

Generic characters in the Polynoinae (Annelida, Polychaeta), with notes on the higher classification of scale-worms (Aphroditacea)

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Introduction

A comparison of Fauvel, 1923 and Hartmann-Schröder, 1971, with Hartman, 1959, 1965 and Fauchald, 1977 shows that the limits of the genus *Harmothoe* and its sub-genera are confused. *Antinoella* Augener, 1928, *Austrolaenilla* Bergström, 1916, *Eucranta* Malmgren, 1865, *Eunoe* Malmgren, 1865 and *Harmothoe* Kinberg, 1855, are variously considered as genera or sub-genera of *Harmothoe sensu lato*. It was decided that this situation should be investigated preparatory to a study of the scale-worms of north-western Europe (George & Muir, in prep.).

The sub-family under consideration in this paper is often referred to as the Harmothoinae Willey, 1902. However, as the categories family and sub-family are co-ordinate according to the International Code of Zoological Nomenclature 1964 (articles 36 and 37), the correct name is Polynoinae Kinberg, 1855.

It should be borne in mind also that the word Polynoinae is often used to refer to that taxon herein called the family Polynoidae, when that family is thought of as a sub-family of the Aphroditidae (e.g. Fauvel, 1923; Day, 1967). The family Aphroditidae as used by these authors is equivalent to Fauchald's (1977) super-family Aphroditacea, i.e. it includes all scale-worms and excludes all others.

Materials and methods

Thirty-four of the genera or sub-genera, including the disputed five, of the Polynoinae were investigated. The type specimens of the type species of each genus were examined, where possible. The other type specimens appear to be either missing or not available on loan. For all except one of these remaining genera it was considered unsafe to rely on early, incomplete descriptions or possibly misidentified specimens from localities sometimes far distant from the type locality.

The exception was made for the important genus *Polynoe*, which provides the stem for the family-group names. *Polynoe scolopendrina*, the species usually cited as the type species (see Muir, 1979), has been described many times and there are many specimens in the collection of the BM(NH). A description was therefore compiled from Savigny, 1822; Fauvel, 1923; Day, 1967; Hartmann-Schröder, 1971 and ZK 1938.5.25.7, a specimen from East London, South Africa, which matches the description of Savigny, 1822. The type locality is 'côtes de l'océan', which refers to the Atlantic coast of France. As Savigny's polychaete type specimens are not in the Museum National d'Histoire Naturelle, Paris (Renaud-Mornant, *pers. comm.*), they have probably been destroyed (see Pallary, 1932).

The nominal genera studied are listed in Table 1, which also gives the Operational Taxonomic Unit (O.T.U.) numbers, i.e. *Bathylevensteinia* was the twenty-fifth taxon to have its details entered into the computer.

Table 1 O.T.U. coding, with a list of material studied

O.T.U. number	Nominal genus	Type species	Material studied
01	<i>Acanthicolepis</i> McIntosh, 1900	<i>Polynoe asperima</i> Sars, 1861	Oslo C 3154, syntypes
02	<i>Adyte</i> Saint-Joseph, 1899	<i>Hermadion assimile</i> McIntosh, 1876	BM(NH) ZK 1921.5.1.498-500, syntypes
03	<i>Antinoo</i> Kinberg, 1855	<i>Antinoo microps</i> Kinberg, 1855	Stockholm Typsaml. 407, holotype
04	<i>Antinoella</i> Augener, 1928	<i>Antinoo sarsi</i> Kinberg in Retzius, 1857	Stockholm 410, 413, syntypes
05	<i>Arcteoobia</i> Annenkova, 1937	<i>Eupolynoe antioestiensis</i> McIntosh, 1874	BM(NH) ZK 1921.5.1.554-5, syntypes
06	<i>Australaugeneria</i> Pettibone, 1969a	<i>Polynoe rutilans</i> Grube, 1878	Pettibone, 1969a & pers. comm.
07	<i>Austrolaenilla</i> Bergström, 1916	<i>Austrolaenilla antarctica</i> Bergström, 1916	Stockholm Typsaml. 590, syntypes
08	<i>Barrukia</i> Bergström, 1916	<i>Gatyania cristata</i> Willey, 1902	BM(NH) ZK 1902.1.8.23-5, syntypes
25	<i>Bathylevensteinia</i> Pettibone, 1976	<i>Macellicephala bicornis</i> Levenstein, 1962	Pettibone, 1976 & pers. comm.
09	<i>Enipo</i> Malmgren, 1865	<i>Enipo kinbergi</i> Malmgren, 1865	Stockholm Typsaml. 2377, syntype
10	<i>Eucranta</i> Malmgren, 1865	<i>Eucranta villosa</i> Malmgren, 1865	Stockholm Typsaml. 2378, syntypes
11	<i>Eunoo</i> Malmgren, 1865	<i>Eunoo oerstedii</i> Malmgren, 1865	Stockholm Typsaml. 2390, 2391, 2395, syntypes
26	<i>Gesiella</i> Pettibone, 1976	<i>Macellicephala jameensis</i> Hartmann-Schröder, 1974	Hartmann-Schröder, 1974 & Pettibone, 1976
12	<i>Gorekia</i> Bergström, 1916	<i>Malmgrenia crassicornis</i> Willey, 1902	BM(NH) ZK 1902.1.8.67-74, syntypes
13	<i>Harmothoe</i> Kinberg, 1855	<i>Harmothoe spinosa</i> Kinberg, 1855	Stockholm Typsaml. 409, syntypes
14	<i>Hartmania</i> Pettibone, 1955	<i>Hartmania moorei</i> Pettibone, 1955	Pettibone, 1955 & pers. comm.
15	<i>Herdmanella</i> Darboux, 1899	<i>Polynoe (?) ascidioides</i> McIntosh, 1885	BM(NH) ZK 1855.12.1.92, holotype
27	<i>Hermadion</i> Kinberg, 1855	<i>Hermadion magalhaensi</i> Kinberg, 1855	Stockholm Typsaml. 532, holotype
16	<i>Intoshella</i> Darboux, 1899	<i>Polynoe (Langerhansia) euptectellae</i> McIntosh, 1885	BM(NH) ZK 1885.12.1.91, ZK 1921.5.1.548, syntypes
28	<i>Kermadecella</i> Darboux, 1899	<i>Polynoe magnipalpa</i> McIntosh, 1885	BM(NH) ZK 1885.12.1.98-98a, syntypes
17	<i>Lagisca</i> Malmgren, 1865	<i>Polynoe rarispina</i> Sars, 1861	Oslo C 3157, syntypes
18	<i>Leucia</i> Malmgren, 1867	<i>Polynoe nivea</i> Sars, 1863	Oslo C 3156, syntypes
19	<i>Melaenis</i> Malmgren, 1865	<i>Melaenis loveni</i> Malmgren, 1865	Stockholm Typsaml. 2383, syntype
20	<i>Nemidia</i> Malmgren, 1865	<i>Nemidia torelli</i> Malmgren, 1865	Stockholm Typsaml. 2379, syntypes
30	<i>Neoholepidella</i> Pettibone, 1969b	<i>Neoholepidella murrayi</i> Pettibone, 1969b	BM(NH) ZK 1937.9.2.29, holotype
21	<i>Paradyte</i> Pettibone, 1969a	<i>Polynoe crinoideicola</i> Potts, 1910	BM(NH) ZK 1924.3.1.85, syntypes
22	<i>Phyllosheila</i> Pettibone, 1961	<i>Phyllohartmania taylora</i> Pettibone, 1961	Pettibone, 1961 & pers. comm.
23	<i>Phyllosheila</i> Pettibone, 1961	<i>Phyllosheila wigleyi</i> Pettibone, 1961	Pettibone, 1961 & pers. comm.
31	<i>Polyeunoo</i> McIntosh, 1885	<i>Polyeunoo laevis</i> McIntosh, 1885	Pettibone, 1961 & pers. comm.
29	<i>Polynoe</i> Savigny, 1818	<i>Polynoe scolopendrina</i> Savigny, 1822	BM(NH) ZK 1885.12.1.55, syntypes
32	<i>Polynoella</i> McIntosh, 1885	<i>Polynoella levisetosia</i> McIntosh, 1885	See text
33	<i>Robertianella</i> McIntosh, 1885	<i>Polynoe (Robertianella) synophthalma</i> McIntosh, 1885	BM(NH) ZK 1885.12.1.105, holotype
34	<i>Scalisetosus</i> McIntosh, 1885	<i>Scalisetosus ceramensis</i> McIntosh, 1885	BM(NH) ZK 1885.12.1.101-2, syntypes
24	<i>Tenonia</i> Nichols, 1969	<i>Tenonia kitsapensis</i> Nichols, 1969	BM(NH) ZK 1885.12.1.85, holotype Nichols, 1969

Details of the external morphology of the worms were examined using a Wild M4A binocular microscope, at a magnification of $\times 60$. Chaetae were examined, after removal of a parapodium and mounting in polyvinyl lactophenol, using a Wild M20 microscope, at a magnification of $\times 500$.

Characters

The characters are discussed here in detail, because there is some confusion of terminology in the literature. Although internal characters have been used in some families (e.g. pharyngeal armature in Nereididae, nephridia in Terebellidae), only external characters have been examined in this study of type material. The character numbers and codings, as used in the data matrix, are listed after the discussion of the possible characters and their states.

Length, width and number of segments

Where possible, the length of the body (including head) and the greatest width (including parapodia, but not including chaetae) were measured. These measurements were then ranged from 0 to 100 (i.e. they were expressed as a percentage of the maximum length or width found). It will be seen from Fig. 1a that *Eunoe* (O.T.U. 11) is longer and wider than any other specimen measured. The other O.T.U.s, however, do not form a straight line between *Eunoe* and the origin. Length and width are therefore not perfectly correlated and must both be considered in the numerical part of this paper, even though width was measured more accurately than length in those cases where specimens were coiled or fragmented.

The relationship of length and width is easier to see in Fig. 1b, where a ranged value of length divided by width is plotted against a ranged value representing the number of segments. The number of segments for this purpose includes all the segments between the head and the pygidium, i.e. it includes the tentacular cirrus segment.

It will be seen that there are two groups along the L/W axis. Most of the O.T.U.s, including *Eunoe*, are grouped between 17 and 62 on this axis. The second group lies between 90 and 100 on the L/W axis and can be thought of as relatively long and thin, as opposed to the first group, which are more oval in shape and more obviously dorso-ventrally flattened.

Another interpretation of this scatter-diagram is that, apart from O.T.U.s 16 and 9, there is a correlation between shape and number of segments. If worm A has more segments than worm B it will probably be **relatively** longer and thinner, although not necessarily longer in **absolute** terms.

Grouping along the S axis is not so obvious as that along the L/W axis, with most of the O.T.U.s between 12 and 54, then *Polyeunoa* (O.T.U. 31) at 65, *Polynoe* (29) at 80 and *Neohololepidella* (30) at 100.

Head appendages

All members of the Polynoinae, when intact, have three antennae; one median antenna attached via a ceratophore to the anterior margin of the head and two lateral antennae attached via their ceratophores sub-distally and ventrally on the head. The lateral antennae appear always to be shorter than the median antenna, so this ratio was not used as a character.

Daly (1973a) has investigated the structure and function of the appendages of *Harmothoe imbricata* and describes the papillae on the surface of the antennae. It is likely that the antennae of all polynoid worms have a similar structure and function, although they are often described as smooth. The antennae, when present, were examined at a magnification of $\times 60$ and described as either smooth or ornamented.

Daly (1973a) has described two different types of papillae on the surface of the palps, although these were not noted by Åkesson, 1963. The palps are described here as smooth or

ornamented at $\times 60$ and their length is compared with that of the median antenna when possible.

The head often carries eyes, usually four in number; a posterior pair and a pair wider apart, often at the sides of the head. I agree with Darboux (1899) that this is not an important characteristic. Not only does the pigment of the eyes fade after prolonged immersion in preserving fluids, so their presence is likely to be missed, but in some polychaetes the number and distribution of eyes is known to vary during the development of one individual, and also between individuals of one species.

Cirri

The various cirri have a similar structure and function to the antennae (Daly, 1973a). All polynoids possess two pairs of tentacular cirri. These structures, looking similar to the antennae, are attached via cirrophores directly to the sides of the first segment behind the head and are directed forward like the antennae. The dorsal pair are generally slightly longer than the ventral pair. The length of the longest tentacular cirrus is compared with that of the median antenna and they are described as smooth or ornamented.

The dorsal cirri are slightly more variable in shape than the antennae, not always having a sub-terminal swelling as the antennae do. They have been described as smooth or ornamented, and their length is compared with that of the parapodial lobes, i.e. if the tip of the cirrus extended further from the body than the lobes of the parapodium, it was described as longer.

Two types of ventral cirri occur in intact specimens. The most anterior pair are usually much longer than the others, and directed forwards, but were usually missing in the specimens studied. The normal ventral cirri are assessed for surface ornamentation, and length in comparison with that of the parapodia.

The anal cirri (sometimes called urites) were almost always missing in the specimens studied. They are usually similar to the dorsal cirri.

Parapodia

In the Polynoidae each segment except that bearing the tentacular cirri bears well-developed parapodia. In some cases the parapodia are distinctly elongated (i.e. the length of the parapodium from the side of the body to its distal extremity approaches the width of the body), so parapodial length was used as a character in the numerical analyses. The elongated state was present in eight of the thirty-four O.T.U.s investigated (23.5%), but is also found in some genera of the other subfamilies of Polynoidae. It is not clear, therefore, at this stage of the investigation, if either state can be called primitive with any degree of certainty.

Several descriptions of polynoids have been published which mention cilia on the parapodia, but cilia were not seen in the present study.

The parapodia bear chaetae (described below) and ventral cirri. They also bear either dorsal cirri or elytra. In one case, *Gesiella jameensis* (Hartmann-Schröder, 1974), the dorsal cirrophores also carry a structure unique among the polychaetes, called by Pettibone (1976) an accessory filamentous sensory organ. The presence or absence of this structure was used as a character in the numerical analyses, and presence was taken as the derived state.

Elytra

The elytra, singular elytron, are the scales which scale-worms carry dorsally. They are attached by short stalks or elytriphores to the dorsal surface of those parapodia which do not carry dorsal cirri. The elytriphores tend to be of greater diameter than the dorsal cirrophores and also to be nearer to the mid-line of the body. Thus the arrangement of the elytra can be discerned even when the elytra are missing.

The arrangement of the elytra has long been regarded as of great importance at the generic level. The arrangement is usually given as a list of the segments which carry the elytra. The

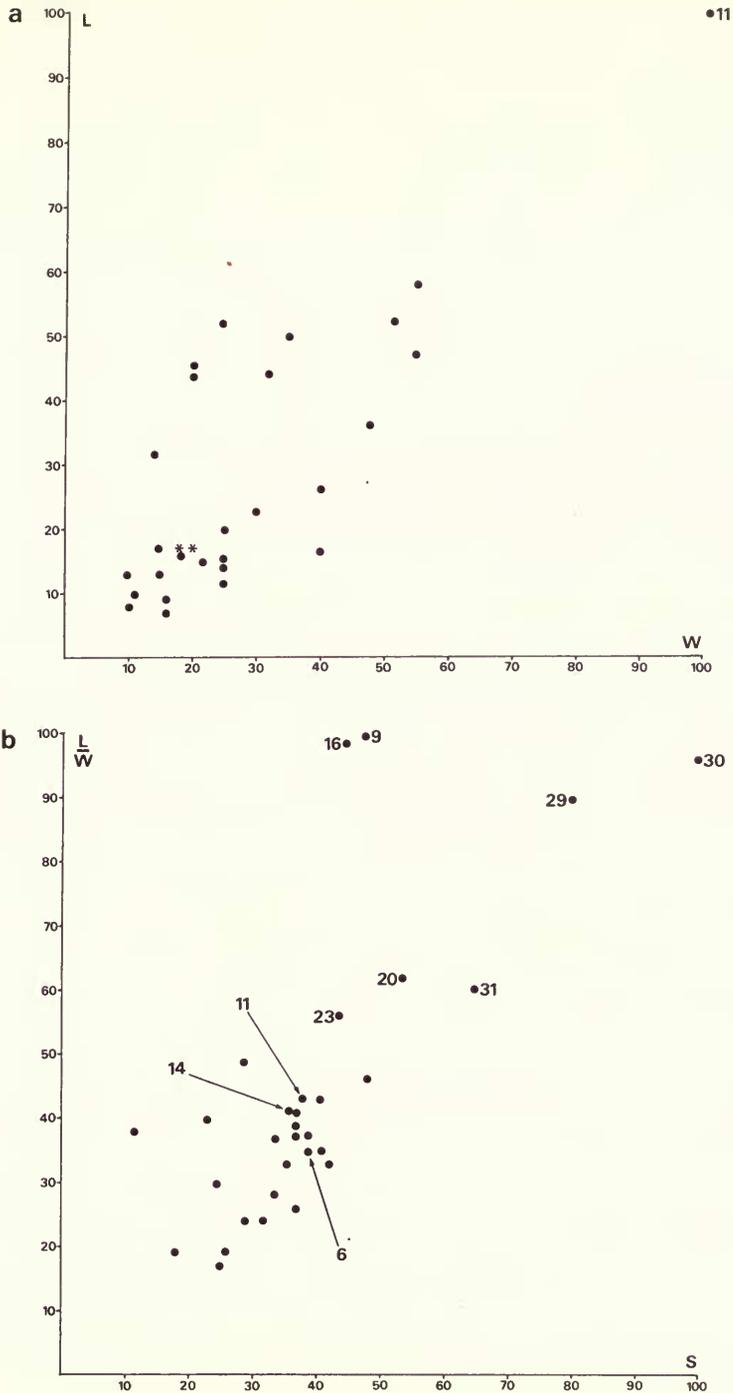


Fig. 1 (a) A scatter-diagram of ranged values of length (L) against ranged values of width (W). An asterisk represents two O.T.U.s. (b) A scatter-diagram of ranged values of length divided by width (L/W) against ranged values of number of segments (S). In both cases only those O.T.U.s especially mentioned in the text are numbered.

use of the term segment by itself is perhaps confusing in this situation, as it is not certain how many segments have been incorporated into the head (see Fauchald, 1974). Other authors have used the term setiger, meaning a segment which carries setae = chaetae. However, the tentacular cirrus segment may or may not display chaetae between the cirrophores, so that an elytron on the segment behind the tentacular cirri may be on setiger 1 or 2. I have therefore used the concept of the parapodial segment, i.e. a segment with distinct parapodia. Using this concept the most anterior elytra are always found on parapodial segment 1, and the standard arrangement of pairs of elytra is: 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 25, 28, 31. A worm with only, say ten segments (including the tentacular cirrus segment) will only have nine parapodial segments, so the elytral arrangement will normally be: 1, 3, 4, 6, 8. This may explain why Darboux (1899) did not regard the number of elytra as a generic characteristic. Many polynoids have more than thirty-one parapodial segments, and these will normally either have a 'tail' region which does not bear elytra, or elytra will continue to be borne on every third segment.

The elytral arrangement has been scored as standard or non-standard in the numerical analyses, but there is a certain subjective element in judging whether an arrangement is standard or not when a minor variation is seen. The observations of Bergström (1916) on the posterior elytra of *Polyeunoa laevis* are of interest in this regard.

Five O.T.U.s were scored as non-standard, but their elytral arrangements were not the same as each other. Thus a certain amount of information has not been presented to the computer. The five arrangements are:

O.T.U. 9 *Enipo* (Right 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 25, 27, 30
(Left 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 25, 28, 31

Asymmetrical, the right side being non-standard.

O.T.U. 12 *Gorekia* 1, 3, 4, 6, 8, 10, 12, (14?), 16, 18, 20, 23, 26, 29

O.T.U. 34 *Scalisetosus* 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 23, 26, 29, 32

Both change to every third segment after number 20 instead of number 22. Cirrophores of parapodial segment 14 of *Gorekia* not clear.

O.T.U. 18 *Leucia* 1, 3, 4, 6, 8, 10, 12, 14, 16 (17, 19, 23, 26, 29, 32)

Type broken at parapodial segment 16, but non-standard due to three non-elytrigerous segments in succession (i.e. 20, 21, 22).

O.T.U. 30 *Neohololepidella* 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 25, 28, 31, 33, 35, 37, 39, 41, 43, 45, 47, 49, 51, 53, 55, 57, 59, 61, 63, 65, 67, 69, 71, 73, 75, 77, 79, 81, 83, 85, 87, 89, 91, 93, 95, 97, 99, 101, 103 (+?)

Returns to every second segment after number 31.

In descriptions of new genera or species of Polynoidae the elytra are usually described in some detail. The shape of any papillae, tubercles etc., on the surface is given, and any hairs or papillae forming a fringe on the postero-lateral rim are also described. It was found that, under increasing magnifications, a so-called hair became a papilla and a papilla could appear as a large tubercle. It was therefore decided to note 1) presence or absence of ornamentation on the dorsal surface. 2) presence or absence of fringe; at a magnification of $\times 60$. The surface structure of the elytra of a range of scale-worms was investigated by Anton-Erxleben (1977) using a scanning electron microscope, and it appears that at very high magnifications the precise shapes of papillae, tubercles and scales, and the presence of pores in some of the Aphroditidae, can be a valuable taxonomic tool. It is not known which states of these characters concerning the elytra are primitive.

Body surfaces

The dorsal and ventral surfaces were both inspected, but no ciliation was observed. All the specimens in good condition showed a longitudinal ventral groove, however, which would be useful as a channel for a respiratory current as described by Dam (1940) for *Aphrodita aculeata*. Segrove (1938) and Lwebuga-Mukasa (1971) have described dorsal currents for

some polynoids, and *Leucia* (O.T.U. 18) shows a dorsal groove from parapodial segment 12. Uschakov (1974) suggests that a dense grating of thin notochaetae (as in *Gattyana*) would protect this dorsal respiratory channel from obstruction in benthopelagic species which swim through water containing large amounts of detritus and suspended mineral particles.

Pettibone has described ciliated structures on O.T.U.s 6, 22 and 26, and other (non-ciliated) structures were seen on O.T.U.s 8, 11, 12 and 19, but these were not entered into the data matrix.

Nephridial Papillae

The nephridial papillae, seen at the postero-ventral base of the parapodia, were much more prominent in some specimens than in others, and this has been used as a character in the data matrix. The papillae were never dorsally directed as shown by Daly (1972) for a ripe female, and were never as elongated as he showed for a ripe male. Thus the specimens used in this study were probably not ripe. Specimens of *Polynoe scolopendrina* from North Uist (identified by McIntosh), Plymouth (Norman), Isles Chausey (Fauvel) and East London, South Africa (Stephenson) were examined, and all of them showed nephridial papillae enlarged but not elongated. As the specimens were of different sizes, and collected at different times from different places, it is unlikely that they were all collected at the beginning of the brief breeding season, and that the enlarged state is a developing stage of the elongated state. The enlarged state of the papillae is therefore probably a specific or generic characteristic rather than a seasonal or sexual one.

Daly (1972) states that the length of the nephridial papillae varies with the size of the individual for *Harmothoe imbricata*. This is shown in a general way by the data matrix, from which it can be seen that the specimens with small papillae have an average ranged length of 19·21, and those with large papillae have an average ranged length of 41·41. This latter figure is, of course, distorted by the presence of *Eunoe* (length 100), but also contains *Australaugeneria* (length 8). Enlarged papillae are shown by 12 (35·3%) of the O.T.U.s in the data matrix, and the distribution of this character in the other sub-families of the Polynoidae is not readily obtainable, so it cannot be said with confidence that one state is primitive or derived.

Colour

Colours and colour patterns are often seen in live and preserved polynoids. Daly (1973*b*), working with live animals, found intraspecific variation in the elytral patterns of *Harmothoe imbricata*. With preserved material, a dark surface can sometimes be seen flaking away from an otherwise colourless elytron. Again, with preserved material, colour is often leached out of the specimen by the preserving fluids. Alternatively, pigment may be dissolved out of the corks often used in the past to close containers and then transferred to the worm inside that container.

Chaetae, especially polynoid notochaetae, are sometimes coloured, and appear to keep their colour well when preserved. This colour varies from a pale yellow tint, through golden- or dark-brown, almost to black, but the range could not be subdivided because of the many intermediates seen.

For all these reasons, colour and colour patterns have not been considered useful taxonomic characters.

Chaetal diameter

Some authors, e.g. Darboux, 1899; Fauchald, 1977, use the relative thickness of the neurochaetae and notochaetae as a generic character. This can, of course, be very difficult to judge when there is a range of chaetae in both groups, and it has not been used as a character here. Bergström, 1916, considered this to be a useful character only at the specific level.

Neurochaetal shape

Unidentate

This common type has a long, thin shaft emerging from the surface of the neuropodium, abruptly widening to form a distinct 'shoulder' to the chaeta (Fig. 2a). The head of the chaeta, distal to the 'shoulder', is shorter than the shaft, and distinctly bent over at the tip, producing the unidentate effect. Between the tip and the 'shoulder' is a region which may bear quite large side-teeth, or may be serrated, or may merely bear faint striations on one side (see Fig. 2a). These states may all be present upon one parapodium, so they are not significant even at the specific level. It is probable that the side-teeth are usually fairly prominent in a newly secreted chaeta, but become worn in older chaetae.

Sesquidentate

This type is similar to the unidentate type (above), but bears a distinct hump below the bent-over tip (Fig. 2b). It is always found in conjunction with the unidentate or bidentate types.

Bidentate

This type is again similar to the unidentate type, but bears a distinct secondary tooth immediately below the bent-over tip (Fig. 2c).

Tridentate

This type is similar to the bidentate type (above), but bears a small tertiary tooth between the primary and secondary teeth (Fig. 2d).

Bergström, 1916 (p. 273 & Fig. 2), united the unidentate, sesquidentate and bidentate neurochaetae under the term 'Grundtypus'. The close relationship between these three types was shown in a startling manner by Hillger and Reish, 1970, in an experiment in which they converted a lepidonotine species with predominantly uni- and sesquidentate neurochaetae to one with predominantly sesqui- and bidentate neurochaetae (and vice versa) by letting amputated parapodia regenerate in warmer or colder water. Gaffney (1973) disagrees with some of the conclusions of Hillger and Reish, e.g. that temperature is the important factor, but it remains true to say that these chaetae are closely related. As Gaffney says, 'Examination of the setae reveals countless intermediates between the purely bifid and entire types, making the task of categorizing them a difficult one'. In my opinion, the tridentate neurochaetae (the *setae mucronatae* of Bergström) can be included with the above as a 'dentate series'. This series, as well as being common in the Polynoinae, is also commonly found in the Lepidonotinae, the other large sub-family of the Polynoidae. It may therefore be argued that possession of dentate neurochaetae can be regarded as a primitive trait.

Capillary Tip

These neurochaetae are similar to the unidentate type, except that the tip, instead of bending over to form a large, sharp tooth, extends into a long, thin filament (Fig. 2e).

Pointed Tip

Again, this is similar to the unidentate neurochaeta, but here the tip is not bent over (Fig. 2f).

Blunt Tip

This is as the pointed tip type, but blunt (Fig. 2g).

For the numerical part of this study I have united these three types as the 'simple tip' series. No work appears to have been published on the mode of formation of, or the effect of wear on, the chaetae of polynoids. However, Michaelis (1978) has shown that in spionid polychaetes chaetae with capillary tips do get worn down through a pointed stage to a blunt stage. This series, like the dentate series, is common to the Polynoinae and the Lepidonotinae, so presence may be a primitive trait, even though it is found less often than the dentate series in the specimens studied.

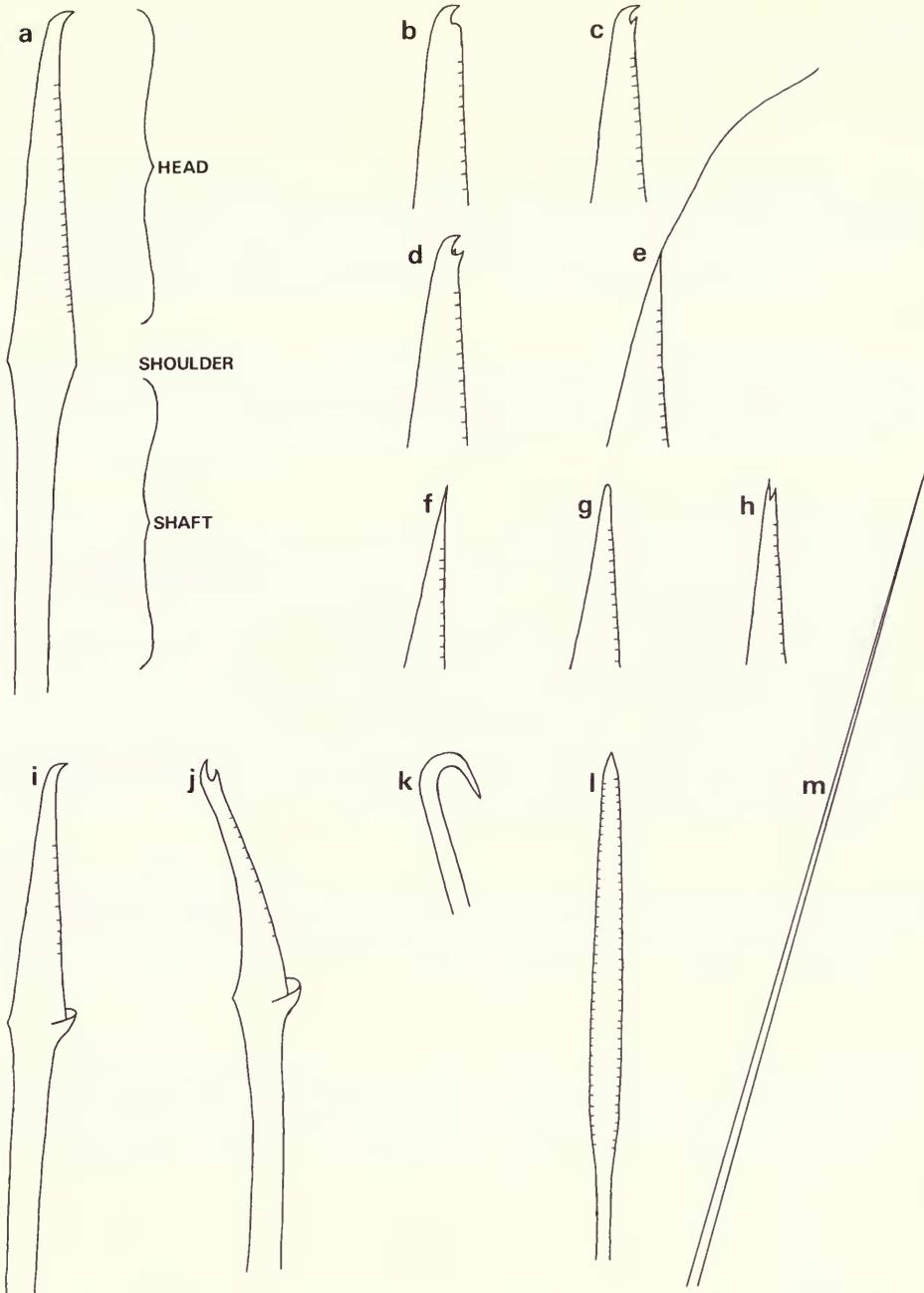


Fig. 2 Neurochaetal types. (a) Unidentate type. Complete chaeta showing regions. (b) Sesquidentate tip. (c) Bidentate tip. (d) Tridentate tip. (e) Capillary tip. (f) Pointed tip. (g) Blunt tip. (h) Unequal furcate tip. (i) Unidentate semi-lunar pocket type. (j) Bidentate, recurved, semi-lunar pocket type. (k) Anterior hook, after Pettibone, 1969a. (l) Flattened type, after Pettibone, 1976. (m) Capillary type.

Strong Type

This type is similar to the pointed, simple tip type, but is much more robust in appearance. It was seen only in *Polynoe scolopendrina*, where it is regarded as an advanced trait.

Unequal Furcate

These neurochaetae are similar to the pointed tip type (above), but in this case the tip is forked (Fig. 2h). The two forks are not divergent, and are not of the same length. The longer tip is not bent over as in the bidentate type. This character is unique to *Melaenis* amongst the Polynoinae. It is not found in the Lepidonotinae, although *Hermenia* is reported as having trifurcate neurochaetae. Its presence is therefore regarded as an advanced state.

Unidentate with Semilunar Pocket

This type is similar to the unidentate type described above, but on the 'shoulder', on the same side as the tooth points toward, bears a structure dubbed by Pettibone (1969a) 'basal semilunar cusp or pocket' (Fig. 2i).

Bidentate, Recurved with Semilunar Pocket

This type is like a bidentate form of the unidentate type with a semilunar pocket but it is usually strongly recurved (Fig. 2j).

I have united these two forms as the 'semilunar pocket' series in the numerical part of this paper. It is only found in two nominal genera of Polynoinae and not in the Lepidonotinae, and its presence is therefore likely to be an advanced trait.

Anterior Hook

Some polynoids possess, on the neuropodia of the first two or three segments, chaetae characterised by Pettibone (1969a) as 'stout golden hooks' (Fig. 2k). Being only found in the genus *Australaugeneria* its presence is an advanced trait.

Flattened

Gesiella jameensis (Hartmann-Schröder, 1974) is the only member of the Polynoinae to possess chaetae described by Pettibone (1976) as 'long, delicate, flattened, finely toothed along lateral borders, with tapered bare tips' (Fig. 2l).

Capillary

Herdmanella ascidioides (McIntosh, 1885) possesses capillary (i.e. long and very thin, see Fig. 2m) neurochaetae. I have regarded this as advanced in the Polynoinae, although it is found scattered throughout the Polychaeta, including *Frennia* (Lepidonotinae). The shape may have been produced many times independently, as it is a relatively simple structure.

Notochaetal shape*Bluntly Pointed*

This is by far the most common type of notochaeta found in the Polynoidae, but does encompass a certain amount of variation. A typical member of this group will be the same diameter all along its length, slightly recurved, with a range of small side-teeth along the distal half of the convex side, and bluntly pointed at its tip (Fig. 3a). Members of this group may be slightly dilated in the region of the side-teeth, the side-teeth can be quite large or almost invisible, and the chaeta as a whole can be almost straight or strongly recurved in the region of the side-teeth. All these variations merge into one another, however, so I feel justified in calling them all one group of chaetae. Presence is a primitive trait in the Polynoidae.

Furcate

This type is similar to the bluntly pointed group of notochaetae, but the tip has a small though definite split which does not appear to be accidental damage (Fig. 3b, c). Its presence is rare and therefore probably an advanced trait in the Polynoinae.

Compressed

This group could be envisaged as flattened representatives of one of the previous two groups. They have fewer, but broader, side-teeth (Fig. 3d) and in *Adyte* and *Paradyte* can be furcate. Its presence is rare and therefore probably an advanced state in the Polynoinae.

Falciger

Fauchald (1977) defines falcigers as distally blunt and curved setae. *Eucranta*, as well as having the usual bluntly pointed notochaetae, has others which are straight almost until the distal end is reached, when they become strongly curved. These chaetae I have called falcigers, and their presence appears to be a derived trait.

Capillary

Several genera possess capillary notochaetae. As with the capillary neurochaetae, this may have been produced several times in the Polychaeta.

Paleae

These chaetae have a narrow proximal portion emerging from the parapodium which abruptly becomes widened and flattened before terminating in a blunt point (Fig. 3e). There are no side-teeth, and no 'shoulder' as seen in the neurochaetae. It is unique to *Antinoe* in the Polynoidea and can therefore be regarded as advanced.

Penicillate

Barrukia possesses normal, bluntly pointed notochaetae, and also others very similar to these but with the tip almost hidden by a mass of fine hairs. It is unique among the Polynoidea and therefore probably a derived character.

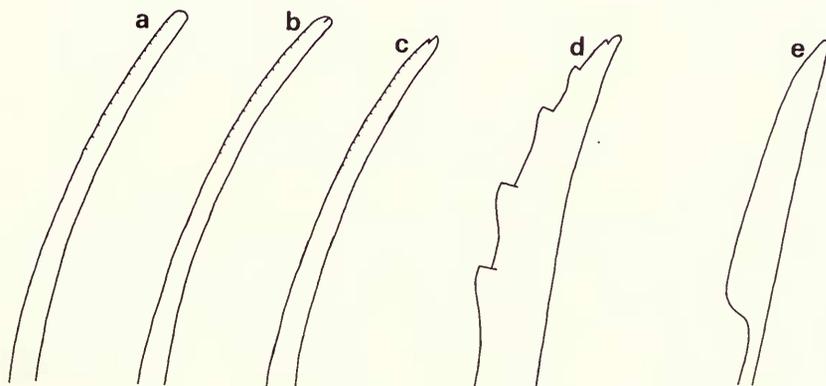


Fig. 3 Notochaetal types. (a) Bluntly pointed. (b) & (c) Two varieties of furcate tip. (d) Compressed type. (e) Palea.

Character coding

The characters used in the numerical part of this study are listed below, with their numbers and the coding used for their different states in the data matrix.

<i>Character</i>	<i>Coding</i>
01 Neurochaetae, simple tip series	0 absent 1 present
02 Neurochaetae, dentate series	0 absent 1 present
03 Neurochaetae, unequal furcate	0 absent 1 present
04 Neurochaetae, semilunar pocket series	0 absent 1 present
05 Neurochaetae, anterior hooks	0 absent 1 present
06 Neurochaetae, flattened	0 absent 1 present
07 Neurochaetae, capillary	0 absent 1 present
08 Notochaetae, bluntly pointed	0 absent 1 present
09 Notochaetae, furcate	0 absent 1 present
10 Notochaetae, compressed	0 absent 1 present
11 Notochaetae, falcigers	0 absent 1 present
12 Notochaetae, capillary	0 absent 1 present
13 Notochaetae, paleae	0 absent 1 present
14 Notochaetae, penicillate	0 absent 1 present
15 Parapodial development	1 normal 2 elongated
16 Dorsal cirrus length: parapodium	1 shorter 2 equal 3 longer
17 Dorsal cirrus ornamentation	0 absent 1 present
18 Ventral cirrus length: parapodium	1 shorter 3 longer
19 Ventral cirrus ornamentation	0 absent 1 present
20 Length (including head and pygidium)	ranged from 0 to 100
21 Width (including parapodial lobes)	ranged from 0 to 100
22 Palp length: median antenna	1 shorter 3 longer
23 Tentacular cirrus length: median antenna	1 shorter 2 equal 3 longer
24 Antenna ornamentation	0 absent 1 present
25 Palp ornamentation	0 absent 1 present
26 Tentacular cirrus ornamentation	0 absent 1 present
27 Elytral arrangement	1 standard 2 non-standard
28 Elytral surface ornamentation	0 absent 1 present
29 Elytral fringe	0 absent 1 present
30 Nephridial papillae	1 small 2 enlarged
31 Accessory filamentous sensory organs	0 absent 1 present
32 Neurochaetae, strong	0 absent 1 present
33 Number of segments	ranged from 0 to 100

Computations and conclusions

Preliminary computations

The characters listed above are of three different types:

1. Those which are apparently derived, in which case absence of that character is not important from a phylogenetic point of view, i.e. two worms without that character are not necessarily similar and the computer will disregard those data. The characters in this group are numbered 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 31, 32. These are all binary characters (either present or absent) which are rarely present in the population under consideration.
2. Character 8 is a binary character which is almost always present in the population under consideration. It is also to be seen in other sub-families of the Polynoidae. This character is therefore regarded as primitive, and absence of this character may sometimes be significant. There are other characters for which it is not clear which states are primitive or

derived. It was therefore thought best that all states should be used in the calculations of overall similarity between the O.T.U.s. These characters are numbered 1, 2, 15, 16, 17, 18, 19, 22, 23, 24, 25, 26, 27, 28, 29, 30.

3. Characters 20, 21 and 33 are quantitative, and all values should be compared with all other values.

The character and O.T.U. codes have been given above. Descriptions of O.T.U.s and the resulting data matrix are available from the author. The data matrix was entered into the BM(NH) Varian mini-computer, a similarity matrix and the position of each O.T.U. on the first five principal coordinate axes were calculated, and the five nearest neighbours of each O.T.U. listed. The nearest neighbours are shown in Table 2.

The first and second coordinates of each O.T.U. were then plotted against each other (Fig. 4) in order to give the best graphical representation of similarities in two dimensions.

Table 2 List of first five nearest neighbours for each O.T.U. Thus the nearest neighbour of O.T.U. 1 is O.T.U. 13, with a similarity of 99.0%, and the second nearest neighbour is O.T.U. 3, with a similarity of 92.3%

O.T.U.	Nearest Neighbours									
	1	2	3	4	5					
01	13	99.0	03	92.3	33	90.9	18	88.3	05	87.3
02	21	99.7	32	76.0	16	72.0	28	71.9	26	69.2
03	01	92.3	13	88.9	28	87.5	05	85.6	33	85.4
04	33	77.6	01	76.7	14	72.7	07	72.7	03	72.3
05	28	92.7	18	92.6	16	92.1	13	92.0	33	91.5
06	24	72.9	09	70.4	32	69.1	33	67.1	12	65.6
07	13	98.4	01	84.9	08	83.9	33	83.5	25	81.3
08	13	90.4	01	86.4	07	83.9	33	82.7	17	80.7
09	15	78.6	06	70.4	24	68.5	32	64.2	26	61.9
10	27	73.9	01	68.7	33	67.3	13	66.0	17	65.4
11	07	80.7	13	78.8	27	74.7	29	73.7	08	73.7
12	18	94.3	28	88.2	30	84.3	16	84.3	05	83.0
13	01	99.0	07	98.4	05	92.0	08	90.4	18	90.2
14	04	72.7	22	65.8	19	64.8	07	61.3	03	58.5
15	09	78.6	24	71.1	32	69.9	28	64.0	16	63.8
16	28	97.2	05	92.1	32	90.7	33	90.3	31	87.3
17	33	87.8	08	80.7	13	80.3	27	78.9	07	75.4
18	12	94.3	05	92.6	28	91.8	30	91.0	13	90.2
19	20	69.5	14	64.8	04	64.3	28	63.2	10	62.6
20	11	72.9	19	69.5	07	67.7	22	64.1	04	62.3
21	02	99.7	32	79.0	16	74.5	28	74.3	26	71.1
22	24	79.3	01	70.8	04	67.2	14	65.8	20	64.1
23	25	79.9	28	72.9	05	71.6	18	70.8	16	70.8
24	22	79.3	05	76.9	32	76.8	25	74.8	28	73.2
25	28	89.7	05	88.8	13	87.5	16	86.8	07	81.3
26	28	83.9	16	78.9	32	78.5	31	77.4	05	77.4
27	13	85.1	33	84.0	17	78.9	08	77.1	01	76.2
28	16	97.2	05	92.7	32	92.4	33	91.8	18	91.8
29	11	73.7	07	70.3	04	70.1	13	67.2	01	64.6
30	18	91.0	16	84.9	12	84.3	01	83.5	13	81.8
31	28	88.8	16	87.3	34	84.2	05	83.7	33	79.4
32	28	92.4	16	90.7	05	86.3	18	85.6	31	84.2
33	28	91.8	05	91.5	01	90.9	16	90.3	13	89.6
34	18	74.2	33	74.0	32	71.8	12	69.1	27	67.0

Conclusions

It will be deduced from Table 2 and Fig. 4 that *Harmothoe* (O.T.U. 13) is very similar to O.T.U.s 1 (*Acanthicolepis*) and 7 (*Austrolaenilla*). *Austrolaenilla* is one of the genera that Hartmann-Schröder (1971) wished to make a sub-genus of *Harmothoe*. The other three genera that she specified (O.T.U.s 4, 10 and 11) are much more dissimilar. It is unfortunate that there are seven variates missing from the syntypes of *Harmothoe*, but as they and the types of *Austrolaenilla* are so similar, and as *Harmothoe* contains 120 species (*vide* Fauchald,

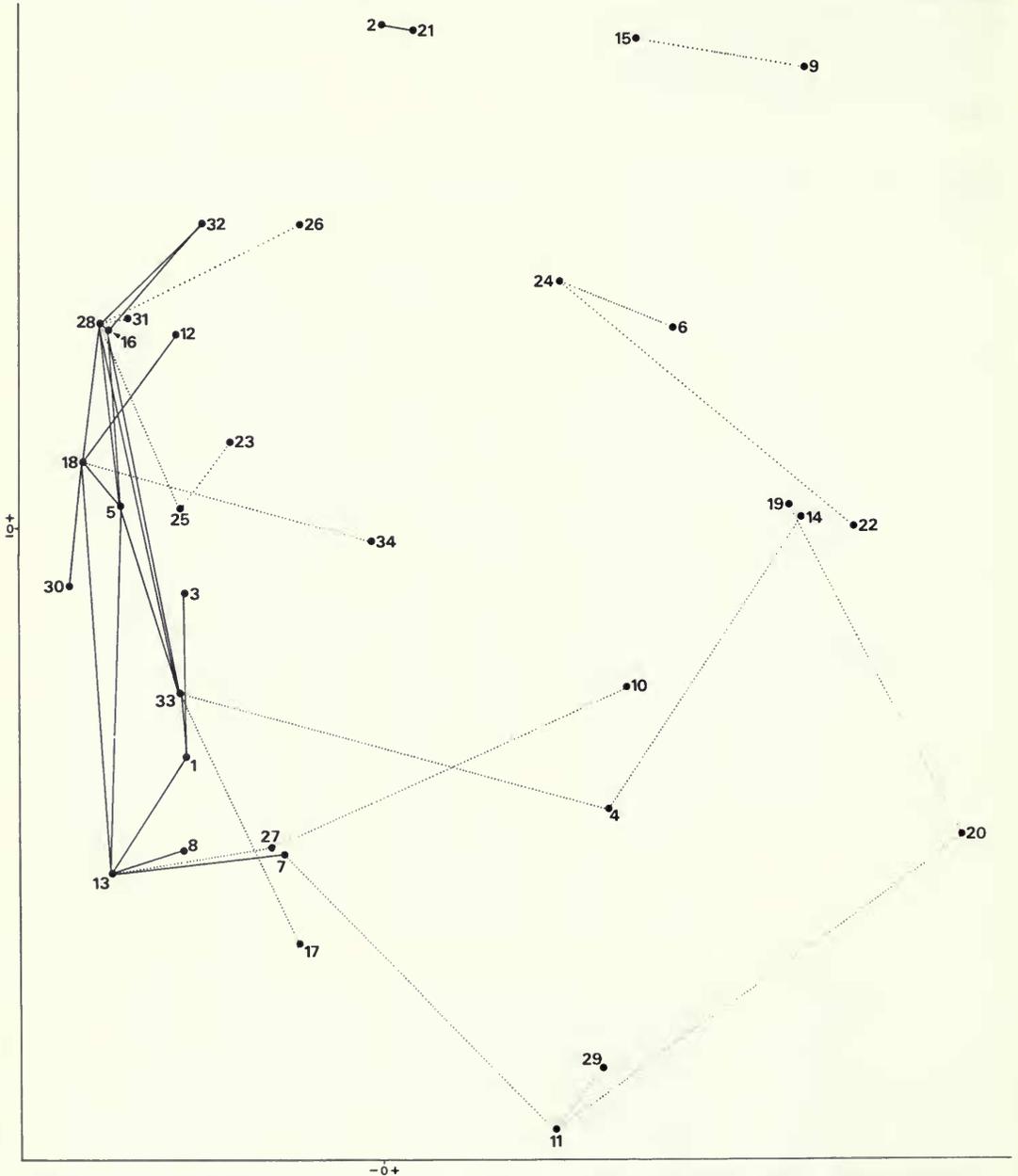


Fig. 4 A scatter-diagram of O.T.U.s plotted on principal coordinate axes 1 (vertical) and 2 (horizontal). Those O.T.U.s which are more than 90% similar to each other are joined by solid lines, the others are connected to their nearest neighbour by a broken line.

1977) and so probably covers a wide range of variation, I would agree with Hartmann-Schröder, who studied a wider range of specimens, that these two genera are synonymous. *Acanthicolepis* was considered a separate genus by Hartmann-Schröder, 1971, and Fauvel, 1923. The types of *Austrolaenilla* and *Harmothoe* are 98.4% similar, but those of *Acanthicolepis* and *Harmothoe* are 99.0% similar, so it would be sensible to synonymize *Acanthicolepis* as well. It would be of value to study the 130 or so species of this group to see if there are any noticeable phenetic gaps between them. *Harmothoe* is the oldest of these three genera, and is the central one in Fig. 4, so nomenclaturally and numerically it would be correct for *Harmothoe* to remain the name of a new enlarged genus.

O.T.U.s 2 (*Adyte*) and 21 (*Paradyte*) are even more similar to each other. *Paradyte* was erected by Pettibone (1969a) for three species with fewer segments than the only species left in *Adyte*, and with both types of semilunar pocket series chaetae (*Adyte* only has the bidentate, recurved type). The number of segments does not appear to be of importance at the generic level from a comparison of Figs. 1 and 4. The two types of semilunar pocket series chaetae are such complex structures, and yet so similar to each other, that I believe they must be closely related. I would therefore synonymize *Paradyte* Pettibone, 1969a with *Adyte* Saint-Joseph, 1899, although perhaps retaining *Paradyte* as a sub-genus.

O.T.U.s 16 (*Intoshella*) and 28 (*Kermadecella*) are also very similar to each other. The main differences between the types lie in the length and number of segments. The median antennae are missing from the types of *Kermadecella*, but the ratio of lengths of the palps and tentacular cirri seems similar to that shown by the types of *Intoshella*. Both genera were erected by Darboux, 1899, probably from the published descriptions of the type species by McIntosh, 1885. The defining characteristic of *Kermadecella* is that the dorsal cirri are alternately long and short. This is by no means obvious from the types, and as *Kermadecella* only has one species, it may safely become a junior synonym of *Intoshella*, which has three species.

O.T.U.s 16 and 28 are 97.2% similar. The next most similar pair of O.T.U.s are 12 and 18 (*Gorekia* and *Leucia*) at 94.3%. *Gorekia* possesses furcate notochaetae as well as the bluntly pointed type, *Leucia* does not. *Leucia* is distinctly wider than *Gorekia*. *Gorekia* shows two annuli per segment dorsally, while *Leucia* has a dorsal longitudinal groove from parapodial segment 12. It was therefore decided that these O.T.U.s represent distinct genera, and that 95% similarity would be a convenient cut-off point for generic identity in this study.

Secondary computations

Because O.T.U.s 1, 7, 21 and 28 have been synonymized with other O.T.U.s (above), it is necessary to run the data for the thirty remaining O.T.U.s through the computer again. Their nearest neighbours are shown in Table 3.

The first and second coordinates have been plotted against each other in Fig. 5. I have also plotted the first coordinates against the third in Fig. 6, to give a better idea of the O.T.U. distribution in multi-dimensional space, and to show why O.T.U.s 14, 19 and 22 are not directly connected to each other on a minimum spanning tree. A tree is a set of straight lines joining pairs of points such that all points are connected to each other, but no closed geometric shapes are formed. The minimum spanning tree uses the shortest possible set of lines in multi-dimensional space, i.e. it links O.T.U.s with high similarities.

Discussions

Previous theories on the inter-relationships of the Polynoinae

Darboux (1899), although considering the Polynoidea to be only one sub-family, split them up into five series. The genera of the Polynoinae that he knew of were put into his series D and E along with some Lepidonotinae. The members of series D were supposed to be long and cylindrical, while the members of series E are short and flattened.

The long, cylindrical group contained O.T.U.s 9, 20, 29 and 31, which are either in the top group or at the top of the lower group in Fig. 1b.

The short, flat group contained O.T.U.s 1, 3, 10, 11, 13, 15, 16, 17, 18, 19, 27, 28, 32, 33 and 34. This group therefore contained the longest genus (*Eunoe*, O.T.U. 11) and the relatively thinnest genus, O.T.U. 16, although this latter (*Intoshella*) was not mentioned in the discussion which followed the listing.

Not only is this division into two series therefore inconsistent with the definitions of the series, but the four genera of series D are well separated on Fig. 5. This shows that the other characters do not segregate along with body shape, and that the two series are therefore an artificial division.

Segrove (1938), basing his ideas on the surface ciliation, considered *Harmothoe* (O.T.U. 13) to show the primitive condition for all scale-worms, with one evolutionary line going through *Lagisca* (O.T.U. 17) to *Polynoe* (O.T.U. 29).

Uschakov (1974, 1977) is the latest author to discuss the phylogeny of this group, and he concentrates on shape and the arrangement of the elytra, which he relates to commensalism, especially commensalism of a polynoid in the tube of another organism. It is interesting to note here the work of Wagner, Phillips, Standing and Hand (1979), which shows that commensalism may not always be the correct term to describe the associations between polynoids and other organisms.

Table 3 List of first five nearest neighbours for each O.T.U. after removal of O.T.U.s 1, 7, 21 and 28

O.T.U.	Nearest Neighbours									
	1	2	3	4	5					
02	32	75.9	16	72.0	26	69.2	31	65.3	05	64.1
03	13	88.9	05	85.6	33	85.4	18	82.3	16	81.5
04	33	77.5	14	72.7	03	72.3	13	71.1	29	70.0
05	18	92.6	16	92.0	13	92.0	33	91.4	25	88.8
06	24	72.9	09	70.4	32	69.0	33	67.1	12	65.6
08	13	90.3	33	82.6	17	80.7	05	80.5	18	77.9
09	15	78.6	06	70.4	24	68.4	32	64.2	26	61.8
10	27	73.9	33	67.1	13	65.8	17	65.4	04	63.4
11	13	78.4	27	74.6	29	73.5	17	73.4	08	73.4
12	18	94.3	30	84.3	16	84.2	05	83.0	32	82.2
13	05	92.0	08	90.3	18	90.2	33	89.6	03	88.9
14	04	72.7	22	65.7	19	64.7	03	58.5	20	58.3
15	09	78.6	24	71.1	32	69.8	16	63.8	22	63.5
16	05	92.0	32	90.6	33	90.3	31	87.2	25	86.7
17	33	87.7	08	80.7	13	80.2	27	78.8	11	73.4
18	12	94.3	05	92.6	30	90.9	13	90.2	16	86.7
19	20	69.4	14	64.7	04	64.2	10	62.6	05	62.4
20	11	72.8	19	69.4	22	64.0	04	62.3	29	61.7
22	24	79.3	04	67.2	14	65.7	20	64.0	15	63.5
23	25	79.8	05	71.5	16	70.8	18	70.7	13	70.6
24	22	79.3	05	76.9	32	76.7	25	74.8	06	72.9
25	05	88.8	13	87.4	16	86.7	18	79.9	23	79.8
26	16	78.8	32	78.5	31	77.4	05	77.4	33	73.1
27	13	84.9	33	83.8	17	78.8	08	77.0	05	75.0
29	11	73.5	04	70.0	13	67.2	08	63.3	27	62.4
30	18	90.9	16	84.8	12	84.3	13	81.7	05	81.4
31	16	87.2	32	84.2	05	83.7	33	79.3	30	78.9
32	16	90.6	05	86.3	18	85.5	31	84.2	33	83.3
33	05	91.4	16	90.3	13	89.6	17	87.7	03	85.4
34	18	74.2	33	74.0	32	71.7	12	69.1	27	66.8

Hartmania (O.T.U. 14) is the only O.T.U. investigated which was found living in tubes (actually burrows of *Neanthes virens*), and it had a standard elytral arrangement. Other O.T.U.s with standard elytral arrangements were found in association with echinoderms (21, 23), ascidians (15), coelenterates (6), sponges (16) or living free (the other twenty-three O.T.U.s). Of the five O.T.U.s with non-standard elytral arrangements, one (30) was in the central cavity of a calcareous sponge. Thus 20% of the O.T.U.s with non-standard arrangements, and 20% of O.T.U.s with standard arrangements (after synonymizations) are 'commensals'. Statistically, therefore, elytral arrangement and 'commensalism' are not correlated.

Two of the 'commensal' O.T.U.s (16, 30) are in the relatively long and thin group of Fig. 1b, and one of the other four or five (23) is near the top of the other group. O.T.U.s 6 and 14 have lower values of ranged L/W. O.T.U.s 15 and 21 were incomplete. Again, this distribution is not statistically significant.

Uschakov actually cites *Polyeunoa* (O.T.U. 31) as a primitive type and *Polynoella* (O.T.U. 32) as an advanced type, but these two genera have similar coordinates (see Figs. 5 & 6).

Groupings within the Polynoinae

One of the obvious features of Figs. 5 and 6 is the 'back-bone' formed by the O.T.U.s which are 90–95% similar to each other. This group has a wide spread on axis 1 but a small spread on vectors 2 and 3.

The group includes O.T.U.s 12, 18 and 30, which have non-standard elytral arrangements. O.T.U. 34 is loosely attached to these three, but the fifth O.T.U. with a non-standard arrangement (O.T.U. 9) is widely separated on vector 2. The arrangement on O.T.U.s 12 and 34 is very similar, and O.T.U. 18 also has similarities. *Neohololepidella* (O.T.U. 30) has a normal arrangement up to parapodial segment 31, and then returns to every second segment rather than every third segment. O.T.U.s 12 and 18 (*Gorekia* and *Leucia*) have other similarities to each other, but O.T.U.s 30 and 34 (*Neohololepidella* and *Scalissetosus*) have many missing data. These O.T.U.s may all be regarded as being derived with respect to this character.

The other 'back-bone' genera with obviously derived character traits are O.T.U.s 8 and 32. O.T.U. 8 (*Barrukia*) has penicillate notochaetae in addition to the bluntly pointed type. These are very similar to each other, and the penicillate type could easily be derived from the usual type. O.T.U. 32 (*Polynoella*) has no notochaetae at all. Loss of a character, in this case bluntly pointed notochaetae, is generally regarded as of little importance from a phylogenetic point of view.

Of the four remaining 'back-bone' genera, O.T.U. 16 (*Intoshella*) has no ornamentation on the elytra, O.T.U. 5 (*Arcteobia*) has surface ornamentation but no fringe, and O.T.U. 13 (*Harmothoe*) has surface ornamentation and a fringe. These data are missing from O.T.U. 33 (*Robertianella*) which, however, has large nephridial papillae, whereas the others have small papillae. These four O.T.U.s could perhaps be regarded as primitive members of the Polynoinae, although none of them, of course, can be called an ancestral form.

A group of O.T.U.s which are weakly linked to each other, but which have important similarities to each other, consists of O.T.U.s 6, 9, 15, 22 and 24, which have positive first and second eigenvector coordinates but are widely spread on eigenvector 3. This group of five O.T.U.s all have elongated parapodia (a trait shared with O.T.U.s 23 and 25 which are also linked to O.T.U. 5; and O.T.U. 20) and do not have bluntly pointed notochaetae (a trait shared with O.T.U.s 2, 32 and 34). O.T.U. 32, as stated above, has no notochaetae, but it has dentate neurochaetae. O.T.U.s 2 (*Adyte*) and 34 (*Scalissetosus*) share character 10 (compressed notochaetae), but have other different, derived characters (semilunar pocket series neurochaetae for O.T.U. 2 and elytral arrangement for O.T.U. 34). O.T.U.s 23 and 25 (*Phyllosheila* and *Bathylevensteinia*) have dentate neurochaetae and bluntly pointed notochaetae (agreeing with the 'back-bone' genera) whereas O.T.U. 20 has simple-tip neurochaetae and bluntly pointed notochaetae (perhaps also a primitive arrangement).

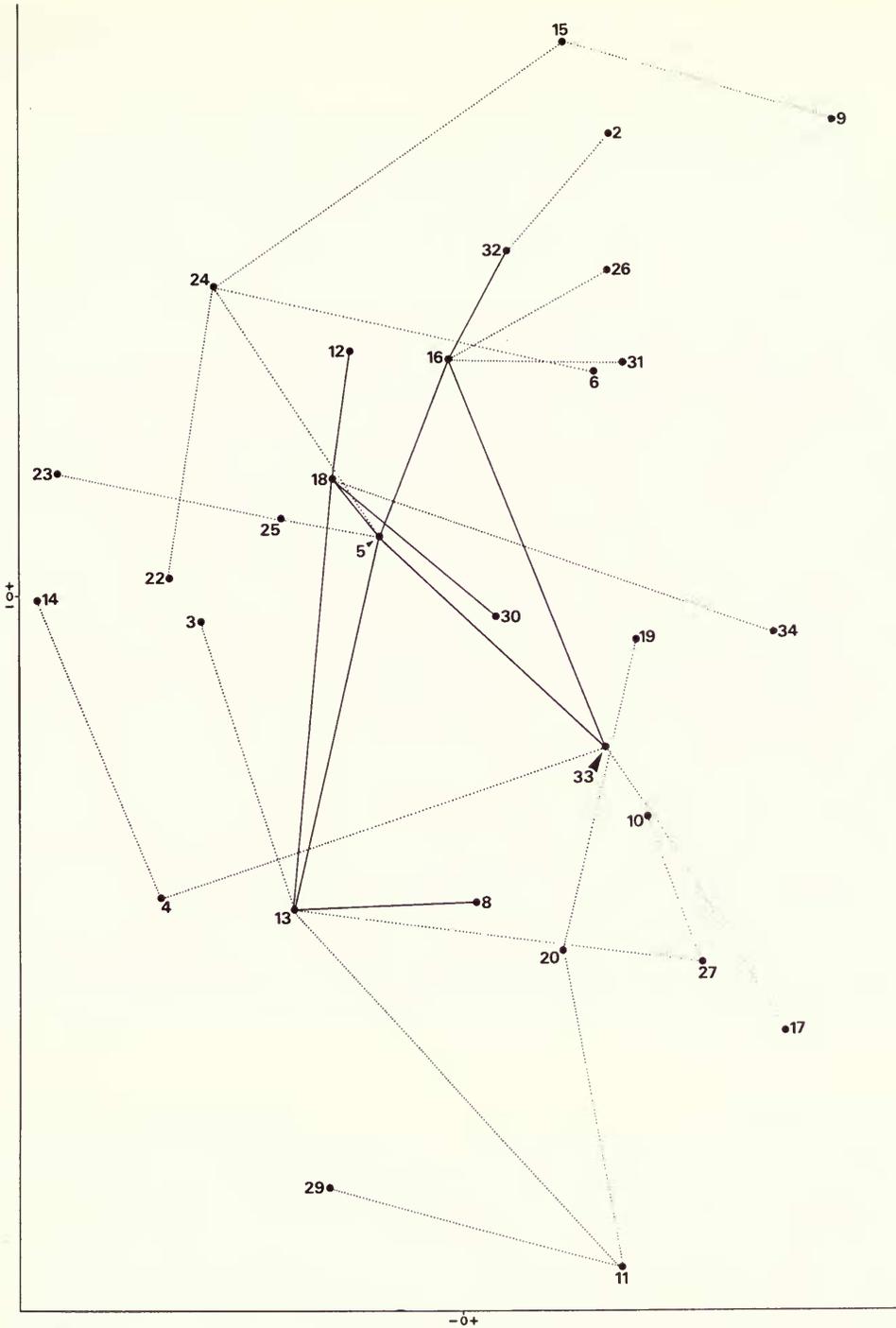


Fig. 6 As Fig. 5, but using principal coordinate axes 1 (vertical) and 3 (horizontal).

O.T.U.s 9 (*Enipo*), 15 (*Herdmanella*), 22 (*Phyllohartmania*) and 24 (*Tenonia*) have capillary notochaetae, whereas O.T.U. 6 (*Australaugeneria*) has furcate notochaetae. Thus they are all derived with regard to notochaetae as well as with regard to parapodial development. O.T.U.s 9, 22 and 24 have primitive neurochaetae. O.T.U. 6 has anterior hooks as well as primitive neurochaetae, and O.T.U. 15 has only got capillary neurochaetae. In my opinion these can be regarded as a distinct, derived group within the Polynoinae, with the possible exception of *Herdmanella*. There is a lot of missing data with regard to this O.T.U. In particular the anterior end is missing, which means that it cannot be referred with certainty to any polynoid sub-family. Pettibone (1976) refers to the genus and species as 'doubtful Polynoidae'.

Uschakov (1977), discussing the Macellicephalinae as defined by Hartmann-Schröder (1971, 1974) states that the characters (*a*) body consistency very soft; (*b*) elytra easily fall off; (*c*) bristles fine and long; (*d*) parapodia greatly elongated; (*e*) dorsal cirri extremely long; all facilitate swimming near the bottom in search of food at abyssal depths. *Herdmanella*, which has all these characters, was found at 2600 fathoms (4755 m) in the branchial chamber of an ascidian. It is possible that this was a hiding place used for protection between feeding forays. The other four members of this group appear slightly less specialized for abyssal life, and at least two of them (O.T.U.s 22 and 24) were found in shallow water. The depths were not given for O.T.U.s 6 and 9. O.T.U. 6 was found in association with the soft coral *Xenia*, so it is possible that the anterior hooks are an adaptation for attachment to the host.

In the bottom half of Fig. 5 there is a group of O.T.U.s which are loosely related phenetically to each other and to the 'back-bone' O.T.U.s. There are three lines of O.T.U.s attached to 'back-bone' O.T.U. 13, (*a*) 11, 29, 20, 19. (*b*) 27, 10. (*c*) 3. O.T.U. 33 gives rise to two lines, (*a*) 4, 14. (*b*) 17. In general, it will be noted that these O.T.U.s are greatly ornamented on some or all of the cirri, antennae, palps and elytra, although there is some missing information for O.T.U.s 3, 4, 10 and 27. All these O.T.U.s also have one or two derived character states and, or, large nephridial papillae. O.T.U. 33 is the only 'back-bone' O.T.U. with enlarged nephridial papillae, so perhaps this trait may also be regarded as derived.

O.T.U. 31 (*Polyeunoa*) is similarly phenetically related to the 'back-bone' at O.T.U. 16, neither of these displaying ornamentation. Again, O.T.U. 31 is not actually a member of the 'back-bone' group because it displays derived states for other characters, i.e. long ventral cirri, and perhaps the short palps and tentacular cirri are also derived.

O.T.U. 26 is similarly placed to O.T.U. 31 for similar reasons. However, whereas the derived states in O.T.U. 31 can be seen to be closely related to primitive states of the same characters in other O.T.U.s, the derived states seen in O.T.U. 26 (*Gesiella*) are completely new structures (flattened neurochaetae with fine lateral teeth and filamentous accessory organs on the dorsal cirrophores).

Out-group comparisons

Of the notochaetae, the bluntly pointed type is probably more primitive than the others, being much more common both in the Polynoinae and in the Lepidonotinae than the other notochaetal types. Of the neurochaetae, the dentate series is present in two-thirds of the specimens studied, and the simple-tip series is present in one-third, with, however, a degree of overlap occurring. The 'back-bone' O.T.U.s only possess dentate series neurochaetae, and the O.T.U.s which have simple-tip neurochaetae but not dentate neurochaetae (O.T.U.s 9, 10, 14, 19, 20 and 22) are far removed from the 'back-bone' because they have other, derived, character states. Does this mean that the dentate series is therefore the most primitive neurochaetal group in the Polynoinae? Both dentate series and simple-tip series neurochaetae are present in the Lepidonotinae, so one might presume that the common ancestor of these two sub-families possessed both types of chaetae. The next stage in this line of investigation is to look for a suitable out-group for comparison in the other families of scale-worms. The Sigalionidae and Peisidicidae both have composite neurochaetae and therefore

are of no help. The Eulepethidae have a different complex of neurochaetae and also other differences from the Polynoidae such as the presence of branchiae and a single anal cirrus. The Aphroditidae again have a different complex of neurochaetae and other characters such as a papillate ventral surface to the body and parapodia, and absence of anal cirri. Several members of the family Polyodontidae have neurochaetae with a distinct 'shoulder', and some of these appear to be identical with the simple-tip neurochaetae with a capillary ending seen in the Polynoinae (see Strelzov, 1968, 1972). The only character which differs between all Polynoidae and all Polyodontidae is the spinning glands which are present in the Polyodontidae. These glands, found in the notopodia, secrete fibres which the worm uses to build a thick tube. Pflugfelder (1934) concluded that the fibres produced by the spinning glands are, in construction and origin, typical chaetae. Capillary notochoetae are also found in at least some polyodontids. The antennae are variable in number and point of insertion, but this is also true of the Polynoidae, especially since the erection of five new sub-families by Pettibone (1976). Some polyodontids have eyes on large ommatophores, but in others (e.g. *Eupanthalis kinbergi*) the eyes look similar to those found in polynoids. Polyodontids have two anal cirri, as do polynoids. The elytra are said to occur on parapodial segments, 1, 3, 4 and then every second segment, a situation seen in *Bathylevensteinia* and approached by *Neohololepidella* among the polynoids studied.

The presence of simple-tip neurochaetae in the Polyodontidae does not necessarily prove that they are more primitive than dentate series neurochaetae but does raise doubts as to the wisdom of retaining the Polyodontidae as a separate family.

- A. If the Polyodontidae are defined by the presence of the spinning glands, then the Polynoidae can only be defined as polyodontids without spinning glands. As the polyodontids are the only polychaetes with spinning glands, this can be regarded as a derived character state. The Polynoidae then become a paraphyletic group, i.e. they consist of all the descendants of a common ancestor except those which evolved spinning glands.
- B. If the Polyodontidae are accepted as a family because of their one unique derived character, why should *Gesiella*, with two unique derived structures as far as the Polynoinae are concerned, only be accepted as a genus?

Three of Pettibone's new sub-families are mono-specific (Pettibone, 1976). On the present evidence it would make sense to raise *Gesiella* to sub-familial status (as Gesiellinae) and to lower the Polyodontidae to the status of a sub-family within the Polynoidae (as Polyodontinae Pflugfelder, 1934 (1855)).

GESIELLINAE sub-fam. nov. Members of the Polynoidae with accessory filamentous sensory organs attached to the dorsal cirrophores. Type genus *Gesiella* Pettibone, 1976.

Key to families of Aphroditacea

- 1 Composite neurochaetae present 2
- All chaetae simple 3
- 2 Elytra, with concentric rings, present on alternate segments along body. One antenna present
PEISIDICIDAE
- Elytra, without concentric rings, on alternate segments anteriorly and all segments
 posteriorly. One to three antennae present
SIGALIONIDAE
- 3 Neuracilae distally hammer-headed
EULEPETHIDAE
- Neuracilae distally pointed 4
- 4 Notochaetae including felt (covering dorsal surface) or erect, harpoon-shaped, flattened
 spines
APHRODITIDAE
- Notochaetae, if present, never as felt or harpoon-shaped
POLYNOIDAE

The family-group name Peisidicidae Darboux, 1899 has priority over Pholoididae Fauchald, 1977 (International Code of Zoological Nomenclature 1964 (articles 36 and 40)).

Key to sub-families of Polynoidea

This key to sub-families is a provisional one. The genus *Cervilia*, according to Fauchald (1977) is of unknown sub-family. As the Polynoinae and Lepidonotinae were originally defined on the position of attachment of the lateral antennae, perhaps *Cervilia* should be placed in a new sub-family Cerviliinae. Alternatively, if the Polynoinae contains groups of species evolving in parallel with groups of species in the Lepidonotinae, perhaps the position of attachment of the lateral antennae is not important and these sub-families could be amalgamated and then broken down again in a more meaningful manner, e.g. *Polynoe scolopendrina* (a polynoine) and *Lepidasthenia elegans* (a lepidonotine) both have dentate neurochaetae with one or two stronger chaetae per segment, they are both long and thin, and they are both often found in terebellid tubes. Obviously much work remains to be done on these groupings.

1	Spinning glands present in some notopodia	POLYDONTINAE	2
-	Spinning glands absent		3
2	Antennae absent		4
-	Antennae present		3
3	Scale-lobe on parapodial segment 5. Elongate parapodia. 7 pairs of pharyngeal papillae	POLARUSCHAKOVINAE	
-	Scale-lobe absent. Notopodia short. 9 pairs of pharyngeal papillae, two of them elongated	BATHYEDITHINAE	
4	Median antenna absent		5
-	Median antenna present		6
5	Lateral antennae attached posteriorly	<i>Cervilia</i>	
-	Lateral antennae attached anteriorly	IPHIONINAE	
6	Only one antenna present (<i>note</i> frontal filaments may be present laterally to the antenna)		7
-	Three antennae present		9
7	Notochaetae present	MACELLICEPHALINAE	
-	Notochaetae absent		8
8	Notopodia greatly reduced	MACELLOIDINAE	
-	Notopodia forming very long, projecting acicular lobes enclosing a very stout acicula	MACELLICEPHALOIDINAE	
9	Pharynx without papillae or jaws. Palps never visible dorsally	BATHYMACELLINAE	
-	Pharynx with papillae and jaws. Palps usually visible dorsally		10
10	Lateral antennae attached distally on prostomium		11
-	Lateral antennae attached ventrally, sub-distally		12
11	Antennal scales, antennal sheath and tentacular sheath present	ADMETELLINAE	
-	These structures absent	LEPIDONOTINAE	
12	Accessory filamentous sensory organs present	GESIELLINAE	
-	These organs absent	POLYNOINAE	

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