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A Middle Miocene primitive octodontoid rodent and its bearing on the early evolutionary history of the Octodontoidea

by

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With 1 plate, 2 text-figures and 1 table

Summary

A new primitive octodontoid rodent from the Middle Miocene Collón Curá Formation of north-western Patagonia, is described. Both its brachydont and pentalophodont cheek teeth, and its incisor enamel with multiserial HSB transitional from acute angle to rectangular plate-like IPM, indicate the new genus and species as a very primitive representative of the Octodontoidea. The transitional state of IPM was more common than previously supposed, because it is also present in several Early - Middle Miocene Patagonian taxa representing different lineages of primitive Octodontoidea; this wider distribution suggests that the rectangular IPM was independently developed in different lineages. This reinforces the hypothesis that early octodontoid evolution was very complex. The fact that the transitional (45°–90°) state of IPM is more widely temporally and taxonomically distributed than previously known, also suggests that rectangular IPM among "caviomorphs" was probably developed after their arrival in South America.

Key words: Rodentia, Miocene, South America, enamel microstructure, evolution.

Zusammenfassung

Aus der mittelmiozänen Collón Curá Formation des nordwestlichen Patagonien werden eine neue Gattung und Art der Nager-Überfamilie Octodontoidea beschrieben. Die niedrigkronigen und pentalophodonten Backenzähne sowie der Inzisiven-Schmelz mit multiserialen Hunter-Schreger-Bändern (HSB) im Übergangsstadium von spitzwinkliger zu rechtwinkliger Interprismatischer Matrix (IPM) zeigen, dass es sich um einen ursprünglichen Vertreter handelt. Dieser Übergangszustand der HSB ist weiter verbreitet als bisher angenommen und wurde bei verschiedenen früh- bis mittelmiozänen Octodontoidea aus mehreren Entwicklungslinien nachgewiesen. Dies zeigt, dass die frühe Stammesgeschichte der Octodontoidea recht komplex war. Die Tatsache, dass HSB im Übergangszustand von spitzwinkliger zu rechtwinkliger IPM (45°–90°) zeitlich und systematisch so weit verbreitet sind spricht dafür, dass HSB mit rechtwinkliger IPM bei den „Caviomorphen" nach deren Ankunft in Südamerika entwickelt wurden.

Schlüsselwörter: Rodentia, Miozän, Südamerika, Schmelzmikrostruktur, Evolution.

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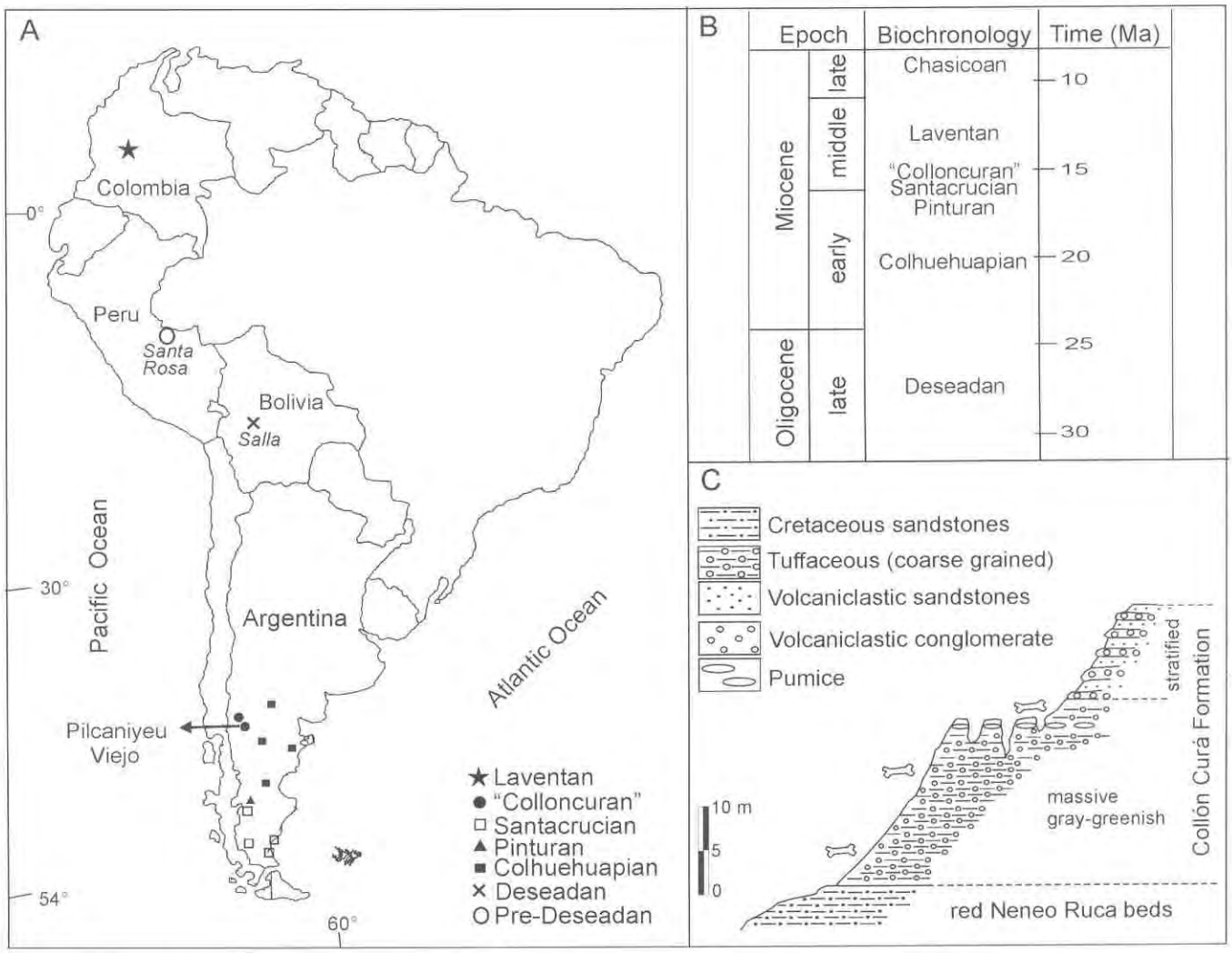
1. Introduction

The South American hystricognath rodents ("caviomorphs") have a good although geographically biased fossil record. For example the Early and Middle Miocene record is essentially Patagonian (southern Argentina) (Text-fig. 1A). This Miocene record of continental mammals begins with those of the Colhuehuapian (Early Miocene) levels of the Sarmiento Formation, followed by those of the lower levels of the Pinturas Formation (late-Early Miocene) (Text-fig. 1A, B). The rodent assemblages of these levels are dominated by taxa with brachy- to protohypsodont cheek teeth of the Erethizontidae, Eocardiidae, Dasyproctidae and several lineages of the Octodontoidea, and have been recently interpreted as characteristic of environments with humid forests (KRAMARZ & BELLOSI 2005). Contrarily, the rodent assemblages of the upper levels of the Pinturas Formation (early-Middle Miocene), as well as those of the slightly younger Santa Cruz Formation (early-Middle Miocene), are dominated by proto- to euhypsodont taxa. They have been interpreted as characteristic of more open environments. The Collón Curá Formation ("Colloncuran", Middle Miocene, Text-fig. 1A-C), slightly younger than Santa Cruz Formation, has a rodent assemblage also dominated by proto- to euhypsodont taxa (BONDESIO et al. 1980, VUCETICH 1984). However, some brachydont echimyids and erethizontids, related to colhuehuepian species, have also been described (PARDIÑAS 1991, VUCETICH et al. 1993, CANDELA 2003).



Text-fig. 1. Localities, time scale and stratigraphy. A. Map of South America showing main fossiliferous localities of Late Oligocene-Miocene mammalian faunas. B. Time scale for Late Oligocene -Miocene South American Land Mammal Ages, modified from FLYNN & SWISHER (1995). C. Stratigraphic profile of Pilcaniyeu Viejo, Cerro San Antonio, Río Negro Province, Argentina.

All this period witnessed a progressive climatic deterioration at low latitudes, and a displacement from wooded to open environments. Accordingly, the rodents of the successive Colhuehuapian, Pinturan, Santacrucian and "Colloncuran" Land-Mammal Ages (Lower – Middle Miocene, Text-fig. 1B) show an increasing proportion of hypsodont taxa. This context of environmental scenario and southerly-biased record, explains why the evolutionary history of derived proto- to euhypsodont rodent lineages is much better known than that of the primitive brachydont ones. But taxa with primitive cheek teeth give a better insight of the early evolution of a group. In this sense, some cases recently reported for Quaternary primitive "caviomorphs" (Vucetich & Verzi 2002, Vucetich et al. 2005) revealed that much higher cladogenesis than supposed occurred in the Brazilian Subregion (Hershkovitz 1958).

In this paper we describe a new genus and species of a primitive octodontoid rodent from the Collón Curá Formation which bears interesting implications on the early evolutionary history of octodontoids, and allow us to speculate about the early development of multiserial HSB subtypes in South America.

2. Material and methods

The following specimens were prepared for the study of the enamel microstructure: MLP 91-V-1-55 (holotype), upper incisor; MLP 91-V-1-4 and MLP 90-V-10-15, lower incisors (see below, Hypodigm); and MLP 91-V-1-43, m1 or m2. Specimens were embedded in artificial resin for easier handling, orientation, and to avoid fractures. Then, they were cut in longitudinal and cross sections, ground with wet grinding paper (600 µm) and powder 1000 µm. Afterwards, they were submerged in 10 % hydrochloric acid (2N HCl) for three or four seconds to enhance morphological details. The enamel microstructure was studied through a Scanning Electron Microscope (SEM) Jeol JSM-T100.

Measurements of the teeth: anteroposterior length (AP), anterior width (AW), posterior width (PW). Enamel measurements taken for each specimen: total enamel thickness, inclination and width of Hunter-Schreger bands (HSB), and angle of interprismatic matrix (IPM) relative to the prism long axes. The inclination of bands is defined as the angle between the intersection of the bands with a line perpendicular to the dentine in the sagittal plane. The proportion of enamel types was also measured.

3. Systematics

Order Rodentia Bowdich 1821

Suborder Hystricognathi Tullberg 1899

Superfamily Octodontoidea Simpson 1945

Family incertae sedis

Plesiacarechimys gen. nov.

Type species: *Plesiacarechimys koenigswaldi.*

Distribution: "Colloncuran" (Middle Miocene) from north-western Patagonia.

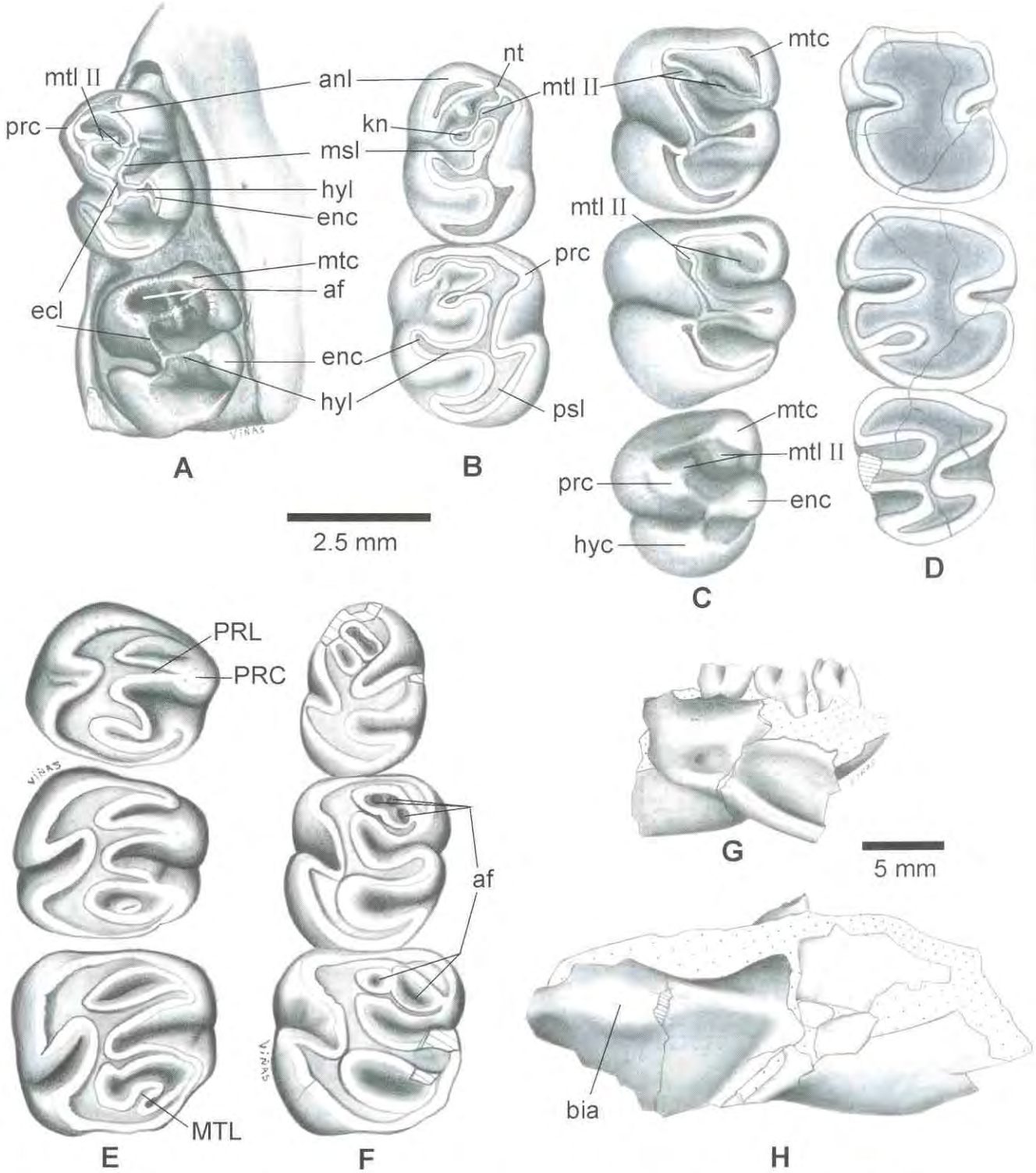
Diagnosis: medium size octodontoid, about 50% larger than the largest species of *Acarechimys* (*A. constans*). Brachydont, with slight unilateral hypsodonty in the upper cheek teeth; lophodont but with cusps well differentiated in young individuals. Pentalophodont upper cheek teeth, with metaloph scarcely developed. Mesoloph oriented toward the metacone, merging with it with little wear. Para- and metacone higher than the rest of the tooth. Lower cheek teeth tetralophodont with the metalophulid II large or diversely reduced but apparently always large in m1, lower than the other lophs, and larger than in *Acarechimys*. Metaconid and entoconid higher than the rest of the tooth. Entoconid anteroposteriorly or only anteriorly expanded.

Etymology: From the Greek plesio = primitive and *Acarechimys*, in relation to its similarity to, although more primitive than this genus.

Plesiacarechimys koenigswaldi sp. nov.

Plate 1, Text-fig. 2

Holotype: MLP 91-V-1-55, very badly preserved fragmentary skull with left DP4-M2 and associated left fragmentary mandible with dp4-m2.



Text-fig. 2. Teeth and mandibular morphology of *Plesiacarechimys koenigswaldi* gen. et sp. nov. A-F. oclusal view. G-H. mandible labial view. A. MLP 91-V-1-19, left mandible fragment with dp4-m1 of a juvenile. B. MLP 91-X-1-42, right mandible fragment with dp4-m1. C, G. MLP 91-V-1-22, left mandible fragment with m1-m3. D, H. MLP 92-V-10-15, right mandible fragment with m1-m3. E-F. MLP 91-V-1-55 (Holotype); E. left DP4-M2. F. left dp4-m2. **af**, anterior fossettids; **anl**, anterolophid; **bia**, base of the incisor alveolus; **ecl**, ectolophid; **enc**, entoconid; **hyc**, hypoconid; **hyl**, hypolophid; **kn**, knob; **msl**, mesolophid; **mtc**, metaconid; **MTL**, metaloph; **mtl II**, metalophulid II; **nt**, notch; **PRC** paracone; **prc**, protoconid; **PRL**, protoloph; **psl**, posterolophid.

Hypodigm: The holotype and MLP 91-V-1-16, right mandibular fragment with m2; MLP 91-V-1-19, left dp4-m1(juvenile); MLP 91-V-1-22, left mandibular fragment with m1-3; MLP 91-V-1-31, right mandibular fragment with m1-2; MLP 91-V-1-42, right mandibular fragment with dp4-m1; MLP 92-V-10-15, right mandibular fragment with m1-3.

Horizon and Locality: All the material comes from a massive grey-greenish tuffaceous sediments of the Collón Curá Formation (Text-fig. 1C); Estancia Cerro San Antonio, Pilcaniyeu Viejo, Río Negro Province, Argentina.

Diagnosis: As for the genus.

Etymology: Name in honour of Prof. Dr. Wighart von Koenigswald.

4. Description

Lower dentition: The dp4 is known in three specimens being that in the holotype (MLP 91-V-1-55) the most worn (Text-fig. 2F). Its anteroposterior diameter almost doubles the transverse one (Table 1, Text-fig. 2A, B and F). Anterior and posterior transverse diameters increase with age (Table 1). Postero- and hypolophid are well developed. The hypolophid can be either quite transverse or curved forward in its lingual portion. In the less worn specimen (MLP 91-V-1-19, Text-fig. 2A), the hypolophid is short and the entoconid is prominent and anteroposteriorly expanded. The anterior portion of the dp4 is more variable than the posterior one. It is shaped as a subcircular lobule, with the fused antero- and mesolophid delimiting a central basin. This central basin is crossed by the metalophulid II (sensu CANDELA 2002, Text-fig. 2A). This structure is similar to that of *Acarechimys* and *Protacaremys*. In MLP 91-V-1-19 the metalophulid II is formed by two portions: a long labial sector and a shorter lingual one. In the holotype, both portions are fused. In specimen MLP 91-V-1-42 (Text-fig. 2B) this structure is not so well defined, because the mesolophid is very short and does not merge with the anterolophid. Though somewhat worn, the notch between the protoconid and the anterolophid is still present (Text-fig. 2B). The labial portion of the metalophulid II is short but connected to a small knob (remnant of the mesolophid or of the lingual portion of the metalophulid II?) in the centre of the tooth.

The m1-2 are similar in structure, although m2 is slightly larger in the holotype (Text-fig. 2F). They are tetralophodont when little to moderately worn, but trilophodont or even bilobated when deeply worn, because of the fusion of crests (Text-fig. 2D). They are somewhat terraced when little to moderately worn, but the occlusion surface becomes flat with increasing wear. The highest part of the crown comprises the meta- and entoconid,

Table 1. Measurements in mm of upper and lower teeth of *Plesiacarechimys koenigswaldi* gen. et sp. nov. AP: anteroposterior length, AW: anterior width and PW: posterior width.

Upper teeth	91-V-1-55	Lower teeth	91-V-1-55	92-V-10-15	91-V-1-16	91-V-1-19	91-V-1-22	91-V-1-31	91-V-1-42
dP4 AP	2.72	dp4 AP	2.98			2.98			2.98
TA	2.80	TA	1.73			1.40			1.65
TP	2.64	TP	2.14			1.65			1.90
M1 AP	2.64	m1 AP	3.07	3.16		2.80	2.96	2.88	2.96
TA	2.64	TA	2.31	2.65		1.65	2.06	2.31	2.23
TP	2.48	TP	2.48	2.75		1.65	2.06	2.48	2.23
M2 AP	3.14	m2 AP	3.22	3.16	2.98		2.64	2.80	
TA	2.80	TA	2.72	3.16	2.23		1.90	2.14	
TP	2.56	TP	2.72	3.16	2.48		1.81	2.56	
M3 AP		m3 AP		2.85			2.40		
TA		TA		2.75			1.81		
TP		TP		2.14			1.65		

though in unworn molars, the protoconid is as high as the metaconid (Text-fig. 2C). The anterior face is straight, while the posterior is much curved. Hypo- and protoconid are aligned. The unworn metaconid is elongated anteroposteriorly, maybe corresponding to the fusion of metaconid and metaconulid. Behind the anterolophid there is a low, complex crest formed by two portions; one arises from the posterior end of the protoconid, and the other from the metaconid (Text-fig. 2A, C). They can be interpreted as the labial and lingual portions respectively of metalophulid II. In m1 both portions are long and merge at the centre of the tooth, except in MLP 91-X-1-42 (Text-fig. 2B) in which the labial portion is not developed, but there is a conspicuous knob at the centre of the tooth (remnant of the lingual portion of metalophulid II?). In the holotype and MLP 91-V-1-19 this structure is associated to a central cusp and one or more crestlets, which are forward oriented producing one or more small anterior fossetids when worn (Text-fig. 2A, F). The entoconid can be anteroposteriorly expanded (Text-fig. 2A) and the hypolophid can be either straight or curved (Text-fig. 2A, B), with anterior concavity. In m2 the metalophulid II is more variable. In MLP 91-V-1-22 the labial portion of the metalophulid II is very short, while the lingual portion bends forward towards the anterolophid (Text-fig. 2C). In the holotype the lingual portion of the metalophulid II is long, while the labial one is shorter. With strong wear, the anterolophid fuses with the metalophulid II, forming a single thick lophid, and the tooth acquires a trilophodont shape. Hypo- and posterolophid are well developed, though the end of the posterolophid always ends more lingually, except with strong wear (Text-fig. 2D). The metaflexid is usually transverse, while the labial portion of the mesoflexid may be inflexed anteriorly when the labial portion of the metalophulid II is short. The hypoflexid is posteriorly oriented and its inner portion is anterior to the metaflexid; its posterior face is straight and short, while the anterior is longer and frequently curved.

The m3 is somewhat smaller than m1-2, with a reduced posterolophid, and both portions of the metalophulid II are reduced to short spurs (Text-fig. 2C). It becomes trilophodont with wear (Text-fig. 2D).

The lower incisor is slender and high (AP diameter approximately twice as transverse). Its base is placed outside and behind the m3, and in some specimens it forms a bulbous prominence at the base of the coronoid apophysis (Text-fig. 2H).

Upper dentition. The upper dentition is only known in the holotype. The DP4 is tetralophodont. The anteroloph is moderately developed, as it does not reach the external edge of the tooth. With little wear, it runs forward from the protocone, and then curves backward reaching the base of the paracone. The latter is a prominent isolated cusp that fuses with the protoloph with moderate wear. The protoloph is straight, and slightly forward directed. The metacone is also prominent and fused to the posteroloph. The mesoloph is short and its labial end curves backward and is free. The posteroloph is slightly curved, with anterior concavity.

M1-2 are similar to DP4 in structure, but the M2 is somewhat larger. The antero- and the mesoloph are not connected to the para- and metacone respectively. The M1 has a remnant of a metaloph, which is free. On the contrary, the M2 has a well-developed metaloph, fused to the posteroloph, though not reaching the labial wall of the tooth.

Mandible. The description of the mandible is based on specimens MLP 91-V-1-22 and MLP 92-V-10-15. The base of the ascending ramus is opposite to m3 and is labially far from the tooth row (Text-fig. 2G, H). The masseteric crest is well developed and the scar for the *M. masseter medialis pars infraorbitalis* (sensu Woods & Howland 1979) is little developed, and placed below the anterior portion of m1.

5. Enamel microstructure of *Plesiacarechimys*

In the upper incisor (MLP 91-V-1-55, holotype), the enamel is 220 µm thick. The inner portion of the enamel (portio interna, PI) is formed by multiserial Hunter-Schreger bands (HSB) with the interprismatic matrix (IPM) at high acute angle (between 45° and 60°). The HSB occupy 85 % of the enamel thickness and are apically inclined at 20°. Each HSB comprises 3 to 5 prisms. The external portion (portio externa, PE) is formed by radial enamel (RE), occupies 15 % of the enamel thickness and the prisms are steeply inclined apically (75°–80°). In the lower incisors (MLP 91-V-10-15), the enamel is 290 µm thick. The HSB that form the PI are more steeply inclined (35°), than those in the upper incisors. Each HSB comprises 3 to 4 prisms, and the angle between IPM and the prism long axes varies from 60° to 90°. The PE is formed by RE and occupies only 10 % of the enamel thickness.

The schmelzmuster (threedimensional arrangement of the different enamel types, KOENIGSWALD 1980) of the lower molar (MLP 91-V-10-43) is formed by two enamel layers: the inner one of HSB that occupies almost 85 % of the enamel thickness, and a thin external layer of RE where the prisms are inclined apically at approximately 30°. The HSB comprise 5 to 6 prisms. The HSB of the leading edge are almost horizontal, but toward the middle of the enamel band their inclination increases up to almost 10°. The HSB of the trailing edge are at 20° to 30°. In the inner enamel zone the angle between IPM and prisms is straight, while it is acute in the external zone. The schmelzmuster with thick HSB present in *Plesiacarechimys* is generalised among "caviomorphs" (KOENIGSWALD 2004, VIEYTES 2003).

6. Discussion

6.1 Relationships of *Plesiacarechimys koenigswaldi*

The position of *P. koenigswaldi* among "caviomorphs" poses some interesting questions. On the one hand its cheek teeth display mostly primitive characters (brachydont with somewhat bulbous walls, wide and shallow flexi/ids, and relatively thick enamel with generalised schmelzmuster) that can be found both in erethizontids and some octodontoids. In contrast, even the most ancient Chinchilloidea and Cavioidea display specialised dental features such as bilaminar or heart-shaped cheek teeth respectively (VUCETICH 1989, WOOD & PATTERSON 1959). On the other hand, some of the characters, such as the very low metalophulid II formed by two portions, produce a very unusual morphology, especially for m1-2. However, the homologies of this second lophid are different from those proposed for the Erethizontidae (CANDELA 2003, 2004). The retention of DP4/dp4 strongly suggests that *Plesiacarechimys* is an Octodontoidea because this is the only superfamily in which these teeth are retained. Moreover, the morphology of the dp4, without the extended anterolophid and the anterior neolophid of the Erethizontidae (CANDELA 2002), also indicates it as an octodontoid.

The enamel microstructure of the incisors can be used to test this hypothesis of relationships. It has proved to be a useful tool for rodent systematics, because of its greater complexity with respect to most other mammals. Moreover, since the incisors have very similar shape in all rodents, their enamel microstructure is not so strongly influenced by biomechanical constraints as in molars (KOENIGSWALD & CLEMENS 1992, MARTIN 1992, 1993, 1994a, 1997, 1999). The incisor schmelzmuster of rodents has generally two layers, a PI with HSB and a PE with RE. The external RE maintains sharp cutting edges because of its high resistance to wear (RENSBERGER & KOENIGSWALD 1980) and the HSB reinforce the structure hindering the propagation of fractures in the enamel (PFRETZSCHNER 1988, KOENIGSWALD & PFRETZSCHNER 1991). Hystricognath rodents have a characteristic type of HSB in the incisors, called multiserial, with thick bands formed by 3 to 8 prisms. The multiserial type is also present in Pedetidae, and advanced Ctenodactyloidea (FLYNN et al. 1986, MARTIN 1993, 1994a). There are three basic subtypes of multiserial HSB, depending on the angle between IPM and prisms (MARTIN 1992, 1997, 1999). In the most primitive subtype (MARTIN 1999), the IPM is parallel to the prisms, and never surrounds them. In the second subtype the IPM is anastomosing, with crystallites at acute angle to prisms, approximately 45°. Based on biomechanical considerations and evolutionary occurrences, MARTIN (1992, 1993, 1994a) stated that the third subtype, in which the IPM is rectangular, plate-like, is the most derived (MARTIN 1999). This structure reinforces the enamel in the third dimension, thus being functionally the best.

The incisor enamel microstructure of rodents including "caviomorphs" has been extensively sampled by MARTIN (1992, 1994b). This author concluded that intraspecific enamel characters are very stable in rodents, and therefore the study of a single specimen can provide adequate insight of the characters in a species.

Among "caviomorphs", both of the most primitive multiserial HSB subtypes are present in the Cavioidea, Erethizontoidea and Chinchilloidea (MARTIN 1992, 1994a). The most derived one is present only in the Octodontoidea and is thus considered a synapomorphy of this superfamily (MARTIN 1992, 1993, 1994a). Likewise, all the octodontoids share HSB 30° to 50° inclined, 3 or 4 (rarely 5) bands width, and almost no difference in the inclination of HSB in upper and lower incisors. Thus, the microstructure of incisor enamel, with IPM reaching 90°, and thin multiserial HSB with high inclination (MARTIN 1994b), reinforces the hypothesis that *Plesiacarechimys* belongs to the Octodontoidea. Nevertheless, the fact that the straight angle is not reached in the upper incisors and only in some sectors of the lowers ones, suggests it is a primitive representative of this superfamily.

The relationships of *Plesiacarechimys* among the Octodontoidea are, obviously, also difficult to establish. The DP4/dp4 is retained in several octodontoid lineages such as Octodontidae, Ctenomyidae and Echimyidae. Classically, octodontoid genera from the Oligocene – Middle Miocene that retain the DP4/dp4 were referred to the Family Echimyidae (WOOD & PATTERSON 1959), but this has recently been challenged, and some of those genera could represent a different (or even more than one) octodontoid family (VUCETICH & KRAMARZ 2003).

Among the Miocene putative echimyids of Patagonia, *Adelphomys* (AMEGHINO 1887), *Stichomys* (AMEGHINO 1887), *Maruchito* (VUCETICH et al. 1993) and *Spaniomys* (AMEGHINO 1887) differ from *Plesiacarechimys* by their laminar and meso- to protohypsodont cheek teeth. *Protadelphomys* (AMEGHINO 1902) and *Willidewu* (VUCETICH & VERZI 1991) differ because the DP4/dp4 is replaced normally, and the lophs/ids are markedly reduced. *Caviocricetus* (VUCETICH & VERZI 1996) differs by its very terraced teeth and the dp4 with deeply split anterior wall. *Protacaremys* (AMEGHINO 1902) and *Prospaniomys* (AMEGHINO 1902), differ by their somewhat more hypsodont cheek teeth with lophs/ids united at their tips forming fossettes/ids.

Similarities are greater with *Acarechimys* (PATTERSON, in KRAGLIEVICH 1965). This genus groups very small species including the smallest "caviomorphs". Originally described for the Santacrucian (PATTERSON & WOOD 1982), species from the Colhuehuapian up to Laventan were later assigned to it (VUCETICH et al. 1993, WALTON 1997). Species are not well defined and an in depth systematic revision is needed. In *Acarechimys* the molariforms are also brachydont, with a slight unilateral hypsodonty and very convex walls. Cusps are well defined and a slightly terraced occlusal surface is seen in juveniles. The metalophulid II is small in the lower molars, and it is almost absent in *A. minutissimus*, the smallest species. In this sense, *Plesiacarechimys* is more primitive than *Acarechimys* because of the persistence of a long, although low, metalophulid II. The dp4 of *Acarechimys* also resembles that of *Plesiacarechimys* in having an anterior lobe defined by the antero- and mesolophid crossed by the metalophulid II (CANDELA 2002). This morphology appears to be common among the octodontoids that retain the dp4.

The shared similarities suggest that *Acarechimys* and *Plesiacarechimys* are related taxa; but the derived structures of *Acarechimys*, which has a longer record including older species (Colhuehuapian – Santacrucian) than *P. koenigswaldi*, pose some doubts. One of these characters is the presence of the most derived multiserial HSB subtype in the enamel incisors of *Acarechimys* (MARTIN 1992). It must be taken into account that a reversal from a rectangular IPM to a more primitive state has not yet been observed (KOENIGSWALD & PFRETZSCHNER 1991, KOENIGSWALD et al. 1993, MARTIN 1993). A possible interpretation is that *Plesiacarechimys* is closely related to *Acarechimys*, but retains several primitive characters. Another possible interpretation is that they represent different lineages, and thus the similarities in gross dental morphology would result from shared plesiomorphic characters (e.gr. brachydont cheek teeth, generalised dp4 morphology). The resolution of this issue depends partly on the finding of more complete materials other than teeth, that allows phylogenetic analyses.

6.2 Implications of *Plesiacarechimys koenigswaldi* on the early evolution of octodontoids

From another point of view, the enamel microstructure of the lower incisors of *P. koenigswaldi*, with an IPM that reaches 90° in only some sectors, is quite revealing. Among "caviomorphs", the enamel subtype with rectangular IPM is exclusively found in Octodontoidea. The only exception known so far was that of the putative echimyid *Sallamys* from the Deseadan of Salla, Bolivia, in which the IPM of the lower incisors is at 45° to 90°. MARTIN (1994b: 126) explained this transitional stage from acute angle to rectangular IPM by the "geological age and its relative close position of *Sallamys* to the common ancestor of the Octodontoidea". In this study we show that in the Colhuehuapian (Early Miocene) genera *Caviocricetus*, *Protadelphomys*, and *Willidewu* the angle of IPM and HSB in the lower incisor is between 60° and 90° (Plate 1: 5). The dental gross morphology of *Caviocricetus* is very different from the other two. It has terraced molars, slender incisors, retention of DP4/dp4, and the dp4 with a peculiar derived morphology. *Protadelphomys* and *Willidewu* are more hypsodont, with loph reduction, replacement of Dp4/dp4, and more robust and crested upper incisors. The differences among these genera, and also with *Plesiacarechimys*, indicate that they represent different lineages that retain a transitional character state of HSB up to the Middle Miocene.

This poses new questions about the early evolution of octodontoids. The multiserial HSB with rectangular IPM could have evolved independently in several octodontoid lineages as a result of an underlying synapomorphy (KOENIGSWALD 1997). Alternatively, it could have evolved once, thus becoming a synapomorphy for the

Acaremyidae, Octodontidae, Echimyidae, Abrocomidae plus some putative Oligo-Miocene echimyids (Vucetich & Kramarz 2003). If this were so, *Caviocricetus*, *Sallamys-Protadelphomy-Willidewu* and *Plesiacarechimys* would represent different lineages within a basal octodontoid stock. Any of these interpretations reinforces the hypothesis that the early evolution of the Octodontoids was more complex than previously supposed (Reig 1989: 262, Vucetich & Kramarz 2003). In this context, the retention of DP4/dp4, which among "caviomorphs" is exclusive of the octodontoids, could have evolved independently in different lineages. But the resolution of these questions requires a more comprehensive analysis.

The wider temporal and systematic distribution of the transitional IPM permit us to speculate about when and were the rectangular IPM was achieved among "caviomorphs". The three multiserial enamel subtypes are already present among the oldest "caviomorphs" (Martin 1992, 1994a, 2004), as well as in the Late Eocene – Early Oligocene Fayum "phiomorphs" (*Metaphiomys*, *Paraphiomys*) (Martin 1992). This led Martin (2004) to postulate two different scenarios for "caviomorph" origin. In one of them, "caviomorphs" would have entered South America quite in advance of the oldest known "caviomorphs", and the different multiserial enamel subtypes would have developed within this continent. The other scenario would imply a later invasion through several waves of taxonomically diverse stem-lineages already possessing the different subtypes of multiserial HSB.

We can imagine a scenario slightly different from the first one. As rodents are capable of a rapid diversification, and with no competition from other rodents in South America, perhaps the "caviomorph" ancestors required only little time to develop a new multiserial HSB subtype in this continent. Thus, the ancestors of "caviomorphs" could have entered South America shortly before the oldest rectangular IPM record in this continent (the pre-Deseadan Santa Rosa fauna in Peru, Frailey & Campbell 2004) having only the most primitive multiserial enamel subtypes. The fact that the transitional (45° – 90°) state of IPM is more widely temporally and taxonomically distributed than previously known, suggests that rectangular IPM among "caviomorphs" could have developed after their arrival in South America. The proposal that rodents did not reach central Patagonia latitudes until the Early Oligocene (Vucetich et al. 2004a, b) is in accordance with this hypothesis, because it suggests that rodents were not in South America during the early Paleogene.

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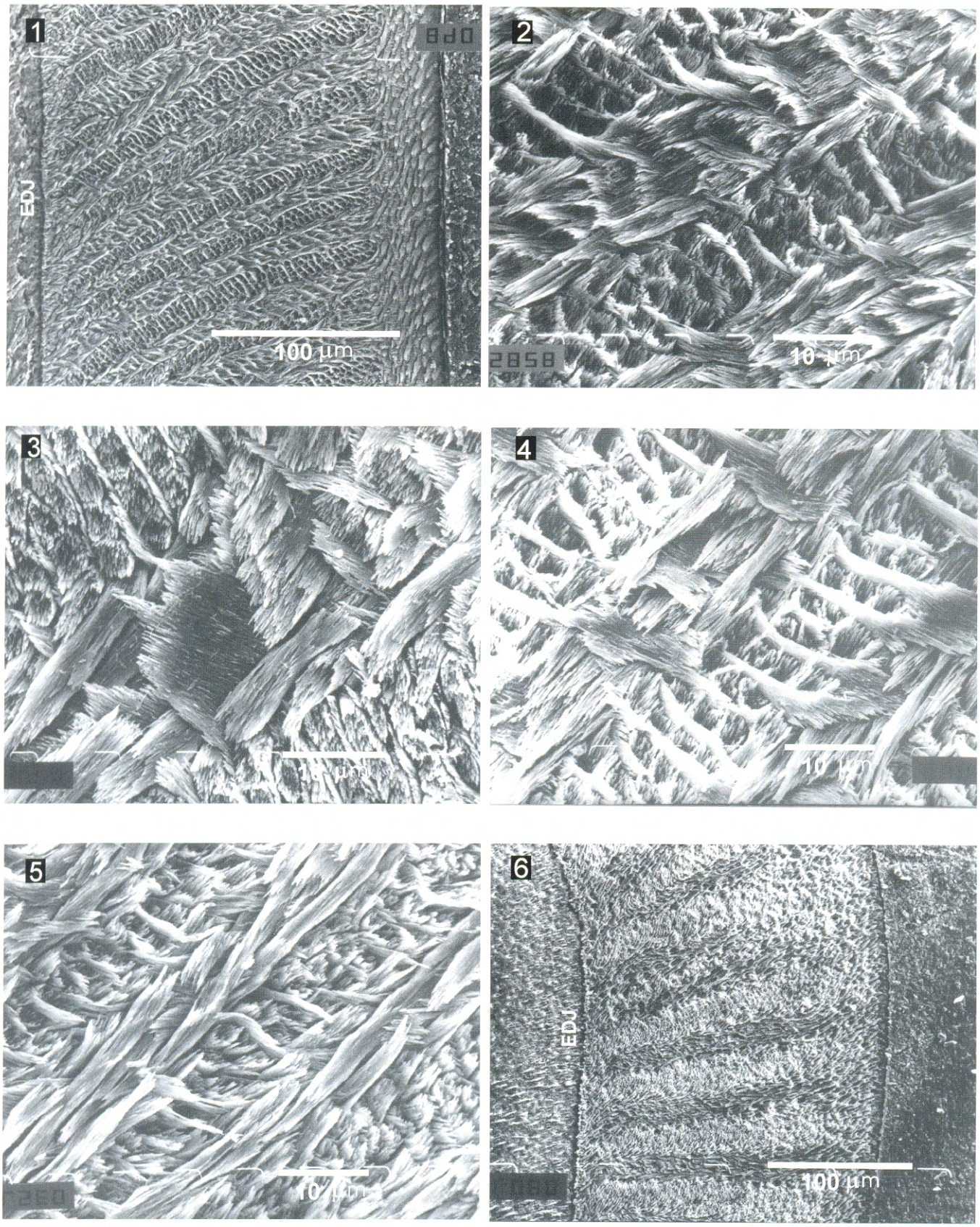
Explanation of Plate 1

Enamel microstructure of *Plesiacarechimys koenigswaldi* gen. et sp. nov. and *Protadelphomys latus*

1. Enamel microstructure in the upper incisor of *Plesiacarechimys koenigswaldi* gen. et sp. nov.
2. Detail of 1 showing the multiserial HSB with high acute angular IPM.
3. Enamel microstructure in the lower incisor of *Plesiacarechimys koenigswaldi* gen. et sp. nov. Detail showing a zone of multiserial HSB with high acute angular IPM.
4. The same as 3 but showing a zone of multiserial HSB with rectangular IPM.
5. Enamel microstructure in the lower incisor of *Protadelphomys.* Detail showing a zone of multiserial HSB with high acute angle IPM.
6. Enamel microstructure in the lower molar of *Plesiacarechimys koenigswaldi* gen. et sp. nov.

All SEM- micrographs are etched vertical sections. The EDJ is on the left, and the tip of the incisor on the top.



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