Annelida

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A major phylum of the Animal Kingdom. The annelids range in size from minute interstitial forms to giant earthworms (up to 10 ft or 3 m), known from the Southern Hemisphere, and they include a few very large marine polychaetes. As the name Annelida suggests, the body is divided into cylindrical rings or segments, with serially arranged organs. The basic body plan is described as a tube within a tube. The inner tube, or digestive tract, is separated from the outer tube, or body wall, by a spacious body cavity, or coelom, lined with mesodermal epithelium. A preoral lobe or prostomium encloses the brain. The first ring or peristomium encloses the ventral mouth. The rest of the trunk is formed by a series of similar segments marked externally by intersegmental lines and internally by transverse septa extending from the body wall to the digestive tract. The posterior lobe or pygidium encloses the anus. Additional segments are added anterior to the pygidium, External segmentation may also be indicated by the presence of serially arranged, movable bristles or setae (Polychaeta, Oligochaeta), and by parapodia, lateral extensions of the body, which bear setae, sensory appendages such as dorsal and ventral cirri, and branchial processes (Polychaeta). Internal segmentation is indicated by the septa and by serially arranged excretory, circulatory, and reproductive organs, as well as by a ganglionated ventral nerve cord. The fundamental pattern may be considerably modified in the Annelida. Some anterior segments may be modified and incorporated with the prostomium and peristomium. The body segments may be secondarily subdivided externally into annuli (leeches and some sedentary polychaetes). Setae may be lacking (leeches, some planktonic and interstitial polychaetes). The coelom may be nearly obliterated by a mesenchymatous packing tissue (leeches). The septa may be mostly lacking (some polychaetes, leeches). The trunk segments may be divided into thoracic, abdominal, and tail regions, with corresponding differences in the parapodia (some burrowing and tube-dwelling polychaetes).

The body wall consists of a simple columnar epithelium, outer circular and inner longitudinal muscle layers, and a coelomic epithelium. The epidermis is overlaid by a collagenous cuticle and rests on a more or less developed basement membrane; it is formed of supporting columnar cells, ciliated cells, glandular mucus-producing cells, and sensory cells. In varying degrees, the epidermis lines the gut and the genital and excretory openings and is infolded to form the setal follicles. Chitinous chaetae, or setae, develop from chaetoblast cells in the epidermal follicles. The epidermal surface may be provided with heavily cuticularized surface papillae. The general body surface is involved in respiratory gascous exchange and may be vascularized in large annelids. The mucus aids in providing a moist surface through which gaseous exchange is accomplished. It

also acts as a lubricant in burrowing and crawling forms.

Annelid worms are able to crawl, burrow, or swim by means of muscular activity. Cilia are rarely used for locomotion except in small interstitial polychaetes and trochophore larvae. The simplest condition is that of a long cylindrical worm with a single fluid-filled cavity in which the septa have been secondarily lost (Arenicola). The body wall encloses a relatively incompressible (coelomic) fluid. The circular and longitudinal muscles are mutually antagonistic, so that contraction of the circular muscles reduces the diameter and extends the worm by means of the pressure generated in the fluid; the recovery of shape is accomplished by contraction of the longitudinal muscles and stretching of the circular muscles. In septate annelids, each segment may function as an independent hydraulic system. The passage of waves of muscular contraction along the body wall of a worm may cause forward or backward motion, or irrigation of a tube or burrow. Supplementary diagonal, setal, and parapodial muscles allow additional movements. The leeches have a flattened body and lack a spacious coelom and setae. They have a layer of oblique muscles between the circular

and longitudinal muscles and have developed anterior and posterior cuticular suckers which they use in their characteristic inchworm type of movement.

The digestive system is composed of the foregut, formed of stomodaeal ectoderm; the midgut, from endoderm; and the hindgut, from proctodaeal ectoderm. The foregut forms the mouth, buccal cavity, pharynx, and esophagus; the midgut, the stomach-intestine; and the hindgut, the rectum. The anus is usually terminal. The structure of the digestive tract is diversified according to the mode of life and the food habits of the worm. A muscular pharynx with chitinous jaws is found in most free-living polychaetes and biting leeches; jaws are absent in tube-dwelling polychaetes, most oligochaetes, and sucking leeches. Leeches have become specialized for a blood-sucking ectoparasitic mode of life. They use their ventral suckers at each end of the body to cling to the host while sucking blood. The midgut forms a large crop with paired diverticula for storage of large quantities of blood.

The excretory system is composed of segmental paired nephridia consisting of straight, looped, or coiled tubes in the coelom that open to the exterior or into the gut. The inner end may be closed by tufts of solenocytes (protonephridia) similar to the flame cells of flatworms, or it may open to the coelom by a ciliated funnel (metanephridia). Both types are ectodermal. A pair of protonephridia constitutes the excretory system of the typical annelid larva; this is considered to be the primitive condition. The nephridia collect waste products and transport them from the coelom to the exterior through the nephridiopores. Paired coelomoducts or mesodermal funnels that function as reproductive ducts

(gonoducts) may be secondarily fused with the nephridia.

The circulatory system is a closed system of vessels. Basically it consists of a series of segmental vessels which join two longitudinal vessels running the length of the body. The dorsal vessel, the chief contractile vessel, moves the blood anteriorly; it has branches to the digestive tract. The ventral vessel moves the blood posteriorly; it gives rise to vessels in each segment which supply the body wall, and it receives vessels from the digestive tract. Blood from the body wall is returned by lateral vessels to the dorsal vessel. In small annelids the blood may be colorless, lacking respiratory pigments. The blood of larger annelids has respira-

tory pigments, such as hemoglobin, dissolved in the plasma.

The fundamental plan of the annelid nervous system is a ladderlike chain of ganglia linked by commissures and connectives extending the length of the body in the ventral midline. Primitively there is a pair of ganglia per segment, connected by transverse commissures. Usually the paired cords and ganglia have fused to form a median, unpaired ventral nerve cord, with ganglion cells concentrated in segmental swellings. The ganglia are supplied with several pairs of lateral nerves. Anteriorly the segmental pattern is modified by the development of a cerebral ganglion or brain located in the prostomium, with paired connectives to a subesophageal ganglion formed by the fusion of ganglia from several segments, and with nerves to the head appendages and mouth. A stomogastric system originates in either the cerebral ganglion or the connectives and innervates the anterior region of the gut. The ventral nerve cord of many annelids is provided with giant nerve fibers which serve as high-speed motor pathways for rapid responses such as escape movements. The brain contains neurosecretory cells of several types; the secretory activities can be related to phases of the life cycle, especially reproduction, growth, and regeneration.

The annelids possess a variety of epidermal and subepidermal sensory cells associated with the reception of tactile, proprioceptive, chemical, and light stimuli. Tactile endings and taste buds are especially numerous on the anterior end of the body. Single photoreceptor cells, sensitive to light, are found in the skin of oligochaetes and leeches over much of their body surface. There is a wide range of photoreception in the annelids, varying from single cells (ocelli) and simple eyespots to elaborate camera-type eyes with lenses and retinas. The nuchal organs of sedentary polychaetes, which take the form of ciliated pits or grooves, are considered to be chemoreceptors. Organs of equilibrium (statocysts) may be present in the form of epidermal invaginations containing sand grains or closed

epidermal pockets with calcareous granules (statoliths).

The sexes are separate in most polychaetes, but hermaphroditic forms are known. The oligochaetes and leeches are characteristically hermaphroditic, with the secondary sexual apparatus reaching its highest degree of development, with adaptations for reciprocal copulation. The majority of the body segments may he fertile (polychaetes), but there is a tendency toward limitation which reaches its culmination in the oligochaetes. In the polychaetes there are usually no permanent gonads, the sex products forming from mesodermal tissue, such as coelomic linings or septa. The products are then discharged into the coelom or genital sacs, where they are nourished by coelomic fluid or chlorogogue cells, or sometimes by nurse cells. The mature sex products escape through coelomoducts or by rupture of the body wall. The eggs may be laid in special structures and undergo direct development, or they may develop into trochophore larvae with a planktonic existence followed by metamorphosis. The oligochaetes and leeches have well-defined gonads with their own ducts opening to the exterior. They have a clitellum which secretes a cocoon for the reception of their eggs. Development is direct. Asexual reproduction by simple fragmentation is known for some freshwater oligochaetes and some polychaetes. The polychaetes and oligochaetes have a high regenerative ability (lacking in leeches). They are able to regenerate new heads and tails.

The phylum includes 3 classes: the Polychaeta (including the aberrant Myzostomida, Poeobiida, and the archiannelid families), the Öligochaeta, and the Hirudinoidea. The Polychaeta are mainly free-living and marine, but they are also found in freshwater and are rarely parasitic and terrestrial. The Oligochaeta are mainly free-living, either terrestrial (earthworms), freshwater, or rarely marine. The Hirudinoidea or leeches are ectoparasitic, freshwater, marine, or rarely terrestrial.

The annelids are considered to have evolved in the sea, with the polychaetes the largest and oldest group. The oligochaetes developed from polychaete stock, perhaps by way of invasion through estuaries into freshwater streams. The leeches, which have the clitellum in common with the oligochaetes, evolved from the latter.

References. R. P. Dales, Annelids, Hutchinson University Library, London, 1963; P. J. Mill (ed.), Physiology of Annelids, Academic Press, New York, 1978.

POLYCHAETA

The largest class of the phylum Annelida; the name refers to the many bristles, or setae, borne on the segments of the body. This is a very diverse group, widely distributed throughout the marine environment; members live in brackish water and freshwater and rarely in moist earth, They are mainly free-living; some are commensal (some Polynoidae, Syllidae, Hesionidae, Spintheridae, Antonbruuniidae, Iphitimidae, Histriobdellidae) and are associated with sponges, coelenterates, echinoderms, mollusks, other polychaetes, and crustaceans; relatively few (some Syllidae, Arabellidae, Ichthyotomidae, Myzostomida) are parasitic on or within other animals (coelenterates, echinoderms, other polychaetes, fishes).

The body varies greatly in form, depending on whether the polychaete is errant, crawling, burrowing, sedentary, tube-dwelling, or pelagic. These worms vary in length from less than 1 mm in some interstitial forms to over 3 m (some Eunicidae, Onuphidae). The number of segments may be few and limited or many and unlimited. New segments develop immediately in front of the pygidium.

The head consists of the preoral prostomium, which may be in the form of a simple lobe or furnished with various appendages, including a pair of ventral palps and frontal,

dorsal, or occipital antennae; sometimes simple eyespots or a pair of well-developed stalked eyes are present (Alciopidae, Polyodontidae). The peristomium, enclosing the ventral mouth, may be formed of one to several fused segments which often lack parapodia and setae and are furnished with a variable number of tentacular or peristomial cirri. The prostomium and peristomium may be more or less fused, and are furnished with a pair of long grooved tentacular palps, ciliated nuchal organs, and a median caruncle extending posteriorly from the prostominm. In the sedentary or tube-dwelling forms, the prostomium may be indistinct and more or less hidden by other structures, such as numerous oral tentacles (Terebellidae, Ampharetidae), enlarged flattened setae or paleae (Amphictenidae, Sabellariidae), or an enlarged branchial plume (Sabellidae, Serpulidae). Usually, each segment following the peristomium is provided with paired parapodia in the form of fleshy lateral outgrowths bearing bundles of setae. When present, the parapodia are uniramous or biramous (dorsal notopodium and ventral neuropodium), and each is supported by a short rod or aciculum. In the burrowing and sedentary forms, the rami may be in the form of low ridges (tori) provided with rows of acicular hooks or

minute setae or uncini. The setae are extremely varied, slender or stout, smooth or dentate, and simple or compound, with basal stems and distal blades of various types. The parapodia may bear accessory structures, such as dorsal and ventral cirri, dorsal scales (Aphroditacea), flattened lobes or ligules (Nereididae), flattened plates or lamellae (Nephtyidae, Spionidae), or filiform or branched branchiae (Eunicidae). The pygidium, containing the dorsal anus, may be simple or may be provided with cirri or flattened

plates.

The epidermis of the body wall is often furnished with ciliated cells which form ciliated tracts and bands; they may set up currents of water, aiding in respiration, and bringing food-laden water and selected particles for tube construction to the mouth. In addition to the circular and longitudinal muscles of the body wall, there may be oblique and transverse muscles, complicated musculature associated with the tentacles and proboscis, and prominent parapodial and setal muscles. The circular muscle layer may be reduced or absent. Slow crawling movement is carried out by the parapodial muscles, rapid crawling and swimming by the parapodia and by undulations of the body which use the well-developed longitudinal muscle bundles. Burrowing may involve two types of anchors; the penetration anclior is a dilation of the upper part of the body that holds the worm against the burrow when the distal region is elongated by contraction of the circular or transverse muscles; this is followed by dilation of the distal region, forming the terminal anchor, which allows contraction of the longitudinal muscles to move the worm into the substrate. The two types of anchors are applied alternately until burial is complete. Polychaetes with elongate narrow bodies and poorly developed parapodia swim by means of undulations which pass along the body and exert a backward thrust against the water in a complex three-dimensional spiral motion or a lateral sinusoidal movement. Irrigation currents are often produced in hurrowing and tube-dwelling polychaetes by muscular means, such as undulations of the body in a dorsoventral plane, or pistonlike swellings which pass up or down the body.

Respiratory exchange takes place over the moist body surface, which may or may not be vascularized. A bloodvascular system is absent in small polychaetes. In larger polychaetes additional vascularized parapodial structures, such as the ligules in the nereidids, increase the surface for respiratory exchange. Special segmental filiform or branched branchiae may occur along most of the body, or they may be confined to the anterior end in tube-dwelling polychaetes. The elaborate branchial crowns in the sedentary polychaetes (Sabellida) serve both as respiratory and as filter-feeding organs. The blood-vascular system has disappeared in the glycerids, and the coelomic fluid functions in respiratory exchange; the septa are reduced, and the coelomic fluid, with hemoglobin-containing corpuscles, is circulated by ciliated tracts on the peritoneum and by movement of the body wall; there may also be coelomic branchial extensions on the parapodia. Respiratory pigments, such as hemoglobin, chlorocruorin, or hemerythrin, may be found in the blood plasma, in coelomic fluid, in corpuscles, and in tissues such as muscle and nerves.

The anterior part of the digestive tract varies greatly, according to the method of feeding and burrowing. In the mobile or burrowing polychaetes, the stomodaeum forms a protrusible proboscis, differing in structure and mode of operation. The most advanced tube dwellers lack a proboscis. The mouth opens into the buccal cavity, which may form a pharyngeal sheath which is lined with papillae. The muscular pharynx may have jaws and papillae. The jaws are formed of sclerotized protein, sometimes mineralized. The main everting force may be provided by contraction of the anterior body wall muscles or partly by specialized anterior septa acting on the coelomic fluid, sometimes supplemented by protractor and retractor muscles. The proboscis may be an eversible nonmuscular sac without jaws; it sometimes bears papillae and is often ciliated. The intestine is usually straight. It may be furnished with numerous paired ceca (Aphroditacea). The anus is generally terminal. Many polychaetes live in more or less permanent tubes which may be formed of hardened mucus, sometimes covered with foreign materials. They may be parchmentlike or calcareous.

The sexes are usually separate. Rarely species are sexually dimorphic. Hermaphrodites are known. Fertilization is often external, the sex products being given off into the water and a more or less extended larval development taking place in the plankton, followed by metamorphosis. At the time of reproduction, some polychaetes undergo changes of varying magnitude, including enlargement of the eyes, associated with greater sensitivity to light, enlargement of the parapodial lobes, addition of capillary setae or replacement of the usual setae with paddlelike swimming setae, and histolysis of the muscles of the body wall and digestive tract. They may become swarming epitokous adults. Polychaetes which do not spawn freely in the sea protect their young to varying degrees. The eggs may be attached to the body of the female in brood chambers, incubated in the parental tube, or laid in gelatinous masses and attached to the substratum; direct development follows. Viviparity is known for a few species. Some may reproduce asexually by fragmentation or fission.

This class includes 87 families, about 1000 genera, and over 8000 known species. The families are herein separated

into 25 orders and 6 superfamilies.

References. R. P. Dales, The polychaete stomodeum and the inter-relationships of the families of Polychaeta, Proc. Zool. Soc. London, 139:389-428, 1962; K. Fauchald, The polychaete worms: Definitions and keys to the orders, families and genera, Natur. Hist. Mus. Los Angeles Co. Sci. Ser., 28: 1-190, 1977; K. Fauchald and P. A. Jumars, The diet of worms: A study of polychaete feeding guilds, Oceanogr. Mar. Biol. Annu. Rev., 17:193-284, 1979; O. Hartman, Catalogue of the Polychaetous Annelids of the World, Allan Hancock Found. Publ. Occas. Pap. 23, 1959, 1965; P. C. Schroeder and C. O. Hermans, Annelida: Polychaeta, in A. C. Giese and J. S. Pearse (eds.), Reproduction of Marine Invertebrates, vol. 3, Academic Press, New York, 1975.

PHYLLODOCIDA

Species in this order have a body which consists of similar segments. The prostomium is distinct, usually with at least one pair of antennae, and often with ventral palps and eyes.

One to several peristomial or tentacular segments enclose the ventral mouth; they usually have tentacular cirri. The pharynx is eversible, muscular, and cylindrical, with or without one or two pairs of jaws. The parapodia are distinct and uniramous or biramous, supported by acicula and usually bearing dorsal and ventral cirri. These worms include errant, swimming, crawling, and burrowing forms.

The order contains 27 families, including 5 in the superfamily Phyllodocidacea (Phyllodocidae, Alciopidae, Lopadorrhynchidae, Pontodoridae, and Lacydoniidae) and 3 aberrant pelagic families (Iospilidae, Tomopteridae, and Typhloscolecidae); 2 in the superfamily Glyceracea (Gly-

ceridae and Goniadidae) and an aberrant family (Sphaerodoridae); 6 in the superfamily Nereididacea (Hesionidae, Pilargidae, Antonbruuniidae, Syllidae, Ichthyotomidae, and Nereididae); 2 in the superfamily Nephtyidacea (Nephtyidae and Paralacydoniidae); 6 in the superfamily Aphroditacea (Aphroditidae, Polynoidae, Polyodontidae, Pholoidae, Sigalionidae, and Eulepethidae) and 2 aberrant families (Chrysopetalidae and Pisionidae).

Phyllodocidacea

These worms are characterized by a distinct prostomium with two to five antennae. The tentacular segments (I-III) bear two to five pairs of tentacular cirri. The proboscis is eversible, cylindrical, and muscular, usually with marginal papillae and rarely with jaws. The parapodia are usually uniramous (rarely subbiramous or biramous), supported by acicula, with fan-shaped bundles of setae and foliaceous dorsal and ventral cirri. They are errant, crawling, and swimming forms.

This superfamily contains 5 families: Phyllodocidae, Alciopidae, Lopadorrhynchidae, Pontodoridae, and Lacydoniidae.

References. R. P. Dales, Pelagic polychaetes of the Pacific Ocean, Bull. Scripps Inst. Oceanogr. Univ. Calif., 7:99–168, 1957; R. P. Dales and G. Peter, A synopsis of the pelagic Polychaeta, J. Natur. Hist., 6:55–92, 1972; N. Tebble, The distribution of pelagic polychaetes across the North Pacific Ocean, Bull. Brit. Mus. (Natur. Hist.), 7:27–492, 1962; P. V. Uschakov, Polychaetes of the suborder Phyllodociformia of the Polar Basin and the northwestern part of the Pacific (families Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae, and Lacydoniidae); in Fauna of the U.S.S.R., vol. 1: Polychaetes, Acad. Sci. U.S.S.R. Zool. Inst. 102, 1974 (Eng. transl. of 1972 publ.).

Phyllodocidae. The body is elongate, slender, somewhat flattened dorsoventrally, and tapering posteriorly, with numerous similar segments (usually over 100, up to 700). The prostomium is subconical, suboval, or cordiform, with four frontal antennae and sometimes an additional median antenna (Eulalia, Eumida), usually with two eyes, and sometimes with a medial nuchal papilla (Phyllodoce) or paired nuchal epaulettes (Notophylum). The anterior one to three peristomial or tentacular segments, which enclose the ventral mouth, show varying degrees of fusion and bear two to four pairs of filamentous or spindle-shaped tentacular cirri; Eteone has two pairs of tentacular cirri on the first achaetous segment; Mystides has three pairs of tentacular cirri on two segments; Paranaitis has the first two segments fused and forming a collar with three of the four pairs of tentacular cirri; Phyllodoce has four pairs of tentacular cirri on three segments, with the first segment reduced dorsally. The proboscis is eversible, tubular, and muscular, and lacks jaws; there is a circlet of papillae around the opening; the proboscis surface is smooth or bears papillae which are distributed diffusely or in the form of longitudinal rows.

The parapodia are uniramous, with the podial lobes supported by a single aciculum, and with fan-shaped bundles of compound setae, the terminal blades tapering to fine tips (compound spinigers). The dorsal and ventral cirri, which emerge from short cirrophores, are flattened, leaflike, or more or less globular. The dorsal cirri may be large and overlapping, more or less covering the dorsum, as in *Noto-* phyllum. Exceptionally, the parapodia are subbiramous, the notopodia represented by additional notoacicula extending in the cirrophores of the dorsal cirri, with or without a few simple capillary notosetae, as in Notophyllum. Rarely, simple hooked setae are present on the anterior segment, as in Chaetoparia. The pygidium, containing the dorsal anus, has a pair of anal cirri.

The sexes are separate. Spawning adults may appear in great numbers on the surface of intertidal flats, showing a type of pseudocopulation, the males and females forming a ball of interlacing bodies. They lay numerous eggs in mucous cocoons anchored to the bottom, and these develop into trochophore larvae before emerging into the plankton. They may have a long pelagic existence. Some, such as Notophyllum, may deposit their eggs on the dorsal side of the body, where they are protected by the large overlapping dorsal cirri. Some, such as Eteone longa, become pelagic at sexual maturity and form modified epitokes, with additional long simple capillary setae mixed with the compound spinigers.

The family contains about 30 genera and 300 species. The phyllodocids are very common in shallow water, associated with hard bottoms. They are very active, moving freely on the surface, and they secrete large amounts of mucus. Some, such as *Eteone*, burrow in soft mud. They are primarily carnivorous; some are known to be bottom deposit feeders. They are widely distributed, from low water to great depths.

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Alciopidae. The body is relatively short and broad (Alciopa) or long, slender, and cylindrical, with numerous segments (up to 270, as in Torrea). Members of this family have regularly arranged pigmented glands which may be associated with pigmented bands (Vanadis) or large pigmented glandular lobes at the bases of the parapodia (Alciopa). The prostomium consists of a small lobe with usually five antennae (four frontal and one medial, sometimes reduced to a rounded tubercle) and a pair of enormous, spherical, highly organized telescopic eyes with large lenses which are directed laterally and capable of extensive vision. The ventral mouth is enclosed by three achaetous tentacular segments which have three to five pairs of tentacular cirri. The proboscis is eversible and cylindrical, bearing marginal papillae and lacking jaws; it may be relatively short (Rhynchonereela) or very long, with two long lateral cirriform appendages for grasping prey (Torrea, Vanadis, Alciopa). Some anterior segments may have rudimentary parapodia (Vanadis).

The parapodia are uniramous; the podial lobes are

long, subconical, and supported by acicula, and sometimes have a single distal cirriform appendage (Rhynchonereela) or two cirriform appendages (Alciopa). The setae form fanshaped bundles of simple capillaries (Naiades) or of compound spinigers (Torrea); or the setae may be of several kinds (Watelio). The dorsal and ventral cirri are large and foliaceous. The pygidium, containing the dorsal anus, has one or two anal cirri.

The sexes are separate. Some of these worms are sexually dimorphic (Alciopa); in the females, the dorsal cirri on segments IV-VI are modified to form large pockets or sperm receptacles; the males have long genital papillae on corresponding segments. Pseudocopulation takes place when the males agglutinate the sperm into a kind of spermatophore and transfer them to the females, where they are stored in the sperm receptacles until required. The young of Alciopina parasitica live parasitically in the pelagic ctenophore Cydippe. The alciopids are rapid swimmers and carnivorous.

This pelagic family contains 9 genera and about 35 species. They occur mainly in the open ocean, chiefly in warm tropical waters. Some species have a very wide distribution.

References. J. H. Day, Family Alciopidae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 172-195, 1967; M. H. Pettibone, Family Alciopidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 91-94, 1963; P. V. Uschakov, Family Alciopidae, in Fauna of the U.S.S.R., vol. 1: Polychaetes, 1. Acad. Sci. U.S.S.R. Zool. Inst. 102, pp. 185-201, 1974 (Eng. transl. of 1972 publ.).

Lopadorrhynchidae. The body is short, flattened, spindleshaped, and semitransparent, with relatively few segments (up to 35). The prostomium is small, with four frontal antennae, sometimes with a pair of nuchal organs, and with or without a pair of small eyes. The prostomium is partly or completely fused with the first or peristomial segment, which has the ventral mouth and two pairs of tentacular cirri (Pedinosoma, Pelagobia), or it may also be fused with the second segment, which has three pairs of tentacular cirri (Lopadorrhynchus, Maupasia); bundles of long setae may be found on the tentacular segment (Pelagobia, Maupasia). In Lopadorrhynchus, the following two segments are enlarged and have modified parapodia bearing large simple hooked setae. The proboscis is eversible and short, with or without papillae, and usually without jaws (with a pair of chitinous styletlike hooks in Pelagobia).

The parapodia are uniramous; the podial lobes are subconical and supported by an aciculum, with fan-shaped bundles of compound setae. The setal blades are oarshaped or spinigerous. The dorsal and ventral cirri are short and conical (in *Lopadorrhynchus*), elongate and digitiform (in *Pelagobia*), or wide and foliaceous (in *Maupasia*, *Pedinosoma*). The pygidium, with the terminal anus, is semicircular and may or may not bear a pair of short anal cirri.

The family includes 4 genera and 16 species. Lopadorrhynchids are exclusively pelagic, probably carnivorous, and widely distributed.

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Pontodoridae. Pelagic family with a single species, Pontodora pelagica. The body is small, slender, and transparent,

with relatively few segments (up to 20). The prostomium is small, rounded, and fused with the first two achaetous segments; it has two antennae, two pairs of tentacular cirri, a pair of small eyes, and a ventral mouth. The proboscis is eversible, short, muscular, and barrel-shaped, with papillae around the opening and on the surface. The parapodia are uniramous; the podial lobes are subconical, supported by an aciculum and extending into a very long digitiform appendage, with fan-shaped bundles of numerous long slender compound setae with spinigerous blades. The dorsal and ventral cirri are small, oblong-oval, and flattened. The pygidium, which contains the dorsal anus, has a pair of long anal cirri.

The pontodorids are carnivorous and are widely distributed in the colder waters of the Pacific and subtropical

References. J. H. Day, Family Pontodoridae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 167–169, 1967; P. V. Uschakov, Subfamily Pontodorinae, in Fauna of the U.S.S.R., vol. 1: Polychaetes, Acad. Sci. U.S.S.R. Zool. 11st. 102, pp. 183–184, 1974 (Eng. transl. of 1972 publ.).

Lacydoniidae. Monogeneric (Lacydonia) family with 4 species. The body is small and linear, with relatively few segments. The prostomium is oval, with two pairs of small subterminal antennae and a pair of ciliated nuchal organs; a small median antenna in the middle of the prostomium and a pair of large eyes may be present or absent. The peristomium or tentacular segment, which encloses the ventral mouth, is distinctly set off from the prostomium; it is achaetous, with a pair of small tentacular cirri. The pharynx is eversible, short-cylindrical, and muscular, with marginal papillae and without jaws. The anterior two or three setigerous segments are uniramous, with neuropodia only. The following parapodia are biramous, with the rami supported by acicula, and with fan-shaped bundles of setae. The rami may be subequal, or the notopodia may be smaller than the neuropodia. The notosetae are simple and capillary; the neurosetae, compound and spinigerous. The dorsal and ventral cirri are small, flattened, leaflike (as in Phyllodocidae), and attached subdistally on the rami. Presetal and postsetal lobes, as well as branchiae, are lacking. The pygidium, with the dorsal anus, is small and rounded and usually bears three short anal cirri.

The lacydoniids are known from a few scattered records from the Mediterranean, the North Atlantic, the northwest Pacific, and the Antarctic, from intertidal zones to abyssal depths.

References. L. Laubier, Lacydonia laureci sp. n., Annelide Polychete nouvelle de l'étage abyssal de Méditerranée orientale, Vie Milieu. 25A:75-82, 1975.

lospilidae (aberrant family)

The body is semitransparent, slender, and short, with a moderate number of segments (up to 60); segmental lines are poorly indicated. The prostomium is small, with two short ventral antennae (palps) and with or without two small eyes; it is fused with the first achaetous segment, which bears two pairs of short tentacular cirri and the ventral mouth. The proboscis is eversible, large, muscular, and sometimes armed with a pair of large chitinous curved hooks (in *Phalacrophorus*). A variable number of anterior segments have reduced parapodia: up to 4 in *Iospilus* and *Paraiospilus*, and up to 10 or 11 in *Iospilopsis* and *Phalacrophorus*. The parapodia are uniramous, with conical podial lobes supported by an aciculum, and with fan-shaped bundles of

long slender compound setae with spingerous blades. The dorsal and ventral cirri are small and rounded. The pygidium is rounded and contains the terminal anus.

The aberrant family includes 4 genera and 7 species. Iospilids are exclusively pelagic and carnivorous; they are

widely distributed in the Atlantic and the Pacific.

References. J. H. Day, Family Iospilidae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 168-171, 1967; P. V. Uschakov, Subfamily Iospilinae, in Fauna of the U.S.S.R., vol. 1: Polychaetes, Acad. Sci. U.S.S.R. Zool. Inst. 102, pp. 183-184, 1974 (Eng. transl. of 1972 publ.).

Tomopteridae (aberrant family)

This pelagic family comprises a single genus, Tomopteris, and about 45 species. The body is transparent, flattened, and widest in the anterior region, tapering posteriorly; it lacks distinct segmental lines and septa and is composed of a moderate number of segments (up to 40). The prostomium is fused with the first two tentacular segments; it has a pair of flattened anterior antennae directed laterally (frontal horns), a pair of deep-set eyes, a pair of ciliated nuchal organs, two pairs of tentacular cirri supported by slender acicula, and the ventral mouth. The first pair of tentacular cirri is short; this pair may be absent or present only in juveniles. The second pair of tentacular cirri, originating from broad subconical bases, extends posteriorly and may be nearly as long as or longer than the body. The proboscis is eversible, short, and unarmed. The parapodia are biramous, with elongated bases and diverging conical notopodial and neuropodial rami, bordered with flattened, finlike, oval membranous plates or pinnules; they lack acicula or setae. The pinnules bear glands of various kinds: rosette organs, hyaline glands, phosphorescent chromophile glands in the neuropodial fins, and spur glands. The posterior end may form a slender cylindrical tail region, with rudimentary parapodia. The pygidium, which encloses the terminal anus, lacks appendages.

The sexes are separate. The tomopterids swim with great swiftness by means of rapid vibrations of the lateral finlike parapodia, darting through the water in all directions. The long tentacular cirri regulate balance and floating. The tomopterids may migrate daily, rising to the surface at night. They are voracious predators in the plankton, widely distributed, and may at times be the dominant form.

References. J. H. Day, Family Tomopteridae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 196-206, 1967; M. H. Pettibone, Family Tomopteridae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mns. 227, pp. 94-98, 1963; P. V. Uschakov, Family Tomopteridae, in Fauna of the U.S.S.R., vol. 1: Polychaetes. Acad. Sci. U.S.S.R. Zool. Inst. 102, pp. 201-208, 1974 (Eng. transl. of 1972 publ.).

Typhloscolecidae (aberrant family)

The body is short, cylindrical, spindle-shaped, and transparent, with relatively few (up to 50) segments. The prostomium is subconical or rounded, and usually extended anteriorly in a slender palpode; it lacks appendages or eyes, but bears a pair of prominent ciliated nuchal organs of variable form, and sometimes a projecting medial papilla or caruncle (in Travisiopsis). In Typhloscolex, the prostomium has large dorsal and ventral transverse ciliated ridges which form a high fringe and function as a rotatory apparatus, allowing the worm to float vertically in the water. Sagitella lacks both a projecting caruncle and ciliated ridges. The

anterior three tentacular segments, which enclose the ventral mouth, are fused to the prostomium and provided with three pairs of foliaceous, spoon-shaped tentacular cirri that are curled anteriorly and enclose the anterior end of the body. The proboscis is eversible, short, and unarmed, with

a glandular retort-shaped organ.

The parapodia are uniramous, with the setal lobes much reduced and only slightly projecting; they are supported by short acicula and have a few (one to three) short simple needlelike setae. In the anterior part of the body the setae are almost totally absent. The dorsal and ventral cirri are large, foliaceous, and nearly square-shaped in the middle part of the body, becoming elongate-lanceolate posteriorly; they function as rowing organs. The pygidium contains the dorsal anus and has a pair of foliaceous anal cirri. The posterior end evidently forms an effective swimming organ.

This aberrant pelagic family contains 3 genera and about 15 species. The typhloscolecids include widely distributed,

mostly deep-sea, pelagic oceanic forms.

References. J. H. Day, Family Typhloscolecidae, in A Monograph of the Polychaeta of Southern Africa, pt. 1: Errantia. Brit. Mus. (Natur. Hist.) 656, pp. 207-213, 1967; M. H. Pettibone, Family Typhloscolecidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 98-101, 1963; P. V. Uschakov, Family Typhloscolecidae, in Fauna of the U.S.S.R., vol. 1: Polychaetes, Acad. Sci. U.S.S.R. Zool. Inst. 102, pp. 208-213, 1974. (Eng. transl. of 1972 publ.).

Glyceracea

The long cylindrical body tapers toward both ends. The prostomium is elongated, conical, and transversely annulated, with four minute antennae in the distal ring. The achaetous peristomium is fused with the basal ring of the prostomium and the anterior few setigerous segments, forming the ventral mouth; tentacular cirri are lacking. The pharynx or proboscis is long and eversible, with jaws and papillae. The parapodia are uniramous or biramous, supported by acicula; the neuropodia have variously developed presetal and postsetal lobes. The notosetae are simple, capillary, or acicular; the neurosetae are compound spinigerous or falcigerous. Dorsal and ventral cirri are short and conical. The pygidium has a pair of anal cirri. The glyceraceads are active burrowers in soft bottom. This superfamily has 2 families: Glyceridae and Goniadidae.

Glyceridae. The body is long, cylindrical, and fusiform, tapering gradually toward both ends, and with biannulate or triannulate segments. The prostomium is sharply conical, longer than wide, and obscurely transversely annulated; the distal ring of the prostomium has four minute, usually biarticulate antennae (the prostomium is wider, with fewer annuli and rather long, nonarticulate antennae, in Glycerella). The prostomium may or may not have minute eyes in the basal and distal rings. The peristomium is more or less fused with the larger basal ring of the prostomium and the anterior few setigerous segments; it has a pair of nuchal organs and a ventral mouth. The eversible pharynx or proboscis is very long, clavate, and strongly muscular, armed distally with four large, dark, hooked, horny jaws, each with an attached rodlike jaw support or aileron; the surface is covered with numerous small, oval and subconical papillae which give it a velvety aspect (the papillae are long and slender in Glycerella).

There are numerous similar body segments with small uniramous (Hemipodus) or biramous (Glycera, Glycerella) parapodia. In the biramous parapodia the rami are indis-

tinctly separated, appearing as a common lobe supported by two needlelike spines (acicula), with variously developed presetal and postsetal lips. The notosetae are simple, thin, and capillary; the neurosetae are compound spinigerous (Glycera. Hemipodus) or compound falcigerous (Glycerella). The dorsal cirri are small and globular, and sometimes inserted well above the parapodia; the ventral cirri are elongate and conical. The branchiae, when present, are thinwalled coelomic extensions which may be saclike or digitiform, stationary or retractile, and simple or branched. There is no true blood-vascular system; the coelomic fluid, containing red blood corpuscles, is freely propelled through the coelomic spaces (including the eversible proboscis and branchiae, when present), giving a pinkish to reddish color to the body. This is the origin of the common name bloodworm. The pygidium is small, with a minute anus and a pair of anal cirri.

The sexes are separate. Spawning occurs when sexually mature worms leave their burrows and either move along the bottom or swim actively at the surface. The body undergoes varying degrees of epitoky: the parapodial lobes are elongated; the setae are elongated and augmented in number, with the addition of some simple setae; the proboscis degenerates and is cast off; and there is atrophy of the intestine and some muscles of the body wall, so that the body becomes a veritable sac filled with sex products which escape through the mouth. The adults die after spawning. Fertilized eggs develop into nectochaete larvae which apparently stay near the bottom, as they are seldom collected in surface plankton.

These worms are active burrowers, found in sandy or muddy bottoms; they seldom appear at the surface except for swarming at the time of reproduction. They shoot out their powerful proboscis with considerable force to aid in hurrowing. Their powerful muscular system allows them to coil in the shape of an open spiral and rotate rapidly with a screwlike motion. They are detritus feeders; food is taken by everting the proboscis, and the large jaws are used to grasp particles; indigestible material is thrown off from the mouth.

The family consists of 3 genera and about 75 species of worldwide distribution. Species are found in all depths; they are common in estuaries. The bloodworm Glycera dibranchiata serves as a commercially valuable marine baitworm in the Maritime Provinces and Maine.

References. M. H. Pettibone, Family Glyceridae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 209-218, 1963.

Goniadidae. Species in this family have a body which is small to large, long, slender, and cylindrical, tapering toward both ends, with numerous segments (up to 300). The segments are uniannulate. The body is usually divided into two regions; the shorter anterior region, with uniramous parapodia; and the longer and usually wider posterior region which has biramous parapodia with well-separated rami. An intermediate transitional region in which the notopodia develop gradually may or may not be present. Rarely the parapodia are all uniramous (Progoniada, Progoniadides). The prostomium is elongated, conical, and transversely annulated, with four very small antennae on the distal ring; it bears a pair of nuchal organs and may or may not have paired minute eyes in the basal and distal or subdistal rings. Rarely the prostomium is short, ovoid, and without antennae (Ophioglycera). The basal prostomial ring, achaetous peristomium, and anterior few setigerous segments are more or less fused and involved in the ventral mouth. The pharynx is very long and tubular, extending through the anterior region of the body; it is eversible, and the distal end has a circlet of soft papillae, a pair of large jaws, and dorsal and ventral arcs of small clawlike teeth. The surface of the proboscis is covered with small papillae or proboscidial organs of various types: all may be similar, or there may be several longitudinal rows of horny spines of remarkable diversity (Glycinde, Bathyglycinde); sometimes there are additional dark horny V-shaped jaw pieces (so-called chevrons) arranged bilaterally on the basal part of the pharynx (Goniada, Goniadella).

The neuropodia, which are supported by one or two acicula, are variously divided into presetal and postsetal lobes; they are much larger and more foliaceous in the biramous regions than in the uniramous regions; the conical ventral cirri are closely united with the neuropodia. The fanshaped bundles of neurosetae are either all compound spinigerous or both compound spinigerous and falcigerous. When present, the notopodia are more or less developed and irregularly lobed, supported by two to four slender acicula, and closely united with the conical dorsal cirri; the notosetae are simple, numerous, and capillary, or few in number and acicular. Branchiae are lacking. The pygidium is minute and tubular, with a pair of anal cirri.

The sexes are separate. When mature, the goniadids may become modified into epitokous swimming forms: the posterior regions become distended with sex products, and the neuropodial lobes become more elongate, with large spreading tufts of simple setae crowded among the compound neurosetae. Developing larvae appear in the plankton.

The family consists of 10 genera and about 75 species. The goniadids are active and predacious and burrow in soft bottoms. They are widely distributed from shallow water to great depths.

References. M. H. Pettibone, Family Goniadidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, 1963.

Sphaerodoridae (aberrant family)

These worms have a body which may be either short, thick, and grub-shaped, with relatively few (up to 30) segments, or long and slender, with more numerous segments (up to 120). The body segmentation is indistinct, except as marked by the parapodia. The integument is more or less covered with globular and filiform papillae. In addition, large spherical glandular capsules or macrotubercles are present. Two macrotubercles per segment, each with a long terminal papilla, may be found dorsal to the parapodia (Sphaerodorum, Ephesiella); or rounded macrotubercles without long terminal papillae may be found dorsally in numbers of four or more per segment (Sphaerodoridium, Commensodorum); they may encircle the dorsum in transverse rows in line with the parapodia, 10-14 per row (Sphaerodoridium minutum). The prostomium, peristomium or tentacular segment, and the first setigerous segment, with the ventral mouth, are not clearly separated; they are covered with papillae, some of which are larger and resemble antennae and tentacular cirri. Subdermal eyes, two to four in number, may be present. The first setigerous segment usually has a pair of stout, curved, hooked setae. The pharynx is unarmed, eversible, smooth, and short-globular or long-cylindrical. The parapodia are uniramous, short, subconical, papillate, and supported by acicula. Some longer papillae may appear as presetal or postsetal lobes and ventral cirri. The setae may be all simple, and slightly hooked (Sphaerodorum, Commensodorum) or compound, with blades short to longer (Ephesiella, Sphaerodoridium). The pygidium has a median papilla and a pair of globular capsules. The sexes are separate. Females may be filled with

large yolky eggs with thick tough shells.

This aberrant family contains only 4 genera with about 55 species. The sphaerodorids are slow, crawling forms which burrow in mixed bottoms, mostly ranging from subtidal regions to great depths. Mature specimens may appear in surface waters. The widely distributed Sphaerodorum flavum (=Ephesia gracilis) is found intertidally, as well as in deeper water.

References. K. Fauchald, Sphaerodoridae (Polychaeta, Errantia) from world-wide areas, J. Natur. Hist., 8:257-289, 1974; M. H. Pettibone, Family Sphaerodoridae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 205-208, 1963.

Nereididacea

Superfamily whose members are characterized by an elongated cylindrical body with numerous similar segments. The prostomium and peristomium are distinct or more or less fused, bearing antennae, palps, and tentacular cirri. The pharynx is muscular and eversible, often with papillae or simple jaws. The parapodia are well developed, supported by acicula; they may be uniramous, subbiramous, or biramous, with dorsal and ventral cirri. The setae are simple or compound. The pygidium encloses the dorsal anus and has anal cirri.

This superfamily contains 6 families: Hesionidae, Pilargidae, Antonbruuniidae, Syllidae, Ichthyotomidae, and Ncreididae. They include active, crawling or burrowing, errant forms. The aberrant family Ichthyotomidae includes external parasites.

Hesionidae. These are small to moderate-sized worms, flattened dorsoventrally and tapered slightly anteriorly and posteriorly, with segments deeply incised, often conspicuously and brilliantly colored. The prostomium is suboval to subquadrangular, sometimes with a posterior notch; it has two or three antennae (rarely none), may or may not have a pair of ventral palps with one to three articles, and usually has two or four eyes (rarely none). The peristomium and few (one to four) anterior achaetous segments show varying degrees of fusion with the prostomium; each segment is provided with two pairs of filiform tentacular cirri (for a total of two to eight pairs) having distinct cirrophores with internal notoacicula. The tentacular segments enclose the ventral mouth; the upper lip may be provided with a conical facial tubercle (Leocrates). The pharynx is cylindrical, muscular, and eversible; it may or may not have few to numerous marginal papillae or fimbriae and horny

The parapodia may be uniramous; or they may be subbiramous, with the notopodia reduced to notoacicula within the cirrophores of the dorsal cirri, sometimes with a few capillary notosetae; or they may be biramous, with the rami equally well developed or with the notopodium forming a distinct lobe on the lower side of the dorsal cirrophore. When present, the notosetae are all simple, capillary or falcate spines. The neurosetae are compound falcigerous or spinigerous, with the terminal blades long to short; there may be some additional simple neurosetae. The dorsal cirri are short to long, and smooth or more or less distinctly articulated. The ventral cirri are short. The pygidium has a

terminal anus, a pair of anal cirri, and sometimes a flattened disk or bilobed plate.

The sexes are usually separate. Swarming at the surface may occur. Large yolky eggs may be laid in mucous masses. The larvae have a relatively short pelagic life. Some small interstitial forms (Microphthalmus, Hesionides) are hermaphroditic; some have complicated male copulatory organs and may form spermatophores.

At least some hesionids are carnivorous. They are highly active and irritable, tending to be fragile and to fragment easily. Some swim readily. A number of hesionids show commensalistic tendencies associated with echinoderms such as starfish, sea cucumbers, and sea urchins; they are found in the burrows of the ghost shrimp (as in *Upogebia*) and of the orbiniid polychaete (as in *Scoloplos robustus*).

The family consists of 31 genera and about 130 species. The hesionids are common in shallow water, and more rarely are found in deep water. They occur in sand or sandy mud and on hard substrates. Some are circumtropical to subtropical and associated with coral reefs (Leocrates chinensis).

References. M. H. Pettibone, Family Hesionidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 101-109, 1963; M. H. Pettibone, Family Hesionidae, in Polychaeta Errantia of the Siboga-Expedition, pt. 4 of Siboga-Expedition, 24, ld, pp. 212-232, 1970.

Pilargidae. The body is cylindrical and somewhat depressed, or long, flattened, and ribbonlike, tapered anteriorly and posteriorly, with the parapodia distinct. Some forms are long and threadlike, with the anterior segments inflated and the parapodia inconspicuous. The integument may be smooth or papillated. The prostomium, peristomium, and first setigerous segment may be more or less fused. The prostomium is small, usually with two or three antennae (these may be very small or absent); when present, the median antenna is on the posterior part of the prostomium; the prostomium also bears a pair of simple or biarticulated palps, consisting of large palpophores, more or less set off from the prostomium, and small buttonlike palpostyles; it sometimes is provided with a pair of small eyes. The achaetous peristomium or tentacular segment has two pairs of tentacular cirri (rarely a single pair or none). The dorsal cirri of the first setiger are often longer than the following ones. The ventral mouth is enclosed in the above two segments. The pharynx is eversible, muscular, and bulbous or cylindrical, usually with a circlet of papillae around the opening; it lacks jaws.

The parapodia are usually well developed (poorly developed in Cabira and Litocorsa) and subbiramous. The notopodia are reduced to embedded notoacicula in the cirrophores of the dorsal cirri, sometimes with additional capillary setae or emergent stout acicular setae which may be straight or strongly hooked; the neuropodia are subconical, with embedded neuroacicula and simple neurosetae which may be capillary or slightly hooked, smooth or spinous. Dorsal cirri are usually present; they are long or short, and conical, ovate, or lamelliform. The ventral cirri are short and tapered or lamelliform. Gills are lacking. The pygidium has a terminal anus and two or three anal cirri (rarely none).

The sexes are separate. The larvae are rarely collected in the plankton. The pilargids are found burrowing in sand or sandy mud, from intertidal zones to great depths. They burrow actively through the sediment and are predators or scavengers. Ancistrosyllis commensalis has been found as a commensal in the burrow of a capitellid polychaete (Notomastus lobatus).

The family consists of 10 genera and about 50 species, forming a rather aberrant and heterogeneous group.

References. T. H. Pearson, Litocorsa stremma, a new genus and species of pilargid (Polychaeta: Annelida) from the west coast of Scotland, with notes on two other pilargid species, J. Natur. Hist., 4:69-77, 1970; M. H. Pettibone, Revision of the Pilargidae (Annelida: Polychaeta), including descriptions of new species, and redescription of the pelagic Podarmus ploa Chamberlin (Polynoidae), Proc. U.S. Nat. Mus., 118(3525):155-208, 1966.

Antonbruuniidae. Family represented by a single species, Antonbruunia viridis, allied to the Pilargidae. The body is moderate in length, depressed, and tapering anteriorly and posteriorly. The prostomium is oval to squarish, with five short filiform appendages (a pair of frontal antennae, a median dorsal antenna, and a pair of ventral palps); eyes are lacking. The peristomium or tentacular segment is achaetous; it bears two paris of short tentacular cirri and encloses the ventral mouth. The pharynx is eversible, short, and cylindrical, with a circlet of a few papillae around the opening; jaws are lacking.

The parapodia are essentially uniramous, the notopodia being represented by embedded notoacicula in the bases of the short dorsal cirri. The neuropodia are well developed, with embedded neuroacicula; they are short, broad, and distally truncate, directed laterally in the anterior region and more ventrally in the posterior region. The neurosetae are simple and distally bifid, with a larger falcate tooth and a more slender, straight secondary one. The ventral cirri are short. The pygidium bears the terminal anus and a pair

of rather long anal cirri.

Antonbruunia viridis is found living commensally in the mantle cavity of the bivalve mollusk Lucina fosteri, collected in the Mozambique Channel; a single sexual pair occurs per host. The males are about half the size of the females.

References. K. Fauchald, Family Antonbruunidae, new name, in The Polychaete Worms Definitions and Keys to the Orders, Families and Genera, Natur. Hist. Mus. Los Angeles Co. Sci. Ser. 28, p. 91, 1977; O. Hartman and K. J. Boss, Antonbruunia viridis, a new inquiline annelid with dwarf males, inhabiting a new species of pelecypod, Lucina fosteri, in the Mozambique Channel, Ann. Mag. Natur. Hist., (13)8: 177-186, 1965.

Syllidae. The body is of small to medium size, linear, flattened ventrally and arched dorsally, tapering slightly anteriorly and posteriorly, with few to numerous segments; some forms are exceedingly tiny and threadlike. The integument is smooth or furnished with adhesive papillae. The prostomium is suboval, with three antennae (rarely one or none), a pair of subconical palps which may be reduced or fused, and two or three pairs of eyes. The achaetous peristomial ring encloses the ventral mouth and has one or two pairs of tentacular cirri (rarely none) and sometimes a pair of nuchal epaulettes that may extend on some anterior segments, or a semicircular nuchal hood which covers the posterior part of the prostomium. The pharynx is eversible; it has a smooth chitinous lining, and is sometimes armed with a single dorsal tooth or a circlet of teeth; it may or may not have a ring of papillae.

The parapodia are uniramous, subconical, and supported by neuroacicula. The setae are mostly compound, with short to long blades; they may be secondarily fused. Addi-

tional simple setae are sometimes present. The dorsal cirri are short or long, smooth, and faintly or distinctly annulated. The ventral cirri are short (rarely absent). The pyidian has two or three and cirri

gidium has two or three anal cirri.

The sexes are separate. Reproduction is extremely varied and may be rather complex. It may be direct (epigamy), as in Odontosyllis, in which mature adults become transformed into epitokes, the whole animal being modified in the process: the eyes are enlarged, long swimming setae develop in newly formed notopodia on a number of segments, and the body is filled with sex products and often becomes luminescent. The epitokes may leave the bottom and swarm in surface waters; the eggs and sperm are given off into the water and develop into pelagic larvae. In some forms, as in Exogone, Brania, and Sphaerosyllis, large yolky eggs are attached to the surface of the female, where they are fertilized and develop into advanced young of five or six segments, resembling the adults. Reproduction may take place indirectly by the asexual formation of stolons: a variable number of posterior segments become modified to form a sexual stolon in which the segments become massed with sex products; long swimming setae develop in newly formed notopodia, and a newly formed head, with four large eyes and various appendages, develops in the anterior part. Stolons may be produced singly or in chains, and they break off from the stem form, the latter regenerating a new posterior end. The male and female stolons may be similar (chaetosyllis stage), as in Syllis, with the head appendages poorly developed; pelagic larvae develop. In some forms, such as Autolytus and Proceraea, the stolons are sexually dimorphic, with well-developed head appendages; the males (polybostrichus stage) have large forked palps; the females (sacconereis stage) have large yolky eggs which are carried in large ventral sacs in which the embryos pass through their early developmental stages.

The syllids are very common shallow-water forms, most numerous on hard substrates. They are carnivorous and live on sponges, hydroids, ascidians, and so forth. They are a large and diverse group of small active worms found creeping on sponges, hydroids, corals, bryozoans, ascidians, and algae. Some live interstitially in sandy and silty bottoms. Some form hardened mucous tubes attached to hydroids. The small grublike aberrant Calamyzas amphictenicola is found as an ectoparasite on the gills of some ampharetid

polychaetes.

The family consists of about 60 genera and 600 species.

References. J. H. Day, Family Syllidae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 233-287, 1967; M. H. Pettibone, Family Syllidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 112-148, 1963.

Ichthyotomidae. Aberrant nereididacead family with a single species (Ichthyotomus sanguinarius) which is an external parasite of eels. The body is elongated, flattened, and slightly tapered posteriorly; it is small (up to 10 mm), with numerous short segments (up to 90). The prostomium is rounded and bears rudimenary papillar appendages consisting of a double-lobed median antenna and a pair of ventral palps. A pair of ciliated sensory organs opens anteriorly, and a pair of small eyes is located on the brain. The peristomium, with the subterminal mouth, forms an oral cone that is capable of being protracted beyond the prostomium and retracted to form a cup-shaped oral sucker. The muscular pharynx has a pair of unique, articulating, scissorlike jaws, each formed of a distal spoonlike stylet

provided with recurved teeth, a middle articulating joint, and a bifurcated basal stem for muscle attachment. When the oral cone is protracted, the stylets project from the opening, pierce the skin of the eel, and attach firmly; then the worm uses its muscular pharynx to suck the blood of the host, which passes into dorsal and ventral hemophilic pharyngeal glands. The peristomium bears the first parapodia, which are each provided with short dorsal and ventral tentacular cirri.

The parapodia are subbiramous. The notopodium is represented by a notoaciculum within the large cylindrical cirrophore of the dorsal cirrus, with a short distal style; the neuropodium is rounded, supported by a neuroaciculum, with a distal stylode and a few setae. The neurosetae are all compound and have three types of blades: spinigerous, short pectinate-tipped, and denticulate hooked. The ventral cirri are large and tapered, with spinning glands opening at the tip, serving to attach the parasite to the host. There are no branchiae, but the dorsal and ventral cirri and podial lobes are strongly ciliated. The pygidium is rounded, with a terminal anus, a ciliated crenulate dorsal lobe, and a pair of long anal cirri.

The sexes are separate. Small-sized young are found on the host. Ichthyotomus sanguinarius is known from the Mediterranean (Naples), where it is found on the fins of several species of eels.

References. H. Eisig, Ichthyotomus sanguinarius, eine auf Aalen schmarotzende Annelide, Fauna Flora Sta. Zool. Naples Monogr. 28, 1906.

Nereididae. Worms in this family have an elongate cylindrical body which is attenuate posteriorly. The prostomium is suboval to subpyriform (the frontal margin is sometimes incised, as in Ceratocephale); it bears two frontal antennae, two ventral biarticulate palps (the appendages are sometimes lacking or poorly developed, as in Micronereis), and four eyes (rarely none). The peristomium is a single long apodous segment (it may be indistinct and fused with the prostomium, as in Micronereis), with three or four pairs of tentacular cirri. The strongly muscular pharynx is eversible; it is differentiated into oral (proximal) and maxillary (distal) rings and terminates distally with a pair of horny falcate jaws whose concave side is smooth or serrated. The surface of the pharynx may be naked (Nicon) or provided with soft papillae (Ceratocephale, Laeonereis), small comblike denticles or pectinae (Platynereis), or conical denticles or paragnaths (Nereis).

There is a moderate to large number of body segments, which are somewhat variable in development along the length of the body. The first two segments are uniramous. The following parapodia are usually biramous, subbiramous (with a notoaciculum only, as in Lycastopsis), or uniramous (Namanereis) with dorsal and ventral cirri (the ventral cirri are sometimes double, as in Ceratocephale) and with varying degrees of development of extra tonguelike extensions or ligules (sometimes lacking, as in Lycastopsis). Some notopodial ligules are expanded, foliaceous, and highly vascularized, serving as branchiae. Rarely, more definite branchial filaments occur, as in Dendronereis and Dendronereides.

The setae are compound spinigers and falcigers; the shafts usually show characteristic chambering; rarely there are some simple falcigerous neurosetae in the posterior segments. The pygidium encloses the terminal anus and bears a pair of anal cirri.

The sexes are usually separate; species are rarely hermaphroditic (Nereis limnicola). They show diverse modes of

reproduction. Sometimes they reproduce in an unmodified atokous stage, with males and females paired in the tube, and eggs laid in the tube, and incubated by the male [Nereis acuminata (=N. arenaceodentata; N. caudata)]; there may be pseudocopulation, with eggs developed in the tube (N. diversicolor); other species may be internal self-fertilizing hermaphrodites, reproducing viviparously [N. limnicola $(=N. \ light)$], slightly modified epitokes (N. urens). or markedly modified epitokes or heteronereids which swarm in surface waters and give off sex products into the water (N. succinea); rarely species reproduce by internal fertilization (Platynereis megalops). Fertilized eggs develop into planktogenic nectochaete larvae. Heteronereids are sexually dimorphic, with extremely enlarged eyes, associated with sensitivity to light; the parapodia of a large region of the body are modified by the extra development of thin foliaceous lamellar plates and the replacement of the usual setae with flattened paddlelike swimming setae; specialized pygidial structures develop in males; extensive histolysis of the muscles of the body wall and digestive tract occurs. Heteronereids die after spawning. Some small forms, such as Micronereis, are sexually dimorphic and show pairing, with eggs deposited in jelly masses attached to vegetation and protected by the female.

Members of this family are typically free-living; they are found on algae or in crevices and burrows where they construct mucous tubes or galleries; the tubes may be formed of threads and incorporated algae, as in *Platynereis*, or secreted mucous material may consolidate the burrow wall, as in Neress. Their general pattern of activity centers around the tube or burrow, from which they extend out and withdraw rapidly. Aggressive behavior and defense of their tubes have been observed in some species. Some species, such as N. fucata and Cheilonereis cyclurus, have been lound living as commensals in snail shells occupied by hermit crabs, and N. grayi has been found in the elongate muddy tubes of the maldanid polychaete Asychis elongatus. These worms may leave the bottom and swim for long distances, not always for the purpose of reproduction. They may be herbivorous, carnivorous, or omnivorous feeders; a modified filter feeding has been observed in N. diversi-

The family contains about 37 genera and 450 species. Members are worldwide in distribution and common in all depths. Species are predominantly marine but are also found in estuaries and freshwater. The sandworm N. virens serves as an important commercial baitworm in Maine. The Japanese palolo, Tylorrhynchus heterochaetus, sometimes becomes a pest in rice fields.

References.M. H. Pettibone, Family Nereidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 148-183, 1963; M. H. Pettibone, Revision of some species referred to Leptonereis, Nicon, and Laeonereis (Polychaeta: Nereididae), Smithson. Contrib. Zool., 104:1-53, 1971.

Nephtyidacea

Superfamily of worms whose body is elongated, linear, tapered posteriorly, and subrectangular in cross section. The prostomium is small, with two pairs of very small frontal antennae and no palps. The first or buccal segment has reduced parapodia and small tentacular cirri (Nephtyidae), or the parapodia and appendages may be lacking (Paralacydoniidae). The ventral mouth is enclosed in the anterior few segments. The eversible pharynx is cylindrical and muscular, with marginal papillae. Jaws are located deep within the pharynx (Nephtyidae), or they are lacking (Paralacydoniidae). The parapodia are biramous, the rami being well developed and supported by internal acicula, with flattened presetal and postsetal lobes or lamellae. The rami are widely separated and ciliated along their interramal horders, forming lateral ciliated grooves along the body. Both rami have fan-shaped bundles of setae. The latter are all simple, cross-barred, and capillary (Nephtyidae), or the notosetae are simple and capillary and the neurosetae are compound spinigerous (Paralacydoniidae). The dorsal and ventral cirri are small. This superfamily comprises 2 families: Nephtyidae and Paralacydoniidae. The nephtyidaceads are adapted to burrowing in sandy mud.

Nephtyidae. In members of this family the body is elongated, linear, and subrectangular in cross section, with numerous short segments; it is tapered posteriorly. The prostomium is small, flattened, and subpentagonal, with two pairs of very short frontal antennae; palps are lacking and eyes, when present, are small and deeply buried; the paired nuchal organs are in the form of eversible ciliated sacs. The first or tentacular segment extends laterally and ventrally to the prostomium; it bears reduced setigerous parapodia and one or two pairs of small tentacular cirri. The ventral mouth is enclosed in the few anterior segments. The eversible pharynx is large, cylindrical, and strongly muscular, with bilobed papillae around the opening and subterminal conical papillae arranged in longitudinal rows; a pair of horny hooked jaws is located deep within the pharynx.

The parapodia are biramous, both rami being equally well developed and widely separated, with ciliated bands along the interramal borders; the lobes are flattened anteroposteriorly and are supported by internal acicula, and there are fan-shaped preacicular and postacicular rows of setae and usually lamellae or flattened plates anterior and posterior to the setae. The setae are simple, cross-barred, and serrated, ending in fine capillary tips; some may be bifurcated (lyrate). Small dorsal and ventral cirri are present on the lower sides of the parapodial rami; they are short and conical or foliaceous. Ciliated curved branchiae occur between the rami on some segments (absent in Micronephthys). The pygidium is the site of the dorsal anus and has a single anal cirrus.

The sexes are separate, and fertilization is external. The larvae pass their early stages in the plankton. The nephtyids are typical inhabitants of sandy mud. They burrow rapidly by means of their eversible muscular proboscis and do not form permanent burrows. They are active swimmers and may leave the substrate for spawning and other excursions. They are predatory and carnivorous. Some, such as *Nephtys incisa*, may be facultative nonselective deposit feeders.

The family comprises 4 genera (Nephtys, Aglaophamus, Micronephthys, and Inermonephtys) with about 110 species. They are widely distributed from intertidal zones to great depths but are particularly prominent in the shallow shore fauna. A few species are found in freshwater.

References. M. H. Pettibone, Family Nephtyidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 186-205, 1963.

Paralacydoniidae. Monogeneric (Paralacydonia) family with 3 species. The body is small, elongated, linear, subrectangular in cross section, and tapered posteriorly. The prostomium is subconical, with two pairs of short frontal antennae; palps and eyes are lacking. The first or buccal segment is achaetous, without appendages. The ventral mouth is enclosed in the few anterior segments. The eversible pharynx

is cylindrical and muscular, with a circlet of marginal papillae; jaws are lacking.

The parapodia of the first setigerous segment are uniramous, with neuropodia only; those of the subsequent segments are biramous, both rami being well developed and supported by internal acicula, with somewhat flattened presetal and postsetal lobes. The rami are widely separated and ciliated along the interramal borders; branchiae are lacking. Both rami have fan-shaped bundles of setae; the notosetae are simple, spinous, and capillary; the neurosetae are compound spinigerous, usually with a few lower simple ones. The dorsal and ventral cirri are short and tapered. The pygidium is bulbous; it bears the terminal anus and a pair of long anal cirri.

The sexes are separate, and fertilization is external. Early stages are passed in the plankton. The paralacydoniids are burrowing forms and are widely distributed in sandy mud, from shallow waters to great depths.

References. M. H. Pettibone, Family Paralacydoniidae, new family, in *Marine Polychaete Worms of the New England Region*, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 184-186, 1963.

Aphroditacea

These worms possess paired dorsal scales or elytra which more or less cover the dorsum; these are borne on cylindrical stumps, the elytrophores, on a certain number of segments (in the Aphroditidae, the elytra may be hidden under a dorsal feltage consisting of setal threads). The prostomium is distinct, bearing one to three dorsal antennae, a pair of ventral palps, and usually two pairs of eyes. The first or tentacular segment is modified and closely associated with the prostomium; the tentaculophores, lateral to the prostomium, are directed anteriorly, each one supported by an aciculum and bearing dorsal and ventral tentacular cirri, sometimes with a bundle of setae. The second or buccal segment bears the first pair of elytra and biramous parapodia; the ventral buccal cirri are longer than the following ventral cirri. The ventral mouth is enclosed in the anterior few segments. The eversible, muscular, cylindrical pharynx has soft sensory papillae around the opening and usually two pairs of chitinous jaws (the jaws are rudimentary in the Aphroditidae). The parapodia are biramous, supported by acicula. The setae are all simple or simple and compound (Pholoidae, Sigalionidae). Dorsal cirri are usually present on the segments lacking elytra (lacking in Pholoidae, Sigalionidae); these same segments have more or less developed nodular dorsal tubercles which are similar in position to the elytrophores. Short ventral cirri are found on all the segments. When present, the branchiae may be cirriform and attached to the elytrophores and dorsal tubercles of most of the segments (Sigalionidae), or numerous filiform processes may occur on some of the parapodia (some Polynoidae). The pygidium usually has a pair of anal cirri.

The sexes are separate. This very large group includes errant, crawling, burrowing, swimming, and carnivorous forms. Some build tubes formed of threads produced by notopodial spinning glands (Polyodontidae, some Sigalionidae).

This superfamily comprises 6 families: Aphroditidae, Polynoidae, Polyodontidae, Pholoidae, Sigalionidae, and Eulepethidae.

References. J. H. Day, Family Aphroditidae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 30-114, 1967.

Aphroditidae. Species in this family have an oval, spindleshaped, or oblong body which is attenuated posteriorly,

with less than 60 segments. Some forms reach large sizes, for instance, Aphrodita japonica, which is up to 220 mm in length and 75 mm in width, with 45 segments. These worms are flattened ventrally and arched dorsally. The ventral surface is thickly beset with globular papillae. The dorsum is covered with large overlapping scales or elytra, but these may be covered by a thick dorsal feltage. The prostomium is small and withdrawn in the anterior few segments; it is spherical, with an anterior median antenna and a pair of long ventral palps; slightly raised oval ocular areas (Aphrodita) or anterior peduncles (Laetmonice), without pigment or with one or two pairs of eyespots, may be present. The first or tentacular segment has large tentaculophores lateral to the prostomium and directed anteriorly, each with a single aciculum, three tufts of setae, and a pair of long dorsal and ventral tentacular cirri; it forms the upper lip of the mouth and is usually provided with a large, oval, papillated facial tubercle wedged between the palps. The second or buccal segment has the first pair of elytra, biramous parapodia, and ventral buccal cirri, which are longer than the following ventral cirri; this segment forms the lateral lips of the mouth. The third segment forms the lower lip. The pharynx is eversible, large, stout, and muscular, with rudimentary jaws in the form of four thickened prominences, and with several rows of very numerous branched papillae around the opening.

The elytra (13-20 pairs, usually 15) are attached firmly to large inflated elytrophores on segments 11, IV, V, and VII, continuing on alternate segments to XXV and then occurring on every third segment. They are thin, smooth, large, and imbricated, and cover the dorsum; their lateral margins are entire or irregularly lobed. The dorsal cirri, with basal cirrophores and long distal styles, are found on the segments lacking elytra; the dorsal tubercles, which correspond in position to the elytrophores, are more or less developed, sometimes with additional fimbriated organs on the posterior margins (Aphrodita). The parapodia are biramous, supported by strong acicula. The setae are all simple. The notopodia form short, wide, rounded lobes which extend dorsally and are usually provided with three groups of notosetae: the notosetae of the first, upper group are long and capillary, sometimes extending dorsally and forming a thick tangled feltage which covers the elytra (Aphrodita); the notosetae of the second group are stout, tapered, and curved over the dorsum, forming a protective armature, with some having barbed or harpoon-shaped tips (Laetmonice), and some being flattened and serrated along the curved margins (Pontogenia); the notosetae of the third group are capillary, often brilliantly iridescent, and extend laterally. The neuropodia are subconical, with stout neurosetae arranged in three tiers. The neurosetae are stout and pointed or slightly hooked, sometimes with basal spurs and fringes or sheaths of hairs. The ventral cirri, attached to the middle of the neuropodia, are short and tapering. The pygidium is minute and lacks anal cirri; the dorsal anus is large, encircled by a few posterior segments and the last pair of elongated elytra.

The sexes are separate; fertilization is external. Early larval stages appear in the plankton. The aphroditids are slow-moving, burrowing or creeping on soft bottoms. They are carnivorous or omnivorous, feeding on a great variety of animals and detritus. Aphrodita, the sea mouse, lives more or less buried in the soft bottom, with the posterior end projecting into the water. Water currents pass through the cavity between the elytra and the thin dorsal side of the body where respiration takes place.

This family includes 9 genera and about 70 species. They

have a wide distribution and are found from shallow water to considerable depths.

References. M. H. Pettibone, Family Aphroditidae, in Marine Polychaete Worms of the New England Region, pt. 1. Bull. U.S. Nat. Mus. 227, pp. 11-15, 1963; M. H. Pettibone, Heteraphrodita altoni, a new genus and species of polychaete worms (Polychaeta, Aphroditae) from deep water off Oregon and a revision of the aphroditid genera, Proc. Biol. Soc. Wash., 79:95-108, 1966.

Polynoidae. The body is relatively short and linear, or oval, or long and vermiform. Some species may reach gigantic sizes, for instance, Eulagisca gigantea from the Antarctic, which may grow to 190 mm in length and 100 mm in width and have 40 segments. These worms are somewhat flattened dorsoventrally, with the dorsum more or less covered by dorsal scales or elytra and not concealed by feltlike setae (as in Aphroditidae). The dorsum may have middorsal tubercles (Polynoe scolopendrina) or elongate pads (Euphione). The ventral surface is usually smooth or rarely papillate (Hermenia). Some species have semilunar ventral lamellae on the bases of the parapodia (Gastrolepidia). The prostomium is oval and slightly bilobed, with the anterior borders rounded, projecting into anterior peaks (Harmothoe) or extended anteriorly to form ceratophores for the lateral antennae (Lepidonotus); it bears one to three (usually three) dorsal antennae and a pair of ventral palps. The eyes are sessile and small to large; there are usually two pairs or sometimes none. The first or tentacular segment has tentaculophores lateral to the prostomium, each with a single aciculum, (several notosetae or none), and a pair of dorsal and ventral tentacular cirri; the upper lip of the mouth has a median facial ridge and sometimes a distinct conical facial tubercle (Eulagisea). The second or buccal segment forms the bulbous lateral lips of the mouth; it has the first pair of elytra and biramous parapodia, and the ventral buccal cirri are longer than the following ventral cirri. A well-developed dorsal nuchal fold may cover the posterior part of the prostomium (Alentia, Eulagisca). The eversible pharynx is large, cylindrical, and muscular, with two pairs of strong, recurved, interlocking jaws and a circlet of marginal papillae.

The paired elytra are attached to prominent elytrophores medial to the notopodia on segments 11, 1V, V, and VII, and they continue on alternate segments in the anterior part of the body, with variable distribution posteriorly. The elytra may be relatively few (7-21 or so pairs) or very numerous; they may be minute and easily overlooked (Hermenia) or large and overlapping; they may cover the dorsum or leave the middorsum and posterior end uncovered. The elytra may be smooth or more or less covered with microtubercles or macrotubercles and may or may not have fringes of papillae along the external margins and surface. Dorsal cirri, with basal cirrophores and distal styles, are found on the non-elytra-bearing segments; dorsal tubercles, corresponding in position to the elytrophores, may be indistinct, inflated and bulbous, transversely elongated and forming pseudelytra (Euphionella), or distally bifurcated (Acholoe). The scales of some polynoids are luminescent (Acholoe). Branchiae are usually absent; numerous digitiform branchial filaments may be present on the anterior and posterior sides of the parapodia (Chaetacanthus).

The parapodia are biramous and supported by acicula; the rami may be equally developed, or the notopodia may be small, bearing few notosetae or none at all. The setae are all simple and vary greatly in size, number, and orna-

mentation. The notosetae may form large radiating bundles; the neurosetae may be short or greatly prolonged. The ventral cirri are short and tapered. The pygidium, with the dorsal anus and a pair of long anal cirri, may be enclosed in the posterior few segments.

The sexes are separate, with fertilization taking place externally. Early larval stages appear in the plankton. Some polynoids may brood their eggs under the elytra (Harmothoe imbricata). Some may enter the plankton during part of their life cycle, while others are wholly pelagic (Drieschia,

Podarmus).

The polynoids are carnivorous, feeding on a great variety of animals. They live under a multitude of conditions. The majority are sluggish, crawling forms and are found under stones, in crevices, and in available tubes or burrows. Many polynoids are commensals, living in close association with other animals, such as coelenterates, mollusks, and especially echinoderms and other polychaetes. They are particularly common in shallow water.

The family comprises about 120 genera and 600 species. The polynoids are one of the most abundant and widely distributed of the polychaete families; they are found from

low water to great depths.

References. M. H. Pettibone, Family Polynoidae, in Marine Polychaete Worms of the New England Region. pt. 1, Bull. U.S. Nat. Mus. 227, pp. 15-45, 1963.

Polyodontidae. These worms have a body which is large, elongated, and flattened dorsoventrally, with numerous segments (300 or more). They are tubicolous, living in loosely constructed tubes formed of thin threads filled with mud, clay, and sand particles. Some species reach gigantic sizes, more than 600 mm in length, with tubes of considerable thickness and over a meter long. Numerous dorsal elytra partially cover the dorsum. The prostomium is oval or slightly bilobed, with a pair of lateral antennae and sometimes a median antenna; it bears a pair of ventral palps and two pairs of eyes. Both pairs of eyes may be subequal in size and sessile (Eupanthalis); or the anterior pair may be very large and located on peduncles or ommatophores, while the posterior pair is small and sessile; the paired ommatophores may be extended anteriorly, dorsal to the lateral antannae and palps (Polyodontes), or they may be extended on the lateral sides of the prostomium (Eupolyodontes). The first or tentacular segment is distinct dorsally, and ventrally it forms the upper lip of the mouth; the tentaculophores are lateral to the prostomium, each provided with one or two acicula and a pair of dorsal and ventral tentacular cirri, with or without setae. The second or buccal segment has the first pair of elytra and biramous parapodia, with the ventral buccal cirri much longer than the following ventral cirri; it forms the lateral lips of the mouth. The eversible pharynx is large and muscular, with two pairs of large jaws, each of which has a main tooth and a row of smaller accessory teeth; there is a row of papillae around the opening, the middorsal and midventral papillae being much longer than the others.

The numerous pairs of elytra overlap along the sides of the body, leaving the middorsum uncovered. They are attached to large bulbous elytrophores on segments II, IV, V, and VII, continuing on every other segment. Dorsal cirri are present on the segments lacking elytra. Branchiae may be present in the form of thin-walled filaments on the dorsal sides of the parapodia (Palyodontes). The parapodia are biramous, supported by acicula; all the setae are simple, not compound. The notopodia are small and clavate on the anterior segments; a bundle of capillary notosetae may or

may not be present. Beginning on segment 1X, the notopodia form wide flattened lobes, with or without small bundles of capillary notosetae, on the anterodorsal sides of the neuropodia, and coiled spinning glands within the notopodia produce soft silky hairs that are used for building the tubes. The neuropodia are well developed and rounded or truncate, and accessory bracts may be present or absent. The neurosetae form two or three groups of various types; some are lanceolate and pilose, and some are strong and acicular, with terminal hairs. The ventral cirri are short and tapered. The pygidium is small and bears a pair of anal cirri.

The polyodontids are carnivorous, pulling out of their tubes to catch their prey. They are predominantly tropical in distribution. This family includes 8 genera with about

45 species.

References. V. E. Strelzov, Polychaete worms of the family Polyodontidae (Polychaeta, Errantia) from the Tonkin Gulf [in Russian], in *Investigations of the Fauna of the Seas*, Acad. Sci. S.S.S.R. Zool. Inst., 10(18):277-328, 1972.

Pholoidae. A family with 2 genera, Pholoe and Pholoides (the latter including Peisidice), and about 15 species. The body may be either small, elongated, and narrow, tapering anteriorly and posteriorly, with numerous segments (up to 90, in *Pholoe*), or short and subrectangular, with up to 50 segments (in *Pholoides*). The ventral surface is papillated. The paired elytra may cover the dorsum or leave the middorsum uncovered. The prostomium is rounded, and withdrawn in and fused to the first or tentacular segment; it bears a single median antenna, a pair of palps, and usually two pairs of sessile eyes. The tentaculophores of the first segment project anteriorly, medial to the palps, each having a single aciculum, a single tentacular cirrus, and a bundle of setae (Pholoides), or a pair of dorsal and ventral tentacular cirri and no setae (Pholoe); there is sometimes a digitiform facial tubercle on the upper lip (Pholoe). The second or buccal segment forms the lateral and posterior lips of the mouth; it has the first pair of elytra, a pair of biramous parapodia, and the ventral buccal cirri, which are larger than the following ventral cirri. The eversible pharynx is large and muscular, with two pairs of interlocking jaws and a circlet of papillae around the opening.

The paired elytra are attached to nodular elytrophores on segments II, IV, V, and VII, continuing on alternate segments to the end of the body (Pholoides) or continuing to segment XXIII, following which they occur on every segment (Pholoe). The elytra are soft and delicate (Pholoe) or stiff and rigid with concentric growth lines (Pholoides). The dorsal tubercles, on the segments lacking elytra, are prominent and knoblike. Dorsal cirri and branchiae are lacking. The parapodia are biramous and supported by acicula. The notopodia are rounded, subconical, and smaller than the neuropodia, with fan-shaped bundles of simple, finely spinous, capillary notosetae. The neuropodia are subconical, bearing compound neurosetae with short falcate blades. The ventral cirri are short and tapered. The pygidium is

small, with a pair of long anal cirri.

The larvae of some pholoids may have a long planktonic existence. These species include crawling forms which are found under rocks, in crevices, and on mud bottoms with shells and debris. They are found from intertidal zones to great depths and are widely distributed.

References. M. H. Pettibone, Genus Pholoe Johnston, in Marine Polychaete Worms of the New England Region, pt. I, Bull. U.S. Nat. Mus. 227, pp. 46-48, 1963; M. H. Pettibone, Genus Pholoe Johnston and Peisidice aspera Johnston, in Some Scalebearing Polychaetes of Puget Sound and Adjacent

Waters, pp. 76-80. University of Washington Press, Scattle, 1953.

Sigalionidae. Species in this family have a body which is long and narrow, tapering posteriorly and quadrangular in cross section, with numerous segments (up to 300). The elytra may cover the dorsum completely or leave the middorsum uncovered. The dorsum and elytra may be thickly covered with sand grains (Psammolyce). The ventral surface may be smooth or papillated. The prostomium is oval to subpentagonal, and fused anteriorly and laterally to the first or tentacular segment, with a pair of long tapering ventral palps and usually three antennae (only a pair of lateral antennae in Sigalion); the median antenna has a distinct ceratophore and sometimes a pair of auricular lobes or ctenidia; the small lateral antennae may be attached to the dorsal sides of the tentacular segment (Sthenelais); one or two pairs of eyes are present, or there are no eyes; sometimes there is a pair of rounded ciliated nuchal organs. The tentaculophores, each with a single aciculum, a bundle of notosetae, and a pair of dorsal and ventral tentacular cirri, are directed anteriorly, dorsal to the palps; the upper lip may have a bulbous facial tubercle. The second or buccal segment has the first pair of elytra, biramous parapodia, and the lateral lips of the mouth, with a pair of buccal cirri longer than the following ventral cirri. The third segment forms the lower lip. The eversible pharynx is large and muscular; it has two pairs of interlocking jaws and a border of papillae around the opening,

Numerous pairs of elytra are attached to knoblike elytrophores on segments II, IV, V, and VII, occurring on alternate segments to XXV or XXVII and then continuing on every segment; they may cover the dorsum or leave the middorsum uncovered; their lateral margins may be smooth or papillated, and their surface is smooth or furnished with microtubercles. Knoblike dorsal tubercles are found on the segments lacking elytra; dorsal cirri are absent, except sometimes on segment III (Sigalion, Neoleanira). Ciliated cirriform branchiae, attached to the lateral sides of the elytrophores and dorsal tubercles, are found on all the segments except for a few anterior ones. Dorsal to the notopodia, concave areas are furnished with three cup-shaped, ciliated cushions or ctenidia, forming ciliated grooves along the laterodorsal parts of the body.

The parapodia are biramous and supported by acicula; the notopodia are subequal to or smaller than the neuropodia. The notopodia are club-shaped, with digitiform papillae or stylodes and long fanlike spreading bundles of simple, finely spinous capillary notosetae which curve dorsally. The neuropodia are subconical, and surrounded by basal bracts with fringes of papillae and distal stylodes. The neurosetae are compound falcigerous or spinigerous; some blades may be long and multiarticled or short and conical; sometimes there are additional simple bipinnate neurosetae. The ventral cirri are short and tapered, sometimes with long accessory papillae on the cirrophores (Willeysthenelais). The pygidium is small and bears a pair of long anal cirri.

The sigalionids are carnivorous. They are able to burrow rapidly in mud and sand. Rarely, as in *Sthenelanella*, they occupy long, tough, fibrous tubes composed of threads formed by notopodial spinning glands (similar to Polyodontidae).

This family includes 20 genera and about 160 species. They are widely distributed, from intertidal zones to great depths.

References. M. H. Pettibone, Family Sigalionidae, in Marine Polychaete Worms of the New England Region, pt. 1,

Bull. U.S. Nat. Mus. 227, pp. 45-54, 1963; M. H. Pettibone, Partial revision of the genus *Sthenelais* Kinberg (Polychaeta: Sigalionidae) with diagnoses of two new genera, *Smithson. Contrib. Zool.*. 109:1-40, 1971; M. H. Pettibone. Two new genera of Sigalionidae (Polychaeta), *Proc. Biol. Soc. Wash.*, 83:365-386, 1970.

Eulepethidae. Members have a flattened subrectangular body which is relatively short and composed of up to 70 segments. The elytra nearly cover the dorsum; the anterior 12 pairs, attached centrally to large cylindrical elytrophores, are arranged on segments II, IV, V, and VII, continuing on alternate segments to XXI and XXIV; they progressively increase in length posteriorly, the last pair being long and subrectangular, and they are usually smooth or have scattered microtubercles; the external margins are notched or fimbriated. The posterior segments have either small elytra attached to small elytrophores by their anterior borders or small lamellae attached to dorsal tubercles. Small subulate dorsal cirri are present on segment III (this segment is not visible middorsally) and segment VI. Branchiae occur on the segments lacking elytra, dorsal cirri, or lamellae; they are inflated dorsal tubercles with distal cirriform processes.

The prostomium and tentacular segment are distinct, withdrawn and wedged between the anterior few segments. The prostomium is globular, provided with three short antennae inserted anteriorly and lacking distinct ceratophores, and a pair of elongate conical palps; eyes, when present, are small and variable in number. Each tentacular parapodium (segment I), lateral to the prostomium, has a pair of dorsal and ventral tentacular cirri, two acicula, two bundles of capillary setae, and a clavate nuchal organ. The ventral mouth is enclosed in segments II and III. The opening of the eversible, strongly muscular pharynx is encircled with soft papillae (about 13 pairs) and provided with 2 pairs of platelike jaws (similar to the Aphroditidae).

The parapodia are biramous; the notopodia are short and cylindrical, with hooked notoacicula, and the neuropodia are thick and paddle-shaped, with neuroacicula provided with hammer-headed distal plates. The setae are all simple; the notosetae are slender, capillary, and smooth or spinous; in addition, there are stout, bent, golden hooks. The neurosetae are pectinate, limbate and nonlimbate capillaries, as well as stout acicular setae. The ventral cirri are short and tapered or globular with filamentous tips. The pygidium, which contains the dorsal anus, has a single extremely long anal cirrus, minutely papillated along one side.

The family comprises 5 genera (Eulephus, Pareulepis, Mexiculepis, Grubeulepis, and Japoeulepis) and about 25 species. Members are burrowing forms, found in sand, silt, mud with muck, shells, and corals. The relatively few species are found in widely scattered areas, mostly in tropical and subtropical waters, from low intertidal regions to moderate depths.

References. M. Imajima, occurrence of species of three families, Eulepthidae, Apistobranchidae, and Heterospinionidae (Polychaeta) from Japan, Bull. Nat. Sci. Mus., 17: 57-64, 1974; M. H. Pettibone, Revision of the aphroditoid polychaetes of the family Eulepethidae Chamberlin (=Eulepidinae Darboux; = Pareulepidae Hartman), Smithson. Contrib. Zool., 41:1-44, 1969.

Chrysopetalidae (aberrant family)

The body is slender, elongated, and depressed, with relatively few (up to 40) or numerous (up to 300) segments.

The dorsum is more or less covered by transverse rows of golden flattened dorsal setae or paleae. The prostomium is small, oval, and withdrawn in the anterior segments; it bears three small antennae, a pair of ventral palps, usually two pairs of eyes, and sometimes a posterior caruncle (Paleanotus). The first or tentacular segment is greatly reduced and achaetous, with one or two pairs of tentacular cirri. The second, or first setigerous, segment may be uniramous, with notopodia only. The ventral mouth is enclosed in segments III to V. The pharynx is eversible and muscular, usually provided with a pair of chitinous stylets.

The parapodia are biramous, with the rami well separated and supported by acicula. The dorsal rami or notopodia form wide low dorsolateral ridges, with flattened, highly ornamented golden notosetae or paleae arranged in fanshaped transverse rows, nearly covering the dorsum. In Dysponetus the notosetae are slender, not flattened; they are held erect and curve over the dorsum. Small dorsal cirri are located below and lateral to the paleae. The neuropodia are short and subconical, with compound spinigerous and falcigerous neurosetae. The ventral cirri are short and tapering. The pygidium bears a pair of anal cirri.

The sexes are separate, and fertilization takes place externally. These worms develop up to an advanced larval stage in the plankton. They are carnivorous and found in crevices of rocks and coral, in holdfasts of algae, in shelly sand banks, and among worm tubes, from intertidal re-

gions to shallow depths.

This aberrant family includes 5 genera (Bhawania, Chrysopetalum, Heteropale, Paleanotus, and Dysponetus) and about 25

species.

References. J. H. Day, Family Palmyridae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 115-119, 1967; M. H. Pettibone, Family Chrysopetalidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 54-55, 1963.

Pisionidae (aberrant family)

These worms show marked adaptations to the interstitial environment. The body is small, slender, elongated, and threadlike, with numerous segments (up to 100). The integument is smooth and transparent, with indistinct annulations. The anterior end is highly modified, with varying degrees of fusion of the small prostomium and the first achaetous or tentacular segment. The tentaculophores of

this segment are directed anteriorly, dorsal to the long paired palps; a small median antenna, medial to the bases of the tentaculophores, may be present (Pisionella) or lacking (Pisione, Anoplopisione); each tentaculophore is supported by a stout aciculum that projects obliquely anteriorly in front of the mouth, and has a long dorsal tentacular cirrus and a small flask-shaped ventral cirrus. The second or buccal segment, which encloses the slitlike ventral mouth, bears the first pair of parapodia, small flask-shaped dorsal cirri, and long ventral buccal cirri. The posterior lobes of the brain extend posteriorly into segments III to V, and there are usually two pairs of closely approximated eyes on the brain (visible through the transparent integument). In Pisionidens the tentaculophores are completely fused medially; the head end appears elongate and subtriangular, with a pair of dorsal tentacular cirri (so-called frontal antennae) and with the paired palps emerging laterally; a median antenna and acicula are lacking; the buccal segment and the following six segments have only dorsal and ventral cirri, without parapodial lobes, and the cirri are small, except for the long ventral buccal cirri on segment II and the long dorsal cirri on segment III. The pharynx is eversible and muscular, with two pairs of chitinous jaws and a circlet of papillae around the opening.

Where the parapodia appear, they are essentially uniramous, supported by one or two acicula; they are subconical and have relatively few setae, the upper one simple and the rest compound falcigerous. The setae may be absent in some adults. Both the dorsal and the ventral cirri are small and flask-shaped. The pygidium has a pair of long anal

The sexes are separate, and there is a highly specialized type of reproduction, involving protrusible copulatory organs in the male. The larvae appear in the plankton. The pisionids are carnivorous; they inhabit sandy areas, from intertidal regions to great depths, and move actively among the sand grains, aided by adhering glands on the parapodia. Each species inhabits a special type of sand. Some species have a wide geographic distribution. This aberrant family includes 4 genera (Pisionella, Pisione, Anoplopisione, and Pisionidens) and about 25 species.

References. B. Åkesson, On the histological differentiation of the larvae of Pisione remota (Pisionidae, Polychaeta), Acta Zool., 42:177-225, 1961; J. H. Day, Family Pisionidae, in A Monograph on the Polychaeta of Southern Africa, pt. 1, Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 132-135, 1967.

AMPHINOMIDA

Members of this order have a body consisting of similar segments. The prostomium is distinct and enclosed in the anterior segments; it bears five appendages (antennae and palps) and a more or less developed posterior extension or caruncle. The peristomium, with the ventral mouth, is enclosed in the anterior segments. The pharynx is unarmed, eversible, and cylindrical. The parapodia are biramous, and the setae are all simple, of various types. Dorsal and ventral cirri, as well as branchiae, are present. This order contains 2 families: Amphinomidae and Euphrosinidae.

Amphinomidae. The body is short, flattened, fusiform or moderately elongated, and subcylindrical or subquadrangular in cross section. The prostomium is suboval and fused with the peristomial or tentacular segment; it bears five short, subulate or filiform appendages: a pair of lateral antennae, a median antenna, and a pair of tentacular cirri. It may or may not bear two to four eyes. There is usually a posterior extension or caruncle on the prostomium, with ciliated bands; the caruncle may be absent, or a small heartshaped or sinuous ridge extending over several segments, or it may be elaborate and convoluted, with upper and lower lobes. The peristomium has the ventral mouth and cushionlike anterior, lateral, and posterior lips, enclosed in two to five setigerous segments. The proboscis is eversible, short, globular or cylindrical, and muscular, lacking papillae and jaws.

The parapodia are biramous, with the rami well separated; sometimes the neuropodia are ventral in position

(Hippowe); the podial lobes are short, supported by acicula. The setae form fan-shaped, radiating groups, of various types, all simple: capillary, spear-shaped, and harpoonshaped, bifurcate with a basal spur, and short, stout hooks. The setae of some species (Eurythoe complanata) are hollow, transparent, and brittle, filled with a poisonous secretion; when irritated, the worm erects its sharp setae, which break when touched and release poisonous contents in the wound, giving rise to the common name fireworms. The dorsal cirri are filiform, one or two in number, posterior to the notosetae; the ventral cirri are short, subulate, and ventral and posterior to the neurosetae (reduced to short cushions in Hipponoe). Paired branchiae occur posterior to the bases of the notopodia, either limited to the anterior region or found along most of the body; they may be arborescent or pinnate. The pygidium has a terminal or subterminal anus and a median oval papilla or pair of short anal cirri. These worms are often brilliantly colored,

The sexes are separate. Some species are protandrous hermaphrodites. Females may show brood care, with the young attached to the adult (Hipponae gaudichaudi. Amphinome rostrata). Some amphinomids have a relatively long planktonic life with gradual morphological transformation from the earliest larvae up to the juvenile stages. The characteristic Rostraria larvae have an elongate conical prostomium, three pairs of eyes, a pair of tentacular palps, a first sctiger with long larval setae, four body segments, and a

pygidium.

Members of this family move rather sluggishly, crawling on rocks, in crevices, and among corals. Some, such as Chloeia, swim well. Amphinomids are omnivorous or carnivorous, feeding on attached animals such as sponges, hydroids, sea anemones, corals, and ascidians; the proboscis is everted, and suction is generated by the muscular pharynx, which sucks out the juices of the prey. Some are active predators (Pherecardia) feeding on other polychaetes. Some (Paramphinome) are found in soft mud. Some are found on floating timbers, algae, debris, and so forth (Hipponoe, Amphinome).

The family consists of 17 genera and about 115 species. These worms are predominantly tropical or subtropical; they are found from low water to great depths. Some are widely distributed (cosmopolitan). Hipponoe gaudichaudi is associated with stalked harnacles (Lepas) on floating objects; members are almost parasitic and are found within the valves of the barnacles upon which they feed.

References. J. H. Day, Family Amphinomidae, in Monograph of Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 120-131, 1967; M. H. Petti-

bone, Family Amphinomidae, in Marine Polychaete Worms, of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 55-62, 1963.

Euphrosinidae. The body is short, oval, more or less convex dorsally, and flat or slightly concave ventrally; it is composed of numerous segments (up to 60). The prostomium is narrow and elongated, wedged between the anterior segments. It is folded over the anterior end, the ventral part having a pair of small eyes, a pair of short lateral antennae which are lateral to the eyes, and a pair of large cushionlike palps; the dorsal part has a short median antenna, a pair of eyes lateral to the median antenna, and a crest-like nuchal organ or caruncle that extends posteriorly on some anterior segments. The ventral mouth is just posterior to the palps and is enclosed in the anterior five segments. The pharynx is unarmed, eversible, elongated, and cylindrical.

The parapodia are biramous, with the rami crestlike and only slightly projecting and separated. The set are all simple. The notopodia form wide transverse ' 3cs that nearly cover the dorsum and bear several trainerse rows of numerous long and short notosetae. The latter may be hollow, cylindrical, and bifurcated, with one branch shorter than the other and with the inner margins often serrated; the short branch may form just a small spur; or the notosetae may be in the form of flattened paleae (Palmyreuphrosyne). The neuropodia have unequally bifurcated neurosetae with a lateral spur. Each notopodium has short digitiform dorsal cirri on the upper and middle parts of the ramus; a ventral cirrus is found posterior to the neurosetae. Transverse rows of branchiae, in the form of simple filaments or branched tufts, are found posterior to the notosetae. The pygidium, which bears the terminal anus and a pair of oval cushionlike anal cirri, is enclosed in the posterior few segments.

Some species of Euphrosine, such as E. borealis, have pelagic development, forming Rostraria larvae that spend considerable time in the plankton. The euphrosinids are creeping forms and are found on mixed bottoms. When disturbed, they curl ventrally, with their numerous setae sticking out, giving the appearance of a bur. They are carnivorous, and commonly found on the sponges upon which they feed. The family contains 2 genera (Euphrosine and Palmyreuphrosyne) and about 50 species.

References. M. H. Pettibone, Family Euphrosimidae (=Euphrosynidae), in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, 1963.

SPINTHERIDA

Aberrant monofamilial (Spintheridae) order with the single genus Spinther and about 9 species. All known species are highly specialized, living as ectoparasites on sponges, to which they cling tightly and which they tend to match in coloration. The body is oval or almost circular, convex dorsally, and flattened or slightly concave ventrally, with relatively few (up to 50) segments. The ventral surface is smooth or papillated. The prostomium is small and inconspicuous, squeezed between the anterior parapodia; there is a globular median antenna which nearly covers the prostomium, and usually two pairs of eyes are found on the base of the antenna. The anterior parapodia are directed anteriorly and fused medially, forming a continuous disk anterior to the prostomium. The ventral mouth is surrounded

by the anterior few segments. The pharynx is unarined and forms an eversible, soft, voluminous, rosettelike sac or funnel; it is very mobile and may extend in a tonguelike fashion, serving to suck in the soft tissue of the sponge.

The parapodia are biramous. The notopodia form elongated transverse ridges which nearly cover the dorsum, with more or less developed, delicate, undulating lamellae supported by transverse rows of spinelike notosetae; the lamellae and notosetae extend laterally, forming notopodial fans which cover the neuropodia. The distal tips of the notosetae are pointed, entire, or furcate. The neuropodia are elongated and cylindrical, supported by several slender acicula and with one or two stout, yellow, compound, and strongly hooked neurosetae. Branchiae and dorsal and ven-

tral cirri are lacking. The posterior parapodia are smaller and directed posteriorly; they enclose the subterminal dorsal anus, which has a pair of thick anal cirri.

The spintherids are semisedentary, and carnivorous or parasitic on sponges; their hooked neurosetae may become embedded in the sponge upon which they feed. They are widely distributed from shallow water to moderate depths.

References. M. H. Pettibone, Family Spintheridae, a Marine Polychaete Worms of the New England Region. pt. 1, Bull. U.S. Nat. Mus. 227, pp. 66-68, 1963.

EUNICIDA

Order composed of the superfamily Eunicacea (with 8 families) and the aberrant family Histriobdellidae. The prostonium is distinct and is usually provided with appendages. The eversible pharynx has an elaborate jaw apparatus

composed of dorsal maxillae and ventral mandibles. The parapodia are distinct, with well-developed neuropodia and reduced notopodia.

Eunicacea

Members of this superfamily have an elongated vermiform body composed of numerous segments. The head is well developed, with a distinct prostomium and peristomium. The prostomium has up to five antennae (there may be none) and variously developed paired palps; the peristomium is composed of one or two apodous segments, with or without a pair of tentacular cirri. The eversible muscular pharyux is armed with a dark chitinous jaw apparatus made up of a pair of ventral plates or mandibles and a dorsal series of maxillae composed of up to six pairs of toothed plates and two or three posterior supports, called maxillary carriers, embedded in the pharyngeal tissue (except in the Dorvilleidae, in which there are two to four longitudinal series of very small and numerous denticled pieces). The parapodia are uniramous or subbiramous, with the notopodia sometimes represented by notoacicula within the bases of small lobes or dorsal cirri; the neuropodia are well developed, usually supported by several neuroacicula. The neurosetae are diverse and may be either simple or compound. Dorsal and ventral cirri and branchiae may be present or absent. The pygidium, which encloses the dorsal anus, has two or four anal cirri. These worms are mostly free-living: some are burrowing forms, and others construct more or less permanent tubes from which they may partially protrude. Exceptionally, a few forms take up a parasitic existence during at least part of their life cycle.

This superfamily is composed of 8 families: Onuphidae, Eunicidae, Hartmaniellidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae, and Dorvilleidae; they are sometimes considered to be subfamilies belonging to the family Eunicidae.

References. J. H. Day, Family Eunicidae, in *The Polychaeta of Southern Africa*, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656. pp. 374-558, 1967; K. Fauchald, Polychaetous annelids of the Families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from Western Mexico, *Allan Hancock Monogr. Mar. Biol.*, 5:1-335-1970; O. Hartman, Polychaetous annelids, pt. 5: Eunicea, *Allan Hancock Pac. Exped.*, 10:1-236, 1944; M. H. Pettibone, Superfamily Eunicea, in *Marine Polychaete Worms of the New England Region*, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 229-276, 1963.

Onuphidae. Worms in this family are characterized by an elongate vermiform body. The prostomium is small and rounded, with five dorsal antennae composed of ringed ceratophores and distal styles. There is a pair of ventral palps, each formed of bulbous basal (labial) and frontal lobes; small eyes may be present or absent. The peristomial ring may or may not bear a pair of short dorsal tentacu-

lar cirri. The eversible pharynx has a pair of ventral mandibles and dorsal maxillae formed of short broad carriers and 4½ pairs of toothed plates. The parapodia of a few anterior segments are more of less modified, with hooked setae, prominent dorsal and ventral cirri, and presetal and postsetal lobes

There are numerous body segments, with subbiramous parapodia; the notopodia are represented by filiform dorsal cirri and internal notoacicula; the neuropodia are subconical, supported by several delicate neuroacicula; and the ventral cirri are in the form of glandular ridges (except in the anterior region). The setae are limbate, capillary, and slender, with comblike tips; they bear subacicular stout hooks in the more posterior segments. Paired branchiae, when present, are attached to the bases of the dorsal cirri as single filaments, or are branched with a pectinate or spiral arrangement. The pygidium has the dorsal anus and two to four pairs of anal cirri.

The sexes are separate. Maturation of eggs is associated with strings or hundles of nurse cells. Some species deposit yolky eggs in their tubes. The larval stages are short. Most species live in tubes (mucous, parchmentlike with attached foreign material, or tough and quill-like) which are embedded in the substrate or are free. The largest onuphids (intertidal Australian beachworms, up to 200 cm in length) have no tubes, and form temporary burrows in shifting sand. These worms are omnivorous scavengers, pulling out of their tubes or temporary burrows and making use of their powerful jaws.

The family contains about 12 genera and 200 species. They are abundant in deep sea but tend to be common at all depths. Their decorated tubes (*Diopatra*) are commonly seen projecting from the bottom. They are found in the thousands intertidally (Australian beachworms), and they serve as scavengers and baitworms.

References. J. H. Day, Subfamily Onuphinae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 405-425, 1967.

Eunicidae. The body is elongate, cylindrical, somewhat flattened, and tapered posteriorly, with numerous segments (up to 600 or more). They are among the largest members of the Polychaeta; Eunice aphroditois reaches more than 2 m in length. These worms fragment and regenerate readily and often show a brilliant iridescence. The prostomium is oval or bilobed, with rather indistinct, fused, globular ventral palps and one, three, or five rather short occipital antennae which lack ringed ceratophores; the antennae are smooth or more or less articulated; two basal eyes (rarely four) are usually present. The peristomium, which contains the ventral mouth, consists of two apodous segments; a pair

of short tentacular cirri may or may not be present on the second one. The pharynx is eversible, with a pair of stout wing-shaped ventral mandibles, the anterior border forming a beveled cutting edge; the dorsal maxillae consist of four or five pairs of plates, the basal pair (M I) in the form of large smooth hooks, and the rest toothed along their inner margins; the right maxillae III and IV are fused, and the paired maxillary carriers are short and broad.

The parapodia are essentially uniramous; the notopodia are sometimes represented by a few notoacicula in the bases of the dorsal cirri. The neuropodia are subconical, supported by a few neuroacicula, usually with longer postsetal lobes. The neurosetae are of several kinds: simple, limbate, and capillary; short, delicate, and comblike; and compound spinigers or falcigers which may be unidentate, bidentate, or tridentate, and hooded; subacicular stout acicular setae are sometimes present in more posterior segments. The dorsal cirri are short and digitiform. When present, the branchiae are attached to the medial sides of the dorsal cirri as simple or branched pectinate filaments. The ventral cirri are short and digitiform to subconical; they may be padlike in more posterior segments. The pygidium encloses the dorsal anus and bears two to four anal cirri.

The sexes are separate. The eggs may be laid in gelatinous masses in which they pass through their early development. In some species fissiparity occurs at sexual maturity, as in the famous palolo worms: the adults live in holes and crevices among rocks and coral on the ocean bottom; the posterior portions of the worms become modified and filled with sex products; the worms back out of their burrows when ready to spawn, and the modified epitokous portions break off and swim tail first to the surface, forming large writhing swarms; after spawning, the epitokes die, while the anterior portions pull back into their burrows and regenerate new posterior genital segments; examples are the Atlantic Palola schemacephala, the circumtropical P. siciliensis, and the Pacific P. viridis, which are gathered by the natives in Fiji and Samoa and used for food.

The eunicids occupy diverse habitats, mostly associated with hard bottoms and shallow water. They may have well-defined burrows which form mucus-lined galleries in cracks and fissures of rocks, sponges, and coral. Some form more or less permanent parchmentlike tubes with a number of lateral openings. They may leave their burrows or extendition anterior ends out of their tubes to feed. They are active and predactious, carnivorous, or omnivorous.

The family consists of 7 genera and about 250 species. They are particularly well represented in tropical and subtropical waters. Many species are associated with corals. Some are cosmopolitan, such as *Marphysa sanguinea*, which is used as a baitworm in England and Japan.

References. J. H. Day, Subfamily Eunicinae, in A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia, Brit. Mus. (Natur. Hist.) 656, pp. 377-404, 1967; M. H. Pettibone, Family Eunicidae (=Leodicidae), in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 234-243, 1963.

Hartmaniellidae. Eunicacead family consisting of a single genus (Hartmaniella) and possibly 2 species. The body is long and slender. The prostomium is suboval, without appendages or eyes. The peristomium is a wide ring lacking appendages, with an additional apodous ring. The pharynx is eversible; it has well-developed dark-colored jaws consisting of a pair of strong ventral mandibles and four pairs of toothed dorsal maxillae attached to a pair of elongate maxillary carriers.

There are numerous body segments, which have subbiramous parapodia; the notopodia are represented by dorsal cirri and internal notoacicula and lack setae; the neuropodia are subconical, with ventral cirri and supra-acicular lobes, and are supported by internal neuroacicula with long mucronate tips. The anterior four parapodia are small and lateral; the following parapodia are shifted dorsally and are provided with dorsal cirri which are elongate and bifid distally; the supra-acicular neuropodial lobes are enlarged and flattened, serving as branchial processes. All of the above characters give the dorsal surface a slashed aspect. The posterior parapodia have dorsal cirri and elongate, cirriform, supra-acicular neuropodial lobes. The neurosetae are simple, slender, capillary and compound spinigerous. The pygidium has a dorsal anus and a pair of long cirri. The family is known from two records in Japan and Madagascar, where specimens were dredged in depths ranging 60 to

References. M. Imajima, A new polychaete family, Hartmaniellidae, from Japan, in Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman, Allan Hancock Foundation. Los Angeles, pp. 211-216, 1977.

Lumbrineridae. Members of this family superficially resemble earthworms. The body is elongate, cylindrical, linear, and threadlike, tapering slightly anteriorly and posteriorly. The prostomium is conical to suboval or long and pointed (Lumbrinerides, Lumbrineriopsis), without appendages and sometimes with one to seven minute nuchal papillae and a pair of nuchal organs which more or less emerge from a pocket between the prostomium and the peristomium; eyes are lacking. The peristomium is formed of two more or less fused apodous segments, without appendages; ventrally, it forms a pair of buccal cushions and the posterior lip of the mouth. The pharyux is muscular and armed with dark chitinized (sometimes also partly calcified) jaw pieces, consisting of a pair of ventral mandibles which are flared anteriorly and (at least in part) fused medially, four pairs of dorsal maxillae, and a pair of short broad maxillary carriers; the basal pair of maxillae (M I) consists of hooked forceps, and there are three pairs of smaller denticled plates (M II to M IV).

The numerous body segments are essentially uniramous; the notopodia may be represented by a few fine notoacicula; the neuropodia are subconical, with few embedded neuroacicula, and the neuropodial lobes may change shape along the length of the body, and, with variable development of the presetal and postsetal lobes, may appear nodular, subconical, auricular, or digitiform. Ventral cirri are lacking, and dorsal cirri are usually lacking (present in Kuwaita): Branchiae are usually lacking but are sometimes present on the postsetal lobes; they are palmately branched (Ninoe) or consist of a single branchial filament (Paraninoe). The setae consist of simple limbate capillaries and simple or compound hooded hooks which are bidentate or multidentate. The pygidium has a terminal anus, with two or four anal cirri, or it may be flattened and rounded, with a dorsal anus and with no cirri (Lumbrinerides).

The sexes are separate. Yolky eggs are laid in gelatinous masses attached to mud or algae, where early development takes place. The lumbrinerids are free-living, creeping between algal holdfasts and in crevices, and burrowing in sand or mud. They are found on various types of bottom but are especially common in muddy sand. Ninoe nigripes forms mucous tubes mixed with mud and sand. They are carnivores, scavengers, and detritus feeders; some appear to be nonselective deposit feeders.

The family consists of 7 genera and about 200 species. Members are widely distributed. They are among the most common polychaetes in sandy and muddy bottoms in shelf depths but are also well represented in deeper waters.

References. M. H. Pettibone, Family Lumbrineridae, in Marine Polychaete Worms of the New England Region, pt. 1,

Bull, U.S. Nat. Mus. 227, pp. 256-268, 1963.

Iphitimidae. Eunicacead family consisting of the single genus Iphitime and 6 species, all found living in the branchial cavities or on the carapaces of decapod crustaceans (crabs and hermit crabs). The body is elongate, flattened dorsoventrally and tapered anteriorly and posteriorly, with numerous segments (up to 200 or more). The prostomium is small and rounded or truncate; it bears a single pair of small frontal antennae and lacks eyes. The peristomium, which contains the ventral mouth, is usually biannulate and lacks tentacular cirri. The pharynx is eversible, armed with a pair of winglike mandibles which are fused medially on the anterior part, and usually with three pairs of maxillae (rarely two pairs); maxillae I are simple, falcate, and fused to a pair of short maxillary carriers.

The parapodia are uniramous, subconical, and supported by several neuroacicula (up to six), with longer postsetal lobes. The setae are short, simple falcate and compound falcate, without hoods; they are adapted for clinging. The branchiae are prominent, dorsal to the neuropodia, digitiform, and simple or branched. The pygidium bears a pair

of short anal cirri.

The sexes are separate. The iphitimids are found adhering to the roof of the branchial chamber of the host, either singly or in groups of several intertwined individuals. There is no clear evidence of parasitism. The crustacean hosts have been found in muddy bottoms in Europe, Japan, and southern California.

References. K. Fauchald, Iphitimidae, new family, in Polychaetous Annelids of the Families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from Western Mexico, Allan Hancock Monogr. Mar. Biol. 5, pp. 118-119, 1970; J. Pilger, A new species of Iphitime (Polychaeta) from Cancer antennarius, (Crustacea: Decapoda), Bull. S. Calif. Acad. Sci., 70:84-87, 1971.

Arabellidae. Family whose members superficially resemble earthworms. The body is elongate and cylindrical, tapering slightly anteriorly and posteriorly. The prostomium is conical or flattened spatulate, without appendages but sometimes with two to four eyespots on the posterior margin. The peristomium is formed of two apodous segments and lacks appendages. The pharynx is eversible, muscular, and armed with dark chitinized jaw pieces which consist of a pair of ventral mandibles, flattened winglike plates (sometimes absent), four or five pairs of dorsal maxillae, a pair of slender maxillary carriers, and an unpaired piece; the maxillae are formed of elaborate toothed plates.

The numerous body segments are essentially uniramous. The notopodia may be represented by minute papillar lobes with a few embedded notoacicula, and the neuropodia are small and subconical, supported by a few neuroacicula; the presetal and postsetal neuropodial lobes are variously developed. Dorsal and ventral cirri, as well as branchiae, are lacking. The setae are all simple; there may be limbate capillary setae only (Arabella), or there may be additional modified acicular setae with asymmetrical tapered hoods (Cenothrix) or additional projecting stout acicular spines (Drilonereis, Notocirrus). The pygidium has a terminal anus and two to four short anal cirri.

The arabellids are widely distributed, from intertidal zones to great depths. They are free-living and burrow readily but rather slowly in sand and mud. They secrete a great deal of mucus, which serves to lubricate their burrows. They are predacious and carnivorous.

Some arabellids show an unusual type of endoparasitism, appearing to be parasitic from very early stages to advanced stages and apparently becoming sexually mature after leaving the host. The mode of entry into the host is unknown. Many worms (Notocirrus spp.) with few to numerous segments may be found in a single host (onuphid and eunicid polychaetes), occupying the body cavities and vascular body walls of the host. Usually there is a single parasite per host, occupying the body cavity and attaining a large size; examples are Oligognathus spp. in echiuroid (Bonellia) and spionid polychaetes, Labrorostratus spp. in syllid polychaetes, Drilonereis spp. in onuphids and eunicids, and Haematocleptes in the peri-intestinal blood sinus of a trichobranchid polychaete (Terebellides). Modifications associated with their parasitic existence include reduction in setae, jaw parts, and mucous glands.

The family consists of 11 genera and about 81 species.

References. M. H. Pettibone, Endoparasitic polychaetous annelids of the family Arabellidae with descriptions of new species, *Biol. Bull.*, 113:170-187, 1957; M. H. Pettibone, Family Arabellidae, in *Marine Polychaete Worms of the New England Region*, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 268-276, 1963.

Lysaretidae. Eunicacead family consisting of 3 genera (Lysarete, Oenone, Tainokia) and 10 species. The body is short to long, with numerous segments (up to 800 or more); it is subcylindrical or flattened dorsoventrally, tapering anteriorly and posteriorly. The prostomium is oval to subconical, partially hidden by the peristomium, and without distinct palps; it usually bears three short occipital antennae (one in Tainokia) and four eyes in a row along the posterior border. The peristomium, which encloses the ventral mouth, is achaetous and usually biannulate, lacking tentacular cirri. The pharynx is eversible, armed with a pair of well-developed, winglike, partially fused mandibles and five pairs of toothed maxillae, which may be somewhat asymmetrical; the paired maxillary carriers are rather short and fused medially, as in Lysarete, or long, narrow, and tapered, with an additional unpaired piece, as in Oenone (=Halla) and Tainokia.

The parapodia are subbiramous, the notopodia represented by notoacicula in the bases of the dorsal cirri. The neuropodia are well developed, subconical and supported by several neuroacicula, with longer postsetal lobes which extend dorsally. The neurosetae are all simple, either consisting only of limbate capillaries, as in *Lysarete* and *Tainokia*, or with some additional subacicular acicular setae in the posterior segments, as in *Oenone*; the acicular setae may be entire, without hoods, or they may be bidentate and hooded. The dorsal cirri are large, flattened, and foliaceous or ligulate. Ventral cirri and branchiae are lacking. The pygidium bears four anal cirri.

The sexes are separate. The lysaretids are carnivorous and are found burrowing in sandy bottoms. They are mainly tropical and subtropical; some attain quite large sizes. Oenone fulgida is circumtropical in distribution, associated with corals. The large O. okudai is an important baitworm in Japan.

References. K. Fauchald, Family Lysaretidae, in Polychaetous Annelids of the Families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from Western Mexi-

co. Allan Hancock Monogr. Mar. Biol. 5, pp. 141-143, 233, 1970; G. A. Knox and K. M. Green, The Polychaetes of New Zealand, pt. 3:Lysaretidae, J. Roy. Soc. N.Z., 2:431-434, 1972.

Dorvilleidae. The body is slender and cylindrical to fusiform; they are mainly small to minute. The prostomium is small and hemispherical to subconical, with a pair of more or less articled dorsolateral antennae and a pair of lateral palps; both pairs are sometimes reduced to papilliform appendages and are rarely absent. The prostomium also bears a pair of indistinct nuchal organs, as many as four eyes (eyes may be absent), and sometimes a nuchal papilla. The peristomium consists of two apodous rings and lacks tentacular cirri; the ventral mouth has prominent lateral lips. The eversible pharynx has chitinized jaws consisting of a pair of dark ventral mandibles, flared and denticulate anteriorly, and dorsal maxillae which are formed of numerous small denticulate plates arranged in two to four longitudinal rows; periodic maxillary replacement occurs.

The number of body segments is moderate to large; and the parapodia are uniramous or subbiramous. The notopodia, when present, are represented by cylindrical cirrophores, with notoacicula, bearing dorsal cirri; the neuropodia are subconical, with neuroacicula and ventral cirri. The upper neurosetae are simple, slender, and capillary or acicular, sometimes with additional short furcate ones; the lower neurosetae are compound, with short to long blades. Branchiae are lacking, but there are segmental transverse bands of cilia. The pygidium has the dorsal anus and two to four anal cirri.

The sexes are usually separate, and there is sometimes a slightly modified, swimming reproductive phase with enlarged eyes and more numerous and longer setae. The gametes are released into the water, and the larvae have a rather short pelagic existence (polytrochal and nectochaetal stages). In some smaller forms, such as Ophryotrocha, reproduction is hermaphroditic, with eggs laid in tubular egg masses; it is rarely viviparous. These worms secrete abundant mucus, burrowing in sand and forming temporary tubes. They are wandering and somewhat pelagic in habit, and young and mature forms are sometimes found at the surface. They are surface deposit feeders.

The family contains about 8 genera and 50 species. Members are common in shallow water but known from greater depths. One species (Eteonopsis geryonicola) is found in the branchial cavities of crabs (Geryon) in the North At-

References. P. A. Jumars, A generic revision of the Dorvilleidae (Polychaeta), with 6 new species from the deep North Pacific, Zool. J. Linn. Soc., 54:101-135, 1974.

Histriobdellidae (aberrant family)

Very aberrant family of the order Eunicida, composed of 2 genera (Histriobdella and Stratiodrilus) and 6 species, all found living epizoically in the branchial chambers or on the surfaces of crustaceans. The body is very small, rarely exceeding 2 mm in length; it is transparent and of atypical polychaete body form, indistinctly and unequally annulated and lacking setae. The prostomium and peristomium are fused to form a rounded head which has five short, tactile,

filiform anterior appendages (corresponding to three antennae and two palps) and a pair of lateroventral appendages which may be nonretractile (Histriobdella) or completely retractile (Stratiodrilus); the ventral mouth is near the anterior end. The cylindrical trunk is separated from the head by a constriction. There are nine trunk segments, as indicated by the segmented ganglia of the ventral nerve cord (not by the indistinct external segmentation). The body is forked posteriorly, forming a pair of large, cylindrical, nonretractile appendages. The anus is found on the dorsal region of the fork. The anterior (head) appendages and posterior appendages or "feet" are flattened distally and equipped with adhesive gland cells to form adhesive disks which aid in locomotion as well as attachment to the host. Short sensory cirri, consisting of three lateral pairs (Stratiodrilus) and a pair on the posterior sides of the posterior feet, may be present. The protrusible pharynx has a very elaborate jaw apparatus which is highly specialized for the collection of microorganisms and consists of: a pair of fixed, parallel ventral mandibles which are flared and serrated anteriorly; dorsal maxillae comprising four pairs of movable articulated denticled pieces; a transverse troughshaped maxillary carrier that slides backward and forward on the mandibles; and a median dorsal rod.

The sexes are separate and sexually dimorphic. The males have a pair of retractile lateral claspers in the middle of the body and a median chitinous ventral penis. Fertilization is internal. The females lay large yolky eggs in capsules and attach them to the egg masses of the host. Development is direct, and the young hatch as immature miniature adults.

The histriobdellids live symbiotically in the branchial chambers of their crustacean hosts, where they attach by their suckerlike feet. They may occur in large numbers in a single host. They have limited powers of locomotion, but they leave the host when conditions are not ideal, and they are able to move from one host to another. They are able to crawl very slowly by a peculiar "walking" movement of the posterior feet. They appear to have a scraping and browsing type of feeding, grazing on the rich microflora (bacteria and blue-green algae) found in the branchial cavities of the host. They are probably beneficial to the host and can be classified as epizoic microphagous cleaning symbionts of crustacea. There is no clear evidence for parasitism.

Histriobdella, with the single species H. homari, is associated with several species of marine lobsters in northern Europe and along the northeastern American coast. Four species of Stratiodrilus are known from freshwater crayfish in Australia, Tasmania, Madagascar, and South and Central America; a fifth species is found on the pleopods of marine iso-

pods in South Africa.

References. S. R. Gelder and J. B. Jennings, The nervous system of the aberrant symbiotic polychaete Histriobdella homari and its implication for the taxonomic position of the Histriobdellidae, Zool. Anz. Jena, 194:293-304, 1975; J. B. Jennings and S. R. Gelder, Observations on the feeding mechanism, diet and digestive physiology of Histriobdella homari van Beneden 1858, an aberrant polychaete symbiotic with North American and European lobsters, Biol. Bull., 151:489-517, 1976.

ORBINIIDA

Order of polychaetes with a single family, Orbiniidae (=Ariciidae) The body is elongate and vermiform. The prostomium is conical or rounded, lacking appendages; it bears a pair of slitlike nuchal organs and sometimes a pair of small, deeply buried eyes. There is an achaetous buccal ring (one or two fused segments) without appendages. The

eversible pharynx is unarmed, soft, saclike, and simple, slightly lobed, or voluminously branched; on small interstitial forms the pharynx is nonevaginable and strongly muscular.

There are numerous segments, with biramous parapodia which lack internal acicula and dorsal and ventral cirri. The body is weakly to sharply separated into two regions: the anterior thorax, which is shorter, wider, flattened, firm, and muscular, attenuated anteriorly, with lateral parapodia; and the posterior abdomen, which is longer and subcylindrical, with the parapodia displaced laterodorsally, giving the dorsum a slashed aspect. The thoracic notopodia have fan-shaped bundles of notosetae and small, buttonlike, subulate to digitiform postsetal lobes; the neuropodia are in the form of low ridges or cushions, with few to many postsetal, subpodal, and ventral papillae. The abdominal neuropodia are elongate, bilobed distally, with or without a subpodal flange, and with a small bundle of neurosetae. There may be interramal cirri on some anterior abdominal parapodia. The setae are all simple, capillary, and with or without transverse denticled plates or serrations; or slender

and furcate; or stout and acicular, smooth or crenulate. Branchiae, when present, are medial to the notopodia, beginning in the anterior region and continuing posteriorly; they are simple (rarely branched), lanceolate, straplike, and ciliated. The pygidium is the site of the dorsal anus and two to four anal cirri.

The sexes are separate. Large yolky eggs are laid in small jelly masses or gelatinous cocoons anchored to the substratum, where early development takes place. A brief pelagic life is followed by settling and burrowing in sand or mud. These are nonselective subsurface deposit feeders; smaller interstitial species are probably selective bottom-deposit feeders. Orbiniids are found from low tidal zones to abyssal depths, sometimes in great abundance. There are about 11 genera and 200 species.

References. K. Fauchald, Order Orbiniida, in The Polychaete Worms: Definitions and Keys to the Orders, Families and Genera, Natur. Hist. Mus. Los Angeles Co. Sci. Ser. 28, pp. 14-18, 1977; M. H. Pettibone, Family Orbiniidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 274-294, 1963.

SPIONIDA

The body is elongate and cylindrical, is tapered posteriorly and has numerous segments, usually divided into more or less distinct regions. The prostomium and the achaetous buccal segment may be fused or distinct, with a pair of long, longitudinally grooved tentacular palps (deciduous) and a nuchal organ or posterior caruncle. The ventral mouth is enclosed in the first setiger. The pharynx or proboscis is unarmed, eversible, and ciliated. The parapodia are bira-

mous or subbiramous and are equipped with simple setae, postsetal lamellae, and interramal sensory organs. Members include tubicolous or burrowing forms and are bottom deposit feeders, using their tentacular palps and ciliated pharynx.

The order includes 5 families: Apistobranchidae, Spionidae, Trochochaetidae, Poecilochaetidae, and Heterospionidae.

Apistobranchidae. Family with a single genus (Apistobranchus) and 2 species. The body is elongate, cylindrical, and tapered posteriorly, with numerous segments (up to 60) which are divided into more or less distinct regions: a wider, somewhat flattened, short anterior thoracic region, and a long fragile posterior abdominal region, with some transitional segments. The prostomium and buccal segment are fused and suboval in shape, bearing a pair of long, contractile, longitudinally grooved tentacular palps (deciduous, may be missing or regenerating and short) and a pair of nuchal folds which are lateral to the palps and project posteriorly on the first setiger. The ventral mouth is enclosed in the lateral and posterior lips of the first setiger. The proboscis is unarmed, eversible, short, and globular.

The parapodia are subbiramous, without notosetae. The parapodia of the anterior thoracic region (seven setigers) have elongate, lanceolate, ciliated notopodia with a delicate internal aciculum (notopodia are lacking on the first setiger). The neuropodia are well developed; they bear thick bundles of amber-colored neurosetae and fimbriated post-setal lamellae which may extend nearly to the midventral line on some segments. Ciliated subconical interramal cirri occur between the notopodia and neuropodia.

The middle or transitional segments (setigers VIII-XI) lack interramal cirri; the notopodia are more slender and may be absent; the neuropodia have smaller bundles of neurosetae and fimbriated subpodal flanges. The posterior abdominal region (which begins on setiger XII) has slender cylindrical notopodia with an internal aciculum; the neuropodia are cylindrical, supported by a few acicula, with a few slender neurosetae and subpodal papillae. The py-

gidium, which encloses the dorsal anus, has two to four anal cirri.

The apistobranchids form loosely constructed burrows in soft bottoms of sand and mud. They are bottom deposit feeders and are widely distributed from shallow water to great depths; at times they may be very abundant.

References. M. H. Pettibone, Family Apistobranchidae, in Marine Polychaete Worms of the New England Region, pt. 1, Bull. U.S. Nat. Mus. 227, pp. 295-298, 1963.

Spionidae. Worms characterized by a body which is elongated and subcylindrical, tapering posteriorly, with numerous short and similar segments which are not clearly divided into distinct regions. Segmental dorsal transverse ciliated bands are usually present. The prostomium is small, reduced to a narrow band, and more or less wedge-shaped; the anterior border is entire, rounded, pointed, bilobed, or produced into prominent frontal horns; posteriorly, it is often prolonged on the anterior few setigers as a ridge or keel which may bear a small occipital tentacle. There may be small eyes. The peristomium, which contains the ventral mouth, is achaetous and large; it surrounds the prostomium as a pair of lateral lobes and is sometimes enlarged to form upturned membranous wings or a hood. The peristomium bears a pair of elongate, extensile, mobile palps with a ciliated longitudinal groove; they are often spirally coiled and easily detached, and they serve as chemoreceptors and for food detection and capture. Paired dorsal sensory nuchal organs occur along the sides of the prostomium and the anterior setigers. The pharynx is unarmed, only slightly protrusible and lobulate, forming a ciliated funnel;

in burrowing forms (Scolelepis) it may form a distinct sac, or

it may be bilobate (Paraprionospio).

The parapodia are biramous and lack embedded acicula; the podial lobes are in the form of glandular cushions or tubercles, and there are interramal sensory organs. Both rami have transverse series of setae; the presetal and postsetal lamellae are more or less developed, decreasing in size posteriorly. On some segments there may be transverse crests connecting the notopodia. Saccessive neuropodia are sometimes united by delicate membranes which form a series of interramal pouches. The setae are all simple, limbate or nonlimbate capillaries; these may be hooded or nonhooded hooks, which may be bidentate to multidentate, in more posterior segments; there are sometimes modified enlarged spines and companion setae on setiger V (Polydora), or a few saberlike neurosetae in the lower part of the bundles, and recurved notosetae on setiger 1 (Spiophanes), or hooked or needlelike notosetae on the posterior setigers (some Polydora). Dorsal and ventral cirri are lacking. Giliated branchiae, dorsal to the notopodia, are variable in occurrence: they may be absent (Spiophanes); there may be a single pair (Streblospio) or relatively few pairs confined to the anterior region (Prionospio); or they may extend along the length of the body (Spio). The branchiae may be free or more or less fused to the dorsal notopodial lamellae, and they may be cirriform, straplike, or pinnate. The pygidium, with the dorsal anus, may be drawn out in the form of blunt lobes, digitiform cirri, a collar, or a funnel.

The sexes are separate and sometimes sexually dimorphic (Pygospio). Fertilization may be preceded by copulation with spermatophores introduced into the seminal receptacles of the female. The sex products may be given off into the water, and pelagic development may follow, the larvae feeding on the plankton; some species have large yolky eggs which develop into lecithotrophic larvae; these mature rather rapidly and are nourished by the yolk until metamorphosis. The eggs may be deposited in mucous masses or capsules attached to the substrate or to the wall of the tube; short or long periods of broad protection by the female follow. Rarely, viviparity occurs, and the eggs are deposited in vascular brood pouches of the female and develop into advanced larvae (Streblospio). Characteristic spionid larvae are well represented in the plankton. Some spionids commonly reproduce asexually by fragmenting into several small pieces, followed by regeneration (Pygospio).

The spionids are found most commonly on muddy or sandy bottoms. They may burrow in shifting sand or may construct fragile solitary or aggregated tubes of sand or mud, with a firm mucoid lining. Some (Polydora) excavate calcareous bodies such as mollusk shells, algae, or rocks, The mechanism by which they bore is thought to be a combination of chemical and mechanical action. Some species of Polydora are pests on oysters, causing mud blisters in the shells or smothering them with numerous mud tubes. They are surface and bottom deposit feeders, taking in minute organisms and organic debris in the water which is brought to their tubes by the ciliary currents of the animals; the organisms and debris are caught by mucus on the palps and carried along ciliated grooves to the mouth; some of the particles are used to build tubes, and others are utilized as food.

The family contains about 32 genera and 320 species. The spionids are most common in shallow depths but are also well represented in deeper waters. They are worldwide in distribution, and many species are cosmopolitan. Their

wide distribution is associated with their long larval planktonic life, and young of considerable size, with long larval setae, may be found in the plankton. They are mostly marine, but a few species are known from freshwater.

References. N. M. Foster, Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea, Studies of the Fauna of Curação and Other Caribbean Islands, vol. 36, pp. 1-183, Martinus Nijhoff, The Hague, 1971; S. A. Haigler, Boring mechanism of Polydora websteri inhabiting Crassostrea virginica, Amer. Zool., 9:821-828, 1969; L. Hannerz, Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden), Zool. Bd. Uppsala, 31:1-204, 1956; J. L. Simon, Reproduction and larval development of Spio setosa (Spionidae; Polychaeta), Bull. Mar. Sci., 17: 398-431, 1967.

Trochochaetidae. Family (=Disomidae) containing a single genus, Trochochaeta (=Disoma) and 7 species. The body is long, slender, and subcylindrical, tapering posteriorly, with numerous (up to 200) segments; it is divided into more or less distinct regions: a short anterior thoracic region and a long abdominal region, with some transitional segments. The prostomium is small and elongate-oval or fusiform, wedged between the anterior setigerous peristomial segments; it usually has a medial crest which extends posteriorly as a narrow caruncle on the first segment or beyond and sometimes bears a small median antenna; there is a pair of long, extensible, longitudinally grooved palps lateral to the prostomium (readily deciduous and often found in varying stages of regeneration). The biramous parapodia of the first segment project anteriorly and dorsally and bear bundles of capillary setae and subconical postsetal lobes; the segment is enlarged ventrally, enclosing the mouth. The second segment is closely allied to the first; the biramous parapodia are shifted ventrally and contribute to the lower lip of the mouth, the postsetal lobes are similar to those of the first segment, and notosetae are usually absent. The pharynx is eversible, unarmed, lobulated, and densely ciliated. In addition to the capillary notosetae and neurosetae, the neuropodia of segment III and sometimes also of segment II have specialized heavy acicular spines. Starting at the fifth thoracic segment, the notopodia have fan-shaped bundles of capillary notosetae; the neuropodial lobes are subcylindrical and are furnished with neurosetae of various types-capillary, lanceolate, acicular, with spiny or hairy sheaths. The postsetal lobes of both rami are oval or platelike, with the borders entire or serrated

In the abdominal region, the body wall becomes markedly thinner and delicate and the notopodia disappear; the neuropodial lobes become smaller, with few heavy acicula and capillary neurosetae, and they have digitiform postsetal lobes that continue posteriorly on each segment as thin flanges. Notopodia reappear in the more posterior abdominal segments in the form of low mounds armed with a bundle of several dark pointed acicular spines; when extended, they may appear as stellate or wheellike organs. The pygidium encloses the terminal anus and is lobulated or encircled by a variable number of anal cirri.

The sexes are separate; the larvae have a long pelagic development. The trochochaetids are tubicolous and live on muddy bottoms. They construct long cylindrical tubes of fine mud particles cemented together by a fibrous secretion. They are bottom deposit feeders, using their long paired tentacular palps and ciliated pharynx.

References. M. H. Pettibone, Contribution to the poly-

chaete family Trochochaetidae Pettibone, Smithson. Contrib. Zool., 230:I-21, 1976; M. H. Pettibone, Family Trochochaetidae, new name (=Disomidae and Disomididae), in Marine Polychaete Worms of the New England Region, pt. I, Bull. U.S. Nat. Mus. 227, pp. 308-316, 1963.

Poecilochaetidae. The body is long and slender, tapering posteriorly, with numerous segments (up to 110), more or less divided into distinct regions. The integument may be smooth or papillated. The prostomium is small and subglobular, enclosed in the first setigerous segments; it usually has four eyespots, a pair of long, extensible, grooved tentacular palps (easily deciduous), and a well-developed trilobed nuchal organ in which the median lobe, or all three lobes, may be elongated and extended posteriorly as ciliated, grooved tentacles with sensory hairs. The ventral mouth is enclosed in the first two setigers; the upper lip has a cirriform facial tubercle projecting anteriorly, appearing as a frontal antenna. The pharynx is eversible, short, spherical, and unarmed. The parapodia of the first setiger are biramous, with long capillary setae directed anteriorly to form a cephalic cage, and with subconical postsetal lobes (sometimes called tentacular cirri).

The biramous parapodia of the anterior region (segments 1 to XVI) have simple setae in the form of slender capillaries, stiff spiny setae (which usually begin on setiger VII), and acicular hooked neurosetae (on setigers II, III, and sometimes IV). The postsetal lobes (sometimes called dorsal and ventral cirri) are subconical, except on setigers VII to XI or XIII, where they are flask-shaped, with a swollen basal part, a thin elongated neck region, and a bulbous tip; they are held stiffly. Small bulbous sensory organs are found between the rami. There may be a chitinous

triangular plate on the dorsal side of setiger IX.

The more fragile abdominal or genital region, which begins on setiger XVII, has biramous parapodia which bear large fan-shaped bundles of simple setae of various types: spinous, pectinate, plumose or featherlike, hooked acicular, and acicular with terminal brush. The postsetal lobes are smaller, irregular in size, and subconical to cirriform. The lateral interramal sensory organs are present but withdrawn in a pit. A few branchial filaments may occur on the posterior sides of the parapodia. The posterior segments are somewhat flattened, with rows of hooked notosetae. The pygidium is bulbous and is the site of the dorsal anus and three or four anal cirri. Elicodasia differs from Poecilochaetus in lacking nuchal organs, in having parapodia on the first two segments, which are reduced and do not form a cephalic cage, in lacking the characteristic flask-shaped postsetal lobes, and in having neuropodial acicular hooks on numerous segments, beginning on setiger III or IV.

The sexes are separate. The eggs are large and yolky, with thick membranes. Development takes place in the plankton, where the larvae remain for long periods until late stages of development (up to 50 segments). The post-larvae produce a mucous feeding string to which bits of particulate matter adhere. They swim, as do the adults when disturbed, by rapid, undulatory, snakelike move-

ments of the whole body.

The poecilochaetids are found on sand, on sand mixed with clay or mud, or in mud-filled crevices. They construct U-shaped burrows lined with stiff layers of mud or clay and mucus. A current of water is brought into the burrow by undulating movements of the body and fanlike beating of the parapodial setae. Some species form friable mucous tubes covered with debris. They are suspension feeders on fine organic particles and small organisms in the water current. The long tentacular palps may extend out of the burrow in search of debris on the bottom.

The family contains 2 genera: Poecilochaetus, with 14 species, and Elicodasia, with a single species, E. mirabilis. The species are mostly tropical or subtropical, living in intertidal regions or shallow depths, but they also extend into deep

and abyssal depths.

References. E. J. Allen, The anatomy of Poecilochaetus, Quart. J. Microsc. Sci., 48:79-151, 1904; J. H. Day, Family Trochochaetidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 519-521, 1967; L. Laubier and J. Ramos, A new genus of Poecilochaetidae (Polychaetous annelids) in the Mediterranean: Elicodasia mirabilis, Proc. Biol. Soc. Wash., 86:69-78, 1973; G. Pilato and G. Cantone, Nuove specie di Poecilochaetus e considerazione sulla famiglia dei Poecilochaetidae (Annelida, Polychaeta), Animalia. 3:29-63, 1976.

Heterospionidae. Family with a single genus (Heterospio) and about 6 species. The body is elongated, slender, linear, and stiff and wiry, divided into three regions: head, thorax, and abdomen. The prostomium is small and subconical to subtriangular, lacking appendages and eyes; it bears a pair of nuchal organs. The peristomium contains the ventral mouth and encloses the prostomium; it is biannulate and provided with a pair of long, longitudinally grooved, spionform tentacular palps (often broken off). The pharynx is eversible, soft, saclike, and unarmed. The anterior thoracic region is somewhat flattened dorsoventrally and composed of seven to nine (usually nine) short crowded segments with biramous parapodia. The podial lobes are weakly developed, with simple, long, flowing, capillary setae in fanshaped bundles in both rami. Six to eight pairs of long branchial filaments are attached dorsal to the notopodia, beginning on setiger II. The posterior abdominal region has greatly prolonged, cylindrical segments; cinctures of short capillary setae may nearly encircle the body, and there are sometimes additional acicular setae with tapered tips (subuluncini). The body terminates in an inflated region consisting of three short segments, each with acicular spines in biramous series; the anus is terminal.

The heterospionids are probably tubicolous and deposit feeders. They are poorly known from widely scattered areas, ranging from shallow water to great depths.

References. O. Hartman, Family Heterospionidae, new family, in *Deep-water Benthic Polychaetous Annelids off New England to Bermuda and Other North Atlantic Areas*, Allan Hancock Found. Publ. Occas. Pap. 28, pp. 162–164, 1965; L. Laubier, C. Picard, and J. Ramos, Les Heterospionidae (Annélides polychètes sédentaires) de Méditerranée occidentale, *Vie Milieu*, 23:243–254, 1972–1973.

CHAETOPTERIDA

Order consisting of the single family Chaetopteridae. The body is elongate, cylindrical, and fragile, composed of numerous segments and divided into three regions; there is a dorsal ciliated groove extending along its length; it produces abundant mucus and is always protected by a tight-fitting tube. The prostomium is small and ovoid or indistinct

and fused; it is enclosed in a broad, glandular, collarlike buccal segment (peristomium) and has a pair of very long and spirally coiled tentacular palps with a deep ciliated groove, and sometimes a pair of small eyes. The mouth is terminal; the pharynx is simple and noneversible. A pair of small tentacular cirri with embedded fine notosetae is sometimes present on the dorsal surface of setiger I (Phyllochaetopterus).

The anterior region (9–18 short segments) is flattened dorsally and rounded ventrally, with a thick glandular epidermis and obliquely truncate uniramous parapodia (notopodia only). The notosetae are simple, lanceolate, or paddlelike, with additional stout, modified, cutting spines on setiger 1V. The secreted tube is formed by the ventral

surface of the anterior region.

The middle region (2-30 segments or more, some very long) has biramous parapodia; the notopodia are unilobed, bilobed, or trilobed and foliaceous, supported by embedded notosetae, with ciliated membranelles which serve to create a current of water through the tube; the medial parts of some notopodia secrete mucus and form one to many mucous bags for straining food from water. The dorsal ciliated groove is enlarged at intervals, forming ciliated cuplike organs (cupulas) which roll up the mucous bags and form food balls for transfer anteriorly to the mouth. The neuropodia are lateroventral, in the form of ridges which bear rows of numerous minute pectiniform neurosetae (uncini).

The posterior region consists of numerous short segments which are sharply divided and usually swollen with genital products, giving a beaded appearance; its parapodia are biramous; the notopodia are cylindrical or digitiform, supported by a few embedded notosetae, and the neuropodia are in the form of bilobed ridges or pinnules bearing uncini. The anus is terminal.

These worms are very closely adapted to tubicolous life. The tubes are formed of secreted organic material and are horny, translucent, leathery, or parchmentlike; they are often annulated distally and sometimes incorporate cemented sand grains. Typically the tubes are embedded vertically in the substratum, with openings projecting above the surface; they have perforated transverse partitions in the lower part and are closed basally. These species are efficient filter feeders. A feeding current of water is brought into the tubes by the beating of cilia on the notopodia, which creates a continuous water current that passes over the dorsal surface of the body and through a series of mucous bags; these strain out suspended detritus and plankton and are then rolled up in cupulas and carried anteriorly to the mouth by periodic reverse beating of the cilia along the ciliated groove. Fecal pellets and foreign material are also carried forward along the ciliated groove, and then transferred to long palps and voided from the

tube; the long tentacular palps have deep ciliated grooves with cilia beating anteriorly toward the tips; they function to remove feces and maintain an unobstructed tube.

The very bizarre and cosmopolitan Chaetopterus variopedatus differs from other members of the family (Mesochaetopterus, Phyllochaetopterus, Spigchaetopterus, Sasekumaria) in a number of respects. It lives in a loose-fitting, U-shaped, parchmentlike tube which has narrower openings projecting from the substratum, forming inhalant and exhalant siphons. The body is large, flabby, and soft, emitting abundant mucus and a blue-violet luminescence. The tentacular palps are short. The dorsal longitudinal ciliated groove is confined to the anterior and middle regions of the body. The middle region is composed of five large segments, the second with large winglike notopodia which secrete a single large mucous bag and have a single cupula; on following segments the notopodia are fused middorsally, forming three large circular fans which drive water through the tube by a pistonlike action; the neuropodial uncinigerous pinnules are fused midventrally, forming suckers and attaching to the tube. The segments of the posterior region are numerous (20-80); the notopodia are digitiform, with embedded setae; the neuropodia have bilobed uncinigerous pinnules. Elongated cylindrical fecal pellets are removed through the exhalant siphon. This species commonly harbors commensal crabs and polynoid polychaetes in its tubes.

The sexes are separate in chaetopterids. The eggs and larvae are found in the tubes. The larvae are pelagic, with a very long planktonic life extending over several months. These large nectochaete larvae are the most unusual larvae of the Polychaeta, with a spherical body clearly divided into three regions: the anterior region, with a broad prostomium and peristomium, terminal mouth, paired eyes, short tentacular palps, and seven setigerous segments with notosetae similar to those of adults; the middle region, with one or two prominent ciliary bands (mesotrochs) and indistinct segments; and the posterior region, which is tapered, with indistinct segments and a terminal cylindrical appendage. They are predacious, feeding on other larvae. Some species reproduce by autotomy and regeneration, in addition to sexual reproduction, forming densely clustered and intertwining tubes on pilings (Phyllochaetopterus prolifica).

The family contains 5 genera and about 45 species. They are widely distributed on sandy and muddy bottoms, ranging from intertidal regions to great depths, from the Arctic

to the Antarctic, Some are cosmopolitan,

References. R. D. Barnes, Tube-building and feeding in chaetopterid polychaetes, *Biol. Bull.*, 129:217-233, 1965. J. H. Day, Family Chaetopteridae, in *A Monograph on the Polychaeta of Southern Africa*. pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 522-532, 1967.

MAGELONIDA

Order with a single family, Magelonidae, and single genus, Magelona, and about 40 species. The body is slender, threadlike, and cylindrical, tapering posteriorly, with numerous segments (up to 150); it is divided into two distinct regions: a short anterior thoracic region, and a long posterior abdominal region. The prostomium is large and oval to subtriangular, sometimes with anterolateral projections (lateral horns) which are flattened and spatulate, supported by two pairs of well-developed longitudinal muscular bun-

dles and appearing as dorsal ridges; it lacks appendages and eyes. The prostomium is fused posteriorly with the achaetous peristomium, which encloses the ventral mouth and bears a pair of very long tentacular palps which have densely crowded, long, capitate papillae along one side for most of their length. The pharynx is eversible, large, globular, and unarmed.

The parapodia are biramous, with lamellar postsetal lobes and ciliated lateral organs between the rami. The

parapodia of the thoracic region (nine setigers) have fanshaped bundles of limbate capillary setae with well-developed postsetal lamellae in both rami; sometimes there are specialized setae on setiger IX. Both rami of the abdominal parapodia have rows of long-handled hooded hooks. The lateral lamellae are confined to the lower part of the notopodia and the upper part of the neuropodia, sometimes with small cirriform lobes (which may be referred to as dorsal and ventral cirri) medial to the rows of hooks. The pygidium bears the subterminal anus and a pair of lateral anal cirri.

The sexes are separate. The larvae have a prolonged pelagic development. The magelonids burrow in sand and muddy sand and form mucus-lined burrows that may be described as fragile tubes. They use their spadelike head and large distensible proboscis to force their way through

the substrate. They are detritus bottom deposit feeders. Their elongate tentacular palps are extended from the openings of their burrows, and food particles gathered on the sticky papillae are brought to the mouth by muscular contraction. The vascular tentacular palps are also important in respiration. Members are widely distributed in shallow waters.

References. M. L. Jones, Four new species of Magelona (Annelida, Polychaeta) and a redescription of Magelona longicornia Johnson, Amer. Mus. Nov., 2164:1-31, 1963; M. L. Jones, On the morphology, feeding and behavior of Magelona sp., Biol. Bull., 134:272-297, 1968; M. I. Jones, Three new species of Magelona (Annelida, Polychaeta) and a redescription of Magelona pitelkai Hartman, Proc. Biol. Soc. Wash., 91:336-363, 1978.

PSAMMODRILIDA

Order consisting of the single aberrant family Psammodrilidae, with 2 genera (Psammodrilus and Psammodriloides), each with a single species. Both species are confined to the interstitial microfauna and show retention of larval characters in the adults, with the parapodia very reduced. The body is transparent, small (up to 9 mm in length and 0.3 mm in width), grub-shaped, and cylindrical, tapering slightly posteriorly, with the segmentation feebly marked; it is divided into three regions: head, thorax, and abdomen. The head, formed of the fused prostomium and peristomium, is bluntly pointed, lacking appendages and furnished with a pair of ciliated nuchal organs and a ciliated T-shaped ventral mouth. The pharynx is noneversible. The following segment is achaetous; in Psammodrilus it is enlarged, forming a collarlike pharyngeal region where the longitudinal muscles act as a suction pump used for feeding on diatoms and detritus (not modified in Psammodriloides). The thorax consists of six segments, with the parapodia reduced to ciliated filiform dorsal cirri (the first three or four are longer), each supported by an internal notoaciculum which is stiff basally and tapers distally to a flexible tip; neuropodia are lacking. The abdominal segments (up to about 30) have low neuropodial ridges with a row of small hooks or uncini (uncinigerous tori); the uncini, up to 16 per torus (in Psammodrilus) or 1 per torus (in Psammodriloides), are sickleshaped, with several distal teeth and a long stem; notopodia

are lacking. The pygidium, with the subterminal ciliated anus, is rounded and lacks cirri. Both the head and the ventral surface are richly ciliated; seven transverse dorsal ciliated rings are present on the head (preoral) and thoracic segments.

The sexes are separate. The females have large yolky eggs. The larvae are ciliated and nonpelagic, showing direct development. These worms may form transparent mucous tubes covered with sand grains, in which they are semisessile, the anterior part extending from the tube and exploring a limited territory (Psammodrilus), or they may be highly mobile (Psammodriloides). They feed on microscopic algae, chiefly benthic diatoms. The family is known from the North Sea to France, and in New England; it is found from intertidal zones to a depth of 65 m in fine sand.

References. K. D. Hobson, Psammodrilidae, in Polychaeta new to New England, with Additions to the Description of Aberranta enigmatica Hartman, Proc. Biol. Soc. Wash. 84, pp. 249-250, 1971; B. Swedmark, Psammodriloides fauvelin. gen., n. sp. et la famille des Psammodrilidae (Polychaeta, Sedentaria), Ark. Zool., 12:55-64, 1959; B. Swedmark, Recherches sur la Morphologie le Développement et la Biologie de Psammodrilus balanoglossoides Polychète Sédentaire de la Microfaune des Sables, Arch. Zool. Exp. Gen., 92:141-220, 1955.

CIRRATULIDA

Species in this order have an clongated, linear body with numerous segments. The prostomium is small but distinct, lacking appendages (sometimes with a median antenna in Paraonidae); it may or may not be provided with eyespots and nuchal organs. The achaetous peristomium, which encloses the ventral mouth, is more or less fused with the prostomium; it lacks appendages in 2 of the 3 families, but has a pair of spioniform tentacular palps or numerous grooved tentacular filaments on the posterior border in Cirratulidae. The pharynx is unarmed and usually nonevaginable (evaginable in Paraonidae). The parapodia are bira-

mous, without internal acicula and with indistinct setal lobes, the setal bundles arising directly from the sides of the body (sometimes there are postsetal lobes in Paraonidae). The setae are all simple (some are pseudocompound in Paraonidae), limbate, capillary, furcate, and acicular. Dorsal and ventral cirri are lacking. When present, the paired branchiae are located dorsal to the notopodia. The pygidium contains the dorsal anus and usually lacks anal cirri. The sexes are separate. These worms are burrowing forms and bottom deposit feeders. The order contains 3 families: Paraonidae, Questidae, and Cirratulidae.

Paraonidae. The body is elongated, slender, and threadlike. The prostomium is subconical to founded, without appendages except for sometimes a median antenna; it has a pair

of ciliated sensory nuchal organs (appearing as slits), sometimes a pair of small eyes, a terminal sensory organ capable of extension and retraction, and transverse bands of cilia.

The peristomial ring is more or less fused with the prostomium. The ventral mouth is enclosed in the peristomium and one or two anterior setigerous segments, which form anterior, lateral, and posterior lips. The pharynx is unarmed, lined with ciliated epithelium, and evaginable as a cylindrical or feebly lobed proboscis. There are numerous body segments with biramous parapodia which are essentially without setal lobes and lack internal acicula. The notopodial postsetal lobes are tuberclelike, conical, cirriform, subulate, or angular. Postsetal neuropodial lobes may be present or absent on some anterior segments. Paired hranchiae, when present, are confined to the anterior part of body, dorsal to the notopodia; the branchiae may be simple, unbranched, and straplike, or wide foliaceous and ciliated. The setae are simple or pseudocompound, capillary, limbate or nonlimbate, and straight or curved. Modified (furcate or modified furcate) setae are sometimes found in the notopodia. Neuropodia of the posterior regions usually have modified setae of several types: acicular, with or without slender tips or aristae. The pygidium is rounded to truncate, and it bears the dorsal anus and a few anal cirri.

The sexes are separate. The females carry relatively few large eggs in the more posterior segments. Mature adults sometimes appear in surface waters. Development of the family is unknown but presumed to be nonpelagic, owing to the large egg size.

These worms are found in soft bottoms of mud or sand, where they construct thin fragile tubes cemented with mucus or are freely moving, forming spiral and meandering burrows. They are sometimes found in very dense populations. They are selective deposit feeders on meiofauna and meioflora.

The family contains about 10 genera or subgenera and less than 100 species. It is universally distributed, from the Arctic to the Antarctic, and from littoral (marine parts of estuaries) to abyssal regions.

References. V. E. Strelzov, Polychaete Worms of the Family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria). Akad. Nauk S.S.S.R., Leningrad, 1973 (Eng. transl., TT 76-52002, Smithsonian Institution and National Science Foundation, Washington DC, 1978).

Questidae. Family containing 2 genera (Questa and Novaquesta), each with a single species, showing affinities to oligochaetes. The body is elongated, slender, and linear, with numerous segments (up to 60). Questids are minute (up to 10 mm in length and 0.4 mm in width). The prostomium is suboval to subtriangular, without appendages or eyes. The peristomium encloses the ventral mouth, is achaetous, and smooth or somewhat biannulate. The pharynx is nonevaginable and unarmed.

The parapodia are biramous, with indistinct lobes, the two bundles of setae arising directly from the sides of the body. The setae are all simple, comprising long serrated capillaries and shorter, thicker bifid hooks which consist of a small apical tooth and a larger tooth at right angles to the shaft, with a membranous guard or hood more basally; additional trifurcate notosetae may be present (Novaquesta) or absent (Questa) in some anterior segments. Dorsal and ventral cirri are lacking. Paired cirriform branchiae may be present on some posterior segments (Questa) or absent (Novaquesta). The terminal anus is enclosed in the pygidium, which lacks anal cirri.

The sexes are separate, and the reproductive structures are confined to a few segments. These worms are sexually dimorphic; the males have a dorsal thickening of the body wall on setigers XIII and XIV, and the females have a few

large yolky eggs in setigers XII and XIII. The questids include interstitial forms and are found on shelf depths in coarse sediments. They are known from a few scattered areas: southern California, British Columbia, and Massachusetts.

References. O. Hartman, Family Questidae, new family, in Quantitative Survey of the Benthos of San Pedro Basin. Southern California. pt. II, Allan Hancock Found. Pac. Exped. 19: 197-198, 1966; K. D. Hobson, Novaquesta trifurcata, a new genus and species of the family Questidae (Annelida, Polychaeta) from Cape Cod Bay, Massachusetts, Proc. Biol. Soc. Wash., 83:191-194, 1970.

Cirratulidae. Members have an elongated, linear, cylindrical body with numerous (up to 350 or more) short similar segments, tapering anteriorly and posteriorly; the posterior segments may be somewhat flattened and inflated. They are mostly small to moderate in size. The prostomium is small, subconical or bluntly rounded, and more or less fused with the peristomium; it lacks appendages and may or may not bear (two to four pairs) eyespots. The peristomium is elongate, formed of at least two fused achaetous segments, sometimes appearing triannulate; it encloses the ventral mouth and is provided either with a pair of large, grooved, spioniform palps on the posterior border (Chaetozone, Tharyx) or with two groups of more or less numerous, more slender, grooved tentacular filaments inserted on one or more anterior setigerous segments (Cirratulus, Cirriformia); both types are furnished with a single blood vessel. The pharynx is noneversible and unarmed.

The parapodia are biramous, with the lobes indistinct, the two bundles of setae arising directly from the sides of the body. The setae are all simple, including capillaries, and additional acicular setae, which may be distally entire and bidentate or multidentate, may be present or absent. Dorsal and ventral cirri are lacking. Branchiae are long, slender, and filamentous, inserted dorsal to the notopodia; there is usually one pair per segment (there may be more than one pair in *Timarete*). The branchial filaments are furnished with two blood vessels (hemoglobin in the plasma) forming a loop, and they are capable of great elongation and contraction. The dorsal anus is enclosed in the posterior few segments and pygidium; there are no anal cirri.

The sexes are separate. Females may deposit their eggs in soft slimy masses of irregular shape which adhere to stones or mud on the bottom; trochophore larvae emerge and either remain close to the bottom or enter the plankton for a short time. Some species free their sex products directly into the water, giving rise to pelagic larvae. Epitokous adults with long capillary setae on both rami may occur. Members of the family may also reproduce asexually by fragmentation and regeneration.

The cirratulids are burrowing, sluggish forms, commonly buried just below the surface in depths of only several centimeters, with their red, filamentous, highly motile tentacular filaments and branchiae extending above the surface and serving for aeration. They secrete abundant mucus and may construct soft muddy tubes. They may be found between or under rocks and nestling among shells and holdfasts in the intertidal zone, as well as in subtidal soft sediments of muddy sand. They are surface deposit feeders, feeding indiscriminately on the detritus of the surface layers of the mud by a kind of suction.

Species of *Dodecaceria*, which burrow in calcareous structures such as calcareous algae, shells of bivalve mollusks,

dead coral colonies, and limestone, differ from other members of the family. They form U-shaped burrows with a single opening, and the body of the worm is curved to fit the burrow. The fused prostomium and peristomium form a hood over the subterminal mouth, with a pair of tentacular palps. The branchiae (2-11 pairs) are restricted to the anterior part of the body. The anterior and posterior ends may extend from the single opening of the burrow. The acicular setae are excavated subdistally (spoon-shaped). In life these are dark green to black worms. They are particularly noted for their complex life histories, which include sexual reproduction by protandrous hermaphroditic atokes (sometimes viviparous), by dioecious and oviparous epi-

tokes, and by parthenogenetic females. They may also reproduce asexually by fragmentation and regeneration, sometimes from only a few segments. *Dodecaceria fistulicola* reproduces asexually and forms boulder-sized colonies.

The family contains 9 genera and about 140 species. They are widely distributed and may be found in great

numbers.

References. J. H. Day, Family Cirratulidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 498-518, 1967; P. H. Gibson, Systematics of Dodecaceria (Annelida: Polychaeta) and its relation to the reproduction of its species, Zool. J. Linn. Soc., 63:275-287, 1978.

CTENODRILIDA

Species in this order have a minute body with relatively few segments. The prostominm lacks appendages. The buccal segment, with the ventral mouth, is distinct. The pharynx is eversible, bulbous, and unarmed. The parapodia are unira-

mous or biramous, lacking distinct lobes and bearing relatively few simple setae. The order is composed of 2 families: Ctenodrilidae and Parergodrilidae.

Ctenodrilidae. Family of worms which may have a short grublike body with relatively few (up to 15) segments (Ctenodrilus, Aphropharynx) or a long threadlike body with more numerous (up to 40) segments (Raphidrilus, Zeppelina). The prostomium is bluntly conical, without appendages or eyespots; a pair of nuchal organs may be present or absent. One or several anterior achaetous segments, usually without tentacles but with one to four tentacles in Zeppelina, may be more or less fused with the prostomium. The ventral side of the prostomium and the anterior achaetous buccal segment may be densely ciliated. The pharynx is eversible and bulbous, used in feeding and movement. The parapodia are biramous, the notopodia and neuropodia represented by reduced bundles of two to four setae per bundle. The setae are simple, capillary, acicular, and dentate or smooth. The pygidium is simple, with a posterior anal pore.

The ctenodrilids commonly reproduce asexually by transverse fragmentation at the segmental boundaries. New prostomia may appear on the dorsal surface of a number of consecutive body segments, forming chains, followed by intrasegmental fragmentation. These worms may also reproduce sexually as protandrous hermaphrodites. Internal gestation of larvae is known for Raphidrilus nemasoma; the emergent larvae have eyes and segmental filiform branchiae. They have short life cycles, reaching sexual maturity within a few days.

The family contains 4 genera (Ctenodrilus, Aphropharynx, Raphidrilus, Zeppelina) and 10 species. They are widely distributed, occurring in clumps of debris, and are commonly found in aquariums of marine laboratories. Ctenodrilus serratus is cosmopolitan; it moves in either direction by slowly creeping.

References. T. Harris, Family Ctenodrilidae, in Unusual Polychaeta from the Isles of Scilly with the description of a new species of *Zeppelina* (Vaillant 1890), *J. Natur. Hist.*, 5:706-711, 1971; O. Hartman, Family Ctenodrilidae, in

Polychaetous Annelids, pt. 6: Paraonidae, Magelonidae, Longosomidae, Ctenodrilidae and Sabellariidae, Allan Hancock Pac. Exped. 10, p. 323, 1944; M. Wilfert, Aphropharynx heterochaeta nov. gen. nov. spec., ein neuer polychet aus der familie Ctenodrilidae Kennal 1882, Cah. Biol. Mar., 15: 495-504, 1974.

Parergodrilidae. Family (=Stygocapitellidae) with 2 monotypic genera: Parergodrilus heideri and Stygocapitella subterranea. The body is very small, with few segments (up to 15); it is cylindrical and grub-shaped, slightly tapered at both ends. The prostomium is oval and lacks appendages and eyes. The ventral mouth is enclosed in the first achaetous buccal segment. The pharynx is eversible and saclike and ends in a pistonlike tongue (Stygocapitella) or a chitinous disk (Parergodrilus). The parapodia are uniramous and ventrolateral, lacking distinct podial lobes. The setae are simple and few in number; they are of three kinds in Stygocapitella: short bilimbate, bilimbate with long whiplike tips, and short furcate; and they are of a single kind in Parergodrilus: stout and acicular, two per bundle. The pygidium, with the terminal anus, is short and rounded, without appendages.

The sexes are separate. In Parergodrilus, the males have copulatory hooks and the eggs are laid in capsules. Stygocapitella lives interstitially in shallow marine sands and is widely distributed. Parergodrilus is terrestrial, crawling by means of the ventral setae and pharynx on humid soils and decomposing plant material (especially of beech trees in Austria).

References. G. Hartmann-Schröder, Familie Parergodrilidae Reisinger, 1960, in Annelida, Borstenwürmer, Polychaeta, vol. 58 of Die Tierwelt Deutschlands und der angrezenden Meeresteil, pp. 403-406, 1971; T. G. Karling, Zur Kenntnis von Stygocapitella subterranea Knöllner und Parergodrilus heideri Reisinger (Annelida), Ark. Zool., 11:307-342, 1958.

COSSURIDA

Order consisting of the single family Cossuridae. The body is small (up to 15 mm), threadlike, and cylindrical, tapering anteriorly and posteriorly, with numerous (up to 120) short similar segments. The prostomium is conical or rounded,

without appendages and usually without eyes (sometimes with a single pair). The peristomium encloses the ventral mouth; it consists of one or two achaetous rings which lack appendages. The pharynx is eversible, soft, and unarmed,

with fingerlike ciliated processes. A single long branchial filament is found on the middorsal surface of an anterior setigerous segment (11-1V); it may be almost as long as the body. The parapodia are biramous; a few anterior segments may be uniramous. The podial lobes are indistinct, lacking embedded acicula and bearing fan-shaped bundles of setae which arise directly from the body wall. The setae are all simple limbate capillaries. Some acicular spines may be found in posterior segments (Cossurella). Dorsal and ventral cirri and lateral branchial filaments are absent. The pygidium bears the dorsal anus and usually three long

anal cirri; there are sometimes additional papillae.

The cossurids are deposit feeders; they burrow in sandy mud and may have membranous tubes. They are found from shallow to abyssal depths.

The family Cossuridae contains 2 genera (Cossura and

Cossurella) and about 18 species.

References. K. Fauchald, Family Cossuridae Day, 1963, in Benthic Polychaetous Annelids from Deep Water off Western Mexico and Adjacent Areas in the Eastern Pacific Ocean, Allan Hancock Monogr. Mar. Biol. 7, pp. 206-213, 1972.

FLABELLIGERIDA

The body has essentially similar segments and is not divided into distinct regions. The integument is more or less densely papillated. The prostomium is reduced, fused to the peristomium, and more or less withdrawn into the anterior setigerous segments. The pharynx is unarmed and noneversible, with a ventral pad. The parapodia are bira-

mous, without embedded acicula, and the podial lobes are reduced or absent, the two bundles of setae arising directly from the body walk These worms include burrowing, sluggishly motile, bottom deposit feeders. The order contains 3 families: Flabelligeridae, Acrocirridae, and Fauveliopsidae.

Flabelligeridae. The body is subcylindrical (Flabelligera); club-shaped with an inflated anterior region and a tapering narrower tail region (Pherusa); short, subfusiform, and grub-shaped (Brada); or stout, flattened, and disk-shaped (Hyphagus). The segments are short, essentially similar, and rather ill-defined. The body has a glandular epithelium and is usually thickly covered with papillae, which may be small wartlike, elongate, filamentous, or club-shaped. The entire body may be covered in a thick mucous mantle through which the pedunculate papillae and setae project (Flabelligera); the mucilaginous coat may be toughened to a cartilaginous consistency (Pycnoderma); or the mucous matrix may be impregnated with sand, mud, and debris. The head is composed of unique complex structures enclosed in a membranous sheath; it is more or less retractable into the anterior setigers and is mostly hidden from view. It is formed of an indistinct prostomium fused with the peristomium, and consists of a prostomial ridge with usually four eyes, a pair of large, very extensible, grooved palps, a semicircular dorsal membrane bearing two groups of ciliated, retractile, filamentous or cirriform tentacles (branchial filaments), and a ventral slitlike mouth enclosed in upper, lateral, and lower lips. The pharynx is unarmed and noneversible, with a ventral muscular pad. The capillary setae and club-shaped sensory papillae of the anterior segments may be elongated and directed anteriorly to form a compact group, the so-called cephalic cage, which serves to protect the buccal apparatus. The latter serves for feeding (ciliary-mucoid), respiration (blood vessels in both palps and tentacles), and excretion (nephridiopores open into the dorsal membrane), and also functions as a sense organ.

The parapodia are biramous, usually with the rami reduced to two widely separated bundles of setae arising directly from the body wall; sometimes the podial lobes are prominent (Flabelligera). The notosetae are simple, crossbarred or smooth capillaries. The neurosetae may be similar to the notosetae or may be composed of more thickened, simple, pseudocompound or compound hooks. Dorsal and ventral cirri are lacking. The pygidium, with the terminal or subdorsal anus, may be slightly crenate. The sexes are separate. Epidemic spawning and rapid larval development in the plankton may occur (F. commensalis).

The flabelligerids are found under stones and in burrows just below the surface of the sand or mud, where they move

rather sluggishly or creep around in a caterpillarlike fashion by means of their hooked neurosetae. They may live in burrows with the posterior end folded back on the body (Pherusa) and may appear in surface waters. They are surface deposit feeders, using their large frilly palps and tentacular filaments to collect food particles from the surface, which are then carried by ciliary-mucoid tracts to the mouth. Flabelligera commensalis lives as a commensal among the spines of sea urchins, where it feeds on fecal material of the host.

The family contains 16 genera and about 130 species. These sluggish mud-loving forms are widely distributed and are found from shallow water to great depths.

References. J. H. Day, Family Flabelligeridae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 652-666, 1967; R. B. Spies, Reproduction and larval development of Flabelliderma commensalis (Moore), in D. J. Reish and K. Fauchald (eds.), Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman, Allan Hancock Foundation, Los Angeles, pp. 323-345, 1977; R. B. Spies, Structure and function of the head in flabelligerid polychaetes, J. Morphol., 147:187-208, 1975.

Acrocirridae. Family of worms which have an elongated slender body with numerous segments. The integument may be rugose and densely papillated. The prostomium is reduced, pentagonal, and pointed anteriorly, lying dorsal to the peristomium and fused to it; it bears a pair of frontal grooved palps, a subterminal ventral mouth, and usually two pairs of eyes. The pharynx is unarmed and noneversible, with a small buccal sac. Usually several anterior segments are crowded and achaetous.

The parapodia are biramous, the setal lobes being mostly very small, with variable development of digitate postsetal lobes and interramal and subpodal papillae. The notosetae are capillary, striated, and spinous. The characteristic neurosetae are stout compound hooks with a hyaline membrane below the tips of the blade, giving a bird's-beak aspect, and a hyaline membrane connecting the blade to the shaft; sometimes there are additional acicular setae and simple hooks on the neuropodia of the posterior segments. Dorsal and ventral cirri are lacking. When present, the branchiae consist of four pairs above the notopodia, begin-

ning on segment II. The pygidium encloses the terminal or slightly dorsal anus and lacks anal cirri.

The sexes are separate. Acrocirrids are found under stones intertidally, as well as in coarse sediments in deeper water. They are selective bottom deposit feeders, food particles being carried along the ciliated grooves of the palps to the mouth.

The family is composed of 3 genera (Acrocirrus, Macrochaeta, and Flabelligella) and about 20 species. It has a worldwide distribution.

References. K. Banse, Acrocirridae n. fam. (Polychaeta, Sedentaria), J. Fish. Res. Bd. Can., 26:2595-2620, 1969; J. M. Orensanz, Poliquetos de la Provincia Biogeografica Argentina, pt. 10 (Acrocirridae), Neotropica, 20:113-118, 1974.

Fauveliopsidae. Flabelligeridad family with a single genus (Fauveliopsis) and about 11 species. The body is short and subcylindrical, or longer and inflated anteriorly, with relatively few (usually up to 40, rarely up to 90) and poorly indicated segments; some forms are firm and stiff, resembling wireworms. The integument is smooth, rugose, or very finely papillated. The anterior end is truncate, the small

prostomium and peristomium being fused and mostly withdrawn in the two anterior setigerous segments; there is a subterminal mouth enclosed in lateral and posterior lips, and palps and oral tentacles are lacking. The pharynx is unarmed and noneversible, with a ventral muscular pad.

The parapodia are biramous, with widely spaced rami and a large rounded interramal papilla; the podial lobes are reduced, and the setae emerge directly from the body wall. The setae are relatively few (one to nine per ramus); they are all simple, smooth, acicular, and straight or slightly hooked, and there are sometimes additional capillaries. Dorsal and ventral cirri are lacking. The posterior end is truncate, with a terminal anus.

These are burrowing forms; they are sluggishly motile and nonselective bottom deposit feeders. Some live in close-fitting tubes of hard cemented sand grains and have been found in scaphopod and gastropod shells surrounded by silt. They chiefly inhabit the bathyal and abyssal zones but are also found in shallow water in the Mediterranean.

References. W. Katzmann, and L. Laubier, Le genre Fauveliopsis (Polychète, Sédentaire) en Méditerrané. Microfauna des Meeresbodens, 50:529-542, 1974.

OPHELIIDA

The body is cylindrical, with similar segments, and is not divided into distinct regions. The segments are usually secondarily subdivided into annuli or areolations. The prostomium and achaetous peristomium are small, lacking appendages and bearing a pair of nuchal organs. The phar-

ynx is eversible, saclike, and unarmed. The parapodia are biramous, with small setal lobes and simple capillary setae; there are segmental interramal sensory organs. These worms are burrowing bottom deposit feeders. The order contains 2 families: Opheliidae and Scalibregmidae.

Opheliidae. The body is cylindrical, tapered anteriorly and truncate posteriorly, with relatively few segments (up to 60); the segments are similar, and not divided into distinct regions. The integument has a thick, tough cuticle which may be smooth or subdivided into annuli or areolations; the intersegmental constrictions are poorly marked. The body may be short, thick, and grub-shaped, lacking a ventral groove (Travisia), inflated anteriorly with the posterior half narrower, with a deep midventral groove (Ophelia), or uniformly slender, with midventral and lateral grooves along the length of the body (Ophelina, Armandia, Polyophthalmus). The prostomium is small and tapered, blunt or conical, sometimes ending in a slender palpode; appendages are lacking; there is a pair of evaginable nuchal organs; and a pair of subdermal eyes may be absent or present. The achaetous peristomium is fused with the prostomium and the following setigerous segment. The ventral mouth is a transverse slit between the anterior and posterior lips, usually on the level of the first setiger. The pharynx is eversible, large, saclike, more or less lobed, unarmed, ciliated, and highly glandular.

The parapodia are biramous; the rami are small, in the form of button-shaped lobes, and they are provided with fan-shaped bundles of simple capillary setae. Dorsal cirri are lacking; short ventral cirri may be present. Segmental cirriform branchiae may be found posterodorsal to the notosetae along most of the body (Travisia, Ophelina, Armandia) or may be confined to the middle part of the body (Ophelia); the branchiae may be branched (Euzonus) or lacking (Polyophthalmus, Kesun). Interramal sensory organs may be present on some segments in the form of small eyespots (Armandia, Polyophthalmus), sensory pits (Travisia), or papillae (Ophelia). A few posterior preanal segments may be achaetous, telescoped, and retractile. The pygidium, which

contains the terminal anus, is often prolonged and tubular, ending with a circle of blunt lobes (*Travisia*), with two stout ventral lobes and a circlet of dorsolateral papillae (*Ophelia*), or with a papillate tube and a long internal cirrus (*Ophelina*, Armandia)

The opheliids are active burrowers and swimmers. They burrow head downward in sand or mud by peristaltic movements of the body. They swim by undulating body inovements. They make no permanent burrows or tubes. Respiratory currents are brought down by peristaltic action and escape along the lateral grooves in which the branchiae are situated. These worms are bottom deposit feeders, engulfing the substrate with their saclike pharynx and utilizing the adhering organic matter. The sexes are separate. Spawning takes place in or on the surface of the sand. Some forms become pelagic as sexually mature epitokes (Armandia, Polyophthalmus). The larvae are planktonic and settle in the substrate at about the five-setiger stage. The opheliids are well known for their localized distribution: they are restricted to soils with a relatively narrow range of particle size. Some are characteristic of fine muds, others of relatively coarse sands; some are found in clean sand (Ophelia, Armandia), and some in muddy bottoms in deep water (Travisia); Polyophthalmus is found in muddy shores of all warm seas. They may be found in great numbers.

The family contains 12 genera and about 150 species. **References.** J. H. Day, Family Opheliidae, in *A Monograph on the Polychaeta of Southern Africa*, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 570-580, 1967; D. P. Wilson, The relation of the substratum to the metamorphosis of *Ophelia* larvae, *J. Mar. Biol. Ass.*, 27:723-760, 1948.

Scalibregmidae. The body is either short, stout, and maggotlike or moderately long (up to 60 segments) and inflated

anteriorly. The segments are usually secondarily annulate (two 10 six annuli per segment) and strongly wrinkled or areolate, superficially resembling Arenicola. The prostomium is small, oval, and bilobed anteriorly; it appears T- or V-shaped, sometimes forming frontal horns; nuchal slits are present, ane eyes may be present or absent. The peristomium is short and achaetous. The ventral mouth is enclosed in the peristomium and the first setiger, which forms the lower lip. The pharynx is eversible, soft, globular, and unarmed.

The parapodia are biramous, with the rami equally developed and widely separated, and with interramal ciliated lateral organs; in the anterior region the setal lobes are poorly developed, indistinct or small, and conical or cushionlike; they are sometimes longer in the posterior part of the body, accompanied by short dorsal and ventral cirri or only by ventral cirri. The setae are all simple, mainly smooth or minutely spinous capillaries; there are a few furcate setae with spinules on the inner margins; sometimes acicular spines are present in the anterior parapodia (one to four segments). When present, the branchiae are branched

and bushy, located posterior to the notopodia and confined to the anterior few segments; there are three to six pairs, beginning on setiger II. The pygidium has a terminal anus, with or without two to seven anal cirri.

The sexes ae separate. Epitokous sexual forms may appear in surface waters, massed with sex products and bearing setae which are more numerous, longer, and finer than usual. These worms burrow in sandy mud or clay and are bottom deposit feeders.

The family contains 12 genera and about 30 species. The scalibregmids are widely distributed but rather rarely collected. They are mostly subtidal, found from intertidal regions to great depths. The cosmopolitan species *Scalibregma inflatum* is found from the Artic to the Antarctic.

References. J. H. Day, Family Scalibregmidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. His.) 656, pp. 583-590, 1967; J. D. Kudenov and J. A. Blake, A review of the genera and species of the Scalibregmidae (Polychaeta) with descriptions of one new genus and three new species from Australia, J. Natur. Hist., 12:427-444, 1978.

STERNASPIDA

Aberrant order with the single family Sternaspidae, the single genus Sternaspis, and about 6 species; it is sometimes considered to have only 1 cosmopolitan species. S. scutata. The body is short, grublike, and variable in shape: it may be inflated and constricted in the middle, with both ends subglobular, or the anterior region may be retracted into the more posterior segments. Distinct parapodial lobes and cirri are lacking. The integument is densely covered with fine filiform papillae. The prostomium is small and knoblike, without appendages. The achaetous peristomial ring encloses the small ventral mouth on a thickened cushion. The pharynx is small, eversible, and unarmed. The following three segments each have a lateral semicircular row of strong, short, yellow simple spines which are arched and pointed to blunt, diminishing in size toward the ventral

side. The middle segments lack setae or are furnished with capillary setae embedded in the body wall. The posterior region, which consists of five or so segments, has a pair of horny trapezoidal ventral plates showing concentric and radiating striae; each plate has about 16 radiating bundles of stiff capillary setae along the lateral and posterior borders. The posterior end bears the terminal anus and is furnished with numerous long anal filaments or branchiae, which are sometimes spiraled. The sternaspids are found burrowing in sand and mud, from shallow water to great depths.

References. J. H. Day, Family Sternaspidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, 1967.

CAPITELLIDA

Members of this order have an elongated cylindrical body. The prostomium is small, and the peristomium or buccal segment, which encloses the ventral mouth, is achaetous; both lack appendages. The pharynx or proboscis is eversible, saclike, unarmed, and papillated. The parapodia are biramous, lacking acicula and bearing simple setae. The neuropodia form raised ridges or tori with transverse rows

of long-shafted hooks or uncini. Dorsal and ventral cirri are lacking. These worms are burrowing forms, sometimes building tubes; they use their eversible saclike proboscis for both burrowing and bottom deposit feeding. The order contains 3 families: Capitellidae, Maldanidae, and Arenicolidae.

Capitellidae. The body is cylindrical, long, and filiform, weakly divided into two regions: a short anterior thoracic region (8-21 segments) which is somewhat inflated, rugose, reticulated, and reddish pink or purplish brown in color (due to red coelomic fluid); and a long posterior abdominal region which is more delicate, fragile, fragmenting easily, with flesh which is yellow to bright red in color. Members of this family superficially resemble earthworms. The prostomium is small, rounded to subconical, and more or less retractile into the anterior segment; it lacks appendages, is furnished with a pair of eversible nuchal organs, and may or may not have small eyespots. The peristomial ring contains the ventral mouth; it is usually achaetous and without appendages. The pharynx is eversible, soft, saclike, glandular, and papillate.

The parapodia are biramous, with the rami well separated, without acicula. The podial lobes of the thoracic region are reduced to small bundles of limbate pointed setae; some males have specialized genital hooks on a few segments (Capitella). The abdominal region has simple long-handled hooks or uncini on slightly raised transverse ridges (tori), and sometimes additional slender pointed setae and specialized terminal spines (Scyphoproctus). The notopodia are sometimes fused medially and the neuropodial ridges are greatly extended laterally and ventrally. The hooks are characteristic, consisting of a main fang and a crest formed of a few rows of denticles, partially enclosed in a hyaline sheath or hood. There are no dorsal or ventral cirri. When present, abdominal branchiae are composed of coelomic extensions in the form of stationary or retractile modifica-

tions of notopodial or neuropodial ridges; they may be simple, papillate, digitiform, or branched filaments and are not always easily discernible. Lateral ciliated sense organs are usually present between the rami. The pygidium, with the terminal anus, has a rounded anal plate, a single elon-

gate digitiform appendage, or several anal cirri.

The sexes are separate. Some are protandrous hermaphrodites. Sometimes conspicuous genital pores appear on the anterior abdominal segments. Sexual dimorphism is known for a few species, and copulation may occur. Eggs are laid in tubes or jelly masses where early development occurs. Adults may exercise brood care during the early stages. Pelagic trochophores develop into polytrochal lecithotrophic larvae with relatively short pelagic life. Members of this family form an important part of the benthos. They are bottom deposit feeders. They burrow in sand or mud, constructing vertical or spiral burrows with a thin layer of mucus; surface markings are indicated by minute black cinder cones. Some (Mediomastus) form closely fitting tubes of debris and mud in which they live with head directed downward and tail upward.

The family is composed of 37 genera and about 140 species. Members are most common in the littoral zone but extend to great depths. They are mostly marine, common in estuaries, and rarely found in freshwater (Eisigella). The cosmopolitan species Capitella capitata is regarded as an excellent indicator of pollution or environmental disturbances; it is easily maintained in the laboratory and has a short generation span (about 1 month), making it an ideal

laboratory animal.

References. J. P. Grassle and J. F. Grassle, Sibling species in the marine pollution indicator *Capitella* (Polychaeta), *Science*, 192:567-569, 1976; O. Hartman, Polychaetous Annelids, pt. 7: Capitellidae, *Allan Hancock Pac. Exped.*, 10: 371-381, 1947.

Maldanidae. The body is elongated, cylindrical, attentuated posteriorly, and truncate at one or both ends; it is not differentiated into regions, and some middle segments are greatly elongated (so-called bamboo worms). The anterior region is furnished with numerous glandular cells, which are either diffused or grouped in clear bands alternating with pigmented rings. Maldanids live in cylindrical membranous tubes which may be thin and horny (Rhodine), or which may incorporate a thin layer of sand grains (Clymenella) or a thick layer of mud (Maldane); the tubes may form a compact mass resembling coral heads (Petaloproctus socialis). The prostomium is poorly defined and fused to the achaetous peristomium or buccal segment; it may be in the form of an ovoid lobe (Nicomache) or an obliquely truncated plate with a membranous border and a median ridge or cephalic keel (Maldane); the anterior end may project as a palpode, lacking appendages but bearing a pair of clongated nuchal slits and sometimes numerous eyespots. The mouth forms a ventral transverse fissure with furrowed lips. The proboscis is eversible, unarmed, globular, papillated, and ciliated.

The parapodia are biramous, the rami being poorly developed, lacking acicula as well as dorsal and ventral cirri. The notopodia are short and rounded, with tufts of limbate, smooth or spinous capillary notosetae. The neuropodia form elongated ridges (tori), usually with a single row of hooks (double rows in *Rhodine*); the hooks are long-shafted, with rows of apical denticles and tufts of stiff hairs below the main fang. The anterior few setigers may lack neurosetae, or they may be furnished with a few acicular spines.

The anterior margins of some anterior segments may extend forward, forming membranous collars, and some posterior segments may form posterior collars (Rhodine). Branchiae are usually absent; some vascular filaments may be present on some segments near the posterior end (Johnstonia). There may be up to 10 posterior achaetous preanal segments. The pygidium may be conical, with a terminal anus (Clymenura); in the form of a symmetrical funnel rimmed with cirri, with the anus in the middle of the funnel (Praxillella); with the anus dorsal to a flattened plate (Maldane); or with the anus dorsal to an oblique spatulate lobe (Asychia).

The sexes are separate. Hermaphrodites are known. The sex products are extruded from the mouth of the tube. Large yolky eggs may be laid in mucous cocoons attached to the tubes, the larvae escaping in the late stages of development, ready to burrow. The maldanids are highly specialized burrowers; they burrow head downward, cementing the surrounding material together and forming compact tubes. The pygidium plugs the entrance of the tube. The eversible proboscis is used for both burrowing and feeding. These worms are selective bottom deposit feeders. Irrigation of the burrow takes place by peristaltic action of the elongated and highly contractile segments. The feces are discharged at the surface.

The family contains about 30 genera and 200 species. They are widely distributed in sand and mud from low wa-

ter to great depths and may be very abundant.

References. J. H. Day, Family Maldanidae, in A Monograph of the Polychaeta of Southern Africa, pt. 2: Sedentaria. Brit. Mus. (Natur. Hist.) 656, pp. 613-647, 1967; J. D. Kudenov, The functional morphology of feeding in three species of maldanid polychaetes, Zool. J. Linn. Soc., 60: 95-109, 1977.

Arenicolidae. Lugworms; the body is thick and cylindrical, with numerous segments, and it is separated into two or three regions: an anterior prebranchial region and a branchial region are present in Arenicolides and Branchiomaldane and an anterior prebranchial region, a branchial region, and a posterior postbranchial, apodous, or tail region are found in Arenicola and Abarenicola. The integument is thick and strongly areolated, with up to five annuli per segment. The prostomium is small and trilobed, lacking appendages and eyes; it may be withdrawn in a nuchal pouch. The peristomial ring and the following segment are achaetous, sometimes provided with a pair of statocysts; they enclose the ventral mouth. The pharynx is eversible, saclike, smooth, and papillate.

The parapodia are biramous and lack acicula. The notopodia are short, erect, and truncate, with simple, limbate, spinous capillary notosetae; branchiae, in the form of arborescent tufts, are located posterior to the notopodia in the branchial region. The neuropodia form lateroventral elongated ridges (tori), with a row of long-shafted hooks or uncini which have poorly marked denticles on the crest, and no hoods; the neuropodia in the branchial region may be long, approaching the midventral line (Arenicola, Arenicolides), or short (Abarenicola, Branchiomaldane). The pygidium forms a simple ring with the terminal anus.

The arenicolids live in muddy sand in the intertidal zone of protected bays and estuaries. They construct L- or J-shaped burrows using their eversible proboscis and the hydrostatic pressure of the coelomic fluid. The walls of the burrow are firm, supported by secretion of the worms. Water is pumped through the burrow by the peristaltic

movement of the body wall, with a pistonlike action. These are bottom deposit feeders; muddy sand is engulfed by the proboscis in the horizontal part of the burrow, resulting in a funnel-shaped depression on the surface of the substrate; the vertical part of the burrow, or tail shaft, is open to the surface and may be marked by coiled castings formed by the worm when it backs up to the surface and defecates.

The sexes are separate. The sex products may be given off into the water or burrow, or the eggs may be laid in gelatinous masses extending from the opening of the burrow, and the elongated cylindrical egg masses may be up to 6 ft (1.8 m) in length (Arenicola cristata). The larvae spend only a short time in the plankton. Some arenicolids may reach gigantic size—up to a meter in length, in A. loveni. They are used as baitworms in some areas.

Specimens of *Branchiomaldane* differ from the rest of the arenicolids in many respects: they are small and thread-like, with a smooth integument; the prostomium is small, and conical, with two groups of small eyespots; the proboscis is globular; the branchiae are confined to the posterior half of the body in the form of a tuft of a few sessile thick filaments; the neuropodial setal hooks have well-marked teeth on the crest. These are hermaphroditic forms, secreting membranous tubes coated with fine sand and living in muddy rock crevices.

The family contains 4 genera and about 30 species and subspecies. They are distributed throughout the world.

References. J. H. Day, Family Arenicolidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 606-612, 1967.

OWENIIDA

Order with the single family Oweniidae. The body is elongate, cylindrical, rigid, and not divided into distinct regions; it is truncate anteriorly and attenuated posteriorly, with relatively few and poorly defined segments indicated only by their setae. The head is composed of the fused rudimentary prostomium and peristomium, which form trilobed lips around the terminal mouth; a pair of eyespots may be present or absent. The head may be rounded and without processes (Myriochele, Myrioglobula); it may be provided with a pair of large grooved palps (Myriowenia) or a ciliated branchial membrane consisting of three to five pairs of dichotomously branched lobes (Owenia). The pharynx is unarmed and noneversible,

The anterior region consists of an achaetous segment, sometimes forming a small collar, and one to three short uniramous setigers with sessile capillary notosetae only. The following segments are biramous, the first five to seven being very long, the rest shorter, with minute tufts of sessile capillary spinulose notosetae and long transverse neuropodial bands with enormous numbers of minute long-shafted hooks or uncini with one to three recurved teeth (uncinigerous tori). Dorsal and ventral cirri and parapodial branchiae are lacking. The pygidium, containing the dorsal

anus, forms a collarlike fold which may have an entire margin or be furnished with a pair of short flaps, a pair of long dorsal anal cirri, or a papillated border.

The sexes are separate, fertilization takes place externally. Pelagic "Mitraria" larvae may remain in the plankton for an extended period of time (up to 4 weeks). The worms may be encased in tight-fitting, tough, flexible membranous tubes with tapering ends, buried upright in the mud and encrusted with niovable overlapping sand grains and shell fragments (Owenia), or the tubes may be thin and mucoid (Myriowenia); a buccal organ is used for tube building. The oweniids are suspension filter feeders, gathering floating particles on their frilly ciliated branchial membranes and conveying them by ciliated grooves to the lips; some are surface deposit feeders, taking up sand and detritus with their lips. They may form compact feeal pellets.

The family consists of 4 genera and about 30 species. They are widely distributed on sand and muddy sand with shells and gravel, from low intertidal zones to moderate depths. Some, such as O. fusiformis, are cosmopolitan.

References. J. H. Day, Family Oweniidae Rioja, 1917, in A Monograph on the Polychaeta of Southern Africa. pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 649-651, 1967.

TEREBELLIDA

Tubicolous, sedentary forms, with the body divided into different regions. The prostomium lacks appendages and is fused with the peristomium; oral tentacles are present which are used in feeding and tube building. Branchiae are usually present on some anterior segments. The parapodia

are biramous, with capillary setae and uncinigerous tori or pinnules. These worms are bottom deposit feeders.

The order includes 6 families: Amphictenidae (=Pectinariidae), Sabellariidae, Ampharetidae, Trichobranchidae, Bogueidae, and Terebellidae.

Amphictenidae. Members have a short conical body with relatively few (about 20) segments; it is circular in cross section, widest anteriorly and tapering posteriorly, encased in free, tapered, sandy tubes which are open at both ends. The integument is soft and translucent. The prostomium, peristomium, and anterior few segments are fused to form the head end, consisting anterodorsally of a semicircular, thick, fleshy, domelike cephalic or opercular plate, with stout, flattened, golden setae or paleae in two obliquely overlapping groups on the anterior margin which serve jointly as an operculum to close the mouth of the tube; the posterior margin of the opercular plate may be smooth (Cistena, Petta) or serrated (Amphictene). Ventrally a thin

semicircular tentacular membrane (cephalic veil) forms a hood in front of the mouth and more or less encloses a group of grooved oral tentacles; the margin of the membrane may be entire (Petta) or fringed with papillae (Cistena. Amphictene); two pairs of short tentacular cirri are found on the lateral sides of the head, followed by two pairs of platelike branchiae.

The following three segments bear uniramous parapodia, having notopodia only, which are provided with winged capillary notosetae and ventral glandular pads. Beginning on setiger IV there is a region of 12 to 15 segments which have biramous parapodia, with neuropodia in the form of projecting pinnules bordered by a single row of

small setae or uncini. The uncini are pectiniform, with teeth of various sizes, in one to four vertical rows. The few following segments may have only notosetae or may be achaetous. The posterior region consists of an achaetous short foliaceous plate or scaphe which is concave dorsally, Iestooned laterally (reduced parapodial lobes), and papillate posteriorly. The scaphe is usually large and set off sharply from the more anterior part of the body (Cistena. Amphictene), but it may be small and tapered gradually (Petta). Lateral groups of stout acicular setae are found on the basal part of the scaphe. A dorsal anal flap or ligule covers the anus; sometimes eyespots occur on the scaphe.

The amphictenids cement individual sand grains, sponge spicules, and shell fragments from the sediment with proteinaceous glue to form conical tubes, one or several grains thick. The tubes are straight or slightly curved, and open at both ends. These worms are mobile bottom deposit feeders. They live with the head downward in the wide end of the tube, the narrower end projecting at an angle just above the surface. The paleae are used for digging; the extensile grooved oral tentacles spread out and, with their prehensile tips, gather detritus from the soft sediment and bring it to the month; some residual sand is used for tube building. Through the upper small end of the tube, sand and feces are discharged by muscular contraction and water is taken in for respiration. The sexes are separate, and fertilization is external. The larvae spend considerable time in the plankton and develop into advanced larvae; they then secrete transparent tubes.

The family (=Pectinariidae) includes 3 genera [Amphictene, Petta, Cistena (=Pectinaria, Cistenides, Lagis)] and about 50 species. They are widely distributed, from low

water to great depths.

References, J. H. Day, Family Pectinariidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 678-685, 1967; C. D. Long, Pectinariidae (Polychaeta) from Caribbean and associated waters, Bull. Mar. Sci., 23:857-874, 1973.

Sabellariidae. One of the most specialized families of the Polychaeta, adapted to tubicolous living. Body is elongate, cylindrical, and divided into four regions: "head," patathoracic region, abdominal region, and caudal region.

Prostomium of the "head" is reduced and partly or wholly concealed by the development of the operculum; it bears a single pair of palps. Peristomium is hypertrophied, forming a pair of stout opercular lobes or peduncles directed anteriorly; rows of numerous oral (feeding) tentacles are located on the ventral sides of the opercular lobes; two pairs of longitudinal setigerous sacs are located within the opercular lobes and form large flattened setae or paleae which are arranged in one to three semicircular rows on the tips of the opercular lobes, serving as a protective operculum or stopper to the tube when the worm retracts. The opercular lohes may remain separated, not fused dorsally; they may bear one to three pairs of stout hooks on their dorsal bases, and a single row of spirally serrated paleae with capillary tips (Phalacrostemma) or two rows of golden paleae (Idanthyrsus, Lygdamis), those of the outer row long and with lateral teeth, those of the inner row smooth and tapering. In other cases the opercular lobes may be fused dorsally, with the operculum placed at nearly right angles to the hody and bearing three rows of golden paleae, those of the external row flattened and with toothed tips, and those of the middle and inner rows geniculate (Sabellaria, Phragmatopoma). In Gunnarea the opercular peduncles may be completely fused dorsally and ventrally, with the opercular crown having two rows of paleae. The mouth is located on the ventral side of the opercular lobes. The first two setigerous segments are small and uniramous, with small neuropodia and capillary setae; the lower lip of the mouth is surrounded by the horseshoe-shaped building organ.

The parathoracic region consists of three or four segments with biramous parapodia, dorsal cirriform gills, and a ventral muscular plate. The notopodia are cylindrical, with stout oar-shaped or spear-shaped notosetae; the neuropodia are small, with capillary setae. The abdominal region has numerous (10 to 45) segments with biramous parapodia, dorsal cirriform gills, and a ventral longitudinal groove; wide notopodial ridges or tori bear rows of minute toothed plates or uncini (six to nine teeth); small ventrolateral neuropodia have capillary setae and lateral fleshy lobes or ventral cirri. The caudal region is narrow and tubular, lacking parapodia and external segmentation; it is reflected ventrally and anteriorly along the ventral groove of the abdominal region. The anus is terminal, at the tip of the cauda.

The tubes are constructed of cemented sand and shell fragments. Sand grains contacting the oral tentacles are passed by cilia to the mouth and then to the building organs, where the grains are coated with cement. The head is protruded and the grain manipulated into position, with the paired grooved palps in front of the mouth assisting the process, and the grain is cemented on the mouth of the tube by the building organ. The cylindrical tubes are closed basally.

The body has abundant ciliary tracts, consisting of dorsal transverse bands on the abdominal and thoracic regions, opercular lobes, and dorsal gills, which move the water anteriorly. Cilia on the ventral surface of the opercular lobes beat anteriorly and serve to reject particles from the mouth. The numerous oral tentacles have rings of cilia. Water is drawn through the tentacles by the lateral cilia, assisted by the current-driving action of the ciliated gills. Feeding is carried out by extracting suspended matter from the surrounding seawater. Food particles are passed along the ciliated ventral grooves of the tentacles to the mouth. A crude sorting mechanism operates, whereby particles too large to be ingested glide over the mouth to be received by the ventral lips, are transferred to the building organ, and are then applied to the ever-growing rim of the tube. When the worm is extended, water is drawn into the tube along the ventral surface of the body. When the worm is disturbed, the oral tentacles contract rapidly, the opercular peduncles bend ventrally to cover them, and the body shortens. Feces are extruded from the anus in the form of continuous strings, associated with peristaltic waves of the cauda. The strings are grasped by the neurosetae, passed anteriorly, and expelled from the tube.

The sexes are separate. The larvae are found in great numbers in the plankton, where they may spend considerable time (many weeks). The trochophore larvae are characterized by two bundles of long barbed provisional setae. The late larval stage has four eyespots on the episphere, a dorsal hump posterior to the eyes, a pair of long tentacles, a well-developed prototroch and telotroch, two bundles of long barbed provisional setae, spiny primary paleae, three parathoracic segments with capillary notosetae, and three abdominal segments with dorsal uncinigerous lobes. At metamorphosis and settlement the provisional setae are lost, the larval tentacles and opercular peduncles with the primary paleae are rotated anteriorly, the heavily ciliated

mouth region and building organ begin to differentiate, and a sandy tube is constructed.

The family contains 7 genera and about 65 species. The sabellariids are widely distributed, settling on rocks, shells, and firm substrates. Their tubes may be solitary or colonial; in the latter case the parallel tubes are agglutinated one against the other, giving a honeycomb appearance. Some species are gregarious and important as reef builders, forming massive wave-resistant reefs in bands between the tidemarks (Sabellaria alveolata, Gunnarea capensis, Phragmatopoma). They are found mostly in shallow water, but solitary forms are found in great depths.

References. J. H. Day, Family Sabellariidae, A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit, Mus. (Natur. Hist.) 656, pp. 667-677, 1967; F. J. Ebling, Formation and nature of the opercular chaetae of Sabellaria alveolata. Quart. J. Microsc. Sci., 85:153-176, 1945; K. J. Eckelbarger, Larval development of Sabellaria floridensis from Florida and Phragmatopoma californica from Southern California (Polychaeta: Sabellariidae), with a key to the sabellariid larvae of Florida and a review of development in the family, Bull. Mar. Sci., 27:241-255, 1977; P. A. Roy, Tube dwelling behaviour in the marine annelid Phragmatopoma californica (Fewkes) (Polychaeta: Sabellariidae), Bull. S. Calif. Acad. Sci., 73:117-125, 1974.

Ampharelidae. The elongated, tapered body is divided into anterior thoracic and posterior abdominal regions. The prostomium forms a flattened hood over the ventral mouth; it lacks appendages, but is provided with a pair of nuchal slits and sometimes a pair of small eyes or two groups of minute eyespots. The achaetous peristomium and the following segment are more or less fused, forming the lower lip of the mouth. Few to numerous mobile, smooth or papillate, oral tentacles, often with a groove along one side, are attached to the upper lip or roof of the buccal cavity: they can be extended from and withdrawn into it. The following few segments are more or less fused or telescoped, furnished with two to four pairs of branchiae which occur on successive segments or are arranged in a transverse row across the dorsum. The branchiae are filiform or subulate, smooth or pinnate. An anterior segment may bear two groups of prominent notosetae or paleae which project anteriorly lateral to the branchiae. The setae are more or less reduced or absent on the buchial segments. One or two pairs of prominent notopodial hooks may be present posterior to the branchiae, as in Melinna.

The following somewhat inflated thoracic segments (9 to 16 in number) are biramous, the notopodia forming conical lobes, with bundles of limbate capillary notosetae and sometimes a small terminal papilla. The neuropodia have the form of small rectangular pinnules bearing a row of small toothed plates or uncini and sometimes an upper papilla or cirrus. The posterior tapering abdominal region (up to 90 segments), bears only neuropodial uncinigerous pinnules, sometimes with a long neuropodial cirrus. The notopodia are rudimentary or absent, without notosetae. The pygidium forms a simple ring; it is sometimes provided with small papillae, a pair of long anal cirri, or a ring of cirri.

The ampharetids construct more or less fragile, membranous tubes covered with mud and agglutinated foreign material. They are bottom deposit feeders, extending from their tubes and gathering food particles from the surface of the sand or mud by means of their oral tentacles, which can be extruded from the mouth. They are found on bottoms of mud in shallow water and are especially common with

increasing depth. The small *Hypaniola florida* may be found in considerable numbers in estuaries of low salinity along the east coast of the United States; they lay large yolky eggs in their tubes and develop into nonpelagic larvae.

The family includes about 70 genera and 230 species. References. J. H. Day, Family Ampharetidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 696-705, 1967.

Trichobranchidae. The body is elongate and vermiform, widest and inflated anteriorly and tapering posteriorly; it is divided into anterior thoracic and posterior abdominal regions. The prostomium and peristomium are fused, forming a more or less developed cephalic ridge which may or may not be provided with numerous eyespots, a pair of horizontal winglike lateral lobes, a ventral tentacular lobe enclosing the mouth, with a frilly margin bearing very numerous grooved oral tentacles, and an inflated grooved lower lip. The anterior few segments are achaetous, bearing branchiae which are sometimes in the form of simple filaments—a single middorsal filament (Unobranchus), two pairs (Filibranchus), three pairs (Trichobranchus, Arctacamella)—and sometimes take the form of a single branchial trunk divided distally into four lamellate lobes (Terebellides).

The thoracic region has hiramous parapodia, with notopodial tubercles bearing capillary notosetae and neuropodial ridges bearing a row of long-handled hooks with dentate crests. Ventral glandular pads are absent. The abdominal region has neuropodia only, in the form of projecting triangular pinnules which bear a row of small avicular uncini. The anus is terminal, with a crenulate opening.

The trichobranchids form membranous tubes coated with mud or fine sand. They are bottom deposit feeders, using their grooved oral tentacles. They form an important part of soft bottom communities and arc most common in cold water. The family includes 8 genera and about 30 species. Some, such as the cosmopolitan *Terebellides stroemii*, are widely distributed.

References. J. H. Day, Subfamily Trichobranchinae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 710-713, 1967; P. Hutchings, Family Trichobranchidae, in Terebelliform Polychaeta of the Families Ampharetidae. Terebellidae and Trichobranchidae from Australia. Rec. Austral. Mus. 31, pp. 23-25, 1977.

Bogueidae. Aberrant terebellidad family with 2 genera, each with a single species and known from a few records in the western Atlantic: Boguea enigmatica is known from shallow muddy bottoms (North Carolina and Florida), and Boguella ornata is known from oozy mud in abyssal depths (off Bermuda).

The body is slender, threadlike, and cylindrical, tapering posteriorly, with relatively few segments (up to 35). The subconical to rounded prostomium is fused with the peristomium, enclosing the ventral mouth; appendages and eyes are lacking. The anterior three (Boguea) or four (Boguella) setigers are uniramous, with notosetae only. The following segments are biramous; the notopodia are small, subconical, or papillar, with limbate capillary notosetae; the neuropodia have small transverse bands of minute hooks or uncini in single and double rows (uncinigerous tori). The uncini are avicular and short-handled, with a main fang and a crest of two rows of small teeth. Dorsal and ventral cirri and branchiae are lacking. The pygidium, with the terminal anus, forms a simple ring (Boguea) or is furnished

with rounded papillae (Boguella). The tubes are weakly chitinized (Boguella) or appear to be absent (Boguea). Large

yolky eggs are found in some segments (Boguea).

References. O. Hartman, Family Oweniidae, in *The Marine Annelids of North Carolina*. Duke Univ. Mar. Sta. Bull. 2, pp. 42-43, 1945; O. Hartman and K. Fauchald, Family Bogucidae, new family, in *Deep-Water Benthic Polychaetous Annelids off New England in Bermuda and Other North Atlantic Areas*, pt. 2, Allan Hancock Monogr. Mar. Biol. 6, pp. 148-151, 1971.

Terebellidae. Species in this family have a subcylindrical, tapered, and delicate body with numerous short segments, usually encased in a mucous tube encrusted with sand or mud. The prostomium is indistinct and fused with the peristomium or buccal segment, forming a head which consists of a semicircular upper-lip, a large, somewhat folded tentacular lobe with numerous filliform, grooved, ciliated oral tentacles which cannot be fully retracted into the mouth, a raised transverse rim or cephalic ridge, sometimes with a series of numerous small eyespots behind the rim, and four lower lips. A large scoop-shaped papillated proboscis is sometimes present (Artacama), but a proboscis is usually absent.

The body is divided into two regions: an anterior thoracic region which is more or less inflated, with biramous parapodia; and a posterior abdominal region which is more or less tapering and usually lacks notosetae. The anterior few segments are achaetous and sometimes furnished with winglike lateral lobes which funtion in tube construction; sometimes there are transverse ridges across the dorsum. Ventral glandular shields or pads are usually present in the anterior region. The thoracic notopodia are subconical and furnished with bundles of notosetae, consisting of limbate capillaries with smooth or serrated tips. The neuropodia consist of long low vertical ridges or tori furnished with numerous small hooked setae or uncini, in single, double, or alternating rows. The uncini are avicular, with ares of denticles above the main fang, or pectinate, with a vertical series of teeth. Rarely setae are absent (Hauchiella). In the abdominal region the neuropodial ridges are more prolonged, forming uncinigerous pinnules. When present, hranchiae include one to three pairs on segments H to IV; they may be numerous and filiform, or branched and arborescent. Rarely, the notopodial lobes are prolonged and vascularized, forming branched branchiae (Enoplobranchus). The pygidium, with the terminal anus, forms a short simple ring; anal cirri are lacking.

The sexes are separate, fertilization is usually external and development is pelagic. Some planktonic larvae form bulky gelatinous tubes (Loimia medusa). In Nicolea zostericola, pair formation between mature adults takes place prior to spawning, and large yolky eggs are deposited in hardened mucous cocoons attached to the substratum or to adult tubes; direct development occurs here and the pelagic phase is omitted; the female remains with the cocoon until hatching occurs.

The terebellids construct more or less permanent tubes of various types: untidy and fragile tubes attached to rocks and composed of sand, mud, fragments of shells, and so forth; compact tubes of coarse sand and gravel (Pista); stout tubes which project above the surface of the mud, with a fan-shaped flattened end decorated with projecting fingers of sand grains (Lanice); U-shaped muddy tubes with both ends opening to the surface (Amphitrite). Some small terebellids make no tubes but creep about, pulling the body around with their tentacles (Polycirrus). Some burrow through silt by means of a papillated proboscis below the mouth (Artacama).

The terebellids are highly adapted selective deposit feeders. Their grooved oral tentacles spread out in sinuous movement in all directions over the mud, exploring actively and moving constantly. Organic particles are picked up by the sticky tentacles and conveyed by ciliary action or by muscular contraction of the whole tentacle (for larger particles) along grooves toward the mouth, where the upper lip acts as a sorting device; some particles are conveyed to the mouth as food, and some are carried to the lower lips and anterior segments, where mucus is added and the particles are applied to the tube.

The family consists of about 60 genera and 375 species. The terebellids are widely distributed, from intertidal regions to great depths, with many cosmopolitan species.

References. J. H. Day, Family Terebellidae, in A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 706-750, 1967; K. J. Eckelbarger, Population biology and larval development of the terebellid polychaete Nicolea zostericola, Mar. Biol., 27: 101-113, 1974.

SABELLIDA

These worms are characterized by a prostomium which is reduced and fused with the peristomium, forming a funnellike tentacular or branchial crown or plume which surrounds the terminal mouth and is composed of ciliated biplimate filaments serving for suspension filter feeding and respiration. The body is divided into anterior thoracic and posterior abdominal regions. The first thoracic segment usually forms a collar, which functions in tube formation.

The parapodia are biramous, with notopodial capillary setae and neuropodial uncini in the thoracic region; in the abdominal region the setae are reversed: notopodial uncini and neuropodial capillaries.

The order comprises 4 families: Sabellidae, Caobangidae, Serpulidae, and Spirorbidae. It includes sedentary tube-dwelling forms.

Sabellidae. Members of this family have a cylindrical hody which tapers posteriorly; it usually has numerous segments and is divided into two distinct regions: anterior thoracic and posterior abdominal. The prostomium is indistinct and fused with the peristomium, forming a funnellike branchial plume or crown which serves for respiration and nutrition, a pair of grooved palps, and upper, lateral, and lower lips around the terminal mouth. The branchial crown consists

of a pair of semicircular or spiraled lobes, each bearing a series of grooved ciliated filaments or radioles (three to numerous); each radiole is furnished with a series of paired, ciliated side branches or pinnules (bipinnate radioles). Some ventral filaments may lack pinnules. The radioles may be dichotomously branched (Schizobranchia), united by a complete membranous web (Myxicola), or united only basally, and they may be provided with a series of ex-

ternal lappets or stylodes (Branchiomma); small eyespots may be arranged regularly in pairs or scattered irregularly on the radioles, and large subterminal compound eyes are sometimes present (Megalomma). The branchial crown is often brightly colored and banded. The branchial lobes may be covered basally by a collar developed on the first setiger or collar segment. The collar is incomplete dorsally and may be two- or four-lobed (notched ventrally and laterally); it is sometimes furnished with a pair of embedded statocysts or eyespots; notosetae only are present (collar setae).

The parapodia are biramous. The thoracic region is composed of relatively few segments (4 to 12); the notopodia are short and cylindrical, with bundles of limbate or winged capillary setae and sometimes additional spatulate setae. The neuropodia are low glandular ridges or tori bearing a row of minute hooked setae or uncini (uncinigerous tori); the uncini may be acicular with long shafts (Fabriciinae) or avicular with short shafts and with or without an anterior row of short companion or hoelike setae (Sabellinae); projecting tori may be lacking (Myxicola). The ventral surface has segmental glandular shields which secrete mucus for tube formation. In the abdominal region (few to numerous segments) the setal types are inverted, with notopodial uncinigerous tori and neuropodial limbate capillary setae. Sometimes interramal eyespots are present. The pygidium, which contains the subterminal anus, sometimes has a pair of bulbous lobes or a subconical dorsal valve; it may or may not have eyespots. The posterior segments and pygidium may form expanded lateral wings (Euchone).

Most sabellids are sedentary and live in more or less permanent cylindrical tubes which are either thick, viscous, transparent, and mucous (Myxicola), or membranous, tough-fibrous, and reinforced with mud, sand, gravel, shells, and debris; they are attached to rocks, in crevices, and in shells; some bore into soft coral. Smaller sabellids (Fabricia, Manayunkia) are capable of moving the posterior end first, dragging their branchial plumes behind; they have a pair of eyes on the pygidium; they form temporary soft, pliable, mucous-muddy tubes. The sabellids are typically suspension filter feeders. When the anterior end is extended from the tube and the trumpet-shaped branchial plume expanded, currents of water carrying suspended food particles are drawn into the funnel, where the food particles are trapped in mucus on the pinnules. Food strings pass down grooves on the inner sides of the radioles to the palps and lips around the mouth, where the particles are sorted by a complex sorting mechanism; smaller particles pass to the mouth as food, larger particles are either ejected or mixed with mucus and incorporated in the tube. Small sabellids (Manayunkia) also may sweep the surface with their tentacular filaments and are primarily deposit feeders. When the tubes are closed posteriorly, fecal pellets are passed from the subterminal anus to the ciliated midventral groove on the abdomen, then to the middorsal surface on the thorax, and finally to the mouth of the tube, where they are ejected.

The sexes are usually separate, fertilization is external, and development is pelagic. Some species deposit their eggs in gelatinous masses, and the larvae enter the plankton in the three-setiger stage. Some (Fabricia. Manayunkia) are hermaphroditic, with reproduction taking place in the parent tubes; yolky eggs are deposited in hyaline mucous capsules, brood care follows, and the embryos hatch as juveniles with no ciliated pelagic phase. These worms may also reproduce asexually by fission.

The family consists of 35 genera and about 300 species. The sabellids are widely distributed, inhabiting a multitude of intertidal and subtidal habitats. They are mostly marine, but some are estuarine and a few are freshwater forms (Manayunkia). The cosmopolitan and estuarine Fabricia sabella may form dense mats of tubes which are associated with heavy pollution.

References. J. H. Day, Family Sabellidae, in A Monograph on the Polychaeta of Southern Africa. Brit. Mus. (Natur. Hist.) 656, 1967; D. B. Lewis, Feeding and tube-building in the Fabricinae, (Annelida, Polychaeta), Proc. Linn. Soc. London. 179:37-49, 1968.

Caobangidae. Aberrant sabellidad family with a single genus (Caobangia) and 7 species. Members are short-bodied (up to 5 mm in length) and club-shaped; they are rounded posteriorly, and the posterior region is widest; the narrower anterior region bears the branchial crown. The saclike body, which lacks obvious segmentation and podial lobes, is divided into two regions: the anterior thoracic region and the posterior abdominal region. The indistinct prostomium and fused peristomium form two semicircular lobes around the terminal mouth, each lobe provided with three radioles; the upper two radioles have bipinnate pinnules, the lower one fewer pectinate pinnules. There is no collar or setae on the basal part of the branchial lobes.

The parapodia are essentially biramous. The thorax consists of seven notopodial setal bundles of short and long limbate capillary notosetae; a row of rather stout palmate neuropodial hooks is found only on the first setiger. A broad pigmented area of glandular tissue is present on the ventral surface of the anterior region. The abdomen has the setal bundles inverted, with paired bundles of one or two limbate capillary neurosetae along most of the abdomen, replaced the the posterior end by neurosetae with blunt brushlike tips. Notopodial bands of numerous small short-necked avicular hooks are found in the anterior abdominal region; they are absent in the middle region; in the posterior region there are a few long-necked avicular notopodial hooks associated with the brush-tipped neurosetae.

The unique feature in the Caobangidae is the presence of an internal recurving digestive tract, with the anus opening in the anterior thoracic region. The ascending gut is visible externally as a longitudinal midventral ridge in the abdominal region; it then curves dorsally and forms a middorsal ridge in the thoracic region; the anus opens anteriorly, about setiger II, into a longitudinal ciliated field between the notosetal bundles and the base of the branchial crown.

The caobangids are sedentary, occupying burrows in the shells of freshwater mollusks. They form blind-ending, teardrop-shaped burrows lined with a thin mucous membrane. They are suspension feeders, using their ciliated branchial crowns. They are hermaphroditic, with internal cross-fertilization. The young develop within the adult body and emerge as larvae with six to eight setigerous segments; at this stage they have segmental bands of cilia, a prostomium with tufts of cilia around the mouth, and a pair of eyes, but no anal opening; they settle on shells, form dome-shaped capsules around themselves, and proceed to bore in. The hosts are freshwater gastropod and bivalve mollusks found in fast-moving streams at an elevation ranging up to 4000 ft (1220 m) in Southeast Asia.

References. M. L. Jones, On the Caobangidae, a new family of the Polychaeta, with a redescription of *Caobangia billeti* Giard, *Smithson. Contrib. Zool.*, 175:1-55, 1974.

Serpulidae. The serpulids are sedentary, living in calcareous tubes which are usually attached to hard objects. The body is cylindrical, tapering posteriorly; it is composed of numerous segments and is divided into two distinct regions, a short anterior thoracic region and a long posterior abdominal region. The prostomium is indistinct and fused with the peristomium, forming a funnellike branchial plume around the terminal mouth. The plume consists of a pair of semicircular or spiraled lobes, each bearing a series of grooved ciliated filaments or radioles which are each in turn provided with a series of paired ciliated side branches or pinnules. The filaments may be free or united basally by a weblike palmar membrane. The most dorsal filament, usually on one side, expands during development to form a stalked operculum which plugs the entrance of the tube when the worm retracts. The mouth is enclosed by ciliated upper, lateral, and lower lips; palps are seldom present. The following segment is expanded to form a high membranous collar which is open dorsally and extended posteriorly as a thoracic membrane or mantle, uniting the thoracic parapodia and forming a ventral frilly apron overlapping the anterior abdominal region. Tuhe-building calcium-secreting glands are associated with the collar. The opercula serve to plug the tubes against instruders and to reduce water loss when the tube is exposed; if lost, they are quickly regenerated. They are fleshy and usually capped by chitinous or calcareous plates. They may be globular, spoon-shaped, conical, or soft funnel-shaped with marginal serrations (Serpula), with a radially ribbed plate bearing a distal whorl of hooked horny spines (Hydroides), or with a calcareous plate bearing two to four branching antlerlike processes (Spirobranchus). The opercular stalk usually lacks pinnules (present in Filograna) and may be cylindrical or flattened, bearing a pair of wings.

The thorax, usually composed of seven segments, begins with a uniramous collar segment with notosetae only (setae sometimes lacking), and the following segments have biramous parapodia; the notopodia have conspicuous bundles of limbate capillary setae, and the neuropodia are in the form of low ridges or tori bearing transverse rows of small saw-shaped toothed plates or uncini (uncinigerous tori), The abdominal region, with numerous segments, has the setae inverted: notopodial uncinigerous tori and small bundles of capillary neurosetae. The pygidium, which contains the slitlike anus, is small and sometimes has one or two pairs of short cirriform lobes. Ciliated fecal grooves are more or less developed: they are midventral in the abdominal region, passing dorsally in the thoracic region to the branchial funnel, serving for passage of fecal wastes and sex products.

The sexes are usually separate, and fertilization takes place externally. The larvae may remain in the plankton for a considerable time. Chitinopoma serrula constructs brood chambers flanking their tubes. Some serpulids, such as Filograna implexa, are hermaphroditic, with the larvae incubated in the tube, Filograna also reproduces asexually by lragmentation, the posterior region separating after forming a new head; this is followed by reorganization of the thoracic and head regions. The serpulids are sessile filter feeders on microscopic organisms and particles in the water current by means of a series of ciliared grooves that move films of mucus along the pinnules and filaments of the branchial plume to the mouth.

The calcareous tubes of the serpulids are more or less cylindrical, and straight, sinuous, or irregularly coiled, and more or less tapered, increasing in diameter with age; they

are mostly attached to hard objects and sometimes erect distally. The deep-water Ditrupa, which lives on a muddy bottom, is an exception in having a free tusk-shaped tube. Some species form dense population by building their tubes vertical to the substrate and cementing the tubes to each other. Some may be embedded in the coral substrate (Spirobranchus). Some may form thick white coralliform encrustations on rocks (Galeolaria in Australia). Filograna forms fine, brittle, threadlike interlacing tubes.

The family consists of about 50 genera and 350 species. The serpulids are widely distributed and form an important part of fouling communities, causing fouling of ships' hulls and harbor structures. Hydroides elegans is the most abundant and widely distributed fouling serpulid all over the world. The cosmopolitan Ficopomatus (=Mercierella) en-

ignaticus is found in estuaries and freshwater.

References. J. H. Day, Family Serpulidae, A Monograph on the Polychaeta of Southern Africa, pt. 2: Sedentaria, Brit. Mus. (Natur. Hist.) 656, pp. 798-820, 1967; J. H. Hall, The feeding mechanism in Mercierella enigmatica Fauvel (Polychaeta: Scrpulidae), Wasmann J. Biol., 12:203-222, 1954; H. A. Ten Hove, Serpulinae (Polychaeta) from the Caribbean, pt. 1: The genus Spirobranchus, Studies on the Fauna of Curação and Other Caribbean Islands, 32:1-57, Martinus Nijhoff, The Hague, 1970; H. A. Ten Hove and J. C. A. Weerdenburg, A generic revision of the brackishwater serpulid Ficopomatus Southern 1921 (Polychaeta: Serpulinae), including Mercierella Fauvel, 1923, Sphaeropomatus Treadwell, 1934, Mercierellopsis Rioja, 1945, and Neopomatus Pillai, 1960, Biol. Bull., 154:96-120, 1978.

Spirorbidae. The spirorbids are sedentary, living in calcareous tubes attached to hard objects. The larvae settle down with the dorsal surface against the substrate; the body is either dextrally or sinistrally coiled and secretes spirally coiled tubes. The body is small and asymmetrical, tapering posteriorly; it is divided into three regions: a short anterior thoracic region (3 to 5 setigers), an achaetons and obscurely segmented preabdominal region, and a rather short postabdominal region (20 or more setigers). The prostomium is indistinct and fused with the peristomium, forming a funnellike branchial plume around the terminal mouth. The plume consists of a pair of semicircular lobes, each bearing a few (three or four) ciliated filaments which are each in turn provided with a series of paired ciliated side branches or pinnules. The second dorsal filament on the concave side of the body expands during development to form a stalked operculum, lacking pinnules. The operculum plugs the entrance of the tube when the worm retracts. The following segment is expanded to form a high membranous collar, open dorsally and extended posteriorly as a thoracic membrane or mantle uniting the thoracic parapodia. Tube-building calcium-secreting glands are associated with the collar. The opercula are fleshy and capped by calcareous plates which are flattened, concave, and saucershaped, sometimes with spinous processes and often with an elongated inner process or talon extending into the stalk. The latter may be expanded to form a brood chamber for developing young. The opercula are periodically molted, sometimes resulting in a series of superimposed disks.

The thorax begins with a uniramous collar segment with notosetae only; on the following two to four segments there are the rudiments of biramous parapodia with capillary notosetae and neuropodial low ridges or tori which bear rows of small rectangular toothed plates or uncini (uncinigerous tori). Notosetae may be missing on the con-

vex side of the last thoracic segment. Following the achaetous preabdominal region, the postabdomen has the setae inverted: notopodial uncinigerous tori and small bundles of capillary neurosetae. The number of abdominal setigers is greater on the concave side of the body; the viscera and developing eggs are pushed to the convex side. Midventral ciliated fecal grooves in the abdominal region pass dorsally in the thoracic region to the branchial region, serving for passage of fecal wastes and sex products. The spirorbids are sessile filter feeders, using the ciliated grooves of the branchial plume to feed on microscopic organisms in the water current.

The calcareous tubes are more or less tightly coiled either to the right or left, in usually flat or somewhat elevated spires. The direction of coiling is constant within a species, with few exceptions. The tubes may be opaque or translucent; porcelaneous, vitreous, dull, or chalky; and smooth or ridged. The spirorbids are hermaphroditic, usually with cross-fertilization from neighboring worms. They form large yolky eggs; there is brood protection to an advanced stage of development, with the free-swimming stage usually lasting only a few hours so that the larvae settle not far from the adults. The eggs and embryos may be incubated in the tube in several ways: egg strings may lie loosely, attached by a thread to the wall of the tube, as in the sinistral Spirorbis spirorbis (=S. borealis); eggs may adhere individually to the tube wall, as in the dextral Circeis spirillum; the egg mass

may be held unattached in the thoracic fecal groove, as in *Paralaeospira*; the egg mass may be attached to the body at the base of the branchial plume by a fingerlike stalk, as in *Protolaeospira*, *Helicosiphon*, and *Romanchella*. A unique method of brood protection is the transfer of the eggs from the abdomen to the operculum, which enlarges and serves as a brood pouch (*Pileolaria*, *Janua*).

The family consists of 16 genera and about 170 species. Spirorbids are widely distributed; they are gregarious and settle on a variety of substrates such as rocks, stones, shells, algae, hydroids, bryozoa, and the carapaces of crustacea. Some species, such as the most generally common spirorbid fanua pagenstecheri, are widely distributed. The Antarctic Helicosiphon lives on a muddy bottom; the tubes are attached by a narrow base, making a few spiral coils and then turning upward for the rest of their length, so that they appear almost uncoiled.

References. P. Knight-Jones, New Spirorbidae (Polychaeta: Sedentaria) from the East Pacific, Atlantic, Indian and Southern Oceans, Zool. J. Linn. Soc.. 64:201–240, 1978; P. Knight-Jones and E. W. Knight-Jones, Taxonomy and ecology of British Spirorbidae (Polychaeta), J. Mar. Biol. Ass. U.K., 57:453–499, 1977; T. G. Pillai, Studies on a collection of spirorbids from Ceylon, together with a critical review and revision of spirorbid systematics and an account of their phylogeny and zoogeography, Ceylon J. Sci., 8:100–172, 1970.

NERILLIDA

Order with the single family Nerillidae. Members are all small (up to 1.5 mm) and transparent, with indistinct segmental lines and relatively few segments (seven to nine). The worms are short and flattened, with parapodia and long slender setae. The ventral surface has a ciliated midventral groove along the length of the body. The dorsal surface may have scattered tufts of cilia and transverse ciliated bands. The prostomium is oval, usually with three filiform frontal antennae (sometimes two or none) which may be annulated (Nerilla), and with a pair of clavate or spoonshaped lateroventral palps (may be lacking in Paranerilla); two pairs of eyes are present or absent; there are paired nuchal organs in the form of ciliated pits. The peristomium or buccal segment, with the ventral mouth in the form of a transverse slit, is usually distinct and bears well-developed parapodia similar to those of the following segments (the parapodia are absent and the segment is fused with the prostomium in Troglochaetus). The eversible muscular pharynx is usually unarmed but is sometimes provided with cuticular stylets or plates. The parapodia are uniramous, in the form of hollow, somewhat retractile outgrowths of the body wall; they are not supported by acicula. Each ramus is provided with upper and lower bundles of long setae separated by a cirriform appendage (Nerilla) or a short conical papilla (Paranerilla). The setae are all simple capillary (Nerilla). all compound with capillary blades (Mesonerilla), or a mixture of the two types (Nerillidopsis). The small pygidium, containing the dorsal anus, usually has a pair of anal cirri.

The sexes are separate. Sperm may be transferred by spermatophores. Groups of fertilized eggs are enclosed in transparent shells and attached to the substratum, and direct development ensues. Some females (Nerillidium) attach a single large egg to the posterior end, where development into an advanced larva takes place. Development may also be pelagic. These worms are found on bottoms of silt, mud, coarse sand and gravel, and algae. They feed on organic debris and microorganisms.

The family contains 12 genera and about 30 species. The nerillids are widely distributed from intertidal regions to greater depths, in marine and brackish waters; and they are found in marine aquaria. The freshwater *Troglochaetus* is found in subterranean waters in central Europe and the Rocky Mountains of Colorado.

References. C. Jouin, Family Nerillidae, in Status of the Knowledge of the Systematics and Ecology of Archiannelida, Smithson. Contrib. Zool. 76, pp. 54-55, 1971; A. Faubel, Neue Nerillidae (Archiannelida) aus dem sublitoral der Nordsee und des Mittelatlantik (Nordwest-Africa), Zool. Scripta, 7:257-262, 1978.

DINOPHILIDA

Order with the single family Dinophilidae, containing 4 genera and about 20 species. These worms are all very small and transparent, with more or less indistinct segmentation indicated by constrictions, and with relatively few segments. They are short and cylindrical (Dinophilus, Diurodrilus) or slender; elongated, flattened, and threadlike

(Trilobodrilus, Apharyngtus). The ventral surface is uniformly ciliated. The dorsal surface has scattered tufts of cilia or transverse ciliated bands, one or two per segment. The head, formed of the prostomium and fused buccal segment, is oval (Dinophilus, Diurodrilus) or three-ringed (Trilobodrilus, Apharyngtus), with transverse ciliated bands

and anterior stiff sensory hairs; it lacks antennae or palps and sometimes is provided with a pair of eyes (Dinophilus). The T-shaped ventral mouth is thickly ciliated, and the muscular pharynx is eversible (lacking in Apharyngtus). The trunk, consisting of 5 to 13 segments, lacks parapodia, setae, and cirri and sometimes bears segmentally arranged stiff hairs and transverse dorsal bands of cilia. The pygidium, with the dorsal anus, may be simple and rounded (Apharyngtus), conical and pointed (Dinophilus), spoonshaped (Trilobodrilus), or bifurcate (Dinophilus). The pygidium is furnished with tactile hairs and adhesive glands which are used for attachment to the substrate.

The sexes are separate. Some species are sexually dimorphic, with the males very small and degenerate. Copulation takes place by hypodermic impregnation, in which

the body of the female is punctured so that internal fertilization may occur. The fertilized eggs are laid in cocoons or capsules and undergo direct larval development.

The dinophilids are marine; some are euryhaline and found in estuaries, on the surface of the sediment, on mud, sand, and shelly sand, among algae. They are predominantly intertidal, and they are common in the algal film of marine aquariums. They move by swimming or ciliarymucus gliding and are well adapted to interstitial life. They feed on microscopic organisms and organic debris. Some species of *Dinophilus* may spend half their lifetime in an encysted state when the environment is unfavorable.

References. C. Jouin, Family Dinophilidae, in Status of the Knowledge of the Systematics and Ecology of Archiannelida, Smithson. Contrib. Zool. 76, pp. 52-54, 1971.

POLYGORDIIDA

Order with the single family Polygordiidae, including a single genus (Polygordius) and 15 species. The body is slender, elongate, and cylindrical, with numerous segments (up to 180). The segmental lines are poorly indicated but are more clearly defined in the posterior region. Parapodia and setae are lacking. The body is covered with a thick and iridescent cuticle, without external ciliation. The head, formed of a rounded or conical prostomium and a peristomium or buccal segment, has a pair of short, stiff, solid frontal tentacles with sensory hairs, and a pair of ciliated nuchal slits; it may or may not bear a pair of eyes. The ventral mouth is triangular or rounded; it is ciliated, with an eversible pharynx. The pygidium is bulbous and enlarged subterminally, often provided with a band of adhesive

glands arranged in longitudinal series which serve to anchor the worm; there is rarely a pair of long anal cirri. The border of the terminal anus is entire, somewhat lobed, or papillated.

The sexes are separate; the sex products are released by rupture of the body wall. Fertilization is external, and development is pelagic. These are active worms which burrow easily by muscular undulating body movements. When disturbed, they twist up into a spiral knot. They feed on diatoms and detritus and are found in coarse shelly sand and gravel, in intertidal and subtidal marine waters.

References. P. Fauvel, Gennus Polygordius, in Faune de France, vol. 16, pp. 415-419, 1927.

PROTODRILIDA

The body is slender, elongate, and flattened dorsoventrally; it is provided with transverse ciliated bands, epidermal glands, sensory hairs, and usually a ventral ciliated groove; segmental lines are distinct or poorly developed. The prostomium and peristomium have a pair of long, mobile, lateral tentacles, a pair of ciliated nuchal organs, and a ventral mouth with ciliated lips and a muscular pharynx. Small

parapodia are present (Saccocirridae) or absent (Protodrilidae). When present, setae are simple. The dorsal anus is enclosed by the pygidium, which is furnished with adhesive lobes or appendages serving for attachment to the substratum. The protodrilidads include small interstitial forms. The order includes 2 families: Protodrilidae and Saccocirridae.

Protodrilidae. The body is small, slender, and flattened dorsoventrally, with a small to moderate number of segments (up to 50). The segmental lines are poorly developed or fairly distinct. Parapodia are completely lacking. Setae are absent (Protodrilus) or present in the form of small sigmoid hooks embedded in the body wall (Protodriloides). Segmental bands of cilia or ciliary tufts are usually present, along with a ventral ciliated groove extending along the length of the body. The epidermis has several kinds of glands, including rodlike or bacillary and adhesive glands. The head, formed of the prostomium and the long peristomium or buccal segment, is rounded and provided with scattered sensory hairs, transverse bands of cilia, and usually a pair of statocysts and a pair of eyes; a pair of nuchal organs in the form of ciliated slits and a pair of actively mobile lateral tentacles with sensory hairs are also present. The tentacles are solid (Protodriloides) or furnished with a fluid-filled canal, with connecting ampullae small or lacking (Protodrilus). The ventral mouth, in the form of an elongated slit, is heavily ciliated. The pharynx is muscular but not eversible. The pygidium bears the dorsal anus and has a pair of fan-shaped or truncate adhesive lobes which are used for attachment to the substratum.

The sexes are separate. The males lack special copulatory organs, the sperm being deposited on the body surface of the female during copulation, and penetrating the epidermis into the body cavity, after which fertilization takes place internally. The eggs may be laid freely in the sand; they develop into swimming larvae. In some species the females have cocoon glands, and large yolky eggs are deposited in cocoons; this is followed by direct development. These are active worms, gliding by means of their ventral bands of cilia, as well as by muscular undulating movements of the body. They use the anal lobes and adhesive glands of the body to attach to the substratum. They feed on diatoms and unicellular algae and live interstitially in very fine to coarse sand.

The family contains 2 genera with about 30 species. They

are widely distributed in marine and brackish waters, rarely in freshwater.

References. C. Jouin, Family Protodrilidae, in Status of the Knowledge of the Systematics and Ecology of Archiannelida, Smithson. Contrib. Zool. 76, 1971.

Saccocirridae. Family with a single genus (Saccocirrus) and 16 species. The body is elongate, slender, and flattened dorsoventrally, with numerous segments (up to 200) and distinct segmental lines. It is highly contractile, with scattered epidermal glands, segmentally arranged sensory hairs, and sometimes a ventral ciliated band on part of the body. The head consists of a small subconical prostomium and a long achaetous peristomium or buccal segment; it is furnished with a pair of eyes, scattered sensory hairs, a pair of nuchal organs in the form of ciliated pits, and a pair of long, mobile, lateral tentacles. The paired tentacles have a central canal connected with a pair of fluid-filled sacs or ampullae and a transverse connecting canal. The ampullae serve as reservoirs for fluid to provide a hydrostatic skeleton for the tentacles, resulting in their lashing movements. The ventral mouth forms a longitudinal slit bordered by ciliated lips; there is usually an eversible muscular pharynx. The parapodia are uniramous, and the parapodial lobes are short, cylindrical, and retractile, and furnished with a single bundle of relatively few setae (up to nine). The setae are simple, of various types: long and capillary, or short and thicker, with bifurcate, trifurcate, or flattened truncate tips. A variable number of posterior segments, forming an area of proliferation, lack parapodia. The pygidium, with the dorsal anus, bears a pair of fleshy pads or paired subtriangular caudal appendages furnished with rows of adhesive papillae along the inner margins, serving for attachment to sand grains; there is rarely a pair of long anal cirri.

The sexes are separate, with a highly complicated reproductive system which includes copulation in coiled clumps. The sperm are transferred from the segmental gonoducts by the penis of the male to the seminal receptacle of the femlae, or they may be transferred through the body wall by hypodermic injections, followed by internal fertilization, with early development taking place in the body of the female and the young escaping as trochophore larvae. The saccocirrids are found interstitially in the surf zone, in coarse shelly sand, and beneath rocks in tide pools. They feed on diatoms, copepods, and detritus. They move actively among the sand grains with jerky leechlike movements, attaching to pebbles or shells by using glutinous secretions from the caudal appendages, body wall, and tentacles. Where ventral ciliated bands are present, they move hy gliding smoothly. They are widely distributed and may reach enormous population densities.

References. J. S. Gray, A new species of Saccocirrus (Archiannelida) from the West Coast of North America, Pac. Sci., 23:238-251, 1969; C. Jouin, Étude de quelques Archiannélides des côtes d'Afrique du Sud, description de Saccocirrus heterochaetus n. sp. (Archiannélide Saccocirrudae), Cah. Biol. Mar., 16:97-110, 1975; G. G. Martin, Saccocirrus sonomacus n. sp., a new archiannelid from California, Trans. Amer. Microsc. Soc., 96:97-103, 1977.

MYZOSTOMIDA

The aberrant body is small, flattened, oval, and disklike, lacking a distinct head and pygidium and without external segmentation. The pharynx is muscular and unarmed. The parapodia are uniramous; there are usually five pairs, each with a single hooked seta and supporting acicular rod. Alternating between the successive parapodia are usually four pairs of suckerlike lateral or sensory organs. Along the lateral borders, cirri or short papillae may be present. Development is pelagic, involving trochophore larvae, which undergo metamorphosis. This is an aberrant group whose members are associated as ectoparasites or endoparasites with

echinoderms, principally crinoids and more rarely asteroids and ophiuroids.

The order includes 7 families: Myzostomidae, Cystimyzostomidae, Pulvinomyzostomidae, Asteriomyzostomidae, Mesomyzostomidae, Protomyzostomidae, and Stelechopidae.

References. P. Fauvel, Myzostomaires, in Faune de France, vol. 16, pp. 445-450, 1927; G. Jägersten, Zur Kenntnis der Morphologie, Entwicklung und Taxonomie der Myzostomida, Nova Acta Regiae Soc. Sci. Upsal., ser. 4, 11(8):1-84, 1940.

Myzostomidae. Family with a single genus (Myzostomum) and over 100 species. The body is small, flattened, oval, and disklike. The dorsal surface is vaulted and may be irregularly furrowed, papillated, or smooth. The ventral surface is flattened or slightly concave. The integument has scattered ciliated cells. The mouth is located terminally or ventrally near the anterior end. The tubular muscular pharynx is eversible and unarmed, usually with a circlet of papillae. The anal or cloacal opening is located ventrally on a papilla near the posterior end. Five pairs of uniramous parapodia, in the form of short cylindrical lobes, are found in semicircular arrangement on the ventral side. Each parapodium is supplied with a stout, strongly hooked seta and a supporting acicular rod with a flattened end plate or manubrium. Alternating between successive parapodia are usually four pairs of suckerlike lateral or sensory organs. Usually 10 pairs of cirri or short papillae are found along the lateral borders; more rarely, there are numerous papillae; some

species have additional long caudal cirri; they may be supplied with tactile hairs or glutinous cells which function as tactile or attachment organs.

The myzostomids are functional hermaphrodites during the greater part of their life. The male openings are situated laterally; the penis is eversible and is often of considerable size. The eggs are poor in yolk and escape through the cloacal opening. Development is pelagic, with trochophore larvae which undergo metamorphosis. These worms are free-living and migratory ectocommensals on crinoids and brittle stars. They are able to move by quick jerky movements on the disks and arms of the host. They are widely distributed in moderate to deep waters.

References. K. Kato, On the development of Myzostome, Sci. Rep. Saitama Univ., 1:1-16, 1952.

Cystimyzostomidae. Family with a single genus (Cystimyzostomum) and more than 10 species. Members live in cysts

or galls formed in the body wall or skeleton of the crinoid host. The cysts are club-, pear-, or sausage-shaped, with hard, rough, or calcareous walls; they may be attached along their length or hang freely, with a small opening on the free side. Usually each cyst is occupied by a single pair of worms, a larger female and a dwarf male. The body is flattened and disklike, somewhat deformed, with the lateral margins curved more or less strongly over the dorsal side. The epidermis has scattered ciliated cells. The mouth is terminal and turned toward the opening of the cyst, where the eversible muscular pharynx may project. The cloacal opening is terminal on the posterior end. The five pairs of parapodia are rudimentary, each furnished with a hooked seta and an accessory acicular rod. Lateral organs and lateral cirri are usually rudimentary or lacking. The sexes are separate or function as protandrous hermaphrodites; the penis is rudimentary or lacking. Movement is confined to the cysts in the adult form.

Pulvinomyzostomidae. Family with a single genus (Pulvinomyzostomum) and 2 species. Members are found living endoparasitically in the stomach of crinoids. The body is oval, much wider than long, with a flat dorsal surface, a vaulted ventral surface, dorsally curved, lateral borders; cirri are lacking. The integumentary epithelium is ciliated. Both the mouth, with the protruding pharynx, and the cloacal papilla are found on the dorsal surface. The five pairs of parapodia on the ventral side are rudimentary, each furnished with a strong projecting hook and a supporting acicular rod. These worms are protandrous hermaphrodites; young males are found on the dorsum of the larger females; a penis is lacking.

Asteriomyzostomidae. Family with a single genus (Asteriomyzostomum) and 2 species. These worms are found living endoparasitically in the body cavity and digestive ceca of starfish. The body is greatly flattened, disklike, transversely elliptical, and broader than long. The epidermis has a cuticle; cilia are lacking. The dorsum is smooth, with somewhat undulating lateral margins, and without cirri. The mouth is ventral near the anterior margin; the muscular pharynx is noneversible. The cloacal opening is on the dorsal surface on the posterior third of the body. The five pairs of parapodia on the ventral side are small and vestigial, each supplied with a large hooked seta and a supporting acicular rod with a cushionlike expansion. Four pairs of small lateral organs alternate with the parapodia. Members of this family are protandrous hermaphrodites; the lateral penis is rudimentary.

References. W. M. Wheeler, A new *Myzostoma*, parasitic in a starfish, *Biol. Bull. Woods Hole*, 8:75-78, 1905.

Mesomyzostomidae. Family with a single genus (Mesomyzostoma) and 2 species. These worms live endoparasitically in the gonads of crinoids. The body is elongate and bandlike, flattened dorsoventrally, without cirri on the lateral margins. The integument is smooth, with a cuticle and without cilia. The anterior mouth is terminal, and the muscular pharynx is noneversible. The posterior cloacal opening is terminal. The parapodia, which number three to five pairs, are vestigial, indicated only by slight protrusions of the dorsolateral or lateral margins; each has a hooked seta and a supporting acicular rod with an expanded end plate. Lateral organs are absent. Members of this family may show a kind of peristaltic movement. They are protandrous hermaphrodites; the penis is rudimentary or lacking.

References. Y. Okada, Mesomyzostoma katoi, n. sp., an interesting myzostome found in the gonad of Comanthus japonicus, Annot. Zool. Japon., 14:185-189, 1933.

Protomyzostomidae. Family which consists of a single genus (Protomyzostomum) and 3 species. Its members live endoparasitically in the oviduct and bursal cavity of basket stars. The body is elongate-oval, flattened dorsoventrally, and without cirri on the lateral margins. The integument is smooth, with a cuticle, and it lacks cilia. The anterior mouth is terminal, and the muscular pharynx is noneversible. The posterior cloacal opening is terminal. The five pairs of parapodia are vestigial, indicated only by slight indentations of the lateral margins of the body; each parapodium has a hooked seta and supporting acicular rod. Five pairs of small lateral organs are situated close to the parapodia. These worms are hermaphroditic; the penis is rudimentary or lacking.

Stelechopidae. Family with a single species (Stelechopus hypocrini). These worms live as ectocommensals on crinoids. The body is long, flat, and bandlike, without cirri on the lateral margins. It is covered with a thick chitinous cuticle which lacks cilia. The mouth is located on the anterior margin between the first pair of parapodia; the muscular pharynx is noneversible. The posterior end, with the cloacal opening, projects as a conical caudal appendage between the last pair of parapodia. The five pairs of parapodia on the ventrolateral sides are subtriangular, and each parapodium is provided with a long hooked seta and a supporting acicular rod. Lateral organs are absent. Stelechopids are hermaphroditic; the penis is rudimentary or lacking.

POEOBIIDA

Order with a single family, Poeobiidae, and a single species, *Poeobius meseres*. It is an aberrant group of uncertain relationship, adapted to a free-swimming pelagic existence. The body is elongate-oval, laterally compressed, and semitransparent, without external segmentation and setae. There are 11 body segments, based on 11 pairs of ganglia in the ventral nerve cord; the body cavity is separated into three areas by two transverse septa. The body wall consists of a delicate cuticle, an epiderinis with scattered sensory papillae and ciliated cells, a very thick gelatinous layer, and circular and longitudinal muscles. The head is fused with the rest of the body and may be completely withdrawn. The indistinct prostomium and peristomium have a pair of long

tentacular palps, each provided with a pair of ciliated glandular ridges, a pair of ciliated nuchal organs, two groups of five to seven cirriform branchiae, a subterminal mouth arched over by heavily ciliated lateral lips, and a heavily ciliated buccal cavity with an eversible muscular pad. The anal opening is terminal on the posterior end and is heavily ciliated.

The sexes are separate. The sex products escape through a pair of coelomic funnels. Fertilization is external. Members of this order feed on detritus and microscopic organisms. Particles are trapped on the tentacular palps by mucus secreted by glandular cells of the ciliated ridges; they are then moved toward the mouth. The distribution of the

poeobiids coincides with that of the North Pacific sub-Arctic water masses and the transitional waters of the California Current, from Alaska to off California.

References. O. Hartman, Poeobiidae Heath, 1930, in Essays in the Natural Sciences in Honor of Captain Allan Hancock, University of Southern California Press, Los Angeles, pp. 52-54, 1955; H. Heath, A connecting link between the

Annelida and the Echiuroidea (Gephyrea armata), J. Morphol. Physiol., 49:223-244, 1930; G. E. Pickford, Histological and histochemical observations upon an aberrant annelid, Poeobius meseres Heath, J. Morphol.. 80:287-320, 1947; D. E. Robbins, The biology and morphology of the pelagic annelid Poeobius meseres Health, J. Zool., 146:197-212, 1965.

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