534

Reprinted from Systematic Zoology
Vol. 21, No. 2, June 1972
pp. 151–173
Made in United States of America

SYSTEMATICS AND EVOLUTION WITHIN THE GNATHOSTOMULIDA[1]

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Abstract

Sterrer, W. (**Bermuda Biological Station for Research, St. George's West, Bermuda**) 1972. Systematics **and Evolution within the Gnathostomulida. Syst. Zool.,** 21:151–173. The present paper is the first classification of the phylum Gnathostomulida, of which 18 genera and more than 80 species are known. Two orders are created, according to the absence (Filospermoidea) or presence (Bursovaginoidea) of a female bursa-vagina-system and paired sensory organs. The latter order is divided into two suborders: Scleroperalia (with a cuticularized bursa) and Conophoralia (with a soft bursa and giant sperm). Presently Filospermoidea comprise 2 families; and the Bursovaginoidea, 6 families. Gnathostomulid evolution, as suggested in this paper, can be characterized by the following trends: shortening of the body and rostrum proportions, differentiation of skin as well as epidermal inclusions and of paired sensory organs, concentration of pharynx musculature, lamellarization of jaws and row-like arrangement of teeth, differentiation of the basal plate, and a more permanent vagina. In the derived phylogeny, *Haplognathia* is the most primitive, and *Austrognatharia* the most advanced type. A hypothetical ancestral form is outlined and possible relationships briefly discussed. A complete and categorized bibliography is given.

INTRODUCTION

Known since the 1920's (Remane) but described only in 1956 by Ax, the marine worm group Gnathostomulida has attracted more and more interest during recent years. Initially, it was their enigmatic systematic position that led to the necessity of separating them from the Turbellaria and the creation of a new class (Ax, 1960). Subsequently, the rapid increase in knowledge of their morphology, biology and worldwide distribution made them one of the major faunistic discoveries of the last few decades.

At present, 18 genera with over 80 species are known to me, of which 12 genera and 40 species are described or in press. However, a systematic survey of the group is still lacking. Riedl's (1969) stimulating paper has already attracted a number of new students of the group especially in the United States, and with the appropriate extracting techniques now available (Sterrer, 1969, Uhlig, 1964, 1968), a considerable increase in new discoveries is to be expected. Zoogeographical considerations make it probable that the total number of gnathostomulid species will exceed 1,000.

Whereas the status of the Gnathostomulida as a group is beyond doubt, their position within the Scolecida (Lower Worms) is still undetermined, because they share characteristics with both Platyhelminthes and Aschelminthes. Owing to their complete ciliation, lack of anus, and rather turbellarioid reproductive system, they have been traditionally associated with freeliving flatworms. Other characters, however, distinguish them from flatworms, especially the pharynx, the quasi-lack of a parenchyma and the monociliary epithelium. Rather conclusive evidence against a close platyhelminth relationship of the Gnathostomulida has been produced recently (Rieger & Sterrer, in press): the presence of only one flagellum, with a 9 + 2 pattern, in the sperm tail of a representative of Filospermoidea. This is in sharp contrast to the well documented finds in Platyhelminthes (Hendelberg 1969, 1971) where biflagellate spermatozoa are the rule (in fact no monoflagellate spermatozoa are known in this group), and sperm flagella have a microtubular pattern devi-

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[1] Contribution number 534 from the Bermuda Biological Station for Research, Incorporated.

ating from 9 + 2 (with the exception of some acoel turbellarians).

The resulting dilemma is obvious. Incorporating the Gnathostomulida into the Aschelminthes would mean depriving an already heterogenous group of one of its few positive characteristics (possession of an anus in the free living groups). Inclusion of Gnathostomulida into the Platyhelminthes, on the other hand, means diluting this very homogenous taxon. Until further positive evidence for their relationship is available, therefore, it seems justified to give Gnathostomulida the rank of a separate phylum, as was first proposed by Riedl (1969).

Possible other relationships of the phylum have been suggested by paleontologists (Durden, Rodgers, Yochelson and Riedl, 1969) who compared gnathostomulid mouthparts with conodonts. Whereas the external resemblance is sometimes rather striking, internal structure and chemical composition need further comparative investigation before Gnathostomulida and Conodontophorida can be considered two classes of the same phylum.

The classification presented here has been arrived at by a stepwise process of recording and comparing of characters of specimens, populations, species and genera. Whenever possible, metric measurements were performed (Sterrer, 1969), and used for indices. It should be pointed out, however, that the hierarchic arrangement has been achieved solely by means of classical phyletics. The following considerations have been at the basis of this classification.

a) Filospermoidea are the only gnathostomulids with a flagellate sperm, and must therefore be the most primitive group with regard to this character.

b) Because the Filospermoidea (and in particular Haplognathiidae) are also the simplest gnathostomulids with regard to most other characters (see below), it is concluded that the general trend in the evolution of the Gnathostomulida was from the simple towards the complicated, rather than a series of reductions.

In order to spare the reader the tedious discussion and evaluation of every single character, the following sections are based on the above assumptions, and the resulting phylogenetic scheme shown in figs. 2–4 and 6. Six new genera that have been discovered by the author but not described as yet have been given roman numerals (genus *II, IV, V, VII, XI, XVI*) so they can be related to this scheme and referred to in future papers. General morphology and terminology are explained in fig. 1, using representatives of the three major groups (Filospermoidea, Scleroperalia, and Conophoralia). The basal plate and jaws of representatives of all described genera are illustrated in fig. 5, whereas fig. 7 gives the main types of spermatozoa.

The aim of this paper is to present data available up to now in a systematic manner (diagnoses of orders through genera), to draw inferred evolutionary patterns (figures and discussions of the different organ systems), and to enhance further work by directing attention to often neglected though important characters.

External Features

As a rule body shape in interstitial faunas is to a high degree an adaptation to the special environment and therefore not a very reliable systematic character. However, this seems to be different in Gnathostomulida. The principal changes of body index (length of body through maximum width) and rostrum index (length of rostrum, i.e., preoral part of the body,

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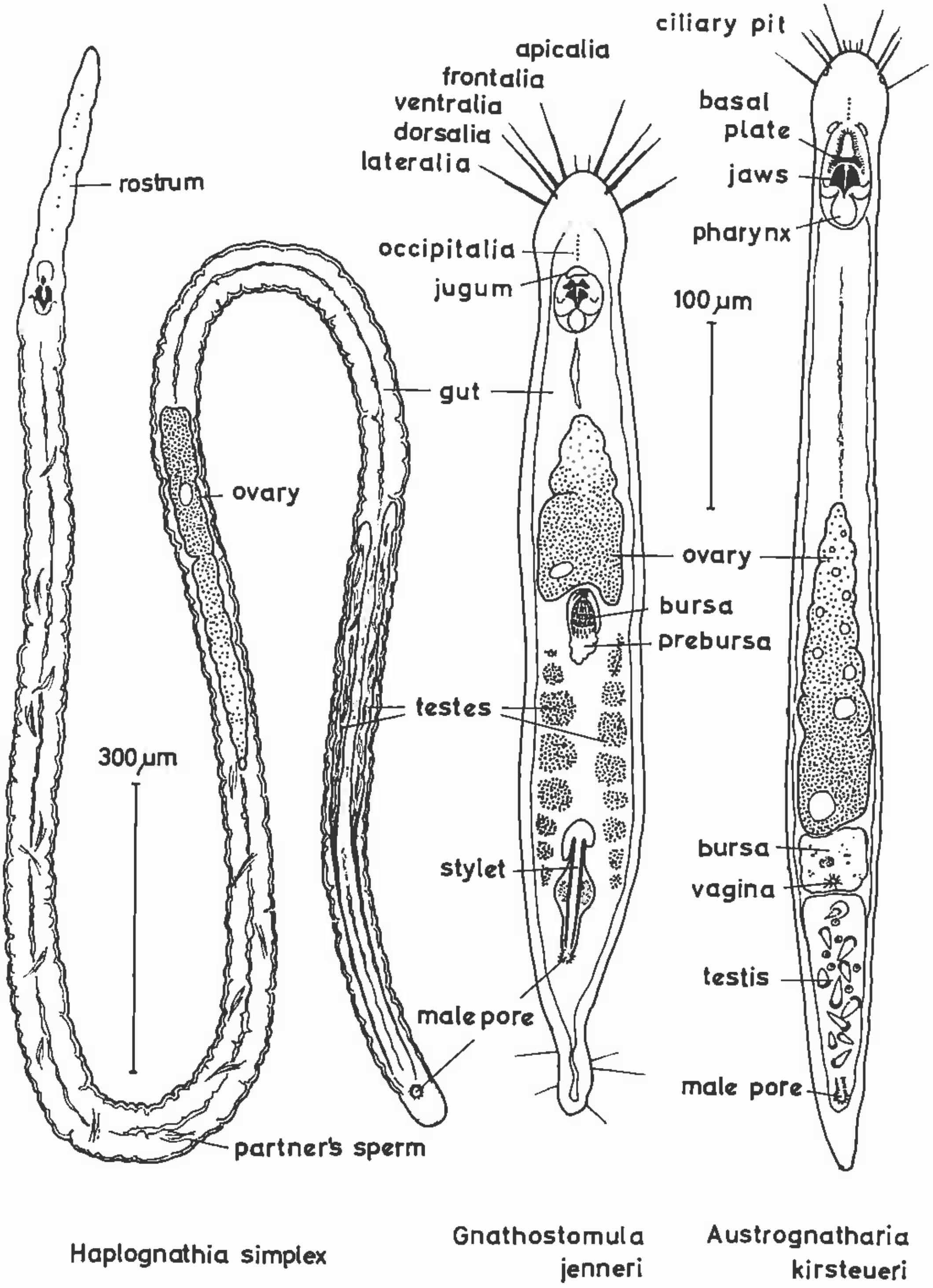
FIG. 1.—General morphology of Gnathostomulida. Representatives of Filospermoidea (*Haplognathia simplex* (Sterrer)), Scleroperalia (*Gnathostomula jenneri* Riedl), and Conophoralia (*Austrognatharia kirsteueri* Sterrer). The two latter are drawn to the same scale.


ciliary pit
apicalia
frontalia
ventralia
dorsalia
lateralia
basal plate
jaws
rostrum
pharynx
occipitalia
jugum
100 µm
gut
ovary
ovary
bursa
prebursa
testes
300 µm
stylet
bursa
vagina
testis
male pore
male pore
partner's sperm
Haplognathia simplex
Gnathostomula jenneri
Austrognatharia kirsteueri

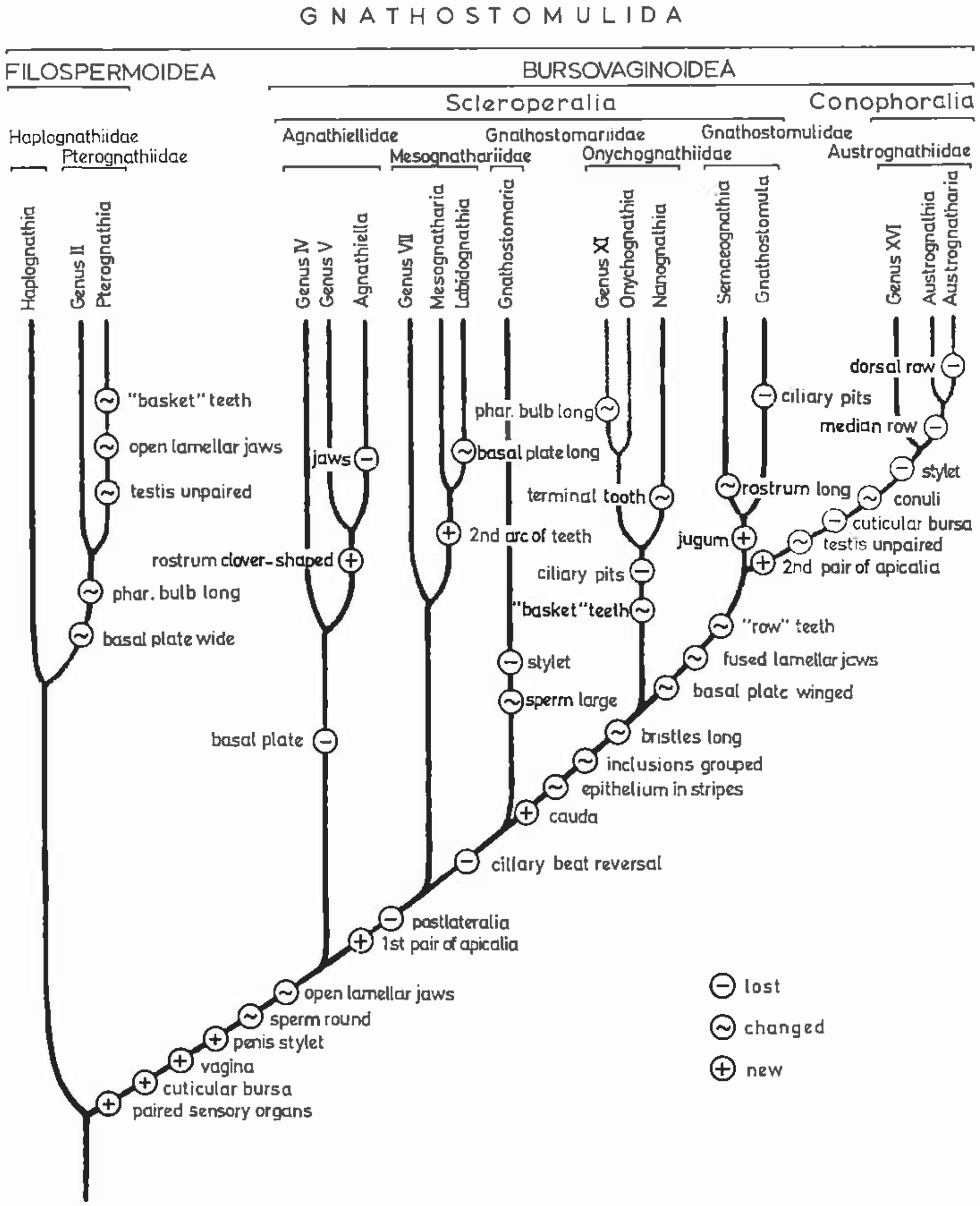


FIG. 2.—Systematics and relationships of Gnathostomulida. All major changes within the phylogeny of their characters are noted along the systematic pathways.

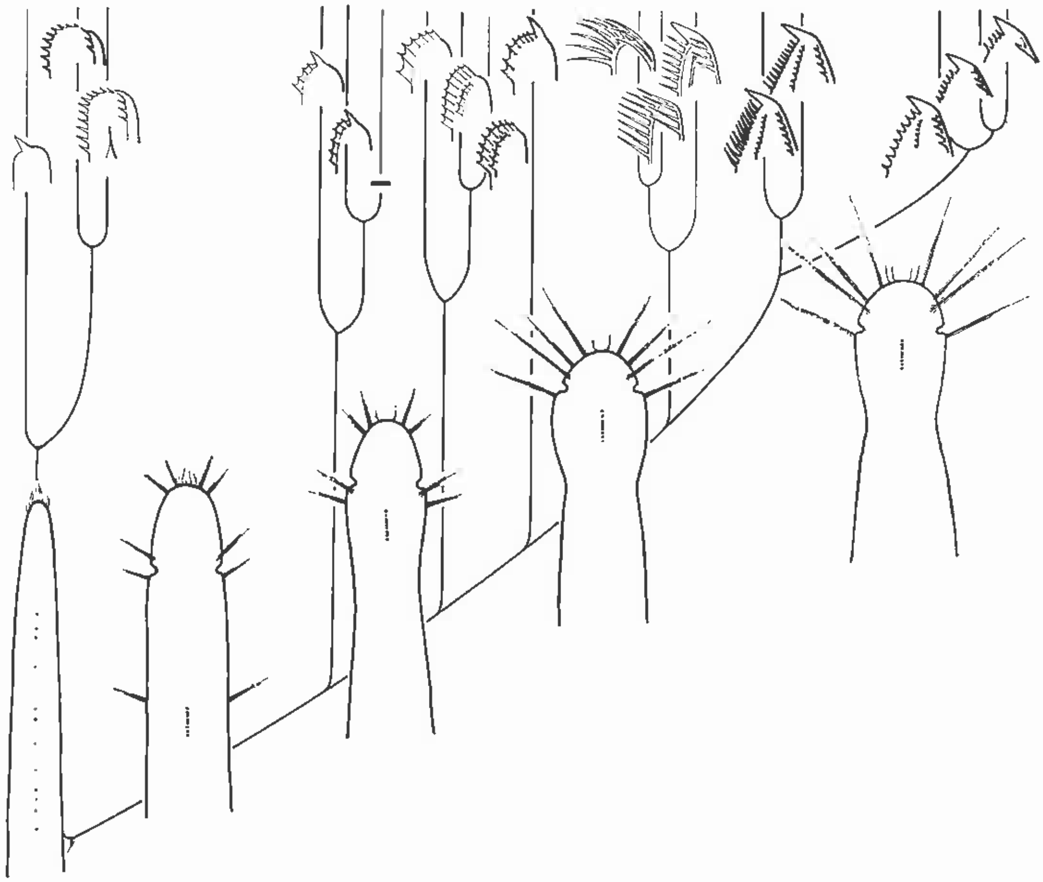


FIG. 3.—Relationship of types of tooth arrangement on jaws (above), and main rostrum and sensorium types (below) in Gnathostomulida.

through its maximum width) conform to the main evolutionary line (fig. 1). The body index, which is very high (up to 80) in the thread-shaped Filospermoidea, decreases steadily within the Bursovaginoidea, being still above 15 in the Mesognathariidae but dropping below 10 in Onychognathiidae, Gnathostomulidae and most Austrognathiidae. The same is true for the rostrum (fig. 1, 3). Whereas the Filospermoidea are characterized by an extremely elongated and pointed rostrum (index between 4 and 7.5), the Agnathiellidae have a much more rounded anterior end (index above 2), which becomes more and more compressed in the Mesognathariidae and Gnathostomariidae (about 1.5). Finally in the Onychognathiidae, Gnathostomulidae and Austrognathiidae, the rostrum index drops below 1, with the peculiar exception of *Semaeognathia* where it is over 2.5. This reduction of relative rostrum length is paralleled by an increase in length of the sensory bristles (fig. 3), which obviously compensates for the former function of the tip of the rostrum as a tactile organ. Other external features (such as color, or presence of a tail region) differentiate only lower systematic categories, without showing any regular pattern.

Skin and ciliation

The one-layered and completely monociliated skin epithelium is one of the most peculiar diagnostic characters of Gnathostomulida. It furthermore yields several clues for the internal classification of the group.

Skin differentiation

In the Filospermoidea and the lower Scleroperalia (including probably the Gnathostomariidae) the epidermal cells are rather large in diameter (4–5 μm), and their arrangement does not show any pattern. In the higher Scleroperalia as well as in the Conophoralia the cells are somewhat smaller (2–3 μm) and arranged in a very regular pattern: rows of 2 to 3 cells width converge in the ventral median line towards the rostrum, and in the dorsal median line towards the tail, thus forming inclined rhomb-like stripes around the body. This peculiar pattern is quite conspicuous on live specimens of Onychognathiidae and Gnathostomulidae, whereas it seems blurred in Austrognathiidae.

Epidermal inclusions

This skin differentiation is parallelled by a grouping of epidermal inclusions. Whereas epidermal inclusions are scattered over the whole body surface (with local concentrations, e.g., in front of the mouth opening) in the Filospermoidea and in the lower Scleroperalia (including the Gnathostomariidae), there are bundles of inclusions in the Onychognathiidae, and rows in the Gnathostomulidae and Austrognathiidae. In the two latter families, the inclusions are lined up in the furrows between the rows of epidermal cells.

There is some evidence that the two types of inclusions are not homologous. Whereas the "scattered" type in the lower Scleroperalia is almost certainly identical with the type called "round epidermal inclusions" (runde Hauteinschlüsse) in *Haplognathia* (Sterrer, 1969), the "grouped" type (which is usually more elongated and rather rhabdoid-like) might correspond to the "spindle-shaped epidermal inclusions" (spindelförmige Hauteinschlüsse) found in all Filospermoidea. As long as there is no further proof for this homology, it may be sufficient to distinguish between "scattered" and "grouped" epidermal inclusions.

Adhesive glands, composed of bundles of spindle-shaped rhabdoids, are to be found in the posterior body region of some Austrognathiidae. They are very probably a local differentiation of the "grouped" inclusions.

The body ciliation is entire. Although the length of cilia is somewhat greater in lower groups (20–25 μm) than in the Conophoralia (about 15 μm), this does not represent a noticeable trend.

Nervous system and sensory organs

The nervous system is probably as systematically important as it is difficult to analyse. It has been described as entirely basiepithelial in *Gnathostomula* (Ax, 1956), and was found to have a well-defined subepithelial brain in the Filospermoidea (Sterrer, 1968). A possible explanation for this discrepancy is that in the process of rostrum shortening and formation of sensory organs in the higher groups, the basal membrane was perforated to the extent that a basiepithelial situation of the nervous system is simulated.

Contrary to earlier descriptions in which the sensory organs were dealt with rather casually, this feature turned out to be of utmost importance (fig. 1,3). Common to all Gnathostomulida is a medio-dorsal row of single cilia (occipitalia). Paired sensory organs, on the other hand, are completely lacking in the Filospermoidea (where the long rostrum probably functions as a tactile organ), whereas they are present in the Bursovaginoidea in the form of ciliary pits and single and united sensory cilia.

Ciliary pits, situated rostrolaterally on the rostrum, are present in all lower Scleroperalia (including *Gnathostomaria*), as well as in the Conophoralia. In contrast, they are secondarily lacking (or reduced below perceptibility with light micros-

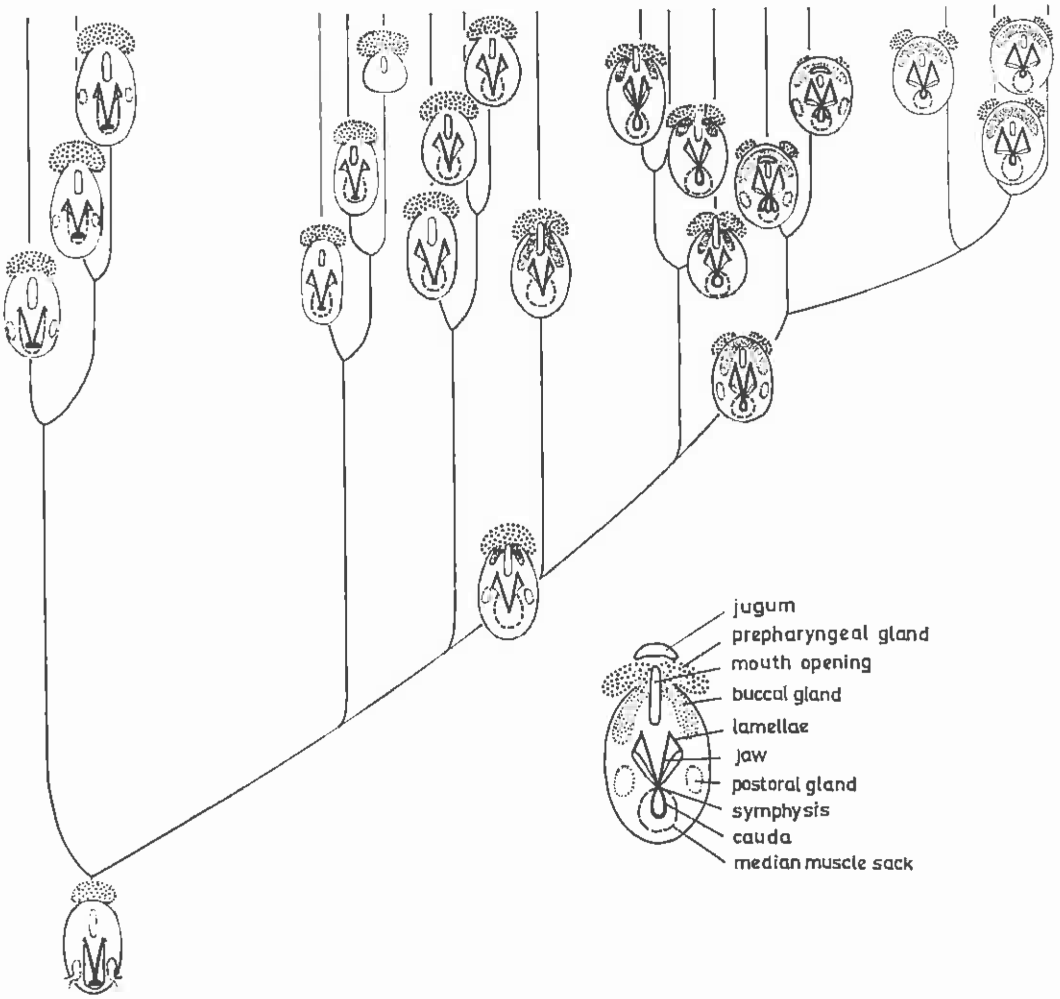


FIG. 4.—Patterns of the relationship of pharynx, jaws and glands in Gnathostomulida (basal plate omitted).

copy) in the Onychognathiidae and in *Gnathostomula*. The occurrence of two pairs of ciliary pits close to each other, as well as an unpaired pit at the tip of the rostrum, both observed in some lower Scleroperalia, are not evident enough to enter phylogenetical considerations.

Single sensory cilia (apicalia) differentiate first within Mesognathariidae (although not very well defined in *Labidognathia*) from a bundle of equal cilia at the tip of the rostrum. They are present throughout the higher Bursovaginoidea as one pair: a second pair is added in the Conophoralia.

Compound sensory bristles are first found at the basis of the Bursovaginoidea. As to their structure and arrangement, 4 trends can be observed. First, a reduction from 5 pairs (including the postlateralia, in *Agnathiella*) to the common 4 pairs (rostralia, ventralia, dorsalia, and lateralia) and even the situation in *Semaeognathia*, where the dorsalia seem to be reduced; second, an increase in length from about 30 μm (e.g., *Mesognatharia*) to over 60 μm (e.g., *Onychognathia*); third, an increase in stability (in the lower families the bristles seem to be less coherent and disintegrate more readily during preparation than in higher groups). Fourth, in addition to a general decrease of distance between the bristles (which goes along with the shortening of the rostrum) a shifting of relative positions takes place. This affects especially the ventralia and dorsalia, which, in lower Scleroperalia, are close to the rostralia and the lateralia, respectively, but in higher Scleroperalia as well as in the Conophoralia are so close to each other that they almost coincide in dorsal view.

The position of the ciliary pits with respect to the dorsalia (rostrally in Mesognathariidae, caudally in all others) seem to have less importance, since these two structures are situated on different vertical body levels and therefore would not interfere with each other in horizontal shiftings along the circumference of the rostrum.

Parenchyma, excretory organs and body musculature

Parenchyma is very poorly developed and reaches measurable dimensions only in the rostrum and around the genital organs.

Excretory organs have been recently found in both of the genera which, so far, have been investigated with ultrastructural techniques, *Gnathostomula* and *Austrognathia* (Graebner, 1968a). They are cyrtocytes of somewhat unusual structure which, in paired groups of 2–3, are situated in the parenchyma laterally to the bursa and the penis.

Body musculature seems to follow a very similar pattern throughout the class and consists of 3–4 paired groups of rather strong longitudinal fibres under a thin layer of fine circular fibres.

All of these structures are either not rich enough in detail or not sufficiently known to be considered in the present discussion.

Pharynx and gut

The pharyngeal apparatus, along with the jaws and basal plate, furnishes important systematic characters, but is still far from being exhausted in this respect. However, only one and probably the simplest pharynx type has been thoroughly analyzed to date (Sterrer, 1969). Therefore, except for simple relations and the conspicuous "jugum", the following considerations have not as yet entered the diagnoses (fig. 4).

Concentration of musculature

Whereas in Haplognathiidae the pharynx musculature can be described as a more or less loose network surrounding the buccal cavity, it becomes progressively centralized in the Scleroperalia and is finally almost capsular in Gnathostomulidae.

Tripartition of pharynx musculature

As was noticed in the first descriptions of *Gnathostomula* (Ax, 1956), the pharynx displays a division into a median and a pair of lateral muscle sacs (fig. 1), which are not present in the Filospermoidea (Sterrer, 1969). Although the exact morphology as well as the functional pattern of this pharynx type is still unknown, it can be said that this tripartition first appears more or less clearly in Mesognathariidae, and is most conspicuous in Gnathostomulidae and Austrognathiidae. The clearness of this arrangement probably depends on the insertion of the median muscle sac at the jaws. Whereas in Mesognathariidae the median muscle sac is rostrally rather open, inserting close to the anterior end of the jaws and surrounding the symphysis, it is closed in the Gnathostomulidae and Austrognathiidae, where it inserts at the symphysis and extends caudally from it. Assuming that the original situation corresponded to the one found in the Haplognathiidae, the muscle which is most likely to correspond would be the abductor (Sterrer, 1969, fig. 30–31, 88–89). This homology, however, would imply a considerable change in the functional pattern of pharynx musculature.

Shorter evolutionary lines are present in Pterognathiidae and Gnathostomulidae. Unlike *Haplognathia,* the Pterognathiidae have a larger pharynx bulb, both absolutely and in relation to the jaw length. This is expressed in the pharynx index (length of pharynx squared, divided by the length of jaws). It is very low in *Haplognathia* (between 0.4 and 6) and reaches a maximum of more than 13 in *Pterognathia,* which can be attributed to the much longer constrictor muscle (Sterrer, 1969).

Jugum

The presence of a "jugum" characterizes only the Gnathostomulidae (fig. 1, 4). This is a cartilaginous, crescent-shaped body situated rostrally to the mouth opening in the epithelium of the mouth cavity. Its function is probably to prevent the mouth opening from being tied off (collapsing) during contraction of the rostral pharynx muscles (especially the protractor of the basal plate).

Glands (fig. 4)

Several buccal or pharyngeal glands have been described, which have been named pre-pharyngeal glands (or preoral glands, in Haplognathiidae and all lower Scleroperalia, including the Onychognathiidae), lateropharyngeal glands (Austrognathiidae), buccal glands (Gnathostomariidae through Austrognathiidae) and postoral glands (Filospermoidea and Gnathostomulidae). The evolutionary line for the glands surrounding the mouth opening (the former three) seems to be the following. During the process of concentration of the pharyngeal musculature an unpaired pre-pharyngeal gland (derived from ectodermal mouth epithelium and present as such in Filospermoidea through Mesognathariidae) is longitudinally divided by the mouth opening. This stage is most clearly represented in the Onychognathiidae but can be observed already in the Gnathostomariidae. Whereas the posterior part now migrates still deeper towards the buccal cavity which it finally surrounds in a horseshoe-like manner, the anterior part, now cut in two, remains outside the pharyngeal capsule. This latter stage is represented in the Austrognathiidae, whereas in the Gnathostomulidae, the paired pre-pharyngeal glands are vestigial in *Semaeognathia* and lacking in *Gnathostomula.* Postoral glands, probably derived from entodermal material, are situated laterally to the jaws and have been found in both the Filospermoidea and Gnathostomulidae. Their homology still remains rather doubtful.

Gut

Apart from several types of seemingly irregular intestinal inclusions, the gut is too uniform within the class to present any phylogenetic clues.

Basal Plate

A common feature of all basal plates (fig. 5) is the somewhat stronger cuticularization of the frontal edge. Two general trends (fig. 6) can further be observed: a decrease of the basal plate index (i.e., decrease of length versus width, leading to a transverse rod or lamella) and a specialization of the median part going along with the differentiation of teeth.

Both of these tendencies are accomplished independently within the Filospermoidea (Pterognathiidae) and the higher Bursovaginoidea (especially the Austrognathiidae). In both groups tooth formation seems to take place at the frontal edge of the basal plate. Whereas the teeth remain there in Gnathostomulidae, they move towards the caudal edge in the Austrognathiidae, *Genus XVI* being a rather conclusive link between the two. The four longitudinal ridges, structures, which, at first sight, one might tend to neglect, seem to be at the basis of a major transformation of the outline. Although the lateral pair may be almost completely reduced, the median pair is present in all basal groups, including the Onychognathiidae. There is strong evidence that the outer parts of the basal plate swung forward to form the rostral wings (strong in the Gnathostomulida, feeble in the Austrognathiidae) and the inner parts extend laterally to form the lateral wings (which are dominant in Austrognathiidae).

Smaller evolutionary sidelines are repre-

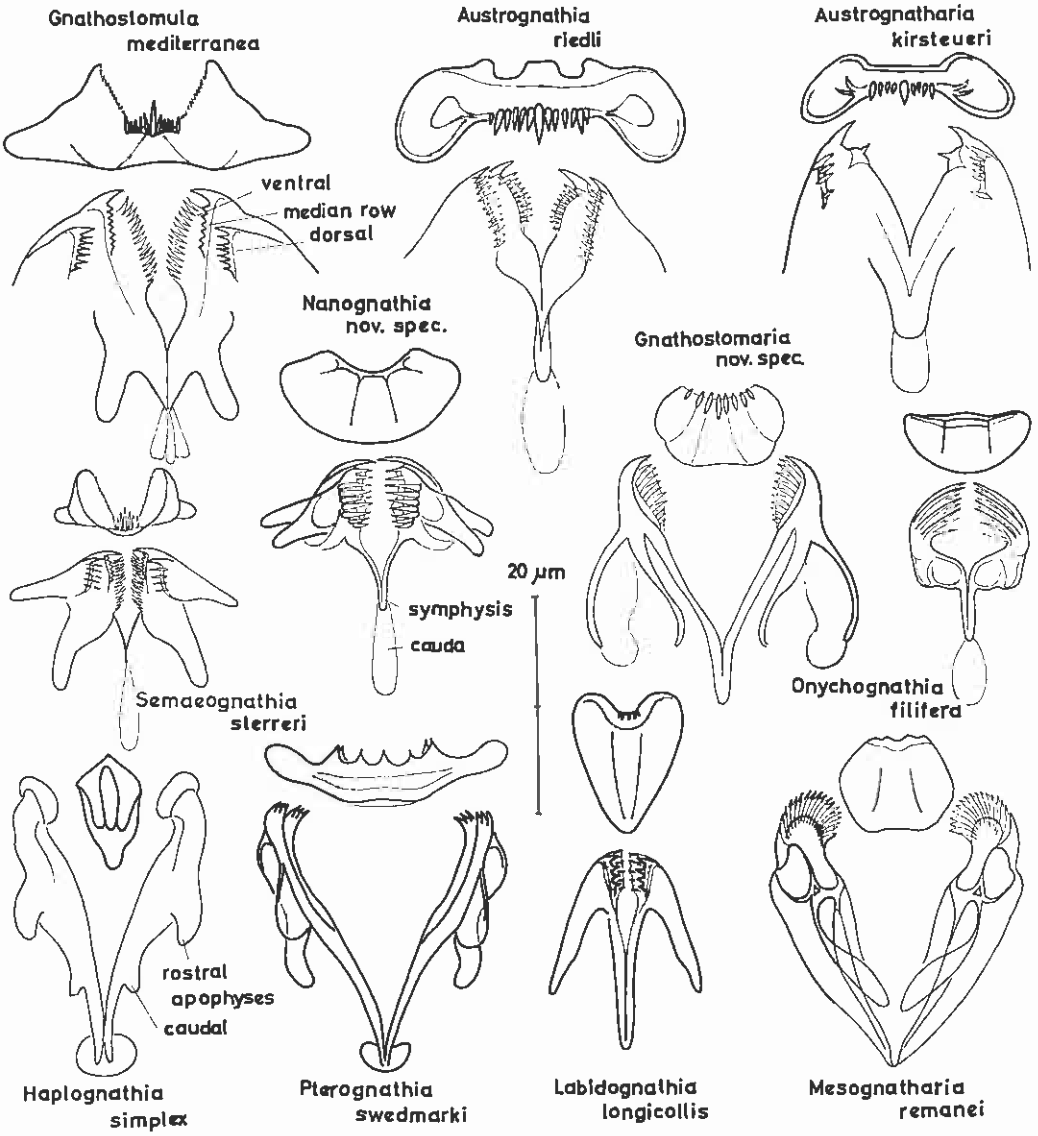


FIG. 5.—Basal plate and jaws of representatives of the described genera of Gnathostomulida. Some in dorsal, some in ventral view. All in the same scale.

sented by the reduction of the basal plate in some Agnathiellidae and Mesognathariidae, and the increase of the basal index in Labidognathia. In spite of a certain structural variety and the extreme difficulty which its analysis often presents, the basal plate can be regarded as a character of high phylogenetic value.

Jaws

The jaws (fig. 5) like the basal plate can be conceived as a local cuticularization of the ventrolateral epithelium of the mouth cavity.

Three major trends can be traced along the evolutionary line (fig. 3). First the rather compact jaws, present in the lower

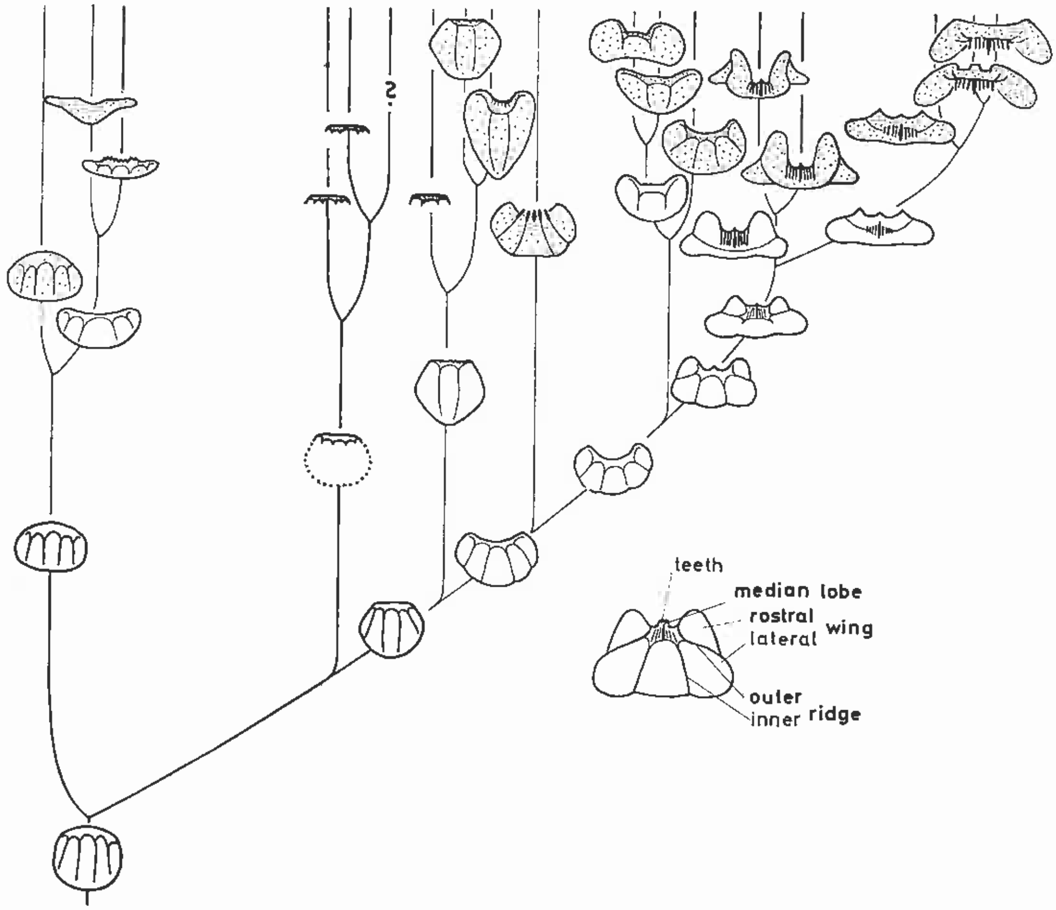


FIG. 6.—Patterns of the relationship of basal plates in Gnathostomulida (hypothetical forms left undotted).

Filospermoidea (Haplognathiidae), tend to become more and more lamellarized both towards Pterognathiidae and the Bursovaginoidea. The functional implication of this process can clearly be seen in the transition from the *Haplognathia* to the *Pterognathia* type (Sterrer, 1969). In *Haplognathia*, the entire lateral surface of the jaws is embedded in the wall of the mouth cavity ("compact type") but the formation of a dorsolateral crista and a ventrolateral lamella in *Pterognathia* makes the jaws protrude much further into the lumen, which results in their greater mobility. The muscles, in this case, insert laterally between the two lamellae. Attained independently and with more or less variation, this "open lamellar type" is represented in the Pterognathiidae and in the lower Scleroperalia, including the Onychognathiidae. In the Gnathostomulidae and Austrognathiidae, however, this process has gone still further. The dorsal and ventral lamellae have fused laterally ("fused lamellar type"), beginning at the anterior tip of the jaw (which stage is almost anticipated in e.g., *Labidognathia*). Consequently, each jaw half forms a hollow cone pointing rostrally and the muscles entering from behind insert interiorly. The lamellarization of the jaws also affects the symphysis, which loses more and more of its substance and is finally a simple suture in the fused lamellar type.

A second trend is manifest in the arrangement (and number) of the teeth. Three types can be distinguished which are comparable with each other.

1. The "arc type" is probably the ancestral type of tooth arrangement. It is characterized by a few teeth bordering the ventro-rostral edge of the jaw. The most anterior tooth can be differentiated as a longer end-tooth, or the teeth are all of more or less equal size. This type is found in most of the Filospermoidea and in the lower Scleroperalia (including the Gnathostomariidae). In the latter group, the teeth are basally interconnected by a cuticular membrane, possibly a very primitive condition in which the teeth are not yet entirely separated. Within the Mesognathariidae, a second and usually very delicate arc of teeth may be developed on the dorsal side of the membrane, possibly as a differentiation of the main teeth.

2. The "basket type" can readily be understood as an arc which is prolonged dorsally so that the teeth, which in this case are also much longer, enclose a semicircular space. It is represented in some Pterognathiidae, and is found in its most extreme form in the Onychognathiidae. In this type, all the teeth are usually of equal size, except in the genus *Nanognathia,* which develops a terminal tooth.

3. The "row type" can be derived from the basket type by assuming that a terminal tooth divides the basket into two, which then flattens. Consequently, the arrangement of teeth becomes row-like. This stage is anticipated to some extent in the genus *Nanognathia.* Very probably, a third (median) row of teeth was added at an early stage of this line, because in both the Gnathostomulida and the Austrognathiidae types with three rows are present.

Evolutionary side-lines of somewhat minor consequence are to be observed in at least three different branches. One is the reduction of jaws in the Agnathiellidae, culminating in their complete loss in the genus *Agnathiella.* A second is a reduction of rows of teeth in the Austrognathiidae, starting at three rows in *Genus XVI*, proceeding to two rows in *Austrognathia* (loss of median row) and ending in the *Austrognatharia,* where the dorsal row is reduced to one single tooth. The third line (fig. 4) starts with the acquisition of a "cauda" (a hyaline caudal appendage of the symphysis) somewhere before the Onychognathiidae, which is also present in Austrognathiidae and Gnathostomulidae. In the latter family, the cauda is bordered by a pair of lateral appendages which are particularly long in *Semaeognathia* (Riedl, 1970b). There is some evidence that the cauda is connected with an incisive change in the muscular pattern of the pharynx.

Although the main line of jaw evolution seems to be well established, many minor points are still obscure. This applies especially to the different apophyses and their homology, and to their exact lines of jaw lamellarization. An intensive three-dimensional analysis of jaw structure on the live animal, complemented by electron microscopy studies, should provide further clues.

Male organs

The male organs basically consist of testes and a more or less developed copulatory organ ending in a subterminal ventral opening (fig. 1).

Paired ventrolateral testes, situated in the posterior body region, can be postulated for the ancestral form. They are independently fused into an unpaired dorsal testis in *Pterognathia* and in the Conophoralia; in the latter case, the origin of the unpaired testis from paired anlagen was observed in an early adult. Whether the more follicular (in Gnathostomulidae and Onychognathiidae) or more tubular testes (e.g., in *Gnathostomaria*) are of higher systematic value, must await more material.

There are three major types of sperm

(fig. 7), which, so far, are structurally very distant from each other.

1. The filiform type (fig. 7F, G), typically consisting of a spiralized head, a middle piece and a tail (Sterrer, 1969) has given its name to the Filospermoidea and is not found anywhere else within the Gnathostomulida.

2. The dwarf type occurs in the Scleroperalia, and can be divided into three subtypes:

a) the small round type, found in *Agnathiella* (fig. 7C), Mesognathariidae and—strange reminiscence—in a *Gnathostomula* species (fig. 7B);

b) the large round type, which is an exclusive feature of Gnathostomariidae (fig. 7A), and functionally connected with the very reduced stylet of this genus; and

c) the droplet type, found in Onychognathiidae (fig. 7D) and with the above exception in the Gnathostomulidae (fig. 7E).

Light as well as electron microscopy (Graebner 1968, 1969; Riedl, 1971b) have shown that these three subtypes basically follow the same structural pattern: a round or more or less elongated sperm body which bears a row or bunch of short, nonciliary filaments.

3. The "conulus" type (fig. 3H), typically consisting of hat, cingulum, body and matrix (Sterrer, 1970a) is still the most puzzling. Whereas there is much evidence for the conulus (which can be up to 45 µm long) being a single giant sperm, it cannot yet be excluded that it represents a spermatophore. However, this does not seem to have too much importance for phylogenetical speculations, because both alternatives can be derived from the dwarf type. As a spermatophore it could have its origin in the pre-bursae (or testes follicles) of, for example, the Gnathostomulidae (Riedl, 1971b), as a giant sperm it could have branched off early in spermatogenesis ("neotenous sperm").

A typology for the male organ (fig. 1) would list two main forms: the simple glandular, non-injectory male opening (which can hardly be called a penis) of the Filospermoidea, and the glandular and muscular penis, provided with a stylet in the Scleroperalia, and without a stylet in the Conophoralia. The stylet which is usually straight, is typically composed of a dozen cuticular rods forming a tube around the male canal. It is elongated, only faintly cuticularized and slightly bent in the Gnathostomariidae, probably in connection with the much larger sperm.

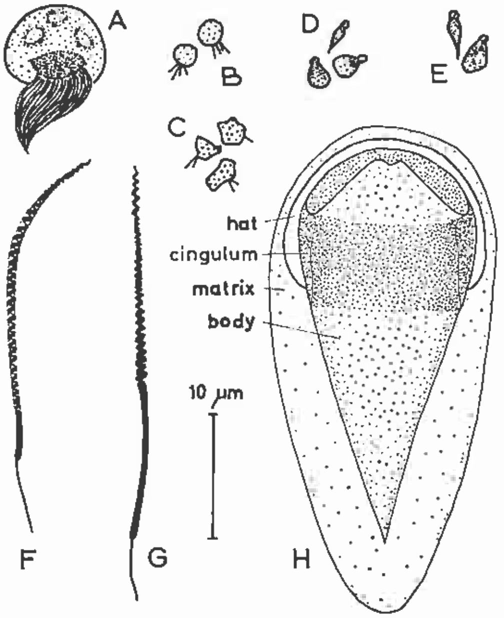


FIG. 7.—Sperm of some representatives of the Gnathostomulida. A. ***Gnathostomaria*** **sp.** nov.; B. ***Gnathostomula*** *jenneri* Riedl; C. *Agnathiella beckeri* Sterrer; D. *Onychognathia filifera* Riedl; E. *Gnathostomula microstyla* Riedl; F. ***Pterognathia swedmarki*** Sterrer; G. *Haplognathia* ***simplex*** (Sterrer); H. ***Austrognathia*** *riedli* Sterrer. All to the same scale.

Glands surrounding the stylet seem to produce at least two types of secretion in the Scleroperalia; a fine granular type which sheathes the stylet, leaving only the proximal part uncovered, and a coarse granular type forming an outer ring around the proximal part. There is strong evidence that a very similar gland structure persists in the Conophoralia, although the stylet there is completely reduced and is compensated for by a much stronger musculature. The exact arrangement of the glands seems to follow a certain trend, but it is not yet possible to incorporate it in these considerations.

A more or less muscular vesicula seminalis is usually more readily recognizable in the lower Scleroperalia than it is in higher; however, no distinct pattern could be traced on the basis of the present material.

Female organs

Three structures have to be dealt with: the ovary, the bursal organ and the vagina (fig. 1).

The ovary is the most conservative feature throughout the class. It is unpaired and situated dorsally in the midbody region, the eggs maturing towards the caudal end. The only trend seems to be that the mature (i.e., the most caudally situated) egg is slightly larger in the lower groups (Filospermoidea and the lower Scleroperalia) than in the higher Scleroperalia and Conophoralia.

The bursal organ is lacking in the Filospermoidea, where sperm from copulation can be found scattered in the gut epithelium and even in the rostral parenchyma. It is present and situated dorsally, behind the ovary, as a cuticularized lamellar sack (which itself, is probably embedded in bursa tissue) in the Scleroperalia (hence the name: Scleros—hard, and peros—sack) or as a soft pouch in the Conophoralia.

The cuticular bursal organ consists of a rather stable anterior part (the bursa sensu stricto, which ends frontally in an even more cuticularized "mouthpiece") and a rather variably shaped posterior part (the bursa appendix or prebursa). This type of a bursal organ is more or less the same in all Scleroperalia, and the differences within the group (e.g., bursa very small in *Semaeognathia*, or presence of a prebursal collar in some *Gnathostomula* species) do not seem to follow a recognisable evolutionary line. Recently, Riedl (1971b) has proposed a very valuable classification of the different stages of bursal organs which can be met within some species of *Gnathostomula*. Assuming that the bursa is formed after the first copulation, and then emptied towards the eggs, each further copulation would add another prebursa which then joins posteriorly and refills the bursa. In a modification of this cycle (which can be found in the same species) the bursa can be completely reabsorbed and is rebuilt from the prebursa injected at the following copulation. This hypothesis, based on comparative measurements of body size and bursa dimensions, is strongly supported by a number of further observations (e.g., the process of fusion between bursa and prebursa, or the presence of a "decay" bursa together with an "early" bursa). Differences in this bursal cycle, already noticed within the genus *Gnathostomula*, are to be expected in other Scleroperalia as well, and may soon provide valuable systematic clues.

Whereas a vagina is completely lacking in the Filospermoidea, such an organ, situated dorsally behind the bursa, is present in the Bursovaginoidea in however a rather scattered distribution. The Conophoralia are the only group which is characterized by a permanent vagina. In the Scleroperalia, the vagina seems to be rather a facultative stage appearing before or after copulation, and becoming more permanent in several scattered species (e.g., in some *Gnathostomula* species, in *Onychognathia filifera*, and probably in *Agnathiella beckeri*). Although a vagina can be assumed for the ancestral type of Bursovaginoidea, its presence or absence is not a character of higher rank within this order.

Ancestral form

On several occasions, the previous discussion converged towards a hypothetical ancestral form. In view of the recent (and most probably future) new discoveries it seems somewhat premature to engage too much in speculations about the origin and relationships of the Gnathostomulida. Nevertheless, the evolutionary tree drawn in the present paper should not be left without taking a brief glance at its roots.

The ancestral form of Gnathostomulida emerges as a fairly slender worm with an equally slender and undelimited rostrum, and without paired sensory organs. The skin is completely monociliated and possesses scattered epidermal inclusions. Excretory organs of the cyrtocyte type are present in a poorly developed parenchyma The pharynx is a simple muscular network, with only fairly cuticularized mouth parts consisting of an almost round, four-ridged basal plate and solid or slightly lamellarized jaws with a few teeth in an arc-like arrangement. An unpaired prepharyngeal and paired postoral glands are present. The ovary is unpaired and dorsally situated in the anterior body region; the eggs mature caudally. No bursa or vagina is developed. The testes are paired, situated ventrolaterally in the posterior body region, and end subterminally in a simple ventral male pore. The sperm has one flagellum, with a 9 + 2 microtubular arrangement.

Without discussing in detail the possible relationships which such an ancestral form might imply, I would like to briefly list the suggestions that have so far been put forward.

A platyhelminth relationship is strongly opposed by the possession of only one spermtail, with a 9 + 2 pattern, in filospermoid Gnathostomulida. The turbellarian order Catenulida, however, shares several morphological features with gnathostomulids: 1. the sparse ciliation as well as the ability to reverse the ciliary beat; 2. the tendency towards aberrant sperm; 3. the quasi-lack of parenchyma. In addition, a new family of marine Catenulida (Sterrer & Rieger, 1972) was found to occur in exactly the same biotope as the Gnathostomulida. This implies a certain similarity in physiological requirements which, in the case of morphological conformity, would strengthen the above argument. It fits into the picture that doubts have been expressed (Sterrer & Rieger 1972) as to the turbellarian or even platyhelminth character of the Catenulida.

Rotatoria and Gnathostomulida show a certain similarity in the ultrastructure of their cuticular mouth parts (Riedl, personal communications). However, as no other taxonomic groups with comparable cuticularisations (such as Nematoda, Gastrotricha, Kinoryncha, Sipunculida and Polychaeta) have been studied in this respect, this evidence cannot be regarded as very strong. It has been suggested that the Conodontophorida are an extinct branch of Gnathostomulida. This conclusion is premature for the only positive evidence so far is a certain degree of likeness in external shape.

As far as other taxonomic groups (Gastrotricha, Archiannelida) are concerned, no further data have been produced that would support a possible relationship.

DIAGNOSES

Phylum Gnathostomulida nov. phyl.

Small free-living, worm-shaped acoelomate Bilateria, with a muscular pharynx usually provided with paired jaws and an unpaired cuticular basal plate. Without an anus. Epidermis monociliated. Parenchyma poorly developed. Hermaphrodites.

Distribution: exclusively marine so far.

Order Filospermoidea nov. ord.

Gnathostomulida with filiform sperm, and without a bursa and vagina. Male opening without an injectory penis. Without paired sensory organs on the rostrum, but with occipitalia. Body usually very elongated (body index at least 25); rostrum pointed and slender (index usually more than 3), and not delimited. Pharynx musculature rather loose; jaws more or less compact, with wing-shaped apophyses and a solid symphysis which is usually wider than long.

TABLE 1. SYNOPSIS OF THE CHARACTERISTIC FEATURES OF THE GENERA OF THE GNATHOSTOMULIDA.

		Genera								
	Characters	Haplognathia	Genus II	Pterognathia	Genus IV	Genus V	Agnathiella	Genus VII	Mesognatharia	Labidognathia
External features	Body index	25–80	?	26–46	?	?	13.3	15.1	22.4	20.0
	Rostrum index	2.5–7.5	5.5	4.5	2.7	2.4	2.0	1.7	1.5	1.7
	Ability to swim backwards	[1] –	–	–	+	?	+	+	?	+
	Epithelium in stripes	–	–	–	?	?	–	–	–	–
	Rhabdoids	–	?	–	?	?	–	–	–	–
	Tail	–	–	–	?	–	–	–	–	–
Sensorium	Ciliary pits	–	–	–	+	+	+	+	+	+
	Apicalia, and number of pairs	–	–	–	?	?	–	1	1	?
	Rostralia	–	–	–	+	+	+	+	+	+
	Ventralia	–	–	–	+	+	+	+	+	+
	Dorsalia	–	–	–	+	+	+	+	+	+
	Lateralia	–	–	–	+	+	+	+	+	+
	Postlateralia	–	–	–	+	?	+	–	–	–
	Occipitalia	+	?	+	?	?	+	+	+	+
	Max. length of bristles, in μm				~30	?	30	30	30	30
	Ventralia—dorsalia approached				?	?	–	–	–	–
Pharynx	Basal plate index	0.40–1.65	0.28	0.29–0.36				0.6	1.0	1.2
	Number of rows of teeth on jaws	0–1	1–2	2	1	1		1	1–2	2
	Jaws lamellarized	–	–	±	–	–		±	+	+
	Cauda	–	–	–	–	?	–	–	–	–
	Jugum	–	–	–	–	–	–	–	–	–
	Pharyngeal bulb 3-partite	–	–	–	–	–	–	–	±	–
Genital organs	Bursa	–	–	–	?	?	+	+	+	+
	Bursa cuticularized				?	?	+	+	+	+
	Permanent vagina	–	–	–	?	?	?	–	–	–
	Number of testes	2	?	1	?	?	2	2	2	2
	Penis stylet	–	?	–	?	?	+	+	+	+
	Sperm, filiform type	+	+	+	–	–	–	–	–	–
	dwarf type	–	–	–	?	?	+	+	+	+
	conulus type	–	–	–	–	–	–	–	–	–

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[1] In Filospermoidea, the caudal cilia beat in reverse; however, this does not result in swimming backwards.

Table 1. *(continued)*

		Genera								
	Characters	Gnathostomaria	Genus XI	Onychognathia	Nanognathia	Semaeognathia	Gnathostomula	Genus XVI	Austrognathia	Austrognatharia
External features	Body index	15.7	8.3	7.8	5.7	10.5	6–10	?	6–13	6–14
	Rostrum index	2.0	1.5	1.0	1.0	2.4	0.7–1.4	0.9	0.9–1.0	0.8–1.4
	Ability to swim backwards	–	–	–	–	–	–	?	–	–
	Epithelium in stripes	–	+	+	+	+	+	?	±	±
	Rhabdoids	-	+	+	+	?	+	?	+	+
	Tail	–	+	+	+	±	+	–	–	-
Sensorium	Ciliary pits	+	–	–	–	+	–	–	–	–
	Apicalia, and number of pairs	1	1	1	1	1	1	2	2	2
	Rostralia	+	+	+	+	+	+	+	+	+
	Ventralia	+	+	+	+	+	+	+	+	+
	Dorsalia	+	+	+	+	±	+	+	+	+
	Lateralia	+	+	+	+	+	+	+	+	+
	Postlateralia	–	–	–	–	–	–	–	–	–
	Occipitalia	+	+	+	+	+	+	+	+	+
	Max. length of bristles, in µm	35	50	60	70	40	65	?	40	55
	Ventralia—dorsalia approached	–	±	±	±	?	+	?	+	+
Pharynx	Basal plate index	0.6	0.3	0.5	0.5	0.5	0.4	0.3	0.3	0.3
	Number of rows of teeth on jaws	1	[2](2)	(2)	(2)	3	3	3	2	1
	Jaws lamellarized	±	+	+	+	+	+	+	+	+
	Cauda	–	+	+	+	[3](+)	(+)	+	+	+
	Jugum	–	–	–	–	+	+	–	–	–
	Pharyngeal bulb 3-partite	±	+	+	+	+	+	+	+	+
Genital organs	Bursa	+	+	+	+	+	+	+	+	+
	Bursa cuticularized	+	+	+	+	+	+	–	–	–
	Permanent vagina	–	–	–	–	–	±	+	+	+
	Number of testes	2	2	2	2	2	2	1	1	1
	Penis stylet	±	+	+	+	+	+	–	–	–
	Sperm, filiform type	–	–	–	–	–	–	–	–	–
	dwarf type	+	+	+	+	+	+	–	–	–
	conulus type	–	–	–	–	–	–	+	+	+

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[2] Teeth arranged in an arc rather than in rows.
[3] Cauda highly modified.

Family Haplognathiidae nov. fam.

Filospermoidea with a short pharyngeal bulb (index usually less than 8.0). Basal plate longer, or equally long as wide, or only slightly wider than long (index more than 0.5), often with teeth or ridges on its dorsal surface. Jaws compact, without a crista, and with no or few teeth arranged in a ventro-lateral arc.

One described genus (*Haplognathia* Sterrer).

Genus *Haplognathia* Sterrer, 1970a

Haplognathiidae with simple and not horizontally bipartite jaws without or with very few teeth (usually not more than 5). Testes paired.

Type species: *H. ruberrima* (Sterrer, 1969).

10 described species: *H. simplex* (Sterrer, 1966a), *H. filum* (Sterrer, 1966a), *H. ruberrima* (Sterrer, 1966a), *H. rubromaculata* (Sterrer, 1969), *H. rosea* (Sterrer, 1969), *H. gubbarnorum* (Sterrer, 1969), *H. lunulifera* (Sterrer, 1969), *H. lyra* Sterrer, 1970a, *H. rosacea*, Sterrer, 1970a.

About 6 undescribed species.

Family Pterognathiidae nov. fam.

Filospermoidea with a long pharyngeal bulb (index usually more than 8.0). Basal plate much wider than long (index less than 0.5), often with teeth at the frontal edge. Jaws often slightly lamellar, with a crista, and with several to many teeth arranged in a ventro-lateral arc or a ventro-rostro-dorsal basket.

One described (*Pterognathia* Sterrer), one undescribed genus.

Genus *Pterognathia* Sterrer, 1966a

Pterognathiidae with more or less lamellar and horizontally bipartite jaws with a crista, with many teeth (usually more than 5). Testis usually unpaired and situated dorsally.

Type species: *P. swedmarki* Sterrer, 1966a.

6 described species: *P. swedmarki* Sterrer, 1966a, *P. meixneri* Sterrer, 1969, *P. atrox* Sterrer, 1969, *P. sorex* Sterrer, 1969, *P. grandis* Kirsteuer, 1969a, *P. ctenifera* Sterrer, 1970a.

About 4 undescribed species.

Order Bursovaginoidea nov. ord.

Gnathostomulida with a bursa and often a vagina, sperm not filiform. Male opening with an injectory penis. With paired sensory organs on the rostrum, and with occipitalia. Body elongated to fairly plump (index smaller than 25); rostrum rather blunt, often plump (index usually less than 3), and mostly delimited by a sulcus. Pharynx musculature concentrated; jaws open-lamellar to fused-lamellar, without wing-shaped apophyses; solid symphysis, if present, longer than wide. Exceptionally, basal plate and jaws are lacking.

Suborder Scleroperalia nov. subord.

Bursovaginoidea with a cuticular bursa and sometimes a vagina. Usually with a male stylet consisting of concentrically arranged cuticular rods. Testes paired, situated ventrolaterally. Sperm small (usually about 3 μm, max. 13 μm), round, polygonal or droplet-shaped, often with a bunch of short filaments. Sensorium consisting of 3–5 pairs of compound bristles and usually one pair of apicalia. Ciliary pits present or reduced.

Family Agnathiellidae nov. fam.

Scleroperalia without paired apicalia, but with 5 pairs of short (30 μm) compound bristles, of which the ventralia originate closer to the rostralia than to the dorsalia. Ciliary pits present. With an unpaired prepharyngeal gland. Epidermal cells not in stripes, epidermal inclusions scattered. Male stylet of the rod type. Sperm small, round or polygonal, usually with a bunch of short filaments. Basal plate usually lacking. Jaws lacking or very delicate, lamellar but not closed, without a cauda, but with a solid symphysis; with teeth connected basally by a cuticular membrane and arranged in a ventro-rostral bow. Without a jugum. With ability to swim backwards.

One described (*Agnathiella* Sterrer), two undescribed genera.

Genus *Agnathiella* Sterrer, 1971a

Agnathiellidae without a basal plate and without jaws. Usually with a clover-shaped rostrum; often with a dorsal protrusion in the posterior body region.

Type species: *A. beckeri* Sterrer, 1971a.

No other species known so far.

Family Mesognathariidae nov. fam.

Scleroperalia without or with one pair of apicalia and 4 pairs of short (30 μm) compound bristles, of which the ventralia originate closer to the rostralia than to the dorsalia. Ciliary pits present. With an unpaired pre-pharyngeal gland. Epidermal cells not in stripes, epidermal inclusions scattered. Male stylet of the rod type. Sperm small, round or polygonal, usually with a bunch of short filaments. Basal plate shield-like and often very delicate; jaws lamellar but not closed, without a cauda; teeth connected basally by a cuticular membrane and arranged in one or two ventro-rostral arcs. Without a jugum. Usually with ability to swim backwards.

Two described (*Mesognatharia* Sterrer, *Labidognathia* Riedl, one undescribed genus.

Genus *Mesognatharia* Sterrer, 1966b

Mesognathariidae with 1 pair of apicalia. Lamellar jaws with ventral apophyses, teeth arranged in one or two ventral arcs. Basal plate shield-like, slightly wider than long.

Type species: *M. remanei* Sterrer.

2 described species: *M. remanei* Sterrer, 1966b, *M. bahamensis* Kristeuer, 1969a.

Genus *Labidognathia* Riedl, 1970a

Mesognathariidae without paired apicalia. Lamellar jaws with long shoulder lamella, teeth arranged in two ventral arcs. Basal plate shield-like, much longer than wide.

Type species: *L. longicollis* Riedl, 1970a.

No other species known so far.

Family Gnathostomariidae nov. fam.

Scleroperalia with one pair of apicalia and 4 pairs of short (max. 35 μm) compound bristles, of which the ventralia originate closer to the rostralia than to the dorsalia. Ciliary pits present. With an unpaired pre-pharyngeal gland. Epidermal cells not in stripes, epidermal inclusions scattered. Male stylet not of the rod type and hardly cuticularized or lacking. Sperm fairly large, round, and with a bunch of fairly long filaments. Basal plate shield-like; jaws more or less lamellar but not closed, without a cauda; teeth connected basally by a cuticular membrane and arranged in a ventro-rostral arc. Without a jugum. Without ability to swim backwards.

One described genus (*Gnathostomaria,* Ax).

Genus *Gnathostomaria* Ax, 1956

Gnathostomariidae with a fairly long rostrum (index about 1.7) and elongated mouth opening. Jaws with crista-like lamellae. Basal plate wider than long, with teeth at its rostral edge. With a muscular seminal vesicle.

Type species: *G. lutheri* Ax, 1956.

One undescribed species.

Family Onychognathiidae nov. fam.

Scleroperalia with one pair of apicalia and 4 pairs of long (50–60 μm) compound bristles of which the ventralia originate equally from or closer to the dorsalia than to the rostralia. Ciliary pits lacking. With an unpaired pre-pharyngeal gland. Epidermal cells in stripes of 2–3, epidermal inclusions often in groups. Male stylet of rod type. Sperm small, droplet-shaped. Basal plate broad; jaws rather lamellar but not closed, with a cauda and long teeth arranged in a ventro-rostro-dorsal basket. Without a jugum. Without ability to swim backwards.

Two described (*Onychognathia* Riedl, *Nanognathia* Sterrer), one undescribed genus.

Genus *Onychognathia*, Riedl, 1971a

Onychognathiidae with a very short rostrum (index about 0.6), and elongated mouth opening. Jaws with long teeth, no terminal tooth developed. Epidermal inclusions in groups, confined to the ventral body surface. Basal plate very delicate, simple, and without a distinct central part. Cauda short, pear-shaped.

Type species: *O. filifera* Riedl, 1971a.

One undescribed species.

Genus *Nanognathia* Sterrer, 1972

Plump Onychognathiidae with fairly short rostrum (index about 0.7), and elongated mouth opening. Epidermal inclusions in groups confined to the ventral body surface. Jaws with fairly long teeth, a terminal tooth is developed. Cauda elongated. Basal plate delicate, simple, and without a distinct central part.

Type species: *N. exigua* Sterrer, 1972.

No other species known.

Family Gnathostomulidae nov. fam.

Scleroperalia with one pair of apicalia and 4 pairs of long (max. 65 μm) compound bristles, of which the ventralia originate closer to the dorsalia than to the rostralia. Ciliary pits present or lacking. Epidermal cells in stripes of 2–3, epidermal inclusions in furrows between the stripes. Male stylet of the rod type. Sperm small, usually droplet-shaped, or round with a bunch of short filaments. Basal plate winged, with a toothed central part and pronounced lateral and rostral wings. Jaws lamellar and closed, usually with 3 horizontal rows of teeth. Cauda delicate, flanked by a pair of elongated appendages. With a jugum in the upper lip. Without ability to swim backwards.

Two described genera (*Gnathostomula* Ax, *Semaeognathia* Riedl).

Genus *Gnathostomula* Ax, 1956

Fairly plump Gnathostomulidae with fairly short rostrum (index about 0.8), and short mouth opening. Doralia normal. Ciliary pits lacking. With or without a permanent vagina. Sperm usually droplet-shaped, or round with a bunch of short filaments. Usually with a well delimited tail region.

Type species: *G. paradoxa* Ax, 1956.

14 species described: *G. paradoxa* Ax, 1956, *G. maldivarum* Gerlach, 1958, *G. murmanica* Mamkaev, 1961, *G. axi* Kirsteuer, 1964, *G. peregrina* Kirsteuer, 1969a, *G. jenneri* Riedl, 1971b, *G. microstyla* Riedl, 1971b, *G. nigrostoma* Riedl, 1971b, *G. brunidens* Riedl, 1971b, *G. mediocristata* Riedl, 1971b, *G. armata* Riedl, 1971b, *G. karlingi* Riedl, 1971b, *G. arabica* Riedl, 1971b, *G. mediterranea* Sterrer, 1970.

About 7 undescribed species.

Genus *Semaeognathia* Riedl, 1970b

Fairly slender Gnathostomulidae with long rostrum (index about 2.6), and short mouth opening. Dorsalia reduced; ciliary pits present. Sperm droplet-shaped. Tail region hardly delimited.

Type species: *Semaeognathia sterreri* Riedl, 1970b.

No other species known.

Suborder Conophoralia nov. subord.

Bursovaginoidea with a soft bursa and mostly a vagina. Penis muscular, without a cuticular stylet. Testis usually unpaired, situated dorsally. Sperm large (usually about 15 μm, max. 45 μm), conical ("conuli"), and without filaments. Sensorium consisting of max. 4 pairs of compound bristles and 2 pairs of apicalia.

Family Austrognathiidae nov. fam.

Conophoralia with two pairs of apicalia and 4 pairs of long (40–55 μm) compound bristles, of which the ventralia originate close to the rostralia. Ciliary pits present. With a pair of pre-pharyngeal glands. Epidermal cells in stripes of 2–3, epidermal inclusions usually in groups. Testis unpaired, situated dorsally. Usually with a vagina. Basal plate winged, with a toothed central part and pronounced lateral, but small rostral wings. Jaws lamellar and closed, with up to 3 horizontal rows of teeth. Without a jugum. Without ability to swim backwards.

Two described (*Austrognathia* Sterrer, *Austrognatharia* Sterrer), one undescribed genus.

Genus *Austrognathia* Sterrer, 1965

Slender to fairly plump Austrognathiidae with jaws with two well developed rows of teeth. Basal plate with a median lobe; teeth of basal plate rather equal in diameter.

Type species: *A. riedli* Sterrer, 1965.

Two described species: *A. riedli* Sterrer, 1965; *A. hymanae* Kirsteuer, 1970.

3 undescribed species.

Genus *Austrognatharia* Sterrer, 1971a

Fairly slender to plump Austrognathiidae. Jaws with only the ventral row of teeth well developed, dorsal row reduced to one tooth (subterminal tooth). Basal plate without a median lobe; teeth of basal plate rather unequal in diameter.

Type species: *A. boadeni* Sterrer, 1971b.

3 described species: *A. boadeni* Sterrer, 1969b, *A. sterreri* (Kirsteuer, 1969a), *A. kirsteueri* Sterrer, 1970a.

About 9 undescribed species.

ACKNOWLEDGMENTS

This paper is dedicated to my teacher and friend Dr. Rupert J. Riedl (Chapel Hill) whose continuous stimulus was of crucial importance throughout my zoological studies. I am also indebted to my wife for criticism and help with illustrations. My work was supported by a Max Kade Fellowship, further by grant No. VF-020–10 of the Research Council of the University of North Carolina, and by National Science Foundation Grants No. XA120–09 and GA-29592.

BIBLIOGRAPHY

Since 1956, more than 60 papers dealing with or mentioning Gnathostomulida have been published (or are in press). Only in 1969 did the first papers begin to appear in American journals and in English, whereas all the earlier literature is scattered over several European journals and almost exclusively in German.

To facilitate further investigation, the complete bibliography is given below, preceded by a classification of the papers into ten major categories.

1. Original descriptions: Ax (1956), Gerlach (1958), Kirsteuer (1964, 1969a, 1970), Mamkaev (1961), Riedl (1970a, 1970b, 1971a, 1971b), Sterrer (1965, 1966a, 1966b, 1969, 1970a, 1971a, 1971b, 1972).
2. Complementary descriptions: Ax (1964a, 1964b, 1965), Graebner (1968a, 1968b, 1969), Riedl (1966, 1969, 1971b), Sterrer (1965, 1966a, 1966b, 1969, 1971b).
3. Mentions (no new contributions): Ax (1966b, 1966c), Riedl (1965), Swedmark (1964).
4. Ecology and distribution (see also "original descriptions"): Ax (1964, 1965), Boaden (1965, 1966), Fenchel & Riedl (1970), Fize (1964), Karling (1962), Kirsteuer (1969b), Müller & Ax (1971), Riedl (1969), Salvini-Plawen (1968), Sterrer (1970b), Swedmark & Teissier (1967), Uhlig (1964, 1968).
5. Cleavage: Riedl (1969).
6. Postembryonic development: Riedl (1969, 1970a, 1971b), Sterrer (1969, 1971b, 1971e).
7. Biology: Müller & Ax (1971), Riedl (1969, 1970a, 1970b, 1971a, 1971b), Sterrer (1969, 1971b, 1971e).
8. Ultrastructure: Graebner (1968a, 1968b, 1969), Riedl (1969), Riedl & Rieger (1972), Rieger & Sterrer (1972).
9. Systematics and relationships: Ax (1956, 1960, 1961, 1964a, 1965, 1966a), Dealamare-Deboutteville (1960), Durden Rodgers, Yochelson and Riedl (1969), Hendelberg (1969), Karling (1963), Mamkaev (1961), Ochietti and Cailleux (1969), Reisinger (1961), Remane (1958), Riedl (1969, 1970a, 1970b, 1971a, 1971b), Steinböck (1958a, 1958b), Sterrer (1965, 1966b, 1969, 1970a, 1971a, 1971c, 1972), Yochelson (1971).
10. Review articles: Ax (1966a), Delamare-Deboutteville (1960), Riedl (1969), Riedl & Sterrer (1970), Sterrer (1970b, 1971b, 1971c), Sterrer & Riedl (1970).

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(Received November, 1969
Revised August, 1971)