

# On the origin of the order Artiodactyla

(Arctocyonidae/Paleocene/Eocene)

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**ABSTRACT** The first known members of the order Artiodactyla appeared suddenly throughout the Holarctic region at the beginning of the Eocene. They are characterized by distinctive cursorial skeletal specializations. Owing to their abrupt appearance and the lack of transitional forms, the origin of the order is problematic. Descent from a “condylarth,” specifically the arctocyonid *Chriacus*, has been suggested based on dental resemblances, but until now postcranial anatomy seemed to preclude close relationship between Arctocyonidae and Artiodactyla. A middle Paleocene specimen of a small arctocyonid (?*Chriacus*) reported here is much more similar to the oldest artiodactyl, *Diacodexis*, in the derived condition of the hindlimb, reviving the possibility that Artiodactyla evolved from an arctocyonid.

Artiodactyla, the even-toed ungulates (pigs, camels, deer, cattle, and their relatives), are the predominant large land mammals of today. The oldest fossil artiodactyls come from early Eocene strata of North America, Europe, and Asia. Their initial appearance seems to coincide with what is increasingly regarded, at least among vertebrate paleontologists, as the beginning of the Eocene on these continents—i.e., the base of the Wasatchian, Sparnacian, or Bumbanian land-mammal ages, respectively (1–6). There is general agreement that the beginning of these land-mammal ages was essentially isochronous.

The earliest artiodactyls are instantly recognizable from their diagnostic double-pulley astragalus, but much of the skeleton also bears the hallmarks of the order, including strongly paraxonic feet and other specializations for cursorial locomotion (7–14). The skull and its bunodont dentition, on the other hand, are relatively conservative in these early forms, exhibiting few if any diagnostic artiodactyl traits.

Early Eocene records of Artiodactyla are referable to *Diacodexis* and closely allied genera variously allocated to Dichobunidae *sensu lato* or Diacodexidae (for oldest North American records, see refs. 3 and 15–18; for Europe, refs. 19–26; for Asia, refs. 1 and 27–30). About the size of a rabbit, these oldest artiodactyls were much smaller than most modern members of the order. The relative abundance, widespread occurrence, and abrupt appearance of artiodactyls at the base of the Eocene make them among the strongest fossil evidence that this boundary has been crossed.

The sudden appearance of artiodactyls in early Eocene Holarctic faunas presents one of the great enigmas of mammalian history: how and where did Artiodactyla originate? They are usually considered to have evolved from “condylarths” (a rather heterogeneous grade of primitive, mostly herbivorous placental mammals often characterized as archaic ungulates even though many bore claws), but no transitional forms have been found—though, admittedly, we still know comparatively little about Paleocene faunas, especially outside of western North America. Two other extant orders—Primates

(i.e., euprimates: lemurs, tarsiers, monkeys, and apes) and Perissodactyla (odd-toed ungulates such as horses, tapirs, and rhinos)—also appeared abruptly and in abundance in early Eocene Holarctic deposits, with little indication of their ancestry. This situation has given rise to speculation that these orders originated in isolation, perhaps in Central or South America, Africa, or India, and that warming climates or breakdown of physical barriers allowed their dispersal into Holarctica (3, 31–33).

Fueling this speculation have been several recent fossil discoveries. These include teeth of an apparent true primate, older than any other, from the late Paleocene of north Africa (34), and the skull of a primitive phenacolephid from the late Paleocene of southern China, which appears to be more closely related to Perissodactyla than the long-held sister group, North American Paleocene Phenacodonta (35–37). More pertinent to the origin of artiodactyls is the discovery of *Diacodexis* in late early–middle Eocene strata of Pakistan and India (29, 30). Though possibly more primitive than the oldest North American and European *Diacodexis*, *Diacodexis pakistanensis* is geologically younger. This evidence, while tantalizing, is still circumstantial, and significant stages in the transition to these modern orders are missing. In short, the geographic source of Artiodactyla remains unresolved.

## Condylarths and Artiodactyla

For more than 50 years, the phylogenetic source of Artiodactyla has been considered to lie among the Condylarthra, a diverse, paraphyletic assemblage that also probably includes the basal stock of other ungulates, including perissodactyls, hyracoids, sirenians, proboscideans, and cetaceans, as well as several extinct orders (36, 38). Derivation from a hyopsodontid condylarth was long believed probable (refs. 39 and 40; see ref. 41 for historical review) but now seems unlikely. Although there is a general dental resemblance between Paleocene hyopsodontids (e.g., *Promioclauenus*, *Litomytus*) and Wasatchian artiodactyls, hyopsodontid postcranial anatomy—primarily based on Bridgerian *Hyopsodus* (42–44)—indicates that they were short-limbed, pentadactyl, clawed mammals of quite disparate adaptation (fossorial or perhaps scansorial) from all early artiodactyls.

Van Valen (41) put forth the most plausible proposal for the phylogenetic source of Artiodactyla, their possible descent from small arctocyonid condylarths near *Metachriacus*, which he then considered to be included in the genus *Tricentes*. This inference was based primarily on dental resemblance (which is closer than that to hyopsodontids), since at that time practically nothing was known of the postcranial skeletons of either small arctocyonids or the most primitive artiodactyls. Later, Van Valen (45) transferred these and several other species of small arctocyonids previously placed in *Tricentes*, *Metachriacus*, and *Spanoxyodon*, to *Chriacus*, which he portrayed as the direct ancestor of Artiodactyla. Subsequent discovery of nearly

complete skeletons of Wasatchian *Chriacus* (*sensu stricto*) and the primitive artiodactyl *Diacodexis* revealed profound differences between them and led to the conclusion that *Chriacus* was not particularly close to Artiodactyla (7, 46). Other arctocyonids for which postcrania are known either resemble *Chriacus* in their skeletal anatomy or differ from early artiodactyls in other ways (47–51).

Rejection of *Chriacus* as the ancestor of Artiodactyla assumes that *Diacodexis* approximates the artiodactyl morphotype. Although it has widely been considered to be the most primitive known artiodactyl (8, 9, 23, 41), some of its postcranial specializations for cursorial–saltatorial locomotion seem to exceed those in certain other primitive artiodactyls. For this reason, *Diacodexis* has sometimes been viewed as closer to selenodont artiodactyls (camels, ruminants, and their kin, whose teeth are characterized by crescentic crests) and therefore unlikely to represent the stem artiodactyl (7, 52). No older or demonstrably more primitive artiodactyl genus is known, however, and the relatively uniform postcranial anatomy of dichobunids suggests that *Diacodexis* does in fact approach the primitive condition for the order. Dental anatomy also supports the basal position of *Diacodexis* (18).

Prothero *et al.* (38) considered Artiodactyla to be the sister group of all other Ungulata (including Arctocyonidae, the next most primitive group), citing addition of a molar hypocone and enlargement and distal shifting of the femoral third trochanter as synapomorphies of all other ungulates. The distribution of these characters among Ungulata, however, renders ambiguous which of the two groups is more primitive. The hypocone is small or absent in the oldest arctocyonids (53, 54) as well as artiodactyls. Although the third trochanter of some ungulates

(e.g., the condylarths *Hyopsodus*, *Phenacodus*, and *Meniscotherium*, as well as perissodactyls) is indeed large and comparatively distal in position, this process differs markedly in size or position in others (e.g., uinatheres, *Arsinoitherium*, anisonchine periptychid condylarths). It is smaller and relatively more proximal in arctocyonids than in phenacodontid condylarths and perissodactyls (48). In *Diacodexis* the third trochanter is very small and slightly more distal than in arctocyonids (7, 8). Nearly all other artiodactyls lack a third trochanter, hence its reduction and loss is inferred to be derived in Artiodactyla. Therefore, both the reduced (artiodactyl) and hypertrophied (perissodactyl) states are probably derived relative to that in arctocyonids.

### New Fossil Evidence

The probability of a close or even sister-group relationship between Arctocyonidae and Artiodactyla is resurrected by a previously undescribed specimen of a small arctocyonid from the middle Paleocene of New Mexico. USNM 407522 (USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC) consists of both dentaries and associated bone fragments including a distal left femur, proximal left tibia, and two vertebrae. The dentaries contain left P<sub>4</sub> and M<sub>2</sub>, right M<sub>3</sub>, and roots of nearly all other teeth (Fig. 1). The specimen was collected in the west branch of Torreon Arrojo [Nacimiento Formation, late Torrejonian, zone To3? (55)], San Juan Basin, New Mexico, by Franklin Pearce, working with C. L. Gazin in 1949. It was not catalogued until much later, however, and its significance was recognized only recently. A label in Gazin's handwriting tentatively identified the speci-

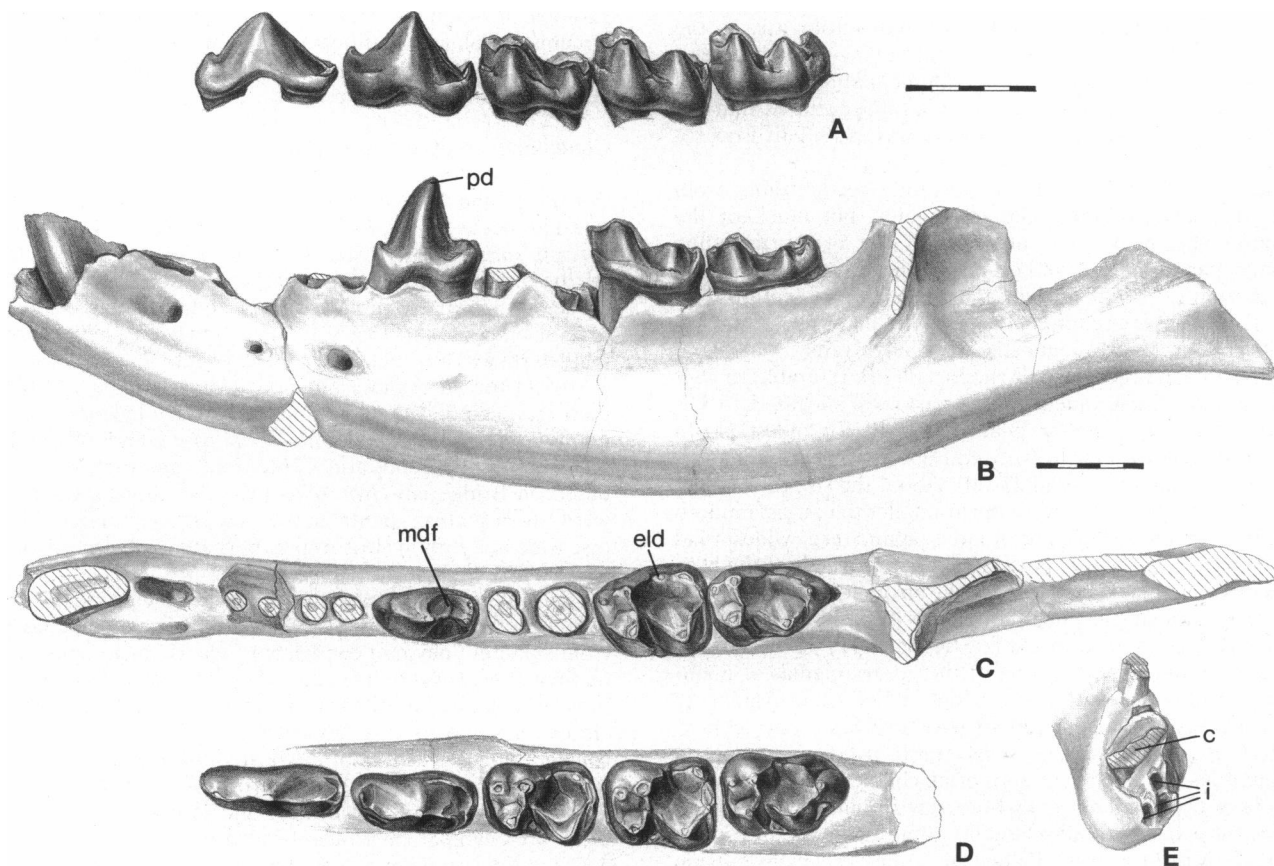


FIG. 1. Comparison of lower dentitions of USNM 407522, a small arctocyonid, and the early Eocene basal artiodactyl *Diacodexis*. (A and D) *Diacodexis secans*, left P<sub>3</sub>–M<sub>3</sub>, in lateral and occlusal views; USGS 16804, P<sub>3</sub> restored from USGS 2352 (USGS, Geological Survey, Denver). (B, C, and E) “*Chriacus truncatus*,” USNM 407522. (B and C). Left dentary with P<sub>4</sub>, M<sub>2</sub>–3, M<sub>3</sub> reversed from the right side; lateral and occlusal views. (E) Anterior part of right dentary showing incisor alveoli. c, Canine root; eld, entoconulid; i, incisor alveoli; mdf, metaconid fold; pd, protoconid. (Bars = 5 mm.)

men as *Chriacus truncatus* Cope, one of five species, previously placed in four different genera, that have recently been regarded as synonyms of *Chriacus baldwini* (Cope) (45, 56, 57).

Considerable confusion surrounds the composition, proper name, and identification of *C. baldwini* specifically and *Chriacus* in general (56, 58), stemming partly from the fragmentary nature or poor quality of many type specimens. The holotype of *C. baldwini* itself is a dentary fragment with P<sub>3</sub>–M<sub>1</sub> in which the molar is heavily worn. Only P<sub>4</sub> is directly comparable with USNM 407522, and the former is larger (18% longer and 40% wider) and differs in structure of the metaconid fold. Available samples are inadequate to assess the significance of these differences. The type and original referred specimens of *C. truncatus* were all upper teeth (and are therefore not directly comparable with USNM 407522), described as “a close copy of *C. baldwini* on a smaller scale” (ref. 59, p. 275). Comparisons of the other holotypes and referred specimens indicate that there is considerable variation in dental anatomy in what is now being referred to *C. baldwini*. Pending much-needed revision of *Chriacus* and related forms, these observations indicate that USNM 407522 represents a small arctocyonid within or close to Van Valen’s concept of *Chriacus* but probably outside the range of *C. baldwini*.

Association of the postcranial fragments with the dentaries is considered reliable on the basis of Gazin’s field records, appropriate size, similar color and preservation, and the individual age of the specimen. That it represents a subadult, but not juvenile, individual is indicated by the fully erupted but little worn M<sub>3</sub>, together with porous surface texture of the limb elements and dentaries, and epiphyses that are unfused (femur) or missing (tibia).

Alveoli preserved in the right dentary show that the incisors were procumbent but somewhat less horizontal than in Clarkforkian–Wasatchian *Thryptacodon* and *Chriacus* (60, 61). Unlike in these, however, the symphyseal region is narrow and the alveoli are crowded together, with one situated above the other two (Fig. 1E); there is no diastema between incisors and canine. The large, laterally compressed canine was followed by four premolars, all but P<sub>1</sub> two-rooted. Judging from the alveoli, a short diastema intervened between P<sub>1</sub> and P<sub>2</sub>, and P<sub>2–3</sub> were noticeably shorter than P<sub>4</sub>, in contrast to *Diacodexis* (Fig. 1A–D). P<sub>4</sub> is relatively shorter than in *Diacodexis*, with a taller protoconid and stronger metaconid fold, but otherwise it resembles that of *Diacodexis* rather closely. M<sub>2–3</sub> resemble those of *Diacodexis* in being low-crowned and bunodont, with wide, basined talonids; but, like *Chriacus* generally, they lack the extent of basal crown inflation characteristic of early artiodactyls. A small entonoulid is present on both M<sub>2</sub> and M<sub>3</sub>, unlike in *Diacodexis*.

The distal femur is similar in size and structure to that of *Diacodexis*, specifically in having a greater anteroposterior than transverse dimension, laterally compressed condyles, and a narrow, elevated patellar trochlea with sharp borders, the medial one more elevated (Fig. 2). These derived traits contrast with the broader and flatter distal femora of Torrejonian and Wasatchian *Chriacus* (16, 46, 59) and, so far as I am aware, all other arctocyonids whose femora have been described (*Anacodon*, *Arctocyon*, *Arctocyonides*, *Claenodon*, *Mentoclaenodon*, *Thryptacodon*; see refs. 47–51), with the possible exception of some specimens of *Arctocyonides trouessarti* (ref. 49, plate 39, figures 10, 11, and 18). Basal artiodactyls are further specialized in having an even more elevated and proximally extensive patellar trochlea and a distinct fossa (for attachment of the common tendon of the extensor digitorum longus and peroneus tertius muscles) between the lateral trochlear rim and lateral femoral condyle (8).

The proximal tibia is slender and laterally compressed and lacks the epiphysis (Fig. 3). The tibial crest is somewhat sharper than that of Wasatchian *Chriacus*, in this respect approaching *Diacodexis*, but its relatively greater length (reflecting more

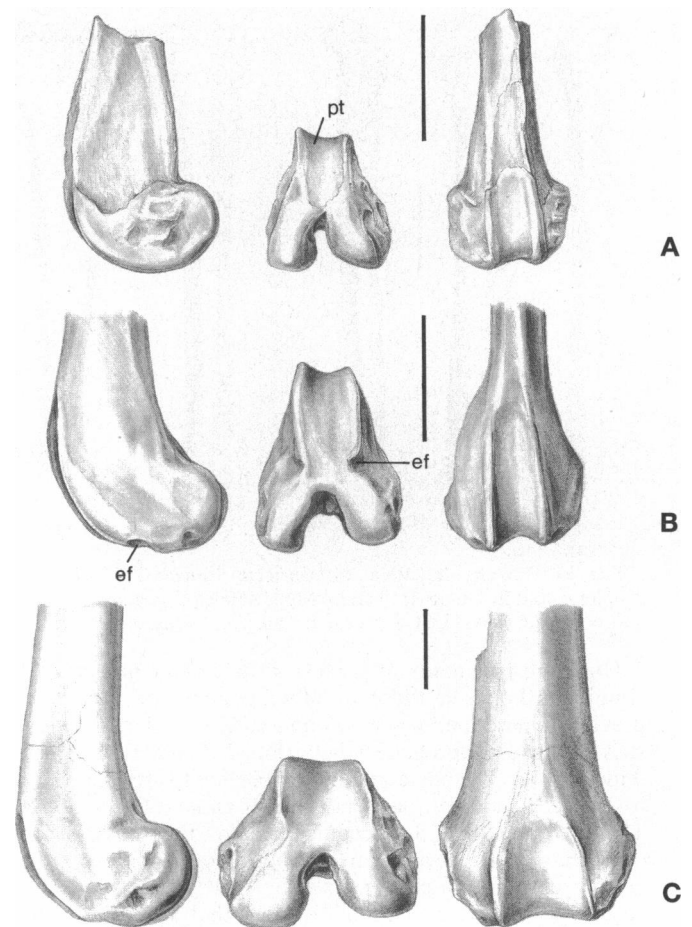


FIG. 2. Distal left femora of “*Chriacus truncatus*,” USNM 407522 (A); *Diacodexis secans*, USGS 2352 (B); and *Chriacus* sp., USGS 21907 (C). Lateral, distal, and anterior views. (B and C) From Wasatchian Willwood Formation, Bighorn Basin, Wyoming. ef, Extensor fossa; pt, patellar trochlea. (Bars = 1 cm.)

distal attachment of the knee flexors semitendinosus, gracilis, and sartorius) is a presumably primitive resemblance to other arctocyonids. Similarly, the mediolaterally compressed shaft with its narrow posterior aspect hollowed toward the medial side resembles that of *Chriacus* and contrasts with the broader, flat posterior surface in *Diacodexis*.

The two vertebrae appear to come from the lumbar and proximal caudal regions but provide little information, except to suggest a somewhat better-developed tail than in *Diacodexis*.

## Conclusions

The dental anatomy of *Chriacus* species (*sensu* Van Valen, ref. 45), including USNM 407522, approaches that of basal artiodactyls as closely or more so than does that of any hyopsodontid. The lower premolars of *Chriacus* are somewhat elongate and pointed (though taller and not as long as in basal artiodactyls), and the molars are relatively low-crowned and broad. As already noted, the hypocone is absent in the oldest artiodactyls and very small or lacking in the most primitive arctocyonids, but this cusp is present on upper M<sup>1–2</sup> of *Chriacus*—a potential obstacle to close relationship if absence of the hypocone in artiodactyls is assumed to be primitive. In ancient artiodactyls, however, these teeth have well-developed pre- and postcingula and often have a small swelling in the region of the hypocone; hence, it is possible that absence (i.e., loss) of the hypocone is a derived trait in artiodactyls. The distribution of this trait among primitive arctocyonids makes positive assessment of its polarity ambiguous.

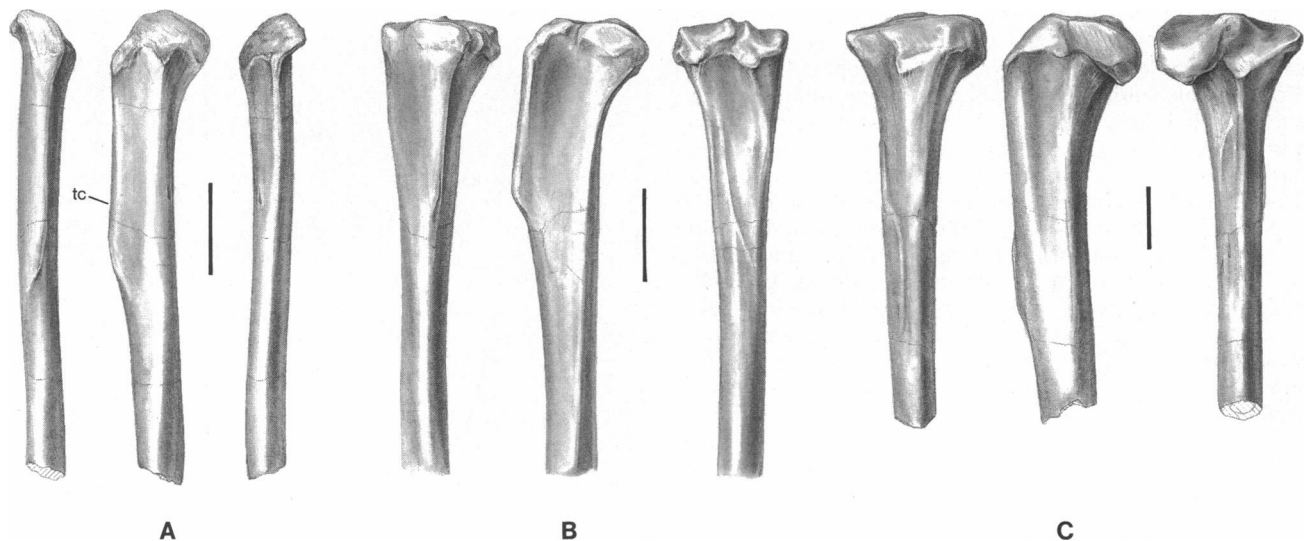


FIG. 3. Proximal left tibiae of "*Chriacus truncatus*," USNM 407522 (A); *Diacodexis secans*, USGS 2352 (B); and *Chriacus* sp., USGS 15404 supplemented by USGS 2353 and AMNH 48006 (*C. gallinae*; Wasatchian San José Formation, San Juan Basin, New Mexico) (C). Anterior, lateral, and posterior views. USGS specimens are from Wasatchian Willwood Formation, Bighorn Basin, Wyoming. tc, Tibial crest. (Bars = 1 cm.)

Hindlimb fragments of USNM 407522 show intermediate conditions between those of other arctocyonids (including previously described *Chriacus*) and early artiodactyls, with a strikingly close approach to the artiodactyl condition in distal femoral form. The postcranial resemblances to artiodactyls are in derived characters associated with cursorial locomotion. These are the first arctocyonid remains that possess such characters, thus providing new support for a possible sister-group relationship between these small arctocyonids and Artiodactyla. Postcranial modifications that would characterize an arctocyonid-artiodactyl transition include progressive elongation and lightening of distal limb segments, reduction in prominence or length of muscular processes and crests, mediolateral compaction of manus and pes with increasing paraxonic arrangement, restriction of joint mobility to a parasagittal plane, and conversion of claws to hoofs.

The occurrence of an artiodactyl-like arctocyonid in the middle Paleocene of New Mexico revives the possibility that Artiodactyla originated in North America during the Paleocene. However, the absence of any other transitional forms leading to Artiodactyla, together with the abrupt appearance of full-fledged artiodactyls across the Holarctic region at the beginning of the Eocene, continue to suggest that the early evolution, if not origin, of the order took place elsewhere. The middle Paleocene age of USNM 407522 provides no support for the origin of Artiodactyla on the Indian subcontinent, which was presumably isolated from Africa since at least the late Cretaceous (33), but it does not preclude the occurrence of artiodactyl-like arctocyonids prior to the middle Paleocene.

Evidence presented here indicates a substantial range of postcranial anatomy and adaptation within animals currently considered to represent the genus *Chriacus* (45, 56, 57). The close similarity of postcranial characters in Wasatchian *Chriacus gallinae* from New Mexico and *Chriacus* sp. from Wyoming, as well as in very fragmentary remains attributed to Torrejonian *C. baldwini* and *Chriacus pelvidens* [AMNH (American Museum of Natural History) 3115 and 3117], supports alliance of these species under the genus *Chriacus*. However, other small arctocyonids recently subsumed under *Chriacus*, such as USNM 407522, differ considerably. This suggests that recognition of more than one genus, as was formerly done, would be a more accurate reflection of known morphological diversity.

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