New data on the Paleocene monotreme *Monotrematum sudamericanum*, and the convergent evolution of triangulate molars

ROSENDO PASCUAL, FRANCISCO J. GOIN, LUCÍA BALARINO, and DANIEL E. UDRIZAR SAUTHIER

We describe an additional fragmentary upper molar and the first lower molar known of *Monotrematum sudamericanum*, the oldest Cenozoic (Paleocene) monotreme. Comparisons suggest that the monotreme evolution passed through a stage in which their molars were "pseudo-triangulate", without a true trigonid, and that the monotreme pseudo-triangulate pattern did not arise through rotation of the primary molar cusps. Monotreme lower molars lack a talonid, and consequently there is no basin with facets produced by the wearing action of a "protocone"; a cristid obliqua connecting the "talonid" to the "trigonid" is also absent. We hypothesize that acquisition of the molar pattern seen in *Steropodon galmani* (Early Cretaceous, Albian) followed a process similar to that already postulated for docodonts (*Docodon* in Laurasia, *Reigitherium* in the South American sector of Gondwana) and, probably, in the gondwanathere *Ferugliotherium*.

Key words: Monotremata, *Monotrematum*, pseudo-triangulate molars, molar structure, Gondwana, Patagonia, Paleocene.

Rosendo Pascual [ropascua@museo.fcnym.unlp.edu.ar], Francisco Goin [fgoin@museo.fcnym.unlp.edu.ar], Lucía Balarino, and Daniel Udrizar Sauthier, Departamento Paleontología Vertebrados, Museo de la Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina.

Introduction

The relationships of Monotremata have been widely debated in recent years, with little apparent consensus (e.g., Kühne 1977; Kielan-Jaworowska et al. 1987; Rowe 1993; Luo et al. 2001). The ornithorhynchid *Monotrematum sudamericanum*, the only non-Australian monotreme and the earliest for which the upper molar pattern is known, is based on a right M2 from the early Paleocene of Patagonia (Pascual et al. 1992a, b). In 1992, another isolated right M2 and a fragment of a right m1, the first lower molar known, were collected from the same locality and level, by a joint Argentinian–Australian expedition. These two additional molars present an opportunity to reconsider the origin of the monotreme molar pattern; and, by implication, the origin and relationships of Monotremata (Pascual and Goin 2001).

Abbreviations.—MLP, Departamento Paleontología Vertebrados, Museo de La Plata, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Paleontología Vertebrados, Trelew, Argentina; SALMA, South American Mammal Age; M, upper molar; m, lower molar; L, length; W, width; R, right.

Systematic paleontology

Monotremata Bonaparte, 1837
Ornithorhynchidae Gray, 1825
Monotrematum Pascual, Archer, Ortiz Jaureguizar, Prado, Godthelp, and Hand, 1992
Monotrematum sudamericanum Pascual, Archer, Ortiz Jaureguizar, Prado, Godthelp, and Hand, 1992

Emended generic and specific diagnosis.—Cheektooth pattern similar to that of *Obdurodon*, the most closely similar ornithorhynchid, but double in size. Posterior lobe of m1 single-rooted, but preserving a vertical anterior sulcus that apparently divided two original roots, which remain well separated in *Obdurodon* species.

Material.—The holotype, MLP 91-I-1-1 (right M2), and the newly-referred MPEF-PV 1634 (right M2) and MPEF-PV 1635 (right m1).

Locality and age.—Punta Peligro, southeastern Chubut province (central Patagonia), Argentina; Hansen Member ("Banco Negro inferior"), Salamanca Formation; early Paleocene (Peligran SALMA, see Bond et al. 1995: fig. 2).

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Measurements.—RM2 (MPEF-PV 1634): W anterior lobe, 10.1 mm; W posterior lobe, 7.5 mm; L 9 mm. Rm1 (MPEF-PV 1635): W posterior lobe, 7.5 mm.

Description and comparisons of the new material

The dental formula of *Monotrematum sudamericanum* is unknown, but the new RM2 (MPEF-PV 1634) does not show any feature suggesting the existence of a succeeding M3. This molar (Figs. 1A–C, 4A) is as extensively worn as the holotype, but more broken. The preserved enamel in the central region shows that the crown pattern is almost identical to that of *Obdurodon* (Fig. 2A): it is composed of two V-shaped lobes, the anterior of which is wider, separated from the posterior one by a valley that connects the lingual and buccal sides of the crown separating the anterior and posterior lobes. There are prominent anterior and posterior cingula, which were involved in the contact between successive molars. In occlusal view, the crowns of both upper and lower molars display lingual and buccal cusp rows; cusps are more numerous in the buccal row of the upper molars, and in the lingual row of the lowers. Both of these rows show a basic cusp-on-line pattern (Fig. 2), wherein one main cusp on each lobe, lingual on the uppers (tentatively identified as B for the anterior lobe and C for the posterior lobe) and buccal on the lowers (tentatively identified as b and c on anterior and posterior lobes, respectively)[1] is connected by blade-like cristae to two smaller, contralateral cusps, yielding a V-shaped configuration. These V-shaped lobes open buccally on the upper molars and lingually on the lowers. The pair of V-shaped lobes on each molar is separated by a large valley, open both lingually and labially. A prominent, columnar lingual cusp is present on M2 (cusp A? in Fig. 2A), as it is on the M2 of *Obdurodon*. With heavy wear (as seen in the holotype), this cusp becomes connected with the posterior arm of the anterior V-shaped lobe (Fig. 1A). Although the base of the specimen is broken, the remains of the roots show that four were present (Fig. 1C).

The Rm1 (MPEF-PV 1635; Figs. 1D–F, 4B) is represented only by the posterior of the two V-shaped lobes. Although broken, its preserved portion is less damaged than the M2, and it is less worn. The relation between its antero-posterior (relatively larger) and transverse diameters correspond to those of a lower molar, and comparison to molars of *Obdurodon* (see Archer et al. 1992: fig. 1) suggests that it is a right m1. Its general dimensions not only correspond to that of MPEF-PV 1634, but are proportionately larger than those of the homologous tooth of *Obdurodon*. As in *Obdurodon*, the lingual and buccal extremes of the V-shaped lobe show, respectively, two lingual cusps and one buccal cusp, the latter more elevated. Below this is the base of an apparently big,
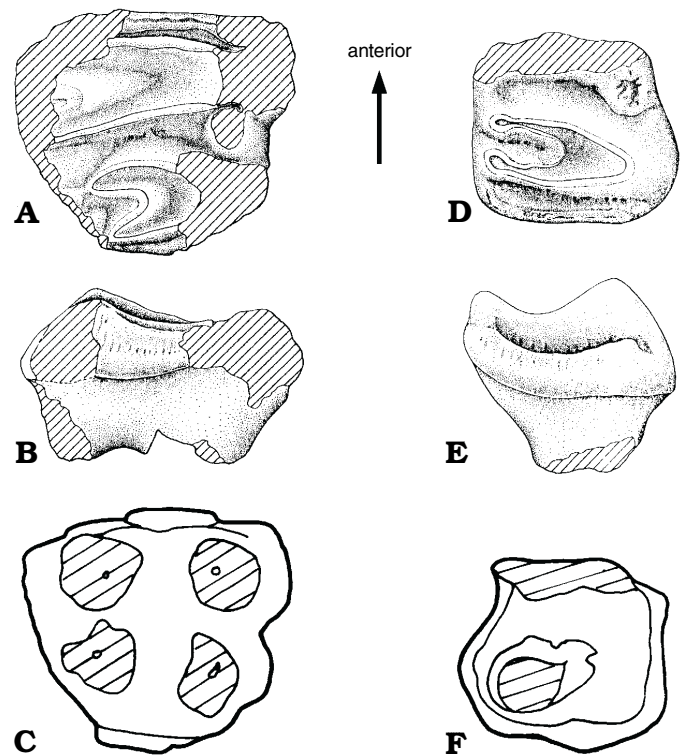
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[1] Cusp terminology after Crompton and Jenkins (1968).

Fig. 1. *Monotrematum sudamericanum* RM2 (MPEF-PV 1634) in occlusal (**A**) and posterior (**B**) views. **C**. Base of crown showing fragment of roots. Rm1(MPEF-PV 1635); occlusal view (**D**), posterior view (**E**). **F**. Base of crown showing fragmentary roots. Not to scale.
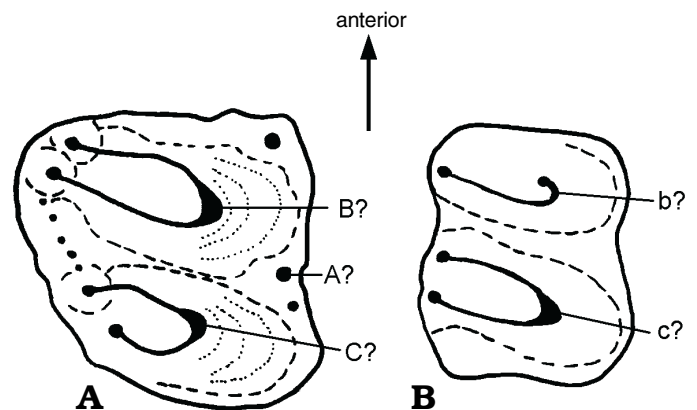

Fig. 2. Schematic occlusal view of the advanced ornithorhynchid *Obdurodon dicksoni*; RM2 (**A**), Rm1 (**B**). The only know m1 of *Monotrematum sudamericanum* is incomplete (Fig. 1D). As both genera show similar crown pattern, we figure here the homologous teeth of *O. dicksoni*. Not to scale.

single root, preserving a vertical anterior sulcus that appears to be either the division of one original root or the fusion of two original ones—as compared to the well-separated roots of *Obdurodon*. Only a trace of the posterolabial root is present in *Obdurodon insignis* (Woodburne and Tedford 1975: fig. 2D). This preserved portion of the root suggests that it was strong, probably deep, and anteroposteriorly compressed. Except for this feature, and for its larger size and more robust appearance, the crown pattern is nearly identical

to that of the homologous tooth in species of *Obdurodon*, and is basically similar to that of the living *Ornithorhynchus anatinus* (see Woodburne and Tedford 1975: fig. 4).

Wear on the buccal portion of the V-shaped blade has resulted in a pattern of dentine exposure similar to that seen in *Obdurodon*, yielding a masticatory surface that is more intensively worn than the surrounding enamel. This wear results in the formation of a transverse basin, deeper lingually than labially, suggesting that the type and extent of wear in both Australian and South American taxa mainly occurred through horizontal jaw movements (see also Pascual et al. 1992b; Archer et al. 1992). The strong, comparatively large roots of m1 in *Monotrematum* (Fig. 1E, F) suggest that its masticatory movements were more intensive than those of *Obdurodon*.

Discussion

Monotremes are distinctive in their retention of some primitive, reptilian characters, and for this reason they have been historically regarded as representing a basal branch of mammals, the subclass Prototheria of Gill (1872). Extinct taxa previously grouped with monotremes in the Prototheria include Triconodonta, Docodonta, and Multituberculata (e.g., Hopson 1970; McKenna 1975). However, more recent studies (e.g., Rowe 1988, 1993) suggest that monotremes have more advanced features than previously believed.

A significant addition to knowledge of the early history of monotremes was the discovery of *Steropodon galmani*, of Early Cretaceous (Albian) age, in the Wallangulla sandstones of Australia (Archer et al. 1985). Because *Steropodon* has lower molars that bear striking resemblance to the tribosphenic pattern characteristic of living therians, Archer et al. (1985: 363) concluded that "...monotremes, one of three groups of living mammals (the other two being marsupials and placentals), are phylogenetically close to the other groups of living mammals". Prior to the discovery of *Steropodon*, the prevailing view was that monotremes were "nontherian mammals" (e.g., Kermack 1967; Hopson 1970; Kielan-Jaworowska 1970; Crompton and Jenkins 1979). On the basis of structural attributes related to occlusion, Kielan-Jaworowska et al. (1987) concluded that *Steropodon galmani* should not be considered tribosphenic because of the apparent absence of an entoconid, and of the absence of wear in the talonid basin, the latter indicating that the upper molars (still undiscovered) lacked a protocone. These authors proposed that *S. galmani* represents a therian derived from a *Peramus*-like form, i.e., a pre-tribosphenic mammal. Following an idea of Bonaparte (1990), Archer et al. (1993: 76), suggested that monotremes "...could be a specialized part of an endemic southern eupantothere if not dryolestoid radiation." As noted by Wible et al. (1995), after the discovery of *Steropodon*, hypotheses on monotreme origins focused on various groups of holotherian mammals (*sensu* Hopson 1994), such as peramurids (Kielan-Jaworowska et al. 1987; Jenkins 1990),
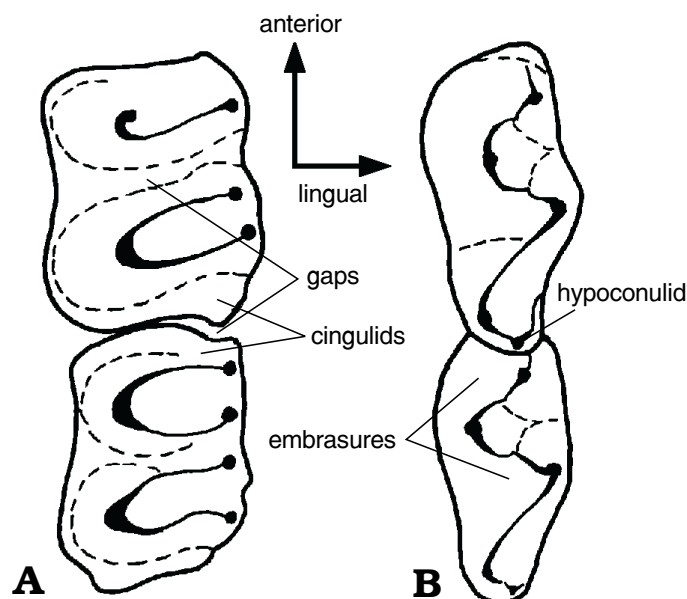

Fig 3. Schematic occlusal view of two left lower molars (m1–m2) of an ornithorhynchid monotreme (*Obdurodon dicksoni*) (**A**), and a pre-tribosphenic peramuran (*Peramus* sp.) (**B**). Note the difference between the "gaps" in A and the "embrasures" in B. In the former the intermolar contact results by mesial and distal cingulids. Not to scale.

dryolestoids (Bonaparte 1990; Archer et al. 1993), and symmetrodonts (Hopson 1994). Based on dental evidence, Rougier (1993) and Wible et al. (1995) denied holotherian affinities for monotremes, despite their possession of the reversed-triangle molar pattern that, according to Hopson (1994: 205, 208), diagnoses the Holotheria.

Recently, Luo et al. (2001) supported the homology of the trigonid cusps among all living mammals, placing monotremes within a group (Australosphenida) for which an independent Gondwanan origin was proposed. In a more comprehensive, follow up study, the same authors (Luo et al. 2002) provided additional derived characters supporting independent origin of a tribosphenic molar pattern in northern (Boreosphenida) and southern (Australosphenida) clades of mammals. They remarked, however, that (p. 26): "…we do not consider the toothed monotremes to have typical tribosphenic molars". But the alternative hypothesis they proposed (p. 26): "[…] implied by the nesting of monotremes within the australosphenidan clade [...], calls for the presence of fully tribosphenic molars in the common ancestor of the stem australosphenidans and Monotremata". Based on this hypothesis, they inferred (p. 26): "[…] that the apical wear of the cristid obliqua and hypoconid of *Steropodon* corresponds to the apical wear of a reduced protocone (= 'valley cusp' as identified by Pascual et al. 1992a, b)".

The cusp identified as a protocone (on the upper molar of *Monotrematum*) by Luo et al. (2002) is, in our judgment, more probably homologous to cusp A of the ancestral "triconodont" pattern, which remained isolated in monotremes that retained it (cusp A? in Fig. 2A).

Specimens described herein support the alternate hypoth-

Fig. 4. *Monotrematum sudamericanum*. **A**. Stereopair of RM2, occlusal view. **B**. Stereopair of Rm1, occlusal view. Anterior is up in A and B.

esis proposed by Pascual and Goin (2001): that a tribosphenic molar pattern is lacking in both *Steropodon galmani* and the more advanced Ornithorhynchidae (= Platypoda *sensu* McKenna and Bell 1997). According to this hypothesis, *Steropodon galmani* did not take origin from a *Peramus*-like ancestor, nor from any other "pre-tribosphenic" taxon. Rather, the hypothesis calls for origin of the bilobed, V-shaped pattern of monotreme molars (both lower and upper) directly from a cusp-on-line pattern like that of *Morganucodon*, through: expansion of the labial cingulum on the upper molars and lingual on the lowers, elevation of cingular cusps, and connection of two such cusps to one of the principal cusps on each lobe—B/b and C/c on the anterior and posterior lobes of upper and lower molars respectively (see Figs. 2 and 3). Pascual and Goin (2001) noted that the relationships between adjacent molars of toothed monotremes are quite different from those of holotherians. In ornithorhynchids and steropodontids, the intermolar contact is established by strong mesial and distal cingula/ids, which lie on a different level than the masticatory surface. Consequently, there is not an embrasure but an intermolar gap between adjacent molars (see Fig. 3). Likewise, the valley that separates molar lobes forms a gap (Fig. 3) instead of the embrasure characteristic of the Zatheria (*sensu* McKenna and Bell 1997).

In short, we regard the resemblances between the pseudo-triangular molar pattern of *Steropodon galmani* and the triangular molar pattern of tribosphenic therians as homoplasic. Our hypothesis is consistent with that of Patterson (1956: 67), who was of the opinion that "The molars of non-therian mammals never went through a reversed triangle stage, their two principal subsidiary cusps being in line with the primary ones". To us, this is the case in *Monotrematum* and *Obdurodon* (i.e., "protocone", "paracone", and "metacone" of Luo et. al. 2002: fig. $4A_1$, C_1, respectively; see Fig. 2A herein). Accordingly, the pseudo-triangular molar pattern of *Steropodon galmani* is, in our view, most plausibly derived from the linear, tricuspate pattern, as seen in *Morganucodon*, which is universally accepted as ancestral for the Mammalia.

The molar pattern of *Steropodon galmani* is structurally antecedent to the bilobed, V-shaped molars of the remaining toothed monotremes.

We previously proposed (Pascual and Goin 2001) that a transformation similar to that of monotremes accounts for the increasing complexity of the molar crown among Gondwanan docodonts, exemplified by *Reigitherium bunodontum* (Docodonta, Reigitheriidae, Pascual et al. 2000; see also Jenkins 1969 for the ancestral Laurasian *Docodon*). The acquisition of pseudotriangular molars may have also occurred in the Gondwanatheria, as exemplified by *Ferugliotherium windhauseni* (Pascual and Goin 2001).

The specimens described herein provide the following new evidence bearing on the origin of the monotreme molar pattern: 1) the lower molar morphology of *Monotrematum sudamericanum* agrees with previous statements that it is a monotreme closely allied with *Obdurodon*; and 2) upper and lower molars of *Monotrematum* lack occlusal attributes (wear facets) characteristic of the tribosphenic molars. Specimen MPEF-PV 1635 closely resembles the lower molar morphology of *Steropodon* and *Obdurodon*, and, together with both upper molars, suggests that the occlusal relationships among monotremes involved patterns and processes distinct from those of tribosphenic mammals and their relatives.

In our opinion, dental evidence contradicts, rather than supports, a close relationship of monotremes and therians, as apparently suggested by basicranial evidence (Wible and Hopson 1993). Consequently, *Steropodon galmani*, *Teinolophos trusleri* (a species recently described by Rich et al. 2001a) and, by extension, the more advanced monotremes, cannot be grouped with Gondwanan tribosphenic mammals, the Ausktribosphenidae (*Ausktribosphenos* and *Bishops*; see Rich et al. 1999, 2001b) and *Ambondro* (Flynn et al. 1999). Luo et al. (2001) proposed that the tribosphenic molar pattern arose independently in Australosphenida (in which they included monotremes) and Boreosphenida (marsupials, placentals, and suspected fossil relatives). For the reasons given above, we suggest that monotremes should be excluded

from the Australosphenida. Monotremes, in our view, followed an independent evolutionary pathway, one that led to a pseudo-triangular morphotype that is not homologous to those of tribosphenic mammals, either Laurasian or Gondwanan.

Acknowledgements

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