Late Miocene Bats from the Juruá River, State of Acre, Brazil, with a Description of a New Genus of Thyropteridae (Chiroptera, Mammalia)[1]

Nicholas J. Czaplewski[2,4] and Kenneth E. Campbell, Jr.[3]

ABSTRACT. We describe a new genus and species of thyropterid bat, *Amazonycteris divisus*, based on an isolated M^1 from upper Miocene deposits cropping out along the Juruá River in western Amazonia. The new taxon lacks a parastyle and stylocone on M^1, a unique derived condition among bats, but otherwise reflects the same M^1 morphology as other thyropterids. The unusual morphology of the specimen suggests a greater than expected diversity within the Family Thyropteridae. A second bat specimen from the same locality is referred to Molossidae genus and species indeterminate.

INTRODUCTION

Collectively, Neogene sedimentary beds with limited exposure along rivers and roadcuts in western Amazonia have provided a high diversity of vertebrate fossils of late Miocene age (Simpson and Paula Couto, 1981; Paula Couto, 1982; Frailey, 1986; Campbell, 1996; Bergqvist et al., 1998; Gaffney et al., 1998; Bocquentin and Melo, 2006; Campbell et al., 2006; Cozzuol, 2006; Kay and Cozzuol, 2006; Latrubesse et al., 2007, 2010; De Iuliis et al., 2011; Góis et al., 2013; Ribeiro et al., 2013; Prothero et al., 2014; Antoine et al., 2016, 2017; Kerber et al., 2016, 2017). The nomenclature and correlation of the relevant strata yielding the fossils in lowland Colombia, Peru, Brazil, and Bolivia, as well as their relationship to tectonic behavior of the central Andes Mountains, are actively described and elucidated (Campbell et al., 2001, 2006, 2010; Gingras et al., 2002; Wesselingh et al., 2002, 2006; Cozzuol, 2006; Latrubesse et al., 2007, 2010; Hoorn et al., 2010a, b; Mora et al., 2010), although there is considerable debate over the age and origin of the youngest deposits of western Amazonia. Many authors seem to agree that the youngest deposits, which comprise the Madre de Dios Formation in Peru and the Içá Formation in Brazil, overlie and are separated from the older Tertiary deposits that comprise the Ipururo Formation in Peru and the Solimões Formation in Brazil by the Ucayali Unconformity (Campbell et al., 2006). The base of the younger formation comprises the Acre Conglomerate (Campbell et al., 1985), from which have come diverse collections of vertebrate faunas of late Miocene age with taxa assignable to the Huayquerian South American Land Mammal Age (SALMA) and the Chasicoan SALMA. Some taxa seem to suggest an even older age, which would be concordant with the geologic history of the region.

Despite the diversity of Miocene mammals and the spectacular diversity of living bats (Chiroptera, Mammalia) in the western Amazon Basin, only a handful of bats are yet known as fossils from the region. Antoine et al. (2016) reported two bat taxa from upper Miocene deposits, as well as other bats in older rocks, in the lowlands of the western Amazon Basin in the extensive Paleogene–Neogene sequence near Contamana, Peru. The late Miocene taxa included a free-tailed bat of the Family Molossidae (Mayoan SALMA), and a sac-winged bat of the Family Emballonuridae (Mayoan–Chasicoan SALMAs), both of indeterminate genus (Antoine et al., 2016). Farther to the south, in younger strata of the Madre de Dios Formation, Czaplewski (1996) reported an extinct species of bulldog bat, *Noctilio lacrimaelunaris*, and a molossid bat of indeterminate genus from the Acre River and Purus River, Peru, respectively, both thought at the time to pertain to the Huayquerian SALMA.

Screen-washing of a small sample of sedimentary deposits in 1995 at a locality along the upper Juruá River in Acre, Brazil (Campbell et al., 2006:fig. 1, locality 3, also known as RJ-95-2 and Natural History Museum of Los Angeles County [LACM] locality 6288; Fig. 1), yielded two late Miocene bat specimens from the Acre Conglomerate Member of the Içá Formation (= Madre de Dios Formation in Peru). Other small mammals recovered from the Acre Conglomerate at this same locality included two erethizontid rodents (Campbell et al., 2006:195) and nearly two dozen other rodent teeth, which are considered to be approximately equivalent in age to the Huayquerian vertebrate fauna from the Acre River and Purus River farther to the southeast. Elsewhere in western Amazonia, other Huayquerian taxa comprise mostly large mammals and do not yet include bats (Bergqvist et al., 1998; Negri et al., 2010; Ribeiro et al., 2013; Kerber et al., 2016, 2017).

The purpose of this paper is to describe two specimens of bats recovered from the Acre Conglomerate along the Juruá River, including a distinctive new taxon of disc-winged bat of the Family Thyropteridae. The previous record of Thyropteridae in the Neogene is limited to two taxa from the middle Miocene (Laventan SALMA) La Venta local fauna, Colombia (Czaplewski, 1997; Czaplewski et al., 2003).

METHODS AND MATERIALS

The Juruá River fossil teeth were compared with resin casts of Neogene fossil bats and museum specimens of modern bats of all families occurring in the western hemisphere (Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Phyllostomidae, Noctilionidae, Thyropteridae, Vespertilionidae). The Juruá River fossil teeth are clearly distinct from all bats except those belonging to the families Thyropteridae and Emballonuridae, thus the comparisons reported below are primarily with those two families. Dental terminology follows Legendre (1985), Sigé et al. (1994), and Kielan-Jaworowska et al. (2004:fig. 11.1). Measurements were made on an Olympus SZX9 stereomicroscope with an eyepiece reticle to the nearest 0.01 mm.

[1] URL: www.nhm.org/scholarlypublications

[2] Vertebrate Paleontology, Sam Noble Oklahoma Museum of Natural History, 2401 Chautauqua Avenue, University of Oklahoma, Norman, Oklahoma 73072, USA.

[3] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA.

[4] Corresponding author: Nicholas J. Czaplewski, E-mail: nczaplewski@ou.edu

ISSN 0459-8113 (Print); 2165-1868 (Online)

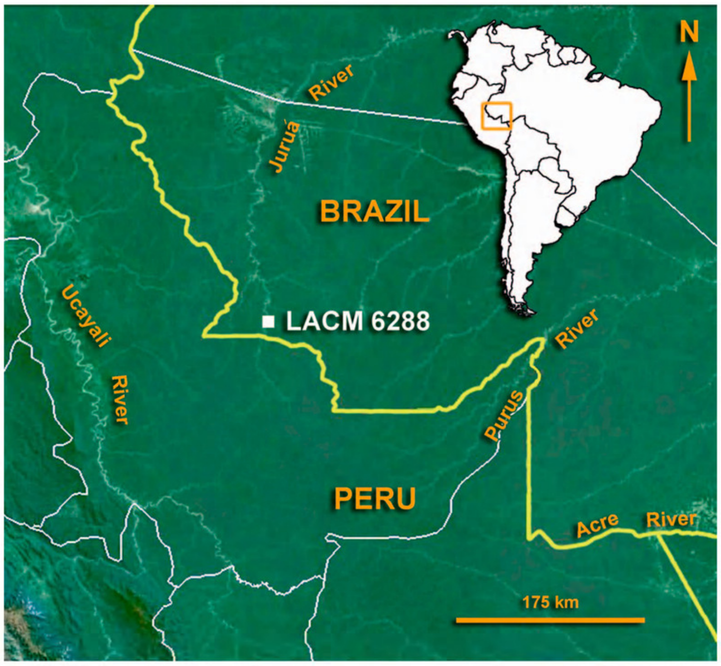

Figure 1 Map of western Amazonia with LACM locality 6288 indicated. Thick yellow lines indicate international borders; thin white lines indicate departmental borders in Peru and state borders in Brazil. Inset figure of South America with orange square shows location of larger image.

Abbreviations: LACM, Natural History Museum of Los Angeles County; Ma, million years ago; SALMA, South American Land Mammal Age.

SYSTEMATICS

Order Chiroptera Blumenbach, 1779

Family Thyropteridae Miller, 1907

Genus *Amazonycteris* new genus

TYPE SPECIES. *Amazonycteris divisus* new species.

INCLUDED SPECIES. Monotypic.

ETYMOLOGY. For the Amazon Basin, and Greek *nykteris*, "bat."

DIAGNOSIS. A small bat with molars approximately the size of those of *Thyroptera tricolor*. The M^1 differs from that of other thyropterids and from nearly all known insectivorous bats, except those of the family Emballonuridae, in having a shortened preparacrista and lacking a stylocone and parastyle. Differs from the M^1 of Neogene and extant members of Emballonuridae in lacking a parastyle on the mesiolabial corner of the tooth, in possessing a hypocone that occupies much of the center of the talon rather than a hypocone on the lingual margin of a deeply basined talon, and in having a strong lingual cingulum extending posteriad from the base of the protocone and continuous with the metacingulum.

***Amazonycteris divisus* new species**
Figure 2

HOLOTYPE. Natural History Museum of Los Angeles County (LACM) 143512, left M^1.

DIAGNOSIS. As for the genus.

TYPE LOCALITY. LACM 6288, Turtle Rock II, 09°16′37″ S, 72°40′47″ W; right bank of Juruá River, approximately 1.6 km upstream from locality Pedra da Tartaruga of Simpson and Paula Couto (1981), State of Acre, Brazil.

HORIZON AND AGE. Upper Miocene Acre Conglomerate of Campbell et al. (1985), which is the basal horizon of the Içá Formation (= Madre de Dios Formation in Peru). Sample taken from a lens just above Ucayali Unconformity (Campbell et al., 2006) on a large slump block sliding into river. Matrix consisted of coarse sand with small clay pebbles and clay, a local facies of the conglomerate noted in several sections along this stretch of the Juruá River by Simpson and Paula Couto (1981). Although the slump block has presumably been swallowed by the river in the 21 years since the fossil was collected, the fossiliferous horizon is probably still present in the remaining cliff.

ETYMOLOGY. From Latin *divisus*, "cut, separated," in reference to the Serra do Divisor/Sierra del Divisor, the low mountain range separating Peru and Brazil; the holotype was found very near the border between the two countries.

MEASUREMENTS. Anteroposterior length, 1.13 mm; transverse width, 1.57 mm.

DESCRIPTION AND COMPARISONS. Labial border of the tooth is markedly oblique, indicating the molar locus as M^1. The tooth is unworn or very lightly worn. It bears a nonbasined talon of moderate size that extends linguad as far as the base of the protocone and distad to a level even with the metastyle. The tooth lacks an anterior lingual cingulum, but it exhibits a posterior lingual cingulum running between the base of the protocone and the talon. Posterior lingual cingulum is continuous with the talon cingulum, which in turn is continuous with the metacingulum. There are no cusps on the talon cingulum (postcingulum). The M^1 postprotocrista extends distad as a relatively strong ridge straight from the protocone apex, ending on a hypocone in the center of the talon. The postprotocrista lacks a rise in height along its length; its posterior terminus would be termed a "metaconule" by Fracasso et al. (2011), but we prefer to call it a hypocone. The M^1 commissures of the W-shaped ectoloph become progressively longer from preparacrista to postmetacrista. A paraconule is lacking, but there is a weak paraloph extending from the base of the paracone toward the protocone. There is a relatively strong, sinuous metaloph extending from the base of the metacone to the postprotocrista and closing off the trigon basin and protofossa posteriorly. Preprotocrista passes labiad from the protocone as a paracingulum, narrowing as it reaches the mesiolabial corner of the tooth. Preparacrista is short; stylocone and parastyle ("paracingulum expansion" of Fracasso et al., 2011) are absent. Mesostyle forms a curved ridge that is slightly elongated mesiodistally. Ectocingulum is indented by ectoflexi on either side of the mesostyle, and bears a small cuspule just mesial to the metastyle.

The M^1 of *Amazonycteris* resembles that of *Thyroptera*, previously the only known genus in the Family Thyropteridae, in most aspects of its morphology except for the mesiolabial corner of the tooth. The M^1 of *A. divisus* shares with that of *Thyroptera devivoi, T. discifera, T. lavali, T. tricolor, T. wynneae,* and the La Venta *Thyroptera* spp. a nearly straight postprotocrista directed posteriad from the protocone; a small talon supporting a hypocone as a swelling beneath the posterior end of the postprotocrista; a short preparacrista; a weak paraloph; a metaloph directed toward the protocone and postprotocrista; a lingual cingulum developed at and posterior to the base of the protocone, and which is continuous with the talon cingulum and metacingulum; a preprotocrista continuous with the paracingulum and extending to the mesiolabial corner of the tooth; and a small ectocingular cuspule anterior to the metastyle. In terms of the M^1, the known species of *Thyroptera* differ only subtly from one another in minor details of dimensions and morphology. In some individuals of *T. discifera* and *T. tricolor*, the lingual cingulum extends a short distance anterior to the base of the protocone, but in most, the lingual cingulum occurs only at the base of

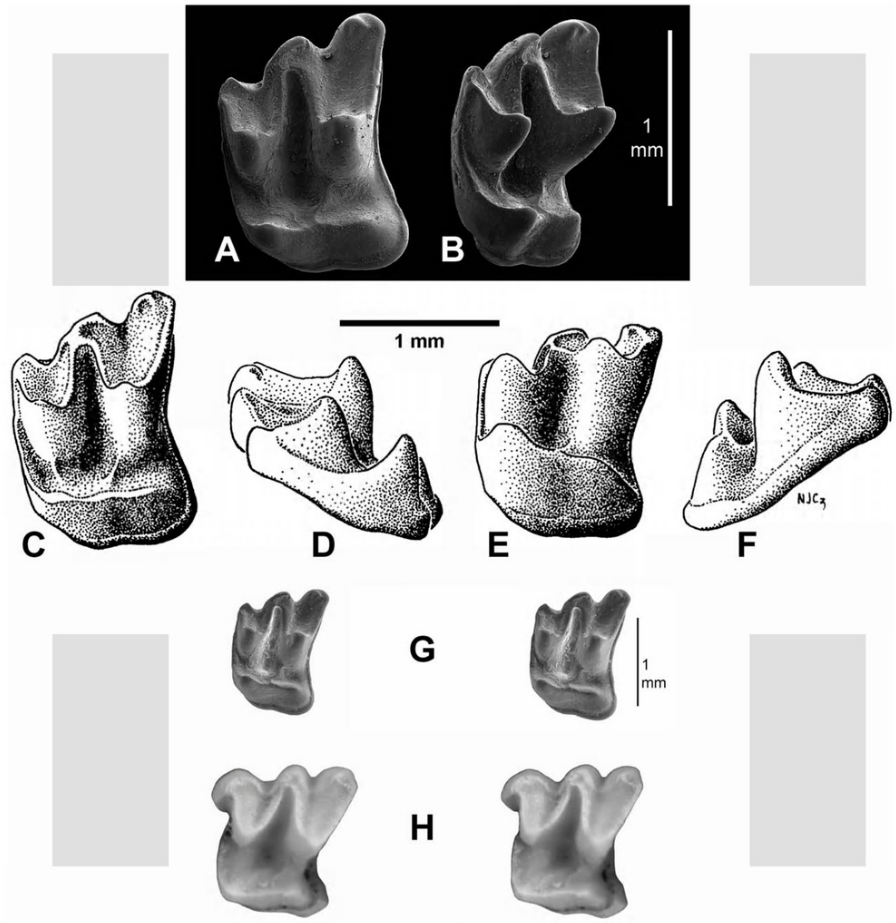

Figure 2 Thyropteridae, *Amazonycteris divisus* new genus and new species, left M^1 (holotype, LACM 143512) from the Juruá River, LACM locality 6288, State of Acre, Brazil; scanning electron micrographs in, A, occlusal and, B, oblique anteroocclusal views; line drawings in, C, occlusal; D, anterior; E, lingual; and F, posterior views; G, stereopair, occlusal view. *Thyroptera tricolor*, H, stereopair of left M1 of a modern specimen for comparison.

the protocone and distally, as in *Amazonycteris*. *Amazonycteris* is distinct from *Thyroptera*, all species of which have a strong M^1 stylocone and parastyle, in having M^1 that lack these structures (compare Fig. 2G and H). The M^1 talon in *A. divisus* is a little better developed than M^1 talons in species of *Thyroptera*, in that it extends slightly farther distad and bears a slightly broader shelf along the distal edge of the tooth confluent with the metacingulum. In *Amazonycteris,* the posterior edge of the M^1 is less constricted distally, so that the talon occupies more area than in *Thyroptera* when seen in occlusal view.

As noted by Simmons et al. (2016), all bats, including archaic Eocene taxa, share dilambdodont tribosphenic molars, with the upper molars having a symmetric W-shaped ectoloph with a strong parastyle, as well as other characters; these characters are probably plesiomorphic for bats. The M^1 of *Amazonycteris* shows a symmetric W-shaped ectoloph, but it differs from the M^1 of almost all insectivorous bats, except those of species of the Emballonuridae, in lacking a parastyle and stylocone. All extant and Neogene Emballonuridae share derived characters of the M^1, in having a shortened preparacrista and lacking a stylocone, but retaining a parastyle (Storch et al., 2002). Paleogene European and Afro-Arabian emballonurids *Vespertiliavus* Schlosser, 1887, *Tachypteron* Storch et al., 2002, and *Dhofarella* Sigé et al., 1994, have a strong M^1 parastyle and often a weak to strong stylocone (*Dhofarella* M^1 has a tiny stylocone and a separate, prominent parastyle; Sigé, 1988; Sigé et al., 1994; Sigé and Menu, 1995; Storch et al., 2002). Despite the superficial resemblance of *A. divisus* to emballonurids, the *Amazonycteris* M^1 further differs from those of most emballonurids in having a lingual cingulum and in the size and shape of the talon. The M^1 talon in *Amazonycteris* is relatively smaller than that in all emballonurids. Unlike emballonurids, the M^1 talon in *Amazonycteris* and other thyropterids has no deep basin; it also has no separate, distinct, and lingually situated hypocone as in the Old World emballonurid genera *Saccolaimus*, *Taphozous*, *Coleura*, and *Emballonura*. Instead, *Amazonycteris* has the hypocone centrally positioned on the talon.

Family Molossidae Gervais, 1856

Genus and species indeterminate
Figure 3

REFERRED SPECIMEN. LACM 143509, right P_2, from locality 6288.

DESCRIPTION AND COMPARISONS. Bears two roots (one broken) that might have been partly coalesced. Shape closely resembles the P_2 of several molossid genera, including *Nyctinomops*, *Eumops*, *Molossops*, *Promops*, and *Mormopterus*. Size is much larger than the P_2s of *Mormopterus kalinowskii* and *Mormopterus phrudus*. It is smaller than the P_2 in *Promops nasutus, Molossops* (*Cabreramops*) *aequatorianus,* and *Nyctinomops laticaudatus*; much smaller and lower in crown height than P_2 of *Molossops greenhallii*; and much smaller than P_2 of the small *Eumops* species *E. patagonicus*, but very close in size and shape to P_2 of *Eumops bonariensis nanus*. Unfortunately, the P_2 is inadequate for referral to one of the above genera.

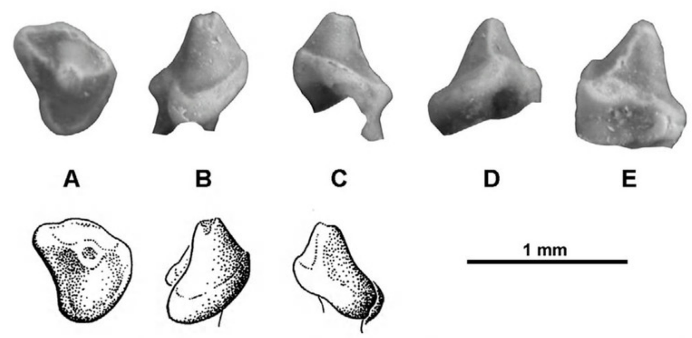

Figure 3 Molossidae, genus and species indeterminate, right P_2 (LACM 143509) from the Juruá River, LACM locality 6288, State of Acre, Brazil; photographs of ammonium chloride–coated specimen and line drawings in, A, occlusal views, mesial to right; B, labial views, anterior to right; C, lingual views; D, anterior view; E, posterior view.

MEASUREMENTS. Anteroposterior length, 0.62 mm; transverse width, 0.72 mm.

DISCUSSION

The known middle Miocene La Venta thyropterids consist of two taxa that were referred to the modern genus *Thyroptera*; one was comparable to an extant species and identified as *T.* sp. cf. *T. tricolor*, and the second was nominated as a new species, *T. robusta* (Czaplewski, 1996, 1997). At that time, only two species of *Thyroptera*, *T. tricolor* and *T. discifera*, were known, both extant. While the volume in which the article naming *T. robusta* eventually appeared was in press (Czaplewski, 1997), another extant species was named *T. lavali* by Pine (1993). A re-examination and comparison of the available fossil teeth of the La Venta *T. robusta* with borrowed skulls of *T. lavali* showed that the teeth of *T. robusta* were the same size and had the same morphology as comparable teeth in *T. lavali*. Because it was not possible to negate the hypothesis that the two samples *T. lavali* and *T. robusta* represented distinct species based on the few available teeth of *T. robusta*, Czaplewski (1996) synonymized *T. robusta* with *T. lavali* (with the synonymization ultimately appearing before the La Venta volume did). Thus, both La Venta fossil thyropterids were tentatively referred to the modern species *T. tricolor* and *T. lavali* pending the discovery of more complete fossil material. Since that time, two more extant species of *Thyroptera*, *T. devivoi* and *T. wynneae*, were named (Gregorin et al., 2006; Velazco et al., 2014). The cheek teeth are exceedingly similar among all five extant species of *Thyroptera* (*T. devivoi, T. discifera, T. lavali, T. tricolor*, and *T. wynneae*), although the incisors differ in details. These species are differentiated mainly on characters of the skull and soft anatomy (Solari et al., 2004; Velazco et al., 2014). Up to four *Thyroptera* species co-occur in western Amazonia today (Velazco et al., 2014); this impressive local diversity within a single genus indicates clearly that they are ecologically and behaviorally more distinct than their conservative dental anatomy indicates. An investigation of the diet of *T. tricolor* indicates that the species is a specialized surface-gleaner, taking tiny, silent, often nonflying arthropods as prey (Dechmann et al., 2006); the foods eaten by the other species of *Thyroptera* are barely known.

A recent species-level time-calibrated phylogenetic analysis of all families of the superfamily Noctilionoidea placed Thyropteridae as the sister taxon to all other noctilionoid families except Mystacinidae (Rojas et al., 2016). The same authors estimated that thyropterids had diverged from other noctilionoids in the later Eocene and that the diversification of the recent species of *Thyroptera* had begun in the Miocene, by about 20 Ma. Few Neogene fossils of thyropterids are yet available to confirm these divergences. The dental similarity among extant thyropterids and that between the extant thyropterids and the La Venta fossils, together with the middle Miocene age of the La Venta fossils, led Velazco et al. (2014) to suggest that the La Venta thyropterids could represent extinct taxa in which little dental evolution has occurred during the last 12 million years rather than long-lasting modern taxa as advocated by Czaplewski (1996) and Czaplewski et al. (2003). Velazco et al. (2014) suggested there was probably a hidden additional diversity in the Neogene fossil record of Thyropteridae but agreed with Czaplewski (1996) and Czaplewski et al. (2003) that more complete specimens would be necessary to demonstrate the extent of that diversity. They further correctly noted that the La Venta fossil bats indicate that the genus *Thyroptera* was distinct by 12.5 Ma, and that the teeth of the five recognized extant species of thyropterids lack many distinguishing characteristics. Reyes-Amaya et al. (2016) confirmed the similarity of the La Venta *T.* sp. cf. *T. tricolor*, at least in most dental measurements, to present-day *T. tricolor*, reinforcing the possibility of a long evolutionary stasis in that species' dentition. The present specimen of *A. divisus*, although geochronologically younger, is not represented by as many specimens as the La Venta fossil thyropterids. Its unusual morphology provides an unexpected glimpse at the late Neogene diversity of this family beyond the face value of the single available tiny tooth.

ACKNOWLEDGMENTS

We thank Brian Davis for scanning electron microscopy and Roger Burkhalter for help in image processing; Bruce Patterson (Field Museum of Natural History), Linda K. Gordon (U.S. National Museum of Natural History), and Nancy B. Simmons (American Museum of Natural History) for loans of comparison specimens; R.L. Cifelli and R.H. Madden for helpful discussions; and G.F. Gunnell and G.S. Morgan for critical reviews. We thank Carl D. Frailey and the late Lidia Romero-Pittman for assistance in the fieldwork, funding for which came from the National Geographic Society and John G. Wigmore.

LITERATURE CITED

Antoine, P.-O., M.A. Abello, S. Adnet, A.J. Altamirano Sierra,P. Baby, G. Billet, M. Boivin, Y. Calderon, A. Candela, J. Chabin, F. Corfu, D.A. Croft, M. Ganerød, C. Jaramillo, S. Klaus, L. Marivaux, R.E. Navarrete, M.J. Orliac, F. Parra, M.E. Pérez, F. Pujos, J.-C. Rage, A. Ravel, C. Robinet, M. Roddaz, J.V. Tejada-Lara, J. Vélez-Juarbe, F.P. Wesselingh, and R. Salas-Gismondi. 2016. A 60 million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Research* 31:30–59.

Antoine, P.-O., R. Salas-Gismondi, F. Pujos, M. Ganerød, and L. Marivaux. 2017. Western Amazonia as a hotspot of mammalian biodiversity throughout the Cenozoic. *Journal of Mammalian Evolution*24:5–17.

Bergqvist, L.P., A.M. Ribeiro, and J. Bocquentin-Villanueva. 1998. Primata, roedores e litopterna do Mio/Plioceno da Amazônia sul-ocidental (Formação Solimões, Bacia do Acre), Brasil. *Geología Colombiana* 23:19–29.

Blumenbach, J.F. 1779–1780. *Handbuch der Naturgeschichte*. Göttingen: Johann Christian Dieterich.

Bocquentin, J., and J. Melo. 2006. *Stupendemys souzai* sp. nov. (Pleirodira, Podocnemididae) from the Miocene–Pliocene of the Solimões Formation, Brazil. *Revista Brasileira de Paleontologia* 9:187–192.

Campbell, K.E., Jr. 1996. A new species of giant anhinga (Aves: Pelecaniformes: Anhingidae) from the Upper Miocene (Huayquerian) of Amazonian Peru. *Contributions in Science, Natural History Museum of Los Angeles County* 460:1–9.

Campbell, K.E., Jr., C.D. Frailey, and J. Arellano-L. 1985. The geology of the Rio Beni: Further evidence for Holocene flooding in Amazonia. *Contributions in Science, Natural History Museum of Los Angeles County* 364:1–18.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 2006. The pan-Amazonian Ucayali peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. *Palaeogeography, Palaeoclimatology, Palaeoecology* 239:166–219.

Campbell, K.E., Jr., M. Heizler, C.D. Frailey, L. Romero-Pittman, and D.R. Prothero. 2001. Upper Cenozoic chronostratigraphy of the southwestern Amazon Basin. *Geology* 29(7):595–598.

Campbell, K.E., Jr., D.R. Prothero, L. Romero-Pittman, F. Hertel, and N. Rivera. 2010. Amazonian magnetostratigraphy: Dating the first pulse of the Great American Faunal Interchange. *Journal of South American Earth Sciences* 29:619–626.

Cozzuol, M.A. 2006. The Acre vertebrate fauna: Age, diversity, and geography. *Journal of South American Earth Sciences* 21:185–203.

Czaplewski, N.J. 1996. *Thyroptera robusta* Czaplewski, 1996, is a junior synonym of *Thyroptera lavali* Pine, 1993 (Mammalia: Chiroptera). *Mammalia* 60:153–156.

Czaplewski, N.J. 1997. Chiroptera. In *Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia*, ed. R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn, 410–430. Washington, D.C.: Smithsonian Institution Press.

Czaplewski, N.J., M. Takai, T. Naeher, N. Shigehara, and T. Setoguchi. 2003. Additional bats from the middle Miocene La Venta fauna of Colombia. *Revista de la Academia Colombiana de Ciencias* 27:263–282.

De Iuliis, G., T.J. Gaudin, and M.J. Vicars. 2011. A new genus and species of nothrotheriid sloth (Xenarthra, Tardigrada, Nothrotheriidae) from the late Miocene (Huayquerian) of Peru. *Palaeontology* 54:171–205.

Dechmann, D.K.N., K. Safi, and M.J. Vonhof. 2006. Matching morphology and diet in the disc-winged bat *Thyroptera tricolor* (Chiroptera). *Journal of Mammalogy* 87:1013–1019.

Fracasso, M.P.A., L. de Oliveira Salles, and F. Araújo Perini. 2011. Upper molar morphology and relationships among higher taxa in bats. *Journal of Mammalogy* 92:421–432.

Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Río Acre region, western Amazonia. *Contributions in Science, Natural History Museum of Los Angeles County* 374:1–46.

Gaffney, E.S., K.E. Campbell, and R.C. Wood. 1998. Pelomedusoid side-necked turtles from late Miocene sediments in southwestern Amazonia. *American Museum Novitates* 3245:1–12.

Gervais, P. 1855 [1856]. Deuxième mémoire. Documents zoologiques pour servir à la monographie des chéiroptères Sud-Américains. Pp. 25–88 in P. Gervais (ed.), Mammifères. In *Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Parà; exécutée par ordre du gouvernement français pendant les années 1843 à 1847, sous la direction du Comte Francis de Castelnau, 1855*, ed. F. de Castelnau, 1(2):1–116, 20 pls. Paris: P. Bertrand.

Gingras, M.K., M. Räsänen, and A. Ranzi. 2002. The significance of bioturbated inclined heterolithic stratification in the southern part of the Miocene Solimões Formation, Rio Acre, Amazonia Brazil. *Palaios* 17:591–601.

Góis, F., G.J. Scillato-Yané, A.A. Carlini, and E. Guilherme. 2013. A new species of *Scirrotherium* Edmund & Theodor, 1997 (Xenarthra, Cingulata, Pampatheriidae) from the late Miocene of South America. *Alcheringa: An Australasian Journal of Palaeontology* 37:177–188.

Gregorin, R., E. Gonçalves, B.K. Lim, and M.D Engstrom. 2006. New species of disk-winged bat *Thyroptera* and range extension for *T. discifera*. *Journal of Mammalogy* 87:238–246.

Hoorn, C., F.P. Wesselingh, H. ter Steege, M.A. Bermudez, A. Mora, J. Sevink, I. Sanmartín, A. Sanchez-Meseguer, C.L. Anderson, J.P. Figueiredo, C. Jaramillo, D. Riff, F.R. Negri, H. Hooghiemstra, J. Lundberg, T. Stadler, T. Särkinen, and A. Antonelli. 2010a. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330:927–931.

Hoorn, C., F.P. Wesselingh, J. Hovikoski, and J. Guerrero. 2010b. The development of the Amazonian mega-wetland (Miocene; Brazil, Colombia, Peru, Bolivia). In *Amazonia, landscape and species evolution,* ed. C. Hoorn and F.P. Wesselingh, 123–142. Oxford, U.K.: Wiley.

Kay, R.F., and M.A. Cozzuol. 2006. New platyrrhine monkeys from the Solimões Formation (late Miocene, Acre state, Brazil). *Journal of Human Evolution* 50:673–686.

Kerber, L., F.R. Negri, A.M Ribeiro, N. Nasif, J.P. Souza-Filho, and J. Ferigolo. 2017. Tropical fossil caviomorph rodents from the southwestern Brazilian Amazonia in the context of the South American faunas: Systematics, biochronology, and paleobiogeography. *Journal of Mammalian Evolution* 24:57–70.

Kerber, L., F.R. Negri, A.M. Ribeiro, M.G. Vucetich, and J.P. De Souza-Filho. 2016. Late Miocene potamarchine rodents from southwestern Amazonia, Brazil, with description of new taxa. *Acta Palaeontologica Polonica* 61:191–203.

Kielan-Jaworowska, Z., R.L. Cifelli, and Z.-X. Luo. 2004. *Mammals from the age of dinosaurs: Origins, evolution, and structure*. New York: Columbia University Press, 630 pp.

Latrubesse, E.M., M. Cozzuol, S.A.F. da Silva-Caminha, C.A. Rigsby, M.L. Absy, and C. Jaramillo. 2010. The late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth-Science Reviews* 99:99–124.

Latrubesse, E.M., S.A.F. da Silva, M. Cozzuol, and M.L. Absy. 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: Biotic and geological evidence. *Journal of South American Earth Sciences* 23:61–80.

Legendre, S. 1985. Molossidés (Mammalia, Chiroptera) cénozoiques de l'Ancien et du Nouveau Monde; statut systématique; intégration phylogénique de données. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 170:205–227.

Miller, G.S. 1907. The families and genera of bats. *Bulletin of the United States National Museum* 57:1–282.

Mora, A., P. Baby, M. Roddaz, M. Parra, S. Brusset, W. Hermoza, and N. Espurt. 2010. Tectonic history of the Andes and sub-Andean zones: Implications for the development of the Amazon drainage basin. In *Amazonia, landscape and species evolution,* ed. C. Hoorn and F.P. Wesselingh, 38–60. Oxford, U.K.: Wiley.

Negri, F.R., J. Bocquentin Villanueva, J. Ferigolo, and P.-O. Antoine. 2010. A review of Tertiary mammal faunas and birds from western Amazonia. In *Amazonia, landscape and species evolution: A look into the past,* ed. C. Hoorn and F.P. Wesselingh, 245–258. Oxford, U.K.: Wiley.

Paula Couto, C. de. 1982. Fossil mammals from the Cenozoic of Acre, Brazil, V. Notoungulata Nesodontinae, Toxodontinae and Haplodontheriinae, and Litopterna, Pyrotheria and Astrapotheria. *Iheringia, Série Geologia* 7:5–43.

Pine, R.H. 1993. A new species of *Thyroptera* Spix (Mammalia: Chiroptera: Thyropteridae) from the Amazon Basin of northeastern Perú. *Mammalia* 57(2):213–225.

Prothero, D.R., K.E. Campbell, Jr., B.L. Beatty, and C.D. Frailey. 2014. New late Miocene dromomerycine artiodactyl from the Amazon Basin: Implications for interchange dynamics. *Journal of Paleontology* 88:434–443.

Reyes-Amaya, N., J. Lozáno-Flórez, D. Flores, and S. Solari. 2016. Distribution of the Spix's disk-winged bat, *Thyroptera tricolor* Spix, 1823 (Chiroptera: Thyropteridae) in Colombia, with first records for the middle Magdalena Valley. *Mastozoología Neotropical* 23:127–137.

Ribeiro, A.M., R.H. Madden, F.R. Negri, L. Kerber, A.S. Hsiou, and K.A. Rodrigues. 2013. Mamíferos fósiles y biocronología en el suroeste de la Amazonia, Brasil. In *El Neógeno de la Mesopotamia Argentina,* ed. D. Brandoni and J.I. Noriega. *Asociación Paleontológica Argentina, Publicación Especial*, vol. 14, 207–221.

Rojas, D., O.M. Warsi, and L.M. Dávalos. 2016. Bats (Chiroptera: Noctilionoidea) challenge a recent origin of extant Neotropical diversity. *Systematic Biology* 65:432–448.

Schlosser, M. 1887. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europaischen Tertiärs und deren beziehungen zu ihren lebenden und fossilen aussereuropäischen verwandten. I Tiel. *Beiträge zur Paläontologie Oesterreich-Ungarns* 6:1–162.

Sigé, B. 1988. Le gisement du Bretou (phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertebres de l'Eocene superieur IV. Insectivores et chiropteres. *Palaeontographica Beiträge zur Naturgeschichte der Vorzeit* 205:69–102.

Sigé, B., and H. Menu. 1995. Le Garouillas et les sites contemporains (Oligocene, MP 25) des phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertebres 5. Chiropteres. *Palaeontographica Abteilung A* 236:77–124.

Sigé, B., H. Thomas, S. Sen, E. Gheerbrant, J. Roger, and Z. Al-Sulaimani. 1994. Les chiroptères de Taqah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. *Münchner Geowissenschaftliche Abhhandlungen (A)* 26:35–48.

Simmons, N.B., E.R. Seiffert, and G.F. Gunnell. 2016. A new family of large omnivorous bats (Mammalia, Chiroptera) from the late Eocene of the Fayum Depression, Egypt, with comments on use of the name "Eochiroptera." *American Museum Novitates* 3857:1–43.

Simpson, G.G., and C. Paula Couto. 1981. Fossil mammals from the Cenozoic of Acre, Brazil III—Pleistocene Edentata Pilosa, Proboscidea, Sirenia, Perissodactyla and Artiodactyla. *Iheringia, Série Geologia* 6:11–73.

Solari, S., R.A. Van DenBussche, S.R. Hoofer, and B.D. Patterson. 2004. Geographic distribution, ecology, and phylogenetic affinities of *Thyroptera lavali* Pine 1993. *Acta Chiropterologica* 6:293–302.

Storch, G., B. Sigé, and J. Habersetzer. 2002. *Tachypteron franzeni* n. gen., n. sp., earliest emballonurid bat from the Middle Eocene of Messel (Mammalia, Chiroptera). *Paläontologische Zeitschrift* 76(2):189–199.

Velazco, P.M., R. Gregorin, R.S. Voss, and N.B. Simmons. 2014. Extraordinary local diversity of disk-winged bats (Thyropteridae: *Thyroptera*) in northeastern Peru, with the description of a new species and comments on roosting behavior. *American Museum Novitates* 3795:1–28.

Wesselingh, F.P., M.C. Hoorn, J. Guerrero, M.E. Räsänen, L. Romero-Pittman, and J.A. Salo. 2006. The stratigraphy and regional structure of Miocene deposits in western Amazonia (Peru, Colombia and Brazil), with implications for late Neogene landscape evolution. *Scripta Geologica* 133:291–322.

Wesselingh, F.P., M.E. Räsänen, G. Irion, H.B. Vonhof, R. Kaandorp, W. Renema, L. Romero-Pittman, and M. Gingras. 2002. Lake Pebas: A palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. *Cainozoic Research* 1:35–81.

Received 6 October 2017; accepted 26 January 2017.