INTRODUCTION

The initial radiations of the orders of eutherian mammals took place during the Paleocene and Eocene according to palaeontological data (e.g., Rose and Archibald, 2005; Wible et al., 2007; Goswami et al., 2011; O’Leary et al., 2013). Mammal fossils from the Paleocene are of particular relevance to the study of the origin and evolution of modern orders (Valen, 1978), because they include representatives of extinct orders that show traits indicating potential relationships to modern orders. The earliest definitive members of modern orders typically appear later.

Procreodi, Matthew, 1915 (= Arctocyonidae Van Valen, 1969; McKenna and Bell, 1997), is a group of more than 20 Paleocene–Eocene genera (Table 1) believed to lie at the base of the radiation of primitive ungulates called ‘condylarths’ (Van Valen, 1978; Rose, 2006). Condylarths are generally considered to include the sister taxa or ancestors of other ungulate clades, most notably the extant orders Artiodactyla and Perissodactyla. Representatives of Procreodi are found in North America, Europe, and possibly Asia, and have been known for over 150 years, the genus Arctocyon itself having been coined by de Blainville in 1841. As the name Arctocyon, meaning ‘northern dog’ or ‘bear dog’ in Greek, suggests, the group was originally associated with Carnivora, specifically with ursids (Gidley, 1919), owing to the well-developed groove below the sustentaculum tali, are shared between A. mumak and Anacodon to the exclusion of Arctocyon and are suggestive of plantigrady and a degree of fossoriality. Univariate and multivariate statistical analyses of six ecomorphological ratios successfully distinguishes a taxonomically diverse group of 47 extant taxa with differing locomotor specializations. When calculated for Arctocyon mumak, these ratios support the view that this taxon was a terrestrial, possibly semi-fossorial taxon. Other taxa within Procreodi are recovered as more arboreal or more terrestrial. Significant ecological and morphological variation exists within this understudied group.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

ARTICLE

GNATHIC AND POSTCRANIAL SKELETON OF THE LARGEST KNOWN ARCTOCYONID ‘CONDYLARTH’ ARCTOCYON MUMAK (MAMMALIA, PROCREODI) AND ECOMORPHOLOGICAL DIVERSITY IN PROCREODI

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ABSTRACT—Procreodi is an order of Paleocene and Eocene mammals thought to lie at the base of the radiation of the paraphyletic ‘condylarths.’ Taxes within the order have been linked to the origins of other condylarth groups, and of some living orders. Within the order, there are specializations indicative of a range of behaviors, and a considerable size range including some of the largest Paleocene mammals. Arctocyon mumak is the largest known arctocyonid. Several craniodental specimens from the Tiffanian of western North America and one partial skeleton, preserving parts of the fore- and hind limbs, pelvic and pectoral girdles, and some vertebrae, with associated teeth and other bony elements, are described here for the first time. Skeletal elements of A. mumak are larger than those of other species of Arctocyon and Anacodon, but are otherwise similar in overall morphology. Certain features of the tarsus, such as the large plantar tuberle on the navicular and the well-developed groove below the sustentaculum tali, are shared between A. mumak and Anacodon to the exclusion of Arctocyon and are suggestive of plantigrady and a degree of fossoriality. Univariate and multivariate statistical analyses of six ecomorphological ratios successfully distinguishes a taxonomically diverse group of 47 extant taxa with differing locomotor specializations. When calculated for Arctocyon mumak, these ratios support the view that this taxon was a terrestrial, possibly semi-fossorial taxon. Other taxa within Procreodi are recovered as more arboreal or more terrestrial. Significant ecological and morphological variation exists within this understudied group.

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The nomenclature of Procreodi has been unstable. McKenna and Bell (1997) recognized two families, Arctocyonidae and Oxyclaenidae, and included in the latter undoubted members of Procreodi such as Chriacus, as well as several Asian genera of questionable relationship to the others (Zhujegale, Astigale, Khashanagale, and Petroleum). More recently, Williamson and Carr (2007) proposed that Oxyclaenidae, which species of the genus, is more closely related to Mesonychia than to arctocyonids, and removed it from Procreodi. Thus, the family Oxyclaenidae does not pertain to Procreodi, and the remaining genera that have been considered oxyclaenids would require a new family name if they are in fact a clade. However, Williamson and Carr (2007) also found that the ‘oxyclaenid’ Carcinodon is polyphyletic. In view of the very unstable state of relationships among the genera that McKenna and Bell (1997) assigned to Oxyclaenidae, we consider most of them to belong to Arctocyonidae sensu lato (see Table 1) for purposes of the present study. Therefore, the term ‘arctocyonids’ henceforth in this article is used essentially as a synonym of Procreodi.

Matthew (1937:15–16) provided the following diagnosis of Arctocyonidae:

“Teeth primitive, tritubercular, varying towards tuberculo-sectorial or bunodont. No carnassials or specialized shear- ing teeth. Premolars mostly simple, acute, an inner cusp on p4, sometimes on p3, canines larges, acute, incisors small. Skull moderately long, brain-case small, sagittal and occipital crests strong, occiput narrow and high, tympanic bulla not ossified. Limbs of moderate length, ulnar and fibular
This diagnosis was retained by Archibald (1998), and is essentially accurate for identifying members of the taxon. However, the likely paraphyletic nature of arctocyonids limits the usefulness of this diagnosis for the study of arctocyonids in an evolutionary context. A revised diagnosis for Arctocyonidae, reflecting current understanding of the family, is clearly needed but is beyond the scope of this study.

Van Valen postulated a connection between arctocyonids and Mesonychia through triisodontines (Van Valen, 1978). A link to Arctodactyla through Chriacus (Van Valen, 1970, 1978), based on dental similarity, was also hypothesized. However, Rose (1987) showed that arboreal adaptations in the postcranial skeleton of Chriacus made such an explicit link unlikely. Other analyses of arctocyonid morphology show an impressive range of specialization, including tooth combs for grooming (Gingerich, 1979, 1980), possible incipient cursorial adaptations in Archibald and Rose, 1979), and possible incipient cursorial adaptations in the lat-

ing the postcranial skeleton of the largest known arctocyonid, Arctocyon mumak (Van Valen, 1978). Van Valen, who based the taxon on a dentary, initially placed the species in the genus Arctocyonides. However, subsequent workers (Archibald, 1998; Secord, 2008) transferred the species to the genus Arctocyon, although no formal explanation for this shift was given. Van Valen’s original taxonomic placement is problematic for two reasons: Arctocyonides is otherwise endemic to Europe, and its principal distinction from Arctocyon is its smaller size and more gracile cranial features (Russell, 1964), whereas Arctocyon mumak is distinguished as the largest and most robust species of Arctocyon, and indeed the largest of all arctocyonids. Therefore, we follow recent authors in placing A. mumak in the genus Arcto-
cy

The taxon is known from several dental and gnathic specimens and a single skeleton from the late Paleocene (Tiffanian) of the northern Bighorn Basin, Wyoming. Associated skeletal remains are very rare in the Paleocene of Wyoming, and though collected a half-century ago, no other skeletal remains of this taxon have been found except for a few isolated teeth. Thus, this spec-
imen remains the sole source of information on the postcranial anatomy of the largest arctocyonid, despite some preservational damage. Its remains are larger than those of the other large-bodied North American arctocyonids, Anacodon, Aphanocyon, and Arctocyon ferox (Matthew, 1915, 1937; Rose, 1990; Secord, 2008). By comparing the known elements of Arctocyon mumak with those of other arctocyonids and of modern taxa of known behavior, inferences about the species’ position within arctocyonids and about its functional morphology can be made. Such information is important to understand the diversity of arctocyonids and their significance to the early radiation of Tertiary mammals.

Inferences from comparative anatomy and description can be augmented through the use of quantitative ecomorphological analysis (Van Valkenburgh, 1994). Ratios provide useful estimates of biomechanically meaningful differences between organisms, in particular by reflecting relative differences in moment arms and input/output levers (Carrano, 1997). They can be measured over a large sample, providing a greater range of comparisons than are typically possible in descriptive work. Univariate and multivariate statistics can be used to test hypothesis of function or ecology, complementing the conclusions of the description (e.g., Janis and Wilhelm, 1993; Van Valkenburgh and Koepfli, 1993). Univariate and multivariate analyses of functionally significant ratios were used to test the inferences made from the postcranial description about the locomotor mode of Arctocyon mumak, and to compare it with other arctocyonids.

MATERIALS AND METHODS

Arctocyon mumak is known from several craniidental speci-

mens (including some reported here for the first time; see also Secord, 2008), but only a single partial postcranial specimen (YPM-PU 18703), which is the main focus of this report. The specimen was prepared out of several blocks collected by Princeton University in 1963 from the Polecat Bench Formation of the northern Bighorn Basin, Wyoming, U.S.A. (NE 1 ½ sec. 11, T56N, R99W, Park County). The location is on the south side of Polecat Bench, approximately 6 miles due north of the town of Powell and 1 mile east of the locality that produced the holotype of A. mumak. The level is dated as late Tiffanian (level T3) (Secord, pers. comm.). The blocks were subsequently transferred to the Yale Peabody Museum. They were identified initially as the re-

The specimen preserves parts of the left scapula, distal left humerus, proximal right and left ulnae, distal left ulna in two fragments, proximal right and left radii, distal radius, parts of the pelvis, left femur, portions of right and left tibiae, right

TABLE 1. Classification of Procreodi, modified from McKenna and Bell, 1997, to include Aphanocyon Secord, 2008.

| Order Procreodi | Matthew, 1915 |
|-----------------|---------------|
| Family Arctocyonidae | Giebel, 1855 |
| Subfamily Loxolophinae | Van Valen, 1978 |
| Subfamily Arctocyoninae | Van Valen, 1978 |
| Subfamily Loxolophinae | Van Valen, 1978 |

- Arctocyonides: Lemoine, 1891
- Lambertocyon: Gingerich, 1979
- Loxolophus: Gilmore, 1919
- Acodon: Patterson and McGrew, 1962
- Mentohaenodon: Weigelt, 1960
- Arctocyonides: Lemoine, 1901
- Landenodon: Quinet, 1968
- Arctocyon de Blainville, 1841
- Anacodon: Cope, 1882
- Aphanocyon: Secord, 2008
- Lambertocyon: Gingerich, 1979
- Family “Oxyclaenidae” Scott, 1892
- Oxyprimus: Van Valen, 1978
- Carciodon: Scott, 1892
- Chriacus Cope, 1883
- Zhunjiegale Zhang and Tong, 1981
- Astigale Zhang and Tong, 1981
- Prolatidens Sudre and Russell, 1982
- Oxytomodon: Gazin, 1941
- Prohystricocodon: Simpson, 1935
- Thryipodon: Matthew, 1915
- Petrolemur: Tong, 1979
- Khashanagale Szalay and McKenna, 1971
- Lantianius Chow, 1964

The taxon is known from several dental and gnathic specimens and a single skeleton from the late Paleocene (Tiffanian) of the northern Bighorn Basin, Wyoming. Associated skeletal remains are very rare in the Paleocene of Wyoming, and though collected a half-century ago, no other skeletal remains of this taxon have been found except for a few isolated teeth. Thus, this spec-
imen remains the sole source of information on the postcranial anatomy of the largest arctocyonid, despite some preservational damage. Its remains are larger than those of the other large-bodied North American arctocyonids, Anacodon, Aphanocyon, and Arctocyon ferox (Matthew, 1915, 1937; Rose, 1990; Secord, 2008). By comparing the known elements of Arctocyon mumak with those of other arctocyonids and of modern taxa of known behavior, inferences about the species’ position within arctocyonids and about its functional morphology can be made. Such information is important to understand the diversity of arctocyonids and their significance to the early radiation of Tertiary mammals.

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MATERIALS AND METHODS

Arctocyon mumak is known from several craniidental speci-
and left proximal and distal fibulae, right and left tarsals, some metatarsals, phalanges, and vertebrae, along with a few teeth (cane and two incisors; see next section). The epiphyses are fused, indicating an adult animal. Although many of the bones have suffered deformation during the process of fossilization, important morphological characters are preserved and can be interpreted with appropriate caution. Prior to photographing, most skeletal elements were coated with ammonium chloride to minimize the visibility of surface damage and irregularities and clarify anatomical details. The skeleton was compared with postcranial details based on the holotype and three previously undescribed specimens (YPM-PU 16150, Fig. 1A–C) and describe additional anatomical features (Supplementary Material 1). These taxa were selected because they encompass a range of locomotor behaviors that should be reflected in the skeletal anatomy (Supplementary Data 1). Taxa were classified into one of six locomotor categories based on the literature. Six functional ratios were calculated (Table 3) based on linear measurements taken with digital calipers (Mitutoyo Abso-

| Taxon | Specimen numbers |
|-------|------------------|
| Fossil | Arctocyon mumak | YPM-PU 16150, 17406 (holotype), 17760, 17761, 18703 (skeleton) |
| Arctocyon primaevus | UCMP 62634, 62635, 62637–62639, 62646–62649, 62651, 62652 |
| Anacodon ursidens | USGS 5026, 5031, 5369, 5902, 6092, 21856, 21857, 25034; USNM 487950, 495292 |
| Arctocyon ferox | AMNH 16543 |
| Chriacus gallinae | AMNH 16223, 48006; UCMP 46640; USGS 2353, 21907, 25113, 25163 |
| Thryptacodon antiquus | USNM 511065, 539522; UW 7421; YPM-PU 14690 |
| Extant | Ailuropoda melanoleuca | USNM-Mammalogy 259027 |
| Gorilla beringei | USNM-Mammalogy 397351 |
| Myrmecophaga tridactyla | USNM-Mammalogy 361028 |
| Taxidea taxus | Johns Hopkins osteological collection |

TABLE 3. Principal specimens described or used for anatomical comparison.

| Ratio | Abbreviation |
|-------|--------------|
| Length of metatarsal III to length of femur | MtIII/Femur |
| Length of metatarsal V to length of metatarsal III | MtV/MtIII |
| Length of proximal pedal phalanx III to length of metatarsal III | PL/MtIII |
| Maximum diameter of radial head to minimum diameter of radial head | RadMin/RadMax |
| Distal humeral articular width to total width | HumArt/HumMax |
| Proximodistal olecranon process length to proximodistal ulna length | OIP/Uln |

The original description and illustration of the holotype of Arctocyon mumak (Van Valen, 1978) were inadequate. Secord (2008) referred several additional specimens (isolated or associated teeth) to the species and expanded the description. Here we provide new images of the holotype dentary and upper teeth (YPM-PU 17406, Fig. 1A–C) and describe additional anatomical details based on the holotype and three previously undescribed dentaries (Figs. 1, 2).

Referred Specimens—YPM-PU 16150 (Fig. 2): left dentary with I1, C, back of P3, M1, and M2 (in separate fragments), from NE ½, sec. 2, T56N, R99W, Park County, Wyoming. YPM-PU 17760 (Fig. 1D, E): left dentary with P3–M2 and alveoli of P4, from Sand Draw, sec. 24, T55N, R97W, Big Horn County, Wyoming. YPM-PU 17761: damaged left dentary with poorly preserved talonid of P4, M1, M3, and roots of canine and some premolars, from Sand Draw, sec. 24, T55N, R97W, Big Horn County, Wyoming. YPM-PU 18703: canine, two left upper(?) incisors, and left P4, associated with the skeleton described below.

Age—Most specimens of A. mumak date from the late Paleocene (later Tiffanian, Ti-4; Secord, 2008), but the skeleton that is the focus of this study may be slightly older (Ti-3), and YPM-PU 16150 is most likely early Tiffanian, although the locality is poorly constrained (Secord, pers. comm.).

Description—All the molars are swollen at the base so that the cusps are set well in from the periphery. They show very low relief, with the primary cusps of the upper molars only slightly higher than the conules and hypocones, and the trigonids of the

NEW DENTAL AND GNATHIC MATERIALS

The application of the techniques of the ecomorphological analysis. In particular, the range of behavioral and morphological variation within Car-
FIGURE 1. Dentitions of *Arctocyon mumak*. A–C, holotype, YPM-PU 17406. A, partial left M1–2; B, C, left dentary with P4–M3, in occlusal (B) and lateral (C) views. D, E, YPM-PU 17760, left dentary in occlusal (D) and lateral (E) views.

The lower molars are longer than the wide and shallow talonid basins. The upper molars have complete cingula encircling the teeth, whereas the cingulids of the lower molars are complete and continuous along the anterior, buccal, and most of the posterior margins, but there is no lingual cingulid. The cingula on both upper and lower molars are relatively high, extending from about half to three-fourths of crown height. The buccal cingulum gives rise to a small mesostyle. As Secord (2008) observed, the crests and cingula, as well as the rest of the enamel surface, are very crenulated. The crenulations are so fine and regular on the crests and cingula that they appear beaded. Overall, the crenulations are more delicate than those of the closely related early Eocene *Anacodon ursidens* (e.g., USGS 5031, USNM 495292).

Three incisors are preserved, one with the holotype and two with the skeleton (YPM-PU 18703). All are presumed to be upper incisors because of their moderately broad crowns and stout roots. Two are broader at the base of the crown and have shorter crowns than the third, which has a larger root and taller, more laterally compressed crown. In all three, the margin of the lingual surface bears a distinct, finely crenulated rim.
The dentary is deep and robust, to accommodate a large, saber-like canine (YPM-PU 16150, 18703). The front of the dentary is moderately deep and conspicuously thickened along its ventral margin from below the canine back to P3 (YPM-PU 16150, 17760, 17761), whereas the broad symphysis extends back to below P2. YPM-PU 17760 and 17761 also show ventral expansion at the front, presumably to form a protective flange for the upper canine, as in Anacodon ursidens, but most of the flange is broken away in these specimens. YPM-PU 16150, though markedly thickened, appears to lack the flange; however, the jaw was reconstructed from several fragments, making the original orientation of the symphyseal region difficult to ascertain. A large mental foramen is situated below I3 at a level just inferior to the I1 alveolus, and a much smaller posterior mental foramen opens at about midlevel below the anterior root of P2 (YPM-PU 16150). The jaw varies in depth and robustness, YPM-PU 17760 being somewhat shallower and more gracile than the others. Together with the mandibular flange and large canine teeth, this is suggestive of sexual dimorphism, but available evidence is inadequate to be compelling.

Axial Skeleton

Vertebrae—The specimen has 24 preserved vertebrae. They are disarticulated and damaged, most preserving only the centrum. We tentatively identify among them six thoracics, five lumbar, eight caudals, and a partial atlas (Fig. 3). Four trunk vertebral bodies are too damaged to assign confidently to either the thoracic or lumbar series. Neither the antilcal nor the diaphragmatic vertebrae can be identified as the spinous processes and zygapophyses are too incomplete.

The left side of the atlas (C1) is preserved, although the transverse process is broken. The cranial surface is dominated by the large, deep articular surface for the occipital condyle. The caudal surface has a ventrally positioned, shallowly concave facet for the axis vertebra. In the neural arch, there is a craniomedially oriented foramen (lateral vertebral foramen; Evans and Christensen, 1979) that presumably transmitted the vertebral artery into the vertebral canal and the first cervical spinal nerve to the suboccipital region (Davis, 1964; Evans and Christensen, 1979).
FIGURE 3. Vertebrae of A. mumak, YPM-PU 18703. A, B, fragmentary atlas (Cl) in dorsal (A) and caudal (B) views; C, D, thoracic vertebra in posterior (C) and right lateral (D) views; E–G, two probable anterior lumbar vertebrae in cranial (E), caudal (F), and right lateral (G) views; H, I, lumbar vertebra in caudal (H) and left lateral (I) views; J, K, lumbar vertebral centrum in caudal (J) and left lateral (K) views; L–O, four caudal vertebrae in ventral (L) and dorsal (M–O) views. Abbreviations: for., foramen; postzyg., postzygapophysis.
Lateral to the articulation for the axis vertebra, where the transverse process meets the vertebral body, is the transverse foramen for the vertebral artery. Both these foramina are described in *Hyracotherium* (Wood et al., 2011). The cranial end of the canal is obscured by matrix. The morphology of the atlas vertebra is very similar to that of *Arctocyon primaevus* as described by Russell (1964).

One thoracic vertebra can be unambiguously identified by the presence of demifacets for the ribs. Other vertebrae were determined to be thoracics based on similarities in central size and shape. The centra are subcylindrical and about as long as they are wide. In accordance with Russell’s (1964) description, the ventral keels are never strong. One vertebra preserves a slender, tall, and strongly caudally inclined spinous process, which Argot (2013) noted is characteristic of the cranial thoracic vertebrae in *Arctocyon primaevus*.

The centra of the lumbar vertebrae are larger than those identified as thoracics, and the floor of the neural canal is wide. There is a distinct ventral keel. A single transverse process is preserved. It arises from the pedicle in the lumbar region and is oriented cranially and laterally, with no discernible ventral component. Two specimens preserve part of the spinous process, showing that it is nearly as long craniocaudally as the centrum. The prezygapophyses are distinctly revolute, and the postzygapophyses are craniocaudally elongate and semicylindrical, suggesting that the diaphragmatic vertebra was in the thoracic series, as in *Arctocyon primaevus* (Russell, 1964). Mammillary processes are present, as in *A. primaevus* (Argot, 2013), although it is difficult to determine how well developed they are. These features are consistent with a lumbar region with limited flexibility in flexion and extension, suggesting that stability and strength, rather than range of motion, were the prime characteristics of this region of the axial skeleton (Zhou et al., 1992; Wood et al., 2011).

The caudal vertebrae appear to have wide, elongated transverse process proximally. More caudally, the transverse processes were evidently expanded at the cranial and caudal ends, creating a bifid transverse process, as observed in *A. primaevus* (Argot, 2013).

Forelimb

Scapula—A partial left scapula is associated with the specimen. Unfortunately, it is too fragmentary to provide much information. It appears to have been similar to that of *Arctocyon primaevus*. The glenoid fossa is pyriform (Fig. 4A, B), much longer than wide (ratio of maximum to minimum diameters is about 1.6). It is more elongate than in *A. primaevus*, in which the glenoid is rounder (Argot, 2013).

Humerus—Approximately the distal third of the left humerus is preserved with the complete ulnar and radial articulations, entepicondyle, ectxepicondyle, and distal part of the supinator crest (Fig. 4C, D). The humerus is robust. A large entepicondyle extends from the level of the distal-most projection of the trocheal lip to well above the proximal border of the articular surface. The distal humerus is wide relative to the articular width (ratio of articular width to maximal distal humeral width = 0.61), owing to the significant medial projection of the entepicondyle, as in *Arctocyon primaevus* (Argot, 2013). The entepicondylar foramen is large.

The supinator crest flares laterally along the entire length of the preserved part of the specimen, and therefore must have originated higher up on the humerus. In *Arctocyon primaevus*, the supinator crest arises along the distal third of the humerus (Argot, 2013). In *Arctocyon mumak*, it extends to the lateral edge of the entepicondyle, and at its widest approximately doubles the width of the shaft.

The trochea is expanded medially, with a sharp, distally and cranially projecting medial edge, and does not extend far proximally either cranially or caudally. In cranial view, it is asymmetric, narrower laterally than medially. In caudal view, it is more open, because the medial crest is less prominent. The olecranon fossa is shallow and not perforated, and the coronoid fossa is equally shallow. The capitulum is spindle-shaped, and projects anteriorly more strongly than in *Arctocyon primaevus* (Argot, 2013). There is a marked lateral extension of the capitulum.

The shaft is somewhat flattened along its caudal surface. In overall proportions, the distal humerus resembles that of the modern badger *Taxidea* at a larger size (ratio of width of distal humeral articular surface to maximum distal humeral width is 0.61 in both *Arctocyon mumak* and *Taxidea taxus*). The prominence of muscle attachment sites is also comparable to the condition in *Taxidea* and *Ailuropoda*. However, features such as the large entepicondylar foramen and the shallowly excavated supra- trocheal region highlight the primitive morphology of the bone. The detail of the shape of the articular surfaces is also quite
different: *A. mumak* having a more open and less extensive articular surface than in the modern taxa, although there are similarities to the wolverine *Gulo gulo*. The anatomy is consistent with powerful forelimb musculature, in particular the flexors and extensors of the forearm, which originate from the entepicondyle and supinator crest, respectively. The anatomy is similar to that of *Arctocyon primaevus* (Russell, 1964; Argot, 2013) and *Arctocyon ferox* (Matthew, 1937). However, *A. mumak* has a more distally projecting entepicondyle, a more pronounced medial trochlear rim, and a wider and more anteriorly projecting capitulum than the other species of the genus. Compared with *Anacodon ursidens*, *Arctocyon mumak* has a steeper medial trochlear rim, a better-defined and narrower trochlea, a wider capitulum, and a possibly less proximodistally extensive medial epicondyle.

**Radius**—Both left and right proximal radii have been identified based on comparisons with the more completely known *Anacodon* (Fig. 5C, D). The distal right radius and part of the radial shaft are also preserved (Fig. 5E–G). The radius is similar overall to that of *Anacodon* and dissimilar to that of *Chriacus* and *Thryptacodon*. It was clearly separated from the ulna throughout its length. The radial head is shallowly concave, almost flat, and distinctly elliptical viewed proximally (ratio of maximum to minimum diameters = 1.7). The ulnar facet is slightly convex, as in *Arctocyon primaevus* (Argot, 2013), and there appears to be a small capitular eminence. There is a marked neck when viewed laterally, and the ulnar margin is broadly convex, both as in the European *Arctocyon primaevus* (Russell, 1964; Argot, 2013). The shaft fragment appears to be from the middle third of the radius, distal to the bicipital tuberosity. It shows that proximally the radius is more rounded in cross-section but expands distally to become more triangular in cross-section with two roughened concave sides and one smooth convex one. This is also the case in *A. primaevus* (Argot, 2013). The two concave sides presumably provided origin for the deep flexors and extensors of the digits, once again suggesting that the musculature of the antebrachium and manus was well developed and powerful. There is a sharp oblique line on the craniomedial surface; in *Anacodon*, this line continues distally to form the margin of a broad excavated expansion proximal to the styloid process. The distal radius in *Anacodon* bears a prominent pronator crest cranially and a marked fossa on the extensor surface that accommodates the pronator quadratus muscle in *Ailuropoda* (Davis, 1964). Close correspondence to the damaged distal radius of *Arctocyon mumak* suggests a similar morphology, as does the radius of *A. primaevus* (Argot, 2013).

The right distal radius preserves a clear styloid process that forms the distal-most extremity of the radius, so that the lateral (ulnar) border of the articulation with the carpals is more
proximal than the medial border. The posterior margin of the distal radius is damaged, obscuring the distal radioulnar articular surface, which is reduced in *Arctocyon primaevus* (Argot, 2013). Overall, the distal radius is rather small, as in *Anacodon* and unlike the more expanded distal radii of *Chriacus* or any of the living Carnivora. The ratio of the mediolateral width of the distal radius to the mediolateral width of distal ulna is 1.15 in *Arctocyon mumak*, whereas it is 1.33 in *Chriacus gallinae* and 1.77 in the modern badger *Taxidea taxus*. Argot (2013) described the distal radius of *A. primaevus* as ‘massive’ and the articular area with the carpals as being ‘wide,’ which does not match our interpretation of *A. mumak*. In the latter, the surface for articulation with the carpals is shallow, triangular, and small, with faint separation into scaphoid and lunate facets, unlike the broad radiocarpal articulation found in *Chriacus* and *Ailuropoda*. The grooves for the muscle tendons are not distinct, although this is likely an artifact of preservation, because they are notable in specimens of *Anacodon* and *Arctocyon primaevus* (Argot, 2013). Although the humeral morphology of *Taxidea* or *Ailuropoda* is very reminiscent of *Arctocyon mumak*, this is not the case for the antebrachial elements, in particular the radius. Thus, although it is reasonable to infer that *A. mumak* had a powerful forelimb based on the large crests of the humerus, inferences about the movements of the forelimbs, and associated behaviors, are less obvious.

**Ulna**—The ulnae are represented by a proximal right ulna preserving the entire olecranon process, semilunar notch, and the proximal-most portion of the shaft (Fig. 5A, B), and a nearly complete left ulna in three parts (Fig. 5H). The ulna is a distinctive bone in the larger arctocyonids: it is craniocaudally deep and mediolaterally compressed throughout its entire length (Russell, 1964; Rose, 1990). *Arctocyon mumak* conforms to this morphology. Overall, the ulna seems to be straight in the mediolateral plane and very slightly curved craniocaudally, with a convex caudal edge. The cranial edge is concave proximally, but straight or even convex caudally, giving a slightly sigmoid appearance overall. The ulna does not taper distally as it does in *Ailuropoda*, but remains deep throughout its length. A similar morphology has been described in the ulna of the South American notoungulate *Anisetomus* (Shockey and Flynn, 2007), in which it is associated with an enlarged pronator crest. This suggests that supination of the manus may have been limited, because motion of the distal radius around the ulna would have been difficult. Such a condition is found in fossorial taxa, which stabilize the manus at the expense of pronation-supination abilities (Hildebrand, 1985). Russell (1964) argued that the similar morphology seen in *Arctocyon primaevus* also suggested limited supination of the wrist.

The olecranon is large and robust. A sharp, midline ridge on the cranial aspect runs from the olecranon tubercle proximally to the anconeal process distally. The caudal surface of the olecranon process is broad, flat, and rugose, with a large medial tubercle that expands to form a flange, probably for the origin of the flexor digitorum profundus and flexor carpi ulnaris muscles (as in *Ailuropoda*; Davis, 1964). The morphology and myological interpretation are similar to those of *Arctocyon primaevus* (Argot, 2013). There is a distinct indentation for the triceps tendon on the proximal-most aspect of the olecranon. The anconeal process is high and sharp, rising above the level of the ulnar shaft. It continues as a distinct oblique ridge, running proximomedial to distolateral to form the proximal edge of the semilunar notch. The olecranon as a whole is craniomedially inflected, unlike the condition in *Ailuropoda* where it is bent slightly caudally. The semilunar notch is marked, but not deep. It is relatively elongate, concave proximodistally and convex mediolaterally. It is more oblique relative to the long axis of the ulna than in either *Anacodon* or *Arctocyon primaevus* (Russell, 1964; Argot, 2013). The proximal and distal borders of the semilunar notch are also oriented at a sharply acute angle relative to the long axis, unlike in *Ailuropoda* where they are situated more or less perpendicular to the long axis of the shaft. The semilunar notch is not constricted in the middle. The coronoid process is broken; what remains indicates that it projected medially, overhanging the medial border of the ulnar shaft. In both *Anacodon* and *Arctocyon primaevus*, the distal portion of the articulation projects prominently over the medial side of the bone, and the coronoid process is distinct, suggesting a similar condition in *Arctocyon mumak*. However, the elongate shape and oblique orientation of the semilunar notch in *Arctocyon mumak* is distinctively different from that in *Anacodon* and *Arctocyon primaevus* (Argot, 2013).

The radial notch is roughly circular, with a shallow depression in its center. These details, which differ from those in *Anacodon*, could be preservational defects, although Argot (2013) described the radial notch in *Arctocyon primaevus* as ‘reduced,’ which is evident in her figure 8.

The ulnar shaft is craniocaudally expanded and mediolaterally compressed throughout its length. The anterior border is rugose and expands mediolaterally in the distal portion, which Russell (1964) and Argot (2013) interpreted in *Arctocyon primaevus* as marking the origin of the pronator quadratus muscle and of the interosseus membrane more proximally. A deep fossa on the cranialateral side, which extends from just distal to the radial notch to just proximal to the styloid process, was presumably the origin of the abductor pollicis longus muscle (Argot, 2013). Proximal to that fossa and caudal to the semilunar notch, a smaller depression probably for the insertion of the anconeus muscle can be discerned. This fossa is bounded caudally by a sharp ridge coming from the olecranon, which may have been the origin of the extensor indicis et pollicis longus muscles, as in *Ailuropoda* (Davis, 1964). In *Ailuropoda*, the proximal portion of the shaft is similarly craniocaudally expanded and excavated, but it tapers distally to become more compact in cross-section. As a result, the ulna-carpal contact is reduced, in contrast to *Arctocyon mumak*. In *A. mumak*, the ulna remains craniocaudally broad throughout; hence, the ulna-carpal contact presumably was large. Russell (1964) noted facets for the triquetrum and the pisiform in *Arctocyon primaevus* and suggested that the radius and ulna contributed equally to the joint between forearm and carpus. Argot (2013) noted that the styloid process of the ulna in *A. primaevus* is reduced relative to the diaphysis, and interpreted this as suggesting a loose articulation with the triquetrum and pisiform. In *Chriacus gallinae*, however, the distal ulna tapers, in conjunction with the enlargement of the distal radius. This may have related to the arboreal adaptations in *A. primaevus*, including enhanced supinatory ability of the forearm (Rose, 1987).

**Manus**—Several poorly preserved fragmentary metapodials—two proximal and four distal ends—as well as one complete metapodial are of slightly smaller size and caliber than the definitive metatarsals, and are tentatively identified as metacarpals. Based on the complete element, tentatively identified as left metacarpal (Mc) III, the metacarpals were robust and neither elongate nor shortened; they are slightly shorter than the metatarsals. The proximal articulation of Mc III is trapezoidal, much wider dorsoventrally than mediolaterally. It is convex dorsoventrally and flat to slightly concave transversely. The proximal lateral aspect is concave, with a narrow facet for Mc IV along the edge of the proximal articular surface; the facet is expanded at the ventral end and probably also at the dorsal end (where it is obscured by poor preservation). Two smaller articular facets appear to be present on the proximomedial surface, one at the dorsal end and one at the ventral. About 1.5 mm from the proximal end, on the dorsomedial aspect, is a low tubercle, probably marking attachment of extensor carpi radialis brevis. Such a tubercle is present in armadillos, palaeanodonts, and various other digging mammals. The metacarpal shaft is deeper dorsoventrally than wide at the proximal end, nearly round at midshaft, and slightly flattened distally. Both metacarpals
compare well with their counterparts in *Arctocyon ferox* but are substantially larger and more robust.

One of the isolated proximal ends may represent left Mc IV. The articular surface is trapezoidal and generally similar to that of Mc III described above; it differs in being wide dorsally and much narrower ventrally; it is convex dorsoventrally and flat to very slightly concave transversely. It bears an extensive and continuous articular facet for Mc V on the proximolateral surface, and two well-separated facets for Mc III on the proximomedial surface, the ventral one larger.

Numerous isolated proximal, intermediate, and terminal phalanges are preserved, but the size differences are minimal and do not allow confident separation between manual and pedal phalanges. They are described with the pes.

**Hind Limb**

**Pelvis**—The ilia of the left and right ossa coxae are preserved, although deformation makes it difficult to determine the orientation of the iliac blade in life. The right ilium is somewhat better preserved than the left, although the latter preserves more of the acetabulum (Fig. 6).

The ilium is prismatic in cross-section, with three distinct surfaces of unequal size, the entire bone being mediolaterally flattened. The cranial end of the ilium is considerably expanded and flares laterally relative to the constricted and distinct neck where it contacts the acetabulum. The shallowly concave lateral surface of the ilium is extensive, providing a significant area of attachment for the gluteal musculature. The gluteal surface is separated from the inferiorly facing iliac surface by a ridge beginning at the acetabulum and extending all the way to the anterior superior iliac spine. Thus, the iliac surface is distinct throughout the length of the ilium, as in the mesonychid *Pachyaena gigantea* (O'Leary and Rose, 1995) and unlike in *A. primaevus*. The iliac surface is the site of origin of the iliacus muscle, which in conjunction with the psoas muscle is the primary flexor of the hip.

The anterior superior iliac spine is enlarged to form a laterally expanded tubercle, which presumably provided origin for the sartorius muscle, as in *Ailuropoda* (Davis, 1964); however, the lateral projection of the tubercle is more likely related to expanding the origin of the gluteal muscles and the tensor fasciae latae (Davis, 1964; Evans and Christenssen, 1979), as well as the trunk muscles attaching to the iliac crest. The lateral flaring of the ilium is more pronounced than in *Arctocyon primaevus* (Argot, 2013). An enlarged surface area for the gluteal musculature is typically associated with powerful extension of the hind limb, terrestrial locomotion, and with well-developed trunk musculature in didelphid marsupials (Argot, 2002).

A distinct anterior inferior iliac spine, site of origin of the rectus femoris muscle, is present in *Arctocyon mumak* just cranial to the acetabulum; however, it is not particularly large and is less prominent than in *Arctocyon ferox* (AMNH 16543) and *Anacodon ursidens*. The iliac crest is curved, thick, and roughened, extending from the enlarged anterior superior iliac spine, and then caudally along the dorsal side of the ilium to the small posterior iliac spine. There is a shallow, smooth greater sciatic notch, as in *A. primaevus* (Argot, 2013).

The medial side of the ilium is insufficiently preserved to allow the auricular surface to be described in detail. It is somewhat cranial to the acetabulum, with a significant portion of the ilium being cranial to it, as in *Arctocyon primaevus* (Russell, 1964).

The cranial portion of the acetabulum is preserved. The lu- nate surface may have been somewhat expanded cranially. It appears that the bony part of the acetabulum did not quite cover the femoral head, based on attempts at articulating the specimen, although the cranial wall of the acetabulum is thick and somewhat buttressed by the anterior inferior iliac spine.

**Femur and Patella**—The bony elements identified as pertaining to the right femur are very damaged and fragmentary; however, the left femur is intact and relatively undeformed (Fig. 7A–C). The shaft is weakly bowed laterally, more so than in *Arctocyon primaevus* (Argot, 2013).
The femoral head is large, with a prominent fovea capitis as in *Anacodon* and *Arctocyon primaevus*. The fovea faces medially and slightly posteriorly, but not quite as posteriorly as in *Anacodon*. The femoral head is somewhat ovoid rather than fully spherical as in *Chriacus*, with a flattened distal border very similar to the state in *Anacodon*, and somewhat different from *Arctocyon primaevus* (Argot, 2013). The femoral head is somewhat ovoid rather than fully spherical as in *Chriacus*, with a flattened distal border very similar to the state in *Anacodon*, and somewhat different from *Arctocyon primaevus* (Argot, 2013). The femoral neck forms a broad angle (roughly 130°) with the main shaft of the femur, so that the medial edge of the femur has a smooth concavity to it. The lesser trochanter projects medially immediately distal to the femoral neck. It forms a distinct, triangular flange extending from just below the femoral neck to just below the distal-most extent of the third trochanter, as in *A. primaevus* (Argot, 2013). The greater trochanter is craniocaudally expanded with a distinct cranial deflection proximally. It does not project above the femoral head, which is similar to the situation in *Anacodon*, *Arctocyon primaevus* (Argot, 2013), and the giant panda *Ailuropoda*. The trochanteric fossa is moderately deep. It was probably deeper prior to deformation, based on comparisons with *Anacodon*, although it is broader and shallower in *Chriacus*.

The third trochanter is distal to the greater trochanter and essentially at the same level along the shaft as the lesser trochanter. It is smaller than the latter, but seems to be relatively larger than in *Arctocyon primaevus*. It projects laterally from the shaft, with a crest-like flange on its cranial border, and is continuous with the sharp posterolateral border of the femoral shaft. However, it does not extend far from the shaft of the femur, so that overall the proximal femur has a wide, flattened appearance. The form and extent of the three trochanters in *Arctocyon mumak* are very similar to what is seen in *Anacodon*, and less similar to *Arctocyon primaevus*. In the latter, the greater trochanter is distinctly lower than the head of the femur, and projects laterad to the same extent or slightly beyond the third trochanter (Russell, 1964; Argot, 2013). The lesser trochanter in *A. primaevus* is broader proximodistally than in *A. mumak*, whereas the third trochanter is more robust and laterally projecting in *A. mumak* than in *A. primaevus*.

The shaft is rounded on its cranial aspect, but its caudal surface is flat, as in *Anacodon*. Medially, the two surfaces form a curved edge, but laterally they meet at a sharp crest that runs from the third trochanter, where it is particularly well developed, down the length of the shaft. This is similar to the situation in *A. primaevus* (Russell, 1964). The shaft is almost semicircular in cross-section in its proximal portion, becoming roughly triangular near its distal end. On its caudal surface, a faint intertrochanteric crest for the insertion of the quadratus femoris muscle, and remnants of the linea aspera, is evident.

The distal femur is slightly distorted by mediolateral shear. The patellar surface extends along the cranial edge of the distal femur slightly more proximally than the condyles, with a regular
proximal border. This contrasts with the proximally extended facet seen in some of the specimens examined by Russell (1964:fig. 38), although Argot (2013) thought this feature may have been age related or aberrant. The patellar groove was possibly compressed somewhat by shear; nevertheless, the trochlear ridges are clearly elevated relative to the shaft, the lateral one extending slightly more proximally and projecting slightly more cranially than the medial one, as in *Anacodon* but unlike *Arctocyon primaevus* (Argot, 2013). It seems to have been relatively narrower and deeper than both the rather shallow, broad patellar groove of *Anacodon* and the better-defined patellar groove of *Arctocyon primaevus* (Russell, 1964; Argot, 2013). The patellar groove is decidedly deeper than the flattened morphology of *Chriacus*, consistent with the larger *A. mumak* having a less arboreal morphology.

The lateral femoral condyle is wider than the medial condyle, although the medial has a greater caudal extent, as is the case in *Anacodon* and *Arctocyon primaevus* (Argot, 2013). The intercondylar groove is narrow, as in *A. primaevus* and *Anacodon*. The medial femoral condyle and supracondylar ridge are well developed, so that a small depression is formed above the medial condyle on the caudal side of the femur. A similar fossa is present just proximal to the lateral condyle. These depressions may have housed a sesamoid bone (fabella) in each head of the gastrocnemius, as in *Canis* (Evans and Christensen, 1979). There are two pits on the lateral condyle just above the border of the distal articular surface (also present in *Chriacus* and *Anacodon*), which probably indicate the origins of the extensor digitorum longus and popliteus muscles.

**Tibia**—The proximal portion of the right tibia is preserved, as is the distal portion of the left tibia (Fig. 8). The proximal portion of the shaft has been mediolaterally compressed postmortem. The preserved portions allow a rough estimate of the length of the tibia. It appears to be of approximately the same length as the femur, as in *Anacodon*. Owing to the distortion of the proximal tibia this interpretation is tentative. Overall, the tibia is very similar to those of *Anacodon*, *Arctocyon primaevus*, and *A. ferox*, though more robust. The tibial tuberosity for the insertion of the patellar tendon is well developed. The tibial condyles are clearly separated and shallow, with the lateral condyle being mediolaterally wider than the medial condyle. The posterior extension of the lateral condylar articular surface identified in *A. primaevus* (Argot, 2013) appears to be present in *A. mumak* as well. There is a distinct intercondylar eminence. The proximal shaft is teardrop-shaped in cross-section, with a prominent, rounded cnemial crest as in *A. primaevus* (Argot, 2013). The medial malleolus projects distally well beyond the level of the lateral border of the tibia. There is a marked pit at its distalmost extremity for the medial collateral ligament, as in *Anacodon*. The articulation with the astragalus is obliquely oriented and shallow but divided into medial and lateral portions by a low, rounded craniocaudal crest, the trochlear ridge, which is more pronounced than in *A. ferox*. The medial portion of this articular surface is longer anteroposteriorly than the lateral portion, and is also more deeply excavated.

**Fibula**—The proximal and distal left and right fibulae are preserved (Fig. 9). The fibula is a strong, separate element in
Arctocyon mumak; it is smaller than the tibia but reasonably robust, with a marked, sharp interosseous crest. The shaft fragments of the fibula of A. mumak are curved, indicating that the fibula was bowed in this taxon, unlike the condition in A. ferox and A. primaevus (Russell, 1964; Argot, 2013).

The proximal articulation for the tibia is flat, slightly medially inclined relative to the long axis of the fibula. The posterior facet that Russell (1964) identified in Arctocyon primaevus and postulated to articulate with a sesamoid cannot be positively identified, because the deformation of the proximal tibia makes articulating the two bones impossible. However, the general shape of the proximal fibula is very similar to that of A. primaevus (Russell, 1964: fig. 41) but significantly more robust, so it seems reasonable to infer that the posterior facet was present in A. mumak.

The distal articulation of the fibula is robust, quadrangular in overall appearance. The facets are not clearly distinguished. The distal tibial facet is small, although a sharp anterior crest on the distal portion of the diaphysis indicates a strong interosseous ligament (Argot, 2013). The astragalar facet is shallow, slightly concave craniocaudally, very slightly concave dorsoventrally, and faces medially. The concave calcaneal facet is positioned more laterally and is somewhat twisted medially.

The fibular malleolus is a distinct process projecting laterad, marking the anterior border of a shallow sulcus for the tendons of the fibularis muscles, plantarflexors, and evertors of the foot, as in Arctocyon primaevus (Argot, 2013). This process is a rounded tuberosity, not hook-like as it is in Arctocyon ferox. In most regards, the fibula of Arctocyon mumak resembles that of A. primaevus, but the latter is smaller, less robust, and straight. The fibular-tarsal contact is well developed and the fibula has significant articulations with both the astragalus and the calcaneus.

Pes—The pes can be reconstructed almost in its entirety, although the precise positions of individual phalanges is conjectural, as is their tentative assignment to the left pes for this reconstruction, rather than the right pes or the manus (Fig. 10). Nevertheless, as noted below, their overall similarity justifies our attempt to provide a pedal reconstruction. Using available elements, only the entocuneiform is missing.
Astragalus—Both astragali are preserved but damaged (Fig. 11). They exemplify Matthew’s (1937) description of the arctocyonid astragals as primitive. The trochlea is shallowly grooved and proximodistally short and wide, suggesting a limited range of motion in the sagittal plane, but little hard tissue constraint on movements outside the sagittal plane. The medial border is the higher and sharper of the two trochlear keels. The medial keel is more rounded. There is a large astragalar foramen in the proximal portion of the trochlea, forming a conspicuous notch at the caudal margin. On the posterolateral side of the body of the astragalus is a deep ovoid depression just above the ectal facet. The pit is conspicuous and deep in A. mumak and Anacodon (also present but not so deep and more central than posterior in Orycteropus). A shallow fossa is evident in this position on the lateral wall in Canis and is the attachment site for the short part of the lateral collateral ligament (talofibular ligament). The size and depth of the pit in A. mumak may reflect a particularly well-developed lateral collateral ligament. This fossa is also present in Arctocyon primaevus (Russell, 1964:fig. 42) but is less clear in Arctocyon ferox. In Anacodon and Arctocyon mumak, the medial face of the astragalus is gently inclined and the proximomedial corner of the astragalar body projects medially almost as far as the medial edge of the astragalar head, resulting in a strongly indented medial profile. This is unlike the condition in Ailuropoda, where the lateral and medial aspects of the astragalus do not project far from the body, giving the bone a more compact aspect. A. primaevus is more similar to A. mumak in this regard (Russell, 1964; pers. observ.). However, in A. mumak the facet for the articulation with the tibial malleolus expands onto this posteromedial projection, probably increasing stability when the foot was plantarflexed. This articulation was characterized as reduced in A. primaevus (Argot, 2013). This feature is obscured by damage in the Arctocyon ferox specimens examined here (AMNH 16543).

The tibioastragalar joint of A. mumak may thus have been most stable in full plantarflexion, which may have had the additional benefit of protecting the contents of the astragalar canal. Bony features that ensure this protection have been noted in other fossil ungulates (Shockey and Flynn, 2007). Although damaged, there seems to be a fossa on the distomedial wall of the trochlea, as in Anacodon, in which it accommodates a spur on the tibial malleolus (Rose, 1990), although no such spur is seen in the A. mumak material, suggesting that the feature may not be analogous.

The astragalar neck is medially offset from the midline of the astragalar body. The angle between the proximodistal axis of the astragalar neck and the distal edge of the astragalar body is slightly greater than 90°. The neck is constricted but short, the total length of the neck and head being slightly less than half the total length of the astragalus. The astragalar head is badly damaged in both the left and right specimens; however, it is clear that it was mediolaterally rounded and somewhat ovoid, being much wider mediolaterally than dorsoplantartly. This is borne out by looking at the shape of the corresponding facet on the navicular. The astragalar head may have been somewhat wider mediolaterally than in either Anacodon or Arctocyon primaevus, but this may be exaggerated by deformation. The mediolateral axis of the astragalar head is parallel to that of the astragalar body, a characteristic of plantigrade taxa (Carrano, 1997). The small cuboid facet is not obviously demarcated from the much larger navicular facet, although there clearly was contact with the cuboid based on examination of the latter. A cuboid facet is variably demarcated in A. primaevus (Argot, 2013). Matthew (1937) noted a similar condition in A. ferox.

A deep groove runs caudally and medially onto the plantar side from the superior astragalar foramen, marking the course of the flexor hallucis longus and flexor digitorum longus tendons, as in Arctocyon primaevus (Argot, 2013). The posterior calcaneal and sustentacular facets are separated throughout by a deep, marked sulcus tali that is continuous at the caudal end with the astragalar canal. The posterior facet is elongated, concave, and very obliquely oriented, facing slightly laterally. The sustentacular facet is small, roughly quadrate and weakly convex, matching the flattened sustentaculum on the calcaneus. However, it bends sharply at its caudal end, forming a narrow articular facet that contacted the proximal surface of the sustentaculum. A similar condition is seen in Anacodon and probably Arctocyon ferox, and may be what Russell (1964) referred to as the S-shaped...
facets in profile in *A. primaevus*. In *Chriacus*, this proximal contact is smaller and less sharply angled. Poor preservation makes it impossible to determine if the sustentacular facet of *A. mumak* was continuous with the cuboid facet laterally, as in *A. primaevus* (Russell, 1964). The sustentacular facet is clearly separated from the cuboid facet in *A. ferox* and *Chriacus*. In *Anacodon*, the facets are either separate or have a very narrow connection. This is suggestive of an unspecialized tarsus, where articulations neither prevented nor facilitated movement in certain planes to the extent seen in more specialized forms, although soft tissue structures may have limited certain movements more than the bone morphology suggests.

**Calcaneus**—Both calcanei are preserved; however, they have been subjected to significant distortion and deformation that complicates their interpretation, particularly as they have been affected differently (Fig. 12A–D, G). The left calcaneus has been compressed and sheared craniocaudally, resulting in very different proportions compared with the right calcaneus (e.g., absolutely and proportionally longer left calcaneal tubercle). Nevertheless, much of the bone surface anatomy is preserved. The right calcaneus is less well preserved, but comparisons with *Anacodon* and *Arctocyon primaevus* suggest that the proportions of the right calcaneus better reflect the original condition. In overall aspect, the calcaneus is a stout, blocky bone. The calcaneal tuberosity is of roughly equal length to the distal portion of the calcaneus extending from the proximal-most part of the ectal facet to the cuboid facet. The morphology is somewhat intermediate between that of *Arctocyon primaevus* and *Anacodon ursidens*. The more specialized features of *Anacodon*, such as the pronounced plantar calcaneal process, do not seem to be present in *A. mumak*.

The calcaneal tuber is large and mediolaterally thicker than in either *Anacodon* or *Arctocyon ferox* but slightly narrower than in *Arctocyon primaevus*. At its proximal end, it expands mediolaterally and dorsoventrally; closer to the ectal facet, it tapers in both dimensions. The proximal end of the tuber is rugose for the attachment of the tendons of the plantar flexors, as in *A. primaevus* (Russell, 1964). The plantar process on the end of the tubercle, though well developed, is less prominent than in *Anacodon* (Rose, 1990), so that the calcaneus of *Arctocyon mumak* does not have the strongly arched profile characteristic of *Anacodon*, which is also observed in large-bodied extant plantigrade taxa such as *Gorilla* and *Myrmecophaga*, but not in *Ailuropoda* or in the fossil *Arctocyon primaevus*.

The distal half of the calcaneus, which articulates with the astragalus and the cuboid, is compact and robust. The ectal facet is twice as long as it is wide, mediolaterally broad, and is bounded medially by a slight proximodistal ridge, as in *Anacodon*; however, there is no bony process or groove to lock the calcaneus and the astragalus together as seen in more derived ungulates. Lateral to the ectal facet is a large, convex, and well-developed fibular
facet, set off from the ectal facet at almost a right angle. The arrangement is very similar to that in *Arctocyon primaevus* (Argot, 2013). The sustentaculum is robust, and projects at a right angle to the calcaneal body. It is situated near the distomedial termination of the bone. The sustentacular facet is triangular, slightly concave, and covers the entire dorsal surface of the sustentaculum and a small strip on its proximal surface, but does not extend onto the calcaneal body. It probably contacted the cuboid facet, as in *A. primaevus* (Argot, 2013). The ectal and sustentacular facets are separated by a deep, rugose calcaneal sulcus that housed the astragalo-calcaneal interosseous ligaments. A distinct peroneal tubercle is preserved on the distolateral side of the left calcaneus. It is much smaller than the sustentaculum tali and apparently less well developed than in *Ailuropoda*, although damage may have obscured its original size. It appears to be larger than the tubercle in *A. primaevus* (Argot, 2013). On the plantar surface, there is a salient tubercle that projects medially under the sustentaculum to help define a deep groove for the flexor hallucis longus tendon. The tubercle and groove are better developed than in *Anancodon* or other *Arctocyon* species. This groove continues distally and indents the cuboid facet, which is also the case in *A. primaevus* (Argot, 2013). A similar morphology is seen in *Gorilla*. The cuboid facet is broadly diamond-shaped and is oblique to the long axis of the bone, facing medially as in *A. primaevus* and *Anancodon*. It is very slightly depressed in the middle, but otherwise almost flat.

**Cuboid**—Both cuboids are preserved with minimal distortion. The middle tarsal segment in *Arctocyon mumak* is short, so the cuboid is a short, prism-like bone, though relatively longer than in *Anancodon* (Fig. 12H, I). The proximal surface is triangular in shape. The medial border of this triangle is sigmoid, corresponding to the contact with the navicular along a narrow articular surface on the medial aspect of the cuboid. The proximal articular surface includes a large, oblong, convex articulation with the calcaneus, and a distinct, dorsoplantarly concave astragalar articulation medially, as in *Arctocyon primaevus* (Argot, 2013).

On the medial aspect, distal to the articulation for the navicular, there is an articular surface for the ectocuneiform, and then a notch, which in *Anancodon* seems to have formed part of a canal running from the plantar to the dorsal surface of the pes. The other half of this canal is clearly visible in the ectocuneiform of *Anancodon*, although it is less clearly defined in *Arctocyon mumak*. The lateral border of the cuboid is composed mostly of a rounded ridge formed by the junction of the dorsal and plantar surfaces. The distal surface of the cuboid is highly triangular, and concave articular surface for metatarsals IV and V; however, there is no clear division of the articular surface.

The plantar tuberosity of the cuboid is very large and extends medially across most of the plantar surface, forming the proximal margin of a deep groove near the distal end of the cuboid for the tendon of the flexor longus muscle. A similar large tubercle delimiting the flexor longus groove is present in *Arctocyon primaevus* (Argot, 2013) and *Anancodon*, although the cuboid is more ovoid and less mediolaterally extensive in the latter. This feature is also present in *Ailuropoda* despite its very different cuboid morphology. Presumably, this groove was for the tendon of the flexor longus muscle (Lessertisseur and Saban, 1967), although Davis (1964) does not find that the tendon goes through the canal in *Ailuropoda*. In this case, the tubercle would have protected the tendon from being crushed by the weight of the animal, and would also have served as the attachment site of the long plantar ligament.

**Navicular**—Both navicular bones are preserved with some damage. The navicular is proximodistally very compressed. The proximal side forms a shallowly depressed, medially broad articulation with the astragalar head. The distal surface is convex, forming, in its present state of preservation, a continuous articular surface for the three cuneiforms (Fig. 12E, F), although the facets are variably distinct in *Arctocyon primaevus* (Argot, 2013). The lateral surface, which is indented, forms the articulation with the cuboid. Ventrally, there is a large plantar tubercle, also present in *Anancodon*, and very prominent in *Arctocyon primaevus* (Argot, 2013).

**Cuneiforms**—The left and right ectocuneiforms, and the right mesocuneiform, are preserved. The ectocuneiform is similar to that of *Arctocyon primaevus*, with a squat, rectangular, slightly concave navicular facet on the proximal end, and a larger, dorsoplantarly more concave facet for the third metatarsal distally. The dorsal surface is trapezoidal, and there is a prominent plantar tubercle that aligns with the one on the cuboid, extending the canal for the fibularis longus tendon and serving for the attachment of plantar ligaments.

The mesocuneiform is a mediallytrolarly narrow bone. The distal face is covered by a concave facet for the articulation with the second metatarsal, which is dorsoplantarly elongate and somewhat inclined proximodorsally to distoplantarly. On the medial and lateral faces, there are distinct long and narrow facets for the ecto- and entocuneiforms. The proximal surface is shallowly concave dorsoplantarly to match the navicular.

**Metatarsals**—Metatarsal (Mt) I is short and robust with a large proximal end. The proximal articulation is more or less quadrate, with a rounded dorsal margin; it is the only metatarsal whose proximal articulation is slightly wider transversely than dorsally. The surface is slightly convex dorsoplantarly, shallowly grooved mediolaterally, and faces proximodorsally. The articular facet for Mt II is damaged, but what remains suggests a slightly abducted hallux. The shaft is relatively wide and flat and its ventral surface is slightly concave. The distal articulation is roughly cylindrical with the keel developed only on the ventral half; it is asymmetrical, the lateral keel wider dorsosventrally than the medial keel.

Mt II is half again as long as the hallucal metatarsal. Its proximal articulation is the narrowest of all the metatarsals, only about half as wide transversely as it is in dorsosventral dimension. It is gently concave transversely and convex and slightly helical dorsosventrally. There is a well-developed, broad, and dorsosventrally slightly concave articular facet for the ectocuneiform all along the proximolateral margin; the facet expands at the dorsal and ventral ends, the latter being larger. The articulation for Mt III is damaged. The shaft of Mt II (and successive metatarsals) becomes flatter and wider distally. The distal articulation is asymmetrical, like that of Mt I. The dorsal surface is smooth and lacks any keel. The lateral face is covered by a concave facet for articulation with the metatarsal (Mt IV) and the plantar surface by a concave facet for articulation with the metatarsal (Mt V). The mediodistal end is more concave than the proximal.

Mt III is twice as long as Mt I and about 20% longer than Mt II. The proximal articulation is trapezoidal, about half again as wide dorsally as ventrally, but much wider dorsosventrally than transversely. It is convex dorsosventrally, flat mediolaterally. Its medial border is notched just dorsal to the midpoint, with a small articular facet at the dorsal end of the proximomedial surface and a larger one ventrally, for articulation with Mt II. The lateral border is markedly concave, with large articular surfaces for Mt IV at the dorsal and ventral ends of the proximolateral aspect. The distal end is relatively wide and symmetrical. Although less well preserved than Mt II, there is no indication of a tubercle on the proximodorsal surface.

Mt IV is of comparable size and robustness to Mt III. A loose distal end, slightly asymmetrical, appears compatible with the proximal part, and would indicate a length comparable to Mt III. The proximal articulation, however, is slightly larger than that of Mt III. It is of similar shape to that of Mt III, but wider and with a conspicuous notch in the medial margin. Dorsal to the notch is a prominent, medially facing articular tubercle that matches the
TABLE 4. Results of the Kruskall-Wallis test of the effect of locomotor mode for each ratio.

| Ratio          | Kruskal-Wallis $\chi^2$ | df | P value | Significantly different post hoc pairs |
|----------------|-------------------------|----|---------|--------------------------------------|
| MitIII/Femur   | 92.4010                 | 5  | >0.0001 | A:C; A:Taq; C:S; C:T; C:Tf; S:Taq; T:Taq; T:Tf |
| MtV/MitIII     | 59.0494                 | 5  | >0.0001 | A:T; A:Taq; A:Tf; C:T; C:Tf; S:T; S:Taq; S:Tf; T:Tf |
| ProxPhal/MitIII| 70.3606                 | 5  | >0.0001 | A:C; A:S; A:T; A:Taq; A:Tf; C:S; C:T; C:Tf; S:Taq; S:Tf; S:Tf |
| RadMin/RadMax  | 86.1515                 | 5  | >0.0001 | A:T; A:Taq; A:Tf; C:S; C:T; C:Tf |
| HumArt/HumMax  | 66.9271                 | 5  | >0.0001 | A:Taq; A:Tf; C:S; C:Taq; C:Tf; S:Taq; T:Taq; T:Tf |
| OIP/UnIL       | 100.6384                | 5  | >0.0001 | A:C; A:S; A:T; A:Taq; A:Tf; C:S; C:T; C:Tf; S:Taq; S:Tf; S:Tf; T:C; T:Taq; C:TEC |

Significant pairs determined by post hoc Bonferroni-corrected Mann-Whitney U tests. Abbreviations: A: arboreal; S: scansorial; T: terrestrial; Tf: semi-fossorial; Taq: semiaquatic; C: cursorial.

proximolateral fossa on Mt III. As in Mt III, the lateral margin is concave, with large articular facets, here to encase the proximalmedial articular surfaces of Mt V. The elements as identified appear to articulate reasonably well, considering the rough condition of the specimen. Nevertheless, in view of the close similarity of the elements we identify as Mt III and Mt IV, and the apparently slightly larger size of Mt IV, it is possible that these elements are switched, and this one is actually Mt III.

Mt V, though robust, is substantially longer than Mt I and about the length of Mt II. It is slightly bowed in the sagittal plane, with a concave medioventral surface. The element displays torsion: the proximal end is twisted laterally relative to the distal end. The proximal articulation is broad and roughly triangular, wider dorsally than ventrally. It is flat transversely and concavo-convex dorsoventrally (slightly convex dorsally, slightly concave ventrally). A large, convex, medially facing facet articulates with the concavity on Mt IV. The distal articulation is asymmetrical, approximately a mirror image of that of Mt I.

Phalanges—Associated with the skeleton are 14 proximal phalanges, nine intermediate phalanges, and 12 terminal phalanges. All are robust. Although there is some size variation among these elements, it is not large enough or consistent enough to allow definitive identification of elements as manual or pedal; hence, they are described together here. The relative consistency in size indicates that the manus and pes were quite generalized, without significant digital reduction except in length of Mc I (Matthew, 1937). The better-preserved elements bear medially oriented facets as indicating what locomotor categories. Thus, it is perhaps best to view these complicated patterns as indicating what taxa. It is worth noting that when values for and within the range of semi-fossorial, semiaquatic, and arboreal taxa from terrestrial and cursorial ones, and relative length of the olecranon process is a very good separator of semi-fossorial versus arboreal taxa, with semi-fossorial taxa having a much longer olecranon relative to ulna length. These findings corroborate long-held observations (e.g., Hildebrand, 1985; Garland and Janis, 1993).

All three forelimb ratios calculated from the specimen of *Arctocyon mumak* fall outside the ranges found in modern arboreal or scansorial forms (Fig. 13). The proportions of the distal humerus are within the ranges of modern semiaquatic and semi-fossorial forms. The proportions of the olecranon process relative to the length of the ulna are at the high end of values observed in modern terrestrial and semi-fossorial forms. The proportions of the radial head are within what is found in modern semi-fossorial, semiaquatic, or terrestrial forms, and are distinct from both arboreal and scansorial forms on the one hand, and cursorial forms on the other. This is consistent with the interpretation of the forelimb of *A. mumak* as having limited supination ability. Modern arboreal forms have the most mobile radiohumeral joints, whereas in most modern cursorial forms the radius is almost entirely immobile.

Conversely, the hind limb ratios do not provide such a clear distinction (Fig. 14). Metatarsal to femur ratio for *Arctocyon mumak* is outside the range of cursorial and semiaquatic forms, but within the range of the other locomotor categories. The relative length of midline to lateral metatarsals is outside the arboreal, scansorial, and cursorial ranges, and within the range of semiaquatic and terrestrial forms, although this ratio is difficult to interpret owing to a very broad spread of values in the terrestrial category. The ratio of proximal phalangeal length to metatarsal V length is outside the range of arboreal, cursorial, and semiaquatic taxa and within the range of semi-fossorial, terrestrial, and scansoreal taxa. It is worth noting that when values for *A. mumak* fall within the ranges of multiple locomotor categories, it is consistently in cases where that ratio is unable to significantly distinguish said locomotor categories. Thus, it is perhaps best to view these complex patterns as indicating what *A. mumak* did not do rather than providing clear indications of what it did. On balance, it is clear that the ratios in *A. mumak* are inconsistent with it having equately preserved, they can be seen to bear a shallow fissure distally.

ECOMORPHOLOGICAL ANALYSIS

The effect of locomotor mode on each of the seven ratios listed in Table 4 was tested using nonparametric Kruskal-Wallis tests. Locomotor mode has a highly significant effect on all seven anatomical ratios (Table 4). Pairwise Bonferroni corrected Mann-Whitney U tests indicate which locomotor groups are distinguished by each ratio. Of particular note, a high metatarsal to femur ratio (characteristic of cursorial taxa) is outside the range of arboreal, semiaquatic, or terrestrial forms, although this ratio is difficult to interpret owing to a very broad spread of values in the terrestrial category.
been a specialized arborealist or a specialized cursorial mammal, and are most consistent with an interpretation of it as a generalized terrestrial or semi-fossorial mammal.

The picture for other arctocyonids is somewhat mixed, with *Chriacus* seeming more arboreal in those indices analyzed that are associated with the forelimb, but more generalized in indices of hind limb, and in fact not easily distinguished from *Arctocyon mumak*. *Thryptacodon* shows a lesser degree of arboreal adaptation, and the larger *Arctocyon primaevus* seems to be more terrestrially adapted based on most indices. *Anacodon* presents a puzzling mix of features, with distal humeral proportions within the ranges of modern arboreal, terrestrial, and cursorial forms, and a proximal radius within the range of modern cursorial, terrestrial, and semi-fossorial forms. This analysis only samples a fraction of the morphological variation in these taxa, and so these results should be treated as preliminary indications; however, they point to significant locomotor diversity in Paleocene and Eocene arctocyonids.

The multivariate analysis only considered *Arctocyon mumak*, because it was the only specimen for which all ratios could be assembled. The MANOVA on the principal component scores was significant for the effect of locomotor mode ($F(5, 147) = 20.04$, Pillai trace = 0.4093, P < 0.0001). Univariate analyses show that principal components (PCs) 1, 3, 4, and 5 are significantly correlated with locomotor mode. Loadings of the ratios on each principal component are given in Table 5.
### TABLE 5. Percent of total variation accounted for by each principal component resulting from the analysis of five ratios.

| Principal component | Percent total variation | MtII/Femur | PL/MtIII | RadMin/RadMax | HumArt/HumMax | OlP/Uln |
|---------------------|-------------------------|-----------|----------|---------------|---------------|---------|
| PC1                 | 45.2                    | 0.487     | -0.388   | -0.755        | 0.187         | -0.388  |
| PC2                 | 22.35                   | 0.796     | 0.47     | 0.186         | 0.148         | 0.275   |
| PC3                 | 15.94                   | -0.162    | -0.868   | 0.404         | -0.931        | 0.867   |
| PC4                 | 10.93                   | 0.151     | -0.185   | 0.211         | 0.251         | 0.187   |
| PC5                 | 5.58                    | 0.283     | 0.248    | 0.211         | 0.251         | 0.867   |

The loading of each initial variable on each principal component is also given.

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**FIGURE 14.** Boxplot of hind limb ratios for extant taxa and fossils. Extremes of boxes are 25% and 75% quartiles. Central tendency lines are medians. Whiskers are 95% confidence intervals. **Abbreviations:** A, arboreal; S, scansorial; T, terrestrial; Tf, semi-fossorial; Taq, semiaquatic; C, cursorial.
In an ordination of PC1 and PC4, A. mumak is placed in the area of the functional morphospace occupied by extant semi-fossorial forms (Fig. 15). PC1 is negatively correlated with radial head index, so that low values of PC1 are more closely associated with a circular radial head, and high values with an elliptical one. Metatarsal to femur ratio is positively correlated with PC1, so that a long metatarsal relative to the femur is associated with high PC1 scores. Thus, when plotted, PC1 distinguishes arboreal taxa with short metatarsals and circular radial heads from semi-fossorial taxa with long metatarsals and elliptical radial heads. PC4 is negatively correlated with distal humeral width index, so that taxa with high PC4 scores have distal humeri that are broad relative to articular width. Thus, PC4 separates robust semi-fossorial taxa from gracile arboreal taxa.

A discriminant function analysis was conducted to test this observation. A discriminant function was calculated on the ratios used for the principal component analysis. Percent correct classification for extant taxa of known locomotor modes ranged from 44% for semiaquatic category to 100% for the semi-fossorial classification for extant taxa of known locomotor modes. Using this discriminant function, A. ferox was classified by locomotor and Arctocyon mumak for graphical comparison. High PC1 scores are associated with an elliptical radial head and a high metatarsal to femur ratio. High PC4 scores are associated with strongly projecting medial and lateral epicondyles.

DISCUSSION

The skeleton of Arctocyon mumak is robust compared with most other Procoreiidae, and has similarities to certain other large Paleocene taxa such as periphyctids and taeniodonts. However, as with the other large arctocyonids, Anacodon ursidens and Arctocyon primaevus, it has proven difficult to interpret the anatomy functionally. The prominent entepicondyle, large and medially directed olecranon process, short metapodials, shallow astragalar trochlea, short astragalar neck, robust and blocky calcaneus, and large plantar tubercles on the calcaneus, cuboid, and navicular all indicate that A. mumak was fully plantigrade (Ginsburg, 1961). The anatomy of the ankle and pes is also consistent with a fully plantigrade stance (Carrano, 1998). Furthermore, the angle of the femoral neck, the asymmetrical femoral condyles, and the shallow semilunar notch suggest that the limbs were held somewhat abducted and flexed, perhaps as in the opossum Didelphis (Argot 2002), or similar to the condition seen in some notoungulates (Shockey and Flynn, 2007). Unlike Arctocyon primaevus (Argot, 2013) and A. ferox, A. mumak had a semilunar notch set obliquely to the long axis of the ulna, asymmetrical femoral condyles, and a bowed fibula. This suggests that the limbs may have been held habitually in an abducted posture, perhaps more so than in other species of the genus Arctocyon.

We confirm Russell’s (1965) and Argot’s (2013) observation of highly interlocking zygaphyses in the lumbar spine, which, combined with the flaring ilium (which is more developed than in Arctocyon ferox), indicates that the lumbar region in the larger species of the genus Arctocyon was powerfully muscled and stabilized against lateral flexion by features of the skeleton and the soft tissue. Thus, flexibility of the lumbar spine was probably limited in these taxa.

Interpreting the behavior of Arctocyon mumak is less obvious. As was noted above, the ungual morphology, which can be a good indicator of behavior, is equivocal both for A. mumak and for Anacodon, suggesting either scansorial or fossorial behavior, or both (MacLeod and Rose, 1993). The pes is quite generalized, with five stout digits. The digits seem to be relatively broader and shorter than those of Arctocyon primaevus, indicative of either scansorial or fossorial habits. Together with evidence from the forelimb (humeral crests, depth of ulna, length of olecranon, tubercle of Mc III), they are more suggestive of semi-fossorial habits.

The fact that the femur and tibia are of comparable length is suggestive of a terrestrial quadrupedal gait similar to that of bears or the wolverine Gulo gulo. In this regard, it may be informative to remember that smaller bears, to which Anacodon has been compared (Rose, 1990), are capable diggers and climbers as well as quadrupedal ambulators. The forelimb musculature was likely powerful, as evidenced by the large crests on the humerus and the deep ulna with pronounced fossae and ridges (Argot, 2013). However, the unusual morphology of the distal forelimb, in particular the laterally compressed and deep ulna and the inferred morphology of the contact between the carpus and the antebrachium, complicates inferences about the motions possible in the forelimb by making analogies with living taxa problematic. Argot (2013) suggested that the unusual ulnar morphology reflects powerful muscle attachments for digital flexors and extensors, and that mechanical stresses from the hand were primarily transmitted via the radius. The asymmetrical morphology of the humeral trochlea, however, in particular the pronounced medial ridge, suggests that the ulna was also buttressed against force transmission in A. mumak. The forelimb thus seems to show
characteristics that reflect powerful musculature for manipulation and adaptation for force transmission.

The ecomorphological analysis provides additional insight into the possible locomotor ecology of *Arctocyon mumak*, as well as how it may differ from other Procreodi. The analysis of multiple ratios proves useful, in that most of them distinguish between some, but not all locomotor modes. Furthermore, we note that the signal is not consistent across all ratios in the fossil taxa. In this regard, it is interesting that although a number of distinctive arboreal morphologies have been detected in *Chriacus*, most notably the capacity for hind foot reversal (Rose, 1987), not all the indices consistently fall within the range of modern arboreal taxa in our comparative sample. The hind limb ratios in particular have similar values for both *A. mumak* and *Chriacus*, and generally fall within the ranges of scansional or terrestrial taxa. Conversely, the forelimb ratios are divergent between the two taxa, with the values for *A. mumak* most often falling within the ranges associated with the fossorial taxa in our modern sample, and those of *Chriacus* falling within the ranges associated with arboreal/scansional taxa in our sample. In particular, the relative length of the olecranon process in *A. mumak* is very similar to that of extant fossorial taxa, whereas in *Chriacus* it is very similar to that of arboreal/scansional forms. Argot (2013) argued that the enlarged olecranon process of *Arctocyon primaevas* was not consistent with the degree of specialization seen in other fossorial taxa (e.g., Rose and Emry, 1983), but this comparison was with some of the most derived fossorial or even subterranean taxa. Fossorial and semi-fossorial mammals encompass a wide range of relative olecranon lengths (Hildebrand, 1985; Hopkins and David, 2009). In this regard, it is notable that Argot (2013) also observed close similarity between the forelimb of *Arctocyon primaevas* and the badger *Taxidea*, but considered the latter a generalist, despite the fact that badger burrows are deep and extensive (Stroganov, 1969). Our multivariate analysis confirms that *A. mumak* is more similar to terrestrial and fossorial taxa in our sample than to arboreal taxa. This is supported by the osteology. In any case, the olecranon process of *A. mumak* is absolutely and relatively larger than that of *A. primaevas*. Other notable differences between *A. mumak* and *A. primaevas* include the shallower and less proximally extensive patellar groove of the latter taxon, the narrower iliac crest, and the less arched medial profile of the proximal calcaneus. If Argot (2013) is correct that such features are associated with scansional and manipulative adaptations, then we conclude that different species of *Arctocyon* display allopatric variation, with the larger *A. mumak* being more terrestrial and using its manipulative, powerfully muscled forelimb for digging and tearing. This is supported by the differing femoral morphologies of the two taxa: the deeper and narrower patellar groove of *A. mumak* being strongly suggestive of terrestrial habits. However, it is also noteworthy that the two ratios we were able to collect on *A. primaevas* (humeral articular width/total distal humeral width and radial head index) give different results for this taxon. The humeral index falls within the range of semi-fossorial and semi-aquatic taxa, together with *A. mumak* and distinct from scansional forms. The radial index is higher for *A. primaevas* and encompasses the range seen in modern terrestrial and scansional forms. This suggests that the manipulative adaptation of the forelimb in both species of *Arctocyon* may have differed slightly, possibly relating to different types of manipulative behavior in the two animals.

An interesting conclusion to come from this work is the observation that although there is a close similarity in morphology between the femur, and particularly the humerus, of *A. mumak* and the living giant panda *Ailuropoda*, such a similarity does not follow in the morphology of the tibia and fibula and, most markedly, the radius and ulna. Some of these characteristics, particularly the distinctive morphology of the ulna, have been considered as distinctive of the large-bodied arctocyonids (Weigelt, 1960; Russell, 1964). The inconsistent results of the ecomorphological analysis, in particular the failure of the hind limb ratios to distinguish the larger-bodied arctocyonids from the smaller ones in terms of function, highlight that Paleogene taxa often show character combinations that are not always entirely commensurate with modern taxa. In this case, the hind limbs may retain a more generalized primitive condition, whereas forelimb anatomy may reflect more specialized substrate preferences. A similar situation is found in the postcranial skeleton of the early Eocene mesonychid *Pachyaena gigantea* (O’Leary and Rose, 1995), which combines primitive morphology in some regards with highly derived and unique cursorial adaptations in others. As a rule, arctocyonid postcrania appear more robust than those of similarly sized modern taxa, with strongly developed crests and processes for muscle attachments. The reasons for this are unclear, although the weak bone-on-bone congruence displayed by many of the joints in these animals suggests that it may have something to do with relying more on muscles and tendons to stabilize the skeleton. It has long been noted that many Paleogene mammals appear to display more robust skeletons, with stronger crests and processes, than extant mammals.

Finally, the ecomorphological analysis of the forelimb provides evidence that the ecology of the large and small-bodied Procreodi in our sample was quite different, with the smaller ones showing more arboreal/scansional traits, and the larger ones more terrestrial/semi-fossorial features. The analysis also highlights the importance of using information from different functional regions of the skeleton to clarify the ecomorphology of these animals, because no single ratio is capable of discriminating between all locomotor modes. Within the larger-bodied group, we note that the tarsals of *Arctocyon mumak*, *A. primaevus*, *A. ferox*, and *Anacodon ursidens* have different morphologies that probably correlate with different ecologies. *Anacodon* in particular is quite distinct from the other large-bodied arctocyonids in its tarsal and femoral morphology. The presence of enlarged, tooth-like canines in *Anacodon*, *Arctocyon mumak*, and *Mento-claenodon* may suggest a link between these three taxa. Further study of the systematics and phylogeny of Procreodi is needed to establish which of these morphologies is primitive or derived. This complex matrix of covarying traits points to a pattern of mosaic evolution in the cranial and postcranial skeleton of arctocyonids. These could provide a source of characters with which to understand the relationships between these taxa. A clearer picture of the phylogenetic relationships of these taxa would permit a better understanding of the ecological and evolutionary significance of this morphological variation. A particular question raised by Argot (2013) concerns whether the scansional-type morphologies seen in these animals reflect a shared ancestry with primitively scansional early eutherians such as *Eomaia* (Ji et al., 2002). O’Leary et al. (2013) reconstructed the hypothetical placental ancestor as scansional based on character optimization. Furthermore, they noted that *Protungulatum donnae*, often considered to be the earliest condylarth, was the earliest undoubted placental mammal known from the fossil record. Thus, there is a distinct possibility that scansional traits in arctocyonids reflect shared ancestry. More detailed phylogenies of Paleogene mammals are required to address these problems. Given the potential importance of arctocyonids in the evolution of modern ungulate orders, such work would doubtless improve our understanding of early ungulate evolution and diversification.

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