# 16. CHORDATE AFFINITIES OF THE CONODONTS

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Until recently virtually nothing was known about the morphology of conodont animals, and zoologic affinities of the group are still regarded as obscure. The present contribution evaluates the hypothesis that agnathan vertebrates are the closest relatives of conodonts. The microstructure of element of conodont apparatuses, their organization into skeletal structures, and the inferred morphology of the soft body parts are compared to the anatomy of early vertebrates. Other problematic phosphatic dermal sclerites are also reviewed.

A complete phosphatic element of the conodont apparatus consists of two distinct parts. The oral part (crown of Nicoll 1977) is developed by centrifugal external accretion. It is rather compact in structure, and its surface is smooth or regularly ornamented. The basal part (basal filling), which is developed by inner accretion, varies greatly in microstructure and morphology. The mode of secretion of the crown tissue is here considered diagnostic for the group; fossil sclerites secreted differently are not considered to be conodont elements (see Bengtson 1976, 1983a, for opposing view).

## CROWN TISSUE

The crown of conodont elements is composed of relatively large, elongated crystallites of apatite. They are parallel to each other, and normal to the element surface *(Fryxellodontus, Cordylodus)* or, most commonly, parallel to the cusp or denticle axis. Frequent disconformities in distribution of lamellae marking subsequent stages in secretion of the crown clearly indicate that the surface of at least platform elements was periodically worn out (Müller and Nogami 1971; Müller 1981). Whether this was caused by mechanical abrasion or chemical resorption, cannot be determined. The shape of apatite crystallites and the pattern of their distribution persisted from the Late Cambrian *Teridontus nakamurai* (Nogami 1967) (see Landing et al. 1980) to the extinction of conodonts (Pietzner et al. 1968; Lindström and Ziegler 1971; Barnes et al. 1973; Müller 1981; Bitter and Merrill 1983). The internal surface of the crown, visible in the basal cavity, always shows distinct growth lines (Pietzner et al. 1968; Lindström and Ziegler 1981).

A basic problem is to explain the function of the conodont elements by allowing for the presence of soft tissue above the crown tissue. Several solutions have been proposed. It is suggested that conodont elements (1) formed a skeleton of the ciliary apparatus (Lindström 1973, 1974; Conway Morris 1976, 1980; Nicoll 1977), (2) grew within epithelial pockets and were protruded while functional (Bengtson 1976; Carls 1977), (3) were covered by a hard horny tissue secreted above the epithelium (Priddle 1974), or (4) originated in a manner analogous to vertebrate teeth and were replaced in ontogeny (Carls 1977; Jeppsson 1980). None of these interpretations is convincing. Bengtson's pocket hypothesis can hardly explain healed fractures of conodont cusps (see Müller and Nogami 1971) and brushlike appearance of platform elements not uncommon in the Devonian (Müller 1981). Carls' concept of ontogenetic replacement implies the occurrence of smaller, regenerating elements in at least some natural assemblages. However, nothing like this has ever been reported. The high rate of evolution and repeated development of platform elements, with their molarlike appearance, are evidence against the filtratory apparatus concept (Dzik 1976; Jeppsson 1979a). Neither were scleritized organic caps covering conodont elements recognized in articulated apparatuses, nor were phosphatic nuclei identified in teeth of Paleozoic hagfishes, to support Priddle's model of the conodont element.

## BASAL FILLING

Unlike the crown, apatite crystallites in the basal filling are roughly isometric and usually do not show any preferred orientation (Pietzner et al. 1968; Lindström and Ziegler 1981). The boundary between the crown and basal filling tissues is always sharp and distinct (Fig. 1).

Most conodont elements lack any remnants of the basal filling. Sometimes, however, a black, carbonized spongy tissue penetrated by meandering canals can be found inside the basal cavity. It may represent shrunken remnants of unmineralized organic matrix of the basal filling tissue (Fig. 1B). In some other cases the basal filling tissue is well mineralized, but its morphology suggests that partial shrinkage occurred during the early diagenesis (Lindström and Ziegler 1971, 1981). Irregular canals and tubuli penetrate this kind of tissue (Barnes et al. 1973). When the tissue underwent more advanced mineralization while alive, the

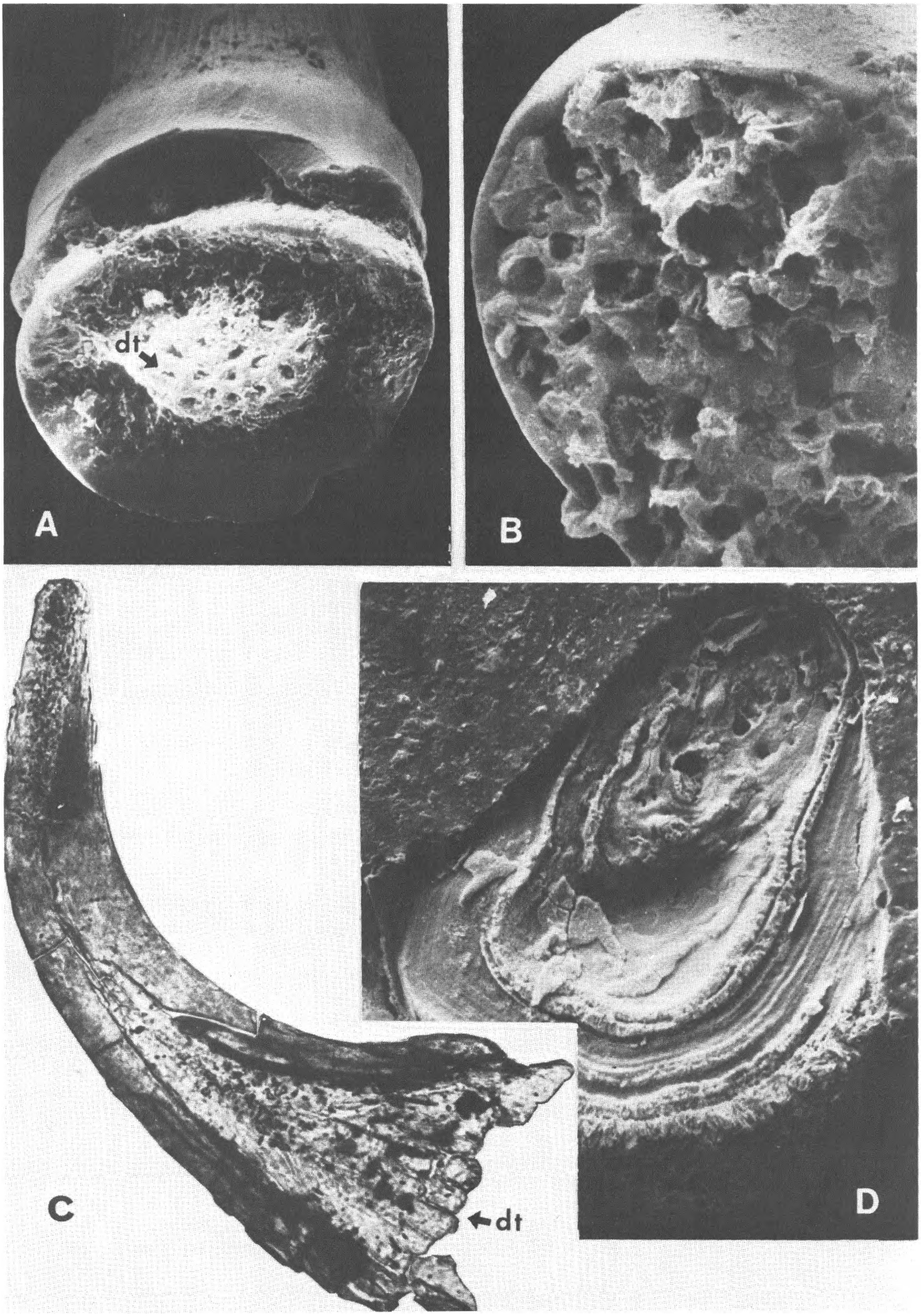

**Fig. 1.** Microstructure of the basal filling in elements of the conodont *Semiacontiodus cornuformis* (Sergeeva 1963) from the Llanvirnian of the Baltic area (glacial erratic boulders). A. Basal view, openings of dentine tubuli (dt) visible, sample E-079. ×300. B. Basal view of a black, unmineralized basal fillilng, sample E-113. ×500. C. Medial thin section, dentine tubuli (dt) in longitudinal section, sample E-079. ×200. D. Etched oblique section through conspicuous callus of the basal filling, sample E-079. ×300.

tubuli appear to be confined to the axial parts of the element and they open basally (Fig. 1A, C). Most commonly, the basal filling tissue shows lamellar organization. Except for growth lines, no other internal structures can be recognized (Müller and Nogami 1971; Lindström and Ziegler 1981). In the histogeny of some primitive Early Ordovician conodonts, such a laminated basal filling tissue followed the spongy tissue (Fig. 1D). Most post-Ordovician conodonts had compact basal filling tissue only. This variation in structure of the basal filling tissue seems to represent consecutive stages in its mineralization.

Generally, the basal filling tissue contributes only a small portion of the total mass. There is only a single group of Ordovician conodonts with the basal filling tissue dominant. *Archaeognathus primus* Cullison 1938 from the Dutchtown Formation (Late Llanvirnian?) of Missouri is the best known representative of this group (Cullison 1938), which is widespread and abundant in North America (Mosher and Bodenstein 1969) and Siberia (Moskalenko 1972, 1976; Barskov et al. 1982). The crown tissue is restricted to the working edge of the element, and it forms only a thin crown, frequently split into coniform denticles. The basal filling reveals a complex internal structure with wide, branching canals (Barskov et al. 1982). Although these so-called coleodontids still await detailed taxonomic description and reconstruction, their conodont nature seems to be well established.

## CONODONT APPARATUSES

The original organization of apparatuses preserved on rock bedding plane (natural assemblages) generally is obscured by sediment compression during lithification. This has prompted many contradictory reconstructions (Jeppsson 1971; Collinson et al. 1972; Lindström 1973, 1974; Nicoll 1977; Hitchings and Ramsay 1978). A fortunate exception in the mode of preservation is represented by the natural assemblage of *Ozarkodina steinhornensis* (Ziegler 1956) described by Mashkova (1972) from Early Devonian limestones. Its elements collapsed obliquely from the sides and are preserved with some relief. As judged after Mashkova's and other natural assemblages (see also Pollock 1969), conodont elements were arranged along both sides of the medial plane, with their processes oriented dorsally and ventrally and the cusps directed toward each other in every pair (Dzik 1976). Two pairs of the elements (*sp* and *oz*) were somehow separated from the remainder of the apparatus and possibly obliquely oriented (Fig. 2).

This general pattern has been confirmed by subsequent discovery of a cluster of seven coniform elements representing one-half of the apparatus of a Late Ordovician species (Aldridge 1982). The clusters illustrated by Briggs et al. (1983) indicate that, despite different arrangement of processes, the cusps of all the elements point in the same direction. Because the *sp* element, at one end of the apparatus, usually is the most robust one (frequently with a platform), while the *ne* element, at the opposite end, usually bears a sharp, swordlike cusp, they were inferred to represent the posterior and anterior ends of the apparatus, respectively (Dzik 1976). A functional gradient along the apparatus, from the grasping function of the *ne* element to the masticatory function of the *sp* element, was proposed. This has been corroborated by the discovery of soft body parts in the conodont animal (Briggs et al. 1983). The pattern of conodont apparatus thus is well established (Fig. 2), although there still are some doubts regarding the position of symmetric (*tr*) elements inside or outside the apparatus. In Mashkova's (1972) apparatus, the *tr* element (identified by Jeppsson 1979b) has the same orientation as the others, and even though its counterpart is not preserved, there is no evidence for its medial positon as proposed by Jeppsson (1971, 1979b). Jeppsson cited the commonness of numerical underrepresentation of *tr* elements to support his reconstruction. Such underrepresentation, however, may be caused by hydrodynamic factors alone, for *tr* elements usually are the most ramified and gracile in the apparatus.

Apparatuses of ramiform conodont elements can be easily homologized in the Early Ordovician (Dzik 1983) through Late Triassic (Sweet 1981). They have 7 pairs of elements each, except for some Late Triassic apparatuses with possibly 10 pairs of elements each [5 pairs of hindeodelliform elements; Ramovš (1978), Dzik and Trammer (1980)] and Devonian *Icriodus* apparatuses, which bear hundreds of coniform elements (Nicoll 1982) and which perhaps represent disintegrated denticles of originally ramiform elements.

The closest functional analog to apparatuses of coniform conodont elements is the grasping apparatus of the Chaetognatha (Fig. 3A; Szaniawski 1982), while apparatuses of ramiform elements have their closest analog in the buccal apparatus of hagfish (Fig. 3B; Priddle 1974). The buccal apparatus of *Myxine* resembles conodont apparatuses (especially *Archaeognathus*) in being bilaterally symmetric and composed of transverse rows of denticles (horny instead of phosphatic) and also in working by scissorlike closing of its lateral parts (Dawson 1963).

## CONODONT SOFT BODY

The first fossils with preserved soft-part anatomy that were claimed to represent the conodont animal include *Lochriea wellsi* Melton and Scott 1973 and other "conodontochordates" from the Carboniferous Bear Gulch Limestone of Montana

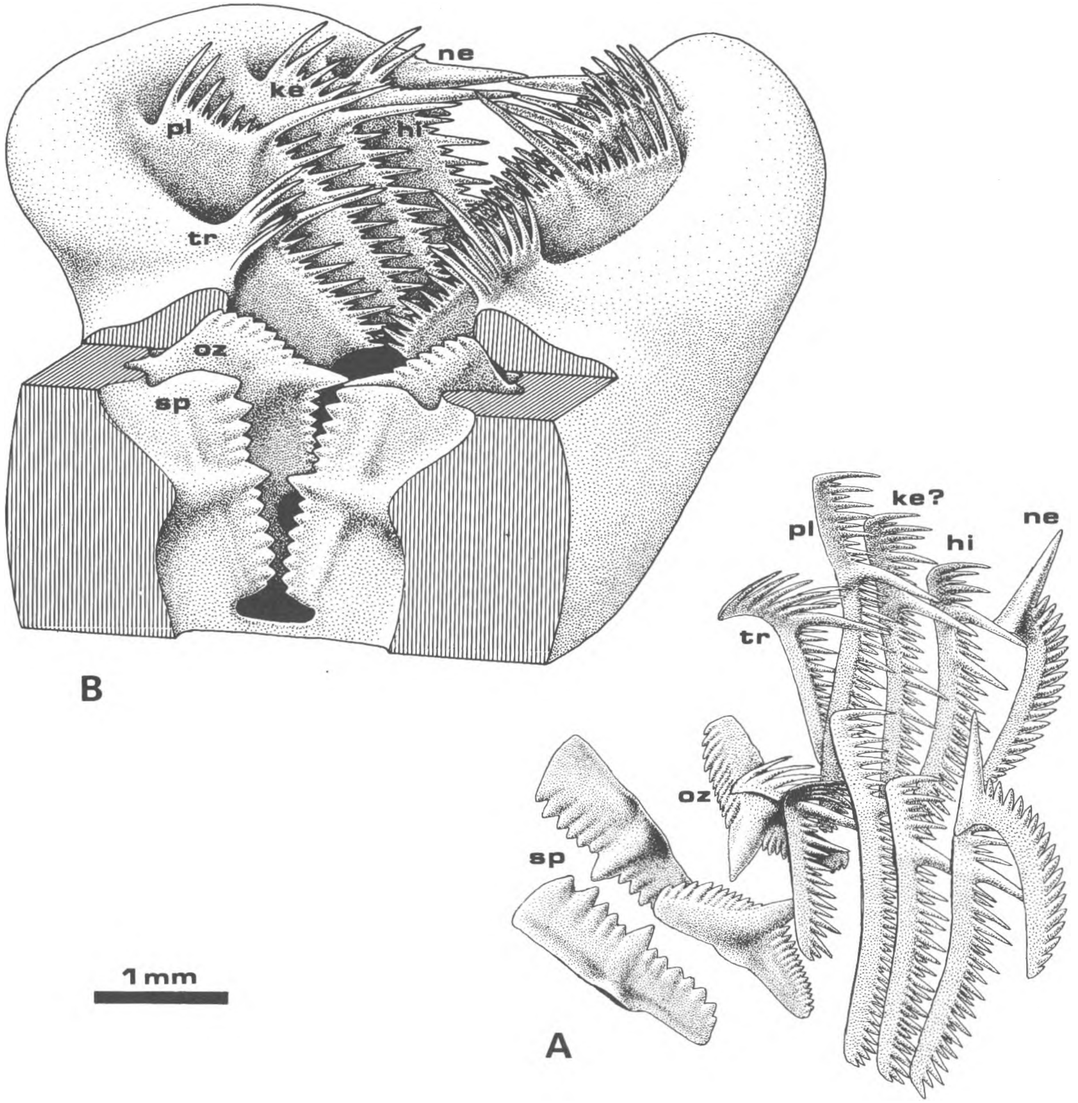

**Fig. 2.** Apparatus reconstruction of *Ozarkodina steinhornensis* (Ziegler 1956) based on the natural assemblage described by Mashkova (1972) from the Early Devonian of Tadjikistan. A. Reconstructed complete set of elements as found on the bedding plane (cf. Mashkova 1972, pl. 1). Identification of the left *tr* element according to Jeppsson (1979b). B. Proposed spatial arrangement of elements in the oral part of the conodont animal (modified from Dzik 1976, fig. 10a), venter up. Note that frequency distribution data suggest presence of unpaired *tr* element.

(Melton and Scott 1973). In having a hypocercal (?) caudal fin with delicate rays, they resemble the Late Devonian, possibly planktic anaspide *Endeiolepsis;* on the other hand, the general shape of the body and the concentration of visceral organs into a globular dense structure (ferrodiscus) indicate the Recent salpae as at least the ecologic analog of these animals. "Conodontochordates" are now generally believed to be conodont-eaters rather than true conodont animals (Lindström 1973, 1974; Conway Morris 1976).

The second fossil with preserved soft-body parts proposed to represent the conodont animal was the Middle Cambrian *Odontogriphus omalus* Conway Morris 1976 from the Burgess Shale of British Columbia (Conway Morris 1976; Chapter 13 by Briggs and Conway Morris, this volume). It is poorly preserved but it shows a looplike organ with coniform teeth in the oral region, two lateral organs with complex internal organization on both sides of the head, a longitudinal digestive (?) tract, and metameric bands in the trunk region. Contrary to the reconstruction by Conway Morris (1976), metamery is invisible at the margin of the trunk, while transverse bands end laterally in dark round spots arranged in rows along both sides of the central, metameric area of the trunk. The caudal area is flexed and partially hidden under the trunk, with no evidence of metamerization.

Leaving aside the problem of the unknown original mineral composition of the denticles of *Odontogriphus*, chordate affinities of this animal seem more plausible than its lophophorate nature proposed originally by Conway Morris (1976, 1980). All Recent and fossil lophophorates are sedentary organisms with a relatively large tentacular apparatus that never has an internal skeleton comparable to the conodont apparatus. By contrast, *Odontogriphus* was free-living and not a suspension feeder. Its body shape seems to have resembled early agnathans, and all its preserved internal structures can be at least tentatively homologized with heterostracans. Metameric bands ending in black spots occur in *Lanarkia* and *Turinia* (Turner 1982), where they are interpreted as remnants of branchial sacs and their openings. The number of proposed branchial sacs in *Odontogriphus* (at least 25) exceeds that in the Heterostraci but still is significantly smaller than in *Amphioxus*. The lateral organs of *Odontogriphus* may represent something related to the osteostracan lateral line organs. Even if its mouth really bore a tentacular organ as proposed by Conway Morris (1976), similar tentacles occur in *Amphioxus*. *Odontogriphus* thus may be a Cambrian naked relative of heterostracans. Its relationship to conodonts cannot be seriously considered unless the microstructure of the oral denticles is known.

The most convincing discovery of a fossil conodont animal with preserved soft-part remnants is *Clydagnathus?* cf. *cavusformis* Rhodes et al. 1969 from the Early Carboniferous of Scotland (Briggs et al. 1983; Chapter 15 by Aldridge and Briggs, this volume). This fossil indicates that the conodont animal was lamprey shaped, probably with a hypocercal caudal fin supported by delicate rays. Like cyclostome agnathans, known also from slightly younger Carboniferous strata (Bardack and Richardson 1977), the conodont animal had V-shaped myomeres. *Clydagnathus?* cf. *cavusformis* has an almost complete apparatus preserved in the oral part of the body. Elements of the apparatus lie transversely to the longitudinal axis of the animal's body as in Mashkova's natural assemblage (1972). The pairs of *sp* and *oz* elements were possibly hidden in the throat, while other elements supported two oval lobes (Fig. 4; Briggs et al. 1983).

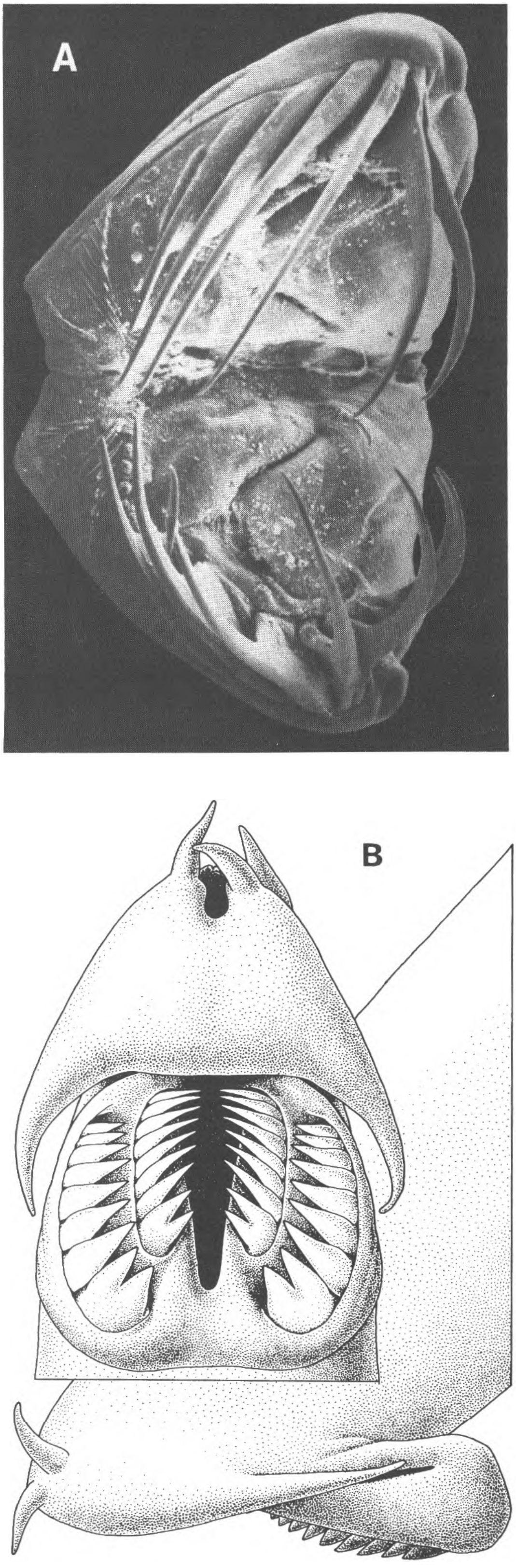

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**Fig. 3.** Closest Recent analogs to conodont apparatuses. A. Grasping apparatus of the chaetognath *Eukrohnia hamata* (Möbius 1875). ×25. B. Jaw apparatus of the hagfish *Myxine* sp. ×5.

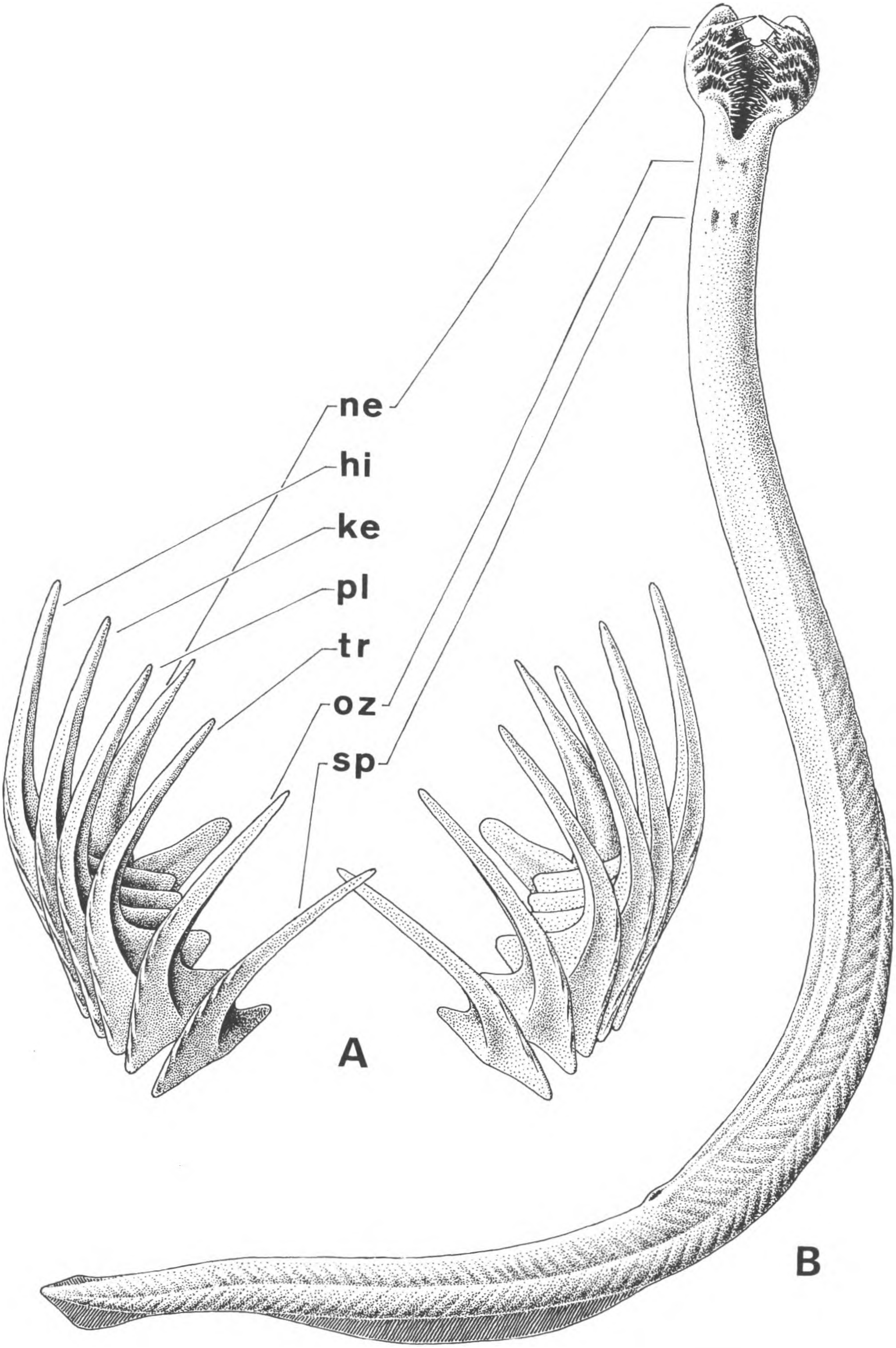

**Fig. 4.** A. Apparatus of the conodont *Besselodus arcticus* Aldridge 1982 from the Late Ordovician of Greenland, reconstructed in life position. Tentative homology of the elements in Jeppsson's notation (1971). Based on data from Aldridge (1982). B. Reconstruction of the body of *Clydagnathus?* cf. *cavusformis* Rhodes et al. 1969 from the Early Carboniferous of Scotland. Based on Briggs et al. (1983).

## HYPOTHESIS OF CHAETOGNATH AFFINITIES OF THE CONODONTS

Morphologic (Figs. 3 and 4A) and proposed functional (Jeppsson 1979a) similarities between conodont apparatuses and grasping apparatuses of the Chaetognatha are striking (Szaniawski 1982). The two animal groups show much similarity in body shape and size (Briggs et al. 1983), and probably occupied similar niches in Paleozoic ecosystems (Seddon and Sweet 1971). As shown by Szaniawski (1982), phosphatized chaetognath grasping spines frequently occur in Cambrian rocks. Thus, chaetognaths stratigraphically precede the oldest true conodonts.

Despite these similarities, however, conodont elements and chaetognath grasping spines developed in basically different ways. The crown tissue of conodont elements was secreted from the outside of the basal cavity, while the tissue of the grasping spine is secreted from the inside. Bengtson (1976) proposed a homology between the conodont basal filling and the tissue of the grasping spine. According to this concept, the grasping spine has become embedded into an epithelial pocket in the course of evolution from chaetognaths to conodonts. The epithelium of the pocket subsequently secreted the crown tissue. The Late Cambrian to Middle Ordovician westergaardodinids ("paraconodonts") have been proposed to represent an intermediate stage of the evolution (see also Andres 1981).

The hypothesis deriving conodont elements from chaetognath grasping spines encounters serious problems, however. First of all, the accidental occurrence and originally late mineralization of the basal filling tissue contradict its proposed primitivism relative to the crown tissue. Among primitive panderodontid and protopanderodontid conodonts, the basal filling tissue was not laminar at the early stages of either phylogeny or histogeny. Moreover, secretion did not take place within the basal cavity in the early westergaardodinid *Furnishina*. Nothing could be homologized with the basal filling. Elements of *Furnishina* developed centrifugally from both the outside and the inside at the very beginning of their histogeny, but in contrast to true conodonts, there is no sharp boundary between the crown and the basal filling tissues. In spite of a similarity in shape, there is a major difference in histogeny between the conodonts, westergaardodinids, and chaetognaths, and there is no evidence for transitions between these groups.

The crucial counterargument to the hypothesis of chaetognath affinities of conodonts is the presence of V-shaped muscular somites in the Carboniferous conodont animal (Briggs et al. 1983; Chapter 15 by Aldridge and Briggs, this volume). This is absolutely incompatible with the mode of locomotion and the body plan of the Chaetognatha. Moreover, the asymmetric fin of the conodont animal suggests that it worked laterally instead of vertically. These two features ultimately reject the hypothesis of conodont relationships to the Chaetognatha.

## HYPOTHESIS OF CHORDATE AFFINITIES OF THE CONODONTS

Neither the presence of an internal skeleton nor its phosphatic composition defines a chordate. The peculiarity of primitive chordate dermal sclerites consists in their secretion within epithelial sacs from the outside by epithelial ameloblasts and from the inside by mesodermal odontoblasts. Calcium and phosphate ions in chordate tissues are persistently in supersaturated solution, but they can precipitate as hydroxyapatite only on matrices that provide nucleation centers. $\beta$-proteins secreted by ameloblasts serve the function of a matrix for precipitation of hydroxyapatite in the enamel (Little 1973). In therian mammals, hydroxyapatite crystalizes into relatively large crystallites organized more-or-less regularly into prisms (Poole 1971). Teeth of lower tetrapods and crossopterygian fish usually have an enamel cover rather homogeneous in structure but with distinct increment lines (Poole 1971; Meinke and Thomson 1983). Other fish teeth are capped with enameloid (or durodentine) tissue that originates by mineralization of mixed collagen (secreted by odontoblasts) and proteins. The enameloid differentiates and begins to calcify before the dentine formation starts; at that time, collagen fibers revert to a labile form and hence are never incorporated into the mineralized tissue (Poole 1971; Shellis and Miles 1976).

The mineralization of dentine occurs on a collagen matrix secreted by odontoblasts. Odontoblasts are not incorporated into mineralized dentine, but their processes (Tomes' fibers) penetrate dentine layers and frequently also the enamel (Schmidt and Keil 1971). The presence of Tomes' fibers in the enamel (and also in the enameloid) seems to be related to the late calcification of the matrix and usually is confined to its deeper, earliest part (Kerr 1955; Schmidt and Keil 1971; Shellis and Miles, 1976). The boundary between the parts of the tooth secreted by ameloblasts and odontoblasts is usually distinct. Sometimes, however—perhaps when the mineralization is very delayed—there is a complete transition between the two tissues. This is why most authors consider enameloid caps to be built with a special kind of dentine (Ørvig 1967; Schmidt and Keil 1971; Poole 1971; Taylor and Adamec 1977). Shellis and Miles (1976), however, demonstrated that at least the external part of the enameloid cap is homologous to the enamel of mammals.

Fossil agnathans with calcified dermal sclerites display diverse histogenetic methods of forming of sclerite caps. In *Astraspis desiderata* Walcott 1892, one of the oldest histologically studied agnathans, the crowns of the dermal tubercles are covered with a tissue that is almost homogeneous and does not contain any fibers or canals (Ørvig 1958; Denison 1967; Halstead 1969). It consists of small, elongated, randomly oriented apatite crystallites (Fig. 5B). The cap is distinctly separated from the underlying dentine (Fig. 5A), which is perforated by numerous tubuli (Halstead 1969) and consists of granular apatite (Fig. 5C). Growth lines visible in the dentine frequently are not parallel to the boundary between the tissues (Denison 1967), suggesting that the dentine grew out from the center of the cavity of the cap after its completion. *Astraspis* ranges from the Early (Lehtola 1973) to Late Caradocian (Denison 1967).

The tubercles of *Pycnaspis splendens* Ørvig 1958, which temporally but not spatially co-occurred with *Astraspis,* differ from those of *Astraspis* in having their caps penetrated by dentine tubuli (Ørvig 1958), but the boundary between the cap and the underlying dentine still is sharp. Even more dentinelike are the caps of tubercles in another Late Ordovician agnathan, *Eriptychius americanus* Walcott 1892. The boundary separating the cap disappeared almost completely, although a thin enamel-like cover still can be recognized in some tubercles (Denison 1967; Halstead 1969). This seems to be typical of post-Ordovician agnathans. An external nondentine cap of the tubercle can be recognized only in polarized light (Schmidt and Keil 1971). In supposedly primitive Silurian thelodonts, scales are almost entirely penetrated by dentine tubuli (Fig. 6; Gross 1967), and the boundary between the parts that originated ectodermally and mesodermally is visible only at its external surface (Fig. 6A). Mineralization probably took place only after the formation of matrix of the whole scale, and a subsequent epithelial increment was insignificant.

Stratigraphic data thus suggest that, contrary to Ørvig (1967), the distinction between enamel and dentine was primitive in vertebrates, while aspidin and true bone were later derivatives of the dentine (Halstead 1969; Meinke and Thomson

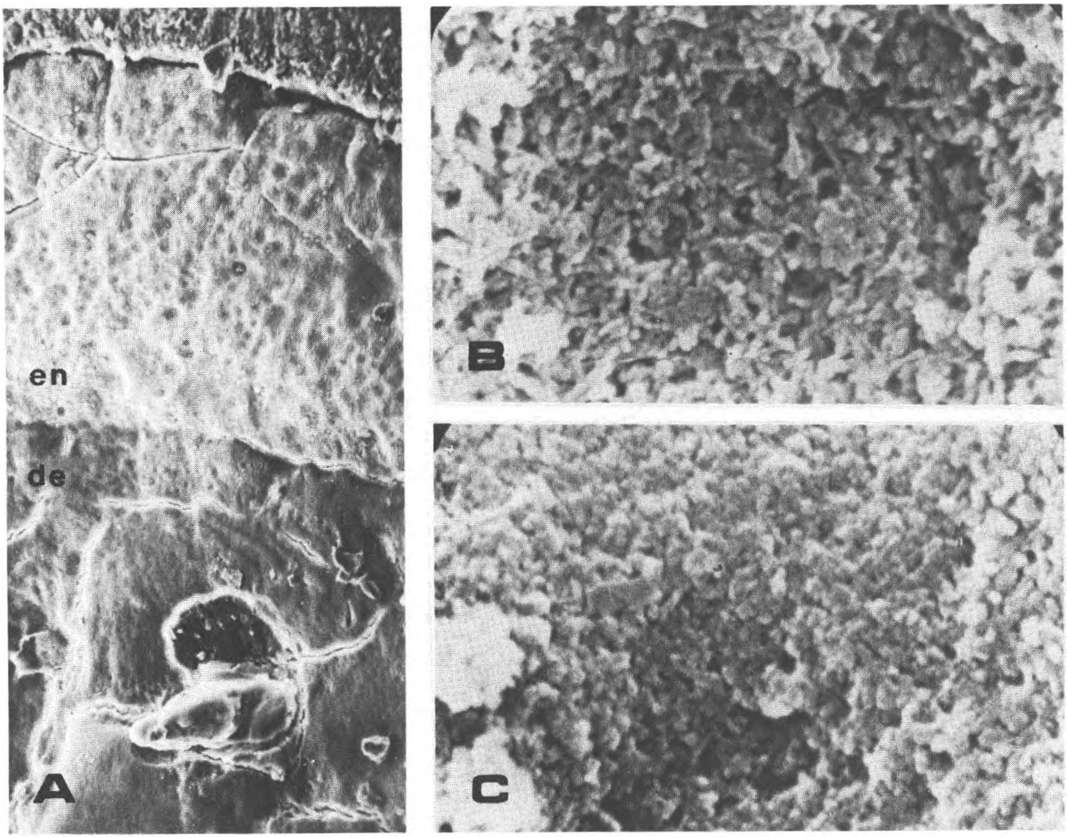

**Fig. 5.** Microstructure of a dental tubercle of the agnathan *Astraspis desiderata* Walcott 1892 from the Late Caradocian Harding Sandstone, Colorado. A. Etched vertical (not exactly medial) section through the cap. Note distinct boundary between the enamel(oid) (en) and the dentine (de). ×500. B. Enamel. ×24,000. C. Dentine. × 24,000.

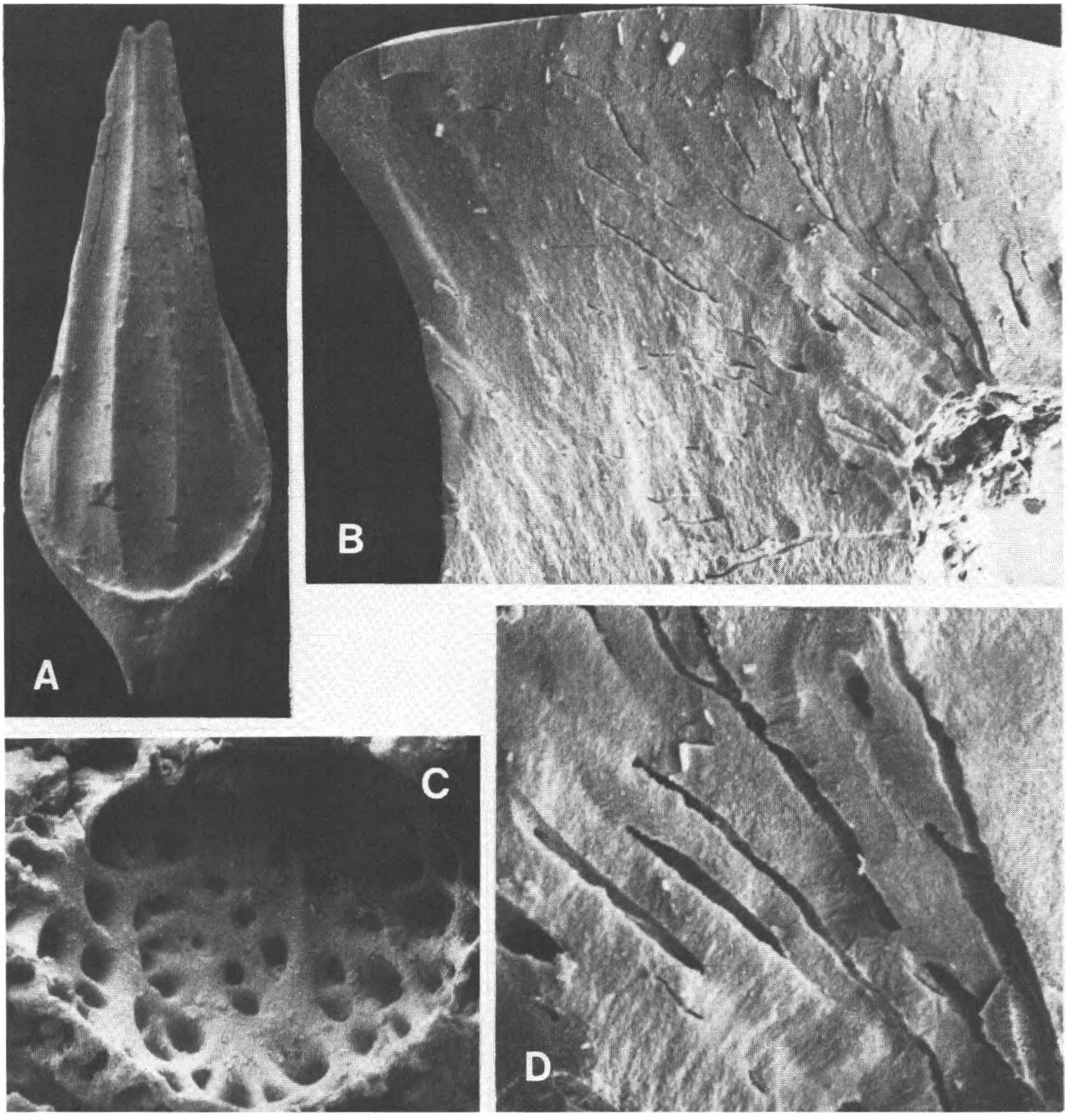

**Fig. 6.** Micromorphology of Late Silurian thelodont scales from the Baltic area (erratic boulder E-279). A. *Logania cuneata* (Gross 1947), scale in upside view. Note distinct boundary between smooth area formed by the epithelium and rough basal part of mesodermal origin (cf. Fig. 1A). ×100. B. Longitudinally broken scale of *Thelodus parvidens* Sgassiz 1844, with well-preserved branching dentine tubuli (cf. Fig. 1C). × 300. C. Pulp cavity of *Thelodus trilobatus* Hoppe 1931, with openings of bunches of dentine tubuli (cf. Fig. 1A). ×750. D. Same as in B. ×1000.

1983). Even more primitive sclerites might then be expected to have a homolog of the enamel as the dominant tissue.

A homology between the conodont crown tissue and the enamel and between the basal filling and the dentine was proposed by Schmidt and Müller (1964; see also Scott 1969; Dzik 1976). A sharp structural distinction between the crown tissue and the basal filling seems to be primitive in the conodonts (but see Bengtson 1976, 1983b). In most conodonts, sporadic mineralization of the basal filling tissue occurs secondarily, usually in large elements probably belonging to older adults. The main argument against agnathan affinities of the conodonts used to refer to the lack of dentine tubuli, spaces after osteocytes, or collagen fibers in tissues of the conodont element (Gross 1954; Denison 1967). As shown above, this argument is no longer valid. Incorporation of collagen fibers, cell processes, or whole cells is not a necessary feature of these mineralization mechanisms in hard tissues of the vertebrates. Furthermore, the basal filling tissue of early conodonts seems to have been penetrated by processes of mesodermal cells.

As shown by the presence of distinct growth lines in the conodont crown tissue, mineralization of organic matrix occurred immediately after or even during its secretion. This makes the crown tissue different from durodentine or enameloid caps of fish and agnathans. However, the enamel cap in *Astraspis,* one of the oldest histologically studied vertebrates, differs from the conodont crown tissue only in smaller size and random orientation of its constituent crystallites (Fig. 5B). It is generally accepted that hydroxyapatite crystallites follow in their orientation the collagen fibers of the matrix (Schmidt and Keil 1971; Shellis and Miles 1976). The crown tissue thus might originate on a collagen matrix, similar to the enameloid of Recent fish. By analogy to the evolution of the enamel in mammals (Koenigswald 1981), one may suggest that the crystallite size and orientation in the conodont cusp were related to its supposed mechanical function (Jeppsson 1979a).

Crystallites in the basal filling tissue differ from those of the crown tissue. At least in the primitive coniform elements, they were arranged in spherulitic aggregates and randomly oriented at the beginning of mineralization. After calcification, numerous tubuli remained in the basal filling (Fig. 1A, C). They do not differ in diameter, mode of branching, and distribution from the tubuli in the dentine of thelodont scales (compare Figs. 1 and 6). The main difference between the basal filling tissue of conodont elements and the agnathan dentine consists in complete disappearance of the tubuli at later histogenetic stages in the former. In this respect, the basal filling tissue can be regarded as an analog of the aspidin.

The hypothesis of chordate affinities of the conodonts has now received much support through the recognition of V-shaped myomeres in the conodont animal body (Briggs et al. 1983).

## CONNECTING LINKS

Agnathans with body armor have been recorded in the Llanvirnian (Ritchie and Gilbert-Tomlinson 1977) and even earlier (Nitecki et al. 1975; Bockelie and Fortey 1976; Repetski 1978), although conclusive histologic evidence still is lacking. The oldest unquestionable conodonts occur in the Franconian (Miller 1980). Except for the doubtful Middle Cambrian *Odontogriphus,* the only older fossil that could be related to true conodonts is *Fomitchella infundibuliformis* Missarzhevsky 1969 from the Early Tommotian of Siberia. *Fomitchella* was interpreted, on purely morphologic grounds, as ancestral to the Ordovician *Pseudooneotodus* (Dzik 1976). Bengtson (1983b) demonstrated that the sclerites of *Fomitchella* had grown centrifugally. He also noted that "the lamellae consist of finely granular apatite without preferred crystallographic orientation" (p. 12). Being similar in shape to early conodont elements and lacking any mineralized mesodermal tissue, the sclerites of *Fomitchella* have almost the same microstructure as the enamel cap of *Astraspis.* It is plausible to derive regularly oriented crystallites of both *Fryxellodontus* type (with crystallite axes normal to the surface) and *Panderodus* type (with crystallite axes parallel to the surface) from the pattern of *Fomitchella.*

The morphologic gap between *Fomitchella* and *Astraspis* can be filled up with a group of Cambrian to Early Ordovician phosphatic sclerites with more balanced contributions of ectodermal and mesodermal mineral tissues. This group includes *Hadimopanella apicata* Wrona 1982 from the Early Cambrian *Bonnia-Olenellus* Zone of Spitsbergen. These sclerites are much smaller in size than *Fomitchella,* but their hyaline, centrifugally growing caps are easily recognizable. Their wide basal cavity is filled by a callus of the basal filling, which is penetrated by an irregular network of very thin horizontal and vertical canals (Wrona 1982). These canals, usually filled by acid-resistant minerals, may represent spaces left by the collagen fibers or organic matrix. *Hadimopanella apicata,* with its single-tipped sclerites, is an end member of a morphocline including the Early Cambrian *Lenargyrion knappologicum* Bengtson 1977 (with several irregularly distributed apices; Bengtson 1977), the Middle Cambrian *Hadimopanella oezgueli* Gedik 1977, the Late Cambrian *Utahphospha sequina* Müller and Miller 1976, and the Early Ordovician *U. cassiniana* Repetski 1981 (with very regular crowns of tubercles: Müller and Miller 1976; Repetski 1981; Boogaard 1983). There is evidence that the caps of *Utahphospha* grew from the outside, centrifugally (Müller and Miller 1976), while the tissue that fills up their basal cavities and links individual sclerites into a continuous body cover has a rather spongy appearance. In *Lenargyrion* the cap is composed of very small, randomly arranged crystallites (Bengtson 1977), as in *Fomitchella* and *Astraspis.*

In *Lenargyrion,* very small sclerites, like those of *Hadimopanella apicata,* have only a single apex, but the number of apices increases proportionately with increase in sclerite size (Bengtson 1977). This ontogenetic pattern resembles the histogeny of some conodont elements (Dzik and Trammer 1980). The correlation of the number of apices to the sclerite size seems to hold also among different species. Sclerites of much larger size than the *Hadimopanella–Utahphospha* group may thus be expected to have more numerous apices. Such a pattern occurs indeed in the Late Cambrian to Late Ordovician *Milaculum* (Fig. 7A).

The external surface of *Milaculum* sclerites is smooth and the basal surface is rough as in *Utahphospha* (Fig. 7C), but a distinct cap tissue has not been recognized. The sclerites are penetrated by vertical canals (Müller 1973) resembling dentine

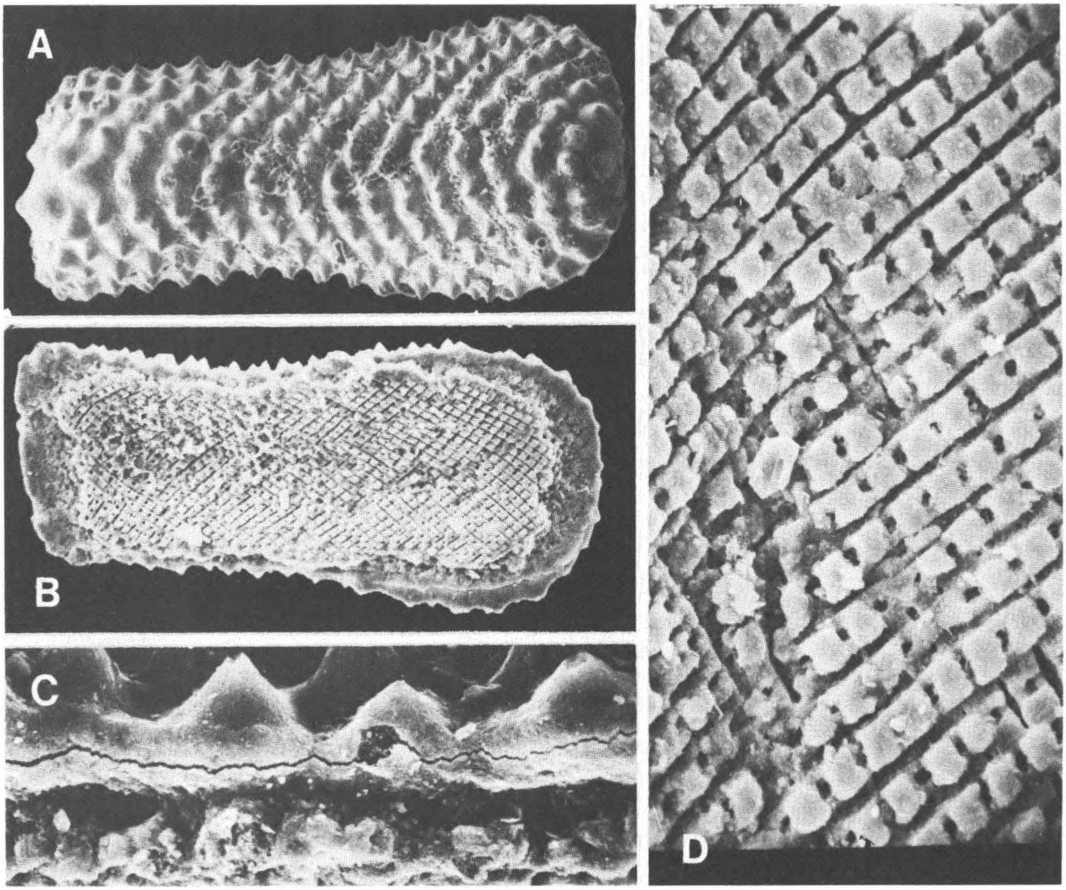

**Fig. 7.** Micromorphology of *Milaculum scandicum* Müller 1973 from the latest Arenigian of Sweden. A. Sclerite in upside view. Note regular distribution of tubercles (cf. Fig. 8B–F). ×200. B. Basal view of the same specimen. Note mineralized basal part. ×200. C. Boundary between the smooth upper surface and the spongy basal tissue. ×1000. D. Basal tissue with layers of perpendicularly oriented horizontal canals (probably free spaces after collagen cords) and vertical dentine (?) tubuli. ×1000.

tubuli. The basal part, which probably was weakly mineralized and thus is rarely preserved, has a rather complex internal structure (Fig. 7D). It is penetrated by horizontal, parallel canals. In each subsequent layer, the canals are oriented perpendicularly to those of the underlying layer. This pattern resembles scolecodonts, that is, jaws of the Eunicida. This may be merely analogy, as is the case, for instance, with the well-known identity in distibution of the collagen fibrils in the cornea of the mammal eye and in the graptolite periderm (Towe and Urbanek 1972). The peculiar distribution of collagen cords in *Milaculum* might be derived from the pattern of collagen cords in *Hadimopanella*. More importantly, the basal part of *Milaculum* sclerites, with its structure obviously related to the mechanical functions of body cover, was incorporated into the skin. This demonstrates that the sclerites were dermal.

## CONCLUSIONS

This overview of phosphatic dermal sclerites suggests that it is the skeletal tissue of ectodermal origin that developed first in phylogeny. There is little basis for speculation concerning its original function. With the initially disorderly arrangement of crystallites and the rather low-conical shape of sclerites taken into account, one may suppose that even if they armored the oral part of the body, they hardly could function as a grasping apparatus. The inferred functional analogy between panderodontid conodonts and chaetonaths may rather reflect subsequent convergent evolution.

The dermal tubercles of *Astraspis* have an enamel microstructure that is similar to that of *Fomitchella* and *Hadimopanella* (Fig. 8). Subsequent histogenetic delay in the mineralization al-

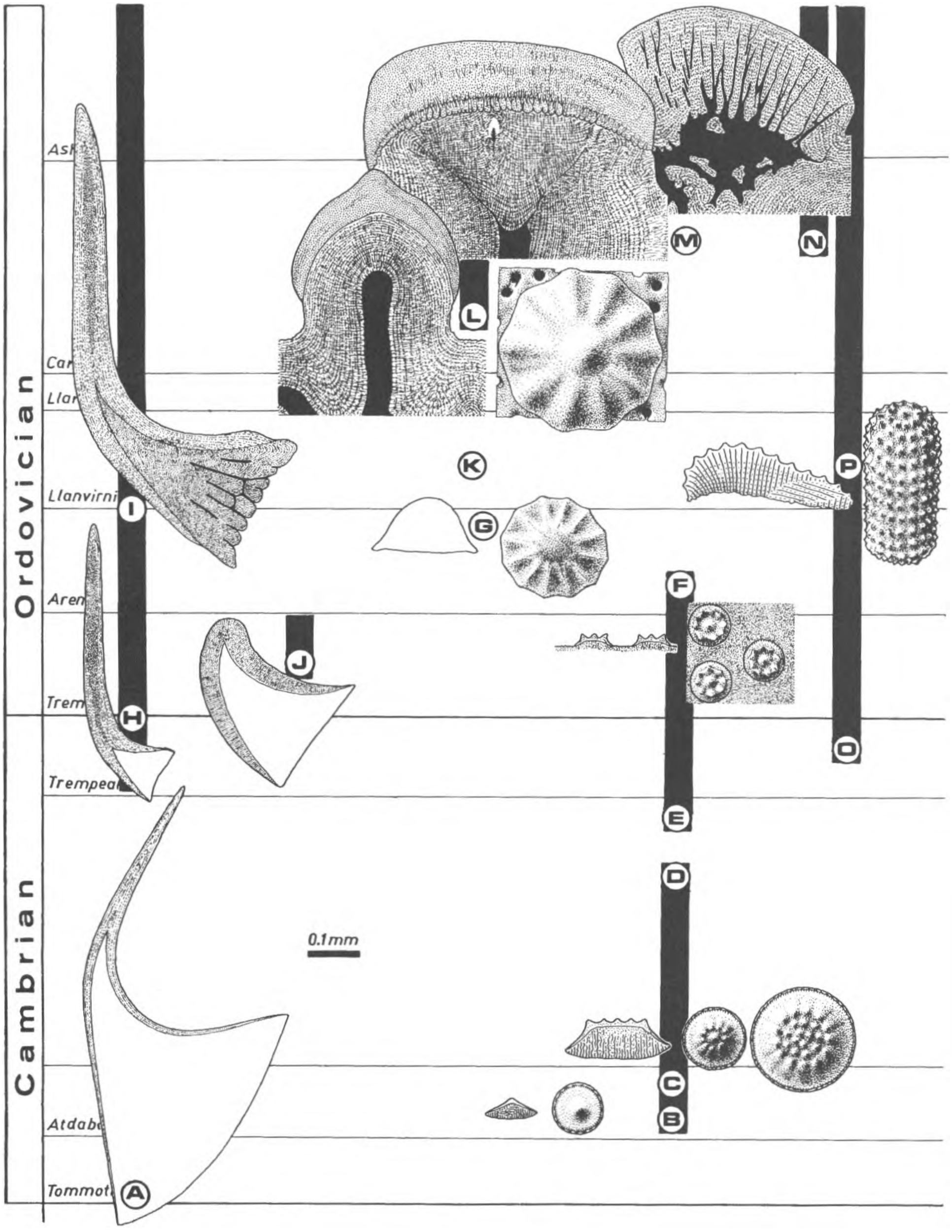

**Fig. 8.** Stratigraphic distribution of centrifugally growing phosphatic dermal sclerites in the Cambrina and Ordovician. Semidiagrammatic drawings of medial sections and oral views of the best known forms. A. *Fomitchella infundibuliformis* Missarzhevsky 1969. Early Tommotian, Siberia (Bengtson 1983b). B. *Hadimopanella apicata* Wrona 1982. *Bonnia-Olenellus* Zone, Spitsbergen (Wrona 1982). C. *Lenargyrion knappologicum* Bengtson 1977. Atdabanian, Siberia (Bengtson 1977). D. *Hadimopanella oezgueli* Gedik 1977. Middle Cambrian, Turkey and Spain (Boogaard 1983). E. *Utahphospha sequina* Müller and Miller 1976. *Elvinia* Zone, Utah (Müller and Miller 1976). F. *Utahphospha cassiniana* Repetski 1981. El Paso Group, Texas (Repetski 1981). G. *?Astraspis* sp. Oil Creek Formation, Oklahoma (Nitecki et al. 1975; Ethington and Clark 1981). H. *Teridontus nakamurai* (Nogami 1967). Wiberns Formation, Texas (Miller 1980; Landing et al. 1980). I. *Semiacontiodus cornuformis* (Sergeeva 1963). Kundan, Baltic area. J. *Fryxellodontus inornatus* Miller 1969. Rabbitkettle Formation, District of Mackenzie (Landing et al. 1980). K. *Arandaspis prionotolepsis* Ritchie and Gilbert-Tomlinson 1977. Stairway Sandstone, Australia (Ritchie and Gilbert-Tomlinson 1977). L. *Astraspis desiderata* Walcott 1892. Harding Sandstone, Colorado (Halstead 1969; Lehtola 1973). M. *Pycnaspis splendens* Ørvig 1958. Harding Sandstone, Wyoming (Ørvig 1958; Denison 1967). N. *Eriptychius americanus* Walcott 1892. Harding Sandstone, Wyoming (Denison 1967; Halstead 1969) O. *Milaculum perforatum* Müller 1973. Mila Group, Iran (Müller 1973) P. *Milaculum scandicum* Müller 1973. Kundan, Sweden.

lowed for the penetration of the enamel by Tomes' fibers and, finally, for the complete structural unification of the enamel with the dentine. This process probably was repeated and reversed several times in chordate phylogeny. One of those lineages where the boundary between ectodermal and mesodermal tissues disappeared was the *Milaculum* lineage. The Agnatha thus developed body armor composed of phosphatic sclerites.

Quite opposite in direction was the evolution of the conodonts. Their sclerites were confined to the oral region of the body. Perhaps the Middle Cambrian *Odontogriphus* was a primitive conodont animal with conical elements in the oral apparatus and with a naked but heterostracan-shaped body. When the oral sclerites began to function in catching prey, as in Recent myxinoids or chaetognaths, a strong selection pressure appeared for elongation and strengthening of the sclerites. It lead to the parallel orientation of crystallites in the cusp. Elongation of the cusp increased in phylogeny, while the basal cavity became progressively shallow. The crown tissue began to dominate. In the primitive coniform conodont elements, the basal filling frequently was penetrated by dentine tubuli, but it soon became compact and rigid.

Evolution of the conodont grasping apparatus probably corresponded to a shift from nectobenthic scavenger to pelagic carnivore niche. This is consistent with the differences in body shape between the Cambrian *Odontogriphus* and the Carboniferous *Clydagnathus*.

There is virtually no feature of the conodonts that would contradict their classification as vertebrates. The structure of skeletal tissues, the mode of their origin, the pattern of medially symmetric oral apparatus, the body shape, and its internal organization with distinct V-shaped somites—all are known in chordates.

### *Acknowledgments*

SEM photographs were taken at the Ohio State University at Columbus, with technical assistance of Mr. Maureen L. Lorenz (Figs. 3A and 7), Geological Institute in Warszawa, Poland (Fig. 5), and Nencki's Institute of Experimental Biology in Warszawa, Poland (Figs. 1 and 6). Specimens of *Astraspis* have been generously provided by Dr. Stig M. Bergström. Dr. Hubert Szaniawski critically read the manuscript and made many valuable and helpful comments.

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