

# Hypsodonty and enamel microstructure in the Paleocene gondwanatherian mammal *Sudamerica ameghinoi*

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Gondwanatherians were the earliest mammals to develop hypsodont cheek-teeth with thick cementum, already by the Late Cretaceous. Hypsodonty occurred independently in Gondwanatheria and Theria; however, very similar biomechanical strategies are observed. The hypsodont molariform cheek-teeth of the early Paleocene *Sudamerica ameghinoi*, the youngest member of the Gondwanatheria, are described. *Sudamerica* had in the lower jaw a continuously growing incisor and, separated by a large diastema, four cheek-teeth which cannot be homologized with premolars or molars, therefore they are regarded as molariforms. The analysis of one fragmentary mandible and 30 isolated molariforms led to the recognition of 8 different morphological categories among them, corresponding to four upper and four lower molariforms. The height of the teeth indicates a relatively high shape of the skull. The molariforms are characterized by transverse lophs; when only slightly worn, they show central enamel islets in the anterior/posterior caps and in the transverse valleys. When the first quarter of the tooth is worn down, these islets disappear and the synclines expand leaving only a narrow central longitudinal ridge. The enamel of the molariforms of *Sudamerica* is one-layered and formed by radial enamel; it resembles the enamel of *Gondwanatherium*. Compared to the enamel of the Gondwanatheria from Madagascar and India, the South American gondwanatherians are distinctly less derived. In turn, the incisor enamel is less derived in *Sudamerica*, although younger, than in *Gondwanatherium*; both show a combination of radial and tangential enamel. The evolution of hypsodonty in gondwanatherians during the Late Cretaceous and early Paleocene cannot be correlated with a grass diet, since grasses were not present during that time. Various lines of evidence including the dental morphology and the inferred habitat for *Sudamerica ameghinoi*, suggest semiaquatic and perhaps a burrowing way of life, similar to that of living beavers.

**Key words:** Hypsodonty, enamel microstructure, enamel islets, Gondwanatheria, *Sudamerica*, Multituberculata.

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## Introduction

In this paper we analyze the cheek-tooth structure and enamel microstructure of *Sudamerica ameghinoi* Scillato-Yané & Pascual, 1984 a gondwanatherian mammal from the early Paleocene of Patagonia. Other representatives of the order Gondwanatheria Mones, 1987, are known from the Late Cretaceous of Patagonia (*Gondwanatherium patagonicum* Bonaparte, 1986 and *Ferugliotherium windhauseni* Bonaparte, 1986), Madagascar (*Lavanify miolaka* Krause, Prasad, Koenigswald & Sahni, 1998) and India (unnamed species). *Ferugliotherium* belongs to the family Ferugliotheriidae Bonaparte, 1986, characterized by brachyodont molars, while three remaining genera to Sudamericidae Scillato-Yané & Pascual, 1984, and are characterized by hypsodont molars. The Sudamericidae constitute the earliest known attempts towards the acquisition of hypsodont cheek-teeth among mammals. Moreover, gondwanatherians are especially interesting since they developed from a non-triangular molar pattern in contrast to all other known mammals with hypsodont dentitions. Hypsodonty is a highly derived dental adaptation developed by many herbivorous mammals among placentals and marsupials. The main advantage of hypsodont teeth is that it provides more tooth material, not for longer life span but for the processing of more abrasive food. Although hypsodonty was developed independently in various mammalian groups, the biomechanical requirements of all hypsodont molars are similar, thus involving similar traits.

In addition to the molariform morphology, we comment on the enamel structure of these teeth in *Sudamerica* and compare it with the enamel structure of Late Cretaceous Gondwanatheria from Patagonia, Madagascar, and India. The incisor enamel of the South American Gondwanatheria is also compared. Finally, we comment on hypsodonty, and morphological features related to hypsodonty, in gondwanatherian molariforms and hypsodont teeth of therian mammals.

*Sudamerica ameghinoi* is of great interest since its highly derived dentition is sufficiently represented by fossil material to be analyzed. The cheek-teeth are hypsodont and are surrounded by cementum. They are well separated from the continuously growing lower incisor by a large diastema (Fig. 1). Such characters occur only much later in most other mammalian groups. The species was initially recognized from a few isolated molars (Scillato-Yané & Pascual 1985), recovered from the early Paleocene Punta Peligro local fauna in Patagonia (Argentina). Because of the advanced hypsodonty (Figs 2, 3), and relative antiquity of this tooth pattern (early Paleocene), relationships to Edentata were assumed in this first description. Later findings of earlier (Late Cretaceous), closely related taxa, *Gondwanatherium patagonicum* and *Ferugliotherium windhauseni* (Krause & Bonaparte 1993), made clear that this highly derived group of mammals was not related to edentates. A diverse array of analyses and phylogenetic speculation regarding the affinities of these peculiar mammals has been formulated in recent years (Scillato-Yané & Pascual 1984, 1985; Bonaparte 1986a, 1986b, 1990a, 1990b; Mones 1987; Sigogneau-Russell *et al.* 1991; Krause & Bonaparte 1990, 1993; Bonaparte *et al.* 1989, 1993; Krause 1990, 1993; Krause *et al.* 1992; 1997; Kielan-Jaworowska & Bonaparte 1996). A recent study of the most complete remains so far known of *Sudamerica ameghinoi* led Pascual *et al.* (in press) to consider the Gondwanatheria as *Mammalia incertae sedis*.

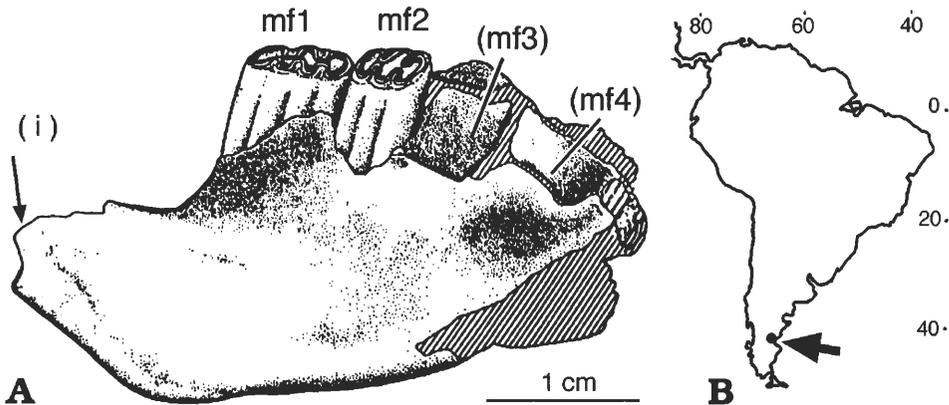


Fig. 1. A. *Sudamerica ameghinoi*, Early Paleocene, Patagonia. Right mandible (MPEFCH 534) in lingual view with an alveolus for a continuously growing incisor (i), the first two molariforms mf1, mf2 and alveoli for other two (mf3), (mf4). B. The map of South America. The arrow indicates Punta Peligro (Central Patagonia, Argentina), the only known location where *Sudamerica* remains have been found.

**Institutional abbreviations:** MLP, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MPEFCH, Museo Paleontológico 'Egidio Feruglio', Trelew, Chubut Province, Argentina; KOE, enamel collection at the Institut für Paläontologie, Universität Bonn, Germany.

**Other abbreviations:** *Molariforms:* MF1, MF2, MF3, MF4, upper molariforms; mf1, mf2, mf3, mf4, lower molariforms. *Enamel structure:* EDJ, enamel-dentine junction; OES, outer enamel surface; IPM, interprismatic matrix; PLEX, prismless outer enamel. For additional terms and definitions on enamel microstructure see Koenigswald & Sander (1997b). All measurements are in mm.

## Materials and methods

For this study a partially toothed mandible, an isolated incisor, and 30 isolated molariforms of *Sudamerica ameghinoi* were examined. The materials and measurements (in mm) are listed in Table 1. All this material comes from Punta Peligro, on the Golfo San Jorge coast, eastern Chubut Province, Argentina, and was collected from the uppermost levels of the Hansen Member (informally known as 'Banco Negro Inferior') of the Salamanca 'Group' or 'Formation' (see Bond *et al.* 1995, and references cited). It belongs to MLP and MPEFCH collections. For the investigation of enamel, tooth fragments were made available by F. Bonaparte from the MACN. As this material turned out to be slightly altered by diagenesis, we decided to prepare serial sections from one uncatalogued upper molariform, from levels of Peligran Age (early Paleocene) at Estancia El Gauchito, some 25 km northeast of Punta Peligro, in order to verify the extension of the enamel islets and to investigate the well preserved enamel. In addition, the enamel structure of *Gondwanatherium patagonicum* could be studied

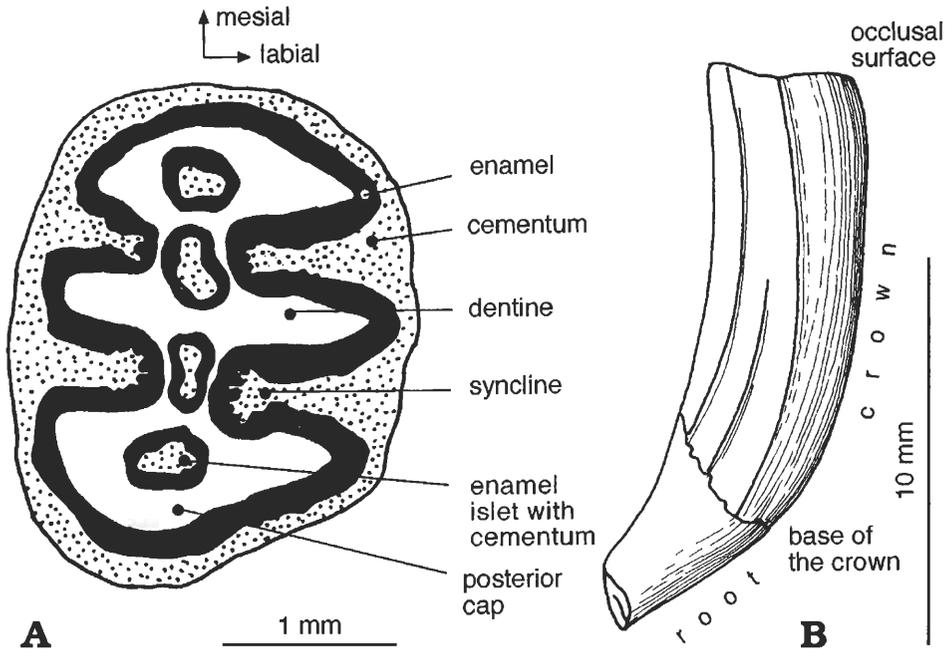


Fig. 2. *Sudamerica ameghinoi*, typical three-lophed molariform (MLP 90-II-12-92, a right MF3) in occlusal (A) and posterior (B) views to indicate the terminology used here (black, enamel; white, dentine; stippled, cementum); synclines showing enamel crenellations at the base and enamel islets are indicated. The specimen belonged to a relatively young individual, as it still has at the occlusal surface enamel islets of the first and second type (see text and Fig. 4). The tooth in posterior view (B) showing the stepped occlusal surface and the base of the lower enamel border, at the base of the crown. The conical root is reconstructed from another specimen.

from a molar fragment (KOE 2862-M) and an incisor fragment (KOE 2862-I). This material comes from Late Cretaceous (Alamitian Age) levels at Los Alamitos, Río Negro Province, Argentina (Bonaparte 1990a, b) and was made available by J.F. Bonaparte from the MACN.

For the serial sections, the uncatalogued specimen was embedded in artificial resin and then sectioned in ten 1 mm thick slices (Fig. 4). A few of these sections were used for enamel investigation as well. A multiple re-embedding into epoxy resin allowed us to make longitudinal, horizontal, and tangential sections with the least amount of material. The specific techniques involved in the microstructural analysis are detailed in Koenigswald & Sander (1997a). Basically, the enamel has to be ground and etched for a few seconds with hydrochloric acid. Observations were made with the aid of a reflecting light microscope and a scanning electron microscope.

## Terminology

In Fig. 2 a typical occlusal surface of a molariform is shown; its transverse lobes, synclines, enamel islets, and other structures mentioned in the text are indicated. Syn-

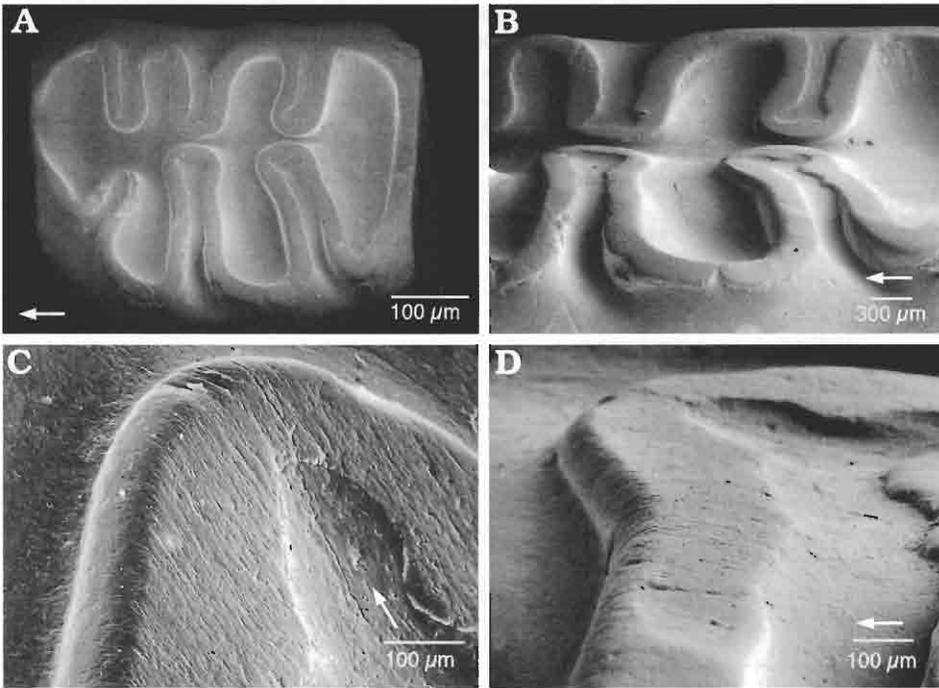


Fig. 3. *Sudamerica ameghinoi*, MF2 (MLP90-II-12-71). **A.** Occlusal surface showing the differently excavated dentine and the thick cementum surrounding the crown. The arrows indicate the direction of jaw motion during mastication. **B.** Detail of **A**, showing the different abrasion of the dentine. In front of the enamel ridge (leading side) the dentine or cementum is deeply excavated while the trailing edge is smooth. **C.** Detail of a leading edge in the center of **B** showing the striation on the enamel surface in longitudinal direction (see arrow). **D.** Another aspect of the same area showing the deep excavation of the dentine in front of the enamel band on the leading side and the soft slope to the cementum behind the enamel band on the trailing side.

clines (or flexae/flexids or reentrant angles) are lateral infolds of the enamel band from the lingual or buccal (= labial) side, which may be filled with cementum. Enamel islets (or fossae/fossids) are deep, funnel-like impressions from the unworn occlusal surface, closed at the bottom (Figs 2, 4). In slightly worn teeth they can be seen as rings of enamel within the dentine, empty or filled with cementum. They might change in their cross-section according to the depth in which the occlusal surface is exposed at the various stages of attrition. Often islets indicate the deepest part of a syncline. In the discussion of hypsodonty, the 'base of the crown' is of significance. It is defined as the area of the lower margin of the enamel and the closure of the synclines.

Previous assignments of gondwanatherian cheek-teeth to premolar or molar loci were strongly influenced by the basic assumption that gondwanatherians were multi-tuberculates. As (1) most known remains of gondwanatherians consist of isolated teeth, (2) there is no indication of milk dentition, and (3) all cheek-teeth show complex, derived morphologies, this problem remains unresolved. In this study we use the term *molariform* for the cheek-teeth of *Sudamerica*. The right mandible MPEFCH 534 has the two anterior molariforms preserved, and alveoli for another two. Since eight

Table 1. Measurements (in mm) of upper and lower molariforms of *Sudamerica ameghinoi*. Abbreviations: mf1–4, lower molariforms; MF1–4, upper molariforms; L, length; W, width; H, height. The column at the extreme right indicates the length/width ratio for each molariform.

	mf1 L	mf1 W	mf1 H	mf2 L	mf2 L	mf2 H	mf3 L	mf3 W	mf3 H	mf4 L	mf4 W	mf4 H	L/W
MPEFCH 534	6.6	3.7	–										1.78
MLP 90-II-12-5	5.3	3.3	11.1										1.6
MLP 90-II-12-94	5.3	3.5	15.2										1.51
MLP 90-II-12-82	6.2	3.5	13.4										1.77
MLP 90-II-12-120	6.2	3.3	17.4										1.87
MLP 90-II-12-100	5.9	3.3	14.5										1.68
MLP 90-II-12-534				4.9	4.5	–							1.08
MLP 90-II-12-561				5.2	4.6	10.6							1.13
MLP 90-II-12-77				4.9	4.6	8.3							1.06
MLP 90-II-12-84				–	4.0	15.2							
MPEFCH 562							4.7	3.7	15.7				1.27
MPEFCH 549							4.5	4.3	10.6				1.04
MLP 90-II-12-86										3.4	3.3	–	1.03
<b>mean</b>	<b>5.9</b>	<b>3.4</b>		<b>5.0</b>	<b>4.4</b>		<b>4.6</b>	<b>4.0</b>		<b>3.4</b>	<b>3.3</b>		
	MF1 L	MF1 W	MF1 H	MF2 L	MF2 W	MF2 H	MF3 L	MF3 W	MF3 H	MF4 L	MF4 W	MF4 H	L/W
KOE 3311	5.7	3.5	–										1.63
MPEFCH 531	5.7	4.0	–										1.42
MLP 90-II-12-96	6.0	3.7	13.4										1.62
MLP 90-II-12-93	5.4	3.8	10.7										1.42
MLP 90-II-12-97	5.8	3.5	13.8										1.65
MLP 90-II-12-81				5.9	4.5	13.0							1.31
MLP 90-II-12-71				5.9	4.9	7.6							1.2
MLP 90-II-12-90							5.0	4.4	13.6				1.13
MLP 90-II-12-80							4.5	4.4	18.0				1.02
MLP 90-II-12-92							5.2	4.4	12.6				1.18
MLP 90-II-12-70							4.7	4.4	12.4				1.07
MLP 90-II-12-102										4.2	4.0	13.6	1.05
<b>mean</b>	<b>5.7</b>	<b>3.7</b>		<b>5.9</b>	<b>4.7</b>		<b>4.8</b>	<b>4.4</b>		<b>4.2</b>	<b>4.0</b>	<b>13.6</b>	

molariform morphological categories have been recognized (see below), it is presumed that four of them belong to lower molariforms (here named mf1, mf2, mf3, and mf4), while the other four correspond to upper molariforms (MF1, MF2, MF3, and MF4). Dimensions and matching occlusal morphologies in these teeth, as well as other positional information as crown structure and implantation, agree with this inference (see below and Table 1).

## The tooth morphology in *Sudamerica ameghinoi*

### The morphology of the lower incisor

As seen in the mandible (MPEFCH 534), the lower incisor of *Sudamerica ameghinoi* is a large, euhypsodont, laterally compressed tooth with a ventro-labially restricted enamel band. Its intra-alveolar portion passes just below the last two molariforms, both of which are bent, the mf3 laterally, and the mf4 posteriorly (Figs 1 and 5). The two anteriormost molariforms, which are straight and very high, are implanted labially to the incisor.

A second specimen, an isolated lower incisor (MLP 90-II-12-560), is assignable to *S. ameghinoi* since it comes from the same early Paleocene levels and locality as the type of *S. ameghinoi*, and its shape, dimensions, and cross-section coincide accurately with the incisor partially exposed in the mandible MPEFCH 534. In cross-section (Fig. 6), the incisor is slightly kidney-shaped, with a shallow concave surface in the mesial face and a gently rounded lateral face. The labial face is also rounded; at this point the enamel is thickest, and continues to the lateral side with reduced thickness is reduced. For comparison, we have an incisor fragment of similar size from Los Alamitos, attributed to *Gondwanatherium* (KOE 2862, see Fig. 6). This fragment indicates that, even though cross-sections are roughly similar, the labial side in *Gondwanatherium* is distinctly more pointed than that of *Sudamerica*. Krause *et al.* (1992) assigned isolated incisors to the small *Ferugliotherium windhauseni* and the larger *Gondwanatherium patagonicum*. They provided important information of the prism cross-section, but a cross-section of the entire tooth showing details of the prism direction and the schmelzmuster was not available. Therefore a comparison here is limited.

### The general morphology of the molariforms

Due to their relatively large size and hypsodont shape, the teeth of *S. ameghinoi* are easy to recognize. Teeth with unworn or only little worn crowns are about four to five times higher than wide in a labial-lingual direction. At first sight, the cheek-teeth seem to be highly variable: there are teeth with two, three, or four transverse lophs. Some show a medial longitudinal loph, while others have central enamel islets. The variability, however, is actually much smaller, since wear stages in hypsodont molars expose different patterns of the occlusal surface due to the level of abrasion. Fig. 4 shows several artificial sections of an isolated molariform of *Sudamerica ameghinoi* (KOE 3311); they illustrate the variation of the occlusal surfaces of the same molariform loci at various levels of abrasion, and are described in detail below.

The morphology of the cheek-teeth varies between two and four transverse lophs according to the tooth position. The lophs are connected by a central crest, visible when the complex surface forming different types of enamel islets is worn down. The occurrence of enamel islets is very obvious in some teeth. In contrast to the number of lophs, the enamel islets do not indicate a specific tooth position. Enamel islets occur in young teeth in the anterior and posterior caps as well as in a central position between the synclines (Fig. 4). The general symmetry of the molariforms in anterior/posterior and lingual/labial direction complicates the identification of individual tooth positions.

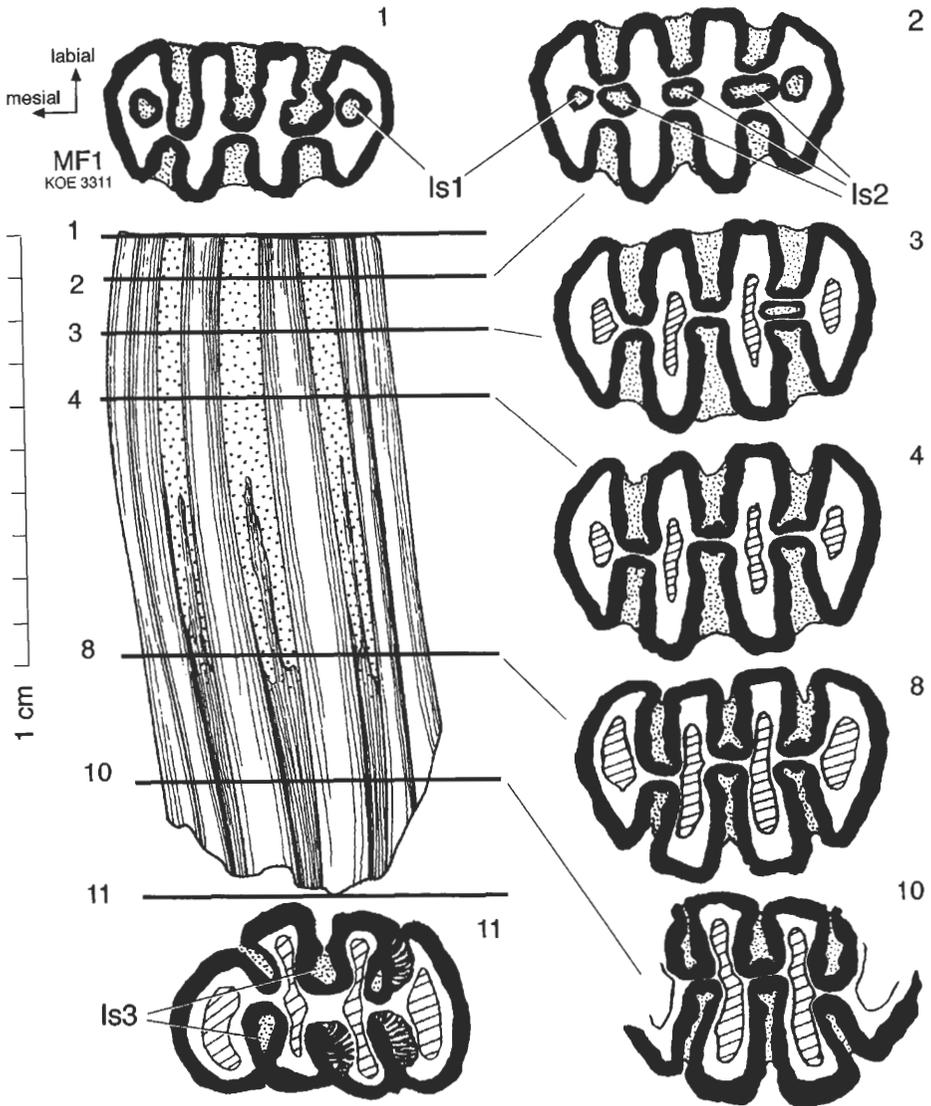


Fig. 4. Changing morphology in one hypsodont molariform (MF1) of *Sudamerica ameghinoi* (KOE 3311), as demonstrated in serial sections of the same tooth. In the lateral aspect of the tooth the position of these sections is indicated. (1) Occlusal surface; (2) section at 0.82 mm from the occlusal surface; (3) at 2.32 mm; (4) at 3.86 mm; (8) at 9.83 mm; (10) at 12.84 mm; and (11) view from below. Enamel islets of the first type (Is1) placed in the anterior or posterior cap can be seen in (1) and (2). Enamel islets of the second type (Is2) deriving from transverse valleys occur in (2) and (3). Enamel islets of the third type (Is3) may occur in heavily worn teeth (11). The increasing enamel thickness at six of these sections is shown in Table 2. (black, enamel; white, dentine; stippled areas, cementum; hatched, pulp cavity).

The molars within the mandible (MPEFCH 534) and a few others show that these teeth were surrounded by a thick layer of cementum. However, in most isolated teeth examined, the cementum has been removed due to post-mortem taphonomical processes.

Facets of contact with neighboring teeth are normally lost together with the cementum; however, at least in one specimen (MLP 90-II-12-71; Figs 3A, 5) they are preserved. The molars are rooted, but the roots covered by cementum are mostly destroyed. The root is partially preserved in one mf1 and in a worn three-lophed molariform (MLP 90-II-12-561). In both cases only one conical root is present, indicating that molariforms of *Sudamerica* were single-rooted despite their complex tooth morphology.

A total of eight discrete morphological categories have been recognized among the cheek-teeth of *Sudamerica ameghinoi*, four as lower molariforms, and four as upper ones (Fig. 5). This is in agreement with the tooth positions known from the mandible MPEFCH 534 (Pascual *et al.* in press). The mf2 and mf3 as well as Mf2 and MF3 are so similar that their allocation is of minor reliability than the other ones. As already mentioned each molariform category shows individual variations in their occlusal morphology, mainly due to the different stages of wear preserved in the specimens. Table 1 shows the individual tooth dimensions (length, width, and height) of all assigned specimens.

**mf1.** — The first lower molariform is represented by the anterior-most tooth in the mandible (MPEFCH 534), and by the following isolated teeth: MLP 90-II-12-75, 82, 94, 100 (right), and 120 (left, Fig. 5). This tooth is characterized by a clear asymmetry: there are three labial and four lingual lochs. The first two lochs are well separated lingually but united labially to form a ‘forked’ pattern. The lingual syncline between them extends down to the base of the crown. A few specimens show, as individual variations, traces of a (very shallow) labial syncline at the anterior cap, which is more obvious in the lower part of the crown. A shallow labial syncline might anticipate a further separation of the anterior lobe. Another individual variation is a keel in the anterior edge of the anterior cap. As mentioned below, special structure, the ‘forked’ structure, of the anterior part of the mf1 is significant since it suggests the homology of this tooth with some molariforms belonging to the most generalized gondwanatherian, *Ferugliotherium windhauseni* (Pascual *et al.* in press).

The occlusal surface of mf1 is flat but somewhat higher in the labial side. Enamel islets can be seen in slightly worn teeth. Labial lobes are also shorter than the lingual ones. In the specimen MLP 90-II-12-82 there is still the basal part of a disappearing islet between the synclines that separates the third and fourth lobe.

In lateral view the tooth is somewhat inclined backwards; therefore, the occlusal surface is oblique to the growing axis. At the very base the tooth curves strongly backwards. This peculiar structure suggests that the mf1 may have erupted somewhat rotationally, upwards and backwards. This, in turn, is an additional argument supporting the inferred backward movement of the jaw during the power stroke (see below).

Although the occlusal surface is multilobed, the mf1 had (as well as all other molariforms) only one conical root, judging from MLP 90-II-12-94 which is the only one preserved at this area.

**mf2.** — It is represented by the second preserved molariform in the mandible (MPEFCH 534), and by the following isolated teeth: MLP 90-II-12-77 (left, Fig. 5), MLP 90-II-12-561 (right), and, probably, by MLP 90-II-12-84 (right). The mf2 is three-lophed and relative symmetrical, with the posterior loph smaller than the anterior two, of which the middle one is larger. The labial lobe of each loph is somewhat higher

and shorter than the lingual one, thus permitting the allocation of each tooth to the left or the right side. Specimen MLP 90-II-12-77 shows an individual variation to this general pattern: the middle labial lobe is incipiently divided by a median groove which disappears shortly before the base of the tooth (Fig. 5). MLP 90-II-12-561 represents a very old individual; it is completely surrounded by cementum and, as the base of the tooth is not broken, it can be assumed that it ends basally in only one root (Fig. 3). Specimen MLP 90-II-12-84, tentatively assigned to a mf2, is broken at the occlusal and posterior faces. The straight bodies of the mf2 and mf3 differentiate them from other three-lobed molariforms.

**mf3.** — Assigned to this molariform locus are specimens MPEFCH 562 (right) and MPEFCH 549 (left; Fig. 5). The mf3 is slightly smaller than mf2. MPEFCH 562 represents a young individual and the tooth bends outwards at the base.

**mf4.** — We regard the specimen MLP 90-II-12-86 (Fig. 5) as a ?left mf4. This two-lobed tooth is relative small and much shorter than mf1-3. Its body is strongly bent backwards, and slightly outwards near the base. Its curvature fits well in form and dimensions in the last alveolus of the mandible (MLP 90-II-12-534). The almost unworn occlusal surface shows an islet in the anterior cap. An additional specimen illustrated in Bonaparte *et al.* (1993: fig. 4D) can be assigned to a mf4, although it was interpreted as a M2 by Krause & Bonaparte (1993: figs 1 and 3C).

**MF1.** — The first upper molar is represented by specimens MLP 90-II-12-531, 93, 96 (left; Fig. 5), and KOE 3311 and MLP 90-II-12-97 (right). Assuming that the elongated lower mf1 should have an antagonist of similar length, the elongated four-lobed molariforms are regarded as MF1's, as indicated in the length/width ratio of these teeth (see Table 1). The MF1 is straight, not curved lingually like MF3 and MF4.

The MF1 has a distinct anterior and posterior cap and two transverse lobes in between. Caps are transversely shorter than the middle lobes. The occlusal surface of the MF1 changes very much during the early stages of wear. A detailed description of the formation of enamel islets is given below. The MF1 forms five enamel islets in the central axis. They are worn away fairly quickly (Fig. 4).

Even though the general structure is four-lobed, at least one of the examined specimens, MLP 90-II-12-96, shows a distinct additional syncline forking the anteriormost lingual lobe, in such a way that the lingual edge is incipiently five-lobed while the labial one is four lobed (Fig. 5). However, this feature is variable. Specimen MLP 90-II-12-97 shows a very slight indication of such a syncline while other teeth to the MF1 locus are rounded in this area.

**MF2.** — The second upper molariform, also four-lobed, is represented by only two left specimens, MLP 90-II-12-81 and 71 (Fig. 5). Interestingly, the specimen MLP 90-II-12-71 shows a much thicker enamel width than most other upper teeth examined. This specimen is heavily worn, indicating an old individual. The enamel becomes slightly thicker towards the base, as seen from the measured sections of KOE 3311 (Table 2). Specimen MLP 90-II-12-71 is four-lobed and the posterior lobe is very small; as it is preserved with all its surrounding cementum layer, it can be seen that on its anterior and posterior faces there are also preserved the contact facets to neighboring teeth (Figs 3, 5). Specimen MLP 90-II-12-81 shows quite a lot of striations in the enamel in ante-

Table 2. Enamel thickness (in mm) of *Sudamerica ameghinoi*, specimen KOE 3311 at six different sections (which correspond to those sections numbered 1, 2, 3, 4, 7, and 10 in Fig. 4). In each section the enamel was measured at six, randomly chosen positions (A, B, C, etc.). Mean values are at the right column.

Sections	A	B	C	D	E	F	mean
1	0.22	0.22	0.22	0.22	0.23	–	<b>0.222</b>
2	0.24	0.24	0.22	0.24	0.24	0.24	<b>0.236</b>
3	0.26	0.26	0.26	0.26	0.28	0.26	<b>0.263</b>
4	0.30	0.28	0.30	0.28	0.30	0.28	<b>0.290</b>
7	0.30	0.30	0.30	0.32	0.30	–	<b>0.304</b>
10	0.30	0.32	0.28	0.30	0.30	0.28	<b>0.296</b>

rior-posterior direction, as well as clearly visible leading and trailing edges revealed by the differentially abraded dentine. Even though its posterior loph is larger than that of MLP 90-II-12-71, it should be noted that there is a posterior groove at its posterior face, suggesting that the profile of the lophs decreases with wear – specimen MLP 90-II-12-81 corresponds to a much younger individual than MLP 90-II-12-71.

**MF3.** — Four three-lophed specimens are assigned to MF3: MLP 90-II-12-90, 92 (right), 70, 80 (left, Fig. 5). Judging for the four preserved enamel islets in each one of them, they belonged to young individuals. The MF3 is more labio-lingually asymmetrical than MF1 or MF2, having the lingual lobes of each loph much shorter than the labial lobes. All the teeth assigned to MF3 are strongly bent lingually, and they are clearly shorter than young individuals assigned to MF1 or MF2. Specimen MLP 90-II-12-92 shows well developed enamel crenellations in the end of each syncline.

**MF4.** — We regard specimen MLP 90-II-12-102 (Fig. 5) as a left MF4. This tooth is only slightly smaller than those assigned to MF3, and it is similar in height. It is also bent lingually. However, it shows shorter and less asymmetrical lophs.

### Upper molariforms and inferred skull shape

Upper molariforms are similar to the lower ones in that the first two (MF1 and MF2) are straight and high, while MF3 and MF4 are laterally bent and somewhat shorter. The two less worn specimens here assigned to MF1 (MLP 90-II-12-96, 97) measure 13.4 and 13.8 mm in height, respectively, while MLP 90-II-12-81, a slightly worn specimen assigned to a MF2, is 13.0 mm in height. As both MF1 and MF2 are straight, this possibly implies that the skull of *Sudamerica* may have been relatively high, as the palatal implantation of the upper molariforms was probably deep. An anatomical consequence of this is that the orbits may have been slightly displaced posteriorly.

### Homologies of the gondwanatherian cheek-teeth

The mf1 of *Sudamerica*, known from the mandible and other isolated specimens (see above), can be homologized with some teeth assigned to the relatively primitive

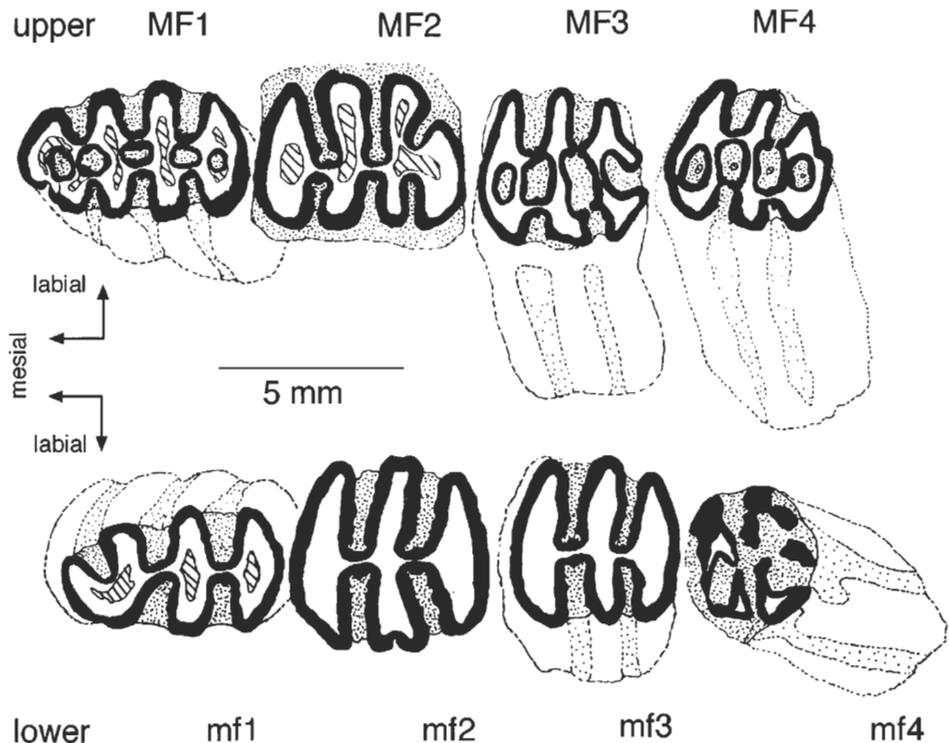


Fig. 5. *Sudamerica ameghinoi*, early Paleocene, Patagonia. Reconstruction of the upper and lower dentition with four molariforms each. The teeth composed to a tooth row come from different individuals; therefore, the degree of abrasion varies (e.g., the MF2 is deeply worn). Most teeth lost the surrounding cementum due to taphonomical processes. Therefore, only in one tooth (the MF2) facets of the adjacent teeth can be observed. We assume MF1, MF2, and mf1 are four-lophed, while MF3, MF4, mf2, and mf3 are three-lophed. The only two-lophed tooth which is strongly bent backwards is regarded as a mf4. MF1, MLP 90-II-12-96; MF2, MLP 90-II-12-71; MF3, MLP 90-II-12-80; MF4, MLP 90-II-12-102; mf1, MLP 90-II-12-120; mf2, MLP 90-II-12-77; mf3, MPEFCH 549; mf4, MLP 90-II-12-86.

*Ferugliotherium windhausenii*, since both show a labial-lingual asymmetry. The two anterior lophs are linked labially, a feature found only in this tooth position. Specimen MACN-RN 174 of *Ferugliotherium windhausenii*, assumed to be right first molar by Krause *et al.* (1992), Krause (1993), and Kielan-Jaworowska & Bonaparte (1996), has four lobes on one side, and three on the other. This is exactly the same pattern of the first lower molariform of *Sudamerica ameghinoi*, which has four lingual and three labial lobes (Fig. 5) – and thus implying that specimen MACN-RN 174 is left, not right (Pascual *et al.* in press). It is interesting to mention that the holotype of the recently described *Lavanify miolaka*, from the Late Cretaceous of Madagascar, also shows a forked pattern (see Krause *et al.* 1997: p. 505, fig. 2a, b).

Upper molariforms of *Sudamerica* may also prove to be homologous to some cheek-teeth assigned to *Ferugliotherium*. For instance, the general pattern of MF1, and specially of specimen MLP 90-II-12-96, shows similarities with specimen MACN-R 248 of *F. windhausenii*, assigned by Krause *et al.* (1992) to a right M1. However, if our

interpretation is correct, this last specimen should be regarded as a left molar. Also, the broken face of this tooth is a posterior face rather than an anterior one. A thorough treatment on the homologies of gondwanatherian cheek-teeth is provided by Pascual *et al.* (in press).

If arguments by Krause *et al.* (1992) and Kielan-Jaworowska & Bonaparte (1996) for assigning these and other molariform teeth of *Ferugliotherium* to first molars prove to be correct, then it would be reasonable to assume that the dental formula of *Sudamerica* is 1.0.0.4. If such was the case, the term 'molariforms', as used here, should be changed to 'molars'.

In their study of a partial dentary recovered from Los Alamos Formation, Kielan-Jaworowska & Bonaparte (1996) assume the multituberculate affinities of *Ferugliotherium windhausenii*. However, it should be noted that no molars of *Ferugliotherium* have yet been found in association with a lower jaw; and molars assigned to *Ferugliotherium* show a pattern similar to that of all other gondwanatherians, even though plesiomorphic. Moreover, *Ferugliotherium* differs from most multituberculates in having upper and lower molars with transverse crests (a character that among multituberculates occurs only in *Essonodon*). The transverse crests are clearly present in all the Sudamericidae. Finally, *Sudamerica* itself shows dentary features resembling closely that of some multituberculates, as pointed out by Pascual *et al.* (in press): '...particularly taeniolabidoid multituberculates such as *Catopsalis* ... and *Taeniolabis* and djadochtatherians such as *Djadochtatherium* and *Catopsbaatar* ... Although the dentary fragment tentatively assigned by Kielan-Jaworowska & Bonaparte (1996) to *Ferugliotherium* is much less complete, comparable parts suggest that it appears to have had a similar morphology. This suite of features, however, is not characteristic of all multituberculates.' In short, the molar morphology of *Ferugliotherium* seems to be closely related to that of Sudamericidae, but lacks hypsodonty. The lower jaws of both *Ferugliotherium* and *Sudamerica* show similarities to that of several multituberculates, but on the basis of available evidence, we concur with Pascual *et al.* (in press) that gondwanatherians are best classified as *Mammalia incertae sedis*.

## Specific characters related to hypsodonty

**Definition of hypsodonty.** — Hypsodonty is defined in different ways. Van Valen (1960) proposed to use the relation between the antero-posterior length and the dorso-ventral height and thus teeth higher than long would be hypsodont. Janis (1988) followed this concept. Koenigswald (1980) preferred to use the relation between the height and the labio-lingual width. This ratio takes into account that in several taxa, e.g. arvicolines or artiodactyls, the first or last tooth of the tooth-row might be elongated. *Sudamerica* has hypsodont cheek-teeth according to both definitions.

We use the term hypsodont in a descriptive form. Moreover, it can be distinguished between rooted and continuously growing teeth. Patterson & Pascual (1972) used the term *hypsodont* for high-crowned teeth with roots, and *hypselodont* for rootless teeth. In turn, Mones (1982) recognized the same morphological criteria, but used *protohypsodont* instead of hypsodont, and *euhypsodont* instead of hypselodont. The discrimination is useful although there is an evolutionary transition from the protohypsodont

to the euhypsodont stages, when roots are formed only by very old individuals. Molars of *Sudamerica ameghinoi* definitely form roots, although they are rarely preserved. Therefore the molariforms, in contrast to the incisor, are not euhypsodont but, rather, are protohypsodont.

It is also useful to distinguish between *external* and *internal* hypsodonty. External hypsodonty is characterized by large extruding teeth, restricted to the anteriormost part of the dentition, like incisors and canines. They serve very different functions, of which food processing is only one. They can be used as weapons or for social interaction, like the saber-teeth in cats or thylacosmilid marsupials, the tusks of elephants, walruses, the enlarged canines or incisors in hippos and of some rhinos. The procumbent incisors of many marsupials (e. g., *Macropus*) and insectivores form another group; most of these teeth do not have antagonists of similar size or shape. A third group of external hypsodont teeth function in pairs of similarly shaped teeth, like rodent incisors. They occur in various groups and are mainly used for food processing, but also for digging and for social contact. Functionally, they form the transition to teeth classified as internally hypsodont.

Internal hypsodonty includes teeth which extrude only very little above the bony rim of the maxilla or mandible, but they provide much material for abrasion. This type of hypsodonty is mainly found among the cheek-teeth, and their function is almost exclusive food processing. These teeth always have antagonists of similar shape. From the functional point of view it is important that the dentine is exposed in the occlusal surface at a very early stage of wear. The exposure of soft dentine and hard enamel forms self-sharpening occlusal surfaces with blade-like cutting edges. Incidentally, it is the tooth-food contact that forms this very efficient surface. A tooth-tooth contact results in a polished occlusal surface without a profile. The cutting edges are in one plane at least in the direction of the power stroke. *Sudamerica* shows an external hypsodonty in its rodent-like incisors and a typical internal hypsodonty in the molars. Internal hypsodonty represents an adaptation not for enlarging the life span but for the processing of abrasive food.

After analyzing different occlusal profiles in hypsodont rodent molars, Koenigswald (1980; see also Koenigswald *et al.* 1994: fig. 23) defined three basic types, describing regularities in the vertical orientation of the enamel plates forming the cutting edges and different ways of reduction. The most primitive condition is called Type A. The transverse lophs are vertical towards the occlusal surface and thus the enamel plates on both sides form cutting edges with the dentine core in between. Gaps between the tooth elements are often filled with cementum. A differentiation of this basic type can be observed when the enamel plate on the trailing side is reduced in thickness (Type B). Thus the thin enamel plate does not form a cutting edge any more. This differentiation is typical for arvicoline molars. In several hypsodont dentitions the transverse lophs are inclined towards the power stroke, as in *Hydrochoerus*. Often, the enamel plate on the leading side of the dentine core is thinner, or even totally reduced (Type C). This can be observed, e. g., in *Chinchilla*. Types B and C are independently derived from Type A. In molariforms of *Sudamerica* the transverse lophs are vertical to the occlusal surface and the enamel thickness is not reduced, thus belonging to the basic Type A condition.

**Jaw motion and functional symmetries.** — The jaw motion can be deduced in fossil dentitions from various sources. If the various aspects indicate the same direction, the reconstruction can be regarded as faithful. The tooth morphology of *Sudamerica ameghinoi* is characterized by transverse lophes. Rensberger (1973, 1975), demonstrated that cutting edges are most effective if oriented perpendicular to the power stroke. Therefore the power stroke in *Sudamerica* was most probably parallel to the tooth row. This argument is supported by striae observed in the enamel of some teeth (e.g., MLP 90-II-12-71; Fig. 3C, D). The occlusal surface of fairly young teeth has several longitudinal steps which can only be produced by an anterior/posterior direction of the power stroke.

Whether the mandible was pushed forwards or backwards during the power stroke can be deduced from the asymmetrical abrasion of the dentine (Costa & Greaves 1981; Koenigswald *et al.* 1994). Most teeth were somewhat altered during taphonomical processes and therefore this trait cannot be observed in all teeth. But there is sufficient material to show that in lower molariforms the dentine (and the cementum) is abraded more deeply on the posterior side of the enamel ridges as in the mf1 (MLP 90-II-12-82) and in the upper molariforms on the mesial side. That is the only way to prove that the mandible, unlike in rodents, was pulled backwards during the power stroke, an observation already made by Krause & Bonaparte (1993). The specific implantation of the MF1 and mf1 also agrees with this inference: while the mf1 is slightly bent backwards, the MF1 is implanted vertically. In arvicolines the M1 is implanted obliquely and the m1 vertically, according to the opposite (anterior) direction of the power stroke.

In several hypsodont dentitions with a power stroke parallel to the tooth row, we find an unbalanced enlargement of teeth. In *Sudamerica* both MF1 and mf1 are distinctly elongated while MF4 and mf4 are much smaller. A similar enlargement of the anterior molars can be observed in arvicolines as well. But in other groups like *Hydrochoerus*, the posterior molars are the enlarged ones – even though throughout the evolution of the group the p4 also shows some enlargement due to the addition of synclines (Pascual & Bondesio 1982). The position of the enlarged molars indicates the most effective zone during mastication.

The high degree of functional similarities of lower and upper molars in many dentitions leads to a morphological similarity, which reflects the direction of the power stroke. This morphological similarity was described as *functional symmetry* (Koenigswald *et al.* 1994). The dentition of *Sudamerica* is highly symmetrical. Under this conditions it is difficult to identify specific examples of functional symmetries. However, in lower molariforms the lingual part of each loph, but especially of the middle ones, is somewhat longer than the labial one. For the upper molars the reverse is true and the labial lobes are longer.

**The enamel islets.** — The formation and disappearance of enamel islets is a distinctive feature of the cheek-teeth of *Sudamerica*. It can be deduced from some isolated teeth representing early stages of wear and serial sections of one tooth. Enamel islets may occur in three different ways. In the little worn occlusal surface, transverse lophes are visible (MPEFCH 562, MLP 90-II-12-80, 120). The anterior/posterior caps show distinct grooves which in later stages of wear will form a first type of enamel islets. At

this very early stage of wear, no connection between the lophs is visible but little spurs indicate sites where, in later stages of wear, a connection may occur.

A second type of islets is formed in the central axis of the tooth during a later stage, but still in the uppermost part of the tooth (less than 1 mm below the unworn surface). The spurs become more distinct and connect the lophs in two parasagittal longitudinal crests. They enclose a central groove, which may be open to one side or the other. The enamel islets of the anterior/posterior caps are well surrounded by an enamel band. At this stage only part of the occlusal surface is worn flat. This early stage of wear is represented in the natural occlusal surfaces of isolated teeth (MLP 90-II-12-80, 120) as well as in the sectioned tooth (Fig. 4: 1).

During further abrasion, the parasagittal crests connect the lophs separating well defined enamel islets in the central axis. These, formed out of a transverse valley, are the second type of enamel islets found in *Sudamerica*. At this stage of wear each valley between lophs, as well as the anterior and posterior caps, show an enamel islet along the sagittal axis of the tooth. This stage is represented in the tooth sectioned at about 1 mm below the reconstructed unworn surface (Fig. 4: 2).

From isolated teeth it can be reconstructed that the islets of the anterior/posterior caps become smaller and disappear earlier than those between the lophs. In section 3 (at 2.5 mm below the reconstructed unworn surface) the islets of the caps have disappeared, as well as most of those between the lophs. Only the very base of one islet is still present even if reduced in size (Fig. 4: 3). In section 4 (at about 4 mm below surface) the enamel islet has disappeared (Fig. 4: 4). The enamel bands of the labial and lingual synclines almost touch each other leaving only a minute band of dentine in between. In this way, a central longitudinal axis with transverse lophs is formed. The number of lophs does not vary within a tooth. The closure of the enamel islets and the expansion of the synclines could be verified in some tooth fragments (MPEFCH 533). They confirm that the enamel islets (regardless if those in the anterior caps or those originating in the valleys between the lophs) disappeared in the upper one/forth of the crown height. All teeth worn more deeply should not have an enamel islet down to the base of the crown.

Due to the prismatic nature of the tooth, further wear does not alter the morphology of the occlusal surface, except when the very base of the crown is reached. This stage of wear is not represented in the fossil material, but it is known from some rodents with a comparable tooth morphology. Therefore this possible pattern will be mentioned here. Towards the very base, the opposing synclines tend to be closed at the outer margin of the tooth (Fig. 4: 10, 11), while in the more mesial part the syncline is somewhat deeper and might form a little basin, which occurs as an enamel islet when this stage of wear is reached. Thus, hypothetically it is probable to find a very worn molariform with a circular or a quadrangular outline, without synclines but with grooves, the third type of enamel islets. These occurred during the ontogeny and phylogeny in some caviomorph rodents (Pascual *et al.* 1965, 1988), notoungulates and many other mammals with hypsodont molars.

So far, three possible kinds of enamel islets can be distinguished. The first type is formed by grooves in the unworn occlusal surface and occurs in the anterior/posterior caps. Such enamel islets are also found in the gondwanatherian tooth fragments from Madagascar and India (Krause *et al.* 1997). The Indian specimen (Fig. 12A) shows that the enamel islet extends much further down into the tooth, approaching the base of the

crown. Among other mammals similar enamel islets are widely distributed, especially in rodents. To our knowledge, the best equivalent is the *Mimomys*-islet of primitive arvicolines (Rodentia). It originates from a lateral syncline, the so called 'islet-fold', of the unworn occlusal surface (Hinton 1926). In some arvicoline taxa these islets penetrate fairly deep into the hypsodont tooth. During further evolution, especially when teeth become euhypsodont, these enamel islets are reduced.

The second type of enamel islets is formed in the transverse valleys separating the lophs. The anterior and posterior walls of the lophs show a pair of little spurs where they connect in later stages of wear to parasagittal crests crossing the transverse valleys. These parasagittal crests surround a central islet and separate the labial and lingual synclines. Since the parasagittal crests differ in height, the enamel islets may remain connected with one or the other syncline somewhat longer. In a slightly later stage of wear the enamel islets are separated from both synclines. In later stages the enamel islets between synclines disappear too and the synclines extend towards the central axis of the tooth.

This is a very unusual condition. In most hypsodont mammals the synclines are deepest in the uppermost stages and become smaller towards the base of the crown. Further, in no other group does increasing abrasion of an islet lead to a replacement by a syncline. The only equivalent we can find is in the p4 of some Lagomorpha like *Necrolagus*, recently discussed by Averianov & Tesakov (1997). Their interpretation that the islet merges into the enlarged syncline (1997: fig. 7.5) has to be rejected since enamel islets always end like a blind sack.

The third type of enamel islets originating at the very base of the tooth from a syncline, is very common in many rodents like *Hystrix* or *Castor*. The cricetid *Rhombomys* should be mentioned here, since it has a strikingly similar tooth morphology compared to that of *Sudamerica ameghinoi*. Here the synclines form such enamel islets in a very late stage of attrition. No tooth of *Sudamerica* so far collected is abraded to expose the base of the crown. However, in the artificial abrasion, the synclines can be shown to end in a shallow enamel islet as well.

**Enamel formation and dental eruption.** — In evolutionary terms, brachyodont teeth, mesodont teeth, and hypsodont teeth form a continuum. The eruption rate of a tooth accelerates with greater height. Within hypsodont teeth there is a gradual transition from rooted teeth (prohypsodont) to continuously growing teeth (euhypsodont). One alternative, seldom discussed in this context, are the dentine teeth of edentates, tubulidentates, elephants, and whales. Here, the enamel cap of these teeth is functionally unimportant; the fast erupting hypsodont body of the tooth is formed by the dentine core continuing into the root. However, for functional reasons most mammals with hypsodont teeth retain their enamel forming very effective cutting edges, which are even self-sharpening. There is one problem with enamel formation from ectodermal tissues: while dentine is formed continuously throughout life, enamel is generally formed only during a very limited time span. Enamel is formed at the tips of the various cones and continues downwards. When the lower rim of the enamel cap is completed, the base of the crown is formed, the enamel organ is reduced and the tooth can erupt and function. This basic pattern of tooth formation is valid for many hypsodont teeth; however, the space available within the jaw limits the maximum size

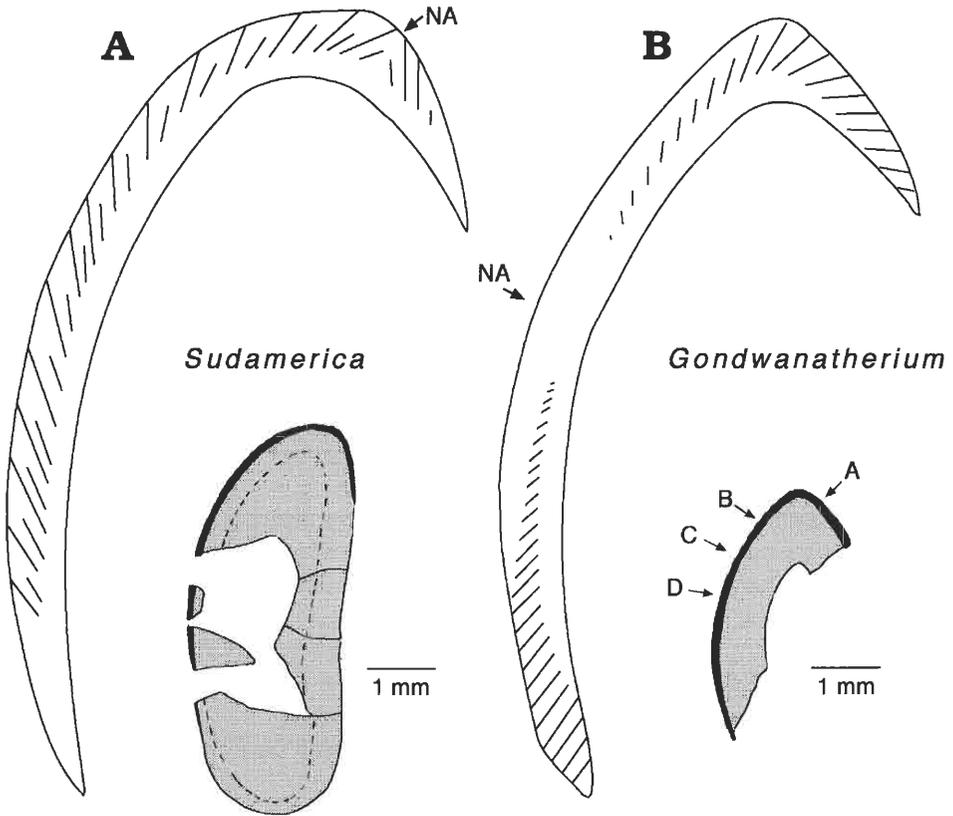


Fig. 6. Cross-sections of isolated lower incisors of *Sudamerica ameghinoi* (A) and *Gondwanatherium patagonicum* (B) with an enlarged schematic indication (not to scale) of the prism orientation in the schmelzmuster. NA indicates the position of the 'neutral area' between two fields of tangential enamel with opposing prism direction. White indicates the radial enamel, hatched areas the tangential enamel with the direction of the prisms. Note that in *Sudamerica* the prisms of the tangential enamel fade away in a thick outer prismless enamel. In B the arrows numbered A–D indicate the position of detailed photos in Fig. 11.

of the crown. The root can be formed when the tooth is already in function. The very high mandible of many mammals with hypsodont teeth reflects the required space. There is a possibility to overcome the limitation set by the jaw morphology. If the enamel organ is not reduced entirely before tooth eruption but continues to add enamel to the dentine core in the lower part, well protected in the depth of the jaw, the tooth can continue to grow. This evolutionary step was reached independently by many mammalian groups. Teeth of that type can grow and form roots at any later time. Several rodents, e.g., *Clethrionomys*, continue to add to the tooth height after eruption and form later roots. This evolutionary step can easily be identified in the fossil record, when younger teeth show no base of the crown but worn teeth normally have roots. There is a transition to continuously growing teeth. The root formation has not had to be reduced, only postponed. It is clearly shown in the South American toxodontid ungulates: the Miocene *Nesodon* develops roots only in the worn molariforms, whereas the Pliocene–Pleistocene *Toxodon*, having the same molar pattern, developed open-rooted,

ever-growing molariforms. In euhypsodont mammals, it is difficult to determine if they are unable to form roots or whether they normally die before roots are formed. The cricetid *Rhombomys* is known to have euhypsodont molars, but in extremely old individuals molars do form roots. Therefore the transition from protohypsodont to euhypsodont teeth forms a classical example of heterochrony (Koenigswald 1982, 1993; Ruiz Bustos 1987; Chaline & Sevilla 1990).

Several slightly worn molariforms of *Sudamerica ameghinoi* show the closure of the synclines at the base of the crown. Since most of the material is rolled or modified slightly by diagenesis, we cannot judge how far roots were formed at that ontogenetic stage. The formation of the base of the crown normally indicates that the full height of the molars is already formed when teeth come into function. Therefore *Sudamerica*, as well as horses, belongs to the first category of hypsodont teeth. Also, indentations of enamel islets are restricted to the first category, since enamel islets cannot be formed when the occlusal surface is no longer covered by tissue.

The formation of enamel islets, characteristic of juvenile molariforms of *Sudamerica ameghinoi*, are very important in hypsodont teeth. To form the enamel within an enamel islet, the tooth has to be covered with growth tissue; therefore, the maximal depth of an enamel island is restricted to the height of the tooth formed before eruption. That might be a constructional reason why teeth of most artiodactyls and perissodactyls, characterized by enamel islets, belong to the first category, and do not evolve into categories two or three. Among rhinos, only *Elasmotherium* developed euhypsodont molars since it reduced the enamel islets and crenellated the outer enamel surface. The length of the functional cutting edges may be contained although enamel islets are reduced when the external enamel is differentiated by synclines. Arvicoline rodents provide a very obvious example of the extensive formation of synclines in hypsodont teeth.

Another interesting conclusion is that, as the molariforms of *Sudamerica* are characterized by fairly shallow enamel islets and deep synclines in their lower part, further evolution of sudamericid molariforms could from a constructional point of view have easily led to euhypsodont teeth. This 'constructional' facility is not present, for instance, in artiodactyls. However, as far as we know, gondwanatherians did not follow this evolutionary pathway.

## The enamel microstructure

Study of eutherian enamel shows that it may differ between teeth of very different morphologies and functions (Koenigswald & Clemens 1992; Koenigswald 1997a). A very obvious example for such a variation at the dentition level is that found regularly in rodents, where incisors and molars, in general, differ fundamentally in their schmelzmuster. Therefore we discuss separately the enamel microstructure of the incisor and the molariforms of each taxon.

In rodent incisors the composition of the different enamel types normally varies only slightly between the lateral and the mesial end of the enamel band. The layer of HSB continues throughout the entire length of the enamel band and is commonly covered by radial enamel. In the Gondwanatheria, however, where the schmelzmuster is

composed of tangential and radial enamel, the orientation of the prisms within the tangential enamel differs between the lateral and the mesial part. A central 'neutral area' of radial enamel only is normally present and important to understand the symmetry. This 'neutral area' of radial enamel between two fields of tangential enamel with prisms oriented in opposite direction seems to be a character linked to some constructional limitation. It can be observed wherever tangential enamel continues over the entire width of a tooth, as in the incisor of the marsupial *Groeberia* (Koenigswald & Pascual 1990), or in the canine of *Thylacosmilus* (Koenigswald & Goin in press). In placentals, the posterior lobe of arvicolid molars shows the same pattern (Koenigswald 1980).

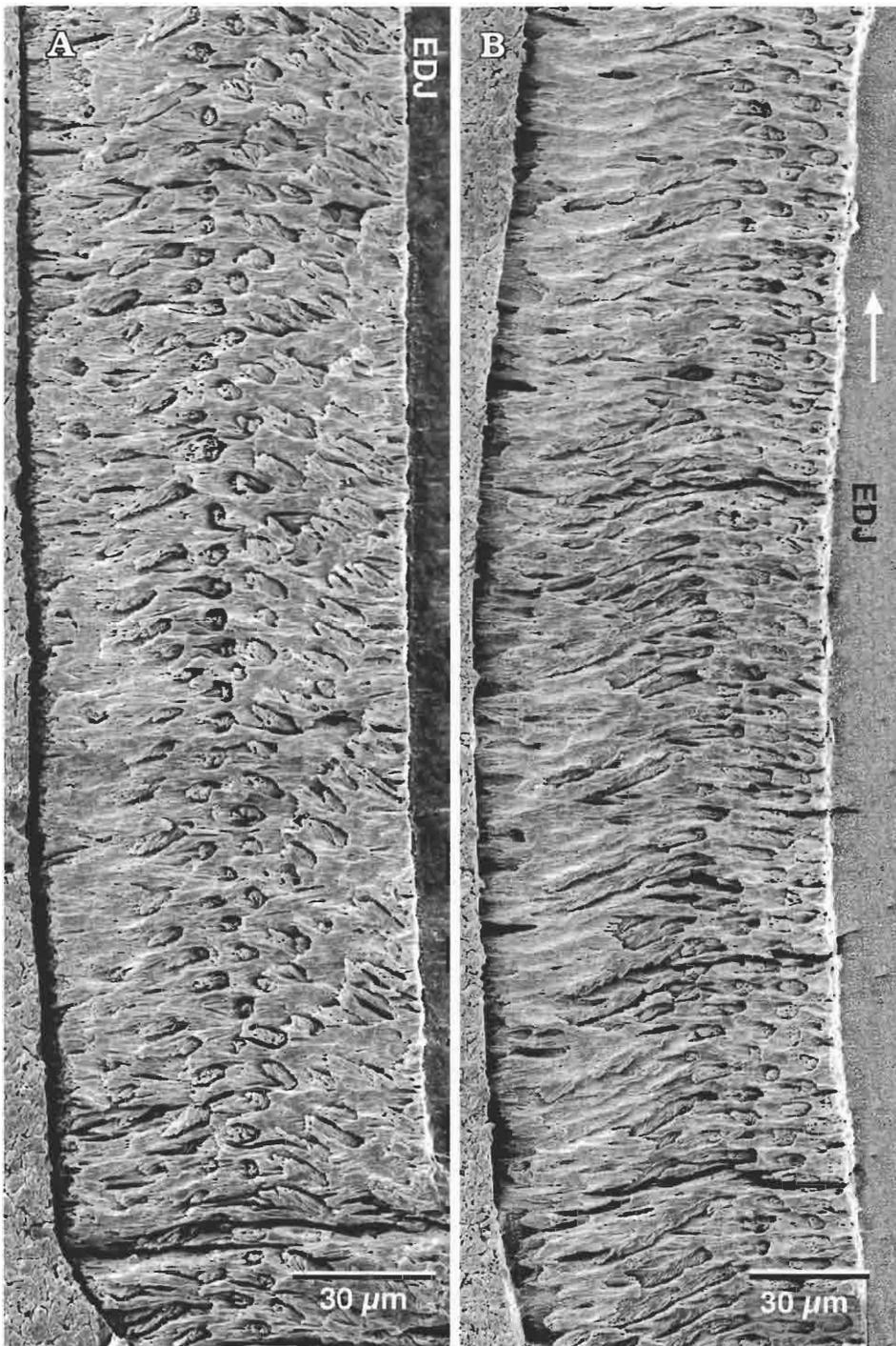
**The enamel of *Sudamerica*.** — The enamel of the incisor in *Sudamerica* is composed of radial enamel, tangential enamel, and a thick PLEX (Fig. 6). Prisms are surrounded by an unusually thick IPM, and are separated by incomplete prism sheaths; therefore, it is somewhat difficult to identify the prism direction. The upward inclination of the prisms is very little and may be even slightly downward. The IPM is straight from the EDJ to the OES and the course of the prisms has a distinct flexion separating an outer from an inner zone (Fig. 7).

Although the prism direction is somewhat difficult to identify, a 'neutral area' of radial enamel can be found somewhat mesial from the most labial point of the enamel band (see Fig. 6A). On both sides of the 'neutral area' we found radial enamel in the inner zone which changed onto tangential enamel in the outer one. The prisms of both fields of tangential enamel are oriented in opposite direction and point towards the neutral area. Towards the OES, the prisms disappear more and more in the thick IPM and most of the outer enamel lacks prisms.

In a set of tangential sections it could be observed that prisms are surrounded by a very thick IPM, and that the prism sheaths are quite open and show often a seam. From sections closer to the OES it appears that the prisms 'fade away', not simultaneously but irregularly. Besides prisms we found very small groups of crystallites surrounded by discontinuities; they may represent the last vestiges of prisms (Fig. 8). The entire enamel of the molariforms is prismatic (Figs 9, 10). In contrast to the incisor, prismless enamel does not play a role. The enamel is always one-layered and consists only of radial enamel. The prisms arise radially with about 45° from the EDJ. The IPM is oriented at a large angle towards the prisms. It anastomoses between the prisms as seen from transverse and tangential section. Near the OES the prisms change direction slightly. The IPM meets the OES almost at a right angle. Retzius lines are well visible in some parts near the outer surface. The prisms have an incomplete prism sheath and show a seam. Their diameter varies between 3.5 and 4.5 µm. Tubuli were observed already by Sigogneau-Russell *et al.* (1991). They occur most frequently near the EDJ. As in *Gondwanatherium*, the prism cross section increases from near the EDJ to the OES (see below).

The enamel band surrounding the cheek-teeth of *Sudamerica ameghinoi* is of almost equal thickness in all areas, measuring 0.2 to 0.3 mm, even though it becomes slightly thicker towards the base (Table 2). The enamel of the enamel islets is slightly thinner. Leading and trailing edges cannot be differentiated from the enamel only, nei-

Fig. 7. Incisor enamel of *Sudamerica ameghinoi* (MLP 90-II-12-560; KOE 2861) in longitudinal (A) and horizontal (B) sections. There are two zones of radial and tangential enamel. The prisms of the tangential



enamel tend to disappear in the very thick interprismatic matrix. The longitudinal section (A) shows that prisms descend in the outer zone.

ther by its thickness nor by its enamel microstructure. Such a differentiation is known from several rodents (Koenigswald *et al.* 1994). In the depth of the synclines, the outer surface of the enamel shows an irregular crenellation. Its functional significance is most probably the firm attachment of cementum. A comparable crenellation was found in other taxa with hypsodont molars, such as the suid *Phacochoerus* and the rhinocerotid *Coelodonta*.

Notes on the microstructure of the enamel of some Gondwanatheria were already given by Sigogneau-Russell *et al.* (1991) and Krause *et al.* (1992). Basically, their results concerning *Sudamerica* can be interpreted in the same way as given above.

**The enamel in *Gondwanatherium*.** — The incisor of *Gondwanatherium* is covered by enamel similar to that of *Sudamerica*. In cross-section, the enamel band is divided into two parts by a sharp bend between the mesial and the labial parts (Fig. 6B). The strong bend differentiates *Gondwanatherium* from *Sudamerica*, in which it is more rounded. The labial and lateral parts of the enamel band are about four times longer than the mesial one. The thickness increases from the lateral end, where it is of about 75  $\mu\text{m}$ , to the bend where the thickness reaches 140  $\mu\text{m}$ . Towards the mesial end, the enamel gets only slightly thinner.

The incisor enamel of *Gondwanatherium* is comprised of radial and tangential enamel (Fig. 11A–D). Since the prisms are well developed in the entire thickness, the schmelzmuster is much more distinct than in *Sudamerica*. A ‘neutral area’ with radial enamel in the entire thickness of the enamel band is found not mesially as in *Sudamerica* but laterally from the most labial point of the enamel band. This ‘neutral area’ is also much more extended than that of *Sudamerica* (Fig. 6B). In the radial enamel the prisms rise towards the occlusal surface. Towards both sides, tangential enamel occurs as a central layer of increasing thickness. The IPM is straight from the EDJ towards the OES, forming a distinct angle with the prisms of the tangential enamel. Towards the mesial side of the tooth, the tangential enamel gradually suppresses the inner and the outer radial enamel in order to fill the entire thickness of the enamel band. Towards the lateral sides, the tangential enamel is underlain by an inner radial enamel for a much longer portion, until finally the tangential enamel covers the entire thickness of the enamel band. The prisms of the tangential enamel are oriented in the mesial part mesially and in the lateral part laterally. The reverse is the case in *Sudamerica*.

Krause *et al.* (1992) were able to study only a longitudinal section of an incisor of *Gondwanatherium* showing only radial enamel. Since no exact position of this section is given, it cannot be evaluated properly. The lateral variation within the schmelzmuster of the Gondwanatheria cannot be demonstrated in a single section. Only the combination of transverse, longitudinal and, if possible, tangential sections allows a three-dimensional reconstruction of the enamel types involved. In rodents, such a lateral variation is less marked, and single longitudinal sections may supply sufficient information.

The enamel of the hypsodont molariforms of *Gondwanatherium* is, as in *Sudamerica*, very thick (0.3 mm), and is formed by radial enamel only (Fig. 11E). The prisms rise in a straight line from the EDJ to the OES. The IPM anastomoses between the prisms. One peculiarity of the enamel of *Gondwanatherium* is that the cross section of the rounded prisms enlarges significantly from near the EDJ to the OES. In a transverse section we observed an increase in the prism width. We measured the maximum

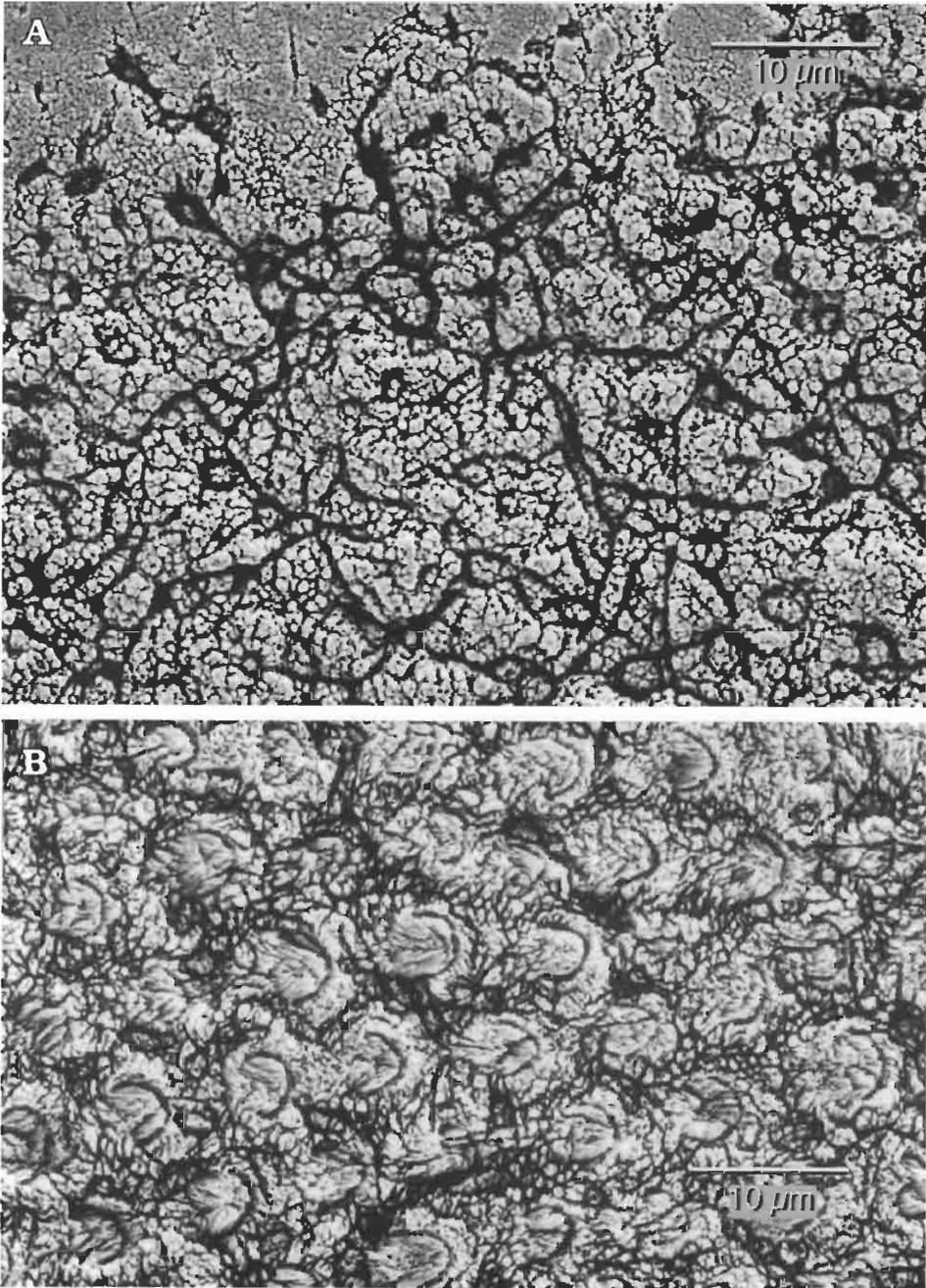


Fig. 8. Two tangential sections of the lateral surface of the incisor of *Sudamerica ameghinoi* (KOE 2861) shown in Fig. 7. **A.** Close to the outer enamel surface, groups of crystallites surrounded by discontinuities occur within the interprismatic matrix. **B.** Much deeper section in which the prisms are fully visible with an incomplete prism sheath and partially a seam. Note that at this level some prisms seem to have disappeared already within the interprismatic matrix.

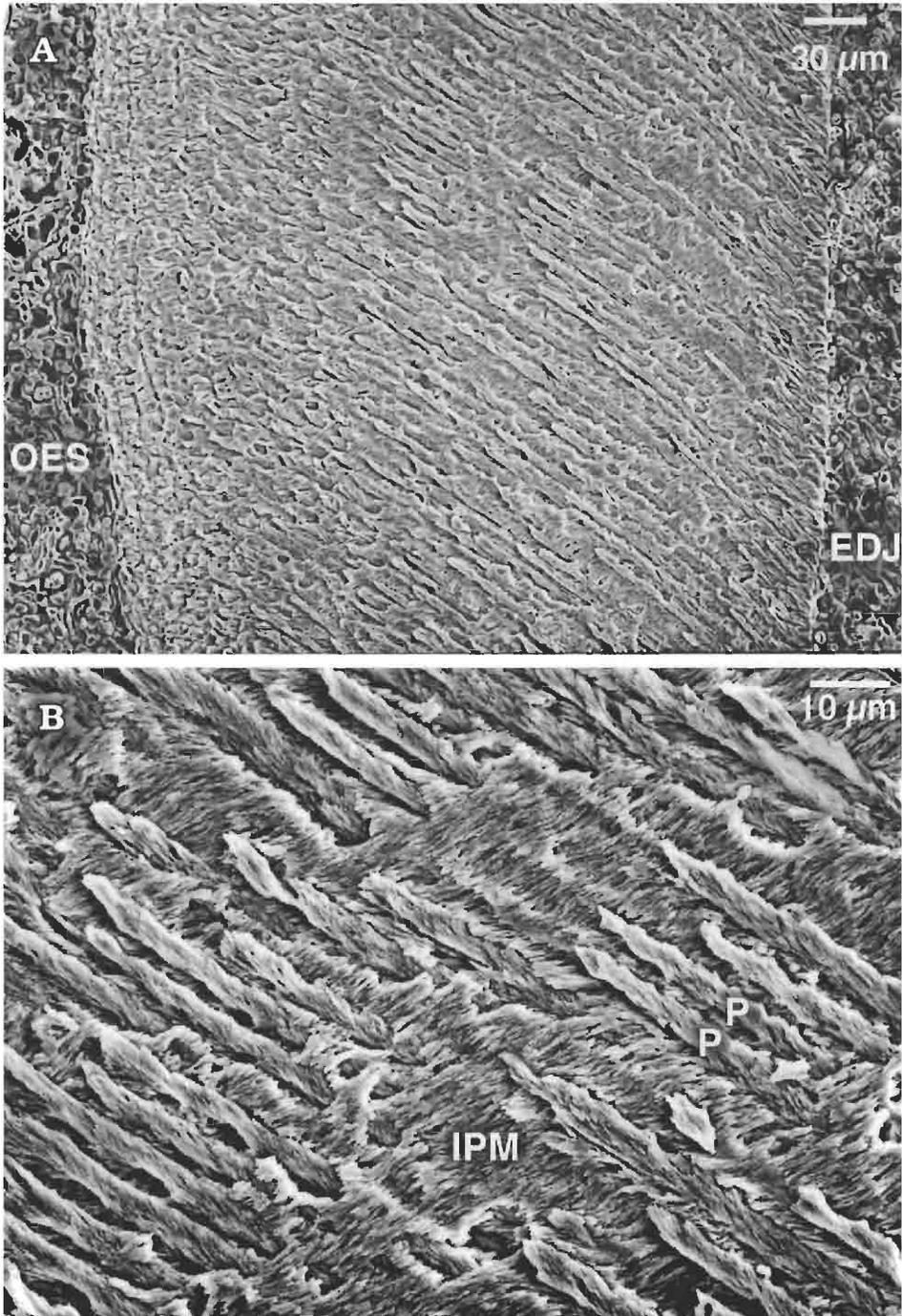


Fig. 9. A. Vertical section through a molariform of *Sudamerica ameghinoi* (KOE 3311) showing the prismatic nature of the entire enamel band and Retzius lines close to the outer enamel surface (OES). B. Detail showing the almost straight angle between prisms (P) and interprismatic matrix (IPM).

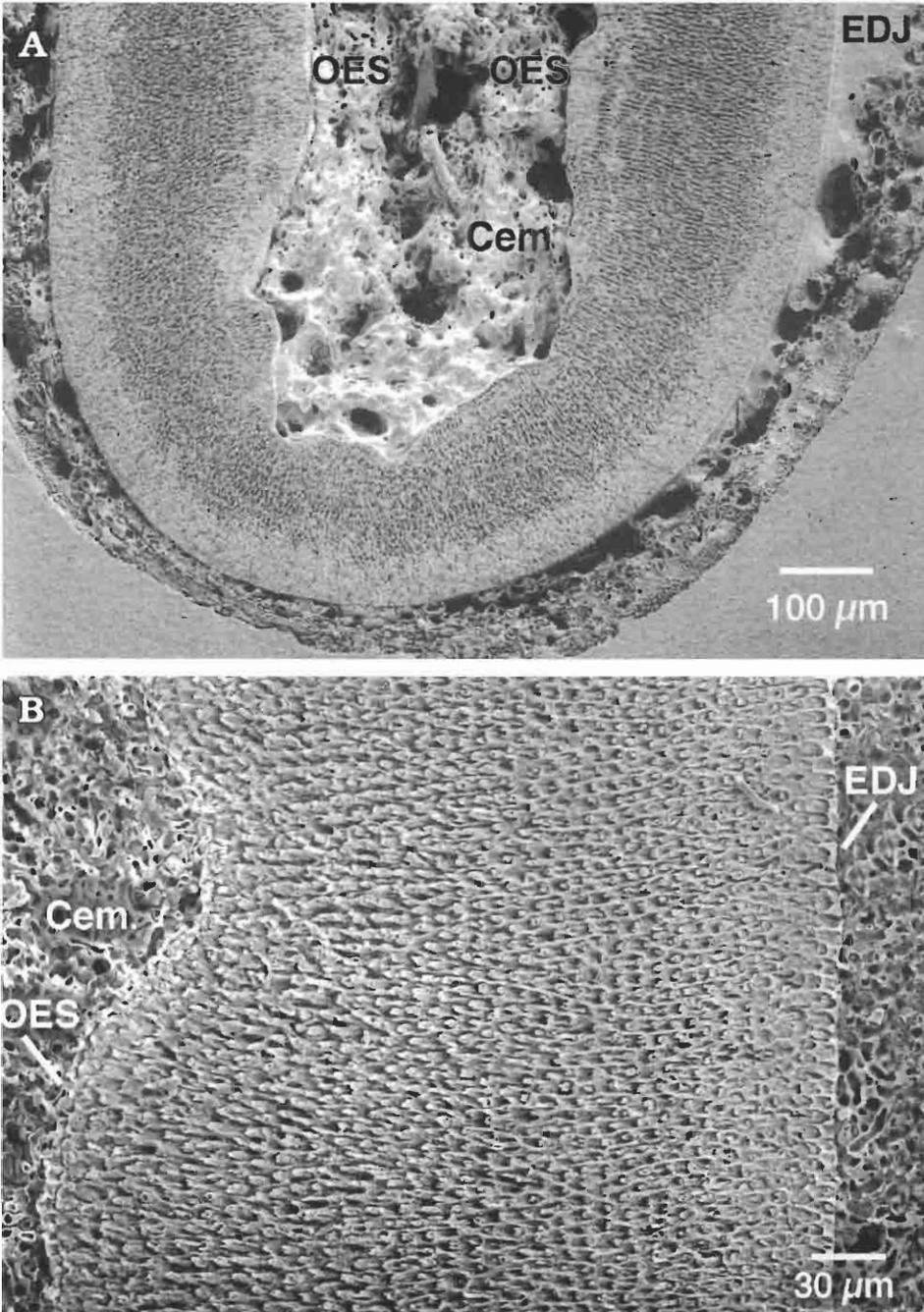


Fig. 10. **A.** Transverse section of a molariform of *Sudamerica ameghinoi* (KOE 3311) showing the radial enamel in the entire thickness of the enamel band. The outer enamel surface (OES) is wrinkled in the depths of a syncline to hold the cementum (Cem). **B.** Detail of the same section showing the radial enamel between the dentine and the cementum (Cem). The specimen is modified by saprophytic organisms.

width of 20 prisms close to the EDJ and calculated a mean of 2.77  $\mu\text{m}$  (ranging from 1.60 to 3.71  $\mu\text{m}$ ). Another 20 were measured in the middle section, with a mean of 4.29  $\mu\text{m}$  (from 3.36 to 5.40  $\mu\text{m}$ ). Finally, near the OES 22 measurements gave a mean of 5.61  $\mu\text{m}$  (ranging from 4.06 to 7.07  $\mu\text{m}$ ; Fig. 11E). The length was neglected because of the angle between the transverse section and the obliquely rising prisms. Such a drastic increase in the prisms diameter has so far not been observed in any other mammal. However, all values are within the range of normal mammalian prisms. Even the largest ones do not reach the size of the 'gigantoprismatic' prisms of some taenio-labidoid multituberculates (Krause & Carlson 1987).

**The enamel in *Ferugliotherium*.** — *Ferugliotherium windhauseni* has very low-crowned molars. The thin enamel (about 0.1 mm) was investigated on a broken edge of a molar by Krause *et al.* (1992). Their pictures clearly indicate radial enamel with anastomosing IPM at large angles. The prism diameter is 4.6  $\mu\text{m}$  according to Sigogneau-Russell (1992). Krause *et al.* (1992) classified the enamel as 'small prismatic enamel'. The size of the prisms is correct but not specific. Whether the prisms have a complete prism sheath cannot be judged from their figures.

**The enamel in *Lavanify*.** — *Lavanify miolaka*, from the Late Cretaceous of Madagascar, is represented by two high-crowned tooth fragments with distinct cementum and a deep enamel islet. The enamel is one-layered and consists of radial enamel with very distinct vertical inter-row sheets formed by the IPM (Krause *et al.* 1997).

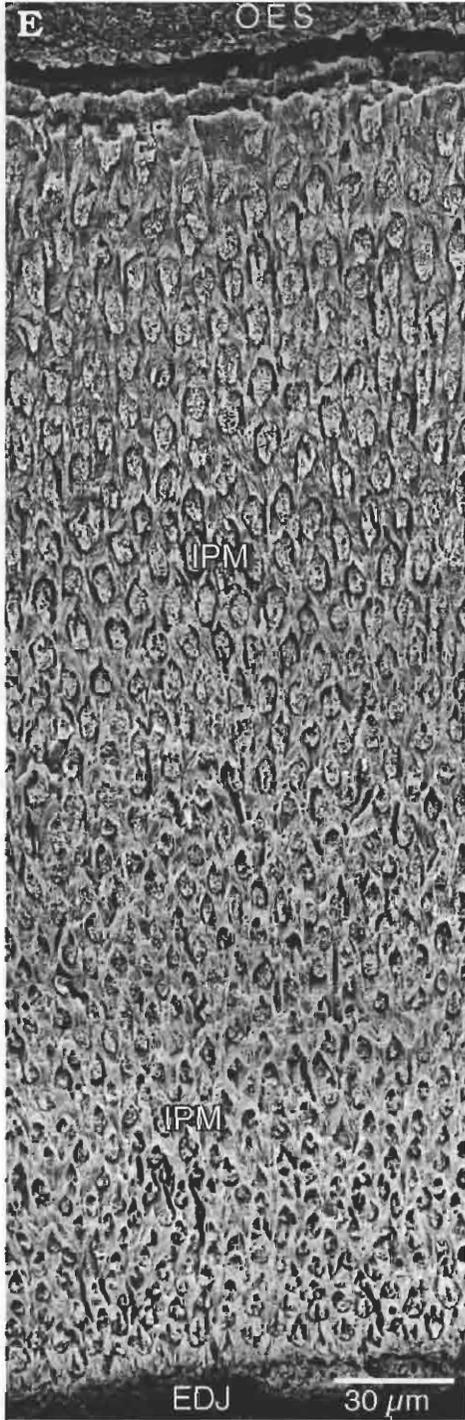
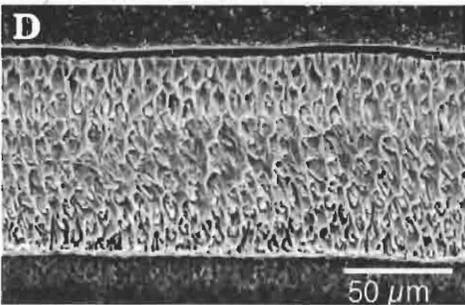
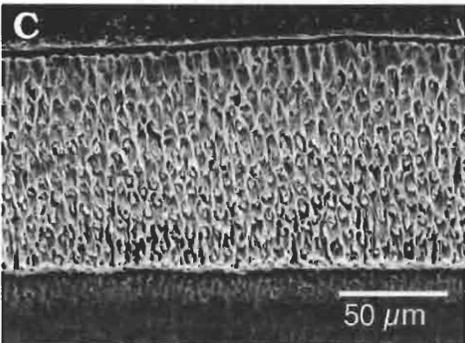
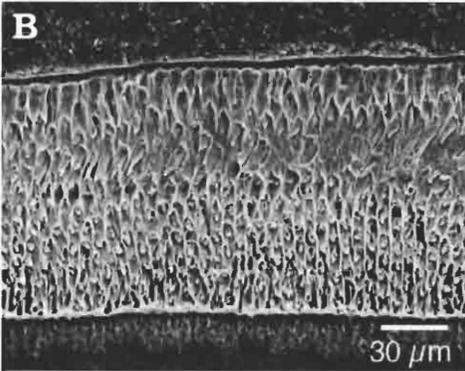
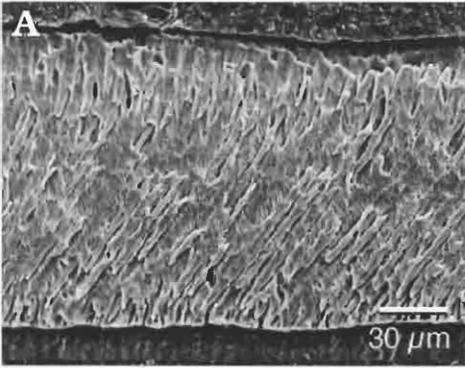
**The enamel of an Indian gondwanatherian.** — This unnamed taxon is represented by an isolated molariform fragment that clearly shows hypsodonty, a deep enamel islet, and cementum (Fig. 12A) (Krause *et al.* 1997). The enamel is about 0.2 mm thick, and mainly formed by radial enamel. Vertical inter-row sheets can be seen in tangential section (Fig. 13A). The transverse section shows that the prisms partly deviate from the radial direction, forming irregular areas of tangential enamel (Fig. 12B). The surrounding enamel of the tooth, which is functionally more important, could not be investigated in detail.

## Comparison of the enamel and tooth morphology of gondwanatherians

Gondwanatherians were regarded as multituberculates until the four molariforms of *Sudamerica* indicated an independent mammalian group. In Multituberculata two different prism types were described (Fosse *et al.* 1978; Carlson & Krause 1985), based on the size and shape of the prism cross-section and termed 'gigantoprismatic enamel' and 'small prismatic enamel'. (Formally these terms refer to prism types and not to

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Fig. 11. Enamel of *Gondwanatherium patagonicum*. **A–D**. Various positions of the transverse section of the incisor showing the different distribution of radial and tangential enamel. The positions of the photos are indicated in Fig. 6B. **E**. Transverse section of a molariform showing the radial enamel with a thick interprismatic matrix (IPM). Note the increasing cross-section of the prisms from the enamel-dentine junction (EDJ) towards the outer enamel surface (OES). Only the widths of the prisms is significant, since the prisms are sectioned at an oblique angle.



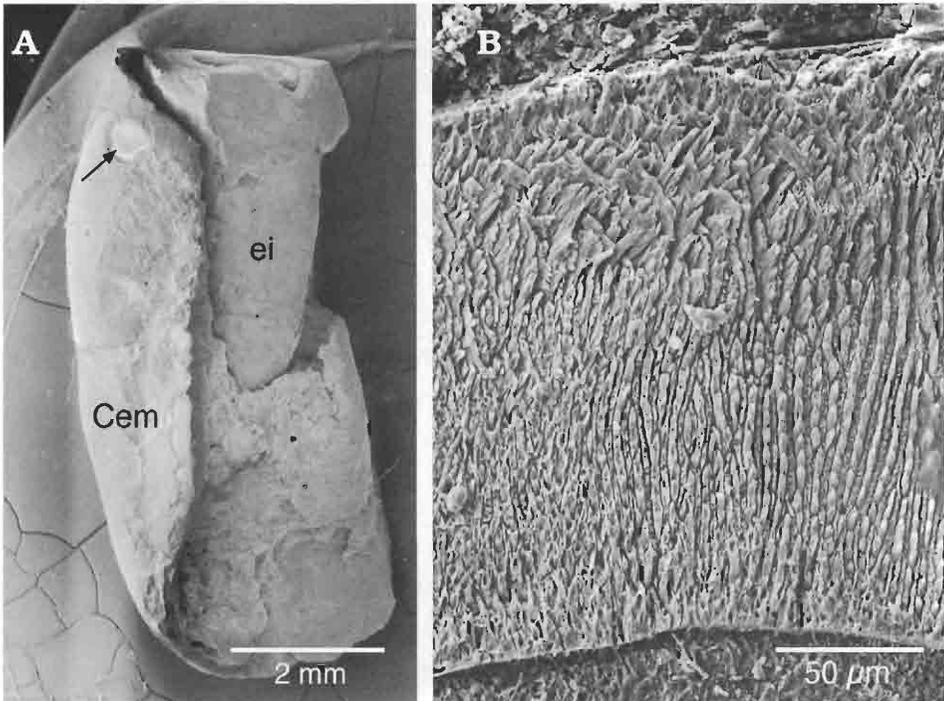


Fig. 12. **A.** The Late Cretaceous, unnamed Indian gondwanatherian tooth fragment (VPL/JU/NKIM/25) with a deep enamel islet (ei) seen from outside at the fracture. The outer enamel is covered by a thick cementum (Cem). The cementum was drilled away (arrow) to obtain the tangential aspect of the enamel shown in Fig. 13. **B.** Cross-section of the enamel band of the same specimen surrounding the enamel islet. It shows radial and tangential enamel and distinct inter-row sheets.

enamel types which are characterized by the orientation of prisms. Therefore, these terms are used here in quotations marks. The prisms of the 'gigantoprismatic enamel' have an open prism sheath and a cross-section between about 6 and 13  $\mu\text{m}$ , with a mean of 8.2  $\mu\text{m}$  (Carlson & Krause 1985). While open prism sheath are very common, the size is exceptionally large for enamel prisms. Such prisms of the 'gigantoprismatic enamel' occur among multituberculates in all Cimolodonta except for Ptilodontoidea, among 'plagiaulacidan' multituberculates in so called 'Morrison' and in *Eobaatar*, and in Arginbaataridae, assigned to a suborder *incertae sedis* (Kielan-Jaworowska & Hurum submitted). The second prism type in multituberculate enamel was described as 'small prismatic'. The prisms have a closed prism sheath and their cross-sections vary between 2 and 5  $\mu\text{m}$ . Carlson & Krause (1985) give a mean value of 3.2  $\mu\text{m}$ . They argue that this prism type derived from 'gigantoprismatic enamel'. This, most probably, is true for multituberculates, but in other mammalian groups prisms normally have between 3 and 4  $\mu\text{m}$  in cross-section and a closed prism sheath can be observed frequently. Therefore the term 'small prismatic' may be useful for the description within multituberculates, but not in comparison with other groups. The prisms of *Ferugliotherium* were described as 'small prismatic' (Krause *et al.* 1992).

None of the gondwanatherian enamels is formed by prisms of the size characteristic for 'gigantoprismatic enamel'. In *Gondwanatherium* a unique increase of prism thickness was observed. But even in the thickest parts they do not reach dimensions as characteristic for 'gigantoprismatic enamel'. Mostly the prism size is much smaller and the prism sheath is normally incomplete. Even in *Ferugliotherium*, the figures given by Krause *et al.* (1992: fig. 3A) do not exclude an incomplete prism sheath. Therefore their identification as 'small prismatic' and thus sharing an apomorphic character with multituberculates may be reconsidered.

At the prism level, the gondwanatherian enamel does not show any specific synapomorphic character with multituberculates nor with any other mammalian group. It cannot be excluded that they developed their prisms parallel to the other mammalian groups.

The schmelzmuster of the incisors can only be compared among the South American gondwanatherians. Similarities between *Gondwanatherium* and *Sudamerica* rely only in the combination of radial and tangential enamel, with an IPM straight from the EDJ towards the OES. If the two specimens available for study are representative, then the older *Gondwanatherium* seems to be somewhat more derived than *Sudamerica* since the tangential enamel is much better developed. It seems to be characteristic that the composition changes from the lateral to the mesial sides of the enamel band. This schmelzmuster is fundamentally different from that of rodent and lagomorph incisors, which are homogeneous throughout and characterized by the presence of Hunter-Schreger bands (Korvenkontio 1934). In marsupials, where Hunter-Schreger bands are generally very rarely developed, enlarged incisors are characterized by the combination of tangential and radial enamel which are linked by simultaneous prism deviations; however, in most species studied (Koenigswald & Pascual 1990; Koenigswald 1994) the IPM is vertical to the prism direction in both enamel types. A combination of radial and tangential enamel was found in ptilodontoid multituberculates (Sahni 1979) and various marsupials (Koenigswald & Pascual 1990; Koenigswald 1994). However, the existence of these two enamel types does not unite these groups as a synapomorphic character, since the arrangement within the schmelzmuster differs.

Even though the schmelzmuster of *Gondwanatherium* and *Sudamerica* is composed of a combination of radial and tangential enamel, they show distinct differences: (1) the 'neutral area' of exclusively radial enamel is very restricted and mesially placed in *Sudamerica*, while in *Gondwanatherium* it is much more expanded and placed laterally in the incisor section. (2) In the tangential enamel of *Gondwanatherium* the prisms are directed away from the 'neutral area', while in *Sudamerica* they do the opposite, pointing towards the 'neutral area'. The enamel seems to be much better differentiated in the Late Cretaceous *Gondwanatherium* than in the Paleocene *Sudamerica*. These differences are substantial, and suggest that both taxa have had long histories of their own, instead of being direct descendants.

All gondwanatherian taxa show radial enamel in their molariforms with IPM at a very distinct angle. The two taxa from Madagascar and India, however, show a more derived feature: prominent inter-row sheets mainly in a vertical direction (Fig. 13A). In the Indian tooth, restricted areas of tangential enamel were observed. In contrast, the South American taxa show anastomosing IPM (Fig. 13B). According to the observation in other mammals, we assume that anastomosing IPM is less derived than typical

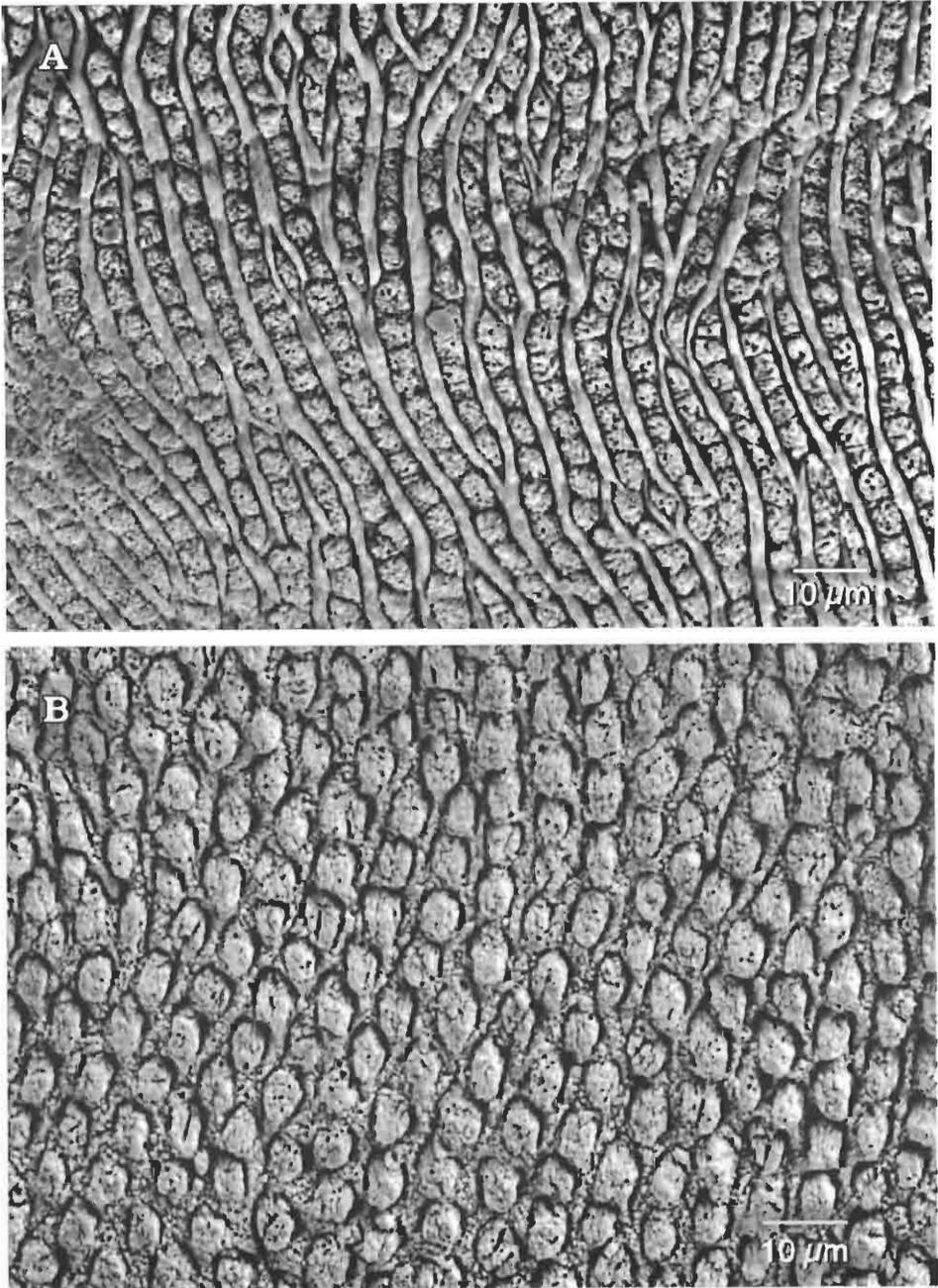


Fig. 13. Tangential aspect of the radial enamel in the unnamed Indian gondwanathere (VPL/JU/NKIM/25) (A) and *Sudamerica ameghinoi* (B) in the same scale. Note that prisms in the Indian specimen are organized in rows separated by inter-row sheets, while in *S. ameghinoi* the prisms are more or less surrounded by interprismatic matrix, although in some parts they show some alignment (KOE 3311).

inter-row sheets (Koenigswald 1997b). These characters indicate that the gondwanatherians from India and Madagascar evolved independently from those in South America and formed, at a very early stage, very deep enamel islets and radial enamel modified by vertical inter-row sheets. The formation of distinct inter row sheets can be regarded as a derived character, at least in marsupial and placental mammals and thus most probably in Gondwanatheria as well.

In turn, each one of the South American taxa can be interpreted as gradual stages of increasing hypsodonty and a very unique formation of shallow enamel islets which are substituted by synclines. They did not modify the radial enamel of the molariforms. Additionally, *Gondwanatherium* and *Sudamerica* are characterized by an unusual increase of the prism thickness from the EDJ towards the OES. The IPM anastomoses between prisms.

Even though simple, it should be noted that the enamel of *Sudamerica* has several derived features that clearly differentiates it from many Mesozoic mammals showing radial enamel but not having the IPM as continuously at a large angle. The reorientation of the IPM at a large angle to the prisms was developed by most mammalian groups independently. Mechanically it functions like a plywood structure. Multituberculates and marsupials developed this character very early, while placentals show this feature only in limited groups. The placentals developed another structure to strengthen the enamel by decussating prisms with prisms (Koenigswald 1995 and in press).

Finally, the molariform gross morphology of gondwanatherians is also coincident with their inferred relations. The forked anterior pattern of the first lower molariform in *Gondwanatherium* and *Sudamerica* is shared by *Ferugliotherium*. *Ferugliotherium* has low-crowned teeth, *Gondwanatherium* is distinctly hypsodont, while *Sudamerica* reached the highest degree of hypsodonty but did not develop continuously growing molars. The enamel islets present in *Sudamerica* are very shallow and as shown above, are replaced by synclines. In this sense (but see above), *Gondwanatherium* might be a good ancestral form. Rodent-like incisors are assumed for all three genera.

Although the morphology of the two taxa from Madagascar and India is difficult to reconstruct, the known fragments clearly show a type of enamel islets different from the South American taxa. They are very deep and not replaced by synclines. In the Indian tooth it can be seen that the islet definitely reaches as far down as the outer enamel (Krause *et al.* 1997: fig. 2C). Therefore the separation seen in the enamel is reinforced by the molar morphology. Nevertheless the gondwanatherians share a number of derived characters such as hypsodonty and cementum.

## **Early Paleocene Patagonian environments and the origin of hypsodonty**

As recently summarized, the close of the Mesozoic Era in southern South America was characterized by far-reaching flooding events which lasted until the Danian (earliest Paleocene). Bond *et al.* (1995: pp. 49–50) stated: 'Epicontinental marine encroachment occurred mainly along the Atlantic side into Patagonia and Southern Cuyo [...] Subaerial domains became drastically reduced and the southern tip of the continent turned into an archipelago, bearing similarities with the modern Java Flores Sea physiography. By the

end of the Danian, conditions shifted toward progressive marine retreat and plate emergence. Because of the prevailing mild tectonic regime, mid-plate relief was still meager, and most of the areas formerly dominated by Maastrichtian–Danian epeiric embayments and seaways turned into a geography featuring extensive loessic plains and large lakes.’ These events set the scene for subsequent colonizations and cladogenetic events that gave rise to the early Tertiary South American mammalian fauna.

The fossil vertebrate assemblage recovered from Punta Peligro (type locality for *Sudamerica ameghinoi*), represents the first regional inhabitants of the terrestrial environments that succeeded that marine retreat. They include remains of undetermined fish, pipid frogs, a very large leptodactylid frog, abundant chelid turtles, alligators, an undetermined crocodile, and, among mammals, the first remains of a South American monotreme, at least two mioclaenid condylarths, a very derived Peligrotheriidae ?condylarth, and the most abundant mammal so far recorded, *Sudamerica ameghinoi* (see Bonaparte *et al.* 1993 for review). Recent work at the same locality led to the recovery of new specimens of all these vertebrates and of three new taxa of small marsupials. The unusually large leptodactylid frog, together with the abundance of chelid turtles and alligators, are strongly suggestive of tropical and aquatic or semiaquatic conditions. On the other hand, judging from their isolated and very fragmentary nature, mammalian remains seem to have undergone some transportation before being deposited (Bonaparte *et al.* 1993). The inferred paleoenvironment for the upper sequence of the fossil bearing Hansen Member (Salamanca ‘Group’ or ‘Formation’; see Bond *et al.* 1995) at Punta Peligro confirms this. Andreis *et al.* (1975) described it as a transitional deposit, probably paralic, alternatively subaerial and brackish subaqueous, and eventually including tidal plains. Palynological records are even suggestive of mangrove, swamp, and woodland environments (Petriella & Archangelsky 1975). In turn, littoral or estuarine environments are suggested by oligohalobian to mesohalobian diatoms (C. Macchiavello personal communication).

With this background, one of the oldest known hypsodont mammals, *Sudamerica ameghinoi* evolved. Traditionally, a close relationship between hypsodonty and grasses has been accepted. Hypsodonty in *Sudamerica* cannot be linked to the presence of grasses since these did not exist (the earliest known record of grasslands dates from the Eocene) or they did not play a significant role at the beginning of the Cenozoic. Interestingly, none of the ungulates so far recorded at Punta Peligro, the already derived ?condylarth *Peligrotherium tropicalis*, and the mioclaenid condylarths *Raulvaccia peligrensis* and *Escribania chubutensis*, are high-crowned, or even mesodont. Hypsodonty in *Sudamerica* involves not only the incisors (which could be engaged in several, not strictly feeding aspects of its life history) but the molariforms, thus directly linking this feature to food-processing. Therefore, it is concluded that nutritional needs including abrasive components, constituted, most probably, a selection pressure towards hypsodonty in gondwanatherians. Judging from the occurrence of hypsodonty in the fossil record, and from extant faunas, hypsodonty and arboreal habits do not go together. In contrast, terrestrial and semiaquatic mammals developed hypsodont molars independently several times. Larger terrestrial animals with hypsodont molars are normally grazers. Smaller terrestrial mammals with hypsodont molars are often fossorial. Hypsodonty in fossorial mammals may be related to food such as roots that contain sediment. Semiaquatic animals such as the murid *Ondatra* and beavers are also

fossorial. These animals feed not only on grasses but on roots, bark and other vegetation containing abrasive components. *Monotrematum sudamericanum*, the only known monotreme outside Australia, and also present in the assemblage from Punta Peligro, may have had similar habits to those of its living relatives, which are semiaquatic and fossorial, as suggested for *Sudamerica*.

Whatever the life history of *Sudamerica ameghinoi* was, the analysis of its cheek-teeth reveals that: (1) its morphology, including the enamel microstructure, was clearly acquired independently from that of therian mammals, (2) it represents the culmination of a process already undergone by other gondwanatherians, (3) this process was already occurring during Late Cretaceous times and before grasses evolved. As such, it leads to the conclusion that hypsodonty among mammals is not (always) a coevolutionary adaptation to grass radiation but, primarily, to specific abrasive components of the diet. In other words: 'habitat preference appears to be more important than dietary preference in determining the degree of hypsodonty' (Janis 1988: p. 367). The increased development of open habitats, and further evolution of grassland environments in Southern South America began in the early Eocene (Pascual & Ortiz Jaureguizar 1990; Pascual *et al.* 1996) and after gondwanatherians had become extinct.

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## **Hypsodontie und Schmelzmikrostruktur der paläozänen *Sudamerica ameghinoi* (Gondwantheria, Mammalia)**

WIGHART v. KOENIGSWALD, FRANCISCO GOIN und ROSENDO PASCUAL

### **Zusammenfassung**

Die Gondwanatheria haben als erste Säugetiergruppe hypsodonte Backenzähne mit dickem Zement entwickelt. Die Evolution der Hypsodontie erfolgte bei den Gondwanatheria unabhängig von den Theria, zeigt aber dennoch die gleichen biomechanischen Konzepte. Unter diesem Aspekt werden hier die hypsodonten Backenzähne von *Sudamerica ameghinoi* aus dem frühen Paläozän von Patagonien, dem jüngsten Glied der Gondwanatheria, beschrieben. *Sudamerica* hat in jeder Kieferhälfte einen immerwachsenden Schneidezahn und, durch eine langes Diastema davon getrennt, vier molariforme Backenzähne. Eine Homologisierung als Prämolaren und Molaren ist nicht möglich. Anhand eines Unterkiefers und 30 isolierter Zähne konnten acht

Zahngruppen unterschieden werden, die den je vier Zahnpositionen des Ober- und Unterkiefers zuzuordnen sind. Aus der Länge der Zähne ergibt sich ein relativ hoher Schädel. Die molariformen Backenzähne sind durch Querjoche gekennzeichnet, die bei geringer Abkautung zentral Schmelzinseln in den Vorder- und Hinterkappen sowie in den Quertälern zeigen. Die Inseln verschwinden mit der Abkautung des oberen Viertels der Zahnhöhe. Bei weiterer Abkautung vertiefen sich die Synklinalen und lassen nur einen schmalen longitudinalen Mittelgrat stehen. Das Schmelzmuster der molariformen Backenzähne von *Sudamerica* ist einschichtig und wird aus radialem Schmelz gebildet. Es besitzt in diesem ursprünglichen Zustand Ähnlichkeit zu *Gondwanatherium*. Gegenüber den Gondwanatheria aus Madagaskar und Indien, die 'interrow sheets' entwickelt haben, ist der Schmelz weniger stark differenziert. Nach dem Schmelzmuster der Inzisiven, das bei *Gondwanatherium* und *Sudamerica* aus radialem und tangentialem Schmelz besteht, ist *Sudamerica* trotz des geringeren Alters weniger abgeleitet. Die Entwicklung der Hypsodontie bei den Gondwanatheria während der Oberkreide kann nicht als Anpassung an eine Grasnahrung betrachtet werden, da es Gräser zu dieser Zeit nur untergeordnet gab. Das Biotop läßt am ehesten eine semiaquatische, eventuell auch grabende Lebensweise, etwa ähnlich einem Biber, für *Sudamerica* vermuten.

## **Hipsodoncia y microestructura del esmalte del mamífero paleoceno gondwanterio *Sudamerica ameghinoi***

WIGHART v. KOENIGSWALD, FRANCISCO GOIN y ROSENDO PASCUAL

### **Resumen**

Los gondwanaterios fueron el primer grupo de mamíferos en desarrollar dientes yugales hipsodontes rodeados de una gruesa capa de cemento, ya desde el Cretácico tardío. La hipsodoncia se desarrolló independientemente en los Gondwanatheria y los Theria, si bien existen muy similares estrategias biomecánicas en ambos. En este trabajo se describen los molares hipsodontes de *Sudamerica ameghinoi* (Paleoceno temprano, Patagonia), el gondwanaterio más joven hasta ahora conocido. La fórmula dentaria inferior de *Sudamerica* incluía un incisivo de crecimiento continuo y, separados por una gran diastema, cuatro dientes cuyas precisas homologías (premolares o molares) son inciertas. El análisis de un fragmento mandibular y de 30 molariformes aislados permitió el reconocimiento de ocho categorías morfológicas distintas para los mismos, cuatro de las cuales corresponden a molariformes inferiores y las otras cuatro a molariformes superiores. De la altura de estos dientes se deduce que el cráneo debió ser relativamente alto. Los molariformes se caracterizan por la presencia de lófos transversales. Cuando no están desgastados, estos dientes muestran sobre la superficie oclusal una serie de islas de esmalte, tanto en los lóbulos anterior y posterior como en los valles transversales. Cuando el cuarto más superior del diente se desgasta, las isletas desaparecen y los sinclinales laterales se expanden dejando solamente un borde central angosto. El esmalte de los molariformes de *Sudamerica* incluye una sola capa de esmalte radial que recuerda a la estructura de

*Gondwanatherium*. En cambio, el esmalte de los incisivos de *Sudamerica* es menos derivado que el de *Gondwanatherium*, e incluye una combinación de esmalte radial y tangencial. Comparado con el esmalte de los gondwanaterios de la India y Madagascar, el de los gondwanaterios sudamericanos es claramente menos derivado. La evolución de la hipsodoncia en los gondwanaterios durante el Cretácico tardío y el Paleoceno temprano no puede ser correlacionada con la de las gramíneas, ya que las mismas no existían en este lapso. Evidencias que incluyen la propia morfología dentaria y el biotopo inferido sugieren para *Sudamerica ameghinoi* hábitos semiacuáticos e incluso fosoriales, similares a los de los modernos castores.

## **Hipsodoncia i mikrostruktura szkliwa u paleoceńskiego ssaka gondwanateriowego *Sudamerica ameghinoi***

WIGHART v. KOENIGSWALD, FRANCISCO GOIN i ROSENDO PASCUAL

### **Streszczenie**

Gondwanatheria były pierwszymi ssakami, które już w późnej kredzie wykształciły wysokokoronowe zęby policzkowe z grubym kostniwem. Hipsodoncja rozwinęła się niezależnie u Gondwanatheria i Theria, można jednak dostrzec podobne strategie biomechaniczne w obu grupach. W pracy opisano trzonowcokształtne zęby policzkowe należące do najmłodszego przedstawiciela gondwanateriów, wczesnopaleo-ceńskiej *Sudamerica ameghinoi*. W żuchwie *Sudamerica* tkwił stale rosnący siekacz, a dalej, oddzielone diastemą, zęby policzkowe, o których trudno powiedzieć, czy są przedtrzonowcami, czy trzonowcami, i dlatego określa się je jako zęby trzonowcokształtne (molariform). Analiza niekompletnej żuchwy oraz 30 pojedynczych zębów policzkowych pozwoliła wyróżnić wśród nich 8 kategorii morfologicznych, odpowiadających czterem górnym i czterem dolnym zębom trzonowcokształtnym. Wysokość zębów wskazuje na to, że czaszka była dość wysoka. Zęby te odznaczają się poprzecznymi listewkami (lophs). Mało zużyte zęby ukazują wysepki szkliwa pośrodku przednich i tylnych guzków i w poprzecznych dolinach. Kiedy pierwsza ćwiartka zęba ulega zużyciu, wysepki znikają, a doliny powiększają się, pozostawiając tylko wąski podłużny grzbiet pośrodku. Szkliwo zębów trzonowcokształtnych *Sudamerica* jest jednowarstwowe i zbudowane ze szkliwa promienistego; przypomina szkliwo kredowego *Gondwanatherium*. W porównaniu z gondwanateriami z Madagaskaru i z Indii, formy południowoamerykańskie są mniej wyspecjalizowane. Szkliwo siekaczy jest mniej wyspecjalizowane u *Sudamerica* niż u *Gondwanatherium*, choć pierwszy z tych rodzajów jest młodszy stratygraficznie. Oba rodzaje wykazują obecność szkliwa zarówno promienistego, jak i stycznego. Ewolucji hipsodoncji u gondwanateriów w kredzie i paleocenie nie da się przypisać trawożerności, gdyż nie było jeszcze wtedy traw. Różne przesłanki dotyczące uzębienia i domniemanego siedliska *Sudamerica ameghinoi* wskazują na ziemnowodny, być może także ryjący tryb życia tego ssaka, zbliżony do współczesnych bobrów.