

Ultrastructure of dental hard tissues of *Gondwanatherium* and *Sudamerica* (Mammalia, Gondwanatheria)

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The ultrastructural study of small dental fragments of the South American mammals *Gondwanatherium* Bonaparte, 1986 (late Cretaceous) and *Sudamerica* Scillato-Yané & Pascual, 1985 (middle Paleocene), tentatively classified in the Paratheria, has shown the same structural characteristics. In the first genus one notes the presence of a thick, well differentiated, prismatic enamel with prisms of pattern 1 of Boyde and interprismatic substance. In places, lines of apposition are visible. The most internal zone of the enamel is very rich in tubules, which become rarer in the peripheral enamel. The dentine presents numerous parallel tubules, sometimes continuing into the enamel. The presence of enamel over the whole height of the tooth fragment indicates that the hypsodonty here would be due almost entirely to lengthening of the crown. While structurally resembling the specimen of *Gondwanatherium*, the dental fragment of *Sudamerica* differs in its enamel locally constituted of open prisms. In spite of the further differences in lobation and enamel folding, the similar kind of hypsodonty met with in both genera studied tends to support their grouping in the order Gondwanatheria Mones, 1987, an order which may well be situated outside the Tribosphenida. On the contrary, the absence, in the fragments under study, of the dental specializations seen in typical Xenarthra, such as enamel reduction, suggest that the morphologic resemblance observed between these genera of the Gondwanatheria and Xenarthra might be a phenomenon of convergence rather than of phyletic relationship. However, diversity within Gondwanatheria, and our poor knowledge of the earliest stages of the complex superorder Xenarthra, do not permit at the moment any definitive statement as to their phylogenetic relationships. □ *Teeth, ultrastructure, Gondwanatheria, Xenarthra.*

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In 1985, Scillato-Yané and Pascual described, on the basis of a hypsodont and polylobate tooth from the early part of the middle Paleocene of Patagonia, a new genus of mammal, *Sudamerica*. They attributed this to a new family of an uncertain order of xenarthran edentates; the origin of this group was thereby pushed back, since the oldest representatives until then were dasypodids from the late Paleocene, also from Patagonia.

Later, one of us (J.B.) described a new mammal from the Los Alamitos Formation, Campanian of Patagonia. Based on several isolated but equally hypsodont molars, the new form, *Gondwanatherium patagonicum* Bonaparte, 1986, was tentatively considered by its author to be related to the Paratheria (Xenarthra plus Pholidota). These molars show a certain number of characters in common with *Sudamerica* ('high

crowns, open root, and nearly flat occlusal surface with enamel lophes'; Bonaparte 1986) and at the same time some differences (number of lophes, enamel configuration). These characters in common led Mones (1987) to group the two genera in a new order of Edentata, the Gondwanatheria, a position adopted later by Bonaparte (1988, 1990). It appeared to us that it would be particularly interesting to study the dental ultrastructure of these two forms, with the aim of confirming or rejecting this ordinal association and possibly documenting their inclusion in the Xenarthra.

Moreover, the Xenarthra has for a long time been thought to have separated very early from the eutherian stem stock ['au voisinage des (ou dans les) Proteuthériens Pantolestidae' Hoffstetter 1982; 'very early eutherian branch' McKenna

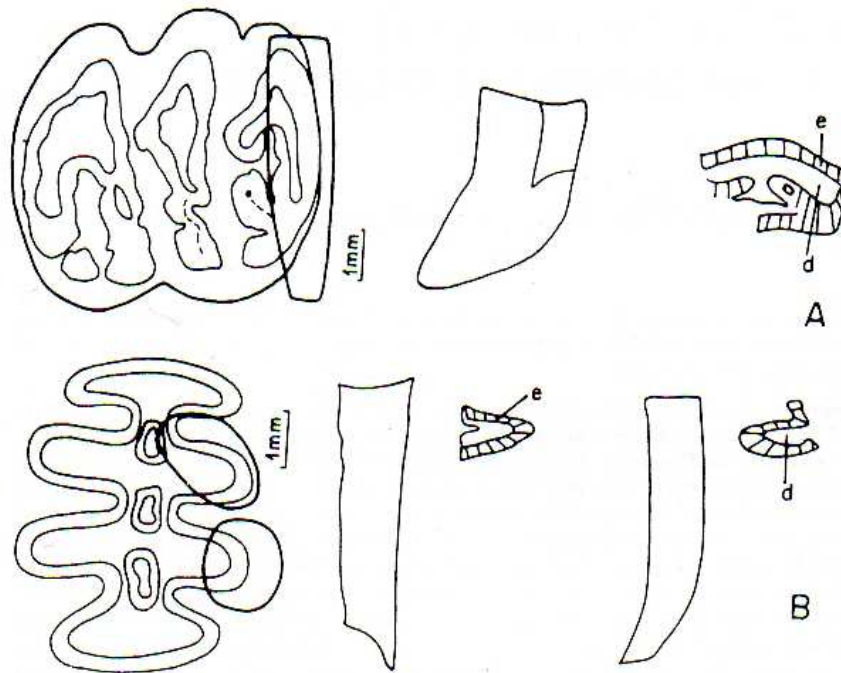


Fig. 1. Localization on the teeth of *Gondwanatherium* (A) and *Sudamerica* (B) of the fragments sectioned in this study.

1987; 'early eutherian offshoot' – Wyss *et al.* 1987] or as the sister group of all the other eutherians in cladistic terms, and this in North America. If *Gondwanatherium* and *Sudamerica* could be included in the Edentata, it could be envisaged with Reig (1981), Bonaparte (1986, 1990) and others before them, that this cohort is more likely to have a South American origin and perhaps, given the age of *Gondwanatherium*, independent of that of the other eutherians; hence the interest of this study.

The xenarthran edentates (about 10 families, mostly extinct, grouped in five orders and two 'grandorders' by Scillato-Yané 1984) constitute a group of mammals that are at the same time archaic (skull, shoulder girdle, thermal regulation, genital apparatus, etc.) and highly specialized; they enjoyed a maximum of diversification during the Neogene, essentially in South America.

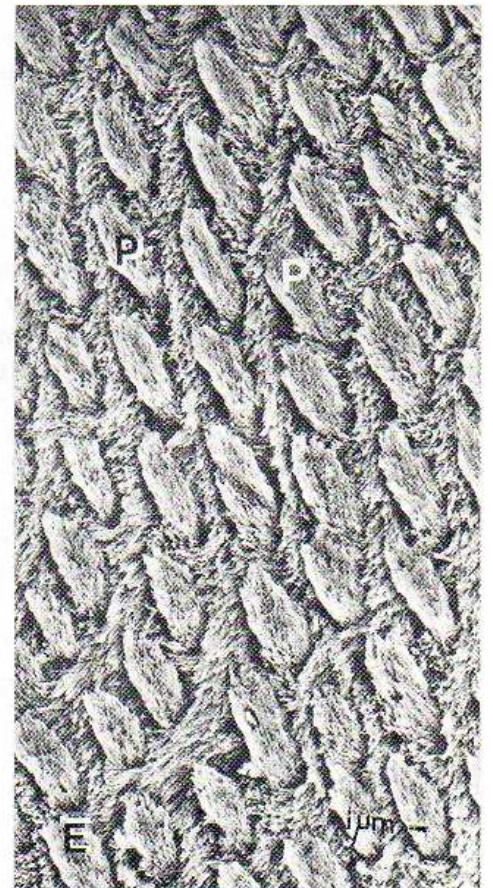
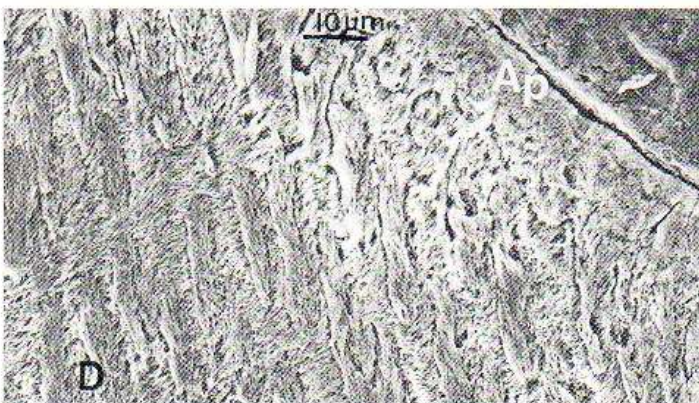
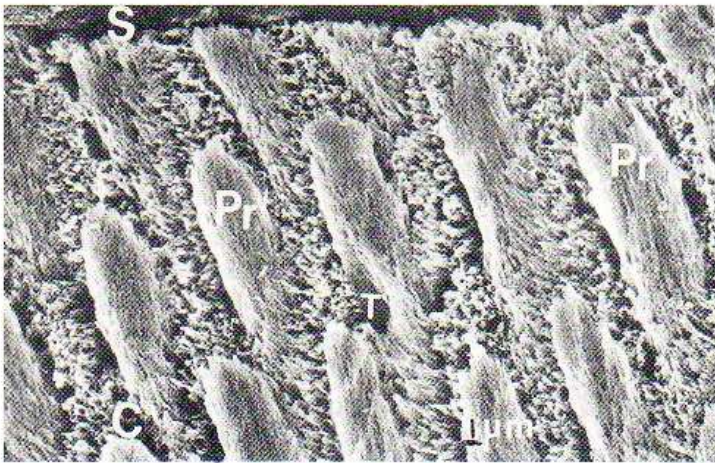
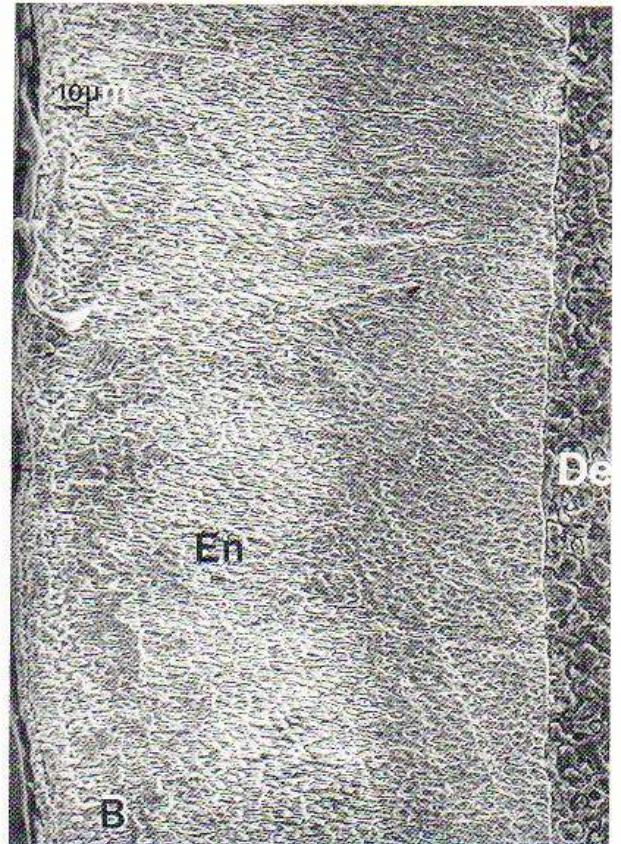
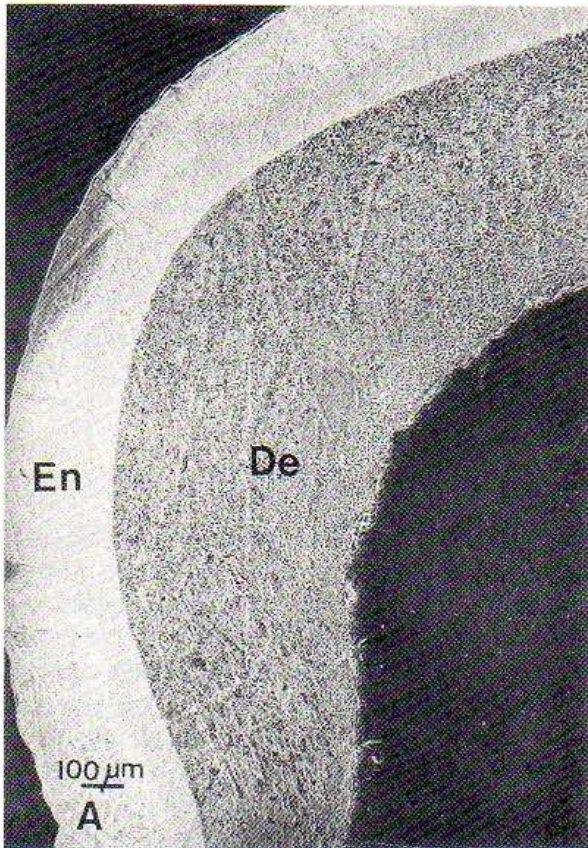
They are characterized by the presence of supplementary zygapophyses on the lumbar and posterior dorsal vertebrae and by the fusion of the ischium-caudal vertebrae-sacrum. Moreover, their teeth are usually reduced in number and in structure (simple crown; homodonty; thinning or

disappearance of enamel; usually a single dentition; sometimes total disappearance of the teeth); certain forms, however, show either polydonty or a specialization of the teeth which are very high, with a thin layer of external cement and an osteodentine center (glyptodonts, megatheriids). Most have an insectivore type of diet, in the broad sense of the term; some, however, are omnivorous while others are herbivorous (glyptodonts, tardigrades).

Two large groups can be distinguished (not taking into account the Vermilingua, a group that no longer possesses teeth, and the Pleiodonta, represented only by *Entelops*), the Loricata or Cingulata and the Tardigrada.

The Loricata include the Glyptodontoidea and the Dasypodoidea (armadillos, which have a wide variety of diets). To the latter belong the oldest edentates (from the Riochican, late Paleocene of Argentina; Hoffstetter 1982). The first known teeth are those of the genus *Uaetus* Ameghino, 1902 (Dasypodidae, Casamayoran, late Eocene); they are oval, elliptic or circular in section with a well-defined crown; the occlusal surface is roof-shaped, with the two sloping surfaces forming a more or less open angle; the lateral faces of the

Fig. 2. □ A. Transverse section of enamel (En) and dentine of a *Gondwanatherium* tooth. □ B. Prismatic nature of enamel (En) of a *Gondwanatherium* tooth. De = dentine. □ C. Prismatic enamel surface layer (S) made of obliquely cut prisms (Pr) separated by relatively large areas of interprismatic substance. *Gondwanatherium*. T = enamel tubule. □ D. An aprismatic surface layer of about 10 µm (Ap) overlays prismatic enamel in a *Gondwanatherium* tooth. □ E. Presence of rows of prismatic enamel (P) with intervening rows of interprismatic substance in a *Gondwanatherium* tooth.



crown are covered with 'unequivocal enamel, unknown on the permanent functional teeth of any other xenarthran, although vestiges have been discovered on the germs of milk teeth of recent armadillos' (Simpson 1948). This enamel is 'thin, simple in structure, with straight prisms all apparently extending through the whole thickness' (Simpson 1948). The enamel of the anterior and posterior faces and of the apex would have disappeared with wear. In the living Dasypodidae (armadillos), the teeth (up to 26 per half jaw in *Priodontes*) also show continuous growth, open roots, but lack enamel, except in milk teeth where it is of an 'extreme thinness . . . which causes it to break off in the process of grinding' (Martin 1916).

In the other superfamily of the Loricata, the Glyptodontoidea (the oldest of which are middle Eocene and derived from armadillos) are armoured forms; their teeth (8 to a half jaw), very hypsodont, are always lacking in enamel and present three rhomboid lobes whose external layer is made of cement, the internal layer of dentine, and the axis of a particularly hard type of dentine, the osteodentine (also found in certain armadillos). There is therefore no more trace of enamel. The pulp cavity is widely open. This structure indicates that the teeth of the Loricata have become hypsodont by radicular growth.

In the Tardigrada Brisson, 1762, grouped, along with the Megalonychidae, the Orophodontidae, the Mylodontidae and the Megatheriidae, which form the Gravigrada Owen, 1842 or ground sloths, are the tree sloths (including *Choloepus*), which derive from the latter.

The teeth of Orophodontidae have a center of hard dentine, like those of Cingulata, but in contrast to those of Gravigrada. In the Megalonychidae the hard dentine forms two transversal crests while the central part is made of vasodentine. The teeth of the Mylodontidae (known since the early Oligocene) are more complicated; they have three components: central vasodentine, thick compact dentine, and a thin layer of peripheral cement (Hoffstetter 1958).

Tree sloth teeth are in the form of a cylindrical

column terminated by a more or less angular surface; in cross section the external layer is made up of cement and the internal layer of a softer vasodentine.

In the Megatheriidae s. st. (which begin in the early Miocene; Hoffstetter 1982), the teeth are high, with two transverse, chisel-shaped crests; in cross section an alternation of thick cement, hypercalcified compact dentine and softer vasodentine can be observed. There, also, the constitution of the teeth seems to indicate that the hypsodonty is 'mostly produced by elongation of the roots' (Van Valen 1988a).

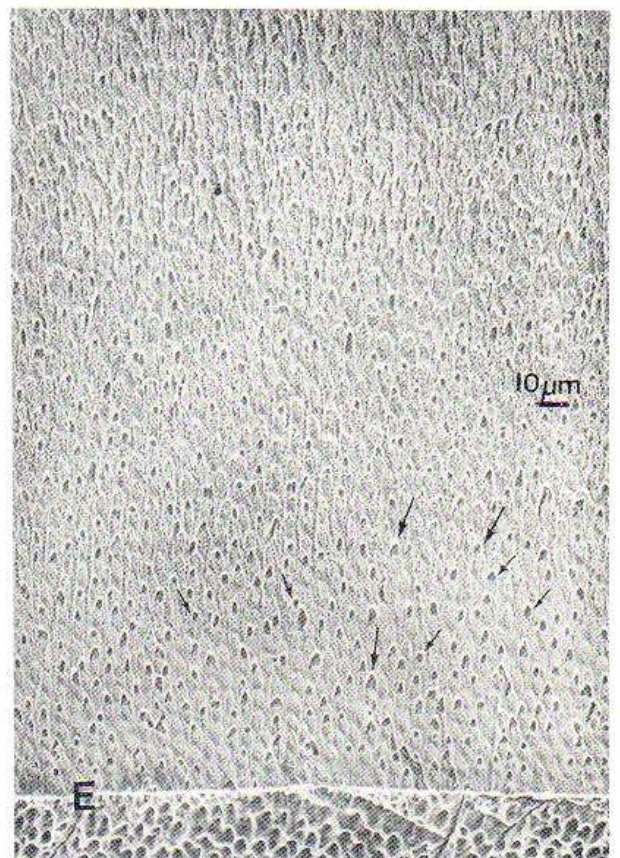
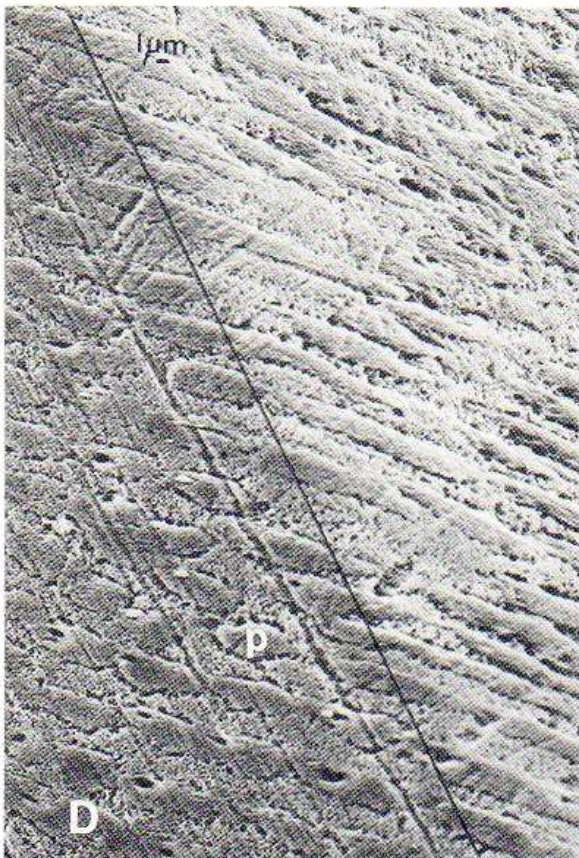
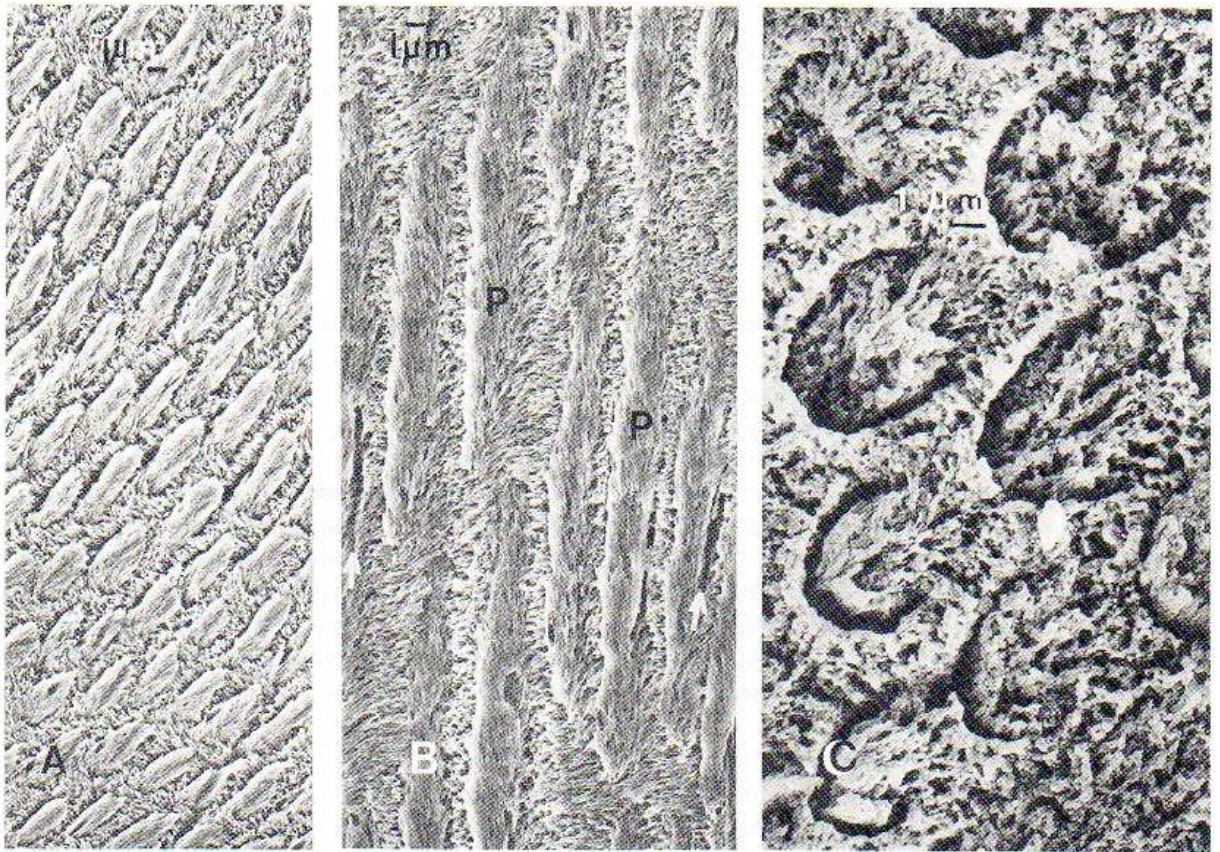
Material and methods

Two dental fragments of *Gondwanatherium* and two dental fragments of *Sudamerica* were used in this study (Fig. 1). The teeth were embedded in Epon 812. Using a Gilling Bronwill grinding machine equipped with a 20 µm thick special rotating circular diamond disk, a longitudinal plane of section was prepared through the whole length of the four dental fragments. One half of each fragment was observed along the longitudinal plane of section so prepared. The other half of each fragment was cut with the Gilling-Bronwill at five different levels in transverse sections regularly distributed from the coronal surface to the apical part. All prepared surfaces were polished with a diamond powder of 0.1 µm particles and etched for 20–30 sec with 20% citric acid solution.

After coating with an Au-Pd layer in a Hummer Junior evaporator, the prepared tooth surfaces were examined with a Jeol JSM 35C scanning electron microscope under 15KV.

A new polished surface was then prepared by grinding off along the same plane a further small portion of the tooth about 20 µm thick. Following the same process of polishing, etching and coating the new surface was studied by SEM. With these progressive steps of grinding and polishing, the dental fragments of *Gondwanatherium* and *Sudamerica* could be systematically studied in longitudinal as well as in transverse sections.

Fig. 3. □ A. Transverse section in prismatic enamel with well-differentiated interprismatic substance of a *Gondwanatherium* tooth. □ B. Longitudinal section in prisms (P) with intervening areas of interprismatic enamel. Presence of enamel tubules (white arrows) in a *Gondwanatherium* tooth. □ C. Presence of arcade-shaped enamel in a *Sudamerica* tooth with prisms and interprismatic substance. □ D. Two planes of sectioning prepared in the enamel of a *Gondwanatherium* tooth. On the right = longitudinal section. On the left = transverse section. P = prism. □ E. Transverse section of a *Gondwanatherium* tooth. Presence of a prismatic enamel with numerous enamel tubules (arrows) in inner enamel. The dentinal enamel junction is straight. Fewer tubules are visible in outer enamel.



In some cases, two planes of sectioning were prepared simultaneously in enamel and/or dentine, which provided two-dimensional aspects of both calcified tissues (Risnes 1987).

Results

It was evident that the *Gondwanatherium* and *Sudamerica* dental fragments studied had a very high crown morphology and that enamel reached the cervical part of the root area. A well differentiated prismatic enamel was present overlying a dentine layer. The dentine-enamel junction was straight (Fig. 2A, B). Enamel thickness measured in *Gondwanatherium* varied between 426 and 140 μm , with a mean value of 261 μm and a standard deviation of $\pm 75 \mu\text{m}$. According to the figures of the tooth of *Sudamerica* by Scillato-Yané & Pascual (1985), enamel thickness would be comparable in this genus. No incremental lines were present in the enamel of *Gondwanatherium*.

This tissue was made up of prisms about 5 μm wide, interprismatic substance and enamel tubules. The prisms were seen in oblique (Figs. 2C, D, 3A) as well as longitudinal (Fig. 3B) and transverse section (Figs. 2E, 3A, 4A). Whereas the inorganic crystals in the prisms were generally oriented with their long axis parallel to the long axis of the prisms, the inorganic crystals in the thick interprismatic substance were oriented with their long axes at 45° to the long axis of the prism (Figs. 2C, E, 3A, B). The prism had generally complete prism boundaries (Figs. 2C, E, 3A) corresponding to the pattern 1 of Boyde (1989). When two planes of longitudinal (to the right) and transverse (to the left) sectionings were simultaneously observed in SEM (Fig. 3D), it appeared clearly that the prisms had a slightly oval cylindrical shape and were separated by a differentiated interprismatic substance. Sometimes rows of continuous interprismatic substance alternated with rows of transversally cut enamel prisms (Fig. 2E at the upper left). In other transversally cut enamel, it was difficult to localize prism boundaries between prism and interprismatic substance (Fig. 4A).

Such a prismatic structure was observed also in *Sudamerica* enamel. In addition to the latter tissue, typical arcade-formed enamel apparently corresponding to pattern 3 of Boyde (1989) could be observed in this genus, too (Fig. 3C).

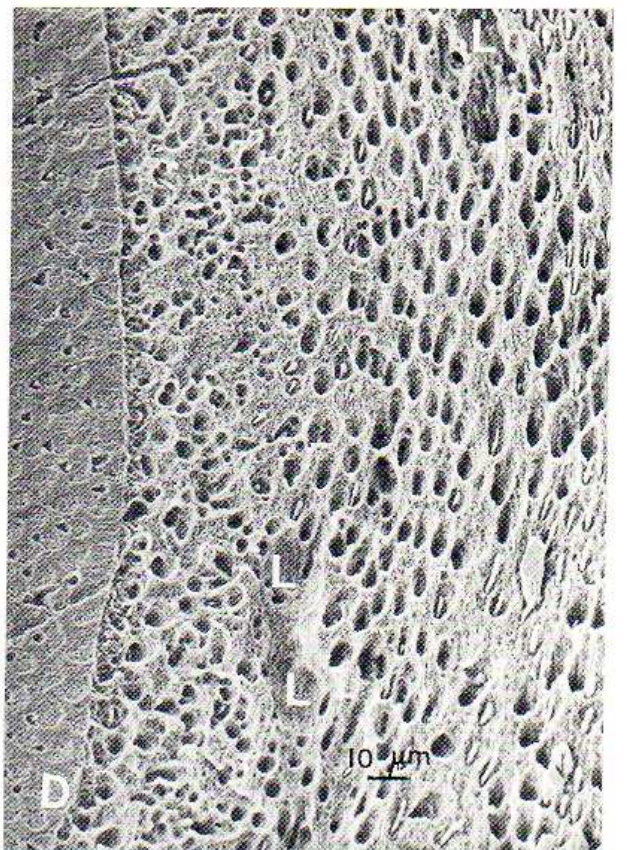
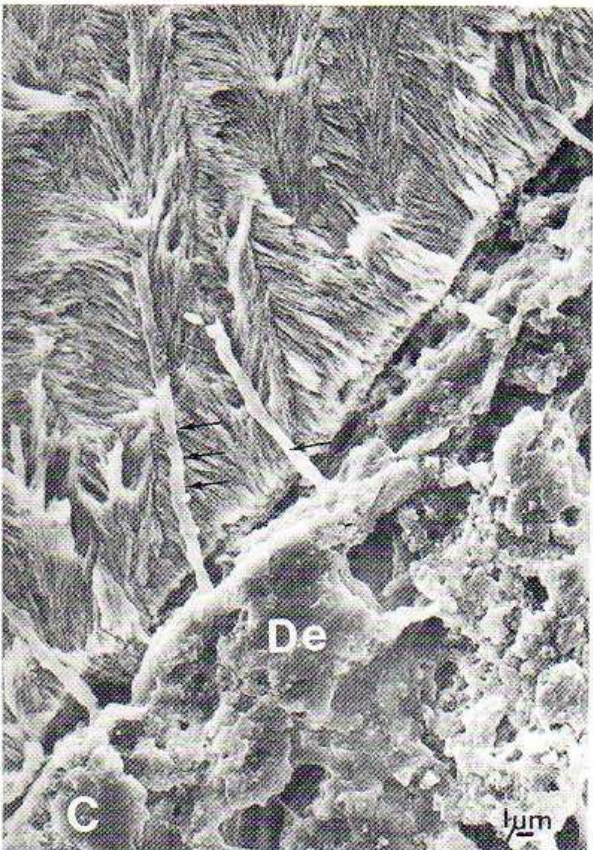
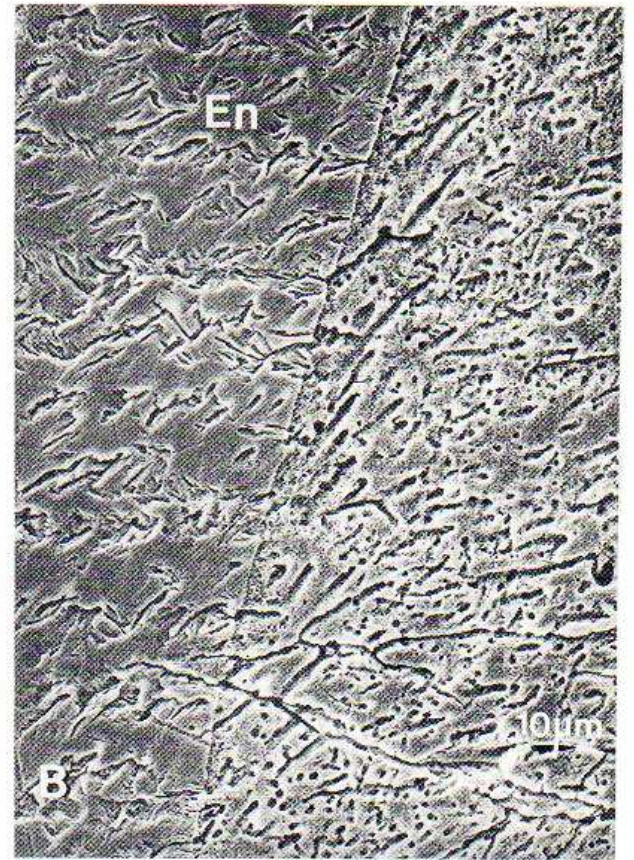
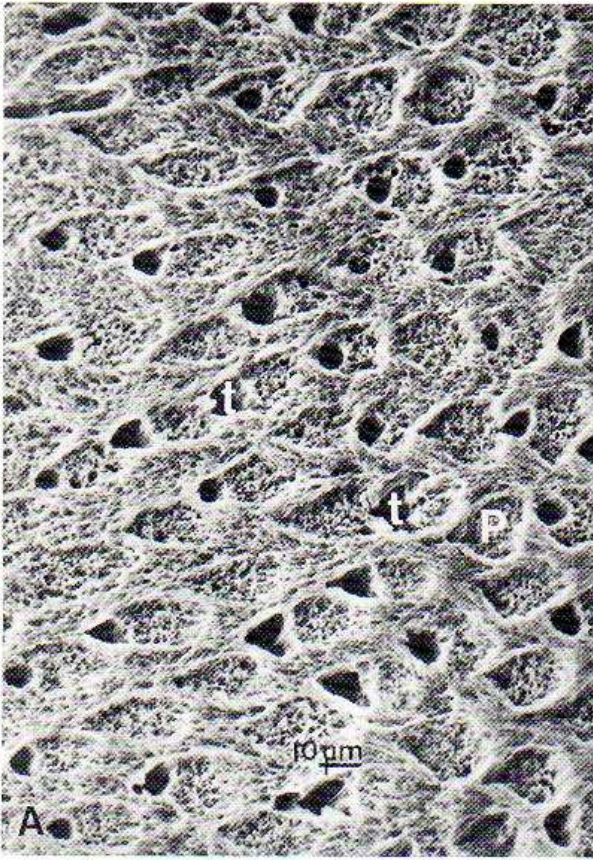
The enamel surface layer of *Gondwanatherium* was generally prismatic and prisms as well as interprismatic substance ended right in the surface layer (Fig. 2C, B). In a few cases an aprismatic surface layer, about 10 μm wide, was found on top of the bulk of prismatic enamel (Fig. 2D). In *Sudamerica* the enamel was prismatic throughout its thickness.

The enamel of both *Gondwanatherium* (Figs. 3D, 4A, B, D) and *Sudamerica* contained typical enamel tubules. These enamel tubules were in direct continuity with dentinal tubules across the enamel-dentine junction (Fig. 4B, C). In general, the enamel tubules were located within the prisms (Fig. 4A) and more precisely in their periphery. More enamel tubules were present in inner enamel than in outer enamel (Figs. 2C, 3E). Measured on transverse sections of *Gondwanatherium* enamel, 3.26 tubules/ $10 \mu\text{m}^2$ (sd ± 3.31) were found in inner enamel, whereas only 2.13 tubules/ $10 \mu\text{m}^2$ (sd ± 2.59) were observed in outer enamel.

Dentine in *Gondwanatherium* as well as in *Sudamerica* presented numerous parallel dentinal tubules which either were empty or contained a calcified dense cylindrical structure (Figs. 4D, 5D). Sometimes on transverse or oblique sections a calcified tube-like structure was present in the tubular lumen (Fig. 5E). As already mentioned, a direct continuity was observed between tubular lumina from dentine to enamel (Fig. 4B). Such a continuity was also observed between calcified tubular contents (Fig. 4C).

Patterns of parallel incremental lines were present across intertubular dentine (Fig. 5A) and were circular around central pulp cavities (Fig. 5C) in *Gondwanatherium* as well as in *Sudamerica* teeth. In the coronal parts of these teeth it was difficult to locate pulp chambers but on transverse sections, narrow pulp cavities completely surrounded by dentine (Fig. 5B, C) could be localized.

Fig. 4. □ A. Transverse section in inner enamel of a *Gondwanatherium* tooth. Presence of prisms (P) and well-differentiated interprismatic substance. Enamel tubules (t) are mostly located within prisms. □ B. Longitudinal section of dentine and enamel (En) showing continuity between dentinal tubules and enamel tubules. The dentine-enamel junction is straight. *Gondwanatherium*. □ C. Longitudinal section through dentine (De) deeply altered by post-mortem lesions and enamel. Continuity of dentinal tubule contents (arrows) across enamel-dentine junction. *Gondwanatherium*. □ D. Transverse section across dentine and enamel. Presence of numerous cross-sectioned dentinal tubules with some post-mortem lesions (L). *Gondwanatherium*.



Various types of post-mortem saprophytic lesions similar to those described by Sognnaes (1963) were observed in the dental fragments of *Gondwanatherium* and *Sudamerica*. They were sometimes discrete and consisted of scattered round or oval-shaped cavities (Figs. 4D, 5A, 6A). But in other cases the dentine structure was deeply modified (Figs. 4C, 5G) with the presence of irregular galleries dug into the tissue (Fig. 5G). Numerous calcified filamentous saprophytic organisms could be localized occasionally in some of the galleries found in the deeply modified dentine.

In the dental fragments of *Gondwanatherium*, a typical cementum layer could be found on the outer part of the root (Fig. 6A). This cementum layer presented oval-shaped cementocyte lacunae with peripheral canaliculi (Fig. 6C). In other parts of the root this cementum layer assumed a more irregular structure with a great number of small cavities presenting various shapes (Fig. 6D). No cementum could be detected in the sectioned fragments of *Sudamerica*.

Finally, at coronal levels of *Gondwanatherium* teeth where deep enamel invaginations were observed (Fig. 6B, E), a circular layer of cementum with typical cementocyte lacunae (Fig. 6E) was found.

Discussion

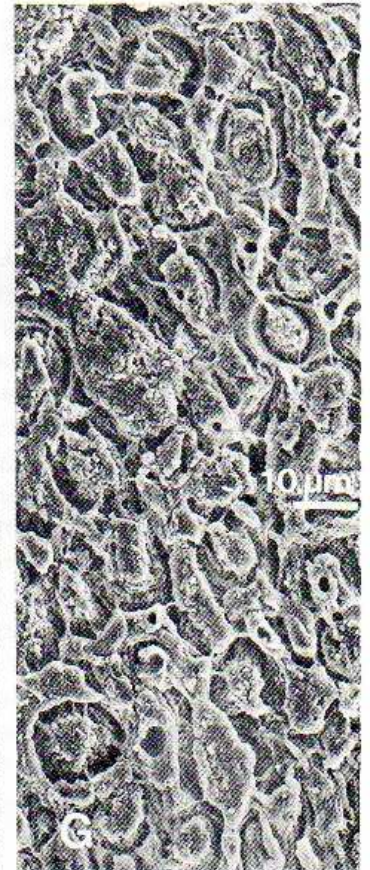
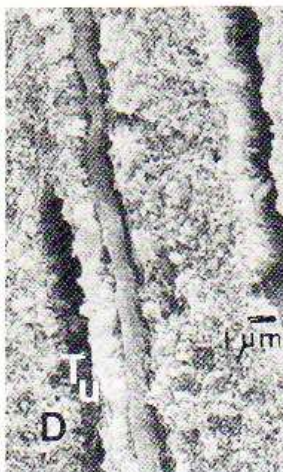
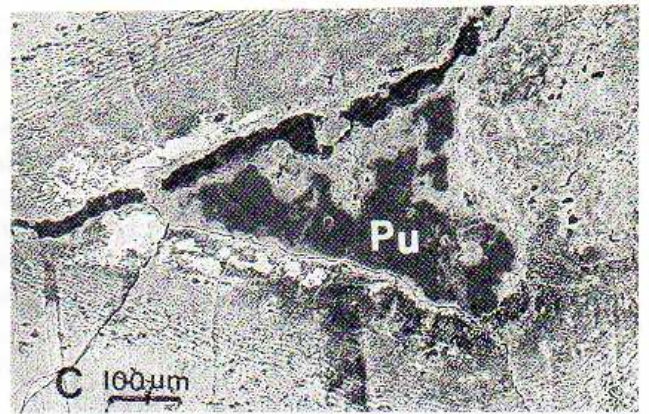
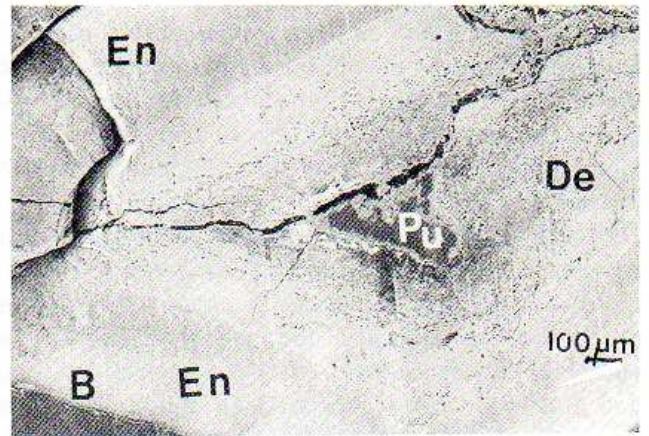
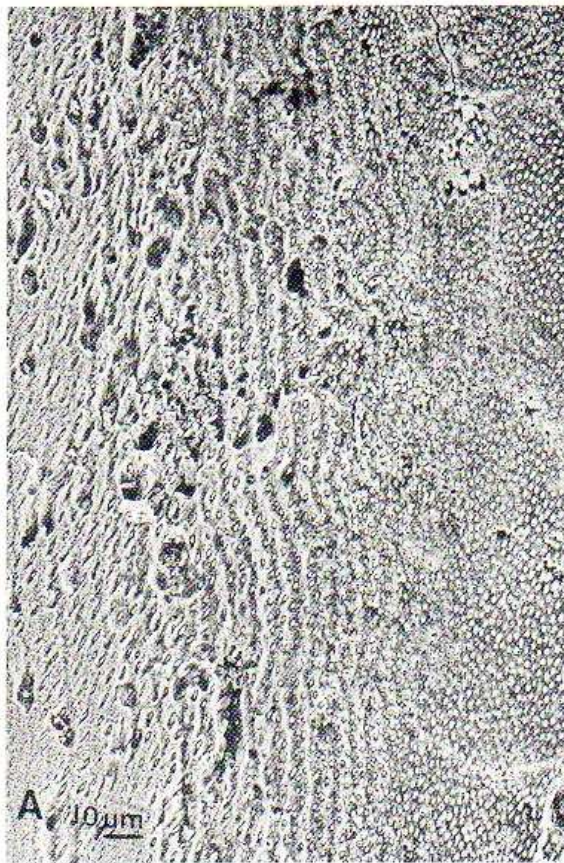
The salient results of this study of the teeth of *Gondwanatherium* and *Sudamerica* are: the presence of a relatively thick enamel, covering most of the height of the tooth, thick interprismatic substance, enamel of type 1 and, locally, possibly of type 3; the presence of cementum at the base of the enamel folds, at least in *Gondwanatherium*, and abundance of enamel tubules. Still to be examined is the degree to which these data contribute to elucidating the relationships of *Gondwanatherium* and *Sudamerica* with respect to one another on the one hand and to the Xenarthra on the other.

Enamel thickness is rarely indicated in ultra-structural studies of teeth. From the measurements we were able to evaluate from the figures given by various authors, it appears that the enamel of early triconodonts is very thin (50 to 70 μm , Peyer 1968; Frank *et al.* 1988); it attains 100 μm in a Jurassic dryolestid tooth figured by Poole (1971), 320 in the Paleocene multituberculate *Taeniolabis* (Carlson & Krause 1985), and 300 in the Paleocene condylarthran *Tetraclaenodon* (Frank *et al.* 1987). In modern mammals, enamel remains thin in certain carnivorous-insectivorous animals (100 μm in a cat, a mole and a bat, Peyer 1968), but thickness increases considerably in other forms (1 to 2 mm in the elephant, 2 mm in man), no doubt in relation to the diet. These measurements of course represent a mean: enamel thickness, as well as other enamel characteristics, can vary according to the area investigated and the plane of the section. In any case, the mean value (260 μm) calculated for *Gondwanatherium* and *Sudamerica* is about the same and approaches that found in other animals of this antiquity. This feature reflects, then, an evolutionary degree, a grade, more than a phyletic relationship.

Of the enamel of the Eocene form *Utaetus*, we know only that it was already 'thin'; but a tendency to thinning is not observed in passing from *Gondwanatherium* to *Sudamerica*. This consequently does not plead in favor of a possible phyletic relationship between the forms studied here and the typical Xenarthra. Consequently, in the case of a filiation between *Sudamerica* and the Xenarthra, as proposed by Scillato-Yané & Pascual (1985), one would have to see in this genus an early, derived member of this order, but not an ancestor of the later Xenarthra.

Similarly, the extension of enamel over most of the height of the teeth, when its distribution is already very limited in *Utaetus*, suggests that the Gondwanatheria (not including *Vucetichia* Bonaparte, 1990) were engaged in a specialization different from that of the known Eocene Xenarthra. From this respective distribution it does appear

Fig. 5. □ A. Transverse section in dentine with numerous cross-sectioned dentinal tubules and parallel incremental lines. Presence of some discrete scattered post-mortem lesions. *Gondwanatherium*. □ B. Transverse section in coronal dentine (De) and enamel (En) with presence of a central pulp chamber (Pu). *Gondwanatherium*. □ C. Slightly higher magnification of the pulp chamber (Pu) surrounded by tubular dentine with incremental lines on the upper left side. *Gondwanatherium*. □ D. Longitudinal section in three dentinal tubules (Tu) of a *Gondwanatherium* tooth. Presence of a calcified odontoblast process in the middle tubule. *Gondwanatherium*. □ E. Transverse section in dentine of a *Sudamerica* tooth. Presence of two calcified tube-like structures in the lumina of two dentinal tubules. □ F. Presence of filamentous saprophytic organisms (SO) in dentine of a *Sudamerica* tooth. □ G. Dentine highly modified by post-mortem lesions. *Gondwanatherium*.



that the hypsodonty of *Gondwanatherium* and *Sudamerica* results mostly from the elevation of the crown, while that of typical xenarthrans, in which the enamel and the crown constitute a minor part of the dental column, is more likely the result of the increase of the roots. Van Valen (1988a, b) has already underlined this difference between *Gondwanatherium* and *Sudamerica* on the one hand and the typical Xenarthra on the other. On the contrary, the probable similar nature of the hypsodonty of *Gondwanatherium* and *Sudamerica* may constitute an argument in favor of a phyletic relationship between the two. It is true that enamel lobation is different in the two cases, *Sudamerica* representing a higher level of specialization, but, considering the time-span separating the two forms and the slight degree to which these teeth are known, the passage from one to the other is not inconceivable.

Moreover, this enamel is, in *Gondwanatherium* and *Sudamerica*, perfectly organized with well-defined prisms and a well-developed interprismatic substance. If the prisms tend to curve towards the outer enamel, they do not form two layers: this so-called radial enamel (Koenigswald 1980) is considered as primitive. Similarly, the predominance of prisms of type I would constitute a primitive character. Finally, the presence, locally in *Sudamerica* (Fig. 3C) of prisms with an incomplete sheath can be regarded as an apomorphy (prisms of type 3) or as a plesiomorphy (open prisms), but certainly not as an enamel regression.

The abundance of enamel tubules is generally regarded as a primitive state; it is found essentially in Multituberculates and Marsupials, but also in late Cretaceous Eutherians in which this feature has been looked for: *Procerberus* and *Protungulatum* (Osborn & Hillman 1979; though denied by Sahni 1979 and Sahni & Lester 1988), as well as in some modern Eutherians, but with a minor density. The situation is not known in *Utaetus*. In any case, this common presence and high frequency in both *Gondwanatherium* and *Sudamerica* again reflects more an evolutionary level than a phyletic relationship.

Finally, the presence of cementum over the enamel at the base of the folds is also known in hypsodont eutherians (perissodactyls, rodents, artiodactyls) 'in which the cheek teeth have to perform particularly punishing functions' (Peyer 1968). In the Xenarthra the cementum remains external.

To conclude, the specializations that unite *Gondwanatherium* and *Sudamerica* remain: (1) the hypsodonty, and a hypsodonty which is apparently of the same nature; (2) the thick interprismatic substance. The other shared characters (relatively thick enamel, well-defined prisms), also met with in contemporary mammals, only reflect a close evolutionary grade. The difference in lobe formation and enamel distribution does not oppose a possible relationship, especially since in that respect *Sudamerica* appears to be more derived. It thus seems justified, given our very limited knowledge of these forms, to maintain the order Gondwanatheria, with two distinct families.

On the contrary, one does not find in *Gondwanatherium* or *Sudamerica* the dental specializations which contribute to the characterization of the Xenarthra: enamel thin or absent, an absence compensated for by the development of two kinds of dentine of different hardness, and an external layer of cement on the crown; moreover, no change in this direction of development is noted in the fragments studied, in going from *Gondwanatherium* to *Sudamerica*. It is to be remembered, however, that one is completely ignorant of the dental formula and the milk dentition of these two genera. In fact, the authors of the latter essentially based their attribution to the Xenarthra on morphologic similarities which are significant; but, as shown by Bonaparte (1986), there also exists some superficial resemblance to the molars of rodents, an observation that serves to emphasize that teeth are subject to convergence.

Thus this admittedly limited study adds no positive element in favor of the attribution of the Gondwanatheria to the Xenarthra. However, one cannot deny that the former may represent an early offshoot from the xenarthran stem stock, or the sister group of the Xenarthra. On the other hand, it is quite possible that *Gondwanatherium* and *Sudamerica* are not eutherians; as suggested by Bonaparte (1990), there may have been no Tribosphenida in the Mesozoic of the southern part of South America. These forms could represent an independent mammalian lineage, probably endemic to that part of Gondwana.

At the present state of our knowledge, it does not appear justified to one of us (D.S.-R.) to see in that lineage the origin of the Xenarthra and hence to argue from that in favor of an origin of the latter independent from that of the Euther-

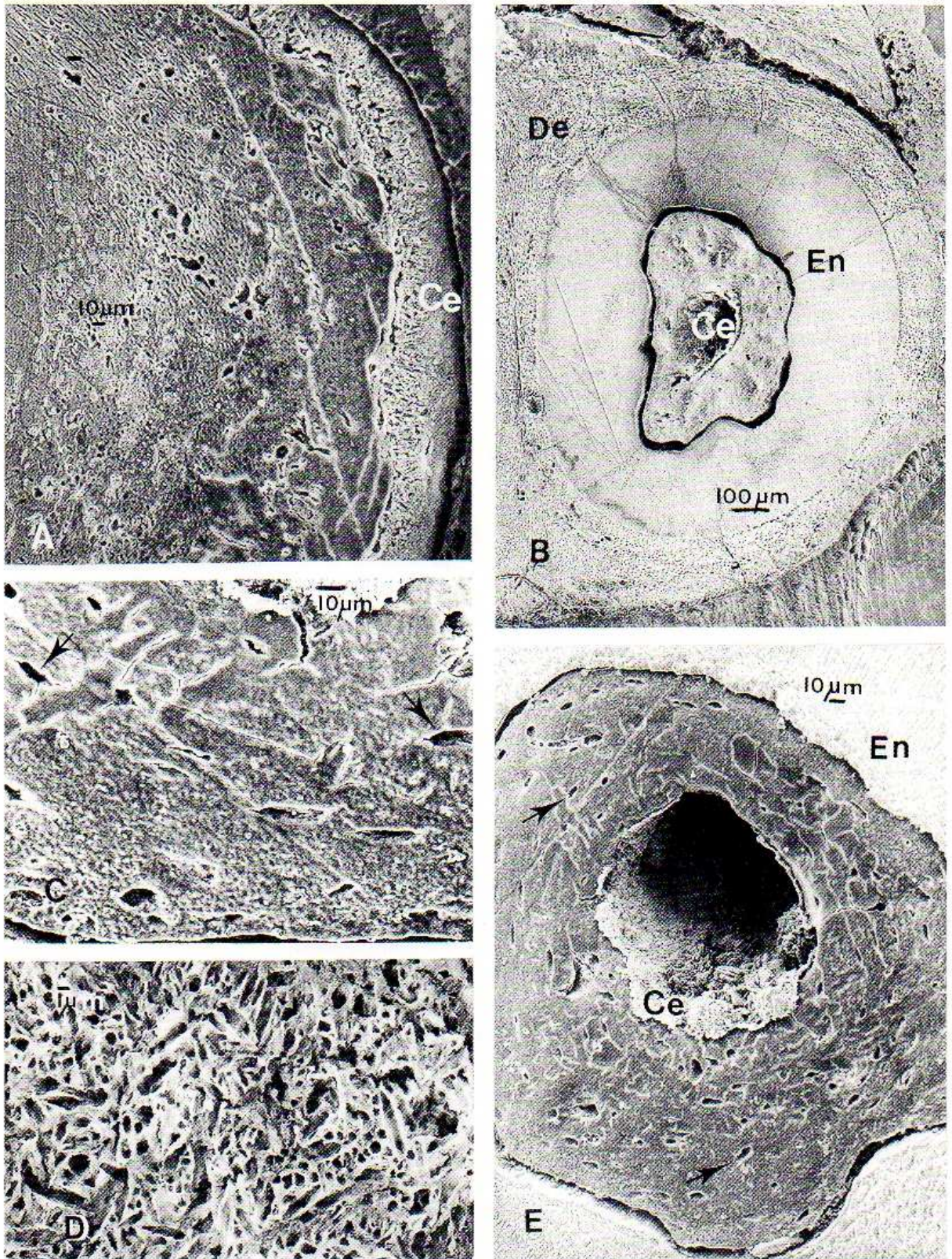


Fig. 6. □ A. Presence of a thin layer of cementum (Ce) on the apical part of a *Gondwanatherium* root. Presence of discrete post-mortem lesions in dentine. □ B. Transverse section in the coronal part of a *Gondwanatherium* tooth. Presence of cementum (Ce) on coronal invaginations of enamel (En). De = dentine. □ C. Presence of typical cementocyte lacunae (arrows) in radicular cementum found on the root of a *Gondwanatherium* tooth. □ D. Irregular structure of cementum found in radicular cementum on the tooth of a *Gondwanatherium* tooth. □ E. Presence of a circular cementum layer (Ce) found all around a coronal enamel invagination (En) of a *Gondwanatherium* tooth. Presence of typical cementocyte lacunae (arrows) within the cementum.

ians. However, as demonstrated by Bonaparte (1990), the Gondwanatheria include species with brachyodont and hypsodont molars, which led him to interpret them as a complex clade of mammals possibly related to the origin of the Xenarthra. This hypothesis remains a challenging possibility, for the confirmation of which a more extensive knowledge of the concerned forms is necessary. In the same line, the ultrastructural study of the teeth of the upper Palaeocene Palaeonodonta, considered by many authors as the source of the Xenarthra, would be of the highest interest.

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