal tube narrow (about 2μ), pharynx oval, with three pharyngeal bars. There is no median cirrus; internal median cirri on base, positioned ventrally to the anterior margin of the head and up to 18μ long; external medial cirri longer (up to 24μ), also on a base, inserted dorsally with respect to the anterior margin of the head. Lateral cirrus A and clava inserted on a common base: usually the clava (27μ) is longer than the lateral cirrus (21-22μ), but in some individuals it is shorter. Laterally exists filaments, approximately in the positions indicated in the genus *Echiniscus* by C, D, E; caudally to filament E, near the insertion of the 4th pair of legs, there is also a short bristle, which departs from a papilla.

The legs are rather slender and increase progressively in length from 1st to 4th pair (the latter, in complete extension, measures about 64μ); their terminal part may be telescopically retractile into the proximal part; at the end of the legs exists 4 slender fingers (digits), 10-11μ long, rather

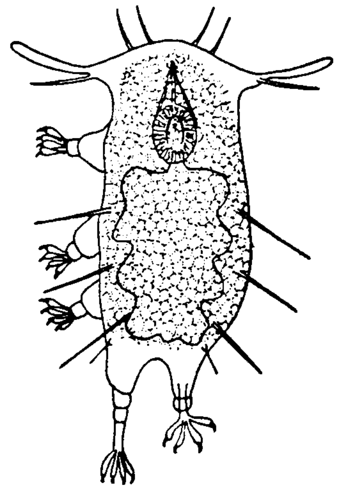


Fig. 297 - *Hal. guiteli* Richters (from Marcus, redrawn).

enlarged into clubs distally and each ending in a robust claw of about 4μ. Eggs unknown.

The species was collected in France, on the Atlantic and Mediterranean coasts, and in the Black Sea.

Typ. loc.: Cancale (S. Malo) and Villefranche (maritime Alps).

HALECHINISCUS INTERMEDIUS Renaud-Mornant, 1967 (Fig. 298).

This species calls to mind *Florarctus salvati* by its cuticular wing-shaped expansions, however much more reduced; it is however part of the genus *Halechiniscus* because of its simple claws and the arrangement of the cephalic appendices.

Length 195μ, ovoid body surrounded -- with exception of the cephalic region -- by lateral and caudal wing-like expansions, which covers the proximal part (not telescopically withdrawn) of the legs.

The cephalic appendices are: median cirrus (20μ), internal (or medial) buccal cirri (22μ), external (or medial) buccal cirri (18μ), lateral cirri A (17μ) and large clavae (50-60μ). All the cirri depart from a large mammillary base and go out from a rather loose sheath: at two-thirds of its length it is reduced to a slender filament. Clava and lateral cirrus A originates -- close together -- from an obvious common mammillary base. The brain has 2 dorsal lobes, which send very visible nerves to the cirri; there are, in the males and females, 3 vesicles surrounding the brain: the frontal is larger and of elongated shape, the two laterals have oval

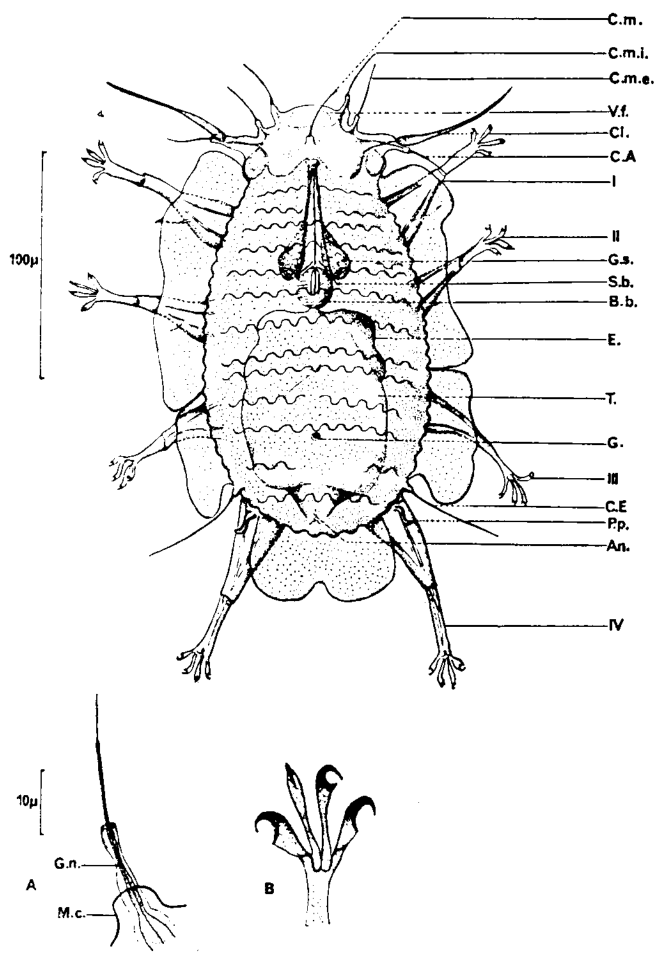


Fig. 298 - *Hal. intermedius* Renaud-Mornant. Above: general view. An., anus; B.b., pharynx; C.A., cirrus A; C.E., cirrus E; C.m.e., external buccal cirrus; C.m.i., internal buccal cirrus; Cl., clava; E., intestine; G., gonopore; G.s., salivary gland; P.p., posterior papilla; S.b., stylet; T., testis; Vf., frontal vesicle; I, II, III, IV, legs. Below: A, cephalic cirrus; G.n., sheath with nerve; M.c., cuticular gibbosity. B, detail of the end of a leg with the digitation (from Renaud-Mornant).

appearance. Ventral mouth, stylets long (50μ) with supports (8μ), and oval pharynx containing 3 rods; the length of the stylets (and of the buccal tube) makes the pharynx very set back from the mouth. A pair of large salivary glands.

The cuticle has -- besides the wing expansions -- a surface ornamentation (sculpture) composed of an extremely fine uniform punctation and of gibbosities spread on all the dorsal surface, which form regular transverse undulations and channels, more or less parallel, with the appearance of festoons at the margins of the cuticle; it is from this festooned margin that the wing expansion originates, not too much different from that of *Florarctus*: the cuticle extends flat and its punctate sculpture becoming still finer. These expansions are 5: one anterio-lateral and one latero-posterior on each side, besides a caudal expansion. There are two dorsal posterior cirri (40μ) in the position corresponding to the appendices E of the *Echiniscus*. The wing expansions differ from those of *Florarctus* by the much smaller size and by being unprovided on the underneath of the massive structures or "glove fingers" present in *F. heimi* and *salvati*.

At the pharynx follows the intestine, multilobed, which ends in a trifid anal aperture. Dorsally, above the intestine, there is the genital gland; the testis covers all the intestine and has two deferentia, one on each side of the rectum, ending then in the rosette ventral gonopore, with 6 platelets.

In the female the ovary may contain 3-4 mature eggs and a score of oocytes in different stages; the oviduct is unpaired, goes around the intestine and joins the gonopore, anterior to the anus.

The legs are similar to those of *Hal. perfectus*, that is they may retract telescopically and have 4 digits, with simple claws. The legs of the 1st pair have a seta on the non-retractile part, seta which is very reduced on the 2nd pair and absent on the 3rd. On the 4th pair of legs there is only a large papilla, near the articulation. The 4 digits have slightly different lengths: the 2 median digits are longer. The claws are simple, curved in a semicircle and do not have a well defined support spur: only a thickening of the cuticle of the digit is noted against the convex part of the claw.

Although the author has had the opportunity to examine individuals of both sexes, he did not see any connection to sex in the size of the clava. The species lived at 4 meters depth, in a coralline detritus sediment, very mobile and rather coarse, from Grand Ténia Island (Saint Vincent Bay -- New Caledonia).

HALECHINISCUS PERFECTUS Schulz, 1955 (Fig. 299).

Length 154-181μ. The cephalic appendices present are: median cirrus, unpaired (17-32μ); internal medial cirrus, paired (20-32μ), inserted rather

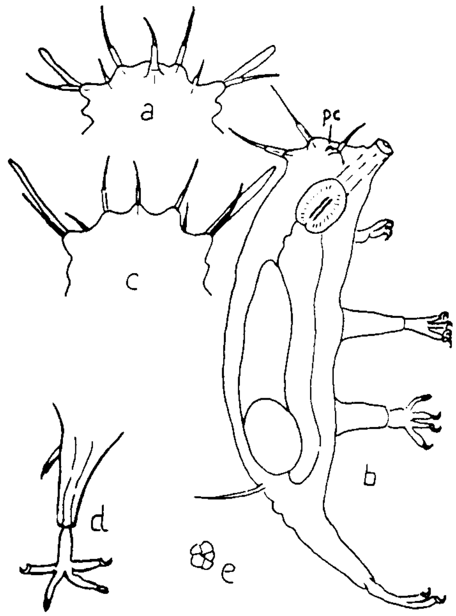


Fig. 299 - *Hal. perfectus* Schulz. a, dorsal view of the cephalic region; b, lateral view: the lateral cirrus and the clava not shown; the digits of the 1st and 4th legs incompletely shown (pc is the cephalic papilla); c, cephalic region -- probably a male -- in dorsal view; d, distal end of the 4th leg; e, gonopore rosette (from Schulz, redrawn).

dorsally; external medial cirrus, paired (16-22μ), positioned ventrally; lateral cirrus A, paired (27-36μ); clava, paired (27-48μ). All these cephalic appendices arise from a papilliform base (for lateralcirrus A and the clava, the base is common): they are constituted of a more enlarged basal part -- cylindrical and with tubular appearance -- and of a more slender distal bristle. Two swollen cephalic papillae (pc) are considered by the author to be between the internal and external median cirri. Unlike *Hal. guiteli*, the median cirrus is present and the clava is not longer than the lateral cirrus, but of equal length, or else less; only in an individual from Napoli, Schulz observed very long clavae (47-48μ), much more than cirrus A, and thinks -- agreeing with the opinion of Richters (1909) -- he was dealing with a male, because the great development of the clava seems to be a secondary sexual character of the males.

The buccal aperture is rostro-ventral; the pharynx contains smooth pharyngeal bars; stylet supports are present. The only cuticular appendices of the body are two dorsolateral caudal robust bristles (spines), positioned approximately in the position where exists -- in the *Echiniscus*

-- the appendices E. The legs increase progressively in length from the 1st to the 4th pair and thus likewise the distal fingering (digits); near to the bases of the first three pairs there is a bristle, while on the 4th pair -- in corresponding position -- there is a finger-shaped papilla, ending in a short bristle, slightly curved.

The species was collected in sand from the French Mediterranean coast at Banyuls (1 individual), in New Caledonia, in the Indian Ocean, and in Italy, near Napoli (3 individuals); according to Schulz (1955) the tardigrades described by Grell (1935) as *Hal. guiteli* and found in the North Sea (Helgoland) are however probably *Hal. perfectus*.

HALECHINISCUS REMANEI Schulz, 1955 (Fig. 300).

The length of the 64 individuals -- examined by the author -- varied between 86 and 120μ, excluding the caudal conical appendix, 12-20μ long. Buccal aperture turned ventrally. The cephalic appendices -- from which the innervation from the brain is obvious -- are as follows:

- median cirrus of 11-16μ;
- internal medial cirri (paired, of 16-19μ) and external median cirri (paired, of 8-12μ) all arising from a base smaller than that existing in *Hal. perfectus*: as in the latter species, the base

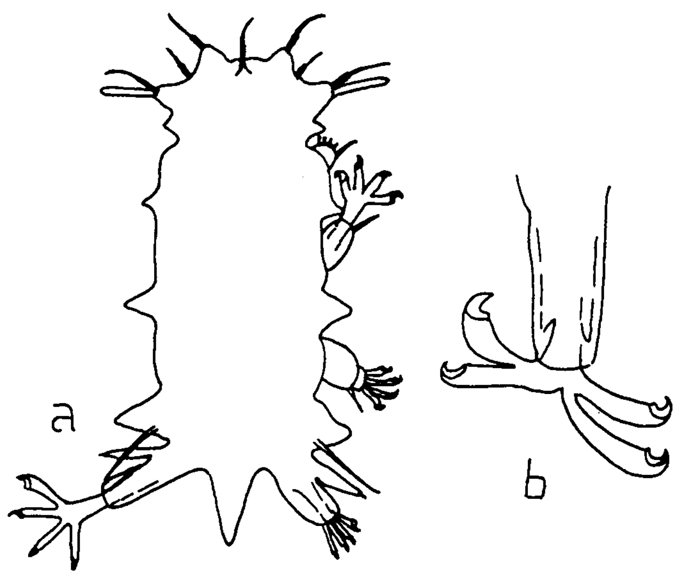


Fig. 300 - *Hal. remanei* Schulz. a, dorsal view; b, distal end of a leg of the fourth pair (from Schulz, redrawn).

of the cephalic cirri is tubular and surrounds their basal part (that which occurs -- according to the author -- also in *Stygarctus bradypus*, *Orzeliscus belopus*, and *Orz. septentrionalis*);

- lateral cirrus A (paired, 22-26μ) and clava (paired, 15-16μ), fixed on a basal conical projection, common to both and about 5μ tall: also the lateral cirrus has a tubular base.

The author has not succeeded in making clear any cuticular processes, which may be interpreted as cephalic papilla. The body has laterally obvious conical projections, positioned respectively -- one per side -- between the cephalic region and the first pair of legs and between the successive legs (that is 4 in total for each side): such processes have increasing length in rostro-caudal sense. In the caudal region of the body -- at about where in the *Echiniscus* exists the appendix E -- there are two laterodorsal cirri (spines), one on each side. The genital pore is separate from the anus and lies 16μ more rostrally from the latter. The legs bear at the distal end 4 fingers (digits), about 14μ long including the terminal claw of 3μ; the first three pairs of legs have a spine, the fourth pair a finger-shaped papilla, 10-11μ long, from which departs distally a robust spine of 4-5μ: within the papilla passes a nerve.

The species, typical of the psammon (i.e., of the psammon environment, or interstitial fauna), is known for Italy (Gulf of Napoli near Baia) and for France (Arcachon and Landes on the Gulf of Guascogna); at Arcachon *Hal. remanei* was collected sometimes between 20 and 40 cm depth (about 5 individuals per 75 cm^3 of sand), sometimes at greater depths, up to 1.50 meters.

Hal. remanei was also collected at 0-20 cm depth in a sandy beach of California (McGinty, 1969) where was also observed young stages with only two digits.

HALECHINISCUS SUBTERRANEUS Renaud-Debyser, 1959 (Fig. 301).

Length about 133μ, cuticle smooth, with a slight fold in correspondence with each pair of legs. The cephalic appendices present are: median cirrus (15μ), unpaired, vertically erect; internal buccal cirrus (14-15μ), paired and in dorsal position; external buccal cirrus (7-8μ), paired and in ventral position; lateral cirrus A (10-13μ), paired; clava (30-32μ), paired. The median cirrus and the buccal cirri have a well developed basal sheath; the lateral cirrus and the clava arise from a common base; cephalic papilla is

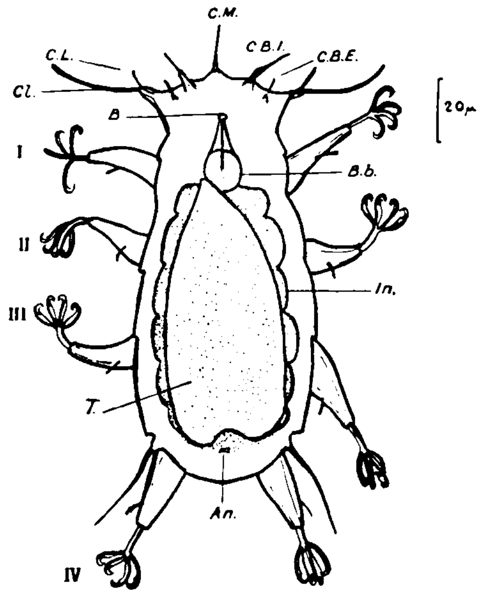


Fig. 301 - *Hal. subterraneus* Renaud-Debyser. An, anus; B, mouth; B.b., pharynx; C.B.E., external buccal cirrus; C.B.I., internal buccal cirrus; C.L., lateral cirrus; Cl., clava; C.M., median cirrus; In., intestine; T., testis; I, II, III, IV, legs (from Renaud-Debyser).

not present. Buccal aperture ventral; stylet supports have not been observed. Intestine with 6 diverticula which -- in dorsal view -- are partly covered by the gonad. The onlycuticular appendices of the body are two long and robust dorsolateral caudal spines, corresponding approximately -- in position -- to the appendices E of the *Echiniscus*. Legs as long as in the other species of the genus, each with 4 digits -- very similar to those of *Hal. remanei* -- ending with a claw without spurs. Each leg bears a short spine.

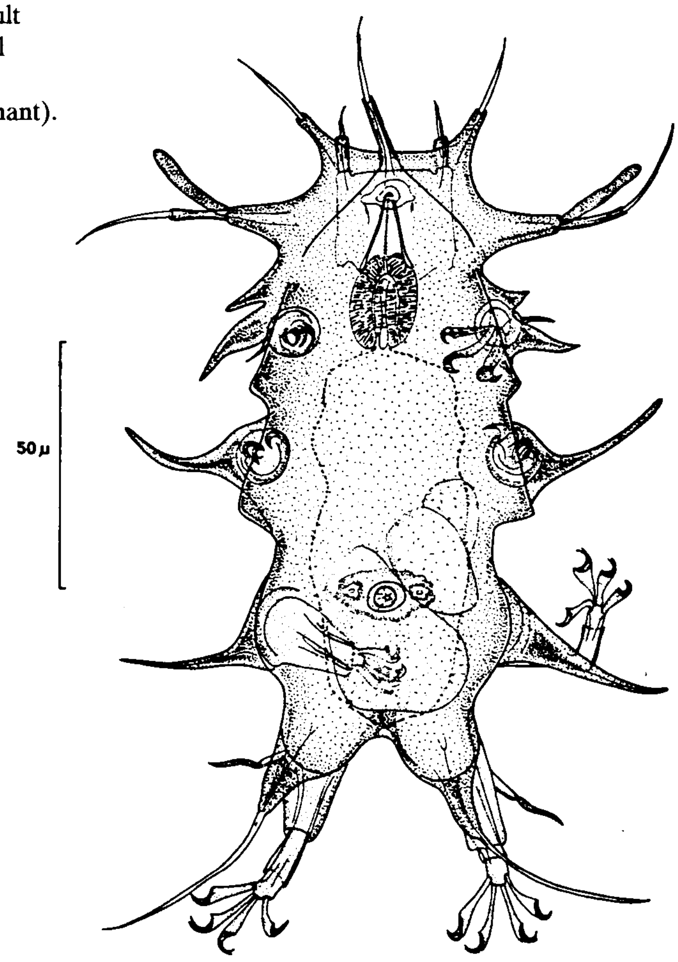
One of the more noticeable differences between *Hal. subterraneus* and the other species of *Halechiniscus* is the very short lateral cirrus A and the very long clava: it is necessary however to remember that the only two individuals examined were both males, and that the very developed clava seems to be a secondary sexual characteristic of the male (Richters, 1909; Schulz, 1955).

The species was collected on the beach of Sharktown on Bimini Island (Bahamas) and was part of the interstitial benthos of the intertidal zone; the two examples were found on the same beach with a separation of one month from each other and at a depth of 50-60 cm, in sand composed of detritus of organisms (foraminifera, polyps, spines of echinoderms, molluscs) and of calcareous algae.

HALECHINISCUS TULEARI Renaud-Mornant, 1979 (Figs. 302, 303).

Rectangular shape, 120μ long, 60μ wide. The head is divided into well defined surfaces: five dorsal lobes bear respectively the unpaired median cirrus, the paired dorsal cirri, and the lateral cirri A, as well as a ventral

Fig. 302 - *Hal. tuleari* Renaud-Mornant. Holotype, adult female, dorsal view (from Renaud-Mornant).



quadrangular lobe, around the mouth, which bears on its anterior border the paired ventral cirri. Each cirrus is borne on a cirrophorus, and is formed of a median portion, ending with a sharpened point. The median cirrus (set very back from the mouth) is 31μ long (14 + 17); the paired, dorsal cirri are 25μ long (10 + 15); the ventral (internal) cirri are 14μ long (6 + 8); cirrus A, 33μ (13 + 20); clava, 20μ. These measurements refer to the holotype (female); in the male which is smaller (92μ, allotype), the clavae are longer (as occurs usually in the genus *Halechiniscus*), that is 33μ, compared with 31 for the cirrus A.

The trunk bears a contraction between the first and the second pair of legs, and another between the second and third.

Laterally on the body, at the level of the first three pairs of legs, exists conical expansions in the shape of large spines, which are double and shorter (8 and 19μ) on the first pair of legs, single and longer (30μ) on the 2nd and 3rd. The caudal conical expansions are ended with the cirrophorus of the cirrus E (12μ) and also the cirrus E (40μ).

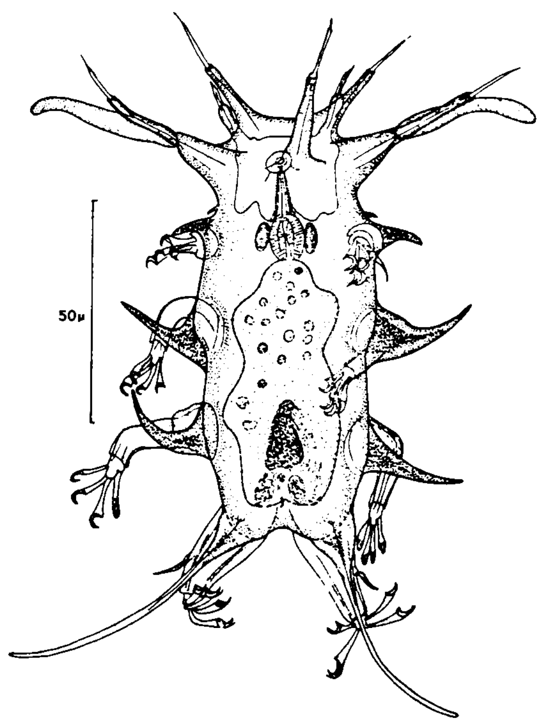


Fig. 303 - *Hal. tuleari* Renaud-Mornant. Allotype, adult male, dorsal view (from Renaud-Mornant).

The telescopic legs have four subequal digits, with claws of crescent shape. The median claws bear a distal spur, very small. The "setae" are present only on the first pair of legs, while on the 4th pair exists a pointed papilla.

Hal. tuleari is very near to *Hal. greveni*, from which it is distinguished especially by the presence of the lateral conical expansions.

The species was collected at Tuléar, on the western coast of Madagascar.

Genus *HAPLOMACROBIOTUS* May, 1948.

Diagnosis: Macrobiotidae with rigid buccal tube, with reinforcement bar; peribuccal lamellae absent. The claws of the first three pair of legs lacking the secondary branch.

HAPLOMACROBIOTUS HERMOSILLENSIS May, 1948 (Fig. 304).

Length 410-650μ, black eye spots in anterior position, cavity globules of reddish orange color, cuticle smooth, pigmentation of dark granules, especially in the mid-dorsal region. The diameter of the buccal aperture is about 7.5μ and that of the buccal tube of about 5μ; the pharynx is ovoid and contains apophyses and 3 macroplacoids: the first is approximately square (2.5μ on a side) and its rostral end is in contact with the apophyses; the second and the third are club-shaped, somewhat more elongated and measure 4μ in length by 2.5 in width; microplacoid absent.

Characteristic is the absence of the doubleclaw: on each foot there are actually two single simple claws, completely separate between their bases, about 20μ long; both the claws have two accessory points at the distal end; there are no lunules.

Only the fourth pair of legs possess a hint of secondary branch, tiny and hardly visible, reduced to a kind of slender spur. Because of its small size it is very difficult to establish the sequence of the legs. Pilato (1973) reports that such sequence is 2121 and therefore considers the claws like *Calohypsibius* type: for this reason he puts the genus *Haplomacrobiotus* within the Hypsibiidae. We do not join in this opinion, for the reasons stated by Maucci (1981).

Typ. Loc.: Hermosillo (Mexico). The species has in addition also been found in California.

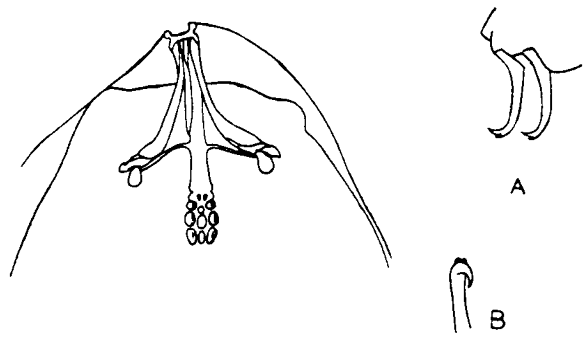


Fig. 304 - *Hapl. hermosillensis* May. Buccal apparatus after treatment with KOH; B, claws; A, claw of 1st pair of legs with the two accessory points, anterior view (from May).

Genus *HEXAPODIBIUS* Pilato, 1969.
= *Hexapodibius* + *Parhexapodibius* Pilato

Diagnosis (amended): Calohypsibiidae with rigid buccal tube, with reinforcement bar; peribuccal lamellae absent; *Calohypsibius* type claws with 2121 sequence; the claws of the fourth pair of legs have a tendency to be reduced even to absent.

KEY TO THE SPECIES

1.	Lacking claws on the fourth pair of legs	2
	Claws (at least one) are present on the fourth pair of legs	3
2 (1).	Buccal tube with a diameter of 3.5-6μ; macroplacoids slender rods	*Hex. micronyx*
	Buccal tube narrow, with diameter of about 2.3μ; macroplacoids in the form of short clubs; 1st-3rd legs have a dorsal gibbosity	*Hex. pseudomicronyx*
3 (1).	On the fourth pair of legs there is a single doubleclaw	*Hex. pilatoi*
	On the fourth pair of legs there are 2 doubleclaws	4
4 (3).	The claws have very reduced secondary branches, and those on the 4th pair of legs often absent	*Hex. castrii*

The secondary branch of the claws is
characteristically present on all the legs 5

5 (4). Three macroplacoids are present, without
microplacoid; eyes absent .... *Hex. lagrecai*
Two macroplacoids and microplacoid are
are present; eyes present .... *Hex. xerophilus*

HEXAPODIBIUS CASTRII (Ramazzotti, 1964) (Fig. 305).
= *Hypsibius* (*Calohypsibius*) *castrii* Ramazzotti, 1964

Maximum length 522μ; more often 300-400μ; cuticle smooth; yellowish green color in reflected light; two large black eye spots, composed of many pigmented granules. Buccal aperture subventral; buccal tube lacking peribuccal lamellae, medially wide (6μ in an individual of 522μ; 4.3 in another of 477μ), with short reinforcement rods and an accentuated curvature; apophyses very developed; stylets with large furcae. Pharynx oval, with length to width ratio variable between 1.35:1 and 1.13:1 (average of 1.23:1), containing 3 macroplacoids of increasing length from 1st to 3rd; the first is often a round granule, sometimes however oval or slightly elongated, the second and third are on the contrary short rounded rods. First and second macroplacoids are close together, the third is more distant.

The species is easily recognized by the particular structure of the doubleclaws: They have in fact the secondary branch very reduced in the

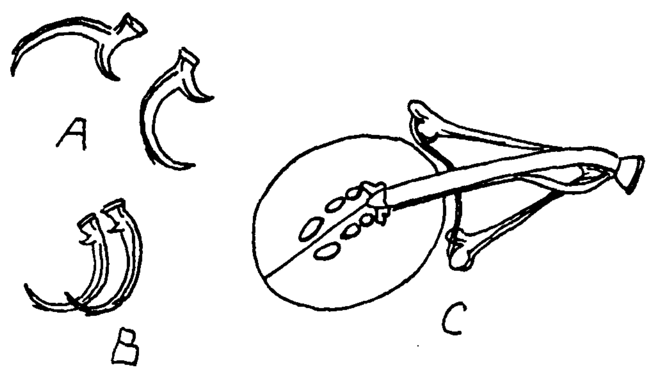


Fig. 305 - *Hex. castrii* (Ramazzotti). A, doubleclaw of the 3rd pair of legs; B, doubleclaws of the 4th pair; C, buccal apparatus and pharynx.

first three pair of legs and quite rudimentary -- sometimes so much that they are almost totally gone -- in the fourth pair; in such cases only the two principal branches remain visible, just as occurs in the genus *Haplomacrobiotus* May. Because of the extreme reduction of the secondary branch, which is often transformed into a simple basal spur of the principal branch, careful observation is required to understand that the doubleclaws are not the *Macrobiotus* type: but the slight difference in size between the two doubleclaws of each leg and the successive space of the branches (principal of the internal doubleclaw -- secondary of the same doubleclaw -- principal of the external doubleclaw -- secondary of the same) establishes the sequence 2121. The doubleclaws are small, in comparison to the dimensions of the tardigrade: for example, the principal branch measures 10-11μ in length on the 4th pair of legs of an animal 520μ long. The principal branches of both of the doubleclaws bear a slender and hard to see accessory point, very displaced backwards with respect to the apex of the claw: it is not possible to distinguish if they are simple or double. Eggs unknown.

The species was collected from terrestrial moss at the entrance of a rodent den (*Lagidium viscasia*) on Cerro del Pajonal (Chile), at an altitude of 4,150 meters.

This species was initially put in the genus *Hypsibius* (because of the sequence of the branches of the claws) and in the subgenus *Calohypsibius* (because of the type of claw).

The presence of the reinforcement bar of the buccal tube rejects this arrangement. Pilato (1973) attempted to put this species in the genus *Haplomacrobiotus* because he considered it to belong to the family Calohypsibiidae. For the reasons expounded by Maucci (1981) we do not acquiesce to the opinion of Pilato, and therefore, while we keep *Haplomacrobiotus* in the family Macrobiotidae, we think it advisable to insert *castrii* in the genus *Hexapodibius*.

HEXAPODIBIUS LAGRECAI (Binda & Pilato, 1969) (Figs. 306 - 308).
= *Hypsibius* (*Calohypsibius*) *lagrecai* Binda & Pilato, 1969
= *Parhexapodibius lagrecai* Pilato, 1969

We have observed 20 individuals, all with smooth cuticle and without eyespots; some colorless, others of brown color; length ranged between 150 and 383μ; according to the authors the size can also be larger, in as much as the longest individual was molting. Mouth subventral, lacking peribuccal lamellae; buccal tube relatively short (40μ in a specimen of

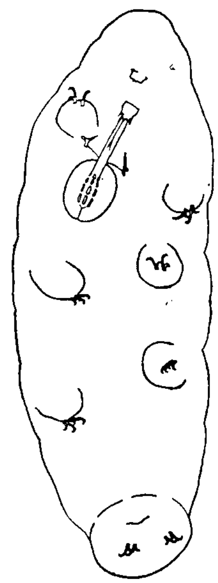


Fig. 306 - *Hex. lagrecai* (Binda and Pilato). Ventral view (from Binda & Pilato).

383μ), with reinforcement bar (that is the *Macrobiotus* type) and of average width (7μ in the aforesaid specimen). Pharynx oval with length/width ratio equal to 1.2-1.3:1 (40 x 37μ in an individual of 330μ).

Apophyses rather developed and 3 macroplacoids (rod-like), of which the first two of about equal length and the third longer (in an individual of 383μ respectively 4.9, 4.3, 5.5μ). The 4th pair of legs (Fig. 308 A) are much shorter and more squat than the other pairs. The doubleclaws (Fig. 307 B) are of the *Calohypsibius* type and rather small; the suture between the principal branch and the secondary branch is very evident nearly to the base of the claw; the principal branch has two small accessory points. The claws of the 4th pair of legs -- contrary to usual -- do not have larger size than the other pairs of legs, but are on the contrary slightly smaller. Exuvia may contain up to 8 smooth, oval eggs (70-77 x 48-54μ).

For this species initially included in the genus *Hypsibius* (subgenus *Calohypsibius*), Pilato (1969) created the genus *Parhexapodibius*.

Hex. lagrecai has been found only in moss from Ustica Island (Sicily).

HEXAPODIBIUS MICRONYX Pilato, 1969 (Figs. 308-310).

Length 228-392μ, more often 300-360μ; colorless, with smooth cuticle. Only 3 pairs of legs are present, with very small doubleclaws, either in relation to the size of the animal, or even in an absolute sense (the

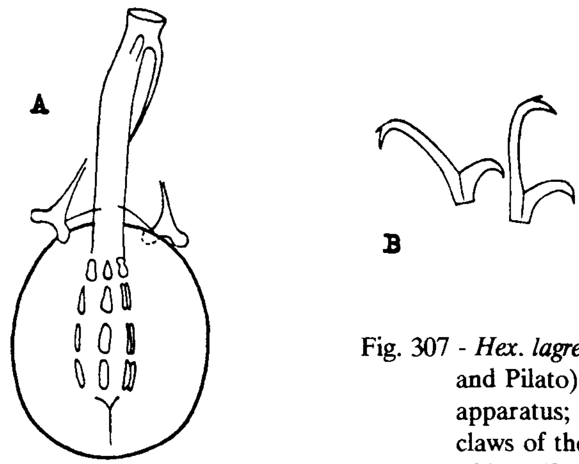


Fig. 307 - *Hex. lagrecai* (Binda and Pilato). A, buccal apparatus; B, doubleclaws of the 3rd pair of legs (from Binda and Pilato).

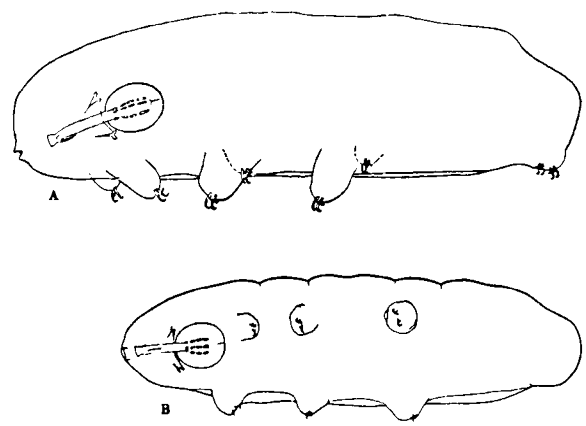


Fig. 308 - *Hex. lagrecai* (Binda and Pilato); B, *Hex. micronyx* Pilato (from Binda and Pilato).

principal branch scarcely reaches 5μ in the larger specimens). Such doubleclaws are of the *Calohypsibius* type: the two branches are fused all the way to the base, with suture very evident almost to the base; the principal branch is a curved hook and the distal part forms an approximate 90μ angle with the rest; the secondary branch is short and likewise forms a 90μ angle with the principal branch. Sometimes there is a squat stump of the 4th pair of legs, however always lacking claws.

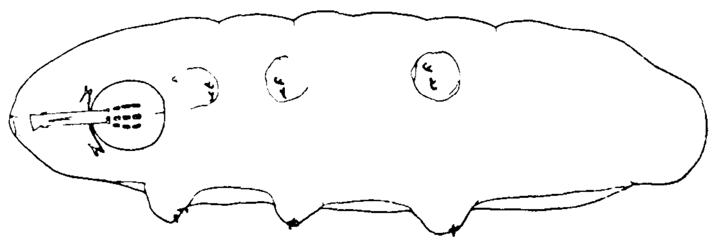


Fig. 309 - *Hex. micronyx* Pilato (from Pilato).

Mouth ventral and forehead steep (as in *Hypsibius*); buccal tube 33-40μ long, 3.5-6μ wide, supplied with reinforcement bar (as in *Macrobiotus*). The pharynx has a length/width ratio of about 1.25-1.35:1 and contains apophyses and 3 macroplacoids (rod-like); the 1st and 2nd are of equal length, or else the 2nd is slightly longer; the 3rd is always a little longer than the others. Microplacoid absent. The eggs are deposited in the exuvium (the only exuvium observed contained 5 smooth, oval eggs of 86 x 70μ).

The species was collected (36 specimens) from moss on fossil sand dunes at Gala (Sicily).

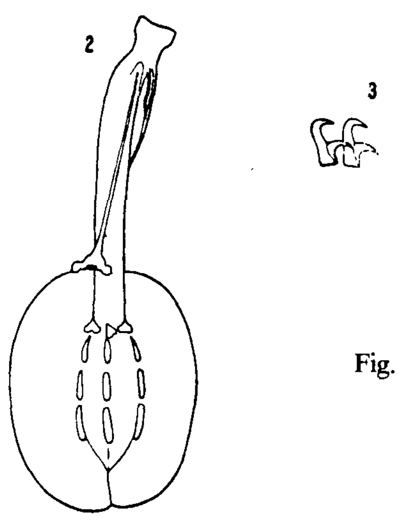


Fig. 310 - *Hex. micronyx* Pilato. Buccal apparatus, pharynx and double-claws (from Pilato).

HEXAPODIBIUS PILATOI Bernard, 1977 (Fig. 311).

Length 245μ; colorless or lightly yellowish, smooth cuticle, without pores, eye spots absent. Buccal tube rather narrow (the width is 6.3% of the length); mouth without lamellae. Pharynx subspherical, with apophyses and 3 macroplacoids, of which the first is a rounded granule, equilateral, the others are slightly elongated, the third longer than the second; microplacoid absent.

Short stumpy legs, with doubleclaws of the *Calohypsibius* type, slender and small; the secondary branch is inserted very near the base, for which the common branch is very short; there are accessory points on the principal branch. The 4th pair of legs, reduced in size, bears on each leg a single doubleclaw, which is similar to that of the other legs, but considerably shorter.

Hex. pilatoi was collected from Gulf Shores (Alabama, U.S.A.).

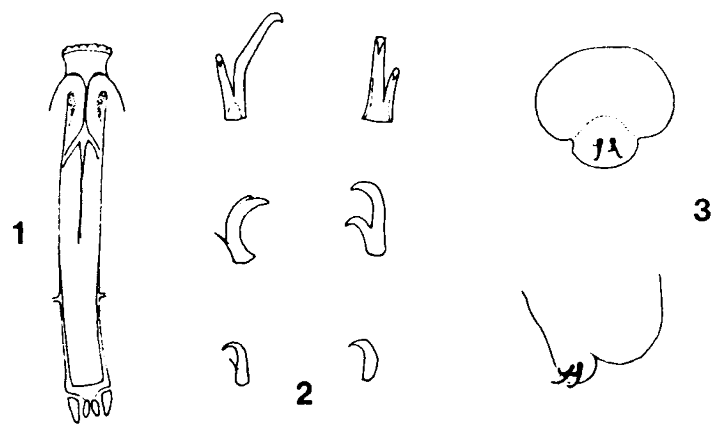


Fig. 311 - *Hex. pilatoi* Bernard. 1, buccal tube, ventral view; 2, claws; 3, leg of the 2nd pair, ventral and lateral view (from Bernard).

HEXAPODIBIUS PSEUDOMICRONYX Robotti, 1972 (Fig. 312).

This species is similar to *Hex. micronyx* in size and general appearance; there is a difference in the following characteristics: the claws have identical size to those of *Hex. micronyx*, but the secondary branch is shorter and more slender, and the accessory points of the principal branch are a little more visible; there are only six legs (the first three pairs) and two stumps of the fourth pair, of variable length; all the legs of the first three

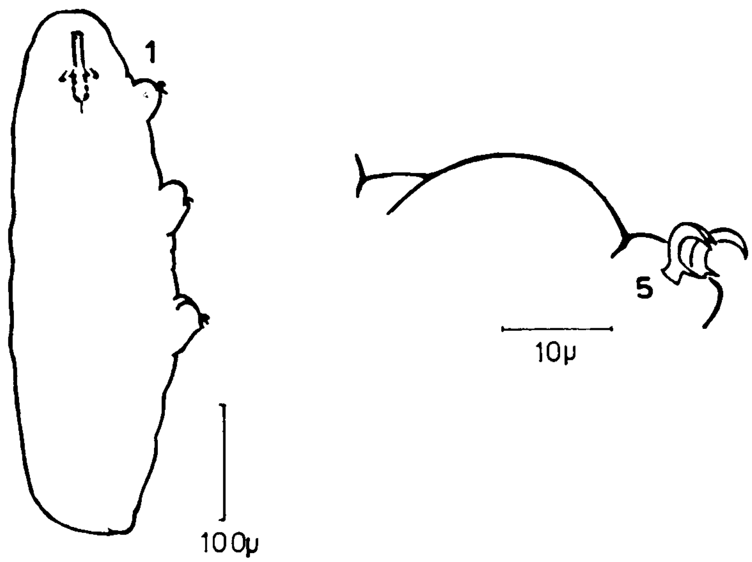


Fig. 312 - *Hex. pseudomicronyx* Robotti. 1, general view; 5, claws and gibbosity on the 3rd pair of legs (from Robotti).

pairs have a dorsal reinforcement; the buccal apparatus is decidedly more narrow (2.35μ in diameter), the macroplacoids have the shape of oval rods, whose line is about a third shorter than in *Hex. micronyx*.

Smooth eggs deposited (up to 9) in the exuvium.

Hex. pseudomicronyx was collected near Avigliana (Piemonte, Italy) in terrestrial moss on a wall near a stream.

HEXAPODIBIUS XEROPHILUS (Dastych, 1978) (Fig. 313).
= *Parhexapodibius xerophilus* Dastych, 1978

Length between 205 and 490μ, white color, smooth cuticle. Eyes present, in posterior position; the eyes were absent in two specimens (of 27 observed). The mouth is situated in an anterio-ventral position, and is without peribuccal lamellae. The buccal tube is 38μ long (in a 342μ specimen), 4μ wide, and has a well developed reinforcement bar. Pharynx oval (33 by 27μ), with apophyses and two macroplacoids in the shape of short rods, the first longer than the second; the first macroplacoid is slightly constricted in the middle. Microplacoid absent. Between the apophyses and the first macroplacoid there are two very slender cuticular

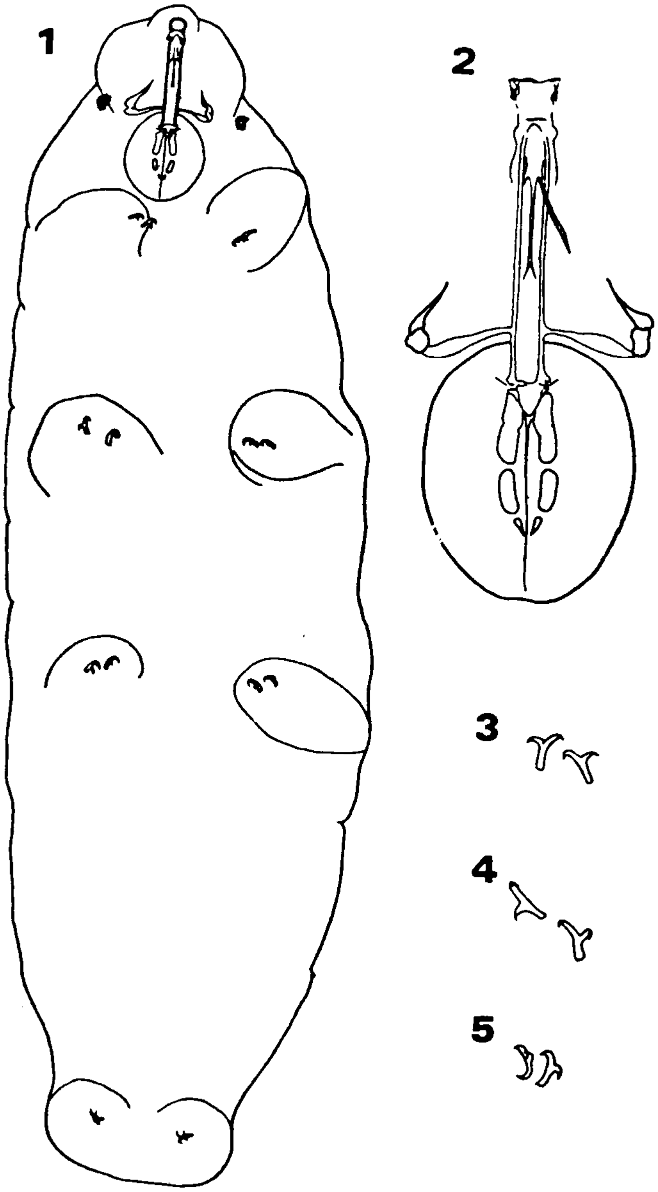


Fig. 313 - *Hex. xerophilus* Dastych. 1, ventral view; 2, buccal apparatus; 3, 4, 5, claws of the 1st, 3rd, and 4th pair of legs (from Dastych).

bars. The claws are of the *Calohypsibius* type, very small and slender. The length of the claws increases slightly from the first to the third pair of legs, while the 4th pair are smaller. The external claws are a little larger than the internal.

The eggs are unknown.

Hex. xerophilus is known from three different localities from east-central Poland.

Typ. loc.: Bialki, near Siedlce; Laskarzew, near Garwolin; Glowacki.

Genus *HYPECHINISCUS* Thulin, 1928.

Diagnosis: Echiniscidae in which the median plates 1 and 2 are transversely divided, not on the contrary the 3rd, which is single, so that 5 median plates in all are visible dorsally; on the terminal plate there is an incision.

KEY TO THE SPECIES

1.	There are no papillae on the 2nd and 3rd pairs of legs; usually there is a single dorsal spine or filament, at times divided (such appendage is absent in the variety *exarmata*)	*Hyp. gladiator*
	Only the papillae on the 2nd and 3rd pairs of legs are present; a single dorsal spine is present	*Hyp. papillifer*

HYPECHINISCUS GLADIATOR (Murray, 1905) (Figs. 314 and 315).

= *Echiniscus gladiator* Murray, 1905

= *Echiniscus* (*Hypechiniscus*) *gladiator* Marcus, 1929

= *Parechiniscus unispinosus* Da Cunha, 1947

Length from 166 to about 300μ, colorless, yellow or pale red; eyes present, sometimes non-pigmented, sometimes black; the sculpture is composed of a very fine granulation, which covers the plates and, less intensely, the cuticle between them; also observed were individuals in which the sculpture was not composed of small dots, but of wide gibbosities, very flat. The plates are faint and poorly delineated: particularly the transverse subdivision of the 1st and 2nd median plates is

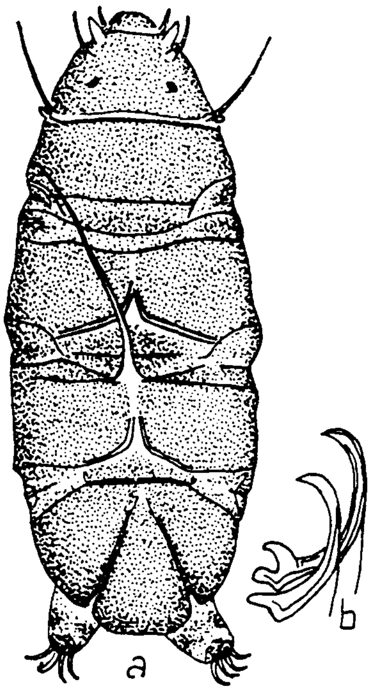


Fig. 314 - *Hyp. gladiator* (Murray). a, dorsal view; b, internal and external claw of the 4th pair of legs (from Petersen, redrawn).

barely visible, sometimes not visible at all. The terminal plate bears two short and deep incisions (notches), which divide it into three wide facets. Other than the usual cephalic appendages (very long cephalic papillae) and the cirrus A, the only cuticular appendage of the body is a robust dorsal spine, or rather a rigid (single) filament, which arises medially from the rostral margin of the second paired plate (II): its length is variable; it can reach or surpass the caudal end of the body, but can also be shorter.

A specimen, collected by Higgins (1960) from North Carolina (U.S.A.) has -- besides the median dorsal filament of 55μ -- also short lateral filaments (25-30μ) arranged asymmetrically.

The legs are slim and the 4th pair is provided with a dentate collar; the internal claws have curved and very robust spurs, which may be

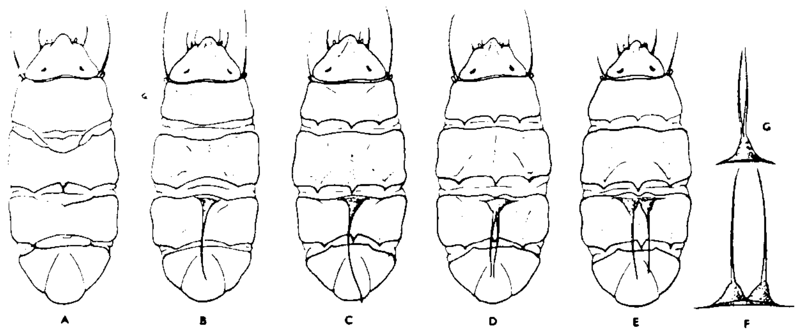


Fig. 315 - Forms of *Hyp. gladiator* (Murray). A, forma *exarmata* (Murray); b, forma nominal; C, forma *spinulosa*; D, forma *fissigladii*; E, forma *bigladii*; F, dorsal appendage of forma *fissigladii*; G, dorsal appendage of forma *bigladii* (from Iharos).

positioned a little under the middle of the claws, or else at the base. The young with two claws measure from 120 to 163μ. The eggs are deposited in the exuvia, generally 3 in number; usually they are oval (70 x 58μ), rarely spherical (diameter of about 60μ).

The species has been collected in a few European localities (Portugal, Ireland, Scotland, Faroe Islands); also in Greenland, in North America (U.S.A. and Canada), in New Zealand, and in Japan. Typ. loc.: Scotland.

Besides the typical form there has been described other different variations, which do not seem to assume the rank of subspecies, also because seldom not present in mixed populations.

Hyp. gladiator forma *exarmata* Murray, 1907, lacks the median dorsal appendage, and has smaller spurs on the internal claws (Ireland, Shetland Island, New Zealand).

Hyp. gladiator forma *bigladii* Iharos, 1973, has small dorsal spines or teeth in positions B, C, and D; the dorso-median filamentous appendage is divided forming two filaments, which arise from two conical projections (Tschann-Pai, Korea).

Hyp. gladiator forma *fissigladii* Iharos, 1973, is similar to the preceding, but the two filaments arise from a single basal projection (the same localities as the preceding).

Hyp. gladiator forma *spinulosa* Iharos, 1973, has a single unpaired dorsal filament, as in the nominal form, but having also small dorsal teeth B, C, and D (same localities as the preceding).

HYPECHINISCUS PAPILLIFER (Robotti, 1972) (Fig. 316).
= *Echiniscus* (*Hyp.*) *papillifer* Robotti, 1972

Length 196-277μ; almost colorless, eye spots black; the sculpture is composed of a fine granulation. A long single dorsal spine (52-59μ) is present. The internal claws are endowed with robust curved spurs, the external claws with small but very distinct sharp spurs, positioned at the base of the claw. On the second and third pairs of legs a rounded papilla is very evident, 2.5μ long with a base 2μ wide.

Hyp. papillifer has been collected (only two specimens) in moss and lichen on rock in Val Piantonetto (Gran Paradiso, Piemonte, Italy) at an altitude of 1,900.

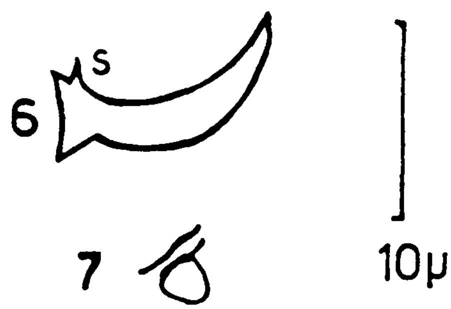


Fig. 316 - *Hyp. papillifer* (Robotti). 6, claw of the 4th pair of legs; 7, papilla of the 3rd pair of legs (from Robotti).

Genus *HYPSIBIUS* Ehrenberg, 1848.

Diagnosis: Hypsibiidae: mouth without peribuccal lamellae, buccal tube short and rigid; cuticle without pores; sequence of the claws 2121; claws of each leg of different form and size; principal branch inserted by means of a flexible junction, not rigid; the common basal branch and the secondary branch form a hooked curve, and are not bent at a right angle; lunule absent.

KEY TO THE SPECIES

1. Cuticle granulated, sculptured or with conical projections 2
   Cuticle smooth 13

2. The cuticle is smooth, but there are two conical papillary projections, caudally, free eggs with spines .... *H. conifer*
   The cuticle is granulated or sculptured with plates, papillae, or tubercular projections 3

3. The sculpture is limited to the caudal zone of the body, posterior to the third pair of legs, and is composed of impressions in the cuticle which have the form of irregular plates or clots .... *H. scabropygus*
   The sculpture extends over all the dorsal and lateral surface, sometimes appearing less distinct on the anterior half of the body 4

4. Epidermis pigmented chestnut, dark brownish-violet, or reddish (which turns purple in KOH), often forming transverse and longitudinal bands (examine adult specimens) 5
   Epidermis not pigmented 9

5. There are dorsal gibbosities .... *H. szeptycki*
   There are no dorsal gibbosities 6

6. Sculpturing very pronounced, constituted of large elements in the form of polygonal plates (diameter 8-9μ) 7
   The sculpturing is a weak granulation, often limited to the caudal half of the body 8

7. The dorsal cuticle is divided into 9 transverse bands which simulate an armor-plating; primary branch of the external claw slender and as long as 17μ . . . . *H. baumanni*

The dorsal cuticle is divided into 10 transverse bands which from the 3rd to the 8th are further divided into a middle zone and two lateral strips; principal branch of the external claw extremely well-developed (up to 45μ) . . . . *H. cataphractus*

8. Pigment distribution in transverse bands but not longitudinal; the eyes are little projected ellipsoids . . . . *H. thulini*

Pigment distribution follows transverse and longitudinal bands, in the pattern of a chess board . . . . *H. oberhaeuseri*

9 (4). The sculpture is composed of a fine and regular granulation; 2 macroplacoids, of which the first is constricted, in the form of a biscuit . . . . *H. biscuitiformis*

The sculpture is composed of polygonal plates, hemispherical tubercles, or papillae 10

10. The sculpture is composed of hemispherical tubercles 11

The sculpture is composed of plates or papillae 12

11. The tubercles of the sculpture are arranged in transverse rows; there are other dark brown granules of various shape and size . . . . *H.* (?) *maculatus*

There are no dark granules . . . . *H. calcaratus*

12. The sculpture is composed of numerous papillae, arranged in transverse rows . . . . *H. runae*

The sculpture is composed of plates of irregular polygonal outline distributed in 7 transverse rows; the plates increase in size from anterior to posterior . . . . *H. camelopardalis*

13 (1). There are three macroplacoids 14

There are two macroplacoids 15

14. The third macroplacoid is shortest; microplacoid present . . . . *H.* (?) *furmanni*

The first macroplacoid is shortest; microplacoid absent . . . . *H. iharosi*

15(13). Epidermis or cavity globules pigmented brown, reddish-brown, violet, or black (examine adult specimens) 16
Unpigmented 22

16. Pigmentation very heavy, dark brown or black 17
Pigmentation fairly pale, brown or reddish-brown 18

17. Body short, reported length:width includes from 3.1:1 to 3.3:1 .... *H. janetscheki*
Body more slender, reported length:width from 4:1 to 5:1 .... *H. klebelsbergi*

18(16). The color is uniformly brown, not deposited in bands 19
The pigment is deposited in transverse and/or longitudinal bands, and turns to purple in KOH 20

19. The macroplacoids are rounded granules .... *H. hypostomus*
The macroplacoids are slightly elongated and are both constricted halfway .... *H. zetlandicus*

20(18). The pigment is deposited in nine transverse (and not longitudinal) bands; eggs smooth, deposited in the exuvium .... *H. novemcinctus*
The pigment is deposited in longitudinal and transverse bands, forming a chess board pattern; eggs free with ornamentation 21

21. The ornamentation of the eggs is spines 5 to 12μ long (known only from Chile) .... *H. anomalus*
The ornamentations are hemispherical (a common and widely distributed species) .... *H. oberhaeuseri*

22(15). The macroplacoids are rods at least two times longer than wide (at least the first) 23
The macroplacoids are rounded or square granules, or slightly elongated (a maximum of one and a half times longer than wide) 28

23. The first macroplacoid is shorter than the second .... *H. giusepperamazzottii*
The first macroplacoid is equal or longer than the second 24

24. The first macroplacoid is two or three times longer than the second; the 2nd is a granule a little longer than wide .... *H. simoizumii*
The two macroplacoids are not very different in length 25

25. Microplacoid present (sometimes very small) 26
Microplacoid absent 28

26. Microplacoid tiny; species usually moss-dwelling 27
Microplacoid visible; species hygrophilic, often aquatic .... *H. dujardini*

27. Eyes present; buccal tube width more than 13% of the length .... *H. allisoni*
Eyes absent; buccal tube width 10% of the length .... *H. convergens*

28(25). Eggs deposited free 29
Eggs smooth, deposited in the exuvium 30

29. The row of placoids surpasses the midlength of the pharynx; claws of each leg different in shape and size; eggs supplied with club-like projections, imbedded in a hyaline layer .... *H. arcticus*
The row of placoids does not reach the middle of the pharynx; claws of each leg almost equal; eggs free, but smooth .... *H. antarcticus*

30(28). The macroplacoids are rods, about two times longer than wide 31
The macroplacoids are rounded or square granules, isometric or barely longer than wide 32

31. Eyes present; buccal tube width 13-14% of the length .... *H. allisoni*
Eyes absent; buccal tube width 10% of the length .... *H. convergens*

32(30). The primary branch of the external claw is inserted very near to the base, for which the common branch is very short (shorter than the secondary branch) .... *H. microps*
The principal branch is inserted higher, for which the common basal branch is longer than the secondary branch .... *H. pallidus*

HYPSIBIUS ALLISONI Horning, Schuster, and Grigarick, 1978 (Fig. 317)

Length between 170 and 365μ, with an average of 283μ (length of the holotype 309μ). Eye spots present. Cuticle smooth. Buccal tube 30μ long, 4 wide. Stylet supports attached 11μ from the base. Pharynx round, 30μ diameter, with apophyses and two macroplacoids, the first a little longer than the second (respectively 6 and 4.5μ). Microplacoid absent, or else present, but very small.

This species, according to the authors, is distinguished from *H. dujardini* and *H. convergens* by the wider buccal tube, with thinner walls, by the presence of eye spots, and by the larger size.

H. allsoni was described in rather summary manner, and the characters do not seem sufficient for distinguishing. The notable variability of the

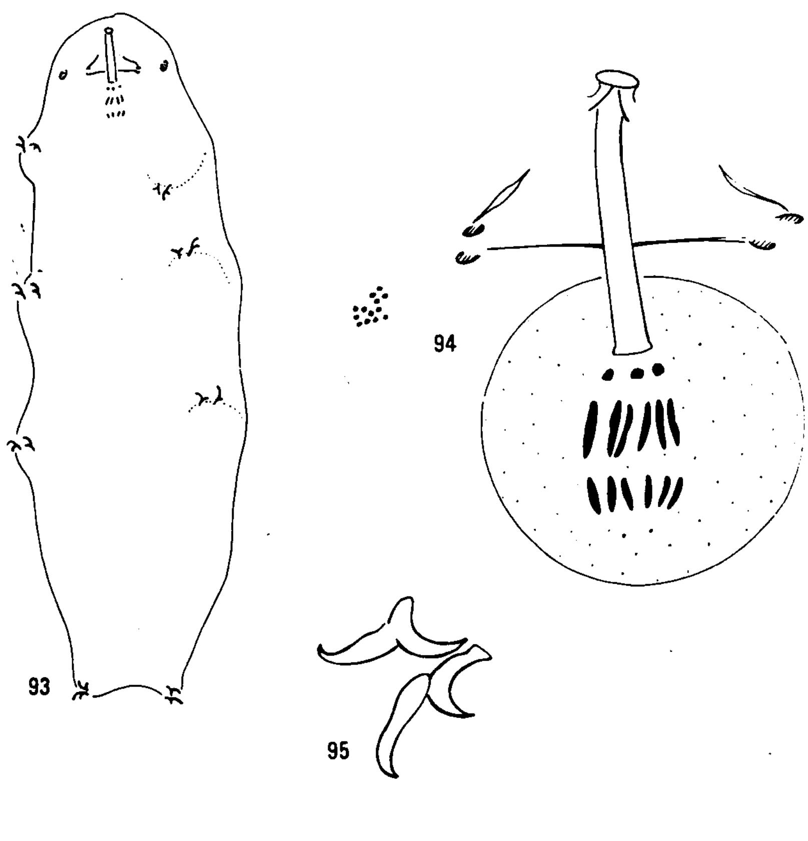


Fig. 317 - *H. allisoni* Horning et al. 93, dorsal view; 94, buccal apparatus and eye spot; 95, claws of the 4th pair of legs (from Horning, Schuster, and Grigarick).

buccal tube width in *H. convergens* leads one to believe that *H. allisoni* probably ought to be considered as a synonym of it.

The species was described from New Zealand.

HYPSIBIUS ANOMALUS Ramazzotti, 1962 (Fig. 318).

Length up to 380μ, more often 300-350μ; eye spots absent. The adult individuals are pigmented reddish-brown, or violet, with longitudinal and transverse uncolored bands; in general aspect they resemble a great deal therefore *H. oberhaeuseri*, with which they are very easy to mistake. But there are only two dorsal longitudinal bands not pigmented (clear), while sometimes, but not always, there are two others on the flanks -- positioned, that is, more laterally -- and fusing into one. Also, *H. anomalus* appears more slender than *oberhaeuseri*, that is the ratio between the maximum length and width -- in dorsal view -- is somewhat greater than in *H. oberhaeuseri*. Treating the tardigrade with KOH, the pigment dissolves and the animals are uniformly colored red-violet; with addition of acetic acid, the coloration turns to a greenish-yellow. The young are barely pigmented, or all colorless; the cuticle, even in the adults, is completely smooth all over, without any granulation.

The buccal tube is narrow (external diameter about 3μ in an animal 380μ long) and its length, from its anterior extreme to its entrance into the pharynx, measures about 26μ (in an individual of 380μ). The stylets have a very pronounced furca; in ventral or dorsal view, the two stylets and the stylet supports delineate a triangle that is approximately equilateral. Pharynx almost spherical (e.g., length 30μ and width 27μ in an animal of 380μ), containing well developed apophyses and 2 macroplacoids, the first a little longer and larger than the second (e.g., respectively about 3μ and 2μ, in a tardigrade of 380μ); in ventral view the first macroplacoid appears almost square and the second rounded.

The doubleclaws are practically indistinguishable from those of *H. oberhaeuseri*; the principal branch of the external doubleclaw (length 15-16μ on the fourth pair of legs, exclusive of the basal part) has two slender accessory points, merging to the back surface of the apices of the claws; they are visible only -- and with difficulty -- using oil immersion; but they occur sometimes also in *H. oberhaeuseri*. The principal branch of the internal doubleclaws have instead very robust and very visible accessory points. Note that the secondary branch of the external doubleclaws is shorter than its basal part; i.e., it is similar to those of *H. oberhaeuseri* and not to those of *H. novemcinctus*.

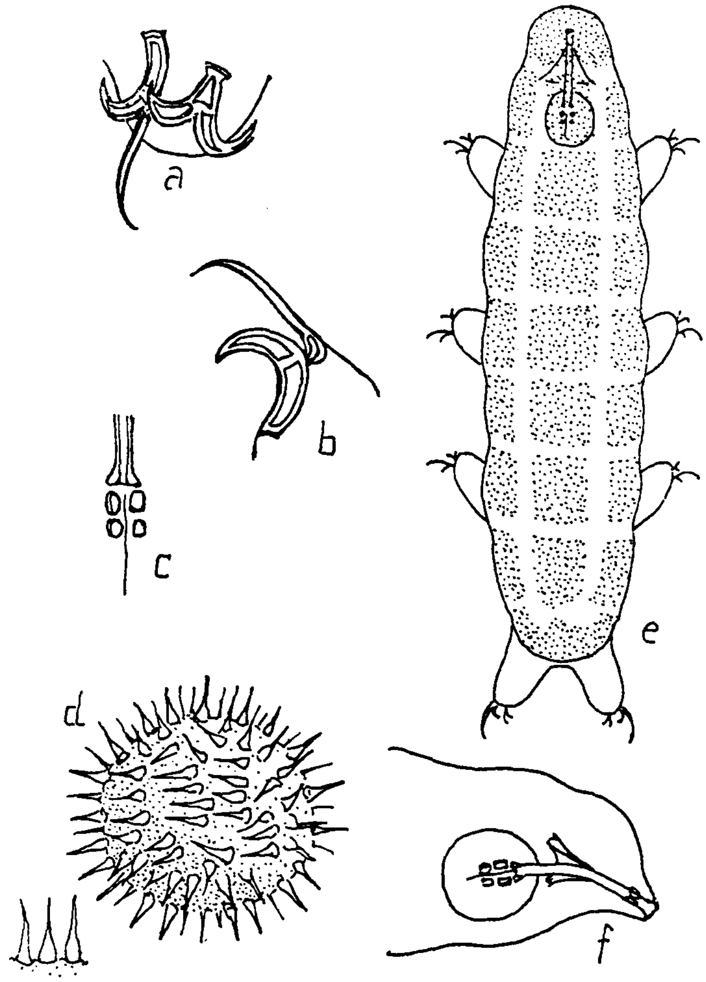


Fig. 318 - *H. anomalus* Ramazzotti. a, doubleclaw of the 4th pair of legs; b, external doubleclaw of the 2nd pair; c, macroplacoids; d, egg and detail of the spines; e, dorsal view (schematic); f, cephalic region in lateral view.

From the preceding information it can be seen that from the examination of a single tardigrade it is not possible to distinguish for certain *H. anomalus* from *H. oberhaeuseri*; the distinct difference consists only in the fact that the longitudinal colorless bands, larger and immediately evident, are reduced to two in *anomalus*: but that does not authorize the establishment of a new species, and not even a variety. The substantial difference between the two species consists instead in the eggs, which are entirely different from those of *oberhaeuseri*. In fact the eggs of *H. anomalus* -- spherical or slightly oval -- have ornamentation in the form of spines, length of 5-12μ, with diameter at the base varying between 2 and 4μ. The spines in general are erect and straight, very rarely with slightly bent apices; the shell, between the spines, appears smooth at medium magnification, but at high magnification -- with the use of oil immersion and phase contrast -- appears finely punctate, not too uniform. The spines are arranged irregularly: in some areas of the shell the distance between them is as much as the diameter of the bases (2-4μ), while in other areas the distance is even 3-4 times the diameter. The belonging of the eggs to *H. anomalus* is certain, because I have examined embryonated eggs, in which the buccal apparatus was perfectly visible and identified as that of the species.

With the discovery of *anomalus*, there exists then at present three species of *Hypsibius* with very similar appearance and they are:

1) *H. oberhaeuseri*, which deposits eggs freely with diameters of 45-57μ and hemispherical projections (the general appearance of the eggs is that of a mulberry or raspberry). The animals reach up to a length of 500μ and have 4 longitudinal and 9 transverse colorless bands. The cuticle is often granulated, especially in the caudal region.

2) *H. novemcinctus*, which deposits smooth eggs in the exuvium; the animals are smaller, not surpassing 240μ in length, lacking the colorless longitudinal bands and having only the eight colorless transverse bands (nine pigmented). The cuticle is smooth everywhere.

3) *H. anomalus*, which deposits eggs freely, with diameters of 64-85μ and ornamentations in the form of spines; the animals have lengths up to 380μ and have 2 obvious colorless longitudinal dorsal bands, sometimes flanked by another colorless longitudinal band, more lateral and less visible. The cuticle is smooth everywhere.

It is however advisable to keep in mind what Baumann (1966) wrote about a possible identity of *H. novemcinctus* with *H. oberhaeuseri*, which we have reported under the description of *novemcinctus*, which we reject. I am of the opinion instead to think -- at least provisionally -- that *H. anomalus* is distinct from the other two species, especially by the notable number of eggs observed, identical in all appearances.

H. anomalus, with many hundreds of individuals and tens of eggs, was observed by me in lichen from rock from Chile (Cerro El Roble), sent by

Prof. F. di Castri Liviero and collected at an altitude of about 1,925 m; the species was accompanied by *E. bigranulatus* and *Miln. tardigradum*, with respective exuvia with eggs.

Recently the species has been discovered by Dastych, also in Afghanistan (with slightly different eggs).

HYPSIBIUS ANTARCTICUS (Richters, 1904) (Fig. 319).

The type species, described by Marcus (1936), is about 336μ, transparent, with smooth cuticle, and eye spots. Stylets are saber-like, pharynx an elongated oval with two macroplacoids, slightly bent and the first a little longer than the second; microplacoid absent. It is a characteristic of this species (in common with very few others) that the line of macroplacoids does not pass the midlength of the pharynx. The doubleclaws of each leg are very different from each other (Fig. 319 C).

The eggs are spherical with a diameter of 80μ, smooth, without any ornamentation, and are usually deposited free. The surface of the egg is sticky so it adheres to the leaves of mosses, or other substrates (Fig. 319 D). However, on one occasion, four eggs were found in an exuvium.

The unique specimen of *antarcticus* collected by Petersen (1951) in Greenland, differs from the above description by having much larger size (540μ), an absence of eyes, and did not have the great differences between the doubleclaws, but as the eggs were not found it seems to us that the inclusion of this specimen in *antarcticus* rather dubious.

Dastych (1973) advanced the hypothesis that *H. antarcticus* might be a synonym for *H. dujardini*, representing an advanced "simplex" stage. We feel we can not agree with this hypothesis, because there are distinct differences between the descriptions of *H. antarcticus* and *H. dujardini*: the size of the claws, the absence of microplacoids. Moreover -- and this for

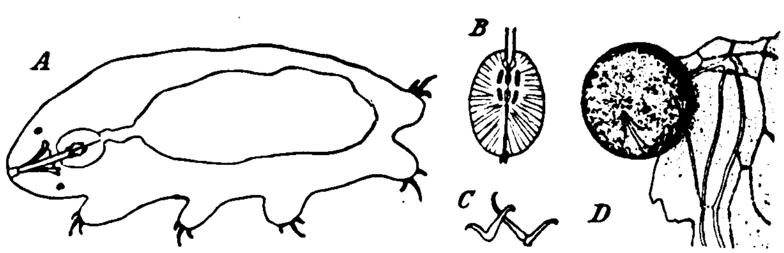


Fig. 319 - *H. antarcticus* (Richters). A, dorsal view; B, pharynx; C, doubleclaws; D, egg stuck to a "leaf" of moss (from Marcus).

us seems decisive -- Marcus (1936) identified the attributes of *H. antarcticus* eggs (deposited free and smooth) in which the characteristic buccal apparatus could be seen, and this is incompatible with a "simplex" stage.

H. antarcticus was observed in Antarctica, but is also found in Poland, Romania, Czechoslovakia, Sweden, Norway, and (perhaps) Greenland. Type Loc.: M. te Gauss (Antarctica).

HYPSIBIUS ARCTICUS (Murray, 1907) (Fig. 320).
= *Macrobiotus heinisi* Richters, 1907

Large size up to 500μ or more, with smooth cuticle, eyed; the immature form is transparent, but the adult individual has some brown pigment. The buccal tube is narrow (1.5μ in an individual of 350μ), the pharynx a short oval with two macroplacoids, in the shape of elongated rods. In the immature form the placoids are reduced to roundish or square granules, in the adults the first macroplacoid is somewhat longer and wider than the second.

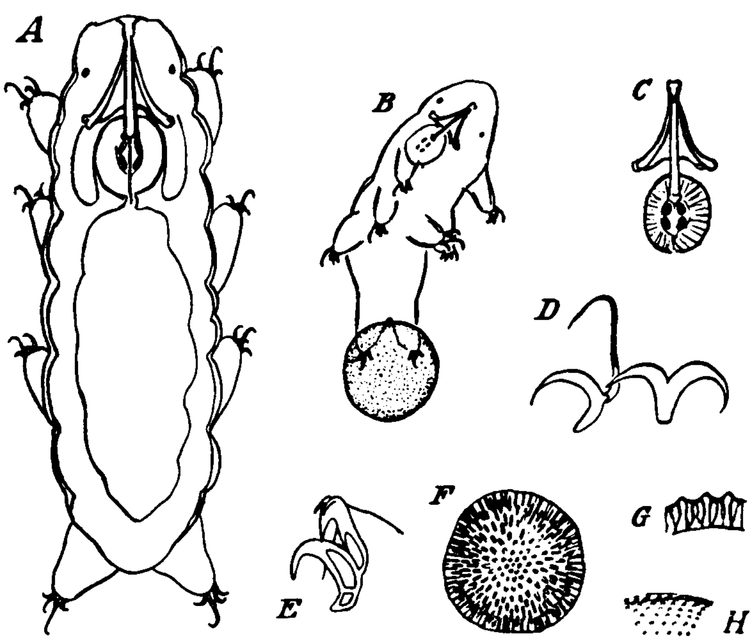


Fig. 320 - *H. arcticus* (Murray). A, dorsal view; B, immature leaving egg; C, buccal apparatus and pharynx of an immature; D, doubleclaw; E, posterior claw of the 4th leg; F, egg; G, H, detail of egg ornamentation (from Marcus).

Both the doubleclaws are large, but very different from each other. The internal (anterior) doubleclaw has a short basal part and a long robust terminal portion which is strongly curved at the tip.

Eggs are short ovals, with a diameter of 76-96μ. The shell is covered in an external hyaline zone in which are immersed (without projections) round headed rods, which when viewed straight on, appear as regularly deposited points of refracted light. The eggs are of two types: those with a shell of major thickness (5-6μ; Fig. 320 F, G), and those with a shell of minor thickness (2-3μ; Fig. 320 H). The eggs may be deposited free or in exuvia (2 or 3 at a time), however, only thin shelled eggs are deposited in the exuvia, while those deposited free may be thick or thin shelled.

The species is cosmopolitan and a few have been found everywhere (not in Italy) either in freshwater or moss. Type Loc.: Terra di Francesco Giuseppe.

HYPSIBIUS BAUMANNI Ramazzotti, 1962 (Fig. 321).

Length 240-315μ, eye spots absent. The sculpture, which covers the entire dorsal and lateral surfaces -- legs included -- is composed of a large granulation, in which the elements assume the appearance of platelets more or less circular or polygonal, especially in the median zone of the dorsum. The individual platelets, which are really tubercles flattened at their apices, may reach 8-9μ in diameter and they resemble, especially those of larger size, what is present on the caudal region of *Diphascon nodulosum* Ramazzotti. In the rostral and caudal regions of the tardigrade and on the legs, especially on the anterior, the platelets diminish in diameter, reduced sometimes (but not always) to a strong granulation of tubercles. The cuticle of the ventral surface, including that of the legs, is smooth.

The animal, observed dorsally, shows 9 transverse bands of reddish brown color, very protruding (with exception of the rostral two); on several of these bands, in particular from the fourth to the eighth, the platelets tend to cluster to form a gibbosity, not always clearly defined in number and position, and variable from one individual to another. Sometimes there is a tuberculated gibbosity also on the 4th pair of legs.

The buccal tube is very narrow (external diameter 1.5-2μ) with very evident apophyses; the pharynx, circular or slightly oval, measures for example 28 x 28μ in an individual 315μ long, 24 x 24 in a 288μ individual, and 24 x 21μ in an individual of 246μ; it contains two square macroplacoids, of which the first is somewhat larger than the first is

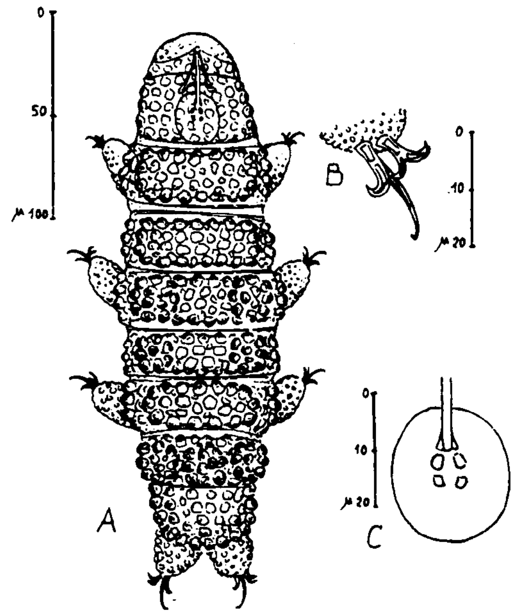


Fig. 321 - *H. baumanni* Ramazzotti. A, dorsal view; B, doubleclaws of the 4th pair of legs; C, pharynx.

somewhat larger than the second; there is no microplacoid. The rows of the macroplacoids are short and do not surpass more than the middle of the pharynx. The doubleclaws resemble those of *H. oberhaeuseri*: the principal branch of the external doubleclaw is slender and long (17μ on the 4th pair of legs of a tardigrade of 246μ) with very small accessory points, visible with difficulty and set back with respect to the end of the claw; the internal doubleclaw is very robust and has distinct accessory points on its principal branch.

H. baumanni, especially at low magnification, resembles in its *H. oberhaeuseri*, but is different in the sculpture characteristics, in the prominent bands, by the more or less distinct gibbosity, and by the lack of colorless longitudinal bands.

Deposited eggs have not been observed and therefore it has not been established if they are free, or else contained in the exuvia; three eggs, visible in the ovary of a female, exhibited small projecting ornamentation, whose shape was not however very distinguishable.

The species was collected in moss and lichen on the trunk of *Aextoxicum punctatum* in two different localities at Fray Jorge (Chile, altitude of about 620 m).

HYPSIBIUS BISCUITIFORMIS Bartos, 1960 (Fig. 322).

Length about 216μ, rather squat, cuticle completely sculptured on the dorsal surface; the sculpture is a fine and regular granulation, which renders the tardigrade barely transparent, or quite opaque. Eye spots present, black and usually in anterior position; slender stylets, with weak curvature; stylet supports inserted somewhat rostrally, so that they are turned back for insertion in the socket of the furca, which is pronounced. Buccal tube rather narrow (external diameter 2.7μ); pharynx short oval, with very evident apophyses and 2 macroplacoids, of which the first is about 4μ long, wide and profoundly notched on both sides, so as to resemble the shape of a biscuit, while the second is a little shorter (about 2.7μ), moderately wide, oval or even spherical (granular); microplacoid absent.

The two doubleclaws of each leg, actually the *Hypsibius* type, do not have very different lengths. An exuvium has been observed containing three eggs.

The species has been collected only in two localities in Hungary, in moss exposed to the sun for many hours of the day.

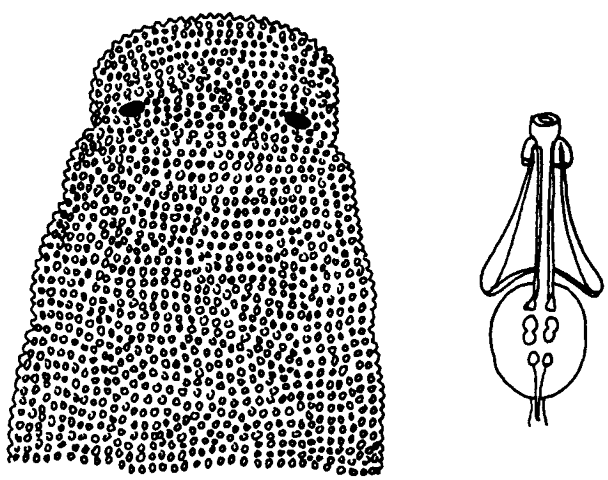


Fig. 322 - *H. biscuitiformis* Bartos. Rostral part of the head and buccal apparatus (from Bartos, redrawn).

HYPSIBIUS CALCARATUS Bartos, 1935 (Fig. 323).

Length 135-200μ; the cuticle of the entire body is granulated and the granulation is composed of minute hemispherical tubercles. Eyes present or absent; when present, the eye spots are small and formed of small granules of pigment (4-10).

Buccal aperture ventral; the buccal tube, Bartos reports, is very short (13.5μ) and narrow (less than 1μ in diameter), however I have seen individuals with buccal tubes longer (22-23μ and somewhat wider (almost 2μ); pharynx approximately spherical, notable small (13.5 x 12.5μ, with 2 macroplacoids, of which the first has a larger size than the second; microplacoid absent. The doubleclaws of each leg are of very different size, especially on the 4th pair of legs; principal branch of the external doubleclaw very developed and slender, with very long and divergent accessory points. Eggs deposited in the exuvium.

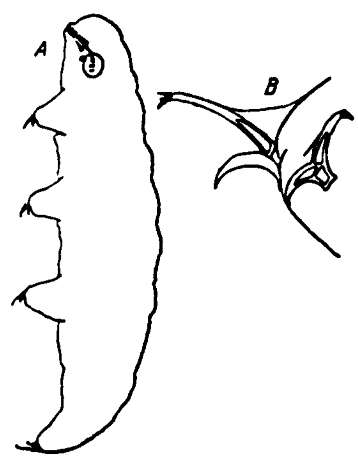


Fig. 323 - *H. calcaratus* Bartos. A, lateral view; B, doubleclaws of the 4th pair of legs (from Bartos).

The species -- when eyeless and the eggs are not present -- is easy to confuse with young, and therefore colorless, individuals of *H. oberhaeuseri*, which have a strong granulation; these can be distinguished -- although somewhat artificially -- by the smaller dimensions of the pharynx and by the greater development of the accessory points on the principal branch of the doubleclaws; the presence of eggs takes away all doubt, because *calcaratus* deposits smooth eggs in the exuvium, while *oberhaeuseri* deposits free eggs and with characteristic ornamentation.

H. calcaratus is known only from a few localities in North America, central Europe, and Italy; the species is probably montane.

Type Loc.: Rozsutec (Czechoslovakia).

HYPSIBIUS CAMELOPARDALIS n. sp. (Fig. 324).

Length as much as 280μ. Colorless, eye spots absent. The cuticle has a rather pronounced sculpture composed of irregular plates roughly polygonal in outline; these plates are distributed in seven transverse bands, of which the first is situated rather anteriorly to the pharynx, the third is at the level of the first pair of legs, the fifth is at the level of the second pair, the seventh is at the level of the third pair; from here the sculpture extends then uniform as far as the caudal end. Between one band and the next, the cuticle is smooth or lightly granulated; the same bands are not however clearly delimited. The plates of the sculpture increase slightly in size in a rostro-caudal direction, so they are clearly larger (up to 6μ) on the caudal area. On the external sides of the legs there is a slight granulation.

The forehead is very bulging, with mouth clearly anterio- ventral, from which the buccal tube (rather narrow, 4μ) makes a curve between the mouth and the entrance into the pharynx. The pharynx is perfectly round, and contains apophyses and two macroplacoids in the shape of granules, of which the first is a very little longer than wide, while the second is equilateral. Microplacoid absent.

The claws of each leg are not very different from each other in shape and size. Claws are rather robust, with short common basal branch and massive principal branch (more than in the species of the *pallidus* "group"), with accessory points. Eggs are unknown.

The species was found on the Iberian Peninsula, in one locality of Portugal (near Nisa), and in one locality of Spain (S.ta Olalla, Andalusia).

Fig. 324 - *H. camelopardalis* n. sp. A, head with buccal apparatus; B, detail of the sculpture, near the caudal end; C, doubleclaws of the 4th pair of legs.

HYPSIBIUS CATAPHRACTUS Maucci, 1974 (Fig. 325).

Length up to 330μ. Intensely and uniformly pigmented violet, without clear bands, neither transverse nor longitudinal; the pigment turns to a bright lilac in the presence of KOH and becomes pale yellow in polyvinyl lactophenol. Eye spots absent. The cuticle appears to be armored, with 10 transverse plates, separated by deep folds, of which the 1st, 2nd, and the 10th are single, while the others are subdivided into three, a dorso-median and two dorso-laterals. The terminal plate has two incisions, similar to those of the *Echiniscus*. The sculpture of the cuticle is a large, dense granulation, composed of hemispherical granules, often touching each other.

The legs are long, the first three pair smooth, the 4th pair with a very fine granulation on their dorsum.

The buccal tube is very narrow (40μ long, 2 wide). Stylets widely spread, short, with large but weak furcae. Pharynx short oval or round, with apophyses and two macroplacoids, of which the first is a little larger

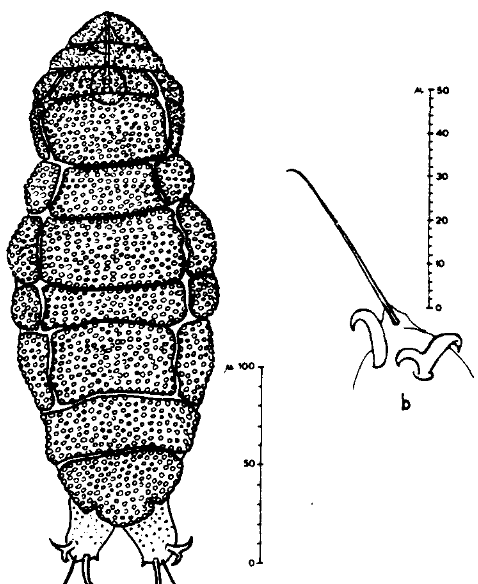


Fig. 325 - *H. cataphractus* Maucci. a, dorsal view; b, claws of the 4th pair of legs (from Maucci).

and of elongated oval shape (two times longer than wide), while the second is short and almost round. Microplacoid absent.

The claws resemble those of *H. oberhaeuseri* but the principal branch of the external claw is extraordinarily long (as much as 45μ), slender, similar to a bristle.

Eggs deposited free, of yellowish color, spherical; the ornamentation is spines with conical bases, then rapidly attenuated: spines about 10-12μ long are irregularly distributed between others not longer than 5-6μ. The diameter of the eggs is 70-75μ, not including the spines.

The species has been collected, without eggs, near the glacier of Grossglockner (Austria). Then it was found again, by Dastych, on Spitzbergen, and in this collection eggs were included.

HYPSIBIUS CONIFER Mihelčič, 1938 (Fig. 326).

Length 200-250μ, colorless, eyed; the cuticle is smooth all over, but caudally there are -- one per side -- two small conical papillary projections; in addition, each of the legs of the 4th pair has dorsally two analogous conical papillae, one proximal and the other distal.

Buccal opening ventral, buccal tube short and narrow, pharynx oval in optical section, sometimes rostrally somewhat flattened; apophyses with a constriction, so that each one of them appears composed of two joined granules; 2 macroplacoids (short rods); microplacoid absent. The two doubleclaws of each leg are of much different size.

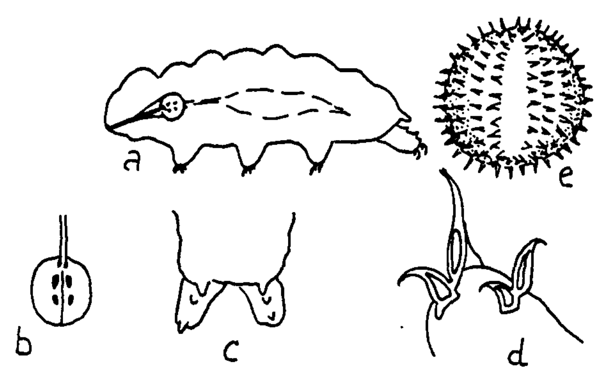


Fig. 326 - *H. conifer* Mihelčič. a, profile view; b, pharynx and placoids; c, caudal region; d, doubleclaws of the 4th pair of legs; e, egg (from Mihelčič and from G. Iharos, redrawn).

The spherical eggs, with numerous spines distributed in regular rows, are deposited free; in the genus *Hypsibius* the existence of eggs with ornamentation is the exception, which has been verified only -- other than in this species -- in *H. anomalus*, *H. arcticus*, *H. fuhrmanni*, *H. oberhaeuseri*, *H. cataphractus*, and *H. thulini*.

H. conifer was collected in Yugoslavia, Hungary, Norway (at the Arctic circle), and in Sicily, in general in moss in the sun on rocks or on houses, but also in damp moss on beech (Sicily).

HYPSIBIUS CONVERGENS (Urbanowicz, 1925) (Fig. 327).

Length up to 400μ; eyes present, sometimes small, sometimes of great size. Buccal tube rather narrow, from 1.5 to 1.7μ in diameter, with appendices of insertion for the muscles in the form of a hook. The pharynx is -- in optical section -- a rather elongated oval (reported length to width ratio of about 1.3;1) and contains apophyses and 2 macroplacoids which are wide rods and the length of the first with respect to the second is reported 3:2; sometimes the first rod appears constricted in the middle and the second assumes the form of an oval granule. In general lacking the microplacoid; when present, it is nevertheless very small. Doubleclaws of each leg of very different size.

The basal branch is inserted very low on the secondary branch, near the base, so that the common branch of the claw is very short.

Deposited in the exuvium are 1 to 7 eggs, smooth, oval or spherical.

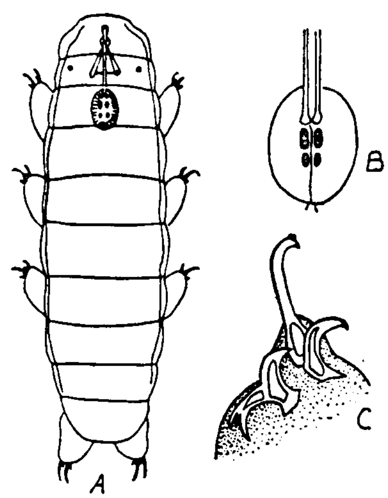


Fig. 327 - *H. convergens* Urbanowicz). A, dorsal view; B, pharynx; C, doubleclaws of the 4th leg.

H. convergens is near to *H. microps* and *H. pallidus*: it can be distinguished from these two species by the elongated pharynx, by the shape of the placoids (which in the other two species are short granules), and by the more massive and divergent claws. It is however advisable to make clear that these characters do not always appear very evident, and in many cases certain determination requires considerable experience. *H. convergens* is also very similar to *H. dujardini*: this last species has however placoids a little more slender and longer, has a more evident microplacoid, and has decidedly more developed claws. Also in this case, especially for material collected in water, in interstitial environment, or in wet moss, a certain determination may be very difficult.

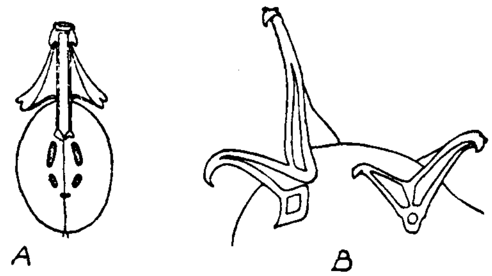
H. convergens has been collected almost everywhere, in Europe (including Italy), North and South America, on Fernando Poo Island (western Africa), on Kerguelen Island, in India, Turkey, at 5,500 m altitude on Himalaya (pigmentation of brown color), in the Arctic: but it is necessary to keep in mind the possibility of possible error in the determination of the species. Type loc.: Wilna (Poland).

HYPSIBIUS DUJARDINI (Doyére, 1840) (Fig. 328).
= *Macrobiotus dujardini* Doyére, 1840
= *Macrobiotus lacustris* + *palustris* Duj., 1851
= *Macrobiotus tetradactylus* Lance, 1896
= *Macrobiotus murrayi* Richt., 1907
= *Macrobiotus breckneri* Richt., 1910
= *Macrobiotus samoanus* Richt., 1908
= *Macrobiotus ursellus* Della Valle, 1915
= *Hypsibius dujardini* + *murrayi* Marcus, 1929

Length up to 500μ, hygrophilic and hydrophilic; usually eyed. Buccal tube short and narrow, of about 2μ diameter and with muscle insertion appendix in the shape of a hook. Pharynx oval, with apophyses and 2 macroplacoids, which are slender rods of about equal length, or else the first -- often with a constriction -- is a little longer than the second; microplacoid usually present, rarely absent (material from Greenland). The two doubleclaws of each leg have very different size, common basal portion of the two branches very short and the principal branch with accessory points.

This species is not exclusively aquatic, but may be found not seldom in damp terrestrial moss, or in shaded habitats; it deposits 2 to 19 eggs in the exuvium; the eggs are oval, smooth and variable in size (larger diameter

Fig. 328 - *H. dujardini* (Doyére). A, buccal apparatus; B, doubleclaws of the 4th pair of legs.



51-73μ; smaller diameter, 42-62μ).

For distinction between *H. dujardini* and the very similar *H. convergens*, refer to the account in the description of *H. convergens*.

The species was collected almost everywhere in Europe, in North America (U.S.A.: Columbia, Illinois, Maryland), in South America, in India, and in the Arctic; in Italy it was also found in freshwater interstitial habitat. Type loc.: Fontainbleau (Paris, France).

HYPSIBIUS (?) FUHRMANNI (Heinis, 1914) (Fig. 329).
= *Macrobiotus fuhrmanni* Heinis, 1914

Length 175-250μ, transparent, eyed. Stylets slightly curved; pharynx oval, containing apophyses, 3 macroplacoids approximately square in shape, of which the third is the smallest, and microplacoid. The claws of each leg are of different length and in both the principal branch is remarkably longer than the secondary. Eggs deposited free, about 72μ diameter, with irregular projections, often with bulbous base and sharpened points.

This species was certainly described in insufficient manner: only the placoid and the egg characteristics may permit eventual identification. Also its classification in the genus *Hypsibius* is considered doubtful: Marcus (1936) includes it in this genus (without however making clear to which subgenus), on the basis of the different length of the claws (cautioning however that the figure of his publication has exaggerated this character, compared with the original diagnosis). One can not exclude that the species belongs instead to *Isohypsibius*, if not quite to *Macrobiotus*.

H. (?) *fuhrmanni* was observed only in South America (Colombia).

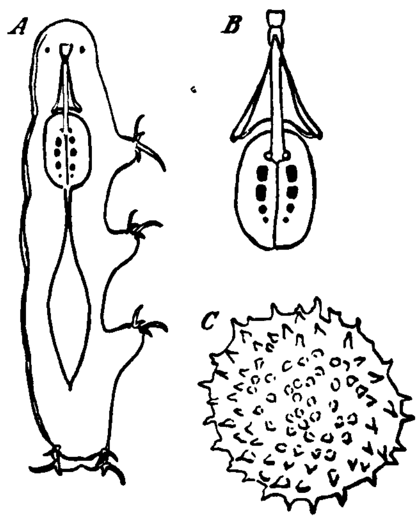


Fig. 329 - *H.* (?) *fuhrmanni* Heinis. A, habitus; B, buccal apparatus; C, egg (from Marcus).

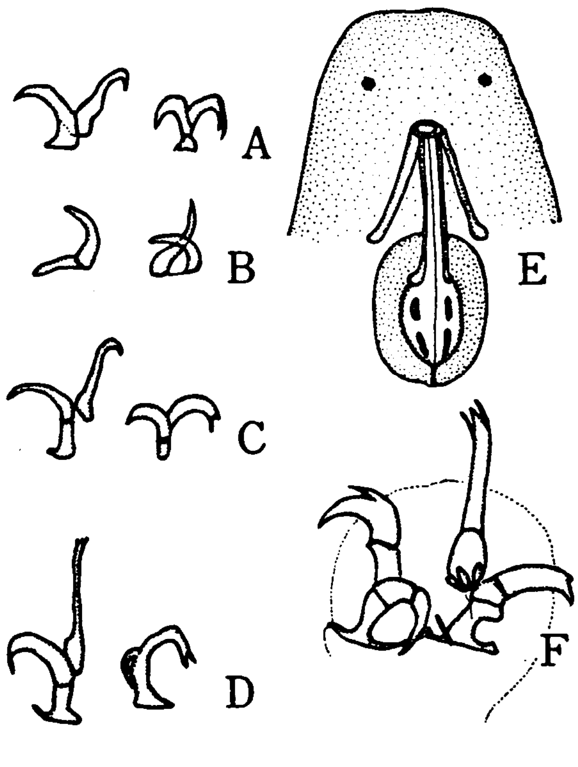


Fig. 330 - *H. giusepperamazzottii* Sudzuki. A, claws of the 1st pair of legs; B, C, D, claws of the 2nd, 3rd, and 4th pair; E, cephalic region; F, claws of the 4th pair of legs (from Sudzuki).

HYPSIBIUS GIUSEPPERAMAZZOTTII Sudzuki, 1975 (Fig. 330).

Length up to 450μ. Eyes present. Buccal tube straight, terminating with large apophyses. Pharynx 38 by 21μ. Two slightly elongated macroplacoids, situated in the posterior part of the pharynx. The first macroplacoid is shorter than the second.

The claws differ according to the legs; those of the 4th pair are typical of *Hypsibius*. The principal branch (of the 4th pair) is 19μ, rather straight, with accessory points; the base is enlarged with two nodular structures; the secondary branch is slightly curved.

Eggs smooth, probably deposited in the exuvium.

H. giusepperamazzottii is an aquatic species, collected only in Japan, in the Tama River, at 13 km from its outlet into the Bay of Tokyo.

HYPSIBIUS HYPOSTOMUS Bartos, 1935 (Fig. 331).

Length up to 270μ, eye spots present, cuticle smooth; cavity liquid and globules of reddish brown color, especially in the larger individuals; the buccal aperture is turned ventrally, so that in profile the "forehead" appears steep, rostrally convex. Buccal tube narrow, with external diameter of about 2μ, strongly curved suddenly before its entrance into the pharynx. The latter is almost spherical (21 x 19μ), with robust apophyses and 2 macroplacoids (rounded granules), of which the first is a little larger than the second; microplacoid absent.

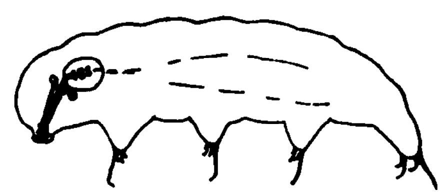


Fig. 331 - *H. hypostomus* Bartos (from Bartos).

External and internal doubleclaw of very different size: secondary branch short and very curved, principal branch long, little curve, with two accessory points. So far only a large smooth egg has been seen, of brown color, deposited in the exuvium. The species resembles *H. novemcinctus*, but it is distinguished easily by the presence of eye spots and by the color of the liquid and of the cavity globules; the same characters, and moreover the smooth egg, without ornamentation, are of value for separation from *H. oberhaeuseri*.

H. hypostomus was collected in the Tatra peaks, where it is very widespread up to the altitude of about 2,500 m, and in Romania.

HYPSIBIUS IHAROSI Bartos, 1941 (Fig. 332).
= *H. montanus* Iharos, 1940 (*not* Mihelčič, 1938)

(This species was described in 1940 by A. Iharos with the name of *Hypsibius* (*H.*) *montanus*, but such description was changed to *H.* (*H.*) *iharosi* by Bartos in 1941, because of the priority of *H.* (*I.*) *montanus*, described by Mihelčič in 1938).

Length 185μ, colorless, eyes present, smooth cuticle. Buccal tube narrow (diameter about 1.5μ); slender and slightly curved stylets; pharynx almost spherical (22.5 x 20μ), with minuscule apophyses and 3 macroplacoids, of which the first is a small rounded granule, while the second and the third are rods; the second macroplacoid is about one and a half times longer than the third; microplacoid absent. Doubleclaws of each leg have different size and short basal part.

The species, easily recognizable by the characteristic macroplacoids, so far has been collected only in the Carpathians, at about 1,800 m altitude, in moss on rock.

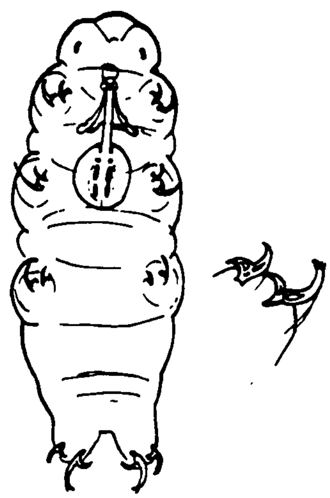


Fig. 332 - *H. iharosi* Bartos. Ventral view and doubleclaws of the 4th pair of legs (from Iharos).

HYPSIBIUS JANETSCHEKI Ramazzotti, 1968 (Fig. 333).

Length 240-400μ, more often 300-350μ, cuticle smooth, eye spots very large and very visible. Characteristic is a very strong pigmentation of these animals, which varies from a very dark brown to almost black. Buccal tube rather narrow (4μ), length up to the apophyses 49μ in a specimen of

400μ. The diameter of the buccal tube may be as small as 2.8μ in an individual 325μ long. Apophyses dot-shaped, practically non-existent. Pharynx oval, with length to width ratio of about 1.5:1, containing 2 macroplacoids in the shape of rods, of which the 1st is longer than the 2nd (for example, in an individual 400μ long they measure: pharynx 37 x 24.5μ; 1st macroplacoid 6.8μ; 2nd macroplacoid 5.5μ; distance between the two macroplacoids about 2μ). Microplacoid absent.

Doubleclaws *Hypsibius* type, small in comparison to the size of the animals; in an individual of 400μ the principal branch of the external doubleclaw of the 4th pair of legs measures about 13.6μ, base included, and the principal branch of the internal doubleclaw about 7μ, also including base; both the principal branches have accessory points. Eggs have not been observed.

This species is certainly very near to *H. klebelsbergi* which was collected in glacial pools (Kryokonitlöcher). On the basis of the first description of this last species there could not exist doubt on the specific separation of *H. janetscheki* from *H. klebelsbergi*. However, after the addition contributed by Mihelčič himself to the description of his species, one can not exclude the possibility that *H. janetscheki* may be a synonym of *H. klebelsbergi*. In expectation of clarification of the question through examination of new material, we keep here the distinction of the two species: the principal difference can be given by the fact that all of the examples of Ramazzotti are eyed, while they are only a quarter of those of Mihelčič; besides *H. janetscheki* is more squat, with reported length to width ratio of 3.3:1 to

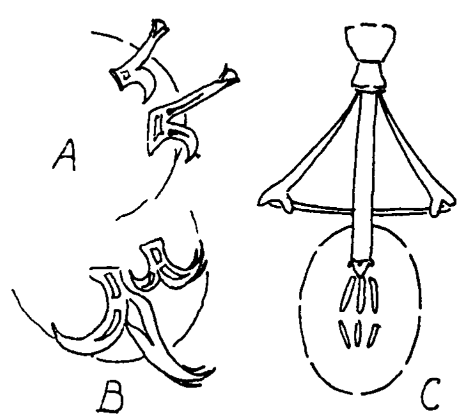


Fig. 333 - *H. janetscheki* Ramazzotti. A, doubleclaws of the 3rd pair of legs; B, of the 4th pair; C, buccal apparatus.

3.1:1 (*H. klebelsbergi* has instead a length to width ratio of about 5:1).

The species was collected by Prof. H. Janetschek in the glacier melt pool (Kryokonitlöcher) of the Nare Glacier (Himalaya).

HYPSIBIUS KLEBELSBERGI Mihelčič, 1959 (Fig. 334).

Length about 600μ, and 130μ wide, that is the animal is very slender with length to width ratio of about 5:1. Eyes in general absent (present in a quarter of the specimens examined). Dark color, as dark as brownish-black or black: often the pigment is deposited in transverse bands of clear and dark. Peribuccal lamellae absent, buccal tube narrow. Pharynx elongated oval, with small point-shaped apophyses and two very slender macroplacoids (rod-shaped); microplacoid absent. Legs long and robust, sometimes with a large gibbosity on the 4th pair (such gibbosity is present in about half of the specimens examined). Doubleclaws of different size, wide and robust, with short common basal branch. Eggs have not been observed.

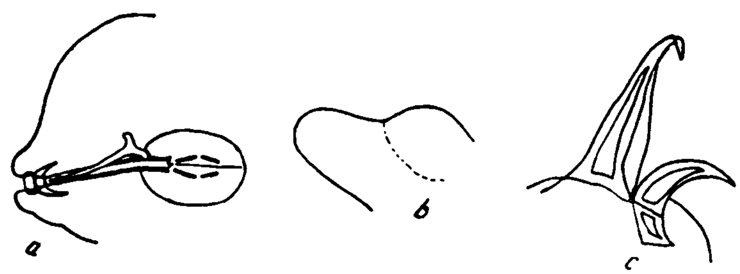


Fig. 334 - *H. klebelsbergi* Mihelčič. a, cephalic region and buccal apparatus; b, gibbosity on 4th pair of legs; c, external doubleclaws of the 4th pair of legs (from Mihelčič).

This description is based on information provided by Mihelčič to Ramazzotti (*in litt.*), and differs slightly from the original description, according to which the eyes were constantly absent and the gibbosity on the 4th pair of legs is always present.

As stated above, the provable difference between this species and *H. janetscheki* could have no value in specific discrimination, in which case *H. janetscheki* could be placed in synonymy with *H. klebelsbergi*. We are willing however, in waiting to examine further material, to preserve here -- at least temporarily -- the two distinct species.

H. klebelsbergi was collected from the water of a frozen melt pool (Kryokonitlöcher) of a glacier in Austria.

HYPSIBIUS (?) MACULATUS Iharos, 1969 (Fig. 335).

Length 200-225μ, color bright lilac, eyes present. The cuticle is covered with low, hemispherical tubercles, arranged in transverse rows, which also cover the legs, on which the tubercles are much smaller. Between the transverse sculpture rows, the cuticle is smooth. Besides the tubercles, the cuticle has numerous granules of a dark brown color, having diverse shape and size (round, oval, or irregular, of full size between 1 and 3.6μ), which are dense and irregularly arranged in the anterior cephalic zone, while they are in two longitudinal rows almost symmetrical on the median longitudinal line of the dorsum and are scattered irregularly on the flanks and on the superficial venter; on the legs they are smaller.

Buccal tube narrow (1.5μ) and long (24μ): almost of the type of that of *Diphascon*, adds the author. The pharynx contains 2 macroplacoids, the first (2μ) a little longer than the second (1.8μ). Microplacoid absent; the pharynx is subspherical (20 x 18μ). Doubleclaws of each leg of different size, which seems to be of the *Isohypsibius* type, but the author does not detail in this regard; the external measures 12μ, the internal 7μ.

It is with much doubt that I keep this species in the genus *Hypsibius*.

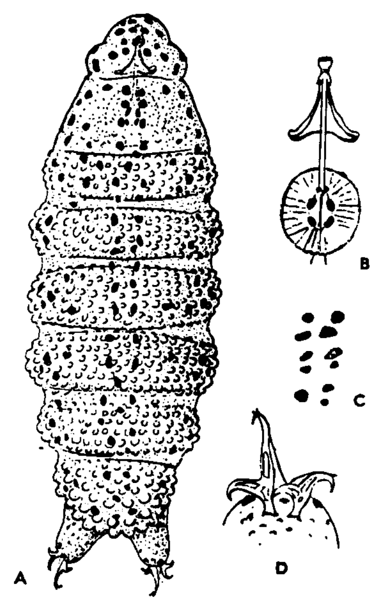


Fig. 335 - *H.* (?) *maculatus* Iharos. A, dorsal view; B, buccal apparatus; C, cuticular granules; D, claws of the 4th pair of legs (from Iharos).

In the original description Iharos does not mention the subgenus, and that leaves it open to doubt. In fact, while the design of the claws does suggest that we treat it as an *Isohypsibius* (and we consider this hypothesis very reasonable), the author insists to the contrary on the affinity of *H. maculatus* with *H.* (or *Calohypsibius*) *ornatus* forma *coelata*. We consider it however very probable that it should be treated as a *Calohypsibius*.

H. maculatus is known from only the Cameroon mountains of Africa.

HYPSIBIUS MICROPS Thulin, 1928 (Fig. 336).
= *H. pallidus* Cuénot, 1932 (in part, of Thulin, 1911)

Length up to 295μ, with maximum diameter between the 2nd and the 3rd pair of legs; colorless, cuticle smooth, eyes constituted of scarce small spots of pigment, separated from each other, or lacking. Buccal tube narrow (external diameter about 1.5μ in an animal 260μ long), with appendices in the form of a hook for muscle insertion; observing the animal in profile, the buccal tube -- starting at the buccal aperture -- runs straight for a certain distance, then curves to enter the pharynx (Fig. 336 B). Pharynx very short oval, almost spherical, with reported length to width ratio of about 1.1:1; there are large apophyses and 2 macroplacoids, the size about equal, in the form of rounded granules and as long as wide, or length 2.5 times the width and slightly curved; microplacoid absent. Doubleclaws large; the principal branch of the external doubleclaw -- particularly in the first three pairs of legs -- is inserted low on the basal portion, almost at a third of its length (Fig. 336 D). Eggs smooth and oval, deposited in the exuvium in numbers of 1-4.

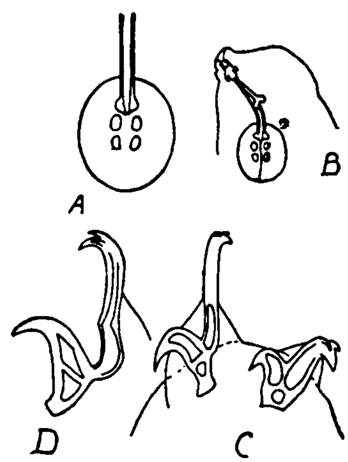


Fig. 336 - *H. microps* Thulin. A, pharynx; B, cephalic region; C, D, doubleclaws of 4th and 3rd legs.

H. microps is one of the more common and distributed species of the genus *Hypsibius*, and together with *H. convergens* and *H. pallidus* constitutes a group of species, apparently related, which to distinguish can be, at times, somewhat difficult (Cuénot, 1932, considered that they ought to be united into a single species *H. pallidus*).

We think that the features of the species are distinct, by which identification can be based upon the following characteristics:

H. convergens has a pharynx more elongated (however this character does not seem very significant) and the placoids are more elongated, in the form of short rods (sometimes, although rarely, there is a tiny microplacoid); the claws, which have, like *H. microps*, a very short common base, are more massive and the two branches are more divergent.

H. pallidus has on the contrary an oval pharynx, slightly elongated, placoids often almost square, and especially the primary branch of the claws is inserted rather high, so that the common branch base is considerably longer than those of *H. microps* and *H. convergens* (in practice equal, or longer, than the secondary branch).

H. microps, leaving out the many probable erroneous identifications, has been observed from many European localities (including Italy), in Turkey, Siberia, Brazil, and India.

Type Loc.: southern Sweden.

HYPSIBIUS NOVEMCINCTUS Marcus, 1936 (Fig. 337).

Length 240μ; the adults have 9 brown transverse bands; the cuticle is smooth, eye spots are absent. Buccal tube very narrow, of about 1μ internal diameter, with appendices to form a hook for the muscle insertions; stylets diverge very little. Pharynx oval, having length to width ratio of 1.25:1, with apophyses and 2 macroplacoids, which are rounded rods, almost granules, of about equal width (1.2μ); the first is a little longer than the second and has a constriction; microplacoid absent. Doubleclaws very similar to those of *H. oberhaeuseri*, with the difference that the secondary branch of the external doubleclaw is longer in its basal part (Fig. 337 C); the principal branch of the same external doubleclaw is very long and slender (about 19μ on the 4th pair of legs), in the form of a crochet hook, and is inserted at about the middle of the basal claw. Eggs smooth, deposited in the exuvium; young unknown: it is unknown then if they are pigmented or colorless.

H. novemcinctus is distinguished from *H. oberhaeuseri* especially because they lack the non-pigmented longitudinal bands (only transverse

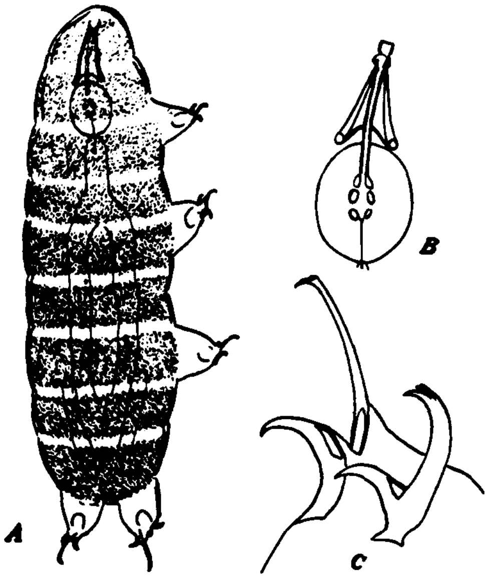


Fig. 337 - *H. oberhaeuseri* Marcus. A, dorsal view; B, buccal apparatus and pharynx; C, doubleclaws (from Marcus).

ones are present) and because the eggs are smooth, without ornamentation.

Nevertheless, Baumann (1966) writes that the species *H. novemcinctus* should be abolished, because he -- in his culturing -- was able to observe females of *H. oberhaeuseri* were able to deposit indiscriminately smooth eggs freely, eggs with ornamentation also free, or even smooth eggs in exuvia, and also see great individual variability in the pigmentation in transverse or longitudinal bands of *H. oberhaeuseri*.

We are of the opinion to maintain separate the two species for the following reasons:

1) One can ascertain the difference in pigmentation, as in the description of *novemcinctus*, accompanied *always* by the deposition of smooth eggs in the exuvium.

2) It is possible that the deposition of smooth eggs freely or of smooth eggs in the exuvium, in the experiments of Baumann can be possibly produced in artificial culturing conditions and not in the natural state.

3) The inspection of an egg-bearing exuvium, collected in Greece by Maucci, confirms acknowledgement of significant difference in the claws, which are more massive, with secondary branch longer and remarkably large, by which they ought to be comfortably enough distinct from the claws of *H. oberhaeuseri*.

The question of the possible synonymy of *H. novemcinctus* and *H. oberhaeuseri* should still however be examined in the future.

The reports of *H. novemcinctus* are scarce, and are limited to a few localities in Scotland, Rhineland, Hungary, and Greece.

HYPSIBIUS OBERHAEUSERI (Doyére, 1840) (Fig. 338).
= *Macrobiotus oberhaeuseri* Doyére, 1840

Maximum length 500μ, however the size is usually less. The cuticle is often granulated, especially in the caudal region of the body, but there are also individuals completely granulated or completely smooth; young colorless, while the adults appear strongly pigmented of brown, or reddish-brown, or brownish-violet, more intense with an increase in age; usually the pigment is deposited in 5 longitudinal bands and 9 transverse, separated by clear bands, of which there are four longitudinal. In animals treated with potassium hydroxide (or, in general, with alkali) the pigment clears and turns to a brisk violet-purple color. The eyes are constantly absent. The buccal tube is very narrow (about 1μ internal diameter) and is supplied with appendices in the form of hooks for the insertion of muscles. The pharynx, short oval, contains apophyses and 2 macroplacoids (granules) about equal, or else the first is a little longer and oval, the second shorter and almost round; the microplacoid is absent.

The two doubleclaws of each leg are very different: the posterior (external), longer, has the principal branch long, slender, straight, with two

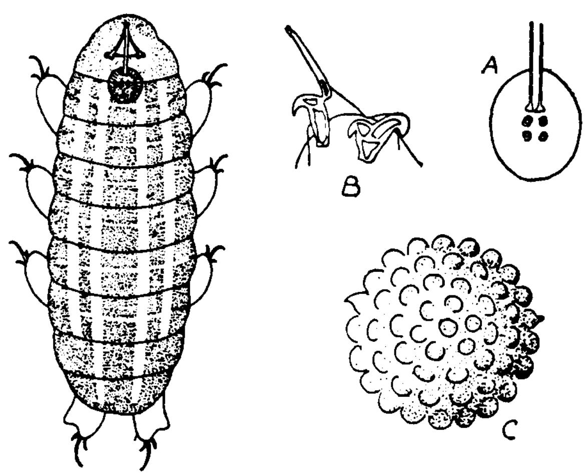


Fig. 338 - *H. oberhaeuseri* (Doyére). Dorsal view; A, pharynx; B, doubleclaw of the 4th legs; C, egg.

accessory points, and thesecondary branch strongly curved; the anterior (internal) doubleclaw, shorter, and constituted of two squat and short branches: the principal branch bears two robust accessory points. The males present, on the lateral external of the 4th pair of legs, a flattened gibbosity, which is lacking -- or is very reduced -- in the female. They deposit small, spherical eggs free, sometimes stuck to each other, with a diameter of 45-57μ, exclusive of the projections, which are numerous and diverse form; in general they are hemispherical and give the egg the appearance of a raspberry, or of a mulberry; sometimes some projections are transformed, here and there, into short cones, or into irregularly truncated cones, or into appendices in the shape of an hour glass. Rarely one is able to find eggs -- with the characteristic projections -- deposited in the exuvium, rather than free; also one can observe *Hypsibius* without eye spots, with transverse (*not* longitudinal) pigment of brown, or reddish-brown, and *smooth* eggs deposited in the exuvia, certainly not to be treated as *oberhaeuseri*, but as *H. novemcinctus*. You see many words, however, in the description of *novemcinctus* about the doubts of Baumann on the real existence of this species.

H. oberhaeuseri is a species spread everywhere, known from numerous locations in Europe (it is also common in Italy), from Greenland, the Arctic and Antarctic, North and South America, Angola, Cyrenaica, Turkey, Afghanistan, and New Zealand.

Type loc.: Greifswald (Pomerania) and Paris.

HYPSIBIUS PALLIDUS Thulin, 1911 (Fig. 339).

Length up to 318μ, colorless or pink, eye spots usually present, cuticle smooth. Buccal tube narrow, with the insertion appendages of the muscles hook-shaped; pharynx very short oval, or almost spherical, containing 2 macroplacoids in the shape of rectangular granules (Marcus, 1936), or else approximately oval (Petersen, 1951); microplacoid absent. Doubleclaws similar to those of *H. oberhaeuseri*: the principal branch has accessory points.

H. pallidus is very near to *H. microps* and the distinction of the two species -- which Cuénot (1932) proposed to unite into one -- is not always easy. For distinction, refer to the description of *H. microps*.

H. pallidus, leaving out the probable errors in determination, is cited from many localities in Europe (including Italy), from the U.S.A. (Colorado), Canada, Greenland, China, and Mexico.

Type loc.: Sweden.

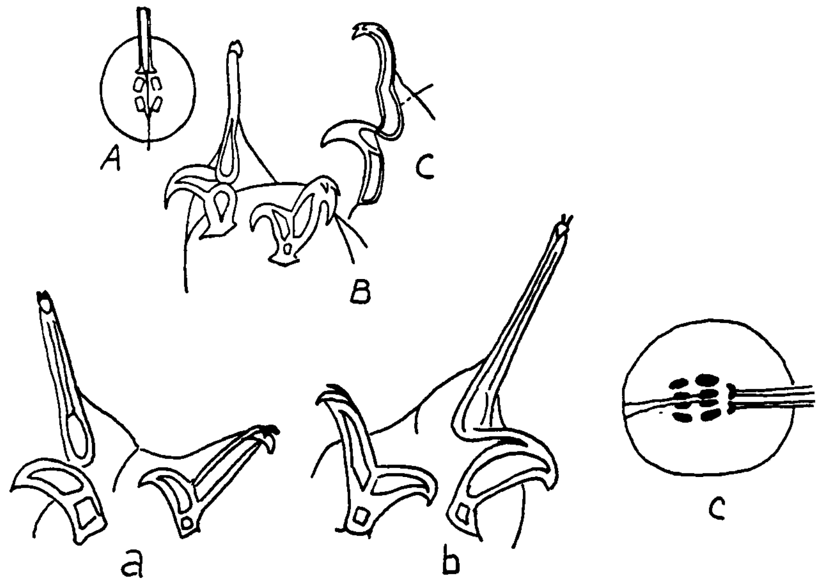


Fig. 339 - *H. pallidus* Thulin. A, c, pharynx; B, b, doubleclaws of the 4th pair of legs; C, posterior doubleclaws of the first legs; a, doubleclaws of the 2nd pair of legs (from Petersen, redrawn).

HYPSIBIUS RUNAE Bartos, 1941 (Fig. 340).

Length 216-230μ, eye spots large and in the posterior position. The body is covered with numerous small papillae, with only the rostral cephalic region, the distal extremities of the legs, and the ventral surface not covered. The papillae are arranged according to transverse bands, each made of several rows fairly close between them: transverse bands composed of papillae larger than the alternating ones that have bands composed of smaller papillae. The cavity liquid is brownish. Buccal tube narrow, its external diameter is about 2μ; pharynx is a short oval (reported length:width equal to 1.1-1.2:1), containing the apophyses and 2 macroplacoids; microplacoid absent. The first macroplacoid (2.7μ) is a little longer than the second (1.8μ). The doubleclaw is very similar to that of *H. convergens*.

The species was cited only in the region of the Carpathians.

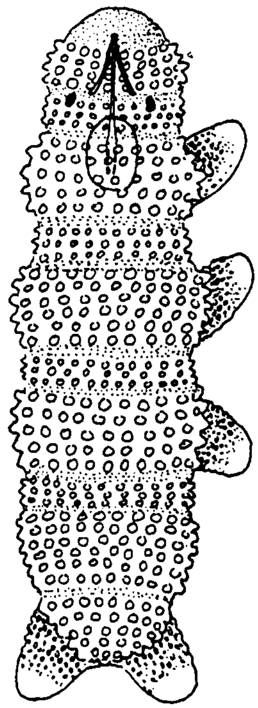


Fig. 340 - *H. runae* Bartos (from Bartos, redrawn).

HYPSIBIUS SCABROPYGUS Cuénot, 1929 (Fig. 341).

Length up to about 320μ, colorless or with pink cavity globules, eyes present in posterior position. The cuticle is smooth from the rostral end to beyond the anterior half of the body, while in correspondence to the 3rd pair of legs is an impression -- on the dorsum and its flanks -- to the caudal region, forming clots, or almost irregular platelets, of yellowish color; sometimes there is a transverse smooth band, which dorsally crosses the sculpture. Immediately after the latter impression is less visible, also because it is then colorless. Buccal tube very narrow, of about 1μ internal diameter, with muscle insertion appendages in the form of hooks. Large pharynx (21 x 18μ), containing apophyses and 2 rounded macroplacoids (granules); microplacoid absent. Doubleclaws rather large: the posterior (that is to say the larger) more slender than the anterior, and likewise on all the legs, but particularly on the 4th pair; principal branch of the posterior doubleclaws long -- about 13μ on the 4th pair of legs and 9μ on the other legs -- with accessory points. From one to 6 smooth eggs, more

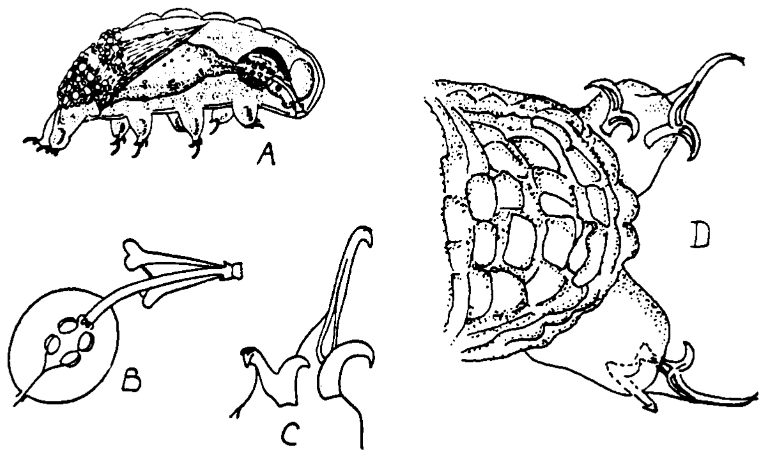


Fig. 341 - *H. scabropygus* Cuénot. A, lateral view; B, buccal apparatus; C, doubleclaws of the fourth pair (from Marcus, redrawn); D, details of the caudal region (from Cuénot, redrawn).

or less oval (52 x 46μ), sometimes of red color, deposited in the exuvia.

The species, easily distinguished from others, is known from various European localities, Italy included, and from southern Africa.

HYPSIBIUS SIMOIZUMII Sudzuki 1964 (Fig. 342).
= *H. mertoni simoizumii* Sudzuki, 1964.

The species *H. mertoni* was insufficiently described, and was therefore considered by Marcus (1936) as *spec. dubia et inquir.*, and was not included in the first edition (1962) of "Phylum Tardigrada." Sudzuki having described and illustrated the variety *H. mertoni simoizumii*, we have retained the subspecific subordination in a species which does not have taxonomic status. We prefer therefore to consider *H. simoizumii* as a valid species, yet proposing the possibility that it could be synonymous with *H. convergens*.

Length about 300μ, body cylindrical, usually transparent; smooth cuticle, eyes present. The buccal tube is straight, robust, rather wide (2.7-3.0μ) and short (ratio of width to length of the bulb: 1.0-1.2); apophyses bifid. Spherical bulb or rather oval (25-28 x 34μ) placed

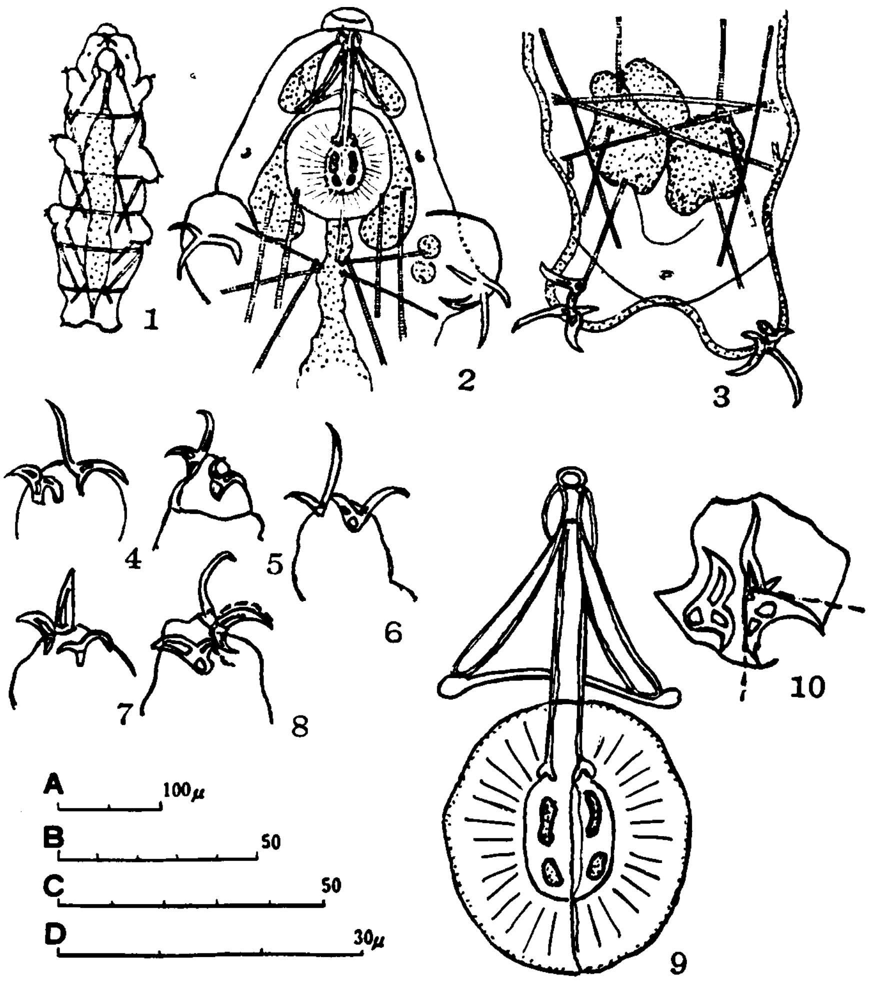


Fig. 342 - *H. simoizumii* Sudzuki. 1, animal; 2, cephalic region; 3, caudal region; 4, doubleclaws of 1st pair of legs; 5, *idem* from 2nd pair; 6, *idem* from 4th pair; 7, *idem* from 2nd pair of another specimen; 8, *idem* from 4th pair; 9, buccal apparatus; 10, doubleclaws of the 1st pair of legs of another example. Scale A for 1; B, for 2 and 3; C, for 4, 5, 6, 7, 8; D, for 9 and 10 (from Sudzuki).

anterior to the 1st pair of legs and containing 2 macroplacoids: the first, with median constriction, and two to three times longer than the second (1st = 3-4 x 2μ; 2nd = 2-3 x 2μ); microplacoid absent.

The two doubleclaws of each leg have very different size, and the external is 2 to 2.5 times longer than the internal (for example, for the doubleclaws of the 4th pair of legs: external, principal branch 16μ, secondary 11μ, internal, principal branch 7μ, secondary 3μ).

From the description of *simoizumii* follows then the sole notable difference between this species and *H. convergens* consists of the wider buccal tube (2.7-3.0μ diameter, while in *convergens* it is only 1.5-1.7μ). But unfortunately *H. convergens* is an extremely variable species, as we have established by observations and by measurement of numerous examples from many different sources (Europe, America, Asia, Antarctica). It is not rare, for example, to come across populations of *convergens* in which the majority of the individuals have narrow buccal tube, while some of these have wide buccal tube, or very wide (from 2.5 to 5.5μ); on the contrary, a few other examples have a small microplacoid, usually absent in *convergens* (and then it is difficult -- and sometimes impossible -- to distinguish from *H. dujardini*). We have numerous other variations, even in the ratio of the length of the two macroplacoids, so that in defining the characteristics and the measurement data of Sudzuki for his *simoizumii* happen to coincide with those of many individuals of *convergens*.

In conclusion: in the present state of our knowledge it is not possible to certainly determine if *simoizumii* is either a species in itself, or else should be identified with *H. convergens*; to be able to do this it would be necessary to examine and measure numerous different populations, especially with regard to the length and the diameter of the buccal tube, the length and width of the bulb and the ratio of these measurements; it would also be indispensable to determine if the difference between the same measurements is not attributed, for example, to sexual dimorphism. The fact remains that at present, examining individuals with wide and short buccal tubes, it is totally impossible to establish if it is the features of *simoizumii* or of *convergens* (we repeat however that the typical *convergens* has narrow buccal tube, however it is really short, that is longer than the bulb, or little more).

It is not, on the other hand, excluding that the two species can be distinguished by the length of the macroplacoids, having in *H. simoizumii* the second placoid much shorter than the first, while in *H. convergens* the difference in length between the two placoids is always modest.

H. simoizumii was observed at Langhovde (Antarctica) in moss.

HYPSIBIUS SZEPTYCKII Dastych, 1980 (Fig. 343).

Length 260μ, light red color with brown pigment. Eye spots absent. The dorsal side has gibbosities arranged in 7 regularly distributed

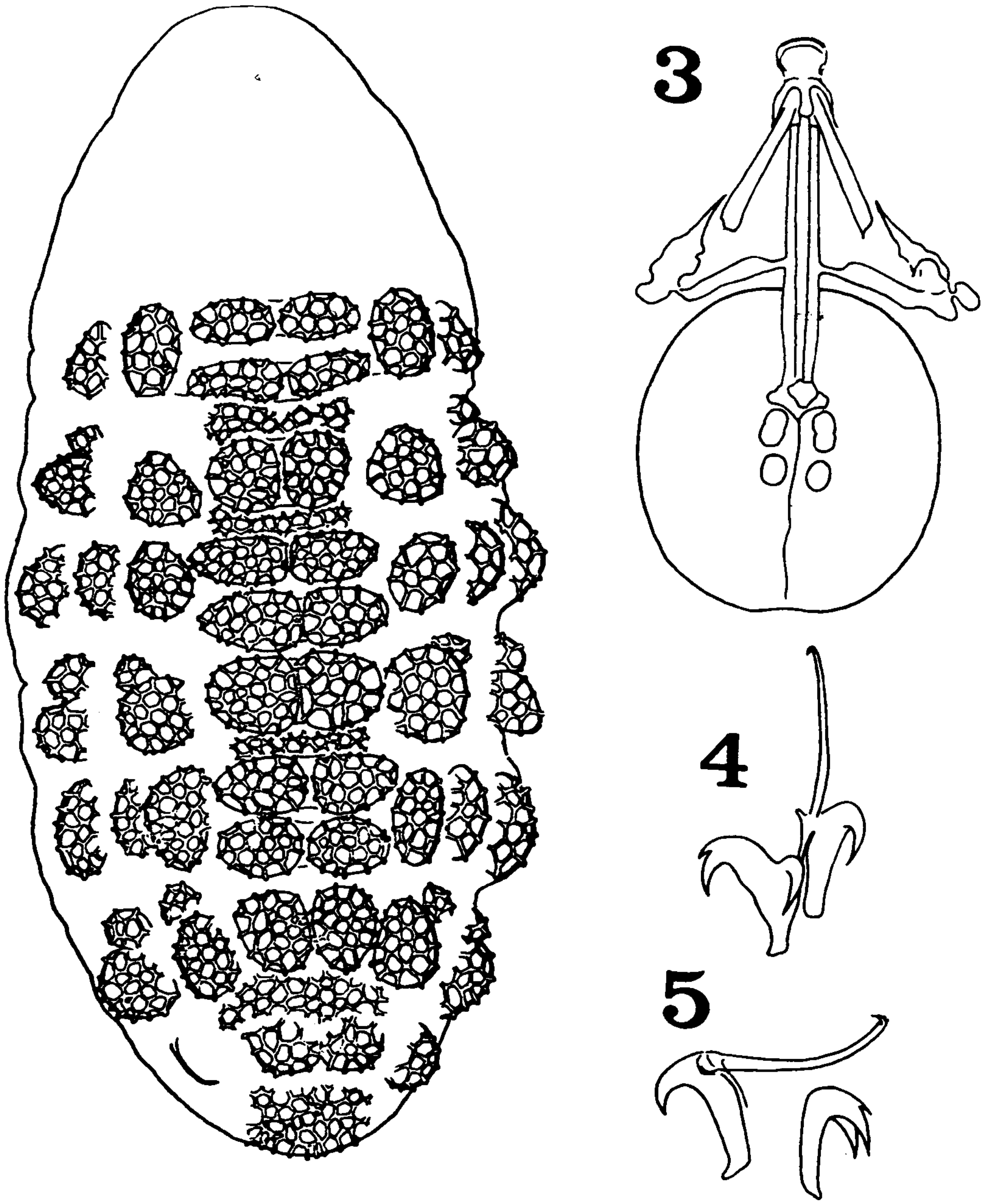


Fig. 343 - *H. szeptyckii* Dastych. Dorsal view. 3, buccal apparatus; 4, doubleclaws of the 1st pair of legs; 5, doubleclaws of the 4th pair (from Dastych).

transverse rows; in the second, fourth, and sixth rows the gibbosities are double. The surface of the gibbosity and sometimes the cuticle between them, sometimes the caudal end of the body has a sculpture which forms a reticulated design composed of slightly projecting border of the cuticle (internal diameter of the mesh 2-5μ). The cephalic end is smooth.

The buccal apparatus is of the *oberhaeuseri* type. Slender buccal tube, 32μ long, 3 wide. Bulb almost round (28 x 27μ), with apophyses and two macroplacoids. Microplacoid absent. The first placoid (4μ long) is very slightly constructed in the middle, the second is 3μ long. The width of the placoids is 2μ.

Claws of the *oberhaeuseri* type. The accessory points of the principal branch are very small and can be recognized only on the 4th pair of legs.

The eggs have not been discovered.

This species belongs, according to the author, to the *oberhaeuseri* group and is rather similar to *H. baumanni.*

The presence of the gibbosities and the reticulated sculpture, observed until now for several species of *Isohypsibius*, constitutes an interesting novelty for the genus *Hypsibius*.

H. szeptycki was collected by Dr. Andrzej Szeptycki, a single example, from Hendriksdaal, in South Africa, at an elevation of about 1400 m.

HYPSIBIUS THULINI Pilato, 1970 (Fig. 344).

Length up to 260-280μ, but in general 220-240; eyes absent, and their position is an ellipsoidal projection, having a size of 7.2 by 4.5μ in larger individuals; pink color or almost brick red in older individuals; caudal zone more strongly pigmented. The pigment is distributed in 8 transverse bands. Cuticular sculpture of tubercles with superior surface in polygonal shape

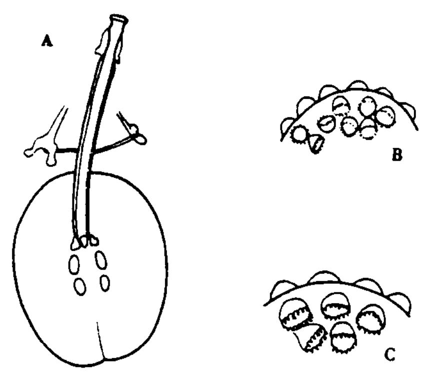


Fig. 344 - *H. thulini* Pilato. A, buccal apparatus; B and C, details of egg probably of *H. thulini* (from Pilato).

and arranged in small projecting transverse bands, in correspondence with the bands of color. The tubercles have larger diameter caudally to the 3rd pair of legs, and the larger measure about 2-3μ; on the legs are very small tubercles. Buccal tube 28-29μ long in the larger specimens, and very narrow (from 1.7 to 1.8μ), with muscle insertion in the shape of a hook with obtuse apex. Apophyses and two macroplacoids of oval granular shape of which the first is a little longer than the second; microplacoid absent.

An egg probably belonging to this species had spherical shape with hemispherical ornamentation, briefly sharpened at the apices; 18 projections in an optical section, smooth shell between the projections; diameter of the egg 60μ without the projections, 68 including these.

The characteristics described eliminates the possibility that this species is the same as *H. oberhaeuseri* (sculptured specimens). The same Pilato (*in litt.*) acknowledges this possibility, however he reserves the right to re-examine the problem, and we have nevertheless retained here -- at least temporarily -- *H. thulini* as a good species.

H. thulini was collected in moss, in a zone of Levigliani (Apuane Alps, Toscana), at 750 m altitude.

HYPSIBIUS ZETLANDICUS (Murray, 1907) (Fig. 345).

Length up to 580μ, brown color, eye spots present. Stylets straight, massive, with large and robust furcae. Short oval pharynx, in which there are the apophyses and 2 short and wide macroplacoids, both with a deep incision at about the middle of the side facing the external of the bulb; lacking microplacoid. Doubleclaws of each leg different in appearance, but both large and robust: the common base to the two branches is rather long, the principal branch of the external doubleclaws (those of larger size) measures about 30μ and bears two accessory points. The eggs, smooth and

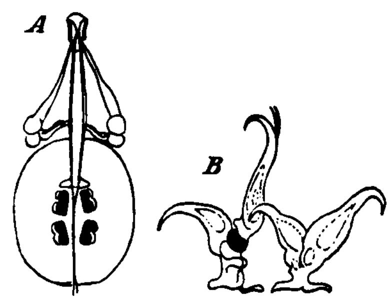


Fig. 345 - *H. zetlandicus* (Murray). A, buccal apparatus; B, doubleclaws (from Marcus).

oval (94 x 75μ), are deposited in the exuvia. J. Murray (1907) stated that he had seen young live tardigrades inside the body of a female, recognizing that this was the first observation of this kind: probably this occurred by an anomalous impediment to the deposition of the eggs (Marcus).

The species was collected in the region of the Carpathians (at an altitude above 2000 m, in damp moss in the shade), in Scotland, on Shetland Island, in Finland, and on the Spitsbergen archipelago.

Genus *ISOHYPSIBIUS* Thulin, 1928.

Diagnosis: Hypsibiidae with rigid buccal tube, without reinforcement bar; appendages for the insertion of the muscles of the crest of the stylet; sequence of claws 2121, "*Isohypsibius* type" claws.

Observations:

1) We note that not always is it easy, especially for an inexperienced eye, to distinguish the "*Isohypsibius* type" of claws from the "*Hypsibius* type": we recommend therefore maximum attention, and, where possible, the examination of many examples.

2) For the species with dorsal gibbosities, belonging to the so-called "*tuberculatus* group", the gibbosities are seldom observed without difficulty, especially in permanent preparations, which do not allow for movement of the animal. We recommend examining especially carefully the caudal portion, where the gibbosities are normally more evident. We think that in the final taxonomy it isn't so much the total number of rows of gibbosities, nor the number of gibbosities in each row, as much as the fact that the gibbosities of the various rows have even or odd numbers, whether or not there is an odd gibbosity medially. That is taken into account in the key.

3) For many species, the original descriptions are somewhat summary and often incomplete. It is especially so with reference to the sculpture of the cuticle, that is sometimes generically "granulated" or "punctated." The same goes regarding the presence or absence of lunules and cuticular bars in the 1st-3rd legs, near the claws. Of these characters, the key takes them into account only where they can be safely verified in the original diagnosis, or in later descriptions.

4) We think it advisable to eliminate the species *I. sattleri*. The original description of this species is so imprecise as to render it impossible to surely identify: it follows that many authors have applied the name

sattleri to many different species, introducing an important and inextricable taxonomic confusion.

N.B.: The marine species *I. itoi* Tsurusaki is not included in the present key, as it's description arrived when the key to the genus *Isohypsibius* was in a finished state.

KEY TO THE SPECIES

1.	Cuticle smooth, without sculpture, swellings, or gibbosities	2
	Cuticle sculptured, with swellings and/or with gibbosities	20
2 (1).	Lunule present	3
	Lunule absent	7
3 (2).	Three macroplacoids are present	4
	Two macroplacoids are present	6
4 (3).	The claws of the 4th pair of legs are considerably greater than the others	*I. macrodactylus*
	The claws of the 4th pair of legs are not greater than the others	5
5 (4).	Macroplacoids in the shape of rods, of which the 3rd is longest; principal branch of the claws with accessory points	*I. saltursus*
	Macroplacoids very short, the first two almost granules, a little elongated; lacking accessory points	*I. deconincki*
6 (3).	Lunule smooth; normal claws of the *Isohypsibius* type	*I. marcellinoi*
	Lunule dentate; claws of the 4th pair have branches fused for a good part and divergent at 180μ so that the claws form almost a triangle	*I. alicatai*
7 (2).	The claws of each leg are considerably different, only the internal claws (smaller) are clearly of the *Isohypsibius* type	8
	Normal claws, both of the *Isohypsibius* type	9
8 (7).	The external claw has the principal branch not connected with the basal and secondary branch	*I. deflexus*
	In the external claw, the principal branch is connected with the secondary, but it is extremely long, slender, bristle-like	*I. renaudi*
9 (7).	There are two macroplacoids, with microplacoid	10
	There are three macroplacoids present	12

10 (9). The two macroplacoids are close to each other even touching, so as to simulate a single placoid .... *I. nipponicus*
The two macroplacoids are clearly distinct 11

11(10). The first macroplacoid is almost twice as long as the second; basal branch of the claw is short .... *I. solidus*
The first macroplacoid is less than one and a half the second; basal branch long .... *I. saracenus*

12 (9). Microplacoid present 13
Microplacoid absent 16

13(12). Not marine; macroplacoids granules, very little elongation; cuticular bar in legs 1-3 .... *I. prosostomus*
Marine; macroplacoids rodlike; without a cuticular bar in the legs 14

14(13). Diameter of the buccal tube 1.5μ; first macroplacoid shorter than the second .... *I. stenostomus*
Diameter of the buccal tube 3μ; first macroplacoid longer than second 15

15(14). The second macroplacoid is shorter than the third .... *I. appelloefi*
The second macroplacoid is equal or longer than the third .... *I. geddesi*

16(12). The principal branch of the external claw is not connected with the basal and secondary branch .... *I. deflexus*
Branches of the claws are connected 17

17(16). Claws of each leg almost equal, very long; macroplacoids very short, almost granules .... *I. tetradactyloides*
Claws of each leg of different size 18

18(17). Mouth anterior; apophyses almost absent; macroplacoids rod-like .... *I. myrops*
Macroplacoids short, oval granules; apophyses obvious 19

19(18). The macroplacoids are granules almost equal, increasing from 1st to 3rd, with divergent positions; principal branch of the external claw very long and slender .... *I. canadensis*
The macroplacoids are oval granules; principal branch of the claws robust .... *I. schaudinni*

20 (1). Cuticle with transverse swellings, without gibbosities 21
Cuticle with sculpture and/or with gibbosities 23

21(20). Three macroplacoids are present .... *I. arcuatus*
Two macroplacoids are present 22

22(21). There are 24 or more transverse swellings; macroplacoids short, the 1st longer than the 2nd; size less than 300μ .... *I. undulatus*
Swellings less developed and less regular; first placoid almost double the second; size more than 400μ .... *I. pseudoundulatus*

23(20). Cuticle sculptured, without gibbosities 24
Cuticle with gibbosities 37

24(23). Cuticle wrinkled; 3 macroplacoids in the form of granules; accessory points only on the internal claw .... *I. lineatus*
Different 25

25(24). Sculpture composed of granules, without reticulated pattern 26
Sculpture with reticulated pattern 32

26(25). Three macroplacoids are present 27
Two macroplacoids are present 28

27(26). The sculpture is a fine granulation; the first two macroplacoids are almost in contact with each other; basal branch of the claws rather long .... *I. granulifer*
The sculpture is composed of hemispherical tubercles; basal branch of the claws shorter .... *I. asper*

28(26). The macroplacoids (at least the 1st) are rod-like, considerably longer than wide 29
The macroplacoids are short and stumpy rods, or else granules 30

29(28). The granulation is composed of tubercles arranged in transverse rows; macroplacoids slender, equal; accessory points on the principal branch of the claw .... *I. annulatus*
The granulation is fine; the 1st placoid is three times longer than the second; claws without accessory points .... *I. fuscus*

30(28). The granulation covers only the caudal area; two granular macroplacoids, which do not reach the middle of the pharynx .... *I. sellnicki*
The granulation is extended over all the body 31

31(30). The granules are extremely fine, without order, present even on the ventral surface .... *I. sculptus*
The granules are arranged in an ordered way to form a pattern; legs and ventral surface not sculptured .... *I. pauper*

32(25). There are two macroplacoids 33
There are three macroplacoids 35

33(32). The macroplacoids are very slender rods, the 1st of the three longer than the 2nd; microplacoid present .... *I. pulcher*
The macroplacoids are short rods; microplacoid absent 34

34(33). Reddish-orange color; without lunule and bar in legs; moss-dwelling .... *I. flavus*
Colorless; there is lunule and cuticular bar in the leg; aquatic .... *I. reticulatus*

35(32). Lunule absent; sculpture of very fine granules, reticulated pattern seen with high magnification .... *I. baldii*
Lunule present 36

36(35). Near the 1st-3rd claws there is a cuticular bar .... *I. brulloi*
The cuticular bar is absent .... *I. wilsoni*

37(23). The dorsal gibbosities are irregularly arranged, not aligned in transverse rows 38
The gibbosities are arranged in transverse rows 40

38(37). The gibbosities are low, irregular, with undulating profile; there is also a hexagonal sculpturing .... *I. hadzii*
Different 39

39(38). Numerous gibbosities, hemispherical, in
contact with others .... *I. gibbus*
A few large gibbosities, others small;
the last two, over the 4th legs, are
covered with tubercles .... *I. montanus*

40(37). All the rows include an even number of gibbosities,
in which there are no dorso-median gibbosities 41
At least some rows have an odd number of gibbosities 59

41(40). The gibbosities are small tubercles,
arranged in about 24 transverse rows
of 8 tubercles each .... *I. indicus*
Gibbosities hemispherical, conical,
or papilliform, arranged in 6-11 transverse rows 42

42(41). All the gibbosities are hemispherical
and not terminated in a point 43
Some gibbosities are conical, mammillary,
or papillose, and terminated in a
point or with a spine 52

43(42). Other than the principal row of
gibbosities (from 6 to 10), there
are no secondary gibbosities 44
There are secondary or lateral gibbosities 50

44(43). There is a cuticular bar in the legs,
near the claws (N.B.! This detail is
ignored by almost all authors; included
here are only the species for which the
bar is explicitly obvious) 45
There is no bar, or it is not obvious 47

45(44). There are 7 transverse rows of gibbosities,
of which the first five have 6 gibbosities,
the last two have 4 .... *I. nodosus*
There are 9 transverse rows of 2 or 4 gibbosities each 46

46(45). The sculpture has a reticulated pattern; maximum size of 300μ .... *I. josephi*
The sculpture is composed of a coarse
granulation, not reticulated; size up to or beyond 400μ .... *I. duranteae*

47(44). Dorsum with transverse swellings
and gibbosities (2 or 4) on the
last six swellings; sculpture
reticulated .... *I. neoundulatus*
There are 9 or 10 rows of gibbosities 48

48(47). Nine rows of gibbosities, the 3rd and the 4th rows have 6 gibbosities, the others 2 or 4; sculpture reticulated . . . . *I. pratensis*
There are 10 rows, all with 2 or 4 gibbosities 49

49(48). Only the 10th row has 2 gibbosities, all the others have 4 . . . . *I. bartosi*
There are 2 gibbosities in the rows 1, 2, 4, and 10 . . . . *I. rudescui*

50(43). Sculpture reticulated; there are 8 rows of gibbosities; there is also 4 lateral cylindrical papillae . . . . *I. theresiae*
There are 10 or 11 transverse rows of larger gibbosities; between these are inserted rows of smaller gibbosities; sculpture reticulated 51

51(50). Lunules are present; cuticular bars are present in the legs . . . . *I. pappi*
Lunules and bars absent . . . . *I. dudichi*

52(42). All the gibbosities are elongated, conical, or mammillary, and have pointed apices 53
Only part of the gibbosities have pointed apices 54

53(52). The gibbosities (arranged in nine rows of 4 or 6 gibbosities each) are conical, pointed, and curved caudally . . . . *I. franzi*
The gibbosities have hemispherical bases, which have papillae at their apices, most often elongated, spine-like . . . . *I. papillifer*

54(52). The dorsal gibbosities are hemispherical, those lateral or dorsolateral are conical, pointed, or papilliform 55
Only the gibbosities of the caudal three rows are conical, pointed 57

55(54). The cuticle is covered with small granules, sometimes transformed into spines; there are 10 transverse rows of gibbosities; the lateral gibbosities of rows 3-8 terminate with a short spine . . . . *I. vejdovskyi*
The sculpture is reticulated 56

56(55). There are 9 rows of gibbosities, each with 2 (6th row), 4, or 6 gibbosities, of which the lateral are pointed cones; reticulated sculpture somewhat coarse; lunule present .... *I. bakonyiensis*
There are 10 rows of 4 or 6 gibbosities, of which the lateral are pointed; the caudal gibbosities are rounded with a short spine at the center .... *I. brevispinosus*

57(54). Granular sculpture; 11 rows of gibbosities, of which the last 3 have conical shape .... *I. gyulai*
Reticular sculpture; 8 or 10 rows of gibbosities 58

58(57). Eight rows of 2 and 4 gibbosities alternating; those in the caudal region are conical .... *I. helenae*
There are ten rows of 4 gibbosities each; the gibbosities of the last 3 rows are of mammillary form, pointed .... *I. mamillosus*

59(40). All the rows have odd numbers of gibbosities, that is there is always a dorsomedian gibbosity 60
Only some of the rows have odd numbers of gibbosities 63

60(59). Granular sculpture, not reticulated; 6-8 rows of gibbosities 61
Reticulated sculpture; 8-9 rows of gibbosities 62

61(60). Six rows of 3 and 5 gibbosities alternating; 2 lateral gibbosities, smaller, anterior to the 1st row, another two posterior to the 6th .... *I. septentrionalis*
Eight rows of 3 or 5 gibbosities .... *I. cameruni*

62(60). Eight rows of gibbosities (5 gibbosities in the 1st-6th rows, 3 in the 7th-8th rows); lunule absent .... *I. trunconum*
Nine rows of gibbosities (5 and 3 alternate in 1st-7th rows, 3 in the last two rows); lunule present ...... *I. novaeguineae*

63(59). Only the first and/or the last row of gibbosities are of odd number 64
There are more odd rows 72

64(63). The first and the last rows are odd 65
The first or the last row is odd 68

65(64). There are lunules and cuticular bars in the legs 66
Lacking lunules; granulate sculpture 67

66(65). Reticulated sculpture; 1st and 10th rows with 5 gibbosities, others alternate 4 and 6, except the next to last (9th) which has only 2 . . . . *I. tuberculatus*
Granulated sculpture; row 1 with 3 gibbosities, last (10th) with only one; the other rows with 4 gibbosities each, except the 2nd which has 2 . . . . *I. elegans*

67(65). There is a cuticular bar in each leg; 1st and 10th rows with 3 gibbosities, all others with 4 . . . . *I. gracilis*
Without the bar in the legs; 1st and 9th rows with 3 gibbosities; 2nd-6th with 6; 7th-8th with 4; between rows of large gibbosities, there are small gibbosities . . . . *I. torulosus*

68(64). Only the first row is odd (3 gibbosities), the others (10 rows in all) have each 2 or 4 gibbosities; reticulated sculpture; lunules and bars in the legs . . . . *I. austriacus*
Only the last row is odd, having 3 gibbosities 69

69(68). Lunules present; 9 or 10 rows of gibbosities 70
Lunules absent; 8 or 9 rows of gibbosities 71

70(69). Smooth cuticle between the gibbosities and on them; there are 9 rows, of which the last has 3 gibbosities, and the others alternate 2 and 4 . . . . *I. eplenyiensis*
Cuticle with reticulated sculpture; bar in legs; there are 10 rows of gibbosities, of which the last has 3, the 1st and sometimes the 2nd, 2, and all others 4 . . . . *I. silvicola*

71(69). Nine rows of gibbosities, of which the last has 3, the others 2 or 4; reticulated sculpture; lacking bar in the legs . . . . *I. basalovoi*
There are 8 rows of which the last has 3 gibbosities, the next to the last 2, all others 4; coelomic fluid violet . . . . *I. latiunguis*

72(63). The gibbosities regularly alternate rows of odd and even rows 73
The gibbosities do not alternate 74

73(72). Nine rows of gibbosities; granulated sculpture; lunules absent . . . . *I. vietnamensis*
Ten rows of gibbosities; lunules present; bar in leg; reticulated sculpture . . . . *I. leithaicus*

74(72). There are 20 rows of gibbosities, the majority of which have even numbers .... *I. tubercoloides*
There are at maximum 12 rows of gibbosities 75

75(74). The 1st and the last row of gibbosities are odd, the others even; there are in all, 10 rows 76
Arrangement different 77

76(75). Only the 8th and 9th are even (2-4 gibbosities), all others are odd; reticulated sculpture; there are no lunules; bar present in legs .... *I. pilatoi*
The first 3 and the last 3 rows are odd; the other four rows have 4 gibbosities each .... *I. bulbifer*

77(75). Sculpture composed of granules, increasing in an anterio-posterior sense; on the caudal end behind the 3rd pair of legs there are only 3 rows of gibbosities with respectively 3, 5, and 2 .... *I. hypostomoides*
Different 78

78(77). Smooth cuticle; 9 rows of gibbosities, of which the 1st two include 2 gibbosities each, all the others 3; there is also a pair of lateral gibbosities .... *I. glaber*
Different 79

79(78). The first and last rows have odd (3) gibbosities 80
The first and last rows have even (2 or 4) gibbosities 82

80(79). Granulated sculpture; lunules absent; bars in legs; 8 rows of gibbosities .... *I. mihelcic*
Reticulated sculpture; 8 or 10 rows 81

81(80). Lunules present; bars in legs; 10 rows of gibbosities, of which the last 3 have 4, 4, 3; also lateral papillae .... *I. lunulatus*
There are 8 rows of gibbosities; the last three have 4, 3, 3; lunules absent .... *I. cyrilli*

82(79). Granular sculpture, not reticulated; 9 rows of conical gibbosities, of which the last 4 have respectively 5, 5, 2, 2 gibbosities .... *I. belliformis*
Reticulated sculpture 83

83(82). There are 8 rows of hemispherical gibbosities; bars in legs .... *I. roncisvallei*
There are 12 rows of conical gibbosities .... *I. effusus*

ISOHYPSIBIUS ALICATAI (Binda, 1969) (Figs. 346 and 347).
= *Hypsibius* (*I.*) *alicatai* Binda, 1969.

The species is easily identifiable, especially by the particulars of the doubleclaws. The animals are colorless, from 246-254μ long, without eye spots. Short buccal tube (26.8μ), with 2.68μ diameter; oval pharynx, about 25μ long, with length/width ratio of 1.1 - 1.5:1, containing apophyses and 2 macroplacoids (rod-shaped), of which the 1st is longer than the 2nd and has a constriction; microplacoid absent.

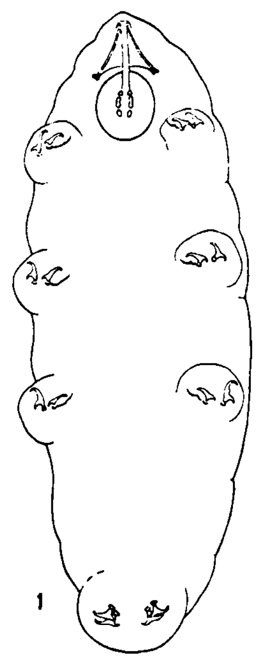


Fig. 346 - *I. alicatai* (Binda). Ventral view (from Binda).

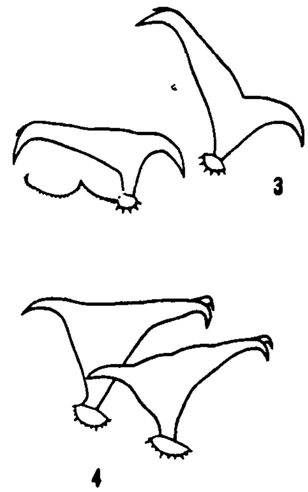


Fig. 347 - *I. alicatai* (Binda). 3, doubleclaws of the 3rd pair of legs; 4, *idem* of the 4th pair (from Binda).

Doubleclaws of the *Isohypsibius* type: in the first three pair of legs there is a slight difference in size between the two doubleclaws of these same legs (principal branch of the external doubleclaws 8-9μ, of the internal 7μ) and the principal branches have two short and slender accessory points. On the 4th pair of legs the external and internal doubleclaws are very similar to each other in shape and size, but very different from those of the first three pair of legs; in fact the branches of each doubleclaw are fused for a good part of their length and forms between them an angle of almost 180μ: as a result the doubleclaws appear to form approximately a single triangular piece, with the proximal angle corresponding to the basal portion and with the two distal angles prolonged into the two branches of the doubleclaws; the principal branch (about 8μ) of the external doubleclaws and of the internals bears short and remarkably robust accessory points.

At the base of all the doubleclaws there is a dentated lunule more developed in the 4th pair of legs: In the first three pair of legs there is also a slender cuticular impression, slightly dentate, which originates near the base of the internal doubleclaws and expires medially at about 10μ.

The species was collected in moss from fossil coastal dunes of Gela (Sicily).

ISOHYPSIBIUS ANNULATUS (J. Murr., 1905) (Figs. 348 and 349).

= *Macrobiotus annulatus* Murr., 1905.

= *Hypsibius annulatus* Thulin, 1911.

= *Hyp.* (*Isohypsibius*) *annulatus* Marcus, 1929 & 1936.

= *Hyp.* (*Isohyp.*) *annulatus* Ramazzotti, 1962 & 1972.

The species is usually aquatic, but collected also in moss in the shade in various localities. Size rather large (length up to 420μ and more); pale yellow color; eyes present. The cuticle is covered with small tubercles (papillae of about equal size, regularly arranged in rings, which encompass the body; the ventral surface is also sculptured, but the tubercles are not in regular rows. In the dorsal and median cephalic regions there is an accumulation of conical papillae, which often adhere to the egg-bearing exuvium after molting (Fig. 348A).

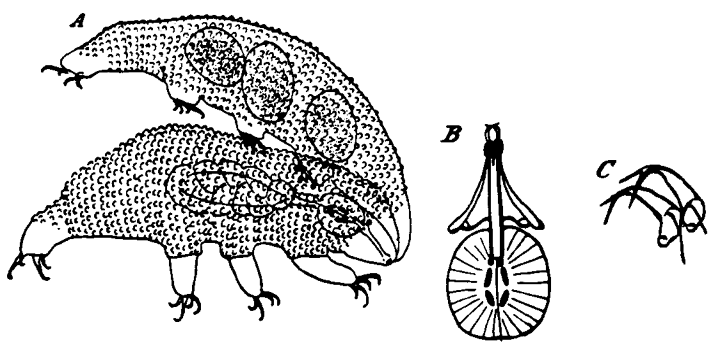


Fig. 348 - *I. annulatus* (Murray). A, female with egg-bearing exuvium; B, buccal apparatus; C, claws (from Marcus).

Stylets robust and curved, pharynx short oval, with very visible apophyses and 2 slender macroplacoids (rod-shaped) of about equal size; microplacoid absent. The two doubleclaws of each leg have little difference in size and the principal branches of both have particularly slender accessory points. The young have unsculptured cuticle.

The oval eggs (67μ long) are deposited in numbers of 3 to 5 in the exuvium, which often (however not always) remains united in the very young, with its rostral end at the maternal cephalic region, where probably is produced a secretion of an adhesive substance.

The species is probably cosmopolitan and was observed in many European localities (also in Italy), in New Zealand, and in the Arctic.

Typ. Loc.: Scotland.

By the name of *Hypsibius* (*Isoh.*) *annulatus* forma *minor*, Ramazzotti (1945) has described a variety very similar to the typical species: different

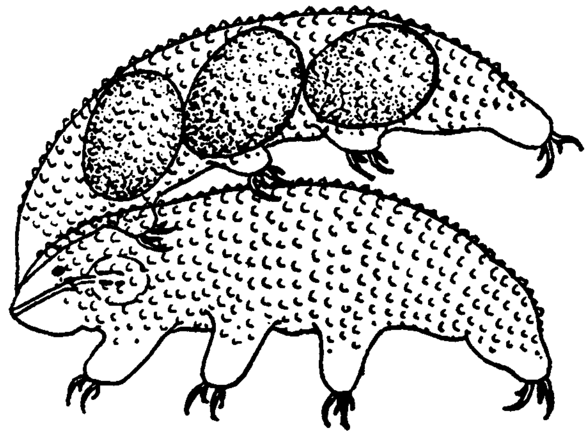


Fig. 349 - *I. annulatus* forma *minor* (Ramazzotti).

only in a smaller size (170μ long), by it lack of color, and by the length of the two slender macroplacoids, of which the first is about twice as long as the second; the diameter of the buccal tube is about 2μ.

The eggs -- in examined populations -- are deposited in the exuvia which remains united to the tardigrade, exactly as happens in *I. annulatus*.

This form was collected in Italy in the water (bottom) of two ponds of the Val Bognanco heights, respectively at about 1600 and 2100 meters altitude; successively was discovered by Rudescu in Romania.

ISOHYPSIBIUS APELLOEFI (Richters, 1908).

= *Macrobiotus apelloefi* Richters, 1908.
= *Isohypsibius apelloefi* Thulin, 1928.
= *Hypsibius* (*Isoh.*) *stenostomus* Marcus, (in part, not Richters, 1908).
= *Hypsibius* (*Isohyps.*) *apelloefi* Hallas, 1971.

Length up to 435μ, according to Hallas, up to 544 according to Richters. Body squat. Cuticle smooth, eye spots present. Buccal tube with a slight ventral curve, more than two times the width that in *I. stenostomus*. Oval pharynx, with large apophyses and three macroplacoids, in the shape of short rods, of which the second is shorter, while the first and third are of equal length, or else the third a little shorter than the first. Microplacoid present. Large claws which vary from one leg to another: those of the 4th pair are always more slender and longer than the others. The doubleclaws of each leg are similar in shape and size. The principal branch is similar to the secondary branch, but is often more slender and bears accessory points which sometimes can be absent on some claws.

This species was placed by Marcus (1936) in synonymy with *Isohypsibius stenostomus*. Then Hallas (1971) in a redescription, did not recognize it as a good species.

This is one of the small marine *Isohypsibius*. It was discovered on coasts of Norway and Sweden.

ISOHYPSIBIUS ARCUATUS (Bartos, 1934) (Fig. 350).
= *Hypsibius* (*I.*) *arcuatus* Bartos, 1934.

Small size: length 178-276μ; eyed. On the dorsum follows 20 annular swellings, alternatively wider and narrower, which surround laterally and to a certain extent the body of the animal; with the exception of these swellings, the cuticle is smooth all over. Cavity globules and liquid of reddish-yellow color. Buccal tube with diameter of 2.5-3μ in a specimen 248μ long, that is rather narrow. Pharynx almost spherical with apophyses very visible and 3 macroplacoids: the first two of about equal length and almost in contact, while the third is somewhat longer and more distant; microplacoid absent. Claws small.

I. arcuatus is differentiated from *I. undulatus* principally by having three macroplacoids, rather than two.

It is a rare species, with few reports in Czechoslovakia and Hungary.

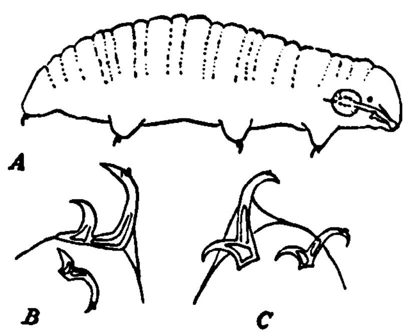


Fig. 350 - *I. arcuatus* (Bartos). A, lateral view; B and C, doubleclaws (from Bartos).

ISOHYPSIBIUS ASPER (Murray, 1906) (Fig. 351).
= *Macrobiotus asperus* Murray, 1906

Large size: length up to 600μ, of dark brown color, with eye spots. The cuticle is dorsally and laterally sculptured with rather big tubercles, semispherical, apparently pliable, arranged without regularity; the cuticle is on the contrary smooth on the ventral surface and on the legs.

Pharynx oval, with 3 macroplacoids in the shape of short rods, about twice as long as wide, of which the first is a little shorter than the others; microplacoid absent. Large doubleclaws (length 24-34μ), whose size increases from the 1st to the 4th pair of legs; the two doubleclaws of each leg have little difference in size between them; however on the fourth pair of legs the principal branch of the posterior (external) doubleclaw is notable larger than the principal branch of the anterior (internal) doubleclaw. It should be noted that the assignment of this species to the genus *Isohypsibius* is very probable, but not entirely certain.

I. asper is known from the south Orkney (typ. loc.), from South Georgia, Poland, the Ukraine, and Rumania.

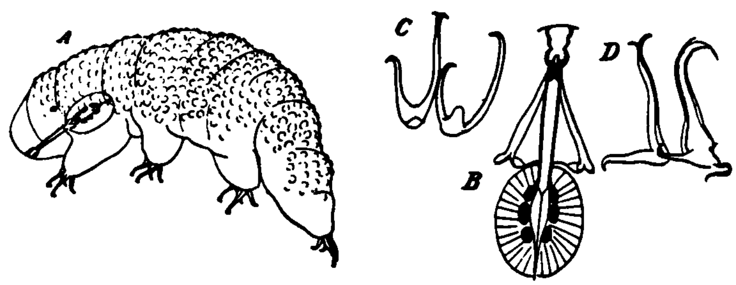


Fig. 351 - *I. asper* (Murray). A. lateral view; B, buccal apparatus and pharynx; C and D, doubleclaws (from Marcus).

ISOHYPSIBIUS AUSTRIACUS (Iharos, 1966) (Fig. 352).
= *Hypsibius* (*I.*) *austriacus* Iharos, 1966.

Length 190-350μ, colorless, eyes absent. The cuticle is sculptured with a reticulated design of large mesh, rather pronounced. The dorsal gibbosities are flattened and arranged in 10 transverse rows, as follows: 2 in rows 2, 10; 3 in row 1; 4 in all the other rows (that is, from 3 to 9). Pharynx elongated oval (32 x 27.5μ) with 2 macroplacoids, of which the 1st is longer and subdivided into two granules in contact with each other. Microplacoid absent.

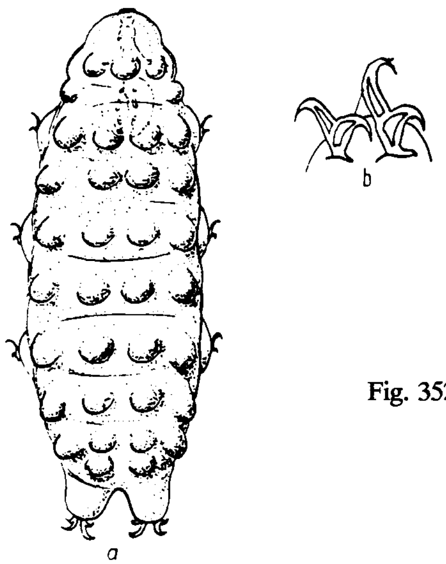


Fig. 352 - *I. austriacus* (Iharos). a, dorsal view; b, claws of the 4th pair of legs (from Iharos).

Doubleclaws of each leg rather large, but not very different. At the base of the claw there is a distinct lunule. Near to the claws of the first three pairs of legs there is a cuticular bar.

Eggs oval, smooth, deposited (in numbers of 8 to 10) in the exuvium.

I. austriacus has been observed in leaf litter in Austria, and then in moss from the Apuane Alps and in Sicily. Typ. loc.: Purbach (M.ti Leitha, Austria).

ISOHYPSIBIUS BAKONYIENSIS (Iharos, 1964) (Figs. 353 and 354).
= *Hypsibius* (*I.*) *sattleri* Auct. (in part).

Length up to 250μ, usually less than 200μ. Colorless, with eyes present. The cuticle has an obvious reticulated sculpture, with varied shape and size of mesh; it appears more prevalent on the dorsal surface and smaller on the sides. The small bands that form the sides of the mesh of the net are in general rather slender, but do not have uniform thickness and width. There are 9 principal rows of gibbosities (even they have reticulated sculpture), four of which are posterior to the third pair of legs. In the first row there are 6 gibbosities (4 in the original description); there follows 6 gibbosities in the second and third rows, 4 in the fourth, 6 in the fifth, 2 in the sixth, 4 in the seventh, eighth, and ninth rows. The median gibbosities

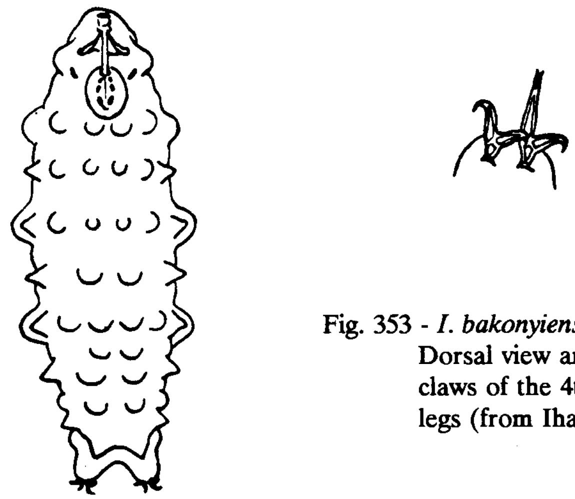


Fig. 353 - *I. bakonyiensis* (Iharos). Dorsal view and double-claws of the 4th pair of legs (from Iharos).

are always more obvious, and have a truncated cone shape; those lateral, smaller, are conical with sharp points. On the sides of the head, anterior to the first row of gibbosities there are two small conical gibbosities, difficult to see. Some gibbosities terminate with a tuft of short and slender spines. Buccal tube short and rather wide. Pharynx oval, with apophyses and 2 macroplacoids, of which the first is profoundly constricted in the middle. Microplacoid absent.

Claws well developed, not much difference in those of each leg. At the base of the claws there is a small lunule, more developed on the 4th pair. There are no other cuticular structures on the legs.

Eggs smooth, deposited in the exuvium.

Pilato (1973), in the redescription of this species (and in its description to which we are referring) puts forth the hypothesis that several authors, in citing *Isohypsibius sattleri*, have had specimens of this species. It is certain that *I. sattleri* was never described in sufficient detail, and certainly to it have been reported different species belonging to the "*tuberculatus* group." We have considered, agreeing with Pilato, to consider *I. sattleri* as a *nomen nudum*.

I. bakonyiensis was described from some localities in Hungary. Later it was found in South America, Canada, North Africa, Sicily and adjacent islands, Apuane Alps, Rome, Carso Trieste, Istria, Lessini Verona, Switzerland and Andalusia (Spain). It is certainly one of the more common species of the "*tuberculatus* group", and currently one of the better described.

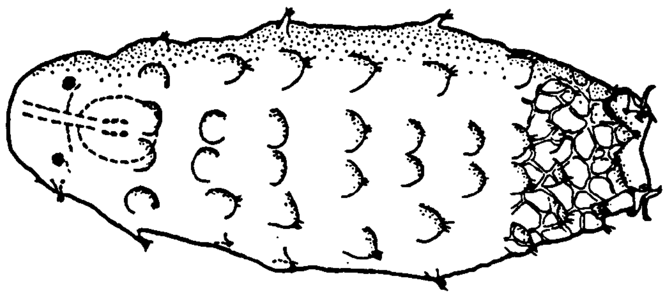


Fig. 354 - *I. bakonyiensis* (Iharos) (from Pilato). The sculpture is drawn only on the caudal end, so the gibbosities can be seen.

ISOHYPSIBIUS BALDII (Ramazzotti, 1945) (Fig. 335).
= *Hypsibius* (*I.*) *baldii* Rammazzotti, 1945.

The species is aquatic, eyed, of small size: the length is always less than 200μ and is usually between 170 and 180μ. The cuticle is sculptured in characteristic manner and the sculpture extends on the dorsum, its flanks and part of the posterior legs, leaving free and smooth the cuticle of the ventral surface of the legs of the first three pair. With low magnification a diffuse granulation, especially very distinct at the margins of the dorsal profile, when the tardigrade is observed laterally. With high magnification this granulation appears composed of small tubercles, which seem to be arranged in the confluence of lines in relief design on the cuticle: thus coming to form a reticulated pattern -- very visible and especially with oil immersion -- composed of small polygonal depressions (the "mesh" of the net).

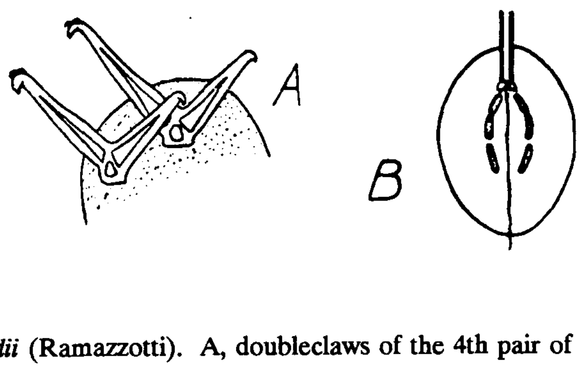


Fig. 355 - *I. baldii* (Ramazzotti). A, doubleclaws of the 4th pair of legs; B, pharynx.

Buccal tube narrow (diameter about 1μ), oval pharynx (24 x 19μ) with three macroplacoids, of which the first two have about equal length and are shorter than the last; microplacoid absent.

The two doubleclaws of each leg have little different size: the posterior (external, or caudal) is slightly larger and its principal branch, on which there are two small accessory points, measuring about 9μ in length.

The eggs are oval and smooth, with diameter of about 40 x 36 to 54 x 34μ, and are deposited in the exuvium in numbers of 3-4.

The species is certainly near to *I. granulifer*, which has however larger size (up to 405μ), sculpture spread also on the ventral surface and on the legs, absent on the reticular pattern of the cuticle, and larger eggs (52 x 41 to 65 x 55μ).

I. baldii has as yet been observed only in Italy from the bottom of Tovel Lake (Dolomiti of Brenta).

ISOHYPSIBIUS BARTOSI (Iharos, 1966) (Fig. 356).

Length 240-270μ, colorless, eye spots absent. Cuticle finely granulated. There are present 10 transverse rows of gibbosities, thus arranged: 2 in the 10th row, 4 gibbosities in each of the other rows (or in 1 through 9).

Pharynx elongated oval (34 x 24μ) with 2 macroplacoids, of which the 1st is longer than the 2nd; microplacoid absent. Doubleclaws of each leg of different length; on the 4th pair of legs the posterior (external) doubleclaws measure 10μ, the anterior (internal) 7μ. They deposit 2-4 eggs in the exuvium.

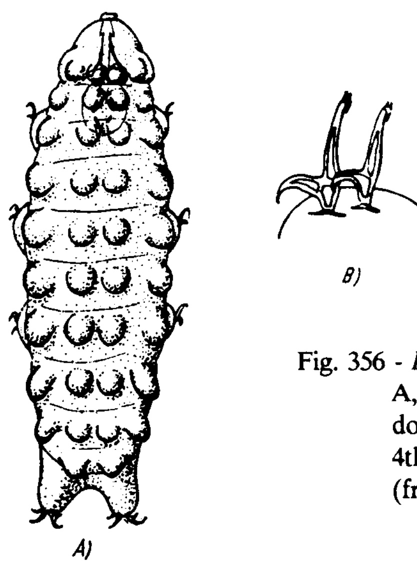


Fig. 356 - *I. bartosi* (Iharos). A, dorsal view; B, doubleclaws of the 4th pair of legs (from Iharos).

The species was collected in leaf litter of the underforest on Badacsony Mountain (Mount Bakony, near Lake Balaton - Hungary).

The description is certainly somewhat summary, and perhaps not sufficient for positive identification of the species. It does not clearly specify the type of sculpture of the cuticle, nor is fact mentioned of lunules, however from drawings they seem to exist. We have also to note that we do not see what significant characters distinguish this species from *I. rudescui*, which likewise has ten rows of equal gibbosities.

ISOHYPSIBIUS BASALOVOI (Durante & Maucci, 1972) (Fig. 357).
= *Hypsibius* (*I.*) *basalovoi* Durante & Maucci, 1972.

Medium size. The specimens examined were minimum of 132μ (juveniles) and a maximum of 280μ. Colorless. Eye spots present. The sculpture of the cuticle is composed of irregular polygonal plates, of variable size, which form a very pronounced network (maximum size of the mesh about 5μ). This sculpture, most evident on the dorsum, is clearly defined, and is absent on the flanks and the ventral side. Besides the plates of the sculpture, the dorsum has flattened hemispherical gibbosities, on each of which the sculpture forms mesh much smaller and denser. The gibbosities are arranged in nine transverse rows, distributed as follows:

1st row: two gibbosities
2nd row: two gibbosities (in a single specimen, 4)
3rd row: four gibbosities
4th row: four gibbosities
5th row: four gibbosities
6th row: two gibbosities (in two specimens, 4)
7th row: four gibbosities
8th row: four gibbosities
9th row: three gibbosities

The buccal tube is rather narrow (23.4μ long and 2μ wide, in the holotype). Muscle appendage attachments in the shape of crests. Slender stylets, with small furcae, very spread. Stylet supports long, straight, slender. Pharynx subcircular (20 by 18μ), at times a little pyriform, having the greatest width in the posterior third. Apophyses are present and three macroplacoids, in the shape of short rounded rods: the first two very close to each other, almost in contact, are very short, equal, or else the second scarcely longer than the first; the third is more elongated. Microplacoid absent.

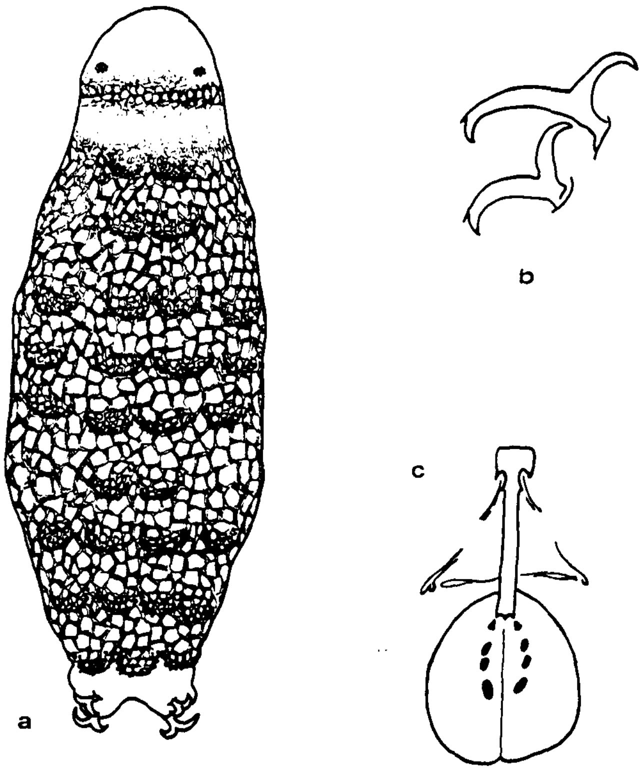


Fig. 357 - *I. basalovoi* (Durante and Maucci). a, dorsal view; b, doubleclaws of the 4th pair of legs; c, buccal apparatus (from Durante and Maucci).

Legs short and stumpy; the fourth pair has a smooth gibbosity on the dorsal side. There is no cuticular bar on the first pair of legs, as present in some species of *Isohypsibius*.

The doubleclaws are large, massive, those of each leg almost equal. The common branch is very short, with an expanded base variously developed, at times scarcely noticeable, spinous, at times large and almost lunuliform. Such enlargement is always more marked on the 4th pair of legs. The two branches, principal and secondary, are almost equally developed, long, robust, with greatest thickness at a certain distance from the common junction. The principal branch runs straight, with an abrupt terminal curvature almost at a right angle, and has two very small accessory points, difficult to see even with oil immersion phase contrast. The secondary branch is strongly arched.

The species, described from some moss samples collected at Basalovo (Verona, Italy), and was later found also near Sundvall (Sweden).

ISOHYPSIBIUS BELLIFORMIS (Mihelčič, 1971) (Fig. 358).
= *Hypsibius* (*I.*) *belliformis* Mihelčič, 1971.

Length from 200 to 300μ, eyes absent (shown in the illustration, not specified), cuticle sculptured with granulation, of which the single elements are round or elongated, of great diversity, but not a reticulated polygonal pattern. Besides this sculpture, there are dorsally rigid cones, covered with the sculpture, and thus arranged: rostrally to the 1st pair of legs 2

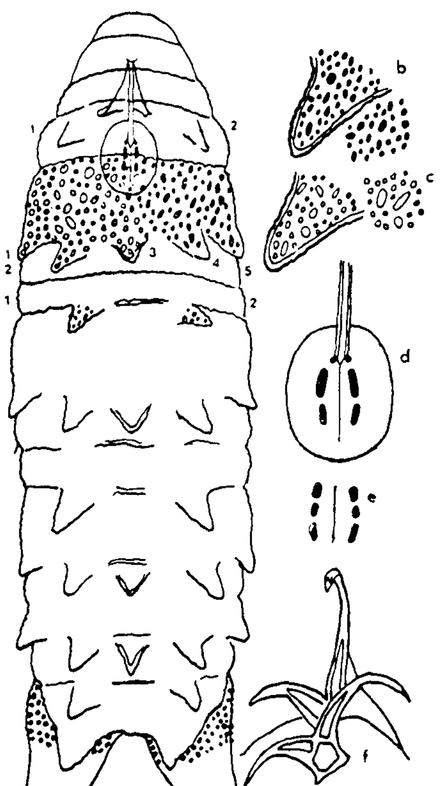


Fig. 358 - *I. belliformis* (Mihelčič). a, habitatus; b, sculpture and sculptured appendage, with low focus; c, *idem*, with high focus; d, pharynx with 2 macroplacoids; e, 3 macroplacoids without the pharynx; f, claws of the 4th pair of legs (from Mihelčič).

gibbosities,above the 1st pair of legs 5 gibbosities, 2 more laterally between the 1st and 2nd pair of legs, also 5 on the 2nd pair, 5 more between the 3rd and 4th, 2 above the 4th pair and also 2 on the caudal end.

Buccal tube with 2.3-3μ diameter, pharynx rounded oval; in dorsal view one sees 2 macroplacoids of unequal length, while in lateral view one sees 3 macroplacoids (granules), the first two of about equal size, the third longer. The description did not cite the claws, and mentioned neither the lunule nor the cuticular bar of the legs.

The species was observed in moss from Amlach (near Lienz, Austria).

ISOHYPSIBIUS BELLUS (Mihelčič, 1971) (Fig. 359).
= *Hypsibius* (*I.*) *bellus* Mihelčič, 1971.

Length 180-280μ. Eyes absent (to judge from the illustration, because it is not specified). Cuticle sculptured, with a granulation of polygonal pattern, always of uniform size. Besides this sculpture there are dorsally 3 [pairs of] hemispherical gibbosities, at the same level as the first three pairs of legs. There are also lateral and caudal conical projections (for their arrangement, see Fig. 359). The polygons of the sculpture are sometimes subdivided into transverse or longitudinal bands.

Pharynx rounded; in lateral view containing 3 unequal macroplacoids (the first two of equal size and wider than long); in dorsal view the visible placoids are only two, wide and of different length. Eggs deposited in the exuvia.

The species was collected in moss and lichen, near Costanza Lake.

We have strong doubts that the above description will allow the identification of this species, which -- I point to the very vague description -- we were not able to include in the identification key.

ISOHYPSIBIUS BREVISPINOSUS (Iharos, 1966) (Fig. 360).
= *Hypsibius* (*I.*) *brevispinosus* Iharos, 1966.

Length 110-150μ, colorless, eye spots present. Cuticle finely granulated, with reticulated design. Dorsal surface covered with 10 transverse rows of gibbosities, which become gradually smaller in a rostro-caudal sense and are thus arranged: 4 in rows 2, 3, 5, 6, 8, 9, 10; 6 in rows 1, 4, 7. The shape of the gibbosities is varied: those dorsal are hemispherical, those lateral pointed and papilliform, those caudal are rounded or flattened and bear in their center a short pointed spine. Also

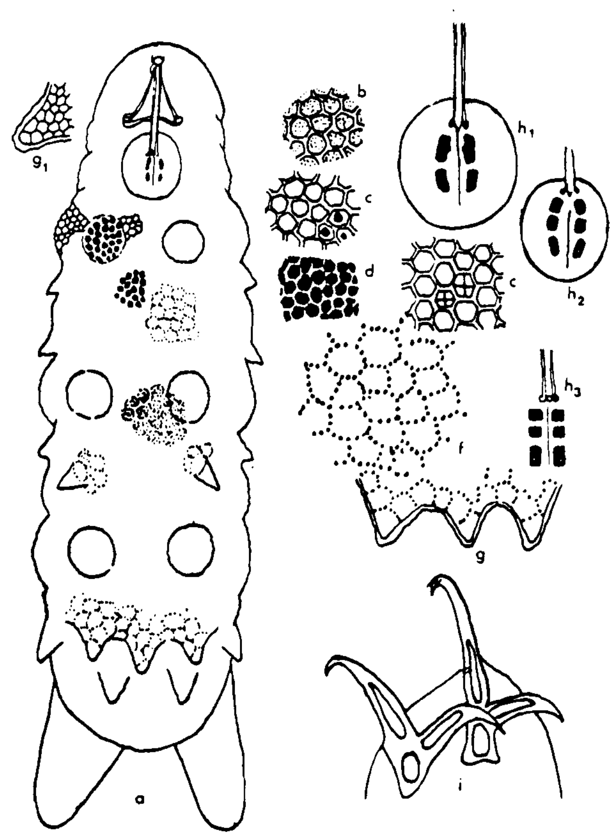


Fig. 359 - *I. bellus* (Mihelčič). a, habitatus; b, sculpture without gibbosities, with high focus; d, *idem*, with low focus; e-f, details of the sculpture; g, the next to last gibbosities; h_1, h_2, h_3, pharynx and macroplacoids, respectively viewed dorsally (h_1), laterally (h_2), and the macroplacoids in lateral view (h_3); i, claws of the 4th pair of legs (from Mihelčič).

on the dorsal surface of the legs are found flattened gibbosities with a small central spine; caudal are rounded or flattened and bear in their center a short pointed spine. Also on the dorsal surface of the legs are found flattened gibbosities with a small central spine; the 4th pair of legs have dorsally a conical pointed gibbosity.

Pharynx elongate oval (15 x 10μ in an individual of 110μ) with 3 macroplacoids (granules), the size increasing from front to back. Microplacoid absent. Doubleclaws of each leg small and of little difference in size; on the 4th pair of legs the external doubleclaws 5μ, the internal 3.5μ. The description does not mention the lunule, which however, according to the illustration can be present. Eggs unknown.

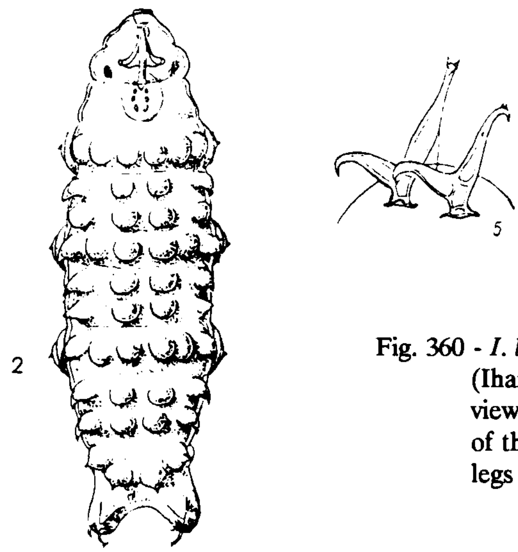


Fig. 360 - *I. brevispinosus* (Iharos). 2, dorsal view; 5, doubleclaws of the 4th pair of legs (from Iharos).

The species was found in moss subject to desiccation, on soil and on rocks and also within lichens, exposed to the sun almost all day in Bakonyako (Hungary) and, later, in South America.

We are willing to consider *I. brevispinosus* as a good species, which sometimes does not substantially differ from *I. bakonyiensis* enough -- according to us -- to differentiate the two species by the slight difference in the number of gibbosities, which are however similar in all the rows for both the species.

ISOHYPSIBIUS BRULLOI Pilato & Pennisi, 1976 (Fig. 361).

Colorless, eye spots absent, length up to 230μ. There are no gibbosities, but the cuticle is sculptured with a net of rather diffuse mesh (the majority has a diameter of about 3.5μ) of irregular shape. The mesh has size almost constant for all the length of the body, but appears less evident on the anterior portion.

Buccal tube rigid, with appendices of the muscle insertion of the stylets in the form of a crest. Buccal lamellae absent. The buccal tube is of medium width (length 25μ and width 3, in a larger specimen). Oval pharynx with apophyses and three macroplacoids in the shape of short rods, of which the second in shortest and the third is longest. Microplacoid absent.

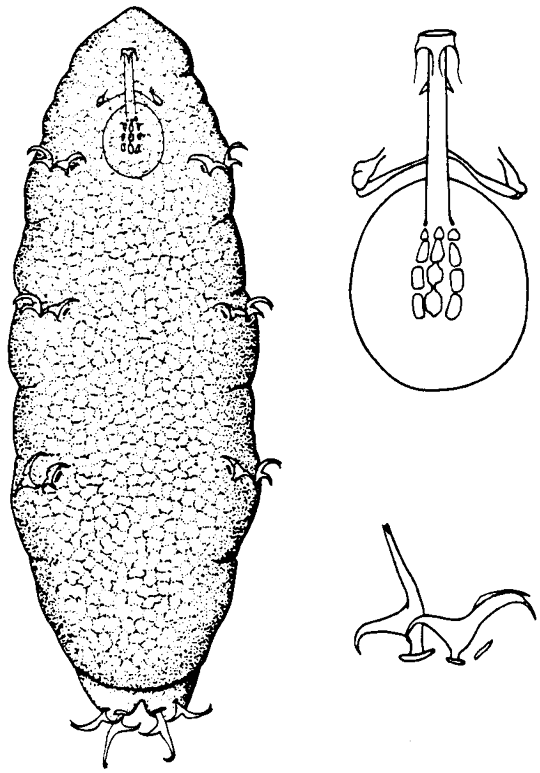


Fig. 361 - *I. brulloi* Pilato and Pennisi (from Pilato and Pennisi).

Claws of each leg somewhat different from the others. The principal branch has slender accessory points. At the base of all the claws is recognizable a lunule, which is most developed on the claws of the 4th pair of legs. On the first three pair of legs, near the internal claws there is a cuticular bar, much shorter than in the other species.

Of this species only three specimens were found near Barce, in Cirenaica (Libya).

ISOHYPSIBIUS BULBIFER (Mihelčič, 1957) (Fig. 362).
= *Hypsibius* (*I.*) *bulbifer* Mihelčič, 1957.

Length 250-270μ, granular cuticle and with 10 transverse rows of gibbosities, thus arranged on the dorsum:

- 3 in each of the rows I, X;
- 4 in each of the rows IV, V, VI, VII;
- 5 in each of the rows II, III, VIII, IX.

Eye spots present, pharynx short oval with 2 macroplacoids (rods), of which the first is longer and sometimes subdivided into two; microplacoid absent. Eggs (3-11) deposited in the exuvium.

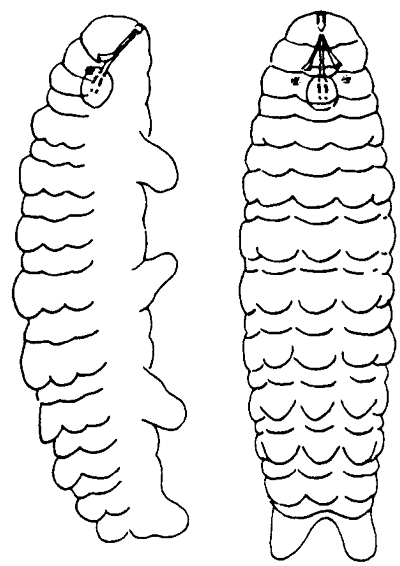


Fig. 362 - *I. bulbifer* (Mihelčič). Lateral and dorsal view (from Mihelčič).

The species is distinguished from *H.* (*I.*) *tuberculatus* and from *H.* (*I.*) *cyrilli* by the number of gibbosities in the various transverse rows, while there is not variance in the details of the buccal tube, the pharynx, of the macroplacoids, and of the doubleclaws.

I. bulbifer has been observed as yet only in Austria (Carinzia), especially in leaf litter.

ISOHYPSIBIUS CAMERUNI (Iharos, 1969) (Fig. 363).
= *Hypsibius* (*I.*) *cameruni* Iharos, 1969.

Length 120-130μ, colorless, eye spots present. Cuticle granulated; on the dorsum and its flanks are 6 to 8 transverse rows of large and flattened gibbosities: in the first row the gibbosities are small, barely visible and may even be lacking. In the rows 1, 3, 5, 7, and 8 there are three gibbosities per row, while in rows 2, 4, and 6 there are 5 each, of which the central gibbosity, flattened, is the largest.

Pharynx oval, with two macroplacoid, the first longer; microplacoid

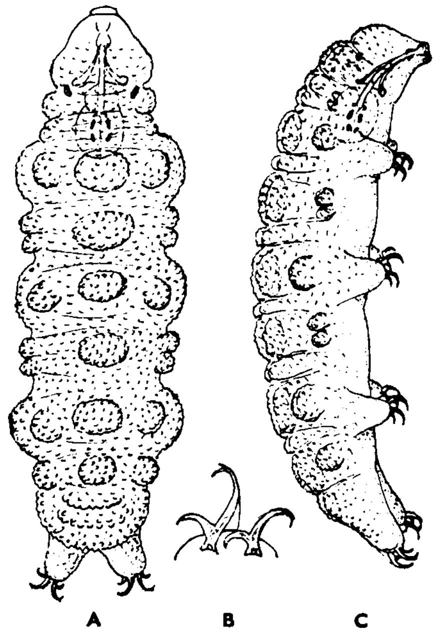


Fig. 363 - *I. cameruni* (Iharos). A, dorsal view; B, doubleclaws of the fourth pair of legs; C, lateral view (from Iharos).

absent. Doubleclaws small and of different size: the external measures 7μ, the internal 4μ. Eggs unknown.

The species was collected in moss in the Cameroon Mountains (western Africa) at 1900-1950 m elevation.

A later report is cited for New Zealand (Horning *et al.*, 1978).

The description is a little imprecise and does not mention some important characteristics. Based on the drawing and the New Zealand specimens, it seems that there are no lunules, neither probably cuticular bars on the legs.

ISOHYPSIBIUS CANADENSIS (Murray, 1910) (Fig. 364).
= *Macrobiotus canadensis* Murray, 1910.

Length up to 225μ, transparent, eyed. The cuticle is usually smooth, but sometimes there are small papillae in the caudal region which may extend somewhat more anteriorly, but without ever covering the whole dorsum. Buccal tube short, pharynx short oval, with apophyses and with 3

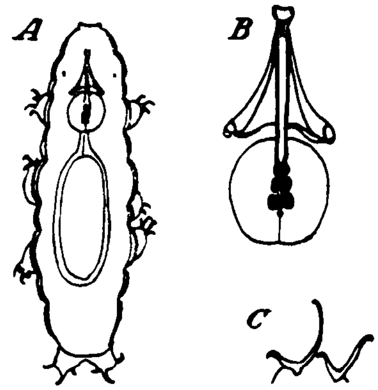


Fig. 364 - *I. canadensis* (Murray). A, dorsal view; B, buccal apparatus; C, doubleclaws (from Marcus).

macroplacoids (granules or short rods), of increasing length from first to third and with the microscope appears almost square; the first macroplacoid is almost adjacent to and parallel to the lumen of the pharynx, and the rows of the macroplacoids diverge only slightly in an anterio-caudal sense; the microplacoid is indistinct or lacking.

The internal doubleclaws are smaller than the external and their principal branch is much longer than the secondary; the external doubleclaws, of larger size, have the principal branch very long and slender, as in *H. oberhaeuseri*, although the structure of the basal claws establish the belonging of the species to the genus *Isohypsibius*; in both the doubleclaws of each leg the principal and secondary branches unite near their bases, so that the basal portion is very short. The eggs (70 x 36μ) are deposited in the exuvium.

The characteristic arrangement and shape of the macroplacoids, the straight buccal tube, and the long, slender principal branch of the caudal doubleclaws, allow an easy separation from the species *I. prosostomus* and *I. schaudinni*.

I. canadensis has been observed only from North America (Vancouver Island, Canada, Virginia, California).

ISOHYPSIBIUS COSTATUS (Mihelčič, 1971) (Fig. 365).
= *Hypsibius* (*I.*) *costatus* Mihelčič, 1971.

Length between 250 and 320μ, color pale yellowish-brown, cuticle sculptured and variable number of gibbosities. Eyes absent. The main characteristic sculpture, which covers even the gibbosities, is composed of slender lines, outlining irregular polygons; sometimes the polygons form rounded or angular structures which the author named "mirrors" and then

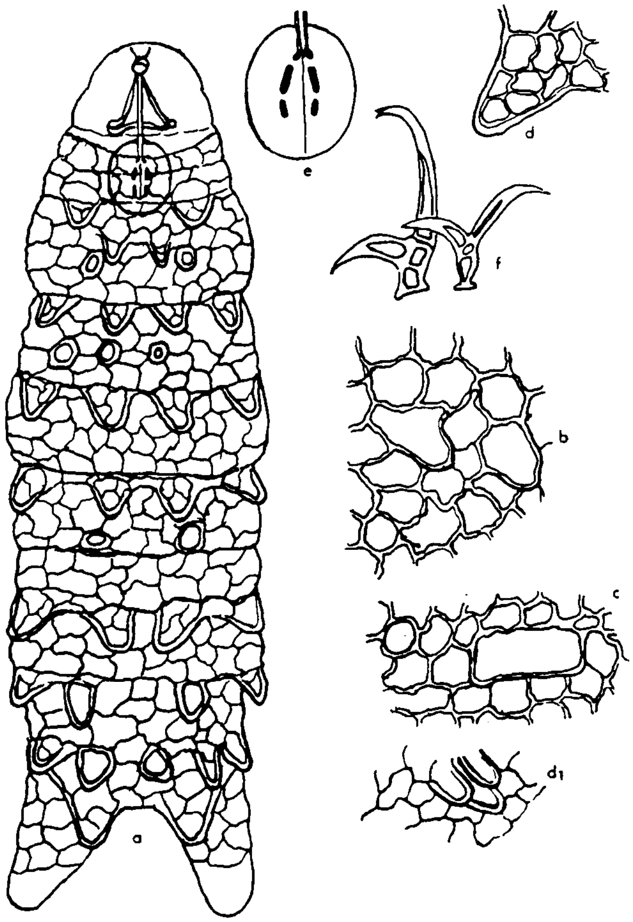


Fig. 365 - *I. costatus* (Mihelčič). a, dorsal view; b, c, d, "mirrors"; d, d_1, gibbosity sculpture; e, pharynx; f, claws (from Mihelčič).

the margins of each polygon are impressed in one or more positions. The gibbosities are rigid, rounded. Pharynx almost spherical and as long as the buccal tube, which is slender, slightly curved. The macroplacoids are two, the first longer than the second, and broken in half. Legs short and squat, covered with polygonal sculpture in the proximal zone. The description does not mention the claws, which, from the drawing we assume rather slender and rather different from each other in shape and size. Lunule presumably absent. Eggs unknown.

The species was observed in moss and soil from Amlach (near Lienz, Austria).

ISOHYPSIBIUS CYRILLI (Mihelčič, 1942) (Fig. 366).
= *Hypsibius* (*I.*) *cyrilli* Mihelčič, 1942.

Length 250-370μ; eyed. The cuticle has a reticulated polygonal design, whose polygons are larger in the dorsal and central regions of the body; there are moreover 8 transverse rows of gibbosities, approximately thus arranged:

- 2 drawn near the center in row II;
- 3 in each of the rows I, III, V, VII, VIII;
- 4 in each of the rows IV, VI.

Diameter of the buccal tube 2-2.5μ; pharynx briefly oval, with robust apophyses and 2 macroplacoids, of which the first is about twice the length of the second and appears interrupted or constricted; stylets slightly curved, with large furcae.

The external doubleclaws have their basal part large and also the principal branch is more robust than usual. An exuvium has been observed with 3 eggs.

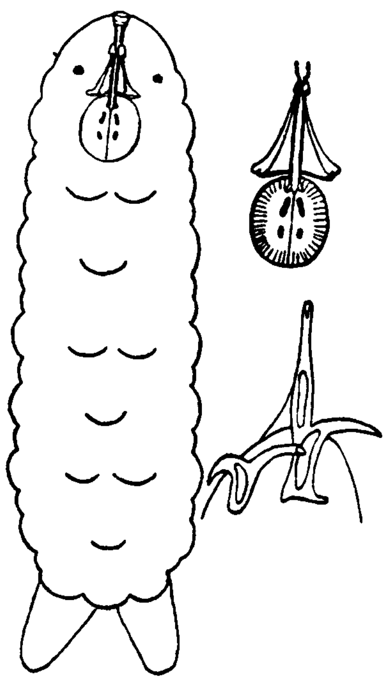


Fig. 366 - *I. cyrilli* (Mihelčič) (from Mihelčič).

The species is known from various localities in Austria; it seems to prefer humid habitat and was collected in leaf litter, in moss, in a cushion of *Saxifraga moschata*, and in soil.

ISOHYPSIBIUS DECONINCKI Pilato, 1971 (Fig. 367).

Length up to 247μ, colorless, eyes absent, cuticle smooth, but with dorsal gibbosities over the 4th pair of legs. Peribuccal lamellae absent, mouth almost terminal, appendages for the insertion of the stylet muscles

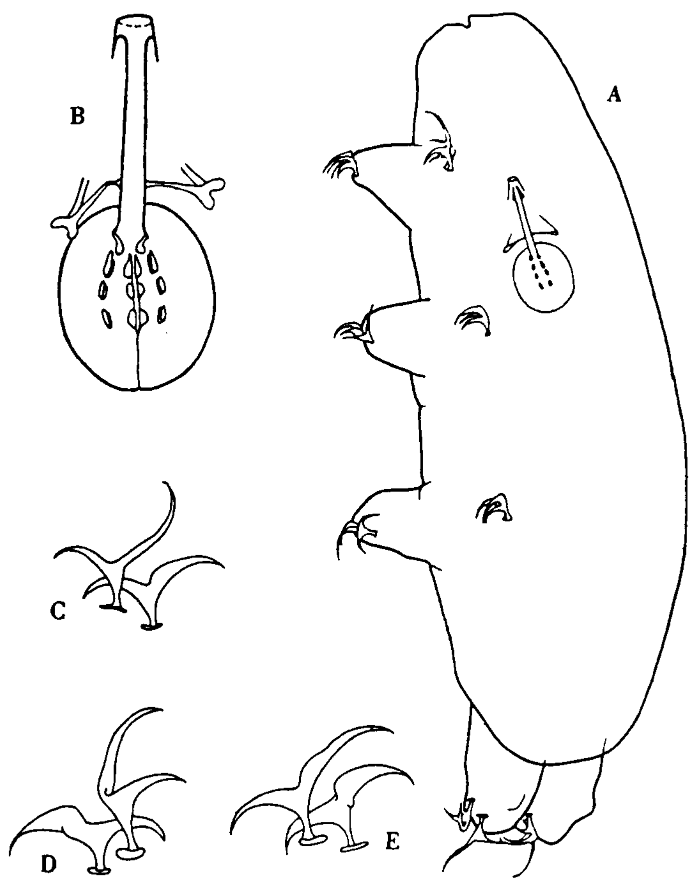


Fig. 367 - *I. deconincki* Pilato. A, habitus; B, buccal apparatus; C, claws of the 2nd pair of legs; D, E, of the 4th pair (from Pilato).

in the form of a crest. Buccal tube 26.8μ long and 3.2μ wide, in a 165μ specimen. Pharynx oval. Three macroplacoids (short rods) of which the first is the longest and the second is the shortest. On the 4th pair of legs the external doubleclaws is 20.4μ, the internal 15.5μ; on the other legs, a little shorter. At the base of the claws exists a lunule, more developed on the 4th pair. There is no cuticular impression ("bar") on the first three pair.

This species, aquatic, was found on the bottom of Simeto River (Randazzo, Sicily), and later in interstitial habitat at Quero (Piave River) and at Zevio (Verona, Adige River).

ISOHYPSIBIUS DEFLEXUS (Mihelčič, 1960) (Fig. 368).
= *Hypsibius* (*I.*) *deflexus* Mihelčič, 1960.

Length 800-900μ, colorless, eyes absent; it is an aquatic species. Buccal opening almost ventral (less than that in *H. hypostomus*), "forehead" in profile very steep. Buccal tube curved near its entrance to the pharynx and having a diameter of about 3μ. The pharynx is oval, with 2 macroplacoids in the form of slender rods of equal length; sometimes the first is longer than the second, or else the first is longer than the second, or else the macroplacoids are 3, and then the longest is the third. Microplacoid absent and apophyses poorly developed. The animal is slender and the maximum width of the body -- in dorsal view -- is in correspondence to the 3rd pair of legs; the legs are not particularly long.

Most characteristic, the external (caudal) doubleclaws which have terminal and basal claws completely separate and independent (in simple terms: the principal and secondary branches are not united to each other);

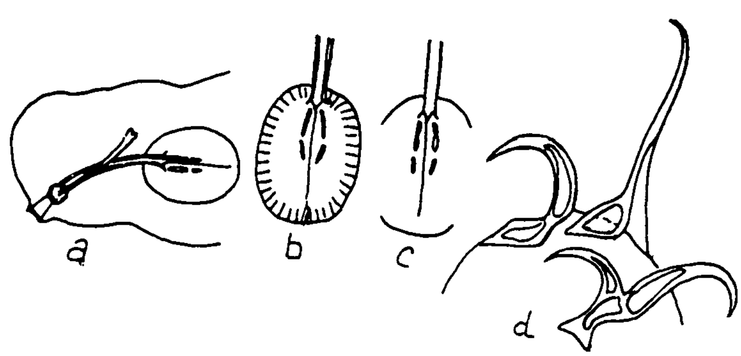


Fig. 368 - *I. deflexus* (Mihelčič). a, cephalic region; b, c, pharynx; d, doubleclaws of the 4th pair of legs (from Mihelčič, redrawn).

the principal branch is very long and slender, slightly curved about the middle, and does not bear accessory points; the secondary branch (basal claw) is much larger and curved. The internal (anterior) doubleclaws are robust and do not appear different from the other species of *Isohypsibius*. The eggs are deposited in the exuvium (12-20 or more).

I. deflexus was collected only in France, in submerged sand from the water of the Mosella, that is in interstitial habitat.

ISOHYPSIBIUS DUDICHI (Iharos, 1964) (Fig. 369).
= *Hypsibius* (*I.*) *dudichi* Iharos, 1964.

Length 180-285μ, colorless, eyes present. The cuticle has a sculpture which outlines a net of rather abundant polygonal mesh, marked by rather slender lines. There are 11 rows of gibbosities, all even, that is without mid-dorsal gibbosity. In the original description the series of rows presented, successively, in an anterio-posterior sense, were 2, 2, 4, 4, 6, 4, 6, 4, 2, 4 gibbosities, plus two lateral gibbosities in front of the eyes, therefore anterior to the first row. In a later letter to Ramazzotti, the author amended as follows the series of gibbosities: 2, 2, 4, 4, 6, 4, 6, 4, 6, 4, 2. Specimens found by Maucci in Austria, and belonging almost certainly to this species, have the following succession: 2, 4, 2, 4, 4, 4, (6), 2(4), 4, 4, 4, 2. Since we know little on the intraspecific variability of the

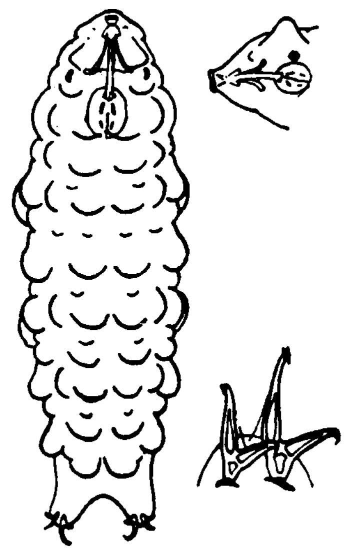


Fig. 369 - *I. dudichi* (Iharos) (from Iharos).

"*tuberculatus* group," we think the aforesaid differences scarcely significant, as opposed to the fact of the 11 rows of even gibbosities.

Between the aforesaid rows of larger gibbosities there are secondary rows of 2 or 4 smaller gibbosities.

Pharynx oval with apophyses and 2 macroplacoids in the form of rods, of which the first is longer than the second; microplacoid absent. Doubleclaws of the *Isohypsibius* type (length on the 4th pair of legs: anterior 8μ, posterior 12μ). They deposit 5-8 eggs in the exuvium.

The species was found in leaves and in moss on rocks and at an altitude of 300 m at Gulacsi-Berg, near the region of Cserszegtomaj (Hungary), and later at Katschbergpass, in Stiria (Austria).

ISOHYPSIBIUS DURANTEAE (Maucci, 1978) (Fig. 370).
= *Hypsibius* (*I.*) *duranteae* Maucci, 1978.

Maximum length 440μ (average of the population 406μ). Colorless, eye spots absent. The sculpture of the cuticle is a coarse irregular granulation. Gibbosities arranged in 9 transverse rows: the first and last rows have two gibbosities, all the others four.

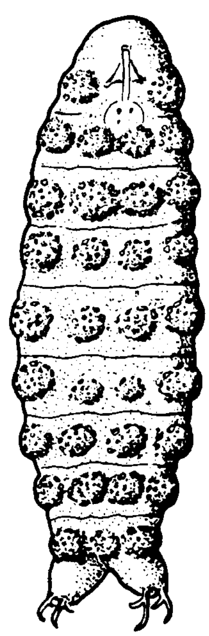


Fig. 370 - *I. duranteae* (Maucci) (from Maucci).

The buccal tube is narrow (40 x 3μ in the holotype, length 360μ). Pharynx short oval, with two macroplacoids in the form of short rods, the first 8μ long and slightly constricted at the middle, the second 5μ long. Microplacoid absent.

The claws are large and massive. The two claws of each leg are little different. The common basal branch, narrow at the base, is enlarged up to the bifurcation; the principal branch, robust and markedly curved, has small accessory points; the secondary branch is notedly long. The basal part plus the principal branch is up to 30μ long, the secondary branch 14μ. At the base of the claw is a lunule, larger on the 4th pair of legs. Near the base of the claws, in the first three pair of legs, there is a large cuticular bar, with granular appearance and running somewhat crooked.

An exuvium has been observed, with five embryonated eggs.

This species has been found in three different localities of eastern Turkey: Horasan, Tahir, Sakcagöz. The population proved more abundant at the last locality.

ISOHYPSIBIUS EFFUSUS (Mihelčič, 1971) (Fig. 371).

The author did not provide information on its length. Eyes absent; the cuticle is sculptured with granules and impressions which delineate polygonal designs, arranged regularly and in uniform size on the cuticular surface. Shape and distribution of the gibbosities is seen in Fig. 371. Two conical gibbosities are placed anteriorly to the 1st pair of legs and 2 on these; anteriorly and posteriorly such gibbosities are connected by transverse impressed lines. The posterior line is interrupted by a wide faintly conical gibbosity. This repeats itself also on the tops of the 2nd pair of legs. Anteriorly to the 3rd pair there are 2 small dorsolateral gibbosities and medially a larger conical gibbosity; the same over the 3rd pair of legs and caudally to them. Above the 4th pair of legs there are two dorsolateral gibbosities and one larger on the median line. Behind these structures are two other gibbosities, nearer each other, and behind them two similar gibbosities, but lateral.

Buccal tube short, length scarcely that of the pharynx. Nothing was written on the placoids, which -- from the drawing -- seems to be two, the first longer than the second and not constricted in the middle. The claws seem to be fairly similar to each other. Eggs unknown.

The species was collected in woods (Carinzia) or in their edges (Osttirol), always in moss.

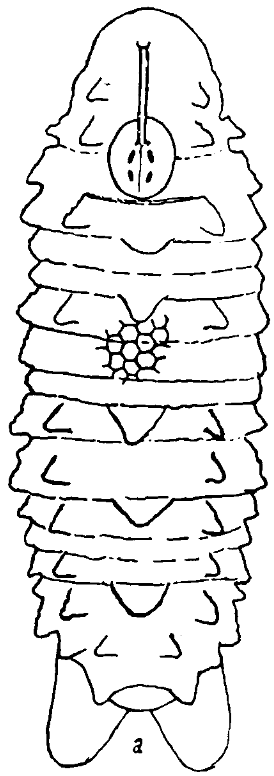


Fig. 371 - *I. effusus* (Mihelčič). a, dorsal view; b, sculpture; c, pharynx; d, claws (from Mihelčič).

ISOHYPSIBIUS ELEGANS (Binda & Pilato, 1971) (Fig. 372).
= *Hypsibius* (*I.*) *elegans* Binda & Pilato, 1971.

Length up to 400μ, eye spots very obvious; cuticle of the dorsum and flanks always densely dotted, even in the newly hatched; the dots have polygonal shape and the larger have a maximum diameter of 1μ, but in general are smaller. Besides this sculpture (barely visible in old preparations) there are hemispherical gibbosities in transverse rows. The number of rows is variable; the individuals which have the maximum number have 10, of which the first has 3 gibbosities, the second with 2, and the successive all with 4, except the tenth with a single median gibbosity. The caudal gibbosities are always more evident (but not larger) and always

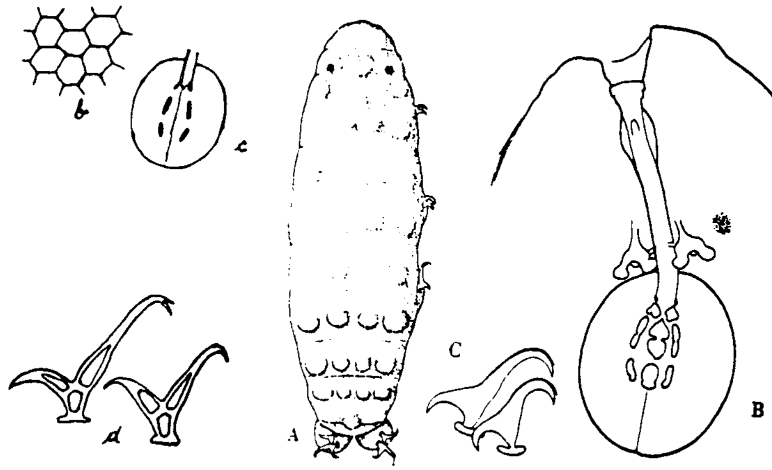


Fig. 372 - *I. elegans* (Binda and Pilato). A, dorsal view; B, buccal apparatus; C, claws of the 4th pair of legs (from Binda & Pilato).

become less evident in a caudo-rostral sense.There are no secondary gibbosities between the principal rows of gibbosities.

Buccal apparatus lacking peribuccal lamellae, buccal tube 39.5μ long in animal of 400μ, with 3.6 diameter, and with muscle attachment appendages of the stylets in the form of crests. Pharynx short oval, containing apophyses and two macroplacoids (rods), of which the first is strongly constricted in the middle, the second shorter, with an apical constriction. Microplacoid absent.

Claws of the *Isohypsibius* type, the principal branch bears accessory points. Lunules at the bases of the claws, more developed on the 4th pair; on the first three pairs of legs there is a cuticular bar, proceeding sinuously.

Eggs smooth and oval, deposited in the exuvia.

I. elegans was collected in moss from pebbles of the avenue in gardens of Catania and Valverde (Sicily). It was later noted from Etna (Sicily), from Favignana and Marettimo (Egadi Island), from Carso Triestino, from Sardinia, and also from Cyrenaica (Derna and Barce) and from Australia (Stanmore, near Sidney).

With the naming of *I. elegans longiunguis*, Pilato (1974) has described some specimens from interstitial habitat, discovered in the stream at Saracena and Reina (Sicily). This subspecies, analogous to the nominate subspecies for almost all the characters, can be distinguished by the absence of dorsal gibbosities (but the author does not concede much importance to this fact, because even in the nominate subspecies the gibbosities can be sometimes scarcely visible) and by the much greater length of the claws, especially those of the 4th pair of legs: the claws of the type subspecies attains less than 50% of the length of the buccal tube, while in the subspecies *longiunguis* such ratio goes up to more than 90%.

ISOHYPSIBIUS EPLENYENSIS (Iharos, 1970) (Fig. 373).
= *Hypsibius eplenyensis* Iharos, 1970.

Length 244-300μ, colorless, eyes present. Cuticle smooth, but with dorsal and lateral gibbosities arranged in 9 transverse rows, thus arranged: 2 gibbosities in the rows 1, 3, 5, 7; 4 gibbosities in the rows 2, 4, 6, 8; 3 gibbosities in row 9. The two dorsal on the median line, as the lateral in row 9, are conical.

Pharynx oval with 2 macroplacoids, of which the first is longer than the second (the description and the figure published does not indicate apophyses). Microplacoid absent. Claws of the 4th pair of different length. It does not mention fact of the lunules, which however clearly appear in the published drawing.

The author has assigned the species to the genus *Hypsibius*, without specifying the subgenus, and therefore Ramazzotti (1974) has cited it as *H.* (*H.*) *eplenyensis*. The gibbosities, the shape of the claws which is inferred

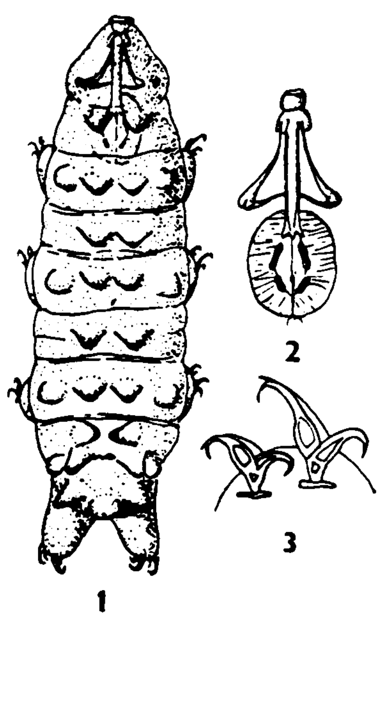


Fig. 373 - *I. eplenyensis* (Iharos). 1, dorsal view; 2, pharynx; 3, claws of the 4th pair of legs (from Iharos).

from the drawing, and the affirmation of the author that the species may be near *Isohypsibius helenae*, clearly indicates that it should be treated as an *Isohypsibius*.

I. eplenyensis was collected only in moss from Mount Bakony (middle-east Hungary).

ISOHYPSIBIUS FLAVUS (Iharos, 1966) (Fig. 374).
= *Hypsibius* (*I.*) *flavus* Iharos, 1966.

Large and massive, length 360-700μ, color red-orange, eyes present. Cuticle very finely punctated, with reticular pattern. Dorsal surface of the body undulated. Pharynx oval (56 x 51μ, in an individual of 560μ), with large apophyses and 2 macroplacoids in the shape of rods (the first 12μ, the second 7.3μ); microplacoid absent. Stylets robust and very curved, with large furcae. Buccal tube wide (7.6μ), with diameter corresponding to about 14% of the length of the pharynx.

Doubleclaws large, rather wide, having little difference in their length: the external 28μ, the internal 24μ (on the 4th pair of legs). The legs bear a smooth gibbosity at the distal end, exactly over the doubleclaws.

This species appears singularly similar to *Doryphoribius citrinus*, for which Maucci has requested and obtained for examination some paratypes of *I. flavus*. It was possible to confirm the diagnosis, establishing in addition the presence of the lunule at the base of the external claws. The only substantial difference between the two species remains still the

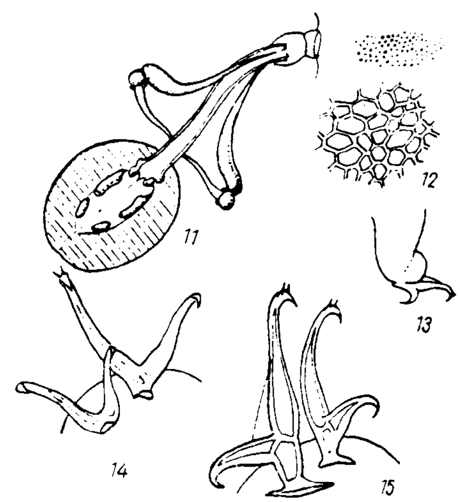


Fig. 374 - *I. flavus* (Iharos). 11, buccal apparatus; 12, punctation and reticular sculpture of the cuticle; 13, leg; 14, doubleclaws of the 3rd pair of legs; 15, of the 4th pair (from Iharos).

reinforcement bar of the buccal tube, absent in *I. flavus*, present instead in *Dor. citrinus*: this is used as noted as a characteristic which is valid for generic discrimination.

The species was observed in moss on rocks subjected to desiccation, near the village Epleny (Hungary).

ISOHYPSIBIUS FRANZI (Mihelčič, 1949) (Fig. 375).
= *Hypsibius* (*I.*) *franzi* Mihelčič, 1949.

Length 240-300μ, eyed. The cuticle, besides having granulations, with sculpture of reticulated appearance (dorsally, laterally and on the legs) present also on the gibbosities, of various numbers and shape. The author considers typical the following distribution of the gibbosities in 9 transverse dorsal rows:

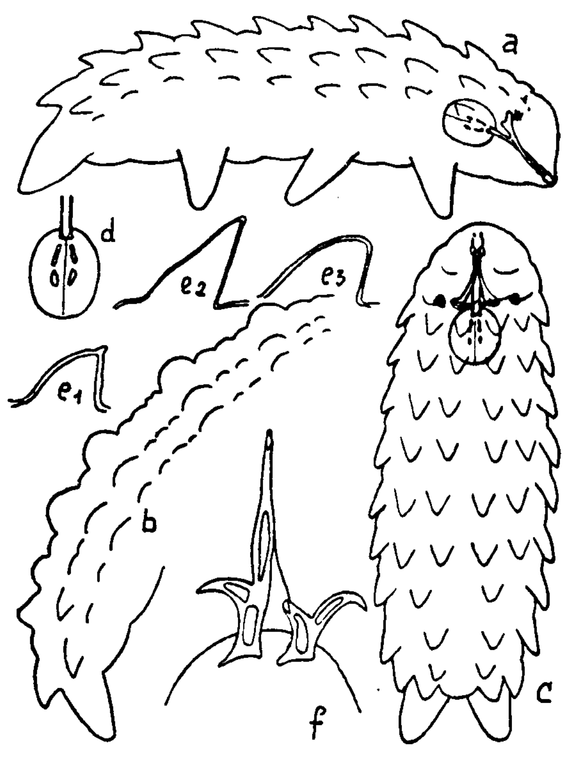


Fig. 375 - *I. franzi* (Mihelčič). a, c, lateral and dorsal view; b, variation in rounded gibbosities; d, pharynx; e, different shapes of gibbosities; f, doubleclaws of the 4th pair of legs (from Mihelčič).

- 4 gibbosities in the rows 7, 8, 9;
- 6 gibbosities in the rows 1, 2, 3, 4, 5, 6.

Sometimes there are also 2 gibbosities, over the fourth pair of legs. In the typical form the gibbosities are not in contact with each other, but between the first 5 rows we observed transverse rows of very small tubercles, which can all be absent: however even in this case the gibbosities are not in contact, and remain therefore free on the dorsum a straight median longitudinal line (because the gibbosities of all transverse lines are in even numbers). In general all the gibbosities are elongated, conical, pointed, sometimes with small papillae at the apex and going caudally, but often those in the anterior region rounded, while only the caudal gibbosities (rows 5-9) preserve the conical and pointed shape, with granulated surface. In the cephalic region there are only two rounded gibbosities covered with small tubercles.

The buccal tube is rather narrow; the oval pharynx contains weak apophyses and 3, or 2 macroplacoids: in this last case the first macroplacoid is longer than the second, and appears interrupted, or constricted; the microplacoid is in general present, but may even be absent. The doubleclaws of all legs have very different appearance.

The species has a great variation and, according to the author, may have the following modifications:

-forms with and without eye spots;
-forms with gibbosities only on the caudal region;
-forms with pointed gibbosities only at the sides of some rows;
-forms with gibbosities reduced to only 4 caudally;
-forms with gibbosities widely spaced in some rows;
-forms with elongated buccal tube, almost of the *Diphascon* type;
-forms with absence of all the gibbosities and only reticulated sculpture;
-forms with gibbosities arranged in smaller number of transverse rows, or else they are only to the sides of the caudal region, above the 4th pair of legs, or else altered into papillae almost spiniform, narrow at the base, very dense in the caudal region and more widely spaced on the rostrum.

Such abundant variability of the species (analogous to that of *Calohypsibius ornatus*) merits to be studied better, especially to define the limits of variability of the various species included in the "*tuberculatus* group" (see No. 2 of the "Observations" in the key to the species).

I. franzi, which seems to prefer shady habitat, was collected in many localities in western Austria, in moss, Phanaerogams of cushion growth, leaf litter (needles and not), soil; in Italy it was observed in moss in the shade and in soil at Pallanza (Lake Maggiore), together with *I. tuberculatus*; it was collected in South America.

ISOHYPSIBIUS FUSCUS (Mihelčič, 1971) (Fig. 376).
= *Hypsibius* (*I.*) *fuscus* Mihelčič, 1971.

Aquatic species. Length between 320 and 450μ, cuticle finely granulated and colored brown at the caudal end. The color is darker on the dorsum than the ventral surface. Body squat and legs rather short. The sculpture is composed of regular granules, which are not grouped to form geometric figures.

Buccal tube wide (9μ in specimen of 400μ); the pharynx is longer than the short buccal tube and has a wide and oval shape; the apophyses are two robust rounded granules; 2 macroplacoids, of which the 1st is three times longer than the 2nd; the macroplacoids are large rods and their rows slightly surpass the middle of the pharynx.

Doubleclaws of all legs of differing shape and size; the external has long and slender principal branch, with extreme and not strongly curved, but rather straight, and supplied with accessory points; the secondary branch is shorter, more robust; the internal doubleclaw is analogous, but with shorter branches.

Eggs smooth, deposited in the exuvium.

I. fuscus was found in interstitial habitat near Ivosjön (Sweden).

ISOHYPSIBIUS GEDDESI (Hallas, 1971) (Fig. 377).
= *Hypsibius* (*I.*) *geddesi* Hallas, 1971.

It is one of the few species of marine *Isohypsibius*, and was observed on the lower part and at the base of Laminaria, at a depth of 0-1 m. Length of 258 to 518μ. Large eye spots, squat body, legs of medium

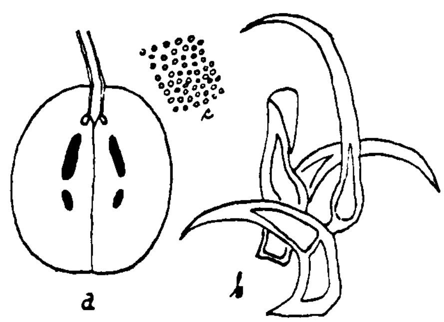


Fig. 376 - *I. fuscus* (Mihelčič). a, pharynx; b, claws of the 4th pair of legs; c, sculpture (from Mihelčič).

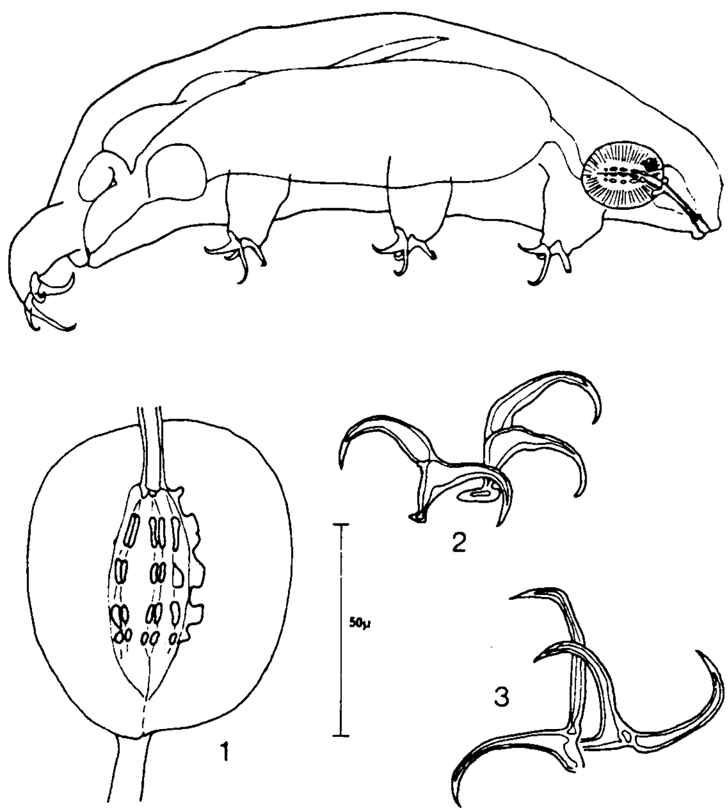


Fig. 377 - *I. geddesi* (Hallas). 1, pharynx; 2, claws of the 2nd pair; 3, claws of the 4th pair of legs (from Hallas).

length. The cuticle may be smooth, but in specimens of larger size they have a fine, dense, and regular granulation. Pharynx oval, containing 3 macroplacoids of rod shape, of which the 1st is longest, the 2nd and the 3rd have equal length, or else the 2nd is longer than the 3rd. The internal diameter of the buccal tube varies from 2.4μ (specimen of 258μ) to 3.3 (specimen of 500μ).

Claws large, little variation between them of each leg.

I. geddesi is very similar to *I. apelloefi* and *I. stenostomus*. It is differentiated from the first by the length of the second macroplacoid which is equal or bigger than the 3rd (the 2nd macroplacoid is shorter than the 3rd in *I. apelloefi*); and from the second by the greater width of the buccal tube.

The species was collected at Frederikshavn (Denmark) and at Grinday, near Tromsö (Norway).

ISOHYPSIBIUS GIBBUS (Marcus, 1928).

= *Macrobiotus tuberculatus* var. *verrucosuc* Della Valle (1915)
= *I. tub.* forma *gibba* Marcus, 1928 & 1936
= *I. tub. gibbus* Ramazzotti 1962 & 1972
= *Hypsibius sattleri* Cuénot (1932) (in part) not Richters, 1902

This species was formerly considered by the author as a variety or subspecies of *I. tuberculatus*. It is distinguished from it by the numerous gibbosities, often in contact with each other and arranged confusedly, that is to say not aligned in transverse rows. He does not mention fact of any types of sculpture of the cuticle. The macroplacoids are three, the first and the second shorter, almost in contact with each other. Microplacoid present. Accessory points were not seen on the principal branch of the doubleclaws.

It is certain that the description is rather incomplete, however the species may be recognized. At the time of the first description *H.* (*I.*) *tuberculatus* was almost the only species known with dorsal gibbosities, and seemed therefore acceptable to consider this form as a variety or subspecies of *tuberculatus*. Actually, with ten described species (probably not all valid) considered to belong to the "*tuberculatus* group", it does not seem acceptable to postulate a subspecies subordination of this form to any of the known species. The disorganized arrangement of the gibbosities, and the presence of the microplacoid justifies, according to us, the validity of *I. gibbus*.

Besides the first report from Della Valley in Italy (Astroni, near Napoli), it is known only from a second report by Bartos, in Bohemia.

ISOHYPSIBIUS GLABER (Durante Pasa & Maucci, 1979) (Fig. 378).

= *Hypsibius* (*I.*) *glaber* Durante Pasa & Maucci, 1979.

Small size; from 110 to 160μ, colorless, eye spots absent. Cuticle smooth, without granulation, nor reticular design, both on the gibbosities and between them. Along the dorsum there are nine rows of gibbosities thus arranged: 2 dorso-lateral gibbosities in the rows I and II; 3 gibbosities, of which the middle one is largest, in row III; 3 gibbosities, plus a pair of small lateral gibbosities, in rows IV, VI, and VIII; 3

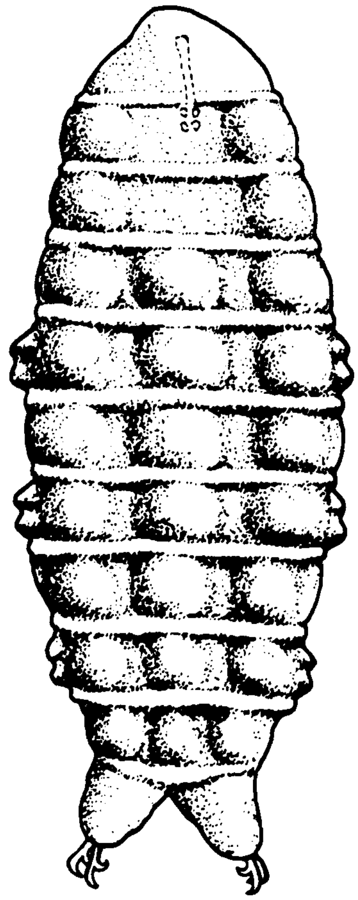


Fig. 378 - *I. glaber* (Durante Pasa and Maucci).

gibbosities in rows V, VII, and IX. Besides the rows of gibbosities, the dorsum has 17 transverse undulations.

Buccal tube of average width, muscle insertion appendages of the stylets in the shape of crests. Pharynx elongated oval, with apophyses and two macroplacoids, of which the first is a little longer than the second andslightly constricted at the middle. Microplacoid absent.

Claws rather small, those of each leg almost equal. Lacking lunule and also absent is the cuticular bar on the legs.

I. glaber was collected near Jävre, in northern Sweden.

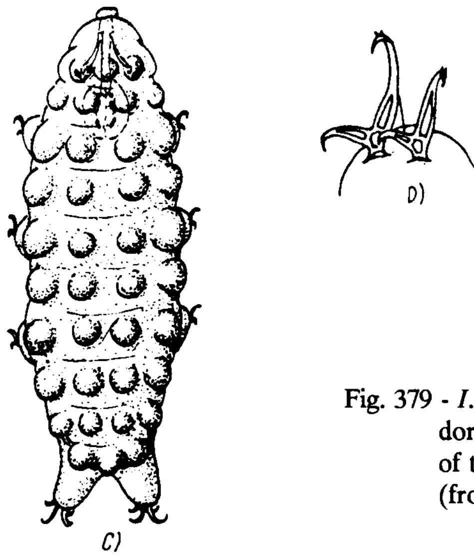


Fig. 379 - *I. gracilis* (Iharos). C, dorsal view; D, doubleclaws of the 4th pair of legs (from Iharos).

ISOHYPSIBIUS GRACILIS (Iharos, 1966) (Fig. 379).
= *Hypsibius* (*I.*) *gracilis* Iharos, 1966.

Length 210μ, eye spots present. Cuticle finely granulated, with 10 rows of dorsal gibbosities, thus arranged in each transverse row: 3 in rows 1, 10; 4 in all the other rows (that is to say from 2 to 9). Pharynx elongated oval (22 x 17μ) with 2 macroplacoids. Microplacoid absent. On the 4th pair of legs the external doubleclaws measure about 12μ, the internal 7μ.

This data given here is the original description, which seems without doubt very summary, and does not mention some important characteristics. Based upon the specimens from Carso, from the Maucci collection, referred to as this species, the diagnosis may be completed as follows. Length up to 300μ; the sculpture is a granulation, regular and dense (without "reticulated" appearance, characteristic of other species), extended on all the cuticle, including the gibbosities.

The claws, rather small, almost equal on the same leg, do not have lunule: only those of the 4th pair, have at the base a light, open cuticular impression, somewhat similar to a lunule. On the legs of the first three pair exists near the base of the claws a slender cuticular bar, long and slightly curved.

The species was collected in needle-shaped leaf litter, at Vaskaputetö in the Bakony Mountains, near Lake Balaton (Hungary), and later in two localities from Carso (Basovizza, near Trieste, and Postumia) in moss.

ISOHYPSIBIUS GRANULIFER Thulin, 1928 (Fig. 380).

A species in general aquatic, however observed sometimes in moss. Length up to 405μ, body slender, legs long, eye spots present. Cuticle covered with a regular granulation, composed of small polygonal granules largest on the dorsal and lateral surfaces, very minuscule on the legs and on the ventral surface. Buccal tube (diameter from 2 to 7μ) barely curved and with appendices in crest shape for the insertion of the stylet muscles. Pharynx oval (length:width ratio varies between 1.1 : 1 and 1.5 : 1), with apophyses and 3 macroplacoids (short rods, or oval granules), of which the first 2 have equal length and the third is longest, or else finally the length increases progressively from the first to the third and the first two are very close together; microplacoid absent. Doubleclaws of each leg large, with basal part slender; principal and secondary branches of the external doubleclaws barely curved; the accessory points of the principal branch may be robust or else slender: they are not found at the distal extremities of the claws, but rather, or quite often, further back. The eggs are smooth and oval (from 52 x 41μ up to 69 x 55μ) and are deposited 6-8 in the exuvium.

It should be noted that the young of *I. granulifer* has cuticle not, or indistinctly, granulated: the granulation becomes instead evident and extends always more -- from the caudal zone to the rostral -- with increase in age and therefore with the size of the animal.

Aquatic individuals similar to *I. granulifer*, but having small size (170-190μ), legs of the first three pair and ventral surface deprived of sculpture, related to *I. baldi*, which has smaller eggs (from 40 x 36μ to 51 x 34μ).

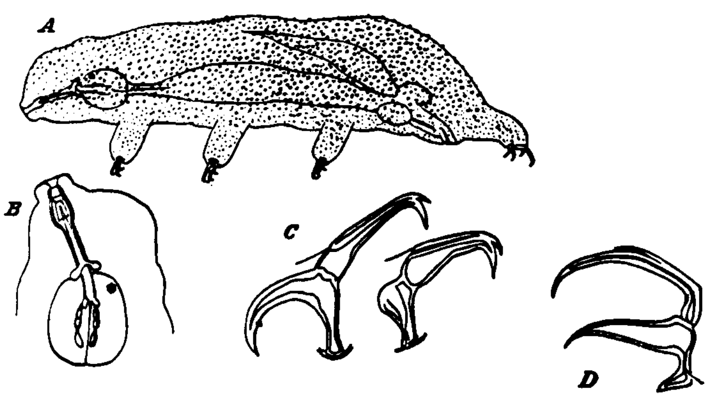


Fig. 380 - *I. granulifer* Thulin. A, lateral view; B, cephalic zone; C, doubleclaws of the 4th pair of legs; D, anterior claws of the 3rd pair of legs (from Marcus).

The species is known from many European locations, where -- except for the report by Bartos in Czechoslovakia and Switzerland -- it has only been observed in water: also in Italy it has been collected only in lacustrine water; it was also found in moss in North America (Colorado) and in water in South America (Brazil), in western Africa (Ivory Coast), and in Baikal Lake.

Typ. loc.: Lund (southern Sweden).

Besides the described nominate subspecies, there are two other described subspecies.

I. granulifer baicalensis Ramazzotti, 1966 (Fig. 381).

Young colorless; with age the pigmentation increases, until a very intense yellowish-brown, sometimes arranged in transverse bands. Maximum length 760μ, but in general (adults) 450-550μ; the young measure 200-210μ. Eye spots very obvious, black.

Cuticle granulated, often very fine and only visible with careful observation, better with phase contrast: the granulation varies from one individual to another and is in general more distinct in clear individuals and of medium size; in larger specimens (650-760μ), the sculpture is sometimes barely visible or absent, other times on the contrary it is very distinct: it is especially evident on the exuvium, where it may be noted that the sculpture is in the form of tiny granules, a little larger in the mid-dorsal and caudal zone, smaller on the proximal legs, on the ventral surface, and in the cephalic region.

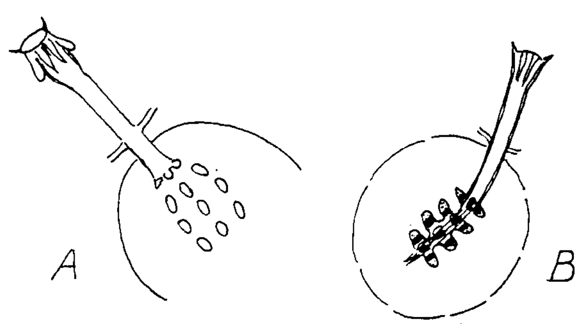


Fig. 381 - *I. granulifer* (Thulin) *baicalensis* Ramazzotti. A, buccal tube, pharynx, and placoids, not deformed; B, appearance of the macroplacoids and the apophyses, after the characteristic deformation.

Pharynx a little longer than wide, with 3 short rods, almost granules, oval; microplacoid absent. It is noted that in this species verification almost always (but not without exception) by a showy and characteristic change in the appearance of the placoids a more or less short time after the preparation (see figure). That is to say that the two parts, of which each macroplacoid is composed, can slide laterally undergoing a transformation: this occurs also to the apophyses and it makes one think of a structure rather different from the usual components of the buccal apparatus. I add that this has not been verified in the typical species *granulifer* from the same Baikal Lake, but only in *granulifer baicalensis*.

Buccal tube provided with peribuccal lamellae, with diameter of 5-7μ in specimens of 450-500μ, but with a certain variability; furcae of the stylets well developed and robust stylet supports. Large doubleclaws of the *Isohypsibius* type; their principal branches with two accessory points; the size of the two doubleclaws of each leg are not very different. You see many females with numerous eggs in the ovary (20-30): on the contrary it was not possible to find egg-bearing exuvia.

This variety was collected in the water of Lake Baikal (Siberia, U.S.S.R.) and differs from *granulifer* by the larger size, by the slightly different macroplacoids (shorter and more oval), by the much more intense pigmentation of the adults.

I. granulifer koreanensis (Iharos, 1971).

Length 220-250μ. Cuticle bright rose color, finely granulated. Eye spots present. Pharynx elongated oval, with three macroplacoids, almost round, equally large; microplacoid absent.

This subspecies is distinguished from the nominate subspecies by the color and by the fact that the granules of the sculpture have equal size not only on the dorsal side and the flanks, but also on the ventral surface and the legs.

I. granulifer koreanensis was found in constantly wet moss on the bank of the Guriong falls, near Kŭm Gan-san (North Korea).

ISOHYPSIBIUS GYULAI (Mihelčič, 1971) (Fig. 382).

Length 200-280μ, colorless, eyes absent. Cuticle sculptured with fine rounded granules on the dorsum and on the legs, but not on the ventral surface. Also, there are gibbosities thus arranged: anterior to the 1st pair

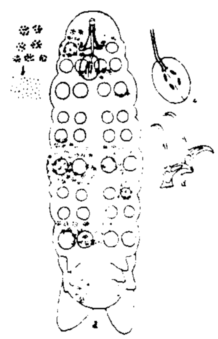


Fig. 382 - *I. gyulai* (Mihelčič).
a. dorsal view; b, sculpture;
c, buccal apparatus; d, claws
(from Mihelčič).

of legs there are two transverse rows, the first with 2 lateral gibbosities (one per side), the second with 2 dorsal and 2 lateral gibbosities, rounded. At the level of the 1st pair of legs, 4 larger gibbosities; equal gibbosities also above the 2nd and 3rd pair of legs; behind the 1st and 2nd pair of legs and for each pair two rows of 4 smaller and rounded gibbosities. Behind the 3rd pair appears to be 4 conical gibbosities per transverse row, and more caudally 2 lateral conical gibbosities per row. The longitudinal median line of the body is lacking gibbosities.

Claws with very obvious accessory points. Buccal tube curved, pharynx oval with obvious apophyses and 2 macroplacoids, of almost equal size. Microplacoid absent.

I. gyulai was collected in moss and lichen in the vicinity of Liez (Austria).

ISOHYPSIBIUS HADZII (Mihelčič, 1938) (Fig. 383).
= *Hypsibius* (*I.*) *hadzii* Mihelčič, 1938.

Length up to 500μ, colorless or greyish, eyed. The cuticle has a hexagonal sculpture; dorsally there are gibbosities of different size and arranged in irregular pattern, which -- observed in profile -- exhibit an undulating contour. The buccal tube is wide; the pharynx, oval and almost spherical contains 3 macroplacoids of about equal size; microplacoid absent. Legs short; doubleclaws of average size, of the *Isohypsibius* type: the principal branch of the external doubleclaw is slender, length almost twice the secondary branch.

The species is known from various localities in Austria, in Yugoslavia, and in Romania.

ISOHYPSIBIUS HELENAE (Iharos, 1964) (Fig. 384).
= *Hypsibius* (*I.*) *helenae* Iharos, 1964.

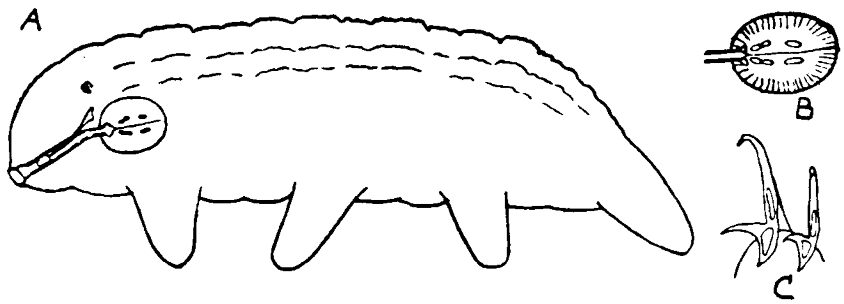


Fig. 383 - *I. hadzii* (Mihelčič). A, lateral view; B, pharynx; C, doubleclaws of the 4th pair of legs (from Mihelčič).

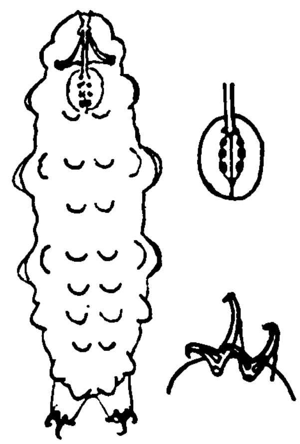


Fig. 384 - *I. helenae* (Iharos). Dorsal view, details of the pharynx and claws of the 4th pair of legs (from Iharos).

Length 140-160μ, color bright yellowish, eye spots present. On the dorsal surface there are 8 transverse rows of gibbosities, hemispherical in the anterior region of the body and conical in the caudal region; they are thus arranged: 2 in the rows 1, 3, 5, 7, and 4 in the other rows (2, 4, 6, 8). Cuticle finely granulated.

Pharynx oval, with three macroplacoids, of regularly increasing length from the first to the third: lacking the microplacoid. Doubleclaws of the *Isohypsibius* type, slender and small: the anterior measures 6μ, the posterior 8μ (on the 4th pair of legs). Eggs oval, deposited in the exuvium.

I. helenae was collected at Ocs-Berg (Bakony Mountains, Hungary) in moss on the ground.

Then this species was collected also in two localities in Sweden (Kila and Ljungby). In the Swedish material the granulation of the cuticle forms small stripes which outline a decided reticular sculpture, with wide and irregular network. Lunule absent, and likewise absent is the cuticular "bar" in the legs.

ISOHYPSIBIUS HYPOSTOMOIDES (Mihelčič, 1971) (Fig. 385).
= *Hypsibius* (*I.*) *hypostomoides* Mihelčič, 1971.

Length 180-250μ. Cuticle with small granules, clear with high focus, dark and encompassing polygons with low focus. The sculpture lacking

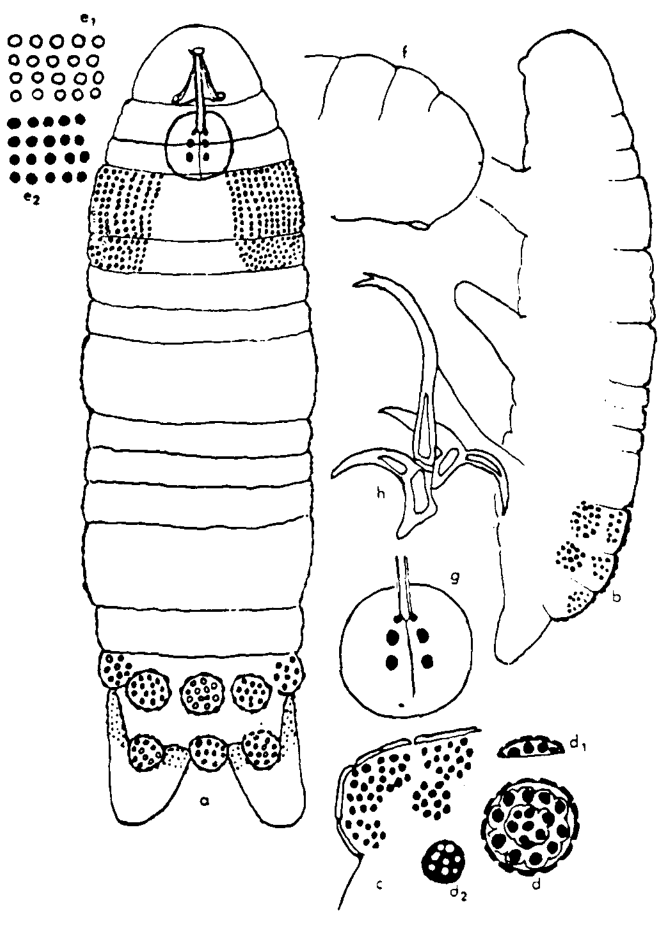


Fig. 385 - *I. hypostomoides* (Mihelčič). a, dorsal view; b, lateral view; c, d, the last segments of the body with "skull-cap" gibbosities, and this view from high; e, sculpture (e_1 with tube high, e_2 with tube low); f, cephalic region; g, pharynx with 2 placoids; h, claws (from Mihelčič).

anterior to the 1st pair of legs and always becoming larger (dorsally) going toward the posterior end.

Over the 4th pair of legs there are three transverse rows of gibbosities: the first row with 5 gibbosities, the second with 3 and the last with 2, smaller; all the gibbosities are low and flattened, in the form of a skull-cap.

Buccal aperture ventro-terminal, buccal tube scarcely as long as the pharynx or a little less. Pharynx almost spherical with apophyses (rounded granules) and two small macroplacoids, rounded, almost equal in size. The rows of placoids are short and surpass a little the middle of the pharynx.

The claws are not mentioned, however from the drawing they seem to be very different on the same leg: principal branch of the external claws very long and slender, with accessory points; lunule almost certainly absent.

I. hypostomoides was observed in moss at Amlach (near Lienz, Austria).

ISOHYPSIBIUS INDICUS (Murray, 1907) (Fig. 386).
= *Macrobiotus indicus* Murray, 1907.

Length about 150μ; on the cuticle there are numerous tubercles, arranged in about 24 transverse rows, each of about 8 tubercles. Pharynx in optical section very short oval (or almost spherical), with distinct apophyses and 2 macroplacoids in the shape of rounded granules; microplacoid absent. The two doubleclaws of each leg have little different size: the secondary branch joins the principal branch (about 7μ long) forming an acute angle. An oval egg (42 x 30μ) was observed deposited in the exuvium.

It is doubtful that the species belongs to the genus *Isohypsibius*; Thulin (1928) indicates the hypothesis that it can be *Calohypsibius* and this is also the opinion of Bartos (1940), who thinks on the contrary probably that *indicus* either is a variety of *C. ornatus* (see the description of that species); Marcus (1936) deems instead to exclude the belonging of *indicus* to the genus *Calohypsibius*, based on the shape and the size of the claws, and especially because J. Murray (1913) observed that the doubleclaws approaches the *Diphascon* type, more than shown in the figure. Only the discovery and study of new material may supply the solution to the problem.

I. indicus was collected on the Himalayas (typ. loc.) and in eastern Africa.

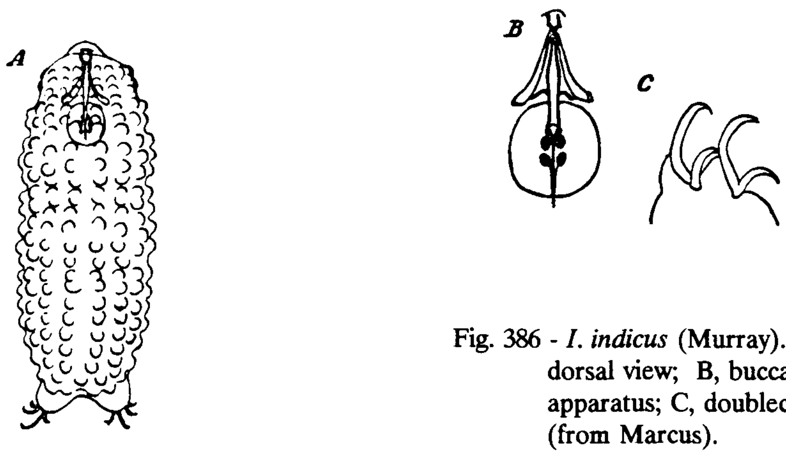


Fig. 386 - *I. indicus* (Murray). A, dorsal view; B, buccal apparatus; C, doubleclaws (from Marcus).

ISOHYPSIBIUS ITOI (Tsurusaki, 1980) (Fig. 387).
= *Hypsibius* (*I.*) *itoi* Tsurusaki, 1980.

Length up to 407μ, colorless, squat shape. Cuticle smooth. Eye spots absent. The buccal tube is rather short and wide (width 13-15% of the length). Pharynx oval, with apophyses and three macroplacoids, of which the second is the shortest, while the first and the third are of about equal length, or else the first is longer than the third. Microplacoid absent.

Claws rather large, those of each leg of unequal size, lacking accessory points.

I. itoi is a marine species, belonging to the "*stenostomus* complex", within which it is very near to *I. appelloefi*. It is differentiated from the other species of the group by the wider buccal tube and by the absence of eye spots and microplacoid.

The species was found in interstitial environment on a beach at Ishikari (Hokkaido, Japan).

ISOHYPSIBIUS JOSEPHI (Iharos, 1964) (Fig. 388).
= *Hypsibius* (*I.*) *josephi* Iharos, 1964.

Length 190-220μ, in the original description; up to 330 in material from Turkey. Colorless, eye spots present or absent; the cuticle has coarse granules, irregularly connected in a manner to permit depressions densely arranged. Dorsally there are nine transverse rows of gibbosities containing four gibbosities each in rows 2-8. The first row has 2 very lateral

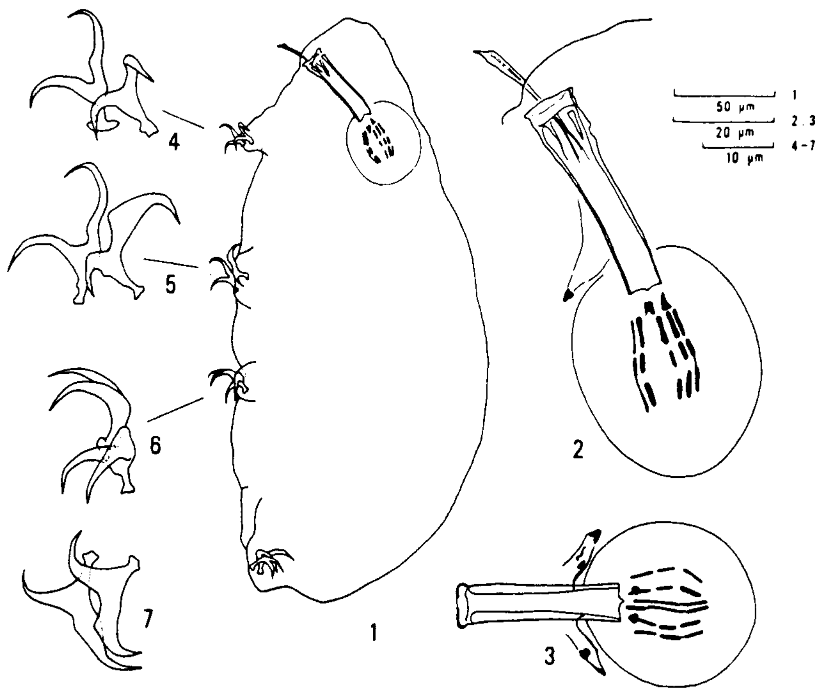
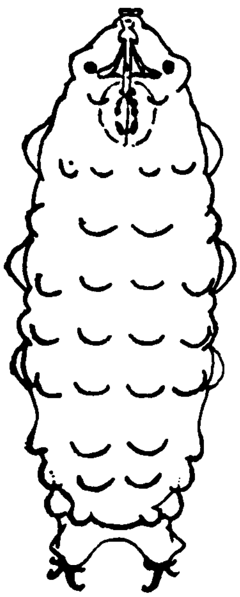


Fig. 387 - *I. itoi* (Tsurusaki). 1, habitus; 2, 3, buccal apparatus; 4, 5, 6, 7, claws of the legs 1-4 (from Tsurusaki).

gibbosities and the last, 3 gibbosities in very small specimens; however there are 3 gibbosities in the first row and only two in the last, in the majority of specimens (in the original description there are 2 gibbosities illustrated in both the first and the 9th row).

Buccal tube short and rather wide (35 x 5μ). Pharynx pear-shaped with 2 macroplacoids, the first twice the length of the second and profoundly constricted at the middle (in the original description: "three macroplacoids: the first two very close"). Lacking the microplacoid. Legs short and stumpy. Claws small, those of each leg about equal, with large lunule, biggest in the 4th pair. Near the base of the claws there is a cuticular bar, long, almost sinuous: contrary to what occurs in other species, this bar is present also on the 4th pair of legs.

The species was observed in moss on rocks in Szentgyörgy-Berg (Hungary), and found later near Van (eastern Turkey). The present description given is based on Turkish material.



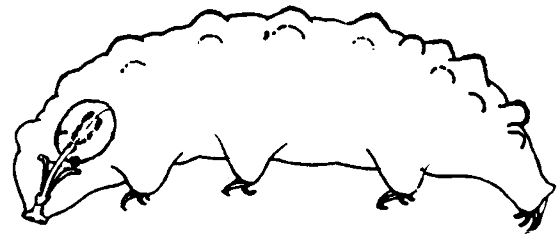
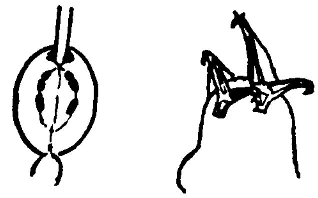


Fig. 388 - *I. josephi* (Iharos). Dorsal view, lateral view, details of the pharynx and doubleclaws of the 4th pair of legs (from Iharos).



ISOHYPSIBIUS LATIUNGUIS (Iharos, 1964) (Fig. 389).
= *Hypsibius* (*I.*) *latiunguis* Iharos, 1964.

Length about 160μ, eyes present. The coelomic liquid of the living animals is in general of violet color. Dorsally there are 8 transverse rows of gibbosities, thus arranged: 2 in row 7; 3 in row 8; 4 in the first 6 rows; there are also -- anterior to the eye spots -- two small gibbosities.

Pharynx oval with 2 macroplacoids, the first longer than the second; lacking the microplacoid. Legs short and fat; doubleclaws of the *Isohypsibius* type, well developed and remarkable for their robustness (the anterior of the 4th pair of legs measures 7μ; the posterior 11μ). Eggs unknown.

The species was observed in moss on soil at Ocs-Berg (Bakony Mountains, Hungary).

ISOHYPSIBIUS LEITHAICUS (Iharos, 1966) (Fig. 390).
= *Hypsibius* (*I.*) *leithaicus* Iharos, 1964.

Maximum length 150μ, colorless, eyes absent. Cuticle sculptured with reticular design; dorsal surface covered with larger and smaller gibbosities,

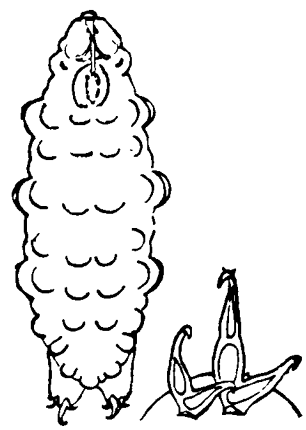


Fig. 389 - *I. latiunguis* (Iharos). Dorsal view and claws of the 4th pair of legs (from Iharos).

arranged in 10 transverse rows as follows: 2 in row 10; 3 in rows 1, 3, 5, 7, 9; 4 in rows 2, 4, 6, 8.

Pharynx oval (15 x 12μ), with 2 macroplacoids (rods), the first longer than the second; microplacoid absent. Doubleclaws rather small: on the 4th pair of legs the posterior (external) doubleclaws measure 7μ, the anterior (internal) measure 5.5μ. Oval eggs (6) deposited in the exuvium.

The species was observed in leaf litter in the Leitha Mountains near Purbach (Austria).

A specimen, found near Resadiye (Turkey) and probably belonging to this species, has a length of 320μ; the sculpture is granulated, indistinct;

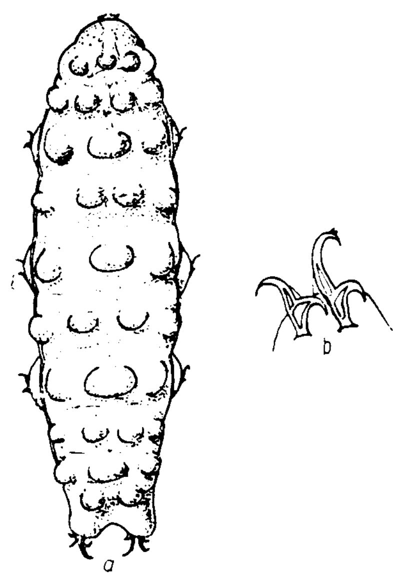


Fig. 390 - *I. leithaicus* (Iharos). a, dorsal view; b, doubleclaws of the 4th pair of legs (from Iharos).

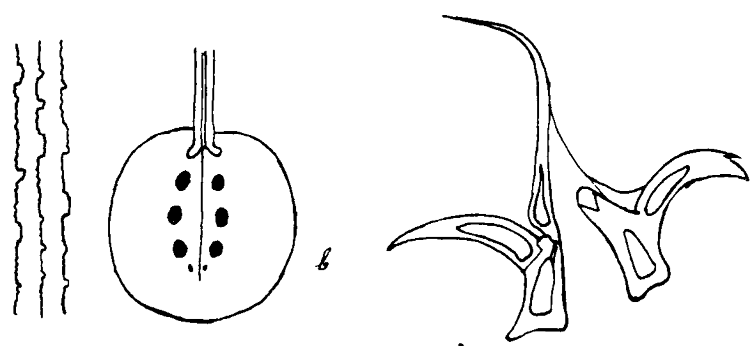
the gibbosities agree with the original description, except lacking the eighth row (the rows are therefore 9 in all, with the following numbers of gibbosities: 3, 4, 3, 4, 3, 4, 3, 3, 2). Large lunules present and slender cuticular bar on the first three pair of legs.

ISOHYPSIBIUS LINEATUS (Mihelčič, 1969) (Fig. 391).
= *Hypsibius* (*I.*) *lineatus* Mihelčič, 1969.

Tardigrade so far observed only in freshwater, and more precisely in sand or in aquatic moss. Length of the animal from 350 to 450μ. Cuticle wrinkled; the sculpture is composed of irregularly undulating lines, which run longitudinally on the body of the tardigrade and they are formed of small granules; such lines are impressed in some points; the undulations are not rounded, but angular, and the impressions are noted at the angles of the "zig-zag". The sculpture is present on the whole dorsum and on the flanks: ventral surface and legs are smooth. Eye spots present.

Pharynx almost circular, only a little flattened anteriorly: it contains 3 short rounded macroplacoids (almost granules) and a microplacoid; buccal tube rather wide. The external doubleclaws have the principal branch with the distal end curved and slender, having the point slender and pointed, almost straight and without accessory points. The internal doubleclaws are very robust and the principal branch has an accessory point.

The species, according to the author, is near to *I. granulifer*, but differs by having the sculpture composed of lines, rather than the granules, by the round pharynx, by having the 3 macroplacoids of equal length, by the presence of the microplacoid and by the very different appearance of the doubleclaws.



a b c

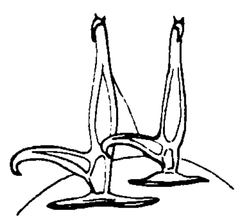
Fig. 391 - *I. lineatus* (Mihelčič). a, sculpture of the cuticle; b, pharynx; c, doubleclaws of the 4th pair of legs (from Mihelčič).

I. lineatus was collected in sand upstream in the Michelbach stream near St. Johann in Walde (Austrian Lienz-Tirolo).

ISOHYPSIBIUS LUNULATUS (Iharos, 1966) (Fig. 392).
= *Hypsibius* (*I.*) *lunulatus* Iharos, 1966.

Length up to 280μ, colorless, eye spots present. Dorsally, its flanks and on the basal portion of the legs, the cuticle is sculptured with big rounded granules or, sometimes, polygons (quadrangular or triangular). There are also 10 transverse rows of large gibbosities. The first row, immediately behind the head, composed of 3 gibbosities, of which the middle is transversely elongated; row 2, only two dorsolateral gibbosities; row 3, at the level of the first pair of legs, 3 large hemispherical gibbosities; row 4, 4 gibbosities, of which the two central are clearly smaller than those lateral; row 5, at the level of the second pair of legs, 3 large gibbosities; row 6, 4 gibbosities, of which the central has size equal to the lateral, and are very close together; row 7, at the level of the third pair of legs, 3 gibbosities; row 8, 4 gibbosities, the central two larger than the lateral; row 9, 2 gibbosities; row 10, 3 gibbosities of which the central is hemispherical, the lateral are transversely elongated.

Fig. 392 - *I. lunulatus* (Iharos). 9, doubleclaws of the 4th pair of legs; 10, dorsal view (from Iharos).



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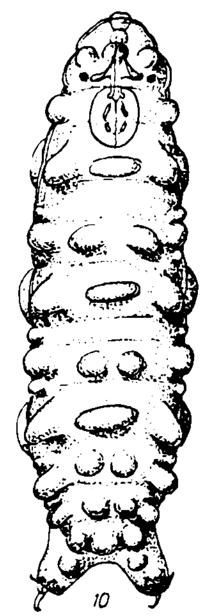

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Between the 3rd and the 4th, between the 5th and the 6th, and between the 7th and the 8th rows, one finds a papilla on each side, of moderate size, but projecting little.

The buccal tube is about 30μ long and width less than 4; the appendage of muscle insertion of the stylet has a crest shape.

Pharynx oval, with robust apophyses and two elongated macroplacoids, of which the first is longer and has a profound constriction at the middle; microplacoid absent.

The doubleclaws of each leg have size and shape little different, and that is more evident on the 4th pair of legs: where the principal branch of the external claws has a basal portion more robust and a more sharpened distal portion, the secondary branch is rather long, and bent in a hook. The principal branch of the internal claws has a size almost constant on all its length. Very small accessory points.

At the base of all the doubleclaws there exists a large smooth lunule. On the first three pair of legs also is noted a cuticular impression in the form of a bar.

I. lunulatus is one of the more clearly described species and easily recognized within the "*tuberculatus* group", and seems also to be one of the more widespread.

The first report was in needle-shaped leaf litter in Uszabänya (Hungary). It was later found and redescribed (with some differences from the original description, which nevertheless does not seem to be determining) from Isole Eolia (Sicily), from Etna, from Nebrodi and Peloritani mountains (Sicily), from Apuane Alps (Toscana), from Carso Triestino, Carnia, Monti Lessini, Istria, from several locations in Austria, from two locations in Sweden, from Greece, French Alps and Pyrenees, from Spain.

ISOHYPSIBIUS MACRODACTYLUS (Maucci, 1978) (Figs. 393 and 394).
= *I. zierhofferi* Dastych, 1979.

Maximum length 440μ (344μ average). Cuticle smooth. Colorless, with numerous irregular granules of black pigment on all the dorsal side. Eye spots absent. The buccal armature is composed only of a posterior band of teeth. Buccal tube rather short and wide: 32μ long and 6μ wide, in the holotype (400μ long). Pharynx almost round. Stylets short, very divergent. Apophyses very robust, and three macroplacoids, the first is the longest, the second the shortest. The first and the second are almost in contact, the third considerably detached. Microplacoid present, very small, barely

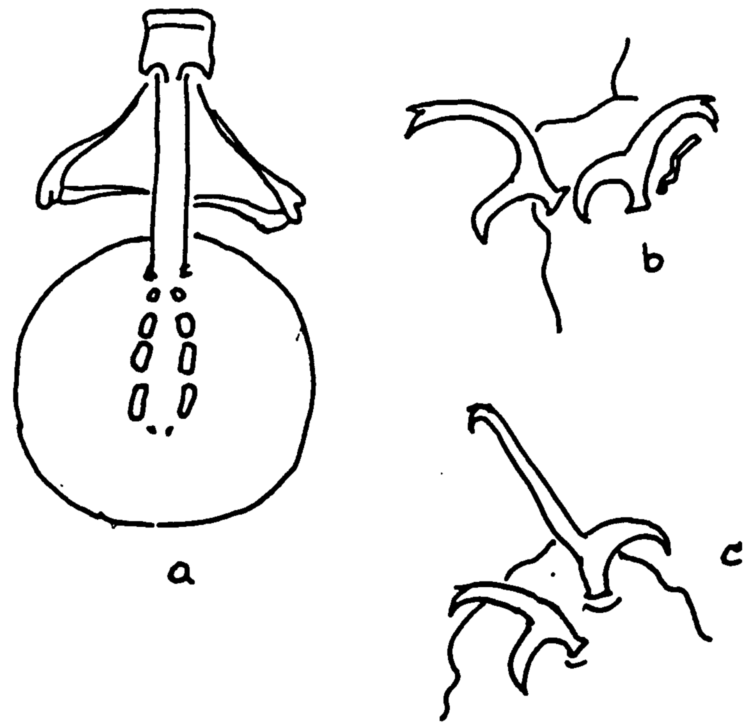


Fig. 393 - *I. macrodactylus* (Maucci). a, buccal apparatus; b, doubleclaws of the 2nd pair of legs; c, doubleclaws of the 4th pair of legs (from Maucci, modified).

visible, and near the third macroplacoid.

The claws are very large (30μ). The common basal branch is long, slender in the external claws, a little more massive in the internal claws; the secondary branch is robust, the principal branch very long, slender, with obvious accessory points. The claws of the fourth pair are considerably longer on the first three pair (45μ). At the base of the claws there is a lunule, which is smooth on the first three pairs, somewhat dentate on the fourth. A cuticular bar, long, sinuous, is found on the first three pair of legs, near the base of the claws, while on the fourth pair a similar bar, but shorter, connected to the base of the two claws.

I. macrodactylus was found in three locations in eastern Turkey (Tahir, Van, Resadiye), as well as from a location from Abruzzo (Italy).

I zierhofferi was found at Pir Scurovski, in the Central Caucasus (Dastych, 1979) and described as follows:

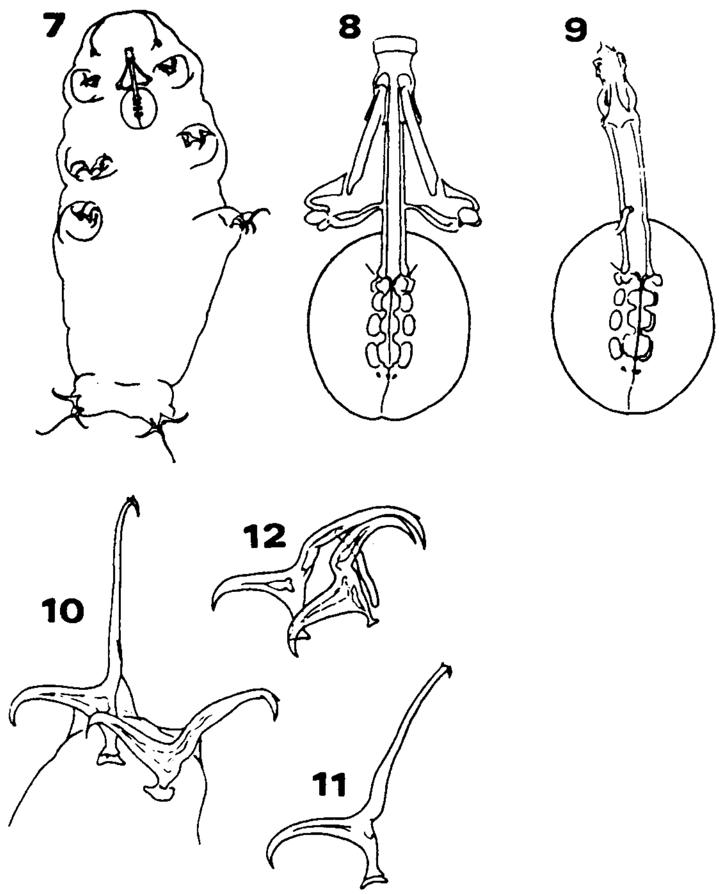


Fig. 394 - *I. zierhofferi* Dastych = *I. macrodactylus* (Maucci). 7, habitus; 8, 9, buccal apparatus, dorsal view and ventral view; 10, 11, doubleclaws of the 4th pair of legs; 12, doubleclaws of the 2nd pair of legs (from Dastych).

Length 190-380μ; white with spots of brown pigment. Eyes present. Cuticle smooth. Buccal aperture terminal, slightly bent in the ventral direction. Buccal tube 34μ long (in a 250μ specimen) and 4 wide. Pharynx oval with large apophyses, three macroplacoids (2.5μ, 3μ, 4μ, respectively, from 1st to 3rd). Claws "*Isohypsibius* type", with lunule and accessory points distinctly developed. Cuticular bar on legs 1-3. The claws of the 4th pair may reach 45μ. Eggs deposited in the exuvium in numbers of four.

It seems that the slight differences (presence of eyes and the size of the buccal tube) does not justify a distinct species), compared with *I. macrodactylus*.

ISOHYPSIBIUS MAMMILLOSUS (Iharos, 1964) (Fig. 395).
= *Hypsibius* (*I.*) *mammillosus* Iharos, 1964.

Length 160-180μ, colorless, eye spots present. There are 10 transverse rows of dorsal gibbosities, of which the lateral have a pointed mammary shape in the caudal region of the body, posterior to the 3rd pair of legs. The gibbosities are in numbers of 4 in all the 10 rows; there is a little gibbosity in the area of the insertion of each leg of the 4th pair. The cuticle is finely granulated, even on the gibbosities, and displays a reticulated pattern.

Pharynx oval (14 x 18μ) with 3 macroplacoids: the microplacoid is absent. The doubleclaws of each leg are not very different in size: on the 4th pair the anterior doubleclaw measures 7μ, the posterior 10μ. There has been observed 5 oval eggs, deposited in the exuvium.

I. mammillosus was collected at Keki-Tal (Alta region of Balatom, Hungary), in lichens on dolomite rocks. Later it was found in Istria and in the Republic of Andorra.

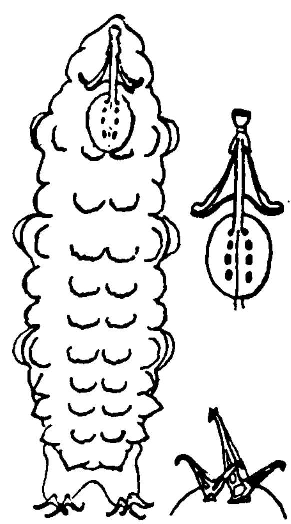


Fig. 395 - *I. mammillosus* (Iharos). Dorsal view, buccal apparatus, and claws of the 4th pair of legs (from Iharos).

ISOHYPSIBIUS MARCELLINOI (Binda & Pilato, 1971) (Fig. 396).
= *Hypsibius* (*I.*) *marcellinoi* Binda & Pilato, 1971.

Maximum length 380μ, colorless, eyes present, smooth cuticle. Peribuccal lamellae absent, buccal tube with stylet muscle insertion appendages in shape of a crest. Buccal tube average width (7.7% of the length). Pharynx short oval, with apophyses and two macroplacoids, the 1st longer than the 2nd. Microplacoid absent.

Doubleclaws of all legs of shape not much different from one another; the external larger than the internal. Smooth lunule at the base of the claws, best developed in the 4th pair of legs; the first three pair of legs have a cuticular bar impression, with one smooth margin and the other notched.

The species was observed in moss near Enna (Sicily), and more recently in aquatic environment, in the Simeto River (Sicily).

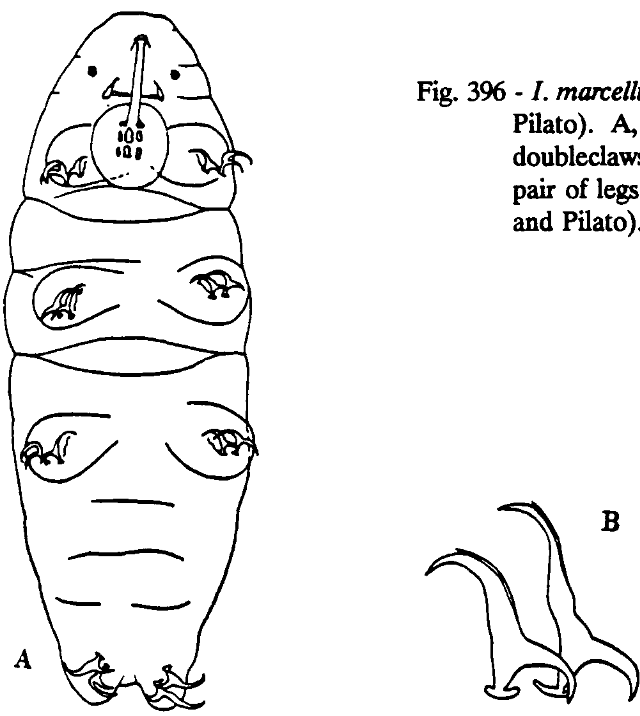


Fig. 396 - *I. marcellinoi* (Binda and Pilato). A, habitus; B, doubleclaws of the 4th pair of legs (from Binda and Pilato).

ISOHYPSIBIUS MIHELCICI (Iharos, 1964) (Fig. 397).
= *Hypsibius* (*I.*) *mihelcici* Iharos, 1964.

Length 165-180μ, colorless, eyes present. Dorsally there are 8 transverse rows of gibbosities: those positioned along the median of the body -- also those unpaired -- are very large and conical, while the others are smaller and hemispherical. The gibbosities are thus arranged: 2 in row 7; 3 in rows 1, 3, 5, 8; 4 in rows 2, 4, 6. Sometimes in the first row the gibbosities may be 4, rather than 3, and in the seventh row 4, rather than 2, as communicated by letter from Dr. Gyula Iharos.

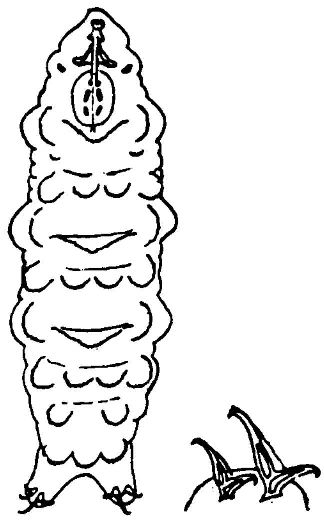


Fig. 397 - *I. mihelcic* (Iharos). Dorsal view and claws of the 4th pair of legs (from Iharos).

Besides gibbosities there is a granular sculpture formed from the lines which outline the reticular mesh.

Pharynx oval with 2 macroplacoids, of which the first is almost twice as long as the second; lacking the microplacoid. Doubleclaws of the *Isohypsibius* type: on the 4th pair of legs the anterior doubleclaws measure 6μ, the posterior 11μ; in this last the principal branch (terminal claws) measure 7.3μ and the basal part 3.7μ.

Lunule absent; on the first three pair of legs there is a cuticular bar. Three oval eggs (55 x 36μ), deposited in the exuvium.

The species was collected at Sarkany-Tal (Alta region of Balaton, Hungary), in moss on dolomite rocks, in India, and later in Istria and Veronese.

ISOHYPSIBIUS MONTANUS (Mihelčič, 1938) (Fig. 398).

Length up to 700μ and more, but often 300-400μ. Eye spots present, cuticle covered dorsally with gibbosities, which are not arranged in regular rows and which have different size between them. The larger gibbosities are scarce in number: those in the dorso-caudal zone are smoother, but change to papillose, especially on the surface facing the back; the last two obvious gibbosities, placed above the 4th pair of legs, or even on them, are covered with tubercles, which have the appearance of nail heads; the remaining legs are smooth. Doubleclaws of all legs of very different size; accessory points have not been observed on the principal branch.

The species is known from Yugoslavia, from Romania and from Austria; it was collected also at an altitude of 1700 and 2700 meters, in moss.

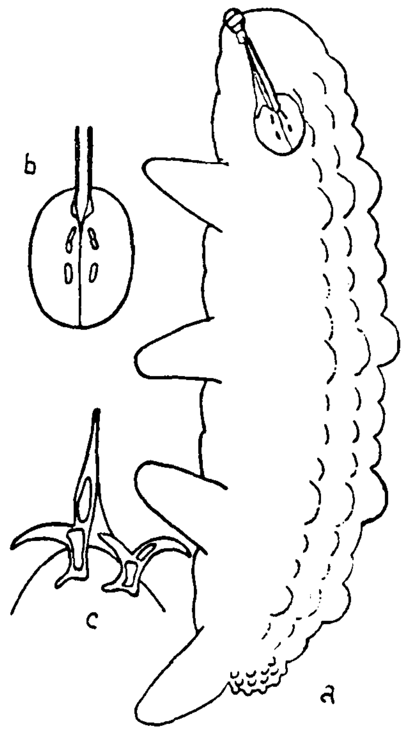


Fig. 398 - *I. montanus* (Mihelčič). a, lateral view; b, pharynx; c, claws of the 4th pair of legs (from Mihelčič).

ISOHYPSIBIUS MYROPS (Du Bois-Reymond Marcus, 1944) (Fig. 399).
= *Hypsibius* (*I.*) *myrops* Du Bois-Reym. Marcus, 1944.

Aquatic tardigrade. Length about 500μ, eye spots absent but -- at their position and in anterior position -- two small globules of fat, having 7μ diameter. Wide buccal aperture and in termino-rostral position, which is not very common in the genus *Isohypsibius* (while it is normal in the genus *Macrobiotus*); peribuccal lamellae absent. Buccal tube of about 4μ in diameter, with appendages in the form of a crest for the muscle insertion; stylets curved. Pharynx oval (length to width ratio equal to 1.3:1) with apophyses almost non-existent and 3 macroplacoids; microplacoid absent. Of the three macroplacoids -- which are slender rods -- the longest is the third (8μ), the shortest the second (5μ); the first (6μ) is a little longer than the second. The two doubleclaws of all legs have different size and their principal branches bear accessory points. They deposit up to 15 smooth and slightly oval eggs in the old cuticle (exuvium).

The species is distinguished from *I. prosostomus* by the little developed apophyses, the absence of eye spots and microplacoid, the more slender macroplacoids and the pharynx somewhat oval (in *prosostomus* the length

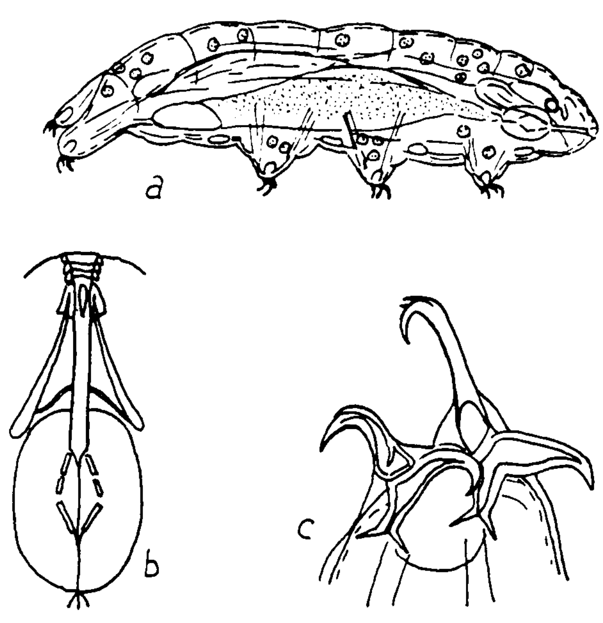


Fig. 399 - *I. myrops* (du Bois-Reymond Marcus). a, lateral view; b, buccal apparatus; c, doubleclaws of the 4th pair of legs (from du Bois-Reymond Marcus, redrawn).

to width ratio is about 1.1 - 1.2:1, that is to say the pharynx is more spherical).

I. myrops was collected in water from various localities in Brazil (State of Sao Paolo).

ISOHYPSIBIUS NEOUNDULATUS (Durante Pasa & Maucci, 1975) (Fig. 400).

= *Hypsibius* (*I.*) *neoundulatus* Durante Pasa & Maucci, 1975.

Size modest (from 180 to 220μ), colorless, eye spots present. The cuticle has a reticular sculpture, very evident, with uniform mesh, indicated by a rather slender design. The dorsal side has flexibility which forms a series of transverse undulations of various thicknesses (from 18 to 24 undulations, along all the dorsum). Besides such undulations there are 6 pairs of gibbosities, all placed in dorsolateral position and precisely:

- a pair of small cephalic gibbosities;
- a pair of large median gibbosities, at the level of the 2nd pair of legs;
- four pair of gibbosities, one for each of the last four undulations of the dorsum.

Mouth in anterio-terminal position. Buccal tube short (30μ, in the holotype, 220μ long), and medium narrow (about 3μ), pharynx short oval, with apophyses and two macroplacoids in the shape of short rods, the first a little longer and constricted at the center. Microplacoid absent.

Claws of the *Isohypsibius* type, rather large and robust, of almost equal size. The two branches of each doubleclaw are of almost equal length. There are no cuticular bars on the legs, near the base of the claws.

The species is very near to *I. undulatus* Thulin, with which it has in common the reticulated sculpture, the undulations of the dorsum, the appearance of the buccal apparatus and the claws. Some difference in the dorso-lateral gibbosities is evident, which are on the contrary constantly absent in *I. undulatus*.

The specimens here described come from a sample of moss on rock in full sunshine, in the vicinity of Uppsala (Sweden). The sample, very rich, contained an abundant population of *Isohypsibius* of the *tuberculatus* group, of which about 2/3 were *I. undulatus* type, 1/3 *I. neoundulatus*. All the specimens examined are clearly recognizable, with or without dorso-lateral gibbosities. It is reasonable to suppose that *I. neoundulatus* represents a mutation (recent probably) of *I. undulatus*. The sympatry of the two forms, without intermediate forms (for example individuals with gibbosities less emphasized, or with smaller number of gibbosities) makes

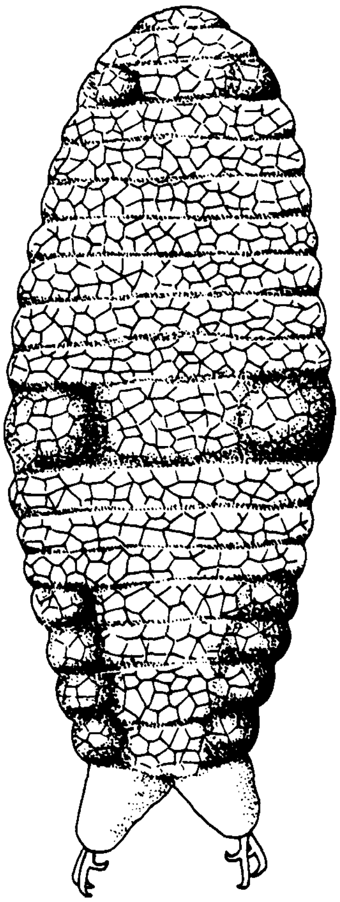


Fig. 400 - *I. neoundulatus* (Durante Pasa and Maucci).

one think that such mutants are intersterile with the non-mutants and that consequently justifies the taxonomic separation, since the specialization is by now complete.

ISOHYPSIBIUS NIPPONICUS (Sudzuki, 1945) (Fig. 401).
= *Hypsibius* (*I.*) *nipponicus* Sudzuki, 1945.

Length 380μ. Buccal aperture rostral. The buccal tube is 39μ long. Pharynx elongated, oval; two elongated macroplacoids and slightly swollen in the posterior half, with a constriction at a third of the length. Microplacoid absent.

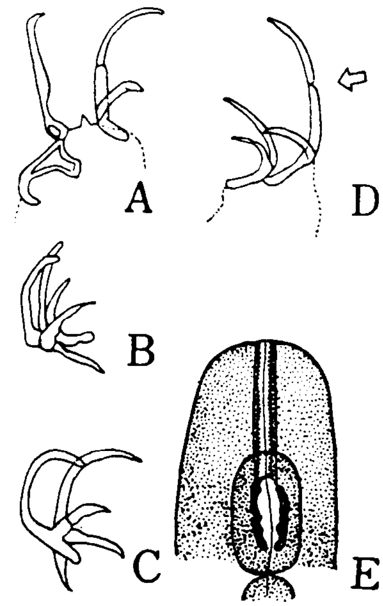


Fig. 401 - *I. nipponicus* Sudzuki. A, B, C, D, doubleclaws of the 1st-4th legs; E, pharynx (from Sudzuki).

Claws of each leg nearly equal in shape and size: the principal branch of the external claw is three times longer than the secondary branch, without accessory points; the secondary branch is strongly curved. On the first legs there is a slender thickening between the claws.

This description is certainly very summary, but the identification of this species is facilitated by the fact that the author considers it "very near, from the shape of the placoids" the following species: *Diphascon belgicae*, *Macrobiotus ferdinandi*, and *Isohypsibius stenostomus* (sic!).

I. nipponicus was found in interstitial environment, on the shore of the Tana River, 28 km from its mouth in the bay of Tokyo.

ISOHYPSIBIUS NODOSUS (Murray, 1907) (Fig. 402).
= *Hypsibius* (*I.*) *nodosus* Murray, 1907.

Length up to 500μ and more, often of yellow color, with black eye spots. The cuticle has, dorsally and its sides, numerous papillose gibbosities, which sometimes are separate between them, while other times touching at their bases: they are arranged in equal numbers within each of the 7 transverse rows (Marcus), symmetrical with regard to the dorsal median line, which remains then, free of gibbosities; in all the transverse rows there are 6 gibbosities, with exception of the last caudal row, which only has 4. The cuticle between successive gibbosities may be smooth, or else finely granulated. The buccal tube has appendages of muscle insertion in the shape of crests; the oval pharynx -- or short oval -- contains rather elongated apophyses and 2 macroplacoids, of which the first is about twice as long as the second; lacking microplacoid.

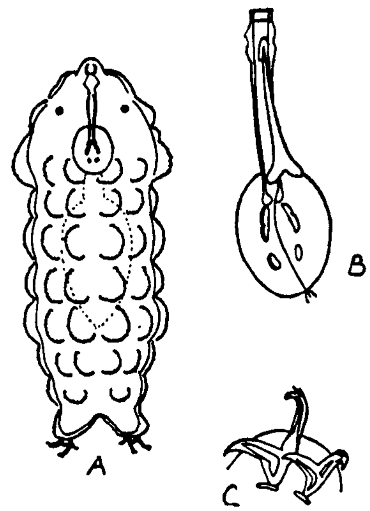


Fig. 402 - *I. nodosus* (Murray). A, dorsal view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs (from Marcus, redrawn).

All the doubleclaws are rather small (30μ in individuals of larger size) and has the principal branch approximately at a right angle with the secondary branch; the two branches differ a little in length and these principals bear two accessory points; at the base of the claws there are small smooth lunules. On the first three pair of legs, near the claws is found a cuticular bar.

At the base of both the doubleclaws there is a transverse cuticular thickening (Fig. 402 C). Deposited in the exuvium up to 9 colorless eggs, or salmon red, or reddish-brown, or brownish.

The species was collected in many localities in Europe (also in Italy), in Java (at 3,000 m altitude), Lombok, eastern and western Africa, Figi and Macquarie Islands, New Zealand, U.S.A., Bolivia (at 1,000-2,000 m altitude), Argentina, etc.

Typ. loc.: Terra del Capo.

ISOHYPSIBIUS NOVAEGUINEAE (Iharos, 1967) (Fig. 403).
= *Hypsibius* (*I.*) *novaeguineae* Iharos, 1967.

Length 160-177μ, colorless, eye spots present. The cuticle has a reticular design of the sculpture of dense and rather coarse mesh; dorsally there are 9 transverse rows of gibbosities; they also are covered with larger granules (2-2.4μ), which appear clear in higher position of the microscope tube and dark in the lower position. The gibbosities are thus arranged in each row: 3 in rows 1, 3, 5, 7, 8, 9; 5 in rows 2, 4, 6.

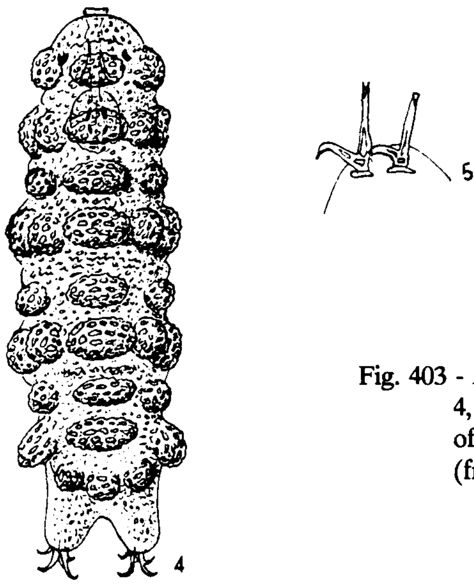


Fig. 403 - *I. novaeguinea* (Iharos). 4, dorsal view; 5, claws of the 4th pair of legs (from Iharos).

Pharynx short oval (15.5 x 13μ) with 2 macroplacoids; microplacoid absent. Doubleclaws of all claws of almost equal size: on the 4th pair of legs the external doubleclaws measure 7.3μ, the internal 6.5μ; the branches of the claws are very slender, lunule present. Exuvia have been observed with 3 ellipsoid eggs (50 x 25μ).

I. novaeguineae was collected in moss on tree trunks from Kaindi Mountains (New Guinea).

ISOHYPSIBIUS PAPILLIFER (Murray, 1905) (Figs. 404, 405, 406).
= *Hypsibius* (*I.*) *papillifer* Murray, 1905.

Length up to 250μ, colorless, eye spots present. The cuticle is covered -- dorsally, laterally, and at the base of the legs -- with isolated mammillary gibbosities, with wide proximal parts, often hemispherical, and terminated at the apices in an appendage in the shape of a spine, sometimes distally rather rounded. Stylets robust and curved; pharynx short oval, nearly spherical, with 3 macroplacoids of about equal size (short rounded rods, almost oval granules, length about twice the width); microplacoid absent. Doubleclaws of all legs of size not much different.

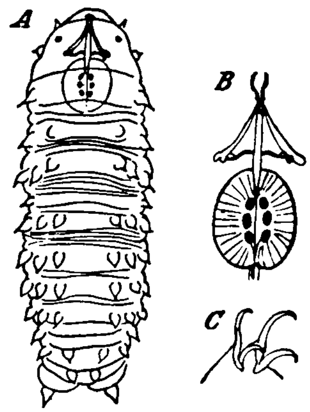


Fig. 404 - *I. papillifer* (Murray). A, dorsal view; B, buccal apparatus; C, doubleclaws (from Marcus).

From the single old figure of the claws (Fig. 404C), it is not possible to deduce the belonging of the species to the genus *Isohypsibius*: the authority to that subgenus on the part of Thulin (1928) and Marcus (1936) was based on the examination of the doubleclaws of *I. papillifer bulbosus*, which is a variety described recently.

Of *I. papillifer* are known reports in many localities from Europe (including Italy), from Brazil, Australia, and New Zealand (Typ. loc.: Scotland).

I. papillifer bulbosus, described by Marcus, 1928, as *Hypsibius* (*I.*) *papillifer* forma *bulbosa*, presents the following characters:

Length about 200μ; as in *I. papillifer* type exists eye spots, the pharynx is short oval, the 3 macroplacoids are short rounded rods, almost oval granules -- of about equal length -- and the microplacoid is absent. The mammillary appendages of the cuticle have however large hemispherical

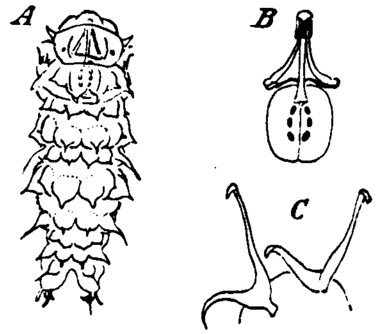


Fig. 405 - *I. papillifer bulbosus* (Marcus) A, dorsal view; B, buccal apparatus; C, doubleclaws (from Marcus).

bases, of which the apices divide into a papilla in the shape of a nipple, often elongated and spiniform. The gibbosities are arranged according to transverse rows: in the rostral region and in the median of the dorsum, they are 6 in number per each row and with their bases in contact; in the caudal region -- posterior to the 3rd pair of legs -- the gibbosities are only 4 per row; the bases of the 4th pair of legs bear a large sharpened papilla with its proximal part hemispherical. The internal and external doubleclaws of all legs are a little different and the angle included between their principal and secondary branches is about 90μ.

The subspecies was collected in Italy, Czechoslovakia, Germany, Scotland, Ireland, and Brazil. Typ. loc.: Scotland and Ireland.

I. papillifer indicus is a further subspecies (Iharos, 1969):

Length 210-230μ, colorless and transparent, eyes present. Dorsally and laterally there are mammillary gibbosities, with a large hemispherical basal part, at the center of which arises a large and wide spine, often very curved. These ornamentations are arranged in 9 transverse rows and becoming longer in a rostro-caudal sense. One other appendage of this type is caudally present, above and between the 4th pair of legs. In each transverse row the ornamentations are arranged as follows: 4 in rows 1, 3, 5, 7, 8, 9; 6 in rows 2, 4, 6.

Pharynx a little longer than wide (22 x 17μ) with 2 macroplacoids, of which the 1st is twice the length of the 2nd (rod-shaped); microplacoid absent. Buccal tube 30.5μ long, with 2μ diameter. Doubleclaws of all legs having little different size; branches of the claws long and slender (15μ for the external doubleclaws, 12μ for the internal).

An exuvium has been observed with 6 oval eggs of rose color (50 x 37μ).

This variety -- according to the author -- is near to *I. papillifer* and to *I. papillifer bulbosus*, but differs by having 2 macroplacoids of rod-shape (instead of 3 short rounded placoids), by having appendages in caudal position and by being devoid of appendages in the cephalic region.

I. papillifer indicus was collected in moss on soil, near the region of Mahableswar (western Ghati, India).

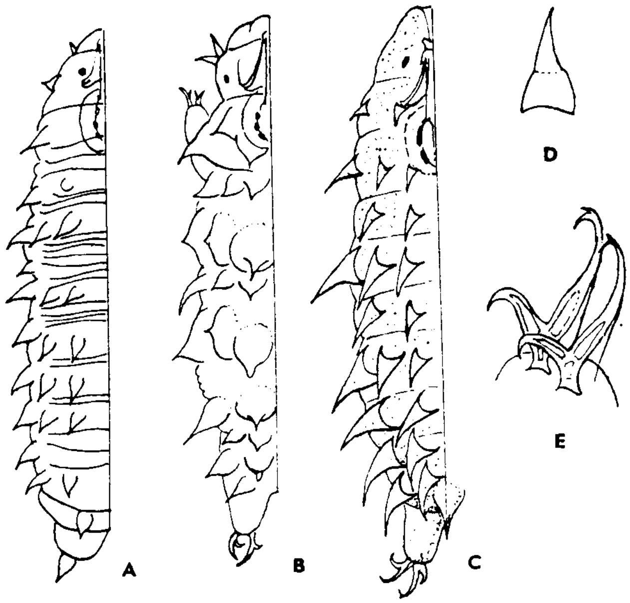


Fig. 406 - Typical form and varieties of *I. papillifer* (Murray). A, *I. p. papillifer* (from Marcus); B, *I. p. bulbosus* (from Marcus); C, *I. p. indicus* (Iharos); D, details of the spinous cuticular appendages of *indicus*; E, doubleclaws of the 4th pair of legs of *indicus* (from Iharos).

We have intentions to keep, for these subspecies, the name proposed by the authors. It is necessary however to observe that such name ("*indicus*") is not valid, in the sense of Article 57 of the International Code of Zoological Nomenclature, in as much as it is a more recent homonym of *I. indicus* (Murray, 1907).

We have not reserved to modify of our initiative the subspecific name, either to eventually abandon the initiative of the same author, or because, it is not all that certain of the assignment of *I. indicus* to the genus *Isohypsibius*, others may place in doubt the subspecific rank of *I. papillifer indicus*.

ISOHYPSIBIUS PAPPI (Iharos, 1966) (Fig. 407).
= *Hypsibius (I.) pappi* Iharos, 1966.

Length 170-400μ, colorless or clear yellowish-green, eyes present. The cuticle has a sculpture of reticular pattern. There are 10 transverse rows of hemispherical gibbosities, as follows: 2 in rows 1 (over the eyes) and 10; 4 in rows 2, 4, 6, 8, 9; 6 in rows 3, 5, 7. There are also smaller gibbosities (tubercles) and precisely: 2 between rows 2-3, 4-5, 6-7 and between rows 5-6 and 7-8. There are however papillae of smaller size between the rows 2-3 and from 4 to 9, positioned laterally and sometimes also dorsally (2 or 4 papillae for each transverse row). In the first half (rostral) of the cephalic region, in the proximity of the buccal apparatus, there is a small papilla on each side.

Pharynx elongated oval (24.8 x 18μ in a specimen of 255μ), containing 2 macroplacoids, of which the first is longer than the second; microplacoid absent. On the dorsal surface of the 4th pair of legs there is a small gibbosity. Doubleclaws of each leg of different size (on the 4th pair of legs the external doubleclaws measure 12μ, the internal 9.5μ).

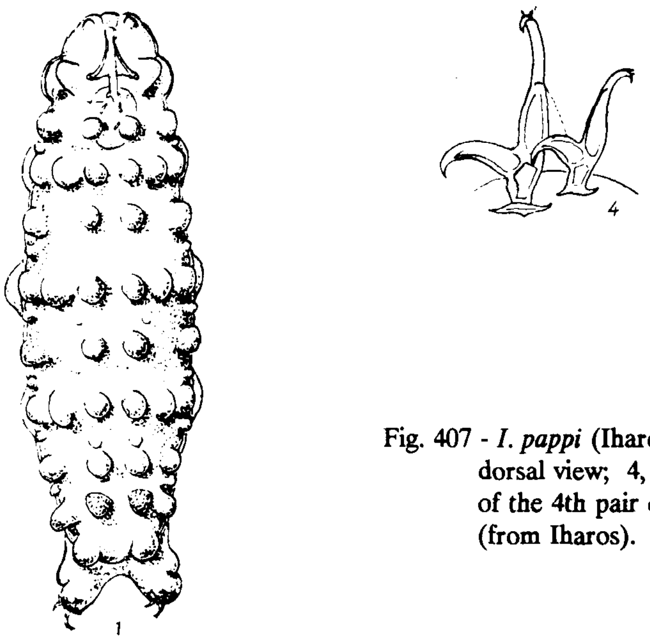


Fig. 407 - *I. pappi* (Iharos). 1, dorsal view; 4, claws of the 4th pair of legs (from Iharos).

At the base of the claws there is a large smooth lunule and, on the first three pair of legs there is a cuticular bar. Eggs (from 4 to 6) smooth, oval, deposited in the exuvium.

I. pappi was collected in various localities from Hungary (Csòt, Herend, Nemesvàmos and Uszabànya) and from Italy (Lignano, Apuane Alps, Sicily, Egadi Island, Sardinia).

ISOHYPSIBIUS PAUPER (Mihelčič, 1971) (Fig. 408).
= *Hypsibius* (*I.*) *pauper* Mihelčič, 1971.

Length 220-280μ, colorless, eyes absent. Cuticle sculptured, but without gibbosities. The sculpture, with microscope tube high, appears as small dark depressions on clear background, while with tube low has the

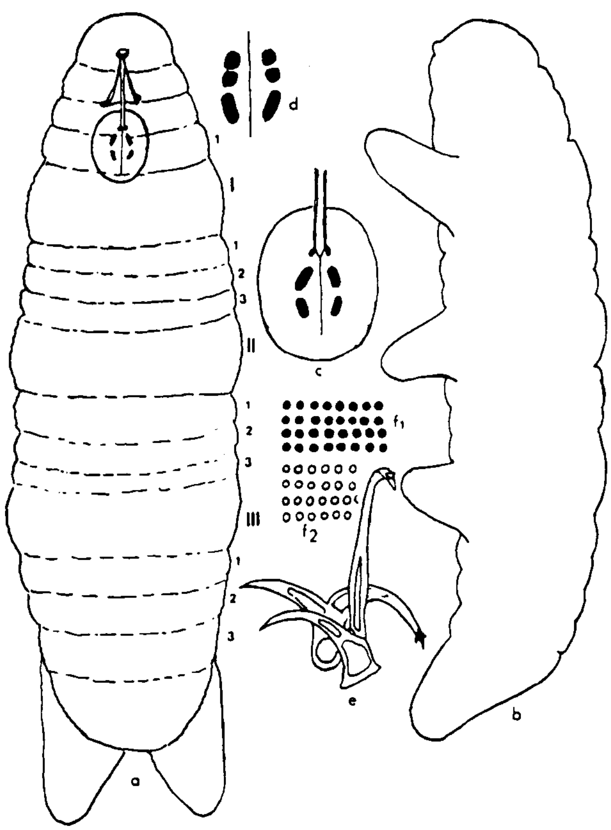


Fig. 408 - *I. pauper* (Mihelčič). a, dorsal view; b, lateral view; c, pharynx with 2 macroplacoids; d, *idem* with 3; e, claws; f_1, sculpture with tube high, and f_2, with tube low (from Mihelčič).

appearance of clear granules (*not* surrounded by polygons) on dark background. The elements of the sculpture outline design of similar size and shape, and are regularly arranged on the surface of the dorsum and on the sides. Some of the segments of the body have thickened cuticle and then projections laterally.

Buccal tube very straight, scarcely as long as the pharynx, which is wide oval; the apophyses are small rounded granules; in dorsal view one sees 2 short macroplacoids of about equal length, while in lateral view the macroplacoids appear to be 3.

The species was observed at Amlach, near Lienz (Tirolo, Austria) in a thin layer of soil under moss and lichen.

ISOHYPSIBIUS PILATOI (Durante Pasa & Maucci, 1979) (Fig. 409).
= *Hypsibius* (*I.*) *pilatoi* Dur. Pasa & Maucci, 1979.

Length from 190 to 270μ, colorless, eyes absent. The cuticle is sculptured with a rather coarse reticular design, with large mesh. There are dorsal gibbosities, arranged in 10 rows as follows: rows 1, 2, and 10, 3 gibbosities each; rows 3, 4, 5, 6, and 7, 5 gibbosities each; row 8, 4 gibbosities; row 9, 2 gibbosities. Characteristic is the even number of gibbosities in the penultimate and ultimate rows, while all the others are unpaired, that is there is a dorso-median gibbosity.

Buccal tube medium width, oval pharynx, with apophyses, and two macroplacoids, of which the first is strongly constricted in the middle. Microplacoid absent. Claws almost equal on each leg. Lunules absent, however a cuticular bar is present on the first three pair of legs.

The species was collected in moss on rock in the sun, near Kvalsund (northern Norway).

ISOHYPSIBIUS PRATENSIS (Iharos, 1964) (Fig. 410).
= *Hypsibius* (*I.*) *pratensis* Iharos, 1964.

Length 170-185μ, colorless, eye spots present. Dorsally there are 9 transverse rows of hemispherical gibbosities, thus arranged: 2 in rows 1, 6; 4 in rows 2, 4, 5, 8, 9; 6 in rows 3, 7. The cuticle is very finely granulated and displays a reticular design.

Oval pharynx with 2 macroplacoids, of which the first is longer than the second; microplacoid is absent. Doubleclaws of a same leg of different size, small and slender; on the fourth pair of legs the anterior

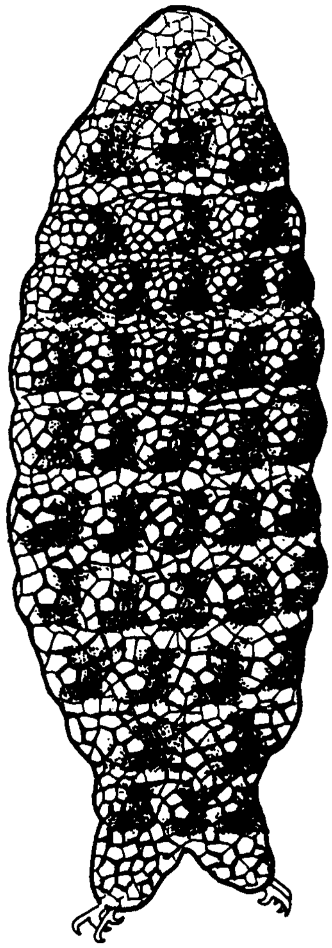


Fig. 409 - *I. pilatoi* (Durante Pasa and Maucci).

doubleclaws measure 6.5μ, the posterior 9μ. Eggs smooth.

I. pratensis was collected in moss on soil at Cser-Tal (Keszthelyer Mountains, Hungary).

ISOHYPSIBIUS PROSOSTOMUS Thulin, 1928 (Fig. 411).

Length of the adults very variable, from 270 to 470μ; colorless, eyes present. The cuticle is almost always smooth, but is faintly granulated in some rare specimens. Buccal tube medium width, of which the diameter is about 3-5μ; pharynx oval, with length to width ratio of 1.2-1.3:1, containing apophyses, 3 macroplacoids and microplacoid; the first

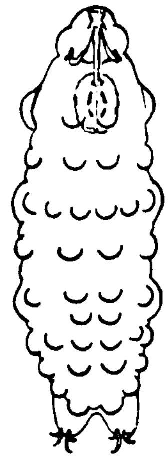


Fig. 410 - *I. pratensis* (Iharos). Dorsal view and doubleclaws of the 4th pair of legs (from Iharos).

macroplacoid is almost in contact with the apophyses, the second is about as long as the first and touching it, the third is a little shorter than the first plus the second. The two doubleclaws of each leg are of very different size; the principal branch of the external doubleclaws bears two small accessory points, is long (about 18-21μ) and more slender than the secondary branch. The characteristics of this species, which renders easy identification and which was so clearly described by Cuénot, is the

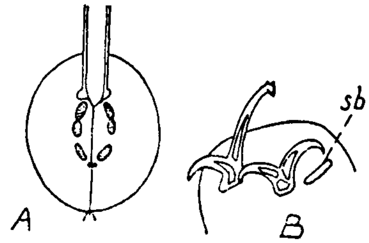


Fig. 411 - *I. prosostomus* Thulin. A, pharynx; B, claws of the third leg; sb, cuticular bar.

presence -- on the first three pair of legs -- of a cuticular thickening in the shape of an oblique bar, which starts about at the base of the smaller doubleclaw (Fig. 411, B); treatment with KOH, or inclusion in Faure liquid, or else in polyvinyl lactophenol, renders the bar even more visible. Eggs smooth, oval (52-70μ x 39-45μ) or sometimes spherical, deposited in the exuvium in various numbers, up to 13.

A species very similar to *I. prosostomus* -- to which Cuénot united it -- is *I. schaudinni*; the principal differences are disclosed in the discussion of this last species.

I. prosostomus is, at least in Europe, the most common and wide spread species of *Isohypsibius*. It is cited from many European localities, and also from U.S.A. and Java. Typ. loc.: Lapland and southern Sweden.

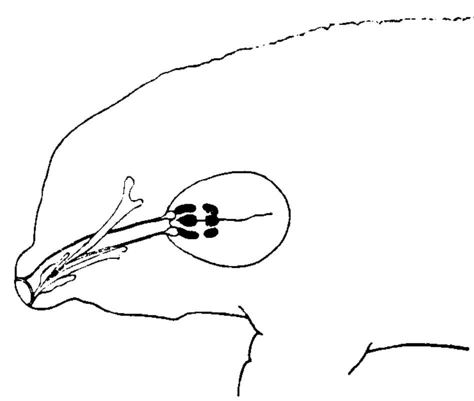
ISOHYPSIBIUS PSEUDOUNDULATUS (Da Cunha & Do Nascimiento Ribeiro, 1946) (Fig. 412).

= *Hypsibius* (*I.*) *pseudoundulatus* De Cunha & Do Nasc. Rib., 1946.

Length up to 405μ; dorsal cuticle with "rings" and poorly developed undulations, less regular than in *I. undulatus*. Eye spots present; the animal has yellowish color. Buccal tube wide, pharynx oval with well developed apophyses and 2 macroplacoids, of which the 1st almost twice the length of the 2nd. Microplacoid absent.

The species very much resembles *I. undulatus*, but the authors consider it distinguished from it by the larger size, by the different relative length of the macroplacoids, and by the less pronounced dorsal undulations. It was collected in moss at Pumba Loge (Angola).

Fig. 412 - *I. pseudoundulatus* (Da Cunha & do Nascimento Ribeiro).



ISOHYPSIBIUS PULCHER (Mihelčič, 1971) (Fig. 413).
= *Hypsibius* (*I.*) *pulcher* Mihelčič, 1971.

Aquatic. Length 300-500μ, eye spots present, rounded. Cuticular sculpture of round granules, clear, very small, which with high magnification appears connected to smooth, clear and describing irregular mesh (square, pentagonal, or hexagonal), which contains a dark field.

The buccal tube is slightly curved in a S, with diameter of 2 to 3μ, and is as long as the pharynx; pharynx oval, with small apophyses and two macroplacoids (slender rods) of which the first is a third longer than the second. Microplacoid present.

Legs short; doubleclaws of each leg not much different from each other in shape and length; basal part short, robust branch; the principal branch of the external claws has the distal extremity elongated and finely dotted; the secondary branch is a little shorter; lacking the accessory points.

The species was collected in water, in Sweden.

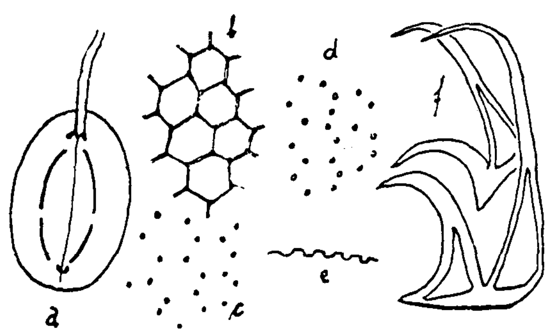


Fig. 413 - *I. pulcher* (Mihelčič). a, pharynx; b, with high magnification; c, with tube low; d, with tube high; e, sculpture in lateral view; f, claws of the 4th pair of legs (from Mihelčič).

ISOHYPSIBIUS RENAUDI (Ramazzotti, 1972) (Fig. 414).

Aquatic. Length 210-340μ, colorless, cuticle smooth, large eye spots. Buccal tube with 2.5-3.4μ diameter, rostrally straight, then with a ventral curve before it enters the pharynx; oval pharynx, with apophyses and 2 macroplacoids (rounded rods) which both have a very clear constriction, in the first at about half its length, in the second more terminal (this last constriction may -- only rarely -- be lacking); the first macroplacoid is very near to the apophyses and length little less than twice the second.

The characteristics more evident of this species -- which allow quick identification without difficulty -- is the enormous length of the principal branch of the external doubleclaw, especially on the 1st pair of legs: this branch may attain the length of 40μ (however never less than 25-35μ), is very slender, to such an extent as to have sometimes the appearance of a cirrus; because of its fragility it often is broken or contorted, and is very curved. Lacking the accessory points. The external claw may closely resemble the claws of the "*Hypsibius*" type. However the internal claw, of normal size and structure, is indisputably of the "*Isohypsibius*" type. Characters of this genus, are also the attachment appendage of the stylet muscles, in the shape of a crest.

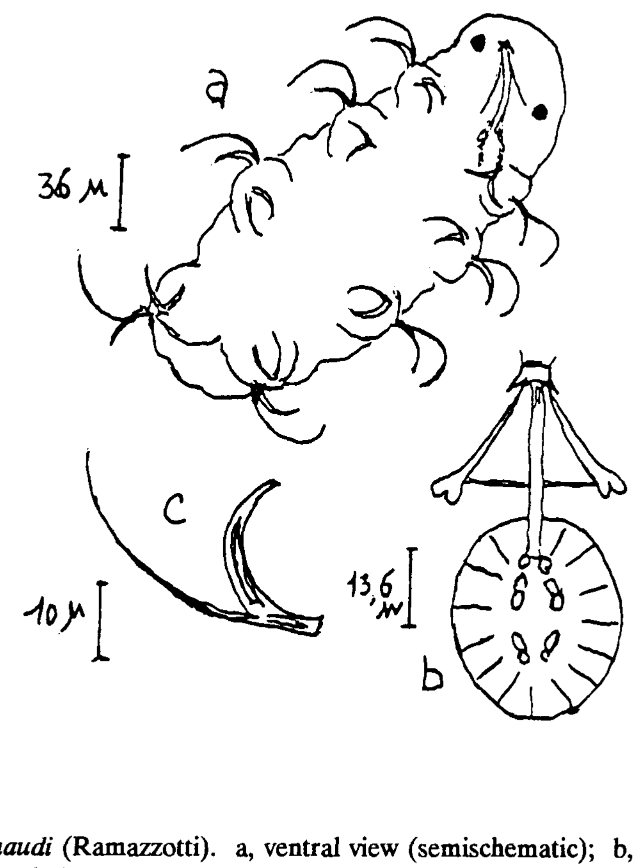


Fig. 414 - *I. renaudi* (Ramazzotti). a, ventral view (semischematic); b, buccal apparatus; c, external claws of the doubleclaws of the 2nd pair of legs (from Ramazzotti).

The species was found in interstitial environment in large sand mixed with fine sand, at the mouth of a stream of water in the Archipelago of the Kerguelen Islands.

ISOHYPSIBIUS RETICULATUS Pilato, 1973 (Fig. 415).

Length up to 380μ, colorless, with eye spots. The cuticle has an elegant reticular sculpture with mesh of different shape and size in the different regions of the body. In the anterior portion at the first pair of legs the mesh are very small (diameter less than 1μ) and have polygonal shape with straight sides; continuing toward the posterior the mesh becomes larger (up to 3.8μ in diameter at the caudal) and the sides of the polygons become bent.

Buccal tube short and rather wide. Appendages of muscle insertion of the stylets in the shape of crests. Pharynx slightly oval, with apophyses well developed and two rod-shaped macroplacoids, of which the first, longer than the second, has a central constriction. Microplacoid absent.

The doubleclaws of the first pair of legs are more developed than the second and the third. The basal portion of all the claws is rather short and strongly reduced near its end; the principal branch of all the claws is provided with small accessory points, difficult to see. At the base of the claws there is a cuticular thickening explainable as a lunule. On the first three pair of legs there is a cuticular thickening in the shape of an undulating bar.

I. reticulatus was found in aquatic environment, in Simeto River (Sicily). An example of which having some differences not important in the design of the sculpture may be attributed to this species, was later found by Maucci, near Kanfanar (Istria), in moss in the sun.

ISOHYPSIBIUS RONCISVALLEI (Binda & Pilato, 1969) (Fig. 416).
= *Hypsibius* (*I.*) *roncisvallei* Binda & Pilato, 1969.

in polygonal shape, which gives it a reticular pattern; the dots increase in size slightly in a rostro-caudal sense: the largest is found in correspondence with the caudal row of gibbosities and reaches a diameter up to 2.4-2.7μ. Posteriorly to this row of gibbosities the dots become smaller.

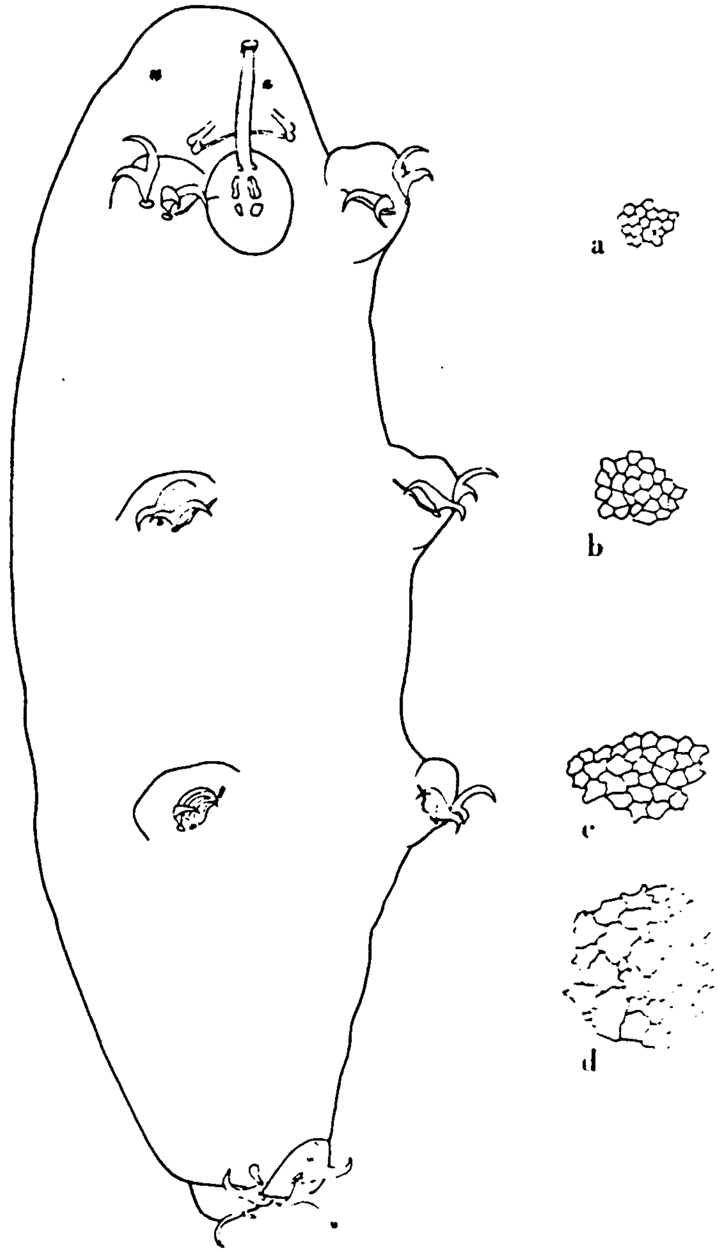


Fig. 415 - *I. reticulatus* Pilato. a, b, c, d, appearance of the sculpture of the cuticle at various levels of the body (Pilato).

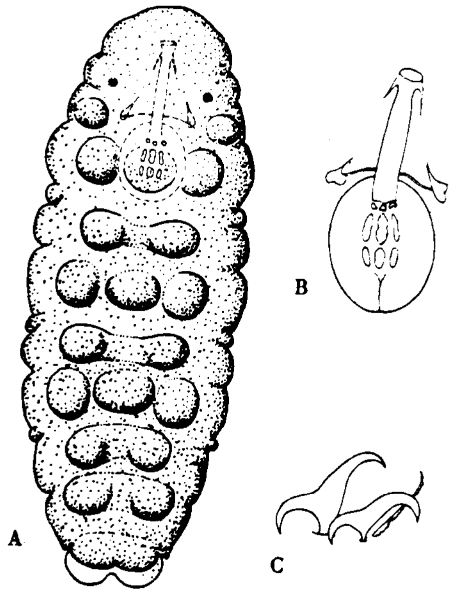


Fig. 416 - *I. roncisvallei* (Binda & Pilato). A, dorsal view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs (from Binda & Pilato).

Dorsally there are 8 transverse rows of large gibbosities, they are however clear and thus arranged: 2 gibbosities in rows 1, 3, 5, 7, 8, and 3 in rows 2, 4, 6. The lateral gibbosities are hemispherical, while the median of rows of three (2, 4, 6) are conical. Between rows 2 and 3, and between rows 4 and 5, and between 6 and 7 there is a small dorsolateral gibbosity on each side.

Along the dorsolateral line of the body there is a longitudinal fold, which clearly separates the dorsal surface, provided with gibbosities, from the lateral regions.

The buccal tube (Fig. 416, B) is 32μ long and about 5μ wide in an individual of 295μ; it has appendages for muscle insertion of the stylet in the shape of crests. While in the same individual the oval pharynx measures 32μ long and 26μ wide (or length to width ratio is about 1.23:1). Present are bifurcated apophyses and 2 macroplacoids (rod-shaped): the first, with profound constriction, is almost twice as long as the second (respectively 8μ and 5μ).

Isohypsibius type doubleclaws: on the 4th pair of legs in a specimen of 295μ, the principal branch of the external doubleclaw is 14μ long; accessory points have not been observed. On the first three pair of legs there is medially a cuticular bar of about 11μ.

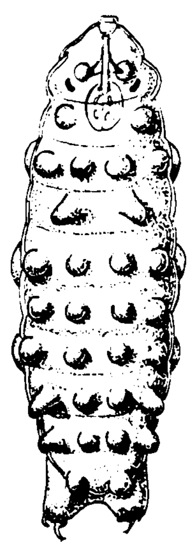
The species was collected in beech soil at Portella Mandrazzi in Peloritani (Sicily).

ISOHYPSIBIUS RUDESCUI (Iharos, 1966) (Fig. 417).
= *Hypsibius* (*I.*) *rudescui* Iharos, 1966.

Length 150-225μ, clear greenish-yellow color, eye spots present. Dorsally there are 10 transverse rows of gibbosities, of which the two dorsal in row 4 and the lateral in rows 8 and 9 are higher than the remaining. The gibbosities are thus arranged in each row: 2 in rows 1, 2, 4, 10; 4 in rows 3, 5, 6, 7, 8, 9.

Oval pharynx (25 x 20μ) with 2 macroplacoids, the first longer than the second; microplacoid absent. Doubleclaws of all legs robust and of different size: on the 4th pair of legs the external doubleclaws measure 11μ, the internal 9.5μ. Eggs not found.

The species lives in moss on soil, exposed to the sun for almost the whole day and subject to frequent desiccation: it was collected on Bagȍ Mountains, in the region of Nemesvàmos (Hungary).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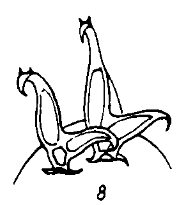
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Fig. - *I. rudescui* (Iharos). 7, dorsal view; 8, doubleclaws of the 4th pair of legs (from Iharos).

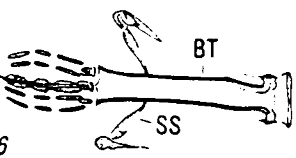

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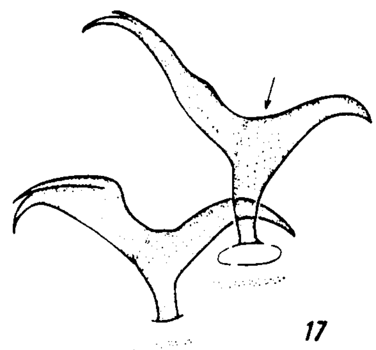
Fig. - *I. saltursus* Schuster, Toftner & Grigarick. 16, buccal apparatus; 17, doubleclaws (from Schuster, Toftner & Grigarick).



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ISOHYPSIBIUS SALTURSUS Schuster, Toftner & Grigarick, 1978 (Fig. 418).

Length up to 710μ; colorless, cuticle smooth or slightly wrinkled; eye spots absent. Mouth not surrounded by lamellae. The buccal tube medium width (length 33μ, width 7μ, in an example of 561μ); pharynx oval, with large elongated apophyses and three macroplacoids of rod-shape, the first two very close, the third farther away; the second macroplacoid is the shortest, the first is the longest; microplacoid absent.

Claws large, with basal part narrowed at the proximal end, and massive branch at their junction, and then rapidly attenuating toward the apices; robust accessory points, especially on the principal branch of the internal claw. The original description did not mention lunules, but they are present, however not very pronounced, and are particularly large on the 4th pair of legs. Eggs smooth, deposited in the exuvium.

I. saltursus has been found only at Pope Beach, on Lake Tahoe, in California.

ISOHYPSIBIUS SARACENUS Pilato, 1973 (Fig. 419).

Size up to 254μ, colorless, eyes absent, cuticle smooth. The mouth opens in an anterio-ventral position and is lacking buccal lamellae. Buccal

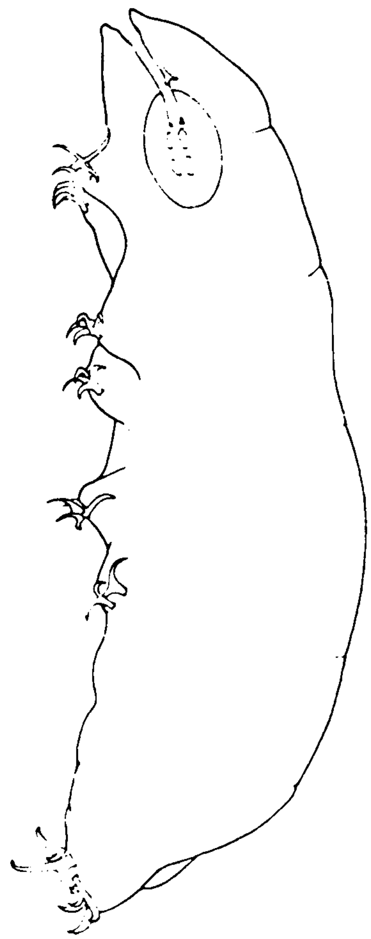
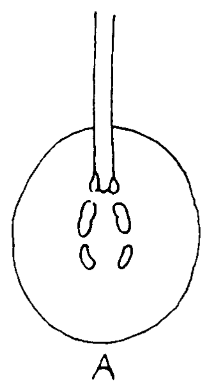


Fig. - *I. saracenus* Pilato
(from Pilato).



tube 26μ long and 5μ wide (in an example of 210μ); insertion appendages of the stylet muscles in the shape of crests. Pharynx very large, elongated oval, with apophyses and two macroplacoids of rod shape, of which the first, which is longer than the second, has a central constriction. Microplacoid absent.

The doubleclaws of each leg are rather different from each other. The basal portion is very long and narrow, especially on the external claws, and the principal branch of this claw is longer and much more narrow than the corresponding of the internal claw. The accessory points are clearly visible on the principal branch of the claws of the 4th pair, less evident on the other claws. There are not lunules present and lacking on all the legs whatsoever cuticular thickening.

The species is aquatic, and was found in the stream of Saracena, near Maletto (Sicily) and later at Ceraino, near Verona (Adige).

ISOHYPSIBIUS SCHAUDINNI (Richters, 1909) (Fig. 420).
= *Hypsibius* (*I.*) *schaudinni* Richters, 1909.

Length up to 368μ, eye spots present. Buccal tube having diameter of about 3μ, with appendages in the shape of crests for muscle insertion. Pharynx short oval, in which there are apophyses, three macroplacoids (oval granules) of increasing size in rostro-caudal sense and small microplacoid, which may be lacking. The two doubleclaws of each leg have different length, with principal and secondary branches united very near the base: on the 4th pair of legs the principal branch of the external doubleclaws is about 20μ long. Smooth eggs (1-3), oval, with largest axis of 70-75μ, deposited in the exuvium.

It is certainly very difficult, on the basis of the description to distinguish *I. schaudinni* from the more common *I. prosostomus*. The principal differences seem to be:

-- in *prosostomus* the buccal tube is straight and the buccal aperture is terminal (as in *Macrobiotus*), while in *schaudinni* the buccal aperture is positioned more ventrally, as usually occurs in *Hypsibius*;

-- in *prosostomus* the first two macroplacoids have about equal length and the third is longer, while in *schaudinni* the macroplacoids are of progressively increasing length from 1st to 3rd;

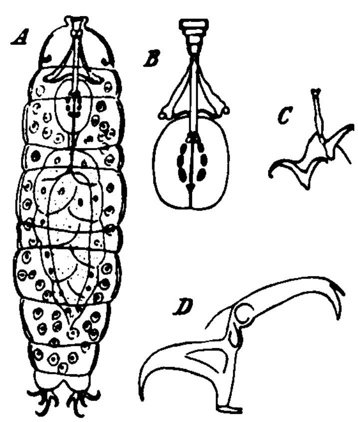


Fig. 420 - *I. schaudinni* (Richters). A, dorsal view; B, buccal apparatus and pharynx; C, doubleclaws; D, posterior doubleclaws of the 2nd pair of legs, after compression (from Marcus).

-- in *prosostomus* the pharynx is somewhat more elongated (length:width ratio = 1.2-1.3:1) than in *schaudinni* (length:width ratio = 1.1-1.2:1).

It is very doubtful that these differences may have an actual taxonomic value, and in fact Cuénot (1932) united the two species into one. Nevertheless an example, discovered at Leinì (Piemonte) and others from Aosta Valley having all the characteristics of *I. schaudinni*, but substantially not distinguishable with certain from *I. prosostomus* are notable for the absence of the cuticular bar on the first three pair of legs. These characteristics can therefore constitute a valid taxonomic difference (the cuticular bar on the legs, for the species that possess it, seems to be an absolutely constant character).

I. schaudinni -- found either in water, or in submerged moss, or in moss subject to desiccation -- is cited from numerous European localities, the Spitzbergen archipelago, Greenland, eastern Africa, India, and South America. One should not however reject any of these citations or from references instead of the more common *I. prosostomus*.

Typ. loc.: Spitzbergen Island.

ISOHYPSIBIUS SCULPTUS (Ramazzotti, 1962) (Fig. 421).
= *Hypsibius* (*I.*) *sculptus* Ramazzotti, 1962.

Length about 200μ, colorless. The cuticle is sculptured and has an extremely fine granulation, diffuse everywhere, even on the ventral surface. The buccal tube is straight and its external diameter is about 2.5μ in a tardigrade of 200μ. Always for an individual of this size the pharynx -- which contains two macroplacoids -- measures 30 x 25μ; the first macroplacoid (4.9μ) is a little longer than the second (4μ) and has a slight median constriction; the microplacoid is absent.

The doubleclaws of each of the first three pair of legs have almost equal size; on the 4th pair of legs the external doubleclaw is a little larger than the internal; note that the appearance of the doubleclaws varies greatly according to the angle viewed. On the fourth pair of legs of an individual of 200μ, the length of the principal branch and that of secondary of the doubleclaws -- measured where they divide at the common base -- may be approximately equal and similar to 7.5μ for the external doubleclaw and 6.3μ for the internal. Eggs unknown.

I. sculptus is distinguished from *I. baldii* Ramazzotti by the different sculpture that forms a reticulated design, it is besides aquatic.

The species was present -- only with few individuals -- in a lichen on

Fig. 421 - *I. sculptus* (Ramazzotti). A, pharynx; B, C, doubleclaws of the 4th pair of legs.

the bark of *Nothofagus* in the Nahuelbuta Cordillera (Chile) at 1,100 m altitude.

ISOHYPSIBIUS SELLNICKI (Mihelčič, 1962) (Fig. 422).
= *Hypsibius* (*I.*) *sellnicki* Mihelčič, 1962.

Length 270-290μ, transparent, with cavity globules of rose or orange-rose color; eyes absent. The cuticle is dorsally and laterally sculptured in the caudal region, smooth on the contrary on all the more rostral zones of the body; the sculpture is composed of a fine uniform punctation (granulation), between which are some small irregularly sparse conical or hemispherical tubercles.

The buccal aperture is ventral, the tube is very narrow (diameter between 1 and 2μ); the pharynx is slightly oval, with length to width ratio of about 1.2:1 and contains two macroplacoids in the shape of rounded granules, of which the first is barely a little longer than the second; the row of the macroplacoids does not caudally reach the middle of the pharynx. Microplacoid absent. Apophyses smaller than the second macroplacoid and rounded.

The fourth pair of legs has dorsally a rounded bulge (not a true and proper gibbosity). Doubleclaws *Isohypsibius* type, robust either internal, or

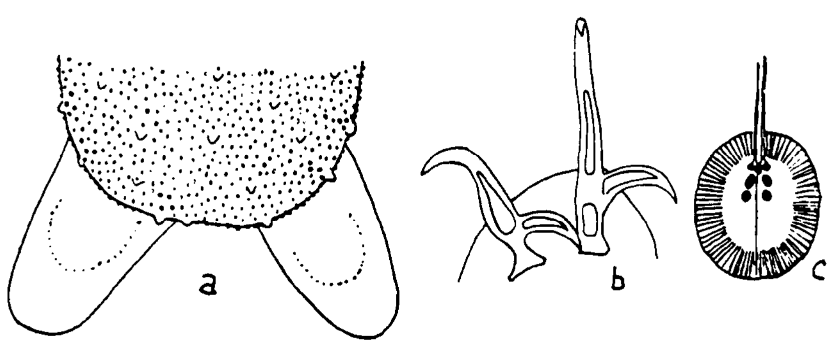


Fig. 422 - *I. sellnicki* (Mihelčič). a, dorsal view of the caudal region; b, doubleclaws of the 4th pair of legs (from Mihelčič).

external, but of different shape. Eggs smooth, deposited in the exuvium in numbers of three.

The species was observed in the lichens *Usnea barbata* and *Ramalina fraxinea* at St. Johann in Walde (Osttirol-Austria).

ISOHYPSIBIUS SEPTENTRIONALIS Thulin, 1928 (Fig. 423).

Length up to 200μ, colorless, eye spots present, but poorly evident. There are present six transverse rows of gibbosities, arranged as follows: row I (corresponding to the 1st pair of legs), 3 gibbosities, plus two small dorso-lateral gibbosities, a little more forward to them; row II, 5 gibbosities; row III (corresponding to the 2nd pair of legs), 3 gibbosities; row IV, 5 gibbosities; row V (corresponding to the 4th pair of legs), 3 gibbosities; row VI, 5 gibbosities; behind row VI there are again two small

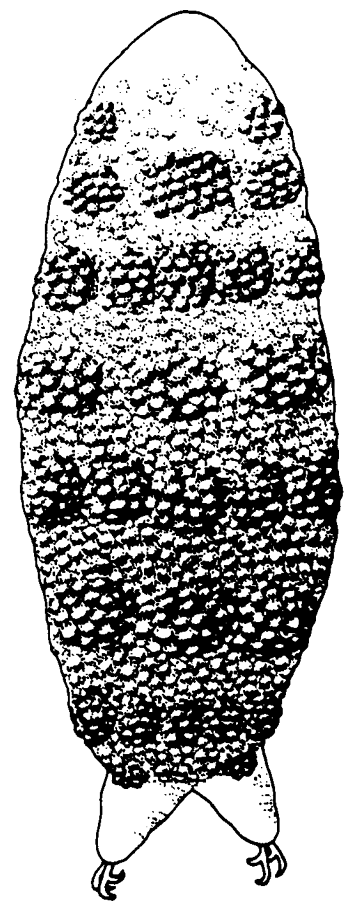


Fig. 423 - *I. septentrionalis* Thulin (from Durante Pasa & Maucci).

dorso-lateral gibbosities. The gibbosities and part of the cuticle between them (more evident on the posterior half of the body) has a sculpture composed of small tubercles, rounded, which touch each other.

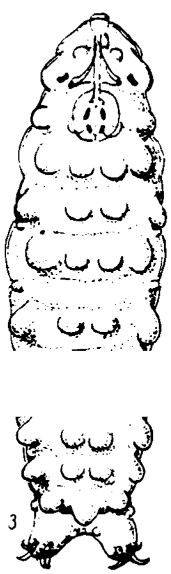
Buccal tube rather slender (length 20μ, width 1.5μ, in an example of 200μ). Pharynx short oval, almost round, with apophyses and two macroplacoids, in the shape of rather elongated granules, the first longer than the second. Microplacoid absent.

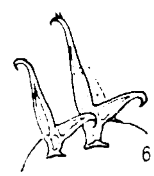
Claws very small, with principal and secondary branches strongly divergent. Lacking lunule, and there are no cuticular bars on the legs.

The original description of this species is rather summary, and was not published with any drawings. The description and the figure published here is attributed to material collected and examined by Durante Pasa and Maucci (1979). The species is known only from Lapland. The "neotype" came from Petäjäski, in Lapland Finland.

ISOHYPSIBIUS SILVICOLA (Iharos, 1966) (Fig. 424).
= *Hypsibius* (*I.*) *silvicola* Iharos, 1966.

Length 180-300μ, colorless, eye spots present. Cuticle finely granulated even on and between the gibbosities, which are hemispherical and arranged dorsally in 10 transverse rows, as follows: 2 in rows 1 and 2;





claws of the 4th pair of legs (from Iharos).

3 in row 10; 4 in rows 3, 4, 5, 6, 7, 8, 9. Sometimes in row 2 there are 4 gibbosities (instead of 2). There are also present smaller lateral papillae (one per each side) between the rows 4-5, 5-6, 6-7, and 7-8.

Pharynx oval (24 x 20μ) with 2 macroplacoids, the 1st (3.6μ) longer than the 2nd (2.4μ); microplacoid absent. Doubleclaws of each leg of different size: on the 4th pair of legs the external doubleclaw is 11μ long, the internal 8.5μ; also on the legs of the 4th pair there is a small papilla at the base and on the internal side. Eggs not seen.

The species was collected in moss in the shade on the ground and on rock, in leaf litter (beech, acacia) and in the soil, in various localities of Hungary (Cseszne, Csȍt) and later in Sicily. Pilato (1973) determined that the sculpture is of reticular type, that the claws have lunules, and that on the first three pair of legs there is a cuticular bar.

ISOHYPSIBIUS SISMICUS (Maucci, 1978) (Fig. 425).

Length up to 560μ (average of the population 500μ). Color sepia brown, with black spots aligned to form two longitudinal dorso-lateral bands. Following treatment with dilute NaOH, the pigment of the spots expands on all the surface and turns into a bluish-black ink. With polyvinyl-lactophenol it becomes again sepia, but darker. Eye spots present, large, in posterior position. The cuticle is sculptured with a dense and regular granulation, which extends on all the dorsum, but sometimes less marked on the cephalic end.

Buccal aperture without lamellae. Buccal tube medium wide (55μ x 6, in the holotype, 500μ long). Stylets short, divergent, with massive furcae. Stylet supports long, straight. Pharynx short oval, with apophyses and two rod-shaped macroplacoids very short, the first 10μ long (sometimes rather constricted at the middle), the second 7μ. Microplacoid absent.

The claws are very large. The basal branch is rather long, and thins basally. The principal branch is longer than the secondary, but this last is more massive. The principal branch bears slender accessory points rather distant from the apex. The claws of the 4th pair are much larger and

first three pair, very large and crenate on the 4th pair. Near the base of the claws of the first three pair of legs exists a cuticular bar, long, sinuous.

The species was found in four samples of moss, near Van, at the foot of the citadel, north side, with abundant population. Also a single example was found in a sample of moss on schist rock, at Ladak-Dras

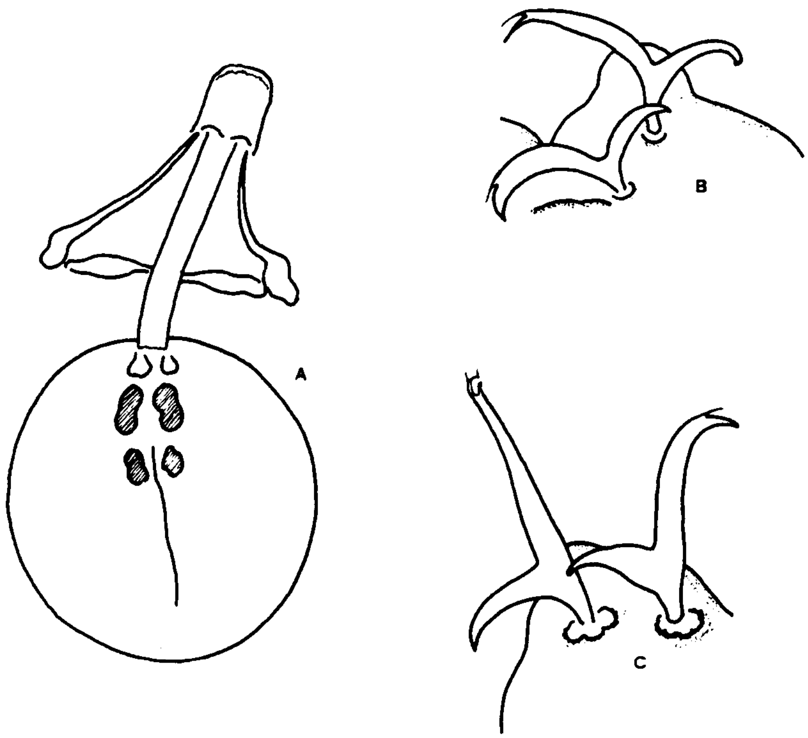


Fig. 425 - *I. sismicus* (Maucci). A, buccal apparatus; B, claws of the 3rd pair of legs; C, claws of the 4th pair (from Maucci).

(Kashmir, India), at 3,300 altitude.

The specific name is inspired by the circumstances that, on the day in which Maucci stayed studying this example, for verification, a short

ISOHYPSIBIUS SOLIDUS (Mihelčič, 1971) (Fig. 426).
= *Hypsibius* (*I.*) *solidus* Mihelčič, 1971.

Length 220-300μ, colorless, eyes absent. Cuticle smooth. Buccal tube short, the length is almost equal to that of the pharynx, which is an

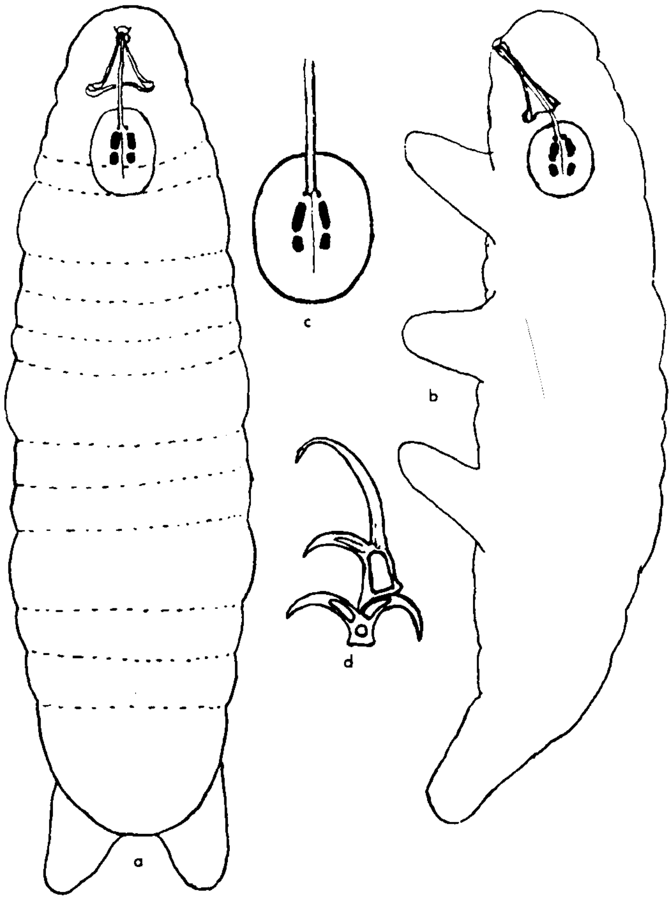


Fig. 426 - *I. solidus* (Mihelčič). a, dorsal view; b, lateral view; c, pharynx; d, claws (from Mihelčič).

elongated oval. Minuscule apophyses, two angular macroplacoids, the 1st almost twice the length of the 2nd; microplacoid absent. Legs short and large, doubleclaws very small, of equal shape and size on each leg; basal part short, principal branch slender. No mention is made of the lunule, nor of the cuticular bar on the legs. Eggs unknown.

I. solidus was observed in moss and in soil under it, near Amlach (Lienz, Austria).

ISOHYPSIBIUS STENOSTOMUS (Richters, 1908) (Fig. 427).
= *Hypsibius* (*I.*) *stenostomus* + *apelloefi* (Marcus 1929 and 1936).

Length 400-500μ, body compressed, legs short. Eye spots present, cuticle smooth (at times lightly granulated in old individuals). Buccal tube rather narrow (1.5μ) and slightly bent ventrally. Pharynx elongated oval, with large apophyses, and three macroplacoids in the shape of slender rods: the first and the third macroplacoids are about equal length, the second is longer and is constricted near its caudal end. Microplacoid present.

The claws are large and may be rather different from one pair of legs to another, having always those of the 4th pair more slender and longer. The claws of each leg are equal in shape and size. The secondary branch and the principal are almost similar, but the principal is often a little more slender and bears accessory points; these last may be small or lacking on some claws.

I. stenostomus is one of the very few species of Eutardigrada that is clearly marine. There are cited various reports from the Baltic Sea and the North Sea, either in sand, or on brown algae.

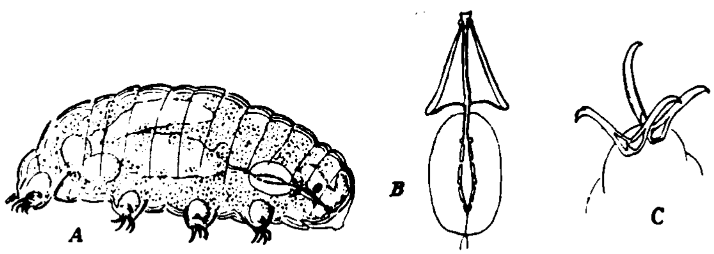


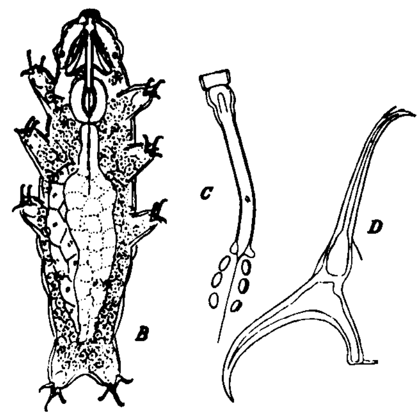
Fig. 427 - *I. stenostomus* (Richters). A, lateral view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs (from Marcus).

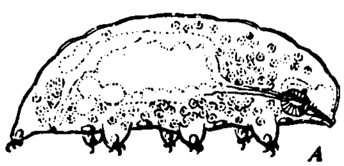
ISOHYPSIBIUS TETRADACTYLOIDES (Richters, 1907) (Fig. 428).
= *Hypsibius* (*I.*) *tetradactyloides* Richters, 1907.

Tardigrades often -- but not always -- aquatic; length up to 400-500μ, eyes present, massive body, legs short. Buccal tube very narrow (internal diameter about 1μ in an animal of 400μ), with appendages in the shape of crests for the insertion of muscles. Pharynx short oval to oval, containing apophyses and 3 macroplacoids; microplacoid absent. The macroplacoids may be short rods of increasing length in rostro-caudal sense, or else the third may be longer and the first two having about equal length; in the young all three have equal length. Doubleclaws of each leg of size not strongly different and of the *Isohypsibius* type. Deposited in the exuvium are 2-8 smooth and oval eggs (largest diameter about 90μ).

The species is known from Italy, Switzerland, Germany, Czechoslovakia, Hungary, western Africa (Ivory Coast), Crozet Island and Heard Island (typ. loc.), Vietnam, and Newfoundland; it was collected either in moss, or in fresh water.

Fig. 428 - *I. tetradactyloides* (Richters). A, lateral view; B, young viewed ventrally; C, buccal tube and placoids of a young still in the egg; D, posterior doubleclaws of the 4th pair of legs (from Marcus).





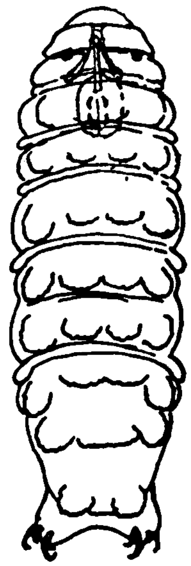
ISOHYPSIBIUS THERESIAE (Iharos, 1964) (Fig. 429).
= *Hypsibius* (*I.*) *theresiae* Iharos, 1964.

Length 180-220μ, colorless, eye spots present. Dorsally there are 8 transverse rows of gibbosities and precisely 4 gibbosities in each of the first seven rows and 2 in the eighth. There are also 4 cylindrical papillae on each side of the animal, in the distance between the 1st and the 4th pair of legs (the author described it "in the shape of a sausage", but has later communicated that there exists also a variety in which it is lacking). The cuticle is finely granulated and has a reticular design, either between the gibbosities, or on them.

Two macroplacoids, as in *I. tuberculatus*; claws are *Isohypsibius* type. The animal deposits up to 5 eggs, smooth and oval, in the old cuticle.

The species was collected at 150-300 m altitude, in forest leaf litter (Gulacsi-Berge and Toti-Berge, Hungary).

Fig. 429 - *I. theresiae* (Iharos) (from Iharos).



ISOHYPSIBIUS TORULOSUS (Mihelčič, 1959) (Figs. 430 & 431).
= *Hypsibius* (*I.*) *torulosus* Mihelčič, 1959.

Length 350-390μ, grayish color, eye spots absent. Buccal tube medium wide, pharynx almost spherical, with apophyses and 2 macroplacoids, of which the first is longer than the second and has a constriction; lacking microplacoid. The tardigrade has sculptured cuticle of a reticular design and bears numerous dorsal and dorsolateral gibbosities, arranged in nine principal transverse rows (that is to say larger gibbosities), which are joined by other transverse rows of smaller gibbosities. The gibbosities are thus distributed in the transverse rows:

- row I, immediately behind the head: 3 large gibbosities, a median and two lateral. There follows two transverse rows of small gibbosities (the first of four and the second of two), not very clear in dorsal view, but very distinct in profile;
- row II, over the first pair of legs: six large gibbosities, three per each side, so that there remains a median dorsal free zone. There follows a transverse row of four smaller gibbosities;
- row III, between the first and the second pair of legs: six large gibbosities;
- row IV, over the second pair of legs: six large gibbosities. There follows a transverse row of 4 smaller gibbosities;
- row V, over the third pair of legs: six large gibbosities, of which those central are positioned more rostrally and the others more caudally;
- row VI, six slightly elongated gibbosities, of which the central four are larger and the lateral two smaller;

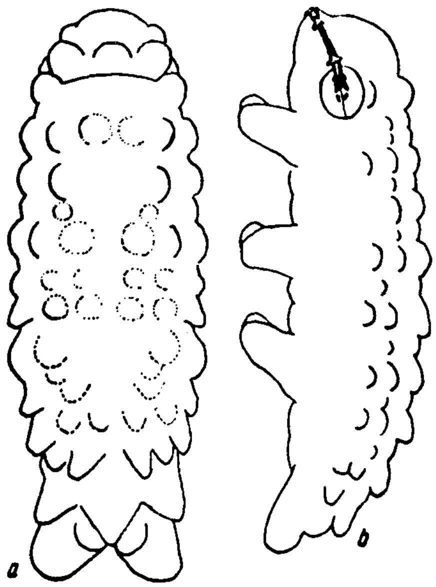


Fig. 430 - *I. torulosus* (Mihelčič). a, dorsal view; b, lateral view (from Mihelčič).

Fig. 431 - *I. torulosus* (Mihelčič). a, pharynx; b, doubleclaws of the 1st pair of legs; c, cephalic region and first segment (dorsal); d, caudal region; e, idem., lateral view; f, doubleclaws of the 4th pair of legs (from Mihelčič).

- row VII, four large gibbosities. There follows a transverse row of small gibbosities;
- row VIII, four large central gibbosities, all elongated in rostro-caudal sense (coniform) and having at the side other smaller gibbosities. There follows a transverse row of small gibbosities;
- row IX, three gibbosities, also elongated one central and two others lateral.

Legs short and large: the first three pair have an anterior gibbosity, the last pair one dorsal gibbosity; doubleclaws of each leg not very different, with basal part rather large.

The species was collected only in Austria (eastern Tirolo), in wet moss on rocks at the margin of woods.

ISOHYPSIBIUS TRUNCORUM (Iharos, 1964) (Fig. 432).
= *Hypsibius* (*I.*) *truncorum* Iharos, 1964.

Length 160-180μ, colorless, eye spots present. Dorsally these are 8 transverse rows of hemispherical gibbosities, thus arranged: 5 in each of the first 6 rows and 3 in rows 7 and 8. The cuticle has a fine granulation and a reticular design.

Pharynx oval, with 2 macroplacoids in the shape of rods, of which the first is longer than the second. Doubleclaws rather small (on the 4th pair of legs the anterior doubleclaws measure 7μ, the posterior 9.2μ). Eggs unknown.

The species was observed in moss on a tree trunk at Felsöerdö (Sudbakony, Hungary) and on the Cansiglio Plateau (Italy).

ISOHYPSIBIUS TUBERCULATUS (Plate, 1888) (Fig. 433).

Length 245-305μ, colorless, eyes present. The cuticle is densely granulated and the individual granules design a reticular structure: there are also dorsal and dorsolateral gibbosities, arranged in 10 transverse rows

- row I, 5 gibbosities
- row II, 4 gibbosities
- row III, 6 gibbosities
- row IV, 4 gibbosities
- row V, 6 gibbosities
- row VI, 4 gibbosities
- row VII, 6 gibbosities
- row VIII, 4 gibbosities
- row IX, 2 gibbosities
- row X, 5 gibbosities.

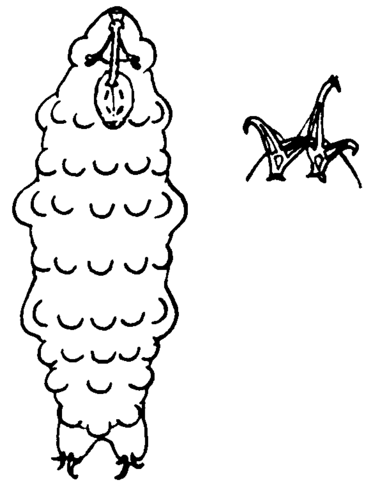


Fig. 432 - *I. truncorum* (Iharos). Dorsal view and doubleclaws of the 4th pair of legs (from Iharos).

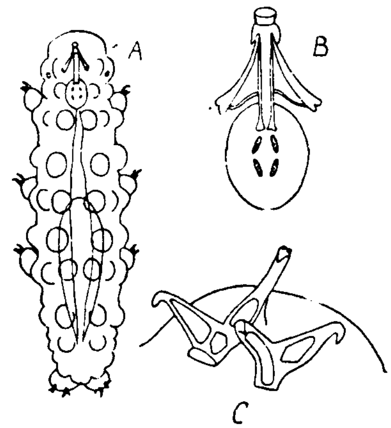


Fig. 433 - *I. tuberculatus* (Plate). A, dorsal view; B, pharynx; C, doubleclaws of the 4th pair of legs (from Marcus, redrawn).

Buccal tube with crest-shaped appendages for muscle insertion; oval pharynx, provided with apophyses and 2 macroplacoids with the appearance of short rods: the first, longer than the second, and sometimes subdivided into two granules in contact with each other; lacking the microplacoid. The branches of each doubleclaw are very divergent and their common basal portion is short; the principal branch has accessory points, at least on the fourth pair of legs. At the bases of the claws there are lunules; on the first three pair of legs there is a cuticular bar.

I. tuberculatus was cited for numerous localities from Europe (including Italy), Shetland Islands, Canary Islands, eastern Africa, North and South America, Spitsbergen Archipelago.

It is very probable, however, that not all the citations refer actually to this species, but rather to one of the numerous others so far described belonging to the "*tuberculatus* group".

Typ. loc.: Marburg (Germany).

ISOHYPSIBIUS TUBERCULOIDES (Mihelčič, 1949) (Fig. 434).
= *Hypsibius* (*I.*) *tuberculoides* Mihelčič, 1949.

Length about 250-300μ, large black eye spots, buccal apparatus similar to that of *I. tuberculatus*; the oval pharynx contains the apophyses and 2 macroplacoids, of which the first is longer than the second; microplacoid absent. The species is easily distinguished from others of

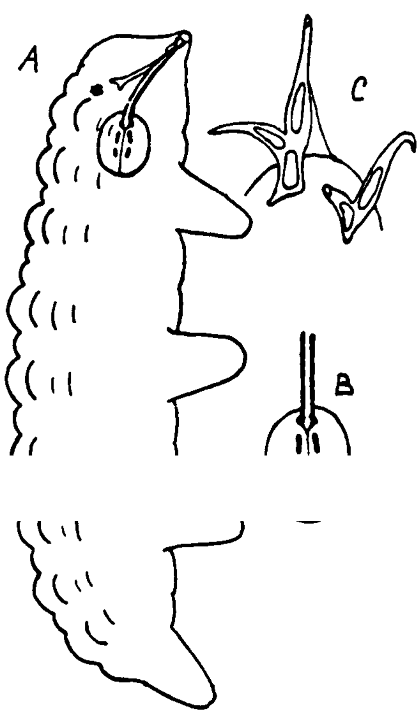


Fig. 434 - *I. tuberculoides* (Mihelčič). A, lateral view; B, pharynx; C, doubleclaws of the 4th pair of legs (from Mihelčič).

the "*tuberculatus* group" by the large number of gibbosities, arranged -- in individuals of complete development -- in 20 dorsal transverse rows; the cuticle is also sculptured with a reticular design. The gibbosities do not all have equal size, but are thus arranged:

-- smaller and more flattened gibbosities in rows 2, 3, 5, 7, 8, 10, 12, 14, 16, 18, 20; more precisely in each of the rows 10 and 20 there are three gibbosities, while there are six in all the other rows;

-- larger gibbosities in rows 1, 4, 6, 9, 11, 13, 15, 17, 19; such gibbosities are arranged as follows: four in each of the rows 1, 9, 19; five in 17; six in each of the remaining rows (4, 6, 11, 13, 15).

In young animals, not yet completely developed, there may be lacking some rows of smaller gibbosities, sometimes even all; in this last case the tardigrade has then only 9 dorsal transverse rows of gibbosities, thus arranged:

-- 4 large gibbosities in rows 1, 4, 9;
-- 5 large gibbosities in row 8;
-- 6 large gibbosities in rows 2, 3, 5, 6, 7.

The doubleclaws are of the *Isohypsibius* type, with basal part common to the principal and secondary branches rather short.

This description of *I. tuberculoides* was compiled on the precise, courteous bases supplied by the author (Mihelčič, in press, 1962), and differs from that published by the same author in 1949, 1951, and 1953; they can still then be taken into consideration for the young to incompletely developed (or variety?) and perhaps -- in some cases -- individuals belonging to a different species.

I. tuberculoides was collected only in Austria, in meadow soil, at about 3 cm in depth: the reports are however too scarce to be able to state that the species is exclusively eu-edaphic.

Length up to 247μ, eye spots present, head large, anteriorly flattened. The cuticle shows a reticular design; the dorsal region is subdivided into transverse folds and appears to be undulating (observe tardigrade in profile): there are inclusively 24 undulations. Buccal tube not excessively narrow (2μ internal diameter), little curved; pharynx short oval, having length to width ratio equal to about 1.1-1.2:1, with apophyses

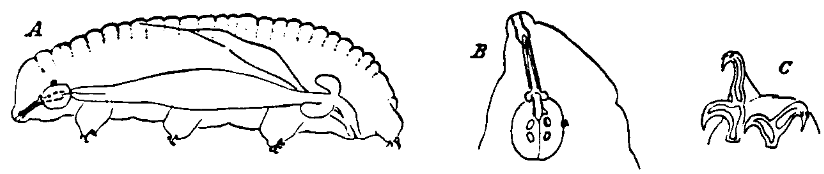


Fig. 435 - *I. undulatus* Thulin. A, lateral view; B, cephalic zone; C, doubleclaws of the 4th pair of legs (from Thulin).

and 2 macroplacoids in the shape of short rods, of which the first is shorter than the second; lacking microplacoid. Doubleclaws of medium size, *Isohypsibius* type. Smooth, oval eggs (38 x 44μ) deposited in the exuvium.

The species was collected in Italy, Hungary, Sweden, and Vietnam. Typ. loc.: Lapland.

ISOHYPSIBIUS VEJDOVSKYI (Bartos, 1939) (Fig. 436).
= *Hypsibius* (*I.*) *vejdovskyi* Bartos, 1939.

Length 110-170μ, colorless, with large black eye spots. The cuticle is finely granulated on all the dorsal surface; the granules are somewhat larger on the cephalic region, where often -- especially laterally -- they are prolonged into small spines. There are besides ten transverse rows of gibbosities, of increasing size in rostro-caudal sense; the last row is found

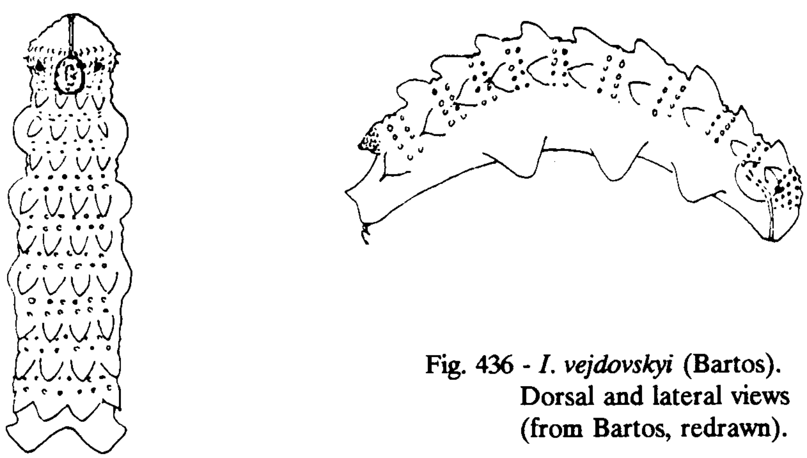


Fig. 436 - *I. vejdovskyi* (Bartos). Dorsal and lateral views (from Bartos, redrawn).

exactly over the fourth pair of legs; in each row there are four gibbosities. Sometimes the lateral gibbosities of rows 3-8 are terminated in a short spine: this happens especially in those individuals which have small lateral spines on the cephalic region. Buccal tube narrow (external diameter about 1.3μ), pharynx short oval, with ratio between length and width equal to 1.1-1.2:1, containing showy apophyses and two macroplacoids, of which the first (2μ) is longer than the second (1.2μ); microplacoid absent.

The legs of the fourth pair bear large tubercles, with blunt ends, on the external dorsal side; the doubleclaws are of the *Isohypsibius* type and similar to those of *I. nodosus*. It deposits 1-2 smooth eggs in the exuvium.

The species was collected many times in the region of the Carpathians, in wet moss.

ISOHYPSIBIUS VIETNAMENSIS (Iharos, 1969) (Fig. 437).
= *Hypsibius* (*I.*) *vietnamensis* Iharos, 1969.

Length 230-310μ. Color dark yellow-orange, eye spots present. The cuticle is finely granulated and has 9 transverse rows of gibbosities, thus arranged: 2 in row 8; 3 in row 9; 4 in rows 2, 4, 6; 5 in rows 1, 3, 5, 7. Buccal tube with diameter of 2.4μ, pharynx elongated oval with 3 macroplacoids (rounded granules), which become larger in rostro-caudal sense. Microplacoid absent. Doubleclaws long and slender: the posterior of 13.4μ, the anterior of 9.7μ. Eggs unknown.

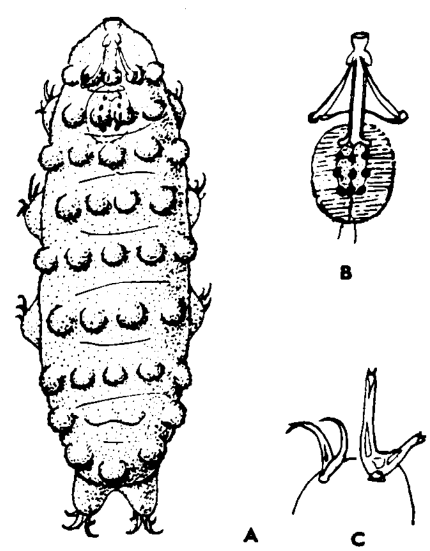


Fig. 437 - *I. vietnamensis* (Iharos). A, dorsal view; B, pharynx; C, doubleclaws of the 4th pair of legs (from Iharos).

The author has described this species with the name *Hypsibius vietnamensis*, without indication of subgenus. Since even the drawing of the claws does not permit a certain identification, this species in the first and second edition of the present "Phylum" was included, however doubtful, in the genus *Isohypsibius*, by the presence of gibbosities, and also because the same author stated explicitly that *H. vietnamensis* belongs to the "*tuberculatus* group".

The species was collected in moss on soil at Huong tich, at about 60 km southwest of Hanoi (Vietnam).

ISOHYPSIBIUS WILSONI (Horning, Schuster & Grigarick, 1978) (Fig. 438).

Length up to 405μ, with an average of 225μ. Colorless, eye spots present or absent. The cuticle is sculptured with a fine reticular design, rather irregular mesh and not polygonal; this design may be sometimes barely evident or absent. Buccal tube 32μ long and 4 wide (in an example of 274μ): may sometimes be proportionally shorter and wider. Pharynx round, with apophyses and three macroplacoids, in the shape of elongated granules, the first two of equal length, the third a little longer; microplacoid absent. Claws large, the principal branch with accessory points. Although the description did not mention features, from the drawing is noted that there is an evident lunule, but only on the external claws.

According to the authors, the species may be near *I. tetradactyloides*.

I. wilsoni was found in different localities in New Zealand.

Genus *ITAQUASCON* Barros, 1939.

Diagnosis: Hypsibiidae, with buccal tube subdivided in a proper

continuous cuticular structures; claws *Hypsibius* type.

Observations: We think that the genus *Itaquascon* should be radically revised. The morphological characters used systematically are so few, that the description of the species so far known results inevitably somewhat vague, and often based on hardly describable gradations. It is

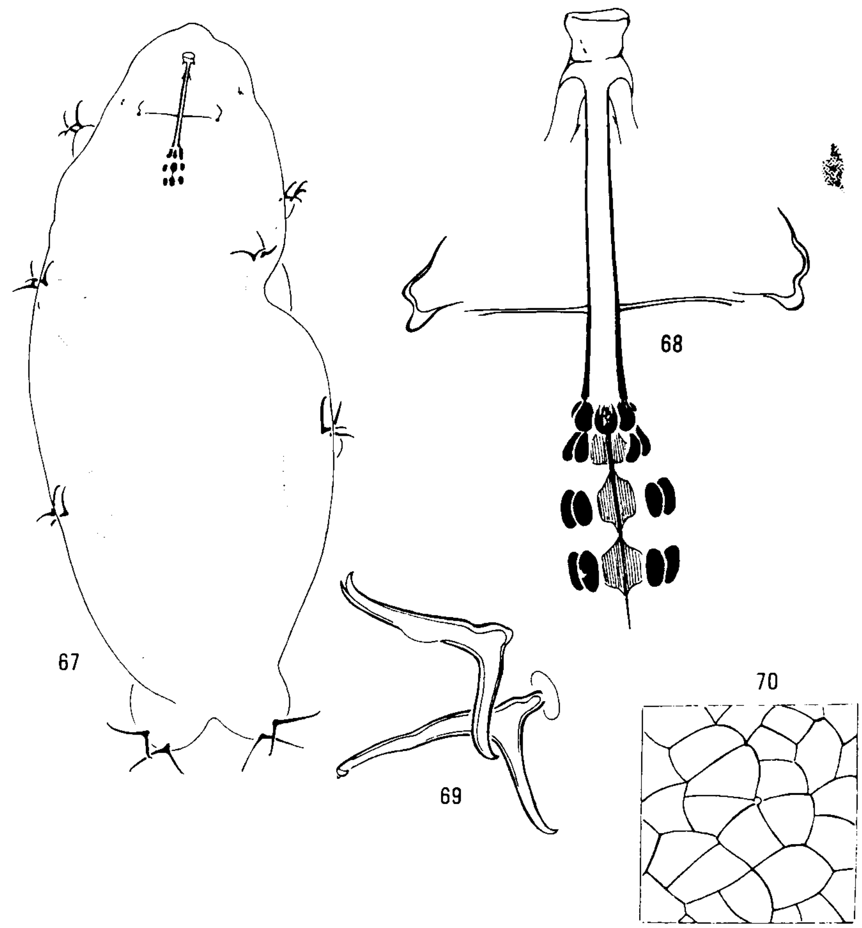


Fig. 438 - *I. wilsoni* (Horning et al.). 67, dorsal view; 68, buccal apparatus; 69, claws of the 4th pair of legs; 70, details of the dorsal sculpture over the 3rd pair of legs (from Horning et al.).

the intraspecific variability. Certain characters used to differentiate some species (length of the salivary glands) are probably of little or no taxonomic importance, being almost certainly tied to physiological situation.

Of the seven species so far described, we think it is possible to be considered valid, with a certain likelihood, *It. umbellinae* (by the presence of the stylet supports), *It. placophorum* (by the dorsal papilla), *It. pawlowskii* (by the long and slender buccal tube, and the round pharynx). *It. tamaensis* does not seem, from the description, clearly differentiated. *It. simplex* was inserted by us in the genus *Itaquascon*, by the absence of placoids, but its description is so insufficient, that it should really be considered as a "*nomen nodum*". *It. bartosi*, *It. trinacriae*, *It. ramazzottii* are probably synonymous (so thinks Dastych, 1973; while Pilato, 1969, limits the synonymy to only *It. ramazzottii* = *It. trinacriae*). There is not, at present, sufficient knowledge to decide the aforesaid question. Nevertheless we have deemed to report all the species described. The identification key should however be used with much prudence, and will always be advisable, in the case of *Itaquascon*, to consult the descriptions of all the species.

KEY TO THE SPECIES

1. Buccal and pharyngeal tube very long and narrow (about 1.5μ) 2
Buccal and pharyngeal tube less narrow (2.5-5μ); pharyngeal tube moderately flexible 4

2. Cuticle sculptured with lines covered here and there with brief dots .... *It. enkelli*
Cuticle smooth 3

3 (2). Pharynx round .... *It. pawlowskii*
Pharynx elongated, somewhat pear-shaped; two rounded lobes at the sides of the head .... *It. simplex*

4 (1). Stylet supports present .... *It. umbellinae*
Stylet supports absent 5

5 (4). Dorsally, between the third and fourth pairs of legs there is a flat triangular papilla .... *It. placophorum*
There is no dorsal papilla 6

7 (6). The salivary glands attain with their caudal end the anterior part of the middle intestine .... *It. bartosi*
The salivary glands attain, at most, the middle of the esophagus (between the pharynx and middle intestine) 8

8 (7). The salivary glands do not surpass the middle of the pharynx, which is oval, with length to width ratio of 2 or more; claws short and massive .... *It. trinacriae*

The salivary glands reach the middle of the esophagus; pharynx elongated oval with length to width ratio of about 1.8; claws long and slender .... *It. ramazzottii*

ITAQUASCON BARTOSI Weglarska 1959 (Figs. 439 and 440).

Length from 220 to 420μ. Colorless, eye spots absent. The body is very slim, almost wormlike, with cephalic end strongly attenuated. Cuticle smooth. The buccopharyngeal tube is medium long, about 50μ, and 5-6 wide. The rigid part (buccal tube) is very short (not more than 12-14% of the entire tube). The flexible part (pharyngeal tube) has the typical spiral structure. The stylets are slender, curved toward the interior. Lacking stylet supports. The pharynx is elongated, cylindrical, with length somewhat more than twice its width. In the interior of the pharynx there are slender cuticular lines, very thin, with thickness not uniform, which may at times be reduced until barely visible. The salivary glands may have length very variable, but they are however considerably long, until reaching caudally the middle intestine. Given the variability of this character, depending on the age and the physiological condition, it does not seem that we can attribute systematic importance to it. The claws of each leg are of considerably different shape and size. The base of the claws has an expansion and the basal branch is sufficiently long; the principal branch, long and slender, has near its insertion an enlargement, strongly refringent. The internal claws have the principal branch much shorter. The accessory points on the principal branch are slender and thin on the external claws, more robust on the internal claws. According to Dastych (1973), near the claws of the second and third pairs of legs there may be however a

the bar is clearly indicated in the drawing). According to Binda (1974) *It. bartosi* does not possess such bar, for which the drawing of Dastych may be the consequence of an error of determination.

Eggs white, smooth.

Dastych (1973) advances the suggestion to consider as synonyms *It. bartosi*, *It. trinacriae* Arcidiacono (and therefore -- implicitly -- also *It. ramazzottii* Iharos). Binda (1974) thinks on the contrary *It. bartosi* a distinct

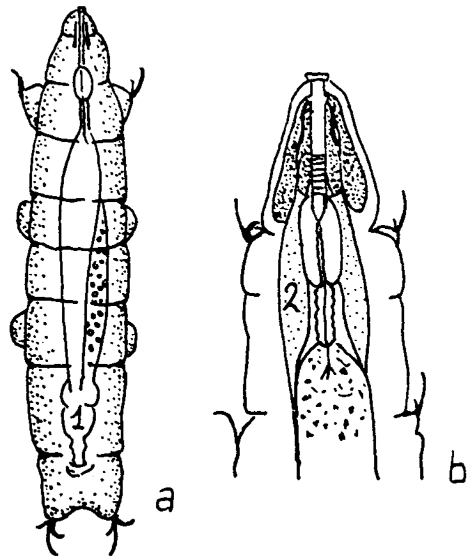


Fig. 439 - *It. bartosi* Weglarska. a, dorsal view: 1, the Malpighian tubule; b, rostral region: 2, the salivary glands (from Weglarska, modified).

species from *It. trinacriae* (this last may be instead synonymous with *It. ramazzottii*), which however may be very near, indicated as differentiating characters the presence of the cuticular bar on the 2nd and 3rd legs in *It. trinacriae*, while such bar would be constantly absent in *It. bartosi.*

We have had occasion to examine all of the three species in question (including some paratypes). It is our opinion that most probably one should follow the account of Dastych and unite the three species under the single name *It. bartosi* (which has priority). However, at the actual state of knowledge, since very little is known on the intraspecific variability of *Itaquascon* (of which never as yet has been found very abundant populations), it is preferable to wait for further observations, and to avoid premature synonymy.

It. bartosi can be distinguished from the other two species almost

on the taxonomic value of this character) and, probably by the less developed principal branch of the external claws. As for the cuticular bar on the 2nd and 3rd legs, we can not share the opinion of Binda (and also of Pilato) that this character is not susceptible to individual variability even as far as to be missing. In our material we have different examples referred to as *It. bartosi*, with bar, therefore like examples with bars noted also by Dastych in Korean material.

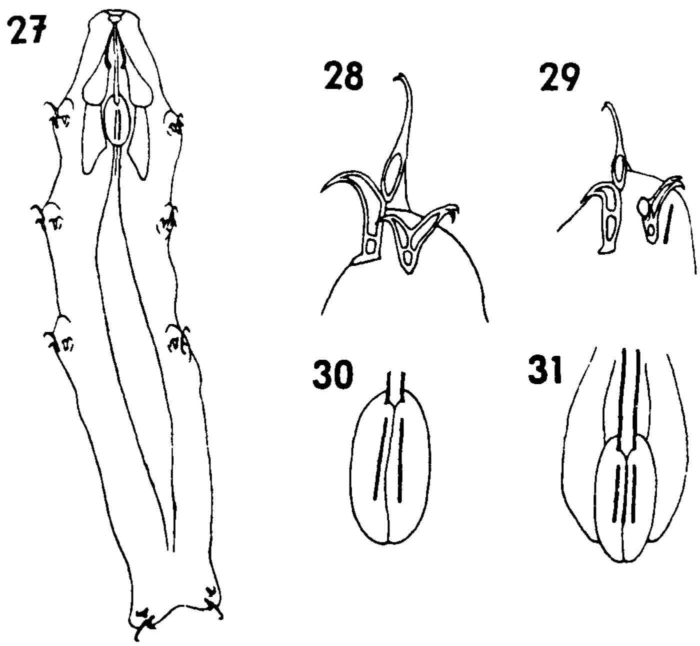


Fig. 440 - *It. bartosi* Weglarska. 27, ventral view; 28, claws of the 4th pair of legs; 29, claws of the 3rd pair of legs; 30, 31, pharynx (from Dastych).

On the contrary we have also examples of *It. trinacriae*, coming from Carso Triestino, deprived on this bar.

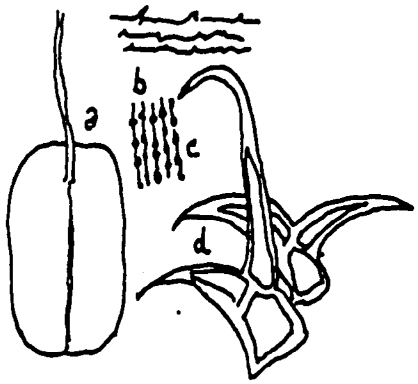
It. bartosi was found on the Tatra Mountains (Poland), in Hungary, Consiglio Plateau and Valtellina (Italy), Austria, Greece, Yugoslavia, North Korea, and South America.

ITAQUASCON ENCKELLI (Mihelčič, 1971-72) (Fig. 441).
= *Hypsibius* (*Diphascon*) *enckelli* Mihelčič, 1971-72.

Aquatic. Flexible pharyngeal tube longer than the pharynx, with diameter of 1.8 to 3μ, depending on the size of the animal, which varies from 450 to 550μ. Pharynx cylindrical, anteriorly and posteriorly truncated, with weak apophyses *and without placoids*.

Cuticular sculpture composed on zig-zag lines which here and there are covered with brief dots or clear dots. Principal branch of the external claws curved, without accessory points and long. Eggs smooth, deposited

Fig. 441 - *It. enckelli* (Mihelčič). a, pharynx; b, c, details of the sculpture; d, claws of the 4th pair of legs (from Mihelčič).



in the exuvium. Collected in interstitial fauna near Ivosjön (Sweden).

We accept with many reservations this species, which was included in the genus *Diphascon*, according to the author, allowing much perplexity.

ITAQUASCON PAWLOWSKII Weglarska, 1973. (Fig. 442).

Length from 130 to 224μ, which makes this the smallest species of *Itaquascon*. Cuticle smooth, eyes absent. Body slender, not very transparent; stylets sharp, delicate. Stylet supports absent. The pharyngeal tube is very long, straight, not very flexible, and furnished with spiral reinforcement. The buccal tube is 10.8μ long, the pharyngeal tube 41.5, in an example of 164μ. Pharynx subspherical, without placoids or apophyese, and without cuticular thickenings.

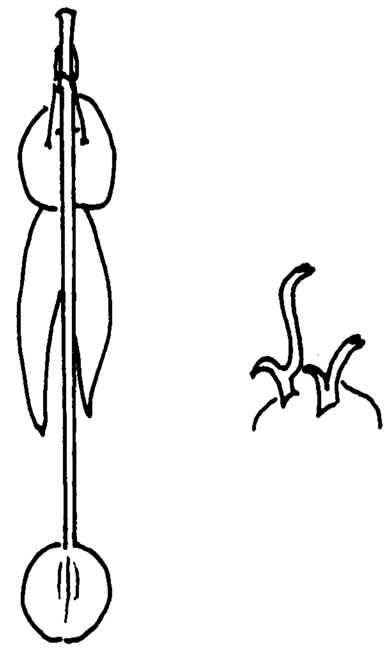
The doubleclaws are similar in all the legs; the principal branch of the external and internal doubleclaws with accessory points. Eggs unknown.

The species was collected at Polana pod Woloszynem (Tatra Mountains, Poland) and at Grimsmark, near Lovanger (Sweden).

ITAQUASCON PLACOPHORUM Maucci, 1972 (Fig. 443).

Length from 315 to 485μ, colorless, translucent. Eye spots absent. The body slender, rostrally tapered, and a little enlarged and abruptly truncated at the caudal end. The cuticle is smooth and has transverse folds, more marked and closer towards the caudal end, upon the 3rd pair

Fig. 442 - *It. pawlowskii* Weglarska. Buccal apparatus and claws of the 4th pair of legs (from Weglarska, redrawn).



of legs. Near the caudal end there is, dorsally, a triangular papilla, pointed, with wide base.

The buccal aperture is very wide, and is surrounded by a cutaneous margin, notched and lobed. Buccal cavity extremely short. The buccal tube is long and straight (length 48μ, width 3, in the holotype, 330μ long). The initial part, rigid, terminated in a reinforced ring, is 16-17% of the tube length. The flexible portion has, in all the length, well defined spiral shaped structure. Stylets weak, almost straight, slightly concave medially, very close to the tube; furca very small, extremely slender. Stylet supports absent.

Pharynx small, markedly elongated oval, length twice the width, without apophyses and placoids. There is a pronounced cuticular thickening, about 15μ long and often almost considerably more pronounced than in the other species of *Itaquascon*.

The salivary glands are larger and wide, strongly rounded and short: it hardly surpasses the caudal end of the pharynx.

The claws of each leg are of very different size. Both the claws have at the base a wide spine-shaped expansion, larger on the external doubleclaws. The basal part and the secondary branch of the external doubleclaw are robust, sickle-shaped, and achieves its maximum thickness in correspondence with the attachment of the principal branch. This last,

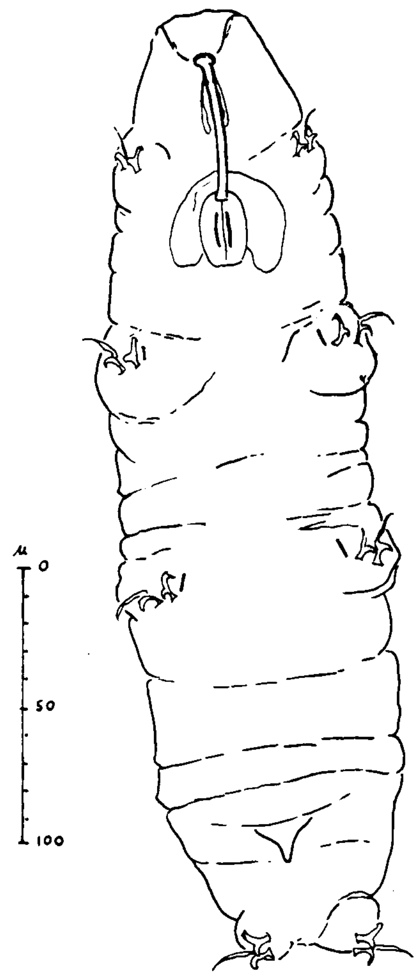


Fig. 443 - *It. placophorum* Maucci (from Maucci).

long and slender, straight as far as the abrupt terminal curvature, has a swelling at its first proximal quarter and carries two extremely small accessory points, barely visible. The internal doubleclaw is very small: both the branches are robust and slightly curved, and the principal branch has two evident accessory points. Near to the internal doubleclaws, the legs of the 2nd and 3rd pairs bear a cuticular thickening in the shape of a linear bar, evident in some examples, less clear in others, and partially faded in a dense irregular granulation.

Eggs unknown.

It. placophorum was described from two localities from Turkey, and was later found also on Carso Triestino, in Austria, and in three localities from Sweden.

ITAQUASCON RAMAZZOTTII Iharos, 1966 (Fig. 444).

Length 450μ, body almost vermiform, elongated, colorless; eye spots absent. Aperture and buccal cavity wide and short. The buccal tube (rigid part of the bucco-pharyngeal tube) is short (12-14% of all the tube), the pharyngeal tube (flexible part) has the spiral structure of the wall, at times difficult to observe, especially in the anterior part of the tube. The

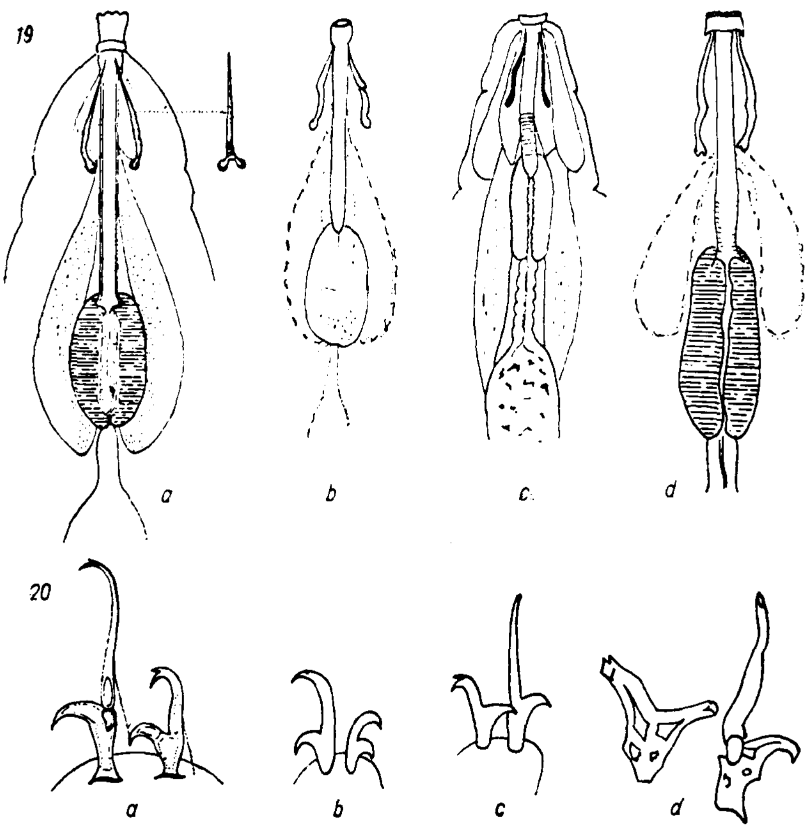


Fig. 444 - Four species of *Itaquascon* compared: 19b, pharynx of *It. umbellinae*; 19c, pharynx of *It. bartosi*; 19d, pharynx of *It. trinacriae*; 20a, claws of *It. ramazzottii*; 20b, claws of *It. umbellinae*; 20c, claws of *It. bartosi*; 20d, claws of *It. trinacriae* (from Iharos).

pharynx is cylindrical, a little less long than double the width, and lacking apophyses and placoids, while present are little cuticular thickenings in the shape of slender lines. Lacking stylet supports. The salivary glands reach in general up to the middle of the esophagus (between the pharynx and the middle intestine). The claws are similar to those of the other species of *Itaquascon*.

Pilato (1969) thinks that *It. ramazzottii* may be identical with *It. trinacriae*. We also -- having examined typical material of both species -- would be of this opinion. We maintain here two separate species in expectation of further observations, with the aim of avoiding a premature synonymy.

It. ramazzottii can perhaps be distinguished from *It. trinacriae* by the small length of the pharynx, by the great length of the salivary glands (however the systematic value of this character is moderate) and probably by the more slender and graceful claws.

The species was collected in the vicinity of Zirc (Hungary) and later -- always by Iharos -- in India and in South America. Pilato (1969) found it in the Apuane Alps (Italy), grounds for judgement however as *It. trinacriae*. There are besides some reports from Maucci -- which may be attributed to *It. ramazzottii* -- from Istria, Carso Yugoslavia, from Greece, and from Spain.

ITAQUASCON SIMPLEX (Mihelčič, 1971) (Fig. 445).
= *Hypsibius* (*Diphascon*) *scoticus simplex* Mih., 1971.

Similar to *Diphascon scoticum*, but length about 500μ. Cuticle smooth; at the sides of the head there are two lobes, one per side. Pharynx very narrow, less wide rostrally than caudally. Two slender cuticular thickenings in the lumen of the pharynx, no microplacoids or septulum.

It was collected in moss in the vicinity of Amlach, near Lienz [illegible]

description is certainly very summary. The authority, as subspecies to *Diphascon scoticum* permits much puzzlement.

ITAQUASCON TAMAENSIS Sudzuki, 1975 (Fig. 446).

Large, length 800μ. Green color due to cavity globules distributed

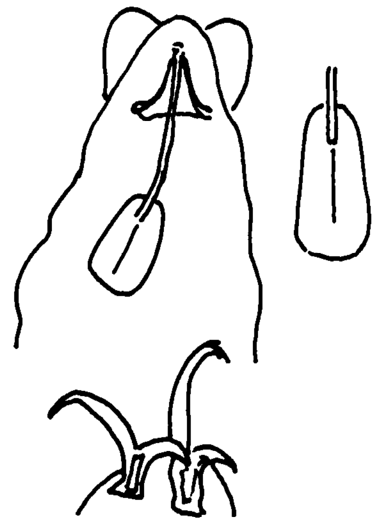


Fig. 445 - *It. simplex* (Mihelčič)
(from Mihelčič, redrawn).

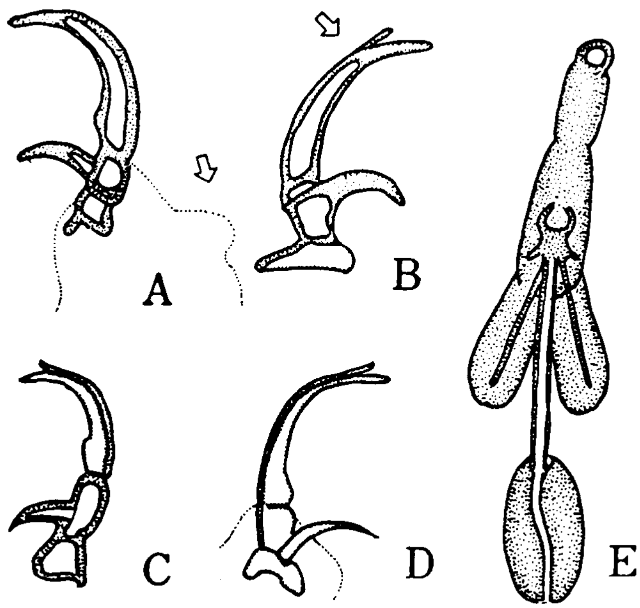


Fig. 446 - *It. tamaensis* Sudzuki. A, C, claws of the first pair of legs; B, D, claws of the 4th pair of legs; E, buccal apparatus (from Sudzuki).

in all the body. Cuticle smooth. There are eye spots, composed of about 80 pigmented dots. Pharynx 60μ x 38, without placoids. No mention is made of cuticular thickenings, nor description of the bucco-pharyngeal tube. Stylets straight, without supports: a pair of salivary glands cover the stylets.

The legs have a small rounded papilla on the dorsal side of the distal end. The claws of each leg are little different in shape and size. The principal branch is weakly curved, to form an arc of a circle. The internal side of this branch is remarkably enlarged at the base; the secondary branch is strongly bent at the apex.

This species is larger than the others, and is the only to have eye spots.

A single example of *It. tamaensis* was collected in interstitial environment, along the Tama-gawa River, in Japan.

ITAQUASCON TRINACRIAE Arcidiacono, 1962 (Fig. 447 & 448).

Length up to 450μ; body very slender with the anterior part thinning. Cuticle smooth, eyes absent.

The buccal tube is clearly differentiated into an anterior rigid part (which represents 12-14% of the entire tube) and a flexible part whose

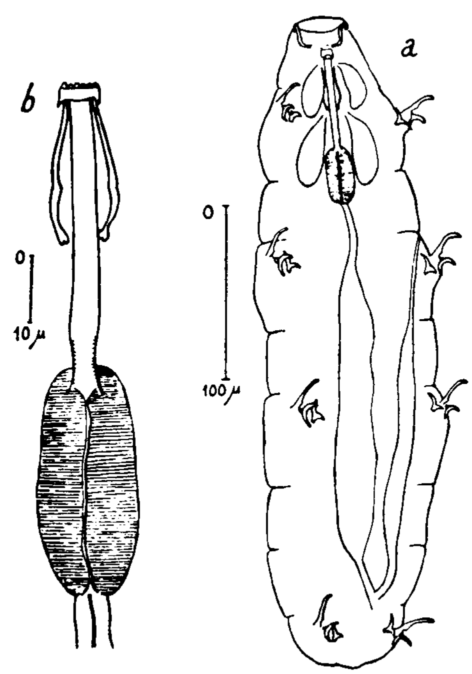


Fig. 447 - *It. trinacriae* Arcidiacono. a, ventral view; b, buccal apparatus and pharynx (from Arcidiacono).

walls are provided with a spiral pattern, clearly visible in the terminal end, but present along all the tube, even though difficult to observe. The tube is 35 to 50μ long, with a width of 3 to 4.6. Lacking the stylet supports.

The salivary glands have somewhat variable length: in general not reaching the caudal end of the pharynx, but at times abundantly surpasses it.

The pharynx is very elongated, without apophyses or placoids, and has a cuticular thickening along the lumen.

The claws are very different on each leg. The principal branch of the external claws is very long, enlarged near its insertion, then very slender and curved. The internal claws are much more massive, with principal branch more robust and shorter; either on the internal claws, or on the external, the principal branch is provided with accessory points.

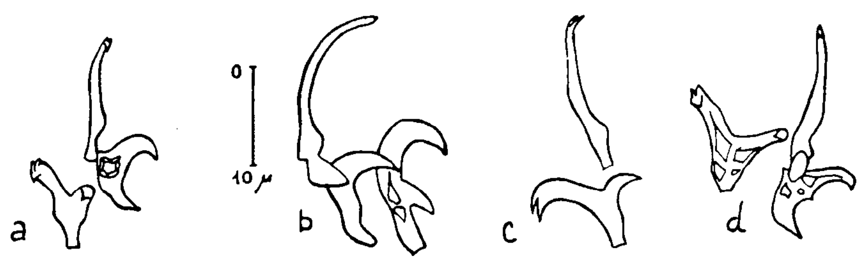


Fig. 448 - *It. trinacriae* Arcidiacono. Doubleclaws: a, from the 1st pair of legs; b, from the 2nd; c and d, from the 4th pair (from Arcidiacono).

On the second or on the third pair of legs there is a cuticular bar about 7μ long, which originates near the base of the internal claws. However Maucci has observed a population, referable as *It. trinacriae*, from Carso Triestino, in which two thirds of the individuals were devoid of such bar.

It. trinacriae was found in Sicily, on the Apuane Alps, on Carso Triestino, and in Abruzzo (Italy). Also in Tennessee (USA) and on the Island of Bali.

For the possible synonymy of this species, see the description of *It. bartosi*.

ITAQUASCON UMBELLINAE Barros, 1939 (Fig. 448).

Length 266-400μ, eye spots absent, cuticle smooth. The body is rather elongated, with maximum width in correspondence with the 3rd pair of legs; sometimes the cavity globules are greenish or brown. The buccal tube is divided into a rigid part and a flexible part, of almost equal length, and the flexible part has its wall with spiral thickening. Stylets weak, with double curvature: there are short stylet supports. The pharynx is elongated oval, with length to width ratio of about 1.6:1. Lacking apophyses and placoids and seems also to lack any cuticular thickening in the lumen. The salivary glands reach almost the posterior margin of the pharynx.

The doubleclaws of each leg are of much different size. There are no cuticular bars on the legs.

It. umbellinae (which can be distinguished from all the other species of the genus by the presence of stylet supports) was found at Itaquaquecetuba in the state of Sao Paulo (Brazil), in Illinois (U.S.A.), and on the Galapagos Islands.

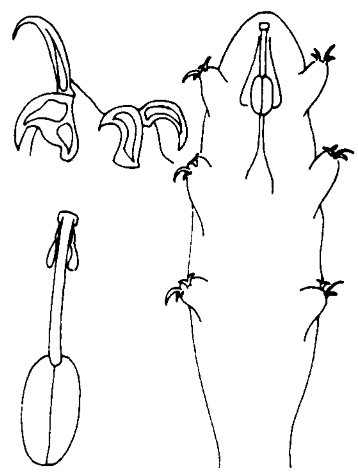


Fig. 449 - *It. umbellinae* Barros (from Puglia, modified).

Genus *LIMMENIUS* Horning, Schuster & Grigarick, 1978.

Diagnosis: Milnesiidae, with four buccal lamellae; the anterior part of the buccal tube is wide and short, the posterior part slender, very elongated, flexible; the stylets enter the tube at the point of constriction, after the wide anterior section; apophyses and placoids absent; claws as in *Milnesium*. (This diagnosis is based on information furnished by Schuster: the original diagnosis is considerably different.)

LIMMENIUS PORCELLUS Horning, Schuster & Grigarick, 1978 (Fig. 450).

Length of 365-675μ, colorless, eye spots present; cuticle smooth. There are present two cephalic papillae, but lacking peribuccal papillae. The mouth has four buccal lamellae (in the original diagnosis is said "lacking buccal lamellae, substituted by one or more membranous flaps"). The buccal tube is composed of a short and wide anterior part (20μ), and of a very elongated, slender, flexible posterior part (also here the original description is different); stylet present, slender, flexible, adhering to the slender part of the buccal tube, stylet supports positioned very back (in the original diagnosis the stylets are given as absent). Pharynx without apophyses and placoids. The claws are as those of *Milnesium*: the two branches of each claw are separate even at the bases; principal branch elongated, slender, apparently without accessory points; the secondary branch, shorter and tripartite apex.

Limmenius porcellus was found only in New Zealand, in five samples of moss (an example in each sample) coming from three stations of South Island.

Genus *MACROBIOTUS* Schultze, 1834.

Diagnosis: Macrobiotidae with a rigid buccal tube, with a

Observations.

The determination of the species within the genus *Macrobiotus* is possible only (in the majority of cases) with the simultaneous presence of their eggs: with the exception of a few species which are endowed with

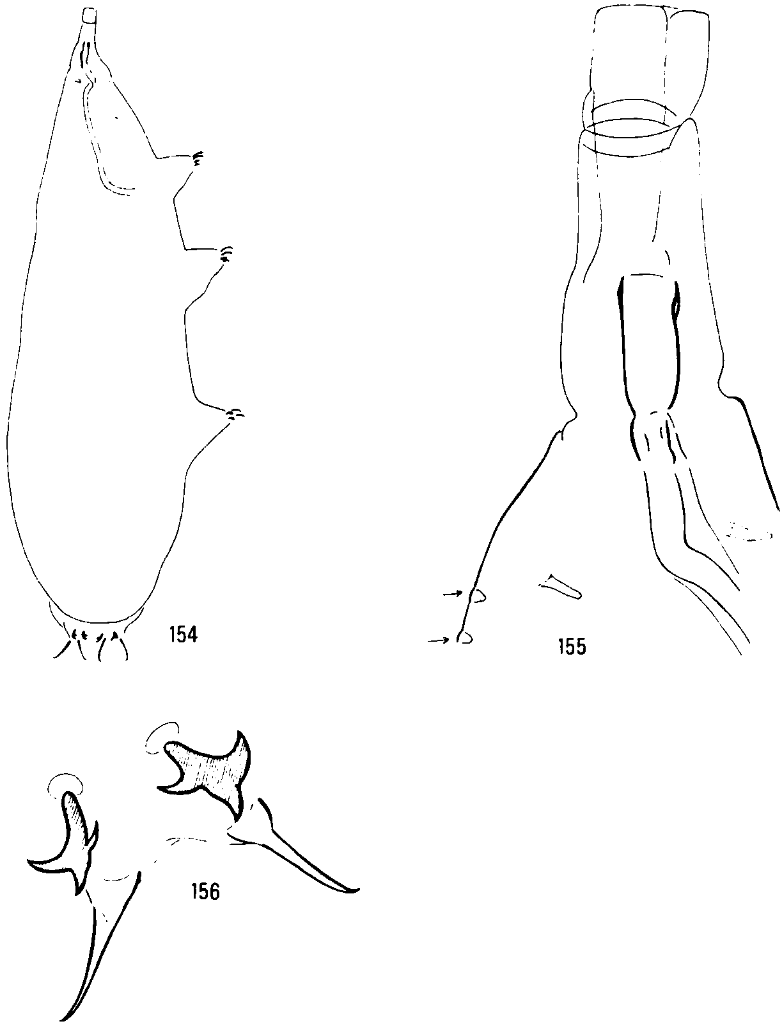


Fig. 450 - *L. porcellus* (Horning et al.). 154, habitus; 155, detail of the head and of the buccal apparatus; 156, claws of the 4th pair of legs (from Horning, Schuster, and Grigarick).

distinct characteristics (sculpturing of the cuticle, large dentate lunules at

We have, however, tried to push forward as much as possible the dichotomy based only on the characteristics of the animal, by introducing the eggs as little as possible before they become indispensable. For some species, the main key leads to the recognition of some "groups": separate keys serve to determine these further.

In the employment of these keys much of the following should be remembered:

1. To those who are beginning the study of tardigrades, it is advised to reread the section dealing with the detail of the buccal apparatus, placoids, claws, and eggs. You are required to know how to distinguish as once -- with only looking at the claws -- a *Macrobiotus* from a *Hypsibius*; in the beginning it is advisable to examine carefully, especially the few critical cases, so as to not mistake the claws of *Calohypsibius* with the claws of *Macrobiotus*, or the claws of *Macrobiotus dispar* (now *Dactylobiotus*) with claws of *Hypsibius*.

2. In the determination of *Macrobiotus* it is advisable, before anything else, to see if the cuticle, especially the caudal region, is either smooth or granulated: however, the key is established by way of a guide to the determination even of the doubtful cases, since the species with little visible granulation, on the cuticle, are often reported in the group of tardigrades with smooth cuticle, rather than those with sculptured cuticle. The simple presence of "pores" or "pearls" on the cuticle ought not to be considered as "granulation" in the use of the key (unless they are deposited in regular lines, or they are very numerous).

3. Remember that the measurements relative to the buccal apparatus and the claws present a notable degree of individual variation. Also, in the species with two macroplacoids, it can occur that the first is constricted until it parts in two, thus giving the appearance of three macroplacoids. Also to this end we again recommend the examination of, if possible, many examples.

4. Remember that some species, that in the previous edition were included in the genus *Macrobiotus*, are now separated into the genera *Dactylobiotus*, *Pseudodiphascon*, and *Adorybiotus*.

5. The following species, included in the previous edition, are eliminated here, due to the original descriptions making identification practically impossible: *M. dubius*, *M. ferdinandi*, *M. luteus*.

6. Some species reported here are described as subspecies by others: we have reserved for consideration, at least provisionally as good species, either by the distinguishing characteristics, in that as much as, in the current state of knowledge it is not possible to decide with certainty

subordination subspecific to a species.

KEY TO THE SPECIES

1. The cuticle is at least partially granulated, dotted, or has gibbosities, or is provided with more or less soft thorny appendages or small papillae 2
   The cuticle is smooth or provided with "pearl like" pores more or less large 14

2 (1). The cuticle shows only a more or less diffuse granulation, without appendages or gibbosities 3
   The cuticle has papillae, gibbosities, or appendages 5

3 (2). There exists a zone of fine granulation, only along the flanks .... *M. hibernicus*
   There is a fine diffuse granulation on the whole dorsal side 4

4 (3). The sculpturing is an indistinct and irregular granulation; 2 macroplacoids and microplacoid .... *M. ovovillosus*
   The sculpturing consists of small stellate structures; 3 macroplacoids; microplacoid absent .... *M. dianeae*

5 (2). The cuticle shows small tubercles on all, or part, of the dorsal surface 6
   The cuticle has gibbosities, plates, papillae, or thorns 8

6 (5). There are tubercles sparsely covering the whole body, each having a central point .... *M. topali*
   The tubercles are restricted to the extreme caudal region 7

7 (6). "Pearl like" pores are present in addition to the tubercles .... *M. granatai*
   There pores are not present .... *M. arguei*

9 (8). The plates are of a brown lenticular form .... *M. hufelandi maculatus*
   The plates form pointed pyramids with polygonal bases .... *M. primitivae*

10(8). The whole body covered with gibbosities .... *M. rollei*
   Papillae or appendages are present on the dorsal surface 11

11(10). There are club-shaped papillae in a
pleated cuticle .... *M. papillosus*
The appendages are spine-like 12

12(11). The appendages of the cuticle spine-like, with
bulbous bases, and arranged in 2 longitudinal
lines along dorsal surface .... *M. julietae*
The appendages are of a conical shape 13

13(12). There exists 3 pairs of spines .... *M. aculeatus*
There is a single pair of spines, near
the posterior end .... *M. subjulietae*

14(1). The cuticle has pores in the form of dimples
which are very dense and/or large 15
The cuticle is smooth, or has small sparse "pearl-like" pores 23

15(14). There are 2 macroplacoids 16
There are 3 macroplacoids 17

16(15). Microplacoid present, lunules dentate .... *M. dentatus*
Microplacoid absent, lunules smooth .... *M. gemmatus*

17(15). Macroplacoids rod-shaped, the third the
longest; microplacoid present .... *M. terricola*
Macroplacoids are equal sized granules 18

18(17). The line of the placoids is short, not
passing the middle of the pharynx 19
The line of placoids passes the middle of the pharynx 20

19(18). The pores are small and circular, laid
in transverse bands .... *M. striatus*
The pores are sub-circular or polygonal,
increasing in size from mid-dorsal to the
rostral and caudal zones where they may
be 6-7μ in diameter .... *M. pustulatus*

20(18). Mouth without lamellae 21
Mouth surrounded by lamellae 22

21(20). Colorless, eggs having projections like the
"head of a screw" enclosed in a transparent capsule ..... *M. intermedius*
Yellowish; eggs with small, dense, soft spines .... *M. furcatus*

22(20). Pores circular or triangular (trilobed triangles),
with a regular diameter of 1.8μ .... *M. pseudofurcatus*
Pores irregular polygons, with diameters of 2-2.2μ .... *M. spallanzanii*

23(14). There are 2 macroplacoids 24
There are 3 macroplacoids 49

24(23). Microplacoid absent 25
Microplacoid present 33

25(24). First macroplacoid clearly constricted in the middle 26
First macroplacoid not constricted, or the constriction is very slight 29

26(25). Moss dweller; there are many small dense "pearl-like" pores; buccal lamellae absent .... *M. occidentalis*
Aquatic; buccal lamellae present 27

27(26). Eggs have projections in the form of goblets, heraldic lilies, or similar, which are immersed, totally or partially, in a transparent zone .... *M. hastatus*
Egg projections are not immersed in a transparent zone 28

28(27). Maximum size 250μ; eggs with projections in the form of small, conical, bent spines, in height about 3μ .... *M. nocentiniae*
Maximum size 560μ; eggs with projections in the form of small conical or mammary tubercles with spaces between .... *M. pullari*

29(25). The 1st macroplacoid is a little longer than the 2nd 30
The 1st macroplacoid is long, about twice the length of the 2nd 31

30(29). Color yellow or orange; cuticle with obvious pores; lunules large, usually dentate or crenate .... *M. islandicus*
Colorless; lunules small and smooth .... *M. annae*

31(29). Aquatic: no buccal lamellae: placoids

32(31). The 1st macroplacoid has a projection pointing toward the midline; eggs have long spines, 11-20μ, which do not touch at their bases .... *M. evelinae*
The 1st macroplacoid has no projection; egg projections are large and angular, arising from hexagonal pattern on the shell .... *M. polyopus*

33(24). Length of the 1st macroplacoid is 2, or more, times that of the 2nd 34
Length of the 1st macroplacoid is less than double the 2nd 37

34(33). The 1st macroplacoid is clearly constricted in the middle 35
The 1st macroplacoid is not constricted, or it is very slight 36

35(34). Red-brown color; lunules small, almost smooth; eggs smooth, deposited in exuvium . . . . . *M. rubens*
Colorless; lunules large, those of the 4th pair dentate; eggs smooth, deposited in the exuvium . . . . . *M. hystricogenitus*

36(34). The two branches of the claws are joined at mid-length, the main branch does not have an accessory point; lunules large and those of the 4th pair dentate . . . . . *M. ariekammensis*
Accessory points are present, the two branches of the claws are joined at the base; lunules very small and incomplete . . . . . *M. polyopus*

37(33). The 1st macroplacoid is not constricted, or it is very slight 38
The 1st macroplacoid is constricted in the middle 41

38(37). The 1st macroplacoid has a projection pointing toward the midline 39
The 1st macroplacoid does not have a projection 40

39(38). Eyes anterior . . . . . *M. spectabilis*
Eyes posterior . . . . . *M. grandis*

40(38). Aquatic; placoids very long and thin; principal branch of the claws has no accessory points; eggs smooth, deposited in the exuvium . . . . . *M. brevipes*
Moss dweller; placoids short; claws have accessory points . . . . . *M. hibiscus*

41(37). Buccal lamellae absent; pores numerous and dense; eggs have small, dense, soft spines with small conical bases and strongly bent tips . . . . . *M. occidentalis*
Buccal lamellae present 42

42(41). In the pharynx, between the apophysis and the 1st macroplacoid, there are 2 thin cuticular bars; eggs have conical ornamentation with large bases and strongly tapered tips ... *M. adelges*
There are no cuticular bars in the pharynx 43

43(42). Lunules large, those of the 4th pair are crenate or dentate 44
Lunules normal or small, not dentate, though possibly those of the 4th pair faintly crenate 45

44(43). Lunules of the 4th pair are crenate; eggs have truncated cones as ornamentation .... *M. tenuis*
Lunules of the 4th pair dentate; eggs with conical projections, or bulbous projections with thin tips .... *M. echinogenitus*

45(43). The eggs have projections in the form of an up-turned egg cup, or they have large conical bases elongated into a cylinder terminating in a small disk .... *hufelandi* group (*hibiscus*, *hufelandi*, *lissostomus*, *persimilis*, *pseudohufelandi*, *rawsoni*)
Eggs different 46

46(45). Length up to 800μ; distance between the stylet supports and end of buccal tube is less than the diameter of the tube; egg ornamentation takes the form of cones with blunt tips .... *M. recens*
Maximum length 500μ; distance between the stylet supports and end of buccal tube is greater than the tube diameter 47

47(46). Eggs have conical projections, and between projections the shell is "tiled" .... *M. aviglianae*
M. pallarii
Eggs different 48

48(47). Eggs have numerous small (about 4μ) projections in the form of truncated cones .... *M. santoroi*
Eggs have projections in the form of elongated cones, the apices of which are subdivided into points or are enlarged into a small notched disk .... *M. andersoni*

49(23). Macroplacoids in the form of almost isodiametric granules 50
Macroplacoids, or at least 2 of them, more or less elongated rods 51

50(49). Microplacoid is absent, or very small, scarcely seen . . . . . *hufelandioides* group (*acontistus*, *artipharingis*, *marcusi*, *hufelandioides*)

Microplacoid present . . . . . *intermedius* group (*allani*, *ascensionis*, *crassidens*, *intermedius*, *subintermedius*)

51(49). One of the macroplacoids is a granule, the others are rod-like 52
All the macroplacoids are rod-like 56

52(51). The 2nd macroplacoid is a granule, 1st and 3rd are rod-like 53
The 1st and 3rd are of granular shape 55

53(52). Aquatic; claws slender with a robust basal basal part; eggs smooth, deposited in exuvium . . . . . *M. norvegicus*
Moss dwelling 54

54(53). Along the dorsal surface are 3 (or 5) longitudinal bands of brown pigment . . . . . *M. virgatus*
Colorless . . . . . *M. potockii*

55(52). The 1st macroplacoid is granular . . . . . *M. insignis*
The 3rd macroplacoid is granular . . . . . *M. porteri*

56(51). Microplacoid absent or very small 57
Microplacoid present 64

57(56). Cavity globules and eggs colored red . . . . . *M. komareki*
Colorless 58

58(57). Buccal lamellae absent . . . . . *M. carsicus*
Buccal lamellae present 59

59(58). Buccal tube narrow (4μ); pores arranged in transverse bands .... *M. bisoctus*
Buccal tube average or very wide (not less than 5μ) 60

60(59). Tube of average width (5-8μ) 61
Tube much wider (9-12μ or more) 62

61(60). Macroplacoids increase in size from 1st to 3rd; eggs have hemispherical projections enveloped in a transparent layer .... *M. mahunkai*
The 2nd macroplacoid is the shortest and the 3rd is the longest; shell of egg is "tiled" and the projections conical .... *M. areolatus*

62(60). Maximum length is less than 500μ; the 2nd macroplacoid does not touch the 1st .... *M. csotiensis*
Maximum length is greater than 500μ; the 2nd macroplacoid approaches, and almost touches, the 1st 63

63(62). Maximum length up to 620μ; the 2nd macroplacoid is much shorter than the others (half the length of the 3rd); eggs have a "stellate" appearance .... *M. tonolli*
Length up to 800μ; the 2nd macroplacoid is long, more than half the length of the 3rd; egg shell has polygonal plates whose edges rise up as rigid spines .... *M. psephus*

64(56). Macroplacoids are short rods (3-5μ) 65
Macroplacoids are longer rods (7-10μ) 66

65(64). The 2nd macroplacoid almost touches the 1st and is shortest, the 3rd longest; eggs have conical projections .... *M. ovidii*
Macroplacoids increase in length from first to last, projections on eggs are immersed in a hyaline zone .... *M. spertii*

66(64). Macroplacoids increase in length from 1st to 3rd 67
Macroplacoids about equal length (the second possibly a littler shorter) 68

67(66). Surface of eggs with reticular design produced by small granular deposits .... *M. kolleri*
Eggs have hemispherical projections which have funnel-shaped depressions .... *M. submorulatus*

68(66). Macroplacoids short rods with rounded ends and arranged in a line concave toward the middle; microplacoid large and placed near the 3rd macroplacoid; cuticle without pores .... *harmsworthi* group (*australis*, *chieregoi*, *furciger*, *gildae*, *harmsworthi*, *liviae*, *mauccii*, *meridionalis*, *montanus*, *nuragicus*, *orcadensis*, *polaris*, *snaresensis*, *stellaris*, *wauensis*)

Different 69

69(68). Buccal tube average width (7μ); eggs have long cones with strongly tapered tips .... *M. willardi*
Buccal tube much wider (15μ or more) 70

70(69). Egg projections are truncated cones or almost hemispherical, shell "tiled" .... *M. richtersi*
Eggs covered with a hyaline layer, in which are partially immersed the ornaments consisting of spine-like cones interspersed with smaller conical or club-shaped projections .... *M. beotiae*

KEY TO THE *HUFELANDI* GROUP

1. Projections of the egg consist of a conical base, surmounted by an extended cylinder that spreads out at the tip 2
Projections are usually in the form of an inverted egg cup 3

2(1). The cylindrical part is shorter than the conical base; lunules occur only in the 4th pair of legs .... *M. pseudohufelandi*
The cylindrical extension is longer than the conical base; lunules are present in all the legs .... *M. lissostomus*

3(1). Between the egg projections the shell is smooth, without pores .... *M. persimilis*
Egg shell has numerous pores between projections 4

4(3). Projections are very close together; a single line of pores runs between neighboring projections .... *M. rawsoni*
Projections are further apart, so more lines of pores run between them 5

5(4). The terminal disk has an entire or only slightly notched margin .... *M. hufelandi*
The terminal disk has a markedly notched margin .... *M. hibiscus*

KEY TO THE *HUFELANDIOIDES* GROUP

1. The buccal tube, viewed laterally, has two angles; eggs are smooth and deposited in the exuvium .... *M. artipharingis*
Different 2

2(1). Projections of the egg are cylindrical with widening tips, and are immersed in a transparent zone .... *M. acontiscus*
Projections of the egg are free 3

3(2). Eggs small, oval, with projections in the form of spines that are enveloped at their bases by a small cuticular capsule .... *M. marcusi*
Egg projections are truncated cone bases with enlarged disk at the distal end .... *M. hufelandioides*

KEY TO THE *INTERMEDIUS* GROUP

1.	Egg projections, in the form of the head of a screw, are all enclosed in a transparent cover	*M. intermedius*
	Egg projections are free	2
2(1).	Egg projections are conical and dense, so there is contact between them, and bear a variable number of small spines at their tips	*M. allani*
	Egg projections do not have subdivided tips	3
3(2).	Eggs have bulbous bases which terminate in a thin undulating apex, similar to a bristle (or hair)	*M. crassidens*
	Ornamentation of the egg has a conical form	4
4(3).	Conical projections are spaced and the shell can be seen between them	*M. subintermedius*
	Projections are packed closely with their bases touching	*M. ascensionis*

KEY TO THE *HARMSWORTHI* GROUP

1.	Buccal tube is very wide (more than 20% of its length)	2
	Buccal tube is only medium wide (less, or much less, than 20% of its length)	8
2(1).	Ornamentation of the egg has tips that are, almost, always subdivided	3
	Tips of the egg ornaments are, almost, never subdivided; ornamentation is in the form of cones or bulbs	4
3(2).	Egg projections are very thin, soft, cones, with tips that are dichotomously, or trichotomously, subdivided	*M. gildae*
	Egg projections are short, squat, cones with the terminal part becoming thin; tips are subdivided into numerous points	*M. nuragicus*

4(2). Projections have a conical form with a constricting collar at the base; there are 8 projections visible in optical section . . . . . . *M. mauccii*
Projections, conical or bulbous, do not have a basal restriction, and there are more than 8 (up to 15) to be seen in optical section 5

5(4). Egg projections are irregular, conical, and sometimes terminated by a filamentous tip; there is also a rectangular pattern on the projections, whose mesh toward the tips forms lines and actual vesicles . . . . . . *M. stellaris*
Tips of the projections do not have vesicles 6

6(5). Egg projections are conical and bulbous, the tips may be elongated and tapering, and in this case the tips are blunt; there are no pores around the base of the projections . . . . . . *M. harmsworthi*
About the base of each projection are small wreaths of pores 7

7(6). Maximum size of the animal 855μ; tips of the projections extend gradually; about the base of each projection are 6-8 large pores . . . . . . *M. snaresensis*
Maximum size of the animal is 650μ; tips of the projections extend abruptly and terminate in a thin point; at the base of each projection are 20-24 small pores . . . . . . *M. harmsworthi coronatus*

8(1). Buccal tube is rather narrow (less than 10% of its length); maximum size 800μ; egg projections are hemispherical or conical . . . . . . *M. polaris*
Buccal tube is wider, 12-18% of its length 9

9(8). Maximum length of the animal is 700μ or more 10
Maximum length of the animal is not greater than 600μ, usually much less 12

10(9). Length up to 700μ; color rose; eggs have few projections, remarkably dispersed, in the form of an elongated drop . . . . . . *M. wauensis*
Colorless; length up to 800μ or more 11

11(10). Buccal tube is wide, 12% of its length or more; eggs have hemispherical projections which have a small, central, disk-like protuberance .... *M. meridionalis*
Buccal tube is wide, 17% of its length; eggs possess from 6 to 8 projections, these are conical and have variously notched bases, the tips are very tapering .... *M. liviae*

12(9). Egg projections are smooth without reticular design 13
Egg projections have a reticular design 15

13(12). Conical projections have tips variously divided into numerous lobes .... *M. furciger*
Tips of the projections are not divided 14

14(13). Projections are bulbous or piriform with distinctly tapering tips .... *M. australis*
Egg projections are hemispherical .... *M. montanus*

15(12). Egg projections are small and conical, with tips subdivided into 2, 3, or more points .... *M. orcadensis*
Projections are large and very high; they are wide based cones which are prolonged into a very tapered tip; the reticular design on the projections is very faint and tends to vanish near the base .... *M. chieregoi*

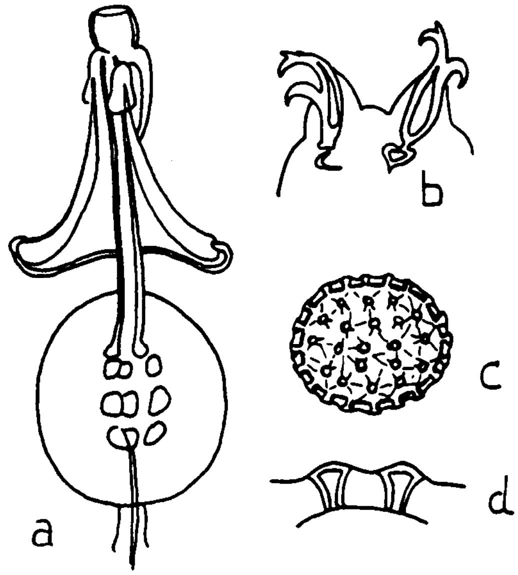
MACROBIOTUS ACONTISTUS Barros, 1942 (Fig. 451).

Size rather small (length about 235μ), colorless, cuticle smooth, eye spots present and in posterior position. Diameter of the buccal tube about 2.5μ; pharynx slightly oval (e.g., 20 x 21μ) with three macroplacoids of granular shape, of which the first is the smallest and the second the largest; microplacoid absent. Claws *hufelandi* type, with small lunule at the base.

The eggs are characteristic, because of the ornamentation of cylindrical shape, flared at the distal end (height about 5μ), are immersed in a transparent zone of the shell, as occurs in the eggs of *M. hastatus*, *M. hibernicus*, and *M. spertii*; the ornamentation of the eggs of *M. acontistus* calls to mind that of *M. intermedius*, which are however singly enclosed in transparent capsule, or free.

The species has so far been observed only in Brazil (Serra Negra, State of Sao Paulo).

Fig. 451 - *M. acontistus* Barros. a, buccal apparatus and pharynx; b, doubleclaws; c, egg; d, detail of the ornamentation of the egg (from Barros, redrawn).



MACROBIOTUS ACULEATUS Murray, 1910 (Fig. 452).

Medium size (length 270-300μ, rarely more); colorless, only the older individuals are pigmented; eye spots in general present. The cuticle -- sometimes with "pearls" -- dorsally displays three pair of pliable conical appendices, or of spine shape with wide bases, in correspondence respectively with the 2nd, 3rd, and 4th pair of legs: these dorsal processes may be reduced to simple obtuse conical projections, or else there may be a single caudal pair, in correspondence with the last pair of legs. Buccal tube narrow; 3 macroplacoids often wider than long, but sometimes even long and slender (Carpathian material); microplacoid present (barely visible) or absent. Claws very slender, of the *hufelandi* type.

The eggs are small and the ornamentations are pliable spines, with minuscule conical bases, distally filiform, wavy, or curved; between the bases of the projections the shell remains free by a larger part of the diameter of the same bases.

So far the species was collected only in Australia (Blue Mounts, New South Wales) and in the Carpathians.

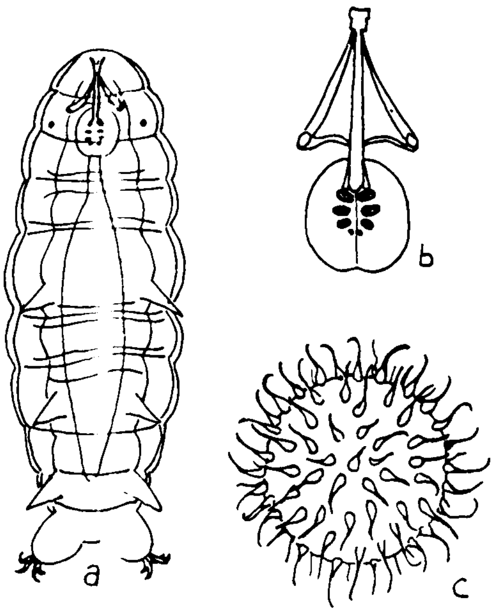


Fig. 452 - *M. aculeatus* Murray. a, dorsal view; b, buccal apparatus and pharynx; c, eggs (from Murray, redrawn).

MACROBIOTUS ADELGES Dastych, 1977 (Figs. 453, 454, 455).

Length 230-754μ. Color clear brown, or violet with brown pigment. Cuticle smooth. Eyes present, in posterior position, rather large. Mouth surrounded by delicate lamellae. The buccal tube moderately wide (width about 11% of the length), slightly folded in two points. Pharynx oval, with apophyses, two macroplacoids, and microplacoid. The first macroplacoid, markedly longer than the second, is slightly constricted at the center. In the pharynx, between the apophyses and the first macroplacoid is noted two slender cuticular bars.

Claws large, especially those of the 4th pair, with long principal branch, and with very small accessory points. Lunules rather large, with wide margins, smooth on the first three pair of legs, dentate on the fourth pair.

Eggs large, white or clear violet; the ornamentations are conical, with wide bases and strongly attenuated apices. There are 31-33 projections visible in optical section. The surface of the projections presents a reticular design, which sometimes is little developed and visible only on the apical part. The apices present some (4-9) very short and

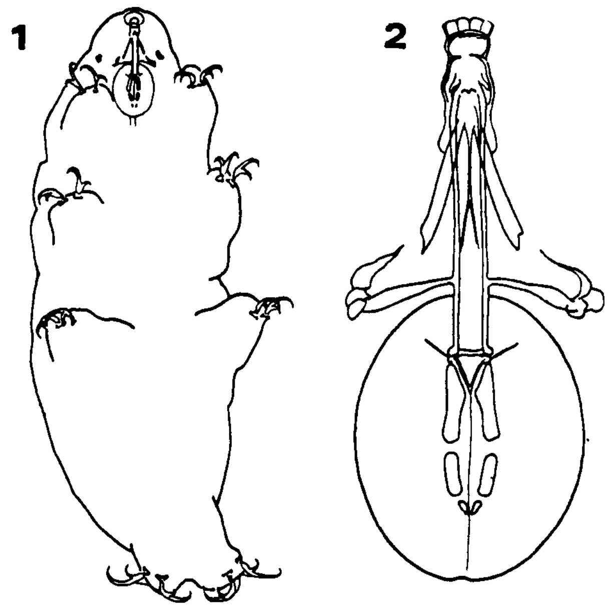


Fig. 453 - *M. adelges* Dastych. 1, ventral view; 2, buccal apparatus (from Dastych).

delicate spines. The bases of the projections are surrounded by dots, while the surface of the egg, between the projections, is smooth.

The species was collected in two localities from Pieniny (Poland).

MACROBIOTUS ALLANI Murray, 1913 (Fig. 456).

Small size (length about 250μ), cuticle smooth, eye spots absent. Buccal tube narrow, with very slender stylets; pharynx almost spherical, with three macroplacoids in the shape of wide granules and microplacoid; claws *hufelandi* type.

The eggs, oval or spherical, are small and have a diameter of about 80μ, including the projections, which are composed of conical processes, densely in contact with each other, each bearing at the distal end a varied number of slender spines, somewhat curved: this last character is the only one which permits the distinction between the eggs of *M. allani* and *M. crassidens*, which possesses instead projections terminated with only one spine.

Typ. loc.: "British East Africa".

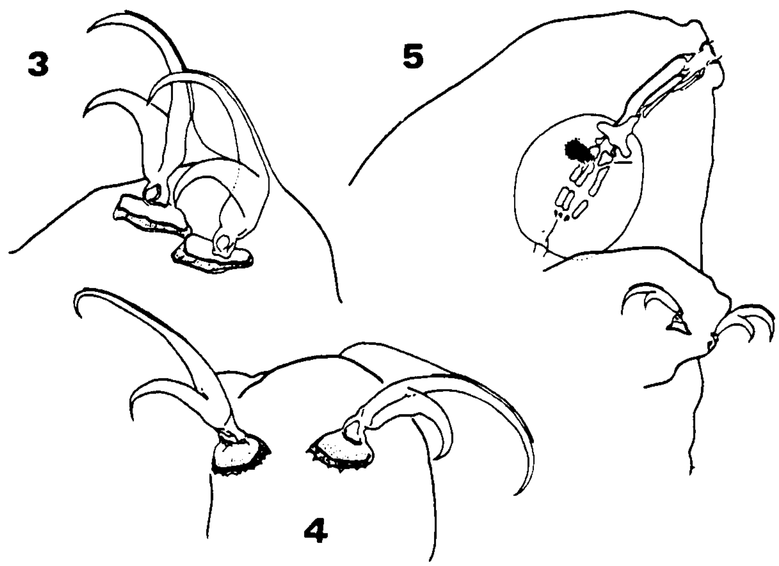


Fig. 454 - *M. adelges* Dastych. 3, claws of the 2nd pair of legs; 4, claws of the 4th pair of legs; 5, cephalic region, lateral view (from Dastych).

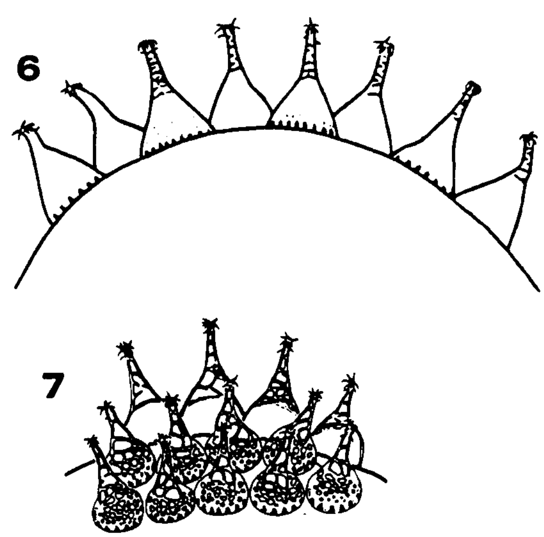


Fig. 455 - *M. adelges* Dastych. Details of the egg.

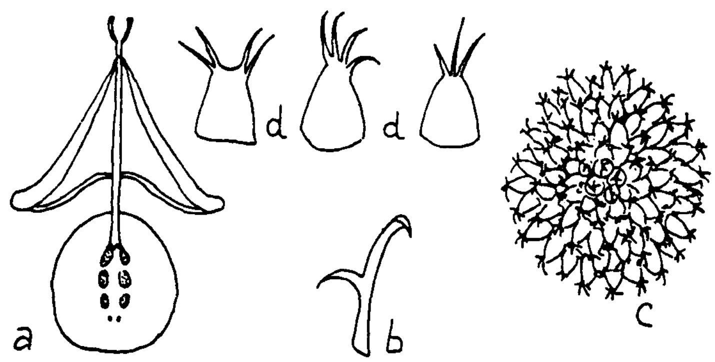


Fig. 456 - *M. allani* Murray. a, buccal apparatus; b, claws; c, egg; d, ornamentation of the egg (from Murray, redrawn).

MACROBIOTUS ANDERSSONI Richters, 1907 (Fig. 457).

The size of the tardigrade was not communicated, but its length should be about 400-450μ, based on the length given of the buccal tube (54μ). The species is colorless, with smooth cuticle and lacking eye spots; buccal tube rather wide (7μ) and pharynx oval, in which exists two macroplacoids of considerable size of rod shape, the first (15μ) curved and somewhat longer than the second (11μ); a large microplacoid is present (4μ). Doubleclaws *hufelandi* type (length 13μ) with obvious accessory points on the principal branch.

Eggs spherical, diameter 81μ, with projections about 18μ high, of bottle (conical) shape, subdivided at the distal end into 2, 3, 4, or more points.

Schuster and Grigarick (Grigarick, Schuster, and Toftner, 1973; Horning, Schuster, and Grigarick, 1978) assigned to *M. anderssoni* examples belonging to the *hufelandi* group, thus described.

Length (including the 4th pair of legs) 470μ. Eye spots present, indistinct. Cuticle smooth, with small sparse pores. Buccal tube 60μ long and 6μ wide; stylet supports attached at 12μ from the base. Pharynx round, with apophyses and two macroplacoids, of which the first, longer, is constricted at a third of its length; microplacoid present, very small. Claws *hufelandi* type; lunules small.

The eggs have 75-80μ diameter, excluding the projections, which are 14-20μ long; the projections are elongated cones, distally terminated in a small disk of notched margin (the projections are not described as subdivided by the authors, but the characteristic is deduced from scanning

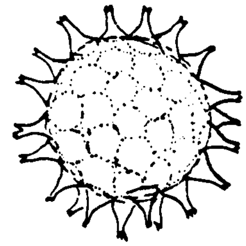


Fig. 457 - *M. anderssoni* Richters.
Egg (from Marcus).

[electron microscope?] photographs. The surface between the projections presents numerous and large pores.

As we see, this description does not correspond exactly with the original description, and seems to refer to a species very near to *M. hufelandi*. It is doubtful therefore that the *Macrobiotus* described by the aforesaid author, can be identified as *M. anderssoni*.

Marcus instead, thinks doubtful the distinction between *anderssoni* and *furciger*. Having had opportunity to see different examples of *furciger*, there does not seem to be doubt about the distinction.

M. anderssoni was collected only in Tierra del Fuego. The examples attributed to *anderssoni* by Schuster *et al.* came from numerous localities in New Zealand. Recently Maucci has found examples and eggs, referable to the description of Schuster, on the island of Crete.

MACROBIOTUS ANNAE Richters, 1908 (Fig. 458).

Medium size (length up to 370μ), transparent, with smooth cuticle; eye spots present. Stylets slightly curved, buccal tube rather narrow (diameter about 3μ), pharynx short oval with two macroplacoids of rod shape, the first longer than the second; microplacoid absent. Claws *hufelandi* type. The eggs, spherical, measuring 108μ in diameter and the ornamentations are slender spines, which each arise from a conical and wrinkled base.

The species was collected the first time at Sumatra and, later, in Hungary.

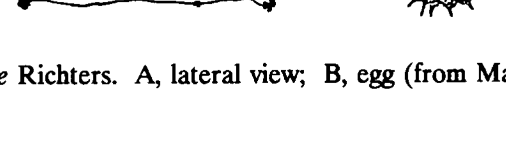


Fig. 458 - *M. annae* Richters. A, lateral view; B, egg (from Marcus).

MACROBIOTUS AREOLATUS Murray, 1907 (Fig. 459).
= *M. echinogenitus* Richters, 1903, in part
(not *M. echinogenitus* Richters, 1904)
= *Hypsibius areolatus* Marcus, 1936
= *M. richtersi*, type 2, Petersen, 1951 (not Murray)
= *M. harmsworthi*, in part, Hallas, 1972 (not Murray)

Size medium to large: length up to 800μ, but often 350-500. Eyes present. Color white, or colorless, cuticle smooth, without "pearls". Mouth surrounded by lamellae, buccal armature composed of an anterior band of small teeth, on top of more rows, and posteriorly of an arrangement of three transverse ventral crests and three dorsal crests, anteriorly to which runs a band of triangular teeth (for greater detail, refer to Pilato, 1972). The buccal tube is rather wide (width up to 14.5% of the length). Pharynx oval, with apophyses and three macroplacoids of rod shape: usually the third is longer, the second shorter. The microplacoid is almost always absent, sometimes present, but extremely small. Claws *hufelandi* type, with lunule of medium size, smooth (sometimes those of the 4th pair slightly crenate).

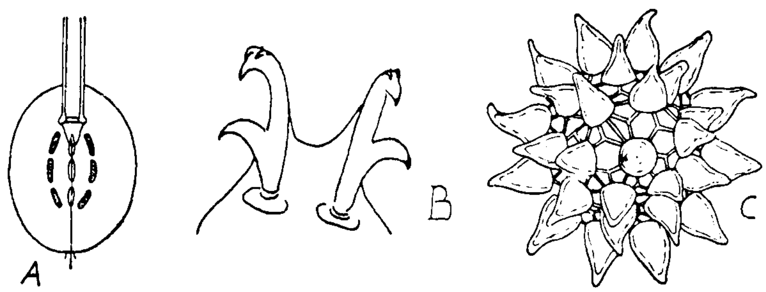


Fig. 459 - *M. areolatus* Murray. A, pharynx; B, doubleclaws; C, egg.

Eggs spherical, with size considerably varied: in general the diameter is 80-100μ, including the projections, but may be larger. The projections are cones, more or less elongated, distally pointed, giving the egg a star appearance. The surface of the projections presents a reticular design of mesh oriented toward the apices of the projections. The shell between the projections presents a tiled appearance, that is to say it appears divided into small polygonal areas, which however seldom appear regular and sometimes indistinct.

This species was placed in the genus *Hypsibius* by Marcus (1936) on the basis of the original drawing of the claws and this assignment was then followed by various authors.

It is no longer possible to doubt the generic position of *M. areolatus*. More recently Hallas (1972) has proposed to unite *M. areolatus*, *M. richtersi*, and *M. harmsworthi*. There i not in any manner possible to accept this unification of clearly distinct species, and -- in our opinion -- not even very remotely wise. *M. richtersi* and *harmsworthi* have a large microplacoid; the eggs of *richtersi* are provided with obtuse projections, hemispherical or cut-off cones, while those of *harmsworthi* have bulbous projections with reticular design of isodiametrical mesh and not oriented, and shell not tiled. In hundreds of populations of our examination, from many varied origin, we have always found each one of the three species associated with eggs of its type.

M. areolatus is an extremely wide-spread and very common species: however in some areas (Scandinavia, Turkey) seems to be very rare.

MACROBIOTUS ARGUEI Pilato and Sperlinga, 1975 (Fig. 460).

Length up to 465μ. Colorless, eyes present. The cuticle is smooth (probably without "pearls"), except near the caudal end of the body where it presents some rounded tubercles whose diameter may reach 1.5-2μ.

Mouth surrounded by lamellae. The buccal tube is rather wide (12.5% of the length); pharynx oval, with apophyses and three macroplacoids of rod shape, the length decreasing from first to third; a rather large microplacoid is present. The buccal armature is similar to that of *M. harmsworthi*.

The claws have two fused branches for a distance less than half their length, presenting accessory points and lunules.

The eggs are spherical and provided with conical projections. The diameter reaches 72μ, excluding the projections, 110 including the same. In optical section they may count 9, or, more often 10 projections, whose height may reach 19μ. The surface of the projections presents a reticular design with mesh almost isodiametrical, very slightly elongated toward the apices of the projections. The shell, between the projections is not tiled, and presents a fine punctation and a reticular design, poorly defined.

The species is very near to *M. harmsworthi*, and perhaps not easy to distinguish, so much so that *M. harmsworthi* is part of a group of related species, perhaps "sibling species" (*montanus*, *orcadensis*, etc.).

M. arguei has been collected in three localities from Sardinia.

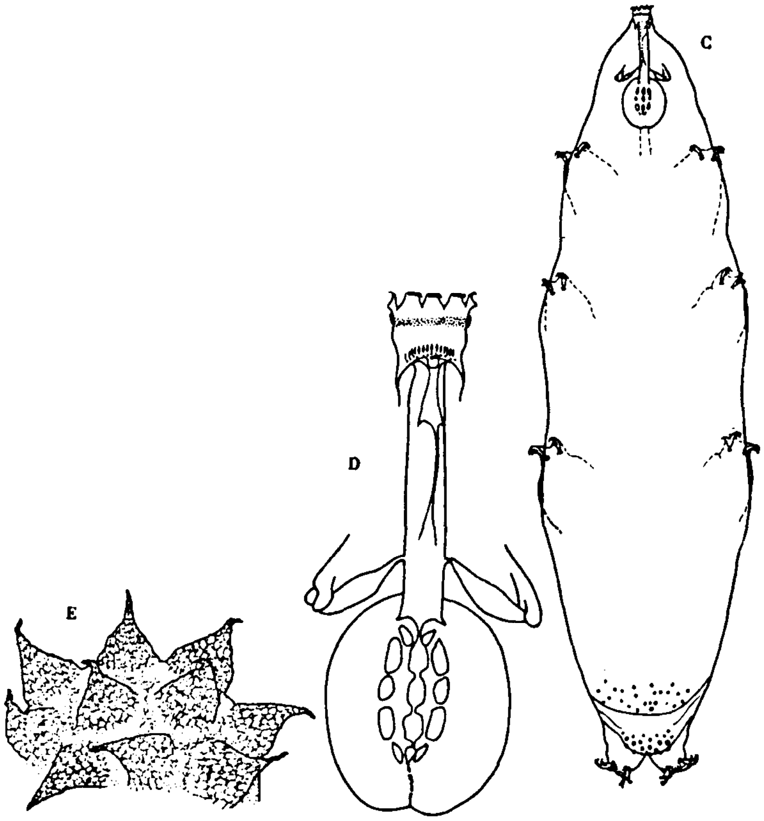


Fig. 460 - *M. arguei* Pilato & Sperlinga. C, dorsal view; D, buccal apparatus; E, egg (from Pilato and Sperlinga).

MACROBIOTUS ARIEKAMMENSIS Weglarska, 1965 (Fig. 461).

Medium length of about 400μ, with a variation between 300 and 450. Cuticle smooth, eyes present, in posterior position. Mouth surrounded by lamellae, in numbers of 12; buccal tube medium wide (about 10% of the length). Stylets slightly curved, with thickened furcae. Pharynx oval (41 x 32μ), with apophyses, 2 macroplacoids of unequal length (the first twice that of the second), and a microplacoid.

The doubleclaws appear to be the *macronyx* type, usually characteristic of some aquatic species, but have at the base smooth lunules on the first three pair of legs, and dentate lunules on the 4th pair. Lacking the accessory points on all the claws. The claws of the 4th pair are considerably larger than the others.

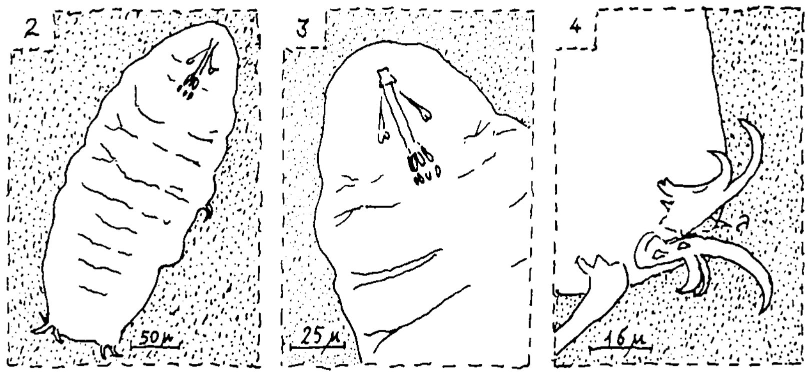


Fig. 461 - *M. ariekammensis* Weglarska. 2, habitus; 3, cephalic region; 4, doubleclaws of the 4th pair of legs (from Weglarska, redrawn).

The eggs are unknown.

The species was collected in a moss near the summit of Ariekammen on Spitsbergen.

MACROBIOTUS ARTIPHARYNGIS Iharos, 1940 (Fig. 462).

Small size: length 150-225μ, smooth cuticle, colorless, sometimes yellowish, eyes present and probably anterior. Buccal tube narrow (1.3-2μ), with two characteristic angles, observed laterally (see figure). Pharynx short oval, with robust apophyses and 3 macroplacoids of rounded granular shape, of which the first and the third (or else the second and the third) are largest, and the second (or else the first) smallest; microplacoid absent.

The eggs are smooth and deposited in the exuvium (4 were observed in a cuticle): this is an extremely rare fact in the genus *Macrobiotus* -- in which the eggs are usually deposited free and have ornamentation -- which joins the case already known of *M. rubens*.

The species has been observed so far only in Hungary, in moss on trees and rocks, and in Rumania.

MACROBIOTUS ASCENSIONIS Richters, 1908 (Fig. 463).

Medium size (length 112-416μ); transparent or colorless; eyes

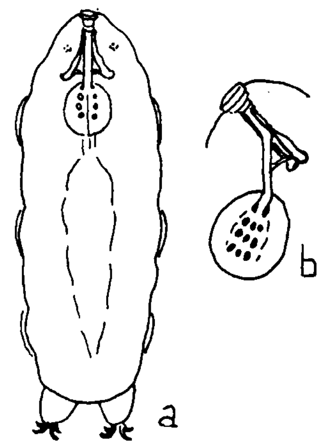


Fig. 462 - *M. artipharyngis* Iharos. a, dorsal view; b, lateral view of the buccal apparatus (from Iharos, redrawn).

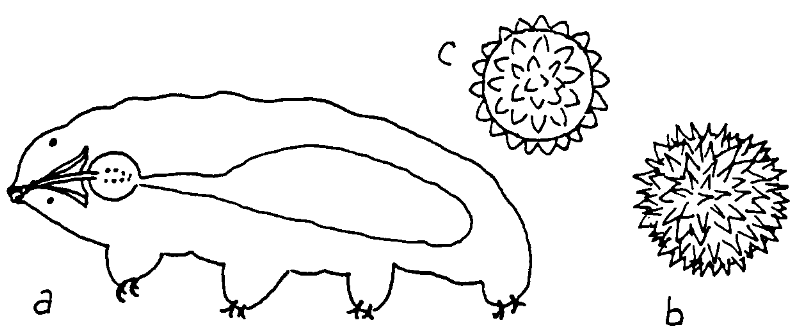


Fig. 463 - *M. ascensionis* Richters. a, lateral view; b, c, two different types of eggs (a, b, from Richters; c, from Heinis, redrawn).

present. Buccal tube very narrow (1-2μ); pharynx approximately spherical, apophyses poorly developed or lacking, 3 macroplacoids with granular appearance and a small microplacoid in the older individuals, which can not be observed with certainty in the young. Claws *hufelandi* type.

Eggs small, spherical, deposited free, with diameter of about 50μ, including the pointed projections of conical shape (Fig. 463 b). It is doubtful that the eggs observed by Heinis (Fig. 463 c) belong to *M. ascensionis*.

The species was collected on Ascension Island and perhaps -- however with much uncertainty -- in south Mexico.

MACROBIOTUS AUSTRALIS Pilato and D'Urso, 1976 (Fig. 464).

Length up to 470μ, colorless; eyes present; cuticle smooth, without "pearls". Mouth surrounded by lamellae; buccal armature composed of three ventral cuticular crests and three dorsal, positioned in the caudal position of the buccal cavity, and with a band of minute teeth situated immediately in front of these crests. Buccal tube wide (more than 16% of its length). Pharynx short oval, with apophyses and three macroplacoids in the shape of rods, of which the second is shortest and the third longest; there is besides a large microplacoid situated very near to the third macroplacoid.

Claws *hufelandi* type, with accessory points and lunule.

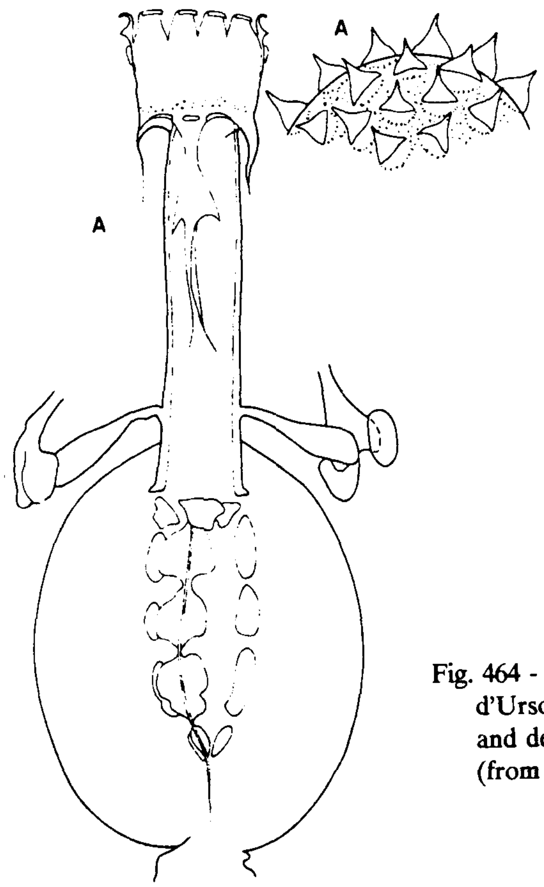


Fig. 464 - *M. australis* Pilato & d'Urso. Buccal apparatus and details of the egg (from Pilato & d'Urso).

The eggs have spherical shape with pear-shaped projections with apices clearly sharpened. The diameter of the eggs may reach 76μ, without the ornamentation, and 96 including the ornamentation, which is 10-11μ high. In optical section there are 19-20 projections. The base of these is surrounded by a ring of large dots, while the shell of the egg has a much finer and irregular punctation. There are no platelets, and the projections are completely smooth.

M. australis, which fits in the *harmsworthi* group, was found at Wallacia, near Sidney (Australia).

MACROBIOTUS AVIGLIANAE Robotti, 1970 (Fig. 465).

Length up to 420μ, in general 400μ. Cuticle smooth, with small irregularly sparse "pearls"; eyes present, posterior. Mouth surrounded by lamellae. The buccal armature consists of three transverse ventral crests and three dorsal crests, in front of that is found a band of small irregularly sparse teeth, with a tendency to be arranged in two parallel rows. Buccal tube moderately wide (about 13% of its length), pharynx oval with large apophyses, two macroplacoids of rod shape, the 1st longer, and almost always slightly constricted, and microplacoid.

Claws *hufelandi* type, with smooth lunules, and accessory points.

The eggs are spherical, with conical projections; diameter excluding projections 80μ, with them 100μ. The cones are 10μ tall, with hexagonal bases: in optical section is contained 15-20 projections. They bear a reticular design. The shell between the projections is tiled in very evident

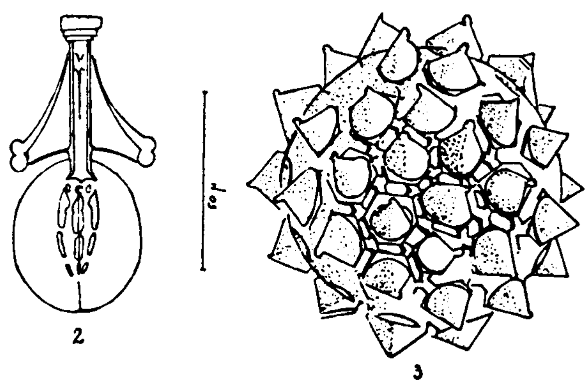


Fig. 465 - *M. aviglianae* Robotti. Buccal apparatus and egg (from Robotti).

and regular manner, all projections being surrounded by hexagonal areas alternatively regular or elongated.

The species is very difficult to distinguish from *M. hufelandi* and related species, in absence of eggs.

It is not excluded that *M. avigliance* may in reality be synonymous with *M. pallarii* Maucci, 1954: however, the type material of *M. pallarii* not being in perfect condition (such that it does not permit a sure identification), Maucci does not think it advisable to sacrifice to an uncertain priority the name of *M. avigliance*, attached to a good recent description, and relied on the abundant typical material.

The species has been collected at Aviglana (Piedmont), and was later found in Sicily, on the Apuane Alps, in Abruzzo, Istria, Norway, Montenegro, and Turkey.

MACROBIOTUS BEOTIAE Durante and Maucci, 1979 (Fig. 466).

Sizes are noteworthy (up to 880μ, with a mean of 700μ), colorless or white. Eye spots absent, cuticle smooth, without "pearls." Mouth surrounded by lamellae. The buccal armature is formed anteriorly of a double row of minute teeth, most of which one finds on the base of the lamellae; posteriorly are 3 dorsal crests, whereas there are no ventral crests, substituted by small round teeth (3-6) irregularly spaced, exceptionally transversely aligned; in front of the dorsal crests and at the ventral teeth exists a row of parallel triangular notches. The buccal tube is short and very wide (up to 25% of the length). Pharynx is large, oval,

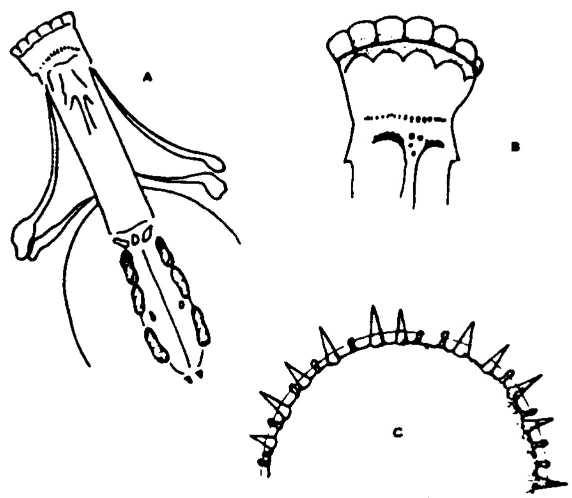


Fig. 466 - ***M. beotiae*** **Durante & Maucci. A, buccal apparatus; B, buccal armature (ventral view); C, surface of the egg (from Durante & Maucci).**

sometimes a little pear-shaped. Small apophyses, 3 rod-like macroplacoids, the first 2 equal and almost in contact with each other; the third, more distant, is longer and terminates caudally with a fold in the median direction; microplacoid oval, large, somewhat distant from the macroplacoids. Between the 2nd and 3rd macroplacoids exists a cuticular spot or plate, placoid-like, slightly smaller than the microplacoid.

Claws of the *hufelandi* type, with strong accessory points, lunules smooth, at times slightly dentate in the 4th pair of legs.

Eggs spherical, yellowish, rather large (145-170μ excluding the projections). The surface of the egg, that appears punctated, is completely surrounded with a thin and uniform hyaline envelope, in which are stuck crater-like dimples, irregularly spaced, while the projections, partially immersed in the hyaline layer, are composed of thin spine-like opaque cones (up to 16μ), alternating with projections shorter, round cylindrical or club-shaped.

The species, in absence of eggs, is very difficult to distinguish from *M. richtersi*. The eggs are always unmistakable.

M. beotiae, found near Levadia, in Beozia (Greece) was successfully collected also at Edessa (Greece).

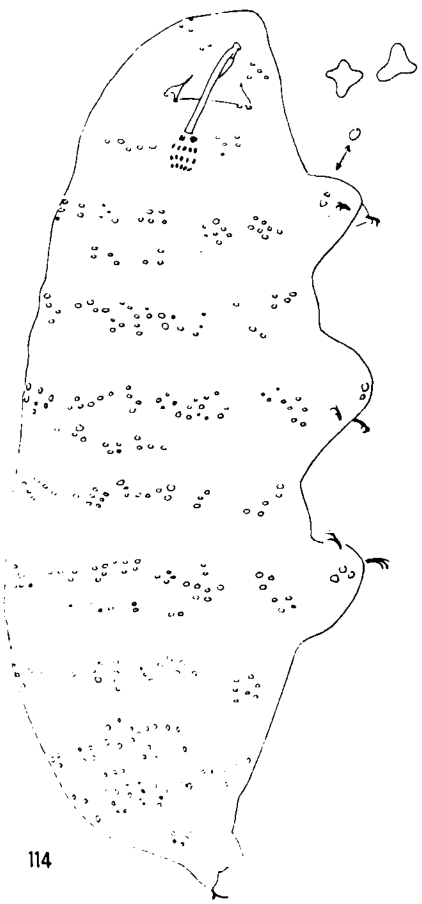
MACROBIOTUS BISOCTUS Horning, Schuster & Grigarick, 1978 (Fig. 467).

Size of 285 to 325μ. Eyes absent. Cuticle smooth, with irregular pores, arranged in fairly distinct transverse bands. Buccal aperture -- it appears -- without lamellae. Buccal tube rather slender (width about 10-11% of the length); there are present apophyses and three macroplacoids of slender and short rod shape of about equal length; the microplacoid seems to be present, somewhat extremely small, dot-shaped. Claws robust, with strong accessory points, and very small lunules, not wider than the base of the claws.

The species (the description of the authors is rather summary, and some information is deduced by observation of the figure) appears to be (according to the authors) near to *M. granatai* and to *M. pustulatus*.

Eggs have not been found.

M. bisoctus has been found in New Zealand.



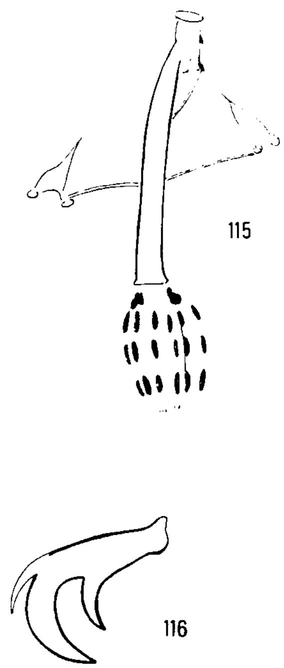
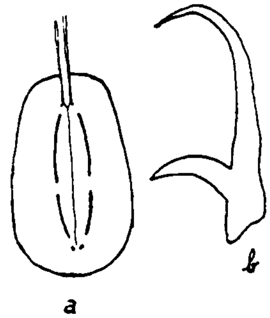


Fig. 467 - *M. bisoctus* Horning *et al.* Dorsolateral view, buccal apparatus, and doubleclaws (from Horning, Schuster, and Grigarick).

MACROBIOTUS BREVIPES Mihelčič, 1971 (Fig. 468).

Length between 250 and 380μ, with short legs, especially those of the fourth pair. Eyes present, posterior. Cuticle smooth. The buccal tube is short and narrow with 1.8-2μ diameter (the length was not cited). Pharynx elongated oval, pear-shaped, that is more narrow rostrally than caudally. Apophyses small, two macroplacoids with appearance of long and slender rods, without constriction, the first a little longer than the second; a small microplacoid is present. Claws small with slender branches: principal branch considerably longer than the secondary, without accessory points. Lunules are not cited, neither peribuccal lamellae.

Fig. 468 - *M. brevipes* Mihelčič. a, pharynx; b, claws of the 4th pair of legs (from Mihelčič).



Eggs smooth, deposited in the exuvium.

This species -- aquatic -- has been observed in the interstitial fauna in Denmark and Sweden.

MACROBIOTUS CARSICUS Maucci, 1954 (Fig. 469).

Length up to 354μ, eyes absent, cuticle smooth, peribuccal lamellae lacking.

Buccal armature composed of a band of triangular teeth, both on the lateral side and on the dorsal (where the teeth are somewhat larger), which follows on the dorsal side a series of three crests arranged transversely, while on the ventral side the crests are replaced by rounded teeth, arranged in transverse row. The buccal tube is rather wide (up to 14% of its length), robust stylets with small furcae; pharynx oval with well developed

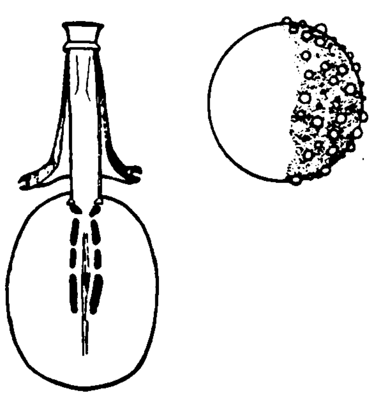


Fig. 469 - *M. carsicus* Maucci. Buccal apparatus and egg (from Maucci).

apophyses and 3 macroplacoids (rounded rods), of which the second is shortest and the third longest; this last has a slight constriction, so that its caudal end appears terminated in a sphere; microplacoid absent. Doubleclaws *hufelandi* type, slender, with small smooth lunule and minuscule accessory points on the principal branch.

The eggs are very characteristic: round, with diameter about 112μ, showing -- in optical section -- about forty yellowish, hemispherical projections, small and widely spaced, not regularly distributed; the shell, between the projections, appears coarsely and densely granulated.

This description is based on a re-examination of the holotype, maintained in the Maucci collection.

This species has as yet been observed a single time and precisely in Italy, in a moss on rock in the sun at about 450 m altitude on Lanaro Mountain (Trieste).

MACROBIOTUS CHIEREGOI Maucci and Durante, 1980 (Fig. 469a).

Length little greater than 300μ (max. 330), colorless, eye spots absent. The cuticle is smooth, without "pearls". Mouth surrounded by lamellae. The buccal armature is composed of an anterior row of teeth, very pronounced; posteriorly a row of large triangular teeth on the ventral

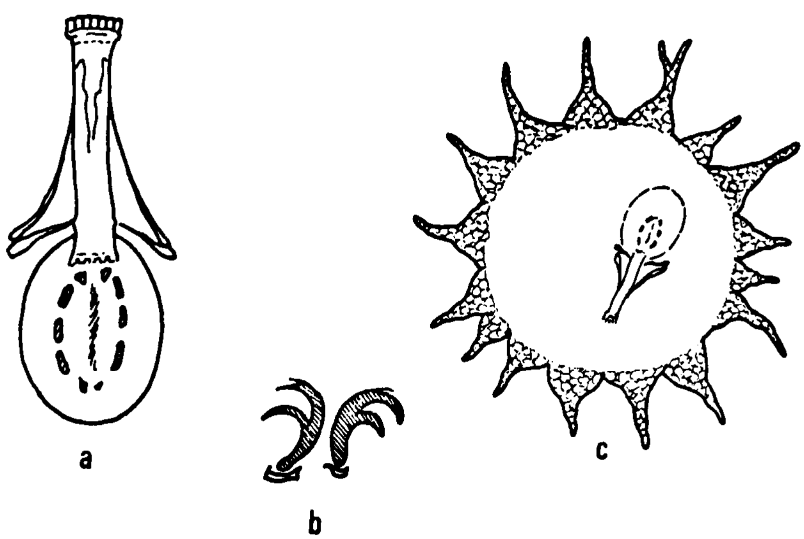


Fig. 469a - *M. chieregoi* Maucci & Durante Pasa. a, buccal apparatus; b, claws; c, embryonated egg (from Maucci and Durante).

side, followed by two short latero-ventral crests and three large teeth at the posterior of the mid-ventral crest; dorsally the row of teeth is followed by the usual three transverse crests. Buccal tube fairly wide (about 15.8% of the length). Oval pharynx very near to the stylet supports, almost in contact with them, with apophyses and three macroplacoids, of rod shape, arranged in rather arched position, as in *M. harmsworthi*: the longest is the third, the shortest the second; the first two placoids are very close to each other, the third is more distant. Microplacoid very small, and rather distant from the macroplacoids.

Claws medium robust: the principal branch is longer than the secondary, and bears weak accessory points; lunule very small, smooth.

The eggs are spherical (72μ without projections, 128 with); the projections (14 in optical section) have a conical base, rather wide, prolonged into a very sharpened apex, terminated in a usual obtuse point, sometimes instead filiform or bifid. The projections have a very slender reticular design, that tends to fade toward the base.

The species -- which is probably near *M. liviae* -- was found a single time, near Port Blair (South Andaman Island).

MACROBIOTUS CRASSIDENS Murray, 1907 (Fig. 470).

Length about 250μ, eye spots absent; the pharynx is oval, with 3 macroplacoids of very wide granular shape, of which the first is in close contact with the apophyses (as in *M. intermedius*); microplacoid present. The doubleclaws are very slender and the principal and secondary branches are not united at the middle of the principal branch, but more rostrally; accessory points have not been observed.

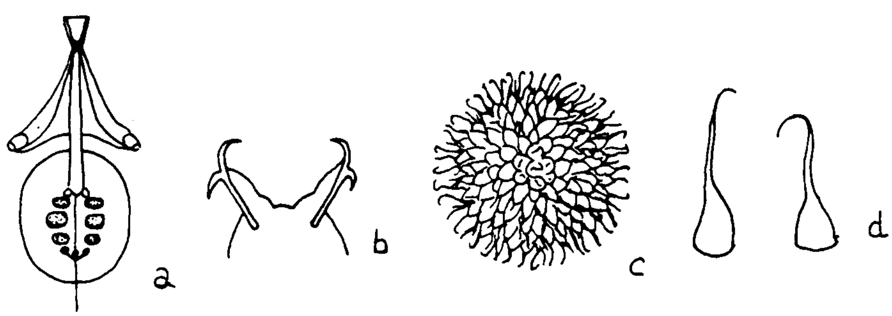


Fig. 470 - *M. crassidens* Murray. a, buccal apparatus; b, doubleclaws of the 4th pair of legs; c, egg; d, ornamentation of the egg.

The eggs, deposited free, are spherical and have a diameter of about 70μ, including the ornamentation, and 50μ excluding these; the ornamentation, enlarged to bulbs toward the bases -- where they are almost in contact -- distally terminated with a slender undulating appendix, of similar appearance to a hair.

The species is distinguished from *M. intermedius* (which it resembles in the pharynx and the placoids) by the different eggs and by the principal and secondary branches of the doubleclaws, united a greater part of the distance; the eggs of *M. allani* differ from those of *M. crassidens*, because the ornamentation distally presents different thorns, and from the eggs of *M. aculeatus*, in which the ornamentations are not in contact at the bases, so that the shell remains visible between them.

M. crassidens was observed in eastern and South Africa, in Australia, in the Hawaiian Islands (Oahu), and in Angola.

Typ. loc.: Cape Town.

MACROBIOTUS CSOTIENSIS Iharos, 1966 (Fig. 471).

Length up to 475μ, colorless, eyes present. Cuticle smooth without "pearls". Mouth surrounded by lamellae. Buccal tube wide (more than 15% of the length). The buccal armature is similar to that of *M. areolatus*.

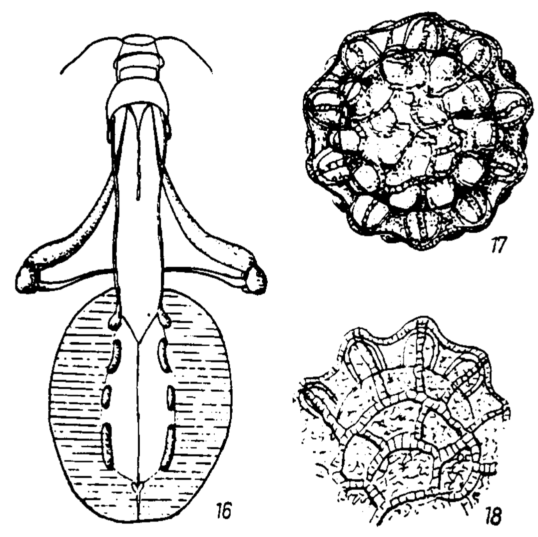


Fig. 471 - *M. csotiensis* Iharos. 16, buccal apparatus; 17, egg; 18, reticular structure of the egg (from Iharos).

Pharynx elongated oval (50 x 40μ) with 3 macroplacoids, of which the 2nd is always shortest, while the longest is the 3rd (in an individual of 475μ the macroplacoids, from 1st to 3rd, measures respectively 7, 5, 10μ); microplacoid absent. Stylets robust and very curved. Doubleclaws *hufelandi* type.

Eggs spherical, with hemispherical ornamentations, positioned very near to each other and covered with a hyaline layer, which is withdrawn (concave) between the projections. The diameter of the egg is 75-80μ including the projections, 60-65μ without these. Surface of the shell finely granulated and with reticular design, of yellowish color. The young measure 120μ in length at the exit from the egg.

The species, recognizable only by the presence of the characteristic egg, was collected in moss subject to repeated desiccation and also on roof of straw and cane, in various localities from Hungary, and also in Sicily.

MACROBIOTUS DENTATUS Binda, 1974 (Fig. 472).

All the specimens colorless and with eyes. The body length barely exceeds 250μ in the adult specimens. The cuticle has pits (holes) generally circular or elliptical and the size varies a lot (the larger have diameters of 2.5μ in the more developed individual); they appear irregularly sparse on the dorsal surface of the body, but on the ventral and lateral they are more numerous in the caudal region. In all the specimens, dorsal to the buccal aperture, one notes 2 elliptical dimples beside one another and this results in bigger size than all the others (about 2.5 x 2.9μ in the more developed individuals). These 2 dimples are quite visible even in the examples still contained within the egg.

The buccal aperture, which surrounds the peribuccal lamellae, is situated in a ventral position so that the front appears steep. The buccal armature is rather plain, in fact, more than in the peribuccal lamellae, in the anterior portion and in that intermediate of the oral cavity are other special cuticular impressions. In the caudal portion, on the contrary, like in many other species, one sees a system of ventral and dorsal transverse cuticular crests. Both dorsally and ventrally because the crest has only as many as two (with respect to the other species, therefore without a crest mid-dorsally or mid-ventrally), and in all specimens one notes that the dorsal crest is more developed than the ventral.

The buccal tube is bent ventrally in the anterior portion and the length is approximately 35μ in the adults (measuring from the base of the apophysis sheath of the stylets results instead in the length of 31-32μ); the

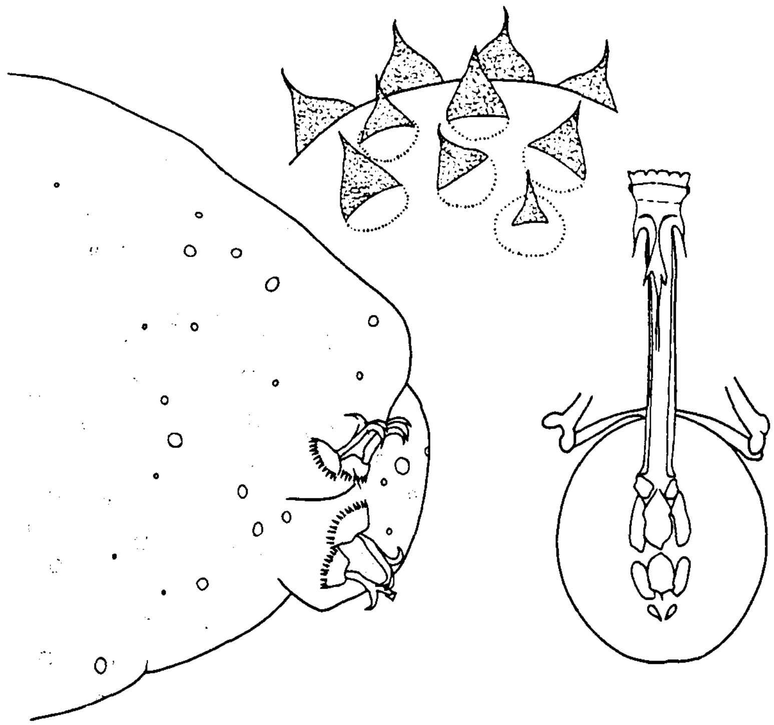


Fig. 472 - *M. dentatus* Binda. Caudal end, detail of the egg and buccal apparatus (from Binda).

internal width is 2.7μ in adults. The pharyngeal bulb is oval and measures about 29 x 25.5μ in adults, with a length:width ratio equal to 1.13:1. It contains large triangular apophyses, 2 macroplacoids (shaped like clubs, sticks) and one microplacoid quite evident. The 1st placoid has a constriction at about a third of the length and the 2nd ends with a swollen circle; in the adult examples the 1st placoid is about 8μ long and the 2nd about 5μ (but in other examples the difference of length between the 2 placoids is less noticeable).

The doubleclaw, of the *hufelandi* type, is small with respect to the total dimensions of the body (approximately 7μ in the adult) and has the principal branch with a large accessory point.

At the base of all the claws is a very developed lunule with margins of about 12 teeth of unusual length.

The eggs of *Macrobiotus dentatus* are spherical and with a starry appearance of protruding small cones. The diameter, exclusive of the cones, is approximately 55μ; including the cones it is about 75μ. The cones have a height of approximately 10μ and a diameter at the base of about 8μ. In an optical section there are 15 to 18 cones. This structure has a conical form with the apex very sharply pointed and generally flexible; at times it also appears bifid. All of the surface of the cones has a delicate entangled (barbed wire) structure with mesh size very small; the base of the cone appears to be surrounded by a corona of dots; but in reality this appearance is in fact where the base of the same cone is slightly disturbed. The shell between the protuberances is completely smooth.

M. dentatus has been collected at Palabione (Valtellina, Italy).

MACROBIOTUS DIANEAE Kristensen, 1982 (Figs. 473 and 474).

Length 230μ (holotype). The mouth is surrounded by ten small lamellae. The buccal tube is relatively wide (3.5μ, with a length of 24μ, in the holotype). The anterior two-thirds of the buccal tube is strongly curved, in relation to the robust reinforcement bar. Pharynx oval (23.1 x 17.6μ). There exists large apophyses, three macroplacoids, lacking the microplacoid. The macroplacoids are, in order, 3.3, 2.2, and 3.8μ long. The first two are in contact with each other.

The doubleclaws have the two branches -- of equal length -- separated at the end of the base, of V shape, that is to say to the *echinogenitus* type. A smooth lunule is present.

Eyes present. Cuticle punctated with small stellate structures, but without "pearls".

The eggs (diameter 30-50μ) present a hyaline zone which forms a regular network of pentagonal mesh. Within this hyaline zone is included projections 4-5μ high, of rod shape with bulbous bases and a constriction at the middle: from the apices, truncated, departs a long and slender spine.

M. dianeae is an aquatic species, and has been found, with many examples, in a warm spring at Unartoq, Disko Island, Greenland.

MACROBIOTUS ECHINOGENITUS Richters, 1904 (Fig. 475).
= *M. crenulatus* Murray, 1907
not *M. echinogenitus* Richters, 1903

This species has been rather drastic taxonomically changed, which can be read in Marcus (1936).

A consolidated taxonomy attributes to *M. echinogenitus* the following description.

Length up to 750μ, but often less, colorless or pigmented brown, eyes

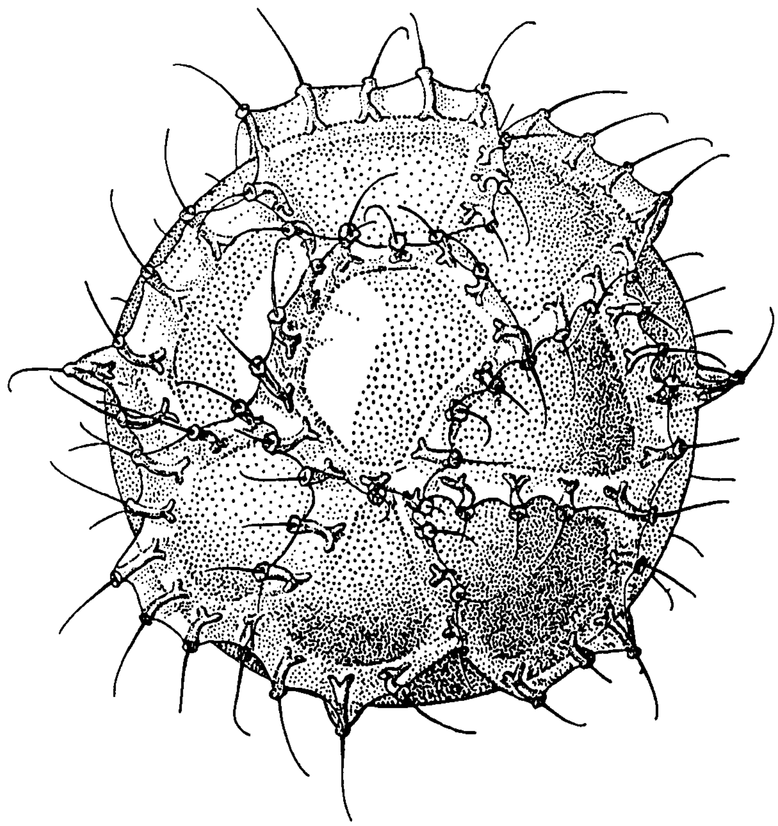


Fig. 473 - *M. dianeae* Kristensen (from Kristensen).

present in posterior position. Buccal tube, with peribuccal lamellae, moderately wide (about 10% of the length of the pharynx or even less); apophyses sometimes well developed, sometimes scarcely visible. The oval pharynx contains 2 macroplacoids of about equal length, or else the first may be longer than the second and may even present a constriction, which may sometimes appear divided in two. Microplacoid present.

Rarely (Scottish material) the legs bear a gibbosity covered with granules or papillae, similar to those of *Dor. evelinae*. The doubleclaws, in young individuals of *M. echinogenitus* are of the *echinogenitus* type (a V, that is with principal and secondary branches separated as far as almost to the base, Fig. 9 G), while in the older individuals they sometimes become the *hufelandi* type (a Y, that is to say with the principal and secondary branches united as far as about half the principal branch); very visible

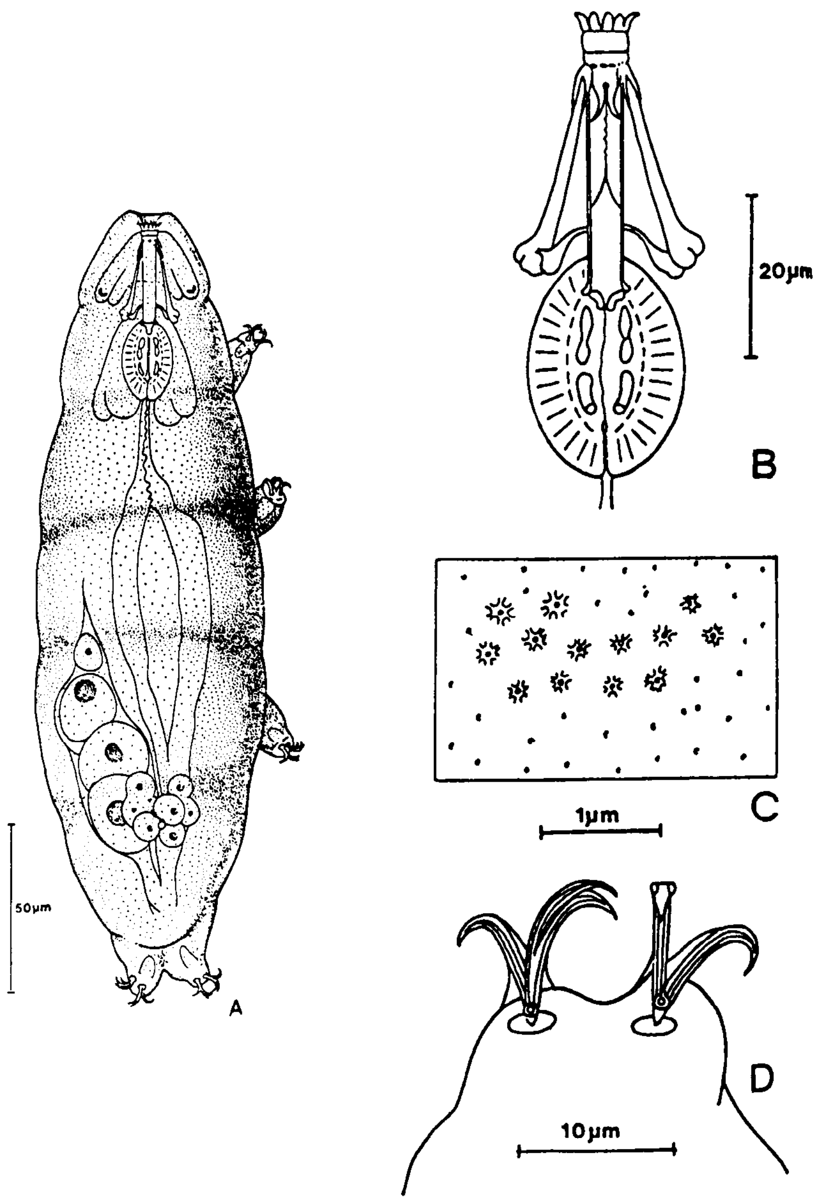


Fig. 474 - *M. dianeae* Kristensen. A, habitus; B, buccal apparatus; C, detail of the cuticle; D, doubleclaws (from Kristensen).

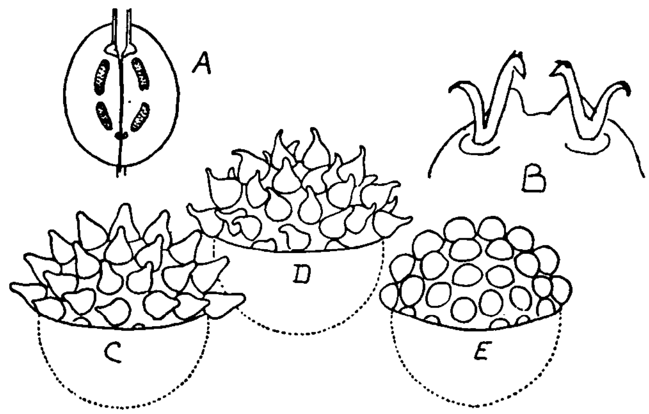


Fig. 475 - *M. echinogenitus* Richters. A, pharynx; B, doubleclaws; C, D, E, various types of eggs.

accessory points on the principal branch; at the base of the claws exists lunules very large and strongly dentate (sometimes crenate). This character is of value to distinguish this species from *M. hufelandi* and related species.

The eggs of *M. echinogenitus* are spherical, with diameter of 65-160μ including the projections (from 14 to 32 in optical section, from 12 to 38μ long), which have very variable shape, conical or onion bulb, punctated or strewn with small papillae, often with apices bent; the shell between the projections -- which rarely are in contact with each other at the bases -- do not have "platelets", and this is the difference from the eggs of *M. areolatus* and *M. richtersi*, whose projections may appear similar (however appears often considerably different to an experienced eye). In exceptional cases the eggs present instead ornaments of rounded cone shape, or almost hemispherical (Figs. 475, C, E).

The species is cosmopolitan and fairly common: it has been found in numerous localities in Europe (also Italy), Greenland, North and South America, Australia, New Zealand, Insulindia, Vietnam, South Africa; it was also observed in soil.

Typ. loc.: Taunus (Austria) and Spitsbergen Island.

MACROBIOTUS EVELINAE Barros, 1938 (Fig. 476).

Length up to 600μ, but on the average 400-450μ; eyes present (posterior); red pigmentation, more intense in the adults. The cuticle has many small pores, especially on the dorsal surface. The buccal tube (diameter 5-6μ) possesses peribuccal lamellae; pharynx large and oval

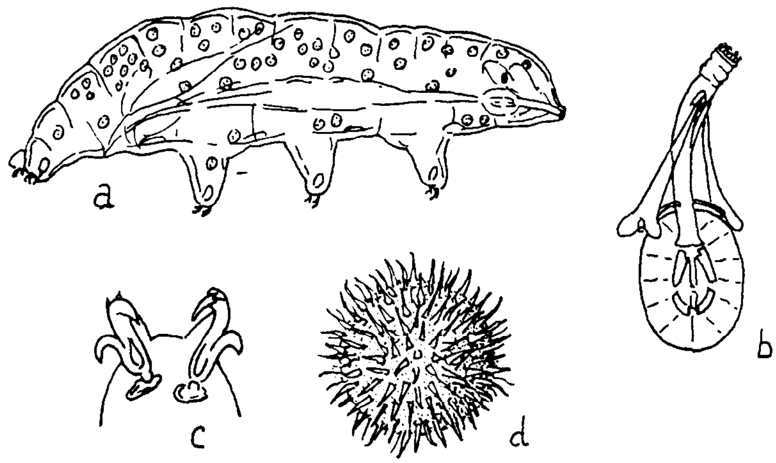


Fig. 476 - *M. evelinae* Barros. a, lateral view; b, buccal apparatus; c, doubleclaws of the 4th pair of legs; d, egg (from du Bois-Reymond Marcus, redrawn).

(39-55μ x 32-47μ) with apophyses and 2 macroplacoids; the first, about twice as long as the second, has a small projection, turned toward the internal part (median); microplacoid absent. Doubleclaws of the *hufelandi* type (a Y), with accessory points on the principal branches and lunules at the bases.

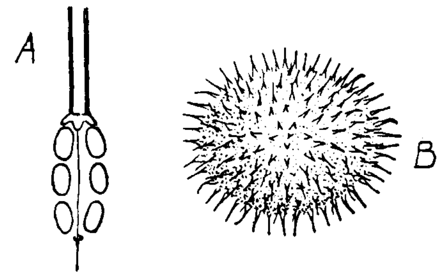
Eggs spherical, of reddish brown color, having diameter of about 86μ, excluding the projections, which are spines 11-20μ long, not in contact at the bases; between the shell remains visible, covered with an irregular granulation. The species was observed in two localities in Brazil (State of Sao Paulo).

MACROBIOTUS FURCATUS Ehrenberg, 1859 (Fig. 477).

Length up to 726μ, more often from about 260 to 430μ; eyed, with eyes posterior; grayish, or more often yellow or orange more or less intense, from carotenoids in the cavity globules.

The cuticle presents pores, much more developed than the usual "pearls", with elliptical shape, or else polygonal (triangular and rhomboidal) with rounded angles, or yet trefoil or four-leaved: these pores are arranged in transverse bands which partially cover even the legs. Peribuccal lamellae absent: buccal tube narrow (not wider than 4% of the length), stylets with maximum curvature toward the middle and caudally robust;

Fig. 477 - *M. furcatus* Ehrenberg. A, placoids; B, egg.



pharynx oval, rather enlarged posteriorly, containing the apophyses and 3 macroplacoids of granular shape, scarcely a little elongated, of which the first is a little shorter than the following two, or else the first two have equal length and the last is a little shorter, or else finally all three have about equal length. The first macroplacoid is very near to the apophyses, so that the external often is partially covered (as occurs, for example, in *M. intermedius*).

The microplacoid may be present or not. Doubleclaws of *hufelandi* type (a Y) with very small accessory points on the principal branch and lunules at the bases, in general smooth, but which may also be dentate. The claws are rather slender and, with respect to the size of the animal considerably long.

Eggs colorless or yellowish, spherical or oval (diameter 52-85μ), with pliable, slightly dentate, about 5μ long, often with curved and sometimes bifurcated apices; the shell between the spines may be punctated.

Cuénot (1932) has rightly noted that *M. furcatus* (with 3 macroplacoids) and *M. occidentalis* (with 2 macroplacoids) are very close species; a limit of overlap between them is supplied in individuals of *occidentalis*, which has the first macroplacoid with a deep constriction, so that it appears divided in two; not only have pure populations of these species been observed, but also mixed populations.

More than to *occidentalis*, however, the species approaches *M. spallanzanii* and *M. pseudofurcatus*, from which, in absence of eggs it is almost impossible to distinguish. *M. spallanzanii* has the buccal tube a little more narrow and shorter, the macroplacoids are more clearly granular shape, and the pores of the cuticle are larger and more pronounced. *M. pseudofurcatus* presents also rather more pronounced pores; the eggs however permit a clear differentiation between these species. Also *M. intermedius* (more easy to distinguish, even in the absence of eggs) probably belongs to this group.

M. furcatus has been collected in various localities of Europe (also in Italy), North America (U.S.A.: Illinois), South America (Brazil), western South Africa, and India. Typ. loc.: Rosa Mountain (Alps).

MACROBIOTUS FURCIGER Murray, 1906 (Fig. 479).
= *M. furcatus* Murray, 1906 (not Ehrbg., 1859).
= *M. ehrenbergi* Heinis, 1921.

Length up to 600μ, cuticle smooth, without "pearls"; colorless or even with 9 transverse brownish bands (variety *vittatus*), of which there are two in the cephalic region, one over each pair of legs, and one on each zone included between the 1st and 2nd, 2nd and 3rd, and 3rd and 4th pair of legs. Eyed, with eyes anterior. Buccal tube provided with peribuccal lamellae, rather wide (diameter equal to about 15% of the length of the pharynx, that is, about $6\text{-}7\mu$); stylets weakly curved and furca little developed; pharynx very little (length 46μ, but probably contracted in the preparations observed and described by Marcus), of oval shape, sometimes almost rhombic, containing apophyses, 3 macroplacoids of about equal length (short rods or oval granules) and a large microplacoid. Doubleclaws

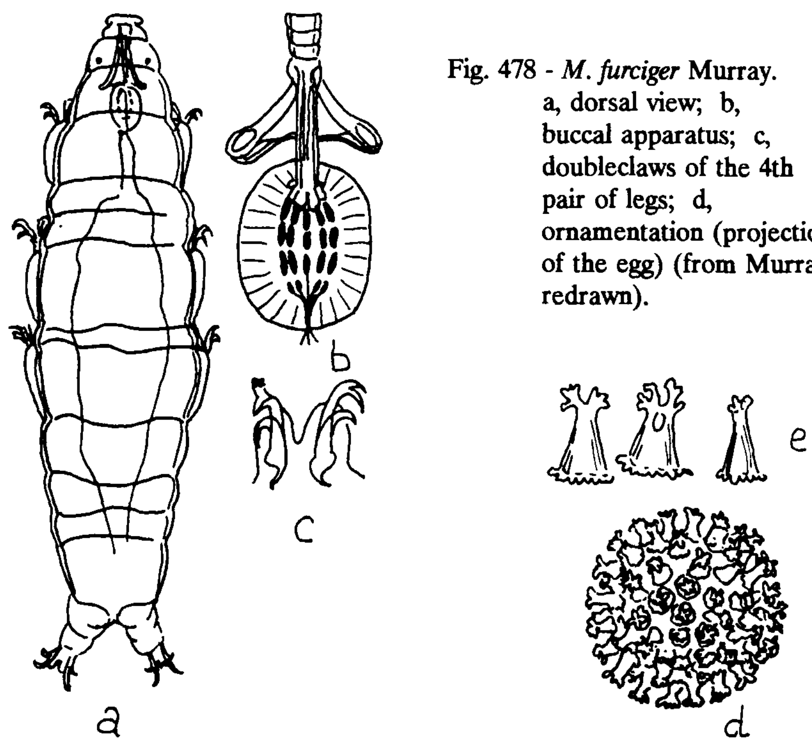


Fig. 478 - *M. furciger* Murray. a, dorsal view; b, buccal apparatus; c, doubleclaws of the 4th pair of legs; d, ornamentation (projections of the egg) (from Murray, redrawn).

of the *hufelandi* type (a Y), with principal branch supplied with very robust accessory points (much more than in *M. hufelandi*).

The eggs are spherical (diameter 103μ including the projections, 83μ without them); the projections are conical, dichotomously subdivided and denticulate at the apices, surrounded at the bases by a ring of dots or of small circles.

The species, in particular by its macroplacoids in the shape of short and obtuse rods, arranged in a rather curved line, and by the large microplacoid very near to the last macroplacoid, belongs to the *harmsworthi* group, a group of very homogeneous species, and difficult to recognize without the presence of the egg: within the limits of this group, *M. furciger* seems near in particular to *M. orcadensis*.

The species was collected in various localities from central Europe and in Romania (not in Italy); also in South America (Tierra del Fuego), in New Zealand, in Antarctica, and recently from Andaman Islands.

Typ. loc.: Southern Orkney.

MACROBIOTUS GEMMATUS Bartos, 1963 (Fig. 479).

Length 254-260μ, color yellowish gray, eye spots black, in posterior position; the cuticle is smooth, but strewn with very visible "pearls". Buccal tube rather narrow (external diameter about 2.7μ, length 27μ), with robust apophyses, reinforcement bar short. Stylets very sharp and slender in their distal half, which run parallel to the buccal tube, and turn laterally out in their caudal half, which always enlarges toward the posterior end. Stylet supports very slender, which depart from the buccal tube at a distance of about 2.7μ from the pharynx. Pharynx spherical (27 x 27μ), caudally notched at the center, containing two large macroplacoids, of which the first (5.4μ) is wide, with a deep constriction a little before its middle while the second (4μ) is also wide, but posteriorly very pointed; lacking the microplacoid. The caudal end of the two rows of macroplacoids reaches beyond two-thirds of the length of the pharynx. Posterior end of the body very thin and terminated in almost square shape.

Doubleclaws of the *echinogenitus* type (a V), about 10.5μ long, with principal branch provided with large accessory points and secondary branches strongly turned out; at the base of the doubleclaws exists smooth lunules.

The eggs are not known for certain, because in the moss examined were also present *M. gemmatus* and *M. insignis* and eggs of the following two different types:

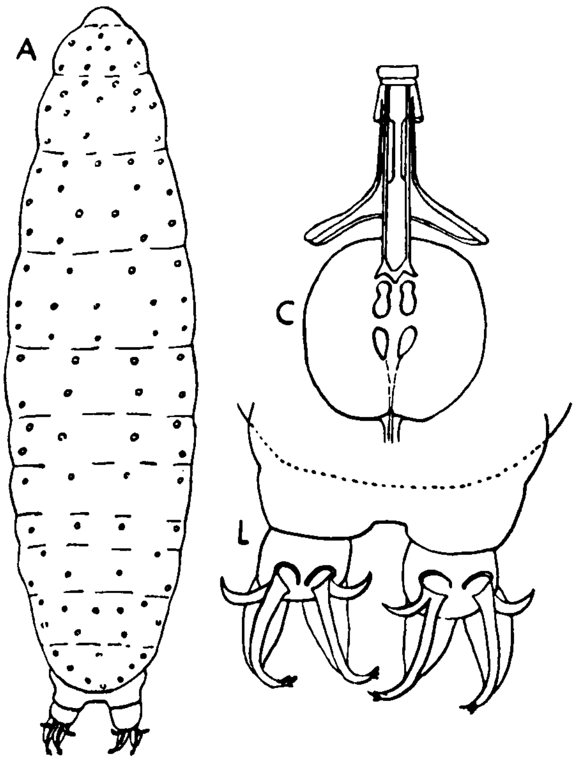


Fig. 479 - *M. gemmatus* Bartos. A, dorsal view; C, buccal apparatus and pharynx; L, detail of the caudal region with legs and doubleclaws (from Bartos).

Type A: Eggs spherical, of grayish yellow color, diameter up to 62μ including the projections which are very slender cones (almost spines), erect, smooth, and empty in the interior, 6μ high, and with diameter of about 2.7μ at the base. These cones are about 8μ apart. Smooth shell.

Type B: Eggs spherical, of clear brownish yellow color, diameter 54μ, shell smooth between the projections: these last -- only 4μ high and 5.4 to 6.8μ apart -- are widely conical in the basal half, while the apical half is composed of a slender and straight extension of about 2μ, of rod shape and always very slanting laterally.

One of these two types of eggs -- according to Bartos -- certainly belongs to *M. gemmatus*. The species was collected on the Ting-chu Mountains near Canton (China) and at Puntiak Pass, between Bogore and Bandung (Java), as well as India.

MACROBIOTUS GILDAE Maucci and Durante Pasa, 1980 (Fig. 479).

Length more than 500μ, colorless. Eye spots present. Cuticle smooth, without "pearls". Mouth surrounded by lamellae, large and long. Buccal armature composed of an anterior band of teeth; posteriorly exists three dorsal crests arranged transversely, almost in contact with each other; ventrally two ventro-lateral slender crests and two large ventro-central teeth; in front of these crests a row of triangular teeth.

The buccal tube is wide (22% of the length); pharynx almost spherical, with apophyses, three rod-shaped macroplacoids, of which the first and the third nearly equal, the second shorter; microplacoid slender and very long (longer than the 2nd macroplacoid). Claws very large, strongly curved, with common basal branch short, principal and secondary branches of almost equal length, and very divergent; the principal branch bears accessory points, very deflected back, along the curvature. Small incomplete lunules on the 1st pair of legs, large, smooth, or weakly crenate

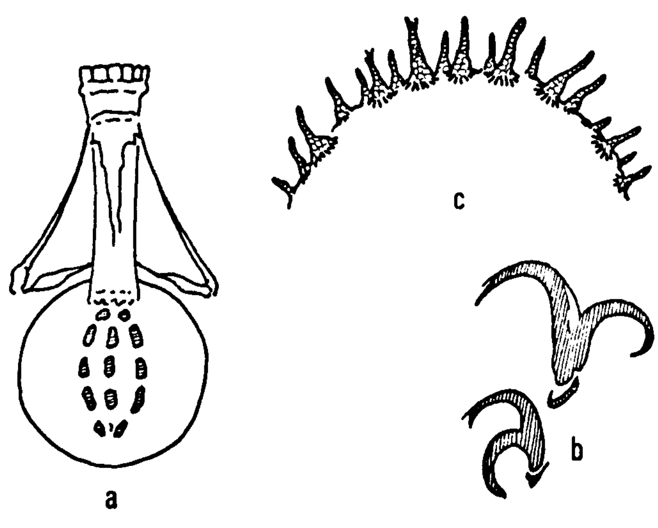


Fig. 479 - *M. gildae* Maucci and Durante Pasa (from Maucci & Durante Pasa).

on the 2nd and 3rd pairs, very large and clearly crenate on the 4th pair.

The only egg examined (clearly belonging to the species, since embryonated) is spherical, with 100μ diameter without the projections, 124 with. The projections have very slender cone shape, with base of 6.5μ and height 16μ, pliable, with apices in general dichotomously divided, or trifid. Each cone bears a reticular design of very irregular mesh, sometimes affecting the entire width of the cone, and in particular toward the apices. The base of each cone is surrounded by a dense radiation of extremely slender streaks, which connect one cone to the others, on the surface of the egg. The embryo, contained in the egg, had buccal tube 40μ long and 7.2μ wide.

M. gildae was found near Port Blair (South Andaman Islands).

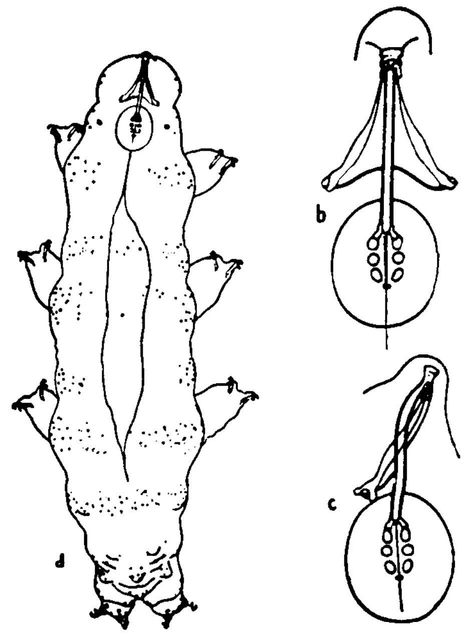
MACROBIOTUS GRANATAI Pardi, 1941 (Fig. 480).

Length up to 335μ; eye spots absent or present: in this last case they are posterior and conspicuous. The cuticle is strewn with brilliant and very refringent granules (pearls?), of various size and round or oval in outline, which are grouped with the tendency to form transverse bands. Caudally the dorsal region shows a complex ornamentation (sculpture), which the author describes composed of:

1. two unpaired and median protuberances, adorned with refringent granules;
2. more paired protuberances, also with refringent granules, of which the caudal pair is more protruding and conspicuous than the others;
3. a cover ring on the legs of the 4th pair, also adorned -- at its margins -- with more refringent granules.

Such sculpture of the dorsocaudal region is present in the adult examples, less evident in the young. Buccal aperture not surrounded by lamellae; buccal tube narrow (internal diameter 1.6μ), with strong apophyses which -- in ventral view -- partially cover the first macroplacoid (as occurs, for example, in *M. intermedius*); stylets robust, with a swelling at about half of their length. Pharynx oval (length:width ratio equal to about 1.2:1); three macroplacoids of granular shape, the first (2.5μ) and the third (2.2μ) somewhat elongated and the second spheroid (1.7μ); a minuscule microplacoid is present. Doubleclaws *hufelandi* type (a Y), with accessory points on the principal branch and with smooth lunules at their base (complete lunule on the 4th pair of legs, incomplete on the others).

Fig. 480 - *M. granatai* Pardi. a, adult in dorsal b, buccal apparatus in dorsal view; c, buccal apparatus in lateral view (from Pardi).



It is probable -- but not certain -- that an egg, found together with *M. granatai*, is attributed to this species: it possessed a smooth shell, without areolation, and was provided with conical based protuberances (ornamentation), smooth and in contact with each other at the bases.

M. granatai was collected at Mega (southern Ethiopia) and was found only in lichen adhering to *Juniperus procera* and on a dry branch of the same *Juniperus*, with scale-shaped and overlapping leaves, on which there were only here and there small lichen patches.

MACROBIOTUS GRANDIS Richters, 1911 (Fig. 481).

It may reach large size (900μ); the cuticle is smooth except on the legs where one notes a fine punctation; the eyes are present in a posterior position. The mouth is terminal and provided with 10 peribuccal lamellae. In specimens 602μ long the buccal tube is 11.5μ wide and has a total length of 68μ (112.9 ms) while measured from the base of the apophyses to the sheath of the stylets, the length is 65μ. The value of the ms index relating to the total length of the buccal tube varies according to Durante and Maucci from 110 to 140. The pharynx is oval with length to width ratio equal to 1.05-1.07:1 and contains normally developed apophyses, two rod-shaped macroplacoids and an obvious microplacoid. The first placoid,

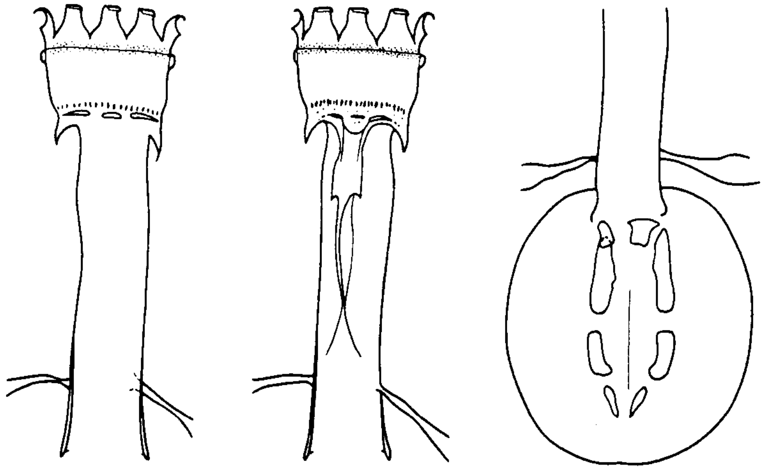


Fig. 481 - *M. grandis* Richters. Buccal armature (dorsal side and ventral side) and pharynx (from Maucci and Pilato).

always longer than the second, has a median projection less evident than in *M. spectabilis* but which may be observed in other species; the second placoid has the caudal end with a sharp curve medially.

In specimens 602μ the first placoid measures 17.2μ and the second 9.5μ; the entire row of macroplacoids is 30μ long and such measurement represents 53% of the length of the pharynx; in the same specimens the microplacoid is 6.6μ. As is noted the length of the placoids and that of the pharynx may vary with the age of the specimen, and such variation may be also considerable (for example for the microplacoid in specimens 602μ long it has a cph index value equal to 11.6, while in specimens 800μ or more long Durante and Maucci have found for the index a value of about 7).

The claws are of the *hufelandi* type and bear accessory points and, at the base, smooth lunules; as is normal, the lunules of the posterior legs are more developed than on the other legs. In specimens 602μ long the external claws of the posterior legs are 15.1μ long and those of the first pair of legs 12.8μ.

The eggs, deposited free, are very similar to those of *M. spectabilis* but not identical with regard to the projections, which have smooth surfaces, not appearing transparent as in this species but having numerous small opaque elliptical surfaces or of irregular shapes (such surfaces are much larger than the minute dots observed on the projections of *M. spectabilis*). The shell between the projections appears tiled exactly as in *M. spectabilis* but appear punctated only along the impressions which delimit the areoles and not at the center of these. The diameter of the eggs is included between 72μ and 132μ excluding the projections (with maximum frequency between 80μ and 100μ), while it is included between 135μ and 190μ including also the projections which have a height of about 38μ and a diameter at the base of about 27μ. In optical section the eggs contain generally 10 projections and only rarely 9 or 11.

The buccal armature of *Macrobiotus grandis* is of the same type as that of *M. spectabilis* but a practiced eye studying the rather minute structures does not have difficulty distinguishing one from the other. In the anterior portion of the oral cavity, besides the ring of peribuccal lamellae, one notes a band of minute teeth; in the posterior portion is seen a ring of triangular teeth and, caudally to this ring, a system of three transverse dorsal crests and three ventral. Between this ring and the system of crests may be present some small supplementary teeth but not ever a true and proper band of such small teeth. In the larger specimens the supplementary teeth are more numerous and in correspondence with the ventral wall may form a row or sometimes almost two very irregular rows, but even in such cases the difference regarding to *M. spectabilis* is very appreciable because the number of teeth in this last species is always greater than that of *M. grandis* and not only in specimens of equal size but also in specimens clearly smaller. The ventrolateral crests may have the lateral portion detached into two or three distinct teeth. The dorsal crests are clearly longer and larger than the corresponding ventral. Posteriorly to the mid-ventral crest, as conspicuous also as *M. spectabilis* and various other species, one can sometimes observe 1-3 supplementary teeth.

M. grandis is cited from Artide (Archipelago Francesco Giuseppe), from Carpazi, Romania, and Switzerland. The present description is based on an examination of an abundant population in Istria (Maggiore Mountains). Other populations have been found in Carso Yugoslavia, in the vicinity of Postumia and Nova Gorica.

MACROBIOTUS HARMSWORTHI Murray, 1907 (Figs. 482, 483).

= *M. echinogenitus* Richters, 1903, in part.
= *M. tetrodon* + *astronenis* Della Valle, 1915.
= *M. echinogenitus* Cuénot, 1932 et al. (not Richters).
= *M. harmsworthi* Hallas, 1972, in part.

Length up to 650μ, but usually between 400 and 500μ; eyes present, in anterior position, sometimes lacking. Colorless or white, smooth cuticle, without "pearls". Buccal aperture surrounded by lamellae. The buccal armature is similar to that of *M. areolatus*. The buccal tube is rather wide,

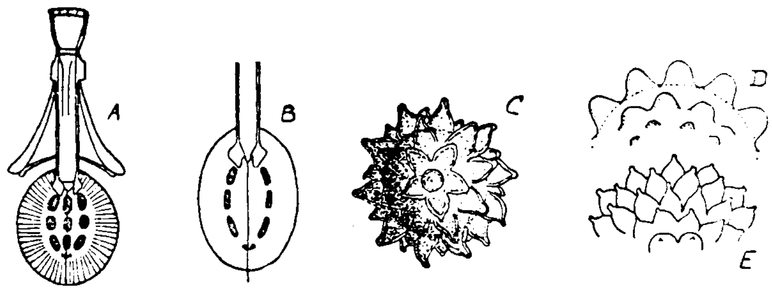


Fig. 482 - *M. harmsworthi* Murray. A, buccal apparatus; B, pharynx; C, typical egg; D, E, other forms of eggs.

or even very wide (almost 20% of the length). The pharynx is oval and contains apophyses and three macroplacoids, in the shape of slightly elongated rods, rounded at the ends, of length almost equal (the third is usually a little longer than the preceding); there is a large microplacoid, very near to the third macroplacoid; the row of placoids has a characteristic bent arc, with medial concavity. Claws of the *hufelandi* type, with strong accessory points on the principal branch. Lunule of medium size, usually smooth, sometimes (in large individuals) slightly crenate on the 4th pair of legs.

The eggs are spherical, with ornamentation in the shape of cones or, more often, a bulb, with apices more or less sharp; this ornamentation has a very fine reticular design but clearly observable with phase contrast, with isodiametrical mesh. Between the ornamentation, when they are not in contact at the bases, the shell has a fine punctation without any hint of "platelets". The diameter of the eggs may be remarkably varied, from 80 to 130μ, including the ornamentation.

M. harmsworthi is a species of extremely wide distribution, probably cosmopolitan (Typ. loc.: Spitsbergen). In absence of eggs the species is practically impossible to distinguish from numerous others, that constitute with it a very homogeneous group: in this we can certainly cite *M. montanus*, *M. orcadensis*, *M. nuragicus*, *M. stellaris*, and perhaps even others.

Clearly distinguishable is on the contrary *M. harmsworthi* from *M. areolatus* and from *M. richtersi*, whose cuticle is also without "pearls", three placoids, and eggs with ornamentation often in conical shape: in fact these two species have egg "platelets", *M. areolatus* does not have microplacoid (or it's extremely small), *M. richtersi* has markedly larger buccal tube, and microplacoid more distant from the third macroplacoid. The unification

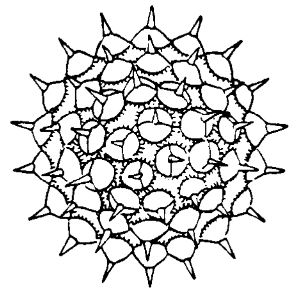


Fig. 483 - *M. harmsworthi coronatus* Barros. Egg.

of these three species, as proposed by Hallas (1972) is therefore, according to us, unacceptable.

With the name of *M. harmsworthi* forma *coronata* Barros, 1942, described populations having characters not distinguishable from *M. harmsworthi*, but different eggs. Spherical shape with ornamentation having a conical or bulbous basal part, prolonged in a slender apex, pointed, similar to a spine, however flexible, sometimes with distal end subdivided into two or three filaments; the base of the projections (that also has a reticular design, similar to those of the typical form) is surrounded by a characteristic ring of elliptical dots. We have been able personally to observe numerous populations referable to this forma (which is not absolutely recognizable in absence of eggs): because we have not ever found mixed populations, we think it may be justified to assign to this forma character of subspecies.

M. harmsworthi coronatus was observed in Brazil (State of Sao Paulo), Tierra del Fuego (Mount Sarmiento), California (Mount Palomar), the Galapagos Islands, in Croazia, Montenegro, on the Andaman Islands, and in other localities from southern Italy.

MACROBIOTUS HASTATUS Murray, 1907 (Fig. 484).
= *Hypsibius hastatus* Thulin, 1928

This is an aquatic species, very wide-spread for example in moss of peat-bogs. Length up to 312μ, eye spots present. Buccal tube medium wide (diameter about 4.5μ), pharynx oval containing the apophyses and 2, or else 3, macroplacoids; microplacoid absent. In general the macroplacoids are 2: the first is longer than the second and is constricted toward the middle, or more caudally, so it appears broken sometimes simulating two distinct macroplacoids in contact with each other; other times the macroplacoids are really three and in such case 1 and 2 are very close, 3 is separated and shorter than 1 + 2.

Doubleclaws of the *echinogenitus* type (a V), with small lunule at the base; principal branch with two accessory points. Eggs, deposited free and very characteristic, round or oval, with diameter about 62-75μ excluding the ornamentations and 75-90μ including the latter. The egg possesses an external transparent zone, in which is immersed -- in all or in part -- the projections of goblet shape, of heraldic fleur-de-lis, etc. The female has clear, but not absolute tendency to deposit the eggs -- two or three at a time -- in the interior of foreign body cavities, for example in shells of Ostracods or Cladocera, in the molt of Acarina (exuvia), etc.

The species was collected in water and in submerged moss in various European localities, Italy included, as well as Sumatra (Typ. loc.: Scotland and Switzerland).

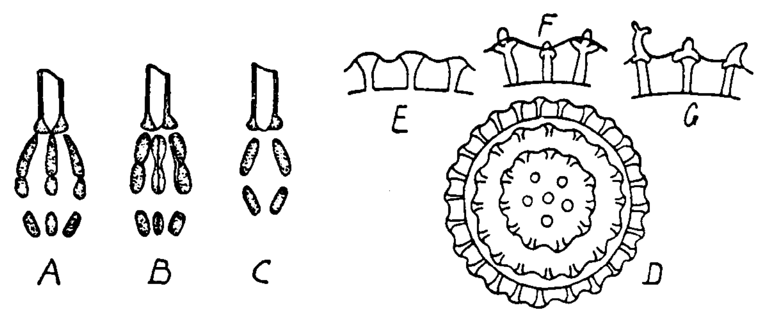


Fig. 484 - *M. hastatus* Murray. A, B, C, placoids; D, egg; E, F, G, various forms of ornamentation of the egg.

MACROBIOTUS HIBERNICUS Murray, 1911 (Fig. 485).

Maximum length about 318μ, colorless, eyes in posterior position. As shown in the figure, the cuticle presents an extremely fine punctation, which covers a dorsal zone over the pharynx and which extends then along the sides, as far as the caudal end: this sculpture is in general very visible only -- and not always with ease -- using the immersion objective and phase contrast. Ramazzotti has also observed Italian specimens (from Val Martello), in which the punctation covers dorsally and laterally the entire

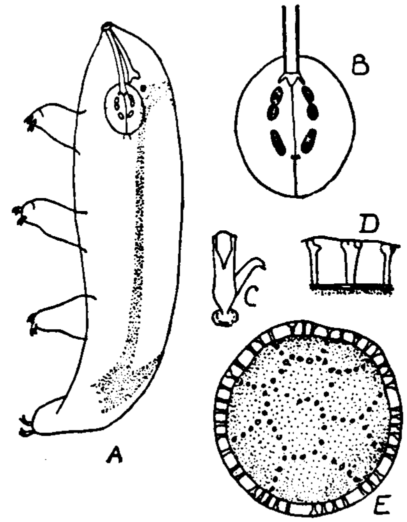


Fig. 485 - *M. hibernicus* Murray. A, lateral view; B, pharynx; C, doubleclaws; D, detail of the ornamentation of the egg; E, egg (from Cuénot, redrawn).

cuticle, without leaving free a zone deprived of sculpture. Peribuccal lamellae present; buccal tube slightly curved and rather narrow (2-3μ); pharynx oval with 3 macroplacoids, of which the first touches the apophyses, the second is of about equal size to the first and almost always in contact with it, the third is longer than the first; other times, instead, the first and the third macroplacoids have about equal length and the second is shortest. Microplacoid absent, or present. Doubleclaws small, of *hufelandi* type (a Y).

The eggs are spherical or oval, sometimes joined two by two, and with diameter of 48 to 70μ; they present an external transport zone, in which is found -- in radial direction -- rods (or tubes) two or three times as long as wide, sometimes with base a little enlarged or rather constricted at the middle, and flared or bilobed end; these rods do not project from the transparent zone, which has a thickness of about 3μ; when observing the back side of the egg, a reticular design is noted, in which the sides of the mesh are composed of rods seen in the front (Fig. 485 E).

The reports of this species are limited to European localities (Czechoslovakia, France, Italy, Ireland, Lapland (typ. loc.), Norway, Poland, Portugal, Hungary, Rumania).

MACROBIOTUS HIBISCUS Barros, 1942 (Fig. 486).

Length up to about 340μ, colorless, eyespots present. Mouth opening consisting of 3 rings (the author does not cite peribuccal lamellae); buccal tube rather short (30μ) and thin (2.5μ); pharynx almost round, with 2 macroplacoids, of variable length and shape, of which the 1st is longer than the 2nd; microplacoid present. The doubleclaw is of the *hufelandi* type (a Y), with accessory points on the primary branch, and is about 8μ long. The eggs are round, with a diameter of about 5.7μ, and have truncated cone-like projections, that get wider distally into a disk at the notched margin; the shell is irregularly punctated.

It is possible that this species is a variety of *M. hufelandi*; in fact, the eggs are practically identical because it is not rare that also in those of *M. hufelandi* the distal disk of the ornamentation is notched and that on the shell is lacking the small crown of points around the base of the projection. The diameter of the buccal tube and the shape of the tube and macroplacoids are also rather variable in *hufelandi*; it seems therefore necessary to study more abundant material, so that this species could be considered valid and truly distinct from *hufelandi*. Of note is also the aberrant form of *M. hufelandoides* with 2 macroplacoids (see the description of this species) which cannot be distinguished from *hibiscus* in some ways.

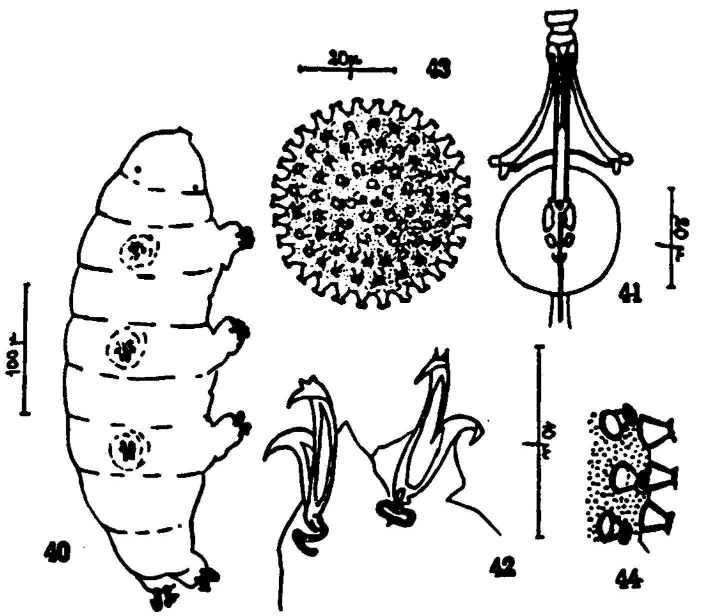


Fig. 486 - *M. hibiscus* Barros. 40, dorsolateral view; 41, pharynx; 42, doubleclaws; 43, egg; 44, detail of the projections of the egg (from Barros).

Schuster and others (Grigarick, Schuster, and Toftner, 1973; Horning, Schuster, and Grigarick, 1978) attributed to *M. hibiscus* animals and eggs described thus:

Length 180-650μ, mean of 362μ; cuticle smooth, eyespots absent. Buccal tube length 54μ and width 6μ (in an example of 400μ). Pharynx nearly round, apophyses and 2 macroplacoids (the 1st 14μ long, the 2nd 10μ); microplacoid present, small (3μ). Claws joined up to half their length, with smooth lunules. Eggs round, with conical projections terminating in an apical disk with jagged edges: the projections are 9-11μ, and are rather distant between each other, the surface between the projections has numerous pores of different sizes.

The identification of these examples with the species described by Barros seems rather dubious. And thus it also seems difficult to distinguish them from *M. hufelandi* (it is of note that the above identification does not refer in particular to the examples from New Zealand, from where the above authors did not cite *M. hufelandi.*

M. hibiscus was cited from a single locality in Brazil (state of Sao Paolo). The examples described by Schuster et al. originated from Tanzania, Italy, Finland, California, and New Zealand. Maucci has attributed, with some doubt, *M. hibiscus* to some samples from Norway (Dombas and Hyerkinn) corresponding to the description of Schuster, and with eggs having small projections, very distant, and with apical disks markedly ravelled.

MACROBIOTUS HUFELANDI Schultze, 1833 (Fig. 487).

This is the most common tardigrade, found everywhere. Average size: many authors, probably repeating each other, refer to the length as up to 1,200μ, that refers probably to reports of other species. The populations of our examinations (many hundreds, with tens of thousands of examples) have average sizes, comprised only between 300 and 450μ, very rarely more; Franceschi and Lattes, in two works on the sizes of populations of *M. hufelandi* (1967; 1968-69) pointed out a minimum number of individuals surpassing 500μ, and none reaching 550μ.

Young individuals are generally colorless, the adults white, often opaque, at times with rows of transverse brownish or grayish pigment; sometimes large individuals have irregular black spots, especially on the posterior part of the body. Eyes are almost always present, in the posterior position. The cuticle is smooth, with pores ("pearls"), rounded small, sparse. Mouth surrounded by lamellae. The buccal armature lacking

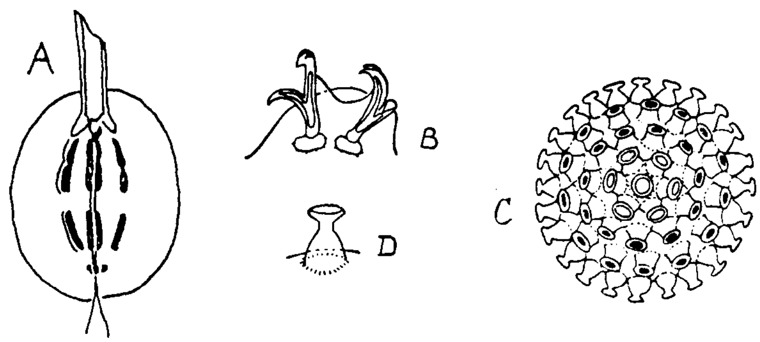


Fig. 487 - *M. hufelandi* Schultze. A, pharynx; B, doubleclaws; C, egg; D, detail of the egg projections.

the anterior band of teeth, while posteriorly exists 3 ventral transverse crests and 3 dorsals, rather thin: the mid-ventral crest is for the most part reduced to a rounded tooth; in front of this crest exists a row of tiny teeth deposited irregularly, without arrangement in parallel rows.

The buccal tube is moderately wide (less than 10% of the length) with a notable individual variability. Stylets robust and slightly recurved; the pharynx is slightly oval and apophyses are present; 2 macroplacoids and a microplacoid; the 1st macroplacoid, which is always longer than the 2nd, often appears, especially in adult specimens, constricted in two; rarely such a constriction divided the placoid, in which case it looks like 3 macroplacoids.

Doubleclaw typical, with primary branch and secondary united up to the middle of the length of the primary branch on which exists robust accessory points. Lunule of medium size, as a rule smooth, rarely lightly crenulate in the old individuals; in these latter ones the legs of the 4th pair often have a sculpture constructed of an irregular very fine punctation.

The eggs are deposited free, sometimes in groups of 2-8 stuck together; the ornamentation is composed of projections shaped of overturned egg cups, namely with a truncated, hemispherical, or bulbous conical base, terminating with a distal extremity widening to a disk, in general smooth and concave, sometimes dentate at the margins. The base of the projections is surrounded by a corona of radial dashes, or of small dots, more or less variously developed. Between the projections, the shell has numerous pores, that renders itself evident like a superficial punctation. Eggs of the type described were also found deposited in numbers of 3-5 in the exuvium. Usually the eggs are round, but oval ones are also found. The dimensions vary a lot, from a minimum of 58μ to a maximum of 140μ

(including the projections). Also the projections are very variable in shape, size, and distribution density, with a minimum of 17 in the optical section to a maximum of 35. This variability made Cuénot (1932) retain the existence of 2 (or more) races of *M. hufelandi.*

Actually numerous other species have been described apparently to a "*hufelandi* group": *hibiscus*, *persimilis*, *pseudohufelandi*, *andersonii*, *rawsoni*. To these descriptions are needed further observations.

M. hufelandi is a cosmopolitan species, spread everywhere, and present in different habitats including terrestrial and sometimes freshwater. The species is cited in all the localities where tardigrades are found (excluding New Zealand). Type locality: Griburgo (Breisgau, Germany).

Iharos (1973) cited as subspecies *M. hufelandi maculatus* some populations collected in diverse samples from Mt. Wilhelm, in New Guinea. This subspecies differs from *hufelandi hufelandi* by the presence, on the cuticle, of lenticular thickenings (of about 6 x 1.2μ) in part irregularly deposited, in part aligned: these thickenings are of dark brown color in living animals, but have a tendency to lose the color in prepared specimens.

M. recens (see that species) can no longer be considered a subspecies of *hufelandi* (as proposed by Marcus) and is now a valid species.

MACROBIOTUS HUFELANDIOIDES Murray, 1910 (Fig. 488).

Length up to 350μ and more, eyes present. Buccal tube thin, diameter about a third that of *M. hufelandi* (lacking more precise indications). Pharynx slightly oval with apophyses and 3 short macroplacoids (short rods or oval granules) of almost equal size and of which the first is in contact with the apophyses. Microplacoid tiny and indistinct, otherwise absent. The doubleclaws, of the *hufelandi* type (a Y), are small and robust, with the secondary branch shorter than the primary: this last one carries distally 2 large accessory points.

The eggs are similar to those of *M. hufelandi*, i.e., with projections with truncated conical bases, widened to a disk at the distal ends, this aspect is like an overturned egg cup; they are surrounded at their bases by rings of dots.

There exists also an aberrant form of *hufelandioides*, without eyes, with only 2 macroplacoids, of which the first is twice the length of the second and has a constriction near the middle. Microplacoid absent; also the doubleclaws are less robust, their primary branches do not show distinct accessory points and finally the projections of the egg do not have a corona

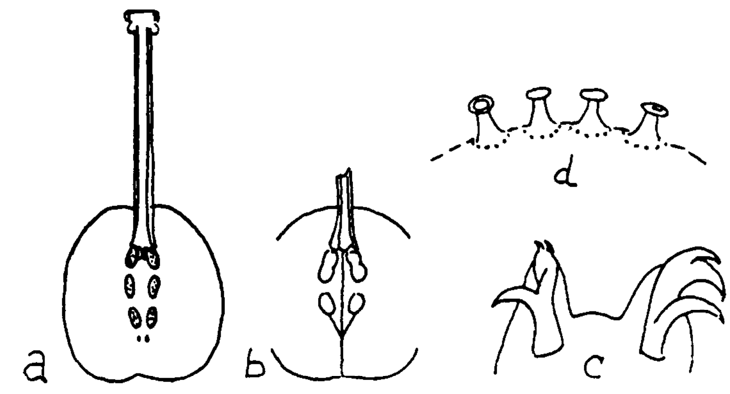


Fig. 488 - *M. hufelandioides* Murray. a, b, pharynx and placoids; c, doubleclaws; d, detail of the ornamentation of the egg (from Marcus, modified).

at their bases.

It seems that the distinction between this aberrant form, *M. hufelandi* and *M. hibiscus* is rather problematical, and that one can say the same about the distinction between *M. hufelandi* with 3 macroplacoids and the typical *M. hufelandioides*; in the last case the difference is limited to the diameter of the buccal tube (a character that presents a large variability) and to insignificant details of the doubleclaws, while also *hufelandi* can have eggs without a corona of dots at the base of the projections. In conclusion, we think that *M. hufelandioides*, like *M. hibiscus* is a species of considerable doubt, needing a more accurate study to establish if these fall within the variability of *hufelandi*, or else remain distinct.

M. hufelandioides, in its typical form with 3 macroplacoids, was only observed in Poland and in Australia; while the aberrant form with 2 macroplacoids was described from Uganda and the Transvaal.

Type locality: Australian Alps.

MACROBIOTUS HYSTRICOGENITUS Maucci, 1978 (Fig. 489).

Length up to 640μ (average of the population 540μ). Color opaque white; eye spots normally absent, sometimes present, with small very sparse dots. Cuticle smooth, without pearls. On the ventral side exists

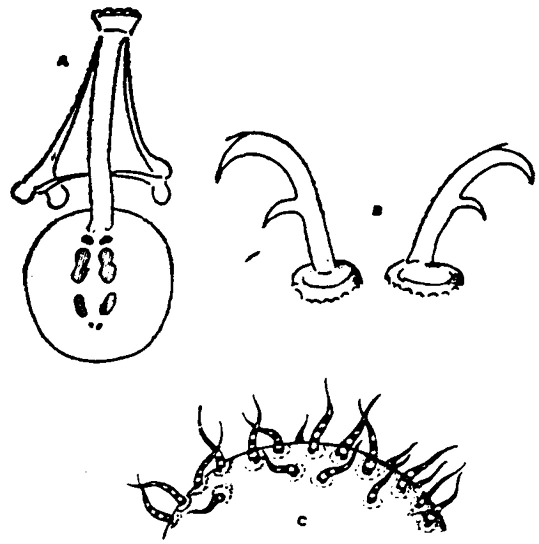


Fig. 489 - *M. hystricogenitus* Maucci. A, buccal apparatus; B, doubleclaws of the 4th pair of legs; C, detail of the surface of the egg (from Maucci).

a finely punctated zone, round or elliptical, arranged with a certain regularity, in transverse rows. Buccal opening wide and short, strongly flared as a funnel. The buccal aperture is surrounded by very small lamellae. The armature is composed only of very slender crests, in the posterior part. The buccal tube is narrow (about 6.5% of its length). Stylets curved, very divergent, with large furcae, stylet supports long, straight. The pharynx is perfectly spherical, with robust triangular apophyses and two macroplacoids of rod shape, of which the first is two times longer than the second, and strongly constricted at the middle. Microplacoid present, slender, elongated.

The legs are stumpy and short. The claws are large and slender, with basal branch considerably long, principal branch strongly arched, with robust accessory points; the secondary branch, short, joined at almost a right angle. Lunules very large and marked, smooth on the first three pair of legs, strongly dentate on the 4th pair.

The eggs, spherical, with 80μ diameter, appear in incident light, neither transparent nor hyaline, rather strongly refringent, white, bright, almost silver. In reflected light they appear instead a very pale yellow-brown. Numerous dense projections, of pliable filament shape, about 3μ wide at the base and then rapidly attenuated to a very slender end, filiform, for a length of 16μ. The base of each projection is contained in a hemispherical hyaline capsule, whose outline presents a clearly punctated circumference. The same projections have an alveolar structure, with evident transverse septa. The surface of the egg is probably covered with a mucilaginous layer, while the projections are considerably fragile: therefore it is rare to find eggs in good condition, being devoid of many appendices and covered with foreign material.

The species is probably very near to *M. tenuis*, which it much resembles. The eggs are however very different, though also appear very refringent as those of *M. tenuis*, golden-yellow and often covered with adhering foreign material.

M. hystricogenitus has been found in one locality in Greece and in two localities in Turkey. Typ. loc.: Mesti (Thrace, Greece).

MACROBIOTUS INSIGNIS Bartos, 1963 (Fig. 490).

Length about 300μ, cuticle smooth, eye spots absent; there exists often on the dorsal surface 9-10 transverse rows of spots, pigmented dirty brown color. Buccal tube rather narrow (external diameter 2.7μ, length 30μ). Stylets slightly curved, with two swellings on each side near the caudal end. Pharynx oval (27 x 24.5μ) with considerably developed apophyses, in which is contained 3 macroplacoids and a microplacoid; the first macroplacoid, small and spherical (diameter 1.5μ), is in direct contact with the apophyses and with the second macroplacoid: this (4.7μ) is wide and has a pronounced constriction toward the middle, so that it seems to be composed of two small spheres. The third macroplacoid (4μ) follows, at a certain distance from the second, and

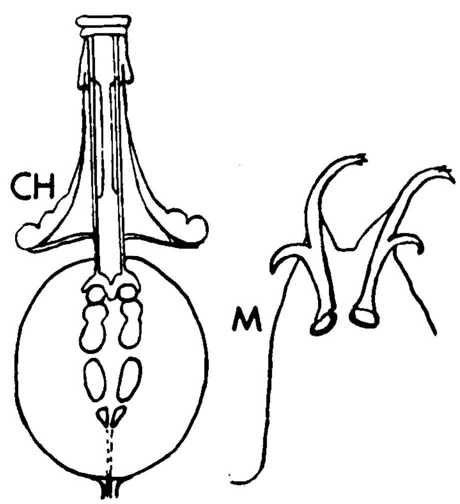


Fig. 490 - *M. insignis* Bartos. CH, buccal apparatus; M, doubleclaws (from Bartos).

has oval shape without constriction. The microplacoid is rather long (1.5μ) and is very pointed caudally.

Doubleclaws of *hufelandi* type (a Y), with smooth lunule and with principal branch provided with robust accessory points. The eggs are not known for certain, because in the mosses examined were always present *M. gemmatus* and *M. insignis* and eggs of the following two different types:

Type A: Eggs spherical, of grayish yellow color, diameter up to 62μ including the projections, which are very slender cones (almost spines), erect, smooth and hollow internally, 6μ high and with diameter at the base of about 2.7μ. These cones are about 8μ apart. Smooth shell.

Type B: Eggs spherical, of clear brownish yellow color, diameter 54μ, smooth shell between the projections: these last -- only 4μ high and 5.4 to 6.8μ from each other -- are widely conical in the basal half, while the apical half is composed of a slender cylindrical and straight extension of about 2μ, of rod shape and always very sloped laterally.

One of these two types of eggs -- according to Bartos -- certainly belongs to *M. insignis*. The species was collected on the Ting-chu Mountains near Canton (China) and at Puntiak Pass, between Bogore and Bandung (Java).

MACROBIOTUS INTERMEDIUS Plate, 1888 (Fig. 491).

Length up to about 350μ, but usually smaller (and one of the smaller species of *Macrobiotus*); color white, sometimes pigmented grayish-brown in transverse bands. All the examples of our observation, from many varied origins, were provided with small eye spots, sometimes very indistinct, however -- according to Marcus and other authors -- the eyes may be lacking. Cuticle scattered with small refringent dots ("pearls"), arranged with a certain regularity: sometimes these dots (which are pores of the cuticle) may be larger, of triangular or rhombic shape, similar to those of *M. furcatus* and *M. spallanzanii*. Viewed in profile the animal shows transverse folds of the cuticle, while the mouth, placed in anterio-ventral position, causing rostrally a steep "forehead", similar to those typical of the *Hypsibius*. Peribuccal lamellae absent.

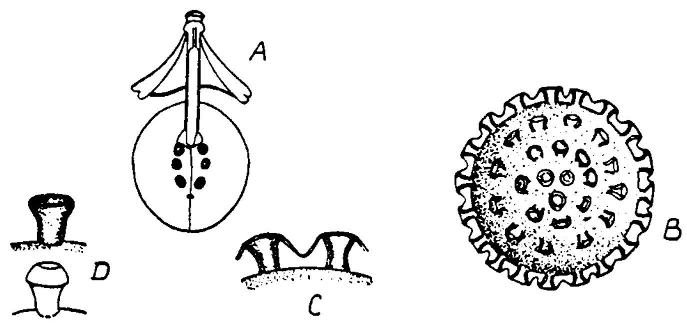


Fig. 491 - *M. intermedius* Plate. A, buccal apparatus; B, egg; C, ornamentation inclosed in capsule; D, ornamentation free.

Buccal armature however absent, that is there exists in the buccal cavity neither teeth nor crests. Buccal tube very narrow (diameter about 1μ) and curved first at its entrance in the pharynx; reinforcement bar especially short, and considerably distant between the stylet supports and the pharynx (2.5-3 times the width of the tube). Almost spherical pharynx containing robust apophyses and 3 macroplacoids of rounded granular shape, of about equal size; small microplacoid. When the tardigrade is observed from the ventral side, the first macroplacoid appears almost hidden by the apophyses, to which it is almost on top. Doubleclaws *hufelandi* type, with principal branch provided with two robust accessory points, and presents at its base a smooth and open lunule, that in incomplete.

The eggs, deposited free, are spherical, with diameter of 40-55μ, and have very characteristic projections, similar to those of the eggs of *M. hufelandi*, but without the basal enlargement, and comparable sometimes to a screw with a large head. Often -- but not always -- the individual projections are enclosed in transparent capsule, or rounded, truncated cone shape, visible only with high magnification and with careful focusing (better with phase contrast). In general the number of projections in optical section is from 17 to 22; however eggs have been found with 34-38 projections, about 3μ high and each contained in gelatinous capsule.

M. intermedius is one of the species of more common tardigrades and widespread everywhere (also in Italy).

The subspecies *julietae* Barros and *subjulietae* Horning et al., having spinose appendices on the cuticle, is here considered -- at least temporarily -- as good species, not being able, at the present state of knowledge to support with certainty any subspecific subordination.

M. intermedius is placed very near to *M. furcatus*, *pseudofurcatus*, and *spallanzanii*, with which probably forms a group of related species.

Typ. loc.: Maribor (Slovenia, Yugoslavia).

For these species, Schuster et al. (1980) has proposed instituting the new genus *Minibiotus*, with the following diagnosis: "Ten peribuccal papulae; without buccal lamellae. Buccal tube short, rigid, without spiral thickenings. Pharynx contains apophyses, macroplacoids, and sometimes microplacoids. Cuticle with or without pores, dorsolateral spines sometimes present... Eggs with processes enclosed in membrane, are deposited free." Besides the type species (*M. intermedius*) the authors think, although not observed by them, that *M. hastatus*, *M. hibernicus*, and *M. spertii* may also belong to the same genus.

We do not think acceptable the genus *Minibiotus*, at the present state of knowledge, both because the characters cited do not seem to be significant at the generic level, and because other different species of *Macrobiotus* have not been found, at this time, and may result in a terminology confusion.

MACROBIOTUS ISLANDICUS Richtersi, 1904 (Fig. 492).
= *Macrobiotus ruffoi* Maucci, 1972

Length 500-560μ, mounted, often with yellow, orange, or yellowish-brown cavity globules; cuticle apparently smooth, but sprinkled with minuscule dots or circles ("pearls"), not very close together and irregularly deposited according to transverse bands, which cover the dorsum and the sides of the animal; it is necessary to attempt to focus the objectives for discerning this very finite sculpture, which becomes more visible in fresh preparations in polyvinyl lactophenol or in Faure's

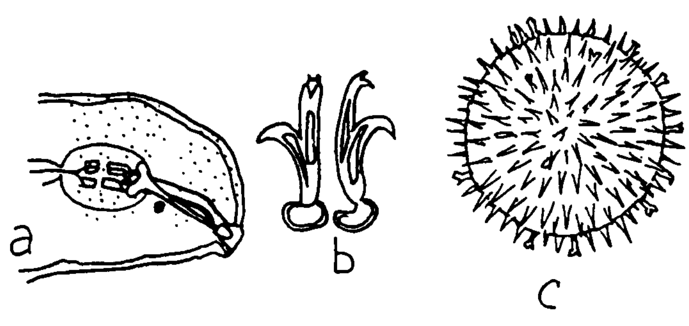


Fig. 492 - *M. islandicus* Richters. a, cephalic region and pharynx; b, doubleclaws of the 4th pair of legs; c, egg (from Marcus, redrawn).

liquid and with the use of phase contrast. Peribuccal lamellae present, buccal tube not very thin (about 14% of the length of the pharynx), with a sharp curvature in the rostral first third and then straight as far as the apophyses. Pharynx oval, with 2 macroplacoids, of which the 1st is longer than the second and which -- in rare cases -- can have a slight constriction; without a microplacoid. Doubleclaw of the *hufelandi* type (a Y); primary branches with robust accessory points, lunule large, in general dentate, sometimes almost smooth. The eggs are round and usually have a diameter of 90-100μ, exclusive of the ornamentation (yet we have seen them larger); the projections of the egg are thin cones, at the bases fairly narrow, often almost spine-like, up to a maximum of 11-12μ, distance between them and their apices not very distinct, having sometimes 2-6 small secondary points.

For the difference between the egg of *M. islandicus* and those of *Adorybiotus coronifer*, see what is said on the subject in the discussion of the latter species.

M. islandicus is a species not found frequently, nor is it very rare. It was observed in Italy, Switzerland, Crete, Yugoslavia, Carpathians, Sweden, Norway, Iceland, Faroe Islands, Spitzbergen Archipelago, Greenland, and U.S.A. Type locality: Iceland.

As for the name of *M. ruffoi*, Maucci (1972) described a population originating from Dikili (western Turkey): a reexamination of the type material made us believe that the difference established did not justify a separate species.

MACROBIOTUS JULIETAE Barros, 1942 (Fig. 493).
= *M. intermedius julietae* Barros, 1942

Length 192-211μ, colorless or slightly brownish, eye spots absent; on the cuticle -- which does not have "pearls" -- exists short appendages of spine shape, with bulbous bases, arranged according to two dorsal longitudinal lines (5 pair of spines) and two dorsolateral longitudinal lines (4 pair of spines); in total they have then 18 spines, arranged as shown in the figure; the very young animals do not have spines. Peribuccal lamellae absent, buccal tube narrow (diameter about 2μ), pharynx short oval, with length:width ratio = 1.1:1, containing 3 macroplacoids of granular shape (about 2μ), equal to each other; microplacoid present. Doubleclaws very small (6μ), with accessory points on the principal branch.

Eggs oval (47 x 50μ) with projections similar to those of *M. intermedius*, that is having cylinders distally flared, or as a screw head, each

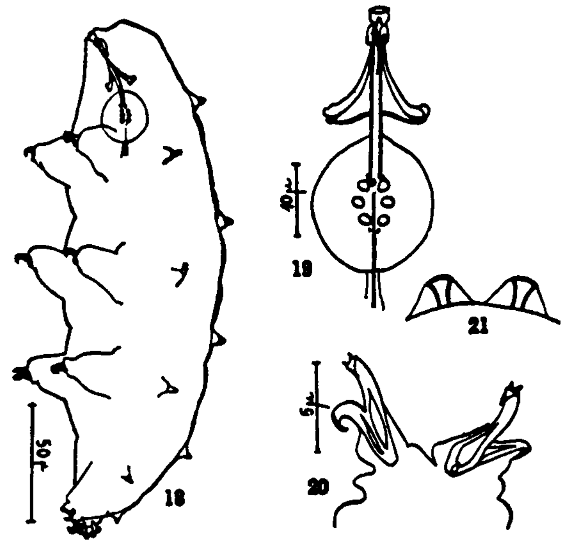


Fig. 493 - *M. julietae* Barros. 18, lateral view; 19, buccal apparatus; 20, doubleclaws; 21, detail of the ornamentation of the egg (from Barros).

enclosed in a capsule of hemispherical shape, or rounded truncated cone; the number of projections, visible in optical section is about 12, that is less than in the eggs of *intermedius*.

The species is known only for two localities in Brazil (State of Sao Paulo).

In spite of the undoubted resemblance of the eggs and of the buccal apparatus, we do not feel it to be hypothetical subspecific subordination of *M. julietae* to *M. intermedius*. The spines of the cuticle and -- especially -- the absence of "pearls" and of pores indicates treatment as different species.

MACROBIOTUS KOLLERI Mihelčič, 1951 (Fig. 494).

Length up to 500μ, cuticle hyaline, eyes present or absent; peribuccal lamellae present, diameter of the buccal tube 5-8μ, pharynx oval with apophyses, 3 macroplacoids of increasing length in rostro-caudal direction, and microplacoid. Eggs of "medium" size (no data given on dimensions), spherical, hyaline. The surface presents a type of sculpture composed of small granules of cap shape, rounded and distinct, with a dark

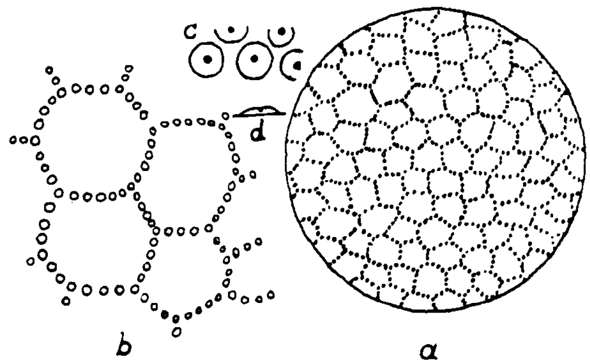


Fig. 494 - *M. kolleri* Mihelčič. a, egg; b, detail of the sculpture of the egg; c, d, individual "cap" granules (from Mihelčič).

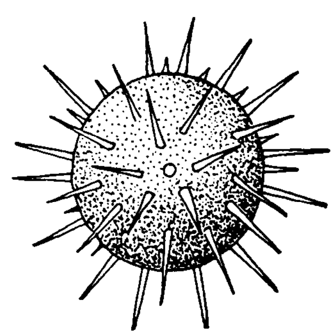
dot in the middle; these granules are arranged to form a type of net with wide mesh.

M. kolleri has been found in Stiria (Austria).

MACROBIOTUS KOMAREKI Bartos, 1939 (Fig. 495).

Length 300-350μ; cavity globules (diameter 12-15μ) intensely colored meat-red; cuticle smooth, but strewn with "pearls", regularly arranged. Stylets robust and very curved; buccal tube medium wide (diameter about 4μ); pharynx oval (25 x 28μ), sometimes pear-shaped, that is somewhat enlarged toward the caudal end, with large apophyses and 3 macroplacoids (rods), of which the second is the longer (5μ) and has a median constriction, while the first is shortest (2.7μ) and rests

Fig. 495 - *M. komareki* Bartos. Egg (from Bartos, redrawn).



against the apophyses; microplacoid absent. Doubleclaws of the *echinogenitus* type (a V). The eggs are very characteristic; their diameter is about 92μ, excluding the projections, and as much as 130μ including the latter; the hollow projections are about 19μ long, narrow at the base, and gradually tapering toward the apex: they have the appearance of smooth spines, clear and very distant from each other, with distal end flexible; between the spines, the yellowish-brown shell appears covered with dark granules; the contents of the eggs has flesh-red color.

The species has been cited for the Carpathians.

MACROBIOTUS LISSOSTOMUS Durante Pasa & Maucci, 1979 (Fig. 496).

Size up to 420μ, with population average of 400μ, hyaline, transparent. Eyes present, posterior, formed of sparse small dot-shaped eyes. Cuticle smooth, generally without "pearls" (these latter are present in a single example). Mouth is anterio-ventral position, surrounded by lamellae of almost trapezoidal shape, pointed. The buccal cavity is narrow, smooth, without either teeth or crests (buccal armature of *M. intermedius* type, Pilato, 1972). The buccal tube, rather narrow, describes a sudden curve after the mouth cavity, then proceeds straight as far as the pharynx. The reinforcement bar, initially large and robust, follows then extremely slender and very short (not ever reaching the middle length of the tube). Stylets slender and very curved, with small furca and thin supports. Pharynx oval or pear-shaped, with two macroplacoids of rod shape, of which the first is longer than the second (sometimes the first, rarely also the second, is slightly constricted at half its length). Microplacoid present.

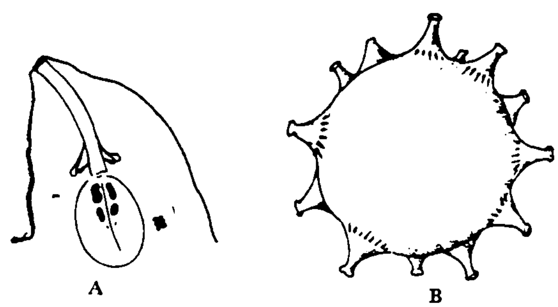


Fig. 496 - *M. lissostomus* Durante Pasa & Maucci. A, buccal apparatus; B, egg (from Durante Pasa and Maucci).

Claws large, with accessory points on the principal branch and extremely small smooth lunule, or absent.

Eggs colorless, spherical, with diameter from 65 to 80μ without projections (from 85 to 120 with the projections). The projections, up to 20μ tall, have a wide truncate conical base, which is prolonged into a cylinder with a flat apex, sometimes bifurcated, sometimes moderately notched. Such projections (surface absolutely smooth) are considerably distant from each other, and present at the base a very obvious ring of crests. The surface of the egg, between the projections is reticulated with rather wide mesh.

M. lissostomus has been found in Epiro, and later at Crete. Typ. loc.: Kerasson (Epiro, Greece).

MACROBIOTUS LIVIAE Ramazzotti, 1962 (Fig. 497).

Length 600-940μ, cuticle smooth and provided with "pearls", eyed. Buccal tube wide (external diameter 14μ in an individual of 940μ), reinforcement bar long. Peribuccal lamellae robust and large, which seems to be arranged as two concentric rings, the external with shorter lamellae than those of the interior ring (different from *M. furcatus*). Pharynx oval, with three macroplacoids and an obvious and triangular microplacoid; the first two macroplacoids are very close to each other, the third is more distant; the first and third have about equal length, the second is shortest. The relative measurements, in a *M. liviae* of 940μ, are: pharynx, 74 x 61μ; length of the 1st and 3rd macroplacoids, 12.7μ; length of the 2nd macroplacoid, 10.5μ; length of the row of placoids, 38μ, excluding the microplacoid, and 47μ including the latter; distance between the pharynx and the insertion of the stylet supports, 8.5μ, that is less than the length of the buccal tube, which is 14μ (different from *M. harmsworthi*).

The doubleclaws seem *almost* of the *echinogenitus* type, because united only for a short distance near the base; they are rather short in relation to the size of the animal (24μ for the principal branch and on the 4th pair of legs) and has two accessory points on the principal branch.

M. liviae is not easily distinguished from other *Macrobiotus* with 3 macroplacoids and wide buccal tube, when the eggs are absent: but these, very characteristic, permit an immediate recognition of the species. They are large (for example with external diameter of 190μ and internal of 97μ) and possess 6 to 8 (in optical section) projections (ornamentations), each composed of a conical basal part (diameter at the base 30-32μ, height about 21μ), which at the apices is continued in a slender appendix of shape

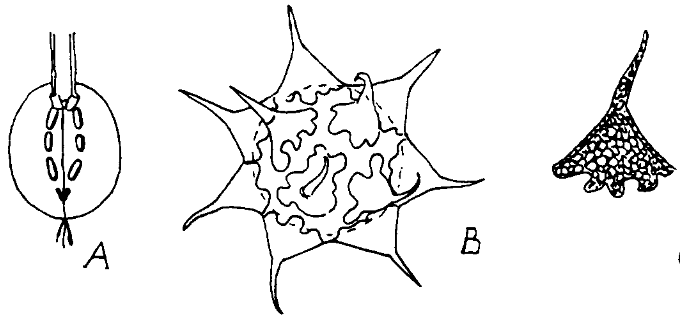


Fig. 497 - *M. liviae* Ramazzotti. A, pharynx; B, egg; C, detail of a projection of the egg.

almost of a spine, sometimes rather bent, in average 32μ long; that is to say the projections measure inclusively 50-55μ in length -- with abundant variation -- and have at their base, where it rests upon the shell, variously notched, often deeply hollowed (even more than shown in Fig. 497) so as to simulate a "tiling", which in reality does not exist. In fact the shell, between the projections, is not "areolated", rather only punctated. The projections have a reticulated sculpture, with mesh of various size, very visible at high magnification: at medium magnification such sculpture bestows on the ornamentation a papillose appearance.

The species -- as described -- was collected in lichen on the bark of *Nothofagus* at Cabrería (Chile -- Nahuelbuta Cordillera), at about 1,100 m altitude; still in Chile, in Los Quenes locality (Curicò, 735 m) exists instead a variety of *M. liviae*, whose eggs have projections a little more numerous (from 8 to 10) and of more slender appearance, because less wide at the base, which is however notched as in the typical species. The eggs have diameter of 160-180μ, including the projections, and 75-80μ without these; the projections are from 45 to 55μ long. The adults observed measured at maximum 650μ and -- with exception of the size a little less -- they are not different from those coming from the Cabrería locality.

MACROBIOTUS LONGIPES Mihelčič, 1971 (Fig. 498).

Aquatic species. Length between 400 and 600μ. Cuticle smooth, eyes absent. Lacking peribuccal lamellae. Buccal tube brief, shorter than the pharynx, and curved first at its entrance in it, medium wide (the author did not furnish measurement of the diameter). Pharynx elongated oval, containing apophyses (which are elongated rods) and 2 slender and thin

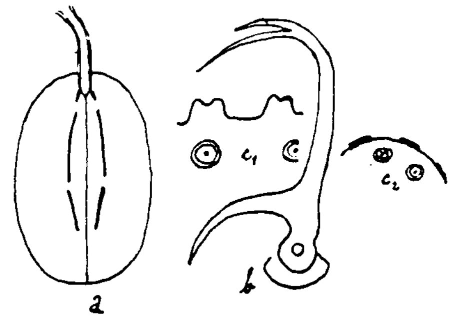


Fig. 498 - *M. longipes* Mihelčič. a, pharynx; b, claw of the 4th pair of legs; c, sculpture of the eggs, respectively deposited and still in the exuvia (from Mihelčič).

macroplacoids, of which the first is about twice as long as the second; microplacoid absent. Legs long and slender; doubleclaws of each leg equal to each other in shape and size; in both, the principal branch is very elongated and much longer than the secondary branch, which is bent downward with long and tapered point.

Eggs deposited free, with projections similar to those of *M. morulatus*, but more distant from each other: that is the distance between the projections is greater than the diameter of their bases; the shell between the ornamentations is smooth.

M. longipes was collected in interstitial environment, in two localities from Sweden.

Although it is difficult to judge either from the description or from the drawing, it is not to be excluded that this species should be placed in the genus *Dactylobiotus*.

MACROBIOTUS MAHUNKAI Iharos, 1971 (Fig. 499).

Length from 380 to 630μ, yellowish color; cuticle smooth with a very fine punctation, arranged in bands. Eyes present. Mouth surrounded by lamellae. Buccal tube 5-8μ wide. Stylets large, strongly curved. Pharynx elongated, with three macroplacoids of increasing length from first to third. Microplacoid absent. Claws of the *echinogenitus* type in young examples, in adult examples becoming the *hufelandi* type. The lunules have a characteristic form (which the author however did not describe).

A single egg is known probably belonging to this species. It is spherical, enveloped in a transparent covering, with reticular design; including such covering the diameter is of 124μ, without it 70μ; on the central, spherical part there are hemispherical projections, 9μ high, yellowish, in contact with each other.

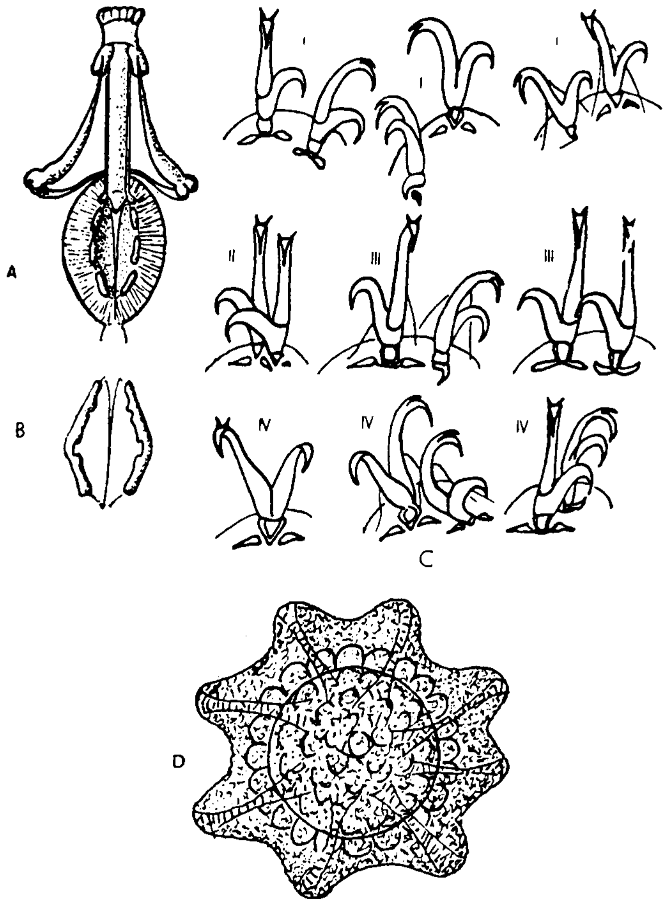


Fig. 499 - *M. mahunkai* Iharos. A, buccal apparatus; B, placoids fused together; C, claws of the 1st-4th legs; D, egg (from Iharos).

M. mahunkai -- which is probably near to *M. csotiensis* -- has been found in constantly wet moss, in different localities of North Korea.

Pilato (1974) puts forth the hypothesis that this species may be near -- or perhaps corresponds -- to *Isohypsibius weglarskae*. From the description and the drawings, the fact seems plausible, in which case the species should be transferred to the genus *Amphibolus*.

MACROBIOTUS MARCUSI Barros, 1942 (Fig. 500).

Length 207μ, color ash grey, eye spots black, cuticle smooth, however with "pearls". Peribuccal lamellae absent. Buccal tube narrow

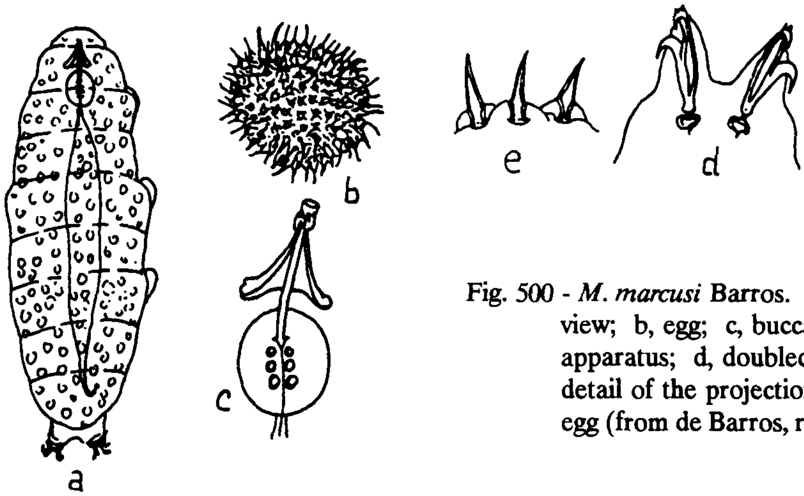


Fig. 500 - *M. marcusi* Barros. a, dorsal view; b, egg; c, buccal apparatus; d, doubleclaws; e, detail of the projections of the egg (from de Barros, redrawn).

(2μ), somewhat curved near its entrance into the pharynx; the latter is oval (18 x 16μ), with apophyses and 3 macroplacoids of granular shape, the size increasing from first to third (the measurements of the granules in microns are respectively: 1.4 x 1.4, 1.6 x 1.6, 2.4 x 1.6). Microplacoid absent. Doubleclaws small (8μ), of the *hufelandi* type (a Y), with two accessory points on the principal branch and small closed lunule.

Eggs oval with projections of spine shape enclosed at the base with a minuscule conical, or hemispherical, cuticular capsule (Fig. 500, b, e), which distinguishes it from the eggs of *M. occidentalis*; diameter of the egg in microns: 55 x 50 including the projections, and 41 x 37 excluding the spines.

The species is probably near to the small *Macrobiotus* of the *intermedius* group, and particularly to *M. subintermedius*.

M. marcusi was collected only in Brazil (State of Sao Paulo).

MACROBIOTUS MAUCCII Pilato, 1974 (Figs. 501 and 502).

Length 450μ; colorless, eyes absent, cuticle smooth, without "pearls". Mouth surrounded by lamellae. The buccal armature is similar to that of *M. harmsworthi*, but differs in that the ventrolateral crests present the distal portion fragmented into a series of teeth, and in which the posterior band of teeth is composed of more rows of teeth. Buccal tube wide (about 22% of the length). Pharynx short oval, with apophyses, 3 macroplacoids of rod shape, and well developed microplacoid. The shape and disposition of the placoids is very similar to those of *M. harmsworthi*:

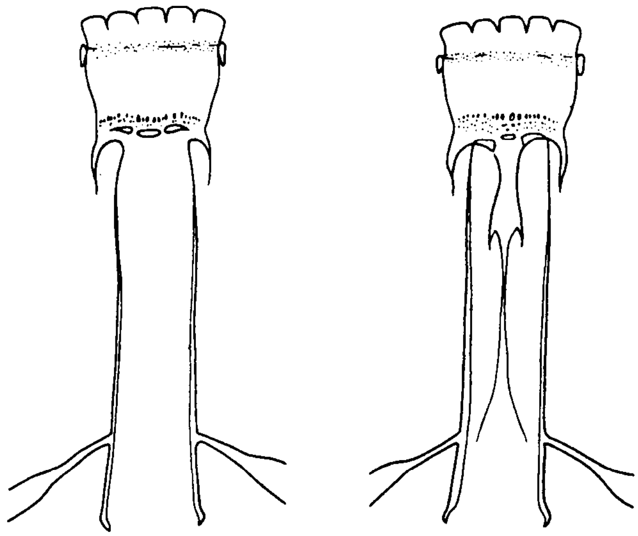


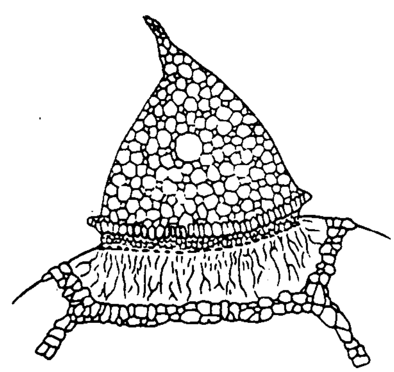
Fig. 501 - *M. mauccii* Pilato. Buccal armature, in dorsal (at left) and ventral view.

the first macroplacoid is longest, the second is shortest.

The claws present two branches united as far as almost half the length, with accessory points on the principal branch. Lunules smooth.

Eggs with obvious projections, conical, which bestows to the egg a stellar appearance. The diameter is 90-100μ including the projections, 60-70 without them. The projections (8 in optical section) have conical

Fig. 502 - *M. mauccii* Pilato. Detail of a projection of the egg (from Pilato).



shape, with a more narrow basal collar. It presents a reticular sculpture with mesh of almost circular shape and varied size.

The shell, between the projections is not tiled, but the base of each projection is surrounded by a polygonal relief, it also with reticular sculpture.

The species is certainly very near to *M. harmsworthi.*

M. mauccii was found the first time in China (near Canton). Later, Maucci found it on Andaman Islands (Cinque Island, South Andaman).

MACROBIOTUS MERIDIONALIS Richters, 1909 (Fig. 503).

Length up to 806μ, large eye spots, robust stylets. Buccal tube rather wide, with diameter 5-6μ and length of 41μ; pharynx oval (44 x 33μ), with apophyses, 3 macroplacoids of about equal length (5μ), in the shape of somewhat curved rods, and microplacoid present.

The doubleclaws are of medium size, of the *hufelandi* type (a Y). The eggs (of which no illustrations are published) have mammary-like projections, or the projections are hemispherical, with a small central projection in the form of a disk, and are 96μ in diameter.

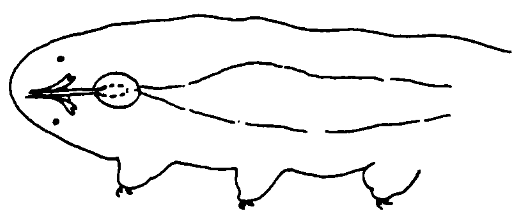


Fig. 503 - *M. meridionalis* Richters (from Marcus, redrawn).

The species (as seen) was insufficiently described and illustrated, however the characteristic projections on the eggs should perhaps permit its identification in the case of new finds. *M. meridionalis* has only been collected from the Antarctic at South Victoria Land, Lat. 77° S.

MACROBIOTUS MONTANUS Murray, 1910 (Fig. 504).
= *M. morulatus* Bartos, 1936.

Length up to 500μ and more but sometimes also about 300μ; colorless when young, more often brownish; eye spots present. Buccal aperture surrounded by lamellae, buccal tube wide or very wide (for example 5μ diameter in an individual of 285μ, 6μ in another of 340μ); stylets robust and curved. Pharynx oval, with length to width ratio of about 1.3:1; containing apophyses and 3 macroplacoids in the shape of oval granules, or of short rods rounded at the ends, of about equal length; may be -- but not always -- a small microplacoid. Doubleclaws of the *hufelandi* type (a Y), large and robust, of which the principal branch has strong accessory points. The spherical eggs have projections of hemispherical shape, almost in contact with each other at their bases, and may measure -- including the projections -- from 55 to 80μ in diameter.

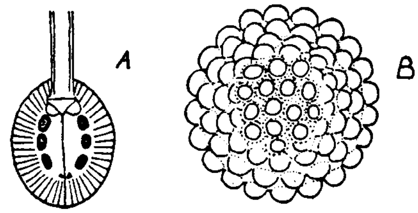


Fig. 504 - *M. montanus* Murray. A, pharynx; B, egg.

The shell between the projections has numerous pores which produce a kind of reticular design.

These pores, which at times describe a ring at the base of the projection, were not cited in the original description, and this has induced Bartos to describe, as *M. morulatus*, examples from the Tatras and Carpathians with eggs of this type (without however having found adult individuals).

We have examined populations of *M. montanus* from various origins and we have *always* found a shell of reticular design. We think therefore it is justified to put *M. morulatus* in synonymy with *M. montanus*.

Schuster (in litt.) relates that the egg of *M. montanus* from California, from his examination, may have the cuticle between the projections smooth, while the eggs from Norway may have the shell punctated. It may be assumed that in reality the European species may be different from the American, and to be precisely *M. morulatus*. We think for the present to leave unprejudiced the question, and to maintain, at least temporarily the synonymy here proposed (not having personally seen the American material of Schuster) in as much as: 1) Grigarick, Schuster, and Toftner (1973), original description of the California material, did mention pores on the surface of the egg; 2) Horning, Schuster, and Grigarick (1978), in the description of New Zealand material, also a "weakly reticular" shell (New Zealand is type locality for *M. montanus*).

M. montanus belongs to the "*harmsworthi*" group, and is very difficult to distinguish from other species of the group in absence of eggs.

This species is not extremely common, however it is cited from many localities from Europe (including Italy), western Africa (Ivory Coast), Canada, California, Galapagos Islands, and New Zealand.

MACROBIOTUS NOCENTINIAE Ramazzotti, 1961 (Fig. 505).

Aquatic tardigrade. Length in general 200-230μ, maximum 245μ; cuticle smooth, eye spots present. Buccal tube -- with peribuccal lamellae -- of length varying between 37-46μ with external diameter from 2μ to 4.2μ, for an animal 208 to 230μ long (this measurement shows, once more, that the dimensions of the buccal apparatus are widely independent of the length of the body and that the indices cph and ms are then unreliable, which we have said in the section "Determination of the Tardigrada and Notes on the Use of the Relative Keys"). Pharynx oval (about 27 x 36μ), with little developed apophyses, however well visible, and 2 macroplacoids: the first about 7μ long, with a constriction a little forward of the middle, and the second somewhat shorter (5μ), not uncommon to be slightly enlarged at the caudal end. Often the constriction of the first macroplacoid is deep, so that the macroplacoids seem to be three, or actually

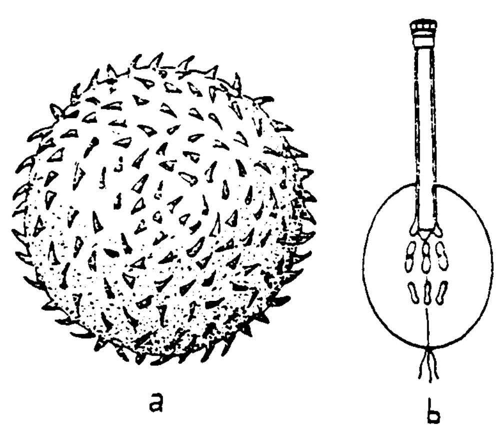


Fig. 505 - *M. nocentiniae* Ramazzotti. a, egg; b, pharynx.

become such: the first two almost in contact with each other and of equal length (sometimes the first a little longer than the second) and the third longest. Doubleclaws of the *echinogenitus* type (a V).

Eggs deposited free, spherical, with diameter of about 61μ without the ornamentation and 67μ including these; the ornamentations (2.5-3.5μ) are about 35-40 in optical section, appear bent in various manner, and have conical shape, but their appearance is that of wide spines, rather than of cones; shell of the egg smooth, even at the base of the projections, where there are not visible rings of dots (not even using immersion objective and phase contrast).

M. nocentiniae is a species probably near to *M. pullari*; it is distinguished from this by the smaller size (*M. pullari* may reach 560μ in length) and especially by the difference in the eggs.

The species has so far been collected only in Italy, on the bottom of Mergozzo Lake (near Maggiore Lake) at depths of 2-7 meters.

MACROBIOTUS NORVEGICUS Mihelčič, 1971 (Fig. 506).

Aquatic. Length 300-380μ; body squat, legs rather short, cuticle smooth. Eyes absent. Lacking peribuccal lamellae. Buccal tube wide (16-19μ) and as long as the pharynx, which is short oval and contains small apophyses, and 3 short, massive macroplacoids: the first is elongated,

Fig. 506 - *M. norvegicus* Mihelčič. a, pharynx; b, claw of the 4th pair of legs (from Mihelčič, redrawn).

very large, and rostrally tapered, the second is small, almost spherical, the third is similar to the first, a little longer and more slender. Microplacoid present.

Doubleclaws slender, with robust basal part; the principal branch is much longer than the secondary, with curved and sharp point and long accessory points.

Eggs smooth, deposited in the exuvium.

The species, collected in Norway, belongs to the interstitial fauna.

MACROBIOTUS NURAGICUS Pilato & Sperlinga, 1975 (Fig. 507).

Length up to 350μ, colorless, smooth cuticle, without "pearls". Eyes present.

Mouth surrounded by lamellae. The buccal armature is similar to that of *M. harmsworthi*. Buccal tube medium wide (15% of the length). Pharynx oval, with apophyses, 3 macroplacoids of rod shape, and an obvious microplacoid. The first and third macroplacoids have almost the same length, the second is shorter.

The claws have the branches fused for a distance less than half the length; the principal branch has obvious accessory points. The lunules are smooth or sometimes dentate.

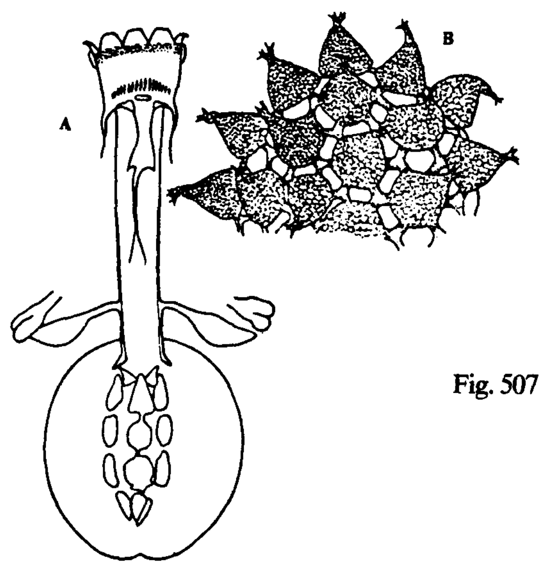


Fig. 507 - *M. nuragicus* Pilato & Sperlinga. A, buccal apparatus; B, egg (from Pilato and Sperlinga).

The eggs are spherical (72μ without projections, 106 with them). The projections are conical, with the terminal part tapered and the apex subdivided into a varied number of points; the surface of the projections presents a reticular design of extremely small isodiametric mesh. The shell of the egg, between the projections, presents a type of tiling composed to thickenings of the shell.

M. nuragicus belongs to a homogeneous group of species, which may be called the "*harmsworthi*" group, and in absence of eggs, it is not easily distinguished from *M. harmsworthi* and *M. orcadensis*.

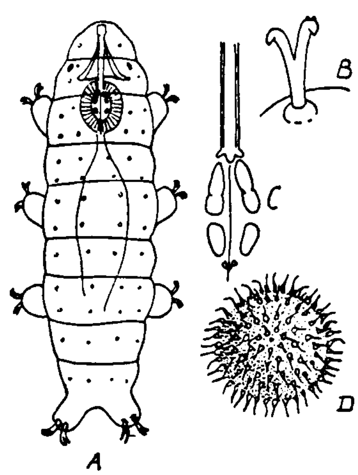
The species was discovered in Sardinia (Villanova). Later it was found in Turkish Mesopotamia (Gaziantep) by Maucci. The examples of this population, all similar (including the eggs) to the typical types, are however considerably larger (average of the population 541.2μ). A further report (Maucci) was from Bali Island.

MACROBIOTUS OCCIDENTALIS Murray, 1910 (Figs. 508 and 509).

This is a species perhaps not yet well defined in its characteristics; and it is probable that the citations of various authors did not always refer to the same species.

Length up to 800μ (according to Marcus; 410μ according to Cuénot; 502μ according to Thulin): examples from the Ramazzotti and Maucci collections rarely surpass a little more than 300μ. Colorless (at least in the young), more often pale yellow, sometimes orange. The cuticle has numerous pores ("pearls") of elliptical shape, larger than those usually

Fig. 508 - *M. occidentalis* Murray. A, dorsal view; B, double-claws; C, placoids; D, egg.



present in other species of *Macrobiotus*, and particularly visible in the caudal part; these pores are, usually, deposited in transversed bands (according to Marcus, these pores could also be missing, yet this does not seem probable, since the "pearls" are usually a constant character for the species which possesses them). Eyes present. Mouth not surrounded by lamellae. Buccal tube not very wide (2-6μ, corresponding to about 10-15% of the length). Pharynx almost round, with apophyses and 2 rod-shaped macroplacoids; the first is very near to the apophyses, and is often constricted in the middle; the second is shorter. The microplacoid is very small, and can also be missing.

The claws are of the *hufelandi* type, rather slender, according to Marcus, markedly massive on the contrary in our material. The principal branch has strong accessory points. The lunules, according to Marcus, are small and smooth in the young examples, regularly dentate in the larger examples. Norwegian examples in the Maucci collection have very large lunules, are strongly dentate (approaching almost those of *coronifer*) also in individuals of smaller length to 300μ. The eggs are spherical, the

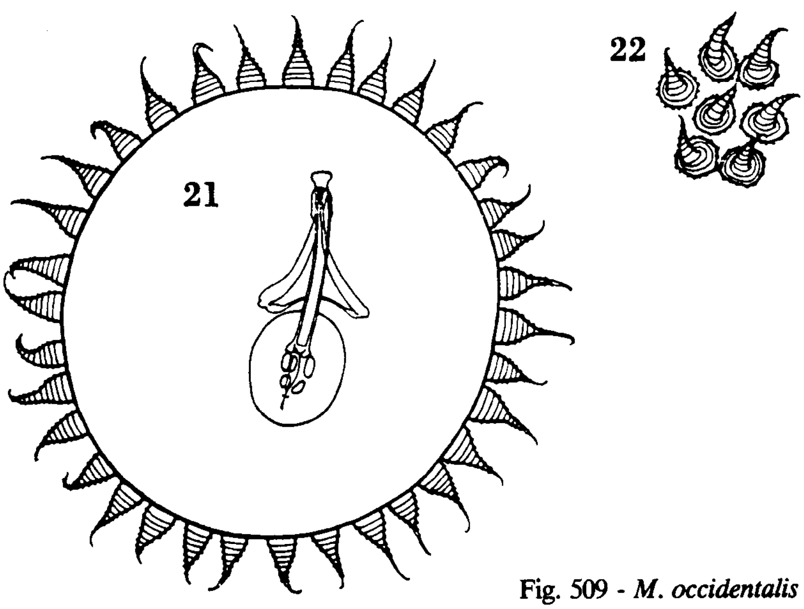


Fig. 509 - *M. occidentalis* forma *striata* Dastych. Egg and details of the ornamentation (from Dastych).

diameter 58-60μ, the color pale yellow to dark orange-red, with flexible thorns, slightly dense, with small conical bases and with the apices often bent.

With the name *M. occidentalis* forma *striata*, Dastych, 1974, described one population having the following characteristics. Size up to 360μ, color clear brown, cuticle smooth (the author did not cite "pearls"); the larger examples had dark brown spots, irregularly distributed. Eyes present. Buccal apparatus like in the typical form. Lunules smooth. Eggs white, with conical projections extended in flexible apices; all the projections had transverse striations, made of thin rings.

The forma *primitivae* Barros, 1942, had sculptured cuticle and a mouth with lamellae, we here consider as a good species.

The typical form is cited for many European localities (also in Italy), for America, Australia, Angola, and the Hawaiian Islands. Typ. loc.: Vancouver (Canada), Australian Alps, Haway. The forma *striata* is noted only from North Korea.

MACROBIOTUS ORCADENSIS Murray, 1907 (Fig. 510).

Length up to 430μ (adult individuals from Scandinavia, which we have been able to observe); eyes present, cuticle smooth without "pearls". Buccal tube of medium width (external diameter 5.5μ in an individual of 378μ), with reinforcement bar long and provided with peribuccal lamellae; pharynx short oval (35 x 31.5μ in an individual of 378μ) containing apophyses, 3 macroplacoids and microplacoid; the macroplacoids are elongated granules, oval, not very different from each other: the second is shortest and the last is slightly enlarged to a sphere at the caudal end; such enlargement is preceded by a slight constriction. Doubleclaws *hufelandi* type (a Y), with accessory points of unusual largeness and robustness on the principal branch; for more of how it shows, see Fig. 169 of the work of Marcus (1936); on the other hand this figure is inaccurate, because both the doubleclaws of each leg have equal size, not different. We ought to however add that sometimes -- and for certain particular conditions -- one doubleclaw appears to be more robust than the other: but it is only an optical illusion, attributed probably to the strongly elliptical section of the branch, that produces the effect of one thickness more or less large according to the angle of observation. At the base of the doubleclaws there is a small lunule, but very clear especially on the 4th pair of legs.

The eggs, spherical, are deposited free and their diameter may vary

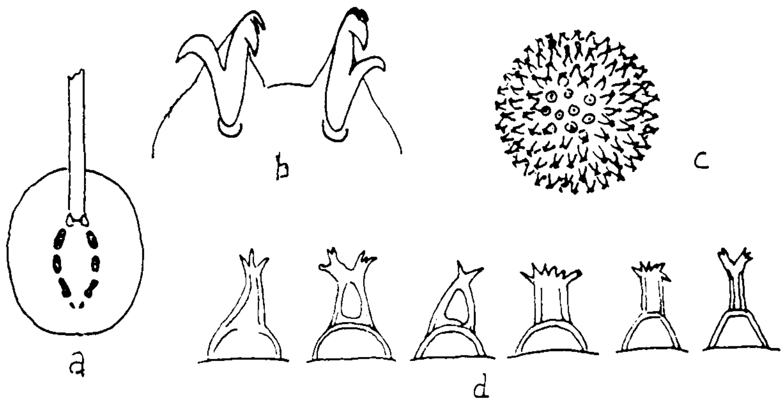


Fig. 510 - *M. orcadensis* Murray. a, pharynx; b, doubleclaws; c, egg; d, various types of ornamentation of the egg.

between 70 and 85μ, including the ornamentation: there are small conical projections (Fig. 510, d) with enlarged base, characterized by the subdivision of their apices into two, three, or more small points. With strong magnification -- better using immersion objective and phase contrast -- renders visible on the shell a circle of dots, or of radial dashes, around the base of each single projection. We have noted that often the eggs adhere so strongly to their substrate, it makes one think very probably the presence of an adhesive secretion.

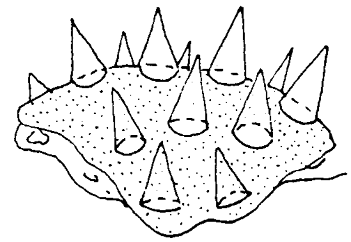
The eggs resemble those of *M. furciger*, from which sometimes (as in material from Chile) they can be distinguished only by being smaller (70-85μ, rather than 100-103μ, including the projections).

The species, which belongs to the *harmsworthi* group and is very near to *M. montanus* (from which, in absence of eggs, it is almost impossible to distinguish), is known from various localities from Scandinavia, Scotland, Orkney Islands, Brazil (State of Sao Paulo), New Zealand, and probably Chile. Typ. loc.: Orkney Islands.

MACROBIOTUS OVIDII Bartos, 1937 (Fig. 511).

Length 270-540μ; young colorless, but adults pigmented brown; eye spots black, cuticle smooth. Diameter of the buccal tube about 4μ, stylets with basal part very wide; pharynx oval, with length:width ratio of about 1.2-1.3:1, containing 3 macroplacoids of rod shape, of which the third (5.5μ) is longest and the second (3μ) shortest; a minuscule microplacoid exists. The first macroplacoid -- almost in contact with the second -- may present

Fig. 511 - *M. ovidii* Bartos. Detail of the egg (from Bartos, modified).



a constriction, which in rare cases is so deep as to divide it in two. Doubleclaws of all legs small, of equal size, with branches very curved and of *hufelandi* type (a Y), with large smooth lunule at the base; the principal branch has accessory points.

Eggs large, yellowish, whose diameter is 116-124μ including the ornamentation, and 100-110μ excluding them; the projections have the appearance of slender sharp and straight cones, never bent, 2.7μ wide at the base and 8-10μ high: they are completely smooth, transparent as glass and positioned considerable distance from each other (about 8μ). The shell -- between the projections -- appear coarsely granulated.

The species is probably near to *M. islandicus*, but differs by the number of placoids, the appearance of the projections of the eggs and the smooth lunules.

The species has been cited from Caliacra Cape (Bulgaria) and from some localities from Dobrugia (Rumania).

MACROBIOTUS OVOVILLOSUS Baumann, 1960 (Fig. 512).

Length of the adults 300-400μ, while the young, barely out of the egg, measures already 259-287μ; colorless, eyes present and in posterior position. The cuticle is indistinctly and irregularly granulated. Buccal tube curved ventrally toward the oral end, so that the buccal opening is anterio-ventral, not rostro-terminal. In the larger individuals, the external diameter of the buccal tube is about 2.5μ, while the pharynx measures 37μ in length and 32μ in width. Two macroplacoids (rods little wider than 1μ), the first (5μ) longer than the second (2.5-3μ) and often with one or two constrictions; a minuscule microplacoid is present. Doubleclaws *hufelandi* type (a Y), lacking accessory points on the principal branches and with small oval lunule at the base.

Eggs deposited free, spherical, brownish, with medium diameter of about 100μ: their surface is covered with a curled filamentous mass,

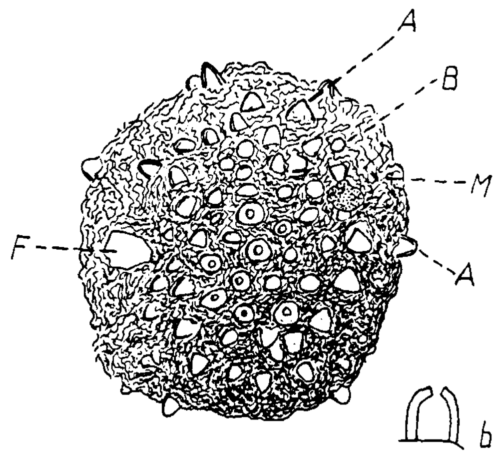


Fig. 512 - Egg of *M. ovovillosus* Baumann. A, a projection viewed in profile; B, a projection viewed frontally; M, filamentous mass; F, particle of detritus; b, detail of one projection of the egg (from Baumann, redrawn).

to which adheres granules of sand and particles of detritus; from this filamentous mass projects -- for a small part of their length -- the ornamentations, each of a narrow parabolic shape, with rather thick walls, open at the distal end. Such processes -- of about 22 in number in optical section -- are about 4μ high, have diameter of 5-7.5μ at the base (circular) and 4-5μ from each other.

The species, which is easily distinguished from all the others by its characteristic egg, was found only in the U.S.A. (Colorado, near Denver), in moss.

MACROBIOTUS PALLARII Maucci, 1954 (Fig. 513).
= ? *M. aviglianae* Robotti.

Length more than 300μ, color white or slightly brownish; cuticle smooth, probably furnished with small pores ("pearls") (the condition of the type material does not allow to establish with certainty the presence of such "pearls"). Peribuccal lamellae present, buccal tube fairly wide (16% of the length), stylets very robust, with small and stumpy furcae. Pharynx almost round, with apophyses and two macroplacoids, of which the first is a little longer than the second; microplacoid present, rather obvious. Claws *hufelandi* type, with small smooth lunules, and accessory points on the principal branches.

Eggs spherical, diameter 80μ without projections, 95 with them. The projections are regular cones, with wide base and pointed apices (14 projections in optical section); the surface of the projections presents a fine reticular design. The surface of the egg is "tiled", that is it is

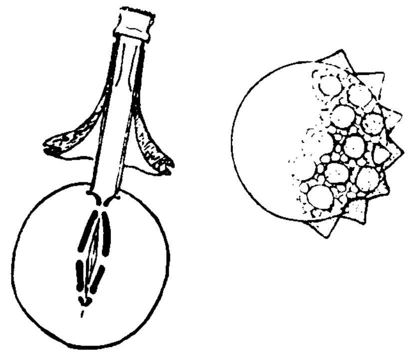


Fig. 513 - *M. pallarii* Maucci. Buccal apparatus and egg (from Maucci).

subdivided into polygonal surfaces (it is not possible, in the type material, to identify exactly the shape of these surfaces, nor their number).

As already said with regard to *M. avigliauae* (see that description), it is very probable that *M. pallarii* and *M. avigliauae* are the same species, in which case naturally *M. pallarii* would have priority. However examination of the type material (preserved in Faure's liquid, and in fairly good condition, but not completely certain) does not permit an absolutely certain identification. Therefore, by being a very probable synonym, we do not think advisable to sacrifice to an unclear priority the name of *M. avigliauae*, entered into use, and supported by a recent good description and abundant type material.

M. pallarii (which therefore we consider *spec. dub. et inquir.*) was collected near Silvano Mansio (Sila, Calabria) at 1,400 elevation.

MACROBIOTUS PAPILLOSUS Iharos, 1963 (Fig. 514).

Length 240-260μ; eye spots absent; color bluish grey; cuticle smooth, but covered -- even on the legs -- with an extremely fine punctation, very refringent and regularly arranged ("pearls"). In the cuticular folds 3, 5, and 7 there exists dorsally small claviform papillae.

Buccal tube medium wide (3.5μ), pharynx elongated oval (30 x 18μ), with 2 macroplacoids of rod shape, the first (10μ) longer than the second (7μ). The author states that there is no microplacoid but well developed septula (?): as yet the presence of the septula has been noted only in the genus *Diphascon*. Stylets robust and curved; doubleclaws of the *echinogenitus* type (a V), with smooth circular lunule. Eggs unknown.

According to the opinion of the author (with which however we are not in agreement) the species is near to *M. hufelandi*, but differs by the coloration, the absence of the eyes (which may however be lacking also in

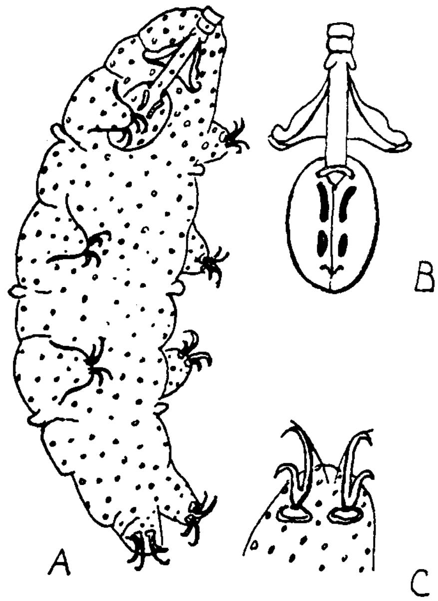


Fig. 514 - *M. papillosus* Iharos. A, habitus; B, buccal apparatus; C, double-claws of the 4th pair of legs (from Iharos, redrawn).

hufelandi), by the shape of the pharynx, the type of doubleclaws and the dorsal cuticular papillae.

M. papillosus was collected in southern Argentina, in moss on rock at 360 m altitude, in a shady forest at the foot of Piltiquitron Mountain, El Bolsòn (Rio Negro Province).

MACROBIOTUS PERSIMILIS Binda & Pilato, 1972 (Fig. 515).

The length reaches and surpasses, not by much, 400μ (in the Greek material, Maucci has found however examples which approach, and even exceed, 500μ). According to the author, this species resembles *M. hufelandi*, however it is differentiated by some characters. Cuticle smooth, with "pearls"; eyes present. Buccal tube moderately wide (16% of the length); pharynx short oval with apophyses, two macroplacoids, and microplacoid. The first macroplacoid is constricted at the middle, and sometimes may be completely divided. The claws have the branches fused for less than half the principal branch, which possesses accessory points. Lunules well developed, especially on the 4th pair of legs, where they are usually slightly dentate. Compared to *M. hufelandi* (Maucci's observations, on Greek and Turkish material) the macroplacoids are somewhat shorter, and the stylet supports are inserted on the buccal tube higher, that is more distant from the end of the tube.

The eggs are similar to those of *M. hufelandi*, with truncated conical

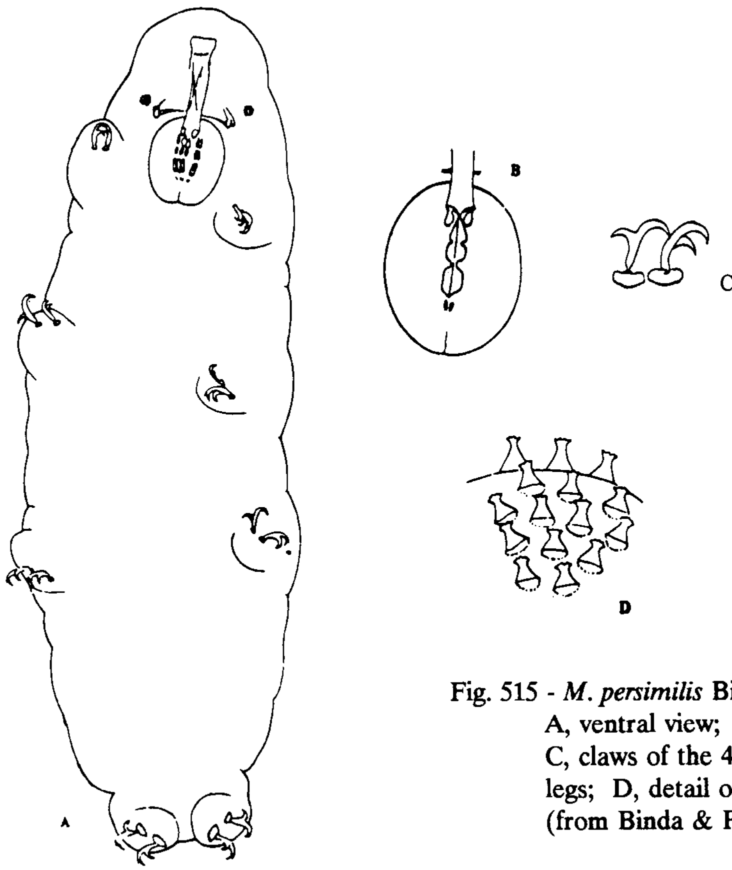


Fig. 515 - *M. persimilis* Binda & Pilato. A, ventral view; B, pharynx; C, claws of the 4th pair of legs; D, detail of the egg (from Binda & Pilato).

projections and distal end with dentated disks. The shell between the projections is all smooth, and this is the principal difference compared to the eggs of *M. hufelandi*.

M. persimilis was collected in moss from various localities in Greece, including the island of Crete (where it seems to be rather frequent), in Turkey, and in one locality in Andalusia (Spain). Pilato and D'Urso (1976) noted it in Australia.

MACROBIOTUS POLARIS Murray, 1910 (Fig. 516).

Length up to 800μ; body slender and elongated, coelomic liquid of pale yellow color, eyes present and usually in an anterior position, cuticle smooth. The buccal tube is rather narrow (about 4μ) in relation to the

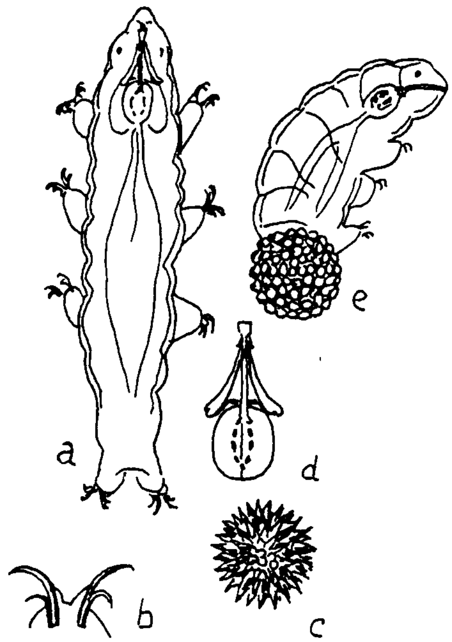


Fig. 516 - *M. polaris* Murray. a, dorsal view; b, double-claws; c, egg; d, buccal apparatus; e, immature leaving egg (redrawn from Marcus).

large size of the animal; the pharynx is a short oval (the length to width ratio is 1.2:1), and contains the apophyses, 3 macroplacoids, in the shape of short rods with rounded ends, of about equal size and length (1.5 to 2.5 times their width), and the microplacoid is present. The doubleclaws are very thin, in relation to the tardigrade; the principal and secondary branches (the length of the latter about half that of the former) are joined some distance from the base at a point a little less than half the length of the principal branch; it would appear that the principal branch has only one accessory point, rather than the usual two.

The eggs, spherical or oval, have a "tile like" shell, consisting of a more or less hexagonal, often deformed mesh; the shell appears as double, subdivided by seven into numerous cells, which outline the above-mentioned mesh. The projections (ornamentations) in the spaces between the hexagonals can be of a hemispherical shape (about 5μ high) giving the egg a total diameter of about 85μ, or the projections may have points, which sometimes terminate with thorns at their tips (about 10μ high), in this case the overall diameter is about 95μ.

The species is noted only from Antarctica (Terre Victoria, between 77°30' and 78° latitude south).

MACROBIOTUS POLYOPUS Marcus, 1928 (Figs. 517 & 518).

Maximum length 300μ, colorless (some examples may present a pigmentation composed of small black dots, arranged in transverse bands); cuticle smooth, without "pearls". Eye spots present. Peribuccal lamellae present. The buccal armature is composed only of two slender transverse crests on the dorsal side and two on the ventral side. The buccal tube is rather narrow (less than 10% of the length); the reinforcement bar, which in the original description was described as very short (only twice of the stylet sheath), may in fact vary somewhat in length, not ever reaching however half the length of the buccal tube. Pharynx oval or a little pear-shaped, with apophyses and two macroplacoids of short rod shape, of which the first is about twice the second, and may be at times slightly constricted at the middle. The microplacoid is often absent; when present it is usually very small, even difficult to see; only in some examples is it normally developed -- however always small, almost dot-shaped or slightly elongated.

The claws are of the *echinogenitus* type, that is the two branches come off of a common base, at an angle of about 30μ between them; the principal branch is little longer than the secondary and bears slender accessory points. The lunules are small, incomplete and smooth.

The eggs are spherical with diameter of about 65μ, including the ornamentations: these are conical projections, low and wide, rather small, whose surface presents ringed relief and, near the base a hint of

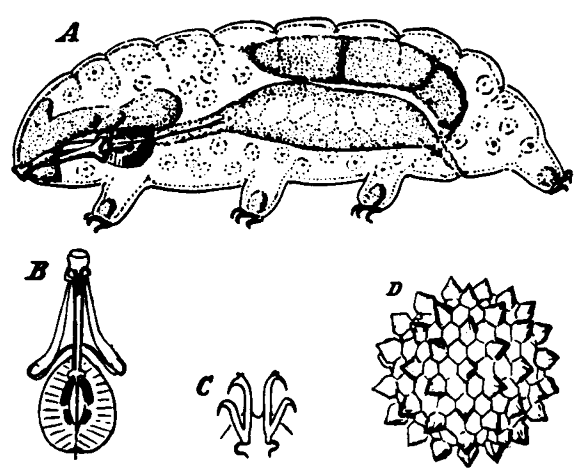


Fig. 517 - *M. polyopus* Marcus. A, lateral view; B, buccal apparatus; C, doubleclaws; D, egg (from Marcus).

longitudinal angle; the ornamentations project alternatively from hexagonal design on the shell; between the projections then remains free a part of the hexagon, and the shell is therefore "tiled"; in a small number of eggs the hexagons of the tiling have the same size as the bases of the projections, in the majority of the cases they are smaller, however each projection is always surrounded by six hexagons.

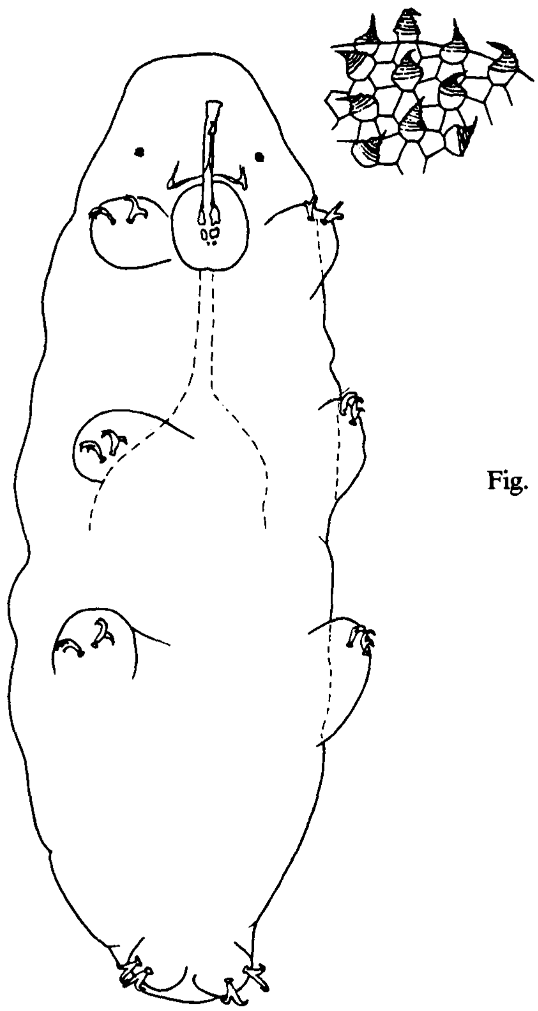


Fig. 518 - *M. mandalae* Pilato
= *M. polyopus*
(from Pilato).

The species was described initially from Sumatra (eastern part), and later from Brazil (State of Sao Paulo). The above-mentioned description is based on abundant material, found at Cinque Island (South Andaman, Andaman Islands) and studied by Maucci. Pilato has described, with the name *M. mandalae*, some examples coming from the vicinity of Canton (China): the modest difference of it compared to the original description (presence of the microplacoid, greater length of the reinforcement bar of the buccal tube, greater development of the accessory points of the claws) does not seem to justify the specific separation, so that this author puts forth the hypothesis that the Sumatra material may belong to the above species, while instead Sumatra is the type country of *M. polyopus*.

MACROBIOTUS PORTERI Rahm, 1931 (Fig. 519).

Length up to 900-1200μ, eye spots present, cuticle smooth, cavity globules very dark, often even intense black color. Buccal tube very wide (diameter 13-17μ); stylets robust, pharynx oval (length:width ratio equal to about 1.2:1), with apophyses, 3 macroplacoids -- of which the 2nd is longest and the 3rd shortest -- and microplacoid. Doubleclaws of 21-25μ, *hufelandi* type (a Y), with lunule (smooth?) at the base and the principal and secondary branch of almost equal length; principal branch with two robust accessory points, strongly sharpened at the apices. Eggs spherical, diameter 131-154μ; the ornamentations are projections often loose and lying down on the shell, arranged in disorganized manner, of different length and shape, but in general composed of slender triangular points.

M. porteri is known only for Chile (near Santiago, up to 1,400 m altitude).

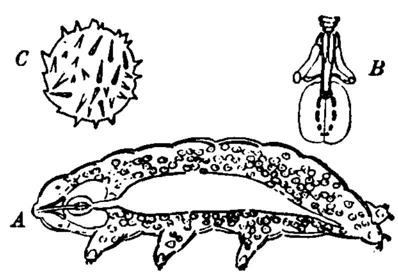
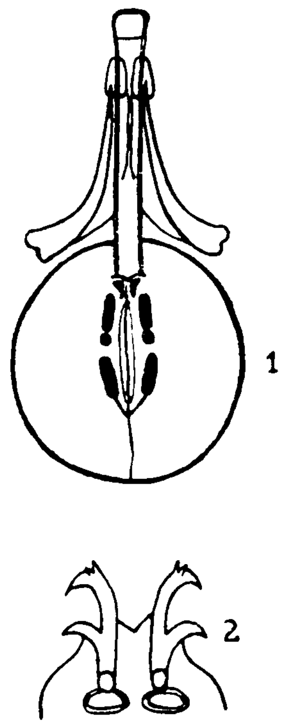


Fig. 519 - *M. porteri* Rahm. A, habitus; B, buccal apparatus; C, egg (from Marcus).

MACROBIOTUS POTOCKII Weglarska, 1968 (Figs. 520 & 521).

Description of the holotype: length 520μ, cuticle smooth, eyes absent; buccal tube straight, 30μ long and 5μ wide. Stylet supports 14μ long, stylets slightly curved with furcae. Pharynx almost spherical (42 x 40μ), in which there are the apophyses and 3 macroplacoids, of which the 1st (6μ) and the 3rd (8μ) have rod shape, while the 2nd (about 2μ) has a granular appearance; microplacoid absent. Doubleclaws rather weak and relatively short, *hufelandi* type: the principal branch measures 12μ, the secondary 7μ; at their base exists a smooth lunule; anterior end of all the legs with a thickened "cushion".

Fig. 520 - *M. potockii* Weglarska. 1, buccal apparatus; 2, doubleclaws of the 4th pair of legs (from Weglarska).



The eggs are spherical and have 140μ diameter including the projections and 100μ without them. The projections (ornamentations) are cones 20μ high with granular surface; each cone is surrounded at the base by a ring of larger granules.

According to the author the species is near to *M. virgatus*: it differs by the lack of pigmentation (*virgatus* has three brown longitudinal bands,

Fig. 521 - *M. potockii* Weglarska.
Egg (from Weglarska).

while *potockii* is colorless in transmitted light and whitish in reflected light), by the shape of the pharynx and of the claws, and by the very small stylets.

The species was found near roots of *Carex sp.* in the Qadzi Deh Valley (Hindukush, Afghanistan), at 3,800 m altitude.

MACROBIOTUS PRIMITIVAE Barros, 1942 (Fig. 522).
= *M. occidentalis* forma *primitivae* Barros, 1942.

Length 300-400μ, eyes present, color lemon-yellow or greenish. The cephalic region, the dorsum and the lateral surfaces of the legs show a sculpture of the cuticle, composed of tubercles of pyramidal points with polygonal bases, whose diameter varies between 3μ (anterior region of the body) and 5μ (posterior region). Buccal tube supplied with peribuccal lamellae, having a diameter of 3-5μ; pharynx oval (length:width ratio of about 1.1:1), containing apophyses and 2 macroplacoids: the first of these possesses a slight external projection -- exaggerated in Fig. 522, c -- and is twice as long as the second, or a little more; the microplacoid may be present or absent. Doubleclaws *hufelandi* type (a Y), 11-14μ long on the 4th pair of legs, with smooth and open lunule. Eggs colorless, deposited free, having diameter of about 60μ including the ornamentations: these are spines 5μ in length, bent at the apices, with enlarged bases of cones and not in contact; between them the shell remains free and deprived of sculpture, completely smooth.

The species has been cited only for Brazil (State of Sao Paulo).

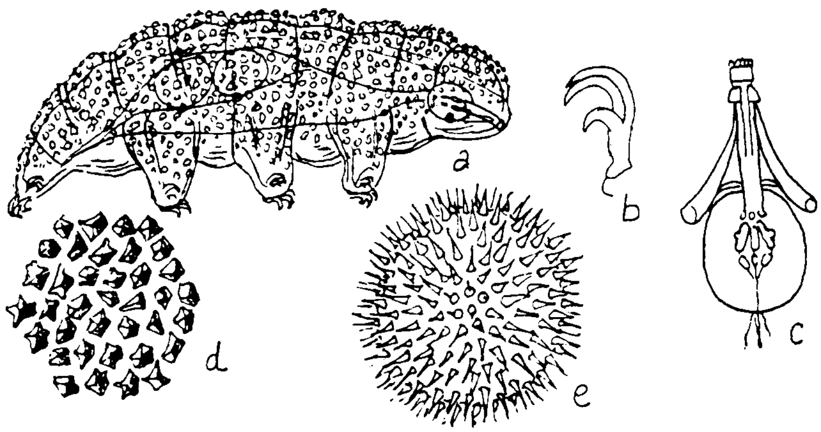


Fig. 522 - *M. primitivae* Barros. a, lateral view; b, doubleclaws; c, buccal apparatus; d, detail of the sculpture of the cuticle; e, egg (from du Bois-Reymond Marcus, redrawn).

MACROBIOTUS PSEPHUS du Bois-Reymond Marcus, 1944 (Fig. 523).

Length up to 800μ, colorless, eyes present in posterior position; mouth opening surrounded by two concentric rings of lamellae: the interior more narrow and the external wider. Buccal tube of large diameter (about 11μ); stylets strongly curved, almost angular. Pharynx oval, having a length:width ratio equal to 1.35:1, with small apophyses and 3 macroplacoids, of which the first and the third have about equal length, while the second -- almost resting on the first -- is shortest (for example, the macroplacoids may measure respectively, from 1st to 3rd: 13, 8.5, 14μ and their width may be 3μ); microplacoid absent. Doubleclaws robust and small (16μ), with accessory points on the principal branches and smooth lunule at the base.

Eggs deposited free, spherical; they have a diameter of about 110μ, including the 14-16μ high ornamentations; these are rigid spines, terminated in a point, or else bifurcated; the shell presents irregular polygonal plates, slightly furrowed, and the spines are from the points of contact of the various plates. A young, extracted by compression of the egg, measured 225μ in length and its buccal tube had a diameter of 4.5μ.

The only report of the species -- easily distinguishable by the very characteristic egg and different from all the others -- was in Brazil (State of Sao Paulo).

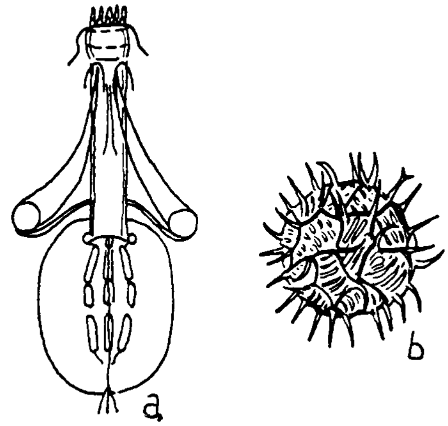


Fig. 523 - *M. psephus* du Bois-Reymond Marcus. a, buccal apparatus; b, egg (from du Bois-Reymond Marcus, redrawn).

MACROBIOTUS PSEUDOFURCATUS Pilato, 1972 (Figs. 524 & 525).

Length up to 340μ, yellow color and large eyes; cuticle with scattered dots very visible, which make up transverse bands; they are more numerous in the dorsal and lateral zones, but exist also on the venter and on the legs; these dots are circular, or elliptical, and a good many have a characteristic triangular trilobate form; the larger ones have pointed form and reach 1.8μ on the side.

The mouth is not terminal, but anterio-ventral; peribuccal lamellae present. Buccal tube ventrally curved in the rostral portion and narrow (12-13% of the length). Reinforcement bar not very long. Pharynx short oval, with apophyses (at their bases there are two lines, like described by Weglarska for *Dor. smreczynskii*), 3 macroplacoids (short and wide rods with rounded corners, almost granular), and small microplacoid.

Doubleclaws of the *hufelandi* type, with small smooth lunule; on the first 3 pair of legs the principal branch is somewhat longer than the second; on the 4th pair of legs the doubleclaws are clearly larger and there is a greater difference in the length of the principal and secondary branches. Accessory points present, more visible on the claws of the 4th pair.

Eggs free, spherical, yellowish, with a diameter -- exclusive of projections -- of 83-90μ; the projections are long flexible cones, smooth; at varying distances from the base, these are bifurcated or divided into three or more terminal filaments, which sometimes branch more; the projections attain a length of 19μ, and sometimes even more.

In absence of eggs this species can be difficult to distinguish from

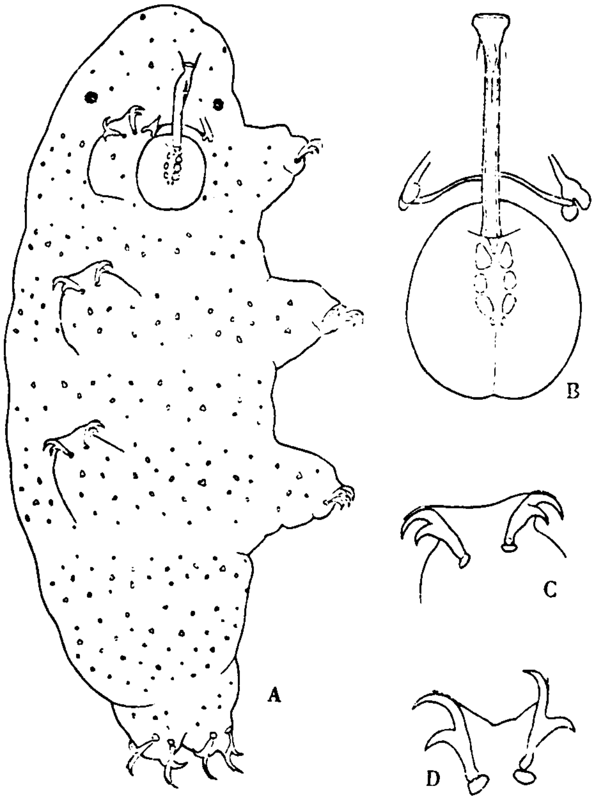


Fig. 524 - *M. pseudofurcatus* Pilato. A, habitus; B, buccal apparatus; C, doubleclaws of the 3rd and, D, the 4th pair of legs (from Pilato).

M. furcatus (which however does not have peribuccal lamellae) from *M. spallanzanii* (which has a little larger pores, and usually polygonal) and perhaps also from *M. pustulatus* (of which the pores reach a diameter of 6-7μ, in the caudal region).

M. pseudofurcatus was observed a single time in lichen on lava rock from Egadi Island (Sicily).

MACROBIOTUS PSEUDOHUFELANDI Iharos, 1966 (Figs. 526-528)
= *M. inermis* Binda & Pilato, 1971

Length as much as 510μ, more often less; cuticle smooth, eyes present. Mouth surrounded by lamellae. Buccal tube medium wide (4μ, in an individual of 350μ), pharynx oval, with apophyses, 2 macroplacoids

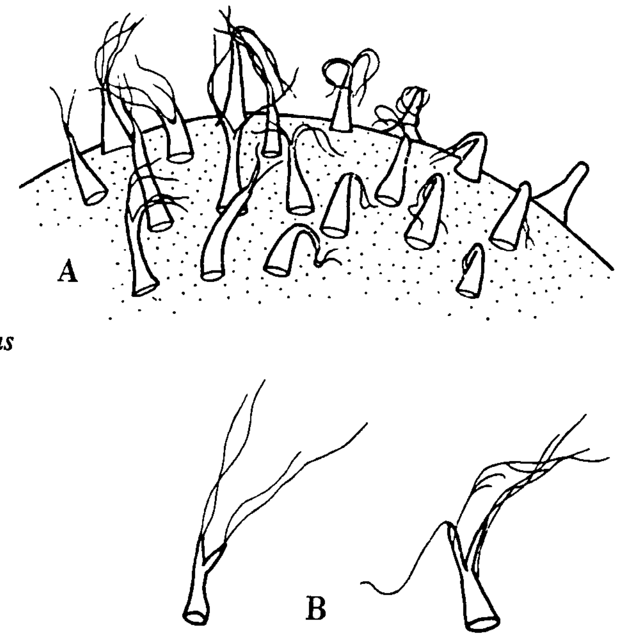


Fig. 525 - *M. pseudofurcatus* Pilato. Detail of the egg and the projections (from Pilato).

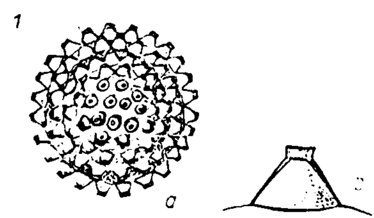


Fig. 526 - *M. pseudohufelandi* Iharos. Egg and detail of a projection (from Iharos).

of rod shape, and microplacoid; the first macroplacoid is always longer than the second and may present a slightly deep constriction. Lunule absent on the first three pair of legs, while it exists on the 4th pair. Claws *hufelandi* type, however the basal portion is very thin, and the principal branch is much shorter, less tapered and with smaller accessory points than in *hufelandi*.

The eggs have 70-100μ diameter excluding the projections and 80-118 including these. The projections are numerous (28-42 in optical

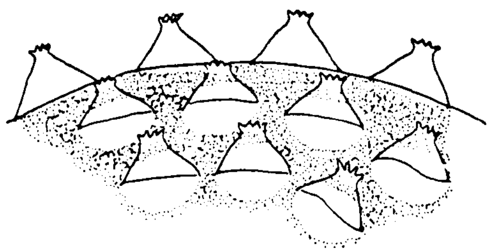


Fig. 527 - *M. pseudohufelandi* Iharos (*M. inermis* Binda & Pilato). Detail of the egg (from Binda & Pilato).

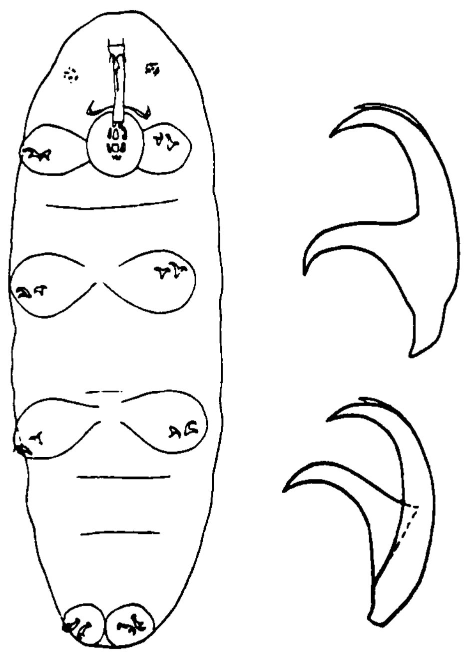


Fig. 528 - *M. pseudohufelandi* (*M. inermis* Binda & Pilato). Ventral view and claws of the 3rd pair of legs (from Binda & Pilato).

section); they have the shape of truncated cones with bases more or less wide and terminated distally with a dentate disk, or else present a basal truncate cone base and distally a short cylindrical part and finally the dentate terminal disk. The shell between the projections has a reticular design of mesh much smaller and less distinct than in *hufelandi*.

This description is taken from the description of *M. inermis*, which Pilato (1973), after comparing with type specimens of *M. pseudohufelandi*, has identified with this last species, even if the original description of Iharos is not exactly corresponding. *M. pseudohufelandi* was collected in Austria, *M. inermis* was found in various localities from Sicily. An egg, coming from Abano Terme, and attributed by Ramazzotti to *M. recens*, belongs perhaps to *M. pseudohufelandi*.

MACROBIOTUS PULLARI Murray, 1907 (Fig. 530).

Aquatic tardigrade; length up to 570μ, but often less (300-400μ). Colorless, or with gray or brown pigmentation, often arranged according to longitudinal and transverse bands; eye spots present, in posterior position. The buccal tube is slightly curved near the buccal aperture, but then proceeds straight until its caudal end, that is, up to the entrance into the pharynx; its diameter is variable, sometimes rather narrow (less than 3μ in individuals of 300-400μ), other times wider (4-4.5μ, also in animals of 300-400μ). Pharynx short oval, with length:width ratio of about 1.1:1; in young animals the pharynx may be almost spherical. Apophyses clearly visible and 2 macroplacoids, of which the first is twice as long as the second and has a constriction (not always in the young); the constriction may be so deep as to divide the first macroplacoid in two, and in that case three macroplacoids are present of equal length; microplacoid absent. Doubleclaws of the *echinogenitus* type (a V), very curved, with very clear accessory points on the principal branch and with small lunule at the base.

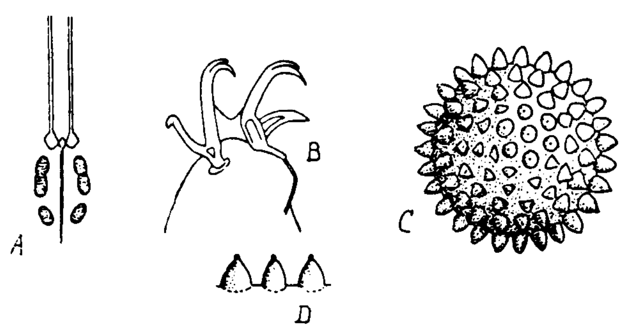


Fig. 529 - *M. pullari* Murray. A, placoids; B, doubleclaws of the 4th pair of legs; C, egg; D, detail of the projections of the egg.

Eggs spherical (diameter 75-90μ, including the ornamentations) or oval (larger diameter about 90μ); the projections are composed of small conical or mammillary tubercles -- 4-7μ high -- rarely with forked points, positioned at a certain distance from each other, in such manner that the shell is visible between these; sometimes there exists a ring of round dots at the base of each cone. The eggs are deposited free and it is not infrequent to find them in cavities, for example in the shells of Cladocera. It has been noted that the eggs of *M. pullari* -- in absence of the animal -- can not practically be distinguished from those of *Da. dispar*; this latter species is however easily recognized by the *macronyx* type claws and -- when they exist -- by the two conical dorsolateral gibbosities between the 3rd and 4th pairs of legs. If then *M. pullari* is found together with *Dactylobiotus* and eggs with the appearance described for those of *pullari*, it is not possible to decide whether the eggs belong to *M. pullari* or *Da. dispar*. It follows that they are not even identifiable from others; in fact if the eggs were deposited by *pullari*, the eggs of the other *Dactylobiotus* present may remain always unknown -- if determined only with the examination of the eggs -- which may then be *Da. dispar* or *Da. ambiguus*: they would only be identified as *Da. dispar*, in fortunate cases when they have the two dorsolateral caudal gibbosities (see also the description of *Da. dispar*). Whenever the material is alive, the doubt may be resolved with the culturing of the female until the depositing of the eggs.

M. pullari was collected in numerous localities from Europe (Italy included), in Africa (Ivory Coast and Kenya), in South America (Colombia) and in Greenland.

MACROBIOTUS PUSTULATUS Ramazzotti, 1959 (Fig. 530).

Maximum length 230μ, colorless, eye spots absent. The cuticle presents dorsally, laterally, ventrally and on the legs a sculpture composed of transverse rows of small cavities, or dimples, whose outline is of variable shape, from subcircular to triangular and to polygonal with rounded angles; the size of these cavities is very variable and from about 1-2μ in diameter for those of the median dorsal zone, to 4-5μ for those of the rostral zone, and 6-7μ and more for those in the caudal region; the margin of the larger cavities appears thick, as if surrounded by a pad.

Buccal tube rather narrow (diameter about 2μ), pharynx short oval with apophyses and 3 macroplacoids, having the appearance of oval granules and about equal size; microplacoid extremely minuscule, barely visible, that may however even be lacking; the shortness of the rows of

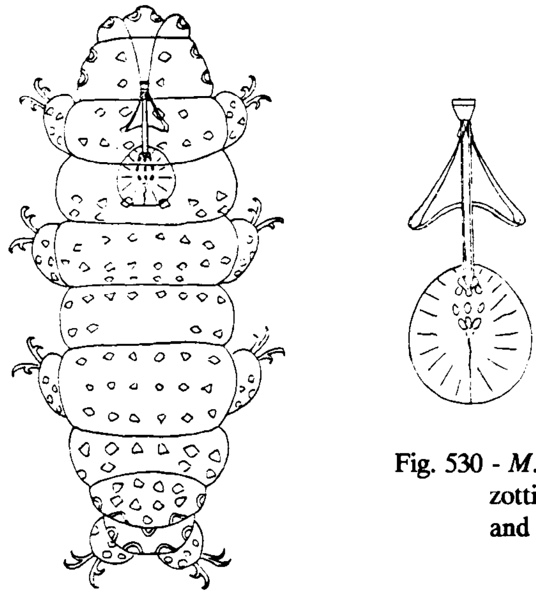


Fig. 530 - *M. pustulatus* Ramazzotti. Dorsal view and buccal apparatus.

macroplacoids is characteristic, which barely surpasses the middle of the pharynx. The first macroplacoid is partially hidden by the apophyses, as occurs for example in *M. intermedius*. Doubleclaws *hufelandi* type (a Y), about 9-10μ long, with small smooth lunules. Eggs with 65μ diameter (80-85μ exceptional) including the projections, which are small conical spines, 4-10μ long, 2μ or less wide at the base, ending in a apex of filiform bristle.

M. pustulatus has so far been collected in Italy (San Martino of Castrozza, western Dolomites, at about 1,500 meters altitude) and in Chile, and is probably near *M. striatus*, which also has very short rows of 3 macroplacoids each and whose apophyses partially mask the first macroplacoid; but the sculpture of the cuticle is much different, since *striatus* has extremely small round pores, similar to dots, which are moreover arranged in different manner and in less number of transverse rows.

MACROBIOTUS RAWSONI Horning, Schuster & Grigarick, 1978.

Length up to 456μ. Eyes present. Cuticle smooth, with some small pores on the posterior third of the body. Mouth probably with lamellae. Buccal tube rather narrow (about 14% of the length). Pharynx round, with apophyses and 2 macroplacoids, rod shaped, the first a little less than twice the second, and constricted in the posterior third; microplacoid present, elongated, very slender. Claws *hufelandi* type, with small lunule.

The eggs are similar to those of *M. hufelandi* and of *M. hibiscus*, with projections of truncated cones, terminated in a disk with dentate margin. These projections are much more numerous and dense than in *M. hibiscus*, and the surface of the egg presents pores; the projections are separated from each other by a single row of pores.

The animals, according to the authors, is not distinguishable from *M. anderssoni* (and -- according to us -- not even from *M. hufelandi*, and from other species of the group, also because the description seems a little summary). However regarding the eggs, we think that -- seeing the considerable variety of the eggs of *M. hufelandi* -- it is not very easy, and perhaps not even certain, to determine a specific distinction from *M. rawsoni* and *M. hibiscus*.

M. rawsoni was observed on the Chatham Islands (New Zealand).

MACROBIOTUS RECENS Cuénot, 1932 (Fig. 531).
= *M. hufelandi* forma *recens* Marcus, 1936
= *M. hufelandi recens* Ramazzotti 1962, 1972
not *M. recens* Grigarick, Schuster & Toftner, 1973
not *M. recens* Horning, Schuster & Grigarick, 1978

Remarkable size: Cuénot cites an adult of 624μ; in Portugese material Maucci has verified lengths up to 800μ. Colorless, cuticle smooth with numerous small, round pores ("pearls"), fairly dense on the caudal part, while more sparse and assume primarily elliptical shape toward the cephalic end. Mouth wide, surrounded by 10 large lamellae. The buccal tube is wide and straight (width as much as 21% of the length). Pharynx large, oval, moderately elongated. Large trapezoidal apophyses, two macroplacoids, and microplacoid. The first macroplacoid has the anterior end pointed and presents a hint of constriction barely beyond the middle; the second is about one-third shorter. The microplacoid, rather close to the second macroplacoid, is long and slender.

Claws of medium size, robust, very massive, with obvious accessory points on the principal branch. The first three pair presents a small, smooth lunule, the 4th pair a lunule more than twice larger, very slightly crenate.

The eggs are colorless or very pale yellow, spherical, with diameter of 95 to 128μ, excluding the projections, from 130 to 160 with these. The ornamentations have the shape of slender cones, around 15μ high, often with 8μ base. The surface of these cones is slightly rough, the apex is blunt, at times bent, at times (but rarely) bifid. At the base of each cone

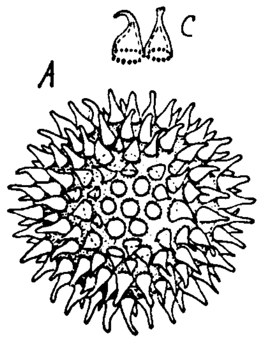


Fig. 531 - *M. recens* Cuénot. A, egg; C, detail of the ornamentation of the egg (from Cuénot).

is found a pronounced ring of dashes, arranged as spokes. Between the projections, the surface of the egg is slightly granulated.

M. recens, which Cuénot considers as a recent variation of *M. hufelandi*, was considered as a "forma" of this last species by Marcus and other authors. It, in reality, is clearly distinct from that species, and recognizable from it, even in absence of eggs, by the wider buccal tube and because the distance between the insertion of the stylet supports on the buccal tube, and end of the buccal tube is often constantly less, or at maximum equal to the width of the tube (in *M. hufelandi*, as also in other similar species -- such as *M. aviglianae* and *M. persimilis* -- such distance is always greater than the width of the tube).

M. recens was described from a locality of Vandea (France). Later it was found in Greece, in Dobrugia (Rumania), and in numerous localities from Portugal and Spain. The reports cited by Schuster et al. (1973) and Horning et al. (1978) from New Zealand do not refer to this species.

MACROBIOTUS RICHTERSI Murray, 1911 (Fig. 532).
= *M. harmsworthi* Thulin, 1911 (not Murray)
= *M. schultzei* Greeff, 1966
= *M. richtersi* Marcus, 1936, in part
= *M. richtersii* Type 1, Petersen, 1951
= *M. harmsworthi* Hallas, 1972 (not Murray), in part

Length as much as 750-1,000μ, often less, but however always considerable size. Colorless, the old individuals sometimes pigmented brown. Cuticle smooth, with very small pores ("pearls"), elliptical, more dense on the caudal part. Eyes almost always absent; if present found in

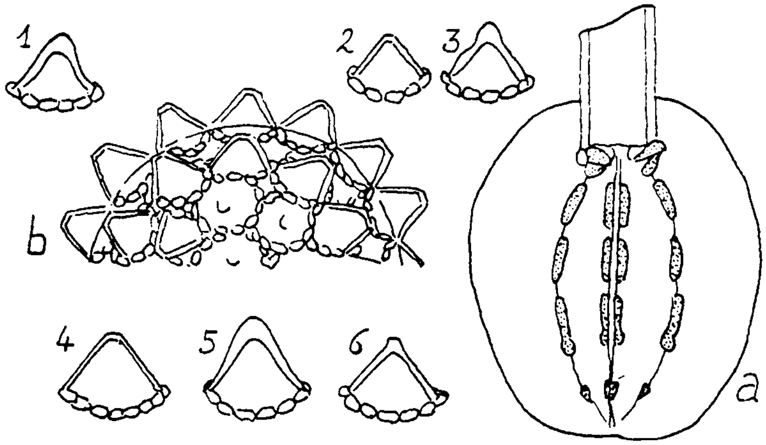


Fig. 532 - *M. richtersi* Murray. a, pharynx; b, detail of the egg; 1-6, different types of ornamentations (schematic).

anterior position. Mouth surrounded by a double ring of lamellae. Buccal tube very wide (one of the widest among the *Macrobiotus*): at least 20% of the length, sometimes even more. Stylets very large and robust; stylet supports inserted on the buccal tube at a distance from the posterior opening of it always clearly less than the diameter of the tube. Pharynx slightly elongated oval with apophyses, 3 macroplacoids and microplacoid. The macroplacoids have rod shape; usually the first and second (very close to each other) have equal length, the third is longer. The microplacoid is positioned rather distant from the macroplacoids, sometimes obvious, more often it is rather small. Claws of *hufelandi* type, robust, with obvious accessory points, and with lunules often smooth, sometimes (especially in the larger individuals) weakly crenate.

Eggs free, of considerably variable diameter. The projections usually have truncate conical shape, sometimes almost hemispherical, at times terminating at the apex with a ring of papillae. The surface of the eggs presents a reticular design; the surface of the egg, between the projections is "tiled", that is divided into polygonal or rounded surfaces.

M. richtersi has been interpreted different by different authors, and is not without confusion with other species. The above description is based on the establishment of a taxonomy that may be considered consolidated. The species appears, in general, easily recognizable, even in absence of eggs (a thing not frequent in the genus *Macrobiotus*), especially by the large width of the buccal tube and the shape and arrangement of the placoids. Compared with *M. areolatus* (with which it has been sometimes confused) it is recognized by the larger width of the buccal tube, and because *M. areolatus* does not have a microplacoid, or has an extremely small one. Compared with *M. harmsworthi* (and other species near it) the distinction is of equal ease: *M. harmsworthi* does not have "pearls", has macroplacoids of almost equal length and arranged in a characteristic curvature, and the microplacoid is much larger and nearer to the macroplacoids.

M. richtersi is one of the more common and more wide spread species. It is cited for many European localities (Italy included), for America, Africa, New Zealand, New Guinea, and diverse localities of Asia. We have found it in almost all the regions from which we have studied samples of moss.

Typ. loc.: Scotland, Ireland, Uganda, South Africa.

MACROBIOTUS ROLLEI Heinis, 1921 (Fig. 533).

Length up to 165μ, eye spots present. The entire dorsal and lateral surface of the body is covered with smooth gibbosities, elongated, not arranged in regular rows, but rather carelessly. Pharynx small, containing

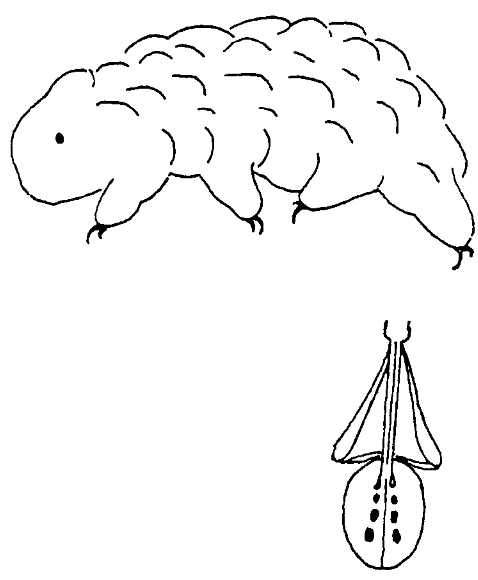


Fig. 533 - *M. rollei* Heinis. Lateral view and buccal apparatus (from Heinis, redrawn).

3 macroplacoids of granular shape. The doubleclaws have reduced size, with principal and secondary branches of almost equal length. Eggs unknown.

The incomplete description and the drawing which represents this species might probably be that of an *Isohypsibius* of the *tuberculatus* group; in fact Thulin (1928) and Cuénot (1932) are of this opinion; Marcus (1936) thinks instead the treatment truly of a *Macrobiotus*, because Heinis perfectly recognized various species of *Hypsibius* with gibbosities, when in 1921 he described *M. rollei*; this appears from preceding publications of this author. We think we can agree with the opinion of Marcus, strengthened by a second report of the species in Hungary, by A. Iharos (1940), who however cited the species without description; he however gives a drawing, according to which the claws -- however not well visible -- seem to be of *Macrobiotus* and precisely of the *hufelandi* type (a Y).

M. rollei was collected in Switzerland (summit of Gornengrad at 3,136 meter altitude), and in Hungary (Köszeg).

MACROBIOTUS RUBENS Murray, 1907 (Fig. 534).

Length 360-430μ, cuticle smooth, eye spots present; cavity globules often of reddish-brown color. Buccal tube narrow (diameter 2.5μ in animal of 368-392μ). Pharynx oval with apophyses and 2 macroplacoids, of which the first is about twice as long as the second and has a more or less deep constriction; microplacoid present. Doubleclaws of the *hufelandi* type (a Y). The eggs are smooth, oval and deposited in the exuvium, which is unusual for the genus *Macrobiotus*.

M. rubens is known from North (Mexico) and South (Colombia, Bolivia) America, Ascension Island, East Africa, Himalaya (at 2,000 m altitude), Australia, and India. Typ. loc.: Himalaya. A female collected at Testigos Islands and attributed by Du Bois-Reymond Marcus (1960) to this species certainly belongs to another species; in fact the size is 660μ, the buccal tube is very wide (16μ), the macroplacoids are three and the microplacoid is absent.

MACROBIOTUS SANTOROI Pilato & D'Urso, 1976 (Fig. 537).

Length as much as over 500μ, colorless with smooth cuticle, provided with circular or elliptical pores ("pearls"). Eyes present. Mouth surrounded with lamellae. Buccal tube moderately wide (11-12% of the length).

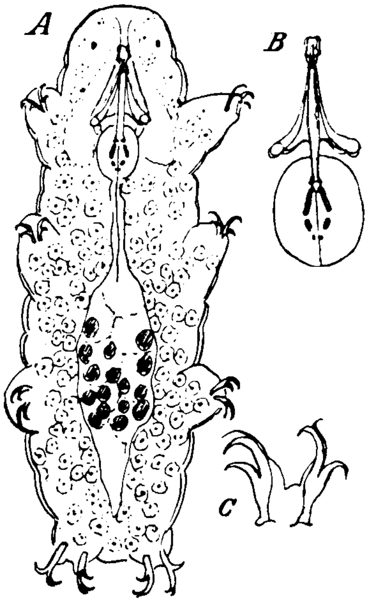


Fig. 534 - *M. rubens* Murray. A, habitus; B, buccal apparatus; C, doubleclaws (from Marcus).

Pharynx short oval, with apophyses, two rod-shaped macroplacoids and microplacoid. The first macroplacoid is longer than the second and has a median constriction.

Claws *hufelandi* type, with the two branches fused for a length equal to half the principal branch, or scarcely less, with accessory points very long on the principal branch, and lunules.

Eggs spherical, diameter 76μ, without projections, 84 with. The projections, numerous and small (4μ high, or a little less) have a truncated conical shape with distal end convex, supplied with a ring of extremely small dots; at times there exists a slight constriction in the distal third. The surface of the projections is smooth, while the shell between the projections has an extremely fine reticular design of extremely small mesh. According to the author the species is certainly near to *M. hufelandi*, from which in absence of eggs it is difficult to distinguish.

M. santoroi was found in Australia (in the vicinity of Sidney).

MACROBIOTUS SNARESENSIS Horning, Schuster & Grigarick, 1978) (Figs. 535 and 536).

Size up to 855μ, with average length of 450. Eye spots absent. Cuticle smooth, without "pearls". Mouth surrounded by lamellae (the description does not mention them, but they are clearly visible in the

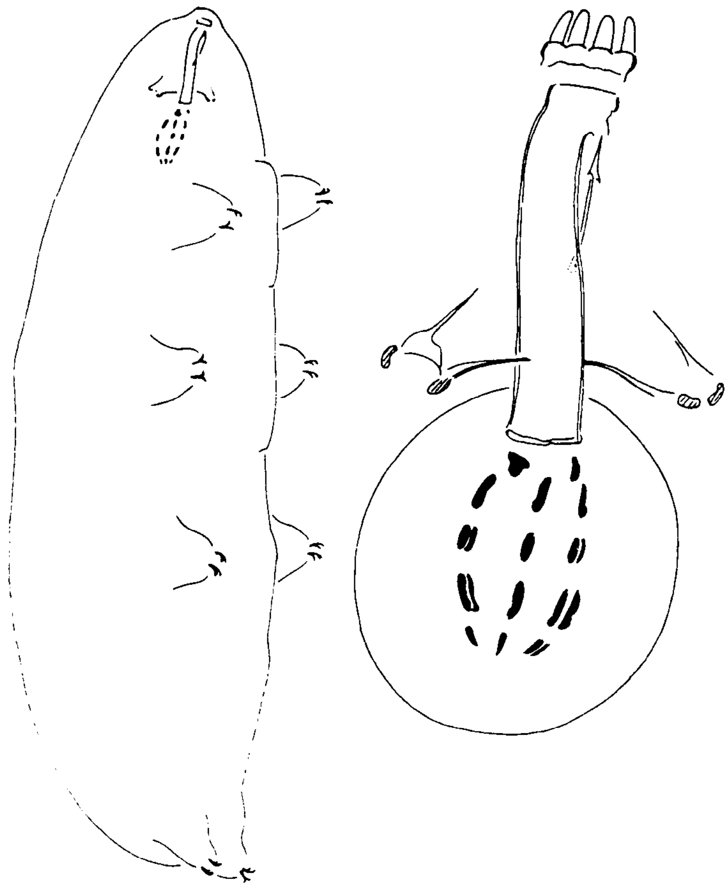


Fig. 535 - *M. snaresensis* Horning et al. Habitus and buccal apparatus (from Horning, Schuster and Grigarick).

accompanying drawing). Buccal tube very wide (22% of the length). Pharynx slightly elongated oval, containing apophyses and three rod-shaped macroplacoids, of which the second is shortest, the first and the third have equal length. Microplacoid present, large (as long as the 2nd macroplacoid).

The claws have common base, and the two branches are divided almost into two claws; the principal branch possesses accessory points. Lunules smooth, those of the 4th pair larger than the others.

The eggs have bulbous projections, with gradually attenuated apices, sometimes -- rarely -- bifid. The surface of the projections has a reticular

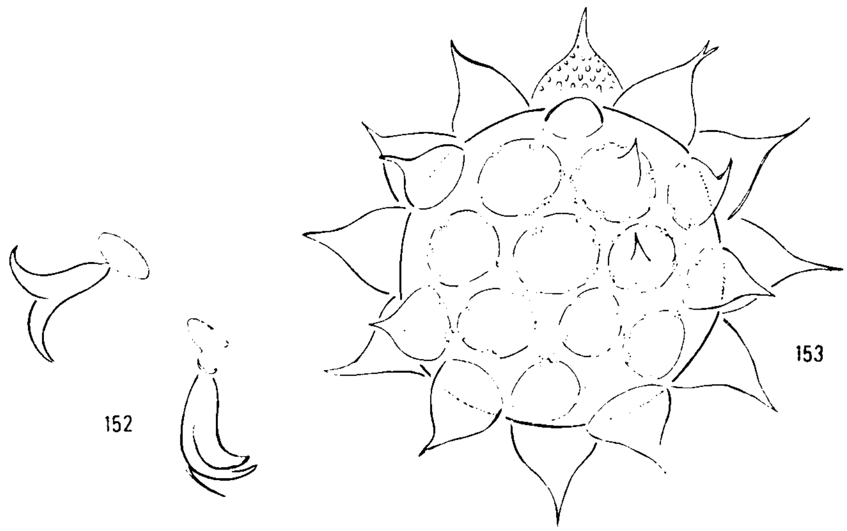


Fig. 536 - *M. snaresensis* Horning et al. Claws and egg (from Horning, Schuster and Grigarick).

pattern. Near the base of each projection is a ring of only 6-8μ pores. Between the projections the surface of the egg has slender protruding crests, but not a true "tiling".

The species is certainly very near to *M. harmsworthi*, and especially to the subspecies *coronatus*. However (apart from the larger size of the animals of *M. snaresensis*), *harmsworthi* does not have the ring of pores around the projections of the eggs, while *coronatus* has 20-24 small pores around each projection.

M. snaresensis was collected on the Snares Islands (New Zealand) where it seems to be the largest and most frequent species of *Macrobiotus*.

MACROBIOTUS SPALLANZANII Maucci, 1973 (Figs. 538 & 539).

Length up to 420μ, globules of intense yellow color, eyes present in posterior position. The cuticle shows pores much more pronounced than the usual "pearls", of irregular polygon, triangle, trapezoid, and rhombus shape, with more or less rounded angles, of size about uniform (from 2 to 2.2μ), except a little larger in size on the caudal portion of the body.

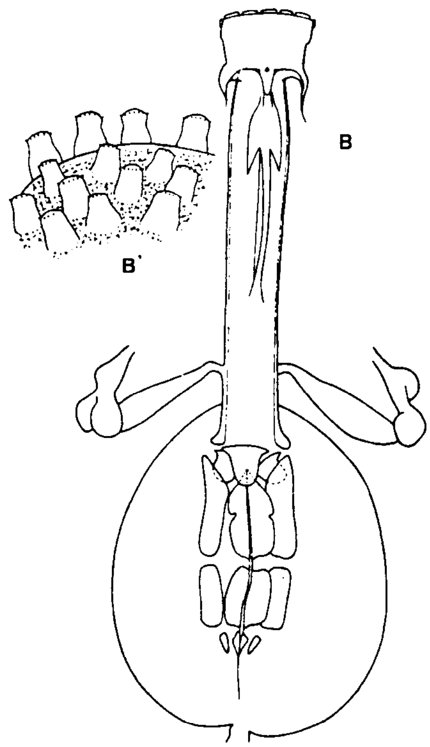


Fig. 537 - *M. santoroi* Pilato and D'Urso. Buccal apparatus and detail of the egg (from Pilato and D'Urso).

Such sculpture forms on the dorsum 8 transverse bands, of which the 3rd, the 5th, and the 7th are more slender than the others. The sculpture covers even the legs, and extends on the sides and on the ventral zone, although rarer and more sparse.

Peribuccal lamellae present. The buccal tube is rather short and straight (40μ long and 3 wide, in an example of 420μ). The buccal aperture is in anterio-ventral position, to which the buccal tube, viewed laterally, has immediate pronounced curvature in its rostral portion, so that the reinforcement bar, which connects as far as the middle of the tube, resulting somewhat removed from this latter. Stylets slender, very divergent, with large but weak furcae. Pharynx round, or subround; apophyses small and rounded; 3 macroplacoids of short granule shape, sometimes round, sometimes -- especially the 3rd -- a little elongated. Microplacoid slender and elongated.

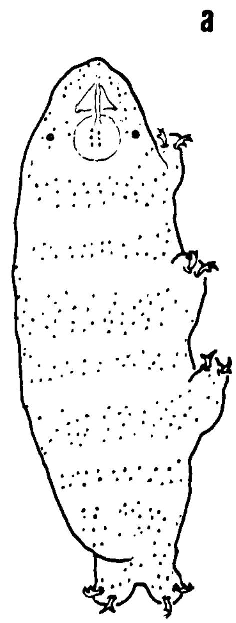
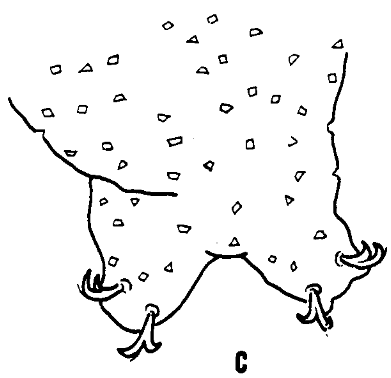
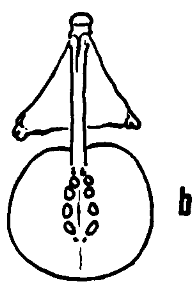


Fig. 538 - *M. spallanzanii* Maucci. a, habitus; b, buccal apparatus; c, caudal end and 4th pair of legs (from Maucci).





Claws *hufelandi* type, rather robust, with evident accessory points on the principal branch; small and smooth lunules on the first three pair of legs, a little larger and dentate on the 4th pair.

Eggs spherical, pale yellow color, with 76-115μ diameter without projections and 104-130 including these. The projections are conical, low (8-12μ) and wide (28-30μ at the base) and have irregularly notched apices, constituting an irregular tuft of papillae; the projections have a reticular design, of dense and irregular mesh; the shell, between the projections,

Fig. 539 - *M. spallanzanii* Maucci. Egg and detail of a projection of it (from Maucci).

which are very distant from each other, have undulating crests, defining irregular depressions, but not such as to constitute a true "tiling".

The species is probably near to *M. furcatus*, *M. pseudofurcatus*, and *M. pustulatus*, and perhaps also to *M. intermedius*. Except for the latter, it is not easy to distinguish from the others in absence of eggs.

M. spallanzanii has been found in different localities of the Trieste and Istrian Carso. Typ. loc.: Trebiciano (Trieste).

MACROBIOTUS SPECTABILIS Thulin, 1928 (Fig. 540).

The size is often considerable (up to 870μ), the cuticle is smooth except on the legs where is noted, as in many other species, numerous small dots.

There are eyes in anterior position. The mouth is terminal and surrounded by 10 obvious peribuccal lamellae. In specimens about 700μ long the buccal tube is 13μ wide and about 74 long (105, 7 *ms*); if one measures from the stylet sheath to the base of the apophyses it is instead 64μ long. The pharyngeal bulb of the same specimen is 65μ long and 53μ wide with a length to width ratio equal to 1.22:1. It contains normally developed apophyses, two macroplacoids in the shape of long rods and a well developed microplacoid. The first macroplacoid has a medial projection of which one thinks of as a structure exclusive of *M. spectabilis*

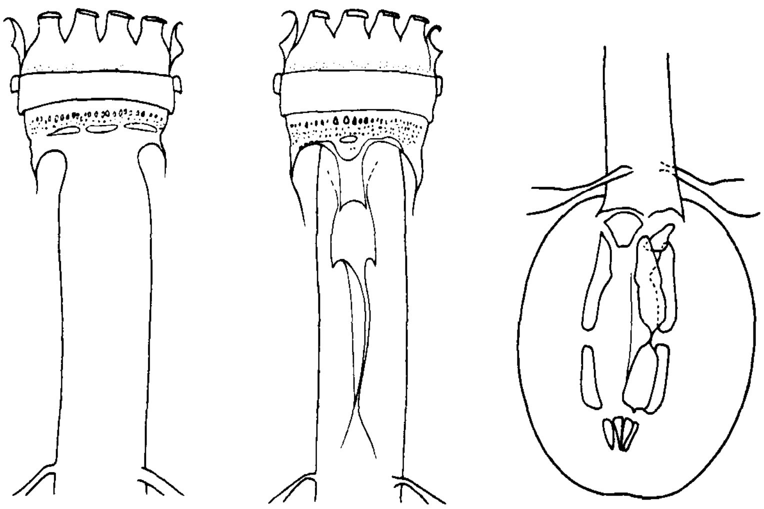


Fig. 540 - *M. spectabilis* Thulin. Buccal armature, dorsal side (from left) and ventral side, and pharynx (from Maucci and Pilato).

but in reality, even if less developed, may be recognized in numerous other species of *Macrobiotus*.

The first placoid has, posteriorly to this projection, a profound constriction, and the second has the caudal end medially bent. In the same specimens of which we have first furnished the measurements relative to the buccal tube and the pharyngeal bulb, the first placoid is 23μ long and the second 16μ; the microplacoid 7.5μ. In the population studied the length of the row of the two macroplacoids represents 58-61% of the length of the bulb.

The claws are of *hufelandi* type with obvious accessory points, and are provided at the base with small smooth lunules which appear more developed on the posterior legs. In specimens about 700μ long the external claws of the posterior legs measure 19.2μ in length, while those of the first pair of legs are 15.8μ.

The eggs, deposited free, are spherical and have stellate appearance due to the presence of obvious conical projections; in optical section they have 11 or, more rarely, 12 projections. These are always completely smooth on the basal half, and sometimes they are also on the distal half where more often they have instead a fine punctation very sparse and irregular.

Very characteristic is the sculpture of the shell between the conical projections: it is composed of a ring of polygons which circle the base of each projection, and since the ring of polygons surrounding the close projections results as contiguous between them, so that between two adjacent projections one always finds two rows of polygons. The shell between the projections is always completely punctated and varying the position of the focus, the single dots appear (however only sometimes) connected between them by very slender and short dashes in a way to give cause to a reticular sculpture of small mesh.

The diameter of the eggs reaches 178μ including in the measurements also the projections, reaches 127μ excluding those structures. The height of the projections may reach 35μ and the diameter at the base 25μ. For the total appearance of the egg of *M. spectabilis* one says usually that it is similar to that of the egg of *M. areolatus* but in reality such resemblance is found only in the existence of conical projections, for all the rest of the egg of the two species appears very different with regard to sculpture of the shell in that the projections of *M. spectabilis* are almost completely smooth while those of *M. areolatus* are always provided with an obvious reticulated sculpture of characteristic appearance for the species.

This species, formerly considered *spec. dubia*, is now known from the redescription carried out by Dastych (1973) and by Maucci and Pilato (1974).

M. spectabilis is known from Siberia (near Lake Telezki, type locality), from Poland, from Italy (Lombardia), and from four localities in Norway.

MACROBIOTUS SPERTII Ramazzotti, 1957 (Fig. 541).

Maximum observed length 580μ, eyes present, cuticle smooth. The buccal tube -- often more cylindrical than appears in Fig. 541, d -- is moderately wide (4.5-7μ) for the size of the animal; peribuccal lamellae are not visible; the pharynx is short oval, sometimes almost spherical, and contains very showy apophyses, 3 macroplacoids (rods) of increasing length from first to third, and rather large microplacoid. Doubleclaws of the *hufelandi* (a Y), rather small (8-10μ in length).

The eggs are very characteristic and -- with size much larger -- calls to mind vaguely those of *M. hastatus*; however, while in *hastatus* there are 2 macroplacoids and the microplacoid is lacking, in *spertii* the macroplacoids are 3 and the microplacoid is present. The ornamentations (projections) of the eggs are generally fifteen in optical section and have the shape indicated in Fig. 541, a, b, c; they are almost completely immersed

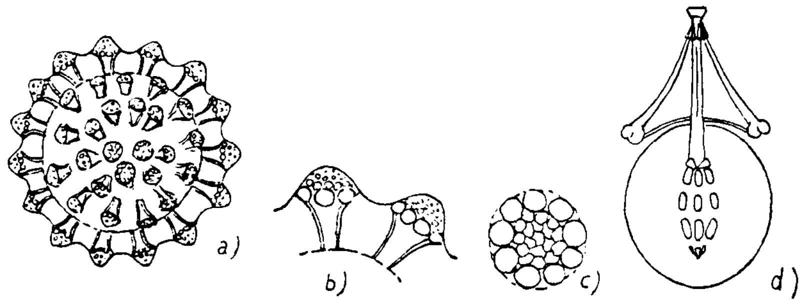


Fig. 541 - *M. spertii* Ramazzotti. a, egg; b, projection of the egg in lateral view; c, projection of the egg in frontal view; d, buccal apparatus.

in a hyaline zone of the shell, a zone which has a thickness of about 21μ in the egg represented; the external diameter of the egg -- including the projections -- may reach 210μ and the inner diameter -- excluding the transparent zone of the shell -- 149μ; the dimensions are however variable. It can be recognized from the other four species having eggs with projections immersed in an external transparent zone: *M. csotiensis*, *M. hastatus* (aquatic), *M. hibernicus*, and *M. acontistus*; however their eggs have a maximum diameter of about 85μ and the thickness of the hyaline zone reaches over 10μ, while in the eggs of *spertii* the diameter may surpass 200μ and the thickness of the hyaline zone 20-22μ; also the shape of the ornamentations is totally different.

The species is known only for a locality of Tierra del Fuego (South Pass of Sarmiento Mountain), where collected in moss.

MACROBIOTUS STELLARIS Du Bois-Reymond Marcus, 1944 (Fig. 542).

Size up to over 600μ (newly hatched scarcely out of the egg measures 200μ). Colorless, cuticle smooth, without "pearls". Eyes present, in anterior position. Peribuccal lamellae present, rather short and wide. Buccal armature "*areolatus* type" (Pilato, 1972). Buccal tube rather short and wide (a little less than 20% of the length). The reinforcement bar of the buccal tube is long, reaching two-thirds of the tube. Stylets slender, with large and heavy furcae. Pharynx short oval, with very small apophyses, 3 macroplacoids, and microplacoid. The first two macroplacoids are very near to each other, the second (which is the shortest) is about twice as long as its width, the first and the third have equal length. The

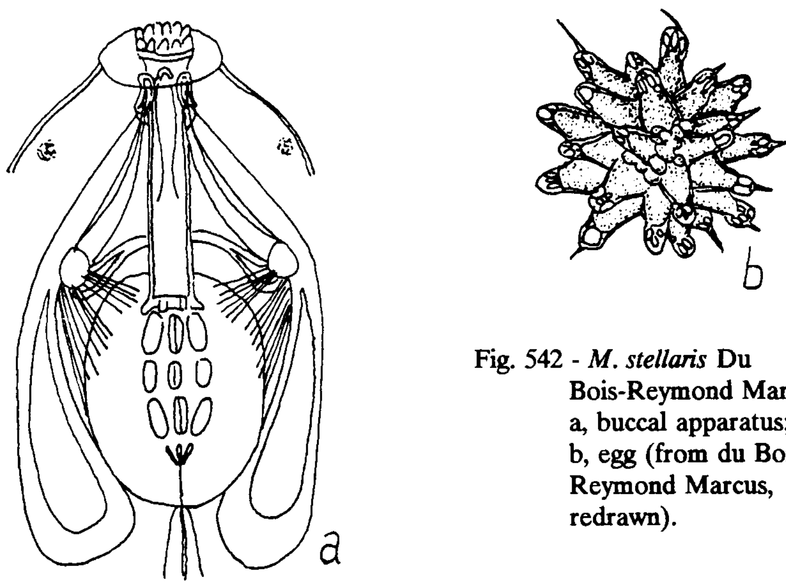


Fig. 542 - *M. stellaris* Du Bois-Reymond Marcus. a, buccal apparatus; b, egg (from du Bois-Reymond Marcus, redrawn).

microplacoid, very large (it is almost as long as the second macroplacoid) is slender and of triangular shape.

Claws short, robust, with large accessory points and smooth lunules, a little larger on the 4th pair of legs.

The eggs, constant in general character, have considerable difference in the size and appearance of the projections. The size (110μ diameter, including the projections, in the original description) reaches 165μ in Turkish material. The projections, large, a little irregular, are conical, end sometimes with a filament at the apex; they have a reticular design, with large and small mesh intermingled; such mesh gets larger toward the apices of the projections, where they become true and proper vesicles (in some examples, prepared in polyvinyl lactophenol, there remains included in such vesicles a bubble of air).

This species, in absence of eggs, is difficult to recognize from others of the *harmsworthi* group, and in particular from *M. harmsworthi* (which has a buccal tube in general a little wider, and rows of placoids proportionally shorter) and from *M. nuragicus* (it also has a wider buccal tube).

M. stellaris was collected in Brazil (State of Sao Paulo, typ. loc.), in one locality from Turkey (Elmali) and in one Greek locality (Peloponneso).

MACROBIOTUS STRIATUS Mihelčič, 1949 (Fig. 453).

Medium size (the length was not published in μ), color yellow, eyes absent. The sculpture of the cuticle consists of dots (small circles) -- which are in reality small pits -- arranged regularly in transverse rows. On the cephalic region there are two double rows of ten small circles each, followed by a single row; in correspondence with the first pair of legs there is a double row of twelve small circles, then a single row of six; in correspondence with the second pair of legs a double row of fourteen small circles, then a single row of seven; in correspondence with the third pair of legs a double row of twelve small circles, followed by two single rows, and finally a row of eight small circles over the fourth pair of legs. There are, moreover, three small circles at the base of each leg.

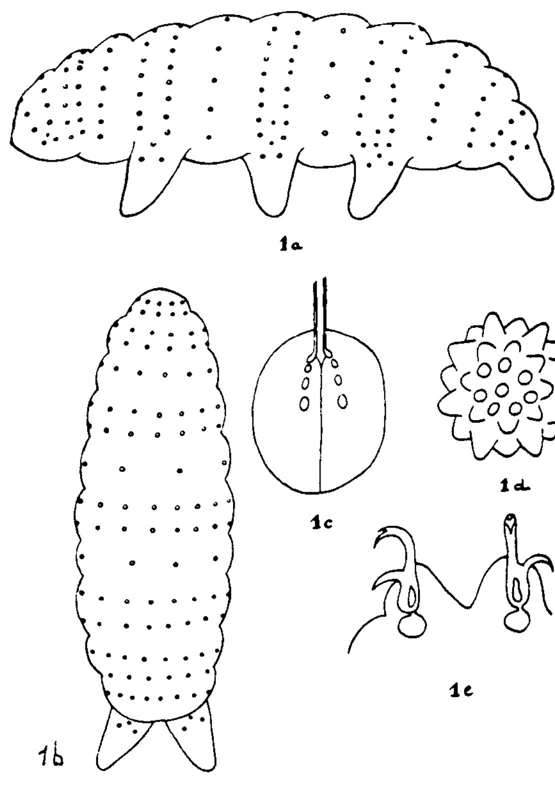


Fig. 543 - *M. striatus* Mihelčič. 1a, lateral view; 1b, dorsal view; 1c, pharynx; 1d, egg; 1e, doubleclaws of the 4th pair of legs (from Mihelčič).

Buccal tube narrow, stylets slightly curved, pharynx short oval with apophyses and three macroplacoids of granular shape; microplacoid absent. The rows of macroplacoids are very short and scarcely reach to the middle of the pharynx; the first macroplacoid is extremely near the apophyses, so that they appear covered by these; the third macroplacoid is largest. The doubleclaws are of the *hufelandi* type (a Y), with smooth lunules; the principal branch is provided with robust accessory points.

Eggs (see Fig. 453, 1d) with conical papillose projections, in narrow contact with each other, of which has not been published the size.

The species -- probably near to *M. pustulatus* (see that description) -- has been collected only in Austria, in needle leaf litter at an altitude of about 1600 meters.

MACROBIOTUS SUBINTERMEDIUS Ramazzotti, 1962 (Fig. 544).

Length up to 290μ; cuticle smooth, small eye spots. The appearance is very similar to that of *M. intermedius*; if lacking eggs, only a very experienced eye may distinguish from this last species, and not always with ease.

The "forehead" is steep (Fig. 544 B), similar that is to that of the *Hypsibius* (as in *M. intermedius*); the buccal tube is very narrow, less than 2μ in tardigrades of 266μ. The pharynx is slightly ovoid, with length:width ratio of about 1.10:1.22, and contains 3 macroplacoids and a minuscule microplacoid, barely visible; analogous with regard to *M. intermedius*, the first macroplacoid appears almost hidden by the apophyses. The macroplacoids are granules, somewhat more quadrangular than in *M. intermedius*; in lateral view often the macroplacoids of one of the rows seems to be very wide in transverse sense, almost rectangular, probably because of the partial overlapping of two rows (this does not happen in *M. intermedius*); in ventral view the granules, still remaining angular, appear more rounded. It should finally be noted that the rows of the macroplacoids are a little shorter than in *M. intermedius*; the difference is however modest; in *M. intermedius* the length of the rows of macroplacoids is in general higher than 64-67% of the length of the pharynx, while it is always less than 60-63% in *M. subintermedius*.

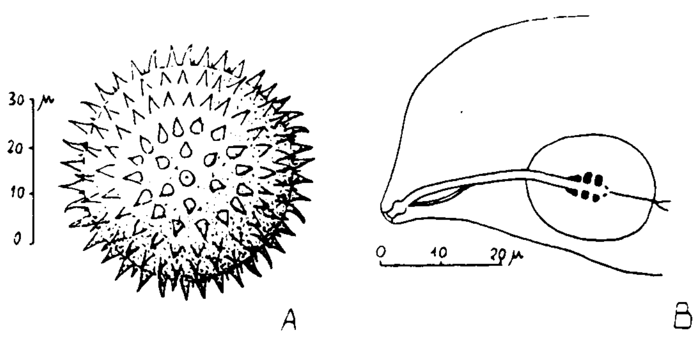


Fig. 544 - *M. subintermedius* Ramazzotti. A, egg; B, detail of the cephalic region.

The doubleclaws are of the *hufelandi* type (a Y), with large accessory points on the principal branch, and have at the base extremely small open lunules; under certain angles of observation the doubleclaws may however simulate the *echinogenitus* type.

The eggs are very different from those, so characteristic, of *M. intermedius*; their diameter is approximately 55μ, including the projections, which have the shape of triangular spines, 2μ or less wide at the base, sometimes a little bent at the apices. The belonging of these eggs to *M. subintermedius* is certain either because they have been observed very embryonated, or because from one of them it was possible to extract for examination a young tardigrade of almost complete development (length 142μ). The species was collected in numerous localities from Chile, where it seems to be very wide spread.

MACROBIOTUS SUBJULIETAE Horning, Schuster & Grigarick, 1978 (Fig. 545).
= *M. intermedius subjulietae* Horning et al., 1978.

The length cited in the original description is of 195μ; an example received as a gift from D. Nelson reached instead 520μ. Colorless. Eyes absent. The cuticle is smooth, without "pearls", but present on the caudal end a zone with irregular tubercles, as well as two conical projections, dorso-lateral, slightly in front of the 4th pair of legs. There are 10 peribuccal lamellae. The buccal tube is rather long, and very narrow (8% of the length); the stylet supports are inserted on the tube slightly beyond half its length. Pharynx almost round, with large apophyses and 3 macroplacoids of granular shape (the macroplacoids have the same size as the apophyses); microplacoid present, rather small. The claws, judging from the published drawing, do not have either accessory points, nor lunules. Eggs unknown.

M. subjulietae was described as a subspecies of *M. intermedius*. It is however our opinion that it should instead be identified with *M. aculeatus* (noted in Australia, and also it may have only one pair of conical projections). *M. subjulietae* is known from different localities of New Zealand.

MACROBIOTUS SUBMORULATUS Iharos, 1966 (Fig. 546).

Length as much as 450μ, colorless, eye spots present, cuticle smooth.

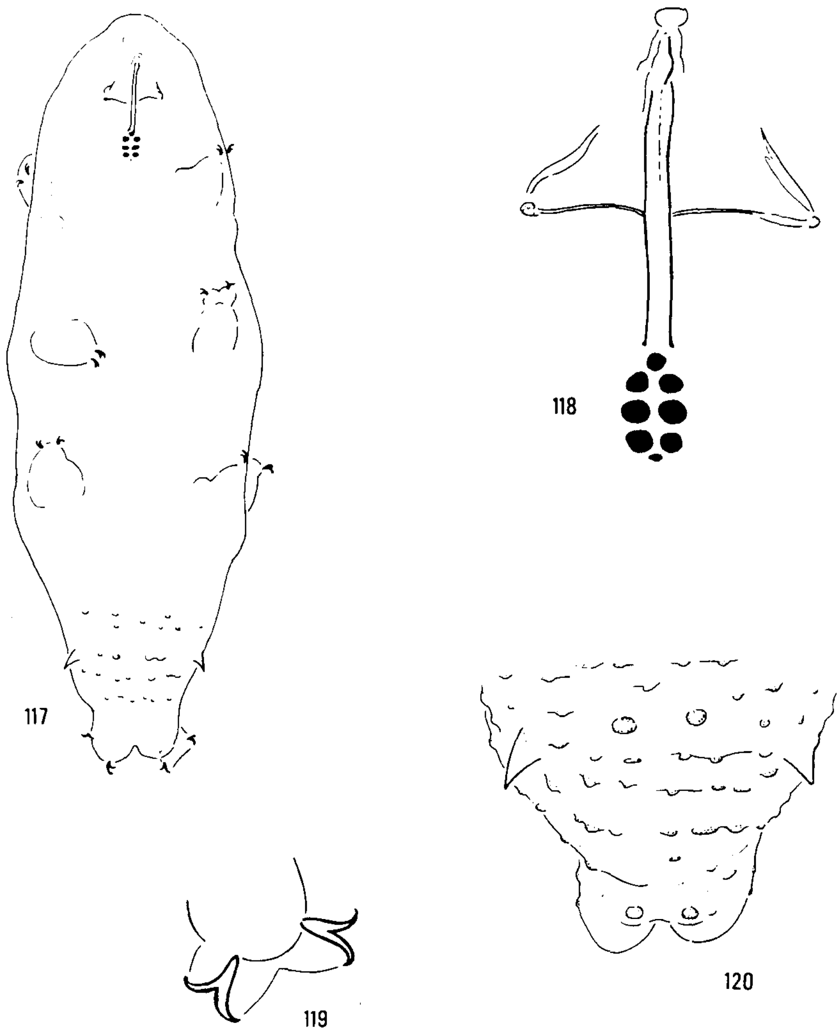


Fig. 545 - *M. subjulietae* Horning et al. 117, dorsal view; 118, buccal apparatus; 119, claws of the 4th pair of legs; 120, detail of the caudal end (from Horning, Schuster and Grigarick).

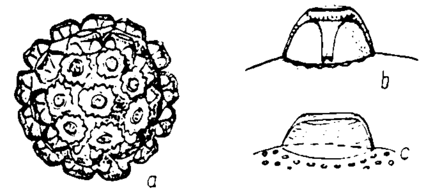


Fig. 546 - *M. submorulatus* Iharos. a, egg; b, projections of egg; c, egg projections of *M. morulatus* (from Iharos).

Pharynx oval (25 x 22μ) with 3 macroplacoids, which increase in length in rostro-caudal sense; small microplacoid. Buccal tube 4μ wide; double-claws *hufelandi* type.

Eggs large, spherical, having 95μ diameter including the projections, which are 7.5μ high and 17μ wide at the base. The surface of the projections is funnel-shaped in the center, that is to say each of the ornaments is sunken as a funnel toward the internal, in its distal central zone; in optical section of the egg there are 12-14 projections visible.

M. submorulatus was collected in moss on dolomite rock in a fir forest at Kalenderberg near Mödling (Austria).

MACROBIOTUS TENUIS Binda and Pilato, 1972 (Fig. 547).

Length from 225μ (neonatal) to 430μ in typical material; in an abundant population studied by Maucci (1972-73) the length was from 160μ (neonatal) to 640μ. Pale yellowish color; smooth cuticle, with "pearls" (without "pearls" in the material of Maucci); eyes present. There is a zone of very fine granulation, composed of dark dots, on the legs and in some positions on the ventral side.

Peribuccal lamellae present. Buccal tube long and slender (from a minimum of 5 to a maximum of 8% of the length). Pharynx almost round, with apophyses and 2 macroplacoids and microplacoid: the apophyses are large, the macroplacoids are small rods, the first almost twice the second, and often strongly incised in the middle.

Claws long, but rather thin; the common basal part is very long, the secondary branch is short and divides almost at a right angle, the principal branch with very thin accessory points, often visible with difficulty. Very large lunule, smooth on the first three pairs of legs, dentate on the 4th

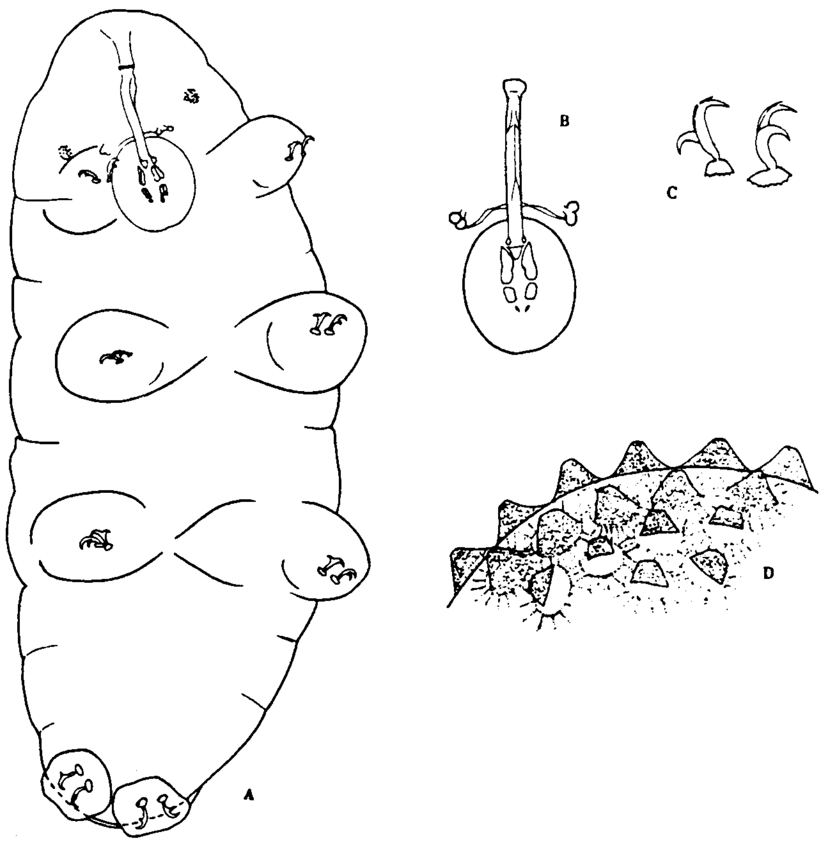


Fig. 547 - *M. tenuis* Binda and Pilato. A, ventral view; B, buccal apparatus; C, double-claws; D, detail of the egg (from Binda and Pilato).

pair.

Eggs spherical, of yellowish color, when viewed under bright incident light; diameter of 92 to 116μ, including projections. The projections are truncate cones and their surface is covered with a reticular design of very dense mesh and of circular shape. The shell between the projections is finely granulated.

M. tenuis is known only from one locality of Sicily (Guarda Mangano, near Catania, typ. loc.), and from the vicinity of Courmayeur (Aosta Valley).

MACROBIOTUS TERRICOLA Mihelčič, 1949 (Fig. 548).

Length 450-600μ, eye spots absent, colorless or whitish-yellow.

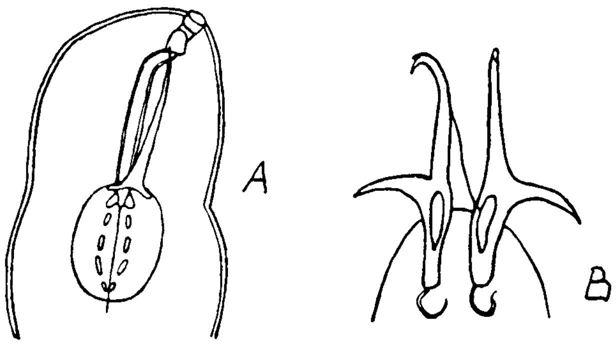


Fig. 548 - *M. terricola* Mihelčič. A, cephalic region and pharynx; B, doubleclaws of the 4th pair of legs (from Mihelčič).

The cuticle is covered -- on the dorsum and its sides -- with a dense sculpture of small round dots, with the appearance of pores. Buccal tube slightly wide (3-4μ diameter), curved, suddenly after the buccal opening, then straight; stylets robust and with strong curvature, furcae large. Pharynx oval with apophyses and 3 macroplacoids; in the second description of the species the author (1951) says that the third macroplacoid is the longest and the second shortest, but in the drawing (Fig. 548) it seems that the three macroplacoids increase in length in rostro-caudal sense. There is a microplacoid. Legs and claws large; the latter are of the *hufelandi* type (a Y) and very robust, with smooth lunules at their bases. The eggs (of which was not given the size, nor published drawing) have obtuse conical projections, with enlarged base in the shape of onion, positioned at a certain distance from each other.

So far the species has always been collected in soil (in Austria; meadow land, or slightly damp); but according to the same author it is perhaps premature to be considered exclusively eu-edaphic.

MACROBIOTUS TONOLLII Ramazzotti, 1956 (Fig. 549).

Length up to 620μ, colorless (white in reflected light), eyed. The cuticle is smooth, but presents dorsally numerous small "pearls", clearly visible only with immersion objective, or with use of phase contrast. The buccal tube is very wide (as much as 12μ diameter) and has peribuccal lamellae; pharynx oval, containing apophyses and 3 macroplacoids, of which the first and the third are about of equal length (11-12μ) and the second shorter (about 6μ) and almost in contact with the first; microplacoid in general absent, but sometimes present, however extremely small

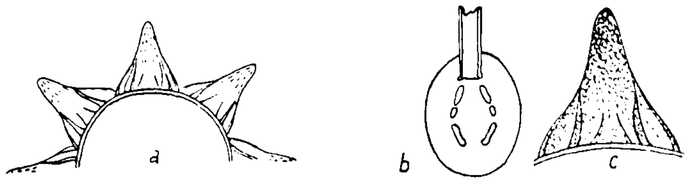


Fig. 549 - *M. tonollii* Ramazzotti. a, egg; b, pharynx with placoids; c, detail of an ornamentation (projection) of the egg.

and visible with difficulty. Doubleclaws *hufelandi* type (a Y), with accessory points on the principal branch and small smooth lunules.

The eggs are characteristic and permit then an immediate recognition of the species; they belong to the "stellate" type, without tiling, but their conical ornamentations (projections), with enlarged bases, possess a rather complex system of ribbing, which we have tried to reproduce in Fig. 549, a, c. In optical section the appendices are not very numerous (from 8 to 10) and that gives the eggs a very elegant appearance, that brings to mind the "alpine star" (*Leontopodium alpinum*). From the base of all projections, to about the middle, runs 6 ribs, of which -- with respect to the level of observation -- two are lateral, two anterior, and two posterior; there are then two ribs shorter and more slender (which sometimes meet at acute angles) in the central zone of each projection, from the base as far as about one quarter, or one third of its height; it is probable that of these small ribs there may be two pair, one anterior and one posterior in optical plane. It results very difficult -- even with the use of phase contrast -- to determine the exact course of the ribs; however Fig. 549, a, c, gives one design rather near to the truth and, when these eggs are viewed even a single time, it is not possible to confuse them with those of other species. Each individual projection, observed with high magnification, shows a complex reticular design (Fig. 549, c), whose mesh has larger size toward the distal end of the projections (height about 32-35μ), is 120-140μ.

M. tonollii is a very common and wide spread species in North America, especially in the eastern United States (Wisconsin, Illinois, Tennessee, North Carolina, etc.) and in Canada. It was also found in Lapland. Typ. loc.: Wisconsin (U.S.A.).

MACROBIOTUS TOPALI Iharos, 1969 (Fig. 550).

Small and squat, length 220-250μ. Coelomic liquid of orange-red color. Eyes present (anterior). The sculpture of the cuticle is composed

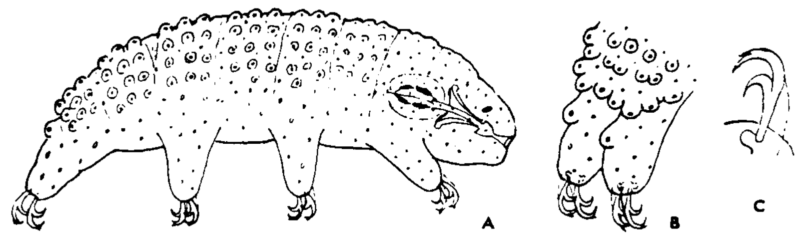


Fig. 550 - *M. topali* Iharos. A, lateral view; B, caudal region; C, doubleclaws of the 4th pair of legs (from Iharos).

MACROBIOTUS TOPALI Iharos, 1969 (Fig. 550).

Small and squat, length 220-250μ. Coelomic liquid of orange-red color. Eyes present (anterior). The sculpture of the cuticle is composed of numerous very refringent dots ("pearls"), irregularly arranged; moreover, beginning at the level of the 2nd pair of legs, starts a dorsal sculpture, composed of small hemispherical tubercles, close to each other and arranged in transverse rows. These tubercles increase in length in anterio-posterior sense and in the caudal region of the dorsum reaches a height of 2-2.4μ; at their center there is a "pearl".

Buccal tube narrow (1.8μ); pharynx elongated oval (22 x 17μ) with apophyses and 2 rod-shaped macroplacoids, the 1st (4.5μ) longer than the 2nd (3μ). Microplacoid absent. Legs long; those of the 4th pair dorsally bear a larger tubercle and many "pearls". Claws *hufelandi* type, 10μ long, with branches of hook shape; small and slender lunules. Eggs unknown.

The species was collected in moss on soil, in a forest at Kurseong (Darjeeling Province, India) at 1,500 m altitude.

MACROBIOTUS VIRGATUS Murray, 1910 (Fig. 551).

Length up to 750μ, robust, eye spots in general present but sometimes absent (Australian material). On the body there are three longitudinal bands of brown pigment, similar to those of *H. oberhaeuseri*, but which do not ever tend to be -- as occurs some times in that species -- to purple color; one of these bands is median, while the other two are positioned at its sides and may be subdivided into narrow bands; there are also slender transverse bands. Buccal tube very wide (9-10μ diameter), which ends in the pharynx with an enlargement of a slightly pronounced

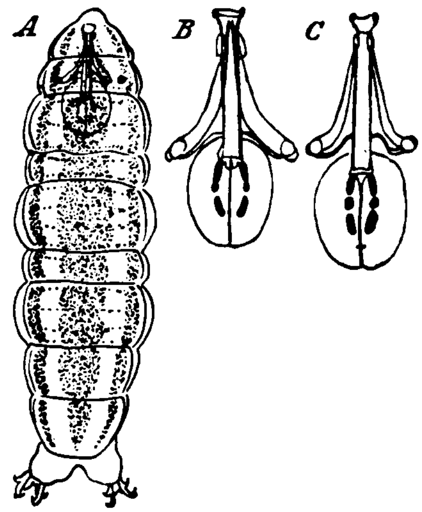


Fig. 551 - *M. virgatus* Murray. A, dorsal view; B, typical pharynx; C, aberrant pharynx with macroplacoids; D, doubleclaws (from Marcus).

longer than wide, or else twice as long as its width; usually lacking microplacoid, which is present instead -- very small -- in the Australian individuals. Doubleclaws very thick; principal and secondary branches of very different length, of the *hufelandi* type (a Y); large accessory points on the principal branch. Eggs unknown.

Bartos (1939) considered as *M. virgatus* individuals collected in the Carpathian region, but they are rather different -- by their characteristics -- from the above reported description; in fact the longitudinal brown pigmented bands were 5 (rather than 3), each subdivided -- by transverse colorless bands -- into about 10 distinct pigmented zones; the animals measured as much as 360μ, the buccal tube had a diameter of 7μ and of the three macroplacoids the longest was the first (5.5μ), while the second and the third had about equal length (4μ); finally the microplacoid reached considerable size (2.7μ), rather than being small or absent; eggs were not found.

The species, not perfectly defined because of lacking knowledge of the eggs, has been cited for the Carpathians, Ireland, Franz Josef Land, Australia, Canada, and Peru; however the belonging of *virgatus* is uncertain for the Australian material and for that of Franz Josef Land; the latter seems to have been assigned to smooth eggs deposited in exuvia (?).

Typ. loc.: Vancouver, Ottawa (Canada).

MACROBIOTUS WAUENSIS Iharos, 1973 (Fig. 552).

Considerable size (675-700μ), rose color. Cuticle smooth; eyes absent. Mouth surrounded by two rings of lamellae. Buccal tube wide

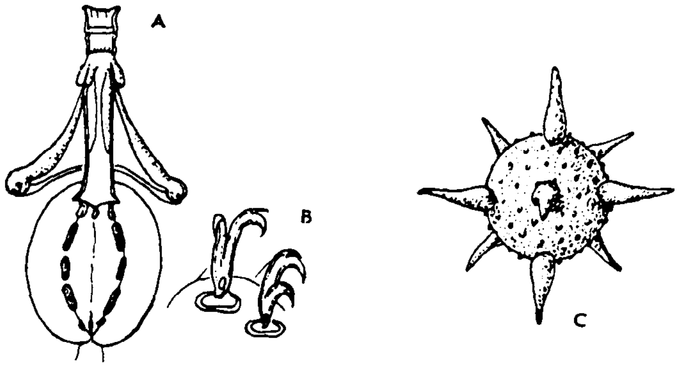


Fig. 552 - *M. wauensis* Iharos. A, buccal apparatus; B, doubleclaws; C, egg (from Iharos).

(12μ); stylets very robust and strongly curved. Pharynx elongated oval, with small apophyses, 3 macroplacoids, and microplacoid. The macroplacoids are rod shaped, the first and the third of equal length, the second shorter; the arrangement and curvature is similar to that of *M. harmsworthi*; the microplacoid is rather small.

Claws of the *hufelandi* type, with smooth lunule.

Eggs spherical, 55μ diameter, without projections. Yellow-brown color. The projections are in the shape of elongated drops, few, and considerably distant. Between these on the surface of the egg, which is smooth, exists small prominent hemispheres.

M. wauensis was found in different localities of New Guinea. Typ. loc.: Mount Wilhelm.

MACROBIOTUS WILLARDI Pilato, 1977 (Fig. 553).

Length as much as a little more than 600μ, colorless, with large eye spots. Cuticle smooth, with "pearls" only on the legs. Mouth supplied with lamellae; buccal tube medium wide (little more than 12% of the length). Pharynx oval, or almost spherical, with apophyses, 3 macroplacoids, and microplacoid; of the macroplacoids the first is longest, the second shortest; sometimes the first two macroplacoids are fused together thus seems only one, strongly constricted in the middle.

Legs short. Claws of *hufelandi* type, with accessory points on the principal branch (more evident on the legs of the 4th pair); lunules well developed, smooth.

Eggs spherical (74-82μ, excluding the projections); the projections (32 in optical section) are long flexible cones (height about 20μ, 6μ wide at the base). The apices are strongly sharpened, and the surface has a

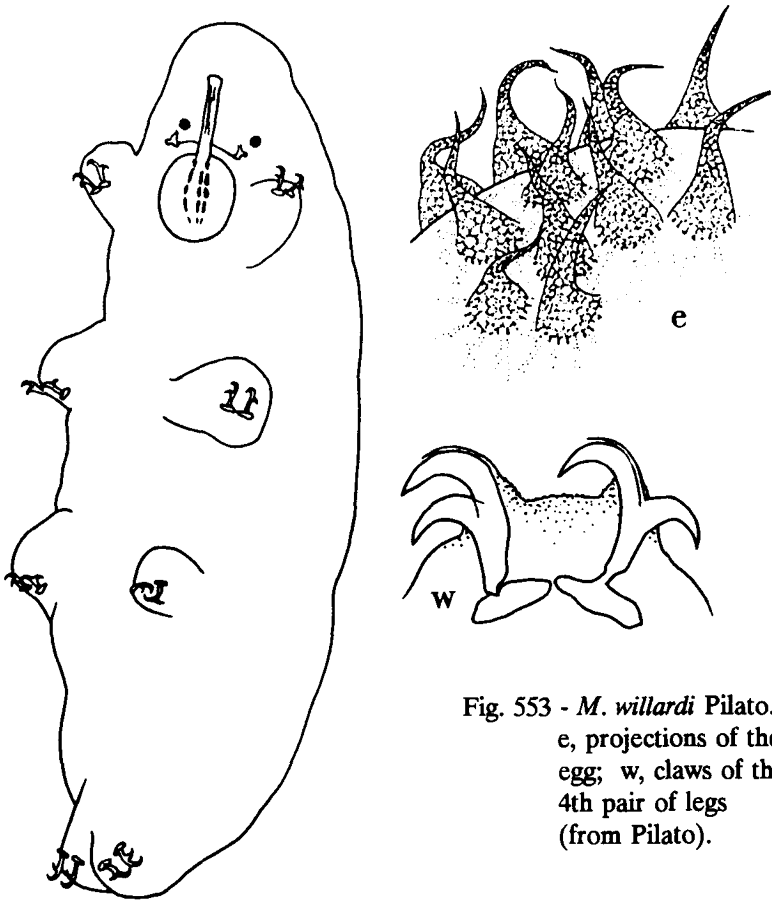


Fig. 553 - *M. willardi* Pilato. e, projections of the egg; w, claws of the 4th pair of legs (from Pilato).

reticular design of isodiametrical mesh. The surface of the egg, between the projections, is finely granulated.

According to the author the species may be somewhat close to *M. tenuis*. *M. willardi* is known from only one locality in Canada (Matador Field Station).

Genus *MEGASTYGARCTIDES* McKirdy, Schmidt, McGinty-Bayly, 1976.

Diagnosis: Stygarctidae with dorsal plates typical of the family (cephalic plate, three trunk plates, caudal plate), with additional intercalated accessory plates, resulting from the fusion of the transverse folds of the cuticle; first three pairs of legs with four claws, 4th pair with two claws; all the claws with one small accessory point; anterior clavae modified into an ovoid structure.

MEGASTYGARCTIDES ORBICULARIS McKirdy, Schmidt, McGinty-Bayly, 1976 (Fig. 554).

Length from 122.4 to 227.6μ, width of the head from 57.3 to 76.9μ. Median cirri 22.3, anterior clavae 12.3, posterior clavae 15.2, lateral cirri A 31.2 (average measurements). All the cephalic cirri are formed of a long, larger proximal section and a distal section terminating in a slender, flexible tip; the anterior clavae are modified to form an ovoid structure, the posterior clavae are elongated, with narrow base; the external cirri depart from ventral rounded tubercles. Mouth ventral, positioned at the end of a telescopic buccal cone; pharynx subspherical, stylets long and slender, without stylet supports. Eyes absent.

The body is more elongated and cylindrical than other species of the family. The cuticle is transparent, very thick, especially in the cephalic region, and forms the typical plates of the family (a cephalic plate, three plates on the trunk, and a caudal plate), but modified by the presence of intercalated plates; these are formed from the fusion of transverse folds of the cuticle. The dorsal cuticle is nearly uniform in thickness, from which the plates are definable as wide areas of smooth cuticle, rather than thickenings of the same.

The cephalic plate has three incisions, one anterior and two lateral, which form cephalic lobes; the two anterior lobes bear the posterior clavae and the lateral cirri. The cephalic plate does not possess pointed processes at the posterio-lateral angles.

The plates of the trunk do not possess lateral expansions, their lateral margins are weakly convex. The caudal plate is semicircular, without spiniform processes; there are cirri E (36.4μ), with thick bases, annulated, inserted on tubercles.

The first three pairs of legs are of about equal length, the 4th pair is considerably longer. The legs are telescopic. There are four claws on the 1st-3rd legs, only two claws on the 4th legs. Each claw has a slender dorsal accessory point and has an expanded base, connected with the leg by means of a basal membrane. The first pair of legs do not have spines, which are instead present, short, on the second and third pairs; the 4th pair has a dorsal, small, rounded tuberance.

The young examples have two claws on all the legs.

Meg. orbicularis belongs to the interstitial fauna and was collected at three stations on the Galapagos Islands.

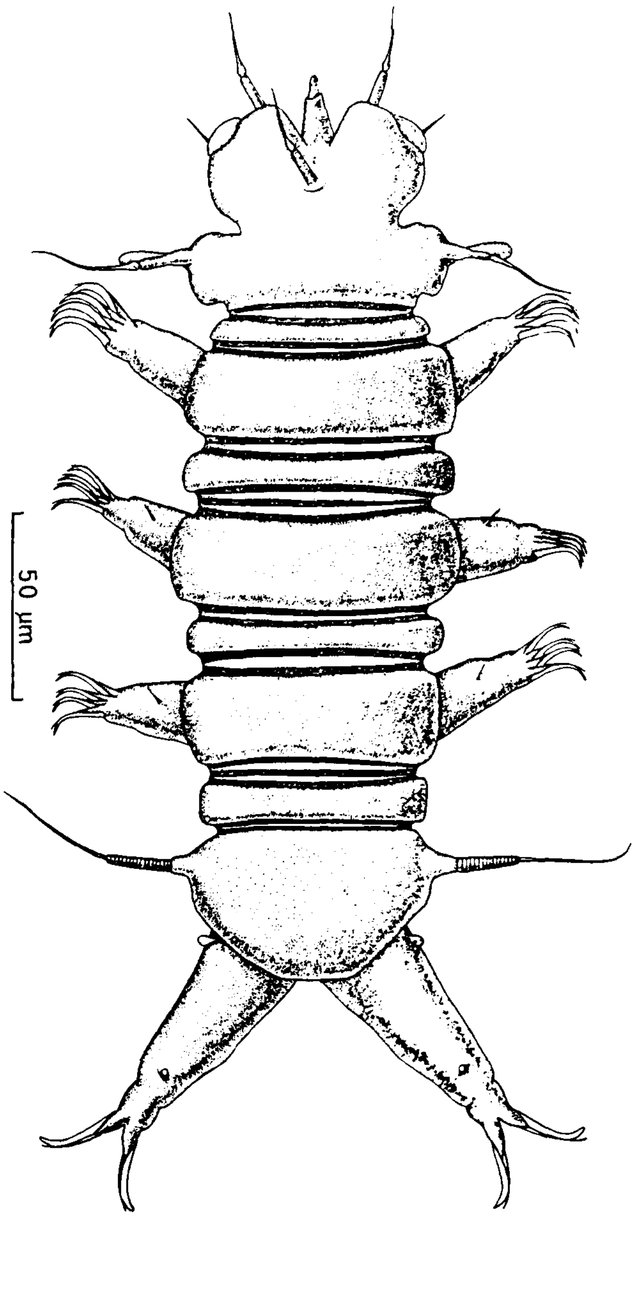


Fig. 554 - *Megastygarctides orbicularis* McKirdy et al. Dorsal view (from McKirdy, Schmidt, McGinty-Bayly).

Genus *MESOSTYGARCTUS* Renaud-Mornant, 1979.

Diagnosis: Stygarctidae; there is a cephalic plate, composed of two parts, three plates on the trunk, with enlarged bases, and a caudal plate without posterior expansion; rudimentary anterior clava; legs with four claws provided with filamentous appendices, the two internal with distal spurs.

MESOSTYGARCTUS INTERMEDIUS Renaud-Mornant, 1979 (Fig. 555).

Length, from the anterior margin of the cephalic plate to the caudal end (in the holotype) 138μ, maximum width (posterior lobe of the head) 55μ. The cephalic part, of hemispherical shape, includes two principal lobes, delimited by a strong thickening of the cuticle. The anterior ventral lobe bears the internal median cirri (15μ) and is separated laterally from the posterior lobe by a cuticular space. The unpaired median cirrus (13μ) is borne on a protuberance of the posterior cephalic lobe; the latter possesses pointed expansions positioned near small cuticular spheres which constitute the anterior clavae. The other cephalic appendices are the following: ventral external median cirri (13μ), frontal internal median cirri (16μ), borne on enlarged bases, cirri A (20μ), and posterior clavae (10μ); these latter are inserted separately on lateral cephalic expansions, supplied with posterior spines.

The buccal cone and the mouth are situated between the internal median cirri. Stylets, with expanded bases, flank the pharynx, which is subspherical.

The three dorsal plates situated on the trunk have trapezoidal shape with the posterior portion wider and supplied with weak lateral points.

The transverse spaces between the plates are ornate with ovoid cuticular thickenings. The caudal plate is more narrow, and bears on its lateral expansions the cirri E (31μ), inserted on an articulation similar to those described for *Pseudostygarctus triungulatus*. Above the anus an indentation divides the plate into two posterior lobes, without expansion. On the insertion of the 4th legs there is a large papilla (9-10μ).

The legs are telescopic, as far as half the length. The distal end, slightly swollen, bears four curved claws 6-8μ long, connected to the foot by means of a membrane. The median claws have a small supplementary spur.

This species presents a general effect of primitive characters, which in the other genera of the family is in general different. *Mesostygarctus*

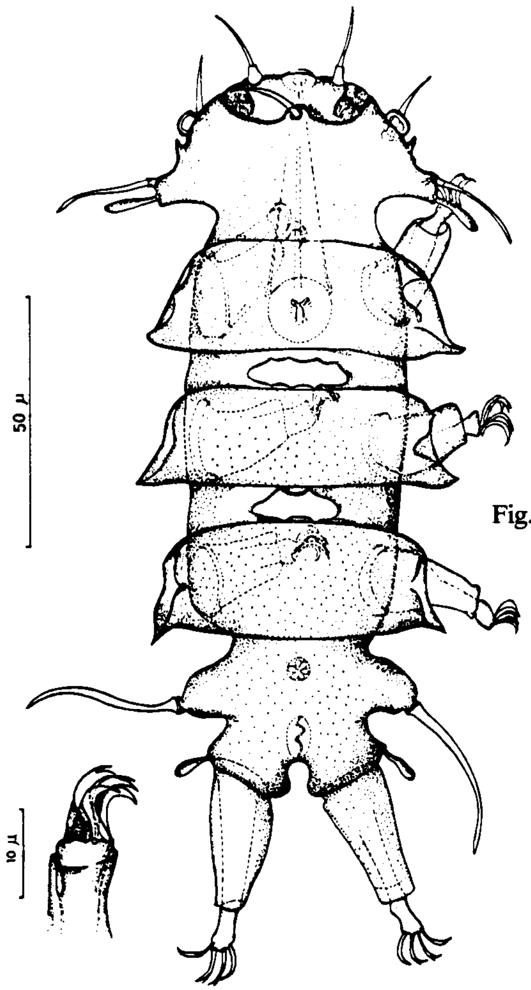


Fig. 555 - *Mesostygarctus intermedius* Renaud-Mornant. Dorsal view of the holotype (female). At left detail of the end of the 2nd leg (from Renaud-Mornant).

comes to be placed therefore in intermediate position between the *Stygarctus-Parastygarctus* group (whose median claws have a filamentous appendix) and the *Pseudostygarctus-Megastygarctides* group, with simple claws or supplied with spurs.

Mes. intermedius has been collected only at Tuléar, on the coast of Madagascar.

Genus *MICROHYPSIBIUS* Thulin, 1929.

Diagnosis: Calohypsibidae, with reduced legs and small claws of *Calohypsibius* type; body abruptly truncated caudally; smooth cuticle; mouth without lamellae or papillae; buccal tube with reinforcement bar or else a slender lamina for the insertion of the muscles.

Observations:

With much reluctance we accept -- in a provisional way -- this genus (as proposed by Kristensen), on whose validity we entertain strong doubt. The type species *Mi. truncatus* does not seem validly separate from *Calohypsibius*, not having significant characters at the generic level, neither the smooth cuticle, nor, still less, the three placoids in place of two. With regard to the two species of Kristensen, the presence of the reinforcement bar seems sufficient character for *not* being included in the same genus with *Mi. truncatus*. Because we have not had occasion to see the two new species, we do not feel they should be arbitrarily included in some other genus, and it is only because of this that we agree here to the genus *Microhypsibius*.

KEY TO THE SPECIES

1. Reinforcement bar on the buccal tube .... *Mi. bertolanii*
   On the buccal tube there is a crest for the insertion
   insertion of the muscles 2

2. There are microplacoids and septula .... *Mi. minimus*
   Neither microplacoids nor septula .... *Mi. truncatus*

MICROHYPSIBIUS BERTOLANII Kristensen, 1982 (Figs. 556 and 557).

Length (holotype) 143μ. Smooth cuticle, eyes absent. The forehead is strongly bulging, with anterio-ventral buccal aperture. Mouth without lamellae or papillae.

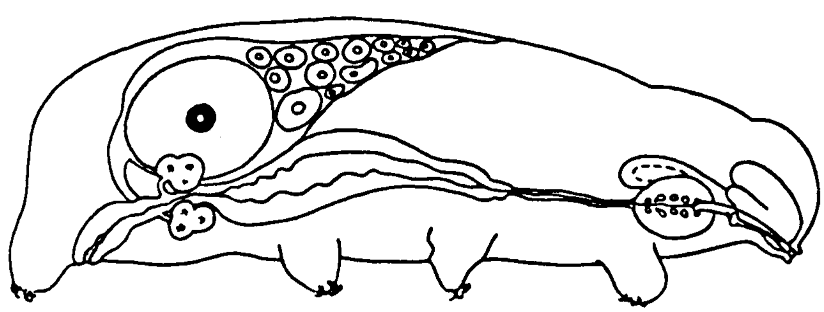


Fig. 556 - *Microhypsibius bertolanii* Kristensen. Lateral view of the holotype (from Kristensen).

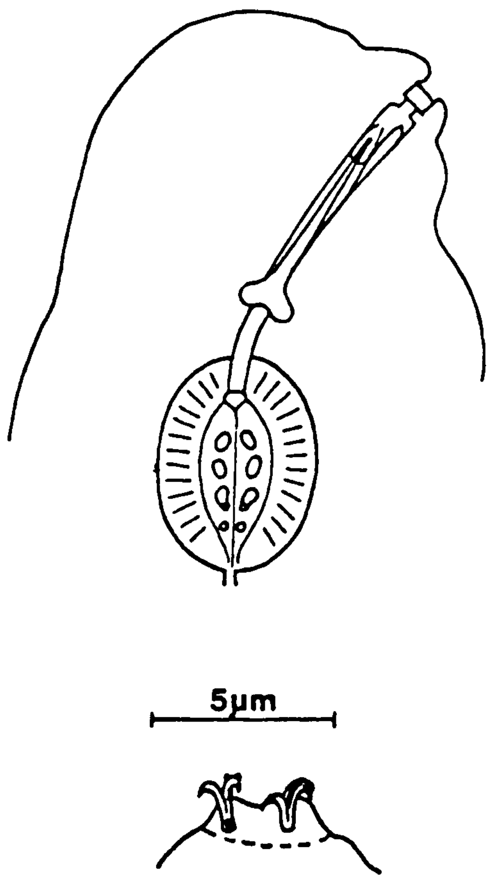


Fig. 557 - *Microhypsibius bertolani* Kristensen. Cephalic end with buccal apparatus, and claws of the 4th pair of legs (from Kristensen).

Buccal tube rather slender, with a thin reinforcement bar. Pharynx oval (10.4 x 8μ), with apophyses and three macroplacoids respectively 0.9, 0.9, 1.5μ long; the third macroplacoid terminates in a drop shape. Microplacoid present.

Legs short, with very small claws.

Eggs are not known.

The species has been collected in hot springs on Disko Island (Greenland). Typ. loc.: Lymnae Lake at Kvandalen, Disko.

MICROHYPSIBIUS MINIMUS Kristensen, 1982 (Fig. 558).

Length from 85 to 130μ. Cuticle smooth, eyes absent. Forehead strongly curved, with mouth anterio-ventral. Mouth without lamellae or papillae. Buccal tube slender, with a crest for muscle insertion. Pharynx oval (10.4 x 5.2μ). There are apophyses, three macroplacoids (1.3, 1.3, 2.6μ respectively), microplacoid and septula.

Claws relatively large, but very slender. The eggs, usually one, smooth, deposited in the exuvia.

The species was found in stagnant water on Disko Island, Greenland. Typ. loc.: Lymnaea Lake, at Kvandaken, Disko.

MICROHYPSIBIUS TRUNCATUS Thulin, 1928 (Fig. 559).
= *Hypsibius* (*Calohypsibius*) *truncatus* Marcus, 1936

Length 145μ, eyes absent, cuticle smooth; the shape of the body is approximately cylindrical, rostrally and caudally tapered; the caudal region appears truncated. Legs short and squat. The buccal tube is slightly curved, narrow (internal diameter 1.5μ). Pharynx elongated oval, with apophyses and three macroplacoids of increasing length from first to third; microplacoid absent.

The claws are very small, those external a little larger than the internal; the claws of the 4th pair are slightly larger. The principal branch has small accessory points.

There are few reports of this rare species. Killin (Scotland), Piemonte, Norway (Arctic Circle); in each of these localities has been found a single example. Later the species was indicated to be as not rare on the British Isles (Scotland, Ireland, Wales) and in Greenland.

Typ. loc.: Killin (Scotland).

Genus *MILNESIUM* Doyére, 1840.

Diagnosis: Milnesiidae; there are present six buccal lamellae and six large peribuccal papillae; buccal tube wide, short, rigid; stylet supports short, large; there are present stylet sheaths; pharynx without apophyses and placoids. Branches of the claws separate, the secondary branch short, two-part or three-part.

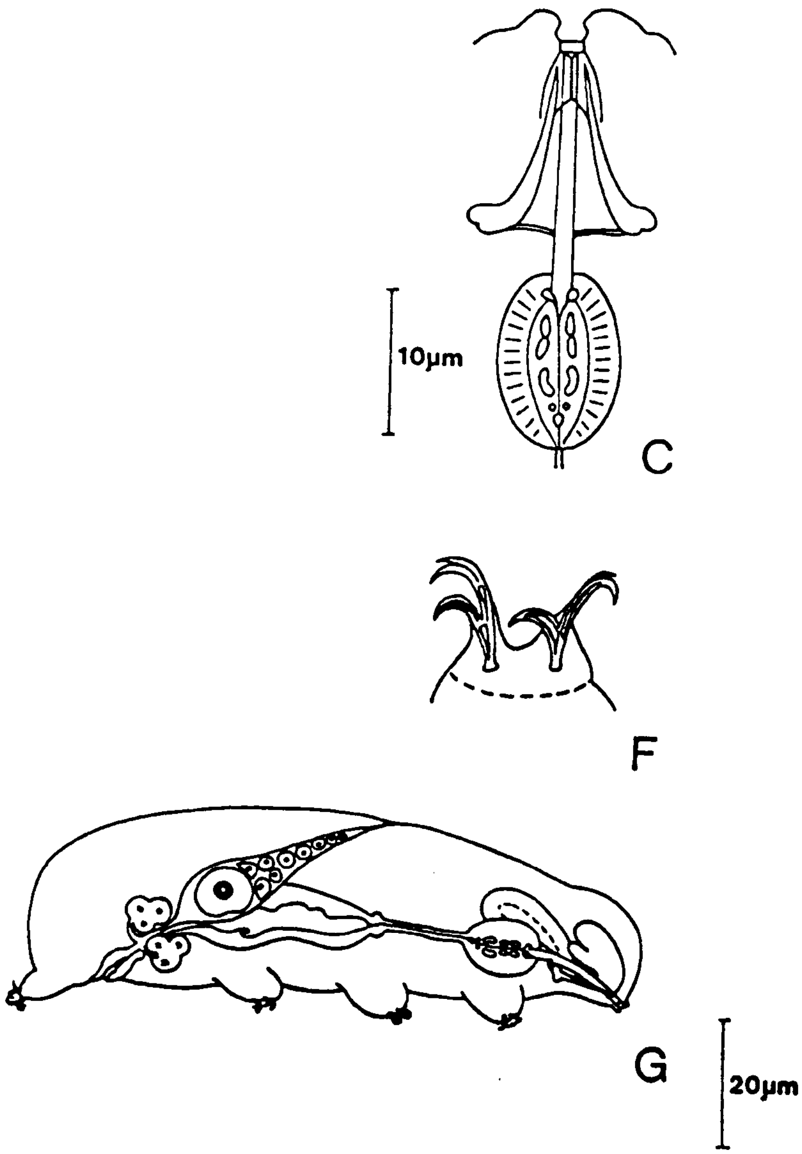


Fig. 558 - *Microhypsibius minimus* Kristensen. C, buccal apparatus (ventral view); F, claws of the 4th pair of legs; G, lateral view of the holotype (from Kristensen).

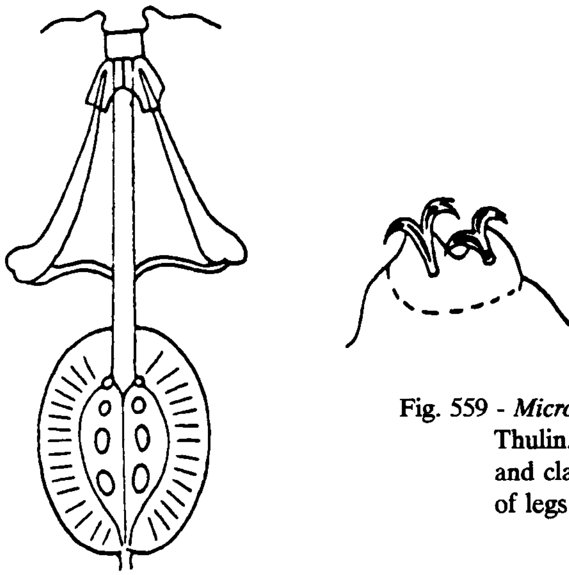


Fig. 559 - *Microhypsibius truncatus* Thulin. Buccal apparatus and claws of the 4th pair of legs (from Kristensen).

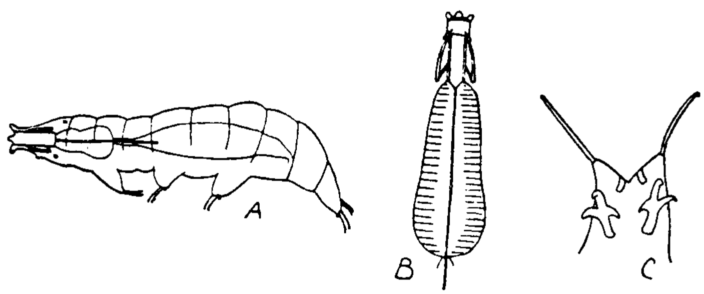


Fig. 560 - *Miln. tardigradum* Doyére. A, lateral view; B, buccal apparatus; C, doubleclaws of the 4th pair of legs (from Marcus, redrawn).

MILNESIUM TARDIGRADUM Doyére, 1840 (Fig. 560).

Length generally 500-600μ; the females sometimes surpass 1,000μ, while the males do not ever surpass 500μ. Body very elongated, which is reduced toward the two ends; cuticle smooth, but appears segmented by folds into unequal rings. Colorless, or reddish, or brownish; treated with potassium hydroxide the pigment turns red-purple and then is released, as in *H. oberhaeuseri*. Eyes present. Buccal aperture terminal; around it there are 6 small rostral papillae, arranged symmetrically, of which the three dorsal are larger than the three ventral; alternating with these -- and to the interior -- there are 6 lobes which, folded, may close the buccal opening. There are then two other papillae, a little more back from the rostral, in lateral position, or ventro-lateral. Buccal tube extremely wide (from 10 to 25μ and more), short; pharynx very elongated, of pear shape, without placoids; stylets short and weak, convex toward the external, with stylet supports.

The first three pair of legs have equal length; those of the 4th pair are very short and very distant from the 3rd pair of legs. Each leg bears two doubleclaws symmetrical with respect to the median plane of the leg and completely divided into basal claw and terminal claw, separate from each other. The end of the leg is bilobed and each lobe bears a very long and slender claw (corresponding to the principal branch of each doubleclaw), supplied with two very small accessory points; at the base of each lobe is found a short and robust claw (corresponding to the secondary branch of each doubleclaw), equipped with 2, 3, or 4 spurs, curved according to different planes; in general the spurs are inclusively 3 (including the apex of the claw proper), but may vary in number also on different legs of the same individual. The males, very rare (1 for every 25 females, according to Marcus, but perhaps even less), have the claws of the 1st pair of legs (Fig. 26) turned rostrally; the shorter claw (that is which corresponds to the secondary branch of the doubleclaw) appears as a rough, robust, simple hook and often bears a small point more downwards. Deposited in the exuvia are up to 18 smooth eggs, spherical or oval, colorless, rosy, or of clear brown color, with diameter about 100-133μ x 70-90μ.

This species, which seems to be exclusively carnivorous, is cosmopolitan and very common everywhere (also in Italy).

The typical form of *Miln. tardigradum* has the cuticle completely smooth. However Ramazzotti has found (in two different localities at Fray Jorge, in Chile) examples with cuticle covered with a fine granulation, at times on all the dorsal surface, at times only on the caudal half of the body (*Miln. tardigradum* var. *granulatum*).

This variety has been found also by Maucci (1973-74) on the Trieste Carso. In this report, as well as in one of the two Chilean reports the variety was intermingled with the nominal form.

Miln. tardigradum forma *trispinosa* Rahm, 1931, is instead a variety characterized by the presence of three dorsal spines, inserted in dorsal position near the caudal end of the body, little more forward of the 4th pair of legs. Also this variety was found intermingled with the nominal form, for which we do not think should be attributed to it rank of subspecies (4 examples with spines, in a population of 233 individuals). There are cited reports in Brazil (State of Sao Paulo) and in Chile (near Santiago, at 1,400 m altitude).

Genus *MOPSECHINISCUS* Du Bois-Reymond Marcus, 1944.

Diagnosis: Echiniscidae with armor-plated cuticle as in *Pseudechiniscus* (that is to say there exists a pseudosegmental plate); the external and internal buccal cirri are absent.

KEY TO THE SPECIES

1. The lateral appendices are in general only spines, especially filaments D. Dorsal appendices, especially in the young (spines, extremely variable in number and position) .... *Mops. imberbis*

Laterally filaments C and D, besides a small projection or point B. No dorsal appendices, with exception of 2 small teeth at the posterior margin (lobe) of the pseudosegmental plate. There are 3 supplementary rounded platelets at the sides of the cephalic plate and others lateral to the scapular plate .... *Mops. granulosus*

MOPSECHINISCUS GRANULOSUS Mihelčič, 1967 (Fig. 561).

Length 288-320μ, color brownish-red, eyes absent; the cephalic region is not rostrally sharpened, as usual in the *Echiniscus*, but is instead rounded and has a facetting. Lacking the buccal cirri and cephalic papilla: in the position of these is seen an oval ring. The lateral cirri A are 80-90μ long, very wide at the base, slender and filamentous at the distal end. Clava short and oval (in one of his letters dated 3-24-1970, Mihelčič communicated that at the bases of the cirrus A -- and at a distance of about half the diameter of A -- there is, in place of the clava, a structure of the shape of a minuscule ring, within which exists sometimes a small projection, with appearance of extremely fine clava -- ? --. In the same letter the author adds that the cephalic "oval rings" are found at the position of the "button" of *Mops. imberbis*).

The cuticle -- according to the author -- is smooth and the apparent sculpture is found *within the* interior of the same cuticle, not at its surface: with the tube of the microscope in high position is seen a clear granulation, composed of granules of equal size; between the individual granules the cuticle appears smooth. With low position of the tube the granules become dark.

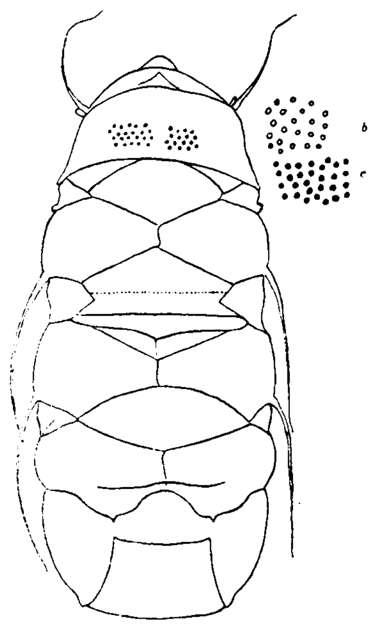


Fig. 561 - *Mops. granulosus* Mihelčič. Dorsal view, and sculpture with high position of the tube (b), and with low position (c) (from Mihelčič).

At each side of the scapular plate there are two supplementary platelets, one whole and the other partially subdivided. Pseudosegmental plate longitudinally subdivided (or else paired), with caudal margin terminated by two mammillary lobes, which distally bear a spine. Median plate 1 whole, having at each side (anteriorly) a supplementary triangular plate. Median plate 2 composed of three parts: the rostral part is largest and has a transverse fold; there is then posteriorly a ribbon-like second part caudally following a curved line of separation and finally the caudal part of the plate 2 is triangular (Mihelčič has however some doubt about the real structure of this median plate 2, because in old preparations in Faure's liquid it appears rather modified). Median plate 3 whole (not subdivided), with anterior margin arched, as median plate 1.

Laterally, besides cirri A, there are short projections B and filaments C (64μ) and D (61μ). Dorsally there are only the cited caudal appendices of the pseudosegmental plate. Terminal plate facetted. There is no dentate collar and the claws do not have spurs.

The species, easily distinguished from *Mops. imberbis*, was collected in lichen on trunks and on rocks, in the Andes of Argentina.

MOPSECHINISCUS IMBERBIS (Richters, 1907) (Fig. 562).

The species was initially collected only in two localities: in South Georgia (Richters, 1907, who thought it belonged to the genus *Pseudechiniscus*) and in Brazil (du Bois-Reymond Marcus, 1944, who created for it the genus *Mopsechiniscus*); actually the characteristics of the *imberbis* of these two reports are so much different that they should be treated as two distinct species, but this conclusion is not followed because of the insufficient number of individuals examined (7 by Richters and 12 by du Bois-Reymond Marcus) and the doubt that the first description by Richters may be inaccurate, especially with regard to the omission of the cephalic "buttons" and of the median cephalic projection.

Later, in 1962, Ramazzotti carefully examined 65 examples of this species in material from Chile, whose characteristics were even different from those of the individuals observed in South Georgia and Brazil. We therefore think it advisable to describe separately the *imberbis* from 3 localities:

Material from South Georgia: Length 272-416μ, robust armor, granulation of the plates scarce and spread out, more dense only on the terminal plate. Lacking the internal and external medial cirri and the cephalic papilla. Laterally, besides cirrus A (about 90μ), there are spines C (5-12μ) and filaments D (about 80μ); dorsally short spines at the posterior margins of the median plate 2 (8μ) and of the pseudosegmental plate (15μ). Dentate collar of the 4th pair of legs absent, internal claws with spurs curved toward the base. Some variations have been observed in the appendices: in C a short filament -- on a single side -- in place of the spine; at the posterior margin of the median plate 2 a long filament -- always on a single side -- rather than a spine; or else a double spine.

Material from Brazil: Length 180-310μ for the 10 individuals observed with 4 claws; the 2 larvae with two claws measured 140-150μ; eyes present, red color, sculpture composed of isolated "dots", however more densely arranged than in the material from South Georgia. The only cephalic appendices are two "buttons" and the median projection, as we have already said. Laterally, besides cirrus A (32-50μ), there are only short spines C (16-19μ), which may be lacking. Dorsally there are no appendices in the individuals of larger size, while a larva of two claws was seen, 140μ long (Fig. 562), with spines at the posterior margins of the median plate 1 (9μ), of the median plate 2 (11μ), and of the pseudosegmental plate (14μ); in another larva of two claws, of 150μ, the spines of the first median plate were lacking, but there were those of the second (10μ) and of the pseudosegmental (14μ); in a young of 4 claws, 180μ long, there were

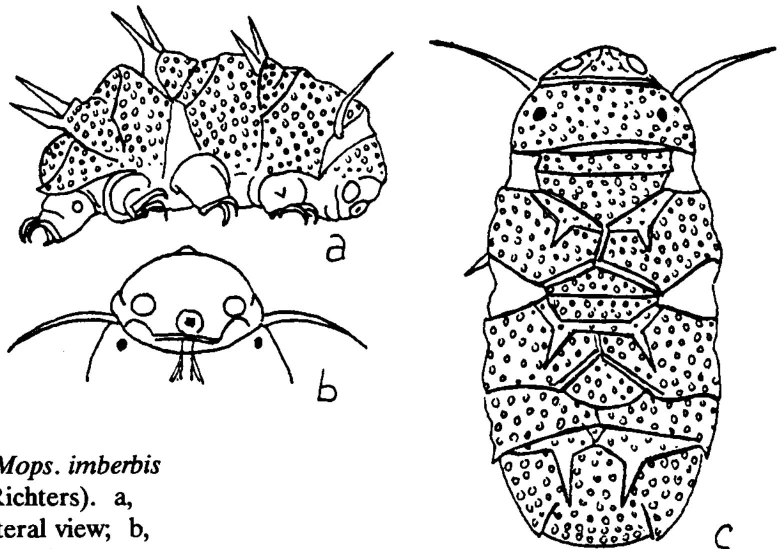


Fig. 562 - *Mops. imberbis* (Richters). a, lateral view; b, cephalic zone; c, dorsal view (from du Bois-Reymond Marcus, redrawn).

dorsally only the spines of the pseudosegmental plate (17μ); in the remaining 9 adult individuals of 4 claws, from 220 to 310μ long, the dorsal appendices were totally absent. It has been verified that the young individuals have a greater number of appendices than the adults, while it is exactly the opposite in the other armored tardigrades (genera *Echiniscus* and *Pseudechiniscus*). At the bases of the legs of the 1st pair there is a spine and at the bases of those of the 4th pair a papilla; there is no dentate collar, but a simple fold; internal claws with spurs.

Material from Chile: The Chilean examples have laterally, besides cirrus A, filaments C and D and -- not always -- small teeth B: they differ in this way both from the Brazilian individuals and those from South Georgia, which exhibit laterally spines C and filaments D. The dorsal appendices (as was noted by Eveline du Bois-Reymond Marcus) decreases in number from larva to adult, as much as disappearing totally in the animals of larger size.

Ramazzotti has seen larvae of two claws (120-130μ) with numerous reductions of the dorsal appendices: that is they were provided only with teeth posteriorly on the median plate 2 and on the pseudosegmental; laterally they had teeth B and spines (not filaments) C and D. Young with

4 claws of 133-170μ still had spines, or triangular teeth, caudally on the median plates 1 and 2 and on the pseudosegmental plate; often dorsal appendices (spines or teeth) also present posterior to the second paired plate (plate III), which has not been observed in *imberbis* so far. In the adults of 200-260μ they remain dorsally only as minuscule teeth at the posterior margin of the pseudosegmental plate, which disappear however in the individuals of larger size (270-314μ). However the species is extremely variable with regard to the number and disposition of the dorsal appendices, yet the fact remains constant that there is a progressive reduction -- as far as totally disappearing -- from the larva to the adult; the presence of the lateral appendices, with exception of B, is instead constant in the Chilean individuals.

The terminal plate has the usual two incisions, in which there is often a tooth ("point" E). For the rest there are no notable differences between the individuals from Brazil and from South Georgia; lacking the internal and external cirri and there are instead the two characteristic buttons; the small median cephalic projection is often very visible; the clava is rather pointed and turned backwards. An egg-bearing exuvium contained 4 oval eggs of red orange color (68 x 53μ).

The Chilean individuals which are cited were collected in two lichens about 1500 meters apart and coming from Nahuelbuta Cordillera. Both the lichens were growing on the bark of *Nothofagus* at an altitude of about 1,100 m (Cabreria locality and its surroundings). More recently other examples of this species have been found on Chiloè Island, also in Chile.

Genus *NECOPINATUM* Pilato, 1971

Diagnosis: Lacking the claws of the 2nd, 3rd, and 4th pairs of legs; the 1st pair of legs has two sclerified parts inserted on the median plane of the leg and together form a pincer, which may also be lacking; reinforcement bar of the buccal tube absent.

NECOPINATUM MIRABILE Pilato, 1971 (Figs. 563 and 564).

Maximum length 203μ, colorless, cuticle smooth, eyes absent; mouth in anterio-ventral position, forehead steep; buccal tube rigid, without reinforcement bar and with appendices for the insertion of the muscles of the stylets of crest shape. The buccal tube is 23μ long, in the

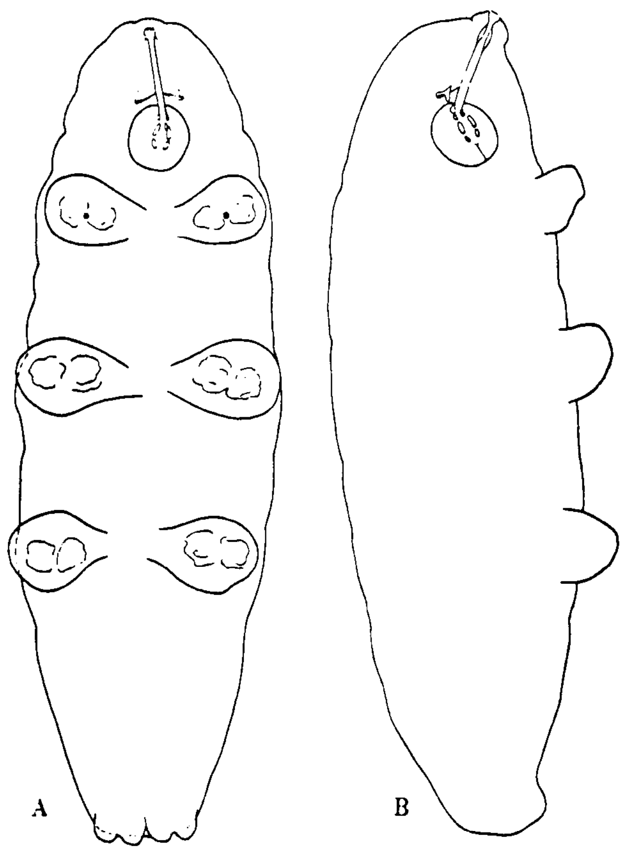


Fig. 563 - *N. mirabile* Pilato. A, ventral view; B, lateral view (from Pilato).

larger examples, with a diameter of 1.7-1.8μ. Pharynx almost spherical, sometimes oval. The tube has a terminal thickening, which follows the apophyses. The macroplacoids are two, of short rod shape, the first a little longer than the second (respectively 3 and 2μ).

Legs rather short, especially the 4th pair, and all bilobed. The legs of the 2nd, 3rd, and 4th pair are devoid of claws or of any sclerified structure; in one of the six examples examined even the 1st pair were without claws; in the remaining examples, the 1st pair of legs have -- in the furrow which separates the two lobes -- two sclerified pieces, which together form an extremely small pincer; the anterior piece (2.3μ) is longer than the posterior (1.2μ) and has the shape of a hook; the posterior

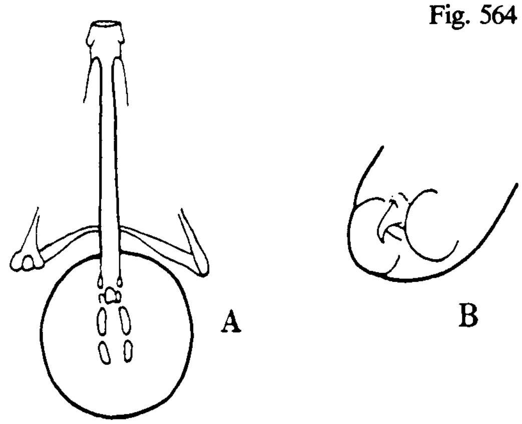


Fig. 564 - *N. mirabile* Pilato. A, buccal apparatus; B, anterior leg (from Pilato).

piece, which is inserted on the leg is well separated from those of that of the anterior part, not exactly coming in contact with the end of this but with its central portion.

Eggs unknown.

N. mirabile was collected a single time, in terrestrial moss, on Etna (Sicily) at about 562 m elevation.

Genus *OREELLA* Murray, 1910

Diagnosis: Oreellidae, with legs ending with four claws; cuticle with armor; body indistinctly subdivided in eight segments; a short caudal median projection is present.

KEY TO THE SPECIES

1. Clava present; the only cuticular appendices of the body is a median caudal projection; cuticle dorsally and laterally granulated or papillose 2

   Clava absent; besides the short median caudal projection there are two conical spines on each side of the body, positioned between the 3rd and 4th pairs of legs; cuticle smooth; length up to 430μ . . . . *O. vilucensis*

2 (1). Stylets long: their caudal end comes almost in contact with the pharynx; internal claws without spurs; length up to 230μ .... *O. mollis*

Stylets short (about a third of the buccal tube), so that their caudal end results distant from the pharynx; internal claws with spurs; length up to 170μ .... *O. minor*

OREELLA MINOR Ramazzotti, 1964 (Figs. 565 and 566).

Length up to about 170μ, colorless, eye spots absent. Cuticle granulated, or covered -- only on the dorsal and lateral regions of the body and on the 4th pair of legs -- with rounded tubercles (0.5-1μ diameter; in a square with sides of 9.5μ are contained 20-26 tubercles). Besides this coarser sculpture there is an extremely fine punctation, visible only with strong magnification, with immersion objective and -- better -- with phase contrast. On the ventral surface and sometimes on the dorsal cephalic region there is only the fine sculpture.

The cephalic appendices are:
- -- internal buccal cirri (3-4μ) in the form of short straight spines;
- -- external buccal cirri (9-10μ), filiform;
- -- cephalic papilla, probably present; it was not however possible to see with certainty in the 8 individuals examined, but rather hypothesized; if it exists, as we are inclined to believe, it should have a very particular structure, to not be in clear evidence not even with phase contrast observation. In the impossibility then of learning exactly the morphology, we have preferred to omit the design of the cephalic papilla;
- -- lateral cirri A, of variable length between 15 and 35μ;
- -- clava, which may be long (11-18μ) and more or less curved, or else short (3.5-5μ) and straight; it is probable that the individuals with long clavae are males and those with short clavae females, according to Richters (1909) and Schulz (1955), who hypothesize an analogous hemisphere for the species of the genus *Halechiniscus*.

The buccal tube is very narrow (external diameter about 1μ) and 15-16μ long; the stylets are very short, about a third or a little more, of the buccal tube: it follows that their caudal end results distant from the pharynx. Stylet supports probably present. Pharynx almost perfectly circular (diameter 10-11μ), with the usual three pharyngeal bars typical of the Order Heterotardigrada.

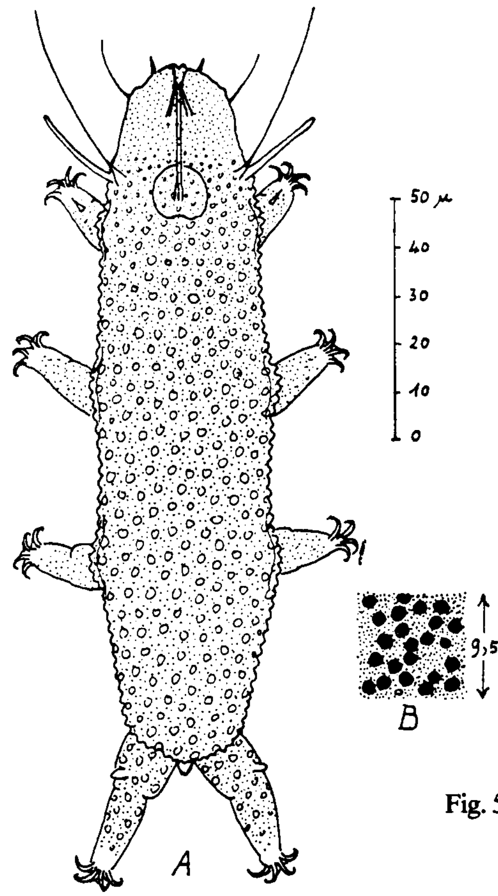


Fig. 565 - *O. minor* Ramazzotti. A, dorsal view; B, detail of the sculpture with phase contrast.

The only cuticular appendix of the body -- other than the cephalic -- is a small caudal conical projection, approximately as in *O. mollis*.

The legs are long, with distal parts probably retractile into the proximal: those of the first pair bear a spine and those of the fourth pair the usual papilla. The claws measure 3-6μ and on the two internals of all the legs is present one curved spur; the insertion of the claws on the legs occurs by way of a papilla, as in the other genera of the Suborder Echiniscoidea. The smaller individuals observed -- only 85μ long -- also had 4 claws.

O. minor is distinguished from *O. vilucensis* by the presence of the clava and by the absence of the lateral conical appendices; from *O. mollis* by the small size, by the shorter stylets, which leaves free a good part of

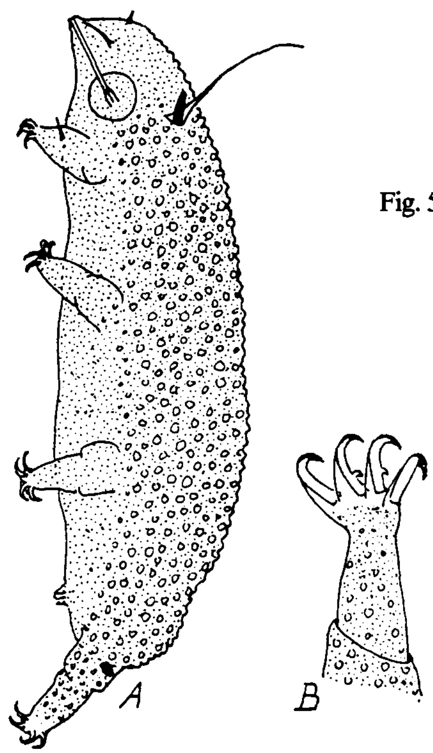


Fig. 566 - *O. minor* Ramazzotti. A, lateral view; B, detail of the legs.

the buccal tube between the stylet supports and pharynx, by the segmentation of the body much less evident, by the double sculpture (but finer sculpture, not easily observed, may have been missed by Richters, present also in *O. mollis*). Also *O. minor* has spurs on the internal claws, absent instead in *O. mollis*.

The species was collected in a moss on a tree trunk at Nal (Chiloe Island, Chile) and was accompanied by *E. bigranulatus*, *P. lateromamillatus*, *Mops. imberbis*, *M. intermedius* (or *subintermedius*?), *M. furciger*, *D. alpinum*.

OREELLA MOLLIS Murray, 1910 (Fig. 567).

Length up to 230μ, eye spots absent, cuticle covered dorsally and laterally by granules, or small rounded papillae, smooth on the ventral surface. The cephalic appendices are the usual internal buccal cirri (somewhat short and conical) and external (long bristles), both arising from

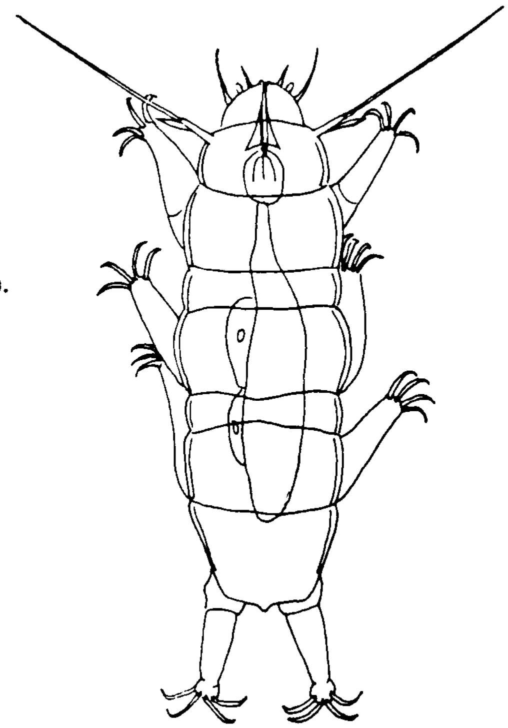


Fig. 567 - *O. mollis* Murray (from Murray, redrawn).

small conical bases: between these exists -- on each side -- a cephalic papilla. The clava, slender and sharp at the apex, and the very long lateral cirri A (about five times that of the clava) arises from a common base. Stylets short, stylet supports present, pharynx short oval, almost spherical, with three pharyngeal bars. The only cuticular appendix of the body is a short median, caudal projection of approximately conical shape with rounded apex. The legs are long and composed of a proximal part, wide and short, and a distal part which becomes slightly sharpened toward the end, enlarged then somewhat in the terminal zone where the four smooth claws, without spurs, are inserted; as always in the Suborder Echiniscoidea, the claws are probably fixed on papillae. Eggs and larvae unknown.

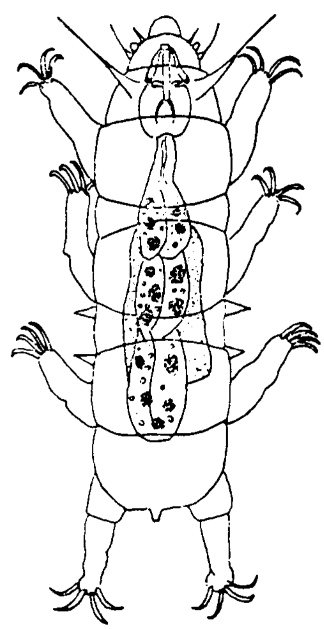
The only sure report of the species comes from Australia, at about 1,000 meters altitude (Blue Mounts, New South Wales); one report, cited by Rahm for Switzerland (Cantone of Friburgo, at over 1,000 meters) is extremely dubious.

OREELLA VILUCENSIS Rahm, 1925 (Fig. 568).
= *O. bonnensis* Rahm, 1932

Length up to 430μ, colorless, eye spots absent; the cuticle is smooth, with papillae (different from *O. mollis*). Median cirrus absent; internal medial (buccal) cirri short and of cone shape, external medial cirri composed of a bristle arising from a common base. Cephalic papilla positioned between the medial cirri, but lying on the interior. Lateral cirri A a third longer than the external medial cirri; clavae lacking (while in *O. mollis* it is present). Stylets short, with stylet supports; the pharynx almost has the appearance of a square with rounded corners. On each side of the body exists -- between the 2nd and 3rd pairs of legs -- two robust conical spines; as in *O. mollis* there is also a short median caudal projection, of shape approximately conical and with rounded point. Legs long, composed of a wide and short proximal part, and of a distal part which is slightly tapered toward the end, enlarged then somewhat in the terminal zone, where are inserted the four smooth claws without spurs: it is probable that -- as always in the Suborder Echiniscoidea -- the claws are implanted on papillae. Eggs and larvae unknown.

The species was cited from Chile (near Conception) and from Germany (Beuel near Bonn): in reality the only example collected in

Fig. 568 - *O. vilucensis* Rahm (from Marcus, redrawn).



Germany was named by Rahm (1932) *Oreella bonnensis*, however Marcus thinks with good reason that this species should be identified as *O. vilucensis*.

Genus *ORZELISCUS* Du Bois-Reymond Marcus, 1952.

Diagnosis: Halechiniscidae, with median cirrus present, the legs have four digits of equal length, lacking claws and ending with a flattened end, of spatula shape, longer than wide.

KEY TO THE SPECIES

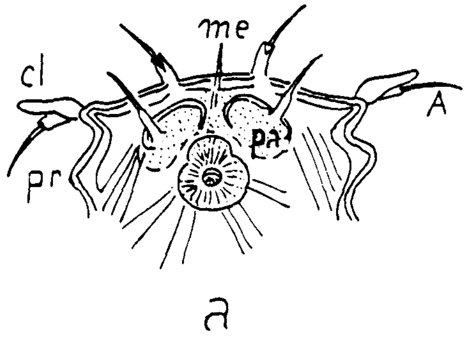
1. The clava has sharpened apex; on the 4th pair of legs exists a papilla terminating in a small bristle .... *Orz. belopus*
   The clava is bigger at the distal end than at the base; lacking the papilla on the 4th pair of legs .... *Orz. septentrionalis*

ORZELISCUS BELOPUS Du Bois-Reymond Marcus, 1952 (Figs. 569, 570).

Marine species, with stocky body, about 200μ long and 90μ wide, and long legs; the cuticle is strongly granulated, with granules arranged more or less regularly, the largest in the dorsal median region, the finest laterally.

The cephalic appendices are: 1 dorsal median cirrus (16μ); 2 internal (buccal) medial cirri on the rostral margin (16μ); 2 external medial cirri, positioned between the anterior margin and the buccal aperture (16μ); 2 lateral cirri at the posterior angles of the rostral margin (25μ); 2 clavae (15μ), each positioned immediately near the lateral cirri and wider at the base than at the distal end; 2 cephalic papillae, situated one per side between the internal and external medial cirri, of convex disk shape (pa in the illustration). Behind the common base of the lateral cirri and the clava there is another slight prominence (pr in the illustration).

The buccal aperture is surrounded by a rounded plate, with two slight sinuosities, and are positioned above a very flat conical projection (buccal cone). The buccal tube is about 25μ long and its diameter is 2μ; the stylets are straight, with obvious supports; pharynx slightly oval with



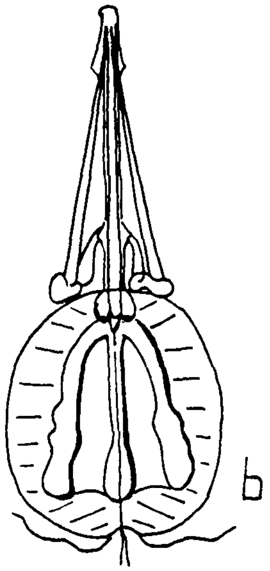


Fig. 569 - *Orz. belopus* du Bois-Reymond Marcus. a, ventral view of cephalic region; b, buccal apparatus and pharynx. A, lateral cirrus; cl, clava; me, median cirrus; pa, cephalic papilla; pr, rostral prominence (from du Bois-Reymond Marcus, redrawn).

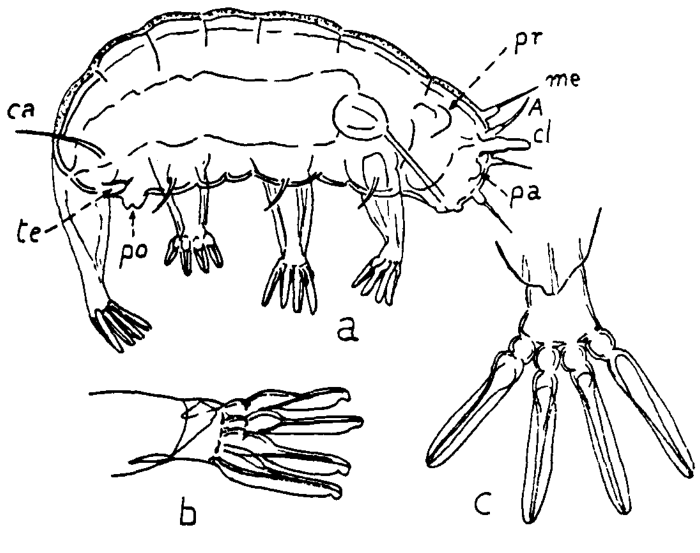


Fig. 570 - *Orz. belopus* du Bois-Reymond Marcus. a, lateral view; b, leg, lateral view; c, leg, dorsal view. A, lateral cirrus; ca, caudal cirrus; cl, clava; me, median cirrus; pa, cephalic papilla; po, gonopore; pr, rostral prominence; te, papilla of the 4th leg (from du Bois-Reymond Marcus, redrawn).

pharyngeal bars 14μ long, not smooth as in genera of the Heterotardigrada, but having the shape indicated in Fig. 569b.

Above the 4th pair of legs there are two conical cirri of 30μ, one per side, and on the first three pair of legs a slender bristle (te in Fig. 570). Legs long, divided in three parts: a sculptured basal part, a more narrow medial, and an expanded terminal bearing 4 digits; each of these digits has a wide base, which is prolonged into a dorsal notching as far as the distal end; their ventral surface is a blunt adhesive peg, 15μ long and with diameter of 2μ, which distally has a slight hollow.

Only females have been found, with dorsal ovary and unpaired oviduct which opens into a ventral gonopore (po in Fig. 570) between the 3rd and 4th pairs of legs.

Orz. belopus was collected various times in Brazil (State of Sao Paulo), near Arcachon in France, in New Caledonia, in Scotland, and on the Galapagos Islands (Santa Cruz Island and San Cristobal Island), always in interstitial environment.

The examples from Galapagos (described by McKirdy et al., 1976) differ from the original description by being smaller (155μ max.), by the clavae more slender at the base, by the presence of two prominences of the shape of lateral bubbles between the third and fourth pairs of legs.

ORZELISCUS SEPTENTRIONALIS Schulz, 1953 (Fig. 571).

Marine tardigrade, 180-225μ long, 90-108μ wide, cuticle granulated. The cephalic appendices are: median cirrus (unpaired), internal and external medial cirrus (paired), cephalic papilla (paired), lateral cirrus A and clava (paired); these appendices greatly resemble those described for

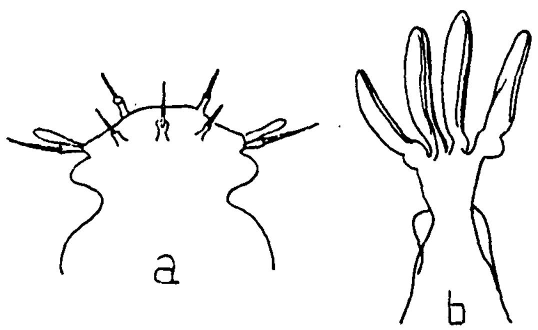


Fig. 571 - *Orz. septentrionalis* Schulz. a, cephalic region; b, distal end of a leg of the 2nd pair (from Schulz, redrawn).

Orz. belopus, however the clava of *septentrionalis* has equal width from the base to the blunt distal end, or sometimes is slightly enlarged at the apex, with club-shaped appearance (while in *belopus* the apical part is more slender); also the papilla, from which arises the lateral cirrus A and the clava, is smaller and less conical than in *belopus*. The buccal aperture is surrounded by a rounded plate with two slight sinuosities, and is positioned on a very flattened conical projection (buccal cone). Buccal tube, stylets, and pharynx approximately as in *belopus*, but the pharynx is a little smaller (20 x 18μ, while in *belopus* measures 22 x 21μ); the shape of the three pharyngeal bars may not be determined as clearly as for *Orz. belopus*.

Above the 4th pair of legs there are two caudal cirri, one per side, and on the first three pair of legs exists a slender bristle, as in *belopus*, however inserted distally; there does not exist however on the 4th pair of legs the finger-shaped papilla ending with a short bristle, which is present in *belopus*. The legs correspond in structure to those of *belopus* and so likewise the 4 digits (also here 15μ long) and the claws.

Of *Orz. septentrionalis* is known 6 individuals, collected near the coast of the North Sea (Amrum Island).

Since the species has not been found later, doubt has been raised (McKirdy et al., 1976; Pollock, 1982) on the taxonomic value of this species, which perhaps may not be distinct from the better known *Orz. belopus*.

Genus *PARASTYGARCTUS* Renaud-Debyser, 1965.

Diagnosis: Stygarctidae, with a cephalic cuticular plate, three dorsal unpaired plates, and a caudal plate; head divided into an anterior part, which bears the buccal cone and the internal cirri, and a posterior with the other cephalic appendices; anterior clava elongated; legs with four claws of which the median are provided with filamentous appendices; caudal spine absent.

KEY TO THE SPECIES

1. The dorsal plates of the trunk bear on each side two pointed appendices .... *Pst. higginsi*
   The dorsal plates of the trunk bear on each side only one appendix .... *Pst. sterreri*

PARASTYGARCTUS HIGGINSI Renaud-Debyser, 1965 (Fig. 572).

Length 250μ. Head divided transversely into two distinct parts: an anterio-ventral (buccal cone), provided with two projections from which departs the internal buccal cirri, and the other composed of a dorsal cephalic plate, subdivided at the margins into 4 large expansions, which bear the remaining cephalic appendices; these appear to be thus arranged:

1. On the buccal cone:
    - Internal buccal cirrus (25μ).
2. On the frontal expansion of the cephalic plate:
    - Cephalic papilla (30μ) morphologically equal to the clava.
    - External buccal cirrus (35μ).
3. On the lateral expansion of the cephalic plate:
    - Lateral cirrus A (45μ).
    - Clava (30μ), with posterior swelling.
    - Robust spine (13μ).
4. In the anterio-median region of the cephalic plate:
    - Unpaired median cirrus (28μ).

The internal and external buccal cirri and the cirrus A are jointed, at about two-thirds of their length, and a long cylindrical base.

Stylets very long (70μ) and very fine; pharynx (15μ diameter) positioned very caudally with respect to the cephalic region and thus in correspondence with the junction between the dorsal plates I and II.

Armor composed -- besides that of the cephalic plate -- of four dorsal plates, each in correspondence with a pair of legs, and separated by an intermediate band. The first three plates are prolonged at each side in two large spines, of which the posterior is longer (50-65μ); there exists no refringent lamellae typical of the genus *Stygarctus*. The fourth (terminal) plate is smaller than the others and bears on each side a large projection, from which departs a long filament (90-100μ), which calls to mind the E of the Echiniscidae. These two filaments have a very characteristic structure: in fact they bear -- on the first third of their length -- a sort of sleeve, provided with fluting, which gives them a complete flexibility. Always on the terminal plate, above the insertion of the 4th pair of legs, there is a large papilla (7-9μ).

The anus is found in posterior position, within a cuticular fold; the gonopore is ventral, anterior to the anus, and is composed of 6 parts arranged in a rosette. The legs are partially retractile and do not possess digits; the claws are inserted directly on the legs and connected to these by a slender basal membrane, as in *Oreella* and in the Echiniscidae. The two internal claws of all the legs bear a slender and long appendix

(20-25μ), curved at its distal end and inserted on a mid-dorsal thickening of the claw (a similar appendix exists also in the genus *Stygarctus*). The cuticle is transparent, colorless and uniformly punctated, both on the dorsal surface and on the ventral.

The species, very characteristic and easily recognized, belongs to the interstitial fauna; about 20 individuals were collected on the beach of Nosy-Komba (Madagascar).

Later the species was collected also on the coast of Malaya.

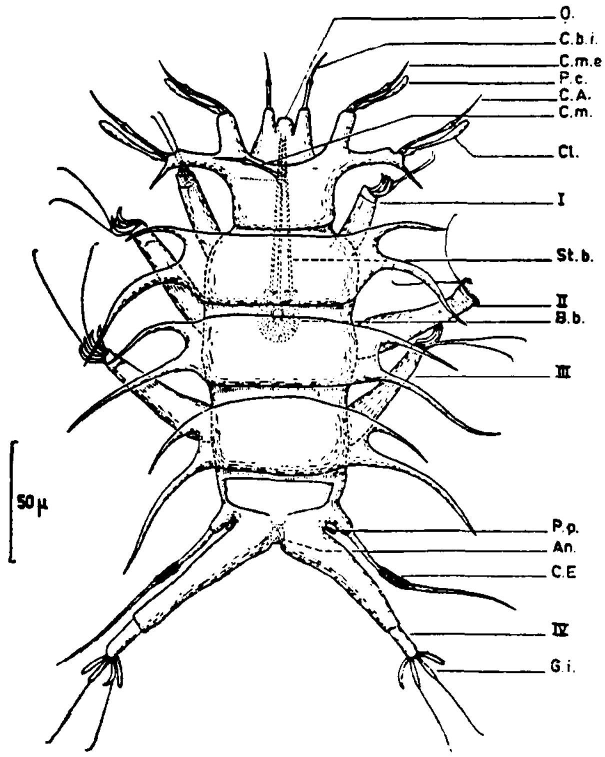


Fig. 572 - *Parastygarctus higginsi* Renaud-Debyser. Dorsal view: An., anus; B.b., pharynx; C.A., cirrus A; C.b.i., internal (medial) buccal cirrus; C.E., filament E; C.m.e., external (medial) buccal cirrus; C.m., unpaired median cirrus; C.l., clava; G.i., internal claw with appendix; O., orifice and buccal cone; P.c., cephalic papilla; P.p., papilla of the 4th leg; St.b., stylet; I, II, III, IV, legs, each corresponding with one of the respective dorsal plates (from Renaud-Debyser).

PARASTYGARCTUS STERRERI Renaud-Mornant, 1970 (Fig. 573).

The body is more squat than that of *Pst. higginsi*, 170μ long and 45μ wide; it is covered laterally (around the trunk and on the legs) with a thick covering of sandy detritus and various particles, and its cuticle has a fine dorsal punctation.

The head is comparable to that of *Pst. higginsi*; the dorsal plate bears the median cirrus (24μ) and forms four large expansions, two frontal with the external buccal cirri (24μ) and the cephalic papillae (19-20μ), and two lateral with cirri A (32μ) and the clavae (25μ); these lateral expansions also bear a spine, turned toward the back; ventrally the buccal cone presents -- on two gibbosities -- the internal buccal cirri.

The cephalic papillae, associated with the external buccal cirri, have size and shape totally similar to the clavae, and have what is considered secondary clavae; the cephalic appendices are similar to those of *Pst. higginsi*, the cirri are articulated and the stalk represents two-thirds of the total length of the appendices.

The trunk is divided into three approximately equal parts corresponding to the first three pair of legs and there is then another caudal portion, clearly differentiated, which bears the 4th pair of legs. The first three parts, composed of plates separated from each other by two transverse folds, give the trunk a segmented appearance; each plate bears a lateral expansion on each side. The posterior part of the trunk (caudal) does not bear lateral expansions of large size: it is narrower, of pentagon shape, and presents two slightly dorsal gibbosities, on which are the cirri E, of 35μ; these are simple, borne on a small cirrophore: the basal part may or may not be annulated. Above the dorsal insertion of each leg of the 4th pair is a spine, 7-8μ long, and 5μ wide at the base.

The telescopic legs bear the claws characteristic of those of *Pst. higginsi*. On the ventral surface is visible the gonopore rosette and the anus.

The first example described was found in the Adriatic (without specific locality given). Later an example was found, perhaps belonging to this species, on Bermuda Island, while further examples were collected at two stations of the Galapagos Islands.

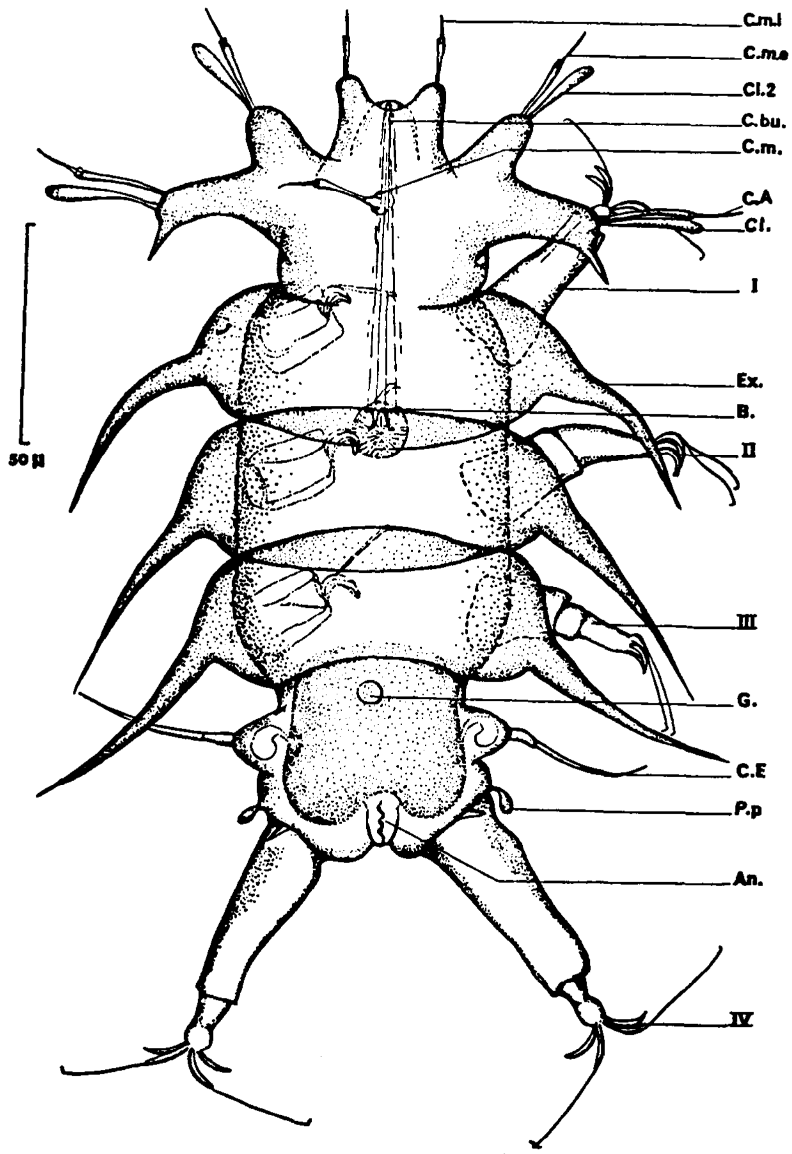


Fig. 573 - *Parastygarctus sterreri*. An, anus; B, pharynx; C.A., cirrus A; C.E., cirrus E; C.bu., buccal cone; C.m., median cirrus; C.m.e., external medial cirrus; C.m.i., internal medial cirrus; Cl., clava; Cl.2, secondary clava; Ex., lateral expansion; G, gonopore; P.p., papilla of the 4th leg; I, II, III, IV, 1st, 2nd, 3rd, 4th legs (from Renaud-Mornant).

Genus *PARECHINISCUS* Cuénot, 1926.

Diagnosis: Echiniscidae, with plates not clearly delimited on the rostral part of the dorsum, and better defined on the caudal part; the terminal plate is clearly visible.

KEY TO THE SPECIES

1. Size up to 200μ. Besides cirrus A, there are no other appendices .... *Par. chitonides*
   Size up to 400μ. Besides cirrus A there is a filament on the terminal plate, not associated with the incision, and then not exactly in position E .... *Par. armadilloides*

PARECHINISCUS ARMADILLOIDES Schuster, 1975.

Size up to 400μ. Larvae of two claws are about 200μ long. The sculpture is composed of small granules densely arranged, much more pronounced from the cephalic end toward the terminal. Cirrus A is 200μ long. The terminal plate is faintly incised. There is a filament 460μ long on the terminal plate, not associated with the incision, and therefore not exactly in position E.

The internal claws of the 4th pair have one or two small basal spines.

The species was collected in Logan Canyon, near Logan, Cache County, Utah (U.S.A.). Rahm (1928) cites, from Switzerland (Kt. Freiburg), a *Parechiniscus chitonides*, provided with filaments at E. Barring error, it should be treated as this species.

PARECHINISCUS CHITONIDES Cuénot, 1926 (Fig. 574).

Length up to about 200μ, colorless or grayish, rather transparent; eye spots present and black. The cuticle is thick dorsally and, in profile, is arranged in a series of crests, with rounded or flattened apices; viewed dorsally, the plates are not well defined in the rostral region of the body, while they are much better defined in the caudal region; extremely clear terminal plate, which is provided with notches.

All the plates are more clearly defined posteriorly than at their anterior margins. The sculpture of the terminal plate is rather coarse,

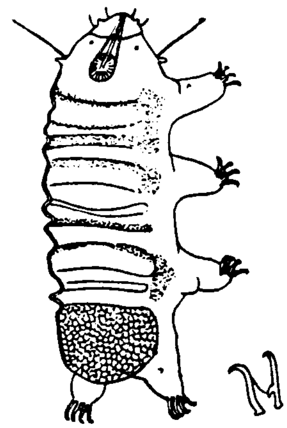


Fig. 574 - *Par. chitonides* Cuénot and external and external claws of the 4th pair of legs.

while it is an extremely fine punctation on the other plates, very visible especially on the scapular, and it extends also to the sides of the animal, especially in the region near the insertion of the legs.

Buccal armature and pharynx similar to that of the *Echiniscus*; stylet supports present. Cirrus A is a long filament and the clava a short papilla. The first pair of legs presents dorsal to their base an extremely small spine, not always easily visible, and at the bases of the 4th pair of legs (which lack the dentate collar) there is a papilla; four claws on each leg, the two internal provided toward the middle -- or a little more basally -- with a strongly curved spur.

Oval eggs are deposited in the old cuticle (exuvium), usually in numbers of two, and have the greater diameter of about 50μ. The larva of two claws measure about 102μ.

The species has been observed only in Europe (many localities of France, Italy, Spain, Switzerland, and from central Europe).

Typ. loc.: Barrois and Ardèche (France).

Genus *PLEOCOLA* Cantacuzène, 1951.

Diagnosis: Halechiniscidae, with digits with simple claws, without spurs; median cirrus and short clavae.

KEY TO THE SPECIES

1. The external buccal cirri are much longer than the internal; eyes absent; size up to 250μ . . . . *Pl. conifera*

The internal and external buccal cirri are
of about equal length; eyes present;
size up to 130μ . . . . *Pl. limnoriae*

PLEOCOLA CONIFERA Renaud-Mornant, 1975 (Fig. 575).

Size of 185 to 250μ (217μ average). The body is three times longer than wide. The cuticle has a punctation caused by uniformly distributed pores both on the dorsal and ventral surfaces. Head hemispherical, delimited by a constriction posteriorly to the cephalic appendices. Eyes absent.

The median cirrus is 9μ long, the internal cirri 10μ, the external 18μ; cirrus A measures 25μ, and is inserted anterior to the clava; the clava, of oval shape (8 x 5μ), is inserted in a semi-invaginated sheath.

The mouth is subterminal. Pharynx subspherical, without cuticular thickenings.

The legs bear dorsal spines, of decreasing length from 1st to 3rd pair (respectively 12, 6, and 2μ). Cirrus E, situated above the insertion of the 4th leg, is 38 to 40μ long, and departs from an enlarged base; anterior to cirrus E exists a papilla ending with a spine.

The legs are slender and bear four unequal digits; the tibia, slender, withdraws telescopically into the femur, which carries the dorsal spine. The external digits are shorter than the internal; the claws are devoid of spurs and are retractile in a membranous sheath, supplied with a distal lobe.

Pl. conifera has been collected in the abyssal meiobenthos in the Indian Ocean at the depth of 1,690 meters.

PLEOCOLA LIMNORIAE Cantacuzène, 1951 (Fig. 576).

Length from 90 to 130μ, 115μ average, with width of 32-35μ toward the middle of the body; colorless, transparent, with two orange-brown eye spots positioned laterally, not far from the base of the clava. The head, very convex, appears truncated when viewed in profile; the buccal aperture, surrounded by a projecting disk, is in anterio-ventral position. The cephalic appendices are: median (unpaired) cirrus, fixed on a base and about 6μ long; internal (dorsal) and external (ventral) buccal cirrus, paired, provided with base, about 12μ long; lateral cirrus A (15-17μ), paired, and oval clava (6 x 3μ), paired, projecting from a common base about 3μ high; lacking cephalic papilla. Buccal tube 15μ long, pharynx

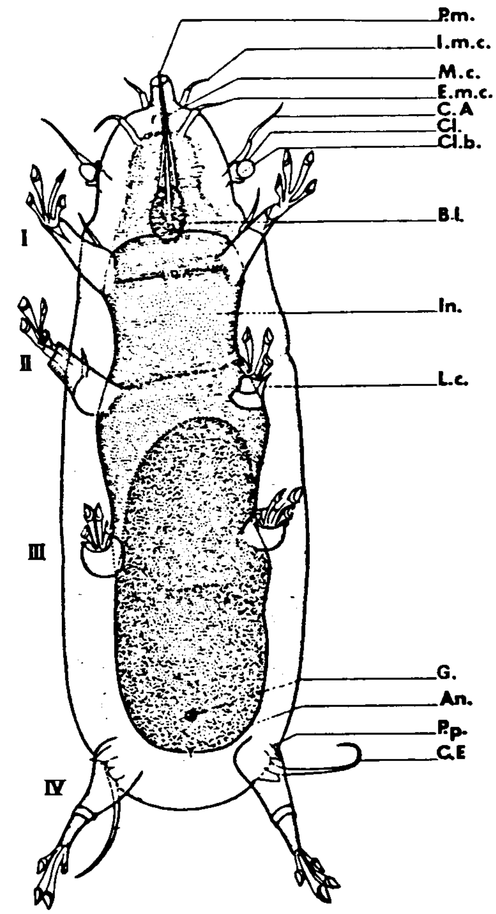


Fig. 575 - *Pl. conifera* Renaud-Mornant. Ventral view. An, anus; B.l., pharynx; C.A., cirrus A; C.E., cirrus E; Cl., clava; Cl.b., base of the clava; E.m.c., external median cirrus; G., gonopore; I.m.c., internal median cirrus; In., intestine; L.c., spine of the leg; M.c., median cirrus; P.m., mouth protracted; P.p., papilla of the 4th leg (from Renaud-Mornant).

oval of 13 x 11μ, with 3 pharyngeal bars; stylets of 15-16μ, having the caudal end enlarged; stylet supports present. There are caudally two dorsal cirri 17-19μ long, approximately in the position where the genus *Echiniscus* has the appendices E.

The legs may in part withdraw telescopically into their wider basal part and are terminated by 4 digits, each bearing at the distal end a robust simple claw (without spurs) and very arched; the two internal digits are longer than the external. All the legs of the first three pair have a small

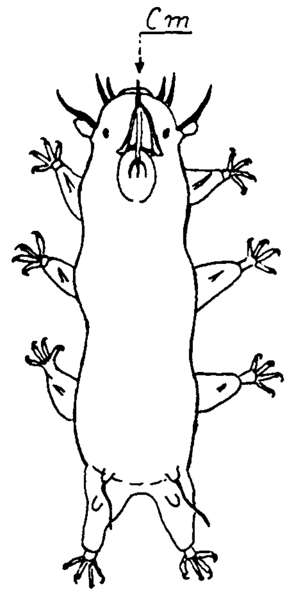


Fig. 576 - *Pl. limnoriae* Cantacuzène. Cm, median cirrus (from Cantacuzène, redrawn).

basal and external spine (longer than of the first pair); the legs of the 4th pair have an oval posterior papilla near their bases. Anal and genital pore distinct; eggs and exuvia unknown; the young animals (larvae) do not show morphological differences from the adults, but have only two claws.

The species was collected in France, on the Breton coast (Roscoff); it is a commensal of the isopod *Limnoria lignorum* (Rathke), localized on the pleotelson and sometimes on the pleopods: it was not ever observed elsewhere, not even in the galleries that the crustacean digs in the wood. On a single isopod there was one or two tardigrades, sometimes even more; the percentage of isopods with *Pleocola limnoriae* was on the average 3%. Later however L. W. Pollock and others observed the species also free, in interstitial environment.

Genus *PSEUDECHINISCUS* Thulin, 1911.

Diagnosis: Echiniscidae; after the second paired plate or after the median plate 3 (if present) follows, before the terminal, a pseudosegmental plate, paired or unpaired; buccal cirri present; cirrus A filamentous.

Observations.

The species *ceratophorus*, *cornutus*, *holmeni*, *lobatus*, *schrammi*, *subcornutus*, *tibetanus*, formerly included in the genus *Pseudechiniscus* (in which some constituted the so-called "*cornutus* group") are separated, to be included in the new genus *Cornechiniscus*.

The subspecies *P. suillus facettalis* has been here considered -- at least provisionally -- as a valid species, not being, in the present state, possibly subordinate with certainty either to *P. suillus* or *P. pseudoconifer*.

We think rather doubtful the actual existence of *P. conifer*, of which there have not been recent valid reports and which can correspond to *P. pseudoconifer*.

According to Dastych (1980), *P. tridentifer* may be a synonym of *P. victor*: the examination of the material in our collections confirm such synonymy, which therefore is used here.

KEY TO THE SPECIES

1. There is only appendix A; no other appendices (neither teeth nor blunt cones) either dorsal or lateral; there are not even lobes on the pseudosegmental, in which the posterior margin is at the most a little sinuous 2
Besides cirrus A there are other appendices, or lobes on the pseudosegmental 8

2(1). Cephalic and terminal plates clearly facetted 3
Cephalic and terminal plates not facetted 4

3(2). Clava well developed, large and rounded; cephalic papilla reduced to a small dome-shaped projection; the sculpture is a fine granulation . . . . *P. clavatus*
Clava and cephalic papilla normal; the sculpture is a granulation with "pearled" appearance . . . . *P. facettalis*

4(2). Head large, anteriorly rounded, 78μ long in a 300μ animal; a sort of papilla between cirrus A and external buccal cirrus . . . . *P. megacephalus*
Head of normal shape and length 5

5(4). Between the scapular plate and median plate 1 exists a row of 4 supplementary platelets; the granules of the terminal plate have a spiny appearance . . . . *P. jiroveci*
Different 6

6(5). The first unpaired plate is transversely divided into three parts . . . . . . *P. dicrani*
The first unpaired is divided into 2 parts 7

7(6). The sculpture is a fine granulation . . . . . . *P. suillus*
The sculpture is a larger granulation, with "pearled" appearance . . . . . . *P. juanitae*

8(1). The pseudosegmental has lobes or teeth on the posterior margin; there are very small lateral teeth, but no other appendices 9
The posterior margin of the pseudosegmental is straight 14

9(8). The pseudosegmental has teeth or lobes; no other dorsal or lateral teeth 10
Besides the lobes of the pseudosegmental, there are also lateral teeth 13

10(9). The scapular plate, the 1st and 2nd paired plates and the pseudosegmental have posteriorly a raised lobe toward the top . . . . . . *P. quadrilobatus*
Only the pseudosegmental has lobes or teeth 11

11(10). Unpaired plates 1 and 2 are undivided, unpaired 3 is absent; 2 small teeth at margin of pseudosegmental . . . . . . *P. bidenticulatus*
Different 12

12(11). The sculpture is composed of large granules, connected between them by lines; there are supplementary lateral plates; posterior margin of the pseudosegmental has two triangular lobes, or an unpaired triangular lobe . . . . . . *P. bartkei*
The sculpture is a fine regular granulation; no supplementary plates; pseudosegmental with 2 triangular lobes, or else a sinuous unpaired lobe, or 2 paired lobes . . . . . . *P. ramazzottii*

13(9). There are triangular teeth at the posterior margin of the scapular plate; short lateral spines B, C, D, E . . . . . . *P. occultus*
There are no teeth on the scapular 15

14(8). Median plates 1 and 2 undivided; pattern of W on cephalic plate; pseudosegmental has 2 rounded lobes; lateral conical processes on D and on terminal plate . . . . *P. scorteccii*
Median plates 1 and 2 are divided transversely; pseudosegmental with lobes in the form of spines, sometimes bifurcated, or else rounded, with or without apical teeth; short lateral conical projections on B, C, D (sometimes only in some of these positions) . . . . *P. novaezeelandiae*

15(13). Lateral projections are short stumps, in the shape of cones; no other appendices 16
There are appendices in the form of spines or filaments 18

16(15). Dorsal plates 2 and 3, under medium magnification, appear strongly granulated 17
Dorsal plates 2 and 3, at medium magnification, appear smooth; in contrast, scapular and terminal plates strongly granulated, but not the rostral region of median plates 2 and 3 . . . . *P. lateromammillatus*

17(16). Third median plate is divided transversely in two; internal claws of the 4th pair of legs without spurs . . . . *P. conifer*
Third median plate not subdivided; cephalic and terminal plates faceted; internal claws of 4th legs with small spurs . . . . *P. pseudoconifer*

18(15). There are no dorsal appendices, not even on the pseudosegmental 19
Both lateral and dorsal appendices 23

19(18). Besides cirrus A, only lateral appendices C 20
Besides cirrus A and an appendix C, there are laterally also other appendices 21

20(19). Size up to 200μ; lateral appendices are robust spines . . . . *P. bispinosus*
Size up to 340μ; lateral appendices C are long filaments; paired plates II and III have triangular points at their anterior margins . . . . *P. transsylvanicus*

21(19). The lateral appendages are long filaments B (which may be lacking), C, and E .... *P. hannae*
The lateral appendages are spines or cones B, C, D, and filaments E 22

22(21). The lateral appendages are conical projections B, C, D, and filaments E; the sculpture is a regular punctation .... *P. pulcher*
The lateral appendages are spines B, C, D, and filaments E; the sculpture has polygonal appearance .... *P. raneyi*

23(18). The dorsal appendices are only spines on the caudal margin of the pseudosegmental plate 24
There are also dorsal spines C and D 25

24(23). Laterally there are spines B, C, D, E; dorsal spines on the caudal margin of the pseudosegmental; the sculpture is formed of transverse and longitudinal lines of small granules .... *P. goedeni*
There are lateral spines B, C, and D and long filaments E; dorsal spines on the pseudo-segmental; the sculpture is formed of dots deposited to form a reticular design .... *P. islandicus*

25(23). There are no appendices E; laterally there are spines or filaments B, C, and E; dorsally there are spines C and D, and filaments posterior to the pseudosegmental plate (?); there may be dorsolateral spines C' and D' .... *P. distinctus*
There are filaments E; lateral spines B, C, D, and filaments E; dorsal spines C and D and two small spines on pseudosegmental; dorsolateral appendices B', C', and D' (or else only D') .... *P. victor*

PSEUDECHINISCUS BARTKEI Weglarska, 1962 (Fig. 577).

Length 150-200μ, orange color, eye spots black and elongated. Cephalic plate with a W pattern; besides the three median plates there are small supplementary plates: two per each side at the side of the median plate 1 and one per side at the side of the median 2. The caudal margin of the pseudosegmental -- which is paired -- has a bilobed process, which ends with two triangular tooth-shaped projections.

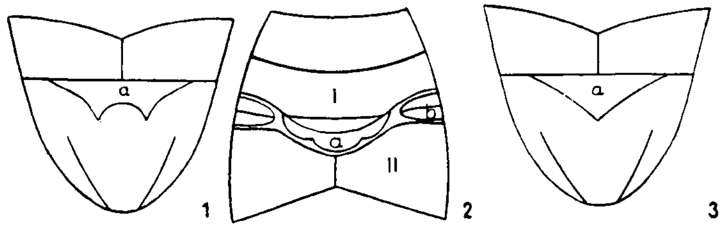


Fig. 577 - *P. bartkei* Weglarska, and its variety *unilobatus* Weglarska. 1, *P. barkei*: a, appendix of the pseudosegmental plate. 2, *P. bartkei*: I, scapular plate; II, first paired plate; b, lateral supplementary platelet. 3, *P. bartkei unilobatus*: a, appendix of the pseudosegmental plate (from Weglarska).

The sculpture of the plates is very characteristic, of the same type found in the Japanese species *E. elegans*, and is composed of densely distributed granules, connected to each other by lines: there is formed in such a manner a design of hexagons, which resembles small wheels of six spokes and which also calls to mind the "net stitch" of embroidery. Terminal plate with facets and with the usual notches. Except for cirrus A of 30μ (in animals 160μ long) there is no other lateral appendices: also dorsally the only existing appendices are the cited processes on the posterior margin of the pseudosegmental plate.

The legs are finely granulated on the basal regions; those of the 4th pair bear the usual papilla, while the dentate collar is absent. Claws normal, the externals with basal spurs, the internals with a small, slender spur. The eggs, 52 x 42μ, are deposited in the exuvium in numbers of 1-2.

The species was observed in moss on calcareous rock at 1,500 meters altitude, in Cha-Pa locality, Lao-Cai Province, in North Viet Nam.

In the same locality, but in a sample of different moss from that in which was observed the nominate subspecies, was collected examples belonging to a different subspecies.

P. bartkei unilobatus Weglarska, 1962.

In general 120-170μ length; the characteristics of this variety, sculpture included, corresponds almost totally with those indicated for *P. bartkei*. The principal differences are:

- the length of cirrus A somewhat larger (40μ in an individual 160μ long, while cirrus A of a *P. bartkei* of 160μ measures 30μ);
- the process on the caudal margin of the pseudosegmental, which rather than being bilobate, is composed of a single triangular structure.

PSEUDECHINISCUS BIDENTICULATUS Bartos, 1963 (Fig. 578).

Length 122μ, color brilliant reddish-yellow, small eye spots black and circular, sometimes indistinct. The sculpture is a regular and uniform granulation, more coarse on the terminal plate. Lateral cirri A of 27μ. Median plates 1 and 2 large, pentagonal and undivided; median plate 3 absent. The caudal margin of the paired plates (II and III) have at their median angle a type of projection (or slight lobe), which connects the right and left caudal margins of these same plates. The pseudosegmental plate is wide and paired, that is divided into two, and bears at its posterior margin two small teeth. The terminal plate is not facetted and has two small deep notches: at their caudal extreme exists a small blunt projection. There are no lateral appendices of the body.

Claws large and provided with spurs. Because the examples examined had strongly retracted legs, the author was not able to observe if having, or lacking, the spine on the 1st pair of legs and the papilla, the spine or the dentate collar on the 4th pair (here is seen the need to always examine individuals in complete extension, using -- if necessary -- some

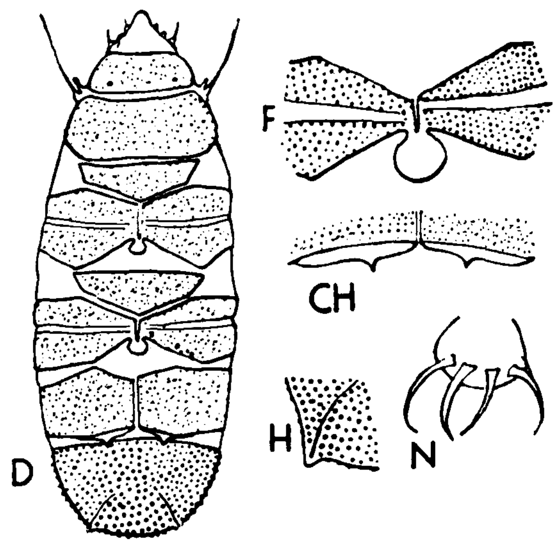


Fig. 578 - *P. bidenticulatus* Bartos. D, dorsal view; CH, detail of the appendices of the pseudosegmental plate; F, detail of a paired plate; H, detail of the terminal plate with incision; N, claws (from Bartos).

drops of about 5% KOH solution to accomplish this). Eggs unknown.

The species is probably near to *P. scorteccii* (which however has undivided median plates 1 and 2) and to *P. ramazzottii*, differing principally by the absence of the median plate 3.

P. bidenticulatus was collected in moss at Puntjak Pass, between Bogore and Bandung, in Java.

PSEUDECHINISCUS BISPINOSUS (Murray, 1907) (Fig. 579).

Small size, length 110-200μ; sculpture composed of a fine punctation on the plates and also on the cuticle between the plates.

Besides the short cirrus A there exists laterally only robust spines C with bulbous bases; there are no dorsal appendices. Terminal plate with notches (incisions); legs lacking dentate collars and claws without spurs.

The species was found only in Brazil and South Africa. Typ. loc.: Cape Colony.

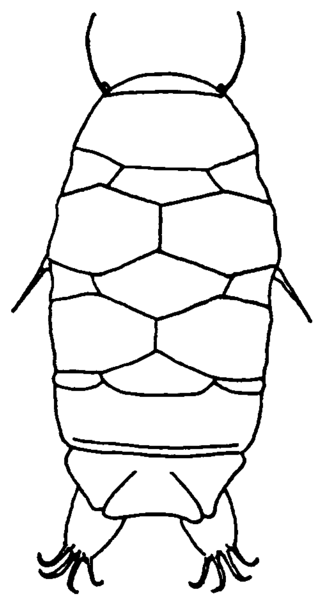


Fig. 579 - *P. bispinosus* (Murray) (from Marcus, redrawn).

PSEUDECHINISCUS CLAVATUS Mihelčič, 1955 (Fig. 580).

Length 200-220μ; the rostral margin is more widely curved than usual, therefore not pointed as in most *Pseudechiniscus*. The clava is large and rounded, while the cephalic papilla is weakly developed and has the appearance of a simple dome-shaped projection of the cuticle between the median (buccal) cirri. The lateral cirrus is a long and robust filament.

The cephalic plate is facetted and the line of demarcation between the cephalic plate and the scapular exhibits a median sinuosity, with the apices turned rostrally. The terminal plate is also facetted and seems to be partially fused with the pseudosegmental (however this is not rare in the genus *Pseudechiniscus*). The sculpture is composed of a very fine granulation.

The illustration shown here of the cephalic region was drawn based on a sketch kindly sent by the author, because the drawing shown in *Zoologischer Anzeiger* of 1955 (Vol. 155, p. 310, Fig. 2a) is wrong.

The species has so far been collected only in Spain (vicinity of Santander) in moss on tree trunks.

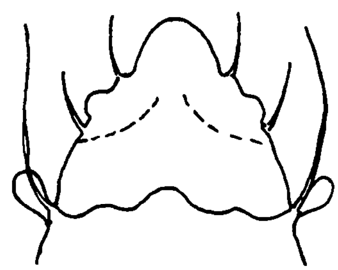


Fig. 580 - *P. clavatus* Mihelčič. Cephalic region.

PSEUDECHINISCUS CONIFER (Richters, 1904) (Fig. 581).

Length about 200μ. The granulation of the plates is rather coarse and is composed of minuscule tubercles; the cuticle between the plates is smooth, not sculptured; the third median plate is present and is subdivided by a transverse fold.

Laterally, besides cirri A, there are small conical projections B, C, D, E. The legs are granulated in the proximal part, smooth in the distal, and does not have dentate collar; the internal claws do not have spurs. The eggs (up to 3) are deposited in the exuvium.

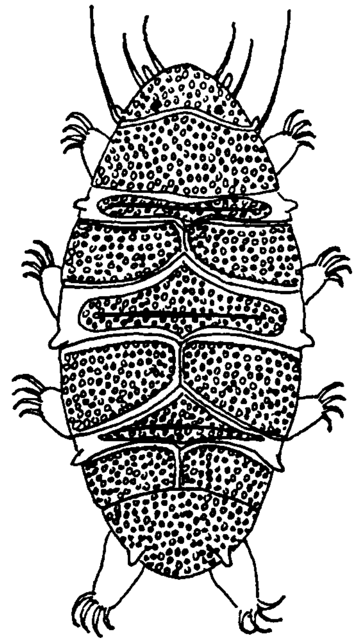


Fig. 581 - *P. conifer* (Richters) (from Richters, redrawn).

The species is easily distinguished from *P. pseudoconifer*, since the latter has the cephalic and terminal plates facetted, not showing transverse fold on the third median plate, has small spurs on the internal claws, and has sculptured cuticle also between the plates.

P. conifer was collected in various localities of Switzerland, Austria, and perhaps Rumania. Typ. loc.: Gandria (Lugano, Switzerland). There remains some doubt however about the possibility that this species was identified with *P. pseudoconifer.*

PSEUDECHINISCUS DICRANI Mihelčič, 1938 (Fig. 582).

Length 260-285μ, color red, eye spots black. The sculpture of the plates and the cuticle is a fine and regular granulation, similar to that of *P. suillus*. The scapular plate has on each side two thickened lines (see Fig. 582); the first median plate is transversely divided into three parts, the median plate 2 is transversely subdivided into two, the third is undivided. Paired plates with transverse bands of more scarce granulation. The pseudosegmental plate is longitudinally divided (paired) and has the posterior margins curved, with the concavity turned caudally, so as to form two dorsolateral lobes, directed posteriorly: sometimes -- but rarely --

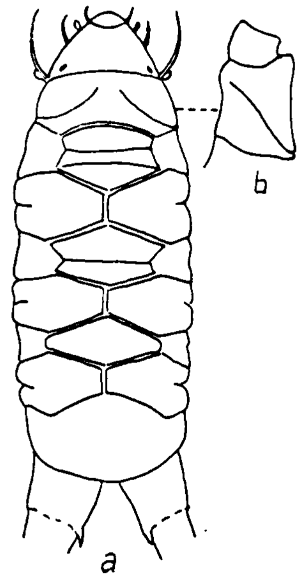


Fig. 582 - *P. dicrani* Mihelčič. a, dorsal view; b, lateral view of the scapular plate (from Mihelčič, redrawn).

these lobes appear thick and bear a tooth or an extremely small spine. Terminal plate not facetted and without notches.

Lateral cirri A are short and scarcely reach the rostral cephalic end; the legs are robust, those of the 4th pair do not have dentate collar, but bear -- in the position which it occupies and on the internal side of the leg -- a small curved spine.

P. dicrani is easily distinguished from the other species of roughly similar *Pseudechiniscus* (*pseudoconifer*, *ramazzottii*, *scorteccii*, *novaezeelandiae*, etc.) by having the first median plate subdivided into three parts.

The species was collected in Yugoslavia in moss of the species *Dicranum undulatum*, and in Rumania.

PSEUDECHINISCUS DISTINCTUS Mihelčič, 1951 (Fig. 583).

Medium size (the measurements in μ are not indicated by the author), of red brown color, with black eye spots. The sculpture of the plates is composed of small depressions, irregularly distributed; the cuticle between the plates is smooth. The three median plates 1, 2, 3, are present, all undivided: the first two have the rostral region unsculptured, the third has a slender median transverse band devoid of sculpture, analogous to

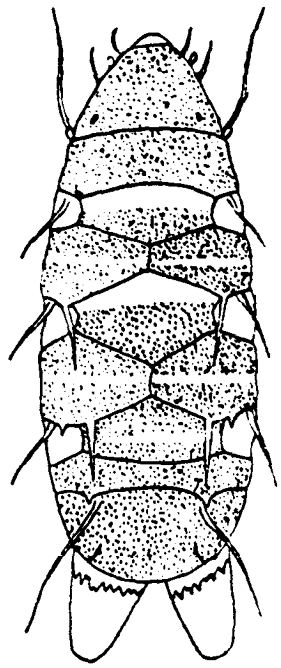


Fig. 583 - *P. distinctus* Mihelčič. Dorsal view (from Mihelčič).

those seen on the paired plates II and III. The pseudosegmental plate, clearly seen only in adult individuals which have reached complete development, is not subdivided longitudinally into two parts (it is then unpaired); the terminal plate has the two notches, or incisions.

The appendices are typical: laterally, long cirrus A and spines of medium length -- or instead filaments -- B, C, D; dorsally spine of medium length C^d and D^d and 2 long filaments -- one per side -- immediately behind the caudal margin of the pseudosegmental plate; dorsolaterally, short spines C' (which may be lacking), D', as well as on the pseudosegmental plate on the outside of the filaments positioned caudal to them. There may be however considerable variation in the appendices and individuals have been observed lacking B, or else B, C, D; others in which B, C, D were short spines; still others in which C^d was reduced to a very short spine; and finally individuals in which D^d was very short.

Legs long with robust claws and spurs on the internals; 4th pair of legs with the usual papilla and dentate collar, composed of numerous unequal teeth, positioned at an irregular distance from each other.

The species is known only for southern Finland and was collected in moss on rock.

PSEUDECHINISCUS FACETTALIS Petersen, 1951 (Fig. 584).
= *P. suillus* forma *facettalis* Petersen, 1951
= *P. pseudoconifer* forma *facettalis* Maucci, 1954
= *P. suillus facettalis* Ramazzotti, 1962 and 1972

Length up to 180μ, red color, or brownish red, black eye spots. Cephalic appendices normal, lateral cirri A rather short (20-30μ). Sculpture composed of a regular granulation, somewhat finer on the median plates and on the caudal zone of the paired plates; the individual granules have larger size in *P. facettalis* than in *P. suillus* and the sculpture is very similar to that of *P. pseudoconifer*. Pseudosegmental plate often -- but not always -- is divided into two (paired); cephalic and terminal plates clearly facetted, legs with sculptured basal parts; those of the 4th pair with the usual papilla; internal claws with spurs, which may be extremely small and difficult to see, but may also have normal size.

Maucci (1954) has proposed to consider this as a form of *pseudoconifer* rather than of *suillus*, on the basis of the facetting of the cephalic and terminal plates, and on the type of sculpture. Since, at the current state of our knowledge, there is not any evidence which supports assignment to a subspecific subordination of one species rather than another, we think it advisable -- at least temporarily -- to elevate *P. facettalis* to the rank of a valid species.

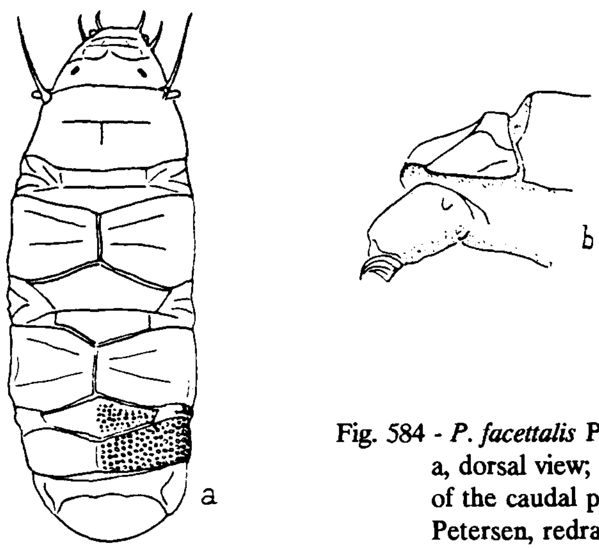


Fig. 584 - *P. facettalis* Petersen. a, dorsal view; b, profile of the caudal plate (from Petersen, redrawn).

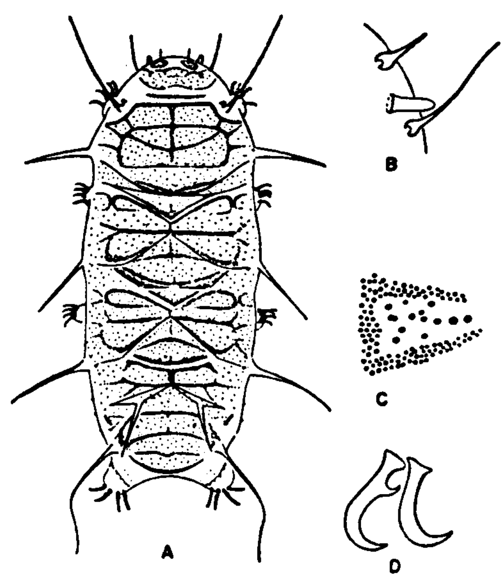
Numerous reports exist of this species from varied localities of Italy, Greenland (typ. loc.), Tierra del Fuego, Yugoslavia, Austria, Turkey, Greece, Republic of Andorra. The *P. suillus* cited by Horning, Schuster, and Grigarick (1978) for New Zealand is also a *P. facettalis*, as seen from the photograph taken with scanning microscope.

PSEUDECHINISCUS GOEDENI Grigarick, Mihelčič, & Schuster, 1964 (Fig. 585).

Length up to 450μ, but usually 350-370μ. The sculpture of the plates is composed of transverse and longitudinal rows of small granules, very close to each other: between there are included smooth zones, in which the granules are larger and arranged in sparse and scattered manner. In the higher position of focus (at 400X with normal or phase contrast illumination) the granulation appears dark on light background, while light on dark background in the lower position. Legs likewise sculptured -- in the armored parts -- with granules of medium size; the cuticle between the dorsal plates and those of the ventral surface is smooth. Pseudosegmental plate medially subdivided, as the dorsal plates.

Laterally are present, besides cirrus A (105μ), lateral spines B, C, D, E (60, 80, 85, 110μ); dorsally there are two spines (40μ) at the caudal margin of the pseudosegmental plate. There are sometimes small

Fig. 585 - *P. goedeni* Grigarick, Mihelčič & Schuster. A, dorsal view; B, cephalic appendices; C, detail of the sculpture; D, claws of the 4th pair of legs (from Grigarick, Mihelčič and Schuster).



supplementary spines at the bases of these dorsal spines and at the bases of the lateral spines C, D, E. The lateral margins of the body, between the spine D and the 4th pair of legs, bears on each side three teeth. The measurements of the cephalic appendices -- in the type -- are: internal buccal cirrus 17μ; external buccal cirrus, 34μ; cephalic papilla, 13μ.

First pair of legs with small basal spine; fourth pair with the usual papilla and dentate collar (8-9 pointed teeth); curved spurs on the internal claws of all the legs. An exuvium was seen containing 3 large eggs of about 100μ diameter.

The species was observed in Oregon (U.S.A.) in lichen on conifers.

PSEUDECHINISCUS HANNEAE Petersen, 1951 (Fig. 586).

Length up to 235μ, color brownish red, eye spots black. The sculpture is a rather coarse granulation, somewhat different from one individual to another (distance between the centers of two granules on the dorsal surface of the scapular plate varies between 1.3 and 1.7μ, in animals having equal size). On all the plates -- including the medians -- as well as on the external side of the legs, the granules have larger size: the sculpture is instead finer on the cuticle between the plates and on the ventral surface, or even on the same plates, where cuticular folds exist.

Sometimes the plates, slightly thick, do not appear distinctly delimited, which occurs fairly often in the genus *Pseudechiniscus*; the

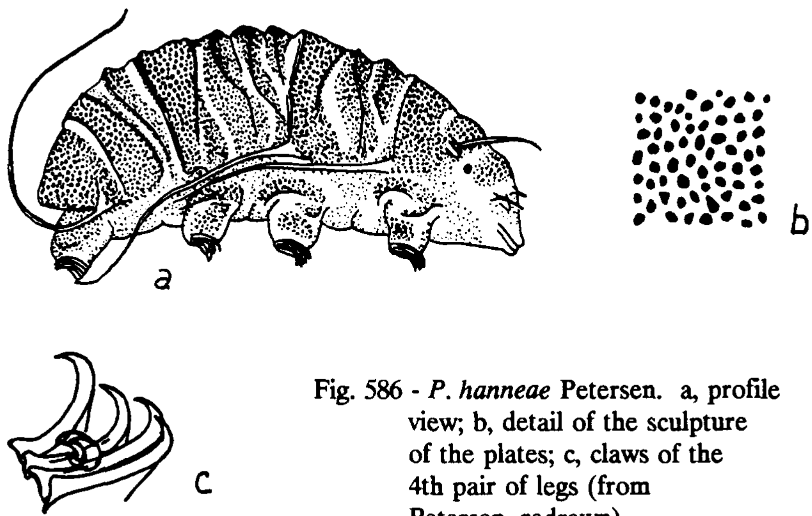


Fig. 586 - *P. hanneae* Petersen. a, profile view; b, detail of the sculpture of the plates; c, claws of the 4th pair of legs (from Petersen, redrawn).

scapular plate and the median plates 1 and 2 have a transverse fold; the terminal plate is not facetted.

The lateral appendices, besides cirrus A (25-30μ), are long filaments B, C, E of progressively increasing length, up to a maximum of 200μ for E; filament B may be lacking: when it is present it measures 30 to 105μ. There are no dorsal appendices. The legs are short and robust: on them there are no papillae, or spines, and even the dentate collar is absent; internal claws with curved spurs. The larvae of 2 claws measure 105-115μ.

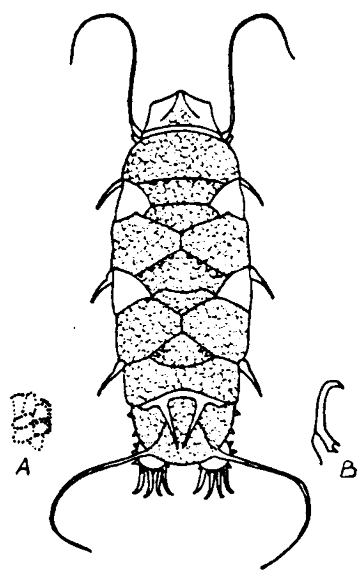
An exuvium has been observed containing two yellowish eggs, subspherical.

The species was collected only in Greenland by Petersen and -- according to this author -- seems to prefer dry habitat; numerous individuals were found in a moss on rock, subject to desiccation.

PSEUDECHINISCUS ISLANDICUS (Richters, 1904) (Fig. 587).

Length 500μ and more; colorless or brownish; sculpture composed of rows of dots, which delineate an irregular reticular design in the center of all the plates. Median plates 1 and 2 divided transversely into two parts,

Fig. 587 - *P. islandicus* (Richters). A, detail of the sculpture of the plates; B, internal claws of the 4th pair of legs (from Murray, redrawn).



median plate 3 undivided; the two notches of the terminal plate are very deep. Laterally exists the following appendices: long cirri A, spines B, C, D, slightly curved (about 48μ), long filaments E; also there are two teeth on each of the lateral margins of the terminal plate IV. Dorsally there is a pair of robust and wide spines (about 55μ) on the caudal margin of the pseudosegmental plate, near the median line, as well as a series of teeth -- in varied number and in dorsomedian and dorsolateral positions -- on the caudal margins of the scapular plate I and on the paired plates II and III; in some individuals the second paired plate (III) bears two straight spines D^d, shorter, more slender and more distant from the median line than those existing on pseudosegmental plate. Small spine on 1st pair of legs; 4th pair with dentate collar, composed of sharp teeth; internal claws with small spurs, curved toward the base; existence of a spine on the external claws very doubtful. Deposits up to 3 eggs, of brownish-yellow color, in the exuvium; the larvae of two claws observed measured a maximum of 304μ.

The species was collected in Switzerland (Cervino), in Scotland, on Shetland and Faröe Islands, on Iceland (typ. loc.), and is probably counted among those "montane."

PSEUDECHINISCUS JIROVECI Bartos, 1963 (Fig. 588).

So far only 5 larvae of two claws (length 50μ) have been collected of this species and it is then possible that the appearance of the adults is different (appearance of the median plates 2 and 3 lacking, of possible cuticular appendices, etc.); however we are in agreement with the author in considering these larvae as belonging to a new species, especially by the characteristic of the dorsal supplementary platelets.

The sculpture is composed of a regular and uniform granulation: on the terminal plate the granules -- with strong magnification -- appear as small thorns. The internal and external buccal cirri arise from a hemispherical base, and the cephalic papilla is also a hemisphere. Cirrus A measures 8.5μ; the clava is minuscule; the eye spots are black, small and round. The cephalic and scapular regions are narrow. Immediately behind the caudal margin of the scapular plate -- and probably derived from this -- there is a transverse row of 4 supplementary platelets, which is followed by median plate 1, large, pentagonal and undivided; lacking median plates 2 and 3 and at their position exists only a narrow band of granulation on the cuticle. Pseudosegmental plate wide and paired; terminal plate not facetted, with two deep notches. Except for cirrus A there are no other lateral or dorsal appendices.

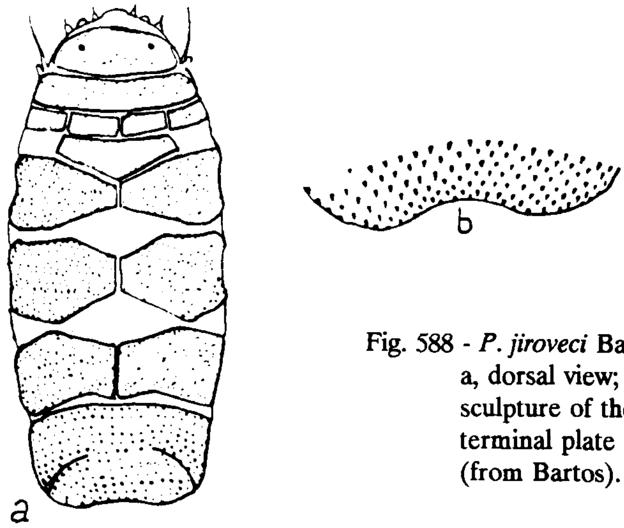


Fig. 588 - *P. jiroveci* Bartos. a, dorsal view; b, sculpture of the terminal plate (from Bartos).

The species was observed in moss from Ting-chu Mountain near Canton in China.

PSEUDECHINISCUS JUANITAE Barros, 1939 (Figs. 589 and 590).
= *P. suillus franciscae* Barros, 1942

Length about 132μ, orange color, eye spots black and rounded. The sculpture is a granulation not very dense, composed of rather large granules, with "pearled" appearance; the individual granules have greater size on the pseudosegmental and terminal plates -- where they are more numerous -- while they are less dense and much smaller on the paired plates, on the caudal part of median plate 2, and on median plate 3 (undivided); the size of the granules decreases -- and the density increases -- on the scapular plate, on median plate 1 and on the rostral part of median plate 2; the sculpture becomes extremely fine on the cephalic plate and on the cuticle between the plates. Two notches are present on the terminal plate; lacking all lateral, with the exception of cirrus A, and dorsal appendices. Legs short; on the 4th pair the dentate collar is absent; claws without spurs. Eggs unknown.

P. juanitae is distinguished from *P. suillus* especially by the sculpture composed of large granules (in *suillus* is found a fine punctation), by the short legs, by the general robust and squat appearance (while *suillus* has the body proportionally less wide and appears then more elongated and more slender).

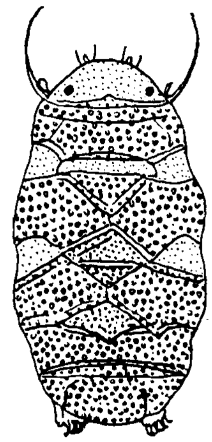


Fig. 589 - *P. juanitae* Barros (from du Bois-Raymond Marcus, redrawn).

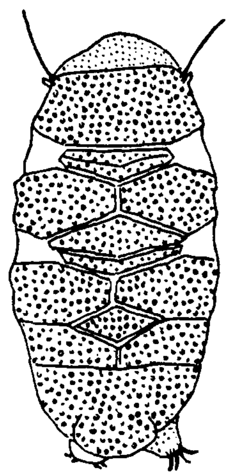


Fig. 590 - *P. suillus* forma *franciscae* Barros = *P. juanitae* (from Barros, redrawn).

Barros has described as *P. suillus* forma *franciscae* a *Pseudechiniscus* with the following characteristics:

Length about 144μ, eyes black and oblong. The sculpture of the plates is composed of rather scarce granules, irregular in shape, size, and distribution; the cuticle between the plates is smooth. Pseudosegmental plate subdivided into two parts (paired), terminal plate not facetted, and with the usual two notches. The basal parts of the legs are sculptured;

internal and external claws smooth, without spurs.

P. suillus forma *franciscae* differs from the typical *suillus* by the coarser sculpture, by the absence of spurs on the internal claws, and by the larger size and robustness of the body; it differs also from *P. juanitae* by having the cuticle between the plates smooth (in *juanitae* it is sculptured) and oblong eyes, rather than round: it is doubtful if this last difference may be considered valid and given the type of sculpture (which in the Echiniscidae has a significant taxonomic value) we prefer to consider *P. suillus franciscae* as synonymous with *P. juanitae*.

P. juanitae was described from Brazil. Subsequent reports are from the Galapagos, Austria, and Italy (National Park of Abruzzo).

PSEUDECHINISCUS LATEROMAMILLATUS Ramazzotti, 1964 (Figs. 591 and 592).

Length up to 140-165μ, color yellowish or yellow-orange, eye spots present. Among the numerous individuals examined no larvae of 2 claws were seen: even the young of only 85μ had 4 claws. *P. lateromamillatus*

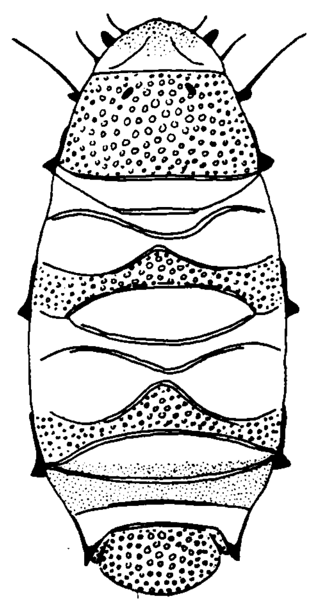


Fig. 591 - *P. lateromamillatus* Ramazzotti. Dorsal view.

is distinguished at first glance from all other *Pseudechiniscus* by the shape and the sculpture of the various plates: even with a diligent examination it is not easy to establish with accuracy their disposition, because of the partial fusion. In fact (see figure) those which in dorsal view seem -- and we think they are -- the rostral parts of the median plates 2 and 3 ("dorsal intersegmental plates" of Marcus), in lateral view may seem instead to make up an integral part of the first and second paired plates (plates II and III): the reason is that such rostral parts of the median plates are prolonged laterally, as far as the lateral margins of the paired plates.

The sculpture is a very large granulation, limited however to the scapular plate, the rostral parts of the median 2 and 3, and the terminal plate, which has the usual two notches. The larger granules are positioned in the central zone of the scapular and terminal plates, where they may reach a diameter of about 2μ. In such zones there are -- in the adults -- from 14 to 19 granules in a square of 9.5μ on a side. In the young the density of the sculpture is instead much larger and this contrasts with what occurs in *E. merokensis*, where on the contrary the density of the granulation increases with the size of the animal (Franceschi and Lattes, 1964).

The pseudosegmental plate is devoid of coarse granular sculpture, but is instead finely punctated and is undivided, with posterior margin straight, or slightly sinuous. The dorsal plates II and III (or however those which have that appearance) are completely smooth -- if observed at medium magnification -- and undivided; only with extremely strong magnification (and not always) appears an extremely fine granulation.

Internal buccal cirri of 5.5-7μ, external of 10-15μ; cephalic papilla considerably developed, width from 2.3 to 3.2μ at the base and 4.2-6.5μ long. Lateral cirri A of 23-29μ, that is rather short. Clava normal.

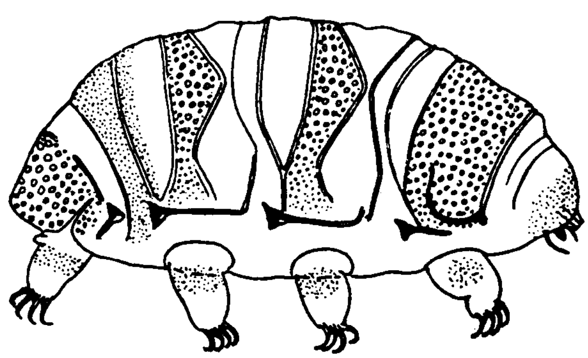


Fig. 592 - *P. lateromamillatus* Ramazzotti. Lateral view.

The only appendices of the body are lateral conical projections B, C, D, and E, the latter positioned on the terminal plate, external to the notches: such appendices are all extended rostrally from a cuticular thickening, lateral to the plates and parallel to their external margins, especially clear in dorsal view. In the young the conical appendices usually bear at the apices a short spine-shaped or cylindrical extension which gives them a mammillary appearance; these occur sometimes also in the adults. The size of these projections varies somewhat, but have in general 4-4.9μ width at the base, with a height of 3.2-4μ.

On the first pair of legs there is a slender spine, visible -- and with great difficulty -- only on some individuals; on the fourth pair exists the usual papilla. The claws are rather short (5-9μ) and those internal on all the legs bear near to the base an extremely slender spur, very sharp and curved, which may easily escape observation.

P. lateromamillatus was collected in moss on trees at Nal (Chiloè, Chile). A recent report from New Zealand (Horning, Schuster, and Grigarick, 1978) is certainly in error, and refers to another species (probably new).

PSEUDECHINISCUS MEGACEPHALUS Mihelčič, 1951 (Fig. 593).

Size about 300μ, color reddish; the cephalic region is well developed, about 78μ long, that is more than a quarter of the entire length of the animal; also the head does not appear rostrally pointed, as for example in *P. suillus*, rather rounded. The internal and external buccal cirri are longer than in *suillus* and arise from small conical bases; the cephalic papilla is large, with mushroom appearance; between the external

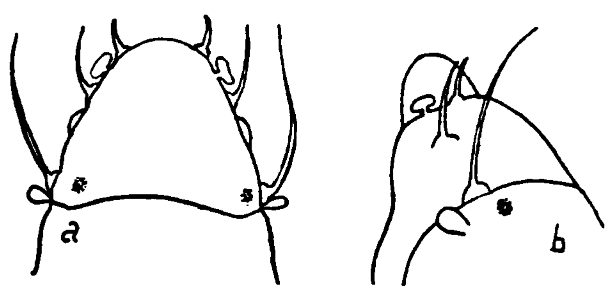


Fig. 593 - *P. megacephalus* Mihelčič. a, dorsal view of the cephalic region; b, the same in lateral view (from Mihelčič).

median cirri and the lateral cirri A exists -- on each side -- a papilliform projection; the lateral cirri A approximately reach, with their apices, the anterior margin of the head, and the clava is similar to that of *suillus*. Plates weakly developed; legs long: on those of the 3rd pair the cuticle is thick and granulated in the proximal zone; claws long and slender, the internals with large and robust spurs.

The species was collected in Austria (east Tirolo) in moss on rock in the shade and -- perhaps -- in Turkey.

PSEUDECHINISCUS NOVAEZEELANDIAE (Richters, 1908) (Figs. 594, 595, 596).

Length in general 190μ, but the size may be larger, up to 210μ and more; eye spots black. The granulation is rather fine, however less than in *P. suillus*; median plates 1 and 2 divided by a transverse line; pseudosegmental plate undivided (unpaired), or else subdivided into two longitudinal line (paired). The caudal margin of the pseudosegmental plate

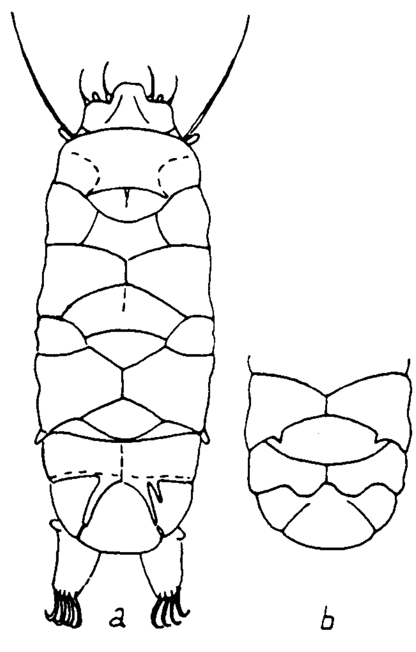


Fig. 594 - *P. novaezeelandiae* (Richters). a, typical; b, with reduced appendices on the pseudosegmental plate (from Murray, redrawn).

bears, near to its median line, two spines -- one on each side -- often bifurcated: these spines may however be reduced to teeth, or a simple lobe, and in such cases the distinction from other close species -- for example *P. pseudoconifer* -- is not easy (perhaps sometimes impossible). Laterally exists short conical projections D and sometimes also B and C. The posterior angles of the paired plates are strongly delimited (Fig. 594, b), so much so as to appear almost tooth-shaped. First pair of legs with a small spine, fourth pair with the usual papilla and lacking the dentate collar; external and internal claws smooth without spurs (a difference from *P. pseudoconifer*, which always has spurs on the internal claws, although sometimes extremely reduced and difficult to see: but precisely because of this the doubt arises that possibly small spurs might have escaped the first observations of *P. novaezeelandiae*). Up to 4 eggs deposited in the exuvium.

P. novaezeelandiae, with its varieties -- listed here below -- is a species which ought to be reexamined in the future, with regard to the taxonomic value of its varieties, the limits of the intraspecific variety, and finally for its relation with other close species, such as *P. pseudoconifer*, *P. scortecci*, and *P. ramazzottii*.

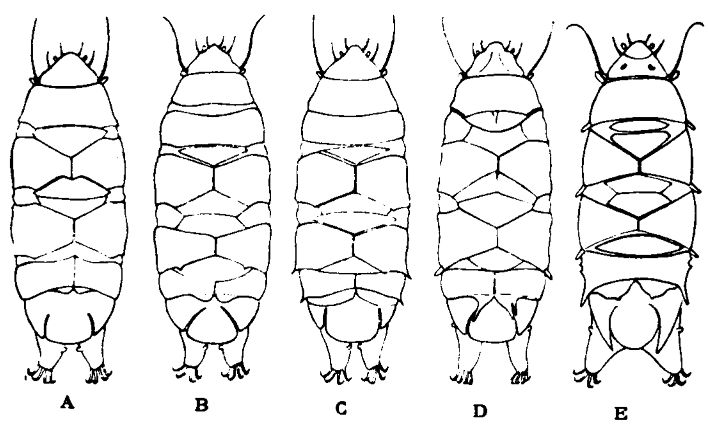


Fig. 595 - *P. novaezeelandiae* (Richters) and its varieties. A, *aspinosus* Iharos; B, *dorsospinosus* (Richters); C, *laterospinosus* Iharos; D, typical form; E, *marinae* Bartos (from Iharos).

There have been described the following varieties:

P. novaezeelandiae forma *aspinosa* Iharos, 1963.

This variety differs from the type species by the complete absence of dorsal and lateral appendices. Also the lobing on the caudal margin of the pseudosegmental plate is poorly developed.

This variety was collected at Mount Piltriquitron near El Bolsòn (Rio Negro Province -- southern Argentina) at 350-400 m altitude.

P. novaezeelandiae forma *laterospinosa* Iharos, 1963.

This variety is distinguished from the typical species because the lateral papillae are absent, while instead present are minuscule lateral spines D on the second paired plate and also at the margin of the pseudosegmental plate: this latter plate presents a well-developed caudal bilobing, however without spines. Small papilla on the internal surface of the 4th pair of legs.

The variety was observed at Mount Piltriquitron near El Bolsòn (Rio Negro Province -- southern Argentina) at 350-400 m altitude.

P. novaezeelandiae forma *marinae* Bartos, 1934.

Length 125-150μ, color reddish-brown, eye spots black, cephalic papilla mushroom-shaped, clava long. Granulation present on the plates and also -- but finer -- on the cuticle between the plates. Pseudosegmental plate undivided (unpaired), bearing at its caudal margin two large lobes, each ending with a small sharp spine, or with a tooth. The terminal plate (IV), external to the notches, is caudally elongated into two pointed processes (see Fig. 596). Laterally, besides cirrus A of about 50μ, there are short conical projections B, C, D, and 2 other analogous projections on each of the two lateral margins of the pseudosegmental plate: the latter has the lateral posterior angles elongated caudally to form two conical appendices, almost spine-shaped. Small spine on the 1st pair of legs and papilla on the 4th pair, which is devoid of dentate collar; external and internal claws smooth, without spurs. Eggs unknown.

P. novaezeelandiae marinae was cited for Czechoslovakia, Rumania, Italy (Valcamonica), Brazil (State of Sao Paulo), and the U.S.A. (Wisconsin); it was noted however that:

1) the individuals of the Italian report (Franceschi, 1952) do not have characteristics in complete agreement with the original description of Bartos;

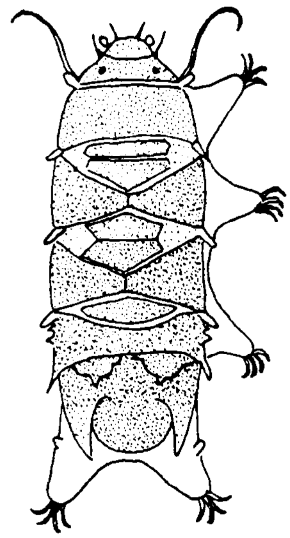


Fig. 596 - *P. novaezeelandiae* forma *marinae* Bartos (from Bartos, redrawn).

2) the examples of one of the two Brazilian reports, to be precise those described by Barros (1942), do not seem to belong to this variety, but rather to *P. pseudoconifer*;

3) the examples from Wisconsin, examined by Ramazzotti, also show some differences from the description of Bartos.

All of this demonstrates the extreme variability -- which we have pointed out many times -- of many species of the genus *Pseudechiniscus* and particularly those of the "*conifer* group" and "*suillus* group."

Reports of the typical form in Europe are only known for the Tatras; other localities of collection are South America (Brazil, Colombia), North America, Hawaiian Islands, Australia, and New Zealand.

PSEUDECHINISCUS OCCULTUS Dastych, 1980 (Fig. 597).

Length 165μ. Color bright red. Eyes present, composed of sparse granules of black pigment. The scapular plate presents a design in the shape of a T and two dorsal spines, short and triangular. The sculpture is composed of an irregular granulation, with larger granules (1.5μ) on the scapular plate and on the first paired plate, and with size decreasing toward the flanks of the body. The terminal plate presents two deep incisions. In positions B, C, D, and E exist small lateral spines (4-7μ), of which the shorter are those in positions B and E. The pseudosegmental plate is

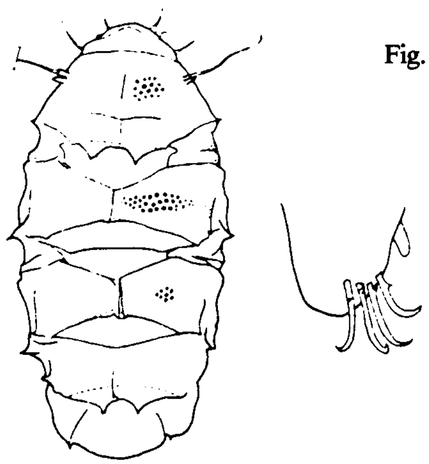


Fig. 597 - *P. occultus* Dastych. Dorsal view and claws of the 4th pair of legs (from Dastych).

partially divided (paired) and bears posteriorly two prominences in the shape of short triangular spines.

Internal buccal cirri 12μ long, external cirri 22μ; cirrus A is 55μ long. Legs without dentate collar; the internal claws of all the legs present a basal spur, the externals of only the 4th pair present a straight spine.

A single example of this species was found in moss on calcareous rock at Mala Dolinka, in the Tatra Mountains (Poland) at 1,650 altitude.

PSEUDECHINISCUS PSEUDOCONIFER Ramazzotti, 1943 (Fig. 598).

Length 150-190μ, color reddish, eyes black. The sculpture of the plates is a more or less fine granulation: sometimes the granules are larger and confer on the sculpture a "pearled" appearance (as in *P. juantiae*), especially on the anterior part of the cephalic plate, on plates II, III, pseudosegmental, and on the terminal IV; on the other plates, and on the cuticle between the plates, the punctation is finer. The pseudosegmental plate often appears subdivided into two by a narrow median longitudinal smooth band, devoid of granulation; it may however be clearly divided (paired), or even undivided (unpaired). The cephalic plate and the terminal are facetted.

Laterally exists small -- but very evident -- conical projections: rarely on C, D, E, more common on C and D, or even only on D; sometimes the scapular plate (I) has the external posterior angles very pronounced, so much so as to simulate another conical projection B. No dorsal appendices; often the pseudosegmental plate shows lobed, or bilobed, caudal margin. The legs have a dorsal and proximal zone strongly granulated, especially those of the 4th pair, on which exists the usual papilla; external claws smooth, internal claws -- often all the legs, and not just the 4th pair -- with very small spurs, at times difficult to see, positioned near the base. The eggs (1-5) are deposited in the exuvium, are oval, of yellowish-red and of variable size (about 43 x 38μ); the larvae of two claws already have conical projections D. Even in the adults lacking the dentate collar.

P. pseudoconifer is distinguished from *P. conifer* by the facetted terminal plate (already in extremely young individuals), by not having transverse fold on median plate 3, by the spurs on the internal claws, and by the sculptured cuticle even between the plates. There is certainly close relation between *P. pseudoconifer* and the other species of the genus *Pseudechiniscus*, in particular *P. conifer*, *P. novaezeelandiae* and its varieties, *P. ramazzotti*, *P. scorteccii*, *P. facettalis*, and perhaps *P. juanitae*.

P. pseudoconifer is known from different localities of Italy, from Yugoslavia, Greece, and Uganda.

Typ. loc.: Belluno and Salsomaggiore (Italy).

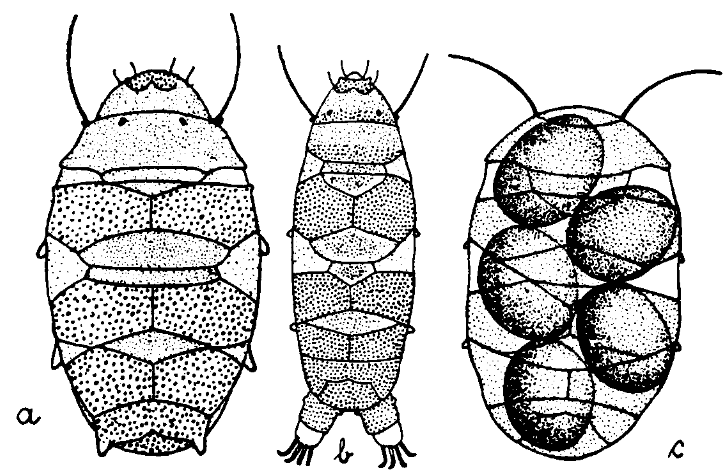


Fig. 598 - *P. pseudoconifer* Ramazzotti. a, b, dorsal views; c, egg-bearing exuvium (in a the animal appears somewhat swollen as a result of Faure's medium, in b, elongated from the action of KOH).

PSEUDECHINISCUS PULCHER (Murray, 1910) (Fig. 599).

Length about 300μ, color red, legs short. The sculpture is a fine punctation; median plate 1 with anterior margin distinct and undivided, median plates 2 and 3 divided according to a median longitudinal line and with anterior margin barely distinct, which tends to merge respectively with the first (II) and the second (III) paired plates. The pseudosegmental plate is narrow in rostro-caudal sense and undivided; the terminal plate has weak and poorly developed notches. Laterally, besides cirri A, there exists obvious conical projections B, C, D, and filaments E of about 100μ. There are no dorsal filaments. Lacking the dentate collar on the fourth pair of legs; the external claws are smooth, the internals have a small spur, very near to the base. The eggs -- up to 9 -- are deposited in the exuvium; there have been observed larvae of two claws of 175μ.

The species was collected only in Australia (Australian Alps), at an altitude of about 2,000 meters.

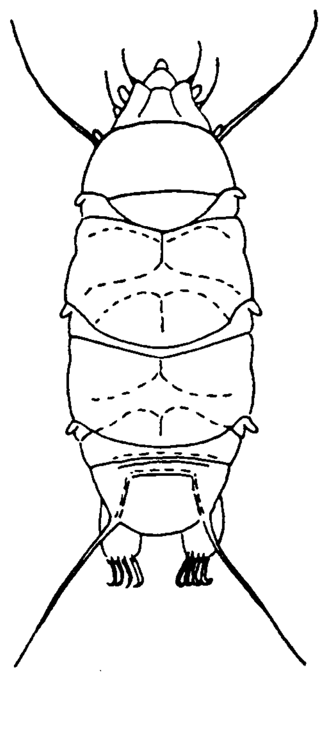


Fig. 599 - *P. pulcher* (Murray) (from Murray, redrawn).

PSEUDECHINISCUS QUADRILOBATUS Iharos, 1969 (Fig. 600).

Small, length 130μ; color orange-red, with black eye spots. The sculpture is composed of small clear dots, regularly arranged. The dorsal plates and the pseudosegmental have at their posterior margins, near the dorsal median line, uplifted lobes (very visible in profile). The more developed of these lobes is found at the margin of the pseudosegmental plate, which is undivided (unpaired). The three median plates are undivided (that is without transverse division). Terminal plate with notches. Internal buccal cirri 7μ long, externals 4μ, and lateral cirri A 30μ. There exists no other dorsal or lateral appendices. At the bases of the 4th pair of legs there is a small spine; lacking the dentate collar and the claws do not have spurs.

The species was collected in moss on tree trunks at Toung Linh (Viet Nam) and is distinguished by the 4 elevated appendices (lobes) of the three dorsal plates and the pseudosegmental.

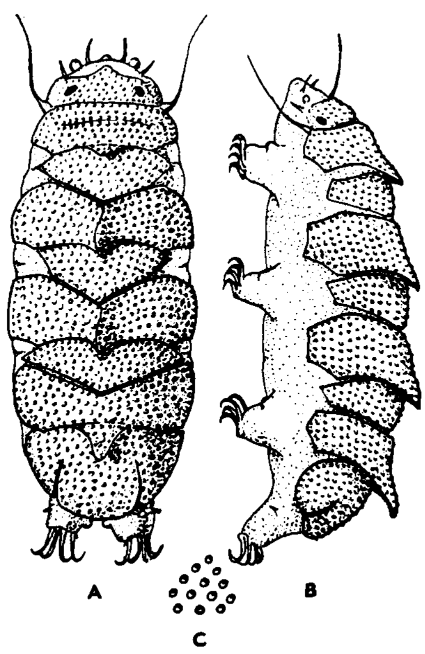


Fig. 600 - *P. quadrilobatus* Iharos. A, dorsal view; B, lateral view; C, sculpture of the plates (from Iharos).

PSEUDECHINISCUS RAMAZZOTTII Maucci, 1952) (Figs. 601 and 602).
= *P. r.* forma *facettalis* Iharos, 1964
= *P. r. facettalis* Ramazzotti, 1962 and 1972
(not *P. suillus facettalis* Petersen, 1954)
= *P. r. lineatus* Maucci, 1973-74

Length in general 150μ, although the larger individuals may reach 196μ; the young with 4 claws measure 131μ. Eyes black, in general oval, rarely round; cephalic appendices normal, cephalic papilla globose and clava long and robust; body slender. The sculpture of the plates is a coarse and uniform granulation, absent only on the frontal plate (not always), on the rostral margin of the scapular plate, and along the caudal margin of the paired plates II and III. Median plates 1 and 2 transversely divided into an anterior part and a posterior one; median plate 3 often fused caudally with the pseudosegmental plate, which is almost always undivided; terminal plate not facetted, with the usual two incisions.

The caudal margin of the pseudosegmental plate bears two lobes of variable appearance, so that the author distinguished three different "forms" which are:

-- form A (type): the two lobes are presented as triangular projections, paired, up to 6μ long and width as much at the bases, medially drawing near (Fig. 601, 1);
-- form B: the two triangular caudal processes of the pseudosegmental plate are reduced to two rounded lobes, barely projecting and separated medially by an incision, more or less deep (Fig. 601, 2);
-- form C: the lobe is single, median, very rounded, sometimes with margin slightly incised medially; this is the more common variety (Fig. 601, 3).

Legs long, sculptured at the bases; the first three pairs without papillae and spines; the fourth pair -- lacking dentate collar -- presents a strong basal spine (more robust than shown in Fig. 601, 1) at the position of the usual papilla; internal claws with strong spurs curved toward the base. There was seen an exuvium containing 2 spherical and yellowish eggs (diameter 45μ).

In material from Switzerland and U.S.A. (Wisconsin) Ramazzotti has observed individuals with very pointed papilla of the 4th pair of legs, however it does not reach the size and robustness of the spine present in *ramazzottii*; also the posterior margin of the pseudosegmental plate had a simple lobing, or double: the above cited author was not able to classify these individuals, as he thought at first they were *ramazzottii*, but which calls to mind also *P. scorteccii* (in which however exists two conical processes on the terminal plate, the papilla of the 4th pair of legs is

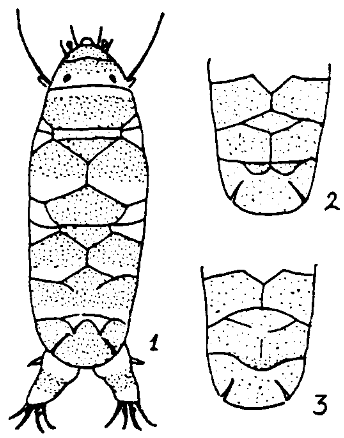


Fig. 601 - *P. ramazzottii* Maucci (from Maucci, redrawn and slightly modified).

rounded, and the frontal plate bears a "W" design). The author considered instead as *P. ramazzottii* (forms B and C) the examples collected in a moss on the SE slope of Focobon (Dolomites of San Martino of Castrozza) at about 2,700 m altitude, with strong spine on the legs of the 4th pair.

The species is known for Italy (Aurisina near Trieste and western Dolomites), Hungary, North and South America.

P. ramazzottii forma *facettalis* was described by Iharos (1964) in the following words: Length 160-185μ, red or orange color, eye spots present and black. The granulation of the plates is rather uniform and even the cuticle between them is finely granulated. Cephalic plate facetted; cephalic appendices as in *P. ramazzottii*. Posterior margin of the scapular plate often arched; pseudosegmental plate medially divided, or else undivided, in which the caudal margin appears more or less bilobed, by the presence of two wide pointed appendices. Terminal plate facetted. Median plates 1 and 2 transversely subdivided, median plate 3 undivided.

Legs long and finely granulated; lacking the dentate collar. At the bases of the legs of the 4th pair -- on their external sides -- exists a spine of medium length; on the internal side there is however a small papilla. Central claws with minuscule spurs turned basally. The red and oval eggs are deposited in the exuvium.

P. ramazzottii facettalis differs from the type principally by the facetting of the cephalic and terminal plates and by the presence of the small papilla on the internal side of the legs: this papilla does not exist in

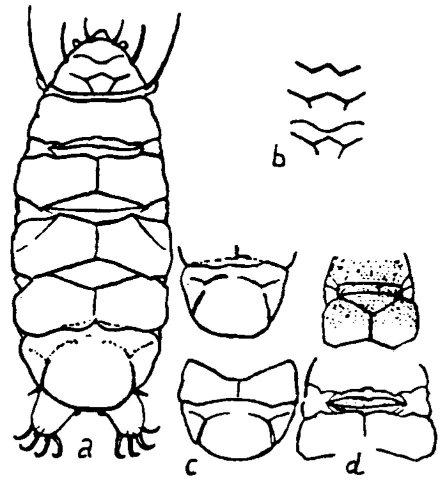


Fig. 602 - *P. ramazzottii* forma *facettalis* Iharos. a, dorsal view; b, different appearances of the cephalic plate; c, terminal plate in two different individuals; d, median plate 1 of *P. ramazzottii* (above) and of the variety *facettalis* (below) (from Iharos).

the individuals described by Maucci and which Ramazzotti has had the opportunity to examine.

The variety *facettalis* was collected at Sarkani-Tal (Alta region of Balaton, Hungary), in moss on dolomitic rock.

Having Ramazzotti (1962) apply to the Tardigrada the trinomial nomenclature, considering then *P. ramazzottii facettalis* as a subspecies, it is necessary to avoid the homonymy with *P. suillus facettalis* Petersen: therefore Maucci proposed (on suggestion from Iharos) the name *P. ramazzottii lineatus* (1973-74).

Recently however Maucci has found different examples of this variety on Carso Triestino and Yugoslavia, intermingled with a population of the type variety. It does not therefore seem justified to speak of subspecies, so it may be valid to return to the name *P. ramazzotti* forma *facettalis*.

PSEUDECHINISCUS RANEYI Grigarick, Mihelčič, and Schuster, 1964 (Fig. 603).

Length in general over 300μ, with a maximum observed of 390μ. Sculpture of polygonal appearance, regularly arranged; the polygons are rather larger near the anterior margin of the dorsal and intersegmental

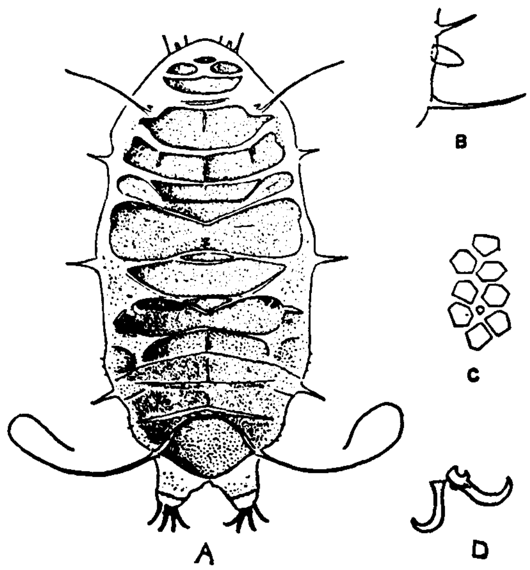


Fig. 603 - *P. raneyi* Grigarick, Mihelčič, and Schuster. A, dorsal view; B, cephalic appendices; C, detail of the sculpture; D, claws of the 4th pair of legs (from Grigarick, Mihelčič, and Schuster).

plates. Cuticle smooth between the plates and on the ventral surface. The cephalic and scapular plates appear subdivided by transverse and longitudinal bands devoid of sculpture, smooth.

Besides cirrus A (57μ) there exists laterally short spines B, C, D (15, 25, 25μ), and long filament E (175μ). In general B, C, D have about equal length, but sometimes the appendix C -- of one, or both sides -- may be as long as filament E. Lacking dorsal appendices, however the caudal and lateral margins of each plate bear numerous teeth of variable size. The measurements of the cephalic appendices -- of the type -- are: internal buccal cirrus 10μ; external buccal cirrus 25μ; cephalic papilla 9μ.

First pair of legs with small basal spine; fourth pair with the usual papilla and dentate collar (8-10 teeth); internal claws of all the legs with curved spurs.

The species was observed in various localities of California and Oregon (U.S.A.) in moss and especially in lichen (up to and above 2,600 meters altitude).

PSEUDECHINISCUS SCORTECCII Franceschi, 1952 (Fig. 604).

Length 148μ. The sculpture of the plates is a granulation, finer on the caudal region of the frontal plate (which bears a design of "W" shape), on the median plates 1 and 2 (undivided), on the median plate 3, and on the pseudosegmental (these last two fused together to form a single plate), as well as on the terminal IV. The sculpture exists also on the cuticle between the plates and is an extremely fine granulation. The caudal margin of the pseudosegmental plate is bilobed and the two rounded lobes are close together on the median longitudinal line of the animal. The terminal plate bears laterally two pointed conical processes. Cephalic appendices normal, lateral cirrus A 23μ long; besides minuscule conical lateral projections D, barely visible, there does not exist other lateral or dorsal appendices. The first pair of legs bear a small spine, the fourth pair the usual papilla; internal claws with spurs, externals smooth.

Concerning the individuals from Wisconsin (U.S.A.) and Sweden, which Ramazzotti has had occasion to examine and which presents some resemblance to *P. scorteccii*, see the description of *P. ramazzottii*.

A single example of *P. scorteccii* was initially collected in Italy (near Edolo, at about 700 meters altitude) in moss; later Weglarska found the

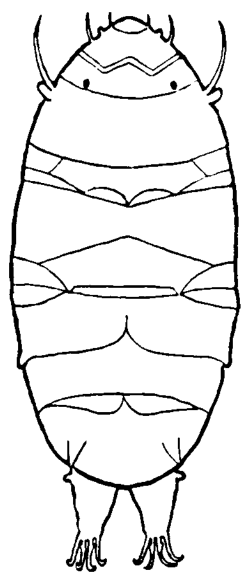


Fig. 604 - *P. scorteccii* Franceschi. Dorsal view (from Franceschi).

species in Viet Nam, in various localities and in extremely numerous examples, as well as exuvia containing 1 or 2 oval eggs (52 x 41μ); the animals measured 150-200μ and were of orange color.

PSEUDECHINISCUS SUILLUS (Ehrenberg, 1853) (Fig. 605).
= *Echiniscus suillus* Ehrenberg, 1953
= *Echiniscus mutabilis* Murray, 1905

Length up to 285μ, reddish, eye spots black; legs very long, with a punctated zone on the upper basal part. The sculpture of the plates and of the cuticle between them consists of a very fine and regular granulation, especially fine on the cephalic plate, on the scapular (I), and on the median plates (1, 2, 3), coarser on the others (sometimes only in the rostral zone) and especially visible on the terminal plate, which is not facetted and possesses the usual two notches. In general the pseudosegmental plate is undivided (unpaired), but there is sometimes a median longitudinal line, along which the granulation is interrupted; also the paired plates (II and III) may be divided longitudinally only by a smooth line, devoid of sculpture.

The posterior margin of the pseudosegmental plate is, normally, straight or else presents a simple sinuosity, barely hinted at.

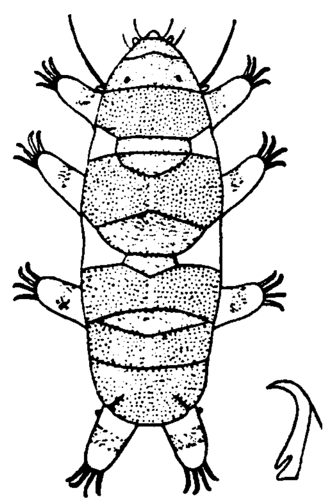


Fig. 605 - *P. suillus* (Ehrenberg). Dorsal view and internal claw of the 4th pair of legs.

The first pair of legs does not normally possess the spine, common in the genus *Echiniscus*: however there exists a variety (*papillatus* Rahm, 1932) in which the three pairs of legs present a basal spine. Fourth pair of legs with papilla, lacking dentate collar; internal claws with small curved spurs. No lateral or dorsal appendices, with exception of cirrus A and the cephalic appendices. Deposited in the exuvium are 1 to 5 oval eggs, yellowish or reddish, with the larger diameter of about 45μ; the larvae of two claws measure from 85 to 120μ and are often colorless.

Not uncommonly the delineation between two or more plates is incomplete, indistinct, or absolutely absent; Franceschi (1952) studied populations of *P. suillus*, collected in the upper Camonica Valley, containing type individuals -- with plates clearly delimited -- ranging to individuals with absolutely no delimitation between all the plates, through a long series of intermediate stages. The disappearance of the limits of the plates (which is verified also in other Echiniscidae) may perhaps be connected -- at least in some cases -- to the phenomenon of ecdysis and appears in an immediately successive stage, when the cuticle is still delicate and the sculpture barely evident.

It is certain that many citations of *P. suillus*, especially by the older authors, do not refer to this species, but to other close species. The diagnosis of *P. suillus* is interpreted in the terms cited above. In particular examples with more coarse sculpture, species of "pearled" appearance do not refer to *suillus*. Therefore it should not be treated as *P. suillus* if the cephalic or the terminal plate, or both, are facetted, if the pseudosegmental presents lobing or teeth, if there exists spines or lateral lobes, even in a single position.

For the distinction of *P. suillus* from other similar species, remember that:

- -- if there are small lateral conical projections and -- in general -- granulation of the plates more pronounced, treat as *P. conifer* or *P. pseudoconifer* (for the separation of these two species see the description of *pseudoconifer*);
- -- if the terminal plate is facetted, the species is *P. facettalis*;
- -- individuals with granulation much larger than usual, especially on the pseudosegmental and terminal (IV) plates, are *P. juanitae* or *P. facettalis*;
- -- individuals with strong lobing or bilobing of the pseudosegmental plate belong to *P. ramazzottii*, if exists a robust spine on the fourth pair of legs, and belong instead to *P. scortecci* if there is the usual papilla at the position of the spine and there are two lateral pointed conical processes on the terminal plate.

It is advisable to always observe with much care and patience the individuals having the general appearance of *P. suillus*, concentrating particular attention to all the species of the "*P. suillus* group."

P. suillus is a cosmopolitan species, known from extremely numerous localities in Europe (and very common also in Italy), in North and South America, Africa, Asia, Australia, New Zealand, Arctic, and Antarctic.

Typ. loc.: Mount Rosa (Alps).

PSEUDECHINISCUS TRANSSYLVANICUS Iharos, 1936 (Fig. 606).

Length up to 342μ, eyed. The sculpture is composed of small dots and is extended on the legs. All the plates of the genus *Pseudechiniscus* are present; the terminal plate possesses the usual two notches and is facetted (so writes the author, although this is not shown in the drawing). The rostral margins of the paired plates II and III bear a triangular point, which is much longer on the second paired plate (III) than on the first (II). The only lateral appendices, other than cirrus A with papilliform base, are the

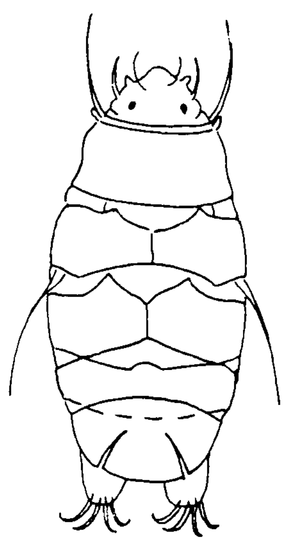


Fig. 606 - *P. transsylvanicus* Iharos (from Iharos, redrawn).

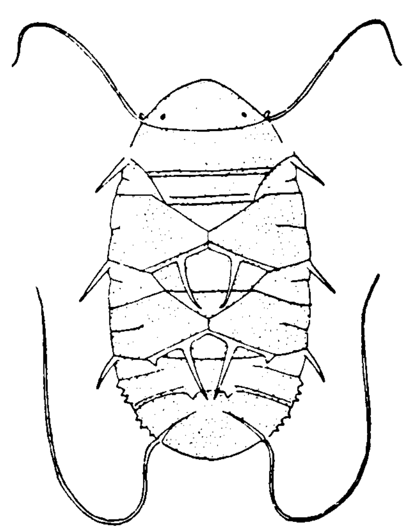
long filaments C. Legs of the fourth pair without dentate collar; claws (18μ) smooth: even the internals do not have spurs. Eggs unknown.

The species, easily recognizable by the triangular point at the anterior margin of the paired plates, is so far known only from the region of the Carpathians.

PSEUDECHINISCUS VICTOR (Ehrenberg, 1853) (Fig. 607).
= *P. tridentifer* Bartos, 1935

Length up to 310μ, color red, eye spots black. The sculpture of the plates is a fairly regular punctation, which is extended also on the cuticle between the plates, more finely punctated. The external buccal cirri is found generally on the ventral side of the head and has the shape of short curved spines; the lateral cirrus A is very long (about 160μ) and the clava is triangular: however external buccal cirri and clava may also be of the usual type. Median plates 1 and 2 divided transversely. The lateral appendices are composed of cirrus A, of curved or straight spines B, C, D, and of a long filament E (which perhaps may sometimes become a spine); also there often exists very minuscule thorns (teeth) on the flanks of the various plates, in variable numbers, and of which the larger are found at the sides of the pseudosegmental plate. Dorsally there are strong spines C^d and D^d, curved toward the median line of the body, a pair of dorsolateral triangular teeth D' and a pair of analogous teeth, positioned

Fig. 607 - *P. victor* (Ehrenberg) (from Marcus, redrawn).



at the caudal margin of the pseudosegmental plate, near the median line. Internal and external claws without spurs.

The fourth pair of legs, in addition to a rounded papilla near the base, bear also a robust straight spine and a dentate collar; however individuals collected by Ramazzotti in the Bognanco Alta Valley (and others collected by Petersen in Greenland) exhibit only two robust spines (teeth), about 10μ long, at the position of the dentate collar, spines which may be reduced to a single in the larvae of 2 claws and in the young. We have seen larvae of 2 claws of 132μ, which already have -- although shorter -- all the lateral and dorsal appendices. Deposited in the exuvium are 3-4 oval eggs.

The species is known from Italy (Bognanco Alta Valley, from 1,700 to 2,300 m altitude), the Alps (Mount Rosa at 3,500 m, typ. loc., Cervino at 3,800 m), Greenland, and various Arctic localities (Spitzbergen Archipelago, Axel Heiberg Island, Franz Josef Land, etc.) as well as for the U.S.A.

Dastych (1980) has indicated the identity of *P. tridentifer* with *P. victor*, and therefore the synonymy of the two species. From the examination of material in our possession (examples determined as *P. tridentifer* from Iceland, and examples of *P. victor* from Bognanco Valley, Axel Heiberg Island -- given by Weglarska -- and Oregon -- given by Schuster -- we can confirm such synonymy.

Genus *PSEUDOBIOTUS* Nelson, Schuster, Grigarick, and Christenberry, 1980.

Diagnosis: Hypsibidae; 30 small irregular buccal lamellae are present; rigid buccal tube with unequal dorsal and ventral crests; claws, in shape and size, of the *Isohypsibius* type.

Observations:

The genus is based on the species *Ps. augusti* and the authors report that to it goes assigned also the other species here reported (without however having been examined). We consider this systematics to be valid. However, more than the peribuccal lamellae, it seems that the characters which unite the four species are either the type of claw (having clearly the *Isohypsibius* type), that they exhibit special characters, or for their large size or for the very articulated method by which the principal branch is inserted on the basal plus secondary branch.

KEY TO THE SPECIES

1.	Two macroplacoids are present	*Pbs. megalonyx*
	Three macroplacoids are present	2
2.	The buccal tube is rather narrow (6.5% of the length); claws without accessory points	*Psb. matici*
	Buccal tube width 8-12% of the length; principal branch of the claws with accessory points	3
3.	The egg-bearing exuvium remains attached to the body of the female; buccal tube width 8-12% of the length; there is no cuticular bar in the legs	*Pbs. augusti*
	The egg-bearing exuvium is free; buccal tube wide (16% of the length; in 1st - 3rd legs, near the base of the claws, there is a cuticular bar	*Pbs. stephaniae*

PSEUDOBIOTUS AUGUSTI (Murray, 1907) (Fig. 608).

= *Macrobiotus augusti* Murray, 1907
= *Macrobiotus lacustris* Wenck, 1914
= *Hypsibius augusti* + *dujardini* (in part) Marcus, 1928
= *Isohypsibius megalonyx* + *augusti* Thulin, 1928
= *Hypsibius* (*I.*) *megalonyx* + *augusti* Marcus, 1936

Colorless, eye spots present, cuticle smooth, except for a papilla present in lateral position on the first three pairs of legs. Length up to 705μ. The buccal opening is provided with numerous (30 according to Schuster) slender lamellae. In the caudal part of the buccal cavity is noted (Pilato, 1974) either dorsally or ventrally a single row of triangular teeth, limited on each side by a tooth of larger size; following, either dorsally or ventrally, are three transverse crests. The appendices for the insertion of the stylet muscles are in the shape of crests and considerably developed. The buccal tube is of average width (width about 8-12% of the length).

Pharynx slightly elongated or almost spherical, with apophyses and three macroplacoids of rod shape, of which the second, which is always situated nearer to the first than the third, appearing sometimes slightly shorter, while the others have similar size. Microplacoid absent.

Legs slim, without cuticular bar or lunule. Claws *Isohypsibius* type, enormously developed, considerably flexible. The principal branch bears accessory points which reach the middle of the same branch. The common basal part is somewhat developed and moderately wide. The basal end is

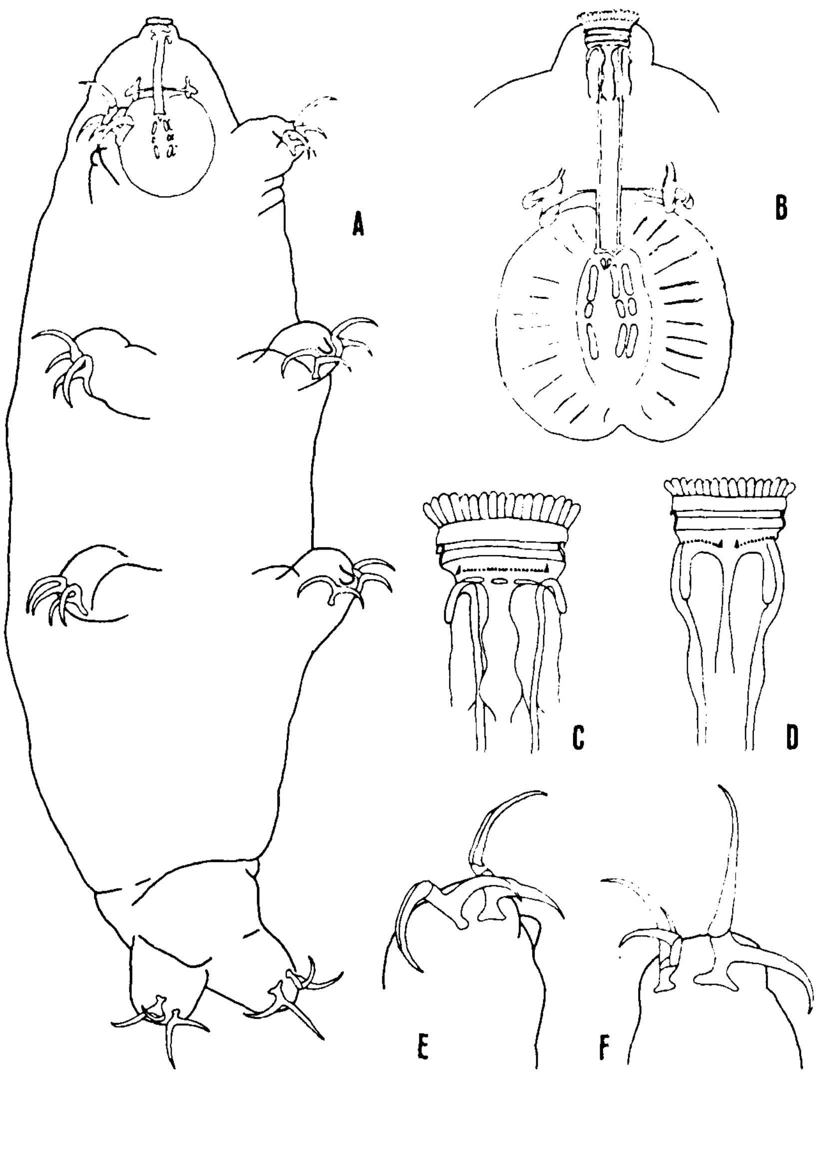


Fig. 608 - *Psb. augusti* (Murray). A, habitus; B, buccal apparatus; C, D, buccal armature in ventral and lateral view; E, doubleclaws of the 1st pair of legs; F, doubleclaws of the 4th pair of legs (from Bertolani).

slightly enlarged in the internal claw, much more in the external.

Eggs smooth, oval, deposited in the exuvium. The animal abandons the exuvium before depositing the eggs, and the exuvium remains then linked around the body, between the third and the fourth pair of legs. Examples have been observed with two successive egg-bearing exuvia attached.

This species, formerly placed in the genus *Macrobiotus*, then in *Hypsibius*, then in *Isohypsibius*, has been now placed in the new genus *Pseudobiotus* Schuster et al. The present description is based on the revision of the species carried out by R. Bertolani (1976).

The species is aquatic and also interstitial. It is probably cosmopolitan, however not all the localities indicated refer with certainty to *Psb. augusti*, giving it uncertain taxonomic existence. Typ. loc.: Franz Joseph Land.

PSEUDOBIOTUS MATICI (Pilato, 1971) (Figs. 609 and 610).
= *Isohypsibius matici* Pilato, 1971

Aquatic. Length 254-317μ. Colorless, cuticle smooth, eyes absent. Peribuccal lamellae present. Buccal tube rather narrow (6.5% of the length) with appendices of insertion of the stylet muscles in the shape of a crest. Pharynx oval, with apophyses, and three rod-shaped macroplacoids, rather short, of which the second is the shortest, and is very close to the first. Sometimes the macroplacoids may seem to be two, of which the very long first is deeply constricted.

Doubleclaws very large; the principal branch of the external claw is very long and is connected to the rest of the claw by means of a slender structure, thus sometimes seemingly separated from the rest of the claw. Microplacoid absent. Lacking the accessory points of the claws and also the lunules are absent.

The species was collected in interstitial environment in Sicily. Typ. loc.: Flascio River (Randazzo).

PSEUDOBIOTUS MEGALONYX (Thulin, 1928) (Fig. 611).
= *Isohypsibius megalonyx* Thulin, 1928
= *Hypsibius* (*Isohypsibius*) *augusti* (in part) Marcus, 1936 (not Murray, 1907)
= *Hypsibius* (*I.*) *augusti* (in part) Ramazzotti, 1962, 1972, and others

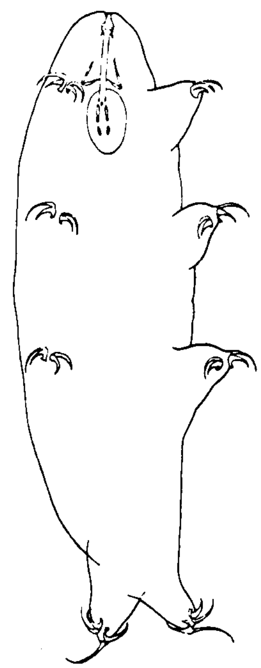


Fig. 609 - *Psb. matici* (Pilato) (from Pilato).

Length up to 830μ, colorless, eye spots present. Cuticle smooth, except for on the first three pair of legs, where exists laterally an obvious papilla. Mouth surrounded by numerous and slender lamellae. The buccal armature is composed of a dorsal and ventral band of teeth, arranged on more rows, followed by three dorsal crests and three ventral arranged transversely. Appendices of insertion of the stylet muscles of crest shape, well developed. The buccal tube is medium wide. Pharynx slightly oval or spherical, with well developed apophyses and two macroplacoids of slender rod shape; the second is always longer than the first (except in very young examples) and presents an angle which follows the internal cavity of the pharynx.

Legs very slender, without cuticular bar or lunule. *Isohypsibius* type claws extremely developed, similar to those of *Psb. augusti*. The common basal branch is longer than in *Psb. augusti*, and the basal end of the claw is less enlarged. In the males the secondary branch of the internal doubleclaws of the first pair of legs is more massive, strongly curved hook, and with two small spurs.

The females deposit from 6 to 34 smooth eggs in the exuvium. Also in this species, as in *Psb. augusti*, the exuvium remains attached to the female.

Fig. 610 - *Psb. matici* (Pilato). Buccal apparatus and claws of the 4th pair of legs (from Pilato).

Psb. megalonyx, described by Thulin (1928) as *Isohypsibius*, was later considered by Marcus (1936) as synonymous with *H.* (*I.*) *augusti*, from which it is distinguished only by the presence of eyes (which are instead absent in *H. augusti*). The unification of the two species was later accepted by various authors (including Ramazzotti, 1962 and 1972). Bertolani (1976) has studied again the two species and has detected constant morphological differences, and especially caryological (3n = 18 in *augusti*; 2n = 10, 3n = 15 in *megalonyx*), which justifies the distinct species.

Given the taxonomic confusion previously existing, it is not possible to know the geographic distribution of this species, which is however probably cosmopolitan.

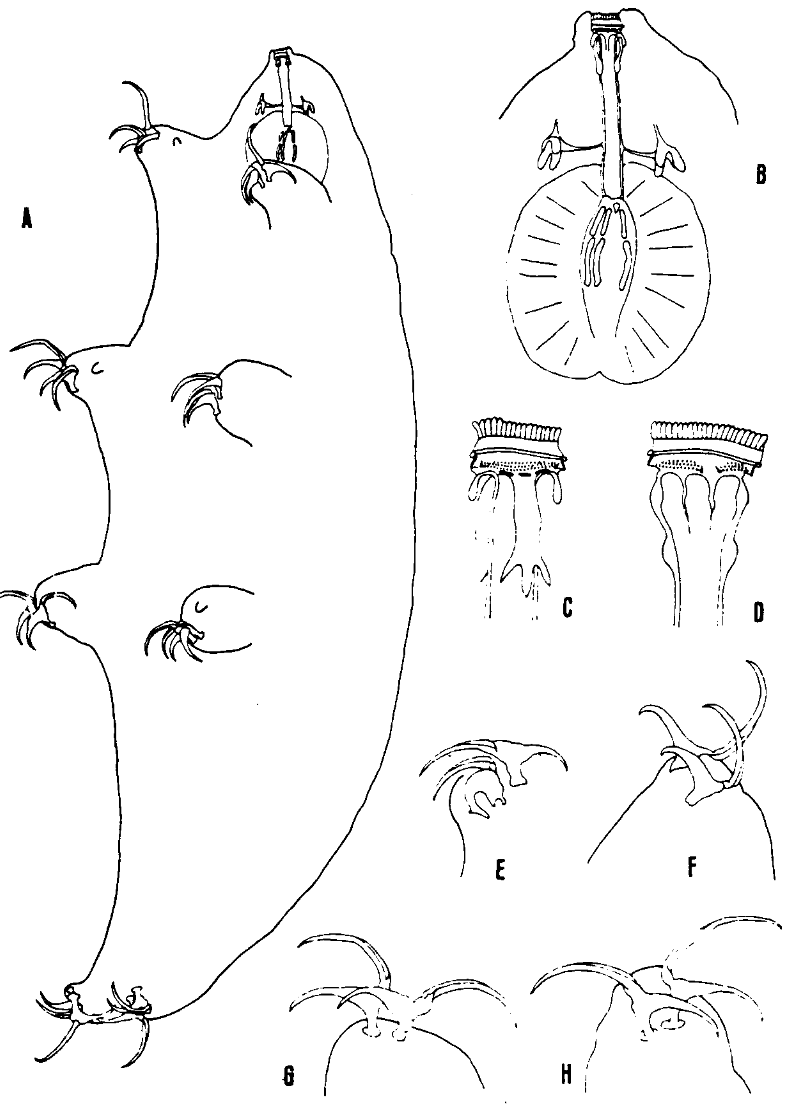


Fig. 611 - *Psb. megalonyx* (Thulin). A, habitus; B, buccal apparatus; C, D, buccal armature in ventral and lateral view; E, doubleclaws of the 1st pair of legs of the male; F, doubleclaws of the 4th pair of legs of the male; G, doubleclaws of the 2nd, and H, doubleclaws of the 4th pair of legs (from Bertolani).

PSEUDOBIOTUS STEPHANIAE (Pilato, 1974) (Fig. 612).
= *Isohypsibius stephaniae* Pilato, 1974

Length up to 640μ. Body slender, cuticle smooth, eyes absent. Mouth provided with lamellae. The buccal tube possesses appendices of insertion of the stylet muscles of crest shape, well developed. The buccal armature is composed of a wide band of teeth irregularly arranged in 3-5 rows, followed by a row of large teeth arranged in a transverse row. The buccal tube is rather wide (about 16% of the length). Pharynx short oval, with apophyses and three macroplacoids of short rod shape, of which the second is always shortest. Microplacoid absent.

Claws *Isohypsibius* type, of considerable size. The two claws of each leg are similar in shape and size. The common basal part is very long, with enlarged base, especially in the external claw; principal branch very slender with extremely slender accessory points. Lunules absent. On the first three pairs of legs, near to the base of the claws, exists a long cuticular thickening.

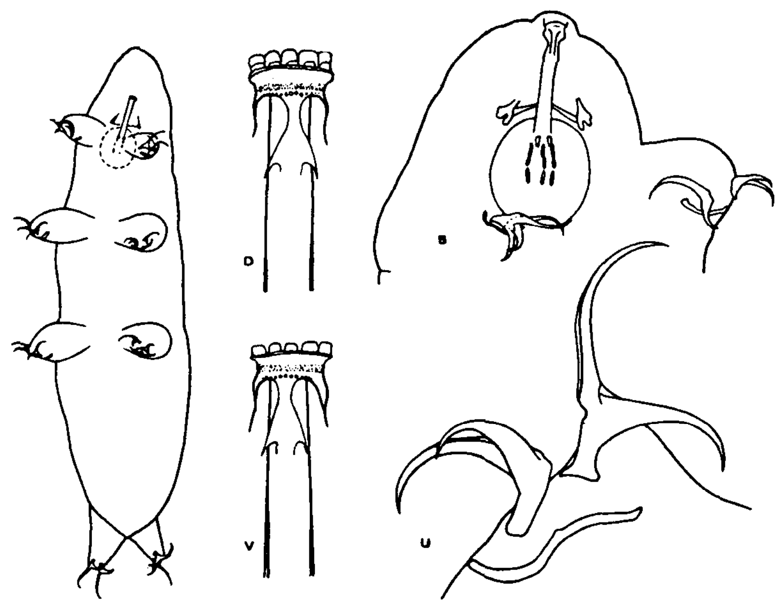


Fig. 612 - *Psb. stephaniae* (Pilato). D, V, buccal armature in dorsal and ventral view; B, cephalic end; U, claws of the 1st pair of legs (from Pilato).

Eggs smooth, deposited in the exuvium.

The species, aquatic, has been found in different localities of Sicily, and later, in interstitial environment, in Adige and in Oglio[1].

Genus *PSEUDODIPHASCON* Ramazzotti, 1964.

Diagnosis: Macrobiotidae; the reinforcement bar of the buccal tube is present; the buccal tube is long and flexible; sequence of the claws is 2112.

Observations:

The two species *Psd. inflexus* and *Psd. diphasconoide* are described in incomplete state, and some important characters are not mentioned. Not cited is the presence of the reinforcement bar (however in *Psd. diphasconoide* the design may be deduced by its absence), not cited is the spiral structure of the buccal tube. Therefore the genus ought to be provisionally accepted with reservation, as its diagnosis remains incomplete, and is not even certain that the three species really belong to the same genus: the only thing which they clearly have in common is the flexible structure of the long buccal tube.

KEY TO THE SPECIES

1. Two macroplacoids are present; lunule present 2
   Three macroplacoids present; lunule absent .... *Psd. bindae*

2. Microplacoid is present; on all the legs there is a large dentate lunule .... *Psd. inflexum*
   Microplacoid absent; the legs each bear a small smooth lunule .... *Psd. diphasconoide*

PSEUDODIPHASCON BINDAE Christenberry & Higgins, 1979 (Fig. 613)

Length 345μ; colorless, cuticle smooth, without pores, eye spots present. Buccal tube 72μ long and 4 wide.

[1]Presently this species has been inserted in the genus *Thulinia* Bertolani (see appendix).

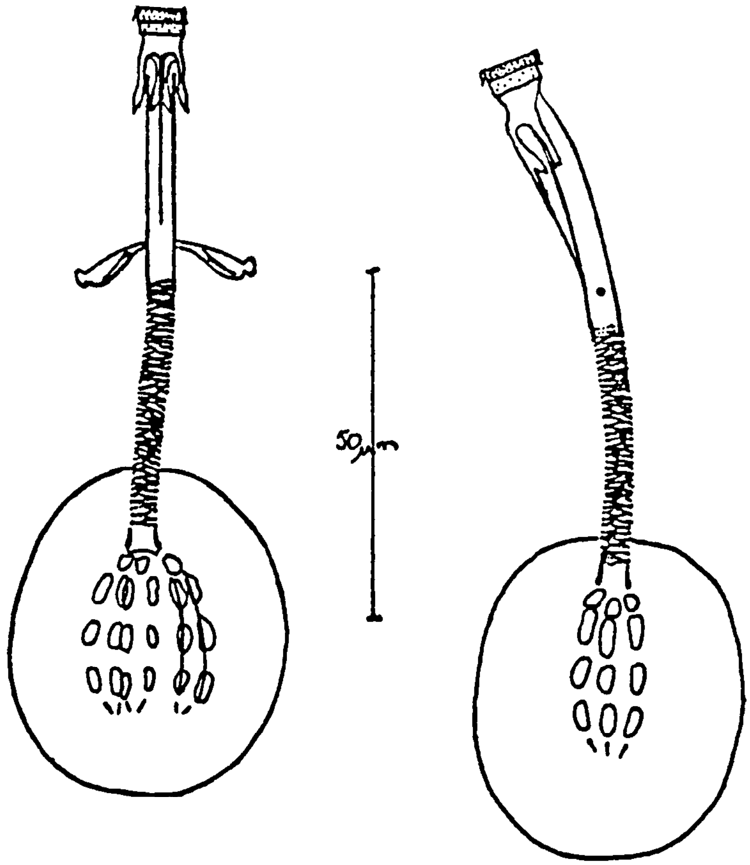


Fig. 613 - *Psd. bindae* Christenberry and Higgins. Buccal apparatus, ventral view and lateral view (from Christenberry and Higgins).

Mouth without lamellae. The buccal tube does not seem divided into a rigid part and a flexible part, at least not clearly, however in its first part (as far as the stylet supports), that is about 34μ, the wall of the tube is solid and smooth; immediately after appears a spiral structure (as in the genus *Diphascon*), at first very fine and close, then (as far as the opening of the pharynx) more scattered. Pharynx short oval, with apophyses and three macroplacoids of rod shape, with length decreasing from 1st to 3rd (the first is clearly longer, the second and third are almost equal); microplacoid present, elongated, slender.

The claws are small, somewhat thin, but not slender; the branches are united for more than half of their length; common branch stumpy, cylindrical, principal branch and secondary branch very divergent, almost equal; accessory points on the principal branch. Lunules absent.

Psd. bindae was collected in Alabama (U.S.A.).

PSEUDODIPHASCON DIPHASCONOIDE (Iharos, 1969) (Fig. 614).
= *Macrobiotus diphasconoides* Iharos, 1969

Length 220μ, colorless, eyes present or absent; cuticle smooth. The buccal tube is very narrow (1.5μ), long (24.5μ), and appears rather flexible. The author thinks that the species should be included in the genus (at that time considered subgenus) *Pseudodiphascon*. However the description does not cite a particular flexibility of the tube (of which is mentioned only the unusual length), nor a possible spiral structure; also, to judge from the drawing it seems to lack the reinforcement bar which also is not mentioned. Stylets slender and very curved, with very small furcae; the author states he was not able to see the stylet supports. Pharynx round, with two small round macroplacoids (apophyses are not mentioned), the first a little larger than the second.

Doubleclaws *hufelandi* type, with small and smooth claws.

On the whole it seems that the belonging of this species to the genus *Pseudodiphascon*, although fairly probable, is -- at the present state -- on the contrary not all that certain.

Psd. diphasconoide was observed in a scrap of mixed terrestrial moss, at Huong tich (Duc Khè, Huong-son) in Viet Nam.

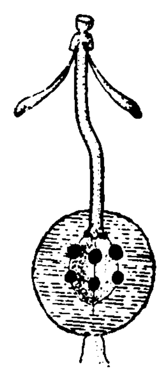


Fig. 614 - *Psd. diphasconoide* (Iharos). Buccal apparatus (from Iharos).

PSEUDODIPHASCON INFLEXUM (Arcidiacono, 1964) (Fig. 615).
= *Macrobiotus inflexus* Arcidiacono, 1964

Length 298-480μ, colorless, cuticle smooth, eye spots present. The buccal tube is flexible, rostrally undulating, describing a curve in its first half, and turns then at a right angle before entering the pharynx. The tube is very narrow (1.8-2.4μ); stylets very long. The author states that it was not possible to observe the furca of the stylet. Also not mentioned are the support bars, nor a possible spiral structure of the tube (Pilato, questioned by Maucci, has observed the type examples, but found them somewhat deteriorated, so that it was not possible to fill the above-mentioned gaps).

Pharynx short oval, with well developed apophyses almost in contact with the first macroplacoid. The macroplacoids are two, angular, wide, of almost trapezoidal shape; the first is longer than the second; microplacoid present, small.

Claws *hufelandi* type, with principal branch considerably longer than the secondary and furnished with accessory points. Large dentate lunules at the base of each doubleclaw, with 8-12 teeth.

Psd. inflexum (of which are so far known only two examples) has been collected in moss at Crasto Castle (Nebrodi Mountains, Sicily).

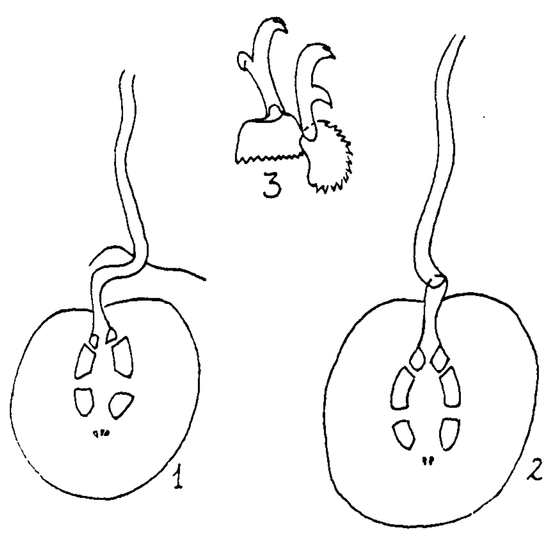


Fig. 615 - *Psd. inflexum* (Arcidiacono). 1, 2, buccal apparatus; 3, doubleclaws of the 2nd pair of legs (from Arcidiacono, redrawn).

Genus *PSEUDOSTYGARCTUS* McKirdy, Schmidt, McGinty-Bayly, 1976.

Diagnosis: Stygarctidae, with dorsal armor formed from a semicircular cephalic plate, three plates of the trunk, and a caudal plate, devoid of spinous processes; anterior clavae of semi-globular structure; legs end with three claws, each with dorsal spurs.

PSEUDOSTYGARCTUS TRIUNGULATUS McKirdy, Schmidt, McGinty-Bayly, 1976 (Figs. 616 and 617).

Length, from the anterior margin of the head to the caudal incisions, from 85 to 138μ, width of the head from 46.4 to 63.4μ. Median cirrus 8.4μ, internal cirri 9.8, external cirri 10.1, anterior clavae 10.1, posterior clavae 11, cirrus A 18 (these measurements refer to the average of the populations). The anterior clava is modified into a semi-globular structure; the cephalic cirri are slender, with a short basal enlarged section; the external cirri are inserted on rounded tubercles; the posterior clavae are elongated, with constricted base. Mouth subterminal, positioned on a retractile buccal cone. Pharynx subspherical. Eyes absent.

The cuticle is transparent and forms the plates characteristic of the Stygarctidae (cephalic plate, three plates of the trunk, caudal plate); the cephalic plate is semicircular, with slight lateral incisions which form five lobes. The internal cirri are inserted on the median lobe; the anterior clavae on the anterio-lateral lobes; the posterior clavae and the lateral cirri on the lateral lobes. The posterior margin of the cephalic plate bears small lateral processes, very short. The three distinct lobes of the trunk each bear two lateral processes with flexible spines. Between the plates exist thin cuticular thickenings. The caudal plate bears two long, flexible cirri E (38.5μ), with bases articulated on prominent tubercles. Dorsal to these tubercles, two pointed processes form the anterio-lateral angles of the caudal plate. There are no caudal spines, but the terminal plate has a median incision.

The legs are telescopic, the first three pairs of equal length, the 4th longer. Each leg bears three terminal claws, supplied with a dorsal accessory spine, very slender, and having an expanded base. There are no spines on the 1st-3rd legs, while the 4th pair bears a dorsal papilla, near the base.

Pss. triungulatus belongs to the interstitial fauna and was found at the Galapagos Islands.

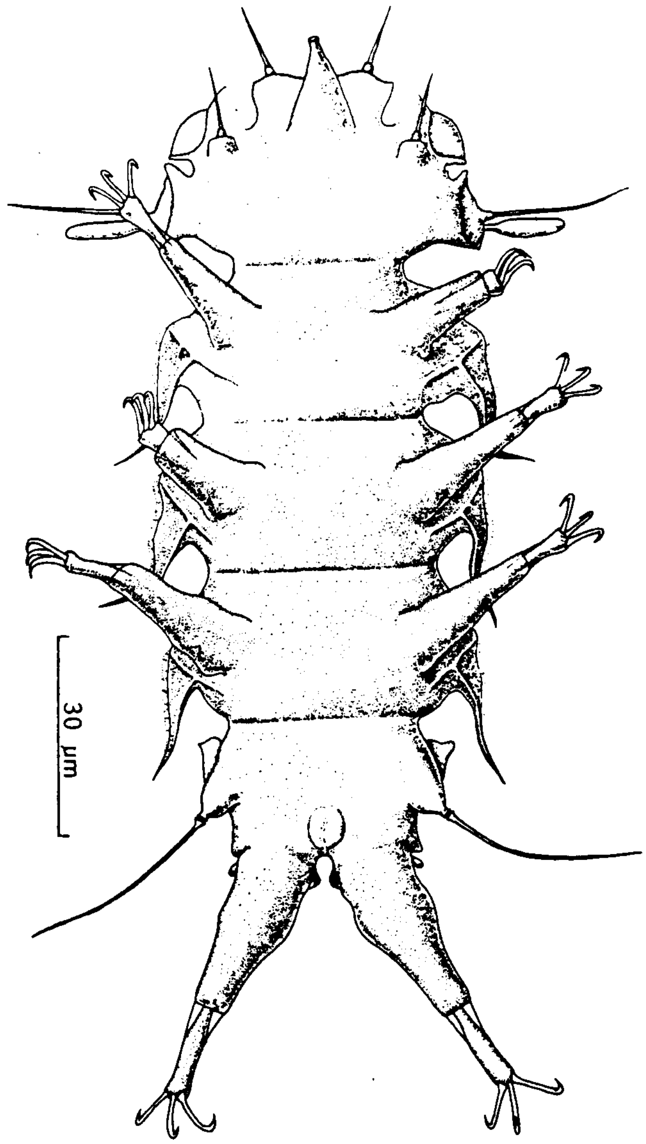


Fig. 616 - *Pss. triungulatus* McKirdy et al. Ventral view (from McKirdy, Schmidt, McGinty-Bayly).

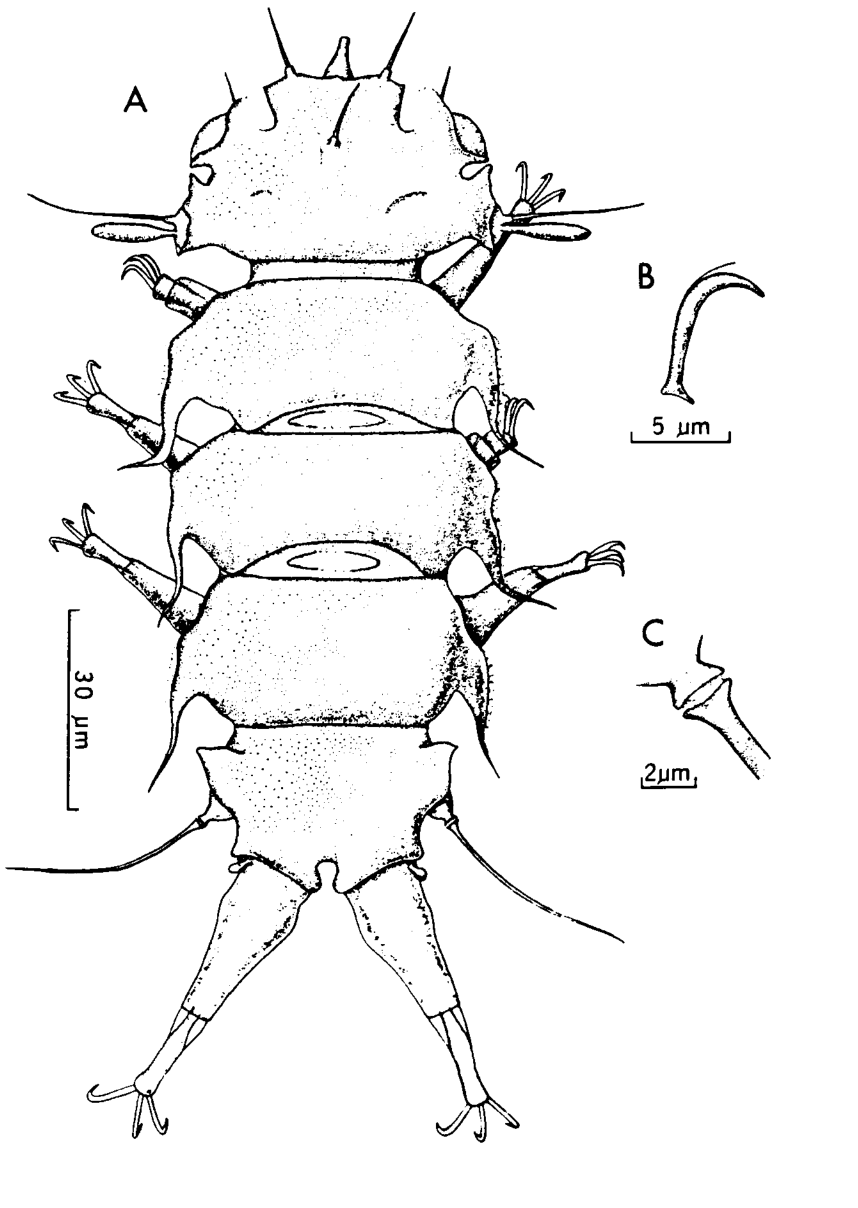


Fig. 617 - *Pss. triungulatus* McKirdy et al. A, dorsal view; B, claw; C, articulation of the cirri E (from McKirdy, Schmidt, McGinty-Bayly).

Genus *STYGARCTUS* Schulz, 1951.

Diagnosis: Stygarctidae; there are dorsal cuticular plates, and more precisely a cephalic plate, three dorsal unpaired plates, and a caudal plate; caudal spines are present; legs supplied with four claws, of which the internals bear a long filamentous appendix; anterior clavae elongated.

KEY TO THE SPECIES

1.	Dorsal spines present on plate II	*S. bradypus*
	Dorsal spines absent on plate II	2
2.	Clava straight	*S. granulatus*
	Clava bent	*S. abornatus*

STYGARCTUS ABORNATUS McKirdy, Schmidt, McGinty-Bayly, 1976 (Fig. 618).

Length (from the apex of the cephalic plate to the base of the caudal process) 97.5μ. The head is 36μ wide (at the bases of the lateral cirri). Median unpaired cirrus, 7.5μ; internal cirri, 11.5μ; external, 12.5μ; anterior clava, 13μ; posterior clava, 6μ; lateral cirri, 11.5μ. The anterior clavae and the external cirri arise from a ventral, rounded protuberance, flanked by the buccal cone. The anterior and posterior clavae are as those of *S. bradypus*. Mouth subterminal, positioned at the apex of a retractile buccal cone. Stylet supports absent, pharynx subspherical. Eyes absent.

The cuticle forms the plates typical of the genus. The cephalic plate, five-lobed, is equal to that of *S. bradypus*; the dorsal plate II, devoid of dorsal posterior spines, is a little smaller than plates I and III. The space between the plates presents localized cuticular thickenings. The plates of the body laterally present expansions with slender lateral margins; the posterior end of these expansions present a process sharper than the anterior margin, and consists of a vertical lamella, which reaches the dorsal surface of the plates. A similar lamella is found at the posterio-lateral margins of the cephalic plate. The caudal plate presents two lateral processes on each side: a small and pointed anterior, and a blunt posterior, somewhat membranous. Two prominent caudal processes are present, 14μ long, that is about half that of the 4th legs. Cirri E 17μ long (or more), arising from a tubercle near the anterior lateral process. All the plates are devoid of sculpture or ornamentation.

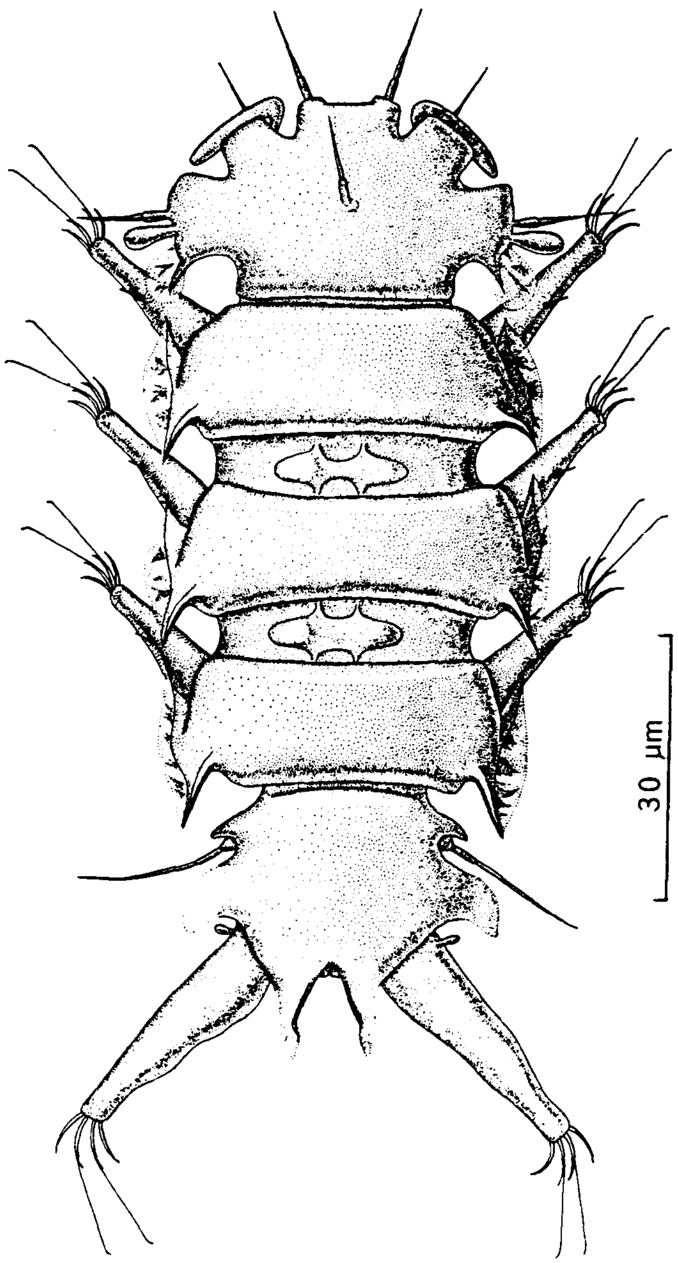


Fig. 618 - *S. abornatus* McKirdy et al. Dorsal view (from McKirdy, Schmidt, and McGinty-Bayly).

The first three pair of legs have about equal length, the 4th pair is longer. The legs are telescopic, ending with four claws, of which the internals present a long filamentous process. The 1st - 3rd legs possess a small spine, the 4th legs a papilla.

S. abornatus is closer to *S. bradypus* than to *S. granulatus*. It is distinguished from *S. bradypus* especially by the absence of the dorsal spines on plate II, and from *S. granulatus* especially by the absence of refringent granules on the cuticle.

S. abornatus is part of the coastal interstitial fauna, and has been found only at the Galapagos Islands.

STYGARCTUS BRADYPUS Schulz, 1951 (Fig. 619).

The size is small, 90-150μ in length, and the body appears clearly segmented into 5 parts: a cephalic region (plate) well delimited, three unpaired dorsal plates, which also encompass the body laterally as far as to cover the bases of the legs, and a terminal plate, not curved at the sides and without notch or incision. At first examination the appearance calls to mind the Echiniscidae, however the type of armor is fundamentally different and the plates do not have sculpture.

The cephalic appendices are: short median (unpaired) cirrus inserted perpendicularly, with it on thick base, in a hollow of the cephalic plate and considerably distant from the anterior margin of it; lateral cirrus (paired) and clava (unpaired), the latter visibly club-shaped, separate from the lateral cirrus, which arises from a thick base; internal, or medial, (paired) and external buccal cirri (paired), also with bases; cephalic papilla (paired) by the side of the buccal aperture, large, composed of a short basal part which continues, after a bend, with a terminal piece larger and longer, narrowly adherent to the external cephalic margin and turned laterally. These cephalic papillae, of unusual shape in tardigrades, gives the impression of palps and may easily escape -- by their position -- a hasty examination. The cephalic appendices are better seen observing the tardigrade frontally (Fig. 619, e, anterior part).

There exists then, at the posterior margin of the cephalic plate and of the three unpaired plates, appendices which -- observed dorsally -- have the appearance of teeth or hooks turned toward the caudal end: it consists of a refringent lamella, which continues as a lamella still more delicate and transparent, visible only with strong magnification and with the diaphragm very closed. From the posterior margin of the second unpaired dorsal plate, near the median line of the animal, departs two spines 23-25μ long,

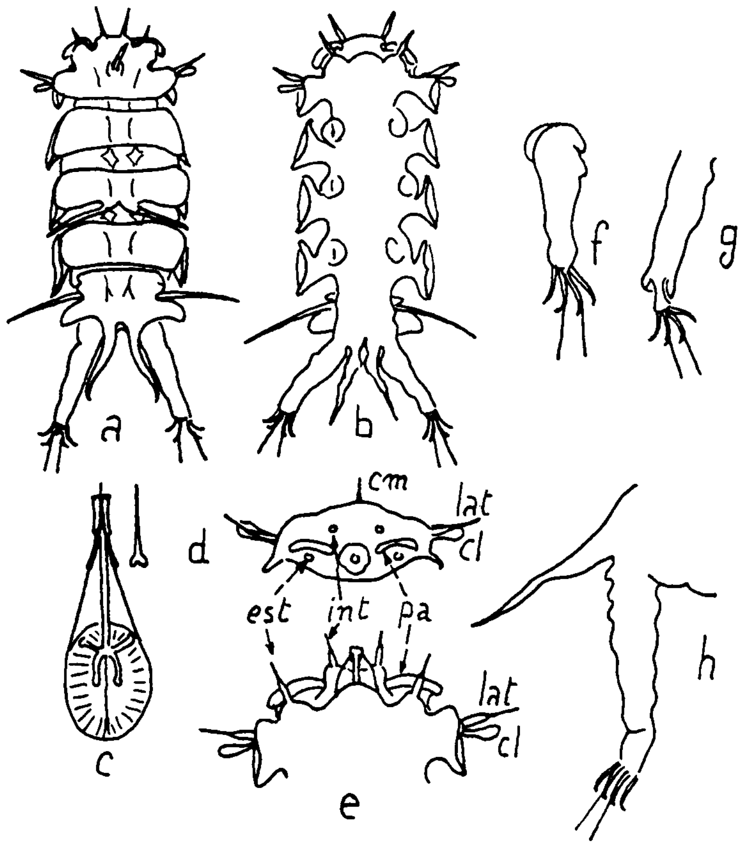


Fig. 619 - *S. bradypus* Schulz. a, dorsal view; b, ventral view; c, buccal apparatus and detail of the stylet; d, frontal view, and e, ventral view of the rostral end of the cephalic region (cl, clava; cm, median cirrus; est, external buccal cirrus; int, internal buccal cirrus; lat, lateral cirrus; pa, cephalic papilla); f, leg of the first pair; g, leg of the 4th pair, with distal end partially retracted; h, leg of the 4th pair and caudal spine, in lateral view (from Schulz, redrawn).

turned transversely toward the lateral margin, which they approximately reach. The terminal plate bears two caudal appendices, in the form of spines, whose length is almost equal to three-fourths of that of the legs of the 4th pair.

The buccal aperture is circular and subterminal, positioned on a buccal cone, which may be retracted or bent (Fig. 619, e): it continues with the buccal tube, about 40μ long, which enters for a short distance into the spherical or oval pharynx (diameter 8-10μ), forming then the pharyngeal bars (Fig. 619, c), whose structure, somewhat different than usual, may not be totally clear. The stylets are straight, or weakly curved, and it seems that the stylet supports are absent.

The legs have the median part telescopically retractile into the proximal and has distinct mobility in various directions: they may also be folded on the dorsum; the legs of the 4th pair are very long. Claws without spurs, straight for three-fourths of their length and only distally curved: on the two internal claws of all the legs exists a pliable bristle, at least as long as the entire claw and inserted on the claw, at the end of the straight part and at the beginning of the curvature; the author named this bristle "*Tasthaare*" [tactile hair], specifying however that it is not intended to refer to their function, of which we know nothing, but only use a convenient expression.

J. Renaud-Mornant and M. N. Anselme-Moizan (1969) in one of their interesting works -- to which one is referred for more details -- decided that there exists 3 larval stages of this species, the 1st of about 70μ length, the 2nd of about 80μ, the 3rd of 90μ. The adults (4th stage) measures from 95 to 110μ. The first two stages present only two claws (the central or internal, since provided with bristles).

S. bradypus belongs to the interstitial fauna of the marine littoral: it was collected in a hole 60 cm deep, hollowed out in the sand of a beach North of List (near Sylt - North Sea) and in the sand of the beach of Eyrac (Arcachon, Guascogna Gulf); in this last locality the maximum density of population (75 individuals in 75 cm^3 of sand) was observed at a depth of 20-30 cm; they were also observed later up to 120 individuals per 50 ml of sand (Renaud-Mornant and Anselme-Moizan, 1969). In the U.S.A. *bradypus* was collected on beaches of Virginia and Massachusetts.

STYGARCTUS GRANULATUS Pollock, 1970 (Figs. 620 and 621).

Length of the holotype 130.2μ, width of the head, 49μ. The cephalic appendices are: a median cirrus, internal buccal cirri 8.2μ, cephalic papillae (or anterior clavae) 7.2μ, external buccal cirri 11.4μ, lateral cirri A 14.7μ, clavae 6.5μ; the bases of all the cephalic cirri are enclosed in tiny cups. Mouth subterminal, on a retractile buccal cone; pharynx subspherical, buccal tube and stylets 27μ, stylet supports absent. Eyes absent.

Cuticle transparent and transformed into a series of dorso-lateral flat strips, with the appearance of dorsal and ventral unpaired plates (one around the head, three around the trunk, and one around the caudal part). There exists slender thickenings between the dorsal plates I and II, and between II and III. Dorsal plates thick, with small sparse refringent structures. The cephalic plate and those of the body are ventro-laterally

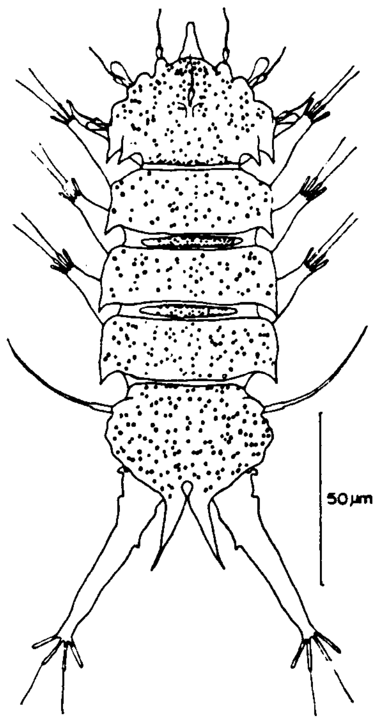


Fig. 620 - *S. granulatus* Pollock. Adult female, dorsal view (from Pollock).

enlarged and form sharp posterior processes in the lateral angles of these plates. Only on the cephalic plate there is a second series of sharp processes, positioned on the posterior margin. The caudal plate has two long and pointed terminal processes of 16.3μ. There exists two long lateral spines (30.4μ), with enlarged bases -- annulated in some examples -- of about 3.9μ inserted on the tubercles near the anterior end of the caudal section of the body.

The first three pair of legs are inserted in round spaces, positioned in the anterior angles of the ventral plates I-III; these legs have equal length (about 25μ); the 4th pair of legs is inserted latero-terminally in space positioned at the posterior angle of the ventral caudal plate; this 4th pair is longer (39.2μ). The simple, terminal claws are four on all the legs, with basal connections; legs not digitated. Each one of the two median claws of each leg with a filamentous process departing along the dorsal surface of the claw, then slightly diverging, with an expansion of 13μ beyond the end of the claw. Claws of the 4th pair of legs 10μ long, those of the other three pair 6.5μ. On the 4th pair of legs there is a small lateral

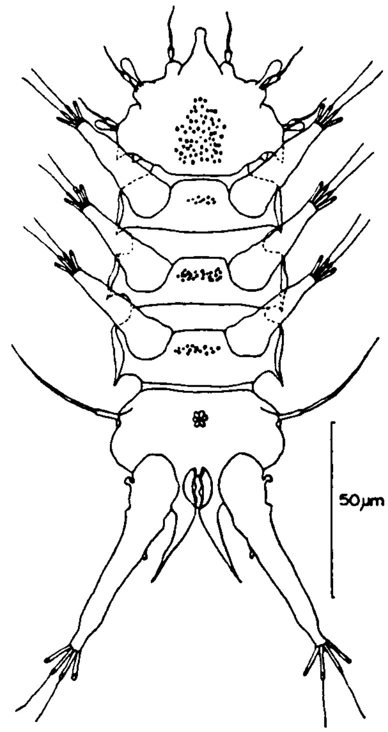


Fig. 621 - *S. granulatus* Pollock. Adult female, ventral view (from Pollock).

papilla, near the junction of the body.

The species was collected in marine sand, at a depth of 20-40 cm on the coasts of Massachusetts and North Carolina (U.S.A.).

Genus *STYRACONYX* Thulin, 1942.

Diagnosis: Halechiniscidae with digits terminating with claws with two spurs; median cirrus short and slender; clavae present.

KEY TO THE SPECIES

1.	Eyes present	2
	Eyes absent	3
2.	Cirri A medium long (13µ)	*Styr. paulae*
	Cirri A long (42µ)	*Styr. hallasi*

3. Cirri A short (7-10μ) .... *Styr. haploceros*
   Cirri A long (about 30μ) .... *Styr. sargassi*

STRYACONYX HALLASI Kristensen, 1977 (Figs. 622, 623).

Length 139.5μ in the male holotype and 150-151, the female. The head is delimited by a constriction behind the clavae. Mouth subterminal, pharynx oval. Eye spots present (visible in the live animal, decompose after treatment with polyvinyl lactophenol). The cephalic appendices are composed of a base followed by a flagellum. Median cirrus short and situated very dorsal (7.5μ), internal buccal cirri 15μ, external buccal cirri 12, clavae 5μ; the cirrus A is rather long (42μ). The cirrus E possesses a bell-shaped base and is 45μ long. The legs consist of four parts: coxa, femur, tibia, and tarsus. The coxal spines, present on the first three pairs of legs, increase in length from 1st to 3rd; on the 4th pair exists an oval papilla, without spine. The digits of each leg are of unequal length, with internal digits longer than external; the internal digits possess at their base a heart-shaped adhesive structure. The claws are retractile into a membranous sheath.

Styr. hallasi has been found in "hot" springs near to the coast line on Disko Island (western Greenland), and appears therefore to be the only species of the genus to live in fresh water.

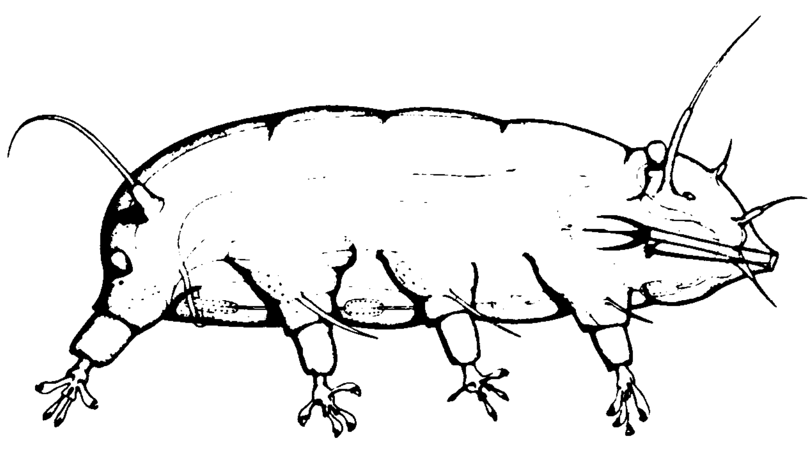


Fig. 622 - *Styr. hallasi* Kristensen. Male, lateral view (from Kristensen).

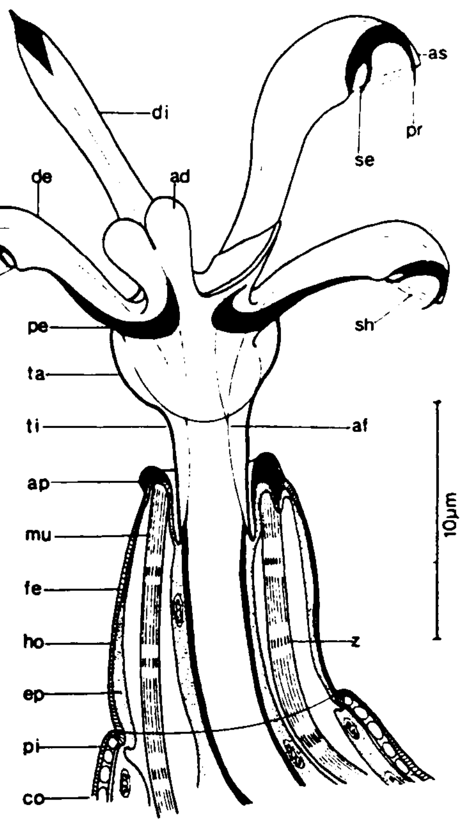


Fig. 623 - *Styr. hallasi* Kristensen. Leg of the 3rd pair, ventral view (from Kristensen).

STYRACONYX HAPLOCEROS Thulin, 1942 (Figs. 624, 625).

Length up to 155μ, maximum width of the body (dorsal view) in correspondence with the 2nd and 3rd pairs of legs and equal to about 30% of the length. The cuticle is very finely punctated and the individual "dots" -- separated by about 0.75μ -- are arranged in regular rows, which are crossed between them; in optical section the dots have the appearance of "pores". Eyes absent.

The cephalic appendices are: median cirrus (unpaired), short and slender, lacking base, situated in dorsal position and somewhat posterior to the anterior cephalic margin; internal medial cirrus (unpaired), and external (paired), also without base, similar to the median cirrus; lateral cirrus A (paired), with enlarged base and having size a little longer than the other cephalic appendices.

The clavae are given as absent in the original description, however Kristensen (1977) doing a re-examination of the type material, established the presence. Also cirrus E, given as absent, is present, at least in some examples.

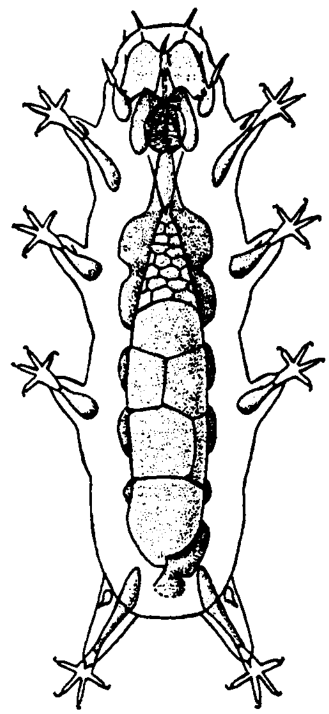


Fig. 624 - *Styr. haploceros* Thulin (from Thulin).

The legs -- ventrolateral -- are slender, rather long and composed, as usual, of a wider basal part, in which may be retracted the terminal portion, which is somewhat enlarged distally and which bears 4 fingers (digits), provided with claws. The claws are characteristic and are prolonged at their base to form a slender stalk, which runs along the digit, reaching the maximum at the base of the digit in the two internal digits, exceeding in the two external digits (Fig. 625). Each claw possesses three points: a distal (accessory point); a central, more robust and developed than the others (principal point); and a basal curve (basal spur). In the proximal region of all legs exists a lateral bristle, which diminishes in length and thickness from 1st to 3rd pair of legs; on the 4th pair of legs there is instead -- rather than the bristle -- an appendix composed of a wide and flat basal part, which is abruptly reduced at the end into a short conical projection; the 4th pair of legs also bear -- at the border with the terminal portion -- a small dorsal conical papilla (distal papilla of Thulin).

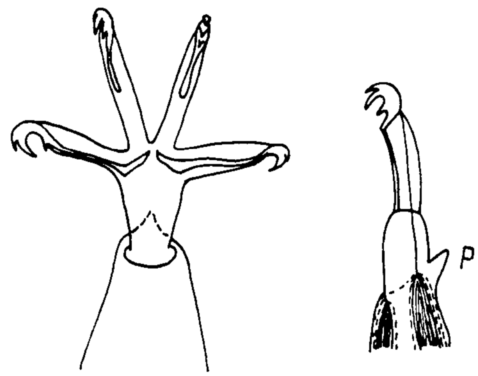


Fig. 625 - *Styr. haploceros* Thulin. Distal end of the 4th leg, ventral view; p, papilla (from Thulin).

The buccal aperture is small and surrounded by a short buccal ring; from it follows a straight and narrow buccal tube (about 1μ diameter) and an oval pharynx, whose length (about $11\text{-}12\mu$) is a little greater (10-20%) than the length of the buccal tube. In the drawing (Fig. 624) is shown -- posterior to the pharynx -- the short esophagus and the intestine with lateral lobes, terminating in a short rectum and the anus; the dorsal ovary also is seen, prolonged into a short oviduct, which opens in a ventral genital papilla, anterior to the anus.

The eggs are unknown. Individuals were seen of 2 claws, $86\text{-}88\mu$ long, while those of 95μ already possessed 4 claws.

The species was observed -- together with *Ec. sigismundi* -- on the Breton coast of France (Saint Malo), in a lichen (*Lichina pygmaea*) containing an alga (*Catenella opuntia*): the lichen was collected on a rock, at an altitude greater than that reached by high tide, and it is then probable that *Styraconyx halploceros* may endure short periods of desiccation, similar to *Echiniscoides sigismundi*.

STYRACONYX PAULAE Robotti, 1971 (Fig. 625, part 2).

Length 105μ; eyes present, color reddish-brown; cuticle with extremely fine granulation and wrinkled in optical section. Buccal aperture ventral, with external diameter of 6μ; buccal tube straight, 10μ long, and narrow (1μ); stylet supports present, pharynx oval and long. Median cirrus in the shape of a bristle (6μ); also the buccal cirri are bristles (internals and externals, both 9μ long). Clava of 9μ, curved conical shape, bearing close to the apex a roundish outgrowth; lateral cirrus A of 13μ; all these appendices do not have basal enlargement.

The first three pair of legs with dorsal spine, 4th pair with long caudal spine (18μ), arising from a base, and blunt conical papilla with short bristle. Legs telescopic, with four digits and claws with two spurs.

Of *Styr. paulae* has been found a single example, on the madreporite of *Coenocyathus dohrni* Död., on the coast of Stromboli Island (Eolie), at a depth of 2 meters.

STYRACONYX SARGASSI Thulin, 1942 (Figs. 625, part 2, 626, and 627).
= *Bathyechiniscus tetronyx* Marcus, 1936, in part (not Steiner, 1926)

Length up to 150μ, width 43μ; eyes absent and -- according to Thulin -- cuticle smooth. However Renaud-Mornant (1967) noted that the cuticle of an egg-bearing female, collected in New Caledonia, was entirely punctated (about 15 dots per 10μ). The buccal aperture is positioned on a conical cuticular projection and is turned ventrally. Buccal tube straight, stylet supports present, pharynx almost spherical with pharyngeal bars. The median cirrus is a long bristle and the internal and external medial cirri are also bristles: the latter (8μ) are inserted dorsally and somewhat back with respect to the rostral cephalic margin. The clava (12μ) is subdivided into two parts: a distal, shorter, and a longer, proximal (see Fig. 626); lateral cirrus twice as long as the clava (30μ). As is characteristic for the genus *Styraconyx*, the cephalic appendices do not have bases and also the clava and the lateral cirri are separate as far as the base, that is, not arising from a common base; but Renaud-Mornant (1967) observed in an example from New Caledonia (female) in which clava and cirri A arose from a small common lateral base.

The first three pairs of legs bear dorsally a rather long spine; at the base of the 4th pair of legs -- where inserted on the body -- exists on each side a long spine arising from a base, while more caudally -- on the same

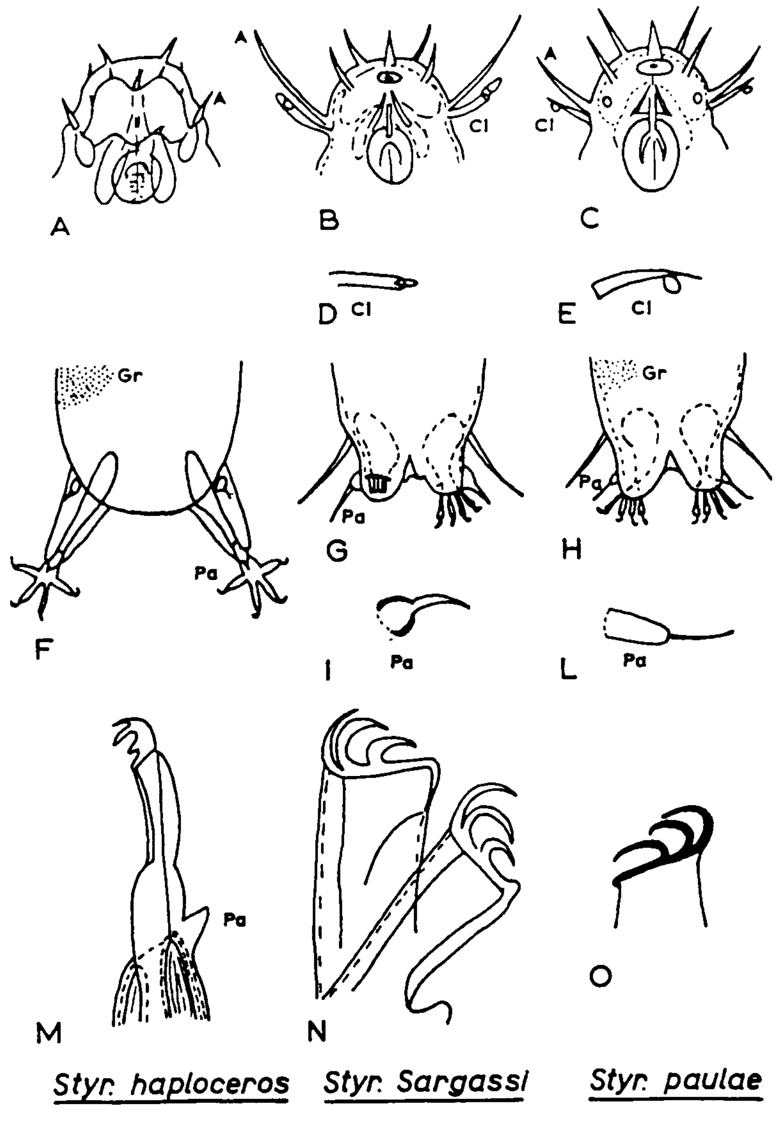


Fig. 625, part 2 - *Styr. haploceros*: A, cephalic end; F, caudal end; M, digit. *Styr. sargassi*: B, cephalic end; D, clava; G, caudal end; I, papilla; N, digit; *Styr. paulae*: C, cephalic end; E, clava; H, caudal end; L, papilla; O, claw. A, lateral cirrus A; cl, clava; Gr, granulation; Pa, papilla. (A, F, M, B, D, G, I, N, from Ramazzotti, 1962, redrawn).

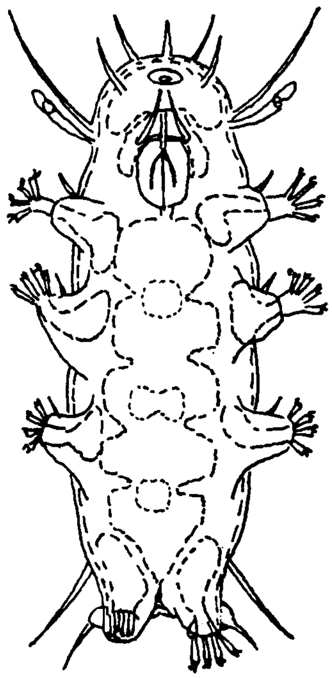


Fig. 626 - *Styr. sargassi* Thulin (from Marcus, redrawn).

leg -- there is a bulbous papilla, almost spherical, which ends in a slender point. The legs are composed of a wider proximal part and a more slender distal, telescopically retractile into the proximal part and which ends with the 4 digits, supplied with claws with two spurs (Fig.. 627). Eggs unknown.

The species -- erroneously united by Marcus (1936) with *Bathyechiniscus tetronyx*, as observed by Thulin (1942) -- was collected in the Sargassum Sea at 43° 4' north latitude and 31° west longitude, on *Sargassum*, as well as in the Gulf of Mexico, on the coast of Texas, on that of

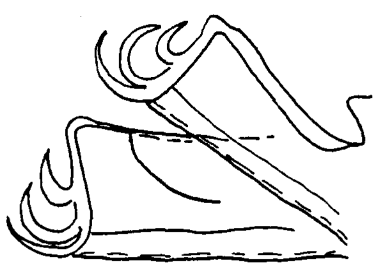


Fig. 627 - *Styr. sargassi* Thulin. Detail of two digits claws (from du Bois-Reymond Marcus, redrawn).

California, on the Atlantic and Mediterranean coasts of Spain, and in the port of Pollensa (Majorca Island), on the coast of New Caledonia, in Polynesia, and on the coast of Madagascar.

Genus *TANARCTUS* Renaud-Debyser, 1959.

Diagnosis: Halechiniscidae with median cirrus present; clavae much longer than lateral cirri A; on the 4th pair of legs, two caudal lobes terminating with extremely long bristles variously adapted; legs telescopic, digitated, with claws.

KEY TO THE SPECIES

(from Renaud-Mornant, 1980, modified)

1. Secondary clavae present 2
   Secondary clavae absent 3

2. The primary clavae are shorter than the total length of the body; the caudal bristles are less than twice the length of the body . . . . *Tan. ramazzottii*
   The primary clavae are longer than the length of the body; the caudal bristles surpass twice the length of the body . . . . *Tan. tauricus*

3. The caudal bristles are simple, not branched, or with only a small proximal spur 4
   The caudal bristles are branched 5

4. The legs bear four subequal digits . . . . *Tan. gracilis*
   The legs bear two digits, flanked by two small cuticular outgrowths . . . . *Tan. heterodactylus*

5. The caudal bristles bear expanded membranous, wing-shaped branches . . . . *Tan. velatus*
   The branches of the bristles have spine shape 6

6. The branches consist of spines secondarily branched . . . . *Tan. arborspinosus*
   The branches consist of strong secondary and tertiary spines . . . . *Tan. dendriticus*

TANARCTUS ARBORSPINOSUS Lindgren, 1971 (Fig. 628).

Length up to 88μ, small, delicate, and flattened. The cephalic cirri and the caudal spines are very developed.

There exists the dorsal median cirrus, directed forward; the internal cephalic cirri are 24-25μ long, the externals are inserted ventral to the cephalic papilla, and are 16-18μ long; lateral cirri and clavae are inserted on a common base. In the original description of this species, as well as of *Tan. tauricus*, it was described as the clavae being short appendices, while those considerably longer were considered as cirri A. Lindgren however, in the description of this species, has advanced the hypothesis that in reality the long appendices are the clavae, and those short, slender, and pointed are in reality the cirri A. This hypothesis was later adopted by other authors, and applied to the descriptions of later species. Nevertheless, more consideration verified that in *Tan. arborspinosus* the cirri A are 8μ long, while the clavae, somewhat flattened, supplied with short bristles, are 205-220μ long.

There exists a short cirrus E (13-17μ) between the 3rd and 4th pairs of legs. The conspicuous posterolateral spines are composed of a principal branch, which reaches 195-210μ, from which branches three (sometimes two or four) secondary branches as well as numerous much shorter branches. The cuticle is transparent, with small uniformly distributed pores. The mouth is ventral.

The legs are telescopic and the first three pair bear a short spine. The digits, with claws, are four per leg, and arise from a bulbous base; the internal digits are longer than the externals.

Tan. arborspinosus belongs to the interstitial fauna and was collected on a beach of North Carolina.

TANARCTUS DENDRITICUS Renaud-Mornant, 1980 (Fig. 630).

Length from 67 to 78μ, width from 30 to 40. The bases of the 1st, 2nd, and 3rd legs are in contact with each other, giving the animal a stellate appearance. The cuticle has small, lateral rods higher than 1μ, in numbers of 20 per 10μ. The head has trapezoidal shape, clearly delimited from the trunk. The cephalic cirri arise from bases 4-5μ high, are very wide at the base and attenuated distally. Unpaired median cirrus, 9μ; internal median cirri (whose bases are connected by a transparent membrane), 20μ; external median cirri, 12μ. The lateral cephalic lobes are slightly prominent, but present a lateral fold forming an outgrowth;

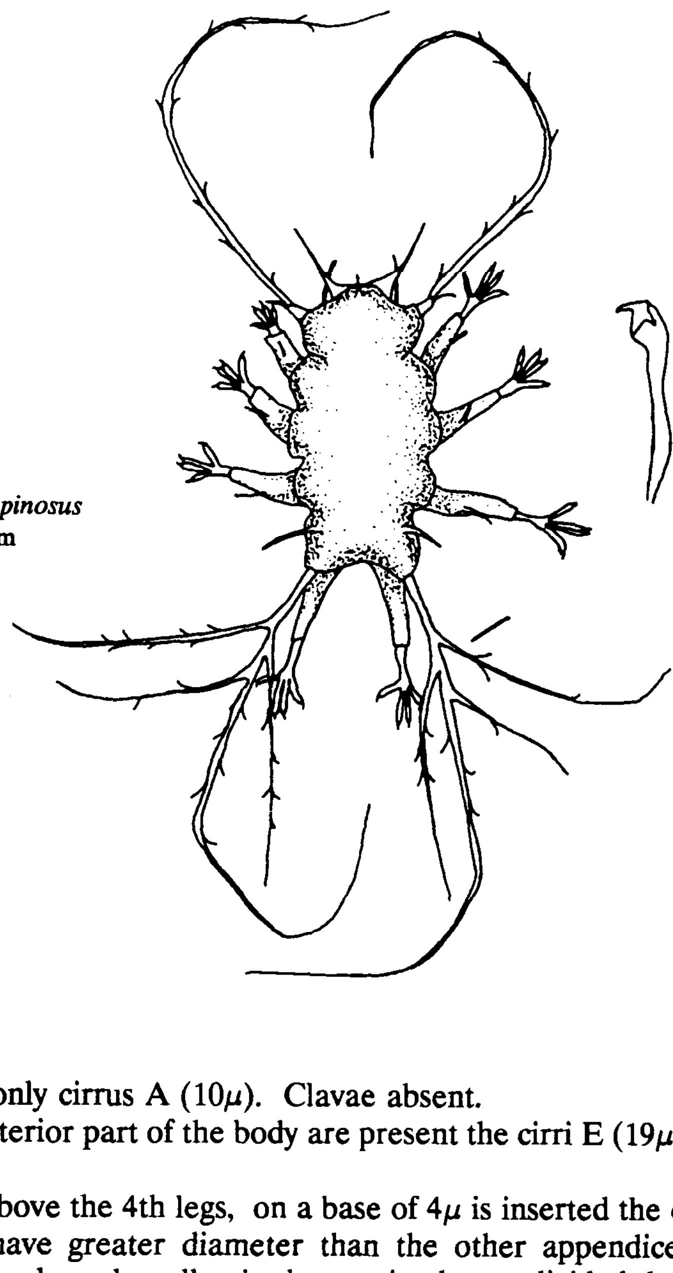


Fig. 628 - *Tan. arborspinosus* Lingren (from Pollock).

these lobes bear only cirrus A (10μ). Clavae absent.

On the posterior part of the body are present the cirri E (19μ), with enlarged bases.

Dorsally, above the 4th legs, on a base of 4μ is inserted the caudal bristles. These have greater diameter than the other appendices and measure 105μ: simple and swollen in the proximal part, divided then into four secondary branches, of which the proximal is branched further into strong tertiary branches.

The legs are conformed according to the general plan for the genus. The internal digits (10μ long) are on a common base, the external digits are 7-8μ long. The claws, sickle-shaped, bear one external spur.

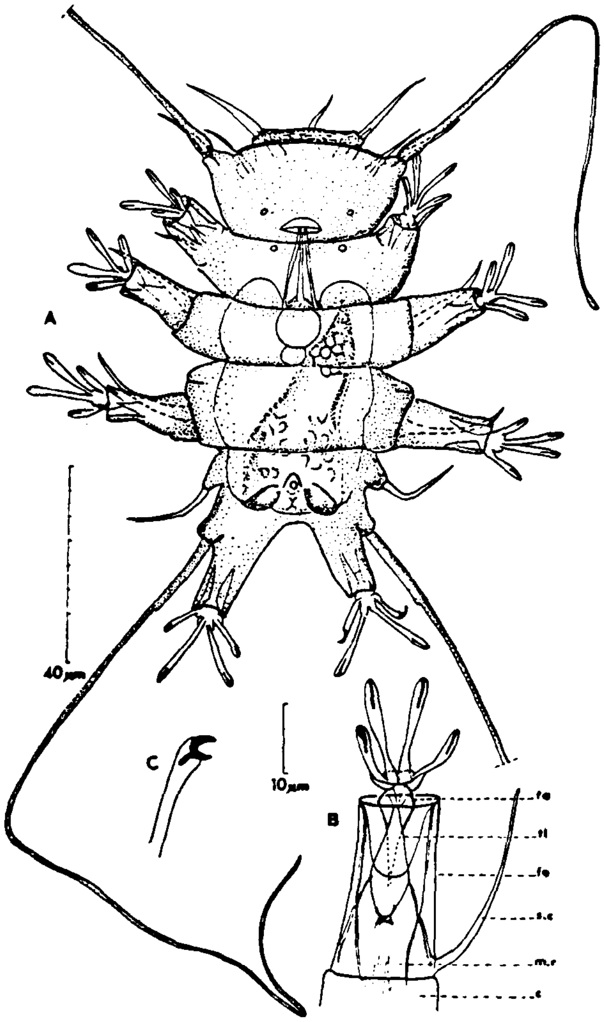


Fig. 629 - *Tan. gracilis* Renaud-Mornant, ventral view. B, retracted leg; C, claw of a median digit (from Renaud-Mornant).

Tan. dendriticus was found in sand, in the Atlantic Ocean, off the coast of North Carolina (U.S.A.) at 4,000 meters depth.

TANARCTUS GRACILIS Renaud-Mornant, 1980 (Fig. 629).

Body oval, 80μ long (excluding the 4th legs), and 40 wide. The head is trapezoidal, with lateral border posteriorly curved; the anterior part of the head is formed from a cuticular membrane, which unites the bases of the internal median cirri. The unpaired median cirrus is 11μ long; the internal median cirri, distally pointed, has enlarged bases, and are 19μ long. Ventrally is found the external median cirri, positioned on a base followed by a constriction; they are 12μ long. The cirri A are dorsal and have size equal to the external median cirri. The clavae, situated on the poorly developed cephalic lobes, are ventral and bear a refringent organ at the base: length 110μ.

The ventral mouth forms a transverse cleft.

Dorsally the cuticle is very finely punctated, while ventrally the body is roughly subdivided by folds at the level of the insertion of the legs. On the posterior part of the body exists cirri E (28μ) inserted on lateral rounded prominences. On the 4th legs is found the long caudal non-branched bristles (220μ).

The telescopic legs consist of a coxal part (with distal filament), a femoral part, and a retractile tibial part. The legs bear four digits of which the internals measure 15μ, the externals 8-9μ; the claws, sickle-shaped, have one external spur.

Tan. gracilis was found (one male and one female) on the coast of North Carolina (U.S.A.) at the depth of 400 meters.

TANARCTUS HETERODACTYLUS Renaud-Mornant, 1980 (Fig. 631).

Length as much as 135μ, width 60μ, oval shape, slender. The cuticle is strongly punctated on the dorsal surface.

The head is trapezoidal, clearly separated from the trunk with a lateral constriction. The cephalic cirri depart from thick bases: unpaired median cirrus, 9μ; internal median cirri (25μ) are united to each other by a translucent membrane; external median cirri, 23μ. The lateral cephalic lobes are poorly developed and bear the cirri A (15μ) and the clavae (155μ), swollen at the bases. The mouth is a transverse fissure, situated ventrally.

The trunk does not bear lateral constrictions. On the posterior part, the cirri E measure 25μ. The caudal bristles, swollen on the proximal part, are not branched and bear a small basal spur: their length is 150μ.

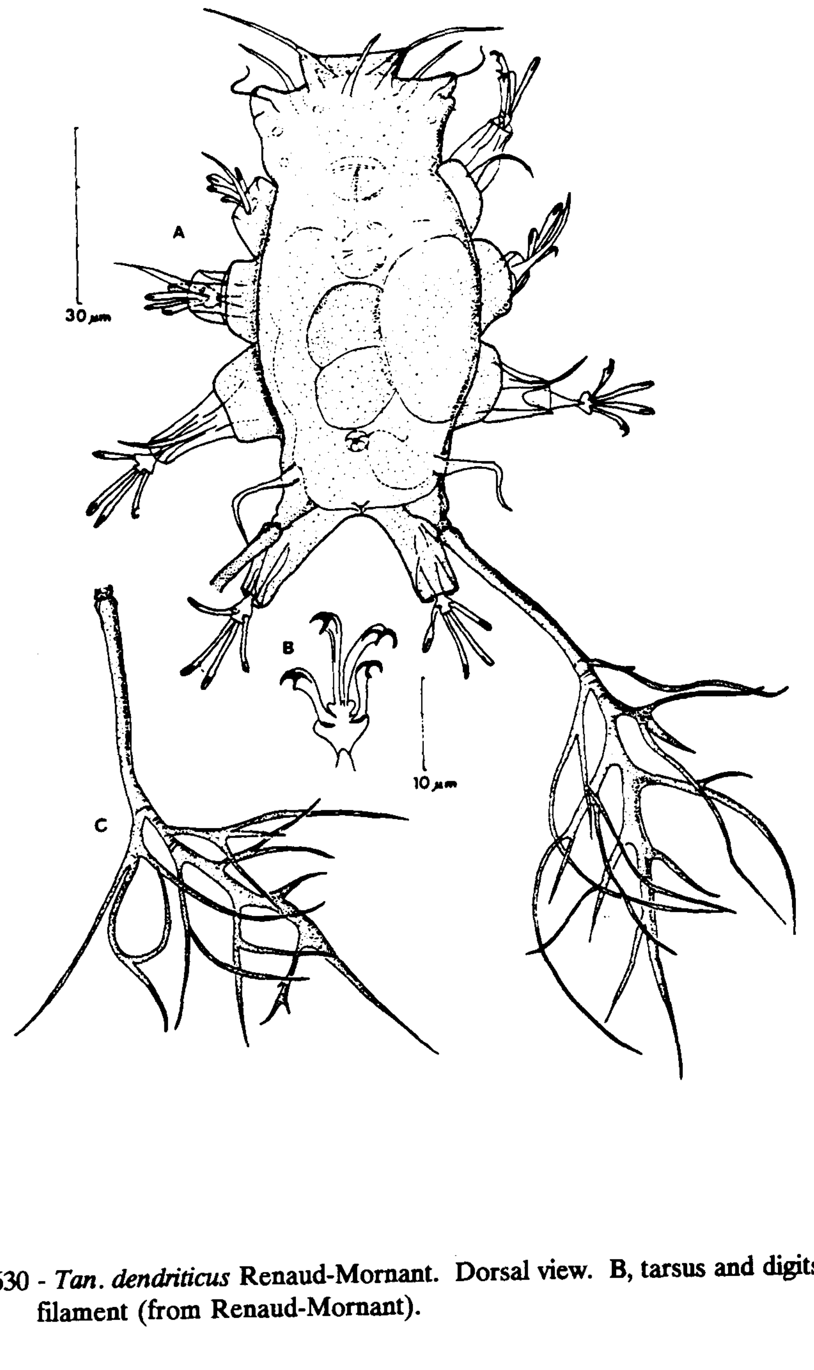


Fig. 630 - *Tan. dendriticus* Renaud-Mornant. Dorsal view. B, tarsus and digits; C, caudal filament (from Renaud-Mornant).

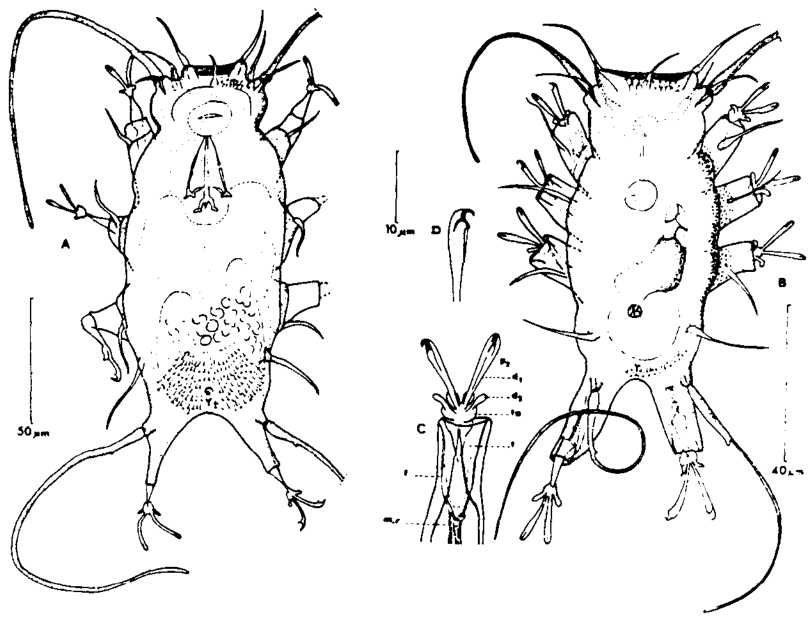


Fig. 631 - *Tan. heterodactylus* Renaud-Mornant. A, male, dorsal view; B, female, dorsal view; C, retracted leg; D, claw of a median digit (from Renaud-Mornant).

The legs are telescopic, and are composed of a coxal part, a femur (with a bristle) of trapezoidal shape, and a tibia, much narrower, ending with a point; the tarsi are triangular. Each leg bears a pair of median digits (10μ), which have at their base a cuticular fold, and bear distally a sickle-shaped claw, with external spur. At the side of the digit exists two small cuticular outgrowths of 4-5μ, without claws.

Tanarctus heterodactylus was found off the shore of North Carolina (U.S.A.), at 400 meters depth, and off the coast of Rio de Janeiro at a depth of 22 meters.

TANARCTUS RAMAZZOTTII Renaud-Mornant, 1975 (Fig. 632).

The two known examples of this species are respectively 80 and 82μ long; the body is short, the bases of the legs are almost in contact with each other; head massive, 35μ wide. The unpaired median cirrus (11μ) is present, inserted on an enlarged base, somewhat back with respect to the anterior margin of the head. The internal cephalic cirri are inserted on basal peduncle, connected by a cuticular membrane; the external cephalic cirri, also with peduncle bases, are ventrally inserted; both the pair of cirri consist of a larger basal part and a slender terminal part. The lateral cirri a are inserted dorsally, on an enlarged base, are 11μ long, and terminated with a sharpened apex. The clavae, 60-65μ long, are flattened and end with a rounded apex. "Secondary clavae" exist, of short oval shape, not inserted on a common base with cirrus A and the principal clavae, but in a position more ventral and median, very near to the bases of the external cephalic cirri.

The mouth is ventral, stylets and subspherical pharynx are present.

Legs long, slender and telescopic. The first three pair possess a long tripartite spine, which is longer on the 3rd legs. The cirrus E (35μ) is situated dorsally, above the insertion of the 4th legs. The strong postero-lateral, or caudal, spines are 145-150μ long, and do not present branching.

The legs bear four digits, of different length, having the internals longer than the externals. The claws are simple.

The cuticle presents pores on the dorsal side, uniformly distributed.

This species, very similar to *Tan. tauricus* (with which it has in common the caudal spine not branched), differs by the small length of the clavae and of the caudal spines.

Tan. ramazzottii was found in the abyssal mud in the Gulf of Biscaglia, at 3,039 meters depth, as well as in infralittoral sand on the coast of northwestern Britain.

TANARCTUS TAURICUS Renaud-Debyser, 1959 (Figs. 633 and 634).

Length 98-100μ, width 35-40μ. Cephalic region very developed, which occupies about a fourth of the length of the body. Cuticle smooth, barely thickened, without visible stripes, with exception of slight ventral furrows in correspondence with the legs; the lateral margin of the body appears smooth, without projections.

The median cirrus does not exist; the other cephalic appendices are: very long internal buccal cirrus (24-25μ), paired, in dorsal position;

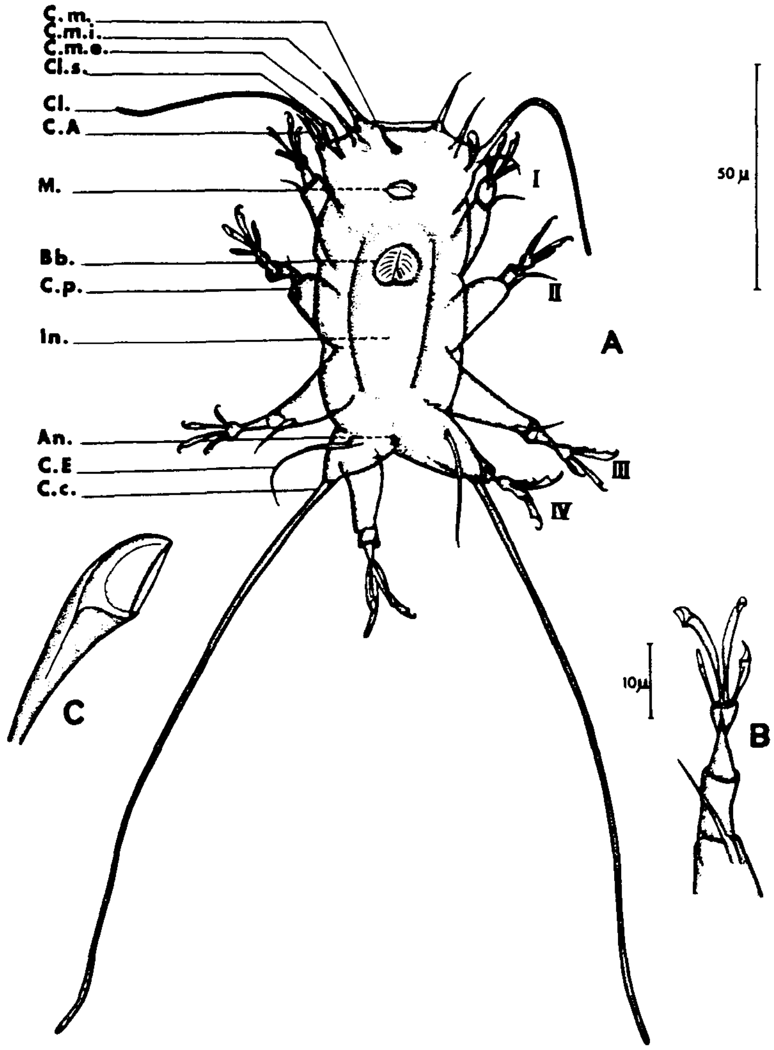


Fig. 632 - *Tan. ramazzottii* Renaud-Mornant. Dorsal view. An, anus; Bb, pharynx; CA, cirrus A; Cc, caudal spine; CE, cirrus E; Cl, clava; Cl.s., secondary clava; Cm, median cirrus; Cm.e., external cephalic cirrus; Cm.i., internal cephalic cirrus; Cp, spine; In, intestine; M, mouth; B, leg of the 3rd pair; C, external digit of the 4th pair of legs (from Renaud-Mornant).

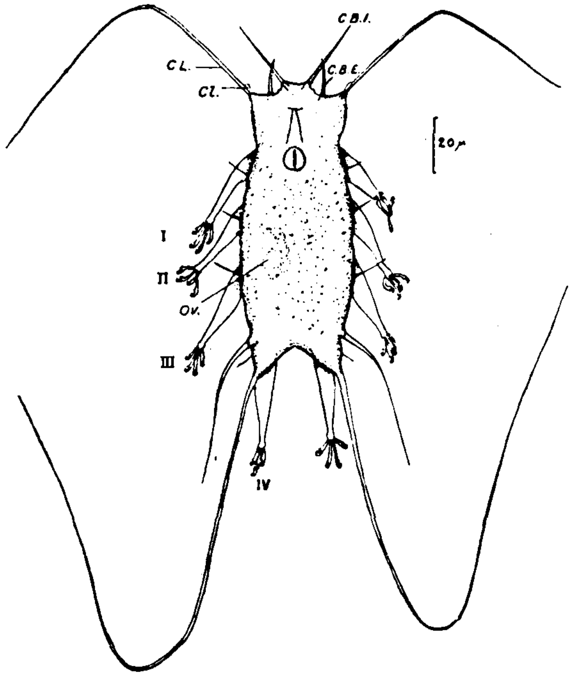


Fig. 633 - *Tan. tauricus* Renaud-Debyser, dorsal view. C.B.E., external buccal cirrus; C.B.I., internal buccal cirrus; C.L., lateral cirrus; Cl, clava (from Renaud-Debyser).

shorter external buccal cirrus (12-14μ), paired, inserted ventrally and curved toward the internal buccal cirrus; paired cephalic papilla, small, positioned between the internal and external buccal cirrus; lateral cirrus A very short (4-5μ) and long clava (95-100μ), inserted on a common base with cirrus A.

In the original description, the long clava was considered as cirrus A, and vice versa. Following the observations of Lindgren (1971), in the genus *Tanarctus* the longer appendix is now considered as homologous to the clava of the other Heterotardigrada, and the short and slender appendix, already called "clava" is at present homologous to cirrus A.

According to the original description the unpaired median cirrus might be lacking; later however the author has acknowledged its presence.

The buccal aperture is situated ventrally and has the appearance of a thin transverse fissure; there was seen two stylets and the pharynx (without further detail), followed by the intestine with 6 lobes and the anus; gonads (with 8 eggs) positioned in correspondence with the 2nd and 3rd pairs of legs: it was not possible to perceive the gonopore.

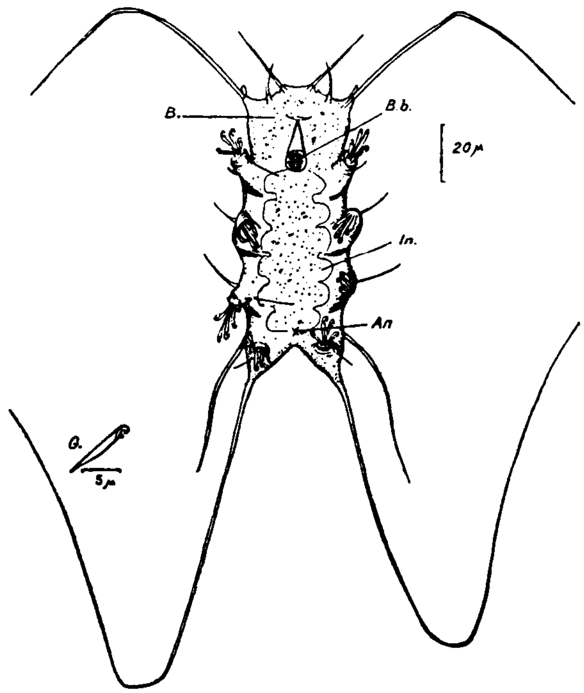


Fig. 634 - *Tanarctus tauricus* Renaud-Debyser. Ventral view of the living animal, with legs almost completely retracted. B.b., pharynx; B., mouth; An., anus; In., intestine; G. digit (from Renaud-Debyser).

Two robust laterodorsal spines -- one per side -- between the 3rd and the 4th pairs of legs, approximately where is inserted the appendices E of the *Echiniscus*. The caudal end of the body is subdivided -- almost bifurcated -- into two large conical lobes, from each of which departs an extremely long filament, or flexible spine (220μ). The legs are all similar to each other, translucent, telescopically retractile, and each one bears a spine; at the distal end of the legs, which is somewhat enlarged, there are 4 digits, of which the two median are longer (9-10μ) and the two external shorter (5-7μ); digits terminate with a claw without spurs.

The species was found in a single example (female) in the sand of the beach of Sharktown on Bimini Island (Bahamas) at a depth between 10 and 20 cm.

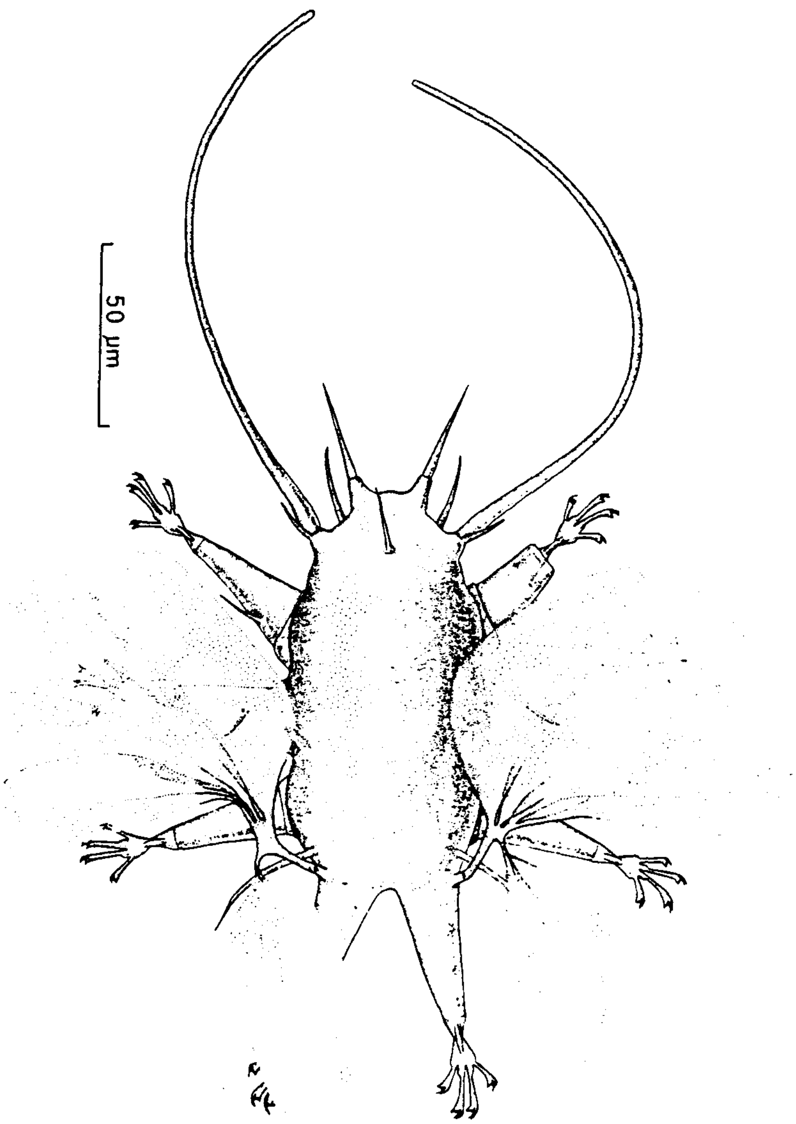


Fig. 635 - *Tan. velatus* McKirdy, Schmidt, and McGinty-Bayly. Dorsal view (from McKirdy, Schmidt, and McGinty-Bayly).

TANARCTUS VELATUS McKirdy, Schmidt, and McGinty-Bayly, 1976 (Fig. 635).

Length 118.3μ. The median cirrus is present (17.5μ long), inserted dorsally, rather set back with respect to the anterior margin of the head; the internal cirri (30.5μ) inserted on a prominent pedestal; external cirri (21μ), ventral, inserted near to the anterior margin of the head; lateral cirri A (12μ) and clavae (151.5μ) inserted on a common base: the clavae are ventral and have an uniform thickness for all the length.

The cuticle is punctated dorsally and, more finely, also ventrally and on the proximal parts of the legs. Cirrus E, 40μ long, between the third and the 4th pairs of legs. The posterolateral, or caudal, appendices are inserted near to the insertion of the 4th legs: they present a proximal part not subdivided for 20μ then are split into a posterior and an anterior branch: the latter is quickly subdivided into numerous branches each expanded into a more slender cuticular structure, wide, similar to a veil; the posterior branch is similarly expanded into a veil, but is not branched.

The legs are strongly telescopic; spines are present only on the 1st and 2nd legs. Each leg bears four digits, of which the internals are longer than the externals. The claws of the internal digits bear a slender spur on the curvature.

Of *Tan. velatus* was found a single example, in interstitial environment, on the island of Santa Cruz (Galapagos).

Genus *TETRAKENTRON* Cuènot, 1893.

Diagnosis: Halechiniscus, with body very flattened in dorsoventral sense; cephalic appendices short, including the median cirrus, which is a short spine; the digits end with a claw supplied with two spurs.

TETRAKENTRON SYNAPTAE Cuènot, 1892 (Fig. 636).

Length up to 200μ, eyes absent, body flattened dorsoventrally and to which remains united the cuticle of preceding molt (?); colorless, with smooth cuticle. The buccal aperture is positioned on a conical projection, widely rounded, and is ventral. Stylets lacking supports, pharynx almost spherical with three pharyngeal bars. Median cirrus very short, with appearance of triangular spine; internal and external median cirri very small; the clava is a short dome-shaped papilla, from which is raised a

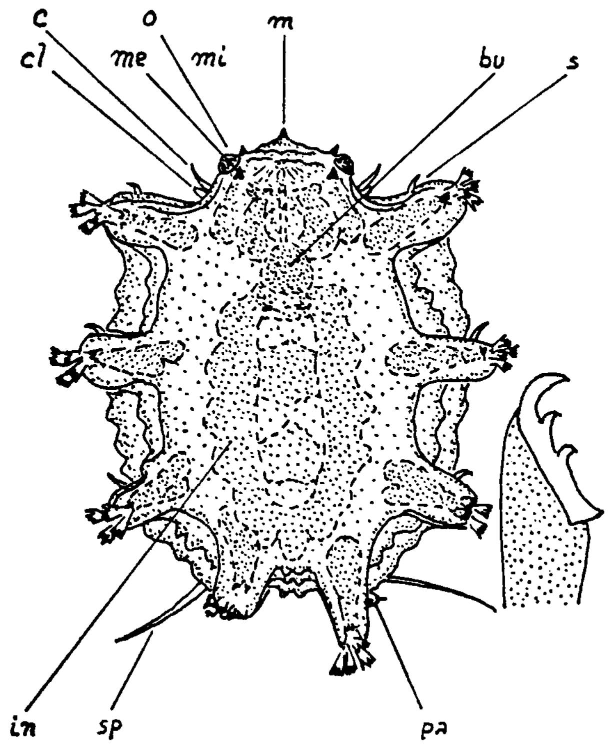


Fig. 636 - *T. synaptae* Cuènot. Ventral view and detail of a claw: bu, pharynx; c, lateral cirrus; cl, clava; in, intestine; m, median cirrus; me, external (buccal) medial cirrus; mi, internal (buccal) medial cirrus; o, sensory organ; pa, papilla of the 4th pair of legs; s, sp, spines (from Marcus, modified).

slender bristle; the lateral cirrus is a wide straight spine. Between the internal and external medial cirri -- that is to say in correspondence with the position occupied by the cephalic papillae -- exists two cuticular hemispherical projections, in which penetrates two nerves.

Legs short, composed of a wider and somewhat conical proximal part, into which may be telescopically retracted the short distal part, ending with four digits; these are short, a little enlarged distally, and bear at their end a claw with 2 spurs. On the proximal and dorsal portions of the first three pairs of legs exists a spine; where the legs of the 4th pair are inserted into the body there is -- on each side -- a long pointed cirrus (the longest appendices of the animal) and caudally to them -- on the proximal part of the leg -- a papilla with base approximately spherical and small point at the apex. Eggs unknown.

T. synaptae is the only parasitic tardigrade. It was found only on the peribuccal tentacles of the holothuroid *Leptosynapta gallienei* Herapath near Roscoff, on the Breton coast.

Genus *THERMOZODIUM* Rahm, 1937

Diagnosis: Cirri A are present; pharynx with placoids; claws not differentiated into principal branch and secondary branch.

THERMOZODIUM ESAKII Rahm, 1937 (Figs. 637 and 638).

This species is the only representative of the Order Mesotardigrada; length 360-490μ, average about 440μ, eye spots present and black, body transparent, with pigmentation slightly reddish. The cuticle is smooth, with dorsal transverse folds, and is thick at the lateral margins of the body,

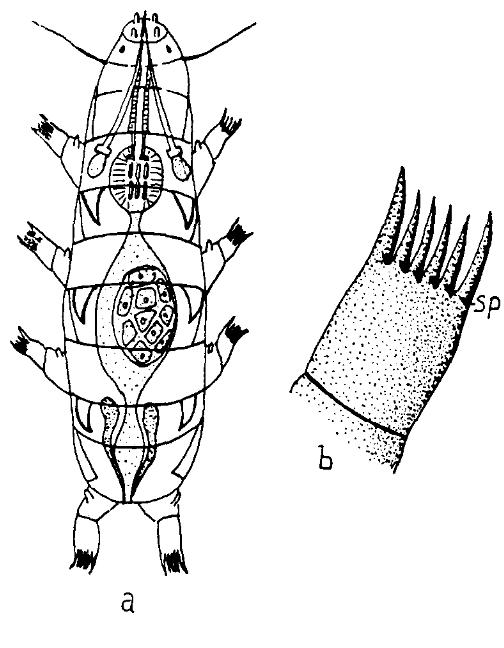


Fig. 637 - *Th. esakii* Rahm. a, dorsal view; b, claws; sp, small spine (from Rahm, redrawn).

rostrally to each pair of legs: the author advances the hypothesis that it can be treated as an initial sign of an armor; in dorsolateral position -- caudal to the first 3 pairs of legs -- there are 3 pairs of robust spines with very wide base.

The cephalic zone bears two not very long lateral cirri A, but the clava is absent. The buccal aperture is wide (diameter about 12μ), surrounded by 2 (?) pairs of fairly developed papillae, which is followed by a funnel-shaped cavity (buccal cavity) and then the buccal tube (diameter $7\text{-}8\mu$), terminating with two large apophyses: besides these, the oval pharynx contains 2 macroplacoids (rods), of about equal length; sometimes the first is somewhat longer than the second. The stylets are rather long, slightly curved, with furca: probably there are stylet supports, but they were indicated with a sketched line in the figure, because their presence can not be determined with certainty. Fig. 638 shows schematically what the author saw at about 1,250 times magnification, but it was not possible to show what the relationship is between the stylet sheaths and the reinforcement bars.

The legs of all the legs bear dorsally, on the proximal part, a small elongated papilla; the claws are 6-10 in number (usually 6 or 8) and the external two slightly surpass in length the internals; they do not have spurs, but sometimes a small spine at their base. Rahm observed up to 10 eggs maturing in the ovary (dorsal); he saw also -- a single time -- its stadium simplex.

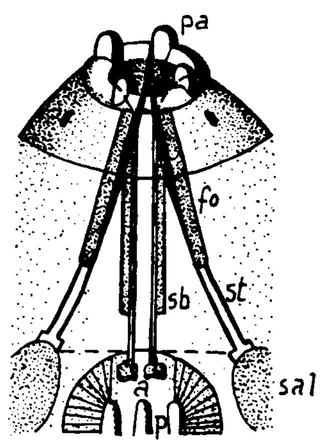


Fig. 638 - *Th. esakii* Rahm. Schematic representation of the rostral region: a, apophyses; b, placoids; fo, stylet sheath; pa, peribuccal papillae; sa, salivary gland; sb, reinforcement bar; st, stylet (from Rahm, redrawn).

The species, which eats algae, was collected at the margin and in the small discharge canal of a Japanese sulphurous thermal spring near Nagasaki (Kyushu Island), with water at the temperature of 65°C; the algae, inhabited by the tardigrades, was penetrated intermittently -- as a consequence of wind -- by hot vapor and reached a temperature between 39.8 and 41.7°C. According to recent reports, it seems that the type habitat has been entirely destroyed by an earthquake.

APPENDIX

APPENDIX

While the printing of this volume was in progress, some new species were described, which -- not included in the text and in the keys -- are cited here. This appendix is up to date as far as to the end of the month of February 1983.

ANGURSA BICUSPIS ABYSSALIS Renaud-Mornant, 1981 (Fig. 639).

This subspecies corresponds to the nominal subspecies as far as the general appearance of the body (however still more vermiform), the characteristics of the head and of the legs. It differs by the presence of a very short median cirrus and by the presence of hemispherical papillae on the 4th pair of legs.

The subspecies has been found in the Atlantic, in abyssal environment, down to and beyond 2,000 meters depth.

ANGURSA LANCEOLATA Renaud-Mornant, 1981 (Fig. 640).

The body, of elongated shape, is 165μ long and 29 wide. The cuticle, punctated, forms poorly accentuated transverse folds at the levels of the 1st, 2nd, and 3rd legs. The head, barely distinct, presents a slight constriction behind the lobes which bear the cirrus A and the clava. The cephalic cirri are composed of a base and a flagellum; the internal median cirri (1 and 2μ) are dorsal and situated at 2μ from the buccal aperture; ventrally, the internal median cirri (2 and 3μ) are longer and situated further back. The median cirrus is inserted more posterior, in front of the cephalic papillae. The cirri A (5 and 6μ) are inserted in front of the clavae; these, leaf shaped (6 x 4μ), are attached to the cephalic lobes by way of a refringent organ. The mouth has a sucker opening. The buccal tube, straight, 27μ long, leads to an oval pharynx containing three slender placoids.

Legs telescopic, the coxal part of the first pair bears a bristle with expanded base. The tibia is narrower than the femur, which has conical shape. The digits are inserted on a barely distinct tarsus, from which departs ventrally two slightly curved peduncles which penetrate into the external digits. Dorsally the internal digits are implanted on a slightly swollen bulb. The digits of the 4th pair of legs are longer than the others. The claws possess two accessory points. The cirrus E is dorsally inserted, in posterior position, and is enlarged distally to form a spear head. The coxal papillae of the 4th pair of legs are simple, elongated.

Ang. lanceolata was found in the southeast Atlantic, off the coast of Angola, in abyssal environment at almost 3,000 meters depth.

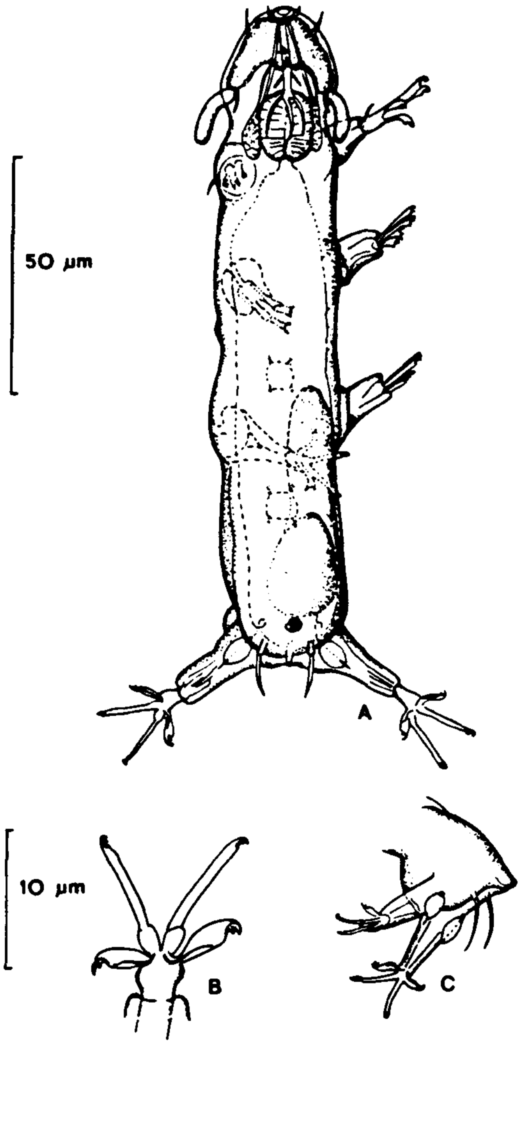


Fig. 639 - *Ang. bicuspis abyssalis*. A, dorsal view; B, leg of the 4th pair; C, caudal part of a specimen (from Renaud-Mornant).

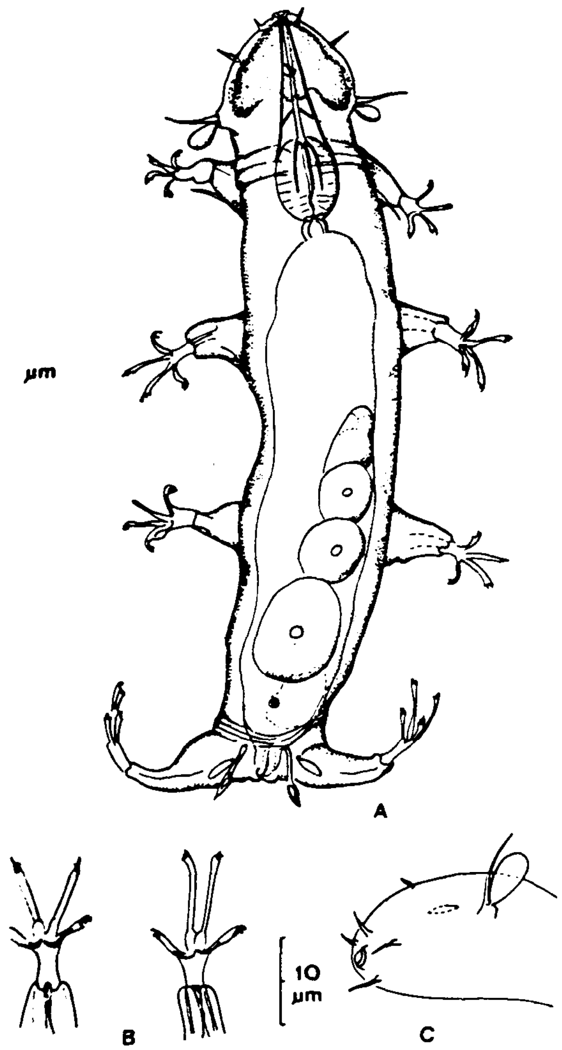


Fig. 640 - *Ang. lanceolata*. A, dorsal view; B, leg of the 3rd pair (at the left) and of the 4th pair (at the right); C, sketch of the cephalic end, with the position of the cephalic appendices and the mouth (from Renaud-Mornant).

BRYODELPHAX DOMINICANUS (Schuster and Toftner, 1982) (Fig. 641).
= *Echiniscus* (*B.*) *dominicanus* Schuster & Toftner, 1982

Length about 100μ (minimum 77, maximum 113, holotype 98). Lacking information on the color and on the presence of eyes. The plates present a sculpture composed of pores distributed in poorly defined transverse rows, more accentuated on the cephalic, scapular, and terminal plates; on the terminal plate exists also an extremely fine granulation. The 4th pair of legs do not possess dentate collar. Internal claws with basal spurs, externals smooth.

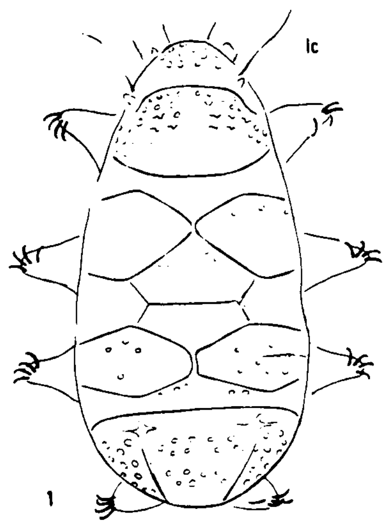


Fig. 641 - *B. dominicanus* (from Schuster and Toftner).

This is the only species of *Bryodelphax* in which the sculpture is composed of pores rather than granules.

E. dominicanus was found in two localities of the Dominican Republic.

Type locality: Constanza (Dominican Republic).

DACTYLOBIOTUS PARTHENOGENETICUS Bertolani, 1981 (Fig. 642).

Length up to 950μ, but generally between 650 and 700. Colorless. Eye spots present. Cuticle finely wrinkled. Between the third and the fourth pairs of legs exists two dorsal conical papillae. The mouth is

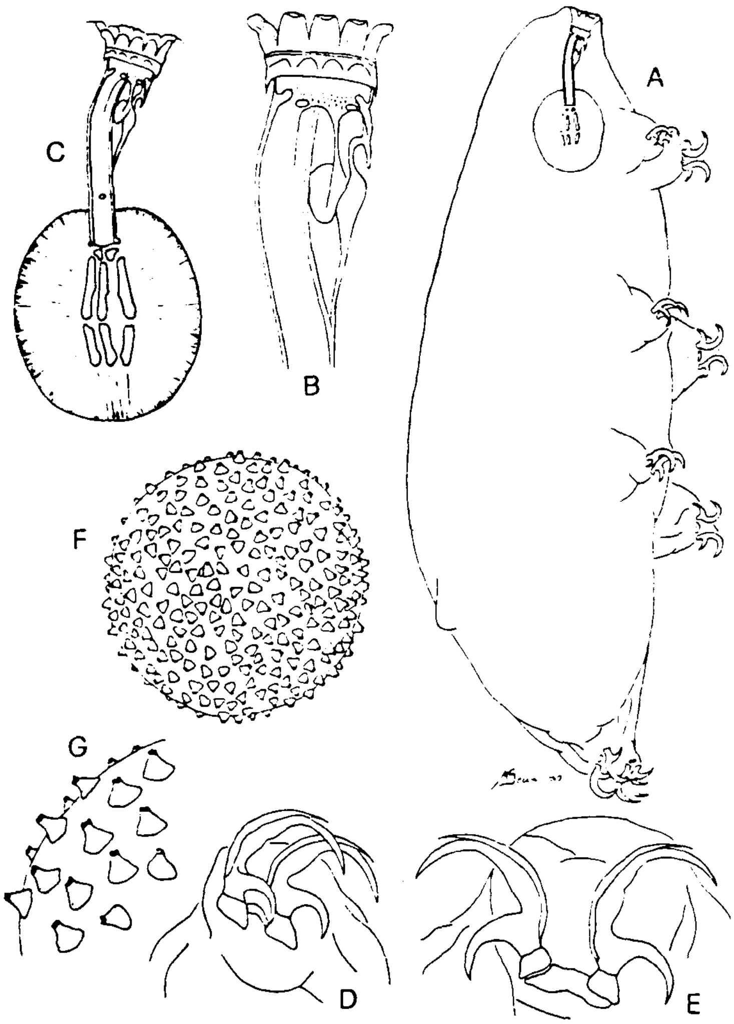


Fig. 642 - *Da. parthenogeneticus*. A, habitus; B, buccal armature and reinforcement bar (in profile); C, profile of the buccopharyngeal apparatus; D, claws of the third pair; E, claws of the fourth pair; F, egg; G, its detail (from Bertolani).

surrounded by 10 lamellae. Buccal tube medium wide (7μ in an example 580μ long), and presents reinforcement bar provided with a robust ventral hook. Pharynx slightly oval, with apophyses and two macroplacoids in the shape of elongated rods: the first, longer than the second, is constricted at the middle, the second presents a prominence. Microplacoid absent.

Claws robust. The basal part is distinct from the rest of the claw by means of a septum; the principal branch possesses accessory points, the secondary branch is rather large and fairly long, more than in the other species of the genus. A cuticular bar connects the bases of the claws of each leg.

The legs are deposited free, sometimes in the exuvium. They possess conical ornamentation 4-4.5μ high, distant from each other, with notched apices. The shell, between the projections, is smooth.

Da. parthenogeneticus, in absence of eggs, is not easy to distinguish from the other species of the genus, from which it is distinguished by the better development of the secondary branch of the claws.

It is an aquatic species, found especially, but not only, on algae and floating phanerogams.

Da. parthenogeneticus is known from Italy (Marche, Lazio, Sardegna) and from Greece. Typ. loc.: Chioggiola (Pavullo, Modena).

DACTYLOBIOTUS SELENICUS Bertolani, 1981 (Fig. 643).

Length up to 740μ. Colorless. Eye spots present. Cuticle slightly wrinkled. Between the third and the fourth pairs of legs are present two dorsal conical gibbosities. Peribuccal lamellae present. The buccal tube is moderately wide (7.4μ in an example 563μ long). The round or slightly oval pharynx presents well developed apophyses and two macroplacoids of elongated rod shape, the first longer than the second, without constriction.

Claws slender and graceful, with principal branch strongly arched and devoid of accessory points. The basal part is distinct from the rest of the claw by means of a septum; the secondary branch is fairly long, however always much less than the principal. A cuticular line connects the bases of the claws of each leg.

Eggs free, spherical, with a diameter of about 85μ, excluding the ornamentation. These are composed of small projections, 2-2.3μ high, distant from each other, of truncated cone shape, with notched and hollowed apices, crater-shaped. The shell between the projections is smooth.

Da. selenicus is an aquatic species, often interstitial. It has been found in Lazio, Abruzzo, in different localities from Adige, Piave, Oglio, and in Costanza Lake. Typ. loc.: Salto River, between Grotti and Casetta (Rieti).

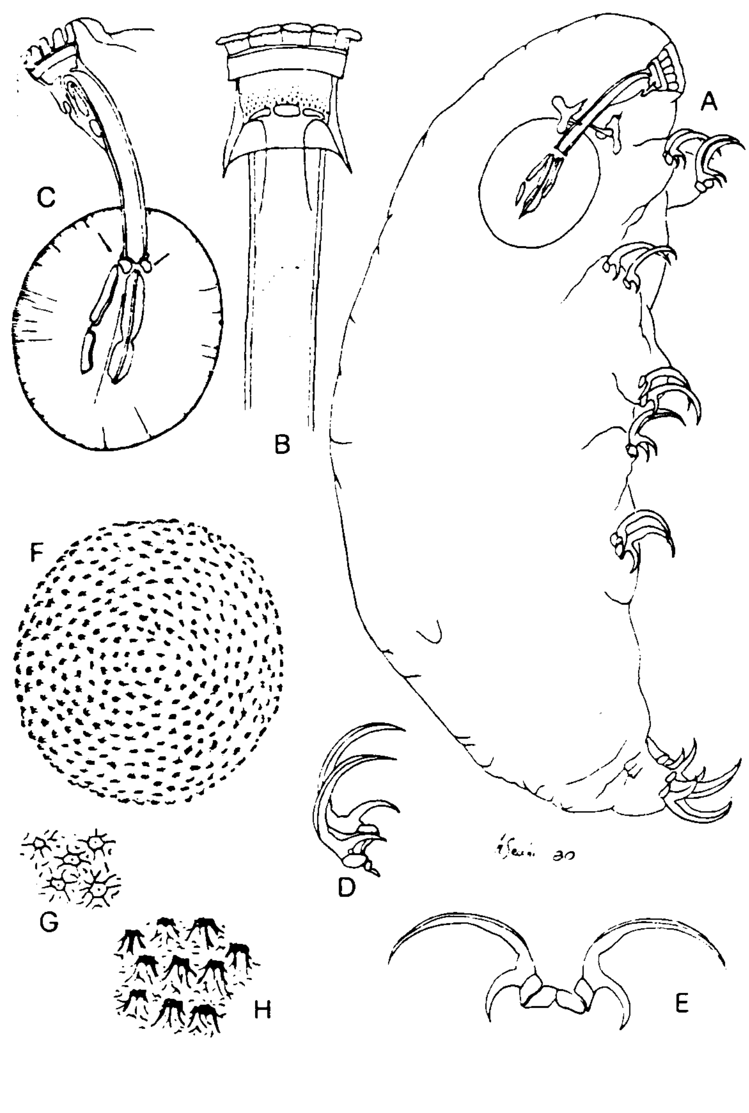


Fig. 643 - *Da. selenicus*. A, habitus; B, buccal armature (dorsal); C, profile of the buccopharyngeal apparatus; D, claws of the third pair of legs; E, claws of the fourth pair; F, egg; G and H, its detail in frontal and profile view (from Bertolani).

NEW KEY FOR THE GENUS *DACTYLOBIOTUS*

1. Eggs smooth, deposited in exuvia .... *Da. macronyx*
Eggs with ornamentation, usually deposited free 2

2(1). The secondary branch of the 1st-3rd claws is extremely reduced, almost a spur; buccal tube wide .... *Da. haplonyx*
The secondary arm of the claws is short, but not excessively; buccal tube of medium width 3

3(2). On the principal branch of the claws the accessory points are lacking .... *Da. selenicus*
The accessory points are present, at least on the claws of the 4th pair of legs 4

4(3). Lacking dorsal, conical gibbosities 5
Two conical, dorsal gibbosities exist, between the 3rd and 4th pair of legs (Attention! In individual specimens these gibbosities may be missing.) 6

5(4). Length up to and over 800μ, claws long and thin. Eggs with projections conical, bulbous, or mammary, with bases that are in contact .... *Da. ambiguus*
Length rarely over 500μ, claws shorter and more stocky. The eggs have large conical projections, hexagonal at the base, with the sides in contact .... *Da. ampullaceus*

6(4). Claws long and thin, with accessory points only on the 4th pair of legs .... *Da. grandipes*
Claws with accessory points on all legs 7

7(6). Claws long and thin. Eggs with conico-ogival [pointed arch] projections and separate from each other, height 4-5μ .... *Da. dispar*
Claws with robust principal and secondary branches. The projections of the eggs have a conical shape, with the apex indented .... *Da. parthenogeneticus*

DORYPHORIBIUS MACRODON Binda, Pilato, and Dastych, 1980 (Fig. 644).

= *Dor. doryphorus* (not Binda and Pilato, 1969) Pilato, 1972; Pilato and D'Urso, 1976.

Length up to 564μ, yellowish color, cuticle smooth, with some caudal undulations; eye spots present. Peribuccal lamellae absent, mouth in anterio-ventral position. The buccal armature is composed of some teeth in posterior position, one of these, mid-dorsal, is clearly larger than

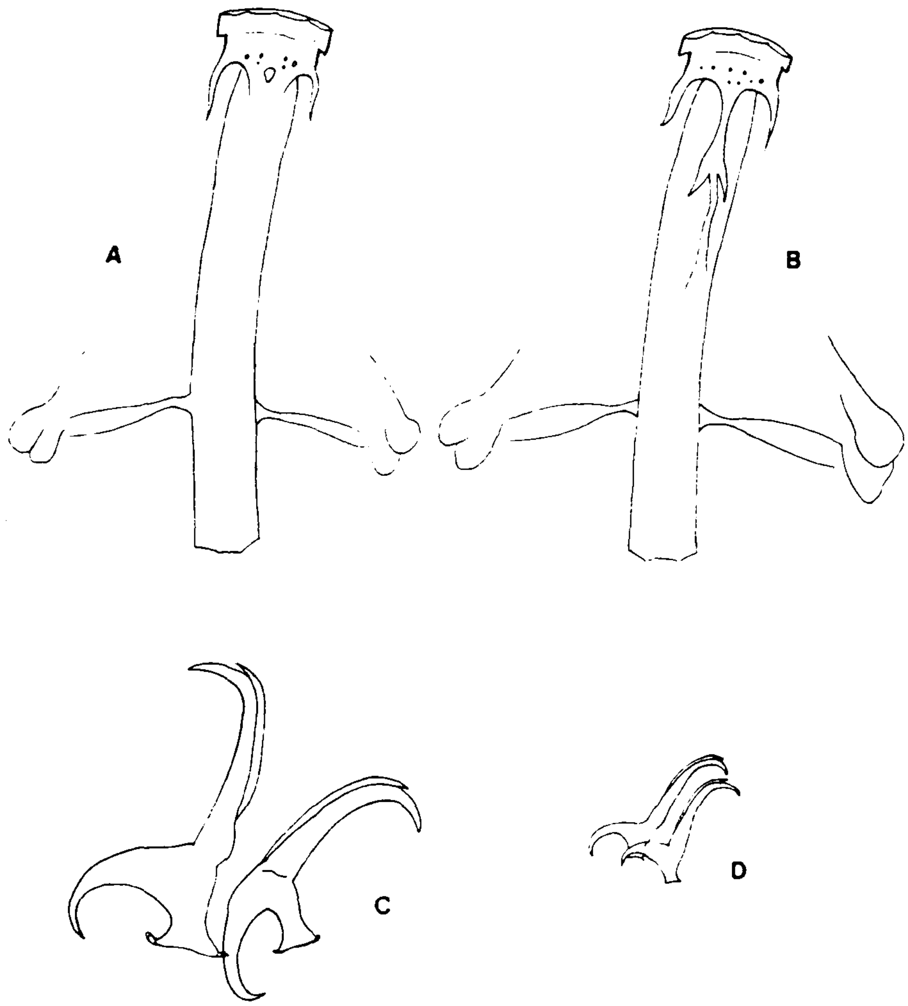


Fig. 644 - A and B, buccal armature of *Dor. macrodon* observed dorsally (A) and ventrally (B). C, claws of the posterior legs of *Dor. macrodon*. D, claws of the posterior legs of *Dor. doryphorus* (from Pilato et al.).

the others. The buccal tube, ventrally bent about a third of its length, is 52μ long and 4.8 wide. The pharynx is short oval and contains apophyses and two macroplacoids, the first of these, constricted at about half its length, is double the length of the second; microplacoid absent.

The claws of each leg have somewhat different size from each other; the basal part and the secondary branch are large and massive, especially on the external claw, the base of the claw is enlarged and presents a very reduced lunule; the principal branch is provided with fairly evident lunule.

The species is rather similar to *Dor. doryphorus* (with which it was initially confused): it differs by the size, by the armature of the buccal cavity, by the shape of the claws, and by the presence of lunules.

Dor. macrodon has been found in Sicily (Adrano, typ. loc.), on Spitzbergen Island, and near Sidney (Australia).

ECHINISCUS MONTANUS Iharos, 1982 (Fig. 645).

Medium size (up to 250μ), color orange. Eye spots present, red. The sculpture is of "polygonal" type. Lacking the median plate 3. The terminal plate is not facetted and does not present notches.

Besides cirrus A (about 70μ long) exists lateral appendices in positions C (112μ), D (105μ), and E (187μ). Dorsally are present long spines in position D (22μ).

The 4th pair of legs presents a dentate collar composed of 6-8 small teeth. The claws, both internal and external have neither spurs nor spines.

The species has been found in some localities of Hungary and North Korea.

Typ. loc.: Kom (Hungary).

ISOHYPSIBIUS MARII Bertolani, 1981 (Fig. 646).

Length up to over 580μ. Colorless. Eye spots present. The cuticle presents dorsally a sculpture composed of a reticular pattern of slender mesh which delimit irregular polygons, of various size. This pattern may disappear in old preparations. The buccal armature is composed of a posterior band of teeth followed by a row of round teeth. The buccal tube is moderately wide (5.3μ in a specimen of 510μ). The pharynx contains apophyses and three macroplacoids in the shape of short and slender rods,

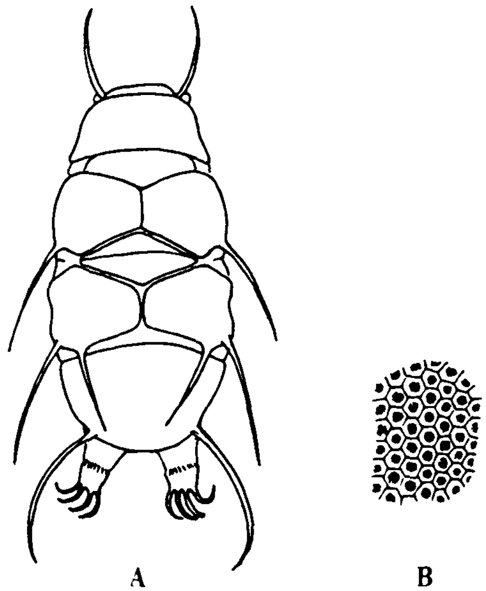


Fig. 645 - *E. montanus*. A, dorsal view; B, sculpture of the plates (from Iharos).

of about equal length. Microplacoid absent.

The claws are long, especially on the 4th pair of legs. The basal branch is slender and straight, with enlarged base on the external claw; the principal branch is a little longer than the secondary and markedly more slender, and possess accessory points. Lunules absent. On the first three pair of legs exists a small cuticular bar, near the base of the internal claw.

Smooth eggs deposited (up to 24) in the exuvium.

I. marii, which is an aquatic species, in known only from Emilia. Typ. loc.: Formigine (Modena).

ISOHYPSIBIUS MONOICUS Bertolani, 1981 (Fig. 647).

Length up to 622μ. Colorless or whitish. Eye spots present. The cuticle presents dorsally a pattern similar to Persian [lamb?] fur. The buccal armature lacks the band of teeth, and is composed of 4-6 large ventral points and of a transverse crest with dorsal arch. The buccal tube is rather narrow (4.3μ in a specimen of 537.5μ). Pharynx almost spherical

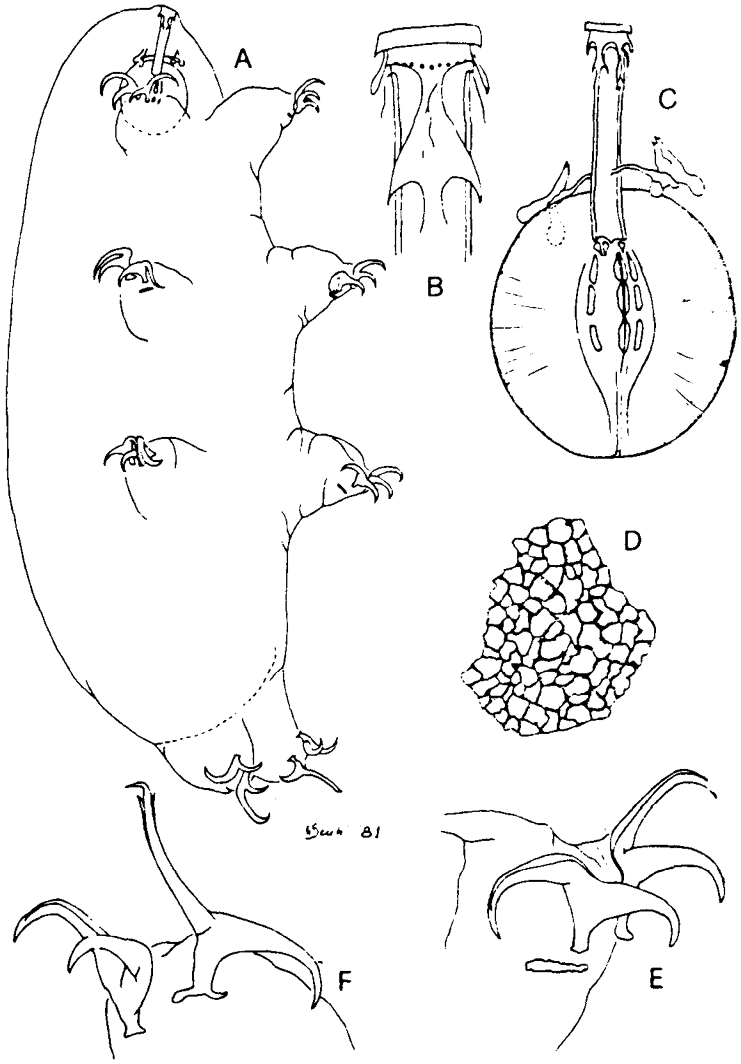


Fig. 646 - *I. marii*. A, habitus; B, buccal armature; C, buccopharyngeal apparatus; D, detail of the dorsal sculpture of the cuticle; E, claws of the third pair of legs and cuticular bar; F, claws of the fourth pair of legs (from Bertolani).

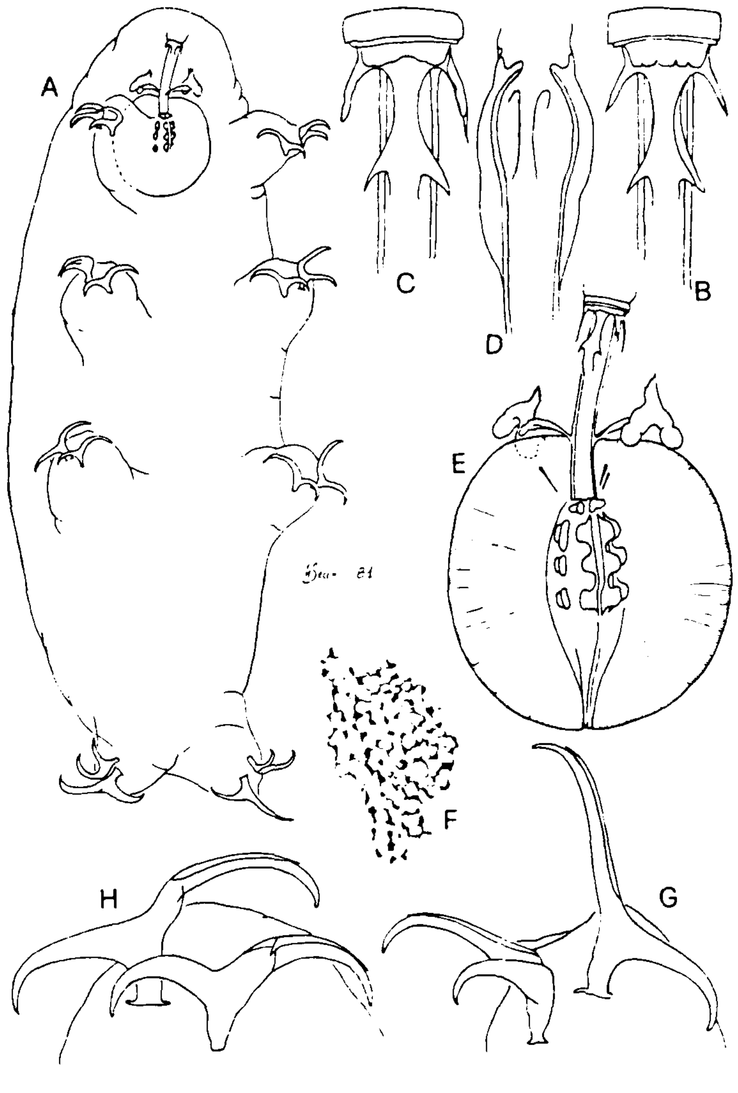


Fig. 647 - *I. monoicus*. A, habitus; B, buccal armature ventral; C, buccal armature lateral; D, profile of the buccal tube with appendices of crest shape; E, buccopharyngeal apparatus (pharynx somewhat compressed); F, detail of the cuticular sculpture; G, claws of the fourth pair of legs; H, claws of the third pair of legs (from Bertolani).

or oval, with apophyses enlarged transversely, and three macroplacoids of oval granular shape, of almost equal size. Microplacoid absent.

Claws very large and slender. On the external claw the basal part is cylindrical with slight basal expansion, on the internal claw pushed back toward the base, without enlargement. The principal branch, somewhat longer and more slender than the secondary, presents accessory points. Lacking both lunules and cuticular bar on the legs.

The eggs are smooth and are deposited (up to 9) in the exuvium.

I. monoicus, which is an aquatic species, has been found in Toscana, Lazio, and Adige, near Verona. Typ. loc.: Corsonna River (Garfagnona, Lucca).

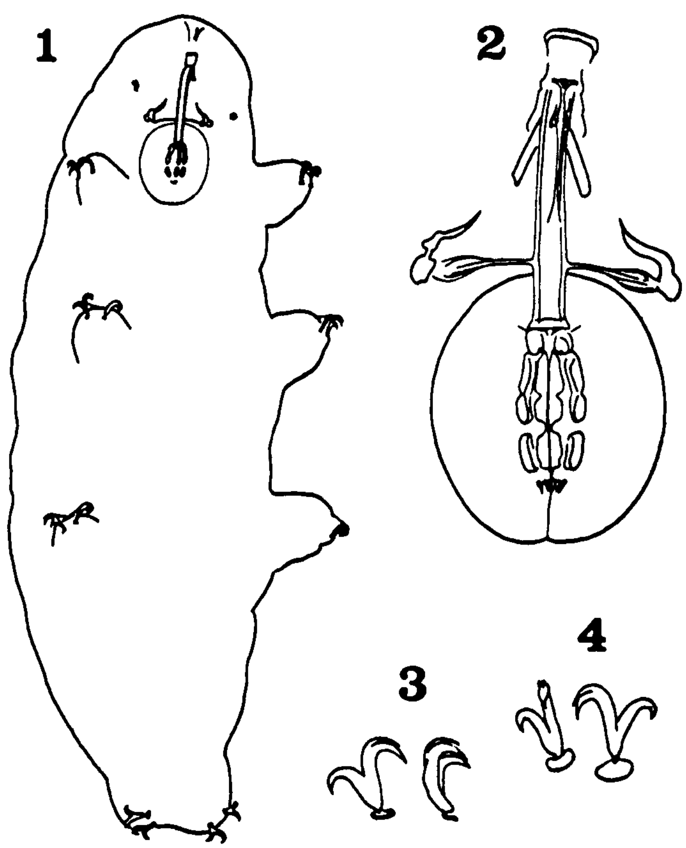


Fig. 648 - *M. kurasi*. 1, habitus; 2, buccal apparatus; 3, claws of the 3rd pair of legs; 4, claws of the 4th pair of legs (from Dastych).

MACROBIOTUS KURASI Dastych, 1980 (Figs. 648, 649).

Length up to 450μ. Color white. Cuticle smooth. Eye spots present. Peribuccal lamellae present, not easily observed. Buccal cavity entirely smooth, without teeth or crests. Buccal tube medium wide. Pharynx oval with apophyses, two macroplacoids and small microplacoid; the first macroplacoid, up to 12μ long, is slightly constricted at the middle, the second is up to 7μ long.

The claws are of the *hufelandi* type and have smooth lunules on the first three pairs of legs, larger and slightly dentate on the 4th pair. The principal branch has accessory points.

Eggs white, with projections of two types: the larger are truncated cones, with apices often papillose, sometimes prolonged into a long, slender appendix, at times bifid; the smaller ornamentations, intermingled with the first, are conical; between the projections, the shell presents an extremely fine reticular design, more visible around the bases of the ornamentation.

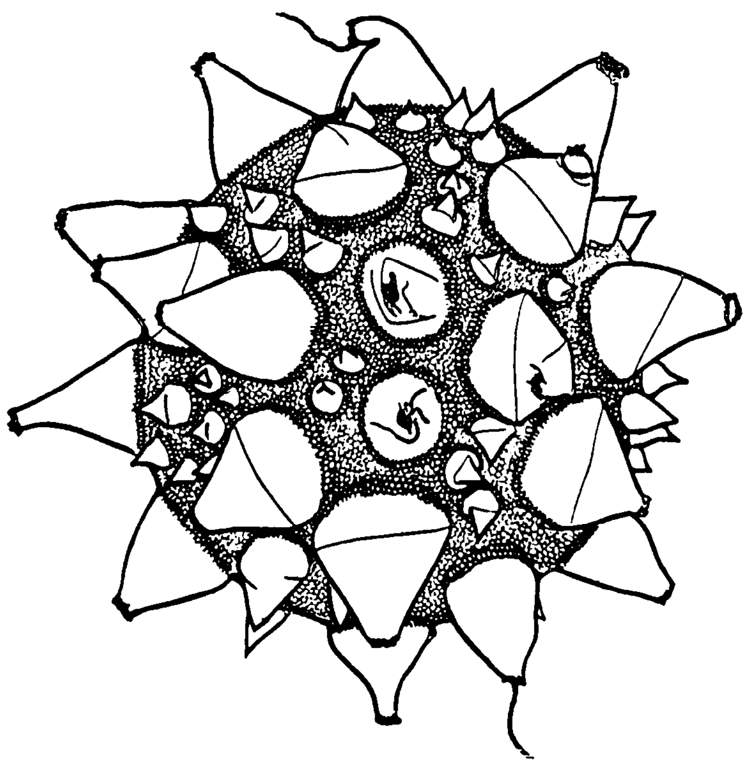


Fig. 649 - *M. kurasi*. Egg (from Dastych).

M. kurasi is very similar to *M. hufelandi*, from which it is distinguished only by the absence of buccal armature and by the smaller microplacoid. The eggs, on the contrary, are clearly different.

The species has been found in some localities of Uganda. Type locality: Mount Ruwenzori, at 4,250 elevation.

Genus *RAIARCTUS* Renaud-Mornant, 1981.

Diagnosis: Halechiniscidae with anterior cephalic border almost straight; cuticular edge sustained by a complex of hairs surrounding the body, situated above the cephalic cirri. Claws with spurs and accessory points.

Type species: *R. colurus* Renaud-Mornant, 1981.

RAIARCTUS AUREOLATUS Renaud-Mornant, 1981 (Fig. 650).

Body oval, 105μ long, 55μ wide. Dorsally exists three transverse furrows. The cuticular border around the body, sustained by hairs, is only interrupted at the level of the lateral cephalic lobes; there are 14 hairs of 5-6μ on the frontal cephalic lobe, 82 hairs of 13-15μ on the rest of the body. Behind the border exists hairs of 1-2μ, and others smaller form a punctation on the dorsum. The head is barely distinct with frontal border weakly undulating. Cephalic cirri of shape and insertion similar to those of *R. colurus*. Cirrus A (10 to 18μ), clava (12μ) oblong, flattened, of oval shape. The cirri E (21μ) are laterally implanted on a cirrophorus, 10μ above the insertion of the 4th pair of legs.

Legs telescopic, similar to those of *R. colurus*. Coxal bristle (15μ) with cirrophorus exists on the first three pairs of legs. On the 4th pair a papilla with distal spine.

This species was found at Tuléar (Madagascar, typ. loc.) in coralline sand and off the coast of Brest (France) at a depth of 130 meters in organic sand.

RAIARCTUS COLURUS Renaud-Mornant, 1981 (Fig. 651).

The body, of oval shape, 112μ long, 53 wide. The head is barely distinct, laterally flattened, with anterior border slightly undulating.

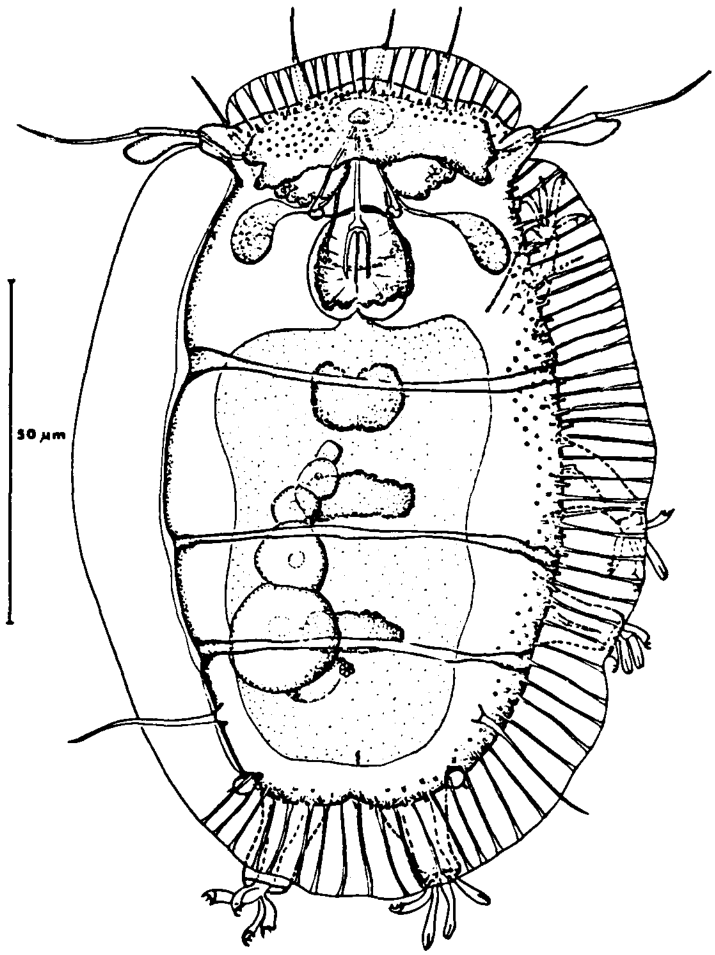


Fig. 650 - *Raiarctus aureolatus*. Dorsal view (from Renaud-Mornant).

Cephalic cirri without cirrophorus, scapus wide and cylindrical, flagellum pointed. The median cirrus (scapus 4μ, flagellum 6μ) and the internal median cirri (6 and 10μ) are ventral, inserted beneath the lateral lobes. The latter, poorly developed, bears cirri A (13μ and 16μ) inserted in front of the clavae; these, distally expanded, have a petaloid appearance.

The anterior cuticular border, sustained by 23 hairs (8μ), is situated anteriorly and dorsally above the cephalic cirri; laterally the border increases in width (18μ at the level of the first pair of legs), then decreases

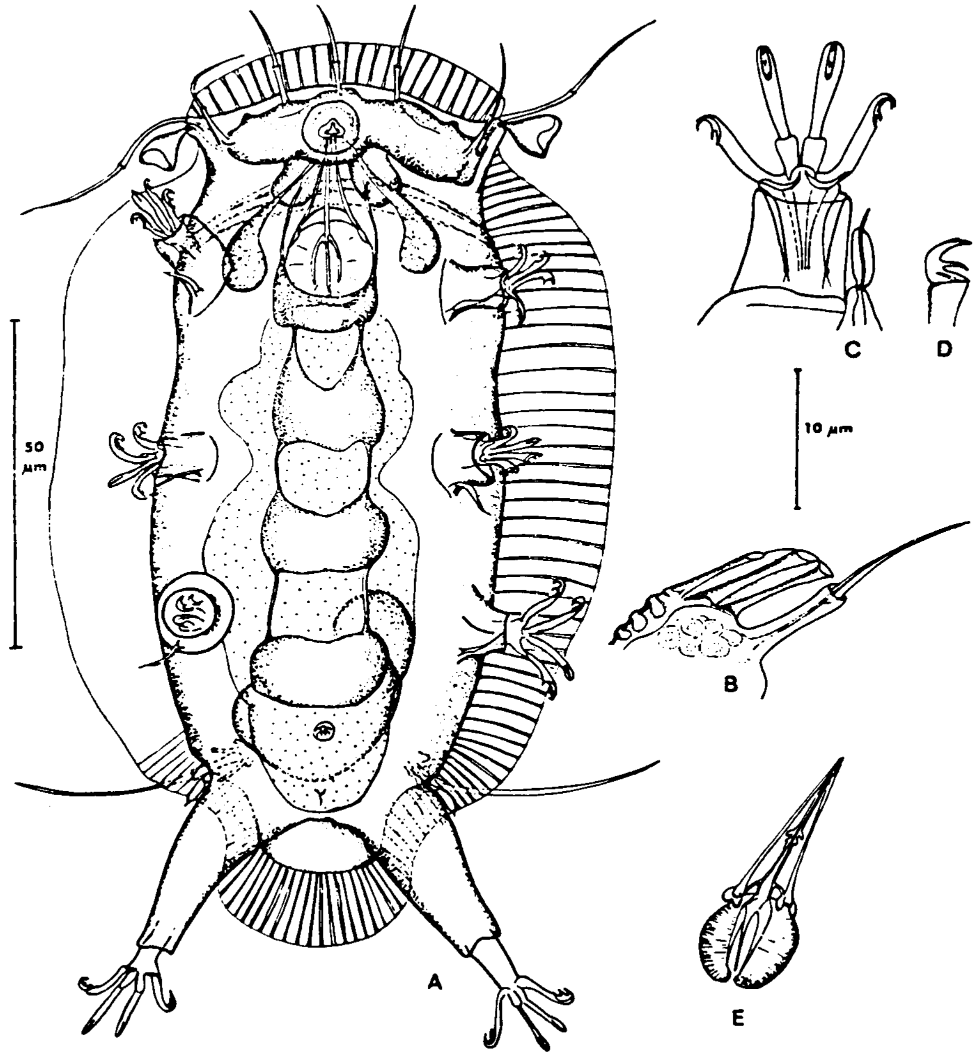


Fig. 651 - *Raiarctus colurus*. A, ventral view; B, anterior collar, in profile; C, leg of the 4th pair, retracted; D, detail of the external claw; E, buccal apparatus (from Renaud-Mornant).

again in caudal direction; the caudal lobe is wider, with 19 hairs. The cuticle is dorsally punctated and on the legs, with small hairs, larger around the insertion of the cirrus E (35μ), which is inserted in a cuticular dimple. The dorsal cuticle presents a series of 4 or 5 transverse folds, between the head and the 1st pair of legs.

Legs telescopic, with cylindrical tibia and barely distinct tarsus, surpassed by the curved peduncle of the base of the external digits. Digits almost equal in size, with claws supplied with accessory points and with a slightly curved basal spur.

R. colurus has been found in interstitial environment, among coralline sand on the coast of the island of Guadalupe.

STYGARCTUS GOURBAULTAE Renaud-Mornant, 1981 (Fig. 652).

Length 100μ; body elongated, slightly curved ventrally. Cuticle transparent and finely punctated dorsally and ventrally. The lateral cephalic lobes divided on the horizontal plane, the median lobes are curved forward; the lateral lobes possess dorsally a weak posterior spine, a clava (6μ) and the cirrus A (11μ), ventrally a funnel structure with membranous lamellae. The frontal cephalic lobes are complex: the median expansion bears internal median cirri (11μ); the lateral expansions oblique, curved ventrally, presenting lobes which surround the mouth, bearing the external median cirri (12μ) and the anterior clavae (15-16μ). The unpaired cirrus (10μ) is situated far back, on a median dorsal outgrowth.

The head is clearly separated from the trunk, which possesses three plates and four more reduced intercalary spaces. The plates possess lines of dorsal ornamentation, while the intercalary zones present a motif of oval shapes. The 1st and 2nd plates have a pair of lamellar prominences (2μ) on the posterior border, and also, the 2nd plate has two large bifid appendices (19μ), enveloped distally by a membrane. The 3rd plate does not possess appendices. The three plates bear in latero-ventral position wide funnel formations surrounded by a cuticular membrane; on the 1st and 2nd plates these formations possess anteriorly a comb-shaped appendix.

The caudal plate is formed of two pairs of lateral lobes, of which the anteriors are smaller; between these is found cirrus E, fixed on a cirrophorus. Two robust caudal spines (15μ) delimit the plate.

The 1st, 2nd, and 3rd legs are telescopic and retractable to a third of their length by means of four folds; lacking the bristle. The 4th legs bear laterally a very small coxal papilla (2μ). The end of the legs is swollen and bears the four claws characteristic of the genus, with long bristle on the median pair.

The species seems linked to coralline sand of the intertidal zone, and has been found on the coast of the island of Guadalupe.

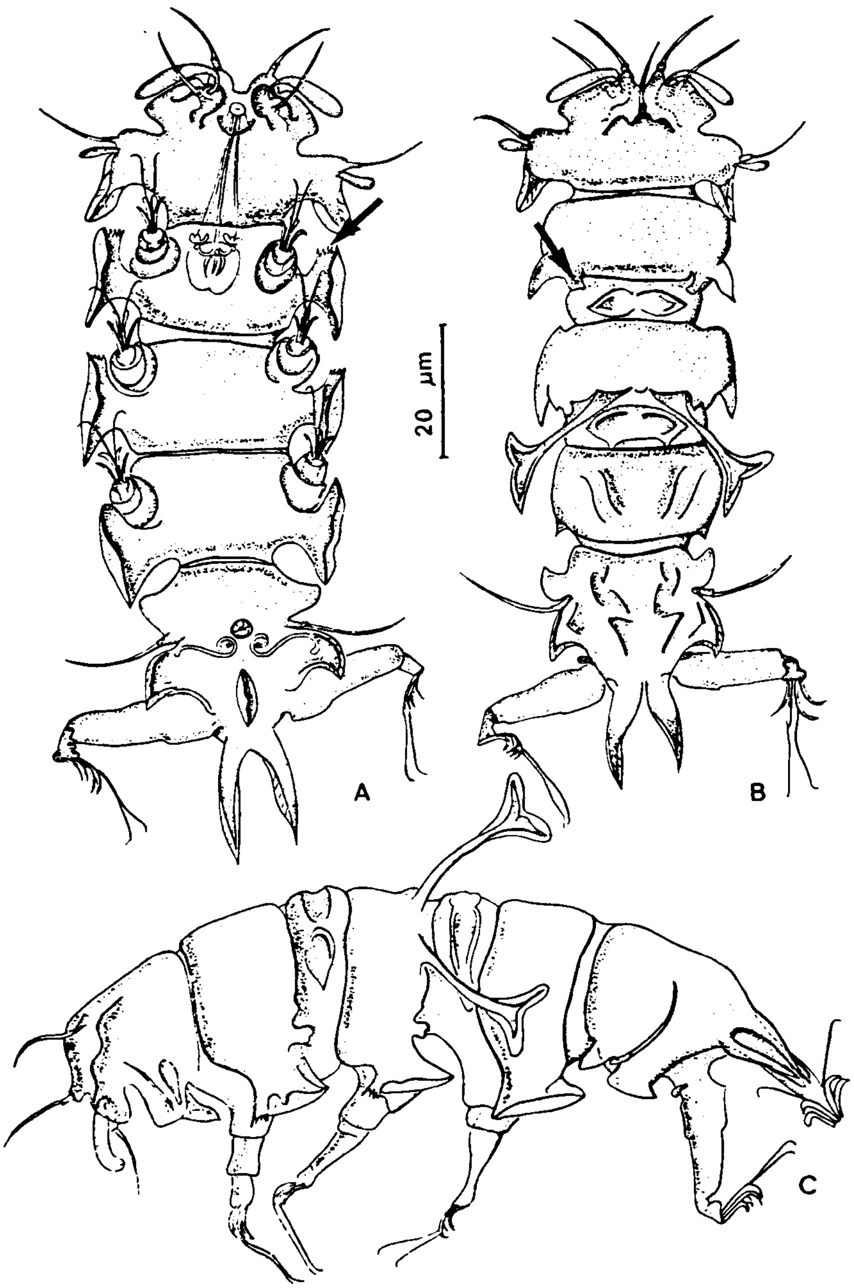


Fig. 652 - *S. gourbaultae*. A, ventral view (adult female); B, dorsal view (adult male); C, adult female, in profile (from Renaud-Mornant).

Genus *THULINIA* Bertolani, 1982.

Diagnosis: Hypsibiidae with "*Isohypsibius* type" claws, mouth surrounded by 12 lamellae; appendices of muscle insertion of the buccal tube of crest shape. Fresh water species.

KEY TO THE SPECIES

1. Claws large and robust, with expanded bases; lunules absent .... *Th. stephaniae*
   Claws of average size, with slender bases, not expanded; lunules present .... *Th. ruffoi*

THULINIA STEPHANIAE (Pilato, 1974).
= *Isohypsibius stephaniae* Pilato, 1974
= *Pseudobiotus stephaniae* Schuster et al., 1980

Description, see page 905.

THULINIA RUFFOI Bertolani, 1981 (Fig. 653).

Length up to and over 550μ, body slender. Colorless. Eye spots absent. Cuticle smooth. There are 12 peribuccal lamellae present. The buccal armature is formed of a posterior band of teeth, followed by a ventral and a dorsal row of round teeth. Buccal tube rather wide (15-17% of the length). Pharynx slightly oval with well developed apophyses and three macroplacoids of thick-set rod shape, of which the first and the third have equal length, the second is shorter. Microplacoid absent.

Claws moderately large. The basal part is long and slender, especially in the external claw, and is slightly expanded at the base; the principal branch long and straight in the external claw, shorter and robust in the internal claw, possessing robust accessory points; the secondary branch is in both the claws larger and shorter than the principal. At the base of the claws exists a small lunule. On the 1st-3rd legs, near the base of the claws, exists a cuticular bar, slender and sometimes divided in half. Typ. loc.: Sesia River, near Vocca (Veralli).

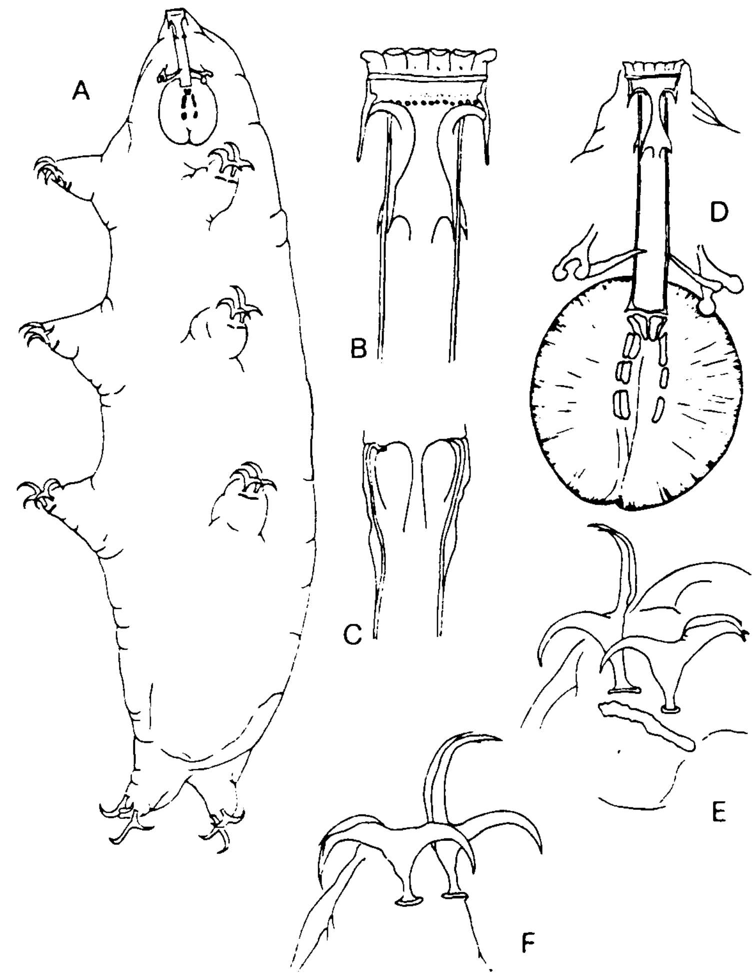


Fig. 653 - *Thulinia ruffoi*. A, habitus; B, buccal armature; C, appendices of the buccal tube of crest shape (profile); D, buccopharyngeal apparatus; E, claws and cuticular bar on the third pair of legs; F, claws of the fourth pair of legs (from Bertolani).

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Note: With the exception of three works which we consider fundamental (CuJnot, 1932, Marcus, 1929 and 1936), the bibliography includes only the works since 1936 because those of preceding years are given in the two works of Marcus.

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