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The Origin of the Mineral Skeleton in Chordates

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INTRODUCTION

Most of the evolution of the vertebrate mineralized dermal skeleton, which has resulted in its present complexity, is traceable within the crossopterygian–tetrapod lineage. In acanthodianlike ancestors of these higher vertebrates the dermal skeleton was restricted to scales, locally coalescing into dermal plates or modified into oral teeth. The basic unit of such primitive vertebrate skeleton is the odontode, a denticle forming at the tip of an ectomesenchymal dental papilla under its ectodermal epithelium (recently reviewed by Smith and Hall, 1993; Smith, 1995). In most fishes and extinct armored agnathans the external layer of mineralized dermal tissue is enameloid, developing as a result of mineralization of a matrix produced by both ectodermal and ectomesenchymal cells of the dental papilla, or histogenetically similar complex tissue. Below this layer, purely ectomesenchymal in origin derivatives of dentine develop. However, in the most primitive actinopterygian fishes, ganoine, an enamel homolog (Sire *et al.*, 1987) develops, instead of enameloid. Odontodes composed of acellular bone (aspidin) and capped with enamel characterize the Ordovician agnathan *Eriptychius* (Smith and Hall, 1990; M. P. Smith *et al.*, 1995; M. M. Smith *et al.*, 1996). The original odontode organization was thus, as can be judged on the basis of this pattern of distribution of ectodermally secreted mineral tissues, a thick and dense cap built of a mineral laminated tissue, ectodermally secreted

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from outside by ameloblasts (Smith, 1995), and less compact basal tissue filling the internal denticle cavity, secreted in a rather irregular way by ectomesenchymally derived odontoblasts, which may or may not be incorporated into the mineral tissue (Smith and Hall, 1990). Such a structure characterizes elements of the oral apparatuses of the conodonts, extinct organisms preceding in their origin the armored agnathans. The conodonts are the oldest and the most primitive chordates bearing a well-developed mineralized dermal skeleton.

The mode of formation of the phosphatic skeleton, which characterizes both the conodont elements and the vertebrate dermal scales, is unique for these two kinds of sclerites and is unknown in any other organisms. Their homology seems to be based on strong evidence (Smith, 1995). It is highly unlikely that this could have evolved independently twice in metazoan phylogeny. Rather, the genetic and developmental patterns that evolved at the earliest stages of phylogeny of the oral apparatus of the common ancestor of the conodonts and agnathans were applied by the latter to the secretion of dermal scales (M. M. Smith *et al.*, 1996; M. P. Smith *et al.*, 1996). This could have been connected with a change from the pelagic to near-bottom mode of life and to a different feeding style, when the weight of newly constructed armor was no longer an obstacle to building a mineral protective armor and there was also no longer a need for a predatory grasping apparatus.

This chapter contains a review of the paleontological evidence available on the earliest evolution of the chordate mineral skeleton and its correspondence to soft anatomy. The data on which the reviewed anatomical and phylogenetic inferences are based are of varied nature, ranging from isolated mineral denticles to complete organisms with details of soft organs preserved. This richness of the fossil record is a rather unexpected result of paleontological research since the late 1980s. It is now possible to merge the information provided by statistical studies on isolated skeletal elements of conodonts (reviewed by Dzik, 1991*a*), articulated skeletal parts (Aldridge *et al.*, 1987, 1995), and complete imprints of the soft body (Briggs *et al.*, 1983; Aldridge *et al.*, 1986, 1993). The Cambrian soft-bodied faunas continue to supply new data on even more primitive chordates (e.g., Dzik, 1995); the Ordovician is also important in discussion of the phylogeny of vertebrates (e.g., Sansom *et al.*, 1996). The available evidence is incomplete, typical of all paleontological material, but is unrivalled because it comes directly from those geological epochs in which the evolutionary diversification actually took place, or at least from a time closely following establishment of the main clades. The fossil record, therefore, regularly provides challenging tests to the relationships between the Recent chordates, established on neontological data (see Forey and Janvier, 1993).

The question of the origin of the mineral skeleton in chordates will start from presentation of the basic data on the organization and evolution of the skeletal structures in the conodont body, their oral apparatuses. An interesting feature of conodont elements is the occurrence of clear imprints of secretory cells on their oral surface. The imprints provide insight, at the cellular level, into developmental processes in these extinct chordates, many of which are up to 500 million years old. An attempt to restore the organization of the secretory organ and mechanisms of morphogenesis of particular morphological structures on the basis of cell imprint distribution is presented. The oral grasping apparatuses of chordates, as well as their elaborate sensory head organs, appear to be even more ancient in origin than those of true conodonts and are present in the Middle Cambrian probable "paraconodont" *Odontogriphus* (Conway Morris, 1976*a*), and perhaps even in the oldest known chordate *Yunnanozoon*, of Early Cambrian age (Dzik, 1995; Shu *et al.*, 1996*a* interpreted another fossil from the same locality as a chordate). These organisms differ strongly from conodonts and more advanced chordates in their anatomy, as well as from the generally assumed ancestral chordate Bauplan (but see Lacalli, 1996; Williams and Holland, 1996). A scenario of possible evolutionary transformations that may explain this deviation from expectations, consistent with the fossil evidence although radically unorthodox from a zoological perspective, is proposed. According to this model, the evolutionary origin of the oral apparatus with its mineralized skeleton took place well within the invertebrate grade of the sequence of events leading to the chordates.

ARCHITECTURE OF CONODONT APPARATUSES

The chordate affinity of conodonts is based on the occurrence of V-shaped muscle blocks and an axial notochord, an asymmetric caudal fin, and paired eyes (Fig. 1*a*; Briggs *et al.*, 1983; Dzik, 1986; Aldridge *et al.*, 1986, 1993; proposed to be otic capsules by Pridmore *et al.*, 1997), as well as the probable homology of their mineralized tissues with those of the vertebrates (Schmidt and Müller, 1964; Dzik, 1976, 1986; Smith, 1995). The conodonts are classified in several orders (Sweet, 1988; Dzik, 1991*b*), most of which are distinguished on the basis of the organization of their oral apparatuses. Soft tissue anatomy is also relatively well known, owing to imprints of representatives of the two most diverse orders. *Clydagnathus* from the early Carboniferous of Scotland (Briggs *et al.*, 1983; Aldridge *et al.*, 1986, 1993) is representative of the Ozarkodinida, whereas *Promissum*, from the late Ordovician of South Africa (Aldridge and Theron, 1993; Gabbott *et al.*,

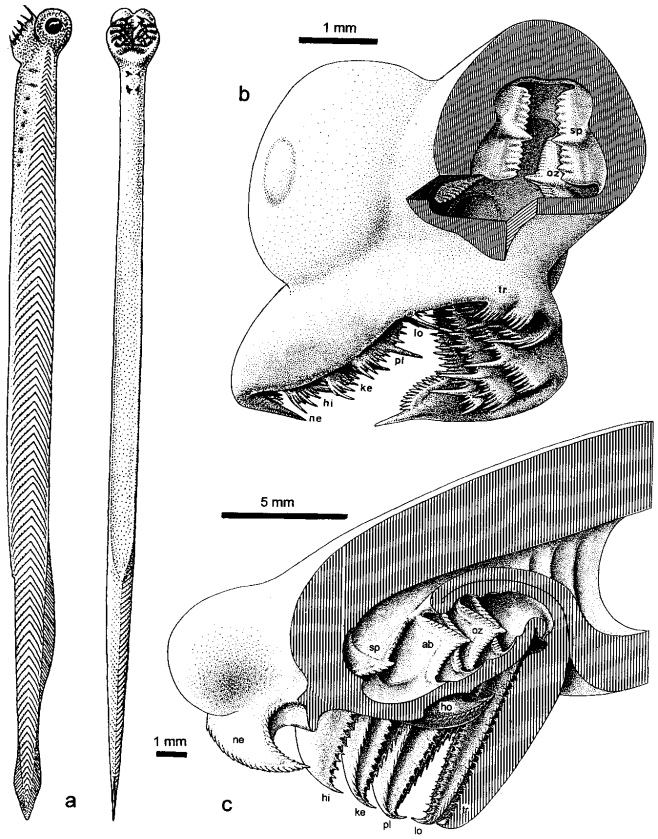


FIG. 1. Soft anatomy of conodonts: (a) conodont *Clydagnathus*? cf. *cavusformis* from the Early Carboniferous (Viséan) Granton Shrimp Bed of Scotland (based on data of Aldridge *et al.*, 1993); (b) restoration of soft parts surrounding the apparatus elements in the Early Devonian (Gedinnian) ozarkodinid conodont *Pandorinellina remscheidensis*; the head is shown in postero-ventral view and is "cut" to expose elements hidden in the throat; the anterior set of elements was oriented more obliquely toward the axis in resting position (from Dzik, 1991*b*); (c) proposed arrangement of elements and their homology in the Ordovician prioniodontid conodont *Promissum pulchrum* (the head is shown sectioned medially; Jeppsson's notation of element locations is modified by adding locations **ab** and **ho**, derived from "ambalodus" and "holodontus" element types of *Amorphognathus*, where they are not differentiated morphologically from elements in locations **oz** and **ne**); three-dimensional arrangement of elements taken from Aldridge *et al.* (1995). Note that in this position the apparatus could not effectively work, as some elements are located in between others. To act as a grasping apparatus, protrusion of the whole set of symmetry transition series elements ("filtratory basket") is necessary; this resulted in an arrangement of elements basically similar to that in the ozarkodinids.

1995) belongs to the Prioniodontida. Despite a rather large taxonomic and time difference between them, these conodonts are similar anatomically (Gabbott *et al.*, 1995). Both show lampreylike outline and well-developed ocular sclerotic rings and differ only in details of apparatus organization. However, these conodonts are highly derived and to restore the ancestral architecture of the conodont apparatus, which may be more meaningful than the rather uniform anatomy in the discussion of early chordate evolution, it is necessary to consider more primitive conodonts. Our understanding of such forms is primarily based on statistical reconstructions of their feeding apparatuses from collections of isolated elements and is subsequently refined by discovery of natural assemblages (for review see Sweet, 1988; Dzik, 1991*b*).

Restorations of the three-dimensional apparatus architecture of ozarkodinid conodonts represent the most reliable source of information regarding primitive conodonts. Findings of complete conodont apparatuses on the surface of bedding planes (natural assemblages) exhibit different directions of post mortem collapse, which enable restoration of the original spatial distribution of individual elements. Such analyses have been performed for the Early Devonian *Pandorinellina* (Fig. 1*b*; Dzik, 1976, 1986, 1991*b*) and several late Carboniferous genera (Aldridge *et al.*, 1987; Purnell, 1993; Purnell and Donoghue, 1997). Sometimes less deformed apparatuses have been recovered by acid dissolution of rock (clusters), where elements are fused together by diagenetic mineral. These provide additional evidence. An iterative method of reconstructing the original spatial arrangement of elements in the apparatus by proposing and then continually refining a model by testing with natural assemblages has proven to be extremely efficient. Little doubt remains that in the ozarkodinid apparatus elements were arranged in pairs, more or less transversely to the body axis, with their cusps opposed. Some minor discrepancies remain that refer to details of the arrangement of particular functional units within the apparatus (see Purnell and Donoghue, 1997). Only Nicoll (1995) continues to support a model where all elements are arranged parallel to the body axis, even though evidence occurs that is clearly contradictory (e.g., Aldridge *et al.*, 1987).

The number of element locations in all the ozarkodinid apparatuses appears to be equal. Also the morphology of elements in those locations are very similar. The late Paleozoic Spathognathodontidae, Polygnathidae, and Idiognathodontidae are a coherent morphological and biological group. Even further derived, Carboniferous species of the Prioniodinidae, representatives of which are well differentiated already in the early Silurian, do not seem to deviate from the ozarkodinid apparatus architecture. The restoration of a plan of their skeletal components proposed by

Purnell (1993) for *Kladognathus* slightly differs from that typical of more generalized members of the order, but it has not been based on assemblages preserving the original arrangement of elements but rather on functional assumptions derived from homology of elements.

Homology of particular element types in the ozarkodinid apparatus can be traced back in time to the late Tremadoc simple-cones *Rossodus* and *Utahconus* (see Dzik, 1991*b* for a review). The numerical ratio of element types seems to be consistent with the model of a 15-component element apparatus, although no statistical study of Ordovician collections has been performed since the early attempts by Marsal and Lindström (1972) and so is difficult to test.

The only direct evidence of prioniodontid apparatus composition (the second largest order of the conodonts, the Prioniodontida, most of which is early Paleozoic) is provided by the late Ordovician conodont *Promissum*. Natural assemblages show that this apparatus differed from those of the late Paleozoic, at least in the presence of two more element pairs: one of incisor-type and another of platform morphology (Aldridge *et al.*, 1995; Purnell *et al.*, 1995). The architecture of the apparatus of *Promissum* is otherwise consistent with that of *Pandorinellina* in the organization of the portion homologous to the symmetry transition series of more primitive conodonts, with one symmetrical and four paired elements (Fig. 1*c*). Numerical data on *Baltoniodus* from the Ordovician Mójcza Limestone of the Holy Cross Mountains (Dzik, 1994, 1996) suggests that duplication of the two element locations, which make prioniodontids different from ozarkodinids, had taken place by the Early Ordovician. After the Ordovician, only the pterospathodontids, which are probably derived from an ancestor close to *Complexodus* or *Icriodella* (Dzik, 1991*b*), flourishing in the early Silurian, had a similar number of elements to *Promissum* (see Männik and Aldridge, 1989).

It is possible to determine homology between apparatuses of ozarkodinids and the Protopanderodontida. The protopanderodontids range back to the latest Cambrian. They are almost certainly ancestral to both the Ozarkodinida and the Prioniodontida and probably, therefore, had a similar apparatus organization. This is supported by evidence from incomplete clusters (reviewed by Dzik, 1991*b*). These clusters do not allow determination of the exact number of element locations, but underrepresentation of the symmetrical elements in samples of isolated elements relative to other element types suggests that they were unpaired. The two robust element types in the apparatus probably correspond to elements of ozarkodinids and prioniodontids traditionally referred to as the platform series. Composition of the protopanderodontid apparatus was, therefore, similar to that

of the ozarkodinids and the prioniodontids. However, this is not the primitive state of true conodonts.

Much lower diversification of coniform elements occurs in the apparatus of the order Panderodontida. The most complete cluster of the panderodontid elements, currently known, consists of 13 elements (Dzik and Drygant, 1986). The only unpaired element in this specimen is strongly asymmetric and was undoubtedly originally paired, the missing element probably lost during processing. All elements were, therefore, originally paired. In several genera of the panderodontid conodonts no symmetrical element was present in the apparatus. The cluster of *Besselodus* described by Aldridge (1982) consists of seven elements, representing one side of the apparatus in close lateral connection, an arrangement unlikely to have developed if the apparatus was similar in organization to that of ozarkodinids or prioniodontids. Even if symmetrical elements do occur in *Panderodus*, their occurrence in number comparable with other elements of the apparatus suggests that they too were paired. In some species they are so rare that they are more likely to have resulted from an atavistic malformation than to represent a normal element type. All of these facts are reconcilable with the chaetognathlike model of apparatus architecture proposed by Dzik and Drygant (1986). It has been proposed (Dzik, 1991*b*) that the primitive 15-element component apparatus can be derived directly from that of the Panderodontida by adding a single medial element to the existing seven pairs of elements. This suggests that the prioniodontid apparatus is derived. Sansom and colleagues (1995), who had at their disposal the only known natural assemblage of *Panderodus*, preferred to arbitrarily reconstruct an apparatus with 17 elements, more than present in the natural assemblage and in any known clusters. The maximum number of element types allowed by their model is nine, but the most observed is seven or fewer. Whether a 19-component apparatus, instead of 15, is primitive or derived is unknown, although at present the second possibility appears more likely.

Symmetrical elements occur in pairs in the apparatus of the Tremadoc conodont *Coeleocerodontus*, known from numerous clusters (Andres, 1988). Its apparatus consists of two pairs of relatively robust elements at one end, at least five pairs of the "symmetry transition series" (including large, paired symmetrical elements), and a pair of elements with a triangular cross-section at the other end. The exact affinity of *Coeleocerodontus* remains obscure (Andres, 1988 suggested that it was a paraconodont, a member of the Westergaardodinida, an order defined on element histology), but its apparatus structure is similar to that of the protopanderodontids. However, occurrence of all elements in pairs suggests that

Coelocerodontus is more closely related to the panderodontids. Perhaps the apparatus of *Coelocerodontus* is representative of the condition from which both the simple panderodontids and more advanced protopanderodontids are derived.

FUNCTION OF CONODONT APPARATUSES

The strong morphological differentiation of the conodont feeding apparatus mirrors the differentiation of element function. The clear analogy between the organization of the conodont apparatus and the dentition of mammals (with posteriorly located molars and anterior canini), as well as the crustacean mandibles (with the anterior incisor, posterior molar regions, and comblike lacinia mobilis in between), strongly suggests a feeding function. Crustacean mandibles are closest in size and in morphology to conodont apparatuses and provide a good functional analog. The presence of the unpaired element in the middle of advanced conodont apparatuses makes their anterior and posterior parts functionally distinct. The anterior set of sharply denticulated elements was probably exposed and could have been used to grasp and possibly perform a filter function, whereas the more robust posterior elements were hidden in the throat of the animal, performing grinding functions.

Although in general this functional interpretation of the conodont apparatus seems well substantiated, it is much more difficult to be more precise about the functional adaptations of particular element types. Purnell (1994) used the positive allometry in development of the platform area in the posteriormost elements in the apparatus of the idiognathodontids and the allegedly negative allometry in the relative growth of the anteriormost elements (the latter being clearly an artifact resulting from the chord instead of the true length of the curved inner process being measured) to support their crushing and grasping functions, respectively, for these elements. Although such a functional differentiation of these elements is generally accepted (Jeppsson, 1979), this does not necessarily imply their morphology being so strictly controlled histogenetically. The histogeny of conodont elements to some degree is recapitulated in their evolution. The reason for the difference between juveniles and adults is historical rather than functional. Both the platform and the icrion (the two basic ways of molarization in conodonts—see Dzik, 1991*a*) are evolutionarily derived structures that in all conodonts originated late in histogeny, gradually expanding in the course of evolution toward earlier and earlier ontogenetic stages. In advanced conodonts (e.g., *Manticolepis* or similar palmatolepi-

dids) growth of the platform is isometric except for the earliest phase of histogeny.

The mammalian jaw or crustacean mandible models are not applicable to the most primitive panderodontid apparatuses, in which the chaetognath grasping apparatus appears to be a much closer analog (Dzik and Drygant, 1986). It has to be noted, however, that the most primitive coniform elements of the Late Cambrian conodonts were generally of more robust appearance than chaetognath grasping spines (including the associated protoconodonts, which probably belonged to the chaetognaths; Szaniawski, 1982). The apparatuses they formed were thus probably relatively robust as well.

GROWTH AND FUNCTION OF CONODONT ELEMENTS

The unique internal structure of the elements of the conodont apparatus is a result of their mode of growth, with successive lamellae of the crown being added from outside. Frequently, within the conical basal cavity (or just below the crown if the basal cavity is inverted) an additional, histologically different kind of skeletal tissue was secreted. The nature of this basal filling tissue, being secreted from inside the basal cavity, was established by Gross (1957). Lindström and Ziegler (1971) have shown that the basal cavity tissue in evolutionarily primitive conodonts was originally rich in organic matter, or was plainly organic in composition, and its mineralization was commonly secondary. Generally, gerontic elements have their basal filling tissue better developed than juvenile ones. Elements of the same species may or may not bear any basal body, depending on the sample. Samples rich in phosphatized fossils frequently yield elements with elaborate structures of this kind, which supports the notion of a significant contribution from a secondary mineralization, but there are many exceptions and the variation in mineralization of the basal bodies remains to be explained.

The lower surface of the basal filling tissue in early Ordovician conodonts is of irregular appearance, with perpendicular branching canals opening to the basal cavity (Lindström and Ziegler, 1971: pl. 4: 6) interpreted as at least analogous to dentine tubuli (Dzik, 1986: Fig. 1*a*; Sansom *et al.*, 1994). Sometimes the tissue is spongy, black, and probably unmineralized (Dzik, 1986: Fig. 1*b*). These features of the basal filling tissue are even more apparent in Cambrian conodonts (Andres, 1988; Fig. 2*b*, this chapter).

The only developmental analog of the crown and basal filling tissues of conodonts (with respect to their mineralogy and mode of secretion) are

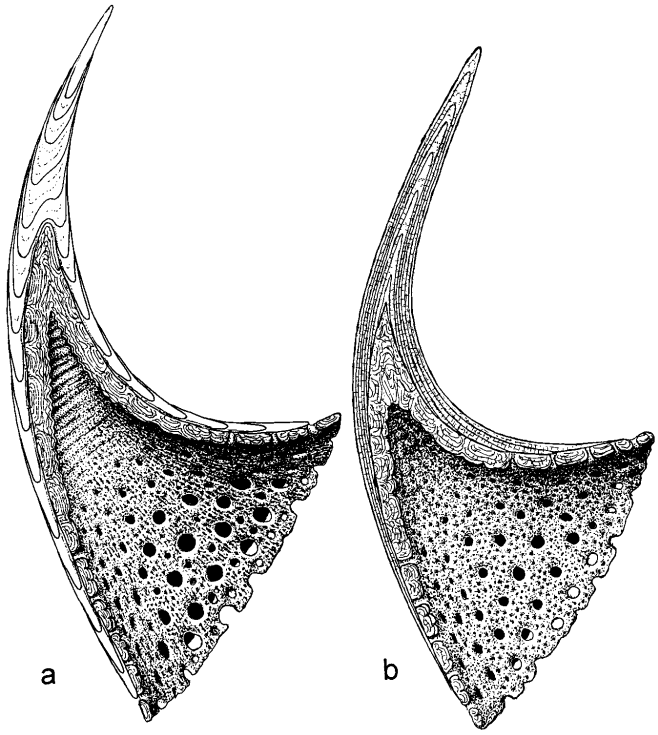


FIG. 2. Diagrammatic medial sections of elements of Cambrian "paraconodonts" and "euconodonts" (based on Andres, 1988): (a) the Late Cambrian westergaardodinid *Problematoconites* sp. (see Andres, 1988: text—Fig. 13, pl. 4: 1–8), note initial rodlike stage in the development of the crown tissue; (b) a primitive late Cambrian cordylodontid (see Andres, 1988: pl., 12: 7–8, 13: 5–6), the crown is conical from its beginning.

the enamel and dentine of vertebrates (Schmidt and Müller, 1964; Dzik, 1976, 1986; Smith, 1995; Sansom, 1996). Since the chordate nature of the conodonts has been established, there have also been other attempts to fit the conodont element microstructure into the classification of vertebrate skeletal hard tissues. Sansom *et al.* (1992) proposed that the "lacunate spaces"

within opaque parts of conodont crown tissue ("white matter") were osteocyte lacunae and thus the tissue was a cellular bone. Secondary development of white matter during late stages of the element's histogenesis (or perhaps even diagenetically), replacing the original lamellar cone-in-cone structure, is well recognized (Sweet, 1988, p. 14; Donoghue, 1998, Fig. 6, proposed that the white matter was developed at the cusp surface during early histogenesis but this is in contradiction with the observed pattern of its distribution in juvenile elements). There cannot, therefore, have been cells within the tissue during secretion. Furthermore, as white matter is invariably covered by intact lamellar crown tissue, there is no way for the putative cells to migrate there (Dzik, 1993). Moreover, the external secretion of the crown tissue makes it rather unlikely to be of ectomesenchymal or mesodermal origin, which is the case with the cellular bone.

The claim that the basal filling tissue of the Ordovician *Chirognathus* is dentine (Sansom *et al.*, 1994) is consistent with the homology proposed by Schmidt and Müller (1964), but usually canals comparable with dentine tubuli are missing in the basal filling. There is also no clear evidence yet that mineralization of the ectomesenchymal organic tissue filling the basal cavity characterized the common ancestor of conodonts and agnathans. This would be necessary to identify the basal filling tissue as dentine. They thus have to remain just analogs.

Ganoid scales of Recent fishes (see e.g., Meunier, 1980) provide probably the closest analog, if not homolog, of the conodont element mineral tissues. The ganoine is a primitive type of enamel (Sire, 1995). The cells of the inner ganoine epithelium are homologous with ameloblasts and can be referred to as such (Sire, 1994). This can be reasonably extended to the secretory cells of the conodont crown tissue. Ganoine secretion proceeds by alternating deposition of a thin organic layer of preganoine, and a subsequent period of mineralization. As a result, distinct growth lines develop at the contact of ganoine with the underlying bony plate. Instead of collagen, preganoine contains fibers of other proteins arranged perpendicularly to the surface, along which ganoine crystals grow (Sire, 1995). It is likely that the histogenesis of conodont elements (e.g., Müller and Nogami, 1971) was homologous, and growth was punctuated by periods of arrest (perhaps daily; Fig. 3*d*; see Zhang *et al.*, 1997). Kemp and Nicoll (1995) argued for the presence of collagen in the conodont element tissues because they stain with Sirius Red, the tetrakisazo dye used in soft tissue histology. It seems to be of importance in this context that simple histological tests failed to identify even structurally preserved Early Paleozoic collagen (Urbanek, 1986) whereas in phosphatic sclerites of Ordovician palaeoscolecid worms, mineralogically similar to conodont elements, collagen fibers are represented only by empty spaces (Dzik, 1986). Sirius Red acts by ion

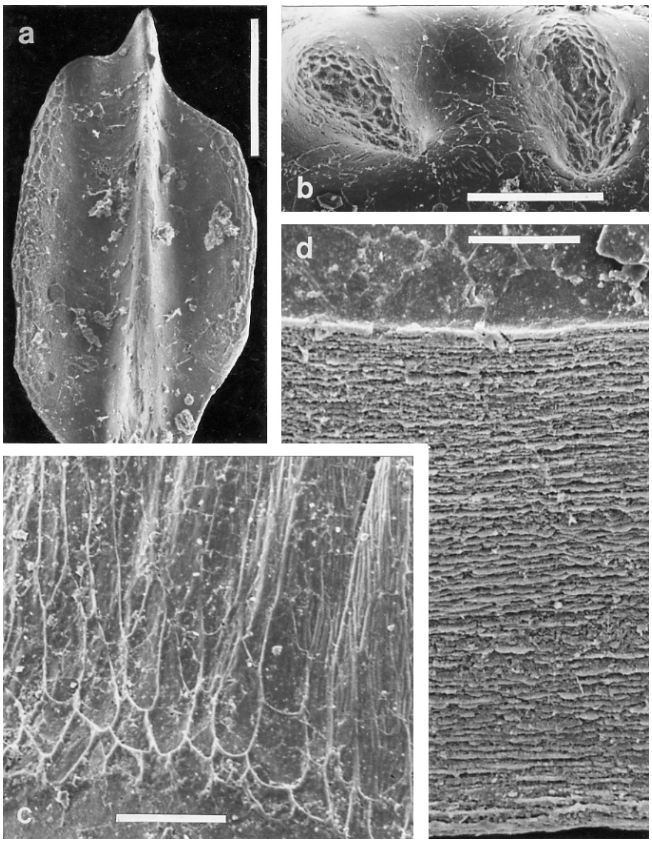


FIG. 3. Localized development of secretory cell imprints (a, b), their elongation with denticle growth (c), and growth increments (d) in conodont elements: (a) juvenile **sp** element of *Polygnathus* s. l. from the Late Devonian (latest Frasnian) of Płucki, Holy Cross Mountains, Poland, in occlusal view showing development of polygonal cell imprints at margins of fast growing platform; bar scale 49μm; (b) juvenile **sp** element of *Icriodus alternatus* from coeval strata in Wietrznia, same region, with polygons developing on fast-growing denticle tips of icrion; bar scale 49μm; (c) adult **hi** element of *Falcodus* sp. from the Early Carboniferous (Tournaisian, sample Dz–15) of Dzikowiec, the Sudetes, Poland, in lateral view showing elongation of secretory cell shapes toward the denticle tips; bar scale 19.6μm; (d) surface of inverted basal cavity in **ne** element of *Ancyrodella* from the Late Devonian (late Frasnian, sample Pl–22) of Płucki showing numerous rhythmic, possibly daily, increments; bar scale 19.6μm.

binding of its sulfonic groups with the basic groups of the collagen molecule (Marotta and Martino, 1985), mainly proline and hydroxyproline, and is also known to stain several other kinds of proteins (Brigger and Muckle, 1975).

Although some irregularities have been documented from the internal record of growth of conodont elements (Müller and Nogami, 1971), well-preserved conodont apparatus elements, like scales of pelagic fish, exhibit no evidence of surface wear (scratches and abrasions, such as illustrated by Purnell, 1995*b*, are uncommon). An active grasping and crushing function of the conodont elements has been inferred from their shapes (Jeppsson, 1979). If the mineral crown tissue of the elements were in a direct contact with food particles this would hardly allow preservation of such intact surfaces unless they were periodically covered by folds of soft secretory tissue, as mentioned by Denham (1944) and as fully elaborated by Bengtson (1976). The pocket theory of secretion fits some peculiarities of the morphology of certain conodont elements (Carls, 1977) but is difficult to apply to complex brush-like morphologies of the occlusal surfaces of some elements and difficult to test. However, some conodont elements record the arrangement of secretory cells on their oral surface, which provides direct insight into the anatomy of the organ responsible for their secretion.

Such imprints were first recognized by Hass (1941), and their value for paleobiological analysis is widely recognized (Pierce and Langenheim, 1970; Burnett, 1988; Conway Morris and Harper, 1988; Burnett and Hall, 1992; von Bitter and Norby, 1994; Zhuravlev, 1994). Their width, usually ranging from 3 to 5 μm, is similar to that of the cells of inner ganoine epithelium (Sire, 1994) and is even closer to ameloblasts in Recent tetrapods where they are of columnar shape, with a height of about 50 μm, and with well-developed Golgi apparatuses (Masuda *et al.*, 1989) crucial to their secretory activity (Matsuo *et al.*, 1992). In conodonts, calcium phosphate was secreted by the whole exposed surface of the cells, which were individually convex at the secreting margin. Where cells were in contact with their neighbors, activities of the cells overlapped, leading to increased deposition of calcium phosphate. This resulted in the development of a polygonal pattern of ridges on the surface of the crown tissue. Not only the size, but also shapes of individual cells can be traced through histogeny (Burnett, 1988) and it appears (Fig. 4) that they were not uniform over the whole area, as would be predicted if the elements were temporarily withdrawn from epithelial pockets (or periodically worn-out and regenerated). Burnett (1988, pp. 414–415) salvaged part of the theory, proposing that "more positively upstanding areas" were emergent during function. His hypothesis is refuted by the presence of polygons on the tips of cusps in icrions of genera

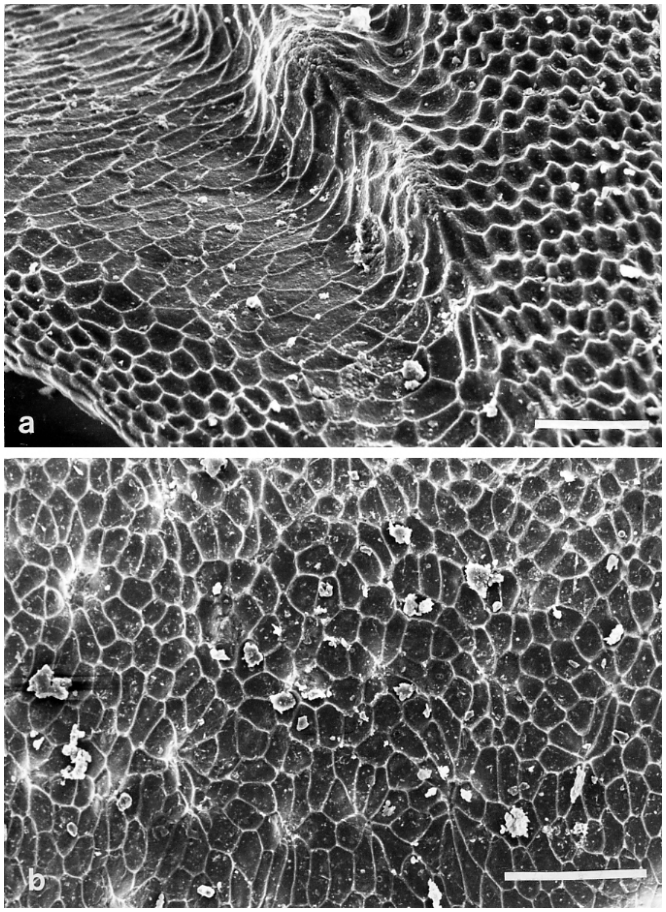


FIG. 4. Distribution of ameloblast imprints on the occlusal surface of the posteriormost (**sp**) elements of the conodont apparatus: (a) *Siphonodella belkai* from the early Tournaisian of Kowala, Holy Cross Mountains, sample Ko–42; note that the epithelial cover passes uninterrupted across the element carina (the main row of denticles) and that their shapes vary specifically; bar scale 19.6μm; (b) *Conditolepis? linguiformis* from the latest Frasnian of Płucki, Holy Cross Mountains; note star-like arrangement of cells at tubercles; bar scale 49μm.

such as *Icriodus* (Fig. 3*b*) or *Lochriea* (von Bitter and Norby, 1994) and on the lateral surfaces of denticles in, among others, *Dinodus*. Cells on the lateral surfaces of denticles were extremely elongated (Fig. 3*c*; contra Burnett, 1988, p. 414). The most reasonable explanation for this pattern is the occurrence of extensional stress generated by the elevated denticle tip during growth, whereas the cell divisions on the lateral surfaces of the denticle were, for some reason, inhibited.

The mode of secretion of the crown tissue in conodonts that develop a prominent pattern of reticulation, sometimes with deep concavities in the center of each polygon (Fig. 4*a*), closely resembles the mode of secretion of enamel in Recent tetrapods (e.g., Boyde, 1978). Conodont crown tissues (for instance *Polygnathus* s. s.), which did not develop polygons, even in the thickest parts of the platform, more closely resemble the ganoine of Recent primitive actinopterygian fishes (e.g., Sire, 1994, 1995). It is possible that in such cases, secretory cells were not in direct contact with the mineralized tissue but were separated from it by a membrane similar to the ganoine membrane. This is a kind of basement membrane, which does not mineralize, and it is rich in proteoglycans that work as a glue keeping epithelial cells in place (Sire, 1995). Presumably in places of extremely high secretion of conodont crown tissue (Fig. 3*a*, 3*b*), the membrane tended to thin or disappear completely. As a result, direct contact of the epithelial cells (ameloblasts) with the secreted tissue led to the formation of a polygonal surface pattern.

In platform elements, concave areas, which had a relatively low secretion rate, are virtually always smooth, lacking imprints of secretory cells. The boundary between areas of smooth and polygonal ornament are distinct, or can be seen as gradual over a very short distance, where the ribs delimiting polygons become more and more indistinct, as if the surface is covered by a thin blanket. This strongly suggests the presence of a basal membrane separating the mineralized matrix and the secretory cells in the areas of the smooth surface. Microstriae also present on the surface of such elements have nothing to do with cell imprints but represent longitudinal folding of the basal membrane, as shown by irregularities in their distribution. The occurrence of cell imprints discernible even in areas such as these indicates that the cells were invariably covered by a secretory epithelium, elements differing only in the extent of the basal membrane. The membrane, therefore, tends to disappear in the fastest growing parts of elements. There is an interesting analogy between this pattern of the secretive epithelium growth and the morphogenesis of salivary glands, as reviewed by Bard (1990, pp. 44–48). After a bulblike bud of the salivary gland covered by a basal lamina is formed, the surrounding mesenchyme produces a neutral hyaluronidase that locally degrades the chondroitin sulfate (one of several

sulfated proteoglycans of an important function in morphogenesis) and the hyaluronic acid of the lamina. Only regions where collagen is attached to the basal lamina are protected and they eventually become the concave areas surrounding the faster growing protrusions.

Reticulate imprints of the secretory cells that developed at the ends of discrete periods of growth are present in cross-sections of the Carboniferous *Siphonodella* elements (Burnett, 1988). This provides additional support to the idea that periods of growth of the conodont element corresponded to sequential secretion of an organic matrix and its subsequent mineralization.

The most important feature of ameloblast distribution in conodonts is that they provided continuous and uniform cover over the whole of the occlusal surface (Figs. 4*a*, 5) making Bengtson's (1976, 1983) pocket theory untenable. This leaves Schmidt's (in Schmidt and Müller, 1964, p. 131; also Priddle, 1974) "horny cup" model the viable paradigm to explain the paradox of growth and function in conodont elements. The epithelial cover of the elements had to perform mechanical functions of the feeding apparatus (Fig. 6). The covering of epithelium over the surface of conodont elements must have been multilayered, as in chaetognaths and in virtually all of the chordates, and may have been produced in a similar manner to keratinous toothlets of *Myxine* and *Petromyzon*. Chordates, like other deuterostomes, lack chitin synthetase (P. Willmer, 1990, p. 80), so whenever a need to develop a firm external skeleton appears, its function is performed by keratinized epidermal cells.

Functional convergence between conodont and cyclostome feeding apparatuses has been invoked by many authors (e.g., Priddle, 1974; Dzik, 1986; Sweet, 1988; Krejsa *et al.*, 1990*a*), but if a homology can be drawn with the toothlets of myxinoids, it must be restricted to the unpreserved (hypothetical) horny caps of conodont elements and not the crown tissue of conodont elements (contra Krejsa *et al.*, 1990*a*, *b*; also Slavkin and Diekwisch, 1996). The structure of the horny caps remains enigmatic, although Schmidt (in Schmidt and Müller, 1964, p. 130) refers to the presence of black stains extending from the tips of denticles in natural assemblages of *Gnathodus* from the Early Carboniferous of Germany. Whether these are the remnants of keratinized epidermal cells (as in *Myxine*) or a chitinous laminar structure secreted by epidermal cells (as in chaetognaths) cannot as yet be determined, although the second possibility seems unlikely because chordates are not able to secrete chitin. Obviously, phylogenetic implications of this distinction would be far reaching, but either structure could have evolved from the other by a change in the secretional behavior of the epidermal cells, from an ability to secrete an external proteoglycan–polysaccharide matrix to a modified keratinous cytoskeleton, or vice versa.

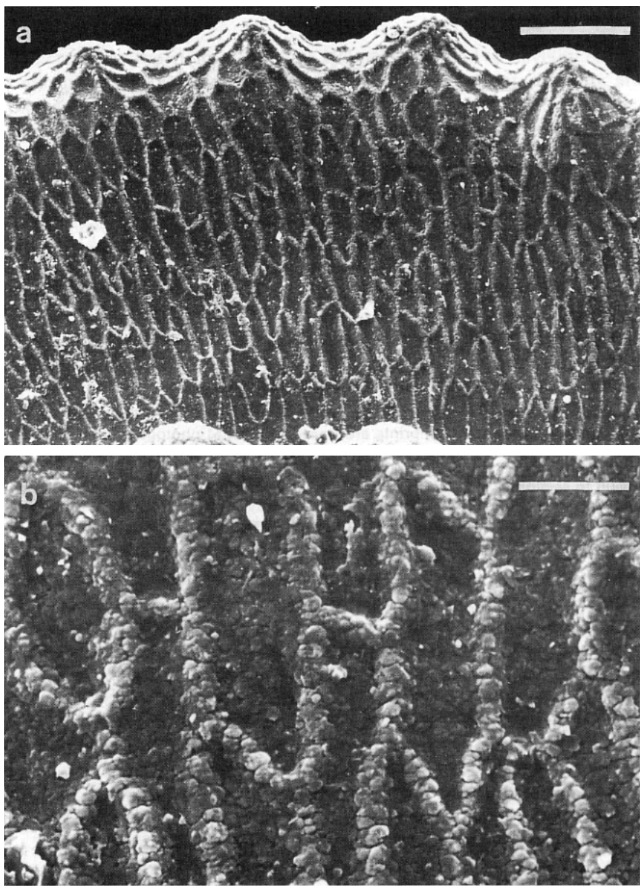


FIG. 5. Relationship between calcium phosphate secretion rate and the size of ameloblasts in *Siphonodella belkai* from the early Tournaisian of Kowala, Holy Cross Mountains, sample Ko–42; (a) platform surface in the specimen illustrated on Fig. 4*a*. The platform margin with tubercles was secreted at the highest rate and ameloblast contact areas are the smallest. At the platform occlusal surface the secretion was much less intense, ameloblast contacts are much wider, and are also mechanically extended in accord with the platform widening; scale bar 19.6μm; (b) a few ameloblast contact areas at higher magnification showing arrangement of calcium phosphate crystals; scale bar 4.9μm.

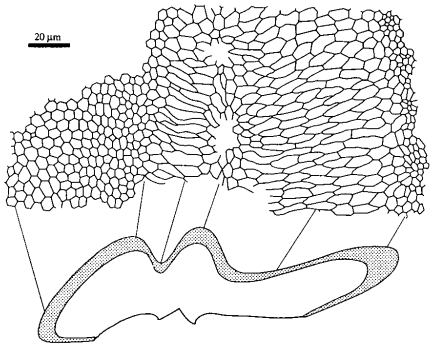


FIG. 6. Ameloblast shapes in the specimen of *Siphonodella belkai* illustrated on Fig. 4*a*; contours of ameloblast imprints are traced from SEM photographs taken at different angles, to keep views of particular cells vertical. The intensity of secretion corresponds to the thickness of laminae in the crown tissue. It would be technically difficult to section exactly the same element, at the surface of which the cell imprints have been traced (and rather unreasonable to destroy it in result) so only a rough estimate of secretion rate can be inferred from the element's shape and its isometric (in short-term) growth.

To avoid a contradiction with the data on the secretory cells imprints discussed previously, it seems reasonable to consider the wear, common on denticle and tubercle tips in isolated conodont elements (Purnell, 1995*b*), as a post mortem taphonomic abrasion.

CONODONT ELEMENT MORPHOGENESIS

The elements of the conodont oral apparatus attain their specific shapes as a result of differential rates of secretion of calcium phosphate by the ameloblasts. Presumably, the ameloblasts first secreted a thin layer of organic matrix followed by precipitation of calcium and phosphate ions, forming crystallites that developed along the axes of protein fibers in the matrix, as in the formation of enameloid (Shellis, 1978; Prostak *et al.*, 1993) and ganoine (Sire, 1994, 1995). The protein fibers are removed from the matrix while it is mineralized. In conodonts, secretion was the most intense (at least during early stages of the histogeny) at the cusp. Most of the elements also bear ridges or crests that arm the inner and outer margins of the cusp, which frequently bifurcate or are supplemented by additional ridges

and crests. At the element margins, the ridges tended to develop element rami (processes) that often dominated the whole element. Typically, after the processes reach a certain size, the sharp occlusal margins develop denticulation. The basal margins of conodont elements are approximately flat, the occlusal morphology resulting exclusively from differential rates of crown tissue secretion.

The ameloblast imprints also provide an insight into the mode of secretion of specific structural features of conodont elements. They show clearly that the size of the contact area of ameloblasts with the element crown tissue surface is inversely proportional to the intensity of secretion. The polygons are smallest at the tips of denticles and on the elevated margins of platforms (Figs. 5, 7). In such areas, the cell imprints are deep and, in extreme cases, a small depression may occur in the center (Fig. 4*a*) that may correspond to Tomes' process in mammalian enamel. This feature is

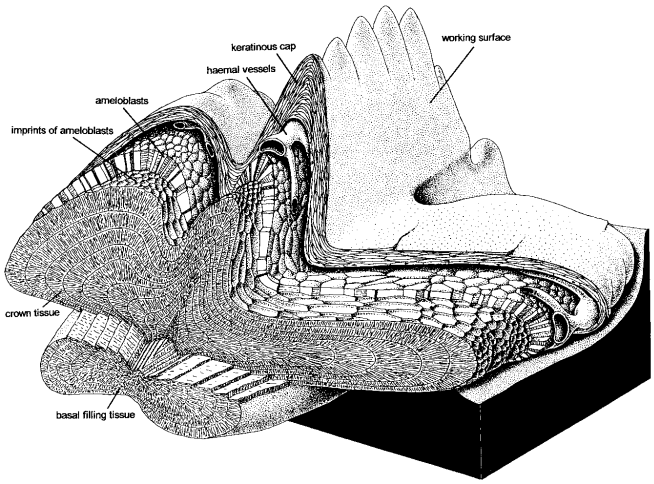


FIG. 7. Hypothetical section through the secreting organ of the conodont element, exemplified by the **sp** element of Tournaisian *Siphonodella*. Shapes of ameloblasts have been inferred from their imprints at the element surface (Fig. 4*a*), the presence of a blood lacuna above the cusp from the inferred control of secretion, the horny cup is required to provide enough strength for biting. Basal filling tissue in conodonts of this group is generally unmineralized but perhaps some structureless organic connective tissue was present in the corresponding place.

present on the tips of rounded tubercles, for instance in *Lochriea* or in *Sweetognathus*.

In elements with wide platforms that develop surface denticulation (e.g., in palmatolepidids), each minor tubercle is marked by an asterisk-shaped radial cell arrangement, commonly with a single minute cell imprint or group of imprints in the center. This suggests that the development of such denticles was preceded by a proliferation of ameloblasts. In higher vertebrates the proliferation of ameloblasts is stimulated by endogenously produced epidermal growth factor (EGF; a low molecular weight polypeptide; see Soler and Carpenter, 1994) that stimulates DNA synthesis (Hu *et al.*, 1992). Tooth cusp formation commences with the development of a cluster of nondividing epithelial cells (enamel knot), which stimulates the growth of surrounding cells by synthesis of fibroblast growth factor FGF–4 (Jernvall *et al.*, 1994), one of the family of single chain polypeptides with evolutionarily conservative structure (see Vainikka *et al.*, 1994). Both of these growth factors transduce their signals by binding to cell surface receptors exhibiting tyrosine kinase activity. The cells of the enamel knot undergo apoptosis after ceasing their regulatory action (Thesleff and Nieminen, 1996). Perhaps the minute polygons at the tip of the tubercles and denticles in conodonts correspond to cells located immediately below an enamel knot. It has to be noted, however, that during growth of the conodont crown there is no apparent increase in the number of secretory cells (von Bitter and Norby, 1994), which were inserted to accommodate the increase in area resulting from growth. One may speculate that a high secretion activity requires DNA replication processes to have ceased. Shape distribution remains constant during growth although adult elements of *Siphonodella* exhibit thicker ribs separating polygons that tend to constrict the contact area, particularly of laterally elongated cells in areas of reduced secretion rate.

A small area of surface contact does not necessarily mean that the cell itself was small. The cells putatively located immediately below the enamel knot could have been tightly arranged, vertically elongate, and columnar, like mammalian ameloblasts. This has already been suggested in connection with the inverse relationship between cell size and secretion intensity. Cells that were laterally elongate, and presumably low in profile, did not contribute much to element growth. Perhaps the cells were equally capable of calcium phosphate secretion and reduced contact area may, therefore, have enabled more intense secretion. The tip of each conodont ameloblast appears to be a functional analog of the Tomes' processes of mammalian ameloblasts, capable of secreting crystallites perpendicularly to its surface (see Masuda *et al.*, 1989).

If this was truly the case, tubercle and denticle morphogenesis was almost exclusively controlled by the supply of a morphogenetic factor, phos-

phate, and calcium. Retinol (vitamin A) may work in tooth morphogenesis as a pattern-generating factor that acts by increasing expression of EGF mRNA (see Smith and Hall, 1993, for review); transferrin is also recognized as the serum protein that is a necessary growth factor for early tooth morphogenesis in vertebrates (Partanen and Thesleff, 1989). A localized increase in the rate of secretion of calcium phosphate requires that the ameloblasts are supplied by other organs of the body. The transport direction was obviously from the element base to its tip, whatever model of the element anatomical organization is assumed. If this process proceeded exclusively by active transport through cell membranes (as is probably the case in the ganoine of *Polypterus*, which is secreted very slowly; see Sire, 1995), the normal gradient would be opposite to the observed secretion intensity. During a presumably short period (not more than a few years; Zhang *et al.*, 1997) each of the cells had to secrete an amount of calcium phosphate several times larger than its volume! It therefore appears reasonable to suggest that some blood sinuses developed above the ameloblasts at tips of denticles to supply the most active ameloblast, and that theses canals were responsible for the supply of food and the stimulation of mitosis and cell fission. Such a network develops above the ganoine epithelium in the Recent fish *Lepisosteus* (Sire, 1994). The development of a sinus preceded, according to this model, the origination of denticles. How tooth (and probably also conodont element) organogenesis is precisely executed remains largely unknown, but the homeobox gene Hox-8 (for a review of homeobox genes in primitive chordates see Holland *et al.*, 1994; Holland and Garcia-Fernandez, 1996) is definitely involved in specifying tooth shape and is expressed in the enamel knot and the epithelium (MacKenzie *et al.*, 1992).

The inferred mode of the morphogenetic control of element shapes suggests the presence of a blood sinus (or an expansion of a capillary) above each area of elevated morphology on the surface of an element. This means that each of the denticles in an element had to have been capped by a soft, fluid-filled cavity, which makes the idea of protective horny caps even more appealing. In fact, the tip of the epithelial papilla, at which the sharp myxinoid teeth (built of keratinized cells; Slavkin and Diekwisch, 1996) or the chaetognath grasping spine develops (composed of α-chitin; Bone *et al.*, 1983; Kapp, 1991), must also be a center of increased skeletal matrix secretion. A way to stimulate the supply of nutrients to exactly the same place has thus to be assumed also for the horny cap.

If this interpretation is correct, the morphology of conodont elements relates directly to morphogenesis of the blood vascular system or otherwise had a reciprocal relationship with it. This requires that dermis was inserted between the external epithelium and the ameloblastic layer, as is the case

in vertebrate teeth and in ganoid scales. The inferred presence of a horny cap above the secretory cells requires higher demands on the oxygen supply than at the surface of fish scales where epithelium is directly exposed to the sea water. It would be expected that in such conditions the distance between blood capillaries was less than 100μm, as is typical of Recent vertebrates, which corresponds quite closely with the distances between ridges in conodont elements. This is exemplified by the histogeny of elictognathid conodonts (Dzik, 1997), where new ridges were developed with uniform spacing and terminate at a level of the cusp (even if the cusp itself is completely reduced). A similar morphogenetic field controlled by an angiogenetic mechanism was probably executed at early stages of the development of the apparatus, after buds of particular elements had been established. The way in which endothelial cells form new blood capillaries possibly explains the bifurcation of processes and ridges in conodont elements (see Dzik, 1994).

Although, in some cases, the distribution of denticles on the surface of conodont element platforms seems to be almost random, this was not the case with the pattern of early denticle growth. A well-defined morphogenetic field was probably generated by a denticle formation centrum (blood lacuna?) that inhibited formation of new denticles in close proximity. The field size increased during the histogeny. This might explain some peculiarities of conodont element growth where earlier formed denticles coalesced and new individual denticles were periodically added to the growing end of an element (Fig. 8; see Dzik and Trammer, 1980).

One may speculate that new denticles started to develop only after the element process base reached a sufficient length to be free of the inhibitory effect of the morphogenetic field of preceding denticles. Only then could a new blood sinus have developed, an ameloblast below which must have begun to proliferate and develop a group of densely packed cells with small secreting areas. Local increase in the secretion of calcium phosphate would then have resulted in elevating the tip ameloblasts and in the mechanical elongation of their neighbors. As a result a rosette pattern of ameloblast distribution would have developed (Fig. 4*b*), and it would have subsequently been obliterated when a denticle developed with smooth sides and a sharply pointed tip.

Therefore, it appears that although conodont hard tissues can easily be homologized with the hard tissues of vertebrate dermal denticles, conodont elements were functionally rather unlike such denticles and teeth. The only possible homolog of the inferred mechanically functional organic cap is the horny teeth of the hagfish (Priddle, 1974). In fact, the genes responsible for amelogenesis are universally distributed among the vertebrates, including the myxinoids (Slavkin and Diekwisch, 1996), and it is reasonable

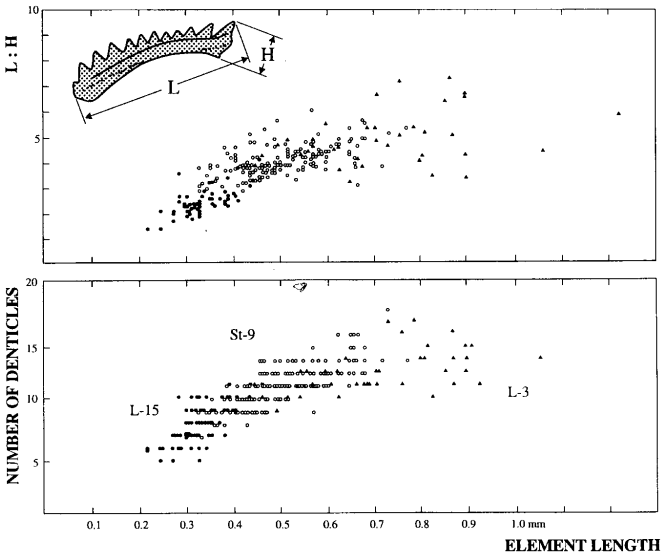


FIG. 8. Scattergrams showing the pattern of conodont element growth as exemplified by **sp** elements of the Middle Triassic *Gondolella mombergensis-G. haslachensis* lineage (from Dzik and Trammer, 1980); specimens are from samples Lesica 3 (*G. mombergensis*; the oldest one), Stare Chęciny 9 (transitional), and Lesica 15 (*G. haslachensis*); the evolution leads toward more and more juvenile morphologies dominating in samples: (a) elongation index (element length: cusp height) against the element length; note that until elements reached a certain size their growth was mostly due to an increase in elongation; (b) number of denticles plotted against element size; element growth proceeded through addition of more and more denticles at the ventral ("posterior" in conventional terminology) end until coalescing of earlier produced small denticles counterbalanced this.

to assume that their ancestors had abilities to secrete enamel. Perhaps these were *Archeognathus*-like conodonts (Dzik, 1986; see also Klapper and Bergström, 1984). The Late Carboniferous *Gilpichthys* shows some features that fit this interpretation in its dorsally attached mouth apparatus of keratinous teeth, six gill pouches, and V-shaped myomeres (Bardack and Richardson, 1977). All Recent vertebrates show rather W-shaped myomeres (Pridmore *et al.*, 1996), but it remains unclear whether this character, generally connected with increased locomotory abilities, developed only once

in the chordate phylogeny. Another fossil chordate that may be related to this lineage, although it had only a pair of conical teeth, is the Early Carboniferous *Conopiscius* (Briggs and Clarkson, 1987). Recent hagfish have developed a powerful muscular system to operate their jaws (Dawson, 1963; Yalden, 1985) that corresponds to the rather robust appearance of their teeth. Such a muscular armament was apparently missing in the typically gracile oral apparatuses of conodonts and its development must have been correlated with an increase in the thickness of their horny caps that perhaps made the internal phosphatic skeleton unnecessary.

Conodonts inhabited various marine environments, mostly pelagic but also reefal or extremely shallow water, but in their long-lasting evolution they never invaded brackish or fresh waters. This indicates that they were not equipped with osmotic regulation organs (renal tubuli) and their blood was apparently isotonic to the sea water. This places them physiologically at the same level as hagfishes, in which tubuli are virtually missing (Fels *et al.*, 1993), but below lampreys and other vertebrates.

In any case, the conodonts were true chordates. Their most obvious chordate character is the V-shaped arrangement of their myomeres (Briggs *et al.*, 1983). Such an arrangement also characterizes the relatively poorly known *Pikaia* (Conway Morris and Whittington, 1979; Whittington, 1985) and *Metaspriggina* (Simonetta and Insom, 1993) from the Middle Cambrian Burgess Shale. Little is known about the anatomy of the oral area of these animals but at least *Pikaia* shows some tentaclelike oral appendages (Conway Morris and Whittington, 1979; Whittington, 1985), which in *Nectocaris*, a possible close relative, may have been scleritized (Conway Morris, 1976*b*). The crucial role of the neural crest in the development of teeth in Recent vertebrates is used as evidence of their origin in chemosensory organs (Smith and Hall, 1990; see also Mallatt, 1996). Perhaps the oral structures in these Cambrian chordates represent such organs, which also performed a grasping function and may be homologous to the oral apparatus of conodonts. An oral apparatus was also present in *Yunnanozoon*, possibly the most primitive chordate.

RELATIONSHIPS OF *YUNNANOZOON*

Yunnanozoon is distinct from both Recent and Cambrian chordates and is presumably more primitive in its anatomical organization. It differs mainly in the dorsal disposition of its metameric blocks, or chambers, of which there were only 23 (Hou *et al.*, 1991), separated by straight vertical myocommata (Figs. 9, 10). They are thus of much simpler organization than

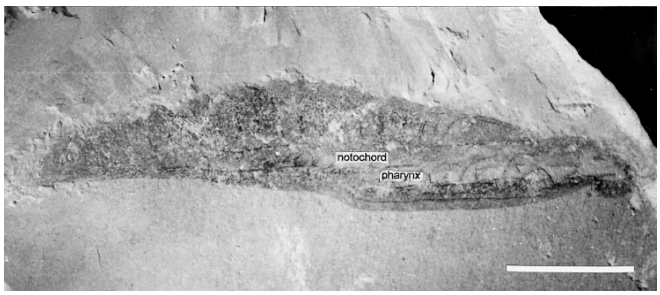


FIG. 9. *Yunnanozon lividum*; Early Cambrian Chengjiang fauna, Yunnan, China, juvenile specimen ELRC 52002, level 5; note the notochord, well delimited with dark lines, located clearly above the sediment-filled pharynx and intestine (contrary to Shu, Zhang, and Chen, 1996; Shu, Conway Morris, and Zhang, 1996), and the laterally compressed mouth apparatus of sclerites arranged in a ring (here laterally compressed). Scale bar equals 4.5 mm (from Dzik, 1995).

in Recent amphioxus. The complex topology of myotomes in higher vertebrates clearly corresponds to their locomotory abilities; there is an evolutionary tendency toward more sophisticated geometries (e.g., Hardisty and Rovainen, 1982, Fig. 11), and the most ancient chordates should be the simplest in this respect. Almost all of the known specimens of *Yunnanozoon* (more than 60) are preserved lying on one side–strongly suggesting that its

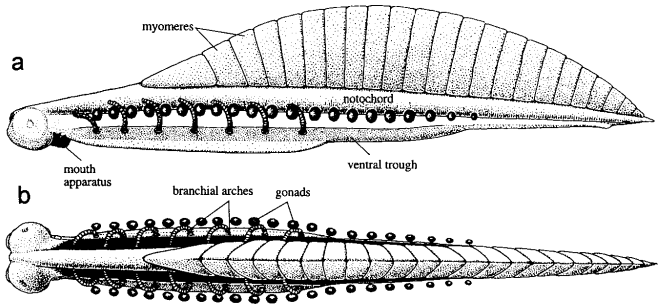


FIG. 10. *Yunnanozon lividum*; Early Cambrian Chengjiang fauna, Yunnan, China, restoration of preserved body organs (from Dzik, 1995).

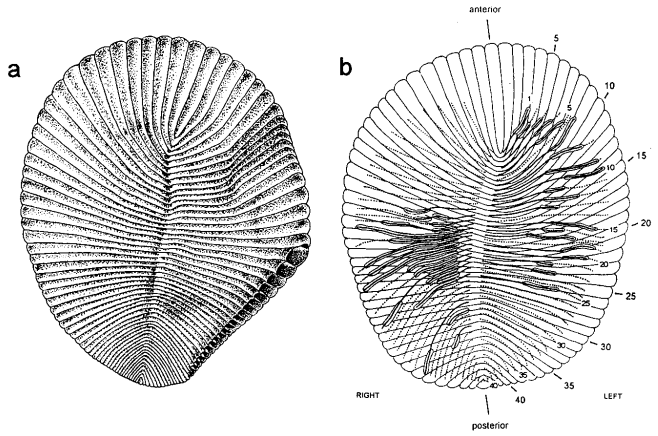


FIG. 11. Probable anatomical organization of the late Vendian *Dickinsonia costata*; (a) arrangement of dorsal chambers based on the specimen from the Ust'Pinega Formation of Russia (based on the specimen illustrated by Fedonkin, 1987); (b) diagrammatic representation of sand-filled metameric caeca of the intestine and dorsal muscular chambers as preserved in the specimen of Ediacara illustrated by Long (1995, p. 15). Boundaries of the dorsal muscular chambers and contours of sand-filled caeca are given in thin lines, the course of caeca inferred from their sand fillings shown as thick lines, their hypothetical occurrences being dotted. Caeca and muscular chambers are consecutively numbered on the left side of the specimen. The caeca diverge at the proximity of the inferred body wall (segment 7 and 8 on left side;) or merge close together (segment 5–7 on left), which means that they were not bound by any mesenteria.

body was laterally compressed. Immediately ventral to the muscular chambers there was a very large notochord that extended to the anterior end of the body (Fig. 9; Chen *et al.*, 1995; Shu *et al.*, 1996*a* claimed that the "supposed notochord appears to have gut contents," which is not the case in any of the studied specimens with this structure, clearly delimited by dark lines, preserved; see Fig. 9). Its weak staining in fossils is suggestive of its being constructed from highly vacuolarized tissue. However, whether the stiffness of the notochord was controlled by the muscular action of stacked cells (as in *Amphioxus*; see Flood, 1975; for review see Jefferies, 1986; Gee, 1996; and Ruppert, 1997) or whether the cells within the sheath were arranged irregularly and, therefore, nonmuscular (as in larval vertebrates) remains unknown. The pharynx in the anterior part of the body was rather narrow

and was bordered on both sides by seven branchial arches, each composed of minute segments, about 20 in number. The arches were convex in lateral aspect and somewhat inclined anteriorly in the dorsal region. The dorsal end of each arch was attached to the midlateral surface of the notochord and was ventrally connected to the ventral trough. The apparent external position of the arches in *Yunnanozoon* suggests that its gill rays were oriented toward the pharynx. This requires that the branchial apparatus of *Yunnanozoon* was dissimilar in organization to the branchial basket of the cephalochordates and the tunicates. Each segment of the arches may have supported its own gill blade. A transverse striation of similar density (approximately 0.15 mm) occurs on longitudinally arranged ridges in the only, incompletely preserved, nematode-like specimen, on the basis of which Shu *et al.* (1996*a*) proposed the new Chengjiang chordate *Cathaymyrus.* Its segmented body exhibits two parallel lines in the middle that means, irrespective of their interpretation, that either the animal was of a round cross-section or it is dorsoventrally compressed. Anyway, it seems premature to assume its chordate affinities or to draw any definite conclusion on the basis of such a problematic specimen—more convincing material is needed.

The pharynx of *Yunnanozoon* was large, probably expanding laterally into gill pouches between arches. The pharynx continued into a straight gut containing helically coiled fecal content. This may indicate the presence of a spiral valve (Shu *et al.*, 1996*b*), which commonly occurs in lower vertebrates. The anus was located in a position similar to that in *Branchiostoma.*

The paired oval bodies, regularly distributed along the body (perhaps corresponding in number to myomeres), resemble the gonads of *Branchiostoma* in their oval shape, high content of organic matter, and metameric distribution restricted to the proposed pharynx and were located outside the gills, immediately below the skin (Dzik, 1995). This closely resembles the organization of the branchiogenital region in the enteropneusts, and like in the enteropneusts, the gonads probably opened to the outside, instead of into the coelom, as in Recent vertebrates, where the gonads are separated from outside by a thick wall of body musculature.

Yunnanozoon also bore a ventral skeletal structure that supplemented the notochord (Dzik, 1995). It had a troughlike shape with angular ventrolateral margins, possibly equipped with additional ribs. Its preservation closely resembles that of the ventral part of the Carboniferous "conodontochordate" *Typhloesus* (Conway Morris, 1990). This ventral structure was more resistant to decay than the body integuments immediately above it. Its walls were rather rigid but elastic, as documented by the observed pattern of deformation, especially in partially decayed specimens. The

ventral trough enclosed a large space that probably contained some kind of visceral organs such as the stomach, intestine, or liver.

The head region of *Yunnanozoon* was structurally complex, although no one specimen provides details of its organization. There is a dark-stained structure that is strongly concave and of a ringlike appearance in some specimens. Others show two large lateral lobes with semicircular lateral margins, each probably with holes in the center. They were compared with eye sclerotic rings of the conodonts (Dzik, 1995). Another, ventrally oriented head structure is subdivided into several sclerotic units, probably in excess of 12 (Dzik, 1995), apparently forming together a ring reminiscent of the oral sclerotic ring of the early Silurian anaspid *Jamoytius* (Ritchie, 1968). The high degree of organization in the head of *Yunnanozoon* is unexpected; the possible presence of eyes and a feeding apparatus requires that the neural system was accordingly developed (which is consistent with the reevaluation of neontological data by Wicht and Northcutt, 1992). If the oval head structures in *Yunnanozoon* are truly eyes, this would imply the presence of the neural tube because vertebrate eyes are bulbous extensions of the brain, the photoreceptors being transformed ependymal cells of the brain cavity. Olfactory sense organs apparently preceded eyes in the phylogeny of chordates. This is suggested by their terminal location in the head. Their sensory epithelial cells produce processes to communicate with the brain, a trait definitely very ancient, reminiscent of the innervation mode of muscle cells in the nematodes and in *Amphioxus*.

The body plan of *Yunnanozoon*, although typically chordate, differs substantially from that of Recent *Branchiostoma*. The low number of gill-slits (probably six) appears to be a very old trait, and the presence of an atrium is certainly a derived feature. In having strictly transverse myosepta and robust myomeres, as well as a small number and probably direct openings of particular gill slits, *Yunnanozoon* is more primitive than any known Recent or fossil chordate. It seems, therefore, that *Yunnanozoon* belongs to a completely extinct branch of the earliest chordates, the main characteristics of which are not preserved even in the ontogeny of Recent chordates, being suppressed by later anatomical acquisitions. The embryological evidence does not seem to be matched by paleontological data deeper than to the Middle Cambrian *Pikaia* and *Metaspriggina*, except for the earliest embryonic stages, when the myocoel develops as metamerically arranged vesicles above the long notochord, unlike succeeding somites, and the first is longitudinally elongated. The somites merge and enclose the neural tube in a way similar to the formation of the collar region in enteropneusts.

The only parts of the enteropneust body that may be comparable to the muscular chambers of *Yunnanozoon* is the proboscis and collar (see Benito and Pardos, 1997). There is some resemblance in shape between the

first muscular block in *Yunnanozoon* and the proboscis, which probably developed from fused paired cavities. The proboscis coelom in the enteropneusts constitutes an unpaired cavity, but the collar coelom develops by invagination from two lateral pouches and may be separated in two parts by both dorsal and ventral mesenteria. The second pair of muscular chambers in *Yunnanozoon* may be a homolog of the enteropneust collar. The collar neural cord of some enteropneusts has a continuous lumen that opens to the exterior at each end by neuropores. This further supports the possible homology with the muscular chambers of *Yunnanozoon*. Their homology with myomeres of later chordates implies that the nerve cord was located in between them. There is no evidence that enteropneusts were already effective burrowers in the Cambrian; the possibility remains that their proboscis and collar developed from structures more similar to the myomeres of *Yunnanozoon*, present in the common ancestor of both organisms.

The large size of the notochord and the strictly dorsal position of the muscular blocks are difficult to reconcile with presently accepted views of the early phylogeny of the chordates. Yet, there is another Cambrian organism, *Odontogriphus* from the Burgess Shale (Conway Morris, 1976*a*), that shows a series of metameric transverse units resembling that in *Yunnanozoon* and possibly dorsal in respect to the straight intestine. There is no evidence of a notochord but it had a mouth apparatus that was armed with denticles resembling westergaardodinid conodont elements (paraconodonts).

PARACONODONTS AND THE EVOLUTIONARY ORIGIN OF THE CONODONT APPARATUS

The elements of the oral apparatus of the westergaardodinid conodonts (paraconodonts; Bengtson, 1976) differ both structurally and functionally from typical conodont elements, as their epithelial cover may have disappeared apically at later histogenetic stages. *Odontogriphus* from the Middle Cambrian Burgess Shale (Conway Morris, 1976*a*) is the only anatomically preserved fossil possibly representing a westergaardodinid. The only known specimen is dorsoventrally compressed, probably corresponding to the original compression of the body (Conway Morris, 1976*a*). Body segments are very short, with clear, strictly transverse boundaries. Although much wider and dorsoventrally compressed, they may be homologous to the muscular chambers of *Yunnanozoon*. Oval dark structures that border the segments in *Odontogriphus* resemble the gonads in *Yun-*

nanozoon. Lateral unsegmented fields may correspond to lateral fins or to the ventral trough of *Yunnanozoon*. The head region of *Odontogriphus* was not segmented and was equipped with a pair of presumably sensory organs ("palps") of unknown function and homology. The intestine is straight and runs along the midline, perhaps under the segments. Earlier suggested chordate affinities of *Odontogriphus* (Dzik, 1976, 1993) may thus find some support in the anatomy of *Yunnanozoon*. The dorsoventrally compressed oval body of this Middle Cambrian organism may be a trait connecting it with some fossils even older and more primitive than *Yunnanozoon*. The mouth of *Odontogriphus* was armed with a bilobate apparatus, apparently ventral in position. Elements of this apparatus are mineralogically altered, making affinities with the westergaardodinids uncertain, but their external shapes and organization of the apparatus fit expectations.

The internal structure of westergaardodinid elements shows that they originated as organic rods within the "dental papilla" of a developing conodont element (Müller and Nogami, 1971; Szaniawski, 1971) with distinct episodes of organic matrix and mineral secretion. Later in histogeny, secretion was restricted to the base of the elements and as a result, a conical structure gradually developed basally (Müller and Nogami, 1971; Szaniawski, 1971). Secretion ceased at the apex of the element and it may have been exposed at this stage. The growth of the element continued to be stadial (possibly in connection with a circadian rhythm of feeding) with concentric wrinkles visible on both external and internal surfaces of the base. In some genera (*Problematoconites*) a special kind of tissue developed later in histogeny within the basal cavity, which may extend to the outside (Fig. 2*a*; Andres, 1988). This tissue is perforated by pores and its surface within the basal cavity is irregular, with wrinkles, ribs, and, perforations. It is thus very different from the regular element tissue of the paraconodonts. Only some elements in samples show the presence of this kind of tissue, others are of typically paraconodont organization (structurally not differentiated type of Andres, 1988).

The typical panderodontid or protopanderodontid conodonts (euconodonts of Bengtson, 1976) co-occurred with the westergaardodinids in the Late Cambrian and they are almost certainly phylogenetically related. The most primitive of the euconodonts (*Proconodontus*; Andres, 1988; Fig. 2*b*, this chapter) have a basal perforated tissue, structurally indistinguishable from that of the paraconodont *Problematoconites*. Szaniawski and Bengtson (1993: Fig. 6: 2), in their schematic drawing of the *Proconodontus* element section, proposed that the basal filling tissue had the same internal structure as the typical westergaardodinid element. This is used to support their hypothesis that the crown tissue of euconodonts was a new

acquisition and that the basal filling tissue of euconodonts was homologous with the whole paraconodont element. However, I have not been able to find any convincing evidence of continuity of growth increments between the basal filling tissue and the crown tissue in Andres' (1988) data. To the contrary, the boundary between the basal filling and the crown tissue appears distinct both internally (see Andres, 1988: pl. 10–13) and at the surface of elements (e.g., Chen and Gong, 1986: pl. 23:, 16, 25: 6, 32:, 15), in *Problematoconites*, in *Proconodontus*, and in later conodonts. In all well-known conodont elements, the basal filling tissue and the crown tissue are structurally distinct. The boundary between them is clear-cut and serrate in cross-section. This closely resembles relationships between ganoine and underlying ectomesenchymal tissues in actinopterygian fish scales. Usually, the conodont basal filling tissue was not mineralized and is missing in fossil specimens.

The enigmatic sclerites of *Fomitchella* are composed of a fully mineralized crown tissue that is of coniform morphology from the beginning of its histogeny. Its appearance in the earliest Cambrian (Bengtson, 1983) makes the primitive nature of the paraconodont element organization somewhat uncertain. The possibility remains that the early Cambrian ancestors of the westergaardodinids could have had elements of euconodont organization, thus identical with *Fomitchella*. A secondarily delayed mineralization of the organic matrix of the crown tissue, so common among higher chordates, could have resulted in developing the peculiar paraconodont histogeny.

There are thus at least three possible scenarios for the evolutionary transitions between paraconodonts and euconodonts.

1. The basal filling tissue of the euconodonts originated by developing a clear-cut difference between the secretive properties of epithelial cells covering the paraconodont element from outside and those within the basal cavity (Bengtson, 1976).
2. The inner part of the paraconodont element developed a porosity and transformed into the basal filling tissue and a secretion of strongly mineralized crown tissue was subsequently initiated from outside, whereas the external secretion of the paraconodont element tissue ceased completely (Szaniawski and Bengtson, 1993).
3. The crown tissue of the euconodont is homologous with the whole paraconodont, being different mostly in timing of calcification in the histogeny, whereas the basal filling tissue was generally not mineralized in the conodonts, and if mineralized then it was generally late in histogeny or even diagenetically (Dzik, 1976, 1986). The

periodicity in secretion of the paraconodont tissue may have resulted from sequential secretion of an organic matrix and its calcification in a mode similar to the ganoine of Recent fishes.

The homology of the paraconodont element tissue with the ectomesenchymally secreted basal filling tissue of typical conodonts, as proposed by Bengtson (1976), implies that the initial paraconodont rods were secreted within a sac built of condensed mesenchyme. This deserves some consideration. In Recent vertebrate teeth a reciprocal signaling between epithelial and mesenchymal tissues controls the morphogenesis (Thesleff *et al.*, 1995). Odontoblasts start their secretive activity before ameloblasts and this may correspond in a way to the proposedly earlier evolutionary origin of the ectomesenchymal mineral tissue in the conodont lineage. Both the stadial mode of secretion and mineralization of the paraconodont element and its morphology are very remote to all known kinds of ectomesenchymal teeth or scale tissues. This, as well as generally weak and late mineralization of the undoubtedly ectomesenchymal basal filling tissue, makes this interpretation difficult to accept. Another interpretation is more appealing to me. The early histogeny of the paraconodont element may be a modified recapitulation of its evolutionary origin. The organic denticle developing inside an epithelial pocket and later puncturing it may have originated from a hook deeply imbedded within the epithelium, in a way similar to nemertinean stylets. This may explain why such epithelial pockets developed in chordates. Presumably both in histogeny and evolution they subsequently enveloped the ectomesenchymal dental papilla, in effect developing a conical shape. The ability to secrete phosphatic tissues seems to be very ancient in the Metazoa. In the lingulide brachiopods, which are "living fossils" presumably preserving now the physiologic mechanisms typical of early Paleozoic organisms, the secretive cells are in direct contact with the mineralized calcium phosphatic tissue (Williams *et al.*, 1994), a relationship analogous to that in the conodont crown and vertebrate enamel. According to Williams and colleagues (1994) apatite granules are exocytosed in brachiopods.

This scenario of the origin of the conodont apparatus also has implications for the ancestry of the chordates. If one accepts the (undoubtedly controversial) idea that *Yunnanozoon* and *Odontogriphus* are the most primitive chordates, some expectations can be also formulated regarding the anatomy of the common ancestor of these organisms. It should bear metamerically arranged muscular chambers with internal cavities separated from each other by transverse myosepta. A cylindrical intestine, with several branchial slits or pouches in the anterior part, should run below this metameric vesicular unit. The notochord may have been an evolutionary

novelty connected with the chordate style of locomotion (by lateral undulations of the body) not necessarily present in *Odontogriphus* and its common ancestor with *Yunnanozoon*. The fossil organism that may appear crucial in these considerations is the Vendian *Dickinsonia*, the only known animal of this geological age with dorsally located metameric muscular blocks and intestinal caeca that could have given rise to both hepatic sacculation of the enteropneusts and branchial pouches.

DICKINSONIA AND THE ANCESTRY OF CHORDATES

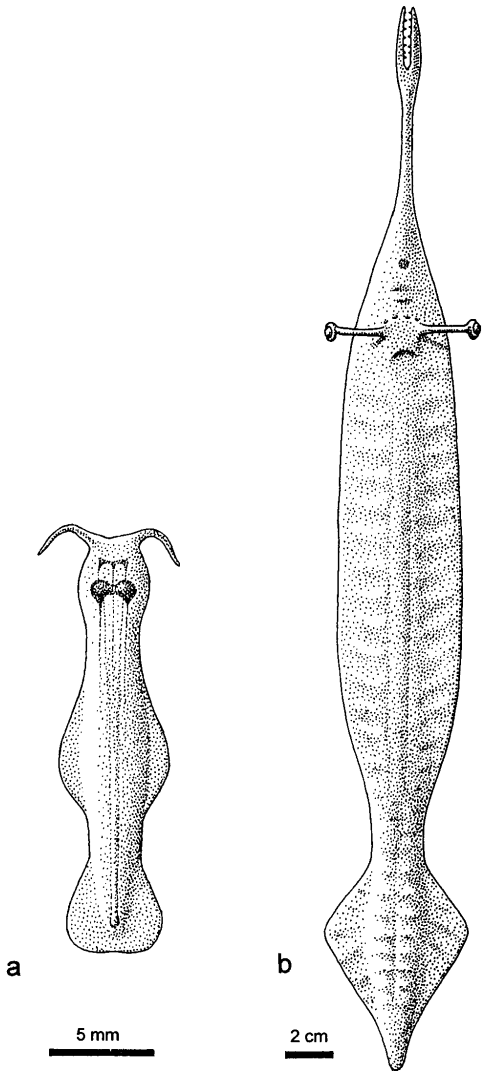
The internal anatomy of *Dickinsonia* remains a matter of dispute and countless interpretations of its relationships have already been offered. Nevertheless, despite its preservation on the bedding planes of coarse sandstone, there is surprisingly rich evidence to interpret. Thus, Seilacher (1989) has convincingly shown that particular "segments" of the body were actually chambers separated from each other by walls and filled with a liquid under pressure during life. In the "quilted pneu structure" of *Dickinsonia* there is an anterior medially elongated unpaired unit. At early ontogenetic stages with a low number of muscular units the anteriormost one was much more elongated and rounded triangular in outline (Runnegar, 1982). Behind, it is followed by transversely elongated modules that seem to be at least subdivided medially by a kind of mesenterium in the center of the body (according to Gehling, 1991, only from one side). The *Dickinsonia* body increased in size by adding new metameric units at its posterior end. Wade (1972) and Runnegar (1980) have pointed out concentric wrinkles and changes in diameter of the body in some specimens that can be explained as a muscular contraction (desiccation being a less likely alternative), with muscle fibers running longitudinally (parallel to the body margin: Runnegar, 1982: Fig. 1e). The ventral and dorsal sides of the quilted structure of *Dickinsonia* were apparently of similar morphology (but see Gehling, 1991); so it can hardly be compared with any complete known organism. Internal structures other than the dorsal metameric quilt are preserved only in a few specimens of *Dickinsonia* among several hundreds collected (Wade, 1972, p. 175). However, some specimens show a presence of sediment-filled cylindrical gut under the quilted structure (Runnegar 1982: Fig. 1c; Jenkins, 1985, 1992: Fig. 14). This is the relationship between muscular blocks and the alimentary tract as in *Yunnanozoon* and, proposedly, in *Odontogriphus*, the main difference being that in adult *Dickinsonia* the body was very strongly dorsoventrally flattened.

If the dorsal segmented quilt of *Dickinsonia* is truly homologous to the muscular blocks of *Yunnanozoon* (Dzik, 1995), the polarity of relationship between the hemichordates and the earliest chordates should be the reverse to that generally assumed. In this case, the origin of branchial slits would be phylogenetically later than the appearance of dorsal muscular coelomic pouches. The enteropneusts and pterobranchs would appear to be derived successors of a *Yunnanozoon*-like ancestor of both hemichordates and chordates, although they undoubtedly preserved several very ancient traits in their anatomy, for instance an organization of cilia closely resembling *Xenoturbella* (Benito and Pardos, 1997, p. 24), the most primitive Recent flatworm. This does not significantly change the pattern of relationships and is not contradicted by other kinds of phylogenetic evidence. Sequence data for 18S rRNA suggests that the pterobranchs are closely related to both the enteropneusts and the echinoderms, being not far from the tunicates, whereas the acraniates cluster together with the vertebrates (Turbeville *et al.*, 1994; Halanych, 1995; the proximity of lampreys to myxinoids is also supported—Stock and Whitt, 1992). This is consistent with the proposed derivation of *Amphioxus* (and tunicates) from anatomically rather advanced extinct chordates (good swimmers—with V-shaped myomeres) by secondary anatomical simplification and of enteropneusts from *Yunnanozoon*-like earliest chordates (Dzik, 1995; a somewhat less radical interpretation is shown on Fig. 13). In fact, Halanych (1995, p. 72) suggested that "ciliated gill slits and the dorsal hollow nerve chord are plesiomorphic features of the Deuterostomia." This would indicate that the stomochord of the enteropneusts is a rudiment of the earlier functional (in *Yunnanozoon*) notochord and the simplicity of the nervous system in the pterobranchs is a neotenous feature, related to their small adult size (Dilly, 1975, p. 11). Obviously, all those extinct animals were much more primitive than any Recent craniates, particularly in having only one *Hox* gene cluster, as in *Amphioxus* (see Garcia-Fernàndez and Holland, 1994).

In any case, to explain the origin of the diagnostic anatomical features of *Odontogriphus*, *Yunnanozoon*, and conodonts as interpreted herein one has to invent a hypothetical organism similar to *Dickinsonia*. Its proposed anatomical organization could easily have produced branchial pores by connecting caeca with the body wall and the segmented dorsal quilt may have been transformed into myomeres. The peculiar mode of innervation of muscular blocks in the most primitive chordates by processes of muscle cells, inherited after ancestral worms and preserved in *Amphioxus*, requires that the main neural cord is in the proximity of the locomotory muscles. The original dorsal position of these blocks might have been the main reason for its dorsal position in the chordates.

Much more difficult to answer is the question of the origin of body organization in *Dickinsonia* and its relationship to other phyla. Its anatomy is reminiscent of some features of the nemerteans, particularly its metameric caeca that lack bounding mesenteria (Glaessner and Wade, 1966: pl. 101: 4; Long, 1995: p. 15; here Fig. 11). The presence of metameric gonads in *Odontogriphus* and in *Yunnanozoon* (Chen *et al.*, 1995; Shu, Zhang, and Chen, 1996) is a trait shared not only with the nemerteans but also with the enteropneusts, which makes it a likely primitive (plesiomorphic) feature of these groups. In *Yunnanozoon*, each gonad probably opened separately at the body surface and between branchial slits that may have developed from serial intestinal caeca (if so, this is exactly as in the nemerteans). Some enteropneusts have serial intestinal caeca (hepatic sacculation) of digestive function (Benito and Pardos, 1997). Jenkins (1992, p. 163, Fig. 13) restored a dorsally located longitudinal intestinal diverticulum in *Dickinsonia*, which may correspond to the notochord or the rhynchocoel. An oral apparatus had no chance of having been preserved in the Ediacaran specimens of *Dickinsonia*, but in Recent nemerteans there are sclerites with some resemblance to paraconodonts (the group to which *Odontogriphus* possibly belongs). The proboscis stylets of the nemerteans originate in epithelium (inside enlarged cells) and are of a shape similar to that of the earliest stages in development of the westergaardodinid elements, being composed of a central organic matrix surrounded by an inorganic cortex containing calcium phosphate (Stricker, 1982). It is generally accepted that the presence of numerous stylets is primitive for the Nemertini (Gibson, 1988; Crandall, 1993). The nemertean features presumably common to the *Dickinsonia*, *Odontogriphus*, and *Yunnanozoon* anatomies recall the old idea of relationships between the Nemertini and Chordata (Jensen, 1960, 1988; E. N. Willmer, 1974, 1975). Some similarities in the excretory and reproductive systems of the nemerteans and chordates have already been pointed out by E. N. Willmer (1974). Perhaps these three Precambrian–Cambrian organisms represent a link connecting these two phyla. The evidence is obviously very weak, as usual in paleontology, but it calls for more attention to be paid to this hypothesis, now considered rather unorthodox. An additional argument in its favor may be the inability of the nemertineans to secrete chitin, shared by them with sipunculans, hemichordates, echinoderms, and chordates (P. Willmer, 1990, p. 80). Molecular phylogenies, however, place nemertineans far from the chordates (Turbeville *et al.*, 1992; Winnepenninckx *et al.*, 1995).

If the Middle Cambrian *Amiskwia* (Fig. 12*a*) belongs to the Pelagonemertini (Conway Morris, 1977, did not find any evidence for a retractable proboscis), they were highly advanced anatomically already in the Cambrian. Recent pelagic nemerteans show several primitive features in their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anatomical organization (Crandall, 1993) and may be a relic group. The enigmatic Carboniferous *Tullimonstrum* (despite various interpretations of its affinities; see e.g., Beall, 1991, and Bousfield, 1995), with its internal metameric body, stalked eyes, and grasping apparatus at the end of its long proboscis (Fig. 12*b*) shows a combination of characters that may express a remote relationship with a nemertean ancestor of the same stock. Most interestingly, the proboscis of *Tullimonstrum* was not retractable but, instead, it was bilobed and armed with scleritized, possibly mineralized denticles (Foster, 1979). The rhynchocoel in which the nemertean proboscis is retracted bears some resemblance to the anterior medial chamber of the quilt of *Dickinsonia* and to the enteropneust proboscis. The origin of the retractable proboscis apparatus could have been preceded by an extension of the anterior segment of the body together with the perioral apparatus (the mouth opening keeping its original position) and *Tullimonstrum* may have preserved to the Carboniferous some features of such a transitional stage. The origin of nemerteans from anatomically more complex coelomates has been already forwarded by Turbeville and Ruprecht (1985).

Possible nemertean ancestry of the chordates is in conflict not only with the traditional view that the anatomical organization of hemichordates, highly ecologically specialized in two opposite directions (tentacle filtration in clonal pterobranchs and mud burrowing in enteropneusts), represents a connecting link between the invertebrates and the chordates. It is also in apparent conflict with the idea that conodont elements originated from grasping spines of the Cambrian chaetognaths ("protoconodonts").

THE PROBLEM OF PROTOCONODONTS

Although the pocket theory of conodont elements functioning is apparently falsified by the microornamental features of the conodont element surface, the idea of protoconodont → paraconodont → euconodont

FIG. 12. Problematic Paleozoic animals of possible nemertean affinities: (a) *Amiskwia sagittiformis*, from the Middle Cambrian Burgess Shale of British Columbia (after Conway Morris 1977); (b) *Tullimonstrum gregarium* from the Late Carboniferous Mazon Creek fauna of Illinois (based on data of Foster, 1979, and Beall, 1991).

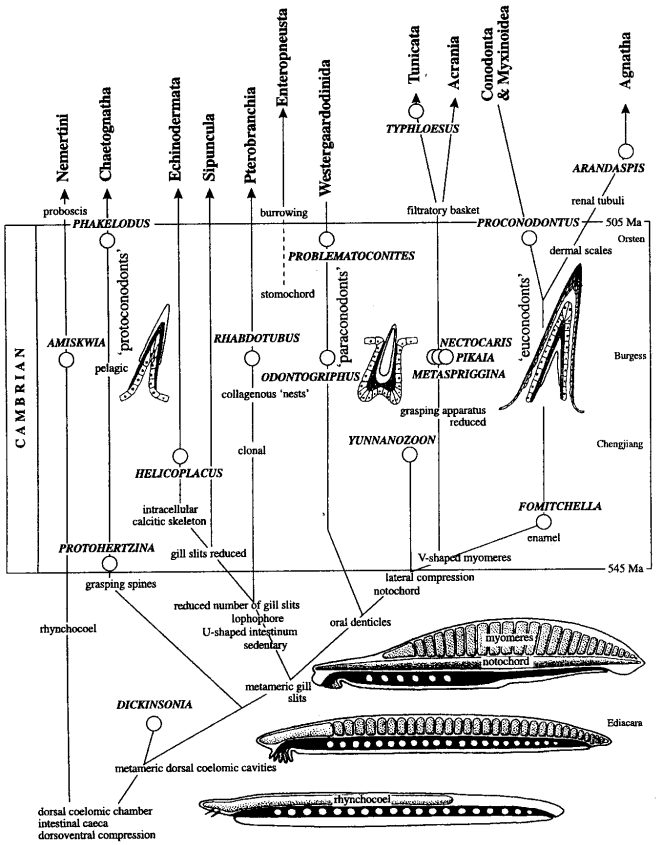

FIG. 13. The most parsimonious "chronophyletic" (see Dzik, 1991*b* for a discussion of methodology) scenario of evolutionary relationships of the chaetognaths ("protoconodonts") and the conodonts ("paraconodonts" and "euconodonts"; diagrammatic sections show their mode of secretion) in respect to other early metazoans. The alternative would be that the grasping apparatuses of the chaetognaths and conodonts are homologous (Bengtson, 1976), which implies that the anatomy of Recent chaetognaths is secondarily simplified (Christofferson and Araújo-de-Almeida, 1994) and they restored ability to secrete chitin; the tail of the probable paraconodont *Odontogriphus* should then be laterally compressed (the specimen is too poorly known to exclude or to prove this) to make it anatomically closer to the conodonts. Another possibility is that the chaetognaths, with their externally secreted chitinous grasping spines, originated from ancestors at the nemertean grade before they lost chitin synthetase and developed internally secreted stylets.

relationship (Bengtson, 1976) does not necessarily need to be connected with the theory and requires a separate discussion. The earlier step in this speculative evolutionary transition is confronted in the following paragraphs with the available evidence and inference based on it.

The protoconodonts are narrowly conical sclerites, known to form grasping apparatuses virtually indistinguishable from those of the Recent chaetognaths and with basically the same internal structure (Szaniawski, 1982). Like the chaetognath grasping spines (built of α-chitin; Kapp, 1991), they were secreted at the surface of long conical soft tissue appendages. The idea of the chaetognath nature of protoconodonts is the most parsimonious solution of the problem of their affinities and as such should be accepted, although it has to wait for corroboration by anatomical evidence. No fossil documents an association of the protoconodonts with any soft parts. It remains possible, even if the protoconodont animals were truly ancestors of the Chaetognatha, that they were anatomically very different from their living relatives. This is suggested by the occurrences of the oldest known protoconodonts of the earliest Cambrian in relatively shallow-water sediments, unlike their Late Cambrian successors, which were generally confined to pelagic black shales and limestones.

The paraconodonts (elements of the westergaardodinid conodonts) are widely conical in shape and their internal structure is basically different from that of the protoconodonts. However profound are the structural differences between the proto-, the para-, and the euconodonts, there is nothing in their structure that would make evolutionary connections between them impossible. The real problem is with the anatomy of their bearers. The most reasonable interpretation of the protoconodonts as chaetognath grasping spines implies that the Cambrian *Protohertzina* or *Phakelodus* were unsegmented animals with bodies stiffened by coelomic fluid pressure and with lateral fins propelling them by dorsoventral undulations of the tail. The mouth is terminal in chaetognaths, the anus being located ventrally, with a tail behind it. In contrast, the conodonts were true chordates with a laterally compressed body stiffened by the internally located notochord and propelled by lateral waving of the tail. Transversely straight segments and a dorsoventrally flattened body characterize the possible westergaardodinid *Odontogriphus* (Conway Morris, 1976*a*). It appears thus that grouping together proto-, para-, and euconodonts, based on structural similarities of their oral sclerites would encompass anatomies of at least two, if not three, phyla. This is, again, not impossible but any hypothesis of homology between these skeletal elements would require that the common ancestor of all these organisms possessed a grasping oral apparatus (Fig. 13).

The inferred presence of an organic cap above the mineralized portion of the conodont element invokes a question of whether the chaetognath

organic grasping tissue is not homologous with this protective structure. The crown tissue of the conodont element would then develop secondarily within the invaginated internal epidermis of the papilla. Such a model does not encompass an explanation of the origin of the ectodermal enamel organ. This is more easily resolved if embedding of an ectodermally derived denticle (stylet) and its subsequent overgrowth by the epithelium is assumed. Any direct relationship between the chaetognaths and the chordates requires that the low number of coelomic compartments in the Chaetognatha was a result of secondary reduction in the number of originally metameric chambers (Fig. 13). In fact, Christoffersen and Araujo-de-Almeida (1994) have proposed that the chaetognaths secondarily lost the gill slits, the notochord, and the endostyle although they do not provide any evidence for this and their ideas are apparently influenced by Bengtson's (1983) interpretation of conodont–protoconodont relationships. Some features of chaetognath anatomy may perhaps be explained in this way, for instance the inverted photoreceptor cells in eyes of most chaetognaths and a multilayered sheath reminiscent of vertebrate myelin, which covers their cerebral ganglion (Bone and Goto, 1991; but nerve fibers in *Myxine* and other agnathans are unmyelinated, with only some overlap of Schwann cells sheath, Peters, 1963). The transverse muscle cells that occur in several chaetognaths, regarded as the more primitive, penetrate the basement membrane to reach nerve terminals in the epidermis (Bone and Duvert, 1991). This is reminiscent of the situation in *Amphioxus* and in nematodes, where muscle cells produce processes that terminate at nerve cords (Wright, 1991). In fact, according to Nielsen and Colleagues (1996, p. 401), the early embryogeny of the chaetognaths is typical of aschelminthes and the chitinous oral teeth closely resemble the mastax of the rotifers. This would make the chaetognaths an early offshoot of the priapulids but does not contradict a distant relationship to the chordates (although molecular data suggest that the chaetognaths are distant from the deuterostome; Wada and Satoh, 1994). It has to be stressed, however, that there is a contradiction between the possible homology of the organic cap of the conodont elements with the teeth of *Myxine* and a suggestion of homology with the grasping spines of the chaetognaths.

CONCLUSIONS

There are several anatomical traits shared by the most primitive Early Cambrian chordates *Yunnanozoon*, the Middle Cambrian probable westergaardodinid *Odontogriphus*, and the Vendian problematicum *Dickinso-*

nia, and their body plans resemble that of the nemerteans. The rhynchocoel of the nemerteans and (at least) the most anterior dorsal chamber of *Dickinsonia* may appear thus homologous, which is consistent with the idea of its homology with the notochord and myocoel of the chordates. The phosphatic elements of the westergaardodinid paraconodont apparatuses seem to represent a stage in the development of mineral skeleton transitional between nemertean stylets and conodont elements. *Odontogriphus* had an oral grasping apparatus composed of such mineralized, probably phosphatic elements. Some kind of oral apparatus of unknown internal structure also occurred in *Yunnanozoon*, which probably also bore complex sensory head organs. *Dickinsonia*, *Odontogriphus*, *Yunnanozoon*, and *Pikaia* may thus represent a developmental series, from muscular dorsal chambers to the organization of myomeres typical for all later chordates (Fig. 13). In this respect even cephalochordates and tunicates are anatomically highly derived. *Amphioxus* and the tunicates share the presence of the filtratory basket surrounded by the atrium, which indicates that they are closely related and evolutionarily late. The earliest, more or less reliable fossil evidence of this structure is in the Carboniferous *Typhloesus*. It shares with Recent salps a very characteristic concentration of the alimentary tract in a globular body (although bilobed in *Typhloesus*). Notably, the latest of the anaspid agnathans with weakly mineralized body covers, the Late Devonian *Legendrolepis*, shows a very elaborate gill apparatus (Arsenault and Janvier, 1991), suggestive of filtratory adaptations. The time order in appearance of these anatomies is consistent with the idea that salps and *Amphioxus* derived from chordates related to the anaspids. This implies a more complex anatomy of the common ancestor of the tunicate and cephalochordate evolutionary branches than is usually assumed, but it is consistent with neontological data by Lacalli (1996) and Williams and Holland (1996).

The mode of secretion of the conodont crown tissue, with its early mineralization, and distribution of shapes of the secretory cells suggest that localized intensity of secretion of calcium phosphate, instead of cell migration, was the main factor controlling the morphology of elements. Calcium phosphate secretion was extremely high at denticle tips, which requires (as phosphate and calcium ion transport took place above the surface of the element) a relatively thick cover of soft tissue to fulfill supply needs. In typical conodonts, this tissue was probably protected on the outside with horny caps. The primitive panderodontid conodonts had a grasping apparatus composed of at least seven element pairs morphologically similar to that of the Cambrian and Recent chaetognaths. Any homology of their crown tissue or the organic cap, with the grasping spines of the chaetognaths (protoconodonts), is unlikely. The typical

organization of the conodont apparatus originated in the early Ordovician within the clade of coniform Protopanderodontida. Their apparatuses were composed of a pair of incisorlike elements in front, a set of four pairs of relatively gracile elements connected into a single unit by one posteriorly located symmetrical element, and two pairs of robust elements hidden within the throat. This apparatus architecture did not undergo any basic modifications in the ozarkodinid and prioniodontid clades. In the most advanced prioniodontids (e.g., *Promissum*) the apparatus was probably evertible, with the throat being sinuously folded at the resting position. Elements of some locations were doubled in these conodonts. A homology between the organic caps of elements of advanced conodonts and horny jaws of Recent hagfish is likely, which would make the Myxinoidea close relatives of the conodonts or even members of their class.

The homology between the crown and basal filling tissues of the conodonts and the enamel and dentine of vertebrates, respectively, implies that the developmental mechanisms that arose at the origin of the conodonts were subsequently used by the agnathans to build up their protective dermal scales.

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