

The early history of the Conodonta

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FOSSILS AND STRATA



Bengtson, Stefan 1983 12 15: The early history of the Conodonta. *Fossils and Strata*, No. 15, pp. 5–19. Oslo ISSN 0300-9491. ISBN 82-0006737-8.

The slender, spine-shaped, apatitic protoconodonts appear in the fossil record near the Precambrian–Cambrian boundary and persist through the Cambrian. Recent work (Szaniawski 1982, *J. Paleont.* 56) suggests that protoconodont elements were homologous to the grasping spines of modern chaetognaths. Paraconodonts are similar to protoconodonts in their mode of growth by basal accretion. However, paraconodonts were more deeply invested in the secreting epithelium, and there are no known transitional forms between the two types. Other Cambrian conodont-like fossils have been investigated to examine the possibility that they may be homologous with paraconodonts. Some of them, such as the funnel-shaped cones of *Fomitchella*, have an internal structure which precludes homology with paraconodonts. Others, such as the cone-shaped sclerites of *Lapworthella*, might have taken on the morphological and structural characteristics of paraconodonts if they became adapted to a tooth or claw function, but there is no direct evidence to support such an interpretation. Morphological, histological and stratigraphical data indicate that euconodonts evolved from paraconodonts during the late Cambrian by acquiring a crown, a dense apatitic tissue secreted over the outer surface of the paraconodont cusp. If the paraconodont and protoconodont animals are closely related, as has been suggested earlier, the paraconodont and euconodont animals may represent a branch of the chaetognaths that had developed pharyngeal denticulation. This concept of conodont origin and early evolution fits well with the recently discovered euconodont animal in the Scottish Carboniferous (Briggs, Clarkson & Aldridge 1983, *Lethaia* 16). □ *Conodonta, Chaetognatha, protoconodonts, Rhombocorniculum, Fomitchella, Lapworthella, microstructure, functional morphology, evolution, Cambrian.*

ECOS III

A contribution to the Third European Conodont Symposium, Lund, 1982

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By the time of their first rise to high diversity in the Ordovician, conodonts had already attained the euconodont grade of element structure, i.e. the elements had developed a crown (term introduced by Nicoll 1977 for what was previously known as the 'conodont proper'). Most of our knowledge of conodont evolution concerns this euconodont grade of organization, which was extant from the late Cambrian (Franconian) until the final extinction of the group in the Triassic. The earlier history of the Conodonta is much less well understood, largely because Cambrian conodonts with their slow evolution and low diversity are unattractive for biostratigraphical purposes and have therefore attracted comparatively little attention, but also because the simple morphology and structure of early conodonts provide little basis for detailed phylogenetic analyses and often may even render their identification as conodonts conjectural.

The present contribution examines evidence for the early evolution of conodonts, in time from the first appearance of conodont-like fossils in the latest Precambrian to the attainment of the euconodont grade in the late Cambrian. The evidence is in some measure equivocal because of the problems of identification just mentioned. It is possible to propose evolutionary lineages between almost any two Cambrian conodont-like fossils, but very difficult to test such hypotheses. Histological characters help to channel speculation, but identifications of non-euconodonts as conodonts must nevertheless involve some degree of appeal to fairly general phylogenetic hypotheses. However, as long as the nature of the

hypothesis is kept in mind, this kind of approach may be fruitful and is, indeed, often the only one available.

In this paper I shall examine the record of conodont-like fossils known from the Cambrian within the framework of a model of early conodont evolution proposed in 1976 (Bengtson 1976). The essentials of this model are: (1) conodont elements were primarily external, secreted by an epithelium, (2) an evolutionary trend during the Cambrian, represented by the sequence protoconodonts–paraconodonts–euconodonts, involved gradual retraction of the elements into pockets of this epithelium, (3) euconodonts were completely engulfed in epithelial pockets, which enabled them to grow holoperipherally and thus to assume more complex shapes that could be retained during ontogenetic growth, and (4) the secreting epithelium adhered only to the basal body of the euconodont, the crown being exposed to the aquatic medium when the apparatus was in use.

The model has a number of implications which may be tested against independent evidence: (1) The tissue of the elements was primarily derived from an ectodermal epithelium, (2) the basal body of early euconodonts is homologous with the 'cusp' of paraconodonts, (3) conodont elements functioned externally rather than as supports for soft tissue, and (4) they alternated between a retracted non-functional growth stage and a protracted functional non-growth stage.

The model was mainly based on histological structure as reflecting the mode of accretion of the elements. The present

study extends the histological comparisons to conodont-like fossils additional to those that were considered in 1976. These comparisons can be used to test and develop the general model. In addition, the well-documented proposals by Jeppsson (1979) on the tooth function of euconodonts and by Szaniawski (1982; Repetski & Szaniawski 1981) on the chaetognath nature of protoconodonts may be combined with the proto–para–euconodont model to produce a more specific hypothesis of conodont evolution that sets up detailed proposals on the origin, affinities and biology of the conodont animal and on the anatomy and functional morphology of the conodont apparatus. In fact, some already published central predictions of this hypothesis have been confirmed by the recent discovery in the Scottish Carboniferous of the first convincing conodont animal with preserved soft parts (Briggs, Clarkson & Aldridge 1983), as will be discussed below.

Cambrian conodont-like fossils

The earliest known unquestionable euconodonts appear in the upper Franconian *Proconodontus tenuiserratus* Zone of western United States (Miller 1980; Miller *et al.* 1982). These forms (*P. tenuiserratus* Miller 1980 and the n. gen. n. sp. of Miller 1980:31–32) are characterized by simple-cone elements with prominent basal bodies and thin hyaline crowns. The histological evolution of crown and basal-body tissue in the late Cambrian is at present under investigation by J. F. Miller and myself and will be the subject of a later publication. Reviews of general euconodont histology have been given by Bengtson (1976), Müller (1981) and Lindström & Ziegler (1981).

Evolutionary transitions can never be *proven* to have occurred. Even if we identify fossils which are highly probably ancestors of euconodonts, there is always a remaining possibility that the ancestors of euconodonts are in fact unrepresented in the fossil record. Keeping this in mind, we may examine the record of conodont-like fossils in the Cambrian, essentially the record of phosphatic, cone-shaped fossils. The general cone shape may in each instance result from either or both of two conditions: (1) accretionary growth and (2) a function requiring a pointed shape (tooth, claw, defensive spine, etc.). Both of these conditions are common, and, consequently, so are instances of morphological convergence in simple cone-shaped fossils. In order to exclude such cases of convergence from the phylogenetic analyses it is necessary to investigate as many independent characters as possible, particularly histological. Although microstructures are not in themselves a more reliable tool for phylogenetic analysis than morphology, they may give crucial information on the origin and mode of formation of the tissue, which in turn may serve to restrict hypotheses concerning homology.

All figured specimens have been deposited at the Swedish Museum of Natural History, Stockholm (SMNH). Specimens sectioned for SEM investigation were polished and etched with 3% HCl for 5–10 seconds before coating with gold–palladium.

Paraconodonts

The term ‘paraconodont’ is here used in the sense of Bengtson (1976:186) to signify conodont-like fossils with the structural

organization specified by Müller & Nogami (1971, 1972; cf. Bengtson 1976:200). The group corresponds only partly to the order Paraconodontida as defined by Miller (1981), since he also included the genera *Amphigeisina* Bengtson 1976 (only genus of the superfamily Amphigeisinae Miller 1981), *Gapparodus* Abaimova 1978, and *Protohertzina* Missarzhevsky 1973, as well as the species ‘*Prooneotodus*’ *tenuis* (Müller 1959) (within the superfamily Furnishinae, family Furnishinidae Müller & Nogami 1971) which all are of the protoconodont grade of structural organization (Bengtson 1976, 1977, and herein; Szaniawski 1982). However, the terms proto-, para- and euconodont as used here are descriptive and do not necessarily imply a direct correspondence with taxonomic groups (although element histology certainly has taxonomic implications).

Morphology and histology. – The paraconodont elements are typically simple cones with more or less flaring bases. A few representatives (notably *Westergaardodina* Müller 1959) have secondary denticles at the base. Finds of bedding-plane associations and fused clusters of *Furnishina* Müller 1959 indicate that paraconodonts formed apparatuses similar to those known in simple-cone euconodonts (Szaniawski 1980a; Andres 1981). Most information about the histology of paraconodont elements derives from the work of Müller & Nogami (1971, 1972); the essential characters are: high organic content, very small apatite crystallites, thick growth lamellae, growth by basal accretion on the outside, on the basal edge, and (in some cases) on the inside of the element.

In one important respect the published accounts of paraconodont histology may have to be modified: Müller & Nogami (1971) stated that in the initial growth stages the lamellae are continuous around the tip of the element. The only specimen that has been adduced to show this is a thin section of *Problematocoenites perforatus* Müller 1959 illustrated by Müller & Nogami (1971, Pl. 1:4). I have studied this section and find no evidence of apically closed lamellae – the structure that may have such an appearance in their Pl. 1:4 is formed by a dark Becke line. Other thin sections of paraconodonts in the Bonn collection (UB246, 325, 326, 328, 343–349, N922) also fail to show apically closed lamellae. The presence of apically continuous lamellae in the early growth stages of paraconodont elements has yet to be demonstrated.

Discussion. – According to the proposed evolutionary model, euconodonts were derived from paraconodonts through the addition of an outer apatitic layer (the crown) deposited from an enveloping epithelial fold. The idea was supported by the close histological similarities between paraconodont elements and the basal body of early euconodont elements. If paraconodonts did indeed have apically closed lamellae in the early growth stages, the evolutionary acquisition of a crown in euconodonts may have been due to a heterochronic process; whereas the possible absence (see above) of such lamellae in paraconodonts would postdate the appearance of the crown and make the suggested homology more exact.

Miller’s (1980) unnamed new genus and species of euconodont found together with the first *Proconodontus tenuiserratus* satisfies the predictions of the hypothesized evolutionary model, for it is a form which differs visibly from associated



Fig. 1. Elements of *Protohertzina*. □A. *P. unguiformis*, Tommot, River Aldan, Yakutia, Precambrian–Cambrian boundary beds, sample 70g (V. V. Missarzhevsky). $\times 70$. SMNH No. X2070. □B. Detail of A, base of internal cavity. $\times 500$. □C. *P. unguiformis*, same locality as A–B, sample 70e (V. V. Missarzhevsky). $\times 130$. SMNH No. X2081. □D. Same specimen in longitudinal section, polished and etched. Position

of E indicated. $\times 130$. □E. Detail of D. $\times 600$. □F. *P. anabarica*, River Kotujkan, Anabar Massif, Yakutia, Nemakit–Daldyn Beds (Precambrian–Cambrian boundary beds), sample M419/12 (V. V. Missarzhevsky). Longitudinal section (perpendicular to plane of curvature), polished and etched. Position of G indicated. $\times 160$. SMNH No. X2082. □G. Detail of F. $\times 1400$.

paraconodonts only in the presence of a thin hyaline crown (Miller 1980:31–32). The new form may be very closely related to '*Coelocerodontus rotundatus* Druce & Jones 1971 described from the Upper Cambrian of Queensland (Druce & Jones 1971); the histology of these forms and of the paraconodonts associated with them is at present under detailed investigation.

Protoconodonts

The term 'protoconodont' was introduced for slender Cambrian elements with only basal–internal growth increments (Bengtson 1976). This structure was demonstrated for Middle Cambrian *Gapparodus bisulcatus* (Müller 1959) and was later (Bengtson 1977) shown to occur also in the widespread Upper Cambrian '*Prooneotodus tenuis*'. The latter species is represented by numerous apparatus-like assemblages (bedding-plane associations or fused clusters) from several continents (e.g. Miller & Rushton 1973; Müller & Andres 1976; Landing 1977; Tipnis & Chatterton 1979; Abaimova 1980; Andres 1981; Szaniawski 1982). Szaniawski (1982) has shown that the patent general similarities between the '*P. tenuis*' apparatus and the grasping apparatus of modern chaetognaths are complemented by detailed morphological and histological similarities.

Protoconodonts are among the earliest cases of biomineralized tissues known from the fossil record. The genus *Protohertzina* is known from pre-Tommotian (i.e. uppermost Precambrian according to current stratigraphical concepts) deposits of the Siberian Platform, Kazakhstan, and Mongolia (Missarzhevsky 1973, 1982; Missarzhevsky & Mambetov 1981), and has also been reported from the base of the 'shelly' succession in China (e.g. Qian 1977; Qian, Chen & Chen 1979; Chen 1979, 1982) and the Canadian Cordillera (Conway Morris & Fritz 1980). The fine structure of *Protohertzina* is thus of particular interest and will be examined in detail here.

Morphology and histology. – Protoconodont elements are long (up to several millimetres), slender, slightly curved, commonly with one or more longitudinal keels (Figs. 1–2). The internal cavity reaches almost to the apex. Well-preserved specimens of *Gapparodus bisulcatus*, *Amphiheisina danica* (Poulsen 1966) and '*Prooneotodus tenuis*' show a three-layered wall structure: a thick, laminated middle layer bounded by thin outer and inner lamellae (Bengtson 1976, 1977; Szaniawski 1982, 1983). Organic content was originally high, and there is evidence to show that only the middle layer was to some degree mineralized with apatite (Bengtson 1976:196–197; Szaniawski 1982, 1983). This layer also demonstrates the basal–internal growth increments referred to above (not observed in *Amphiheisina*, however).

Three elements of *Protohertzina unguiformis* Missarzhevsky 1973 from the River Aldan, Yakutia, one of *P. anabarica* Missarzhevsky 1973 from the River Kotuj, Anabar Massif, and one each of *P. anabarica* and *P. cultrata* Missarzhevsky 1977 from Malyj Karatau, Kazakhstan, have been available for histological investigation. All are from Precambrian–Cambrian boundary deposits except for the *P. cultrata*, which is from the Upper Atdabanian. Two thin sections and four polished and etched sections were made. The observations indicate a consistent structure in *P. unguiformis* and *P. anabarica*: the

main layer of the wall is composed of lamellae arranged slightly obliquely to the wall in a manner indicating basal–internal accretion (Fig. 1D–G). The lamellae have a fibrous appearance, as they consist of acicular apatite crystallites with long axes parallel to the lamellae. This direction corresponds to that of the *c* axes; the structure is highly birefringent. (The fibrous structure can also be observed in an unsectioned specimen, Fig. 1B; the fibres are here probably enlarged by secondary apatite deposition.) The thin sections (one of each species) show an impersistent dark-coloured outer portion of the wall with no birefringence at all or with *c* axes perpendicular to the lamellae. This may represent recrystallized or originally less mineralized portions of the wall. There is no persistent outer layer visible; the thin crust seen in Fig. 1G is of uncertain origin.

In the specimen of *P. cultrata* the lamellae are non-fibrous (Fig. 2), as in *Gapparodus bisulcatus* and '*Prooneotodus tenuis*'. There is also a secondary apatitic lining of the internal cavity with surface-normal (i.e. perpendicular to the outer surface) acicular crystallites (Fig. 2C). A similar layer of surface-normal to spherulitic apatite has also been observed in the internal cavity of elements of *P. unguiformis* and *P. anabarica*.

Discussion. – Szaniawski (1982) compared the structure of grasping spines of modern *Sagitta* with that of Upper Cambrian '*Prooneotodus tenuis*' elements. He found a three-layered structure in the wall around the pulp cavity of *Sagitta* spines that is strikingly similar to the structure in protoconodonts. Probable growth increments, reflected on the surface as well as in the structure of the thick middle layer, are present in *Sagitta*, as in protoconodonts. The main differences are that *Sagitta* spines are unmineralized, and the middle layer is fibrous. These fibres consist of chains of highly crystalline α -chitin (Atkins, Dlugosz & Foord 1979). It is interesting to note that a fibrous structure is indeed present in the earliest protoconodonts, i.e. the *Protohertzina unguiformis* and *P. anabarica* figured here. (Although it is a protoconodont too, the younger *P. cultrata* differs considerably from the two older species both morphologically and histologically; it may in fact not be so closely related to them that it deserves placement in the same genus.) Fibres consisting of acicular apatite crystallites and chitin chains, respectively, are not likely to be strictly homologous, but the fibrous structure as such may reflect similarities in the organization of the tissues responsible for formation of the spines.

Bone, Ryan & Pulsford (in press), studying spines and teeth of *Sagitta setosa* Müller 1847, discovered complex structures (fibrils or lamellae, probably representing aggregated crystalline sheets of α -chitin) traversing the middle layer and connecting the outer and inner layers of the wall. They also found high concentrations of silicon in the tip, and of zinc in the tip and the outer and inner layers of the wall. Such features have not yet been found in protoconodont elements. However, their presence need not be expected in apatitic elements even if they are homologous to chaetognath spines, for in the latter these features probably all serve to strengthen and harden the unmineralized spines (Bone, Ryan & Pulsford, in press).

Outer and inner layers are not clearly visible on the *Protohertzina* specimens investigated here. Thin organic layers, if present, are generally not likely to be preserved, and one

must be cautious when interpreting thin crusts on surfaces of fossil specimens – they may well be diagenetic, as is evident in the case of the inner apatitic crusts seen in many specimens of *Amphiheisina* (Bengtson 1976, Figs. 1A–B and 3) and *Protohertzina* (Fig. 2C herein). Such a crust is usually characterized by growth of acicular crystallites normal to the encrusted surface, with tell-tale spherulitic growth around irregularities on the surface. The fused lamellae reported as primary tissue in clusters of '*Prooneotodus*' *tenuis* by Tipnis & Chatterton (1979) are typical of such diagenetic structures (cf. also Repetski & Szaniawski 1981:170–171).

Although some paraconodonts (and euconodonts) have slender shapes approaching those of protoconodonts, none of the forms investigated so far could be interpreted as morphological–histological intermediates between proto- and paraconodonts (cf. Bengtson 1977:43). For this reason the evolutionary transition between these two groups is more hypothetical than the transition from para- to euconodonts.

RHOMBOCORNICULUM

Rhombocorniculum Walliser 1958 is a widely distributed fossil in the upper Lower Cambrian, first reported from Shropshire, England (Cobbold 1921; Walliser 1958). It is found as phosphatic sclerites, narrowly conical or broadly triangular, with a characteristic rhomboidal surface microsculpture (Fig. 3). The type species, *R. cancellatum* (Cobbold 1921), has been interpreted as having two kinds of elements, slender and broad, which occur in the same deposits (Walliser 1958; Landing, Nowlan & Fletcher 1980). (Mambetov 1977, however, considered the broad element to represent a separate species, *R. walliseri* Mambetov 1977.) Missarzhevsky (*in* Missarzhevsky & Mambetov 1981) has described another species, *R. insolutum* Missarzhevsky 1981, characterized by slender elements with rounded cross-section and spinose surface sculpture.

Morphology and histology. – Walliser (1958) and Landing, Nowlan & Fletcher (1980) described the morphology and histology of *R. cancellatum* in detail. The elements are up to a couple of millimetres long, usually asymmetrical, more or less twisted, with a narrow internal cavity. A slender element is figured herein (Fig. 3A) showing the characteristic surface ornament. The internal structure is coarsely fibrous (Walliser 1958, Pl. 15:6–7; Landing, Nowlan & Fletcher 1980, Figs. 3–4; Fig. 3B–C herein). The fibres are arranged obliquely to the walls, those from opposing walls converging in the apical direction, i.e. the inclination agrees with that of the fibrous lamellae in *Protohertzina unguiformis* and *P. anabarica*. The composition is apatitic (Walliser 1958), and observations under a petrographic microscope show that the fibres are composed of highly birefringent crystals with *c* axes parallel to the longitudinal direction of fibres. The presence of outer (Walliser 1958) and inner (Landing, Nowlan & Fletcher 1980) organic lamellae has been reported, but information on these structures is not sufficient to allow a more detailed determination of their nature.

Discussion. – Apart from some apparently arbitrary assignments to groups such as the blatantly polyphyletic Cambro-

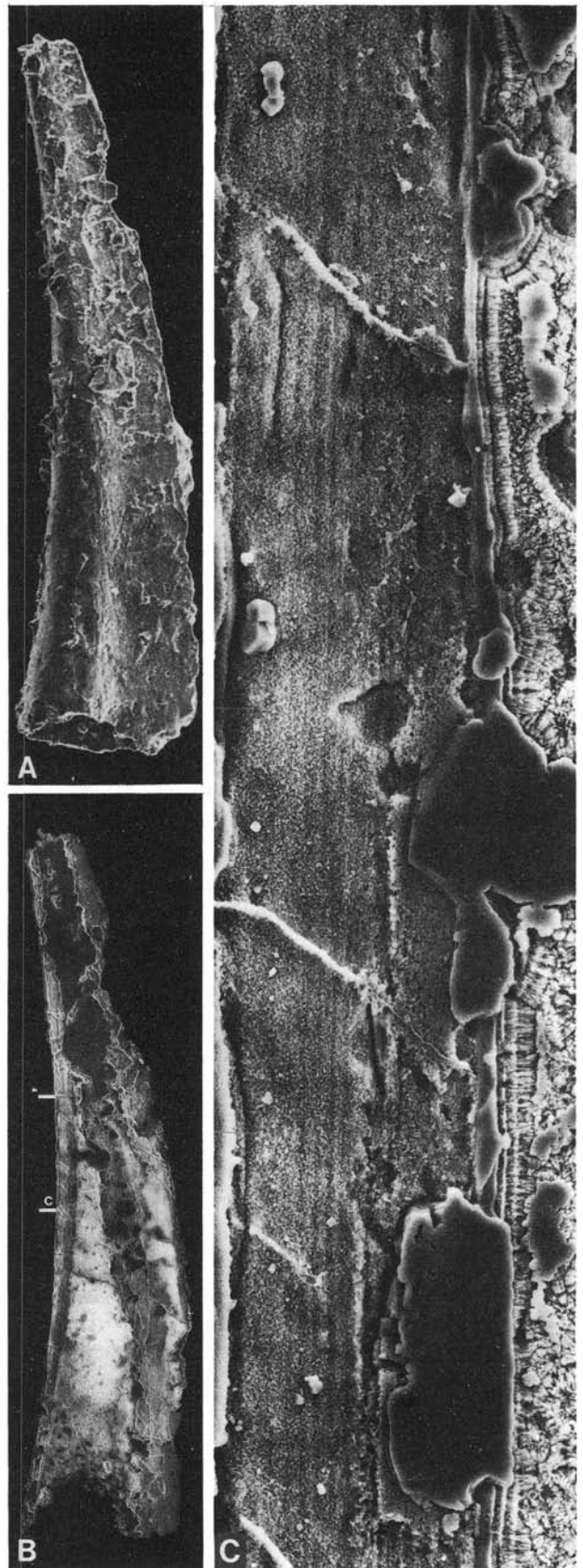


Fig. 2. Element of *Protohertzina cultrata*, Aktugaj, river Shabakty, Malyj Karatau, Shabakty Formation (upper Atdabanian), sample M52 (A. M. Mambetov). SMNH No. X2083. □A. ×65. □B. Longitudinal section, polished and etched. Position of C indicated. ×65. □C. Detail of B. ×900.

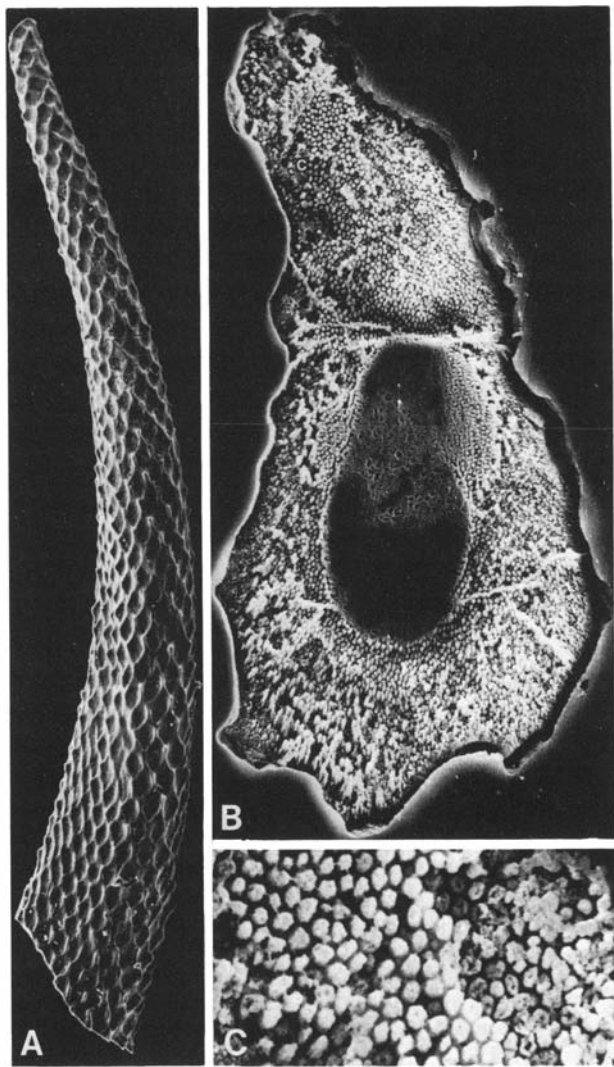


Fig. 3. Slender elements of *Rhombocorniculum cancellatum*. □A. Fortune River, Burin Peninsula, Newfoundland, Brigus Formation, ca. 10 m above base, sample Can79-30-SB. $\times 100$. SMNH No. X2084. □B. Achchagyj-Kyyry-Taas, River Lena, Yakutia, Transitional 'Formation', 2nd Member (upper Atdabanian), sample Sib73-2-SB. Transverse section, polished and etched. Position of C indicated (upper left). $\times 500$. SMNH No. X2085. □C. Detail of B. $\times 2000$.

scleritida Meshkova 1974 (Meshkova 1974; Mambetov 1977; cf. Bengtson 1977:60–61) or the Halkieriidae Poulsen 1967 (Missarzhevsky 1977; Missarzhevsky & Mambetov 1981), *Rhombocorniculum* has generally been left without a suprageneric assignment. Müller (1962) originally assigned it to his order Paraconodontida together with *Problematocoenites* Müller 1959 and *Pygodus* Lamont & Lindström 1957, but subsequent histological investigations led to a considerable emendation of the Paraconodontida, to include a number of Cambrian forms structurally similar to *Problematocoenites*, and to exclude *Rhombocorniculum* and the euconodont *Pygodus* (Müller & Nogami 1971). Landing, Nowlan & Fletcher (1980) introduced the (seemingly expletive) term 'pseudocodont' for *Rhombocorniculum* sclerites and discussed the general similarities with protoconodont and euconodont apparatuses, concluding that the *Rhombocorniculum* elements 'may have served a similar function and had a broadly comparable morphology in an unrelated organism'. I agree

with this conclusion, except that the fibrous structure of *Protohertzina* described herein certainly allows for the interpretation that *Rhombocorniculum* was derived from an early protoconodont. Thus a near relationship with conodonts is conceivable, but the available characters do not allow a strict assessment of this possibility. There are no known forms that show any evidence of being descendants of *Rhombocorniculum*.

FOMITCHELLA

The phosphatic cones of *Fomitichella infundibuliformis* Missarzhevsky 1969 (Fig. 4) were described by Missarzhevsky (*in* Rozanov *et al.* 1969) from the lower part of the Tommotian Stage in Siberia, i.e. basal Cambrian beds as currently understood. In 1977 Missarzhevsky described a second species, *F. acinaciformis*, from these beds, and similar forms are now known also from approximately age-equivalent beds in Mal'j Karatau (Missarzhevsky & Mambetov 1981), eastern Massachusetts (Landing & Brett 1982) and southeastern Newfoundland (Bengtson & Fletcher 1983). [Other reports of *Fomitichella* appear questionable on the evidence of published illustrations, viz. the *Fomitichella* sp. of He (*in* Yin *et al.* 1980, Pl. 19:7), the *F. rugosa* and *F. cf. infundibuliformis* of Jiang (*in* Luo *et al.* 1982, Pl. 17:14–15 and Pl. 17:16, respectively), and the *F. yankonensis* of Yuan & Zhang (1983, Pl. 1:6); also the *Paraformichella* [sic!] *orientalis* of Qian & Zhang (1983, Pl. 2:15–17).] *Fomitichella infundibuliformis* is very conodont-like and has even been suggested as the stock from which all later conodonts, including paraconodonts, arose (Dzik 1976, Fig. 1).

Morphology and histology. – Specimens of *F. infundibuliformis* have also been illustrated by Missarzhevsky (*in* Rozanov *et al.* 1969, Pl. 6:12, 15, 16), Meshkova (1969, Pl. 56:1–5, as '*Oneotodus?*' sp.); *in* Repina *et al.* 1974, Pl. 17:5) and Matthews & Missarzhevsky (1975, Pl. 3:8). They are hollow cones, usually slightly flattened laterally, with widely flaring bases and narrow, drawn-out tips. The internal cavity is large and the walls consequently very thin (down to 5 μm) but the cavity does not extend into the narrow tip. Outer and inner surfaces are practically smooth; a faint radial ornament is sometimes visible on the outside.

In longitudinal section (Fig. 4B–D) the cones are seen to consist of very fine (0.5–2 μm) lamellae parallel to the outer surface of the cones. These lamellae wedge out towards the inner side, so that the innermost lamellae are restricted to the apical part. The lamellae appear finely granular under the SEM, and the substance shows very weak birefringence in polarized light, suggesting that individual crystallites are very small with a *c* axis orientation which is only to a degree preferential (tangentially in the cross-sectional plane). There may be fine (about 1 μm in diameter) tubules piercing the lamellae (Fig. 4D, top), but these may have been produced *post mortem* by boring organisms.

Discussion. – If the lamellae are taken to represent successive growth increments, their arrangement shows that secretion took place on the *outside* of the cone, i.e. that the outer side was covered with secretory tissue. This is similar to the condition in the euconodont crown (cf. Fig. 5), but fundamentally different

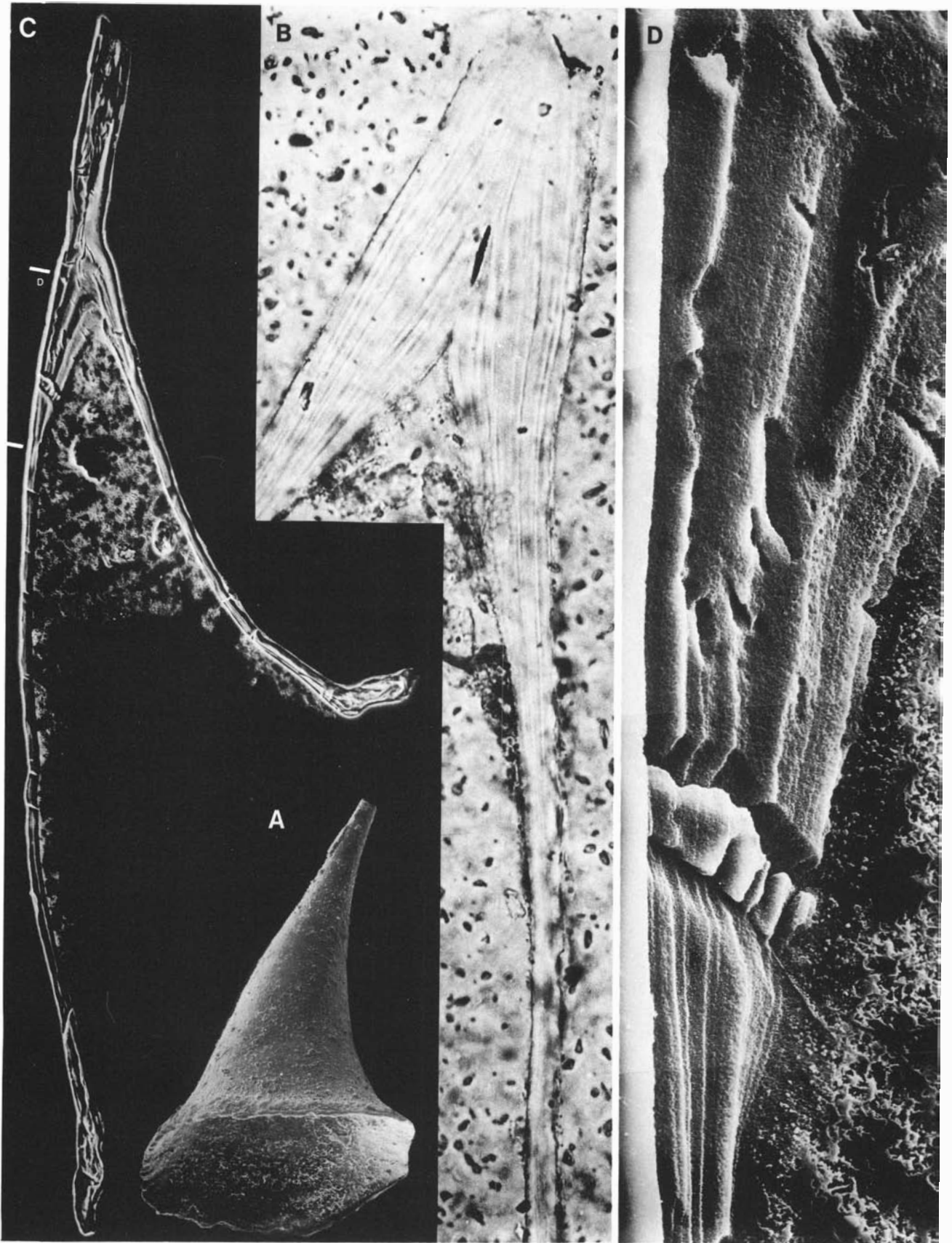


Fig. 4. *Fomitchella infundibuliformis*. River Fomich, Anabar Massif, Zone of *Aldanocyathus sumnagicus* - *Tiksitheca lici*; sample M314/4 (V. V. Missarzhevsky). □A. $\times 100$. SMNH No. X2086. □B. Longitudinal

thin section in transmitted, plane-polarized light. $\times 600$. SMNH No. X2087. □C. Longitudinal section, polished and etched. Position of D indicated. $\times 200$. SMNH No. X2088. □D. Detail of C. $\times 1500$.

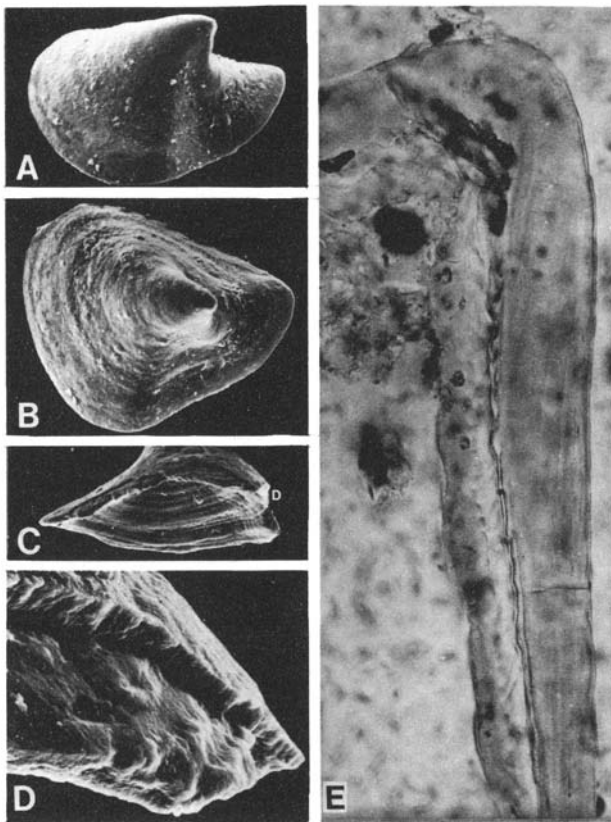


Fig. 5. Elements of *Pseudooneotodus* cf. *mitratus* (Moskalenko 1973), 'elf caps' of Winder (1976). Colbourne Quarry, Ontario, upper Trenton Group (Caradoc), coll. C. G. Winder. □A–B. $\times 100$. SMNH No. X2089. □C. View from below showing basal body and thin crown. Position of D indicated. $\times 100$. SMNH No. X2090. □D. Detail of specimen in C, showing partly exfoliated crown on basal body. $\times 800$. □E. Thin section in transmitted, plane-polarized light, showing crown (top and right) and basal body. $\times 400$. SMNH No. X2091.

from that in the Cambrian paraconodonts. In fact, there seems to be no possibility that the elements of, e.g., *Furnishina furnishii* Müller 1959 and *Prooneotodus gallatini* (Müller 1959) could be derived from the morphologically somewhat similar, but histologically different, cones of *Fomitchella infundibuliformis*. There is a radical difference in mode of secretion which hardly permits the structures to be interpreted as homologous.

This similarity between *Fomitchella* and euconodonts presents a challenge to the hypothesis that euconodonts evolved from paraconodonts in the late Cambrian. There are four possible interpretations:

(1) Late Cambrian euconodonts did not evolve from paraconodonts but from *Fomitchella infundibuliformis* or a close ancestor in common with *Fomitchella*.

(2) Euconodonts did in fact evolve from paraconodonts, but considerably earlier than supposed, in the late Precambrian rather than the late Cambrian. *Fomitchella* is an early euconodont. The stratigraphic order of appearance of the other forms misrepresents their evolutionary order of appearance.

(3) The euconodont grade of organization was attained more than once and at different times, *Fomitchella* representing an early such example. The euconodont animals are polyphyletic and the crown not truly homologous between different euconodonts.

(4) *Fomitchella* is not a member of the conodont stock, and the similarity to euconodonts is convergent or fortuitous.

The first interpretation would reduce the similarities between paraconodont elements and the basal bodies of euconodonts documented by Müller & Nogami (1971, 1972; cf. Bengtson 1976) to convergence or chance, and it would negate the hypothesis that euconodonts evolved from paraconodonts by the acquisition of a crown. Against this interpretation there stands the orderly stratigraphic succession in the Upper Cambrian of paraconodonts, euconodonts with thin crown and prominent basal body (e.g. *Proconodontus* Miller 1969) and euconodonts with thicker crown and smaller basal body (e.g. *Terodontus* Miller 1980, *Eoconodontus* Miller 1980, *Cambroistodus* Miller 1980) as documented by, e.g., Miller (1969, 1980; Miller *et al.* 1982). The complete absence of a basal body in the well-preserved Tommotian *Fomitchella* contrasts with the prominent basal bodies present in the earliest appearing late Cambrian euconodonts (*Proconodontus* and the n. gen. et sp. of Miller 1980:31–32).

The second interpretation is also at variance with the observed stratigraphical succession. Whereas such stratigraphical misrepresentations are theoretically possible, they are not very likely in the present case of commonly abundant microfossils whose distribution has been investigated in detail in key sections in North America (e.g. J.F. Miller 1969, 1978, 1980; Derby, Lane & Norford 1972; R. H. Miller & Paden 1976; R. H. Miller *et al.* 1981; Fähræus & Nowlan 1978; Landing, Ludvigsen & von Bitter 1980; J. F. Miller *et al.* 1982), northern Europe (Müller 1959; Szaniawski 1971, 1980b; Bednarczyk 1979), Kazakhstan (Abaimova & Ergaliev 1975; Abaimova *et al.* 1978; Abaimova 1978; Dubinina 1982), Iran (Müller 1973), China (Xiang *et al.* 1981), and Australia (Druce & Jones 1971; Druce, Shergold & Radke 1982). The lack of a trace of a basal body in *Fomitchella* is also inconsistent with this interpretation.

The third interpretation is somewhat strained, again because of the lack of a basal body in *Fomitchella*.

The fourth interpretation fits the available data, but at the price of an *ad hoc* assumption that *Fomitchella* has nothing to do with conodonts. This assumption can be partly defended by the fact that *Fomitchella*, apart from the anomalous stratigraphic position, differs in some respect from early euconodonts. First, in spite of the good preservation (no sign of etching, recrystallization, mechanical abrasion or heating) and the deep internal cavity there is no trace of a basal body. Second, the lamellae consist of finely granular apatite without preferred crystallographic orientation, whereas euconodont crowns typically show a strong preferred orientation of crystallographic *c* axes, usually in connection with acicular crystallites. None of these differences can be taken to prove that *Fomitchella* is not a euconodont, but it must be remembered that the remaining similarities to the euconodont crown are of a simple and general nature, making convergence or fortuitous resemblance a not unlikely possibility.

In summary, *Fomitchella* is not a paraconodont or a paraconodont ancestor, but its possible euconodont nature cannot be ruled out by its characters alone. In view of the total stratigraphical and histological evidence on the origin of euconodonts, however, acceptance of *Fomitchella* as a conodont

strains credulity much more than the alternative assumption that it is no close relative of conodonts.

If not a conodont element, the phosphatic cone of *Fomitchella* may be interpreted as a supporting cup for an organism having secreting soft tissue extending over the outside of the mineralized structure. This organism may have been a colonial animal, the cones secreted by a coenenchyme, but there is no direct comparison with the superficially similar laminated phosphatic linings of some bryozoan zoecia (Martinsson 1965) because the lamination indicates that these were secreted by the zooids themselves (Martinsson 1965; Eisenack 1964).

LAPWORTHHELLA

The phosphatic cones of *Lapworthella* Cobbold 1921 are not strictly conodont-like, but a case could be made for a *Lapworthella*-like animal as an ancestor of paraconodonts; this possibility and its implications will be dealt with here.

Species of *Lapworthella* are known from Lower Cambrian (and some possibly Middle Cambrian) deposits in north-western Europe, eastern North America, the Siberian Platform, Mongolia, South China, and South Australia (species list in Bengtson 1980; new occurrences reported by Landing, Nowlan & Fletcher 1980; Yin *et al.* 1980; Landing & Brett 1982; Voronin *et al.* 1982; Luo *et al.* 1982; Bengtson & Fletcher 1983; Qian & Zhang 1983). Sclerites typically show very large morphological variation within samples (this has led to some taxonomic oversplitting). Several lines of evidence suggest that the sclerites were parts of a composite exoskeleton similar to that inferred for mitrosagophorans (Bengtson 1977:58–60); *Lapworthella* is generally considered to be closely related to the mitrosagophorans and some other Cambrian animals with composite phosphatic exoskeletons, such as *Dailyatia* Bischoff 1976 and the Kelanellidae Missarzhevsky & Grigor'eva 1981. The choice of *Lapworthella* for the present comparison with paraconodonts is mostly for the sake of illustrating a point; its sclerites are most similar to paraconodonts, but because detailed morphology may not be relevant at this level of comparison, any of these other forms could have been chosen.

Morphology and histology. – *Lapworthella* sclerites (Fig. 6A–B; see also Matthews 1973 for examples of morphological variability) range from broadly pyramidal to narrowly conical. In most species there are very pronounced annulations as well as finer growth lines present (Fig. 6C). A section through a specimen of *L. dentata* Missarzhevsky 1969 (Fig. 6D–E) shows that the fine growth lines correspond to a fine lamination, confirming that growth took place by basal–internal accretion. Under a petrographic microscope, the walls in this species are seen to be made up of highly birefringent apatite with *c* axes aligned parallel to the growth axis of the sclerite. The etching pattern (Fig. 6E) suggests very small (in the size order of tenths of micrometres) isodiametric crystallites; there is no sign of acicular structures.

Discussion. – In general terms, *Lapworthella* sclerites resemble paraconodont elements in gross morphology, composition and inferred external mode of formation. The main differences are the pronounced surface sculpture and lack of basal growth

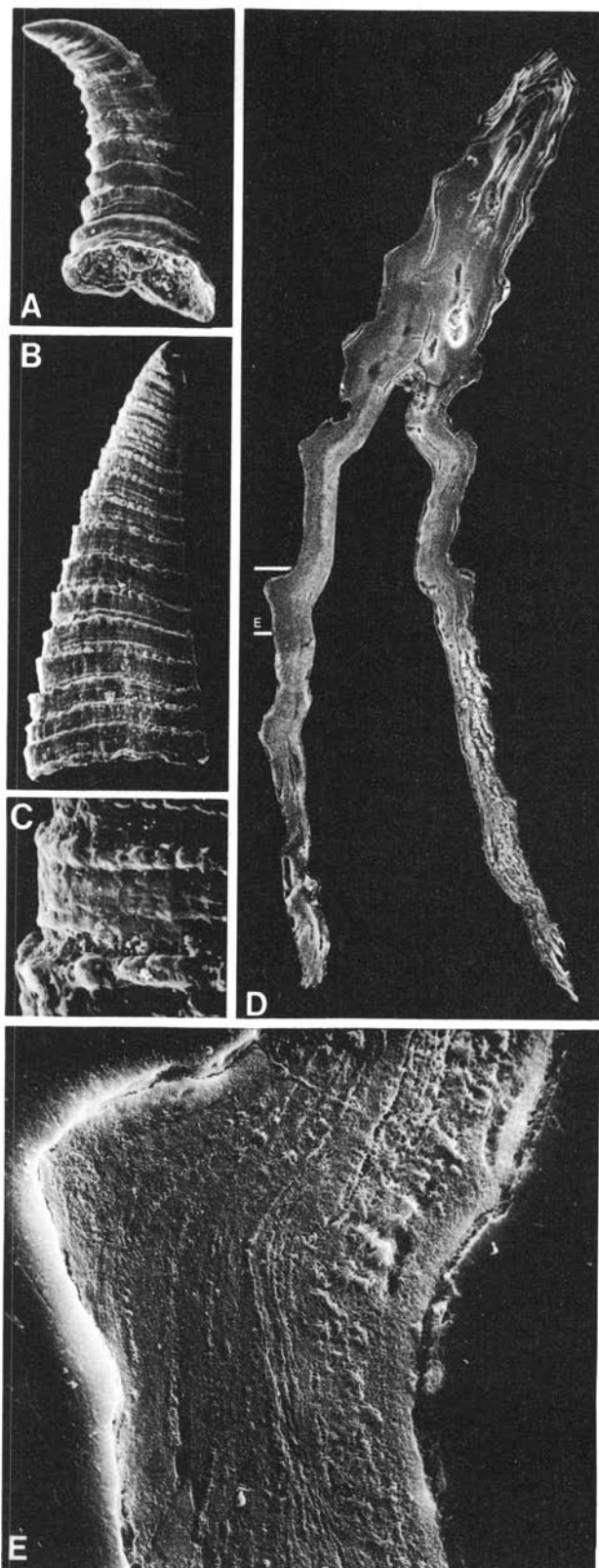


Fig. 6. Sclerites of *Lapworthella dentata* Missarzhevsky, Achchagyj-Kyyry-Taas, River Lena, Yakutia, Transitional 'Formation', 3rd Member (upper Atdabanian or lower Lenian). □A. Sample M49/106 (V. V. Missarzhevsky). ×60. SMNH No. X2092. □B. Same sample as A. ×30. SMNH No. X2093. □C. Detail of B. ×200. □D. Sample Sib73-1-SB. Longitudinal section, polished and etched. Position of E indicated. ×200. SMNH No. X2094. □E. Detail of D. ×1 500.

increments deposited on the outside. None of the similarities are necessarily indicative of close relationship (they are common features of external sclerites), and the differences indicate a significant difference in function at least: *Lapworthella* sclerites were probably passive protective devices (the sculpture would have interfered with an active function as teeth or graspers) whereas paraconodont elements, judging both from their morphology and their probable homology with euconodont elements, most likely were mouth parts.

Nevertheless, at first an evolutionary transition between the two does not seem entirely unlikely – it could be regarded as a process analogous to the odontode–tooth transition in vertebrates (cf. Ørving 1977). In the absence of plausible transitional forms leading to paraconodonts (contrast the state of the evidence bearing on the paraconodont–euconodont transition) both the hypothesis of a protoconodont ancestry and that of a *Lapworthella* ancestry (as well as other alternative hypotheses) of paraconodonts must be evaluated along less direct lines of evidence. Such indirect evidence, however, seems to favour protoconodont rather than *Lapworthella* ancestry:

(1) Although in terms of shift of growth loci the adjustment to the paraconodont mode is about the same from both protoconodonts and *Lapworthella*, the derivation of a paraconodont apparatus from a protoconodont apparatus would be considerably simpler in terms of arrangement and probable function than its derivation from the sclerite armour of *Lapworthella*.

(2) Various lines of evidence suggest that the euconodont animal was an active nektic or planktic predator (e.g. Seddon & Sweet 1971; Jeppsson 1979; Briggs, Clarkson & Aldridge 1983). This is much more in keeping with a derivation from the chaetognath-like protoconodonts (Szaniawski 1982) than from *Lapworthella*, which with its heavy mail of sclerites was probably a sluggish or sessile benthic organism.

These considerations would not contradict a more distant relationship between *Lapworthella* with relatives on one side and the conodonts on the other, for example the sharing of a close common ancestor. However, at the level of comparison the similarities only amount to such general characters as the presence of external phosphatic sclerites, and at present there seems to be no practical possibility of testing any such hypothesis.

Other conodont-like fossils

The remaining Cambrian conodont-like fossils to be discussed here are too poorly known to play a role in the evaluation of the proto–para–euconodont evolutionary model. They indicate areas where more investigation is needed and also serve as a reminder that more fossils with some bearing on the conodont problem may yet turn up in the Cambrian.

Odontogriphus omalus Conway Morris 1976 is represented by a single specimen with preserved soft-tissue remains in the Middle Cambrian Burgess Shale. The specimen has been described in great detail by Conway Morris (1976) who interpreted it as a paraconodont animal in keeping with the hypothesis advanced by Lindström (1973, 1974), that conodont elements were tentacle supports in a lophophorate-like animal. The presumed conodont elements in the specimen are, however, too poorly preserved to be identified as

paraconodonts or even conodont-like structures (composition and histology are unknown, and the structures may owe their apparent shape largely to their position between the lobate structures interpreted by Conway Morris as remains of tentacles). The evidence for tentacles is also equivocal. Until we can with some confidence refute or confirm the presence of conodont elements, *Odontogriphus* is of very dubious relevance to questions of the history and nature of the Conodonta. (See also discussions on the interpretation of *Odontogriphus* by Landing 1977:1082–1083; Conway Morris 1980; and Jeppsson 1980.)

Mongolodus rostriformis Missarzhevsky 1977 was described from the base of the Lenian Stage of Western Mongolia (Missarzhevsky 1977). It is represented by claw-shaped, curved, laterally compressed sclerites with a base strongly expanded in the plane of curvature. The internal cavity is large and the walls thin. There is a suggestion of ‘cone-in-cone’ lamellation indicating growth by basal–internal accretion, but the histology is not known in detail. *Mongolodus* is possibly related to the protoconodonts, but the available evidence does not permit a firm evaluation of this possibility.

Yunnanodus doleres Wang & Jiang 1980 was described (in Jiang 1980) from phosphorite beds in the upper part of the Meishucunian Stage in eastern Yunnan. The sclerites of this species have a straight ‘cusp’ attached to a basal plate set with irregularly arranged smaller denticles. The original composition and histology are not known. Jiang (1980) suggested conodont affinity. Although *Yunnanodus* is vaguely conodont-like, it does not show any distinctive conodont features, and certainly none that suggest any affinity with known Cambrian conodonts. Some attention should be given to the possibility that it is related instead to the Zhijinitidae Qian 1978 (=Cambroclavitidae Mambetov 1979), known from the upper Atdabanian Stage of Kazakhstan (Mambetov & Repina 1979; Missarzhevsky & Mambetov 1981) and the upper Meischucunian Stage of China (Qian 1978; Qian, Chen & Chen 1979; Luo *et al.* 1982). The sclerites of this enigmatic group are composed of a straight or curved ‘cusp’ attached to a distinct basal plate. Finds of articulated sclerites show that they united to form a complex palisade-like aggregate (Mambetov & Repina 1979, Pl. 14:6, 8, 9) with no resemblance to a conodont apparatus.

In a recent publication, Chen (1982) described some new presumed conodonts from the Meishucunian of Emei-shan, Szechuan. Of these, *Emeidus primitivus* Chen 1982 appears morphologically similar to *Protohertzina*, whereas the two serrate species of *Paracanthodus* Chen 1982 are more difficult to place in a high-level taxonomic group on the basis of the published illustrations. The fragment of a curved rod with three processes illustrated as ‘Conodont Form A gen. et sp. indet.’ appears to have little claim to recognition as a conodont.

A reassessment of the evolutionary model

The search among Cambrian conodont-like fossils has not yielded a more likely ancestor for the euconodonts than a paraconodont, or a more likely ancestor for the paraconodonts than a protoconodont. *Rhombocorniculum* may be envisaged as

derived from a protoconodont, but not itself as a paraconodont ancestor. *Fomitchella* cannot be envisaged as a protoconodont or a paraconodont ancestor, and hardly even as an ancestor of the simplest euconodonts (*Proconodontus* and Miller's new genus) – and if it were an ancestor of other conodonts this would falsify not only the evolutionary model under assessment, but also the identification of almost all Cambrian conodonts, including the earliest euconodonts. *Lapworthella* (or another animal with external phosphatic protective sclerites) can be envisaged as a paraconodont ancestor, but much less easily so than any protoconodont.

Thus the proto–para–euconodont model has passed the test in good condition: any alternative interpretation of the phylogenetic relationships of Cambrian conodont-like fossils appears less probable than the one shown in Fig. 7. The remaining possibilities that either euconodonts or paraconodonts (or both) evolved directly from other, perhaps unknown, forms, are more difficult to assess. That euconodonts should not be derived from paraconodonts seems very unlikely, but the possibility will be further appraised in the current work on the histology of the apparent transitional forms. Paraconodont derivation from something other than a protoconodont is more of a possibility. At present it can only be assessed indirectly, through the way in which the implications of the protoconodont model are compatible with new evidence. These implications can be made considerably more specific and testable by reference to the proposed close affinity between Cambrian protoconodonts and modern chaetognaths (Szaniawski 1982).

It should be noted that a simple list of character similarities between two groups does not suffice for systematic purposes. Comparisons with other groups, both those closely related (to exclude similarities due to symplesiomorphy) and those more distantly related (to rule out similarities due to convergence) are required. In the case of grasping spines it has not yet been shown whether structures similar to those found in chaetognaths and protoconodonts may also occur by convergence in cuticular spines or teeth of other groups (e.g. priapulids, acanthocephalans, gymnosomatous pteropods). However, the available evidence certainly supports Szaniawski's proposal, and the fibrous structure of *Protohertzina* reported herein serves to strengthen the case.

Chaetognath grasping spines sit laterally on the head of the animal, well outside the mouth. The action of the grasping apparatus is well integrated with the action of the whole head in feeding (Kuhl 1932), and it is obvious that the morphologically more complex conodonts could not have functioned in an identical way. Nevertheless, the evolutionary model under consideration postulates that no radical change in function is necessary to explain the burgeoning of conodont element morphology in the early Ordovician (Bengtson 1976:202). Jeppsson (1979) has pointed to a number of analogies between euconodont elements and teeth (*sensu lato*) in various groups of animals (and included reference to structures that had previously been quoted as arguments *against* a tooth function of conodont elements), which suggest similarities of function. (See Conway Morris 1980; Jeppsson 1980; Bengtson 1980, 1983; and Briggs, Clarkson & Aldridge 1983 for a recent discussion of the tooth model *versus* the tentacle-support model of conodont function.)

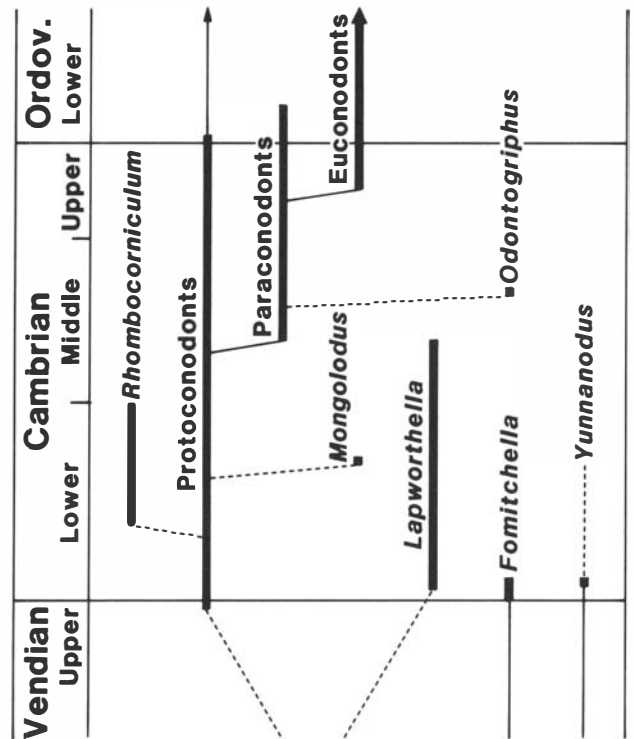


Fig. 7. Proposed phylogenetic relationships of Cambrian conodont-like fossils discussed in the text. Proto-, para- and euconodonts informally grouped as taxa. Bars show known stratigraphic ranges of 'taxa'. Unbroken lines indicate proposed evolutionary lineages; broken lines indicate possible but insufficiently corroborated lineages. *Fomitchella* and *Yunnanodus* are thus shown as independently derived from Vendian ancestors, whereas the possibility of a near common ancestry for *Lapworthella* (and other related forms) and protoconodonts is indicated by the divergence of broken lines.

Three central predictions of the hypotheses in question appear to have been verified by the recent discovery in the Scottish Carboniferous of a conodont animal with preserved soft parts (Briggs, Clarkson & Aldridge 1983):

- (1) Contrary to customary reconstructions (e.g. Rhodes & Austin 1981), an apparatus with ramiform and pectiniform elements should have the ramiform, not the pectiniform, elements anteriormost (Jeppsson 1971:101, 120, Fig. 4).
- (2) The conodont apparatus, when not in function, should be stored in a retracted resting position (Bengtson 1976:203; Jeppsson 1979:167–168).
- (3) The euconodont animal should show chaetognath affinities (Repetski & Szaniawski 1981).

The first two predictions have been confirmed by the Scottish animal (Bengtson 1983). The suggestion of verification of the third one can be challenged, in that the chaetognath-like characters seen in the Scottish animal are not exclusively indicative of chaetognath affinity, and there is one feature – the oblique (possibly V-shaped) regularly repeated structures in the posterior part of the trunk – that cannot easily be matched with any known chaetognath character. In a chordate model they could represent myotomes (Briggs, Clarkson & Aldridge 1983:10); in a chaetognath model they could possibly be cuticular bandings or gonad structures, but both of these interpretations offer problems. Further finds are not likely to solve this problem directly (although gonad structures may be expected to show varying development in

different individuals depending on the stage of maturity), but might, one would hope, provide an answer to the important question of the orientation of the animal. If the Scottish animal has a dorso-ventrally flattened chaetognath-type tail, further finds should show the symmetry of the (lateral) fins; if it has a laterally flattened chordate-type tail, the asymmetry of the (sagittal) fins is likely to show up as a consistent pattern. It should be kept in mind, however, that the conodont animals may yet show significant deviations from the body plan of their closest living relative; thus fin morphology may not be conclusive evidence against either chordate or chaetognath affinity.

The question of conodont affinity is thus unresolved even by the find in the Carboniferous of Scotland, but there are now sufficient grounds for developing the proto-para-euconodont model around the possibility of chaetognath affinity. The model can then be reformulated as follows:

(1) Predatory chaetognaths first appeared no later than at the Vendian-Cambrian transition. They were equipped with a grasping apparatus of essentially modern aspect. Individual spines, the protoconodont elements, were at least in some cases mineralized with calcium phosphate.

(2) No later than early middle Cambrian a branch of the chaetognath stock evolved, characterized by a robust denticulation around the mouth or in the pharynx. The individual denticles, the paraconodont elements, were derived either from the lateral spines or from a weaker denticulation around the mouth of the ancestor (cf. the teeth of modern chaetognaths). The denticles were deeply invested in the epithelium of the mouth-pharynx, and grew during the course of the animal's ontogeny by secretion of mineralized tissue from this epithelium. They were partly or wholly enveloped in epithelial folds when the animal was not feeding and the pharynx was in a constricted resting position.

(3) In the middle late Cambrian there appeared forms in which the secretory activity of the pharyngeal epithelium in the folds around the denticles created favourable conditions for deposition of a thin apatite crust on the free surface of the denticle during periods when the pharynx was not expanded for feeding. Denticles so invested were the first euconodont elements.

(4) Soon after the first appearance of this new tissue – the crown – it began to be utilized for more complex constructional needs. Initially it formed cutting edges (keels), then it took over more and more of the construction of the cusp. This involved increasing biological control of the formation of the tissue, probably through an increasingly structured organic matrix. As the plastic potential of this new mode of growth began to be realized (Bengtson 1976:202), the euconodont elements grew more complicated, and the enfolding of the pharynx into the rest position became increasingly complex. This change was accompanied by a diversification of feeding habits and life modes, but the denticles, the euconodont elements, continued to function as teeth (*sensu lato*; Jeppsson 1979).

In regard to the systematic position of the Conodonts, the model outlined allies them closely to the Phylum Chaetognatha, but as formulated here it does not touch on the interesting possibility of a

close relationship between chaetognaths and chordates. If one accepts that taxonomic groups may be paraphyletic (i.e. if one is not an ardent cladist) it is possible to argue for a separate paraconodont-euconodont Phylum Conodonts, derived from the protoconodont Phylum Chaetognatha. But with regard to the total phenotype, the presence or absence of pharyngeal denticulation is only a detail, and if further finds of well-preserved conodont animals were to confirm closer adherence to a chaetognath body plan, the Conodonts would be better placed as a subphylum or class within the Phylum Chaetognatha.

This model is sufficiently specific to be both informative and testable. Unfortunately for the latter aspect, however, it suggests that there may be an evolutionary discontinuity between the protoconodont and paraconodont elements, in that the latter may not have evolved from the former, but from histologically similar but morphologically different structures nearer to the mouth. Thus there may be no prospect of finding an evolutionary series between these two types of elements (and there is no evidence that any species was provided with both protoconodont grasping spines and paraconodont denticles). Nevertheless, in other respects the model allows clear inferences on the early evolution of conodont elements and their histogenesis. It precludes the possibility that the primary mineralized tissue of conodont elements was formed by cells homologous to vertebrate osteogenic cells; any mesodermally derived mineralized tissue would have had to be secondarily added to the primarily ectodermal elements. (The recent suggestion by Barskov, Moskalenko & Starostina 1982 that vertebrate bony tissue is present in Ordovician conodonts would need to be strengthened – with regard to the conodont nature of their specimens of *Coleodus* as well as to the morphology and identity of the alleged cavities after osteocytes, osteoblasts and osteoclasts – before it would offer any threat to the idea that conodont elements were derived from an ectodermal epithelium.) It further suggests that element morphology in euconodonts may be analyzed specifically in terms of (1) function in the manipulation of prey, (2) storage within a collapsed pharynx, and (3) growth within epithelial folds.

Questions concerning the origin and early evolution of conodonts can thus be seen to be in continuous association with the wide spectrum of problems of euconodont biology. Many answers to the current problems of the early history of conodonts, including the further testing of the evolutionary model presented here, are likely to come from improved insights into the nature of post-Cambrian conodonts.

Acknowledgements. – My work has been financed through grants from the Swedish Natural Science Research Council. I thank Vladimir V. Missarzhevsky (Moscow), Amanbek M. Mambetov (Frunze) and Gordon C. Winder (London, Ontario) for providing material indispensable for this investigation. Quentin Bone (Plymouth), Derek E. G. Briggs (London) and Hubert Szaniawski (Warsaw) kindly gave me access to unpublished manuscripts. Of the many colleagues who have helped me with information and critique I would especially like to mention Simon Conway Morris (Milton Keynes), Lennart Jeppsson (Lund) and Klaus J. Müller (Bonn). Simon Conway Morris, Anders Martinsson (Uppsala), S. Crosbie Matthews (Uppsala) and James F. Miller (Springfield, Missouri) read the manuscript and provided many helpful suggestions; it is with grief that I record that Anders Martinsson and Crosbie Matthews both died shortly before this volume went to the press.

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Patterns and processes in conodont evolution: a prospectus

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Since their discovery, conodonts have become highly regarded as useful biostratigraphic tools, and correlation may always be the principal *raison d'être* of conodont work. More recently, multielement taxonomic concepts and examinations of paleoecologic controls seem to have lent truly organismal status to conodonts, now climaxed by the discovery of the new conodont animal (Briggs, Clarkson & Aldridge 1983). Examinations of conodont evolution have been largely restricted to the determination of phylogenetic relationships, usually as a codominant or subordinate theme to biostratigraphy (e.g. Sweet & Bergström 1981; Bergström 1982; Fåhræus 1982).

Abundant stratigraphic and geographic distributional data are available for conodonts in many parts of the geologic column. These data lend themselves to a closer examination of conodont evolution, namely recognition of patterns and processes of morphologic change.

Such recognition, however, is heavily dependent on several kinds of data, including (1) precise stratigraphic limits of range, (2) ontogenetic development and (3) range and kind of intraspecific variation.

Stratigraphic data must be precise to document the extent of local teilzones and show physical stratigraphic relations between supposed ancestor and descendant species. The answerable questions become: Is there stratigraphic overlap? At all occurrences? The answers suggest patterns of lineage branching, if present, and possible dispersal gradients of newly developed morphotypes (see, e.g., Fåhræus 1982). Single collections 'characteristic' of entire formations or large intervals ('bag biostratigraphy' of W. C. Sweet, 1982, personal communication) are grossly inadequate.

Detailed knowledge of ontogenetic development of discrete conodont elements is vital to the recognition, not only of ancestor–