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Placental nature of the alleged marsupial from the Cretaceous of Madagascar

ALEXANDER O. AVERIANOV, J. DAVID ARCHIBALD, and THOMAS MARTIN

A recently (Krause 2001) reported fragmentary mammalian lower molar (University of Antananarivo, UA 8699) from the Late Cretaceous (Maastrichtian) of Madagascar, was attributed to Marsupialia, for which far reaching paleobiogeographical conclusions were made. The five characters used to identify UA 8699 as a marsupial are not exclusive to Late Cretaceous marsupials, but are found also in some placental mammals, notably in Late Cretaceous ungulatomorph zhelestids, known from various Upper Cretaceous strata in Asia, Europe, and North America (Nessov et al. 1998). Identification of UA 8699 as a zhelestid placental is in keeping with myriad other faunal similarities between Europe and Africa/Madagascar.

Zhelestid molars, as well as UA 8699 and marsupials (Krause 2001), have the following: a postcingulid extending from the base of the hypoconid toward the hypoconulid apex (Fig. 1C) (although its prominence varies across the diverse zhelestids), a talonid that is as wide or wider than the trigonid (Fig. 1A), a low trigonid (Fig. 1C), and mostly horizontal wear. A lingually situated hypoconulid, noted by Krause (2001) as characteristic of UA 8699 and marsupials is problematic. The position of the hypoconulid in UA 8699 (Fig. 1B) is slightly lingual compared to some Cretaceous eutherians, but is in the same location as in zhelestids (Fig. 1A). By contrast, in all known Late Cretaceous marsupials the hypoconulid and entoconid are "twinned." These cusps are always very close at the posterolingual margin of the molar (Fig. 1E, F) or both lie along the lingual margin of the tooth, unlike that in UA 8699. In total, the similarities are closer between UA 8699 and zhelestid placentals, than between UA 8699 and Late Cretaceous marsupials.

UA 8699, although heavily worn, is remarkably similar to the lower molars of the zhelestid *Lainodon orueetxebarriai* (Fig. 1A, B), from the Maastrichtian Laño locality, northern Spain (Gheerbrant and Astibia 1994, 1999) and could be referred to a closely related taxon. UA 8699 is similar to *L. orueetxebarriai* and most other early metatherians and eutherians in having a greater trigonid angle, with the protocristid more posterolingually oriented compared to the more derived, but geochronologically older Middle Asian zhelestids (Archibald 1996; Nessov et al. 1998). Gheerbrant and Astibia (1999) interpreted the more compressed trigonid of the Asian zhelestids as the ancestral state; however, Nessov et al. (1998) and Archibald (1996) argued that the less antero-posteriorly compressed trigonid such as in the European zhelestids is ancestral because this state is found more widely in both early metatherians and eutherians.

The Maastrichtian faunas of Laño and Madagascar have other faunistic similarities, such as the madtsoiid snakes *Madtsoia laurasiae* Rage, 1999 and *M. madagascariensis* Hoffstetter, 1961, and the titanosaurid sauropods *Lirainosaurus* Sanz et al., 1999 and *Repetosaurus* Rogers and Forster, 2001. Taxa of Gondwanan origin in the late Campanian–Maastrichtian faunas of Europe include the neoceratosaurian (?abelisaurid) theropod *Tarascosaurus* from Southern France (Le Loeuff and Buffetaut 1991), an unnamed neoceratosaurian theropod from Romania (Csiki and Grigorescu 1998), the titanosaurid sauropods *Magyarosaurus* Nopsca, 1915 (Weishampel et al. 1991) and *Ampelosaurus* Le Loeuff, 1993 from Romania and France, respectively, and bothremyid pelomedusid turtles from Spain (Lapparent de Broin and Murelaga 1999; Lopez Martinez et al. 2001). All these indicate a significant exchange between European and Gondwanan (specifically, African) terrestrial biotas during the latest Cretaceous (Le Loeuff 1997). Our identification of UA 8699 as a zhelestid lends further credence to this previously known connection between Maastrichtian European and Malagasy vertebrate faunas. Although marsupials were reported from the Campanian fauna of the Iberian Peninsula (Antunes et al. 1986), this determination was based on a few imperfect specimens and is now doubted (Gheerbrant and Astibia 1999). Currently marsupials are not known from the Late Cretaceous of Europe nor Madagascar. Gheerbrant and Astibia (1999: 319) predicted the existence of *Lainodon*-like mammals in Africa.

Institutional abbreviations.—CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; L1AT, Museo de Ciencias Naturales de Alava, Spain; UA, University of Antananarivo, Madagascar; UCMP, University of California Museum of Paleontology, Berkeley, California.

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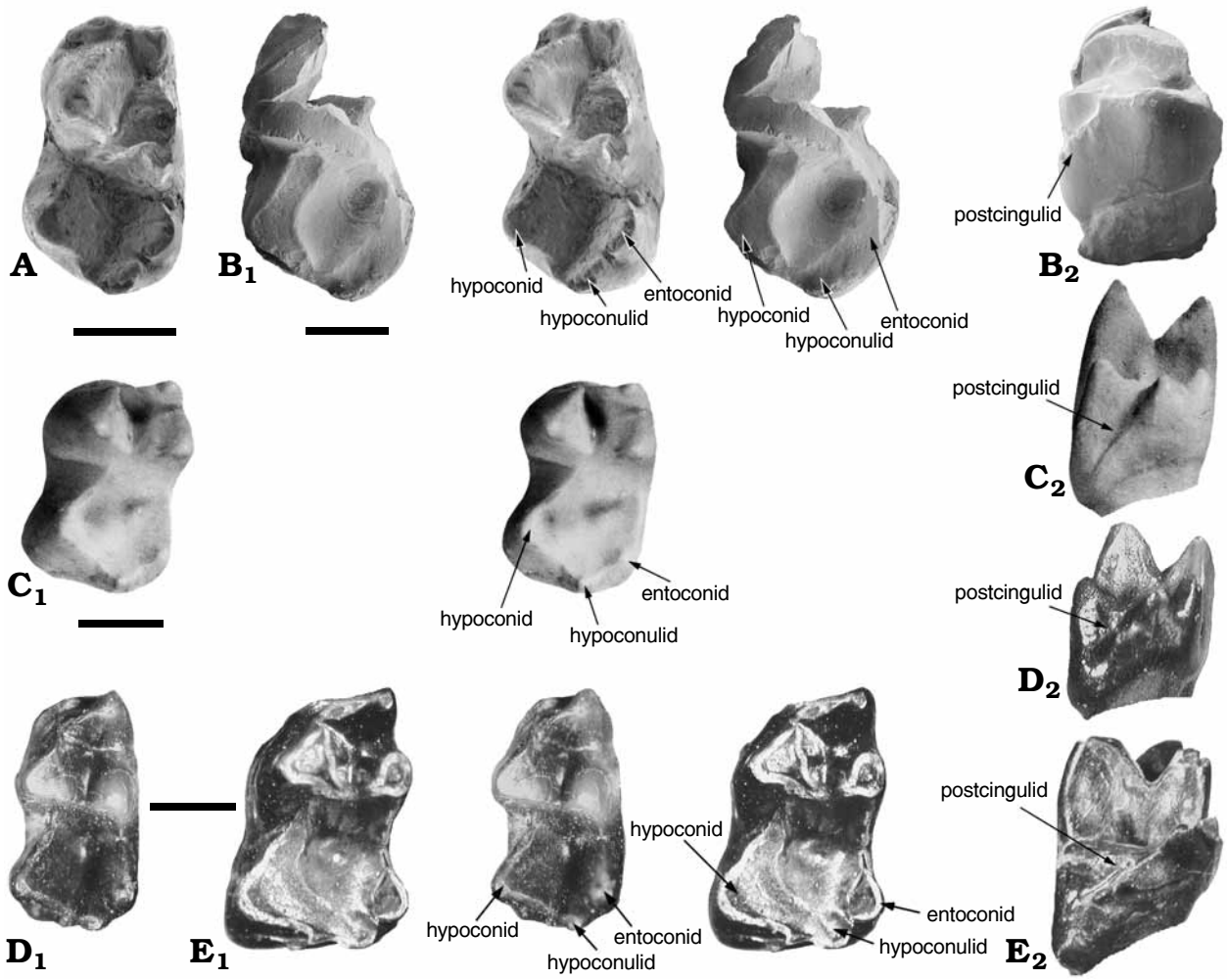

Fig. 1. Lower molars of therians. **A**. *Lainodon orueetxebarriai*, zhelestid placental mammal, Late Cretaceous, Spain, left m1?, stereo occlusal view (L1AT 14, holotype). **B**. Therian mammal, Late Cretaceous, Madagascar, left molar, (UA 8699), B_1, stereo occlusal view, B_2, posterior view. **C**. *Sorlestes budan*, zhelestid placental mammal, Late Cretaceous, Uzbekistan, right molar (reversed), (CCMGE 3/12176, part of holotype dentary), C_1, stereo occlusal view, C_2, posterior view. **D**, **E**. *Pediomys hatcheri*, marsupial mammal, Late Cretaceous, United States, D_1, right m1 (reversed) (UCMP127642), D_2, the same, posterior view, E_1, left m2 or 3 (UCMP 135217), E_2, the same, posterior view. Scale bars, 1 mm.

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Alexander O. Averianov [sasha@AA1923.spb.edu], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia;
J. David Archibald [darchibald@sunstroke.sdsu.edu], Department of Biology, San Diego State University, San Diego, California 92182-4614, USA;
Thomas Martin [tmartin@zedat.fu-berlin.de], Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität, Malterserstrasse 74-100, D-12249 Berlin, Germany.