

On the morphology of the genus *Flota* Hartman, 1967 and corroboration of the family status of Flotidae Buzhinskaja, 1996 (Polychaeta)

G.N. Buzhinskaja

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Comparative description of the genus *Flota* is given, including additional data on the anatomical structure of the digestive tract, female gonad, ventral nervous cord, as well as refining of external morphology. The organization of *Flota* is compared with that of representatives of other families of polychaetes. The arguments for family status of Flotidae are based on features of structure, differentiating *Flota* from all other polychaetes (triramous non-grooved palps, enormous ventro-lateral pharyngeal organ of peculiar structure and ventral nervous cord with numerous ganglia on connectives). Apart from being differentiated by these characters *Flota* differs from Flabelligeridae and close families in the structure of the head, digestive tract, parapodia and pygidium, presence of buccal tentacles and surface arrangement of the ventral nervous cord. Discovery of additional specimens of this genus and other representatives of Flotidae, further study of their anatomy and also investigation of the larval development will allow establishing the place of this family among polychaetes.

G.N. Buzhinskaja, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St.Petersburg 199034, Russia. E-mail: polychaeta@zin.ru

Polychaetes are mostly benthic marine animals. Many of them are able to swim in search for food and during breeding period. Up to 120 species of polychaetes living pelagically are known, which is approximately 1% of the total number of polychaete species. It is assumed (Dales, 1962; Uschakov, 1972) that the ancestors of the majority of these highly specialized planktonic species were free-moving errant benthic polychaetes of the order Phyllodocida, in particular of the family Phyllodocidae. Transition to exceptionally pelagic mode of life brought about profound reorganization of the animals structure; in connection with this nearly all planktonic species were placed in separate pelagic families or subfamilies (Hartman, 1959; Uschakov, 1972; Pettibone, 1982; Støp-Bowitz, 1987; Fauchald & Rouse, 1997, and others).

At present, species of pelagic polychaetes that have apparently originated from sedentary forms inhabiting bottom grounds are known. Some of them have certain features of similarity with representatives of the family Flabelligeridae. For instance, *Poeobius meseres* was initially described as an intermediate form between annelids and echiurids (Heath, 1930), and even a separate phylum Poeobioidea (Fisher, 1946) was es-

tablished for it. Meanwhile, more detailed morphological studies showed *Poeobius* to have structural features in common with flabelligerids (Hartman, 1955; Robbins, 1965). In contrast to flabelligerids, however, this translucent animal is completely devoid of parapodia, chaetae, or any traces of external segmentation, and has only retained two septa dividing the coelomic cavity. *Poeobius* is commonly regarded as a separate family within the order Flabelligerida (Hartman, 1955; Fauchald, 1977) or a separate order (Pettibone, 1982; Uschakov, 1985; George & Hartmann-Schröder, 1985).

Some features of similarity with Flabelligeridae are found also in the pelagic genus *Flota*, which means "swimming". This similarity is reflected in the name of the species *F. flabelligera*, which was caught in the Pacific Ocean near Southwestern Chile and described by the American researcher Hartman (1967). Originally she placed *Flota* in the family Flabelligeridae, then, in the close family Fauveliopsidae (which she had established), based upon the absence of cephalic cage and retractile gills characteristic of flabelligerids (Hartman, 1971). In the catalogue of genera of polychaetes Fauchald (1977) regarded *Flota* as a genus without placing it in a particular

family. Subsequently, an opinion was proposed that *Flota* was reminiscent of *Poeobius* (Rouse & Fauchald, 1997b, p. 140).

In 1977 the author described from the Kuril – Kamchatka trench a second species of this genus, *F. vitjasi* Buzhinskaja. Mostly external structure was examined in both the species. O. Hartman described the digestive tract very briefly, providing no drawings. However, all the specimens examined by her were damaged and error crept into the description. Thus, she denoted the ventro-lateral pharyngeal organ as a proboscis, and described the oesophagus as a pharynx. Nearly 18 years later, after the description of *F. vitjasi*, the author discovered, in the collections of the Zoological Institute of the Russian Academy of Sciences, two specimens labelled *Planctoflabelligera pacifica* Uschakov gen. et sp. nov., which because of the poor preservation had not been described. These specimens turned out to belong to the genus *Flota*; one of those had digestive tract thrown out of the body completely. Based upon the study of the new material and refining the data obtained earlier, the author published a brief paper noting some unique characteristic features of the organization of *Flota* and establishing a new family of polychaetes Flotidae Buzhinskaja, 1996. But Rouse (in Rouse & Pleijel, 2001) considers the family Poeobiidae and the genus *Flota* (out of any family) together “because both are pelagic and they share a number of features with Flabelligeridae”. He does not use the name Flotidae since “it is redundant” and places both taxa close to flabelligerids in the order Terebellida, clade Cirratuliformia.

The present paper deals with additional anatomical features of this family concerning the structure of the digestive tract, female gonad and ventral nervous cord, refining of external morphology, comparison of the organization of *Flota* with that of representatives of other families of polychaetes, and arguments for family status of Flotidae.

Material

Type material. *Flota vitjasi*. Holotype: No. 1/43261, R/V “Vityaz”, 1.VII.1953, st. 2218, Pacific Ocean, Kuril-Kamchatka trench, 43°40'N, 149°31'E, Ring travel, depth 6000–0 m. Paratype: No. 2/43262, R/V “Vityaz”, 23.V.1953, st., 2119, Pacific Ocean, Kuril-Kamchatka trench, 46°11'N, 154°56'E, Ring travel, depth 4000–0 m.

Flota flabelligera. Holotype: No. 55548, 30.VIII.1962, st.190, Pacific Ocean, off Southwestern Chile, 34°46'–35°05'S, 74°53'–74°29'W, 2891 m depth.

Additional material. *Flota vitjasi*. 1 specimen No. 3/11651, R/V “Vityaz”, 28.VIII.1954, st. 3116, Pacific Ocean, Kuril-Kamchatka trench, 51°46'N, 161°48.2'E, Ring travel, horizontal catch at a depth of 5760–5550 m.

Flota sp. 1 specimen No. 2/11652, R/V “Vityaz”, 25.X.1954, st. 3214, Pacific Ocean, Japan trench, east of

the Honshu Island, 38°18.4'N, 143°55.9'E, Ring travel, horizontal catch at a depth of 5700 m; 1 specimen No. 3/50521, R/V “Academician Keldysh”, 4.X.1990, st. 2358, Pacific Ocean near Peninsula California, 27°12'N, 115°31'W, depth 3000–3750 m.

Specimens of *F. vitjasi* and *Flota* sp. are deposited at the Zoological Institute, Russian Academy of Sciences, St. Petersburg. The holotype of *F. flabelligera* is deposited at the National Museum of Natural History, Washington.

The studies were conducted using German binocular microscopes of the firm Karl Zeiss (Jena). The photographs were made by Nikolai Lebsky using camera “Zenit10” and by I.S. Smimov using “Nikon 4500”.

Family FLOTIDAE Buzhinskaja, 1996

Type genus: *Flota* Hartman, 1967.

Diagnosis. Pelagic polychaetes. Small number of segments. Upper layer of cuticle gelatinous, penetrated by long and short papillae. Prostomium simple lobe fused with peristomium. Pair of trilobed structure (palps) arranged dorso-laterally to mouth. Numerous oral tentacles in buccal cavity. First segment larger than others. Parapodia biramous with short stem. Notopodia and neuropodia fused. Dorsal, ventral cirri and parapodial branchia absent. Chaetae of two kinds: thin capillaries and thick, long, transversely barred chaetae. Aciculae absent. Large pharynx with enormous ventral pharyngeal organ inside cavity of first setigerous segment. Nephridial papillae on some segments. Pygidium as a cylindrical funnel. Double ventral nervous cord with numerous ganglia.

Remark. It has been recently established that *Buskiella abyssorum* McIntosh, 1885 also belongs to Flotidae (S. Salazar-Vallejo, oral communication). Thus, the family is considered to include two genera.

Genus *Flota* Hartman, 1967

Type species: *F. flabelligera* Hartman, 1967.

Diagnosis. Body short, flattened. Nine segments; segmentation distinct. Body surface ornamented by ridges, strips and tubercles. Numerous additional small ganglia on connectives of nervous cord and accumulations of nervous cells on segmental nerves.

Remarks. According to the description and drawings (McIntosh, 1885), the genus *Buskiella*, in contrast to *Flota*, has long segments and non-ornamented body surface. The presence of additional small ganglia on connectives of nervous cord is possibly a common feature of both the genera, but *Buskiella* is a poorly studied genus.



Fig. 1. *Flota vitjasi*, paratype (photo), habitus, dorsal view.

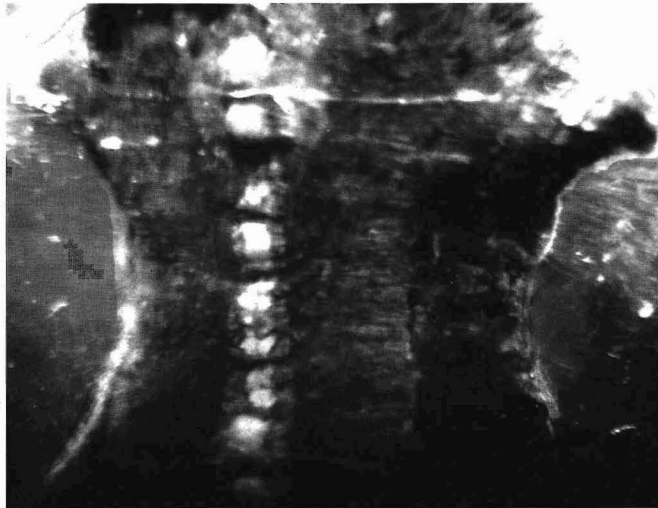
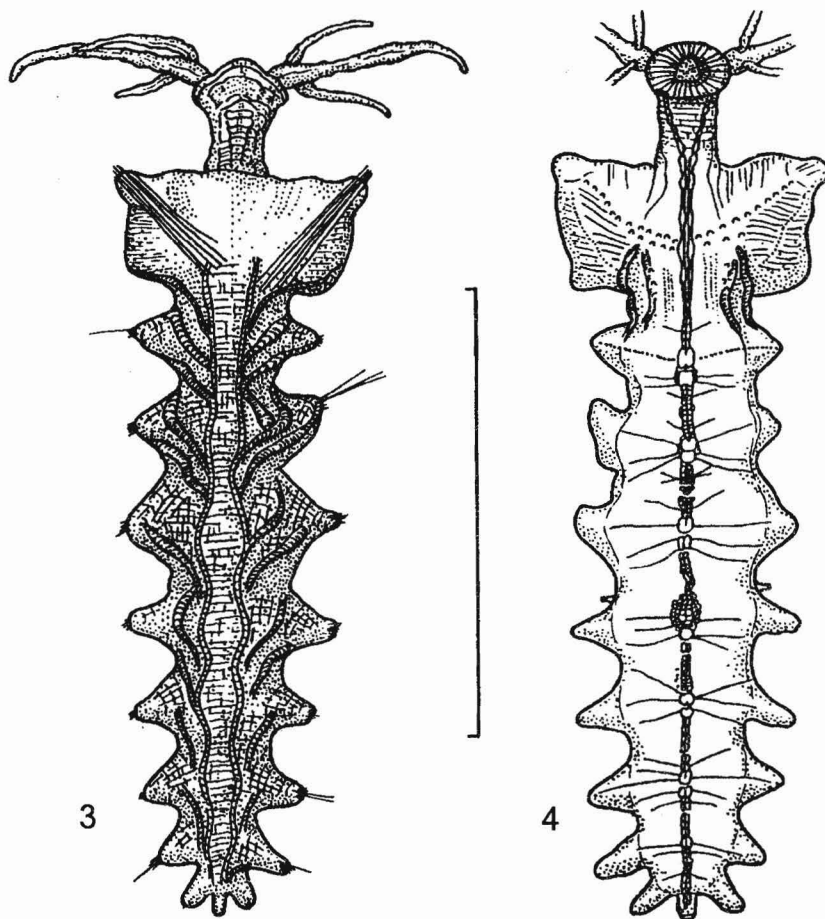


Fig. 2. *Flota vitjasi*, paratype (photo), segment of the body
(ventral nervous cord in the centre).



Figs 3, 4. *Flota vitjasi*, holotype. 3, dorsal view; 4, ventral view. Scale bar: 10 mm.

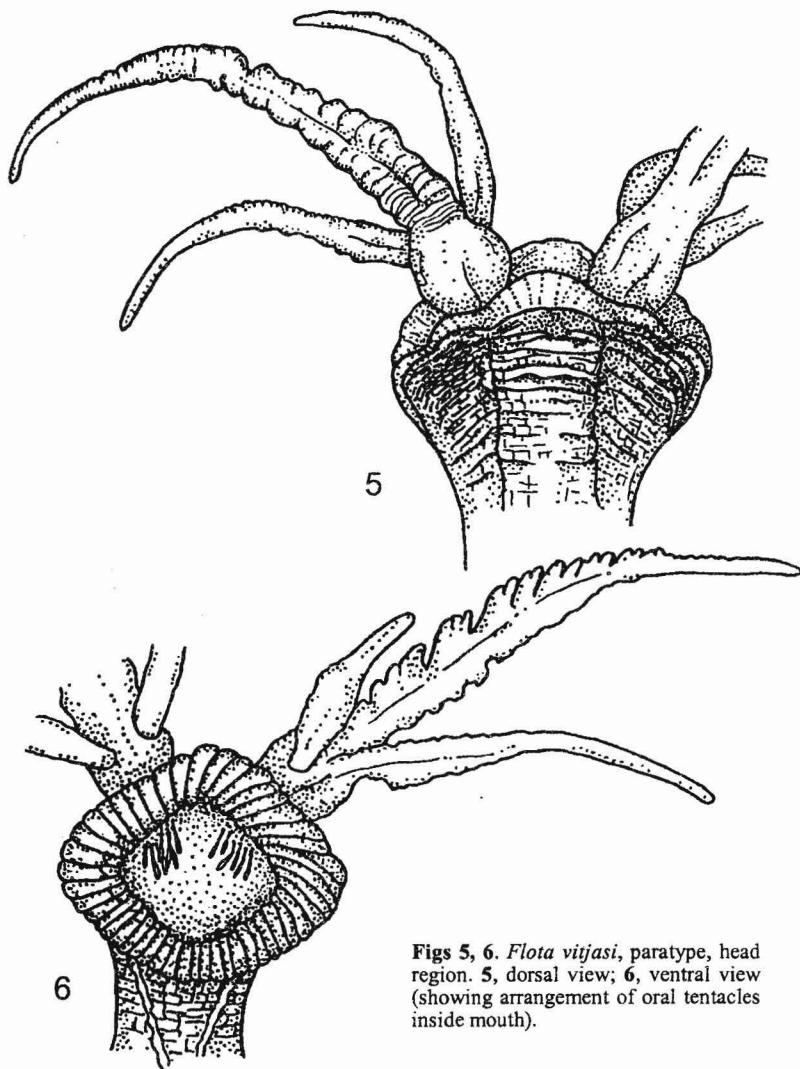
Sizes, regions of body, segmentation, cuticle. Body short, flattened, length 20-30 mm, width 4-8 mm, consists of head region, 9 chaetigers, and pygidium (Figs 1, 3). Segments are distinctly separated from one another. The first chaetiger is the largest, sizes of segments decreasing towards the posterior end.

Cuticle is wrinkled. *F. vitjasi* has on the dorsal side pronounced ornament in the form of two central wavy stripes going along the entire body, and along both sides of these large oblique folds or ridges, 1-2 per each segment, are arranged (Fig. 3). On the ventral side, 4 longitudinal crests are visible, which are stretching laterally from the middle of the first chaetigerous segment up to the beginning of the second chaetiger (Fig. 4). Less pronounced are the dorsal folds in the holotype of *F. flabelligera*. Hartman (1967) noted two transversal ridges on each segment and considered body segments to be two-ringed. How-

ever, development of such crests mostly on the dorsal side does not conform to the secondary annulated state (false segmentation), which is characteristic of some species of benthic polychaetes (e.g. Glyceridae, Opheliidae, Scalibregmatidae, etc.).

Body colour of well-preserved specimens of *F. vitjasi* is red-brown; along the medial line the body is semi-translucent. Other specimens are not coloured. Body and a part of the head are covered by a thick translucent gelatinous layer, which repeats the body shape and is pierced with numerous epithelial papillae of different shapes (Figs 1, 13). This gelatinous layer is so closely connected with the worm's body that, when it is removed, papillae and ends of setae are torn away. Apparently, this layer should be regarded as a part of the cuticle, but not as simply a mucous cover or a sheath.

Papillae are scattered over the entire body. Particularly numerous are pedunculate papillae, but

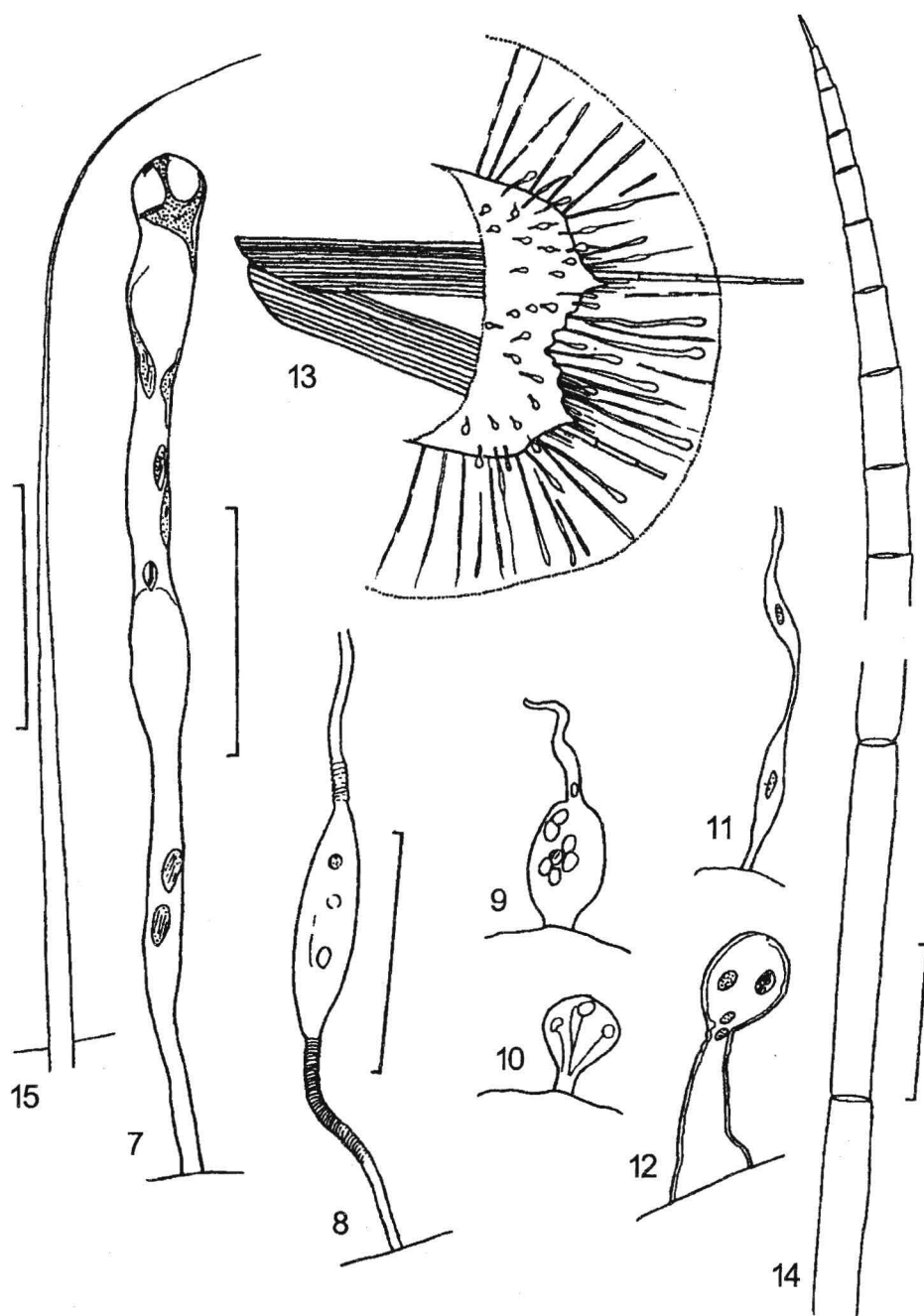


Figs 5, 6. *Flota vitjasi*, paratype, head region. 5, dorsal view; 6, ventral view (showing arrangement of oral tentacles inside mouth).

there occur also short spherical papillae (Figs 7-12). Pedunculate papillae apparently perform an excretory function. The pedunculate papillae and gelatinous layer are observed also in flabelligerid polychaetes of the genus *Flabelligera* (see Quatrefages, 1849; McIntosh, 1915, and others). The gelatinous cover, with sensory papillae visible on its surface, is also a part of the cuticle of *Poebius* (Robbins, 1965).

Head region and head structure. The prostomium is indistinct as a ridge or small lobe, fused to the peristomium forming the head. Latero-ventrally from the prostomium (latero-dorsally from the mouth), two large flattened processes consisting of three rami are situated (Figs 5, 6). In *F. vitjasi* the middle branch is long and

wide with a dilated base, from which a pair of shorter and narrower branches diverges ventrally. In *F. flabelligera* the middle branch is short (Hartman, 1967). The longitudinal grooves and cilia on these processes are absent. Hartman (1967) proposed that the middle branches are palps, whereas the lateral ones, fused with them, are branchia; this assumption, however, remains ungrounded so far. Palps are most characteristic appendages of the prostomium in polychaetes. These are normally non-ramous formations; however, it should be noted that serpulids in their development go through the larval stage with tri-ramous palps (Salensky, 1882; Sentsz-Braconnet, 1964; Crisp, 1977). In all probability, the cephalic appendages in *Flota* are also ramous

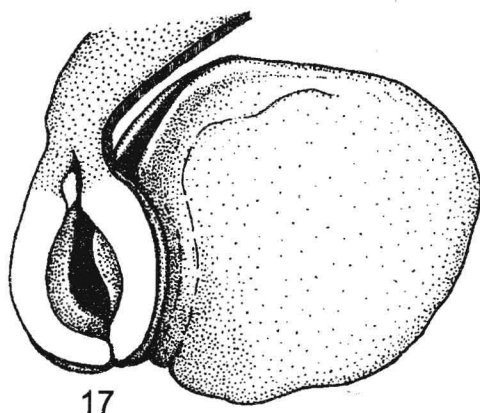
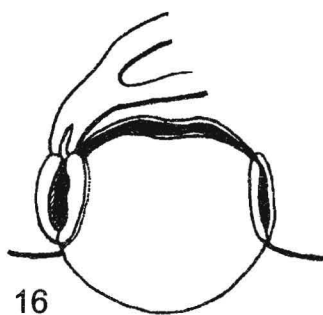


Figs 7-15. *Flota vitjasi*. 7-12, epithelial papillae; 13, parapodia (the ends of chaetae are broken); 14, cross-barred chaeta; 15, capillary chaeta. Scale bars: 0.1 mm (7-12, 15), 0.3 mm (14).

palps, which perform sensory and respiratory functions, even though to reach the final conclusion it is necessary to study their innervation and presence of coelome. In contrast to *Flota*, the palps of flabelligerids, Fauveliopsi-

dae and *Poeobius* are simple uniramous with a longitudinal groove.

The peristomium of *Flota* narrows towards the 1st chaetigerous segment. Situated subterminally is a large mouth, surrounded by a circular fold-



Figs 16, 17. *Flota vitjasi*, ventral pharyngeal organ. 16, lateral view (scheme); 17, view from behind.

ed lip, having ring musculature and capable of stretching (Fig. 6).

The structure of the cephalic region of *Flota* is sharply distinct from that of Flabelligeridae, Fauveliopsidae and Poeobiidae, in which it retracts to a certain degree into the anterior segments. In *Flota* the head is too large for that purpose, and most part of body cavity of first chaetigerous segment is occupied by a huge pharynx. The dorsal part of the peristomium of flabelligerids comprises a branchial membrane bearing nephridiopores, two groups of branchia differing in structure (Spies, 1975) and nuchal organs, which are lacking in *Flota*. The nuchal organs have been described also for fauveliopsids and poeobiids (Robbins, 1965; Riser, 1987). In *Poeobius*, on the anterior end, there are 5 pairs of branchia, nephridia open anteriorly from branchia (Heath, 1930; Robbins, 1965). In the opinion of some authors (Rouse & Fauchald, 1997), the arrangement of branchia in *Poeobius* conforms to the arrangement of branchia in flabelligerids.

Parapodia and chaetae. Parapodia are elongated lateral projections of body (Figs 3, 4). They

are biramous, without aciculae, dorsal and ventral rami are similar, fused with each other (Fig. 13). Parapodia of segment 1 are directed slightly forward and laterally (antero-laterally), others are directed laterally. All chaetae are delicate and translucent. In both the rami of the parapodia there are two types of chaetae: narrow capillaries (Fig. 15) and wide very long, gradually tapering towards the distal end cross-barred chaetae (Fig. 14). Length of the external stem of the chaetae of the 2nd type attains 14 mm, which exceeds notably the body width. Each podial branch counts up to 15 cross-barred chaetae and up to 40 capillary chaetae. The chaetae may have fan-shaped arrangement which favours hovering in water column.

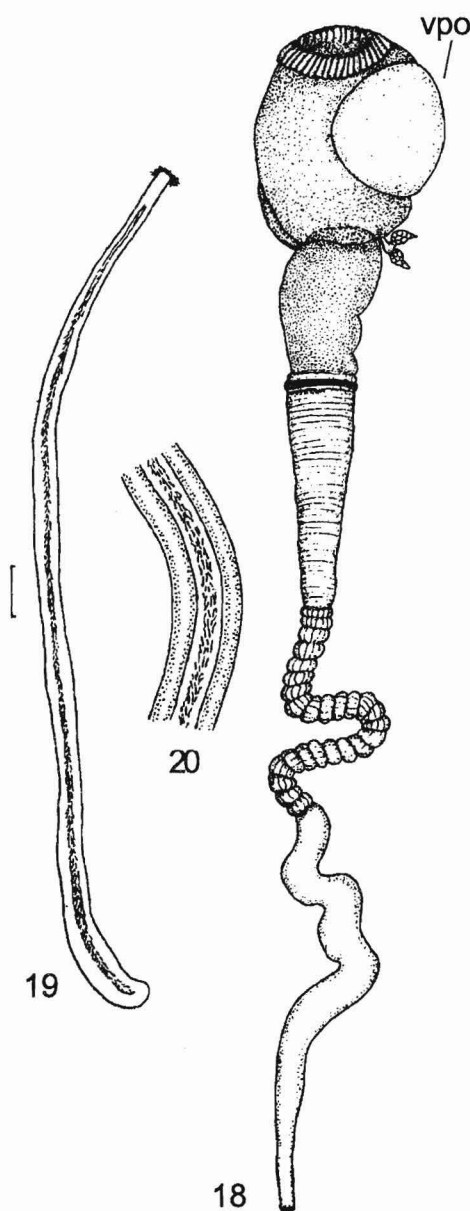
It is noteworthy that parapodia of flabelligerids, in contrast to *Flota*, do not have an elongated stem, branches of parapodia in them are not fused and are set widely apart. They are weakly developed except for those in the genus *Flabelliderma* (Hartman, 1960), which has an elongated dorsal parapodial branch. Articulated chaetae are characteristic of Flabelligeridae, although among this family a species with non-articulated chaetae has been noted (oral communication of S. Salazar-Vallejo). It is interesting to note that the long chaetae of Tomopteridae, confined in tentacular cirri of segment 2, have internal septa, lending them flexibility (Uschakov, 1972, fig. 7, 10). Transverse barred aciculae have been described in *Bruunilla natalensis* Hartman, 1971. The above author considered this genus to be close to the family Flabelligeridae, based upon the presence of such aciculae (Hartman, 1971, p. 1413, fig. 3f). The species, however, appeared to belong to the subfamily Macellicephalinae (Polynoidae), its representatives having pelagic or semi-pelagic mode of life at great depths (Pettibone, 1979). Among the benthic polychaetes, Sigalionidae have articulated appendages of compound chaetae.

Pygidium has the shape of a short straight anal tube or funnel; anus is terminal, anal cirri lacking. It is noteworthy that tubular pygidium in polychaetes is rare; it occurs, in particular, in some Opheliidae and in all species of Sabellariidae (see Kirtley, 1994). The genus *Armandia* (Opheliidae) has tubular pygidium evidently resulting from fusing two lobes and has marginal papillae and a long ventral cirrus. In sabellariids, a long cauda is formed having the appearance of cylindrical appendage. However, pygidium in *Flota* apparently does not conform to cauda of sabellariids. According to Wilson (1929), the cauda in *Sabellaria alveolata* contains 50-60 transversal ventral septa.

Digestive tract. In the buccal cavity of the holotype and paratype of *F. vitjasi* buccal tenta-

cles arranged dorso-laterally in two groups were discovered; approximately 50 tentacles in each group (Fig. 6). The tentacles are thin, brown, dilated on the distal end, hollow, U-shaped in cross section and have ciliated path, located in a longitudinal groove (Figs 19, 20). The mouth cavity leads into a huge sack-like muscular black pharynx (Fig. 18). A large part of the pharynx is occupied by a very large, 3×4 mm, ventro-lateral organ of pink colour, reminiscent of half-open bursa (Figs 16, 17). This multilayer glandular formation has longitudinal and transversal fibers, epithelial layer above the muscular tissue and is covered by a membrane. Edges of the organ are muscular, the more powerful musculature is situated on the posterior part of the organ, facing the oesophagus. From the posterior dorsal part of the organ a non-paired formation (septa) diverges, which is then bifurcated and extends along the lateral parts of the internal surface of pharynx (lateral ridges). This formation is morphologically not different from the tissue lining the internal side of the pharynx and contains muscular fibers. The external side of the organ is freely situated within the body cavity. This muscular organ is evidently able to turn inside out. According to Hartman (1967), the organ turned inside out is shovel-like. It is noteworthy that thin oral tentacles of *Flota*, by means of ciliated grooves, can only catch very small particles and direct those to the ventral organ. In all probability, the tentacles serve for sucking in, i.e. they create water flows, and the ventral organ catches larger prey, when the mouth is widely open and the pharynx is evaginated. Moreover, the open organ apparently accumulates food particles. After a food bolus is formed it is closed forming a thick tube, and pushes the food to the oesophagus by muscular effort. Thus, the buccal tentacles are functioning mostly as a ciliary water-moving apparatus for attracting food, and the ventral apparatus catches, accumulates and transports food.

At the boundary with the oesophagus, one duct of paired salivary glands falls into the pharynx (Fig. 18). Behind the pharynx, in II and III chaetigers, a wide, black oesophagus is stretching, its length is approximately 4 mm, and width approximately 3 mm. The oesophagus is lined by black folded glandular epithelium. The oesophagus is followed by an elongated (about 5.5 mm) glossy pink stomach with strongly developed ring musculature. Width of the stomach is declining gradually towards the intestine. At the boundary with the oesophagus the stomach has a noticeable ringed dark thickening. The intestine is white, bends irregularly and consists of two parts (Fig. 18). The first part, 8.5 mm in length, is characterized by metamere structure and abundance of



Figs 18-20. *Flota vitjasi*. 18, digestive tract (vpo – ventral pharyngeal organ); 19, buccal tentacle; 20, fragment of buccal tentacle. Scale bar: 0.1 mm (19).

ringed and longitudinal musculature. The second, posterior end, or rectum, about 11 mm in length, is a smooth wide tube tapering towards the anus. Total length of the digestive tract notably exceeds the body length. Thus, body length being 20 mm, its length is equal to approximately 34 mm. Anus is terminal.

Structure of the digestive tract of *Flota* differs sharply from that of flabelligerids and apparent-

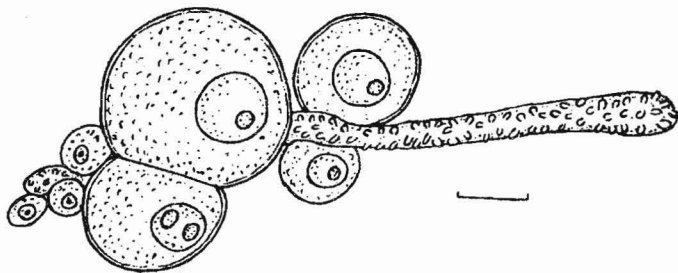


Fig. 21. *Flota vitjasi*, female gonad. Scale bar: 0.1 mm.

ly of fauveliopsids, which feed gathering food particles from surface layers of ground by means of grooved palps, dorso-lateral ciliary structures and ventral bulbus (Schlieper, 1927; Spies, 1975; Wilfert, 1975; Riser, 1987; Purschke & Tzetzlin, 1996). In the structure of the mouthparts and pharynx pelagic *Poebius* is also similar to them (Heath, 1930; Robbins, 1965). Oral tentacles are absent in these families. Numerous feeding oral filaments, or tentacles, are only found in representatives of the family Sabellariidae (order Sabellariida according to Pettibone, 1982 and Uschakov, 1985; Terebellida according to George in George & Hartmann-Schröder, 1985 and Kirtley, 1994; Sabellida according to Fauchald & Rouse, 1997) and in the families Pectinariidae, Ampharetidae, Alvinellidae, Trichobranchidae and Terebellidae from the order Terebellida. However, in contrast to *Flota*, buccal tentacles in these families collecting food particles from surface of ground layers are arranged in one or two groups antero-dorsally in relation to the mouth (Djakonov, 1913; Hessle, 1917; Heimler, 1978; Orrhage, 1978; Desbruyeres & Laubier, 1991; Kirtley, 1994; Zhadan et al., 2000). Ciliary tentacles of Cossuridae have no groove and are situated in the posterior dorsal part of the pharynx (Fournier & Petersen, 1991; Tzetzlin, 1994). Ciliated oral tentacles of Sabellariidae also have no groove. These tentacles are situated at the ventral side of the opercular podia and arise from buccal flap along both sides of the buccal cavity (Kirtley, 1994). According to Orrhage (1978), they are "extended lateral parts of the upper lip of the mouth" and therefore are part of peristomium (see Heimler, 1983). Oral tentacles of species of above-mentioned families of Terebellida are supplied with ciliary groove nearly always, but can be of cylindrical shape. There is no general agreement concerning initial place of tentacles of Terebellida. The arrangement of oral tentacles inside the mouth is regarded as a plesiomorphic state by Hessle (1917) on the basis of the data on their innervation. Holthe (1986) and Orrhage (2001) assume pharyngeal origin of buccal tentacles of this order. The hypothesis about

origin of oral tentacles from prostomial or peristomial palps is argued by Nilsson (1912), Fauchald & Rouse (1997), Rouse & Pleijel (2001), and others. In the process of larval development, first oral tentacles arise in front of mouth (Eckelbarger, 1974; Cazaux, 1982; Heimler, 1983; Lambert & al., 1996) and therefore are a part of prostomium. As to the genus *Flota*, to judge by the arrangement of oral tentacles on the dorsal side of the buccal cavity, they belong to peristomium.

A profound study of the ventro-lateral pharyngeal organ of *Flota* is needed. In the arrangement and presence of medially longitudinal invagination it is reminiscent of an analogous organ of Amphinomidae (see Gustavson, 1930; Dales, 1962). In *Flota* this organ is characterized by large size and deep invagination, i.e. it in fact has its own cavity. It possesses muscular anterior and posterior edges, lateral ridges diverging from it, and it has no gross rugosity in contrast to the pharyngeal organ of amphinomids.

The pharynx of *Flota* differs from the pharynx of flabelligerids also in the presence of paired pharyngeal glands. The oesophagus of *Flota* is much wider; the blind sack, characteristic of flabelligerids, falling into the anterior part of the stomach on the boundary with the oesophagus is absent. Moreover, in flabelligerids the intestine is similar everywhere, its structure is not metamorous (Quatrefages, 1849; Schlieper, 1927).

Female gonad and nephridial papillae. Female gonads (Fig. 21) have been discovered in the paratype of *F. vitjasi* on V and VI chaetigers. The remaining segments have not been studied. A gonad is a cord with numerous oocytes and 7 eggs. The eggs are polylecithal with a large nucleus and a thin membrane. Colouration is white. There are 1 or 2 nucleoli in the nucleus. Shape of eggs is spherical. Diameter of the largest egg is about 250 μm .

Nephridia of *Flota* have not been studied. Two pairs of long tubular, possibly nephridial papillae are arranged in *F. flabelligera* and *Flota* sp. from the Japan Trench on the ventral side of III and IV chaetigerous segments (Hartman, 1967); in *F. vitjasi*, only one pair of such papillae on the

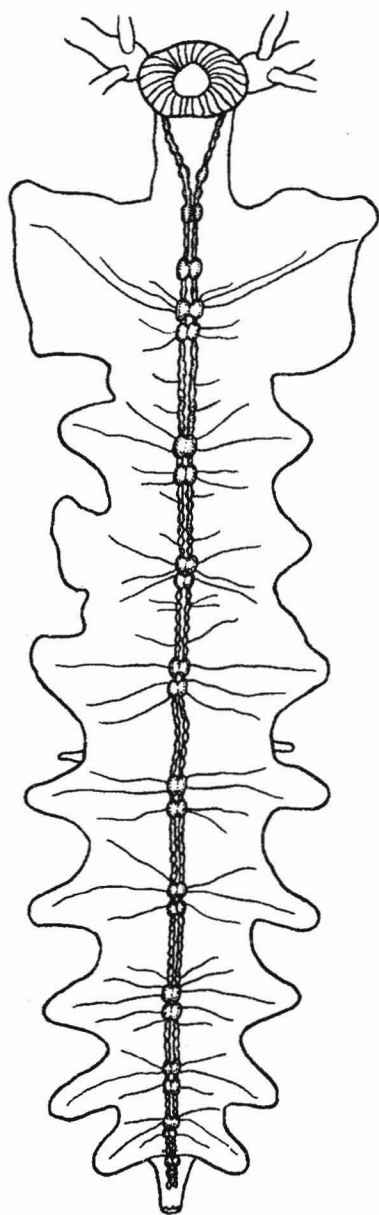


Fig. 22. *Flota vitjasi*, circumpharyngeal connectives and ventral nervous cord (scheme) (from Buzhinskaja, 1996).

posterior side of IV chaetiger has been discovered. In the majority of flabelligerids and *Poeobius*, the only pair of nephridia opens in the anterior end of the body (Schlieper, 1927; Robbins, 1965). Species of the genus *Brada* (Flabelligeridae), according to the data of many taxonomists, also possess a pair of prominent papillae on IV or V chaetigerous segments. *Diversibranchius nicolaji* Buzhinskaja and some other species of

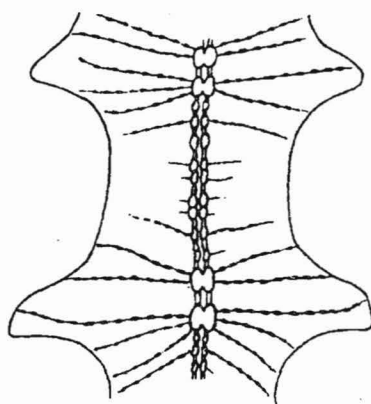


Fig. 23. *Flota vitjasi*, fragment of ventral nervous cord.

flabelligerids have short "nephridial" papillae or pores on 10-11 segments of the body, however, no anatomical studies of these formations have been performed. In *Poeobius*, there is a pair of gonoducts in the middle coelome (Robbins, 1965).

Circumpharyngeal connectives and ventral nervous cord. Circumpharyngeal connectives (Fig. 22) have three pairs of ganglia. In contrast to Flabelligeridae with ventral nervous cord lying between layers of musculature (Haswell, 1892; Schlieper, 1927) and *Poeobius* with ventral nervous cord in coelome (Robbins, 1965), the ventral nervous cord of *Flota* retains a primitive subepithelial position. Nervous stems are paired, but situated close to each other. The large paired segmental ganglia are fused with one another, but the boundaries between the right and the left halves are noticeable. In segment I there are 3 pairs of large ganglia, in all others there are 2 pairs in each; in the pygidial funnel there are also 2 pairs. Moreover, circumpharyngeal connectives and connectives of nerve cord of *Flota* are covered throughout their length by minute ganglionic swellings (Figs 2, 22, 23). Nerves diverge at least from some small ganglionic swellings as well as from large ganglia (Figs 22, 23). Hartman did not describe the ventral nervous cord of *F. flabelligera*, however, Carl Petterson who performed drawings of this species depicted the large ganglia and also the numerous nerves diverging not only from large ganglia, but also from connectives (Hartman, 1967, pl. 38, fig. A). In a typical case, one pair of ganglia is formed on the ventral nervous cord in each segment of body of polychaetes, including also flabelligerids and *Poeobius*. Segments of studied species of Sabelariidae, Sabellidae and Serpulidae contain 2 pairs of ganglia (Pruvot, 1885; Meyer, 1887, 1888). In Pectinariidae only a part of the segments have 2

pairs of ganglia and some, even 3 pairs, others, one pair (Nilsson, 1912). Additional numerous ganglionic swellings on connectives of the ventral nervous cord were only found among polychaetes of the genus *Flota* (Buzhinskaja, 1996). Such multiple ganglionization is possibly connected with the intensification of locomotory functions in an ancestral form of this genus with transition from sedentary mode of life to swimming and with the change of mode of feeding. Among invertebrates, possibly a similar process of concentration of nervous cells on connectives was described in larvae of *Echiurus abyssalis* in the class Echiurida (Korn, 1960). Ganglionization or concentration of nervous cells to form nodes is a criterion of the progress of the nervous system (Beklemishew, 1952). Apart from the numerous ganglia *Flota vitjazi* have swellings (aggregations of nervous cells) on the segmental nerves (Fig. 23).

Discussion

Thus, the genus *Flota* possesses characteristic structural features, differentiating it from all other polychaetes. Those include triramous non-grooved sensory palps, enormous ventro-lateral pharyngeal organ of peculiar structure and ventral nervous cord with numerous ganglia on connectives. Apart from being differentiated by these characters, *Flota* differs from flabelligerids and close families in the structure of the head region, presence of buccal tentacles, structure of the digestive tract, parapodia and pygidium, surface arrangement of the ventral nervous cord. Based on the knowledge available, it can be stated that similarity of *Flota* and flabelligerids is restricted by the structure of articulated chaetae and cuticle having a gelatinous layer penetrated by papillae, similarly to one of flabelligerid genera. It is noteworthy that the type of chaetae does not always determine to what family or order the genus belongs. It is known, for instance, that dentate platelike chaetae, uncini, are characteristic of polychaetes of different families and orders and also of Pogonophora. As concerns articulated chaetae, as has been shown above, they can also arise separately in different families and orders of polychaetes. Pedunculate excretory papillae have been found only in genera *Flabelligera* and *Flota*, which seems to bring *Flota* closer to flabelligerids. However, the characteristic structural features of *Flota* concerning organs of vital importance suggest that Flotidae are a separate taxon. Oral tentacles of *Flota* are similar in structure with grooved tentacles of above-mentioned families of Terebellida, but they differ in location. At present, it is difficult to name a group close to which Flotidae should be placed. It is

not improbable that discovery and study of new specimens of this remarkable genus and other representatives of Flotidae, further study of anatomy and investigation of the larval development will allow establishing the place of this family among polychaetes.

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References

- Beklemishew, W.N. 1952. *Osnovy sravnitel'noy anatomii bespozvonochnykh* [Fundamentals of the comparative anatomy of the invertebrates], Moskva: Sovetskaya Nauka. 698 p. (In Russian).
- Buzhinskaja, G.N. 1977. *Flota vitjazi* sp.n., a new deep-water pelagic species of the family Fauveliopsidae (Polychaeta, Annelida). *Issled. Fauny Morey*, 20(28): 9-12. (In Russian).
- Buzhinskaja, G.N. 1996. Unique characters of structure of some deepwater pelagic polychaetes. *Dokl. Akad. Nauk SSSR*, 347(1): 133-135. (In Russian).
- Cazaux, C. 1982. Développement larvaire de l'ampharetidae lagunaire *Alkmaria romijni* Horst. 1919. *Cah. Biol. mar.*, 23: 143-157.
- Crisp, M. 1977. The development of the serpulid *Pomatoleios krausii* (Annelida, Polychaeta). *J. Zool. London*, 183:147-160.
- Dales, R.Ph. 1962. The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proc. zool. Soc. London*, 139: 389-428.
- Dales, R.Ph. 1963. *Annelids*. London: Hutchinson University library. 200 p.
- Desbruyères, D. & Laubier, U. 1991. Systematics, phylogeny, ecology and distribution of the Alvinellidae (Polychaeta) from deep-sea hydrothermal vents. *Ophelia*, 5(suppl.): 31-45.
- Djakonov, A.M. 1913. Anatomisch-histologische Untersuchungen des Darmes von *Amphictelis gunneri* Sars (Polychaeta, Ampharetidae). *Tr. imp. Sankt-Peterburg. Obshch. Estestvoisp.*, 42(4): 297-346. (In Russian).
- Eckelbarger, K.J. 1974. Population biology and larval development of the terebellid polychaete *Nicolea zostericola*. *Mar. Biol.*, 27: 101-113.
- Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera. *Natur. Hist. Mus. Los Angeles Cty Sci. Ser.*, 28: 1-188.
- Fauchald, K. & Rouse, G. 1997. Polychaete systematics: Past and present. *Zool. Scripta*, 26(2): 71-138.
- Fisher, W.S. 1946. Echiuroid worms of the North Pacific Ocean. *Proc. U.S. nat. Mus.*, 96: 215-292.
- Fournier, J.A. & Petersen, M.E. 1991. *Cossura longicirrata*: Redescription and distribution, with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta: Cossuridae). *Ophelia*, 5(suppl.): 63-80.
- George, J.D. & Hartmann-Schröder, G. 1985. Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synopses of the British Fauna (New Series)*, 32. Linnean Soc. London. 221 p.
- Gustafson, G. 1930. Anatomische Studien über die Polychäten-Familien Amphinomidae und Euphrosynidae. *Zool. Bidr. Uppsala*, 12: 305-471.

- Hartman, O. 1955. Endemism in the north Pacific Ocean, with emphasis on the distribution of new or little known species. In: *Essays in the Natural Sciences in honour of Captain Allan Hancock*: 39-60. Los Angeles: University of the Southern California Press.
- Hartman, O. 1959. *Catalogue of the polychaetous annelids of the world*. Pt. 1. Los Angeles: University of the Southern California Press. 353 p.
- Hartman, O. 1967. Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises chiefly from Antarctic seas. *Allan Hancock Monogr. mar. Biol.*, 2: 1-387.
- Hartman, O. 1971. Abyssal polychaetous annelids from the Mozambique Basin off Southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. *J. Fish. Res. Bd. Canada*, 28(10): 1407-1428.
- Haswell, W.A. 1892. Observations on the Chloraemidae with special reference to the certain Australian forms. *Proc. Linn. Soc. N.S. Wales.*, 6(ser.2): 329-356.
- Heath, H. 1930. A connecting link between the Annelida and the Echiuroidea (*Gephyrea armata*). *J. Morphol.*, 49: 223-249.
- Heimler, W. 1978. Über Bau und Function der Larvalentakel bei *Lanice conchilega* (Polychaeta, Terebellomorpha). *Zool. Jb. Anat. Ont. Tiere*, 99: 59-63.
- Heimler, W. 1983. Untersuchungen zur Larvalentwicklung von *Lanice conchilega* (Pallas, 1766) (Polychaeta, Terebellomorpha). Teil III: Bau und Struktur der Aulophore-Larve. *Zool. Jb. Anat. Ont. Tiere*, 110: 411-479.
- Holthe, T. 1986. Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with catalogue of the taxa and a bibliography. *Gunneria*, 55: 1-236.
- Kirtley, D.W. 1994. A review and taxonomic revision of the family Sabellariidae Johnston, 1865 (Annelida, Polychaeta). *Sabecon Press*, 1(sci. ser.): 223 p.
- Korn, H. 1960. Ergänzende Beobachtungen zur Struktur der Larve von *Echiurus abyssalis* Skor. *Z. wiss. Zool.*, 164: 197-237.
- Lambert, R., Retiere, C. & Lagadeuc, Y. 1996. Metamorphosis of *Pectinaria koreni* (Annelida: Polychaeta) and recruitment of an isolated population in the English Channel. *J. mar. Biol. Assoc. U.K.*, 76: 23-36.
- McIntosh, W.C. 1915. *A monograph of the British Annelids*. Pt. 1. Polychaeta, Opheliidae to Amphicteniidae. London: Ray Soc. 368 p.
- Meyer, E. 1887. Studien über den Körperbau der Anneliden. *Mitt. Zool. Stn Neapel*, 7: 592-741.
- Meyer, E. 1888. Studien über den Körperbau der Anneliden. *Mitt. Zool. Stn Neapel*, 8: 462-658.
- Nilsson, D. 1912. Beiträge zur Kenntnis des Nervensystems der Polychaeten. *Zool. Bidr. Uppsala*, 1: 85-161.
- Orrhage, L. 1978. On the structure and evolution of the anterior end of the Sabellariidae (Polychaeta, Seden-taria). With some remarks on the general organization of the polychaete brain. *Zool. Jb. Anat.*, 100: 343-374.
- Pettibone, M.H. 1982. Annelida. In: *Synopses and classification of living organisms*, 2: 1-43. McGraw-Hill, New York.
- Pettibone, M.H. 1979. Redescription of *Bruunilla natalensis* Hartman (Polychaeta: Polynoidae) originally referred to Fauveliopsidae. *Proc. biol. Soc. Wash.*, 92(2): 384-388.
- Pruvot, G. 1885. Recherches anatomiques et morphologiques sur la système nerveux des Annelides Polychètes. *Arch. Zool. exp. gen. Paris* (sér. 2), 3: 211-336.
- Purschke, G. & Tzetlin, A.B. 1996. Dorsolateral ciliary folds in the polychaete foregut: structure, prevalence and phylogenetic significance. *Acta zool.*, 77: 33-49.
- Quatrefages, M.A. 1849. Types inférieurs de l'embranchement des Annelés. Mémoire sur la famille des Chlorémiens, Chloraemae, Nob. *Ann. Sci. natur.* (sér. 3), 12: 277-306.
- Riser, N.W. 1987. A new interstitial polychaete (Family Fauveliopsidae) from the shallow subtidal of Zealand with observations of related species. *Bull. biol. Soc. Washington*, 7: 211-216.
- Robbins, D.E. 1965. The biology and morphology of the pelagic annelid *Poeobius meseres* Heath. *J. Zool.*, 146: 197-212.
- Rouse, G.W. & Fauchald, K. 1997. Cladistics and polychaetes. *Zool. Scripta*, 26(2): 139-204.
- Rouse, G.W. & Pleijel, F. 2001. *Polychaetes*. New York: Oxford University press. 354 p.
- Salensky, W. 1882. Études sur le développement des Annelides. *Arch. Biol. Paris*, 3: 345-378.
- Schlieper, C. 1927. *Stylarioides plumosus*, eine monographische Darstellung. *Z. Morphol. Ökol. Tiere*, 7: 320-383.
- Sentz-Braconnet, E. 1964. Sur le développement des serpulidae *Hydroides norvegica* (Gunnerus) et *Serpula concharum* Langerhans. *Cah. Biol. mar.*, 5: 385-389.
- Spies, R.B. 1975. Structure and function of the head in flabelligerid polychaetes. *J. Morphol.*, 177: 187-208.
- Step-Bowitz, C. 1987. A new genus and species (*Yndolacia lopadorrhynchoides*) of pelagic polychaetes. Representative of a new family, Yndolaciidae. *Bull. biol. Soc. Washington*, 7: 128-130.
- Tzetlin, A.B. 1994. Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta, Cossuridae) from the White Sea. *Mém. Mus. nat. Hist. natur.*, 162: 137-143.
- Uschakov, P.V. 1972. Polychaetes of the suborder Phyllo-dociformia of the Polar Basin and the North-Western part of the Pacific (Families Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae, and Lacydoniidae). *Fauna SSSR* (n. ser.), 102: 1-272. (In Russian).
- Uschakov, P.V. 1985. About the classification of the Polychaeta. *Issled. Fauny Morey*, 34(42): 5-9. (In Russian).
- Wilfert, M. 1975. Nachweis eines Pharynx bulbus bei Polychaeten aus der Familie Flabelligeridae. *Helgoländer wiss. Meeresunters.*, 27: 313-323.
- Wilson, D.P. 1929. The larvae of the british Sabellari-ans. *J. mar. Biol. Assoc. U. K.*, 16: 221-268.
- Zhadan, A.E., Tzetlin, A.B. & Safronova, M.A. 2000. Anatomy of some representatives from the family Alvinellidae (Polychaeta, Terebellidae) from the Pacific hydrothermal habitats. *Zool. Zh.*, 39(2): 141-160. (In Russian).

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