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A new porcupine (Rodentia, Hystricognathi, Erethizontidae) from the Early and Middle Miocene of Patagonia

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Abstract. A new erethizontid, *Branisamyopsis australis* gen. et sp. nov., from Colhuehuapian sediments (early Miocene) of the Sarmiento Formation cropping out at Gran Barranca, Chubut Province, Argentina, is described. The new genus is also identified in the middle Miocene (Collón Cura Formation) at Cañadón del Tordillo (Neuquén, Argentina). The comparative study of the mandibular and tooth morphology of erethizontids indicates that *Branisamyopsis australis* gen. et sp. nov. is closely related to Patagonian porcupines *Eosteiromys* Ameghino and *Steiromys* Ameghino. *Branisamyopsis australis* gen. et sp. nov. shows that extinct erethizontids reached their greatest taxonomic diversity during the Colhuehuapian. The cheek-tooth morphology of Patagonian Colhuehuapian erethizontids could correspond to different dietary adaptations. The temporal and geographic distribution and the phylogenetic affinities of *Branisamyopsis*, *Eosteiromys* and *Steiromys* suggest that Patagonia was a marginal area of differentiation for the family, unconnected with the radiation of living porcupines.

Resumen. UN NUEVO PUERCO ESPÍN (RODENTIA, HYSTRICOGNATHI, ERETHIZONTIDAE) DEL MIOCENO TEMPRANO Y MEDIO DE PATAGONIA. Se describe un nuevo eretizóntido, *Branisamyopsis australis* gen. et sp. nov., proveniente de sedimentos colhuehuapenses (Mioceno temprano) de la Formación Sarmiento aflorante en Gran Barranca (Chubut, Argentina). El nuevo género se identifica también en el Mioceno medio (Formación Collón Cura) de Cañadón del Tordillo (Neuquén, Argentina). El estudio comparativo de la morfología mandibular y dentaria de los eretizóntidos indica que *Branisamyopsis australis* gen. et sp. nov. está cercanamente vinculada a los puerco espines patagónicos *Eosteiromys* Ameghino y *Steiromys* Ameghino. *Branisamyopsis australis* gen. et sp. nov. muestra que los eretizóntidos extintos alcanzaron su mayor diversidad taxonómica durante el Colhuehuapense. La morfología dentaria de los eretizóntidos patagónicos colhuehuapenses podría corresponder a diferentes adaptaciones dietarias. La distribución temporal y geográfica y las afinidades filogenéticas de *Branisamyopsis*, *Eosteiromys* y *Steiromys* sugieren que Patagonia sirvió como un área marginal de diferenciación para la familia no vinculada con la radiación de puerco espines vivientes.

Key words. Rodentia. Erethizontidae. Systematics. Early and Middle Miocene. Patagonia. Argentina.

Palabras clave. Rodentia. Erethizontidae. Sistemática. Mioceno Temprano y Medio. Patagonia. Argentina.

Introduction

Erethizontidae (the New World porcupines) is a basal clade of Hystricognathi rodents (Woods, 1972; Bugge, 1971; Bryant and McKenna, 1995; Candela, 1999). Known from the late Oligocene of Argentina and Bolivia to the present (Wood and Patterson, 1959; Candela, 2000), they are the most widespread Hystricognathi of the New World, occurring in South, Central and North America. Presently, Neotropical porcupines comprise about fifteen species, all of which are strictly arboreal (Emmons, 1997), and are essentially restricted to the Brazilian Subregion (*sensu* Hershkovitz, 1958; figure 1). Extinct erethizontids had a wider distributional range, including localities at low latitudes such as La Venta (Walton, 1997), and in central, northern and southern Patagonia (figures 1, 3). Patagonian porcupines are found from the late Oligocene to middle Miocene, an interval during which they experienced significant diversification, and therefore appearing in numerous mammal assemblages (Ameghino, 1887, 1902; Scott, 1905; Patterson, 1958; Wood and Patterson, 1959; Vucetich *et al.*, 1993; Candela, 2000). Despite their importance, with the exception of few recent contributions (Candela, 1999; Candela and Vucetich, 2002), most Patagonian erethizontids have not been restudied since their original description nor analyzed from a paleobiological perspective. Consequently, their systematics and paleoenvironmental significance are not completely understood.

This paper describes a new genus and species of erethizontid from the Sarmiento Formation (Early Miocene) outcropping at Gran Barranca, the south-

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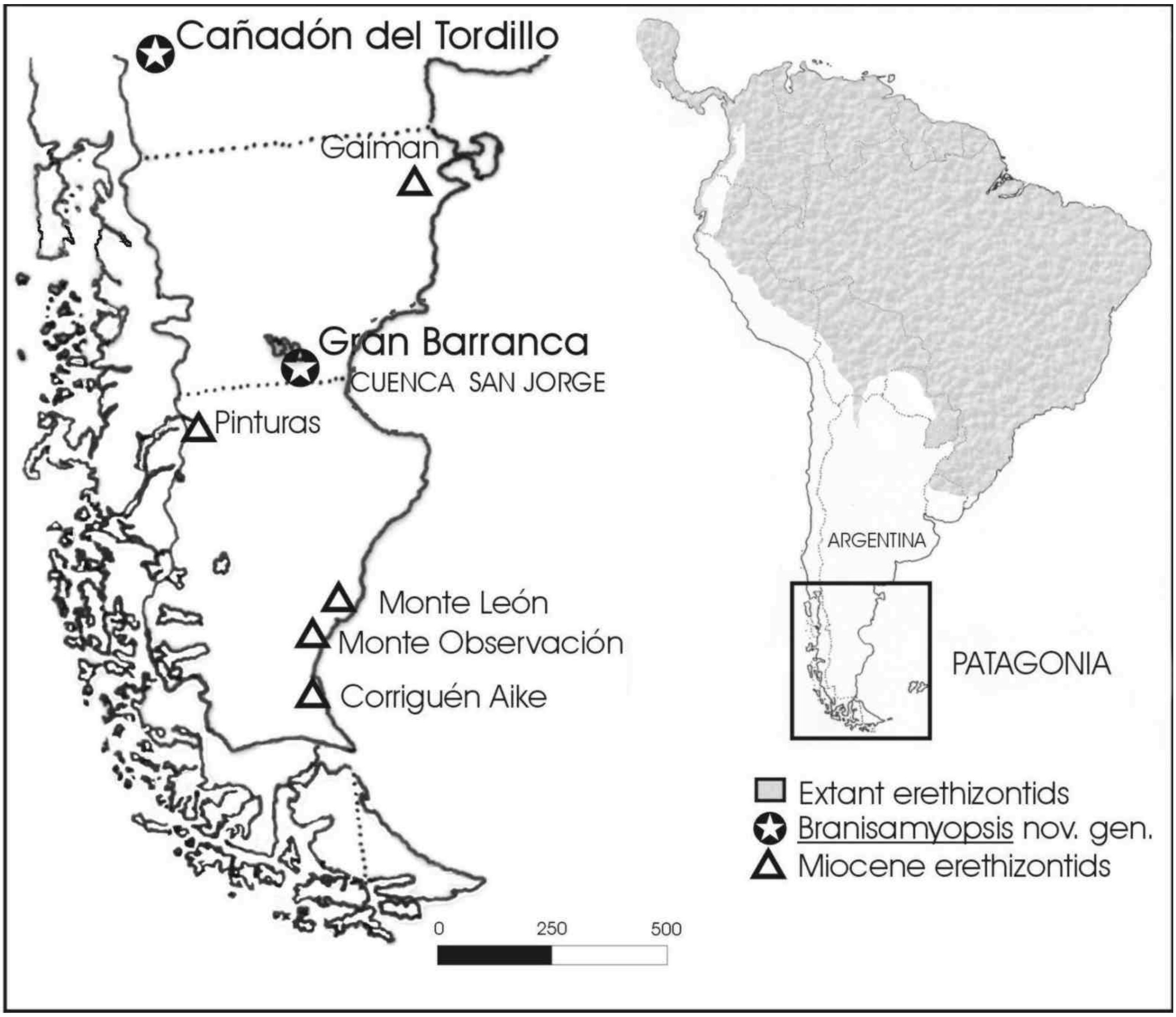

Figure 1. Map of South America showing the geographical location of *Branisamyopsis* gen. nov. and remaining Miocene erethizontids of Patagonia, and the distribution of extant Neotropical erethizontids. / *Mapa de América del Sur mostrando las localidades de Branisamyopsis gen. nov. y otros eretizóntidos miocenos de Patagonia, y la distribución de los eretizóntidos neotropicales vivientes.*

ern cliff face bordering Colhué Huapi Lake, Chubut Province, Argentina (figure 1). This genus is also recorded in the Collón Cura Formation (Middle Miocene) at Cañadón del Tordillo, Neuquén Province, Argentina. The tooth and mandibular morphology of this porcupine provides new information on the evolutionary and biogeographical history of the erethizontids.

Abbreviations

MLP, Museo de La Plata, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina; MMP, Museo Municipal de Mar del Plata "Lorenzo Scaglia", Argentina; MEF, Museo Paleontológico "Egidio Feruglio", Trelew, Argentina; MNHN, Museum National d'Histoire Naturelle, París. APD, maximal anteroposterior diameter; TD, maximal transverse diameter; PTD, posterior tranverse diameter; ATD, anterior transverse diameter.

Material and methods

Specimens of all taxa of extinct erethizontids of Argentina were analyzed. The only exceptions are the specimens from the Río Pinturas valley (Santa Cruz Province), which are currently being studied by others (Kramarz, com. pers.). Terminology of cusps, flexi, flexids, lophs and lophids of upper and lower cheekteeth follows the nomenclature of Candela (1999, 2000, 2002; figure 2). Measurements are in millimeters. Data on geographic and temporal distribution of erethizontids from the Oligocene and Miocene of South American are included in figure 3.

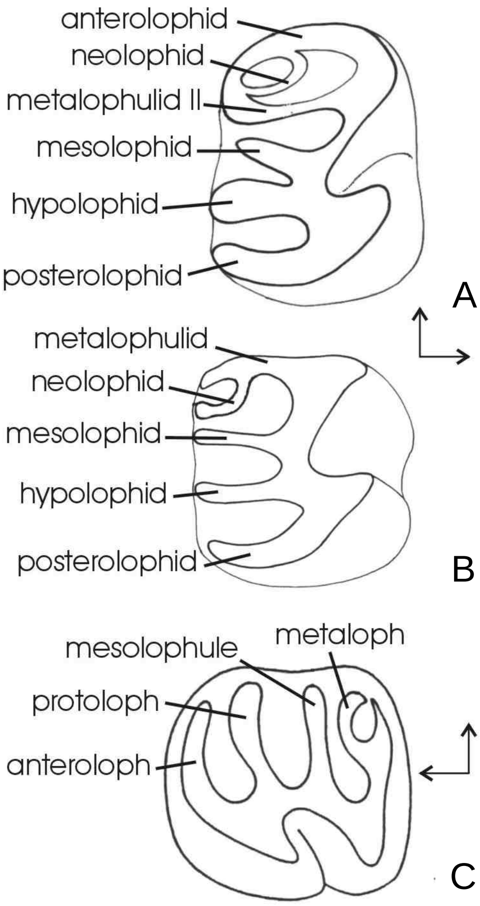

Figure 2. Terminology used for upper and lower cheekteeth of the Erethizontidae (after Candela, 1999, 2000, 2002). **A**: lower deciduous teeth; **B**: lower molar; **C**: upper molar. Arrows show anterior and lingual sides. / *Terminología utilizada para los dientes superiores e inferiores de los Erethizontidae (según Candela, 1999, 2000, 2002).* ***A:*** *dientes deciduos inferiores;* ***B:*** *molar inferior;* ***C:*** *molar superior. Las flechas señalan los lados anterior y lingual.*

Systematics

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Family ERETHIZONTIDAE Thomas, 1897

Branisamyopsis gen. nov.

Type species. *Branisamyopsis australis* gen. et sp. nov.

Etymology. From genus *Branisamys* Hoffstetter and Lavocat, 1970 and from Greek *opsis*: similar to.

Stratigraphic, chronologic and geographic occurrence. Colhuehuapi Member, Sarmiento Formation, Colhuehuapian Age (early Miocene), Chubut Province, Central Patagonia, Argentina, and Collón Cura Formation, Colloncuran Age (Middle Miocene), Neuquén, northern Patagonia, Argentina (Vucetich, *et al.*, 1993; Flynn and Swisher, 1995; Kay *et al.*, 1999).

Diagnosis. cheekteeth with shallow and narrow flexi, flexids, fossettes, and fossetids. Upper molars with the hypoflexus connected to the paraflexus, short mure, protocone and anteroloph with subcircular contour, and TD larger than APD. Pentalophodont lower molars, having a short and oblique ectolophid and a well developed neoconid. dp4 and p4 hexalophodont. P4 having a well developed mesoconid but not ectolophid, protoconid and anterolophid unconnected, and hypo-and mesoflexid connected. Mandibular body more robust and deeper than that of living erethizontids but less robust and lower than in *Steiromys* species. Lack of crest and insertion fossa for the pars posterior of the medial masseter, chin projected ventrally, ventral edge of the angular region flat and oriented lateromedially in its middle and posterior portions. Lower incisors wider and proportionally longer than those of *Eosteiromys.*

Branisamyopsis australis sp. nov.
Figures 4-6

Type. MMP 937, nearly complete right hemimandible, with the incisor and the p4-m3 series.

Etymology. In reference to its geographic distribution in the southern region of South America.

Hypodigm. The type and the following specimens: MNHN col. 96a, right isolated M1 or 2; MNHN col. 96b, right M1 or 2; MNHN col. 96c, left M1 or 2; MNHN col. 96d, left M1 or 2; MNHN col. 74a, right M3; MNHN col. 98a, right M3; MNHN col. 97, right p4; MNHN col. 99b, left p4; MLP 82-V-2-46a and b, two left mandibular fragments with m1-2; MLP 85 VII-3-34a, left M1 or 2; MLP 85-VII-3-34b, left M1 or 2, MLP 85 VII-3-34c, right M1 or 2; MMP 131, left M3; MEF 5790a, left mandibular fragment with m1; MEF 5790b, mandibular fragment with m3; MEF 5790c, left m3; MEF 5790d, right m1; MEF 5790e, left m1; MEF 5791a, left upper cheekteeth; MEF 5791b, left M1; MEF 5791c, left M1; MEF, 5791d, right M3; MEF 5791e, left M1; MEF 5792a, right p4; MEF 5792b, right dp4; MEF 5810, left m1; MEF 5812a, un right p4; MEF 5812b, left p4; MEF 5812c, left m1; MEF 5812d, left m1; MEF 5818, right M1; MEF 5825, left M1.

Stratigraphic, chronologic and geographic occurrence. Colhuehuapi Member, Sarmiento Formation, Colhuehuapian Age, early Miocene, Gran Barranca, southern cliff of Lake Colhué Huapi, Chubut Province, Argentina.

Diagnosis. The same as the genus by monotypy.

Description. The mandibular body is robust, high with regard to mandibular length (table 1) and labially convex (figure 4.A). The diastema is excavated and ascending from the alveolar edge of p4. The masseteric notch is located above the half of mandibular height, and at the level of the posterior end of m1. The masseteric fossa is moderately deep. The lateral crest is well marked, extending from the masseteric notch to the base of the coronoid process. The anterior edge of this process originates somewhat before m2-3, making the m2 visible in labial view. Masseteric crest

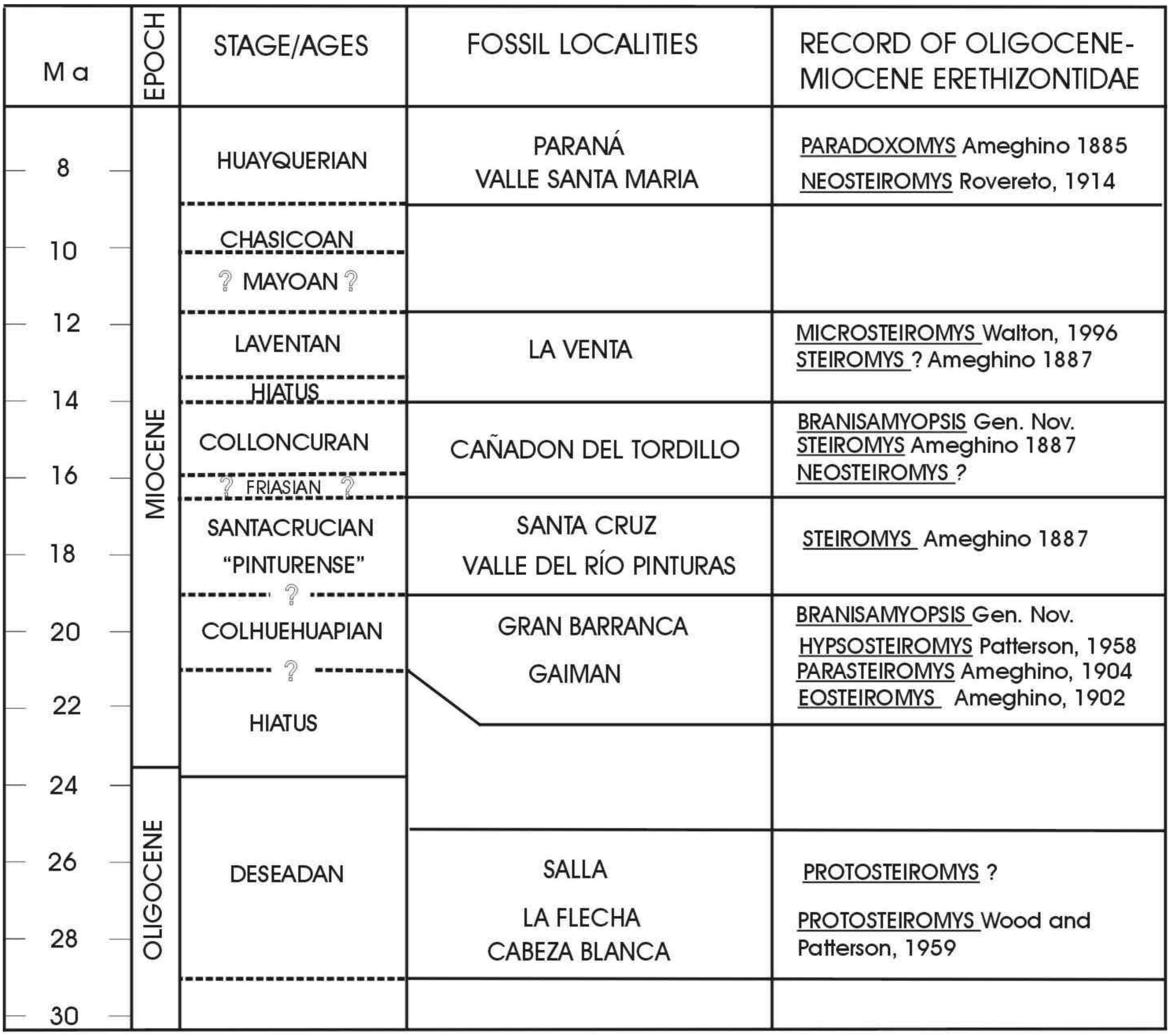

Figure 3. Temporal and geographic records of erethizontids from the Oligocene and Miocene of South America. Chronology according to Flynn and Swisher / *Registros temporales y geográficos de eretizóntidos del Oligoceno y Mioceno de América del Sur. Cronología según Flynn y Swisher.*

is fairly developed and is unconnected to the masseteric notch. There is no fossa for insertion of the pars posterior of the medial masseter (Woods, 1972). The condyle, of which only the basal portion has been preserved, is elongated anteroposteriorly. The anterior portion of the ventral edge of the angular region is rounded, while its medial and posterior portions are clearly flat and oriented lateromedially. An anterior projection of a line bisecting the cheekteeth intersects the incisor (figure 4.B). The alveolar sheath of the incisor is very broad, beeing clearly distinct from the angular region of the mandible (figure 4.C). The curve of the incisor alveolus suggests that its base extends to the vicinity of the condyle. Pterygoid shelf is very narrow. The symphysis is very wide anteriorly, narrowing posteriorly. The posterior end of the symphysis continues posteriorly by a short, rough and conspicuous projection of the muscular insertion. The chin has a ventral projection.

The incisor is large in relation to cheektooth size (table 2); its anterior surface is almost flat and has a slight crest on its external edge.

Table 1. Measurements of the mandible of the type (MMP 337) of *Branisamyopsis australis* gen. et sp. nov. / *Medidas de la mandíbula del tipo de* Branisamyopsis australis *gen. et sp. nov.*

	MMP 937 (type)
Length of diastema	12.10
Length of symphysis	28.7
Mandibular height at p4	22.81
Mandibular height at m1	17.57
Mandibular height at m1-2	16.07
Condyle-angular process depth	30.9
Maximal mandibular length*	61.70

*Measured from the anterior end of diastema to posterior edge of post-condyloid process.

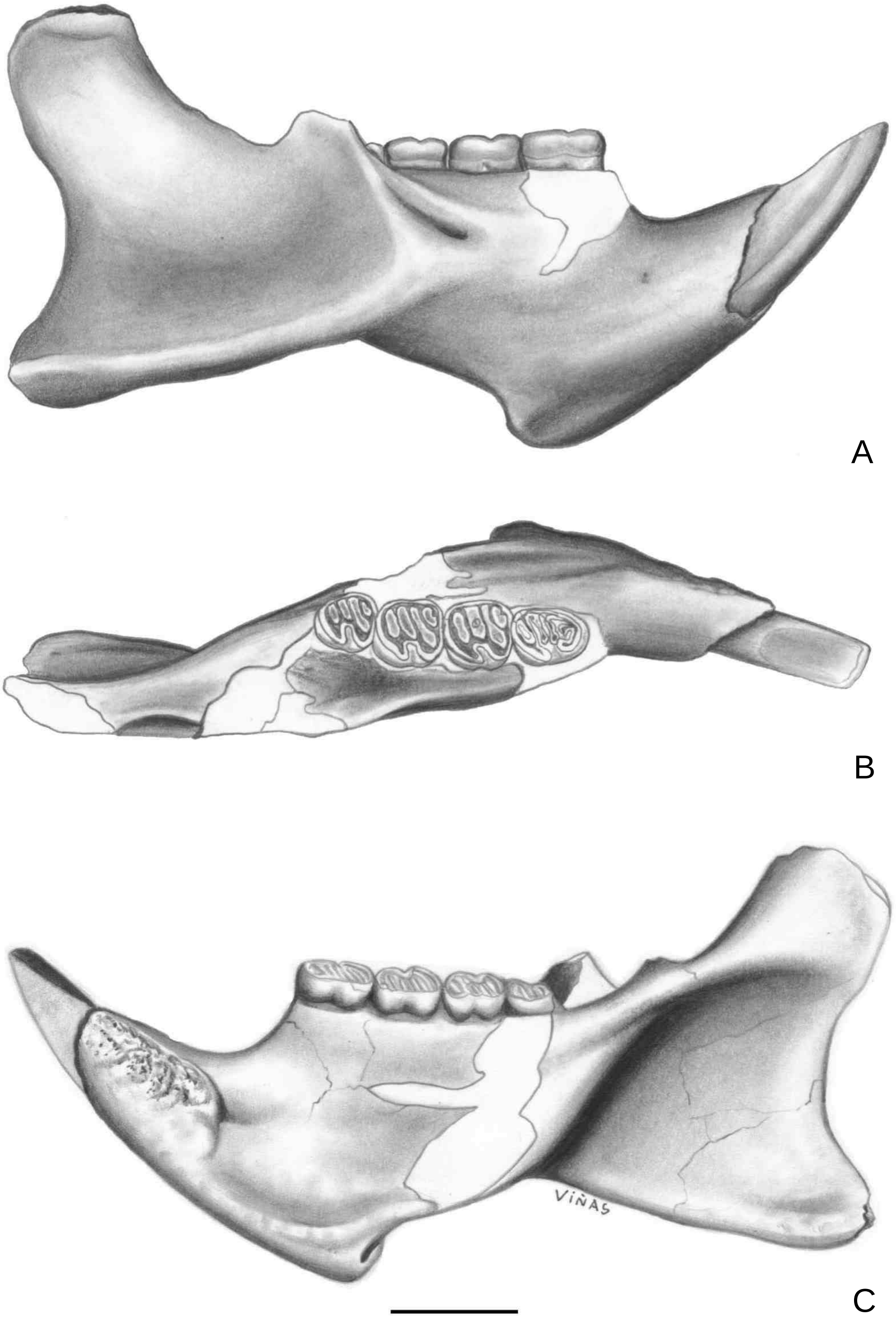

Figure 4. ***Branisamyopsis australis*** gen. et sp. nov. (type MMP 937), hemimandible in lingual **(A),** labial **(B),** and occlusal **(C)** views / *hemimandíbula en vistas lingual **(A),** labial **(B)** y oclusal **(C)***. Scale 1 cm / *Escala* 1 cm.

Cheekteeth are characterized by their shallow and narrow flexi, flexids, fossettes, fossetids, and clearly individualized cusps.

The dp4 (figure 5.A; table 2) is hexalophodont. The protoconid is separated from the anterolophid by a small incision. The anterolophid extends towards the metaconid with a semicircular shape. The neolophid is united to the anterolophid, while its remaining end is free in the interior of the anterofossetid. The metalophulid II and mesolophid are well developed. The ectolophid is separated from the protoconid by a narrow and shallow incision. The mesoconid is smaller than the protoconid and located lingually with respect to it. The hypoflexid is connected to the mesoflexid.

Figure 5. Lower cheekteeth of *Branisamyopsis australis* gen. et sp. nov. **A,** MEF 5792a, right dp4; **B,** MEF 5792b, right p4; **C-D,** MLP 82-V-2-46a, m1 **(C)**, m2 **(D)**; **E,** p4-m3 of MMP 937 (type). Scale 1 mm / *Escala* 1 mm.

The p4 (figures 5.B, E) is subrectangular and hexalophodont. The anterolophid is separated from the protoconid by a deep notch (e g. MPEF 5792a, figure 5.B), which becomes less evident with wear (e. g. MMP 337, figure 5.E). The neolophid is variable, ranging completely developed (MEF 5812a) to reduced (MNHN col. 99b). The metalophulid II is transversally oriented or slightly posterolingual. The

Figure 6. Upper molars of *Branisamyopsis australis* gen. et sp. nov., **A,** MLP 85-VII-3-34b, left M1 or 2; **B,** MLP 85-VII-3-34a, left M1 or 2; **C,** MLP 85-VII-3-34c, right M1 or 2 showing labial cusps; **D,** MNHN col. 74a, right M3. Scale 1 mm / *Escala* 1 mm.

mesoconid is very developed, lingually located with respect to the proto- and hypoconid, and unconnected to these cusps. Therefore, the ectolophid is solely represented by the mesoconid, and the hypoflexid continues lingually with the mesoflexid-metafossetid. The mesolophid may be either completely (MLP 337, MPEF 5792a, MPEF 5812b) or partially developed (MNHN col. 97). A very shallow and narrow mesoflexid is found in MEF 5812b, but in specimens MEF 5792a, MMP 337, and MEF 5812b the mesoflexid has become a mesofossetid.

The m1 (figures 5.C, E) is pentalophodont, with TD subigual or larger than APD (table 2). The metalophulid is transverse. The neolophid joins lingually with the neoconid (*sensu* Candela, 2000), this latter clearly visible behind the metaconid in little-worn teeth (e. g. MPEF 5812c, MLP 82-V-2-46a; figure 5.C), and may be interrupted in its middle portion (figure 5.C). The mesolophid joins lingually the mesostylid, the latter being somewhat larger than the neoconid. The ectolophid is short and rather oblique. The m2 (figure 5.D, E) is very similar to the m1; slightly larger than m1 in MLP 82-V-2-46a and MLP 82-V-2-46b; and slightly smaller in MMP 337. A very narrow and shallow communication between the hypoflexid and the posterofossetid may be observed (e. g. m1 of MLP 82-V-2-46a; figure 5.D). The m3 is smaller than m1-2, with PTD smaller than ATD (figure 5.D).

The M1-2 (figures 6.A-C) are pentalophodont with a sigmoid shape due to the communication between the hypoflexus and the paraflexus/parafossette. This condition is even evident in worn teeth (figure 6.B). Their TD is larger than APD (table 3) and the mure is very short. Labial cusps are well differentiated, a feature especially noticeable in molars with little wear (figures 6.A, C). The protocone joins the anteroloph displaying a subcircular configuration. The protoloph is anterolabially oriented until its union with the paracone. The mesolophule (*sensu* Candela, 1999) is narrower and shorter than the protoloph and extends more or less transversally to the mesostylid, which is lower than the para- and metacone. At the lingual end of the mesolophule in specimens with little wear (e. g. MLP 85 VII-3-34c; figure

Table 2. Measurement of lower cheekteeth of *Branisamyopsis australis* gen. et sp. nov. / *Medidas de los dientes inferiores de* Branisamyopsis australis *gen. et sp. nov.*

	TD	APD	APD	ATD	PTD	APD	ATD	PTD	APD	ATD	PTD	APD	ATD	PTD	APD	ATD	PTD
	I	I	dp4	dp4	dp4	p4	p4	p4	m1	m1	m1	m2	m2	m2	m3	m3	m3
MMP 337 (type)	4.8	5.5				5.9	4.4		5.3	5.4	5.4	5.2	5.3	5.2	4.9	4.7	4.3
MEF 5815	4.7																
MEF 5792a			6.1	4.1	4.5												
MEF 5792b						6.2	3.3	3.9									
MEF 5810										4.6							
MEF 5812a						5.8	4.1	4.3									
MEF 5812b						6.2	4.3	4.5									
MEF 5812c									5.1	5.4	5.2						
MEF 5812d									5.2	5	5.1						
MLP 82-V-2-46a									4.9	4.9	4.8	5.1	5	5			
MLP 82-V-2-46b									5	5.2	5.1	5.2	5.5	5.4			
MEF 5790a										4.4							
MEF 5790b															4.8	4.3	4
MEF 5790c															4.7	4.4	4
MEF 5790d									4.9	4.7	4.8						
MEF 5790e										5	4.8						
MNHN col. 97						5.7	3.7	4.4									
MNHN col. 99 b						5.8	4.2	4.5									

6.C) the metaconulid is recognized. The metaloph is well developed, its lingual end is almost at the level of the lingual end of the mesolophule. When wear is limited, the posteroloph is lower than the metaloph and the metacone. The M3 (figure 6.D) shows a prepentalophodont design (*sensu* Candela, 1999), i.e. the mesolophule is partially developed and the metaloph is either disconnected from the posteroloph and joined to the mure, or joined to the posteroloph and the mure. The M3 is somewhat smaller than M1-2 and has the hypocone fairly more labially than the protocone.

Comparisons and affinities of *Branisamyopsis*

Colhuehuapian erethizontids, i. e. *Eosteiromys* Ameghino, 1902, *Parasteiromys* Ameghino, 1904, *Hypsosteiromys* Patterson, 1958, are mainly known by isolated teeth. The mandibular rests of these taxa are scarce and poorly preserved. In this sense, the mandible of *Bransamyopsis australis*, the best preserved among the Colhuehuapian erethizontids, allows a more comprehensive analysis of the mandibular characters of this family.

The mandible of *B. australis* is somewhat smaller than that of the living *Coendou prehensilis* (Linnaeus, 1758), notably smaller than that of Santacrucian *Steiromys duplicatus* Ameghino 1887, and comparable in size to that of *Eosteiromys homogenidens* Ameghino 1902 and the Santacrucian *Steiromys detentus* Ameghino 1887. Likewise *E. homogenidens* and *Steiromys* species, *B. australis* differs from living erethizontids (see Voss and Angermann, 1997: fig. 15; Candela, 2000: volume II, figs. 17, 34, 36) in possessing a more robust and relatively deeper mandibular body, absence of insertion fossa for the pars posterior of the medial masseter, pterygoid shelf more reduced, wider symphysis showing a distinctive posterodorsal projection, deeper masseteric fossa, more remarkable masseteric crest, more ventrally projecting chin, and ventral edge of the angular region characterized by a distinctive flat surface, latero-medially oriented. In *B. australis*, this condition is evidenced in the middle and posterior portions of this region, being rounded in its anterior portion, while in *Steiromys* the entire ventral edge is flat (in *Eosteiromys* this feature is missing).

The mandible of *Neosteiromys* Rovereto, 1914, the late Miocene giant porcupine from northwestern Argentina, differs from that of *B. australis* and the remaining Patagonian erethizontids in several features, the most remarkable being its greater size and robustness, the greater depth of the masseteric fossa, noticeable development of the lateral and masseteric crests, higher anterior extension of the retromolar fossa, and more anterior position of the masseteric notch (located below the posterior end of p4).

Therefore, in relation to the other erethizontids, the mandibular characters of *Branisamyopsis* are closer to those of *E. homogenidens* and *Steiromys* species. It should be noted that a recent cladistic analysis of erethizontids based on cranial and mandibular characters indicates the existence of two clades: one represented by the living *Coendou* and *Erethizon*, and the other by the extinct taxa from late Oligocene-late Miocene (Candela, 2000, 2001). According to this proposal, *Neosteiromys* would be the sister taxon of the Patagonian clade represented by *Eosteiromys* and *Steiromys*. The shared mandibular characters of *Eosteiromys*, *Steiromys* and *Branisamyopsis* (see above) indicate that these three genera would be closely related. *Branisamyopsis*, in turn, shows a set of stages of mandibular characters considered to be plesiomorphous in comparison to those of *Eosteiromys* and

Figure 7. ***Branisamyopsis*** gen. nov., MLP 91-IX-1-7a, a left isolated DP4? Scale 1 mm / *Escala* 1 mm.

Steiromys (Candela, 2000). In fact, *Branisamyopsis* has a longer diastema, lower mandibular ramus (feature not preserved in *S. detentus* and *E. homogenidens*), less robust mandibular body, somewhat more posterior masseteric notch, an incisor less deeply implanted, and anterior end of the ventral edge of the angular region more rounded (features not completely preserved in *S. detentus*, *E. homogenidens*). In this sense, *Branisamyopsis* is closer to the ancestral condition of this clade than are *Steiromys* and *Eosteiromys*.

With reference to the cheekteeth, unlike *Branisamyopsis*, lower molars of *Eosteiromys* and *Steiromys detentus* are tetralophodont, the ectolophid is well developed and the hypoflexid is wider. Just as in *Branisamyopsis*, lower molars of *S. duplicatus* are pentalophodont but the neolophid and lingual cusps are less developed. The p4 of *Eosteiromys* and *S. detentus* is distinguished from that of *Branisamyopsis* by the presence of a well developed ectolophid and flexids and fossetids wider and deeper. Additionally, the P4 of *E. homogenidens* is tetralophodont. Unlike *Branisamyopsis*, the p4 of *S. duplicatus* is proportionally shorter and the ectolophid is well developed. Incisors of *Branisamyopsis* are somewhat wider and proportionally longer than those of *Eosteiromys*. Their general appearance is very similar to that of *S. duplicatus* incisors.

Upper molars of *Branisamyopsis* distinguish from those of *Steiromys* and *Eosteiromys* by the hypoflexus-paraflexus communication, protocone and anteroloph with a subcircular configuration, less depth and amplitude of flexi and fossettes, higher TD, and shorter mure. It should be noted that upper molars of *Neosteiromys* show the hypoflexus-parafossette communication, just as in *Branisamyopsis*. Nevertheless, the cheekteeth of *Neosteiromys* can be distinguished from those of *Branisamyopsis* in several features, i.e. their larger size, lack of cusps and the tendency to the early closure of labial and lingual flexi/ids.

The analysis of *Branisamyopsis* characters indicates that this taxon is more closely linked to the Patagonian genera *Steiromys* and *Eosteiromys*. Therefore, the hypoflexus-paraflexus/parafossette communication would represent a feature independently acquired in *Neosteiromys bombifrons* Rovereto, 1914 and *Branisamyopsis*. Note that *Neosteiromys*? *tordillense* Vucetich, Mazzoni and Pardiñas, an erethizontid recovered from Collón Cura Formation (middle Miocene) from Neuquén, would also present the hypoflexus-parafossette connection, a feature that allowed the species to be tentatively linked to *Neosteiromys bombifrons* (Vucetich *et al.*, 1993). However, *N.*? *tordillense* is distinguished from *N. bombifrons* by several characters, among the most distinctive being the persistence of labial and lingual flexi/ids and the connection between hypo- and mesoflexid of p4. Notably, both features are also present in *B. australis*. In addition, *N. bombifrons* has many distinctive cranial and mandibular features which cannot be detected in *N.*? *tordillense*, because the latter is solely represented by isolated teeth. This scenario suggests that *N.*? *tordillense* would be more closely linked to *Branisamyopsis* than to other erethizontids. This hypothesis will only be tested by finding more complete remains of *N.*? *tordillense*.

Branisamyopsis *in the Colloncuran Age*

Two specimens, the MLP 91-IX-1-7a (a left isolated DP4?; figure 7) and the MLP 91-IX-1-7b (a left isolated m3), from Upper Member of Collón Cura Formation outcropping at Cañadón del Tordillo, are assigned to *Branisamyopsis* gen. nov. The upper tooth is pentalophodont, with the TD (5.89 mm) larger than the APD (5.62 mm), the hypoflexus connected to the parafossette, the protocone continuous with the an-

Table 3. Measurement of upper cheekteeth of *Branisamyopsis australis* gen. et sp. nov.

	APD M1 or 2	ATD M1 or 2	PTD M1 or 2	DAP M3	ATD M3	PTD M3
MLP 85-VII-3-34a	4.7	5.8	5.8			
MLP 85-VII-3-34b	4.7	5.9	5.7			
MLP 85-VII-3-34c	4.7	5.4	5.3			
MEF 5825	4.7	5.3	5.5			
MEF 5818	5.5	5.8	5.7			
MEF 5791a	5.1	5.3	5			
MEF 5791b	4.7	5.9	5.8			
MEF 5791c	5.1	6.1	6.1			
MEF 5791d				4.5	5.2	5
MEF 5791e	4.9	6.1	5.6			
MNHN col. 96a	4.7	5.6	5.3			
MNHN col. 96b	4.9	5.5	5.3			
MNHN col. 96c	4.8	5.5	5.2			
MNHN col. 74a				4.9	5	4.8
MNHN col. 98a				4.8	5.2	4.8

teroloph showing a subcircular contour, labial cusps scarcely developed, the metaloph very close to the posteroloph, and the fossettes relatively wide and shallow. The general appearance of the tooth, its extremely low crown and thin enamel, suggest that it could be a deciduous tooth. The m3 is pentalophodont, some longer (APT: 5 mm) than wider (ATD: 4.57 mm) and posteriorly narrower (PTD: 4.49 mm), with very shallow flexids and fossetids and thin enamel. The neolophid is not completely developed, and the bottom of the hypoflexid is continuous lingually with the posterofossetid. The hypo-paraflexus / parafossete connection, the subcircular contour of the proto- and anteroloph, the presence of neolophid and the shallow flexi and fossetids displayed by the two specimens allow to assign them to *Branisamyopsis* gen. nov. Both specimens differ from those assigned to *Branisamyopsis australis* gen. et sp. nov. in at least two features considered derived for the erethizontids (Candela, 2000): less developed cusps and lack of mure. However, to analyze the presumed diagnostic value and evolutionary significance of these differences, the finding of a more complete sample of Colloncuran specimens is needed.

Discussion

Some features of the molar pattern of *Branisamyopsis australis* are primitive in relation to the remaining Erethizontidae and Hystricognathi: persistence of cusps, specially the metaconule, pentalophodonty of M1-2, and M3 with a prepentalophodont design (Candela, 1999: figs. 6, 8). Although these features are not significant for establishing phylogenetic relationships, they are of great importance for understanding the evolution of the upper molar pattern of erethizontids and the remaining Hystricognathi (Candela, 1999). The persistence of the metaconule identified in *Branisamyopsis australis* confirms that the third loph of upper molars of the Hystricognathi is homologous to the mesolophule (Bryant and McKenna, 1995; Candela, 1999). The M3 of *Branisamyopsis australis* would represent a more generalized pattern than the typical pentalophodont design (e. g. *Mesomys*, *Lonchotrix*, *Neoreomys*). This latter pattern would have been acquired through the complete development of the mesolophule and the exclusive connection of the metaloph with the posteroloph (Candela, 1999: figure 8).

On the other hand, the sigmoid design shown by *Branisamyopsis* seems to have been independently acquired in different lineages and at different times during the evolutionary history of the South American Hystricognathi. This design is observed, for instance, in the dasyproctids *Incamys* (Hoffstetter and Lavocat, 1970), *Scleromys* Ameghino 1887, and *Australoprocta* Kramarz 1998, the octodontoid *Willidewu* (Vucetich and Verzi, 1991), and the dinomyid? *Branisamys* (Patterson and Wood, 1982, but see Lavocat, 1976). It should be noted that many cranial and dental features (especially those of the dp4) of *Branisamys* are shared with erethizontids in general and Patagonian *Steiromys* and *Eosteiromys* in particular (personal observation). This suggests its affinities lie with Erethizontidae. If this hypothesis is confirmed, the inclusion of *Branisamys* in a phylogenetic analysis of all erethizontids will determine if the sigmoid design present in this genus and in *Branisamyopsis* was independently acquired or not.

Paleoenvironmental and biogeographic considerations

Living Neotropical porcupines are strictly arboreal, inhabiting different types of forests (e. g. deciduous, evergreen, gallery, and Atlantic forests; Emmons 1997); their feeding habits are based mainly on fruits, seeds, and soft leaves (Charles-Dominique *et al.* 1981; Emmons 1997). With the exception of *Chaetomys subspinosa* Olfers (apparently a member of this family; Emmons, 1997), the cheekteeth of the different extant Neotropical species are very similar (Alberico *et al.*, 1999; Voss and Angerman, 1997). Conversely, Patagonian porcupines show remarkable differences in their molar patterns, and their cranial and mandibular anatomy indicate diverse masticatory strategies (Candela, 2000). The different occlusal patterns found among Patagonian erethizontids could indicate different dietary adaptations, specially during Colhuehuapian Age, the time when they show their greatest taxonomic diversification (figure 3). *Hypsosteiromys*, for instance, displays a tendency to hypsodonty and to the reduction of its cusps and metaloph, a tendency that has been interpreted as an adaptive response related to a diet of harder and more abrasive food, available even in more open environments than those in which living porcupines currently live (Candela and Vucetich, 2002). A different response to a more abrasive diet could have involved an increase of enamel thickness and in the number of lophids. *Eosteiromys homogenidens* has well developed cusps, and its upper and lower molars are pentalophodont and tetralophodont, respectively. Specimens of a new species of *Eosteiromys* show smaller, slender upper molars with tetralophodont morphology (Candela, 2000). *Branisamyopsis australis* has, instead, increased the number of lophs, resulting in pentalophodont upper and lower molars. Upper molars of *Parasteiromys* are larger than those of *B. australis* and *E. homogenidens*, having less developed cusps and thicker enamel. In sum, unlike the conservative dentition of living Neotropical porcupines, the cheekteeth morphology of Patagonian Colhuehuapian erethizontids could correspond to different dietary adaptations. The differing molar patterns displayed by Patagonian erethizontids may reflect the environmental diversification inferred for central Chubut during the Colhuehuapian, which would have been characterized by forested areas interspersed with open areas, with an optimum balance for park savanna (Pascual *et al.*, 1996).

The clade of Patagonian erethizontids from the late Oligocene-middle Miocene (Candela, 2000, 2001) indicates that Patagonia represented an area of marginal differentiation in the evolutionary history of the family, unrelated to the radiation of living porcupines. The temporal distribution of *Branisamyopsis* reveals that it would have differentiated very early from the lineage that produced Santacrucian species of *Steiromys*, at least in the Early Miocene. In this regard, it should be mentioned that during the early Oligocene-early Miocene, central Patagonia experienced significant tectonic movements and changes of the sea level, that deeply affected the region, with ever-increasing marine transgressions in central Patagonia (see Bellosi, 1995 and literature cited therein). Transgressions represented geographic barriers that certainly affected biotas, promoting vicariance and diversification events (Bellosi, 1995: 65). It is possible that vicariance phenomena have limited the occurrence of *Branisamyopsis* to the north and northwest of massif Deseado and the presence of *Steiromys*, frequently found at more austral localities in the Santa Cruz coastline (figure 1), to the south of the area affected by transgressions. The presence of *Branisamyopsis* in the Colhuehuapian of Chubut and Colloncuran of Cañadón del Tordillo, apparently absent during the Santacrucian, seems to be consistent with that interpretation.

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