

AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Warren, L. M., P. A. Hutchings and S. Doyle, 1994. A revision of the genus *Mediomastus* Hartman, 1944 (Polychaeta: Capitellidae). *Records of the Australian Museum* 46(3): 227–256. [17 November 1994].

doi:10.3853/j.0067-1975.46.1994.6

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

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A Revision of the Genus *Mediomastus* Hartman, 1944 (Polychaeta: Capitellidae)

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ABSTRACT. The genus *Mediomastus* is redefined, and nine species are recognised. Three of these are new species, and one, *M. deductus*, is transferred from the genus *Heteromastus*. Three further species probably belong in *Mediomastus* but there is insufficient information available to confirm this. Two further species originally placed in *Mediomastus* are shown to belong in other genera. A full description of each species is given, based upon the re-examination of type material. Two tables indicating all the relevant diagnostic characters of all described species of *Mediomastus* are given. Comments are made on the validity of the characters that have been used traditionally in capitellid taxonomy. Setal characteristics are the most diagnostic and these should be examined by SEM as well as by light microscopy. However, identification of species of *Mediomastus* requires a combination of diagnostic characters.

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Hartman (1944) erected the genus *Mediomastus* with the following characteristics, a thorax of 11 segments, including a well-developed asetigerous peristomial ring; segments 2 to 5 with capillary setae and segments 6 to 11 with hooded hooks. *Mediomastus californiensis* Hartman was designated as the type species. This genus has been well accepted and nine additional species have subsequently been assigned to it.

The original description of *Heteromastus filiformis* (as *Capitella filiformis*) by Claparède (1864) referred to

ten thoracic segments, the first four with capillary setae and the following six with hooded hooks, which conforms to the above definition of *Mediomastus*. However, according to Eisig's (1887) original diagnosis of *Heteromastus*, there are 11 thoracic setigers, of which the first five have capillary setae. This definition has been followed by all subsequent workers. Hutchings & Rainer (1981) designated a neotype of *Heteromastus* in accordance with Eisig's definition, to legitimise the use of *Heteromastus* Eisig. Hutchings

& Rainer (1981) have thereby also eliminated the potential confusion between these two common genera.

Mediomastus occurs commonly in intertidal and shallow subtidal environments and is frequently collected in ecological surveys. The identification of the genus appears to cause difficulties as the individuals are small (3-31 mm in length and 0.3-1.0 mm in width) and have few obvious characters. Determination to species level has been difficult partially as the current species' descriptions are often inadequate. Recently, large populations of *Mediomastus* have been found throughout Australia. While attempting to identify the material it became apparent that additional morphological characters were needed to satisfactorily separate species within this genus. In this revision of the genus all species are redescribed, together with the description of three new species. Species originally described as belonging to the genus but currently assigned to other genera, are also considered.

Within the family Capitellidae the number of thoracic segments and the arrangement and type of setae (thoracic setal formula) have been the primary generic diagnostic characters. These have formed the basis for identification keys and charts (Fauchald, 1977; Amaral, 1980). Recently there has been a proliferation of monospecific genera based on these two characters; however, in many cases it appears that there is no clear external boundary between the thorax and the abdomen and often the material is not mature. This is important as in some genera the number of thoracic setigers with capillary setae increases with age and juvenile worms cannot, therefore, be reliably assigned to a genus using this character (George, 1984; Warren & George, 1986). This phenomenon we suspect is widespread within the family but, to date, the development of only a few species has been studied in detail. We therefore propose that the generic diagnosis of capitellid genera refer to the number of thoracic setigers with capillary setae occurring in adults and that considerable caution should be used in stating the total number of thoracic setigers in those genera in which the distinction between the thorax and the abdomen is indistinct. For some genera this may lead to a range in the number of thoracic setigers being given. We follow Warren (1991) in quoting the number of thoracic setigers rather than segments as has been done by earlier workers (Hartman, 1947). References to the presence or absence of an asetigerous peristomium have led to considerable confusion in the past because of the effect that this character has on thoracic segment counts and for this reason we have omitted it from the thoracic setal formulae, although the presence or absence of an asetigerous segment is still an important character. While the structure of thoracic and abdominal hooks may vary under the SEM the differences are not readily seen with light microscopy and therefore we have not included this in the generic diagnoses.

Diagnostic Characters

A wide range of external characters has been used to differentiate species of capitellids. Large amounts of preserved material of some species of *Mediomastus* were available to us and we were able to undertake a detailed evaluation of the taxonomic utility of these external characters. However it must be stressed that several species of *Mediomastus* are currently known only from type material which could not be dissected or examined under the SEM. Although molecular studies may reveal additional species of *Mediomastus*, which are morphologically similar (cf. *Capitella*, Grassle & Grassle, 1976), such data could not be obtained for most species and therefore we have based our revision on external characters only. Our two tables of the diagnostic characters are designed to facilitate the identification of species of *Mediomastus* by benthic ecologists. A schematic diagram of an anterior portion of *Mediomastus* is given by Day (1967: 600, fig. 28.2n).

Prostomium. The size and shape of the palpoae have been used as diagnostic characters for species of *Mediomastus*. However variation due to fixation completely invalidates the use of this character when dealing with preserved material. This has been confirmed by Méndez & Cardell (1992) who have shown experimentally that the appearance of the prostomium in *Capitella* is strongly influenced by the method of fixation.

Proboscis. In all the material examined the proboscis is papillated; however, the number and size of papillae can be a useful character in some species, but only if the proboscis is everted, as it cannot be easily dissected.

Peristomium. The presence or absence of eye spots and their position on the peristomium is species specific; however, the eye spots often fade in alcohol and this feature should not be relied upon as a key character for species identification.

Colour. Alcohol preserved animals show no consistent colour patterns. In some species the abdomen or the entire animal is transparent. This is related to the development of the body wall musculature.

Body shape. The general body shape differs significantly between species. In some species the thorax is widest at setiger 2 or 3, in others the thoracic setigers are all more or less the same width. The abdomen may be coiled or nearly straight; this is species specific and does not appear to be significantly affected by method of preservation.

Body size. Total body length is a diagnostic feature, but is of limited use for identification purposes because complete worms are rarely collected, and individuals can regenerate lost abdominal segments. Thoracic length is

the most practical measure provided that the boundary between thorax and abdomen is clear. Thoracic width also gives an indication of size but the difference between the smallest and largest species of *Mediomastus* is so slight that this character is of no practical use.

Size and shape of segments. The ratio of length to width for segments in different body regions and the shape of the abdominal segments have been used in species diagnoses. Both these characters are highly variable however, and are dependent on the state of contraction, regeneration and the effects of fixation (Doyle, 1991).

Presence of nephridiopores and lateral organs. The anatomy of the nephridia can be diagnostic in polychaetes. For example, Hesse (1917) used the structure of nephridia as a means of distinguishing genera of terebellids and recently Smith (1992) has found consistent differences in the number and arrangement of nephridia in species of *Pista* (family Terebellidae). Nephridiopores and lateral organs have been described in some species of *Mediomastus* but these are difficult to see with confidence. Consequently we have not been able to evaluate their taxonomic significance.

Thoracic setal formulae. The presence of four capillary setigers is common to all species; all remaining thoracic setigers have hooded hooks only. The only differences in the thoracic setal formulae between species relate to the number of thoracic setigers (see Thorax/abdomen junction).

Number of setae within fascicles. The number of setae within a fascicle is size dependent but the relative numbers of capillary setae and hooks, and the number of setae in the notopodia relative to the number in the neuropodia can be a useful feature. However, this sort of analysis is dependent upon the availability of large amounts of undamaged material and we have only been able to determine these ratios in a few species. Therefore we are unable to state if the variation between species is greater than that occurring within a species.

Structure of setae. There are winged thoracic capillary setae in all species. The width of the wings varies both within and between species, but the variation between species is significantly greater. The structure of the hooded hooks varies between species and, although these differences can be seen under light microscopy, examination by SEM is recommended when describing a new species in order to clarify the structures observed under the light microscope. Differences exist between the hooks present on the thorax and those on the abdomen; there can also be differences between the noto- and neuropodial hooks in the same setiger. Species vary in the length of the shaft; the presence or absence of a constriction and a shoulder; the proportions of the hood; the size and shape of the main fang; and in the arrangement of the teeth (Fig. 1). Figures 1a and 1b show

a generalised hooded hook from lateral and frontal view respectively. Some of the features identified are not apparent in all hooks and the proportions may differ. Figures 1c and 1d illustrate extreme forms within the normal range. Hooks can vary in the length and width of the shaft; the prominence of a proximal constriction and a distal shoulder; the proportions of the hood; the length of the fang and the arrangement of the teeth. Thoracic hooks, as in Figure 1d, are typically long and straight with no obvious shoulder and no constriction. The hood is long and tight fitting surrounding a small fang. In those species in which there is a difference between thoracic and abdominal hooks, the typical abdominal hook (Fig. 1c) is much shorter and stouter with a marked constriction and a definite shoulder. The hood is shorter but much more voluminous and the fang is much larger. In some species the hooks may be modified further by great elongation so that they appear superficially as spines (Fig. 1f). The presence of a hood, albeit very tight fitting, is often the best indication of the true nature of these setae. In two species, the detailed structure of the hooks is diagnostic. Thus the notosetal hooks in *M. acutus* appear bifid (Fig. 1e) and the abdominal hooks in *M. thomassini* n.sp. are curved downwards into a beak with the teeth stacked very steeply (Fig. 1g). The dental formula has been used in the past but we found it to be variable both within a row of hooks and along the body. Interpretation is also dependent on the orientation of the preparation making this a difficult character to use. We have, therefore, decided that it is of little use in a key for distinguishing between species in this genus.

In the species descriptions which follow the details of setal structure given are based upon in most cases on numerous setal mounts and the accompanying SEM photographs may not show all the details given in the text. Attempts to remove the hoods of the hooded hooks without damaging the underlying hook proved impossible, however sometimes in oil emersion mounts the hoods were partially damaged or accidentally had been removed during the preparation of the mount. Attempts to orientate the hooded hooks also proved impossible due to the small size of the setae. The SEM photographs of which only a selection are used in this paper often confirmed structures which could almost be seen under oil emersion. For all species examined with the SEM preserved material had to be used, only in the case of *M. australiensis* n.sp. was fresh material available which could be carefully collected in order to minimise contamination from fine particles which adhere to the mucous sheath which coats the animals. Cleaning of preserved material often resulted in damaging the fragile setae. As well as illustrating the setae with SEM photographs, highly schematic diagrams are provided to illustrate the diagnostic features of the setae but they should be used in conjunction with the SEM photographs. These schematic diagrams do not illustrate the often highly textured surface of the hood.

Thorax/abdomen junction. Members of the genus are

typically described as having ten thoracic setigers. In some species, however, it is difficult to determine the exact number of thoracic setigers. This may be because there is no abrupt change of function between the thoracic and abdominal setigers. The following characters are different in thoracic and abdominal segments – body wall musculature, gut, hook structure and position, development of parapodial ridges (Hartman, 1947). The setiger on which the change occurs, however, is not necessarily the same for each of these characters (although it is consistent within a species), so that it is not possible to see where the thorax ends and the abdomen begins. In most species, it is possible to see a distinct discontinuity at low magnification. This is because the intersegmental groove at the thorax/abdomen boundary is deeper than those between other segments. If picked up, the specimen may bend at this point. More detailed examination may reveal the transitional mix of characters listed above. For the purposes of the descriptions, however, the intersegmental groove is taken to be the boundary, and references to the boundary being distinct or indistinct refer to this feature.

Asetigerous segments. In some species the number of asetigerous segments immediately anterior to the pygidium has been indicated. However, examination of a wide range of material of some species shows that the distribution of setae in extreme posterior segments is highly variable especially as many specimens have regenerated posterior ends, which initially lack setae.

Branchiae. Parapodia on posterior segments can be swollen and may have a respiratory function but no physiological investigation of their role has been undertaken.

Caudal cirrus. In all species the pygidium is terminal with a midventral caudal cirrus the length of which is of diagnostic value. The cirrus is easily detached, leaving no obvious scar, and is contractile.

Egg diameter. Morphologically similar species of *Capitella* differ in the number and size of eggs produced. This is related to reproductive strategy. Within a species of *Capitella*, sizes are usually consistent. Overall, the genus *Mediomastus* exhibits less variation in egg diameter than in the genus *Capitella*, and egg diameter is diagnostic for a particular species of *Mediomastus*.

Methyl green staining. Ewing (personal communication) has used this staining technique to distinguish between species of *Mediomastus* in the same sample but to date the technique has not been rigorously tested. We suspect that fixation and preservation may influence the staining patterns observed and comparisons should only be made between individuals subjected to identical fixation and preservation. Furthermore, the technique is only of use for small worms where the body wall is relatively thin so that the stain can be viewed using transmitted light. With larger

species such as *M. fragilis* and *M. deductus*, it is impossible to detect bands of stain.

We did, nonetheless, submit specimens of a number of species to this treatment during the course of this study. In each case preserved worms (previously fixed in formalin but now stored in alcohol) were placed in a weak solution of methyl green in 70% alcohol (prepared by sprinkling a few grains of the powdered stain on to the surface of the liquid) for one or two minutes until the whole surface of the worms had taken up the stain. The worms were then rinsed in several changes of alcohol and observed under a dissecting microscope at regular intervals as the stain was progressively washed out. The colour is not lost evenly and gradually prominent bands of colour, sometimes in the form of dots (presumably indicating the presence of glandular cells) are all that remain. This colour pattern was recorded on a chart as shown in Figure 2. Only the staining bands on the posterior part of the thorax have been indicated in Figure 2. In some species there may be fainter bands around anterior setigers, especially setiger 2 but these are not consistent and fade very quickly. Density of stain is indicated by the closeness of the shading lines. For those species in which the staining is restricted to dots in some places, this is indicated by dots on the figure. There may be considerable individual variation, especially in the number of setigers stained. The diagrams are based upon individual worms considered representative of the species rather than a composite picture covering all variations for the species. Numbers refer to setigers.

Habitat. While all species occur in soft sediments, the precise requirements are largely unknown.

Locality. Because the geographical range of each species is unknown, the locality cannot be used as a reliable character for species identification. It can, however, provide an indication as to the likely species. The known distributions of each species are given in Figure 12.

Summary of character utility. The most decisive character is the setal structure. There is little individual variation and treatment of the specimen has no effect on the morphology as viewed with light microscopy. It is not, however, easy to use. Setae are small and orientation may be difficult. Some features can only be detected with confidence using the SEM. For this reason, it is necessary to make additional use of some of the other characters. Using a combination of diagnostic characters it should be possible to identify specimens to species level using Tables 1 and 2 (Appendix) which contain the diagnostic characters of the species of *Mediomastus*. We considered this approach preferable to the more conventional dichotomous key using one or two diagnostic characters at each stage. This would have been unworkable, partly because specific variations in each character are so slight and partly because of the common occurrence of incomplete worms.

Abbreviations. The following abbreviations have been used in the text: LACM-AHF – Allan Hancock Foundation, Los Angeles (collection now housed in The Los Angeles County Museum); AM – The Australian Museum, Sydney; BMNH – British Museum (Natural History), London; CAS – California Academy of Sciences, San Francisco; HZM – Zoologisches Institut und Zoologisches Museum der Universität, Hamburg; MNHN – Museum National d’Histoire Naturelle, Paris; NMWZ – National Museum of Wales, Cardiff; RSM – Royal Museum of Scotland, Edinburgh; SAM – South African Museum, Cape Town; USNM – United States National Museum, Washington.

SEM – scanning electron microscope.

Tables 1 and 2 are listed in the Appendix.

Taxonomy

Generic Diagnosis

Mediomastus Hartman

Mediomastus Hartman, 1944: 264.–Hartmann-Schröder, 1962: 143, fig. 119e.–Fauchald, 1977: 34.

Capitita Hartman, 1947: 408-409.

Diagnosis. Body small and thread-like consisting of numerous setigers. Abdomen often highly coiled and posterior setigers often bell-shaped. Prostomium with elongated, round-tipped palpode. Proboscis eversible with papillae. Peristomium asetigerous with or without eye spots. Thorax of 9-11, usually 10 setigers of which the first 4 bear winged capillary setae in both noto- and neuropodia; subsequent thoracic setigers with long-shafted hooded hooks in both noto- and neuropodia. Junction between the thorax and abdomen may or may not be distinct. Number of abdominal setigers variable with size and age. Abdominal setigers with hooded hooks and sometimes with long capillary setae in notopodia of posterior segments. Abdominal hooded hooks structurally different from thoracic hooks although differences may be slight. Modified paddle-like setae sometimes present. Pygidium terminal with midventral caudal cirrus.

Type species. *Mediomastus californiensis* Hartman, 1944 by original designation.

Comments. We have modified the generic diagnosis of *Mediomastus* to accommodate species which we consider to belong in the genus and yet do not have a clear demarcation between the thorax and abdomen. Included, are species having nine or ten thoracic setigers with setiger 10 being transitional, and one species, *M. fragilis*, in which setiger 11 shows some features typical of anterior setigers. The generic diagnosis has been expanded to include the fact that structural differences occur in the hooded hooks, and that modified paddle-

like notosetae as found in *Mediomastus acutus* may be present.

The original diagnosis of the genus *Mediomastus* has been modified several times since Hartman (1944) erected the genus. Hartman (1960) expanded the definition to include a new species, *Mediomastus glabrus*, which has the first four to six thoracic setigers with capillary setae and the last six to four thoracic setigers with hooded hooks. Hartman (1969) subsequently removed *M. glabrus* from *Mediomastus* and erected a new genus, *Neomediomastus* for this species; and the original generic diagnosis of *Mediomastus* was reinstated. Hartmann-Schröder (1959) enlarged the generic definition to include species with ten thoracic segments and simple notopodial setae in posterior abdominal segments. In 1962, she reverted to Hartman’s (1944) original generic definition of 11 thoracic segments, at the same time expanding the diagnosis to include species with branchiae. Hartmann-Schröder also synonymised the genus *Capitita* Hartman, 1947, with *Mediomastus*. Fauchald (1977) however, while agreeing with this synonymy, repeats Hartman’s (1944) definition of *Mediomastus* and this is still widely used.

We have looked at all the available type material of species that are presently, or have been, included in the genus *Mediomastus*, and conclude that there are at least nine valid species, including three newly described ones. Type material of three of the species was in such poor condition or so incomplete that we are unable to comment on their status. Two species do not belong to *Mediomastus*. The status of each species may be summarised as follows:

Mediomastus acutus Hartman, 1969

Mediomastus ambiseta (Hartman, 1967) – original genus
Capitita

Mediomastus australiensis n.sp.

Mediomastus branchiferus Hartmann-Schröder, 1962
species inquirenda

Mediomastus californiensis Hartman, 1944

Mediomastus calliopensis n.sp.

Mediomastus capensis Day, 1961

Mediomastus caudatus Hartman, 1974 – removed to
Heteromastus

Mediomastus cirripes Ben-Eliahu, 1976 – *species inquirenda*

Mediomastus deductus (Pillai, 1961) – original genus
Heteromastus

Mediomastus fragilis Rasmussen, 1973

Mediomastus glabrus Hartman, 1960 – removed to
Neomediomastus

Mediomastus setosus Hartmann-Schröder, 1959 – *species inquirenda*

Mediomastus thomassini n.sp.

Mediomastus acutus Hartman

Figs 1e, 3a–f, 4a–f, 5a–c, 12; Tables 1, 2

Mediomastus acutus Hartman, 1969: 385, figs 1-3.

Type material examined. HOLOTYPE (LACM-AHF 6731-59, Poly 0451), PARATYPE (LACM-AHF 6731-59 Poly 1327) 5.2 km from Ventura Pier light, California, USA, 34°17'53"N 119°21'05"W, 6 Dec. 1959, 9 m, fine silty sand, both incomplete, holotype female.

Additional material. USA – 4.4 km from Standard-Humble oil platform, 34°23'02"N 119°30'40"W, several, mounted for SEM examination (LACM-AHF 6721-59) 4 Dec. 1959, 10 m; Imperial Beach, 32°28'N 117°08'W (LACM-AHF) 28 Aug. 1984, 9 m, complete, 17.5 mm long and thorax of 2.5 mm long and 0.25 mm wide.

Description. Holotype lacks anterior end and consists of only a few abdominal segments and lacks caudal cirrus. Paratype consists of single posteriorly incomplete specimen with thorax and 23 abdominal segments; 4 mm in length; no coelomic gametes visible. As the non-type material closely resembles the incomplete type material this description is a composite one. Detailed information on setal structure was obtained from AHF 6721-59 examined under SEM, which was collected from close to the type locality for the species. Alcohol preserved material pale cream.

Thread-like, with abdomen loosely coiled. Thorax abdominal boundary distinct between setigers 10 and 11. Prostomium long and pointed with elongated, pointed palpode. Eversible proboscis with poorly developed papillae. Peristomium with or without eye spots.

Thorax with 10 setigers; maximum width at about setiger 2-3; from setiger 6 segments markedly biannulated and about half as long as wide (Fig. 3a). Nephridiopores not seen.

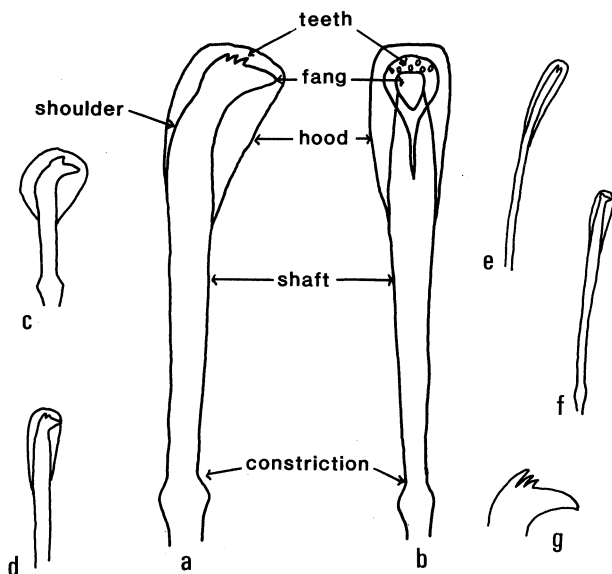


Fig. 1. Structure of the hooded hooks: a – generalised hooded hook, lateral view; b – generalised hooded hook, frontal view; c – typical abdominal hooded hook; d – typical thoracic hooded hook; e – *Mediomastus acutus* notosetal “hook”; f – *M. ambiseta* abdominal “spine-like” hook; g – *M. thomassini* n.sp. abdominal hooded hook.

Setigers 1-4 with expanded winged capillary setae (Figs 3b, 5a), setigers 5-10 with hooded hooks in neuropodia (Figs 3c, 4b) and hooded hooks in notopodia of setigers 5-7 (Fig. 4a) and modified paddle-like notosetae on setigers 8-10 (Figs 3d, 4c,d, 5b). Notosetae and neurosetae in 4 equally spaced fascicles at mid-segment level on setigers 1-7 (Fig. 4e). From setiger 8 the 2 notopodial rami merge to form a single mediodorsal notopodia (Fig. 4f). In addition all fascicles on setiger 10 inserted more posteriorly than preceding ones. Paratype with 5-6 capillary setae per fascicle and 3-5 hooded hooks per fascicle.

Capillary setae appear short-shafted, winged, spatulate-like with smooth tips (Fig. 3b). Notosetae of setigers 6-7, long-handled hooks (Fig. 4a). From setiger 8 onwards the notosetae appear bifid under light microscopy (Fig. 1e). However under SEM, the structure of these notosetae appears as follows, base of hood elongated proximally with the side of the hood flared and enrolled around shaft; instead of a hook there is an acicular type seta almost concealed by flared hood (Figs 3d, 4c,d, 5b). Thoracic neurosetae shorter, hooded hooks, hood not extended proximally (Figs 3c, 4b, 5c).

Abdomen with anterior segments rounded in cross

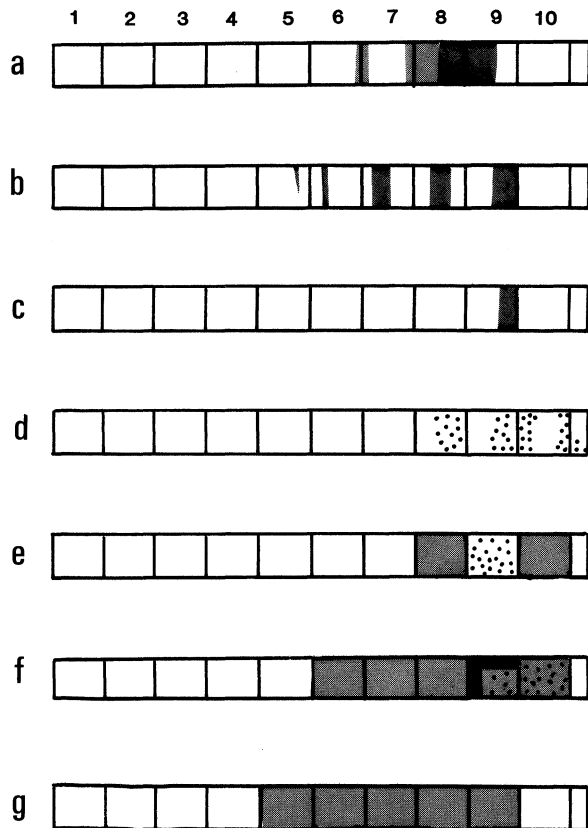


Fig. 2. Methyl green staining: a – *Mediomastus ambiseta*, Buzzards Bay, Massachusetts; b – *M. californiensis* type; c – *M. capensis* type; d – *M. thomassini* n.sp. type; e – *M. calliopensis* n.sp. type; f – *M. cirripes* type; g – *M. australiensis* n.sp. type.

section, posterior segments markedly bell-shaped. Pygidium smooth ring with short caudal cirrus. Setiger 11 with 8 setae per fascicle in both noto- and neuropodia, setiger 21 with 5-6 setae per fascicle in notopodium and 13 in neuropodium, extreme posterior setigers with 1-2 setae. Abdominal neurosetal hooks resemble neurosetal thoracic hooks (Fig. 3f). Anterior abdominal setigers initially have a fused notopodium with paddle-like notosetae (Fig. 3e). However there is some evidence on the material available to us, for SEM examination, that posterior abdominal segments have 2 notopodia, only one of which has paddle-like notosetae. It was not possible to determine exactly where the single notopodium splits into the typical 2 notopodia.

Gravid female (Imperial Beach) with coelomic oocytes of 60 μm in diameter.

Comments. The presence of paddle-like notosetae has not previously been reported in *Mediomastus* and

necessitates a modification to the generic diagnosis. It is not surprising that these type of setae have not previously been reported as it is only when these setae are examined under the SEM that this paddle-like structure can be observed. Under light microscopy they appear as partially bifid structures. The presence of a single fused notopodium in anterior abdominal setigers is a unique feature in this species.

Habitat. Type locality is 9 m in very fine silty sand and other specimens have been collected from fine sand sometimes among onuphid (*Diopatra*) tubes. The species has also been reported in shallow seagrass beds of *Zostera marina* (Harris, personal communication).

Distribution. Species known only from California, USA, (34°23'02"N 119°30'40"W to 32°28'N 117°08'W) (Fig. 12).

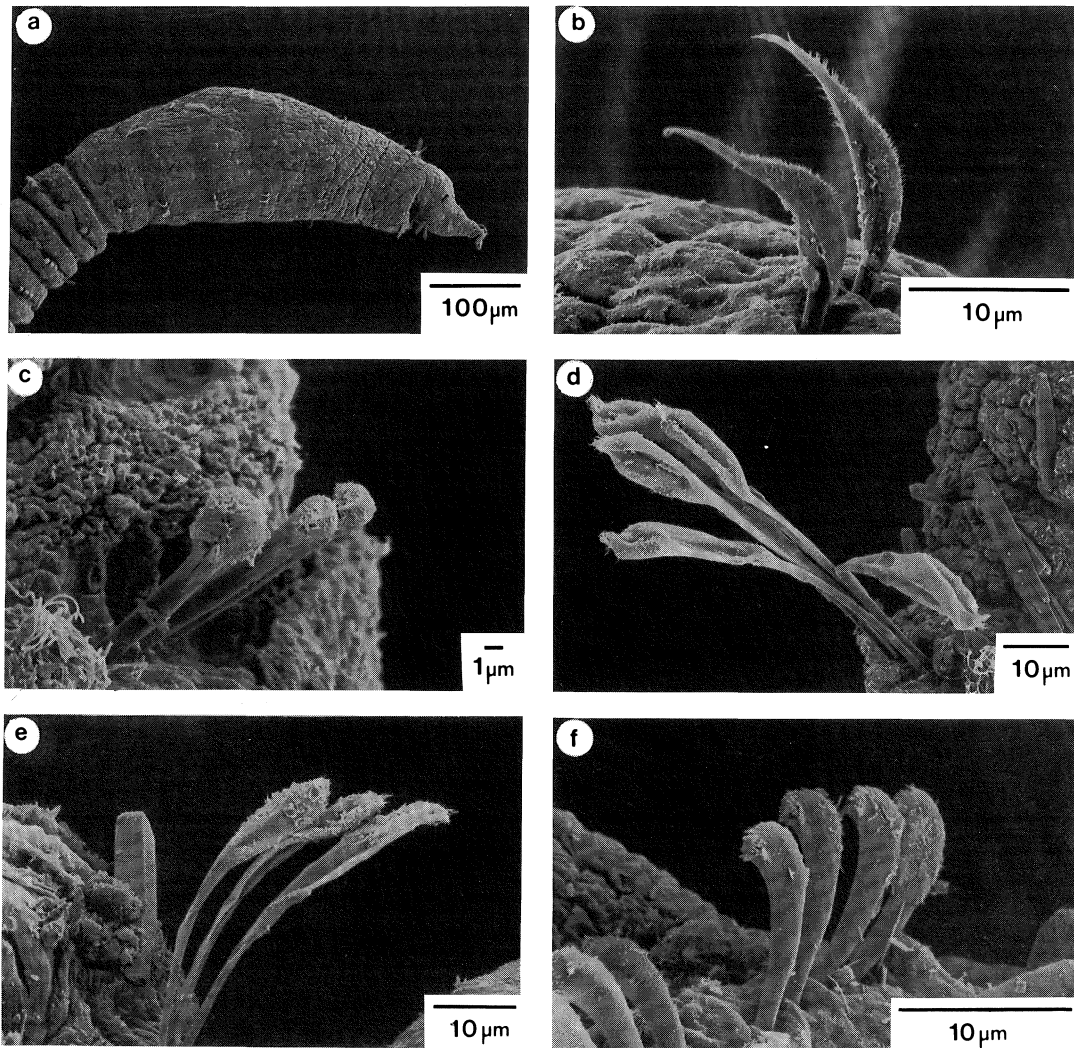


Fig. 3. *Mediomastus acutus*: a – prostomium and anterior thoracic segments; b – thoracic setiger 1 showing capillary setae; c – thoracic neurosetae setiger 10; d – thoracic notosetae setiger 10; e – notosetae setiger 32; f – neurosetae setiger 31-32.

Mediomastus ambiseta (Hartman)

Figs 2a, 5d-f, 6a-f, 12; Tables 1, 2

Capitula ambiseta Hartman, 1947: 409-410, pl. 45, figs 1-4.
Mediomastus ambiseta Hartmann-Schröder, 1962: 143, fig. 18.

Type material examined. HOLOTYPE (LACM-AHF 1451-42, Poly 0499), PARATYPES (LACM-AHF 1451, Poly 0450), Newport Harbour, Corona del Mar, California, USA, 33°36'04"N 117°52'48"W, 2 June 1942, intertidal.

Additional material. USA – Newport Bay, north, 33°36'58"N 117°54'12"W to 33°37'12"N 117°53'25"W, (LACM-AHF 1442-41) intertidal, sandflats along shore, mounted for SEM examination; Oxnard Beach, 34°11'N 119°15'W, 1 (LACM-AHF) A36, Sept. 1974, 30 m; Ace Mission Bay, 32°47'N 117°15'W, 4 (LACM-AHF) St.B.9.IV, 6 June 1980; San Diego Bay, 32°45'N 117°10'W, 3 (LACM-AHF) Aug. 1986, 3 m; northern Monterey Bay 36°53.6'N

121°57.5'W, 1 (CAS 0513 Cat 005168) 34.5 m; Massachusetts, Buzzard Bay, 41°30'N 70°53'W, 9 (AM W12045) 20 m; Outer New Bedford Harbour, 41°40'N 70°50'W, 4 (BMNH ZB 1990 53-56).

Description. Holotype consists of anterior thorax, connected to few abdominal segments by poorly preserved strand, far posterior segments and caudal cirrus absent. Paratypes consist of 5 anterior fragments, 3 midabdominal fragments and an extreme posterior fragment with caudal cirrus.

This description is based, in part, on non-type material collected from southern California which is the type locality. The east coast material from Massachusetts compares closely with this material.

Body length to 14 mm; length of thorax to 1.1 mm; width of thorax to 0.15 mm; up to about 70 segments. Thread-like; abdomen highly coiled. Thorax/abdomen boundary distinctive. Setigers 5-9 all of similar shape and size; setiger 10 shorter and narrower. Abdominal setigers

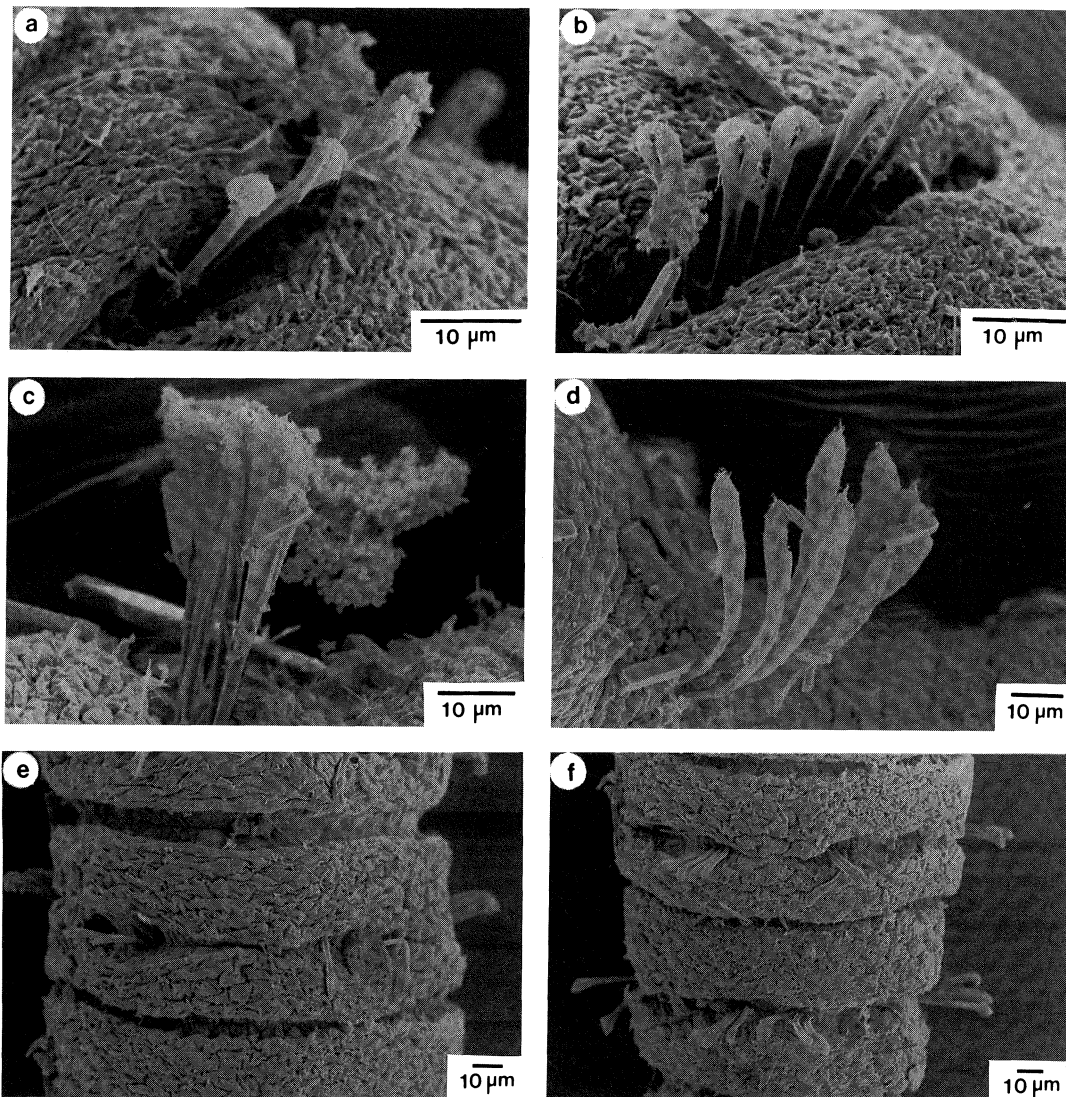


Fig. 4. *Mediomastus acutus*: a – thoracic notosetae setiger 6; b – thoracic neurosetae setiger 7; c – thoracic notosetae setiger 9; d – thoracic notosetae setiger 10; e – thoracic setiger 6 showing four rami; f – thoracic setigers 7 and 8 with the notopodial rami merging and the beginning of paddle-like notosetae at setiger 8.

much paler. From setiger 11 segments thin walled and variable in shape, often with prominent ventral gutter. Colourless and transparent in alcohol. Methyl green staining on posterior of setigers 6 and 7, setiger 8 and anterior of 9; strongest staining on posterior of setiger 8 and anterior part of setiger 9; weakest on 2 (Fig. 2a).

Prostomium small, conical with slightly elongated, round-tipped palpode. Eversible proboscis with low, indistinct papillae. Peristomium slightly longer than first thoracic setiger. Eyes not apparent.

Thorax of 9 setigers (Fig. 6a,b); setiger 10 may be transitional. Thoracic setigers half as long as wide; setiger 10 shorter and narrower. Epidermis of anterior thorax smooth, posterior setigers clearly biannulated. Shape of thorax variable, may be cylindrical or widest at setiger 5. Nephridiopores not visible. Setigers 1-4 with smooth, broadly winged capillary setae only; tips may be curved to form small hook. Setigers 5-9 with hooded hooks only. Setigers in 4 equally spaced fascicles at mid-segment level; no raised tori. Numbers of capillary setae per fascicle range from 2-7 in notopodia and 1-10 in neuropodia; hooded hooks number from 1-4 in notopodia and 2-6 in neuropodia. Thoracic hook straight with slight shoulder proximal to long neck; no constriction; small fang surmounted by 2 rows of teeth; tight fitting hood about 2-5 times as long as wide (Figs 5d, 6c).

Number of abdominal segments not fixed, commonly about 30 but may reach 70. Shape of abdominal segments varies; anterior abdominal segments about as long as wide; may decrease in posterior abdomen to 0.5 times width. Parapodial ridges more or less distinct at posterior margins of all segments except for setiger 10 where setae at mid-segment level. Branchiae absent. Pygidium a smooth ring with long midventral cirrus the length of which may reach 0.5 times thoracic length (Fig. 6f).

All abdominal segments with setae; no posterior asetigerous segments. Neuropodia with hooded hooks only, ranging from 5-10 per fascicle anteriorly to 2-6 posteriorly (Figs 5e, 6e). Notopodia with hooded hooks, ranging from 3-5 in anterior abdomen. Notopodial hooded hooks in mid-abdomen may be long and spine-

like (1 or 2 per fascicle); may be accompanied by single, long, unwinged capillary setae (Figs 5f, 6d). Posterior notopodia with 1-2 capillary setae per fascicle only. Abdominal setal formula varies considerably between individuals; spine-like hooks may be absent but usually begin on fifth to sixth abdominal segment; capillary setae begin on 12th-20th abdominal segment and may not be present on all segments posterior to their first appearance.

Neuropodial hooks short, stout, with prominent shoulder and constriction; large fang with at least 2 rows of minute teeth. Hood shorter and wider than in thorax; length about 2-3 times width. Hooks on anterior notopodia similar. Spine-like hooks are very elongated hooded hooks, much longer and slightly thinner than thoracic hooks; minute fang with very short, tight-fitting hood just visible under oil immersion. Abdominal capillary setae about 0.5 times width of spines and 1.5-2 times length; flexible or stiff, not winged.

Gravid females with large numbers of small eggs in coelom. Egg diameter 50 μm or greater.

Comments. The material described differs from the type description in terms of the number of setae present per fascicle. Hartman (1947) describes four to six or more capillary setae present in the thoracic notopodia and three to six or more in the thoracic neuropodia with six to 11 thoracic hooded hooks per fascicle. However, the material examined exhibits considerable variation between individuals. The thorax/abdomen boundary is also different in the type material and the additional material examined here. Hartman (1947) describes ten thoracic setigers, of which the tenth is transitional, comparable in length to the thoracic setigers but with the setae positioned as in the abdominal setigers. The opposite is the case in the material examined. For further comments on this feature, see the discussion of diagnostic characters above.

Habitat. *Mediomastus ambiseta* occurs in shallow water and intertidally in mud and muddy sand. It may occur in clam beds. Hartman (1947) recorded it in

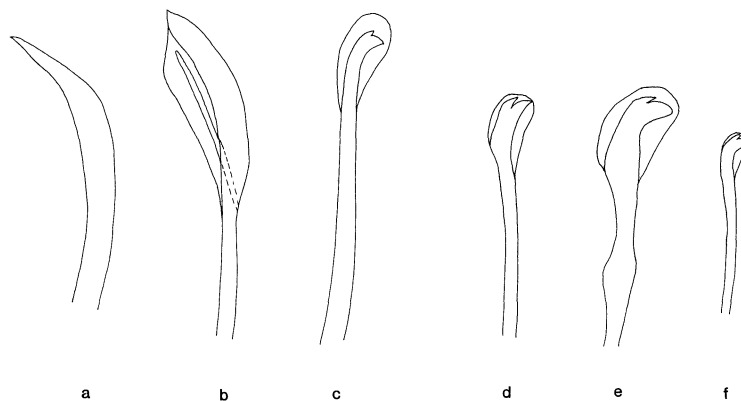


Fig. 5. Schematic figures of setae. *Mediomastus acutus*: a – modified winged capillary, lateral view; b – paddle-like notoseta, lateral view; c – neurosetal thoracic hooded hook, lateral view. *Mediomastus ambiseta*: d – thoracic hooded hook, lateral view; e – neuropodial abdominal hooded hook, lateral view; f – spine-like abdominal notopodial hooded hook, lateral view.

association with the spionids *Streblospio benedicti* Webster, 1879 and *Spiophanes missionensis* Hartman, 1941. It lives in a mucus tube vertically in the sediment; worms lie head downwards with the caudal appendage sticking out from the sediment.

Distribution. North America, west and east coasts (Fig. 12). Dauer & Simon (1976) record its presence in the Gulf of Mexico, however we have not examined this material to confirm the identification.

***Mediomastus australiensis* n.sp.**

Figs 2g, 7a–b, 8a–f, 12; Tables 1, 2

Mediomastus californiensis.—Hutchings & Rainer, 1979: 779.—Hutchings & Rainer, 1980: 45.—Hutchings & Murray, 1984: 81.—Collett *et al.*, 1984: 124–125.—Day & Hutchings, 1984: 277.—non Hartman, 1944: 264–265, pl. 25, figs 64–65.

Mediomastus sp. Melbourne Metropolitan Board of Works *et al.*, 1973: 370.

Mediomastus sp. Hutchings & Recher, 1974: 105.

Type material examined. HOLOTYPE (AM W20589) complete, 21 mm long 1 mm wide, 95 setigers, gravid; PARATYPES 2 (USNM 136597) both complete, 20 mm long, 1 mm wide, about 72 setigers, gravid, 18 mm long, 1 mm wide, about 60 setigers; 2 (BMNH ZB 1994.4793–4794) both complete, 15 mm long, 1 mm wide, about 90 setigers, 21 mm long, 1 mm wide, about 90 setigers; 2 (LACM-AHF 1648) 20 mm long, 1.2 mm wide, about 145 setigers, 21 mm long, 1 mm wide, about 85 setigers with regenerated posterior end; 3 (AM W20590) all complete, 18 mm long, 1 mm wide, about 90 setigers, 15 mm long, 0.8 mm wide, about 70 setigers, 20 mm long, 1 mm wide, about 90 setigers. All type material from the same lot, Merimbula, seaward side of bridge, NSW, Australia, 36°54'S 149°53'E, Oct. 1976, 2–3 m, *Posidonia australis* seagrass beds. (Remaining material from this lot of 40+ individuals (AM W11347) is thus available for any subsequent SEM examination).

Additional material. Australia – South Australia – Upper Spencer Gulf, 33°12'S 138°E, 3 (AM W20593) Aug. 1979, 4.1 m, 795-A4/7, *Posidonia sinuosa* seagrass beds; 2 (AM W20596) 795-B2/2, Aug. 1979, intertidal, *Zostera* spp seagrass beds; 1 (AM W20594) 801-A3/5, March 1980, 3.6 m, *Posidonia australis* seagrass beds; 1 (AM W20595) 795-A4/4, Aug. 1979, 4.1 m, *Posidonia sinuosa* seagrass beds. Victoria – Port Phillip Bay, Hobsons Bay, 37°58'S 144°54'E, few (AM W5645) Stn 1224. New South Wales – Merimbula, 36°54'S 149°53'E, 40+ (AM W11347), 30+ (AM W11427), 30+ (AM W11449) July 1976, 2–3 m, *Posidonia australis* seagrass beds; Jervis Bay, Murrays Basin, 35°08'S 150°45'E, 1 (AM W17529), 4 (AM W17532), 4 (AM W17528) Oct. 1972, 3–4 m, *Posidonia* seagrass beds; Port Hacking, 34°05'S 151°07'E, 10 (AM W195277) 1974, sand; Silver Beach, Kurnell, 34°01'S 151°08'E, several (AM W17697) intertidal; Georges River 34°00'S 151°05'E, 3 (AM W7647) 3 m, mud; Careel Bay, 33°37'S 151°20'E, 1 (AM W8361) 11 Dec. 1973, 1–2 m, *Posidonia australis* seagrass beds; Port Stephens, 32°41'S 152°04'E, 9 (AM W12634), 15 (AM W12622) 27 July 1976, *Posidonia* seagrass beds; Wallis Lake, 32°13'S 152°30'S, 1 (AM W12790) July 1976, 2–3 m, *Posidonia* seagrass beds. A selection of

material examined.

The following material was mounted for examination by SEM, in all cases only part of the registered lot was used: Victoria – Corio Bay, Port Phillip Bay, 38°07'S 144°29'E (AM W unregistered). New South Wales – Merimbula, 36°54'S 149°53'E, 2 (AM W11357); Jervis Bay, Hole in the Wall, Plantation Point 35°08'S 150°45'E, several (AM W unregistered); Towra Point, Botany Bay, 34°01'S 151°08'E, 24 (AM W10842) sand; Weeney Bay, 34°01'S 151°10'E, 4 (AM W12378) 4 June 1977, *Zostera* seagrass beds; Kogarah Bay, 33°59'S 151°07'E, many (AM W7605) 3 m, mud; Silver Beach, Kurnell, 34°01'S 151°08'E, several (AM W17253), intertidal, 25 Feb. 1980; Wallis Lake, 32°13'S 152°30'E, several (AM W unregistered) *Zostera* seagrass beds.

Description. Based on type material and material examined by SEM. Body length exceeds 31 mm; length of thorax 3.5 mm; width of thorax to 0.55 mm. Incomplete specimen with 71 segments. Thorax cylindrical or slightly inflated at setiger 2. Abdomen not coiled. Thoracic segments markedly biannulated; setae at mid-segment level on setigers 1–9; in posterior third of segment 10. Abdomen swollen, thinner walled; segments not biannulated, ie, clear demarcation between 10 and 11. Setiger 9 is 0.75 as long as wide; setiger 10 (0.5–0.75) and setiger 11 (0.75). Slight lateral furrow present on thorax. Small nephridiopores between setigers 7 and 8, 8 and 9 and possibly 9 and 10. Robust thorax and anterior abdomen, remaining abdominal segments not as robust and solid. Holotype with midabdominal segments distended with sediment. Colour in alcohol pale yellow. Methyl green staining produces a band of staining over segments 5–9 (Fig. 2g).

Small prostomium with long round-tipped palpode, in holotype obscured by partly everted proboscis. Proboscis finely papillated. Peristomium longer than first setiger. Eyes not apparent.

Setigers 1–4 with 6–12 narrow winged capillary setae in notopodia and 5–8 in neuropodia. Remaining thoracic setigers with 5–8 notopodial hooks and 6–9 neuropodial hooks. No mixed thoracic fascicles present. Thoracic notopodial and neuropodial hooks with distinct neck and shoulder but no constriction present. Hood wide with curved opening (Fig. 8a,b,c). Setal rows uneven so as to appear double in places (Fig. 8d). Hooks with at least 3 rows of teeth above main fang, but typically hood covering hooks; surface of hood textured (Figs 7a, 8c).

Abdominal segments square to rectangular anteriorly, becoming longer posteriorly. Posterior abdominal segments becoming progressively narrower and bell-shaped towards pygidium. Caudal cirrus appears annulated and equal in length to last 7–8 segments. Abdominal hooks with more obvious fang which is long and pointed and slightly beaked. Setiger 10 has hooks like those on more anterior setigers. At mid-abdomen 7 hooks in notopodia and 14 in neuropodia. Abdominal noto- and neuropodial hooks similar with slight constriction, distinct shoulder and short hood, shaft thickened. Hoods flared with margins upturned, strongly textured. Large prominent main fang (Figs 7b, 8e,f).

Structure of abdominal hooded hooks similar throughout abdomen.

Lives in fine mucus tube. Gravid, egg diameter 80 μm .

Comments. *Mediomastus australiensis* n.sp. closely resembles *M. californiensis*, with which it has been confused in the past, but it can be clearly distinguished by the shape and structure of the hooded hooks. In *M. californiensis* the hood is elongated and there are numerous accessory teeth above the main fang, whereas in *M. australiensis* the hood is short and there are few teeth above the main fang. *Mediomastus australiensis* can also be distinguished from the other species of *Mediomastus* using the characters shown in Tables 1 and 2.

It appears that along the east coast of Australia there is a southern species of *Mediomastus*, *M. australiensis* and a more northerly species *M. calliopensis* (Fig. 12). *Mediomastus californiensis* Hartman does not occur in Australia.

To date only a few specimens of *Mediomastus* have been collected from the Perth region. This Western Australia material was incomplete and too dirty to examine under the SEM. So at this stage it is not known whether *M. australiensis* extends westward of Upper Spencer Gulf in South Australia.

Some of the type material which was collected in October 1976 was gravid, with the coelomic oocytes concentrated in the posterior segments.

Etymology. The specific name refers to the geographical region in which this species occurs.

Habitat. Often occurs in sheltered bay and estuarine situations where salinity levels are high, in muddy substrates and often is associated with species of *Posidonia* and *Zostera* seagrasses. The species can occur in extremely high densities.

Distribution. East coast of Australia from Wallis Lake, NSW to Upper Spencer Gulf, SA (Fig. 12).

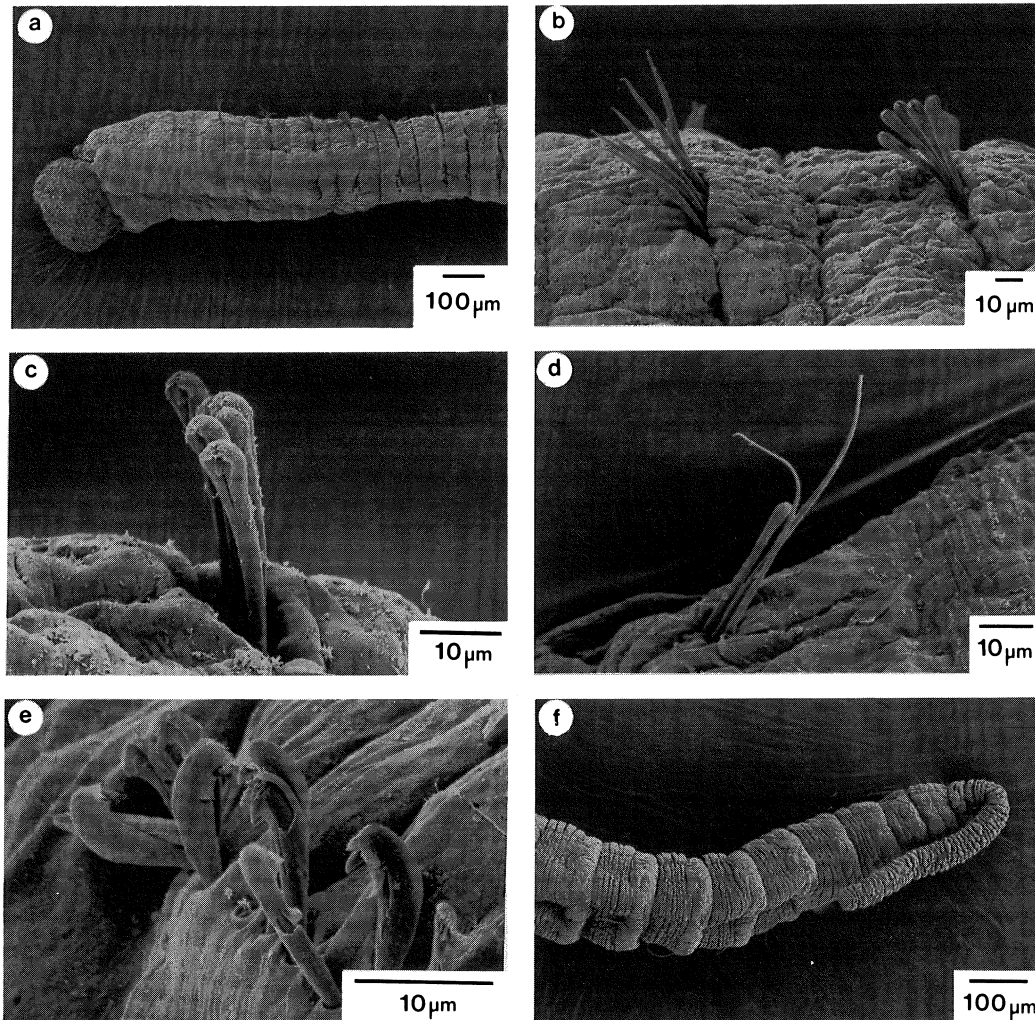


Fig. 6. *Mediomastus ambiseta*: a – prostomium with partially everted proboscis and anterior thoracic segments; b – thoracic setiger 4 (left) and setiger 5 (right) showing transition from capillary setae to hooded hooks; c – thoracic setiger 6; d – Posterior abdominal notosetae; e – posterior abdominal neurosetae; f – posterior segments with caudal cirrus.

Mediomastus branchiferus Hartmann-Schröder

Fig. 12; Tables 1, 2

Mediomastus branchiferus Hartmann-Schröder, 1962: 142-143, pls 17-19.

Type material examined. HOLOTYPE (HZM P-19158), Callao between Punta and El Camotal, Peru, 34°56'S 72°14'W, Stn C2 11 20, coll. Noodt, 29 May 1956, consists of 3 fragments which may constitute an entire specimen; anterior thoracic fragment 1 mm long, 0.5 mm wide, middle fragment 1 mm long, posterior fragment 1.5 mm long; total number of setigers present 35.

Additional material. Chile – Punta Iloca, 34°56'S 72°14'W, 3 (HZM P-15097) incomplete specimens, 12 mm long, for 44 setigers, gravid, 8 mm long for 47 setigers, gravid, 4 mm long for 24 setigers, not gravid.

Description. Type material is in poor condition,

holotype consists of 3 fragments, and paratypes examined consist of 3 incomplete specimens. Prostomium with small rounded palpode, eye spots not seen. Proboscis not everted. Asetigerous peristomium.

Thoracic setigers 1-4 with 2-5 winged capillary setae per fascicle. Thoracic setigers 5-8 with 2-3 hooded hooks; a single row of 2 teeth above the main fang; with no constriction in shaft; long narrow hooded hooks, hoods 3 times as long as wide. Junction between thorax and abdomen very damaged. Nephridiopores not visible. Abdomen with hooded hooks, with 1-3 per fascicle in anterior abdominal notopodia; neuropodia with 6-8 per fascicle. Posterior fragment of holotype with 18 setigers, notopodia with single notosetae plus 1 or 2 hooded hooks, very small and deeply embedded in epidermis, shaft difficult to see, but no obvious constriction, long narrow hood.

Comments. Hartmann-Schröder (1962) originally described an intact worm. The holotype is now in three

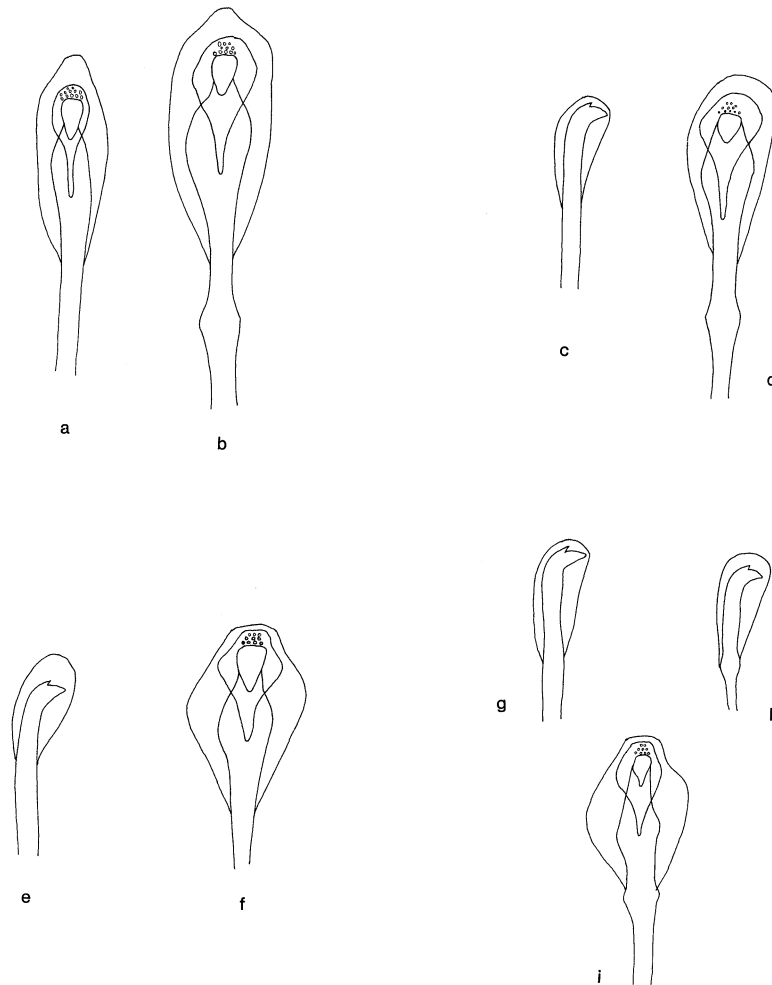


Fig. 7. Schematic figures of setae. *Mediomastus australiensis*: a – thoracic hooded hook, head on view; b – abdominal hooded hook, head on view. *Mediomastus californiensis*: c – thoracic hooded hook, lateral view; d – abdominal hooded hook, head on view. *Mediomastus calliopensis*: e – thoracic hooded hook, lateral view; f – abdominal hooded hook, head on view. *Mediomastus fragilis*: g – thoracic hooded hook, lateral view; h,i – abdominal hooded hook, lateral and head on views.

fragments, and it is not possible to confirm the presence or absence of the transitional zone between the thorax and the abdomen. Eyes are not visible on the type material although they are mentioned in the original description.

Because of the damaged nature of the abdominal segments we cannot confirm the presence of two or more long papillae or thread-like processes on the short posterior abdominal segments situated dorsally above the notopodia which Hartmann-Schröder describes as branchiae. The presence of branchiae would enable this species to be easily distinguished from all other described species of *Mediomastus*. Until additional complete material from the type locality can be collected and described, we have referred to the species as a *species inquirenda*.

However, we have included the species in Tables 1 and 2.

Habitat. Collected from the holdfasts of *Macrocystis*.

Distribution. Known only from the type localities in Peru and Chile (Fig. 12).

Mediomastus californiensis Hartman

Figs 2b, 7c–d, 9a–d, 12; Tables 1, 2

Mediomastus californiensis Hartman, 1944: 264-265, pl. 26, figs 64, 65.—Hartman, 1947: 408, pl. 46, figs 3-4.—Hartman, 1969: 387-388, figs 1-4.—Ewing, 1984 (Ch.14): 14-16, figs 14-9, 14-10a-c.

Mediomastus capensis.—Fournier & Levings, 1982: 36 (not Day, 1961).

Type material examined. HOLOTYPE (LACM-AHF 63 (n 747) Poly 0428) Tomales Bay, California, USA, 28°25'N 123°W, 8 June 1941, intertidal, 1 individual in 2 fragments, anterior fragment 13 mm long, 0.5 mm wide anterior thorax, 0.3 mm wide posterior thorax, for 34 setigers, posterior

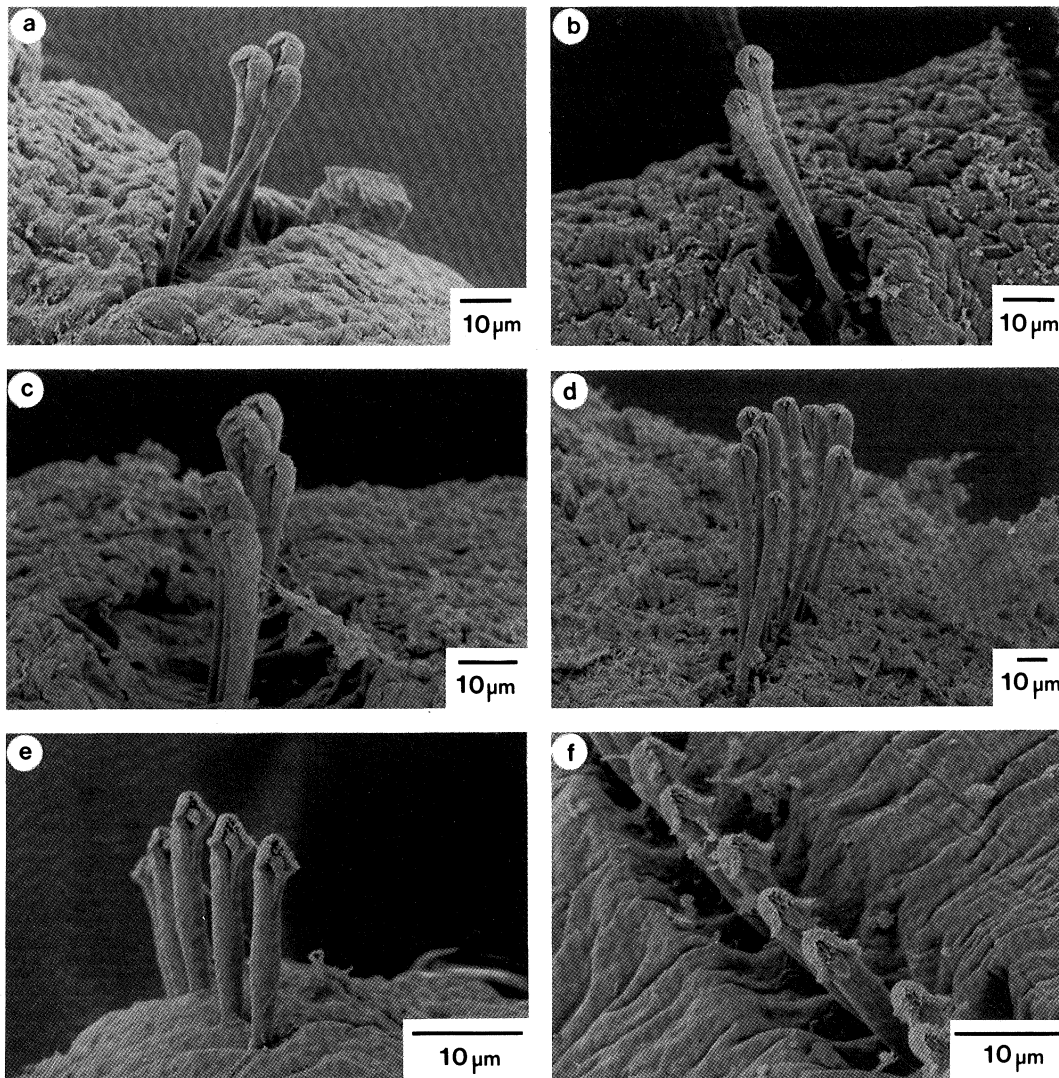


Fig. 8. *Mediomastus australiensis* n.sp.: a – thoracic neurosetae setiger 5; b – thoracic neurosetae setiger 6; c – thoracic neurosetae setiger 6; d – thoracic notosetae setiger 5; e – notosetae setiger 23; f – neurosetae setiger 14.

fragment 20 mm in long, 0.5 mm wide tapering gradually, extreme posterior setigers 0.2 mm wide, 83 setigers, caudal cirrus missing.

Additional material. USA – California – (LACM-AHF n 1488), several mounted for SEM examination; San Diego Bay, 32°45'N 117°10'W, 5 (LACM-AHF) to 20 m Stn F2 + N2; Florida – Hutchinson's Island, St Incie Co., 27°22'08"N 80°13'46"W, several (AM W12047) 10.3 m; North Carolina – off Beaufort 34°34'N 76°25'W, several (AM W12046) 20 m. Canada – British Columbia – (as *M. capensis*) Cousins Inlet 52°17.2'N 127°45.8'W, 4 (AM W18393) 90 m, silt, gravel; Cousins Inlet 52°18.1'N 127°45.3'W, 5 (AM W18394) 70 m, silt, gravel; Graham Reach, Swanson Bay 53°08'N 128° 30.5'W, 7 (AM W18385) 51 m, sand; Graham Reach, Swanson Bay, 53°0.6'N 128°30.6'W, 3 (AM W18396) 66 m, wood debris under 2-3 cm sand.

Description. As type material is incomplete the following description is a composite one based on all the material examined including some examined under the SEM. All the material examined had been collected and identified by Hartman. Body length to 35 mm; length of thorax to 3 mm; width of thorax to 0.5 mm. Number of segments may exceed 100. Worm solid and muscular; widest at second and third setigers (Fig. 9a); tapers slightly to end of body. Abdomen loosely coiled. Thorax/abdomen boundary readily recognisable by sudden constriction caused by change in size and shape of segments. In the holotype first abdominal segment inflated posteriorly, narrowed anteriorly; in all other material last thoracic setiger posteriorly narrowed. Pale yellow or colourless in alcohol; abdomen not usually transparent. Staining

with methyl green produces a distinct band on setigers 7, 8 and especially posterior part of 9, and faint bands on setigers 5 and 6, setiger 10 unstained (see Fig. 2b).

Small prostomium with more or less elongated, round-tipped palpode. Eversible proboscis with widely scattered low papillae that may appear prominent or be inconspicuous. Peristomium as long or longer than wide; longer than anterior setigers. Two small eye spots mid-dorsally in anterior peristomium; not always apparent.

Thorax of 10 setigers; setigers 1-4 about 0.5-1 times as long as wide (Fig. 9a); setiger 5 shorter, about 0.5 times as long as wide; setiger 6-10 gradually increasing in length to 0.75-1 times as long as wide. Setigers 2 and 3 slightly wider than other thoracic setigers. Thoracic setigers biannulated, markedly so from setiger 5. Holotype with deep midlateral groove on all thoracic setigers.

Nephridiopores between setigers 7 and 8, 8 and 9 and possibly 6 and 7, and 9 and 10; not always apparent. Setigers 1-4 with narrow, smooth winged capillary setae only; setigers 5-10 with hooded hooks only. Fascicles of setigers 1-7 inserted posterior to mid-segment; those on setigers 8-10 progressively more posterior. Number of setae per fascicle variable within and between individuals; capillary setae range from 5-15 per fascicle in notopodia, 5-11 in neuropodia; thoracic hooks range from 4-8 in notopodia, 5-10 in neuropodia. Thoracic hooks long and prominent; long shaft with no obvious shoulder, tapering slightly distally; no proximal constriction; small fang surmounted by several rows of teeth; 2 or more large

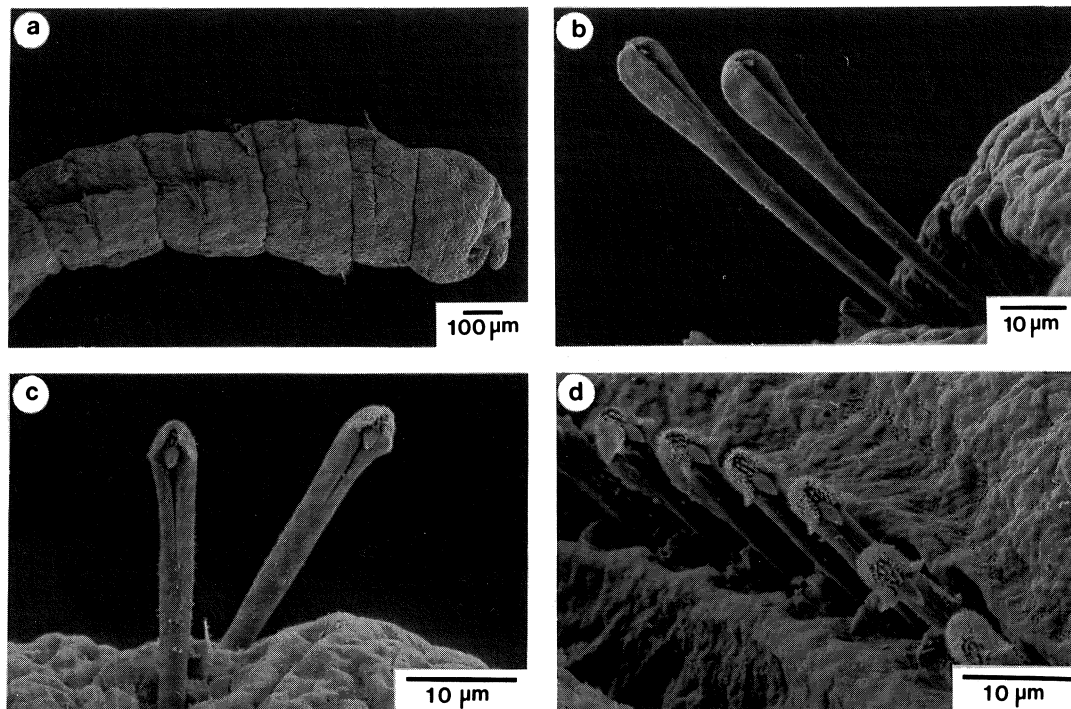


Fig. 9. *Mediomastus californiensis*: a – prostomium and anterior thoracic segments; b – thoracic hooded hooks on setiger 5; c – hooded hooks on setiger 14; d – hooded hooks on setiger 38.

teeth in basal row. Hood long, gently tapering into shaft. Length 3 times width (Fig. 9b). Number of abdominal segments not fixed; may exceed 100. Anterior segments slightly wider than posterior thoracic segments; about 1-1.5 times as long as wide; increasing in length in mid-abdomen, decreasing posteriorly to 0.75 times width. Abdominal segments multi-annulated with posterior parapodial ridge; posterior abdominal segments slightly wider posteriorly; bell-shaped. Branchiae absent. Pygidium with midventral caudal cirrus.

Abdominal setigers with hooded hooks only. Anterior setigers with 5-7 hooks per fascicle in notopodia and 8-10 in neuropodia; midabdominal setigers with 4-5 hooks in notopodia, 8-12 in neuropodia; posterior setigers with 2 hooks in notopodia, 4 in neuropodia. Abdominal hooks similar to thoracic hooks, with slight shoulder; slight constriction; not always clear. The arrangement of teeth above the main fang, as viewed under oil immersion, varies within a torus. Majority of hooks with squat triangular cap of teeth; at least 3 rows of about 12 irregularly arranged teeth. At least 3 teeth in basal row. Single hook in each fascicle with slightly enlarged teeth in basal row. Hood slightly shorter than in thoracic hooks (Fig. 7c,d).

Gravid female with large number of small eggs in the coelom; egg diameter about 60 μm .

Comments. The holotype is incomplete posteriorly and in two fragments, an anterior end with 34 setigers, 13 mm long and an abdominal fragment of 83 setigers, 20 mm long. Complete specimens fitting the description have been recorded extensively from North America.

Mediomastus californiensis may easily be distinguished from *M. ambiseta*, whose distribution it overlaps, by its much more muscular, solid appearance, even if the lack of a posterior end prevents comparison of notopodial setigers. It is also unlike other species in that the structure of thoracic and abdominal hooks is similar. Fournier & Levings (1982) identified Canadian specimens of this species as *M. capensis* (material examined by us) but they may be distinguished by the distinctive setal morphology of *M. capensis* (see below). See Table 1 for other features which distinguish *M. californiensis* from other species of *Mediomastus*.

Habitat. *Mediomastus californiensis* occurs in sandy mud flats at low water, sometimes associated with the capitellid *Notomastus tenuis* (Hartman, 1944). Hartman (1963) also records the species from depths of 517 m off southern California but we doubt the authenticity of this record.

Distribution. North America from both the west and east coast (Fig. 12) and the Gulf of Mexico (Ewing, 1984). However, we have not examined Ewing's material and therefore have not substantiated the species presence in the Gulf of Mexico.

Mediomastus calliopensis n.sp.

Figs 2e, 7e-f, 10a-f, 12; Tables 1, 2

Mediomastus californiensis.—Saenger *et al.*, 1980: 160 (not Hartman, 1944).

Mediomastus sp. Saenger *et al.*, 1980: 159.—Moverley *et al.*, 1986: 227-321.

Type material examined. HOLOTYPE (AM W20591) complete, 14 mm long, 1.0 mm wide anteriorly and 0.4 mm posteriorly, about 90 segments, PARATYPES 2 (BMNH ZB 1994.4795-4796) both complete, 10 mm long, 0.5 mm wide anteriorly, 0.2 mm posteriorly, about 51 segments, 8 mm long, 0.6 mm wide anteriorly, 0.3 mm posteriorly, about 60 segments; 2 (USNM 136598) both complete, 12 mm long, 1.0 mm wide anteriorly, 0.3 mm posteriorly, about 75 segments, 20 mm long, 1.2 mm wide anteriorly, 0.4 mm posteriorly, about 85 setigers, 2 (LACM-AHF 1649) both complete, 12 mm long, 1.0 mm wide anteriorly, 0.3 mm posteriorly, about 69 segments, 8 mm long, 1.0 mm wide anteriorly, 0.3 mm posteriorly, about 60 segments, 14 (AM W 20592) all complete; all type material from Calliope River, Gladstone, Queensland, Australia, 24°01'S 150°59'E, collected between 1974 and 1983, 7-8 m, 3.8 km upstream, sandy mud.

Additional material. From same batch as type material, many (AM W 199325), some of this material is gravid, and some has been mounted for SEM examination.

Description. Small fragile worm strongly tapering towards posterior end. Body length to 27 mm, length of thorax to 2.6 mm, width of thorax to 0.3 mm. Up to about 100 segments. Thread-like, thorax cylindrical, solid, segmental grooves not indented whereas in abdomen clear segmental demarcation present caused by intersegmental grooves. Abdomen not coiled. Clear demarcation between thorax and abdomen between setigers 10 and 11. Colourless in alcohol with transparent abdomen. Methyl green staining produced stippled staining on segment 9 and weak staining on segments 8 and 10 (Fig. 2e).

Small prostomium with elongate palpode with rounded tip. Eversible proboscis with low papillation. Peristomium longer than thoracic segments. Eyes not apparent. Nephridiopores not seen.

Thorax of 10 setigers increasing in length from setiger 5 from 0.33 times width to 1-1.5 times width at setiger 10. Clear demarcation between setigers 10 and 11, first 10 setigers more muscular than subsequent segments. In some type material distinct lateral groove extending from setiger 1 to end of setiger 10, posteriorly body wall unconstricted. Anterior abdominal segments rectangular and clearly demarcated segmentally but posterior abdominal segments bell-shaped and extreme posterior segments narrow and extremely compressed. Alimentary canal clearly visible through posterior abdominal walls and body walls appear thinly muscularised. Marked colour change from cream on first 10 setigers to darker brown on posterior setigers, ventral glandular stripe present pale cream. Setigers 1-4 with narrow, smooth, winged capillary setae only (Fig. 10a), 5-14 per bundle;

setigers 5-10 with hooded hooks only. Number of hooks per torus range from 4-13. No differences in setal numbers between thoracic noto- and neuropodia.

Setal fascicles situated at mid-segment level except for those on setiger 10 where positioned posteriorly on segment.

Thoracic hooks with stout, short straight shaft, head small, hood wide with wide opening (Figs 7e, 10b-c).

Anterior abdominal setigers same size as posterior thoracic setigers but thereafter length increases greatly to 4 times width but is variable within type material. Towards posterior end, segments relatively shorter with parapodial ridges.

Abdominal setigers with hooded hooks only, numbering 12-13 per bundle anteriorly, 16-17 in mid-abdomen, 5-8 posteriorly in neuropodia and about 5 per bundle in notopodia. Hooks may be absent from last few segments, possibly as a result of regeneration.

Abdominal hooks shorter than thoracic hooks with curved, prominent shoulder and long fang (Figs 7f,

10d-f). Hood only 1-2 times as long as wide and much shorter than in thorax. Caudal cirrus narrow, thin, length of last 5-7 segments.

Type material includes 2 specimens with sperm morulae in coelom, and non-type material includes coelomic oocytes 50-57 μm in diameter.

Comments. *Mediomastus calliopensis* can be easily distinguished from *M. australiensis* by the structure of the hooded hooks and the general body form. *Mediomastus calliopensis* is a small fragile worm in contrast to the robust *M. australiensis*. The thoracic hooded hooks have longer hoods than those found in *M. australiensis*, and the abdominal hooded hooks in *M. calliopensis* have more flared bases than those present in *M. australiensis*. For further distinguishing characters and how it can be separated from other described species of *Mediomastus* see Tables 1 and 2.

The species currently has a restricted geographical range, but it should be stressed that few if any shallow

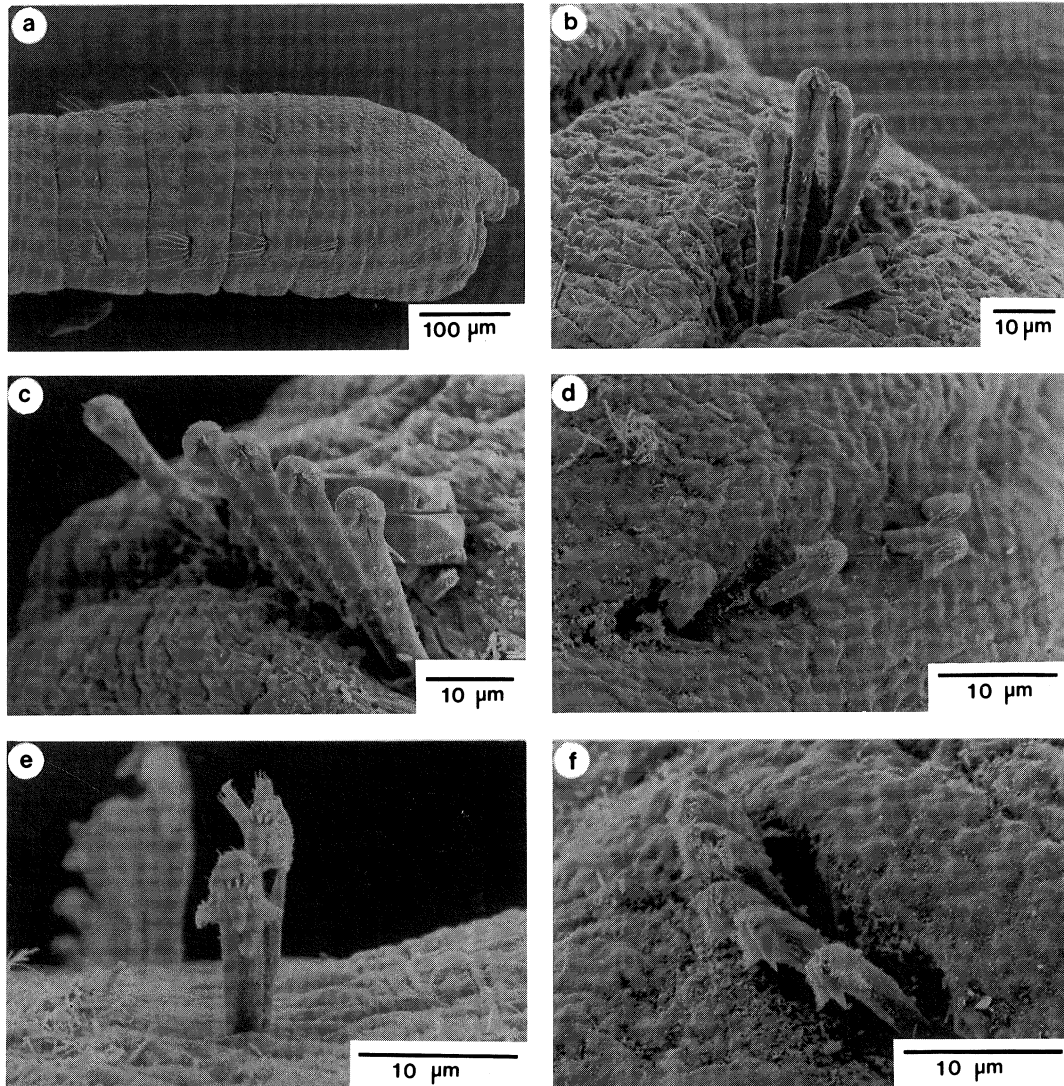


Fig. 10. *Mediomastus calliopensis* n.sp.: a – prostomium and anterior thoracic segments; b – thoracic neurosetae setiger 7; c – thoracic notosetae setiger 10; d – notosetae setiger 23; e – notosetae setiger 27; f – neurosetae setiger 38.

coastal polychaete collections have been made in Queensland or estuarine tropical Australia (Fig. 12).

All the material was collected during an environmental survey of Calliope River carried out by Saenger *et al.*, during the years of 1974 to 1983, and the species was restricted to Sites 19 and 22 (for site details see Saenger *et al.* (1980)). However all the material which was deposited in the AM had been pooled so that details of actual dates of collection are unknown. Some material was sexually mature but it is not known when this was collected. Sexually mature material was not larger than non sexually mature material.

Etymology. The specific name is derived from the type locality, the Calliope River.

Habitat. Estuarine in muddy sediments, salinity range from 6.53 p.p.t. to 37.94 p.p.t.

Distribution. Known only from Calliope River, central Queensland (Fig. 12).

Mediomastus capensis Day

Figs 2c, 12; Tables 1, 2

Mediomastus capensis Day, 1961: 518-519, fig. 11a-d.—Day, 1967: 600-601, fig. 28.2n-p.—Hartmann-Schröder, 1974: 187. not *M. capensis*.—Thomassin, 1970: 80, fig. 5a-d. not *M. cf. capensis*.—Gibbs, 1971: 186. not *M. capensis*.—Fournier & Levings, 1982: 36-37.

Type material examined. HOLOTYPE (SAM A-20587) Cape SB 211F, Univ. Cape Town Ecol. Survey, South Africa, 33°03'5"S 18°01'5"E, 1 May 1960, incomplete posteriorly, 14 mm long, 0.9 mm wide, gravid; PARATYPES (BMNH 1961.9 558-604) St WCD 61J, 63N, 68R, 70H, 82G grab, Univ. Cape Town Ecol. Survey, South Africa, 32°05'–32°44'S 17°56'–18°06'E, 21 Sept. 1960, 95 m, 11, all posteriorly incomplete; 4 (SAM A-20588) anterior fragments plus an abdominal fragment, 4 mm long, thorax plus 15 abdominal segments, 5 mm, thorax plus 16 abdominal segments, 3 mm long, thorax plus 12 abdominal segments, 3 mm long, thorax plus 7 abdominal segments, gravid; 2 (SAM A-20589) 1 complete with regenerating posterior end, 10 mm long, 0.9 mm wide, about 44 segments, incomplete, 7.5 mm long, 0.8 mm wide, about 28 setigers.

Additional material. Mozambique – Lourenço Marques 25°48'S 32°51'E, (HZM P-15100).

Mediomastus sp. cf. *capensis* Solomon Islands, Marovo lagoon, New Georgia, 8°50'S 158°20'E (BMNH:1970-711), 18 m, mud.

Description. Body length 14 mm for 60 setigers; length of thorax to 4 mm; width of thorax to 0.9 mm. Thorax widest at setigers 2-3 narrowing anteriorly; narrower but cylindrical posteriorly. Abdomen loosely coiled. Thorax/abdomen boundary apparently clearly marked by change in width and shape of segments

after setiger 10. Setiger 10 is transitional, however, in that its size and shape is like anterior setigers but the position of the setae is like that found on abdominal setigers. Pale brown in alcohol; thorax not transparent, abdomen slightly transparent. In methyl green, a distinct band around posterior half of setiger 9 (Fig. 2c).

Prostomium with small round-tipped elongated palpode. Eversible proboscis with indistinct papillae; may appear smooth. Peristomium about same length as first setiger. Eyes may or may not be apparent.

Thorax of 10 setigers; posterior segments slightly longer, about as long as wide. Setigers 1-3 show a gradual increase in width to maximum at setiger 3 which is about two-thirds as long as wide; setiger 4 gradually narrows; setigers 5-10 are all similar in width. Segments biannulated, markedly so from setiger 5; epidermis otherwise smooth or crenulated. Nephridiopores between setiger 8 and 9; 9 and 10; may not be apparent. Setigers 1-4 with winged capillary setae, curved into minute hooks at tip. Setigers 5-10 with hooded hooks only. Setae in 4 equally spaced fascicles, inserted midsegmentally on setigers 1-9; more posteriorly on setiger 10. Number of capillary setae per fascicle ranges from 6-13 in notopodia; 6-12 in neuropodia. Number of hooded hooks ranges from 5-11 in notopodia; 3-10 in neuropodia. Thoracic hooks very prominent with long straight shaft without shoulder. Small fang surmounted by at least 3 irregular, steeply banked rows of teeth with 5-8 in first row. Voluminous hood, tapering into shaft, length about 2-3 times width.

Anterior abdominal segments slightly shorter than posterior thoracic segments, length about 0.75 times width; length increasing to 1.5 times width posteriorly. Segments thin walled with prominent ventral gutter. Posterior margin of segments with parapodial ridge. Branchiae absent. Abdominal setigers with hooded hooks only, 5 per fascicle in notopodia and 11 in neuropodia. Hook not very different from thoracic hook; slightly shorter with slight shoulder, more obvious in more posterior segments; no constriction. Main fang only slightly larger than in thoracic hooks, surmounted by at least 2 steeply banked rows of teeth, first row with 2 or 3 large teeth. Hood shorter than in thoracic hook, length about 2 times width.

Holotype is gravid with large number of immature small eggs. Diameter of eggs floating freely in coelom is 40 μ m.

Comments. The type material is described by Day (1961) as "fairly complete", but he also gives details of the posterior with a caudal cirrus, although he does not describe the posterior setae. We have only examined one paratype which was complete but this specimen was regenerating and posterior setae were not visible; the holotype is now in two pieces and incomplete posteriorly. The type locality is given in Day (1961) as Stn SB 232 Saldanha Bay 33°04'S 18°00'E, depth 8-12 m, bottom

khaki sand but the holotype and paratypes are labelled Stn SB 211F and Stn WCD 61J, 63N, 68R, 70H, 82G with slightly different latitudes and longitudes. In the published description, Stn SB 211F is listed as having one juvenile only. The number of paratypes (12+3 posterior ends) examined is greater than listed by Day (1961) for the paratype material (8). Day (1961) indicates that the types would be deposited in the South African Museum but no material could be located; instead the holotype was found in the Zoology Department, University of Cape Town, together with some paratypes and additional paratypes were located in the BMNH. The types located in the Zoology Department have now been deposited in the South African Museum. However all the type material examined was collected from within the same geographical area and are the same species. The discrepancies between the labels and the published description appear to be typographical.

In Day's original description (1961) the dental formula of the hooded hooks is given as MF:5-6:3-4 but in Day (1967) the dental formulae is given as MF:8:3-4. We observed at least three irregular rows of teeth present above the main fang. *Mediomastus capensis* may be distinguished from other species by its hooked capillary setae and by its hooded hooks, which do not differ markedly between those present in the thorax and abdomen. They are very prominent, with voluminous hoods, small fangs and a crest of teeth which gives them an almost bifid appearance at the tip. It must be emphasised, however, that the abdominal hooks on more posterior segments might not conform to this pattern, as no posterior fragments were available for examination.

For comparisons of *M. capensis* with other species of *Mediomastus* see Tables 1 and 2.

Mediomastus capensis has also been recorded from the Mediterranean (Italy, Spain, France – see, for example, Giangrande & Gambi, 1986, Campoy, 1979, Willsie, 1986) but this material has not been examined. Material from British Columbia (Fournier & Levings, 1982) is indistinguishable from *M. californiensis* Hartman. The only records which have we have substantiated as *M. capensis* are those from Mozambique (Hartmann-Schröder, 1974).

Gibbs (1971) recorded *Mediomastus* sp. cf. *capensis* from the Solomon Islands but it is an incomplete specimen, and cannot be identified with any certainty to species. However it seems unlikely from the known distribution of *M. capensis* that this anterior fragment is in fact *M. capensis*.

Thomassin (1970) recorded *M. capensis* from Madagascar. Re-examination of this material has shown it to be a new species *M. thomassini* which we describe in this paper.

Habitat. *Mediomastus capensis* is recorded as occurring in sand at shallow depths (Day, 1961).

Distribution. South Africa and Mozambique (Fig. 12).

Mediomastus cirripes Ben-Eliahu

Figs 2f, 12; Tables 1, 2

Mediomastus cirripes Ben-Eliahu, 1976: 138, fig. 6a-c.

Type material examined. HOLOTYPE (BMNH. ZB.1976. 161) Shavei Zion, Israel, 32°59'N 35°05'E, 347.2 km north of Bet Ha'Emek creek, 8 May 1971, *Dendropoma* infauna, incomplete, 3.3 mm long.

Description. Holotype consists of an anterior end with a complete thorax and 6 abdominal setigers. The thorax is 1.6 mm long, 0.4 mm wide at widest point (setiger 3). The boundary between thorax and abdomen marked by a deep intersegmental groove between setigers 10 and 11 but setiger 10 shows some features typical of abdominal setigers. Colourless in alcohol and transparent. Methyl green staining (Fig. 2f) produced a solid band of colour extending from setiger 6 to the midsegmental groove on setiger 9 with the heaviest staining on setiger 9. This intense stain extended posteriorly on the dorsal surface of the rest of setiger 9. The remainder of setiger 9 and setiger 10 less intensively stained; with darkly stained dots in addition. Abdominal setigers with a narrow band of colour at the extreme posterior end.

Prostomium small, conical with prominent, elongated round-tipped palpode. Eversible proboscis with low, poorly defined papillae. Peristomium 1.5 times longer than first setiger. Two red eye spots, dorsally on peristomium.

Thorax of 10 setigers of which the tenth is transitional. Setigers 1-9 about 0.5 times as long as wide; setiger 10 slightly longer. Setigers clearly biannulated; additional annulations on setiger 10. Nephridiopores not visible. Setigers 1-4 with broad-winged, pointed capillary setae which may be stiff or flexible; those on setiger 1 less prominent than the rest. Numbers of capillary setae range from 2-5 in notopodia and 2-4 in neuropodia. Setigers 5-10 with hooded hooks only, numbering 2-5 in notopodia and 2-4 in neuropodia. Setae in 4 equally spaced fascicles placed slightly posterior to mid-segment level in setigers 1-9, further back on setiger 10.

Thoracic hooks with long, straight shaft with no shoulder and no constriction, surmounted by a small fang with at least 3 rows of small teeth; hood wide, about 2-3 times as long as wide.

Anterior abdominal setigers slightly longer than setiger 10; up to about as long as wide; multi-annulated; setae situated near posterior margin of setiger; 4-5 setae per fascicle. Abdominal setigers with hooded hooks only, not very different from those on thorax but shaft slightly shorter with a slight shoulder and slight constriction. Fang slightly longer and more pointed than in thoracic hooks. Hood wide, but not as wide as in thorax; shorter than in thorax.

The holotype is a gravid female with eggs still attached in gonad; egg diameter approximately 65 μ m but not fully rounded.

Comments. The original description refers to a rounded pygidium, without a caudal cirrus. It appears, however, that the worm had lost its posterior end some time prior to collection. The holotype differs from specimens of other species of *Mediomastus* by the morphology of the hooks on thorax and abdomen; the shape of the setigers including the thorax/abdomen boundary; and the prominent palpode. With the possible exception of the hook morphology, however, these characters may well be variable within the species and without further material it is impossible to speculate on the likely range. Furthermore, the specimen lacks most of its abdominal setigers which might contain other diagnostic features. The locality and the habitat, however, suggest that this might be a separate species. Nevertheless, because we have been unable to give a complete description we prefer to refer to *M. cirripes* as a *species inquirenda*. However we have included this species in Tables 1 and 2, and have listed the known characteristics of the species and how it compares with other species. Collection of additional material from the type locality may substantiate this species.

Habitat. Associated with vermetid reefs of *Dendropoma*.

Distribution. Known only from the type locality on the Israeli coast in the Mediterranean (Fig. 12).

Mediomastus deductus (Pillai)

Fig. 12; Tables 1, 2

Heteromastus deductus Pillai, 1961: 29-30, figs 9j-k, 10b-c.

Type material examined. HOLOTYPE (BMNH 1960.3.13.24) Tambalagam Bay, Sri Lanka, 8°28'N 81°07'E, oyster beds, brackish water in centre of lake, Nov. 1959, 1 incomplete anterior end, 12 mm long and 1 abdominal fragment, 25 mm long.

Description. The anterior end consists of a thorax with 15 abdominal segments; total length of about 12 mm (abdomen highly coiled and, therefore, difficult to measure accurately); length of thorax 4 mm; width 0.8 mm. Abdominal fragment of 47 segments; about 25 mm long; incomplete posteriorly. Thorax/abdomen boundary very indistinct; abdominal segments more wrinkled and with parapodial ridge. Setiger 10 is typical of thoracic setigers in shape and hook morphology. Methyl green staining did not produce any staining patterns.

Small, conical prostomium with long round-tipped palpode. Eversible proboscis with very distinct low papillae. Peristomium as long as first setiger; no eye spots.

Thorax of 10 setigers. Setigers 1-6, 0.5 times as long as wide; biannulated. Setigers 7-10 longer, length 1.25-1.75 width. Thorax cylindrical; all segments the same width. Nephridiopores not visible. Setigers 1-4 with

narrow winged capillary setae; some with hooked tip. Setigers 6-10 with hooded hooks only. Setiger 5 badly damaged; 3 of the parapodia appear to have been cut out, no setae visible on remaining thoracic setigers. Setae in 4 equally spaced fascicles at mid-segment level in setigers 1-6, gradually further back on setiger in remaining thoracic segments. Capillary setae and hooks range in number from 2-4 per fascicle.

Thoracic hooks not very prominent; shaft straight without shoulder or constriction; small fang with a low lying crown of small teeth in at least one row; hood very long and wide, length about 4 times width.

Anterior abdominal segments same length as posterior thoracic segments; multi-annulated and wrinkled in appearance; posterior segments longer. Distinct parapodial ridge from first abdominal setiger; much less obvious in the abdominal fragment. Setae positioned near posterior end of setiger. Abdominal segments with hooded hooks only; 1-2 on anterior segments increasing to 4 on more posterior segments.

Abdominal hooks very short and difficult to detect; distinctive shoulder; constriction not apparent; stout, prominent fang with a very indistinct row of small teeth; hood tightly fitting with fang protruding through opening.

Both fragments contained mature eggs floating freely in the coelom; egg diameter 65 μ m.

Comments. The original description refers to an incomplete worm, 34 mm long for 80 segments. Both the description and the figure show setiger 5 with hooded hooks and no capillary setae. Although *M. deductus* is known only from two fragments, they exhibit sufficient characters to characterise the species. *Mediomastus deductus* may be distinguished from all other species of *Mediomastus* by its very short abdominal hooks. Although we cannot confirm the thoracic setal formula and the possibility therefore remains that this is a species of *Heteromastus*, the original description is very clear in its reference to the fifth setiger having hooded hooks only and emphasises the fact that this is unusual for a species of *Heteromastus*. For this reason we feel justified in believing this to be a valid species of *Mediomastus* rather than a *species inquirenda* and have included it in Tables 1 and 2.

Habitat. Found in amongst oyster beds, in 2 m deep brackish water.

Distribution. Known only from the type locality in Sri Lanka, Indian Ocean (Fig. 12).

Mediomastus fragilis Rasmussen

Figs 7g-i, 11a-f, 12; Tables 1, 2

Mediomastus fragilis Rasmussen, 1973: 115-116.—Rasmussen, 1956: 64-74, figs 20-23.—Warren, 1979: 757-760, fig. 1.—Capaccioni-Azzati, 1985: 50-51, figs 3-5.

Material examined. Denmark – Vellerup Vig, Isefjord, 55°44'N 11°52'E, 0.5 m, silty sand, (Rasmussen's private collection from type locality). Norway – Oslofjord (BMNH ZB 1993.130.133) 59°19'N 10°30'E; England – Liverpool Bay (NMWZ 1993.060) 53°30'N 3°50'W, muddy sand/mud, 9-35 m; Grimsby (BMNH ZB 1993.134-143) 53°30'N 0°10'E; Scotland – Scalloway Voe, Shetland (BMNH ZB 1993.144-149) 60°08.5'N 01°16'W, muddy gravel near low water mark; Cambuscurrie Bay, Dornoch Firth (BMNH ZB 1993.150-155) 57°52'N 4°10'W, in fine to medium sand at low tide level, near to freshwater; Northern Ireland – Mulroy Bay (BMNH ZB 1993.121-123) 55°6'N 7°45'W. Ireland – Cork (BMNH ZB 1993.20 and 88-89) 51°40'N, 8°18'W.

Description. Body length to 60 mm; length of thorax to 4 mm; width of thorax to 0.8 mm. Number of segments may exceed 100. Thread-like; thorax cylindrical or tapering very slightly posteriorly. Abdomen may be coiled. Thorax/abdomen boundary indistinct, most clearly indicated by slight change in segment size and by change

in size and position of hooks. Setigers 10 and 11 may be transitional. Colourless in alcohol and often transparent. Methyl green staining did not produce any distinctive staining pattern.

Small prostomium with elongated round-tipped palpode. Eversible proboscis with low, prominent papillae. Peristomium longer than thoracic segments and not clearly marked off from first setigers. Two red eyes mid-dorsally near posterior margin (not always visible) of peristomium.

Thorax of 10 setigers; all more or less the same width; may increase in length from 0.5 times width anteriorly to 1 times width posteriorly. Segments biannulated with clear intersegmental grooves; epidermis otherwise smooth. Nephridiopores not visible. Setigers 1-4 with smooth winged capillary setae only (Fig. 11a); setigers 5-10 with hooded hooks only. Setae in 4 equally spaced fascicles just posterior to midline of segment. Number of setae per thoracic fascicle variable within and

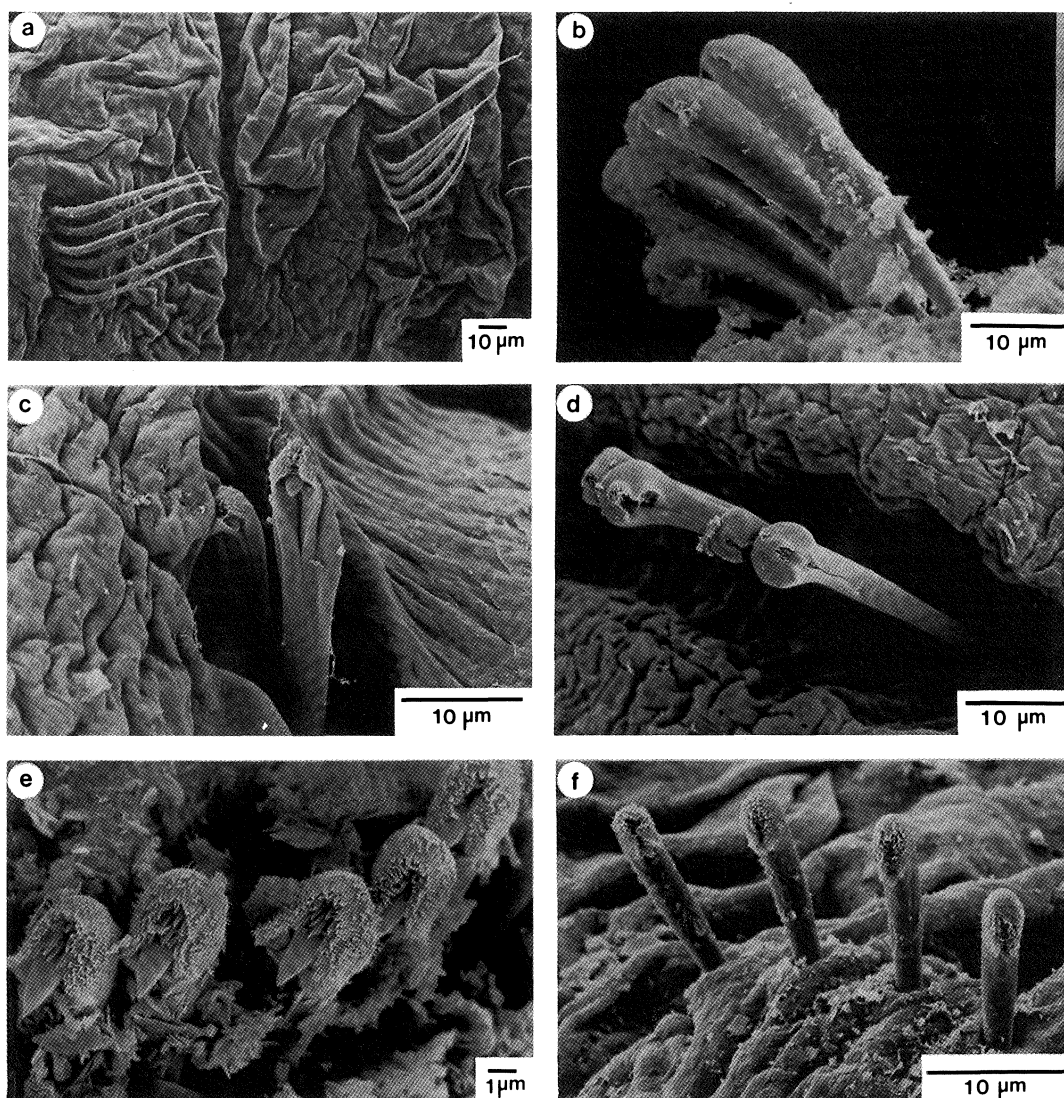


Fig. 11. *Mediomastus fragilis*: a – thoracic notosetal capillary setae on setigers 3 and 4; b – thoracic hooks on setiger 5; c – thoracic notosetae on setiger 6; d – thoracic neurosetae on setiger 9; e – hooded hooks on setiger 12; f – neurosetae on setiger 22.

between individuals; capillary setae ranging from 1-11 in notopodia and 2-12 in neuropodia; range seldom exceeding 2 or 3 in an individual. Thoracic hooks range from 2-9 per fascicle in noto- and neuropodia, with similar variation present within an individual.

Thoracic hook with long, more or less straight, shaft tipped with a small fang surmounted with smaller teeth arranged in at least 2 rows with 3-5 evenly sized teeth in the first row. Constriction not apparent on thoracic hooks except, perhaps, for those on setiger 10. Hood length about 3-5 times width, tapering gradually to shaft (Figs 7g, 11b-d).

Anterior abdominal segments about same width as thoracic segments, length ranging from 0.75-1.5 times width. Length of midabdominal segments may exceed 3 times width; segments narrower than anterior segments. Posterior segments may be very small, possibly indicating regeneration. All abdominal segments multi-annulated, probably reflecting an ability to change shape. Anterior segments cylindrical; posterior segments with longer posterior margins than anterior margins, thus bell-shaped and squarish in cross section. Branchiae absent but posterior noto- and neuropodia enlarged. Pygidium smooth ring with midventral caudal cirrus.

Abdominal setigers with hooded hooks only. Fascicles positioned just posterior to mid-segment in first few setigers; in posterior third of segment thereafter and in distinct parapodial ridge around margin of segment in posterior setigers. Anterior segments with 1-3 or 3-4 hooks per fascicle even in specimens with high thoracic setal counts. Numbers may decrease to 1 per fascicle

posteriorly. It is not always possible to detect hooks in all posterior segments but hooks are known to occur to at least penultimate segment.

Abdominal hooks shorter than thoracic hooks. Shaft may show slight, indistinct constriction. Fang much larger than in thoracic hooks; surmounted by large number of very small teeth. Hood length 1.5 times width; wider than in thoracic hooks (Figs 7h-i, 11e,f).

Gravid females with large number of eggs distributed throughout body coelom. Egg diameter about 70 μm .

Comments. The range in thoracic setal numbers per fascicle is much greater than for any other species of *Mediomastus*. The difference may not be significant as far more material of this species was available for detailed examination. For several other species only type material was available.

A comparison of the features of *M. fragilis* with other described species is given in Tables 1 and 2.

Habitat. *Mediomastus fragilis* occurs in shallow waters and intertidally in a variety of sediments but appears to prefer mud or muddy sand where it can attain densities of 1000 m^2 .

Distribution. North Sea, Irish Sea and Baltic (Fig. 12). *Mediomastus fragilis* has also been recorded from the Mediterranean (Capaccioni-Azzati, 1985), but we have been unable to examine any of this material for comparison and so cannot confirm these identifications.



Fig. 12. Distribution of species. Species distributions are indicated by cross hatching. Species are identified by numbers, a key to which is given below. Unsubstantiated records of species have not been included. It should be noted that material of *Mediomastus* from Malaysia has been recorded but we have been unable to examine material; we have no other records from South-east Asia. 1. *M. acutus*; 2. *M. ambiseta*; 3. *M. australiensis* n.sp.; 4. *M. branchiferus*; 5. *M. californiensis*; 6. *M. calliopensis* n.sp.; 7. *M. capensis*; 8. *M. cirripes*; 9. *M. deductus*; 10. *M. fragilis*; 11. *M. setosus*; 12. *M. thomassini* n.sp.

Mediomastus setosus Hartmann-Schröder

Fig. 12; Tables 1, 2

Mediomastus setosus Hartmann-Schröder, 1959: 169-172, figs 173-177.

Material examined. El Salvador – Estero Jaltepeque near La Herradura, between 13°17'N 89°02'W and 13°13'N 88°54'W, TYPE (HZM P-19159) mud, intertidal, Feb. 1955, salinity 15.7 p.p.t several incomplete fragments, anterior fragment of thorax and 3 abdominal setigers, middle fragment of 5 abdominal, posterior fragment with caudal cirrus. Non-type material from type locality, gravid fragments (HZM P-15099).

Description. Description based on fragmented type material. Prostomium with elongated, blunt-ended palpode, proboscis papillated. Eye spots present. Thorax with asetigerous peristomium, 10 thoracic setigers. Transition from thorax to abdomen marked by an increase in length of setigers and slight change in orientation of fascicles.

Setigers 1-4 with capillary setae and setigers 5-10 with hooded hooks. Capillary fascicles with 2-4 setae in notopodia and 3-5 setae in neuropodia; hooded hook fascicles with 2-3 in notopodia and 3-5 in neuropodia. Abdominal notopodia with 3-4 hooks per fascicle and 6-9 in notopodia.

Posterior setigers with 1 or 2 hooded hooks per fascicle, last 5 setigers in addition have 1 long seta per noto- and neuropodial fascicle, seta appears simple. Immediately prior to caudal cirrus 3 asetigerous segments. Post-setal regions of posterior setigers glandular, somewhat expanded, and posteriorly rounded. Pygidium small semi-circular, with finger shaped caudal cirrus.

No evidence of gametes was observed.

Comments. Hartmann-Schröder (1959) in describing this new species of *Mediomastus* had to emend the generic diagnosis to include the possession of simple setae in the notopodium of the posterior abdominal setigers. Unfortunately the type material is incomplete and the detailed structure of the simple setae in the posterior setigers cannot be determined. Thus this species must remain incompletely known and additional complete material from the type locality is needed to describe this species adequately. In the meantime we consider it to be a *species inquirenda*. However we have included the species in Tables 1 and 2.

Habitat. Occurs in salinities of 15.7 to 31.4 p.p.t and is not dependent upon a particular substrate; lives in tube made of fine sediment which does not completely encase the animal.

Distribution. Known only from the type locality in El Salvador (Fig. 12).

Mediomastus thomassini n.sp.

Figs 1g, 2d, 12; Tables 1, 2

Mediomastus capensis.—Thomassin, 1970: 80-81, fig. 5a-d (not Day, 1961).

Type material examined. HOLOTYPE (MNHN UC234) Stn 80, 4 Nov. 1965, 3-4 m, sandy shallow lagoonal substrate between coral patches; PARATYPES (MNHN UC235) Stn 66, 20 Oct. 1965, intertidal, sand bank; Grand Recif Barrier Reef, Tuléar, Madagascar, 23°20'S 43°41'E.

Description. Length 8 mm for 17 segments; length of thorax 3 mm; width of thorax 0.5 mm at setiger 2. Thorax/abdomen boundary marked by change in shape of segments, and size and position of hooks. Abdominal segments thinner-walled and variable in shape with obvious width increase posteriorly. Pale brown in alcohol; may be transparent. Methyl green staining (Fig. 2d) produced mauve-striped staining of posterior of setigers 8 and 9 and anterior and posterior of 10. Staining continued ventrally into the anterior abdomen.

Small conical prostomium with long pointed palpode. Eversible proboscis with low, widely spaced papillae; not prominent. Peristomium longer than first setiger; boundary between them indistinct. No eyes, but some scattered pigmentation on one of the paratypes.

Thorax of 10 setigers; setigers 2 and 3 slightly wider than others; length approximately 0.5-0.75 width. Boundary between segments indistinct; segments not obviously biannulated; epidermis smooth. Nephridiopores not visible. Setiger 1-4 with very long, narrowly winged capillary setae only; capillary setae flexible and whiplike; not stiff. Setigers 5-10 with hooded hooks only. Fascicles just posterior to mid-segment. Number of capillary setae range from 5-11 in notopodia and 4-8 in neuropodia; hooks range from 6-8 in notopodia and 6-10 in neuropodia. Thoracic hook with long, more or less straight, shaft tipped with a small fang surmounted by small teeth in at least 2 rows; front row with 3-5 equally sized teeth. Hood tight fitting and narrow, at least 5 times as long as wide, tapering gradually into shaft; long, narrow opening in hood.

Anterior abdominal segments slightly wider and larger than thoracic segments. Length of midabdominal segments variable but may exceed 4 times width. All abdominal segments increase in width posteriorly in region of hooks. Branchiae absent. Abdominal setigers with hooded hooks; fascicles near posterior margin of segment in all setigers. Anterior segments with 6-8 hooks per fascicle in notopodia and 7-11 in neuropodia; 15th abdominal segment with 6-7 hooks in notopodia and 16 in neuropodia. Hooks shorter than thoracic hooks. Shaft with slight but distinctive shoulder just proximal to fang; marked constriction about half way down length of shaft. Fang much larger than in thoracic hooks; down-curved at tip; beak-like; surmounted by at least 2 rows of teeth; those in first row with 3 teeth, larger than those in row above. Hood

wider distally than in thoracic hooks and shorter, length about 3 times width.

Holotype with many maturing ova, about 60 μm in diameter but not fully rounded.

Comments. *Mediomastus thomassini* n.sp. can be distinguished from *M. capensis* Day, 1961 by its prominent palpode, smooth thorax without secondary annulation, distinctive capillary setae, and the marked differences between thoracic and abdominal hooks.

None of the specimens are complete posteriorly. The holotype is an anterior end with 17 segments and a midabdominal section of 17 segments; paratypes have 13 and 16 abdominal segments respectively. The lack of a posterior end means that the description cannot be complete but the material is considered sufficiently distinctive to merit the erection of a new species.

This new species can be distinguished from all other species of *Mediomastus* by the structure of the setae. The capillary setae are long, narrow and whiplike unlike those described for any other species of *Mediomastus* see Table 2. The thoracic hooded hooks have very long straight shafts, with the hood five times as long as wide and tightly fitting, and in this character they resemble those present in *M. fragilis* however this species has smooth thoracic capillaries unlike the whiplike setae present in *M. thomassini*. The abdominal hooks of *M. thomassini* are shorter than the thoracic hooded hooks and have a prominent shoulder and constriction together with a large beak-like fang and the hood is three times as long as the width of the hood. These abdominal hooded hooks are unlike those found in any other species of *Mediomastus* (see Table 2).

Habitat. *Mediomastus thomassini* occurs in intertidal and subtidal sand banks off the inner coral reef slope. For details of the associated fauna occurring with this species see Thomassin, 1978.

Etymology. The species is named after Dr Bernard Thomassin who collected the material and kindly allowed us to examine it.

Distribution. Known only from the type locality of Tuléar, Madagascar (Fig. 12).

Heteromastus Eisig

Heteromastus Eisig, 1887: 839, 841-843.—Hutchings & Rainer, 1981: 373-380.

Diagnosis. Thorax of 12 segments; 1 asetigerous segment present; first setiger complete. Segments 2-6 with capillary setae only (ie, first 5 setigers with capillary setae only), from segment 7, all setae hooks. Notopodial branchiae present.

Type species. *Capitella filiformis* Claparède, 1864 by subsequent designation by Eisig (1887).

Comments. Hutchings & Rainer (1981) designated a neotype of *Capitella filiformis* Claparède, 1864, in order to clarify the status of the genus *Heteromastus* Eisig, 1887. This was necessary as no type material of Claparède appears to exist and some potential confusion existed between the generic diagnosis given by Eisig which is widely used and the original description of *Capitella filiformis*. For more details see Hutchings & Rainer (1981).

Heteromastus caudatus (Hartman) new combination

Mediomastus caudatus Hartman, 1974: 237-239, fig. 13a-b.

Material examined. Arabian Sea – 5 km north of Cochin Harbour, Kerala State, RH14, TYPE (LACM-AHF Poly 1328), meiobenthos, 33 specimens, 23 m, silty clay, 5 March 1964; Madagascar – Tuléar, 23°20'S 43°41'E, 10 Aug. 1964, AB 363Z (LACM-AHF unregistered). intertidal sand, muddy sand, into mangrove areas; Arabian Sea 25°17'N 59°05'E, 29 Nov. 1963, AB 251B (LACM-AHF unregistered) 35 m.

Comments. The type material consists of a number of small worms, some of which are complete. Some of these specimens have capillary setae on the first five thoracic setigers thus complying with the diagnosis for *Heteromastus* and not *Mediomastus*. Hartman's (1974) description is not very detailed but, as far as could be determined, the specimens are those referred to in her description. The conspicuous projecting uncinial spines in the posterior segments, which she described, are clearly visible in some specimens. They take the form of greatly elongated hooded hooks with a minute head and very short hood, similar to those found in *M. ambiseta*.

The material labelled AB 251B, also referred to by Hartman in her description, consists of numerous anterior fragments.

AB 363Z is a complete worm of about 60 segments. It appears to have the correct thoracic setal formula for *Mediomastus* (although setae on setigers 1-4 could not be detected) but is not gravid. It does not come from the type locality, however. Its small size, together with the fact that it is slightly dehydrated, made it impossible to see any details of the setae but there is no sign of the uncinial projections referred to by Hartman. While this specimen may be a species of *Mediomastus*, it is not the species described by Hartman, and is in too poor a condition to describe.

We conclude therefore, that *Mediomastus caudatus* is a species of *Heteromastus*. The spine-like uncini probably mean that it is not synonymous with any described species of *Heteromastus* but we have not examined type of material of other species of *Heteromastus* to confirm this.

Recently it has been decided that the bulk of this Indian Ocean Expedition, R/V Anton Brun Cruise 4B will be lodged at the LACM-AHF with a voucher

collection being deposited in the USNM (Fauchald, personal communication).

Neomediomastus Hartman

Neomediomastus Hartman, 1969: 392.

Diagnosis. Thorax with 11 segments; 1 asetigerous segment present; first setiger complete. Up to segment 7 with capillary setae only, (ie, first 6 setigers with capillary setae) then all setigers with hooks. Small notopodial branchial processes present in far posterior setigers.

Type species. *Mediomastus glabrus* Hartman, 1960, by original designation.

Comments. Hartman (1969) does not give a formal generic description of *Neomediomastus*. However as *N. glabrus* is currently the only species assigned to this genus we have based the generic diagnosis on this species. We have included a full description of *N. glabrus* based on examining type material as it was originally described as a species of *Mediomastus* and some characters were omitted from the type description.

Neomediomastus glabrus (Hartman)

Mediomastus glabrus Hartman, 1960: 138-139.

Neomediomastus glabrus Hartman, 1969: 391-392, fig. 1.

Type material examined. HOLOTYPE (LACM-AHF Poly 0426) Stn 2850, PARATYPES (LACM-AHF Poly 0427) Stn 2850-54, 1135 m; Santa Catalina Basin, southern California, USA, 33°30'N 118°35'W. All type material posteriorly incomplete.

Description. Body length 5.5 mm for 33 segments; length of thorax to 2.2 mm, width of thorax 0.4 mm at setiger 3. Abdomen may be coiled. Thorax/abdomen boundary indistinct; marked by change in shape of segments. Body wall musculature thicker in thorax; abdominal segments thinner walled and not of fixed shape. There may also be marked discontinuity in segment size, first abdominal segment being wider or narrower than last thoracic segment. Abdominal notopodia are slightly lateral to thoracic notopodia. Red in alcohol, epidermis with slight sheen.

Prostomium triangular with broad base, tip rounded; no palpode. Large eversible proboscis, divided into 2 equal lobes by deep constriction. Anterior lobe slightly papillated; posterior lobe with distinct, long, pointed papillae; basal part with small papillae. Peristomium about same length and width as first setiger. Anterior margin evaginated mid-dorsally. No eyes. Thorax of 10

setigers; setigers 1-4 about one-third as long as wide; setigers 5-10 slightly narrower, length increasing gradually so that setiger 10 as long as wide. Setigers 1-4 clearly biannulated; epidermis otherwise smooth.

Nephridiopores not visible. Setigers 1-6 with capillary setae only. Capillary setae long, distally fine and flexible. Setigers 7-10 with hooks only. Setae in 4 equally spaced fascicles; dorsal capillary setae at angle such that lateral ends of notopodia are anterior to other ends. Hooks in an uneven row, appearing as double row in places. Numbers of capillary setae range from 6-13 in notopodia, 6-14 in neuropodia. Numbers of thoracic hooks range from 4-9 in notopodia; 6-11 in neuropodia.

Thoracic hook almost spine-like with long, more or less straight shaft and minute fang surmounted by indistinct rows of teeth. Hood tight fitting and long; length at least 6 times width; long narrow opening.

Size and shape of abdominal segments varies. Segment length usually 0.75-1.25 times width but may be much longer. Segments swollen dorsally, and sometimes ventrally in region of setae. Parapodial ridges increasingly more prominent after about sixth abdominal segment; notopodia each develop a posteriorly directed digitate lobe that may have branchial function.

Abdominal setigers with hooded hooks only; fascicles at mid-segment level in anterior segments, posteriorly thereafter. Anterior abdominal segments with 5-9 hooks per fascicle in notopodia; 10-11 in neuropodia; 15th abdominal segment with 6-8 hooks. Abdominal hooks shorter than thoracic hooks; shaft with a distinct shoulder but no constriction. Fang larger than in thoracic hooks; surmounted by at least 2 rows of regularly arranged, very small teeth, about 5 in each row. Hood short and tight fitting about 2 times as long as wide. Abdominal hooks are shorter.

Comments. None of the type specimens are complete, although Hartman (1960) refers to posterior segments. The holotype is a juvenile with only five thoracic setigers with capillary setae. None of the specimens is gravid. It is possible, therefore, that all specimens are juveniles. Nevertheless, the distinctive proboscis, the arrangement and structure of the setae; the notopodial "branchiae", together with the deep ocean habitat, suggest that the material is representative of a species sufficiently distinct from other capitellids to merit its own genus, *Neomediomastus* as diagnosed by Hartman (1969).

Habitat. *Neomediomastus glabrus* occurs at depths exceeding 1000 m.

Distribution. Deep basins and submarine canyons off southern California and western Mexico.

Discussion

The genus *Mediomastus* occurs throughout the world except in extreme high latitudes. Species are typically

geographically isolated (Fig. 12). Morphological differences between species are small, as is typical of the family Capitellidae. Generic determination of *Mediomastus* is dependent upon the thoracic setal formula and it is essential to examine mature individuals in order to avoid the possibility of confusion with *Heteromastus* as juvenile *Heteromastus* have the same thoracic setal formula as adult *Mediomastus*.

The morphology of the posterior end of *Mediomastus* is diagnostic for some species and only complete, sexually mature individuals can therefore be determined with any certainty. Thus, ideally, only sexually mature, complete individuals should be described as type material.

We know little of the geographical variation exhibited within species of *Mediomastus* as most species are known from a few limited localities often occurring in large numbers. We consider that the morphological differences between individuals from different localities represent discrete species and not geographical variation within one cosmopolitan species. Instead *Mediomastus*, which occupies similar shallow water habitats throughout the world, appears to have evolved into a number of discrete species without undergoing extensive morphological radiation. In support of this hypothesis, it may be noted that extensive intertidal and shallow subtidal collecting in some parts of the world has failed to reveal species with widespread distributions. Rather species have discrete geographical distributions when examined in detail. Based on published material that we have examined, records of certain species outside their geographical range have been shown to be erroneous. Furthermore, the presence of morphologically similar species is common within capitellids (Doyle, 1991; Grassle & Grassle, 1976). This may be a reflection of the evolutionary consequences of the opportunistic reproductive strategies employed by certain members of this family. For example populations of *Capitella* can expand rapidly after disturbance (Grassle & Grassle, 1974). We must emphasise, however, that no detailed studies of the reproduction of *Mediomastus* have been carried out. Nevertheless, *Mediomastus* increase in numbers in response to environmental stress (Dauvin, 1982) where such a strategy would be appropriate. Another factor responsible for the presence of morphologically similar species within the family may be that most species of capitellids occupy similar habitats, ie, muddy sediments, and have similar feeding strategies etc, which restricts the need for morphological adaptations.

Electrophoretic studies may be a useful tool, for separating members of a genus by increasing the range of diagnostic characters available for consideration. Such techniques have proved useful in separating morphologically similar species of *Scyphoproctus* in Australia (Doyle, 1991).

While species of *Mediomastus* are difficult to separate, the genus is easily recognised by its body shape and form, thoracic setal formula and the presence of a caudal cirrus. It could be confused with juvenile

Heteromastus which may have the same thoracic setal formula (Fredette, 1982, but see also Hutchings & Rainer, 1981). *Parheteromastus* Monro, 1937 has the same number of thoracic setigers with capillary setae but has additional thoracic setigers with hooded hooks, ie, a different thoracic formula. We believe that these genera are closely related, together with *Barantolla* Southern, 1921 and *Neomediomastus* Hartman, 1969, and form a discrete group within the family. We have examined material from each of these genera and have concluded that none is synonymous with *Mediomastus*. The closest is *Parheteromastus* but there is no doubt from the type material of the type species, *P. tenuis* Monro, 1937, that the 11th setiger is part of the thorax. The material is also much larger than any of the *Mediomastus* we have examined. It is possible that the increase in the number of posterior thoracic segments as exhibited by *Parheteromastus*, is related to the development in some species of *Mediomastus* of transitional posterior thoracic segments. It is worth noting, in this respect, that the largest species of *Mediomastus*, *M. fragilis*, is transitional on setiger 11. We have not, as yet, carried out a detailed study of these similar genera and cannot, therefore, comment further on possible inter-relationships.

This review is an attempt to clarify the taxonomy of *Mediomastus* as far as is possible given the material available. It is not intended to be a definitive work. Only four species are represented by large collections from several localities; five are known only from the type locality and, of these, four are known only from a single specimen or few specimens. For several species, the type material is incomplete or badly damaged. Wherever possible we have examined representative setae under SEM because we believe that setal morphology is very useful as a diagnostic tool. It is not often practical, however, so we have based the key on other features. We must emphasise that the key is not necessarily exhaustive, but hopefully will facilitate the identification of additional material as it becomes available.

Distinguishing between Species of *Mediomastus*

The most difficult species to distinguish between, even with good material, are *M. californiensis*, *M. capensis* and *M. fragilis*, which are all large species. *Mediomastus ambiseta*, which is also large and has a similar distribution to *M. californiensis*, is readily distinguished by the presence of capillary setae and spine-like hooks in the abdomen. As these may start from about setiger 15, the distinction should be apparent even in most incomplete worms. *Mediomastus acutus*, which also occurs in California, may be distinguished by its paddle-like notosetae and by the shape of its prostomium. *Mediomastus californiensis* and *M. fragilis* are best distinguished by the fact that the thoracic and abdominal hooks are morphologically different in *M. fragilis* but very similar to one another in *M. californiensis*. Despite its name, *M. fragilis* is the

largest, most robust species in the genus. This may explain why setiger 11 as well as setiger 10 appears transitional in some specimens. It is possible that smaller specimens might be confused with *M. thomassini*. It is difficult to make comparisons between a species known only from incomplete type material and one that is commonly occurring but, on the evidence currently available, *M. thomassini* may be distinguished by the long down-curved fang on the abdominal hooks and by the prominence of all its setae which appear unusually long relative to its body size. *Mediomastus capensis* is similarly quite difficult to distinguish from *M. californiensis* but has differences in setal morphology. Three species have abdominal capillary setae. The best known of these, *M. ambiseta*, also has spine-like hooks. As far as is known these are not present in *M. branchiferus* nor *M. setosus*. In Australia, currently two species are known which can easily be separated, *M. australiensis* is a robust species in contrast to *M. calliopensis*, in addition the structure of the hooded hooks differs.

ACKNOWLEDGMENTS. We should like to thank the following people and institutions for lending us material: Alex Muir and David George, Natural History Museum, London; California Academy of Sciences, San Francisco; Sue Williams, Leslie Harris, formerly Allan Hancock Foundation now the Los Angeles County Museum, Los Angeles; Bernard Thomassin, Marine Station D'Endoume, Marseille; Gesa Hartmann-Schröder, Zoologisches Institut und Zoologisches Museum der Universität, Hamburg; Sebastian Rainer, Division of Fisheries, CSIRO, Perth; Meredith Jones, United States National Museum, Washington; Zoology Dept, University of Cape Town and The South African Museum, Cape Town; Eric Rasmussen, Zoological Museum, Copenhagen; John Berge, University of Oslo; Charlotte Fuller, Woods Hole Oceanographic Institution; Julian Hunter, Highlands River Purification Board; Tony Walker, University of North Wales. Sebastian Rainer provided encouragement in the early stages of this paper and provided comments on the manuscript. Jane McRae prepared Figure 10. The Royal Society of London provided funds to one of us (LW) to visit Australia during the preparation of this paper.

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Table 1. Summary of diagnostic characters of species of *Mediomastus* (except setae). n.d. - no data

SPECIES	LOCALITY	LENGTH (mm)	EGG DIAMETER (μ m)	ABD. CAPS	ABD. SPINE-LIKE HOOKS	PROSTOMIUM	PAPILLAE ON PROBOSCIS	BRANCHIAE
<i>M. acutus</i>	California, USA	4 incomplete	60	-	-	long and pointed	poorly developed	-
<i>M. ambiseta</i>	North America east and west coast	14	50	+	+	small, conical	low, indistinct	-
<i>M. australiensis</i> n.sp.	south-east Australia to south Australia	21+	80	-	-	long, rounded tipped	finely papillated	-
<i>M. branchiferus</i>	South America Pacific Ocean	3.5	n.d.	+	-	small rounded palpode		+
<i>M. californiensis</i>	North America east and west coast Gulf of Mexico	35	60	-	-	small	widely scattered low, more or less distinct	-
<i>M. calliopensis</i> n.sp.	Gladstone Qld, Australia	27	50-57	-	-	small	low	-
<i>M. capensis</i>	South Africa Indian Ocean	14 incomplete	40	-	-	small, elongated palpode	appears smooth, very indistinct	-
<i>M. cirripes</i>	Mediterranean	3-5, type, incomplete	65+	-	-	small, conical with long palpode	low, poorly defined	-
<i>M. deductus</i>	Sri Lanka Indian Ocean	37, type, incomplete	65	-	-	small, conical	very distinct	-
<i>M. fragilis</i>	North Sea, Baltic ? Mediterranean	60	70	-	-	small	low prominent	-
<i>M. setosus</i>	El Salvador Pacific Ocean	4	n.d.	+	-		present	-
<i>M. thomassini</i> n.sp.	Madagascar Indian Ocean	8 incomplete	60+	-	-	small conical	widely spaced, low, not prominent	-

Table 2. Setal characteristics of species of *Mediomastus*. n.d. - no data; for abdominal caps and spine-like hooks + = present, - = absent; for thoracic abdominal hooks, + = same, - = different; ± = more or less the same.

SPECIES	THORAX AND ABD. HOOKS SAME	THORAX/ABD. BOUNDARY	THORACIC HOOK	ABDOMINAL HOOK	CAPILLARIES (THORACIC)
<i>M. acutus</i>	+	distinct setiger 10/11	long straight shaft paddle-like notosetae, plus hooded hooks, neurosetae different, shorter	neurosetae same as thoracic neurosetal hook, abdominal notosetae included paddle-like notosetae and typical hooded hook	short, spatulate, smooth tipped
<i>M. ambiseta</i>	-	distinct setiger 10/11, setiger 10 same shape as 9, transitional in size	long, straight shaft slight shoulder; no constriction, small fang; 2 rows of teeth; tight hood 2-5 times long as wide	short, stout shaft prominent shoulder prominent constriction hood short and wide 2-3 times long as wide	broad winged recurved tip
<i>M. australiensis</i> n.sp.	-	clear demarcation	distinct neck and shoulder; no constriction hood wide with curved opening, surface of hood textured	similar to thoracic but fang longer pointed, slightly beaked; hoods flared with upturned margins strongly textured	narrow winged capillaries
<i>M. branchiferus</i>	n.d.	damaged, n.d.	long straight shaft; no constriction; hood 3 times as long as wide	n.d.	n.d.
<i>M. californiensis</i>	±	distinct 10/11	long straight shaft, no constriction; small fang; several rows of teeth in first row, hood tight 3 times long as wide	slight shoulder, slight constriction, otherwise like thoracic	narrow smooth winged
<i>M. calliopensis</i> n.sp.	-	distinct 10/11 position of setae transitional on 10	stout, short shaft; small fang, hood wide	shorter and smaller, prominent shoulder, long fang, shorter hood	narrow smooth winged

Table 2 (cont'd).

SPECIES	THORAX AND ABD. HOOKS SAME	THORAX/ABD. BOUNDARY	THORACIC HOOK	ABDOMINAL HOOK	CAPILLARIES (THORACIC)
<i>M. capensis</i>	±	distinct 10/11 setiger 10 same size and shape as 9; setae in same position on 11	long straight shaft; small fang; 3 steep rows of teeth voluminous hood 2-3 times long as wide	slightly shorter, slight shoulder, no constriction, fang slightly larger, 2+ steep rows of teeth	hooked tip
<i>M. cirripes</i>	±	distinct 10/11 setiger 10 transitional	long straight shaft; no constriction, small fang, 3+ rows of teeth, hood wide very long and wide, 4 times long as wide	slight shoulder and constriction, fang slightly larger, hood narrower	broad winged
<i>M. deductus</i>	-	indistinct setiger 10 like 9	not prominent; no shoulder, no constriction, small fang, 4 times long as wide	very short; indistinct shoulder, prominent fang, tight hood	narrow winged, may be recurved
<i>M. fragilis</i>	-	indistinct setigers 10+11 both transitional hook intermediate	long, straightish shaft, no constriction, small fang; 2+ rows of teeth, hood 3-5 times long as wide	short indistinct constriction, larger fang, many teeth, hood one and a half times long as wide	smooth
<i>M. setosus</i>	n.d.	? distinct	n.d.	n.d.	n.d.
<i>M. thomassini</i> n.sp.	-	more or less distinct	very long straight shaft, small fang; 2 rows of teeth, first row with 3-5 teeth, hood tight; 5 times long as wide	shorter; shoulder and constriction large fang-beak-like 2+ rows of teeth; wide hood 3 times long as wide	long, narrow whiplike