Hydrobiologia **496:** 269–278, 2003.
E. Sigvaldadóttir, A.S.Y. Mackie, G.V. Helgason, D.J. Reish, J. Svavarsson, S.A. Steingrímsson & G. Guðmundsson (eds), Advances in Polychaete Research.

Comparative study of the diaphragm (gular membrane) in Terebelliformia (Polychaeta, Annelida)

Anna E. Zhadan & Alexander B. Tzetlin
Department of Invertebrate Zoology, Biological Faculty, Moscow State University, Moscow, 119992, Russia
Fax: (7095) 939-4309. E-mail: azhadan@mail.ru; tzetlin@soil.msu.ru

Key words: diaphragm, coelom, anatomy, ultrastructure, Terebelliformia

Abstract

The structure and location of the diaphragm (gular membrane) was studied in five families of Terebelliformia: Terebellidae, Trichobranchidae, Pectinariidae, Ampharetidae and Alvinellidae, using dissections, histology, and scanning and transmission electron microscopy. Position, shape, and structure of the diaphragm differ in these taxa. In Terebellidae and Pectinariidae the diaphragm is straight. In Trichobranchidae, Ampharetidae and Alvinellidae it is funnel-shaped. Diaphragm possesses two contractile sacs in Terebellidae and Pectinariidae, one in Alvinellidae and none at all in Trichobranchidae. The relative size and form of the sacs varied. Representatives of the family Ampharetidae have one or two sacs or none at all. Four kinds of the diaphragm can be distinguished: strait with two sacs, funnel-shaped with two sacs, funnel-shaped with one sac, funnel-shaped without sacs. In some Alvinellidae, the diaphragm is fenestrated, while in all other taxa it is continuous. The wall of the sacs is more muscular than the wall of the remaining diaphragm. The diaphragm is attached to the body wall at different levels: between the third and fourth segments in pectinariids or between the fourth and fifth in terebellids, ampharetids, alvinellids and trichobranchids. In most cases, the diaphragm contains two coelothelial layers with a well-developed extracellular matrix in between, and one or two muscle layers. The maximum development of the muscle fibres occurs in Terebellidae; probably related to the length of buccal tentacles. Significance of morphological and ultrastructural peculiarities of the diaphragm is discussed.

Introduction

The diaphragm (gular membrane) is one of the important characteristics of internal anatomy in Terebelliformia. It is an anterior septum that distinctly differs from other septa. The presence of a diaphragm in Polychaeta is often connected with such eversible structures as a pharynx, palps, and tentacles (Fauchald & Rouse, 1997). In addition, the diaphragm divides the anterior coelom where funnels of excretory nephridia open, from posterior one where gametes mature and funnels of gonoducts are located (Smith, 1992).

Although the diaphragm has been found in all terebelliform polychaetes (Hessle, 1917; Fauchald & Rouse, 1997), its structure has been poorly studied. According to Meyer (1887) and Hessle (1917), in Ampharetidae and Terebellidae the diaphragm attaches to the body wall between the fourth and the fifth segments and in Pectinariidae between the third and the fourth ones. In Terebellidae, the diaphragm is a straight partition with two blind muscular expansions. They contract and pump coelomic fluid in the cavity of the buccal tentacles, thus providing for their extension (Meyer, 1887). In *Melinna* sp. (Ampharetidae) only one such expansion was observed (Hessle, 1917). Hessle (1917) supposed that the relatively short buccal tentacles of ampharetids and pectinariids extend due to contraction of the whole diaphragm as he did not observe the muscular expansions. In many Terebelliformia, especially in *Terebellides* (Trichobranchidae), diaphragm is funnel-shaped. According to Heimler (1983), the diaphragm appears in aulophora larvae of *Lanice conchilega* (Pallas) between the third and the fourth chaetigers simultaneously with the first tentacle. He supposed that prediaphragmal section was represented by the larval segments.

In Alvinellidae the diaphragm looks like a sac with a rear blind projection covering the anterior part of the digestive and vascular systems. In *Alvinella pompejana* Desbruyeres & Laubier, *A. caudata* Desbruyeres & Laubier, *Paralvinella palmiformis* Desbruyeres & Laubier, and *P. grasslei* Desbruyeres & Laubier the diaphragm is fenestrated and coelomocytes can penetrate through numerous openings (Jouin-Toulmond et al., 1996; Zhadan et al., 2000). In *Paralvinella dela* Detinova and *P. pandorae pandorae* Desbruyeres & Laubier no holes were observed in diaphragm (Zhadan et al., 2000). The diaphragm wall in Alvinellidae consists of two epithelial layers with an extra-cellular matrix between them (Jouin-Toulmond et al., 1996). No data on the ultrastructure of the diaphragm in the other terebelliform families is available.

The present study was aimed at investigation of the variety of the shape and structure of the diaphragm in representatives of different Terebelliformia taxa.

Materials and methods

Twenty-four species of Terebelliformia were studied (Table 1). Material came from collections of the Department of Invertebrate Zoology and Department of Hydrobiology of the Moscow State University, Moscow, and the collection of the National Museum of Natural History, Washington DC.

Animals were dissected and examined with a stereomicroscope. Particular body fragments were dried using the critical point method, coated with platinum-palladium and examined with a HITACHI 400A scanning electron microscope. Four specimens of *Paralvinella palmiformis* were fixed in 4% formalin solution; after paraffin embedding and serial cross sectioning, the slides (5 μm thick) were stained with Heidenhain's iron haematoxylin. They were examined with an OPTON MC 63s light microscope. Adult specimens of *Ampharete finmarchica* (Sars) and *Polycirrus medusa* Grube and juveniles of *Pectinaria hyperborea* (Malmgren), *Proclea malmgreni* (Ssolowiew) and *Terebellides stroemi* Sars were embedded in Epon. The specimens were used for preparation of the semi-thin and thin sagittal sections that were examined with a light microscope and a Jeol JEM 100-CX transmission electron microscope.

Results

Family Alvinellidae

In *Paralvinella pandorae pandorae* the funnel-shaped diaphragm is not perforated and stretches to the 12th chaetiger. It has a vermiform sac at its posterior edge (Fig. 1A–B).

In *Paralvinella dela* the funnel-shaped diaphragm stretches to the 33th chaetiger and possesses a single short rounded sac in the rear. The diaphragm is represented by a continuous fibreless film, which is not perforated (Fig. 1C–D).

In *Paralvinella palmiformis* the funnel-shaped diaphragm is attached to the body wall between the second and the third chaetigers. It stretches to the 16th chaetiger, where a single sac is situated. The diaphragm is perforated and consists of fibres 0.2–1 μm wide. The holes are elongated, 3–4 μm long and 0.5–1.5 μm wide (Fig. 1E). The nuclei are also elongated and approximate 8 μm in length. Coelomocytes on the diaphragmal surface are rounded and reach about 9 μm in diameter.

In *Alvinella caudata* the funnel-shaped diaphragm with a single sac at its posterior edge stretches to the 11th chaetiger. The diaphragm consists of two layers. The external one includes cells with cytoplasmic extensions forming a net with rounded and elongated holes 12–15 μm in diameter. The nuclei are 5–8 μm long. The internal layer is also perforated, but the holes are considerably smaller with their diameter approximately 3 μm (Fig. 1F).

Family Ampharetidae

In all representatives studied, the diaphragm is thin, more-or-less funnel-shaped and at least anterior parts of the oesophagus and heart are located inside the funnel (Figs 2 and 3A–B, D–E).

In *Amphicteis gunneri antarctica* Hessle the diaphragm is attached to the body wall between the second and the third chaetigers.

In *Melinna pacifica* McIntosh the diaphragm envelopes the oesophagus almost near the place of its transition into the intestine. The only sac is located medially approximately half way along the oesophagus. (Figs 2 and 3D). With SEM the diaphragm looks like a film of a fine-fibred structure and the sac consists of interlacing fibres 3–5 μm thick.

In *Melinnopsis collaris* (Hartman), *Amphicteis gunneri antarctica* and *Melinantipoda antarctica* Hartman only one sac was observed. In *Ampharete*

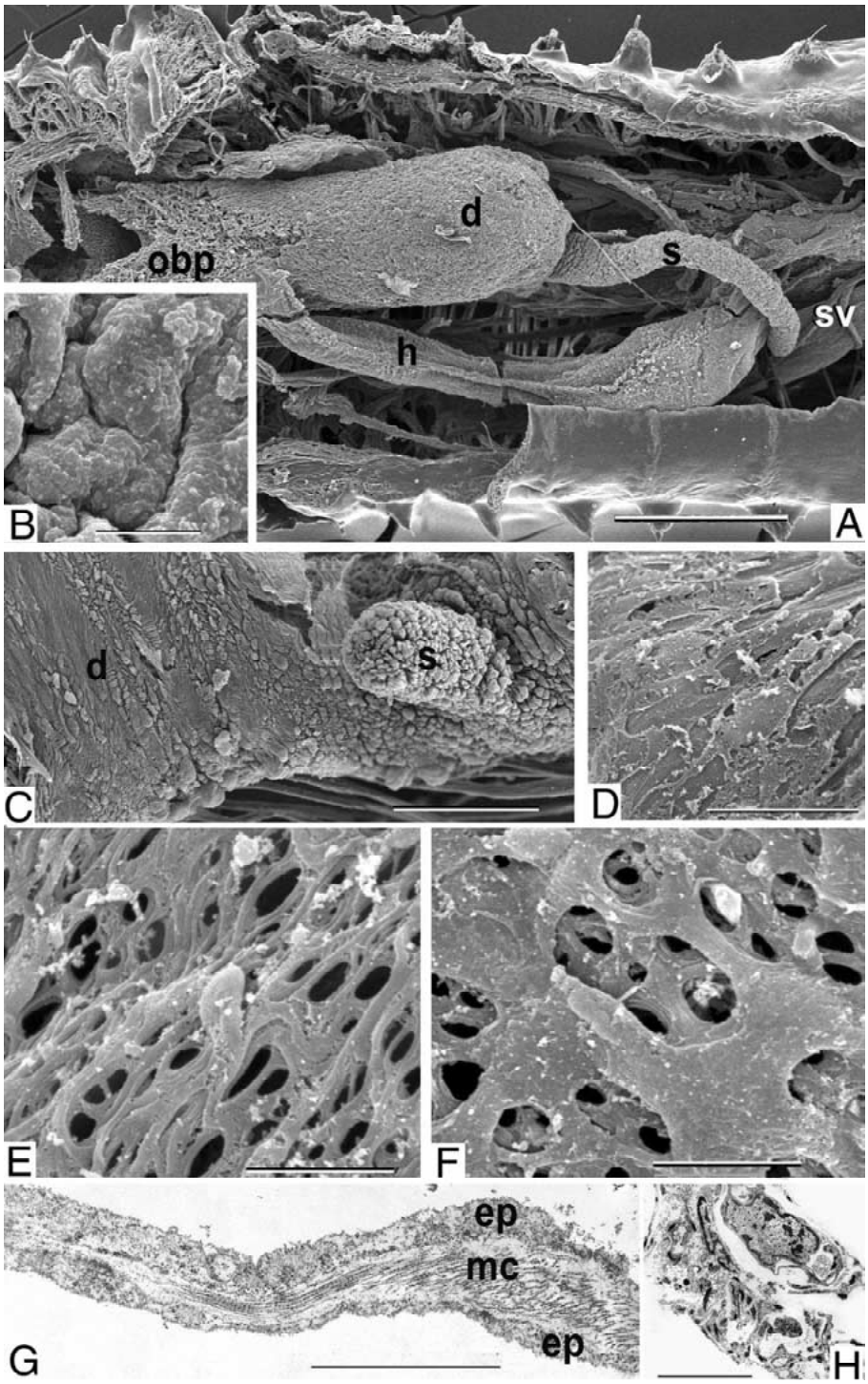

Figure 1. (A – F) SEM micrographs. (A, B) *Paralvinella pandorae pandorae,* dissections of the anterior end of the body. (B) surface of the diaphragm. (C, D) *Paralvinella dela,* dissections of the anterior end of the body. (D) surface of the diaphragm. S – sac, d – diaphragm, h – heart, obp – peri-oesophageal blood plexus. (E) *Paralvinella palmiformis,* surface of the diaphragm, note elongated holes. (F) *Alvinella caudata,* surface of the diaphragm, note two layers with holes of different size. (G) *Pectinaria hyperborea*, sagittal section via diaphragm, TEM micrograph. Note two epithelial layers (ep) and muscle layer (mc) in the middle. (H) *Polycirrus medusa*, sagittal section of the diaphragm, TEM micrograph. The cells possess numerous outgrowths. Scale: A – 400 μm, B, D E, F – 10 μm, C – 300 μm, G – 3 μm, H – 6 μm.

Table 1. Material examined and methods

Family	Species	Number of specimens studied by			
		Dissec-tion	SEM	TEM	Light microscopy
Ampharetidae	*Ampharete finmarchica*	4	2	1	
	Ampharete reducta	1		1	
	Samythella elongata	2	2		1
	Amphicteis gunneri antarctica	1	1		1
	Sabellides borealis	2	1		
	Melinantipoda antarctica	2			
	Melinnopsis collaris	2			
	Melinna pacifica	2	2		1
Alvinellidae	*Paralvinella pandorae pandorae*	3	3		
	Paralvinella dela	3	3		
	Paralvinella palmiformis	8	4		4
	Alvinella caudata	2	1		
Terebellidae	*Proclea malmgreni*	5	2		1
	Neoamphitrite figulus	4	1		
	N. groenlandica	1	1		
	N. robusta	3	1		
	A. cirrata	2	1		1
	Artacama proboscidea	3	2		
	Artacama coniferi	3			
	Polycirrus medusa	4	3		1
	Thelepus crispus	2	1		
Trichobranchidae	*Terebellides stroemi*	15	10	1	3
Pectinariidae	*Pectinaria hyperborea*	3	3	1	1
	P. koreni	3	3		

reducta Chamberlin, *A. finmarchica*, and *Sabellides borealis* Sars the funnel-shaped diaphragm is lacking any sacs. In *Samythella elongata* Verrill two vermiform sacs protrude from the posterior part of the diaphragm (Fig. 3E). The diaphragm looks like a continuous fibreless film and the sacs consist of interlacing fibres about 5 μm thick (Fig. 3F–G).

Family Pectinariidae

In both representatives studied, *Pectinaria koreni* (Malmgren) and *P. hyperborea,* the diaphragm is very thin, straight, and it has two poorly developed sacs (Fig. 3C). It is attached to the body wall behind the second pair of tentacular cirri. The thickness of the diaphragm is 1–4 μm. In some parts of the diaphragm three layers can be distinguished: two 1-μm epithelial ones and a muscular layer, about 2 μm thick, with the sagittal fibres (Fig. 1G). There are only two layers in the other parts, and the muscle fibres are transversally oriented. Epithelial cells contain nuclei about 2 μm in diameter.

Family Terebellidae

In all the representatives studied, except for *Artacama* species, the diaphragm forms a straight partition transversal to the body axis and distinctly visible in dissections. It possesses two muscular sacs. They differ slightly in relative size and shape in different species (Fig. 4A–B). Nephridial channels are often found inside the sac. The shape of sacs also depends on fixation and condition of the animal. They are rounded in *Neoamphitrite figulus* (Dallyell) and *N. groenlandica* (Malmgren), slender and elongated in *Thelepus crispus* Johnson, and triangular with a wide base and drawn-out top in *Neoamphitrite robusta* (Johnson), *Amphitrite cirrata* O.F. Müller and *Pista cristata* (O.F. Müller). In *Polycirrus medusa* the sacs are small and located slightly above the heart (Fig. 4C). Using SEM

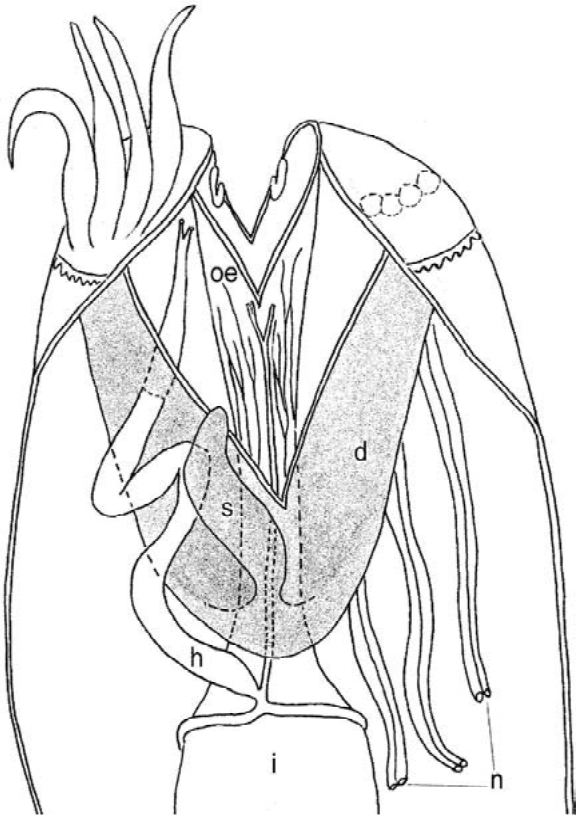

Figure 2. Melinna pacifica, dissections of the anterior end of the body, schema. S – sac, d – diaphragm, h – heart, i – intestine, n – nephridium, oe – oesophagus with perioesophageal blood plexus.

the diaphragm looks like a continuous fibrous film with the fibres in the sacs better developed (Fig. 3I).

The diaphragms vary in their structure and location in the representatives of different subfamilies of Terebellidae. In *Proclea malmgreni* (Terebellinae) it is thick and muscular. It attaches to the body wall between the first and the second chaetigers. In *Polycirrus medusa* (Polycirrinae) the diaphragm is about 12 μm thick. It attaches to the body wall between the third and the fourth chaetigers. Its surface is rough and seems to be covered with coelomocytes in the light and SEM micrographs (Fig. 3H). The cells of the diaphragm possess numerous outgrowths, which are distinct in TEM micrographs (Fig. 1H). The nuclei are elongated and approximate 8 μm in length.

In *Artacama proboscidea* Malmgren and *A. coniferi* Moore the oesophagus and heart lie in the proboscis and the diaphragm is situated in front of the oesophagus (Fig. 5). The sacs were not observed. The diaphragm is continuous; the fibres are thin and slightly branched.

Family Trichobranchidae

In *Terebellides stroemi* the diaphragm is hardly visible. It is funnel-shaped and covers the oesophagus and the anterior part of the heart. The first pair of nephridia is located inside the diaphragm funnel. There are no sacs (Fig. 6). In the SEM diaphragm looks like a thin film without fibres.

The fine structure of the diaphragm of *T. stroemi* is shown in Figure 4D. The diaphragm is about 5 μm thick and consists of four cell layers. The external layer is epithelial, about 2 μm thick. The cells contain elongated nuclei up to 6 μm in length and are connected by desmosomes. An extracellular lamina is developed beneath the epithelial cells. The second layer is 1.0–1.5 μm thick, it contains sagittal and transversal muscle fibres and mitochondria. The third layer also contains sagittal muscle fibres and mitichondria, its thickness is about 1.2–1.6 μm. An extracellular lamina is developed between the two muscle layers. One more epithelial layer is situated below them and divided from them by an extracellular lamina. The cells are connected by desmosomes.

Discussion

Location of the diaphragm

According to our data, in *Proclea malmgreni* (Terebellidae) the diaphragm is located behind the first chaetiger. According Orrhage's data for the genus *Pista* based on investigation of innervation of the anterior end, the first chaetiger is the fourth segment (Orrhage, 2001). So, the diaphragm is situated between the 4th and 5th segments, if in *Proclea* the arrangement of segments is equal to that in *Pista*.

Similarly, in *Amphicteis gunneri* (Ampharetidae) the diaphragm is located between the second and third chaetigers, i.e. between the 4th and 5th segments, according to Orrhage (2001). In *Pectinaria hyperborea* (Pectinariidae) the diaphragm is situated behind the second pair of tentacular cirri, i.e., according to Orrhage (2001), between the 3th and 4th segments.

There is no data on innervation of the anterior end of Alvinellidae and Trichobranchidae. Fauchald & Rouse (1997) assume that in alvinellids and trichobranchids the first chaetiger is the third body segment.

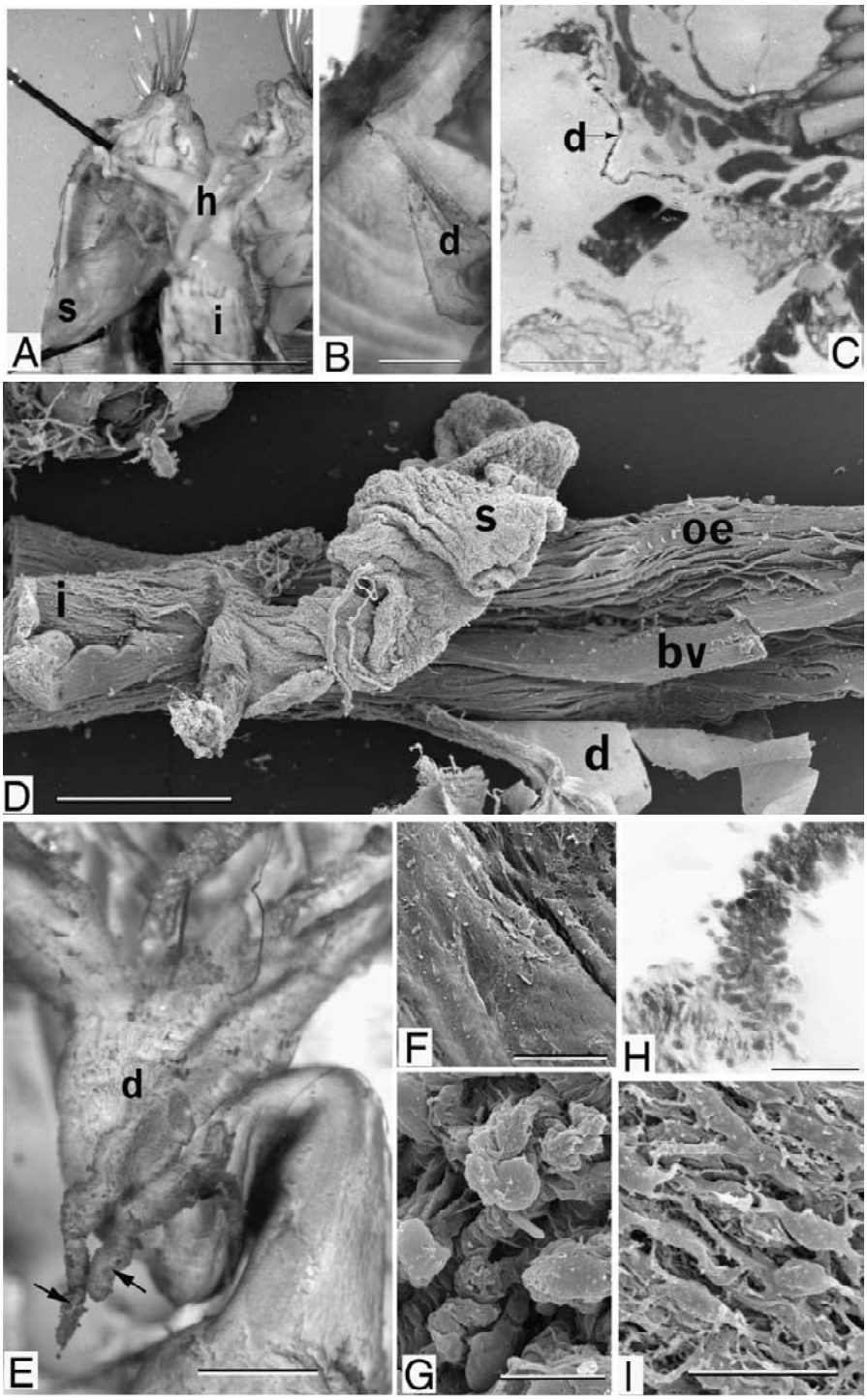

Figure 3. (A, B) *Amphicteis gunneri*, dissections of the anterior end of the body, light photographs. S – sac, d – diaphragm, h – heart, i – intestine. (B) attachment of the diaphragm (d) to the body wall. (C) *Pectinaria hyperborea*, sagittal section of the anterior end, light micrograph showing the diaphragm (d). (D) *Melinna pacifica*, dissection of diaphragm (d), SEM. Note the sac (s) and the blood vessels (bv) covering the oesophagus (oe), i – intestine. (E – G) *Samythella elongata*, E - dissections of the anterior end of the body. Note the diaphragm (d) covering the oesophagus, and two sacs (arrows). (F, G) – SEM micrographs. (F) surface of the diaphragm, (G) surface of a sac. (H) *Polycirrus medusa*, sagittal section via diaphragm, light micrograph. Note the rough surface of the diaphragm. (I) *Amphitrite figulus*, surface of a sac, SEM. Scale: (A) 800 μm, (B) 200 μm, (C) 200 μm, (D) 800 μm, (E) 500 μm, (F, G, I – 10 μm, (H) 50 m.

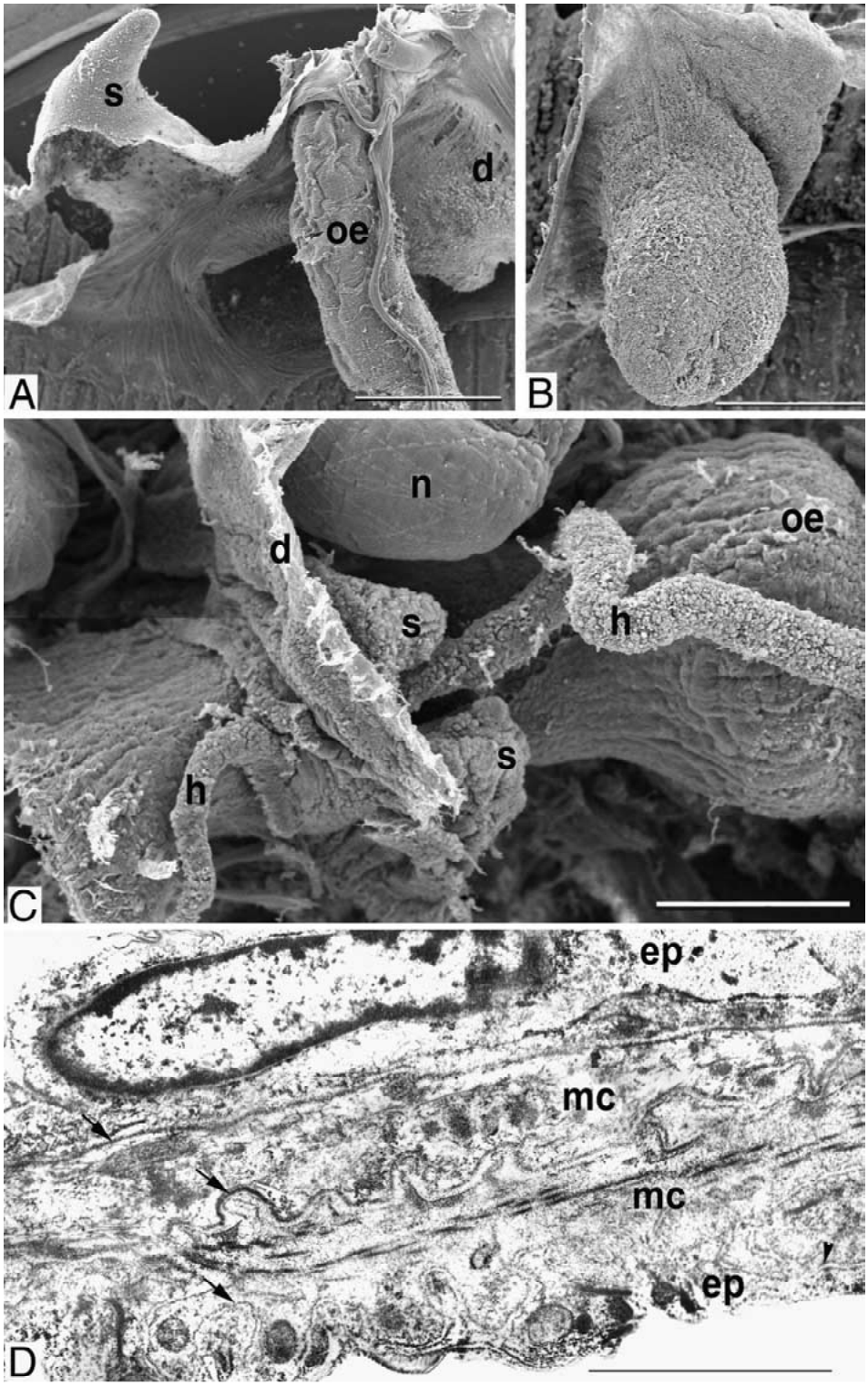

Figure 4. (A–C) SEM photographs. (A) *Neoamphitrite robusta,* diaphragm (d) with sac (s), oesophagus (oe). (B) *Neoamphitrite figulus,* sac of the diaphragm. (C) *Polycirrus medusa,* dissections of the anterior end of the body, s – sacs, d – diaphragm, h – heart, n – nephridium, oe – oesophagus. (D) – *Terebellides stroemi*, sagittal section ofthe diaphragm, TEM micrograph. Note two epithelial layers (ep), two muscle layers (mc) in the middle and extracellular laminae (arrows). Scale: A – 1 mm, B – 400 μm, C – 200 μm, D – 2,5 μm.

Table 2. Characteristics of the diaphragm in Terebelliformia taxa

	Location	General shape	Number of sacs	Structure
Alvinellidae	between the second and third setigers	funnel-shaped	1	perforated or continuous
Ampharetidae	between second and third setigers	funnel-shaped	0–2	continuous
Pectinariidae	behind the second pair of tentacular cirri	straight	2	continuous
Terebellidae	behind the first setiger	straight (except *Artacama)*	2	continuous
Trichobranchidae	between second ant third setigers	funnel-shaped	0	continuous

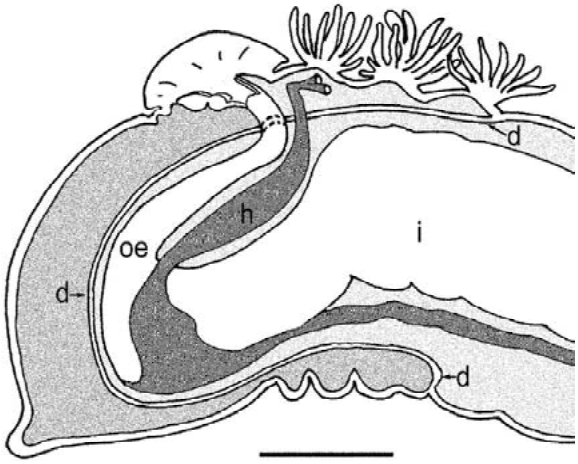

Figure 5. Artacama coniferi, sagittal section of the anterior end of the body, schema. d – diaphragm shifted anterior to oesophagus (oe), h – heart, i – intestine. Scale: 2 mm.

In *Paralvinella palmiformis* (Alvinellidae) the diaphragm is located between the second and third chaetigers, i.e. between the 4th and 5th segments. In *Terebellides stroemi* (Trichobranchidae) the diaphragm is found between the second and third chaetigers, i.e. between the 4th and 5th segments.

Therefore, now we can suppose that the diaphragm is situated between the fourth and the fifth segment in Terebellidae, Trichobranchidae, Alvinellidae and Ampharetidae, whereas in Pectinariidae it is located between the third and the fourth segment. This assumption supports early findings of Hessle (1917). The diaphragm could have developed from different septa independently in Pectinariidae and other families. Other possibilities are: the diaphragm could be homologous in all terebelliform taxa but has migrated in Pectinariidae; or some anterior segments in pectinariids could be fused. More extensive and detailed studies of the anterior end of different Terebelliformia and their development are required.

Shape of the diaphragm

In the species studied, the diaphragms differ in their general shape (straight or funnel-shaped) and the number of sacs (0–2). The straight diaphragm seen in Terebellidae and Pectinariidae seems to be the plesiomorphic condition, because a diaphragm of the same shape is found in other polychaete families such as Arenicolidae (Dales, 1962) and Maldanidae (Green, 1994) and closely resembles a common septum.

The plesiomorphic number of sacs remains uncertain. Terebellids (except *Artacama*) and pectinariids have diaphragms with two sacs, alvinellids – with one, and the diaphragms of different ampharetids may either lack sacs, or have one or two sacs. *Terebellides stroemi* (Trichobranchidae) lacks sacs on its diaphragm. The straight diaphragm of terebellids (except *Artacama*) and pectinariids possesses two sacs, so this particular number of sacs could be supposed to represent the plesiomorphic state.

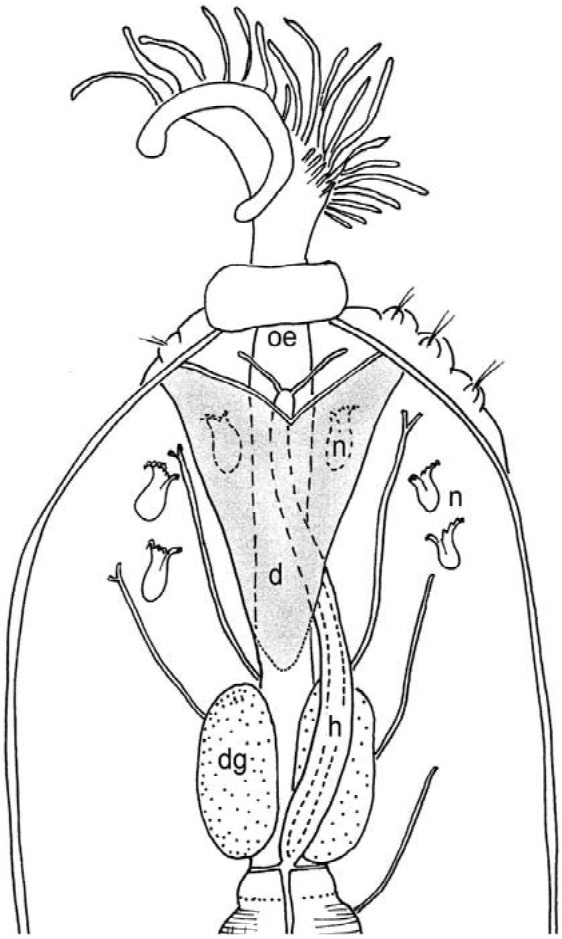

Figure 6. Terebellides stroemi, dissections of the anterior end of the body, schema. d – diaphragm, dg – digestive gland, h – heart, n – nephridia, oe – oesophagus.

Structure of the diaphragm

In most cases the diaphragm consists of two epithelial layers with one or two layers of muscular cells between them. In *Polycirrus medusa* (Terebellidae) the diaphragm is comprised of an uncertain number of layers of cells with cytoplasmatic processes.

The walls of the sacs contain more muscle fibres than the other part of the diaphragm. The most muscular diaphragm and well-developed sacs were observed in Terebellidae. This may be connected with the fact that the longest buccal tentacles are found in Terebellidae compared to other Terebelliformia. Two *Artacama* species have relatively short tentacles (Dales, 1955) and a diaphragm without sacs pressed to the proboscis wall by the oesophagus. This fact favours the idea of correlation of development of muscle fibres and sacs of the diaphragm with the length of the mouth tentacles.

The diaphragms of four Alvinellidae species (*Alvinella pompejana, A. caudata, Paralvinella grasslei,* and *P. palmiformis*) are perforated, whereas in two other species (*Paralvinella dela* and *P. pandorae pandorae*) it is continuous (Jouin-Toulmond et al., 1996; Zhadan et al., 2000; this study). The continuous diaphragm is, evidently, a plesiomorphic state because it occurs in the overwhelming majority of studied terebelliform and perforated one is not known for any other polychaete taxa.

Function of the diaphragm

A muscular diaphragm produces extra hydrostatic pressure necessary for protraction of the buccal tentacles (Meyer, 1887; Dales, 1955). The hydraulic function of the diaphragm is confirmed by correlation between the length of the mouth tentacles and development of the muscle fibers and sacs.

The perforated diaphragm of some Alvinellidae apparently has another function: it contains a hypertrophied peri-oesophageal capillary plexus and coelomic erythrocytes both taking part in the sulfide detoxication (Jouin-Toulmond et al., 1996). Moreover, erythrocytes can be oxygenated in the cavity of the mouth tentacles which is connected with the prediaphragmal (anterior) coelom, penetrate through holes in diaphragm, reach the posterior coelom and provide internal organs and, particularly, developing gametes with oxygen (Jouin-Toulmond et al., 1996). The reasons for the differences in the structure of the diaphragmal wall in different alvinellids are still under question.

The funnel-shaped diaphragm of ampharetids and alvinellids correlates with ability of their tentacles to invert into the oesophagus (Holthe, 1986; Zhadan & Tzetlin, 2002). Probably the shape of the diaphragm is a synapomorphy within these two families as well as their inversible tentacles (Zhadan & Tzetlin, 2002).

The location of the diaphragm, its shape and, in some cases, peculiarities of its structure is important taxonomic characteristics in the Terebelliformia (Table 2). The members of every family have diaphragms of a particular type.

Acknowledgements

We are indebted to Dr I. Zhirkov (Hydrobiology Department of Moscow State University) and Dr L. Ward

(NMNH) for supplying us with Terebellids' 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 for various support during the stay of junior author in Smithsonian Institute (U.S.A.). We would like to thank Dr K. Fauchald and G. Rouse for fruitful discussion at the initial stage of the project, I. Ivanov for providing us with sections of alvinellids and A. Popovkina for critically reviewing the English version of the manuscript.

The work was supported by the following grants: Russian Foundation for Basic Research þ 01-04-49093, and Short Time Visiting Program of Smithsonian Institution.

References

Dales, R. P., 1955. Feeding and digestion in terebellid polychaetes. J. mar. biol. Ass. U.K. 34: 55–79.

Dales, R. P., 1962. The polychaete stomodeum and the interrelation of the families of Polychaeta. Proc. zool. Soc. Lond. 139: 389–428.

Fauchald, K. & G. W. Rouse, 1997. Polychaete systematics: past and present. Zool. Scr. 26: 71–138.

Green, K., 1994. The head of Maldanidae polychaetes of the subfamily Maldaninae. In Dauvin, J.-C., L. Labier & D. Reish (eds), Actes de la 4ème Conferénce internationale des Polychètes. Mem. Mus. natn. Hist. nat. 162: 243–250.

Heimler, W., 1983. Untersuchungen zur Larvalentwicklung von *Lanice conchilega* (Pallas), 1766 (Polychaeta/Terebellomorpha). Part III: Bau und Struktur der Aulophora-Larve. Zool. Jb. Anat. Ontog. Tiere 110: 411–478.

Hessle, C., 1917. Zur Kenntnis der terebellomorphen Polychaeten. Zool. Bidr. Upps. 5: 39–258.

Holthe, T., 1986. Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography. Gunneria 55: 1–236.

Jouin-Toulmond, C., D. Augustin, D. Desbruyeres & A. Toulmond, 1996. The gas transfer system in alvinellids (Annelida Polychaeta, Terebellida). Anatomy and ultrastructure of the anterior circulatory system and characterization of a coelomic, intracellular, haemoglobin. Cah. Biol. Mar. 37: 135–151.

Meyer, E., 1887. Studien über Körperbau der Anneliden. Mitt. Zool. Stat. Neapel 7: 592–741.

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

Smith, R., 1992. Three nephromixial patterns in polychaete species currently assigned to the genus *Pista* (Annelida, Terebellidae). J. Morph. 213: 365–393.

Zhadan, A. E., A. B. Tzetlin & M. A. Safronova, 2000. Anatomy of some representatives from the family Alvinellidae (Polychaeta, Terebellida) from the Pacific hydrothermal habitats. Zool. zhurn. 79: 141–160 [in Russian].

Zhadan A. & A. Tzetlin, 2002. Comparative morphology of the feeding apparatus in the Terebellida (Annelida: Polychaeta). Cah. Biol. Mar. 43: 149–164.