Journal of Vertebrate Paleontology 25(4):990–993, December 2005

NOTE

THE OLDEST RECORD OF SOUTH AMERICAN BATS

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A new Paleogene mammal fauna was recently recovered in northwestern Chubut Province, Patagonia, Argentina. The mammal-bearing strata belong to the Middle Chubut River volcanic-pyroclastic complex (Fig. 1), of Paleocene-Eocene age (Aragón and Mazzoni, 1997). The site, named Laguna Fría, is about 50 km west of the town of Paso del Sapo, on the property of Estancia San Ramón (Fig. 1), and has produced hundreds of vertebrate fossils, especially mammals. Among the Laguna Fría taxa, there are several species referable to almost all the South American marsupial orders, including Peradectia (Peradectidae, Caroloameghiniidae), Sparassodonta (Borhyaenidae), Microbiotheria (Microbiotheriidae), Polydolopimorphia (Glasbiidae, Gashterniidae, Polydolopidae), Didelphimorphia (Protodidelphidae, Derorhynchidae, Sternbergiidae), and Paucituberculata (family indet.). Also, dasypodid xenarthrans are represented, as well as several orders of South American 'ungulates' such as 'condylarths,' litopterns, notopterns, notoungulates, and astrapotheres. However, a remarkable new occurrence is the oldest record of bats for South America, described herein. The specimens are deposited in the paleontological collection of the LIEB (Laboratorio de Investigaciones en Evolución y Biodiversidad), Facultad de Ciencias Naturales, Sede Esquel, Universidad Nacional de la Patagonia "San Juan Bosco".

Geochronological data taken from nearby volcanic deposits indicate that the fauna is not younger than Early Eocene age. Alkaline basalts exposed southeast of Laguna Fría, which are related to the alkaline basalts (Andesitas Huancache) that overly the fossiliferous level, have given Ar^{40}/Ar^{39} dates of 52 Ma (Alric, 1997). Also, a K/Ar age was obtained from a sample of whole rock of the underlying Barda Colorada ignimbrite, giving an age of 58.6 Ma (Archangelsky, 1974, corrected with 1978 constants). Thus, the Laguna Fría vertebrate fossils are presently bracketed by dates of 58.6 and 52 Ma.

We report here the discovery of bats at Laguna Fría, represented by two lower molars, a well preserved left m?2 (LIEB-PV 999; Fig. 2a, b, c) and a right talonid (LIEB-PV 1000; Fig. 2d), apparently belonging to the same species. Bats appear in the fossil record by the Early Eocene in North America (Jepsen, 1966; Novacek, 1985; 1987; Habersetzer and Storch, 1989), Europe (Russell et al., 1973), and Australia (Hand et al, 1994). Until now, the oldest South American record was of Middle or Late Eocene age at Santa Rosa locality (?Yahuarango Formation), in Perú (Czaplewski and Campbell, 2004).

RESULTS AND DISCUSSION

Of the two specimens recovered, the broken talonid (LIEB-PV 1000) is virtually identical in size and shape to the talonid portion of the nearly complete molar. The intact molar (LIEB-PV 999) probably represents m2. The isolated talonid is more heavily worn on the hypoconid, entoconid, and cristid obliqua than the complete tooth. The tips of the paraconid and metaconid of LIEB-PV 999 are missing, but their bases remain and give an indication of the relative sizes of these two cusps. Some of the enamel is etched from the crown of LIEB-PV 999.

The Laguna Fría specimens are identified as bats because they have a complete labial cingulum extending continuously from the anterior base of the paraconid to the hypoconulid; this character was noted by Hand et al. (1994) as a probable synapomorphy of early bats. The molar cusps are strongly merged into the molar crests rather than being individualized and rather conical. The trigonid is anteroposteriorly compressed. The paraconid is small and low, much smaller and slightly less lingually situated than the metaconid. The talonid is not strikingly lower than the trigonid. The entoconid is moderate in height; it bears a straight entocristid (in occlusal view). The cristid obliqua extends from the hypoconid to a point low on the posterior wall of the trigonid slightly labial to the midline of the tooth. The postcristid extends from the hypoconid to a small hypoconulid (the "nyctalodont" condition; Menu and Sigé, 1971) and is separated from the entoconid by a small groove. The hypoconulid is fully merged into the postcristid and is not distinguishable as a separate cusp; it merely forms the posteriorly curving lingual terminus of the postcristid and is positioned directly posterior rather than posterolabial to the entoconid.

In the Laguna Fría specimens, the talonid shows a derived condition relative to the primitive tribosphenic arrangement of distinct talonid cusps (entoconid, hypoconid, and hypoconulid) and a medially or submedially situated hypoconulid. The primitive tribosphenic condition is present in the archaic bats *Ageina*, *Archaeonycteris*, *Eppsinycteris*, *Hassianycteris*, *Honrovits*, *Icaronycteris*, and *Necromantis* (Simmons and Geisler, 1998; Czaplewski, pers. obs.). However, the same derived configuration of the postcristid-hypoconulid as in the Laguna Fría bats is also found in other Eocene bats such as *Dizzya* (Philisidae), *Lapichiropteryx*, and *Stehlinia* (Palaeochiropterygidae), and certain fossil and extant representatives of Emballonuridae, Furipteridae, Miniopteridae, some Molossidae, Mormoopidae, Natalidae, some Phyllostominae, some Rhinolophidae, Rhinopomatidae, and some Vespertilionidae. A very similar condition, in which the hypoconulid is merged into the postcristid but is situated medial or posterolabial rather than posterior to the entoconid, occurs in Craseonycteridae, some Hipposiderinae, and extant Megadermatidae. It is different from the myotodont condition (postcristid connecting hypoconid with entoconid, hypoconulid more-or-less separate) in which the hypoconulid is a rearward-jutting small cusp posterior or posterolabial to the entoconid, as seen in *Palaeochiropteryx* (Palaeochiropterygidae), *Philisis* (Philisidae), some Molossidae, Mystacinidae, Myzopodidae, Noctilionidae, Thyropteridae, and some Vespertilionidae.

In *Cecilionycteris* (Palaeochiropterygidae) there is yet another configuration, at least in unworn specimens: the postcristid extends from the hypoconid to a small hypoconulid situated low and directly posterior to the entoconid, but there is also a small, curved, sharp crest extending back to the hypoconulid from the entoconid.

It is not possible to make comparisons of the Laguna Fría bat teeth with teeth of the Eocene bats *Chadronycteris* (Vespertilionoidea), in which the lower molars are unknown, and *Tanzanycteris* (Tanzanycteridae; Gunnell et al., 2003), in which the teeth are as yet unknown.

Among mammals other than bats, a rather similar morphological pattern of the lower molars is present in several insectivores such as some erinaceomorphs (Erinaceidae, Dormaliidae, Amphilemuridae, Talpidae) and soricomorphs (Soricidae). Isolated teeth of many members of these groups can be very difficult to distinguish. Certain plagiomenid ?dermopterans (*Plagiomene*, *Elpidophorus*) also bear a complete labial cin-

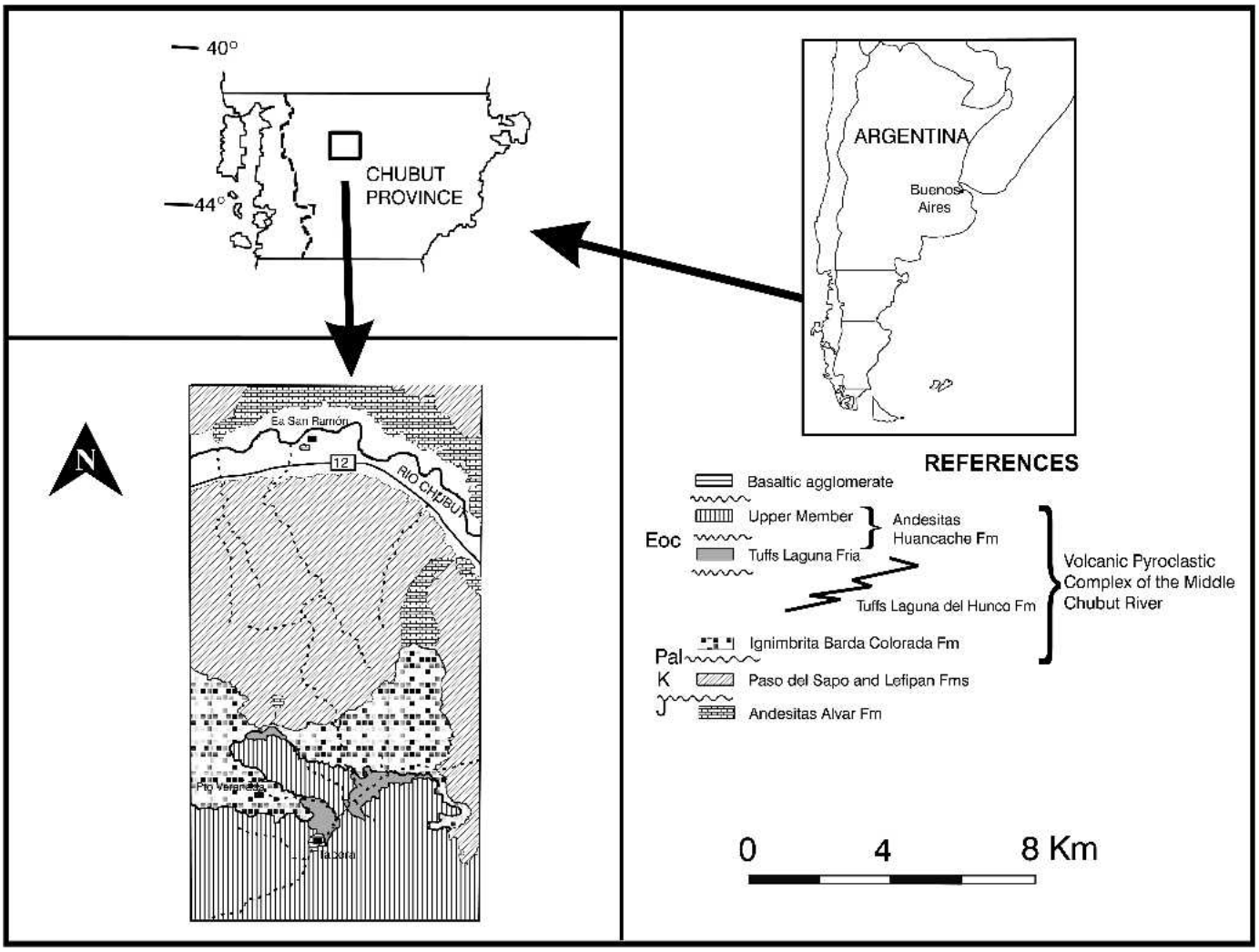

FIGURE 1. Map, stratigraphic column, and geology of the area mentioned in the text.

gulum on the lower molars, but these teeth are otherwise not particularly similar to the Laguna Fría bats; they have crenulated enamel, prominent hypoconulids or multiple cusps in the hypoconulid position that are centrally not lingually situated, and often a mesoconid and other accessory cusps are present.

In our examination of insectivorans, we find that some erinaceomorph lower molars bear a labial cingulum but it is usually strongest on the anterior (mesial) end of the molars and is weak or absent labially and posteriorly (with a reduced or absent postcingulum). Erinaceid molars characteristically show exodaenodonty (basal swelling of the labial cusps) that is also lacking in the Laguna Fría molars. Dormaliid and amphilemurid erinaceomorphs, although they may possess weak labial cingula on lower molars and are not exodaenodont, have medially situated or no hypoconulids, and the talonids are much wider than the trigonids. Moreover, the most significant differences are in the arrangement of the entoconulid/hypoconulid and the shape and height of the entoconid with respect to the hypoconid. The hypoconulid does not form the posteriorly curving lingual terminus of the postcristid and is not placed posterior to the entoconid, as in the bats described here. Instead, the tiny hypoconulid of erinaceids is always positioned centrally in the postcristid, as in some bats with primitive tribosphenic molars but not in the Laguna Fría bats. The entoconid in erinaceids is columnar, prominent, and higher than the hypoconid (in some m2s, the entoconid and hypoconid are subequal), instead of being poorly developed with respect to the higher hypoconid, with a straight entocristid running to the distal wall of the trigonid, as in the bats.

As discussed by Hutchison (1968:18, Fig. 6), two major patterns occur in the lower molars (m2-m3) of talpids: (1) one in which the cristid obliqua joins the trigonid at or near a well developed metastylid and the talonid basin is open lingually, and (2) one in which the cristid obliqua joins the protolophid, the metastylid is weak or absent, and an entocristid often closes the talonid basin lingually. The first type differs greatly from lower molars of most insectivorous New World bats (except noctilionids; Czaplewski, 1996) in the long cristid obliqua and presence of a metastylid; in the bats, the cristid obliqua runs from the hypoconid to the middle back wall of the trigonid and a metastylid is absent. Moles in which the metastylid is absent may possess a hypoconulid situated directly posterior to the metaconid (at least on m1 and m2) and a labial cingulum on the lower molars, but the labial cingulum is usually incomplete and a distal cingulum is lacking, unlike the condition in bats.

The only fossil talpid that seems to have an m2 that bears a continuous mesial, labial, and distal cingulum and a hypoconulid situated immediately posterior to the entoconid is the Miocene North American species *Mystipterus vespertilio*. Interestingly, the genus *Mystipterus* originally was identified on a dentary fragment with m3 as a bat (hence the name; Hall, 1930), but was later called a shrew (Patterson and McGrew, 1939), and finally referred to the talpid subfamily Uropsilinae (Hutchison, 1968). Additional specimens from the type locality in Fish Lake Valley, California, have been referred to *Mystipterus*, including upper and lower molars and postcranial bones. Furthermore, additional species of moles have been named (*Mystipterus pacificus*; Hutchison, 1968:40) or placed in synonymy with *Mystipterus* (*Mydecodon martini* Wilson, 1968; Hutchison, 1968:36). However, these specimens and taxa agree with other moles in having the second pattern mentioned above with a longer cristid obli-

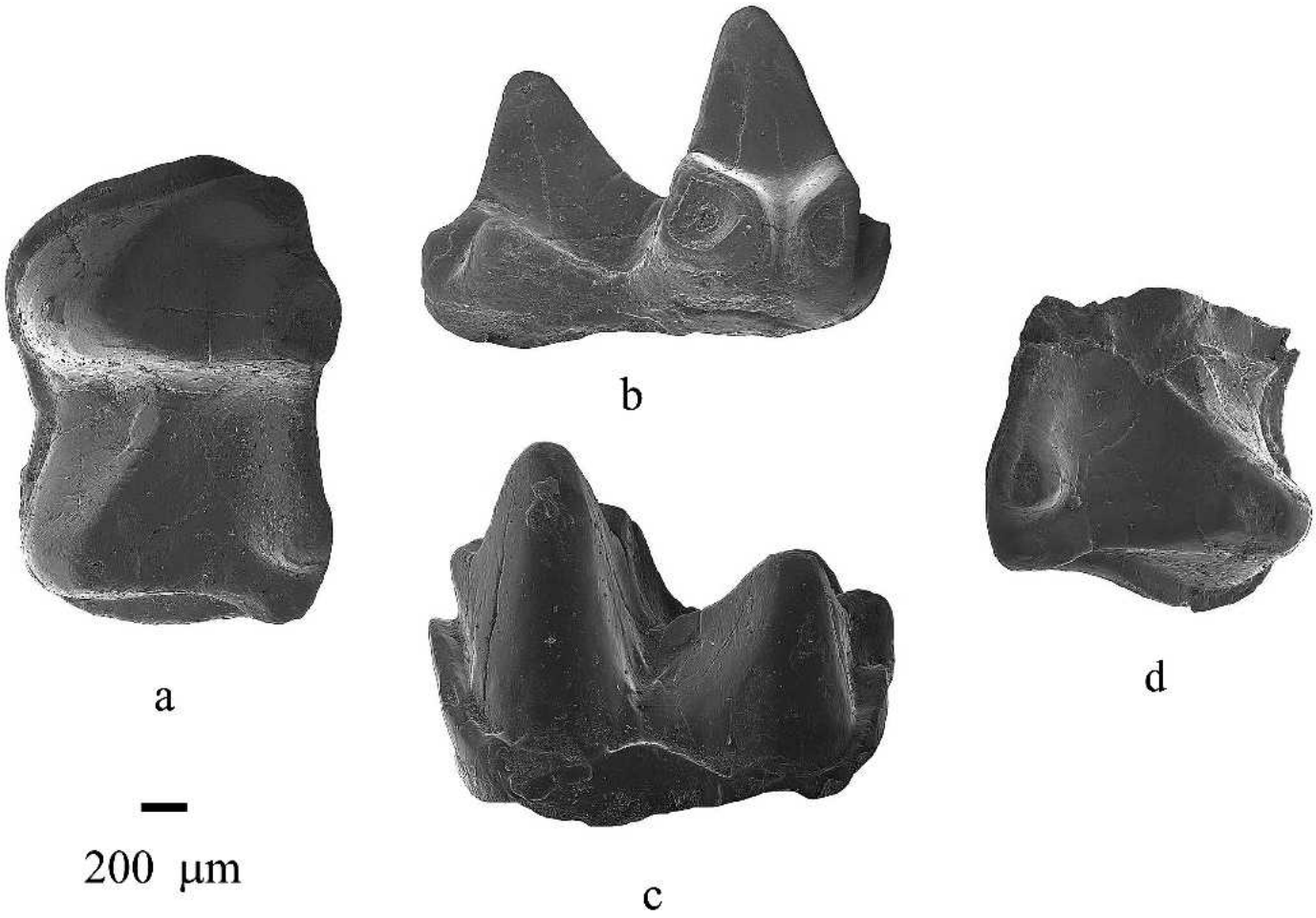

FIGURE 2. Teeth of Eocene Chiroptera from Laguna Fría, Argentina. LIEB-PV 999 in occlusal (a), lingual (b), and labial (c) views. LIEB-PV 1000 (d) in occlusal view. Scanning electron micrographs of resin casts sputter-coated with gold-palladium.

qua that approaches the metaconid (as well as other dental and osteological characters), instead of a shorter one that meets the back wall of the trigonid centrally as in the Laguna Fría bats. More importantly, except for Hall's (1930) superficial comparison of the original fossil of the genus *Mystipterus* with a single taxon, a modern specimen of the long-fingered bat *Miniopterus schreibersii*, no author has attempted to compare the type specimen with any bats. Such comparisons are beyond the scope of this paper, but there remains a possibility that the type specimen of *Mystipterus vespertilio* actually represents a bat not a mole, and probably the fragmentary type specimen should be considered insufficient for a diagnosis and a nomen vanum. The other named species referred to *Mystipterus* do truly represent moles, as do the more recently collected specimens referred to *M. vespertilio*. These moles may require a new name, but in any case, they do not resemble the Laguna Fría bats.

In soricids, the appearance of the postcristid especially in unworn soricid molars may resemble that in many bats; the entoconid is similarly separated from the postcristid (except on m3s) and it similarly bears an entoconid crest (Repenning, 1967). However, as in erinaceids, the soricid entoconid is prominent and higher than the hypoconid. The labial side of the lower molars of soricids is much more developed than the lingual side. In contrast to the bats, which have a vertically deep hypoflexid that opens at the level of the labial cingulum, soricids have the hypoflexid much shallower in the vertical plane, with the foot of the valley opening well above the labial cingulum. In labial view all soricids have a strongly curved protoconid base that is swollen anterolabially beneath the paracristid, especially the labial half. This and the shallow hypoflexid give an inflated appearance to the crown base of soricid lower molars compared to the bats. By contrast, the labial side of the protoconid in the complete Laguna Fría molar (LIEB-PV 999) appears straight, vertical, and columnar down to its base in labial view, and does not look swollen. In soricids there is a well-developed anterobasal cingulum, but a reduced or absent labial cingulum. When present, the labial cingulum in soricids is narrower and much shallower than in the bats. Moreover, in the soricids a weak but continuous lingual cingulum is present, whereas in the Laguna Fría bat teeth (and in virtually all insectivorous bats) a continuous lingual cingulum is absent from the lower molars. Unlike the condition in bats, the trigonid of all three lower molars in soricids is long due to the anteriorly expanded paracristid.

There are several records of Eocene insectivores, but in all cases the morphological differences from the bats described here are the same as for the extant insectivores.

Given the few specimens and characters available in the teeth, and their similarity to numerous extinct and extant bats from several lineages, we are unable to assign the Laguna Fría specimens to a taxon. However, judging from the observable morphology, its size and lower molar features indicate insectivorous feeding habits. In this respect, it is noteworthy that the Laguna Fría mammal assemblage is probably contemporary to the very rich early Eocene Laguna del Hunco flora (Wilf et al., 2003) located a few kilometers northwest of Laguna Fría, which in turn suggests that the early radiation of modern angiosperm lineages in Patagonia, as well as their insect pollinators, had already begun by early Paleogene time.

Acknowledgments—We thank Brian Davis, Richard Lupia, and Amy McClain for help in scanning electron microscopy and image processing. Special thanks go to Mr. Rafael Nicolletti and Mrs. "Coca" San Martín for allowing us to work in Estancia San Ramón, and Sergio Vincon and Gabriel Martin for their help in the field. NJC also acknowledges funding from National Science Foundation grants DEB 9981512 to NJC and G. S. Morgan, and DBI 0100317 to R. Lupia, R. Cifelli, NJC, and S. Westrop. This is LIEB publication number 7.

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Submitted 10 May 2005; accepted 26 May 2005.