

Cambrian chaetognaths recognized in Burgess Shale fossils

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Oesia disjuncta, one of the species of the soft-bodied fauna collected and described by Walcott (1911) from the Middle Cambrian Phyllopod Bed (Burgess Shale, British Columbia, Canada) is recognized as a chaetognath. For anatomical comparisons many specimens of Recent chaetognaths were specially compressed and dried to obtain forms similar to the fossils preserved in shales. The most characteristic features shared by the fossil and Recent specimens include: strongly elongated, transversely striated and very flexible body, large size, and characteristically diversified shape of head, pronounced intestine and horizontally oriented caudal fin. Possible traces of other chaetognath structures—grasping apparatus, lateral fins, seminal vesicles, ventral ganglion, ovaries and anus—are also present but preserved in one specimen only. Among extant genera, those showing the closest similarity to *Oesia* Walcott, 1911 are the hyperbenthic *Archeterokrohnia* Casanova, 1986¹, and *Heterokrohnia* Ritter-Záhony, 1911, which are considered by some authors as evolutionarily most primitive.

Key words: Chaetognatha, *Oesia*, soft-bodied fossils, protoconodonts, Cambrian, Burgess Shale, Canada.

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Introduction

Chaetognaths, commonly known as arrow worms, are a small phylum of exclusively marine, bilaterally symmetrical, invertebrates. They have a rounded or sub-triangular head and strongly elongated body (up to 120 mm in length) (Figs. 1D–F, 4). The head is armed with a feeding apparatus composed of strong, chitinous grasping spines and small teeth (Fig. 3A–F, H). The body is circular in cross section, filled with a fluid and usually translucent. Additionally, the animals are equipped with horizontally arranged lateral and tail fins. They live in all marine habitats. Most are planktonic, some are benthic or hyperbenthic but all have a similar structure. Because of their mass occurrence and predatory mode of life, chaetognaths play an important role in the marine food web. Paleontological as well as molecular data indicate their very ancient origin (see Szaniawski 1982, 2002; Telford and Holland 1993, 1997), but despite extensive investigations the old statement of Darwin (1844: 1), that the animals are “remarkable for the obscurity of their affinities” is still valid (Bone et al. 1991; Ghirardelli 1994, 1995; Telford 2004). It is not clear even if chaetognaths are closer to protostomes or deuterostomes. It has been long known that during embryogenesis they exhibit deuterostomy and some other features characteristic for the deuterostomes. However, most of the recent molecular studies suggest their closer relationship with protostomes (Telford and Holland 1993; Wada and Satoh 1994; Halanych 1996; Helfenbein et al. 2004; Papillon et al. 2004). According to Telford (2004) it is

probable that chaetognaths inherited some features directly from a common ancestor of both of the groups, protostomes and deuterostomes, but “[...] more genetic data need to be gathered in the expectation that the picture will continue to become clearer” (Telford 2004: 256). Therefore it is very important to learn more about their origin, evolution and phylogeny. Unfortunately, the fossilization potential of the delicate bodies of chaetognaths is very low, and consequently their fossil record is poor. Only the chitinous grasping apparatus has a somewhat greater chance to become fossilized. Such apparatuses and their detached elements, commonly known as protoconodonts, occur quite commonly in rocks of late Proterozoic to Early Ordovician age (Szaniawski 1982, 2002). Recently, they were found also in Carboniferous strata (Doguzhaeva et al. 2002). All of the hitherto known fossil grasping spines of chaetognaths are secondarily phosphatized. Some other, non-phosphatized fossils have been described as possible chaetognath bodies but none of these are really convincing (see Szaniawski 2002). The stratigraphically oldest of these fossils was recently reported from the Lower Cambrian of South China (Chen and Huang 2002). However, preservation of the single specimen, described as *Eognathacantha ercainella* Chen and Huang, 2002 is insufficient for certain determination. The most important features suggesting its affinity with chaetognaths are traces of structures resembling grasping spines. However, their nature is uncertain because somewhat similar traces, in addition to those in the head region, also occur near the supposed anus of the specimen.

¹ According to Kapp (1991) *Archeterokrohnia* is a junior synonym of *Heterokrohnia*

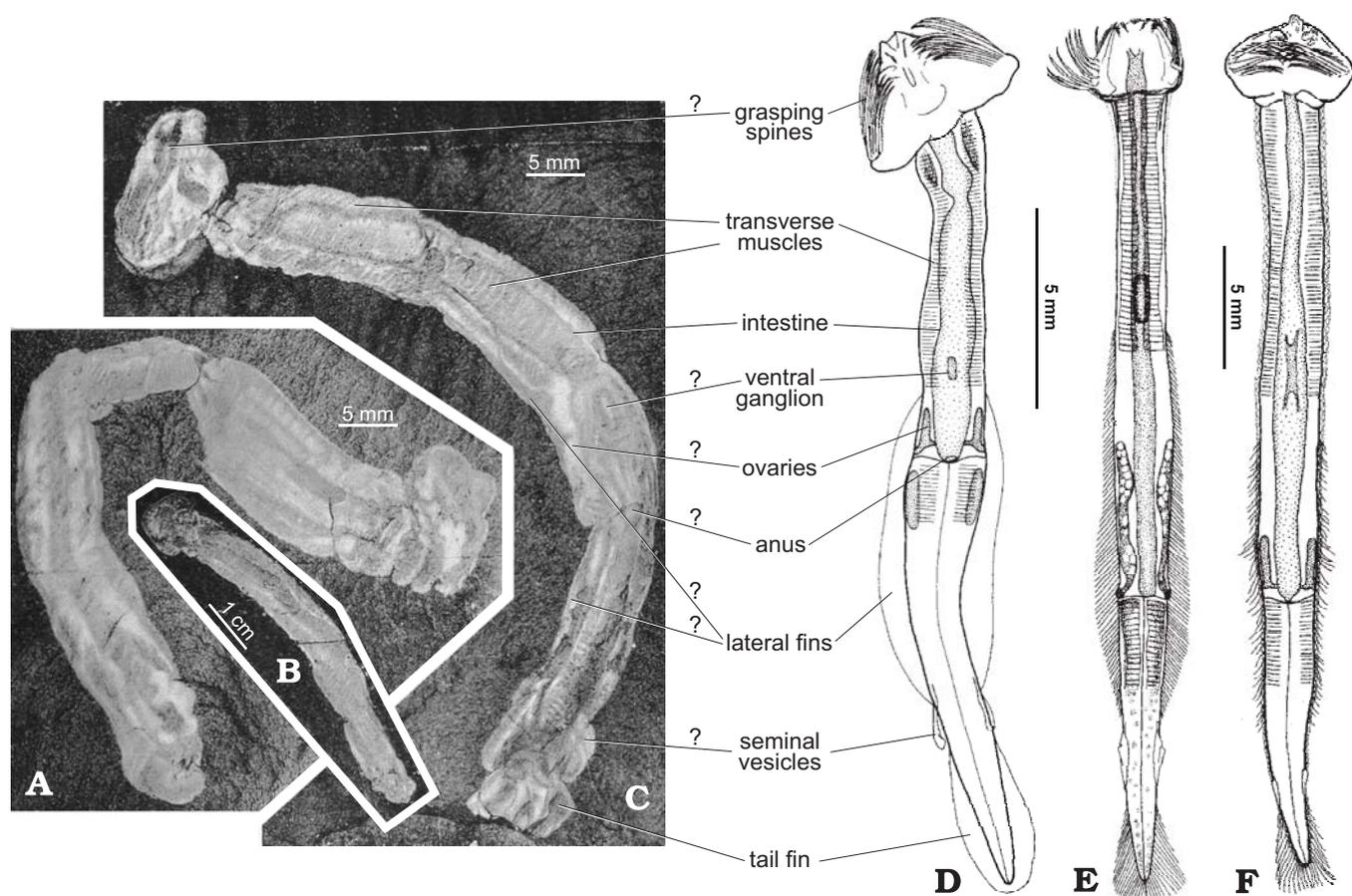


Fig. 1. A–C. *Oesia disjuncta* Walcott, 1911. A. USNM 57631. B. USNM 57632. C. USNM 57630, lectotype. D. *Archeterokrohnia rubra* Casanova, 1986. E. *Heterokrohnia mirabilis* Ritter-Záhony, 1911. F. *H. furnestine* Casanova and Chidgey, 1987. A–C, after Walcott (1911); D–F, after Kapp (1991).

In most old text books of paleontology, *Amiskwia sagittiformis* Walcott, 1911 has usually been cited as the only fossilized chaetognath. This species was described in one of the classic papers of Walcott (1911), among many other excellently preserved fossils from the famous Middle Cambrian Burgess Shale of British Columbia. However, the systematic position of the species has been challenged subsequently (Owre and Bayer 1962; Conway Morris 1977; Bieri 1991).

Anatomical-comparative studies of selected fossils from Walcott's collection and Recent chaetognaths have confirmed an earlier supposition (Szaniawski 2002) that among fossil chaetognaths, it is not *A. sagittiformis* but rather *Oesia disjuncta* Walcott, 1911, that is most similar to Recent chaetognaths and thus should be assigned to this phylum. In the original description *Oesia* was assigned to the polychaete annelids. Later, Lochmann (1922) interpreted it as a tunicate, but Tarlo (1960) favoured the original determination of Walcott.

Institutional abbreviations.—USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

Walcott's collection of these fossils is housed in the U.S. National Museum of Natural History in Washington, D.C. Originally, nine specimens in the collection were identified as *O. disjuncta*, but only the three specimens illustrated in his paper (Walcott 1911: pl. 20: 3–5; this paper Fig. 1A–C) are comparatively well-preserved. Preservation of all other specimens does not allow recognition of structural details. Two of them are illustrated in the present paper (Fig. 2B, F). In addition, there are some other specimens in the same museum drawer originally determined as "Miscel. worms, Genus indet. Sp. indet.". Two of these are determined herein as *O. disjuncta* (Fig. 2A, E).

Four of the specimens illustrated in this paper (Figs. 1B, C and 2B, C, E, G) are represented in the collection by part and counterpart. Specimen USNM 57630, illustrated in Figs. 1C, 2C is chosen here as the lectotype of *O. disjuncta*.

The collection of Recent chaetognaths used for comparative anatomical studies is stored in the Institute of Paleobiology, Polish Academy of Sciences in Warsaw. The last two numerals used for the specimens in this collection indi-

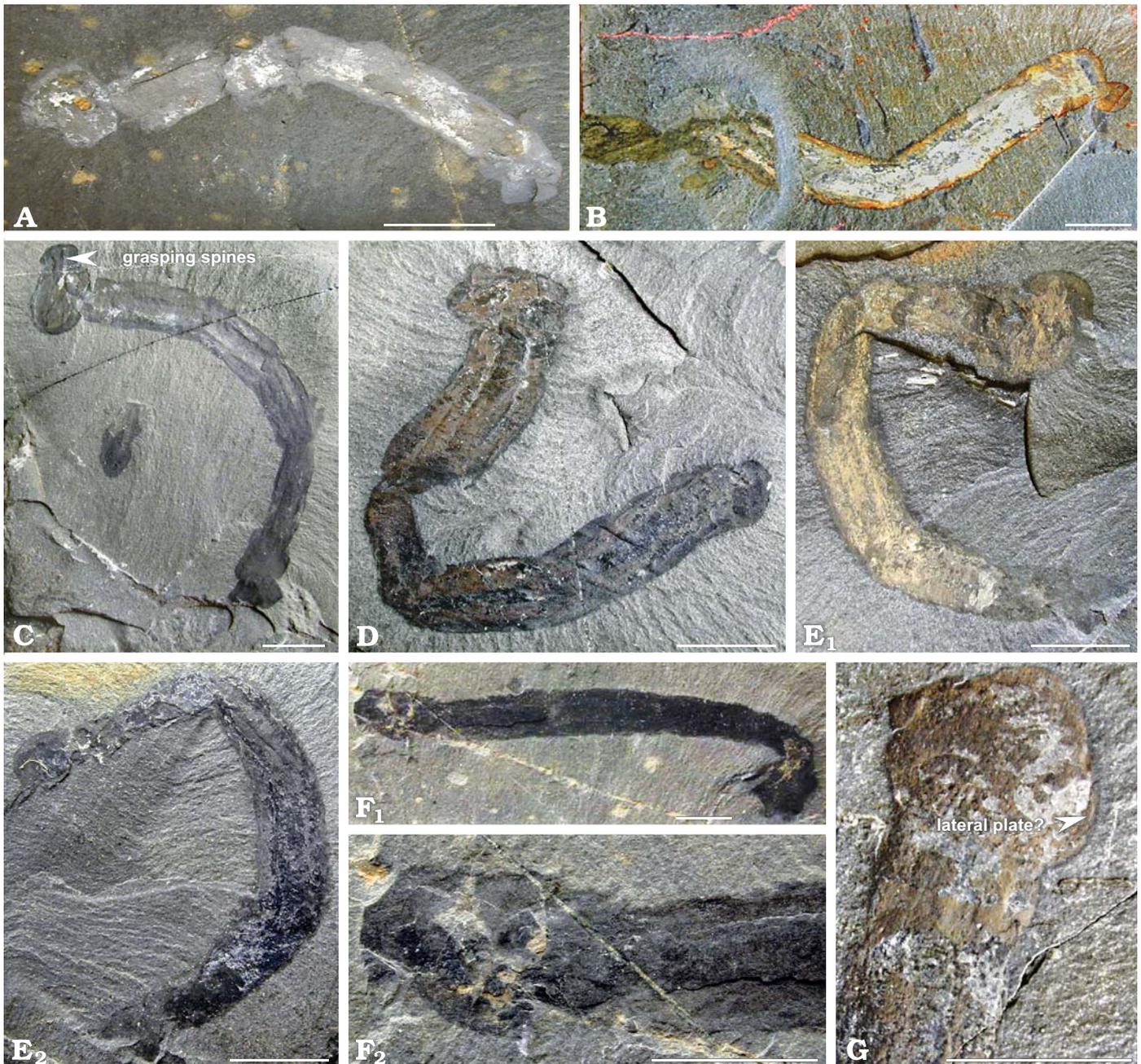


Fig. 2. *Oesia disjuncta* Walcott, 1911. A. USNM 277849. B. USNM 200552. C. The same specimen as on Fig. 1C in slightly different view. D. The same specimen as on Fig. 1A in slightly different view. E. USNM 277842 (E₁) and USNM 277841 (E₂), part and counterpart of the same specimen. F. USNM 203021, whole specimen (F₁), and anterior part in higher magnification (F₂). G. Anterior part of the counterpart of the specimen illustrated on Fig. 1B. Scale bars 1cm.

cate the number of the SEM stub and of the specimen on the stub (e.g., 147.5 means specimen no. 5 on the stub no.147).

Studies of the fossils are based on the illustrations published by Walcott (1911) and on numerous digital photos made recently using various angles and styles of illumination.

Studies of Recent chaetognaths were based on the rich collection of chaetognaths, gathered during Polish Antarctic Expeditions. About twenty five comparatively large specimens of different taxa (*Sagitta* Quoy and Gaimarad, 1827,

Eukrohnia Ritter-Záhony, 1909, *Heterokrohnia*, and undetermined) were selected for comparative anatomical investigations. In order to simulate deformations similar to those usually observed in soft-bodied fossils preserved in shales, about twenty of the specimens were washed in water and/or alcohol, placed between two pieces of glass (or between pieces of paper covered by glass), slightly compressed, and air dried. Some of the specimens before compression were stained for better visibility of the inner structure. The remain-

der were washed in water, partly dehydrated in alcohol and attached to SEM stubs using sticky, electro conductive tape. Rapid attachment of wet specimens to the sticky tape protected them from strong deformation during drying.

During processing some of the specimens became damaged but it was still possible to make some observations and photograph them under binocular and/or scanning electron microscopes.

Results of comparative anatomical studies

Comparative studies showed numerous close structural similarities between *Oesia disjuncta* and all the experimentally deformed Recent chaetognaths that are almost certainly not coincidental.

An anatomical interpretation of *O. disjuncta* is shown in Fig. 1.

The most characteristic feature of *O. disjuncta* is the strong variation in the outline of the head. This feature was mentioned in the original description of Walcott (1911). A strikingly similar diversity in head shape was also characteristic for the dead bodies of Recent chaetognaths, especially after drying and compression (Fig. 3). This variability in shape occurs because shape depends on the arrangement of the grasping apparatus, which is diverse during life (resting or active position) and is often strongly deformed after death.

Moreover, the head of the compressed and dried chaetognaths is usually much wider than the rest of the body (Fig. 3B, H), similar to what is observed in *O. disjuncta* (Fig. 1A, C). This is because the grasping apparatus often became extended laterally due to postmortem muscular contraction and also because the head is much more resistant to contraction during drying than the rest of the body.

The specimens of *O. disjuncta* do not have well-preserved feeding apparatuses. Although Walcott (1911: 133) noted "Traces of minute hooks at the anterior end [...] of one specimen", his observation is probably erroneous because unquestionable hooks can not be identified in any of the museum specimens. Probable traces of a grasping apparatus, occur in the specimen illustrated in Figs. 1C and 2C, yet not in the form "of minute hooks". The shape of the head of this specimen indicates that the apparatus was in resting, laterally extended position, as in specimens of Recent chaetognaths illustrated in Figs. 1F, 3B.

Despite the fact that the feeding apparatus of *O. disjuncta* is preserved only in the form of unconvincing remnants, the

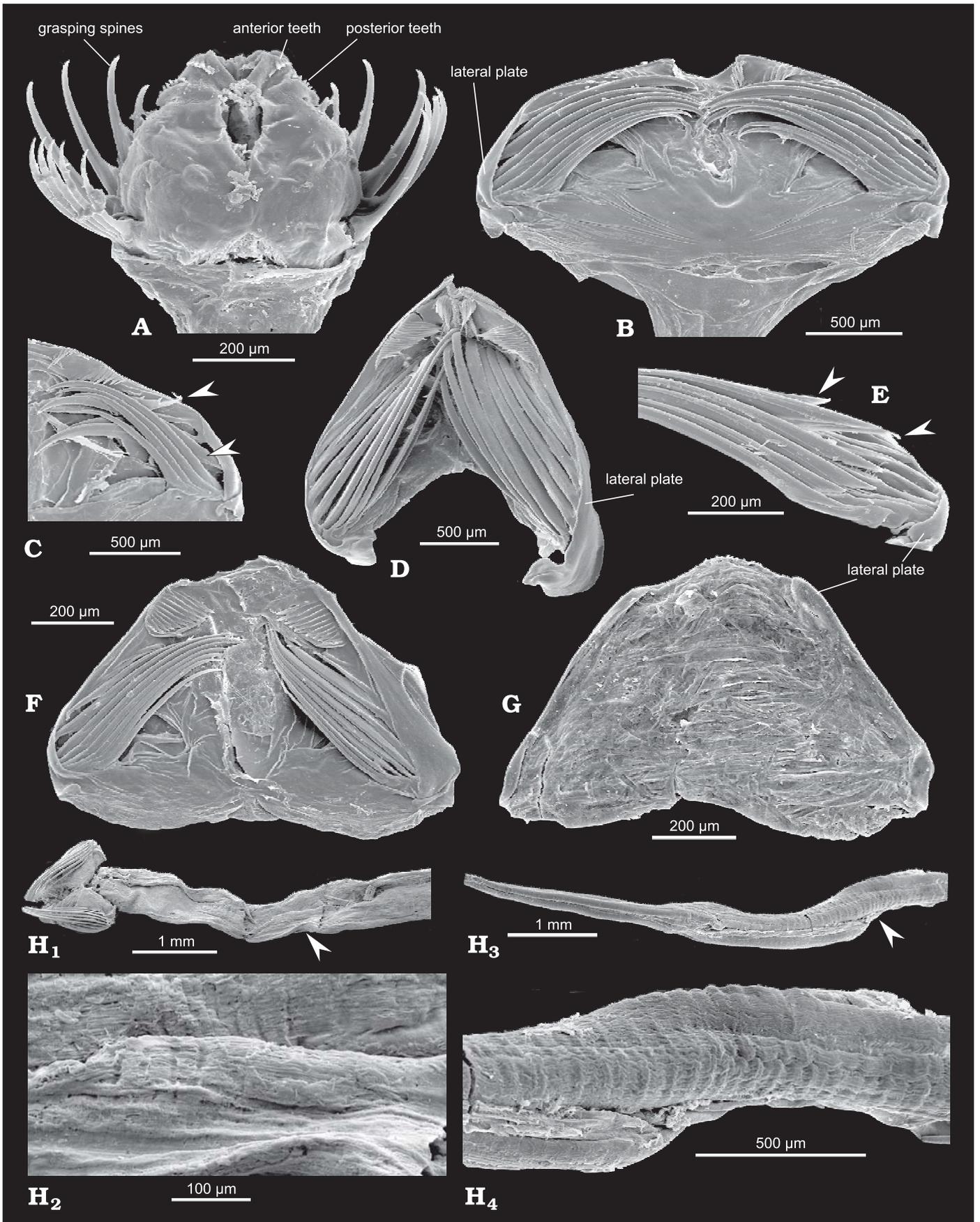
differentiation of the shape of head suggests that the species possessed an apparatus very similar in structure to the grasping apparatus of Recent chaetognaths. The fact that this is not preserved can be explained in two ways: (1) during taphonomic processes, the comparatively rigid, chitinous spines could be lost; experiments conducted on extant chaetognaths show that the drying of flattened specimens often causes their grasping spines to be partly pulled out of the relatively flexible cuticular pockets (Fig. 3C, E); (2) the apparatus certainly would not be fossilized in a similar manner to the rest of the body because of the difference in chemical composition. The grasping spines and teeth are composed mainly of crystalline α -chitin (Atkins et al. 1979) which, during long-term fossilization processes undergo chemical changes completely different from those affecting the soft tissues. The fossilization conditions for chitin in the Burgess Shale fauna were not as favorable as for the soft tissues, despite the fact that chitin has much greater decay resistance (Butterfield 1990; Briggs 1999; Petrovich 2001). As mentioned above, fossilized grasping apparatuses of chaetognaths are known only in the form of secondarily phosphatized spines (Szañkowski 1980, 1982, 2002; Doguzhaeva et al. 2002) while "...the depositional setting of the Burgess Shale was different from settings that favor phosphatisation" (Petrovich 2001: 705).

Therefore, the original presence and arrangement of the feeding apparatus in the specimens of *O. disjuncta* can be recognized mainly from the outline of the heads. In contrast to transversely elongated head of the specimen illustrated in Figs. 1C and 2C the apparatus of the specimen illustrated in Figs. 1B and 2G was arranged, after death, in the natural resting position, somewhat similarly to the Recent chaetognaths illustrated in Fig. 3D, H.

Most of the specimens of *O. disjuncta* are strongly twisted, and some of them seem to be twisted completely around, e.g., the specimen illustrated in Figs. 1A and 2D. Bodies of dead chaetognaths often are similarly twisted. In life, the body is supported only by a hydroskeleton (Bone and Duvert 1991; Kapp 1991), and because of this it quickly collapses after death when the drop in internal pressure of the fluid filling the body cavity causes the body to become very flexible.

Traces of the intestine of *O. disjuncta* are clearly visible in all three of the best-preserved specimens (Figs. 1A–C, 2C, D). Judging from these the intestine was very wide and long. The intestine possibly protruded through the trunk/tail septum, as in some extant chaetognaths such as *Heterokrohnia longicaudata* (Hagen and Kapp, 1986), then narrowed but

Fig 3. A–G. Heads or fragments of heads of undetermined Recent chaetognaths; A–F, in ventral view. A. Air dried head with grasping apparatus in acting position; ZPAL Cg.1/147.5. B. Compressed head with laterally extended grasping apparatus in resting position; ZPAL Cg.1/142.1. C, E. Fragments of the compressed heads with grasping apparatus in resting position. Arrows point on the spines pulled out of the cuticular pockets, ZPAL Cg.1/146.2 and ZPAL Cg.1/143.1. D. Grasping apparatus in resting position; ZPAL Cg.1/141.3. F. Compressed head with grasping apparatus in resting position, partly extended laterally; ZPAL Cg.1/147.9. G. Compressed head with grasping apparatus in similar arrangement as in F but in dorsal view. H. *Heterokrohnia* sp. ZPAL Cg.1/141.1. H₁, slightly compressed anterior part of the specimen in ventral view, arrow points to the fragment magnified on H₂; H₃, posterior part of the same specimen but not compressed, arrow points to the fragment magnified on H₄. →



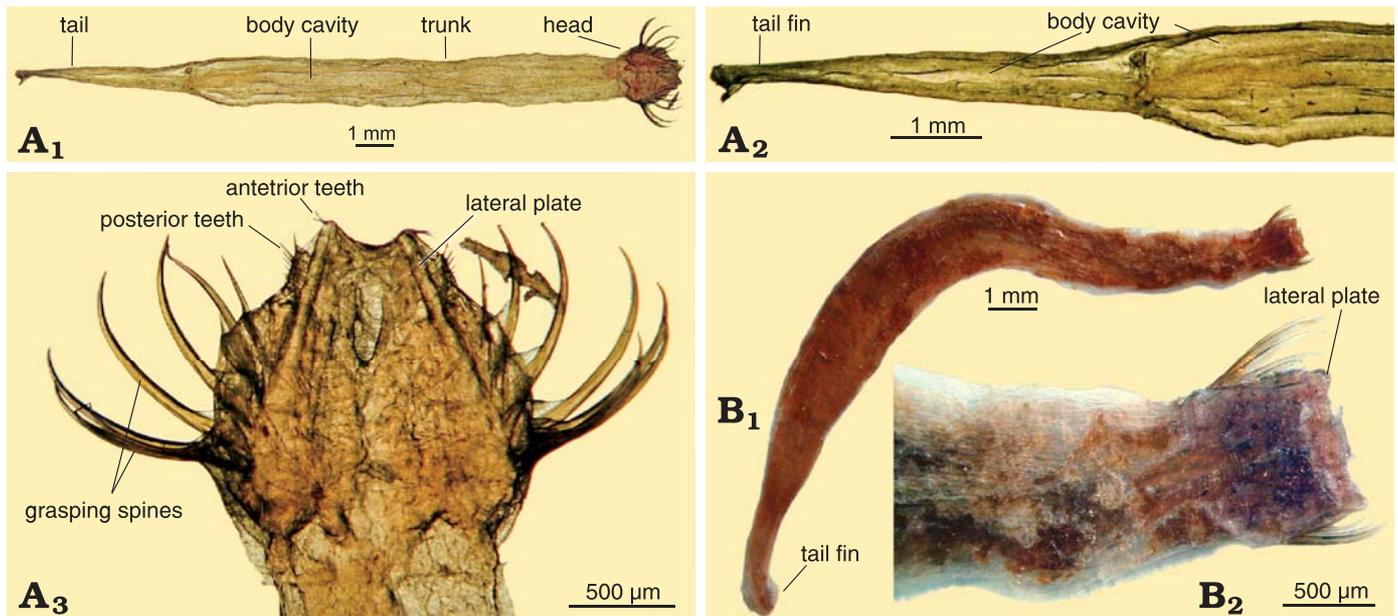


Fig. 4. A. *Sagitta* sp., compressed specimen in transmitted light, dorsal view; ZPAL Cg.1/146. Whole specimen (A₁); magnification of the posterior part (A₂); magnification of the head (A₃). B. ?*Sagitta* sp., stained and compressed specimen in reflected light, dorsal view; ZPAL Cg.1/146.1. Whole specimen (B₁); magnification of the anterior part (B₂).

continued far to the posterior.² The intestine of Recent chaetognaths is also very prominent.

The body of *O. disjuncta*, or at least part of it, is cross striated (Figs. 1A, C, 2C, D). This striation was interpreted by Walcott (1911) as segmentation. However, the unclear preservation suggests that it reflects a rather delicate, most probably internal structure. Similar striation occurs in modern chaetognath muscles and is easily visible in their dried bodies (Figs. 1D–F, 3H). Striation is especially well-developed in taxa possessing not only longitudinal but also transverse muscles. Such musculature occurs in those genera which, contrary to the majority of chaetognaths, lead benthic (*Paraspadella* Salvini Plawen, 1987; see Bowman and Bieri 1989), epibenthic (*Spadella* Langerhans, 1880) or hyperbenthic (*Archeterokrohnia*, *Heterokrohnia*, and some *Eukrohnia*) modes of life. According to some authors (Tokioka 1965; Kassatkina 1980; Casanova 1986; 1996; Casanova and Duvert 1996, 2002), these are evolutionarily primitive forms.

The caudal fin of *O. disjuncta*, like that of chaetognaths, is horizontally oriented and has a similar shape and size. The fin is comparatively well-preserved in the specimens illustrated in Figs. 1C, 2C, F. In other specimens it is strongly deformed (Fig. 2A, B, E) or insufficiently differentiated (Figs. 1A, B, 2D).

Lateral fins are not well preserved in any of the *Oesia* specimens. Probable remnants of them occur only in the specimen illustrated in Figs. 1C, 2C. The poor preservation of the fins can be explained by the experiments made on extant chaetognaths, which show that lateral fins are usually

preserved much more poorly than caudal fins. Lateral fins usually become damaged or “glued” to the body and invisible during processing and drying of a specimen. The fins of chaetognaths are very flexible and delicate and in some species are completely rayless. It is obvious that their fossilization cannot be easily accomplished.

Probable seminal vesicles are comparatively well preserved in the lectotype only (Fig. 1). Interpretation of such delicate structures as the ventral ganglion, ovaries and anus, based on the same specimen, is even less certain.

Oesia is compared here to the Recent hyperbenthic genera *Archeterokrohnia* and *Heterokrohnia* because only these genera have transverse muscles developed in both trunk and tail and therefore are considered to be phylogenetically most primitive (Casanova 1986; Casanova and Duvert 2002). Benthic genera and some species of the partly hyperbenthic genus *Eukrohnia*, possess these muscles in the trunk only, while the majority of chaetognaths lack them altogether.

The hypothesis that *Heterokrohnia* is primitive is also supported by paleontology. Recently described phosphatised Carboniferous chaetognath grasping spines (Doguzhaeva et al. 2002) are denticulated in a manner similar to the spines of juvenile *Heterokrohnia longidentata* Kapp and Hagen, 1985. In both the fossil and Recent forms the denticles are inclined towards the tips of the spines. Among other Recent chaetognaths, similar denticulation of grasping spines occurs only in some species of juvenile *Eukrohnia*, which is probably closely related to *Heterokrohnia* (Casanova and Duvert 1996). Furthermore, species of *Serratogitta* Tokioka, 1965

² According to some authors “Chaetognaths are not tripartite as sometimes suggested” (Bone et al. 1991: 3) and the caudal, transversal septum “... is clearly a secondary separation” (Ghirardelli 1995: 168).

possess spines with denticulation but which are inclined toward the base, whereas the spines in the vast majority of chaetognths are not denticulated.

Obviously there are some differences between *Oesia* and Recent chaetognaths. The tail of Recent forms gradually narrows posteriorly, a feature that cannot be seen in *Oesia*. However, in some Recent chaetognaths, e.g., *Flaccisagitta Tokioka*, 1965 and *Parasagitta Tokioka*, 1965, the tail is very short and does not show a pronounced narrowing. Most species of Recent forms are smaller in size than *Oesia*, but adult forms of some species are larger. Similarly, most of the Recent forms are comparatively narrow, but some representatives of benthic species are wide. The seminal vesicles of most of Recent chaetognaths is small compared to the supposed vesicles of *Oesia*, but in some benthic species (e.g., *Spadella gaetanoi* Alvariano, 1978 and *Paraspadella schizoptera* (Conant, 1895)) the vesicles are of a similar size to those of *O. disjuncta*.

Archeterokrohnia and *Heterokrohnia* lead a hyperbenthic mode of life in deep waters (usually 1000–4000m), while most of the fauna preserved in the Phyllopod Bed of the Burgess Shale belong to a benthic community that inhabited moderately deep water (Conway Morris 1986; Petrovich 2001). Thus it is very probable that the morphological differences between the fossil and Recent forms compared herein are the results not only of evolutionary development but also of different environments and modes of life.

It is interesting to note that Walcott when studying *Oesia disjuncta* (1911: 133) gained the impression that the species “[...] lived in an irregular tube that was so thin the annelid shows through it”. In fact Recent chaetognaths have a tube-like shape and their body is covered by a thin and translucent epithelium.

Acknowledgements

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