Chaetognath grasping spines from the Upper Mississippian of Arkansas (USA)

LARISA A. DOGUZHAEVA, HARRY MUTVEI, and ROYAL H. MAPES

Previously unidentified tiny (about 0.5 mm in length), hollow, gently curved, serrated spines probably originally composed of horny, organic fibers from the Upper Mississippian (Middle Chesterian = Namurian A equivalent or lower Serpukhovian) of Arkansas (USA) are described, and their probable chaetognath affinities are discussed. The specimens are preserved in an oval accumulation (about 15 mm long and 6 mm wide) of approximately 200 specimens within a small (about 25 mm in length) phosphatic concretion. For comparison, the grasping spines of the Recent chaetognath *Eukrohnia hamata* were examined. The Arkansas specimens are named *Eoserratosagitta serrata* gen. et sp. nov., and this genus is assigned to the Phylum Chaetognatha. The Upper Mississippian spines are also compared with protoconodonts. This comparison supports the hypothesis that the chaetognaths may have existed in the Cambrian.

Key words: Chaetognatha, organic spines, protoconodonts, phosphatized fossils, Mississippian.

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Introduction

SEM studies of numerous well-preserved, tiny, horny, uni-cusped spines from the Upper Mississippian (Middle Chesterian, or Lower Serpukhovian) of Arkansas (USA) show definite similarity in general morphology and ultrastructure with the grasping spines of living chaetognaths. These fossil spines exhibit a larger number of similar morphological characters than the fossil spines that have been previously compared with those of Recent chaetognaths (Szaniawski 1982: 807, text-fig. 1A–H; Dzik and Drygant 1986: 134, fig. 1).

Chaetognatha is a small phylum of small, elongate, dorsoventrally flattened marine planktonic carnivorous invertebrates considered to be one of the most isolated groups among the metazoans (Nielsen 1995). The chaetognaths may also be phylogenetically related to the conodonts as well (Rietschel 1973; Szaniawski 1996). However this assignment remains problematic at the present time (Donoghue et al. 2000). The Early Paleozoic uni-cusped spines assigned to protoconodonts have recently been considered as remnants of ancient chaetognaths (Szaniawski 1980, 1982, 1983, 1996, 2002; Repetski and Szaniawski 1981; Bengtson 1983; Kraft et al. 1999).

The living chaetognaths comprise around 140 species, grouped in 20 genera, 5 families, 2 orders and a single class Sagittoidea Claus and Grobben, 1905 (Kasatkina 1982; Bieri 1991). They inhabit the oceans and the seas with normal salinity from shallow to great depths (Vinogradov 1968). Their arrow-like body is adapted for quick and comparatively long leaps. The great majority of chaetognaths use their fins to maintain non-stop movement. Their main food is larvae of herring, copepods, decapods, amphipods and fry of chaetognaths. Some feed on prey larger than themselves, and some are organic suspension feeders. In their turn chaetognaths are food for adult herring (Kasatkina 1982). To capture prey, the chaetognaths use a grasping apparatus formed by a set of grasping spines and a set of biting teeth (Fig. 5A, B). They also have "hardened" lateral and ventral plates within the head for support and muscle attachment (*fide* Briggs et al. 1983). General morphology of the grasping spines is strongly constant in the phylum with an exception of *Krohnitta*, which has spines that are much more curved than in all other genera. The spines and teeth are similar in inner structure but differ in shape and size in that the spines are much larger than the teeth. The number of spines and teeth change with body growth, seasonality, and with food habits (Ghirardelli 1968: 274).

Material and methods

This described material is an accumulation of fossil spines in a phosphate concretion that was recovered from a black shale in the bed of Cove Creek near the base of the Fayetteville Formation (Upper Mississippian) near the community of Leslie in northern Arkansas, USA (see Mapes 1979, locality M-22 for more details). The grasping spines of Recent chaetognath *Eukrohnia hamata* from Antarctic (Gerhache
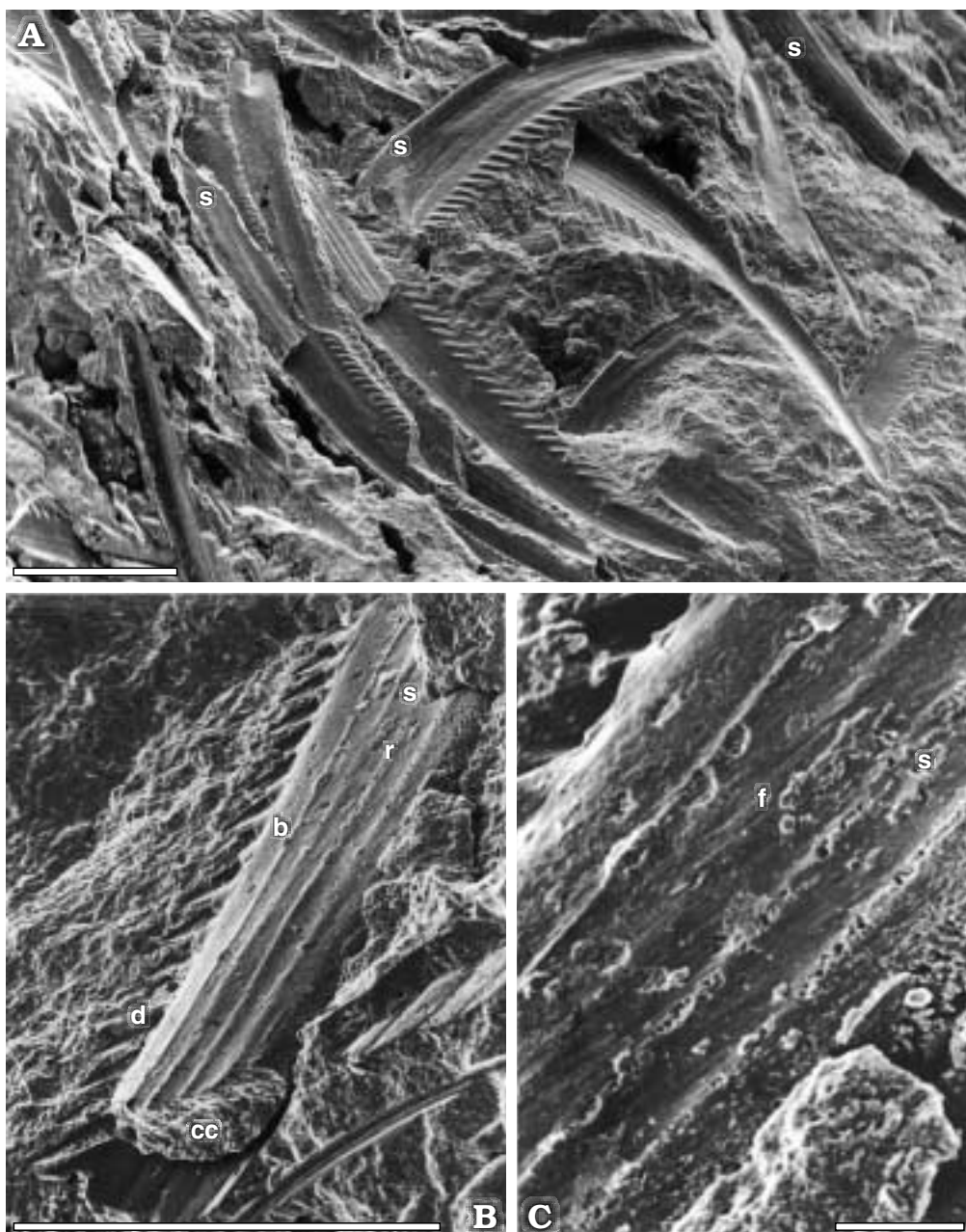
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Fig. 1. *Eoserratosagitta serrata* gen. et sp. nov., Cove Creek (Arkansas, USA), Middle Chesterian (Namurian A equivalent). **A**. A concretion fragment showing part of the accumulation of spines (s), scale bar 0.1 mm. **B**. A fragment of the middle part of a spine showing the concretion filled central cavity (cc), a row of bullet-like, hollow (now concretion-filled) denticles (d) on the concave side (to the left), and five longitudinal bands (b) separated by fine ribs (r) on the outer surface of the spine wall, scale bar 0.1 mm. **C**. Close-up of B showing fiber (f) impressions, scale bar 0.01 mm. All SEM micrographs.

Strait, Hughes Bay, Antarctic Peninsula) were collected in March 20, 1987.

After examination with a light microscope, the spines were studied with SEM. For this latter process the two halves of the concretion were coated with gold.

Fifteen specimens of *E. hamata* (grasping apparatuses together with the heads and soft bodies) were embedded into plastic and cut through the head. The sections showing more than one spine were polished and etched with 5 per cent hydrogen peroxide. To disintegrate the horny material into fibers the spines were boiled about 10–15 minutes in 5 per cent hydrogen peroxide. The material was studied with a Philips 35 scanning electron microscope (SEM) at the Swedish Museum of Natural History, Stockholm.

Institutional abbreviations.—The fossil specimens are reposited in the Ohio University Zoological Collections (OUZC) in Athens, Ohio, USA. Recent specimens are stored at the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm (SMNH).

Geological setting and environments of deposition

The stratigraphic horizon that yielded the concretion that contains the fossil spines is the Fayetteville Formation (Mississippian–Middle Chesterian = Lower Serpukhovian). The fossil

bearing black platy shale is estimated to be 1–3 m above the base of the formation. At this interval, there is a moderately diverse assemblage of crushed goniatites and other less common cephalopods. Sometimes the fossils are preserved within small (20–40 mm diameter) phosphate concretions. Of the thousands of concretions recovered and broken open, only one contained an accumulation of spines; however, others sometimes contain fossil nuclei including ammonoid shells, cephalopod mandibles and rarely their radulae. The preservation, taphonomy, and phylogenetic significance of these mandibles and radulae have been studied by Mapes (1987), Tanabe and Mapes (1995), and Doguzhaeva et al. (1997).

At the locality there is a series of shale exposures on the banks and in the bed of Cove Creek. A prolific cephalopod fauna is known from this and similar exposures (see Gordon 1964; Mapes 1979; and Meeks and Manger 1999 for a nearly complete list of cephalopod taxa from this unit). No benthic organisms such as crinoids and brachiopods were found at this interval in the formation. The Fayetteville Formation is interpreted as having a strongly dysoxic to anoxic bottom environment because of the black color of the shale, the common occurrence of pyrite and phosphate, and the lack of a benthic fauna.

Preservation

The Mississippian spines from Arkansas were preserved as an accumulation in the center of a small spherical phosphate concretion with a diameter of about 25 mm. The accumulation is 15 mm in length and 6 mm in width containing approximately 200 spines. The spines are shiny dark brown to nearly black with no regular orientation (Figs. 1A, 2A).

There are no other faunal remains in the concretion with the exceptions of three specimens (Fig. 3B, E, F), which might be either a set of the same spines exposed from the rounded convex side, or other spines resembling the protoconodont *Phakelodus* Miller, 1984. One of these specimens (Fig. 3B) represents an assemblage formed by six juxtaposed coniform-like, slightly curved, hollow spines that are oval in cross section. The other two specimens are encrusted internal moulds of distal fragments of isolated spines (Fig. 3E, F) similar in shape and size to those that appear to be joined together (Fig. 3C). The rest of the accumulation contains unidentified debris.

The spine accumulation is probably a concentration preserved in a coprolite produced by a predator. Indeed, some of the spines in the concretion were damaged prior to the formation of the phosphate concretion (Fig 3A, C). This damage probably took place when the spine-bearing animal was eaten by the coprolite producing predator. From this interval of the Fayetteville Shale, between 90 and 95% of the phosphate concretions have coprolite nuclei. A probable producer of the coprolite with the spine accumulation could be an ammonoid since these animals are the most abundant macro faunal element in the interval. Additionally, like modern *Nautilus*, which is a scavenger and opportunistic predator, the ammonoids were probably similar in food gathering, and this is supported by their jaws structure and stomach contents. They apparently ate small benthic and planktonic biota (Nixon 1988, 1996; Lehmann and Weitschat 1973; Lehmann, 1988; Jäger and Fraaye 1997). In their turn the ammonoids in the Carboniferous were probably attacked by sharks or other carnivorous fish (Lund and Mapes 1984, Mapes et al. 1995), which have been recovered at this horizon in the shale (Mapes, unpublished personal observations).

The spines were observed on both surfaces of the split concretion. The inner and outer surfaces of the spines were mainly preserved as imprints on their moulds (Figs. 1A, B, 2A–C). Tangential and cross sections of spines were observed in broken specimens at different distances from the pointed tip (Figs. 1A, B, 2A, B, 3D). These specimens are constructed with a long central cavity and hollow denticles along a concave side. The actual wall of the spine was preserved in only a few cases (Fig. 2B, 3A, C). Most of the spines were diagenetically encrusted (Figs. 2B, 3D, F). Fig. 2B (enlarged detail of the spine illustrated on Fig. 2A) shows the thin wall of a spine that is coated by a comparatively thick mineralized (phosphate?) crust with an uneven irregular outer surface. Here the crust has a branch that does not follow the surface of the spine but extends at an angle of 60 degrees to its surface. This provides additional proof that the mineralized coating of the spines is not biomineralogical but an abiotic structure. The crust on the spines, however, could be erroneously interpreted as the spine wall if the material was extensively diagenetically altered.

Morphology and ultrastructure

The maximum exposed length of the spines is about 0.4–0.5 mm and the maximum width about 0.05–0.06 mm. The spines are gently curved (Figs. 1A, 2A, 4A). Their outermost side is broader than the inner side (Fig. 3D). The central cavity of the spine is long and seems to extend to its tip. The wall of the spine is thin (Fig. 2B, C); in places it shows plastic deformation (Figs. 2A, 3A, C) that in combination with dark color and the fibrous impressions supports the conclusion that the spine was originally composed of fibrous, organic horny material. The outer layer of the spine wall bears lines that are intrepreted to be the impressions of fiber bundles that extend obliquely at an angle of 25–39 degrees to the long axis of the spine (Figs. 1B, C, 2B). These fibrous bundle impressions are less distinct on spines showing plastic deformation (Fig. 3A, C).

The spine has five to six slightly imbricated bands. The term band as used here describes relatively flat regions on both the inner and outer surfaces of the spine that are usually bounded by narrow ridges that are nearly parallel to the length of the spine. The appearance of the bands appear in different ways depending on the mold/cast preservation. The ridges are raised rib-like structures on the outer surfaces of the spine (Figs. 1B, C, 3B, C) and grooves on the mould sur-
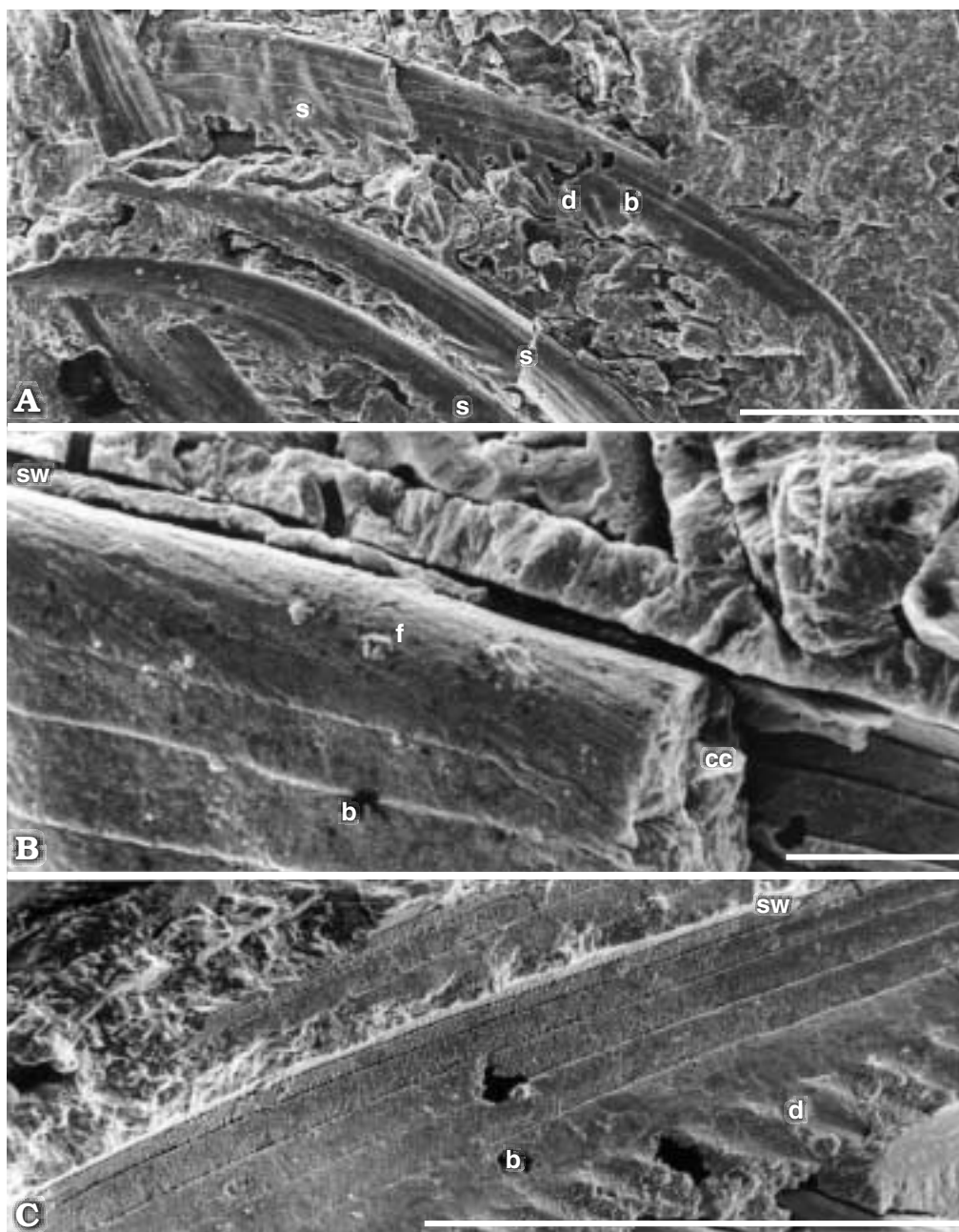
Fig. 2. *Eoserratosagitta serrata* gen. et sp. nov., Cove Creek (Arkansas, USA), Middle Chesterian (Namurian A equivalent). **A**. Three large fragments of spines (s); the uppermost one is the holotype (OUZC 4002/A); it is preserved as imprint of a distal part and a mould of the middle part. The latter bears traces of plastic deformation (wavy pattern on surface); the spine has five longitudinal bands (b) and bullet-like denticles (d) on concave side. Note that the distal part near the pointed tip of the spine is smooth and lacks denticles, scale bar 0.1 mm. **B**. Enlarged view of a holotype segment with the edge of the internal mold showing the replaced spine wall (sw) which is covered by a mineral (phosphate concretion?) coating (compare with the outermost layer of the spine wall in the living chaetognath *Eukrohnia hamata* on Fig. 6A, B, herein). The inner surface shows a distinct oblique pattern of fibers (f) in bundles. Five longitudinal bands (b) are visible and the central cavity (cc) is infilled by concretion material, scale bar 0.01 mm. **C**. The mold of the outer surface of a spine with a row of uniformed bullet-like denticles (d) along the concave side, five gradually narrowed distinctly separated bands (b) on the lateral side, and the thin spine wall (sw) along the convex side (compare with the outermost layer of the spine wall in the living chaetognath *E. hamata* on Fig. 6A, B, herein), scale bar 0.1 mm. All SEM micrographs.
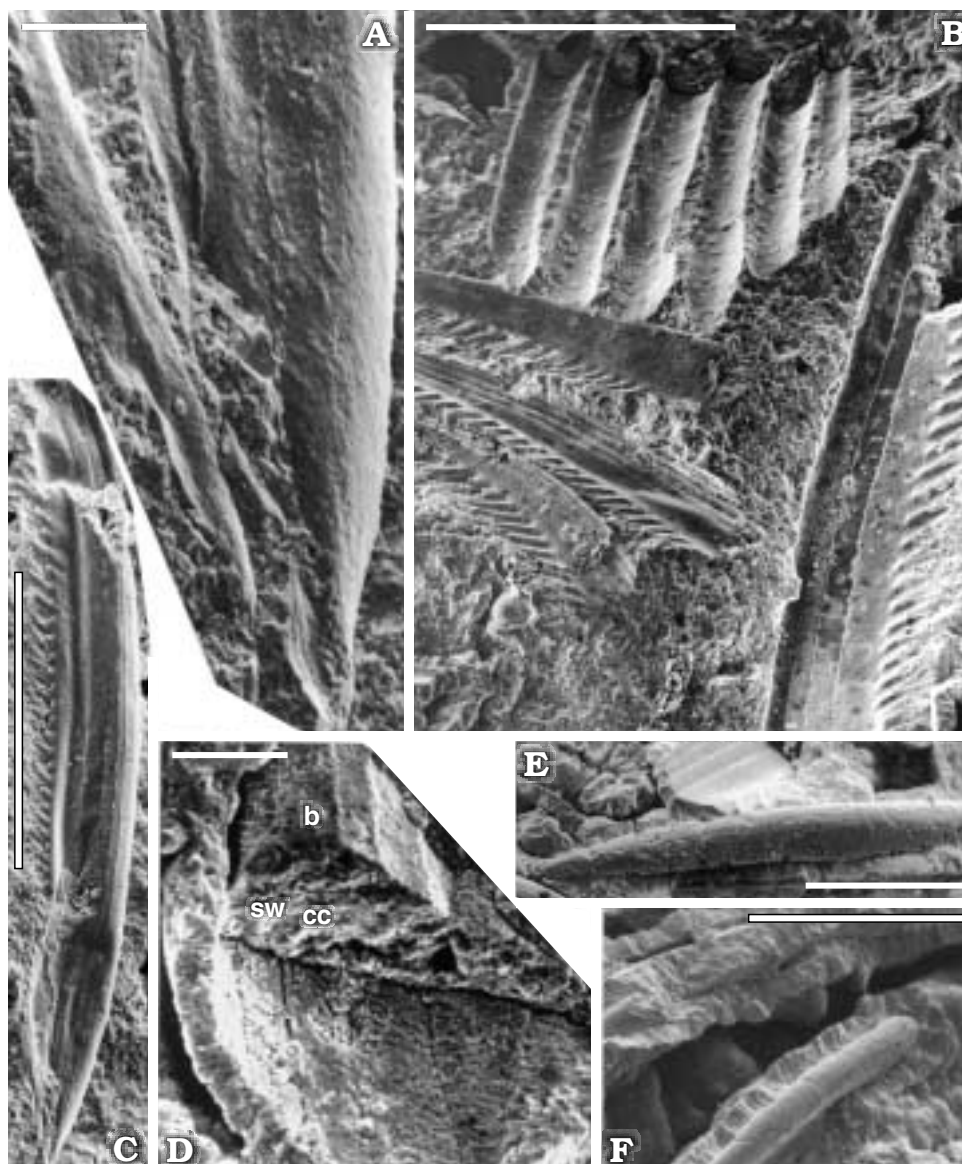
faces (Figs. 2B, C; 3D). When bands are visible on the molds they show distinct indications of the fibrous pattern (Figs. 1C, 2C, 4A, B). The fibrous pattern seems to reflect the fibrous structure of the principal middle layer of the wall. The very tip of the spine is formed by only one band, the innermost band forming its concave side. The second band appears at a short distance from the tip. The third band appears at nearly half of the distance between the tip and the first denticle. The fourth band appears at the level where the first denticle occurs. The fifth and the sixth bands appear at the level of 7th–10th denticles (Fig. 2A). Usually the first band is broader than the rest, and the width of the band regularly decreases toward the outer side (Fig. 2C). The outermost band is rolled in a way that forms the outer side of the spine (Fig.

2B). The inner, or concave, side of the spine bears numerous, uniformly sized, bullet-like, hollow denticles, which are inclined towards the distal end of the spine with an angle of about 60° (Figs. 1A, B, 2C, 3B, C). These denticles cover approximately 2/3 of the spine length; the distal portion of the spine lacks denticles (Figs. 1A, 2A).

Comparison with grasping spines of Recent chaetognaths

In Recent chaetognaths the grasping apparatus includes 7–11 pairs of spines and 2–38 pairs of teeth (in rare cases the teeth

Fig. 3. *Eoserratosagitta serrata* gen. et sp. nov., Cove Creek (Arkansas, USA), Middle Chesterian (Namurian A equivalent). **A**, **C**. Lateral view of a plastically deformed and incomplete spine showing that it has been broken prior to fossilization. The spine has overlapped, unfused edges that have been pressed together by compaction, scale bars: **A**, 1.0 mm, **C**, 0.1 mm. **B**. Unidentified assemblage of tube-like spines in the coprolite that resemble the Cambrian paraconodont *Prooneotodus* or are perhaps the rounded convex side of the new genus and species described herein, scale bar 0.1 mm. **D**. The cross section of the fractured spine shows the triangular outline with a rounded convex (external) side and acute concave (internal) side, central cavity (cc), thin spine wall (sw) and longitudinal bands (b) on inner surfaces of the spine. There is a thick mineral encrustation that provides a mold of the outer surface of the spine, scale bar 0.01 mm. **E**, **F**. Unidentified cone-like structure of a problematic remain resembling the paraconodont-like spine of the assemblage seen in B above, scale bars 0.05 mm. All SEM micrographs.

are absent). The spines as well as the teeth are arranged in a single row on each side (Fig. 5A, B). In some genera the spines are of equal or slightly different length (up to 2 mm); however, the spines in others can be strongly differentiated. Muscles are attached to a structure called the basis, which is the proximal widest part of the spine (Fig. 5A, B). The remaining part of the spine, if present, is the hook, the latter being equipped with a talon (Fig. 5B). The spine has a central cavity (Figs. 5C, D, 6A, B) infilled by pulp. The internal concave side (facing the mouth) is usually smooth, but in all species of *Serratosagitta* and few species of *Eukrohnia* (both from the family Sagittidae), it is serrated with denticles (Kasatkina 1982). Both the chitinous spines and denticles contain significant amounts of zinc and silicon (Bone et al. 1983).

The spines of chaetognaths differ from those in polychaetes; the latter have much less spinal curvature and no widen basis for muscle attachment. Besides, "the persistent pulp cavity sets the chaetognaths teeth and spines apart from such other chitinous structures as ... the setae of polychaetes [are] ... secreted by a basal cell or cells" (Bone et al. 1983: 939). On the ultrastructural level the grasping spines of chaetognaths are in some ways similar to those of annelids, pogonophorans and brachiopods. The resemblance is assumed to be a result of parallel development (Buzhinskaya and Lebskiy 1974; Buzhinskaya et al. 1980). In *Eukrohnia* (Dzik and Drygant 1986: fig. 4C; herein Fig. 5A, B) as well in *Sagitta* (Szaniawski 1982: text-fig. 2A–C) the wall of the spine is shown to be mainly formed by a comparatively thick fibrous layer protected from the outside by cuticle and from the inside by a thin compact layer (Szaniawski 1982: text-fig. 3A–I; herein Figs. 5C, 6A–C). The fibers form bundles (Figs. 5E, 6A–C) that are both longitudinal and oblique to the longitudinal axis of a spine.

The spines are not conjoined (Fig. 5A, B); however, there is a platform-like structure called the lateral plate and the spines are attached to this feature by muscles. In resting posi-
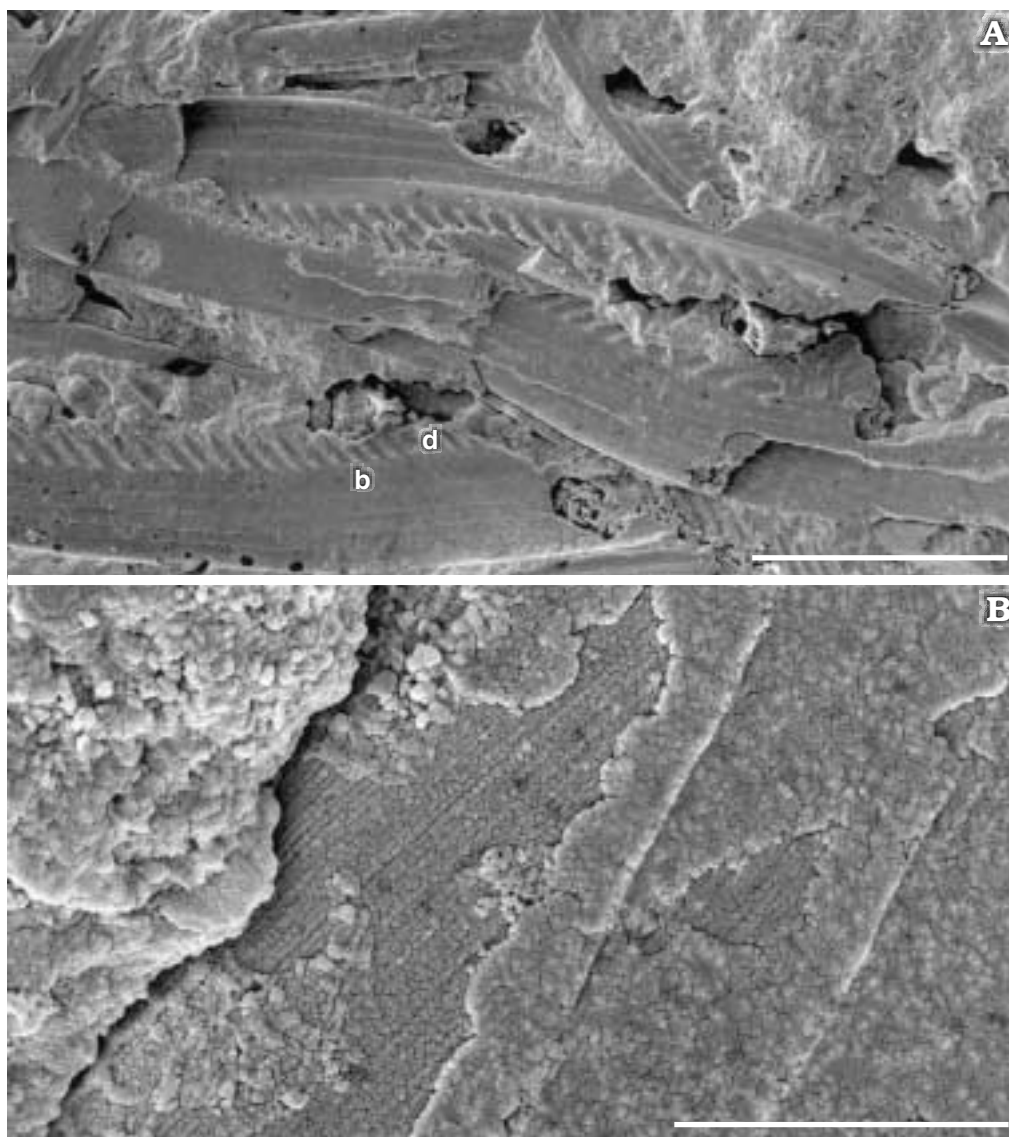
Fig. 4. *Eoserratosagitta serrata* gen. et sp. nov., Cove Creek (Arkansas, USA), Middle Chesterian (Namurian A equivalent). **A**. Three relatively complete paratypes (OUZC 4002/B, C, D from top to bottom, respectively) with nearly identical basic morphology including bands (b) and bullet-like denticles (d), scale bar 1.0 mm. **B**. Enlargement of the lower right segment of paratype OUZC 4002/B showing the phosphate replaced, fibrous ultrastructure of the spine wall, scale bar 0.1 mm. All SEM micrographs.

tion the spines are drawn into the soft tissues of the hood, which can be extended forward to cover the entire head (Szaniawski 1982: text-fig. 2A–I).

The long central cavity of the Mississippian spines (Figs. 1A, B, 2A, B, 3D) did not allow us to consider these fossils as remnants of polychaetes. However, this long central cavity is a common feature of both the fossil spines and modern chaetognaths (compare Figs. 1B, 2B, 3D and Figs. 5C, 6A, B). The wall of the Mississippian spines is also composed of fibers that are oblique to the long axis of the spine (Figs. 1B, C, 2B, 3A, C, 4B). Because of their fibrous structure, brown color and plastic deformation (Fig. 3A, C), an interpretation that the spines were originally organic horny material seems warranted.

Modern chaetognath spines show longitudinal bands on their lateral side, the width of which gradually decreases toward the outer rounded side (Szaniawski 1982: text-fig. 3B, G; herein Fig. 5A, B). The Mississippian spines have similar bands (compare Figs. 1B and 5C). Also, modern chaetognath

spines have an interruption in their wall layers, which in cross section looks like a radial split, directed from the central cavity to the concave side (Szaniawski 1982: text-fig. 3I; herein Fig. 5D). A similar feature may have been present in the Mississippian spines (Fig. 3A, C, D).

In summary, there are numerous morphological characters that are common to both the modern cheatognaths and in the Mississippian age fossil spine specimens. Because of these similarities, we have concluded that the Mississippian spines belong to animals that can be placed in the Phylum Chaetognatha.

Comparison with the spines of Late Cambrian *Phakelodus*

In *Phakelodus* (*Prooneotodus*? previously) *tenuis* the gently curved hollow spines (up to 3 mm in length) have three layers
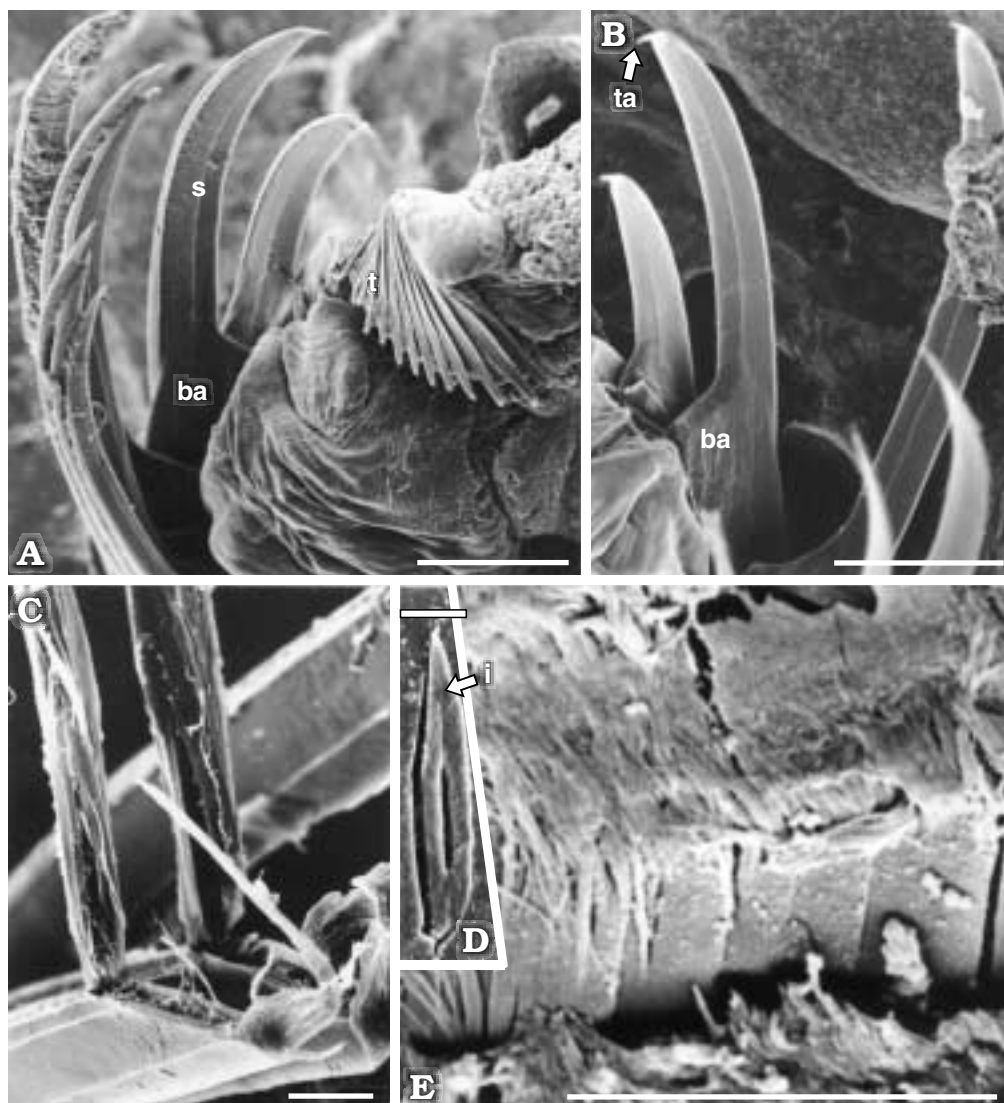
Fig. 5. Part of the head region of the Recent chaetognath *Eukrohnia hamata*, Gerhache Strait, Hughes Bay, Antarctic Peninsula; SMNH X-3525. Scale bar 0.1 mm for all except E. **A**. General view of a half of the grasping apparatus consisting of eight pairs of grasping spines (s) with a broad basis (ba) to the left and more than 10 pairs of teeth (t) (in the center). **B**. Five spines showing the talon with the slightly recurved tip. **C**. Broken spine showing the three layers of the wall and the fibers, which make up the central layer of the spine. **D**. Cross section of a spine showing oval outer edge (bottom) and acute inner edge (top), as well as the central cavity and the line between the central cavity and acute inner edge. **E**. A split spine showing the fibrous bundles in the middle layer, scale bar 0.01 mm. All SEM micrographs.

in the wall, exhibit oblique growth rings on the outer surface and faint lamination of the thick middle layer; the latter in cross section shows an indistinct interruption of the layers (Szaniawski 1982: text-fig. 1A–H). Also, the fibrous structure of the middle layer in *P. tenuis* has been observed (Szaniawski 2002). Thus, not only in general morphology (Müller and Andres 1976; Müller 1981), but in the wall ultrastructure as well, these spines are similar to the grasping spines of living chaetognaths (Szaniawski 1982: text-figs. 2A–C, 3A–I). The growth lines of *P. tenuis* illustrated on text-fig. 1F (Szaniawski 1982) show an oblique pattern (not mentioned by the author) that seems to reflect the fibrous structure of spines. In *P. elongatus* the spines were observed with the teeth that are somewhat similar in shape to the Mississippian spines but smaller (Szaniawski 1996: text-fig. 1). This observation supports the conclusion that chaetognaths were present in Cambrian time.

The Mississippian spines under consideration are similar to those of *P. tenuis* in that both are gently curved, hollow with what appears to be the impressions of three fibrous layers in the wall, and oblique growth lines on the surface (Figs. 1B, C, 2B, 3A, C). Contrary to *P. tenuis* and *P. elongatus*, these Mississippian spines show five to six longitudinal bands on their outer surface and a serrated concave (internal, in relation to mouth) side. Besides, the plastic postmortem deformations and even rolling of the broken end observed in exposed specimens of the Mississippian spines (Figs. 3A, C) and originally fibrous structure (Fig. 4B) is good evidence of an organic composition.

Thus, the Mississippian spines under consideration and the Late Cambrian ones of *P. tenuis* and *P. elongatus* are similar in structure and both possess features that are characteristic of the spines observed in living chaetognaths.

Systematic paleontology

Phylum Chaetognatha Leuckart, 1854
Class, Order, and Family uncertain

Genus *Eoserratosagitta* nov.

Type species: *Eoserratosagitta serrata* sp. nov., by monotypy.

Derivation of name: From Greek *eos*, dawn, and the name of a Recent genus *Serratosagitta* characterized, in part by having a saw-like edge on the chaetae.

Diagnosis.—Small horny gently curved spines with a long central cavity and fibrous wall; lateral sides weakly convex, with five to six longitudinal bands and fine oblique growth lines; concave (or inner) edge acute and serrated with more than 20 straight, conical, hollow denticles, inclined towards the pointed tip, distal portion non-serrated; convex (or distal) edge rounded and smooth.

Age.—Upper Mississippian (Middle Chesterian = Lower Serpukhovian).

Eoserratosagitta serrata sp. nov.

Figs. 1A–C, 2A–C, 3A–D, 4A, B.

Holotype: OUZC 4002/A, (Fig. 2A, B). Paratypes (OUZC 4002/B, C, D; Fig. 4).

Type locality: Cove Creek locality (See Mapes 1979, locality M-22) in northern Arkansas (USA).

Type horizon: Middle Chesterian (Namurian A equivalent), Upper Mississippian (Lower Serpukhovian). The phosphate concretion that contains the specimens is estimated to have come 1 to 3 m above the base of the formation in a black platy shale exposed in the banks and in the bed of Cove Creek.

Derivation of name: From the Latin *serra,* meaning saw, based on the saw-like inner edge of the spine bearing numerous denticles.

Diagnosis.—Small horny spines (approximate length 0.4–0.5 mm and width 0.05–0.06 mm); gently curved; central cavity long; with convex side rounded and concave side acute; five to six longitudinal bands on each lateral side; concave side serrated, with more than 20 straight, conical hollow denticles, inclined towards the pointed tip; distal portion (1/3 to 2/5 of total length) not serrated. The ratio between length of denticle and width of spine 2/5 (proximally) to 1/2 (distally). Denticles closely spaced, being in contact with each other in their proximal parts. Shape of denticles bullet-like: proximal portion, 2/3 of their length, cylindrical, and remaining distal portion conical, strongly pointed; ratio between maximum diameter and length 1/3–1/4.

Fossil record of proposed chaetognaths

The scarce fossil record of chaetognaths results from their almost complete lack of hard tissues. The morphological exceptions to this generalization are the horny grasping spines, biting teeth and "hardened" lateral and ventral plates within the head for muscle attachment and head support. These "hardened parts" and the possibility of soft body impressions are the only realistic potential fossil evidence of the ancient representatives of the Chaetognatha in the fossil record.

For a long time, *Amiskwia sagittiformis* from the Middle Cambrian of British Columbia, Canada, was assumed to be the most ancient chaetognath. It was preserved as a single imprint of the soft body in the Burgess Shale (Walcott 1911). The specimen does not show any spines and was therefore thought to present a young stage. However, the chaetognath affinity was later questioned and the similarity with nemertines was emphasized (Beklemishev 1952; Owre and Bayer 1962; Hekker 1964). Later the specimen was redescribed as a nemertine, mainly on the basis of a pair of long tentacles (Conway-Morris 1977). However, *Amiskwia* is indeed similar to young chaetognath hatchlings, and its assignment to the Chaetognatha cannot be completely excluded (Kasatkina 1982).

The Lower–Middle Ordovician *Titerina rokycanensis* from Bohemia that is assumed to belong to the chaetognaths (Kraft and Mergl 1989; Kraft et al. 1999) is known from three imprints of the body. The body is minute, and elongate, and its anterior end is distinctly differentiated, with one pair of robust spines.

The Middle Pennsylvanian *Paucijaculum samamithion* from the Mazon Creek area, Illinois, USA has been assigned to the chaetognaths with reservations (Schram 1973). It is known from few soft body imprints with some indications of grasping spines. *Paucijaculum samamithion* possesses a nearly circular body outline, a tail fin, but unlike living chaetognaths (except *Spadella*) the lateral fins are only incipiently developed if at all (Schram 1973).

The Lower Paleozoic protoconodonts (Paraconodontida) are interpreted as possible chaetognaths (Szaniawski 1980, 1982, 1983, 1996, 2002; Repetski and Szaniawski 1981; Bengtson 1983; Sweet 1988; Kraft et al. 1999; McIlroy and Szaniawski 2000), although, on the basis of gross morphology, they are often assigned to conodonts. This view is based on the similarities between the grasping spines of chaetognaths and Cambrian protoconodonts. Müller and Andres (1976) for the first time attracted attention to the similar construction of the spines of protoconodont *Prooneotodus*? (presently *Phakelodus*) *tenuis* and living chaetognaths. They considered the spines not as an indication of *Ph. tenuis*—chaetognaths affinity but as a convergent evolution similarity. Nevertheless, *Phakelodus* differs from the true conodonts (see Bengtson 1976: fig. 11; Szaniawski 1982: text-fig. 1A, B). in being usually preserved as assemblages of nearly identical, gently curved, uni-cusped, hollow spines (Abaimova 1980) and having a long central cavity. It is significant that in *Ph. elongatus* the spines and teeth were found together (Szaniawski 1996), which is a strong evidence of the similar structure of the grasping apparatuses in protoconodonts and living chaetognaths. Nevertheless, the relationship of the protoconodonts and euconodonts (= true euconodonts) is not presently well defined. Using structural differences in protoconodonts (= spines with long central cavity coming to the tip), paraconodonts (= spines with short central cavity ending at some distance from the tip) and euconodonts (no central cavity; two structural units can be distinguished: basal body and conodont proper. Bengtson (1976) showed the possible
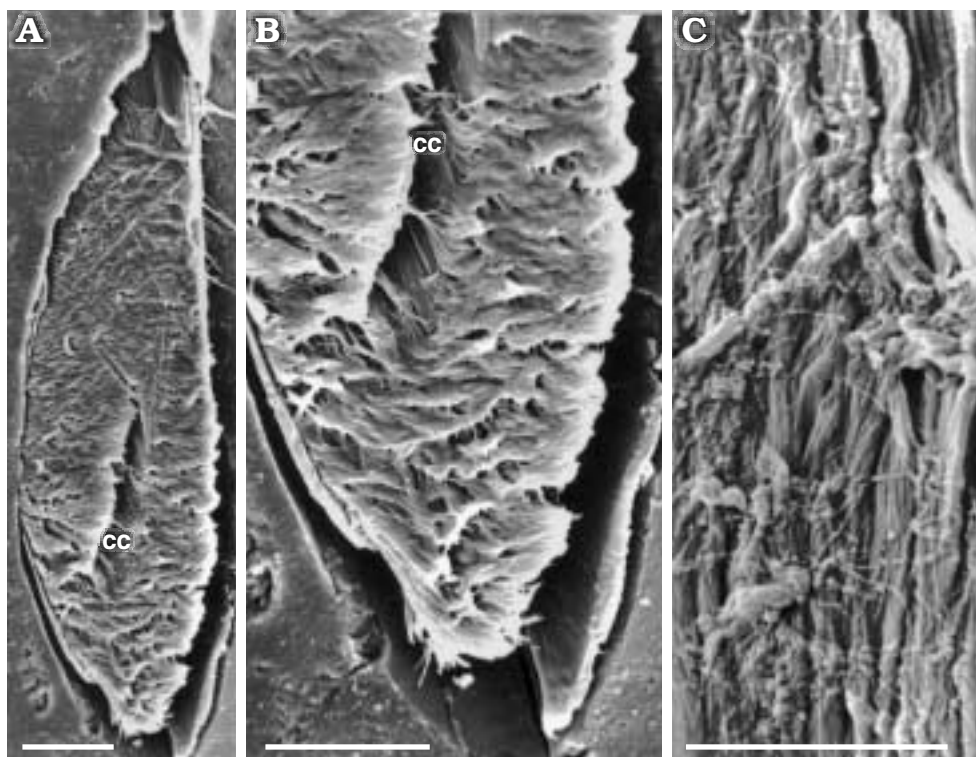
Fig. 6. Recent chaetognath *Eukrohnia hamata*, Gerhache Strait, Hughes Bay, Antarctic Peninsula; SMNH X-3526. **A**, **B**. Transverse section of a grasping spine, showing the hollow central cavity (cc), fibrous structure (f) in middle layer, and the thin partly removed solid-appearing outer layer. The thin inner organic layer has been removed by hydrogen peroxide, scale bars 0.01 mm. **C**. Longitudinal fracture of a spine showing the internal view of the fibers (f) grouped in bundles, scale bar 0.01 mm. All SEM micrographs.

trend in evolutionary transformation of the spine secretion and the phylogenetic relationship between them. On the assumption that they are the representatives of the same group he would derive the euconodonts via paraconodonts from protoconodonts. Due to the secreting epithelium lining the central cavity, the protoconodonts are assumed to grow by basal-internal accretion (Bengtson 1976: fig. 11A–C). Paraconodonts might have grown at early ontogenetic stages by concentric accretion, later by semi-concentric accretion (with the exception of the tip which was outside the secreting epithelium) (Müller and Nogami 1971; Bengtson 1976: fig. 11D–F). In euconodonts, the concentric accretion seemed to occur at all ontogenetic stages with a pause before the conodont proper was formed (Bengtson 1976: fig. 11G–I). This leads to the conclusion that protoconodonts were the starting construction for euconodonts (Bengtson 1976). Later it was emphasized that conodonts were not chaetognaths *sensu stricto* but they and chaetognaths seemed to have common ancestors (Bengtson 1983; Szaniawski 1987). The detailed morphological analysis of the Lower Silurian (Mikulic et al. 1985) and Lower Carboniferous (Briggs et al. 1983; Aldridge et al. 1986) imprints of the conodont soft bodies prompted a comparison with the primitive jawless craniates rather than chaetognaths, so that the possibility of a relationship between the euconodonts and chaetognaths was discounted (Aldridge et al. 1986). Contrary to the dorsal-ventrally flattened body of the chaetognaths, in the conodonts the body seemed to be laterally flattened, with the posterior fins extending further along one margin than the other. According to Aldridge et al. (1986: 290) the conodonts are "either a sister group of the

myxinoids, or lying between them and the heterostracans" and "There is no longer justification for retaining a phylum Conodonta".

In summary, the Late Mississippian *Eoserratosagitta serratum* gen. et sp. nov. is an accumulation of well-preserved spines, which exhibit a larger number of similar ultrastructural and morphological features with spines in living chaetognaths than to any other fossil so far described. Therefore, we conclude that the fossil spines from Arkansas belong to the Chaetognatha, and that these fossils provide convincing evidence for the existence of chaetognaths in the Paleozoic.

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