

AN EARLY EOCENE ARCTOSTYLOPID (MAMMALIA: ARCTOSTYLOPIDA) FROM THE GREEN RIVER BASIN, WYOMING

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Arctostylopidids are an enigmatic group of small, herbivorous early Cenozoic mammals (Cifelli et al., 1989; Cifelli and Schaff, 1998) initially described as members of the endemic South American order Notoungulata (Matthew, 1915). Cifelli et al. (1989) considered the resemblances between arctostylopidids and notoungulates to be convergent, placing the family in a new order to recognize their distinctiveness. Similarities of the arctostylopid tarsus to the anagalidan *Pseudictops* were noted by Cifelli et al. (1989) and Cifelli and Schaff (1998), but in both cases, the order's higher level affinities were left unresolved. With regard to possible anagalidan relationships, it should be noted that Meng et al.'s (2003) recent analysis of anagalidan and gliroid interrelationships does not even consider the possibility of a relationship between arctostylopidids and anagalidans. The group has most recently been placed in the ungulate mirorder Eparctocyna, along with artiodactyls, whales, and a number of taxa traditionally placed in the paraphyletic order "Condylarthra" (McKenna and Bell, 1997). Prior to the present work, arctostylopidids were known from the early Paleocene to early Eocene of Asia (e.g., Matthew and Granger, 1925; Zhai, 1978; Zheng, 1979) and the late Paleocene of North America (Matthew, 1915; McKenna, 1980; Rose, 1981; Cifelli et al., 1989; Cifelli and Schaff, 1998). The first appearance of arctostylopidids in North America in the late Paleocene Tiffanian North American Land Mammal Age (NALMA) is coincident with the appearance of other Asian taxa, particularly Dinocerata (Rose, 1981).

While arctostylopidids are relatively abundant in some Asian faunas, they remain extremely rare in North America. Cifelli et al. (1989) reported eight specimens of *Arctostylops steini*—until now the only North American representative of the family—seven from the Tiffanian and Clarkforkian of the Clarks Fork Basin of northwest Wyoming and a molar trigonid from the Clarkforkian near Togwatee Pass in northwestern Wyoming (McKenna, 1980). At least one additional specimen is now known (Bloch, 1999), but *A. steini* is still one of the most infrequently encountered North American late Paleocene mammals. To some extent, this rarity may account for the lack of a previous early Eocene record in North America. However, the number of mammalian specimens from the early Eocene Wasatchian NALMA vastly outnumbers that from the late Paleocene of the Tiffanian and Clarkforkian NALMAs.

The specimen described in this paper was collected by a field party led by C. L. Gazin in 1961, but was not previously identified or described. It comes from one of several localities southwest of Rock Springs originally prospected by Roehler (Gazin, 1965). I encountered the specimen in a small block of coarse-grained sandstone with the field number 10–61 while searching through uncatalogued material from the Green River Basin. Gazin's field catalogue entry for 10–61 indicates derivation from low in the local Wasatch section and would appear to correspond to one of two faunules described as coming from "well below the Tipton Tongue" (Gazin, 1965:176). The lithology of the fragments with the 10–61 field number does not match Roehler's (1992) description of the lowest locality in this area, and derivation from the higher of the two localities, identified as locality 2a59 in Roehler (1992), appears more likely. However, I have not had the opportunity to visit this locality to confirm this. Other uncatalogued blocks with the same field number include *Hyracotherium* sp. and *Hyopsodus* sp., supporting an early Eocene age. This fauna appears to be early Wasatchian based on the presence of *Haplomyilus*, which makes its last appearance

in Wa-4 of the Bighorn Basin (Schankler, 1980; Clyde, 2001), but further age refinement is not currently possible.

Institutional Abbreviations—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **USGS**, United States Geological Survey, now in the collections of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **USNM**, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

EUTHERIA Huxley, 1880
ARCTOSTYLOPIDA Cifelli et al., 1989
ARCTOSTYLOPIDAE Schlosser, 1923
genus and species indeterminate
(Fig. 1a, b)

Referred Material—USNM 521803, heavily worn left M?2.

Horizon and Locality—Early Eocene (Wasatchian) of the Main Body of the Wasatch Formation; USGS locality 2a59, southwest of Rock Springs, Green River Basin, Wyoming.

Description—USNM 521803 is an isolated and heavily worn left upper molar that retains three large, relatively vertical roots (Fig. 1A, B). Based on comparisons with other arctostylopidids, it is probably an M2. The advanced state of wear has removed most crown morphology, but enough remains to confidently identify the specimen as an arctostylopid and to discuss its relationships to named taxa. In occlusal view, the crown is trapezoidal, with its greatest mesiodistal length buccally and with the lingual end noticeably shorter. Overall, the crown is relatively elongate for its width. The most striking feature of USNM 521803 is its high-crowned but featureless ectoloph (Fig. 1B). There is no development of folds on the buccal surface of the ectoloph nor is there any trace of a buccal cingulum. The only notable feature on the buccal surface of the crown is an inflection in the ectoloph where the parastyle joins the paracone. Based on the position of this flexure, the parastyle was relatively elongate.

The central portion of the crown is very heavily worn and almost no morphology remains (Fig. 1A). However, the pattern of wear resembles that seen in arctostylopidids in that the ectoloph bears a single, steeply inclined wear facet. On the lingual margin of the worn central portion of the crown are the small and largely confluent protocone and pseudohypocone (following the terminology of Cifelli et al., 1989), which are divided lingually by a faint sulcus, morphology virtually identical to that of *Arctostylops steini*. The pseudohypocone was apparently smaller than the protocone and more buccally positioned, again as in *A. steini*. More distal but closely appressed to the pseudohypocone is a tall, nearly lophate distal cingulum, which extends farther lingually than the pseudohypocone and protocone and is taller, but otherwise similar to that of *A. steini*. In contrast to the latter taxon, while the lingual margin of the distal cingulum is inflected mesially, it does not continue as a true lingual cingulum, nor is there any trace of a mesial cingulum, although the latter may have been removed by wear. The lingual margin of the crown is tall, although not so tall as the ectoloph, and nearly vertical, but slightly inflated basally.

Measurements—Length: 4.8 mm; width: 5.2 mm.

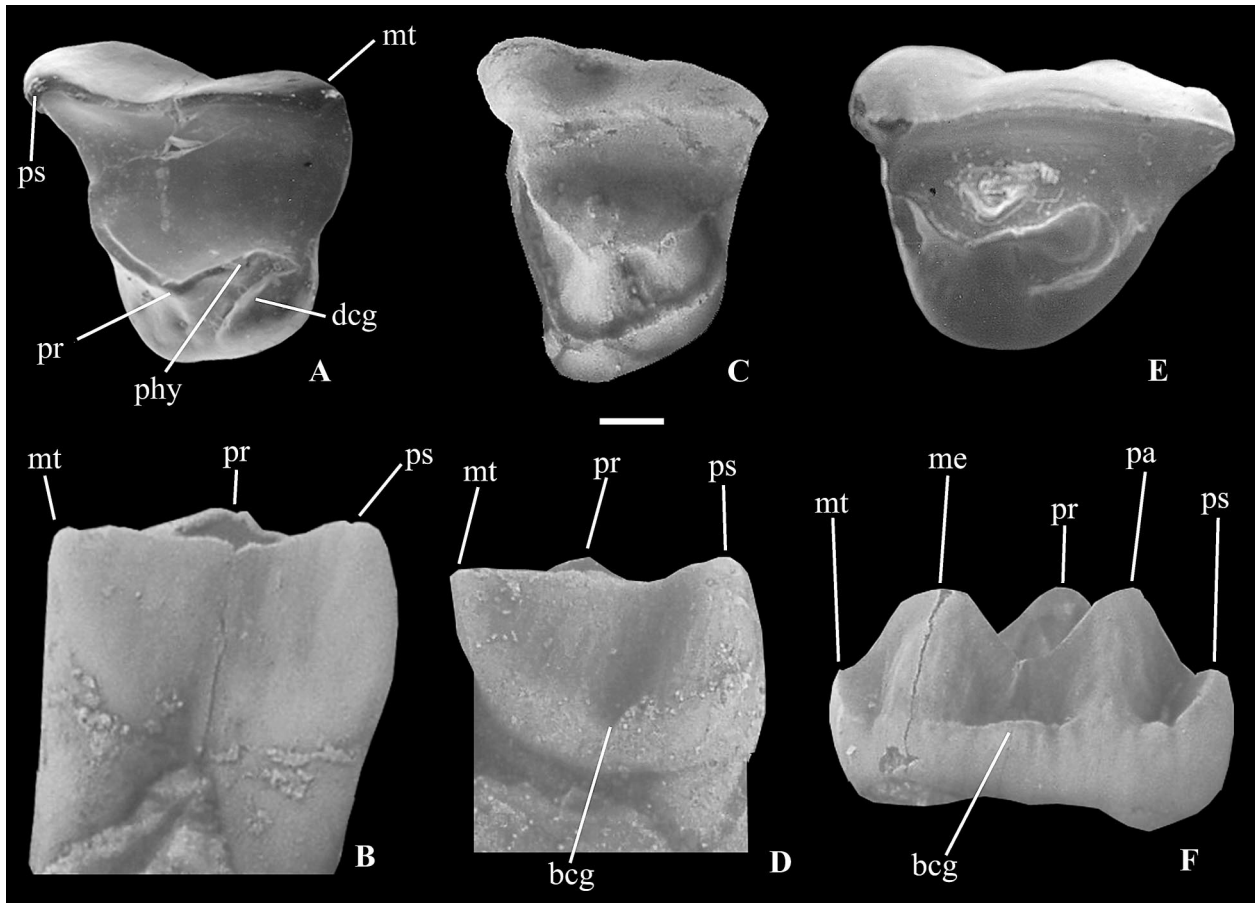


FIGURE 1. Comparison of USNM 521803, left M₂, Arctostylopidae indet. (A, B) with MCZ 20004, right M₂ (reversed), *Arctostylops steini* (C, D), IVPP 4357, left M₂, *Anatolestylops dubius* (holotype) (E), and USGS 13288, left M₂, *Hyopsodus powellianus* (F). A, C, E, occlusal view; B, D, F, buccal view. Note the contrast in buccal view between the arctostylopid (A and C) and *Hyopsodus* (F). Although the strength of particular features varies, other “condylarths,” perissodactyls, artiodactyls, and primates are comparable to *Hyopsodus* in ectoloph morphology and differ dramatically from USNM 521803 and other arctostylopid. Scale equals 1 mm. **Abbreviations:** bcg, buccal cingulum; dcg, distal cingulum; me, metacone; mt, metastyle; pa, paracone; phy, pseudohypocone; pr, protocone; ps, parastyle.

Discussion—Referral of USNM 521803 to Arctostylopidae is based on the following features that are not, in combination, found in any other group of Paleocene or Eocene mammals: relatively hypsodont crown, particularly buccally; buccal wall of crown featureless, lacking either a buccal cingulum or folds in the positions of ectoloph cusps (compare Fig. 1B, D with Fig. 1F); crown elongate and substantially longer buccally than lingually; protocone and pseudohypocone relatively small and closely appressed; distal cingulum tall and lophate; crown inflated at lingual basal margin.

The morphology of the buccal margin of the crown, essentially reduced to a vertical wall, is particularly unusual in an early Tertiary mammal. Aside from arctostylopid, the only other group to show any close morphological similarity is Notoungulata. The most similar notoungulates, those of the family Notostylopidae, differ in retaining at least a paracone fold connected to a weak buccal cingulum, in having less strongly developed distal cingula, and in having relatively larger lingual cusps, resulting in molars that are somewhat more transverse and less noticeably elongate buccally.

Among Wasatchian mammals previously known from North America, USNM 521803 most closely resembles hypsodontid and some phenacodontid “condylarths,” perissodactyls, primates, and artiodactyls in observable crown morphology. The squared proportions and prominent parastyle of USNM 521803 are suggestive of deciduous premolars. However, the retention of three large roots in an isolated tooth argues against this. Moreover, deciduous premolars are generally lower crowned than molars of the same taxa. As USNM 521803 is higher crowned than molars of any of the taxa that invite close comparison, it is unlikely that it represents a deciduous tooth of one of these forms.

Perissodactyls and the phenacodontid “condylarths” *Meniscotherium* and *Ectocion* resemble USNM 521803 in being relatively lophodont for Wasatchian mammals and, in particular, in having tall ectolophs. However, these taxa are larger, lower crowned (except for the largest perissodactyls), have V-shaped centrocrisae in buccal view, and, except for phenacodontid M3s, large connate hypocones. M3s of *Ectocion* and *Meniscotherium* typically lack hypocones, but there is no development of a lophate distal cingulum that terminates lingual to the protocone. Perissodactyl molars retain prominent paracone and metacone folds, and the hypocone of all molars forms part of a transverse metaloph, all features lacking in USNM 521803. *Ectocion* molars have prominent mesostyles and retain paracone and metacone folds on the buccal surfaces of their ectolophs, while *Meniscotherium* also has large mesostyles and incipiently selenodont molars, with W-shaped ectolophs in buccal view.

Unlike phenacodontids and perissodactyls, hypsodontid “condylarths” are more similar to USNM 521803 in size. All three North American Wasatchian genera (*Hyopsodus*, *Haplomylys*, and *Apheliscus*) are much lower crowned, more bunodont, and have strong ectoloph cusp relief (Fig. 1F). *Hyopsodus* has a well-developed hypocone and relatively transverse crowns, both in contrast to USNM 521803. *Apheliscus* has more quadrate crowns and a very weak hypocone, but has a low weak distal cingulum that ends buccal, rather than lingual to the level of the protocone. *Haplomylys* has a crest between the protocone and hypocone that, when worn, gives the impression that a pseudohypocone is present. However, the distal cingulum is low and terminates at the hypocone, rather than being lophate and continuing to the lingual margin of the crown.

Some adapid primates have well-developed pseudohypocones, which invite comparison with USNM 521803. However, adapid molars are much more transverse and low crowned than USNM 521803, retain prominent buccal cingulae and paracone and metacone folds, have V-shaped centrocristae in buccal view, and do not develop a lophate distal cingulum. Finally, early Eocene artiodactyls are bunodont, much lower crowned, have more transverse upper molars, have prominent ectoloph cusp relief, and lack a lophate distal cingulum, all in contrast with USNM 521803. Overall, USNM 521803 is much more similar to arctostylopids than to any previously recognized North American Wasatchian mammal.

Within the Arctostylopidae, USNM 521803 appears to be new at least at the specific level. In contrast to *Arctostylops steini* (Fig. 1C, D), previously the sole known North American arctostylopid (Matthew, 1915; Rose, 1981; Schaff, 1979; McKenna, 1980; Cifelli et al., 1989), USNM 521803 has a completely featureless buccal wall (traces of a buccal cingulum are retained in *A. steini*), a stronger, more lophate distal cingulum, and lacks a lingual cingulum. USNM 521803 also has more vertically oriented lingual slopes of the protocone and pseudohypocone, indicating a more hypsodont crown. However, the extreme wear on USNM 521803 makes it difficult to assess the magnitude of this difference. Despite these differences, USNM 521803 is similar to *A. steini* in size and crown proportions. In particular, both taxa have relatively transverse crowns and large, mesiobuccally directed parastyles.

The extreme simplification of the ectoloph, absence of the lingual cingulum, and degree of hypsodonty seen in USNM 521803 are found in the two named Eocene arctostylopids from Asia, *Anatolostylops dubius* Zhai, 1978, and *Stenostylops xiangensis* Huang et al., 2001. The large parastylar region of USNM 521803 is also found in *Stenostylops*, while *Anatolostylops* (Fig. 1E) has a relatively small parastyle. However, USNM 521803 differs from *Stenostylops* in having a less reduced lingual portion of the crown, in retaining at least a weak sulcus between the protocone and pseudohypocone, and in having a distal cingulum that is less well separated from these cusps, all features shared with *Anatolostylops dubius* and *Arctostylops steini*. USNM 521803 differs from both Asian forms in its more transverse crown, which appears to result chiefly from a less distally elongate ectoloph.

Overall, USNM 521803 is most similar to *Arctostylops steini*. The major differences from the latter taxon are the greater hypsodonty in USNM 521803 and the reduction of basal crown features, which is not atypical of hypsodont mammals. Additional material is needed to be certain, but the similarities between USNM 521803 and Asian Eocene arctostylopids are at present best regarded as parallelism. USNM 521803 almost certainly represents a new taxon, but I refrain from naming it due to the very incomplete nature of the only known specimen.

DISCUSSION

The discovery of the first Wasatchian arctostylopid in North America after well over a century of collecting raises the obvious question of why the group has not been recorded earlier, particularly in the extraordinarily well-sampled Willwood Formation of the greater Bighorn Basin, which has yielded almost all known North American Paleocene arctostylopids. The simplest explanation is that the ecological requirements of the family were not met in the basin-center floodplains sampled by most North American early Eocene deposits. Cifelli and Schaff (1998) have suggested that arctostylopids were specialized herbivores, possibly adapted to a diet of fibrous vegetation. The hypsodont dentition of the specimen reported here (and of other Eocene arctostylopids) is consistent with a fibrous diet, although high dietary abrasives such as plant phytoliths or exogenous grit could also be responsible (Williams and Kay, 2001). Described arctostylopid postcrania suggest terrestrial habits (Cifelli et al., 1989; Bloch, 1999), a potential source of the second class of abrasives, although many other early Eocene taxa that show evidence of terrestrial habits (Rose, 1990, 2001) are not hypsodont. Meng et al. (1998) have argued that late Paleocene Mongolian faunas, in which arctostylopids are abundant, sample more open, less heavily forested environments than contemporary North American faunas, in which arctostylopids are exceedingly rare. A preference for relatively open habitats would explain the combination of hypsodonty and terrestrially adapted postcrania seen in arctostylopids.

If, as argued above, the new taxon is most closely related to *Arctostylops steini* among named arctostylopids, the family was probably continuously present in North America from the Tiffanian through the Wasatchian, despite its poor record on this continent. This suggests that suitably open habitats were present throughout this time. However, the

poor record of arctostylopids suggests that such habitats are infrequently sampled and are probably not associated with the proximal floodplain deposits that constitute most fossiliferous Paleocene and early Eocene deposits in western North America (Gingerich, 1989). The occasional presence of arctostylopids in such deposits suggests, however, that suitable habitats may not have been geographically distant.

The discovery of an arctostylopid in the early Eocene of Wyoming also has implications for reconstructions of the biogeographic history of arctostylopids. While the morphology of the new specimen is most compatible with a sister-taxon relationship to North American *Arctostylops*, the resemblances to Asian *Anatolostylops* and *Stenostylops* could be indicative of a separate Asian origin for the new form. Either way, the recovery of a North American Eocene arctostylopid indicates that the North American history of the group remains poorly known, probably due to a preference for infrequently sampled environments. The negative evidence for the absence of the group from North America prior to the late Paleocene should be viewed with caution, particularly in the evaluation of a relationship between Asian/North American arctostylopids and South American notoungulates.

Acknowledgments—Thanks go to Dr. R. J. Emry and R. Purdy for facilitating the loan of USNM 521803 and for permission to describe it, to C. Schaff for providing a cast of MCZ 20004, to Dr. K. D. Rose, Dr. M. C. McKenna, Dr. J. I. Bloch, Dr. Z.-X. Luo, T. Penkrot, and F. Therrien for helpful reviews and discussions, to Dr. M. F. Teaford, T. Penkrot, and B. Auerbach for SEM assistance, and to Dr. C. B. Ruff for access to a digital camera.

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Received 19 May 2003; accepted 12 August 2003.