

THE EVOLUTION OF THE MOLAR PATTERN OF THE
ERETHIZONTIDAE (RODENTIA, HYSTRICOGNATHI) AND THE
VALIDITY OF *PARASTEIROMYS* AMEGHINO, 1904

by

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Mots-clés: Porcs-épics, Erethizontidae, Hystricognathi, Rodentia, Argentine, Systematique, Miocene, evolution des molaires.

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ABSTRACT

The genus *Parasteiromys* AMEGHINO, 1904 is revalidated, and *P. friantae* sp. nov. (Hystricognathi, Erethizontidae) from Colhuehuapian (early Miocene) sediments of the southern cliff of Colhue-Huapi Lake (Province of Chubut, Argentina), is described. The molar morphology of these taxa and of living porcupines adds new elements to understand the dental evolution of the Erethizontidae, and to propose the hypothetical ancestral molar pattern for this family. This pattern does not correspond to any of the morphologies traditionally proposed as ancestral for South American hystricognathous rodents. The proposed pattern is characterized by a metaloph disconnected from the posteroloph and oriented towards the hypocone, and the third loph incompletely developed with the lingual portion homologous to the mesolophule of Baluchimyinae (Chapattimyidae) from the Miocene of Pakistan. The inferred steps of the molar evolution of erethizontids towards the pentalophodont condition, considered derived for the family, are illustrated. This study strengthens the hypothesis placing erethizontids in a basal position among rodents of the suborder Hystricognathi.

RESUME

Le genre *Parasteiromys* AMEGHINO, 1904 (Hystricognathi, Erethizontidae) est revalidé et on décrit *P. friantae* sp. nov., découvert dans les sédiments du Miocène inférieur (Age Colhuéhuapien) du Ravin Sud du Lac Colhué-Huapi (Province de Chubut, Argentine). La morphologie des molaires de ces taxons et des Porcs-épics vivants ajoute des compléments pour mieux comprendre l'évolution du plan dentaire des éréthizontidés, et conduit à proposer un schéma du patron dentaire hypothétique pour cette famille. Ce patron se caractérise par la possession d'un métalophe déconnecté du postérolophe et orienté vers l'hypocône; le troisième lophe est incomplètement développé, et sa portion linguale est homologue du mésolophule des Baluchimyinae (Chapattimyidae) du Miocène du Pakistan. Les stades successifs de l'évolution de ce patron dentaire vers la condition pentalophodonte sont illustrés; le stade pentalophodonte doit être, considéré dérivé pour cette famille. Cette étude renforce l'hypothèse qui envisage que les éréthizontidés occupent une position basale parmi les rongeurs du sous-ordre Hystricognathi.

INTRODUCTION

Neotropical porcupines represent a primitive lineage of hystricognathous rodents that occur now different kinds of forest ranging from southern Mexico to northern Argentina. They are represented by three genera and about eleven species (see Woods, 1993) fully adapted to arboreal life (Emmons, 1997). Fossil representatives recorded since the Deseadan (late Oligocene) are known mainly from the Argentine Patagonia (Wood & Patterson, 1959; Patterson, 1958). Their relationships with other families of the Suborder Hystricognathi have not been satisfactorily understood and their complete isolation from other South American hystricognathous rodents is broadly recognized (Bugge, 1974; Bugge, 1985; Luckett & Hartenberger, 1985; Wood & Patterson, 1959; Patterson & Wood, 1982; Woods, 1972; Woods & Hermanson, 1985; Moody & Donninger, 1955; Vanzolini & Guimaraes, 1955; George & Weir, 1974; Nedbal *et al.*,

1994). This fact suggested they represent an early separated branch of the latter (Wood & Patterson, 1959; Patterson & Wood, 1982; Wood, 1985), or even that they arrived independently in South America (Bugge, 1974; Woods, 1972; Moody & Donninger, 1955). Recently, Bryant & McKenna (1995) placed erethizontids at the base of the radiation of the suborder (African and South American hystricognathous rodents) and supported the hypothesis that they represent an independent dispersion event from the Old World into South America. The evolutionary and biogeographic history of this family may be better understood if the fossil representatives are taken into account. The molar morphology of fossils has not been used extensively for testing the different hypothesis mentioned above.

This is the first study of a series that aims to elucidate the evolutionary history of Erethizontidae. The genus *Parasteiromys* AMEGHINO, 1904 is revalidated, and a new species of this genus is described, from the early Miocene (Colhuehuapian Age) of central Patagonia. The molar morphology of these taxa together with that of certain living erethizontids supplies new evidence to propose an hypothetical ancestral molar pattern of the family, to analyze the evolution of this pattern, and to discuss the homologies of their cusps and lophs, and the rising mode of the third loph.

ABBREVIATIONS

MLP: Museo de La Plata, Argentina; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina; MPEF: Museo Paleontológico Egidio Feruglio, Argentina; MMCN: Museo Municipal de Ciencias Naturales "L. Scaglia", Mar del Plata, Argentina; MNH: Museo de Monte Hermoso, Argentina; MNHN: Museum National d' Histoire Naturelle, Paris; MNRJ: Museo Nacional de Rio de Janeiro, Brazil; MG: Museo Paranense Emilio Goeldi, Belém, Brasil. DP3: deciduous third upper premolar; DP4: deciduous fourth upper premolar; P4: definitive fourth upper premolar; M: upper molar.

MATERIALS AND METHODS

The analyzed taxa were compared with the entire fossil erethizontid genera and species of Argentina. In the case of *Steiromys* AMEGHINO, 1887 all the species assigned to this genus were studied, i. e., *S. detentus* AMEGHINO, 1887, *S. duplicatus* AMEGHINO, 1887, *S. annectens* AMEGHINO, 1901, and *S. intermedius* SCOTT, 1905 (*S. principalis* AMEGHINO, 1901 could not be found). *S. duplicatus* was analyzed with more detail because the remaining species need an update revision. The genus *Disteiromys* AMEGHINO, 1904 from the middle Miocene of Chubut, was not considered in view of its uncertain position (Vucetich, 1984). The terminology of cusps, valleys and lophs used in this study was adapted from the standard rodent dental terminology of Wood & Wilson (1936), Patterson & Wood (1982, fig. 1A), and Lavocat (1976), with modifications made in this study (see Fig. 1 and Discussion). All measurements are in

millimeters (mm).

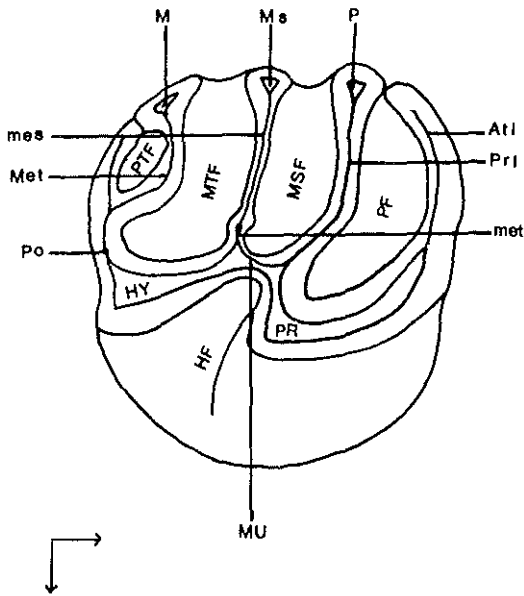


Figure 1.— Key to the terminology applied to cusps, lophes and valleys of upper molar (right) in Erethizontidae. Abbreviations: AtI: anteroloph; HF: hipoflexus; HY: hypocone; M: metacone; mes: mesolophule; met: metaconule; Met: metaloph; MU: mure; Ms: mesostyle; MSF: mesoflexus or mesofossette; MTF: metaflexus or metafossette; P: paracone; PF: paraflexus or parafossette; PR: protocone; Pri: protoloph; Po: posteroloph. PTF: posterofossette. Arrows show anterior and lingual.

SYSTEMATICS

Order **RODENTIA** BOWDICH, 1821
Suborder **HYSTRICOGNATHI** TULBERG, 1899
Family **ERETHIZONTIDAE** THOMAS, 1897

PARASTEIROMYS AMEGHINO, 1904

Steiromys PATTERSON, 1958 *non* AMEGHINO, 1887

Type species: *Parasteiromys uniformis* (AMEGHINO, 1903)

Distribution: early Miocene of Central Argentina.

New diagnosis: it differs from the remaining erethizontids in the following combination of characters: DP3 present; hypocone of the molariforms placed lingually to the protocone; lack of mure with the consequent communication between hypo- and mesoflexus; labial cusps scarcely developed; early closing of para- and metafossettes; posteroloph higher than metaloph; lingual face of the protocone parallel or slightly oblique respect to the anteroposterior axis of the tooth; upper incisor with anterior face slightly convex.

Parasteiromys uniformis (AMEGHINO, 1903)

(Fig. 2a, b)

Eosteiomys uniformis AMEGHINO, 1903

Steiomys uniformis PATTERSON, 1958; WOOD & PATTERSON, 1959

Type and only known specimen: MACN A 52-178, a left maxillary fragment with DP3 alveoli, DP4-M1 complete and isolated upper right incisor.

Horizon and locality: Southern cliff of Colhue-Huapi Lake, Chubut province, Argentina; Sarmiento Formation, Colhuehuapian Age, early Miocene.

Measurements: DP4: length: 6.52; anterior width: 6.60; posterior width: 6.30. M1: length: 6.90; anterior width: 8; posterior width: 7.58. Incisor: width: 4.88.

Diagnosis: it differs from *P. friantae* sp. nov. in the following features: larger size, subcircular shape of the lingual face of the protocone, larger width of the parafofsette, and protoloph connected with the posterior end of the protocone.

Description

The specimen is a left maxillary fragment with DP4-M1 complete (Fig. 2a). A major part of the maxillary fosse lies in the anterior portion; it is moderately deep and is limited anteriorly by a longitudinal crest. The lower zygomatic root rises laterally, the posterior edge of which is placed in front of the DP4. In the anterior portion, it has a deep furrow of the surface originated by the superficial masseteric tendon and masseter lateralis (*sensu* Woods, 1972). Two small holes that seem to belong to the alveoli of the DP3 are in front of the DP4 (see below). They are very close to each other and to the DP4, and separated by a thin bony wall; the anterior one is placed externally to the posterior one and is clearly larger than the latter. The anterior face of the upper incisor is slightly convex and smooth.

The DP4 (see Measurements and Fig. 2b) is subrectangular in occlusal view. The tooth is scarcely worn, with the dentine exposed only at its posterolabial surface. The anteroloph is strongly curved from the anterior end of the protocone to the anterior slope of the paracone, labially closing the parafofsette, though remains of a very slender and superficial paraflexus can be observed in occlusal view. The protoloph extends from the posterior portion of the protocone, slightly oblique posterolingually-anterolabially, to join labially the lingual slope of the paracone. This cusp is not much developed, it is larger than the metacone and the mesostyle, and scarcely rises above the occlusal surface. The "mesolophule" (third loph) is the lowest and thinnest loph, and its lingual end is separated from the anterolabial end of the hypocone by the metaconule (see Discussion). This cusp is small though clearly distinct and shows a small anterior projection. The labial end of the "mesolophule" is associated with a small and low mesostyle. The metaloph joins the posteroloph labially and lingually, bounding small subcircular posterofossette. Consequently, the labial end of the metaloph is not united with the metacone, as in the remaining erethizontids, but only to the posteroloph. In front of the posterofossette and behind the "mesolophule" there is a short and wide spur extending anterolingually from the metacone. This spur may represent the labial portion of the metaloph, which may have released its lingual portion. This latter may have

joined the posteroloph labially and lingually. The metacone, scarcely differentiated, is anterolabially-posterolingually directed, very close to the mesostyle, and its lingual and posterior slopes are continuous with the short spur and the posteroloph respectively. This latter loph is higher than the metaloph and its lingual end is separated from the hypocone by a small posterior inflexion, from where it is posterolabially directed describing a semicircle. The parafofsette is wider than the mesoflexus and has its labial and lingual ends approximately of the same anteroposterior diameter. The metaflexus is very narrow labially (suggesting the early formation of the metafofsette), and deeper in its lingual half. The mesoflexus is narrower than the metaflexus and its walls are subparallel and slightly oblique anterolabially. The protocone has a crest in its posterolingual end, and its lingual face is subcircular and parallel to the anteroposterior axis of the tooth. This cusp forms with the anteroloph a semicircular contour.

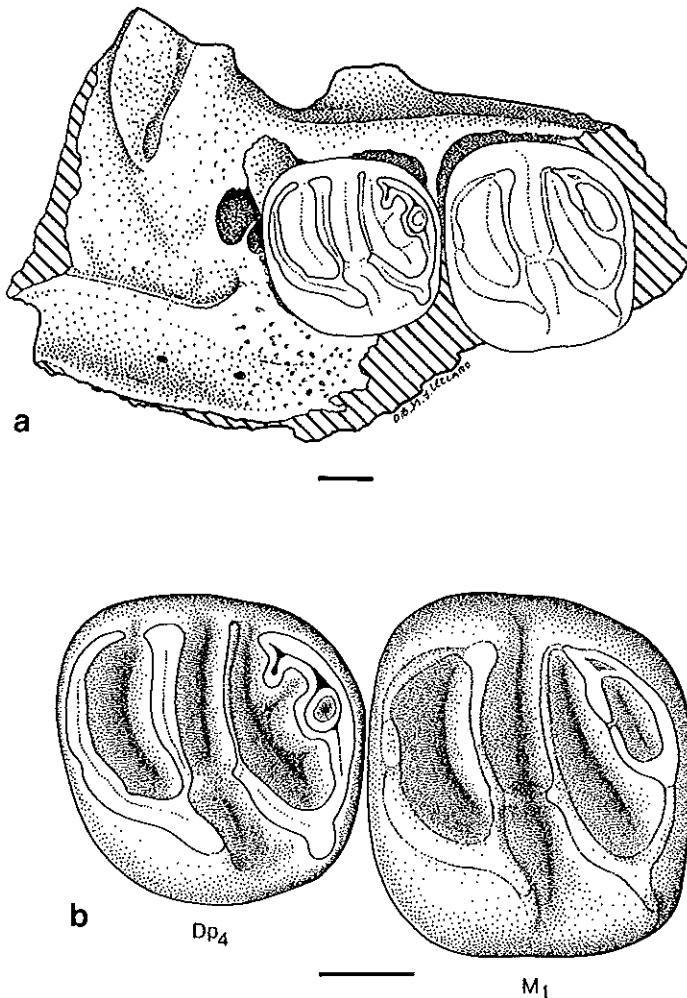


Figure 2.— Maxillar fragment and cheek teeth of *Parasteiromys uniformis* AMEGHINO, 1904, type MACN A-52-178, a: left maxillar fragment with DP3 alveoli, and complete DP4-M1; b: view occlusal only DP4-M1. Scale: 2mm.

The hypocone is lesser extended anteroposteriorly than the protocone and is placed lingually to the latter. Its anterolabial end is clearly defined by the metaconule, and its posterolingual end extends like a wide and rounded crest. The hypoflexus continues with the mesoflexus, due to the absence of mure. The anterior labial root (Fig. 2a) is anterolabially extended. Consequently, it can be seen in occlusal view, projected in front and externally to the external anterior edge of the crown.

The M1 (see Measurements and Fig. 2b) is pentalophodont, larger than the DP4, less worn and subquadrangular in occlusal view. Like the DP4, the M1 has no mure, and consequently hypo- and mesoflexus are continuous. However, the hypoflexus is anterolabially-posterolingually directed, while the mesoflexus is transverse. Besides, the boundary is marked by the metaconule, separating the anterolabial end of the hypocone from the lingual end of the "mesolophule". The orientation of anteroloph, protoloph and "mesolophule" is similar to that in DP4, though the labial end of the anteroloph is closer to the paracone, closing the parafossette labially. The size, position and relative height of the labial cusps are similar to those described for the DP4, though the mesostyle is smaller in the latter and closer to the metacone, closing the metaflexus labially. Likewise, M1 and DP4 are similar in size, orientation and relative position of the proto- and hypocone. Unlike the DP4, the M1 lacks the short spur joined to the lingual slope of the metacone, and the metaloph joins this cusp labially. Consequently, the metaloph does not have the subcircular shape of the DP4. Instead, it runs from the posteroloph anterolabially towards the metacone, defining a more developed and oblique posterofossette.

Validity of *Parasteiromys* AMEGHINO, 1904 and comparison with other erethizontids

In 1903, Ameghino figured the species *Eosteiomys uniformis* for the first time, and discussed certain features of its dentition. Though he did not describe it as a new species, the brief mention (pages 126-7) and figure (Fig. 47) are enough to refer the species to this work. A year later, Ameghino (1904) proposed the genus *Parasteiromys* and formally described *Parasteiromys uniformis* nov. gen. et sp. The following are the main features that may be deduced from Ameghino's diagnosis: presence of the DP3 alveoli (his m3), hypoflexus united to the mesoflexus, and presence of a metafossette. Patterson (1958) considered that *Parasteiromys uniformis* was a species of the genus *Steiomys* Ameghino 1887, and a year later he published the arguments supporting this statement (Wood & Patterson, 1959: 378). These authors considered that: a- the anterior holes of the DP4 of *Parasteiromys uniformis* may correspond to vascular foraminae rather than to alveoli, as similar holes are observed in young specimens of living erethizontids, in which no tooth anterior to the DP4 has ever been observed; b- the presence of metafossette (neofossette according to them) is common in other erethizontids; and c- the union of hypo- and mesoflexus does not seem to be a feature with generic meaning.

The analysis of these characters led to the following conclusions: the anterior holes of the DP4 may correspond to alveoli of the DP3, as the absence of this tooth in living erethizontids does not imply its absence in fossil erethizontids. In addition, the holes in *Parasteiromys uniformis* and in other fossil erethizontids (e.g. *Steiomys*

detentus, MACN 4147) are too conspicuous to belong to vascular holes. The presence of metafossette is frequent among erethizontids (e.g. *Steiromys duplicatus*) and consequently, it is not a diagnostic feature either. However, the absence of mure with the consequent union hypoflexus-mesoflexus and the lingual position of the hypocone respect of the protocone are exclusive features of this genus (see below). Likewise, the slight development of labial cusps and the greater height of the posteroloph respect of metaloph, also characterize *Parasteiromys*. Besides, *Parasteiromys uniformis* has relatively narrow upper incisors compared with the molars, and their anterior faces are more convex than those of the species of *Steiromys* and *Eosteiromys*. The incisors of *Hypsosteiromys* are also convex but much narrower compared to the molar size. Summing up, these features and their combination with those pointed out in the diagnosis are distinctive enough to justify the validity of the genus *Parasteiromys*.

The species of the genus *Steiromys* AMEGHINO, 1887 (Fig. 3a) differ from *Parasteiromys* by the labial position of the hypocone respect of the protocone and the presence of mure, with the consequent separation of hypo- and mesoflexus. Besides, *Parasteiromys* differs from *Steiromys* because the former has a proportionally narrower mesoflexus and wider para- and metafossettes; relatively higher posteroloph; and earlier closing of the paraflexus than the latter. In turn, the lingual facet of the protocone in the species of *Steiromys* is flat, markedly oblique respect of the anteroposterior axis of the molars and separated from the anteroloph by a marked inflexion. Finally, the parafossette of *Parasteiromys* does not narrow labially as in the species of *Steiromys*, and the labial cusps are less developed. Despite the great intra- and interspecific variability seen within *Steiromys*, differences of the species of this genus from those assigned in this paper to the genus *Parasteiromys* (see below) are distinctive enough as to justify their generic separation. The specimen of the species *S. duplicatus* figured in this paper was especially selected for this comparison, as it is as worn as *Parasteiromys uniformis* allowing a reliable evaluation of the differences observed in the studied species.

Parasteiromys differs from *Eosteiromys* AMEGHINO, 1902 (Fig. 3b; *E. homogenidens* is the single species of the genus) in the following features: absence of mure with union of meso- hypoflexus; posteroloph higher than metaloph; hypocone placed lingually respect of the protocone; labial cusps less developed; and oval and more developed posterofossette. In addition, the mesoflexus of *Parasteiromys* is proportionally narrower than that of *E. homogenidens* and the metaloph of the M1 is slightly more oblique; the paraflexus of *Parasteiromys* closes very early, unlike that of *E. homogenidens*, which continues with a moderate wear. Finally, the hypocone of the molars of *E. homogenidens* is not crested and its anterolingual face is less convex.

Hypsosteiromys PATTERSON, 1958 (Fig. 3c; *H. axiculus* is the single species of this genus) differs from *Parasteiromys* because the former has higher crowned molariforms. The loph of the molariforms of *Hypsosteiromys* are more oblique, and their fossettes and flexi are deeper. The DP4 of *H. axiculus* (MMCN 113) is longer than the M1, unlike in *P. uniformis*. The hypocone of the molariforms of *H. axiculus* is placed labially respect of the protocone, and the mure separates hypo- from mesoflexus, which is wider than the metafossette and the paraflexus, and has divergent walls. *H. axiculus* is also characterized by a pronounced angle between the protocone and the

anteroloph.

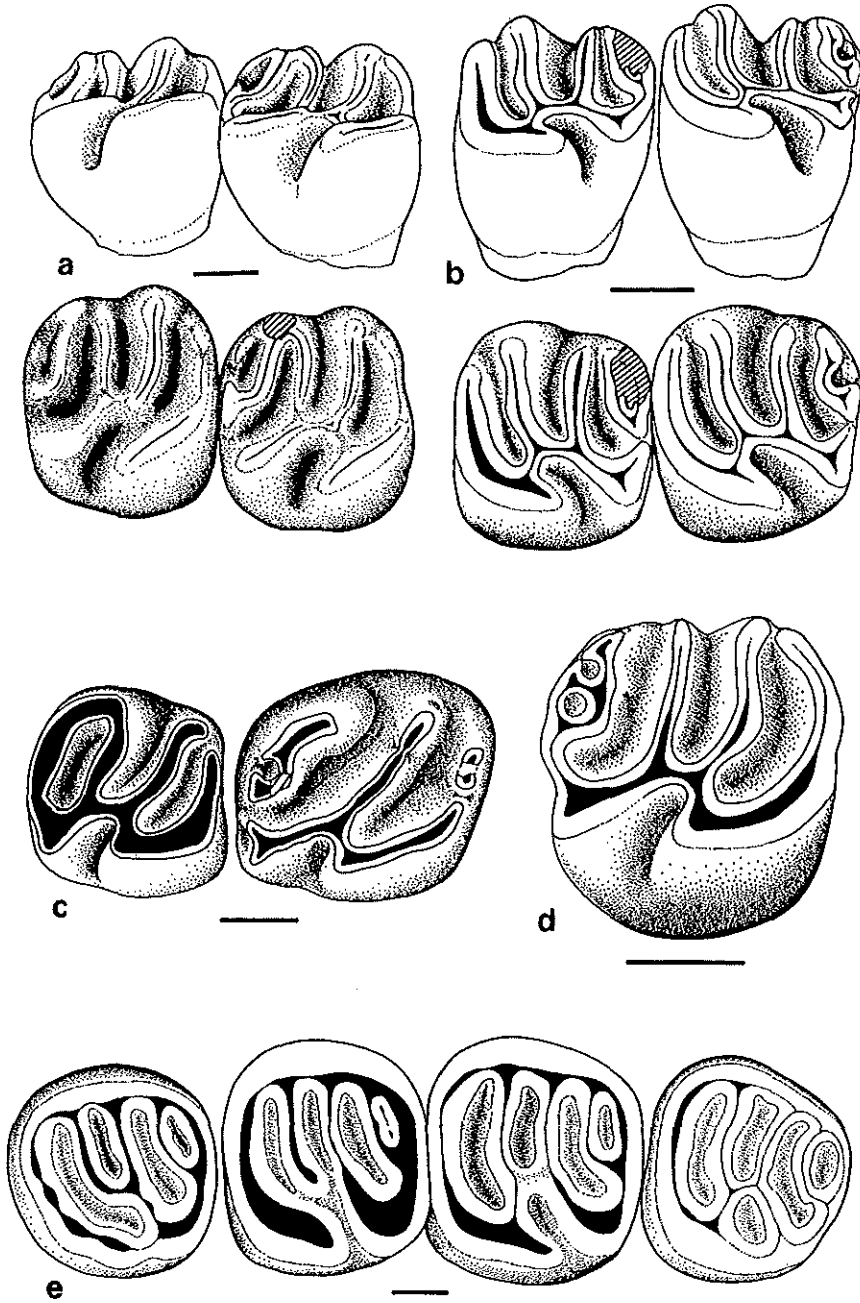


Figure 3.— Upper molariforms of a: *Steiromys duplicatus* AMEGHINO, 1887, specimen MLP 15-355, occlusal and lingual-occlusal views of right M1-2; b: *Eosteiomys homogenidens* AMEGHINO, 1902, type MACN A-52-165, in occlusal and lingual-occlusal views, only left M1-2; c: *Hypsosteiomys axiculus* PATTERSON, 1958, trace of MNHN col. 49, occlusal view of P4-M1; d: *Protosteiomys medianus* WOOD & PATTERSON, 1959, type MACN 52-111, isolated upper right molar (M1 or 2) in lingual-occlusal view; e: *Neosteiomys bombifrons* ROVERETO, 1914, specimen MNH 92-1-1 occlusal view of left P4-M3. Scale: 2 mm.

Parasteiromys differs from *Neosteiromys bombifrons* ROVERETO, 1914 (Fig. 3e; *N. bombifrons* is the single undoubted species of the genus) by its smaller size, smaller enamel thickness, the persistence of the mesoflexus, the absence of mure and the lingual position of the hypocone respect of the protocone. In *N. bombifrons* the hypoflexus is united to the paraflexus, and the flexi and fossettes are shallow. These latter features clearly differentiate this genus from *Parasteiromys*.

Parasteiromys differs from *Protosteiromys* WOOD & PATTERSON, 1959 (Fig. 3d; *P. medianus* is the type species of the genus, and the only species with known upper molars) by its larger size, the absence of mure, deeper flexi and fossettes, and more convex anterolingual face of the hypocone. Though the hypocone of the molars of *P. medianus* is displaced more lingually than in most erethizontids (in which the hypocone is placed labially respect of the protocone), it is in the same anteroposterior line of the protocone and not lingually respect of this cusp as in *Parasteiromys*.

Parasteiromys friantae sp. nov.

(Fig. 4)

Holotype and only known specimen: MPEF 5501, an isolated upper right molariform.

Horizon and locality: early Miocene, Colhuehuapian Age, South Cliff of Colhue-Huapi Lake, Chubut province, Argentina.

Etymology: in honor to Madeleine Friant for her contribution to the study of Erethizontidae.

Measurements: length: 6.30 mm; anterior width: 5.61 mm; posterior width: 5.53 mm.

Diagnosis: it differs from *P. uniformis* in the following features: smaller size; lingual face of the protocone plane and slightly oblique respect of the anteroposterior axis of the tooth; shallower flexi and fossettes; more developed mesostyle; metaloph not connected to the posteroloph, with its lingual end free and oriented toward the hypocone; and narrower parafofsette.

Description

The holotype is an single upper right tooth (Fig. 4), subrectangular in occlusal view, with its anterior labial root very anteriorly displaced. Both features are characteristic of DP4 of erethizontids. However, as it is an isolated molariform, it is difficult to assign it undoubtedly to any of the molariforms of the dental series (except for the M3 that narrows markedly towards its posterior end). The holotype has shallow flexi and a slight worn, which is more clearly observed at the hypocone. The lingual face of this cusp is rounded, less extended anteroposteriorly than the protocone, and is placed lingually respect of the latter. The lingual face of the protocone is plane. This cusp is somewhat oblique to the anteroposterior axis of the molar. A strangling marks the limit between the protocone and the lingual end of the anteroloph. The labial end of this loph continues with the anterior slope of the small paracone, closing the parafofsette labially. The protoloph has also a strangling in its lingual end that marks the limit with the medial zone of the protocone. It runs transversely, becoming wider level with the paracone and rising slightly when approaching to this cusp. There is no

mure between proto- and hypocone, consequently the hypoflexus continues with the mesoflexus, though the boundary may be established by their orientation: while the hypoflexus is posterolingually-anterolabially oriented, the mesoflexus is transverse to the longitudinal axis of the tooth. In turn, the boundary with the "mesolophule" may be established in the anterolabial end of the hypocone, because a clear widening marks the presence of the metaconule (see Discussion). From this cusp the "mesolophule" runs transversely ending labially in a mesostyle similar in size to the paracone. Both cusps are very close to each other, so the mesoflexus is almost closed labially. The metaloph is not clearly separated from the posteroloph by its lingual end. It is free instead, oriented towards the hypocone, while in its labial end, slightly curved backwards, it joins the metacone. The metacone is not delimited respect of the posteroloph. It is anteriorly extended respect of the metaloph and oblique posterolingually-anterolabially. The posteroloph is semicircular and in spite of being worn in its labial half, it is somewhat higher than the metaloph. The metaflex is continuous with the lingual bottom of the posterofossette because the lingual end of the metaloph is not connected with the posteroloph.

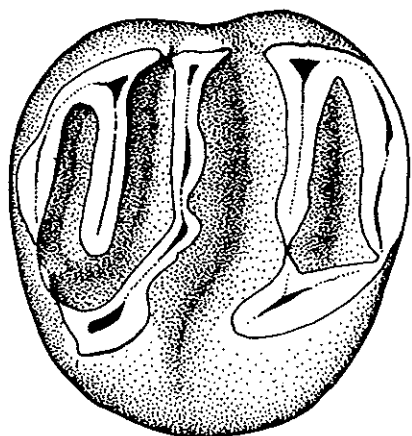


Figure 4.— Occlusal view of *Parasteiromys friantae* sp. nov., MPEF 5501, holotype, an isolated upper right molariform. Scale: 2mm.

Comments

The features that allow the assignment of this new species to the genus *Parasteiromys*, are: communication of hypo- with mesoflexus due to the absence of mure, lingual position of the hypocone respect of the protocone, and posteroloph higher than metaloph. A characteristic feature of *P. friantae* sp. nov., though not exclusive, is the disconnection between the lingual end of the metaloph and the posteroloph. This feature, seen also in living erethizontids, is here interpreted as a primitive condition of the molar pattern of the family (see Discussion). On this account, *P. friantae* may be the most primitive species of the genus. However, in view that it is known only by a single tooth, further information may probably modify its diagnosis.

DISCUSSION

Affinities of *Parasteiromys* AMEGHINO, 1904

Parasteiromys has unique features like the absence of mure, and the lingual position of the hypocone respect to the protocone, that render difficult the establishment of its phylogenetic relationships. However, the closest affinities of this genus seem to be with the genus *Protosteiomys*, in view of the following shared characters: scarce development of labial cusps, parallel or slightly oblique position of the protocone respect of the longitudinal axis of the tooth, a semicircle formed by the protocone with the anteroloph (more clearly seen in *P. uniformis*), and the trend to the early closing of the parafossette, (see comparisons and Fig. 3d). *Protosteiomys*, known through two Deseadan (late Oligocene) species of Patagonia, from La Flecha (Santa Cruz province) and Cabeza Blanca (Chubut province), was considered the most generalized erethizontid (Wood & Patterson, 1959). However, the trend towards the reduction of the labial cusps and the early closing of the parafossette do not seem to be primitive characters, while to date it is difficult to evaluate the evolutionary state of the remaining features shared by both genera. Consequently, *Protosteiomys* should not be taken as the most primitive representative of the family until further information about all the fossil genera is provided. On the contrary, a distinct metaconule and the disconnection of the metaloph from the posteroloph (only present in *P. friantae*) in *Parasteiromys* suggest the possibility that this genus is one of the most generalized porcupines.

THE MOLAR PATTERN OF ERETHIZONTIDAE. HOMOLOGIES AND PHYLOGENETIC IMPLICANCES

Pentalophodonty versus Tetralophodonty

Two hypotheses on the identification of the ancestral molar pattern of South American Hystricognathi are currently cited. One of them (Fig. 5a) proposes pentalophodont morphology, with the third and fourth lophs respectively homologous to the meso- and metalophs of the African Hystricognathi (Hoffstetter & Lavocat, 1970; Lavocat, 1973; Lavocat *in* Wood, 1974; Hoffstetter, 1975; Lavocat, 1976). This hypothesis was used to support the African origin of South American Hystricognathi. The other, supported by Wood & Patterson (Patterson & Wood, 1982 and references therein), dismisses that idea and proposes a tetralophodont ancestral pattern, in which the third loph corresponds to the metaloph, and consequently, it is not homologous of the third loph or mesoloph of the African Hystricognathi. According to this proposal, the pentalophodont occlusal design of South American hystricognaths is a derived condition acquired by the addition of a neomorphic crest, the neoloph, between meta- and posteroloph (Fig. 5b). Jaeger (1989), supporting in part the first of these hypothesis, sustains that the pentalophodonty is the ancestral molar pattern at least for some South American Hystricognathi, and that the third loph corresponds to the mesoloph, though its origin is different from that of African Hystricognathi. Thus, Jaeger suggests that the

dispersal of South American Hystricognathi took place prior to the development of their mesoloph. Buttler (1985) also questions the fourth loph of the pentalophodont South American hystricognaths as a neomorph loph, because it requires that para- and metacone be closer each other than proto- and hypoconid. Reig (1986) supported the pentalophodont ancestral pattern, though without further justifications. Vucetich & Verzi (1994), proposed a pentalophodont ancestral pattern, on the base of different evidences, in agreement with the homologies of Lavocat, though they do not affirm that it may be homologous to that of the African Hystricognathi. Recently, Bryant & McKenna (1995) argued that in both South American and African hystricognaths the third crest corresponds neither to the mesoloph nor to the metaloph, but to the mesolophule, and that a five crested molar pattern is the ancestral one for all the Hystricognathi. The mesolophule was defined by Flynn *et. al.* (1986: 8, 20) for the Chapattimyidae Baluchimyinae of the Miocene of Pakistan (Flynn *et. al.*, *op. cit.*; Flynn & Cheema, 1994; McKenna & Bell, 1997), as a crest occupying the third place from the anterior margin, extending from the metaconule up to the labial side of the tooth, between proto- and metaloph (Fig. 6a). In view of the aforementioned opinions, it is clear that the establishment of the homologies of the third and fourth lophs of South American Hystricognathi, and the identification of the ancestral molar pattern could not be defined yet.

The occlusal surface of *P. uniformis* and *P. friantae* sp. nov., as well as that of certain living porcupines, supplies additional significant data to clarify this problem.

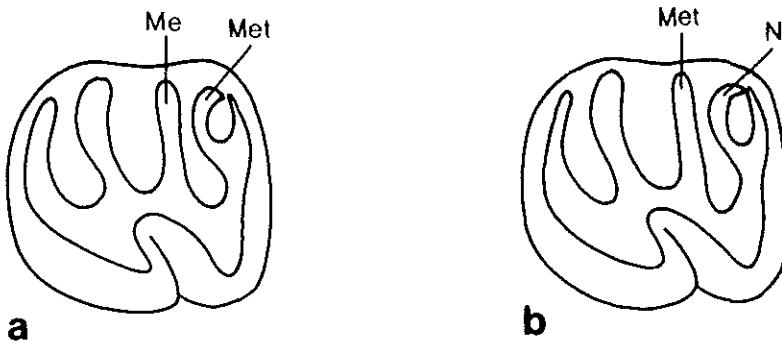


Figure 5.— Upper molar of a South American pentalophodont hystricognath illustrating homologies of the third and fourth lophs, a: after Lavocat; b: after Wood & Patterson. Abbreviations: Me: mesoloph; Met: metaloph; N: neoloph.

Homologies of cusps and the third loph

The identification of well developed molar cusps of diverse fossil and living erethizontids is the key to establish the homologies of the associated lophs. The scarcely worn teeth of *P. uniformis* and *P. friantae* sp. nov. show three labial cusps (anterior, middle and posterior) less developed than in other erethizontids but completely distinguishable. The anterior cusp may be homologous to the paracone, in view of its

position and relations, while there are two possible homologies for the middle and posterior cusps. These may correspond to mesostyle-metacone, or either to metacone respectively. The first of these two interpretations, mesostyle-metacone, is strengthened by the following points: if the middle cusp were the metacone, and the posterior one the neocone, the former would have shifted anteriorly from its primitive position in most generalized rodents, that is, facing the hypocone. According to Butler (*op. cit.*), this is functionally incorrect. Besides, in pentalophodont erethizontids, the middle cusp is always smaller and lower than the posterior one. Consequently, if the middle cusp were the metacone, this would have not only shifted forwardly, but also have reduced its size and height. If the metacone would have undergone all these changes the formation of a new cusp, the neocone, in the place left by the metacone, with similar characteristics to those originally shown by the latter, is at least surprising. It seems more parsimonious to suppose that the metacone kept its original position as well as its size and height, and that a new cusp, the mesostyle, appeared in a middle position, as it occurs in many African Hystricognaths (e.g. *Paraphiomys*, *Phiomys*, *Metaphiomys*). In this way, this interpretation leads to the same conclusions of Lavocat (1973) respect of labial cusps, rather than those of Wood & Patterson. Bearing in mind these homologies, the loph that joins para- and protocone is homologous to the protoloph (second loph), and the loph that extends lingually from the metacone (fourth loph) on, the end of which may either remain free -as in *P. friantae* sp. nov.- or join the posteroloph -as in most pentalophodont Hystricognathi-, is homologous to the metaloph. The loph that occupies the third position and is labially linked with the mesostyle may have two possible correspondences: mesoloph or mesolophule. The mesolophule of chapattimyid baluchimine - the probable nearest outgroup of the Hystricognathi (Flynn *et al.*, *op. cit.*; Jaeger, 1988) - extends labially from the hypocone through the metaconule, between the proto- and the metaloph. Conversely, the mesoloph, that occupies the same position between the proto- and the metaloph, is related lingually to the mesocone, a neomorphic cusp level with the mure. Therefore, the correct identification of a metaconule or mesocone is the key to establish the correct homology of the third loph of pentalophodont hystricognaths. In *Parasteiomys uniformis* and *P. friantae* sp. nov. a small but quite distinguishable cusp is placed in the anterolabial end or anterior ramus of the hypocone (see Description). This cusp is not placed in the position of the mesocone, due to the absence of mure. It occupies instead the position of the metaconule in the Baluchimyinae (fig. 6a). The metaconule has never been previously distinctly expressed in South American Hystricognathi. However, Wood (1949) cited a metaconule for *Plattipitamy*s, and later (Wood, 1974) he interpreted its presence in the middle portion of the third loph (its metaloph) in *Sallamys* Hoffstetter & Lavocat, 1970 and *Protosteiomys*, but there are not enough evidences to identify this cusp in these genera. Besides, *Parasteiomys* shows a metaconule, and not a mesocone, in a position more similar to that of Baluchimines than to Phiomorpha of Fayum in which this cusp is connected to the posterior cingulum rather than to the hypocone (Wood, 1968). In view of these reasons, the third loph of the porcupines is not homologous to the mesoloph, nor to the metaloph, but to the mesolophule of the Baluchimyinae - at least in its lingual portion - as proposed by Bryant & McKenna (*op.cit.*). The labial portion of the third loph, instead, seems to correspond to an extension of the mesostyle (see below), resulting in a third loph that, when completely formed, would have a mixed origin, represented lingually by the mesolophule and a

commonly smaller neomorphic labial portion.

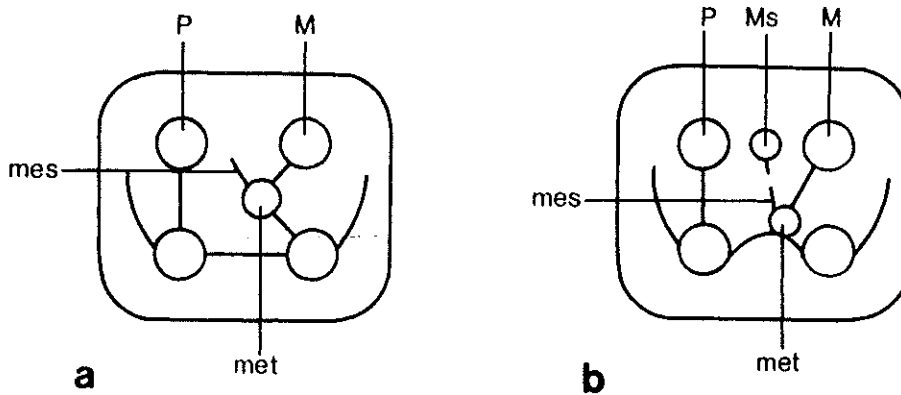


Figure 6.— a: hypothetical baluchimyine ancestral molar pattern modified from Flynn *et al.* (1986: fig. 7); b: hypothetical erethizontid ancestral molar pattern. Abbreviations: P: paracone; M: metacone; Ms: mesostyle; met: metaconule; mes: mesolophule.

The ancestral molar pattern of porcupines. Evolution of the occlusal design and phylogenetic aspects

Based on the similarities of the molar pattern, the Baluchimyinae were considered the probable sister group of the African Thryonomyioidea hystricognaths (Flynn *et al.*, 1986), or the Hystricognathi as a whole (Jaeger, 1988). Bryant & Mackenna (*op.cit.*) considered that the baluchimyines might be even a group of the Hystricognathiformes, a taxon including *Tsaganomys* and all living Hystricognathi. On this account, baluchimyines are adequate for the comparative analysis of molar morphology of Hystricognathi. Flynn *et al.* (*op.cit.*) proposed a hypothetical baluchimyine occlusal pattern characterized by a labially extended mesolophule from the metaconule, and a metaloph lingually directed from the metacone towards the hypocone and united to the metaconule (Fig. 6a). Among erethizontids, *P. friantae* sp. nov. shows an occlusal design with the metaloph directed towards the hypocone, like in the baluchimyine pattern. This, it may represent a morphology close to the primitive condition of the erethizontids. Several living porcupines have, in addition to this condition, an interrupted third loph, with a lingual portion related to the metaconule -here homologous to the mesolophule- and a labial portion, generally shorter, related to the mesostyle (The Fig. 7 show different development stages of both portions). The possible formation process of the third loph may be then inferred: it may grow lingually from the mesostyle and labially from the metaconule. Based on these observations, the hypothetical ancestral molar pattern for the erethizontids is proposed (see Fig 6b), with the fourth crest or metaloph disconnected from the posteroloph and oriented towards the hypocone, reaching the metaconule; and with the third loph represented by a lingual portion united to the metaconule and a labial portion related to the mesostyle. This pattern is here named "prementalophodont" and basically differs from the primitive molar pattern proposed for the Baluchimyinae by the presence of the mesostyle, smaller development of the metaconule, and the differentiation of a distinct lingual sinus

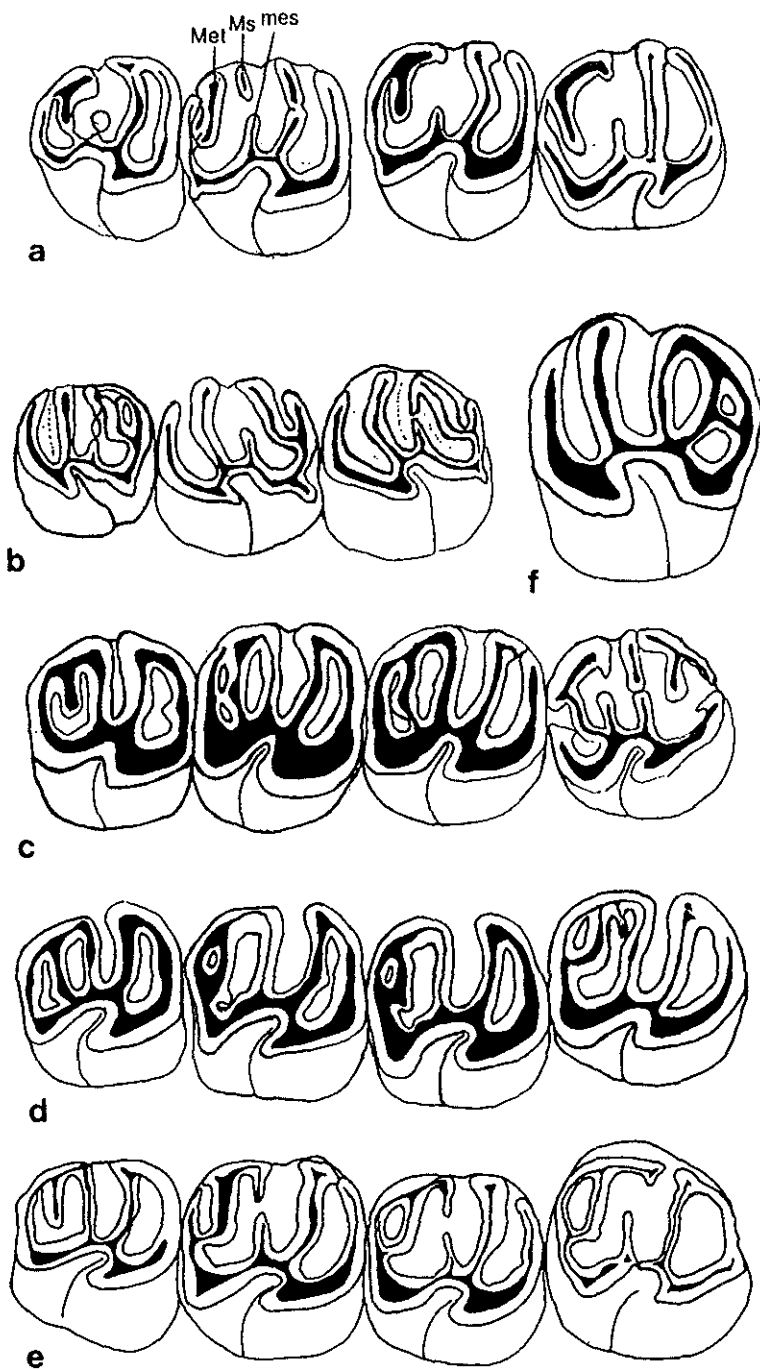


Figure. 7.— Lingual-occlusal views of upper molariforms of living erethizontids. a: *Coendou prehensilis* (LINNAEUS, 1758), specimen MNRJ 4923, right P4-M3; b: *Coendou* sp., specimen MNRJ 2670, left DP4-M2; c: *Coendou* sp., specimen MNRJ 2665, right P4-M3; d: *Coendou* sp., specimen MNRJ 34504, right P4-M3; e: *Coendou prehensilis* (LINNAEUS, 1758), specimen MG 12494, right P4-M3; f: *Coendou bicolor* (TSCHUDI, 1844), specimen MNRJ 4915, left M3. Abbreviations: Met: metaloph; Ms: mesostyle; mes: mesolophule.

or hypoflexus. Likewise, the "prepentalphodont" pattern differs from most pentalphodont Hystricognathi in the disconnection of the metaloph from the posteroloph, the persistence of the metaconule and the incomplete development of the third loph. Finally, this pattern is similar to that of North African *Protophiomys* which has been considered either early phiomyid thryonomyoid (Jaeger, 1988; Jaeger *et.al.*, 1985) or a chapattimyid of baluchimyinae affinity (Flynn *et. al.*, 1986).

Erethizontids demonstrate how a pentalphodont pattern (e.g. *Steiromys duplicatus*, *Parasteiromys uniformis*, *Protosteiromys medianus*) may derive from one "prepentalphodont", the evolution of which would imply the following steps: 1) formation of the third loph both from the metaconule -its lingual portion- and the mesostyle -its labial portion-, resulting in a completely developed third loph; 2) the progressive disconnection of the lingual end of the metaconule's metaloph and its orientation towards the posteroloph until its complete union with this latter loph (Fig. 8 a, b, c). Successive states of this process are observed in certain living erethizontid (Fig. 7 a, b, c, d, e and f), in which intermediate conditions, represented by the metaloph connected both to the mure and to the posteroloph, and different states of the development of the third loph, are showed (see Figs. 7 f, e; and 8 b).

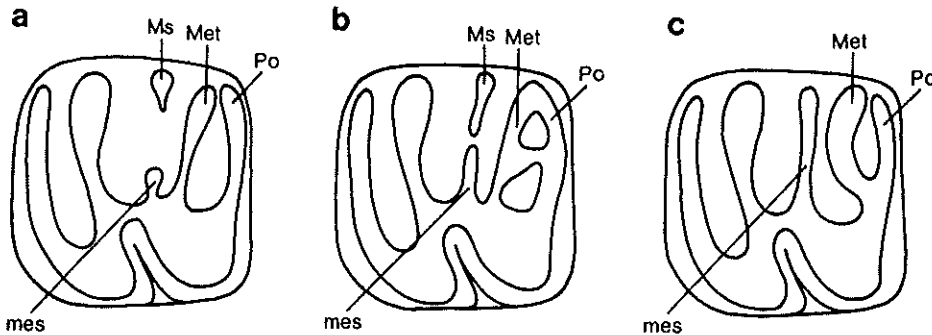


Figure 8.— Schematic illustration of supposed transforming states in the evolution of the upper molar pattern of Erethizontidae. a: primitive state, "prepentalphodont" design, with metaloph directed towards the hypocone; and the third loph incompletely developed, with a lingual portion united to the metaconule and a labial portion united to the mesostyle; b: intermediate state, with the metaloph united both to the mure and to the posteroloph, and the third loph more developed; c: derived state, pentalphodont design, with the metaloph connected with the posteroloph and the third loph fully developed. Abbreviations: Met: metaloph; Ms: mesostyle; mes: mesolophule; Po: posteroloph.

In sum, the ancestral molar pattern of erethizontids does not respond to those traditionally proposed, i.e. tetralophodont, or pentalphodont in which the metaloph is always united to the posteroloph and the third loph corresponds to the mesoloph (Lavocat, in Wood, 1974; Vucetich & Verzi, 1994: 64). It may responds instead, to a pattern with the metaloph disconnected from the posteroloph and the third loph in growing process. Erethizontids seem to have a more primitive molar pattern, closer to that of the Baluchimyinae than to any other Hystricognathi. This idea agrees with the recent proposal of Bryant & McKenna (*op. cit.*) placing erethizontids in a basal position respect of the remaining Hystricognathi. As these authors said: "because of the

possibility that Erethizontidae may share a common ancestor with other Hystricognathi in Asia (because the basal node of Hystricognathi is not fully resolved), the possibility exists that the dispersal of porcupines to New World was not from an African ancestor" (Bryant & McKenna, 1995: 36). The dispersal of Erethizontidae would have been prior to the development of third loph as Jaeger (1988) suggested for all Hystricognathi.

The homology of the third loph of Hystricognathi with the mesolophule depends on the identification on the metaconule. Since this cups is recognized in erethizontids, they are the only group in which the mesolophule may be undoubtedly verified. But this homology must not be extensive to all the families of the suborder as Bryant & McKenna stated until the presence of metaconule could be checked in each particular group. If the Baluchimyinae, with mesolophule, represent the nearest outgroup of Hystricognathi, or even a member of Hystricognathiformes, this would not support the presence of this loph in all Hystricognathi.

CONCLUSIONS

Parasteiromys AMEGHINO, 1904, considered in this study a valid Erethizontidae genus, probably represents one of the most generalized porcupines, the closer affinities of which seem to be with the genus *Protosteioromys*.

The molar pattern of the species of *Parasteiromys* and of certain living erethizontids leads to interpret the third loph of erethizontids as a mixed structure; its lingual portion would be homologous to the mesolophule of Baluchimyinae.

The inferred ancestral molar pattern of erethizontids would not respond to any of the morphologies traditionally proposed as ancestral for South American Hystricognathi, but to a "prepentalphodont" pattern characterized by the presence of a metaloph disconnected from the posteroloph and directed towards the hypocone, and the third loph in rising process. This pattern is closer to that of Baluchimyinae from the Miocene of Pakistan, a possible sister group of Hystricognathi, than to the remaining members of the suborder. Erethizontids would have separated from the remaining Hystricognathi before acquiring the typical pentalphodont pattern. This fact agree with the early divergence and basal position of the family within the suborder, and supports the hypothesis of an independent arrival of the family in South America.

The inferred evolution process of the erethizontid molars may illustrate the possible progressive modifications that enabled the establishment of the molar pattern in other lineages of South American Hystricognathi.

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