Polychaeta

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Introduction

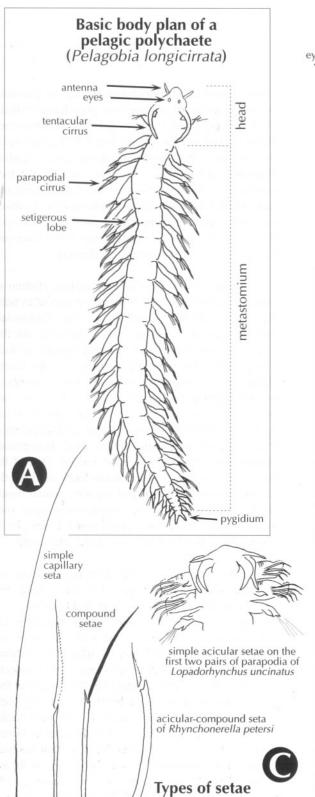
As some other marine phyla that comprise mostly benthic forms, the Annelida contain a small minority of species that have evolved to spend all their life in the pelagic realm. These holoplanktonic Polychaeta have developed a number of special adaptations to live in the planktonic environment including small size, long setae, enormous and complex eyes, flattened or gelatinous bodies, a high degree of transparency, sperm storage in females, etc. (Fig. 1). Pelagic polychaetes are found mainly in the open sea, but they also occur in neritic regions. They inhabit the entire water column from surface layers to abyssal depths. Most research has been undertaken on their distribution and taxonomic relationships, and very little is known about other aspects of their biology and ecology.

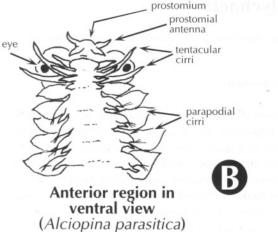
The holoplanktonic species are mainly active predators which attack their prey with the rapidly everted proboscis. However, filter-feeders or phytophagous forms are also known, for example some species of the family Iospilidae (Day, 1967). Judging from their behavior and their strong proboscides, the Alciopidae are active predators, but there are no direct observations of alciopid feeding. They are assisted in their search for prey by telescopic eyes, which enable them to orient themselves in different directions, as well as to recognize the size and form of the prey. The tomopterid polychaetes have very short pharynges, and can either consume their prey whole or suck out the internal body fluids. The long cirriform appendages of the second segment in the tomopterid polychaetes may play a role in prey (or predator) detection. Remains of herring fry, fragments of siphonophores, chaetognaths and appendicularians have been found in their digestive tracts (Rakusa-Suszczewski, 1968). Many other species have no obvious prey-catching organs, and possibly they feed on microscopic prey or eggs in the plankton (Day, 1967). The aberrant polychaete Poeobius meseres captures falling detrital matter using a mucous web (Uttal-Cooke, 1992). Members of the family Typhloscolecidae may be neotenic forms in connection with their transition to ectoparasitism, and their pharynx is modified into a characteristic suctorial organ.

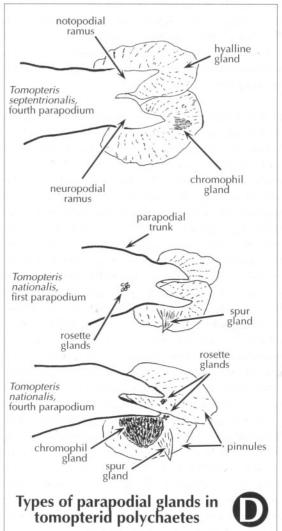
A few studies have been undertaken on the physiology and biochemistry of pelagic polychaetes (Ikeda, 1974; Thuesen and Childress, 1993; Childress and Thuesen, 1993). The active forms of pelagic polychaetes have very high metabolic rates, leading Thuesen and Childress (1993) to suggest that they may have the highest rates of all deep-sea pelagic animals. High levels of activity by alciopid and tomopterid polychaetes are supported by *in situ* observations (Video Archive Library, Monterey Bay Aquarium Research Institute, Monterey, California).

As in almost every other pelagic marine phylum of animals, bioluminescence has been observed in pelagic species of the Annelida. In the Alciopidae, Alciopina and Krohnia are bioluminescent, but this ability is probably present in other genera as well. Clark (1970) describes the histology of the mucus glands of Rhynchonerella angelini, and he mentions the possible relationship of these organs with the bioluminescence in this species. In the Tomopteridae, there are photogenic organs located on the parapodia which give off an unusual yellow light. This phenomenon is present in Tomopteris nisseni. One of the biological functions of bioluminescence is likely the attraction between males and females, which would be of great importance for pelagic forms since they usually do not form dense populations. Dales (1971) has reviewed this vital function in pelagic worms.

One of the most unique aspects of pelagic polychaetes is the evolution of eyes in the family Alciopidae. These complex eyes are very large and telescopic, and each eye has a lens that is controlled by muscles which can change the direction of its axis. The eyes can apparently determine not only the intensity and direction of light, but also the outline and size of objects. This must be of great advantage to the species in this pelagic family since it enables them to survey their surroundings in different directions. The first studies of these complex structures were undertaken by Greeff (1876) and Demoll (1909), and their function has been described by Hermans and Eakin (1974) and Wald and Rayport (1977). The eyes of these annelids are remarkably similar to those of cephalopods and vertebrates,







and because of their different developmental origin, they have been cited as an extreme example of convergent evolution (Salvini-Plawen and Mayr, 1977). Wald and Rayport (1977) have emphasized the extraordinary evolutionary convergence represented by the possession of accessory retinas in alciopid polychaetes, cephalopods and deep-sea fishes. Recent findings of a small multi-gene family of packed box-containing genes (Pax genes) in different metazoan phyla, which play an important role in embryonic development in the nervous system, has revealed that their expression is structurally similar in different visual systems, yet ontogenically distinct (Zuker, 1994).

Uschakov (1972) pointed out, correctly, that in the general economy of the sea, the role of the 8000+ species of Polychaeta is tremendous because they represent a very important link in all processes of the production of living matter, and in particular, they are the basic food, rich in calories, of numerous fishes. Although Uschakov was referring to benthic or meroplanktonic species, it is clear that holoplanktonic polychaetes play an important role in the pelagic ecosystem.

Methods

Mero- and holoplanktonic species of polychaetes are common in plankton communities, and they are collected by commonly used methods, such as standard and horizontal hauls with open or opening-closing nets of different mesh sizes (0.2-0.5 mm). Many species of pelagic polychaetes are very fragile and are often damaged during collection. Nets with large volume: mouth ratios, large cod ends and slow towing speeds improve the condition of the fragile species. Samples are best preserved immediately in 4-5% formalin in filtered seawater neutralized with a boraxsaturated solution. Although, long-term preservation in an ethanol solution is not recommended for gelatinous worms, "working specimens" may be kept in a 70% ethanol solution. The glands in the parapodia of the tomopterid polychaetes can be seen with the naked eye, but this requires care and some practice. The chromophil glands stain deeply with haematoxylin which helps to observe these structures.

Geographic distribution

Since the middle part of the twentieth century, strong correlations between the distributions of planktonic animals and the movements of water masses in the oceans have been established. Tebble (1960) has demonstrated such correlations for some species of pelagic polychaetes in the South Atlantic Ocean, and Tebble (1962) and McGowan (1960) for pelagic polychaetes in the North Pacific Ocean. Støp-Bowitz (1948) found differences between the pelagic polychaete fauna in the western and eastern parts of the North Atlantic Ocean, the western part being richer, both in species and abundance. In addition, some species occur only in the eastern half while they are absent in the western half, and vice versa. Orensanz and Ramírez (1973) have studied the distribution of pelagic polychaetes in the southwestern Atlantic Ocean. They recorded 27 species from the families Lopadorhynchidae, Iospilidae, Alciopidae, Typhloscolecidae and Tomopteridae, and also some larval and epitokous forms. Orensanz et al. (1974) described the distribution of nine polychaete species from antarctic waters near Argentina. Støp-Bowitz (1992) has documented the distribution of pelagic polychaetes in the eastern South Atlantic off the coast of the Africa between the equator and about 20°S.

The distributions of some holoplanktonic species have been mapped by Tebble (1960) in the South Atlantic Ocean. He discusses their zoogeographical patterns, and describes endemic, cosmopolitan and tropicalsubtropical species. Tebble (1960) concluded that although there were three endemic species of antarctic pelagic polychaetes, there were no endemic species of pelagic polychaetes in the subantarctic Atlantic. He also noted that the Subtropical Convergence was not a barrier to the distribution of any planktonic polychaete species. Five species (Tomopteris planktonis, T. septentrionalis, Typhloscolex mulleri, Travisiopsis levinseni and Pelagobia longicirrata) were found in all the investigated hydrological zones of the South Atlantic Ocean. The Discovery samples that Tebble (1960) analyzed also included some specimens collected with opening-closing nets, and he provided some depth distribution data. However, much more work is needed in order to properly elucidate the bathymetric ranges of

Fig. 1. Morphologic details and characters used for the identification of pelagic Polychaeta. From Fernández-Álamo (1983).

pelagic polychaetes. Distribution records of 63 species of pelagic Polychaeta in the South Atlantic Ocean are shown in Fig. 2.

Morphology, identification and systematics

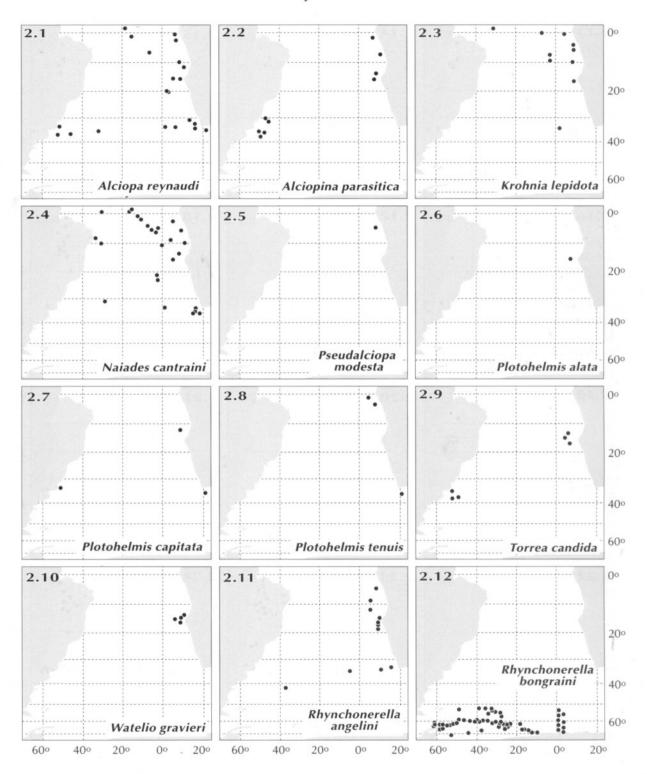
Morphology and identification

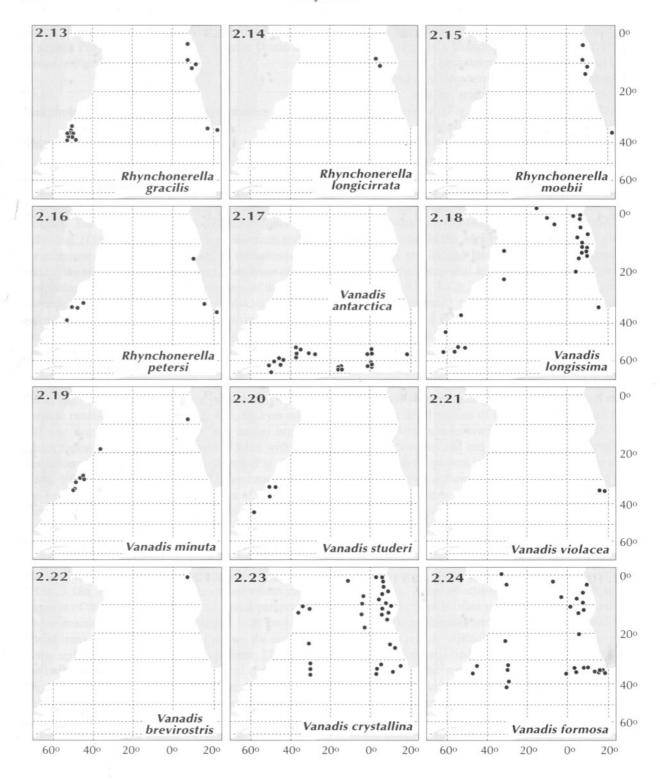
The body plans of polychaete worms often reflect their habits and habitats. This is shown in the great diversity of structural forms that deviate from the basic metameric body. The basic polychaete body plan includes the following: (1) a head consisting of a prostomium and a peristomium; (2) a segmented body or metastomium; and (3) the anal segment or pygidium. Variations of the morphological characteristics of these parts of the body are important for the identification of polychaetes. The holoplanktonic species are highly specialized for pelagic life, and the main morphological characters used for their identification will be described briefly.

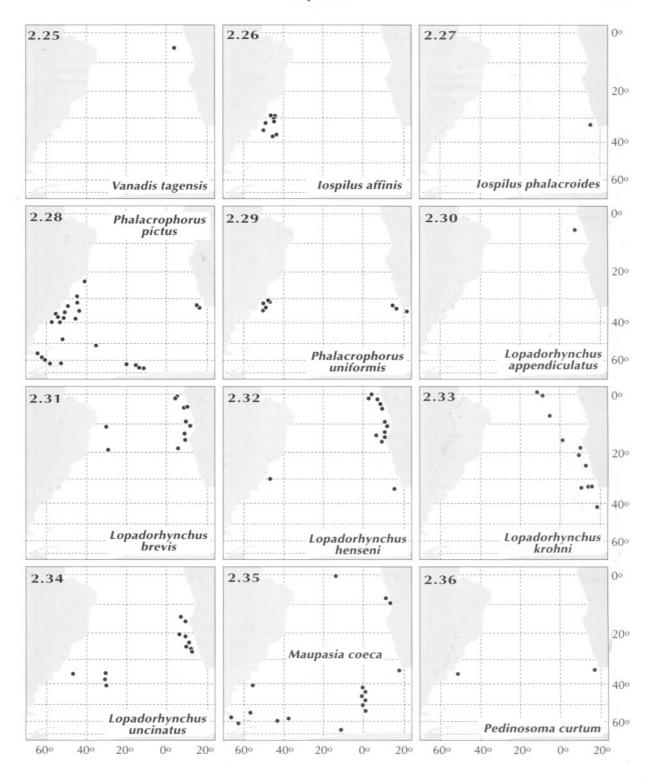
The basic body plan of a pelagic polychaete is illustrated in Fig. 1. The head presents a prostomium with a variable number of antennae (1, 2, 4, 5, 6), eyes with different degrees of development, and nuchal organs which appear as ciliated pits, grooves or lobes with different forms in typhloscolecid polychaetes (Fig. 3.53a, 3.54a, 3.55a, 3.56a, 3.57b, 3.59b). The peristomium of the head is usually integrated by fusion of some segments with well developed food-gathering appendages referred to as tentacular cirri (Fig. 1B). There is often an eversible buccal cavity or proboscis that may have chitinous jaws (Fig. 3.24b). Proboscides are variable in size and in the distribution of their papillae (Fig. 3.9a, 3.15a, 3.18a, 3.19a, 3.20a). In the metastomium each segment of the body bears a pair of lateral parapodia. These structures are typically biramous with the parapodial trunk dividing into a dorsal ramus, the notopodium, and a ventral ramus, the neuropodium. This biramous condition is present in tomopterid polychaetes (Fig. 1D), but in the other holoplanktonic families the parapodia are uniramous. Each ramus consists of a setigerous lobe supported by a stout internal chitinous rod or aciculum, and a bundle of chitinous setae which show an infinite variety of forms (Fig. 3.lb, 3.4b, 3.29b, 3.27b, 3.32c). Setae are also referred to as chaetae by some zoologists. Holoplanktonic families present two main kinds of setae: simple and compound. Simple setae are capillary setae (slender hair-like structures,

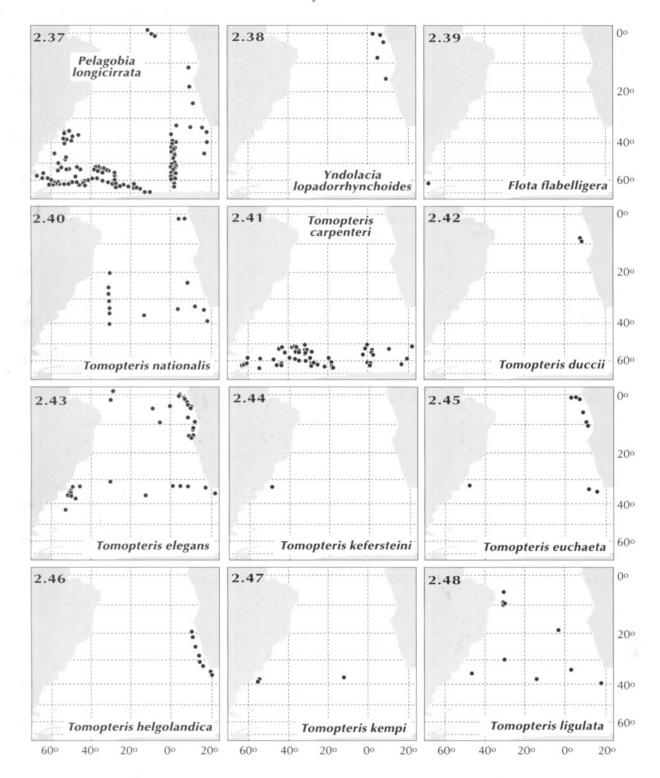
Fig. 1C) and simple acicular setae (stout, similar to the aciculum, Fig. 1C). Compound setae consist of a basal and distal parts. The distal part may be flattened to form a blade, and may have serrations (Fig. 1C). Compound setae may also be acicular, as in some species of Rhynchonerella (Fig. 1C). Fauchald (1977) has remarked on the importance of accurate examination of these structures through precise microscopic observations. Each parapodium may bear dorsal and ventral structures named parapodial cirri that are variable in form and size. In addition, some glands are associated with the parapodia, and they have taxonomic importance in the holoplanktonic families Alciopidae and Tomopteridae. In the Alciopidae, the segmental glands or organs are located laterally, dorsally or ventrally between the parapodial lobes on most body segments (Fig. 3.6b, 3.7b, 3.12b, 3.15a, 3.16b, 3.20a, b). Usually they are pigmented and their form and pigmentation pattern are used in the identification of some species (Fig. 3.17a). In the Tomopteridae, there are various types of parapodial glands located in the notopodial and neuropodial pinnules which are membranous structures adapted for swimming (Fig. 1D). Chromophil glands are always present in all species, and occur only in the ventral or distal regions of neuropodial pinnules, from the third parapodia on toward posterior (Fig. 1D). They are often swollen and can be stained by haematoxylin. Spur glands are present in some species. They are alone in the first two or three parapodia, but associated with chromophil glands in the subsequent parapodia (Fig. 1D). In some species, rossete glands are present in the trunks of the first two parapodia (Fig. 1D) and in the notopodial and neuropodial pinnules of later parapodia (Fig. 1D). Hyaline glands occur near the apex of the pinnule as clear areas around a yellowish spot (Fig. 1D). These structures are very difficult to see because the spot is often missing. Day (1967) recommends a brief staining with haematoxylin to make the clear area readily visible. This basic plan of the parapodia can be modified whereby any part of the parapodium may be suppressed. All the setae may be lacking (achaetous) as in tomopterid polychaetes. The setigerous lobes may not be present, leaving only dorsal and ventral cirri (apodous), as the first parapodia in the genus Vanadis (Fig. 3.15, 3.20a). The cirri may be lost, such as the ventral cirrus in the first parapodia in some species of the genus Lopadorhynchus (Fig. 3.32b, 3.33b), or the cirri may be well developed, as in all species of the family Typhloscolecidae (Fig. 3.51a, 3.54a).

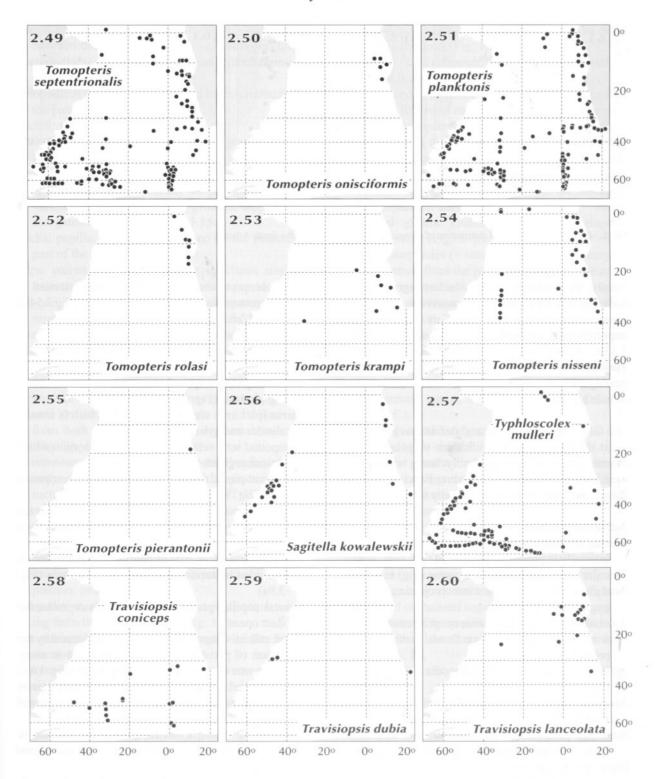
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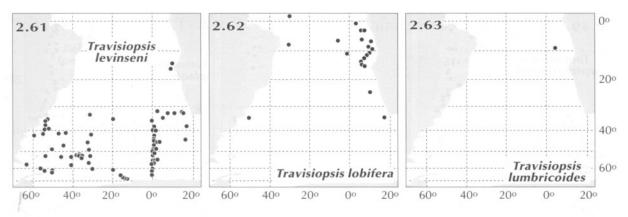


Fig. 2. Charts of the horizontal distribution of pelagic Polychaeta species in the South Atlantic.

Finally, the pygidium which is the last segment of the body that bears the anus, only conserves a pair of cirri named anal or pygidial. They are taxonomically important only in the family Typhloscolecidae (Fig. 3.53b, 3.54b, c, 3.55b, 3.56b, 3.59a). In the Tomopteridae, the pygidial region may be elongated bearing rudimentary parapodia and receives the name of tail (Fig. 3.36a).

The following list of terms and definitions is given to assist the reader with identification of pelagic polychaetes. Several sources of polychaete terminology were used for definitions, including Fauchald (1977), Pleijel and Dales (1991), and Glasby (1996).

Achaetous: see asetigerous.

Acicula (pl. aciculae): supportive chitinous rod found internally in projecting parapodial rami (Fig. 3.30c). Acicular setae: stout, projecting setae (Fig. 1C).

Anal cirrus (pl. anal cirri): cirrus projecting from the pygidium (Fig. 3.56b).

Antenna (pl. antennae): sensory projection arising from the dorsal, lateral or frontal surface of the prostomium (Fig. 1A).

Achaetous paddles: wide parapodia without setae (Fig. 1D).

Apodous: segments without parapodia.

Asetigerous: segment without setae (Fig. 1D).

Biramous parapodium: parapodium with two branches, a notopodium and a neuropodium (Fig. 1D).

Blade: distal, flattened portion of a compound or simple seta (Fig. 1C).

Capillary setae: long slender setae tapering to a fine point (Fig. 1C).

Caruncle: protuberance from the posterior section of the prostomium carrying nuchal organs (Fig 3.54a).

Chaeta (pl. chaetae): see seta.

Chaetiger: see setiger.

Chromophil gland: a densely staining gland in the ventral pinnule of *Tomopteris* (Fig. 1D).

Chromatophore: a special cell or group of cells carrying pigment (Fig. 3.12b).

Cirrus (pl. cirri): sensory appendage which is usually slender and cylindrical (Fig. 1A, B).

Compound seta: seta having a terminal portion which articulates with the shaft (Fig. 1C).

Distal end-piece: the terminal section of a compound seta (Fig. 1C).

Eye: light sensing organ which usually occurs on the prostomium but may occur elsewhere on the body or appendages (Fig. 1A, B).

Eversible proboscis: part of pharynx capable of being extended by turning the inner part outwards (Fig. 3.9a).

Genital papilla: projection on which a reproductive duct opens.

Head: collective term used for a structure formed by the fusion of peristomium, prostomium and in many cases, one or more cephalised segments (Fig. 1A).

Hyaline gland: gland in the pinnules of certain species of *Tomopteris*; usually translucent, sometimes with a yellow spot in the center (Fig. 1D).

Intermediate cirrus: a cirriform structure attached to the body wall between the notopodium and neuropodium.

Jaws: simple or complicated hardened apparatus with opposable units situated in the eversible pharynx.

Lobe: conical process of a parapodium (Fig. 1A).

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- Metastomium: segmented portion of the body between the prostomium and pygidium (Fig. 1A).
- Neuropodium (pl. neuropodia): ventral branch (ramus) of a parapodium
- Notopodium (pl. notopodia): dorsal branch (ramus) of the parapodium.
- Nuchal: pertaining to the neck.
- Nuchal lappet: nuchal organs forming posterior outgrowths from the prostomium.
- Nuchal organs: paired chemosensory structures usually situated postero-laterally on the prostomium, variously developed as pits, grooves, lappets, or elongated ridges (Fig. 3.53a, 3.55a).
- Nuchal papilla: dorsal papilla found on the posterior part of the prostomium.
- Palps: paired sensory or feeding structures arising from the ventro-lateral surface of the prostomium.
- Palpode: an anterior papilla-like prolongation of the prostomium in typhloscolecids (Fig. 3.52).
- Parapodium (pl. parapodia): one of a pair of lateral appendages (sometimes greatly reduced) from a body segment, often with a main trunk and two branches (rami), usually bears setae (Fig. 1A, D).
- Peristomial cirri (= tentacular cirri): paired elongated cirri on the peristomium which may be derived from both pre-segmental and segmental sources (Fig. 1A, B).
- Peristomium: strictly, the pre-segmental region of the body surrounding the mouth. In practice also includes segments fused to the rear of the peristomium. Sometimes bears cirri and food-gathering tentacles.
- Parapodial cirrus: appendage, often sensory, of the parapodium (Fig. 1A, B).
- Parapodial rami: branch of the parapodium (cf. neuropodium, notopodium).
- Parapodial trunks: the portion of the parapodium arising from the body segment (Fig. 1D).
- Peristomium: the pre-segmental region of the body surrounding the mouth.
- Pharynx: anterior portion of the digestive tract modified for feeding.
- Pinnules: membranous projections of the neuropodia and notopodia of *Tomopteris* used as swimming paddles and bearing glands (Fig. 1D).
- Proboscis (pl. proboscides): eversible, non-muscular part of the pharynx (strictly); often used interchangeably with pharynx.
- Prostomium (pl. prostomia): anteriormost, pre-segmental region of the body, may bear eyes, antennae and palps, and encloses part of the brain (Fig. 1B).

Pygidium: post-segmental terminal part of the body bearing the anus (Fig. 1A).

- Ramus (pl. rami): branch, used about the dorsal or ventral branch of a parapodium (Fig. 1D).
- Rosette gland: yellowish star-shaped gland found in the two first rami and in the pinnules of some species of *Tomopteris* (Fig. 1D).
- Segment: one of the serially repeated units comprising the trunk, separated internally or externally by septa.
- Segmental organ: organs occurring in segmental arrangement, specifically used about the nephridia and nephridial ducts.
- Segmental glands: glands occurring in segmental arrangement (Fig. 3.7b).
- Seminal receptacles (= receptacula seminis): receptacles formed from the parapodial lobes of the most anterior parapodia which receives and stores spermatozoa in some female alciopids (Fig. 3.16a, 3.18a, 3.19b, 3.20b).
- Seta (pl. setae): chitinous bristle protruding from a pocket in the body wall (Fig. 1C).
- Setigerous lobe: the projection or part of the notopodium or neuropodium which bears the setae (Fig. 1A).
- Shaft: proximal part of a compound or simple chaeta (Fig. 1C).
- Setiger: segment bearing setae (Fig. 3.1b).
- Spathulate: blade-shaped, like a spatula.
- Spur glands: gland with a spur-like projection, situated alone on the ventral side of the first pair of neuropodial pinnules and distally to the chromophil gland in posterior parapodia (Fig. 1D).
- Spiniger: seta that tapers to a fine point, usually referring to a compound seta (third seta from left in Fig. 1C).
- Setigerous (= chaetigerous): bearing setae.
- Tentacular cirrus: dorsal and/or ventral cirri of parapodia of cephalised segments, often more elongate than those of more posterior parapodia; have been confused in the literature with peristomial cirri (Fig. 1A, B).
- Tentacular segment: segment bearing tentacles (Fig. 1B).
- Unarmed pharynx: pharynx without chitinous hooks (Fig. 3.10a).
- Uniramous parapodium: parapodia with only one branch, usually the neuropodium (Fig. 3.34b).

Systematics

Overviews of the systematics of the pelagic polychaeta are given by Greeff (1876), Bergström (1914), Fauvel

(1916), Wesenberg-Lund (1935, 1939), Støp-Bowitz (1948), Dales (1957), Day (1967), Uschakov (1972), Rice (1987), and Pleijel and Dales (1991). Uschakov (1972) suggested that the pelagic families, despite their biological differences and external morphologies could be placed in the suborder Phyllodociformia using the name proposed by Levinsen in 1882 without systematic rank. This suborder belongs to the order Phyllodocemorpha (Livanov, 1940, fide Uschakov, 1972), which includes the marine polychaetes with the most primitive characters. Pleijel and Dales (1991) have considered that holoplanktonic families of uncertain phylogenetic affinities belong to the superfamilies Phyllodocoidea (Alciopidae, Lopadorhynchidae and Pontodoridae), Iospiloidea, Typhloscolecoidea and Tomopteroidea in the order Phyllodocida.

Fauchald (1974) reviewed the morphological and anatomical features used in the taxonomy of recent polychaetes, and discussed some principles of their phylogeny. He proposed that the evolution of the different polychaete families was a rapid radiation from several ancestors adapted to life in the semi-consolidated detritus layer above the sea bottom. Støp-Bowitz (1984) has discussed the systematic problems in the families Alciopidae, Tomopteridae Typhloscolecidae. Pleijel (1991) suggested that holoplanktonic families are derived from benthic phyllodocid polychaetes. The systematic study of some of these families are included in major works, such as Greeff (1876), Bergström (1914), Uschakov (1972), and Pleijel and Dales (1991).

Eight families of holoplanktonic polychaetes have been recorded from the South Atlantic Ocean. *Pontodora pelagica* has not yet been recorded in this region, and it belongs to a monogeneric and monospecific family, Pontodoridae. The phylogenetically isolated polychaete *Poeobius meseres* has only been found in the North Pacific Ocean. The diagnostic characters of the families and recorded species from the Atlantic Ocean are given below.

Outline classification

Order **Phyllodocida** Clark, 1969
Family **Alciopidae** Ehlers, 1864
Genera *Alciopa* Audouin and Milne Edwards, 1833; *Alciopina* Claparède and Panceri, 1867; *Krohnia* Quatrefages, 1866; *Naiades* Delle

Chiaje, 1830; Plotohelmis Chamberlin, 1919; Pseudalciopa Støp-Bowitz, 1991; Rhynchonerella Costa, 1864; Torrea Quatrefages, 1850; Vanadis Claparède, 1870; Watelio Støp-Bowitz, 1948 Family Iospilidae Bergström, 1914 Genera Iospilus Viguier, 1886; Phalacrophorus Greeff, 1879 Family Lopadorhynchidae Claparède, 1870 Genera Lopadorhynchus Grube, 1855; Maupasia Viguier, 1886; Pedinosoma Reibisch, 1895; Pelagobia Greeff, 1879 Family Pontodoridae Bergström, 1914 Genus Pontodora Greeff, 1879 Family Tomopteridae Grube, 1848 Genus Tomopteris Eschscholtz, 1825 Family Typhloscolecidae Uljanin, 1878 Genera Sagitella Wagner, 1872; Travisiopsis Levinsen, 1885; Typhloscolex Busch, 1851 Family Yndolaciidae Støp-Bowitz, 1987 Genus Yndolacia Støp-Bowitz, 1987 Order Fauvelopsida Fauchald, 1977

Identification

Order **Phyllodocida** Family **Alciopidae**

Family Flotidae Buzhinskaya, 1996

Genus Flota Hartman, 1967

The main diagnostic character of the members of this family is a single pair of large and complex eyes. Prostomium small with four, five or six antennae. Three, four or five pairs of tentacular cirri and an eversible proboscis, with short papillae or long terminal horns. Body slender and elongate with numerous segments, almost always broken into fragments in zooplankton samples. Parapodial glands are present, laterally, dorsally or ventrally between the parapodial lobes on most body segments; these are referred to as "segmental glands". The glands range in size from small oval projections in some species to elongated kidney-shaped structures extending from the dorsal to the ventral cirrophore. A pair of anal cirri is present, but it is usually difficult to see due to body damage. It is assumed by the presence of the eversible muscular proboscis, sometimes provided with a pair of lateral projections for grasping prey, that alciopid polychaetes are predators; however, the nature of the prey is unknown (Day, 1967). By the presence of this structure, their complex eyes, and their behavior, Uschakov (1972) suggested they are active predators. Rice

(1987) describes the behavior, *in situ*, of some species of this family from the Bahama Islands in the Western Atlantic Ocean, and gives new information on morphology using electron microscopy and discusses aspects of reproduction, and systematics. He added two new taxonomic characteristics (sperm type and body transparency), and constructed an evolutionary tree of the alciopid polychaetes. In general, he agrees with Støp-Bowitz (1949) in the generic relationships, dividing the genera of this family into two somewhat distinct groups on the base of the type of setae.

Key to genera and species

Key	to genera and species
1	Setigerous lobe without a cirriform appendage
	2
1a	Setigerous lobe with a single cirriform appendage
	3
1b	Setigerous lobe with two cirriform appendages
	4
2	Setae capillaries only: Naiades cantraini Delle
	Chiaje, 1830 (Fig. 3.1)
2a	Setae compound spinigers only: Torrea candida
	(Delle Chiaje, 1841) (Fig. 3.2)
2b	Setae capillaries and simple aciculae: Alciopina
	parasitica Claparède and Panceri, 1867 (Fig. 3.3)
2c	Setae compound spinigers and simple aciculae:
	Plotohelmis5
3	Setae capillaries and simple aciculae: Krohnia
	lepidota (Krohn, 1845) (Fig. 3.5)
3a	Setae capillaries and compound spinigers:
	Watelio gravieri (Benham, 1929) (Fig. 3.4)
3b	Setae compound spinigers only: Vanadis12
3c	Setae compound spinigers and simple or com-
	pound aciculae: Rhynchonerella8
4	Setae capillaries and compound spinigers:
	Alciopa reynaudi Audouin and Milne Edwards,
	1829 (Fig. 3.6)
5	Segmental glands with ventro-lateral chromato-
	phores6
5a	Segmental glands without ventro-lateral chro-
	matophores7
6	Chromatophores ventro-lateral branching on the
	ventrum. Males with four pairs of genital papil-
	lae on ventral region of segments 12 to 15:
	Plotohelmis capitata (Greeff, 1876) (Fig. 3.12)
6a	Chromatophores ventro-lateral but no bran-

ching. Males with ten pairs of genital papillae on

ventral region of segments 13-22: Plotohelmis

alata Chamberlin, 1919 (Fig. 3.13)

7	Prostomium	large	and b	oulbous,	divided	into	
	hemispheres	by a	media	n groov	e. Segm	ental	
	organs as lateral bars behind the basis of the pa-						
	rapodia. M	ales	withou	ut genit	al papi	llae:	
	Plotohelmis tenuis (Apstein, 1900) (Fig. 3.14)						

- 8b Two kinds of compound setae.....11
- 9 Segments 4-6 with only 2-7 simple acicular setae and their dorsal cirri much larger and more rounded than later ones: *Rhynchonerella moebii* (Apstein, 1893) (Fig. 3.10)
- 9a Simple acicular setae and compound capillary setae present from the first parapodia. The first few dorsal cirri not obviously different from later ones: *Rhynchonerella gracilis* Costa, 1861 (Fig. 3.9)
- 10 Distal end-pieces of acicular setae small and simple. Prostomium and dorsum strongly pigmented: *Rhynchonerella angelini* (Kinberg, 1866) (Fig. 3.7)
- 10a Distal end-pieces of acicular setae large and clearly serrated. Head not pigmented: *Rhynchonerella petersi* (Langerhans, 1880) (Fig. 3.11)
- 11 Compound setae with smooth or denticulate end-piece on the first seven or eight parapodia. Cirriform appendages on the pedal lobe are very small. Segmental glands are seldom pigmented: *Rhynchonerella bongraini* (Gravier, 1911) (Fig. 3.8)
- 12 Prostomium with 4 antennae......13
- 13 Proboscis with a pair of lateral horns. Females with a pair of seminal receptacles14
- 14 First 6-7 pairs of parapodia modified, achaetous with very small dorsal and ventral cirri. Segmental glands lightly pigmented before segment 12, if at all: *Vanadis minuta* Treadwell, 1906 (Fig. 3.18)
- 14a First 5-6 pairs of parapodia modified. Segmental glands as vertically pigmented bands before segment 7: *Vanadis studeri* Apstein, 1893 (Fig. 3.20)
- 15a Proboscis terminated by 12 triangular marginal papillae. Segmental glands present from segment 5, never pigmented and body uniform violet when fresh: *Vanadis violacea* Apstein, 1893

- 15b Proboscis terminated by two long horns and a varying number of small papillae......17
- Dark bars around body every five or ten segments: *Vanadis longissima* (Levinsen, 1885) (Fig. 3.17)
- 16a Dark bars across dorsum at intervals of two or three segments: *Vanadis antarctica* (McIntosh, 1885) (Fig. 3.21)
- 17 Parapodia well developed and with setae from the third foot posteriorly: *Vanadis formosa* Claparède, 1870 (Fig. 3.16)
- 17a Parapodia well developed and with setae from the seventh to tenth parapodia posteriorly: *Vanadis crystallina* Greeff, 1876 (Fig. 3.15)
- Proboscis with 12 terminal papillae, of which two lateral pairs are longest. Four pairs of tentacular cirri: *Vanadis tagensis* Dales, 1955 (Fig. 3.19)

In addition to those included in the key above, alciopids reported from the South Atlantic include three more species described recently from the Gulf of Guinea by Dr. Støp-Bowitz (1991), most of them with only one specimen: *Pseudalciopa modesta* Støp-Bowitz, 1991, *Rhynchonerella longicirrata* Støp-Bowitz, 1991, and *Vanadis brevirostris* Støp-Bowitz, 1991.

Family Iospilidae

Small worms with prostomium rounded, without antennae. Two minute palps and two eyes. Proboscis eversible, with or without a pair of lateral chitinous hooks. First two or ten segments of the body with reduced parapodia. Later parapodia uniramous with short dorsal and ventral cirri, a longer setigerous lobe and compound spinigerous setae. Day (1967) mentions that species of the genus *Iospilus* include some of the few holoplanktonic polychaetes which feed on diatoms, and species of *Phalacrophorus* which have chitinous hooks are possibly predators. Uschakov (1972) suggested that these jaws are developed as adaptive structures to pelagic life, for catching rapidly moving planktonic organisms.

Key to genera and species

- 1 Proboscis unarmed: Iospilus2
- 1a Proboscis armed with jaws: *Phalacrophorus*.....3
- 2 First two chaetigers without cirri, and small lobes with few setae: *Iospilus affinis* (Viguier, 1911) (Fig. 3.23)
- 2a First two chaetigers with cirri: *Iospilus phala-croides* Viguier, 1886 (Fig. 3.22)

- First two chaetigers reduced, only with small lobes and few short setae: *Phalacrophorus pic*tus Greeff, 1879 (Fig. 3.25)
- First seven chaetigers reduced only with small lobes and few short setae: *Phalacrophorus uniformis* Reibisch, 1895 (Fig. 3.24)

Family Lopadorhynchidae

Worms with flattened body. Prostomium broad with four antennae, no palps and poorly developed eyes. Eversible proboscis, simple and unarmed. With three tentacular cirri on the first one or two segments which may lack setae. Parapodia uniramous with dorsal and ventral cirri. Setae mainly compound with serrated end-pieces. The serrations are of taxonomic importance and must be examined in lateral view (Pleijel and Dales, 1991). Pygidium without cirri.

Practically nothing is known of the biology of this group. None have ever been found with food in the gut, but certainly they do not feed on phytoplankton (Day, 1967). Uschakov (1972) speculated that the simple hook-shaped setae of the first modified parapodia of *Lopadorhynchus* might hold the prey.

Key to genera and species

- 2 Prostomium triangular with four small antennae and a pair of eyes. Tentacular segment with a few setae and two long, tapered cirri. Later parapodia with a conical setigerous lobe and longer dorsal and ventral cirri essentially similar, more or less cylindrical. Compound setae with basal joints smooth: *Pelagobia longicirrata* Greeff, 1879 (Fig. 3.35)
- 2a Body small and flattened with few segments. Round prostomium with two pairs of lateral antennae. Tentacular cirri without setae. All subsequent parapodia with cordate dorsal cirri, conical setigerous lobes and lanceolate ventral cirri. Setae all fine and compound: *Pedinosoma curtum* Reibisch, 1895 (Fig. 3.26)

- 3 First two pairs of parapodia modified, with curved and simple acicular setae......4
- 4 First two pairs of parapodia are large and stout with strong acicular setae which are rounded at the base by a collar-like expansion: *Lopador-hynchus uncinatus* Fauvel, 1915 (Fig. 3.30)
- 4a First two pairs of parapodia are stout, but not larger than subsequent ones, with a linear series of stout simple, hooked acicular setae and lack ventral cirri: *Lopadorhynchus krohni* (Claparède, 1870) (Fig. 3.31)
- 4b First two pairs of parapodia stouter and shorter than subsequent ones, with simple acicular setae. The ventral cirri are partially fused to the inferior margin of the setigerous lobes: *Lopadorhynchus henseni* Reibisch, 1893 (Fig. 3.32)
- 4c First two pairs of parapodia are short with inconspicuous, hooked setae. The ventral cirri are present partially fused to the setigerous lobes. Ventral cirri on the four and subsequent parapodia with a long filiform tips: *Lopadorhynchus appendiculatus* Southern, 1909 (Fig. 3.33)
- 5 Setigers 1-3 shorter and stouter than subsequent ones, they have only simple acicular setae and lack ventral cirri: *Lopadorhynchus brevis* Grube, 1855 (Fig. 3.34)
- 5a Setigers 1-3 shorter and stouter the subsequent ones, with simple acicular setae. They have the ventral cirri partly fused to the distal inferior margin of setigerous lobes: *Lopadorhynchus nationalis* Reibisch, 1895 (Kim, 1967, has considered this species synonymous with *L. brevis* Grube, 1855).
- 6 Posterior parapodia with dorsal cirri foliaceous and ventral cirri lanceolate: *Maupasia coeca* Viguier, 1886 (Fig. 3.27)
- 7 Dorsal tentacular cirri of segment 2 longer than twice the body width: *Maupasia gracilis* Reibisch, 1893 (Fig. 3.28)
- 7a Dorsal tentacular cirri of segment 2 less than twice the body width: *Maupasia isochaeta*

Family Pontodoridae

A monogeneric and monospecific family with a small and slender pelagic polychaete, whitish and fragile body. Rounded prostomium with four antennae, and very small eyes. Two pairs of tentacular cirri present. Uniramous parapodia with slender, elongated pedal lobes that are extended until the long composite setae; dorsal and ventral cirri are oval and small.

Pontodora pelagica Greeff, 1879 (Fig. 3.29) has not yet been recorded in the South Atlantic Ocean. It has been reported from warm waters in the Atlantic Ocean (Dales and Peter, 1972), the Agulhas and Mozambique Currents (Day, 1967), and from warm and cold waters in the Pacific Ocean (Treadwell, 1943; Uschakov, 1955; Berkeley and Berkeley, 1960; Fernández-Álamo, 1983, 1992).

Family Tomopteridae

Polychaetes characterized by parapodial reduction to biramous achaetous paddles with notopodia and neuropodia modified for swimming into membranous structures named pinnules. These structures may carry various types of glands including chromophils, hyalines, rosettes and spurs. Dales (1957) gives a good description of these organs. Prostomium with one pair of antennae and simple eyes. First two segments fused with the prostomium and carrying cirri supported by aciculae. Second segment with long cirriform appendages. Short and unarmed pharynx.

Very little information about the biology of the members of this family is available. In general, nothing is to be seen in the transparent gut. Uschakov (1972) believes that they are voracious predators.

Key to species

Abbreviations used in key, Pin: Pinnules; Hy: Hyaline glands; Ros: Rosette glands; Chr: Chromophil glands; Sp: Spur glands.

- 1a Without tail.....5
- Pin restricted to the parapodial rami. Ros present in the trunks of the first two parapodia and at apices of both rami of later parapodia. Chr large and swollen from the third parapodia and subsequently on all parapodia. Sp present from second parapodia onwards (from the third are associated with Chr): *Tomopteris nationalis* Apstein, 1900 (Fig. 3.36)
- 3a Pin extended on the distal ends of parapodia trunks. Hy present in the apices on dorsal and

- ventral Pin from the third parapodia. Chr voluminous situated in the inferior half of the ventral Pin from 3-4 parapodia onwards: *Tomopteris krampi* Wesenberg-Lund, 1936 (Fig. 3.37)
- 3b Ros present in the trunks of the first two parapodia and in both pinnules of the following parapodia. Chr large from the fifth parapodia and subsequently on all parapodia. Sp well developed from the third parapodia located in the inferior part of the ventral Pin: *Tomopteris duccii* Rosa, 1907 (Fig. 3.38)
- 4 Pin broad with an inner clear area and a narrow frilly outer margin containing the glands. Glandular outer edge not extending between the rami in juveniles. Hy present towards the distal end of the inferior part of the ventral Pin from the third foot onwards. Chr swollen from fourth parapodia: *Tomopteris euchaeta* Chun, 1887 (Fig. 3.43)
- 4a First pair of cirri present in juveniles. Pin restricted to the parapodial rami. Ros in the trunks of the first two parapodia and near the tips of both rami thereafter. Sp present from 2-3 parapodia. Chr large and start on the third parapodia: *Tomopteris dunckeri* Rosa, 1908 (Fig. 3.44)
- 4b Body large and flaccid. Nuchal organs well marked. Parapodia swollen with short, conical rami. Black spots present on the dorsal and ventral Pin from the third to subsequent parapodia. Chr well marked from the third parapodia: *Tomopteris kempi* Monro, 1930 (Fig. 3.45)
- 4c Body large, tail long. Pin reduced to a fringe bordering the parapodia. Hy in variable position very ventral and dorsal Pin. Chr prominent, present from the fourth parapodia posteriorly. Cirriform appendages of second segment may exceed length of body: *Tomopteris nisseni* Rosa, 1908 (Fig. 3.46)
- 4d First cirri present in juveniles, absent in adults. Pin oval. Ros present from the first parapodia on the inner side of the Pin, next to the apex of each ramus. Chr inconspicuous from the first parapodia: *Tomopteris helgolandica* Greeff, 1879 (Fig. 3.47)
- 5 First cirri present6
- 6 Parapodial trunks long and slender with oval Pin. Chr well developed from fourth parapodia, situated towards the apical ventral region of Pin. Hy restricted to the dorsal Pin of the third and

- fourth parapodia: *Tomopteris elegans* Chun, 1887 (Fig. 3.39)
- 6a Pin rounded and restricted to parapodial rami. With brownish pigment at the tips of both dorsal and ventral rami. Chr situated ventrally in the Pin: *Tomopteris kefersteini* Greeff, 1879 (Fig. 3.41)
- 6b Pin oval. Ros in the trunks of the first two parapodia and near the tips of both rami thereafter. Chr rounded situated ventrally from the third parapodia: *Tomopteris rolasi* Greeff, 1882 (Fig. 3.42)
- Pin oval and restricted to parapodial rami. Chr well developed, from fourth parapodia, with a triangular form, and situated at the proximal end of the ventral region of the Pin. Hy and Ros absent: *Tomopteris planktonis* Apstein, 1900 (Fig. 3.48)
- 7a Pin oval the dorsal extending onto the distal end of the parapodial trunk. Hy present at the apices of ventral Pin from 2-4 parapodia. Chr not compact situated between the ventral and apical region of Pin from the fourth parapodia onwards: *Tomopteris septentrionalis* Quatrefages, 1865 (Fig. 3.49)
- 7b Body very large, Pin oval, frilly and extend on to the distal ends of the parapodial trunks. Hy deeply pigmented from the third parapodia in the superior half of ventral Pin. Chr large and voluminous from the fourth parapodia, in inferior half of Pin: *Tomopteris carpenteri* Quatrefages, 1835 (Fig. 3.50)
- 7c Pin continuous with dorsal and ventral ridges along the parapodial trunks. Hy in a dorsal position from the third ventral Pin. Chr ventrally from the fourth parapodia: *Tomopteris ligulata* Rosa, 1908 (Fig. 3.40)

In addition to those listed in the key, *Tomopteris circulosa* Støp-Bowitz, 1992, *T. congolana* Støp-Bowitz, 1992, *T. guineensis* Støp-Bowitz, 1992, *T. guineensis* Støp-Bowitz, 1992, *T. lutea* Støp-Bowitz, 1992, and *T. simplex* Støp-Bowitz, 1992, have been described recently from the Gulf of Guinea by Dr. Støp-Bowitz (1992), most of them from only one specimen. According to Day (1967), *T. apsteini* Rosa, 1908 is probably synonymous with *T. nationalis* Apstein, 1900. *Tomopteris cavalli* Rosa, 1907 was not considered valid by Tebble (1960). Day (1967) put *Enapteris euchaeta* within the genus *Tomopteris* on the basis of a careful description of the parapodia.

Tomopteris onisciformis Eschscholtz, 1825, the type species of the genus, has been considered as indeterminable; it was reported by Støp-Bowitz (1992), but its characteristics are very similar to *T. rolasi* Greeff, 1882 (cf. Orensanz and Gianuca, 1974) in the same paper, and it is important to clarify if the latter is synonymous with the first.

Family Typhloscolecidae

Worms highly specialized, with fusiform and transparent body. Prostomium indistinct from the rest of the body and projected forward into a small papilla. Without eyes, with well developed nuchal organs which often form free posterior projections. Pygidium with a pair of flattened anal cirri.

These worms have been considered to be ectoparasites of gelatinous animals, such as chaetognaths and medusae. The characteristic suction apparatus that replaces the proboscis may indicate that they are semi-parasites (Uschakov, 1972). Feigenbaum (1979) has regarded the possibility that typhloscolecids are predators of chaetognaths.

Key to genera and species

- 2 Prostomium blunt and bearing a small asymmetrical palpode. Ciliated lobes almost as broad as the head, the dorsal one with a pair of small rounded nuchal lappets at the sides: *Typhloscolex mulleri* Busch, 1878 (Fig. 3.59)
- 3 Prostomium with a small palpode. Head with a pair of semicircular nuchal ridges on dorsal region but no free nuchal lobes: Sagitella kowalewskii Wagner, 1872 (Fig. 3.51)
- 4 Nuchal organs extended backward as rounded lobes. Anal cirri oval: *Travisiopsis dubia* Støp-Bowitz, 1848 (Fig. 3.53)

- 4a Nuchal organs extended backward as lobes simple and digiform. Anal cirri long and ovate: *Tra*visiopsis lanceolata Southern, 1911 (Fig. 3.54)
- 4b Nuchal organs extended backward as lobes digiform and parallel. Anal cirri subtriangular: *Travisiopsis lobifera* Levinsen, 1885 (Fig. 3.56)
- 4c Nuchal organs extended backward as lobes semicircular. Anal cirri spathulate: *Travisiopsis levinseni* Southern, 1911 (Fig. 3.55)
- 4d Nuchal organs extended backward as branched lobes. Anal cirri spathulate: *Travisiopsis coni*ceps (Chamberlin, 1919) (Fig. 3.52)

In addition to the above, Støp-Bowitz (1991, 1992) recorded only one specimen of *Travisiopsis lumbricoides* Reibisch, 1895 (Fig. 3.57) in the tropical waters (10 m depth) of the Gulf of Guinea.

Family Yndolaciidae Støp-Bowitz, 1987

Worms with short and flat body; reduced prostomium without antennae, palps or eyes. Proboscis short, unarmed with deep ventral slit. Peristomium and following segment with a pair of large tentacular cirri; body segments with biramous parapodia with dorsal and ventral cirri in needle form; compound setae, each with a long slender blade.

 Yndolacia lopadorrhynchoides Støp-Bowitz, 1987 (Fig. 3.58) is the only species in the family. It is bathypelagic (800-900 m depth), and found in the equatorial region off the coast of Africa.

Order Fauvelopsida

Family Flotidae

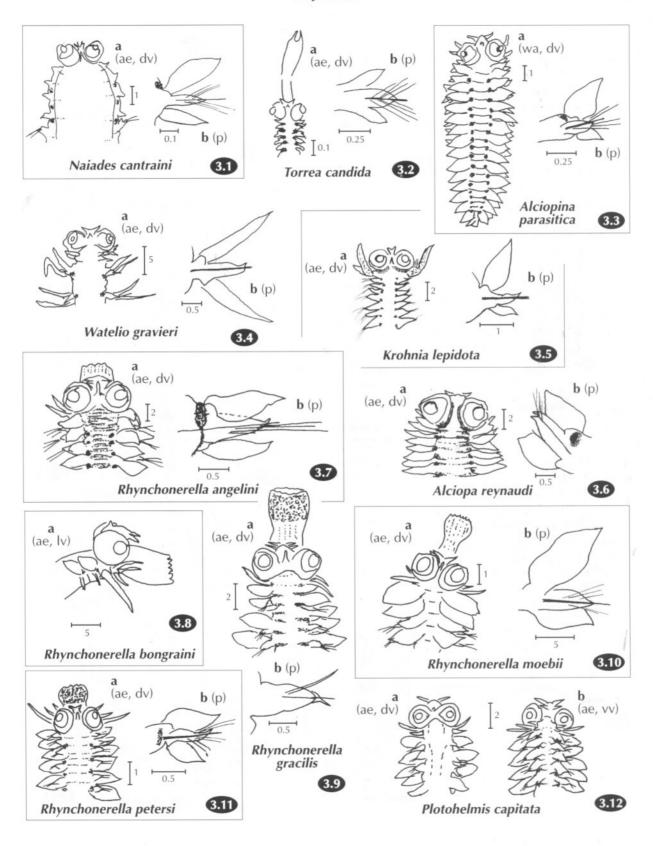
Nine segments, parapodia biramous, with setae characteristically cross-barred. Body and parapodia completely encased in transparent gelatinous sheath. Bathy- to abyssopelagic.

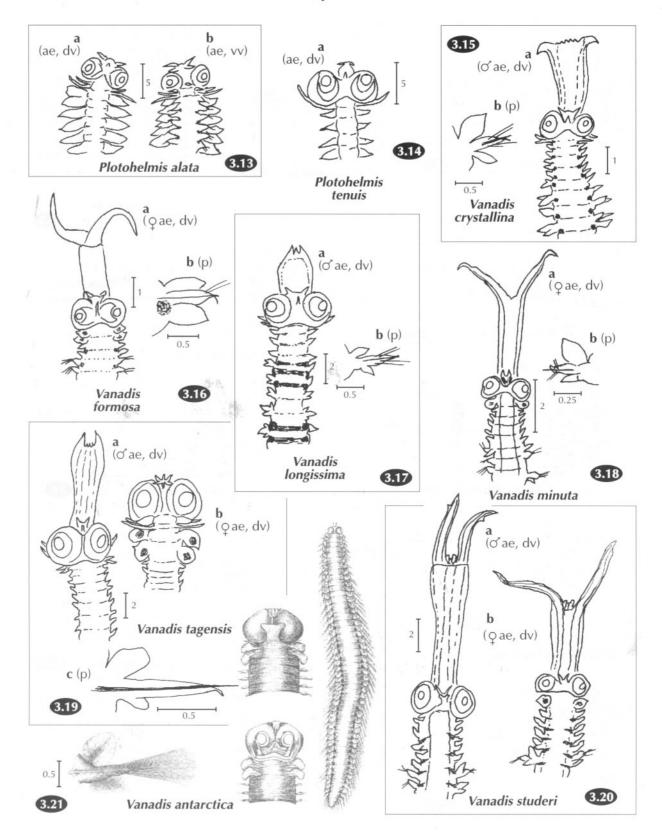
Flota flabelligera Hartman, 1967 (Fig. 3.60). At a total length of 25 mm, it has been found off the coast of southwestern Chile and off Cape Horn (Hartman, 1967). It will most likely be found at abyssal depths in the southern section of the South Atlantic Ocean. One other species in this family has been described, Flota vitjasi Buzhinskaya, from the western North Pacific Ocean.

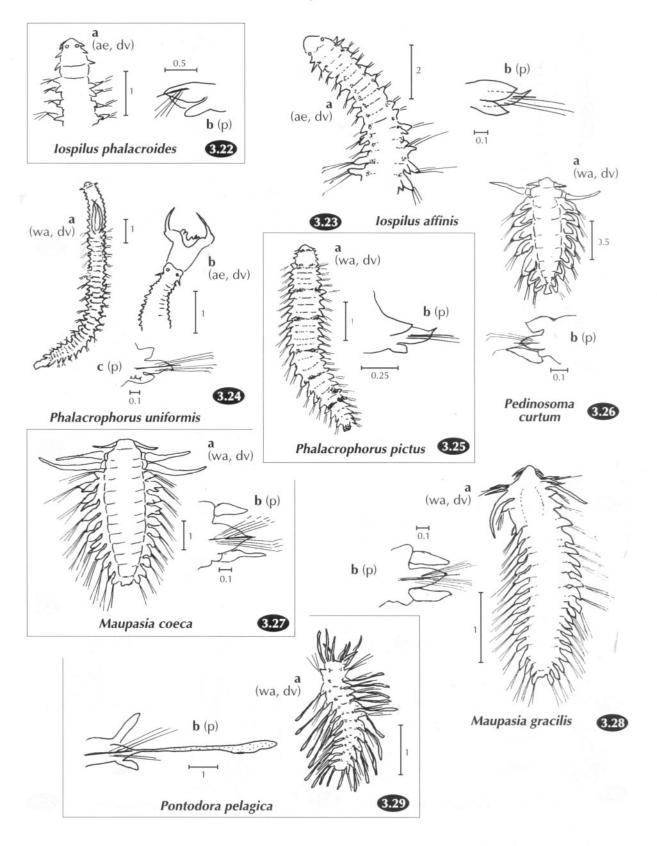
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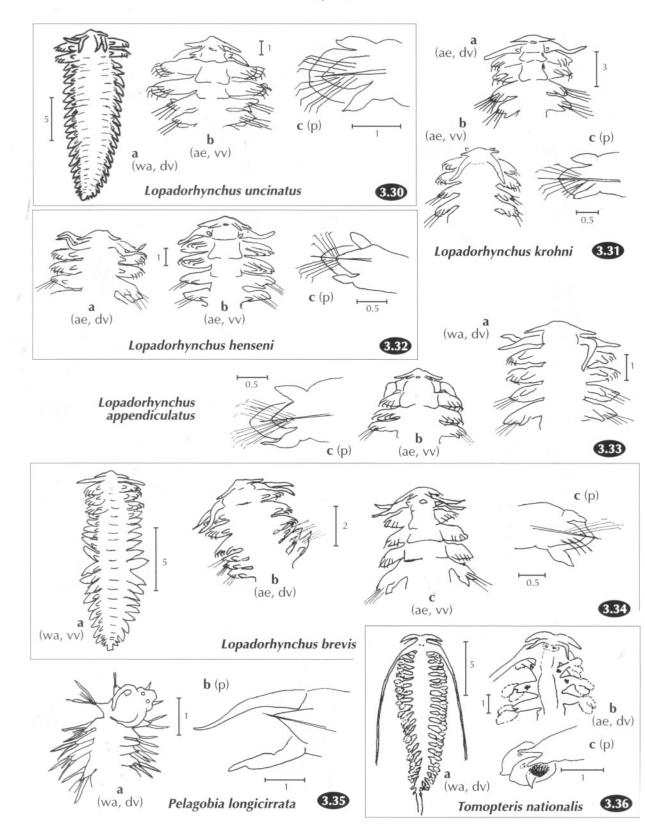
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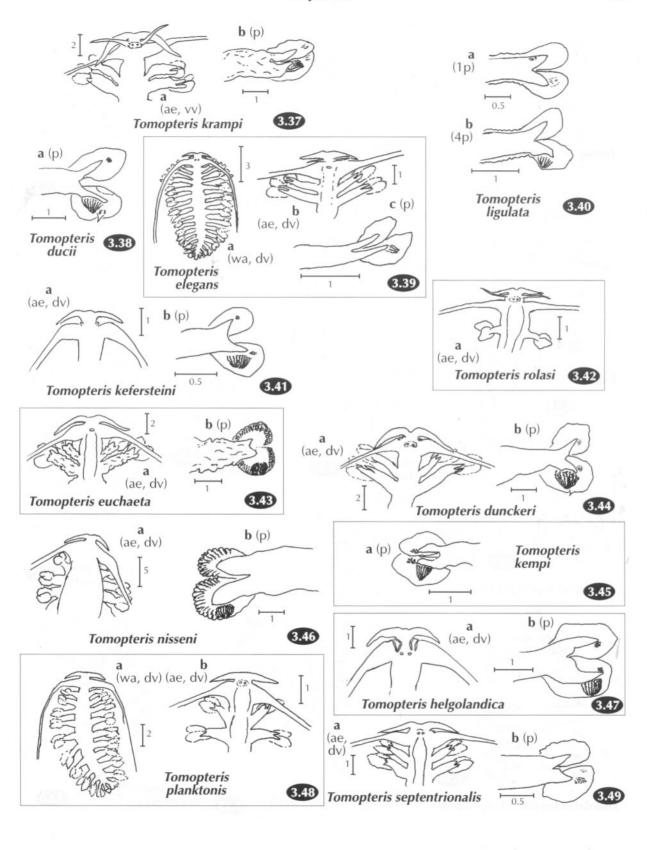
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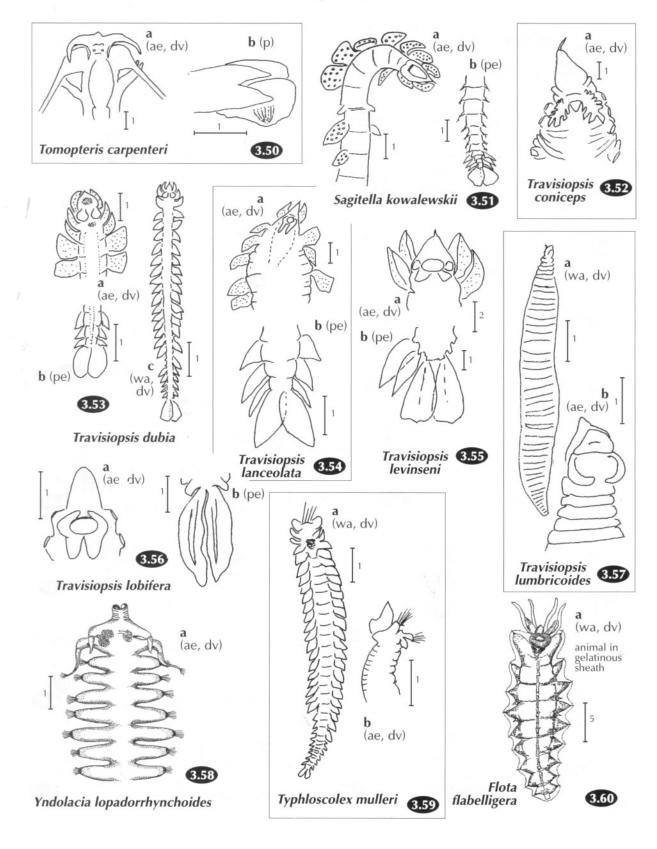


Fig. 3. Illustrations of the species. All scales are in mm. 1p: first parapodium; ae: anterior end; dv: dorsal view; lv: lateral view; p: parapodium; pe: posterior end; vv: ventral view; wa: whole animal. All figures redrawn; sources: after Benham (1929): 8, 50; after Chamberlin (1919): 52; after Fernández-Álamo (1983): 1, 3-7, 9-20, 22, 24-37, 39, 43, 44, 46, 48, 49, 51, 53, 54, 59; after Hartman (1967), composite by M.T. Biondi: 60; after Malaquin and Carin (1922): 42; after McIntosh (1885): 21; after Monro (1930): 45; after Monro (1936): 56; after Reibisch (1895): 57; after Rosa (1908): 38, 40; after Støp-Bowitz (1987), composite by M.T. Biondi: 58; after Viguier (1911): 23; after Wesenberg-Lund (1935): 41, 47; after Wesenberg-Lund (1936): 55; after Wesenberg-Lund (1939): 2.