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A large new collection of *Palaeostylops* from the Paleocene of the Flaming Cliffs area (Ulan-Nur Basin, Gobi Desert, Mongolia), and an evaluation of the phylogenetic affinities of Arctostylopidae (Mammalia, Gliriformes)☆,☆☆

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ABSTRACT

Arctostylopids are enigmatic mammals known from the Paleocene and Early Eocene of Asia and North America. Based on molar similarities, they have most often been grouped with the extinct Notoungulata from South and Central America, but tarsal evidence links them to Asian basal gliriforms. Although *Palaeostylops* is the best-known arctostylopid genus, some points of its content and species level taxonomy remain uncertain. Here we report 255 upper and lower jaw fragments of *Palaeostylops*, five calcanea, three astragali, as well as the first known arctostylopid distal tibia. This new material was collected from the late Paleocene of the Flaming Cliffs area in Mongolia, in a single lens almost exclusively containing arctostylopid remains. Our study of the morphology and size of the new *Palaeostylops* dental material confirms the validity of two species, *P. iturus* and *P. macrodon*, and illustrates their morphological and biometrical variability and diagnostic differences. The distal tibia of *Palaeostylops* is relatively unspecialised and resembles the Asian gliriforms *Pseudictops* and *Rhombomylus*. We also review the relevance of the historically important genus *Palaeostylops* in view of other, more recently described but less abundant arctostylopid genera. *Palaeostylops* remains the reference taxon for the arctostylopid anterior dentition and postcranial morphology. For both anatomical regions, arctostylopids differ significantly from notoungulates, and present a mosaic of characters also seen in basal gliriforms. The notoungulate-like molars of *Palaeostylops* are highly specialized for arctostylopids and the arctostylopid molar morphotype is therefore better illustrated by the early middle Paleocene *Asiostylops*. This morphotype does not present any similarities to notoungulates, but shares a number of derived characters with basal gliriforms. Among gliriforms, the primitive arctostylopid morphotype is most similar to *Astigale* from the early Paleocene of South China, and we suggest that Arctostylopidae may therefore be more closely related to Astigalidae than to any other group.

1. Introduction

The late Paleocene and early Eocene Arctostylopidae are diverse and typical elements of Asian mammal faunas, as well as exceedingly rare elements in North American faunas where they were first discovered (Cifelli et al., 1989; Wang et al., 2007). Based on striking molar resemblances, arctostylopids were initially grouped with the South and Central American Notoungulata (Matthew, 1915). This grouping implies early Tertiary mammal dispersal between North and South America. Arctostylopids have therefore figured prominently in various intercontinental dispersal hypotheses (Patterson and Pascual, 1972; Cifelli, 1983; Gingerich, 1985).

In 1989, interest in arctostylopids was revived by a phylogenetic revision of the group by Cifelli et al. (1989). This paper featured the first arctostylopid tarsal bones, and based on dental and tarsal morphology, Cifelli et al. (1989) placed Arctostylopidae in a new order Arctostylopida, distinct from Notoungulata and all other mammals. Thereby they also dismissed the faunal exchange between North and South America during the late Paleocene or early Eocene. Another part of their study handled the classification of the two best-known arctostylopids, *Palaeostylops iturus* and *Palaeostylops macrodon*. Since their discovery, these two species

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had always been reported to co-occur, both in Mongolian and Chinese late Paleocene sites (Matthew and Granger, 1925; Matthew et al., 1929; Russell and Zhai, 1987; Meng et al., 1998; Missiaen and Smith, 2008). This co-occurrence in otherwise species-poor communities, of two taxa differing only by their size seemed to suggest the presence of a single, sexually dimorphic species. Cifelli and co-authors raised the possibility of sexual dimorphism, but quickly dismissed it. Presenting a number of novel morphological differences between both forms, they concluded that they represented two distinct species and genera: *P. iturus* and "*Gashatostylops*" *macrodon* (Cifelli et al., 1989).

Since then, the validity of a separate genus "*Gashatostylops*" has been accepted by some studies (Ting, 1998; Meng et al., 1998), and rejected by others (Kondrashov and Lucas, 2004; Ni et al., 2007; Missiaen and Smith, 2008; this paper). Similarly, some researchers have accepted the placement of Arctostylopidae in a separate order Arctostylopida (Ting, 1998; Zack, 2004; Wang et al., 2008), while others have suggested to group them with Notoungulata based on unpublished new material (Bloch, 1999) or a rebuttal of the arguments of Cifelli and co-workers (Kondrashov and Lucas, 2004). Missiaen et al. (2006) published additional arctostylopid tarsals, assigned to *P. iturus* from Inner Mongolia and *Arctostylops* from North America. Based on the tarsal evidence, they supported the exclusion of Arctostylopidae from Notoungulata, and moreover placed the family Arctostylopidae within the superorder Gliriformes.

Here we report on the discovery of 255 upper and lower jaw fragments of arctostylopids recovered from a small sandy lens in the late Paleocene of the Flaming Cliffs area in Mongolia (Fig. 1). This collection contains specimens referable to both *P. iturus* and *P. macrodon* based on dental morphology and measurements, and represents a large, single sample from the type area of both forms. This collection is therefore perfectly suited to study the morphological and size variability of both forms, and to assess whether they represent two genera, two species or even one sexually dimorphic species.

In addition to the abundant dental remains, this lens also yielded a limited number of postcranial elements, including the previously unknown arctostylopid distal tibia, which provides additional data for reconstructing the higher-level phylogenetic position of arctostylopids. In view of more recently described but less well-known arctostylopids and of the new hypotheses on arctostylopid evolution, we critically review the relevance of the historically important and abundant *Palaeostylops* fossils from Gashato for our understanding of arctostylopid evolution.

2. Material and methods

Abbreviations: AMNH: American Museum of Natural History, New York, USA; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; IMM: Inner Mongolian Museum, Hohhot, China; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MLP: Facultad de Ciencias Naturales y Museo de La Plata, División Paleontología de Vertebrados, Buenos Aires, Argentina; MPC-M: Mongolian Paleontological Center-Mammal Collection, Academy of Sciences of Mongolia, Ulaanbaatar, Mongolia.

2.1. Material

The famous Flaming Cliffs area in Mongolia has long been known to yield abundant late Cretaceous (Djadokhta Formation) and early Paleogene (Khashat Formation = Gashato Formation) vertebrates (Matthew and Granger, 1925). During fieldwork at the Gashato locality in 1999, a small fossiliferous sandy lens ($< 1\ m^3$) in the late Paleocene Member 1 of the Khashat Formation was discovered and completely excavated and screenwashed by two of us (G.E. and J.-L.H.) and the late D. Dashzeveg (Fig. 1). Except for a few rare teeth of a large mixodont and one dentary fragment of a sarcodontid, the fossil mammal teeth in this lens belong exclusively to arctostylopids. A total of 730 teeth (canines, premolars and molars) in 255 upper and lower jaw fragments were recorded, representing a minimum number of individuals (MNI) of 48. In addition, this lens yielded a very limited number of identifiable postcranial remains. These include five calcanea and three astragali, which are attributed to *Palaeostylops* based on their abundance and their close similarity to the previously published tarsals of *P. iturus* (Missiaen et al., 2006). The distal part of a left tibia is also attributed to *Palaeostylops*, based on its articulation with the *Palaeostylops* tarsals. The distal part of a humerus can be attributed to the typical late Paleocene multituberculate *Lambdopsalis bulla*, which is not represented by dental specimens in this collection. Finally, a large phalanx and the proximal part of a femur could not be identified with certainty.

Among the arctostylopid dental remains, two different morphotypes can be recognised, corresponding to *P. iturus* and *P. macrodon* as originally described from this area (Matthew and Granger, 1925; Matthew et al., 1929). When possible, dental remains were attributed to either of both morphs based on the enlarged M2/m2, the only criterion universally accepted as diagnostic between both forms (Matthew et al., 1929; Cifelli et al., 1989; Kondrashov and Lucas, 2004; Missiaen and Smith, 2008). Using this method, 111 of the 255 upper and lower jaw fragments, representing 376/730 teeth and a MNI of 32, were unambiguously identified as *P. iturus*, whereas 40/255 jaw fragments, representing 154/730 teeth and a MNI of 14, were identified as *P. macrodon*.

2.2. Biostatistical analyses

Parallel to the comparative analysis of cheek tooth morphologies, all arctostylopid teeth in this collection were measured using a binocular microscope with a graded eyepiece with a precision of 0.1 mm. Length and/or width was determined for 697/730 measurable teeth, of which 497 were unambiguously identified as either *P. iturus* or *P. macrodon*. In order to quantitatively describe and compare length and width measurements for each available cheek tooth position, we computed standard statistics using PAST v. 2.01 (Hammer et al., 2001), including:

- usual univariate descriptive statistics;
- bivariate (Doornik and Hansen omnibus) tests for normality;
- Kolmogorov-Smirnov nonparametric test for two-sample univariate distribution comparison;
- Wilks' λ test for multigroup multivariate comparison (here, two groups [*P. iturus* and *P. macrodon*] and two variables [length and width cheek tooth dimensions]).

Computation of two-group bivariate Wilks' λ (formally identical to an Hotelling's T^2-test) was preferred to the more usual combination of two univariate Student *t*-tests because several univariate distributions show significant departure from normality (results not shown), whereas all but one cheek tooth positions (*P. iturus*' P4) appear bi-normally distributed at the 95% confidence level (Table 1). Thus, based on the available sample distributions, the association of bivariate Wilks' λ with univariate Kolmogorov-Smirnov statistics offers the best possible compromise between power and robustness in order to test for significance both sample mean and individual distribution differences for each position.