# THREE NEW THIOBIOTIC GASTROTRICHA

by

### P. J. S. Boaden

The Queen's University, Marine Biology Station, Portaferry, Co. Down, U.K.

#### Résumé

Trois nouveaux Gastrotriches Macrodasyoidea *Turbanella reducía* n.sp., *Turbanella thiophila* n.sp. et *Thiodasys sterreri* n.gen.n.sp. sont décrits et leur position systématique discutée. Ces espèces se rencontrent dans la communauté biotique des sables marins riches en sulfures et présentent une adaptation à la vie dans ce thiobios

#### Introduction

Recent investigations of the sulphide and redox-potential discontinuity layers of marine sands (see Fenchel & Riedl 1970, Boaden & Platt 1973) have revealed the presence of a fairly large number of organisms belonging to diverse and often primitive taxa. The most successful of the metazoan phyla in this thiobios are the Gnathostomulida, the Platyhelminthes (represented by many of the more simply organised Turbellaria) and the Aschelminthes. The latter are represented by a large number of Nematoda and a lesser number of Gastrotricha.

This paper describes three of these new species of Gastrotricha. Two of these belong to the genus *Turbanella*. The third belongs to a new genus *Thiodasys* (of which there are known to be several other undescribed species — communication from Christiana Sterrer and personal observation). These three species illustrate the transition in "lebens-form typen" between Gastrotricha living in undisturbed anaerobic or poorly oxygenated sands and those such as *Turbanella cornuta* Remane 1925 living in well oxygenated surface sand.

Type specimens have been deposited in the Ulster Museum, Belfast.

### TURBANELLA REDUCTA n.sp.

Five specimens were found in grey and black sand taken from 4-12 cm depth in a 44.5 mm diameter sand core taken from about low water neap level in the gulley at the south end of Firemore Beach, Loch Ewe, Scotland (5° 42' W. 57° 49' N.) on 22nd July, 1971. For

CAHIERS DE BIOLOGIE MARINE Tome XV - 1974 - pp. 367-378 further details of this beach, see McIntyre and Murison 1973. Holotype Ulster Museum Mh1.

Adult specimens are about 420  $\mu m$  long when moving freely. The fairly transparent body is about 30  $\mu m$  wide over most of its length, being only slightly narrowed at the posterior (Fig. 1A). The head is just over 30  $\mu m$  long. There is only a very slight constriction between the head and main part of the body. The sensory hairs around the mouth are relatively long and a pair of 30-35  $\mu m$  forwardly directed sensory hairs arises near the base of the head lateral appendages which are about 7  $\mu m$  long (Fig. 1B).

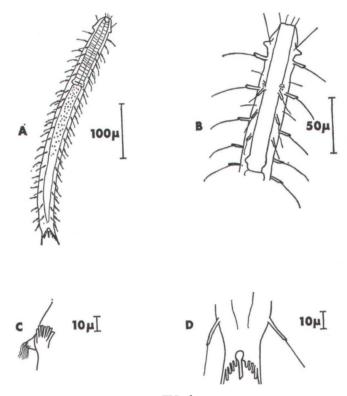


FIG. 1
Turbanella reducto n. sp.

A: habit; B: head end, dorsal view to show lateral and dorso-lateral tubules; C: head lobe and anterior tubules, ventral view; D: tail, dorsal view to show posterior and median tubules.

There is a paired anterior group of 7 ventro-lateral tubules (Fig. 1C). The adhesive tubules of the body are found in a lateral and a dorso-lateral row down each side. There is no third paired dorsal row like that in *T. cornuta*. The tubules are rather fine reaching a length of 14-18  $\mu m$ . The last lateral pair is rather longer (20  $\mu m$ ) and more posteriorly directed in the three adult specimens (Fig. 1D). The body tubules bear sensory hairs often twice the length of the tubule. There are also shorter stiffer sensory hairs arising directly from the body surface. There is a small group of granules near the

base of the first dorso-lateral tubule which occurs about as far along the body as the second lateral tubule. There are about eighteen tubules in each row.

The posterior tubules are shown in Figure 1D. There are five tubules on each side, the longest (about 10  $\mu$ m) forming the point of the tail fork. There is a median tubule of about the same length with a prominent gland at its base.

The gut is much the same as in other species of *Turbanella*. The pharynx occupies about a third of the total gut length. Ciliation is also similar but sparser. None of the specimens found contained eggs although three contained sperm.

Turbanella reducta is obviously very closely related to T. otti Schrom 1972. However the body in T. reducta is much slimmer, being only half the width of T. otti. T. reducta has seven compared with six anterior tubules and up to eighteen compared with ten to fifteen tubules in the lateral and dorso-lateral rows. The tail is acutely forked whereas in T. otti the tail lobes are so oblique as to be almost straight across the hind end of the animal. The specific name of T. redacta refers to its occurrence in the redox-potential discontinuity layer and in the upper reduced layers of sand.

## TURBANELLA THIOPHILA n.sp.

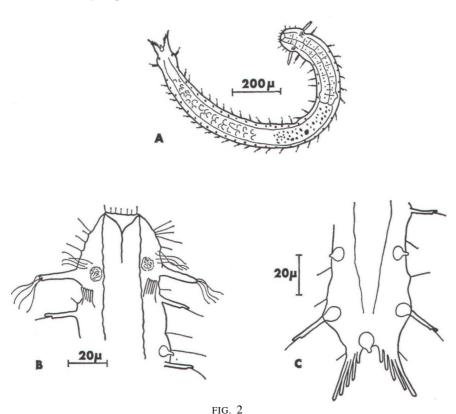
Eight specimens were found in black sand taken from 8-16 cm depth in the same core from Firemore Beach. Holotype Ulster Museum Mh2, paratypes Mh3, 4, and 5.

Adult specimens reach a length of just over 1.2 mm although the smallest **egg** bearing specimen was 815  $\mu m$  long. The body is transparent with many refringent glands and a generally vacuolar appearance. The adults are about 45  $\mu m$  wide in the pharyngeal region but then taper to about 30  $\mu m$  near the hind end; the body then swells out before narrowing into the tail (Fig. 2A).

The head (Fig. 2B) is about 35  $\mu$ m long and separated from the body by a small but obvious constriction. The head bears a pair of 17-20  $\mu$ m long lateral appendages with a tuft of fairly long cilia at their end. The longest sensory hairs on the head are 10  $\mu$ m long and those fringing the mouth are about 5  $\mu$ m. The head also has a pair of finely granular dorsal glands near the base of the tentacles.

The number of anterior adhesive tubules varied from four to eight on each side, most specimens having five rather thin tubules inserted just posterior to the head constriction. The lateral tubules occur in a single paired lateral row. They are spaced fairly evenly along the body although the number is rather variable. The maximum number seen was in a 815  $\mu$ m long adult which had twenty three lateral tubules on each side, the largest specimen found (1224  $\mu$ m) had twelve tubules on the left and thirteen on the right of the body. The tubules are 13 -16  $\mu$ m long and bear short 7-10  $\mu$ m sensory hairs. The sensory hairs on the body reach twice this length but are more usually between 10-15  $\mu$ m.

There is a dorso-lateral row of glands opening through short projections and more or less alternating with the lateral tubules (Fig. 2 B, C). Some of these glands which are 6-8  $\mu m$  in diameter contain dark granules but they are usually transparent, sometimes with a slight green colour. These glands are very similar in appearance to glands which can be seen at the base of some of the adhesive tubules (Fig. 2C) and hence may represent reduced tubules.



Turbanella thiophila n. sp.

A: habit; B: head end, ventral view to show anterior tubules and head appendages, median cilia omitted; C: tail, dorsal view to show posterior and lateral tubules and the dorso-lateral "tubule-glands".

The tail is deeply forked (Fig. 2C). In one small specimen, there were only four tubules on each side but there are five in adults. The outermost tubule which forms the point of the tail is 18-  $20\,\mu$  lun long. The other tubules decrease in length toward the mid line the shortest being 5-10  $\mu$ m. Occasionally the tubules appear fused to neighbouring tubules along part of their length. There is a small medium "tubule-gland" similar in appearance to the dorso-lateral glands.

The mouth cavity is very small. The adult pharynx/total gut length ratio is unusually variable ranging from 1:2.6 to 1:4.25. The anterior third of the intestine contains many small green granules and various brown inclusions. The posterior gut is of very vacuolated appearance.

Only one specimen was seen with a mature egg. This was situated at about three-quarters of the distance from the head to tail and was ovoid with a maximum diameter of  $70\,\mu m$ .

Details of ciliation were not observed but the ventral cilia are long and few in number.

Turbanella thiophila resembles T. veneziana Schrom 1972 and T. italica Gerlach 1953 in the reduction of the tubule rows but differs from both these species in carrying sensory hairs at the end of the tubules. It is also a much larger and elongated species. The very long lateral head appendages are unlike those in any other Turbanella species but recall those of Pseudoturbanella stylifer d'Hondt 1968. The status of the genus Pseudoturbanella must now be in doubt since the only character remaining to separate it from Turbanella is the deeply cleft nature of the tail producing a pair of caudal peduncles. It is easy to see how this condition could be derived by elongation of that in T. thiophila. The specific name of the new species refers to its occurrence in sulphide rich deoxygenated sand.

## THIODASYS STERRERI n.gen. n. sp. (1).

Thiodasys — macrodasyoid gastrotrichs with an attenuated body at least twenty times as long as broad, laterally paired ovary, posterior ventrally opening bursa, posterior ventrally opening receptaculum, paired testis, penis absent, ventral male pore, sperm transferred in bundles or spermatophores, flexible non-cuticularized mouth cavity, anterior tubule group absent or reduced, tail flat and either bilobed or pointed.

Type species: *T. sterreri*.

Many specimens have been found in grey and black sand in beaches on the County Down coast of Northern Ireland as well as from the Firemore beach gully core in which eight specimens were found at 8-16 cm depth. The type locality is at Green Island, Barr Hall Bay at the entrance to Strangford Lough (5° 32'W, 54° 20'N) where specimens occur in pockets of detritus rich medium to coarse shell sand near low water mark. Holotype Ulster Museum Mh6, paratype Mh7.

Adults (Fig. 3A) reach a length of 3 mm but are usually between 1.7-2.5 mm long. The animal is very contractile and can shorten to about half its normal free moving length. Width (40-50  $\mu m$ ) is fairly constant along the worm. The body is fairly transparent, sometimes colourless, especially when young, but may be greenish or more often yellowish-brown. The colour is concentrated in the pharynx, intestine and dorsal glands. Specimens look rather hairy especially under phase contrast.

The head is not very distinct from the rest of the body. There is a slight ciliated indentation in the ventro-lateral area on each side of

<sup>(1)</sup> Note added in proof: Schmidt, P., 1974. — Interstitielle Fauna von Galapagos IV Gastrotricha. *Mikrofauna Meeresbodens*, 26, pp. 1-76 has described a new genus *Megadasys*. The male reproductive system of this is not fully described, otherwise it may prove to be congeneric with *Thiodasys*.

the head just in front of the first lateral adhesive tubules. Apparently there are only 0-2 pairs of forwardly directed head sensory hairs.

There is no distinct group of anterior tubules either on or immediately behind the head. The most anterior tubules simply being the first of the ventro-lateral row. The lateral tubule row is not very well developed and there is only a scattering of dorso-lateral tubes along the body in the older specimens. Thus without careful examination the tubules would appear to be restricted to a paired ventro-lateral row. Even this is difficult to make out and rather variable but there

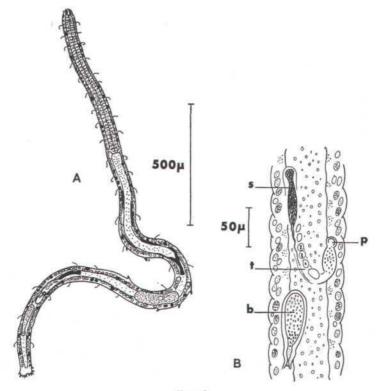


Fig. 3
Thiodasys sterreri n. gen. s. sp.

A: habit; B: region of bursa and receptaculum, dorsal view; b: bursa; r: receptacular pore; s: received sperm bundle; t: receptacular tract.

are often 25-40 tubules in each row. When *Thiodasys sterreri* adheres, the whole region close to the sticking tubules is often stretched towards the point of adhesion. The tubules reach a maximum length of 7  $\mu$ m but are often only about 4  $\mu$ m. They do not bear sensory hairs.

The posterior tubules are variable in arrangement. Young specimens often have only three to five tubules around a rounded or slightly pointed hind end but the number of tubules increases to about twenty in large specimens. In adults, the hind end tends to be bilobed with about ten tubules on each lobe (Fig. 3A).

The body is well equiped with sensory hairs about half to twothirds as long as the body width. The ends of the hairs are invariably curled back towards the body.

There are well developed dorsal glands (diameter up to 10  $\mu m)$  occurring in a roughly aligned pair of dorso-lateral rows. In adults, these glands usually contain brown granular material and sometimes are quite full of larger reddish brown granules. Some specimens have a pair of large apparently empty glands in the head dorsal to the ventro-lateral pits.

The dorsal surface of the body seems to have many small papillae though this appearance may possibly be due to fine granules immediately below the integument. These granules occur in broad ventral and dorso-lateral paired bands. The papillae aid adhesion especially in the anterior region. A distinct layer of large vacuolar cells with fine granules in constant motion is often visible below the epidermis.

Very long cilia are borne on the ventral body surface but the ciliation is very sparse. Below the head, the cilia are thinly scattered over all the surface but there are more cilia towards the sides of the head. The ciliation arches up around the head in the region of the ventro-lateral indentations but does not give a complete band across the dorsal surface. Behind the head the ventral cilia are restricted to two narrow longitudinal bands, four to five cilia wide at the most and narrowing to only one to three cilia behind the pharyngeal region.

The mouth is more or less terminal but somewhat inclined to the ventral surface. The mouth cavity is variable in appearance since the anterior part of the pharynx is continued to form a thin muscular wall which can constrict to close the cavity. However when open the mouth cavity is fairly large being 12-15  $\mu m$  long and 7-10  $\mu m$  in diameter.

The pharynx is rather granular and often has a yellowish colour. The pharynx total gut ratio is usually about 1:3.5 but in the longest specimens may only be 1:4.5. There are no clearly defined regions in the gut, the walls of which contain many fine granules.

The reproductive system of *Thiodasys sterreri* is of great interest. Like the majority of macrodasyoid gastrotrichs, the species is hermaphrodite.

There is a pair of lateral ovaries situated just behind the middle of the body. In mature specimens, two to four egg cells can usually be seen on each side of the gut. They are linearly arranged and the most anterior is the most mature. The paired oviduct leads to a large common uterus which is dorsal to the gut and in which the eggs mature. The mature eggs are oval in outline with a maximum length of 250  $\mu m$  and width of 35  $\mu m$ . There is often only one mature egg in the uterus, but there are occasionally two, in which case the posterior one is usually smaller (about 20-25  $\mu m$  long).

There is a well developed bursa (Fig. 3B) opening to the ventral surface by a pore about one fifteenth of the total body length forward from the posterior end. The bursa is thick walled and up to 120  $\mu m$  long. Three regions can usually be distinguished. The bursa opens into a short finely granular region of about one sixth of the bursa

length. It then widens to an equally long region of coarse appearance and ends in a sac like portion filled with fairly coarse granules. The bursa arches around the gut towards the dorsal surface.

Close to the anterior border of the bursa, there is a muscular pore opening to the dorsal surface. This pore leads into a fairly thick walled 40-50  $\mu m$  long granular structure which might at first be thought to be a penis. It is however a seminal receptacle and opens into a peculiar duct or specialized tract of tissue. This tract is lined with large vacuoles apparently filled with a clear fluid. These decrease in size towards the anterior part of the "sperm tract" and the more anterior vacuoles have a rather hyaline appearance, often containing a darker dumb-bell shaped structure (Fig. 3B). These vacuoles are probably of a nutritive or enzymatic nature. The sperm tract is often more sinuous than shown in the diagram especially when *Thiodasys* is contracted.

The most anterior part of the receptacular structure contains a sperm bundle oriented with the sperm heads to the anterior. This bundle is about 75  $\mu m$  and of an attenuated pear shape with a slight constriction about a quarter of the distance from the head end. In a few specimens, a single slowly vibrating sperm may be seen protruding forwards from the sperm bundle. These may well be in transit to the ova.

The male system consists of a paired lateral testis with a vas deferens leading back along each side of the gut to the mid body region. In adults, sperm may always be seen aggregated in fairly large groups in the vas deferens. On reaching the mid body region, the vasa deferentia curve towards the mid ventral line and fuse.

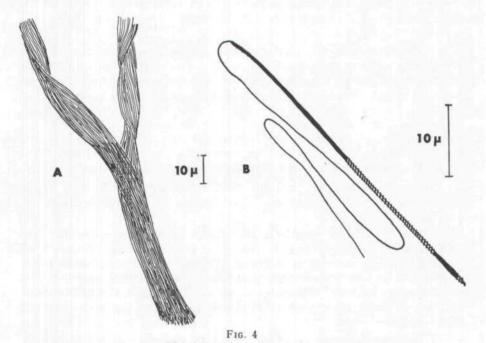
At this point, the sperm aggregations from the two sides come together to form a characteristic Y-shaped sperm bundle or spermatophore (Fig. 4A). The head (stalk) part of this is about 70-75  $\mu m$  long, 8-10  $\mu m$  wide and consists of the sperm heads and part of the sperm tails. The two arms are more variable though usually of about the same dimensions and consists largely of sperm tails formed into a spiral bundle. No male copulatory organ or pore is visible.

Individual sperm separate out from the sperm bundle fairly readily when live preparations of *Thiodasys sterreri* are squashed. The mature spermatozoon (Fig. 4B) is about 125  $\mu m$  long. The sperm head is about 47  $\mu m$  long and less than 0.4  $\mu m$  wide at is widest point. High power phase contrast observation reveals a typical and probably species characteristic spiral patterning. The point of the sperm has three turns like the point of a cork-screw; there is then a wider portion about 4.2  $\mu m$  long on which the spiral marking is very faint. There is next an obvious spiral portion with about forty turns extending back to almost the mid point of the head. The rest of the head appears smooth except for a faint spiral trace on the last 8  $\mu m$ .

There can be little doubt that the sperm are transferred in complete sperm bundles from the ventral surface of one *Thiodasys* to the dorsal receptaculum of another. They are then stored until maturation of the ova. The function of the "bursa copulatrix" is problematical.

The species is named after Christiane and Wolfgang Sterrer who gathered many specimens from the type locality during a visit to Portaferry in 1966.

The new genus *Thiodasys* is so named because of its occurrence in sulphide rich sediment. It obviously belongs to the order Macrodasyoidea (see Remane, 1936; Boaden, 1963; d'Hondt, 1971). At present there are held to be six or seven families within this order. These are the Dactylopodellidae, Lepidodasyidae, Macrodasyidae, Planodasyidae, Thaumostodermatidae and the Turbanellidae. With the exception of the Planodasyidae (Chandrasekhara Rao and Clausen, 1970), these were all defined by Remane (1929). It is probable that the genus *Chordodasys* Schöpfer-Sterrer 1969 with its peculiar chordoid organ and cuticular head shield is representative of a new family. There



Thiodasys sterreri n. gen. n. sp.
A: typical sperm bundle before transmission; B: spermatozoon.

is undoubtedly a need for revision or redefinition of these families but this is beyond the scope of this present paper.

The presence of a paired ovary in *Thiodasys* excludes it from the Thaumastodermatidae and the Lepidodasyidae as does the apparent midway position of the male pore.

The general body form and, in particular, the long pharynx which is not contained within an enlarged head region exclude *Thiodasys* from the Dactylopodellidae.

The new genus does not have a recurved anteriorly opening vas deferens but possesses a copulatory bursa so on both these grounds does not belong to the Turbanellidae.

The Macrodasyidae are said to have a ventral uterus (d'Hondt, 1971) but this is not known to be the case in two of the three genera (Macrodasys, Remane 1924; Pleurodasys, Remane 1927 and Urodasys, Remane 1926). The same author also states that the pharyngeal pores are situated in the mid pharyngeal region in this family, but this is not the case in several of the described species of Macrodasys. Macrodasys species all have a well developed penis, Urodasys is characterised by a very long median tail process and Pleurodasys by specialized pharyngeal knobs. Hence, Thiodasys is not closely allied to any existing members of the Macrodasyidae although this family is ill defined and heterogenous.

Thiodasys shows the greatest affinities with the genus Crasiella Clausen 1968 which has been assigned to a new family—the Planodasyidae—by Chandrasekhara and Clausen in 1970, in conjunction with their description of a new genus *Planodasys*. They define the family as follows:

Body dorso-ventrally flattened and ribbon-like, without cuticular armament. Pestle organs absent. Hind end with paired tail lobes flanked by adhesory tubules. Anterior tubules occur in two diagonal rows. Lateral tubules numerous. Testes and ovaries paired, lying lateral to the intestine in the middle third of the body region. Vasa deferentia directed backwards and the male genital pore located on the central surface just posterior to the egg cells. Penis absent. Posterior bursa copulatrix. Seminal receptacle present or absent. Pharyngeal pores at the hind end of pharynx. Anus subterminal.

It seems unwise to have included forms apparently with (Crasiella) and without (Planodasys) a receptaculum seminis in the same family.

Adult *Thiodasys* would fit this family diagnosis except for its lack of a pestle organ and an anterior tubule group. The tail of adult *Thiodasys sterreri* is nothing like the two distinct oval lobes in *Planodasys* but if somewhat more deeply cleft would resemble the condition in *Crasiella*. However, in young *Thiodasys*, the tail is more rounded or pointed as in many Lepidodasyidae and the macrodasyoid *Pleurodasys*.

Thiodasys does not seem to have a true pestle organ but merely a ciliated pit; this is close to Clausen's original description (two pits with long protruding cilia) of Crasiella. The position of the bursa and, probably of the receptaculum (imperfectly known in Crasiella) in these two genera, is also similar.

The lack of any anterior group of tubules in *Thiodasys sterreri* would seem to be an obvious difference from the condition in the Planodasyidae (and also from the Lepidodasyidae and Macrodasyidae). However, in *Crasiella*, the anterior tubules are in a paired irregular longitudinal group that could almost as well be described as a thickened lateral row.

The flexible non-cuticularized mouth cavity, the large sperm bundles, complex receptaculum and the extreme size and attenuation of the body in *Thiodasys* are more obvious differences. Inclusion of this new genus in the Planodasyidae would blurr any distinction between the already random assortment of genera comprising the Piano-

dasyidae and Macrodasyidae. Until there is more information on new or previously described members of these families which will enable reclassification and redefinition *Thiodasys* must be left *incertae sedis*.

#### Discussion

The three new species may be taken as a series showing an increase in morphological characteristics associated with thiobiotic life. For example, whereas *Turbanella cornuta*, which occurs in aerobic yellow sand at Firemore and many other localities, has well developed ventro-lateral, lateral and dorso-lateral rows of adhesive tubules, *T. reducta*, which is characteristic of the grey RPD sand, has far less tubules, these occurring in lateral and ventro-lateral rows. In *T. thiophila* from the black sand, the tubules are restricted to the lateral rows, although there are dorso-lateral glands which may represent reduced tubules.

These three *Turbanella* species also form a series showing decreased ciliation, increased body sensory hairs and marked elongation as conditions become increasingly anaerobic.

These trends are at their extreme in *Thiodasys sterreri*. This species also shows specialized sperm production and transference which is paralleled in the Gnathostomulida (see Fenchel and Riedl, 1970) a group more or less restricted to sulphide rich habitats.

There can be little doubt that such thiobiotic forms are also adapted at the cellular and biochemical levels. *Thiodasys sterreri* has been kept in sealed jars of anoxic sand for over two months. Preliminary electron microscopy and autoradiography indicate that *Thiodasys* has a low number of cristae in its mitochondria and that it has the ability to fix CO<sub>2</sub> from sea water.

There are reasons for assuming that many of the taxa represented in the thiobios are of primitive origin and are "lebens-ort" types for such habitats (Fenchel and Riedl, 1971). Further studies of sulphide rich marine habitats can confidently be expected to produce much information about early evolution and systematic relationships within the lower Metazoa.

### Acknowledgements

I wish to thank Wolf and Christiane Sterrer, Bob Bleakley, and Cathy Maguire for collection of material and Alasdair McIntyre and the Department of Agriculture and Fisheries of Scotland for help and hospitality at Firemore. Part of the material was collected during investigations financed by a National Environmental Research Council grant. Some of the information was presented at the Second International Meiofauna Conference at York in July 1973.

## Summary

Three new macrodasyoid gastrotrichs, *Turbanella reducta* n. sp., *Turbanella thiophila* n. sp. and *Thiodasys sterreri* n. gen. n. sp. are described and their systematic position discussed. The species come from the biotic community of sulphide rich marine sand and show adaptations to life in the thiobios.

## REFERENCES

- BOADEN, P.J.S., 1963. Marine Gastrotricha from the interstitial fauna of some North Wales beaches. Proc. Zool. Soc. London 140, pp. 485-502.
- BOADEN, P.J.S. and PLATT, H.M., 1971. Daily migration patterns in an intertidal meiobenthic community. 6th Eur. Mar. biol. Symp., Thalassia Yugoslavica 7, (1), pp. 1-12.
- CHANDRASEKHARA RAO, G. and CLAUSEN, c., 1970. Planodasys marginalis gen. et sp. nov. and Planodasyidae fam. nov. (Gastrotricha Macrodasyoidea). Sarsia 42, pp. 73-82.
- CLAUSEN, C., 1968. Crasiella diplura gen. et sp. n. (Gastrotricha, Macrodasyoidea). Sarsia 33, pp. 59-64.
- D'HONDT, J.-L., 1968. Contribution à la connaissance des Gastrotriches intercotidaux du Golfe de Gascogne. Cah. Biol. Mar. 9, pp. 387-404.
- D'HONDT, J.-L., 1971. Gastrotricha. Oceanogr. Mar. Biol. Ann. Rev. 9, pp. 141-192. FENCHEL, T.M. and RIEDL, R.J., 1970. — The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar. Biol., 7, pp. 225-268.
- GERLACH, s., 1953. Gastrotrichen aus dem Kustengrundwasser des Mittelmeeres.
- Zool. Anz 150, pp. 203-211.

  MCINTYRE, A.D. and MURISON, D.J., 1973. The meiofauna of a flatfish nursery ground. J. mar. biol. Ass. U.K. 53, pp. 93-118.
- REMANE, A., 1924. Neue aberrante Gastrotrichen I: Macrodasys buddenbrocki nov. gen. nov. spec. Zool. Anz 61, pp. 289-297.
- REMANE, A., 1925. Neue aberrante Gastrotrichen II: Turbanella cornuta nov. spec. und Turbanella hyalina M. Schultze, 1853, Zool. Anz. 64, pp. 309-314.
- REMANE, A., 1926. Morphologie und verwandschaftbeziehungen der aberranten
- Gastrotrichen I. Z. Morph. ökol. Tiere 5, pp. 625-754.
  REMANE, A., 1927. Neue Gastrotricha Macrodasyoidea. Zool. Jb. (Syst.) 54, pp. 203-242.
- REMANE, A., 1936. Gastrotrichen. Bronn's Klassen 4, 2, AB. 1, B. 1, 2. pp. 1-242. SCHROM, H., 1972. Nordadriatische Gastrotrichen. Helgoländer wiss. Meeresunters.
- 23, pp. 286-351.