Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): Evolutionary significance

ADRIANA MAGDALENA CANDELA

Cusp and lophid homologies of the lower deciduous teeth (dp4) in erethizontids and other Hystricognathi are specified. On this basis, a new nomenclature for these structures is proposed. The probable primitive condition and evolution of the occlusal patterns of these teeth are also analyzed. In contrast to previous proposals, it is concluded that the mesoconid, mesostylid, and mesolophid of the dp4 of erethizontids can be recognized since the Early Miocene. The anteriormost three lophids of the pentalophodont dp4 of the Erethizontidae would be homologous to the anterolophid, metalophulid II, and mesolophid, respectively. In addition, it may be proposed that the lophids of the dp4 of the Baluchimyinae and Old World Hystricognathi are homologous to those of the erethizontids and the remaining South American Hystricognathi. The pentalophodont pattern is probably the primitive condition of the dp4 of the Hystricognathi.

Key words: Rodentia, Hystricognathi, Erethizontidae, deciduous teeth, homology, evolution.

Adriana Magdalena Candela [acandela@museo.fcnym.unlp.edu.ar], Departamento Científico Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina.

Introduction

The rodents of suborder Hystricognathi, mainly those of the New World (traditionally known as Caviomorpha, but see Bryant and McKenna 1995; McKenna and Bell 1997), have lower deciduous teeth (dp4) with variable designs, usually more complex than those of molars (e.g,. Dinomyidae, Dasyproctidae, several octodontoids). These features obscure the identification of crest homologies, and consequently phylogenetic and evolutionary significance of crown morphology remain uncertain for most of the lineages of the suborder.

The Erethizontidae, the New World porcupines, are a clade early differentiated from the other Hystricognathi (Bugge 1971; Woods 1972; Bryant and McKenna 1995; Candela 1999; but see Nedbal et al. 1994; Huchon and Douzery 2001). This family shows primitive characters, such as cheekteeth with distinctive cusps, which are the key elements to recognize homologies (Jernvall 1995; Butler 1985). These conditions make the erethizontids a very important group in the understanding of the dental evolutionary patterns of the Hystricognathi. As noted by Wood and Wilson (1936: 388) "One large order of mammals, the rodents, has certain characteristic patterns that seem to be found on a few main cusps, and these cusps need to be identified before much progress can be expected in the study of the evolution of the order". Thus, the cusp homologies of the Hystricognathi are essential to elucidate those characters of the cheekteeth that may be reliably comparable in the phylogenetic analysis.

In this study, the homologies of the dp4 of porcupines and other Hystricognathi are recognized, and a new terminology of their cusps and lophids is proposed. Upon this basis, the probable primitive condition and the changes of the occlusal designs of these teeth are analyzed. This data source increases the information available to clarify patterns of dental evolution in the Hystricognathi.

Institutional abbreviations.—MLP, Museo de Ciencias Naturales de La Plata (Argentina); MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina); MPEF, Museo Paleontológico Egidio Feruglio (Trelew, Argentina); MNRJ, Museu Nacional de Río de Janeiro (Río de Janeiro, Brazil); PUC, Pontificia Universidad Católica de Minas Gerais (Bello Horizonte, Brazil); MNHN, Museum National d'Histoire Naturelle (Paris); MCZ, Museum of Comparative Zoology (Cambridge, Massachusetts, USA); AMNH, American Museum of Natural History (New York, USA); FMNH, Field Museum of Natural History (Chicago, USA).

Materials and methods

The term homology is used to mean comparable structures (for a survey of the notion of homology see Patterson 1982; Rieppel 1988, 1994; de Pinna 1991; Nelson 1994). Topology and connectivity have been the conceptual tools employed to guiding observation in the search for homologies (Rieppel 1994). In this sense, the recognition of cusps of the deciduous teeth was based upon the following statements: (1) "...homology cannot be treated as an observational fact, but only as an hypothesis of similarity based on topological relations and with potential phylogenetic information content to be tested

Acta Palaeontol. Pol. 47 (4): 717–723, 2002

http://www.paleo.pan.pl/acta/acta47/app47-717.pdf

by congruence" (Rieppel 1994: 93); and (2) "The empirical basis of homology is rooted in the observation of topological equivalence..." (Rieppel 1994: 93). The nomenclature system of Wood and Wilson (1936) provides a reference.

Because the monophyly of the New World Hystricognathi, traditionally known as Caviomorpha (grouping the Erethizontidae with the remaining South American Hystricognathi), is currently argued (e.g., Bryant and McKenna 1995; Huchon and Douzery 2001) the term "Caviomorpha" is used here with quotation marks.

The dp4 of the following specimens of the living porcupine *Coendou prehensilis* (Linnaeus, 1758) were studied: MNRJ 2667, MNRJ 11467, MNRJ 2671, MNRJ 34502, MNRJ 2670, PUC 507, PUC 307, PUC 515, MACN 50275, MLP col. 36 and MLP 1436.

The dp4 of the following specimens of extinct erethizontids were added: *Eosteiromys homogenidens* Ameghino, 1902 (Early Miocene) MNHN col. 38, MNHN col. 99a, MLP 85-VII-3-33f; *Eosteiromys* sp. (Early Miocene) MPEF 5644; Gen. nov. MPEF 7592b (Candela 2000); *Eosteiromys*? sp. nov. (Early Miocene) MPEF 5811d, MPEF 5090a, and several isolated dp4 housed in MACN still without collection number; *Steiromys detentus* Ameghino, 1887 (Early-Middle Miocene) MLP 15-293, MLP 15-339, MLP 15-233, MLP 82-XII-1-20, MLP 15-227, MACN A 6; *Steiromys duplicatus* Ameghino, 1887 (Early Miocene) MLP 15-282, MACN 4150-3, *Steiromys* sp. MLP 92-V-10-2; *Neosteiromys*? *tordillensis* Vucetich, Mazzoni, and Pardiñas, 1993 (Middle Miocene) MLP 91-IV-17d; *Hypsosteiromys axiculus* (Ameghino, 1902) (Early Miocene) MPEF 5798a, MPEF 5798b, MPEF 5798c, MLP 83-III-10-1, MACN A 52-176, and *Hypsosteiromys nectus* (Ameghino, 1902) (Early Miocene) MACN A 52-177.

Previous proposals

Patterson and Wood (1982) accomplished one of the most significant studies to shed light on the evolutionary patterns of the dp4 of "Caviomorpha". These authors proposed a sequence of morphological change, though not phylogenetical, from the tetralophodont dp4 towards a condition of more
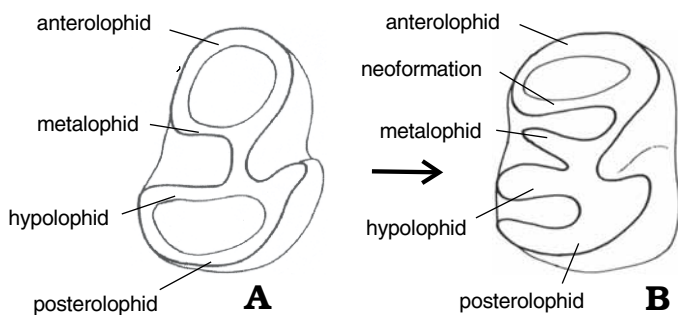

Fig. 1. Lophid homologies for lower deciduous teeth (dp4) of "caviomorphs" according to Patterson and Wood (1982). The arrow points in the direction of the change from tetralophodonty (**A**) towards pentalophodonty (**B**). All drawn as if from the right side.
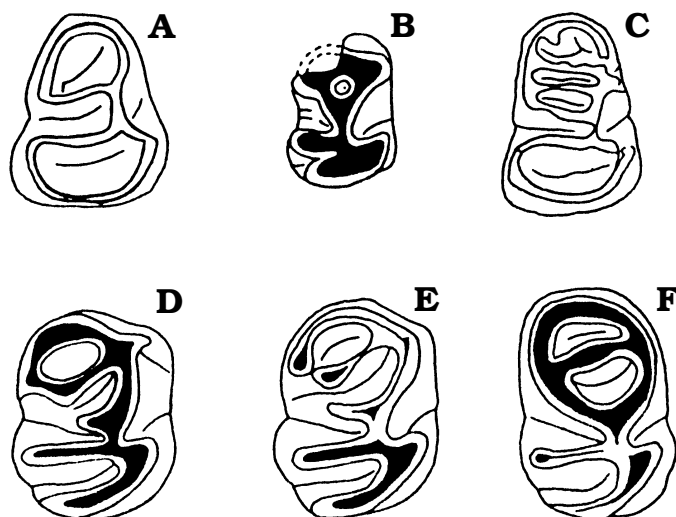

Fig. 2. Schematic drawings of lower deciduous teeth of selected "caviomorphs" taken from Patterson and Wood (1982). **A**. *Erethizon dorsatum* MCZ no. 51367. **B**. *Prospaniomys priscus* AMNH no 29697. **C**. *Erethizon dorsatum* MCZ no. B 7752. **D**. *Protacaremys prior* AMNH 29707. **E**. *Protacaremys prior* FMNH P 13295. **F**. *Protacaremys prior* AMNH 29692.

complexity (Fig. 1). In the simplest pattern, the lophids were homologized, from front to back, as anterolophid, metalophid, hypolophid, and posterolophid (Fig. 1A). This pattern was recorded in some specimens of the Holarctic living erethizontid *Erethizon dorsatum* (Linnaeus, 1758), some "early" erethizontids, the extinct Acaremyidae *Sciamys* Ameghino, 1887 and some extinct Echimyidae, such as *Prospaniomys* Ameghino, 1902 and *Eumysops* Ameghino, 1888 (Fig. 2A, B; Wood and Patterson 1982: fig. 31A, E). Somewhat more complex tetralophodont patterns were identified in the dp4 of the extinct Echimyidae *Paradelphomys*, Patterson and Pascual, 1968, *Spaniomys* Ameghino, 1887 and *Stichomys* Ameghino, 1887. A greater complexity was found in the pentalophodont dp4 of the extinct Echimyidae *Protacaremys* Ameghino, 1902 in which the second lophid, crossing the anterofossettid, was recognized as a new structure, with the metalophid being third in position (Figs. 1B; 2D–F; Patterson and Wood 1982: 501; fig. 31B–D). The dp4 of *Sallamys* Hoffstetter and Lavocat, 1970 (Echimyidae), *Cephalomys* Ameghino, 1897 (Cephalomyidae), and *Branisamys* Hoffstetter and Lavocat, 1970 (considered a dasyproctid by Lavocat, 1976, or a dinomyid by Patterson and Wood 1982), were considered as the most complex and derived designs (Patterson and Wood 1982: fig. 31F–H).

Additionally, Patterson and Wood (1982) outlined the marked variability in the dp4 of *Erethizon dorsatum*, identifying different types of occlusal patterns: (1) tetralophodont (Fig. 2A), (2) with a variably developed spur crossing the anterofossettid, and (3) with "apparent" mesoconids and mesolophids, interpreted as neoformations recently acquired in *Erethizon* Cuvier, 1822 (Fig. 2C; Patterson and Wood 1982: 502; but see below).

Concerning the Old World Hystricognathi, Wood (1968)

suggested that in the Oligocene Phiomyidae from Fayum, the pentalophodont dp4 would be the primitive condition. Later, Patterson and Wood (1982) pointed out that the dp4 of both Oligocene petromurids (including the subfamily Phiomyinae) and Miocene thryonomyoids were very different from those of the "caviomorphs". Therefore, they considered that the dp4 of the Old and New World Hystricognathi do not show any evidence to support the monophyly of these rodents.

Results

Cusp and lophid homologies of the dp4 of Erethizontidae.— The dp4 of extinct and living porcupines have tetra, penta- or hexalophodont occlusal designs. In the most usual pattern (Fig. 3), the posterior region of the dp4 comprises the hypolophid, extending from hypocone to entoconid, and the posterolophid on the posterior margin of the teeth. The anterior region is more complex. There are two cusps on the labial side in front of the hypoconid. The anterior cusp is larger and placed more labially than posterior one. Because of their topology, both cusps can be homologized with the protoconid and mesoconid, respectively. The ectolophid is usually separated from the protoconid by a narrow flexid. On the lingual side of the tooth, in front of the entoconid, there are also two cusps. The anterior cusp, somewhat larger than the posterior one, is opposite the protoconid, though slightly posterior to the latter. Because of their topology, both lingual cusps can be homologized with the metaconid and mesostylid, respectively.

Regarding the connections with these cusps, the anterior lophids may be homologized as follows (Fig. 3A, B): (1) The anteriormost lophid, extending from the protoconid to the lingual margin of the tooth, can be homologized to the anterolophid. It may be separated from the protoconid by a narrow flexid. (2) The second lophid, extending from the posterior part of the protoconid to the metaconid, can be homologized with the metalophulid II (*sensu* Wood and Wilson 1936; in MLP 15-339 this lophid is connected to the third lophid, Fig. 3A). (3) The third lophid is narrower and lower than the other lophids, extends from the mesoconid to the mesostylid, and can be homologized with the mesolophid (in MPEF 7592b the ectolophid continues lingually by a short and narrow lophid, which joins the middle part of the mesolophid, Fig. 3B). (4) A small lophid, variably developed, is usually found into the anterofossettid. A similar lophid in the same position is also present in the m1–3 of some extinct species of porcupines (e.g., *Steiromys duplicatus*). This latter lophid cannot be homologized with any structure of the most generalized rodents, consequently, it is recognized as a newly formed structure: the neolophid.

Deciduous teeth variability among living and extinct erethizontids.—There is some variability in the basic pattern described above, expressed mainly in the degree of development of the neolophid and mesolophid (Fig. 4). (1) Among the species of the extinct genus *Hypsosteiromys* Patterson, 1958, the
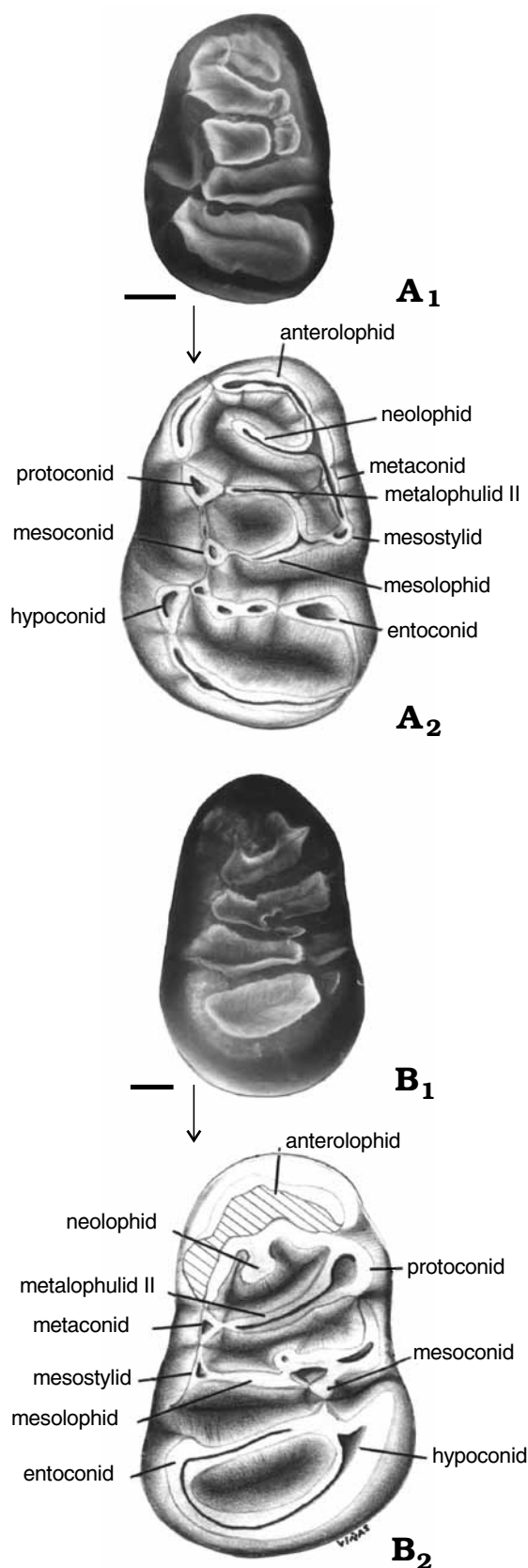

Fig. 3. Nomenclature for cusps and lophids of lower deciduous teeth (dp4) of the Erethizontidae. **A**. *Steiromys detentus* MLP 15-339, left dp4. **B**. Gen. and sp. nov. MPEF 7592b, right dp4. Scale bars 1 mm. Below each photomicrographs (A$_1$, B$_1$), enlarged interpretive drawings (A$_2$, B$_2$) are shown.
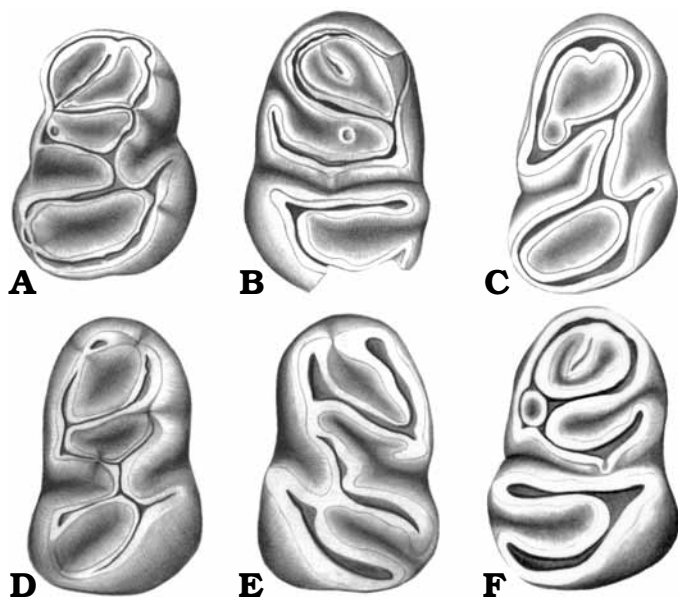
Fig. 4. Lower deciduous teeth (dp4) of Erethizontidae. **A**. *Steiromys detentus* MLP 15-293, right dp4. **B**. *Eosteiromys*? sp. nov. MPEF 5090a, left dp4. **C**. *Hypsosteiromys nectus* MACN A 52-177 (type specimen), right dp4. **D**. *Eosteiromys homogenidens* MLP 85-VII-3-33f, right dp4. **E**. *Eosteiromys homogenidens* MNHN col. 99a, left dp4. **F**. *Eosteiromys*? sp. nov. MPEF 5811d, right dp4. Not to scale.

dp4 present a simple tetralophodont pattern, lacking neolophid, mesoconid or mesolophid (Fig. 4C). This pattern is also recognized in some specimens of *Erethizon dorsatum* (Patterson and Wood 1982). (2) Among extinct and living erethizontids, penta- and hexalophodont patterns are the most usual conditions. The mesolophid may be fully developed, as in *Coendou prehensilis* MNRJ 2671, *Eosteiromys homogenidens* MLP 85 VII-3-33f, MNHN col. 38, and *Steiromys detentus* MLP 15-293 and MLP 15-227 (Fig. 4A, D). Patterns with partially developed mesolophid are also found in *Coendou prehensilis* PUC 307, and *Eosteiromys homogenidens* MNHN col. 99a (Fig. 4E).

The position, distinctness and size of the neolophid are also variable. In the dp4 of some erethizontids there is no evidence of a neolophid, as in *Eosteiromys homogenidens* MLP 85-VII-3-33f (Fig. 4D). An incipient neolophid connected with the anterolophid is observed in *Steiromys detentus* MLP 15-227, *E. homogenidens* MNHN col. 38, and Gen. nov. MPEF 7592b (Fig. 3B). Inside the anterofossettid of *Eosteiromys*? sp. nov. MPEF 5090a, there is a small neolophid isolated from the anterolophid (Fig. 4B). In *Coendou prehensilis* MNRJ 2667 and *Eosteiromys*? sp. nov. MPEF 5811d, the neolophid is more developed (Fig. 4F). In *Steiromys detentus* MLP 15-339 and MLP 15-233, the neolophid is well developed and connected with the lingual margin of the tooth, though separated from the anterolophid (Fig. 3A). In *Steiromys detentus* MLP 293 and *Steiromys duplicatus* MLP 15-282 the neolophid is fully developed, extending from the lingual margin of the tooth up to the anterolophid (Fig. 4A). In these cases, the neolophid accounts for the acquisition of an hexalophodont pattern.

Discussion

New proposal of homologies.—The dp4 of the extinct erethizontids indicate that the variability of their occlusal patterns was reached early during the evolutionary history of the family, at least by the Early Miocene. Although no mesoconid was identified in the "caviomorph" rodents (Patterson and Wood, 1982), this study indicates that the mesoconid and mesolophid of the dp4 of the erethizontids may be also recognized, at least since the Early Miocene (Fig. 3). Upon this basis, it can be proposed that in the more complex dp4 of *Erethizon dorsatum* the supposed new structures correspond, in fact, to the mesoconid, mesolophid, and neolophid in different degrees of development. Likewise, the three anterior lophids of the pentalophodont dp4 of erethizontids seem to be homologous to the anterolophid, metalophulid II, and mesolophid, respectively (Fig. 3). This hypothesis differs from that of Patterson and Wood (1982) for the pentalophodont dp4 of "caviomorphs", like *Protacaremys* (i.e. anterolophid, neoformation, and metalophid, respectively; Fig. 1B).

The primitive condition of the dp4 in Erethizontidae.— During the evolutionary history of the erethizontids, the morphological change in dp4 could have occurred from tetralophodonty towards penta- and hexalophodonty successively, or from pentalophodonty towards tetra- and hexalophodonty independently. In contrast to previous proposals, the second hypothesis is supported by the following reason: the dp4 of the Miocene Baluchimyinae from Pakistan (Flynn et al. 1986; Flynn and Cheema 1994), the probable sister group of the Hystricognathi (Jaeger 1988) or a member of the Hystricognathiformes (i.e., *Tsaganomys* Matthew and Granger, 1923 and the living Hystricognathi; Bryant and McKenna 1995), show, from front to back, the anterolophid, metalophulid II, an incipient (*Baluchimys* Flynn, Jacobs, and Chemma, 1986) or well developed (*Lindsaya* Flynn, Jacobs, and Chemma, 1986) mesolophid, hypolophid, and posterolophid, respectively (Fig. 5A; Flynn et al. 1986: figs. 17J, 18J). Interestingly, in the pentalophodont dp4 of the erethizontids, the same lophids connected to the same cusps are identified (see above). Upon this basis, it can be proposed that the pentalophodont design (with anterolophid, metalophulid II, and at least an incipient mesolophid) was not acquired independently by the Baluchimyinae and erethizontids, but it was already present in the common ancestor of these rodents. Thus, the hexalophodont dp4 of the erethizontids would result from the acquisition of a neolophid (Fig. 6A, B), while the tetralophodont dp4 would result from occlusal simplification (Fig. 6A, C), as seems to be the case in *Hypsosteiromys* and some specimens of *Erethizon dorsatum*.

The dp4 of the Old World Hystricognathi.—It is worth analyzing fossil dp4 showing comparable structures, such as the Oligocene Phiomyidae from Fayum. For these rodents pentalophodonty was considered the primitive condition, and the dp4 of *Phiomys andrewsi* Osborn, 1908 AMNH 13271 was considered the standard pattern of the Phiomyidae (Wood, 1968). It is
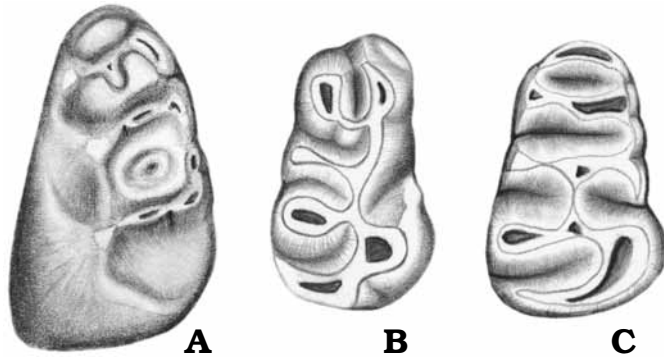
Fig. 5. Lower deciduous teeth (dp4) of: **A**. *Baluchimys ganeshapher* (left dp4). **B**. *Phiomys andrewsi* (right dp4). **C**. *Gaudeamus aegyptius* (right dp4). A from Flynn et al. (1986: fig. 17J); B, C from Wood (1968: figs. 1G, 15E).

characterized by a metalophid (posterior margins of protoconid and metaconid joined), anterolophid, mesolophid, hypolophid, and posterolophid or posterior cingulum (Fig. 5B; see Wood 1968: 39, fig. 1F, G). Interestingly, the same lophids can be recognized in the dp4 of the erethizontids (see above). *Phiomys andrewsi* also presents dp4 with a simpler morphology, usually without mesolophid or mesoconid (Wood 1968: fig. 2B). However, the most complex morphology, with mesolophid and mesoconid, was regarded as the most generalized for this species. *Gaudeamus aegyptius* Wood, 1968, another Oligocene Phiomyidae, has also a pentalophodont dp4, and its lophids were homologized to those of the complex dp4 of *Phiomys andrewsi* (Fig. 5C; see Wood 1968: figs. 14D, G; 15E, G). As noted before, an evident mesoconid and mesolophid, both supposedly absent in the dp4 of "Caviomorpha" (Patterson and Wood 1982), may be clearly distinguished in the erethizontids, and their remaining structures would be essentially identical to the standard pattern of the Phiomyidae.

The dp4 of Miocene Thryonomyoids has been also considered very different from those of "caviomorphs", taking as examples the dp4 of *Neosciuromys africanus* Stromer, 1922, *Elmerimys* Lavocat, 1973, and *Myophiomys* Lavocat, 1973, which have a very simple morphology, and of *Diamantomys* Stromer, 1922, and *Pomonomys* Stromer, 1922, which have very complex patterns (Patterson and Wood, 1982). However, in all cases their morphologies diverged from the gener-

alized patterns, and consequently the homologies are not reliably established.

Likewise, any similarity between the dp4 of the Old and New World Hystricognathi, such as between *Gaudeamus*, *Branisamys*, and *Erethizon*, was regarded as convergence phenomenon (Patterson and Wood, 1982). However, the lophids and cusps of the pentalophodont dp4 of *Phiomys andrewsi* AMNH 13271 (Fig. 5B), *Gaudeamus* (Fig. 5C), *Branisamys* (see below), and erethizontids seem to have identical topological characteristics, and nothing seems to justify why the same lophids with the same connections would be different structures.

The dp4 of "Caviomorpha".—The homologies of the dp4 of different "caviomorph" lineages, such as the Echimyidae (Dactylomyinae and Echimyinae), Octodontidae (Ctenomyinae and Octodontinae), Caviidae, Neopiblemidae, Hydrochaeridae, Capromyidae, Abrocomidae and Chinchillidae, are difficult to establish because their morphologies are quite modified and usually lack cusps. However, the following comments are pertinent to the more generalized patterns of the dp4 of the "caviomorpha".

(1) In view of their topology, and in contrast to previous proposals, the second and third lophid of the pentalophodont dp4 of the "Caviomorpha" (as those of the extinct Echimyidae *Protacaremys* and *Acarechimys* Patterson [in Kraglievich, 1965], living Echimyidae *Mesomys* Wagner, 1945 and *Lonchothrix* Thomas, 1920, and the living and extinct dasyproctids *Dasyprocta* Illiger, 1811 and *Neoreomys* Ameghino, 1887), may be homologized as the metalophulid II and mesolophid, respectively (Fig. 7A, B). The position, distinctness, and size of the mesolophid are also variable. Patterns without a fully developed mesolophid are observed, as in *Acarechimys* which presents a small "spur" connected to the ectolophid (Fig. 7C).

This pattern seems to be essentially equivalent to the pentalophodont dp4 of the Baluchimyinae, erethizontids, and *Phiomys andrewsi*, suggesting that the pentalophodonty was present in the dp4 of the ancestor of the Hystricognathi.

(2) The supposedly primitive tetralophodont dp4 of "Caviomorpha", as in the acaremyid *Sciamys*, and the echimyids *Prospaniomys* and *Eumysops*, lack distinctive cusps, preventing the identification of their lophids (Fig. 7D,
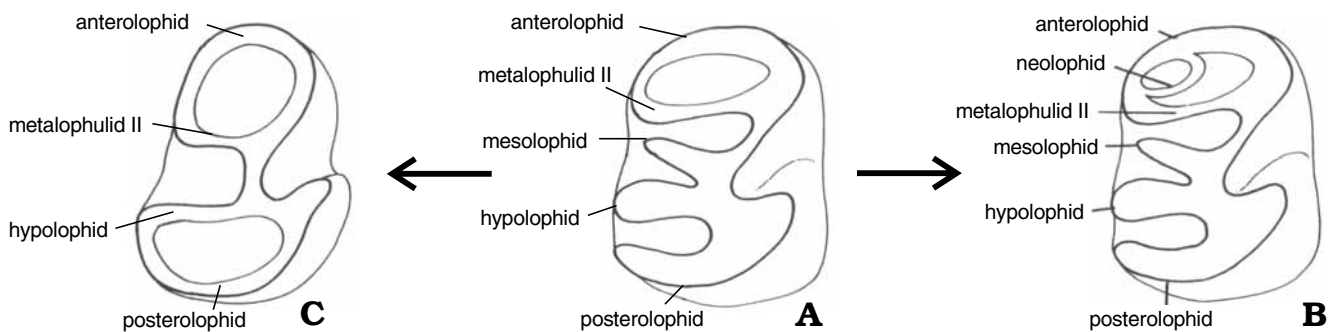

Fig. 6. Lophid homologies for lower deciduous teeth (dp4) of Erethizontidae according to this study. The arrows point in the direction of the change from pentalophodonty (**A**) towards tetra- (**B**), and hexalophodonty (**C**). All drawn as if from the right side.
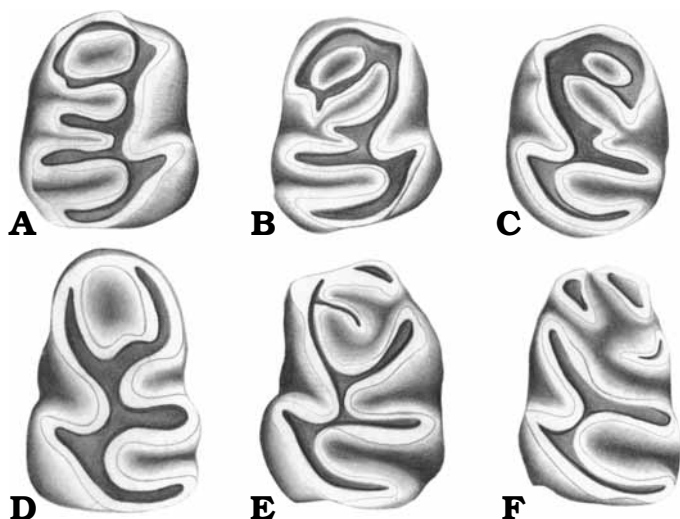
Fig. 7. Lower deciduous teeth (dp4) of "caviomorphs". **A**, **B**. *Protacaremys*; MLP 85-VII-131 (right dp4) (**A**); MLP 85-VII-3-128 (right dp4) (**B**). **C**. *Acarechimys* MLP 82-XII-1-6 (left dp4), **D**, **E**. *Sciamys*; MLP 82-V-2-33 (left dp4) (**D**); MLP 15-197 (left dp4) (**E**). **F**. *Protadelphomys* MPEF 5050 (left dp4). Not to scale.

Fig. 8. Lower deciduous tooth of *Branisamys luribayensis* (GN 014, type of *Villarroelomys bolivianus*), from Patterson and Wood (1982), showing the homologies proposed in this study (**A**), and by Patterson and Wood (1982) (**B**).

E). Likewise, the lophids of the tetralophodont dp4 of the adelphomyine echimyids *Paradelphomys*, *Spaniomys*, and *Stichomys* are also difficult to homologize. The dp4 of *Paradelphomys* lacks distinguishable cusps and, as in its lower molars, the last lophid is isolated (Patterson and Pascual 1968: fig. 3). The dp4 of *Spaniomys* (Patterson and Pascual 1968: fig. 1) also lacks distinguishable cusps, and has wide flexids, strong lamination, and a tendency to hypsodonty. This also occurs in *Stichomys* (Scott 1905: pl. LXV: 20a). Certain octodontoids, like *Protadelphomys* Ameghino, 1902, have simpler dp4 morphologies (Fig. 7F). Therefore, since the homologies of the lophids of these teeth are uncertain, it is not possible to test whether tetralophodonty is the primitive condition.

(3) The occlusal pattern of the dp4 of *Branisamys* (supposedly the most derived condition; Patterson and Wood 1982) is essentially similar to that of the pentalophodont erethizontids (Fig. 8). Because of their topology, it may be proposed that in the dp4 of *Branisamys* the anteriormost labial cusp corresponds to the protoconid and the anteriormost lingual cusp corresponds to the metaconid. Thus, the "protoconid", as was interpreted by Patterson and Wood (1982), would actually be the mesoconid, and the "metaconid" would be the mesostylid, placed behind the metaconid (Fig. 8A, B). Therefore, as in the erethizontids, the first three lophids of the dp4 of *Branisamys* may be homologous to the anterolophid, metalophulid II, and mesolophid, respectively. Notably, skull and dental characters of *Branisamys* (Lavocat 1976; Patterson and Wood 1982) are similar to those of extinct erethizontids (personal observation), suggesting the possibility that this genus belongs to the Erethizontidae.

In sum, on the basis of comparable structures, it may be proposed that the pentalophodont pattern of the dp4 in porcupines and other South American Hystricognathi is homologous.
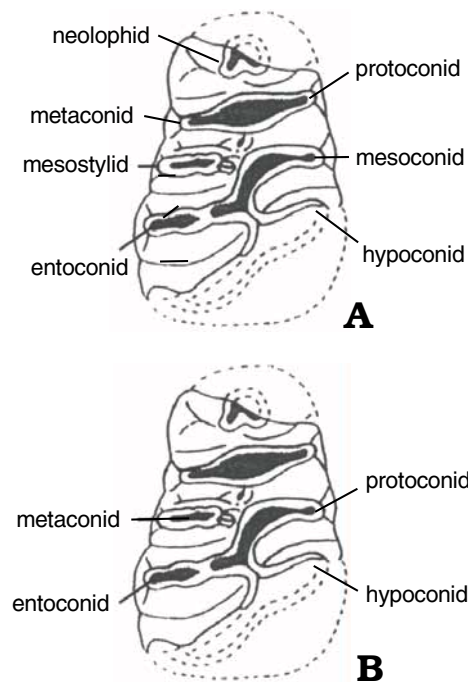
Concluding note

The dp4 of the Hystricognathi differ from the generalized rodent molars, but most of their cusps can readily be homologized to those of the tribosphenic pattern. As noted by Butler "…rodent molars have passed through a tribosphenic stage in their evolution, and the Osbornian name can be applied confidently to their cusps" (Butler 1985: 386).

In contrast to previous proposals (Patterson and Wood 1982), it is concluded that the mesoconid, mesostylid, and mesolophid of the dp4 of the erethizontids can be recognized at least since the Early Miocene. The lophids of the pentalophodont dp4 of the erethizontids would be homologous to the anterolophid, metalophulid II, mesolophid, hypolophid, and posterolophid. This pattern seems to have identical topological characteristics than those of the dp4 of the Baluchimyinae, suggesting that pentalophodonty was already present in the common ancestor of these rodents. In addition, on the basis of comparable structures, it may be proposed that the pentalophodont dp4 of the Old World Hystricognathi are homologous to those of the erethizontids and the remaining South American Hystricognathi.

In sum, the pentalophodont pattern is probably the primitive condition of the dp4 for the Hystricognathi rodents. However, "It is obvious from the above that not enough is known about lower deciduous teeth of caviomorphs to be of great significance in unraveling their interrelationships" (Patterson and Wood 1982: 503). This study attempts to identify the homologies of the dp4 of the Hystricognathi to develop them as a source of characters in future phylogenetic analyses.

Acknowledgments

References

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1888. *Lista de las especies de mamíferos fósiles del Mioceno superior de Monte Hermoso hasta ahora conocidas*. 21 pp. Buenos Aires.

Ameghino, F. 1897. Mammifères Crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium. Boletín del Instituto Geográfico Argentino* 18: 406.

Ameghino, F. 1902. Enumération synnoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia de Ciencias de Córdoba* 13: 259–452.

Bryant, D. and Mckenna, M.C. 1995. Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia: Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. *American Museum Novitates* 3156: 1–42.

Bugge, J. 1971. The arteries system in sciuromorphs with special reference to the systematic classification of rodents. *Acta Anatomica* 80: 336–361.

Butler, P.M. 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. *In*: W.P. Luckett and J.L. Hartenberger (eds.), *Evolutionary Relationships among Rodents. A Multidisciplinary Analysis*, 381–401. Plenum Press, New York.

Candela, A.M. 1999. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *Parasteiromys* Ameghino 1904. *Palaeovertebrata* 28: 53–73.

Candela, A.M. 2000. *Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina. Sistemática e historia evolutiva y biogeográfica*. 357 pp. Ph.D. dissertation, Facultad de Ciencias Naturales y Museo.

Cuvier, F. 1822. Examen des espéces du genre porc-épic, et formation des genres ou sous-genres *Acanthion, Erethizon, Sinethere* et *Sphiggure. Mémoires du Muséum National d'Histoire Naturelle* 9 (6): 413–437. Paris.

De Pinna, M.C.C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7: 367–394.

Flynn, L.J., Jacobs, L.J., and Cheema, I.U. 1986. Baluchimyinae, a new Ctenodactyloid rodent Subfamily from the Miocene of Baluchistan. *American Museum Novitates* 2841: 1–58.

Flynn, L.J., and Cheema I.U. 1994. Baluchimyine rodents from the Zinda Pir Dome, Western Pakistan: systematic and biochronologic implications. *In*: Y. Tomida, C.K. Li, and T. Setoguchi (eds.), *Rodent and Lagomorph Families of Asian Origins and Diversification*, 115–129. National Science Museum Monographs 8, Tokyo.

Hoffstetter, R. and Lavocat, R. 1970. Découverte dans le Déséadien de Bolivie de genres pentalophodontes appuyant les affinités africaines des rongeurs Caviomorphes. *Comptes Rendus de l'Académie des Sciences, Paris* 271: 172–175.

Huchon, D. and Douzery, E.J. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. *Molecular Phylogenetics and Evolution* 20: 238–251.

Illiger, C. 1811. *Prodromus systematis Mammalium et Avium additis terminis zoographicis utriusque classis, eorumque versione Germanica*, i–xviii + 1–302. C. Salfield, Berlin.

Jaeger, J.J. 1988. Rodent phylogeny: new data and old problems. *In*: M.J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods*, Vol. 2,

177–199. The Systematics Association, Special Volume No. 35B, Clarendon Press, Oxford.

Jernvall, J. 1995. Mammalian molar cusp patterns: Developmental mechanisms of diversity. *Acta Zoological Fennica* 198: 1–61.

Kraglievich, L. 1965. Speciation phylétique dans les rongeurs fossiles du genre *Eumysops* Amegh. (Echimyidae, Heteropsomyinae). *Mammalia* 29: 258–267.

Lavocat, R. 1973. Les rongeurs du Miocène d'Afrique Orientale. *Mémoires et travaux de l'Ecole Pratique des Hautes Etudes, Institut de Ecole Montpellier* 1: 1–284.

Lavocat, R. 1976. Rongeurs Caviomorphes de l'Oligocene de Bolivie. II. Rongeurs du Bassin Deseadien de Salla-Luribay. *Palaeovertebrata* 7: 15–90.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Tomus I. Editio decima, reformata. Holmiae: Laurentii Salvii.

Matthew, W.D. and Granger, W. 1923. New Bathyergidae from the Oligocene of Mongolia. *American Museum Novitates* 101: 1–5.

Mckenna, M. and Bell, S.K. (eds.) 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.

Nedbal, M.A., Allard M.W., and Honeycutt R.L. 1994. Molecular systematics of hystricognath rodents: Evidence from the mitochondrial 125 rRNA gene. *Molecular Phylogenetics and Evolution* 3: 206–220.

Nelson, G. 1994. Homology and systematics. *In*: B.K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology*, 101–149. Academic Press, New York.

Osborn, H.F. 1908. New fossil mammals from the Fayûm, Egypt. *Bulletin of the American Museum of Natural History* 24: 265–272.

Patterson, B. 1958. A new genus of erethizontid rodents from the Colhuehuapian of Patagonia. *Breviora* 92: 1–4.

Patterson, B. and Pascual, R. 1968. New Echimyid Rodents from the Oligocene of Patagonia, and a synopsis of the family. *Breviora* 301: 1–14.

Patterson, B. and Wood, A.E. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of Museum of Comparative Zoology* 149: 371–543.

Patterson, C. 1982. Morphological characters and homology. *In*: K.A. Joysey and A.E. Friday (eds.), *Problems of Phylogenetic Reconstruction*, 21–74. Academic Press, London.

Rieppel, O. 1988. *Fundamentals of Comparative Biology*. 202 pp. Birkhäuser Verlag, Basel.

Rieppel, O. 1994. Homology, Topology, and Typology: the history of modern debates. *In*: B.K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology*, 63–100. Academic Press, New York.

Scott, W.B. 1905. Paleontology. Glires, Part III. Reports of the Princeton University Expeditions to Patagonia (1896–1899) 5: 243–245.

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltier-Reste aus Deutsch-Südwestafrika. S.B. Bayerischen Akademie der Wissenschaften 1921: 331–340.

Thomas, O. 1920. A new genus of Echimyinae. *Annals of the Magazine of Natural History*, Serie 9 (6): 113–115.

Vucetich, M.G., Mazzoni, M.M., and Pardiñas, U.J. 1993. Los roedores de la Formación Collón Curá (Mioceno Medio), y la Ignimbrita Pilcaniyeu. Cañadón del Tordillo, Neuquén. *Ameghiniana* 30 (4): 361–381.

Wagner, J.A. 1845. Diagnosen einiger neuen Arten von Nagern und Handflüglern. *Weigmann's Archiv für Naturgesch* 11 (1): 145–149.

Wood, A.E. 1968. Early Cenozoic mammalian faunas, Fayum province, Egypt. Part II. The African Oligocene Rodentia. *Peabody Museum of Natural History Bulletin* 28: 29–105.

Wood, A.E. and Wilson, R.W. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. *Journal of Paleontology* 10: 388–391.

Wood, A.E. and B. Patterson. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin Museum of Comparative Zoology* 120: 281–428.

Woods, C.A. 1972. Comparative myology of jaw, hyoid and pectoral appendicular regions of New and Old World Hystricomorph rodents. *Bulletin of the American Museum Natural History* 147: 115–198.