



A New Specimen of the Genus *Octodontobradys* (Orophodontidae, Octodontobadyinae)

From the Late Miocene-Pliocene of the Southwestern Amazon Basin, Brazil

Um Novo Espécime do Gênero *Octodontobradys* (Orophodontidae, Octodontobadyinae) do Mioceno Superior/Plioceno da Amazônia Sul-Ocidental, Brasil

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Abstract

This study presents an almost complete mandible of *Octodontobradys* sp. from the late Miocene-Pliocene of the Solimões Formation from a locality on the border between Brazil and Bolivia, in southwestern Amazonia. The two almost complete mandibular rami, together with fragments of fossils from other taxa, were found on the left bank of the Abunã River, upriver from the town of Plácido de Castro, in the Brazilian state of Acre. The form of the symphyseal region of the mandible, and the elongated and bilobated outline of the alveoli of the m2-3-4 molariforms place the specimen clearly in the genus *Octodontobradys*. However, the new specimen differs from *O. puruensis* in (a) the anterior position of the posterior external aperture of the mandibular canal, and (b) the wider and more anteriorly inclined symphyseal region. The mandible described here represents the first specimen of the genus *Octodontobradys* found outside of the holotype locality, Talismã, in the Brazilian state of Amazonas and enabled us to emend the diagnoses of Subfamily Octodontobadyinae.

Keywords: Orophodontidae; ground sloth; Solimões Formation

Resumo

Apresenta-se aqui uma mandíbula quase completa de *Octodontobradys* sp., proveniente do Mioceno superior/Plioceno da Formação Solimões, na fronteira Brasil/Bolívia, sudoeste da Amazônia. Os dois ramos mandibulares quase completos além de outros fragmentos fósseis pertencentes a diferentes táxons foram encontrados na margem esquerda do rio Abunã à montante da cidade de Plácido de Castro, Estado do Acre, Brasil. A forma da região sínfisiária da mandíbula e o contorno alongado e bilobado dos alvéolos dos molariformes m2-3-4 não deixa dúvida de que este novo espécime pertence ao gênero *Octodontobradys*. *Octodontobradys* sp difere de *O. puruensis* pelos seguintes caracteres: (a) abertura do canal mandibular posterior externo situado mais anteriormente e (b) região sínfisiária mais ampla e inclinada anteriormente. A mandíbula descrita aqui representa o primeiro achado de material pertencente ao gênero *Octodontobradys* fora do sítio Talismã, no Estado do Amazonas, de onde provém o holótipo deste táxon e nos permitiu ampliar a diagnose da Subfamília Octodontobadyinae.

Palavras-chave: Orophodontidae; Preguiça terrestre; Formação Solimões

1 Introduction

The early history of the Orophodontidae is poorly documented. *Orophodon haploides* Ameghino, 1895 and *Octodontherium grandae* Ameghino, 1895, known only from the Deseadan (Oligocene) of Argentina, are the oldest sloths of this family. *Octodontobradys puruensis* Santos, Rancy & Ferigolo, 1993, represented by a skull fragment and an almost complete mandible from the Late Miocene-Pliocene of the Solimões Formation in southwestern Brazilian Amazonia, is included in the Octodontobradyninae, a subfamily of the Orophodontidae. The phylogenetic relationships of the family remain unclear and the position of many low-level taxa is uncertain.

The orophodontids have been linked to the Cingulata (e.g. Ameghino, 1895; Kraglievich, 1940; Kraglievich & Rivas, 1951), Paleopeltidae (e.g. Gaudry, 1906), Paragravigrades (e.g. Hoffstetter, 1954, 1956, 1958) and Mylodontidae (e.g. Romer, 1966; Simpson, 1945; Hirschfeld, 1985). Scillato-Yané (1977) includes the octomylodontine species *Octomylodon aversus* Ameghino, 1904 and *O. robertoscagliai* Scillato-Yané, 1977 in the Mylodontidae. Until a thorough phylogenetic review becomes available, we will consider the

Orophodontidae to be a member of the superfamily Orophodontoidea, following Hoffstetter (1956) and McKenna & Bell (1997).

The mandible described below was generously provided to us by a resident of Plácido de Castro, a town in the eastern extreme of the Brazilian state of Acre, in the southwestern Amazon basin (Figure 1). The specimen was collected during the summer of 2003. According to the collector, the specimen and the associated fossil remains, which included a number of fragments of postcranial vertebrate, were removed from an argillaceous outcrop on the left bank of the Abunã River, near the Bolivian border (approximately 67°12'00"W; 10°20'00"S; Figure 1). All material is deposited in the collection of the Laboratório de Pesquisas Paleontológicas (LPP) at the Universidade Federal do Acre (UFAC). This mandible represents a new specimen of the genus *Octodontobradys*, first described by Santos *et al.* (1993). The material provides new evidence of the presence of orophodontids in the Solimões Formation of southeastern Acre, and may provide the basis for a reconsideration of the relationship between *Octodontobradys* and the orophodontids from the Deseadan of Argentina described by Ameghino (1895, 1897) on the basis of histological structures and tooth morphology.

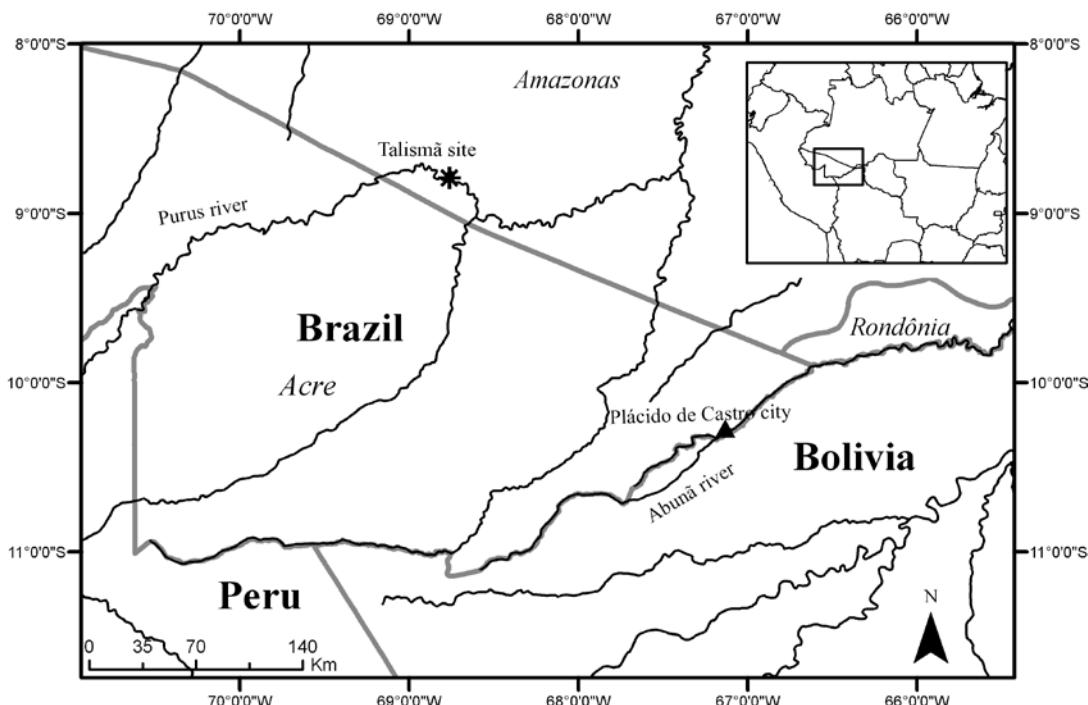


Figure 1 Geographic map of the Southwestern Amazon, showing the location of the city of Plácido de Castro (Acre) and Talismã site (Amazonas State) quoted in the text.

2 Materials and Methods

This study presents a detailed description of the mandible UFAC 5643, assigned to the genus *Octodontobradys*, collected on the left bank of the Abunã River in Brazil/Bolivia border. This specimen was compared with the type specimen of *Octodontobradys puruensis* Santos, Rancy & Ferigolo, 1993 (UFAC 1803), collected at Talismã site, on the right bank of Purus River, in the Brazilian state of Amazonas (Santos *et al.*, 1993).

Abbreviations. Institutional abbreviations: UFAC = Federal University of Acre, Rio Branco, Acre, Brazil; LPP = Laboratory of Paleontological Research. For dental notation, we use lower case letters for the lower teeth (*e.g.*, m1 indicates a lower first molar).

3 Systematic Paleontology

Superorder XENARTHRA Cope, 1889
 Infraorder MYLODONTA McKenna & Bell, 1997

Superfamily OROPHONTOIDEA

Ameghino, 1895

Family OROPHONDONTIDAE Ameghino, 1895
 Subfamily OCTODONTOBRADYINAE Santos, Rancy & Ferigolo, 1993

Emended Diagnosis: Orophodontid of large size distinguished from all the other members of the family by the presence of elongated and bilobate molariforms m2-4 in the mandible and M2-5 in the maxilla; elongated symphyseal spout; posterior end of the symphysis anterior to the third tooth; ascending ramus anteroposteriorly broad; condyloid process of moderate length with posterior edge nearly vertical, condylar articular surface expanded mediolaterally and orientated orthogonally to the long axis of the mandible.
Species included: *Octodontobradys puruensis* Santos, Rancy & Ferigolo, 1993 and *Octodontobradys* sp.

Known Distribution: Late Miocene and Pliocene of the Solimões Formation, southwestern Amazon Basin, Brazil.

Genus: *Octodontobradys*, Santos, Rancy & Ferigolo, 1993.

Diagnosis: The same as the subfamily.

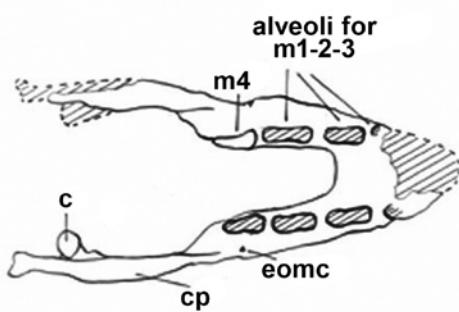


Figure 2 *Octodontobradys* sp., UFAC 5643, incomplete mandible, in dorsal view. Dashed outline indicates estimated extension of the symphysis and the left ascending ramus.
 Abbreviations:
 c - condyle;
 cp - coronoid process;
 eomc - posterior external opening of mandibular canal;
 m - molariform.

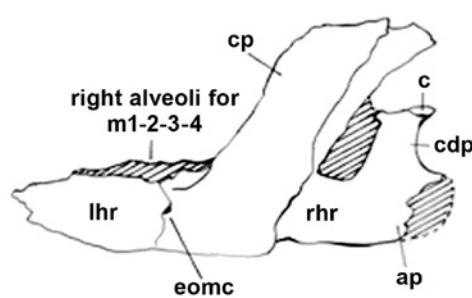
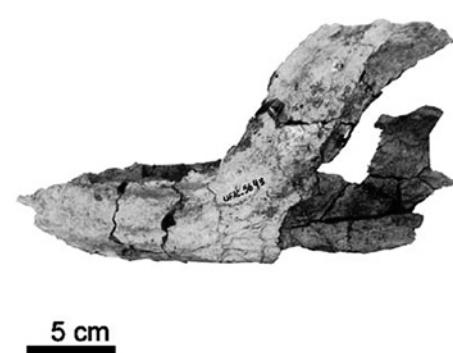


Figure 3 *Octodontobradys* sp., UFAC 5643, incomplete mandible, in left posterolateral view. Dashed outline indicates estimated anterior extension of the symphysis and the restoration of the right ascending ramus.
 Abbreviations:
 ap - angular process;
 c - condyle;
 cp - coronoid process;
 cdp - condyloid process;
 eomc - posterior external opening of mandibular canal;
 Ihr - left ramus;
 rhr - right ramus;
 m - molariform.

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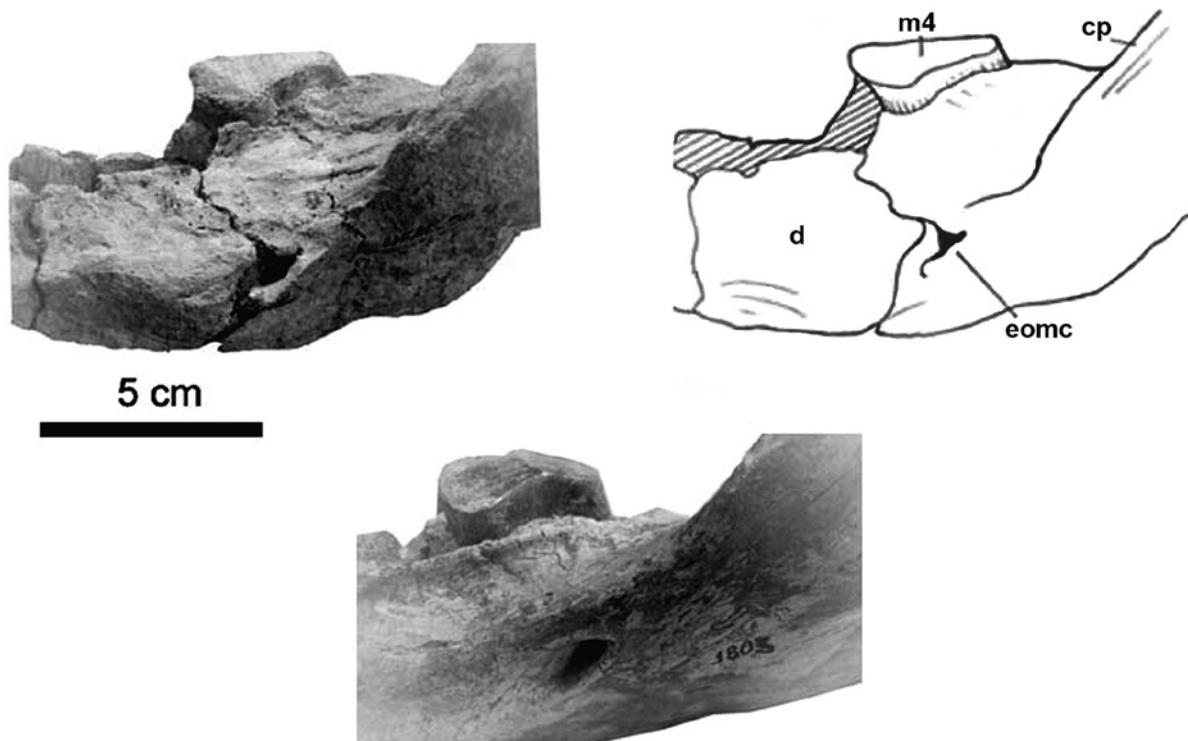


Figure 4 Region of the external orifice of the mandibular canal, in left lateral view (top: *Octodontobradys* sp., UFAC 5643); (bottom: *Octodontobradys puruensis*, UFAC 1803). Abbreviations: cp - coronoid process; d - dentary; eomc - posterior external opening of mandibular canal; m4 - molariform 4 badly damaged.

Measures	<i>Octodontobradys</i> sp. (UFAC 5643)	<i>O. puruensis</i> (UFAC 1803)**
Length of the mandible as preserved	244	262
Height of the right horizontal ramus above ventral border at alveolus for m3	44	59
Thickness of the right horizontal ramus at alveolus for m3	32	33
Thickness of the symphysis	21	25
Width of the condylar articular surface	29	31,5
Length right m2	27*	26
Anterior width right m2	11*	11
Posterior width right m 2	13*	14
Length right m3	29*	29
Anterior width right m 3	12*	15.5
Posterior width right m 3	12*	15.5
Least width right m3	11*	11.5
Length left m4	32	27
Anterior width m4	14	16.5
Posterior width m4	9	11

* Measurements of the alveolus

** From SANTOS et al. (1993)

Table 1 Measurements (in mm) of the mandibles and the lower teeth of *Octodontobradys* sp. (UFAC 5643) and *Octodontobradys puruensis* Santos, Rancy & Ferigolo, 1993 (UFAC 1803).

Specimen: UFAC 5643, incomplete mandible with damaged left m4, incomplete alveoli for left m1-2-3 and right m1-2-3-4. It lacks of the left ascending ramus, both angular processes and the anterior end of symphysis. Collected in 2003 (Figures 1-4; Table 1).

Geographic and stratigraphic location: Municipality of Plácido de Castro in the state of Acre, Brazil (Figure 1), late Miocene and Pliocene (Land Mammal age Huayquerian and Montehermosan) of the Solimões Formation (Latrubesse *et al.*, 1997, 2007).

Description of the specimen: The incomplete mandible (UFAC 5643; Figures 2 and 3) is stoutly built and has a heavily fused symphysis. The distance between the anterior end of symphysis (as preserved) to the posterior end of the condyle measures 244 mm. The symphysis itself is broken anteriorly, but the incomplete symphyseal suture is wide, with an anterodorsal inclination of 30° from the horizontal plane. The symphysis extends posteriorly to m2 and is 21 mm thick. The right horizontal ramus extends 44 mm above the almost straight ventral margin. The posterior external opening of the mandibular canal opens laterally, midway up the horizontal ramus, anterior to the coronoid process. The ascending process is broad anteroposteriorly, and rises at approximately 50° to the alveolar plane. The tip of the right coronoid process projects posteriorly and extends to the posterior of the head of the condyle. The condyloid process is of moderate length with a nearly vertical posterior edge. The condyle is situated just above the level of the tooth row. In the dorsal view, the condyle is expanded mediolaterally. In the posterior view, the condyle is convex medially and concave laterally. In the dorsal view, the condyle is oriented orthogonally to the long axis of the mandible.

The dentition of *Octodontobradys* sp. appears to be closely similar to that of *O. puruensis*, although the tooth rows are parallel. Diastemas are not noticeably present. On the right side, the alveoli for the hypsodont m2-3-4 are implanted vertically. Although it is broken, enough of the alveolus of the first right molariform has been preserved to indicate that the tooth had a reniform cross-section oriented at about 45° to the midline. The alveolus of m2 cannot be distinguished from that of m3. They are elongated, somewhat subretangular in the occlusal line, with a constriction in the middle which indicates that the teeth were slight bilobated. The flattened cross-section of the damaged left m4 is T-shaped with the occlusal surface perpendicular to the long axis of the tooth. The badly damaged crown has a marked

constriction in the middle of the tooth that connects the larger anterior and smaller posterior lobes. The occlusal surface of the left m4 of *Octodontobradys* sp. has the same wear pattern as that of the teeth of *O. puruensis*, with a thin layer of cementum on the outer surface of the tooth, a thick layer of orthodentine and modified orthodentine in the core (Santos *et al.*, 1993; Ferigolo, 1985). Standard measurements of the lower dentition are given in Table 1.

4 Discussion

4.1 Comparisons of the new specimen of *Octodontobradys* with other Deseadan sloths

The new specimen of *Octodontobradys* and *O. puruensis* are related to the Deseadan sloths *Orophodon* and *Octodontotherium* on the basis of their dental histological structure, as recognized by Ameghino (1891), and by the morphological design of the molariforms, as indicated by Hoffstetter (1954, 1956), Hirschfeld (1985) and Gaudin (2004). The teeth of these species present a central island of compact dentine, which is more resistant to wear than the surrounding dentine that covers most of the tooth. They also have a relatively resistant outer layer of cementum. The cross section of the hypsodont molariform m4 of *Orophodon* and m3-4 of *Octodontotherium* is bilobate, with an antero-posterior elongation. As in the pampatheres, these flattened molariforms have a mesiodistally-oriented island of resistant dentine that enhances shearing efficiency. It should be noted that *Octodontobradys* sp. shares a number of features with *Octodontotherium* that are best assessed as primitive features retained from their common ancestor. The shared features retained by *Octodontobradys* sp. include the position of the posterior external opening of the mandibular canal, which opens laterally in the horizontal ramus and two characters that Gaudin (2004) incorporated in his cladistic analysis of the Tardigrada. One is the position of the condyle just above the tooth row and the second is the shape of the coronoid process, which is intermediate in development (ratio of height to length >1.0 and ≤ 1.25).

Octodontobradys sp. is nevertheless distinct from *Octodontotherium* due to its parallel-sided suture (in the occlusal view). This is consistent with the most marked trends in the evolution orophodontoid morphology observed since the Deseadan – the shift from oblique to parallel tooth rows and from peg-like to bilobate teeth. However, no taxa known from

the Colhuehuapian or Santacrucian periods present morphological characteristics which might link the orophodontines with *Octodontherium* or *Orophodon*. While the records of ground sloths from La Venta include lineages of a variety of taxa, there is no evidence of an ancestral link with the Amazonian orophodontids, which are also different in shape and wear from the octomylodontines of the late Miocene of Argentina. This is particularly impressive considering the time-span between the upper Deseadan (29 m.y) and the Huayquerian-Montehermosan, at 9-4 m.y. (McKenna & Bell, 1997).

4.2 Comparisons of the New Specimen of *Octodontobradys* with *O. puruensis*

Numerous features of *Octodontobradys* sp. point to a close relationship with *O. puruensis*. These include a close similarity in overall morphology, the presence of bilobated alveoli for m₂₋₃ and the flattened T-shaped cross-section of m₄. However, if the major features of the mandible of *Octodontobradys* sp. confer with those of the holotype of *O. puruensis* (UFAC-1803), and justify the inclusion of the new specimen in the Octodontobradyninae, a more detailed comparison reveals conspicuous differences. The morphological and dental features of the UFAC 5643 mandible that characterize it as *Octodontobradys* sp. and differ from *O. puruensis* include: (a) the anteriorly position of the posterior external opening of the mandibular canal on the horizontal ramus (in *O. puruensis*, this canal opens posteriorly to the ascending ramus) (Figure 4); (b) the parallel tooth rows in the occlusal view (in *O. puruensis* the tooth rows converge anteriorly); (c) the symphyseal spout is wider and more inclined than in *O. puruensis*; (d) the m₁ alveolus is curved anterolabially, whereas in *O. puruensis*, it is reniform and relatively lobate, and elongated anteroposteriorly.

5 Final Considerations

The phylogenetic relationships among the orophodontoids cannot be determined precisely, but the Amazonian sloths (Octodontobradyninae) present the closest affinities with those of the Deseadan. The anterior progression of bilobation is considered to be an important character for the construction of phyletic

sequences. In *O. puruensis* the slightly bilobate cross-section of the m₁ is elongated anteroposteriorly and the posterior external aperture of the mandibular canal opens anterolaterally on the ascending ramus. Based on these morphological characters, *O. puruensis* is clearly different from the new specimen described here, which leads us to believe that it may be a new species of *Octodontobradys*, which lived in sympatry with *O. puruensis* in the southwestern Amazon basin. If this is true, they may have avoided interspecific competition through different dietary preferences, which might also imply differential habitat use. While precise information is lacking, the available evidence indicates that the region was characterized by vast tracts of rainforest interspersed with savanna and gallery forests (Campbell *et al.*, 2006; Latrubesse *et al.*, 2007). The masticatory dentition of both *Octodontobradys* sp. and *O. puruensis* indicates that they were grazers, with a relatively mobile mandible and well-developed masseter muscles designed to process vegetation.

Janis & Ehrhard (1988) consider a wide muzzle to be an indicator of grazing in ungulates. Considering the pre dental spout in the sloth mandible as equivalent to the ungulate muzzle (McDonald, 1997), the flared and relatively wide mandibular symphysis of *Octodontobradys* sp. can be interpreted as the result of an adaptive shift to grazing, with far greater emphasis on the crushing, rather than the cutting phase. This suggests that the orophodontids had diversified to fill a variety of niches in the late Miocene of the Solimões Formation. We suggest that *O. puruensis*, with its long and narrow pre dental spout, was adapted for the processing of tender shoots, twigs, and leaves of trees. The presence of animals such as *Neoeublema* rodents, primates (Atelidae), lizards (Teiidae; cf. *Paradracena* sp.) associated with *O. puruensis* in the local fauna of the Talismã (Santos *et al.*, 1993; Bergqvist *et al.*, 1998; Hsiou *et al.*, 2009) suggests that this locality was covered in forest gallery (Labrubesse *et al.*, 2007).

Our evaluation of the evidence suggests that *Octodontobradys* sp. inhabited savanna grasslands rather than forests. An alternative hypothesis is that the species were not sympatric but occupied the same geographical zone during different times in a zone that may have shifted in response to changes in temperature and conditions of moisture (Campbell *et al.*, 2006). The absence of detailed stratigraphy and location data for the associated specimens collected with the mandible is a problem. However, the presence of fragments of a large femur and

incomplete neurocranium of an unknown sloth, and remains of the large-bodied alligatorid *Purussaurus brasiliensis* Barbosa Rodrigues, 1892, *Mourasuchus* Price, 1964 (Nettosuchidae) and the dinomyiid rodent *Neoepiblema ambrosettianus* Ameghino, 1889 enable us to place the new locality in the late Miocene-Pliocene of the Solimões Formation.

There has been much disagreement over the taxonomic status of the Orophodontidae. This confusion stems in part from the unclear relationship between the available orophodontid material and the osteoderms of *Palaeopeltis* Ameghino, 1895 discovered in the Deseaden of Argentina (Hoffstetter, 1954, 1956). We have never found large osteoderms at localities in the Brazilian state of Acre.

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