Growth, function, and the conodont fossil record

Philip C. J. Donoghue*†
School of Earth Sciences, University of Birmingham, Birmingham B15 2TT, UK
Mark A. Purnell†
Department of Geology, University of Leicester, Leicester LE1 7RH, UK

ABSTRACT

Interpretation of the fossil record of conodonts hinges on whether conodont elements were retained through the life of the animal or were periodically shed and replaced. Many quantitative analyses of conodont paleoecology and statistical techniques in conodont taxonomy, for example, rely on an assumed correspondence between numbers of elements and numbers of animals, but the possibility that conodonts shed their elements may undermine this assumption. As with many aspects of conodont paleobiology, hypotheses of shedding versus retention of elements have been difficult to test. Here, we describe recurrent patterns of damage resulting from element function in vivo which indicate that internal discontinuities within an element represent periods of use followed by further growth. The cyclical alternation of phases of growth and function provides compelling evidence that elements were retained through the life of the animal.

INTRODUCTION

The importance of the conodont fossil record as a biostratigraphic database is well known, but it is also gaining increasing paleobiological significance as the record of the evolutionary and paleoecological history of a diverse and long-lived clade of extinct jawless vertebrates. The vertebrate affinity of conodonts is still viewed by some as controversial because it challenges established hypotheses for the origin of the vertebrate skeleton (Smith et al., 1996). The evidence from conodonts agrees broadly with earlier models which contend that a mineralized dermal skeleton preceded a mineralized endoskeleton (e.g., Patterson, 1977). However, the data suggest that the primitive patterning unit of the dermal skeleton first evolved not as external armor, but in the mouth or pharynx of conodonts or the common ancestor of conodonts and other vertebrates (cf. Smith et al., 1996).

Despite recent advances, we have barely begun to understand many aspects of conodont paleobiology, such as how the skeleton grew (Donoghue, 1998) and functioned (Purnell, 1995), or even whether conodont feeding elements were permanently retained or periodically shed and replaced through the life of the animal. This uncertainty has significant ramifications beyond the study of conodont paleobiology as the question of the permanence of the dentition is fundamental to interpretation of the conodont fossil record. Paleoecological and paleobiogeographic analyses incorporating abundance data (e.g., Ji and Barnes, 1994, and examples in Clark, 1984) implicitly assume that numbers of elements can be taken to indicate numbers of animals. However, if elements were periodically shed and replaced (Carls, 1977; Krejsa et al., 1990), this assumption may be undermined as different taxa may have shed elements at different rates. Similarly, if different parts of the apparatus of an individual conodont were shed at different rates, then statistical approaches to reconstructing multielement conodont taxa (see, e.g., Sweet, 1988, for a review) will be flawed.

The view that conodont elements were permanent was clearly articulated by Hass (1941, p. 80) who considered each element to represent "the last stage of the ontogeny that was reached before the death of the conodont-bearing animal." However, Gross (1954) suggested that conodonts might have shed their elements, repeatedly forming new ones of increasing size during ontogeny. Carls (1977) later adopted this hypothesis to explain the difference between ratios of element types in complete apparatuses preserved as natural assemblages and those observed in collections of discrete

elements. These differences, however, can probably be explained by hydrodynamic sorting of elements (Broadhead et al., 1990). More recently, Krejsa et al. (1990) proposed that the conodont crown and basal body are, respectively, homologous to the functional keratin cap of the deciduous myxinoid "tooth" and the developing replacement tooth beneath it. However, this hypothesis is incompatible with conodont element growth (Donoghue, 1998).

Natural assemblages of conodont apparatuses provide a potential test of hypotheses of shedding, as replacement elements that developed before their functional counterparts were shed should be recognizable. No such assemblages have been recorded, although some are found with less than a complete set of 15 elements. There is also no evidence for differential growth of elements in natural assemblages (Purnell, 1993). Nevertheless, these data do not rule out the possibility that conodonts shed the entire apparatus before beginning to grow replacement elements. In this case, testing hypotheses of permanent versus deciduous elements becomes difficult. It may not be possible to find direct evidence that conodont elements were not shed, but evidence for retention of elements with multiple phases of growth would make shedding unlikely.

## GROWTH DISCONTINUITIES AND HYPOTHESIS TESTING

It is conventionally accepted that conodonts grew their "teeth" in a manner distinct from other vertebrates (Gross, 1954). This hypothesis is based on the occurrence of internal discontinuities within the crown tissue of the elements (Figs. 1, 2). These internal discontinuities have been interpreted as the result of accidental damage followed by repair (Hass, 1941), episodes of resorption (Müller and Nogami, 1971), or abnormal deformation during growth (Rhodes, 1954, p. 431). They have also tentatively been interpreted as evidence of alternating phases of growth and function (Purnell, 1995; cf. Jeppsson, 1979). Each of these hypotheses allows us to make testable predictions concerning the nature of the internal discontinuities.

Rhodes's (1954) hypothesis can be rejected because it is unlikely that the elements could be damaged during growth without the mineral-secreting organ also being damaged. Such an injury would produce abnormal growth of crown tissue subsequent to the event that caused the discontinuity; no such pathologies have been described in the literature or observed by us.

If the discontinuities represent episodes of resorption, they should have irregular pitted surfaces similar to those that characterize resorption in other hard tissues. Vertebrate teeth, for example, exhibit pits ranging in diameter from ~10 to >100 μm (Jones et al., 1986; Boyde and Jones, 1987). Furthermore, discontinuities in elements from different individuals would not occur

*Present address: Department of Geology, University of Leicester, Leicester LE1 7RH, UK.
†E-mail: pcjd2@le.ac.uk, map2@le.ac.uk.
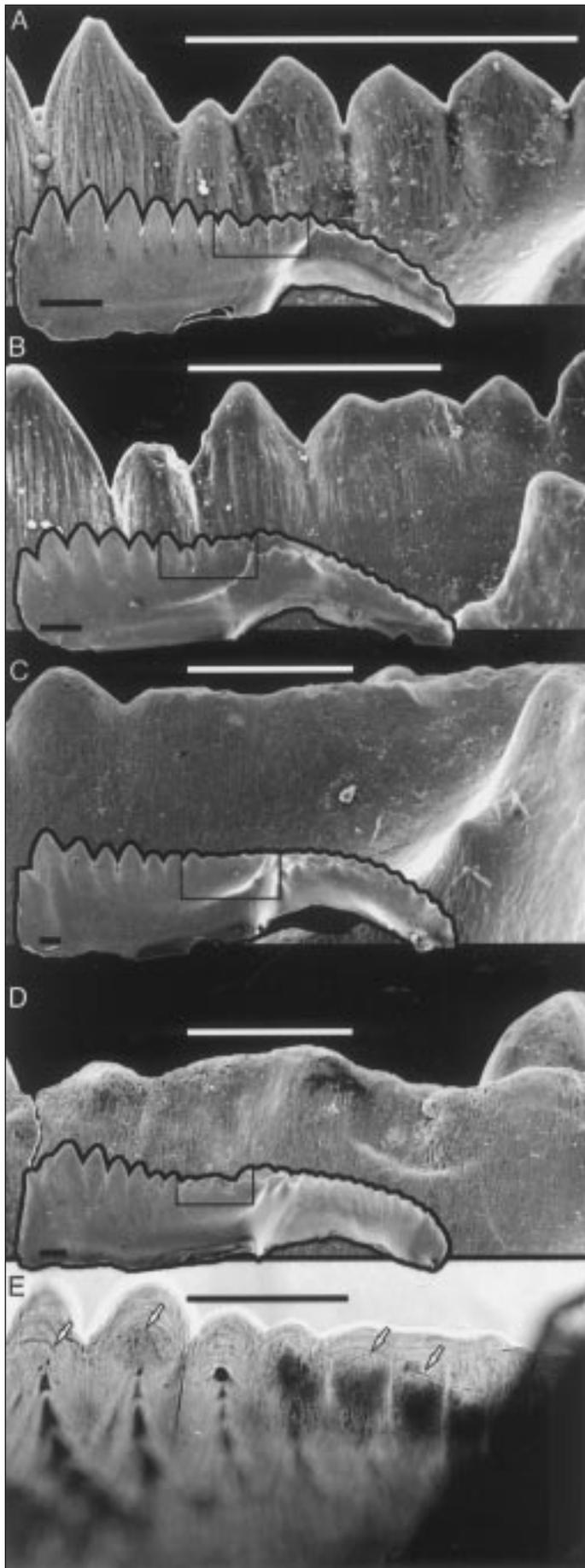
consistently in the same part of the element; resorption should occur randomly or affect the whole surface of the element. The polygonal micro-ornament on the surface of the crown tissue of some conodont elements is not the product of resorption and, instead, has been linked with secretion (von Bitter and Norby, 1994).

If the internal discontinuities are simply the result of random, accidental damage during life (Hass, 1941), they should not exhibit recurrent patterns of distribution, consistent between specimens.

If the discontinuities are the result of wear or surface damage caused during normal use of the elements in feeding, they should consistently occur on functional surfaces where opposing elements repeatedly came into contact or where elements were in contact with food. They should not occur on nonfunctional surfaces. Functional surfaces can be recognized by using independent evidence derived from studies of surface damage and microwear (Purnell, 1995) and integrated functional morphology (Donoghue and Purnell, 1999).

The function of the platform or Pa elements of *Idiognathodus* has recently been considered in great detail (Donoghue and Purnell, 1999). The opposed Pa elements of this genus exhibit precise occlusion and developed considerable surface damage and wear during function, particularly along the crest of the denticles at the junction between the blade and the platform (Fig. 1, and Figs. 3 and 8 of Donoghue and Purnell, 1999). This pattern of damage is very common in *Idiognathodus* Pa elements, and if internal discontinuities represent earlier phases of function followed by wear, they should also occur in the area where the blade joins the platform. Figure 1E shows an example of this denudation and subsequent compensatory growth. There is no evidence of pitting along the plane of the discontinuity (expected in resorption), and the consistent correlation between the distribution of surface damage caused by function and the distribution of internal discontinuities argues strongly against accidental damage as a cause.

Microwear on the blade-shaped Pa elements of *Ozarkodina confluens* indicates that these elements performed a shearing function (Purnell, 1995), with wear facets and other surface damage occurring particularly in the dorsal part of the element. Figure 2 shows examples of this recurrent pattern of surface wear and damage related to function, as well as examples showing conspicuous discontinuities in the same dorsal part of the element. As in *Idiognathodus*, there is no evidence of pitting along the plane of the discontinuities, and the consistent correlation between the distribution of functionally related surface damage and internal discontinuities argues strongly against accidental damage. We interpret the discontinuities in *O. confluens* and *Idiognathodus* as successive phases of function followed by periods of growth and repair.

Published examples are also consistent with our hypothesis. Accidental damage cannot be ruled out for most of Hass's (1941) examples, but Müller and Nogami (1971) illustrated thin sections of ozarkodinids (Pl. 9, Fig. 5; Pl. 19, Fig. 2; Pl. 22, Fig. 4) exhibiting a series of discontinuities beneath the oral surface of the element only. Furthermore, these discontinuities occur only in areas that studies of element morphology and pairing

Figure 1. Recurrent patterns of wear and surface damage (A–D, scanning electron micrographs), and internal discontinuities (E, transmitted light) in Pennsylvanian *Idiognathodus* Pa elements. Scale bars represent 100 μm. All from Elk County, Kansas; Royal Ontario Museum Specimens ROM 49777–49780, 53445. A: Wear is limited to removal of primary ribbed surface texture from tips of denticles at dorsal (occlusal) end of blade (toward right in close-up). B: Denticle tips at dorsal end of blade are worn smooth; some denticles are merged owing to previous damage of occlusal surface. C: Repeated damage has reduced denticulate area at dorsal end of blade to flat ridge; surface damage is evident. D: Dorsal end of blade is reduced to undulating ridge; surface damage is evident. E: Internal discontinuities (arrowed) underlying surface of dorsal part of blade.

have identified as being occlusal (Nicoll, 1987; Weddige, 1990; Donoghue and Purnell, 1999). The growth increments overlying the discontinuities can be traced throughout the elements; in nonocclusal areas, such as the margins of the elements, they are conformable with the underlying incremental layers. The close correlation between discontinuities in the ozarkodinid elements illustrated by Müller and Nogami (1971) and the occlusal surfaces identified by Nicoll (1987; reappraised in Donoghue and Purnell, 1999) provides strong evidence against accidental damage or resorption and indicates that the discontinuities are most likely to have resulted from wear and damage during feeding.

Thus, the internal discontinuities are worn and damaged functional surfaces that have been subsequently overgrown. This finding strongly supports the hypothesis that the elements were retained, not periodically shed and replaced.

GROWTH AND FUNCTION, ONTOGENY, AND LIFE CYCLE

Our interpretation of the internal discontinuities also has implications for hypotheses of element growth and function and of the ontogeny and life cycle of conodonts.

Discontinuities do not occur through the whole growth record of conodont elements; they are restricted to specific levels corresponding to episodes of function, between which growth was uninterrupted. The duration of periods of *function* cannot be determined, but if analogy can be drawn between incremental growth lines in conodont elements and those of other vertebrate hard tissues (see Zhang et al., 1997, and references therein), then the low number of increments constituting the phases of *growth* is likely to represent no more than a few weeks. The alternating phases of growth and function are comparable to cyclical variations observed in the thickness of conodont crown-tissue lamellae (Müller and Nogami, 1971; Zhang et al., 1997). The regularity of the cyclicity in some of these examples indicates that the growth phases were of equal duration.

A similar interpretation is possible for Jeppsson's (1976) plot of size distribution of *Ozarkodina confluens* Pa elements. This shows three discrete clusters along a single line, which probably represent successive generations. The clusters remain discrete because phases of growth were tightly regulated, were of equal duration, and took place over a very short period of time relative to the episodes of function (cf. Jeppsson, 1976). However, of the numerous biometric analyses of conodont elements, only Jeppsson's (1976) exhibits clear size clustering.

Alternate phases of growth and function were implicit in Bengtson's (1976) model for growth of conodont elements, which addressed the paradox that appositional growth of elements required tissue cover, yet their tooth function (then equivocal) required elements to be exposed. Bengtson proposed that between phases of growth, elements grew within epithelial pockets; they were everted from this soft tissue only during function and were subsequently retracted. A similar idea is implicit in Jeppsson's (1979,
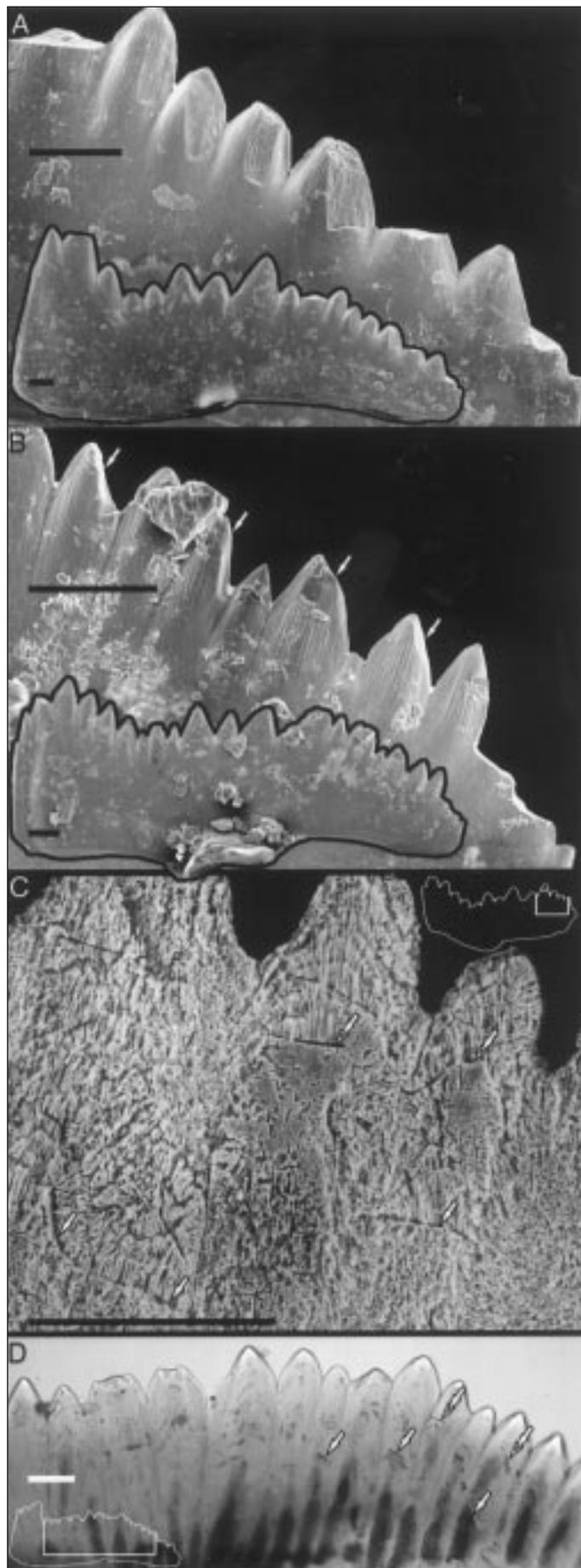
Figure 2. Recurrent patterns of wear and surface damage (A, B) and internal discontinuities (C, D) in Silurian *Ozarkodina confluens* Pa elements (A–C, scanning electron micrographs; D, transmitted light). Scale bars represent 100 μm. A: Almost all denticles at dorsal end of this element (toward right) are damaged, but those toward ventral end are not; this difference cannot be explained by postmortem processes. Natural History Museum, London (NHM) specimen X-2834, from Aston Munslow, Shropshire, England. B: Denticles at dorsal end of element exhibit wear facets and damage; arrows indicate more subtle facets. NHM specimen X-1299 from Prior's Frome, Worcestershire, England. C: Thin section through dorsal part of element (see inset line drawing); two levels of discontinuities are indicated, one by arrows, the other by double-headed arrows. NHM specimen X-2835. D: Two levels of discontinuities in dorsal part of element are indicated, one by arrows, the other by double-headed arrows. NHM specimen X-2836. C and D from Botvide, Gotland, Sweden.

p. 166) hypothetical explanation reconciling a toothlike function with perceived lack of wear in conodonts: "Since elements grew during the animal's entire life by adding lamellae to the surface, any type of superficial wear on one lamella would be covered by the following lamella." However, our evidence indicates that functional episodes were probably a good deal longer than the intervening phases of growth. Furthermore, Smith et al. (1996) have suggested that each conodont element is homologous to an odontode (i.e., a tooth or nongrowing scale), the basic building block of the vertebrate dermal skeleton, and Donoghue (1998) found that multidenticulate elements are grown by marginal accretion and/or envelopment by successive odontodes. Thus, Bengtson's (1976) epithelial pocket model is untenable. Usually, when odontodes erupt (e.g., in the case of teeth), the enamel organ is destroyed; even in those instances in which the enamel organ continues to secrete enamel after eruption, secretion is limited to new growth, not repair (e.g., rodents). In the case of ozarkodinid conodont elements, postfunctional growth is likely to have been facilitated by the growth of a new odontode, the first lamellae completely enveloping the preexisting element. For this to occur, the element must have been returned to the epidermal layer, and the whole process of odontogenesis repeated, as though a new conodont element was to be grown (Donoghue, 1998). A similar hypothesis has been proposed for scale growth in extinct acanthodian fishes (e.g., Reif, 1982).

CONCLUSIONS

Recurrent patterns of wear and damage resulting from element function in vivo indicate that internal discontinuities within an element represent prolonged episodes of use. These were separated by short intervals of growth, each interval probably of equal duration. This model differentiates continued growth from continuous growth, finally resolving the paradox that elements functioned as teeth yet continued to grow.

During the intervals of growth, when they were covered by soft tissue, elements could not have been used in food acquisition or processing. The alternation of growth and function suggests that at regular intervals (?annually) ozarkodinid conodonts underwent a phase of fasting and perhaps dormancy. Such episodes were not necessary in ancestral taxa that grew their elements by marginal accretion of odontodes (see Donoghue, 1998). However, ozarkodinid conodonts became the most diverse group of jawless vertebrates, and their success may have been linked to their complex mode of growth. This enabled ozarkodinids to regenerate the functional surfaces of their elements, and without this ability they could probably not have evolved complex interpenetrative occlusion and the most sophisticated mechanisms of food processing of any jawless vertebrate.

The cyclical alternation of growth and function in ozarkodinids provides compelling evidence that elements were retained permanently. This conclusion has broad paleoecological implications: Pa element abundance can be taken as an indicator of the number of conodonts in an environment; shedding of Pa elements cannot explain their overrepresentation in faunal residues; element size can be taken as a proxy for age. It may now be possible to determine the absolute age of conodonts at death, opening up new avenues, such as rigorous analysis of mortality and population structure, for future research.

REFERENCES CITED

Bengtson, S., 1976, The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function: Lethaia, v. 9, p. 185–206.

Boyde, A., and Jones, S. J., 1987, Early scanning electron microscope studies of hard tissue resorption: Their relation to current concepts reviewed: Scanning Microscopy, v. 1, p. 369–381.

Broadhead, T. W., Driese, S. G., and Harvey, J. L., 1990, Gravitational settling of conodont elements, implications for paleoecologic interpretations of conodont assemblages: Geology, v. 18, p. 850–853.

Carls, P., 1977, Could conodonts be lost and replaced?—Numerical relations among disjunct conodont elements of certain Polygnathidae (Late Silurian–Lower Devonian, Europe): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 155, p. 18–64.

Clark, D. L., editor, 1984, Conodont biofacies and provincialism: Geological Society of America Special Paper 196, 340 p.

Donoghue, P. C. J., 1998, Growth and patterning in the conodont skeleton: Royal Society of London Philosophical Transactions, ser. B, v. 353, p. 633–666.

Donoghue, P. C. J., and Purnell, M. A., 1999, Mammal-like occlusion in conodonts: Paleobiology, v. 25 (in press).

Gross, W., 1954, Zur Conodonten-Frage: Senckenbergiana Lethaea, v. 35, p. 73–85.

Hass, W. H., 1941, Morphology of conodonts: Journal of Paleontology, v. 15, p. 71–81.

Jeppsson, L., 1976, Autecology of Late Silurian conodonts, in Barnes, C. R., ed., Conodont paleoecology: Geological Association of Canada Special Paper 15, p. 105–118.

Jeppsson, L., 1979, Conodont element function: Lethaia, v. 12, p. 153–171.

Ji, Z., and Barnes, C. R., 1994, Conodont paleoecology of the Lower Ordovician St. George Group, Port au Port Peninsula, western Newfoundland: Journal of Paleontology, v. 68, p. 1368–1383.

Jones, S. J., Boyde, A., Ali, N. N., and Maconnachie, E., 1986, Variation in sizes of resorption lacunae made in vitro: Scanning Electron Microscopy, v. 1986, p. 1571–1580.

Krejsa, R. J., Bringas, P., and Slavkin, H. C., 1990, A neontological interpretation of conodont elements based on agnathan cyclostome tooth structure, function, and development: Lethaia, v. 23, p. 359–378.

Müller, K. J., and Nogami, Y., 1971, Über die Feinbau der Conodonten: Kyoto University, Faculty of Science, Memoirs, Series of Geology and Mineralogy, v. 38, p. 1–87.

Nicoll, R. S., 1987, Form and function of the Pa element in the conodont animal, in Aldridge, R. J., ed., Palaeobiology of conodonts: Chichester, Ellis Horwood, p. 77–90.

Patterson, C., 1977, Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton, in Andrews, S. M., Miles, R. S., and Walker, A. D., eds., Problems in vertebrate evolution: London, Academic Press, Linnean Society Symposium Series no. 4, p. 77–122.

Purnell, M. A., 1993, Feeding mechanisms in conodonts and the function of the earliest vertebrate hard tissues: Geology, v. 21, p. 375–377.

Purnell, M. A., 1995, Microwear on conodont elements and macrophagy in the first vertebrates: Nature, v. 374, p. 798–800.

Reif, W. E., 1982, Evolution of dermal skeleton and dentition in vertebrates: The odontode regulation theory: Evolutionary Biology, v. 15, p. 287–368.

Rhodes, F. H. T., 1954, The zoological affinities of the conodonts: Biological Reviews, v. 29, p. 419–452.

Smith, M. M., Sansom, I. J., and Smith, M. P., 1996, "Teeth" before armour: The earliest vertebrate mineralized tissues: Modern Geology, v. 20, p. 303–319.

Sweet, W. C., 1988, The Conodonta: Morphology, taxonomy, paleoecology, and evolutionary history of a long-extinct animal phylum: Oxford, Clarendon Press, Oxford Monographs on Geology and Geophysics No. 10, 212 p.

von Bitter, P. H., and Norby, R. D., 1994, Fossil epithelial cell imprints as indicators of conodont biology: Lethaia, v. 27, p. 193–198.

Weddige, K., 1990, Pathological conodonts: Courier Forschungsinstitut Senckenberg, v. 118, p. 563–589.

Zhang, S., Aldridge, R. J., and Donoghue, P. C. J., 1997, A Triassic conodont with periodic growth?: Journal of Micropalaeontology, v. 16, p. 65–72.