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A phylogenetic and biogeographic study of *Euniphysa* (Eunicidae, Polychaeta)

HUA LU†‡ and KRISTIAN FAUCHALD‡

†*Department of Biological Sciences, the George Washington University, Washington, DC 20052, USA; email: hualu@gwu.edu*
‡*Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA*

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Fourteen species have either been described in, or referred to, the genus *Euniphysa*. Seven of these are here re-described based on type material and two new species, *E. quadridentata* and *E. filibranchia*, are described. *Euniphysa oculata* is found to be a subjective synonym of *E. spinea*, and *E. unicusa* is a subjective synonym of *E. aculeata*. *Euniphysa taiwanensis* and *E. megalodus* are correctly assigned to the genus, but cannot be described due to lack of material. *Euniphysa misakiensis*, *E. tubicola* and *E. tubifex* are transferred to *Eunice*. A key is given to the nine identifiable species retained in *Euniphysa*. Coding strategies for polymorphic and inapplicable characters, as well as problems associated with shared absences, are discussed. A phylogenetic analysis of *Euniphysa* based on 24 morphological characters yielded two most parsimonious trees (CI = 0.902, RI = 0.905). The tree topology separates *Euniphysa* into two distinct groups. Group I includes *E. filibranchia* n. sp., *E. italica*, *E. jeffreysii*, *E. quadridentata* n. sp. and *E. spinea*, it is supported by five equivocal similarities. Group II is supported by five unequivocal synapomorphies and two equivocal similarities, it includes *E. aculeata*, *E. auriculata*, *E. falciseta* and *E. tridontesa*. Based on the phylogenetic topology, *Paraeuniphysa* and *Heterophysa* are considered as junior synonyms of *Euniphysa*. The recognition of a separate family for *Euniphysa* is not warranted. All species of *Euniphysa* are fragile, shallow, warm water species. They have been collected mainly from sandy sediments of the Northern Hemisphere. The greatest diversity is from the South China Sea area; other species are found throughout the Indian Ocean, the Mediterranean Sea and the East Atlantic Ocean coasts suggesting the genus may have originated in the Tethys Sea. A few species have also been found in the Gulf of Mexico and the West Atlantic Ocean coast again suggesting a Tethyan origin associated with the westward drift of the North American continent.

KEYWORDS: Biogeography, coding, ecology, *Euniphysa*, Eunicidae, jaw, phylogeny, Polychaeta.

Introduction

The genus *Euniphysa* was named by Wesenberg-Lund (1949) for a single species, *E. aculeata*, which she described from the Gulf of Iran. The species was re-described

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and its distribution extended by Pettibone (1970). The next species to be recognized, *E. oculata*, was described by Wu *et al.* (1979) from the South China Sea. Miura (1986) reviewed the genus and referred to it four previously described species of *Eunice* Cuvier, 1817, *E. jeffreysii* (McIntosh, 1903), *E. spinea* (Miura, 1977), *E. tubicola* (Treadwell, 1921) and *E. tubifex* Crossland, 1904; a year later (Miura, 1987) he added one more species, *E. misakiensis*, from Japan. Wu and He (1988) described a new genus, *Paraeuniphysa*, for their new species, *P. taiwanensis* from Central Taiwan Strait. Shen and Wu (1990) added *E. unicusa* and *P. falciseta* and described a new genus, *Heterophysa*, for their new species, *H. tridontesa*. Cantone and Gravina (1991) described *E. italica* from the Mediterranean. Fauchald (1992) moved two additional species of *Eunice*, *E. auriculata* Treadwell, 1900 and *E. megalodus* Grube, 1878 to *Euniphysa*.

Shen and Wu (1990: 765; see also Shen and Wu, 1991: 129) created a new family, Euniphysidae, for *Euniphysa*, *Heterophysa* and *Paraeuniphysa*. Their definition of the new family read *in toto*:

'1. Five occipital tentacles, with short basal part, distributed unequidistantly, the distance between the inner and the outer lateral tentacles is shorter than that between the median tentacle and the inner lateral tentacles.

2. The maxillary formula. The jaw consists of six pairs of maxillary plates. On the right side Mx-III is fused with Mx-IV. The teeth of the maxillary plates Mx-III to Mx-V are not serrate, and the teeth are moderately developed and U-shaped.

3. The body may be divided into anterior region without compound chaetae and a posterior region with compound chaetae.

4. Dorsal cirri are conical. Lower part expanded, base fairly slender, forming a short stem.'

Each character used by Shen and Wu (1990) is discussed below using the numbering in the original description.

(1) The distribution of the antennae mentioned is present in many species of *Eunice* and is not present in all *Euniphysa* species. Thus the character cannot by itself distinguish *Euniphysa* from *Eunice* at the generic, or familial level. According to our observations (see later description), only four of the nine species have their palps and antennae distributed unevenly (e.g. *E. aculeata*); the other five species have evenly spaced palps and antennae (e.g. *E. jeffreysii*). Documentation of different patterns of antennal distribution can be found illustrated in many publications, even if the pattern has only rarely been specifically described. Hartman (1944), Fauchald (1970) as well as Miura (1986, 1987) showed the antennal distribution for many species of *Eunice*.

(2a) All species of *Eunice* have four (or five) paired and one unpaired jaw, called Mx-I, Mx-II, Mx-III, Mx-IV and Mx-V (or plus Mx-VI). Mx-III is unpaired, being present only on the left side when viewed from the dorsum. In all *Euniphysa* species, most jaw-pieces carry at least one distinct tooth or fang. However, Mx-VI is edentate on both sides. All species of *Euniphysa* have, in addition to the jaws, paired or unpaired sclerotinized accessory plates lined outside of Mx-IV or Mx-III. Documentation and illustrations of different (apparent) number of jaws can be found in McIntosh (1885) and Treadwell (1921, 1922).

(2b) In species of *Euniphysa* examined here, including the type species, no evidence shows that Mx-III is fused to Mx-IV. We assume that 'Mx-III to V not being serrate' means that these jaw-pieces have only one or a few long, curved fang-like teeth each, rather than the more numerous 'molar-like' teeth usually present in species of *Eunice*. The shape of these teeth is one of the features that may characterize the genus *Euniphysa* (see below).

(3) All nine *Euniphysa* species examined lack compound chaetae (but may have pseudocompound chaetae) in anteriormost chaetigers. Thus Shen and Wu's (1991) observation is correct. However, to use shared absences as a shared derived similarity (synapomorphy) appears dubious: such absences are difficult to test by observation in contrast to 'present' features which can be compared by direct observation (see below).

(4a) The 'dorsal cirri' of all eunicids are notopodia and notopodial cirri. Separation between notopodia and notopodial cirri may be more or less distinct. In some taxa a cincture is present; in others, the separation is marked only by an abrupt narrowing of an otherwise digitate or conical notopodial cirrus. In some species the notopodial cirri are so slender that a distinctly narrowed base cannot be identified (Fauchald, 1992). Notopodial structures vary within the two major genera, *Eunice* and *Marphysa*; in less species-rich genera, they tend to be uniform.

(4b) The pendant lobe at the ventro-lateral base of the notopodial cirrus in *Euniphysa*, first described by Treadwell (1900), has been suggested to be a sensory organ (Hayashi and Yamane, 1994); it is known to be present in other eunicids, but also more generally among other euniceans. It is not a unique feature of *Euniphysa*.

According to a preliminary study of Eunicida, *Euniphysa* falls well inside the family Eunicidae (unpublished data). Giving *Euniphysa* separate family status would leave the remaining Eunicidae paraphyletic. The characters mentioned by Shen and Wu (1991) may be sufficient to function as synapomorphies for *Euniphysa*, there are currently no adequate grounds for supporting separate familial status for this genus without distorting familial concepts in the order Eunicida. A detailed study of morphological characters and a reconstruction of phylogeny for all *Euniphysa* species may provide a better testable pattern for the taxonomy of this group. The relationship between *Euniphysa*, *Heterophysa* and *Paraeuniphysa* is discussed below.

Abbreviations used in the text

The antennae have traditionally been abbreviated as A-I to A-III; however, the demonstration by Orrhage (1995) that the outer pair (A-I) are palps, makes this pattern of abbreviation unnecessary; the five prostomial appendages are here called palps, lateral antennae and median antenna.

The jaws (figure 1) are conventionally observed *in situ* from the dorsal side and are numbered from posterodorsal towards the antero-ventral side. Mx-I, first maxillae; Mx-II, second maxillae; Mx-III, unpaired, third maxilla present on left side only; Mx-IV, fourth maxillae; Mx-V, fifth maxillae; Mx-VI, sixth maxillae.

The species are described below in a format similar to the one used in Fauchald (1992). The body width always refers to the widest part around the anterior region.

Phylogenetic characters of *Euniphysa*

A study of the Eunicida (unpublished data) shows that *Euniphysa* is a sister group to species of *Eunice* with six paired jaws, such as *Eunice rullieri* Fauchald 1992. For that reason, a specimen of *Eunice rullieri* (USNM 100202) was studied in detail, in parallel with the study of *Euniphysa*, and is used as outgroup during the analysis.

The species of *Euniphysa* can be easily recognized by the combination of the following characters:

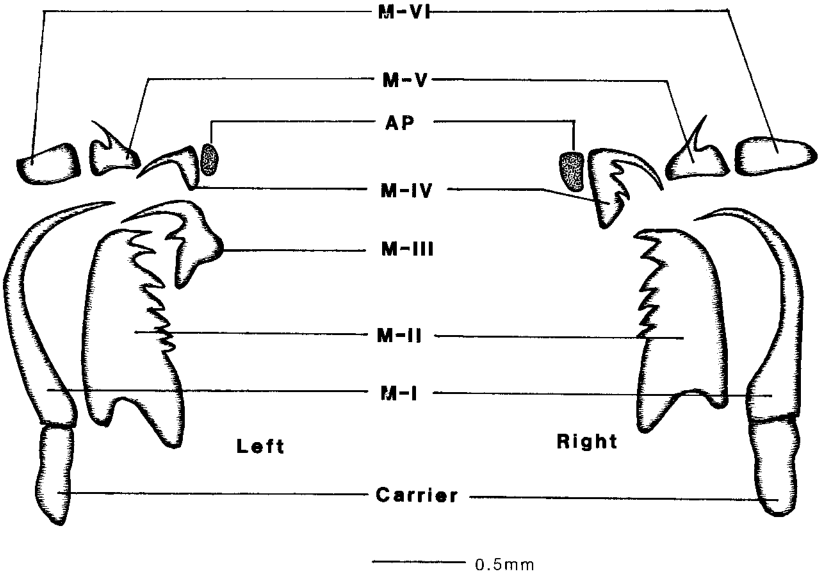

FIG. 1. Diagram of maxillae of *Euniphysa* (*E. auriculata*, USNM 37716). Maxillary formula of this set of jaws is 1 + 1, 7 + 6, 2 + 0, 1 + 3, 1 + 1 and 1 + 1. AP = accessory plate.

(1) The main teeth on Mx-III, Mx-IV and Mx-V are fang-shaped and reduced in number, left Mx-III usually has two teeth with the distal one much longer than the proximal one.

(2) All have slender and smooth palps and antennae.

(3) All have compound spinigers.

(4) The chaetal lobes have a small knob dorsal to the aciculae.

Among the above features, only the jaw structure (character 1) has not been observed in any of the other eunicids (pers. obs., also review of the literature), and this character is the proposed synapomorphy for *Euniphysa* (unpublished data). Another 'similarity' for *Euniphysa* species is the shared absence of compound chaetae in anterior parapodia (Shen and Wu, 1990). Shared absences may be considered as negative similarities, and, specifically, it is difficult to apply similarity criteria to such similarities and we would prefer to avoid using them in tree construction. It is however worthwhile noting that, as far as we know, all other eunicids do have compound chaetae in anterior parapodia.

Twenty-one morphological and three morphometric (22, 23 and 24) characters are included in the analysis. The characters and character states are:

(1) The distribution of palps and antennae: 0—evenly spaced, 1—lateral antennae and median antenna separated by larger gap than lateral antennae and palps.

(2) Shape of palps and antennae: 0—stout, 1—slender (and relatively smooth).

(3) Shape of maxillae: 0—molar shaped, 1—fang shaped (figure 2a–c).

(4) Mx-III with two teeth (figure 1): 0—no, 1—yes. All *Euniphysa* species examined have two teeth on Mx-III except for *E. italica*. Of the two specimens available of this species, one had two teeth, the other had a tiny proximal tooth in addition to the two normal teeth.

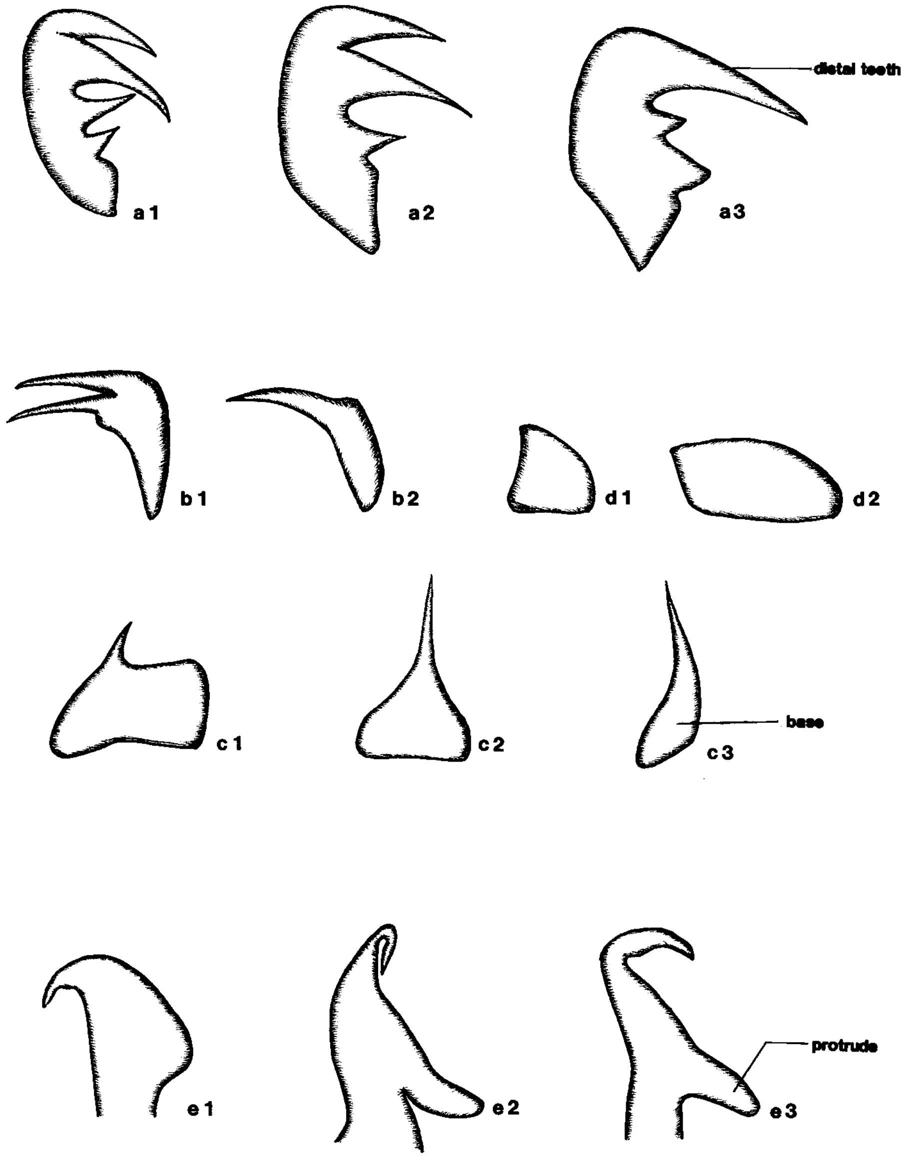

FIG. 2. Diagram of various features of *Euniphysa*. (a) right Mx-IV; (b) left Mx-IV; (c) Mx-V; (d) Mx-VI; (e) dorsal cirri.

(5) Number of teeth in right Mx-IV: 0—more than five teeth, 1—four teeth (figure 2a1), 2—three teeth (figure 2a2, a3).

(6) Shape of teeth in right Mx-IV: 0—all similar, 1—second from distal one longest (figure 2a1, a2), 2—second from distal one shortest (sometimes nearly absent, figure 2a3).

(7) Number of teeth in left Mx-IV: 0—more than two, 1—two (figure 2b1), 2—one (figure 2b2).

(8) Shape of both Mx-V: 0—a short, tapering tooth on a large base (figure 2c1), 1—relatively long, slender tooth on a small base (figure 2c2, c3).

(9) Width to length ratio of Mx-VI: 0—less than one or close to one (figure 2d1), 1—more than two (figure 2d2).

(10) Sclerotinized accessory plate (figure 14j) outside of left Mx-III: 0—present, 1—absent. Coding this character will lead to problems associated with shared absences.

(11) Chaetal lobe with small fleshy knob (figure 3c, d) dorsal to aciculae: 0—absent, 1—present.

(12) Dorsal cirri in anterior region with finger-shaped protrusion: 0—absent

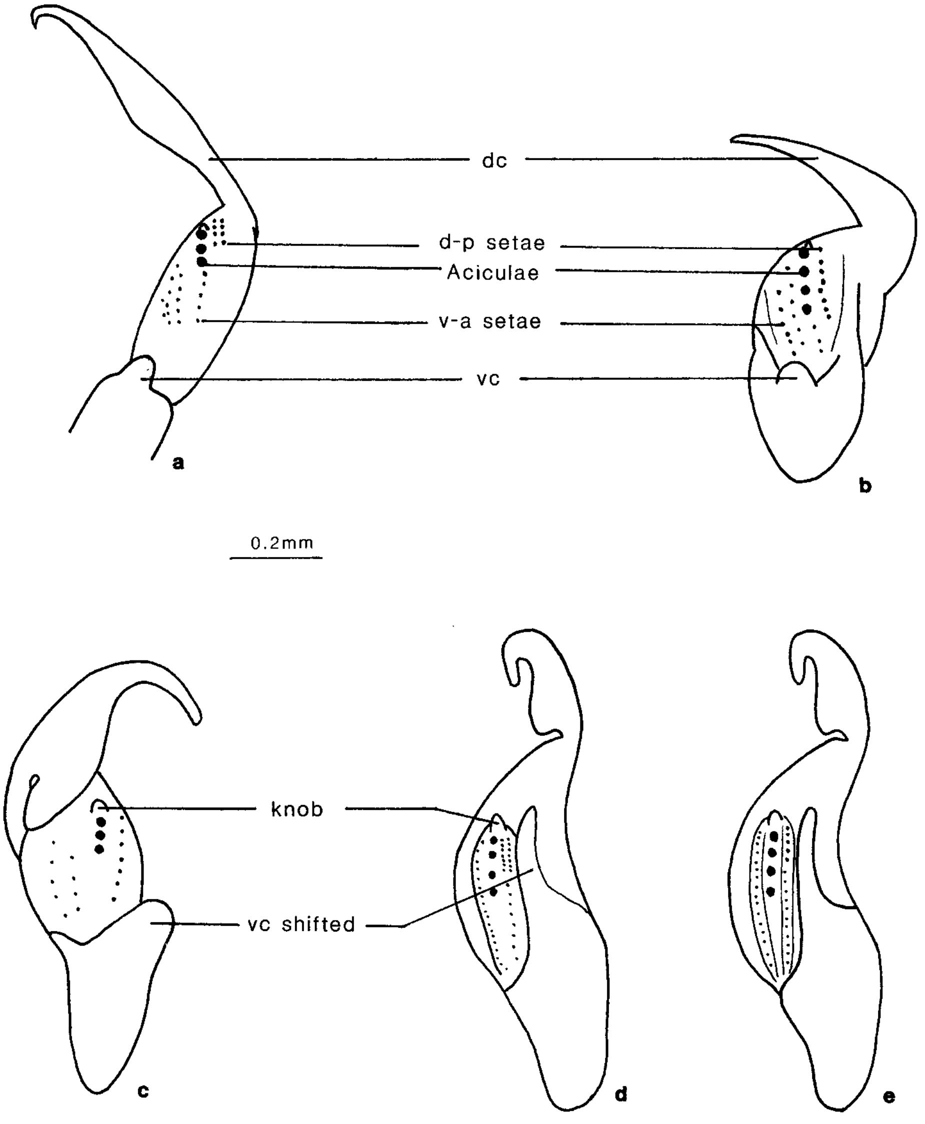

Fig. 3. Diagram of various parapodia (lateral view) of *Euniphysa* showing different ventral cirri and chaetae arrangement patterns: (a) parapodium 18 of *E. aculeata*; (b) parapodium 5 of *E. quadridentata*; (c) parapodium 8 of *E. auriculata*; (d) parapodium 5 of *E. aculeata*; (e) parapodium 4 of *E. aculeata*. dc = dorsal cirrus; vc = ventral cirrus; dp = dorsal-posterior; va = ventral-anterior.

(figure 2e1), 1—present (figure 2e2, e3). An expansion on the ventral side sub-basally on the dorsal cirri is more or less distinct in all *Euniphysa* species examined (especially in *E. aculeata* and *E. tridontesa*); in *E. auriculata* and *E. falciseta* it is uniquely large and finger shaped.

(13) In anterior chaetigers ventral cirri located in part on posterior face of parapodium (figure 3c–e): 0—absent, 1—present.

(14) Number of anterior chaetigers with posteriorly located ventral cirri: 1—nine, 2—ten, 3—six.

(15) Shape of posteriorly located ventral cirri: 0—with free cirri-form tip (figure 3c), 1—completely fused to chaetal lobe and visible as a ridge on the posterior face of chaetal lobes (figure 3d, e). For taxa without posteriorly located ventral cirri we here face the problem of inappropriate coding for the two last characters.

(16) Arrangement of dorso-posterior simple chaetae in anterior parapodia: 0—in two rows (figure 3a, d), 1—in one row (figure 3b, c, e).

(17) The chaetae posterior to aciculae curved around upper half of the chaetal lobe: 0—absent (figure 3a, b), 1—present (figure 3c, e).

(18) The chaetae anterior to aciculae curved around lower half of the chaetal lobe: 0—absent (figure 3a–c), 1—present (figure 3d, e).

(19) Type of ventral chaetae on anteriormost parapodia: 0—compound falcigers, 1—pseudocompound spinigers, 2—simple chaetae.

(20) Chaetal type in middle and posterior region: 0—compound falcigers, 1—compound spinigers.

(21) Number of subacicular hooks in anterior chaetigers: 0—multiple, 1—always single except for replacements.

(22) First subacicular hook (figure 4) in a 2.5 mm wide specimen first present from: 0—chaetiger 25, 1—chaetiger 35, 2—chaetiger 20. The distribution of character states is based on a morphometric study. In Eunicidae and Onuphidae many morphological features, such as the first occurrence of subacicular hooks, are size-dependent (Fauchald, 1991; Lu and Fauchald, 1998). The first occurrence of subacicular hooks in *Euniphysa* while size-dependent, shows distinctive patterns: *E. quadridentata*, *E. jeffreysii* and *E. italica* form one group in which subacicular hooks start from about chaetiger 35 for a 2.5 mm wide specimen, while the rest of the species (except for *E. tridontesa*) form another group in which subacicular hooks start from about chaetiger 25 for a 2.5 mm wide specimen. *E. tridontesa* is clearly very similar to 'state 0', but a gap remains, so a unique state is given to this species. Since nearly half of *Euniphysa* species were described from only one or two specimens, we have to make the assumption that the features of these specimens are normal and they represent the populations properly in some sense. The assumption should be tested on more specimens. The above discussion is also applicable to the next two characters.

(23) Distribution of last distinct ventral glandular tab (figure 5) in a 2.5 mm wide specimen: 0—inappropriate, 1—chaetiger 32, 2—chaetiger 55, 3—around chaetiger 20, 4—around chaetiger 42. For this character, *E. quadridentata*, *E. jeffreysii* and *E. italica* form one group in which ventral tab ends at about chaetiger 55 in a 2.5 mm wide specimen; *E. aculeata*, *E. auriculata*, *E. falciseta* and *E. spinea* form another group in which ventral tab ends at about chaetiger 32 in a 2.5 mm wide specimen. The ventral tab patterns of *E. filibranchia* and *E. tridontesa* (state 3 and 4) are similar to 'state 1', but gaps remain, so a unique state is given to each of these two species.

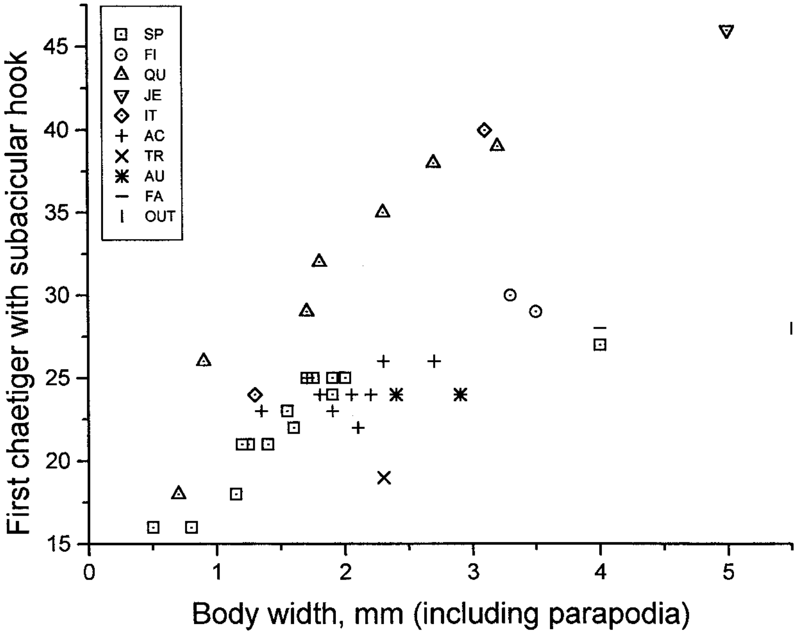

FIG. 4. The relationships between maximum body width (mm) and the start position of subacicular hooks in nine *Euniphysa* species: SP = *E. spinea* (*n* = 14), FI = *E. filibranchia* n. sp. (*n* = 2), QU = *E. quadridentata* n. sp. (*n* = 7), JE = *E. jeffreysii* (*n* = 1), IT = *E. italica* (*n* = 2), AC = *E. aculeata* (*n* = 8), TR = *E. tridontesa* (*n* = 1), AU = *E. auriculata* (*n* = 2), FA = *E. falciseta* (*n* = 1), OUT = outgroup.

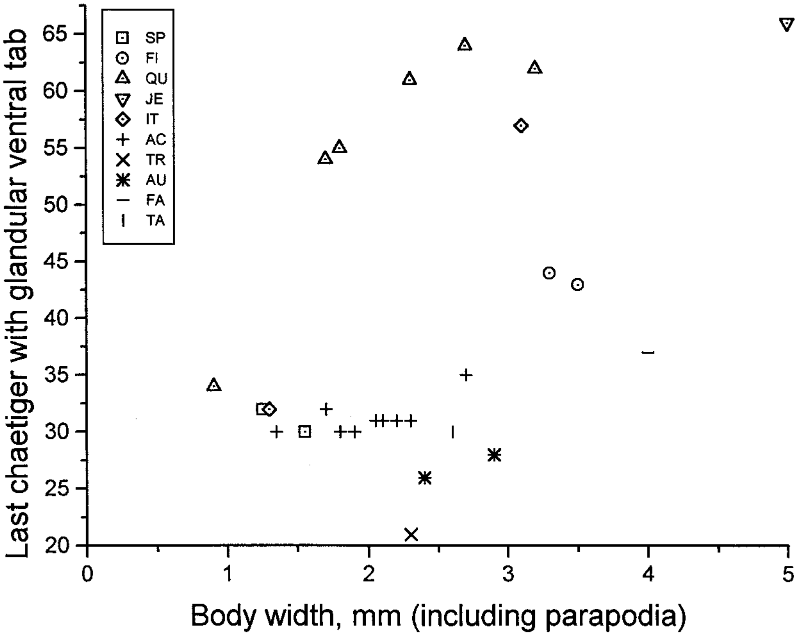

FIG. 5. The relationships between maximum body width (mm) and the ending position of ventral glandular tabs in 10 *Euniphysa* species. Abbreviations as in figure 4, TA = *E. taiwanensis* (*n* = 1).

(24) First branchiae (figure 6) in a 2.5 mm wide specimen start: 0—chaetiger 10 or less, 1—chaetiger 17, 2—chaetiger 24 or later. Again, for this character, *E. quadridentata*, *E. jeffreysii* and *E. italica* form one group in which branchiae start around chaetiger 25 for a 2.5 mm wide specimen; *E. aculeata*, *E. auriculata* and *E. falciseta* form the second group in which branchiae start around chaetiger 17 for a 2.5 mm wide specimen; *E. spinea*, *E. tridontesa* and *E. filibranchia* form the third group in which branchiae start around chaetiger 9 for a 2.5 mm wide specimen.

The distribution of the last chaetigers in which double aciculae (per parapodium) were present, was also studied (figure 7). There is some evidence that the differences among the several species generally match the pattern of other morphometric characters (22–24). For example, compared to their occurrence in other species, the double aciculae continue to more posterior chaetigers in *E. quadridentata* n. sp., *E. jeffreysii* and *E. italica*. However, no distinctive gaps can be identified, so this character was not used in the phylogenetic analysis.

Coding strategies for polymorphic characters and in situations where inapplicable characters are present have recently been discussed (Pleijel, 1995; Rouse and Fauchald, 1997); however, no agreement has been reached. Discussions on the potential problems in scoring shared absences are rarer, but are also of importance for interpreting phylogenetic studies. Thus before constructing the data matrix, we decided to discuss and choose appropriate coding methods for problematic data.

Coding of absences and polymorphic characters

A problematic entry in a data matrix may belong to any one of the following three categories:

(1) The data cannot physically be observed on current material, for example,

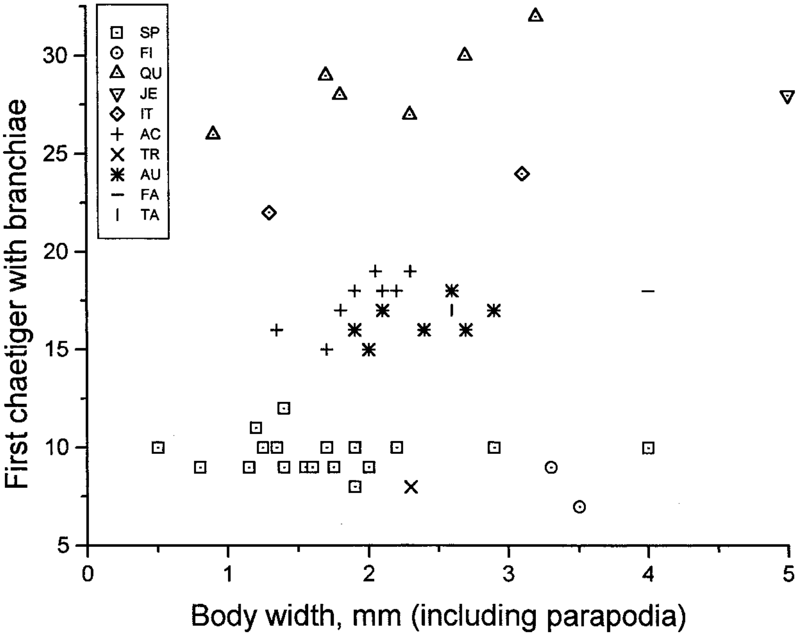

FIG. 6. The relationships between maximum body width (mm) and the start position of branchiae in 10 *Euniphysa* species. Abbreviations as in figure 4, TA = *E. taiwanensis* ($n = 1$).

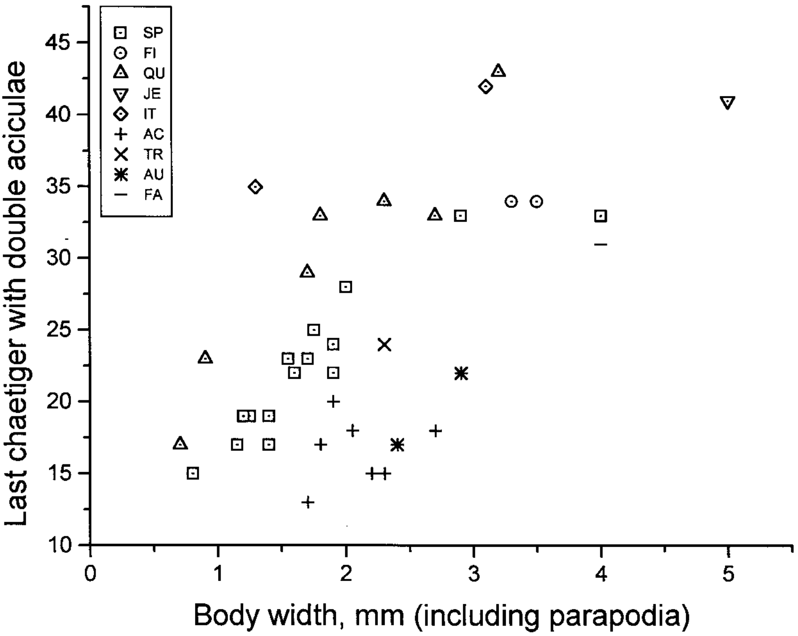

FIG. 7. The relationships between maximum body width (mm) and the ending position of multiple aciculae in nine *Euniphysa* species. Abbreviations as in figure 4.

structures of the posterior end when the specimens studied are incomplete. This is coded as '?'.

(2) The character is polymorphic, i.e. more than one character state is present in a single (terminal) taxon. This condition is also coded as '?'.

(3) A major feature is absent in some taxa, but present in others. When present the feature is subject to additional analysis; when absent, the inappropriate characters are coded as '–'. Current analysis programs (Hennig86, PAUP) will treat '–' as '?'.

Platnick *et al.* (1991) analysed the logical differences among these three categories and concluded that 'for a binary character, unknown data could be either 0 or 1, inapplicable characters are neither 0 nor 1, polymorphisms are both 0 and 1'. Therefore, it appears that the three logically different categories are indiscriminately treated similarly in traditional coding. Many papers have been published on this issue (Nixon and Davis, 1991; Maddison, 1993; Pleijel, 1995; Rouse and Fauchald, 1997) but no agreed solution appears to have been found yet.

Nixon and Davis (1991) indicated that the solution for polymorphic data was to divide the taxa into subunits that were monomorphic for each character used in the analysis. This proposal works well when the polymorphism occurs above the level of the terminal taxa. However, polymorphism may be present within the terminal taxa, for example, all individuals of a species have feature X, but in some individuals it is red, in others it is blue. According to the phylogenetic species concept (Nixon and Wheeler, 1990), for feature X, this species has only an attribute but no definite character state. Consequently, it is appropriate to treat within-taxon polymorphism as unknown data, scored as '?', for a given character. This of course, assumes that one has convincing evidence that the taxon in question is monophyletic.

Inapplicable characters are a consequence of a need for scoring both the presence/

absence of a given feature and, for taxa in which the feature is present, to specify a condition of the feature. One way of resolving the problem is to consider the absence as one of the character states otherwise detailing the feature in a multi-state character (Fitzhugh, 1989). However, there does not appear to be complete agreement that this is appropriate; many authors prefer to treat presence/absence as a separate character and detail the feature in additional characters. For example, given a group of six taxa A–G (including five ingroup members and one outgroup), and considering a particular structure X, it is present and red in A and B, present and blue in C–D and absent in E and F. Traditionally (Sneath and Sokal, 1973; Swofford, 1985; Farris, 1988), feature X is coded as having two characters.

(1) Feature X: absent (0)/present (1).

(2) Colour of feature X: inapplicable (?)/red (0)/blue (1).

The character 'colour' for taxa E and F may not always be inapplicable, it depends on the nature of 'absence' in these taxa—whether the character was initially absent or represents a secondary loss. If the absences in E and F are due to secondary loss, this would imply that E and F used to have feature X, but of unknown colour. Thus while E and F could be considered as having the attribute, the state for character 'colour' would be unknown and a '?' would be appropriate for this character. Only when E and F or their ancestors never had feature X, does the character 'colour' become truly inapplicable (Sneath and Sokal, 1973). Logically, one cannot assign states to features that have never been present; thus neither 'red' nor 'blue' can in any meaningful sense have been present. However, coding 'colour' with a '?' means they have to be either 'red' or 'blue' since no other options are available. Without additional information, it is of course impossible to decide whether a given observation of 'absent' can be considered secondarily lost or not.

According to Maddison (1993) the potential conflict may result in 'long distance attraction' and thus potentially an incorrect tree. 'Long distance attraction' may be relatively rare according to Maddison's (1993) analysis, and it can be noted and taken into account by manually checking the cladogram. To avoid relying on manual checks, Maddison (1993) advocated using a single multi-state character to code feature X: absent (0)/red (1)/blue (2). In this coding, the problem with 'long distance attraction' is avoided, but the observed similarity information 'the presence of general feature X in A–B and C–D' is lost.

Pleijel (1995) proposed an alternative binary A/P coding in which all features were treated as multiple binary characters (present /absent):

Feature X: absent (0)/present (1).

Red colour: absent (0)/present (1).

Blue colour: absent (0)/present (1).

Pleijel (1995) noted that there is no justification for the automatic redundancy in coding certain states. One similarity (such as the absence in E and F) is repeated multiple times, and this problem may become severe if the 'shared absence' similarity is non-homologous. Another problem in A/P coding is that it severs the natural connection between character states and consequently causes information loss. The connection between character states comes from observation and involves two assumptions: firstly, the character states came from the same ancestral state; secondly, they are modifiable among each other. The sub-character (absence/presence of feature X) will indirectly test the homology of varied character states through the testing of the homology of varied X, so the first assumption is tested; on a phylogenetic tree, these character states can always change from one to the other, here the second assumption is also tested. Therefore, Pleijel's (1995) concern on the testability of the homology statements among different character states becomes irrelevant.

At this point, the better solution to the problem appears to be the traditional coding (Sneath and Sokal, 1973; Swofford, 1985; Farris, 1988) and to check the cladogram manually for the presence of 'long distance attraction'.

Phylogenetic reconstruction is based on an analysis of observed shared similarities. Structural similarities may be tested through the application of a set of specifiable criteria, such as position, details in (microscopic) structure, genetic similarities and so forth. There are two primary types of similarities, shared presences and shared absences of a given feature. It is obviously difficult to apply any similarity criteria to check a similarity based on shared absences. Shared absences may or may not result from a single loss, but such losses are never observable. If the phylogeny is to be based on observable, testable information, shared absences cannot provide group information. For example, if the shared absences are present only in ingroup members, the most common coding method is to give these shared absences an identical code; consequently these shared absences do input group information during the tree construction process, and this may be undesirable coding' (Lu and Fauchald, 1998) may be an alternative choice in this case. According to it, the shared absences in the ingroup members will be assigned separate autapomorphic character states, hence they cannot provide group information during tree construction. This of course does not imply that the shared absences cannot be homologous. After construction of a tree which is solely based on observable shared presences, the origin(s) of the shared absences can be hypothesized *a posterior*.

Phylogenetic analysis of *Euniphysa*

As a consequence of the above theoretical considerations, the following decisions were made about scoring different characters.

(1) The polymorphism in character 4 of 'left Mx-III tooth number' in *E. italica* is coded as '?' implying that we at this point assume that *E. italica* is a monophyletic taxon.

(2) The multi-state feature 'ventral cirri' is treated as having three associated characters (characters 13, 14 and 15) and when inapplicable these are scored with a '?'. The 'long distance attraction' was checked by manual inspection.

(3) The shared absences of 'accessory plates lateral to Mx-III' in character 10 in four ingroup species are given individual states. Based on the cladogram, they are hypothesized *a posterior*.

Sufficient materials of nine species were available to be used in the analysis; two indeterminable species were omitted. The data matrix for the *Euniphysa* group is shown in Appendix A.

All characters are treated as unordered. Using the exhaustive search option of PAUP 3.1.1 (Swofford, 1993), two most parsimonious trees (TR = 41, CI = 0.902 (0.862 excluding uninformative data) HI = 0.098 (0.138 excluding uninformative data) and RI = 0.905) were found. The trees do not show evidence of 'long distance attraction' (Maddison, 1993) caused by '?' assignment to 'inapplicable' characters. Tree 1 is shown in figure 8; tree 2 differs from tree 1 in that the trichotomy in tree 1 is resolved in tree 2. The topology of tree 2 is (((*auriculata*, *falciseta*), (*tridontesa*, *aculeata*)), (*spinea*, (*filibranchia*, (*italica*, (*jeffreysii*, *quadridentata*))))). The strict

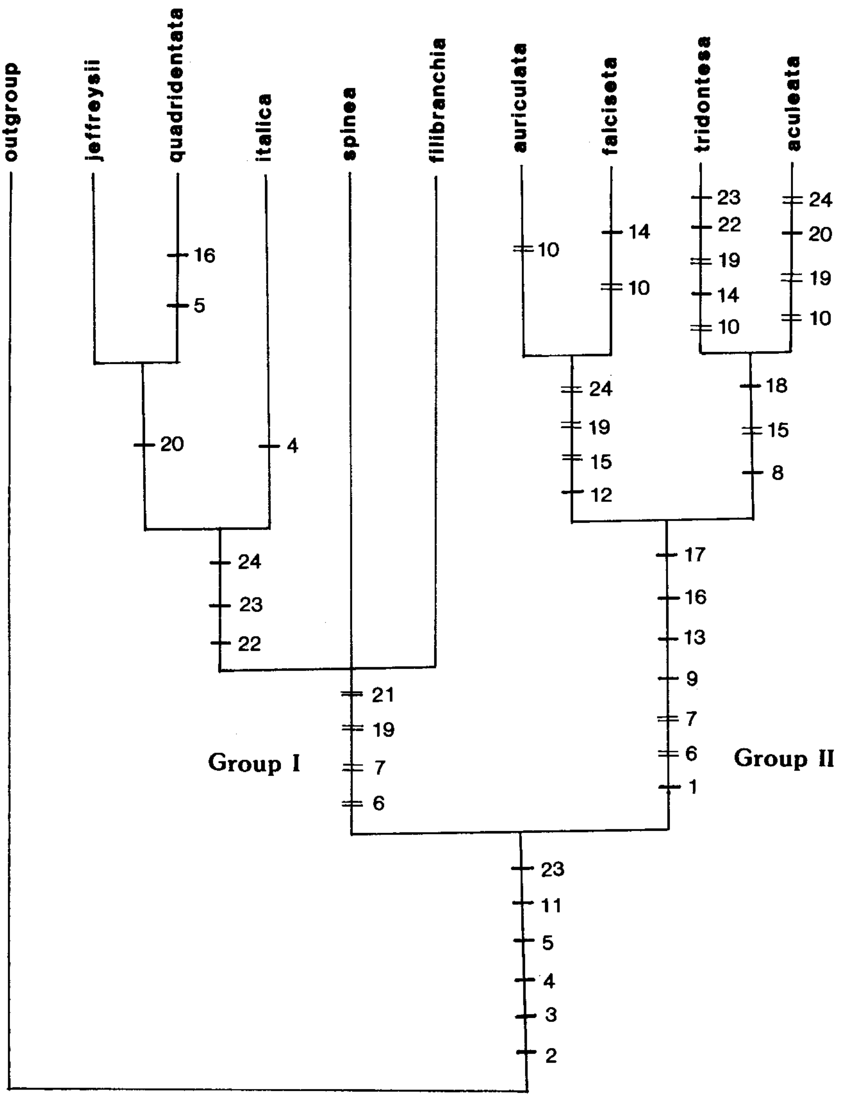

FIG. 8. One of the two most parsimonious cladograms of *Euniphysa* based on 24 morphological characters. The numbers on the tree are the character numbers. '_' represents unequivocal character state change, ' = ' represents equivocal character state change.

consensus tree has the same topology as tree 1. The following interpretation of *Euniphysa* phylogeny and biogeography is based on tree 1.

The four species lacking accessory jaw plates lateral to Mx-III are members of a monophyletic group characterized by seven synapomorphies of which five are unequivocal. We therefore believe, *a posteriori,* that character 10, 'loss of accessory plate lateral to left Mx-III' in *E. aculeata*, *E. tridontesa*, *E. auriculata* and *E. falciseta* can be better explained as having originated as a single event, and therefore may represent another synapomorphy for the group. The number of teeth in left Mx-III, a character polymorphic in *E. italica* is a modification from the common state in which two teeth are present in Mx-III.

Euniphysa is separated into two groups (figure 8). Group I includes *E. spinea*, *E. filibranchia* n. sp., *E. italica*, *E. jeffreysii* and *E. quadridentata* n. sp. It is supported by four possible synapomorphies all of which are equivocal: 6, the median tooth is longest in right Mx-IV; 7, two teeth in left Mx-IV; 19, presence of pseudocompound spinigers; and 21, subacicular hooks single at least in the first chaetigers in which the hooks occur. The branch (*E. italica*, *(E. jeffreysii*, *E. quadridentata*)) is supported by three unequivocal characters: 22, 23 and 24, all are morphometric features.

Group II includes *E. aculeata*, *E. tridontesa*, *E. auriculata* and *E. falciseta*, it is supported by eight possible synapomorphies, among which six are unequivocal: 1, palps and antennae unevenly distributed; 9, the Mx-VI width is twice its length; 10, loss of accessory plate lateral to Mx-III; 13, anterior ventral cirri attached posteriorly; 16, dorso-posterior chaetal bundle a single row of simple chaetae; 17, dorso-posterior chaetae in a fascicle enclosing the acicular lobe in anterior chaetigers (figure 3c, e). In *E. aculeata* and *E. tridontesa*, the chaetae of the antero-ventral bundle is also arranged as a fascicle enclosing the acicular lobe in anterior chaetigers (figure 3d, e). One can postulate a character transformation series for the distribution of the anterior chaetae from a presumed ancestral type (figure 3a) through a primary modified type (figure 3d) to the secondary modified type (figure 3e) which in fact follows the character state reconstruction. However, in a single specimen of *E. aculeata* (USNM 37716) all three patterns are present: the most modified type (figure 3e) from parapodia 2 to 4; the less modified type (figure 3d) present from parapodia 5 to 9 and the plesiomorphic type (figure 3a) present from parapodia 10 to posterior. The same phenomenon has also been observed in the other three species in this group. All polychaetes add chaetigers posteriorly, thus the morphologically 'oldest' chaetigers are the anteriormost ones.

The indeterminable species *E. megalodus* probably belongs to Group I. The shape of right Mx-IV resembles that of members of this group, especially *E. spinea* and *E. filibranchia*. The branchial pattern is also similar to that of members of this group (starting at parapodia 8). The other indeterminable species, *E. taiwanensis* may be a member of Group II. The information available in the original description (Wu and He, 1988) makes it impossible to separate it from *E. auriculata*, but is incomplete, and the two may differ in characters not mentioned by Wu and He (1988). The problem can only be solved by studying more materials of *E. taiwanensis*.

The ecology and biogeography of *Euniphysa*

All species of *Euniphysa* are found in warm water. Most of them live in the tropical or subtropical area. The highest latitude is 42°N for *E. italica* off the Latium coast of Italy, Mediterranean Sea; the next highest is at 33°N for *E. spinea* from the Japanese coast. The Mediterranean Sea is historically derived from a warm water area, and *E. spinea* lives right within the range of influence of the warm Kuro Siwo current. Except for one population of *E. aculeata* found just south of the equator (7°25'S, 113°16'E), all other records of *E. aculeata* and all other species of *Euniphysa* have been found in the Northern Hemisphere. No species have been reported from Central or Eastern Pacific regions.

All records are from shallow water. Most specimens were dredged from areas less than 100 m depth. The deepest one is 162 m for *E. taiwanensis* from the middle of the Taiwan Strait, East China Sea.

Unlike species of its sister taxon *Eunice* which are often associated with hard substrata, records of *Euniphysa* are exclusively collected from soft bottom sediment.

All of them were reported (data available for eight species) from sandy areas, with grain size ranging from coarse through fine to silty; fine to muddy sand is most frequently mentioned. At least two *Euniphysa* species were found with tubes. The tube of *E. auriculata* (USNM 15899) consists of an inner thin secreted layer (0.1 mm) and an outer thick layer (2 mm) of fine sand. In *E. tridontesa*, the tube consists of an inner secreted layer and an outer layer of silty sand, both layers are about 0.1 mm thick. The secreted layer of the tubes may come from the glandular swollen bases of the ventral cirri of the anterior parapodia, it is yellow-coloured in some species (e.g. *E. jeffreysii*).

All species of *Euniphysa* studied are fragile. Of the roughly 50 specimens examined, only a single specimen (*E. aculeata*) is nearly complete (but still without anal cirri), most of them consist of the head and less than 60 anterior chaetigers.

When the *Euniphysa* cladogram is mapped with their geographic distribution (figure 9), five well-characterized species from both Groups I and II and both of the indeterminable species, *E. taiwanensis* and *E. megalodus*, are found to live in the South China Sea and adjacent waters. The other four species have been found, one in each area, in the Mediterranean Sea, on both coasts of the Atlantic Ocean and in the Gulf of Mexico. This distribution pattern matches the Tethys Sea patterns documented for other marine organisms (Ekman, 1953). The equatorial Tethys Sea stretched in an easterly and westerly direction and connected today's West Pacific with the Indian Ocean, the Mediterranean and the Atlantic Ocean during the Mesozoic Era (245 million years), or even from as early as Lower Cambrian (Ekman, 1953). The number of records is very low, and the pattern can be no more than suggestive of a geographically interesting distribution.

Euniphysa members are exclusively shallow and warm water species, both the Atlantic and the seas off the southern extremities of Africa appear impassable to them. In *Palola* Gray 1847 (in the same family as *Euniphysa*), the embryos settle to the bottom immediately after fertilization; in Onuphidae (sister group of Eunicidae), the larvae either are brooded in the mother tube or they develop directly in the sea bottom (Hsieh and Simon, 1987). It is also quite possible that no real pelagic larvae exist in *Euniphysa* for dispersal. Large amounts of fossilized Eunicida jaws were found from Ordovician to Silurian strata (Kielan-Jaworowska, 1966; Szaniawski, 1974; Bergman, 1989), which is earlier than the existence of the Tethys Sea and the westward drift of the North America continent. Continental drift is a possible reason for the separation of *E. auriculata* and *E. quadridentata* from their sister groups across the Atlantic Ocean and eastwards.

Based on the tentative relationships suggested between phylogeny and recorded distribution, both dispersal and vicariance may explain part of the current geographical distribution.

Euniphysa Wesenberg-Lund, 1949

Euniphysa Wesenberg-Lund, 1949: 305; Miura, 1986: 312–313.
Paraeuniphysa Wu and He, 1988: 123.
Heterophysa Shen and Wu, 1990: 765; Shen and Wu, 1991: 138.

Diagnosis. Eunicids with a pair of palps and three antennae, all slender and tapering without distinct articulations. Peristomial cirri present. Anterior jaw elements (Mx-III, IV and V) fang-like with slender, pointed tips, number of teeth in each piece is low (two to four). Branchiae present. Notopodia with a narrow

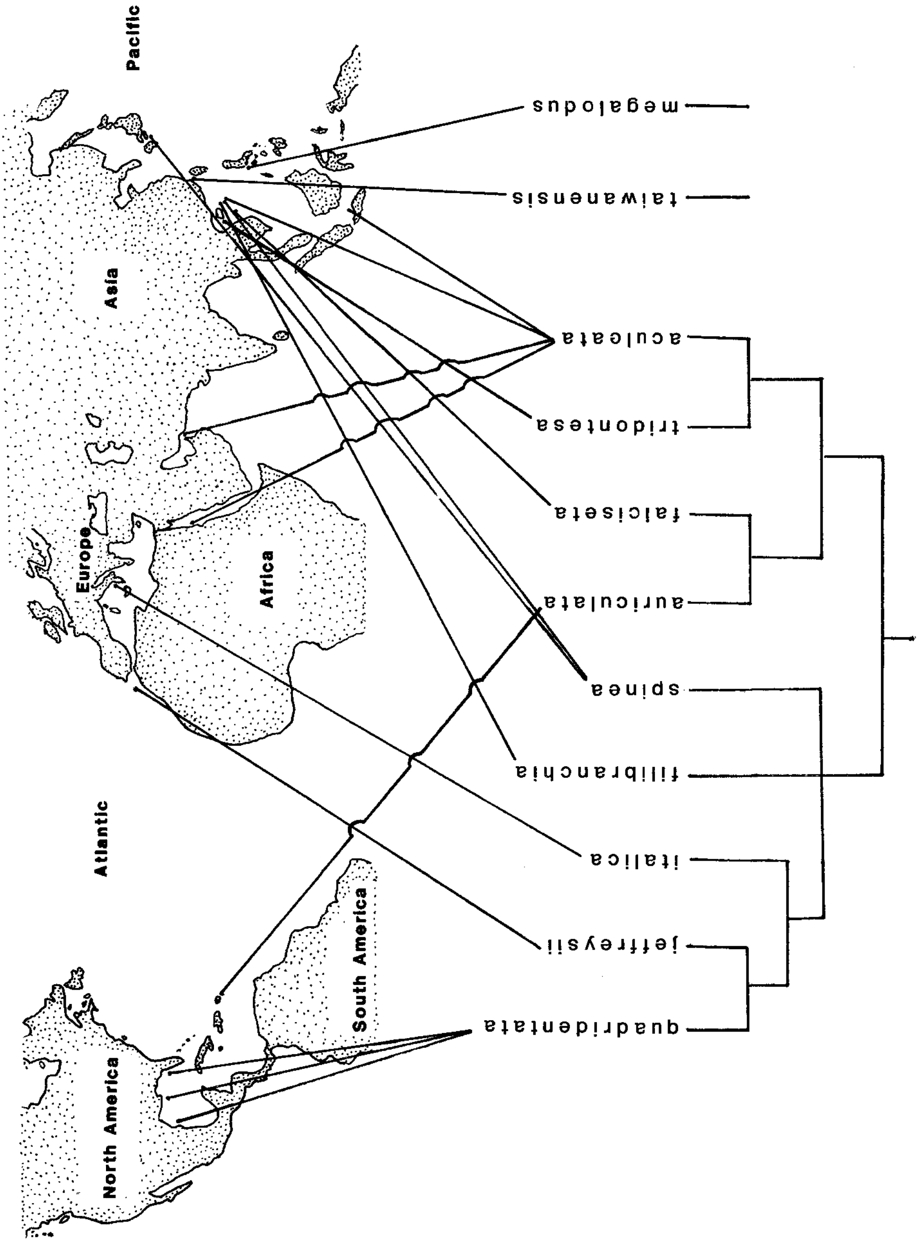

FIG. 9. The biogeographic mapping of the phylogeny and distributions of *Euniphysa*.

cirrophore and a tapering cirrostyle; base of cirrostyles distinctly enlarged and glandular at least in some median chaetigers, sometimes forming distinct pendant lobes. A small, fleshy knob present dorsal to aciculae on the acicular lobe. Limbate chaetae, pectinate chaetae, aciculae, subacicular hooks and compound spinigers always present; pseudocompound spinigers and compound falcigers present in some species.

Discussion. Wesenberg-Lund (1949) pointed out the structure of the maxillae as being unusually important in defining her new genus; she described Mx-III, IV and V from outside to inside (traditionally, Mx-III, IV and V are described from inside to outside, see figure 1), and named Mx-VI as chintinous plates.

Species of *Euniphysa* are most readily recognized by the combination of long palps and antennae tapering to slender tips and the thick, rather enlarged-looking anterior end. Other easily observed features are the long, fang-like teeth in the maxillary apparatus. The unique fang-shaped jaws with reduced teeth number is the proposed synapomorphy for *Euniphysa*. Species of *Palola* have similarly very low number of teeth, one or two in some cases (Fauchald, 1992). However, the shape of the jaws is entirely different in members of this genus and a preliminary analysis of all the Eunicida suggest that this may be homoplasious.

The presence of both compound spinigers and peristomium cirri is another character thought to be unique for *Euniphysa* (Wesenberg-Lund, 1949). Based on the above diagnosis, Miura (1986, 1987) treated *Eunice tubicola*, *Eunice tubifex* and *Eunice misakiensis* as members of *Euniphysa*. If this is the case, then *Eunice impexa* Grube, 1878 should be included in this group as well. Defining a genus by a unique combination of features is unsatisfactory, since the genus could easily be paraphyletic. We agree with Shen and Wu (1991) that 'The above three species proposed by Miura have all five pairs of maxillary formulae and the teeth of maxillary plates are all serrate instead of claw-shaped. They are not similar to *Euniphysa* and should still be kept in *Eunice*'.

In this study, only those with the *Euniphysa* synapomorphy (fang-shaped jaws) are recognized as *Euniphysa* species.

Type species, by monotypy: *Euniphysa aculeata* Wesenberg-Lund, 1949.

Synonyms. According to Shen and Wu (1990, 1991), *Euniphysa*, including three species, *E. aculeata*, *E. unicusa* and *E. oculata*, lacks compound falcigers completely and lacks all compound chaetae in the anterior nine chaetigers. Both synapomorphies according to Shen and Wu (1991) are thus shared absences. *Euniphysa aculeata* and *E. unicusa* both lack compound falcigers, as claimed by Shen and Wu (1991), and they always lack compound chaetae in the first nine chaetigers; in fact we are unable to separate the two which are here treated as subjective synonyms (see description below). *Euniphysa oculata*, which is a subjective synonym of *E. spinea* (see description below), actually has compound falcigers. Furthermore, the number of anterior chaetigers without compound chaetae is size-dependent and is normally far more than nine, usually around 20. These three species do not form a single branch on our phylogenetic tree (figure 8). Consequently, Shen and Wu's (1990) concept of *Euniphysa* is paraphyletic.

The two recently erected genera, *Paraeuniphysa* (Wu and He, 1988) and *Heterophysa* (Shen and Wu, 1990) were first and foremost characterized jointly by the presence of compound falcigers in addition to the compound spinigers. Shen and Wu (1990) separated *Heterophysa* from *Paraeuniphysa* on the start position of the compound chaetae. Compound chaetae, either spinigers or falcigers, are supposed to start at chaetiger 11 in *Paraeuniphysa* and from chaetiger 7 in *Heterophysa*. In *Marphysa*, one of the major genera of eunicids, species may have either compound spinigers or falcigers or both. Thus, the presence of both kinds of compound chaetae is insufficient to recognize a separate genus, at least at this point in our analysis of the family. *Paraeuniphysa* (Shen and Wu, 1990) includes *E. taiwanensis*, *E. falciseta* and *E. spinea*. The first occurrence of compound chaetae is size-dependent in *E. spinea*, and as mentioned above is around chaetiger 20 for a 2 mm wide specimen. In our analysis *E. spinea* does not fall out as the sister species to the other two species originally included in *Paraeuniphysa* (figure 8); consequently, as defined (Wu and He, 1988; Shen and Wu, 1990) this genus is polyphyletic.

As mentioned above, *Heterophysa* (Shen and Wu, 1990) was erected for the first occurrence of compound chaetae in chaetiger 7, but also for its unique Mx-I morphology which has three teeth. Both features are present, but are autapomorphies rather than synapomorphies. Recognizing a separate genus does not provide more systematic information for the phylogeny of *Euniphysa*, in addition it makes that genus paraphyletic (figure 8).

Thus, recognition of *Paraeuniphysa* and *Heterophysa* does not reflect the phylogenetic relationships among species; the consequence is that taxa become paraphyletic. Both *Paraeuniphysa* and *Heterophysa* are here considered synonyms of *Euniphysa*.

Key to species of *Euniphysa*

1 Two accessory plates present, left Mx-IV with a single tooth; subacicular hooks multiple in anterior parapodia 2
– Three accessory plates present, left Mx-IV with two teeth, subacicular hooks single in anterior parapodia 5

2 Anterior parapodia with only simple chaetae; pseudocompound spinigers absent; compound falcigers present 3
– Anterior parapodia with pseudocompound spinigers; compound falcigers absent . . . . *E. aculeata*

3 Ventral cirri of first six parapodia fused to posterior face of acicular lobe, visible only as a ridge; Mx-I with three teeth . . . . *E. tridontesa*
– Ventral cirri of first nine or 10 parapodia attached on posterior face of acicular lobe, but are free with distinct free tip; Mx-I falcate 4

4 Only limbate chaetae present in first nine parapodia; ventral cirri attached on posterior face in same chaetigers . . . . *E. auriculata* + *E. taiwanensis*
– Only limbate chaetae present in first 10 parapodia; ventral cirri attached on posterior face in same chaetigers . . . . *E. falciseta*

5 Right Mx-IV with four teeth; limbate chaetae arranged in one row in anterior parapodia . . . . *E. quadridentata* n. sp.
– Right Mx-IV with three teeth; limbate chaetae arranged in two rows in anterior parapodia 6

6 Branchiae first present from around chaetiger 10 7
– Branchiae first present after chaetiger 20 8

7 Anterior branchiae with single filament . . . . *E. spinea*
– Anterior branchiae with multiple long filaments . . . . *E. filibranchia* n. sp.

8 Compound falcigers present . . . . *E. italica*
– Compound falcigers absent . . . . *E. jeffreysii*

Description of species

Euniphysa aculeata Wesenberg-Lund, 1949
(figures 3a, d, e, 4–7, 10, 11)

Euniphysa aculeata Wesenberg-Lund, 1949: 305–310, figures 27–30; Pettibone, 1970: 247–251, figures 41–46.

Euniphysa unicusa Shen and Wu, 1990: 767, figure 1; Shen and Wu, 1991: 129–140, figure 1. New synonymy.

Material examined. PARATYPES: USNM 37716 ($n = 4$), Gulf of Iran, Sta. 75A, 20 nautical miles W by N of the buoy at Jask, 25°43′N, 5°722′E, 34 m, 21 April 1937, coll. G. Thorson.

Other material examined. USNM 37717 ($n = 2$), Siboga Sta. 2, Madura Strait, 7°25′S, 113°16′E, 56 m, 8 March 1899. USNM 96436 ($n = 2$), Gulf of Suez, Red Sea, 28°57′N, 33°10′E, October 1980, coll. J. Hartley.

Holotype of Euniphysa unicusa. SSBT 0034, Beibu Bay, the South China Sea, 21°20′N, 109°21′E, 12 m, mud and sand.

Comments on material examined. The description is mainly based on the paratype material in USNM 37716. Numerical values inside parentheses are for the specimen of *E. unicusa* examined. One specimen of USNM 96436 is complete, the only complete specimen seen for any species of *Euniphysa*, so its features, especially those of the posterior part, are described separately.

Description. Incomplete specimen with 68 (85) chaetigers; total length 16 mm; maximum width 1.8 (1.9) mm at chaetiger 10. Length through chaetiger 10, 1.7 (1.9) mm. Body flattened ventrally in anterior end, becoming increasingly cylindrical further back. Remnants of dark pigment present anteriorly.

Prostomium wider frontally than posteriorly; distinctly narrower than peristomium; vaguely divided into a posterior and anterior region; fronto-ventral area distinctly set off as upper lips (figure 10a). Each prostomial half frontally obliquely rounded; posterior end gently convex; anterior region straight or slightly flaring towards anterior end. Median sulcus very shallow; continued as a distinct suture to base of middle antennae. Eyes absent. Antennae and palps in deep horseshoe; Palps and lateral antennae close to each other, similar in thickness. Palpophores and ceratophores short and ring-shaped; without articulations. Palpostyles and ceratostyles slender, tapering; without articulations. Palps reach chaetiger 3 (1), lateral antennae chaetiger 5 (5) and median antenna chaetiger 8 (10). Peristomium large, folded; more than twice as long ventrally as dorsally. Separation into rings distinct dorsally and laterally and vaguely indicated ventrally. Anterior ring two-thirds of total peristomial length. Peristomial cirri located nearly laterally; short, digitiform; reaching middle of anterior peristomial ring. Peristomial cirri without articulations.

Maxillae (exposed in paratype from USNM 37716, figure 10g) with slender, sharply pointed teeth; light reddish to tan-coloured; without distinct calcifications. Maxillary formula ($n = 8$): 1 + 1, ‘4–6’ + ‘4–6’, 2 + 0, 1 + 3, 1 + 1, 1 + 1. One accessory plate present on left and one accessory plate on right side. Mx-VI represented by flat sclerotinized patches. Mx-III very small, proximal to left Mx-II. The middle tooth of right Mx-IV very small in some specimens. All Mx-III, IV and V with long, slender fangs. Mandibles decalcified, flat with widely flaring frontal edge.

Branchiae present from chaetiger 17 (18); occurring sporadically in first several branchiated chaetigers; parapodia 22–27 with two filaments, 28–38 with three

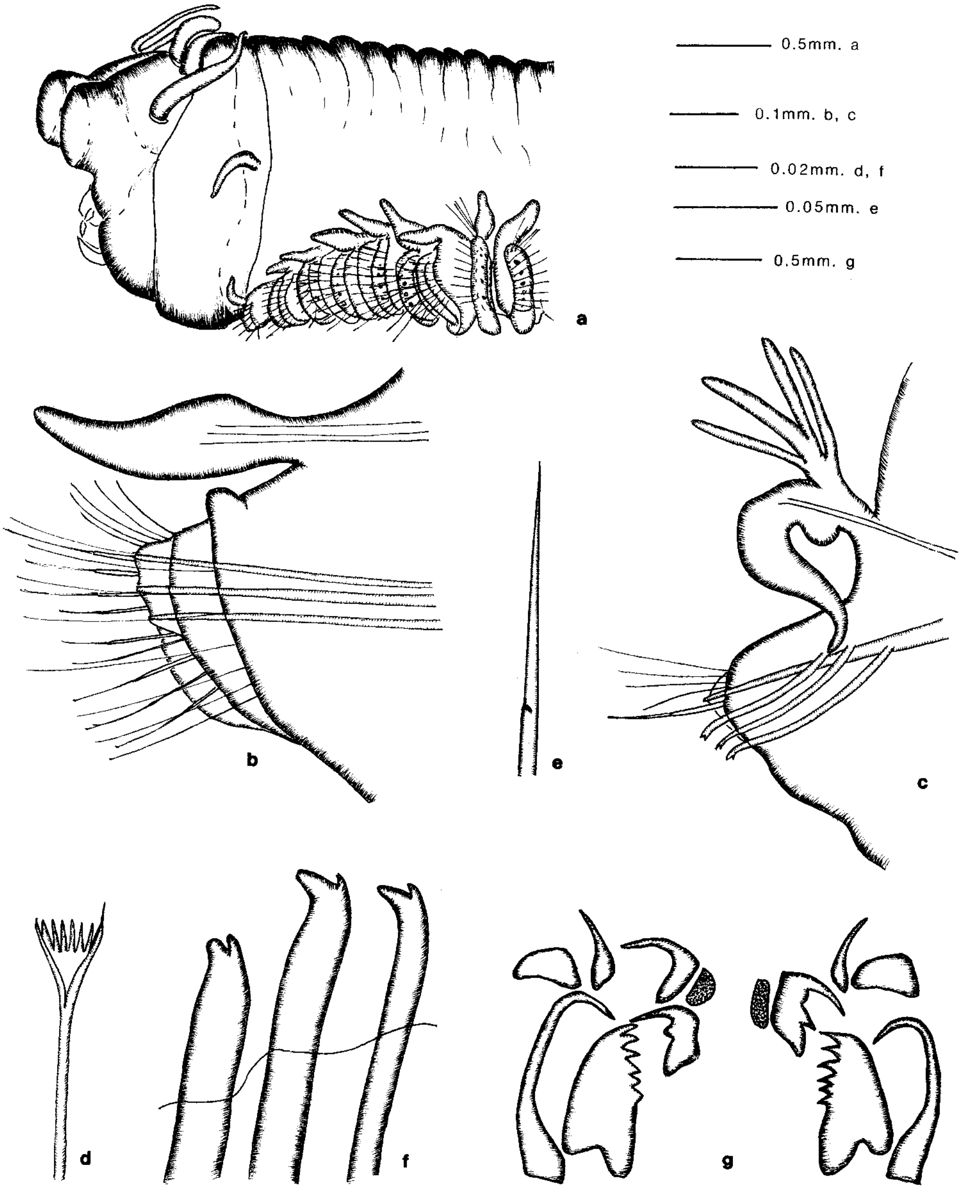

FIG. 10. *Eunice aculeata* (paratype, USNM 37716). (a) Anterior end; (b) parapodium 5; (c) parapodium 35; (d) pectinate chaetae; (e) pseudocompound chaetae; (f) subacicular hooks; (g) maxillae.

filaments, 39–45 with four filaments, up to five (five) filaments from parapodium 46 (73). Branchiae always shorter than dorsal cirri.

First parapodium with bilobed acicular lobes; superior section slightly longer than inferior section. Both pre- and postchaetal lobes low, transverse folds. Acicular lobes obliquely truncate; with distinct superior free tab through about chaetiger 20; becoming increasingly symmetrically conical posteriorly. Both pre- and postchaetal lobes becoming increasingly longer in posterior chaetigers; tracking the outline of acicular lobes closely in posteriormost chaetigers. Slender, digitiform ventral cirri present in first chaetiger only; completely fused to (figure 10b) posterior face of acicular lobe in chaetigers 2–9 (2–9); re-emerging as short, conical free cirrus from chaetiger 10. Lower edge of parapodia increasingly glandular from chaetiger 10 (10), presumably representing completely incorporated bases of ventral cirri. Glandular base and free cirrus reduced from about chaetiger 25; Glandular bases totally missing posterior to chaetiger 31 (figure 10c). Where present all ventral cirri tapering to slender tips; articulations absent. First notopodium with distinct narrow base; enlarged in lower one-third and tapering to slender tip; supported by four slender aciculae. Notopodial cirri posterior to chaetiger 10 with distinct basal enlarged region on ventral side.

First nine parapodia with distinct pre- and postacicular fascicles; preacicular fascicle with short, tapering pseudocompound chaetae (figure 10e) in a fan-shaped arrangement. Postacicular fascicle with dorsal limbate chaetae and ventral pseudocompound spinigers in fan-shaped arrangement; limbate chaetae in one row (figure 3e) on parapodia 1–4 and slightly longer than pseudocompound ones; in two (two) rows (figure 3d) on parapodia 5–9 (5–9) becoming twice as long as pseudocompound ones. Pseudocompound spinigers with distinct obliquely transverse line; barely enlarged at level of joint; marginally smooth. From chaetiger 10 (10), compound spinigers completely replacing pseudocompound spinigers; arranged in three preacicular ventro-lateral rows. Limbate chaetae remaining in two postacicular dorsal-lateral rows in relation to aciculae; such a pattern persisting until about first occurrence of subacicular hooks (figure 3a). Compound spinigers with distally enlarged shafts, marginally serrated; without distinct distal beak. Appendages very long, finely tapering, without marginal serrations. Pectinate chaetae (figure 10d), first present posterior to chaetiger 15, very small; with slender shafts; distally flaring and furled; eight to ten teeth present, one marginal tooth longer than others. Compound falcigers absent. Notopodial aciculae present in all chaetigers; slender, brown; numbering three or four in all parapodia. Neuropodial aciculae tapering, blunt; brown, without distinct core and sheath construction; multiple in anterior parapodia, single from middle part of body. Subacicular hooks (figure 10f) from chaetiger 25 (23); chestnut-coloured; parapodia 24–26 with single hook, 27 with two hooks, 28–32 with three hooks, 29 with four hooks, most posterior parapodia with three hooks (parapodia 23–26 with single hook, 27–28 with two hooks, 29–34 with three hooks, 35 with four hooks, 36–38 with three hooks, 39–40 with four hooks, 41–63 with three hooks, from 64-end with two hooks). All hooks similar; brown; bidentate; proximal tooth very much larger than distal tooth; tapering, unless worn; directed laterally. Distal tooth short, very much narrower than proximal tooth; directed obliquely distally. Guards truncate.

Complete specimen USNM 96436 with 170 chaetigers with two pairs of anal cirri, all broken. Widest part 1.9 mm, first ten chaetigers 1.7 mm. Branchiae from chaetiger 19 to near posterior end; single filament in first branchiate parapodium, chaetiger 20 with two filaments, as many as seven filaments on chaetiger 150; initially filaments shorter than dorsal cirri, becoming twice as long as dorsal cirri near posterior end. Aciculae in multiples in anterior region (figure 11). Subacicular hooks (figure 11) from parapodium 24. Compound spinigers present from parapodium 10 through posterior end of body. Compound falcigers not seen.

Remarks. *Euniphysa aculeata* is unusual among eunicids in that the chaetae are arranged in fascicles, rather than bundles in several anterior chaetigers. Furthermore,

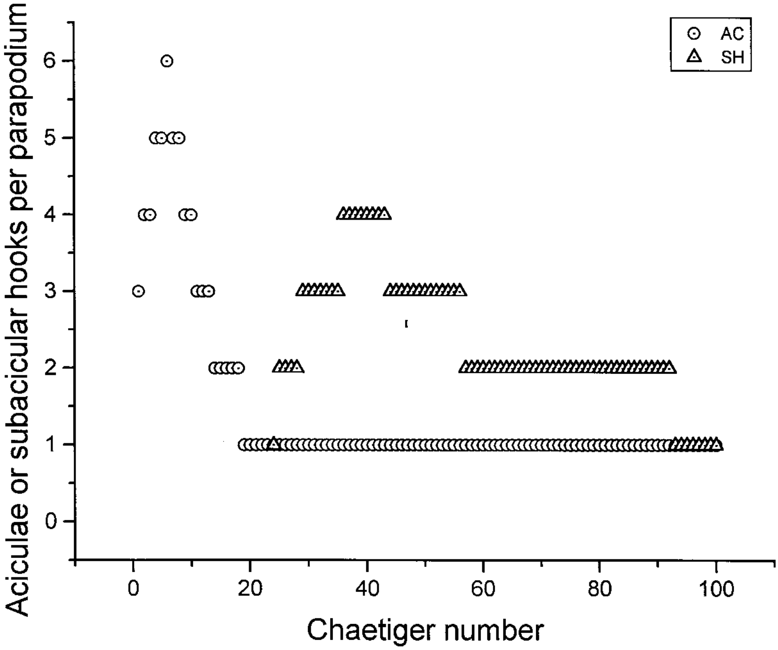

FIG. 11. The distribution pattern of aciculae and subacicular hooks in the anterior 100 chaetigers of the complete specimen of *Euniphysa aculeata* (USNM 96436). AC = aciculae; SH = subacicular hooks.

ventral cirri emerge from the posterior face of the parapodia and are united with the acicular lobe in chaetigers 2–9.

Certain morphological characters are size-dependent (figures 4–7) in *E. aculeata* ($n = 8$). The first occurrence of branchiae varies from parapodia 15–19; first occurrence of subacicular hooks varies from parapodia 22–26; last occurrence of multiple aciculae varies from parapodia 13–21.

After careful examination of a paratype specimen of *Euniphysa unicusa* (SSBT-0034), and comparing all its morphological characters with those of *E. aculeata*, we find that all morphometric features of *E. unicusa* fall well within the range of those of *E. aculeata*. According to Shen and Wu (1990, 1991), *E. unicusa* differs from *E. aculeata* in the following features: presence of papillae on dorsal cirri; presence of simple unidentate chaetae (= pseudocompound spiniger); short-stemmed pectinate chaetae and in the first occurrence of the subacicular hooks. Our observations show that the papillae of the dorsal cirri are only present randomly in some dorsal cirri and are not a fixed feature; pseudocompound spinigers are also present in *E. aculeata* in the same pattern (fascicle) and position (on parapodia 2–9) as in *E. unicusa*, they had not been correctly described by previous authors (Wesenberg-Lund, 1949; Pettibone, 1970); stem length of the pectinate chaetae is variable even within a parapodium and certainly among parapodia of a single specimen; first occurrence of the subacicular hooks is a size-dependent feature, subacicular hooks start from parapodia 22–24 for a 2 mm-wide *E. aculeata* (figure 4), it starts from the parapodium 23 for the similar-sized specimen of *E. unicusa* studied. We cannot find consistent differences between the two and for that reason consider *E. unicusa* to be a junior subjective synonym of *E. aculeata*.

Euniphysa auriculata (Treadwell, 1900)
(figures 1, 2e2, 12a–i)

Eunice auriculata Treadwell, 1900: 342–343; Treadwell, 1901: 196–197, figures 33–36b.

Material examined. Two syntypes, USNM 15898, Fish Hawk Sta. 138, Mayaguez Harbor, Puerto Rico, 16–17 fms, 1899. Five syntypes plus tube fragments, USNM 15899, Fish Hawk Sta. 139, Mayaguez Harbor, Puerto Rico, 20 January 1899, 97–120 fms.

Comments on material examined. The syntypes from USNM 15899 have all been dried out at one time and only characters unaffected by this, such as the jaw structure, were observed. The specimen described in detail is the larger of the two syntypes from USNM 15898.

Description. Syntype incomplete, consisting of 62 chaetigers, 20 mm long and 2.4 mm wide at widest; length through chaetiger 10, 2.2 mm. Anterior end to about chaetiger 15 enlarged and thickened with chaetigers crowded; further posteriorly all chaetigers about as long as wide and body cylindrical.

Anterior part of prostomium (figure 12a) consisting of two well-separated, dorsally flattened lobes; posterior part with antennae broad and slightly enlarged. Antennae and palps very slender, tapering to whip-like tips without articulations. Palps reaching chaetiger 1; lateral antennae reaching about chaetiger 7 and median antenna reaching chaetiger 16. Eyes not observed.

Peristomium trumpet-shaped in all specimens; all specimens with major portion of jaw apparatus everted, which may have distorted the prostomial shape. Peristomium consisting of two rings, of which anterior ring about five-sixths of total length; separation between two rings distinct only dorsally; ventral separation possibly hidden by expanded lower lip. Peristomial cirri enlarged basally and tapering to a whip-like tip and reaching front edge of peristomium; without articulations.

Jaws (figure 1) everted in all specimens. Teeth de-calcified and soft. The maxillary formula ($n=8$): 1 + 1, '6–7' + 6, 2 + 0, 1 + 3, 1 + 1, 1 + 1. Two black accessory plates present. Mx-III located between left Mx-II and left Mx-IV; posterior tooth short, nearly triangular; anterior tooth long and slender. Mx-IV, V and VI form an arc on each side; different jaws separated by barely visible furrows. On left side all distinct teeth fang-like; on right side two posterior teeth on Mx-IV triangular, flattened; other teeth slender fangs.

Branchiae first present from chaetiger 16 (figure 12c) and present on all later chaetigers. In most branchiate chaetigers one or two filaments present; some posterior chaetigers with up to three branchial filaments in a rudimentary pectinate arrangement.

Anterior parapodia broadly truncate with pre- and postchaetal lobes represented by low folds. By chaetiger 10 parapodia becoming distally rounded. A short supra-acicular knob present in all anterior parapodia. Parapodia becoming increasingly pointed in posterior chaetigers in all fragments present. Notopodia stalked basally, with a distinct enlarged region with a distinctive digitiform shape (figure 2e2) in parapodia 2–9. Distally, notopodia finally tapering to slender tips. Near base of enlarged region a glandular structure starting out as small knob from about chaetiger 10 (figure 12b, c). By last chaetigers present glandular knob increased to large, ball-shaped, solid structure. Ventral cirri cirriform and in normal position in chaetiger 1; emerging from the posterior face of the acicular lobes in chaetigers 2–9 and represented by a round knob; in normal position again from chaetiger 10 to the last chaetigers present.

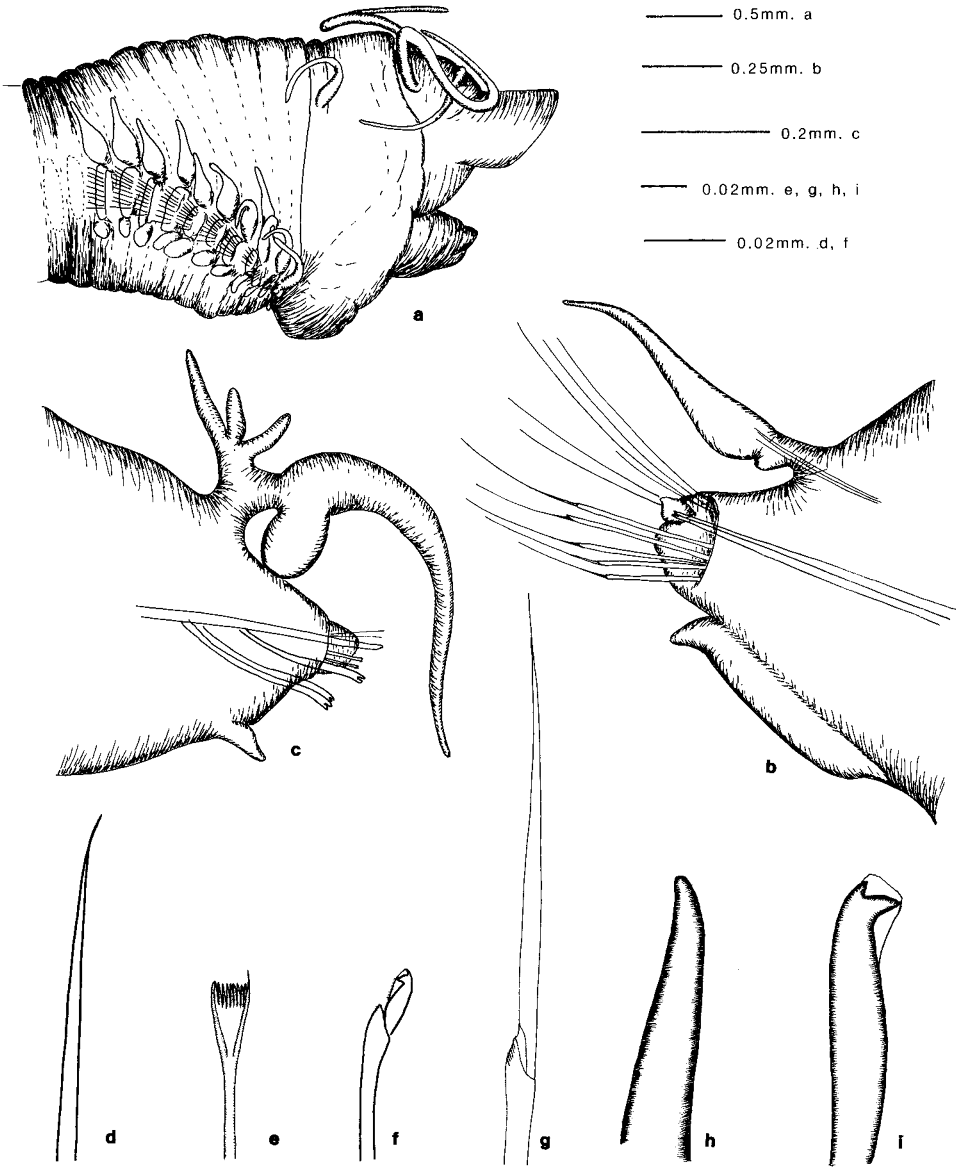

FIG. 12. *Euniphysa auriculata* (syntype, USNM 15898). (a) Anterior end; (b) parapodium 12; (c) parapodium 56; (d) simple chaetae; (e) pectinate chaetae; (f) compound falciger; (g) compound spiniger; (h) acicula; (i) subacicular hook.

Slender smooth limbate chaetae (figure 12d) in all chaetigers, at least on dorsal side of parapodia; first nine parapodia with only limbate chaetae. Limbate chaetae similar in length or posterior-dorsal ones slightly longer than others. In chaetigers 1–7 antero-ventral limbate chaetae arranged in two rows, postero-dorsal limbate chaetae in a single row; in chaetiger 8, antero-ventral limbate chaetae in three rows, postero-dorsal limbate chaetae in single row. In chaetiger 9 antero-ventral limbate chaetae in three rows and postero-dorsal limbate chaetae in two rows. From chaetiger 10 to the last chaetigers present, antero-ventral limbate chaetae replaced by three or four rows of compound spinigers and postero-dorsal limbate chaetae remaining in two rows, but arrangement of limbate chaetae indistinct from about chaetiger 23. Pectinate chaetae (figure 12e) not observed in anterior chaetigers, but present in posterior chaetigers. Each pectinate chaeta distally distinctly flared, very small and slender, with a scoop-shaped distal end consisting of about ten teeth, one marginal tooth longer than others. Compound spinigers (figure 12g) with slender, distally somewhat enlarged, marginally serrated shafts; appendages very long and slender with whip-like tips. Compound falcigers (figure 12f) present from chaetiger 26; each with distally enlarged shaft and short, bidentate appendage with bluntly pointed guards; teeth similar in size and distinctly curved in relation to long axis of appendage. Aciculae (figure 12h) honey-coloured or very light brown and distally straight; multiple in number in anterior parapodia; posterior parapodia with single, light brown, distally pointed acicula; posterior aciculae slightly curved dorsally. Light brown, bidentate subacicular hooks (figure 12i) present from chaetiger 24 to end of the body; chaetiger 25–29 with two hooks, 30–44 with three hooks; 45 with four hooks, from chaetiger 51 to end of fragment each chaetiger with three hooks. Each hook with large main fang and very much smaller distal tooth; truncate guards present.

Remarks. The species was first named and recognizably described in a short paper mentioning the characteristic rounded smooth glandular organ attached ventrally on the notopodia. A more complete description was published the following year and has been considered the original description by most authors. Hartman (1956: 308) indicated that Treadwell misspelled the specific name in the first publication; this is incorrect.

Euniphysa falciseta (Shen and Wu, 1990) n. comb.
(figures 2e3, 13a–i)

Paraeuniphysa falciseta Shen and Wu, 1990: 768–769, figure 2; Shen and Wu, 1991: 134–136, text figure 2, 1–10.

Material examined. One paratype, SSBT-0016, South China Sea, off Nansha Islands, 111 m, sandy mud (locality information quoted from Shen and Wu, 1991: 136).

Description. Paratype incomplete, with 56 chaetigers. Total length 29 mm; maximum width 4 mm at chaetiger 15; length through chaetiger 10, about 3.2 mm.

Body tapering from anterior end; jaw apparatus fully everted, distorting shape of prostomium and anterior end. Parapodia of first two chaetigers ventro-lateral; from chaetiger 3 parapodia fully lateral, becoming ventro-lateral again from about chaetiger 15. Dorsum slightly convex; anterior venter convex, becoming flattened from about chaetiger 15.

Prostomium (figure 13a) frontally truncate; probably excavate with thickened margins (distorted due to eversion of pharynx); median sulcus shallow. Eyes absent. Palps and antennae in a horseshoe, palps closer to lateral antennae; median antenna thicker than others and isolated by distinct gap; palpophores and ceratophores short and ring-shaped; without articulations; palpostyles and ceratostyles slender, tapering to slender tips, without articulations. Palps reaching chaetiger 3; lateral antennae reaching chaetiger 8 and median antenna reaching chaetiger 15. Peristomium distorted; anterior ring enlarged and about 90% of total peristomial length. Peristomial cirri basally enlarged, tapering to slender tips; reaching posterior edge of prostomium.

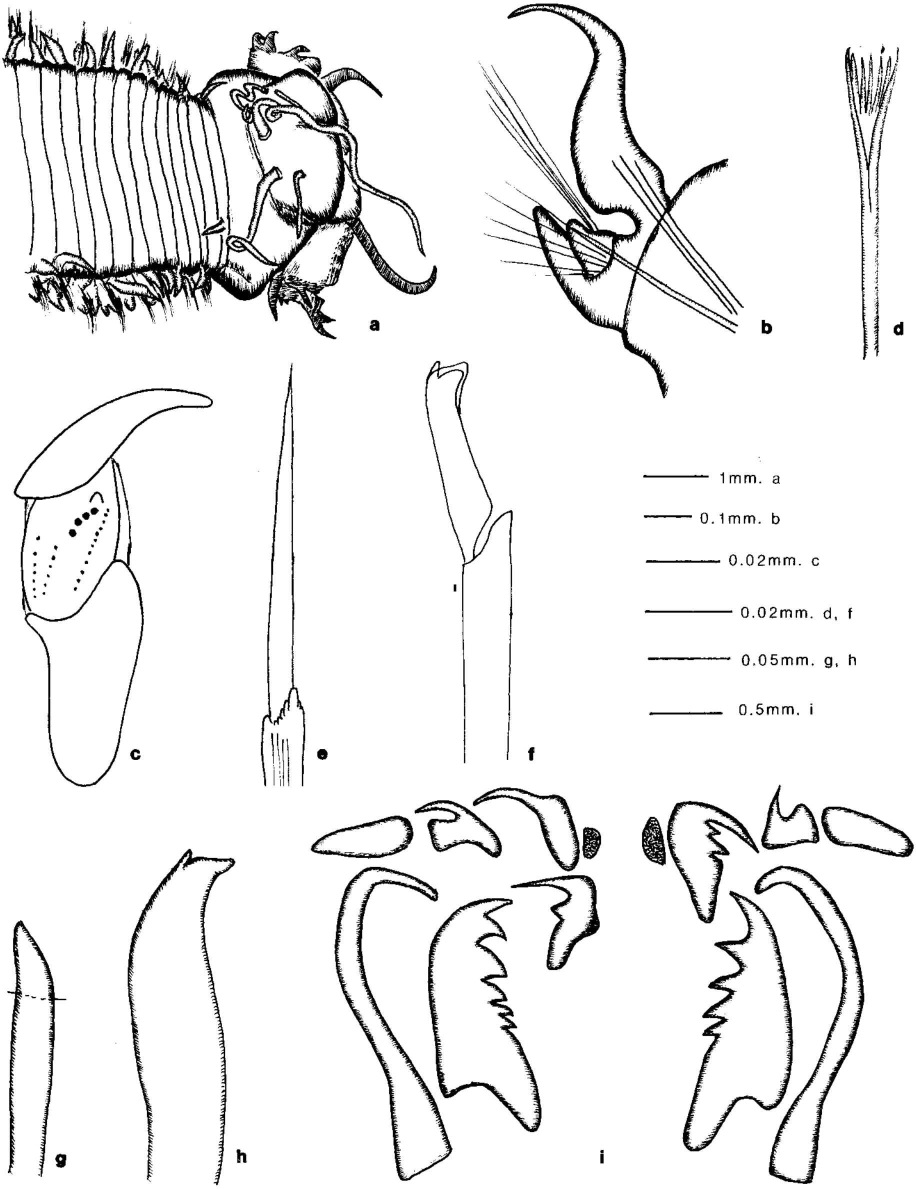

FIG. 13. *Euniphysa falciseta* (holotype, SSBT-0016). (a) Anterior end; (b) parapodium 1; (c) parapodium 4, lateral view; (d) pectinate chaetae; (e) compound spiniger; (f) compound falciger; (g) acicula; (h) subacicular hook; (i) maxillae.

Maxillary formula (figure 13i) 1 + 1, 6 + 5, 2 + 0, 1 + 3, 1 + 1, 1 + 1. Two black accessory plates present. Two proximal teeth of right Mx-IV small; most other teeth slender, curved fangs.

Branchiae present from chaetiger 18 to end of fragment; all branchiae palmate with very short, stubby filaments; chaetigers 18–26 with two filaments, 27–34 with three filaments, chaetiger 35 with four filaments, from chaetiger 36 to end of fragment each chaetiger with three branchial filaments. Branchial stem very short, button-shaped. Branchiae less than half length of notopodial cirri in all chaetigers.

Anterior acicular lobes obliquely truncate; aciculae emerging dorsal to midline. Median acicular lobes (posterior to chaetiger 25–30) distally rounded, barely elevated above body wall; with aciculae emerging at midline. Anterior-most prechaetal lobes low, transverse folds, becoming rounded in mid-anterior chaetigers and obliquely rounded in median chaetigers. All postchaetal lobes short, rounded tabs posterior to and slightly above acicular lobes enclosing postero-dorsal fascicle of chaetae. First three ventral cirri (figure 13b) tapering, becoming basally enlarged through next two to three chaetigers; enlarged region thick, transverse welts, becoming withdrawn into ventral body-surface in median chaetigers; free tips present in all parapodia; each tip short, sharply tapering from a broad base ventral to acicular lobe; ventral cirri or its free tips emerge from posterior face of parapodia in chaetigers 1–10; glandular enlarged base present through chaetiger 38. Notopodia with distinct aciculae in all chaetigers. Anterior notopodia basally with narrow stalk; a distinctly finger-shaped structure is present sub-basally (figure 2e3) in chaetigers 2–10; notopodial cirri tapering distally to slender tips. Median notopodia less distinctly enlarged near base; with a distinct, sensory structure attached ventrally.

Narrow limbate chaetae present in postero-dorsal bundles in all chaetigers, each chaeta tapering to slender, whip-like tips. First 10 chaetigers exclusively with limbate chaetae. Chaetigers 1–10 with two rows of limbate chaetae (figure 13c) on antero-ventral side of acicula lobes, and one fascicle of limbate chaetae on postero-dorsal side of acicular lobe. From chaetiger 11 to posterior end antero-ventral limbate chaetae replaced by three or four rows of compound spinigers and the postero-dorsal limbate chaetae become arranged in two rows. Shafts of compound spinigers (figure 13e) slightly enlarged; with distinct distal beak, marginally serrated with serrations continued as internal striations. Pectinate chaetae (figure 13d), seen in median chaetigers only, small, located at base of postero-dorsal limbate chaetae. Each pectinate chaeta furled, tapering; one marginal tooth longer than other teeth; about seven to ten teeth present in each. Compound falcigers (figure 13f) present from chaetiger 31; their shafts tapering, marginally smooth, thicker than shafts of compound spinigers. Appendages bidentate with proximal teeth larger than distal teeth; proximal teeth directed laterally, tapering; distal tooth directed obliquely distally, tapering; Guards distally truncate; marginally smooth. Aciculae (figure 13g) tapering to slightly oblique tips; copper-coloured; chaetiger 1 with two aciculae, chaetigers 2–25 with three aciculae, 26–31 with two aciculae, and chaetiger 32 to the end of fragments with single acicula. Aciculae and subacicular hooks without distinct separation of core and sheath. Subacicular hooks (figure 13h) first present from chaetiger 28; as many as six hooks present in a single chaetiger (41). Each hook subdistally thickened, tapering to small head, bidentate. Proximal tooth larger than distal one; directed laterally, slightly uptilted distally. Distal tooth small, slender, tapering; directed obliquely distally.

Remarks. This description differs from the one given by Shen and Wu (1991) in the following details:

(1) Median antenna extends to chaetiger 15 rather than to chaetiger 10.

(2) Branchiae are present from chaetiger 18 rather than from chaetiger 14; they are not pectinate, but palmate, with short branchial filaments emerging close together from a short stem.

(3) Parapodium 50 has many compound spinigers and a few compound falcigers;

parapodium 45 lacks compound spinigers altogether. The chaetal distribution cited by Shen and Wu (1991) is different.

(4) Subacicular hooks are present from chaetiger 28 and number up to six in a parapodium rather than four and first present from about chaetiger 31.

(5) The maxillary formula is slightly different.

These differences may be important since differences in the characters listed above under points 1, 2 and 4 were used to separate *Paraeuniphysa taiwanensis* from *P. falciseta* by Shen and Wu (1991). The description by Shen and Wu was based on the holotype (SSBT-0015) rather than the paratype (SSBT-0016); this may be the cause of some of the reported differences.

Euniphysa falciseta resembles *E. auriculata* in most morphological characters. The main difference is that *E. falciseta* has ten anterior parapodia with exclusively limbate chaetae and posteriorly located ventral cirri, while all eight *E. auriculata* specimens examined consistently have nine parapodia with exclusively limbate chaetae and posteriorly located ventral cirri.

Euniphysa filibranchia n. sp.
(figures 4–7, 14a–j, 15, 16)

Material examined. Type specimens: SSBT-0017 ($n = 2$), South China Sea.

Comments on material examined. No detailed locality information, is available, but the specimen probably was collected near Nansha Island according to the label number. The materials will be deposited in the South China Sea Institute of Oceanography, Academica Sinica, China. The following description was mainly based on the larger specimen.

Description. Both types (holotype and paratype) incomplete, of unknown sex with 48 and 45 chaetigers and similar in size. Maximum width 3.5 mm. Length through chaetiger 10, 2.6 mm.

Anterior end (figure 14a) through chaetiger 5 rounded, becoming flattened thereafter. Frontal edge of prostomium rounded; median sulcus shallow. Prostomium about as long as peristomium, distinctly narrower and less than half depth of peristomium. One pair of black reniform eyes present, located lateral to lateral antennae and posterior to bases of palps. Palps and antennae in shallow horseshoe, evenly spaced; increasing in thickness from median through lateral antennae and to palps. Palpophores and ceratophores ring-shaped. Palpostyles and ceratostyles slender, tapering to fine tips, without articulations but with slightly irregular wrinkles. Palps reaching first chaetiger; lateral antennae reaching chaetiger 7; median antenna longer than others but broken. Separation between peristomial rings distinct on all sides (forming a complete cincture). Anterior ring about four-fifths of total peristomial length on dorsal side. Peristomial cirri slender, tapering to very fine tips; without articulations; reaching middle of prostomium.

Maxillary formula (figure 14j): $1+1$, $5+4$, $2+0$, $2+3$, $1+1$, $1+1$, and in addition three black accessory plates. All teeth long, slender, tapering. Mx-VI smooth, without distinct teeth.

Branchiae (figure 14b) from chaetiger 7 (9 in paratype) to end of fragment. Chaetiger 7 with one branchial filament, chaetigers 8–17 with two filaments, chaetiger 18 with three filaments, remaining chaetigers with two filaments (as many as four filaments on chaetigers 12–27 in paratype). Filaments two to three times longer than dorsal cirri; flat.

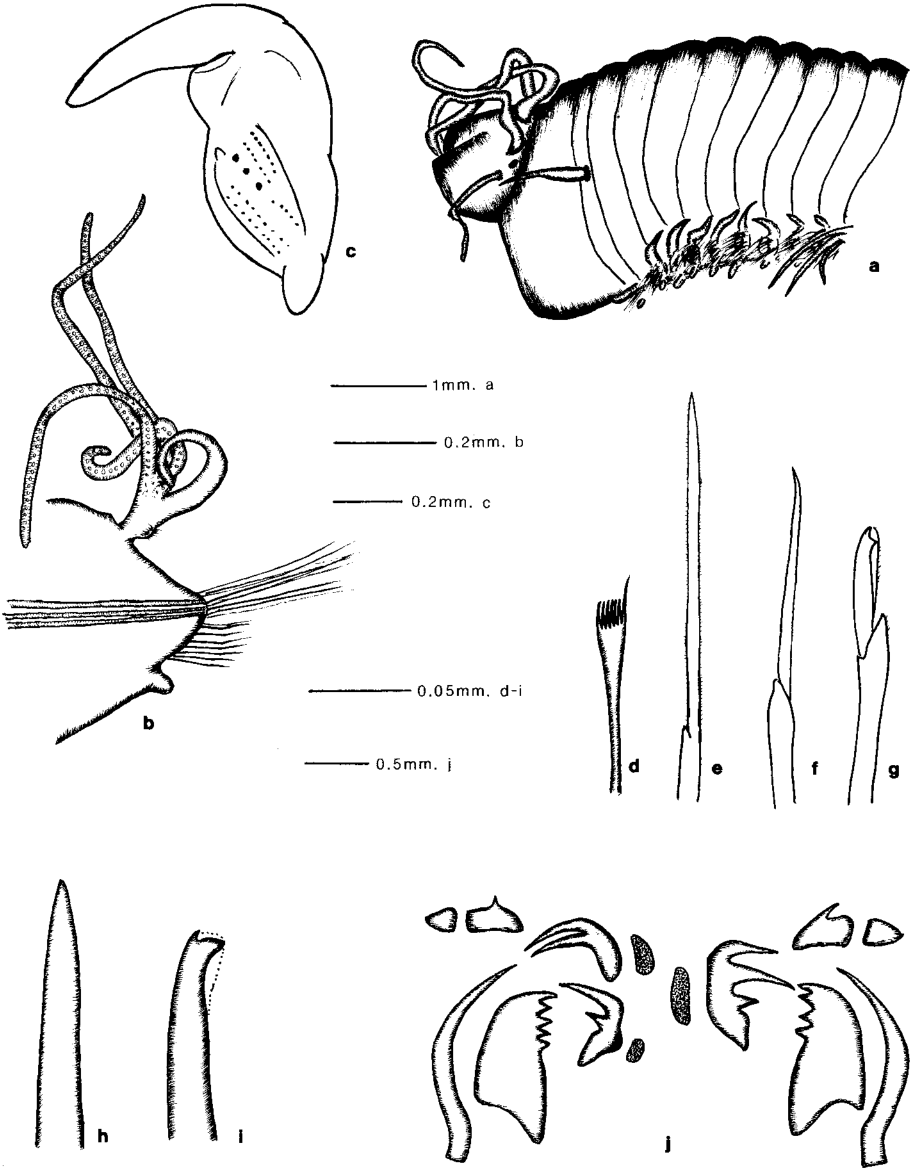

FIG. 14. *Euniphysa filibranchia* n. sp. (syntype, SSBT-0017). (a) Anterior end; (b) parapodium 15; (c) parapodium 4, lateral view; (d) pectinate chaetae; (e) pseudocompound spiniger; (f) compound spiniger; (g) compound falciger; (h) acicula; (i) subacicular hook; (j) maxillae.

All notopodia with distinct, light brown aciculae. Anterior notopodial cirri fusiform; tapering to slender tips. Median notopodial cirri similar, but rather more slender, with a rounded pendant sensory structure near base. Sensory structure distinct in all median chaetigers. A small knob present dorsal to aciculae in anterior parapodia. Ventral cirri slender on first chaetiger, becoming smaller from parapodium 2; from parapodium 7, bases of ventral cirri strongly enlarged through about chaetiger 42.

Dorso-posterior, slender limbate chaetae in two rows (figure 14c) in anterior chaetigers. Anterior pectinate chaetae not seen. Median pectinate chaetae (figure 14d) tapering or very gently flaring; with about seven teeth; one marginal tooth longer than other teeth. Antero-ventral chaetae serrated pseudocompound spinigers (figure 14e) in three rows in chaetigers 1–24 (in paratype). Pattern of rows becoming obscure from chaetiger 25. Compound spinigers (figure 14f) replacing pseudocompound spinigers starting at chaetiger 22 ending by chaetiger 43; compound spinigers marginally hirsute (rather than serrated). Bidentate, compound falcigers (figure 14g) first present from chaetiger 33; totally replacing compound spinigers by chaetiger 44. All aciculae (figures 14h, 15) brown to very dark brown; tapering to straight, pointed or blunt tips; multiple in number in first 34 chaetigers. Subacicular hook (figure 14i) present from chaetiger 29 (right) or 31 (left); single in all chaetigers present. Proximal tooth larger than distal tooth; directed laterally, slightly uptilted distally. Distal tooth tapering, directed obliquely laterally, tapering.

Remarks. The types of this species were labelled as one of the type-lots of *E. falciseta*. The differences between these two species are remarkable: *E. falciseta* has two accessory plates, a single tooth on left Mx-IV and multiple subacicular hooks in anterior parapodia; while *E. filibranchia* has three accessory plates, two teeth on left Mx-IV and single subacicular hook in anterior parapodia.

Euniphysa filibranchia resembles *E. spinea* in nearly all morphometric characters such as the distribution of branchiae, subacicular hooks, enlarged portion of ventral cirri, the various kinds of chaetae (figures 4–7, 16) and the jaw structure. The only significant difference is that in anterior chaetigers in similarly sized (around 3.5 mm wide) specimens, *E. spinea* has only one short branchial filament, but *E. filibranchia* has three to four long branchial filaments.

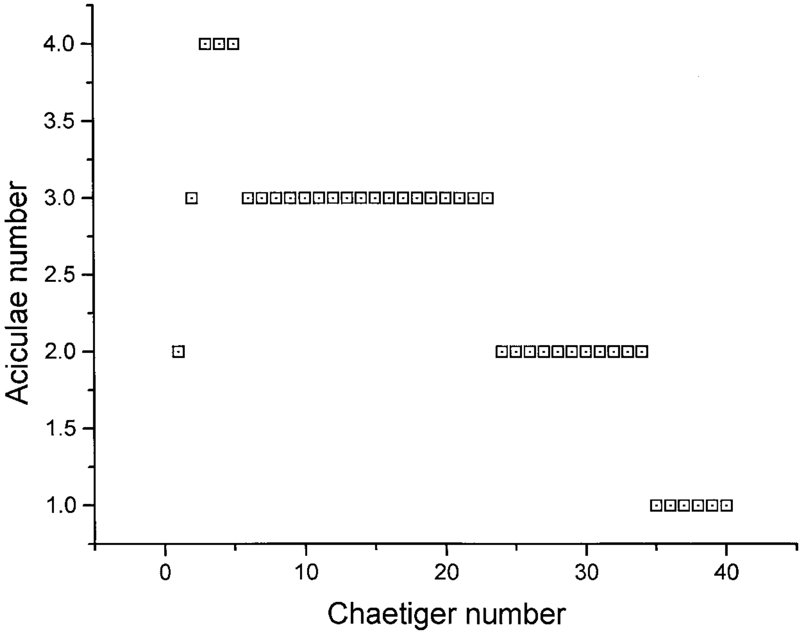

FIG. 15. The distribution pattern of aciculae in the anterior 40 chaetigers of *Euniphysa filibranchia* n. sp. (SSBT-0017).

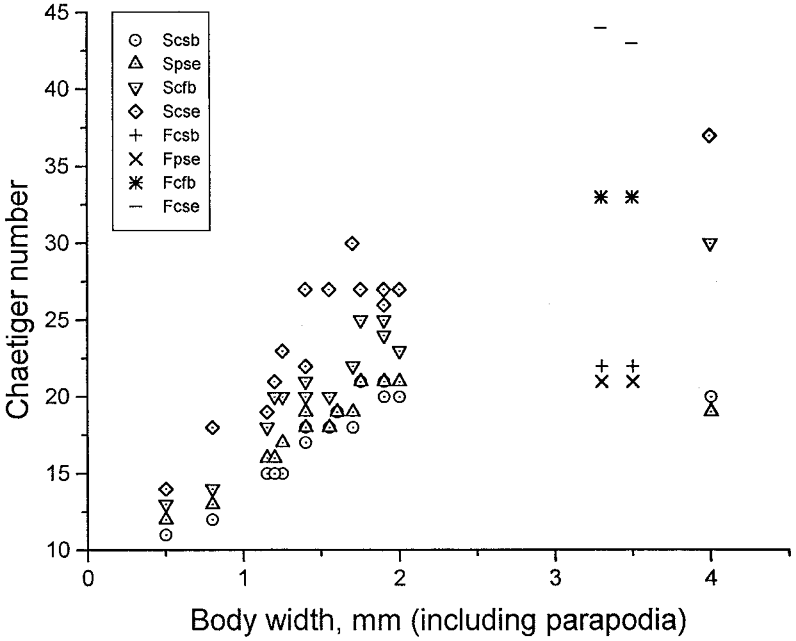

FIG. 16. The relationships between maximum body width (mm) and various chaetae positions in *Euniphysa filibranchia* n. sp. (F, $n=2$) and *Euniphysa spinea* (S, $n=15$): Fcsb = start position of compound spiniger in F, Fpse = ending position of pseudocompound spiniger in F, Fcfb = start position of compound falciger in F, Fcse = ending position of compound spiniger in F; Scsb = start position of compound spiniger in S, Spse = ending position of pseudocompound spiniger in S, Scfb = start position of compound falciger in S, Scse = ending position of compound spiniger in S.

Etymology. This species is named for the long, slender branchial filaments present in anterior parapodia.

Euniphysa italica Cantone and Gravina, 1991
(figure 17a–h)

Euniphysa italica Cantone and Gravina, 1991: 229–235, figures 1, 2.

Material examined. HOLOTYPE, 26E/IX 89, Mediterranean Sea off Latium, Italy, 42°10′N, 12°30′E. PARATYPE, 12B/ VII 89 ($n=1$), Mediterranean Sea, Italy.

Comments on material examined. The description is mainly based on the holotype specimen. The values in the parentheses are for the smaller paratype.

Description. Holotype incomplete, with 68 (52) anterior chaetigers. Total length 22 mm; first ten chaetigers 2.9 (1.7) mm long, widest part (with parapodia) measures 3.1 (1.3) mm.

Prostomium (figure 17a) anteriorly bilobed, with deep sulcus dorsally; about as long as peristomium; distinctly narrower and less than half depth of peristomium. One pair of black reniform eyes situated between palps and lateral antennae. All prostomial appendages, except right palp and right lateral antenna incomplete; nearly evenly spaced. Palpophore and ceratophore short and stout; remaining palpostyle and ceratostyle long and smooth; palps reaching chaetiger 6 and lateral antenna reaching chaetiger 9. First ring of peristomium about five-sixths (laterally)

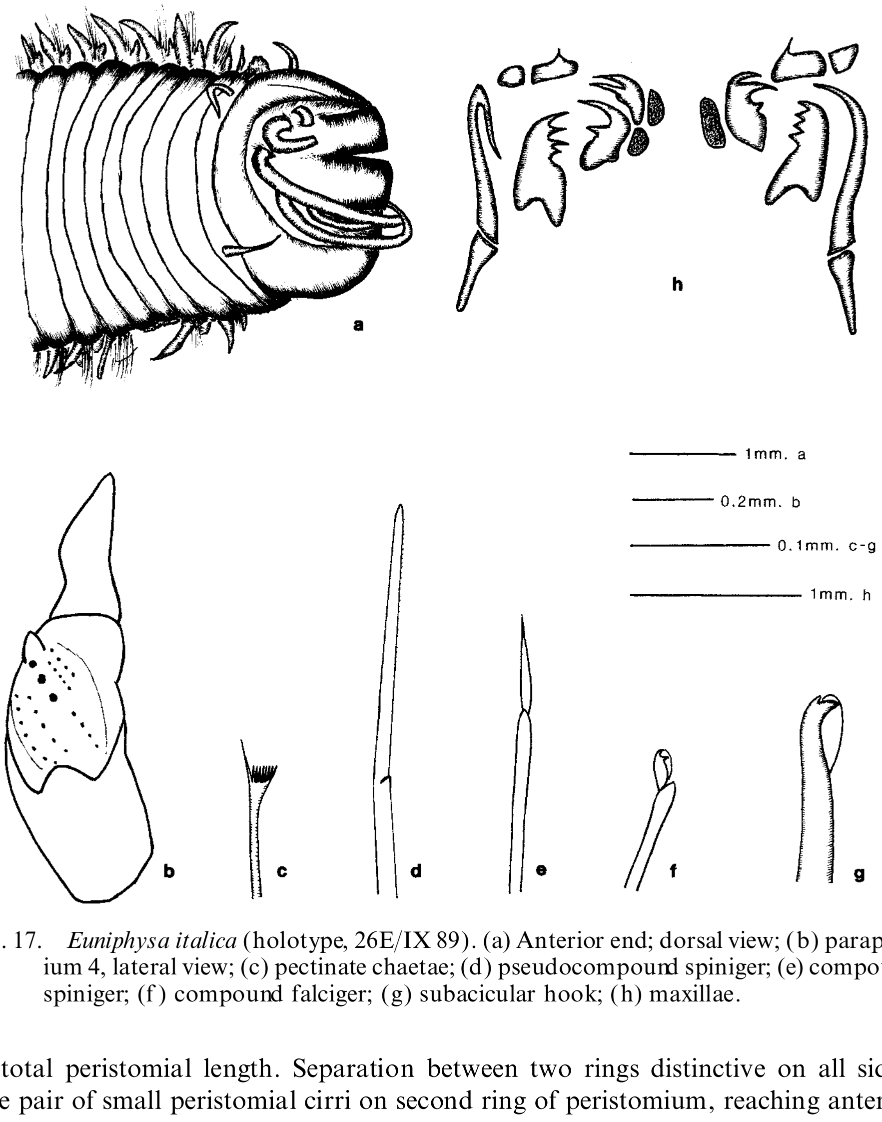

FIG. 17. *Euniphysa italica* (holotype, 26E/IX 89). (a) Anterior end; dorsal view; (b) parapodium 4, lateral view; (c) pectinate chaetae; (d) pseudocompound spiniger; (e) compound spiniger; (f) compound falciger; (g) subacicular hook; (h) maxillae.

of total peristomial length. Separation between two rings distinctive on all sides. One pair of small peristomial cirri on second ring of peristomium, reaching anterior end of prostomium.

Maxillary formula (figure 17h): 1 + 1, 4 + 4, 3(2) + 0, 2 + 3, 1 + 1, 1 + 1. Accessory plates black; two present on left and one on right side. Proximal tooth of Mx-III very small; absent in smaller specimen. Teeth in fang shape.

Branchiae present from chaetiger 23 (22); present in all remaining chaetigers of incomplete specimens; always with single filament. First filament shorter than dorsal cirri, gradually increasing in length to become near same length as or even slightly longer than, dorsal cirri.

First two pairs of parapodia, especially first pair, smaller than following ones. A small protrusion present dorsal to aciculae. Dorsal cirri long throughout remaining chaetigers. A small (sensory) knob on ventral side of dorsal cirri near base; size of knob increasing in size posteriorly. Ventral cirri of chaetigers 1–2 finger-shaped; enlarged bases present from chaetiger 3; bases largest in median of chaetigers present, decreasing in size posteriorly and absent from chaetiger 55.

Dorso-posterior limbate chaetae in two rows (figure 17b), always serrated. Pectinate chaetae (figure 17c) with nine teeth, one marginal tooth bigger and longer than other teeth. Ventro-anterior pseudocompound spinigers (figure 17d) arranged in three rows; pattern distinct through first 28 (20) chaetigers. Compound spinigers (figure 17e) first present from chaetiger 27 (20) and co-occurring with pseudocompound spinigers on two (one) chaetigers; replacing pseudocompound spinigers completely from chaetiger 29 (21). Most posterior chaetae broken. Bidentate compound falcigers (figure 17f) observed in several parapodia (e.g. chaetiger 46; in the smaller specimen, compound falcigers first present from chaetiger 25 and completely replacing compound spinigers from chaetiger 28). Aciculae dark honey-coloured; distal end bluntly pointed; Chaetiger 1 with two aciculae, chaetigers 2–9 with three aciculae, chaetiger 10 with four aciculae, chaetigers 11–13 with three aciculae, 14–15 with four aciculae, 16–19 with three aciculae, 20–42 with two aciculae, from about parapodia 43, most parapodia with single acicula. Subacicular hooks (figure 17g) first present from parapodia 40 (24); always single. Colour light golden brown to black; distal end bidentate, small, distal tooth small erect, proximal tooth relatively large and directed obliquely or directly laterally.

Remarks. Cantone and Gravina (1991) did not mention or illustrate the presence of Mx-VI.

Euniphysa italica resembles *E. jeffreysii* in most features, the most obvious difference is that compound falcigers are present in *E. italica* and absent in *E. jeffreysii*.

Euniphysa jeffreysii (McIntosh, 1903)

(figure 18a–e)

Eunice jeffreysii McIntosh, 1903: 137–140.
Euniphysa jeffreysii: Miura, 1986: 312; Fauchald, 1992: 182.

Material examined. HOLOTYPE, BM(NH) ZK 1921, 5 January 1986. Tangiers Bay, Morocco, Atlantic, 35°50′N, 5°49′W, 30 fms, dredged, Porcupine 2 July 1870.

Comments on material examined. A. I. Muir, BM(NH) noted that the date must be in error, since Porcupine did not leave England until 4 July and was in Tangiers in early August of that year, the date of collection may have been 2 August, rather than 2 July.

Description. Holotype incomplete, with 63 chaetigers; total length 25 mm; maximum width 5 mm. Length through chaetiger 10, 5 mm. Maxillary apparatus strongly everted and whole anterior end vastly expanded. Chaetigers very short and crowded and body flattened, appearing in shape as one of larger species of *Marphysa*.

Prostomium (figure 18a) a flattened lobe, about half as wide as peristomium and limited to upper one-third of body depth. Anterior end of prostomium separated into two triangular projections. One pair of small black eyes present between palps and lateral antennae. Antennae and palps slender and irregularly wrinkled. Palps reaching middle of first peristomial ring; lateral antennae reaching chaetiger 5 and median antenna reaching chaetiger 10. Peristomium flaring anteriorly with lower lip scalloped; separated into two rings of which anterior ring five-sixths of total length of peristomium; separation well marked dorsally and ventrally and present, but indistinct laterally. Short peristomial cirri basally enlarged.

Jaws fully everted; with slender, sharply pointed teeth; generally horn-coloured.

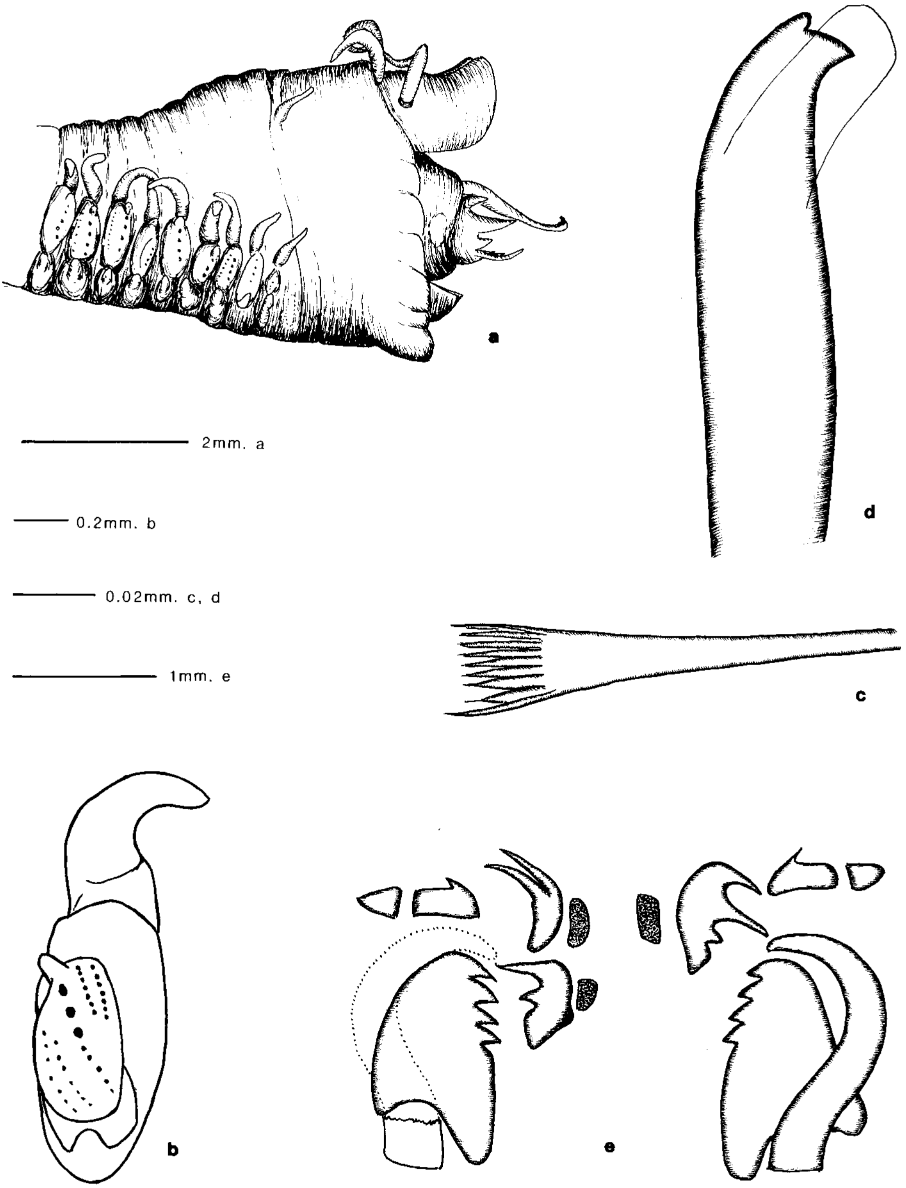

FIG. 18. *Euniphysa jeffreysii* (holotype, BM ZK 1921, 5.1.1986). (a) Anterior end, lateral view; (b) parapodium 4, lateral view; (c) pectinate chaetae; (d) subacicular hook; (e) maxillae.

Maxillary formula (figure 18e): 1 + 1, 4 + 4, 2 + 0, 2 + 3, 1 + 1, 1 + 1, and three black accessory plates. Mx-III very short.

Branchiae first present from chaetiger 28; most chaetigers with single branchial filaments, but some scattered chaetigers with two filaments. All branchial filaments digitiform.

Anterior parapodia distally very wide, obliquely truncate and with a small knob dorsal to emergence of aciculae; knob present through chaetiger 46. Pre- and postchaetal lobes low, transverse folds, postchaetal lobes very nearly as high as acicular lobe. By chaetiger 30 acicular lobes increasingly pointed and pre-and postchaetal lobes reduced to low, nearly basal folds. Notopodia pyriform in all chaetigers due to presence of sub-basal sensory organ. Sensory organ increasingly indistinct in posterior chaetigers. Ventral cirri thick and tapering in first few chaetigers, but becoming basally enormously enlarged from about chaetiger 5. Enlarged regions long, narrow ridges well set off from body wall ventrally and continued dorsally as a small, free tip. Enlarged condition of ventral cirri retained in all chaetigers present.

All chaetae, with exception of a few pectinate chaetae and subacicular hooks broken off. Multiple aciculae arranged in a dorso-ventral row in anterior parapodia; chaetigers 1–3 with two aciculae, 4–9 with three aciculae, 10–23 with three or four aciculae, 24–39 with two aciculae, later chaetigers all with single acicula. In anterior parapodia, two rows of chaetae in dorso-posterior bundle, three rows in ventro-anterior bundle (figure 18b). In one chaetiger, shaft of one compound chaeta retained; distally enlarged and marginally smooth. Pectinate chaetae (figure 18c) distally transverse with about ten teeth, one marginal tooth longer than others. Dark, horn-coloured subacicular hooks (figure 18d) present from chaetiger 49; bidentate with proximal tooth larger than distal one; flattened and a subdistal region expanded in relation to shaft and head; always single in remaining chaetigers in incomplete specimen.

Remarks. McIntosh (1903) described and illustrated exclusively compound spinigers for *E. jeffreysii*, but indicated that those of anterior and posterior ends had different shapes. Comparing his illustration of spinigers with the spinigers (both pseudocompound and compound) present in *E. spinea* and *E. italica*, we found that the anterior spinigers in *E. jeffreysii* are morphologically closer to pseudocompound rather than compound spinigers of these species in that the appendage is long, straight, sword-shaped and finely serrated; the pseudo-articulated region is not much wider than the rest of the shaft. The presence of pseudocompound spinigers can easily be overlooked and the chaetae were first described for *E. spinea* by Miura (1987). In earlier described species, such as *E. aculeata* Wesenberg-Lund, 1949, and *E. oculata* Wu, Sun and Chen 1979, the anterior pseudocompound spinigers were mis-interpreted as compound ones. We believe that in the anterior region of *E. jeffreysii*, the spinigers are pseudocompound rather than compound ones, based on the above considerations.

This species was transferred to *Euniphysa* by Miura (1986: 312). Shen and Wu (1991: 137–138) retained this species in *Eunice* on the grounds that it showed five pairs of 'serrated' rather than 'claw-shaped' maxillae. *Euniphysa jeffreysii* has six pairs of fang-like maxillae which resemble those of other species of *Euniphysa* closely.

Euniphysa megalodus (Grube, 1878)

Eunice megalodus Grube, 1878: 156–158, pl. 9, figure 5.
Euniphysa megalodus: Fauchald, 1992: 217.

Remarks. Grube had a single, posteriorly incomplete specimen consisting of 53 chaetigers being 35 mm in length, collected from Pandanon, Philippine Islands (11°45′N, 122°10′E). The specimen is no longer available. The following summary includes all that is known about the species.

The prostomial antennae are slender, long and lack articulations and reach beyond the peristomium; the median antenna is the longest. The peristomial cirri reach the front margin of the peristomium. The jaw structure appears to be unusual;

the maxillary formula appears to be 1 + 1, 3 + 3, 2 + 0, 2 + 3 and 1 + 1, perhaps with Mx-VI present in front of Mx-V. Three accessory plates present. Mx-III through Mx-V are well developed and have strongly falcate distal teeth as illustrated by Grube. Both the description and illustration of plate 9, figure 5 by Grube show that the right Mx-IV has three teeth of which the middle tooth is the longest; Mx-III has two teeth of which the distal tooth is much longer than the proximal one.

Branchiae are present from chaetiger 8; where best developed, at about chaetiger 24, they have nine slender filaments.

Chaetae include fascicles of compound spinigers and simple limbate chaetae. Aciculae are dark-coloured and the subacicular hooks appear to be bidentate.

Grube specifically mentioned that the notopodial cirri have enlarged bases equipped with rounded lower lobes.

The shape of the jaw-apparatus, the chaetae as described and the structure of the notopodial cirri are all features of the genus *Euniphysa*. The presence of the third accessory plate outside of Mx-III, the shape of right Mx-IV with the middle tooth the longest and the branchial distribution (starting from chaetiger 8) suggest that this species most closely resembles *E. spinea* and *E. filibranchia*. All three have been reported from the South China Sea or neighbouring waters.

The information available is not sufficient to distinguish the species from other species in this genus and is here considered indeterminable.

Euniphysa quadridentata n. sp.

(figures 3b, 19a–i, 20, 21)

Euniphysa sp. Gathof 1984: 40.29–40.30, figures 40–27, 28a–j.

Material examined. Holotype, USNM 090047, Sta. IV-2423, off Apalachicola River, Florida, MAFLA, Gulf of Mexico, 29°37′N, 84°17′W, 19 m, August 1984, collected for BLM. Paratypes, USNM 090045 (*n* = 1), USNM 090046 (*n* = 1), Gulf of Mexico; USNM 090048 (*n* = 1), USNM 090049 (*n* = 1), Sta. IV-3, MAFLA, off Port Isabel, Texas, STOCS, Gulf of Mexico, 26°10′N, 96°24′W, 91 m, November 1977, collected for BLM; USNM 090050 (*n* = 1), SOFLA; USNM 54713, Hutchinson Island, Florida.

Description. Holotype with 74 anterior chaetigers. First ten chaetigers 2.3 mm long, widest part (around chaetiger 5) 3.8 mm (with parapodia).

Prostomium (figure 19a) anteriorly bilobed, with deep sulcus dorsally; narrower than, less than half depth of, and almost same length as, peristomium. One pair of black reniform eyes situated lateral to lateral antennae. Palps and antennae nearly evenly distributed (palps and lateral antennae slightly closer to each other than lateral antennae to median antenna). Palpophores and ceratophores short and stout; palpostyles and ceratostyles long and slender without articulations. Palps more slender than antennae; reaching second ring of peristomium. Lateral antennae reaching chaetiger 4 and median antenna reaching chaetiger 7. First ring of peristomium about three-quarters (dorsally) or four-fifths (laterally) of total peristomial length. Peristomial cirri small, reaching three-quarters across first peristomial ring.

Maxillary formula (figure 19i): 1 + 1, 4 + 4, 2 + 0, 2 + 4, 1 + 1, 1 + 1. Two black accessory plates present on left and one on right side. Mx-III, Mx-IV and Mx-V with slender, sharp teeth. Formula identical in all seven specimens examined.

Branchiae first present from chaetiger 30; present on all remaining chaetigers (specimen incomplete, observed on right-hand side of specimen). Most branchiae

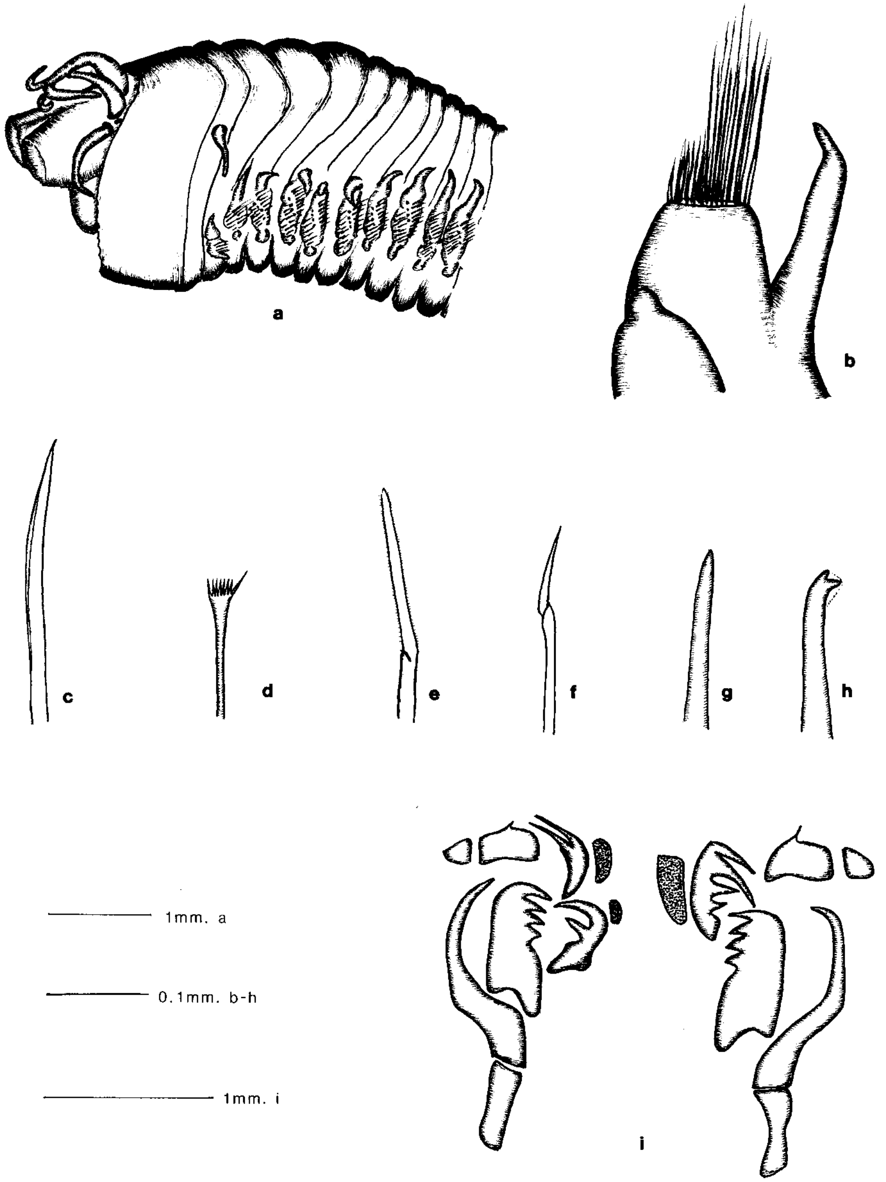

FIG. 19. *Euniphysa quadridentata* n. sp. (holotype, USNM 090047). (a) Anterior end; (b) parapodium 5; (c) limbate chaetae; (d) pectinate chaetae; (e) pseudocompound spiniger; (f) compound spiniger; (g) acicula; (h) subacicular hook; (i) maxillae.

with single filament, but on chaetiger 46 and from chaetiger 68 to end of specimens, two filaments observed. Initially filaments shorter than dorsal cirri, reaching approximately same length as dorsal cirri in last chaetigers present.

First three pairs of parapodia (especially first pair) smaller than following ones. A small fleshy knob present dorsal to aciculae. Dorsal cirri (figure 19b) long throughout remaining body. First ventral cirri large; becoming ventrally enlarged from chaetiger 2, but retaining a free triangular tip in all following chaetigers. Enlarged region best developed in median region, decreasing in size toward posterior end.

Dorso-posterior limbate chaetae (figure 19c) interspersed with pectinate chaetae (figure 19d) in one row (figure 19b). Limbate chaetae always serrated. Pectinate chaetae (observed as far anterior as chaetiger 6) with eight to 11 teeth, one marginal tooth much thicker and longer than other teeth. Antero-ventral pseudocompound spinigers (figure 19e) arranged in three rows (figure 19b) in anterior chaetigers, rows becoming indistinguishable at chaetiger 38, just anterior to start of subacicular hooks (chaetiger 39). Compound spinigers (figure 19f) starting three to four chaetigers anterior to start of subacicular hooks; co-occurring with pseudocompound spinigers on these three to four chaetigers; replacing pseudocompound ones completely on parapodia with subacicular hooks. Acicular colour (figures 19g, 20) varying from dark honey-coloured to black; present in multiples in first 32 chaetigers. Subacicular hooks (figure 19h) first present from chaetiger 39 in holotype; always single; colour varying from dark honey to black; distal end bidentate with small teeth. Distal tooth small and erect; proximal tooth relatively large and directed obliquely laterally. Compound falcigers absent.

Remarks. Some of the morphological features of *E. quadridentata* vary with specimen size (figures 4–7, 21, $n=7$). Starting position of branchiae varies from chaetigers 26–33 (branchiae are absent in a small 0.7 mm wide specimen, USNM 090049); The first occurrence of subacicular hooks varies from chaetigers 18–39. The last chaetiger with multiple aciculae varies from chaetigers 17–33; the first occurrence of compound spinigers varies from chaetiger 15–36; the last pseudocompound spiniger can be found in chaetigers 17–37. Note that the last four items occur within several neighbouring parapodia. *Euniphysa quadridentata* resembles *E. jeffreysii* in most features, the significant differences are that: the dorsal limbate chaetae of the anterior parapodia are arranged in one row in *E. quadridentata* but

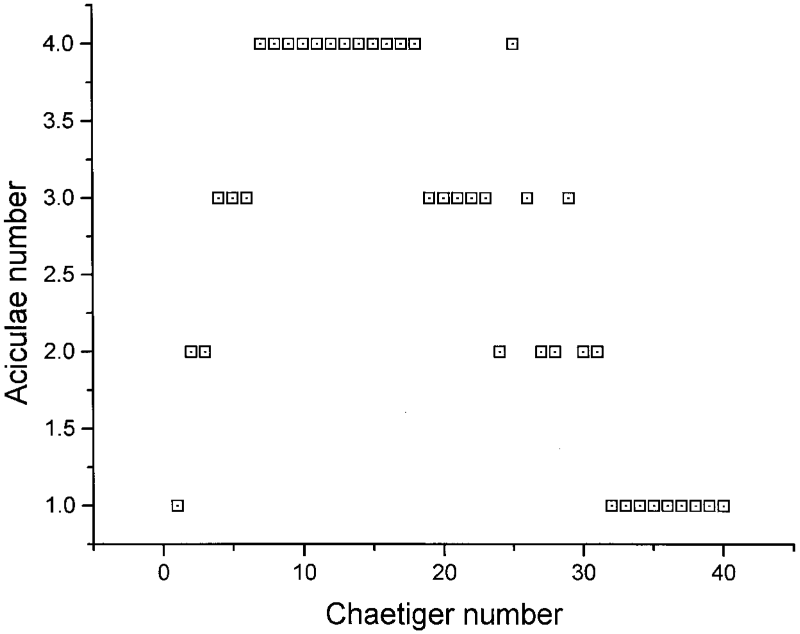

FIG. 20. The distribution pattern of acicula in the anterior 40 chaetigers of *Euniphysa quadridentata* n. sp. (USNM 090047).

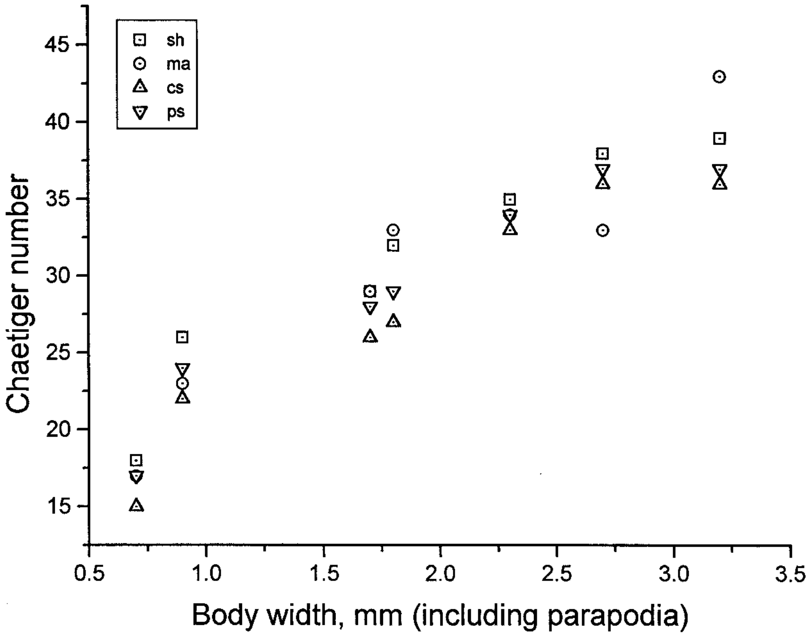

FIG. 21. The relationships between maximum body width (mm) and various chaetae positions in *Euniphysa quadridentata* n. sp. ($n=7$): sh = start position of subacicular hook, ma = last chaetiger with multiple acicula, cs = start position of compound spiniger, ps = ending position of pseudocompound spiniger.

in two rows in *E. jeffreysii*; the right Mx-IV has four teeth in *E. quadridentata* and three teeth in *E. jeffreysii* as in all other *Euniphysa* species known to date.

Etymology. This species is named for the presence of four teeth on right Mx-IV; all other species known in the genus have three.

Euniphysa spinea (Miura, 1977)
(figures 4–7, 16, 22a–k)

Eunice spinea Miura, 1977: 64-67, figure 2.
Euniphysa oculata Wu, Sun and Chen 1979: 89–92, figures 1, 2; new synonymy.
Euniphysa spinea: Miura, 1986: 312–315, figures 35–37.
Paraeuniphysa spinea: Shen and Wu, 1991: 136–138, figure 3.

Material examined. PARATYPES, USNM 400271 ($n=11$). USNM 100219 ($n=7$), Bungo Channel, Japan, Pacific Ocean, 33°06′N, 132°08′E, 89–91 m, September 1984, coll R. Yamamoto. N20513-36,

Type of Euniphysa oculata. Near Xisha Island, South China Sea, Cruise 101, area 9, Sta. 6187, 162 m, sand and mud, trawl, coll. Liu.

Comments on material examined. The specimen described in detail is from USNM 100219. The values inside parentheses are for the type of *E. oculata*.

Description. Specimen described incomplete, of unknown sex with 30 (37) chaetigers. Maximum width 1.75 (4) mm. Length through chaetiger 10, 2.9 (5) mm.

Anterior end (figure 22a) of body dorsally enlarged, ventrally flattened becoming dorso-ventrally flattened from about chaetiger 12. Frontal edge of prostomium apparently rounded; dorsal surface apparently excavate with thickened rim; median sulcus shallow. One pair small black eyes present posterior to bases of palps. Palps

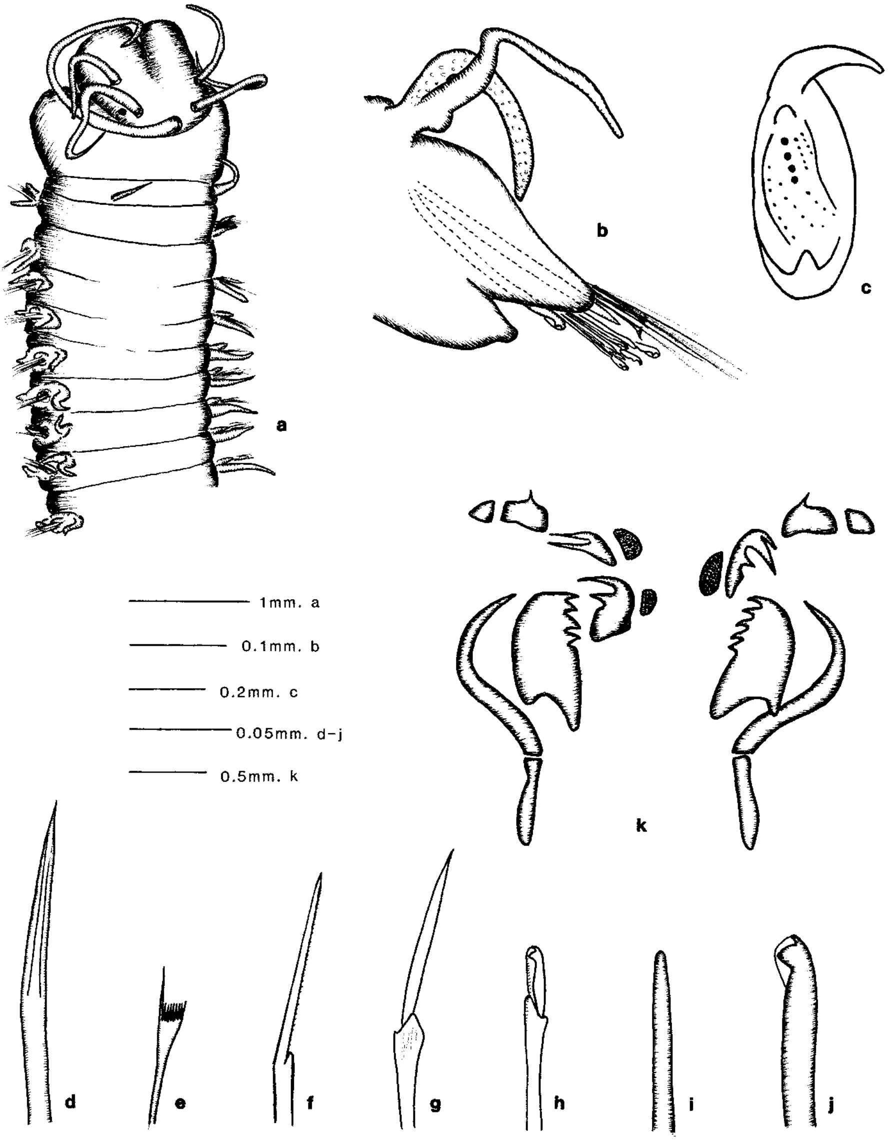

FIG. 22. *Euniphysa spinea* (paratype, USNM 100219, No.2). (a) Anterior end; (b) parapodium 24; (c) parapodium 4, lateral view; (d) simple chaetae; (e) pectinate chaetae; (f) pseudocompound spiniger; (g) compound spiniger; (h) compound falciger; (i) acicula; (j) subacicular hook; (k) maxillae.

and antennae in shallow horseshoe, evenly spaced; middle antenna slightly thicker than lateral antennae and palps. Palpophores and ceratophores ring-shaped and distinct. Palpostyles and ceratostyles slender, tapering to fine tips, without articulations. Palps reaching posterior end of first ring of peristomium; lateral antennae reaching chaetiger 3; middle antenna reaching chaetiger 9. Separation between peristomial rings distinct on all sides (forming a complete cincture). Anterior ring approximately four-fifths of total peristomial length on dorsal side. Peristomial cirri slender, tapering to very fine tips; without articulations; reaching anterior end of first ring.

Branchiae from chaetiger 10 (10) to end of fragment. Branchiae single; filament initially shorter, later slightly longer than dorsal cirri (in some specimens, branchial filaments always slightly longer than dorsal cirri).

Anterior acicular lobes distally obliquely rounded with aciculae emerging distinctly dorsal to mid-line. Prechaetal lobes low oblique folds; postchaetal lobes following outline of acicular lobes closely. Median acicular lobes broadly rounded with aciculae forming a conical projecting point; aciculae emerging in midline. Prechaetal lobes low, transverse folds; postchaetal lobes free, very nearly as high as acicular lobes; distally truncate with rounded corners. First four ventral cirri tapering from a wide base; triangular, slightly flattened; becoming basally enlarged from about chaetiger 5. Enlarged bases (figure 22b) thick, large transverse welts located entirely on ventral surface. Tips tapering, excavate on dorsal side to contain subacicular hooks.

All notopodia with distinct, light brown aciculae. Anterior notopodial cirri fusiform; tapering to slender tips. Median notopodial cirri similar in shape, but rather more slender, with the exception of rounded pendant tab near base. Pendant tabs distinct in all median chaetigers.

Limbate chaetae in two rows (figure 22c, d) on dorsal-posterior side of chaetal lobe in anterior chaetigers; each slender, with slightly geniculated shaft. Anterior pectinate chaetae not seen. Median pectinate chaetae (figure 22e) tapering or very gently flaring; with about nine teeth; one marginal tooth longer than other teeth. Serrated pseudocompound spinigers (figure 22f) arranged in three rows on anterior ventral side of chaetal lobe in anterior parapodia 1–20, such a pattern obscure from parapodia 21 (20) with presence of compound spinigers. Shafts of anterior compound spinigers slender, tapering; distal enlarged region absent; slight internal striation visible; appendage slender, gently tapering for most of length; distally abruptly tapering to slender tip. Shafts of median compound spinigers, distinctly enlarged (figure 22g); distal beak distinct; marginally hirsute; with distinct internal striations. Compound falciger (figure 22h) present from parapodia 25 (30), co-existing with compound spiniger in three chaetigers, completely replacing compound spinigers from parapodium 28; bidentate with hood. All aciculae (figure 22i) brown to very dark brown; tapering to straight, pointed or blunt tips; parapodia 1–2 with two aciculae, 3–7 with three aciculae, 8 with four aciculae, 9–18 with three aciculae, 19–26 with two aciculae, 27-end with single acicula. Both aciculae and subacicular hooks with coloured cores and clear sheaths. Subacicular hook (figure 22j) present from chaetiger 25 (27); single in all chaetigers present; small in relation to size of aciculae; bidentate with distinct guards. Proximal tooth larger than distal tooth; directed laterally, slightly uptilted distally. Distal tooth tapering, directed obliquely laterally, tapering.

Maxillary formula: $1+1$, $4+4$, $2+0$, $2+3$, $1+1$, $1+1$, plus three black accessory plates. Above formula is true for 12 out of 14 specimens examined; in two of the exceptions, Mx-II with five teeth (figure 22k). All teeth long, slender, tapering. Mx-VI smooth, without distinctive tooth.

Remarks. Certain morphological features of *E. spinea* are size-dependent (figures 4–7, 16): the first occurrence of subacicular hooks varies from parapodium 16 in a 0.5 mm-wide specimen to 27 in a 4 mm-wide specimen; the end position of multiple aciculae varies from parapodium 15 in a 0.8 mm-wide specimen to 33 in a

4 mm-wide specimen; the start position of compound spinigers varies from parapodia 11–21; the ending position of pseudocompound spiniger varies from parapodia 12–21; the start position of compound falciger varies from parapodia 13–30; the ending position of compound spiniger varies from parapodia 14–37. The last four items occur in several neighbouring chaetigers in each specimen.

Shen and Wu (1991) mentioned 'This species (*E. spinea*) is quite similar in its external form to *Euniphysa oculata...*', they also indicated that the main difference should be that *E. oculata* lacks pseudocompound spinigers and compound falcigers while *E. spinea* possesses them. After careful examination of the type specimen N20513-36 deposited in Institute of Oceanology, Academica Sinica in Qingdao, we find two features were not described accurately by Wu *et al.* (1979): spinigers in the anterior 20 chaetigers are pseudocompound rather than compound and compound falcigers are present, from chaetiger 30, rather than absent. *E. oculata* has exactly the same jaw structure (numbers of teeth, shape and position) as *E. spinea*. When other size-dependent features (figures 4–7, the largest specimen of *E. spinea* is the type of *E. oculata*), such as the first occurrence of subacicular hooks, the first occurrence of branchiae, the last occurrence of pseudocompound spinigers, and the first and last occurrence of compound spinigers, are considered, no significant difference between the two species can be identified. The specimen of *E. oculata* (5 mm wide) is larger than all the *E. spinea* specimens (less than 3 mm) available and what differences there are, match the kinds of size-related differences present within other species. Consequently, *E. oculata* is here considered a junior subjective synonym of *E. spinea*.

Euniphysa taiwanensis (Wu and He, 1988) n. comb.

Paraeuniphysa taiwanensis Wu and He, 1988: 123–126, figures 1–15.

Remarks. Despite several attempts to borrow, the type material has not been available for examination. The following is a summary of information in the description and illustrations given by Wu and He (1988).

The specimens were dredged from 162 m deep sandy and muddy bottom in the middle of Taiwan Strait of East China Sea.

Holotype incomplete, with 84 chaetigers; total length 34 mm; maximum width 2.6 mm. Prostomium frontally rounded, median sulcus shallow. Palps and antennae in a shallow horseshoe; palps and lateral antennae close to each other, separated by a distinct gap from middle antenna; similar in thickness. Palpophores and ceratophores distinct, short and ring-shaped. Palpostyles and ceratostyles, slender, tapering to very slender tips; without articulations. Palps reaching about chaetiger 3; lateral antennae reaching chaetiger 12–13 and middle antenna reaching chaetiger 20. No eyes.

Peristomium apparently flaring anteriorly. Anterior ring making up four-fifths of total peristomial length. Separation between rings apparently distinct on all sides. Peristomial cirri reaching middle of prostomium; slender, tapering, without articulations.

Maxillary formula $1+1$, $6+6$, $2+0$, $2+3$, $?+1$, $1+1$; two sclerotinized accessory plates. The missing illustration of Mx-III suggests that this piece may be reduced and located behind left Mx-II. Mandibles flat.

Branchiae first present from chaetiger 17 (18 in abstract), at first with short, stubby filaments; by chaetiger 73 with six long, slender filaments. Branchiae presumably continued to near the posterior end.

Anterior neuropodial acicular lobes appear conical; prechaetal lobes are low, rounded folds; postchaetal lobes not characterizable from illustration. Median and posterior neuropodial acicular lobes bluntly conical; pre- and postchaetal lobes not characterizable based on illustrations. Anterior chaetigers with ventral glandular tab until parapodium 30.

Limbate chaetae present dorsally in all parapodia. Pectinate chaetae present. Compound spinigers present from chaetiger 10; compound falcigers from chaetiger 25. Aciculae paired in anterior and median chaetigers; single in posterior chaetigers. Bidentate subacicular hooks present from chaetiger 31; each parapodium with three to four hooks.

Note that in the figure legends, the legends for figures 9, 10 and 11 have been reversed.

Of the 24 characters used in our phylogenetic analysis, Wu and He (1988) did not specifically describe the shape and the arrangement of the first several parapodia (character 11–18). Otherwise, in all remaining characters, even the three morphometric ones such as the distribution of subacicular hooks, enlarged bases of ventral cirri and branchiae, *E. taiwanensis* closely resembles (figures 4–6) *E. auriculata*. No known characters separate these two species. *Euniphysa taiwanensis* is not included in our analysis; clearly it is very similar to *E. auriculata* and probably has several anterior parapodia with ventral cirri emerging from the posterior face of the parapodia and dorso-posterior limbate chaetae arranged in one or more fascicles; finally we also anticipate that the left Mx-IV has a single fang-shaped tooth.

Euniphysa tridontesa (Shen and Wu, 1990) n. comb.
(figure 23a–i)

Heterophysa tridontesa Shen and Wu, 1990: 765–773, figure 4; Shen and Wu, 1991: 138–140, figure 4.

Material examined. Holotype, SSBT-0031, Xieyang Island, Beibu Bay, the South China Sea, 15 m, muddy sand.

Description. Specimen incomplete, with 65 anterior chaetigers. First ten chaetigers measure 2.3 mm, widest part measures 1.9 mm (with parapodia).

Prostomium anteriorly bilobed, with a deep dorsal sulcus. Prostomium distinctly narrower than peristomium and less than three-quarters depth, but nearly same length as peristomium. Eyes absent. Palps and antennae unevenly distributed with palps and lateral antennae emerging close to each other. Palpophores and ceratophores short and stout; palpostyles and ceratostyles long and smooth. Palps reaching first ring of peristomium; lateral antennae reaching chaetiger 5 and median antenna broken (reaching chaetiger 8 according to Shen, 1990). First ring of peristomium about three-quarters (dorsally) or five-sixths (laterally) of total peristomial length. Peristomial cirri reaching anterior end of first ring.

Maxillary formula (figure 23i): 3 + 3, 5 + 5, 2 + 0, 1 + 3, 1 + 1, 1 + 1; two black accessory plates present. Mx-I with three sharp teeth. Most teeth fang-like.

Branchiae first present from chaetiger 8; present in all remaining chaetigers; chaetigers 8–10 with two filaments; chaetigers 11–13 with three filaments; chaetiger 14 with four filaments; up to six filaments on chaetiger 60. Filament slightly longer than dorsal cirri.

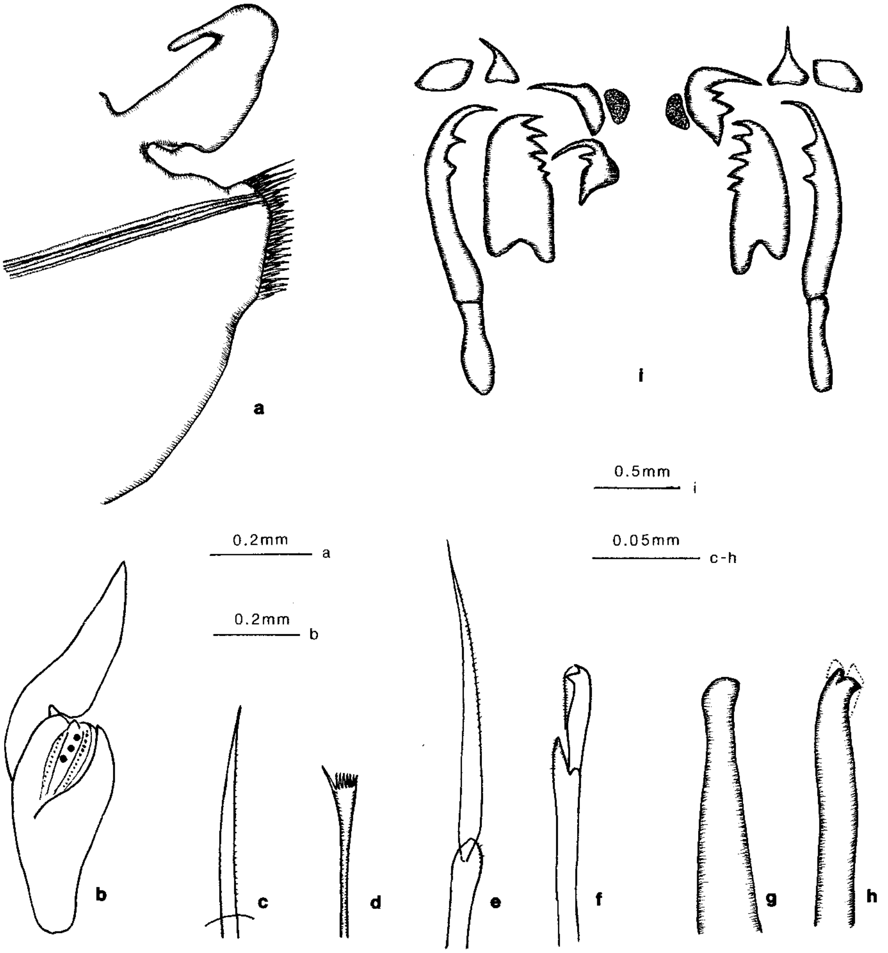

FIG. 23. *Eunice tridontesa* (paratype, SSBT-0031). (a) Parapodium 5; (b) parapodium 4, lateral view; (c) simple chaetae; (d) pectinate chaetae; (e) compound spiniger; (f) compound falciger; (g) acicula; (h) subacicular hook; (i) maxillae.

First parapodium with bilobed acicular lobe; superior section slightly longer than inferior section. Both pre- and postchaetal lobes low, transverse folds. Acicular lobes obliquely truncate; with distinctive superior free tab in anterior chaetiger; ventral cirri emerging from posterior face of parapodia and completely fused to the acicular lobe (as if missing) in parapodia 1–6 (figure 23a, b); re-emerging as short, conical free cirrus from chaetiger 7. Lower edge of parapodia with increasingly glandular enlarged region from chaetiger 7, presumably representing completely incorporated bases of ventral cirri. Enlarged region reduced from about chaetiger 16 and totally missing posterior to chaetiger 21; free cirrus retained in all chaetigers present. All notopodial cirri tapering to slender tips; articulations absent. First several notopodia with distinct narrow base; enlarged in lower one-third and tapering to slender tip; supported by four slender aciculae. Notopodial cirri posterior to chaetiger 7 with distinct basal enlarged sensory region on ventral side.

Finely serrated limbate chaetae (figure 23c) arranged in two fascicles around acicular lobe in chaetigers 1–6; dorso-posterior chaetae longer than others which are barely emerging out of chaetal fold. From chaetiger 7 long limbate dorso-posterior chaetae present in two rows; all ventro-anterior chaetae compound spinigers (figure 23e) arranged in three or four rows; pattern becoming obscure by chaetiger 13. Compound falcigers (figure 23f) co-occurring with compound spinigers from chaetiger 21; numbers increasing from one to several toward posterior chaetigers. Pectinate chaetae (figure 23d) with seven to eight teeth, one marginal tooth longer than others. Acicula (figure 23g) darkly honey-coloured; blunt tipped anteriorly becoming hammer-headed from chaetiger 10; parapodium 1 with two aciculae, parapodia 14–37 with three aciculae, parapodium 7 with four aciculae, parapodia 8–24 with two to three aciculae, from chaetiger 25 all parapodia with single acicula. Bidentate, subacicular hooks (figure 23h) first present from chaetiger 19; each darkly honey-coloured; chaetigers 19–22 with single hook, chaetigers 23–27 with two hooks, chaetigers 28–30 with four hooks, chaetigers 31–37 with three hooks, chaetigers 38–43 with two hooks, from chaetiger 44 each parapodium with a single hook.

Remarks. Our description of the holotype differs from that of Shen and Wu's (1991) in the following features: ventral cirri emerging from posterior face of parapodium and fused to the parapodium from chaetiger 1 rather than from chaetiger 2; branchiae present from chaetiger 8 rather than 20; ventral cirri with distinct tip from chaetiger 7 to the end of the fragment rather than being absent from chaetiger 31; it does become smaller and lacks the basal enlarged region from chaetiger 21. The small paired eye-spots described by Shen and Wu (1991) were not seen by us probably due to degradation of eye pigment by alcohol.

The presence of three teeth on Mx-I has never been seen in any adult eunicid as far as we know (pers. obs.).

Species previously referable to *Euniphysa*

Eunice impexa Grube, 1878

Eunice impexa Grube, 1878: 159–160, pl. 9, figure 6; Fauchald, 1992: 174–176, figure 57a–m, tables 52, 53.

Remarks. This species agrees with members of *Euniphysa* in that the compound chaetae include both spinigers and falcigers, but is here retained as a member of *Eunice* based on the following characters. The maxillae have short, triangular teeth, not the long pointed teeth present in *Euniphysa*. The occipital antennae are relatively short, without the slender tips characteristic of members of *Euniphysa* and are distinctly articulated, rather than smooth.

The species is included in this overview, because of its close resemblance to *Eunice tubifex*, a species that was transferred to *Euniphysa* by Miura (1986).

Eunice misakiensis (Miura, 1987) n. comb.

Euniphysa misakiensis Miura, 1987: 6–9, figures 4, 5.

Remarks. *Euniphysa misakiensis* does not belong to *Euniphysa* as here defined, but is a member of the genus *Eunice* related to *E. tubifex* and *E. impexa* in that it combines the presence of compound spinigers and falcigers with the jaws characteristic of a member of the genus *Eunice*. Mx-III is long and located directly behind left Mx-II (Miura, 1987, figure 4n) and the teeth are short and blunt, rather than fang-like as in members of *Euniphysa*.

Eunice tubicola (Treadwell, 1921)

Leodice tubicola Treadwell, 1921: 139–142, figures 17–23, pl. 3, figures 1–6.
Eunice tubicola: Fauchald, 1992: 325–327, figure 11, tables 52, 53; Shen and Wu, 1990: 770.
Euniphysa tubicola: Miura, 1986: 312–313.

Remarks. This species has short palps and antennae; it has short, molar-like teeth as in common species of *Eunice*; the sensory organ associated with the notopodial cirri characteristic of *Eunice* is developed, but rather than being the large structure present in species of *Euniphysa*. Shen and Wu (1990) suggested that this species should be retained in *Eunice* based on jaw structure and this is in agreement with our concept of the two genera. Consequently, the transfer of the species to *Euniphysa* proposed by Miura (1986) is not accepted.

Eunice tubifex Crossland, 1904

Eunice tubifex Crossland, 1904: 303–310, figures 52–55, pl. 21, figures 1–8; Fauchald, 1992: 327–329, figure 112, tables 52, 53; Shen and Wu, 1990: 770.
Euniphysa tubifex: Miura, 1986: 312–313.

Remarks. This species has short, stubby occipital antennae; the teeth on Mx-IV and V are short, and molar-like; Mx-III is long and has seven teeth. In *Euniphysa*; antennae are long and tapering; teeth on the anterior jaw-pieces are slender and fang-like; Mx-III has two teeth. Shen and Wu (1990) suggested that this species should be retained in *Eunice* based on jaw structure; we agree. Consequently, the transfer of the species to *Euniphysa* proposed by Miura (1986) is not accepted here.

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Appendix A

The data matrix for *Euniphysa*, which includes 10 taxa and 24 characters. '?' = species level polymorphism; '–' = inapplicable entry; '≠' = shared absence, each is treated as unique character state in calculation.

Taxon	Characters
Outgroup	0000000000000—000000000
jeffreysii	0111111000100—000111112
quadridentata	0111211000100—100111112
italica	011?111000100—000101112
spinea	0111111000100—000101020
filibranchia	0111111000100—000101040
auriculata	111112201 ≠ 11110110200021
falciseta	111112201 ≠ 11120110200021
tridontesa	111112211 ≠ 10131111200230
aculeata	111112211 ≠ 10111111110021