



ANATOMICAL REVIEW OF *EIRA BARBARA* (CARNIVORA, MUSTELIDAE) FROM THE QUATERNARY OF SOUTHWESTERN BRAZILIAN AMAZONIA

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ABSTRACT – Most species of mustelids currently found in South America descend from North American immigrants that arrived during the Great American Biotic Interchange, following the rise of the Isthmus of Panama. However, previous works indicate that the genus *Eira* arrived in South America before this event, through an island bridge in Central America. The tayra *Eira barbara* (Mustelidae, Carnivora), the only species of the genus, currently has a wide geographic distribution, from Mexico to northern Argentina. Here, we redescribe a fossil of *E. barbara* collected close to the municipality of Marechal Thaumaturgo, Acre State, Brazil. The southwestern Brazilian Amazonia is mostly characterized by the older sediments of Solimões Formation (Neogene deposits), although on the riverbanks of the Upper Juruá River a typical Quaternary vertebrate fauna is also found, mainly represented by fossil mammals. The specimen UFAC PV-36 is a right hemimandible with the p4 preserved *in situ*, and it was compared to fossil and extant specimens of *E. barbara*, as well as with other carnivorans. The review of the fossil record shows that this taxon is restricted to the Quaternary of Brazil, in the states of Bahia, Minas Gerais and Acre, and of Argentina, in the Entre Ríos Province. In this way, our study contributes to a better understanding of the origin and distribution of the genus in the Quaternary of South America.

Keywords: Acre State, Upper Juruá River, Solimões Formation, South America, Brazil.

RESUMO – A maioria das espécies de mustelídeos atualmente encontradas na América do Sul são descendentes de imigrantes norte-americanos que chegaram durante o Grande Intercâmbio Biótico Americano, após a ascensão do Istmo do Panamá. No entanto, trabalhos previos indicam que o gênero *Eira* teria chegado na América do Sul antes deste evento, através de um conjunto de ilhas na América Central. A irara *Eira barbara* (Mustelidae, Carnivora), a única espécie do gênero, atualmente tem uma ampla distribuição geográfica, desde o México até o norte da Argentina. Neste trabalho, redescrivemos um fóssil de *E. barbara* coletado em torno do Município de Marechal Thaumaturgo, Estado do Acre, Brasil. O sudoeste da Amazônia brasileira é principalmente caracterizado pelos sedimentos mais antigos da Formação Solimões (depósitos neógenos), embora nas margens do Alto Rio Juruá também é encontrada uma típica fauna de vertebrados do Quaternário, representada principalmente por fósseis de mamíferos. O material UFAC PV-36 é uma hemimandíbula direita, com o P4 preservado *in situ*, e foi comparado com espécimes fósseis e viventes de *E. barbara*, bem como com outros carnívoros. A revisão do registro fóssil reconhece que este táxon está restrito ao Quaternário do Brasil, nos estados da Bahia, Minas Gerais e Acre, e da Argentina, na Província de Entre Ríos. Assim, nosso estudo contribui para uma melhor compreensão da origem e da distribuição do gênero no Quaternário da América do Sul.

Palavras-chave: Estado do Acre, Alto Rio Juruá, Formação Solimões, América do Sul, Brasil.

INTRODUCTION

The fossil record indicates that the biogeographic history of mustelids is determined by numerous intercontinental dispersions, originating mainly in Eurasia, where the early fossils of the family (from the late Oligocene) were found (Wolsan, 1999; Tedford *et al.*, 2004; Koepfli *et al.*, 2008).

Koepfli *et al.* (2008) infer that paleoenvironmental and biotic changes driven by climate variations during the second half of the Neogene promoted two bursts of cladogenesis within mustelids. The first would have occurred during a ~3.7 million year interval, from the middle to late Miocene (12.5–5.8 Ma), and the second burst of diversification would have occurred during the Pliocene (5.3–1.8 Ma).

Most of the genera and species of mustelids currently found in South America descend from North American immigrants that arrived as part of the Great American Biotic Interchange (**GABI**), following the rise of the Isthmus of Panama, at about 3.0–2.5 Ma (Marshall & Sempere, 1993; Coates & Obando, 1996; Hunt, 1996; Koepfli *et al.*, 2008). In the case of *Eira*, this genus is closely related to the North American extinct taxa *Trigonictis* and *Legionarictis* (see Tseng *et al.*, 2009), corroborating this interpretation.

Based on mitochondrial data, Young (2018) reports that the process of diversification within *Eira* occurred at 6.3–4 Ma, coinciding with the end of the first or the beginning of the second diversification bursts detected by Koepfli *et al.* (2008). In this scenario, *Eira* would have arrived at South America earlier than other mustelids, before the complete formation of the Isthmus of Panama, coinciding with the presence of the Choco-Panama islands bridge (see Galvis, 1980). Alternatively, the rise of the Isthmus occurred earlier than most widely accepted, during the Miocene, as indicated by Montes *et al.* (2015).

The species *Eira barbara* (Linnaeus, 1758) is the only species of the genus and currently has a wide geographic distribution, from Mexico to northern Argentina (Figure 1), inhabiting tropical and subtropical forests (Reis *et al.*, 2006; Tortato & Althoff, 2007; Branco *et al.*, 2013; Castro *et al.*, 2014).

Fossils of *Eira barbara* in South America are relatively scarce and restricted to the Quaternary. In Brazil, the first record of the species was cited by Lund (1843), who named *Galictis barbara* (= *Eira barbara*), from the “Lapa da Escrivânia”, municipality of Lagoa Santa, in the Minas Gerais State (Figure 1A). Posteriorly, Rancy (1991) reported a specimen from the Upper Juruá River, in the Acre State (Figures 1B, 2), and Lessa *et al.* (1998) reported a fossil from “Gruta dos Brejões”, municipality of Morro do Chapéu, Bahia State (Figure 1C). Further reports include Castro *et al.* (2014), from the cave Gruta do Ioiô, municipality of Palmeiras, Bahia State (Figure 1D), and Vasconcelos (2015), who describes a specimen found in the “Maciço Escrivânia”, municipality of Prudente de Moraes, Minas Gerais State (Figure 1E). The most recent fossil record of the taxon is reported by Schiaffini *et al.* (2017), from Entre Ríos Province, Argentina (Figure 1F).

Although Rancy (1991) reported the fossil assigned to *Eira barbara* from the Upper Juruá River, Acre State, the anatomy and the taxonomic criteria used to identify the specimen were

presented only briefly. Therefore, the main goal of our study is to describe the specimen UFAC-PV 36, characterizing it in a taxonomic and systematic context.

MATERIAL AND METHODS

The specimen UFAC PV-36 (Figure 3) is housed at the paleontological collection of the Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre (**UFAC**), Rio Branco, State of Acre, Brazil. The material is a right hemimandible with the p4 preserved *in situ*, and it was compared to fossil and extant specimens of *Eira barbara*, as well as with other species of carnivorans (see Appendix 1). Osteological nomenclature follows Paula-Couto (1979) and the Nomina Anatomica Veterinaria, International Committee on Veterinary Gross Anatomical Nomenclature (2012). Dental nomenclature follows Paula-Couto (1979) and Smith & Dodson (2003). The systematic arrangement follows Bryant *et al.* (1993), Marmi *et al.* (2004) and Koepfli *et al.* (2008).

The material was collected near the municipality of Marechal Thaumaturgo, southwestern Amazonia, Acre State, Brazil (Figure 2). According to Latrubbles & Rancy (1998) and Cozzuol (2006), younger vertebrates from southwestern Brazilian Amazonia occur in several localities together with Neogene fossils, because Pleistocene terraces are developed on older Cenozoic sediments that were bisected by the same rivers that produced these terraces (Hsiou & Albino, 2011). The Solimões Formation contains a Miocene vertebrate fauna (see Cozzuol, 2006; Bissaro-Júnior *et al.*, 2018), while younger (Quaternary) bone-bearing conglomerates, as defined by Simpson & Paula-Couto (1981), are exposed unconformably over this unit. The Quaternary vertebrate fauna at these localities includes mainly fossil mammals, represented by carnivorans, notoungulates, xenarthrans, proboscideans, sirenians, perissodactyls and artiodactyls (Simpson & Paula-Couto, 1981; Ranzi, 2000, 2008; Hsiou & Albino, 2011). Both fossiliferous assemblages can be found along the Upper Juruá River in the State of Acre (Latrubbles & Rancy, 1998). The mammals recovered from Juruá River are often mixed by reworking of the deposits, hindering the establishment of specific levels in the locations (see Simpson & Paula-Couto, 1981; Paula-Couto, 1981, 1982a, 1982b, 1983; Latrubbles & Rancy, 1998; Ribeiro *et al.*, 2013).

Institutional abbreviations. **FUMDHAM**, Fundação Museu do Homem Americano, São Raimundo Nonato, Piauí, Brazil; **LPRP**, Laboratório de Paleontologia de Ribeirão Preto, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil; **MCL**, Coleção de Paleontologia, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil; **MCN-M**, Coleção de Mastozoologia, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil; **MNRJ**, Setor de Mastozoologia, Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; **MPEG**, Coleção de Mastozoologia, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; **MZUSP**, Coleção de Mastozoologia,



Figure 1. Records of *Eira barbara* in the South American Quaternary (A–F) and the current distribution of the species (gray shade). A, Lapa da Escrivanânia, Lagoa Santa, Minas Gerais, Brazil; B, Upper Juruá River, Acre, Brazil; C, Gruta dos Brejões, Morro do Chapéu, Bahia, Brazil; D, Gruta do Ioiô, Palmeiras, Bahia, Brazil. E, Maciço Escrivanânia, Prudente de Moraes, Minas Gerais, Brazil; F, Entre Ríos Province, Argentina.

Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil; UFAC, Universidade Federal do Acre, Acre, Brazil; UFAC-CZM, Coleção Zoológica de Mamíferos da Universidade Federal do Acre, Rio Branco, Acre, Brazil.

Anatomical abbreviations. c, lower canine; p2, second lower premolar; p3, third lower premolar; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

CARNIVORA Bowdich, 1821

MUSTELOIDEA Fischer von Waldheim, 1814

MUSTELIDAE Fischer von Waldheim, 1817

GULONINAE Gray, 1825

Eira Smith, 1842

Eira barbara (Linnaeus, 1758)
(Figure 3)

Referred specimen. UFAC-PV 36, an incomplete right hemimandible with the p4 preserved *in situ*.

Locality and age. The material was collected near the municipality of Marechal Thaumaturgo, southwestern Brazilian Amazonia, Acre State. Although the collection has not precise information about its stratigraphic origin, additional material was collected on the same terraces, allowing its attribution to the Quaternary (see Material and Methods).

Description. UFAC-PV 36 is a partial right hemimandible preserving a single premolar. It was briefly described by Rancy (1991), who referred this tooth as p3; however, the present analysis considers that it corresponds to the p4. Therefore, the specimen exhibits the entire p4 *in situ* and part of the root of the p3 (Figure 3). The fossil exhibits highly fragmented surfaces. The irregular aspect of fractures might be associated with transport and/or reworking of the bioclast. The presence of some rounded surfaces (at the condylar and angular process) is probably caused by dissolution processes (Holz & Simões, 2002). The dark coloration acquired by the material was

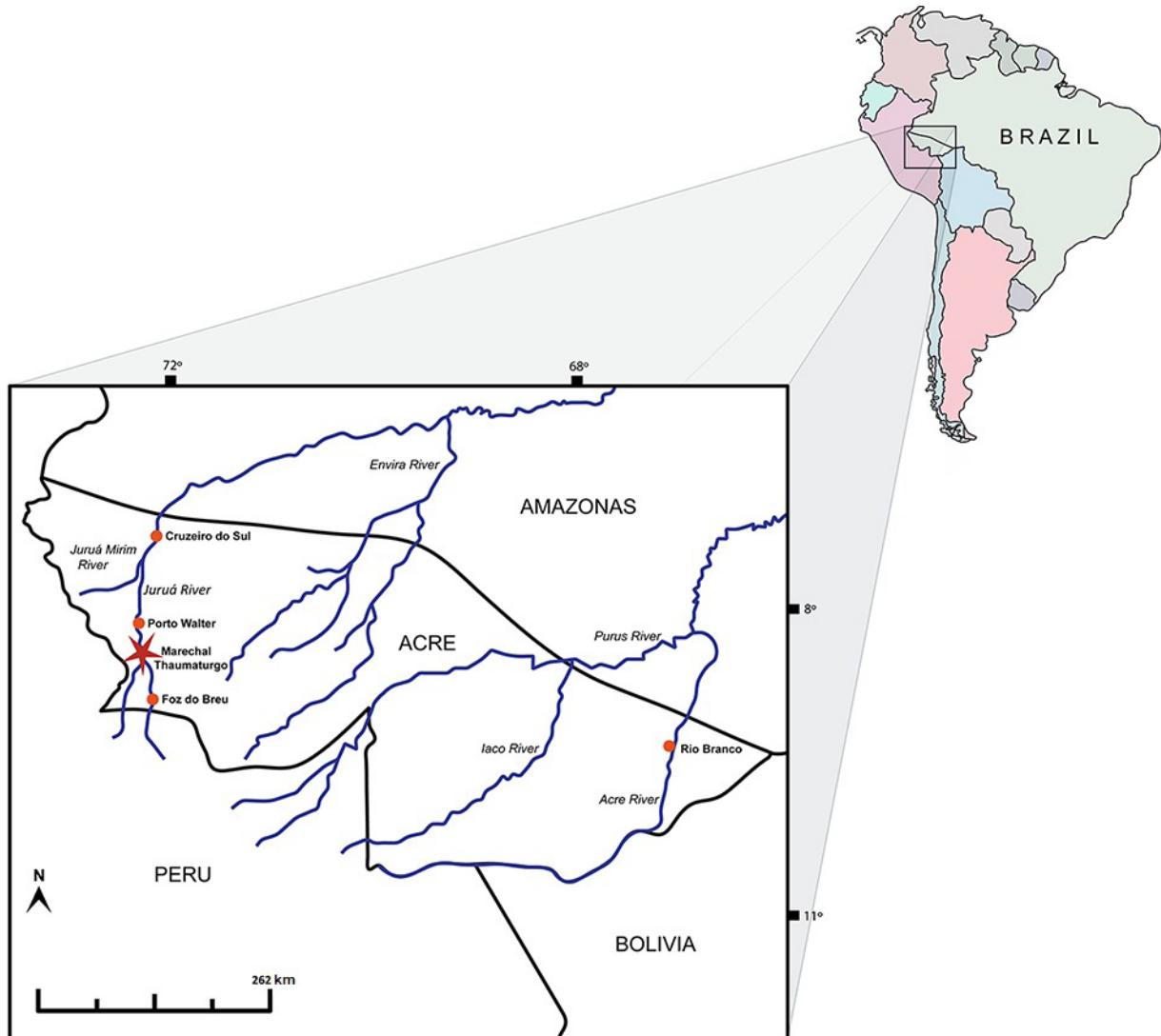


Figure 2. Acre State, southwestern Brazilian Amazonia, showing the collection site of the fossil UFAC PV-36 (red star).

possibly the result of manganese oxide impregnation during later diagenesis (Bissaro-Júnior, pers. com.).

The ventral and dorsal margins of the mandibular body are slightly curved. In the anterior portion of the lateral surface, there are three mental foramina, which vary in size and shape (Figures 3A,D). The masseteric fossa is shallow, extending above the level of the alveolus of m_2 and being limited by the anterior masseteric crest (Figures 3A,D). In medial view, the small mandibular foramen is posteriorly continued by an elongated groove that extends posteriorly towards the mandibular ramus. This foramen is located ventroposteriorly to the posterior margin of the alveolar process, between the angular process and the condyle (Figures 3B,E). The coronoid process and the posterior part of the condyle are broken. The angular process is curved and slightly prominent, while the angular notch is slightly curved dorsoventrally (Figures 3A,B,D,E). As the coronoid process is broken, only a small portion of the pterygoid fossa can be

observed. It is shallow and dorsally limited by the alveolar process and posteroventrally by the groove that extends from the mandibular foramen (Figures 3B,E). The alveolar process extends from the posterior margin of the symphysis until the anterior margin of the coronoid process. The alveolus of c , p_{2-3} , and m_{1-2} are present, being very close to each other (Figure 3C). As for its dental roots, the c , p_2 and m_2 are single-rooted teeth, and the p_{3-4} and m_1 are two-rooted teeth. The mandibular symphysis is short and extends posteriorly to the anterior level of p_2 (Figures 3B,E). The p_4 (Figure 3) has a small and slightly elongated crown. The mesial cingulum is narrower and more elongated than the distal cingulum. This tooth has small fractures on the apex of the crown, distal cingulum, and tooth neck. In lateral view (Figures 3A,D), the tooth is gently convex in cross-section, differently from the medial view, where the surface appears to be slightly convex in the anterior portion and slightly depressed in the middle and posterior portions (Figures 3B,E).

Measurements (in mm). Length from the anterior end of the mandibular symphysis to the posterior end of the condylar process: 69.7; height of the mandibular body at the distal edge of m1: 16.2; maximum height of p4: 6.85; width of p4: 4.3; length of p4: 5.5; length of the alveolar process: 30.7.

Morphological and taxonomical comparisons. The fossil UFAC-PV 36 described here, as well as living specimens of *Eira barbara*, present morphological characteristics that resemble mainly the mandibular anatomy of *Galictis vittata*. However, the following characters allowed the taxonomic determination: the mandibular body of both species are slightly arched, but its height is smaller in *G. vittata* than in *E. barbara*;

the mandibular symphysis in *G. vittata* may extend to the distal border of p4, while in *E. barbara* the symphysis is restricted to the distal border of p2; the alveolar process of *E. barbara* shows a small space between the alveolus of p2 and of the canine, whereas in *G. vittata* this gap is absent, making the p2 and canine very close; the p4 of both species are very similar, but *G. vittata* has a much wider distal cingulum than *E. barbara*.

Misinterpreted fossil record of *Eira barbara*. Two post-Pliocene fossils from the United States of America were misinterpreted as belonging to this taxon, under the names of “*Galera perdicida*” and “*G. macrodon*” (Cope, 1868a–c). However, after a reappraisal, *G. perdicida* was assigned to the genus *Mephitis* (Alston, 1882) and *G. macrodon* was attributed to *Trigonictis*, an intermediate form between the genus *Galictis* and *Eira*, probably in the same lineage of these two genera (Presley, 2000; Ruiz-García et al., 2013). Guérin et al. (1993) described a fossil from Toca de Cima dos Pilão from the São Raimundo Nonato, Piauí State, Brazil, with doubts about its taxonomic attribution, probably due to the high degree of fragmentation. Our analysis of photos of this specimen (FUMDHAM 19993) indicates that the mandibular and dental morphology does not agree with *E. barbara*; since its preservation prevents a better taxonomic assignment, it can be assigned to Musteloidea indet.

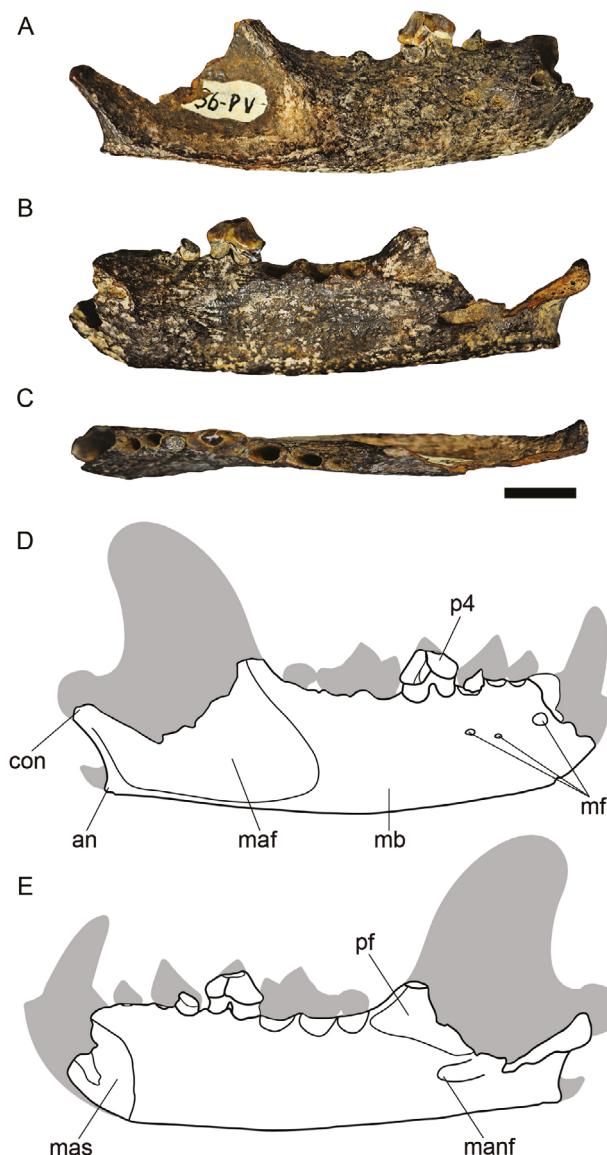


Figure 3. Right hemimandible of *Eira barbara* (UFAC PV-36). A, lateral view; B, medial view; C, occlusal view; D, schematic drawing of the lateral view; E, schematic drawing of the medial view. The outlines in gray in figures D and E represent the missing structures of the hemimandible (UFAC PV-36) when compared to an extant adult specimen. Abbreviations: an, angular process; con, condylar process; maf, masseteric fossa; manf, mandibular foramen; mas, mandibular symphysis; mb, mandibular body; mf, mental foramina; pf, pterygoid fossa; p4, fourth lower premolar. Scale bar = 1 cm.

FINAL CONSIDERATIONS

The present paper describes the specimen UFAC-PV 36 from the Quaternary of Upper Juruá River, Acre, Brazil. The fossil corresponds to a right hemimandible with p4 preserved and assigned to *Eira barbara*. The revision of previous records indicate that fossils of the species are restricted to the Quaternary of Brazil, in the states of Bahia (Lessa et al., 1998; Castro et al., 2014.), Minas Gerais (Lund, 1843; Vasconcelos, 2015) and Acre (Rancy, 1991), and in Entre Ríos Province, Argentina (Schiaffini et al., 2017). Thus, the paleogeographic distribution of *E. barbara* was broader than the current one.

Considering that the fossils of *Eira barbara* known so far, including UFAC-PV 36, do not have their precise age determined, we consider a broad Quaternary age. However, although UFAC-PV 36 is a resedimented material, it was collected *in situ*, but reworked, we suggest that it has a Late Pleistocene age, for the following reasoning: according to Latrubesse & Rancy (1998), the Upper Juruá River presents a Upper Pleistocene facies, defined by Simpson & Paula-Couto (1981) as “bone-bearing conglomerate”, with colors ranging from black to red-brown due to the precipitation of iron oxides; this condition is very similar to that observed in UFAC-PV 36.

Latrubesse & Rancy (1998) point out that according to the radiocarbon ages recorded in the Ucayali, Madre de Dios and Caqueta rivers, the Pleistocene sediments deposited in the upper Rio Juruá may be tentatively correlated with the Middle Pleniglacial of the Last Glaciation. For Van der Hammen & Absy (1994), during the Middle Pleniglacial the Amazonian climate was cooler or colder and with higher rainfall, changing to a drier and markedly cold climate during the Late Pleniglacial (Latrubesse & Rancy, 1998).

However, the results of Latrubesse & Rancy (1998) indicate that the climatic shift in the lowlands of the southwest of the Amazon began before the Late Pleniglacial period of the Last Glaciation. Vertebrate fossil records from Juruá River are inconclusive, as some were associated to drier savannas and others to less arid conditions (see Latrubesse & Rancy, 1998). According to the authors, the sedimentological phase of Late Pleistocene deposition, recognized in other Amazonian rivers and associated with the climatic changes produced during deglaciation, was not identified in the Basin of Juruá River. Certainly, further stratigraphic and geochronologic works will provide a more complete paleoenvironmental frame for the Neogene and Quaternary of western Amazonia.

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Appendix 1. List of specimens analyzed and compared to UFAC PV-36.

Species	Specimens
<i>Eira Barbara</i> (extant)	MPEG 134; MPEG 838; MPEG 276; MPEG 331; MPEG 836; MPEG 837; MPEG 1523; MPEG 1843; MPEG 4216; MPEG 1208; MPEG 4218; MPEG 4247; MPEG 5510; MPEG 07900; MPEG 6519; MPEG 7112; MPEG 5621; MPEG 5622; MPEG 5623; MPEG 5624; MPEG 5625; MPEG 5629; MPEG 5626; MPEG 5627; MPEG 5628; MPEG 5630; MPEG 5631; MPEG 5632; MPEG 6517; MPEG 9210; MPEG 10013; MPEG 10032; MPEG 10014; MPEG 10245; MPEG 10473; MPEG 11903; MPEG 20184; MPEG 22400; MPEG 22654; MPEG 6518; MNRJ 3100; MNRJ 3102; MNRJ 3106; MNRJ 3107; MNRJ 4904; MNRJ 4907; MNRJ 5163; MNRJ 5512; MNRJ 5619; MNRJ 5649; MNRJ 5791; MNRJ 5959; MNRJ 5960; MNRJ 6085; MNRJ 6088; MNRJ 6089; MNRJ 7611; MNRJ 10990; MNRJ 25686; MNRJ 29976; MNRJ 29977; MNRJ 30003; MNRJ 51650; MNRJ 63452; MNRJ 68357; MNRJ 68358; MNRJ 68365; MNRJ 68625; MNRJ 74385; MNRJ 75096; MZUSP 468; MZUSP 144; MZUSP 2469; MZUSP 3184; MZUSP 1693; MZUSP 1438; MZUSP 1087; MZUSP 22391; MZUSP 2061; MZUSP 27682; MZUSP 22390; MZUSP 20192; MZUSP 22387; MZUSP 21626; MZUSP 22392; MZUSP 22389; MZUSP 22388; MZUSP 2976; MZUSP 445; MZUSP 19817; MZUSP 2975; MZUSP 1807; MZUSP 19818; MZUSP 7699; MZUSP 837; MZUSP 2848; MZUSP 2974; MZUSP 3760; MZUSP 1163; MZUSP 6811; MZUSP 488; MZUSP 1162; MZUSP 2924; MZUSP 1161; MZUSP 2972; MZUSP 2726; MZUSP 5933; MZUSP 2237; MZUSP 2727; MZUSP 2728; MZUSP 6584; MZUSP 19814; MZUSP 3826; MZUSP 4243; MZUSP 3918; MZUSP 4244; MZUSP 3917; MZUSP 4242; MZUSP 4294; MZUSP 6316; MZUSP 7029; MZUSP 2653; MZUSP 5855; MZUSP 3375; MZUSP 22901; MZUSP 20056; MZUSP 20068; MZUSP 5188; MZUSP 5185; MZUSP 5192; MZUSP 5191; MZUSP 19797; MZUSP 5194; MZUSP 5140; MZUSP 5193; MZUSP 926; MZUSP 5189; MZUSP 5186; MZUSP 5194; MZUSP 19798; MZUSP 19809; MZUSP 19802; MZUSP 3672; MZUSP 5187; MZUSP 5275; MZUSP 19799; MZUSP 19807; MZUSP 10143; MZUSP 10145; MZUSP 19806; MZUSP 10144; MZUSP 19805; MZUSP 19800; MZUSP 19803; MZUSP 19808; MZUSP 19804; MZUSP 19810; MZUSP 19801; MZUSP 19845; MZUSP 5183; MCN-M 2981; MCN-M 3012; MCN-M 1915; MCN-M 1987; MCN-M 1898; MCN-M 1746; MCN-M 1897; MCN-M 1745; UFAC-CZM 016; UFAC-CZM 36; UFAC-CZM 154; UFAC-CZM 151.
<i>Eira barbara</i> (fossil)	MCL 1849-01; MCL 21.170 01-02; LPRP 0728; FUMDAM 19993.
<i>Galictis vittata</i>	MPEG 4221; MPEG 4222; MNRJ 75066.
<i>Galictis cuja</i>	MPEG 22230; MPEG 22188; MNRJ 3115; MNRJ 29989.
<i>Lontra longicaudis</i>	MPEG 4245; MPEG 4244; MPEG 4238; MPEG 4242; MNRJ 50799; MNRJ 50800.
<i>Mustela africana</i>	MPEG 6526; MPEG 6515.
<i>Pteronura brasiliensis</i>	MPEG 671; MPEG 5603; MPEG 685.
<i>Conepatus chinga</i>	MPEG 22190; MPEG 22232.
<i>Nasua nasua</i>	MPEG 1531; 58; MPEG 4295.
<i>Potos flavus</i>	MPEG 4340; MPEG 4347.
<i>Procyon concrivorus</i>	MPEG 4207; MPEG 721.
<i>Conepatus semistriatus</i>	MNRJ 29990.
<i>Gulo gulo</i>	MNRJ 3492.
Musteloidae ident.	FUMDHAM 19993