Non-tribosphenic Gondwanan mammals, and the alternative development of molars with a reversed triangle cusp pattern

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Abstract. Several lineages of non-holotherian Gondwanan mammals developed complex, tribosphenic-like molars, but not tribosphenic occlusion. The reversed triangle occlusal pattern, characteristic of holotherian lineages leading to tribosphenic occlusion, could have been acquired without a cusp rotation process. A review of the molar structure in primitive monotreme prototherians and gondwanathere allotherians suggests that a tricuspid pattern could have been accomplished by expansion of cingula, elevation of their cusps, and connection by ridges of two of the latter to one of the original ones, leading to a triangular pattern in some, or all, their molars. This cusp and ridge arrangement is already outlined in the lower cheekteeth of *Steropodon galmani* Archer et al., the oldest (Early Cretaceous) and most primitive Platypoda so far known. Similarly, one isolated lower molariform of the primitive gondwanathere *Ferugliotherium windhauseni* Bonaparte (Late Cretaceous) shows its anterolabial cusp connected by two ridges to two lingual cusps, forming a V-shaped, trigonid-like structure.

Key words. Mammals. Monotremata. Gondwanatheria. Gondwana. Molar pattern. Evolution.

Introduction

In relation with the Laurasian record, the Gondwanan Mesozoic record of land mammals is extremely poor, both chronologically and geographically, although it is currently increasing and becoming richer, mainly because of new discoveries in Cretaceous beds of southern South America (Patagonia). Although the mammalian record in the remaining Gondwanan continents is even less complete, its comparison with that of South America suggests that there was a markedly regional differentiation, e.g., between South America and Australia, and even within the present Gondwanan continents. For example, the Mesozoic record from Patagonia and that from the present intertropical regions of the South American continent indicate that, by the Late Cretaceous, both represent distinct biogeographic regions, the latter more closely allied to Africa, while the former more closely allied to the Eastern Gondwanan continents (Crisci et al., 1993), as it is at present (Crisci et al., 1991).

The earliest stages of mammalian evolution in Gondwana are unknown, since the oldest remains come from Middle Jurassic of Madagascar (Flynn et al., 1999), Upper Jurassic of Africa (Heinrich, 1998, 1999), Early Cretaceous of Australia (Archer et al., 1985; Kielan-Jaworowska et al., 1987; Flannery et al., 1995; Rich et al., 1999), Africa (e.g., Sigogneau-Russell, 1995), and South America (Patagonia; Bonaparte, 1986, 1988, 1996; Rougier, 1990; Rougier et al., 1992). The next and younger record comes from Late Cretaceous beds of southern South America (Patagonia; Bonaparte, 1996 and references therein; Pascual et al., 2000), Madagascar and India (Krause et al., 1997; Prasad and Sahni, 1988; Pascual et al., 1999). Except for a few Early Cretaceous records from Australia (Rich et al. 1997, 1999), and one from the Early Cretaceous of Patagonia (Bonaparte, 1986, 1988; Rougier, 1990), all remaining known Cretaceous mammals of Gondwana are from the Late Cretaceous, and pertain to non-tribosphenic groups. Both the Early and Late Cretaceous records attest to a distinct Gondwanan history (Pascual, 1996; Pascual, 1998; Vizcaíno et al., 1998), a partially hidden evolutionary experiment because, with the exception of Monotremata and probably the Xenarthra, the Mesozoic Gondwanan radiation left no representatives in modern communities. So distinct was this faunal radiation that we called it "the other history" (Pascual, 1997), not only because none of the ancestors of the peculiar Cenozoic South American Tribosphenida (sensu McKenna and Bell, 1997) were recorded, including the primordial, presumably native xenarthrans (Pascual, 1988), but because primitive non-tri-

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bosphenic mammals such as the Prototheria, Allotheria (Gondwanatheria), Triconodonta, and Docodonta evolved endemic taxa, including some peculiar ecological specializations (compared to their Laurasian counterparts). Furthermore, some holotherians (*sensu* McKenna and Bell, 1997), probably the Dryolestida, differentiated taxa with a mosaic of therian-like features, which makes their phylogenetic relationships quite problematic when compared with that of Laurasian mammals. Some examples are the Lower Cretaceous Patagonian *Vincelestes* (Bonaparte, 1986, 1988; Rougier, 1990; Rougier *et al.*, 1992), and the Australian *Ausktribosphenos* (Rich *et al.*, 1997, 1999). Even some non-tribosphenic mammals, such as the Docodonta, persisted longer than in Laurasia, and gave origin to more advanced types than their Laurasian relatives (Pascual *et al.*, 2000). Others, like the Gondwanatheria, developed quite multituberculate-like forms (Pascual *et al.*, 1999); remarkably, the last and most advanced gondwanatheres (early Paleocene) became equally rodentiform as the most advanced rodents presently known (Pascual *et al.*, 1993, 1999; Koenigswald *et al.*, 1999).

With the probable exception of the Xenarthra, this peculiar "other history" left the Monotremata as the only living Gondwanan mammals.

Raising the issue

Admitting,

(1) Crompton and Jenkins' (1968) hypothesis that the common ancestor of both docodonts and therians (i.e., holotherians *sensu* McKenna and Bell, 1997) may have been an early morganucodontid with a molar pattern like that of *Morganucodon* —the tricuspid cusp-on-line pattern; see figure 1.A—, and

(2) that one of the basic modifications leading to the docodont molar pattern included the lingual expansion of both upper and lower molar's cingula (Jenkins, 1969; see figure 1.C).

it is then theoretically admissible that similar processes would have occurred more than once in the history of non-holotherian mammals. Thus, a triangular pattern of the first lobe in the lower molars, similar to that inferred as differentiated in *Docodon* in Laurasia (Jenkins, 1969), and in *Reigitherium* in Gondwana (Pascual *et al.*, 2000), may have been developed more than once in the history of non-holotherian mammals. A new look to some Gondwanan taxa, as the Australian monotreme *Steropodon galmani* and the South American gondwanathere *Ferugliotherium windhauseni*, led us to find evidence suggesting that this same process actually happened (see below).

Molar morphology in Monotremata and Gondwanatheria

Monotremata

Archer *et al.* (1985) described a fragment of a lower jaw with three molars of the Early Cretaceous monotreme *Steropodon galmani* Archer *et al.* (figure 1.C), by then dubiously assigned to the Ornithorhynchidae. *Steropodon* molars were interpreted as tribosphenic, and thus supposedly derived from a relatively advanced stage in therian evolution. Two years later, Kielan-Jaworowska *et al.* (1987) examined a cast of the holotype, and on the basis of wear facets (figure 1.C) and other morphological features they concluded that its teeth are not tribosphenic, but pertain to a Theria (sic) "...derived from therians before the development of tribosphenic teeth, possibly during the Jurassic period".
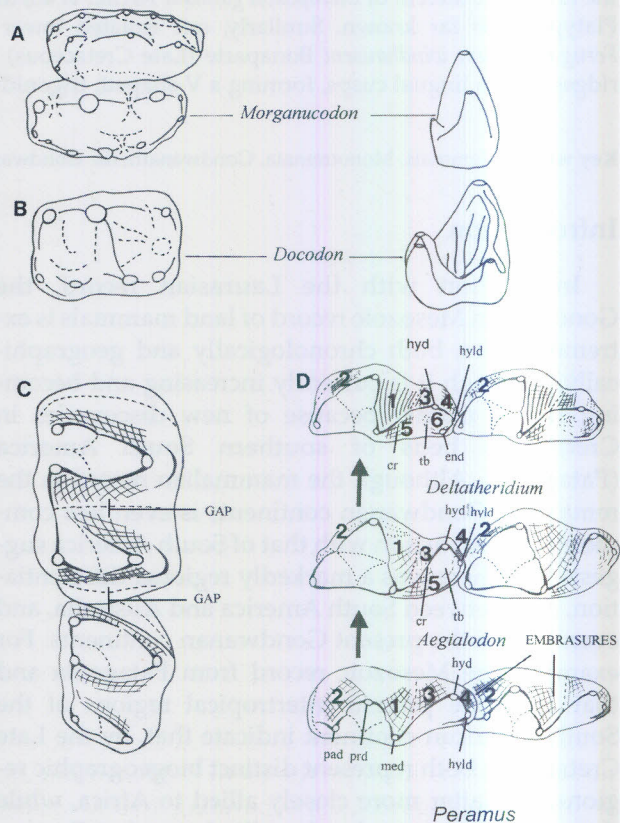
Figure 1. Lower molar morphology in early non-tribosphenic, pre-tribosphenic, and tribosphenic mammals. **A,** *Morganucodon* (left, occlusal view; right, anterior view); **B,** *Docodon* (left, occlusal view; right, anterior view); **C,** *Steropodon* (occlusal view of m2-3); **D,** occlusal views of m2-3's in *Peramus* (below), *Aegialodon* (center), and *Deltatheridium* (above). Arrows in D indicate inferred successive stages in the evolution of the tribosphenic lower molar (Kielan Jaworowska *et al.*, 1987, fig. 1). **References:** 1, 2, 3, 4, 5, 6, shearing surfaces of the pretribosphenic and tribosphenic molar in *Peramus*, *Aegialodon*, and *Deltatheridium*; **cr,** cristida obliqua; **end,** entoconid; **hyd,** hypoconid; **hyld,** hypoconulid; **med,** metaconid; **pad,** paraconid; **prd,** protoconid; **tb,** talonid basin. C and D, modified from Kielan-Jaworowska *et al.* (1987, fig. 1). Drawings are not to scale.
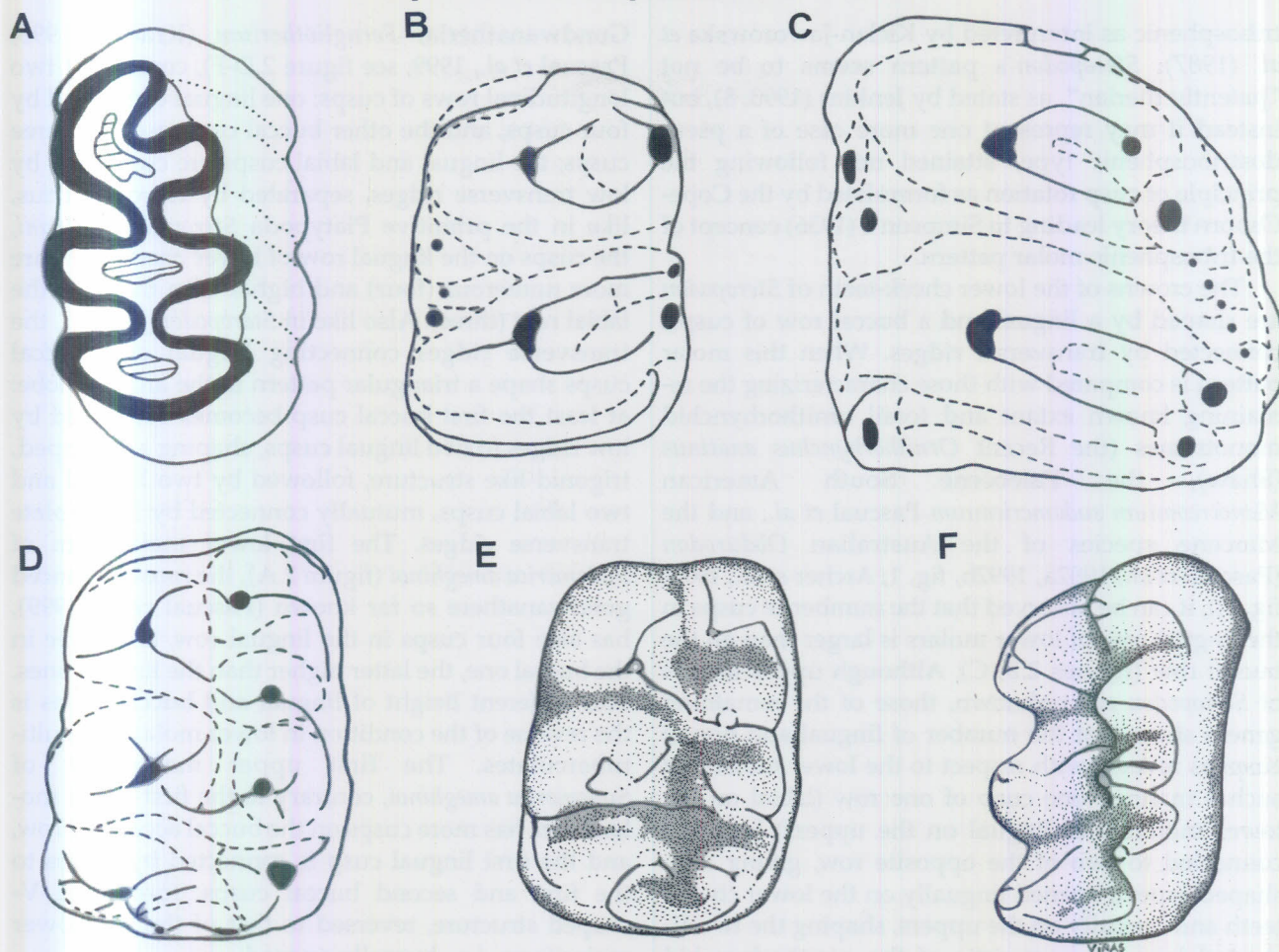
Figure 2. Molar morphology in non-tribosphenic Gondwanan mammals. **A,** first lower left molariform of *Sudamerica ameghinoi* Scillato-Yané and Pascual (Sudamericidae, Gondwanatheria) in occlusal view; **B-C,** occlusal views of lower and upper molars of *Obdurodon dickinsoni* Woodburne and Tedford (Monotremata, Ornithorhynchidae; **B,** left lower molar, **C,** left upper molar; **D-F,** first lower left molar of *Ferugliotherium windhauseni* Bonaparte (Ferugliotheriidae, Gondwanatheria; **D** and **E,** occlusal views; **F,** occlusal-lingual view). Anterior side of each tooth at the top, labial side at left (except in C, where labial is at right). Drawings are not to scale.

These authors noted that the lower molars of *Steropodon galmani* developed two major areas of shear (figure 1.C):

(1) "The first, between the distal surface of the (supposed) trigonid and mesial surface of the (supposed) hypoconid (facets 1 and 3), is a greatly enlarged embrasure (hypoflexid) for the paracone" (Kielan-Jaworowska *et al.*, 1987: 871). In fact, there is no such embrasure since the tooth is opened lingually by a gap (figure 1.C), separating two V-shaped lobes, as it happens in a typical ornithorhynchid as Obdurodon (figure 2B.C). Because of this, facets 1 and 3 are clearly separated, not being homologous to the unitary facet that in tribosphenic molars is formed by the wearing action of the paracone. Obvioulsy, there is not a cristid obliqua and, consequently, there was not the demarcation of occlusal areas for the protocone (lingually) and paracone (labially) (figure 1.C). We concur with Kielan-Jaworowska *et al.* (1987: 871) in that their view "strengthens the interpretation that a protocone was not developed in *Steropodon*". However, following the same reasoning

it can be concluded that neither a protocone nor a paracone were developed.

(2) The second area of shear locates between the distal surface of the (supposed) talonid and mesial surface of the (supposed) trigonid of the adjacent tooth (facets 4 and 2; figures 1.C, D). Again, and contrary to tribosphenic molars, this is not a close triangular "embrasure" but instead a greatly enlarged gap which is lingually opened. Because of this gap, the posterior wear facet (facet 4 of Kielan-Jaworowska *et al.*, 1987; figure 1.C) is unconnected and set well apart from the facet built up on the anterior face of the subsequent molar (facet 2 of Kielan-Jaworowska *et al.*, 1987). In brief, it is not homologous to the area of shear of the metacone of tribosphenic mammals, but the gap between the posterior V-shaped lobe of a molar and the anterior likewise V-shaped lobe of the subsequent molar. The intermolar contact by means of mesial and distal cingulids support this interpretation (figure 1.C).

Thus, we suggest that *Steropodon* was neither tribosphenic as inferred by Archer *et al.* (1985), nor pre-

tribosphenic as interpreted by Kielan-Jaworowska *et al.* (1987). *Steropodon´s* pattern seems to be not "patently therian", as stated by Jenkins (1990: 8), but instead it may represent one more case of a pseudostribosphenic type, attained not following the principle of cusp rotation as formulated by the Cope-Osborn theory leading to Simpson's (1936) concept of the tribosphenic molar pattern.

The crowns of the lower cheek-teeth of *Steropodon* are shaped by a lingual and a buccal row of cusps, connected by transversal ridges. When this molar pattern is compared with those characterizing the remaining known extant and fossil ornithorhynchid monotremes (the Recent *Ornithorhynchus anatinus* (Shaw), the Paleocene South American *Monotrematum sudamericanum* Pascual *et al.*, and the Miocene species of the Australian *Obdurodon* [Pascual *et al.*, 1992a, 1992b, fig. 1; Archer *et al.*, 1992, fig. 1]), it can be observed that the number of cusps in the lingual row of lower molars is larger than on the buccal row (figures 2.B, C). Although upper molars of *Steropodon* are unknown, those of the remaining genera show that the number of lingual and buccal cusps is reverse with respect to the lower molars. In such a manner, one cusp of one row (labial on the lower molars and lingual on the uppers) becomes connected to two of the opposite row, giving a V-shaped aspect, opened lingually on the lower cheek-teeth and buccally on the uppers, shaping the two V-shaped lobes characteristic of the ornithorhynchid cheek-teeth. This cusp and ridge arrangement is already outlined in the known lower cheekteeth of *Steropodon galmani* (figure 1.C; Archer *et al.*, 1985, fig. 1; Jenkins, 1990, fig. 2; Kielan-Jaworowska *et al.*, 1987, fig. 1), and shapes an apparent "pre-tribosphenic" state. Their shearing surfaces and other features suggest that, like in the more advanced ornithorhynchids (Jenkins, 1990, fig. 2), the molar occlusion was also performed by a reversed-triangle pattern of cusps and ridges, which explains the non-tribosphenic shearing surfaces remarked by Kielan-Jaworowska *et al.* (1987). In such a manner, one of the branches of the two V-shaped lobes in upper molars (Kielan-Jaworowska *et al.*'s " transverse loph-like") occludes on the open "embrasure" (gap, "hypoflexid") between the two lower V-shaped lobes, while the other one on the likewise open intermolar "embrasure" (gap).

In short, *Steropodon galmani* did not develop the embrasure-shearing occlusion that was one of the basic characters that led to the Tribosphenida (*sensu* McKenna and Bell, 1997).

Gondwanatheria

An unworn left m1 of the most primitive Gondwanatheria, *Ferugliotherium* (Krause, 1993; Pascual *et al.*, 1999; see figure 2.D-F), consists of two longitudinal rows of cusps: one lingual composed by four cusps, and the other buccal composed by three cusps; the lingual and labial cusps are connected by low transverse ridges, separated by furrows. Thus, like in the primitive Platypoda *Steropodon galmani*, the cusps on the lingual row of lower cheek teeth are more numerous (four) and higher than those on the labial row (three). Also like in *Steropodon galmani*, the transverse ridges connecting lingual and buccal cusps shape a triangular pattern in the anterior lobe: at least the first buccal cusp becomes connected by low ridges to two lingual cusps, shaping a V-shaped, trigonid-like structure, followed by two lingual and two labial cusps, mutually connected by incomplete transverse ridges. The first lower molariform of *Sudamerica ameghinoi* (figure 2.A), the most advanced gondwanathere so far known (Pascual *et al.*, 1999), has also four cusps in the lingual row, and three in the buccal one, the latter higher than the lingual ones. This different height of lingual and buccal cusps is the reverse of the condition in lower molars of multituberculates. The first upper molariform of *Sudamerica ameghinoi*, contrary to the first lower molariform, has more cusps on the buccal accessory row, and the first lingual cusp is connected by ridges to the first and second buccal cusps, forming a V-shaped structure, reversed to that of the first lower molariform, i.e., buccally opened.

Conclusions

Recognition of the fact that therian molars were originally reversed triangles led Patterson (1956: 43) to ask if this condition was inherited or if it evolved within the order Symmetrodonta. To him, the "great age" (sic) of the oldest known symmetrodont ("Duchy 33", from the European latest Triassic or earliest Jurassic) suggests that this type was inherited from the Therapsida. However, the reversed triangles occlusal pattern of the non-therian *Docodonta* (Jenkins, 1969; figure 1.B), and of the Gondwanan ornithorhynchid and Gondwanatheria, evolved from non-mammalian Mammaliaformes, probably from an early morganucodontid with a molar pattern like that of *Morganucodon*, with the triscuspid cusp-in-line pattern and with cuspidate cingula (figure 1.A), where the number of lingual and buccal cusps on each cingulum is reverse in the upper and lower molars.

The Gondwanan examples analyzed here suggest that, in non-holotherian mammals, a triangular pattern of the first lobe could have been accomplished by expansion of cingula, elevation of their cusps, and connection by ridges of two of the latter to one of the

original ones, thus shaping a triangular pattern without passing through the cusp rotation of the ancestral triangular stage leading to the tribosphenic molar (Crompton and Jenkins, 1968). Further, these features also suggest that the reversed triangle occlusal pattern, characteristic of the lineages leading to the tribosphenic occlusion, could have been acquired without such reversed cusp rotation in upper and lower molars; in some cases (*e. g.*, *Steropodon galmani*), developing a complex, "tribosphenic-like" pattern, but not tribosphenic occlusion.

Acknowledgements

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