

Hypsosteiromys (Rodentia, Hystricognathi) from the Early Miocene of Patagonia (Argentina), the only Erethizontidae with a tendency to hypsodonty

Hypsosteiromys (Rodentia, Erethizontidae), un porc-épic très particulier du Miocène inférieur de l'Amérique du Sud

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Abstract

Hypsosteiromys is the only New World porcupine that shows a tendency to hypsodonty. It is recorded exclusively from the Colhuehuapian Age (Early Miocene) of central Patagonia (Argentina). In addition to the type species, a second one, *Hypsosteiromys nectus* (AMEGHINO, 1902), is recognized, from the southern cliff of Colhuehuapi Lake (Chubut province). It differs from the type species in the lesser development of the anterolabial and posteroflexid notches of the m1-3, shorter p4 and dp4, and more slender incisors. Dental morphology suggests that the species of *Hypsosteiromys* lived in more open areas than most fossil and living Erethizontidae. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Hypsosteiromys est le seul porc-épic sudaméricain qui montre une tendance à l'hypsodontie. Il est connu exclusivement dans le Colhuehuapien (Miocène inférieur) du centre de la Patagonie. Une seconde espèce, en plus de l'espèce type, est reconnue: *Hypsosteiromys nectus* (AMEGHINO, 1902), qui provient des reliefs Sud du Lac Colhué Huapi (Chubut). Cette espèce diffère de l'espèce type par un développement moindre des 'notches' antérolabiales et des postéroflexides des m1-3, p4 et dp4 plus courts, et des incisives plus graciles. La morphologie dentaire suggère que les espèces d'*Hypsosteiromys* auraient vécu dans des régions plus ouvertes que la plupart des Erethizontidae fossiles et vivants. © 2002 Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Rodentia; Erethizontidae; Systematics; Palaeoenvironments; Early Miocene; Patagonia; Argentina

Mots clés: Rodentia; Erethizontidae; Systématique; Paléoenvironnement; Miocène inférieur; Patagonie; Argentine

Abbreviations: MLP, Museo de La Plata, Argentina; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina; MMP, Museo Municipal de Ciencias Naturales 'L. Scaglia', Mar del Plata, Argentina; MNHN, Museum National d'Histoire Naturelle (Paris); MPEF, Museo Paleontológico Egidio Feruglio, Argentina; DAP, anteroposterior diameter; DTA, anterior transverse diameter; DTP, posterior transverse diameter; DT, maximum transverse diameter

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1. Introduction

The caviomorph, the New World Hystricognathi, are immigrants in South America, and they are first recorded from the Tinguiririca faune which is at least old as 31.5 Ma (Vucetich et al., 1999). Among them, the Erethizontidae (the New World porcupines) are probably a basal clade of this suborder, which would have emigrated to South America independently of the other New World Hystricognathi (Woods, 1972; Bugge, 1971, 1974; Bryant and McKenna, 1995; Candela, 1999, 2000). The living North American porcupines are represented by a single semi-arboreal species, *Erethizon dorsatum*, distributed from northern Mexico to Alaska and Canada (Roze, 1989). The living porcupines of Neotropica are essentially restricted to the Brazilian Subregion (sensu Herskovitz, 1958), which extends from Uruguay to middle America. They are strictly adapted to arboreal life and inhabit different types of forests, as well as more open areas such as the cerrado, high caatinga, Venezuelan llanos, and Bolivian chaco (Emmons, 1997; Anderson, 1997).

Erethizontids are first known from the Late Oligocene of Argentina and Bolivia (Wood and Patterson, 1959; Candela, 2000). According to the fossil record, they lived in Patagonia (Argentina) at least up to the Middle Miocene (Vucetich et al., 1993), reaching their highest diversity during the Early Miocene (Colhuehuapian; Candela, 1999, 2000). During the Colhuehuapian, porcupines showed, for once in their history, an increase in cheektooth crown height. This is an exclusive feature of the genus *Hypsosteiromys* PATTERSON, 1958 and makes this porcupine one of the most easily recognizable erethizontids.

In the present paper, the species *Hypsosteiromys nectus* (AMEGHINO, 1902) is revalidated, the type specimens of ‘*Steiromys*’ *nectus*, ‘*S.*’ *tabulatus* and ‘*S.*’ *axiculus* are figured for the first time, and the paleoenvironmental significance of this genus is evaluated.

2. Materials and methods

Terminology of cusps, flexi/ids, and loph/ids of upper and lower cheekteeth follows the nomenclature of Candela (1998, 1999). Illustrations were made with the camera

lucida of a Wild M-5 stereoscope. All measurements are in millimetres and were taken with a digital caliper with 0.1 mm precision.

In order to determine the number of species within the supposedly monospecific genus *Hypsosteiromys* (PATTERSON, 1958), we used the multivariate method of cluster analysis (Johnson, 1998). The ‘unweighted pair-group average’ method using euclidean distances was applied. The multivariate analysis was used as an additional source of information for qualitative characters.

Six juvenile specimens (Table 1) were analysed. Four only have the deciduous premolar (dp4): MACN A 52-176, MPEF 5798a, MPEF 5798b, and MPEF 5798c. Two have dp4-m2: MACN A 52-177 and MLP 84-III-10-1. A joining cluster analysis was developed with DAP and DTA of dp4. Another joining cluster analysis was performed on 11 adult specimens (MACN A 52-172, MACN A 52-175A, MACN A 52-175B; MNHN, col. 50, MMP 113, MLP 82-V-2-47a, MLP 82-V-2-47b, MLP 82-V-2-47c, MLP 83-VII-3-39, MPEF 5802 a, MPEF 5802 b) using the variables DAP and DTA of permanent premolars (p4) (Table 2). Analyses were made with the software STATISTICA (StatSoft, Inc., 1996).

3. Previous work

Ameghino (1902: 109–110) recognized within the genus *Steiromys* AMEGHINO, 1887, in which all fossil Patagonian erethizontids were then grouped (i.e. *S. annectens*, AMEGHINO, 1901, *S. principalis*, AMEGHINO, 1901, *S. detentus*, AMEGHINO, 1887, and *S. duplicatus*, AMEGHINO, 1887), four new species: ‘*Steiromys*’ *axiculus*, ‘*S.*’ *tabulatus*, ‘*S.*’ *nectus*, and ‘*S.*’ *segregatus*. Later, Patterson (1958) created the genus *Hypsosteiromys* to group ‘*S.*’ *axiculus*, ‘*S.*’ *nectus* and ‘*S.*’ *tabulatus*, which he considered synonymous, keeping as type species *H. axiculus*. It is noteworthy that a few years earlier Patterson himself (unpublished catalogue, 1952) had recognized, in agreement with Ameghino (1902), the validity of *H. nectus*, but he did not state this idea in his paper of 1958. In her dissertation, Candela (2000) gave the arguments for the validity of *H. nectus* (AMEGHINO, 1902) and proposed a diagnosis for each of the two species of the genus.

Table 1
Mandibular and dental measurements of juvenile specimens of *H. nectus* and *H. axiculus* (AMEGHINO, 1902). (*) Type specimen of *H. nectus*. The others are *H. axiculus*.
Mesures mandibulaires et dentaires des exemplaires juvéniles d’*Hypsosteiromys nectus* (remarqués avec un astérisque) et *H. axiculus* (AMEGHINO, 1902).

Specimens	DT incisor	DAP incisor	DAP dp4	DTA dp4	DAP ml	DTA ml	Mandibular height at dp4	Mandibular height at dp4ml	Mandibular height at ml
MACN A 52-177*	2.46	3.1	7.1	3.3	5.0	4.3	12.08	11.13	10.53
MLP 84-III-10-1	3.42	3.73	8.5	3.6	6.4	4.8	14.64	12.76	11.34
MACN A 52-175A			8.2	3.9					
MPEF 5798a			8.0	4.0					
MPEF 5798b			8.4	4.1					
MPEF 5798c			7.9	3.7					

Table 2

Mandibular and dental measurements of adult specimens of *H. nectus* and *H. axiculus* (AMEGHINO, 1902). (*) Specimen of *H. nectus*. Mesures mandibulaires et dentaires des exemplaires adultes d'*H. nectus* (remarqués avec un astérisque) et *H. axiculus* (AMEGHINO, 1902).

Specimens	DT Incisor	DAP incisor	DAP p4	DTA p4	DAP m1	DTA m1	Mandibular height at p4.	Mandibular height at p4-m1
MACN A 52-171	3.45	3.65			5.60	4.64		
MACN A 52-172*			7.1	5.2	5.3	4.9		
MACN A 52-175A*			7.4	4.3				
MACN A 52-175B			8.9	5.3				
MNHN col. 50*			7.0	4.4				
MMP 113			8.2	4.3	6.07	4.90	6.30	5.30
MLP 82-V-2-47a			8.7	5.4				
MLP 82-V-2-47b			8.6	5.3				
MLP 82-V-2-47 c			8.4	5.0				
MLP 83-VII-3-39	3.69	4.13	8.5	5.2				
MPEF 5802a			8.4	5.1				
MPEF 5802b			8.6	5.2				
MLP 85-VII-3-4*					5.9	4.7		

4. Systematic paleontology

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Family ERETHIZONTIDAE Thomas, 1897

Genus *Hypsosteiromys* PATTERSON, 1958

Locality and horizon – Gran Barranca, southern cliff of Lake Colhué Huapi, and Bryn Gwyn, Chubut Province, Argentina; Sarmiento Formation, Colhué Huapi and Trelew Members, Colhuehuapian Age, Early Miocene.

Hypsosteiromys nectus (AMEGHINO, 1902) nov. comb.

Fig. 1; Fig. 2a, d

Steiromys nectus AMEGHINO, 1902: 109.

Steiromys tabulatus AMEGHINO, 1902: 109–110.

Hypsosteiromys axiculus PATTERSON, 1958: 3. *Partim*

Type – MACN A 52-177, right mandibular fragment with the incisor root, and dp4-m2 series (m2 not completely erupted).

Hypodigm – The type and the following specimens: MACN A 52-172, left mandibular fragment with p4-m3 (lectotype of '*S.*' *tabulatus* AMEGHINO, 1902 sensu Patterson, 1958); MACN A 52-175A, isolated right p4; MNHN col 50, isolated left p4; MLP 85-VII-3-4, isolated left m1 or 2.

Locality and horizon – Gran Barranca, southern cliff of Lake Colhué-Huapi, Chubut Province (Argentina); Sarmiento Formation, Colhué Huapi Member, Early Miocene (Colhuehuapian Age).

Revised diagnosis – *H. nectus* differs from *H. axiculus* in the lesser development of the anterolabial notches of the m1-3, shallower posteroflexids and smaller DAP of p4 and dp4, and smaller DT of the incisor.

Description – m1-2 of this species display low variability and essentially the same pattern as the type specimen (MACN A 52-177). Mandibular features are better preserved in this specimen, which is described below.

The dp4 is elongate anteroposteriorly with DTA less than DTP. The occlusal pattern is tetralophodont, with lophids somewhat oblique posterolingually. The metalophulid has a

small 'spur' directed into the anterofossettid. This lophid is semicircular and extends from the protoconid to the lingual side of the tooth, where it merges with the lingual end of the second lophid. The second lophid is anterolabially–posterolingually oblique and has a small 'spur' near the lingual end projecting into the anterofossettid. As its lingual end is not connected with a cusp, it is difficult to determine whether it is a metalophulid II or a mesolophid. The anterofossettid is widest anteroposteriorly, the mesoflexid is moderately wide and the posterofossettid is clearly closed. Hypoconid and protoconid are separated by a wide hypoflexid; the ectolophid is more or less parallel to the anteroposterior axis of the tooth. The hypolophid is slightly oblique anterolabially–posterolingually, and the posterolophid is semicircular.

The m1 is scarcely worn, with the dentine exposed almost exclusively on the areas of the protoconid and hypoconid. This tooth differs from the dp4 in being shorter and having DTA and DTP subequal, and the hypoflexid and the ectolophid shorter. The metalophulid has a very superficial anterolabial notch. Both the antero- and the posterofossettid are clearly closed and the borders of the mesoflexid are subparallel.

The m2 is in eruption, so it has no wear. It differs from m1 in the presence of cusps, which are scarcely developed. The hypoconid is the tallest and largest cusp of the tooth. The posteroflexid is almost closed. There is a small but clearly distinguishable cusp of uncertain homologies laterolingual to the hypoconid. On the occlusal surface, the enamel is crenulate with rugosities similar to small cusplules.

The incisor is deeper than wide, gracile relative to the size of cheekteeth, and its anterior face is convex.

The preserved portion of the mandible (Fig. 1) is shallow and elongate relative to the size of the cheekteeth. The diastema is long and the retromolar fossa (sensu Woods and Howland, 1979) is narrow and shallow. The base of the coronoid process is lateral to the m2, though its inclination and development are unknown. The notch for the medial masseteric tendon (sensu Woods, 1972) is below the

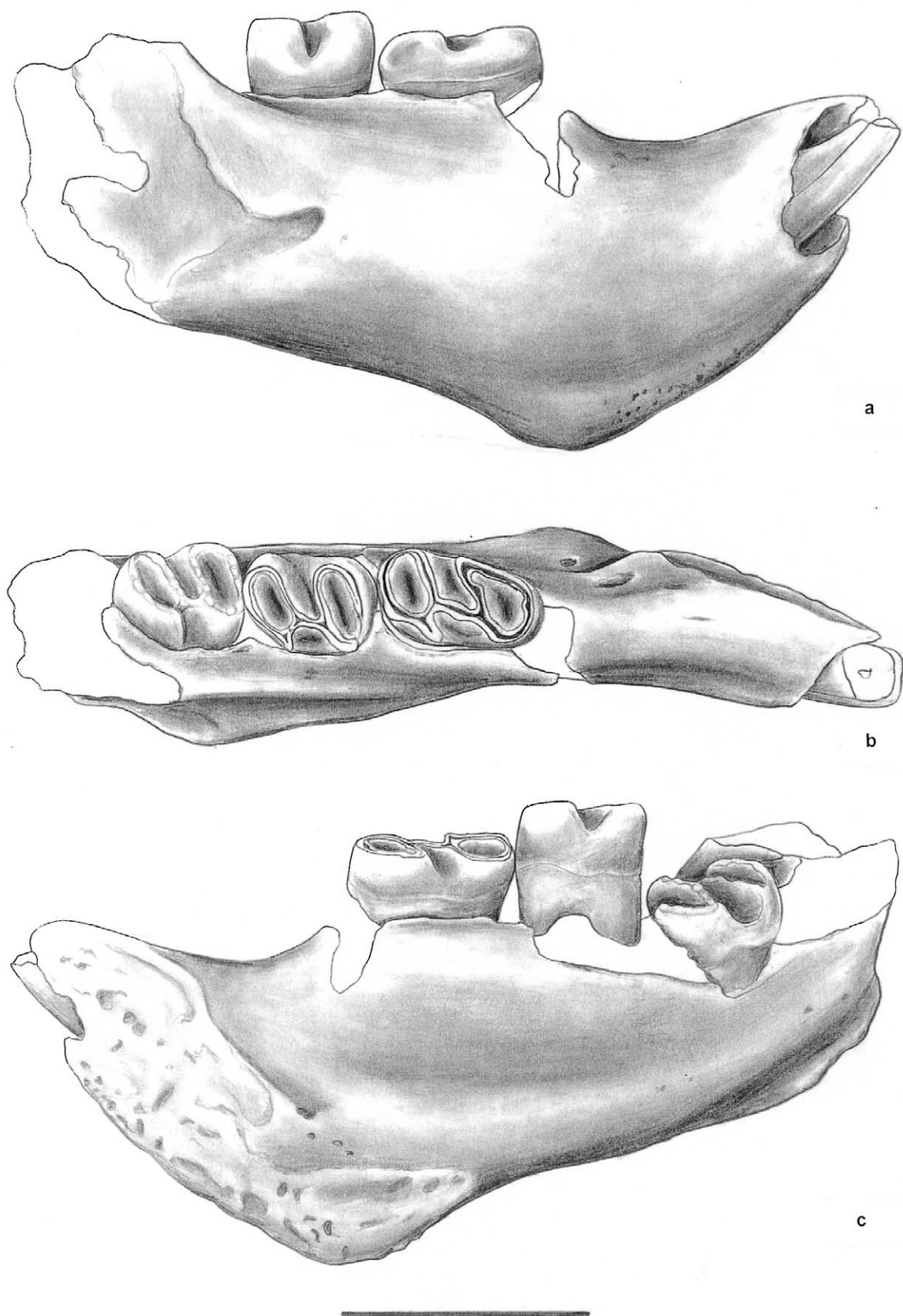


Fig. 1. Labial (a), occlusal (b) and lingual (c) views of specimen MACN A 52-177, type of *H. nectus* (AMEGHINO, 1902) with dp4-m2. Scale: 1 cm.
 Vues labiale (a), occlusale (b) et linguale (c) de l'exemplaire MACN A 52-177, type d'*H. nectus* (AMEGHINO, 1902) avec dp4-m2. Échelle: 1 cm.



Fig. 2. Oclusal views of lower cheekteeth of *H. nectus* (a, d) and *H. axiculus* (b, c); a. Right dp4-m2, MACN A 52-177 (type); b. Right dp4-m2, MLP 84-III-10-1; c. Right m1-3, MACN A 52-171 (type); d. Left p4-m3, MACN A 52-172 (lectotype of '*S.*' *tabulatus* AMEGHINO, 1902). Scale: 2 mm.

Vues occlusales des molariformes inférieures d'*H. nectus* (a, d) et d'*H. axiculus* (b, c); a. dp4-m2 droites, MACN A 52-177 (type); b. dp4-m2 droites, MLP 84-III-10-1; c. m1-3 droites, MACN A 52-171 (type); d. p4-m3 gauches, MACN A 52-172 (lectotype de '*S.*' *tabulatus* AMEGHINO, 1902). Échelle: 2 mm.

anterior limit of the m1, at approximately half the mandibular height. It is subhorizontal and continues backward with the scarcely developed lateral crest. This latter is directed posterodorsally to the base of the coronoid process. The masseteric crest limits a shallow masseteric fossa. The mandibular symphysis extends up to the posterior end of the dp4.

Other specimens – The p4 (MACN A 52-172, MACN A 52-175A, MNHN col. 50; Fig. 2d) is subrectangular in

occlusal view, with DAP greater than DT. The protoconid is more extended anteroposteriorly than the hypoconid. The posterolingual end of the protoconid area extends lingually toward the mesolophid, which is more or less transverse with respect to the anteroposterior axis of the tooth. The lingual end of this lophid merges with the lingual end of the anterolophid, closing the anterofossettid lingually. The ectolophid is short, and slightly oblique. The hypolophid runs anterolabially–posterolingually and its lingual end rises

smoothly toward a small entoconid. The convex posterolophid extends from the hypoconid; its lingual end curves slightly forwardly not reaching the hypolophid and, consequently, the posteroflexid is still evident. The hypoflexid is wide and in MACN A 52-175 A contacts the posteroflexid through a very narrow and superficial furrow.

In MLP 85-VII-3-4 (an isolated left m1 or 2), the posteroflexid is completely closed and the anterolabial notch is scarcely evident.

5. Validity of *Hypsosteiromys nectus* (AMEGHINO, 1902)

5.1. Qualitative characters

In the molar of the type specimen of *H. nectus* (MACN A 52-177; Fig. 2a), the anterolabial notches are more superficial than those of the type specimen of *H. axiculus* (MACN A 52-171; Fig. 2c) and the posteroflexid is closed in m1 and almost closed in m2. These two characters change with wear, becoming more superficial and closed, respectively, in more worn cheekteeth. Consequently, it may be expected that the type of *H. nectus*, a younger specimen (with m2 in eruption) than the type of *H. axiculus* (with m2 erupted and m3 in eruption), would have a more open posterolophid and deeper anterolabial notches. However, just the contrary is observed. Accordingly, in the specimen MLP 84-III-10-1 (Fig. 2b) of *H. axiculus*, the anterolabial notches are clearly deeper, and the posteroflexids clearly more open than the type of *H. nectus*, despite both showing the same eruption stage of their molars (m2 erupted). This strengthens the diagnostic significance of both characters.

Likewise, the incisors of the Erethizontidae increase in size up to approximately the time of the loss of the dp4 (about two years old, Candela 2000 and literature therein). Consequently, this feature has to be analysed in specimens with the same ontogenetic stage. The incisor of the type of *H. nectus* is thinner than that of specimen MLP 84-III-10-1 (Table 1). Additionally, in the type of *H. nectus*, the symphysis area is placed more anteriorly in labial view, with respect to the dp4 than in specimen MLP 84-III-10-1, in which the symphysis area is level with the dp4. This is why the mandibular height, at this level, differs markedly in both specimens. The height of the mandible of both specimens is also different at the m1 level. However, because the most anterior part of the mandible of the type of *H. axiculus* is not preserved, these differences are not included in the diagnosis of *H. nectus* until more complete mandible remains are available.

5.2. Quantitative characters

In order to test the previous results (i.e. the existence of two species, *H. nectus* and *H. axiculus*, within the genus *Hypsosteiromys*) cluster analyses were performed (see Ma-

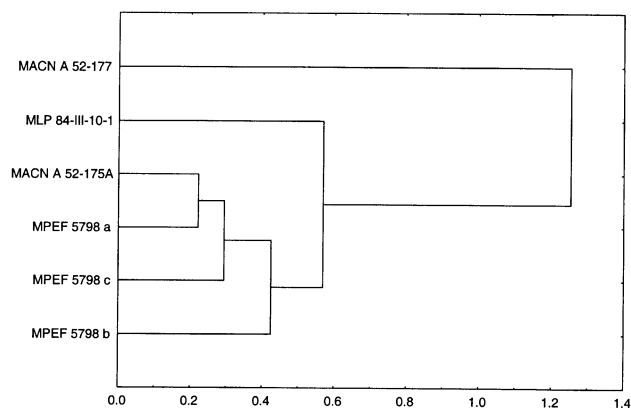


Fig. 3. Dendrogram obtained from the cluster analysis of juvenile specimens.

Dendrogramme obtenu à partir de l'analyse des conglomérats hiérarchiques agglomératifs des exemplaires juvéniles.

terials and methods). The cluster analysis of the juvenile specimens (Fig. 3) separates MACN A 52-177 (type of *H. nectus*) from the remaining specimens. This separation shows the smaller DTA and DAP of dp4 of the type specimen of *H. nectus* with respect to the other specimens (Fig. 4). These latter are assigned to *H. axiculus* because they have open posteroflexids and well-developed anterolabial notches (see Qualitative characters).

The dendrogram obtained from the cluster analysis of adult specimens (Fig. 5) separates two major groups: one comprised of MACN A 52-172, MACN A 52-175A and MNHN col 50; the other group, of the remaining specimens. This separation shows the smaller size of p4 of the first three specimens (Fig. 6). Student's *t*-test shows that only DAP of p4 is statistically significantly different between the two groups ($P < 0.01$). The smaller DAP of the p4 of the first three adult specimens seems to agree with the smaller DAP of the dp4 of the type of *H. nectus*. The remaining adult specimens, besides having a larger p4, show features of *H. axiculus* (e.g. anterolabial notches and well-developed posteroflexids). In short, the groups obtained from cluster analyses agree with the results of the qualitative characters.

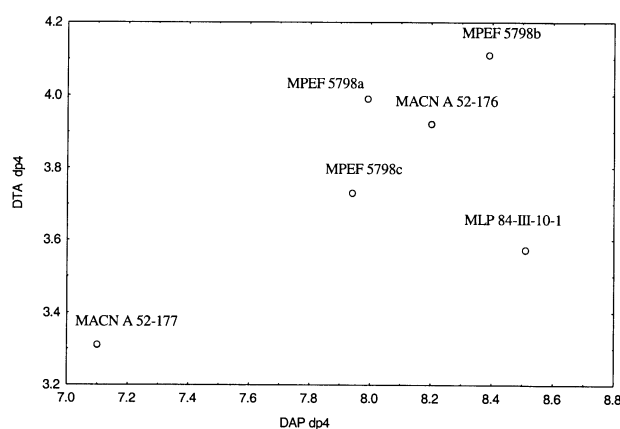


Fig. 4. Scatterplot of DAP and DTA of the dp4 of juvenile specimens. Scatterplot du DAP et DTA du dp4 des exemplaires juvéniles.

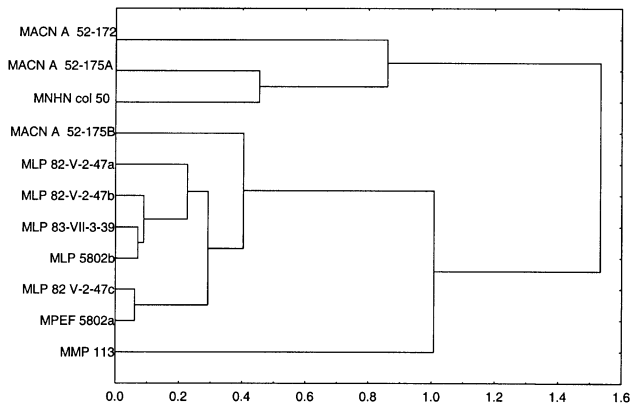


Fig. 5. Dendrogram obtained from the cluster analysis of adult specimens. Dendrogramme obtenu à partir de l'analyse de conglomerat hiérarchique des exemplaires adultes.

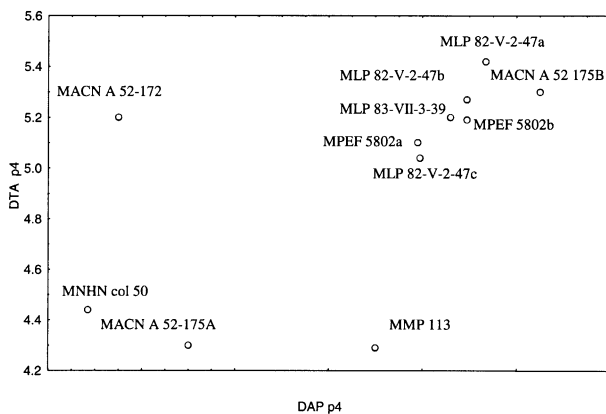


Fig. 6. Scatterplot of DAP and DTA of the p4 of adult specimens. Scatterplot du DAP et DTA du p4 des exemplaires adultes.

6. Paleoenvironmental significance

The cheekteeth of erethizontids are medium to large sized, with thick enamel layers, primitive occlusal patterns (Candela, 1999), and cusps that may be distinguished until late stages of wear (Candela, 1998). They are markedly brachydont except for the genus *Hypsosteiromys*. The slight tendency to hypsodonty of *Hypsosteiromys* is a key feature used to estimate, in comparison with living porcupines, its probable feeding adaptations and its paleoenvironmental significance.

Traditionally the presence of erethizontids in the fossil record has been linked to warm, forested environments (Pascual and Ortiz Jaureguizar, 1990). However, Candela (2000) pointed that, since porcupines live in such different environments as tropical forest and arctic tundra, the paleoenvironmental significance of fossil erethizontids has to be based on rigorous studies of feeding strategies and/or locomotive habits.

Living Neotropical porcupines represent one of the several radiations of mammals adapted to arboreal life, inhabiting different types of forests (e.g. deciduous, ever-

green, gallery, Atlantic forests; Emmons, 1997). Some species, such as *Coendou prehensilis*, also live in more open areas such as the cerrado, the caatinga, the Venezuelan llanos (Emmons, 1997), and the Bolivian chaco (Anderson, 1997). Surprisingly their cheekteeth are as markedly brachydont as those of species restricted to forest areas. The very few studies on the natural history of the Neotropical species point to a feeding habit based mainly on fruits, seeds, buds and soft leaves (Charles-Dominique et al., 1981; Miles et al., 1985; Emmons, 1997).

In contrast, *Erethizon dorsatum*, the single living North American porcupine, is semi-arboreal and is mainly distributed in temperate woodlands, but also occurs in the taiga forests, the tundra (Roze, 1989) and desert habitats (Sweitzer and Berger, 1993; Jones and Genoways, 1969). Accordingly with these environments, *E. dorsatum* is a generalist, feeding mainly on bark, coniferous leaves and seeds (Woods, 1984; Roze, 1989), all of which are harder than the soft fruits and leaves on which Neotropical species feed. Their cheekteeth are essentially as brachydont as those of Neotropical species.

According to Candela (2000), the cheekteeth of *Hypsosteiromys*, not only are mesodont (Mones, 1982), but also have reduced cusps, forming an occlusal surface that suggests a more abrasive diet than that of the living species, one that is probably related to more open areas than Neotropical, tropical and subtropical forests. The trend in *Hypsosteiromys* to increase the crown height may be an adaptive response related to a diet of harder and more abrasive food, available in even more open environments than those in which *C. prehensilis* currently live.

In sum, the cheekteeth morphology of *Hypsosteiromys* suggests that this erethizontid more probably lived in open environments than in forested areas. This agrees with the paleoenvironment suggested for central Chubut during the Colhuehuapian, characterized by forested areas mixed with open areas, with optimum balance for park savanna (Pascual, 1986; Pascual et al., 1996). Other coeval mammals recorded from the same localities also display a hypsodonty trend, which was interpreted as an adaptation to open environments, strengthening this paleoenvironmental inference; they are the marsupials *Patagonia* and *Argyrolagidae* gen. et sp. nov., and the rodents *Willidewu*, *Protadelphomys*, *Cephalomyopsis*, and *Acaremys* (Pascual and Carlini, 1987; Pascual et al., 1989; Vucetich and Verzi, 1991; Vucetich and Verzi, 1994; Vucetich, 1985).

Another factor that may have influenced the development of hypsodonty in these groups from the Lower Miocene of central Chubut is the dust added to the food. An important component of the sedimentary sequence of Gran Barranca is volcanic ash, that may have been deposited on vegetation in a dry and windy climate (Kay et al., 1999). This particular combination of conditions is what may have triggered this single tendency to hypsodonty in erethizontids.

. Biblio non appelée

(Patterson, 1952)

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