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## SHORT COMMUNICATION

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# Asian gliriform origin for arctostylopid mammals

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**Abstract** Arctostylopids are common in Late Palaeocene and Early Eocene mammal faunas of Asia, but they are rare in North America. From the time of their first discovery, arctostylopids were grouped with the strictly endemic South American Notoungulata based on their strikingly similar dental morphology. This relationship was challenged based on dental morphology of more recently discovered arctostylopids and on supposed tarsal morphology (based on unassociated material) of the Asian arctostylopid *Palaeostylops*. Therefore, Arctostylopidae were placed in a separate order, Arctostylopida, of enigmatic affinities. Many authors, however, continue to unite Arctostylopidae and Notoungulata based on dental simi-

larities. In the Late Palaeocene Subeng site in Inner Mongolia, we identified the *Palaeostylops* tarsals based on their size and abundance. This identification is supported by comparison to unpublished *Arctostylops* tarsals from the North American Clarkforkian, derived from a semi-articulated skeleton also including dental material. Tarsal morphology shows moderate similarity to the gliriform *Pseudictops*, and strong resemblance to the tarsally conservative gliroid *Rhombomylus*. Hence, Arctostylopidae may best be grouped with Asian non-gliroid Gliriformes, which we interpret as having dispersed into North America in the Late Palaeocene.

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## Introduction

Arctostylopidae are common and diverse elements of Asian Late Palaeocene and Early Eocene mammal faunas (Cifelli et al. 1989; Ting 1998) but are exceedingly rare in North America where they were first discovered. Based on striking dental resemblances, arctostylopids were immediately grouped with the strictly endemic South American Notoungulata, and they were considered the first compelling evidence for Early Tertiary mammal dispersal between North and South America (Matthew 1915). Since then, Arctostylopidae have figured prominently in various intercontinental dispersal scenarios (Patterson and Pascual 1972; Cifelli 1983a; Gingerich 1985; Beard 1998).

Cifelli et al. (1989) published a revision of Arctostylopidae including the first arctostylopid tarsals, attributed to the Asian Late Palaeocene *Palaeostylops iturus*. These authors argued that dental similarities to Notoungulata were caused by convergence. Their discussion of the arctostylopid ankle morphology noted the lack of certain notoungulate tarsal synapomorphies and a limited similarity to the Asian endemic *Pseudictops*. In conclusion, Cifelli et al. (1989) placed Arctostylopidae in a new, separate order Arctostylopida. Preliminary observations on a semi-articulated partial skeleton of North American *Arctostylops* by Bloch (1999) renewed the discussion on arctostylopid phylogeny, and Kondrashov and Lucas (2004) restored

Arctostylopidae as a family within Notoungulata. Ninety years after their first discovery, the affinities of arctostyloids remain controversial.

The Late Palaeocene mammals from the Subeng site in Inner Mongolia have only recently been studied in detail (Smith et al. 2004; Missiaen and Smith 2005). In this locality, dental material from *P. iturus* is highly abundant, and we identified the isolated tarsals from *P. iturus* (Fig. 1) based on their size and abundance (Fig. 2). This identification is supported by their similarities to the tarsals of *Arctostylops* (Fig. 3), the only arctostyloid tarsals known directly associated with dental material (Bloch 1999). In this study, we fully illustrate, describe and compare the *Palaeostylops* tarsals, and discuss their functional interpretation and phylogenetic and biogeographic implications.

### Systematic palaeontology

Gliriformes Wyss and Meng, 1996

Arctostylopidae Schlosser, 1923

*Palaeostylops* Matthew and Granger, 1925

*Palaeostylops iturus* Matthew and Granger, 1925

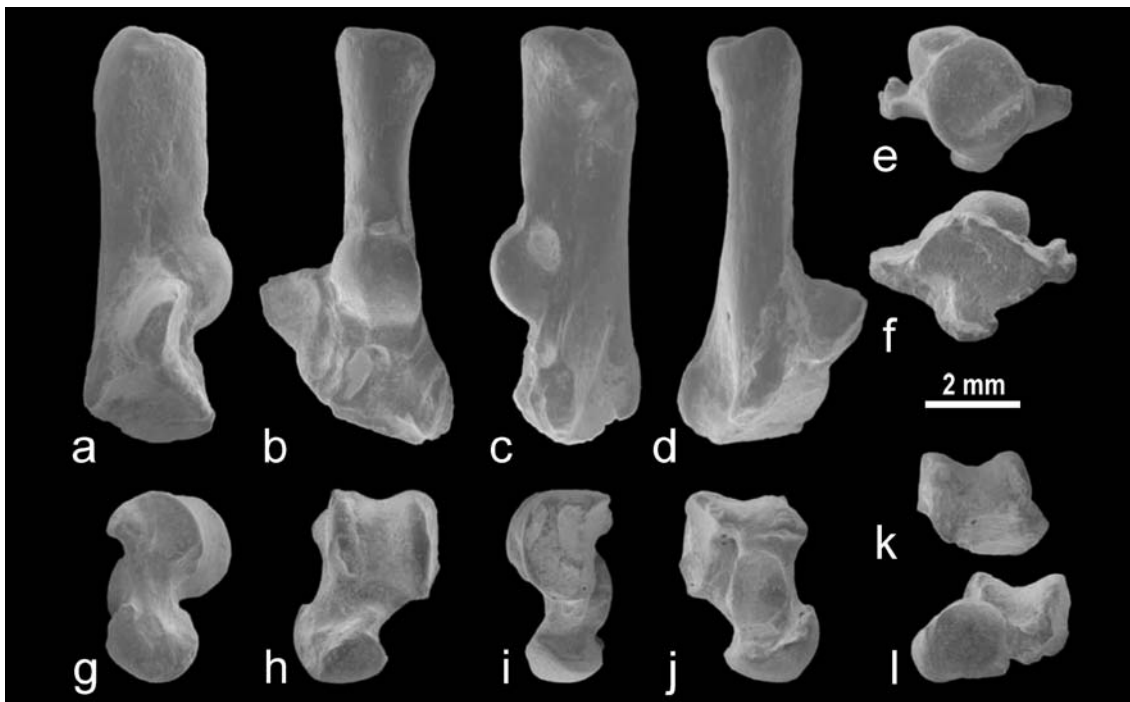
### Referred material

Three complete astragali and a proximal part of an astragalus (IMM 2004-SB-4 to 8); three complete calcanea and a distal part of a calcaneum (IMM 2004-SB-9 to 12).

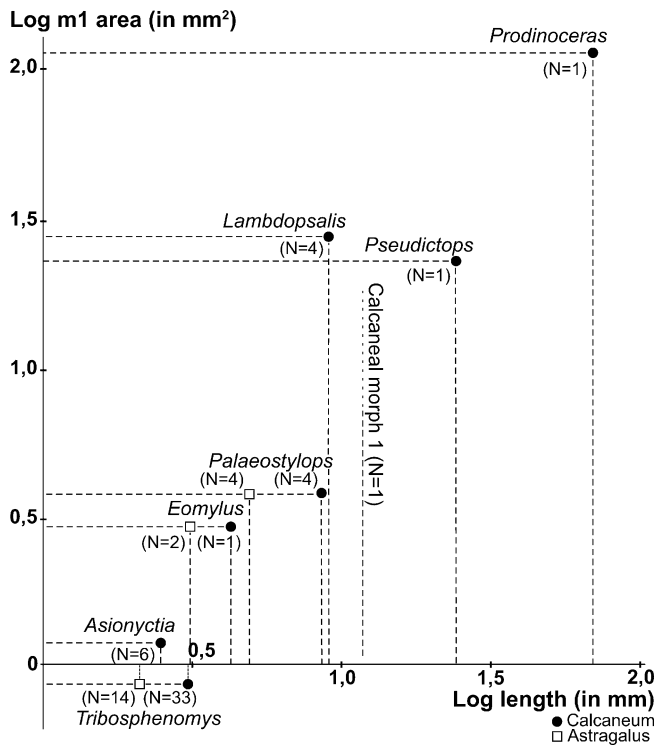
### Description (Fig. 1)

The astragalar trochlea is marked and slightly asymmetrical, with the lateral crest somewhat longer than the medial crest. The body is semicylindrical without a dorsal foramen. The lateral side bears a semicircular fibular facet and a small lateral process, and the medial side has a small tibial process. The neck is relatively long and somewhat constricted. The small head bears a narrow cuboid facet, a long, dorsoventrally oriented navicular facet and a medial facet extending far on the medioplantar side. These three facets are not sharply delimited, but neither one is confluent with the sustentacular facet. This facet is slightly proximodistally elongated and weakly convex. The long ectal facet faces lateroplantarly and is strongly concave.

The calcaneum is robust in lateral outline, with a long, somewhat compressed tuber. The ectal and fibular facets are large and conspicuous, strongly convex and roughly parallel to the long axis. The ectal facet is rounded and dorsoventrally inclined, facing partially medially with an angle similar to that of the astragalar ectal facet. The fibular facet is rectangular in dorsal view, somewhat shorter anteroposteriorly than the ectal facet and slightly dipping medioventrally. The proximal border of the sustentaculum is situated midway of the ectofibular facet and is almost perpendicular to the long axis; the distal border is more obliquely oriented and reaches the medialmost limit of the cuboid facet. The cuboid facet has an oblique distomedial orientation and a subrhomboid outline. The distal plantar tubercle is small but clearly visible. A small but prominent peroneal process is present on the distalmost lateral end. There is no transverse calcaneal canal.



**Fig. 1** SEM micrographs of *P. iturus* tarsals from Subeng. Left calcaneum (IMM 2004-SB-9) and left astragalus (IMM 2004-SB-4) in medial (a, g), dorsal (b, h), lateral (c, i), ventral (d, j), proximal (e, k) and distal (f, l) views



**Fig. 2** Diagram illustrating association of tarsal and dental specimens based on their dimensions. X-axis shows dimensions and number of all tarsal morphs at Subeng, and Y-axis shows dimensions of corresponding dental specimens. Dimensions taken in millimeters and log-transformed. *N* = number of specimens for the specific morph

### Comparison

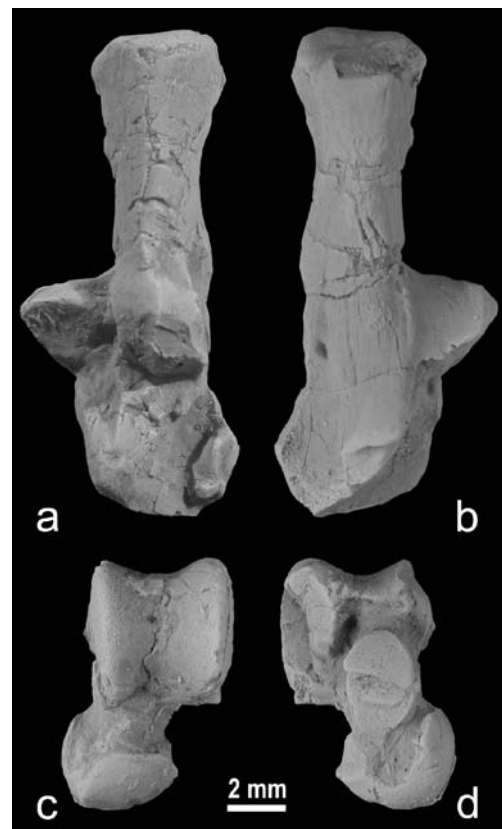
The new *Palaeostylops* tarsals show several differences from those figured by Cifelli et al. (1989). Many of the observed differences could be due to wear, breakage or differences in orientation, and at least some errors occurred during the drawing process (note the inversion of the left calcaneum, which was depicted as a right calcaneum in the ventral view). We have not seen these materials and so refrain from judging the association made by Cifelli et al. (1989; criticised by Kondrashov and Lucas 2004).

Comparison of the *Palaeostylops* tarsals to those of Notoungulata is of primary interest. The oldest unambiguous Notoungulata are *Colbertia*, *Itaboratherium* and *Camargomendesia* from the Late Palaeocene Itaborai fauna in Brazil, and the tarsals have been identified for all three genera (Bergqvist 1996). These tarsals exemplify the notoungulate morphotype that is characterised by the following synapomorphies (Cifelli 1983b, 1993; Bergqvist 1996). The astragalus has a long, constricted neck with an oblique dorsal crest, a large medial protuberance, a sulcus leading laterally from the dorsal astragalular foramen and a well-developed contact of sustentacular and navicular facet. The calcaneum has a conspicuous beak on the dorsal distomedial end and a deep groove between the sustentacular and ectal facet. Out of all these characters, the *Palaeostylops* tarsals only match the long, constricted

astragalular neck, equally observed in other groups, ranging from Palaeocene leptictids to Recent elephant shrews and including *Pseudictops*, *Rhombomylus* and *Palaeolagus* (Fig. 4). The *Palaeostylops* tarsals do not exhibit any other notoungulate synapomorphy and thus do not, by themselves, provide support for placement of Arctostylopidae within the Notoungulata.

We made extensive comparisons with tarsals of most extinct and modern mammal orders, finding that the arctostyloid tarsals are characterised by the following features. The astragalus has a well-defined and fairly symmetrical trochlea without dorsal foramen, a neck that is moderately long and somewhat constricted and a navicular facet that is not confluent with the astragalular sustentacular facet. The calcaneum has a long, laterally compressed tuber, large ectal and fibular facets oriented roughly parallel to the long axis, a moderate peroneal process and an obliquely oriented cuboid facet.

This combination of diagnostic characters is only met by the Early Eocene eurymylid *Rhombomylus*, which also exhibits the best overall resemblances to the *Palaeostylops* tarsals. Meng et al. (2003) published a detailed description of *Rhombomylus*, and their comprehensive analysis of



**Fig. 3** Associated left calcaneum and astragalus of *Arctostylops* from the Clarks Fork Basin in dorsal (a, c) and ventral (b, d) views. These tarsals form part of University of Michigan Museum of Paleontology specimen UM 82359, a semi-articulated partial skeleton reported previously by Bloch (1999), and are thus found in direct association with dental material. Note the striking similarities to the *Palaeostylops* tarsals, confirming the association of these materials found in isolation

Glires and associated taxa is followed throughout this paper. The Asian endemic eurymylids are basal Glires, and arctostylopids and Glires share the following derived characters: absence of the dorsal astragal foramen and the roughly parallel orientation of the ectal and sustentacular facet on the astragalus (Meng et al. 2003). The *Palaeostylops* tarsals differ from *Rhombomylus* by the more dorsoventrally oriented navicular facet on the astragalus, and by the more longitudinal ectal facet and the broader and more dorsally facing fibular facet on the calcaneum. However, these features are derived characters shared with *Pseudictops*, a contemporaneous Asian endemic gliriform which also exhibits considerable overall similarities to *Palaeostylops* and *Arctostylops* (Sulimski 1968).

### Functional interpretation

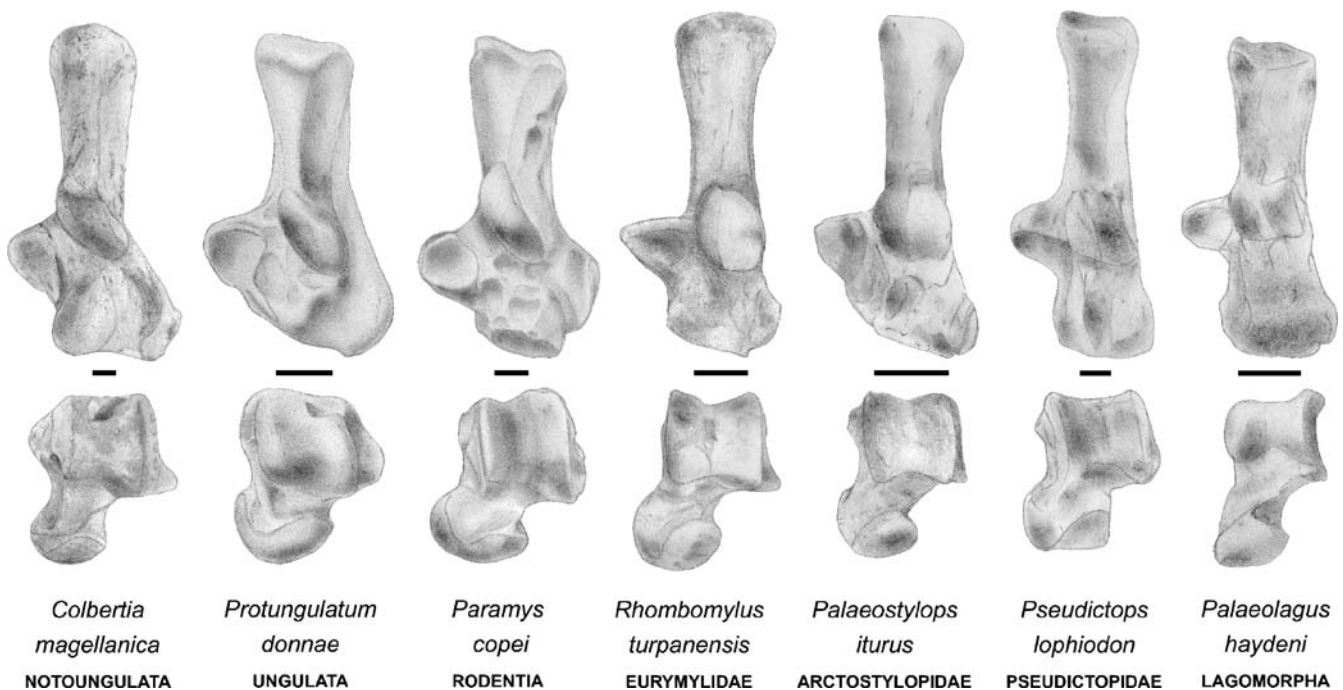
Almost all of the distinctive tarsal characters cited above to group *Palaeostylops* and *Rhombomylus* enhance lateral stability and suggest a cursorial or saltatorial locomotion (Tabuce et al. 2006). The more dorsoventral astragal navicular facet and the more longitudinal calcaneal ectofibular facet, which differentiate *Palaeostylops* from *Rhombomylus*, are observed in *Pseudictops* as well as in Lagomorpha, and may therefore suggest that *Palaeostylops* was even slightly more specialised than was *Rhombomylus*. *Palaeostylops* was thus moderately specialised for fast running or jumping in terrestrial conditions and possibly digitigrade.

### Phylogenetic and biogeographic implications

Traditional views of relationships have united Arctostylopidae with Notoungulata based on their strikingly similar teeth. The close similarity of the *Palaeostylops* and *Rhombomylus* tarsals may therefore seem surprising especially because of their strongly divergent dentitions.

True Glires such as *Rhombomylus* are uniquely characterised by their specialised gnawing dentition with enlarged incisors and reduced dental formula. Basal gliriforms such as *Anagale* and *Pseudictops*, however, retain a complete dental formula with the upper and lower dentition forming an evenly graded series, as is also the case in arctostylopids. Moreover, Cifelli et al. (1989) proposed an arctostyloid dental morphotype, differing from advanced arctostylopids by weaker molar lophes, no molar hypocone and p3 without metaconid. These characters would separate arctostylopids from Notoungulata, but are also present in basal Gliriformes (Meng et al. 2003), and may bridge the morphological gap with Gliriformes. Therefore, the arctostyloid dentition immediately prevents their association with true Glires but not necessarily with non-gliroid Gliriformes.

Tarsal morphology of arctostylopids described in this study does not support their notoungulate affinities. Instead, it compares moderately well to the Asian gliriform *Pseudictops*. Similarity is even greater to the Asian gliroid *Rhombomylus*, for which the conservative tarsal morphology does not differ significantly from the gliriform stage (Meng et al. 2003; Asher et al. 2005). We suggest



**Fig. 4** Dorsal view of left tarsals illustrating basal morphotypes of notoungulates, ungulates and different gliriform groups. Scale bar equals 2 mm. Illustrations based on Sulimski (1968), Szalay (1977, 1985), Bleefeld and McKenna (1985), Meng et al. (2003) and on personal observations



Arctostylopidae may be a family of non-gliroid Gliriformes, conserving the primitive dental formula and the gliriform tarsal characters cited in the “[Comparison](#)” section. As in other groups during the expansive radiation of Gliriformes, the dentition may have evolved more rapidly than postcranial morphology, and adaptation to a particular type of herbivory led to the evolution of molar lophs, divergent from other gliriforms.

We propose that Arctostylopidae is part of a Palaeocene radiation of endemic Asian Gliriformes. During the Late Palaeocene, arctostyloids migrated from Asia into North America, giving rise to the genus *Arctostylops*, but never achieved the diversity and success of their Asian relatives (Cifelli et al. 1989; Zack 2004). A comprehensive analysis that includes both postcranial and dental morphology is needed to really test the affinities proposed here. Likewise, description of the skeleton of *Arctostylops* is underway (Bloch et al. in preparation) and will provide a robust test of the hypotheses presented here.

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