Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta, Cossuridae) from the White Sea

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ABSTRACT

Morphology of the feeding structures and construction of the anterior part of the body cavity of *Cossura* sp. from the White Sea were studied using TEM and SEM techniques. Buccal tentacles are the only feeding structures in the spacious buccal cavity. They are situated on the dorsal surface of the buccal cavity near the esophageal opening. There are about 15 buccal tentacles covered by long cilia inside the proboscideal cavity. In cross sections every tentacle consists of columnar epithelial ciliated cells and in the central part, inside a ring of basal membrane, there are two longitudinal muscle cells and two cells without contractile filaments. The space between body wall and tissues of digestive tract is occupied by the non-contractile cytoplasmic parts of longitudinal muscle cells of the body wall. Buccal tentacles cannot be protracted by hydrostaic pressure of the body cavity, as there is no free coelomic space either in the anterior part of the body or inside the tentacles. Also *Cossura* sp. has not circular muscles in the body wall which are usually necessary for hydrostatic skeleton. It seems that natural position for the buccal tentacles during feeding processes is partly projected from the very widely open mouth. According to our observations on living specimens, the long unpaired dorsal branchial filament never takes part in feeding, it is always stretched along the trunk, and has presumably a respiratory function.

RÉSUMÉ

Morphologie fine de l'appareil alimentaire de *Cossura* sp. (Polychète, Cossuridae) de la mer Blanche

La morphologie des structures trophiques et la constitution de la partie antérieure cavitaire du corps de *Cossura* sp. de la mer Blanche ont été étudiées en utilisant les techniques de miscroscopie électronique à transmission et de microscopie électronique à balayage. Les tentacules buccaux sont les seules structures servant à l'alimentation, présentes dans la vaste cavité buccale. Il y a environ 15 tentacules couverts de longs cils à l'intérieur de la cavité proboscidéale. En coupe, chaque tentacule est constitué par des cellules épithéliales ciliées en forme de colonnes et dans la partie centrale, à l'intérieur d'un anneau de la membrane basale, il y a deux cellules musculaires longitudinales et deux cellules sans filaments contractiles. L'espace entre la paroi du corps et les tissus du tractus digestif est occupé par les parties cytoplasmiques non contractiles des cellules musculaires longitudinales de la paroi du corps. Les tentacules buccaux ne peuvent être développés par la pression hydrostatique de la cavité corporelle, tout comme il n'y a pas d'espace coelomique libre ni dans la partie

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antérieure du corps ni dans les tentacules. De même, *Cossura* sp. n'a pas de muscles circulaires dans la paroi du corps, lesquels sont habituellement nécessaires pour le squelette hydrostatique. En position naturelle durant les phases d'alimentation, les tentacules buccaux semblent être partiellement projetés hors de la bouche très largement ouverte. Suivant nos observations sur des animaux vivants, le long filament branchial dorsal ne joue aucun rôle dans l'alimentation. Il est toujours accolé le long du tronc et a, probablement, une fonction respiratoire.

INTRODUCTION

The Cossuridae is one of the most poorly studied polychaete families. We have very nearly no information even about the general anatomy of these worms. In addition there is almost no information about life style and feeding in these animals (FAUCHALD & JUMARS, 1979; FOURNIER & PETERSEN, 1991). THULIN (1921) and later FOURNIER & PETERSEN (1991) described the ciliated "buccal tentacles" of the pharyngeal cavity of *Cossura* as the feeding apparatus of these polychaetes. Up to this time the construction, position in the pharyngeal cavity and functioning of the cossurid mouth parts have remained unknown.

This paper deals with the fine morphology of the feeding structures and the construction of the anterior part of the body cavity of *Cossura* sp. from the White Sea.

MATERIALS AND METHODS

All material (about 100 specimens) was collected within 20 km of Velikaya Salma Straight (Kandalaksha Bay, the White Sea, 66° 30'N, 33° 30'E), in the depths varying from 20 to 30 m by means of SCUBA.

The White Sea *Cossura sp.* inhabits the upper layer (1-2 cm) of muddy sediment in depths of more than 20 m. Previously, this species was identified as *Cossura longocirrata* Webster & Benedict (TZETLIN,1981), but according to PETERSEN (personal communication) the White Sea animals must be referred to another, possibly new species.

Live worms were examined in the Laboratory of the White Sea Biological Station of Moscow University. The observations on the *Cossura sp.* were made in a small aquarium with a 3 cm sediment layer transferred from the depth of 25 m.

Animals were fixed with 2,5 % glutaraldehyde, buffered with 0,2 M Na-cacodylate buffer (pH = 7,2-7,4) with the addition of 0,131 g sucrose per 1 ml of solution (1 hour) and postfixed with 1 % osmiumtetroxide solution in the same buffer. For SEM observations specimens were critical-point dried after dehydration in an ethanol series and with acetone and then after coating with gold. They were studied with a Hitachi S 405 microscope. For TEM fixed specimens were dehydrated in an ethanol series, treated with acetone and embedded in Epon. Semithin sections were made with glass knifes on a Dupont Ultracut microtome and stained in 1 % toluidine blue. Ultrathin sections for TEM observations were cut on a LKB-3 Ultracut microtome with diamond knife, stained in lead citrate and uranylacetate and then examined with a JEM-100b microscope. More than 50 specimens were studied by light microscopy in living condition, 25 specimens were observed with SEM. Fifteen of them were cut in the sagittal plane by microsurgery knife and the dissected worms examined with SEM. Four specimens (two sagittal and two transverse series) were examined with TEM techniques.

RESULTS

CONSTRUCTION OF THE FEEDING APPARATUS. — *Cossura* sp. are slender polychaetes of 20-30 mm length, with 50-60 setigers. The T-shaped mouth opening is located in the fissure between two secondary "segments" of the peristomium. The only external appendage on the anterior part of the body is the dorsal branchial filament, which originates from the border between the second and third setigers. The branchial filament bears a longitudinal row of cilia. The inner part of the branchial filament contains longitudinal muscle cells, and two blood vessels. There is also a narrow coelomic space.

The spacious buccal cavity stretches from the anterior border of peristomium to the border between setigers 2 and 3. In the last area is also the junction between foregut and intestine. The extremely short esophagus is represented by short funnel with relatively narrow lumen between stomodeum and intestine (Fig. 1A).

Stomodeal epithelium consists of squamous (1,6 μm) cells rarely covered by short microvilli (Fig. 1B-C; Fig. 3, C-D). A collagenous matrix on the surface of the stomodeal epithelium is poorly developed. There are electron dense secretory spherulae (D =0,5-0,4 μm) in the epithelial cells. The epithelium is underlain by a thin basal

lamina (0,4 μm) and peritoneal cells. The wall of buccal cavity lacks muscle cells (Fig. 1, B-C; Fig. 3, C-D). Epithelial cells in the back region of the stomodeum are covered with cilia (Fig. 1, A, B). These cells are similar to epithelial cells of the esophageal region and anterior part of intestine.

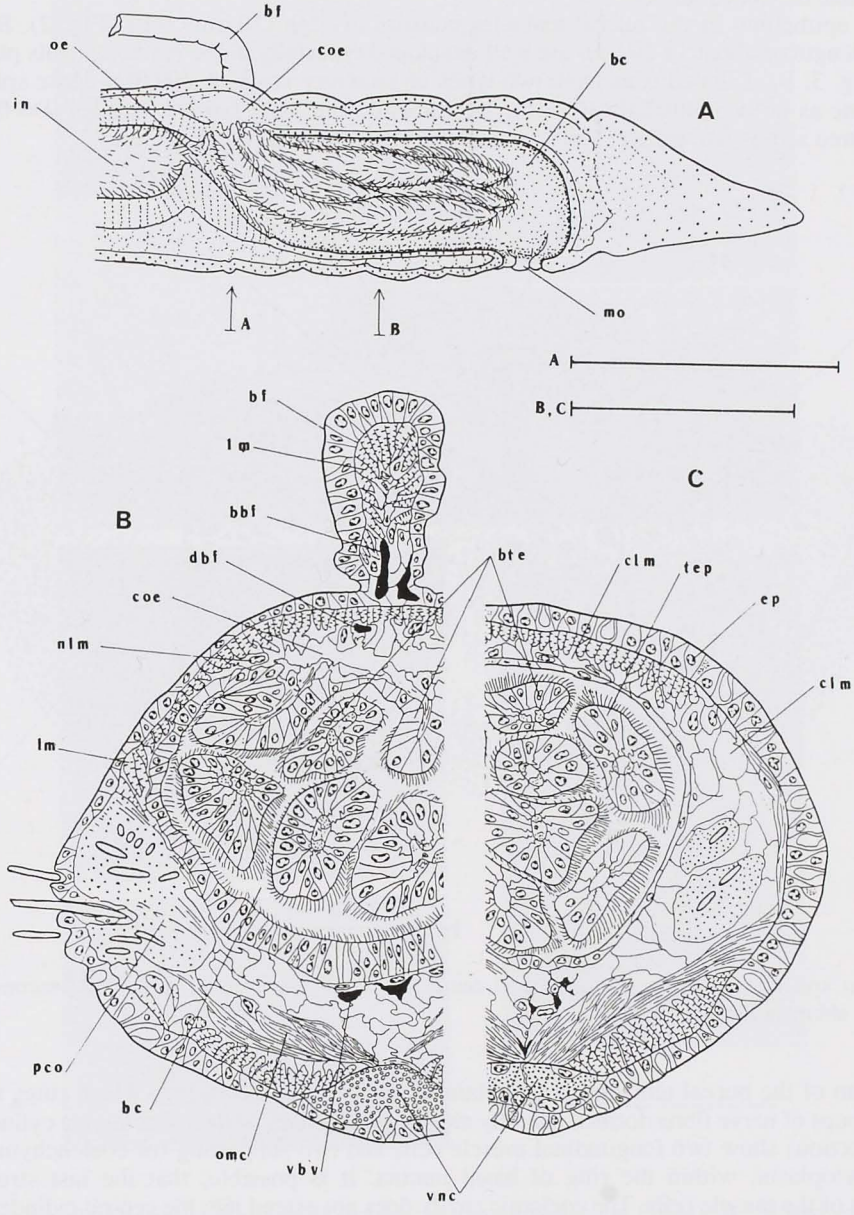

FIG. 1. — *Cossura* sp. **A**. : scheme of sagittal section. Arrows **B, C** show position of transverse sections. **B, C** - transverse sections through the region of the foregut (hemischeme, after TEM-reconstructions). Scale: A - 0,5 mm, **B, C** - 0,1 mm. bc: buccal cavity. bf: branchial filament. bbf: blood vessel of the branchial filament. bte: buccal tentacle. bz: basal zone of the buccal tentacle. c: cilia. ch: chaeta. clm: cytoplasmic expansion of the longitudinal muscle cell. coe: coelomic cavity. dbv: dorsal blood vessel. ep: epitermal epithelium. in: intestine. lm: longitudinal muscle cell. mo: mouth opening n: nucleus. nf: nerve filament. nlm: nucleus of the longitudinal muscle cell. oe: oesophagus. omc: oblique muscle cell. pco: parapodial complex. r: rootlets. step: stomodeal epithelium. sg: secretory granulae. tep: tentacular epithelium. vbv: ventral blood vessel. vnc: ventral nerve cord.

Buccal tentacles, the only feeding structures, are located in the spacious buccal cavity. They are attached to the dorsal surface of the buccal cavity near the opening into esophagus. There are about 15 buccal tentacles covered with long cilia occupying almost all space inside the buccal cavity (Fig. 1, A, B, C). The length of the buccal tentacles is 0,6 - 0,7 mm and the width about 0,05 mm. The ventral and lateral surfaces of tentacles are more densely ciliated than the dorsal surface.

The ciliated epithelium of the buccal tentacles consists of high (20 μm) cells (Fig. 2). Basal bodies and rootlets (with a length of about 18-20 μm) are well developed especially in the epithelial cells placed laterally on the tentacles (Fig. 3, B). Ciliated cells have two types of secretory vesicles: electron dense spherulae (D= 0,5-0,4 μm), the same as in the epithelial cell of the buccal wall. The other type of vesicles (D= 0,8 μm) is full of gray, non-structured serous-like matter. The epithelial cells have large nuclei (D= 5 μm).

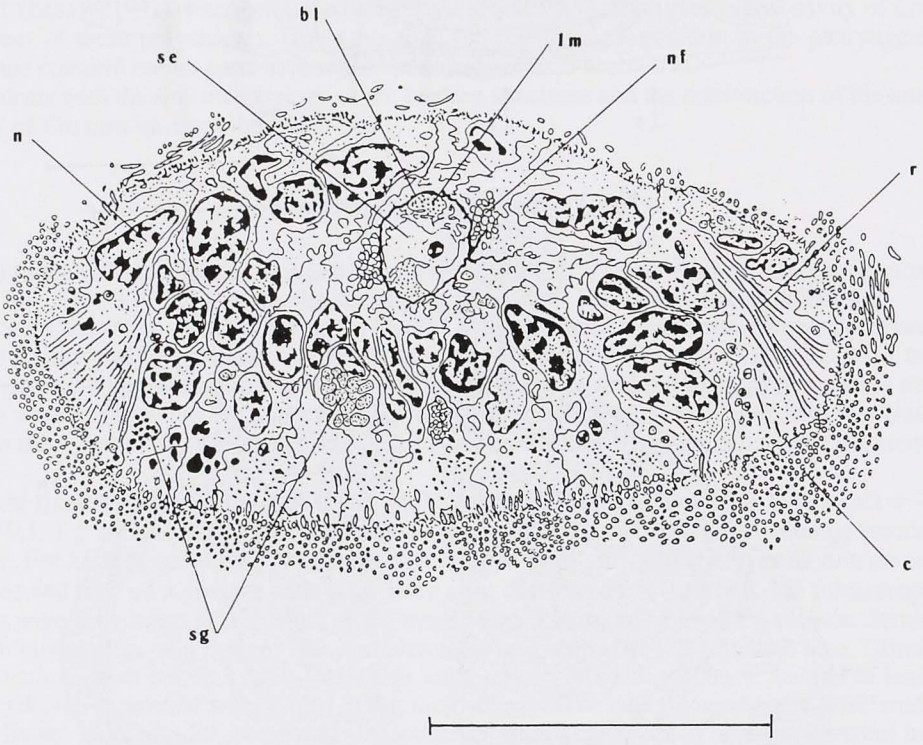

FIG. 2. — *Cossura* sp.: Cross-section of the buccal tentacle (slightly schematic, after TEM-reconstruction). Scale: 0,025mm. For abbreviations, see Figure 1.

The epithelium of the buccal tentacles is underlain by basal lamina (0,16 μm) which rings the central zone. There are two groups of nerve fibres located laterally along the both sides of the basal lamina cylinder.

Transverse sections show two longitudinal muscle cells and two supporting (or coelenchyme-like) cell with almost empty cytoplasm, within the ring of basal lamina. It is possible, that the last structures are only cytoplasmic parts of the muscle cells. The coelomic cavity does not extend into the central cylinder of the tentacles (Fig. 3, A).

CONSTRUCTION OF BODY WALL AND COELOMIC LINING OF THE ANTERIOR END OF THE TRUNK. — There are only longitudinal muscle cells in three bundles (two ventro-lateral and one unpaired dorsal longitudinal bundle) under the ectodermal epithelium and basal lamina. Circular muscles are very poorly developed and could be seen only in the areas of inter-segmental fissures. Oblique muscles are located in the region of the parapodial complexes. All longitudinal muscle cells have a spacious non-contractile cytoplasmic expansion in which the nucleus is found. These cytoplasmic extension occupy all the space of the body cavity in the anterior setigers and fit closely to the peritoneal cells which surrounds the foregut (Fig. 3, C). The little space free of cell bodies is

only in the dorsal region of the third setiger. It is directly connected to the coelomic cavity of the branchial filament.

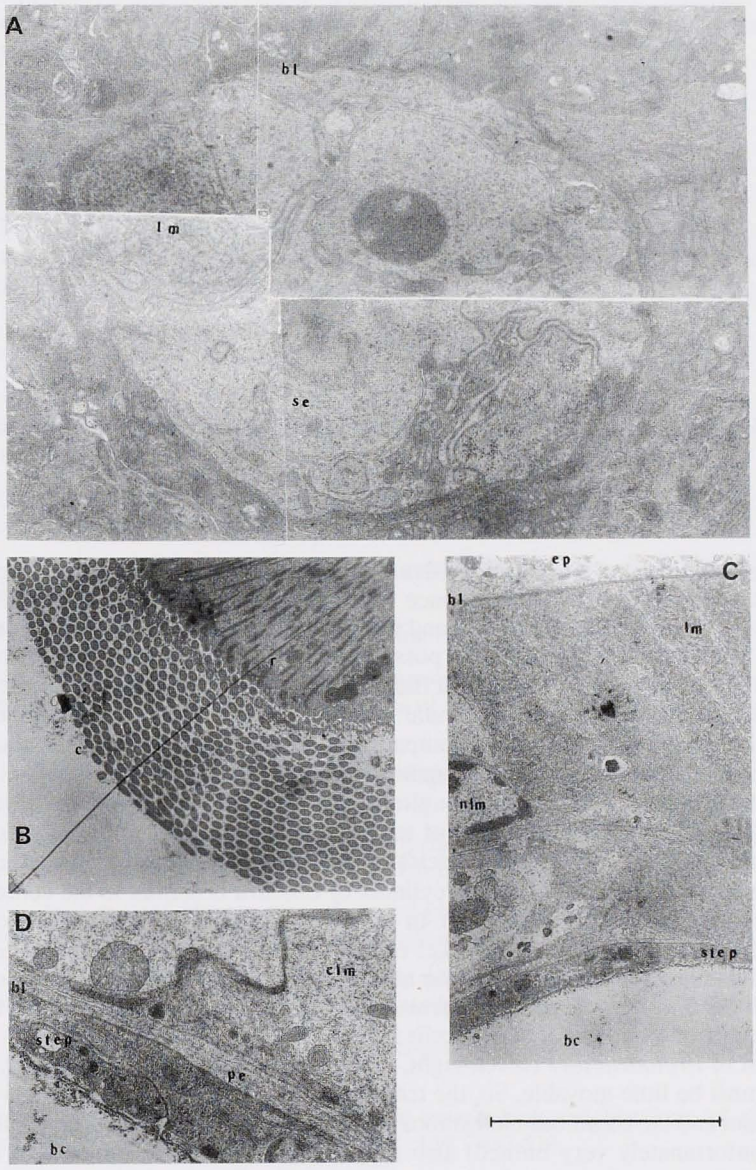

FIG. 3. — *Cossura* sp.: **A**, Central part of buccal tentacle in transverse section (TEM); **B**, ciliated epithelial cell of the buccal tentacle (TEM); **C**, part of a transverse section through anterior part of the body (TEM); **D**, part of the epithelium of the middle part of the buccal cavity (TEM). Scale: **A**, 0.003 mm, **B, C**, 0.014 mm, **D**, 0.0045 mm. For abbreviations, see Figure 1.

LIVING OBSERVATION. — The worms do not build massive tubes, but continuously produce mucus which is always covered with sediment particles. The long dorsal branchial filament never takes part in feeding, being always stretched along the trunk inside the mucous tube presumably having only a respiratory function. After extraction from the sediment the worms usually break up into fragments and die rapidly.

Buccal tentacles are normally located inside the buccal cavity. Only few worms with buccal tentacles extended from the mouth were observed. The tentacles were motionless and non-contractile. All these animals were in bad condition and convulsively contracted the anterior end. These worms were unable to retract their buccal tentacles.

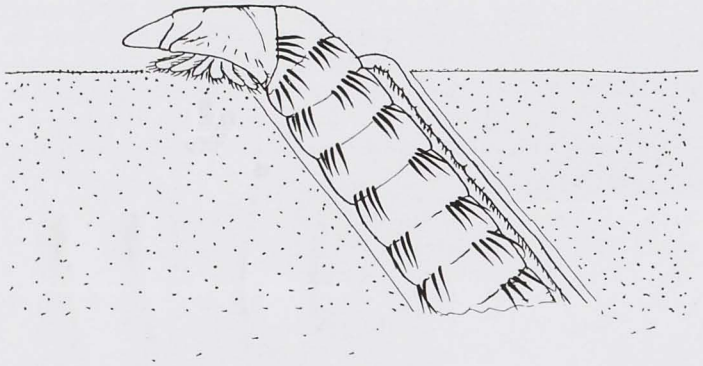

FIG 4. — *Cossura* sp.: Hypothetical position of *Cossura* sp. during feeding processes. For abbreviations, see Figure 1.

DISCUSSION

The central cylinder of the buccal tentacles of *Cossura* consists of longitudinal muscle elements and supporting (coelenchyme-like) elements. A small coelomic space free from the cell bodies in the dorsal region of the third setiger was found (between the branchial filament and the base of the buccal tentacles), but no coelomic space is present in the buccal tentacles. It is theoretically possible that powerful contractions of the longitudinal body muscles, coupled with a contraction of the branchial filament could cause the extrusion of the buccal apparatus. In a great number of polychaetes, extrusion of tentacular or palpal structures when hydrostatic pressure is used, is strongly correlated with the presence of special compartments of the coelom with muscular walls (ampullae of Spionida, Protodrilidae and Saccocirridae and diaphragms in the Terebellida).

Thus, it is unlikely that contraction of the longitudinal body muscles, coupled with a contraction of the branchial filament may be the normal mechanism of tentacle elongation. It is more probable that the supporting elements of the central cylinder of the buccal tentacles form a kind of chord, supporting the constant shape and volume of the tentacle. Construction of the central cylinder of *Cossura* is similar to the construction of the palpal canal of *Protodriloides chaetifer* (PURSCHKE, 1993). In both cases there are longitudinal muscle elements (without circular elements) and supporting (coelenchyme-like) elements. *P. chaetifer* and *P. symbioticus* differ from other Protodrilida (Protodrilidae and Saccocirridae) by the absence of ampullae and circular muscle in the wall of the palpal canal. Although the diameter of the buccal tentacles of the *Cossura* is twice as large as that of the palp of *Protodriloides*, the number of longitudinal muscle cells in the central cylinder (two in a cross-section) is rather less than in the palpal canal of *Protodriloides* (seven-eight, PURSCHKE, 1993). Considering their structure, the buccal tentacles of *Cossura* must be little movable. So, the tentacles of *Cossura* are not able to move actively along the surface of the substratum and the enormous elongations so typical for tentacles of the Terebellida (SUTTON, 1957). Living observation (unfortunately very limited) also support this conclusion. Protraction of the whole buccal cavity as a component of normal feeding behavior (as suggested by THULIN, 1921 and FOURNIER & PETERSEN, 1991) is hardly probable since we did see observe any system of retractors connected to the tentacles or the foregut. The only possible hypothesis seems to be that the buccal tentacles will be exposed to the substratum when the mouth is opened very wide (Fig. 4). In this case tentacles may be pressed down onto the sediment. The high density of cilia on the lateral and ventral surfaces of buccal tentacles supports this assumption. However, the mechanism of contact of the feeding apparatus of *Cossura* with sediment is not absolutely clear.

From a functional point of view the cossurid tentacular apparatus appears similar to the ciliated pharynx of adult Orbiniidae (FAUCHALD & JUMARS, 1979). In morphological terms, the buccal tentacles of the Cossuridae differ considerably from the tentacular apparatus of the Terebellida both in position and way of action. In the Terebellidae and Alvinellidae tentacles are located on the outer surface of the upper lip, in the Pectinariidae on the

level of mouth opening, and in Ampharetidae the tentacles are on the inner surface of the upper lip of the mouth (FAUVEL, 1897; DALES, 1962, DESBRUYÈRES & LAUBIER, 1986). In contrast, the tentacles of the cossurids are situated on the dorsal surface of buccal cavity near the esophageal opening. The hydrostatic mechanism of tentacle elongation is associated with a special organ in the body cavity of Terbellida, in the form of a muscular diaphragm with paired reservoirs (DALES, 1962; SUTTON, 1957). Such devices are absent in Cossuridae. The ciliated tentacles of Cossuridae may be derived from ciliated structures on the dorso-lateral surfaces of buccal cavity common in a number of different polychaete families (PURSCHKE, 1984, 1985, 1987; TZETLIN, 1991).

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REFERENCES

DALES, R.P., 1962. — The polychaete stomodeum and the interrelation of the families of Polychaeta. *Proc. Zool. Soc. London*, **139** : 389-428.

DESBRUYÈRES, D., & LAUBIER, L., 1986. — Les Alvinellidae, une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines: systématique, biologie et écologie. *Can. Journ. Zool.*, **64** : 2227-2245.

FAUCHALD, K., & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** :193-284.

FAUVEL, P., 1897. — *Recherches sur les Ampharétiens*. Lille, Imp. L. Danel, 230pp.

FOURNIER, J.A., & PETERSEN, M.E., 1991. — *Cossura longocirrata*: redescription and distribution with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta, Cossuridae). *Ophelia*, Suppl. **5** : 63 -80.

HOLTHE T., 1986. — Evolution, systematics and distribution of the Polychaeta Terebellomorpha, with a catalogue of the Taxa and a Bibliography. *Gunneria*, **55** : 1-236.

PURSCHKE, G., 1984. — *Vergleichende anatomische und ultastrukturelle Untersuchungen ventraler Pharynx Apparate bei Polychaeten und ihre phylogenetische Bedeutung*. Ph. D. Diss., Gottingen, 372pp.

PURSCHKE., G., 1985. — Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). 2. The pharynx of Nerillidae. *Mikrofauna Mar.*, **2** : 23-60.

PURSCHKE., G., 1987. — Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). 4. The pharynx and jaws of the Dorvilleidae. *Acta Zool.*, Stokh., **68** : 85-105.

PURSCHKE., G., 1993. — Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphology*, **113** : 1-20.

SUTTON, M.F., 1957. — The feeding mechanism, functional morphology and histology of the alimentary canal of *Terebella lapidaria* L. Polychaeta). *Proc. Zool. Soc. Lond.*, **129** : 487-523.

THULIN, G., 1921. — Biologisch-faunistische Untersuchungen aus dem Vresund. V1. Über *Cossura longocirrata* Webster & Benedict und über die Rohren von *Disoma multisetosum* Oersted. *Lunds Univ. Ersskr. N.F.*, Avd. 2, Bd.**17**, 10 : 2-15.

TZETLIN, A.B., 1981. — *Fauna and distribution of the polychaetes of the White Sea*. Ph. D. diss., Moscow, 1- 355 (in Russian).

TZETLIN, A.B., 1991. — Evolution of the feeding apparatus in the order Capitellida (Annelida, Polychaeta). *Zool. Zhurn.*, **70** : 10-22 (in Russian).