TOOTH ENAMEL MICROSTRUCTURE OF A LATE CRETACEOUS GONDWANATHERIAN MAMMAL FROM INDIA

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ABSTRACT

Hypsodont molars of a sudamericid (Gondwanatheria) from the Late Cretaceous of India were studied for enamel microstructure. The present specimens differ from other hypsodont sudamericids such as *Sudamerica ameghinoi*, *Gondwanatherium patagonicum* and *Lavanify miolaka* in having radial enamel, tangential enamel and a prismless outer enamel zone (PLEX). The presence of radial enamel with prisms originating from the Enamel Dentine Junction (EDJ) running apically to meet the occlusal surface and turning perpendicularly towards the outer enamel surface, has been inferred as a reinforcement against abrasion. In the present specimen, wave-like inter-row sheets in the inner radial enamel, with interprismatic matrix crystallites oriented nearly at a right angles to those of the prisms, have been observed. These features and the difference in orientation of prisms as we move from the enamel dentine junction to the outer enamel surface, were probably related to adaptation against propagation of cracks in these hypsodont teeth as early as in the Late Cretaceous.

Key words : Tooth enamel, microstructure, functional significance, Late Cretaceous.

INTRODUCTION

Gondwanatheria Mones, 1987 is represented in the Late Cretaceous (*Gondwanatherium patagonicum* and *Ferugliotherium windhhauseni* Bonaparte, 1986) and Palaeocene (*Sudamerica ameghinoi* Scillato-Yane and Pascual, 1984) of Argentina and in the Late Cretaceous of Madagascar (*Lavanify miolaka* Krause, Prasad, Koenigswald, Sahni, and Grine, 1997) and India (Sudamericidae indet., Krause *et al.*, 1997). The Indian specimens are isolated and fragmentary cheek-teeth recovered from Naskal, Andhra Pradesh, where the Late Maastrichtian Deccan Intertrappean sequences are exposed.

Among the mammals, gondwanatheres are the first to have acquired hypsodont cheek teeth, already by the Late Cretaceous (Mones, 1987; also see Koenigswald, Gain and Pascual, 1999). In hypsodont teeth the crown height is more as compared to its antero-posterior or labio-lingual length (Van Valen, 1960; Koenigswald, 1980). It is widely considered that hypsodonty developed in response to intake of more abrasive food material such as grasses and even roots. Janis (1988) proposed that it is the preference of habitat rather than the dietary habit, which plays an important role in determining the degree of hypsodonty. By developing high-crowned dentition herbivorous mammals and Gondwanatheres provide more tooth material to compensate the damage due to abrasion.

The present study originates from the idea that irrespective of the taxonomic affiliation of the mammalian group, the biomechanical requirements of all hypsodont cheek-teeth (molars) should be the same. Therefore the objectives are 1) to document the complexity of the enamel microstructure of the Indian sudamericid 2) to compare its microstructure to those of other hypsodont gondwanatheres (ex. *Gondwanatherium patagonicum*, *Sudamerica ameghinoi* and *Lavanify miolaka*) and some therian extant and fossil mammals such as murids (*Bandicota bengalensis*) and gerbillids (*Tatera indica*), and 3) to draw functional inferences of the enamel microstructure.

Sudamericids have transverse lophs on their molars (Krause and Bonaparte, 1993;

Koenigswald *et al.*, 1999), a condition favourable for cutting food material provided the power stroke of the lower jaw is perpendicular, i.e. forward or back-ward or both (for a detailed explanation see Rensberger, 1973, 1975). Transverse lophs of harder enamel and softer dentine (of both mandibular and maxillary teeth) are self-sharpening devices, and like scissors, the shearing contact moves across the food material. In many rodents, the transversely arranged enamel crests in the upper dentition curve in a direction opposite to that of occluding crests in the lower dentition, providing a minimum and rather constant area of contact and consequently maximum pressure (Rensberger, 1973, p. 518). Unlike in rodents, the power stroke in sudamericids has been found to be backward (Krause and Bonaparte, 1993; Koenigswald *et al.*, 1999). Keeping in mind the fragmentary nature of the present specimens from India, the jaw movement direction is difficult to find out, therefore it is assumed here that one of the transverse lophs (fig.1) could be

a part of the leading edge and the other could be the trailing edge.

Koenigswald and Clemens (1992) proposed that the enamel microstructure can be studied at various hierarchical levels. These levels include the crystallite, prism, enamel type, schmelzmuster and dentition. All mammals have their dental enamel made up of hydroxyapatite '*crystallites*'. These crystallites are fiber-like and are arranged almost parallel to each other to form bundles called '*prisms*'. These prisms in turn are surrounded by '*interprismatic matrix*' (IPM). Interprismatic matrix is also made up of crystallites (fig. 2). The crystallites of IPM may or may not run parallel to the prism they surround. Distinct prism boundary called as '*prism sheath*' is formed due to the difference in the orientation of prism and interprismatic crystallites. Prisms originate at the enamel dentine junction (EDJ), travel through the entire thickness of the enamel, terminating at the outer surface (fig.2). '*Enamel types*' are defined by the arrangement of groups of prisms in space. The part of the enamel in which prisms run parallel to each other is termed the '*radial enamel*' (RE). In most of the mammals, prisms are arranged in layers or zones, and when prisms of alternate layers run in different directions, a decussating structure is produced called the '*Hunter-Schreger Bands*' (HSBs) (fig. 4d). Complexly interwoven bundles of prisms are called as '*irregular enamel*'. When parallel prisms have a strong lateral deviation relative to the enamel surface they are termed as '*tangential enamel*'. The three dimensional arrangement of different enamel types within a tooth define its '*schmelzmuster*'. The variation of schmelzmuster from tooth to tooth defines the '*dentition*' level of the enamel microstructure hierarchy. With increasing levels of complexity (from crystallite to the dentition level), the significance of enamel microstructure for taxonomic and phylogenetic studies increases
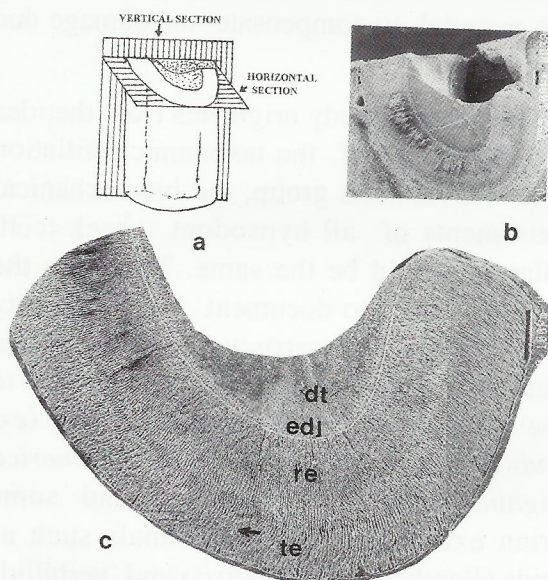

Fig. 1. a. The Indian sudamericid specimen (Das Sarma/GSI) and the orientation of sections; b, section parallel to the occlusal surface (horizontal); c, section magnified; dt, dentinal tubules; edj, enamel-dentine junction; re, radial enamel; te, tangential enamel, arrow indicating change in orientation of prisms.
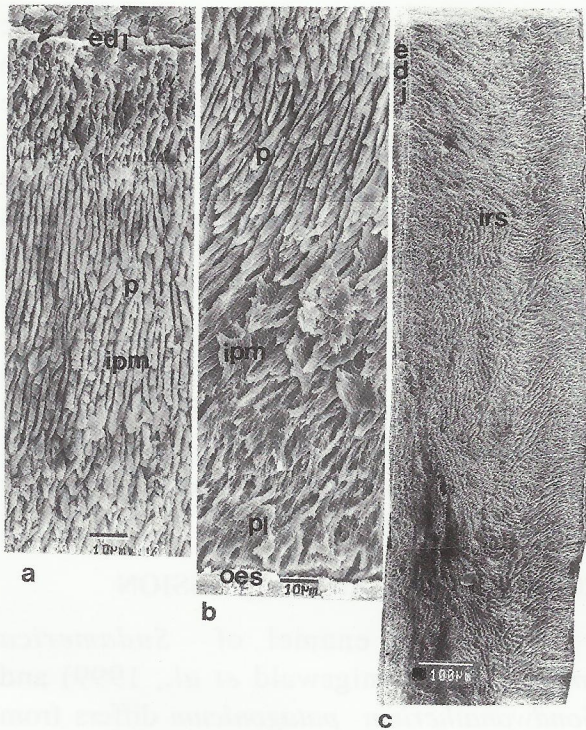
Fig. 2. a. magnified view of the inner enamel layer in occlusal section; edj, enamel-dentine junction; p, prism; ipm, interprismatic matrix; arrow showing the presence of prism sheath. b, magnified view of the outer enamel layer in occlusal section; pl, PLEX; oes, outer enamel surface. c, longitudinal (vertical) section; edj, enamel-dentine junction; irs, inter-row sheets.

(Koenigswald and Clemens, 1992; Koenigswald and Sander, 1997).

MATERIAL AND METHODOLOGY

The gondwanathere specimen (Das Sarma/GSI) studied here in detail is a fragment of an isolated cheek-tooth, loaned by Dr. D.C. Das Sarma of Geological Survey of India for enamel microstructure studies. The other specimen (VPL/JU/NKIM/25) used here for comparison was jointly studied by Profs. Ashok Sahni and W.v. Koenigswald and has been partly described in Krause et al., (1997) and Koenigswald et al., (1999). The specimen (Das Sarma/GSI) was embedded in a polymer and sections parallel and vertical (longitudinal) to the occlusal surface were made. The polished sections were etched for 10 seconds using 5% Hydrochloric Acid. Longitudinal sections of hypsodont molars of muroid rodents belonging to families muridae and gerbillidae were used for comparison. Enamel microstructure terminology is adapted from Koenigswald and Clemens (1992).

OBSERVATIONS

The sudamericid specimen (Das Sarma/GSI) is an isolated molariform fragment showing hypsodonty. In a section parallel to the occlusal surface (fig.1 a & b) a predominantly radial enamel can be seen with prisms arising from the enamel-dentine junction (EDJ) radially and ending at the outer surface. But lateral deviations in prism orientation can be observed forming a kind of wave pattern particularly near the bend of the enamel (fig. 1 b, shown by the arrow). This deviation formed by both prisms and IPM is quite distinct and can be termed the 'tangential enamel'. The parallely oriented prisms are bounded by very thick interprismatic matrix forming inter-row sheets occupying most of the central part of the enamel thickness. The entire width of the enamel from EDJ to the outer surface can be divided into four parts depending upon the orientation of IPM and prisms (figs. 1, 2). Very near to the EDJ, prisms are surrounded by the IPM and distinct prism sheaths can be observed (fig. 2a; fig. 3a, shown by arrows). Dentinal tubules are concentrated near the EDJ; they are mostly empty, but sometimes found filled with calcified cylindrical structures (fig. 1b). Sigogneau-Russel, Bonaparte, Robert and Escriobano (1991) observed continuity of calcified tubular contents of dentine and enamel in *Gondwanatherium* and *Sudamerica* (also see Sahni and Lester, 1988 for similar observations in Therapsids). When we move further towards the outer enamel surface the radially oriented prisms get bounded on two sides by very thick (around 1.5 µm) IPM (figs. 2a, 3b). IPM crystallites are almost at right angles to those of prisms (fig. 3b, c). Then prisms and IPM
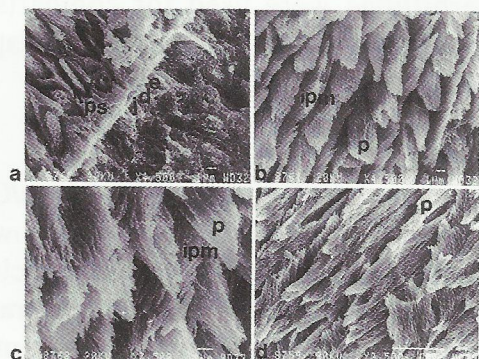
Fig. 3. Magnified view of enamel layer in occlusal surface; edj, enamel-dentine junction; ps, prism sheath; ipm, interprismatic matrix; p, prism.

deviating laterally can be observed (fig. 2b, 3d). In most of the portion, this lateral deviation is not uniform. To begin with, first the prisms and IPM of the inter-row sheets tend to deviate in one direction and then forming a wave they turn and orient themselves in entirely opposite direction (fig. 1b). The outermost part comprise a thick PLEX, with crystallites of IPM changing their orientation, running perpendicularly towards the outer enamel surface, and prisms showing the propensity of disappearing into the thick IPM (fig. 2 b).

In a vertical section, prisms originating from the EDJ, making an angle of about 45 ^{0} (fig. 4a) and running towards the occlusal surface, can be observed (fig. 2c). In this section, the enamel band can be broadly divided into three parts, radial, tangential and PLEX. All along the vertical section, change in orientation (three dimensional) of inter-row sheets forming wave-like pattern can be seen (fig. 2c). In general, the planes of inter-row sheets are vertically oriented as seen on the section parallel to the occlusal surface. These planes are not uniform and form wave-like pattern, as indicated by the lateral deviation of prisms and IPM (figs. 2c, 4a). The inter-row sheets keep on changing their orientation throughout the entire thickness of the

enamel (figs. 4 and 5). Whatever may be the orientation of the planes of inter-row sheets, the IPM crystallites are always at a very high angle (nearly right angles) to those of the prisms (figs. 4 b, c, 5 a, b, c, d). For a comparison, we have selected Recent *Mus* molars, where the HSBs are very distinct and the IPM crystallites run almost perpendicular to those of the prisms (fig. 4 d). The prisms of outermost part of inter-row sheets become more distinct (fig. 5 a, c, d) before fading away into the PLEX, where IPM crystallites tend to orient in a direction parallel to those of prisms and perpendicular to the outer enamel surface (fig. 5 a).

COMPARISONS AND DISCUSSION

The molar enamel of *Sudamerica ameghinoi* (Koenigswald *et al.*, 1999) and *Gondwanatherium patagonicum* differs from
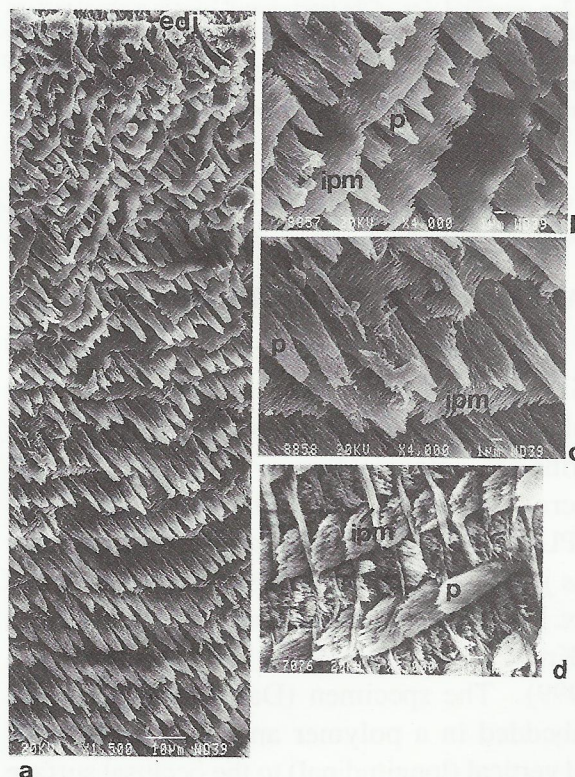

Fig. 4. a, magnified view of inner enamel layer in longitudinal section; b, innermost layers of inter-row sheets magnified; c, middle layers of inter-row sheets magnified; d, HSBs as seen on a horizontal section of a Recent *Mus* molar.
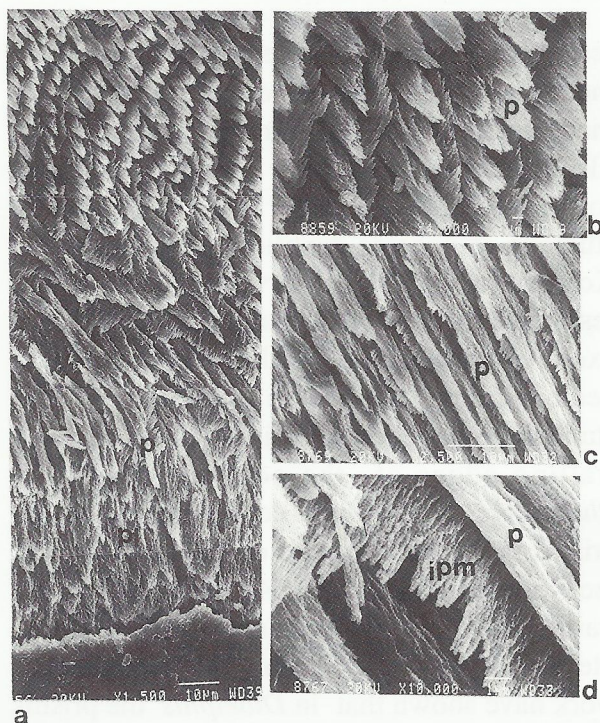
Fig. 5. a, magnified view of the outer enamel layer in longitudinal section; b, vertically oriented inter-row sheets magnified; c, magnified portion of the enamel showing change in orientation of prisms; d, a portion of fig. 5 c magnified.

that of the present specimen in having only one-layered radial enamel, whereas in the Indian form, besides having radial enamel, presence of tangential enamel and zone of PLEX has been noticed. Prisms in the molars of the South American taxa are surrounded by anastomosing IPM and in the Indian form they show inter-row sheets. Prisms in *Sudamerica* and *Gondwanatherium* run straight towards the outer enamel surface after starting from the EDJ, whereas those of the Indian form make wave-like pattern before reaching the outer enamel surface. The prism diameter in *Sudamerica* and *Gondwanatherium* increases from EDJ towards the outer enamel surface (Koenigswald *et al.*, 1999). No significant variation in the prism diameter of the Indian forms has been noticed. The taxa from the Late Cretaceous of Madagascar *Lavanify miolaka* differs from the present form in having only one layer of radial enamel, but resembles in having distinct vertical

inter-row sheets formed by the IPM (Krause *et al.*, 1997).

Gondwanatherians were regarded as multituberculates (Krause and Bonaparte, 1990; 1993). Recently, Pascual, Gain, Krause, Ortiz-Jaureguizar and Carlini (1999; also see Koenigswald *et al.*, 1999), based on finds of *Sudamerica* with four molariform dentition, have argued that the Gondwanatheria should be considered to be an independent mammalian group. At the prism level, the present gondwanathere does not show any similarity to 'gigantoprismatic' or 'small prismatic' enamel described for the multituberculates (Carlson and Krause, 1985; Krause, Kiela-Jaworowaska and Bonaparte, 1992). However, at the schmelzmuster level the present specimen resembles ptilodontid multituberculates (Sahni, 1979) and various marsupials (Koenigswald and Pascual, 1990; Koenigswald and Goin, 2000) in having a combination of radial and tangential enamel. Koenigswald *et al.* (1999) argued that as the arrangement within the schmelzmuster differs, the existence of these two enamel types cannot be taken as a synapomorphic character and does not really unite these groups. The distinct vertical inter-row sheets formed by the IPM in the present specimen, *Lavanify miolaka* (Krause *et al.*, 1997), marsupials and placentals (Koenigswald, 1997) can be regarded as a derived character.

The basic function of the dentition is to aid in breaking down the food material and to accommodate various stresses generated due to loads exerted on different portions of the teeth from different directions (Rensberger, 1973, 1975). Forces may be horizontal or oblique to the occlusal surface depending upon jaw movement, cutting and grinding edges, etc. (Rensberger, 1997). Forces acting vertically during mastication in low-crowned teeth result in rise of horizontal stresses, which in turn result in growth of vertical cracks (Koenigswald,
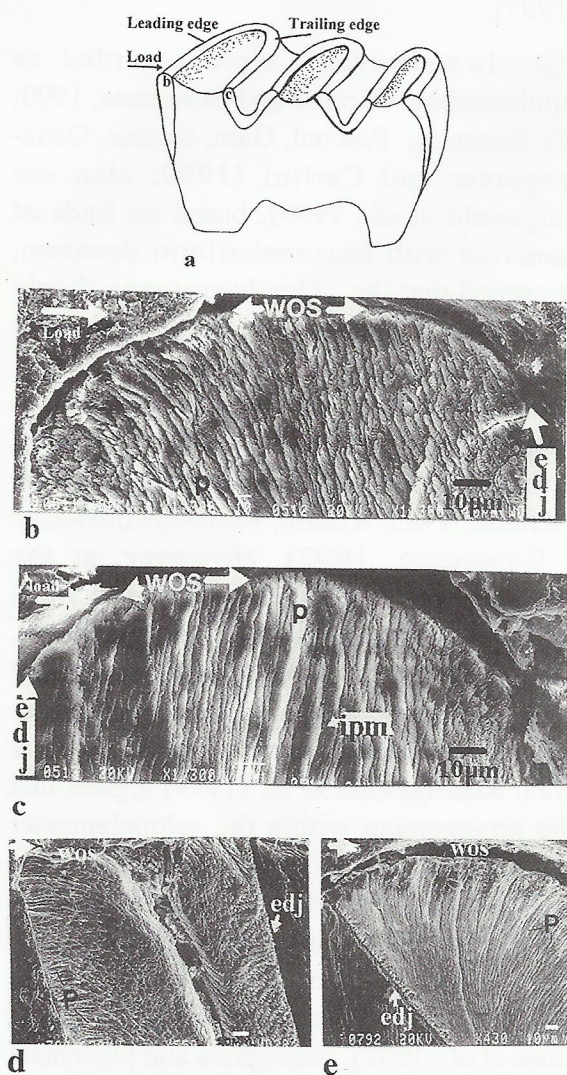
Fig. 6. a, sketch of the first lower molar of *Tatera indica* showing leading and trailing edges, ; b, a portion of the leading edge enamel (also see fig. 6 a), wos, worn occlusal surface, edj, enamel-dentine junction, p, prism; c, a portion of the trailing edge (also see fig. 6 a); d & e, leading and trailing edge enamel on *Bandicota bengalensis*.

Rensberger and Pfretzschner, 1987; Pfretzschner, 1988; Rensberger, 1992; Srivastava, Ahmed and Rao, 1999).

Apatite crystal is anisotropic when it comes to its hardness. The face of apatite crystal that is perpendicular to the c-axis (long axis) is harder than to those which are perpendicular to the short axes (a & b, see Rensberger, 1997). In other words, apatite crystals offer more

resistance to forces parallel to the c-axis than those parallel to a and b axes. Since prisms are made up of more or less parallely bound fiber-like crystallites, they offer more resistance to forces parallel to their long axes. While studying rhinoceros dentition, Rensberger and Koenigswald (1980) observed that maximum resistance to abrasion is attained when the long axes of prisms are parallel to the abrasion vector. Young, McGowan and Daley (1987) studied the direction of prisms in leading and trailing edges of the occlusal ridges in *Phascolarctos*. They have demonstrated that the prisms in the leading edge of the enamel meet the worn surface at about 64 ^{0} and those in the trailing edge are perpendicular to the surface. Stern, Crompton and Skome (1989) in a similar work have shown that in *Didelphis* the prisms of anterior face of the protoconid form an angle of about 46^0 and those of the posterior face tend to form an angle of about 21^0, which they consider it to be the optimum prism alignment required to resist abrasion on both the faces. Koenigswald (1980) and Koenigswald, Sander, Leite, Mors and Santel (1994) showed the presence of various types of enamel (radial, tangential, irregular, lamellar and HSBs) in leading and trailing edges, in response to the jaw movement in hypsodont rootless rodents. Koeinigswald *et al*. (1994) found that the radial enamel with its abrasion resisting properties has been invariably found to occupy the push sides of the leading edges.

In order to understand the functional significance of prism orientation, hypsodont rooted molars of *Tatera indica* (the Indian gerbill) and *Bandicota bengalensis* (bandicoot rat) were studied for enamel microstructure (fig. 6 a,b and c). In these muroid rodents the effective jaw movement (proal) and the direction of load is known (Butler, 1985). It has been found in these molars that in response to load the prisms orient themselves in a direction

optimum to resist abrasion (being described in detail elsewhere). The leading edge (fig. 6 a, b) of *Tatera indica* comprises prisms originating at the EDJ at an angle of about 70^0 and meeting the pull side of the worn occlusal surface at a very high angle (70^0 acute angle). In the trailing edge they tend to move away from the load direction (fig. 6 c). Prisms present on the push side tend to orient themselves towards the load and meet the worn occlusal and outer enamel surface at right angles (fig. 6 b). In the leading edge of *Bandicota bengalensis* (fig. 6 d), prisms are arranged in inter-row sheets, originate from the EDJ making an angle of about 70^0 and run towards the worn occlusal surface. Gradually, they turn towards the load direction and tend to make an angle of 90^0 with the outer enamel surface. The orientation of prisms in the trailing edge is in the direction (fig. 6 e) opposite to that seen in the leading edge.

With this background, it can be safely assumed that the orientation of prisms in the present sudamericid specimen has functional significance. The design consisting of radial enamel with prisms originating from EDJ, making an angle of about 45^0, meeting the occlusal surface at about 45^0, turning towards the outer enamel surface to meet it perpendicularly, is to offer maximum resistance to abrasive forces. This could be true for *Sudamerica* and *Gondwanatherium* as well. It is usually considered that hypsodonty is related to the advent of grasses. But, as in the Late Cretaceous time, grasses were not present, it has been suggested (Koenigswald *et al.*,1999) that hypsodonty in small fossorial mammals may be related to food such as roots that contain sediments. In determining the degree of hypsodonty, habitat preference could be more important than dietary preference (Janis, 1988). This phenomenon probably explains the presence of hypsodonty in gondwanatheres (Koenigswald *et al.*, 1999).

It has been observed that the radial enamel, which is made up of prisms running parallel to each other is at a high risk of giving way to an incoming crack, that can proceed easily along the prisms (Boyde, 1978; Pfretzschner, 1988). Therefore, abrupt change in the orientation of prisms dissipates the energy concentrated at the tip of the crack and this risk is further reduced in enamel with interprismatic matrix crystallites running at an angle (or perpendicular in the third dimension) to the prisms (fig. 4d). Also, with prisms frequently changing their course as in HSBs, alter the direction of progressing cracks resulting in loss of considerable energy (Koenigswald *et al.*, 1987; Rensberger, 1992). HSB with prisms of alternate bands decussating, usually oriented in a direction perpendicular to the load direction/parallel to the tensile stress, resist the growth of cracks (Pfretzschner, 1988; Srivastava, *et al.*, 1999).

CONCLUSIONS

1. As early as the Late Cretaceous, gondwanatheres developed hysodonty and enamel lophs arranged transversely (perpendicular) to the jaw movement direction.

2. At the megascopic level this was an adaptation towards eating abrasive food material.

   This adaptation is reflected at the microscopic level with prisms arising from EDJ running towards the occlusal surface and finally meeting the outer enamel surface at a very high angle. This adaptation has been found to be common to both gondwanatheres and hypsodont muroid molars.

3. The modification of the sudamericid inner radial enamel into wave-like inter-row sheets with IPM crystallites oriented almost perpendicular to those of the prisms, and

change in orientation of prisms, was perhaps a reinforcement against the propagation of cracks.

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