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New Studies of Enamel Microstructure in Mesozoic Mammals: A Review of Enamel Prisms as a Mammalian Synapomorphy

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Characters from enamel microstructure have not been used in recent phylogenetic analyses of Mesozoic Mammalia. Reasons are that enamel characters have been perceived as (A) variable without regard to systematic position of taxa, (B) inconsistently reported within the literature, and (C) simply scored as either prismatic or not prismatic in earlier mammals. Our work on Mesozoic mammals such as *Sinoconodon*, *Gobiconodon*, Triconodontidae, *Docodon*, *Laolestes*, and others suggests that synapsid columnar enamel (SCE) structure was easily transformed into plesiomorphic prismatic enamel (PPE) and that PPE may be described with at least five independent character states. Two PPE characters—a flat, open prism sheath and a planar prism seam—were present in the cynodont *Pachygenelus* and in several Jurassic and Cretaceous mammals. We propose that appearance of a prism sheath transforms SCE into PPE and that reduction and loss of a prism sheath reverse PPE into SCE, in both phylogeny and ontogeny. We further propose that no amniote vertebrates other than the trithelodontid cynodont, *Pachygenelus*, plus Mammalia have ever evolved an ameloblastic Tomes process capable of secreting PPE and that the genetic potential to secrete PPE is a synapomorphy of *Pachygenelus* plus Mammalia, whether or not all lineages of the clade have expressed that potential.

KEY WORDS: mammalian synapomorphy; enamel microstructure; prismatic enamel; Mesozoic mammals.

INTRODUCTION

The first mammals lived during the Late Triassic, perhaps 225 million years ago [for convenience, we follow the more inclusive definition of Mammalia of Lucas and Luo (1993)]. Mammals coexisted with dinosaurs until 65 million years ago and then appear to have radiated into the extant orders and families (but see Gibbons, 1998). During the Mesozoic most mammals remained small and more or less scansorial in habit. More complete skeletal remains have been recovered in recent years (e.g., Kielan-Jaworowska, 1977, 1979; Jenkins and Schaff, 1988; Krebs, 1991; Novacek *et al.*, 1997; Hu *et al.*, 1997), but since the last century a majority of Mesozoic mammals have been known mainly from dental remains (Lil-

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legraven *et al.*, 1979). Microscopic patterns in tooth enamel have therefore been an obvious target of investigation, with the hope that more information would be added toward our understanding of the origin and basal diversification of Mammalia. Enamel has not been a useful component of recent computer-assisted phylogenetic analyses of mammalian characters (Wible, 1991; Luo, 1994; Sidor and Hopson, 1998), but it is our hope from this work that enamel characters will be a useful part of such analyses in the future.

Background—Multiple or Single Origins of Prismatic Enamel?

Stern (1989) studied animals on either side of the cynodont-to-mammalian transition (see Stern and Crompton, 1995). She found plesiomorphic prismatic enamel (PPE) in one nonmammalian cynodont, the trithelodontid *Pachygenelus* (reported earlier by Grine and Vrba, 1980), and also in the Late Triassic–Early Jurassic morganucodontid mammal, *Megazostrodon*. Since other workers had found enamel without prisms in several other early mammals (Sigogneau-Russell *et al.*, 1984; Fosse *et al.*, 1985; Frank *et al.*, 1988; Lester and Koenigswald, 1989), it again raised the question (first articulated by Grine and Vrba, 1980) of whether prisms evolved once, rather than several times, within Mammalia.

Krause and Carlson (1986), in a thorough survey of enamel in multituberculates, had interpreted the phylogenetic distribution of patterns within the group and several outgroups to mean that prismatic enamel evolved as a new pattern within Multituberculata (from ancestors with prismless structure). This interpretation would require a multiple origin of prismatic enamel within Mammalia. Carlson (1990) provided a general overview of enamel biology and phylogeny which remains an excellent general reference on the subject.

Rowe (1988) and Wible (1991) began discussions of mammalian phylogeny which have led to a continuing series of contributions to and revisions of mammalian phylogeny [see Hu *et al.* (1997) for a list of current references on the subject]. Rowe included prismatic enamel as a mammalian synapomorphy, but Wible excluded enamel characters as phylogenetically unreliable and as inconsistent within the literature. Koenigswald and Clemens (1992) summarized the issues and supported the multiple origins of prismatic enamel within Mammalia.

At a workshop on enamel structure and evolution at Andernach, Germany, in 1994 (see Koenigswald and Sander, 1997a), three contributions specifically addressed the occurrence of the earliest prisms in mammalian and nonmammalian synapsids. Wood and Stern (1997) summarized the distribution of prismatic and prismless enamel in early mammals and their immediate ancestors or sister taxa. In view of the spate of new cladograms for mammalian relationships after Carlson (1990), Wood and Stern generated a new distributional map of enamel characters. For the first time, they reported prisms in a derived symmetrodont mammal. Originally reported as *Symmetrodontoides foxi*, the specimen should now be referred to the closely related cf. *Spalacotheridium* sp. (R. Cifelli, personal communication). Prismatic enamel in spalacotheres would seem to indicate that prisms were ancestral for all mammals further up the phylogeny. Multituberculates are problematic but otherwise the question is about the origin of prisms more basal to the clade—*Pachygenelus* and *Megazostrodon* are at the bottom. Wood and Stern (1997) reiterated the alternatives that (1) prisms evolved once with several early reversals or that (2) prisms evolved several times, before and after multituberculates. Wood and Stern advocated the first alternative.

Sander (1997) reviewed a comprehensive sample of nonmammalian synapsids and thus took the "bottom-up" approach to the question of prism origins. He found that synapsids have a unique enamel pattern among amniote vertebrates, which he named synapsid columnar enamel (SCE). He advocated the alternative of multiple origins for prisms within Mammalia. An important issue is Sander's (1997) observation that the early mammals that have no prisms have SCE nevertheless. The implication would be that, if these mammals had lost prisms, perhaps they would have some prismless pattern other than SCE. Sander also indicated that we have yet to identify the actually ancestral enamel stages between SCE and PPE. Sander (1997), nevertheless, held open the possibility of seams-only enamel (without sheaths) although—at that time—it was undocumented in the fossil record.

Clemens (1997) summarized the arguments of Sander (1997) and of Wood and Stern (1997). While he advocated investigating multiple working hypotheses, he leaned toward the alternative of multiple origins. Clemens especially emphasized prismatic enamel distribution within a detailed look at multituberculate phylogeny (referring especially to Simmons, 1993), indicating that ancestral multituberculates are prismless and that small prisms (more like our PPE) would seem to have evolved four times from multituberculate ancestors with a non-PPE pattern. The apparently basal multituberculate prismatic pattern has been called "gigantoprismatic" (Krause and Carlson, 1986) because prism diameters average around 8 μm, as opposed to PPE diameters more often in the 2- to 4-μm range.

MATERIALS AND METHODS

We have undertaken further work on additional Mesozoic mammals in order to obtain more data for the lower parts of the mammalian clade. Table I provides data for these and other specimens described below. (See Table II for the abbreviations used in this report.) It may be best to observe enamel structure in several individuals per species where possible, and at several locations within the dentition of a single individual, but in these early mammals this often is not possible. Specimens for several of these taxa are rare and it is sometimes very fortunate to have even a single specimen which can be sacrificed for enamel studies. Among extant species with relatively simple enamel structure, we have the general impression that the greatest variation in pattern is with depth in the single layer of enamel on the individual tooth (see Maas, 1993, 1994; Dumont, 1997) and that less variation seems to be present among individuals in a species or between teeth in the dentition (although more research may need to be done on a wider variety of tribosphenic species to confirm this). We must assume, for now, that enamel structure among the teeth of earlier mammals is no more variable than it is for extant mammals. It is nevertheless important to be sure of comparing equivalent teeth and views of those teeth (i.e., planes of section and zones of enamel) when drawing generalized conclusions from this work. All illustrations in this paper are from horizontal sections (frontal plane in quadrupeds) of lower molariform teeth unless otherwise noted (see Table I).

For the subtleties of structure in many of these specimens, best results are usually obtained by embedding the specimen in laboratory resin. The resin holds the specimen firmly so that it may be sectioned and then polished to a high degree. We have used a Buehler wheel with a 600-grit abrasive disk, followed by a felt disk and 0.05-μm alumina polishing medium. Frequent checking with a dissecting microscope allows finer control;

Table I. Specimen Data for this Report

Taxon	Cat. No.	Tooth	Locality	Age
Philander opossum	MVZ154359	Rm2	Guatemala	Recent
Marmosa robinsoni	MVZ135235	Rm2	Colombia	Recent
Caluromys sp.	MCZ9418	Rm2	?Panama	Recent
Dromiciops gliroides	MVZ163432	Rm2	Argentina	Recent
Alphadon sp.	MCZ uncat.	Lm2 or 3	Bug Creek Anthills, Montana	K/T boundary
Pediomys sp.	MCZ uncat.	Lm2 or 3	Bug Creek Anthills, Montana	K/T boundary
Didelphodon vorax	UCMP52291	Rm4?	V5620, Lance Fm., Wyoming	Maastrichtian, Cretaceous
Tribotherian undet., Met.–Euth. grade	OMNH24632	Rm2 or 3	Straight Cliffs Fm., Utah	Turonian, Cretaceous
Cf. *Spalacotheridium* sp.	OMNH26709	Rm	Cedar Mtn. Fm., Utah	Late Albian, Cretaceous
Cf. *Laolestes eminens*	AMNH101127	Lm	Morrison Fm., Como Bluff, Wyoming	Late Jurassic
Gobiconodon ostromi	4MCZ19860	PM, isolated	Cloverly Fm., Montana	Albian, Cretaceous
Sinoconodon sp.	IVPP8691	Lower molariform	Lower Lufeng Fm., China	Liassic
Sinoconodon sp.	IVPPV8693	Upper last molariform	Lower Lufeng Fm., China	Liassic
Triconodontid (unnamed)	MCZ20024	m	Cloverly Fm., Montana	Albian, Cretaceous
Triconodontid, cf. *Jugulator*	OMNH25792	m	Cedar Mtn. Fm., Utah	Late Albian, Cretaceous
Docodon victor	AMNH104799	Rm	Morrison Fm., Como Bluff, Wyoming	Late Jurassic

with experience one can judge progress by the degree of light reflectivity on the polished surface. Experience has also shown that in the subtlest structure at the prism and crystallite level, it is often impossible to see the accurate orientation of crystallite fabric and small-scale features such as tubules, or even prism seams, except by treatment with the Prophyjet™ airpolishing device (see Boyde, 1984a, b). This machine directs an air-driven stream of soft abrasive (mainly sodium bicarbonate) at the specimen, surrounded by a "doughnut" of water. Dentine will be eroded rapidly with this device, and care must be taken to avoid very thin or badly cracked enamel; but on ordinary enamel about 20 sec of airpolishing on the mechanically polished surface gives optimum results. After 20 sec it is difficult to detect any further effects on the enamel, but the surrounding resin (and dentine) will continue to erode and leave the enamel layer standing in relief.

It may also be noted that stereophotography greatly helps in the observation of subtle structures. We have found that a divergence of about 10° between stereo pairs provides the best view of relief in the etched enamel fabric.

Final steps in specimen preparation include acid etching (stopped by immersion in running tap water) and a brief ultrasonic (ethanol) bath followed by air-drying. Different researchers have used a variety of etching agents (Carlson and Krause, 1985; Grine,

Table II. Abbreviations Used in this Report

	Museums
AMNH	American Museum of Natural History, New York
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
MCZ	Museum of Comparative Zoology, Harvard University
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
OMNH	Oklahoma Museum of Paleontology, Norman
UCMP	University of California Museum of Paleontology, Berkeley
	Teeth
R	Right
L	Left
m	Lower molar
M	Upper Molar
PM	Upper premolar
	Enamel
PPE	Plesiomorphic primsatic enamel
SCE	Synapsid columnar enamel
DEJ	Dentine–enamel junction
OES	Outer enamel surface
AP	Aprismatic enamel zone (outer) [=PLEX of Koenigswald and Sander (1997)]
p	Prism (or prismatic crystallites)
ip	Interprismatic area (or interprismatic crystallites)
sh	[Prism] Sheath
sm	[Prism] Seam
pr	Prism row
irs	Interrow sheet
mgph#	Micrograph Number (C.B.W. archive)

1986; Grine *et al.*, 1987). For consistency we have chosen always to use 1% phosphoric acid, with the etch time depending on the degree of relief desired. We also suspect that fossilization may sometimes result in differing degrees of resistance to acid and therefore require more or less etch time than may be necessary for unfossilized specimens. Our etch times have ranged from less than 5 to more than 90 sec. It is a better strategy to begin conservatively, with a shorter etch time. If the structure is not yet distinct enough, the surface can be repolished and reetched for a longer period of time.

After sputter coating of the specimens with platinum or palladium–gold, most of our SEM photography of them has been at between 20 and 25 kV. Micrographs with "MCZ" preceding the number (see figure captions) were made at Harvard University, by Ed Seling, operator, on an AMR 1000 microscope. The others were done by C.B.W. on an ISI DS130 (LaB_6 filament) at the University of California, Berkeley.

RESULTS

Enamel Character Polarity in Didelphimorph Marsupials

Enamel studies in mammals have a history almost coincident with that of modern microscopes (e.g., Owen, 1845; Tomes, 1849), but truly phylogenetic studies of enamel

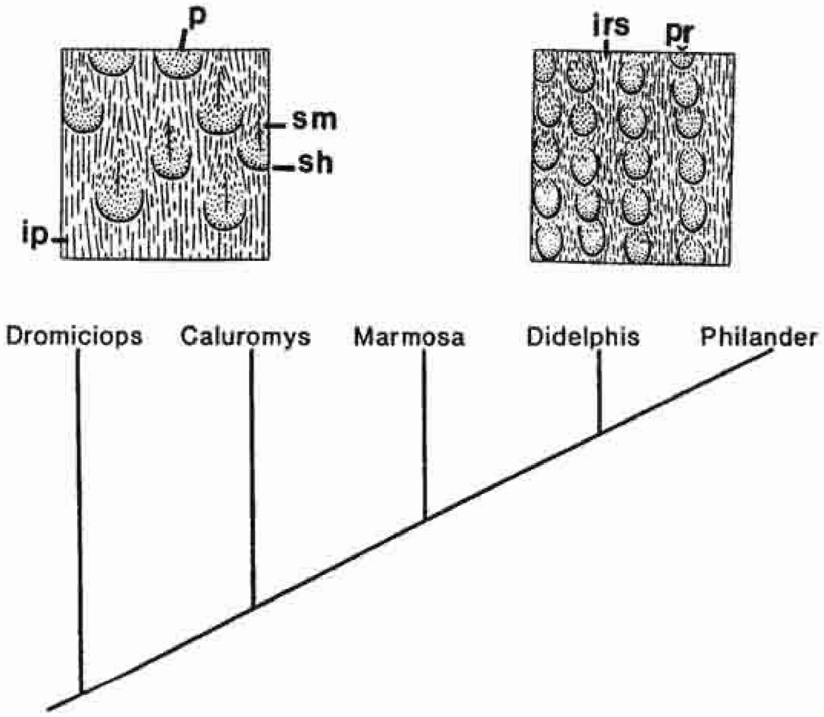

Fig. 1. Diagrammatic representation of enamel microstructure trends in selected extant didelphimorph marsupials. Although character states and nodes are not indicated on this phylogram, Wood (1992) found that enamel character transformations were congruent with cladograms generated by Reig *et al.* (1987). Prisms (p) and interprismatic (ip) areas are separated by prism sheaths (sh), which are surfaces of discontinuity between enamel crystallites in differently oriented sets (dashes when in plane of section, dots when cut by plane of section). Interrow sheets (irs), prism rows (pr), and seams (sm) are structural features described and defined in text and figures that follow; see Table II for a list of all abbreviations used in this report.

pattern are more recent. During the 1960s to 1980s some workers began to consider character polarities in general (Boyde, 1964, 1976a; Poole, 1971) and in Mesozoic mammals specifically (Moss, 1969; Sahni, 1979; Clemens, 1979; Lester and Koenigswald, 1989), but no systematic study had been attempted for any group known to have lived from the Mesozoic through the present. Therefore, one of us undertook a dissertation on didelphimorph marsupials toward that end (Wood, 1992).

Stern *et al.* (1989) had related enamel structure to molar function in *Didelphis virginiana*. Extant didelphids are relatively diverse in Central and South America and had recently been subjected to phylogenetic analysis from combined molecular, karyotypic, and morphological characters (Reig *et al.*, 1987). Selecting certain taxa from the published phylogeny (and accepting the phylogeny as given) Wood (1992) mapped variations of enamel structure on the phylogeny as a first attempt to understand polarities within the extant taxa (Fig. 1). Didelphids have radial enamel (see Koenigswald and Sander, 1997b) which does not have prism decussation or other complex patterns seen in many derived placental mammals [nor do most other marsupials (see Koenigswald, 1994, 1997)],

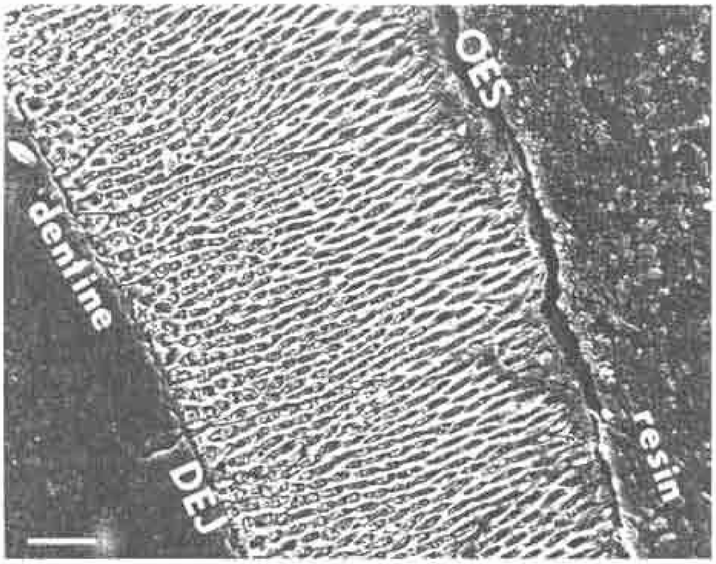

Fig. 2. Enamel structure in *Philander opossum* (see Table I for specimen data). Entire enamel layer in a cross section; prisms arranged in linear fashion, with prism rows separated by distinct interrow sheets of interprismatic crystallites. *Didelphis* has a similar structure but not as compactly separated as this. Note that in this species prisms toward the outer enamel surface (OES) are tilted at a lower angle to the plane of section and are thus more ovate. Note, also, the lack of a distinct aprismatic zone toward the OES. DEJ, dentine–enamel junction. Micrograph (Mgph)# 4168 (archive maintained by C.B.W.); bar = 16.9 μm.

but *Philander* has a very tightly woven, almost laminated enamel (alternating layers or rows of prisms and anastomosing interrow sheets of interprismatic crystallites; Figs. 2–4); *Didelphis* has stacked prisms with distinct interrow areas (Stern, 1989; Stern *et al.*, 1989), but not as exaggerated as in the outer parts of the *Philander* crown. There were intermediate patterns (*Marmosa, Caluromys;* Figs. 5 and 6), and *Dromiciops* had arc-shaped prisms bisected by linear prism seams, arranged in an open, hexagonal pattern (Fig. 7).

Wood's (1992) survey also included Late Cretaceous didelphimorph genera from North America. The survey of extant genera indicated that the pattern in *Dromiciops* could be closer to the ancestral pattern, and indeed all the Cretaceous animals so far examined have variations on that design (Fig. 8; also Figs. 9–13). Wood and Stern (1997) call this enamel pattern plesiomorphic prismatic enamel, hereinafter referred to as PPE (a full characterization of PPE is reviewed below).

New (Mesozoic) Taxa Sampled

Laolestes

Laolestes is a dryolestid mammal from the Late Jurassic of North America (see Prothero, 1981). Dryolestids are at a more primitive dental grade than are placental and marsupial mammals though related more closely to them than most other Jurassic mam-

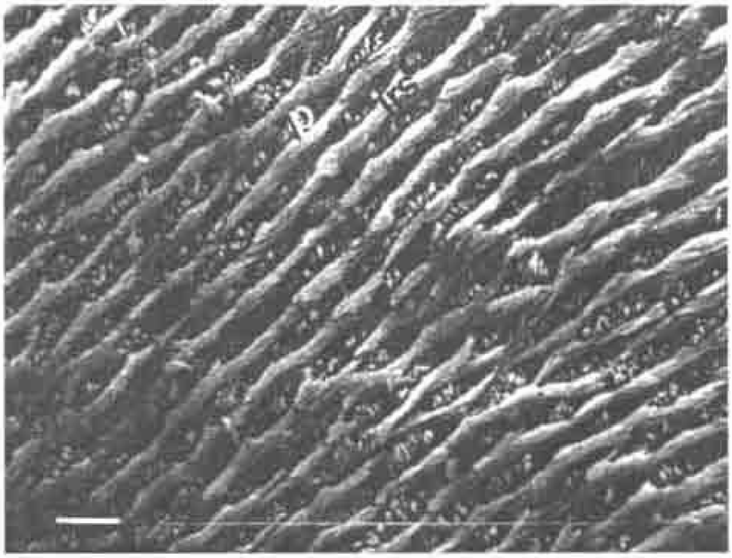

Fig. 3. Enamel structure in *Philander opossum*, higher magnification of structure toward the outer enamel surface (elsewhere on the cusp but same plane of section as in Fig. 2). Here the prisms (p) are much less distinct (and not because of leaning toward the OES) so that the enamel has a much more laminated, and therefore "composite," type of structure. irs, interrow sheet. Mgph# 4176; bar = 5.05 μm.

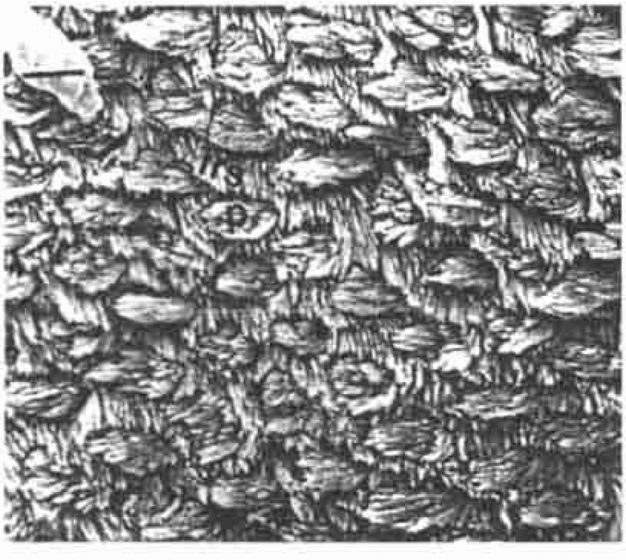

Fig. 4. Enamel structure in *Philander opossum* (a different plane of section through the same specimen as Figs. 2 and 3) showing the cross-woven fabric of prismatic (p) and interrow sheet (irs) crystallites at about 90° to one another. Mgph# 4180; bar = 5.00 μm.

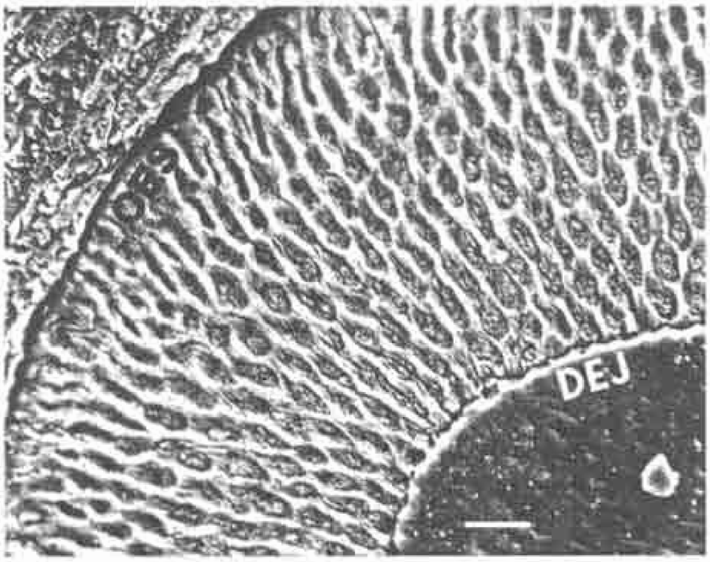

Fig. 5. Enamel cross section in *Marmosa robinsoni*. Prisms are arranged in linear rows, separated more or less by interrow sheets, but not as tightly as in *Didelphis* or *Philander*. There is no distinct outer aprismatic zone but the outer prisms become smaller and are more tightly squeezed together with interprismatic layers. Mgph# 3801; bar = 11.7 μm.

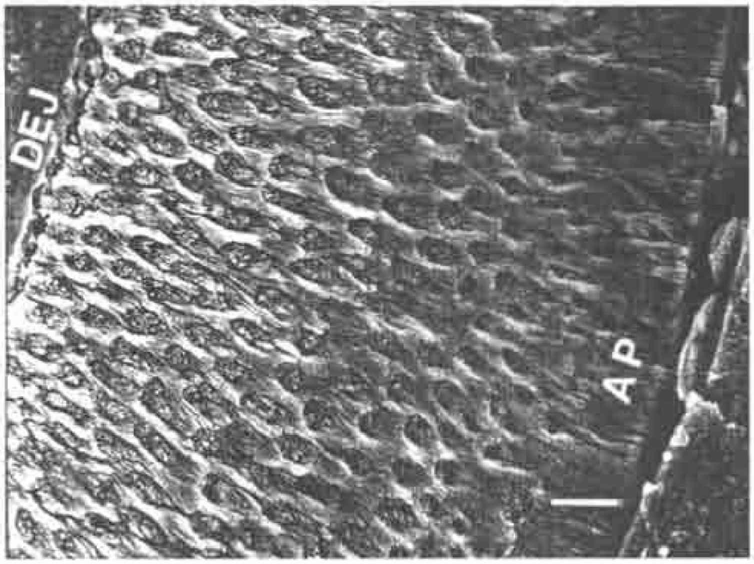

Fig. 6. Enamel cross section in *Caluromys* sp. Prisms are less clearly arranged in linear rows, with each prism more open toward the OES; there are very indistinct or no interrow sheets, and outer prisms become progressively smaller so that there is an outer aprismatic (AP) zone. Mgph# 3947; bar = 10.1 μm.

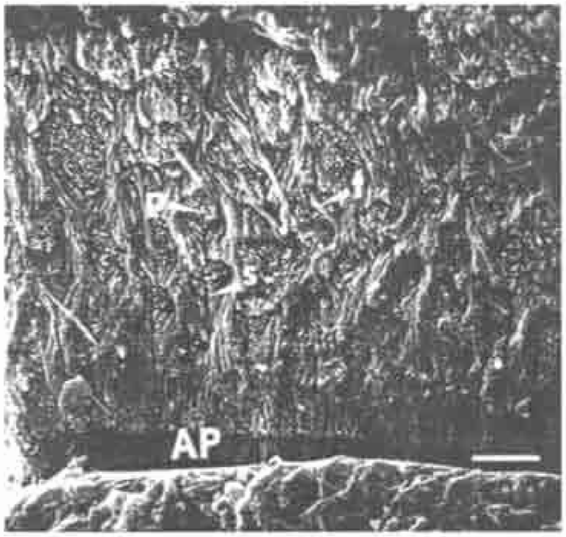

Fig. 7. Enamel cross section in *Dromiciops gliroides*. This species has plesiomorphic prismatic enamel (PPE), with hexagonally arranged, open prisms (p) that are bisected by strong prism seams (s). There is a thin but clearly layered AP zone below the OES. t, tubule filling of flexible resin, injected during embedment, and left after etching of specimen with acid. Mgph# 4480; bar = 5.29 μm.

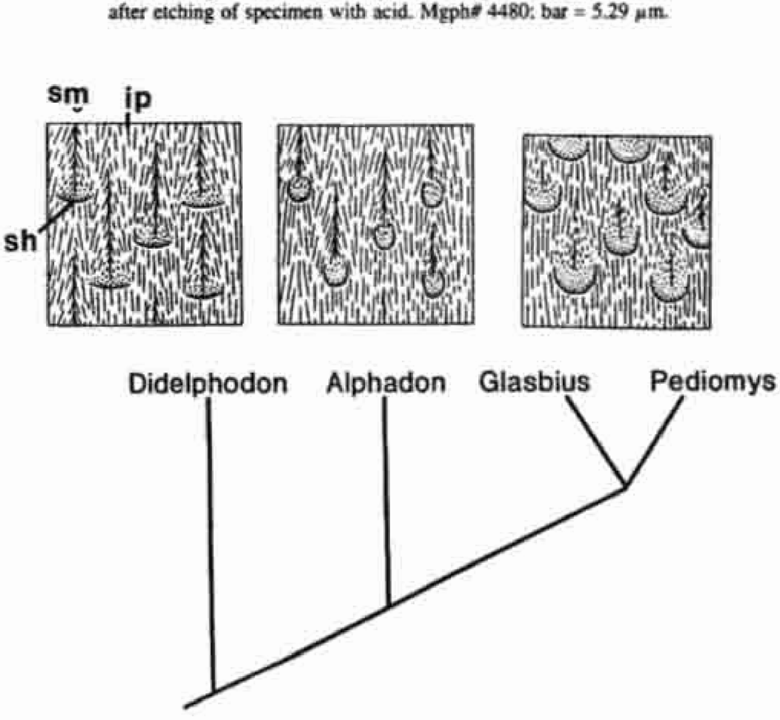

Fig. 8. Diagrammatic representation of enamel microstructure in selected Late Cretaceous marsupials. Note that all display PPE but that there are subtle variations in prism size and shape of prism sheaths (sh). ip, interprismatic matrix; sm, seam.

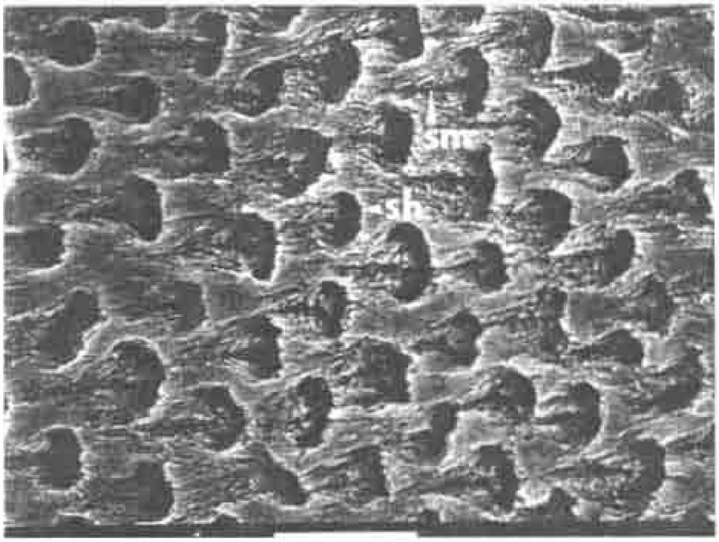

Fig. 9. PPE in a Late Cretaceous specimen of *Didelphodon vorax* (stagodontid marsupial). Prism seams (sm) are very strong and the packing pattern is hexagonal to erratic. Prism sheaths (sh) may be fully semicircular but in many other places they are relatively flat (see diagrammatic representation in Fig. 8). Mgph# 008 71194 MCZ; bar = 10 μm.

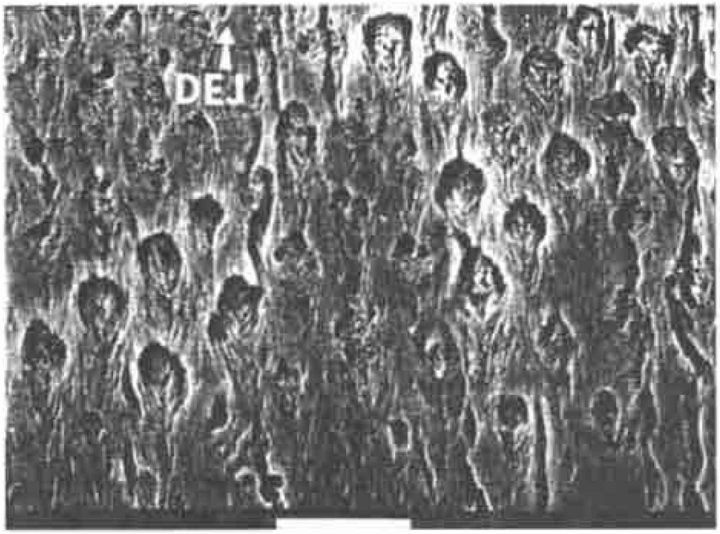

Fig. 10. Enamel structure from a specimen of *Alphadon* sp., a Late Cretaceous peradectid marsupial. Note that the seams have some variability between sheath and tubule-like structures at the ends toward the DEJ. Mgph# 120 31594 MCZ; bar = 10 μm.

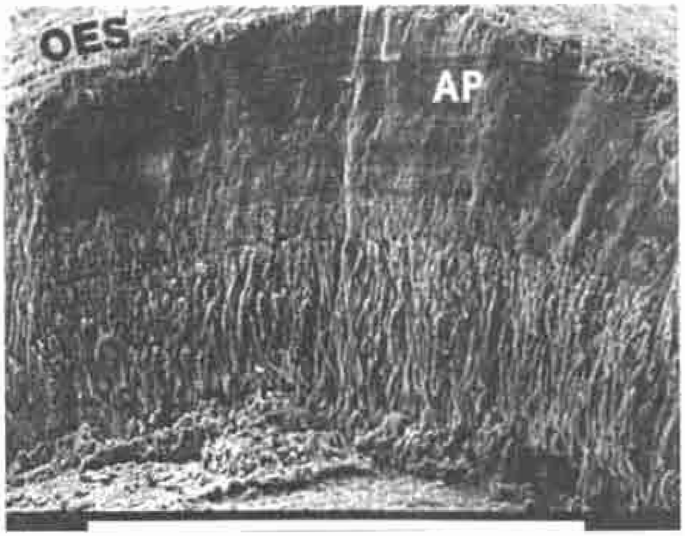

Fig. 11. Broken cross section of enamel in *Pediomys* sp. (Latest Cretaceous marsupial). Although the specimen has been etched, the specimen has not been polished, and the prismatic layer closer to the dentine has an ambiguous structure with this kind of preparation. There is, nevertheless, a clear, thick outer AP zone with very distinct incremental lines or layers. Mgph# 003 11233 MCZ; bar = 100 μm.

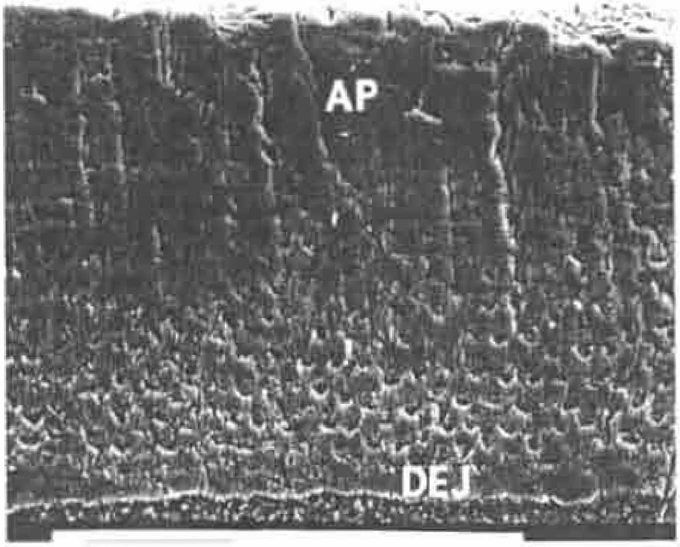

Fig. 12. Polished and etched enamel cross section from an undetermined, "Earliest Late" Cretaceous tribosphenic mammal which may be either marsupial, placental, or neither ("Metatherian–Eutherian grade"). The outer AP zone is extremely thick in this specimen, and the prism sheaths are flattened as in *Didelphodon*. Mgph# 005 11094 MCZ; bar = 100 μm.

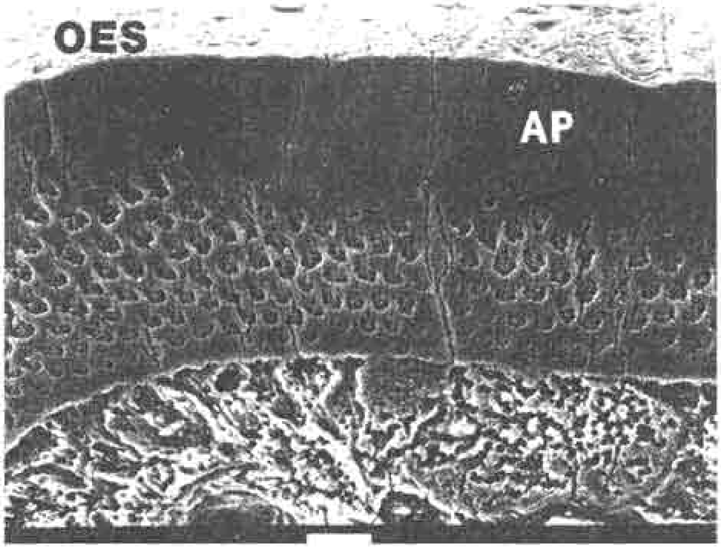

Fig. 13. Very well-polished and -etched specimen of cf. *Spalacotheridium* sp. ("Middle" Cretaceous) previously reported (Wood and Stern, 1997) as the closely related *Symmetrodontoides foxi*. These mammals do not have tribosphenic teeth. The specimen is extremely small for a mammal but the enamel is, nevertheless, quite reminiscent of enamel in the "Metatherian–Eutherian grade" mammals (Fig. 12) as well as in stagodontid marsupials (i.e., *Didelphodon*). Mgph# 012 01594 MCZ; bar = 10 μm.

mals. One or two other dryolestids are known to have PPE (Lester and Koenigswald, 1989), and Crompton *et al.* (1994) published on two unusual Late Cretaceous South American "dryolestoids" which have interesting variations on that pattern. We chose *Laolestes* in order to extend the sample from the basal part of the Dryolestoidea.

Laolestes (Fig. 14) demonstrates some important caveats about conclusions drawn based upon what is seen or not seen depending on preparation technique. In the embedded specimen (Fig. 15) it is clear that the enamel is divided into two layers and that the outer layer has incremental lines. The nature of the inner layer was not clear until extremely fine polish on the surface was buffed (prior to brief etching with 1% phosphoric acid; see above) with the soft-abrasive airpolishing unit. Arc-shaped prism sheaths, bisected by linear seams, are evident (Fig. 16) but are actually quite subtle. On a less-well-polished surface (Fig. 15), the sheaths and seams are present but not obvious.

Gobiconodon

Gobiconodon is an Early Cretaceous triconodontan (therefore, strictly nontherian) mammal of uncertain affinities within the order Triconodonta (Jenkins and Schaff, 1988). It may or may not be closely associated with the more typical members of family Triconodontidae. *Gobiconodon* has a rather peculiar version of PPE (Figs. 17–19). There are both sheaths and seams but these are erratically spaced. Sheaths are quite variable in size and there are examples of seams with almost no visible sheath (though a tubule-like opening may be present at the beginning of a seam instead). Overall we believe

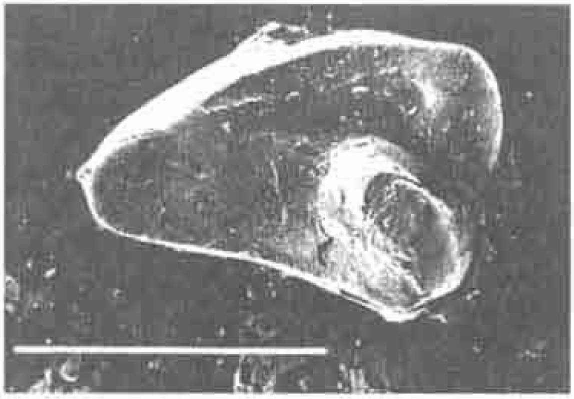

Fig. 14. *Laolestes* (Late Jurassic dryolestoid), crown view of specimen before embedment; the specimen is broken posteriorly so that the talonid is not visible. Mgph# 019 31996 MCZ; bar = 1 mm.

that this enamel is prismatic, if faintly and incompletely so. In Fig. 10, which illustrates enamel from a specimen of *Alphadon*, a North American Cretaceous marsupial, we also see considerable variability in prism sheath dimensions, spacing, or occurrence.

Sinocondon

Figure 20 illustrates enamel from *Sinoconodon*, one of the earliest and most basal mammals (Crompton and Luo, 1993), which was also illustrated by Wood and Stern

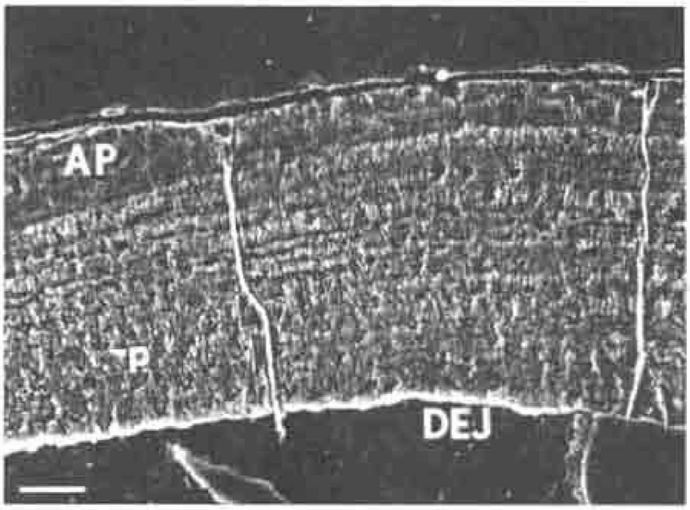

Fig. 15. Enamel in *Laolestes*, in cross section, with light polishing. A distinct outer AP zone is present, but the inner prismatic zone has an ambiguously prismatic structure with this preparation. Mgph# 006 41696 MCZ; bar = 10 μm.

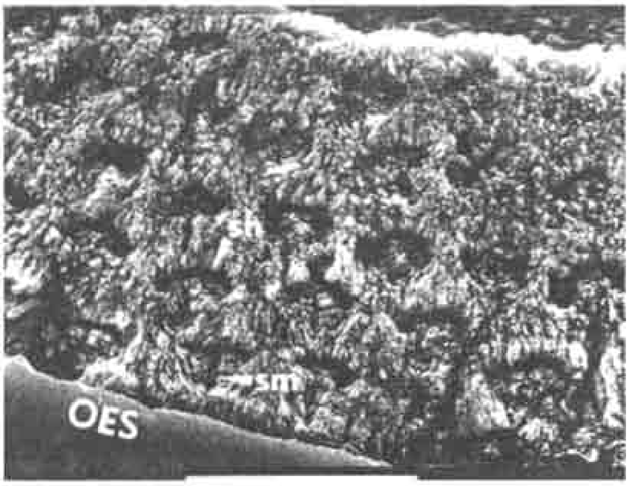

Fig. 16. Enamel in *Laolestes*, highly polished enamel cross section (same plane as in Fig. 15), lightly etched. The enamel is thinner on this part of the tooth than in that illustrated by Fig. 15, and an outer AP zone with incremental lines is not present, but small prism sheaths (sh) and seams (sm) are clearly present. Mgph# 009 41696 MCZ; bar = 10 μm.

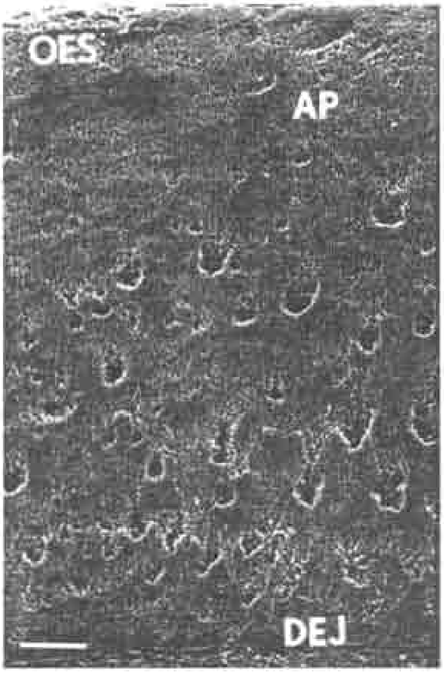

Fig. 17. Highly polished cross section of enamel in *Gobiconodon ostromi* ("Middle" Cretaceous). Note that there is a thick outer AP zone and that prisms are erratic in size, packing geometry, and definition. Mgph# 015 32696 MCZ; bar = 10 μm.

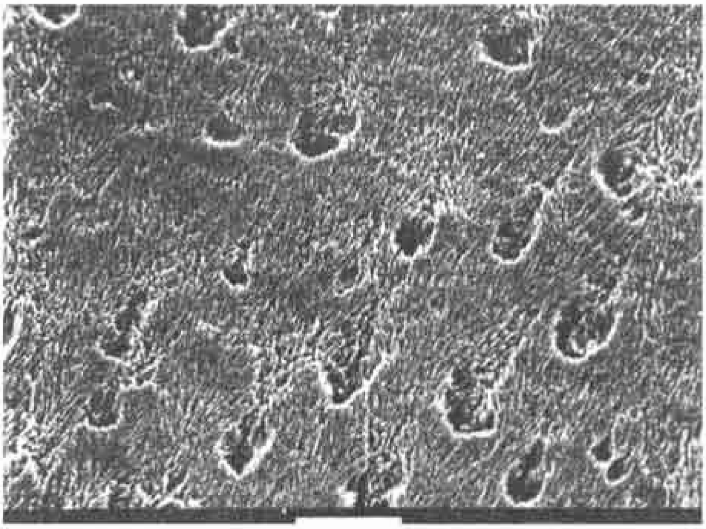

Fig. 18. Higher magnification within the field of view from Fig. 17. Seams are a more constant feature of the structure than sheaths, but note that some seams are marked toward the DEJ end by fully developed sheaths, while others are marked by more tubule-like openings. It is unlikely that this variation represents etch artifact because the entire surface was etched in the same medium all at once. Mgph# 019 32696 MCZ; bar = 10 μm.

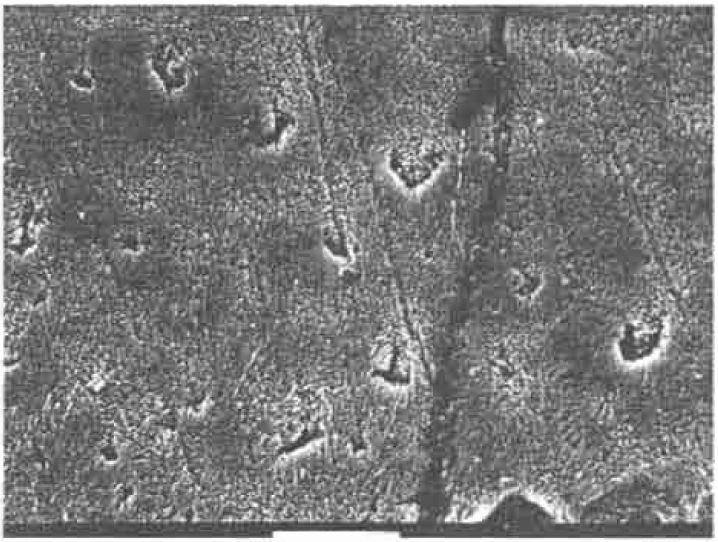

Fig. 19. Another view of enamel in the same specimen and plane as the other two *Gobiconodon* views (Figs. 17 and 18). Here the prismatic structure is more subtle (long linear grooves are polishing artifacts) and compares well with that seen in some views from the triconodontid cf. *Jugulator* (see Fig. 26.). Mgph# 014 22096 MCZ; bar = 10 μm.

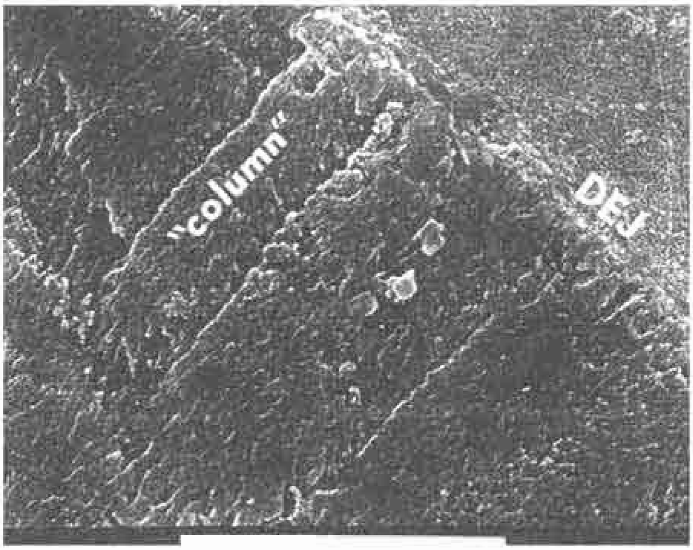

Fig. 20. Enamel cross section from *Sinoconodon* sp. (Liassic, China), in a specimen reported earlier (Wood and Stern, 1997) in which the linear (actually planar) discontinuities (defining "columns") appear to extend almost the whole thickness of the enamel. This version of the structure in *Sinoconodon* appears very similar to Synapsid Columnar Enamel (Sander, 1997). Mgph# 029 30194 MCZ; bar = 10 μm.

(1997); see also Zikui and Wending (1991) for an earlier illustration. Wood and Stern reported that available views were inconclusive as to presence of true prisms and that more views were needed (specimens are rare and academically valuable), but Sander (1997) included *Sinoconodon* in his SCE category [based on the illustration presented by Wood and Stern (1997)]. *Sinoconodon* has a "triconodont" crown morphology but this may be coincidental to more derived triconodont mammals such as members of Triconodontidae. Figure 21 is a new preparation of *Sinoconodon* enamel. As reported by Wood and Stern (1997) there are distinct radial, linear/planar discontinuities present, but with occasional widenings at the dentine–enamel junction (DEJ) end. We consider this to be a transitional structure between SCE and PPE, and further comparison is included below (see p. 195).

Triconodontidae

Triconodontids are significant for at least two reasons: (1) they have a dental morphology similar to that of both *Gobiconodon* and *Sinoconodon*, and (2) recent studies of basicranial characters (Rougier *et al.*, 1996) place Triconodontidae closer to the stem of therian mammals than previously suggested. Other "triconodontan" mammals such as *Morganucodon* and *Dinnetherium* probably are much more basal to the clade Mammalia. Several reports have shown *Morganucodon* to have prismless enamel (Frank *et al.*, 1988; Lester and Koenigswald, 1989; Wood and Stern, 1997), and we found (thanks to the

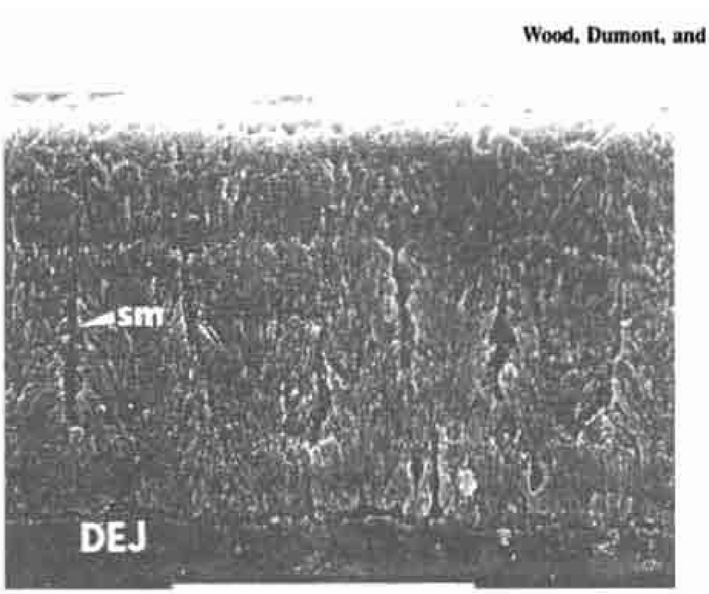

Fig. 21. Enamel cross section from *Sinoconodon* sp. (Liassic, China), new preparation of specimen in horizontal section, showing strong linear features widened at the DEJ end. These are spaced like prism seams in PPE enamel and interpreted here as essentially seams (sm) without a clear sheath. Mgph# 026 30194 MCZ; bar = 10 μm.

generosity of F. A. Jenkins, Jr.) that *Dinnetherium* also has very thin enamel (not illustrated) which is prismless and otherwise similar to that of *Morganucodon*.

Figures 22 and 23 are from an unnamed but very well known Early Cretaceous triconodontid from Montana (Crompton and Luo, 1993; Cifelli *et al.*, 1998). The enamel is columnar and quite reminiscent of the view obtained from *Sinoconodon* enamel except

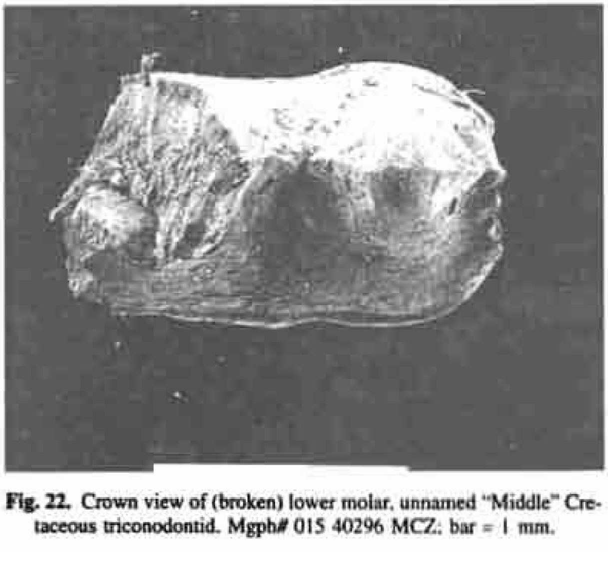

Fig. 22. Crown view of (broken) lower molar, unnamed "Middle" Cretaceous triconodontid. Mgph# 015 40296 MCZ; bar = 1 mm.

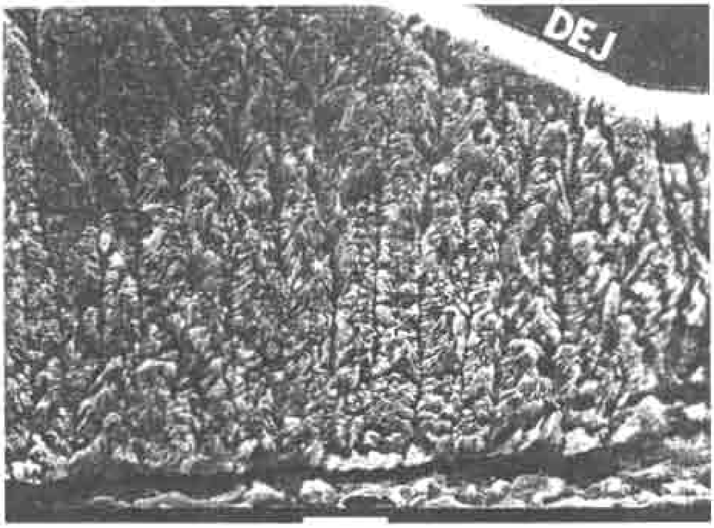

Fig. 23. Embedded, polished cross section of enamel in same specimen as in Fig. 22. The structure is columnar; note, however, that the surface is not as smoothly polished as those in Figs. 21 and 25. Mgph# 026 41696 MCZ; bar = 10 μm.

for not being polished as flat. Figure 24 is a related triconodontid from Utah (Cedar Mountain Formation), slightly younger than the first (personal communication from R. Cifelli, who generously donated the specimens). Lines which define columns (Fig. 25) are more reminiscent of prism seams in the *Gobiconodon* micrographs; although strong prism sheaths are not evident, overall the appearance is similar to the *Gobiconodon* structure but with yet more subtle (or incipient) prisms. The structure also resembles that of *Sinoconodon* (compare Fig. 26 to Fig. 21). Two points may be evident in these results: (1) this is incipient prismatic enamel, expressed with maximal subtlety, and (2) this (including the structure in *Gobiconodon* and *Sinoconodon*) represents the previously unknown transition between SCE and PPE (Sander, 1997, see especially p. 55). The differences between transitional PPE and SCE are minor but include widening (homologous to sheaths) at the base of some seam planes and less continuity of seam planes from the dentine–enamel junction (DEJ) to the outer enamel surface (OES) in the transitional PPE.

Docodon

The Docodontidae is a family of Jurassic mammals with rather unusual dental morphology [Fig. 27; see Jenkins (1969)]. It is not a diverse family; only two genera (*Docodon* and *Haldanodon*) are known from abundant material. The phylogenetic position of the family has been unclear. Lillegraven and Krusat (1991) described the basicranium of *Haldanodon* (Late Jurassic, Guimarota Mine, Portugal) and concluded that docodonts were a very basal offshoot of Mammalia (sister group to *Sinoconodon* plus Morganucodontidae and other mammals), whereas Luo (1994) placed *Haldanodon* beyond *Sinoconodon* (before Morganucodontidae) and Rougier *et al.* (1996) place it beyond Morganucodontidae (before montremes). Lester and Koenigswald (1989) ex-

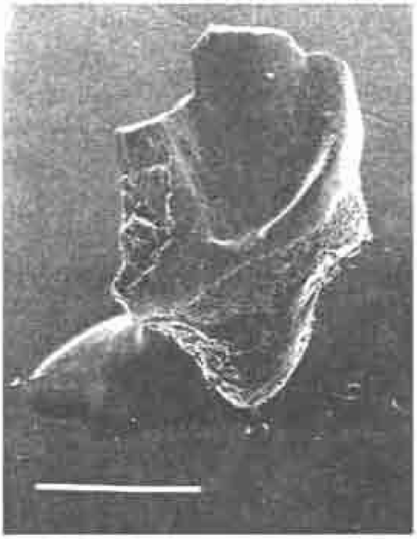

Fig. 24. Lateral view of broken lower molar, "Middle" Cretaceous triconodontid, cf. *Jugulator*. Mgph# 014 11256 MCZ: bar = 1 mm.

amined enamel from *Haldanodon* and found it to be without prisms. Sander (1997) indicates that *Haldanodon* has SCE.

Until now *Docodon* had not been examined with SEM [but see Moss (1969), who used polarized light microscopy]. Figures 28–30, from a Late Jurassic (Como Bluff,

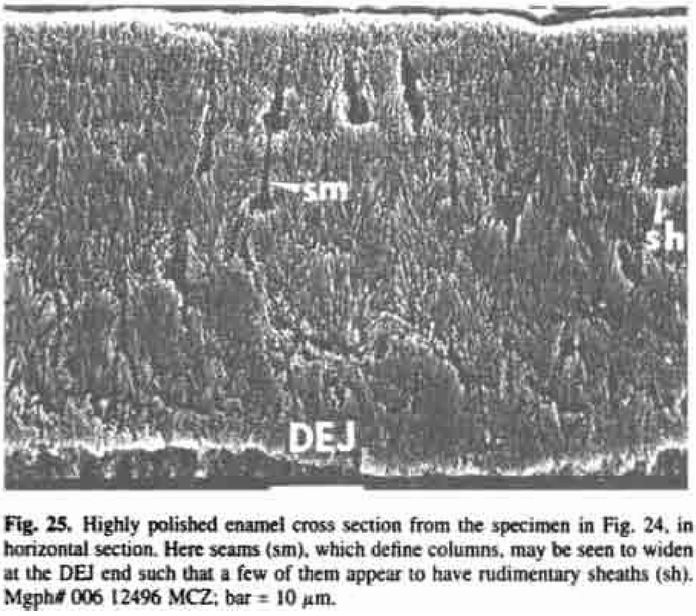

Fig. 25. Highly polished enamel cross section from the specimen in Fig. 24, in horizontal section. Here seams (sm), which define columns, may be seen to widen at the DEJ end such that a few of them appear to have rudimentary sheaths (sh). Mgph# 006 12496 MCZ; bar = 10 μm.

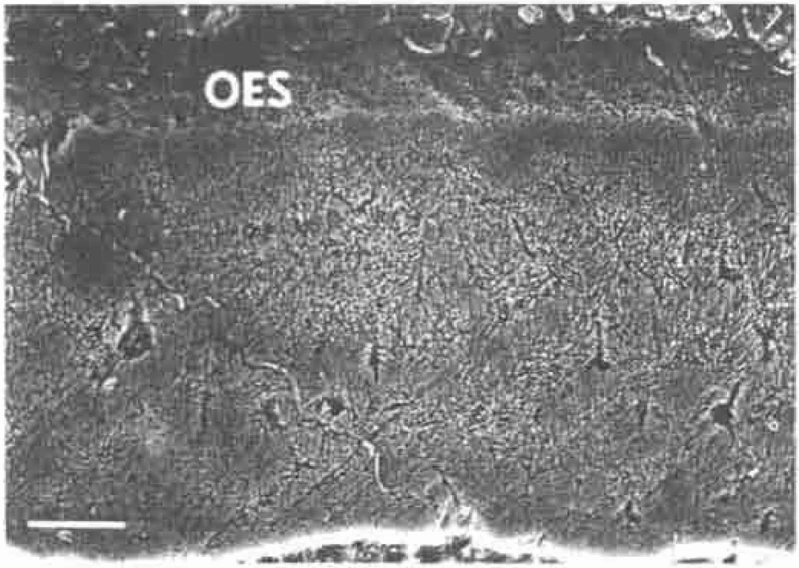

Fig. 26. Another view of the section in Fig. 25, with erratically spaced seams and ?sheaths; this is comparable to the structure seen in parts of the *Gobiconodon* specimen (see Fig. 19). Mgph# 003 12496 MCZ; bar = 10 μm.

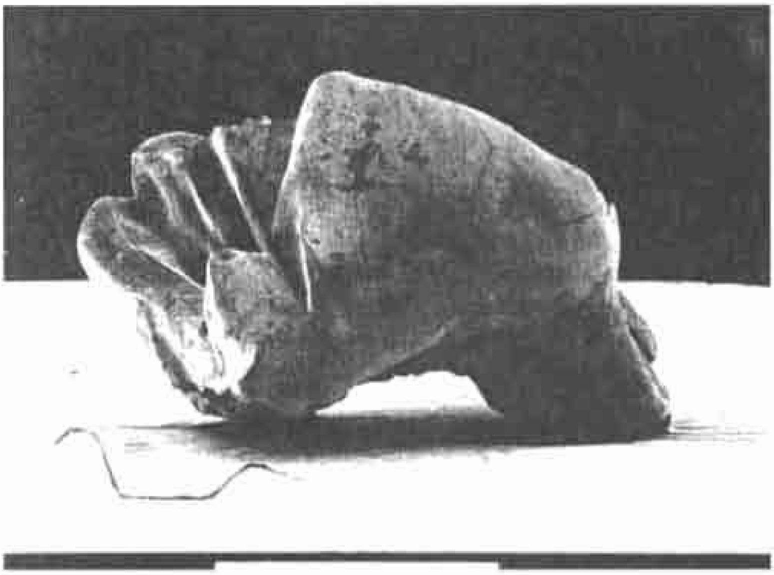

Fig. 27. *Docodon victor* (Late Jurassic), oblique view of lower molar. Mgph# 006 31996 MCZ; bar = 1 mm.

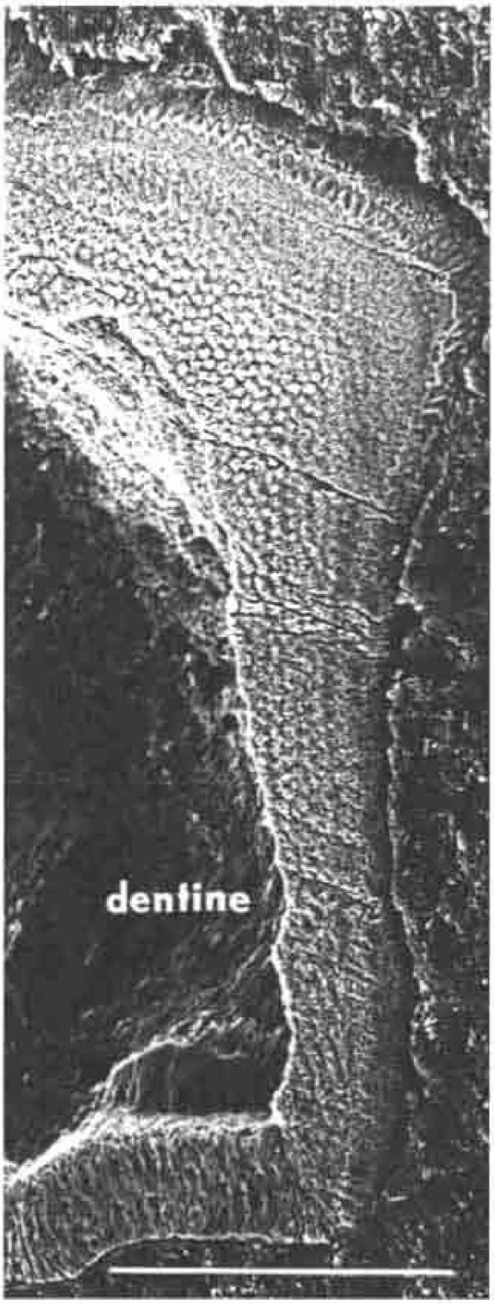

Fig. 28. Montage of part of embedded specimen of *Docodon* (Fig. 27), with moderate polish and moderate etch. There is a distinct change of direction of subtle columnar/prismatic structure from the top to the bottom of the figure. Mgph# 008 and 005 40996 MCZ; bar = 100 μm.

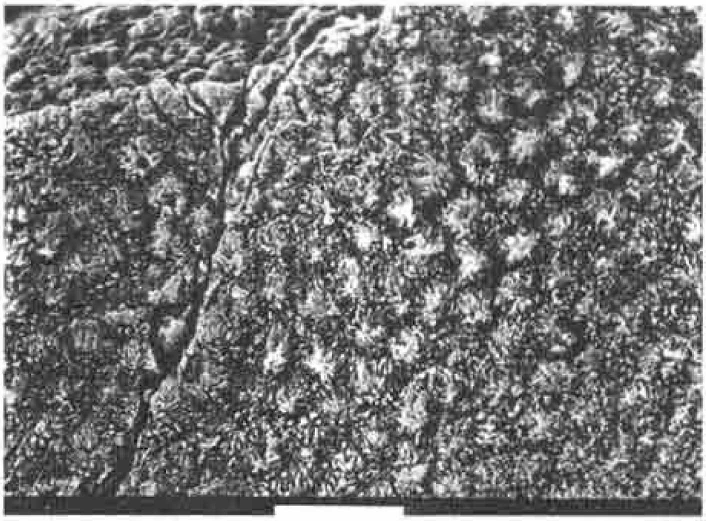

Fig. 29. Higher magnification within the top part of the montage of *Docodon* in Fig. 28. Mgph# 004 40996 MCZ; bar = 10 μm.

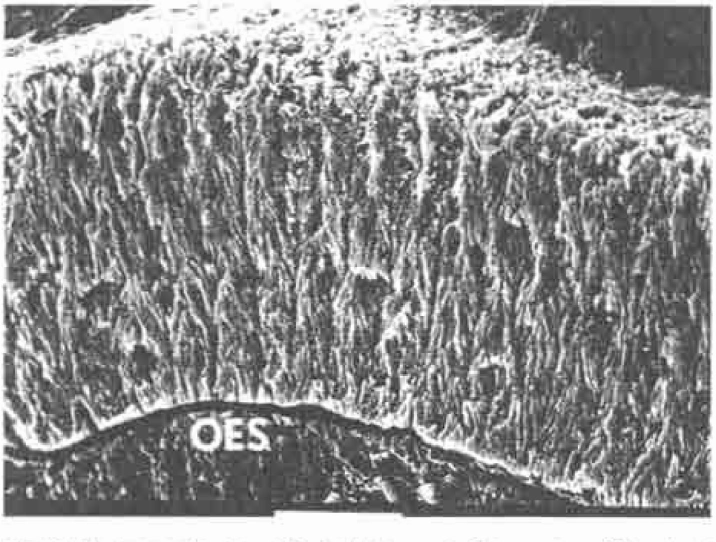

Fig. 30. Higher magnification within the bottom part of the montage of *Docodon* in Fig. 28. Here the structure is columnar, with very subtle sheath-like discontinuities at right angles to the seams which define columns. Mgph# 007 40996 MCZ; bar = 10 μm.

Wyoming) specimen of *D. victor*, demonstrate another variety of very subtle, if incipient, prismatic enamel that is visible through a combination of polishing, airpolishing, and light etching with acid.

DISCUSSION

Definition of PPE

Since the review by Wood and Stern (1997) it is clear that plesiomorphic prismatic enamel (PPE; see Fig. 31B) is not a single character state that may be scored as either present or absent. Rowe (1988) scored prismatic enamel as either present or absent in his phylogenetic analysis; although this was a necessary first step in the cladistic analysis of mammals, and of enamel, it also allowed Wible (1991) to dismiss prismatic enamel rather easily in his rebuttal to Rowe.

Koenigswald and Clemens (1992) and Koenigswald *et al.* (1993) have shown that for thorough understanding, enamel must be characterized at several hierarchical levels of organization, including crystallite, prism, enamel type, schmelzmuster, and dentition. Accordingly, Wood and Stern (1997) discussed PPE in terms of five character states, which may be summarized as follows.

(1) PPE prisms usually range from about 2.5 to 5.5 μm in diameter and are clearly delimited from a radial "sea" of interprismatic crystallites by arc-shaped prism sheaths visible in tangential or horizontal sections [see Koenigswald and Sander (1997b) for a glossary of terms]. A prism may be defined by the presence of a sheath. In PPE the sheath is a semicylindrical discontinuity within the enamel, caused by the ends of radial interprismatic crystallites as they abut the long sides of crystallites within the prism bundle. Sheaths could be defined by other circumstances or materials in more derived or in extant mammals, but in earlier mammals it appears that the presence and distinctness of a sheath may be directly correlated with the angle between prism and interprism crystallites—the lower the angle, the less distinct the sheath (and therefore the prism; see below). Enamel with prisms in any layer or position upon the tooth crown may be called prismatic enamel, even when prisms are absent in large portions of the crown. Regardless of other structure, Sander (1997) and Wood and Stern (1997) have advocated that the word "prismless" be applied to enamel that has no clear prisms anywhere on the tooth crown. Sander (1997) adds further commentary to the definition of prism and prismatic enamel; there is a clear consensus that words such as "preprismatic" and "pseudoprismatic" should be abandoned to avoid further confusion.

(2) In the same planes of section (tangential and horizontal) as sheaths, a strong linear or planar "prism seam" (Lester and Koenigswald, 1989) bisects part of the prism within the sheath, usually extending through the open ends of the sheath arc toward the outer enamel surface (OES), and often well into the interprismatic area toward the next prism sheath. Prism seams are so widespread in early mammals and in all earliest representatives of extant subclasses that they must certainly be considered a plesiomorphic enamel feature, as suggested by Lester and Koenigswald (1989) and Lester (1989). This would mean that any prisms without seams (Fig. 31C) would represent a derived condition, regardless of other attributes of the enamel at the prism level or higher levels of organization.

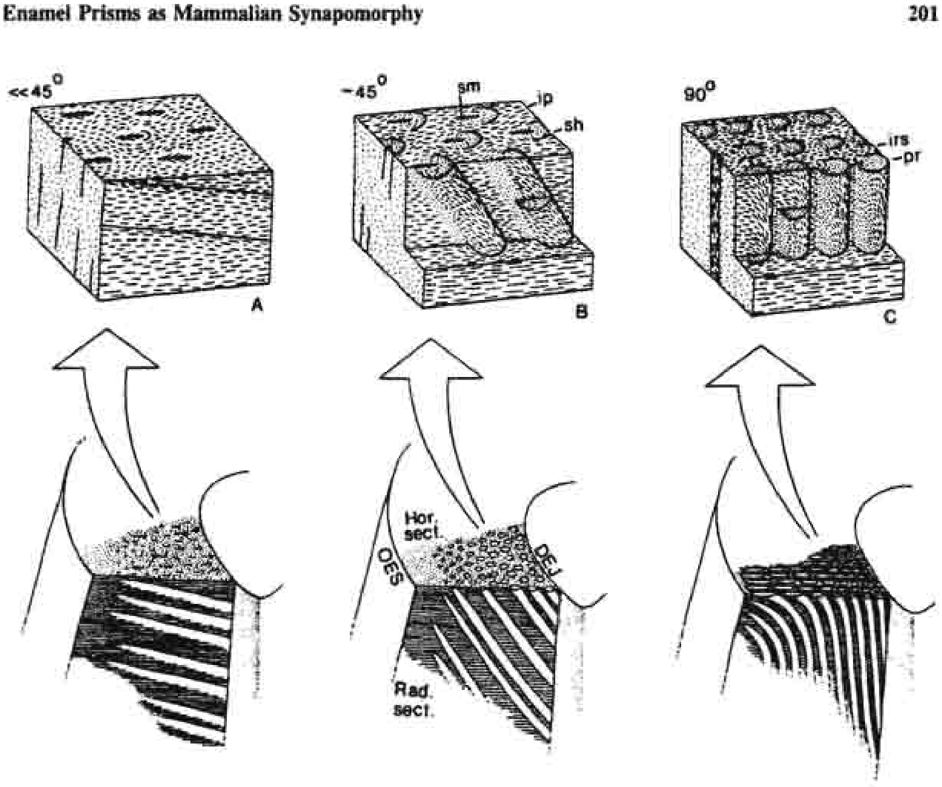

Fig. 31. Schematic diagram to represent transformations from "transitional," almost-synapsid columnar enamel (SCE) structure, through plesiomorphic prismatic enamel (PPE) structure, to derived prismatic structure such as seen in *Didelphis*. The lower part of the figure represents a tooth cusp in horizontal section (Hor. sect.) and in radial section (Rad. sect.) to illustrate enamel structure in the layer between the dentine–enamel junction (DEJ) and the outer enamel surface (OES) for each of the upper, magnified enamel blocks. (A) "Transitional" structure, such as that seen in triconodontids or *Sinoconodon*. Seams and "prismatic" crystallites are inclined at much less than 45° to radially oriented "interprismatic" crystallites, and thus sheaths are indistinct or absent. (B) PPE structure, as in *Spalacotheridium*, *Pediomys*, and *Dromiciops*, in which prism seams (sm) and crystallites are inclined at about 45° to the interprismatic "matrix" (ip); prism sheaths (sh) are therefore distinct between the two sets of crystallites. The prisms are "open" toward the OES, due to a gradual change in direction of prismatic crystallites (to become parallel to interprismatic crystallites) in that area. (C) Derived prismatic structure, such as in *Didelphis*. Here the prisms stand at about 90° to the interprismatic crystallites. Prism seams have disappeared and the prisms are lined up in rows (pr) so that interprismatic crystallites now separate the rows in distinct interrow sheets (irs). Although prismatic crystallites here gradually change direction toward the OES (as in PPE), in other derived mammals there may be an abrupt change in direction on the OES side also, which gives those prisms a "closed" or "circular" shape.

(3) PPE prisms are usually well separated by broad areas of interprismatic crystallites, with prisms usually arranged in a roughly hexagonal packing pattern, but also likely to be irregularly arranged. Prisms stacked in rows (Fig. 31C) or packed so closely together as almost to exclude interprismatic areas [e.g., human and elephant enamel (see Carlson, 1990)] represent a derived condition relative to PPE.

(4) In many Mesozoic taxa with PPE, including representatives of at least Placentalia, Marsupialia, "Tribotheria," Dryolestoidea, and spalacotheriid Symmetrodonta, there is a thick outer layer of aprismatic or AP enamel ("PLEX" of Koenigswald and Sander, 1997b). This is sometimes comparable in thickness to the layer of prismatic enamel below

it toward the dentine–enamel junction (DEJ; see Figs. 11–13). Thick, outer AP enamel is present in *Pachygenelus* and in *Megazostrodon* (though not to the degree of some later mammals), which suggests that it is a constant element of PPE and also that relatively thick outer AP enamel is plesiomorphic to both Marsupialia and Placentalia. It is possible, nevertheless, that many extant mammals with thick outer AP may have secondarily derived this character from Cenozoic ancestors which had earlier decreased or even lost the outer aprismatic zone (see discussion below).

(5) No prism decussation or simple change of direction of prisms has been observed in mammals with PPE; instead the prisms are arranged in a simple parallel, radial orientation outward from the DEJ, and tilted toward the apex of the cusp or crest at an angle of around 45° to a more horizontally oriented interprismatic matrix. In extant didelphimorph marsupials such as *Didelphis* and *Philander*, prisms often stand at nearly 90° to the interprismatic crystallites (Fig. 31C; see Wood, 1992). Such high angles clearly are derived with respect to PPE, as are complex or simple decussations of prism rows or of prisms and inter-row sheets. As indicated elsewhere in this report, lower angles between prism and interprism crystallites begin to obscure prism sheaths, and thus prisms (Fig. 31A), but we believe that this can be true of either ancestral or derived enamel with respect to PPE.

Phylogenetic Implications

Figure 32 represents the mammalian cladogram from Wood and Stern (1997), modified and updated with the new information presented above. The position of *Gobiconodon* is not certain—it could arise at a more basal point than indicated because of dental replacement characters not discussed in this paper. It is now known also that haramiyoids may be unlikely associates or close relatives of multituberculates (Jenkins *et al.*, 1997).

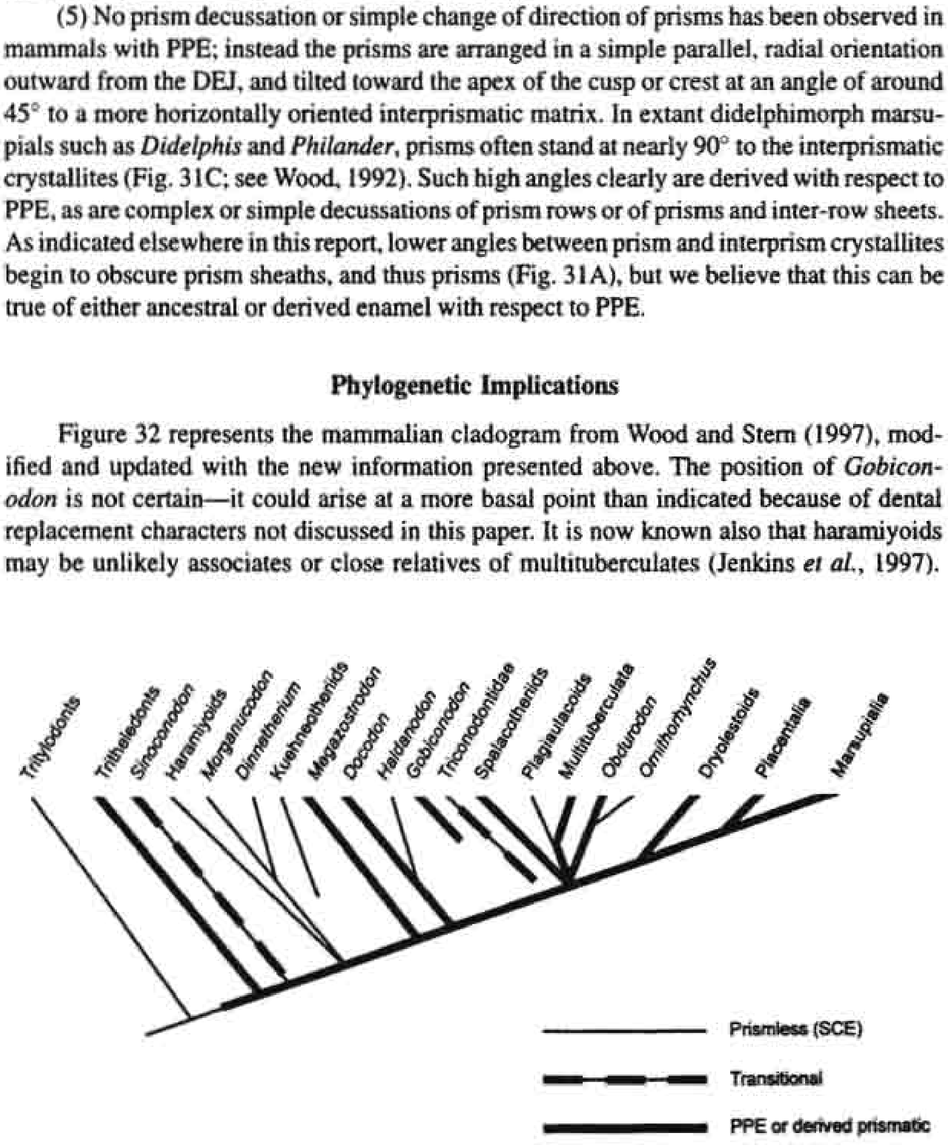

Fig. 32. Generalized cladogram with enamel structures mapped as interpreted in this report. See text for discussion and explanation. We follow Lucas and Luo (1993) for convenience, so that Mammalia begins after tritheledonts and before *Sinoconodon*. At present, enamel microstructure has been observed only for *Pachygenelus* among trithelodontids and only for *Kuehneotherium* among kuehneotheriids.

Wood and Stern's (1997) cladogram supported both single and multiple origins of prisms in mammals with equal parsimony—six transformational steps in either case (not counting later steps such as in *Ornithorhynchus* and possibly several times among whales); preference for multiple or single origins remained a matter of personal choice. In the cladogram in Fig. 32 a single origin of prisms now becomes more parsimonious than multiple origins. At most this diagram shows five steps required for single origin, as opposed to the necessity of seven steps (or more) for multiple evolution of prisms. Indeed, it may even be possible that kuehneotheriids, *Morganucodon–Dinnetherium*, and haramiyoids represent a single, autapomorphic step of reversal, in which case the count would become three to seven in favor of single origin as most parsimonious.

Despite competing interpretations of their phylogenetic position within Mammalia, nearly every recent phylogeny would show Multituberculata bracketed on both sides by sister groups with PPE. In Clemens (1997, Fig. 3; see also Simmons, 1993) the so-called ancestral gigantoprismatic origin of prismatic enamel in the group is actually bracketed by a plesiomorphic sister group (*Ferugliotherium*) with small prisms. "Plagiaulacida" is indicated with prismless enamel, but according to Simmons (1993), several important Jurassic taxa remain unsampled. At most, small prisms evolve four times. Another scenario is that gigantoprismatic enamel evolves once and that there are three later reversions to small prisms. We do not know how likely this may be. All multituberculates are extinct and no extant animals are known to have gigantoprisms. No living ameloblasts large enough to secrete enamel into a single gigantoprism have been observed. The ontogeny of gigantoprisms therefore remains a mystery, as does any possible mechanism for the conversion of one to a small prism, or vice versa.

"Underlying Synapomorphy"

In all contending cladograms, *Pachygenelus* (a nonmammalian, trithelodontid cynodont) and *Megazostrodon* are among the most basal members to the mammalian clade, and both exhibit fully developed PPE (Stern and Crompton, 1995; Sander, 1997; Wood and Stern, 1997).

Koenigswald (1997; with reference to Saether, 1979) raises an interesting new concept for enamel evolution called "underlying synapomorphy." Although Koenigswald applies the concept to the recurrent origins of more complex structural types in several groups of placental mammals, the concept may also apply to this discussion. Simply stated, the idea implies that the genetic potential for a certain structure appears once in an ancestor that may not express that genetic potential itself, and in later descendants several lineages show the structure, whereas others do not. Koenigswald (1997) concludes that interpreting phylogeny based on presence or absence of the structure is greatly complicated by this possibility. This kind of occurrence may seem to represent an untestable hypothesis at the moment, but it will in fact be testable in the future when the genetic basis for enamel pattern has been fully worked out. We suggest that it may be biologically most parsimonious (see Wood and Stern, 1997) for the genetic basis for PPE to have appeared only once in the common ancestor of *Pachygenelus* and all mammals and that the early versions of the structure are simple enough structurally and ontogenetically to be suppressed easily; thus, not all later lineages (especially early branches) may have expressed the structure ontogenetically.

In other words, we propose that the genetic basis for prismatic enamel is synapomorphic for *Pachygenelus* plus Mammalia, whether expressed in all descendants or not. Sander (1997) has shown that no other synapsids have true prisms. He and others have shown that—with one exception—no other nonsynapsid amniotes have anything like truly prismatic enamel. The single, exceptional occurrence of prism-like structures is in the agamid lizard, *Uromastyx* (Cooper and Poole, 1973). In this case, when examined in detail, the prisms are not at all like those in mammalian PPE. It is obvious, therefore, that the structure in *Uromastyx* is (uniquely) analogous to but in no way homologous to prisms in mammals. There is great diversity and complexity of enamel structure among sauropsid amniotes, especially among archosaurs, and this should be studied for its own sake. Nonmammalian amniotes have evolved many ways to strengthen enamel within a variety of functional contexts, but none are known to have evolved a Tomes process capable of secreting PPE.

Phylogenetic Reversal

Phylogenetic reversal implies the evolution of a derived structure or character back to its plesiomorphic state. For a complex or large structure such as a tetrapod limb, evolution back into a fin can occur but the fin is not anatomically identical to the fin in a pretetrapod ancestor. It is rather widely held in vertebrate paleontology, furthermore, that once a complex structure such as a limb has been lost, it is unlikely or impossible for one to reevolve.

For a numerical character, such as molar tooth count, developmental mechanisms may produce supernumerary teeth (e.g., in *Otocyon*) but it is not clear whether this should be regarded as a reversion to an ancestral count—it remains unclear whether the ancestral placental or tribotherian count was four molars instead of three (Kielan-Jaworowska and Nessov, 1990; Marshall and Kielan-Jaworowska, 1992; Cifelli, 1993), and it is unclear whether the developmental mechanism responsible for supernumerary teeth has anything to do with the mechanism for determination of tooth number in the ancestor.

In the case of microscopic, relatively simple, structures such as SCE (synapsid columnar enamel) and PPE, however, the transformation of either type into the other seems by comparison a less forbidding possibility. Both enamel patterns are the result of the shape and function of only part of a single cell, the Tomes process of the secretory ameloblast. The mature enamel in SCE is not very different from that in PPE. The qualitative differences between them may be clearly described and the number of differences would be small by any measure one might choose. It is apparent that rather subtle differences in the shape of the Tomes processes of ancestor and descendant would result in the consequent enamel patterns and that the return of the Tomes process to the ancestral shape would cause a reappearance of the ancestral pattern in the mature enamel of a descendant. In fact, it has been suggested (Lester and Koenigswald, 1989) that such a transformation of the Tomes process may be inferred during development in extant species that have relatively thick outer AP enamal, such that the outer AP enamel at least superficially resembles a less derived condition than the middle zones of the enamel deposited earlier on the same tooth.

Causes of Reversal from PPE to SCE

At least two ways may be considered for reversal of mature enamel from PPE to SCE. Whether these possibilities are mutually exclusive is an open question; conceivably both could occur together in the reversion of PPE to SCE.

Low Angle Between Prismatic (P) and Interprismatic (IP) Crystallites in PPE

In PPE a visible, etched prism sheath is the main feature for defining a prism and thus the presence of prismatic enamel. In this enamel the sheath is visible only because of the abrupt difference in direction of prism and interprism crystallites. That is, the sheath represents the discontinuity of the long sides of prism crystallites where they abut the ends of radial, interprism crystallites; this discontinuity is enlarged and therefore made more visible by etching with acid (Figs. 32B and C). It follows from these observations that no sheath will be visible unless there is a distinct angle between prism and interprism crystallites sets and that, if the angle approaches zero, prisms disappear into the interprismatic (IP) fabric (Fig. 32A). In Figs. 16 and 28, the enamel of *Laolestes* and *Docodon* (see also certain sectors of enamel in *Gobioconodon;* Fig. 19) shows subtle or incomplete prism sheaths (and thus prisms) because of a low angle between the two crystallite sets. With careful preparation, however, it can be seen that the equivalent of a relatively strong planar prism seam still remains in the enamel and that this may still divide the enamel into a columnar pattern in horizontal section (see illustrations of *Sinocondon* enamel in Figs. 20 and 21). These columns are the "pseudoprisms" of Lester and Koenigswald (1989) and Lester (1989), and we submit that these columns may define SCE as well.

A relatively minor change in the shape of the Tomes process would be enough to cause a visible sheath to appear or disappear around the constant feature of the planar seam. To put it another way, PPE in an ancestor like *Pachygenelus* could easily be reversed into SCE by this means.

Increasingly Thick Outer Aprismatic (AP) Zone

In most known species with PPE there is also a relatively thick outer AP (aprismatic, or PLEX) zone of enamel in which prisms are either indistinct or absent. In some species the inner, prismatic zone may be coequal in thickness to the outer AP (see Figs. 11–13). In other species [e.g., *Dromiciops gliroides* (see Wood, 1992)] as one traces the enamel toward its cervical, thinner margins, the prismatic layer becomes less of the total thickness until, near the margin, it is absent and only AP enamel is present. It would seem reasonable therefore that some species could evolve in which the AP expands (or the prism layer diminishes, or both) to the point that enamel on the entire tooth crown becomes prismless. This is admittedly a speculative scenario, with currently no evolutionary sequence to document it. Some Mesozoic mammals, e.g., *Morganucodon* and *Dinnetherium*, have prismless enamel which is also very thin even when compared to the small size of the tooth; this thinning suggests the possible inhibition of developmental mechanisms which might otherwise produce a prismatic layer. Explanations for such changes in enamel layers would include adaptive scenarios regarding the function of prismatic and aprismatic components. Several of these are outlined in the following section.

Functional/Adaptational Considerations

A thick layer of secondarily derived, aprismatic enamel is characteristic of some toothed whales (Werth and Stern, 1992; Sahni and Koenigswald, 1997; Boyde, 1980; Ishiyama, 1984, 1987), fruit and vampire bats (Lester and Hand, 1987; Lester *et al.*, 1988; Dumont, 1993), and the platypus (Lester *et al.*, 1987). Because the teeth of many of these taxa are reduced from their ancestral condition, aprismatic enamel is frequently considered to be a product of tooth degeneration (Lester and Boyde, 1986; Lester *et al.*, 1987; Maas and Thewissen, 1995). From this perspective, aprismatic enamel is not considered to be of functional significance. This view is perhaps not unexpected given the extraordinary variety of mechanical adaptations that have been documented for more complicated forms of prismatic enamel (Pfretzschner, 1994; see for a recent review Rensberger, 1997). However, the assumption that aprismatic enamel is an incidental result of tooth degeneration may not apply to all lineages in which aprismatic enamel occurs.

Sharp Cutting Edges. Stern *et al.* (1989) and Crompton *et al.* (1994) have analyzed the morphological details of molars with a triangular outline in occlusal view and have suggested that enamel structure varies in predictable ways on the shear and grinding surfaces of these teeth. Crompton *et al.* (1994) suggested that prismatic enamel arose coincidentally with precise, interlocking occlusion in which shear surfaces trap food and cut it in a manner analogous to scissor or paper cutter blades. Such blades require sharp edges maintained by flattened surfaces meeting at 90°. If such edges become worn so that the edges are rolled over and thus blunted, then the shearing ability is greatly diminished. The orientation of prismatic and interprismatic crystallites in opposition is such that wear is inhibited on the shear facet more than on the apical surface of the worn enamel-to-dentine cross section [see Figs. 6 and 7 of Crompton *et al.* (1994)] and this differential wear becomes a highly adaptive, self-sharpening mechanism. Mechanical testing of this result is difficult because of scale, but some experimental work has been conducted by Maas (1991).

Observational difficulties with this hypothesis are that some species (e.g., *Morganucodon*) with wear facets do not have any prismatic enamel and that most known early mammals which maintain sharp shearing blades are ones in which the sharp edge actually develops in the outer AP zone (e.g., see Figs. 7 and 11–13). Self-sharpening edges may indeed develop from the orientation of the enamel fabric but this may not by itself be an adequate explanation for the origin of prismatic enamel in synapsids.

In *Morganucodon* (and presumably *Dinnetherium*) effective shear is not established until the teeth are thoroughly worn (Crompton and Jenkins, 1968; Crompton, 1995). It is possible that prismatic enamel, if it reduced wear in these animals, could actually impede the development of shear.

Enamel Strength Against Crack Propagation, and Rate of Tooth Wear. As mammals evolved from nonmammalian cynodonts, their teeth were subjected to greater stresses from chewing (instead of simply puncturing or holding) and mechanisms would be needed to keep enamel from cracking away from the tooth. There are at least two reasons that chewing in mammals generates greater stress: (1) molar occlusion, in which shear and tooth-to-tooth contact occur, and (2) the fact that occlusion is unilateral. As a result of unilateral occlusion, muscle force from both sides can concentrate on one bite point; nonmammalian cynodonts are not capable of this (reviewed by Crompton, 1995).

Koenigswald (1980, 1988), Pfretzschner (1992, 1994), Rensberger (1992, 1995), and others (see review by Rensberger, 1997) have conducted studies which show that prismatic enamel is a composite material which (though brittle) has greater resistance to cracking than a noncomposite (prismless) enamel. The first appearance of this structure in synapsids coincides with the appearance of precise occlusion and shear facets (*fide* Crompton *et al.*, 1994), but this may not be the whole story because herbivorous ornithopod and ceratopsian dinosaurs also have effective shear yet lack prismatic enamel. Grine and Vrba (1980) suggested that prisms may also be associated with reduced rates of tooth replacement (i.e., the origin of diphyodonty in mammalian synapsids), where greater strength due to prismatic structure may also reduce the rate of tooth wear overall. Those herbivorous dinosaurs most adapted to shearing function evolved toward ever greater rates of tooth replacement than ancestral dinosaurs, rather than toward any obvious mechanism which would slow down rates of tooth wear. In this context it is interesting to note that *Uromastyx*, the herbivorous agamid lizard which develops prism-like structures in its enamel, has wear facets, shear, and also greatly reduced tooth replacement (Cooper and Poole, 1973).

Gomphodont cynodonts, with prismless SCE enamel, wore out their molariform teeth rapidly. They compensated by continuous replacement at the back of the tooth row to keep pace with loss of molariform teeth in the front. Mammals, because they suckle, can compensate for growth by a single replacement of the milk dentition plus the addition of molars without replacement. Once occlusion is established, replacement of the molars would lead to malocclusions (Crompton, 1972, 1995). Tougher teeth, with enamel more resistant to wear, would appear to be adaptive in this set of circumstances.

Size and Total Load. A mostly uninvestigated question is whether smaller mammals with small teeth (that do not shear) would be likely to lose prisms over time. Extant examples which come to mind include *Myrmecobius* (marsupial numbat) and *Proteles* (aardwolf), both of which have secondarily simplified molars as an apparent adaptation to a diet of termites. A similar question is whether it may be adaptive to lose prismatic enamel in larger mammals (i.e., odontocete whales) that do not load the teeth by means of shear or other functions, such as powerful grasping of prey.

We have examined specimens of *Myrmecobius* and *Proteles* (not illustrated), and although they do not have derived composite enamel patterns (i.e., prism decussation), they do have a prismatic enamel otherwise comparable to their respective noninsectivorous relatives. We have briefly examined molars of the pinniped genera *Eumetopias* and *Phoca* as examples of large mammals with tricuspid molars that lack shear facets; both have prismatic enamel with some degree of prism decussation. Rensberger's (1997, 1999) study of hyena canines indicates that a more or less conical tooth may have highly derived prismatic enamel as a response to vertical loading (and slight bending), despite having no shear function comparable to a normal molar. It is conceivable, therefore, that *Eumetopias* and *Phoca* might retain a derived prismatic enamel as a response to stress generated from the powerful grasping of food items prior to ingestion. Although considerable variation in prismatic and prismless structure has been reported in odontocete whales (e.g., Sahni and Koenigswald, 1997; Ishiyama, 1987), it would be very interesting to correlate this variation with data on feeding in the genera which have been studied. An obvious question is whether the genera that have weak or no development of prismatic enamel are also ones which minimize or lack grasping of prey prior to ingestion (see Werth and Stern, 1992).

The Chemical Environment of the Mouth. It has been clearly documented in the clinical literature that people who are frequently exposed to dietary, stomach, or environmental acids experienced high rates of enamel erosion (Zero, 1996), which can lead to increased tooth wear and eventually tooth loss (Nunn, 1996; Sorvari *et al.*, 1996). Withi the oral cavity, pH need only drop below 5.5 before enamel erosion occurs (Newbrun, 1989). Fruits, in particular, have pH values well below 5.5 (Grobler, 1991; Ungar, 1995), suggesting that frugivore teeth are frequently exposed to erosive acids.

One potential protective mechanism in frugivore mouths is saliva, which has intrinsic pH and buffering systems that play important roles in maintaining oral health (Birkhead and Heinz, 1989). Because frugivore teeth are likely to be exposed to frequent dietary acids, the saliva of frugivores might be expected to be alkaline and well buffered as a means of compensation. In fact, the saliva of many frugivores is routinely more acidic and more poorly buffered than that of either insectivores or folivores (Dumont *et al.*, 1997; Dumont, 1997). In the absence of salivary protective mechanisms, aprismatic enamel may function to protect frugivore teeth from erosion.

The performance of enamel under etching regimes has been of interest to clinical researchers because erosion is the cornerstone of many oral health problems (Shellis and Hallsworth, 1987; Frank, 1990). SEM studies have revealed that prismatic and aprismatic enamel perform differently under the same etching regimes. Prismatic enamel erodes quickly as acids penetrate along prism boundaries and remove large areas of enamel (Haikel *et al.*, 1983; Shellis and Hallsworth, 1987; Frank, 1990; Nelson, 1990). In contrast, a diffuse, irregular dissolution pattern is characteristic of aprismatic enamel exposed to acid (Haikel *et al.*, 1983; Boyde, 1984b; Shellis and Hallsworth, 1987; Meurman and ten Cate, 1996).

The resistance of aprismatic enamel to erosive wear may be attributed to the dense packing of crystallites. Ichijo *et al.* (1992) report that surface aprismatic crystals in humans are more irregular in size and shape and more densely packed than crystals within deeper, prismatic enamel. Aprismatic surface enamel also is harder and more highly mineralized than underlying prismatic enamel (Hodge and McKay, 1933; Caldwell *et al.*, 1957; Newbrun and Pigman, 1960; Gwinnett, 1967; Newbrun, 1989). Gwinnett (1992) viewed this feature as additional evidence that aprismatic enamel is more resistant to demineralizing agents than is prismatic enamel. Given this evidence that aprismatic enamel is more resistant to erosion than is prismatic enamel (at least in humans), it seems appropriate to consider the possibility that secondarily thick layers of aprismatic enamel in some species represent an adaptation for an acidic diet.

Clearly more data summarizing salivary chemistry, food chemistry, and the distribution of aprismatic enamel within lineages are needed to support this hypothesis. Such analyses of frugivores are currently in progress (Dumont, in preparation). Nevertheless, it is also clear that while the impact of chemical milieu of the mouth has not been considered a significant factor in enamel evolution, it may, in fact, have significant implications in some lineages.

Ontogenetic Factors. Whatever the force that drives thickened layers of aprismatic enamel, the mechanism of its formation lies in tooth development. Hydroxyapatite crystals, the basic building blocks of enamel, form within enamel matrix proteins perpendicular to the secretory fronts of ameloblast cells (Boyde, 1964, 1969, 1976b; Wakita and Kobayashi, 1983). Prismatic enamel forms when the secretory poles of ameloblasts are protruded, and aprismatic enamel forms when secretory poles of ameloblasts are flat. In mammalian teeth, aprismatic enamel forms at the enamel–dentine junction and outer enamel surface as ameloblasts begin and end their secretory phase (Ripa *et al.*, 1966; Gwinnett, 1967; Martin, 1983; Fortelius, 1985; Martin *et al.*, 1988). This supports

Boyde's (1964) hypothesis that the formation of aprismatic enamel is associated with reduced levels of ameloblastic activity.

Secondarily derived aprismatic enamel appears to result from a shift in the timing of the reversion to flat-ended ameloblasts during dental development. Determining the cause of the timing shift is a difficult task. Thick layers of aprismatic enamel could result from a slowdown in ameloblastic activity that represents metabolic savings during the development of nonfunctional teeth. Alternatively, the early reversion to flat-ended ameloblasts may be selected for in cases where aprismatic enamel serves a protective function. Choosing between these alternatives will require additional information regarding the rates of deposition of aprismatic enamel in mammals as well as a more detailed understanding of dental function in groups such as bats and whales.

CONCLUSIONS

A morphological sequence from synapsid columnar enamel (Sander, 1997; see especially p. 55) to incipient, through fully-developed plesiomorphic prismatic enamel (Wood and Stern, 1997) is illustrated in Figs. 20, 21, 25, 18, 13, 9, and 5 (also Fig. 32). This is not a phylogenetic sequence in the taxa illustrated, but we suggest that PPE has been easily derivable from and reversible into SCE by similar transformations of structure. Whereas only one nonmammalian synapsid (the trithelodontid *Pachygenelus*) and no other nonmammalian amniotes have PPE, it is clear that the ability or potential of an ameloblastic Tomes process to secrete PPE is synapomorphic to *Pachygenelus* plus all derived sister groups [Mammalia (*sensu* Lucas and Luo, 1993)], whether or not that potential is expressed in all descendants. Unfortunately, this result does not clarify the relationship of tritylodontid and trithelodontid cynodonts to one another and to mammals. Tritylodontids do not have prismatic enamel (Stern and Crompton, 1995; Wood and Stern, 1997). This observation could place tritylodontids either within (after *Pachygenelus*, because of structural reversal) or outside of (due to plesiomorphic ameloblasts) the clade *Pachygenelus* plus Mammalia. At this time we favor the suggestions (Shubin *et al.*, 1991; Crompton and Luo, 1993; Lucas and Luo, 1993; Luo, 1994) that Trithelodontidae (including *Pachygenelus*) are closer to the mammals.

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