

The position of the phyla Chaetognatha and Euconodontophylea in the classification of Metazoa

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Kasatkina, A.P. & Buryi, G.I. 1999. The position of the phyla Chaetognatha and Euconodontophylea in the classification of Metazoa. *Zoosystematica Rossica*, 8(1): 21-26.

The types of the fossil Chaetognatha *Paucijaculum samamithion* (Schram, 1973) found by F.R. Schram from Illinois Pennsylvanian in 1973 and euconodont imprints found by D.E.G. Briggs and others from Carboniferous Granton shrimp bed of Edinburgh are redescribed and reconstructed. Transverse muscular system and apatite composition is observed in different groups of vertebrates and cannot be a ground for undoubted insertion of euconodonts into Chordata. Many similar morphological features (head structure; presence of an intestine and gut diverticle; ventral ganglion; lateral fins flattened in dorso-ventral direction; grasping spines, and spermatophores) allow consideration of euconodonts as animals similar to Chaetognatha. However, such features as terminal position of mouth and anus, and the differences of the tooth apparatus structure give every reason to distinguish euconodonts as an independent phylum, Euconodontophylea. Unique fine structure of the muscular tissue and the structure of the intercellular contacts may indicate early separation of Chaetognatha from the common stem of Metazoa and commencement of original pathway of tissue perfection with preservation of the minimum organ amount. Apparently in Pre-Cambrian, before the skeletization, Chaetognatha and Euconodontophylea had a common ancestor. Both similar phyla belong to a single ancient independent branch, the superphylum Chaetodonta.

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INTRODUCTION

The position of the Chaetognatha and euconodonts in the Metazoa classification is under discussion. It is known that Chaetognatha are a small phylum (about 140 species) of carnivorous marine animals ranging in size from 2 to 120 mm. Most of them are planktonic, constituting a significant proportion of the plankton biomass and consuming large quantities of small copepods and fish fry. The affinities of the phylum have been debated for more than 200 years. Most of recent workers have concluded that the Chaetognatha are distant relatives of the three major deuterostome phyla (Hemichordata, Echinodermata and Chordata) (Hyman, 1959; Ducret, 1978; Ghirardelli, 1981). Telford & Holland (1993, p. 660, fig. 1) based on the molecular analysis "propose that the lineage leading to the chaetognaths

arose prior to the advent of the coelomate Metazoa".

Euconodonts, considered to be extinct, and proto- and paraconodonts have for a long time been attributed to the problematic remains of unknown marine animals, conodont-bearer, which lived from Cambrian to Triassic inclusive. Szaniawski (1982) found that protoconodonts were the grasping spines of Chaetognatha. The affinities of paraconodonts have not been determined yet, but, in our opinion, paraconodonts also represent isolated denticles of Chaetognatha. Euconodonts differ histologically from proto- and paraconodonts (Bengtson, 1976) and on this basis homology between them is absent. At present, many investigators refer euconodonts to primitive vertebrates (Aldridge et al., 1993; Purnell et al., 1995). They give the following arguments in favour of relation of euconodonts with vertebrates: the

presence of a thick muscular system arranged transversely, as in fishes, and similarity of chemical composition of fish teeth and skeletal elements of euconodonts. The purpose of this article is to contribute to the debate on origin and relation of Chaetognatha and euconodonts. We redescribe the imprints of fossil chaetognaths and euconodonts and compare them with recent representatives of the phylum Chaetognatha.

REDESCRIPTION OF CHAETOGNATHA IMPRINTS

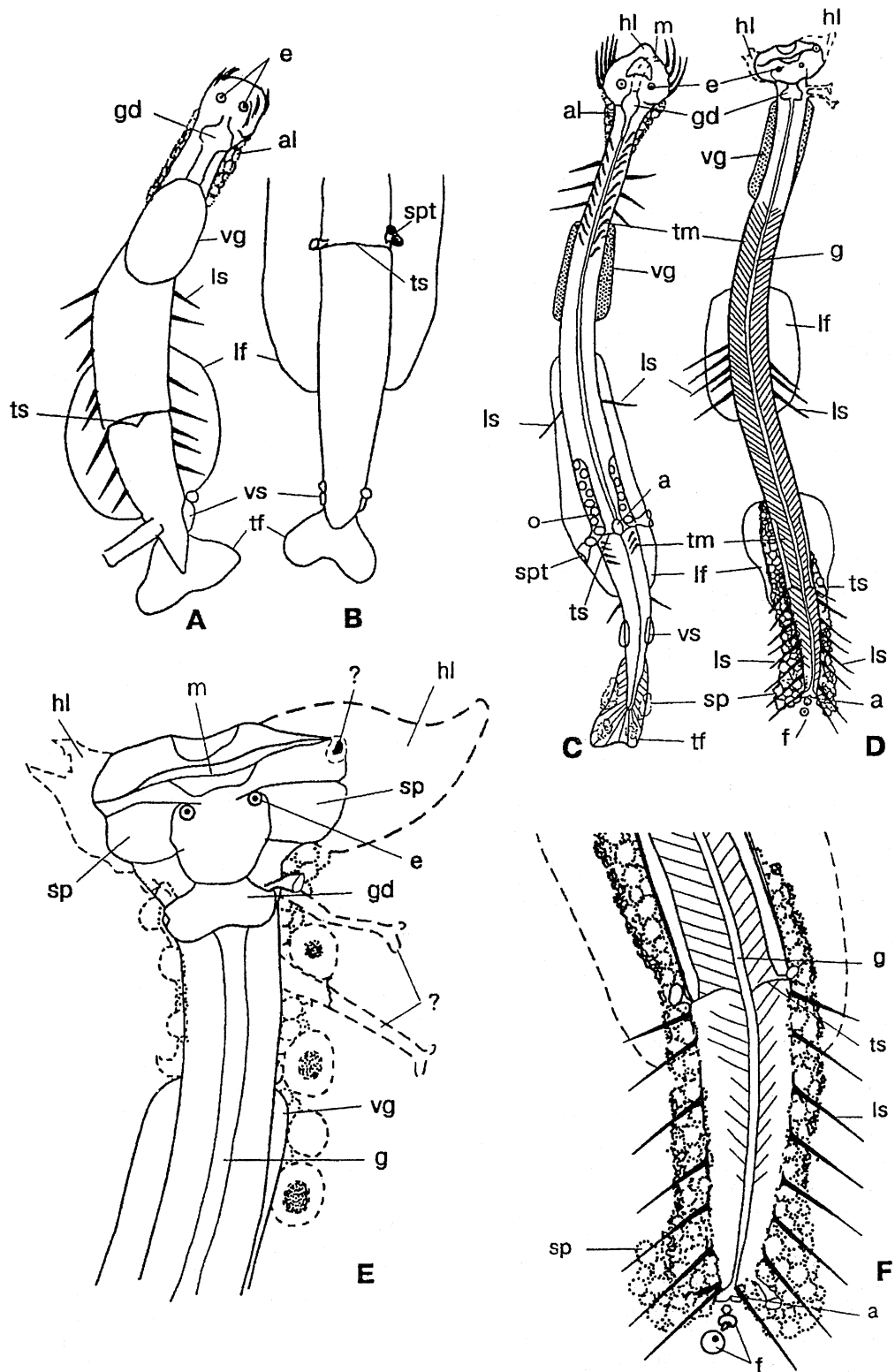
Our redescription is made from Schram's types of *Paucijaculum samamithion* (Schram, 1973) full imprint (PE 11640) and a fragment of the tail division (PE 12835) from the Pennsylvanian. The unique full imprint of *P. samamithion* (PE 11640) is about 22.5 mm long. Only the dorsal (back) part of the animal body is observable. At magnification, one can see paired eyes (Fig. 1A, *e*) and alveolar tissue (Fig. 1A, *al*) – the ectoderm derivative covered with cuticle only. The muscular pharynx (Fig. 1A, *gd*) is less distinctly visible. The large ventral ganglion extends beyond the body boundaries (Fig. 1A *vg*). Because of the relatively small size and dorsal position of the animal, its grasping spines and denticles are observed only as strips. The difference in colour of body and tail divisions suggests that at the instant of the animal's death, the tail division was filled with sperma, and so it is darker than the body division (as in recent Chaetognatha). On the boundary of the body and tail divisions, there are convexities which may be interpreted as spermathecae (Fig. 1B, *spt*). On the tail division (where a mote lies across the body), there is a seminal vesicle (Fig. 1A-B, *vs*), an organ for releasing spermatophores. It is impossible to observe any longitudinal or transverse muscular fibre and ovaries in the body divisions. Ovaries could be undeveloped as it is, for example, observed in the recent protandrous Eukrohniidae, in which the sperms mature much earlier than ova.

Fins (Fig. 1A-B, *lf* and *tf*) have been preserved much better in specimen PE 12835. However, the fin boundaries are not distinct (dash lines) and fins have no thick rays. On the body divisions, below the ganglion, and the tail division there are paired structures in the form of straight large spines. Spines of similar appearance are present in recent Chaetognatha. After Horridge & Boulton (1967), they perform locomotor function. Cytological data (Duvert & Salat, 1991) suggest that rays and fins have different structure: fins are the prominences of a basal membrane, and rays show cellular structure. In ontogenesis, they appear earlier than the structureless component of fins (Elpatyewski, 1913). Thus, we may suggest that the fins of ancient Chaetognatha represented the projections of basal membrane. Body spines were arranged separately from fins. Joining of body spines with projections of basal membrane resulted in the fins of the recent Chaetognatha. It is of interest that a notch on the tail fin is clearly seen in both imprint specimens. It is known that the intestine of Chaetognatha is formed from mouth to terminal part in the tail division. Originally, the anus opened not on the body-tail septum but terminally, in the tail part of the body, and so the tail fin could not be continuous, it had to be in the form of paired lobes on each side of anus. In the course of evolution, when obliteration (closing) of the intestine in the tail part occurred, the tail lobes grew together and formed a continuous tail fin. However, in some species, a notch remained as atavism.

REDESCRIPTION OF EUCONODONT IMPRINTS

This redescription is made from the best preserved specimen of *Clydagnathus* from Carboniferous Granton shrimp bed of Edinburgh (No. 6, RMS GY 1992. 41.2) (Aldridge et al., 1993). The animal lies on the ventral side and only the dorsal (back) side of *Clydagnathus* is accessible. In the

Fig. 1. Chaetodonta morphology (*a*, anus; *al*, alveolar tissue; *e*, eye; *f*, feces; *g*, gut; *gd*, gut diverticle; *hl*, head lobe; *lf*, lateral fin; *ls*, locomotor spines; *m*, mouth; *o*, ovaries; *sp*, spermatophores; *spt*, spermatheca; *sp*, skeletal plate; *tf*, tail fin; *tm*, transverse muscles; *ts*, tail septum; *vg*, ventral ganglion; *vs*, seminal vesicle; the question mark refers to the unknown morphological structures). **A-C.** Chaetognatha: **A**, new interpretation of the fossil *Paucijaculum samamithion* (Schram), specimen PE 11640 Mazon Creek area Middle Pennsylvanian, Illinois, based on the illustration published by Schram (1973); **B**, the tail fragment of the fossil *P. samamithion* (Schram), specimen PE 12835, the same location; **C**, the recent *Praeteterokrohnia* sp. **D-F.** Euconodontophylea, a new interpretation of *Clydagnathus*, the specimen No. 6, RMS GY 1992. 41.2, Carboniferous Granton shrimp bed of Edinburgh, Scotland: **D**, general view; **E**, fragment of the head; **F**, the tail fragment.



head region, the ectoderm derivatives, paired eyes (Fig. 1D-E, *e*) are visible. The slit-like mouth (Fig. 1E, *m*) is in terminal position. On mouth sides there are cephalic hunting lobes (Fig. 1D-E, *hl*). They consisted of soft tissues, so their contours are not distinct. Around neck there are structures (Fig. 1E, *?*) similar to the alveolar tissue of chaetognaths. They could give buoyancy to the heavy head. Deep inside the head there are paired head skeletal plates (Fig. 1E, *sp*) which are interpreted by other authors as eyes. Chaetognaths also have the head skeletal plates, however they are less thick, transparent. In Chaetognaths, they serve as attachments of muscles of the grasping spines and the muscle of the single lobe acting as a hood. Probably, skeletal plates of euconodonts had the same function. The tooth apparatus is arranged along the pharynx, its most massive P elements are in its most widened and apparently muscular part (Fig. 1D-E, *gd*). As is shown by Purnell et al. (1995), the P elements act as a crusher and pulverizer (scissors type) of food, and this is confirmed by small round faecal pellets going out from anus. Chaetognaths evolution resulted in reduction of transverse muscular system, and favoured development of other abilities – swallowing of a large prey (sometimes larger than Chaetognaths itself). A large ventral ganglion extends beyond the body boundaries (Fig. 1D-E, *vg*). Different colour allows separation of the animal body into trunk and tail divisions. The tail division makes about 17% of the total body length. A darker colour of the tail division suggests that it was filled with male sexual products, because immature animals show the same colour over the whole body. Delicate cloudy structures hanging on the tail locomotor spines in abundance testify that the animal died at the moment of spermatophore releasing. Abundant, rather large locomotor spines are arranged on sides of the body mostly in the tail division. Probably, the locomotor spines on the body performed the same function as in Chaetognaths. However, it is clear that the tail locomotor spines act as a device for supporting and bearing spermatophores. This specimen has two distinct pairs of fins. The fins, being a more delicate tissue, suffered in greater extent and are preserved worse compared to the muscular system. The tail fin is absent. Instead of it, on sides of the anus there are large spines, probably protecting the anus from damage. The anus (Fig. 1F, *a*) shows a

structure resembling opening flower petals. The animal died at the moment of defecation, and round faecal masses are going out from anus (Fig. 1F, *f*). A light band which may be undoubtedly interpreted as an intestine canal goes upwards from the anus.

DISCUSSION

When describing the imprint of the fossil Chaetognaths, Schram (1973) has supposedly found the similarity between *Paucijaculum samamithion* and recent Spadellidae. However, the analysis of morphology and proportions of different organs relative to the total body length indicate the propinquity of this fossil to another family of Chaetognaths.

(1) *P. samamithion* has rather short tail division, about 27-28% of the total body length. Apparently the proportions are not the same as in Spadellidae in which it is more than 45%, but such a short tail is found in other families of living Chaetognaths.

(2) The ventral ganglion is unusually large, about 23% of the total body length. Such a large ganglion is found in the recent genus *Aberrospadella* of the family Eukrohniidae (Kasatkina, 1982), but is not characteristic of any species of recent Spadellidae.

(3) The head division makes up about 12% of the total body length, which characterizes primitive Spadellidae and Eukrohniidae (*Aberrospadella* and *Tokiokaispadella*).

(4) The relatively large seminal vesicle (about 11% of the total body length and about 45% of the tail division length) suggests relationship of the fossil animal to Eukrohniidae. In addition, a similarity in the tail fin morphology is observed. In both fossil *Paucijaculum samamithion* and recent *Aberrospadella* there is a small notch on the centre; rays are absent. The imprint does not show any transverse muscular system. However, judging from the animal's flexion in lateral direction, a transverse muscular system must be present in *P. samamithia*, as the body of all Chaetognaths in which the transverse muscular system is absent can bend only in dorso-ventral, but under no circumstances in lateral direction.

(5) In our opinion, the imprint of the fossil euconodont shows similarity rather to Chaetognaths and not to vertebrates. The presence of a transverse muscular system in euconodonts is not a convincing argument to place them in vertebrates. Such a muscular system is present in many animal groups including primitive Chaetognaths.

METAZOA

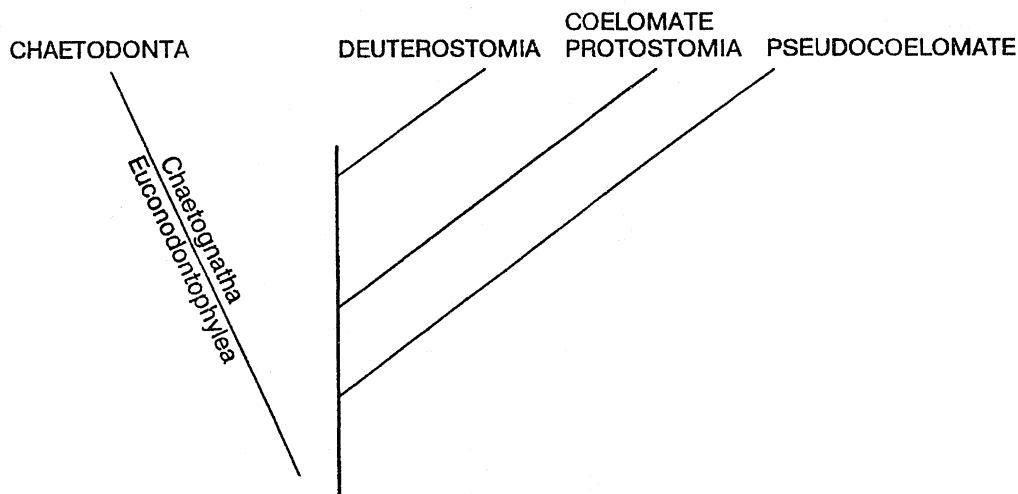


Fig. 2. The scheme of the Metazoa phylogeny.

(6) Not only fish teeth and euconodont elements, but also brachiopod lingulid (*Pleuropigia*) shells show the apatite composition. The similarity of chemical composition of fish teeth and euconodont skeletal elements cannot be considered as homology. Such is the case with the similar chemical composition of lipids in *Chaetognatha* and vertebrates, that we do not consider as homology (Kostetsky, 1985). The description of the euconodont imprint illustrates the absence of a chord in them, because the light structure piercing the animal along its centre is undoubtedly an intestine as it is in *Chaetognatha*. The head lobes of euconodonts are homologous with the hood of *Chaetognatha*, which serves to create streamline for swimming.

In addition to the arguments presented above, there is another feature making euconodonts and *Chaetognatha* similar: the presence of skeletal plates in their heads. Earlier, these plates in euconodonts were interpreted as eyes (Aldridge et al., 1993; Purnell et al., 1995).

(7) Fins in euconodonts and *Chaetognatha* are flattened in dorso-ventral, but in fish in lateral direction. Thus in fish and euconodonts fins are not homologous, which also contradicts to the idea of similarity of these groups.

(8) Apical position of mouth and distal position of anus in euconodonts indicate

their more primitive structure as compared with *Chaetognatha*. However, embryonic data show that the intestine of *Chaetognatha* develops up to the distal end. It testifies that initially the anus was on the distal end of the body as in euconodonts.

New data obtained with ultramicroscopy of *Chaetognatha* tissues (Duvert, 1969; Stolyarova & Kasatkina, 1988; Kapp, 1991; Bone & Goto, 1991) show this type to be undoubtedly ancient. In spite of the great similarity of transverse muscles of *Chaetognatha* and vertebrates, and quick wing muscles of insects (Basurmanova & Kasatkina, 1987), their fine structure demonstrates differences and unique muscular system in *Chaetognatha*. Unique peculiarity is shown also by the structure of the *Chaetognatha* intercellular contacts the diversity of which in metazoans (including plants and animals) is not large: 6 types at all. The seventh type of intercellular contacts has been found in adult primitive *Chaetognatha*, this can be taken as evidence of early separation of these animals from the common stem and commencement of an early, peculiar pathway of tissue development with preservation of the minimum organ number (Stolyarova & Kasatkina, 1988). Data on molecular biology (Telford & Holland, 1993) showed that *Chaetognatha* do not belong to Deuterostomia stem, and they separated before Protostomia, broke away from Deuterostomia. Comparison of

new data on morphology, molecular structure, and ultramicroscopy of Chaetognatha tissues with paleontological data on the electron microscopy of Conodonts, and recent findings of imprints of them allowed the conclusion that these animal groups have many similar features in morphology. However, the primitiveness of euconodont structure (mouth and anus show terminal position and thus they are not homologous to those in Chaetognatha) does not allow consideration of this group as a class of the phylum Chaetognatha and gives every reason to distinguish euconodonts as an independent phylum Euconodontophylea (Kasatkina & Buryi, 1996a, 1996b). In euconodonts, the major axis of symmetry is along the digestive canal, but Chaetognatha (Beklemishev, 1964) are typically bilateral animals with a pronounced dorso-ventral symmetry. Apparently, in Pre-Cambrian, before skeletization, Chaetognatha and Euconodontophylea had a common ancestor. Both similar phyla belong to a single ancient independent branch. We propose to name it superphylum Chaetodontia (Fig. 2).

Acknowledgements

We thank Academician O.G. Kussakin and Prof. I.I. Starobogatov for consultations, Prof. Yu.D. Zakharov and Prof. H. Szaniawski for valuable advice. The paper has been carried with the support of the Russian Foundation for Basic Research (grant No. 98-04-49355a).

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Received 24 June 1998