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Generic Revision and Relationships of the Family Onuphidae (Annelida: Polychaeta)

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ABSTRACT. The general morphology, reproduction and development of the family Onuphidae are reviewed and supplemented with new observations, emphasizing ontogenetic changes. The following features were found to be associated with the juvenile state: distinctive colour pattern, ceratophores of antennae with few rings, absence of frontal palps and tentacular cirri, presence of eyes, smaller number of modified setigers, lesser developed branchiae, early occurrence of subacicular hooks, presence of compound falcigers in anterior and far posterior setigers.

Five new genera are described, bringing the number of recognized genera in the family to 22. A key, diagnoses and illustrated definitions to all genera are given.

The relationships within the family are analyzed using morphological, ecological and life history characters. Two subfamilies: Hyalinoeciinae, n. subf., and Onuphinae are erected. The two subfamilies differ in the presence or absence of notosetae, position of subacicular hooks and lower limbate setae, number of anal cirri, primary envelope of oocytes and arrangement of their nurse cells. Two groups of genera are recognized in each subfamily. The Hyalinoeciinae includes the *Nothria* group (consisting of *Nothria* and *Anchinothria,* n. gen.) and the *Hyalinoecia* group (consisting of *Hyalinoecia; Leptoecia; Neonuphis; Hyalospinifera).* The Onuphinae includes the *Diopatra* group (consisting of *Notonuphis; Paradiopatra; Diopatra; Epidiopatra; Brevibrachium,* n. gen.; *Longibrachium,* n. gen.; *Rhamphobrachium; Americonuphis)* and the *Onuphis* group (consisting of *Australonuphis; Hartmanonuphis,* n. gen.; *Hirsutonuphis,* n. gen.; *Aponuphis; Kinbergonuphis; Mooreonuphis; Onuphis; Heptaceras).*

It is hypothesized that the Onuphidae have a southern centre of origin and radiated from epifaunal habitats to world-wide distributions from the shallowest to the deepest depths.

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CONTENTS

Members of the family Onuphidae (order Eunicida) are mostly tubicolous, range from a few centimetres to the longest polychaetes ever reported (3 metres) and occur in all oceans from intertidal to the deepest depths. Onuphids used to be considered as predominantly deep-water species (McIntosh, 1910) that lived permanently in rather sturdy tubes (Pettibone, 1963). However, many shallow water species with fragile tubes are now known (Fauchald, 1980). A number of species, some of large size with very fragile, temporary tubes occur in sandy beaches, predominantly in the southern oceans. The largest of these, species of *Australonuphis,* occur in Central and South America and in eastern Australia. They are known as 'beachworms' in Australia and are highly sought after for fishing bait, collected from surf beaches during low tides by amateurs and professional collectors. The study of these beachworms (Paxton, 1979) has led to the present revision of the family.

Order Eunicida. The order Eunicida includes seven of the 81 extant families of polychaetes (Fauchald, 1977) and eight of the extinct families (Kielan-Jaworowska, 1966). Members of the order share the possession of a ventral eversible pharynx with a complex jaw apparatus consisting of ventral mandibles and dorsal maxillae. The jaws are composed, to a large extent, of calcium and magnesium carbonates and, to a smaller extent, of sclerotized proteins (Jeuniaux, 1975). The jaw apparatus is an autapomorphic feature, marking the Eunicida as a monophyletic group. Although a number of other polychaete families have jaws (see Wolf, 1976), their chemical composition differs markedly from that of the Eunicida, suggesting that the Eunicida represent a "phylogenetic line distinct from that of other 'errant' predacious polychaetes" (Voss-Foucart *et al.,* 1973).

The jaw apparatuses of Eunicida consist of four types: Placognatha (Kielan-Jaworowska, 1966), Ctenognatha (Kielan-Jaworowska, 1966), Prionognatha (Ehlers, 1868) and Labidognatha (Ehlers, 1868). The former two types are characterized by having rows of maxillae with gaping basal cavities. The placognath type is extinct, while the ctenognath type is represented by one extant family, the Dorvilleidae. Prionognatha and Labidognatha have fewer maxillae with much reduced basal cavities. The two halves of the prionognath type maxillae are more or less symmetrical and arranged in parallel rows; extant families are the Arabellidae and Lysaretidae. The labidognath type maxillae are asymmetrical and so arranged as to form a semicircle in the retracted state; extant families are the Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae, Eunicidae and Onuphidae.

The Eunicida has been treated as a family (Ehlers, 1868; Fauvel, 1923; Day, 1967), superfamily (Kinberg, 1865; Hartman, 1944; Fauchald, 1970) or order (Dales, 1962; Fauchald, 1977); the last mentioned is followed in this paper. Historical reviews of the taxonomic studies on the Eunicida can be found in McIntosh (1910) and Hartman (1944). The phylogeny of the fossil Eunicida has been discussed by Kielan-Jaworowska (1966). She concluded that the placognath and ctenognath maxillae, which were well established by the Ordovician, were the most primitive types. She stated that Recent prionognath families could be derived from several extinct prionognath families, while the Recent labidognath families—Eunicidae, Onuphidae and possibly Lumbrineridae—arose from the Palaeozoic Paulinitidae. The relationships between the extant families have never been elaborated. However, the similarity between larval onuphid and eunicid maxillae and adult dorvilleid maxillae has been interpreted as an indication of the ancestral position of the Dorvilleidae (Monro, 1924).

Family Onuphidae. The family Onuphidae was erected by Kinberg (1865) as 'Onuphiaea' and has remained unchanged, although it was treated as a subfamily by several authors (McIntosh, 1910; Fauvel, 1923; Day, 1963). Kinberg erected the family for those members of his superfamily Eunicea with 7 maxillae, 5 tentacles, 2 antennae, 2 palps and a single buccal segment, to contain the genera *Onuphis* and *Diopatra.* The number of genera increased rapidly to a dozen by 1919. This number remained the same for more than 50 years, with most authors accepting only eight to ten (e.g. Hartman, 1944, 1945; Day, 1967).

The characters employed for generic separation were presence or absence of tentacular cirri, presence or absence of branchiae, and the structure of branchial filaments when present. The modification of the anterior parapodia and their specialized setae were generally not used as characters, except for *Rhamphobrachium* Ehlers, 1887.

About 220 species have been described; most of these have been in the genera *Onuphis* and *Nothria,* which contained 60 and 40 species respectively as accepted by Fauchald (1977). The division between *Onuphis* and *Nothria* on the basis of their branchial structure (*sensu* Hartman, 1944) was presumed artificial (Fauchald, 1968) but was retained for convenience. The unsatisfactory state of the generic classification was expressed repeatedly (e.g. Hartman, 1944; Pettibone, 1970).

A new phase of revisionary work started in the 1970's with redefinitions of *Nothria* and *Paradiopatra* by Pettibone (1970). New genera were described by Fauchald (1973), Orensanz (1974) and Hartmann-Schröder (1975). The most extensive revisions were carried out by Kucheruk (1978) and Fauchald (1982a). Kucheruk remarked on the unsatisfactory characters of earlier definitions and included the setae and nature of the tubes to arrive at a more natural classification. He described three new genera and gave definitions and a key to all genera. He remarked on the polyphyletic nature of the genus *Onuphis,* but did not attempt to subdivide it. Fauchald (1982a) revised the genera *Onuphis, Nothria* and *Paradiopatra* based on type material. By using the structure and length of antennae and putting more emphasis on setal structures, he redefined *Onuphis* and described three new genera (*Kinbergonuphis, Mooreonuphis, Sarsonuphis*), bringing the number of nominal genera to 24.

Cladistic analyses, although uncommon in polychaete studies, have been carried out to establish intrageneric (Westheide, 1977) and intergeneric relationships (Westheide, 1982; Westheide & Riser, 1983; ten Hove, 1984). Fauchald (1982a) used cladistic techniques to arrange the onuphids studied by him in patterns suggesting relationships within and between the genera examined, but the relationships between all genera of the family Onuphidae have never been examined.

The aim of the present study is to carry out a generic revision of the family Onuphidae. The study has three main objectives: (1) to provide an account of the comparative morphology and ontogenetic changes of the family; (2) to define the taxa on a wider range of characters; and (3) to elucidate the phylogenetic relationships within the family.

MATERIALS AND METHODS

This study is based mainly on museum collections. The material examined consists of type species (whenever possible), Australian species, and selected species from other geographic areas. Abbreviated collection data for the material examined is listed with the respective genera, except for *Brevibrachium, Longibrachium* and *Rhamphobrachium*. Full collection data for these genera are given together with species descriptions in Paxton (1986).

The order of taxa is according to the classification recognized in this study. Body length (measurements and numbers of setigers) of incomplete specimens are followed by plus signs, width is of setiger 10 without parapodia. All drawings were prepared with the aid of a camera lucida.

Scanning electron microscopy (SEM) examination was carried out on specimens originally fixed in formol saline. Specimens were dehydrated in a graded ethanol series, dried in a Sorvall critical point dryer using liquid CO_2, and gold coated in a Polaron sputter coating system. They were photographed in a JSM-T20 using a Robinson backscattered electron detector.

The observed ontogenetic changes of *Rhamphobrachium* Ehlers, 1887 are based on 20 specimens of *R. ehlersi* Monro, 1930, and 29 specimens of *R.* sp. The length for each *R. ehlersi* stage is based on a single complete specimen (except stage 4 where no complete specimens were available), while the width is based on several incomplete specimens.

Taxonomic account. Differential diagnoses and definitions are given for all taxa. The species recognized as members of a genus are listed under 'remarks'. This information is provided for most genera, except those in need of revision, and is based on the literature and examination of specimens. The species listed include a number of new species from Australia which will be described in a forthcoming paper (Paxton, in preparation).

All keys are artificial and for adults only. A key to genera is given, as well as keys to species for a number of genera of particular interest to the author. Reference is made to recently published keys for other genera. However, no keys are available for a number of genera which are in need of revision.

Phylogenetic relationships. A brief outline of the theory and terminology of cladistic analysis, and its application to polychaetes can be found in ten Hove (1984).

The character states were determined by fossil evidence from the literature, ontogenetic changes observed in this study, and outgroup comparison. The outgroup comparison was based on examination of species of Eunicidae (listed below) and information from the literature: *Eunice aphroditois* (Pallas, 1788)—**Australia:** New South Wales—2 (AM W.1765-6) and others. *E. australis* Quatrefages, 1865—**Australia:** Western Australia—1 (AM W.5642). *E. tubifex* Crossland, 1904—**Australia:** New South Wales—1 (AM W.3528); **New Caledonia**—1 (AM W.198980). *Marphysa sanguinea* (Montagu, 1815)—**Australia:** New South Wales—2 (AM W.4881) and others. *Nematonereis unicornis* (Grube, 1840)—**Australia:** Queensland—2 (AM W.199003) and others.

A Wagner tree was constructed using a programme by George McKay (MU) modified from Farris (1970). Autapomorphies were included in the analysis to define endbranches; a hypothetical, all-primitive ancestor was included.

Abbreviations

AHF	Allan Hancock Foundation, Los Angeles, Calif., U.S.A.
AM	Australian Museum, Sydney, NSW, Australia
BMNH	British Museum (Natural History), London, U.K.
CM	Canterbury Museum, Christchurch, New Zealand
MU	Macquarie University, North Ryde, NSW, Australia
MCZ	Museum of Comparative Zoology, Cambridge, Mass., U.S.A.
MNHP	Museum National d'Histoire Naturelle, Paris, France
NMV	Museum of Victoria, Melbourne, Vic., Australia
NMW	Naturhistorisches Museum Wien, Austria
NZOI	New Zealand Oceanographic Institute, Wellington, New Zealand
PML	Portobello Marine Laboratory, Portobello, New Zealand
QM	Queensland Museum, Brisbane, Qld, Australia
RNH	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
UC	University of Canterbury, Christchurch, New Zealand
UNC	University of North Carolina, Chapel Hill, N.C., U.S.A.
UNH	University of Hawaii, Honolulu, Hawaii, U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
UT	University of Tromsö, Tromsö, Norway
WAM	Western Australian Museum, Perth, WA, Australia
ZMB	Zoologisches Museum, Berlin, E. Germany
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg, W. Germany
ZMO	Zoologisk Museum, Oslo, Norway

GENERAL MORPHOLOGY

Some notes on the general morphology of onuphids can be found in most polychaete treatises and onuphid revisions. The aim of this section is to bring the information together, to supplement it with new observations, and to detail the characters utilized in the taxonomic accounts below. The general characters of Onuphidae are discussed and illustrated with reference to one of the earliest described and best known species, *Onuphis eremita* Audouin & Milne Edwards, 1833 (Figs 3, 6–8, 10) and other species examined in this study.

Colour patterns. While pigments are usually lost through preservation, onuphids often have a dark brown pigmentation that remains. The patterns are prominent in shallow-water forms, where they may consist of a pigmented peristomium and dorsal bands on the anterior segments (Fig. 34m).

Body shape. The anterior part of the body is generally cylindrical due to accommodation of the eversible pharynx (Fig. 1). Fauchald (1982a) stated that the median and posterior parts have one of three different body shapes: (1) slight dorsal flattening, almost circular in transverse section; (2) strong dorsal flattening, semicircular in transverse section; (3) convex dorsal and ventral surface, oval in transverse section. He related (1) and (2) to the development of branchiae and stated that species of (1) have poorly developed branchiae and fit closely into their tubes, while those of (2) have well developed branchiae. This categorization appears justified as far as permanent tube dwellers are involved. Animals of (1) need little space to aerate their branchiae (*Onuphis holobranchiata,* Fig. 2a), while animals of (2) need more space to use their branchiae efficiently (*Diopatra aciculata,* Fig. 2b). However, it may be a function of size since animals of (1) are generally smaller than those of (2). Many shallow-water species with fragile temporary tubes live in sandy beaches and have been termed beachworms (Paxton, 1979). Although these species have well developed branchiae, some are of (1) (*Onuphis eremita,* Fig. 2c), others of (2) (*Hirsutonuphis mariahirsuta,* Fig. 2d). Beachworms have very well developed longitudinal muscles, particularly the ventral bundle.

Species of *Nothria* (Fig. 2e) and allied forms with flattened tubes were considered as group (3) by Fauchald. The species examined in this study are more or less oval in transverse section; however, their ventral surface is not convex but flat. Their longitudinal muscles are extremely reduced.

The type of body shape may not only be related to the branchial development but also to the size of the animal, its mode of living (tubicolous or burrowing) and associated specializations (e.g. muscular development).

Prostomium

The prostomium is oval to rounded, usually wider than long. Anteriorly it can be smoothly rounded (Fig. 27a), slightly incised (Fig. 34a), or extended (Fig. 3b). The prostomial appendages consist of five dorsal antennae and a pair of frontal and ventral labial palps each.

Antennae. The antennae have been termed 'occipital tentacles' (Hartman, 1944; Fauchald, 1968) or 'occipital antennae' (Day, 1960; Fauchald, 1982a). Since they are the only antennae, the term occipital is redundant. The individual antennae have been referred to as 'paired outer and inner lateral' and 'median unpaired' (Hartman, 1944; Fauchald, 1968; 1982a). The term 'outer lateral' is misleading since their position is more often anterior (e.g. *Onuphis*) rather than lateral (e.g. *Rhamphobrachium*) to the second pair. It is preferable to refer to the five antennae as (1) pair of anterior lateral, (2) pair of posterior lateral and (3) single median.

The antennae often form a crescent over the posterior half of the prostomium; in *Rhamphobrachium* and *Paradiopatra* this crescent has shifted more anteriorly. Fauchald (1982a) noted that in most *Nothria* and *Paradiopatra* (=*Anchinothria*) the two anterior antennae are in a more anterior and median position and form a circle with the frontal palps when viewed from the dorsal side. This arrangement is not limited to these two genera, but occurs in most. Sometimes the anterior antennae are placed so far forward as to be in a ventral position (Fig. 30b). In the shallow-water genera the antennae are very thick, almost covering the dorsal part of the prostomium. While in most genera the median antenna is the most posteriorly placed, in *Heptaceras* (Fig. 36a) the median antenna has moved anteriorly and is placed centrally among the five.

The antennae consist of proximal ceratophores and distal styles. Although CERATOPHORES may be smooth in small species, they usually have circular constrictions, giving them an annulated or ringed appearance. The constrictions usually terminate subdistally, so that the terminal ring is several times as long as the others. The ceratophores range from short (2–3 rings) to very long (more than 30 rings). While the former are shorter than the prostomium, the latter are several times its length. The number of rings is reasonably constant (± 5) in most genera. Some small species of *Onuphis, Epidiopatra* and *Diopatra* have relatively few rings (5–10) while most have 15–20. The greatest variation is found in *Heptaceras,* where the number ranges from 20–60.

Some species of *Diopatra, Epidiopatra* and *Paradiopatra* have lateral projections on the ceratophores of the posterior lateral and median antennae (Fig. 24k) which Day (1960) considered as branching. These are limited to small species and may represent a neotenic condition.

The STYLES range from short (Fig. 30c) to moderately long (Fig. 3a) to very long (*Hyalinoecia*). The anterior lateral pair is the shortest, sometimes shorter than its ceratophore (Fig. 3a). The posterior lateral styles may be equal, shorter or longer than the median one. While the overall length of styles is relatively constant for some genera, in others there is considerable variation.

The styles are covered by combined sensory/secretory structures referred to as 'Sinnesknospen' or sensory buds by Pflugfelder (1929). He described their histology for *Diopatra* sp., showing that cilia project through the cuticle from a central sensory cell and that the ciliated cell is accompanied by one or two serous glands opening to the surface. SEM photomicrographs show that the sensory buds, although at times very inconspicuous, are present in all species of Eunicidae and Onuphidae examined. In most genera they are irregularly scattered (Fig. 4a,b), while in species of *Diopatra* the sensory buds are arranged in rows (Fig. 4c,d). The serous glands and their openings can be more numerous than in the species examined by Pflugfelder and are present as a semicircle

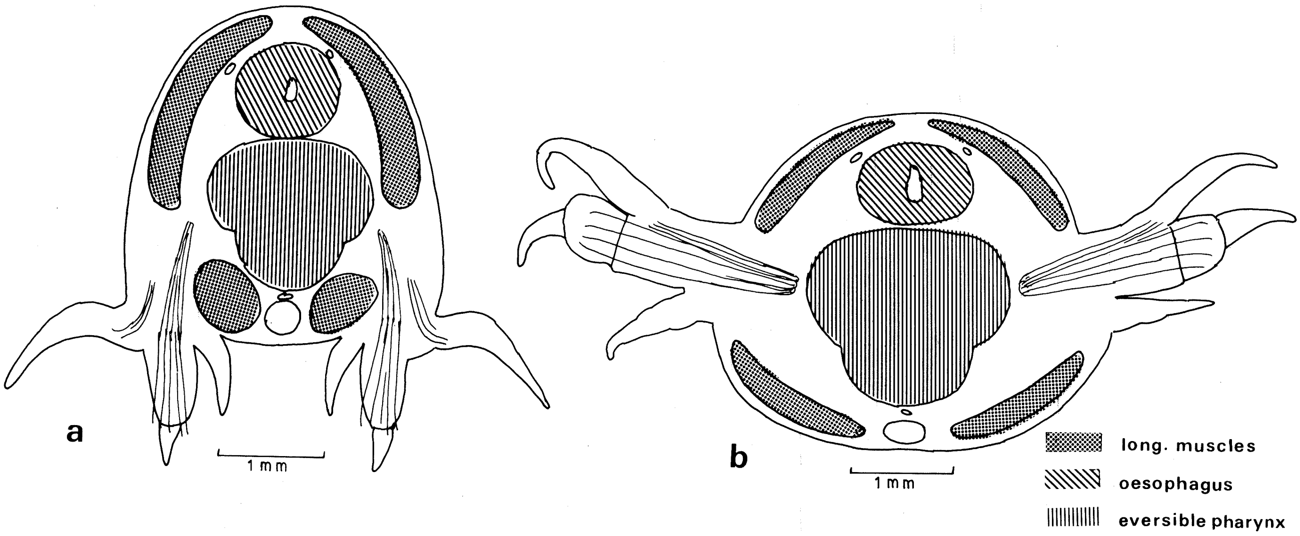


Fig. 1. Transverse sections through proboscideal region: **a,** *Diopatra* n. sp. 2, setiger 4; **b,** *Australonuphis teres,* setiger 3.

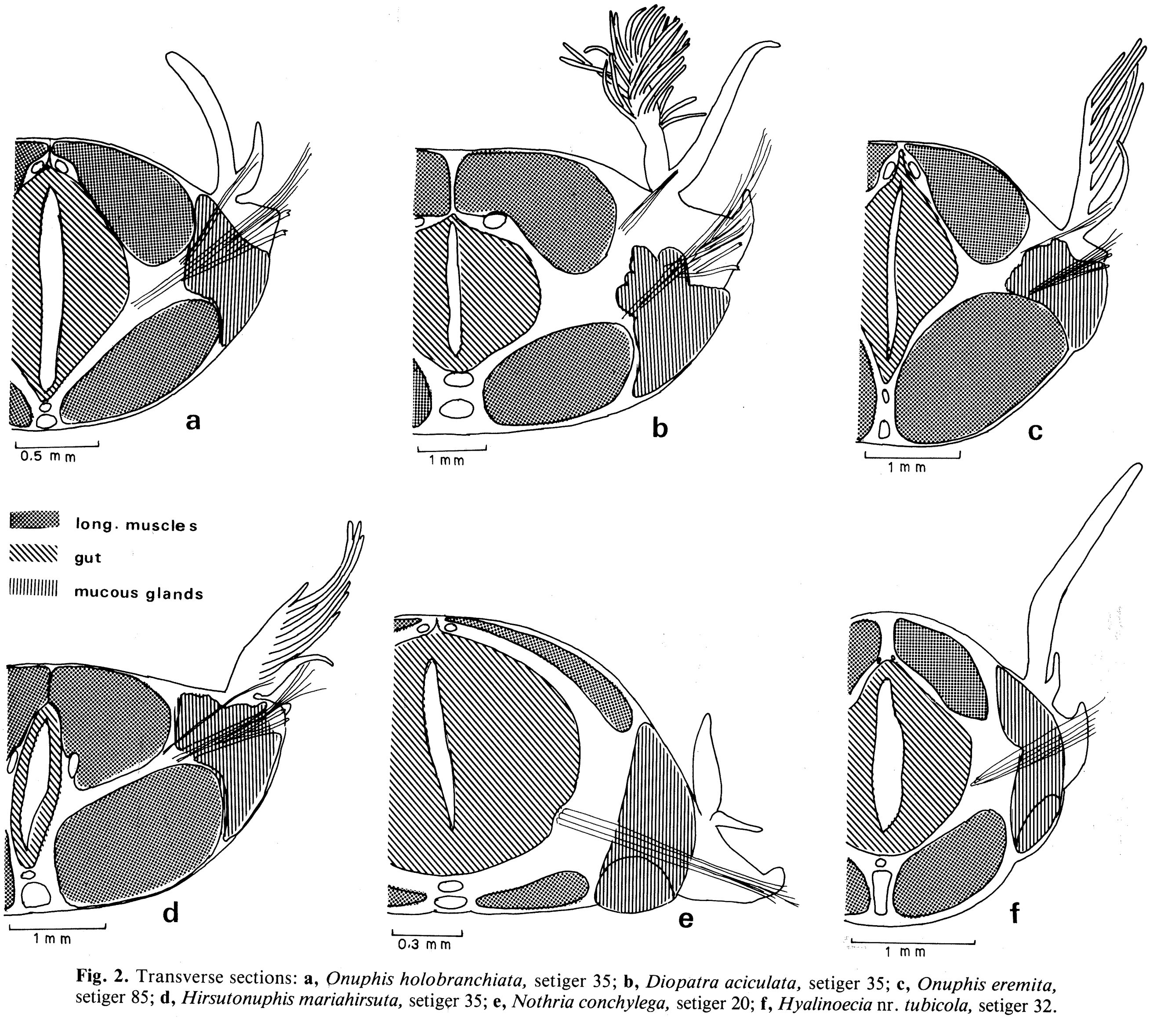


Fig. 2. Transverse sections: **a,** *Onuphis holobranchiata,* setiger 35; **b,** *Diopatra aciculata,* setiger 35; **c,** *Onuphis eremita,* setiger 85; **d,** *Hirsutonuphis mariahirsuta,* setiger 35; **e,** *Nothria conchylega,* setiger 20; **f,** *Hyalinoecia* nr. *tubicola,* setiger 32.

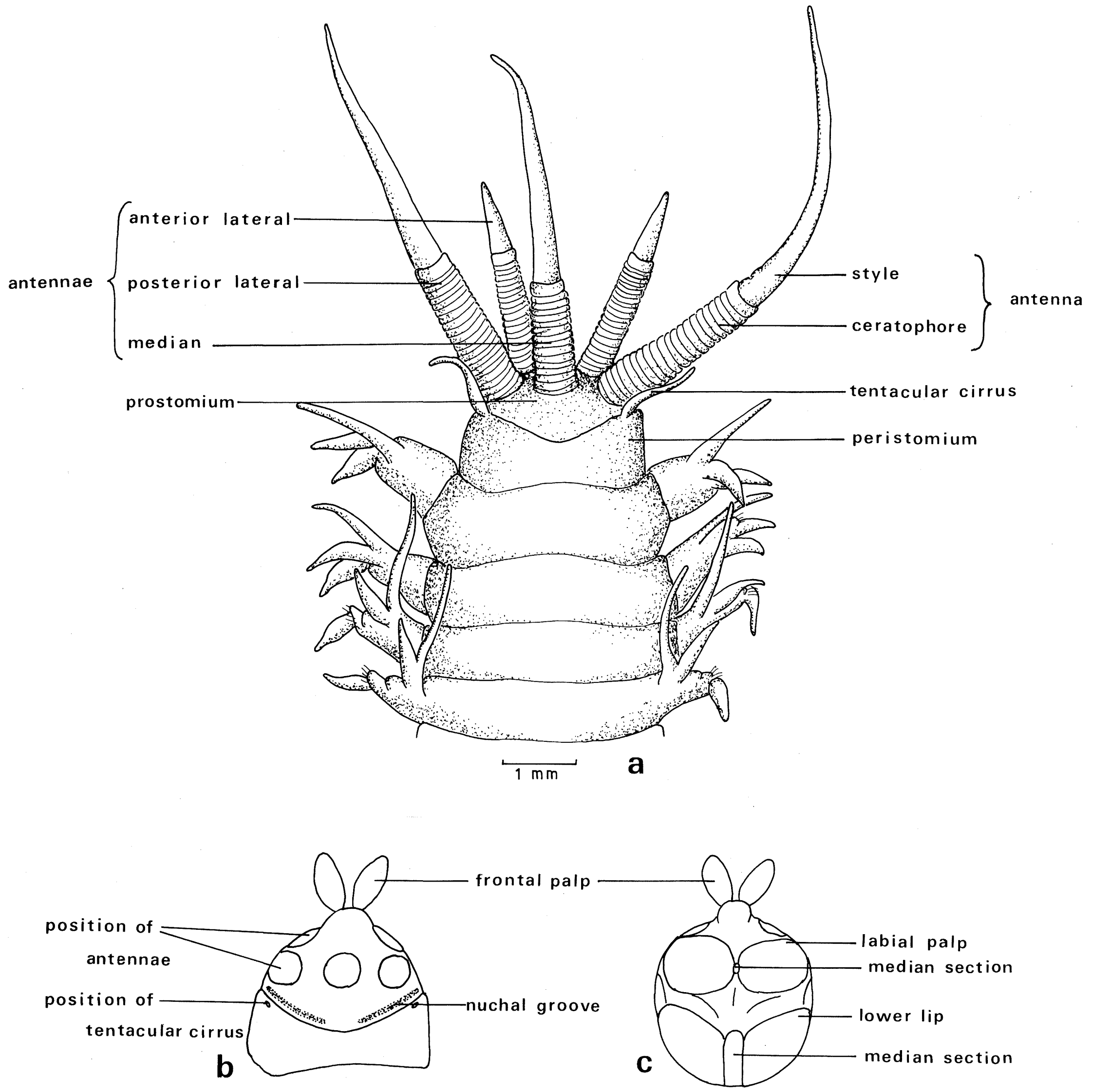


Fig. 3. *Onuphis eremita* (BMNH ZK 1928.4.26.290): **a**, anterior end, dorsal view; **b**, stylized diagram of prostomium and peristomium, dorsal view; **c**, same, ventral view.

(Fig. 4e) or a complete circle around the ciliated area (Fig. 4f). In some species the sensory buds are located on little papilla-like protruberances (Fig. 5a,b). The pattern of distribution of these 'papillae' was used by Hartman (1944) as a taxonomic character and described for a number of species. The configuration and arrangement of the sensory buds appear to be species-specific in *Diopatra* and are being utilized in a forthcoming revision of the genus (Paxton, in preparation).

Palps. The FRONTAL PALPS were referred to as antennae until von Haffner (1959) histologically demonstrated that they are palps and hypothesized that they evolved by a subdivision of the labial palps. Frontal palps are generally present, but reduced to absent in *Neonuphis* and *Leptoecia*. The frontal palps are short, inflated and range in shape from round (Fig. 27a) to oval (Fig. 30a) to subulate or subtriangular (Fig. 23a). The two frontal palps may be close together (Fig. 27a) or slightly separated (Fig. 34a).

The LABIAL PALPS are oval to rectangular, and can be medially separated (Fig. 34b) or touching (Fig. 30b). A more glandular distal area may be slightly set off (Fig. 34b) or form a distinct distal lobe (Fig. 28b). The area between the palps may be free (Fig. 17b) or folds may outline a 'median section'. This median section may be anterior, i.e. close to the frontal palps (Fig. 27b), or it may be in the centre between the two labial palps (Fig. 3c).

Eyes. Eyes, when present, are situated between the bases of the anterior and posterior lateral antennae. They range from small pigment spots (Fig. 33a) that can be found in some members of most genera, to large eyes with lenses (Fig. 17a). The juvenile anterior eyespots are retained in the adults of some small species.

Nuchal organs. The nuchal organs are chemoreceptors (Mill, 1978) located at the posterior part of the prostomium in the form of ciliated grooves. In

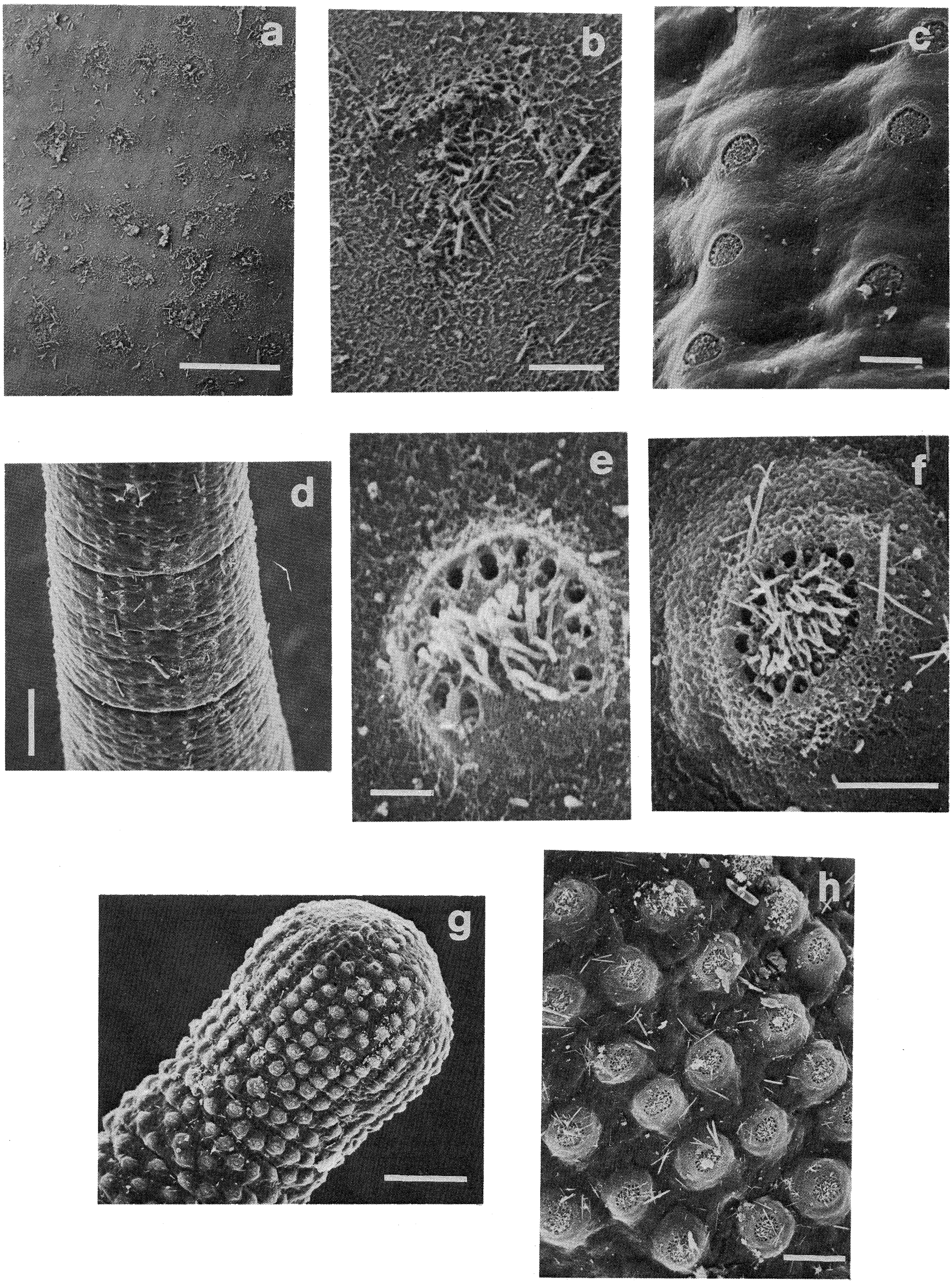


Fig. 4. Scanning electron micrographs of antennae: **a,** irregularly scattered sensory buds of *Hirsutonuphis mariahirsuta* (scale 50 μm); **b,** enlarged sensory bud of same (scale 5 μm); **c,** rows of sensory buds of *Diopatra ornata* (scale 10 μm); **d,** same of *D. cuprea* (scale 100 μm); **e,** enlarged sensory bud of *D. cuprea* (scale 2 μm); **f,** same of *D. dentata* (scale 5 μm); **g,** tip of antenna of *Diopatra dentata* showing sensory buds on papilla-like protruberances (scale 100 μm); **h,** same, enlarged (scale 20 μm).

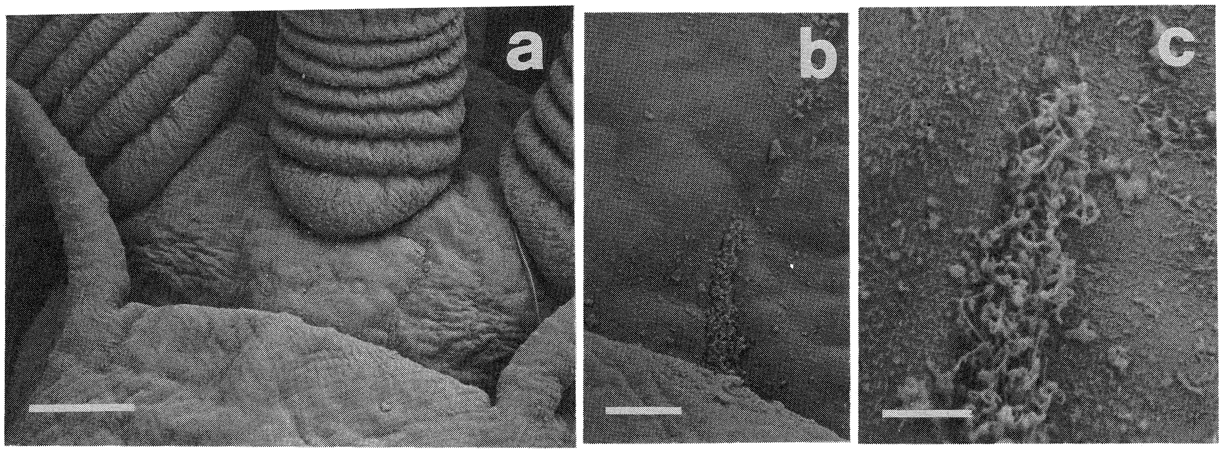


Fig. 5. Scanning electron micrographs of nuchal grooves: **a,** prostomium and peristomium of *D.* n. sp. 1 showing nuchal groove (scale 100 μm); **b,** same, enlarged (scale 20 μm); **c,** nuchal groove of same, enlarged (scale 5 μm).

Hyalinoecia tubicola they are associated with the hindbrain in a way similar to that reported for *Eunice* (von Haffner, 1959), as they probably are in all onuphids. The ciliated grooves can be recognized as such in SEM preparations (Fig. 5a-c) and are visible with light microscopy since they stand out as dull bands in the otherwise shiny cuticle (Fig. 3b). The grooves generally run from the position of the eyes (between the anterior and posterior lateral antennae) along the anterior fold of the peristomium and meet middorsally. The grooves may be almost straight and come close together so as to have a small (Fig. 28a) or wide middorsal separation (Fig. 26a), or have a wide separation and curve anteriorly towards the base of the median antenna (Fig. 30a). In species of *Epidiopatra* (Fig. 24a) and *Diopatra* (Fig. 23a) the grooves are short and the lateral and median parts of the grooves are curved anteriorly, forming an arc between and posterior to the median and lateral antenna in the former and almost a circle in the latter genus. This form of nuchal groove was often mistaken for eyes (Hartman, 1944).

Peristomium

The apodous peristomium forms a complete ring. It is dorsally entire in all genera except *Heptaceras* (Fig. 36a) where it has a middorsal notch, and a median raised ridge runs from the peristomium to the median antenna. The peristomium ranges from short (Fig. 19a) to moderately long in most genera (Fig. 3a). The dorsal anterior fold in Americonuphis (Fig. 28a) is wrinkled and expansible, forming a protective collar over the nuchal grooves as in *Eunice*. In most genera, the anterior fold is distinct but does not form a collar, while *Australonuphis* (Fig. 30a), *Hartmanonuphis* and *Hirsutonuphis* lack an anterior fold and the peristomium appears to extend middorsally towards the median antenna along the curved nuchal grooves. Ventrally, the peristomium forms a large semilunar to triangular lower lip. A distinct median section (Fig. 3c) is present in many genera but absent in others (Fig. 15b). The furrows outlining the median section are formed by a zone without glands in the otherwise glandular lower lip (Eulenstein, 1914).

Tentacular cirri. Tentacular cirri, when present, occur dorsally on the peristomium. In *Americonuphis* (Fig. 28a) they are situated in the middle of the peristomium, in some genera subdistally (Fig. 15a), while in most genera they emerge distally at the anterior margin of the peristomium.

Parapodia

Polychaete parapodia are typically biramous, consisting of noto- and neuropodia. In the Onuphidae the notopodia are reduced, represented only by the base of the branchiae and the dorsal cirri, thus being subbiramous.

Within the Eunicidae, all segments are rather similar with respect to their length, parapodia and setae. In the Onuphidae, however, the anterior one to eight pairs of parapodia are different from the subsequent ones in their orientation, length, parapodial lobes and types of setae. These anterior parapodia are here referred to as 'modified' to mark their distinction from the subsequent 'unmodified' ones. In genera with a smaller number (2–3) of more highly modified setigers (e.g. *Nothria, Rhamphobrachium*) the change is more abrupt than in genera with a larger number (5–7) of less modified setigers (e.g. *Kinbergonuphis*). Hence, it is hard to establish the exact number of modified parapodia in some genera or species since the modifications become gradually less. Therefore, the number of modified parapodia is here defined as the number of parapodia in which the lower setae consist predominantly of hooks.

In many genera, the modified parapodia are directed anteroventrally, ranging from slightly so (Fig. 21c), to moderately (Fig. 1a), to almost touching midventrally (Fig. 29a). As a result of this rotation, the morphologically anterior surfaces are facing each other (Fauchald, 1982a). In another group of genera, the modified parapodia are directed anterolaterally to -dorsally (Fig. 1b), reaching their maximum development in the beachworms (Fig. 32j). The orientation of the last modified or early unmodified parapodia changes gradually, giving the unmodified parapodia a lateral to dorsolateral orientation. The modified parapodia are of about the same length as the

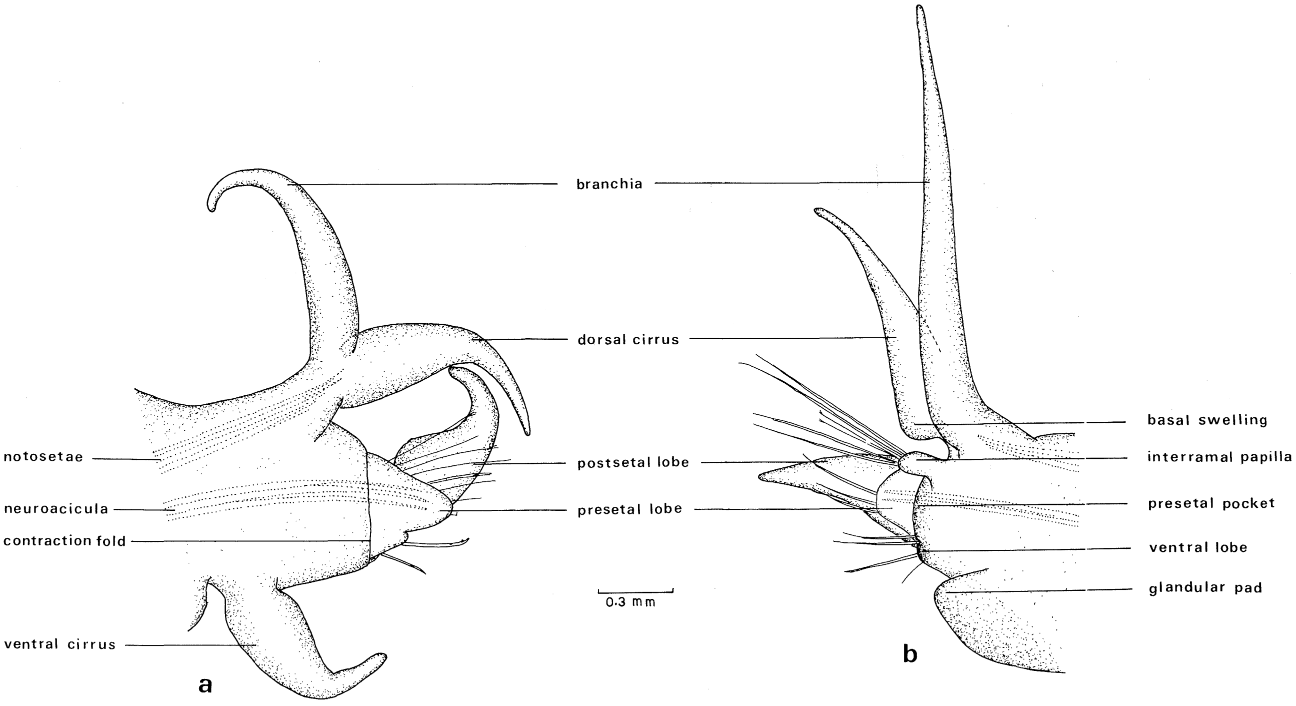


Fig. 6. *Onuphis eremita* (BMNH ZK 1928.4.26.290): **a**, parapodium 1, anterior view; **b**, parapodium 8, same view.

median ones (Fig. 3a) or are prolonged. The prolongation ranges from slight (Fig. 34m) to moderate (Fig. 30c) to great (*Longibrachium*). When the parapodia are prolonged, often the first is the longest, or the first three are equally long, and the remaining modified parapodia become gradually shorter. However, in *Australonuphis* and related genera parapodia 2-4 are longest.

The modified parapodia can be extensile, and their length differs with their state of contraction. Contracted parapodia often show furrows or even rings (Fig. 26c). A transverse fold, often present below the presetal lobe, referred to earlier by Fauchald (1968) as a 'low transverse fold', was subsequently designated a 'contraction fold' since it is not a structural feature but can be present or absent depending on the state of contraction (Fauchald, 1980). In the modified parapodia the contraction fold (Fig. 6a) remains as such or can at times be totally extended leaving no fold. However, with the beginning of the unmodified setigers this fold becomes a fixed, often glandular structure (*Rhamphobrachium, Australonuphis*) and will be referred to as a presetal pocket (Fig. 6b).

Prolonged modified parapodia are usually also thicker and stouter because of better developed muscles. However, the first segments are generally not much longer, except in *Hyalinoecia* and allied genera, where especially setiger 1 is considerably longer than the following setigers.

Parapodial cirri. The anterior parapodia bear subulate or digitiform VENTRAL CIRRI (Fig. 6a) which are replaced in median and posterior parapodia by ventral glandular pads (Fig. 6b). The number of setigers with ventral cirri usually agrees with the number of modified setigers. The transition zone between ventral cirri and glandular pads may be short and consists of one or two setigers with globular ventral cirri (*Onuphis*) or glandular pads with reduced cirri (*Hirsutonuphis*). However, species of *Australonuphis* and *Hartmanonuphis* (Fig. 31d) have a long transition zone of glandular pads with reduced cirri (until setigers 14-25), similar to the condition in the Eunicidae.

DORSAL CIRRI are usually present on all setigers and bear internal setae. However, in *Hyalinoecia* and allied genera these cirri lack setae and are posteriorly reduced or absent. Dorsal cirri are usually best developed in the modified parapodia, where they are often of subulate shape and long; these cirri reach their greatest development in the genus *Hirsutonuphis* (Fig. 32j), where in *H. gygis* they approximate the antennae in thickness and length. The dorsal cirri often have a basal swelling (Fig. 6b), which is elaborated into a digital process in some genera (Fig. 30e).

Parapodial lobes. The parapodial lobes consist of acicular, presetal and postsetal lobes and are recognized as such by most authors.

The ACICULAR LOBE is distally truncate or rounded, supported by internal acicula which emerge from its tip.

The PRESETAL LOBE is anterior to the acicular lobe. It is found in all genera, except in the highly modified anterior parapodia of *Rhamphobrachium* and allied genera. In some genera the presetal lobe is very short and follows the outline of the acicular lobe closely, making the two lobes almost indistinguishable. Day (1960) referred to this apparently single lobe in *Diopatra* as the 'setigerous lobe' and stated that the presetal lobe is not developed in the anterior four parapodia. This terminology was followed by Knox & Hicks (1973) but is not followed here. The presetal lobe can have a moderately large, free distal end (Fig. 36c), or form a hood-like, auricular lobe over the setae as in *Hyalinoecia* and its allies. While the presetal lobes are usually rounded, they may be bilobed (Fig. 23c), trilobed (Fig. 32c), or have a distal extension (Fig. 28b).

The presetal lobes become reduced after the modified parapodia, and the original presetal lobes disappear by setiger 10 to 30. In most species they remain lost, but in a number of larger species they become replaced by the new presetal lips which can be formed in two different ways: (1) In some species of *Onuphis* (Fig. 6b), *Australonuphis* and *Hirsutonuphis* an interramal papilla appears at the base of the dorsal cirrus immediately after the modified region. In the latter two genera this papilla enlarges ventrally, fuses with the presetal pocket and thus forms a new presetal lip. *Onuphis eremita* develops in addition to the interramal papilla a small ventral lobe, the two of which fuse and form the presetal lip. (2) In species of *Hartmanonuphis* (Fig. 31d), *Americonuphis* and *Diopatra,* a ventral lobe appears in the early unmodified parapodia, increases dorsally and becomes the new presetal lip. This structure was referred to by Day (1960) as the 'true presetal lobe', and is termed here 'new presetal lip' following Rozbaczylo & Castilla (1981).

The highly modified anterior parapodia of *Rhamphobrachium* and *Longibrachium* lack presetal lobes. However, separate papillae-like lobes are present at the point of emergence of each of the enlarged hooks and are referred to here as papilliform lobes.

POSTSETAL LOBES (Fig. 6) are usually single, of triangular shape with a flattened base and a subulate to digitate distal part. In some species of *Diopatra* and *Brevibrachium* (Fig. 25b) they are double, consisting of a larger upper and a smaller lower accessory lobe. In *Rhamphobrachium* and *Longibrachium* the postsetal lobe is in a more ventral position than in other onuphids and it is likely that it represents the lower part of the double lobe, while the upper lobe has been lost. In juvenile *R. ehlersi* the lower postsetal lobe develops when the parapodium becomes modified (see p. 18), suggesting a separate origin from the usual one. Postsetal lobes are best developed in the modified region, becoming reduced thereafter. In some species, the absence of the postsetal lobes is correlated with the origin of the subacicular hooks *(Rhamphobrachium),* while in others the reduced lobes are continued to the end of the body.

Branchiae. Branchiae are present in the majority of species and occur as outgrowths of the dorsal cirri. The branchiae can be simple, branched, pectinate or spiralled. Simple branchiae (Fig. 17d) are present in small to moderately sized species. The single filaments are often long (overlapping middorsally), and relatively wide and flat. This type has been referred to as 'simple strap-like branchiae' (Fauchald, 1968) and may differ morphologically from others (Fauchald, 1982a). Dichotomously branched branchiae have been found only in two species of *Anchinothria* (Fig. 16d). The most common type are pectinate branchiae. They originate usually as single filaments (Fig. 6) in the anterior body region, and usually rapidly increase their number of filaments by the addition of new ones to the distal part of the main stem (Fig. 7). Spiralled branchiae (filaments attached spirally around the central trunk) are only found in *Diopatra* (Fig. 23d) and *Epidiopatra* (Fig. 24d).

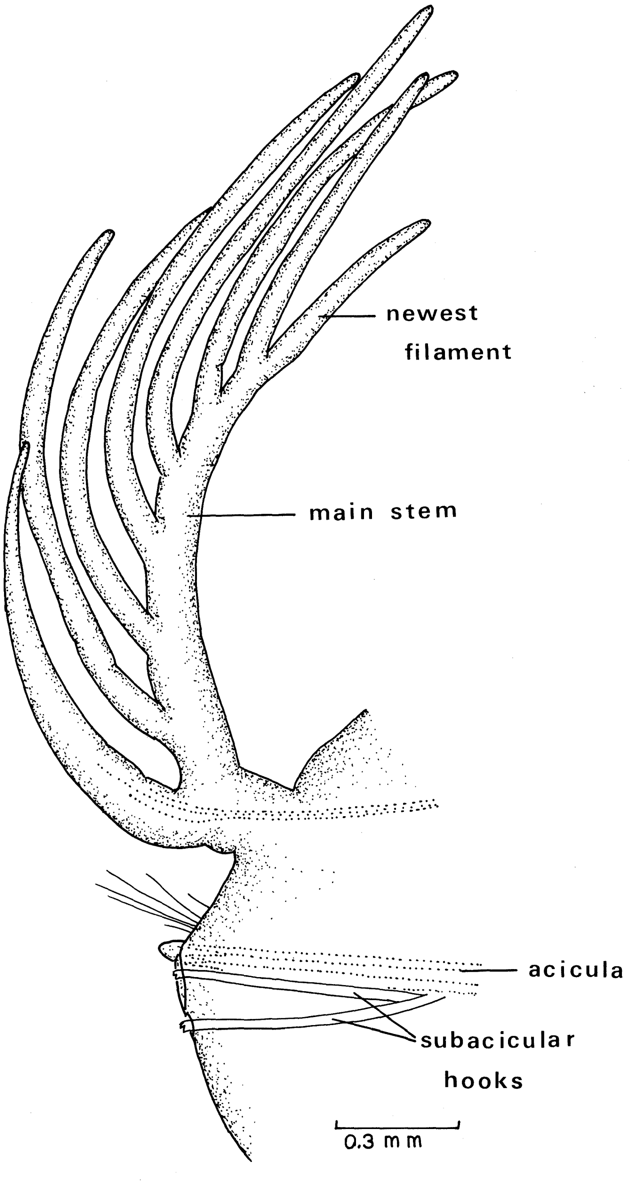


Fig. 7. *Onuphis eremita* (BMNH ZK 1928.4.26.290): parapodium 53, anterior view.

Branchiae may be present from the first setiger or later; in many shallow-water species they start on or about the sixth setiger, while in deep-water ones they often occur after the tenth. In *Diopatra* and related genera the branchiae are well developed in the anterior part of the body and restricted to single filaments from setiger 40–60.

Setae

In the Onuphidae the notosetae are reduced to internal setae in the dorsal cirrus or absent. When present, they are usually short in the modified parapodia (Fig. 6) and longer in the median and posterior region (Fig. 7).

The neurosetae are anchored to the acicula, which number from one to about five. Newly emerged acicula have a filiform tip which may be retained (Fig. 25g) or more commonly, break off, leaving a bluntly rounded tip. In some species the tip projects at an angle *(Diopatra).* The setae of the median and posterior region project dorsolaterally in most genera (Fig. 2a–d,f). However, species of *Nothria* and *Anchinothria* have ventrolaterally directed setae (Fig. 2e). The setae generally consist of an upper bundle, dorsal and posterior to the acicula, and a lower bundle, ventral and anterior to the acicula. The setal sac is usually contained within the segment from which it originates, except species of the *Rhamphobrachium* complex where the setal sac projects into the following or subsequent segments. The most extreme degree of development of this arrangement occurs in *Longibrachium* and *Rhamphobrachium* where the setal sacs extend to setiger 50–70, where they lie in the body cavity next to the gut and slide anteriorly and posteriorly depending on the state of extension or retraction. These long setal sacs were thought by McIntosh (1910) to be secreted fibres; Hoagland (1920) recognized them as retractor muscles with attached hooks, and Berkeley & Berkeley (1938) gave a detailed description of the setal sacs.

Upper bundle of setae. The upper bundle of setae consists of simple limbate and pectinate setae.

The UPPER LIMBATE SETAE (Fig. 8a) are long, with narrow wings, often appearing as capillaries. In some species of *Rhamphobrachium, Neonuphis* and *Leptoecia* (Fig. 18f) they are densely covered with spines, giving them a spiky or hairy appearance. The upper limbate setae are generally present from the first setiger. However, in *Rhamphobrachium* and *Hyalinoecia* and their respective allies, they do not emerge from the modified parapodia, but are internal supports.

PECTINATE SETAE occur in many genera from the first setiger onwards and throughout the body. The distal pectinate edge may be at either a right angle (transverse) (Fig. 30g) or an oblique angle (Fig. 8c) with the shaft of the seta. The comb of the seta is usually flat, but may be rolled up in anterior parapodia (Fig. 32k). In *Nothria* (Fig. 15l) and *Anchinothria* the lateral distal parts of the seta are flared towards each other

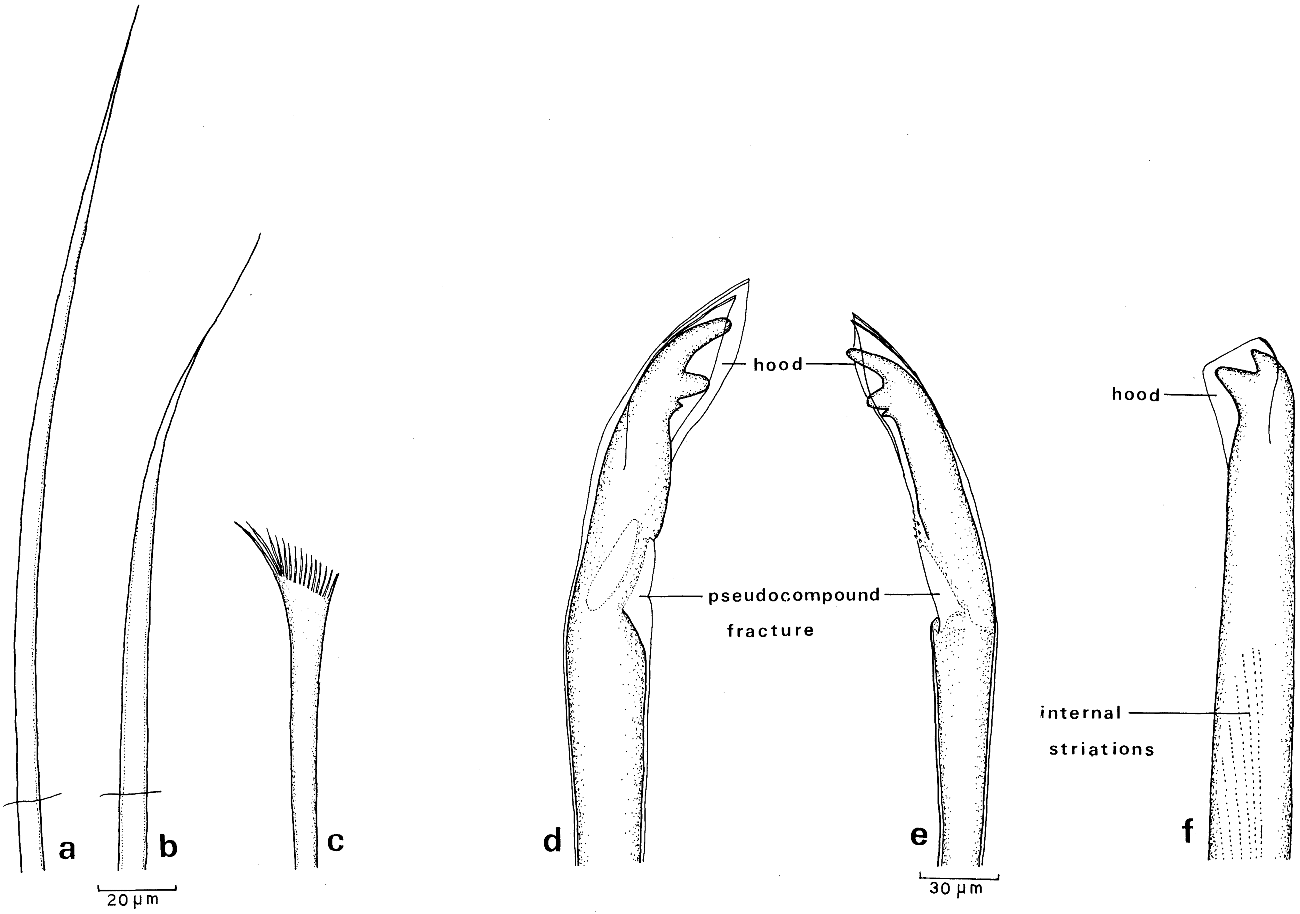


Fig. 8. *Onuphis eremita* (BMNH ZK 1928.4.26.290): **a,** upper limbate seta from setiger 4; **b,** lower limbate seta from same; **c,** pectinate seta from setiger 3; **d,** median pseudocompound hook from setiger 3; **e,** lower pseudocompound hook from same; **f,** subacicular hook from posterior setiger.

forming an 'open scoop', and are termed 'scoop-shaped' (Fauchald, 1982a). Pectinate setae are very numerous in *Hyalinoecia* and allied genera, while their number can vary greatly in other genera.

The number of teeth on pectinate setae was at times considered a good taxonomic character and was used particularly to separate species of *Diopatra* (see Hartman, 1944: 51 for a review). When the number of teeth is low (less than 10) it seems to be a good character, since it aligns *Diopatra neapolitana* and a group of species which also share a number of other features. However, when the number is large (15–30), the variation can be more than 10 teeth in a single specimen so that the number is of little taxonomic value.

Lower bundle of setae. The lower bundle of setae consists typically of hooded bi- to tridentate pseudocompound hooks in the modified parapodia, followed in the unmodified parapodia by short, simple to pseudocompound limbate setae which may remain throughout or become replaced by hooded subacicular hooks. A number of modifications to this basic plan are found and discussed below.

The HOOKS range from pseudocompound to simple. In the majority of species the hooks are pseudocompound; the fracture is completely ankylosed but visible (Fig. 8d,e), or is represented by a clear area (Fig. 23e,j,l). In some species the shaft of the hook shows no sign of fracture, and appears as simple (Fig. 15d,e).

The appendage, or distal part of the anterior hooks can be unidentate (falcate), bidentate or tridentate. The unidentate hooks are found in a number of genera (Fig. 30f). Several authors have considered unidentate hooks as worn bi- or tridentate hooks (e.g. Fauchald, 1982a). However, setae are continually replaced and unidentate replacement hooks are found (Fig. 15c). If the teeth had been lost through wear, certainly the delicate hoods would be lost also, which is not the case (Fig. 15f). unidentate hooks have the distal falcate end and an additional lower second tooth which may be smaller (Fig. 23e), equal in size (Fig. 29c), or thicker (Fig. 36i,j) than the distal tooth. In the tridentate condition (Fig. 8d,e), a usually smaller tooth is present below the second one.

The distal end of the hook is generally covered by a pair of valve-like hoods which range from short and closely fitting (Fig. 8d,e) to long and pointed (Fig. 22c,d).

One or two slightly thicker median hooks (Fig. 8d), located immediately below the acicula, are present in a number of genera from setiger 1. In *Kinbergonuphis* and *Mooreonuphis* (Fig. 35e) these hooks differ from others further in having a more distal pseudoarticulation, and in the shape and orientation of their teeth: the distal tooth is shorter, and the median and lower teeth are blunter and point downwards. They have been referred to as 'precursors of simple tridentate hooks' (Paxton, 1979). The pseudocompound fracture usually becomes weaker and moves more distally in the following segments, and by setiger 3–7 the hook is simple (Fig. 35g). These large median hooks often remain until the occurrence of the subacicular hooks. The larger hooks were termed 'acicular hooks' or 'tridentate simple hooks' (Hartman, 1944), and 'large hooks' (Fauchald, 1982a). The latter term is modified here to 'large median hooks', and also includes the precursors.

The most modified anterior hooks are found in *Rhamphobrachium* and allied genera. Two species of *Brevibrachium* have regular, hooded uni- to tridentate hooks but the hooks of *B. maculatum* and all species of *Longibrachium* and *Rhamphobrachium* (Fig. 27d,e) have strongly recurved or scythe-like distal ends.

The shafts of hooks have a smooth surface in most genera; in *Rhamphobrachium* and allies they have rows of spines. However, the shafts that appear smooth when viewed with light microscopy show small, irregularly distributed spines in SEM preparations (Fig. 9a). In some species of *Diopatra* (Fig. 9b), some of these spines have lengthened and become oriented into two rows. These rows of spines are well developed in some *Brevibrachium, Longibrachium* (Fig. 9c,d), and particularly in *Rhamphobrachium,* where they are moveable (Fig. 9e,f).

The beginning of the unmodified parapodia is marked by the replacement of hooks by LOWER SIMPLE LIMBATE SETAE (Fig. 8b) that are wider and shorter than the upper ones, and may be cultriform (Fig. 23g) to spine-like (Fig. 24g). In some genera the lower limbate setae are weakly pseudocompound to compound (i.e. spiniger) (Fig. 35h). The lower limbate setae are present throughout the median and posterior region in *Hyalinoecia* (Fig. 17d) and allied genera. However, in *Onuphis* (Fig. 7) and related genera, the lower limbate setae are absent after the appearance of subacicular hooks.

Some species of *Rhamphobrachium* also have COMPOUND FALCIGERS, strongly reminiscent of eunicid falcigers in the first two unmodified pairs of parapodia.

SUBACICULAR HOOKS occur in all onuphids examined and start from setiger 8 to 80. They occur either in a ventral or median position in the fascicle. Fauchald (1982a) restricted the term 'subacicular hooks' to the former, and referred to the latter as 'intrafascicular hooks'. However, since the two types appear to be homologous and both occur in a subacicular position, it is recommended that the established name be retained for both types.

Both types of subacicular hooks are simple and show clear internal striations. Both types are hooded and bidentate (Fig. 8f), except in *Australonuphis* (Fig. 30j) where the hooks are distally entire and lack a hood. In most genera they number two per parapodium from their origin and continue as such. In *Hyalinoecia* they originate as one per parapodium, increase to two, and rarely three, after several segments. A similar pattern occurs in *Rhamphobrachium,* while in two species of this genus they increase to a maximum of three to six, and then decrease to the typical two per parapodium, which is then retained.

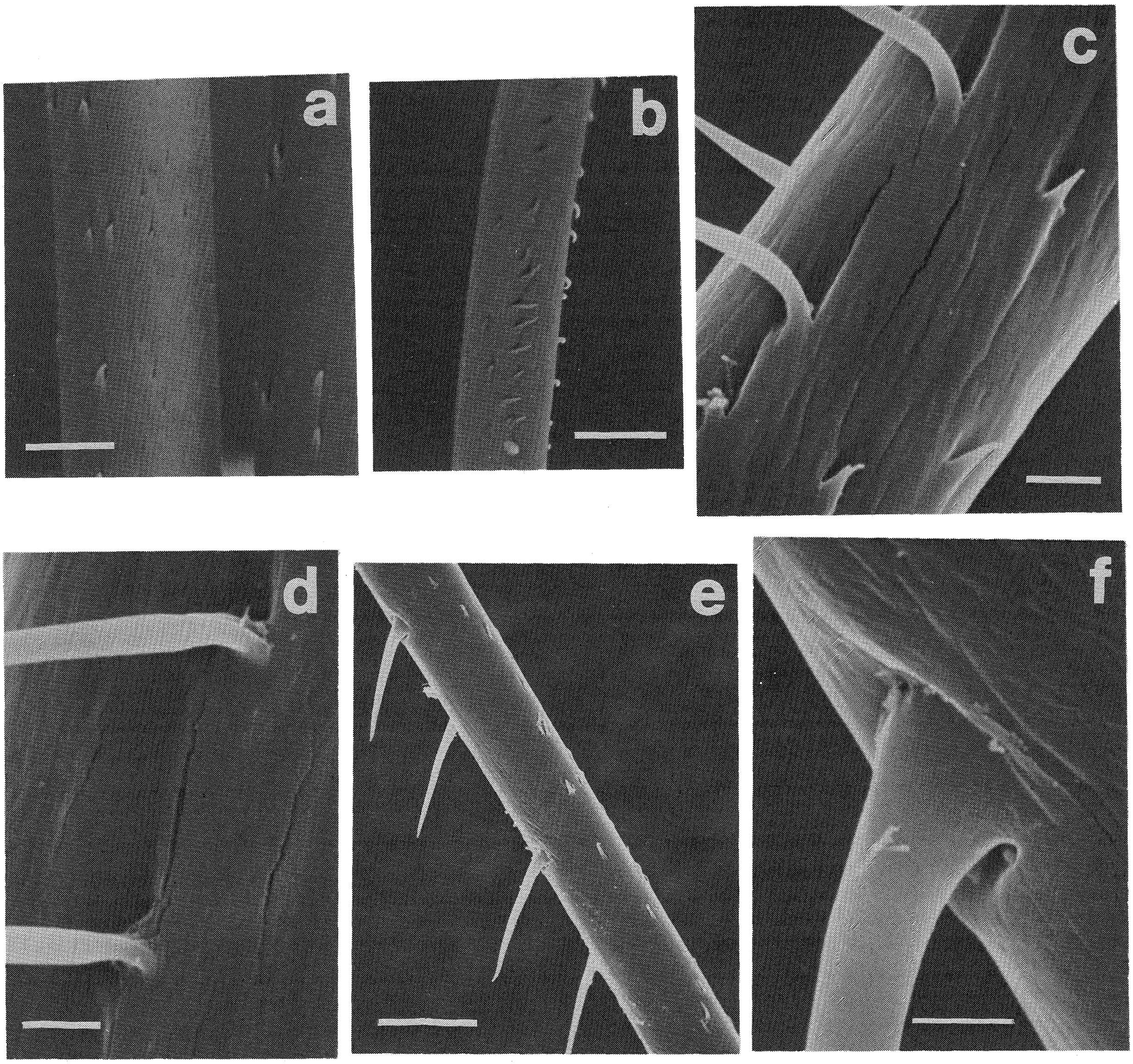


Fig. 9. Scanning electron micrographs of setal hooks: **a,** shafts of *Brevibrachium maculatum* (scale 5 μm); **b,** shaft of *Diopatra* n. sp. 1 (scale 5 μm); **c,** shaft of small hook of *Longibrachium longipes* (scale 2 μm); **d,** shaft of large hook of same (scale 2 μm); **e,** shaft of *R. (Rhamphobrachium) longisetosum* (scale 20 μm); **f,** same enlarged (scale 2 μm).

Ventral subacicular hooks occur in most genera. The upper subacicular hook runs parallel to the lowest aciculum, while the lower subacicular hook originates at, or slightly above, the acicula, emerging usually considerably lower, thus forming an acute angle to the upper subacicular hook and the acicula (Fig. 7). Lower limbate setae are absent from the start of the subacicular hooks, and the latter are now the most ventral setae in the fascicle. As was noted by Fauchald (1982a), the ventral subacicular hooks are round in transverse section, and usually barely emerge from their setal sacs.

Median subacicular hooks are found in *Hyalinoecia* (Fig. 17d) and related genera. They originate just below the acicula and follow it closely, emerging parallel to it in the middle of the parapodium. The median subacicular hooks do not replace the lower limbate setae, which continue ventrally to the subacicular hooks until the end of the body. The median subacicular hooks are oval in transverse section (Fauchald, 1982a) and emerge much further from their setal sacs than the ventral hooks.

Eversible Pharynx

The eversible onuphid pharynx is a ventral structure projecting backwards under the oesophagus as a muscular sac (Dales, 1962). A detailed study of the eversible pharynx of *Hyalinoecia tubicola* was made by von Haffner (1959). The eversible pharynx contains an elaborate jaw apparatus consisting of a pair of ventral mandibles and 4½ to 5½ pairs of dorsal maxillae.

Mandibles. The mandibles (Fig. 10a) are solid structures consisting of long shafts widening into anterior cutting plates which are connected to each other

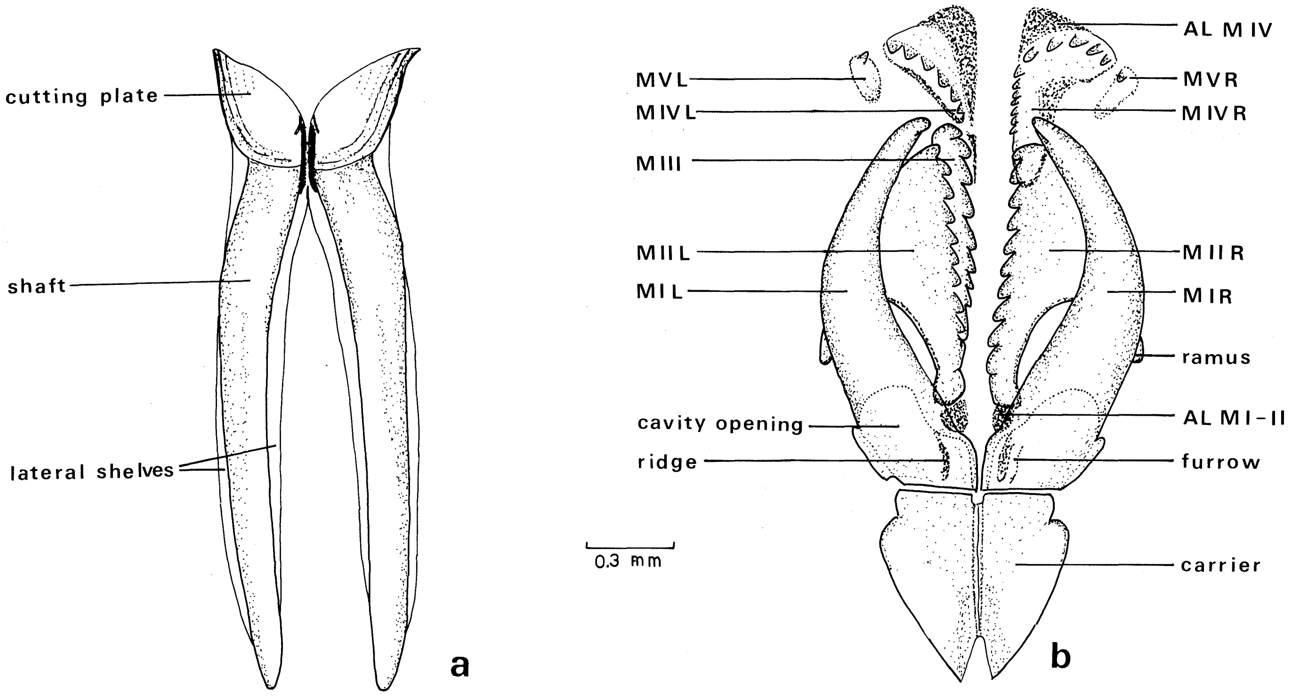


Fig. 10. *Onuphis eremita* (BMNH ZK 1928.4.26.290): **a,** mandibles, decalcified, ventral view; **b,** maxillary apparatus, dorsal view (AL = attachment lamella, L = left; M = maxilla; R = right).

by a ligament. The length of the mandibles equals, in most genera, the length of the maxillary carrier and maxilla I together. However, in some groups the mandibles seem disproportionately large (Fig. 15m). The shafts are centrally thickened and often have distinctly thinner lateral shelves. The cutting plates consist of a sclerotized dorsal matrix and a thick, ventral layer of calcium carbonate that is usually twice as long as the matrix and often anteriorly serrated (Fig. 24i).

Maxillary apparatus. The maxillary apparatuses (Fig. 10b) range from the most delicate, translucent, hardly sclerotized or calcified structures of small species (Fig. 19h) to the robust, opaque, highly sclerotized and calcified structures of large species (Fig. 23k). The apparatus is made up of a pair of medially hinged posterior carriers and anterior maxillae. The hardened part of the maxilla provides an exoskeleton for the internal living tissue which is in contact with the soft structure of the pharynx through basal cavity openings. The latter range from relatively small (Fig. 10b) to very large (Fig. 19h). The maxillae (abbreviated as Mx) are conventionally enumerated in Roman numerals in an anterior direction. Maxillae I, II and IV are each paired, while III is a single left plate. The right Mx IV is larger than the left Mx III and was considered a fused right Mx III and Mx IV by Hartman (1944), and followed by Day (1967) and Fauchald (1968). However, as pointed out by Kielan-Jaworowska (1966), while there is no support for this interpretation from Recent material, it is contradicted by fossil evidence.

The numbers of median teeth on the maxillary plates are described by the dental formula, where the numerals represent the number of teeth on the respective left and right maxillary plates. The dental formula for *Onuphis eremita* (Fig. 10b) is thus represented as follows: Mx I = 1 + 1; Mx II = 9 + 9; Mx III = 8 + 0; Mx IV = 6 + 12; Mx V = 1 + 1. The absence of a plate is indicated by a zero, e.g. 'Mx III = 8 + 0' states that the left Mx III has 8 teeth, while the right Mx III is absent.

The maxillae I (or forceps) are attached to the carriers by hinges. Proximally, the left Mx I has a ridge which fits into the corresponding furrow of the right Mx I, interlocking like a 'Druckknopf' (Hartmann-Schröder, 1967) or snap. This basal ridge is interpreted as the remnant of the laeobasal plate in fossil eunicids (Kielan-Jaworowska, 1966). The lateral ramus of the Mx II is usually covered by the Mx I but is protruding in some genera (Fig. 10b). The Mx II are attached posteriorly to the Mx I by an often darkly sclerotized attachment lamella. The more anterior maxillae are usually free from each other. The Mx III may originate posteriorly at the same level as Mx II (Fig. 17l), or more anteriorly (Fig. 31i). It is usually longer anteriorly than Mx II (Fig. 10b), except in *Nothria* (Fig. 15n) and *Anchinothria* (Fig. 16k). The distal tooth of Mx II is sometimes enlarged, forming a fang (Fig. 16k).

The Mx IV are disproportionately large in some groups (Fig. 19h). The attachment lamellae of the Mx IV (Fig. 10b) have been elaborated into large sclerotized areas that were also termed 'Schwielen' (Heider, 1925) or 'callosités' (Desière, 1967). Mx V are small plates having one tooth each. They can be very small (Fig. 10b) or larger (Fig. 23k); Mx VI are present in some genera as toothless plates (Fig. 27l), or even bear a small tooth each (Fig. 28d), but are absent in most genera.

Pygidium

The pygidium is generally a small lobe with a dorsal anus, while in *Hyalinoecia* it consists of an enlarged glandular structure. The pygidium bears anal cirri which are a single pair in *Hyalinoecia* and allies (Fig. 15j), while in other genera there is a larger ventral and smaller dorsal pair.

Kinbergonuphis pygidialis (Fauchald, 1968) was described as having a single anal cirrus with a bifid tip. I have not observed any other specimens with only one anal cirrus and presume that the single specimen upon which the description was based, was aberrant or damaged in this respect.

Tubes

The tubes are generally round in transverse section and longer than their inhabitants. Flattened tubes occur in *Nothria, Neonuphis* and *Leptoecia.* The tubes usually consist of an inner lining secreted by its inhabitant, and an outer layer of foreign particles. The internal lining of *Diopatra* and other genera consists of a tough, parchment-like material, while that of *Onuphis* and others consists of a softer mucous substance which is extremely fragile in some groups. Only rarely is the outer layer absent as in the quill-like tubes of *Hyalinoecia.* The chemical composition of the *Hyalinoecia* tubes was found to be a combination of onuphic acid and a mucoprotein (Defretin, 1971). *Hyalinoecia* tubes are also unique in having internal valves.

The outer layer of the tube consists of sand grains, fragments of hard parts from other animals, or plants. Fauchald (1982a) stated that some selection of particles apparently takes place since the particles attached to the tube are usually larger than the mean particle size in the surrounding medium.

Size

Species of *Nothria* are short-bodied, measuring up to 5 cm for less than 100 setigers, even though their width can attain up to 6 mm. Most onuphids have a length of about 10 cm (up to 200 setigers), and a width of up to 3 mm, while species of the *Rhamphobrachium* complex and *Diopatra* can measure up to 30 cm long (up to 250 setigers) and up to 8 mm wide. However, the longest of all onuphids are species of *Americonuphis* and the beachworms, which can attain a length of 70 cm (1000 segments), width of 10 mm, and live specimens can measure up to 300 cm.

REPRODUCTION AND DEVELOPMENT

Knowledge of the reproductive biology of onuphids is scant. Reference to many of the earlier studies can be found in Richards (1967). Additional or newer papers are listed in Table 1. Of the 27 species in the combined listing, accounts for 10 species merely reported the presence of gametes or brooding, while studies of the remaining species dealt with various aspects of reproduction, development and life history. The fact that many species live in great depths and that even littoral species cannot be collected and kept easily in the laboratory explain the gaps in our understanding of their life history.

Onuphid eggs are relatively large (175 to 1,170 μm in diameter); development is either by lecithotrophic planktonic larvae, direct development with brood care in the parental tube, or viviparity. While the sexes are usually separate without sexual dimorphism, cases of hermaphroditism (Lieber, 1931) and male dwarfism (Hartman, 1967a) have been observed. Very small specimens of the Antarctic *Rhamphobrachium ehlersi* Monro, 1930 observed in the present study contained sperm morulae and free sperm, suggesting that the species is a protandric hermaphrodite. Asexual reproduction has not been reported. The following discussion is limited to aspects of development of features of taxonomic importance and their relevance to intergeneric relationships.

Reproduction

During oogenesis, onuphid oocytes are associated with nurse cells (Schroeder & Hermans, 1975) which occur in two different types of arrangement. In *Onuphis* and other genera the nurse cells are attached to the oocyte as two strings of cells (Fig. 11a), while in *Hyalinoecia* and allies they are attached in a cluster (Fig. 11b). When viewed with light microscopy the primary envelope of mature eggs in the former group appears smooth, while that of the latter group is densely pitted (Bergmann, 1903: pl. 17 figs 17–19).

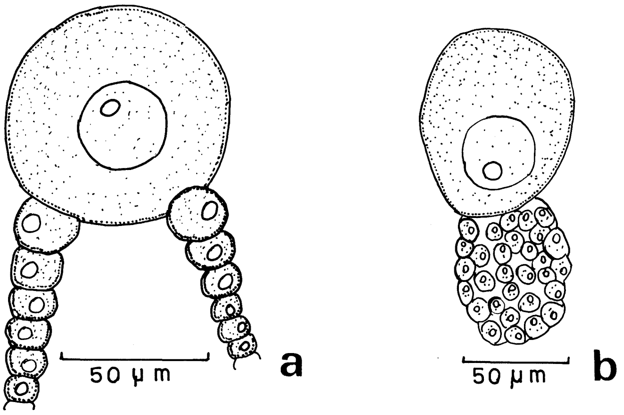


Fig. 11. Oocytes: **a**, oocyte of *Australonuphis teres* with strings of nurse cells; **b**, oocyte of *Hyalinoecia tubicola* with cluster of nurse cells.

Fauchald (1983) discussed life diagram patterns in benthic polychaetes and included onuphids of four different genera in the category of perennial species, characterized by: low reproductive effort, moderately large to large eggs, and non-planktotrophic development. The species listed by him have relatively few eggs per spawning (less than 3,200). However, large individuals of the Australian beachworms, *Australonuphis teres* (Ehlers, 1868), examined during the present study contained more than 100,000 eggs in their body cavity, making this one reproductive effort higher than the lifetime investment considered as

Table 1. Summary of Reproduction, Development and Life History Studies in the Family Onuphidae

Species	Location	Observation	Reference
Nothria conchylega	North Sea	Oogenesis.	Eulenstein, 1914
N. nr. *conchylega*	S. Shetland Islands	Eggs in adult tube.	Hartman, 1967a
Hyalinoecia araucana	Central Chile	45-69 larvae (3-13 setigers) in adult tube.	Carrasco, 1983
H. tubicola (as *Onuphis tubicola*)	Naples, Italy	Oogenesis.	Bergmann, 1903
H. tubicola	Sweden	Sperm morphology.	Franzén, 1956
Notonuphis antarctica (as *Paronuphis antarctica*)	Antarctic	Eggs 1.17 mm diameter and up to 24-setiger juveniles in adult tube; pygmy ♂ (4 mm long) firmly appressed to ♀.	Hartman 1967a, b
Diopatra nr. *amboinensis*	Java	Oogenesis	Lieber, 1931
		Yellowish-white eggs and up to 6-setiger larvae in adult tubes; eggs singly attached on inside of tube near distal end; juveniles build own tube on outside of parental one.	Pflugfelder, 1929
D. cuprea	North Carolina, U.S.A.	Artificial fertilization.	Just, 1922
	Florida, U.S.A.	Eggs 200 μm diameter; 1600-3200 eggs/spawning; 4 spawnings/life of ♀.	Fauchald, 1983
D. nr. *cuprea*	Sumatra	Oogenesis.	Lieber, 1931
D. neapolitana	?Naples, Italy	Oogenesis.	Lieber, 1931
D. ornata	S. California, U.S.A.	Eggs 235 μm diameter; 900 eggs/spawning; 4 spawnings/life of ♀.	Fauchald, 1983
D. variabilis	India	Osmoregulation of eggs and larvae.	Krishnamoorthi, 1963
D. n. sp.	Sumatra	♂♂, ♀♀, and hermaphrodites with ♂ and ♀ gonads in the same segments; oogenesis.	Lieber, 1931
		Three generations of tubes together.	Pflugfelder, 1929
Brevibrachium maculatum (as *Rhamphobrachium* sp.)	Victoria, Australia	Summer breeding season; eggs 300-500 μm diameter and up to 28-setiger juveniles in lateral chambers of adult tube.	Smith and Jensz, 1958
Americonuphis magna (as *Onuphis magna*)	North Carolina, U.S.A.	Eggs in gelatinous strings (2 m or more).	Hartman, 1945
Australonuphis teres	Eastern Australia	Eggs light green; 260 μm diameter; 'primitive' sperm.	Paxton, 1979
A. pareteres	Eastern Australia	Eggs cream with green spots; 280 μm diameter; 'primitive' sperm.	Paxton, 1979
Hirsutonuphis mariahirsuta (as *Onuphis mariahirsuta*)	Eastern Australia	Eggs 240 μm diameter.	Paxton, 1979
Kinbergonuphis notialis (as *Nothria notialis*)	Antarctic	2-3 eggs and up to 29-setiger juveniles in each of numerous lateral capsules of adult tube.	Hartman, 1967a, b
K. pulchra	Belize, Central America	Eggs 330 μm diameter; 74 eggs/spawning; 3 spawnings/life of ♀; non-planktotrophic.	Fauchald, 1983
K. taeniata (as *Onuphis taeniata*)	Queensland, Australi	Eggs 240 μm diameter.	Paxton, 1979
K. simoni (as *Onuphis simoni*)	Florida, U.S.A.	Eggs and up to 20-setiger juveniles in adult tube.	Santos *et al.*, 1981
		Eggs 360 μm diameter; 46 eggs/spawning; 3 spawnings/life of ♀; non-planktotrophic.	Fauchald, 1983
Mooreonuphis jonesi	Bermuda	Eggs 175 μm diameter in body cavity; 50-60 up to 10-setiger juveniles in brood chamber of adult tube.	Fauchald, 1982b
		22 eggs/spawning; 3 spawnings/life of ♀.	Fauchald, 1983
Onuphis elegans (as *Nothria elegans*)	California, U.S.A.	Eggs 230 μm diameter; 'primitive' sperm; lecithotrophic planktonic larvae; feeding delayed until just prior to settlement at 6 days; artificially fertilized and reared through 60-setiger juveniles.	Blake, 1975
		789 eggs/spawning; 4 spawnings/life of ♀.	Fauchald, 1983
Onuphis eremita oculata	Florida, U.S.A.	Eggs 210 μm diameter; 4 spawnings/life of ♀; non-planktotrophic.	Fauchald, 1983

characteristic for perennial species by Fauchald (1983).

The directly developing worm in an egg mass or parental tube, limiting its dispersal, is defined as an embryo, while free-spawned eggs develop into a larva; both types become juveniles when they enter the adult environment (Schroeder & Hermans, 1975).

Juvenile Development

Juveniles in various stages of growth, of many species, were observed. For one species, the Antarctic *Rhamphobrachium ehlersi,* a complete growth series of juveniles together with adult specimens was obtained from a single sample. This fortunate find allowed the elucidation of juvenile *Rhamphobrachium* development, leaving no doubt as to the conspecificity of the various stages. An incomplete series of juveniles of an undetermined species of *Rhamphobrachium* from Australia showed the same basic growth pattern, but some variations in the setal pattern. This section will firstly describe juvenile states of *Rhamphobrachium ehlersi* and *R.* sp., to be followed by a discussion of general juvenile characters.

The juveniles of *R. ehlersi* can be divided into four stages (Table 2).

Stage 1. Antennae present, ceratophores not ringed. Frontal palps beginning to develop, tentacular cirri absent. Only parapodium 1 prolonged, three characteristic spiny hooks protruding. Parapodium 2 short with internal spiny hooks, low postsetal lobe starting to develop. Parapodium 3 short with limbate setae. Subacicular hooks present from setiger 6–8, branchiae absent.

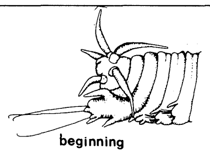
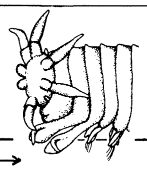
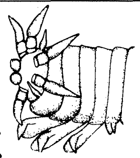
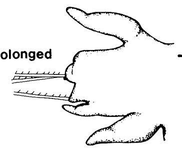
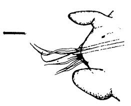
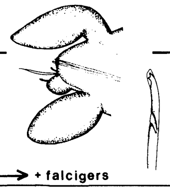
Stage 2. Frontal palps present, tentacular cirri ranging from absent to short. Both parapodia 1 and 2 prolonged with protruding spiny hooks. Parapodium 3 short, bearing limbate setae. Subacicular hooks present from setiger 8–10. Single branchial filaments present from setiger 11–13, about the same origin as in adults.

Stage 3. Prostomial parts similar to stage 2. Parapodia 1 and 2 same as in stage 2. Parapodium 3 short, its low postsetal lobe starting to develop. Limbate setae and 1 to 4 compound falcigers present in parapodium 3. Subacicular hooks present from setiger 10–13.

Stage 4. Prostomium and parapodia 1 and 2 as before. Parapodium 3 short, low postsetal lobe has lengthened; ventral falcigers lost, replaced with internal spiny hooks. Subacicular hooks present from setiger 14–16.

Adult. Three pairs of prolonged parapodia with protruding spiny hooks, subacicular hooks start on setiger 15–16. Branchiae start on setiger 10–12 as single filaments, becoming bifid by setiger 20.

Table 2. Ontogenetic changes of *Rhamphobrachium ehlersi*

Character	Stage 1	Stage 2	Stage 3	Stage 4	Adult
Anterior end		————		————→	
Frontal palps	beginning	present ————	————→	————→	
Tentacular cirri	absent	absent to short ————→		present ————→	
Parapodium 1	prolonged 	————	————	————→	
Setae	protruding spiny hooks ————	————	————	————→	
Parapodium 2	short 	prolonged ————	————	————→	
Setae	internal spiny hooks	protruding spiny hooks ————	————	————→	
Parapodium 3	short — 	————		————→ 	prolonged
Setae	limbate ————	————→	+ falcigers	internal spiny hooks	protruding spiny hooks
Subacicular hooks from set.	7-8	8-10	10-13	14-16	15-16
Branchiae from setiger	absent	11-13	11-14	11-14	10-12
Length (mm); setigers (no.)	12 ; 31	15 ; 50	19 ; 57	15^+; 41^+	45 ; 72
Width (mm)	0.7-1.0	1.0-1.3	0.8-1.3	1.1-1.8	1.8-3.5

***Rhamphobrachium* sp.** Juveniles of stages 1 and 2 range in length from 10–22 mm for 50–100 setigers. Frontal palps, tentacular cirri and branchiae absent in all specimens. Parapodia 1 and 2 range from short to prolonged, with internal to protruding spiny hooks. Parapodium 3 and subsequent ones short with upper limbate setae and 6–8 lower simple bidentate hooks with wings (Fig. 13c). These setae considered as precursors of subacicular hooks, because of their similar shape and position. Wings largest on hooks of setiger 3, becoming gradually smaller in subsequent segments until hooks resemble adult subacicular hooks, becoming reduced to 2 per parapodium by setiger 20–25, retained as such until the last few segments. In terminal 2 to 3 setigers, simple precursor subacicular hooks may be replaced by compound precursor subacicular hooks.

General Juvenile Characters of Onuphidae

Colour pattern. Many shallow-water onuphids have dark brown dorsal pigmentation, the pattern of which spreads in a definite sequence. The most common type is a series of dorsal horizontal bands (Fig. 34m). Initially there are two lateral patches per segment which spread towards the middle and form the band. *Diopatra aciculata* has a more complex pattern which starts with a median anterior patch and two lateral posterior patches on each segment (Fig. 12a). Both groups of patches spread, the anterior one laterally and the lateral ones medially (Fig. 12b), to be followed by a breaking up of the anterior lines into patches (Fig. 12c), the middle of which is the most distinctive and is usually the only one remaining in adults. Juveniles sometimes have a dark band on the peristomium (Fig. 12a) which is absent in adults.

Antennae. The development of antennae in embryos and larvae has been documented for a number of species, e.g. *Nothria elegans* (= *Kinbergonuphis elegans;* Blake, 1975). In juveniles the ceratophores are smooth, indistinctly ringed, or have less rings than in adults. The styles of young juveniles can be inflated and clavate (*Australonuphis;* Paxton, 1979: figs 59, 60) or subulate (*Hyalinoecia artifex;* Mangum & Rhodes, 1970: fig. 4), later becoming tapered and more slender. Fauchald (1982a) noted that small specimens usually have longer antennae than larger specimens of the same species relative to the total length of the body.

Frontal palps and tentacular cirri. Both sets of structures are absent in young juveniles. Their development is independent; in some species the frontal palps are formed first (Fig. 12), in others the tentacular cirri appear first (*Australonuphis*). Frontal palps appear as two protrusions marked off by a furrow from the labial palps, and then elongate (Paxton, 1979). The tentacular cirri start as lateral outgrowths on the anterior part of the peristomium, and elongate (Fig. 12b,c).

Eyes. A pair of anterior eyespots develops early in larvae (e.g. *Kinbergonuphis elegans;* Blake, 1975) and embryos (e.g. *Diopatra variabilis;* Krishnan, 1936). These eyespots may be followed by another posterior

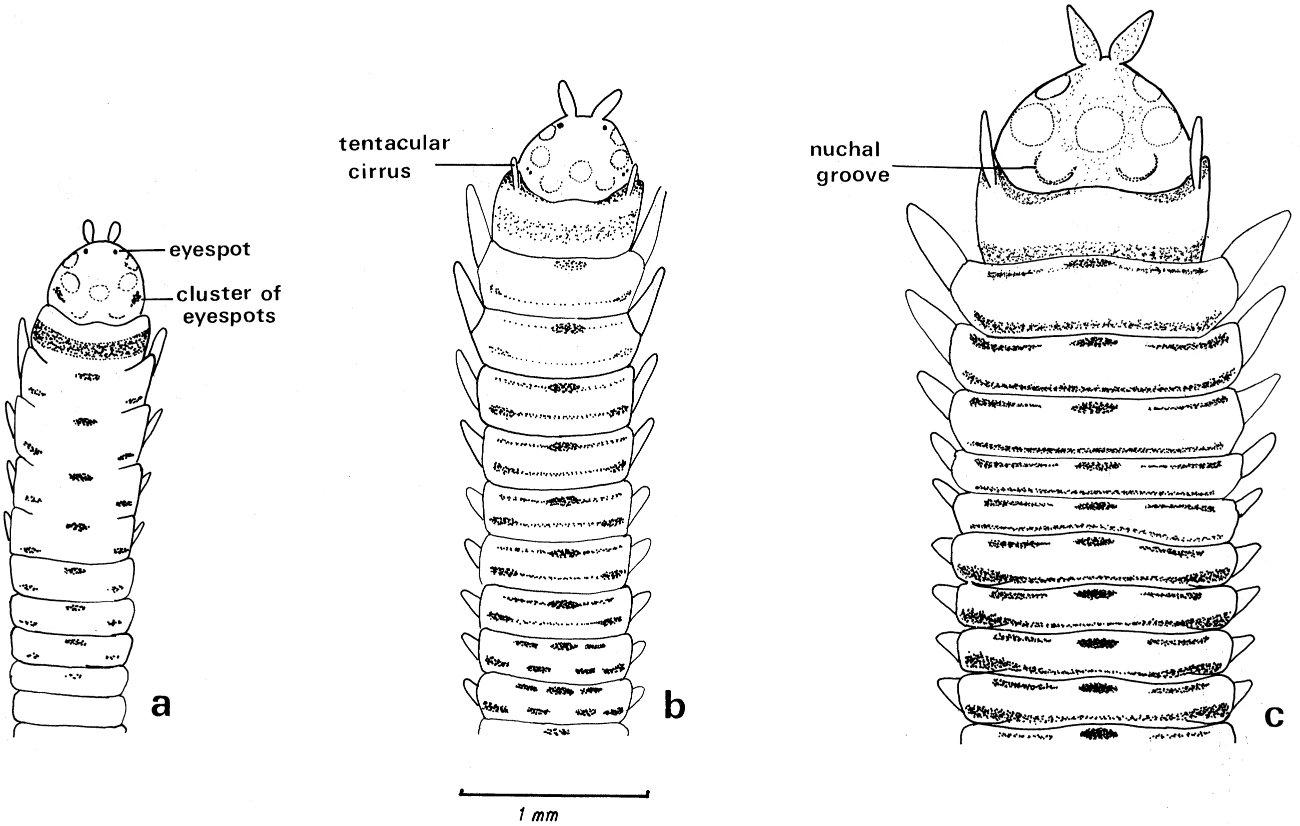


Fig. 12. Juveniles of *Diopatra aciculata* (parapodial detail and branchiae omitted): **a**, young juvenile; **b**, juvenile; **c**, young adult.

pair. The anterior pair is usually distinct while the posterior pair can consist of two clusters of eyespots (Fig. 12a). The anterior eyespots are retained only in the adults of some small species, while they are generally lost; the posterior ones are more often present in adults, but may be lost as well.

Nuchal grooves. Nuchal grooves are straight in small juveniles. They either remain as such *(Onuphis)* or become curved towards the median antenna (Fig. 30a). In species of *Diopatra* (Fig. 12) the grooves curve anteriorly at both ends, developing into a semicircle in small species, or an almost complete circle in large species (Fig. 23a).

Modified anterior parapodia. In *Rhamphobrachium ehlersi* the development of specialized setae precedes the prolongation of the modified parapodia. The number of modified parapodia in juveniles is less than in adults, where it is more or less stable within a species.

Branchiae. Young juveniles may develop ciliated juvenile branchiae on setigers 6–8 soon after the formation of these segments (Blake, 1975; Fauchald, 1982b). The juvenile branchiae may be retained and adult branchiae added, first posteriorly and later anteriorly when the worms are considerably larger, as in *Kinbergonuphis elegans* (Blake, 1975); or the larval branchiae are lost, the juveniles are abranchiate for a period of time and adult branchiae develop later, as in *Mooreonuphis jonesi* (Fauchald, 1982b). The development of adult branchiae can start as early as in 10-setiger worms (*Diopatra variabilis;* Krishnan, 1936), or not before they reach 50 setigers (*R. ehlersi*) or later. Species with compound branchiae add filaments as they grow, but remain within a certain range of development that is characteristic for the species.

Setae. The setal progression occurring in larvae, embryos and juveniles has been documented for *Diopatra variabilis* (Krishnan, 1936), *D. cuprea* (Allen, 1959), *Kinbergonuphis elegans* (Blake, 1975) and *Hyalinoecia araucana* (Carrasco, 1983).

The setal development in onuphids does not follow a single pattern; considerable differences occur even within one genus as is demonstrated for *R. ehlersi* and *R.* sp. above. Although these processes are not completely understood, an attempt is here made to identify general trends.

The presence of certain types of setae in larvae and juveniles that are absent in adults has been noted by several authors and referred to as 'provisional' setae by Krishnan (1936), as opposed to 'permanent' or adult setae. The provisional setae (Fig. 13) are reminiscent of eunicid setae, indicating their relict nature.

Simple provisional setae have been observed in *Rhamphobrachium* sp. and species of *Diopatra.* In *R.* sp. these consist of bidentate winged hooks (Fig. 13a) (see above). The two species of *Diopatra* studied were reported to have 'pointed setae' (Krishnan, 1936: fig. 12c) or 'curved pointed' (Allen, 1959: pl. V figs 29–32) in parapodium 1 and 'blunt-tipped' (Krishnan, 1936: fig. 12b) or 'short-tipped winged' (Allen, 1959: pl. V figs 32–34) in parapodia 2 to 4–7 in embryos and larvae. The newly formed posterior segments carry permanent or adult setae and, by the time the juveniles of *Diopatra* consist of 15 setigers, most provisional setae have been replaced by permanent setae. However, the distribution of these permanent setae is different from the adult pattern.

The provisional setae of *K. elegans* and *H. araucana* consist of compound falcigers. While adult-like setae of parapodium 1 also appear in about the 15-setiger juveniles in these two species, the remaining provisional setae are retained longer than in *Diopatra.*

Compound provisional setae (or falcigers) were observed in the present study in juveniles of *Rhamphobrachium, Onuphis, Kinbergonuphis* and *Hyalinoecia,* and thus appear to be more common than the simple types.

The provisional setae are the precursor setae for the hooks of the modified parapodia and for the subacicular hooks. Permanent or adult hooks are restricted to the first parapodia in young juveniles. From the second parapodia onwards the provisional setae are present until they are replaced by the adult hooks which appear sequentially until the typical number of parapodia with hooks for the particular species is attained. For instance, small juveniles of *K. taeniata* have permanent pseudocompound hooks on setigers 1–3 and provisional compound falcigers on setigers 4–7, while adults of the same species have seven setigers with pseudocompound hooks.

In species of *Rhamphobrachium,* the provisional falcigers are sometimes present for only a short period of time (e.g. *R. ehlersi,* stage 3). Rarely, compound falcigers are retained as a presumably neotenic feature in the first unmodified setigers of adults (e.g. *R. diversosetosum*); however, generally the presence of falcigers in anterior parapodia indicates the juvenile state of the specimen.

The 'large median hooks' characteristic of *Kinbergonuphis* and *Mooreonuphis* are absent in juvenile *K. taeniata,* and presumably in other species as well. These hooks may represent a relatively recent specialization, thus developing late in ontogeny.

Subacicular hooks start as one or two hooks in embryos or small juveniles either from setiger 6–8 in their adult form *(R. ehlersi, Diopatra* spp.), or as a provisional form from setiger 2–5 to be replaced by the adult form from about setiger 8. The provisional form is compound in *Onuphis* (Fig. 13a) and *K. elegans* (Blake, 1975: fig. 6c), and simple in *Rhamphobrachium* sp. (Fig. 13c). The anterior permanent subacicular hooks of *Diopatra* are parallel to the acicula and project far from their setal sacs (Fig. 13d).

Compound provisional subacicular hooks in the most posterior setigers of *Hyalinoecia tubicola* were observed a long time ago (Langerhans, 1880; Saint-Joseph, 1906; Eulenstein, 1914) and attributed to the juvenile state of the specimens, a statement that is supported here (Fig. 13e).

The origin of subacicular hooks remains at setiger

8–10 in the adults of a number of species, while in others the origin will move posteriorly until the adult origin is reached. This size dependent variation in the origin of subacicular hooks has been noted previously (Hobson, 1971; Amoureux, 1982; Fauchald, 1982a). In most species the adult origin of subacicular hooks is constant; however, in *Australonuphis* it continues to be displaced posteriorly, with subacicular hooks starting at setiger 70–80 in very large specimens.

Limbate and pectinate setae were found only in their permanent form. Limbate setae are present early in development, while pectinate setae usually appear later.

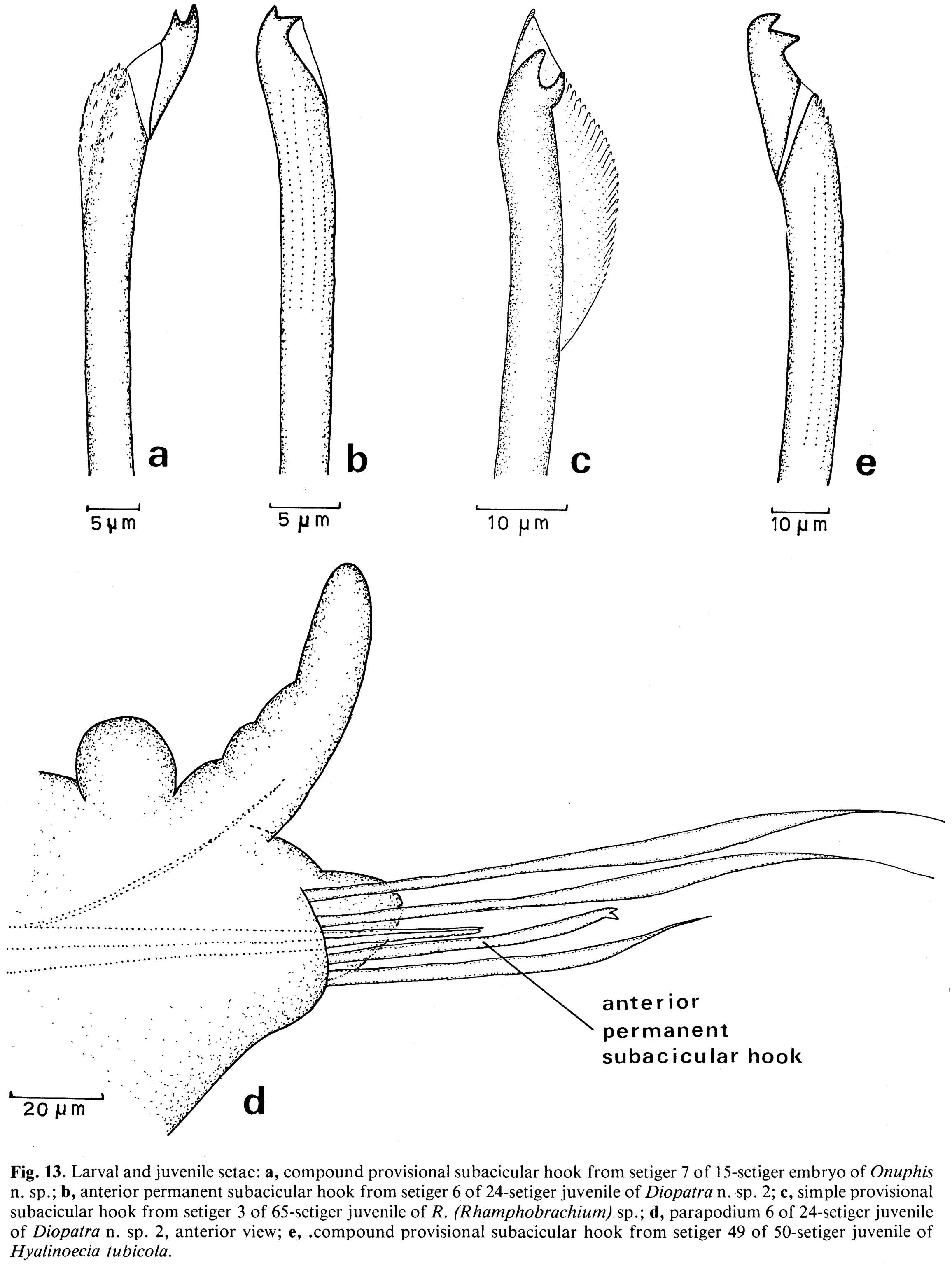


Fig. 13. Larval and juvenile setae: **a,** compound provisional subacicular hook from setiger 7 of 15-setiger embryo of *Onuphis* n. sp.; **b,** anterior permanent subacicular hook from setiger 6 of 24-setiger juvenile of *Diopatra* n. sp. 2; **c,** simple provisional subacicular hook from setiger 3 of 65-setiger juvenile of *R. (Rhamphobrachium)* sp.; **d,** parapodium 6 of 24-setiger juvenile of *Diopatra* n. sp. 2, anterior view; **e,** .compound provisional subacicular hook from setiger 49 of 50-setiger juvenile of *Hyalinoecia tubicola.*

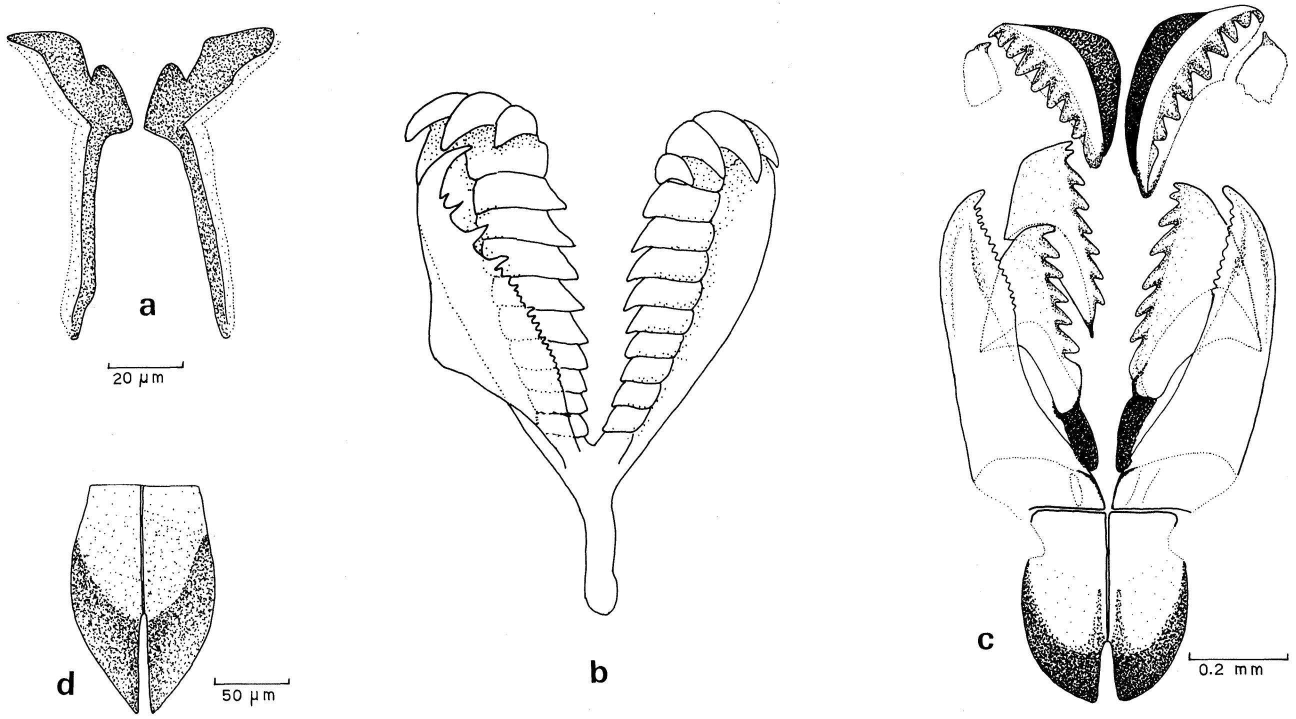


Fig. 14. Larval and juvenile jaws: **a,** mandibles of 40-setiger juvenile of *Diopatra* n. sp. 2; **b,** maxillae of 11-setiger embryo of *Diopatra cuprea* (= *D.* sp.), X680 (from Monro, 1924: fig. 6); **c,** maxillae of 170-setiger juvenile of *Australonuphis* sp. (Mx III to Mx V not in natural position); **d,** carriers of 40-setiger juvenile of *Diopatra* n. sp. 2.

Jaws. The larval mandibles are sclerotized and can be noted as a dark, X-shaped structure (Fig. 14a) through the body wall. This part will be enlarged by the exterior deposition of sclerotized proteins and carbonates, throughout life, at the areas in contact with the cuticular epithelium, i.e. ventrally and laterally. The initial part is still visible in adults dorsally as small dark lines, or in some species it can even be seen in a ventral view through the carbonate layer (Fig. 49g). In decalcified mandibles the initial structures are sometimes longer than the sclerotized plate and have been referred to as 'Stacheln' or thorns by von Haffner (1959).

The development of the larval maxillary apparatus has been described for several species (e.g. *K. elegans;* Blake, 1975) and its function has been observed in live specimens of *Diopatra cuprea* (Allen, 1959). The larval maxillary apparatus (Fig. 14b) can be recognized in a 5-setiger worm and consists of narrow carriers, a pair of maxillae consisting of a series of separate, adjoining pieces, each one with a tooth, and a single left maxilla with small proximal and larger distal teeth. The juvenile apparatus (Fig. 14c) has the typical adult complement of maxillary plates but differs from the adult in detail and proportions. Most of it is very delicate and hardly sclerotized, while the lamellae connecting MxI and Mx II, and the attachment lamellae of Mx IV stand out through their dark sclerotization. Juvenile carriers (Fig. 14c,d) are often posteriorly extended and darkly sclerotized.

Although only on circumstantial evidence, it was assumed that the maxillary apparatuses grow during the lifetime of the animal (Paxton, 1980) and are not replaced as was previously suggested. Paxton (1980) showed that the number of teeth on Mx II and Mx III increased by the addition of new distal teeth to the plates. Fauchald (1982b) found larval jaw apparatuses in the gut of brooded larvae of *Mooreonuphis jonesi* and interpreted them as shed larval apparatuses. It is likely that the larval jaw apparatus is discarded and replaced by the juvenile one which grows and is retained throughout life. The shedding of the larval maxillae is supported by the lack of observed transition stages between larval and juvenile apparatuses, and the similarity of the larval maxillae to the more ancestral ctenognath maxillae of the family Dorvilleidae which are replaced periodically.

TAXONOMIC ACCOUNT

Evolution within the family Onuphidae has resulted in a radiation of species within a number of evolutionary lines. During the course of this radiation, changes have occurred in the morphology of the various groups as well as their tube consistency and construction, and morphology of oocytes. The taxonomic categories recognized within the family are defined below on the basis of these criteria and consist of two subfamilies and 22 genera (see Table 3 for synopsis).

Table 3. Classification Synopsis of the family Onuphidae

Subfamily	Group	Complex	Genus	Synonym
HYALINOECIINAE new subfam.	*Nothria*		*Nothria* Malmgren, 1866	*Northia* Johnston, 1865
			Anchinothria n. gen.	—
	Hyalinoecia		*Hyalinoecia* Malmgren, 1866	*Paronuphis* Ehlers, 1877
			Leptoecia Chamberlin, 1919	*Parhyalinoecia* H.-Sch., 1975
			Neonuphis Kucheruk, 1978	—
			Hyalospinifera Kuch. 1979b	—
ONUPHINAE	*Diopatra*		*Notonuphis* Kucheruk, 1978	—
		Diopatra	*Paradiopatra* Ehlers, 1887	*Sarsonuphis* Fauch., 1982a
			Diopatra Aud. & M.Edw., 1833	—
			Epidiopatra Augener, 1918	—
		Rhamphobrachium	*Brevibrachium* n. gen.	—
			Longibrachium n.gen	—
			Rhamphobrachium Ehlers, 1887	*Paranorthia* Moore, 1903
	Onuphis	*Australonuphis*	*Australonuphis* Paxton, 1979	*Americonuphis* Orens., 1974
			Hartmanonuphis n. gen.	—
			Hirsutonuphis n. gen.	—
			Aponuphis Kucheruk, 1978	—
			Kinbergonuphis Fauch., 1982a	—
			Mooreonuphis Fauchald, 1982a	—
			Onuphis Aud. & M. Edw., 1833	—
			Heptaceras Ehlers, 1868	*Tradopia* Baird, 1870

Key to Genera of Onuphidae

1. Tentacular cirri present (Fig. 3a). 2

——Tentacular cirri absent (Fig. 17a). 16

2. Branchial filaments arranged spirally (Fig. 23d). .... *Diopatra*

——Branchial filaments arranged otherwise or absent. 3

3. Peristomium middorsally incised (Fig.36a). .... *Heptaceras*

——Peristomium complete. 4

4. Modified parapodia with extensile setae (shafts extending back through at least 5 segments), usually with spiny shafts and distally recurved. 5

——Modified parapodia with short setae (shafts limited to one segment), usually without spiny shafts, distally uni- to tridentate. 7

5. Three pairs of modified parapodia (with 3 setae each) with spiny shafts and distally recurved (Fig. 27e). .... *Rhamphobrachium*

——Four to 5 pairs of modified parapodia (with 4 or more setae each) with spiny shafts, or 3 pairs of modified parapodia with smooth shafts. 6

6. Antennae moderately long, to setiger 6–15 (Fig. 26c); 4 pairs of modified parapodia with single postsetal lobes and setae with spiny shafts and distally curved. .... *Longibrachium*

——Antennae short, to setiger 1; 3–5 pairs of modified parapodia with double postsetal lobes (Fig. 25b) and setae with spiny shafts and distally uni- to tridentate (Fig. 25e,k) or with smooth shafts and distally recurved. .... *Brevibrachium*

7. Setiger 1 and its parapodia usually enlarged; scoop-shaped pectinate setae (Fig. 15l). 8

——Setiger 1 not enlarged; flat pectinate setae (Fig. 29e). 9

8. Modified parapodia with large, auricular presetal and subulate postsetal lobes (Fig. 15c). .... *Nothria*

——Modified parapodia with bi- to trilobed presetal and short, subconical postsetal lobes (Fig. 16c). . . . . *Anchinothria*

9. Tentacular cirri inserted in middle of peristomium (Fig. 28a); modified parapodia directed strongly anteroventrally, ventral cirri of setiger 5 almost touching in ventral midline (Fig. 29a). . . . . *Americonuphis*

——Tentacular cirri inserted subdistally to distally on peristomium; modified parapodia directed anteroventrally to -laterally or -dorsally, ventral cirri of setiger 5 far apart. 10

10. Pseudocompound hooks of modified parapodia with long, pointed hoods (Fig. 22c,d,j). . . . . *Paradiopatra*

——Pseudocompound hooks of modified parapodia with short or without hoods. 11

11. Middorsal part of peristomium with anterior fold, separating it from prostomium (Fig. 3a). 12

——Middorsal part of peristomium without anterior fold, appearing to extend to median antenna (Fig. 30a). 14

12. Ceratophores of antennae with 10–25 rings, anterior styles shorter than their ceratophores; large median hooks absent. . . . . *Onuphis*

——Ceratophores of antennae with 3–7 rings, anterior styles longer than their ceratophores; large median hooks (Fig. 35g) often present. 13

13. Compound limbate setae (= spinigers) (Fig. 35h) present in anterior unmodified setigers. . . . . *Mooreonuphis*

——Compound limbate setae absent. . . . . *Kinbergonuphis*

14. Pseudocompound (Fig. 30f) and subacicular hooks (Fig. 30j) distally entire and without hoods. . . . . *Australonuphis*

——Pseudocompound hooks uni- to tridentate, subacicular hooks bidentate, both types hooded. 15

15. Ceratophores of antennae with 10–15 rings; branchiae from setiger 6–9; maxillary carriers with darkly sclerotized lateral triangles (Fig. 32i). . . . . *Hirsutonuphis*

——Ceratophores of antennae with 6–8 rings; branchiae from setiger 1; maxillary carriers without darkly sclerotized lateral triangles (Fig. 31i). . . . . *Hartmanonuphis*

16. Branchial filaments arranged spirally (Fig. 24d). . . . . *Epidiopatra*

——Branchiae absent or as single filaments. 17

17. Ceratophores of antennae with 10–20 rings; anterior 5 setigers with hooks. . . . . *Aponuphis*

——Ceratophores of antennae with 2–5 rings; anterior 1–3 setigers with hooks. 18

18. Modified parapodia with low presetal lobes (Fig. 21d); subacicular hooks in ventral position in fascicle, starting on setiger 9–10. *Notonuphis*

——Modified parapodia with large, auricular presetal lobes (Fig. 17c); subacicular hooks in median position in fascicle (Fig. 17d), starting on setiger 12–35 or later. 19

19. Frontal palps well developed; tough, quill-like tubes. *Hyalinoecia*

——Frontal palps reduced or absent; fragile tubes. 20

20. Branchiae as single filaments; anterior hooks with pointed hoods (Fig. 20f,g). *Hyalospinifera*

——Branchiae absent; anterior hooks with short, blunt hoods. 21

21. Ceratophores of antennae short (⅓ to ½ length of prostomium); tubes flattened with lateral supports. . . . . *Leptoecia*

——Ceratophores of antennae very short (1/10 length of prostomium); tubes round in transverse section without lateral supports. . . . . *Neonuphis*

Family ONUPHIDAE Kinberg

Onuphiaea Kinberg, 1865: 560. Type genus: *Onuphis* Audouin & Milne Edwards, 1833.
Onuphidae Malmgren, 1867: 180.

Diagnosis. Prostomium with 5 dorsal antennae with ceratophores, and 2 frontal palps.

Definition. Prostomium oval to triangular, wider than long; 5 dorsal antennae: pair of anterior lateral, pair of posterior lateral and single median; smooth to ringed ceratophores and distal styles; 2 pairs of ventral palps: smaller frontal palps (rarely absent) and larger posterior bulbous labial palps; eyes present or absent. Nuchal grooves straight to almost circular. Peristomium apodous; pair of dorsal tentacular cirri present or absent; large semilunar lower lip ventrally.

Anterior 1–8 pairs of parapodia modified, with subulate to digitiform ventral cirri, followed by a transition zone of globular ventral cirri, or ventral pads with reduced cirri, thereafter only glandular pads. Dorsal cirri present throughout or reduced to absent on posterior setigers. Branchiae, when present, with simple, pectinately or dichotomously branched, or spirally arranged filaments.

Parapodia subbiramous (with or without reduced notosetae in dorsal cirri). Modified parapodia with simple to pseudocompound hooks, pectinate and/or limbate setae present or absent; setae of unmodified parapodia pectinate, simple to compound limbate (spinigers), rarely falcigers, subacicular hooks. Anal cirri 2 or 4.

Jaws consisting of ventral mandibles and dorsal maxillae formed of 4½–5½ pairs of toothed plates and pair of short carriers. Mostly tubicolous. Nurse cells associated with oocytes in 2 strings or cluster.

HYALINOECIINAE n. subf.

Type genus: *Hyalinoecia* Malmgren, 1866.

Diagnosis. Lower limbate setae present to end of body; subacicular hooks in median position in fascicle.

Definition. Frontal palps usually present, rarely absent. Nuchal grooves straight to slightly curved. Peristomium with middorsal anterior fold, ventral lip without median section.

Setiger 1 longer than following setigers. Anterior 1–3 pairs of parapodia modified and directed anteroventrally, parapodia 1 usually prolonged. Presetal lobes of modified parapodia usually auricular, as long as postsetal lobes. Dorsal cirri without basal swelling or process; often reduced to absent in posterior parapodia. Branchiae, when present, with single or dichotomously branched filaments.

Parapodia subbiramous (dorsal cirri without internal notosetae). Hooks of modified parapodia uni- to bidentate. Lower limbate setae simple, present to end of body. Subacicular hooks in median position in fascicle. Two anal cirri.

Mandibles often longer than maxillary carriers and Mx I together. Maxilla III long; Mx VI absent. Nurse cells associated with oocytes attached in single cluster. Tubes circular or oval in transverse section, of translucent substance without external covering; or parchment-like or translucent inner layer, outer layer of foreign particles.

Genus Nothria Malmgren

Fig. 15a–n

Nothria Malmgren, 1866: 66. Type species: *Onuphis conchylega* Sars, 1835: 61, by original designation. Gender: feminine.
Northia Johnston, 1865: 136. Preoccupied by *Northia* Gray, 1847 (Mollusca).

Material examined. *Nothria conchylega*—**Norway:** Ramfjord near Tromsφ—5 (AM W.198975) and 2 (AM W.198976). *N.* n.sp.—**Australia:** Queensland: Fraser Island—4 (AM W.198982).

Diagnosis. Modified parapodia with large, auricular presetal lobes; pectinate setae scoop-shaped.

Definition. Prostomium (Fig. 15a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with smooth ceratophores or with 3–5 rings, and moderately long to long posterior styles: longest (median) to setiger 5–13. Frontal and labial palps oval, latter with small or without median section (Fig. 15b). Nuchal grooves straight with small middorsal separation; peristomium short to moderately long, with distally to subdistally inserted tentacular cirri.

Anterior 2–3 pairs of parapodia modified; parapodia 1 (Fig. 15c) prolonged, with large auricular presetal and subulate postsetal lobes. Anterior dorsal cirri subulate to digitiform, more posterior ones reduced; ventral cirri subulate on anterior 2–3 setigers. Branchiae from setiger 8–13 as single, strap-like filaments, or absent.

Hooks of modified parapodia uni- to bidentate, simple to pseudocompound, with or without blunt hoods (Figs 15d–f,k); scoop-shaped pectinate setae (Fig. 15l) and limbate setae (Fig. 15g,h) from setiger 2; subacicular hooks (Fig. 15i) from setiger 8–14. Pygidium with 2 anal cirri (Fig. 15j).

Jaws with mandibles (Fig. 15m); maxillae (Fig. 15n) with left Mx II with or without distal fang; Mx III distally shorter than left Mx II. Short, flattened tubes, consisting of translucent or parchment-like inner lining and outer layer of foreign particles. Latter consist usually of sand and shell fragments, attached with the flat or concave side to the lining, thus making a flattened

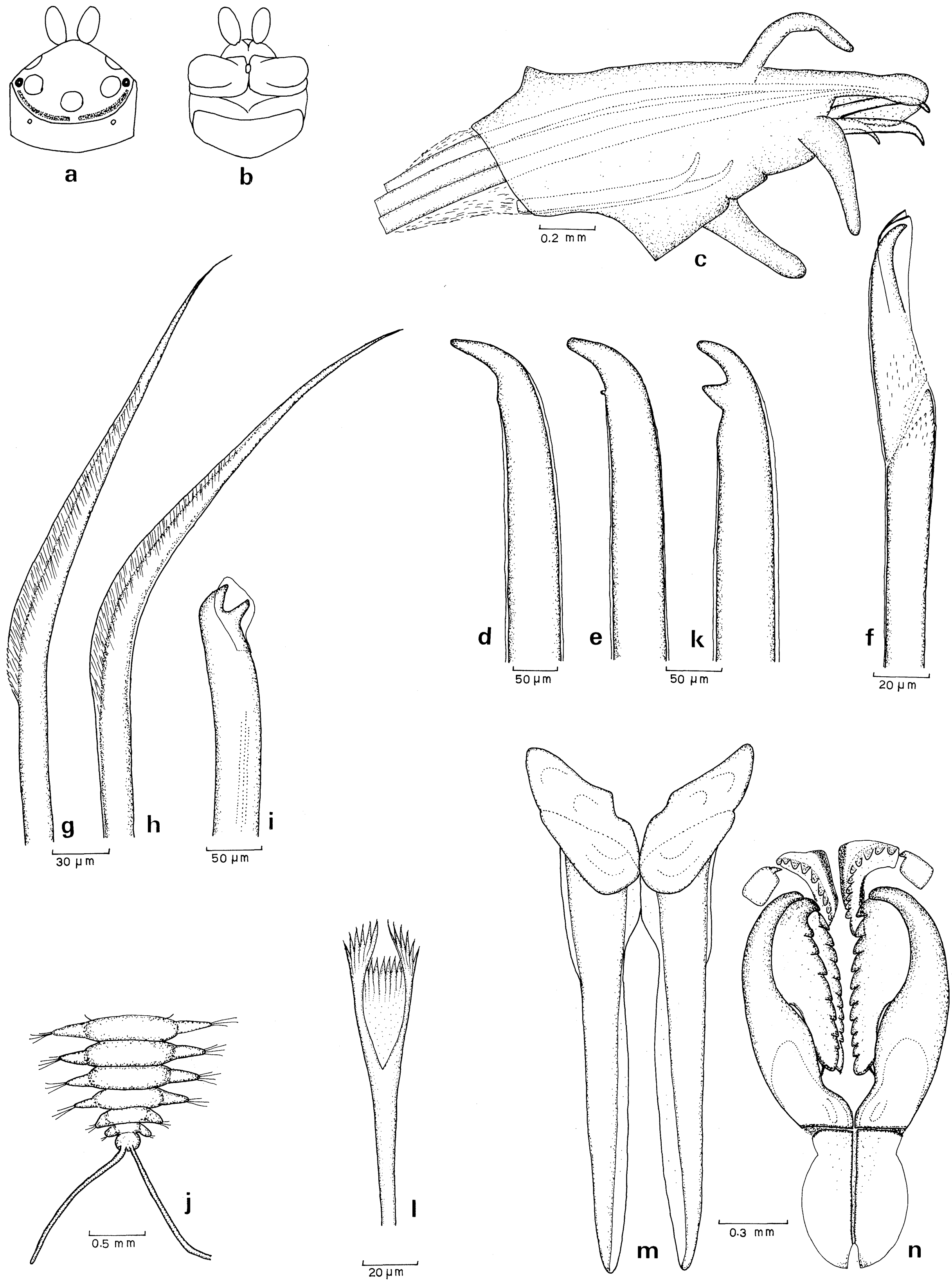


Fig. 15. *Nothria conchylega* (AMS W.198975): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, posterior view; **d**, unidentate simple hook from setiger 1; **e**, bidentate simple hook with tiny secondary tooth from same; **f**, unidentate pseudocompound hook from setiger 3; **g**, upper limbate seta from setiger 13; **h**, lower limbate seta from same; **i**, subacicular hook from setiger 30; **j**, posterior end. *Nothria* n. sp. (AMS W.198982): **k**, bidentate simple hook with large secondary tooth from setiger 1; **l**, scoop-shaped pectinate seta from setiger 12; **m**, mandibles; **n**, maxillae.

tube; rod-like lateral supports absent.

Size. Short-bodied with limited number of segments; length to 52 mm for 63 setigers, width to 6 mm with parapodia.

Remarks. Johnston (1865) erected the genus *Northia* for species with single branchial filaments, and included *Nereis tubicola* and *Onuphis conchylega* Sars, 1835. However, *Northia* was preoccupied (*Northia* Gray, 1847 in Mollusca) and was changed to *Nothria* by Malmgren (1866) and the latter species was designated type species. The definition of *Nothria* remained the same and contained species with tentacular cirri, anterior parapodia that were not markedly modified, and branchiae with single filaments or absent. Although it was generally recognized that this was an unnatural grouping and *Nothria* was perhaps a synonym of *Onuphis,* the taxon was retained to separate the large group of species (Hartman, 1944; Fauchald, 1968; 1972; 1977). Some authors treated *Nothria* as a subgenus (Pettibone, 1963; Day, 1967). In 1970 Pettibone redefined *Nothria* on the basis of its type species, *N. conchylega,* and showed that it is characterized by its modified anterior parapodia with specialized setae and flattened tube. This redefinition was followed by Orensanz (1974), Kucheruk (1978), Fauchald (1982a) and is accepted here.

Fauchald (1982a) recognized eight species and gave a key to these. *Nothria abyssia, Onuphis africana* and *Paronuphis solenotecton,* referred by Fauchald (1982a) to *Paradiopatra (= Anchinothria)*, are here considered as species of *Nothria.* Although the types were not examined, the original illustrations show the characteristic auricular presetal lobes. The following species are recognized: *N. conchylega* (Sars, 1835); *N. abyssia* Kucheruk, 1978; *N. africana* (Augener, 1918); *N. anoculata* Orensanz, 1974; *N. atlantica* (Hartman, 1965); *N. australatlantica* Fauchald, 1982c; *N. britannica* (McIntosh, 1903); *N. hawaiiensis* Pettibone, 1970; *N. hyperborea* (Hansen, 1878); *N. mannarensis* Rangarajan & Mahadevan, 1961; *N. occidentalis* Fauchald, 1968; *N. solenotecton* (Chamberlin, 1919); *N. textor* Hartman & Fauchald, 1971; *N.* n.sp.

Distribution. World-wide; shallow to 5200 m.

Anchinothria n. gen.

Fig. 16a–k

Type species: *Diopatra pourtalesii* Ehlers, 1887: 74. Gender: feminine.

Material examined. *Diopatra pourtalesii*—**Cuba:** near Havana—SYNTYPE (MCZ 687); off Cuba—SYNTYPE (MCZ815); **Caribbean:** S of Rebecca Channel—SYNTYPE (tube only) (MCZ 785); Sta. Lucia—2 (ZMH PE-779, PE-782); **U.S.A.**: Florida—SYNTYPE (MCZ 874). *Paranorthia fissurata* —**Mexico:** Lower California—HOLOTYPE (USNM 19151). *A. sombreriana*—**Caribbean:** Sta. Lucia—3 (ZMH PE-782a).

Diagnosis. Modified parapodia with bi- to trilobed presetal lobes; pectinate setae scoop-shaped.

Definition. Prostomium (Fig. 16a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with smooth ceratophores or with 2–5 rings and moderately long to long posterior styles: longest (median) to setiger 5–13. Frontal and labial palps oval, latter with or without distinct distal lobe, without median section (Fig. 16b). Nuchal grooves straight with small middorsal separation; peristomium short to moderately long, with subdistally to distally inserted tentacular cirri.

Anterior 2–3 pairs of parapodia modified; parapodia 1 (Fig. 16c) usually prolonged, with bi- to trilobed presetal and short, subconical postsetal lobes; parapodia 2–3 with shorter presetal and longer, digitiform postsetal lobes. Dorsal cirri subulate to digitiform; ventral cirri subulate on anterior 2–3 setigers. Branchiae from setiger 8–17, as simple strap-like or dichotomously branched filaments (Fig. 16d), or absent.

Hooks of modified parapodia uni- to bidentate, simple to pseudocompound, with or without blunt hoods (Fig. 16e); scoop-shaped pectinate setae (Fig. 16f) and limbate setae (Fig. 16g,h) from setiger 2; subacicular hooks (Fig. 16i) from setiger 8–14.

Jaws with mandibles (Fig. 16j), and maxillae (Fig. 16k) with left Mx II with distal fang, Mx III distally shorter than left Mx III. Short to moderately long, round or flattened tubes, consisting of translucent or parchment-like inner lining, with or without thin outer layer of mud, and with scattered foreign materials. Latter consisting often of rod-like pieces, e.g. glass sponge spicules, echinoid spines, even pine-needles, often used as lateral supports.

Size. Short-bodied with limited number of segments (complete specimen of *A. cirrobranchiata* measures 35 mm long for 55 setigers, 3 mm wide) to moderately long (up to 112 mm for 100 setigers, width 7 mm).

Etymology. The name *Anchinothria* is derived from the Greek *anchi* for near and *Nothria,* emphasizing the close relationship between the two genera.

Remarks. The genus *Anchinothria* is erected for those species that were referred by Pettibone (1970) and Fauchald (1982a) to *Paradiopatra* Ehlers. As discussed below (see 'Remarks' for *Paradiopatra)* the first designated type species of *Paradiopatra, Diopatra (Paradiopatra) fragosa* Ehlers, 1887, is not congeneric with the species of *Paradiopatra* as defined by Pettibone (1970) and Fauchald (1982a).

The type species of *Anchinothria, Diopatra pourtalesii,* can be recognized by its characteristic tubes, which are flattened, have laterally attached supports consisting of echinoid spines or skeletal parts of other animals and are sometimes covered with transversely attached glass sponge spicules. This type of tube was first mentioned by Pourtalès (1869), and the tube only was described by Ehlers (1879) as *Diopatra pourtalesii* in a preliminary report. Ehlers (1887) gave a complete description of the animal and listed seven localities in the Caribbean for his specimens, most of which are in the collections of the MCZ. These syntypes were

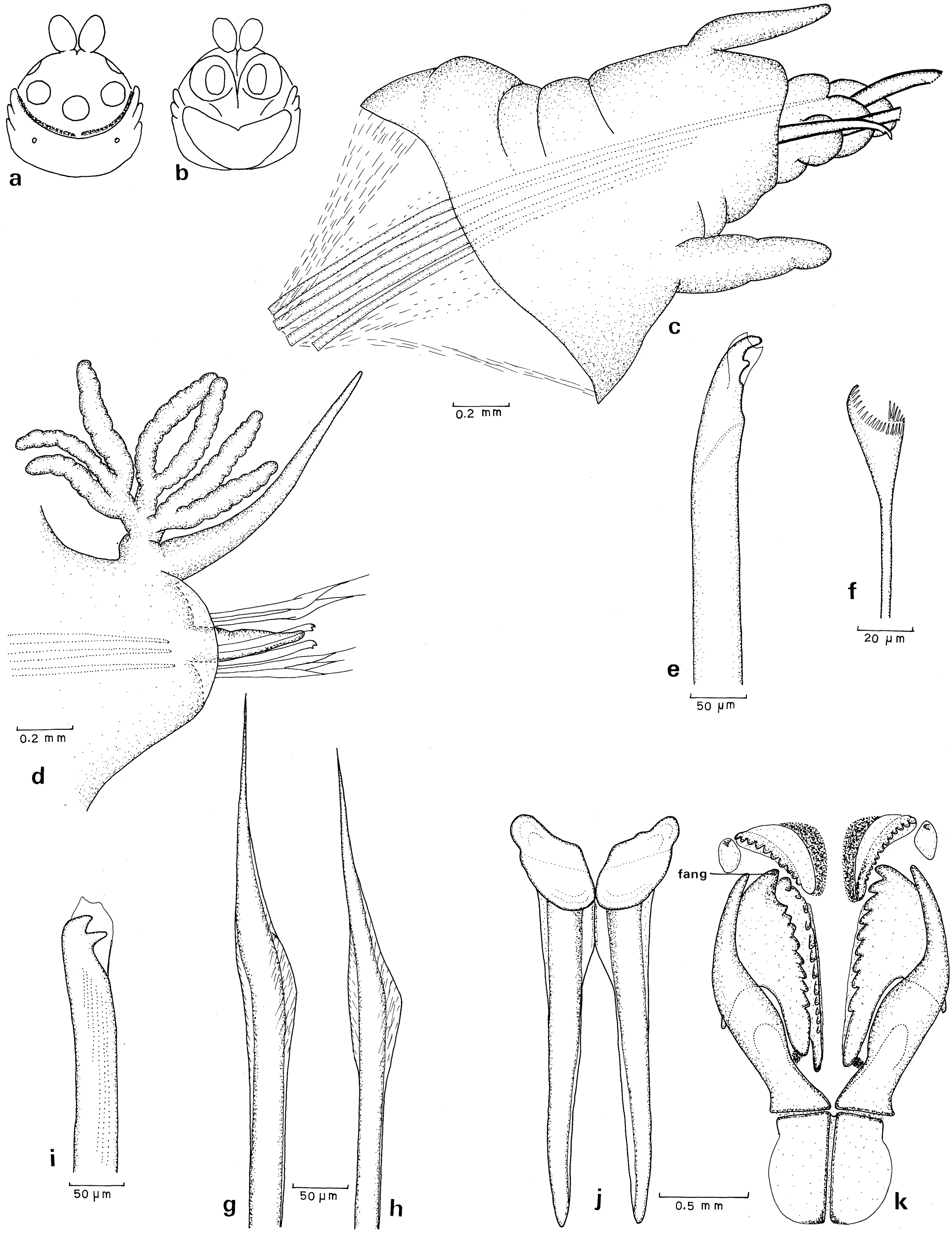


Fig. 16. *Anchinothria pourtalesii* (ZMH PE-779): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 1, anterior view; **d,** parapodium 14, anterior view; **e,** bidentate pseudocompound hook from setiger 1; **f,** scoop-shaped pectinate seta from setiger 14; **g,** upper limbate seta from same; **h,** lower limbate seta from same; **i,** subacicular hook from same; **j,** mandibles; **k,** maxillae.

examined by Fauchald (1982a) who stated that none were specifically mentioned by Ehlers (1887). Two specimens, not listed among the original localities, with the following label: 'Diopatra Pourtalesi Ehl., Depth 422 fms., Sta. Lucia, A. Agassiz 1878/79', were apparently retained by Ehlers and are now in the collections of the ZMH. The branchiae commence at setiger 9–10 in one specimen (PE-779) and 11 in the other (PE-782), and have a maximum of 7–9 filaments. The syntypes at the MCZ have branchiae from setiger 9–12, and maximally 4–5 filaments. In the description, Ehlers stated that branchiae originate on setigers 7–9, and have maximally 8 filaments, while in the figured specimen (pl. 19 fig. 6), they start at setiger 10. It is more likely that the description is based on the specimens retained in Germany (and Fig. 6 on specimen PE-782) than those deposited at the MCZ.

The anterior pseudocompound hooks are bidentate (Fig. 16e) but they are unusual in that the hood originates far distally from a protrusion that could be interpreted as a third tooth, as was done by Fauchald (1982a). The branchiae (Fig. 16d) appear in a bundle with each initial branch usually giving rise to two, rarely three filaments. This arrangement has been clearly illustrated by Ehlers (1887: pl. 19 fig. 10) and Pettibone (1970: figs 61h,k). Fauchald (1982a) described the branching as 'clearly pectinate'. The syntypes were examined in the present study and found to have dichotomously branched branchiae as well. However, since they have only 4-5 branchial filaments, the true pattern is not as obvious as in the larger specimens.

The following species are referred to *Anchinothria.* This list is, with some modifications, based on Fauchald (1982a) who gave a key to species (= *Paradiopatra): Diopatra pourtalesii* Ehlers, 1879; *Nothria abranchiata* McIntosh, 1885; *Paranorthia antarctica* Hartman, 1967b; *Onuphis cirrobranchiata* Moore, 1903; *Onuphis cobra* Chamberlin, 1919; *Onuphis crassisetosa* Chamberlin, 1919; *Paranorthia fissurata* Fauchald, 1972; *Diopatra (Paradiopatra) glutinatrix* Ehlers, 1887; *Nothria hiatidentata* Moore, 1911; *Nothria macrobranchiata* McIntosh, 1885; *Nothria pycnobranchiata* McIntosh, 1885; *Nothria sombreriana* McIntosh, 1885.

Distribution. World-wide; in 36–3931 m, most species deeper than 500 m (see Fauchald, 1982a).

Genus *Hyalinoecia* Malmgren

Fig. 17a–l

Hyalinoecia Malmgren, 1866: 67. Type species: *Nereis tubicola* Müller, 1776: 18, by monotypy. Gender: feminine.

Paronuphis Ehlers, 1887: 78. Type species: *Onuphis (Paronuphis) gracilis* Ehlers, 1887: 78, by monotypy.

Material examined. *Hyalinoecia tubicola*—**Australia:** Tasmania—4 (AM W.198988) and 2 (NMV). *H.* nr *tubicola*—**Australia:** Western Australia—6 (WAM 57-79) and others (WAM). *Paronuphis bermudensis*—**Bermuda:** HOLOTYPE (AHF Poly 0734); **Brazil:** Pernambucco—5 (AHF). *H. ?brevicornis*—**Australia:** Queensland: Fraser Island—9 (AM W.198987). *H.* sp.—**Australia:** New South Wales: off Wollongong—4 (AM W.198989).

Diagnosis. Frontal palps well developed; subacicular hooks in median position; maxilla V present; tubes secreted entirely by inhabitants, round in transverse section, without lateral supports.

Definition. Prostomium (Fig. 17a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with ceratophores with 2–5 rings and long styles: longest (median) to setiger 8–14. Frontal palps rounded to subulate; labial palps rounded, without median section (Fig. 17b). Nuchal grooves straight with small to moderately large middorsal separation; peristomium short to moderately long; tentacular cirri absent.

Anterior 2–3 pairs of parapodia (Fig. 17c) modified; parapodia 1 (often also 2 and 3) prolonged, with large auricular presetal and subulate postsetal lobes. Anterior dorsal cirri large, later ones reduced; ventral cirri digitiform on anterior 3–4 setigers. Branchiae from setiger 18–33, as single, strap-like filaments (Fig. 17d), or absent.

Hooks of modified parapodia uni- to bidentate, simple to pseudocompound, with or without hoods (Fig. 17e,f); flat pectinate setae (Fig. 17g) and limbate (Fig. 17h,i) setae from setiger 2; subacicular hooks (Fig. 17j) from setiger 15–30.

Jaws with mandibles (Fig. 17k) and maxillae (Fig. 17l). Tubes longer than inhabitants, round in transverse section, quill-like, with internal valves; of translucent, usually tough substance, without external covering of foreign particles.

Size. Small to moderately large; length to 18 cm, width to 6 mm.

Remarks. Blainville (1828) provided the name Nereitube as a genus for *Nereis tubicola* Müller. However, this name is vernacular and thus considered as invalid.

Paronuphis Ehlers, 1887 was characterized as an abranchiate, *Hyalinoecia*-like genus. Augener (1906) pointed out that the type species, *O.(P.) gracilis,* represented a juvenile *Hyalinoecia* and referred it to this genus, a decision which has more recently been supported by Mangum & Rhodes (1970) who believed that *O.(P.) gracilis* is an intermediate between juvenile and adult forms of *H. artifex.*

Hartman (1965) described the abranchiate *Paronuphis bermudensis* and distinguished it from *O.(P.) gracilis* by having long-appendaged, composite falcigers in the anterior parapodia, and very short-appendaged, composite falcigers (= compound subacicular hooks) in posterior segments. These typical juvenile characters are present in the holotype while larger specimens from station Ch35Dr12 have simple to short-appendaged pseudocompound hooks in setigers 1 and 2, but still have compound posterior subacicular hooks and are still abranchiate. Hartman mentioned a specimen from sta. Be7 with ova and embryos in its body cavity, demonstrating the maturity of these small specimens. Unfortunately, this particular specimen cannot be located [Williams (AHF), personal communication].

Small abranchiate species are found in several onuphid genera in which most species have branchiae. This condition is not considered to be of generic status. Hence, in agreement with Kucheruk (1978), *Hyalinoecia* is here defined as having single branchial filaments or being abranchiate, and *Paronuphis bermudensis* Hartman, 1965 is referred to *Hyalinoecia*.

Fauchald (1977) recognized 20 species.

Distribution. World-wide; shallow to 2448 m.

Genus *Leptoecia* Chamberlin
Fig. 18a–h

Leptoecia Chamberlin, 1919: 319. Type species: *Leptoecia abyssorum* Chamberlin, 1919: 320, by original designation. Gender: feminine.

Parhyalinoecia Hartmann-Schröder, 1975: 65. Type species:

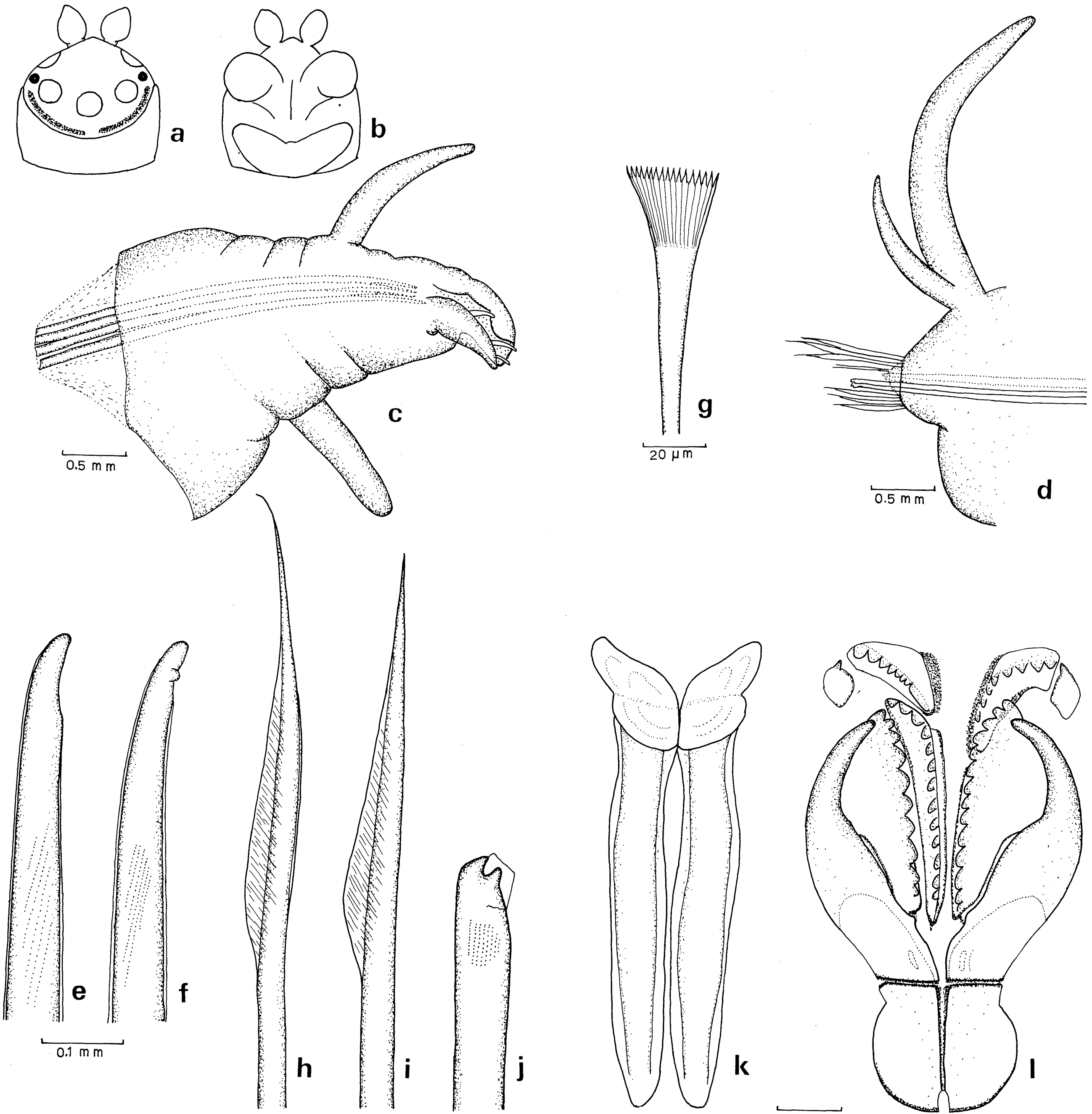


Fig. 17. *Hyalinoecia tubicola* (AM W.198988): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, posterior view; **d**, parapodium 29, anterior view; **e**, unidentate simple hook from setiger 1; **f**, bidentate simple hook from same; **g**, pectinate seta from setiger 29; **h**, upper limbate seta from same; **i**, lower limbate seta from same; **j**, subacicular hook from same; **k**, mandibles; **l**, maxillae.

Parhyalinoecia apalpata Hartmann-Schröder, 1975: 65, by original designation.

Material examined. *Leptoecia abyssorum*—**Ecuador**—Holotye (USNM 19406). *Parhyalinoecia apalpata*—**Portugal**-Holotype (ZMH P-13630).

Diagnosis. Frontal palps reduced or absent; tubes secreted entirely by inhabitants, oval in transverse section, with lateral thickenings on both sides.

Definition. Prostomium (Fig. 18a) anteriorly rounded. Posterior antennae on posterior part of prostomium with short ceratophores (⅓-½ length of prostomium), smooth or with 2-4 indistinct rings, and long styles. Frontal palps reduced to ventral semicircular protrusions, or absent; labial palps reduced (Fig. 18b). Nuchal grooves slightly curved; peristomium short to long with weakly defined ventral lip; tentacular cirri absent.

Anterior 1-2 pairs of parapodia modified. Parapodia 1 (Fig. 18d) prolonged, with auricular presetal and subulate postsetal lobes; parapodia 2 shorter, presetal lobes low, postsetal lobes subconical to digitiform. Dorsal cirri subulate on anterior setigers, reduced in median and absent in posterior region; ventral cirri subulate on anterior 2 setigers. Branchiae absent.

Hooks of modified parapodia uni- to bidentate, simple with hoods (Fig. 18c,e); flat pectinate setae and limbate setae (Fig. 18f) from setiger 2; subacicular hooks (Fig. 18g) from setiger 35 or later.

Mandibles with large initial parts; Mx I to Mx III with large cavity openings (Fig. 18h), left Mx II with distal fang, long Mx III, Mx V absent. Tubes thin, translucent,

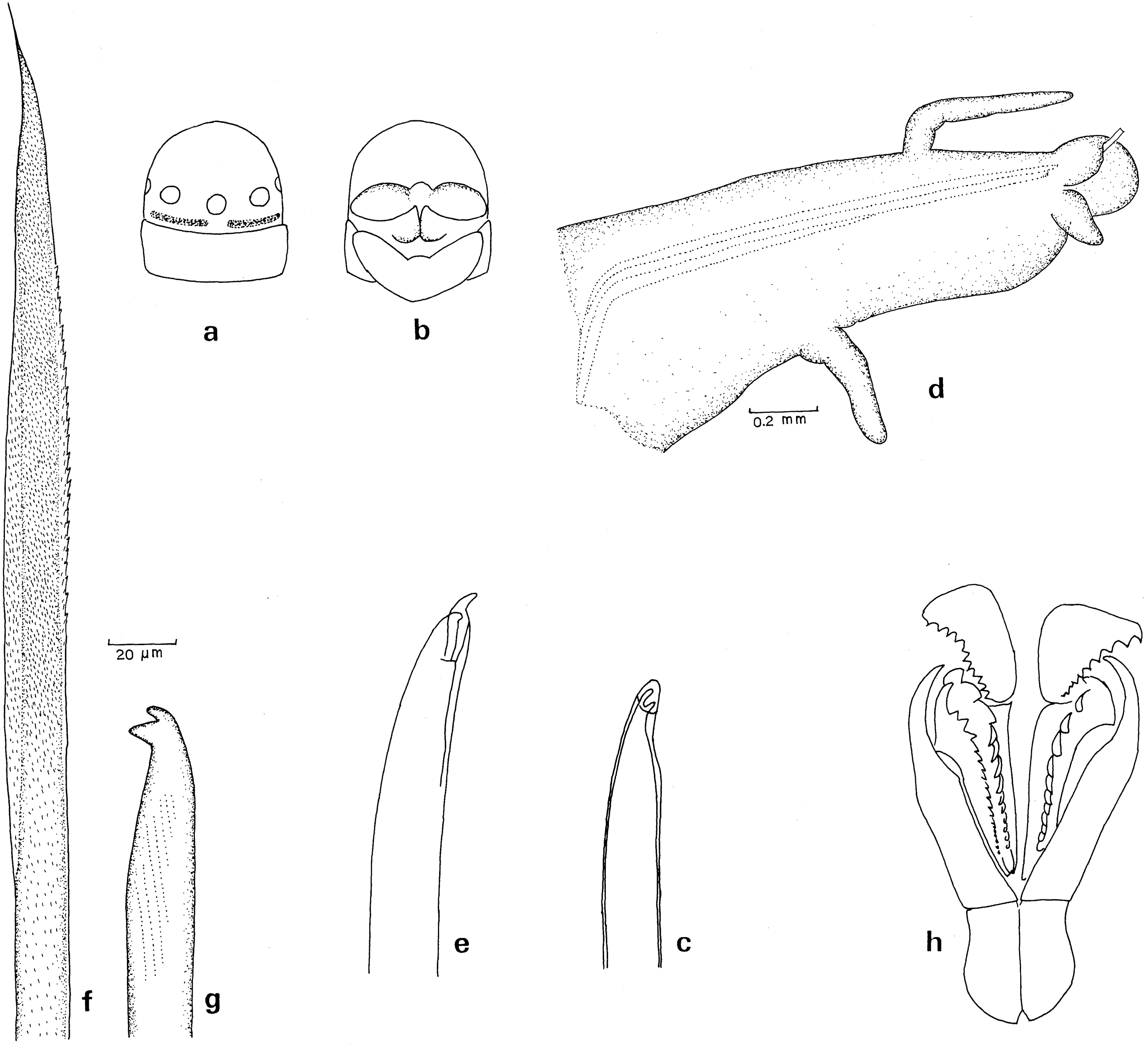


Fig. 18. *Leptoecia apalpata* (a, b, holotype ZMH P-13630; c, from Hartmann-Schröder, 1975: fig. 36): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** bidentate simple hook from setiger 1. *Leptoecia abyssorum* (d, f, g, holotype USNM 19406); e, h, from Chamberlin, 1919: figs 8, 3): **d,** parapodium 1, posterior view; **e,** unidentate simple hook from setiger 1; **f,** spiny limbate seta from setiger 2; **g,** subacicular hook from setiger 49; **h,** maxillae.

longer than inhabitants; oval in transverse section, with thickenings on both sides; without external covering of foreign particles.

Size. Small; to 42 mm for 70 setigers, width 1.75 mm.

Remarks. *Leptoecia* was considered as a junior synonym of *Paronuphis* Ehlers, 1887 (Hartman, 1965; Fauchald, 1977). However, *Paronuphis* is an invalid genus (see 'Remarks' for *Hyalinoecia).* Kucheruk (1978) resurrected *Leptoecia,* emphasizing not only morphological characters but also the method of tube construction in the definition of the genus.

Hartmann-Schröder (1975) described the monotypic genus *Parhyalinoecia,* characterized by the absence of frontal and labial palps. The holotype of *P. apalpata* was examined and found to lack frontal palps but weakly defined labial palps are present. The ceratophores of the antennae are longer than shown by Hartmann-Schröder (1975: fig. 32). *Parhyalinoecia apalpata* is insufficiently different from *L. abyssorum* to warrant separate generic status. Both species construct the characteristic tubes, distinct from those known for any other onuphids. Kucheruk (1978) erroneously stated that *P. apalpata* constructs round tubes. *Parhyalinoecia* is here considered a junior synonym of *Leptoecia.*

The following species are recognized: *L. abyssorum* Chamberlin, 1919; *L. apalpata* (Hartmann-Schröder, 1975).

Distribution. Pacific Ocean: Mexico, Galapagos Islands, Ecuador, Coral Sea, Tasmania; Indian Ocean: Arabian Sea; North Atlantic Ocean: Portugal; in 2880–5275 m.

Key to Species of *Leptoecia*

——Peristomium as long as setiger 1; unidentate hooks (Fig. 18d) on setiger 1 only. . . . . *L. abyssorum*

——Peristomium half as long as setiger 1; bidentate hooks (Fig. 18c) on setigers 1 and 2. . . . . *L. apalpata*

Genus *Neonuphis* Kucheruk

Fig. 19a–h

Neonuphis Kucheruk, 1978: 93. Type species: *Neonuphis oxyrhinchus* Kucheruk, 1978: 93, by original designation. Gender: feminine.

Material examined. *Hyalinoecia benthaliana*—**New Zealand:** SE of North Island—LECTOTYPE (BMNH ZK 1885.12.1.233). *Neonuphis benthaliana*—**Antarctica:** South Shetland Islands—2 (USNM 58396); Antarctic Peninsula—2 (USNM 58399); Mid-Pacific Antarctic Basin—2 (USNM 58405).

Diagnosis. Frontal palps reduced or absent; maxilla V absent; tubes secreted entirely by inhabitants, round in transverse section, without lateral thickenings.

Definition. Prostomium (Fig. 19a) anteriorly rounded or pointed. Posterior antennae on posterior part of prostomium, with very short, smooth ceratophores ($\frac{1}{10}$ length of prostomium), and short to moderately long styles: longest (median) to setiger 2–8. Frontal palps reduced to ventral semicircular protrusions or absent; labial palps reduced (Fig. 19b). Nuchal grooves slightly curved, with moderate middorsal separation; peristomium short; tentacular cirri absent.

Anterior 1–2 pairs of parapodia modified. Parapodia 1 (Fig. 19c) prolonged, with auricular presetal and subulate postsetal lobes (latter may be absent in *N. oxyrhinchus);* parapodia 2 shorter, presetal lobes low, postsetal lobes longer, digitiform. Dorsal cirri subulate on anterior setigers, reduced or absent from setiger 7–14; ventral cirri subulate on anterior 2 setigers. Branchiae absent.

Hooks of modified parapodia bidentate, simple to pseudocompound with hoods (Fig. 19d); flat pectinate setae and limbate setae (Fig. 19e) from setiger 2; subacicular hooks (Fig. 19f) from setiger 12–30.

Mandibles (Fig. 19g) with large initial parts; Mx I to Mx III with large cavity openings (Fig. 19h), left Mx II with or without distal fang, long Mx III, Mx V absent. Tubes translucent; longer than inhabitants; round in transverse section, without external covering of foreign particles.

Size. Small; length to 42 mm for 75 setigers, width to 1.5 mm.

Remarks. *Neonuphis* was described by Kucheruk as a monotypic genus for *N. oxyrhinchus,* and defined as lacking frontal and labial palps, possessing one pair of prolonged anterior parapodia with large rounded postsetal lobes, bidentate compound hooks, and constructing *Hyalinoecia*-like, round, translucent tubes. Unfortunately, the specimens were not available for examination. Auricular presetal lobes are present in all genera of the Hyalinoeciini. The lobes designated as 'postsetal' by Kucheruk appear as typical presetal lobes in his figures and are here considered as such. The 'real' postsetal lobes, usually of subulate shape, may have been lost; it is unlikely that they are absent in *N. oxyrhinchus.*

Neonuphis, as presently defined, is very close to *Leptoecia.* The distinguishing characters are the longer ceratophores in *Leptoecia,* and different tube construction. As more material becomes available, *Neonuphis* may prove to be a junior synonym of *Leptoecia.*

Kucheruk (1978) erroneously stated that *Parhyalinoecia apalpata* Hartmann-Schröder, 1975 construct similar tubes to *Neonuphis.* He distinguished *Parhyalinoecia* from *Neonuphis* by the presence of spiky limbate setae and dorsal cirri on all segments in the former, and smooth limbate setae and absence of dorsal cirri after setiger 7–8 in the latter. Kucheruk (1978) referred *Hyalinoecia benthaliana* McIntosh, 1885 and *Paronuphis ultraabyssalis* Kucheruk, 1977 to *Parhyalinoecia. Parhyalinoecia* was found to be a junior synonym of *Leptoecia* (see 'Remarks' for *Leptoecia*);

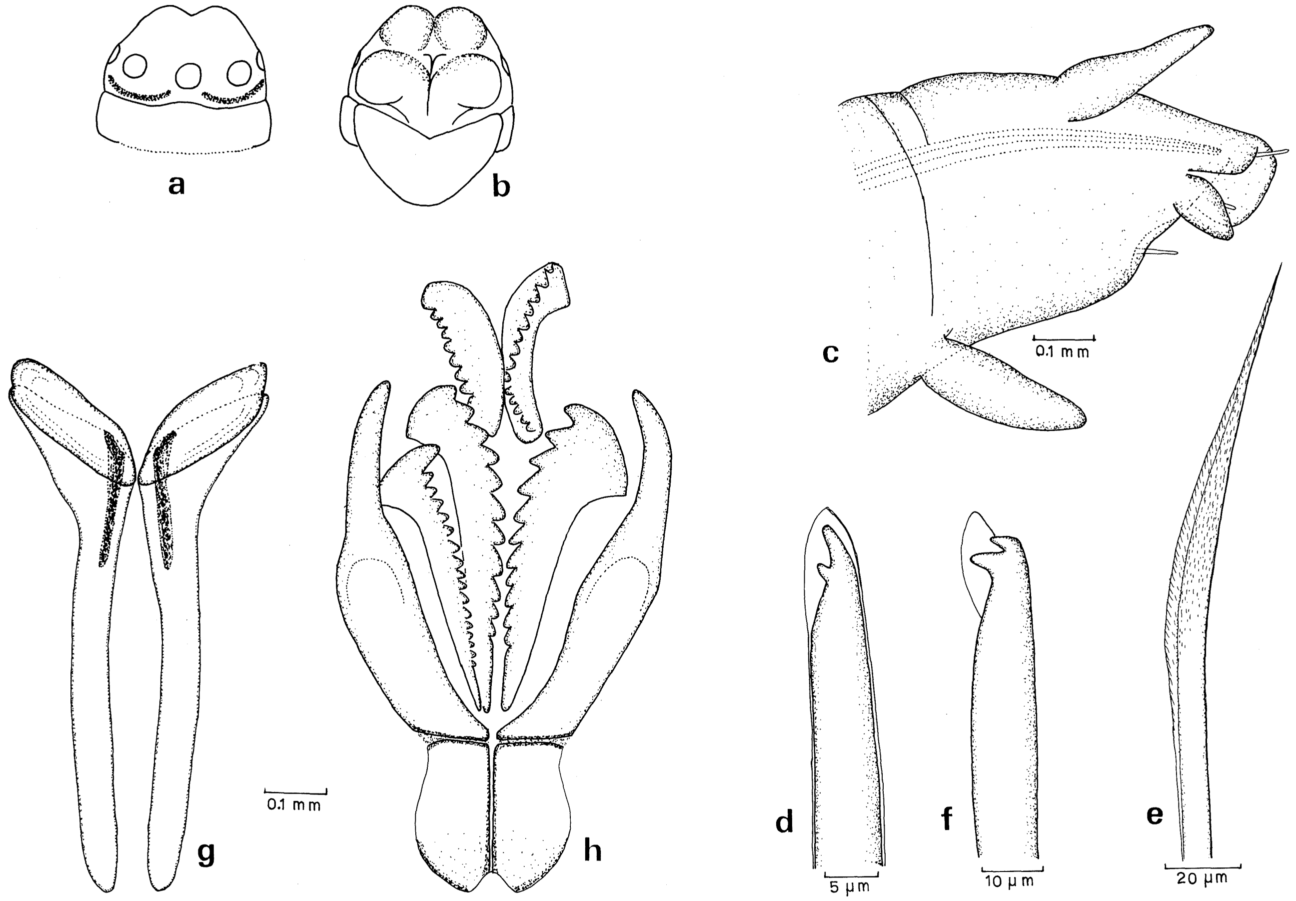


Fig. 19. *Neonuphis benthaliana* (a–c, g–h USNM 58405; d–f, lectotype BMNH ZK 1885.12.1.233): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 1, posterior view; **d,** bidentate simple hook from setiger 1; **e,** limbate seta from setiger 8; **f,** subacicular hook from median setiger; **g,** mandibles; **h,** maxillae.

it constructs tubes which are flattened and are supported by two lateral thickenings. Spiky limbate setae are not considered a distinctive generic character as they occur in species of other genera (e.g. *Rhamphobrachium diversosetosum).* Dorsal cirri are reduced or absent after the anterior setigers in most Hyalinoeciinae, as indeed they are also in *Parhyalinoecia apalpata.*

Hyalinoecia benthaliana and *Paronuphis ultraabyssalis* are herewith referred to *Neonuphis.*

The two syntypes of *H. benthaliana* were examined; both specimens are in poor conditions. One syntype(BM ZK 1885.12.1.233) is in three pieces; part of the prostomium and the jaw apparatus is missing. Part of the tube is preserved and consists of translucent fragments without lateral thickenings. This is the specimen from station 168 upon which McIntosh based most of the description, and it is herewith designated the lectotype. The other syntype (BM ZK 1885.12.1.234) is the dried specimen from station 158. It consists of part of the prostomium and 10 segments, although an unknown number of anterior segments is missing. With the specimen is part of a tube, consisting of a yellowish, translucent substance with a thickening on one side as characteristic of Hyalospinifera. McIntosh stated that the specimen had simple branchiae, a character that is also present in *Hyalospinifera,* but absent in the lectotype of *Hyalinoecia benthaliana.* However, most setae are broken and the anterior parapodia which carry the characteristic hooks with pointed hoods in *Hyalospinifera spinosa* are lost. No definitive identification can be made and the specimen is herewith designated as *Hyalospinifera* sp.

Some of the specimens reported by Hartman (1967b) as *Paronuphis benthaliana* were examined and found to agree with the original description and the remains of the lectotype.

The following species are recognized: *N. oxyrhinchus* Kucheruk, 1978; *N. benthaliana* (McIntosh, 1885); *N. ultraabyssalis* (Kucheruk, 1977).

Distribution. Pacific Ocean: Philippino Trough, New Zealand, South of Australia, Antarctic; Atlantic Ocean: Antarctic; in 720–6330 m.

Key to Species of *Neonuphis*

1 . Prostomium anteriorly pointed; dorsal cirri absent after setiger 7–8. . . *N. oxyrhinchus*

——Prostomium anteriorly rounded (Fig. 19a); dorsal cirri distinct to setiger 14 or later. 2

2. Bidentate hooks of setiger 1 simple (Fig. 19d); subacicular hooks from setiger 22–29. . . . . *N. benthaliana*

——Bidentate hooks of setiger 1 pseudocompound; subacicular hooks from setiger 12–13. . . . . *N. ultraabyssalis*

Genus *Hyalospinifera* Kucheruk

Fig. 20a–n

Hyalospinifera Kucheruk, 1979b: 1585. Type species: *Hyalospinifera spinosa* Kucheruk, 1979b: 1585, by original designation. Gender: feminine.

Material examined. *Hyalinoecia benthaliana*—**Australia:** S of Australia—SYNTYPE (BMNH ZK 1885.12.1.234).

Diagnosis. Frontal palps reduced; anterior hooks with pointed hoods; tubes secreted entirely by inhabitants, egg-shaped in transverse section, with lateral thickenings on one side.

Definition. Prostomium (Fig. 20a) anteriorly rounded. Posterior antennae on median part of prostomium, with short ceratophores with 3–4 indistinct

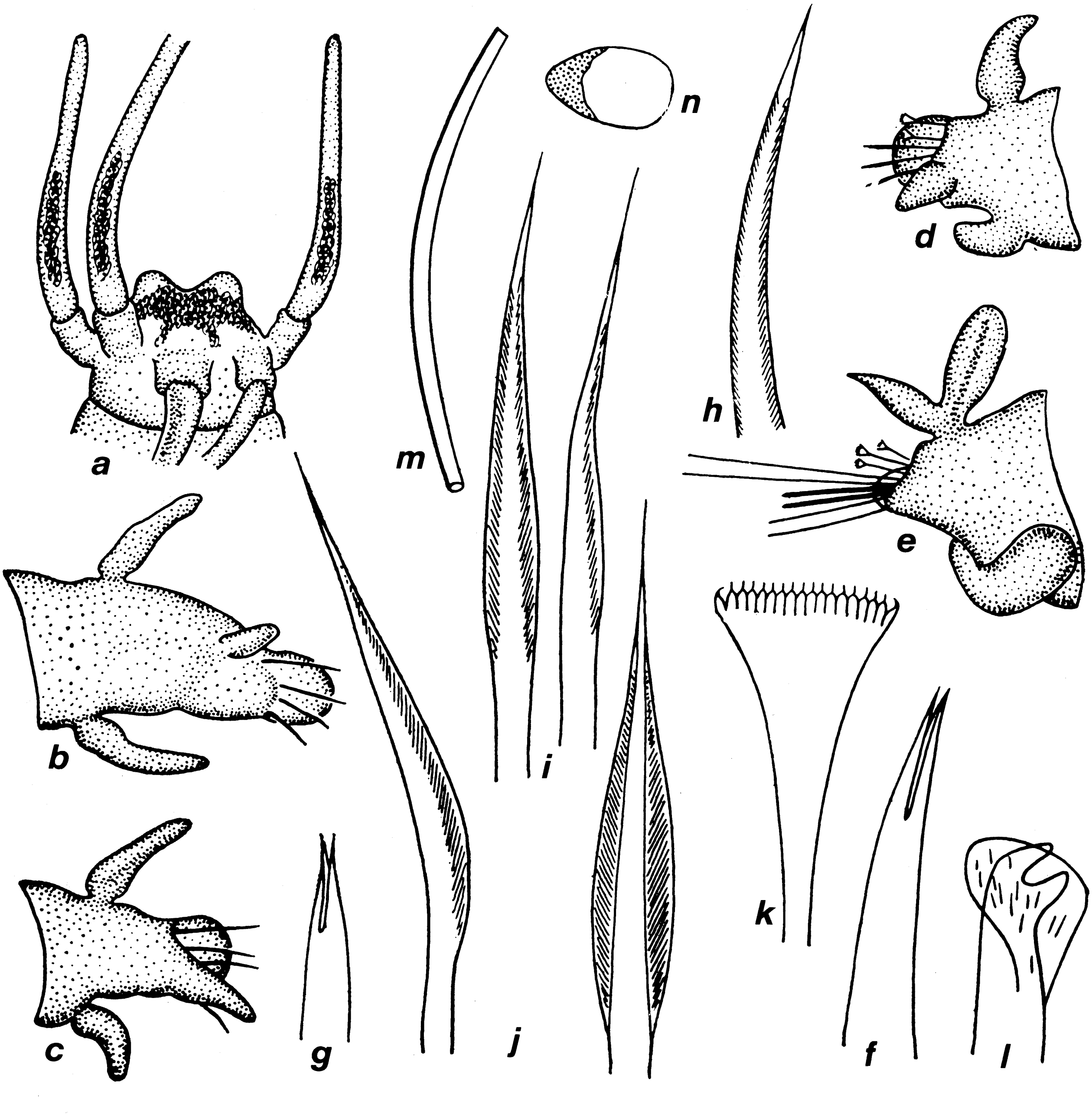


Fig. 20. *Hyalospinifera spinosa* (from Kucheruk, 1979: figs 1–14): **a**, prostomium, dorsal view; **b**, parapodium 1, posterior view; **c**, parapodium 2, same view; **d**, parapodium 3, same view; **e**, parapodium 25, anterior view; **f**, simple hook with pointed hoods from setiger 1; **g**, same from setiger 2; **h**, limbate seta from setiger 1; **i**, same from setiger 3; **j**, same from setiger 18; **k**, pectinate seta from setiger 3; **l**, subacicular hook from setiger 25; **m**, tube; **n**, transverse section of tube.

rings, and long styles. Frontal palps semicircular, labial palps rounded. Nuchal groove presumably straight; tentacular cirri absent.

Anterior 2 pairs of parapodia modified. Parapodia 1 (Fig. 20b) prolonged, with auricular presetal and short, digitiform postsetal lobes; parapodia 2 and 3 (Fig. 20c,d) shorter, presetal lobes shorter, postsetal lobes longer, subconical. Dorsal cirri subulate to digitiform, ventral cirri digitiform on 2-3 setigers. Branchiae (Fig. 20e) from setiger 16-18, simple filaments throughout.

Hooks of modified parapodia with pointed hoods (Fig. 20f,g) on setigers 1-2; limbate setae (Fig. 20h-j) from setiger 2; flat pectinate setae (Fig. 20k) from setiger 3; subacicular hooks (Fig. 20l) from setiger 18-19.

Details of jaw apparatus not known. Tubes (Fig. 20m) bent, translucent; egg-shaped in transverse section (Fig. 20n) with thickening on one side; without external covering of foreign particles.

Size. Small; length of incomplete holotype 20 mm for 42 setigers, width 1.3 mm.

Remarks. No specimens were available for examination. One syntype of *Hyalinoecia benthaliana* (BM ZK 1885.12.1.234) is considered as an unidentifiable species of *Hyalospinifera* (see 'Remarks' for *Neonuphis).*

Distribution. Southern Indopacific: Arabian Sea, Bay of Bengal, Indonesia, South of Australia; in 850-3294 m.

Subfamily ONUPHINAE

Type genus: *Onuphis* Audouin & Milne Edwards, 1833.

Diagnosis. Lower limbate setae absent posterior to origin of subacicular hooks; subacicular hooks in median position in fascicle.

Definition. Frontal palps present. Nuchal grooves straight to almost circular. Peristomium with or without middorsal anterior fold, ventral lip with median section.

Setiger 1 usually same length as following setigers. Anterior 2-8 pairs of parapodia modified. Presetal lobes of modified parapodia usually short, half as long as postsetal lobes. Dorsal cirri present on all setigers; often with basal swelling, rarely with basal process. Branchiae, when present, with simple, pectinately branched or spirally arranged filaments.

Parapodia subbiramous, dorsal cirri usually with internal notosetae (absent only in *Notonuphis).* Hooks of modified parapodia uni- to tridentate. Lower limbate setae usually simple, rarely pseudocompound or compound (=spinigers), absent posterior to origin of subacicular hooks; latter in ventral position in fascicle. Four anal cirri.

Mandibles as long as maxillary carriers and Mx I together. Maxilla III short to long, Mx VI rarely present. Nurse cells associated with oocytes attached in 2 strings. Tubes circular in transverse section, parchment-like or mucous inner layer, outer layer of foreign particles usually present.

Genus *Notonuphis* Kucheruk

Fig. 21a-i

Notonuphis Kucheruk, 1978: 93. Type species: *Leptoecia antarctica* Monro, 1930: 133, by original designation. Gender: feminine.

Material examined. *Notonuphis antarctica*—**Antarctica:** Bransfield Strait—many (USNM 58411). *Nothria minuta*—**New Zealand**—HOLOTYPE (BMNH ZK 1885.12.1.227).

Diagnosis. Frontal palps globular; tentacular cirri absent; branchiae absent; setiger 1 not prolonged.

Definition. Prostomium (Fig. 21a) short, anteriorly rounded. Posterior antennae on posterior part of prostomium, with ceratophores with 3-4 rings, with moderately long styles: longest styles (posterior laterals) to setiger 5-9. Frontal and labial palps rounded, latter without distal lobes or median section (Fig. 21b). Nuchal grooves straight, peristomium moderately long, with middorsal anterior fold, ventral lip with small median section. Tentacular cirri absent.

Anterior 3 pairs of parapodia modified, not prolonged (Fig. 21c,d). Dorsal cirri without internal setae; ventral cirri subulate on anterior 2-3 setigers, short transition zone of globular ventral cirri. Branchiae absent.

Hooks of modified parapodia pseudocompound to simple, uni- to bidentate with long hoods (Fig. 21e). Pectinate setae (Fig. 21f) from setiger 10, upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 21g) from setiger 9-10.

Jaws with mandibles, and maxillae (Fig. 21h) with long Mx III, Mx V moderately large, Mx VI absent. Tubes consisting of tough inner parchment-like layer and outer layer of mud.

Size. Small; length to 65 mm (115 setigers), width to 1.5 mm.

Remarks. *Nothria minuta* McIntosh, 1885 was considered an indeterminable species of *Hyalinoecia* by Fauchald, 1982a. The holotype, which is lacking its prostomium and immediate anterior setigers, was examined in the present study. The median setigers (Fig. 21i) lack branchiae and dorsal setae, have oblique pectinate setae, and subacicular hooks with very short upper teeth. The original description and illustrations showed that the animal lacked tentacular cirri and possessed simple, curved bidentate hooks with long pointed hoods on setiger 1, and the maxillary apparatus had a long Mx III. The combination of these characters marks *Nothria minuta* a member of *Notonuphis,* to which it is referred herewith as the second known species of the genus.

Distribution. Southern oceans: Antarctic and New Zealand; 175-1437 m.

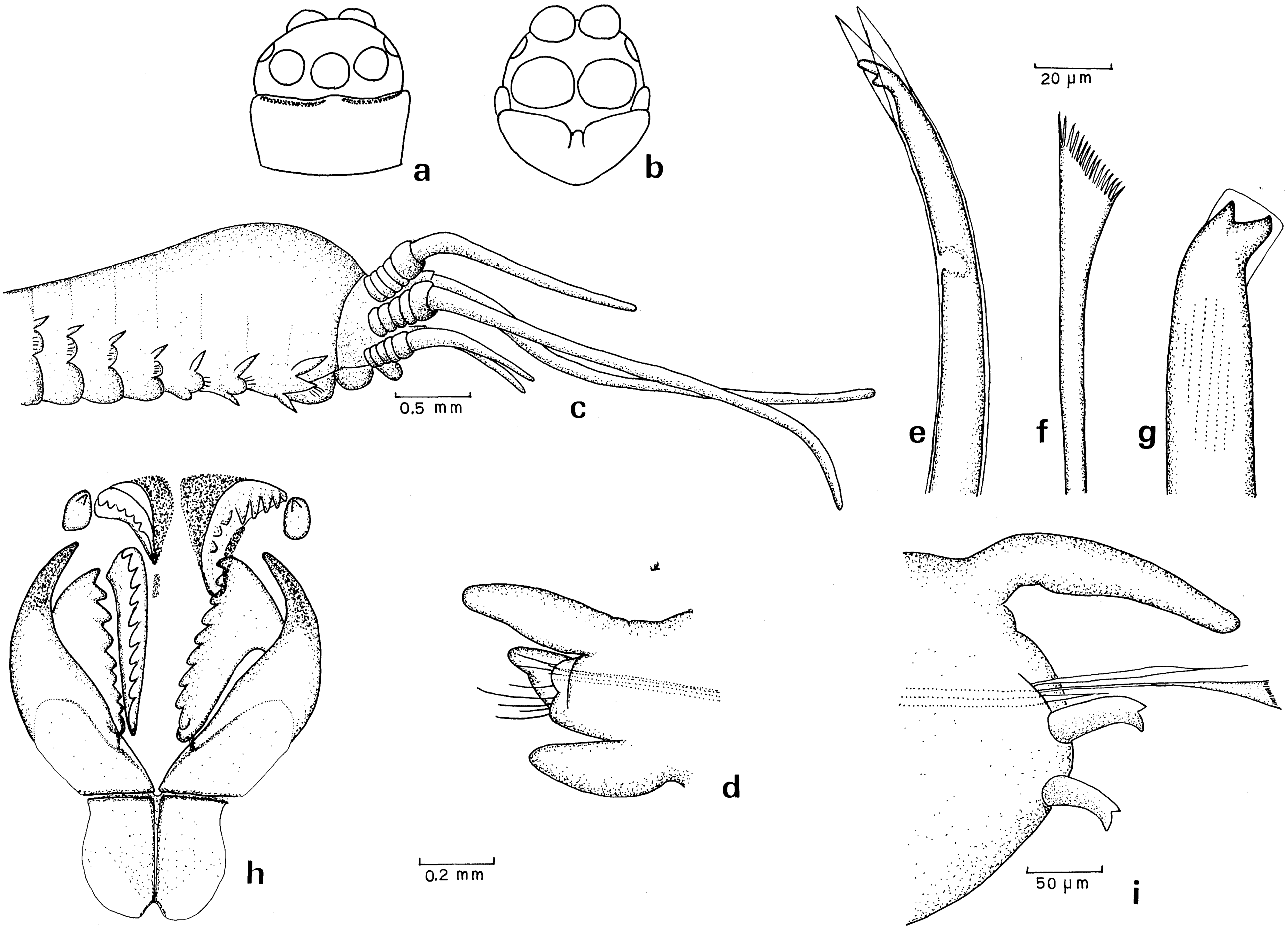


Fig. 21. *Notonuphis antarctica* (USNM 58411): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, anterior end, lateral view; **d**, parapodium 1, anterior view; **e**, pseudocompound hook from setiger 1; **f**, pectinate seta from setiger 30; **g**, subacicular hook from same; **h**, maxillae. *N. minuta* (holotype BMNH ZK 1885.12.1.227): **i**, median setiger.

Key to Species of *Notonuphis*

——Pseudocompound hooks on setiger 1 (Fig. 21e). .... *N. antarctica*

——Simple hooks on setiger 1. .... *N. minuta*

Genus *Paradiopatra* Ehlers

Fig. 22a–k

Diopatra (Paradiopatra) Ehlers, 1887: 73. Type species: *Diopatra (Paradiopatra) fragosa Ehlers, 1887: 75, by subsequent designation of Hartman, 1959: 305. Gender: feminine.*

Sarsonupis Fauchald, 1982a: 64. Type species: *Onuphis quadricuspis* M. Sars, in G.O. Sars, 1872: 407, by original designation.

Material examined. *Paradiopatra fragosa*—**Caribbean:** off Marquesas—juvenile SYNTYPES (MCZ 656); off Bahia Honda—2 SYNTYPES (MCZ 857); **U.S.A.**: Florida: off Sand Key—SYNTYPE (MCZ 766). *P. amoureuxi*—**Africa:** off Ivory Coast—2 (MNHP). *Onuphis lepta*—**Panama**—HOLOTYPE (USNM 19425). *Onuphis quadricuspis*—**Norway:** Drøbak, Oslofjord—5 PARALECTOTYPES (ZMO C3172); southwest—8 (AM W.198970); Bergen—2 (BMNH ZK 1921.5.1.1827).

Diagnosis. Tentacular cirri present; branchiae absent or with pectinate filaments; anterior hooks with long pointed hoods.

Definition. Prostomium (Fig. 22a) anteriorly rounded. Posterior antennae on anterior to median part of prostomium, with ceratophores with usually 3–5 (rarely up to 9) rings, sometimes indistinct or smooth, or with lateral projections; styles of antennae usually short to moderately long, rarely long, longest styles (usually posterior laterals) to setiger 3–9, rarely to 20. Frontal and labial palps oval, latter without distal lobes or median section (Fig. 22b). Nuchal grooves curved laterally, widely separated middorsally. Tentacular cirri inserted distally or subdistally on moderately long peristomium, peristomium with middorsal anterior fold, ventral lip with median section.

Anterior 3 (rarely 4–5) pairs of parapodia modified, not prolonged. Dorsal and ventral cirri long and digitiform (Fig. 22k), latter on anterior 2–4 (rarely 7–8) setigers; short transition zone of globular ventral cirri. Branchiae rarely absent, usually present from setiger 2–18, pectinate filaments; often restricted to anterior part of body (absent after setiger 30–50).

Hooks of modified parapodia uni- to tridentate (usually bidentate), pseudocompound with long, pointed hoods (Figs. 22c,d); shafts of hooks sometimes with 2 rows of minute spines (Fig. 20j). Pectinate setae (Fig. 22e) from setiger 2 or later, upper limbate setae (Fig. 22f) from setiger 1, lower limbate setae simple (Fig. 22g); bidentate hooded subacicular hooks (Fig. 22h) from setiger 9–28 (usually 9–10).

Jaws with mandibles, and maxillae (Fig. 22i) with distally slender Mx I, left Mx II sometimes with distal fang, moderately long Mx III, Mx V large, Mx VI present or absent. Tubes with soft to tough inner parchment-like lining, often with thick outer layer of mud; other foreign particles may be attached at right angles, similar to *Diopatra* tubes.

Size. Usually small, length of most species less than 10 cm, width less than 2 mm.

Remarks. *Paradiopatra* was described as a subgenus of *Diopatra* for *D. (P.) fragosa* Ehlers, 1887 and *D. (P.) glutinatrix* Ehlers, 1887. The subgenus was characterized as *Diopatra*-like without branchiae. Hartman (1959)

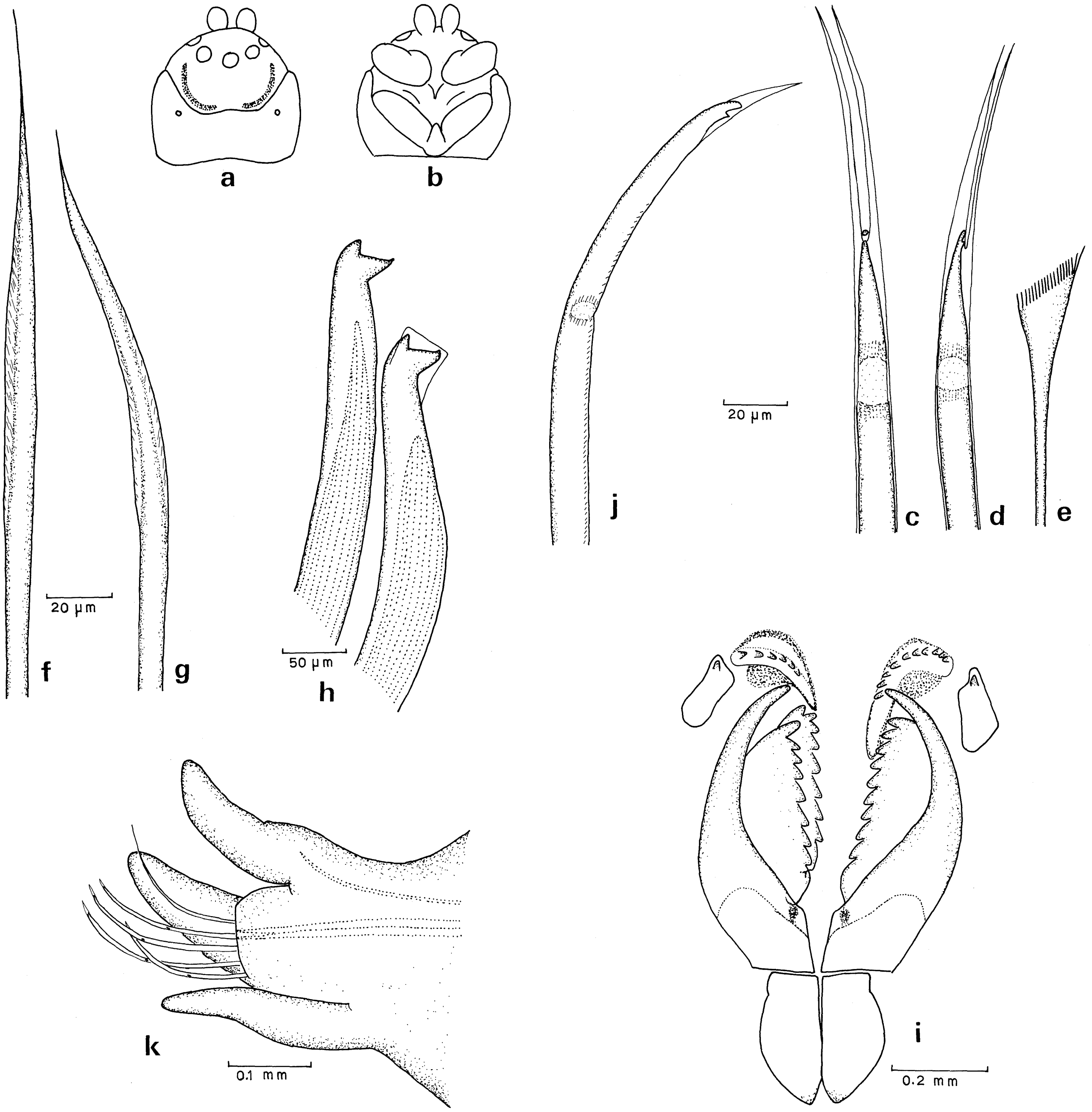


Fig. 22. *Paradiopatra quadricuspis* (AM W.198970); **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, pseudocompound hook from setiger 1, frontal view; **d**, same, lateral view; **e**, pectinate seta from setiger 42; **f**, upper limbate seta from setiger 4; **g**, lower limbate seta from same; **h**, subacicular hooks from setiger 21; **i**, maxillae. *P. fragosa* (syntype MCZ 766): **j**, pseudocompound hook from setiger 1; **k**, parapodium 1, anterior view.

designated *P. fragosa* the type species without giving reasons. Pettibone (1970) found the type specimens of *P. fragosa* in poor condition and considered the species doubtful. Although she stated that according to the original illustrations the two species appeared to belong to different genera, she overlooked Hartman's designation, designated *P. glutinatrix* the type species and redefined *Paradiopatra* on this basis as having two modified pairs of parapodia with specialized hooks, tentacular cirri, and branchiae present or absent. Fauchald (1982a) revised the genus, accepted *P. glutinatrix* as the type species and referred 10 more species from *Onuphis* to *Paradiopatra.*

Fauchald (1982a) examined the type specimens of *P. fragosa.* In addition to the two brittle syntypes, that were found unsatisfactory by Pettibone (1970), he located a third lot of syntypes in better condition. He stated, 'the types are certainly not in particularly good condition but they can be recognized and the additional original material makes it possible to characterize the species' and referred *P. fragosa* to the new genus *Sarsonuphis* (type species *Onuphis quadricuspis* M. Sars) which he described in the same paper.

The syntypes of *P. fragosa* were examined in the present study. The two lots of brittle syntypes appear to be adults and the third lot consists of juveniles of the same species. Since *P. fragosa* is the first designated type species of *Paradiopatra,* the name *Sarsonuphis* must be considered a junior synonym of the former genus, and the species referred to *Sarsonuphis* by Fauchald (1982a) are herewith referred to *Paradiopatra.*

The group of species referred to Paradiopatra by Pettibone (1970) and Fauchald (1982a) are referred to a new genus, *Anchinothria,* which is described above.

Fauchald (1982a) stated in the diagnosis of *Sarsonuphis* that large hooks were rarely present. The holotype of *P. lepta,* the only species for which he reported large hooks in setigers 4-9, was examined and no such hooks were found.

Onuphis (Onuphis) amoureuxi Intes & Le Loeuff, 1975 was considered by Fauchald (1982a) to resemble species of *Australonuphis* since it has similar presetal pockets. Glandular presetal pockets are found in several genera [e.g. *Rhamphobrachium, Onuphis* (see Fig. 6b)] and are not considered to be of generic importance. *Onuphis amoureuxi* has anterior pseudocompound hooks with long pointed hoods, and maxillae with distally slender Mx I, typical of the genus *Paradiopatra.* It is unusual, however, in being large (specimens examined measured 5-7 mm in width) and in having more digitiform ventral cirri and a later origin of subacicular hooks than other species of the genus. However, these differences may be due to its large size, and *O. amoureuxi* is herewith referred to *Paradiopatra.*

The following species are referred to *Paradiopatra.* This list is based on Fauchald (1982a), who gave a key to species (=*Sarsonuphis): Diopatra (Paradiopatra) fragosa* Ehlers, 1887; *Onuphis (Onuphis) amoureuxi* Intes & Le Loeuff, 1975; *Nothria armandi* McIntosh, 1885; *Onuphis bihanica* Intes & Le Loeuff, 1975 (? juvenile *P. amoureuxi); Nothria ehlersi* McIntosh, 1885; *Nothria fiordica* Fauchald, 1974; *Onuphis furcatoseta* Monro, 1937; *Nothria hartmanae* Kirkegaard, 1980; *Nothria hispanica* Amoureux, 1972; *Onuphis (Onuphis) iberica* Hartmann-Schröder, 1975; *Onuphis lepta* Chamberlin, 1919; *Onuphis litabranchia* Chamberlin, 1919; *Onuphis pachyctmema* Chamberlin, 1919; *Onuphis papillata* Kucheruk, 1979a; *Onuphis parva* Moore, 1911; *Diopatra paucibranchis* Ehlers, 1908; *Onuphis pauli* Annenkova, 1952; *Onuphis quadricuspis* M. Sars, 1872; *Onuphis socia* Chamberlin, 1919; *Onuphis parva striata* Uschakov, 1950; *Nothria willemoesii* McIntosh, 1885.

Distribution. World-wide, in 95-5270 m, most species deeper than 500 m (see Fauchald, 1982a).

Genus *Diopatra* Audouin & Milne Edwards
Figs 9b, 23a-l

Diopatra Audouin & Milne Edwards, 1833: 229. Type species: *Diopatra amboinensis* Audouin & Milne Edwards, 1833: 229, by subsequent designation of Malmgren, 1866: 180. Gender: feminine.

Material examined. *Diopatra aciculata*—**Australia:** Victoria: Port Phillip Bay—HOLOTYPE (NMV G1748); Western Australia: Bunbury—10 (AM W.5606) and others (WAM); South Australia—several (AM, SAM). *D. cuprea*—**U.S.A.**: North Carolina—10 (AHF n1642). *D. dentata*—**Australia:** New South Wales—1 (AM W.3826), 2 (AM W.198984) and others (AM). *D. heterodentata*—**Chile:** Punta Ronca—7 (ZMH P-13820). *D. monroi*—**South Africa:** Bay of Luderitz—1 (ZMH P-14284). *D. monroviensis*—**West Africa:** Monrovia—5 (ZMH V736-7). *D. musseraensis*—**Angola:** Mussera—HOLOTYPE (ZMH V907). *D. neapolitana*—**Italy:** Naples—4 (ZMH V10722). *D. ornata*—**U.S.A.**: California—many (AHF Velero sta. 5709-56). *D. rhizoicola*—**Peru:** San Lorenzo near Lima—PARATYPE (ZMH P15273). *D. spiribranchis*—**West Indies**—HOLOTYPE (ZMH PE-781). *D.* n.sp. 1—**U.S.A.**: Hawaii—10 (AM W.198985). *D.* n.sp. 2—**Australia:** Queensland—6 (AM W.198986) and others (AM, QM). *D.* n.sp. 3—**Australia:** New South Wales—2 (AM W.196435) and others (AM).

Diagnosis. Tentacular cirri present; branchial filaments arranged spirally around trunk.

Definition. Prostomium (Fig. 23a) anteriorly rounded to slightly extended. Posterior antennae on median part of prostomium, with ceratophores with 5-20 rings (sometimes with lateral projections), with moderately long to long styles. Frontal palps subulate; labial palps oval with distinct distal lobes and median section (Fig. 23b). Nuchal grooves rounded to almost circular, widely separated middorsally; tentacular cirri inserted distally on moderately long peristomium, middorsal part of peristomium with anterior fold; ventral lip with median section.

Anterior 3-5 (rarely 7) pairs of parapodia (Fig. 23c) modified, slightly prolonged; rarely with double postsetal lobes. Ventral cirri subulate on anterior 4-6 setigers, short transition zone of globular ventral cirri; dorsal cirri long to very long. Small ventral lobes on setiger 5-25 in some species. Branchiae from setiger 4-5,

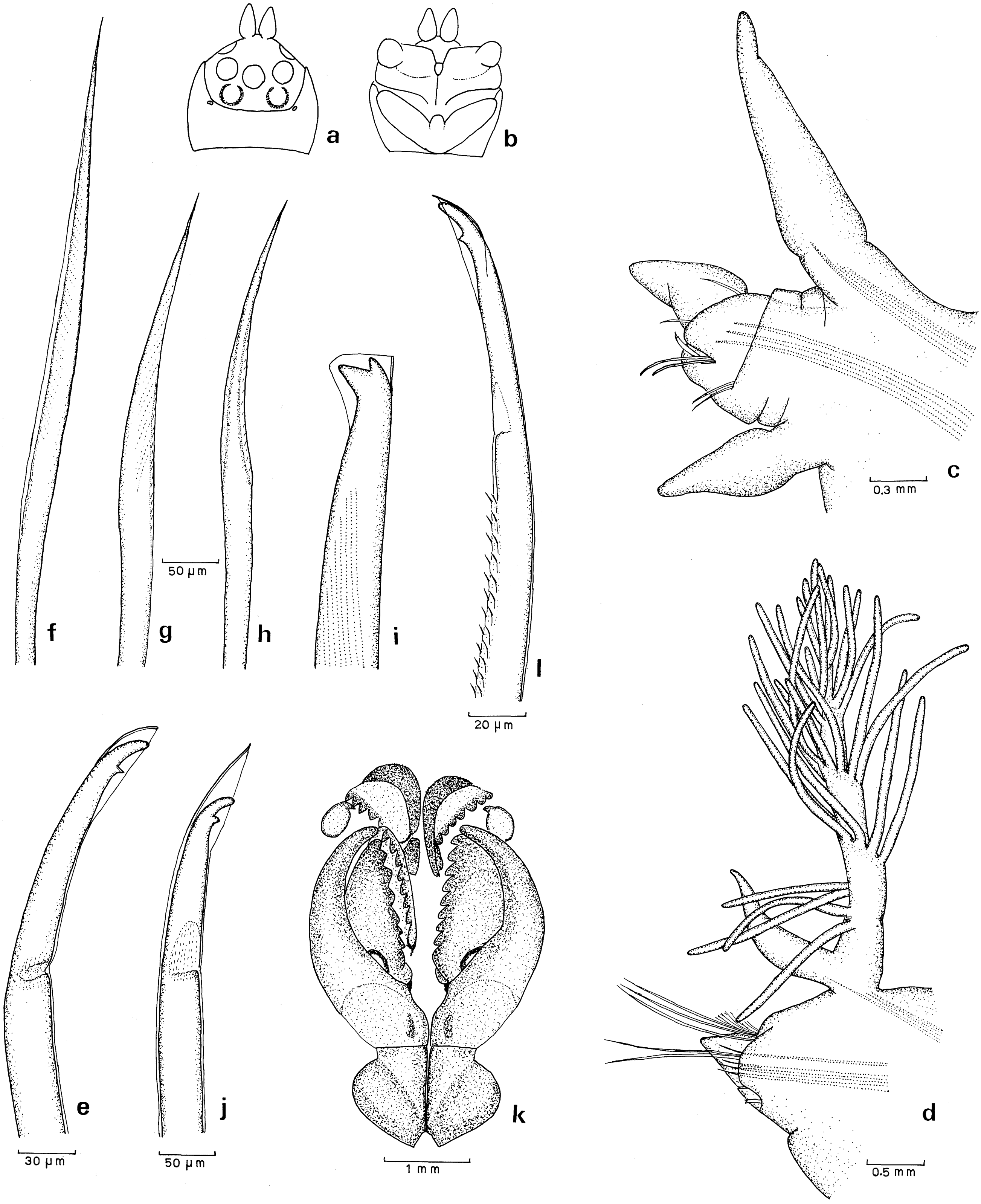


Fig. 23. *Diopatra cuprea* (AHF n1642): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, anterior view; **d**, parapodium 38, same view; **e**, pseudocompound hook with short hood from setiger 1; **f**, upper limbate seta from setiger 21; **g**, lower cultriform limbate seta from same; **h**, lower spine-like limbate seta from same; **i**, subacicular hook from setiger 36. *D. aciculata* (AM W.5606): **j**, pseudocompound hook with long hood from setiger 1; **k**, maxillae. *D. heterodentata* (ZMH P-13820): **l**, pseudocompound spiny hook from setiger 2.

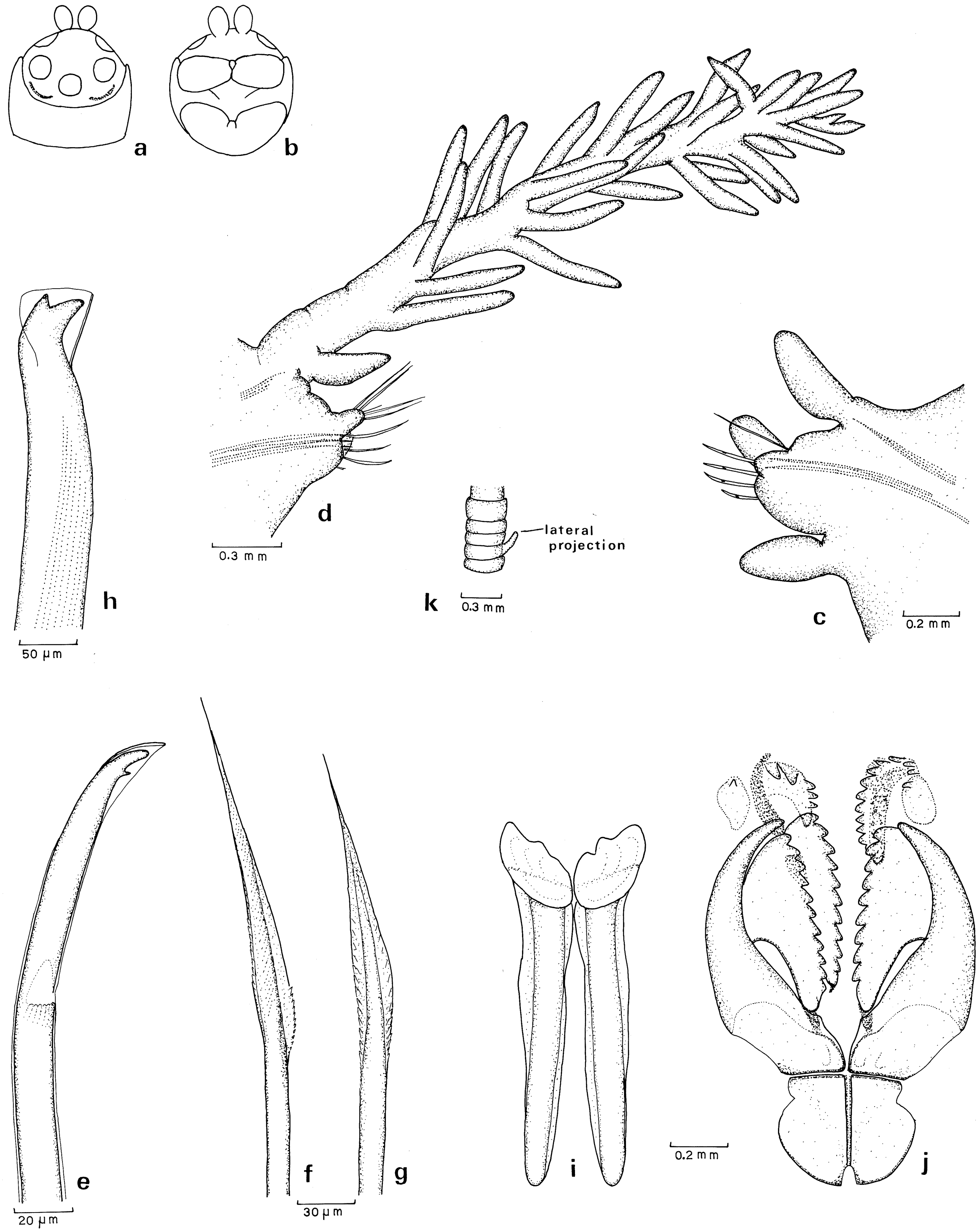


Fig. 24. *Epidiopatra hupferiana* (AM W.198962): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 3, anterior view; **d**, parapodium 5, posterior view; **e**, pseudocompound hook from setiger 1; **f**, upper limbate seta from setiger 9; **g**, lower spine-like limbate seta from same; **h**, subacicular hook from setiger 29; **i**, mandibles; **j**, maxillae. *E. gilchristi* (paratype BMNH ZK 1963.1.85): **k**, ceratophore of left posterior lateral antenna.

filaments arranged spirally around trunk (Fig. 23d); well developed only on anterior part of body, single filaments from setiger 40–60.

Hooks of modified parapodia uni- to tridentate, pseudocompound with short (Fig. 23e) to long (Fig. 23j) hoods; shafts of hooks sometimes with 2 rows of minute to small spines (Figs 9a, 23l). Pectinate setae from setiger 5 or later, upper limbate setae (Fig. 23f) from setiger 1, lower limbate setae simple (Fig. 23g,h); bidentate hooded subacicular hooks (Fig. 23i) usually from setiger 15–20 (rarely 12–30).

Jaws with mandibles, and maxillae (Fig. 23k) with moderately long Mx III, Mx V large, Mx VI absent. Tubes robust, consisting of inner parchment-like layer and outer layer of foreign particles, often attached at right angle.

Size. Moderately large to large, length to 30 cm (250 setigers), width to 8 mm.

Remarks. Audouin & Milne Edwards (1833) did not designate a type species for *Diopatra*. The description of the genus was followed by that of *Diopatra amboinensis* with a note that *Nereis cuprea* delle Chiaje also belonged to the genus *Diopatra*. Milne Edwards (1838: 564) gave a short description of the genus and listed only one species, *Diopatra amboinensis*. This reference was taken as a type designation by Malmgren (1866) and stated as such. Hartman (1944) listed *Diopatra cuprea,* and Hartman (1959) *D. amboinensis* the type species, and either of the two designations have been followed by subsequent authors. The first author to unequivocally state the type species for the genus is Malmgren and his subsequent designation is herein accepted.

Although the genus *Diopatra* is well defined, the taxonomy is not clear at the specific level. Fauchald (1977) recognized 40 species. A complete revision of the genus is underway (Paxton, in preparation).

Distribution. In all major oceans, best represented in warmer waters; intertidal to shallow depths.

Genus *Epidiopatra* Augener

Fig. 24a–k

Epidiopatra Augener, 1918: 355. Type species: *Epidiopatra hupferiana* Augener, 1918: 355, by subsequent designation of Hartman, 1959: 300. Gender: feminine.

Material examined. *Epidiopatra hupferiana*—**Australia:** New South Wales—3 (ZMH V9570) and 3 (AM W.198962-3). *E. gilchristi*—**South Africa**—PARATYPE (BMNH ZK 1963.1.85).

Diagnosis. Tentacular cirri absent; branchial filaments arranged spirally around trunk.

Definition. Prostomium (Fig. 24a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with ceratophores with 3–20 rings sometimes with lateral projections (Fig. 24k), with short to long posterior styles. Frontal and labial palps oval, latter without distal lobes, with small median section (Fig. 24b). Nuchal grooves slightly curved, with large middorsal separation; peristomium moderately long, with middorsal anterior fold; ventral lip with small median section; tentacular cirri absent.

Anterior 3–4 pairs of parapodia (Fig. 24c) modified, not prolonged. Dorsal and ventral cirri digitiform, latter on anterior 3–5 setigers, short transition zone of globular ventral cirri. Branchiae from setiger 4–5, filaments arranged spirally around trunk (Fig. 24d); only on anterior part of body, last filaments from setiger 20–40.

Hooks of modified parapodia uni- to tridentate, pseudocompound with short to long hoods (Fig. 24e); shafts of hooks sometimes with 2 rows of minute spines. Pectinate setae from setiger 5 or later, upper limbate setae from setiger 1 (Fig. 24f), lower limbate setae simple (Fig. 24g); bidentate hooded subacicular hooks (Fig. 24h) from setiger 9–14.

Jaws with mandibles (Fig. 24i), and maxillae (Fig. 24j) with moderately long Mx III, Mx V large, Mx VI absent. Tubes consisting of tough inner parchment-like layer and outer layer of foreign particles, or only opaque tough substance with widely spaced rings (*E. gilchristi* and *E. tenuissima).*

Size. Small; length to 60 mm, width to 3 mm.

Remarks. Juvenile specimens of *Diopatra* have been confused with *Epidiopatra* and the validity of the latter genus has been questioned by Day (1960) and Intes & Le Loeuff (1975). The present study shows that species of *Epidiopatra* are not merely juveniles of *Diopatra* but represent a valid genus, possessing such neotenic and specialized features as the absence of tentacular cirri and the construction of opaque tough tubes respectively.

The following species are recognized: *E. hupferiana* Augener, 1918; *E. drewinensis* Augener, 1918; *E. gilchristi* Day, 1960; *E. papillosa* Day, 1967; *E. rugosa* Kucheruk, 1979a; *E. tenuissima* (Grube, 1868).

Distribution. Southern oceans: Africa, Australia; North Pacific: Japan; 20–1660 m.

Brevibrachium n. gen.

Figs 9a; 25a–k

Type species: *Rhamphobrachium capense* Day, 1960: 355. Gender: neuter.

Diagnosis. Anterior 3–5 pairs of parapodia prolonged, with more than 3 hooks each; hooks smooth, distally recurved, or uni- to tridentate with 2 rows of immoveable spines; setal sacs extending to setiger 4–8.

Definition. Prostomium anteriorly rounded. Posterior antennae on anterior to median part of prostomium, with ceratophores with 2–4 rings, with very short styles (to setiger 1). Frontal and labial palps oval, latter without distal lobes or median section (Fig. 25a). Nuchal grooves curved laterally, widely separated middorsally. Tentacular cirri inserted distally on short peristomium; peristomium with middorsal anterior fold; ventral lip without median section.

Anterior 3–5 pairs of parapodia modified (Fig. 25b,c),

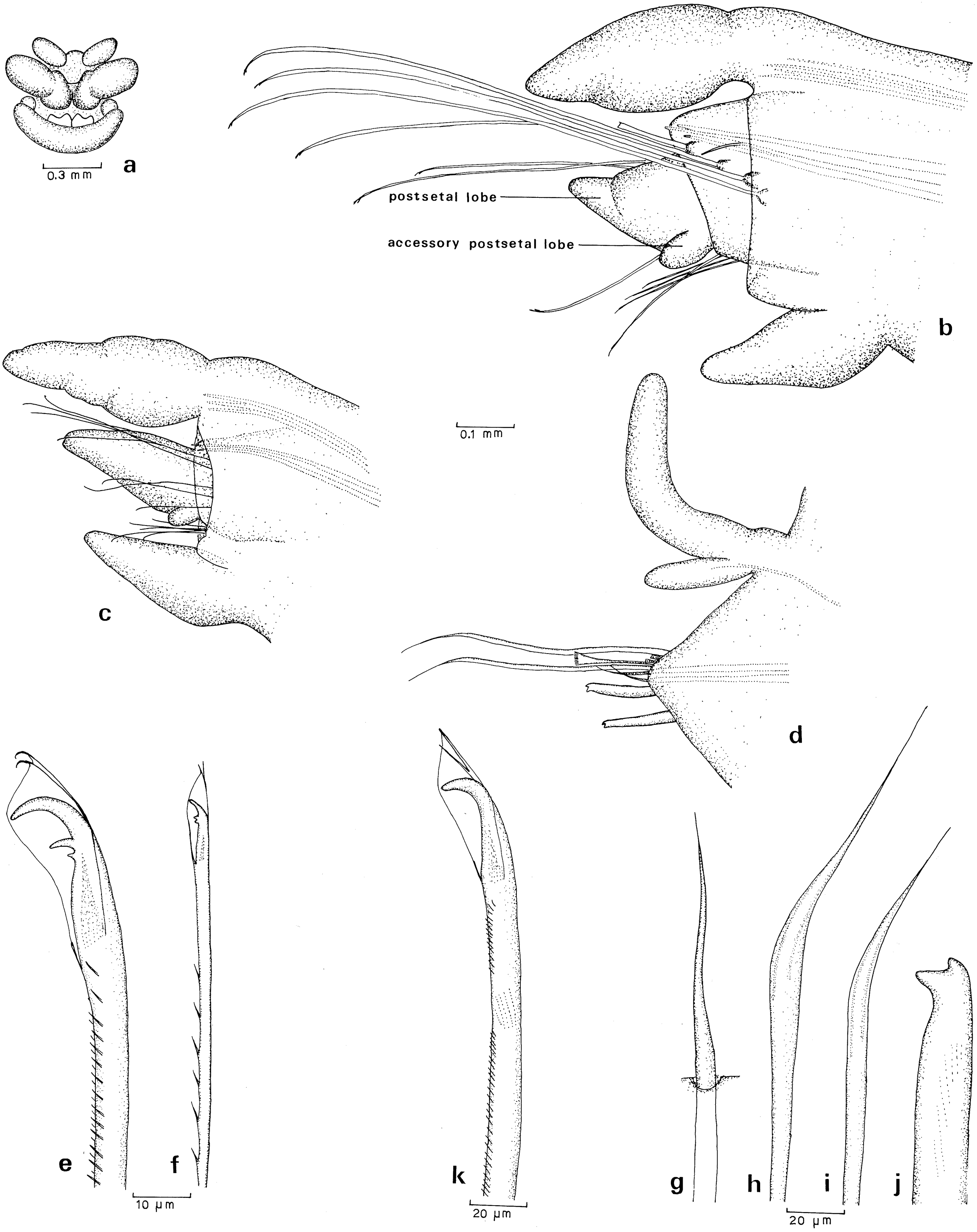


Fig. 25. *Brevibrachium capense* (a-j, paratype BMNH ZK 1961.20.4-7; k, paratype BMNH ZK 1961.20.14): **a,** prostomium and peristomium, ventral view; **b,** parapodium 1, anterior view; **c,** parapodium 4, anterior view; **d,** parapodium 60, posterior view; **e,** large tridentate spiny hook from setiger 1; **f,** small tridentate spiny hook from same; **g,** aciculum, from setiger 6; **h,** median limbate seta from same; **i,** lower limbate seta from same; **j,** subacicular hook from setiger 60; **k,** large unidentate spiny hook (number of setiger unknown).

moderately prolonged. Dorsal and ventral cirri subulate, latter on anterior 3–5 setigers, short transition zone of globular ventral cirri. Branchiae from setiger 2–40, single (Fig. 25d) or pectinate filaments.

Modified parapodia with more than 3 hooks each; hooks simple, smooth (Fig. 9a), recurved; or simple to pseudocompound, uni- to tridentate with hoods, shafts with 2 rows of immoveable spines (Fig. 25e,f,k); setal sacs of both types of hooks prolonged, extending to setiger 4–8 in body cavity. Internal capillary setae from setiger 1, pectinate setae from setiger 5 or later, limbate setae (Fig. 25h) from setiger 4–6, lower limbate setae (Fig. 25i) simple. Bidentate hooded subacicular hooks (Fig. 25j) from setiger 8–10.

Jaws with mandibles, and maxillae with moderately long Mx III, large Mx V, Mx VI absent. Tubes with mucous or parchment-like lining and outer layer of foreign particles; or burrows in limestone rock.

Size. Small; length to 42 mm (107 setigers), width to 2 mm.

Etymology. The name refers to the relatively short, modified parapodia; Latin *brevis* (short) and *brachium* (arm). The combination also emphasizes that *Brevibrachium, Longibrachium* and *Rhamphobrachium* are a group of related genera.

Remarks. *Brevibrachium* shares with *Rhamphobrachium* Ehlers, 1887 and *Longibrachium,* n. gen. the possession of modified parapodia with long setal sacs, and hooks with two rows of spines (spines in all but one species of *Brevibrachium).* These spines are immoveable in *Brevibrachium* (when present) and *Longibrachium,* and moveable in *Rhamphobrachium. Brevibrachium* differs most markedly from *Longibrachium* in having relatively short modified parapodia with setal sacs extending to setiger 4–8, while those of *Longibrachium* are very long with setal sacs extending to setiger 20–60.

Three species, *Rhamphobrachium capense* Day, 1960, *R. maculatum* Estcourt, 1966 and a new species are referred to the new genus and described in Paxton (1986).

Distribution. Southern oceans: South Africa, Australia and New Zealand; intertidal to 90 m.

Longibrachium n. gen.

Figs 9c,d; 26a–e

Type species: *Rhamphobrachium atlanticum* Day, 1973: 55. Gender: neuter.

Diagnosis. Anterior 4 pairs of parapodia prolonged, with more than 3 distally recurved hooks each; hooks with 2 rows of immoveable spines; setal sacs extending to setiger 20–60.

Definition. Prostomium (Fig. 26a) anteriorly rounded; posterior antennae on posterior part of prostomium, with ceratophores with 4–7 rings, with moderately long styles: longest style to setiger 6–15. Frontal palps globular; labial palps oval, without distal lobes, with median section (Fig. 26b). Nuchal grooves

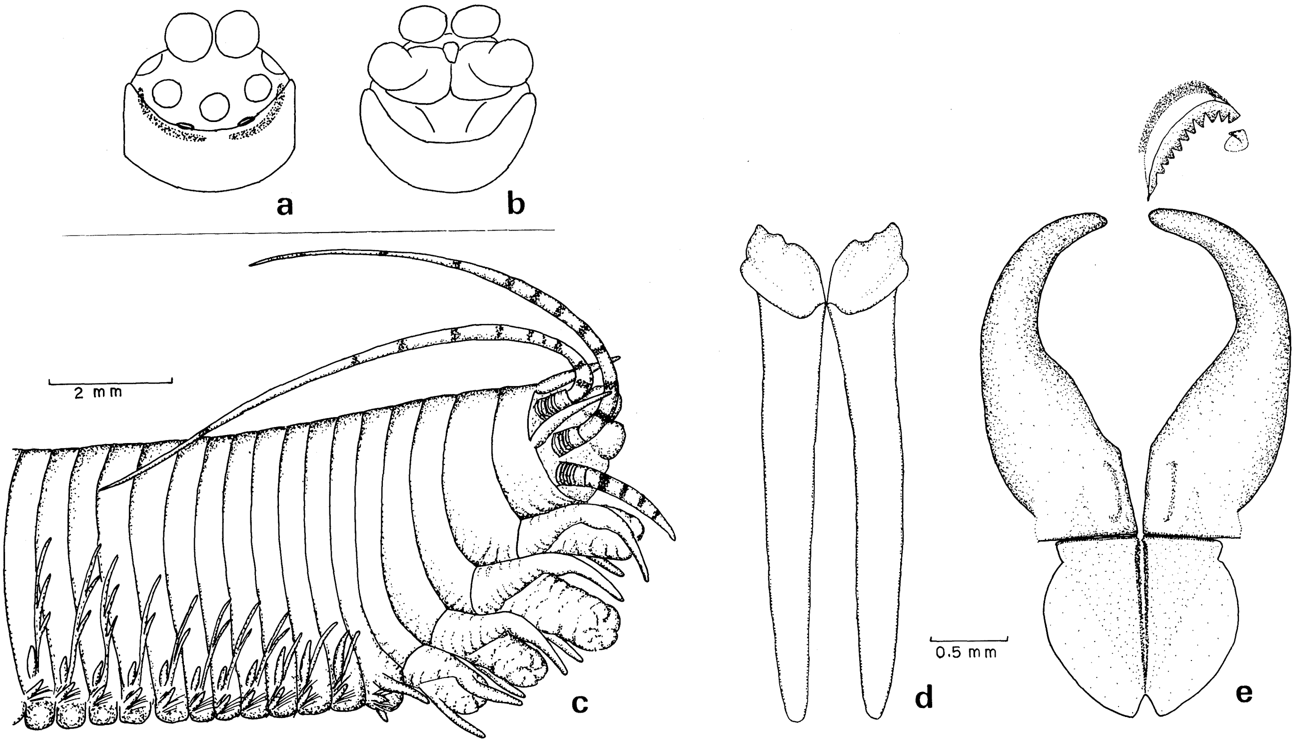


Fig. 26. *Longibrachium atlanticum* (holotype USNM 43124): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, anterior end, dorsolateral view; **d**, mandibles; **e**, part of maxillae.

straight, with small to large middorsal separation. Tentacular cirri inserted distally on moderately long peristomium; peristomium with middorsal anterior fold; ventral lip without median section.

Anterior 4 pairs of parapodia modified, moderately (Fig. 26c) to greatly prolonged. Dorsal cirri subulate and long on modified parapodia, later with basal swelling (rarely with basal process); ventral cirri subulate on anterior 4–5 setigers, short transition zone of globular ventral cirri. Small interramal papillae on setigers 7–12. Branchiae from setiger 6–7; pectinate filaments (maximum 6).

Modified parapodia with more than 3 hooks each; hooks simple, distally recurved, shafts with 2 rows of immoveable spines (Fig. 9c,d); setal sacs extending to setiger 20–60 in body cavity. Internal capillary setae from setiger 1, pectinate setae from setiger 5 or later, limbate setae from setiger 5, lower limbate setae simple. Bidentate hooded subacicular hooks from setiger 16–26.

Jaws with mandibles (Fig. 26d), and maxillae (Fig. 26e) with moderately long Mx III, Mx V small, Mx VI present or absent. Tubes with parchment-like inner lining and outer layer of foreign particles.

Size. Moderately large; length unknown, width to 6 mm.

Etymology. The name is suggested by the long anterior parapodia. Hence the Latin *longi* (long) and *brachium* (arm).

Remarks. The relationships of *Longibrachium* to *Brevibrachium* and *Rhamphobrachium* are discussed in 'Remarks' for *Brevibranchium.*

Three species, *Rhamphobrachium atlanticum* Day, 1973, *R. quadripes* Kucheruk, 1979 and a new species are referred to the new genus and described in Paxton (1986).

Distribution. Western North Atlantic, South Pacific, Gulf of Tonkin; 12–157 m.

Genus *Rhamphobrachium* Ehlers

Figs 9e,f; 27a–l

Rhamphobrachium Ehlers, 1887: 70. Type species: *Rhamphobrachium Agassizii* Ehlers, 1887: 70, by subsequent designation of Hartman, 1944: 47. Gender: neuter.

Paranorthia Moore, 1903: 448. Type species *Paranorthia brevicornuta* Moore, 1903: 448, by subsequent designation of Hartman, 1959: 306.

Diagnosis. Anterior 3 pairs of parapodia prolonged, with 3 distally recurved hooks each; hooks with 2 rows of moveable spines, setal sacs extending to setiger 30-60.

Definition. Prostomium (Fig. 27a) anteriorly rounded; posterior antennae on anterior to median part of prostomium, with ceratophores with 2-5 rings, with short styles (to setiger 2-5). Frontal palps globular; labial palps oval, without distal lobes, with distinct (Fig. 27b) to indistinct anterior median section. Nuchal grooves curved laterally, with small to large middorsal separation. Tentacular cirri inserted distally to subdistally on moderately long peristomium, ventral lip without median section.

Anterior 3 pairs of parapodia modified, moderately prolonged. Dorsal and ventral cirri subulate, latter on anterior 3–4 setigers. Branchiae from setiger 6–17, single or pectinate filaments.

Modified parapodia with 3 long, simple to pseudocompound, distally recurved hooks (Fig. 27d,e) each, projecting from papilliform lobes; shafts with 2 rows of moveable spines (Fig. 9e,f); setal sacs extending to setiger 30–60 in body cavity. Internal capillary setae from setiger 1, pectinate and limbate setae (Fig. 27f,g) from setiger 4; lower limbate setae simple (Fig. 27h) to pseudocompound to compound (= spinigers). First 1–2 unmodified parapodia (Fig. 27c) rarely with falcigers. Bidentate hooded subacicular hooks (Fig. 27i,j) from setiger 10–16.

Jaws with mandibles (Fig. 27k), and maxillae (Fig. 27l) with moderately long Mx III, Mx V small to large, Mx VI present or absent. Tubes with parchment-like inner lining and outer layer of foreign particles.

Size. Small to large; length to 19+ cm (190+ setigers), width to 7 mm.

Remarks. *Rhamphobrachium* was erected by Ehlers (1887) for his previously described *Onuphis brevibrachiatum* and two new species, *R. chuni* and *R. agassizii.* The characteristics of the genus were given as three prolonged anterior pairs of parapodia with spiny, recurved hooks. This definition was later expanded by Monro (1937), Estcourt (1966) and Kucheruk (1979a) with the inclusion of species with two pairs of prolonged parapodia (*R. bipes),* with spineless recurved hooks (*R. maculatum),* and with four pairs of prolonged parapodia (*R. quadripes).*

The elucidation of *Rhamphobrachium* development (see p.18) has shown that specimens with two pairs of modified parapodia are juveniles. *Rhamphobrachium maculatum* and several species with four or five pairs of modified parapodia differ also in a number of additional important characters (types of spines, distal ends of setae, length of setal sacs, prostomial characters, etc.). These species represent different lineages from the genus *Rhamphobrachium* (type species *R. agassizii)* and are referred to two new genera *Brevibrachium* and *Longibrachium* described above. The definition of *Rhamphobrachium* is here restricted to species with 3 pairs of modified parapodia, each with 3 hooks with moveable spines, and long setal sacs (extending to setiger 30–60).

Moore (1903) described *Paranorthia* for his new species *P. brevicornuta.* He defined *Paranorthia* as intermediate between *Nothria* and *Rhamphobrachium* by possessing two pairs of prolonged parapodia, but lacking the long recurved setae. The holotype of *P. brevicornuta* has been examined in the present study. Although the setae of the modified parapodia are broken off, their internal long shafts are present and bear the two rows of moveable spines characteristic of the genus *Rhamphobrachium. Paranorthia brevicornuta* was referred to *Rhamphobrachium* by Kucheruk (1979: 119), and *Paranorthia* considered a junior synonym of the latter genus, a decision that is supported by the present study.

A complete revision of *Rhamphobrachium,* providing a key to and descriptions of the 12 currently recognized species is published separately (Paxton, 1986).

Distribution. World-wide; intertidal to 2165 m.

Genus *Americonuphis* Fauchald

Figs 28a–d, 29a–e

Americonuphis Fauchald, 1973: 22. Type species: *Diopatra magna* Andrews, 1891b: 286, by original designation. Gender: feminine.

Material examined. *Americonuphis magna*—**U.S.A.**: North Carolina—2 (AM W.198971-2). *A. reesei*—**Panama:** Gulf of Panama—HOLOTYPE (AHF Poly 0729); Naos Island—1 (AHF).

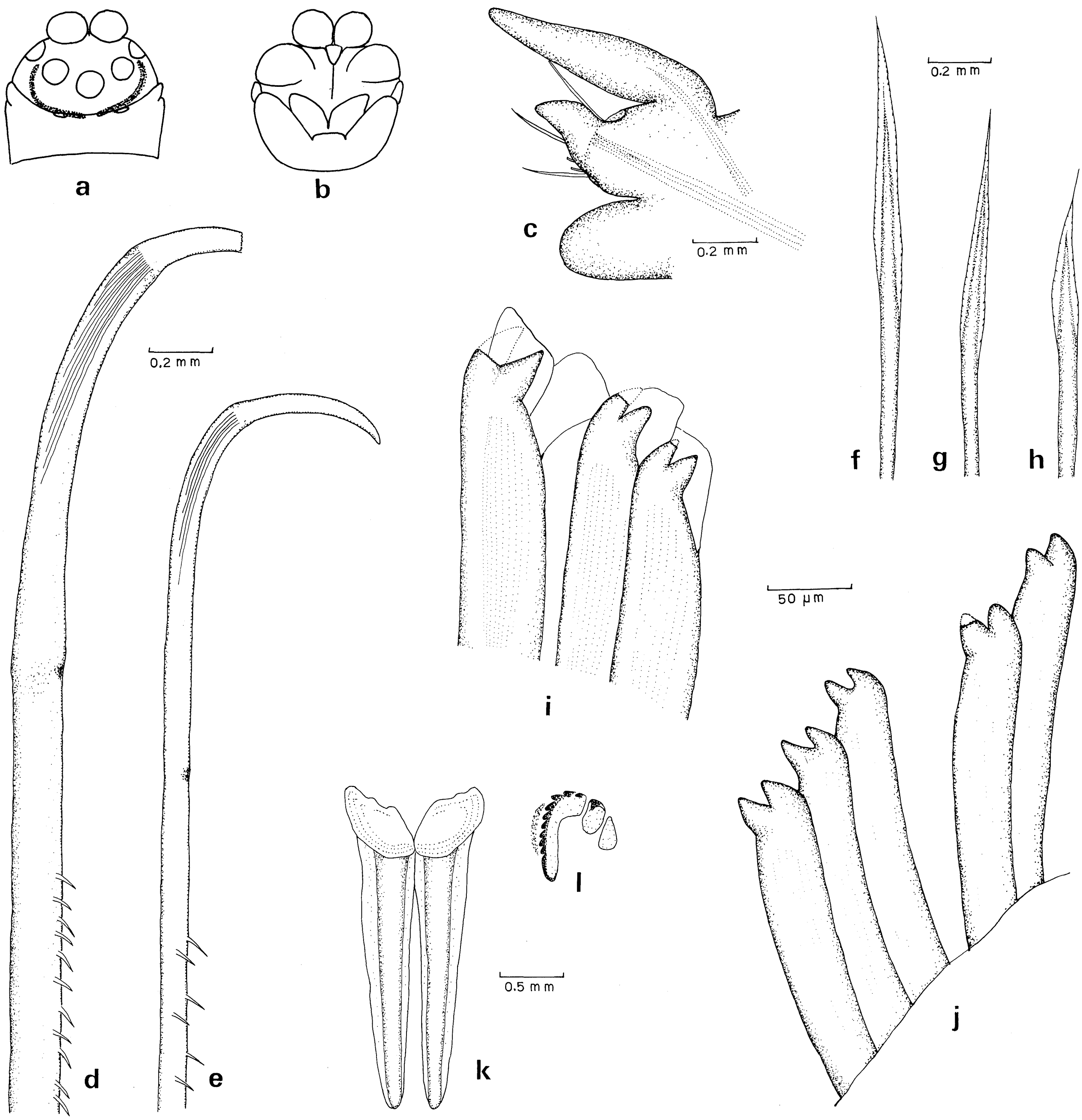


Fig. 27. *R. (Rhamphobrachium) agassizii* (c, e, f–h, j, USNM 20070; d, i, k, l, lectotype MCZ 789): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 4, posterior view; **d,** recurved hook (tip broken) from parapodium 1 of lectotype; **e,** same from specimen from Puerto Rico; **f,** upper limbate seta from setiger 13; **g,** median limbateseta from same; **h,** lower spine-like limbate seta from same; **i,** subacicular hooks from setiger 17 of lectotype; **j,** same from setiger 19 of specimen from Puerto Rico; **k,** mandibles; **l,** right Mx IV, V and VI.

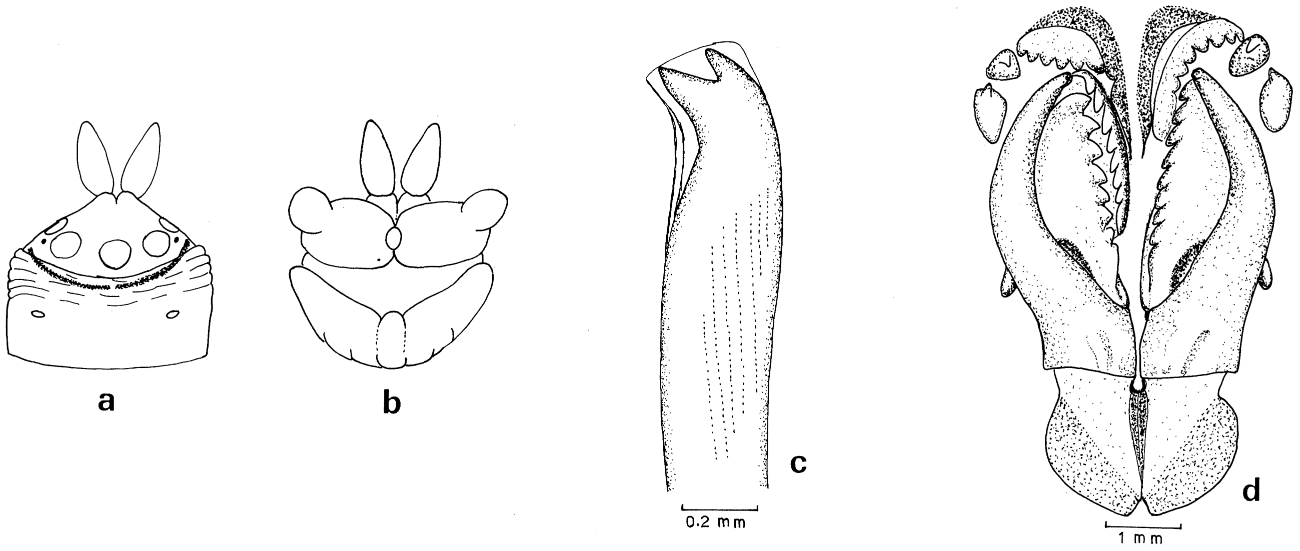


Fig. 28. *Americonuphis magna* (AM W.198971): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** subacicular hook from setiger 95; **d,** maxillae.

Diagnosis. Tentacular cirri inserted in middle of expansible peristomium; modified parapodia directed strongly anteroventrally, ventral cirri of setiger 5 almost touching in ventral midline.

Definition. Prostomium (Fig. 28a) very short, weakly incised and anteriorly extended. Posterior antennae on posterior part of prostomium, with ceratophores with 5–8 rings, and with short to moderately long styles: longest style (median) to setiger 4–9. Frontal palps subulate; labial palps oval with distinct distal lobes and median section (Fig. 28b). Nuchal grooves straight, with small middorsal separation, covered by anterior folds of expansible peristomium; tentacular cirri inserted in middle of moderately long peristomium; ventral lip with median section.

Anterior 3–5 pairs of parapodia (Fig. 29b) modified, slightly prolonged, directed strongly anteroventrally, ventral cirri of setiger 5 almost touching in ventral midline (Fig. 29a); dorsal and ventral cirri subulate, latter on anterior 4–5 setigers. Branchiae (Fig. 29d) from setiger 6; thick stem, pectinate filaments (maximum 7–12).

Hooks of modified parapodia bidentate, pseudocompound with hoods (Fig. 29c). Pectinate setae (Fig. 29e) from setiger 5 or later, upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hoods (Fig. 28c) from setiger 16–18.

Jaws with mandibles, and maxillae (Fig. 28d) with moderately long Mx III, Mx V moderately large, Mx VI present. Tubes consisting of inner parchment-like lining and outer layer of foreign particles.

Size. Large; length to 73 cm, width to 10 mm.

Remarks. The following species are recognized: *A. magna* (Andrews, 1891); *A. reesei* Fauchald, 1973.

Distribution. Western North Atlantic Ocean: Gulf of Mexico, Caribbean; intertidal to 45 m.

Key to Species of *Americonuphis*

——Anterior part of body with brown pigment spots; maximum of 12 filaments per branchia. .... *A. magna*

——Anterior part of body without pigment spots; maximum of 7 filaments per branchia (Fig. 29d). .... *A. reesei*

Genus *Australonuphis* Paxton

Fig. 30a-l

Americonuphis Orensanz, 1974: 100. Type species *Americonuphis casamiquelorum* Orensanz, 1974, by original designation (preoccupied by *Americonuphis* Fauchald, 1973).

Australonuphis Paxton, 1979: 270. Type species: *Americonuphis casamiquelorum* Orensanz, 1974, by original designation (replacement name for *Americonuphis* Orensanz, 1974). Gender: feminine.

Material examined. *Diopatra teres*—**Australia:** New South Wales—HOLOTYPE (ZMB 6727). *Australonuphis teres*—**Australia:** New South Wales—8(AM W.16051) and others. *A. parateres*—**Australia:** New South Wales: Narrabeen near Sydney—HOLOTYPE (AM W.11798), 5 PARATYPES (AM W.15069-73) and others (AM); Queensland—many (AM W.16550) and others.

Diagnosis. Antennae with moderately long ceratophores (about 10 rings) and short styles; anterior hooks uni- to weakly bidentate; distally entire subacicular hooks from setiger 50–80.

Definition. Prostomium (Fig. 30a) anteriorly rounded. Posterior antennae almost covering dorsal part of very short prostomium (Fig. 30b), with ceratophores with about 10 rings and short styles: longest style (median) to setiger 3–4, anterior lateral styles as long as their ceratophores. Frontal and labial palps oval,

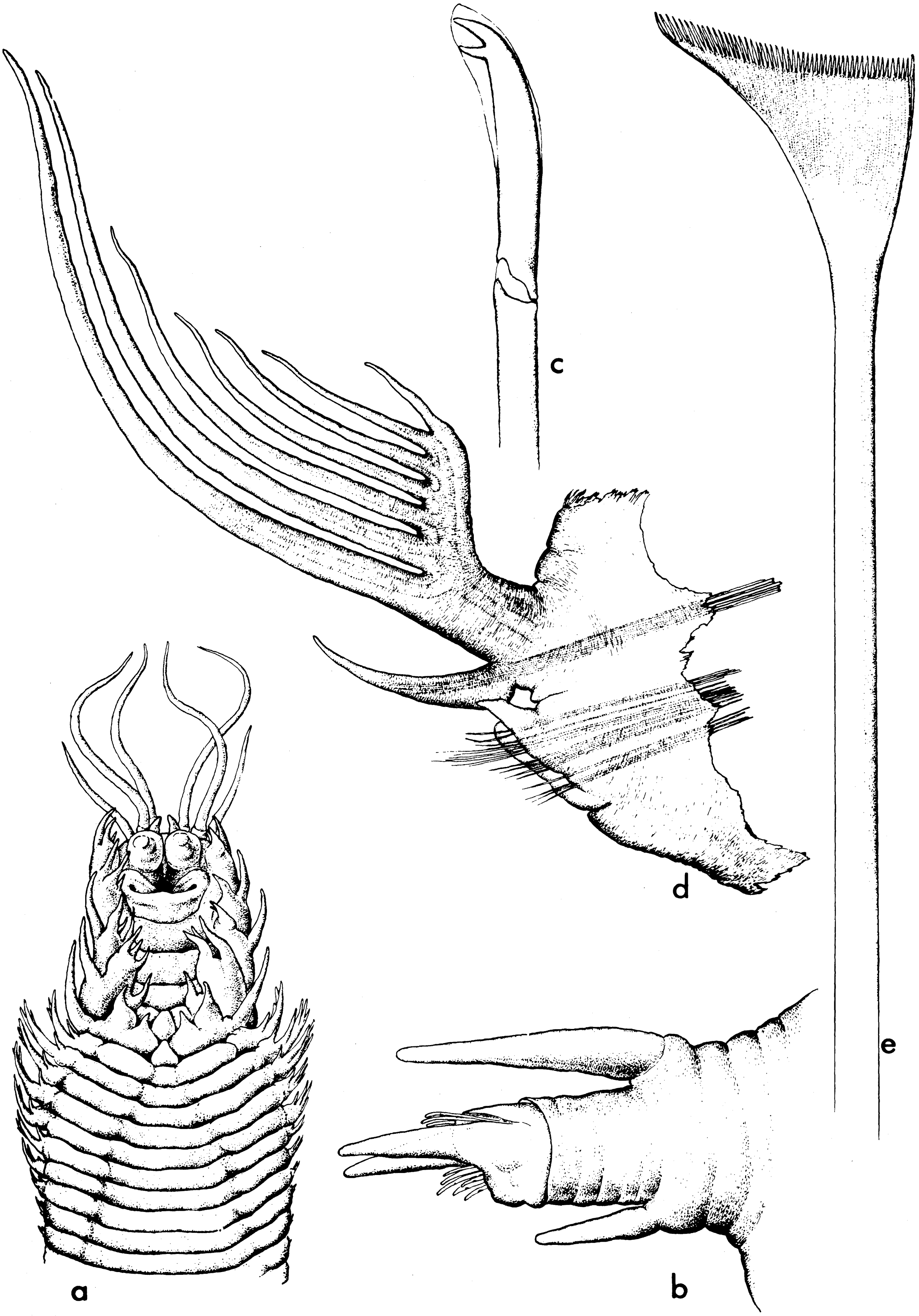


Fig. 29. *Americonuphis reesei* (from Fauchald, 1973: fig. 3a–e): **a,** anterior end, ventral view; **b,** parapodium 1, posterior view; **c,** pseudocompound hook from setiger 1; **d,** branchial parapodium, posterior view; **e,** pectinate seta.

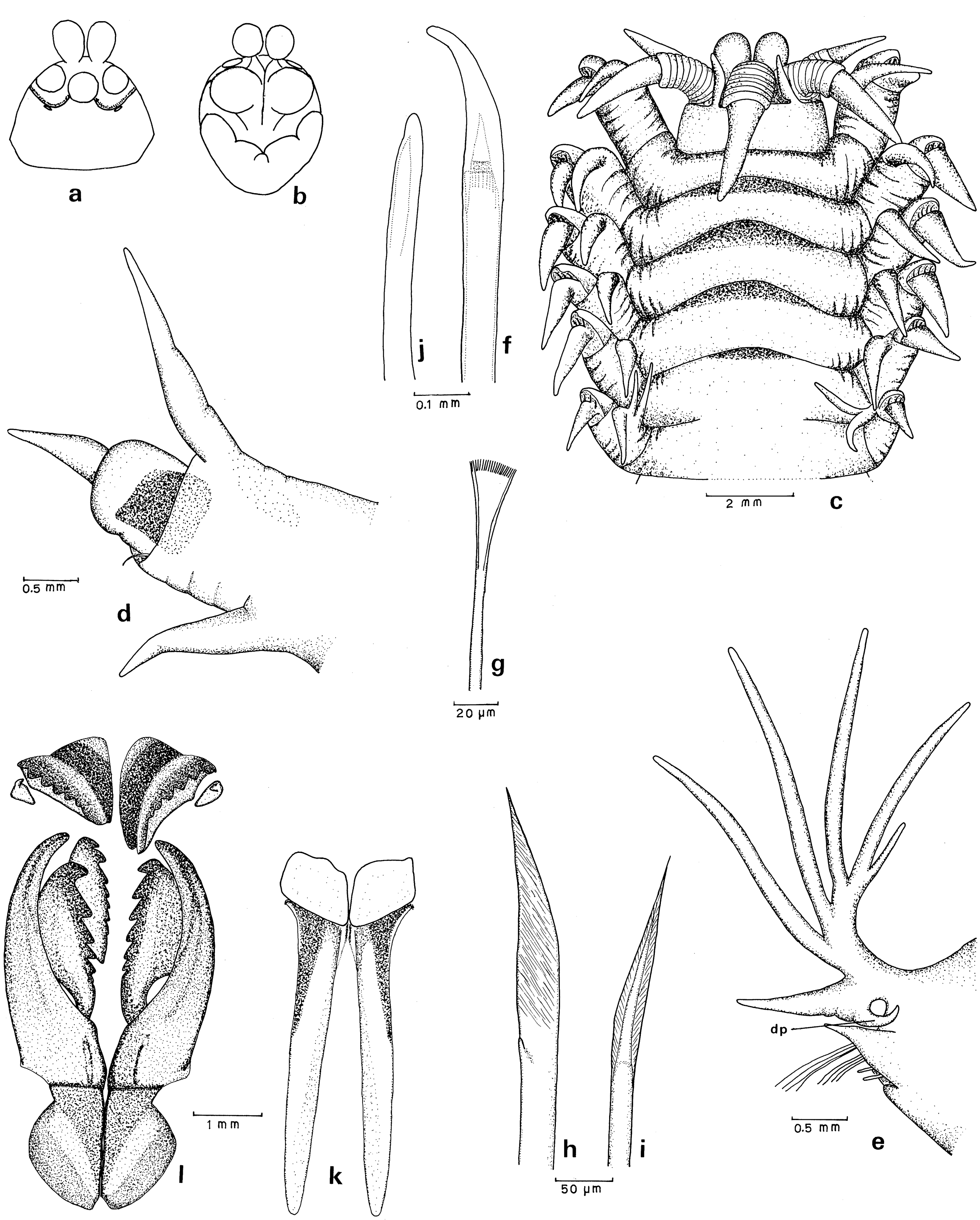


Fig. 30. *Australonuphis parateres* (c–j from Paxton, 1979: figs 9, 10–12, 15, 16): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** anterior end, dorsal view; **d,** parapodium 1, anterior view; **e,** parapodium 84, posterior view (dp = digital process); **f,** pseudocompound hook from setiger 1; **g,** pectinate seta from setiger 84; **h,** weakly pseudocompund cultriform limbate seta from setiger 17; **i,** spine-like limbate seta from setiger 65; **j,** subacicular hook from setiger 84. *Australonuphis teres* (from Paxton, 1979: figs 6, 7): **k,** mandibles; **l,** maxillae (Mx III to Mx V not in natural position).

latter without median section. Nuchal grooves widely separated in midline, curved towards base of median antenna. Tentacular cirri inserted distally on moderately long to long peristomium; middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna, ventral lip with indistinct median section.

Anterior 5–8 pairs of parapodia modified, moderately prolonged (parapodia 2–4 longest) (Fig. 30c,d). Ventral cirri subulate on anterior 6–8 setigers, long transition zone of glandular pads with reduced cirri (until setigers 15–25). Dorsal cirri moderately long, with basal swelling from setiger 6–7, gradually developing into digital process (Fig. 30e). Interramal papilla from setiger 6–7, moving ventrally, forming new presetal lip by setiger 15–20, and fusing with ventral pad by setiger 40–70. Branchiae from setiger 6 with thick stem and pectinate filaments (maximum of 6–7).

Hooks of modified parapodia uni- to weakly bidentate, pseudocompound without hoods (Fig. 30f); large median hooks absent. Pectinate setae (Fig. 30g) from setiger 6–7; upper limbate setae from setiger 1; lower limbate setae weakly pseudocompound, cultriform (Fig. 30h) to simple, spine-like (Fig. 30i). Distally entire subacicular hooks without hood (Fig. 30j) from setiger 50–80.

Jaws with strongly sclerotized mandibles (Fig. 30k), and maxillae (Fig. 30l) with short Mx III, small Mx V, Mx VI absent. Tubes thin and temporary, consisting of inner mucous and outer layer of sand.

Size. Large; length of live worms to 300 cm, width to 2.5 cm; preserved to 70 cm long (1065 setigers); 10 mm wide.

Remarks. The following species are recognized: *A. casamiquelorum* (Orensanz, 1974); *A. hartmanae* (Friedrich, 1956); *A. parateres* Paxton, 1979; *A. teres* (Ehlers, 1868); *A. violacea* Rozbaczylo & Castilla, 1981.

Distribution. Pacific Ocean: eastern Australia, El Salvador, Chile; Atlantic Ocean: Brazil and Argentina; intertidal to 14 m.

Key to Species of *Australonuphis*

1. Five anterior setigers with weakly bidentate pseudocompound hooks. 2

——Six to eight anterior setigers with unidentate pseudocompound hooks (Fig. 30f). 3

2. Peristomium and modified segments dark blue-violet; pseudocompound hooks distally curved and blunt. . . . . *A. violacea*

——Peristomium and modified segments grayish-green; pseudocompound hooks distally less curved and pointed. . . . . *A. casamiquelorum*

3. Seven to eight anterior setigers with pseudocompound hooks. . . . . *A. hartmanae*

——Six anterior setigers with pseudocompound hooks. 4

4. Brown transverse bands after setiger 8; frontal palps at least partly brown. . . . . *A. teres*

——No brown bands after setiger 8; frontal palps white. *A. parateres*

Hartmanonuphis n. gen.

Fig. 31a–i

Type species: *Onuphis pectinata* Knox & Hicks, 1973: 289. Gender: feminine.

Material examined. *Onuphis pectinata*—**New Zealand:** Timaru—HOLOTYPE (CM); Banks Peninsula—2 PARATYPES (CM). *Hartmanonuphis pectinata*—**New Zealand:** Kaitaia—2 (AM W.198977) and 1 (USNM 98883).

Diagnosis. Antennae with short ceratophores (6–8 rings) and moderately long styles; short anterior dorsal cirri; long transition zone of ventral glandular pads with reduced cirri (until setiger 14–16); anterior hooks bidentate; bidentate subacicular hooks from setiger 29–31.

Definition. Prostomium (Fig. 31a) with anterior median incision. Posterior antennae almost covering dorsal part of short prostomium, with ceratophores with 6–8 rings, and short styles: longest styles (posterior laterals) to setiger 3–5, anterior lateral styles shorter than their ceratophores. Frontal and labial palps oval, latter without median section (Fig. 31b). Nuchal grooves widely separated in midline, curved towards base of median antenna. Tentacular cirri inserted distally on moderately long peristomium. Middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna; ventral lip with distinct median section.

Anterior 6 pairs of parapodia modified, moderately prolonged (parapodia 2–4 longest) (Fig. 31c). Ventral cirri subulate on anterior 6 setigers, long transition zone of glandular pads with reduced cirri (until setiger 14–16) (Fig. 31d). Dorsal cirri moderately long, with basal swelling. Ventral lobe from setiger 9–12, enlarging dorsally and forming new presetal lip by setiger 25. Branchiae from setiger 1, with thick stem and pectinate filaments (maximum 9–11).

Hooks of modified parapodia bidentate, pseudocompound with hoods (Fig. 31e); large median hooks absent. Pectinate setae (Fig. 31f) from setiger 2; upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 31g) from setiger 29–31.

Jaws with strongly sclerotized mandibles (Fig. 31h), and maxillae (Fig. 31i) with short Mx III, small Mx V, Mx VI absent. Tubes thin and temporary, consisting of inner mucous and thin outer layer of sand.

Size. Large; width 3.5 to 8 mm; length to 50 cm (800 setigers).

Etymology. Named in honour of Dr Olga Hartman, who has introduced and encouraged me to the study of polychaetes.

Remarks. The new genus is closest to *Australonuphis* and *Hirsutonuphis* (described below) with which it shares the prolonged anterior parapodia and curved nuchal grooves. It differs mainly from *Australonuphis* by having bidentate, pseudocompound and subacicular hooks instead of distally entire hooks, and from *Hirsutonuphis* by having shorter dorsal cirri, shorter

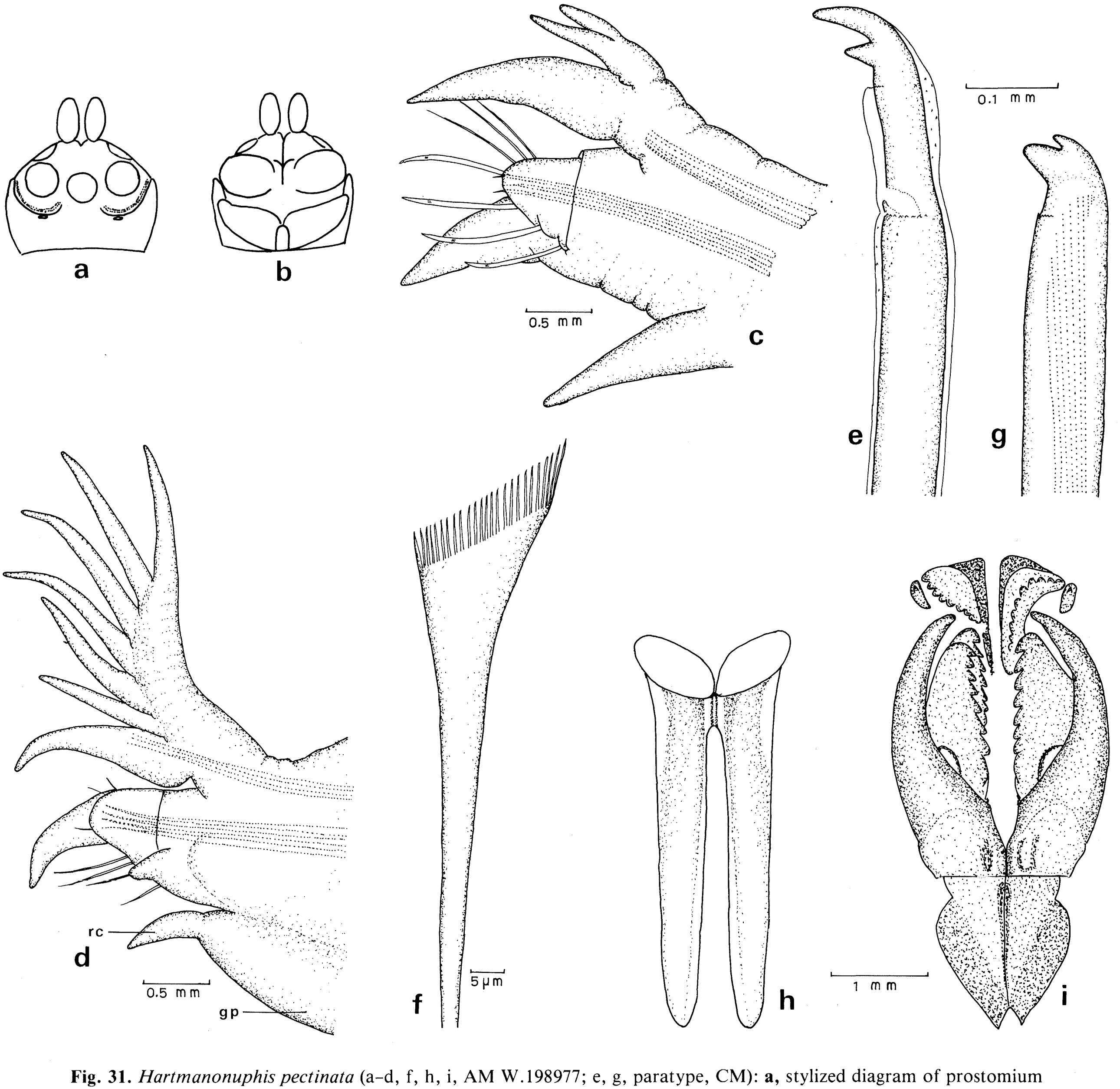


Fig. 31. *Hartmanonuphis pectinata* (a–d, f, h, i, AM W.198977; e, g, paratype, CM): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, anterior view; **d**, parapodium 12, anterior view (gp = glandular pad; rc = reduced cirrus); **e**, pseudocompound hook from setiger 2; **f**, pectinate seta from setiger 200; **g**, subacicular hook from setiger 50; **h**, mandibles; **i**, maxillae.

ceratophores and uniformly sclerotized, instead of the characteristically sclerotized, maxillary carriers.

The type specimens of *O. pectinata,* the only known species in the genus, were examined. The modified parapodia contain 3–4 upper limbate setae instead of 12 as described by Knox & Hicks (1973).

Distribution. South Pacific Ocean: New Zealand; intertidal to 85 m.

Hirsutonuphis n. gen.

Fig. 32a–l

Type species: *Onuphis mariahirsuta* Paxton, 1979: 277. Gender: feminine.

Material examined. *Onuphis mariahirsuta*—**Australia:** New South Wales: Coffs Harbour—HOLOTYPE (AM W.11799), 5 PARATYPES (AM W.15083-7) and others (AM). *Onuphis geminata*—**Central America:** Belize—2 PARATYPES (USNM 061240). *Onuphis gygis*—**Australia:** Queensland: Fraser Island—HOLOTYPE (AM W.15103) and 2 PARATYPES (AM W.15104-5). *Onuphis zebra*—**Mexico:** Lower California: Punta Gorda—HOLOTYPE (USNM 32898). *Hirsutonuphis* n. sp. 1—**Australia:** New South Wales: Botany Bay near Sydney—2 (AM W.13768), 2 (AM W. 13775) and others (AM); Queensland—several (AM). *H.* n.sp. 2—**Australia:** New South Wales—1 (AM W.6258), 2 (AM W.6263) and others (AM).

Diagnosis. Antennae with moderately long ceratophores (10–15 rings) and moderately long styles; long to very long anterior dorsal cirri; maxillary carriers with darkly sclerotized median part and lateral triangles.

Definition. Prostomium (Fig. 32a) with anterior median incision. Posterior antennae almost covering dorsal part of short prostomium, with ceratophores with 10–15 rings and moderately long styles: longest styles (posterior laterals) to setiger 4–10, anterior lateral styles shorter to longer than their ceratophores. Frontal palps oval; labial palps oval to rectangular, with or without median section (Fig. 32b). Nuchal grooves widely separated in midline, curved towards base of median antenna. Tentacular cirri inserted distally on short to moderately long peristomium. Middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna; ventral lip with median section.

Anterior 5–8 pairs of parapodia modified, moderately prolonged (parapodia 2–4 longest) (Fig. 32j). Ventral cirri subulate on anterior 6–8 setigers, short transition zone of glandular pads with reduced cirri (until setiger 9–11). Dorsal cirri long to very long (Fig. 32c,j) with basal swelling (Fig. 32d). Interramal papilla on setigers 11–18 in H. zebra. Branchiae usually from setiger 6 (rarely 8–9), with thick stem and pectinate filaments (maximum of 8–12).

Hooks of modified parapodia bi- to tridentate, pseudocompound with hoods (Fig. 32e,f); median hooks usually slightly larger but not becoming simple or remaining into unmodified parapodia. Pectinate (Fig. 32k,l) and upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 32g) usually from setiger 20–30 (rarely 15 to after 35).

Jaws with mandibles (Fig. 32h), and maxillae (Fig. 32i) with moderately long Mx III, short Mx V, Mx VI absent. Carriers heart-shaped; lateral triangular area between Mx I and carriers, and anterior median region of carriers strongly sclerotized. Tubes thin, temporary, consisting of inner mucous and outer layer of sand.

Size. Small to large; width 1.1 to 6 mm; longest complete specimen (type species) measures 56 cm for 1040 setigers.

Etymology. The modified parapodia with their long dorsal cirri give the animals a 'hairy' appearance, hence the first part of the name. This is combined with *Onuphis,* the first described genus in the family.

Remarks. *Hirsutonuphis* is the only onuphid genus that has diagnostic maxillary carriers. It is most closely related to *Hartmanonuphis,* which has been described above and their relationships discussed.

The holotype of *O. zebra* was examined and found to contain no compound spinigers, contrary to Fauchald (1980; 1982a).

The following species are referred to *Hirsutonuphis: Onuphis mariahirsuta* Paxton, 1979; *Onuphis acapulcensis* Rioja, 1944; *Onuphis (Onuphis) geminata* Fauchald, 1980; *Onuphis gygis* Paxton, 1979; *Onuphis zebra* Berkeley & Berkeley, 1939; *H.* n.sp. 1; *H.* n.sp. 2.

Distribution. Pacific Ocean: eastern Australia, Guatemala, Mexico; Atlantic Ocean: Caribbean Sea; intertidal to 36 m.

Key to Described Species of *Hirsutonuphis*

1. Anterior dorsal cirri as thick as antennae (Fig. 32j); pseudocompound hooks of anterior setigers bidentate. . . . . *H. gygis*

——Anterior dorsal cirri much thinner than antenna (Fig. 32c); pseudocompound hooks of anterior setigers bi- to tridentate (Fig. 32e,f). 2

2. Conical interramal papilla on setigers 11–18; subacicular hooks after setiger 35. . . . . *H. zebra*

——Interramal papilla absent; subacicular hooks from setiger 15–26. 3

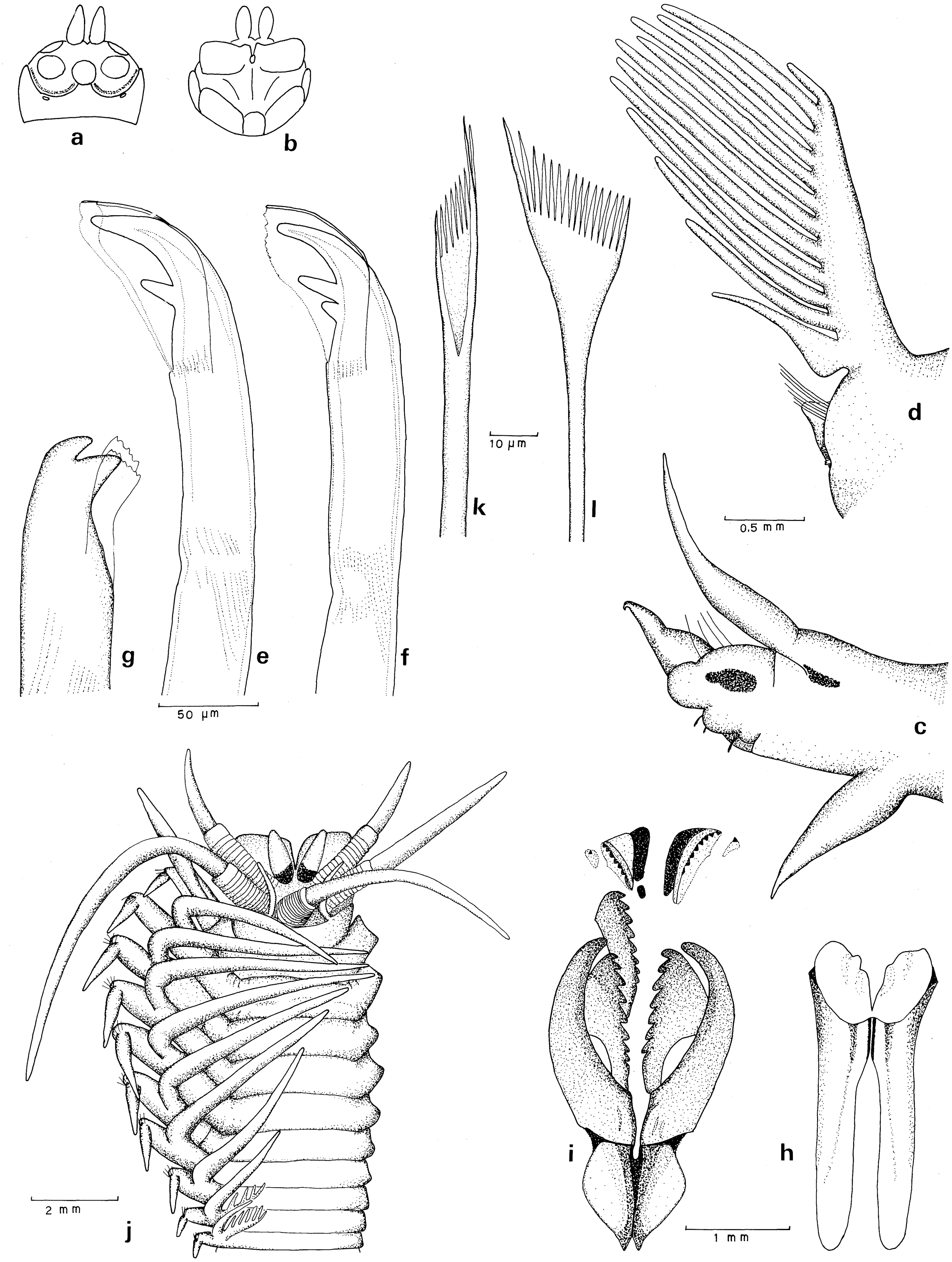


Fig. 32. *Hirsutonuphis mariahirsuta* (c–i from Paxton, 1979: figs 24, 26, 27, 29, 31–33): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, anterior view; **d**, parapodium 60, same view; **e**, bidentate pseudocompound hook from setiger 1; **f**, tridentate pseudocompound hook from same; **g**, subacicular hook from setiger 60; **h**, mandibles; **i**, maxillae (Mx III to Mx V not in natural position). *H. gygis* (from Paxton, 1979: figs 34, 38, 39): **j**, anterior end, dorsal view; **k**, rolled up pectinate seta from setiger 1; **l**, flat pectinate seta from median region.

3. Subacicular hooks from setiger 15–18; all pseudocompound hooks tridentate. .... *H. acapulcensis*

——Subacicular hooks from setiger 20–26; peudocompound hooks bi- and tridentate. .... 4.

4. No brown middorsal bands (Fig. 32j) after setiger 6. .... *H. mariahirsuta*

——Brown middorsal bands from setiger 2–50. .... *H. geminata*

Genus *Aponuphis* Kucheruk
Fig. 33a–h

Aponuphis Kucheruk, 1978: 91. Type species: *Hyalinoecia bilineata* Baird, 1870: 358, by original designation. Gender: feminine.

Material examined. *Hyalinoecia bilineata*—**U.K.**: off Cornwall—3 SYNTYPES (BMNH ZH 1867.1.7.2). *Aponuphis bilineata*—**Ireland:** off Cork—1 (BMNH ZB 1983.314).

Diagnosis. Antennae with moderately long to long ceratophores (10–20 rings); branchiae absent or as single filaments; tentacular cirri absent.

Definition. Prostomium (Fig. 33a) anteriorly extended. Posterior antennae on median to posterior part of prostomium, with ceratophores with 10–20 rings and moderately long to long styles (to setigers 8–20), anterior lateral styles shorter to longer than their ceratophores. Frontal palps oval; labial palps rectangular without median section (Fig. 33b). Nuchal grooves straight, small middorsal separation. Tentacular cirri absent. Peristomium moderately long, middorsal part of peristomium with anterior fold; ventral lip with weakly defined median section.

Anterior 5 pairs of parapodia (Fig. 33c) modified, not prolonged. Ventral cirri subulate on anterior 5–7 setigers, short transition zone of globular ventral cirri; dorsal cirri moderately long. Branchiae, rarely absent, usually present from setiger 4, rarely 1–7; single filament.

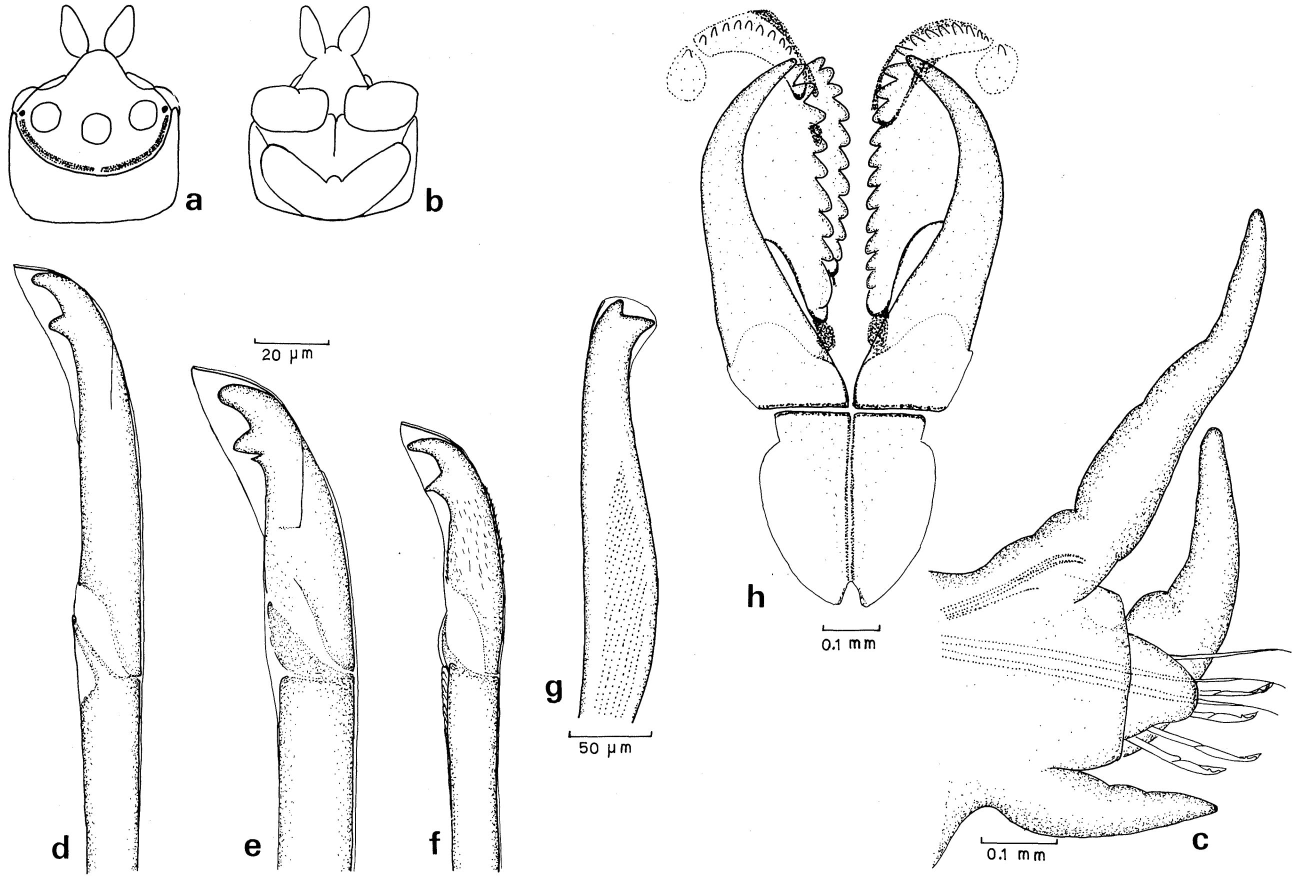


Fig. 33. *Aponuphis bilineata* (c, f, syntype BMNH ZH 1867.1.7.2; d, e, g, h, BMNH ZK 1983.314): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 1, anterior view; **d,** lower bidentate pseudocompund hook from setiger 1; **e,** median tridentate pseudocompound hook from same; **f,** lower bidentate pseudocompound hook from setiger 5; **g,** subacicular hook from posterior setiger; **h,** maxillae.

Hooks of modified parapodia bi- to tridentate, pseudocompound with hoods (Fig. 33d-f); median hooks slightly larger, remaining to setiger 7 but not becoming simple. Pectinate setae from setiger 6-7; upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 33g) from setiger 8-20.

Jaws with mandibles, and maxillae (Fig. 33h) with moderately long Mx III, large Mx V, Mx VI absent. Tubes thin, consisting of inner mucous and outer layer of sand or broken shells.

Size. Small; length to 80 mm (250 setigers), width less than 1.5 mm.

Remarks. Bellan (1964) considered all subspecies and related species of *A. bilineata* as ecological 'forms' and synonyms of that species. In view of the differences involved, this judgement appears very conservative, and the species are retained until more conclusive evidence of their conspecificity is available.

The following species are recognized: *A. bilineata* (Baird, 1870); *A. brementi* (Fauvel, 1916); *A. fauveli* (Rioja, 1918); *A.* grubii (Marenzeller, 1886); *A. ornata* (Fauvel, 1928); *A. rigida* (Claparède, 1868); *A.* sp., abranchiate (see Bellan, 1964).

Distribution. Eastern North Atlantic Ocean and Mediterranean Sea; in shallow depths.

Genus *Kinbergonuphis* Fauchald
Fig. 34a-o

Kinbergonuphis Fauchald, 1982a: 10. Type species: *Onuphis tenuis* Hansen, 1882: 10, by original designation. Gender: feminine.

Material examined. *Onuphis tenuis*—**Brazil:** off Rio de Janeiro—LECTOTYPE and PARALECTOTYPE (RNHL). *Onuphis taeniata*—**Australia:** Queensland: Mackay—HOLOTYPE (AM W.15102) and 7 PARATYPES (AM W.15095-101). *Kinbergonuphis taeniata*—**Australia:** Queensland: Moreton Bay—3 (QM GH570, 572, 574). *K.* n.sp.—**Australia:** Queensland: Moreton Bay near Brisbane—1 (QM GH573); Halifax Bay, N of Townsville—1 (AM W.198983) and others (AM).

Diagnosis. Antennae with short to moderately long ceratophores (3-10 rings); anterior lateral styles longer than their ceratophores; short transition zone of ventral glandular pads with reduced cirri (to setiger 7-9, rarely 11-13) or globular ventral cirri; large median hooks often present.

Definition. Prostomium (Fig. 34a) anteriorly incised or extended. Posterior antennae on median to posterior part of prostomium, with ceratophores with usually 3-7 rings (rarely 8-10 or smooth), and with short to long styles: longest (usually posterior laterals) to setiger 5-25, anterior lateral styles as long as or longer than their ceratophores. Frontal and labial palps oval, with or without median section (Fig. 34b). Nuchal grooves straight, small to large middorsal separation. Tentacular cirri inserted distally on short to moderately long peristomium, middorsal part of peristomium with anterior fold; ventral lip with median section.

Anterior 5-7 (rarely 3) pairs of parapodia modified, short to slightly prolonged (Fig. 34c,m). Ventral cirri subulate on anterior 2-7 setigers, short transition zone of glandular pads with reduced cirri to setiger 7-9 (rarely 11-13), or globular ventral cirri; dorsal cirri short to moderately long, with or without basal swelling. Branchiae rarely absent, usually present from setiger 6, rarely before or after; rarely single, usually pectinate filaments; branchial stem usually thin (Fig. 34d).

Hooks of modified parapodia usually tridentate (sometimes uni- to tridentate), pseudocompound with hoods (Fig. 34e). Median hooks slightly larger, usually becoming simple and changing to 'large median hooks' (see p. 13) (Fig. 34f-h), present usually in anterior unmodified parapodia, often until origin of subacicular hooks. Pectinate setae (Fig. 34i) from setiger 1 or later; upper limbate setae (Fig. 34j) from setiger 1, lower limbate setae (Fig. 34k) simple; bidentate hooded subacicular hooks (Fig. 34l) usually from setiger 12-20 (rarely later, up to 40).

Jaws with mandibles (Fig. 34n), and maxillae (Fig. 34o) with moderately long Mx III, short Mx V, Mx VI absent. Tubes usually thin, consisting of inner mucous and outer layer of sediment; rarely tough, with parchment-like lining.

Size. Most species are small, less than 10 cm, width less than 2 mm. Width of largest species to 5 mm with parapodia.

Remarks. The genus was recently described by Fauchald (1982a). His diagnosis is accepted in the present definition but a greater emphasis is placed on the large median hooks of anterior setigers. Fauchald stated that pseudocompound hooks were present in the first five setigers of the type species and that large hooks were absent. An examination of the type specimens of *K. tenuis* revealed the presence of large median hooks (Fig. 34a) in setigers 6-8. The large median hooks develop late in ontogeny and are absent in young juveniles (see p. 20). This may account for several small species, listed below, that lack the characteristic hooks.

The following list of recognized species is based on Fauchald (1982a) who gave a key to species. *Onuphis vexillaria* Moore, 1911 is here referred to *Kinbergonuphis* due to the possession of the following characters: antennae with short ceratophores, large number of ventral cirri, numerous branchial filaments, large median hooks and late origin of subacicular hooks. The species marked with an asterisk have long pointed hoods (except *Nothria atlantisa* Hartman, 1965 which lacks hoods) and lack large median hooks. They should probably be referred to the genus *Paradiopatra: K. tenuis* (Hansen, 1882); **K. abyssalis* (Fauchald, 1968); ?*K. arctica* (Annenkova, 1946); **K. atlantisa* (Hartman, 1965); *K. cedroensis* (Fauchald, 1968); *K. difficilis* (Fauchald, 1982d); *K. dorsalis* (Ehlers, 1897); *K. fragilis* (Kinberg, 1865); *K. gorgonensis* (Monro, 1933); *K.*

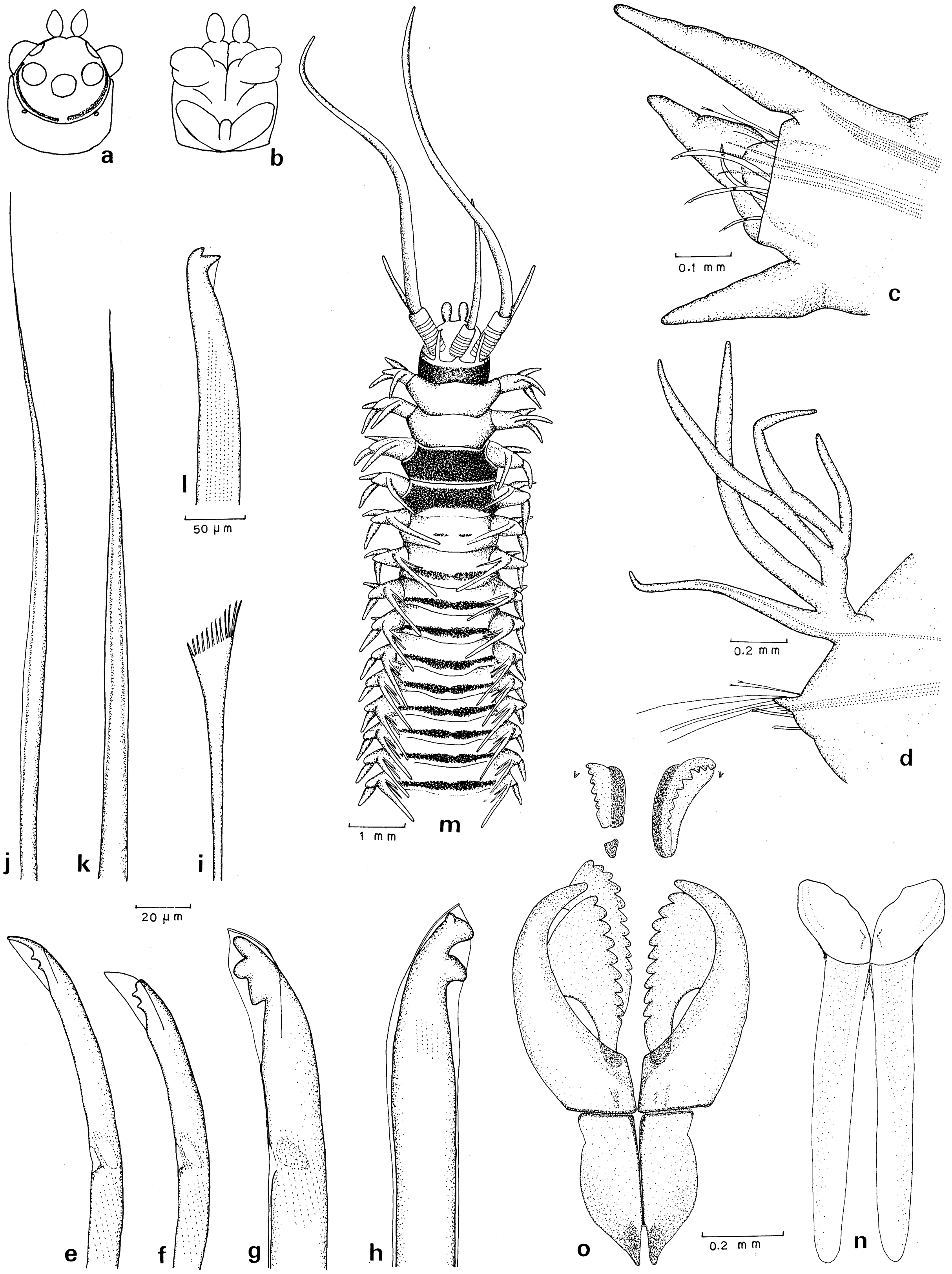


Fig. 34. *Kinbergonuphis tenuis* (d, f, g, lectotype; e, h–m, paralectotype RNHL): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 1, anterior view; **d,** posterior parapodium, posterior view; **e,** upper pseudocompound hook from setiger 1; **f,** median pseudocompound hook from setiger 1; **g,** pseudocompound 'large median hook' from setiger 4; **h,** simple 'large median hook' from setiger 8; **i,** pectinate seta from posterior setiger; **j,** upper limbate seta from setiger 6; **k,** lower limbate seta from same; **l,** subacicular hook from posterior setiger. *Kinbergonuphis taeniata* (from Paxton, 1979: figs 43, 54, 55): **m,** anterior part, dorsal view; **n,** mandibles; **o,** maxillae (Mx III to Mx V not in natural position).

heterouncinata (Hartmann-Schröder, 1965) (? juvenile); *K. investigatoris* (Fauvel, 1932); *K. jenneri* (Gardiner, 1976); *K. lineata* (Fauchald, 1980); *K. microcephala* (Hartman, 1944); **K. mixta* (Fauchald & Hancock, 1981); ?*K. multidentata* (Hartmann-Schröder, 1960); *K. nannognathus* (Chamberlin, 1919); *K. notialis* (Monro, 1930); *K. oligobranchiata* (Orensanz, 1974); *K. orensanzi* (Fauchald, 1982d); *K. paradiopatra* (Hartman, 1944); *K. pigmentata* (Fauchald, 1968); *K. proalupus* (Chamberlin, 1919); *K. pseudodibranchiata* (Gallardo, 1968); *K. pulchra* (Fauchald, 1980); K. *pygidialis* (Fauchald, 1968) (? juvenile); *K. rubrescens* (Augener, 1906); *K. simoni* (Santos, Day & Rice, 1981); *K. taeniata* (Paxton, 1979); *K. tenuisetis* (McIntosh, 1885); *K. vermillionensis* (Fauchald, 1968); *K. vexillaria* (Moore, 1911); *K. virgata* (Fauchald, 1980); *K.* n.sp.

Distribution. World-wide, in all depths; most species occur in the western Atlantic Ocean, in intertidal depths (see Fauchald, 1982a).

Genus *Mooreonuphis* Fauchald

Fig. 35a–j

Mooreonuphis Fauchald, 1982a: 55. Type species: *Onuphis nebulosa* Moore, 1911: 269, by original designation. Gender: feminine.

Material examined. *Onuphis nebulosa*—**U.S.A.**: California: Monterey Bay—2 PARATYPES (USNM 17062) and 4 (USNM 17432).

Diagnosis. Anterior hooks bi- to tridentate; lower limbate setae compound (= spinigers).

Definition. Prostomium (Fig. 35a) anteriorly weakly incised or extended. Posterior antennae on median to posterior part of prostomium with ceratophores with up to 5 rings, rarely smooth, with short to long styles: longest (usually posterior laterals) to setiger 3–13, anterior lateral styles longer than their ceratophores. Frontal and labial palps oval, without median section (Fig. 35b). Nuchal grooves straight, small middorsal separation. Tentacular cirri inserted distally on short to moderately long peristomium, middorsal part of peristomium with anterior fold; ventral lip with median section.

Anterior 3–5 (rarely 7) pairs of parapodia modified, not prolonged (Fig. 35c). Ventral cirri subulate on anterior 3–6 setigers (rarely up to 10), short transition zone of globular ventral cirri; dorsal cirri short to moderately long. Branchiae usually present after setiger 17 (rarely from 6 or 7); usually single, rarely pectinate filaments.

Hooks of modified parapodia usually tridentate (rarely bi- and tridentate), pseudocompound with hoods (Fig. 35d–f). Median hooks slightly larger (Fig. 35e), sometimes becoming simple and changing to 'large median hooks' (see p. 31) (Fig. 35g), and present in anterior unmodified parapodia. Pectinate setae from setiger 6–7, upper limbate setae from setiger 1, lower setae compound (= spinigers) (Fig. 35h) until replaced by bidentate hooded subacicular hooks (Fig. 35i) from setiger 13–29.

Jaws with mandibles, and maxillae (Fig. 35j) with moderately long Mx III, small Mx V, Mx VI absent. Tubes range from thin mucous to tough parchment-like inner layer with outer layer of sediment.

Size. Small; length less than 10 cm, width up to 2.2 mm with parapodia.

Remarks. The following list of recognized species is based on Fauchald (1982a) who gave a key to species. *Nothria exigua* Shisko, 1981 and *Onuphis segmentispadix* Shisko, 1981 possess spinigers and are here referred to *Mooreonuphis: M. nebulosa* (Moore, 1911); *M. cirrata* (Hartman, 1944); *M. dangrigae* (Fauchald, 1980); *M. exigua* (Shisko, 1981); *M. guadalupensis* (Fauchald, 1968); *M. intermedia* (Kinberg, 1865); *M. jonesi* Fauchald, 1982c; *M. litoralis* (Monro, 1933); *M. microbranchiata* (Fauchald, 1968); *M. pallidula* (Hartman, 1965); *M. peruana* (Hartman, 1944); *M. segmentispadix* (Shisko, 1981); *M. stigmatis* (Treadwell, 1922); *M. veleronis* (Fauchald, 1980).

Distribution. Eastern Pacific and western Atlantic Oceans: Americas; in intertidal to shelf depths (see Fauchald, 1982a).

Genus *Onuphis* Audouin & Milne Edwards

Figs 3, 6–8, 10

Onuphis Audouin & Milne Edwards, 1833: 225. Type species: *Onuphis eremita* Audouin & Milne Edwards, 1833: 226, by subsequent designation of Malmgren, 1866: 180. Gender: feminine.

Material examined. *Onuphis eremita*—**France:** Noiremoutier, near St. Nazaire—2 (BMNH ZK 1928.4.26.290-1). *O. aucklandensis*—**New Zealand:** Auckland—several (UC). *O. holobranchiata*—**Australia:** Queensland—many (AM); Victoria: Phillip Island—1 (AM W.3584) and others (NMV); Western Australia: Cockburn Sound—1 (WAM 23-74) and others. *O.* n.sp., abranchiate—**Australia:** New South Wales: Botany Bay near Sydney—10 (AM W.13117) and others (AM).

Diagnosis. Antennae with moderately long to long ceratophores (10–25 rings) and short to moderately long styles; anterior lateral styles shorter than their ceratophores; branchiae usually from setiger 1.

Definition. Prostomium (Fig. 3a,b) often anteriorly extended. Posterior antennae on median to posterior part of prostomium, with ceratophores usually with 10–25 rings (rarely less than 10), with short to moderately long (rarely long) styles: longest (posterior laterals) to setiger 5–12 (rarely to 25), anterior lateral styles shorter than their ceratophores. Frontal and labial palps oval, with or without median section (Fig. 3c). Nuchal grooves straight, small to wide middorsal separation. Tentacular cirri inserted distally on moderately long peristomium. Middorsal part of peristomium with distinct anterior fold; ventral lip with median section.

Anterior 3–4 (rarely 2 or 5) pairs of parapodia modified, not prolonged (Figs 3a, 6a). Ventral cirri subulate on anterior 4–6 setigers, short transition zone of globular ventral cirri; dorsal cirri moderately long, with basal swelling. Interramal papillae (Fig. 6b) on setigers 4–10 in type species. Branchiae rarely absent, usually present from setiger 1, rarely 3–6; usually thin stem (Fig. 7), single or pectinate filaments (maximum 8).

Hooks of modified parapodia usually tridentate (rarely only bidentate, sometimes bi- and tridentate), pseudocompound with hoods (Fig. 8d,e); median hooks usually slightly larger (Fig. 8d) but not becoming simple or remaining into unmodified parapodia. Pectinate setae (Fig. 8c) and upper limbate setae (Fig. 8a) from setiger 1 or later; lower limbate setae (Fig. 8b) simple; bidentate hooded subacicular hooks (Fig. 8f) usually from setiger 10–12 (rarely 9–18).

Jaws with mandibles (Fig. 9a), and maxillae (Fig. 9b) with moderately long Mx III, small Mx V, Mx VI absent. Tubes usually thin, consisting of inner mucous and outer layer of sediment; rarely tough with parchment-like lining.

Size. Most species are small, width less than 3mm. Length of largest species is up to 30 cm (more than 200 setigers) width up to 4 mm.

Remarks. Audouin & Milne Edwards (1833) did not designate a type species for *Onuphis*. The description

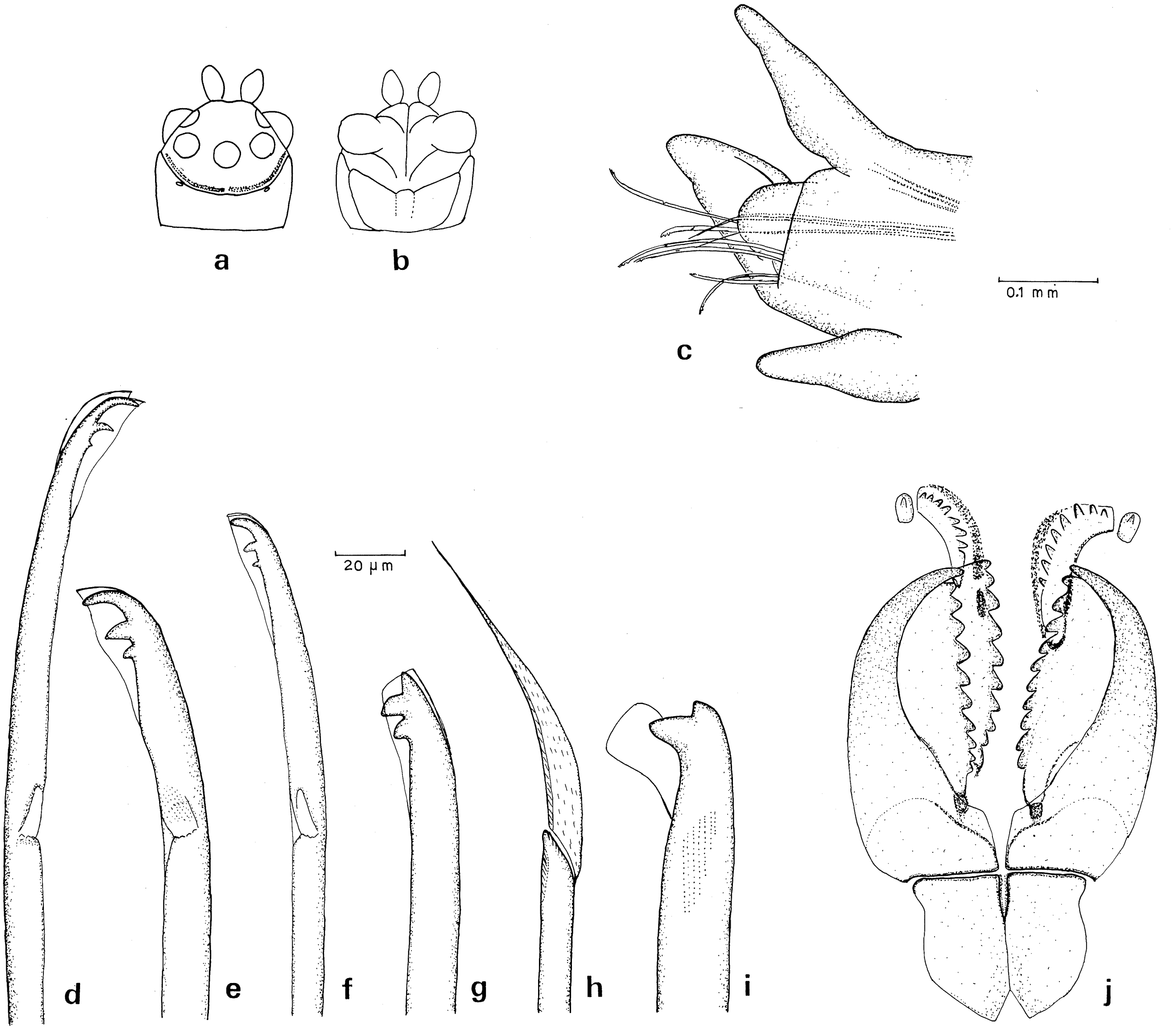


Fig. 35. *Mooreonuphis nebulosa* (a–g, i–j, USNM 17432; h, paratype USNM 17062): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 1, anterior view; **d,** upper pseudocompound hook from setiger 1; **e,** median pseudocompound hook from same; **f,** lower pseudocompound hook from same; **g,** simple 'large median hook' from setiger 9; **h,** compound lower limbate seta from setiger 12; **i,** subacicular hook from posterior setiger; **j,** maxillae.

of the genus was followed by that of *Onuphis eremita* with a note that *Nereis tubicola* Müller also belonged to the genus *Onuphis*. Therefore, *O. eremita* cannot be considered as type species by monotypy as has been stated by some authors. Milne Edwards (1838: 564) gave a short description of the genus and listed only one species, *Onuphis eremita*. This reference was taken as a type designation by Malmgren (1866) and stated as such. Thus, the first author to unequivocally state the type species for the genus was Malmgren and his subsequent designation is herein accepted.

The genus was recently revised by Fauchald (1982a), whose diagnosis is largely accepted in the present definition. However, the discovery of an abranchiate new species (Paxton, in preparation), fitting the definition of the genus *Onuphis* in all other criteria, requires the emendation of the genus to include abranchiate species.

The following list of recognized species is based on Fauchald (1982a) who gave a key to species: *O. eremita* Audouin & Milne Edwards, 1833; *O. eremita oculata* Hartman, 1951 (? juvenile *O. eremita); O. eremita parva* Berkeley & Berkeley, 1941; *O. aucklandensis* Augener, 1924; *O. branchiata* Treadwell, 1931; *O. chinensis* Uschakov & Wu, 1962; *O. declivorum* Fauchald, 1982c; *O. dibranchiata* Willey, 1905; *O. elegans* (Johnson, 1901); *O. falesia* Castelli, 1982; *O. farallonensis* Hobson, 1971; *O. geophiliformis* (Moore, 1903) (? juvenile); *O. heterodentata* Fauchald, 1982c; *O. holobranchiata* Marenzeller, 1879; *O. iridescens* (Johnson, 1901); *O. lithobiformis* Fauchald, 1982c; *O. mexicana* (Fauchald, 1968); *O. multiannulata* Shisko, 1981; *O. opalina* (Verrill, 1873); *O. pallida* (Moore, 1911); *O. rullieriana* (Amoureux, 1977); *O. shirikishinaiensis* (Imajima, 1960); *O. similis* (Fauchald, 1968); *O. texana* Fauchald, 1982c (? juvenile); *O. vibex* (Fauchald, 1972); *O.* n.sp. (abranchiate.)

Distribution. World-wide, in all depths; most species occur in the western Pacific Ocean, in shelf depths (see Fauchald, 1982a).

Genus *Heptaceras* Ehlers

Fig. 36a–j

Heptaceras Ehlers, 1868: 284. Type species: *Diopatra phyllocirra* Schmarda, 1861: 133, by monotypy. Gender: neuter.

Tradopia Baird, 1870: 355. Type-species: *Tradopia maculata Baird, 1870: 355, by monotypy.*

Material examined. *Diopatra phyllocirra*—**Sri Lanka:** south west, Bentota Beach—NEOTYPE designated herein (BMNH ZK 1953.11.10.8). *Heptaceras phyllocirrum*—**Sri Lanka:** south west, Bentota Beach—1 (BMNH ZK 1953.11.10.1-7); **Arabia:** south coast-3 (BMNH ZK 1937.9.2.341-2). *Tradopia maculata*—**India:** Madras-2 SYNTYPES (BMNH ZK 1868.5.27.1). *Onuphis quinquedens*—**South Africa:** Natal: Umpanganzi—HOLOTYPE (BMNH ZK 1961.16.34).

Diagnosis. Antennae with long to very long ceratophores (20–60 rings); peristomium with deep middorsal notch.

Definition. Prostomium (Fig. 36a) with frontal extension forming palpophores for frontal palps. Posterior lateral antennae on posterior part of prostomium, median antenna in more anterior position; ceratophores very wide (almost covering dorsal part of prostomium) and long (20–60 rings), styles short to moderately long: longest (posterior laterals) to setiger 3–10; anterior lateral styles shorter than their ceratophores. Frontal palps oval; labial palps rectangular, with small median section (Fig. 36b). Moderately long peristomium with deep middorsal notch; ventral lip with median section. Nuchal grooves following edge of peristomium including notch, separated in midline by raised ridge between base of notch and base of median antenna. Tentacular cirri inserted distally on peristomium on each side of notch.

Anterior 3 pairs of parapodia modified, slightly prolonged (Fig. 36c). Ventral cirri subulate, present on anterior 5 setigers, short transition zone of globular ventral cirri; dorsal cirri moderately long, with basal swelling, small basal process present (Fig. 36d) or absent. Small interramal papilla from setiger 6–10 in type species. Branchiae from setiger 1, with thick stem and pectinate filaments (maximum of 12).

Hooks of modified parapodia bi- to tridentate, pseudocompound with hoods (Fig. 36e,f,i,j); median hooks slightly larger but not becoming simple or being present in anterior unmodified parapodia. Pectinate setae from setiger 6–8; upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 36g) from setiger 9–10.

Jaws with mandibles, and maxillae (Fig. 36h) with moderately long Mx III, small Mx V, Mx VI absent. Worms make mucous-lined vertical burrows (Day, 1967), i.e. temporary tubes.

Size. Moderately large; width to 4 mm; length to 20 cm (500 setigers).

Remarks. The genus *Heptaceras* was erected by Ehlers (1868) for *Diopatra phyllocirra,* described by Schmarda (1861) from the east and south coasts of Sri Lanka. It has not been reported since its original description and has been considered a probably aberrant form by Kucheruk (1978).

Ehlers defined the genus as having long, filiform frontal palps, resembling the antennae, instead of the short frontal palps present in *Diopatra.* However, Schmarda never stated that the frontal palps of *D. phyllocirra* were as long as the antennae, on the contrary, he compared their length to that of the tentacular cirri which he described as small, 'hardly larger than those of the forehead'.

He described the head as small, with two eyes at the base of the median antenna, and next to them the tentacular cirri. He stated that branchiae were present from setiger 1 as a single filament, becoming spiralled later. Spiralled branchiae are known to occur only in *Diopatra* and *Epidiopatra,* where they are spiralled from their origin on setiger 4–5. The filaments in Schmarda's illustration (fig. f) appear more pectinately branched

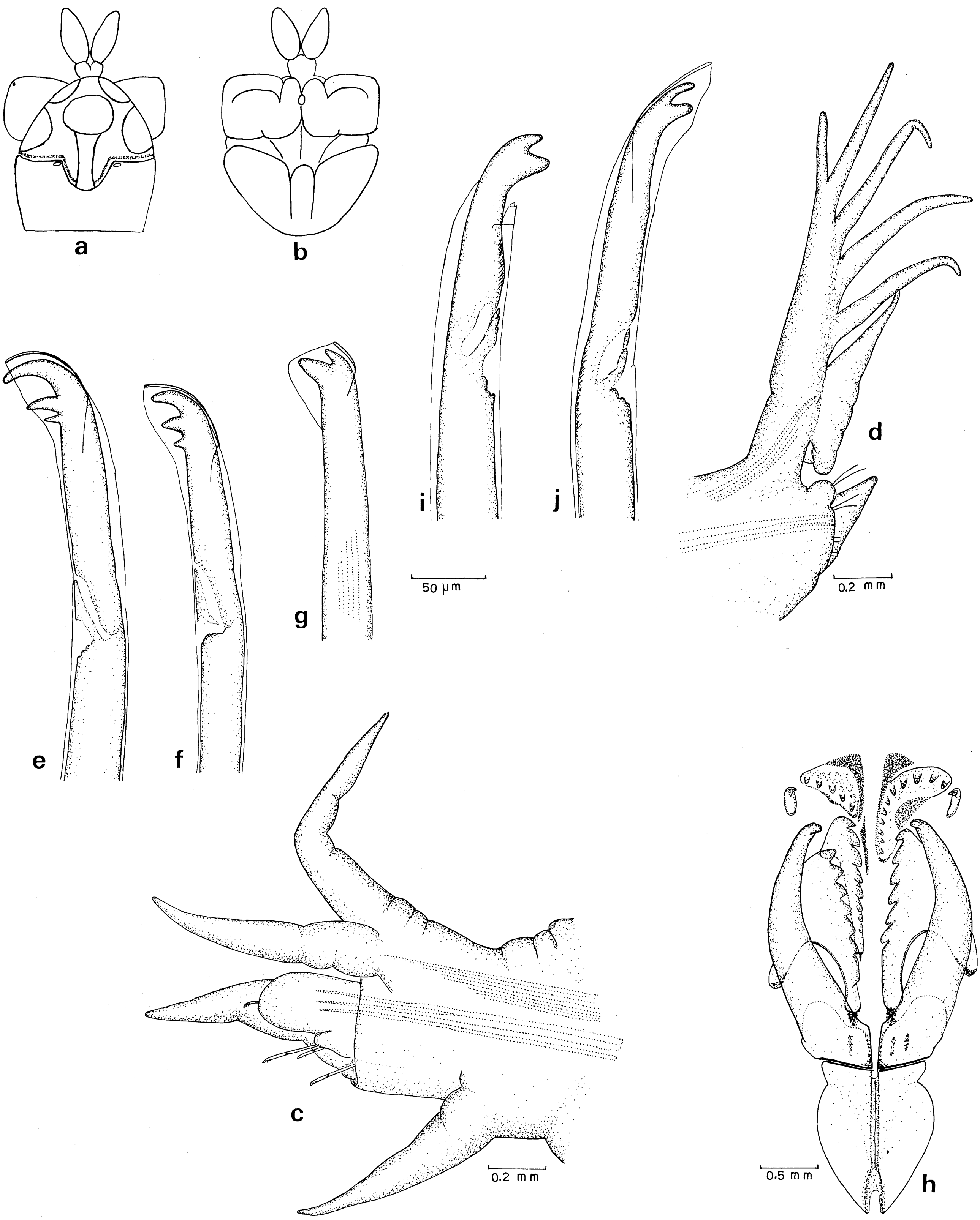


Fig. 36. *Heptaceras phyllocirrum* (BMNH ZK 1953.11.10.1-8): **a,** stylized diagram of prostomium and peristomium, dorsal view; **b,** same, ventral view; **c,** parapodium 1, anterior view; **d,** parapodium 17, anterior view; **e,** median tridentate pseudocompound hook from setiger 1; **f,** lower tridentate pseudocompound hook from same; **g,** subacicular hook from setiger 98; **h,** maxillae. *Heptaceras quinquedens* (holotype BMNH ZK 1961.16.34): **i,** median bidentate pseudocompound hook from setiger 2; **j,** lower bidentate pseudocompound hook from same.

than spiralled. Another characteristic of the species was the leaf-like, uneven heart-shaped dorsal cirrus (Schmarda, 1861: fig. f).

Baird (1870) described the genus *Tradopia* for his new species *T. maculata*. The genus was considered invalid and *T. maculata* referred to *Onuphis* (Hartman, 1959; Fauchald, 1977). The species had not been reported since its original description. This may be attributed to Baird's insufficient description which was not accompanied by any illustrations. Examination of the type material shows that *T. maculata* has a small prostomium, almost completely covered by the large ceratophores of the antennae, has dorsal cirri with basal processes (giving a heart-shaped appearance), has branchiae from setiger 1, which become pectinately branched from setiger 10, and its subacicular hooks are of the same shape as those illustrated by Schmarda (1861: fig. c) for *D. phyllocirra*. Although *T. maculata* lacks eyes, the depressions next to the median ridge between the peristomium and the base of the median antenna flanked by the tentacular cirri could have been interpreted as eyes. It appears certain that *T. maculata* is a junior synonym of *D. phyllocirra*.

Onuphis basipicta Willey, 1905: 275, from southwest Sri Lanka, is also referred to the latter. Although the type material is not available (Fauchald, 1982a), its identity appears clear from the description. Furthermore, specimens from Bentota Beach, S.W. Sri Lanka, have been identified as the same species in the present study, marking it as a common species on the Sri Lankan coasts. However, it also occurs on the South Arabian coast [it had been misidentified by Monro (1937: 292) as *O. eremita]* and near Madras, so that it is much more common and widespread than was previously suspected.

Since the types of *D. phyllocirra* are lost [Kritscher (NMW), personal communication] I am here designating the complete specimen from Bentota Beach, south west Sri Lanka (BMNH ZK 1953.11.10.8), neotype of *Diopatra phyllocirra* Schmarda, 1861.

The genus *Heptaceras* is redefined, placing emphasis on its notched peristomium and very long ceratophores, and is considered a well characterized, valid genus.

The following species are recognized: *H. phyllocirrum* (Schmarda, 1861); *H. fukianensis* (Uschakov & Wu, 1962); *H. quinquedens (Day, 1951).*

Distribution. Indo-Pacific Oceans: South Africa, Arabia, Sri Lanka, India, Taiwan Strait; intertidal to 22 m.

Key to Species of *Heptaceras*

1. Ceratophores of antennae with brown pigment spots; all pseudocompound hooks tridentate (Fig. 36e,f). .. *H. phyllocirrum*

——Ceratophores of antennae without pigment; pseudocompound hooks bi-, or bi- and tridentate. 2

2. All pseudocompound hooks bidentate (Fig. 36i,j); bifid branchial filaments from setiger 9. .... *H. quinquedens*

——Pseudocompound hooks bi- and tridentate; bifid branchial filaments from setiger 47. .... *H. fukianensis*

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships within the family Onuphidae are analyzed following the principles of Hennig (1966), where only the derived or apomorphic states of characters are utilized. The character states are determined by outgroup comparison, fossil evidence, and observed ontogenetic changes.

The most useful method is by outgroup comparison. The closest relative or sister group of the Onuphidae is the family Eunicidae. The synapomorphies they share are a similar jaw apparatus, parapodial structures and the possession of antennae. The members of the Onuphidae compose the 'ingroup', while members of the Eunicidae form the 'outgroup'. Since the Onuphidae is more specialized in having distinct frontal palps and antennae with well developed ceratophores, and thus represents the most derived family of the order Eunicida, the comparisons are limited to 'below' (more primitive than) their level of structural organization. The outgroup comparison is based on the examination of representative species of eunicids (see 'Materials and Methods'), and information from the literature.

The Eunicida is the order of polychaetes best represented in the fossil record. Although these are generally limited to isolated maxillae (scolecodonts) and mandibles, complete jaw apparatuses (Kielan-Jaworowska, 1966) and a few complete animals with impressions of parapodial structures and setae (Kozur, 1971; Thompson & Johnson, 1977) are known.

Ontogenetic character transformations can be used to determine adult character states. In a transformation from a more general to a specialized character, the former can be regarded as ancestral and the latter as derived (Nelson, 1978). This method confirms some of the decisions based on the other two criteria utilized.

The analysis is based on 46 morphological and ecological characters which are listed and discussed below. While examination is limited to type species and other selected species, information from the literature is also taken into account. However, some characters used in this analysis (e.g. prostomial features, ultrastructure of setae) have not been described before, so that their possible irregular distribution within genera could provide a source of error. For a number of characters (character 31–33) the derived state could not be determined with certainty. However, these characters have been included, since they are considered important in the definition of taxa.

Some characters have been noted to occur infrequently and are considered retained plesiomorphies with widely spread derived states (34–43). The determination of the state of the last three characters (44–46) is rather speculative. It is not based on the eunicids as an outgroup, but on the assumption that the state that occurs in both subfamilies is plesiomorphic, unless it has arisen independently.

Discussion of Characters and Their States

The following notation is used: (0) = plesiomorphic state, (1) = apomorphic state, C = by outgroup comparison, F = fossil evidence, J = ontogenetic changes. The distribution of the character states among the genera is tabularized (Table 4).

1. Frontal palps absent (0), present (1); C, J. Some species of *Eunice* (e.g. *E. aphroditois*) have labial palps which are medially incompletely subdivided, but do not represent distinct frontal palps which are absent throughout the family Eunicidae. Frontal palps are absent in young onuphid juveniles and are often the last prostomial structures to develop (see p. 19).

2. Ceratophores absent, or very short, one-ringed (0), present, longer, sometimes smooth, usually with 2 or more rings (1); C, J. The antennae of eunicids have usually a small, more or less defined promixal division which might be considered as a primitive, one-ringed ceratophore. However, it never develops into a 2-ringed or longer structure. Ceratophores are poorly formed in otherwise well developed juvenile onuphids (see p. 19), demonstrating their derived character state.

3. Lower limbate setae present after origin of subacicular hooks (0), absent (1); C. The lower bundle of setae in eunicids consists of compound falcigers and/or limbate setae (= spinigers). These lower setae are present throughout the median and posterior region in eunicids and in the onuphid subfamily Hyalinoeciinae. Their loss in the median and posterior region of the Onuphinae is seen as a specialization to their tubicolous mode of living.

4. Notosetae present (0), absent (1); C, F. Reduced notosetae are present or absent in the Eunicidae. A well preserved fossil eunicid from the Upper Carboniferous, described as a new genus, *Esconites* Thompson & Johnson, 1977, was characterized by the possession of well developed noto- and neuropodia. However, it is clear from the photograph of the setal impressions (Thompson & Johnson, 1977: fig. 8) that the setae referred to as notoacicula are neuroacicula, and the setae referred to as neuroacicula are subacicular hooks. The notosetae were either absent or left no impression, and the species is uni- or subbiramous like other Eunicida. Since the polychaete parapodium is typically biramous, the presence of notosetae in the Onuphinae is considered as the ancestral condition.

5. Subacicular hooks in ventral position (0), median position (1); C, F. In the former condition, the hooks originate at or slightly above the acicula and emerge lower, thus forming an acute angle (see p. 14). This condition is found in all Recent eunicids, and also in fossil eunicids (see above). The subacicular hooks of the fossil genus *Eunicites* Ehlers, 1868 were referred to as small acicula, running at an acute angle to the large acicula (Kozur, 1971). Anterior permanent subacicular hooks of very young *Diopatra* juveniles are in a median position parallel to the aciculum (see p. 20). The same position in adults of the Hyalinoeciinae is considered as a neotenic condition. The character is considered derived in agreement with Fauchald (1982a), who referred to them as intrafascicular hooks (see p. 13).

6. Hooks without rows of spines (0), with 2 rows of spines (1); C. Small, irregularly distributed spines are present on the shafts of eunicid and onuphid hooks (see p. 13). However, in some genera of onuphids these spines are lengthened and oriented into two lengthwise rows, which is considered a derived condition.

7. Branchiae present throughout (0), limited to anterior region (1); C. Although branchiae are present throughout in all eunicids examined, a number of species are reported in the literature in which the branchiae are limited to the anterior region. The latter condition is considered derived and presumed to have arisen independently in the two families.

8. Lateral projections on ceratophores absent (0), present (1); C. Eunicids lack well developed ceratophores and lateral projections. In the Onuphidae the projections are limited to some species of *Diopatra, Epidiopatra*, and *Paradiopatra*. They are present in small species and may represent a neotenic feature, which is considered apomorphic.

9. Rings on ceratophores 10 or less (0), more than 10 (1); C, J. As stated above (character 2), while one-ringed ceratophores may be present in Eunicidae, well developed ones occur only in the Onuphidae. Most genera have short ceratophores with less than 10 rings, which is interpreted to be the ancestral condition, while long ceratophores with many rings (up to 25–60 in some species of *Onuphis* and *Heptaceras*) are interpreted to be the derived condition in agreement with Fauchald (1982a). This is not a unique development but has arisen independently also in *Hirsutonuphis, Diopatra* and *Epidiopatra.*

10. Branchial filaments simple or branched (0), spiralling around a central trunk (1); C. Spiralled branchial filaments are a unique development in the Eunicida, restricted to *Diopatra* and *Epidiopatra*, and is a synapomorphy.

11. Tentacular cirri present (0), absent (1); C, J. Tentacular cirri are present in *Eunice* (Eunicidae) and generally in onuphids. In some species they develop relatively late in ontogeny (see p. 19), and their complete absence is considered a derived neotenic character that has evolved independently several times in the Onuphidae.

12. Setal sacs of modified parapodia to setiger 1 (0), to setiger 5 or beyond (1); C. Setal sacs in eunicids and usually onuphids are limited to their respective setiger. However, in genera of the *Rhamphobrachium* complex the setal sacs lie in the body cavity to setiger 5 or later (up to setiger 70), and slide anteriorly when protruded. The structure and function of this setal arrangement is so specialized that it is thought to have evolved only once, and is considered apomorphic.

Table 4. Data used in computing the Wagner tree; the characters and their states are defined in the text. 0.0 = plesiomorphic or unknown state; 0.5 = apomorphic state present in some species of the genus only; 1.0 = apomorphic state. The data was read into the program in the order shown.

Character Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Ancestor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nothria	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0
Anchinothria	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0
Hyalinoecia	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptoecia	0.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neonuphis	0.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hyalospinifera	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notonuphis	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paradiopatra	1.0	1.0	1.0	0.0	0.0	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diopatra	1.0	1.0	1.0	0.0	0.0	0.5	1.0	0.5	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epidiopatra	1.0	1.0	1.0	0.0	0.0	0.5	1.0	0.5	0.5	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brevibrachium	1.0	1.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Longibrachium	1.0	1.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhamphobrachium	1.0	1.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Americonuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Australonuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0
Hartmanonuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Hirsutonuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0
Aponuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kinbergonuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Mooreonuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Onuphis	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heptaceras	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0

Character Genus	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Ancestor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nothria	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.0	1.0	0.0	0.0	0.0
Anchinothria	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.0	1.0	1.0	0.5	1.0	0.5	0.0	0.0
Hyalinoecia	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	1.0	1.0	0.5	1.0	0.5	0.5	0.5	1.0	0.0	0.0	0.0	0.0
Leptoecia	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	1.0	0.5	1.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Neonuphis	0.0	0.0	1.0	0.0	1.0	1.0	0.0	0.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	0.5	0.5	0.5	1.0	0.0	0.0	0.0	0.0
Hyalospinifera	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Notonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Paradiopatra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.5	0.5	1.0	0.5	1.0	0.5	1.0	1.0	1.0	0.0	1.0	0.5	1.0
Diopatra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	0.5	1.0	0.5	0.5	1.0	1.0	0.0	1.0	1.0	1.0
Epidiopatra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.5	1.0	0.5	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0
Brevibrachium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.5	0.5	1.0
Longibrachium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.5	0.0	1.0	0.5	0.0	1.0	1.0	1.0
Rhamphobrachium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.5	1.0	1.0	1.0	0.5	1.0	0.0	0.5	1.0	0.0	0.5	0.5	1.0
Americonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.5	1.0	0.0	1.0	1.0	0.0	1.0	0.0	0.0	1.0	1.0	1.0
Australonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	0.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0
Hartmanonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0
Hirsutonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.5	0.5	1.0	0.5	1.0	1.0	1.0	0.0	1.0	1.0	1.0
Aponuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	0.0	0.0	1.0	1.0
Kinbergonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	1.0	1.0	0.5	1.0	1.0	1.0	0.0	1.0	1.0	1.0
Mooreonuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	1.0	0.0	0.5	1.0	1.0	1.0	0.0	0.5	0.5	1.0
Onuphis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	0.5	1.0	1.0	1.0	1.0	0.5	0.0	0.5	1.0	1.0
Heptaceras	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	1.0	0.0	0.0	1.0	1.0	1.0

13. Setal sacs of modified parapodia to setiger 1–5 (0); to setiger 20 or beyond (1); C. The very long setal sacs of *Rhamphobrachium* and *Longibrachium* are here considered an extreme specialization of the two genera.

14. Hooks with immoveable spines (0), with moveable spines (1). Rows of spines are absent in eunicid hooks, which can therefore not be used as the outgroup for this character. The immoveable spines (see p. 13) present in a number of genera are of a simpler type than the highly specialized moveable spines which are only found in *Rhamphobrachium.* Although it cannot be proven at the present time, the former are considered ancestral and the latter derived.

15. Modified parapodia positioned more ventrally than unmodified ones and directed ventrally to anteroventrally (0), anterolaterally to -dorsally (1), C. All eunicid parapodia are similar but the anterior ones are positioned more ventrally and are in contact with the substratum, allowing a crawling method of locomotion. This ventral position of the parapodia has been maintained in some onuphid genera (e.g. *Notonuphis, Paradiopatra*). Members of other genera retained the ventral position but developed prolonged anterior parapodia [e.g. *Diopatra* (Fig. 1a), *Rhamphobrachium, Nothria*] which became anteroventrally directed. Both types are considered ancestral, while the anterolateral to -dorsal position and direction of *Australonuphis* (Fig. 1b) and related genera is considered derived.

16. Mx V large or Mx VI present (0), Mx V small and Mx VI absent (1), C. Maxilla VI is present in some but not all species of *Eunice.* Mx V is large in all eunicid species examined, and has also been illustrated as such in the literature. The small Mx V of the *Onuphis* group is interpreted here as a derived character.

17. Anterior peristomial fold present (0), absent (1); C. A distinct dorsal anterior fold is present in all eunicids and most onuphids. In *Australonuphis* and related genera the peristomium lacks this fold, appearing to extend along the curved nuchal grooves toward the median antenna. This condition is considered as an adaptation to the beach habitat and thus an apomorphic condition.

18. Maxillary carriers uniformly sclerotized (0), median and lateral strong sclerotization (1); C. The maxillary carriers of eunicids and all other genera of onuphids are uniformly sclerotized; the unique sclerotization found in *Hirsutonuphis* is considered an autapomorphy.

19. Subacicular hooks distally bidentate (0), distally entire (1); C. Subacicular hooks are distally bidentate in all but one species of eunicids examined, as they are in most reported species of the family and in all onuphid genera except *Australonuphis.* The distally entire hooks are considered an apomorphy that evolved independently in some species of *Eunice* and *Australonuphis.*

20. Peristomium complete (0), with deep anterior middorsal notch (1); C. The peristomium of eunicids and all other genera of onuphids is anteriorly complete, and the deep middorsal notch found in *Heptaceras* is considered an autapomorphy.

21. Large median hooks absent (0), present (1); C, J. Large median hooks (see p. 13) are not present in the Eunicidae. Their presence in two genera of Onuphidae is here considered derived, as it was by Fauchald (1982a). The late development of large median hooks (see p. 20) also supports their derived state.

22. Pectinate setae flat (0), scoop-shaped (1); C. Pectinate setae are flat or slightly rolled up in all eunicids and onuphids except *Nothria* and *Anchinothria.* In these two genera the lateral distal parts are flared towards each other forming an 'open scoop' (see p. 12), which is considered an apomorphic character in agreement with Fauchald (1982a).

23. Maxilla III distally shorter than left Mx II (0), longer (1); C. In the species of Eunicidae examined, and probably all species of the family, the Mx II is distally shorter than Mx III as it is in all genera of Onuphidae except *Nothria* and *Anchinothria.* This condition is considered plesiomorphic, and the distally longer Mx II a synapomorphy of the latter two genera.

24. Tubes absent, of parchment-like material, or consisting of inner secreted and outer layer of foreign particles, round in transverse section (0), flat tubes with outer layer of foreign particles attached with the flat or concave side to the lining (1); C. Most eunicids have no tubes while some species construct completely organic, parchment-like tubes. While the *Nothria* tubes consist of a secreted inner layer and an outer layer of foreign particles like most onuphid tubes, they are characteristic in their orientation and attachment of the particles and are here interpreted as autapomorphic.

25. Branchial filaments simple or pectinate (0), dichotomously branched (1); C. Dichotomously branched branchial filaments are not found in any eunicids or other onuphids, and are considered autapomorphic in species of *Anchinothria.*

26. Tubes (see plesiomorphic state of character 24) (0), consisting of a clear material composed of onuphic acid and mucoprotein (1); C. Completely organic tubes of an opaque parchment-like material are secreted by eunicids and two species of *Epidiopatra* (Onuphinae), and are considered plesiomorphic, while the clear tubes of the Hyalinoeciinae are considered apomorphic.

27. Tubes without internal valves (0), with internal valves (1); C. The presence of internal valves in *Hyalinoecia* tubes is unique in the order Eunicida, and thus an autapomorphic character.

28. Maxillary cavity openings short to moderately elongated (0), very elongated (1); C, F. The maxillary cavity openings are short to moderately long in the species of Eunicidae examined and in literature reports of extant and extinct members of the family. The maxillae I to III of *Neonuphis* and *Leptoecia* have extremely large cavity openings, a condition assumed to occur also in *Hyalospinifera*, and is considered derived.

29. Maxillae V present (0), absent (1); C, F. Maxillae V are present in all eunicids examined, presumably in

all Recent and fossil species. Their absence in *Neonuphis, Leptoecia* and presumably *Hyalospinifera* is considered a secondary loss and thus derived.

30. Tube without secreted lateral rods (0), with 1 or 2 secreted lateral rods (1); C. Tubes with secreted lateral rods are constructed only by species of *Leptoecia* and *Hyalospinifera* and thus represent a derived character.

31. Oocytes with a single cluster of nurse cells (?0), two strings of nurse cells (?1). Within the order Eunicida, nurse cells are present only in the Dorvilleidae (one cell per oocyte) and Onuphidae. Strings of nurse cells have not been reported for any other group and may represent an autapomorphy of the Onuphinae.

32. Pygidium with four anal cirri (?0), two anal cirri (?1). Anal cirri number two or four in the Eunicidae and no deduction as to the ancestral state can be made based on outgroup comparison. However, it is likely that the ancestral condition was four cirri and became reduced to two in each family independently.

33. Primary envelope of mature oocytes smooth (?0), densely pitted (?1). The more complex surface of the primary envelope may represent the derived condition.

34. Tentacular cirri inserted on second asetigerous segment to subdistally on peristomium (0), distally on peristomium (1); C. Tentacular cirri, when present in the Eunicidae, are inserted far from the anterior margin of the peristomium. In *Americonuphis* the tentacular cirri are inserted in the middle of the peristomium, and in some other genera subdistally. This is considered ancestral, and the distal insertion found in most onuphids is considered derived.

35. Four or more pairs of modified parapodia (bearing hooks) (0), 1–3 pairs (1); C, J. Fauchald considered three to five pairs of parapodia with pseudocompound hooks as plesiomorphic and '(a) two or less' or '(b) more than 5' as apomorphic. In eunicids, all setigers have compound spinigers and/or falcigers. The restriction of hooks to the anterior parapodia and the fusion of the fracture is a specialization of onuphids. I consider it a gradual process with a large number of modified parapodia the ancestral, and a small number the derived condition. Several genera in the Onuphinae retain the plesiomorphic condition. Since the parapodia that have retained hooks usually also bear subulate ventral cirri, the same states are accepted for this character. Agreement between the two characters has been defined as the plesiomorphic, and its absence as the apomorphic condition by Fauchald. As discussed above (see p. 10) the number of setigers with hooks usually agrees with the number of setigers with ventral cirri, while the absence of agreement is usually due to the fact that the first glandular pads also carry reduced cirri (see character 36). Juveniles sometimes bear transitional falcigers in early unmodified parapodia that later disappear (see p. 20). They are considered relicts of the ancestral state, where a greater number of parapodia bore hooks.

36. Long transition zone between subulate ventral cirri and glandular pads (0), short transition zone (1); C. Glandular pads with reduced cirri is the ancestral condition found in eunicids. In some genera of onuphids this condition is present as a transition zone between ventral cirri and glandular pads. The long transition zone of reduced cirri is considered ancestral, and the short transition zone of either reduced subulate or globular cirri is considered derived.

37. Anterior hooks distally only bidentate (0), tridentate or otherwise (1); C. The ancestral pseudocompound to compound hooks are thought to have been distally bidentate. Fauchald (1982a) took the tridentate condition as primitive, and either unidentate or bidentate alone, or unidentate or bidentate together with tridentate as the apomorphic condition. The hooks of eunicids are bidentate as they are also in some genera of onuphids. Tridentate hooks are absent in the Hyalinoeciinae but common in the Onuphinae, particularly in conjunction with bidentate hooks. The bidentate condition is here taken as the ancestral condition; uni- and tridentate hooks probably evolved independently several times.

38. Compound limbate setae (= spinigers) present (0), absent (1); C. Fauchald (1982a) considered the presence of spinigers in Mooreonuphis as an apomorphy. Spinigers are found in a number of eunicids and their presence in onuphids is here considered a retained plesiomorphic character.

39. Late origin of subacicular hooks (after setiger 20) (0), early origin (setiger 8–19) (1); C, J. The origin of subacicular hooks in the eunicids examined ranged from 20–79, and occurs after setiger 20 in most species. The hooks start on setiger 6–8 in small juveniles (see p. 20) and subsequently become displaced more posteriorly. The early origin found in adult onuphids is interpreted as a derived neotenic feature that has arisen many times.

40. Subacicular hooks start as one per parapodium (0), two per parapodium (1), C. In the eunicids examined, subacicular hooks start as one per parapodium. This condition is found in members of the *Diopatra* group and some Hyalinoeciinae, and is considered ancestral, while the common pattern of two hooks per parapodium from their first appearance, as in most onuphids, is considered derived.

41. Three or more subacicular hooks in some parapodia (0), always two (1); C. In some eunicids the subacicular hooks increase to 3–5 per parapodium, a feature that occurs rarely in members of both onuphid subfamilies, and is interpreted as plesiomorphic.

42. Maxilla II wide with laterally protruding ramus (0), narrower ramus not protruding (1); C, F. The wide Mx II with usually laterally protruding ramus is found in Recent and fossil eunicids (see Kielan-Jaworowska, 1966) and considered ancestral, while the narrower Mx II is considered derived. The state is unknown for *Hyalospinifera* and assumed derived as in related genera.

43. Adults consisting of more than 100 segments (0), short-bodied, less than 100 segments (1), C, F. Extant and extinct eunicids consist of a great number of segments (200–1000) which is considered plesiomorphic, while the shortened bodies of some onuphids are

considered apomorphic, in agreement with Fauchald (1982a).

44. Branchial filaments single, strap-like (0), branched or spiralled (1). Fauchald (1982a) considered two or more filaments plesiomorphic and single ones apomorphic. This is a logical assumption, considering the widespread occurrence of pectinate branchiae in eunicids. However, the absence of pectinate setae in the Hyalinoeciinae and presence of single strap-like branchiae in both subfamilies demonstrates the ancestral state of the single strap-like type.

45. Origin of branchiae relatively late (after setiger 10) (0), early (setiger 1–9) (1). Fauchald (1982a) considered the start of branchiae 'on or after setiger 5 but before setiger 10' as plesiomorphic and '(a) on or before setiger 4 (b) after setiger 10' as apomorphic. Some support for this reasoning is found in ontogeny, in that larval branchiae in some species appear at setiger 6 and later spread anteriorly and posteriorly (see p. 20). However, the late occurrence of branchiae in the Hyalinoeciinae (when they are present) and some members of the Onuphinae is here taken as an indication of plesiomorphy.

46. Proximal origin of Mx II and Mx III equal (0), Mx III more anterior (1). The common proximal origin of Mx II and Mx III is found in members of both subfamilies and thought to represent the ancestral condition, while Mx III starting at a more anterior level is thought to be derived.

Relationships Within the Onuphidae

The relationships within the Onuphidae are depicted in a Wagner tree (Fig. 37) and summarized in Table 3. The family includes about 220 species, here placed in 22 genera and considered a monophyletic group with the autapomorphies of possession of frontal palps [1 (number indicates character discussed above—apomorphic state)] and antennae with ceratophores (2). Frontal palps are reduced or absent in *Leptoecia* and *Neonuphis* but this is interpreted as secondary loss as a result of neoteny. The family can be divided into two groups, based on conservative characters, and two subfamilies are erected: Onuphinae and Hyalinoeciinae. The parapodia of Onuphinae generally have notosetae; subacicular hooks are in a ventral position and lower limbate setae are absent posterior to the origin of the former (3); they have four anal cirri; immature eggs have two strings of nurse cells (31) and the primary envelope of mature eggs is smooth. In the Hyalinoeciinae notosetae are absent (4); subacicular hooks are in a median position in the fascicle (5) and lower limbate setae continue to the end of the body; they have two anal cirri (32); nurse cells occur in a single cluster and the primary envelope of eggs is pitted (33).

Relationships within the Hyalinoeciinae. The Hyalinoeciinae consists of about 50 known species, most of them of small size and living at great depths. Some members display neotenic characters, e.g. reduction and loss of frontal palps, and loss of tentacular cirri and branchiae. Much of this analysis is based on the characteristic tubes that the individual groups construct.

The Hyalinoeciinae falls into two groups: the *Nothria* group and the *Hyalinoecia* group. In members of both groups, the first setiger and its pair of parapodia are enlarged. The latter have claw-like hooks, allowing the animals to be mobile and to pull their protective tubes around with them (Fauchald & Jumars, 1979). *Nothria* and *Anchinothria* share the scoop-shaped pectinate setae (22) and maxilla III which is distally shorter than maxilla II (23), two characters which are unique within the Eunicida. In discussing the relations among *Nothria* and *Paradiopatra* (= *Anchinothria*), Fauchald (1982a) considered the short tubes and foliose presetal lobes of *Nothria* as apomorphic conditions. The short tubes of *Nothria* are characteristic and unique, as is their method of construction which renders them flat and smooth (24). Foliose presetal lobes are found in all Hyalinoeciinae except *Anchinothria*, where they may have been secondarily lost. This loss may represent an apomorphic rather than a plesiomorphic condition. However, the state cannot be definitely assigned and thus the character has not been used. Two species of *Anchinothria* have dichotomously branched branchiae (25), which is unique.

The loss of tentacular cirri (11) and the construction of clear tubes, secreted completely by its inhabitant without addition of foreign materials (26), are the apomorphies that define the *Hyalinoecia* group. The round, quill-like tubes with internal valves are a characteristic of *Hyalinoecia* (27). *Neonuphis, Leptoecia* and presumably *Hyalospinifera* share the possession of maxillae I to III with extremely large cavity openings (28), and the absence of Mx V (29). The three genera occur in abyssal depths and are poorly known. *Neonuphis* constructs round tubes without lateral supports, while both *Leptoecia* and *Hyalospinifera* construct tubes with secreted lateral supporting rods (30). The absence of frontal palps in *Leptoecia* and *Neonuphis* is considered a secondary loss.

Relationships within the Onuphinae. The Onuphinae is by far the more speciose subfamily, with approximately 170 species in 17 genera. Although the individual genera can be satisfactorily defined by autapomorphic characters and grouped into larger units on morphological and ecological characteristics, it is difficult to define these larger units by unequivocal synapomorphies. The genera fall into two broad groups: the *Diopatra* group and the *Onuphis* group.

Members of the *Diopatra* group have representatives at all depths and share a number of characters. The anterior three to five pairs of parapodia are directed anteroventally, the tubes have a parchment-like lining, an additional jaw piece, maxilla VI, and bifid postsetal lobes occur in some species. However, these characters are either ancestral and found already in the Eunicidae, or specialized but not present in all members. The best represented derived character (6) is the presence of two rows of spines on the anterior hooks, found in all but one species of the *Rhamphobrachium* complex and in some members of *Diopatra, Epidiopatra* and *Paradiopatra.*

The *Diopatra* group is here considered to consist of *Notonuphis,* the *Diopatra* complex, the *Rhamphobrachium* complex, and *Americonuphis. Notonuphis* is the only onuphine that lacks notosetae (4) and that has maxillae with Mx II and Mx III originating at the same point. The former character is here interpreted as having evolved parallel to the Hyalinoeciinae, while the latter is taken as a retained plesiomorphic state. *Notonuphis* lacks tentacular cirri (11), a character that has evolved independently several times in the family.

Paradiopatra, Diopatra and *Epidiopatra* make up the *Diopatra* complex. Some members of all three genera have branchiae limited to their anterior region (7) and

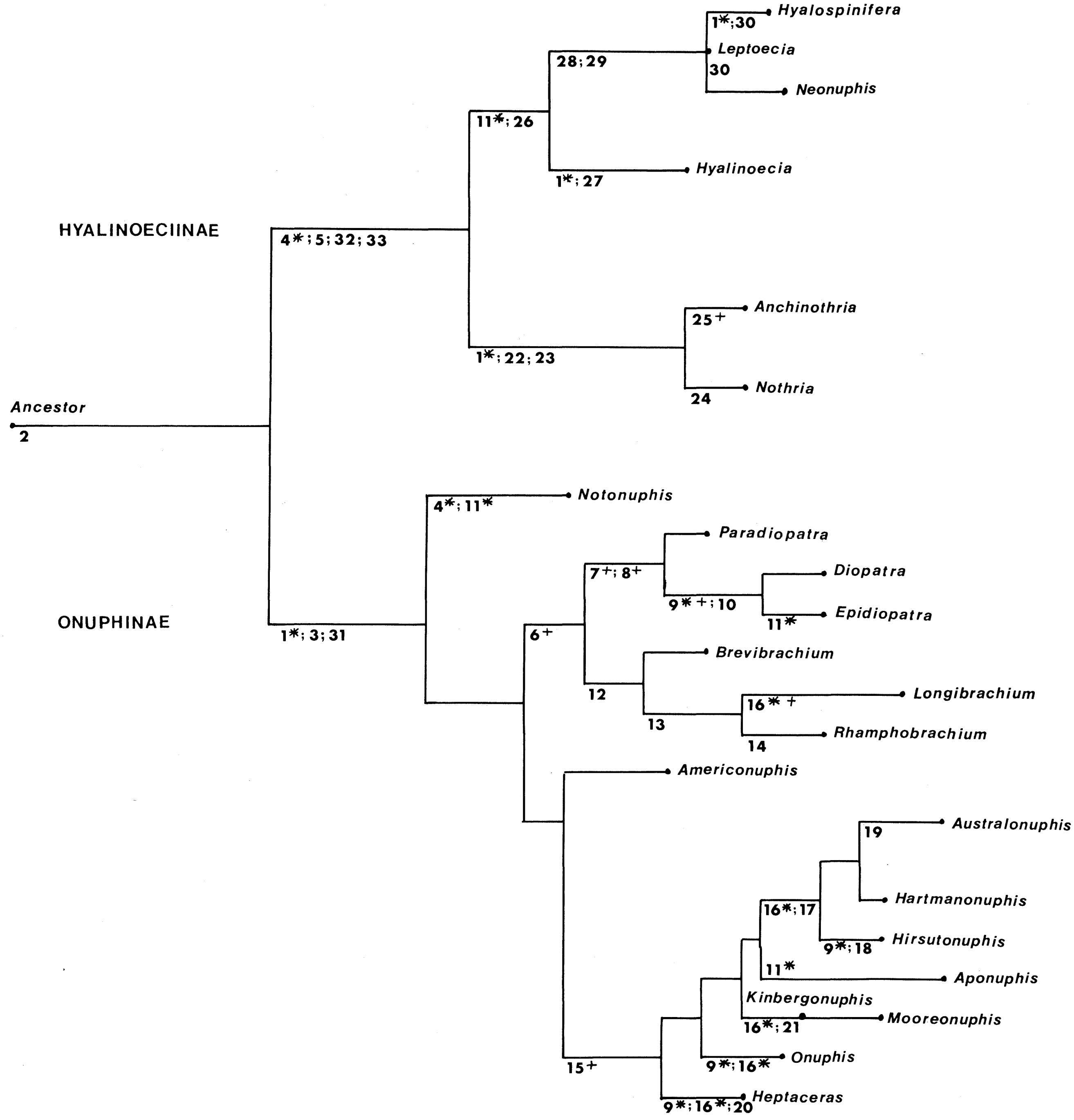


Fig. 37. Wagner tree of Onuphidae computed on basis of 46 characters; overall consistency 0.48 (total length of tree = 92.0). Horizontal lines between linkage levels drawn in proportion to evolutionary distances. All-primitive *Ancestor* at left; taxa on right more derived. Numbers refer to apomorphic characters (1–33) described in text. Characters 34–46 with widespread apomorphic states not indicated here. * = parallelism; + = character not present in all species.

lateral projections on their ceratophores (8), characters which are not found in any other genera. The puzzling aspect of the lateral projections is their presence in so few species. Anterior hooks with long pointed hoods are present in all species of *Notonuphis, Paradiopatra,* some species of *Diopatra, Epidiopatra* and some Hyalinoeciinae. This type of hood was considered apomorphic by Fauchald (1982a). Long pointed hoods as well as short blunt hoods occur in the Eunicidae so that the state of this character cannot be determined.

Diopatra and *Epidiopatra* share the possession of spiral branchiae (10) and some species of both genera have ceratophores with many rings (9). The former character is unique while the latter character is very plastic and has been attained in a number of genera. *Diopatra* is highly specialized in having well developed sensory buds on its antennae, and almost circular nuchal grooves. *Epidiopatra* lacks tentacular cirri (11); some of its species live in deep water and construct completely organic tubes, suggesting a long independent evolution from its sister group *Diopatra.*

Members of the *Rhamphobrachium* complex share the possession of prolonged modified parapodia which reach their maximum development in species of *Longibrachium.* These parapodia bear long protrusible hooks, the shafts of which extend in long setal sacs in the body cavity (12). In *Brevibrachium* the setal sacs are relatively short (to setiger 5), while in *Longibrachium* and *Rhamphobrachium* they extend to setiger 20–70, representing an extreme specialization (13). Although species of *Brevibrachium* and *Longibrachium* share some features (hooks with immoveable spines and similar subacicular hooks), the few species display a great variation of morphology, marking them as survivors of a plastic group. One species of *Longibrachium* has a small maxilla V and lacks Mx VI (16). This state is typical for the *Onuphis* group, and is thought to have evolved independently in *L. atlanticum.* Species of *Rhamphobrachium* are more numerous and morphologically very similar to each other, giving the impression of a more general but successful genus. This is also borne out by their hooks which are very uniform in morphology and unique in having moveable spines (14).

Americonuphis is the genus with the fewest derived characters and is reminiscent of the Eunicidae with its collar-like peristomial fold and posterior emergence of tentacular cirri. Its anterior parapodia are positioned very far ventrally, a condition that is approached in species of the *Rhamphobrachium* complex. It shares the possession of a Mx VI with members of *Longibrachium* and *Rhamphobrachium (R.)* but lacks the prolonged anterior hooks of the *Rhamphobrachium* complex.

Most members of the *Onuphis* group are characterized by the anterolateral to -dorsal direction of the anterior three to eight pairs of parapodia (15) and small maxillae V (16). The former character is best developed in *Australonuphis, Hartmanonuphis, Hirsutonuphis, Heptaceras,* some species of *Onuphis* and *Kinbergonuphis.* It is not obvious in some small species of *Onuphis, Kinbergonuphis* and *Mooreonuphis* and is attributed to the smaller size. The majority of species live in shallow water and have rather temporary tubes, consisting of a thin mucous lining and adhering sand grains or mud.

The *Onuphis* group contains eight genera of which only three (*Australonuphis, Hartmanonuphis, Hirsutonuphis*) can be defined by a synapomorphy and are here referred to as the *Australonuphis* complex. The nuchal grooves are curved towards the base of the median antenna and are widely separated middorsally. The peristomium lacks a distinct anterior fold, appearing to extend along the nuchal grooves toward the median antenna (17). The parapodia of the anterior five to eight setigers are moderately prolonged and all genera are limited to shallow water habitats. *Hirsutonuphis* is defined by its uniquely shaped and sclerotized maxillary carriers (18). Distally entire subacicular hooks are an autapomorphy of *Australonuphis* (19).

Aponuphis is the only genus in the *Onuphis* group that lacks tentacular cirri (11). Although it resembles *Onuphis* with respect to setal morphology and anteriorly extended prostomium, the two genera do not share any derived characters.

Most of the species of *Kinbergonuphis* and all of *Mooreonuphis* live in shallow water and build temporary tubes. Some species of *Kinbergonuphis* have slightly prolonged parapodia and appear close to the *Australonuphis* complex. Most of the members of the two genera (including the type species) bear the characteristic large median hooks (21). These hooks were reported to be rarely present in *Onuphis (O. vexillaria)* and *Sarsonuphis (= Paradiopatra) (P. lepta)* (Fauchald, 1982a). The former species is here placed with *Kinbergonuphis* for reasons stated in 'Remarks' for the genus *Kinbergonuphis.* My re-examination of *S. lepta* showed that large median hooks are not present in that species, and are thus restricted to *Kinbergonuphis* and *Mooreonuphis.*

Onuphis and *Heptaceras* share setal and prostomial similarities and the possession of many ceratophoral rings (9). The latter genus is unique in having an incised peristomium (20). *Heptaceras* and some species of *Onuphis* share the beachworm habits of members of the *Australonuphis* complex. They also share some morphological features, such as interramal papillae and dorsal cirri with basal processes, with the latter group. However, the former feature is present in very few species, and the latter is found also in *Longibrachium* and *Americonuphis,* indicating an ancestral state. While members of the *Australonuphis* complex have five to eight pairs of modified parapodia and a very late origin of subacicular hooks, *Heptaceras* and most species of *Onuphis* have only three pairs of modified parapodia and a very early origin of subacicular hooks, both of which may be neotenic features.

Identikit Picture of the Uronuphid

While generalized hypothetical ancestors have no value in considering relationships (Anderson, 1982), the reverse process, tracing the ancestor from a previously accepted phylogeny, is an interesting exercise. In the case of the Onuphidae, where there are two clear cut lineages, one can assume that characters in their plesiomorphic condition in both lineages reflect the state of the ancestor.

The prostomium had five antennae, borne on short ceratophores [9 (number indicates character discussed above)]; two frontal palps (1) and two labial palps. The nuchal grooves were straight, with a small middorsal separation. The peristomium had a distinct anterior fold (17), probably even collar-like, covering the nuchal grooves; tentacular cirri were inserted subdistally (34).

A relatively large number (four or more) pairs of parapodia were modified (35) and directed anteroventrally (15) but not prolonged. These parapodia bore subulate dorsal cirri with embedded notosetae (4) and digitate ventral cirri, followed by glandular pads, the most anterior of which may have had additional reduced cirri (36). Branchiae started either around setiger 6, or more likely relatively late (after setiger 10) (45) and consisted of single, strap-like filaments (44).

All modified parapodia bore compound to pseudocompound, distally bidentate (37), hooded hooks. Flat, pectinate setae (22) and several upper narrow limbate setae were present from setiger 1. It is hypothesized here that the lower setae, from the termination of the hooks to the beginning of the subacicular hooks, consisted of spinigers (38). Most modern onuphids have simple limbate setae in the lower position which, I think, evolved from the spinigers by fusion of the fracture, and are morphologically different from the upper limbate setae. The lower limbate setae were continued till the end of the body (3). Bidentate (19), hooded, subacicular hooks probably started late (after setiger 20) (39). The subacicular hooks were in a ventral position (5), may have started as one per parapodium (40), increasing to two and even three to five subsequently (41).

Mandibles were much like Recent ones. Maxillae II were wide with laterally protruding rami (42); Mx III started proximally at the same level as Mx II (46); Mx V were either relatively large plates or each was separated into two plates (16). The tubes were longer than their inhabitants, consisting of a parchment-like inner layer (24) to which foreign particles may have adhered on the outside.

The animals were probably moderately large; they consisted of a great number of segments (more than 100) (43), and probably lived in shallow coastal waters.

ZOOGEOGRAPHY AND CONCLUSION

Members of the family Onuphidae can be found in all world oceans, at all depths. Although some genera have a world-wide distribution, and are found from the shallowest to the deepest depths, most have a limited geographic and depth distribution.

The family is much better represented in the southern hemisphere than in the northern. Four genera (*Hartmanonuphis, Brevibrachium, Notonuphis* and *Neonuphis*) are limited to the southern oceans, and another three (*Australonuphis, Heptaceras* and *Hyalospinifera*) have only been reported south of 25°N. On the other hand, only *Aponuphis* and *Americonuphis* are limited to the northern hemisphere. This strong southern representation might suggest a southern centre of origin.

The oldest fossil records of the order Eunicida are from the Ordovician and consist of jaw pieces of a number of now extinct families. Of these, only the Paulinitidae (records till early Triassic) shows strong similarity to the Recent Eunicidae and Onuphidae and can be regarded as their possible ancestor (Kielan-Jaworowska, 1966). Isolated palaeozoic onuphid and eunicid jaw pieces have been reported, and completely fossilized specimens of a eunicid are known from the Upper Carboniferous (Thompson & Johnson, 1977). Considering the similarity of the maxillary apparatuses between some Recent representatives of eunicids and onuphids, it may be impossible to distinguish fossil jaw elements of the two families.

The family Eunicidae is a large and successful group. Some members are burrowers, but most are epifaunal on hard substrates, crawling under rocks, invading crevices, and some constructing tubes.

All parapodia of eunicids are similar, directed ventrally, and allow the animal to crawl in an onychophoran-like manner. The most anterior ventral cirri are conical and are replaced by glandular pads with reduced conical cirri which are in contact with the substratum and aid locomotion. The lower setae consist of a bundle of compound hooks, in addition to which the median and posterior regions have two or more subacicular hooks projecting at an angle, thus making them the most ventral setae and providing the *points d'appui*.

Eunicid tubes, when present, consist of parchment-like material, secreted by the animal, without the incorporation of foreign materials. Most eunicids occur in shallow, quiet waters, are most numerous in warm areas, and have occupied these habitats since the Mesozoic (Kozur, 1971) and probably earlier.

A number of onuphid genera (*Americonuphis, Longibrachium, Australonuphis, Hartmanonuphis, Hirsutonuphis, Heptaceras*) each with very few, widely geographically separated species, of moderately large to large size, with eunicid-like plesiomorphic characters, may represent the survivors of more ancestral onuphids. These genera are all highly specialized in certain features, which may have removed them from the main stream of onuphid evolution. The present distribution of these genera is consistent with the existence of the southern landmass, Gondwanaland, which lasted at least until the Jurassic (Seyfert & Sirkin, 1973) and supports the hypothesis of a southern origin of the Onuphidae.

While the earliest onuphids were probably mainly epifaunal on hard substrates, the elaboration of their tubes allowed them to become members of the infauna found mainly in soft substrata and rubble (Fauchald & Jumars, 1979). The ancestral onuphids probably were shallow water inhabitants. Many Recent genera occur from intertidal to great depths, suggesting that the deeper waters were invaded independently several times. The genera *Notonuphis, Neonuphis, Leptoecia* and *Hyalospinifera* consist of very few species each and occur in deep, mainly Antarctic waters, indicating that they may be survivors of less successful lines.

One of the most interesting genera is *Diopatra.* It is a speciose genus that is not found beyond shelf depths, while even its sister group, *Epidiopatra,* has deep-water representatives. *Diopatra* has a high number of derived characters which allow it to compete successfully and coexist with eunicids in the warmer, shallow waters to which it is limited.

Most of the remaining genera have world-wide geographic distributions, can be found at all depths, and are relatively speciose. *Paradiopatra, Rhamphobrachium, Nothria* and *Anchinothria* are largely limited to deeper waters. *Onuphis* and *Kinbergonuphis* have a few deep, but mostly shallow-water species, while *Mooreonuphis* and *Aponuphis* are found only in shallow waters. The latter four genera occur mainly in temperate to warmer waters, with *Onuphis* best represented in the western Pacific, *Kinbergonuphis* in the western Atlantic Ocean and *Mooreonuphis* restricted to the Americas. These three genera consist of many closely related, small-sized species, living in thin, temporary tubes. The individual species have relatively limited geographic distributions and may be the result of comparatively recent speciation after reinvading the shallow-water habitats.

While the onuphids have a very similar body plan, jaw apparatus and probably diet to the eunicids, it is mainly the development of more elaborate sensory structures and the specialization of their parapodia that allowed them to compete successfully in habitats where eunicids were already established, and to invade new habitats. The eunicid antennae are short and lack ceratophores, while most onuphids have muscular ceratophores that allow the styles to be well controlled and participate in feeding (Fauchald & Jumars, 1979: fig. 15) and in new activities, such as the selection and manipulation of foreign particles to construct more elaborate tubes (Linville, 1903). The nuchal grooves are covered by the collar-like peristomium in eunicids while they are exposed in most onuphids. The separation of the frontal palps and the more anterior position of the tentacular cirri in onuphids add more sensory structures to the head region.

Another focal point of the onuphid radiation was the modification of the anterior parapodia. They became strengthened for burrowing (beachworms), prolonged for grasping (*Rhamphobrachium*), or enlarged (Hyalinoeciinae) for better crawling. The setae of these parapodia also became specialized. Most onuphids construct permanent tubes, while some burrowing groups live in a mucus-lined hollow, or temporary tube. The inner lining of the tubes is secreted by the glandular ventral pads. The reduced cirri of the eunicids were lost as a consequence in the truly tubicolous groups and retained only in more mobile groups like the beachworms.

The lower bundle of setae, an important aid in the locomotion of eunicids, became modified in two different ways in the onuphids. In the Onuphinae the lower bundle was lost. It is hypothesized that this allowed the subacicular hooks more space, so that they could get a better hold on the inside walls of the tube and act like the uncini of the sedentary tubicolous families. The start of the uncini-like hooks shifted more anteriorly in most onuphines, thus allowing a greater part of the body to grip the tube. The hyalinoeciines retained the lower bundle of setae and adopted the juvenile position of the subacicular hooks in a median position in the fascicle parallel to the acicula. The animals have become mobile through the remarkable development of the first and sometimes second pair of parapodia. These have been greatly enlarged; even the first setiger is enlarged to accommodate the better developed muscles and longer setal sacs. The enlarged parapodia are analogous to the legs of caterpillars, as they crawl around, pulling their protective tube with them.

The hyalinoeciines adopted various ways to overcome the absence of ventral subacicular hooks. Species of *Hyalinoecia* have well developed longitudinal muscles and their body is circular in transverse section (Fig. 2f). The body is closely appressed to the walls of the tube and the whole setal fascicle seems to provide the *points d'appui.* Most of the remaining genera of Hyalinoeciinae have poorly developed longitudinal muscles giving their body an oval shape in transverse section (Fig. 2e). The animals construct flattened tubes to accommodate the oval shape and seem to offset the poor muscular system by a shortened body.

As mentioned above, the reproductive strategies of onuphids are not well known. The large eunicid-like *Americonuphis* spawn large numbers of eggs, which develop in huge egg masses, while species of *Australonuphis* produce even greater numbers of eggs and may be free-spawning. The latter strategies are similar to those of members of the Eunicidae (see Richards, 1967) and can be considered ancestral, thus supporting the conclusions based on the morphological and ecological information.

Most genera have smaller numbers of eggs, which are often brooded in the parental tube. This type of reproduction and development was a preadaptation for invading the deeper waters and probably played an important role in the radiation of the onuphids.

It is concluded that the plasticity of the anterior parapodia and their setae, together with the elaboration of palps and antennae, played a major part in the radiation of the Onuphidae. The resultant specializations allowed the group to invade the infauna, or provided greater efficiency where the epifaunal habitat was maintained. The tubicolous life allowed for brood care in the parental tube, thus opening the way to the deeper waters. While the onuphids probably evolved in the southern, shallow, warmer waters, they radiated world-wide, inhabiting all depths, and some lines may at present be diversifying in the shallow waters of the northern hemisphere.

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References

Allen, M. J., 1959. Embryological development of the polychaetous annelid, *Diopatra cuprea* (Bosc). The Biological Bulletin of the Marine Biological Laboratory Woods Hole 116: 339-361.

Amoureux, L., 1972. Annélides polychètes recueillies sur les pentes du talus continental, au large de la Galice (Espagne). Campagnes 1967 et 1968 de la "Thalassa". Cahiers de Biologie Marine 13: 63-89.

———1977. Annélides polychètes errantes recueillies sur les pentes du talus continental, à l'entrée de la Manche, avec la description de deux espèces nouvelles. Campagne 1973 de la "Thalassa". Cahiers de Biologie Marine 18: 391-411.

———1982. Annélides polychètes recueillies sur la pente continentale de la Bretagne à l'Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre especes nouvelles pour la science. Cahiers de Biologie Marine 23: 29-51.

Anderson, D.T., 1982. Origins and relationships among the animal phyla. Proceedings of the Linnean Society of New South Wales 106(2): 151-166.

Andrews, E. A., 1891a. Reproductive organs of *Diopatra.* Journal of Morphology 5:113-124.

———1891b. Report upon the Annelida Polychaeta of Beaufort, North Carolina. Proceedings of the United States National Museum 14: 277-302.

Annenkova, N.P., 1946. New species of Polychaeta from the Arctic Ocean. **In** 'Works of the drifting ice-expediton in the central Arctic Ocean in the Ice-Breaking Steamer *G. Sedov,* 1937-1940' (ed. V.K. Buinitski): 185-188. Akademia Nauk SSSR, Moscow. (In Russian.)

———1952. New species of polychaetous annelids (Polychaeta). Trudy Zoologicheskogo Instituta Azerbaidzhanskii filial Akademia Nauk SSSR 12: 148-154. (In Russian.)

Audouin, J.V. & H. Milne Edwards, 1833. Classification des annélides, et description de celles qui habitent les côtes de la France. Annales des Sciences Naturelles (Paris) (1) 29: 195-269.

Augener, H., 1906. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the United States, 1877 to 1880, by the U.S. Coast Survey Steamer "Blake", Lieut. Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 42. Westindische Polychaeten. Bulletin of the Museum of Comparative Zoology at Harvard College 43(4): 91-196.

———1918. Polychaeta. **In** 'Beiträge zur Kenntnis der Meeresfauna West-Afrikas' (ed. W. Michaelsen). Vol. 2(2): 67-625. Friedrichsen & Co., Hamburg.

———1924. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-16. 18. Polychaeta II. Polychaeten von Neuseeland. I. Errantia. Videnskabelige Meddelelser fra Dansk naturhistorisk Fφrening i Kjφbenhavn 75: 241-441.

Baird, W., 1870. Remarks on several genera of annelides belonging to the group Eunicea with a notice of such species as are contained in the collection of the British Museum and a description of some others hitherto undescribed. Journal of the Linnean Society of London 10: 341-361.

Bellan, G., 1964. Contribution à l'étude systématique, bionomique et écologique des annélides polychètes de la Mediterranée. Recueil des Traveaux, Station Marine d'Endoume, Bulletin 33: 1-371.

Bergmann, W., 1903. Untersuchungen über die Eibildung bei Anneliden und Cephalopoden. Zeitschrift für wissenschaftliche Zoologie 73:277-301.

Berkeley E. & C. Berkeley, 1938. *Rhamphobrachium longisetosum,* sp. n., with some observations on the regeneration of the specialized anterior setae. Annals and Magazine of Natural History (London), (11) 1: 428-435.

———1939. On a collection of Polychaeta, chiefly from the west coast of Mexico. Annals and Magazine of Natural History (London) (11) 3: 321-346.

———1941. On a collection of Polychaeta from southern California. Bulletin of the Southern California Academy of Sciences 40: 16-60.

Blainville, H. de, 1828. Ver. **In** 'Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement a l'utilité qu' en peuvent retirer la médecine, l'agriculture, le commerce et les art. Suivi d'une biographie des plus célèbres naturalists.' Vol. 57: 1-628. Levrault, Strasbourg.

Blake, J.A., 1975. The larval development of Polychaeta from the northern California coast. II. *Nothria elegans* (Family Onuphidae). Ophelia 13: 43-61.

Carrasco, F.D., 1983. Description of adults and larvae of a new deep water species of *Hyalinoecia* (Polychaeta, Onuphidae) from the southeastern Pacific Ocean. Journal of Natural History 17: 87-93.

Castelli, A., 1982. *Onuphis falesia,* a new species of Onuphinae (Polychaeta, Eunicidae). Bollettino di Zoologia 49(1-2): 45-49.

Chamberlin, R.V., 1919. The Annelida Polychaeta. Memoirs of the Museum of Comparative Zoology at Harvard College 48: 1-514.

Claparède, E., 1868. Les annélides chétopodes du Golfe de Naples, premier partie. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 19(2): 313-584.

Dales, R.P., 1962. The polychaete stomodeum and the interrelationships of the families of Polychaeta. Proceedings of the Zoological Society London 139: 389-428.

Day, J.H., 1951. The polychaet fauna of South Africa. Part I. The intertidal and estuarine Polychaeta of Natal and Mosambique. Annals of the Natal Museum 12(1): 1-67.

————1960. The polychaet fauna of South Africa. Part 5. Errant species dredged off Cape coasts. Annals of the South African Museum 45: 261-373.

————1967. A monograph on the Polychaeta of southern Africa. Part I. Errantia. British Museum (Natural History) Publications 656: 1-458.

————1973. New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service Circular 375: i-xiii + 1-140.

Defretin, R., 1971. The tubes of polychaete annelids. Comprehensive Biochemistry 26C: 713-747.

Desière, M., 1967. Morphologie de l'organe buccal ventral de *Marphysa bellii* (Audouin & Edwards) (Polychète, Eunicidae). Annales de la Société Royale Zoologique de Belgique (Bruxelles) 97: 65-90.

Ehlers, E., 1868. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Engelmann, Leipzig, pp. 269-748 (pp. 1-268 of this work were published in 1864).

————1879. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mecico, by the United States Coast Survey Steamer "Blake", Lieutenant-Commander C. D. Sigsbee, U.S.N., commanding. 4. Preliminary report on the worms. Bulletin of the Museum of Comparative Zoology at Harvard College 5: 269-274.

————1887. Reports on the results of dredging, under the direction of L.F. Pourtales, during the years 1868-1870, and of Alexander Agassiz, in the Gulf of Mexico (1877-78), and in the Caribbean Sea (1878-79), in the U.S. Coast Survey Steamer "Blake", Lieut.-Com. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 31. Report on the annelids. Memoirs of the Museum of Comparative Zoology at Harvard College 15: 1-335.

————1897. Polychaeten. **In** 'Ergebnisse der Hamburger Magalhaenischen Sammelreise' 2(1): 1-148. Friedrichsen & Co., Hamburg.

————1908. Die bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899 16(1): 1-167.

Estcourt, I.N., 1966. A new polychaete from Three Kings Islands. Transactions of the Royal Society of New Zealand. Zoology 7(15): 205-207.

Eulenstein, F., 1914. Über Onuphiden der Nordsee. Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel, neue Folge 16: 129-172.

Farris, J.S., 1970. Methods for computing Wagner trees. Systematic Zoology 19: 83-92.

Fauchald, K., 1968. Onuphidae (Polychaeta) from western Mexico. Allan Hancock Monographs in Marine Biology 3: 1-82.

————1970. Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from western Mexico. Allan Hancock Monographs in Marine Biology 5: 1-335.

————1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. Allan Hancock Monographs in Marine Biology 7: 1-575.

————1973. Polychaetes from Central American sandy beaches. Bulletin of the Southern California Academy of Sciences 72: 19-31.

————1974. Deep-water errant polychaetes from Hardangerfjorden, western Norway. Sarsia 57: 1-32.

————1977. The Polychaete Worms. Definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County Science Series 28: 1-188.

————1980. Onuphidae (Polychaeta) from Belize, Central America, with notes on related taxa. Proceedings of the Biological Society of Washington 93(3): 797-829.

————1982a. Revision of *Onuphis, Nothria* and *Paradiopatra* (Polychaeta: Onuphidae) based upon type material. Smithsonian Contributions to Zoology 356: i-vi + 1-109.

————1982b. Description of *Mooreonuphis jonesi,* a new species of onuphid polychaete from shallow water in Bermuda, with comments on variability and population ecology. Proceedings of the Biological Society of Washington 95(4): 807-825.

————1982c. Some species of *Onuphis* (Polychaeta: Onuphidae) from the Atlantic Ocean. Proceedings of the Biological Society of Washington 95(2): 238-250.

————1982d. Two new species of *Onuphis* (Onuphidae: Polychaeta) from Uruguay. Proceedings of the Biological Society of Washington 95(1): 203-209.

————1983. Life diagram patterns in benthic polychaetes. Proceedings of the Biological Society of Washington 96(1): 160-177.

———— & P.A. Jumars, 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology: an Annual Review (London) 17: 193-284.

———— & D. Hancock, 1981. Deep-water polychaetes from a transect off central Oregon. Allan Hancock Monographs in Marine Biology 11: 1-73.

Fauvel, P., 1916. Deux polychètes nouvelles (*Disoma watsoni* n. sp., et *Hyalinoecia brementi* n. sp.). Bulletin d'institut oceanographique (Monaco) 316: 1-10.

————1923. Polychètes errantes. Faune de France, Paris 5: 1-488.

————1928. Annélides polychètes nouvelles du Maroc. Bulletin de la Société Zoologique de France (Paris) 53: 9-13.

————1932. Annelida Polychaeta of the Indian Museum, Calcutta. Memoirs of the Indian Museum (Calcutta) 12(1): 1-252.

Franzén, Å., 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zoologisce Bidrag Uppsala 31: 355-482.

Friedrich, H., 1956. Mitteilungen über neue und wenig bekannte Polychaeten aus Mittel- und Südamerika. Senckenbergiana Biologica 37(1/2): 57-68.

Gallardo, V.A., 1968. Polychaeta from the Bay of Nha Trang, South Viet Nam. NAGA Reports, Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand 1959-1961 4(3): 35-279.

Gardiner, S. L., 1976. Errant polychaete annelids from North Carolina. Journal of the Elisha Mitchell Scientific Society 91(3): 77-220.

Grube, A.-E., 1868. Über eine Reihe neuer Anneliden. Jahresbericht der Schlesischen Gesellschaft für vaterländische Cultur (Breslau) 45: 50-52.

Haffner, K. von, 1959. Über den Bau und den Zusammenhang der wichtigsten Organe des Kopfendes von *Hyalinoecia tubicola* Malmgren (Polychaeta, Eunicidae, Onuphidinae), mit Berücksichtigung der Gattung Eunice. Zoologische Jahrbücher, Abteilung für Anatomie 77(2): 133-192.

Hansen, G.A., 1878. Annelider fra den norske Nordhavsexpedition i 1876. Nyt Magazin for Naturvidenskaberne (Christiana) 24: 1-17.

————1882. Recherches sur les annélides, recueillies par M. le professeur Édouard van Beneden pendant son voyage au Brésil et à la Plata. Mémoires couronnés et mémoires des savants étranges publiés par l'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique (Bruxelles) 44(3): 1-29.

Hartman, O., 1944. Polychaetous annelids. Part 5. Eunicea. Allan Hancock Pacific Expeditions 10: 1-238.

————1945. The marine annelids of North Carolina. Duke University Marine Station Bulletin 2: 1-54.

————1951. The littoral marine annelids of the Gulf of Mexico. Publications of the Institute of Marine Science (Port Aransas) 2(1): 7-124.

————1959. Catalogue of the polychaetous annelids of the world. Allan Hancock Foundation Occasional Paper 23: 1-628.

————1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Allan Hancock Foundation Occasional Paper 28: 1-378.

————1967a. Larval development of benthic invertebrates in Antarctic seas: early development of *Nothria notialis* (Monro) and *Paronuphis antarctica* (Monro) in Bransfield Strait, Antarctic Peninsula. Proceedings of the Symposium on Pacific-Antarctic Sciences. JARE Scientific Reports, Special Issue 1: 205-208.

————1967b. Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic seas. Allan Hancock Monographs in Marine Biology 2: 1-387.

———— & K. Fauchald, 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Part 2. Allan Hancock Monographs in Marine Biology 6: 1-327.

Hartmann-Schröder, G., 1960. Zur Polychaeten-Fauna von Peru, Part I. Beiträge zur Neotropischen Fauna 2: 1-44.

————1965. Die Polychaeten des Sublitorals. **In** 'Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden (mit Bemerkungen über den Einfluss sauerstoffarmer Strömungen auf die Besiedlung von marinen Sedimenten)' (G. Hartmann & G. Hartmann-Schröder). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 62: 59-305.

————1967. Feinbau und Funktion des Kieferapparates der Euniciden am Beispiel von *Eunice (Palola) siciliensis* Grube (Polychaeta). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 64: 5-27.

————1975. Polychaeten der Iberischen Tiefsee, gesammelt auf der 3. Reise der METEOR im Jahre 1966. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 72: 47-73.

Heider, K., 1925. Über *Eunice,* Systematisches, Kiefersack, Nervensystem. Zeitschrift für wissenschaftliche Zoologie 125: 55-90.

Hennig, W., 1966. Phylogenetic systematics. University of Illinois Press, Urbana, pp. 269.

Hoagland, R. A., 1920. Polychaetous annelids collected by the United States Fisheries Steamer "Albatross" during the Philippine Expedition of 1907-1909. Bulletin of the United States National Museum 100 1(9): 603-635.

Hobson, K.D., 1971. Some polychaetes of the superfamily Eunicea from the North Pacific and North Atlantic Oceans. Proceedings of the Biological Society of Washington 83: 527-544.

Hove, H.A. ten, 1984. Towards a phylogeny in serpulids (Annelida; Polychaeta). **In** 'Proceedings of the First International Polychaete Conference, Sydney' (ed. P.A. Hutchings): 181-196. The Linnean Society of New South Wales, Sydney.

Imajima, M., 1960. Description of a new polychaete, *Nothria shirikishinaiensis* n. sp. of the family Eunicidae. Publications of the Seto Marine Biological Laboratory 8(1): 55-58.

Intes, A. & P. Le Loeuff, 1975. Les annélides polychètes de Côte d'Ivoire. I.-Polychètes errantes-compte rendu systématique. Cahiers de la Office de la Recherche Scientifique et Technique des outre mer (Oceanographie) 13(4): 267-321.

Jeuniaux, C., 1975. Principes de systématique biochimique et application à quelques problèmes particuliers concernant les aschelminthes, les polychètes et les tardigrades. Cahiers de Biologie Marine 16:597-612.

Johnson, H.P., 1901. The Polychaeta of the Puget Sound region. Proceedings of the Boston Society of Natural History 29: 381-437.

Johnston, G., 1865. A catalogue of the British non-parasitical worms in the collection of the British Museum. London, pp. 366.

Just, E.E., 1922. On rearing sexually mature *Platynereis megalops* from eggs. American Naturalist 56: 471-478.

Kielan-Jaworowska, Z., 1966. Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. Palaeontologia Polonica 16: 1-152.

Kinberg, J.G.H., 1865. Annulata nova. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar (Stockholm) 21: 559-574.

Kirkegaard, J.B., 1980. Abyssal benthic polychaetes from the northeast Atlantic Ocean, southwest of the British Isles. Steenstrupia, Zoological Museum, University of Copenhagen 6(8): 81-98.

Knox, G.A. & K. Hicks, 1973. The polychaetes of New Zealand. Part 5. Onuphidae. Journal of the Royal Society of New Zealand 3(2): 281-294.

Kozur, H., 1971. Die Eunicida und Phyllodocida des Mesozoikums. Freiberger Forschungshefte (C) 267: 73-111.

Krishnamoorthi, B., 1963. Volume regulation in eggs, larvae and adults of a brackish-water polychaete, *Diopatra* *variabilis* (Southern). Proceedings of the Indian Academy of Sciences B57: 1275–1289.

Krishnan, G., 1936. The development of *Diopatra variabilis* (Southern). Zeitschrift für wissenschaftliche Zoologie 147: 513–525.

Kucheruk, N.V., 1977. On the specific composition and distribution of the deep-sea genus *Paraonuphis (sic)* (Polychaeta, Eunicidae). Trudy Institutyi Okeanologii Akademia Nauk SSSR 108: 44–51. (In Russian.)

————1978. Deep-water Onuphidae (Polychaeta) from the collections of the 16th cruise of the R/V *Dmitry Mendeleev* (to the generic classification of the family Onuphidae). Trudy Institutyi Okeanologii Akademia Nauk SSSR 113: 88–106. (In Russian.)

————1979a. New species of the family Onuphidae (Polychaeta) from the Pacific. Zoologichesky Zhurnal, Akademia Nauk SSSR 58: 1227–1230. (In Russian.)

————1979b. A new genus and species of polychaetes (Onuphidae). Zoologichesky Zhurnal, Akademia Nauk SSSR 58: 1585–1587. (In Russian.)

Langerhans, P., 1880. Wurmfauna von Madeira. Zeitschrift für wissenschaftliche Zoologie 33: 267–316.

Lieber, A., 1931. Zur Oogenese einiger Diopatraarten. Zeitschrift für wissenschaftliche Zoologie 138: 580–649.

Linville, H.R., 1903. The natural history of some tube-forming annelids (*Amphitrite ornata, Diopatra cuprea).* **In** 'Mark Anniversary Volume' (ed. G.H. Parker): 225–235. Henry Holt & Co, New York.

Malmgren, A.J., 1866. Annulata Polychaeta Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita. Frenckelliana, Helsingfors, pp. 127.

Mangum, C. & W.R. Rhodes, 1970. The taxonomic status of quillworms, genus *Hyalinoecia* (Polychaeta: Onuphidae), from the North American Atlantic continental slope. Postilla (Yale Peabody Museum of Natural History) 144: 1–13.

Marenzeller, E. von, 1879. Südjapanische Anneliden. I. Dankschrift der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschafdten (Wien) 41(2): 109–152.

————1886. Poriferen, Anthozoen, Ctenophoren und Würmer von Jan Mayen. **In** 'Die internationale Polarforschung 1882–1883. Die österreichische Polarstation Jan Mayen ausgerüstet durch seine Excellenz Graf Hanns Wilczek geleitet vom K.K. Corvetten-Capitän Emil Edlen von Wohlgemuth'. Beobachtungs-Ergebnisse herausgegeben von der Kaiserlichen Akademie der Wissenschaften (Wien) 3(B): 9–24.

McIntosh, W.C., 1885. Report on the Annelida Polychaeta collected by the H.M.S. *Challenger* during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the Years 1873–1876 under the Command of Captain George S. Nares, R. N., F.R.S. and the Late Captain Frank Tourle Thomson, R.N., Zoology 12(34): 1–554.

————1903. Notes from the Gatty Marine Laboratory, St. Andrews, no. 25. Annals and Magazine of Natural History (London) (7) 12: 128–166.

————1910. A monograph of the British annelids. Polychaeta. Syllidae to Ariciidae. Ray Society (London) 2(2): 233–524.

Mill, P.J., 1978. Sense organs and sensory pathways. **In** 'Physiology of annelids' (ed. P.J. Mill). Academic Press, London, pp. xvi + 683.

Milne Edwards, H., 1838. Les annélides. **In** 'Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particulièrs de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie' (J.B.P.A. de Lamarck), 2nd ed. by G.P. Deshayes & H. Milne Edwards, vol. 5:1–699. Bailliere, Paris.

Monro, C.C.A., 1924. On the post-larval stages of *Diopatra cuprea,* Bosc, a polychaetous annelid of the family Eunicidae. Annals and Magazine of Natural History (London) (9) 14: 193–199.

————1930. Polychaete worms. Discovery Reports 2: 1–222.

————1933. The Polychaeta Errantia collected by Dr. C. Crossland at Colon in the Panama region and the Galapagos Islands during the expedition of the S.Y. St. George. **In** 'Proceedings of the General Meetings for Scientific Business of the Zoological Society of London'. London, pp. 96.

————1937. Polychaeta. The John Murray Expedition 1933–34 Scientific Reports 4(8): 243–321.

Moore, J.P., 1903. Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. Proceedings of the Academy of Natural Sciences of Philadelphia 55(2): 401–490.

————1911. The polychaetous annelids dredged by the U.S.S. "Albatross" off the coast of southern California in 1904: III. Euphrosynidae to Goniadidae. Proceedings of the Academy of Natural Sciences of Philadelphia 63: 234–318.

Müller, O.F., 1776. Zoologica Danicae prodromus seu animalium Daniae et Norvegiae indigenarum characters, nomine et synonyma imprimis popularium. Havniae, pp. xxxii + 274.

Nelson, G.J., 1978. Ontogeny, phylogeny, paleontology and the biogenetic law. Systematic Zoology 27: 324–345.

Orensanz, J.M., 1974. Los anelidos poliquetos de la provincia biogeografica Argentina. V. Onuphidae. Physis (Buenos Aires) A33(86): 75–122.

Paxton, H., 1979. Taxonomy and aspects of the life history of Australian beachworms (Polychaeta: Onuphidae). Australian Journal of Marine and Freshwater Research 30: 265–294.

————1980. Jaw growth and replacement in Polychaeta. Journal of Natural History 14: 543–546.

————1986. Revision of the *Rhamphobrachium* complex (Polychaeta: Onuphidae). Records of the Australian Museum 38(2): 75–104.

————Revision of the Genus *Diopatra (*Polychaeta: Onuphidae). (In preparation).

————Onuphidae (Polychaeta) from the Australia-New Zealand Region. (In preparation).

Pettibone, M.H., 1963. Marine polychaete worms of the New England region. 1. Aphroditidae through Trochochaetidae. Bulletin of the United States National Museum 227(1): 1–356.

————1970. Polychaeta Errantia of the Siboga-Expedition. Part IV: Some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Eunicidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species. Siboga-Expeditie Monographie 24(1d): 199–270.

Pflugfelder, O., 1929. Histogenetische und organogenetische Prozesse bei der Regeneration polychaeter Anneliden. I.

Regeneration des Vorderendes von *Diopatra amboinensis* Aud. et M. Edw.. Zeitschrift für wissenschaftliche Zoologie 133: 121-210.

Pourtalès, L.F. de, 1869. Contributions to the fauna of the Gulf Stream at great depths. Bulletin of the Museum of Comparative Zoology at Harvard College 1: 103-120.

Rangarajan K. & S. Mahadevan, 1961. On a new species of *Nothria* Malmgren (Polychaeta, Annelida) from the Gulf of Mannar. Journal of the Marine Biological Association of India 4: 179-185.

Richards, T. L., 1967. Reproduction and development of the polychaete *Tauronereis rudolphi,* including a summary of development in the superfamily Eunicea. Marine Biology 1: 124-133.

Rioja, E., 1918. Datos para el conocimiento de la fauna de anelidos poliquetos del Cantabrico. Trabajos de museo nacional de ciencias naturales (Madrid) (Zoologica) 29: 1-111.

————1944. Estudios anelidologicos, XI: Notes sobre algunas especies de poliquetos de las costas mexicanas del Pacifico. Anales Instituto Biologica (Mexico) 15: 139-145.

Rozbaczylo, N. & J.C. Castilla, 1981. *Australonuphis violacea,* a new polychaete (Onuphidae) from the southeast Pacific Ocean. Proceedings of the Biological Society of Washington 94(3): 761-770.

Saint-Joseph, A. de, 1906. Les annélides polychètes des côtes de France. Annales des Sciences Naturelles (Paris) (9) 3: 145-260.

Santos, S.L., R. Day & S.A. Rice, 1981. *Onuphis simoni,* a new species of polychaete (Polychaeta: Onuphidae) from South Florida. Proceedings of the Biological Society of Washington 94(3): 663-668.

Sars, G.O., 1872. Diagnoser af nye Annelider fra Christianiafjorden, efter Professor M. Sars's efterladte Manuskripter. Videnskabsselskabet i Christiania Forhandlinger 1871: 406-417.

Sars, M., 1835. Beskrivelser og iagttagelser over nogle maerkelige eller nye i havet ved den Bergenske kyst levende dyr af Polypernes, Acalophernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne arter og deres forekommen. Bergen, pp. xii + 81.

Schmarda, L.K., 1861. Neue Turbellarien, Rotatorien und Anneliden beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Zweite Hälfte. Wilhelm Engelmann, Leipzig, pp. 164.

Schroeder, P.C. & C.O. Hermans, 1975. Annelida: Polychaeta. **In** 'Reproduction of Marine Invertebrates' (eds. A.C. Giese & J.S. Pearse). Vol. III Annelids and Echiurans: 1-213. Academic Press, New York.

Seyfert, C.K. & L.A. Sirkin, 1973. Earth history and plate tectonics, an introduction to historical geology. Harper and Row, New York, pp. viii + 504.

Shisko, J.F., 1981. Five new polychaetes of the families Eunicidae and Onuphidae, collected in 1975 and 1976 during the southern California Baseline Project. Proceedings of the Biological Society of Washington 94(4):968-983.

Smith, B.J. & R.L. Jensz, 1968. Unusual mode of reproduction in a new species of polychaete. Nature 218: 777.

Thompson, I. & R.G. Johnson, 1977. New fossil polychaete from Essex, Illinois. Fieldiana Geology 33(25): 471-487.

Treadwell, A.L., 1922. Polychaetous annelids collected at Friday Harbor, state of Washington in February and March, 1920. Publication of the Carnegie Institute of Washington 312: 171-181.

————1931. Contributions to the biology of the Philippine Archipelago and adjacent regions: four new species of polychaetous annelids collected by the United States Fisheries Steamer Albatross during the Philippine Expedition of 1907-1910. Bulletin of the United States National Museum 100, 6(5): 313-321.

Uschakov, P.V., 1950. Polychaetous annelids (Polychaeta) of the Sea of Okhotsk. Issledovanii Dal'nevostochnykh morei SSSR 2: 140-324. (In Russian.)

———— & B.-L. Wu, 1962. Littoral fauna of polychaete worms of the provinces of Fukian and Chekian. Studio Marine Sinica 1: 89-108. (In Chinese and Russian.)

Verrill, A.E., 1873. Results of recent dredging expeditions on the coast of New England. American Journal of Science (New Haven) (3) 5: 98-106.

Voss-Foucart, M.-F., M.-T. Fonze-Vignaux & C. Jeuniaux, 1973. Systematic characters of some polychaetes (Annelida) at the level of the chemical composition of the jaws. Biochemical Systematics 1: 119-122.

Westheide, W., 1977. Phylogenetic systematics of the genus *Microphthalmus* (Hesionidae) together with a description of *M. hartmanae* nov. sp. **In** 'Essays on polychaetous annelids in memory of Dr. Olga Hartman' (eds. D.J. Reish & K. Fauchald): 103-113. Allan Hancock Foundation, Los Angeles.

————1982. *Ikosipodus carolensis* gen. et sp. n., an interstitial neotenic polychaete from North Carolina, U.S.A., and its relationships within Dorvilleidae. Zoologica Scripta 11(2): 117-126.

———— & N.W. Riser, 1983. Morphology and phylogenetic relationships of the neotenic interstitial polychaete *Apodotrocha progenerans* n. gen., n. sp. (Annelida). Zoomorphology 103: 67-87.

Willey, A., 1905. Report on the Polychaeta collected by Professor Herdman, at Ceylon, in 1902. Supplementary report 30. **In** 'Report to the government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar with supplementary reports upon the marine biology of Ceylon by other naturalists' (ed. W. A. Herdman). Part 4: 243-324. Royal Society, London.

Wolf, G., 1976. Bau und Funktion der Kieferorgane von Polychaeten. Private printing, Hamburg, pp. i + 70.

————1980. Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). Senckenbergiana Maritima 12(1/4): 1-182.

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