

New evidence for the protoconodont origin of chaetognaths

HUBERT SZANIAWSKI



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An earlier hypothesis concerning the origin of chaetognaths from protoconodonts found additional support in new discoveries and in recent structural, chemical and molecular investigations. The new findings show that the head armature of protoconodonts was composed not only of grasping spines but also of much smaller spicules corresponding in size and shape to the chaetognath teeth. Grasping spines of protoconodonts were originally built mainly of an organic substance. Their original composition was changed by secondary phosphatisation. The thickest layer of the protoconodont spines was originally constructed of organic fibrils, similar to those in the corresponding layer of chaetognaths. Recent molecular investigations show that the chaetognath lineage separated in the early stage of metazoan radiation, which fits the presented hypothesis. Described are some previously unknown structural details of chaetognath grasping spines, including composition of the outer layer and the origin of their distinctive tips.

Key words: Chaetognatha, Conodonta, protoconodonts, problematic fossils, Metazoan phylogeny, Cambrian, Ordovician.

Hubert Szaniawski [szaniaw@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Chaetognaths, commonly called arrow worms, are small, bilaterally symmetrical, marine animals of enigmatic origin and unknown systematic position (for review see Bone et al. 1991; Ghirardelli 1994). They live in different environments and may be planktonic or benthic, but all of them are predatory and similar in structure. The chaetognath body consists of a rounded or somewhat triangular, flattened head and an elongated, fluid-filled trunk. The head is usually armed with one or two paired rows of small teeth located antero-ventrally and a group of big grasping spines (“hooks”) situated on the postero-lateral sides. The trunk bears one or two pairs of lateral fins and a terminal, horizontally oriented, “tail” fin (Fig. 1). Some authors are of the opinion that “Chaetognaths are not tripartite as sometimes suggested” (Bone et al 1991: 3) but their body consists only of a head and trunk.

The length of the animals ranges from 2 to 120 mm. As they often occur in great abundance, they constitute a very important component of the marine food web. Nearly 200 species of chaetognaths have been described (Ghirardelli 1997), but their phylogenetic relationships are still unknown and their origin is commonly regarded as enigmatic.

No uncontroversial chaetognath body fossils are known, despite some published supposed finds. The chaetognath nature of *Amiskwia sagittiformis* Walcott, 1911, from the Cambrian Burgess Shale, was challenged by Owre and Bayer (1962), Conway Morris (1977), and Bieri (1991). However, recently Butterfield (1990) returned to the original opinion stating (p. 272) that: “... it may in fact be a chaetognath ...”.

Paucijaculum samamithion Schram, 1973 from the Pennsylvanian of Illinois is presently the only extinct species quite commonly accepted as a chaetognath, but preservation of the illustrated specimens (Schram 1973: pl. 1: 7, pl. 2: 5) does not permit a reliable interpretation. Bieri (1991) supported the chaetognath affinity of *Paucijaculum*, but did not provide new data.

The preservation of three specimens described as *Titerina rokycanensis* Kraft and Mergl, 1989 from the Lower Ordovician of Bohemia (Kraft and Mergl 1989; Kraft et al. 1999) is also insufficient for a good reconstruction. Moreover, the head of this species is more poorly differentiated than in the chaetognaths and its armature consists of one pair of comparatively short, forceps-like “spines”, which are different from the grasping spines of extant chaetognaths.

In my opinion to the list of body fossils possibly related to chaetognaths should be added *Oesia disjuncta* Walcott, 1911, from the Burgess Shale, originally described as an annelid. However, the problem needs further study.

The lack of a good fossil record of chaetognaths is quite understandable because they are completely devoid of mineralized skeleton and have a soft body covered by very thin integument. Unusually for invertebrates, the trunk and the dorsal surface of chaetognath head are covered by multi-layered epidermis and devoid of cuticle. A mono-layered epidermis producing cuticle occurs only on the ventral surface of the head (see Ahnelt 1984; Kapp 1991). The construction of the trunk supports only a “hydroskeleton” (Bone and Duvert 1991). It is obvious that the fossilization potential of these animals is extremely low. Only the chitinous elements

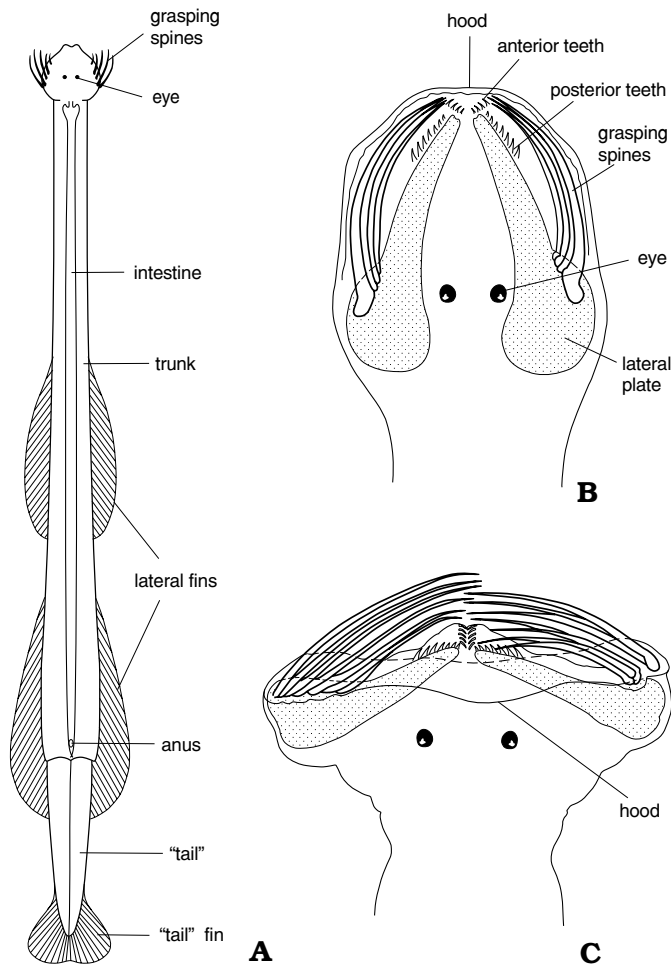


Fig. 1. Diagrams of the chaetognath body (A) and arrangements of the head armature in ventral view (B, C). B. The armature arranged in resting position, enclosed by hood. C. The hood withdrawn, the head enlarged and the grasping half-apparatuses arranged against themselves. (A, after Kapp 1999, simplified, B, and C, after De Beauchamp 1959, simplified).

of the head have a slightly better chance of being fossilized (Fig. 1B, C).

In the early eighties I published a hypothesis that some of the Lower Palaeozoic microfossils usually assigned to the informal group of protoconodonts¹ represent in fact grasping spines of chaetognaths or animals closely related to them (Szaniawski 1980, 1982; Repetski and Szaniawski 1981). The assumption was based on great morphological and structural similarity of the isolated spines and architecture of the whole grasping apparatus of the fossil and recent forms. The hypothesis has been commonly accepted or seriously considered (e.g., Dzik 1986; Sweet 1988; Bengtson 1990; Bone et al. 1991; Berezinskaya and Malakhov 1994; Kasatkina and

Buryi 1997; Kraft et al. 1999, Doguzhaeva et al. 2002) but some authors expressed an opinion that all the similarities could be the result of convergence (e.g., Andres 1988; Müller and Hinz 1991).

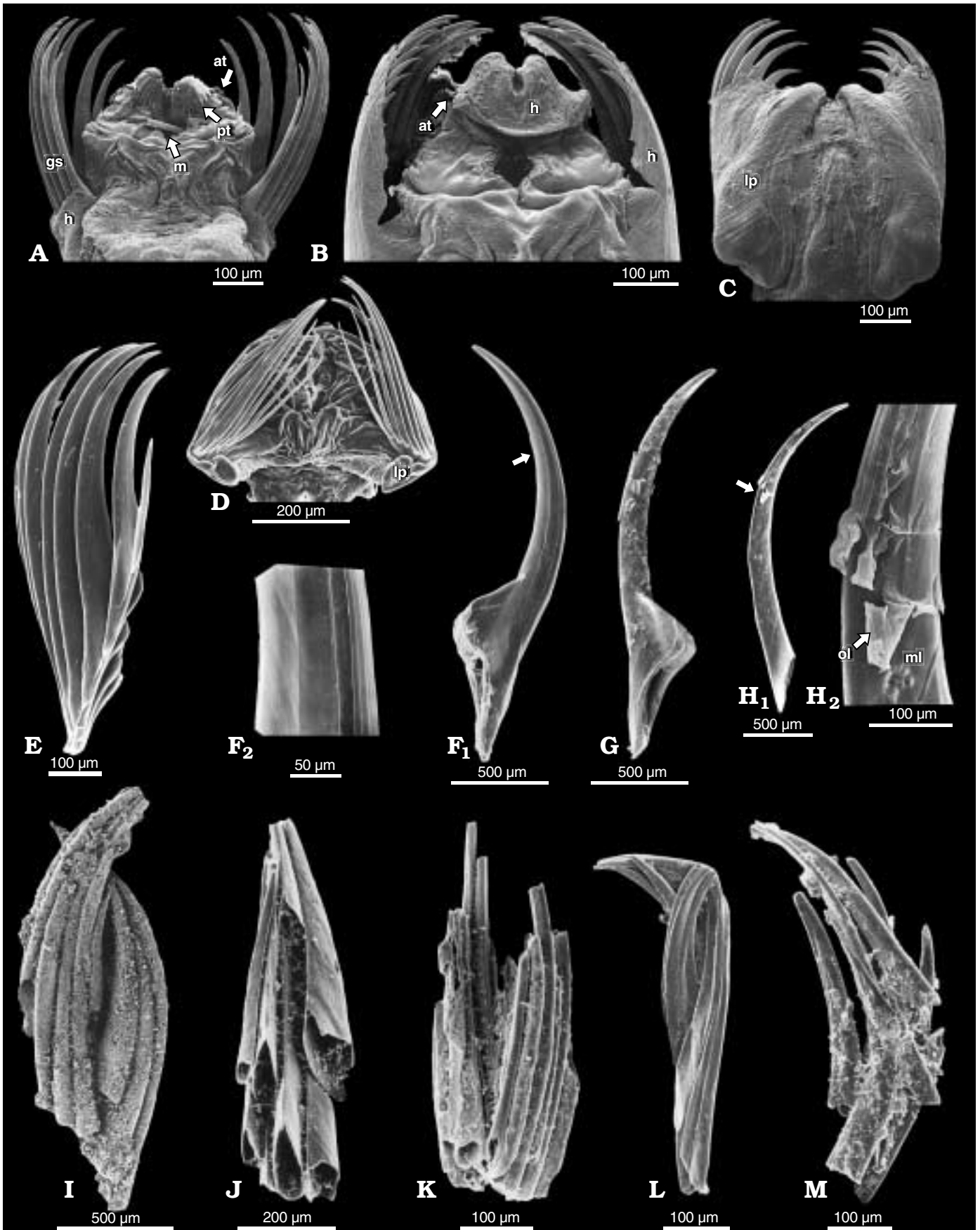
During the past twenty years the knowledge of the structure, diversity, and occurrence of protoconodont elements has greatly increased. Also, some new data about the structure and composition of the grasping spines of recent chaetognaths have been obtained. The new data seem to support the hypothesis of the chaetognath origin from protoconodonts. However, it is understandable that it can not be finally accepted until the protoconodont grasping spines are found in association with other fragments of the animals. A special search for such evidence has produced some interesting results. A partial grasping apparatus of a Cambrian protoconodont has been found in natural association with three small spines corresponding in shape and size to chaetognath teeth. The discovery was announced at the Sixth European Conodont Symposium (Szaniawski 1996), and another, similar specimen has subsequently been found (see Fig. 7G).

The objective of this paper is to summarize the current knowledge on chaetognath and protoconodont head armature, to compare and discuss recently discovered structural details, to present results of new chemical studies of protoconodonts, and to discuss recently published ideas on the origin of the chaetognaths based on molecular investigations.

Most of the results presented herein, concerning fossil

Fig. 2. A–D. Head of Recent *Sagitta* sp., showing arrangement of the armature, soft parts deformed because of drying. A. Ventral view, hood withdrawn, grasping apparatus in position of action; ZPAL C.IV/6.20. B. Ventral view, grasping apparatus in resting position, hood slightly damaged, almost completely enclosing the grasping spines and teeth; ZPAL C.IV/6.27. C. Dorsal view, grasping apparatus in resting position, incompletely enclosed by partly damaged hood; ZPAL C.IV/6.23. D. Ventral view, basal part of the head enlarged, hood withdrawn, grasping apparatus in intermediate position; ZPAL C.IV/6.28. E. *Sagitta* sp., grasping half-apparatus in dorsal view; ZPAL C.IV/1.1. F–H. Recent *Sagitta maxima* Conant, South Shetland Islands. F₁. Isolated grasping spine in dorsal view showing opening of the pulp cavity; ZPAL C.IV/118.25. F₂. Fragment of the same in slightly different position, showing longitudinal ridges and oblique lines reflecting direction of the fibrils of the middle layer. G. Grasping spine treated briefly with KOH solution; note relationship of the spine to the partly damaged basal pocket; ZPAL C.IV/4.3. H. Grasping spine after more prolonged treatment with KOH solution; ZPAL C.IV/4.2. Whole spine without the basal pocket and most of the outer layer damaged as a result of the treatment (H₁). Magnification of the fragment showing partly damaged outer layer and well preserved middle layer underneath (H₂). I–M Grasping-spine apparatuses of protoconodonts. I. Almost complete apparatus of *Phakelodus tenuis* (Müller); ZPAL C.IV/6.2. J. Incomplete half-apparatus of *Phakelodus savitzkyi* (Abaimova) in inner lateral view showing keels of the spines; ZPAL C.IV/9.13. K. Partly damaged apparatus of *Phakelodus tenuis* (Müller); ZPAL C.IV/6.1. L. Deformed apparatus of gen. et sp. indet.; ZPAL C./117.14. M. Disturbed half-apparatus of *Phakelodus* sp.; ZPAL C./1.7. I–K and M from the subsurface Upper Cambrian of northern Poland. L. Lower Tremadocian of Öland Island, Sweden. (E, F, and H after Szaniawski 1982; fig. 3A–G). Abbreviations: at, anterior teeth; gs, grasping spines; h, hood; lp, lateral plate; m, mouth; ml, middle layer; ol, outer layer; pt, posterior teeth. Arrow without caption shows fragment magnified on next illustration.

¹ The informal term "protoconodonts" (introduced by Bengtson 1976) is used for slender, organophosphatic sclerites commonly occurring in the Cambrian and Lower Ordovician. Similar fossils were recently found also in the Upper Mississippian (Doguzhaeva et al. 2002). The protoconodonts are often treated as ancestors of conodonts but they differ in structure and composition and their affinity with conodonts is not certain.



ized material, are based on collections obtained from the subsurface Upper Cambrian of northern Poland (deep drillings: Żarnowiec-1, Żarnowiec-4, Darżlubie, Hel). Collections from Upper Cambrian and Lower Ordovician outcrops in Sweden (Västergötland and Öland Island) were also studied. The extant chaetognaths were collected in the North Sea and Antarctic region. All of the investigated Recent specimens belong to *Sagitta* Quoy and Gaimard, 1827. Most useful were specimens of *Sagitta maxima* Conant, 1896, because of their comparatively large size.

Because of the variable preservation of protoconodonts, different methods for their preparation had to be used (see Szaniawski 1983, 1987). Good results were often obtained by etching the sectioned or fractured specimens in chromium sulphide or 3% hydrochloric acid. To avoid deformation, the critical point method of drying has been often used. The prepared specimens of protoconodonts were studied by optical (biological and petrographic) microscopy, and scanning electron microscopy. For chaetognaths, transmission electron microscopy was also used.

The investigated collection is housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw (ZPAL) and in the Swedish Museum of Natural History, Stockholm (SMNH). The Arabic numerals indicate the number of the SEM stub and of the specimen on the stub (e.g., 6.15 means specimen no. 15 on the stub no. 6).

Skeletal structure of the chaetognath head

Grasping spines, teeth and head plates (ventral and lateral) are the only hardened structures of the chaetognaths. They are composed of chitin (Atkins et al. 1979) and are more resistant to damage than the rest of the body. The strongest of them are grasping spines. These are comparatively large and have a solid and complex structure.

Grasping apparatuses of all chaetognaths are similar in shape and construction. They consist of two symmetrical half-apparatuses composed of 4 to 14 spines arranged in arched rows on both sides of the head (Figs. 1, 2A–D). The spines are long, slim and inwardly curved (Fig. 2E–H); in some species serrations are present along the sharp inner margin (= keel). Within each half-apparatus the spines are differentiated in length, width and degree of curvature (Fig. 2E). The base of each spine is mounted in a pocket of weakly sclerotized cuticle. The pockets are attached to the lateral plates (Fig. 1B, C). When not in use, the spines of each half apparatus are in juxtaposition (Figs. 1B, 2B, C). In action they spread and form a kind of basket, surrounding the prey from all sides (Fig. 2A). In cross section, the spines are wedge-shaped, tapering toward the inner margin (Figs. 3A, 6G)

The morphology and anatomy of the grasping spines as observable with optical microscopy was described a long time ago (Krumbach 1903; Schmidt 1940). However, some

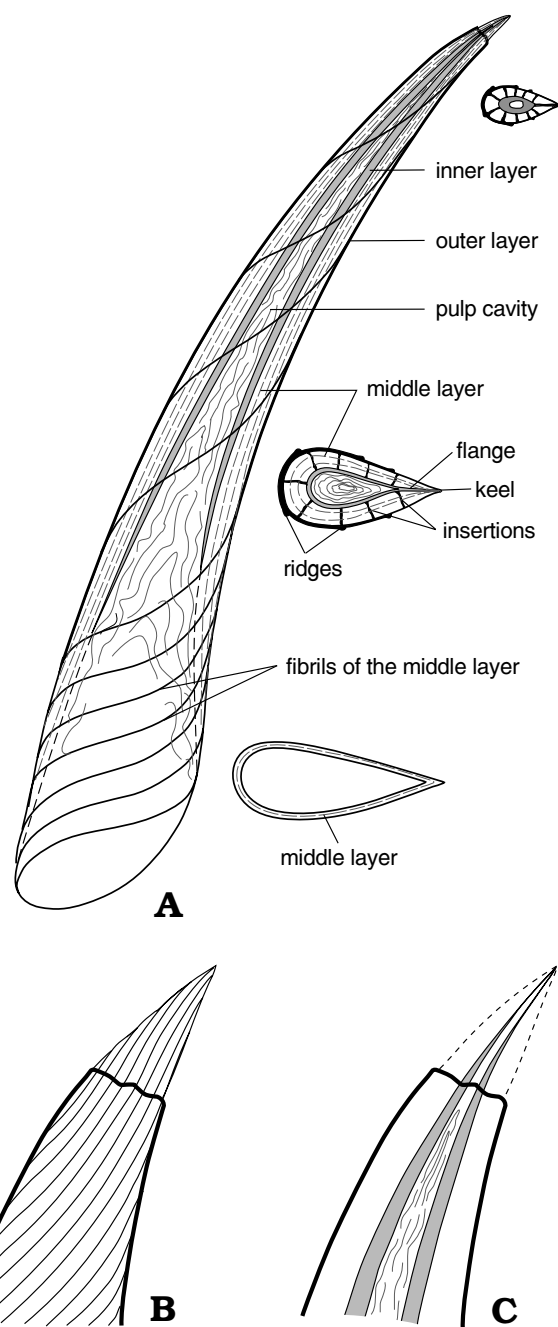


Fig. 3. Diagrams showing internal structure of the chaetognath grasping spines. A. Whole grasping spine and its cross sections. B, C. Distal portion of grasping spine showing structure of its tip.

details of their inner structure could be detected only with the electron microscope (Szaniawski 1982; Bone et al. 1983; Ahnelt 1984; Berezinskaya and Malakhov 1994). Some new observations are presented here.

Unlike teeth and jaws or setae of other animals, the grasping spines and teeth of chaetognaths are built of three different layers: the outer, thin, apparently homogenous, electron-dense layer, the middle, comparatively thick fibrous layer and the inner, again thin and electron-dense but laminated layer. The layers surround a large pulp cavity extending from the base up to the tip of the spines (Fig. 3).

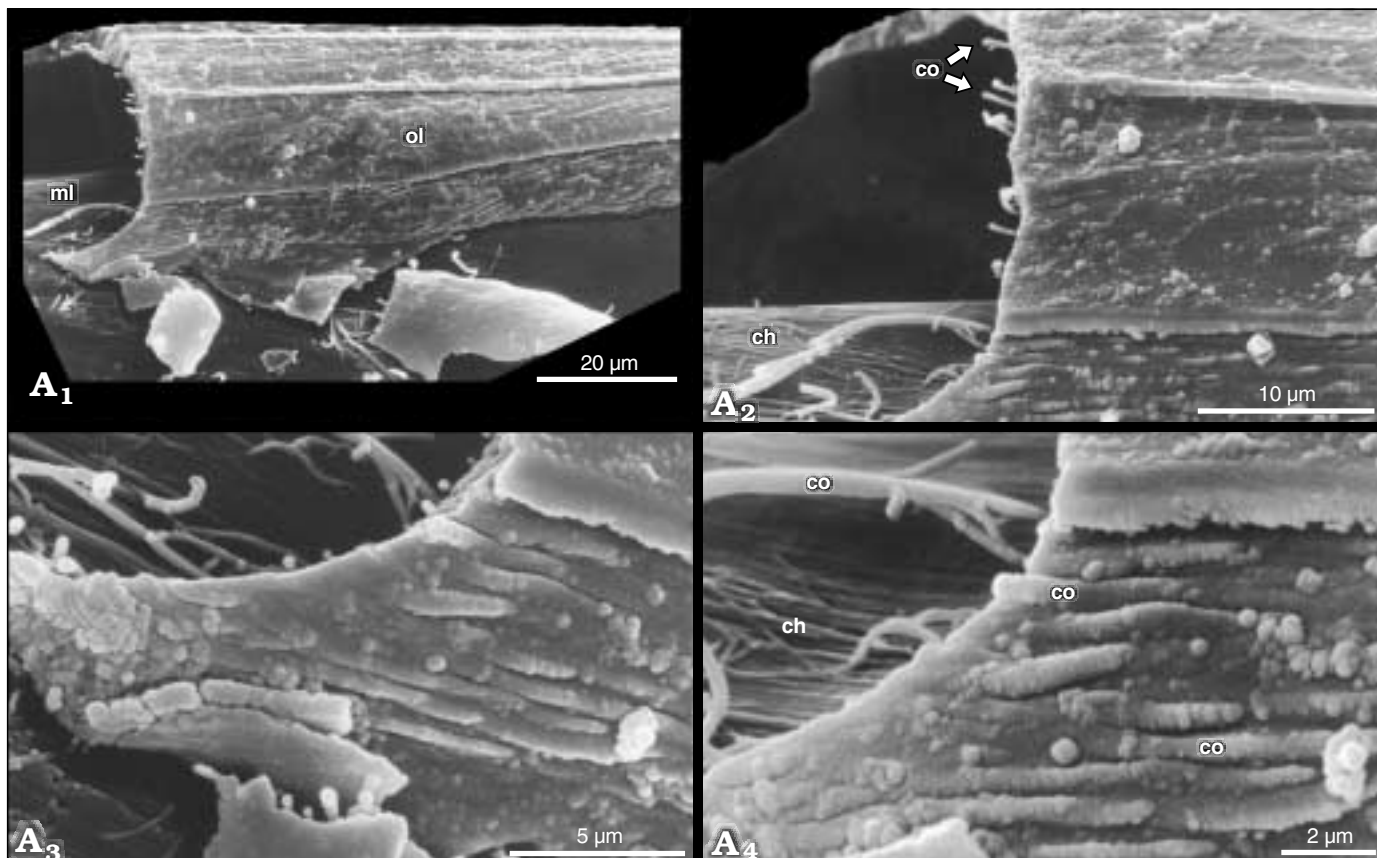


Fig. 4. Grasping spine of Recent *Sagitta maxima*, etched in KOH solution (same specimen as shown in Fig 2G); ZPAL C.IV/4.3, South Shetland Islands. **A₁**. Fragments of the outer layer partly detached from the inner layer. **A₂**. Fragment of the same in slightly different position and higher magnification. **A₃**. Fragment of the same in different position and higher magnification; note branching of some of the coarse strands. **A₄**. Fragment of **A₂** in higher magnification. Abbreviations: ch, chitinous fibrils of the inner layer; co, coarse (collagen-like) fibrils of the outer layer; in, inner layer; ol, outer layer.

The outer layer is strengthened from the outside by longitudinal ridges (Fig. 2F). Ultrastructure of the layer is not well recognized. Some preparations observed in high magnification shows that it is not homogenous but constructed of several thin laminae that are composed, at least in part, of comparatively coarse and irregular fibrils (Fig. 4). Cross striations (not quite certain) and branching of the fibrils shows some similarity to the collagen strands of the chitino-phosphate shells of brachiopods (see Williams et al. 1994). They are much coarser than the chitinous fibrils of the middle layer. Moreover, in some of the laminae a very fine palisade-like structure is visible (Fig. 5D). The outer layer is thicker at the outer side of the spine, where it is most probably constructed of a greater number of laminae (Fig. 3A).

The fibrils of the middle layer are arranged in strips and the strips in thin laminae. The individual fibrils run obliquely around the spine but probably do not form complete loops. Toward the inner margin of the spine they gradually change to a more apical direction and continue along the margin toward the tip (Fig. 3A, B). As a result, the middle layer does not form a complete tube but is “dissected” along the inner margin of the spine where the outer and inner layers merge. The course of the fibrils changes also from the base toward

the tip of the spine, from more transversal to more longitudinal. This reflects the direction of the spine growth in different stages and explains the reason of their oblique fracturing (Fig. 5A, B), although the three-layer structure, and elasticity of the fibrils (Fig. 5C), makes the spines very resistant to fracture.

The inner layer consists of a coating of the pulp. Toward the apex it becomes thicker and faintly laminated. Moreover, the inner and outer layers are connected by thin irregular insertions oriented more or less perpendicularly to the spine surface (Figs. 3A, 6G). The insertions probably pass through the middle fibrous layer, between the fiber strips. The wall of the spine at its base is very thin and the pulp cavity large. Distally the cavity is narrower and the wall thicker. In some species the inner margin of spines is serrated.

The tip of the completely developed spine has a different appearance compared to the rest of the element. According to Bone et al. (1983: 931) it “is clearly of different structure”. However the difference seems to be caused by the lack of the outer layer only. The tip is usually constructed of the “naked” fibrils of the middle layer (Figs. 3B, C, 6A–C). The fibrils are directed apically and arranged in form of a brush. The distal border of outer layer is usually irregular. Possibly the spine

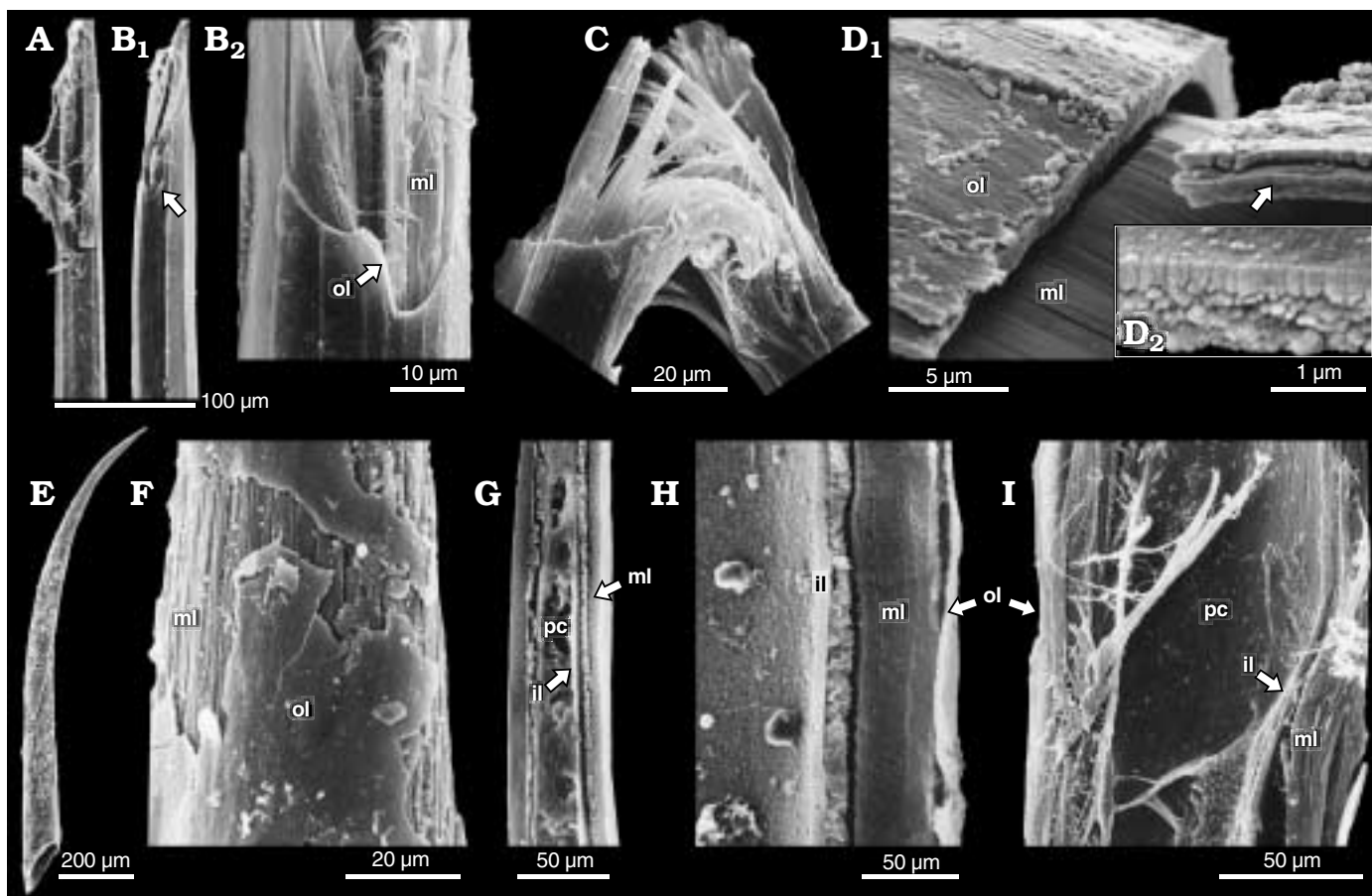


Fig. 5. Structure of the grasping spines of Recent *Sagitta*, North Sea (A–D, I) and *Phakelodus* from the Upper Cambrian subsurface of northern Poland (E–H). A–C. Fragments of three spines of the same apparatus specially fractured to show the oblique direction of fracturing (A, B₁), and inner structure of the spines (B₂, C), note that in C most of the fibrils of the middle layer are strongly bent; ZPAL C.IV/ 6.15. D. Fragment of a spine slightly treated with KOH solution showing fractured outer layer and well preserved middle layer underneath (D₁) and very fine ultrastructure of the lower part of outer layer (D₂); ZPAL C.IV/6.28. E. Grasping spine in lateral view with outer layer preserved fragmentarily; ZPAL C.IV/4.13. F. Fragment of a grasping spine with partly damaged outer layer and the middle layer visible underneath; ZPAL C.IV/92.22. G. Fragment of etched, longitudinal section of grasping spine, the outer layer not preserved, the space between the middle and inner layer, as well as the pulp cavity, partly filled with minerals of secondary origin; ZPAL C.IV/81C.1. H. Fragment of longitudinally fractured and etched grasping spine, the space between middle layer and inner layer filled with minerals of secondary origin, note longitudinal lines on the middle layer; ZPAL C.IV/21.37. E–H. Subsurface Upper Cambrian of northern Poland. I. Irregular, longitudinal fracture of grasping spine of *Sagitta* sp. shortly treated with KOH, showing its ultrastructure, the fibrils of the middle layer are partly disintegrated; ZPAL C.IV/6.13. (H after Szaniawski 1983: fig 3A). Abbreviations: il, inner layer; ml, middle layer; ol, outer layer; pc, pulp cavity; arrow without caption shows fragment magnified on next illustration.

tips of juvenile specimens possess also the outer layer which later on gets abraded by use. The described structure of the grasping spine tips suggests that not only the teeth, as it has been supposed, but also the spines can be used for injection of venom to paralyze the victims (see Bieri et al. 1983; Thuesen and Kogure 1989; Thuesen and Bieri 1996). In many species the tip of spines is curved (Fig. 6A₂) and according to Nagasawa and Marumo (1979) its shape has taxonomic value.

The teeth of chaetognaths are very small (usually 15–200 μm), spine-shaped, situated on the surface of the head, anterior to the mouth (Figs. 1B, C, 7A–F). Their number, size and shape are variable, depending on the nutritional specialization of the species (Moreno 1979; Furnestin 1982). Especially differentiated is the outer ornamentation and morphol-

ogy of their apical part, which in many species is multicuspitate (Fig. 7C, F). Most of the species have two paired rows of teeth but some have three, or only one, or none at all. In the species having two rows, the posterior teeth are usually longer, more numerous (up to 40) and different in shape from the anterior teeth.

The function of the teeth is not well known, but they assist in capturing prey. They are used also to pierce the exoskeleton or epidermis of the prey, and possibly, to inject venom to paralyze them (Bieri et al. 1983; Thuesen and Bieri 1986). The inner structure of the teeth is probably similar to that of the grasping spines; however, it is not so well characterized, mainly because of their very small size. The preparation illustrated in Fig. 7E shows that at least one layer has fibrous structure.

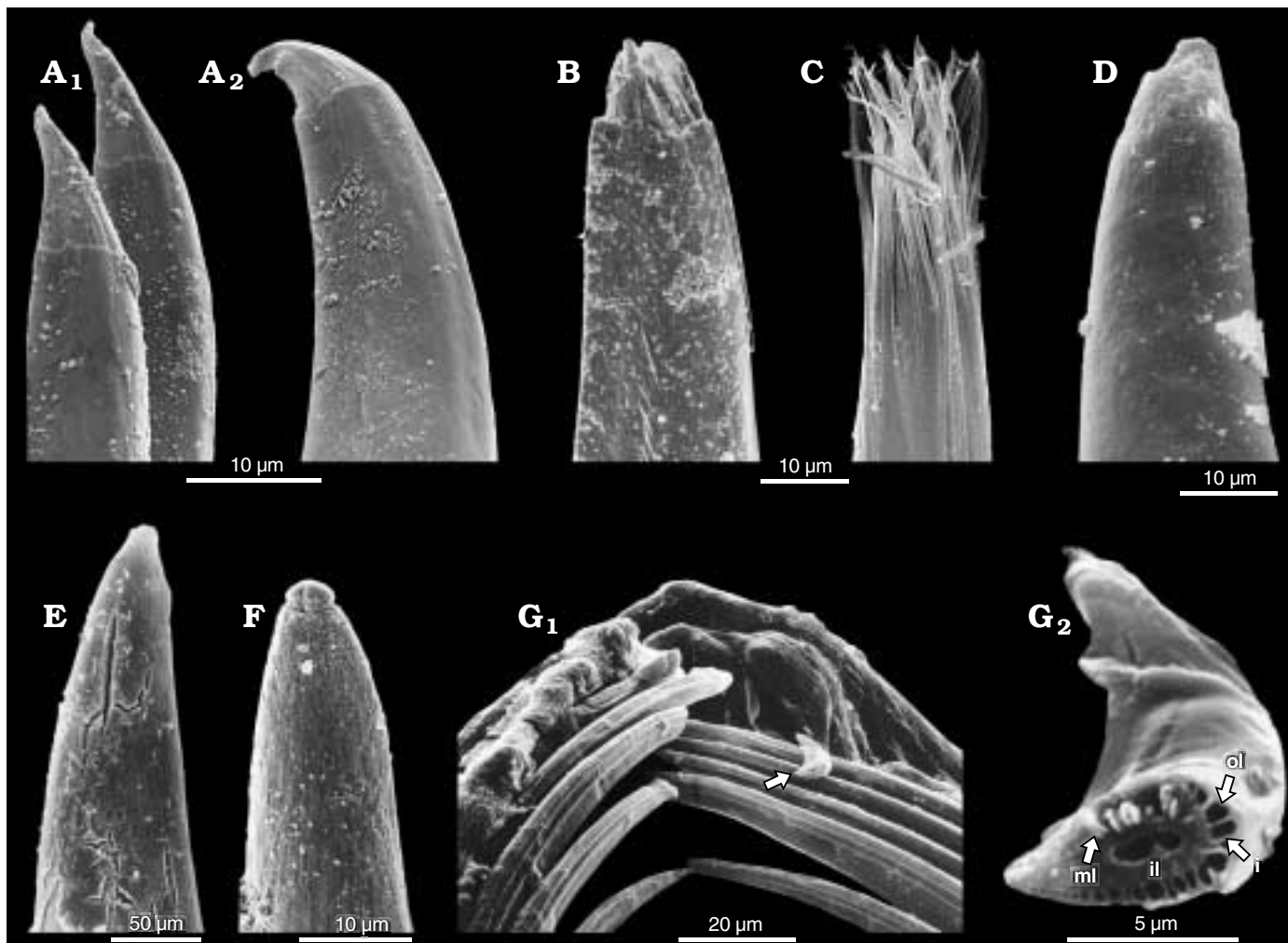


Fig. 6. Distal portions of grasping spines of Recent *Sagitta* (A–C, G) and Cambrian *Phakelodus* (D–F). A. Three spines of the same grasping apparatus showing irregularity of the anterior margin of outer layer and fibrous structure of the tips, note that tip of A_2 is much more strongly curved than those of A_1 ; ZPAL C.IV/6.16. B. Specimen treated shortly with KOH solution, in result the fibrils of tip are slightly disintegrated; ZPAL C.IV/ 4.7 C. Specimen treated longer with KOH solution, the outer layer not preserved, fibrils of the middle layer continue up to the tip where they are strongly disintegrated; ZPAL C/100.14. D–F. Specimens with tips looking differently from rest of the spines (the spine illustrated in F belongs to the natural assemblage illustrated in Fig. 7L). D, F. Subsurface Upper Cambrian of northern Poland; ZPAL C.IV/1.6; ZPAL C.IV/108.4 respectively. E. Upper Cambrian, Trolmen quarry, Kinnekulle, Sweden; SMNH X3519, 95.17. G_1 . Anterior portion of a head in ventral view, note that distal portion of one of the spines is broken off and accidentally attached to other spines. G_2 . Magnification of the fragment pointed by arrow in G_1 , note comparatively small pulp cavity, thick inner layer and well developed insertions connecting the inner and outer layer, the middle layer preserved fragmentarily, structure of the tip not well visible; ZPAL C.IV/2.15. Abbreviations: il, inner layer; ml, middle layer; ol, outer layer.

According to Atkins et al. (1979), the teeth and spines are composed of pure α -chitin crystallites. However, it seems probable that there is a difference in the composition between the outer and inner layers and the middle layer, given the fact that they differ so strongly in structure and resistance (see also the discussion on p. 5). Besides, the teeth and spines contain a significant admixture of silicon and zinc (Bone et al. 1983). The silicon is concentrated mainly in the fibrous tip while the zinc is in the inner and outer layers, along the whole length of the spine. Most probably the admixtures make the structures more hard and tough.

Other hard structures of the head are the lateral and ventral plates. The lateral plates support the teeth and grasping

spines and serve for muscle attachment. They extend from the anterior end of the head along almost its entire length, getting wider posteriorly (Figs. 1B, C, 2C, D, 7A). The ventral plates are subtriangular and serve for muscle attachment in the posterior part of the head. The dorsal and lateral surfaces of the head are covered by a fold of the body wall forming a kind of hood. The hood can be withdrawn when the grasping apparatus is in action (Fig. 2A). This unique feature of the chaetognaths gives them a more hydrodynamic shape and protects their grasping apparatus when not in use.

It is well known that grasping spines preserve well in the stomach contents of chaetognaths' predators (mainly fishes), and can be identified even to the species level (see Nagasawa

and Marumo 1979). Sporadically the lateral plates are also preserved, but, as far as I know, the teeth and ventral plates have not yet been found in any predator's stomach.

Experimental treatment of the chaetognath body with an oxidizing solution shows that only the grasping spines, teeth and lateral plates have comparatively strong resistance to oxidation. After longer treatment with such solution the teeth, lateral plates, basal pockets of the grasping spines, and their outer and inner layers gradually disappear (Fig. 2G, H). The most resistant is the fibrous layer of the spines, which during the treatment becomes transparent but preserves the shape of the spine much longer. The shape slightly changes because the sharp, inner edge (keel) becomes damaged and the brush-like arrangement of the fibrils of the tip gets splintered (Fig. 6C).

Neither the grasping spines nor the teeth are fused. Therefore they usually become isolated in the taphonomic process. However, the grasping spines have a better chance for preservation in natural assemblages because they are stronger, and better enveloped by the comparatively thick "hood" (Fig. 2B) which, until completely decayed, keeps them in a natural arrangement.

Grasping apparatuses of protoconodonts and chaetognaths

Unlike true conodont elements, protoconodont spines occur comparatively often in fused clusters. Initially, they were found in the form of compressed assemblages on Cambrian shale surfaces, in Great Britain (Miller and Rushton 1973) and in Sweden (Müller and Andres 1976). Later, some three-dimensionally preserved clusters were obtained by chemical processing of carbonate rocks from North America (Landing 1977). Since that time more reports about their occurrence in the Cambrian and Lower Ordovician of different regions have been published.

The collections obtained from the Baltic region are exceptionally numerous. Among them are well preserved clusters of grasping spines in natural arrangements (Andres 1981; Szaniawski 1982, 1988; Müller and Hinz 1991). Most hitherto collected protoconodont clusters were assigned to *Phakelodus tenuis* (Müller, 1959) (formerly *Prooneotodus tenuis*), and *Ph. elongatus* (Zhang in An et al. 1983); however, some of them probably need taxonomic revision.

Müller and Andres (1976) noticed the similarity in construction of the *Phakelodus* apparatus and the grasping spine

apparatus of chaetognaths, but they were convinced that the fine structure of the spines composing the apparatuses was completely different and concluded that the similarity resulted from convergence. However, anatomical comparative studies have shown that, in fact, the internal structure of the spines in both groups is very similar (Szaniawski 1982, 1983, 1987). The similarity in architecture of the whole grasping apparatus of *Phakelodus* and those of the Recent chaetognaths concerns several characters. Some of the similarities were mentioned in the papers cited above. Here they are summarized:

1. Both Recent apparatuses of chaetognaths and fossil apparatuses of *Phakelodus* are built of two symmetrical parts (often called half-apparatuses) and have similar size and arrangement.

2. The half-apparatuses are composed of about the same number of spines (4–16 in Recent and up to 14 in fossil forms) and have similar length- to width proportions.

3. The spines of fossil and modern forms are very similar in shape, morphology and inner structure.

4. The spines of each half-apparatus are similarly differentiated in length, width and arching, and their middle elements are the longest.

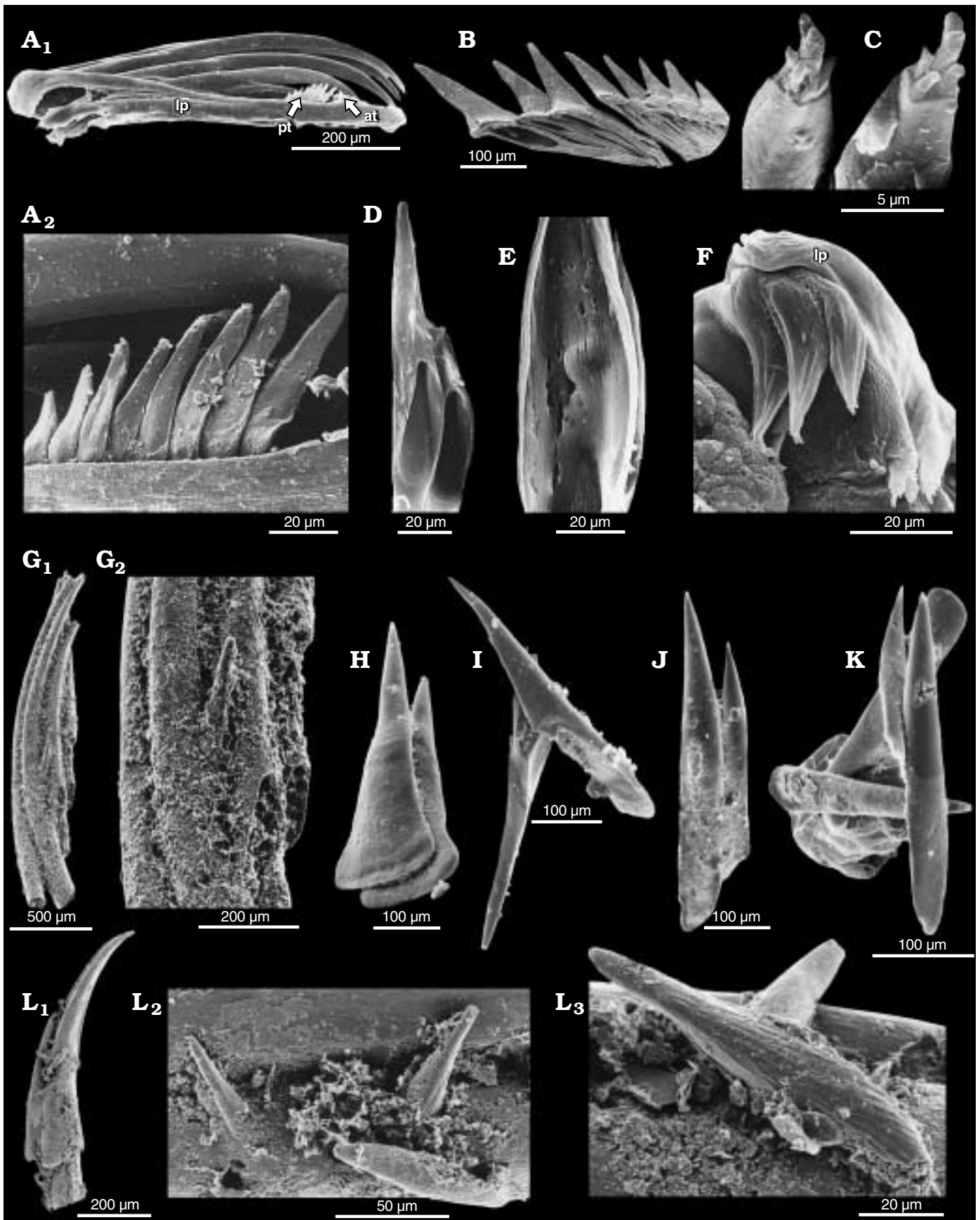
5. Spines of the half-apparatuses of fossil forms are most often arranged in juxtaposition. In recent forms this arrangement corresponds to the resting position of an apparatus in which it is enclosed by the hood.

6. The two half-apparatuses, in both fossil and Recent forms, are usually arranged along the plane of symmetry (Figs. 1B, 2A–C, I, K, L). However, in some cases they are arranged obliquely or nearly perpendicularly to the sagittal plane (Figs. 1C, 2D). In these cases the apical parts of spines of the two half-apparatuses may interfinger (Andres 1981: fig. 6).

7. Clusters of naturally arranged *Phakelodus* grasping spines are comparatively common and often composed of both half-apparatuses. This suggests that the apparatus after the death of the animal has been protected against quick disintegration for some time, just as the hood protects the apparatus of recent chaetognaths. In some cases the time was enough for burial of the specimen in sediment and/or phosphatisation of its grasping apparatus.

All of these similarities show that the apparatus of *Phakelodus* could function in the same manner as apparatuses of recent chaetognaths. This means that protoconodonts were probably the earliest advanced predators that evolved a composite head armature for active capturing of prey (see

Fig. 7. A–F. Recent *Sagitta* sp., different elements of the head armature. A₁. Complete half-apparatus in dorsal view, the lateral plate and anterior teeth deformed. A₂. Magnification of the posterior teeth attached to lateral plate; ZPAL C.IV/2.19. B. Isolated posterior teeth; ZPAL C.IV/6.9. C. Tips of two anterior teeth; ZPAL C.IV/6.18. D. Two posterior teeth showing pulp cavities, distal part of one of the teeth broken off; ZPAL C.IV/1.3. E. Surface of the pulp cavity of a posterior? tooth treated with KOH solution, note the fibrous structure; ZPAL C.VI/4.4. F. Fragment of a head with the anterior teeth; ZPAL C.IV/6.18. G–L. Natural assemblages composed of Late Cambrian grasping spines and teeth-like spicules, subsurface Upper Cambrian of northern Poland. G. Grasping half-apparatus of *Phakelodus* with one attached spicule; ZPAL C.IV/118.1. H–K. Assemblages composed of similar spicules, in natural arrangement (H, J) and displaced (I, K); ZPAL C.IV/6.7; 8.1; 1.10; 8.2, respectively. L. Natural assemblage composed of three grasping spines of *Phakelodus* and three teeth-like spicules. L₂, L₃. Magnifications of the spicules in different views; ZPAL C.IV/108.4. (I, J after Szaniawski 1987: pl. 2.1: 3, 4).



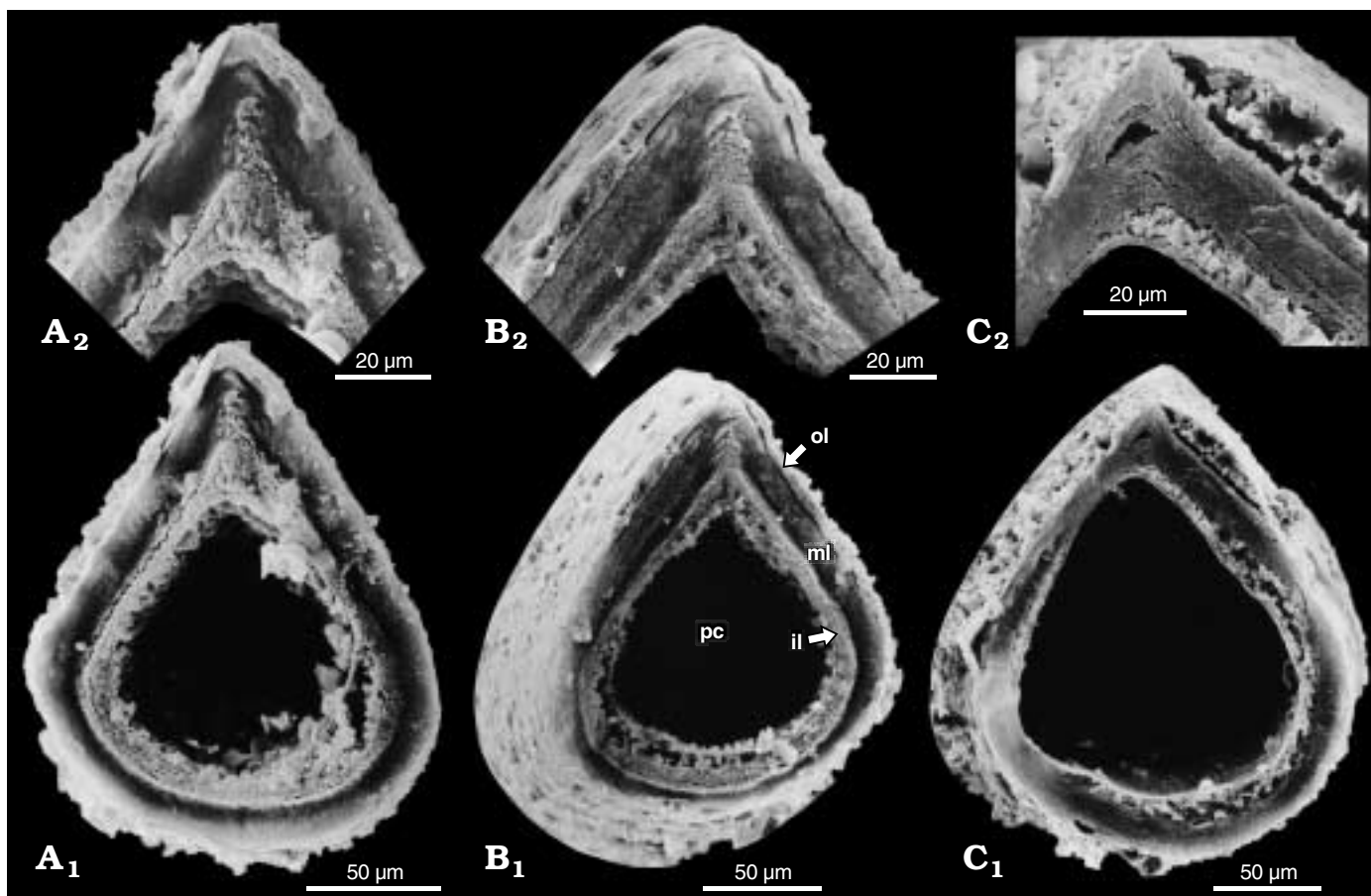


Fig. 8. **A₁**, **B₁**, **C₁**. Etched cross fractures of *Phakelodus* grasping spines showing their inner structure. Outer and inner layers partly overgrown with minerals of secondary origin. **A₂**, **B₂**, **C₂**, enlarged upper parts of **A₁**, **B₁**, **C₁**, respectively. Note that the middle layer, on the inner side of A and B, is interrupted by a flange of the inner layer. All from the subsurface Upper Cambrian of northern Poland; ZPAL C.IV/ 21.3; 21.2; 21/33 respectively (A and C after Szaniawski 1983: fig. 2A, B). Abbreviations: il, inner layer; m, middle layer, ol, outer layer, pc, pulp cavity.

also Szaniawski 1982; Bengtson 1990; McIlroy and Szaniawski 2000).

Anatomical comparison of the chaetognath and protoconodont grasping spines

Comparative studies based on specimens of modern *Sagitta* and Cambrian *Phakelodus* have shown that their grasping spines have a very similar shape, morphology and internal structure. They also have similar longitudinal ridges on the surface and similar inner cavities, open at the base and continuing up to the tip. The fossil spines, like the modern ones, are built of three different layers, of which the outer is thin and usually poorly preserved, the middle comparatively thick and faintly laminated and the inner again thin but in some of the investigated specimens composed of several lamellae. The thickness of the whole wall, in both modern and fossil forms, decreases toward the basal margin.

In some cross sections of the *Phakelodus* spines it is clear that the middle layer, as in chaetognaths, does not form a complete ring. At the tapering side of such sections it is “dissected” by a flange of the inner layer which joins directly with the outer layer (Fig. 8A, B).

Only the fibrous structure of the middle layer, which is very characteristic for chaetognaths, was not well documented in protoconodonts. A poorly preserved fibril-like structure has been observed in the earliest protoconodont genus *Protohertzina* Missarzhevsky, 1973 and in *Phakelodus* (Bengtson 1983; Szaniawski 1983). However, their organic nature was not certain. The supposed “fibrils” are much coarser than the fibrils of chaetognath spines and, at least in some cases, they are composed of “acicular apatite crystallites” (Bengtson 1983:8). Later on, better preserved fibrous structure in *Phakelodus* elements was illustrated by Andres (1988: pl. 1: 7, 5), but the nature of the fibrils was still unclear. Recent structural investigations of very well preserved specimens of the same genus indicated that in some cases the fibrils preserve well even after complete decalcification of the specimens (Szaniawski 1996). Here they are illustrated

for the first time (Fig. 9B–D). The fibrils, originally organic in composition (see below), have about the same diameter as in spines of the chaetognaths and are similarly arranged in micro-layers. Some preparations suggest that their orientation in succeeding micro-layers is different (Fig. 9B_{3,4}).

The tip of the protoconodont spines is rarely well preserved. It is therefore difficult to determine if it is devoid of the outer layer as in chaetognaths. However, some of the specimens suggest that it has a somewhat different structure from the rest of the spine (Fig. 6D–F).

Protoconodont teeth in clusters with grasping spines

As the teeth of chaetognaths have similar structure to the grasping spines, they should also have similar fossilization potential. However, the possibility of finding the fossilized teeth is much smaller because of their minute size. Small spicules and their clusters, similar to the chaetognath teeth, are known (Fig. 7H–K). However, it is very difficult to distinguish isolated protoconodont teeth from similar elements of juvenile paraconodonts (Szaniawski 1987)². Studies of their structure are difficult because of their minute size. The teeth-like clusters are usually composed of only two or three elements of the same shape but slightly different size. The elements are most often arranged in rows and adhere to each other with their lateral margins (Fig. 7J), similarly as the teeth of chaetognaths (Fig. 7A, B, D, F).

Fossil chaetognath teeth are most likely to be correctly identified if occurring in association with grasping spines. The teeth operate independently of the grasping spines and are not attached to them, but are situated very close to the spines (Fig. 7A). Post-mortally they may be kept together by the hood and in some cases can be “glued” to them by taphonomic and diagenetic processes.

A special search for teeth-spines associations resulted in finding two specimens of such clusters. The discovery of the first and more complete specimen has been briefly announced (Szaniawski 1996). The specimen is composed of three small spines, very similar to the chaetognath teeth, attached to three joined grasping spines of *Phakelodus* (Fig. 7L). The grasping spines are in natural arrangement while the supposed teeth are slightly displaced but situated closely together. It seems very likely that all the elements belonged to one animal. Occasionally different fossils can be diagenetically “glued,” but in this case it is rather improbable. The odds that three isolated and uncommon, but nearly identical, sclerites have attached by accident to one cluster belonging to another animal are very low. Moreover, both types of elements of the assemblage have the same mode of preservation.

² Paraconodonts is the informal name for conodont-like fossils differing from the true conodonts and protoconodonts in their inner structure, commonly considered as ancestors of conodonts (see Bengtson 1976; Szaniawski and Bengtson 1993).

The second specimen of that type is less convincing. To a cluster composed of six grasping spines one small spicule is attached (Fig. 7G). However, the probability that the spines and the spicule belonged to the same specimen of chaetognath-like animals is supported by their identical preservation and the size proportion corresponding well to the proportions of the elements in the Recent chaetognaths.

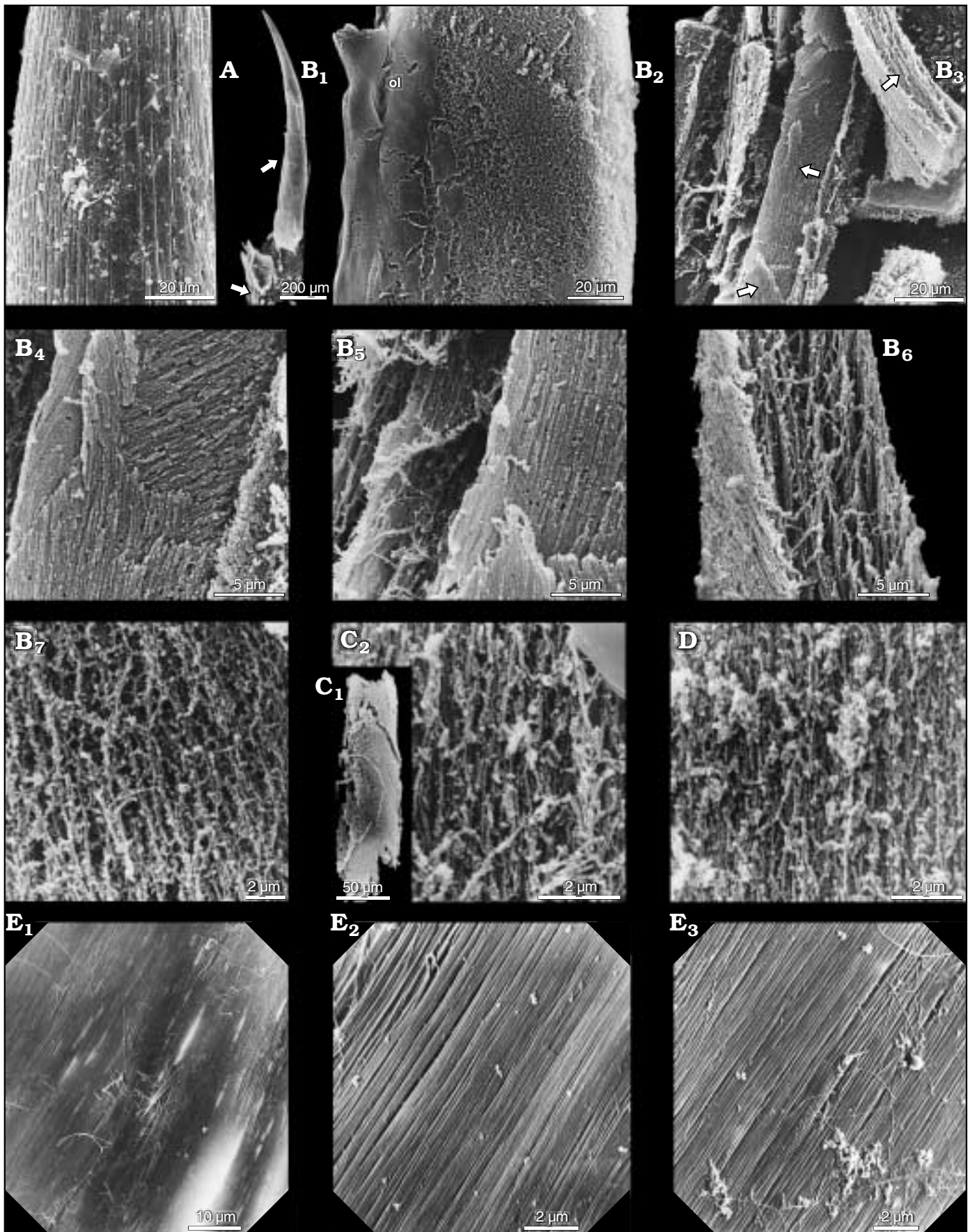
Chemical composition

According to published information, the grasping spines of chaetognaths are composed of chitin (Atkins et al. 1979, see also p. 411), while those of fossilized protoconodonts consist of calcium phosphate (apatite) with an admixture of organic material (Clark and Miller 1969; Bengtson 1976; Szaniawski 1982). This can be considered as one of the most important arguments against the hypothesis positing a close relationship between the two. Another possible argument could be based on the absence of protoconodonts in rocks younger than Ordovician (with only one exception, see the foot note 1). However, there are two possible explanations of both inconsistencies.

1. During the Ordovician, grasping spines of protoconodonts underwent chemical evolution from phosphatic to organic and, as a result, their fossilization potential became greatly reduced (see also Clark and Miller 1969). This would not be extraordinary, because phosphatic skeletons were very common among invertebrates in the Early Paleozoic while later on most of them disappeared. We know fossils of these animals that developed another mineral skeleton, like brachiopods or ostracods, but probably we do not know many of those that lost it.

2. The protoconodont spines were originally built mainly of organic material and became secondarily phosphatised during the fossilization process. Such fossils are very common in the Cambrian and Lower Ordovician.

New EDAX analyses of many Upper Cambrian protoconodont spines from borecores in northern Poland have been made. Examined were: sections of the rock samples yielding numerous protoconodont elements, sections of individual spines embedded in the rocks, spines isolated from the rocks with acetic acid, and spines isolated and decalcified with mineral acids. The results have shown that the rock containing protoconodonts is composed of Ca, O, and C (calcium carbonate), irregularly distributed crystals of pyrite? and barite?, and small admixtures of some other elements. The grasping spines (those embedded in the rocks as well as those isolated, but not etched), beyond Ca, O, and C contain relatively high proportions of P (about 12 Wt%) and F (about 3 Wt%) suggesting presence of calcium phosphate (probably fluoroapatite). Comparatively great amount of C (about 11 Wt%) suggests a substantial admixture of organic matter (occurrence of calcium carbonate is not probable because in the case of isolated spines the CaCO₃ would have been dissolved during processing in acetic acid). The specimens that have



been isolated and decalcified consist mainly of C (about 50 Wt%) and O, with varying admixtures of Na, Mg, Si, S, Fe, Cu, and Zn.

The results suggest that the original composition of protoconodont grasping spines was mainly organic. The common occurrence of the apatite crystals in their inner cavities and the co-occurrence of the spines with many secondarily phosphatized fossils suggest that at least part of the calcium phosphate now present in the spines, is of diagenetic origin (see also Repetski and Szaniawski 1981). For this reason the specimens with well preserved organic matter can retain their shape and fibrous structure even after complete decalcification (Fig. 9B–D).

Moreover, some of the isolated spines and even their clusters are strongly deformed (Fig. 2L), which suggests their great flexibility before fossilization. Some other specimens have a much wrinkled outer layer, evidently the result of contraction. Such flexibility would not be possible if the spines were built mainly of crystalline calcium phosphate.

Bone et al. (1983) stated that significant admixtures of Zn and Si occur in the spines and teeth of recent chaetognaths. The occurrence of Zn, and also of Fe and Cu, has been described earlier in the spines of Upper Cambrian protoconodonts (Szaniawski 1982). As noted above, admixtures of Si and some other elements were presently confirmed. However the new investigations show that their amount vary greatly and it is not possible to determine how much of them are of primary origin.

Protoconodont—chaetognath relationship

Chaetognaths possess many unusual structural features and their systematic position has always been an intriguing puzzle. Darwin (1844: 1) noted that these animals “are remarkable... [for] the obscurity of their affinities”. In the history of

investigations their relationship with almost every phyla of animals, including chordates, has been proposed (Ghirardelli 1994). In the last decades they were most often considered as relatives of the Deuterostomata. However, that opinion has been based mainly on some of their embryological features, and most of the recent molecular studies do not support it. The investigations of Telford and Holland (1993: 674) show “...that the most likely position of the chaetognaths is as descendants from an early metazoan branch possibly originating prior to the radiation of the major coelomate groups”. Wada and Satoh (1994) and later on Halanych (1996) came to similar conclusions.

Further investigations by Telford and Holland (1997) confirmed the earlier results and let them to state (p. 135): “The chaetognaths are extraordinarily homogenous phylum of animals ...” and (p. 143) that “...the lineage leading to chaetognaths separated from other phyla early in metazoan radiation, probably in the Precambrian” Recently Yasuda et al. (1997) investigated expression of actin genes in one chaetognath species and in the result came back to the common previous opinion that chaetognaths (p. 953): “... exhibit features characteristic to both deuterostomes and protostomes, and their ancestry therefore remain unknown.”

All these conclusions are compatible with the hypothesis that chaetognaths originated from some of the protoconodonts. The group belongs indeed to the earliest metazoans and differentiated at the beginning, or even before, the great Cambrian evolutionary explosion.³

Comparatively notable morphological diversification of the protoconodont spines suggests that in the Cambrian and Early Ordovician the protoconodont animals were much more diversified than recent chaetognaths. Presently 13 genera of them are recognized and the existence of some more has been announced (Müller and Szaniawski 1998).

Of the all known protoconodont spines the most similar to chaetognath grasping spines are those of *Phakelodus*. They are very common and distributed throughout the world. They occur comparatively often in clusters, and because of that the whole grasping apparatus of the genus is well known. Other genera of protoconodonts are known only from isolated spines and in some cases of singular or few clusters (see McIlroy and Szaniawski 2000).⁴ Their grasping apparatuses were certainly slightly different from that of *Phakelodus*. Phylogenetic relations among protoconodonts are not known, but they constitute several evolutionary lineages. Most probably the lineage of *Phakelodus* gave rise to recent chaetognaths while the others died out or evolved in other directions. A relationship also to paraconodonts and euconodonts (= true conodonts) is not excluded but the problem is beyond of the scope of the present paper.

³ Protoconodonts originated in the late Precambrian or early Cambrian. It is not possible to determine the age more precisely, because the Pr/C boundary is still not well established in some sections.

⁴ The apparatus structure is well known also in the genus *Coelocerosodontus* Ethington, 1959, which possibly should be assigned to protoconodonts.

← Fig. 9. Fibrous structure of grasping spines of Cambrian *Phakelodus* (A–D) and Recent *Sagitta* (E). A. Surface of a fragment of spine devoid of the outer layer; SMNH X3320, 92.10, Stenbrottet, Västergötland, Sweden. B₁. Demineralized spine with specially crushed basal part for to study its inner structure, arrows point to the fragments magnified in B₂ and B₃. B₂. Magnification of a fragment showing still preserved remains of the outer layer. B₃. Fragment of the specially crushed basal part, arrows point to fragments magnified in B₄, B₅, and B₆. B₄, B₅. Central and lower fragments of B₃ showing slightly differentiated orientation of the fibrils in succeeding laminae. B₆. Upper right fragment of B₃ showing oblique section of the middle layer at basal part of the spine. B₇. Fibrous structure seen on a fragment of the spine surface devoid of the outer layer; SMNH X3521, 95/14, Trolmen quarry, Kinnekule, Sweden. C₁. Partly damaged, demineralized spine. C₂. Fragment of the spine showing fibrous structure of its inner layer; SMNH X3522, 92/9, Uddagården, Västergötland, Sweden. D. Fibrous structure of the inner layer of demineralized specimen; SMNH X3523, 95/17, Trolmen quarry, Kinnekule, Sweden. E. Outer surface of the middle layer of a spine treated with KOH solution (whole spine of same specimen is illustrated in Fig. 2H); ZPAL C.IV/4.2.

Conclusion

- The head armature of the protoconodont genus *Phakelodus* was composed not only of a grasping apparatus, similar to that of chaetognaths, but also of small spicules corresponding in size, shape and morphology to the teeth of chaetognaths.
- Grasping spines of some protoconodonts were similar to the spines of chaetognaths not only in shape, inner structure and morphology but also in their chemical composition. Originally they were mainly built of an organic substance; most probably the calcium phosphate is partly of diagenetic origin.
- The hypothesis of a protoconodont-chaetognath relationship proposed earlier is supported by new observations on the micro- and ultrastructure of the spines in both groups.
- Molecular investigations of the chaetognath origin suggest that they should have originated at about the same time as protoconodonts.
- Judging from their head armature, protoconodonts are the only known extinct animals that could have had a mode of feeding similar to that of chaetognaths.
- Protoconodonts of the evolutionary lineage of *Phakelodus* are probably a stem group of chaetognaths.

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