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. Paleoeological 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 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.
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: Dentine 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,
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