Hydrobiologia (2005) **535/536:** 199–225
T. Bartolomaeus & G. Purschke (eds), Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa

Pharynx and intestine

Alexander Tzetlin[1] & Günter Purschke[2,*]
[1] *Department of Invertebrate Zoology, Moscow State University, 119899 Moscow, Russia*
[2] *Spezielle Zoologie, Fachbereich Biologie/Chemie, Universität Osnabrück, D-49069 Osnabrück, Germany*
*(*Author for correspondence: E-mail: purschke@biologie.uni-osnabrueck.de)*

Key words: pharynx, axial pharynx, ventral pharynx, dorsolateral folds, dorsal pharynx, intestine, enteronephridia, jaws

Abstract

The alimentary canal of polychaetes consists of a foregut, midgut, and hindgut. The alimentary canal shows different specializations even in homonomously segmented polychaetes. The foregut gives rise to the buccal cavity, pharnyx and oesophagus, the midgut may be divided into a stomach and the intestine proper. Since polychaetes use a wide spectrum of food sources, structures involved in feeding vary as well and show numerous specializations. In the foregut these specializations may be classified as one of the following types: dorsolateral folds, ventral pharynx, axial muscular pharynx, axial non-muscular proboscis and dorsal pharynx. The latter, typical of oligochaetous Clitellata, occurs rarely in polychaetes. The structure, evolution and phylogenetic importance of these different types are described and discussed. Axial muscular and ventral pharynges may be armed with jaws, sclerotized parts of the pharyngeal cuticle. Terminology, structure, occurrence and development of the jaws are briefly reviewed. Special attention has been paid to the jaws of Eunicida including extinct and extant forms. Conflicting theories about the evolution of the jaws in Eunicida are discussed. The epithelia of the intestine may form a pseudostratified epithelium composed of glandular cells, absorptive cells and ciliated cells or only one cell type having similar functions. A conspicuous feature in the intestine of certain polychaetes is the occurrence of unicellular tubular structures, called enteronephridia. So far these enteronephridia are only known in a few meiofauna species.

Introduction

The alimentary canal of polychaetes consists of three parts: foregut, midgut and hindgut. Foregut and hindgut are of ectodermal origin, being formed by stomatodeal and proctodeal invaginations of the ectoderm and thus usually bearing a cuticle. The midgut is derived from the endoderm. The structure of the gut is correlated with adaptations to feeding and life style of polychaetes. Usually the alimentary canal shows different specialized parts even in homonomously segmented taxa (Fig. 1A–C). The foregut gives rise to the buccal cavity, pharynx and oesophagus, the midgut may be divided into a stomach and the intestine proper (Fig. 1B and C), and only the hindgut normally forms a single part. The length of the different regions varies among species according to their specific adaptive needs. Usually the intestine is no longer than the body, but in taxa with comparatively short or stout bodies the intestine may be coiled (Fig. 1B) or bear caeca to provide sufficient digestive surfaces. The gut system is attached to the body wall by means of septa and mesenteries which, however, may be more or less reduced or absent when the intestine is coiled or involved in extensive longitudinal movements. In contrast to Clitellata, no polychaete taxon is known to date in which a digestive tract is completely absent. However, in Siboglinidae (formerly

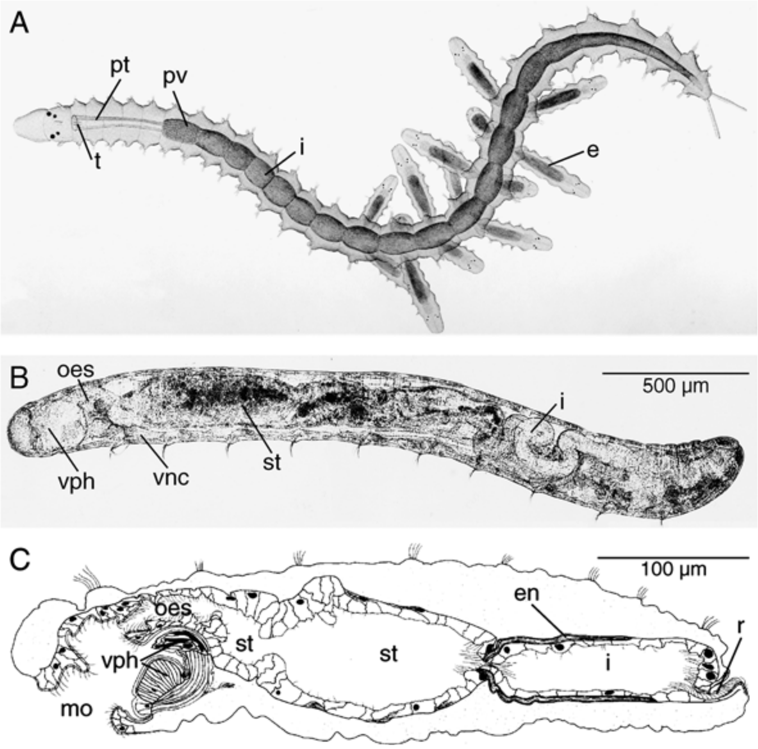

Figure 1. Different patterns of gut structure in polychaetes. (A) '*Exogone rubescens*' (Syllidae). Intestine (i) forms a straight tube. Pharynx differentiated into pharyngeal tube (pt) and proventricle (pv); e developing embryos. (B) *Stygocapitella subterranea* (Parergodrilidae). Gut divided into ventral pharynx (vph), oesophagus (oes), stomach (st), coiled intestine (i), rectum (r), and ventral nerve cord (vnc). (C) *Trochonerilla mobilis* (Nerillidae). Digestive tract comprises ventral pharynx (vph), oesophagus (oes), anterior and posterior stomach (st), enteronephridia (e), intestine (i) and rectum (r). Enteronephridia open into the gut at the border between stomach and intestine. (mo) mouth. A after Ørsted (unpubl.) from Wolff & Petersen (1991), B from Struck et al. (2002), C from Tzetlin et al. (1992).

Pogonophora, now considered to belong to Polychaeta) it is highly modified to form the trophosome housing symbiotic bacteria (Southward et al., 2005) and in *Parenterodrilus taenioides* the gut is residual and non-functional (Jouin, 1979, 1992).

The literature on the anatomy, morphology and physiology of the polychaete digestive system and feeding biology is copious and has been reviewed by Dales (1963), Jeuniaux (1969), Michel & DeVillez (1978), Fauchald & Jumars (1979), Michel (1988), Purschke (1988a), and Saulnier-Michel (1992).

Pharynx and foregut

Polychaetes use a wide spectrum of food sources and show a great diversity of feeding habits (Fauchald & Jumars, 1979). Accordingly, structures involved in feeding vary as well and show numerous specializations (for recent reviews see Purschke, 1988a; Saulnier-Michel, 1992). These specializations include the structural differentiation of the foregut proper and presence or absence of accessory structures, which can include ciliated tracts, ciliated fields or tentacles. Although feeding tentacles differ considerably between taxa, they mostly represent specialized palps and, thus, can be regarded as homologous (Orrhage & Müller, 2005).

However, in Ampharetidae, Pectinariidae and Terbellidae the feeding tentacles are considered not be modified palps (Orrhage, 2001). Moreover several other tentacle-like structures may be present such as the buccal tentacles of Cossuridae, which originate from the stomodeal epithelium (Tzetlin, 1994).

The mouth region of the larvae may give rise to a variety of adult structures often together termed the buccal organ (Rouse, 2000). In many species the foregut is more or less protrusile and thus called a proboscis, which in turn may be composed of several parts (e.g., Purschke, 1988a; Saulnier-Michel, 1992). The term pharynx is generally restricted to the muscular regions of the foregut. Since the foregut is derived from the ectoderm, its epithelium is usually covered by a cuticle. In several taxa, areas of this cuticle have become thickened, sclerotized and mineralized to form distinct jaws or tooth-like structures (p. 209). Although the structure of the foregut varies widely among the polychaete taxa, these different structures have until recently been classified as only three types of buccal organs (Fauvel, 1959; Dales, 1962; Saulnier-Michel, 1992): (1) axial muscular proboscis (pharynx), (2) ventral pharyngeal organ and (3) axial non-muscular proboscis. However, Purschke & Tzetlin (1996) described a previously unrecognized, comparatively simply structured foregut as another distinct plan of organization, which has been called dorsolateral ciliary folds. Rouse (2000) subdivided the ventral pharyngeal organs into simple ventral buccal organs and ventral buccal organs with well-developed musculature, the latter only occurring in Eunicida and Amphinomida. Moreover, the simple, tube-like foregut present in Sabellidae and Serpulidae (as well as Spirorbidae and Sabellariidae?) has been classified as absence of a buccal organ by Rouse (2000). Recent investigations of the foregut in the enigmatic terrestrial polychaete *Hrabeiella periglandulata* confirmed the presence of a dorsal pharynx in this species, elsewhere only known in and characteristic of oligochaetous Clitellata (Rota, 1998; Purschke, 2002, 2003).

Dorsolateral ciliary folds

In many polychaete species the dorsolateral walls of the foregut are differentiated into protrusible ciliated folds (Fig. 2A–H). Although sometimes briefly mentioned in the literature (e.g., Orrhage, 1964; Purschke & Jouin, 1988; Tzetlin, 1989), their importance as a distinct type of feeding structure in polychaetes has not been recognized for a long time. One reason might be their simple structure and another reason, that these folds most often occur together with a ventral pharyngeal organ (Purschke & Tzetlin, 1996). Since there are species in which these folds are the only differentiation of the foregut used for feeding, they are described separately.

These folds are always positioned dorsolaterally and are usually heavily ciliated (about 5–8 cilia per μm^2; Fig. 2D and H). As a rule the ciliated cells are associated with numerous gland cells, which may either be randomly distributed over the folds or are clustered to form distinct pharyngeal or salivary glands. The ciliation of these folds may either be restricted to the foregut or represent a continuation of ciliary fields present on the ventral side of the prostomium (Fig. 2F–H). Usually these folds take the form of a pair of inner lips, separated by an unciliated pouch from the lips surrounding the mouth (Fig. 2B–E). Musculature is only weakly developed and consists of a thin layer of transverse and longitudinal fibres. A few retractor fibres are present as well.

For feeding, the folds can be everted through the mouth opening and brought into contact with the substrate (Fig. 2B, C and E). This is mainly achieved by contraction of the musculature of the body wall without changes of the hydrostatic pressure in the body cavity (Purschke & Tzetlin, 1996). Food particles not adhering firmly to the substrate are kept and retained with mucus, collected by means of the action of the cilia of the folds, transported and sorted along the folds into the mouth and further to the oesophagus. Clearly, these structures are primarily adapted to microphagy and the organisms may be classified as surface deposit feeders (Fauchald & Jumars, 1979). With this mode of feeding, food particles attached to the substrate cannot be ingested and the area which can be grazed is comparatively small, not exceeding the width of the body. Only in species also possessing a ventral pharyngeal organ is it possible for food particles adhering to the substrate to be abraded by the action of the bulb and then to be ingested by the beating of the ciliary folds (Fig. 3B). Both modes of feeding may occur in one species (Jennings & Gelder, 1969; Schmidt & Westheide, 1972; Gelder & Uglow, 1973; Westheide & Schmidt, 1974). Given these considerations, it is not surprising that dorsolateral folds are present only in small epibenthic or interstitial species, usually not exceeding a few millimeters in length, or in juveniles of larger species. In the latter, other types of microphagous feeding structures such as feeding tentacles or a non-muscular

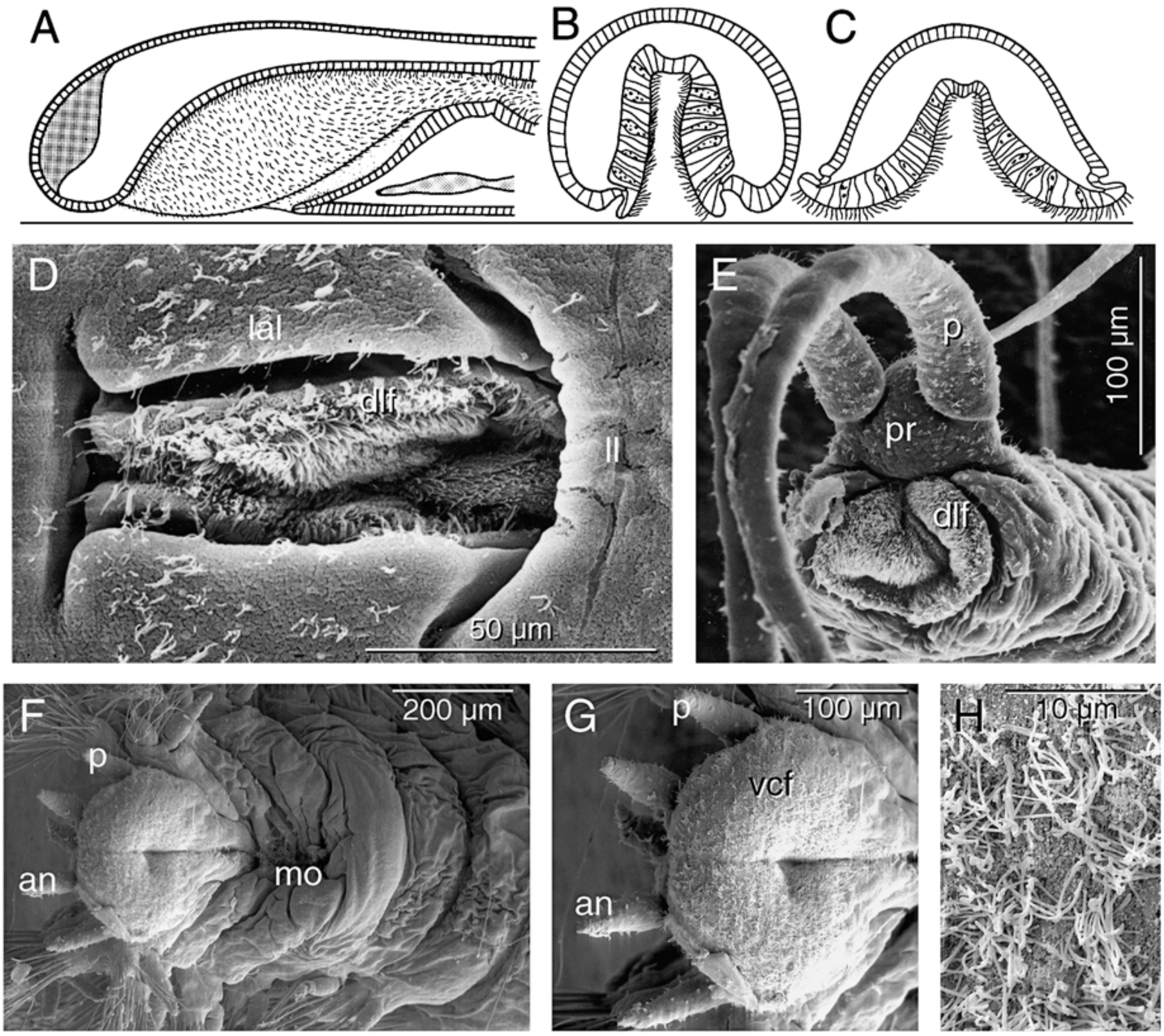

Figure 2. Foregut. Dorsolateral folds. (A–C) Schematic representation. (A) Sagittal section. (B) Cross-section in the resting position. (C) Cross-section in the feeding position. (D, E) *Saccocirrus papillocercus*. (D) Mouth opening with lateral and lower lips (lal, ll) and dorsolateral folds (dlf) in the resting position. (E) Dorsolateral folds everted for feeding. p palp, pr prostomium. (F–H) *Eurythoe complanata*. (F) Ventral view of anterior end, mo mouth. (G) Enlargement of prostomium with ciliary fields (vcf) leading into mouth; an antenna, p palp. (H) Ciliation of prostomium. A–E modified from Tzetlin et al. (1992), micrographs F–H S. Raabe.

axial proboscis develop later during ontogeny (Eisig, 1914; Dales, 1957; Heimler, 1983; Purschke, 1988b).

Ventral pharynx

Ventral pharyngeal organs are widespread within polychaetes. They exhibit a high degree of diversity among the different taxa and several types may be distinguished (Purschke & Tzetlin, 1996; Purschke, 1988a,b, 2002). Situated below the oesophagus, these organs are made up of different parts divided by a few blind-ending pouches. These are situated in the ventroposterior region of the foregut (Fig. 3A and B). The invaginations are lined by specialized epithelia and are covered by structurally differentiated cuticles. Most characteristic is the presence of transverse plate-like muscle fibers underneath one of these invaginations (Figs 3C and 4A). These transverse fibers usually form a compact muscle structure, called muscle bulb. Above this bulb a tongue-like organ may be present. A group of longitudinal fibres runs semicircularly around the ventral pharynx from the lower lip to the dorsalmost parts underneath the oesophagus. These fibers are either called sagittal muscle or, since they envelope the entire ventral pharynx, investing muscle (Purschke, 1988a). The ultrastructure of ventral pharyngeal organs is comparatively well known (Rieger & Rieger, 1975; Jouin, 1978a; Michel, 1978; Purschke, 1985a,b, 1987a,b, 1988a,b; Tzetlin, 1987, 1989, 1991; Tzetlin et al., 1987, 1992; Purschke & Jouin, 1988; Saulnier-Michel et al., 1990; Müller et al., 2001).

Ventral pharynges are used for scraping or licking off food particles from the substrate or they function as devices for processing food particles inside the oesophagus. Usually parts of the cuticle in the ventral pharynges are differentiated for this purpose. In these areas it is comparatively thick, frequently forming tooth-like structures, and microvilli do not reach the surface of the cuticle (Fig. 3B). In spite of this function the cuticle is not sclerotized in most taxa; the only exception is Eunicida which possess a characteristic jaw apparatus described below (p. 211). The stylets typical of Nerillidae are actually intracellular skeletal elements and are not cuticular jaws (Purschke, 1985b; Tzetlin & Larionov, 1988; Tzetlin et al., 1992; Müller et al., 2001). The bulb and/or the tongue-like organ are everted through the mouth, dislodging food particles; in contrast to axial pharynges these structures usually cannot be protruded very far.

The bulbus muscle serves as a firm but elastic cushion supporting the epithelial areas used for scraping. In the bulbus muscle only transverse fibers are present and antagonistic fibers do not exist. The bulb is usually surrounded by a comparatively thick extracellular matrix and several types may be distinguished. Currently six different types of ventral pharynges may be distinguished on the basis of the structure of the bulb. Amphinomida, Eunicida, Dinophilidae, Diurodrilidae and Nerillidae each possess their own type of ventral pharynx.

Type 1

In the most common type, plate-like muscle cells and interstitial cells alternate in the bulb (Fig. 3C–E). In the interstitial cells there is a prominent system of intermediate filaments oriented dorsoventrally, i.e., these filaments are perpendicular with respect to the myofilaments. In certain species these interstitial cells have voluminous cell bodies containing only the nucleus and a few organelles (Fig. 3C and D; Heimler, 1983; Tzetlin, 1987; Purschke, 1988b). Histological observations indicate that this type of bulbus muscle occurs in many species and may thus be the most frequent type. In Protodriloidae, Protodrilidae and Saccocirridae interstitial cells with prominent bundles of tonofilaments are present as well, but the cell bodies are small (Fig. 3E; Purschke & Jouin, 1988). In this type the muscle fibers contract against the extracellular matrix surrounding the bulb, opposing the internal pressure of the interstitial cells and their dorsoventral tonofilament system (Purschke, 1988b). Because these filaments do not allow a dorsoventral extension of the bulb, cushions of varying firmness and elasticity are achieved. In Parergodrilidae a similar bulbus muscle is present (Purschke, 1987a, 1988b). However, in *Stygocapitella subterranea* the bulb is small and more or less replaced by a voluminous multicellular gland. In the terrestrial *Parergodrilus heideri* the muscle bulb is lacking, completely replaced by this gland and the investing muscle fibres are transformed to make up the complex musculature of the tongue-like organ.

Type 2

In a second type of bulbus muscle a similar function is realized by bulbus muscle fibers in which the two myofilament systems are perpendicular to each other and run from right ventrolateral to left dorsolateral and vice versa (Fig. 3F and G). This bulb is found in Dinophilidae (Rieger & Rieger, 1975; Purschke, 1985a, 1988a).

Type 3

In Nerillidae a dorsoventral tonofilament system is present in each muscle fiber, crossing the myofilaments at a right angle (Fig. 4A and B; Purschke, 1985b, 1988a; Tzetlin et al., 1992; Müller et al., 2001). Very often the muscle fibers making up the bulbus are of the circomyarian type, with a central core of sarcoplasm housing mitochondria and nucleus; this fibre type is usually found in Hirudinea (Lanzavecchia et al., 1988).

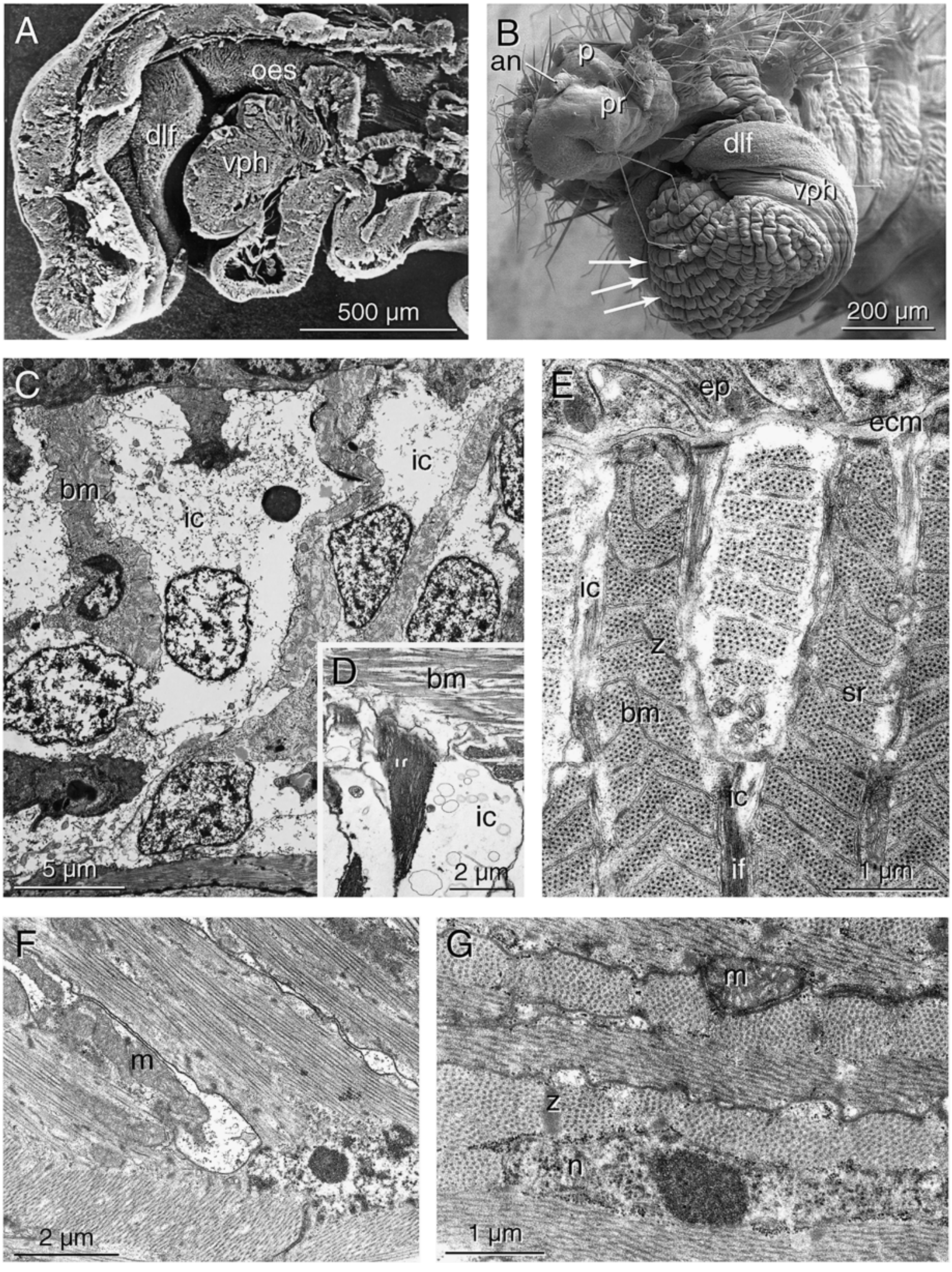
A
oes
dlf
vph
500 µm
B
an
p
pr
dlf
vph
200 µm
C
bm
ic
ic
5 µm
D
bm
ir
ic
2 µm
E
ep
ecm
ic
z
bm
sr
ic
if
1 µm
F
m
2 µm
G
m
z
n
1 µm

Figure 3. Foregut. Ventral pharyngeal organ. (A) *Nicomache minor* (Maldanidae). Sagitally dissected specimen showing ventral pharynx (vph), dorsolateral folds (dlf) and oesophagus (oes). (B) *Eurythoe complanata* (Amphinomidae). Everted ventral pharynx (vph), surface of the bulb supplied with transverse ridges (arrows) used for scraping off food particles; an antenna, dlf dorsolateral folds, p palp, pr prostomium. (C) *Scoloplos armiger* (Orbiniidae). Longitudinal section of muscle bulb composed of large voluminous interstitial cells (ic) and bulbus muscle fibers (bm). (D) *Ctenodrilus serratus* (Ctenodrilidae). Muscle bulb (bm), large interstitial cells (ic) with prominent bundles of intermediate filaments (if) crossing myofilaments at a right angle. (E) *Saccocirrus papillocercus* (Saccocirridae). Bulb made up of small interstitial cells (ic) and plate-like muscle fibers (bm); ecm extracellular matrix, ep epithelium, if intermediate filaments, sr sarcoplasmic reticulum, z z-rod. (F, G) Dinophilidae, muscle bulb consisting of muscle fibers only; myofilaments perpendicular in both halves of the fibers. (F) *Trilobodrilus axi.* (G) *Dinophilius gyrociliatus*; m mitochondrion, n nucleus, z z-rod. A modified from Tzetlin et al. (1992); B micrograph S. Raabe, C modified from Purschke (1988a).

Type 4
In Dorvilleidae the bulbus muscle fibers are of this type as well but without tonofilaments or interstitial cells in between them (Purschke, 1987b).

Type 5
Most likely another type of pharyngeal bulb is present in Diurodrilidae, characterized by a large ventral pharyngeal gland cell and poorly developed musculature (Kristensen & Niilonen, 1982). Unfortunately, from the brief description it cannot be concluded whether this type may have been evolved from one of those mentioned above and has be included in one of the types mentioned above.

Type 6
The pharynx of Amphinomida appears to be completely different from all structures described above. Unfortunately, the highly muscularized structure has not yet been described at the ultrastructural level. It ventrally has a series of distinct transverse lamellae with a thickend and transformed cuticle (Dales, 1962; Purschke & Tzetlin, 1996).

The investing muscle fibres are not that diverse and typically are obliquely striated. In certain species the myofilament system is not helically arranged so that in sections only one myofilament system appears to be present, e.g., Nerillidae (Purschke, 1985b; Müller et al., 2001). Usually nuclei are located in posterior extensions where the fibers turn but in some species their positioning can also be of the Hirudinean type (see above).

Additional muscle fibers may be present in the tongue-like organs, which are pistil-shaped, lateral folds or flat structures attached to the lateral walls of the foregut. Intracellular skeletal elements are present in many (all?) Nerillidae. Situated in epithelial cells, they measure up to 55 μm in length and up to 3 μm in diameter. These skeletal rods are initially made up of tonofilaments which fuse to form striations with a period of 65–70 nm (Purschke, 1985b; Tzetlin et al., 1992; Müller et al., 2001). Depending on the diameter they are recognizable in the light microscope or not. In Parergodrilidae the cuticle of the tongue-like organ forms a rod-like posterior extension serving as attachment area of the musculature (Purschke, 1987a). In other ventral pharynges such specializations are unknown.

Axial non-muscular pharynx

An axial non-muscular proboscis is present in many of the sand- or mud-swallowing species of Arenicolidae, Maldanidae, Capitellidae, Opheliidae, Orbiniidae and Paraonidae (Fig. 4D and E; Purschke & Tzetlin, 1996; Rouse, 2000). These pharynges are composed of epithelial, glandular and sensory cells but musculature is weakly developed (Purschke, 1988a; Saulnier-Michel, 1992). The epithelium is unciliated and forms papillae in Arenicolidae, Maldanidae and Capitellidae. Ultrastructural studies are rare and have only been made in one species, *Notomastus latericeus* (see Michel, 1972; Saulnier-Michel, 1992). Everting movements of the proboscis are achieved by changes in hydrostatic pressure in the anteriormost compartments of the body cavity. The pressure increase effected by contractions of the musculature of the body wall is limited to the anterior part of the body cavity by the presence of a strong muscular septum in Capitellidae and Arenicolidae (Purschke & Tzetlin, 1996). The proboscis is withdrawn by the activity of retractor muscles.

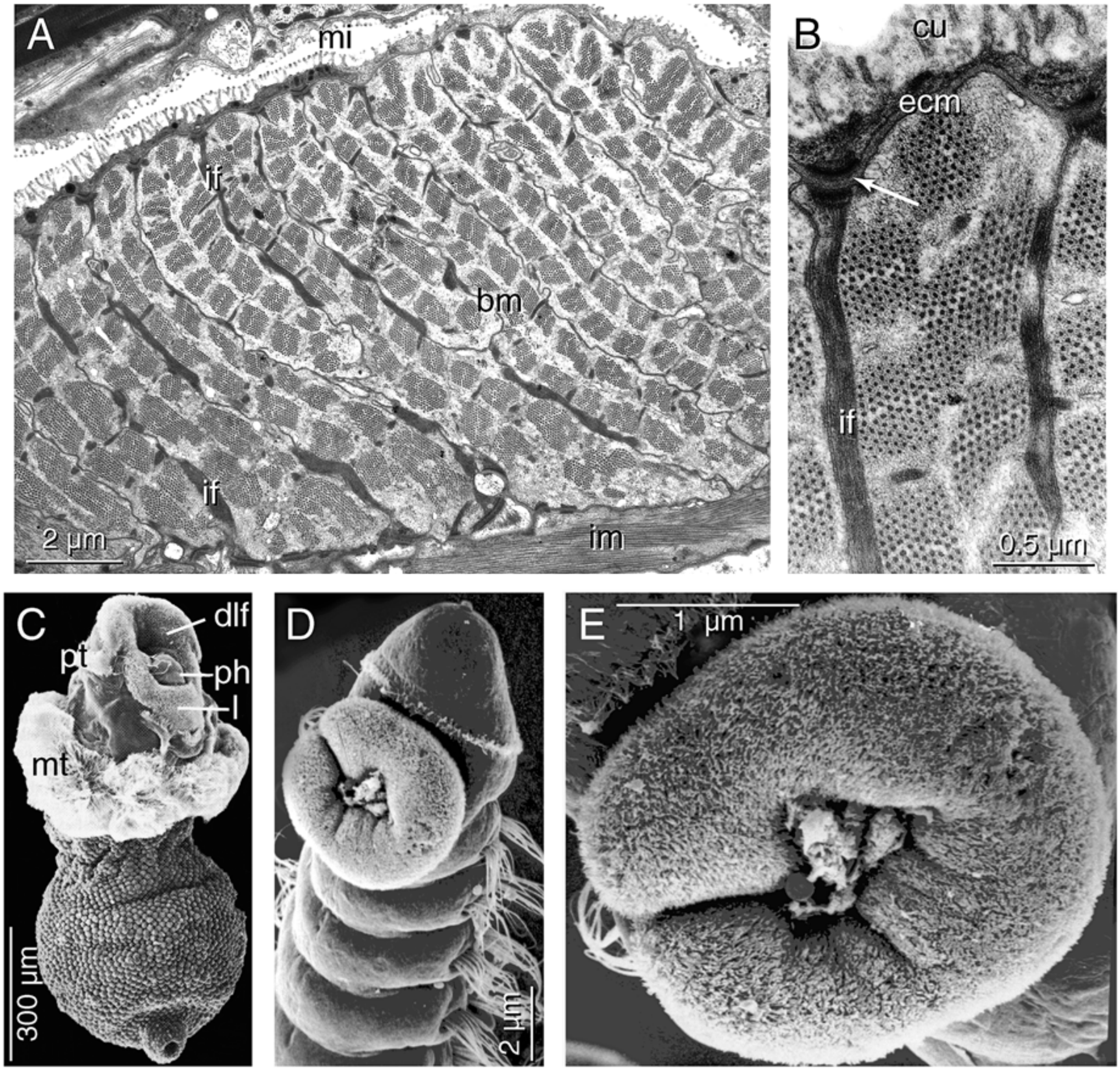

Figure 4. Foregut. (A, B) *Nerillidium troglochaetoides* (Nerillidae). (A) Muscle bulb composed of plate-like muscle cells (bm); myofilaments oriented transversally and parallel; im investing muscle, mi median invagination, if intermediate filaments. (B) Enlargement of bulbus muscle fibre with bundles of intermediate filaments (if) perpendicular to myofilaments. Note myopithelial junction (Arrow); cu cuticle, ecm extracellular matrix. (C) *Phascolosoma agasszii* (Sipuncula). Pelagosphera larva with ventral pharynx (ph); dlf dorsolateral folds, l lower lip, mt metatroch, pt prototroch. (D, E) *Paraonella nordica*. (D) Everted non-muscular axial proboscis. (E) Ciliated epithelium of proboscis. C modified from Rice, 1985.

During ontogeny, individuals of *Arenicola marina*, *Ophelia* spp., and *Scoloplos armiger* (as well as other Orbiniidae) pass through a juvenile stage possessing dorsolateral ciliary folds and a ventral pharyngeal organ (Eisig, 1914; Anderson, 1959; Purschke & Tzetlin, 1996). Later in development these structures are replaced by axial non-muscular proboscides. Interestingly, in some species of Maldanidae the adults have a foregut with a typically developed ventral pharynx and dorsolateral folds (e.g., *Nicomache minor*), whereas other species exhibit various stages of development of axial proboscis-like structures in addition to more or less reduced ventral pharynges (e.g., *Nicomache lumbricalis*, *Praxillela praetermissa*) or even possess only a non-muscular axial proboscis (*Axiothella rubrocincta*) (Fig. 5; Tzetlin, 1991). A similar situation has been observed in Orbiniidae by Eisig (1914).

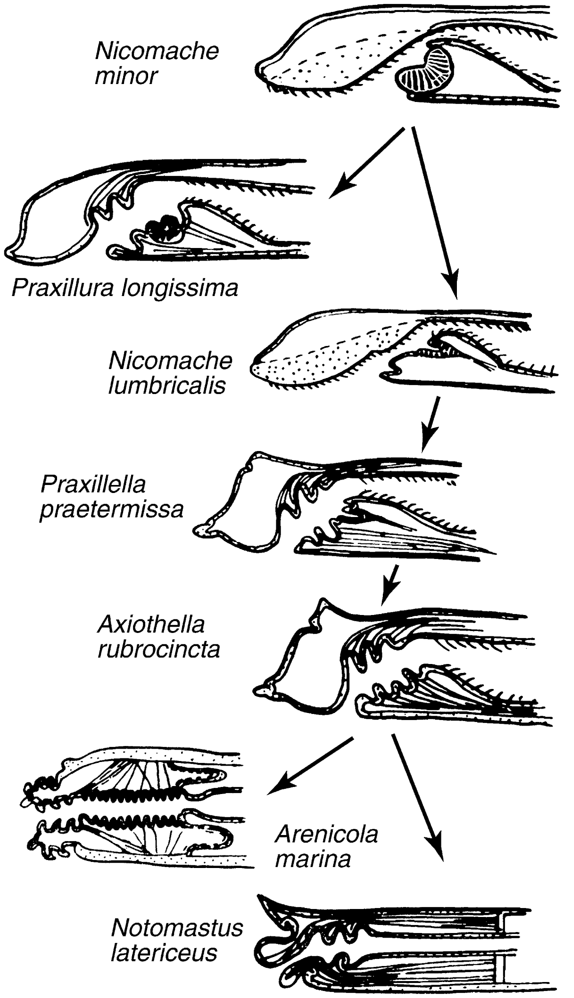

Figure 5. Tentative outline of evolutionary changes of the buccal organ in Capitellida. Subsequent and gradual transformation of ventral pharyngeal organ into non-muscular axial proboscis. Septum separating anterior compartment of the coelom only present in Capitellidae and Arenicolidae but absent in Maldanidae (e.g., *Axiothella rubrocincta*). Modified from Tzetlin (1991).

Dorsal pharynx

A dorsal pharynx is typical of oligochaetous Clitellata, and *Hrabeiella periglandulata* is the only non-clitellate annelid possessing this type of pharynx (Jamieson, 1992; Rota, 1998; Purschke, 1999, 2002, 2003). It is characterized by a conspicuous thickening of the dorsal wall of the foregut owing to epithelial cells, gland cells and muscle fibers (Purschke, 2003). This dorsal pad is densely ciliated whereas the buccal cavity is always unciliated and, further posterior, only the oesophagus has an epithelium with motile cilia (Fig. 6). In *H. periglandulata* a complex system of muscle fibers serving as protractors and retractors is attached to the dorsal ciliated pad. The cell bodies of the gland cells form four pairs of lobes situated on the dorsal side of the foregut between the muscle fibers. They send long, thin processes ventrally, the openings of which are situated exclusively between the ciliated cells of the pad. The epithelial cells are characterized by a well-developed cytoskeleton consisting of bundles of intermediate filaments running in the apical-basal direction. The ciliary rootlets are connected to this filament system. The ciliary pad is surrounded by a cuticular fold and is made up of comparatively short cilia (about 5 μm long, approximately 12 cilia/μm^2) This type of pharynx is obviously adapted to ingestion of decaying plant material and detritus in terrestrial habitats (Westheide & Müller, 1996; Purschke, 2003). This pharynx is structurally rather similar to dorsolateral ciliary folds in that the ciliated and glandular area is restricted to a dorsal pad and additionally supplied with a well-developed system of pro- and retractor fibers.

Axial muscular pharynx

An axial pharynx with a well-developed muscular region is usually present in Phyllodocida (Fig. 1A; see Purschke, 1988a; Saulnier-Michel, 1992). The mouth gives rise to the buccal cavity, called proboscidian sheath (see Purschke, 1988a), which houses the muscular region of the pharynx in the resting position (Fig. 8D). These organs can often be protruded to a great distance, and at the junction of the muscular with the non-muscular region of the buccal organ jaws may be present, as in Nereididae, certain Hesionidae, Pisionidae, Glyceridae or Polynoidae (Figs 7A and C, 10A–D). This region represents the physiological mouth opening in these taxa. In many species of Pisionidae, Hesionidae, Pilargidae and Syllidae the tip of the muscular region is differentiated into a number of finger-like papillae, each bearing a set of sensory cells (Figs 7C–H, 8A–F and 10A, C). The proboscidian sheath covers the pharynx externally when everted. It often bears soft papillae, sclero-

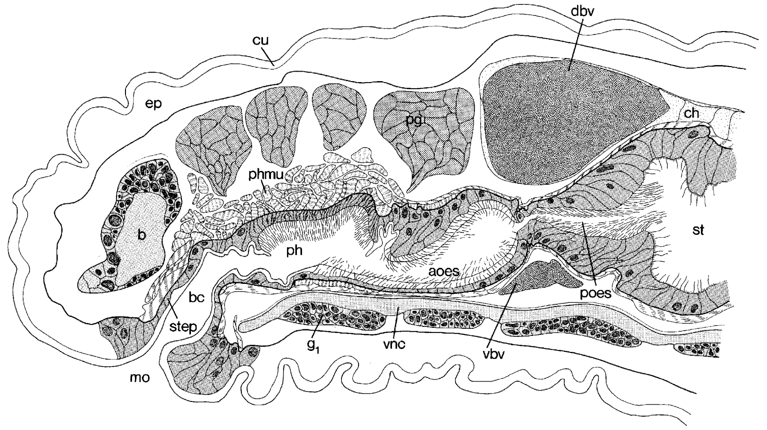

Figure 6. Foregut, dorsal pharynx. *Hrabeiella periglandulata*. Reconstruction of foregut with dorsal pharynx (ph) composed of ciliary pad, pharyngeal musculature (phmu) and pharyngeal glands (pg). Note unciliated buccal cavity (bc); aoes anterior oesophagus, b brain, ch chloragocyte, cu cuticle, dbv dorsal blood vessel, ep epidermis, g1 ganglion 1, mo mouth, poes posterior oesophagus, st stomach, step stomodeal epithelium, vbv ventral blood vessel, vnc ventral nerve cord. From Purschke (2003).

tized papillae or paragnaths (Figs 7A and B, 10D). Such papillae with sclerotized parts (onglets) are especially well developed in Glyceridae and Goniadidae and bear species-specific characters (Böggemann, 2002). Comprising two to three sensory cells with a few penetrative cilia and supportive cells, the papillae of Glyceridae are partly covered by a sclerotized cuticle often forming fingernail-like structures (Fig. 7B) (Bantz & Michel, 1971, 1972; Böggemann et al., 2000). In the sensory cells the ciliary rootlets fuse to form a single, extremely large rootlet extending through the entire papilla. This type also incorporates numerous gland cells, both serous and mucous, which assist adhesion and the digestion of food (Saulnier-Michel, 1992). The most complex axial pharynx is found in Syllidae. The anterior part of the digestive tract consists of a buccal cavity (proboscidian sheath), pharyngeal tube, proventricle and ventricle (Figs 1A, 7G and H; see Purschke, 1988a). The ventricle, sometimes supplied with caeca, is regarded as part of the intestine. The axial proboscis is divided into a long non-muscular part, the pharyngeal tube, followed by a shorter muscular part with prominent radial musculature, the proventricle. At the opening of the pharyngeal tube a circle of soft papillae is often present (Fig. 10A). This region is followed by differently arranged jaws or teeth (Fig. 10A and see below) or may be unarmed (e.g., *Syllide* sp., Fig. 7D). The pharyngeal tube is of different length and thus may be straight or coiled in the resting position.

In axial pharynges, the proboscidian sheath and the muscular region are covered by the cuticle, which may be modified in comparison to that present on the trunk. Especially regions subjected to mechanical stress possess protective structures such as the lamellar layers in Hesionidae (Fig. 8B, C, E and F; Westheide & Rieger, 1978; Purschke, 1988a). In Glyceridae such a lamellar layer is also present on the trunk (Bantz & Michel, 1971, 1972; G. Purschke & Koldehoff, unpublished data).

The musculature of this type of buccal organ is complex: circular, longitudinal and radial fibers are present, allowing sucking and swallowing movements (Fig. 8D). Among these fibers the radial ones predominant. Although usually a component of obliquely striated musculature as is typical for Annelida, these fibers exhibit several specializations: nucleus and mitochondria are often located centrally as in Hirudinea and usually a T-system is present (Purschke, 1988a). In *Nephtys* and Syllidae membrane-bounded granules containing crystalline calcium phosphate are present in the central cytoplasm (Briggs et al., 1985; Bryan & Gibbs, 1986; Purschke, 1988a). In Syllidae the radial fibres of the proventricle are not oblique-striated but cross-striated. The number of sarcomeres varies from one to about 20 depending on species. Sarcomeres may be as long as 60 μm, the longest sarcomeres found in Metazoa so far (Del Castillo et al., 1972; Smith et al., 1973; Wissocq, 1974).

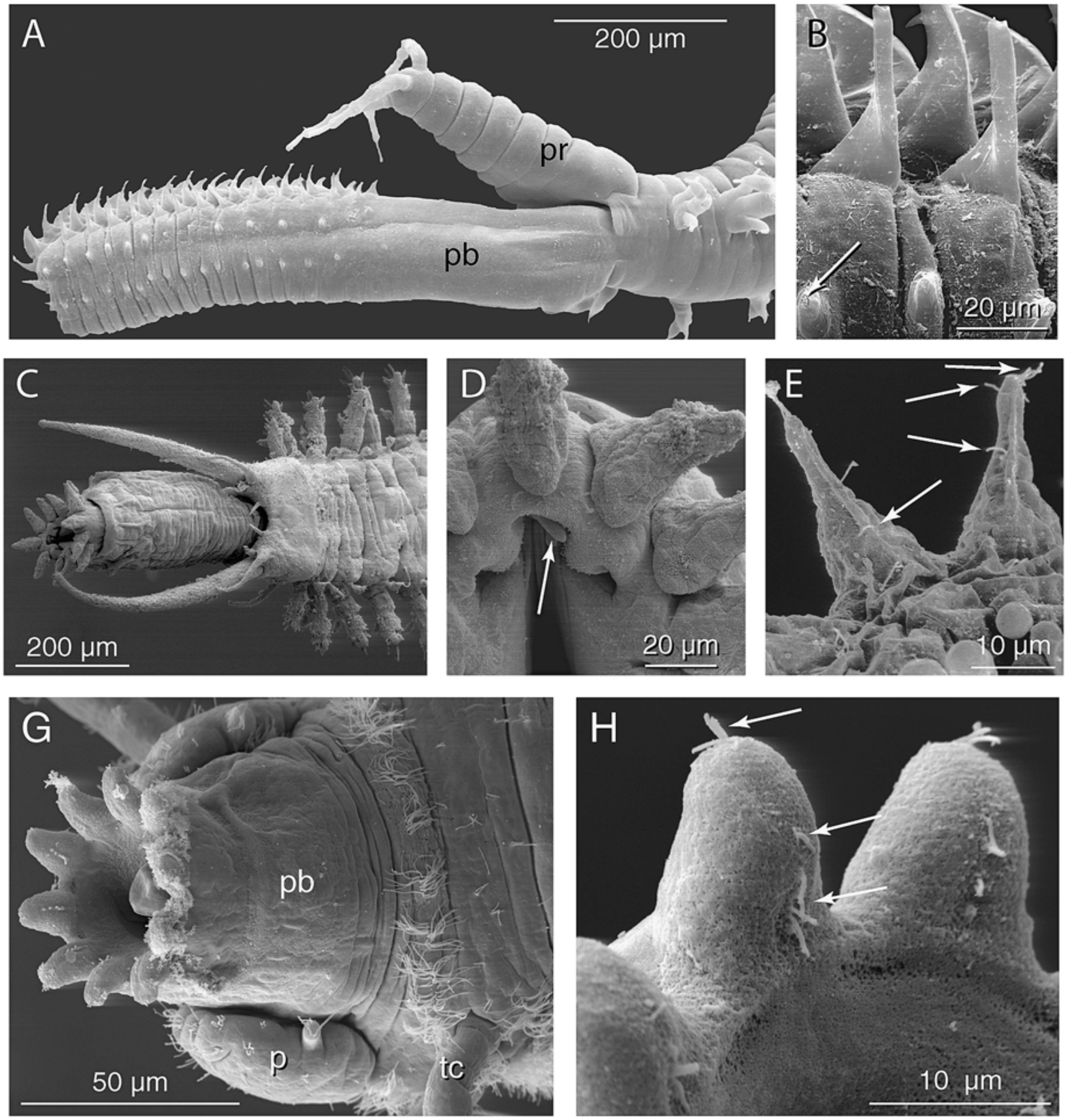

Figure 7. Foregut; axial muscular pharynx. (A, B) *Goniadides falcigera* (Goniadidae). (A) Proboscis (pb) partly everted, densely covered with finger-like papillae; pr prostomium. (B) Enlargement of papillae. Note sensory cilia on top of papillae (arrow). (C, D) *Pisione remota* (Pisionidae). (C) Specimen with everted pharynx bearing 14 terminal papillae. (D) Enlargement of papillae and pharyngeal opening with tip of jaw (arrow). (E) *Microphthalmus listensis* (Hesionidae). Two of ten pharyngeal papillae with cilia of sensory cells (arrows). (G, H) *Syllides caribica* (Syllidae); unarmed pharynx. (G) Everted proboscis with 10 soft papillae; p palp, tc tentacular cirrus. (H) Enlargement of two pharyngeal papillae with cilia of sensory cells (arrows). Micrographs A,B M. Böggemann, C, D S. Raabe, G, H M. Kuper.

Phylogenetic remarks

The phylogenetic importance of the different foregut structures is still under discussion. Dales (1962) in his comprehensive study was among the first to use the structure of the foregut as a basic criterion for grouping the polychaete families. Whereas an axial muscular proboscis is present

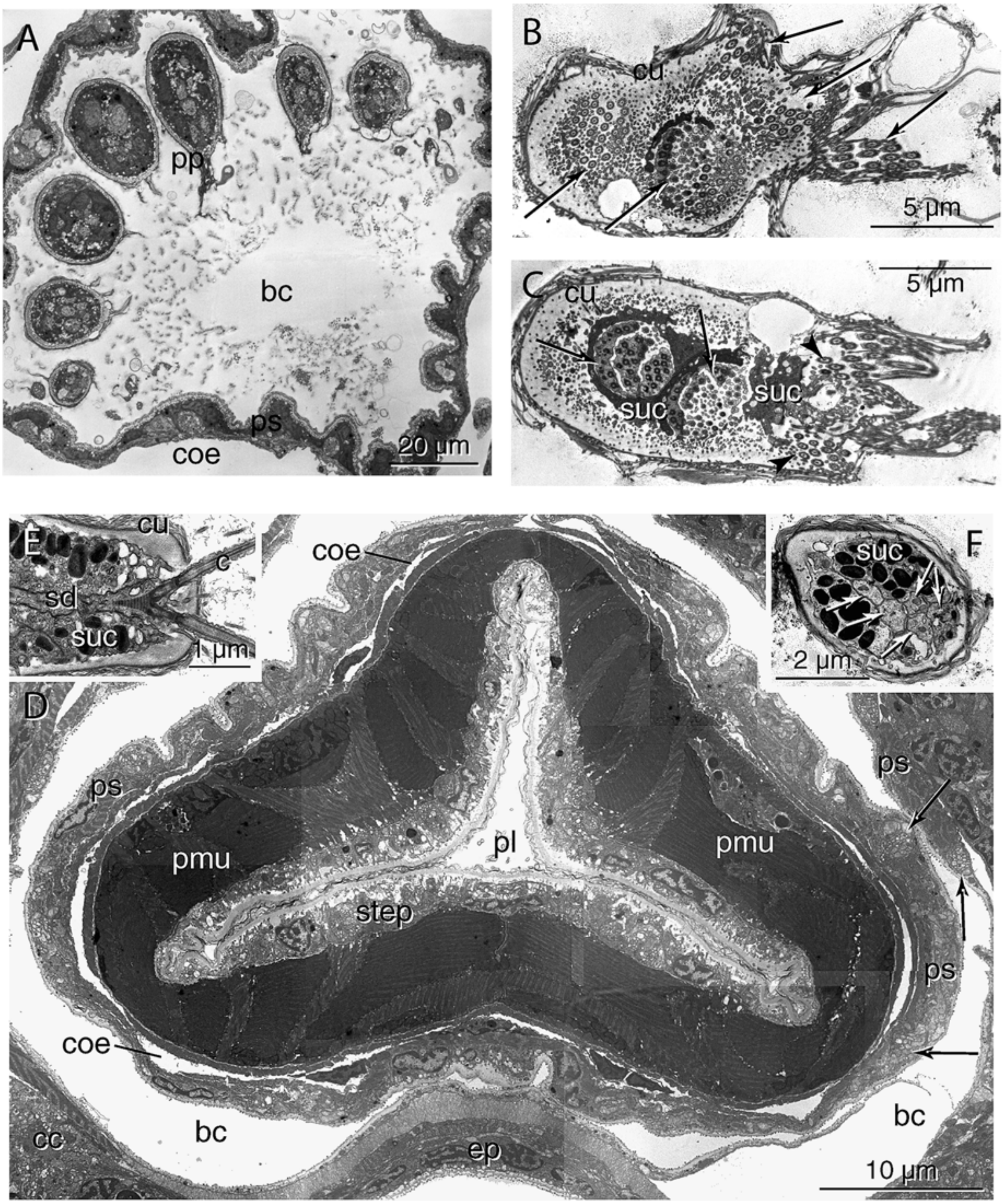

Figure 8. Foregut; axial muscular pharynx. TEM. (A–C) *Kefersteinia cirrata* (Hesionidae). (A) Buccal cavity (bc) with transverse sectioned pharyngeal papillae (pp); coe coelom, ps pharyngeal sheath. (B) Transverse section of papilla with numerous sensory cilia (arrows), pharyngeal cuticle (cu) with several epicuticular lamellar layers. (C) Somewhat deeper section with supportive cells (suc), two central groups of sensory cells (arrows) and a few peripheral sensory cells (arrowheads). (D) *Hesionides arenaria* (Hesionidae). Muscular part of pharynx; bc buccal cavity, cc circumoesphageal connective, coe coelom, ep epidermis, pl pharyngeal lumen, ps pharyngeal sheath, pmu pharyngeal musculature, step stomodeal epithelium. (E, F) *Microphthalmus listensis* (Hesionidae). (E) Tip of pharyngeal papilla, sensory dendrite (sd), two sensory cilia (c) attached to one common rootlet, cuticle (cu) with lamellar cover, suc supportive cell. (F) Cross section of pharyngeal papilla with 5 sensory dendrites (arrows), suc supportive cell.

only in Phyllodocida (and Myzostomida, a taxon of questionable affinities; see Eeckhaut & Lanterbecq, 2005), the other higher taxa of polychaetes do not exhibit such a uniform distribution of foregut structures. Even in a given family taxon different types of buccal organs may be present (Purschke & Tzetlin, 1996). Due to their structural diversity, the homology assumption of ventral pharyngeal organs (e.g., Dales, 1962, 1977) was challenged. Therefore, fine-structural studies have been conducted to elucidate whether ventral pharyngeal organs are in fact homologous or evolved convergently (Rieger & Rieger, 1975; Jouin, 1978a,b; Michel, 1978; Purschke, 1985a,b, 1987a,b, 1988b; Tzetlin, 1987, 1989, 1991; Tzetlin et al., 1987, 1992; Purschke & Jouin, 1988; Tzetlin & Larionov, 1988; Saulnier-Michel et al., 1990). These investigations confirmed great structural differences among the various polychaete taxa examined, making an overall homology unlikely. However, as more was learned about these organs, it became possible to demonstrate a plausible origin of these pharyngeal structures from only a few, convergently evolved, different types (Purschke, 1988b; Purschke & Tzetlin, 1996). Moreover, there is strong evidence that non-muscular axial buccal organs represent derived structures, most likely to have been evolved from foreguts with a ventral pharyngeal organ (Tzetlin et al., 1987; Tzetlin, 1991). Evidence is drawn from the fact that in most cases a ventral pharynx present in larvae is subsequently retained only if the adult of the species is small; it is replaced by a non-muscular proboscis in larger species. In the clade formed by Arenicolidae; Maldanidae and Capitellidae the proboscis is developed from the region in front of the ventral pharynx, in Orbiniidae behind it (Eisig, 1914; Tzetlin, 1991). In the former the epithelium of the proboscis is unciliated, whereas in Opheliidae and Paraonidae it is ciliated (Hartmann-Schröder, 1958; A.B. Tzetlin, unpublished data; Fig. 4D and E). Moreover, in taxa with appendages used for feeding (e.g., Spionidae, Ampharetidae, Terebellidae), a ventral pharynx is present in juveniles as well and may be retained by the adults.

The existence of a comparatively simple feeding structure in polychaetes was recognized by Purschke & Tzetlin (1996), namely the so-called dorsolateral ciliary folds, which are widespread among polychaetes. These microphagous feeding structures are most often found together with a ventral pharynx but may also occur alone. They are present in larvae, juveniles and adults of small species but are usually replaced by other feeding structures in larger species. In connection with their widespread occurrence, these observations strongly indicate that dorsolateral ciliary folds and a ventral pharynx represent the plesiomorphic condition for Annelida (Purschke & Tzetlin, 1996). All other types of feeding structures may have been evolved from these folds, as is indicated by structural and developmental data (Fig. 9; see Purschke & Tzetlin, 1996). Since these folds are obviously restricted to individuals of small body size in extant Annelida, it follows that the annelid stem species either was comparatively small and microphagous, or at least had a life cycle that included a developmental stage showing these characteristics (Purschke & Tzetlin, 1996; Purschke, 2002). Although it seems conceivable that dorsolateral ciliary folds might already have been present in the stem species of Annelida, it is questionable whether they are an autapomorphy of Annelida or, more probably, a plesiomorphy (Ax, 1999). The latter interpretation is supported by the presence of such ciliary folds and a ventral pharynx (buccal organ) in pelagosphera larvae of Sipuncula (Fig. 4C; Rice, 1973, 1976). Homology of these structures in Sipuncula and Annelida remains to be proven but appears to be likely. However, the position of Sipuncula is still uncertain: in analyses using morphological data they usually fall outside Annelida (Rouse & Fauchald, 1997; Ax, 1999), whereas molecular data often suggest placement of Sipuncula within Annelida (e.g., Winnepenninckx et al., 1998; Martin, 2001).

Jaws

General

Polychaete jaws are cuticular structures formed on the surface of specialized epithelial cells, often called gnathoblasts. Usually jaws are sclerotized parts of the pharyngeal cuticle which may be highly mineralized in some taxa, but chitin is absent (Saulnier-Michel, 1992). Jaws occur in Phyllodocida and Eunicida (Wolf, 1980; Paxton, 2000, Rouse, 2000; Rouse & Pleijel, 2001) and

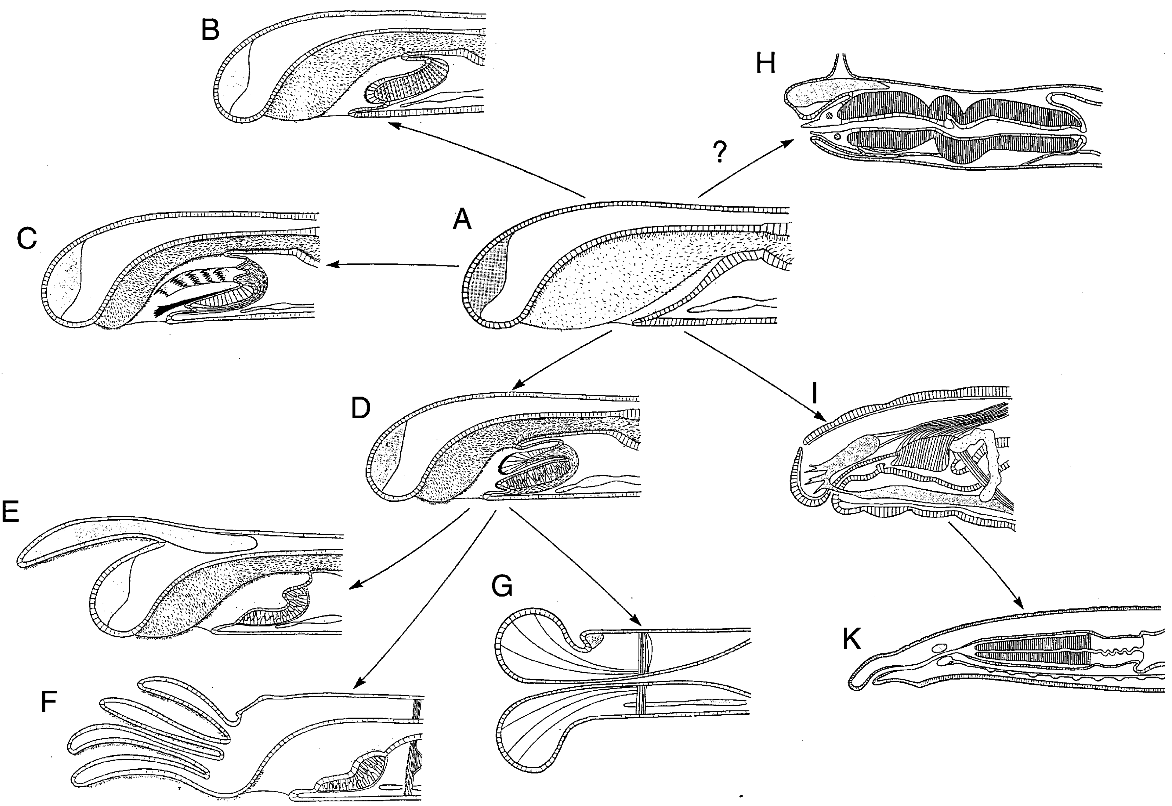

Figure 9. Schematic representation of different foregut structures in polychaetes related to dorsolateral folds (DLF). Arrows indicate probable phylogenetic pathways, some of which can be followed during ontogenesis. (A) DLF only feeding structure present (e.g., Polygordiidae). (B–E) DLF and different ventral pharyngeal organs (VPO). (B) VPO composed of muscle cells only (e.g., Dinophilidae). (C) VPO with jaw apparatus (Eunicida). (D) VPO consisting of muscle bulb, tongue-like organ and investing muscle (e.g., Orbiniidae, Ctenodrilidae, Protodrilidae). (E) VPO and additional feeding appendages (palps) (e.g., Spionidae). (F) VPO Ventral organ and numerous feeding appendages. DFG absent in adults, anterior compartment of coelomic cavity separated by muscular septum (e.g., Terebellidae). (G) DLF and VPO replaced by non-muscular axial proboscis, anterior part of the body separated by muscular septum (e.g., Maldanidae, Capitellidae, Arenicolidae). (H) DLF replaced by axial muscular pharynx (Phyllodocida). (I) DLF modified to dorsal ciliated glandular pad (oligochaetous Clitellata, *Hrabeiella periglandulata*). (K) Dorsal pharynx replaced by axial muscular pharynx (Hirudinea). Modified from Purschke (2002).

more recently jaws were found in certain Ampharetidae (Desbruyères, 1978; Mackie, 1994).

Various aspects of jaw structure are traditionally used as taxonomic and phylogenetic characters. Special attention has been paid to the jaws of Eunicida ever since the fossil scolecodonts were identified as jaws belonging to extinct Eunicida (Pander, 1856; Ehlers, 1868). First Kozlowski (1956) presented a reconstruction of a fossil jaw apparatus directly comparable with extant ones. So far, the palaeozoic jaws of Eunicida are the most abundant fossil material in Annelida (Croneis & Scott, 1933; Kielan-Jaworowska, 1966; Kozur, 1970; Mierzejewski & Mierzejewska, 1975; Mierzejewski, 1978, 1984; Colbath, 1986, 1988; Zaslavskaya, 1989). Hence the comparative analysis of extant and fossil jaw apparatuses is highly important for our understanding of evolutionary trends among polychaetes. Fossil jaws that can be referred to extant polychaete genera are Mesozoic and belong to Glyceridae, Goniadidae and Dorvilleidae (*Ophryotrocha*) (Szaniawaski, 1974), or later fossils from the lower Miocene (Szaniawaski & Wrona, 1987).

Phyllodocida

In Phyllodocida the jaws are represented as more or less numerous tooth-like structures located on the axial muscular proboscis, usually at the beginning of the muscular part (Fig. 10A–D). Jaws have been described for Acoetidae, Aphroditidae, Eulepethidae, Polynoidae, Pholoidae, Sigalonidae, Pisionidae, Chrysopetalidae, Hesionidae, Nereididae, Syllidae, Goniadidae, Glyceridae, and Nephtyidae. In most cases they are used to capture and hold the prey, and in tearing off pieces of algae or decaying matter. The number of jaws may be one, two, four or rather more (Rouse & Pleijel, 2001). Scale worms such as Polynoidae, Sigalonidae, Eulepethidae and Aphroditidae possess two pairs of dorso-ventrally oriented jaws which are more or less well-developed; ultrastructural studies of the jaws are lacking (Saulnier-Michel, 1992; Rouse, 2000). In Syllidae there may be single mid-dorsal jaw (tooth; e.g., *Exogone*, *Sphaerosyllis*, *Syllis*), a series of teeth in a ventrolateral arc (sometimes combined with the large mid-dorsal tooth, e.g., *Odontosyllis, Eusyllis*; Fig. 10A) or a complete ring of teeth called trepan (e.g., most *Autolytus* spp.) situated somewhat behind the pharyngeal papillae (Fig. 10A). In several syllid species the pharynx may be unarmed (e.g., *Syllides*, Fig. 7G); hence pharyngeal structures are highly important for taxonomy in Syllidae (e.g., Licher, 1999; Glasby, 2000). The syllid tooth is scarcely sclerotized and primarily consists of a thick cuticle (Purschke, 1988a; Saulnier-Michel, 1992). There is no experimental evidence that these teeth may be chitinized as sometimes found in the literature. In Hesionidae some taxa possess a pair of jaws (Fig. 10C), the fine structure of which is unknown. One pair of lateral jaws is also present in Nereididae, Nephtyidae, and Pisionidae and all possess heavily sclerotized jaws (Fig. 10B–D; Michel et al., 1973; Purschke, 1988a; Saulnier-Michel, 1992). In Nereididae additional hard structures, the paragnaths, are present (Fig. 10B). Other types of buccal pieces are found Goniadidae: The chevrons are additional, serially arranged v-shaped hard structures situated more basally on the muscular proboscis (Fig. 10E).

A more conspicuous jaw apparatus is found in Glyceridae (Fig. 10D): the two pairs of jaws are always associated with venom glands and each of the venom ducts opens at the tip of the jaw, with an additional series of pores on the ventral side. The jaws are situated at the end of the eversible proboscis and each bears a supporting structure called the aileron (Böggemann et al., 2000). In addition to scleroproteins the jaws are highly mineralized (see Saulnier-Michel, 1992; Böggemann et al., 2000). In the closely related Goniadidae the jaws are completely different and comprise a pair of larger jaws (macrognaths) associated with smaller ones (micrognaths) forming a complete circle (e.g., Rouse, 2000).

Ampharetidae

In a few, small species of Ampharetidae jaws were found: *Gnathampharete paradoxa*, *Ampharete* sp., and *Adercodon pleijeli* (Desbruyères, 1978; Uebelacker & Johnston, 1984; Mackie, 1994). In all species the jaws consist of a transversal row of denticles located on the posterior edge of the ventral bulb (Fig. 10I). Nothing is known about how Ampharetidae use their jaws.

Eunicida

In Eunicida the jaw apparatus consists of a pair of mandibles, located on the ventral muscle bulb of the ventral pharynx, and one or two paired rows of maxillary plates located on lateral folds of the ventral pharyngeal organ (Fig. 10F and G; Wolf, 1980; Purschke, 1987b; Paxton, 2000). In all known extant and fossil Eunicida the mandibles are paired longitudinal structures usually with denticulated frontal edges (Fig. 10F). They are anchored in deep epidermal follicles. There is an articulation in the anterior part between left and right mandible, sometimes forming a ligament-like structure or a symphysis (Hartmann-Schröder, 1967; Purschke, 1987b). Although such an articulation is present, the main movements are in the anterior–posterior direction.

The maxillary apparatus varies between different Eunicida and several types may be distinguished (Figs 12 and 13). In general, one or two pairs of longitudinally arranged rows of maxillary plates are present, which may be connected caudally by carriers or carrier-like structures (Fig. 12D–H). The individual maxillary plates are usually denticulated or, rarely, single toothed. The number of maxillary plates in each row varies from

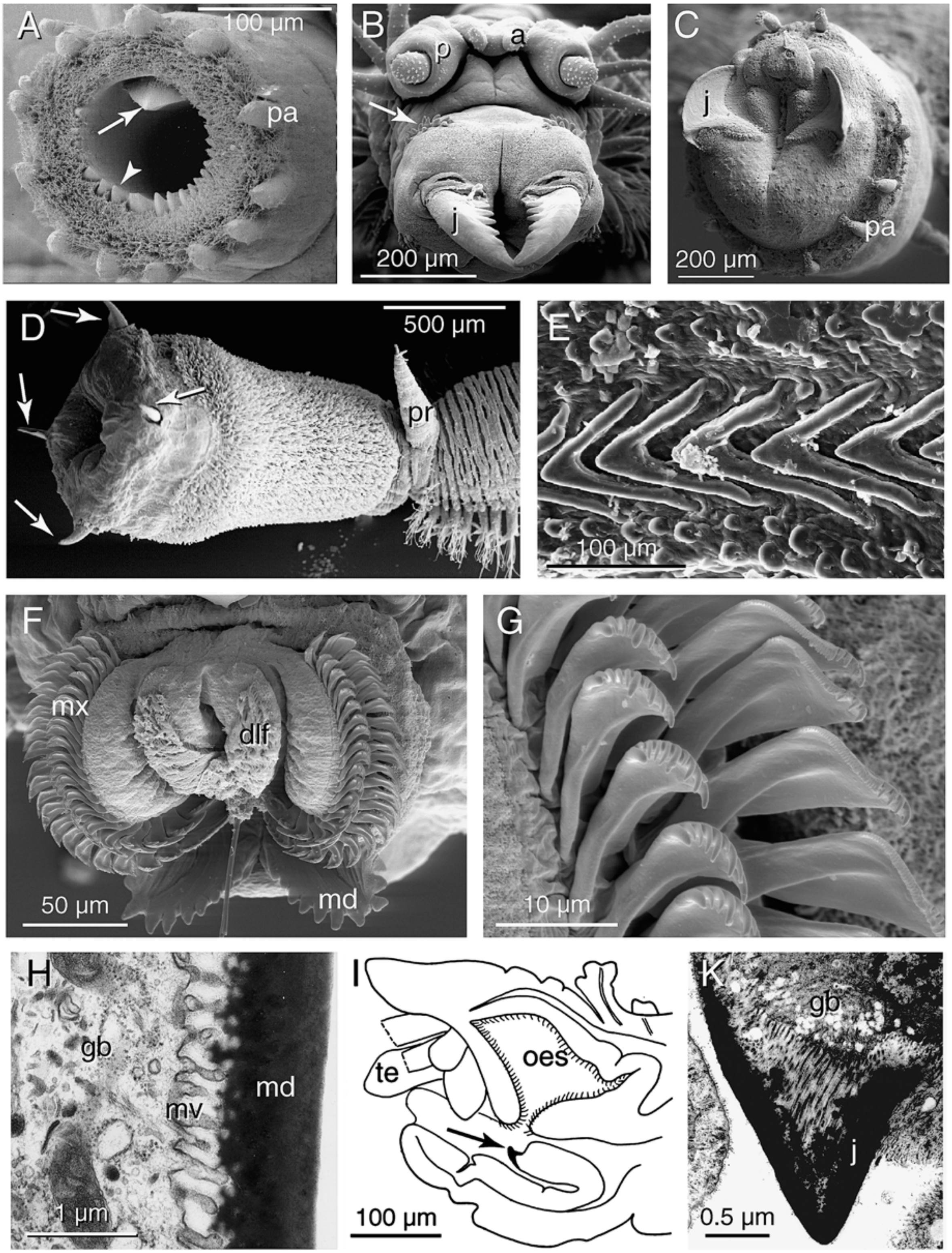
A
100 µm
pa
B
p
a
j
200 µm
C
j
pa
200 µm
D
500 µm
pr
E
100 µm
F
mx
dlf
md
50 µm
G
10 µm
H
gb
mv
md
1 µm
I
te
oes
100 µm
K
gb
j
0.5 µm

Figure 10. Jaws. (A) *Eusyllis blomstrandi* (Syllidae), pharyngeal tube with circle of papillae (pa), cilia and dorsal tooth (arrow) and row of smaller teeth (arrowhead). (B) *Nereis* sp. (Nereididae), jaws (j) and first group of paragnaths (arrow). a antenna, p palp. (C) *Syllidia armata* (Hesionidae), shovel-like jaws at the tip of everted pharynx, note unequal distribution of pharyngeal papillae (pa). (D) *Glycera alba* (Glyceridae), specimen with completely everted pharynx showing the four jaws (arrows) and numerous external papillae. pr prostomium. (E) *Goniada maculata* (Goniadidae), chevron. (F–H) *Protodorvillea kefersteini* (Dorvilleidae), jaw apparatus consisting of mandibles (md) and two rows of maxillary plates (mx). dlf dorsolateral folds. (G) Close up of maxillary plates. (H) TEM-micrograph of mandible (md), note short microvilli (mv) of gnathoblast (gb). (I–K) *Adercodon pleijeli* (Ampharetidae). (I) Position of jaws in the foregut (arrow), oes oesophagus, te tentacle. (K) TEM-micrograph of jaw (j), gnathoblast (gb) with long microvilli. Micrographs D, E M. Böggemann, I modified from Mackie (1994).

four in Lumbrineridae to 50 and even more in Dorvilleidae (Figs 10F and G, 12A–H). Mandibles and maxillae can be moved independently. The movements of the jaws are complex (Hartmann-Schröder, 1967; Wolf, 1980). In most cases Dorvilleidae use their jaws, especially the mandibles, for scraping off food particles from hard substrates and, predominantly the maxillae, for capturing and holding these particles (Tzetlin et al., 1987; A.B. Tzetlin & G. Purschke, unpubl. obs.). Larger extant Eunicida (Lumbrineridae, Onuphidae, Eunicidae) are macrophagous animals using their jaws for capturing and holding food (Jumars, 1974).

Since the mandibles are very similar among the different taxa in Eunicida, classification of eunicidan jaws is based on the structure of the maxillae. The first classification of jaw structures in Eunicida was introduced by Ehlers (1864–1868). A more detailed classification was done by Kielan-Jaworowska (1966) in her outstanding monograph on fossil polychaete jaws: (1) placognath jaws, (2) ctenognath jaws, (3) labidognath jaws and (4) prionognath jaws (Figs 12A–H, 13A and C–E). Later a fifth type, xenognath jaws, was introduced by Mierzejewski & Mierzejewska (1975) (Fig. 13B).

(1) The placognath maxillary apparatus is characterized by asymmetrically arranged denticulated plates in the posterior part and two symmetric anterior rows of apparently free maxillary plates (Fig. 13A). Carriers are lacking. Placognath jaws are only known from Ordovician until the Upper Devonian. Kielan-Jaworowska (1966) and Mierzejewski (1978) described moulting of the maxillae in Mochtyellidae. Jaws of this type appear to be unique within Eunicida and are difficult to compare with other jaws.

(2) Ctenognath jaws consist of small, symmetrically arranged basal plates in the posterior part and four rows of numerous, presumably free, so-called denticles anteriorly (Figs 11, 12A–C and

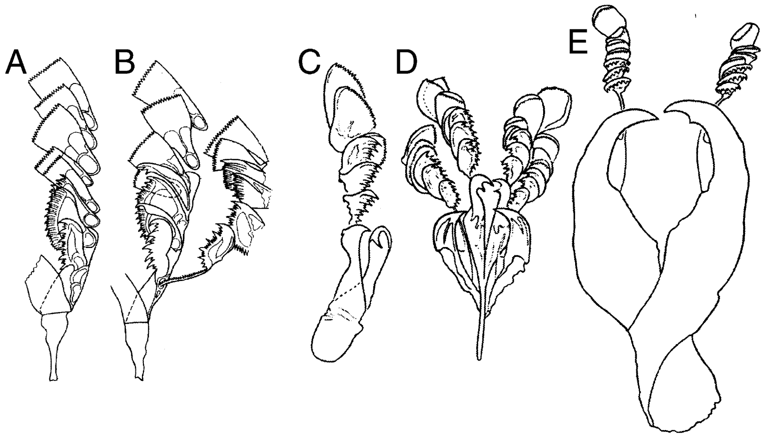

Figure 11. Different jaws of *Ophrytrocha* spp. (Dorvilleidae). (A, B) *O. irinae*. (A) Juvenile p-type maxillae. (B) Adult maxillary apparatus with two rows of plates without shedding of the juvenile plates (PP-type). (C–E) *O. dimorphica*. (C) Maxillae of 7 chaetiger juvenile with bidentate MI. (D) Juvenile during replacement to adult jaw apparatus. (E) Adult maxillae with large MI (forceps; K-type). A, B after Tzetlin (1980a), C–E after Zavarzina & Tzetlin (1986).

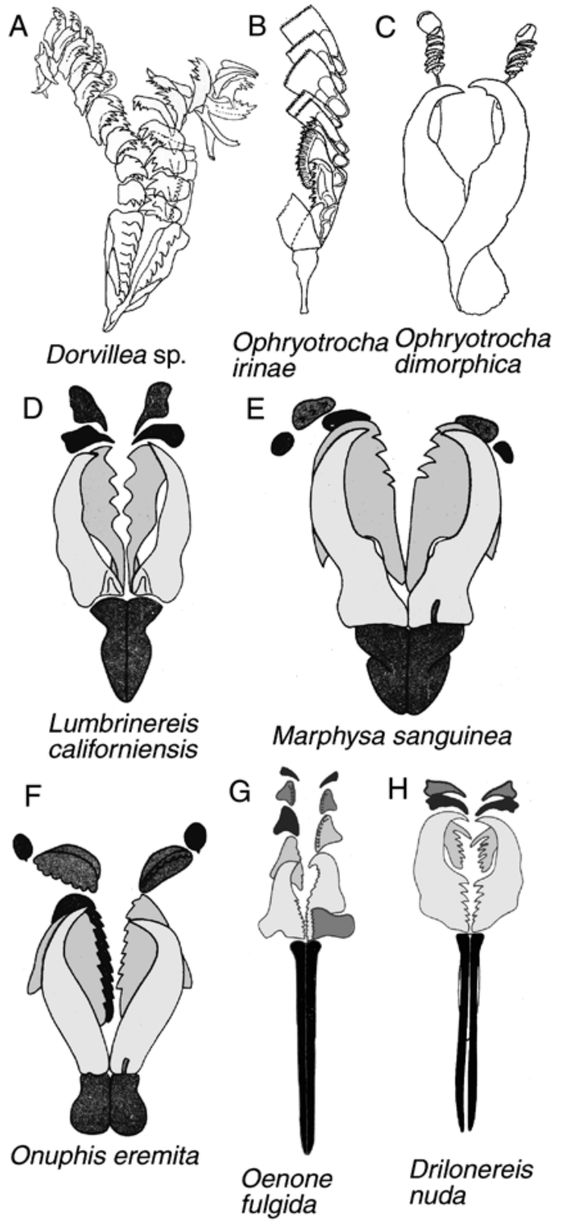

Figure 12. Diagramatic outline of different types of maxillary apparatuses present in extant and extinct Eunicida. (A–C) Ctenognath maxillae (Dorvilleidae). (A) Polymeric maxillae arranged in four rows (B) Oligomeric maxillae arranged in two rows. (C) K-type maxillae of *Ohryotrocha*. (D–F) Labidognath maxillae (D) Lumbrineridae. (E) Eunicidae. (F) Onuphidae. (G, H) Prionognath maxillae; Oenonidae (formerly classified in Lyseratidae and Arabellidae). Redrawn after Kilan-Jaworoswska (1966), Tzetlin (1980a, b), Zavarzina & Tzetlin (1986).

13C). These rows form longitudinal series extending for more than half of the length of the maxillary apparatus. Typical carriers are lacking. Ultrastructural studies of extant material have shown that all maxillary plates are fused and form one piece (Purschke, 1987b). Thus a distinction between basal plates and denticles appears to be difficult and uncertain. According to, e.g., Åkesson (1976) the neutral term 'maxillary plate' should be favored. Posterior jaw pieces (denticles and base plates) possess narrow open pulp cavities. These are present in extant (Dorvilleidae, Histriobdellidae; see Jennings & Gelder, 1976; Tzetlin, 1980b; Purschke, 1987b) and fossil forms (Tetraprionidae from Ordovicium; Kielan-Jaworowska, 1966). According to Tzetlin (1980b) the jaws of Polychaetaspidae and Paulinitidae (Fig. 13D) also belong to this type, but see Kielan-Jaworowska (1966) who classified these jaws as labidognath.

(3) Jaws of the labidognath type are arranged in a semicircle when retracted (Ehlers, 1864–1868). Labidognath maxillae have short, broad carriers embedded in the pharyngeal tissues (Kielan-Jaworowska, 1966). There are 4–5 right and 4–6 left maxillary plates (Figs 12D–F and 13D). Jaws of this type are present in Eunicidae, Hartmaniellidae, most Lumbrineridae and Onuphidae but are known from extinct forms as well (Hartman, 1944; Paxton, 2000).

(4) Prionognath maxillae (extant and extinct) are arranged in two parallel rows of up to 5 maxillary plates and possess long slender carriers, slightly longer than or as long as the group of maxillary plates (Figs 12G, H and 13E). This type is found in Oenonidae among the extant Eunicida. Sometimes the jaw apparatus of Histriobdellidae is also assigned to this type (see Paxton, 2000).

In recent material prionognath and labidognath maxillae differ not only in the maxillary arrangement but also in the structure of the posterior maxillary plate (MI; numbering from posterior to anterior). In the prionognath type it is denticulated on the inner surface, like the anterior ones, whereas in labidognath maxillae MI is forceps-like and lacks teeth. However, if the classification of Kielan-Jaworowska (1966) of the maxillae as labidognath in Polychaetapsidae and Paulinitapsidae is correct, this distinction does only apply for recent taxa. In both extant and fossil labidognaths and prionognaths, the maxillae are two-rowed jaw apparatuses each consisting of only a few denticulated or non-denticulated cuticular maxillary plates.

(5) Xenognath maxillae were described for *Archeoprion quaristata* by Mierzejewski & Mierzejewska (1975). Maxillae of this type consist of two symmetrical plates with a few transverse rows of numerous denticles (Fig. 13B). This jaw apparatus has comparatively long and slender carriers, sometimes regarded as pseudocarriers.

Maxillae in Ophryotrocha

Another classification of the maxillae was introduced to describe the pharyngeal armature in *Ophryotrocha* (Dorvilleidae). Species of this genus like other dorvilleids replace maxillae sequentially during ontogeny (maturation, changes of sex, etc.). When leaving the egg mass, juveniles possess only a few achaetigerous segments. The pharyngeal armature in this stage consists of rudiments of paired mandibles and two rows of maxillary plates (Åkesson, 1967, 1976; Tzetlin, 1980b). Initially there are only 3–4 maxillary plates in every row, but soon 7–8 pairs of denticulated maxillary plates have been produced (Fig. 11A; Åkesson, 1973a, 1976; Tzetlin, 1980b). Carriers are very weakly developed at this stage. This type of maxillae was named P-type (Düsing, 1961; Müller, 1962). Periodically, maxillae of the P-type are replaced by new ones of the same type. A number of species have such jaws throughout life, such as *Ophryotrocha geryonicola, O. gracilis* and *O. cosmetandra.*

In *Ophryotrocha irinae* juveniles have a two-rowed P-type maxillary apparatus, and later a second pair of P-type maxillae appears, while the old ones are not shed (Fig. 11A and B; Tzetlin, 1980b). As a result the maxillary armature consists of four almost equal rows of maxillary plates. Later this four-rowed maxillary apparatus may be replaced by a new one also consisting of four rows of maxillary plates (PP-type). This jaw type has been

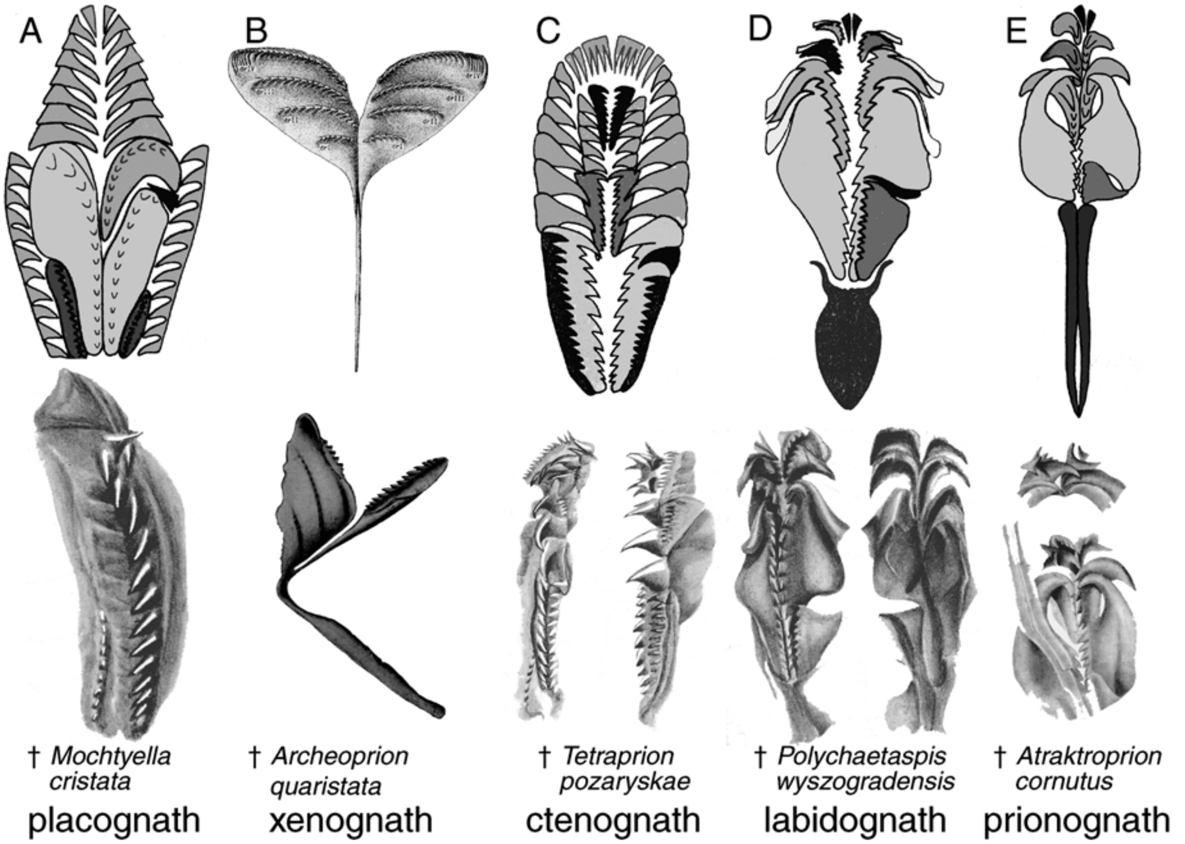

Figure 13. Types of maxillary plates found in fossil Eunicida. Upper row: reconstructions of jaws, lower row: drawings of specimens. Modified from Kielan-Jaworowska (1966) and Mierzejewski & Mierzejewska (1975).

regarded as homologous to the four rows of maxillary plates present in the maxillary apparatus of the other genera of Dorvilleidae by Tzetlin (1980a).

In other species of *Ophryotrocha*, such as *O. dimorphica* and *O. puerilis*, juveniles bear P-type maxillae and then change to another type of jaws – K-type – upon replacement (Düsing, 1961; Müller, 1962). This type of maxillae consists of a pair of large forceps (MI) and two rows of maxillary plates (MII–MVIII) identical with the juvenile P-type (Fig. 11C–E). The MI maxillary plates are rooted in carriers, and are connected with MII – MVIII by a narrow strip of sclerotized cuticle. The MI plates have unidentate or asymmetrical prongs. After K-jaws have formed they are not replaced any more. Very often development of the big MI forceps is connected with sexual maturation or change of sex in sequentially hermaphrodite species (Düsing, 1961; Müller, 1962; Åkesson, 1976; Zavarzina & Tzetlin, 1986). The general appearance of the K-type maxillae is consistent with labidognath jaws apparatus (Fig. 12C–F; Tzetlin, 1980a). During differentiation of the K-type maxillae the forceps (MI) appear after the development of MII – MVIII maxillae has been completed.

In some species (e.g., *Ophryotrocha schubravyi*), maxillae are formed that have relatively small MI (forceps) with bidentate prongs, and then after the next replacement, typical K-type large MI forceps with unidentate prongs appear (sometimes asymmetrical: one branch bi-, the other uni-dentate; Fig.11C and D). The term T-type maxillae (transition) was created for maxillae apparatus having relatively small bidentate MI by Tzetlin (1980a) while others regard these maxillae as P-type.

The maxillae present in other taxa of Dorvilleidae may be classified as P- and PP-type jaw apparatuses, while K- and T-types are only known among species of *Ophryotrocha*. P-type maxillae occur in many species of the genus *Ophryotrocha*, in all known juveniles of Dorvilleidae and in adults of several dorvilleid genera: *Petrocha*, *Pusillotrocha*, *Arenotrocha*, *Apophryotrocha, Exallopus*, *Westheideia*, *Pseudophryotrocha, Parophryotrocha* (Jumars, 1974; Westheide & Nordheim, 1985; Wolf, 1986; Nordheim, 1987; Hilbig & Blake, 1991). PP-type are found in *Ophryotrocha irinae*, and in *Dorvillea, Schistomeringos, Pettibonea, Protodorvillea*. Relatively large species of *Dorvillea* and *Schistomeringos* have more then 30 maxillary plates in each of the four rows (Hilbig & Blake, 1991).

Evolution of jaws in Eunicida

It is beyond discussion that Dorvilleidae represent the most ancient living members of Eunicida (Orensanz, 1990; Paxton, 2000). Usually polymeric maxillary apparatuses of large Dorvilleidae, such as are present in *Dorvillea* and *Schistomeringos*, were considered as plesiomorphic for Dorvilleidae and all Eunicida (Kielan-Jaworowska, 1966; Jumars, 1974; Orensanz, 1990; Eibye-Jacobsen & Kristensen, 1994; Paxton, 2000). According to Jumars (1974) the most primitive jaw apparatus consisted of numerous maxillary plates which were arranged in six rows. The evolutionary trends of the jaws in dorvilleids were (1) decrease in the number of maxillary plates and (2) subsequent reduction of number of rows from four to finally two rows of maxillary plates. This evolutionary trend was strongly supported by the finding of a number of intersitial dorvilleid taxa with reduced or even lacking jaws (*Arenotrocha*, *Westheideia*, *Pusillotrocha*, *Petrocha* and *Apodotrocha*) (Westheide & Riser, 1983; Westheide & Nordheim, 1985; Wolf, 1986; Nordheim, 1987). Dorvilleidae is thought to represent a well-defined monophyletic group (Rouse & Fauchald, 1997). The morphological basis for this hypothesis is the presence of a ctenognath jaw apparatus. However, if this jaw apparatus was already present in the stem species of Eunicida, it is a plesiomorphy of Dorvilleidae and hence cannot support monophyly of this group. Non-monophyly of Dorvilleidae is also suggested by recent molecular data (Struck et al., 2002).

A completely different theory was proposed by Tzetlin (1980b). According to this hypothesis based on a different interpretation of dorvilleid jaws there is no support for a basal polymeric ctenognath jaw apparatus. The main arguments are: (1) Among fossil jaw apparatuses there are no polymeric forms with irregular maxillae. All known Palaeozoic Eunicida have two or four rows and no more than 10 maxillary plates in each row, in most cases rather less (Fig. 13). (2) Data on the development of ctenognath and labidognath apparatuses show that always oligomeric ctenognath-like jaws are formed in the first ontogenetic stages (Åkesson, 1967, 1973a, 1976; Hsieh & Simon, 1987; Tzetlin, 1980a). Due to the resemblance of K-type maxillae of Ophryotrocha with labidognath jaws it was concluded that they most likely evolved from oligomeric ctenognath jaws (Fig. 12B–F). (3) Four rows of maxillae in Dorvilleidae most likely evolved from two-rowed jaws by prevention of shedding of the old maxillae during the processes of replacement (Fig. 12A and B). Oligomeric organization with two rows of maxillae of the P-type should thus be suggested as the plesiomorphic maxillary apparatus of Eunicida. (4) The life style of extinct Paleozoic Eunicida very likely was similar to that of extant *Ophryotrocha* sp.: i.e., small animals that feed by scraping off microfouling and other debris from hard substrates. However, this theory has not been accepted and was criticized by e.g., Orensanz (1990). Additional investigations appear to be necessary to resolve Eunicidan relationships and thus evolution of the different types of jaws.

Jaw histogenesis

Despite the great diversity in number and composition of the jaws in the different taxa there is only little information about their formation. Jaws of Phyllodocida, Eunicida and Ampharetidae are basically different and probably evolved independently. In Eunicida mandibles and maxillae are different as well. However, growth appears to be similar and only two types of jaw histogenesis and growth are known: in the first the gnathoblasts possess comparatively long microvilli and the jaws continue to grow throughout the animal's life (Fig. 10K). The gnathoblasts continuously produce new portions of the cuticular collagen matrix, which later becomes sclerotized by formation of scleroproteins. They may be calcified by calcite (Lumbrinereidae), aragonite (Onuphidae, Eunicidae) (Colbath, 1986) or otherwise mineralized by heavy metals such as iron, copper and zinc in Phyllodocida (Michel et al., 1973; Bryan & Gibbs, 1979, 1980; Gibbs & Bryan, 1980a, b; Böggemann et al., 2000). In Phyllodocida jaw growth is restricted to the basal parts (Olive, 1977, 1980). Since these jaws have a lifelong growth period, growth-lines can usually be observed (Kirkegaard, 1970; Olive, 1977, 1980; Tzetlin, 1990; Britaev & Belov, 1993; Britaev et al., 2002). Jaws of this type are the only ones found in Phyllodocida and applies for the mandibles in Lumbrinereidae, Onuphidae, Eunicidae and Ampharetidae as well (Wolf, 1980; Colbath, 1986; A.B. Tzetlin, unpublished observations).

A different type is typical for the maxillary apparatus in Dorvilleidae. It is characterized by gnathoblasts with very short microvilli or without microvilli (Fig. 10H; Damas, 1987; Purschke, 1987b). Jaws of this type do not grow after they have been formed. In many cases species with this type of jaws replace them regularly. The new ones are formed by newly developed groups of gnathoblasts (Damas, 1987; Purschke, 1987b). The old ones are shed and eliminated from the pharynx via the digestive tract (Tzetlin, 1980a; Hsieh & Simon, 1987). Whether maxillae are replaced in the other Eunicida is seen controversially and appears not to be resolved yet. Kielan-Jaworowska (1966) suggested replacement of labidognath maxillae which was refuted by Paxton (1980) who found evidence for growth throughout life without replacement in Onuphidae. Colbath (1987) suggested that Oenonidae have a fine structure of the jaws that is inconsistent with continuous growth and probably undergo regular shedding and replacement of maxillae. Replacement of maxillae has been described in Onuphidae by Hsieh & Simon (1987). So there is certain evidence indicating that shedding of the maxillae is typical of all Eunicida (Colbath, 1987; Hsieh & Simon, 1987) but further experimental evidence and ultrastructural investigations are required.

Intestine

In polychaetes the midgut may be differentiated into a stomach and intestine. Structure and function have been reviewed by Michel (1988) and Saulnier-Michel (1992) and only a few new results have since been obtained. Therefore, only a short summary is given here. The endodermal epithelia making up this part may form a pseudostratified epithelium, and rest on an extracellular matrix followed by the peritoneal lining. This lining comprises longitudinal and circular muscle fibers as well. Blood spaces are frequently found in the extracellular matrix between the two epithelia to form the blood sinus of the gut.

A distinct stomach representing a glandular or muscular organ is present in many microphagous polychaetes traditionally referred to as sedentary polychaetes (Fig 1B and C). This part of the alimentary canal is the site of extra- and intracellular digestion. It may be composed of glandular cells, absorptive cells and ciliated cells or only one cell type having similar functions. In Phyllodocida an anatomically separated stomach cannot be distinguished (Fig. 1A).

The stomach is followed by the intestine, which mostly forms a straight tube. In certain polychaetes it may be coiled (e.g., Parergodrilidae; Fig. 1B) or bear lateral caeca (e.g., Aphroditidae). The epithelium often comprises absorptive cells and gland cells but in certain species only one cell type may be present (Heffernan, 1988; Michel, 1988; Saulnier-Michel, 1992; Tzetlin et al., 1992). Usually the intestinal cells are equipped with cilia and a well-developed brush border of microvilli. Additional excretory cells filled with spherocrystals have been described for a few species (see Michel, 1988). A ciliated gutter separated from the intestine by a phalanx of straight microvilli has been described ultrastructurally in the meiofaunal polychaetes *Dinophilus gyrociliatus* and *Nerillidium troglochaetoides* (see Oster, 1986; Tzetlin et al., 1992) but a similar structure is present in many macrofaunal species as well (Saulnier-Michel, 1992). In *Notomastus latericeus* this gutter gives rise to an accessory intestine of uncertain function (Saulnier-Michel, 1992). Sometimes a posterior intestine characterized by a progressive numerical increase in absorptive cells and decrease in gland cells can be distinguished.

A conspicuous feature in the intestine of most Nerillidae is the occurrence of unique tubular structures, discovered and called 'entéronéphridies' by Jouin (1967). These enteronephridia have been reported for the taxa *Meganerilla*, *Mesone-*

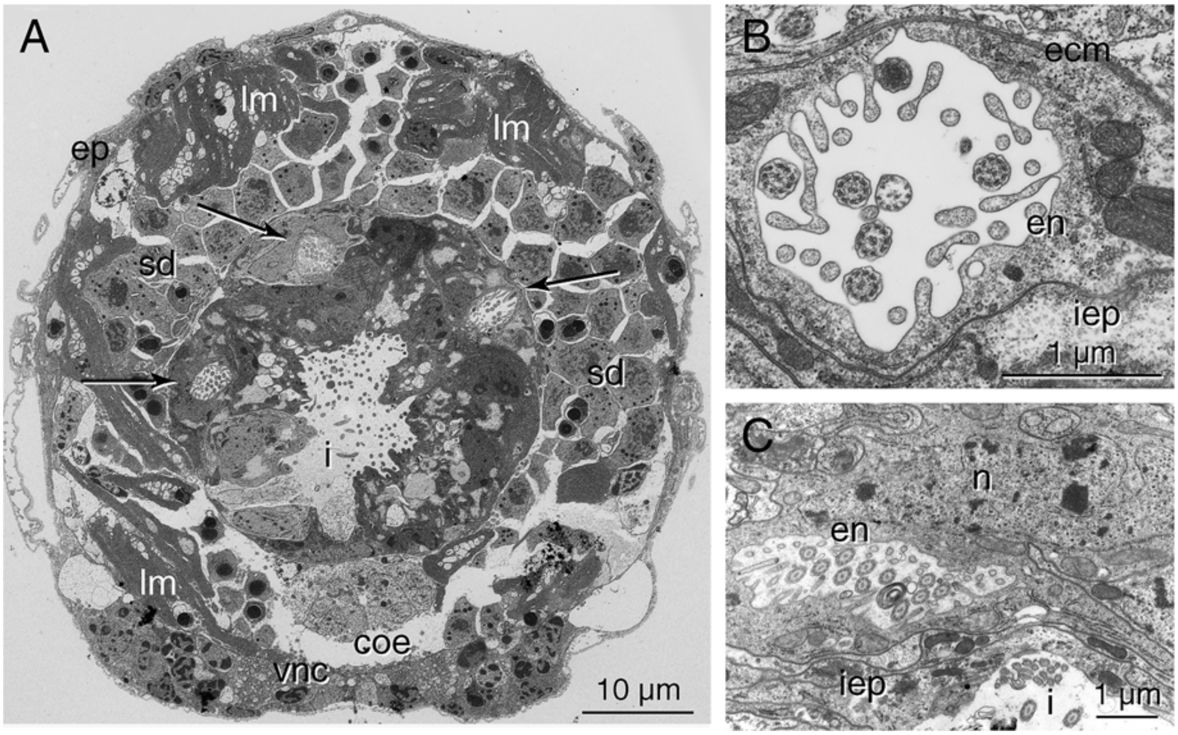

Figure 14. Enteronephridia of Nerillidae. (A–B) *Nerillidium troglochaetoides*. (A) Cross-section of entire specimen to show position of the three enteronephridia (arrows) in the epithelium of the intestine (i); coe coelom, ep epidermis lm longitudinal musculature, sd spermatids, vnc ventral nerve cord. (B) Enlargement of entronephridium (en) with microvilli and cilia, cross section; ecm extracellular matrix, iep intestinal epithelium. (C) *Troglochaetus beranecki*, limnetic species. Section with nucleus (n) of enteronephridium (en) close to opening into intestine (i).

rilla, *Nerillidium*, *Akessoniella*, *Trochonerilla*, *Aristonerilla* and *Troglochaetus* (Jouin, 1967, 1968; Tzetlin & Larionov, 1988; Tzetlin & Saphonov, 1992; Tzetlin et al., 1992; Müller, 2002). In larger species, such as *Nerilla antennata,* enteronephridia are lacking. These structures are blind-ending ciliated intestinal canals, which open into the posterior stomach and run posteriorly all along the intestine (Figs. 1C and 14A–C). Situated in the periphery of the gut, they are embedded between the regular epithelial cells (Tzetlin et al., 1992). The number of enteronephridial canals differs between species and ranges from 3 to 13. Ultrastructural investigations revealed that they are unicellular structures, each cell measuring up to 130 μm in length and approximately 5 μm across (Tzetlin et al., 1992). The canal is formed by the invaginated cell apex and is present throughout the length of the enteronephridia. The luminal cell surface bears a well-developed brush border of microvilli and a few cilia. The apical membrane is characterized by endo- or exocytic vesicles but there is no increase of the basal surface by means of basal folds or a basal labyrinth. These cells are attached to the adjacent cells of the stomach by typical junctional complexes, indicating that the enteronephridia belong to this part of the gut. The enteronephridia resemble protonephridial or metanephridial ducts (Fig. 14B and C), although all species investigated possess protonephridia (Smith, 1992; see Chapter 8). The function of these structures is presumed to be excretory, but experimental evidence is lacking. So far these organs have not been found in any other taxon of Annelida: The enteronephridia described for Megascolecida are structurally different: they are true metanephridia opening into the intestine (see Tzetlin et al., 1992). The only known species with structurally similar organs is *Jennaria pulchra* (see Tzetlin et al., 1992), a taxon with annelid affinities but uncertain systematic position (Rieger, 1991).

Rectum

The rectum is the ectodermal posterior part of the gut (Saulnier-Michel, 1992). It may be short, not exceeding the length of the pygidium, or may extend over several segments. Generally the epithelium bears a cuticle of varying thickness and may be ciliated as well. The anus usually opens terminally, dorsally or ventrally and often possesses a sphincter formed by circular fibres.

Acknowledgements

Thanks are expressed to Dr Hannelore Paxton and Prof. Dr Valadimir Malkhow for fruitful discussions and suggestions. Helpful comments of two anonymous referees are gratefully acknowledged. Part of the studies of the senior author (A.T.) was supported by the Russian fund for basic researches (N-03-04-48598 and 01-04-49093-a). We thank Dr M. Böggemann, Dr M. Kuper and S. Raabe for material or micrographs. Technical assistance by Anna Paul, Werner Mangerich, Martina Biedermann, Anja Ritz and Andrea Noel is gratefully acknowledged.

References

Åkesson, B., 1967. On the biology and larval morphology of *Ophryotrocha puerilis* Claparède & Metschnikov (Polychaeta). Ophelia 4: 111–119.

Åkesson, B., 1973a. Morphology and life history of *Ophryotrocha maculata* sp.n. (Polychaeta, Dorvilleidae). Zoologica Scripta 2: 141–144.

Åkesson, B., 1973b. Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). Zoologica Scripta 2: 145–155.

Åkesson, B., 1976. Morphology and life cycle of *Ophryotrocha diadema*, a new polychaete species from California. Ophelia 15: 23–35

Anderson, D. T., 1959. The embryology of the polychaete *Scoloplos armiger*. Quarterly Journal of microscopical Science 100: 89–166.

Ax, P., 1999. Das System der Metazoa II. Fischer, Stuttgart, 383 pp.

Bantz, M. & C. Michel, 1971. Revètement cuticulaire de la trompe chez *Glycera convoluta* Keferstein (Annélide Polychète). Zeitschrift für Zellforschung 118: 221–242.

Bantz, M. & C. Michel, 1972. Les cellules sensorielles des papilles de la trompe chez *Glycera convoluta* Keferstein (Annélide Polychète). Anatomie microscopique et ultrastructure. Zeitschrift für Zellforschung 134: 351–366.

Böggemann, M., 2002. Revision of the Glyceridae Grube 1850 (Annelida: Polychaeta). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 555: 1–249.

Böggemann, M., D. Fiege & G. Purschke, 2000. Ultrastructure of the proboscidial papillae in some *Glycera* species (Annelida: Polychaeta: Glyceridae). Cahiers de Biologie Marine 41: 143–153.

Briggs, R. T., J. E. Chaffee & M. Anderson, 1985. Calcium containing granules in myoepithelial cells of the polychaete

Syllis spongiphila: possible tonic modulators. Tissue and Cell 17: 923–928.

Britaev, T. A. & V. Belov, 1993. Determination of the age of polychaetes fam. Polynoidae by the jaws growth-lines. Zoologicheskii Zhurnal 72: 15–21 (in Russian).

Britaev, T. A., M. Pluscheva & A. Buyanovski, 2002. Size-age structure of populations of *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae) in the White Sea. Zoologicheskii Zhurnal 81: 285–291 (in Russian).

Bryan, G. W. & P. E. Gibbs, 1979. Zinc – a major inorganic component of nereid polychaete jaws. Journal of the Marine Biological Association of the United Kingdom 59: 969–973.

Bryan, G. W. & P. E. Gibbs, 1980. Metals in nereid polychaetes: the contribution of metals in the jaws to the total body burden. Journal of the Marine Biological Association of the United Kingdom 60: 641–654.

Bryan, G. W. & P. E. Gibbs, 1986. Occurrence, composition and function of intracellular calcium phosphate granules in the musculature of nephtyid polychaetes (Annelida). Journal of the Marine Biological Association of the United Kingdom 66: 343–365.

Colbath, G. K., 1986. Jaw mineralogy in eunicean polychaetes (Annelida). Micropaleontology 32: 186–189.

Colbath, G. K., 1987. Evidence for shedding of maxillary jaws in eunicoid polychaetes. Journal of Natural History 21: 443–447.

Colbath, G. K., 1988. Taphonomy of recent polychaete jaws from Florida and Belize. Micropaleontology 34: 83–89.

Croneis, C. & H. W. Scott, 1933. Scolecodonts. Bulletin of the Geological Society of America 44: 207.

Dales, R. P. 1957. The feeding mechanism and structure of the gut of *Owenia fusiformis* D.Ch. Journal of the Marine Biological Association of the United Kingdom 36: 81–89.

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

Dales, R. P. 1963. Annelids. Hutchison University Library, London, 200 pp.

Dales, R. P., 1977. The Polychaete stomodeum and phylogeny. In Reish, D. J. & K. Fauchald (eds), Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman. Allan Hancock Foundation, Los Angeles: 525–546.

Damas, D., 1987. Étude cytologique, histochimique et microanalytique des pieces maxillaires d'*Ophryotrocha puerilis* (Annélide, Polychète, Eunicidae). Bulletin of the Zoological Society of France 111: 61–73.

Del Castello, J., M. Anderson & D. S. Smith, 1972. Proventriculus of a marine annelid: muscle preparation with the longest recorded sarcomere. Proceedings of the National Academy of Sciences of the United States of America. 69: 1669–1672.

Desbruyères, D., 1978. Un Ampharetidae (Annélides Polychètes sédentaires) à structure buccale aberrante: *Gnathampharete paradoxa* gen., sp. n. Comptes Rendus de l'Académie des Sciences Paris, D 286: 281–284.

Düsing, H., 1961. Die Umwandlung des Kauapparates in Abhängigkeit vom sexuellen Zustand bei *Ophryotrocha puerilis* Claparde et Metschnikoff. Naturwissenschaften 3: 532–533.

Eeckhaut, I. & D. Lanterbec, 2005. Myzostomida. A review of the phylogeny and ultrastructure. Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 251–273.

Ehlers, E., 1864–1868. Die Borstenwürmer nach systematischen und anatomischen Untersuchungen dargestellt. Wilhelm Engelmann, Leipzig: 1–748.

Ehlers, E., 1868. Über eine fossile *Eunice* aus Solnhofen (*Eunicites avitus*) nebst Bemerkungen über fossile Würmer überhaupt. Zeitschrift für wissenschaftliche Zoologie 18: 421–443.

Eisig, H., 1914. Zur Systematik, Anatomie und Morphologie der Ariciiden nebst Beiträgen zur generellen Systematik. Mitteilungen aus der zoologischen Station zu Neapel 21: 153–593.

Eibye-Jacobsen, D. & R. M. Kristensen, 1994. A new species and genus of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. Zoologica Scripta 23: 107–131.

Fauchald, K. & P. A. Jumars, 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology Annual Review 17: 193–284.

Fauvel, P., 1959. Classe des Annélides Polychètes. In Grassé, P.-P. (ed.), Traité de Zoologie, Vol. 5. Masson, Paris: 13–196.

Gelder, S. R. & R. F. Uglow, 1973. Feeding and gut structure in *Nerilla antennata* (Annelida: Archiannelida). Journal of Zoology 171: 225–237.

Gibbs, P. E. & G. W. Bryan, 1980a. Copper – the major metal component of glycerid polychaete jaws. Journal of the Marine Biological Association of the United Kingdom 60: 205–214.

Gibbs, P. E. & G. W. Bryan, 1980b. A note on the element composition of the jaws of *Goniada maculata* (Polychaeta: Goniadidae). Journal of the Marine Biological Association of the United Kingdom 60: 541–542.

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

Hartmann-Schröder, G., 1958. Zur Morphologie der Opheliiden (Polychaeta sedentaria). Zeitschrift für wissenschaftliche Zoologie 161: 84–143.

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

Heffernan, P., 1988. Ultrastructural and histochemical studies of the digestive system of *Pholoë minuta* (Polychaeta: Sigalionidae). Journal of the Marine Biological Association of the United Kingdom 68: 447–464.

Heimler, W., 1983. Untersuchungen zur Larvalentwicklung von *Lanice conchilega* (Pallas) 1766 (Polychaeta/Terebellomorpha) Teil III. Bau und Struktur der Aulophora-Larve. Zoologische Jahrbücher. Anatomie 110: 411–478.

Hilbig, B. & J. A. Blake, 1991. Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a genric revision of *Ophryotrocha*. Zoologica Scripta 20: 147–183.

Hsieh, H.-L. & J. L. Simon, 1987. Larval development of *Kinbergonuphis simoni*, with a summary of development patterns in the family Onuphidae (Polychaeta). Bulletin of the Biological Society of Washington 7: 194–210.

Jamieson, B. G. M., 1992. Oligochaeta. In Harrison, F. W. & S. L. Gardiner (eds), Microscopic Anatomy of Invertebrates. Vol. 7 Annelida. Wiley-Liss, New York: 217–322.

Jennings, J. B. & S. R. Gelder, 1969. Feeding and digestion in *Dinophilus gyrociliatus* (Annelida, Archiannelida). Journal of Zoology 158: 441–457.

Jennings, J. B. & S. R. Gelder, 1976. Observations on the feeding mechanism, diet and digestive physiology of *Histriobdella homari* van Veneden 1958: an aberrant polychaete symbiotic with North American and European lobsters. Biological Bulletin 151: 489–517.

Jeuniaux, C., 1969. Nutrition and Digestion. In Florkin, M. & B. T. Scheer (eds), Chemical Zoology. Vol. 4. Academic Press, London, New York: 69–91.

Jouin, C., 1967. Étude morphologique et anatomique de *Nerillidopsis hyalina* Jouin et de quelques *Nerillidium* Remane (Archiannélides Nerillidae). Archives de Zoologie Expérimentale et Genérale 108: 97–110.

Jouin, C., 1968. Sexualité et biologie de la reproduction chez *Mesonerilla* Remane and *Meganerilla* Boaden (Archiannélides Nerillidae). Cahiers de Biologie Marine 9: 31–52.

Jouin, C., 1978a. Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Archiannelida). I. Muscles and myo-epithelial junctions. Tissue and Cell 10: 269–287.

Jouin, C., 1978b. Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Archiannelida). II. The stomodeal epithelium and its cuticle. Tissue and Cell 10: 289–301.

Jouin, C., 1979. Description of a free-living polychaete without gut: *Astomus taenioides* n.gen., n. sp. (Protodrilidae, Archiannelida). Canadian Journal of Zoology 57: 2448–2456.

Jouin, C., 1992. The ultrastructure of a gutless annelid, *Parenterodrilus* gen. nov. *taenioides* (= *Astomus taenioides*) (Polychaeta, Protodrilidae). Canadian Journal of Zoology 70: 1833–1848.

Jumars, P., 1974. A generic revision of the Dorvilleidae (Polychaeta), with six new species from the deep North Pacific. Zoological Journal of the Linnean Society of London 54: 101–135.

Kielan-Jaworowska, S., 1966. Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. Acta Palaeontologica Polonica 16: 1–125.

Kirkegaard, J. B., 1970. Age determination of *Nephtys* (Polychaeta: Nephtydae). Ophelia 7: 447–496.

Kozlowski, R., 1956. Sur quelques appareils masticateurs des Annélides Polychètes Ordoviciens. Acta Paleontologica Polonica 1: 3–16.

Kozur, H., 1970. Zur Klassifikation und phylogenetischen Entwicklung der fossilen Phyllodocida und Eunicida (Polychaeta). Freiburger Forschungsheft C 260: 35–81.

Kristensen, R. M. & T. Niilonen, 1982. Structural studies on *Diurodrilus* Remane (Diurodrilidae fam. n.), with description of *Diurodrilus westheidei* sp.n. from the arctic interstitial meiobenthos, W. Greenland. Zoologica Scripta 11: 1–12.

Lanzaveccchia, G., M. de Eguileor & R. Valvassori, 1988. Muscles. In Westheide, W. & C. O. Hermans (eds), The Ultrastructure of Polychaeta. Microfauna Marina 4: 71–88.

Licher, F., 1999. Revision der Gattung *Typosyllis* Langerhans, 1879 (Polychaeta: Syllidae). Morphologie, Taxonomie und Phylogenie. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 551: 1–336.

Mackie, A. S. Y., 1994. *Adercodon pleijeli* gen. et.sp. nov. (Polychaeta, Ampharetidae) from the Mediterranean Sea. In Dauvin, J. C., L. Laubier & D. Reish (eds), Actes de la 4ème Conférence internationale des Polychètes. Mémoires du Muséum National d'histoire Naturelle 162: 243–250.

Martin, P., 2001. On the origin of the Hirudinea and the demise of the Oligochaeta. Proceedings of the Royal Society of London B 268: 1089–1098.

Michel, C., 1972. Étude ultrastructurale et histochimique des papilles de la gaine de la trompe de *Notomastus latericus* Sars (Annélide Polychète Sédentaire). Zeitschrift für Zellforschung 128: 428–503.

Michel, C., 1978. Étude histologique, histochimique et cytologique du stomodeum chez le Polychète Sédentaire, *Audouinia tentaculata* (Montagu). Cahiers de Biologie Marine 19: 433–446.

Michel, C., 1988. Intestine. In Westheide, W., & C. O. Hermans (eds), The Ultrastructure of the Polychaeta. Microfauna Marina 4: 157–175.

Michel, C. & E. J. DeVillez, 1978. Digestion. In Mill, P. J. (ed.), Physiology of Annelids. Academic Press, London, New York: 509–554.

Michel, C., M.-T. Fonze-Vignaux & M.-F. Voss-Foucart, 1973. Données nouvelles sur la morphologie, l'histochimie et la composition chimique des mâchoires de *Glycera convoluta* Keferstein (Annélide, Polychète). Bulletin biologique de France et de la Belgique 107: 301–321.

Mierzejewski, P., 1978. Molting of the jaws of the early Paleozoic Eunicida (Annelida: Polychaeta). Acta Palaeontologica Polonica 23: 73–88.

Mierzejewski, P., 1984. *Sycnlinophora synclinalis* Eisenack – the oldest arabellid polychaete. Review of Paleobotany and Palynology 43: 285–292.

Mierzejewski, P. & G. Mierzejewska, 1975. Xenognath type of polychaete jaw apparatuses. Acta Palaeontologica Polonica 20: 437–443.

Müller, H., 1962. Über die Sexualität des Polychaeten *Ophryotrocha puerilis*, ihre Determination und Kauapparatentwicklung. Zeitschrift für Morphologie und Ökologie der Tiere 52: 1–32.

Müller, M. C. M., 2002. *Aristonerilla*: a new nerillid genus (Annelida: Polychaeta) with description of *Aristonerilla* (*Micronerilla*) *brevis* comb. nov. from a seawater aquarium. Cahiers de Biologie Marine 43: 131–139.

Müller, M., J. M. Bernhard & C. Jouin-Toulmond, 2001. A new member of Nerillidae (Annelida: Polychaeta), *Xenonerilla bactericola* gen. et sp. nov., collected off California. USA. Cahiers de Biologie Marine 42: 203–217.

Nordheim, H. v., 1987. *Petrotrocha notogaea* gen. et sp. n., a neotenic interstitial polychaete (Dorvilleidae) from the Hauraki Gulf, New Zealand. Zoologica Scripta 16: 33–38.

Olive, P. J. W., 1977. The life-history and population structure of the polychaetes *Nephtys caeca* and *Nephtys hombergii* with special reference to growth rings in the teeth. Journal of the Marine Biological Association of the United Kingdom 57: 133–150.

Olive, P. J. W., 1980. Growth lines in Polychaeta jaws. In Rhoads, D. C. & R. A. Luts (eds), Skeletal Growth of Aquatic Organisms, Plenum, New York: 561–592.

Orensanz, J. M., 1990. The eunicemorph polychaete annelids from antarctic and subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the Southern Indian Ocean. Biology of the Antarctic Seas 21: 1–183.

Orrhage, L., 1964. Anatomische und morphologische Studien über die Polychaetenfamilien Spionidae, Disomidae und Poecilochaetidae. Zoologiska Bidrag fran Uppsala 36: 335–405.

Orrhage, L., 2001. On the anatomy of the central nervous system and the morphological value of the anterior appendages of Ampharetidae, Pectinariidae and Terebellidae (Polychaeta). Acta Zoologica (Stockholm) 82: 57–71.

Orrhage, L. & M. C. M. Müller, 2005. Morphology of the nervous system of Polychaeta. Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 79–111.

Oster, U., 1986. Microfilament-supported macrovilli in the hindgut of the polychaete *Dinophilus gyrociliatus*. Zeitschrift für Naturforschung C41: 1139–1143.

Pander, C. H., 1856. Monographie der fossilen Fische des Silurischen Systems des Russisch-Baltischen Gouvernements. St. Petersbourg: 1–91.

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

Paxton, H., 2000. Eunicida. In Beesly, P. L., G. J. B. Ross & C. J. Glasby (eds), Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO, Melbourne: 89–104.

Purschke, G., 1985a. Anatomy and ultrastructure of the ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). I. The pharynx of the Dinophilidae. Zoomorphology 105: 223–239.

Purschke, G., 1985b. Anatomy and ultrastructure of the ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). II. The pharynx of the Nerillidae. Microfauna Marina 2: 23–60.

Purschke, G., 1987a. Anatomy and ultrastructure of the ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). III. The pharynx of the Parergodrilidae. Zoologische Jahrbücher für Anatomie 115: 331–362.

Purschke, G., 1987b. Anatomy and ultrastructure of the ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). IV. The pharynx and jaws of the Dorvilleidae. Acta Zoologica (Stockholm) 68: 83–105.

Purschke, G., 1988a. Pharynx. In Westheide, W. & C. O. Hermans (eds), The ultrastructure of Polychaeta. Microfauna Marina 4: 177–197.

Purschke, G., 1988b. Anatomy and ultrastructure of the ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). V. The pharynges of the Ctenodrilidae and Orbiniidae. Zoomorphology 108: 119–135.

Purschke, G., 1999. Terrestrial polychaetes – models for the evolution of the Clitellata (Annelida)? Hydrobiologia 406: 87–99.

Purschke, G., 2002. On the ground pattern of Annelida. Organisms Diversity and Evolution 2: 181–196.

Purschke, G., 2003. Is *Hrabeiella periglandulata* (Annelida, 'Polychaeta') the sister-group of Clitellata? Evidence from an ultrastructural analysis of the dorsal pharynx in *H. periglandulata* and *Enchytraeus minutus* (Annelida: Clitellata). Zoomorphology 122: 55–66.

Purschke, G. & C. Jouin, 1988. Anatomy and ultrastructure of the ventral pharyngeal organs of *Saccocirrus* (Saccocirridae) and *Protodriloides* (Protodriloidae fam. n.) with remarks on the phylogenetic relationships within the Protodrilida (Annelida: Polychaeta). Journal of Zoology, London 215: 1–28.

Purschke, G. & A. B. Tzetlin, 1996. Dorsolateral ciliary folds in the polychaete foregut: structure, prevalence and phylogenetic significance. Acta Zoologica (Stockholm) 77: 33–49.

Rice, M. E., 1973. Morphology, behaviour, and histogenesis of the pelagosphera larva of *Phascolosoma agassizii* (Sipuncula). Smithsonian Contributions to Zoology 132: 1–51.

Rice, M. E., 1976. Larval development and metamorphosis in Sipuncula. American Zoologist 16: 563–571.

Rice, M. E., 1985. Sipuncula. Developmental evidence for phylogenetic interference. In Conway Morris, S., J. D. George, R. Gibson & H. M. Platt (eds), The origins and relationships of lower invertebrates. Clarendon, Oxford: 274–296.

Rieger, R. M., 1991. Neue Organisationstypen aus der Sandlückenfauna: die Lobatocerebriden und *Jennaria pulchra*. Verhandlungen der Deutschen Zoologischen Gesellschaft 84: 247–259.

Rieger, R. M. & G. E. Rieger, 1975. Fine structure of the pharyngeal bulb in *Trilobodrilus* and its phylogenetic significance within Archiannelida. Tissue and Cell 7: 267–279.

Rota, E., 1998. Morphology and adaptations of *Parergodrilus* Reisinger and *Hrabeiella* Pizl & Chalupsky, two enigmatic soil-dwelling annelids. Italian Journal of Zoology 65: 75–84.

Rouse, G. W., 2000. Morphology and Physiology. In Beesly, P. L. Ross, G. J. B. & C. J. Glasby (eds), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO, Melbourne: 9–32.

Rouse, G. W. & F. Plejel, 2001. Polychaetes. Oxford University Press. New York: 1–354.

Rouse, G. W. & K. Fauchald, 1997. Cladistics and polychaetes. Zoologica Scripta 26: 139–204.

Saulnier-Michel, C., 1992. Polychaeta: Digestive System. In Harrison, F. W. & S. L. Gardiner (eds), Microscopic Anatomy of Invertebrates. Vol. 7. Annelida. Wiley-Liss, New York: 53–69.

Saulnier-Michel, C., G. Gaill, A. Hily, P. Alberic & M. A. Cosson-Mannevy, 1990. Structure and functions of the digestive tract of *Alvinella pompejana*, a hydrothermal vent polychaete. Canadian Journal of Zoology 68: 722–732.

Schmidt, P. & W. Westheide, 1972. *Dinophilus gyrociliatus* (Polychaeta). Nahrungsaufnahme und Fortpflanzung. Begleitveröffentlichung zum Film E1750. Encyclopaedia Cinematographica: 1–16.

Smith, D. S., J. Del Castillo & M. Anderson, 1973. Fine structure and innervation of an annelid with the longest recorded sarcomere. Tissue and Cell 5: 281–302.

Smith, P. R., 1992. Polychaeta: Excretory system. In Harrison, F. W. & S. L. Gardiner (eds), Microscopic Anatomy of Invertebrates. Vol. 7. Annelida. Wiley-Liss, New York: 71–108.

Southward, E.C., A. Schulze & S. L. Gardiner, 2005. Pogonophora (Annelida): Form and function. Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 225–249.

Struck, T. H., W. Westheide & G. Purschke, 2002. Progenesis in Eunicida ('Polychaeta', Annelida) separate evolutionary events? Evidence from molecular data. Molecular Phylogenetics and Evolution 25: 190–199.

Szaniawski, H., 1974. Some mesozoic scolecodonts congeneric with recent forms. Acta Palaeontologica Polonica 19: 179–199.

Szaniawski, H., & R. Wrona, 1987. Polychaete jaws from the Cape Melville formation (Lower Miocene) of King George Island, West Antarctica. Acta Palaeontologica Polonica 49: 105–125.

Tzetlin, A. B., 1980a. Two new species of the fam. Dorvilleidae from the White and the Barents Seas. Zoologicheskii Zhurnal 59: 1817–1822 (in Russian).

Tzetlin, A. B., 1980b. *Ophryotrocha schubravyi* sp.n. and the problem of evolution of the mouth parts in the Eunicemorpha (Polychaeta). Zoologicheskii Zhurnal 59: 666–670 (in Russian).

Tzetlin, A. B., 1987. Fine morphology of the pharynx apparatus in the larvae of *Nicolea zostericola* (Polychaeta, Terebellidae). Doklady Akademia Nauk SSSR 293: 1505–1509 (in Russian).

Tzetlin, A. B., 1989. Morphological analysis of the structure of the feeding apparatus in polychaetes of the genus *Praxillura* (Maldanidae). Doklady Academia Nauk SSSR 309: 757–760 (in Russian).

Tzetlin, A. B., 1990. To the taxonomical status of the *Lumbrineris* Blainville (Polychaeta: Lumbrineridae) from the White Sea. In: Biological Resource of the White Sea, Izdatel'stvo Moskovskogo Universiteta, Moscow: 99–107 (in Russian).

Tzetlin, A. B., 1991. Evolution of feeding apparatus in the polychaetes of the order Capitellida. Zoologicheskii Zhurnal 70: 10–22 (in Russian).

Tzetlin, A. B., 1994. Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta: Cossuridae) from the White Sea. In Dauvin, J. C., L. Labier & D. Reish (eds), Actes de la 4ème Conferénce internationale des Polychètes. Mémoires du Muséum national d́Histoire naturelle, Paris. 162: 137–143.

Tzetlin, A. B. & V. V. Larionov, 1988. Morphology of a new archiannelid *Akessoniella orientalis* gen. et. sp.n. (Nerillidae). Zoologicheskii Zhurnal 67: 846–857 (in Russian).

Tzetlin, A. B. & M. V. Saphonov, 1992. *Trochonerilla mobilis* gen. et sp. n. – a meiofaunal nerillid (Annelida: Polychaeta) from a marine aquarium in Moscow. Zoologica Scripta 21: 251–254.

Tzetlin, A. B., E. G. Zavarzina & M. V. Saphonov, 1987. Morphofunctional analysis of the pharyngeal structures of the several annelids. Doklady Academia Nauk SSSR 294: 1008–1011 (in Russian).

Tzetlin, A. B., G. Purschke, W. Westheide & M. V. Saphonov, 1992. Ultrastructure of enteronephridia and general description of the alimentary canal in *Trochonerilla mobilis* and *Nerillidium troglochaetoides* (Polychaeta: Nerillidae). Acta Zoologica (Stockholm) 73: 163–176.

Uebelacker, J. M. & P. G. Johnson, 1984. Taxonomic guide to the polychaetes of the Northern Gulf of Mexico. Vol. VI. Barry A Vittor & Associates, Mobile: 39-1–44-37.

Westheide, W. & H. v. Nordheim, 1985. Interstital Dorvilleidae (Annelida: Polychaeta) from Europe, Australia and New Zealand. Zoologica Scripta 14: 183–199.

Westheide, W. & P. Schmidt, 1974. *Trilobodrilus axi* (Polychaeta). Nahrungsaufnahme und Fortpflanzung. Begleitveröffentlichung zum Film E1955. Encyclopaedia Cinematographica 1–12.

Westheide, W. & R. M. Rieger, 1978.Cuticle ultrastructure of hesionid polychaetes (Annelida). Zoomorphologie 91: 1–18.

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

Westheide, W. & M. C. Müller, 1996. Cinematographic documentation of enchytraeid morphology and reproductive biology. Hydrobiologia 334: 263–267.

Winnepenninckx, B. M. H., Y. van de Peer & T. Backeljau, 1998. Metazoa relationships on the basis of 18S rRNA sequences: a few years later … American Zoologist 38: 888–906.

Wissocq, J. C., 1974. Étude ultrastructurale d'un organe musculaire constitué de fibres possédant les plus longs sarcomères du règne animal: Le proventricule des Syllidiens (Annélides Polychètes). Journal de Microscopie 19: 285–306.

Wolf, G. 1980. Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). Senckenbergiana maritima 12: 1–182.

Wolf, P. S. 1986. Four new genera of Dorvilleidae (Annelida: Polychaeta) from the Gulf of Mexico. Proceedings of the Biological Society of Washington 99: 616–626.

Wolff, T. & M. E. Petersen, 1991. A brief biography of A. S. Ørsted, with notes on his travels in the West Indies and Central America and illustrations of collected polychaetes. Ophelia Supplement 5: 669–685.

Zaslavskaya, N. M., 1989. Reconstruction of the phylogenesis of the family Hartmaniellidae (Polychaeta). In: Phylogenetic aspects of Paleontology, 35th session of the USSR Paleontological Society, Moscow. Abstracts: 18–19.

Zavarzina, E. G. & A. B. Tzetlin. 1986. Biology of *Ophryotrocha dimorphica* sp.n. (Polychaeta, Eunincida) from Peter the Great Bay (the Japan Sea). Zoologicheskii Zhurnal 65: 1808–1817 (in Russian).