Cah. Biol. Mar. (2002) 43 : 149-164

Comparative morphology of the feeding apparatus in the Terebellida (Annelida: Polychaeta)

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Abstract: The morphology of buccal parts was studied in twenty representative species of Terebellida belonging to the families Terebellidae, Ampharetidae, Trichobranchidae and Pectinariidae. The ultrastructure of the ventral pharyngeal organ was studied in *Ampharete lindstroemii* and juveniles of *Nicolea zostericola* and *Pectinaria hyperborea*. The ventral pharyngeal organ consists of investing muscle fibres and a bulbous muscle including muscle and interstitial cells. A glandular ridge is found in the posterior part of the bulbous muscle. No such structures were observed in *Pectinaria hyperborea*. The upper lip in representatives of Terebellidae, Trichobranchidae, Ampharetidae, and Alvinellidae is similar in structure. It consists of an area of tentacle attachment and a free edge. In contrast, the upper lip in Pectinariidae has no free edge. A hypothesis on the evolution of the buccal apparatus in the Terebellida is proposed. A distinct prostomium and tentacles located on the upper lip outside the mouth (as in Ampharetidae with everted tentacles) are considered to be a plesiomorphic pattern. The ciliated surface of the dorsal part of the buccal cavity in the Terebellida is considered to be homologous to the dorso-lateral folds found in most polychaete taxa.

Résumé : *Morphologie comparée de l'appareil buccal chez les Terebellida (Annelida: Polychaeta).* La morphologie de l'appareil buccal a été étudiée chez vingt espèces représentatives de l'ordre des Terebellida, appartenant aux familles des Terebellidae, Ampharetidae, Trichobranchidae et Pectinariidae. L'ultrastructure de l'organe pharyngien ventral a été étudié chez *Ampharete lindstroemii* et chez des juvéniles de *Nicolea zostericola* et *Pectinaria hyperborea*. Cet organe comprend une enveloppe de fibres musculaires autour d'un muscle bulbaire formé de cellules musculaires et de cellules interstitielles. Une crête de cellules glandulaire se trouve à l'arrière du muscle bulbaire. Aucune de ces structures n'est observée chez *Pectinaria hyperborea*. La lèvre supérieure des représentants des Terebellidae, Trichobranchidae, Ampharetidae, et Alvinellidae présente une structure semblable. Elle comprend une zone d'attache des tentacules et un bord libre. Au contraire, la lèvre supérieure des Pectinariidae n'a pas de bord libre. Une hypothèse sur l'évolution de l'appareil buccal des Terebellida est proposée. Un prostomium distinct et des tentacules situés sur la lèvre supérieure, en dehors de la bouche (comme chez les Ampharetidae avec des tentacules extroversés) est une disposition considérée comme plésiomorphe. La surface ciliée de la partie dorsale de la cavité buccale chez les Terebellida est considérée comme homologue des replis dorso-latéraux qui sont présents chez la plupart des Polychètes.

Keywords: Terebellida, feeding apparatus, morphology, ultrastructure, evolution.

Reçu le 12 octobre 2000 ; accepté après révision le 9 avril 2002.
Received 12 October 2000; accepted in revised form 9 April 2002.

Introduction

The order Terebellida comprises five families: Terebellidae, Trichobranchidae, Pectinariidae, Ampharetidae and Alvinellidae. The Ampharetidae are divided into Ampharetinae and Melinninae. Four subfamilies: Terebellinae, Thelepodinae, Artacaminae and Polycirrinae, are distinguished within the Terebellidae (Holthe, 1986b). Some authors consider the Trichobranchidae a subfamily of the Terebellidae (see Zhirkov, 1989). The structure of the anterior part of the body is one of the key characteristics of families and subfamilies in the Terebellida (Holthe, 1986b). The feeding apparatus of the Terebellida is composed of numerous buccal tentacles, peristomial upper and lower lips and a ventral pharyngeal organ located in the buccal cavity. The buccal tentacles have different positions. They are located on the upper lip, or dorsally behind it, in Terebellidae and Trichobranchidae, on the eversible upper lip in Ampharetidae (Fauvel, 1897; Djakonov, 1913) and Alvinellidae (Desbruyères & Laubier, 1993; Zhadan et al., 2000), or on the ventral surface of the cephalic veil in Pectinariidae (Holthe, 1986b).

A generally accepted terminology for the terebellid anterior structures is lacking. Different authors used different names for the same structures and, vice versa, the names of different structures were sometimes very similar (Table 1).

Holthe (1986b) defined the upper lip as "a muscular brim between the tentacles and the mouth". According to this author the tentacles of ampharetids and alvinellids are located on the upper lip and can invert into the mouth together with the lip. In the Trichobranchidae and Polycirrinae (Terebellidae), the tentacles are also attached to the upper lip, but there is no distinct muscular brim between tentacles and mouth. That must be why Holthe (1986b) called their upper lip a "tentacular lobe". The upper lip of other Terebellidae (Terebellinae, Thelepodinae, and Artacaminae) does not bear the buccal tentacles that rest behind it.

To avoid misunderstanding, in the present paper we use the term "upper lip" for the area including the zone of tentacle attachment and the free edge in front of this zone.

The homology between the various parts of the feeding apparatus, both within the taxon Terebellida and between

Table 1. Terminology used in descriptions of the tentacular apparatus of the order Terebellida.
Tableau 1. Terminologie utilisée dans les descriptions de l'appareil tentaculaire des Terebellida

Family, subfamily	Terminology used for the upper lip of Ampharetidae, Terebellidae, Trichobranchidae and Alvinellidae	Sources
Ampharetidae	Lèvre supérieure	Fauvel, 1897
	Upper lip	Djakonov, 1913; Mackie, 1994
	Dorsal curtain	Fauchald & Rouse, 1997
	Tentacular membrane	Orrhage, 2001
Terebellidae	Upper lip, tentacular lobe, prostomium	Holthe, 1986b
Terebellinae	Upper lip	Zhirkov, 1989
	Prostomium, upper lip, anterior lip, tentacular lobe	Hutchings, 1990
	Upper lip, dorsal ridge	Orrhage, 2001
Thelepodinae	Tentacular lobe, upper lip	Holthe, 1986b
	Upper lip	Zhirkov, 1989
	Tentacular lobe, prostomium, upper lip	Hutchings, 1990
Polycirrinae	Tentacular lobe, tentacular ridge, upper lip	Holthe, 1986b
	Upper lip	Zhirkov, 1989
	Tentacular membrane, tentacular lobe	Hutchings, 1990
Trichobranchidae	Tentacular lobe, tentacular ridge, upper lip	Holthe, 1986b
	Upper lip	Zhirkov, 1989
Alvinellidae	Buccal membrane	Desbruyères & Laubier, 1993
	Terminology used for the cephalic veil of Pectinariidae	
Pectinariidae	Tentakelmembran	Hessle, 1917
	Antennularmembran	Nilsson, 1928
	Tentacular membrane	Holthe, 1986b; Orrhage, 2001
	Buccal membrane	Zhirkov, 1989
	Cephalic veil	Lambert et al., 1996; Fauchald & Rouse, 1997

Terebellida and other Polychaeta, has not yet been ascertained. The homology of the Terebellida buccal tentacles to any other structure of the polychaete anterior part, as well as their evolutionary origin and primary location, is still vague. Binard & Jeener (1928) considered the buccal tentacles as multiplied palps. Holthe (1986a) suggested that the buccal tentacles evolved from "pharyngeal papillae", which are unknown in other Polychaeta. He considered the tentacle location within the pharynx (as found in ampharetids) a plesiomorphic pattern. He supposed that the state of the Terebellidae with tentacles outside the mouth is a secondary eversion resulting from an increase of the animal's size: the pharynx cannot provide enough space for numerous and long tentacles (Holthe, 1986a).

According to the assumption of Fauchald & Rouse (1997), the buccal tentacles are multiplied palps, peristomial in Ampharetidae, Alvinellidae and Pectinariidae, and prostomial in Terebellidae and Trichobranchidae, hence, they were originally located outside the mouth and the ampharetid possibility of introversion of the tentacles in the pharynx is secondary.

Orrhage (2001) has studied the anatomy of the central nervous system and of the anterior appendages of the Ampharetidae, Pectinariidae and Terebellidae. He concluded that representatives of these taxa bear no antennae and no palps and that their buccal tentacles belong to the alimentary canal.

It is not clear whether the upper lips are homologous through all the families of Terebellida (Holthe, 1986a), in particular whether the ampharetid upper lip is homologous to the terebellid one.

According to Fauchald & Rouse, 1997, in terebellids and trichobranchids prostomium and peristomium are fused marginally and the tentacles are attached along the fusion line. These are produced from the latero-posterior corners of the fusion line and migrate with the growth of the worm into increasingly more dorsal positions.

Purschke & Tzetlin (1996) described dorso-lateral ciliated folds for most of the polychaete taxa. However, it was still unknown which part of the terebellid feeding apparatus is homologous to the dorso-lateral folds of other polychaetes and if those structures are even developed.

In all the species of Terebellida there is a ventral pharyngeal organ (VPhO). In juvenile stages, the pharyngeal organ is used to scrape off microfouling (Tzetlin, 1987), while it is used for food sorting and swallowing in adults (Dales, 1955; Sutton, 1957). It is relatively small in pectinariids and trichobranchids (Watson, 1928; Michel et al., 1984) and well-developed in ampharetids, terebellids and alvinellids (Wirén, 1885; Fauvel, 1897; Djakonov, 1913; Saulnier-Michel et al., 1990; Zhadan et al., 2000). Cuticular papillae, unknown in other Terebellida, have been described in the pharyngeal organ of *Alvinella* (Alvinellidae) (Saulnier-Michel et al., 1990, Zhadan et al., 2000). Transverse rows of teeth at its surface are also found in the ampharetids of the genera *Gnathampharete* (see Desbruyères, 1978), *Adercodon* (see Mackie, 1994), and *Ampharete* (see Uebelacker, 1984). There are no data about the fine structure of the pharyngeal organ in most Teberellida except for a few juveniles of Terebellidae and smaller Ampharetidae (Heimler, 1983; Tzetlin, 1987; Tzetlin & Mackie, unpubl. obs.). According to these data, the VPhO in both families is composed of not only muscular, but also interstitial cells, reinforced with strong tonofilaments, and lacking contractile elements. A study of the juveniles' ventral pharyngeal organs is of special interest because they are used for scraping food (Tzetlin, 1987) like VPhO of many other polychaetes (see Purschke, 1988; Purschke & Tzetlin, 1996).

The aim of our study was to investigate the diversity of structures of the feeding apparatus in different families of Terebellida. A comparative analysis of the location of buccal tentacles and the structure of the ventral pharyngeal organs could clarify the homology of different elements of the feeding apparatus and their synonymy.

Material and methods

Twenty species of Terebellida were studied (Table 2). The material used comes from collections of the Department of Hydrobiology of Moscow State University, Moscow (Barents Sea, Okhotsk Sea), from the collection of the National Museum of Natural History (NMNH), Washington, D.C., from material collected by the authors in the White Sea (White Sea Biological Station of Moscow State University), during summer 1999-2000.

Specific identification of the juveniles was possible because *Pectinaria hyperborea* is the only species of the genus found in the central deep part of the White Sea where the specimens were collected and *Nicolea zostericola* is the only species of the genus in the White Sea as well.

Animals were fixed with a 10% formalin solution, dissected and examined with a stereomicroscope. Ampharetids were dissected both from ventral and dorsal sides for the study of the tentacle attachment. Selected fragments of the anterior region were dried using the critical point method, coated with platinum-palladium and examined with a HITACHI 400 A scanning electron microscope. One specimen of *Hypania invalida* from river Moscow was fixed in 4% formalin solution; after paraffin embedding and serial cross-sectioning (5 µm thick sections), the slides were stained with Heidenhain's iron haemotoxylin. They were examined with an OPTON MC 63s light microscope. Anterior body parts of an adult

Table 2. Material examined and methods. Dis.: dissections; SEM: scanning electronic microscopy; TEM: transmission electronic microscopy; LM = light microscopy.

Tableau 2. Materiel examiné et méthodes. Dis. : dissections ; SEM : microscopie électronique à balayage ; TEM : microscopie électronique à transmission ; LM = microscopie photonique.

Family, subfamily, species	Locality, catalogue number	Number of specimens studied by			
		Dis.	SEM	TEM	LM
Ampharetidae					
AMPHARETINAE					
Ampharete reducta Chamberlin, 1920	Okhotsk Sea, 55°N 156° E	1	1		
Ampharete finmarchica (Sars, 1865)	Barents Sea, 74°30' N, 22°30' E	4	2		1
A.kudenovi Jirkov, 1994	Okhotsk Sea, 48°16'N, 154°55'E	5	3		
A. lindstroemii (Malmgren, 1867)	White Sea, 66°30' N, 33°30' E	2	2	1	1
Amphicteis gunneri antarctica Hessle, 1917	NMNH no. 56799, 59°50' S, 26°41' W	1	1		
A. ninonae Jirkov, 1985	Barents Sea, 71°30'N, 30°00'E	1			
Hypania invalida (Grube, 1860)	River Moscow, 55°45' N, 37°35' E				1
Sabellides borealis Sars, 1856	Barents Sea, 70°45' N 51°30' E	2			
Samythella elongata Verrill, 1873	Barents Sea, 71°30'N, 30°00'E	2	2		
MELINNINAE					
Melinna pacifica McIntosh, 1885	NMNH no. 17421	2	2		
Terebellidae					
AMPHITRITINAE					
Proclea malmgreni (Ssolowiew, 1899)	White Sea, 66°30' N, 33°30' E	5			
Nicolea zostericola (Oersted, 1844)	White Sea, 66°30' N, 33°30' E			2	
ARTACAMINAE					
Artacama proboscidea Malmgren, 1866	White Sea, 66°30' N, 33°30' E	3	2		
POLYCIRRINAE					
Polycirrus medusa Grube, 1850	White Sea, 66°30' N, 33°30' E	4	2		1
THELEPODINAE					
Thelepus crispus Johnson, 1901	NMNH no. 44623	2	1		
Trichobranchidae					
Artacamella hancocki Hartman, 1955	NMNH no. 123316	2			
Terebellides stroemii Sars, 1835	White Sea, 66°30' N, 33°30' E	15	10		2
Trichobranchus glacialis Malmgren, 1865	White Sea, 66°30' N, 33°30' E	1	1		
Pectinariidae					
Pectinaria hyperborea (Malmgren, 1866)	White Sea, 66°30' N, 33°30' E	3	3	1	1
P. koreni (Malmgren, 1866)	White Sea, 66°30' N, 33°30' E	3	3		

specimen of *Ampharete lindstroemii* and of *Pectinaria hyperborea* and *Nicolea zostericola* juveniles were embedded in Epon. They were used for preparation of semithin and thin sagittal sections which were examined with a light microscope and a Jeol JEM 100-CX transmission electron microscope.

Results

Ampharetidae (Figs 1; 2 A – E, G; 3; 4; 5 A–C; 9 C, D)

Tentacular apparatus

In all representatives of the ten species examined the tentacles were attached to the eversible upper lip. When inverted, this lip closely abuts on the dorsal part of the oesophagus and the tentacles attach to it from below. As is evident from ventral dissections, the upper lips vary slightly in shape according to species. The upper lip is semi-cylindrical in *Ampharete finmarchica*, *Amphicteis gunneri antarctica* (Fig. 1 A), and *Melinna pacifica*; its distal edge (facing the intestine when inverted) may be obtuse-triangular (*Ampharete kudenovi,* Fig. 1 B), or almost straight (*A. reducta*). The tentacle bases do not occupy the whole surface of the upper lip, the distal edge of which is tentacle-free. Thus, the upper lip can be divided into two zones: the area of tentacle attachment and the edge of the upper lip which is devoid of tentacles, hence the term free edge. The area of tentacle attachment may stretch along a narrow belt (less than one third of the overall length of the upper lip), as in *Amphicteis gunneri antarctica* (Fig. 1 A). This area may be fairly wide in the genus *Ampharete* (Fig. 1 B). In the transverse section of the oesophagus of *Hypania*

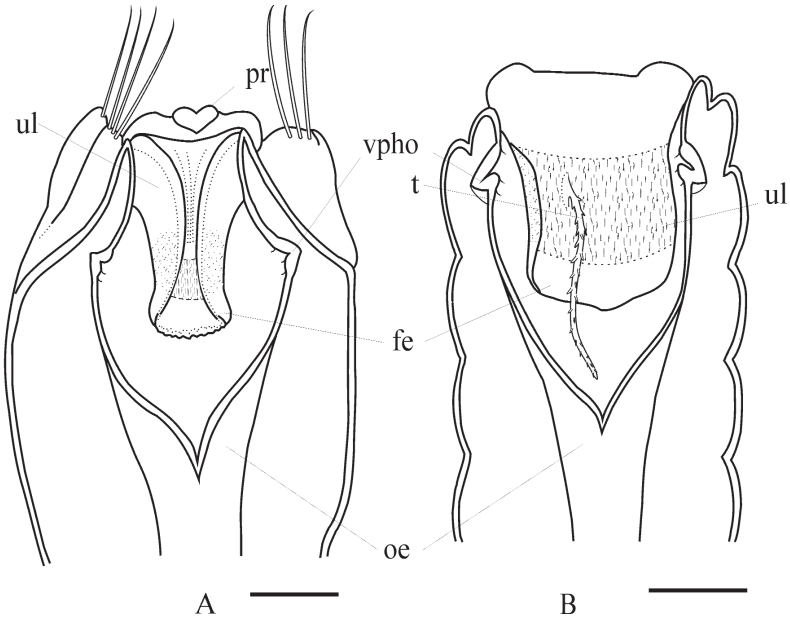

Figure 1 A, B. Ampharetidae dissected from the ventral side to show the inverted upper lip. Most of the tentacles are removed. Zone of buccal tentacle attachment (shaded areas) and free edge can be distinguished. **A**. *Amphicteis gunneri*. **B**. *Ampharete kudenovi*. (*fe*) free edge; (*oe*) oesophagus; (*pr*) prostomium; (*t*) tentacle; (*ul*) upper lip; (*vpho*) ventral pharyngeal organ (dissected). Scale bars: A = 5 mm; B = 2 mm.

Figure 1 A, B. Ampharetidae, dissection en vue ventrale montrant la lèvre supérieure en position introversée. La plupart des tentacules ont été retirés. La zone d'attache des tentacules buccaux (hachurée) et le bord libre sont visibles. **A**. *Amphicteis gunneri*. **B**. *Ampharete kudenovi*. (*fe*) bord libre ; (*oe*) oesophagus ; (*pr*) prostomium ; (*t*) tentacule ; (*ul*) lèvre supérieure ; (*vpho*) organe pharyngien ventral (sectionné). Echelles : A = 5 mm ; B = 2 mm.

invalida, the inverted upper lip is horseshoe-shaped with a small gap below. The surface of the upper lip facing the oesophagus is ciliated (Fig. 2 A, B).

When the upper lip is everted, the tentacles are located on its upper surface and the free edge is situated between the tentacles and the mouth, thus corresponding to the definition of the upper lip by Holthe (1986b). The free edge may be rounded (*Melinna pacifica*, Fig. 2 C), or may form two small longitudinal folds (*Samythella elongata*, Fig. 2 D). The lower surface of the everted upper lip is ciliated; cilia also cover the upper free edge of the upper lip (Fig. 3).

The prostomium is well developed in all the studied species of Ampharetidae and clearly separated from the upper lip by a distinct groove (Figs 2 D, E, G; 3).

Structure of the ventral pharyngeal organ (Figs 2 E, G; 3; 4; 5 A-C)

The pharyngeal organ located in the buccal cavity, ventrally to the oesophagus consists of a bulbous muscle and investing muscle fibres. In all ampharetids examined, the bulbous muscle consists of an anterior and a posterior parts. They are delimited a transverse fold that is subtended by a thin partition crossing the bulbous muscle (Fig. 5 B). The nature of this partition (extracellular matrix, or tonofilaments, or muscle fibre) cannot be determined at present. On a sagittal section of *Ampharete lindstroemii*, the anterior part of the bulbous muscle is about 420 µm long and 140 µm high and the posterior part is about 250 µm long and 150 µm high (Fig. 4).

The pharyngeal organ is covered with the pharyngeal epithelium that lines the large median invagination. The average thickness of this epithelium approximates 12 µm and the nuclei have 7-8 µm in diameter. The epithelium of the anterior part of the bulb is thicker (up to 100 µm high) (Fig. 5 A). The 7.5 µm-thick cuticle consists of an electron-lucent basal cuticle (5.6 µm) and an epicuticle (1.9 µm).

In the posterior part of the bulbous muscle, just near the dorsal invagination, the epithelium forms a narrow transverse ridge composed of glandular cells about 45 µm high. The ridge is separated from the adjacent tissues by a narrow invagination in front and by a deep one from behind (Fig. 5 C).

The bulbous muscle contains transverse muscle cells and interstitial cells. Contractile parts of muscle cells are located at the periphery of the bulb; they are about 12-14 µm high in the upper part of the bulb and about 18-20 µm high in its lower part, while noncontractile parts, in the central zone of the bulb contain nuclei about 10 µm in diameter. Interstitial cells run from the basal lamina of the epithelium down to the internal edge of the bulb. They are fairly thin along the periphery of the bulb and expanded in its central part. These cells have nuclei (12 µm in diameter) and tonofilaments, about 100 µm long, stretching from the epithelium to the ventral edge of the bulbous muscle.

The investing muscle cells form one or two layers below the bulbous muscle. They are about 15-30 µm thick and possess nuclei about 13 µm in diameter.

Morphology of the intestine

A characteristic trait of the intestine morphology, already noted by Fauvel (1897) for *Ampharete acutifrons,* has been found in all examined specimens of *Ampharete* spp.: their intestine envelops the oesophagus at the sides and from below. The same intestinal folds were found also in *Sabellides borealis*. The intestine of other ampharetids (see Table 2) forms no such folds and does not embrace the oesophagus.

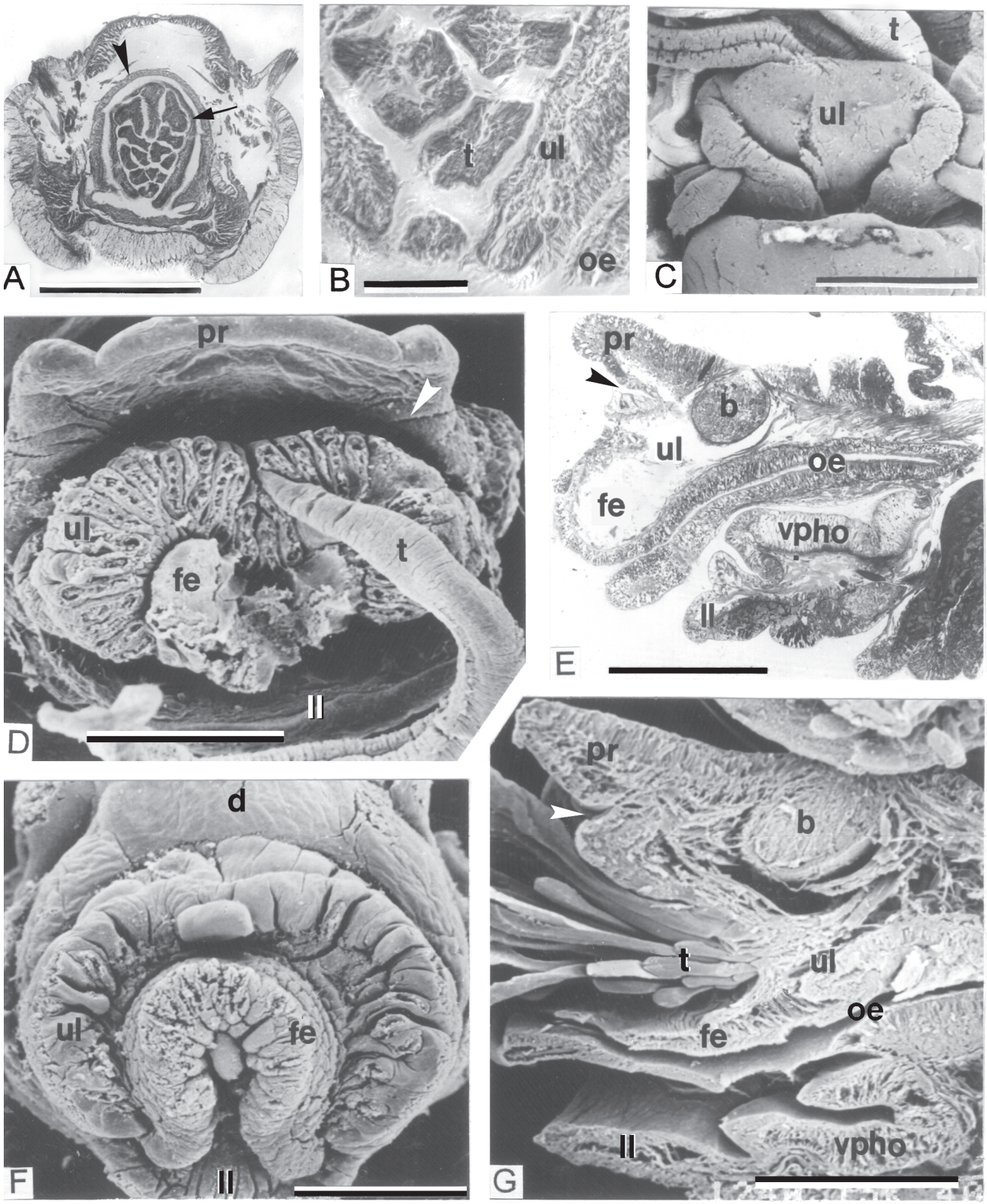
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Figure 2 A, B. *Hypania invalida,* Ampharetidae, histological cross section of the anterior part of the body showing the ciliated oesophagus (*arrowhead* on A), inverted upper lip (*arrow* on A) and buccal tentacles. **C, D, F, G** SEM. **C**. *Melinna pacifica,* Melinninae, ventral view, showing extruded upper lip and buccal tentacles. **D.** *Samythella elongata,* Ampharetinae, anterior view of extruded upper lip showing the free edge and the area of tentacles attachment. The tentacles are removed except one. **E.** *Ampharete lindstroemii,* Ampharetinae, semi-thin parasagittal section of the head, upper lip is extruded. **F.** *Proclea malmgreni,* Terebellidae, anterior view of upper lip and free edge. **G.** *Ampharete finmarchica,* Ampharetinae, sagittal section of the head. Upper lip is extruded. (*arrowhead*) in D and E: prostomium-peristomium border. (*b*) brain; (*d*) dorsal side; (*fe*) free edge; (*ll*) lower lip; (*oe*) oesophagus; (*pr*) prostomium; (*t*) tentacle; (*ul*) upper lip; (*vpho*) ventral pharyngeal organ. Scale bars: **A, E** = 500 µm; **B** = 50 µm; **C** = 1 µm; **D** = 600 µm; **F, G** = 400 µm.

Figure 2 A, B. *Hypania invalida,* Ampharetidae, coupe histologique transversale de la région antérieure du corps montrant l'œsophage cilié (tête de flèche en A), la lèvre supérieure en position interne (flèche en A) et les tentacules buccaux. **C, D, F, G** Microscopie électronique à balayage (MEB). **C**. *Melinna pacifica,* Melinninae, vue ventrale montrant la lèvre supérieure extroversée et les tentacules buccaux. **D.** *Samythella elongata,* Ampharetinae, vue antérieure de la lèvre supérieure extroversée montrant le bord libre et la zone d'attache des tentacules, tous retirés sauf un. **E.** *Ampharete lindstroemii,* Ampharetinae, coupe semi-fine parasagittale de la tête, la lèvre supérieure est extroversée. **F.** *Proclea malmgreni,* Terebellidae, vue antérieure de la lèvre supérieure et du bord libre. **G.** *Ampharete finmarchica,* Ampharetinae, coupe sagittale de la région antérieure, la lèvre supérieure est extroversée. (*tête de flèche*) en D et E : limite prostomium-péristomium ; (*b*) cerveau ; (*d*) côté dorsal ; (*fe*) bord libre ; (*ll*) lèvre inférieure ; (*oe*) oesophage ; (*pr*) prostomium; (*t*) tentacule ; (*ul*) lèvre supérieure ; (*vpho*) bulbe pharyngien ventral. Echelles : **A, E** = 500 µm ; **B** = 50 µm ; **C** = 1 µm ; **D** = 600 µm ; **F, G** = 400 µm.

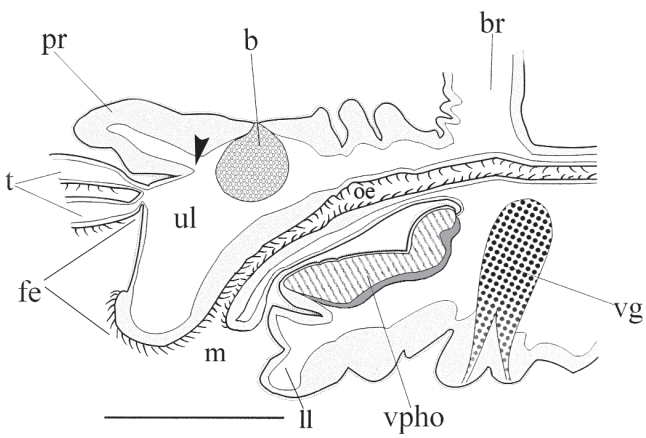


Figure 3. *Ampharete lindstroemii*, parasagittal section of the head, schematic. The upper lip with buccal tentacles is everted. (*arrowhead*) prostomium-peristomium border; *(b)* brain; (*br*) branchiae; (*fe*) free edge of the upper lip; (*ll*) lower lip; (*oe*) oesophagus; (*pr*) prostomium; (*t*) tentacles; (*ul*) upper lip; (*vg*) ventral gland; (*vpho*) ventral pharyngeal organ. Scale bar = 500 µm.

Figure 3. *Ampharete lindstroemii*, coupe parasagittale de la région antérieure, schéma. La lèvre supérieure portant les tentacules est extroversée. (*tête de flèche*) limite prostomium-peristomium ; *(b)* cerveau ; (*br*) branchies ; (*fe*) bord libre de la lèvre supérieure ; (*ll*) lèvre inférieure ; (*oe*) oesophage ; (*pr*) prostomium ; (*t*) tentacules ; (*ul*) lèvre supérieure ; (*vg*) glande ventrale ; (*vpho*) bulbe pharyngien ventral. Echelle = 500 µm.

In both representatives of *Amphicteis* studied (*A. gunneri antarctica* and *A. ninonae*), the blind invagination (coecum) described by Wirén (1885) and Djakonov (1913) is formed on the ventral side of the intestine not far from its beginning. The coecum stretches to the end of the intestine.

Terebellidae (Figs 2F; 5D-F; 6A; 9E, G, H)

Tentacular apparatus

Members of Terebellinae and Thelepodinae have a free edge of the upper lip and an area of tentacle attachment ("tentacular lobe", Hutchings, 1990). These two structures (Fig. 2 F) closely resemble the everted upper lip of Ampharetidae. The free edge of the upper lip is wide and movable; the immovable area of tentacle attachment is situated behind it. The lower surface of the upper lip is ciliated as in ampharetids.

Fine structure of the ventral pharyngeal organ of a juvenile Nicolea zostericola (Fig. 5 D, F)

In the juvenile specimen studied, which had a length of 1,1 mm, the ventral pharyngeal organ is about 70 µm long and 40 µm high. It consists of a bulbous muscle and investing muscle fibres. A transverse fold crosses the middle part of the bulbous muscle that is not subtended by a partition. The fold is about 7 µm deep.

Muscle cells alternate with interstitial cells in the bulbous muscle of *Nicolea zostericola* (Fig. 5 D). On parasagittal sections, the muscle cells reach the height of about 25 µm and have nuclei with a diameter of about 8 µm. The interstitial cells have nuclei measuring 7.5 µm in diameter and contain tonofilaments (Fig. 5 D, F), stretching from the epithelium to the ventral edge of the bulbous muscle.

The thickness of the pharyngeal epithelium that covers the VphO averages 4 µm, but in the anterior part of the bulb, it may reach 12 µm. An epithelial ridge approximately 7 µm high runs along the posterior edge of the bulb. The epithelium that covers the bulbous muscle has a cuticle approximately 0.7 µm thick. The cuticle is serrated, particularly in the anterior region of the bulb and in the area of the posterior ridge.

In adult terebellids the bulbous muscle consists of two parts divided by a thin partition of undetermined nature. Sometimes the pharyngeal organ is fairly extensive, e.g. it reaches a height of 1.3 mm and a length of 1.8 mm in *Thelepus crispus* (Fig. 5 E).

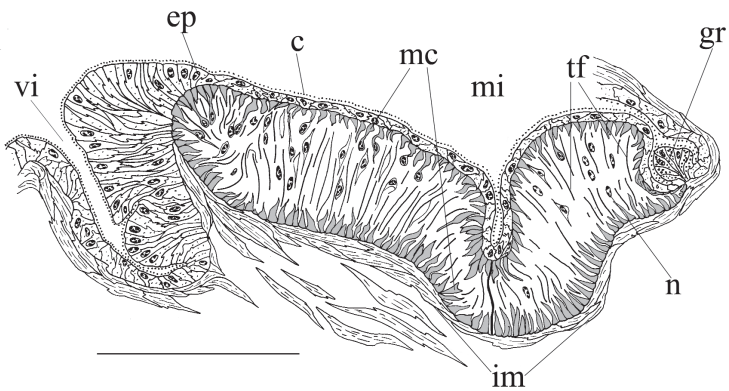


Figure 4. *Ampharete lindstroemii,* drawing of an histological sagittal section of the ventral pharyngeal organ. (*c*) cuticule; (*e*) epithelium; (*gr*) glandular ridge; (*im*) investing muscle; (*mi*) median invagination; (*n*) nucleus; (*mc*) muscle cells; (*tf*) tonofilaments in interstitial cells; (*vi*) ventral invagination. Scale bar = 200 µm.

Figure 4. *Ampharete lindstroemii,* dessin d'une coupe sagittale du bulbe pharyngien ventral. (*c*) cuticule ; (*e*) épithélium ; (*gr*) crête glandulaire ; (*im*) muscle d'enveloppe ; (*mi*) invagination médiane ; (*n*) noyau ; (*mc*) cellules musculaires ; (*tf*) tonofilaments dans des cellules interstitielles ; (*vi*) invagination ventrale. Echelle = 200 µm.

Upper lip in the Artacaminae and Polycirrinae

Members of the Artacaminae (*Artacama proboscidea*) (Figs 5 F, 9 G) are characterized by a prominent anterior extension of their bodies called the proboscis (Holthe, 1986b). The surface of the proboscis is covered with papillae. The mouth and other structures, which normally have a frontal position, are shifted to the dorsal side. Nevertheless, the upper lip looks like that of the Terebellinae with a free edge distinct from the zone of tentacle attachment (Dales, 1955). The small ventral pharyngeal organ is about 320 µm long.

In *Polycirrus medusa* (Polycirrinae), the upper lip is fairly long, wide and movable. It is trefoil-shaped with the central lobe larger than the lateral ones. Each lobe is longitudinally folded forming an almost closed groove (Fig. 6 A, arrowheads). The ventral surface of the upper lip is ciliated (Fig. 9 H). The zone of tentacle attachment expands almost all over the dorsal surface of the upper lip, leaving free only a narrow belt on the peripheral edge (Fig. 6 A). The ventral pharyngeal organ is relatively small. It reaches about 380 µm in length and 180 µm in height.

Trichobranchidae (Figs 6 B, C; 7; 9 H)

Tentacular apparatus

In *Terebellides stroemii* the upper lip is less developed than in the Polycirrinae, but much more developed than in the Terebellinae. It has a narrow free edge with a band of short cylindrical tentacles along it. The ventral surface of the upper lip is ciliated. It is folded and forms one longitudinal groove (Fig. 6 B).

In *Trichobranchus glacialis* the upper lip is smaller than in the previous species and only slightly larger than in terebellins. It forms two shallow grooves (Fig. 6 C).

A relatively small ventral pharyngeal organ is present in both species examined.

Structure of the intestine

In *Terebellides stroemii*, numerous folds of the anterior intestine envelop the oesophagus forming the "digestive gland" (Wirén, 1885, Michel et al., 1984). In *Trichobranchus glacialis* the anterior intestine also envelops the oesophagus in two or three folds, but the digestive gland is not so distinct. In *Artacamella hancocki* the intestine also forms two folds around the oesophagus (Fig. 7).

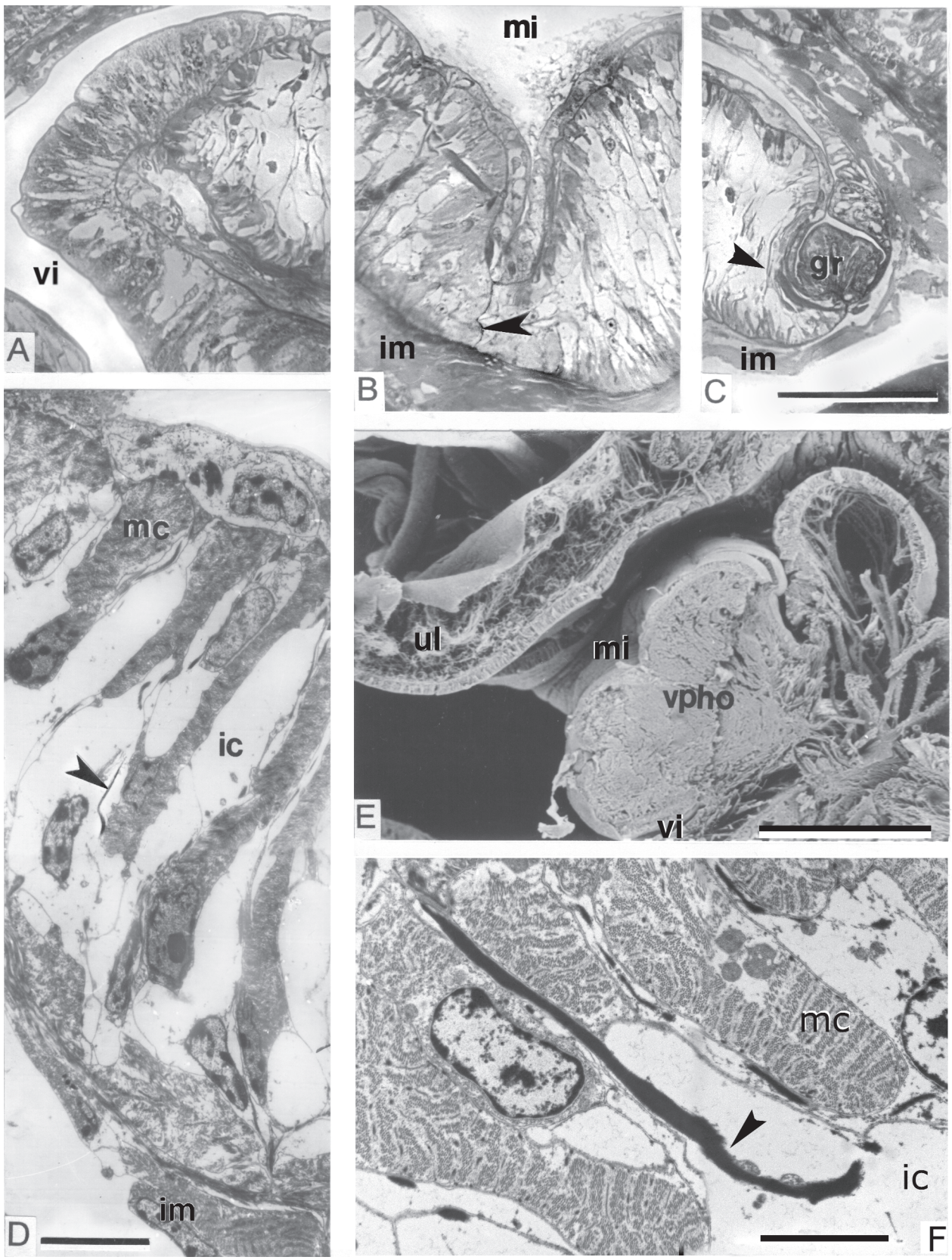
Pectinariidae (Figs 8; 9 B)

Tentacular apparatus

In both species examined (Table 2), the buccal tentacles are attached to the ventral surface of the cephalic veil. No structures resembling the solid upper lip with extended free edge like in terebellids and ampharetids have been found between the tentacles and the mouth. The upper lip is represented only by the zone of tentacle attachment. The

Figure 5. A-C. *Ampharete lindstroemii,* Ampharetinae, sagittal histological section of the ventral pharyngeal organ. **A.** Anterior part, **B.** Median part, showing the partition (*arrowhead*) dividing VPhO into two areas, **C.** posterior part with glandular ridge at the end of median invagination, (*arrowhead*) interstitial cells containing tonofilaments. **D, F.** *Nicolea zostericola*, Terebellidae, sagittal section of the pharyngeal organ, TEM. **E.** *Thelepus crispus,* Terebellidae, sagittal section of the head, SEM. (*di*) dorsal invagination; (*gr*) glandular ridge; (*ic*) interstitial cell containing tonofilaments (*arrowhead*); (*im*) investing muscle; (*mc*) muscle cell; (*mi*) median invagination; (*ul*) upper lip; (*vi*) ventral invagination; (*vpho*) ventral pharyngeal organ. Scale bars: **A** – **C** = 500 µm; **D** = 10 µm; **E** = 1 mm; **F** = 5 µm.

Figure 5. A-C. *Ampharete lindstroemii,* Ampharetinae, coupe sagittale du bulbe pharyngien. **A.** Partie antérieure, **B.** Partie moyenne, montrant la cloison (*tête de flèche*) qui partage le muscle bulbaire en deux parties, **C.** Partie postérieure montrant la crête glandulaire au fond de l'invagination médiane et les cellules interstitielles contenant des tonofilaments (*tête de flèche*) ; **D, F.** *Nicolea zostericola*, Terebellidae, coupe sagittale du bulbe pharyngien MET. **E.** *Thelepus crispus,* Terebellidae, coupe sagittale de la région antérieure, MEB. (*di*) invagination dorsale ; (*gr*) crête glandulaire ; (*ic*) cellule interstitielle contenant des tonofilaments (*arrowhead*); (*im*) muscle d'enveloppe; (*mc*) cellule musculaire ; (*mi*) invagination médiane ; (*ul*) lèvre supérieure ; (*vi*) invagination ventrale ; (*vpho*) bulbe pharyngien. Echelles : **A** – **C** = 500 µm ; **D** = 10 µm ; **E** = 1 mm ; **F** = 5 µm.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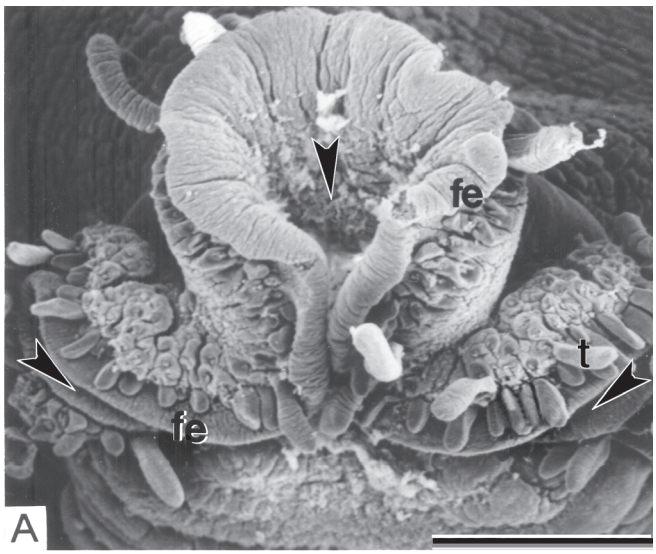
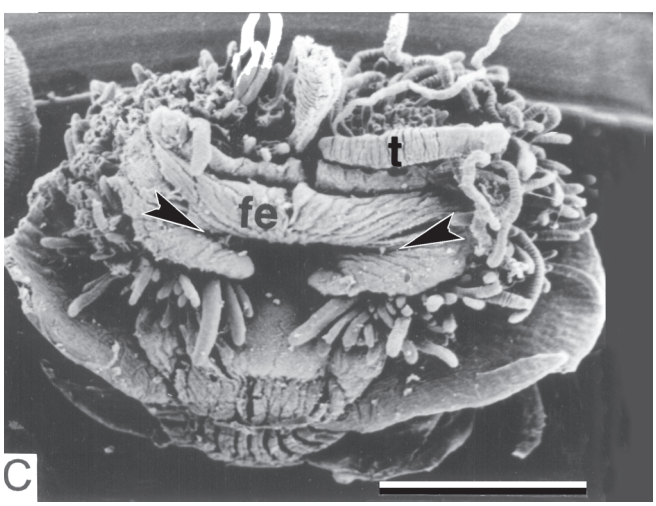




cephalic veil is situated behind the tentacles. The zone of tentacle attachment is curved and forms two arcs above the mouth. Their lower edges are located on the level of the mouth or even protrude slightly below it, thus imitating a complete encircling of the mouth by the tentacles (Fig. 8 C).

Fine structure of the pharyngeal organ of the early juvenile Pectinaria hyperborea *(Fig. 8 A, B).*

The length of this juvenile was 1 mm. The pharyngeal organ consists of a bulbous muscle and investing muscle cells. A tongue-like organ is lacking and there is no dorsal invagination. The ventral (about 20 µm long) and dorsal parts (about 12 µm long) of the pharyngeal organ are separated by the median invagination. There is ventrally a small ventral invagination. The investing muscle cells are 2-5 µm thick. Their nuclei (4.5-5.5 µm in diameter) are located in the dorsal part of the pharyngeal organ.

The bulbous muscle contains about 20 muscle cells and 1-2 interstitial cells. The latter contain no visible tonofilaments and have an electron-lucent cytoplasm and nuclei 3.5-4 µm large. There is no transverse fold in the bulbous muscle. The sagittal section shows that the dorsal part of the bulb is built of three layers of investing muscle cells and a group of three transverse muscle cells.

The pharyngeal organ is covered with an epithelium with an average thickness of 1.5-3 µm (5 µm in the dorsal part) and with spherical nuclei about 2-µm in diameter. The thickness of the cuticle is about 0.4 µm.

In an adult worm the pharyngeal bulb consists of an anterior and a posterior parts. The former is about 40 µm and the latter is about 35 µm long.

Figure 6. A-C SEM**. A**. *Polycirrus medusa,* Terebellidae, anterior view showing the free edge of the upper lip, which forms three grooves (*arrowheads*). Most of the buccal tentacles are removed. **B.** *Terebellides stroemii,* Trichobranchidae, anterior view, the free edge of the upper lip forms one groove (*arrowhead*). Buccal tentacles removed as in A. **C.** *Trichobranchus glacialis,* Trichobranchidae, anterior view, the free edge of the upper lip forms two grooves (*arrowheads*). (*fe*) free edge of the upper lip; (*t*) buccal tentacles. Scale bars: **A, C** = 800 µm; **B** = 400 µm.

Figure 6. A-C MEB**. A**. *Polycirrus medusa,* Terebellidae, vue antérieure montrant le bord libre de la lèvre supérieure formant trois sillons (*têtes de flèches*). La plupart des tentacules ont été retirés. **B.** *Terebellides stroemii,* Trichobranchidae, vue antérieure : le bord libre de la lèvre supérieure forme un seul sillon (*tête de flèche*). Tentacules retirés comme en A. **C.** *Trichobranchus glacialis,* Trichobranchidae, vue antérieure : le bord libre de la lèvre supérieure forme deux sillons (*têtes de flèches*). (*fe*) bord libre de la lèvre supérieure ; (*t*) tentacules buccaux. Echelles: **A, C** = 800 µm ; **B** = 400 µm.

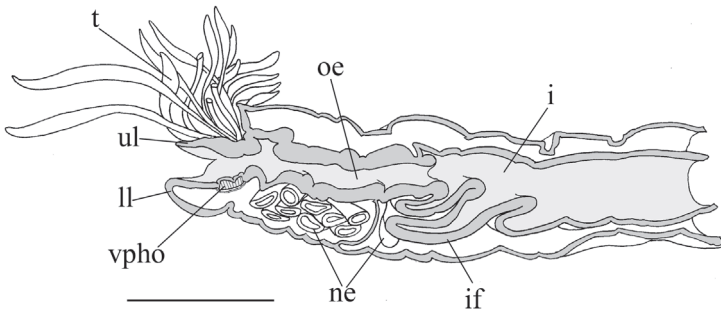


Figure 7. *Artacamella hancocki,* Trichobranchidae, sagittal section of the anterior part of the body, drawing. (*i*) intestine; (*if*) intestinal folds; (*ll*) lower lip; (*ne*) nephridia; (*oe*) oesophagus; (*t*) buccal tentacles; (*ul*) upper lip; (*vpho*) ventral pharyngeal organ. Scale bar = 1 mm.

Figure 7. *Artacamella hancocki,* Trichobranchidae, dessin d'une coupe sagittale de la partie antérieure du corps. (*i*) intestin ; (*if*) repli de l'intestin ; (*ll*) lèvre inférieure ; (*ne*) néphridies ; (*oe*) oesophage ; (*t*) tentacules buccaux ; (*ul*) lèvre supérieure ; (*vpho*) bulbe pharyngien. Echelle = 1 mm.

Discussion

In general, the organization of the feeding apparatus is similar in all members of the Terebellida. All of them have buccal tentacles attached to the upper lip, and all have a ventral pharyngeal organ in the buccal cavity. However, some details differ both among and within the families. To simplify the discussion, we consider two groups of these structures: the tentacular apparatus itself and the organs of the buccal cavity comprising the pharyngeal organ and the ciliated epithelium that covers the inner surface of the upper lip and the dorsal part of the pharyngeal cavity.

Location of the buccal tentacles and shape of the upper lip

Members of Ampharetinae and Melinninae (Ampharetidae) have a feeding apparatus of a similar construction. The entire upper lip is eversible; the area of tentacle attachment occupies 1/2 to 1/3 of its overall surface. The arrangement of the feeding apparatus is the same in Alvinellidae (Zhadan et al., 2000). The well developed prostomium, which is typical for all Ampharetidae, allows us to define its border with the peristomium behind the zone of tentacle attachment (Figs 2 D, E, G; 3). It means that both tentacles and upper lip of the Ampharetidae belong to the peristomium.

The prostomium of Terebellidae and Trichobranchidae is reduced and fused with the peristomium; the exact position of the border between them could be hardly defined in adults. The arrangement of the tentacular apparatus is more variable in representatives of Terebellidae. The following patterns are observed: a) the free edge of the upper lip is wide and movable; the immovable area of tentacle attachment is situated behind the free edge (Terebellinae, Thelepodinae, Fig. 9 E, and Artacaminae, Fig. 9 G); b) the upper lip is very large and movable, its free edge is narrow; the tentacles occupy almost the entire upper surface of the lip and move together with it (Polycirrinae, Fig. 9 H).

In the Artacaminae the mouth and associated structures are located on the dorsal side of the body because of the enormous frontal proboscis. Nevertheless, the animals have numerous buccal tentacles and their upper lip looks like that of the Terebellinae with a free edge distinct from the zone of tentacle attachment (Fig. 9 G).

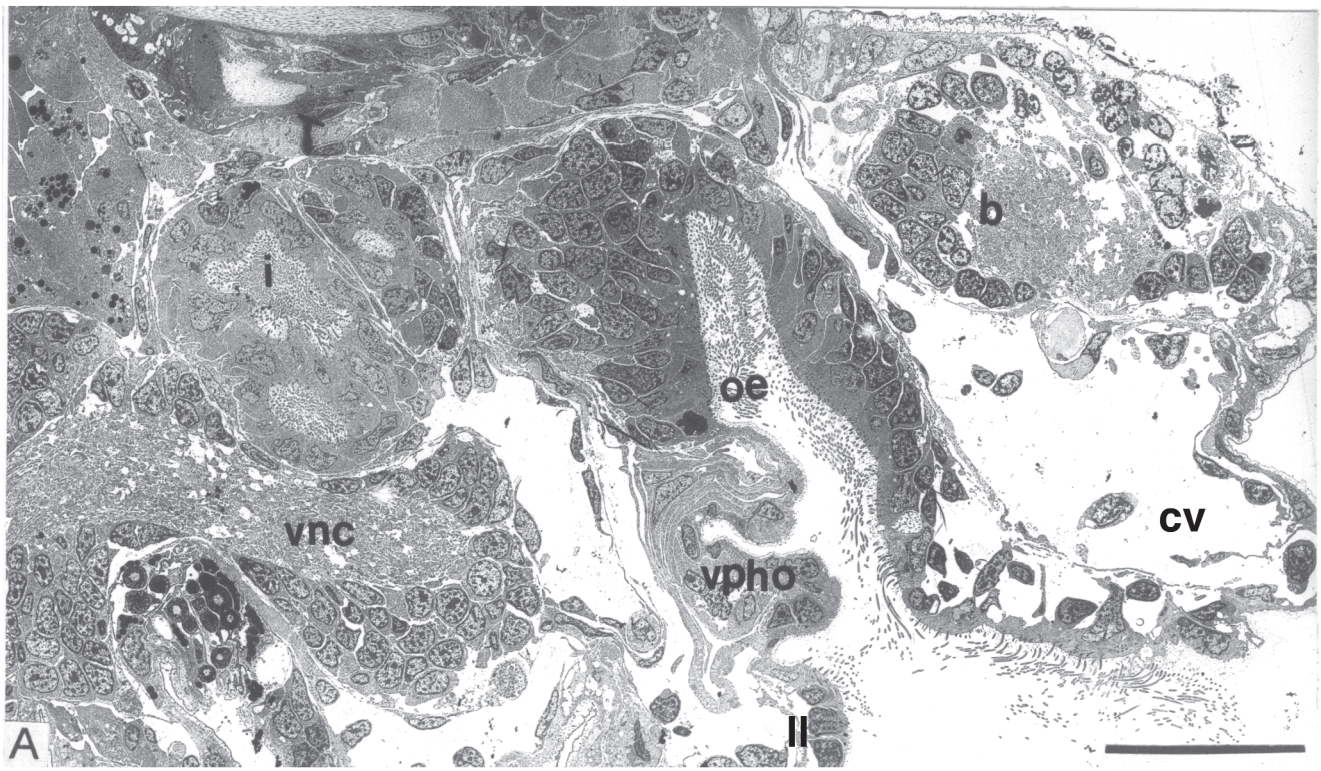
In the Trichobranchidae the shape of the upper lip is intermediate between the Terebellinae and Polycirrinae. In *Terebellides stroemii*, the upper lip is expanded and in contrast to that of *Polycirrus medusa*, it does not form trefoil lobes. The upper lip in *Trichobranchus glacialis* is only slightly larger than in species of Terebellinae and has a relatively wide free edge. In the Terebellidae and Trichobranchidae neither parts of the upper lip, nor tentacles are able to invert into the buccal cavity.

In the Pectinariidae the free edge of the upper lip is not developed and the buccal tentacles are attached to the ventral side of the cephalic veil around the mouth. Tentacles inverted into the buccal cavity were never observed.

The histological structure of the upper lip is similar in all examined families. Its ventral surface and free edge are ciliated, whereas the area of tentacle attachment is not ciliated. This feature favours the concept of homology of the upper lip in all the Terebellida.

In spite of the diversity of the buccal apparatus in different groups, a transitional pattern can be proposed (Fig. 9). The question is, what position of the upper lip could be considered plesiomorphic. We may suppose that the upper lip originated from the bulging body wall at the antero-dorsal edge of the buccal cavity, where the ciliated epithelium gives way to the nonciliated external one. In this case, the external position of the upper lip, as in the Terebellidae and Ampharetidae with everted tentacles, is the plesiomorphic state. The development of the upper lip is significant for the expansion of the area of tentacle attachment. The tendency continued with the development of the long and wide upper lip (tentacular lobe) of trichobranchids and polycirrins. Another evolutionary trend is the development of an introverted upper lip in ampharetids and alvinellids. The ability of the upper lip to invert (turn inside the mouth) seems to be a synapomorphy for these two families. This ability could ensure protection of tentacles from injuries by predators and mechanical damage during crawling.

The state of the pectinariid buccal apparatus is uncertain. The buccal tentacles are located directly on the lower surface of the cephalic veil. The question whether pectinariids have experienced a reduction of the free edge of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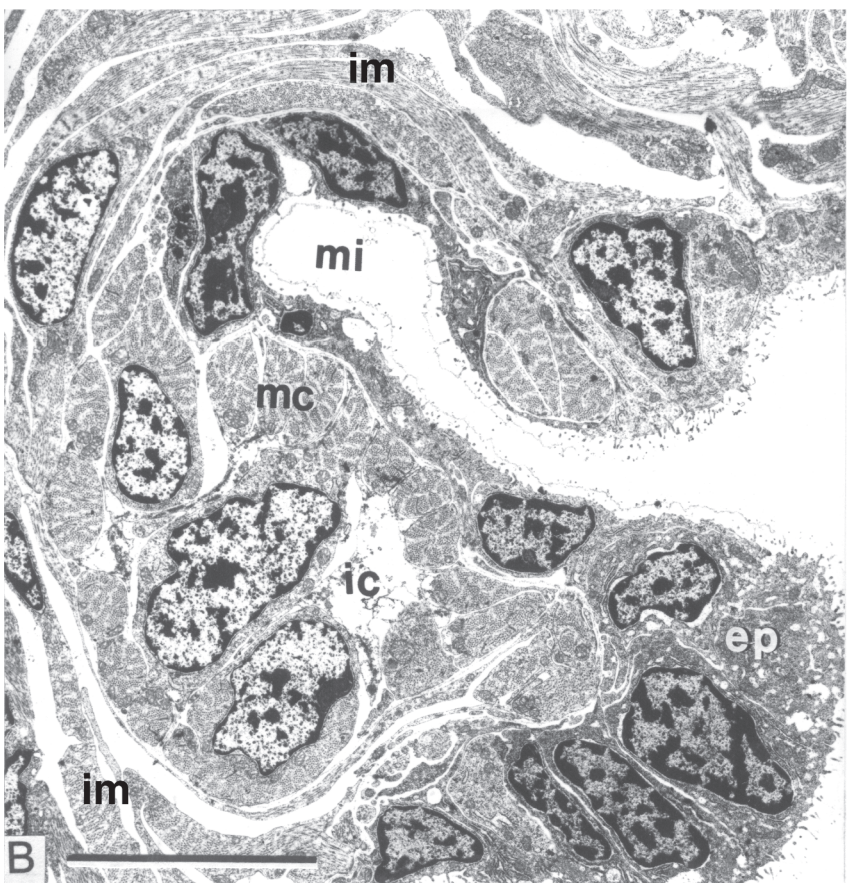
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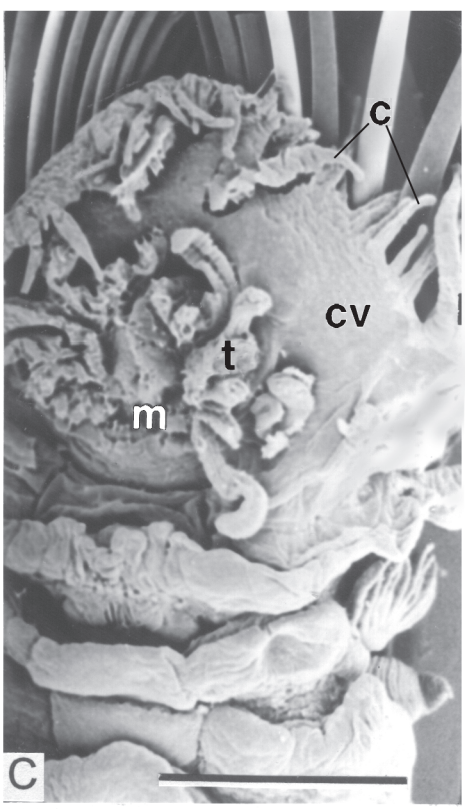
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Figure 8. A, B. *Pectinaria hyperborea,* Pectinariidae, juvenile, TEM. **A.** Sagittal section of the anterior part of the body (anterior end on the right). **B.** Detail of the ventral pharyngeal organ. **C.** *Pectinaria koreni,* Pectinariidae, anterior view. (*b*) brain; (*c*) peripheral cirri of the cephalic veil; (*cv*) cephalic veil; (*ep*) epithelium; (*i*) intestine; (*ic*) interstitial cell; (*im*) investing muscle; (*m*) mouth; (*mc*) muscle cells; (*mi*) median invagination; (*oe*) oesophagus; (*t*) buccal tentacles; (*vnc*) ventral nerve cord; (*vpho*) ventral pharyngeal organ. Scale bars: **A** = 20 μm; **B** = 5 μm; **C** = 1 mm.

Figure 8. A, B. *Pectinaria hyperborea,* Pectinariidae, juvénile, MET. **A.** Coupe sagittale de la partie antérieure du corps (l'avant est à droite). **B.** Détail du bulbe pharyngien. **C.** *Pectinaria koreni,* Pectinariidae, vue de la région antérieure. (*b*) cerveau ; (*c*) cirres périphériques du voile céphalique ; (*cv*) voile céphalique ; (*ep*) épithélium ; (*i*) intestin ; (*ic*) cellule interstitielle ; (*im*) muscle d'enveloppe ; (*m*) bouche ; (*mc*) cellules musculaires ; (*mi*) invagination médiane ; (*oe*) oesophage ; (*t*) tentacules buccaux ; (*vnc*) chaîne nerveuse ventrale ; (*vpho*) bulbe pharyngien. Echelles : **A** = 20 μm ; **B** = 5 μm ; **C** = 1 mm.

the upper lip or whether their state is plesiomorphic still has no answer.

Orrhage (2001) homologized the pectinariid cephalic veil with the ampharetid prostomium (= tentacular membrane). Our data confirm Orrhage's conclusion on the cephalic veil homology. Its position corresponds to that of the ampharetid prostomium. The brain of pectinariids is located at the base of the cephalic veil (Fig. 8 A) and the brain of ampharetids is located at the base of the prostomium (Fig. 2 E, G).

Combining the plesiomorphic characteristics could produce the image of the anterior part of the body of the hypothetical common ancestor of all Terebellida. According to Holthe (1986a), its prostomium was well developed and the tentacles could be retracted. We suppose that it had a well developed prostomium but, on the contrary, non-retractable tentacles at the border of the peristomium (Fig. 9).

Ciliated structures in the buccal cavity

In all species examined, the dorsal and lateral surfaces of the buccal cavity are covered with a ciliated epithelium. It covers the lower surface of the upper lip and runs up to the ciliated epithelium of the oesophagus. There is always a gap between the ciliated surface of the upper lip and the ciliated grooves of the buccal tentacles (Fig. 3).

In alvinellids, a ciliated-glandular dorsal organ is located on the dorsal surface of the buccal cavity and oesophagus (Desbruyères & Laubier, 1993). This organ represents a number of folds of the oesophageal dorsal wall covered with a thickened glandular ciliated epithelium (Saulnier-Michel et al., 1990; Zhadan et al., 2000). Some ampharetids (e.g., *Ampharete finmarchica*) also have ciliated folds of the dorsal part of the oesophagus (pers. unpublished data). In adult Terebellidae, the ciliated fields of the upper lip and the pharyngeal cavity serve for the transport of food from tentacles into oesophagus (Dales, 1955; Sutton, 1957). In juveniles, the ciliated field covering the buccal cavity and the rudimentary upper lip, along with the unciliated pharyngeal organ, takes part in food gathering and forming the food bolus (Tzetlin, 1987). The exact position, structure and functions of the ciliated fields covering the pharyngeal cavity and the upper lip (including the dorsal organ in the Alvinellidae) correspond to those of the dorso-lateral folds of other polychaetes (Purschke & Tzetlin, 1996). Consequently, the ciliated fields must be homologous to those folds.

Ventral pharyngeal organ (VPHO)

In all the terebellid families, the ventral pharyngeal organ consists of an investing muscle and a bulbous muscle. In contrast to *Protodrilus hypoleucus* (see Jouin, 1978), *Ctenodrilus serratus* and juvenile of *Scoloplos armiger* (see Purschke, 1988), a grating plate system, or tongue-like organ, is lacking in the Terebellida, as it is, for instance, in the Dinophilidae (Purschke, 1985). The VPhO is divided into two parts by a deep transversal fold. The pharyngeal organ of many examined terebellids has a partition running from the epidermal epithelium of the transversal fold down to the investing muscles and dividing the bulb into two parts. The nature of this partition is still undefined. Its location is very similar to that of the pillar muscle described by Sutton (1957) in the "transverse muscle" of *Terebella lapidaria*. No such partition has been found in the juvenile specimens of *Nicolea zostericola* and *Pectinaria hyperborea*, though it is distinct on the sagittal sections of the adult ampharetids, terebellids and alvinellids (Fig. 5 B, E; Zhadan et al., 2000, figs 5b, 10a).

The bulbous muscle of the Terebellida is composed of muscular and interstitial cells. Purschke (1988) considers this trait to be primitive. The structure of the VPhO is similar in many families, such as the Spionidae, Poecilochaetidae, Cirratulidae, Orbiniidae, Ctenodrilidae, Flabelligeridae, and Poeobiidae (Purschke, 1988). The epithelium of the terebellid pharyngeal organ contains no glandular cells common to Orbiniidae and Ctenodrilidae. In *Ampharete lindstroemii*, glandular cells are accumulated in the posterior ridge, reflecting one of the evolutionary trends in the development of the VPhO in the Polychaeta (Purschke, 1988). A posterior ridge has also been found in *Nicolea zostericola*, though its glandular nature is not obvious. No such ridges have been observed in other members of the Terebellida.

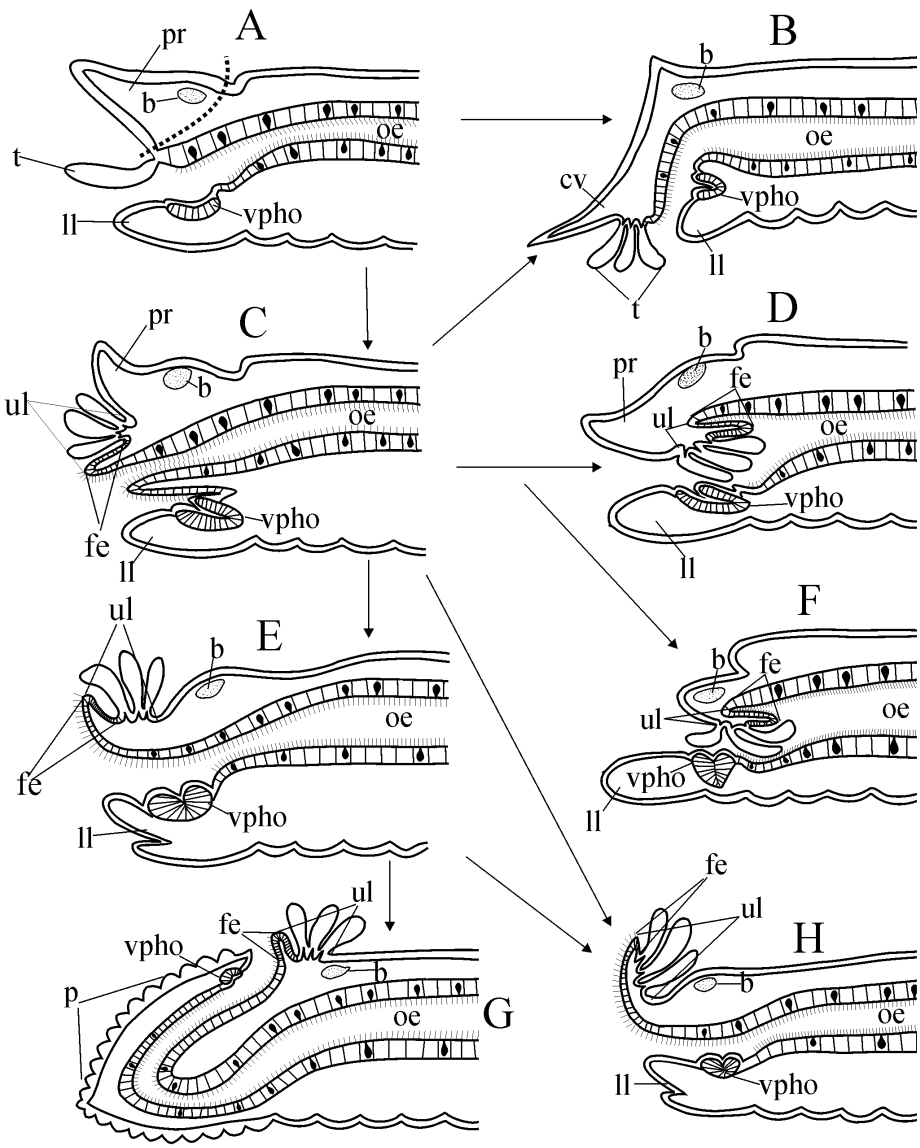

Figure 9. Hypothetical morphological sequences illustrating possible evolutionary pathways of changes in the buccal apparatus of the Terebellida. **A.** Hypothetical common ancestor with a developed prostomium (limited by a dotted line) and tentacles on the border of peristomium. **B.** Developed cephalic veil and numerous tentacles near the mouth (Pectinariidae). **C.** and **D.** Two different possible positions of the upper lip in the family Ampharetidae; prostomium and upper lip are developed, numerous tentacles are located on the upper lip with a wide free edge: **C.** Upper lip is everted, **D.** Upper lip is inverted into the pharyngeal cavity. **E.** Reduced prostomium and developed non-inversible upper lip (Terebellinae, Thelepinae). **F.** Reduced prostomium, upper lip inversible (Alvinellidae). **G.** Reduced prostomium, well-developed non-inversible upper lip, the anterior part of the body is pushed into the proboscis, covered with papillae (Artacaminae). **H.** Upper lip is non-inversible, very large and movable; the free edge is narrow, the tentacles move together with the upper lip (Polycirrinae). (*b*) brain; (*cv*) cephalic veil; (*fe*) free edge of upper lip; (*ll*) lower lip; (*oe*) oesophagus; (*p*) papillae; (*pr*) prostomium; (*t*) buccal tentacles; (*ul*) upper lip; (*vpho*) ventral pharyngeal organ.

Figure 9. Série hypothétique illustrant l'évolution possible des changements morphologiques intervenus dans l'appareil buccal de différentes familles de Terebellida. **A.** Ancêtre commun hypothétique ayant un prostomium développé (limité par une ligne en pointillé) et des tentacules à la limite du péristomium. **B.** Voile céphalique developpé et nombreux tentacules près de la bouche (Pectinariidae). **C.** et **D.** Deux positions possibles de la lèvre supérieure chez les Ampharetidae ; prostomium et lèvre supérieure sont développés, de nombreux tentacules sont situés sur la lèvre supérieure qui possède un large bord libre : **C.** Lèvre supérieure extroversée, **D.** Lèvre supérieure introversée dans la cavité pharyngienne. **E.** Prostomium réduit et lèvre supérieure développée non introversible (Terebellinae, Thelepinae). **F.** Prostomium réduit, lèvre supérieure introversible (Alvinellidae). **G.** Prostomium réduit, lèvre supérieure bien développée, non-introversible, la partie antérieure du corps est poussée dans le proboscis, couvert de papilles (Artacaminae). **H.** lèvre supérieure non introversible, très grande et mobile; le bord libre est étroit, les tentacules sont mobilisés en même temps que la lèvre supérieure (Polycirrinae). (*b*) cerveau ; (*cv*) voile céphalique ; (*fe*) bord libre de la lèvre supérieure ; (*ll*) lèvre inférieure ; (*oe*) oesophage ; (*p*) papilles ; (*pr*) prostomium ; (*t*) tentacules buccaux ; (*ul*) lèvre supérieure ; (*vpho*) bulbe pharyngien.

Development of tonofilaments in the interstitial cells of the VPhO is one more trend in the evolution of the VPhO in polychaetes (Purschke, 1988), observed in Ampharetidae and Terebellidae. The presence of tonofilaments in the interstitial cells of Trichobranchidae and Alvinellidae is still under question. Another tendency is the reduction of both interstitial cells and tonofilaments which probably occurs in the Pectinariidae (only one interstitial cell and no tonofilaments are seen on the sagittal section of the juvenile pharyngeal organ, though the structure of adult VPhO may be quite different).

Homology of the buccal tentacles

There are two views on the origin and homology of the buccal tentacles in the Terebellida (see above). 1. Buccal tentacles are homologous to the paired palps of other polychatetes (Binard & Jeener, 1928; Fauchald & Rouse, 1997). 2. Buccal tentacles originate from unknown structures of the alimentary canal such as pharyngeal papillae (Holthe, 1986a) or outgrowths of the dorsal lip (Orrhage, 2001).

According to our data, in adult Terebellida the buccal tentacles are not connected with the pharyngeal ciliated field, i.e., with the dorso-lateral folds of other polychaetes. The buccal tentacles of all Terebellida families are situated on the outer surface of the upper lip, which more probably belongs to the peristomium (see above).

Data on ontogenesis also demonstrate that the tentacles of the Terebellida develop as peristomial or prostomial appendages (Cazaux, 1972, 1982; Eckelbarger, 1974; Heimler, 1983; Clavier, 1984; Desbruyères & Laubier, 1986; Tzetlin, 1987; Lambert et al., 1996), independently from any pharyngeal structures. These data support the hypotheses according to which the buccal tentacles are homologous to the paired palps of other polychaete families (Binard & Jeener, 1928; Fauchald & Rouse, 1997).

One more indirect argument is provided by data on the internal morphology. A few characters are shared by the Terebellida and two families having paired palps, the Cirratulidae and Flabelligeridae. These taxa have a gular membrane, heart body, similar construction of the vascular system and a ventral pharyngeal organ (Rouse & Fauchald, 1997). The only known family with representatives possessing pharyngeal tentacles is the Cossuridae (Tzetlin, 1994) with a rather different organization.

Orrhage's point of view on the origin and homology of the buccal tentacles of the Terebellida is based on the study of their innervation. The investigation of innervation is the most important tool for defining the homology of organs. At the same time, the conclusions drawn by Orrhage (2001) contrast with the distribution of a number of other anatomical characters, including patterns of the pharyngeal ciliature, discussed in the present paper and, finally, with developmental evidences.

Thus the question of the buccal tentacles origin is still under scientific debates, and further developmental and anatomical studies of the Terebellida are required.

Acknowledgements

We are indebted to Dr. Igor Zhirkov (Hydrobiology Department of Moscow State University) and Ms. Linda Ward (NMNH) for providing access to terebellid collections; the crews of R/V Kartesh and R/V Kuznetsov (Zoological Institute, St. Petersburg) for their help in sampling. We are grateful to Dr. Kristian Fauchald, Dr. Günter Purshke, and Anna Stein for various kinds of support during our work at the Smithsonian Institution (USA) and the University of Osnabrück (Germany). We would like to thank Dr. K. Fauchald for fruitful discussion at the initial stage of the project, Dmitry Milyutin for supplying us with a paraffin section of *Hypania invalida,* and Anastasia Popovkina and Joen Turnbull for reviewing the English version of the manuscript. We express our gratitude to the anonymous reviewers and the Executive Editor of CBM Dr. Jouin-Toulmond for valuable comments and help.

The work was supported by the following grants: Leonard Euler's Program (Germany), Russian Foundation for Basic Research N° 98-04-49950 and 01-04-49093 and the Smithsonian Institution's Short Visit Program.

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