

THE OLDEST SPECIES OF *DIDELPHIS* (MAMMALIA, MARSUPIALIA, DIDELPHIDAE), FROM THE LATE MIOCENE OF AMAZONIA

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The oldest known species of the genus *Didelphis* (Mammalia, Marsupialia, Didelphidae) is described here. The holotype and only known specimen comes from the late Miocene deposits of the Solimões Formation at Patos, Acre River, Brazil. The new species is one of only a few marsupials known from this assemblage. The new species differs from other known species by its smaller size, low mandibular ramus, smaller molars relative to premolars, and p3 with inflated crown. The last feature suggests more frugivorous habits than in other species of the genus.

Key words: Acre, Amazon, *Didelphis*, late Miocene

Living species of *Didelphis* Linnaeus, 1758 (Mammalia, Marsupialia, Didelphidae), the largest and most conspicuous marsupials of the Americas, range from Canada to Patagonia. *D. virginiana* Kerr, 1792, is distributed from British Columbia to Costa Rica. *D. marsupialis* Linnaeus, 1758, is known from Mexico to tropical South America. The remaining 2 species are strictly South American. *D. albiventris* Lund, 1841, occurs through a mostly peri-Amazonian belt from Colombia and Venezuela to Argentina, whereas *D. aurita* Wied-Neuwied, 1826, is from southeastern Brazil (Brown 2004). Two Pampean (Argentina), extinct species of this genus also have been reported, the late Pliocene (Chapadmalalan South American Land Mammal Age) *D. crucialis* (Ameghino, 1904) and the late Pliocene–early Pleistocene (Chapadmalalan–Ensenadan South American Land Mammal Ages) *D. reigi* Simpson, 1972 (Goin 1991; Goin and Pardiñas 1996).

Goin (1991) postulated that the evolutionary history of *Didelphis* could be traced back in time to the beginning of the Neogene. Because of the reduced exposures and consequently relatively poor fossil record for tropical regions of the Americas, most of the Neogene history of this (and many

other didelphid genera) remains obscure. Remains of didelphid marsupials were reported for the Acre region of Brazil (Czaplewski 1996), but no identification at generic or lower levels was possible. Here we report the oldest record of a species of *Didelphis*, coming from the late Miocene deposits of the Amazonian region in Brazil.

MATERIALS AND METHODS

Locality, geology, associated fauna, and age.—Specimen UFAC 5180 was collected from the Solimões Formation at Patos, at the border between Peru and Brazil along the upper Acre River (10°55'55"S, 69°55'20"W) in a riverbank cut that was approximately 38 km upriver from the towns of Assis Brasil (on the Brazilian side) and Iñapari (on the Peruvian side; Fig. 1). The outcrop is visible only during the dry season and consists of an intraformational conglomerate with clasts of clay and silt. It is part of a large paleochannel (Fig. 2). The base of the unit is not visible and its upper part is covered by vegetation.

The Solimões Formation, of Tertiary age, has a large regional extent in southwestern Amazonia. From sediment cores, the formation has a maximum thickness of 1,800 m and is about 800 m thick in the Acre region. Surface outcrops occur along road cuts and banks of the main rivers in this region, reaching a maximum thickness of 70–100 m. Latrubesse et al. (1997) interpret the Solimões deposits as being part of a megafan system with its headwaters in the Peruvian Andes. The system was a sedimentary response to tectonic movements in the Andean foreland basin. The relevant tectonic phase was initiated in the Bolivian and Peruvian Andes approximately 10 ± 2 million years ago (Jordan et al. 1983; Marshall and Sempere 1993).

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FIG. 1.—Location of the type locality of *Didelphis solimoensis*.

The temporal interval of deposition for the formation has been reported as spanning from Paleocene to Pleistocene but examination of recent data indicates that its range may be from late early Miocene to late Miocene (Cozzuol, in press; Hoon 1993, 1994a, 1994b, 1995; Hoon et al. 1995). Outcrops in the Acre region, including the ones containing the specimen studied here and other vertebrates, are considered to be of late Miocene age (time equivalent to Huayquerian South American Land Mammal Age) based on the amniote taxa (Cozzuol, in press). Recent radiometric dates from ashes in sediments correlative to the Solimões Formation at 2 Peruvian localities close to the Brazilian border gave dates of 9.01 and 3.12 million years ago (Campbell et al. 2001). The dates are consistent with the age indicated by the fossil vertebrates, but the precise stratigraphic position of the lower ash is not clear (Campbell et al. 2000:77).

Other specimens found at Patos (mostly under study), include pombatrygonid rays; catfishes of the families Callichthyidae, Doradidae, and Pimelodidae; characiform fishes of the family Characidae; crocodiles of the families Alligatoridae and Gavialidae; aquatic turtles; and mammals. Among the latter are primates of the families Cebidae and Atelidae (Kay and Cozzuol 2006), xenarthrans of the families Dasypodidae and Glyptodontidae, as well as indeterminate sloths. Rodents are represented mainly by teeth but some more-complete specimens also were recovered. They belong to the families Caviidae, Erethizontidae, Dinomyidae, Dasyproctidae, and Echimyidae. Fragmentary remains of notungulates also were found. Frailey (1986) provides a faunal list from the same locality that is generally consistent with ours.

The geological interpretation is consistent with and age-equivalent to the Huayquerian South American Land Mammal Age (9–6.8 million years ago) for the mammalian faunas (Flynn and Swisher 1995; Marshall et al. 1983). According to this chronology, the temporal constraints placed on the age of the specimen described here make it 3–6 million years older than previous records of *Didelphis*.

Abbreviations and terminology.—We used the following abbreviations: UFAC, Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco, Acre, Brazil; MLP, División Paleontología Vertebrados, Museo de La Plata. Dental nomenclature and terminology for length (L) and width (W) of teeth follows Goin et al. (2003). Measurements with an asterisk are estimated. All measurements are in millimeters.

RESULTS

Superorder Marsupialia Illiger, 1811
 Order Didelphimorphia Gill, 1872
 Family Didelphidae Gray, 1821
 Genus *Didelphis* Linnaeus, 1758
Didelphis solimoensis, new species
 Figs. 3a–c

Type.—UFAC 5180, fragment of right dentary with alveoli of p1, roots and posterior one-third of p2, and complete p3–m2.

Hipodigm.—The type only.

Etymology.—*solimoensis*, after Solimões Formation, which yielded the holotype and only known specimen.

Locality and age.—The type comes from Patos, along the upper Acre River (10°55'55"S, 69°55'20"W), in a riverbank cut approximately 38 km upriver from the towns of Assis Brasil (on the Brazilian side) and Iñapari (on the Peruvian side). Solimões Formation, late Miocene (equivalent to Huayquerian South American Land Mammal Age).

Measurements (in mm).—Lp1–p3: 12.5*; Lp1–m2: 19.5*; Lp2: 5.3; Wp2: 1.7; Lp3: 4.2; Wp3: 2.1; Lm1: 3.9; Wm1: 1.8; Lm2: 4.0; Wm2: 2.1.

Diagnosis.—Differs from all other species of *Didelphis* in the following features: smaller size, low horizontal ramus, p3 with inflated crown, smaller molars relative to the premolar series.

Description.—Even though incomplete, the completely erupted p3 suggests that the holotype of *D. solimoensis* belonged to an adult or subadult individual. Thus, the gracility of the dentary bone distinguishes this species among the others in the genus. The lingual face of the dentary is relatively flat. At its posterior end, the symphysis reaches a point located below the anterior root of p2. The labial face of the dentary is convex and relatively wide, even below the premolar teeth. The anterior mental foramen is proportionally larger than that of other species of *Didelphis*, and is located below the anterior root of p2. Judging from the preserved roots it can be appreciated that, even though absent, p1 was not very much reduced in relation to p2. In turn, and judging from the length and the size of its root, p2 (which is almost completely broken) was larger than p3, as in all modern didelphids. The most obvious feature of the crown of p3 is its bulbous, swollen aspect. This single feature clearly distinguishes *D. solimoensis* from all other species of the genus. The p3 is single-cusped and has its posterior crest longer and slightly more subvertical than the anterior one. Another feature that easily distinguishes *D. solimoensis* from other species of the genus is the proportionally smaller size of the lower molars, both in absolute measures as well as relative to the premolar teeth. The 2 preserved molars are only slightly worn; on m1 the paraconid is somewhat labio-

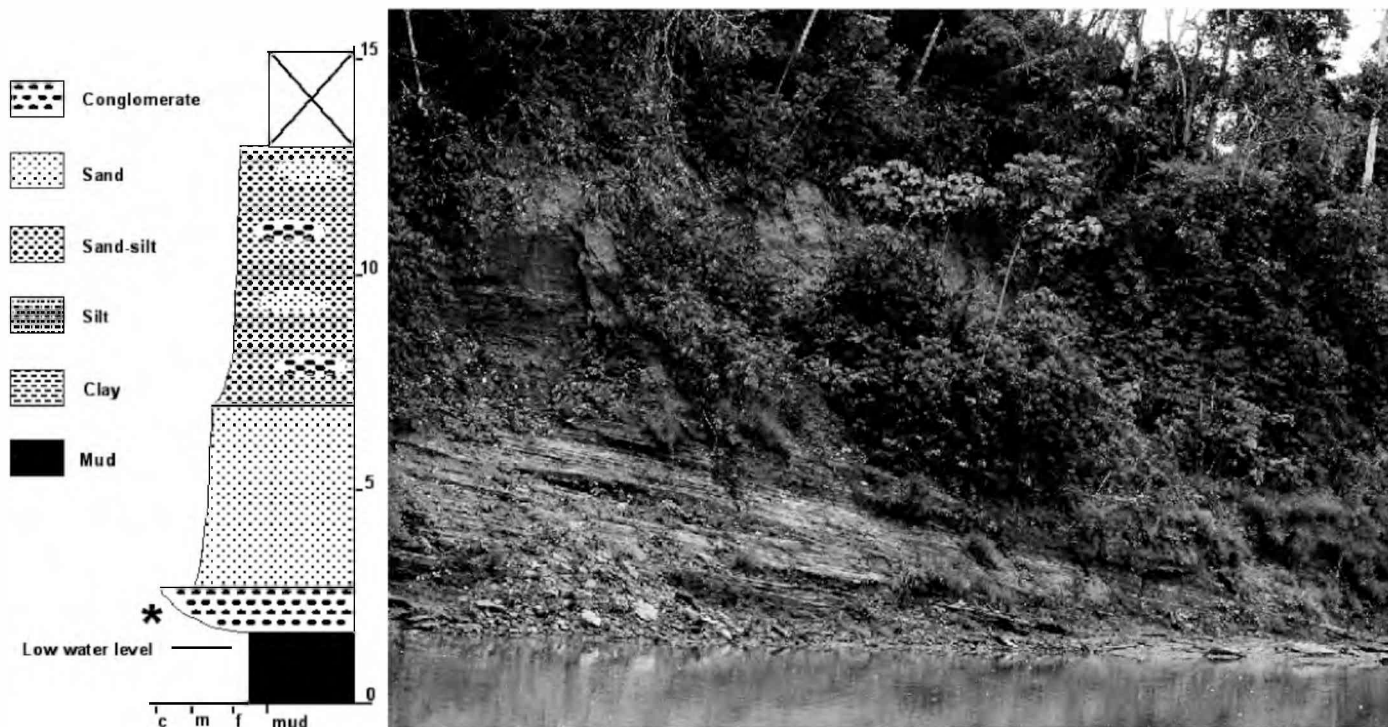


FIG. 2.—View of collection site and, on left, geologic section of the outcrops of Patos, along the Acre River on border between Peru and Brazil, from which the holotype of *Didelphis solimoensis* was recovered. Vertical scale in meters; horizontal scale indicates sediment granulometry: c = coarse, m = medium, f = fine; asterisk indicates level in which the specimen was found. Photo by C. Simon Gutstein.

lingually compressed, more so than in living species of *Didelphis*. The talonid of this molar is proportionally larger than that of m2. The entoconids of both molars are well developed, and their hypoconids are only slightly salient laterally. Both molars have a small, labial, single-cusped cingulid at the crown base between the hypoconid and the entoconid. The anterobasal cingulid is well developed on both molars, being narrower than that of other species of the genus.

Comparisons.—The new species can only be assigned to the genus *Didelphis*. Species of *Lutreolina* have the p2 much larger (higher and longer) than the p3, all premolars are laterally compressed, and molars have shorter talonids and more reduced entoconids. The new species differs from *Philander* because in the latter the p2 and p3 are laterally compressed and have more vertical anterior and posterior crests. Molars also are more laterally compressed and have comparatively longer paracristids. When compared with extinct didelphids, the only similarity between *Hyperdidelphis* and *D. solimoensis* is a short diastema between p1 and p2 (because of the former's carnivorous adaptations—see a review in Goin and Pardiñas [1996]). In contrast, the premolars of *Hyperdidelphis* are more laterally compressed than in *Didelphis*; the molars have more robust trigonids with trenchant paracristids, and short, reduced talonids. Finally, the extinct *Thylophorops* is very large, its p3 has a well-developed “talonid” posterior to its posterior crest, and its molars are wider and more robust than those of any *Didelphis* (see also Goin and Pardiñas 1996).

Didelphis solimoensis is the smallest known species of *Didelphis*; its p3 is comparatively wider and more bulbous, whereas m1 and m2 are proportionally smaller and have

narrower trigonids than in other members of the genus. Even comparing the holotype of *D. solimoensis* with juvenile specimens of other species of the genus, the diastema between p1 and p2 is shorter in the former. Other than these most obvious features, the fragmentary nature of the holotype of *D. solimoensis* makes very difficult other comparisons with living or extinct species of *Didelphis*. Compared with the living ones, *D. solimoensis* shows closer resemblances with *D. marsupialis*: the length of the diastema between p1 and p2 is smaller in *D. marsupialis* than in other living species; the crown of its p3 is proportionally more swollen (although not as much as in *D. solimoensis*), and its posterior talon is less developed; and the anterobasal cingulum in m1 and m2 is well developed. The extinct Pampean Neogene species of the genus *Didelphis*, *D. reigi*, is much larger, its p1 is poorly reduced, the p3 is much more trenchant, the diastema between p1 and p2 is proportionally larger, and the lower molars are stronger, compared to *D. solimoensis*. In turn, *D. crucialis* is more similar in size to *D. solimoensis*; however, its molars are stronger, p2 is proportionally larger, and p3 has a better developed, more trenchant anterior crest.

In short, *D. solimoensis* is the smallest known species of *Didelphis*. Its known dental and mandibular features suggest closer affinities with *D. marsupialis* than to any other species of this genus.

DISCUSSION

Living species of *Didelphis* have omnivorous, opportunistic feeding habits that frequently show seasonal variations. In

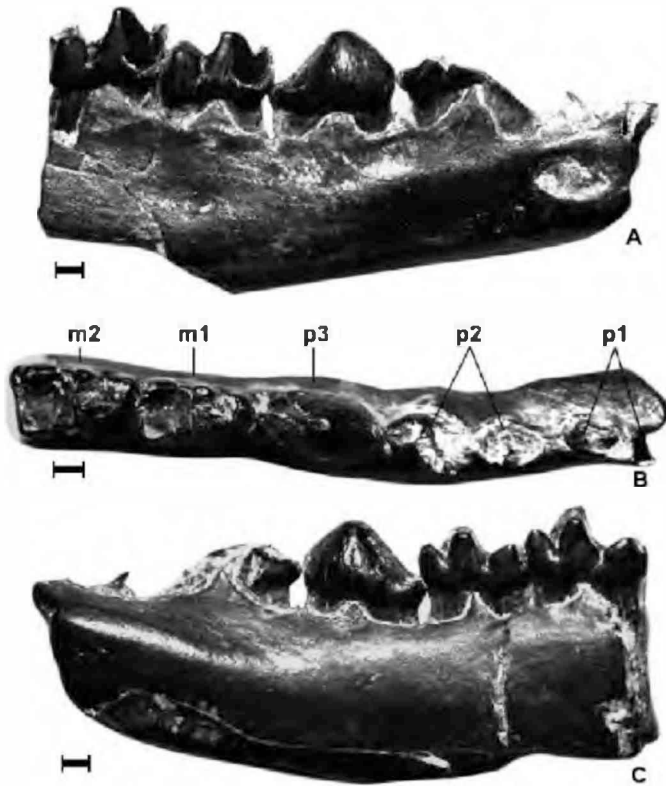


FIG. 3.—Holotype of *Didelphis solimoensis* (specimen UFAC 5180). A) labial, B) occlusal, and C) lingual views of anterior part of dentary. The black bar is 1 mm.

neotropical forests, the diet of *D. marsupialis* consists of a wide variety of items, including insects, frogs, birds, small mammals, earthworms, fruits, and other types of plant material (Cordero and Nicolas 1987). Even gum exudates from several tree species have been reported as a feeding item of *D. albiventris* from the Atlantic forests of southeastern Brazil (Aléssio et al. 2005). Interestingly, Cáceres (2002) noted that *D. albiventris* from southern Brazil is an effective seed disperser. Analyzing scat contents produced by this species, he found fruit remains in 76% of the scat sample (compared to 100% occurrence of invertebrates and 58% occurrence of small vertebrates). Seeds of several plants remained viable (as later tested through germination experiments) after passing through the opossum's guts. The inflated p3 of *D. solimoensis*, as well as the weak development of crests in the lower molars, may be interpreted as an indication of more strictly frugivorous feeding habits in this extinct, Amazonian species. Such habits already have been inferred for several taxa of extinct (Paleocene) "opossum-like" marsupials bearing an enlarged p3 (Marshall 1987).

Because of their generalized postcranial skeleton, species of *Didelphis*, as well as many other didelphids, are capable of a wide range of locomotory patterns, including arboreal, terrestrial, and aquatic (McManus 1974). If more strictly frugivorous, it could be the case that *D. solimoensis* was adapted for a more arboreal locomotion, such as that characteristic of living caluromyids (Bucher and Hoffmann 1980). This hypothesis needs to be tested with (still unknown) postcranial materials of *D. solimoensis*. Judging from comparable parts, *D. solimoensis*

probably resembled in size and body weight the living *Caluromys* and *Philander*, whose mean body masses have been estimated between 275 g (*Caluromys derbianus*) and 531 g (*Philander opossum*—Gordon, 2003).

Summing up, *D. solimoensis*, from the late Miocene of Amazonia, is the smallest known species of the genus. Its dental specializations suggest more frugivorous feeding habits than its living counterparts. It shares more features in common with *D. marsupialis* than with any other known species of *Didelphis*, living or extinct. *D. solimoensis* may represent an early offshoot of the *Didelphis* clade, with no ecological counterparts among the living species of the genus.

RESUMO

Descreve-se aqui a espécie mais antiga do gênero *Didelphis* (Mammalia, Marsupialia, Didelphidae). O holótipo e único espécime conhecido procede dos depósitos da Formação Solimões, Mioceno superior, na localidade de Patos, alto rio Acre, Estado do Acre, Brasil. A nova espécie é um dos poucos marsupiais conhecidos para esta associação. Esta nova espécie difere das outras conhecidas pelo seu menor tamanho, ramo mandibular baixo, molares pequenos comparados aos premolares e p3 com a coroa inflada. Esta última característica sugere hábitos mais frugívoros quando comparada as outras espécies do gênero.

ACKNOWLEDGMENTS

We thank the Laboratório de Pesquisas Paleontológicas of the Universidade Federal de Acre (UFAC) for allowing us to study the material and for providing other information related to the locality. The specimen here described was collected with funding from a grant from Conselho Nacional de Pesquisas Científicas e Tecnológicas, the Brazilian Science Council, to MAC. M. Tomeo prepared the photograph of the holotype.

LITERATURE CITED

- ALESSIO, F. M., A. R. MENDES PONTES, AND V. L. DA SILVA. 2005. Feeding by *Didelphis albiventris* on tree gum in the northeastern Atlantic forest of Brazil. *Mastozoología Neotropical* 12:53–56.
- BROWN, B. E. 2004. Atlas of New World marsupials. *Fieldiana, Zoology* (New Series) 102:1–308.
- BUCHER, J. E., AND R. S. HOFFMANN. 1980. *Caluromys derbianus*. *Mammalian Species* 140:1–4.
- CÁCERES, N. C. 2002. Food habits and seed dispersal by the white-eared opossum, *Didelphis albiventris*, in southern Brazil. *Studies on Neotropical Fauna and Environment* 37:97–104.
- CAMPBELL, K. E., C. D. FRAILEY, AND L. ROMERO-PITMAN. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the Great American Faunal Interchange. *Boletín Instituto Geológico Minero y Metalúrgico, Serie D, Estudios Regionales* 23:1–152.
- CAMPBELL, K. E., M. HEIZLER, C. D. FRAILEY, L. ROMERO-PITMAN, AND D. R. PROTHERO. 2001. Upper Cenozoic chronostratigraphy of the southwestern Amazon Basin. *Geology* 29:595–598.
- CORDERO R., G. A., AND R. A. NICOLAS B. 1987. Feeding habits of the opossum (*Didelphis marsupialis*) in northern Venezuela. Pp. 125–131 in *Studies in neotropical mammalogy: essays in honor of Philip Hershkovitz* (B. D. Patterson and R. M. Timm, eds.). *Fieldiana: Zoology* 39:i–vii + 1–506.

- COZZUOL, M. A. In press. The Acre vertebrate fauna: age, diversity and geography. *Journal of South American Earth Sciences*.
- CZAPLEWSKI, N. J. 1996. Opossums (Didelphidae) and bats (Noctilionidae and Molossidae) from the late Miocene of the Amazon Basin. *Journal of Mammalogy* 77:84–94.
- FLYNN, J. J., AND C. C. SWISHER III. 1995. Cenozoic South American land mammal ages: correlation to global geochronologies. Pp. 317–333 in *Geochronology, time scales, and global stratigraphic correlation* (W. A. Berggren, D. V. Kent, M.-P. Aubry, and J. Hardenbol, eds.). Special Publication 54, Society for Sedimentary Geology, Tulsa, Oklahoma.
- FRAILEY, C. D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Rio Acre region, western Amazonia. *Contributions in Science, Natural History Museum of Los Angeles County* 374:1–46.
- GOIN, F. J. 1991. Los Didelphoidea (Mammalia, Marsupialia) del Cenozoico tardío de la Región Pampeana. Ph.D. dissertation, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina.
- GOIN, F. J., A. CANDELA, AND C. DE MUÍZON. 2003. The affinities of *Roberthoffstetteria nationalgeographica* (Marsupialia) and the origin of the polydolopine molar pattern. *Journal of Vertebrate Paleontology* 23:869–876.
- GOIN, F. J., AND U. F. PARDIÑAS. 1996. Revisión de las especies del género *Hyperdidelphys* Ameghino, 1904 (Mammalia, Marsupialia, Didelphidae). Su significación filogenética, estratigráfica y adaptativa en el Neógeno del cono sur sudamericano. *Estudios Geológicos* 52:327–359.
- GORDON, C. L. 2003. A first look at estimating body size in dentally conservative marsupials. *Journal of Mammalian Evolution* 10:1–21.
- HOORN, C. 1993. Miocene incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105:267–309.
- HOORN, C. 1994a. Fluvial palaeoenvironments in the Amazonas Basin (early Miocene–early middle Miocene, Colombia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 109:1–54.
- HOORN, C. 1994b. An environmental reconstruction of the palaeo-Amazon river system (middle–late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 112:187–238.
- HOORN, C. 1995. Comment on late Miocene tidal deposits in the Amazonian foreland basin by Räsänen, M., Linna, A.M., Santos, J.C.R., Negri, F.R. *Science* 273:122–123.
- HOORN, C., J. GUERRERO, G. A. SARMIENTO, AND M. A. LORENTE. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* 23:237–240.
- JORDAN, T., B. L. ISACKS, R. W. ALLMENDINGER, I. A. BREWER, V. A. RAMOS, AND C. J. AANDO. 1983. Andean tectonics related to geometry of subducted Nazca plate. *Bulletin of the Geological Society of America* 94:321–361.
- KAY, R. F., AND M. A. COZZUOL. In press. New platyrrhine monkeys from the Solimões Formation (late Miocene, Acre State, Brazil). *Journal of Human Evolution*.
- LATRUBESSE, E. M., J. BOQUENTIN, C. R. SANTOS, AND C. G. RAMONELL. 1997. Paleoenvironmental model for the late Cenozoic south-western Amazonia: paleontology and geology. *Acta Amazonica* 27:103–118.
- MARSHALL, L. G. 1987. Systematics of Itaboraian (middle Paleocene) age 'opossum-like' marsupials from the limestone quarry at Sao José de Itaboraí, Brasil. Pp. 91–160 in *Possums and opossums: studies in evolution* (M. Archer, ed.). Vol. 1. Surrey Beatty & Sons Pty. Limited and the Royal Zoological Society of New South Wales, Sydney, Australia.
- MARSHALL, L. G., R. HOFFSTETTER, AND R. PASCUAL. 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata, Mémoire Extra (Montpellier)* 1–93.
- MARSHALL, L. G., AND T. SEMPERE. 1993. Evolution of the neotropical Cenozoic land mammal fauna in its geochronologic, stratigraphic, and tectonic context. Pp. 329–392 in *Biological relationships between Africa and South America* (P. Goldblatt, ed.). Yale University Press, New Haven, Connecticut.
- McMANUS, J. J. 1974. *Didelphis virginiana*. *Mammalian Species* 40:1–6.

Submitted 29 August 2005. Accepted 19 January 2006.

Associate Editor was Carey Krajewski.