Journal of Paleontology, 86(1), 2012, p. 25–43
Copyright © 2012, The Paleontological Society
0022-3360/12/0086-0025$03.00

NEARLY COMPLETE SKELETON OF *TETRACLAENODON* (MAMMALIA, PHENACODONTIDAE) FROM THE EARLY PALEOCENE OF NEW MEXICO: MORPHO-FUNCTIONAL ANALYSIS

PETER E. KONDRASHOV[1] AND SPENCER G. LUCAS[2]
[1]A.T. Still University of Health Sciences, Kirksville College of Osteopathic Medicine,
800 W. Jefferson St., Kirksville, Missouri 63501, USA, <pkondrashov@atsu.edu>; and [2]New Mexico Museum of Natural History,
1801 Mountain Road, Albuquerque, New Mexico 87104, USA, <spencer.lucas@state.nm.us>

ABSTRACT—We describe the relatively complete skeleton of *Tetraclaenodon* undoubtedly associated with its dentition, from the Torrejonian interval of the Nacimiento Formation in the San Juan Basin, New Mexico. *Tetraclaenodon* is the most primitive and oldest genus of the family Phenacodontidae and is very important for assessing the phylogenetic relationships of the family. The newly described skeleton belonged to a lightly built terrestrial mammal that could use trees for shelter. The structure of the ulna, manus, femur, crus, and pes corresponds to that of a typical terrestrial mammal, while morphological features such as the low greater tubercle of the humerus, long deltopectoral crest, pronounced lateral supracondylar crest, and hemispherical capitulum indicate some scansorial adaptations of *Tetraclaenodon*. The postcranial skeleton of *Tetraclaenodon* does not exhibit the cursorial adaptations seen in later phenacodontids and early perissodactyls. Phylogenetic analysis did not recover monophyletic "Phenacodontidae"; instead, phenacodontids formed a series of sister taxa to the Altungulata clade. *Tetraclaenodon* is the basal-most member of the "Phenacodontidae" + Altungulata clade.

INTRODUCTION

ASSOCIATED REMAINS of teeth and postcrania of Paleocene archaic ungulates are uncommon and if found contain a tremendous amount of morphological information for functional and phylogenetic analysis. Archaic ungulates, including the phenacodontid 'condylarths', are thought to be ancestral to several groups of ungulate mammals. Phenacodontidae, in particular, are considered by some researchers to have been ancestors of the order Perissodactyla (Radinsky, 1966; Sloan, 1970; Gingerich, 1976; Thewissen and Domning, 1992). *Tetraclaenodon* Scott, 1892 is the most primitive and oldest genus of the Phenacodontidae, so it is of key importance to assessing the phylogenetic relationships of the family. *Desmatoclaenus* Gazin, 1941 is known by fragmentary remains from the Paleocene of North America (Gazin, 1941; Van Valen, 1978) and was referred to Phenacodontidae by West (1976). This referral was not supported by later researchers and *Desmatoclaenus* was excluded from Phenacodontidae (Thewissen, 1990; Cifelli, 1983; Archibald, 1998). Indeed, *Desmatoclaenus* appears to be much closer to loxolophine arctocyonids than to phenacodontids in its premolar morphology and in having wrinkled enamel.

Despite the fact that *Tetraclaenodon* dental remains are very common in the lower Paleocene deposits of North America, little is known about the postcranial anatomy of representatives of this genus. Most of the previously published information about the postcrania of *Tetraclaenodon* comes from Matthew (1897, 1937), Osborn (1898), and Radinsky (1966). Few associated postcrania have been described for other phenacodontids (Cope, 1884a; Matthew, 1897, 1937; Osborn, 1898; Thewissen, 1990; Rose, 1996a, 2001). Both major revisions of Phenacodontidae were based on dental material (West, 1976; Thewissen, 1990).

Discovery of a nearly complete, partially articulated skeleton of *Tetraclaenodon* allows us to address the question of whether *Tetraclaenodon* was a stem taxon for Perissodactyla as suggested by Radinsky (1966). The phenacodontid ancestry of perissodactyls was questioned by Prothero and Schoch (1989) based on the description of *Radinskya* McKenna, Chow, Ting and Luo, 1989. Rose (1996a) designated *Radinskya* as the closest outgroup to Perissodactyla, with the next closest outgroup being the Phenacodonta (phenacodontid and meniscotheriid 'condylarths'). Beard (1998) suggested that *Radinskya* was a stem perissodactyl but Hooker and Dashzeveg (2003) and Hooker (2005) rejected that idea and regarded *Radinskya* as a "primitive phenacolophid embrithopod with apomorphies distinct from any perissodactyl" (Hooker, 2005, p. 210). Hooker (2005) argued that the discovery of the Asian genus *Lophocion* Wang and Tong, 1997, which shared more dental characters with early perissodactyls, provided some support for the Asian origin of the order. Rose (2006) mentioned that the most likely source of Perissodactyla is phenacodontid condylarths, possibly *Ectocion* Cope, 1882a or *Lophocion*.

Phenacodontids have been recently included in a number of phylogenetic analyses that considered several extant clades, such as artiodactyls, perissodactyls, hyraxes, and macroscelideans (Thewissen and Domning, 1992; Geisler, 2001; Tabuce et al., 2001, 2007; Froehlich, 2002; Asher et al., 2003; Zack et al., 2005; Asher, 2007; Penkrot et al., 2008; Holbrook, 2009). In several of the analyses, phenacodontids showed close affinities to Paenungulata and other condylarths (e.g., Tabuce et al., 2001, 2007; Asher et al., 2003; Asher, 2007), while in others, phenacodontids formed a monophyletic group with perissodactyls (e.g., Thewissen and Domning, 1992; Zack et al., 2005; Penkrot et al., 2008).

Here, we provide a detailed description and functional analysis of the postcranial anatomy of *Tetraclaenodon*. The new material allows us to assess the position of this genus within Phenacodontidae and calls into question ideas about the possible ancestral relationships of the family Phenacodontidae with the order Perissodactyla.

MATERIAL

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, U.S.A.; BR, Berru collection at Muséum national d'Histoire naturelle, Paris, France; CR, Cernay collection at Muséum national d'Histoire naturelle, Paris, France; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; KUVP, University of Kansas, Museum of Paleontology, Lawrence, Kansas, U.S.A.; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; UCMP, University of California Berkeley, Museum of Paleontology, Berkeley, California, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; WA, Walbeck collection at Martin-Luther-Universität, Institut für Geowissenschaften, Halle-Wittenberg, Germany.

From NMMNH locality 02635 (Nacimiento Formation in the San Juan Basin, New Mexico, the Big Pocket locality of Wilson (1949) in Kutz Canyon): NMMNH P-20949, skeleton with a skull and mandible including left and right C1–M3, left c1, p2–m3, right i1–i3 roots, c1–m3; left humerus without the distal portion; right humerus; right ulna; right distal radius; right metacarpals II–IV in a concretion; partial left metacarpal I; left metacarpal IV; partial left metacarpal V; shaft portion of left radius and distal portion of left ulna in natural articulation; proximal forelimb phalanx of digit 3; middle forelimb phalanx of digit 3; proximal forelimb phalanx of digit 2 or 4; large block containing partial and concreted pelvis, left femur, left tibia, left fibula, right femur, proximal right tibia, sacrum, concreted thoracic vertebrae and ribs; shafts of the right tibia and fibula; right calcaneus; right talus; left partial talus; block with distal tarsals; right cuboid; right navicular; block with right metatarsals II–IV, proximal hind limb phalanx of digit 2 or 4, middle hind limb phalanx of digit 2 or 4, ungual hind limb phalanx of digit 2 or 4; proximal hind limb phalanx of digit 3; middle hind limb phalanx of digit 3; left navicular; six caudal vertebrae. Judging from the erupting p4, the skeleton belonged to a young, possibly subadult individual. Besides coming from the same nodule, the elements of the skeleton were preserved either in natural articulation (e.g., right ulna and right radius, left femur and left tibia, etc.) or articulate well with each other (e.g., right talus and calcaneus, right humerus and right ulna, etc.), so there is little doubt that all the bones belong to one individual.

Parts of the skeleton are encased in an intractable 'ironstone' (hematite-limonite-goethite) crust. Attempts to prepare this crust indicate that it is not simply encasing cortical bone, but in many places has invaded the cancellous bone. Thus, removal of it would necessitate damage and partial-to-wholesale destruction of some elements. Therefore, after hundreds of hours of preparation it was deemed advisable to discontinue attempted removal of some of the ironstone, pending the possibility that a way to remove it without damaging the fossil will be discovered in the future.

METHODS

In order to identify the type of locomotion of *Tetraclaenodon*, we compared its skeletal elements to the corresponding bones of extant mammals with different types of locomotion as well as to the published data on various mammalian groups. Mammalian skeletons used for comparison are listed in the Part 1 of the supplemental data file available on-line (www.journalofpaleontology.org). Skeletal adaptations to different types of locomotion have been widely discussed in the literature (e.g., Taylor, 1974, 1976; Van Valkenburg, 1987; Hildebrand and Goslow, 2002; Sargis, 2002a, 2002b; Salton and Sargis, 2008). Many studies are devoted to skeletal adaptations to scansorial and arboreal locomotion (Emry and Thorington, 1982; Jenkins and Krause, 1983; Rose, 1987; Beard, 1991; Argot, 2001, 2002), fossorial, or digging, adaptations (Vinogradov and Gambaryan, 1952; Gambaryan, 1960; Taylor, 1978; Barnosky, 1982; Rose and Emry, 1983, 1993; Rose et al., 1992; Stein, 2000), and cursorial, or running, adaptations (Hopwood, 1947; Gambaryan, 1974; Penkrot et al., 2008). Less data have been published on the skeletal morphology of generalized terrestrial mammals and mammals with aquatic adaptations (Howell, 1970).

Postcranial terminology used in this paper follows the International Committee on Veterinary Gross Anatomical Nomenclature (2005). Dental terminology follows Van Valen (1966) and more recent works (e.g., Lopatin, 2006).

For phylogenetic analysis, we used PAUP Version 4.0b8/4.0d78 (Swofford, 2002) to analyze the matrix. Characters and character states used in the phylogenetic analysis are listed in the supplemental data file (Parts 2 and 3). Characters were scored by direct observations of specimens listed in Part 4 of the supplemental data file and supplemented by descriptions from the literature (Cope, 1884a; Osborn, 1898; Schlosser, 1911; Matthew, 1937; Gazin, 1965, 1968; Szalay and Decker, 1974; Rose, 1985, 1987, 1996a, 1996b, 2001; Thewissen, 1990; Court, 1995; Szalay and Lucas, 1996; Geisler, 2001; Froehlich, 2002; Zack et al., 2005; Delmer et al., 2006; Penkrot et al., 2008; Holbrook, 2009; Ladevèze et al., 2010). The data matrix was analyzed using the branch and bound algorithm of PAUP. Branch robustness was assessed by determining branch support, or number of additional steps required to collapse each node. Branch supports were calculated by instructing PAUP to retain trees progressively longer than the most parsimonious tree in increments of one step. At each incremental step a strict consensus tree was generated. The data matrix file is published on Morphobank website at www.morphobank.org.

SYSTEMATIC PALEONTOLOGY

Family "PHENACODONTIDAE" Cope, 1881a
Genus TETRACLAENODON Scott, 1892

Protogonia COPE, 1881a, p. 492.
Tetraclaenodon SCOTT, 1892, p. 299; MATTHEW, 1937, p. 187.
Euprotogonia Cope in EARLE, 1893, p. 378.

Type species.—*Phenacodus puercensis* Cope, 1881a.

Diagnosis.—Tooth formula i3/3 c1/1 p4/4 m3/3. The upper incisors are small, upper canines slightly enlarged, P1–P2 simple, P3 with a vestigial protocone, P4 protocone better expressed, there usually is a very small metacone. Upper molars with six cusps, hypocone and conules are large and well-expressed. No mesostyle on upper molars. M3/ is slightly reduced, without a hypocone. P/4 with a well-developed metaconid, vestigial paraconid and large talonid with two cuspids: hypoconid and entoconid. Lower molars with a much reduced paraconid. Talonid is as wide as the trigonid, but usually lower. The talonid is not basined. Hypoconulid is present on all molars, largest on M/3. Differs from *Phenacodus* Cope, 1873 and *Copecion* Gingerich, 1989 in lacking the mesostyle on upper molars, also differs from *Copecion* in having relatively shorter molars.

Included species.—*Tetraclaenodon puercensis "puercensis"* (Cope, 1881a); *Tetraclaenodon puercensis "pliciferus"* (Cope, 1882b).

Occurrence.—Lower Paleocene (Torrejonian) of North America.

Discussion.—There are two distinct size groups of *Tetraclaenodon*, a larger form and a smaller form that differ very little in morphology. The size difference is often more than 20–30%. It is possible that the two size groups represent two distinct species but until the entire sample of Torrejonian *Tetraclaenodon* is analyzed we use the subspecies name '*pliciferus*' for the smaller size group and '*puercensis*' for the larger size group, as was suggested by Williamson (1996). The

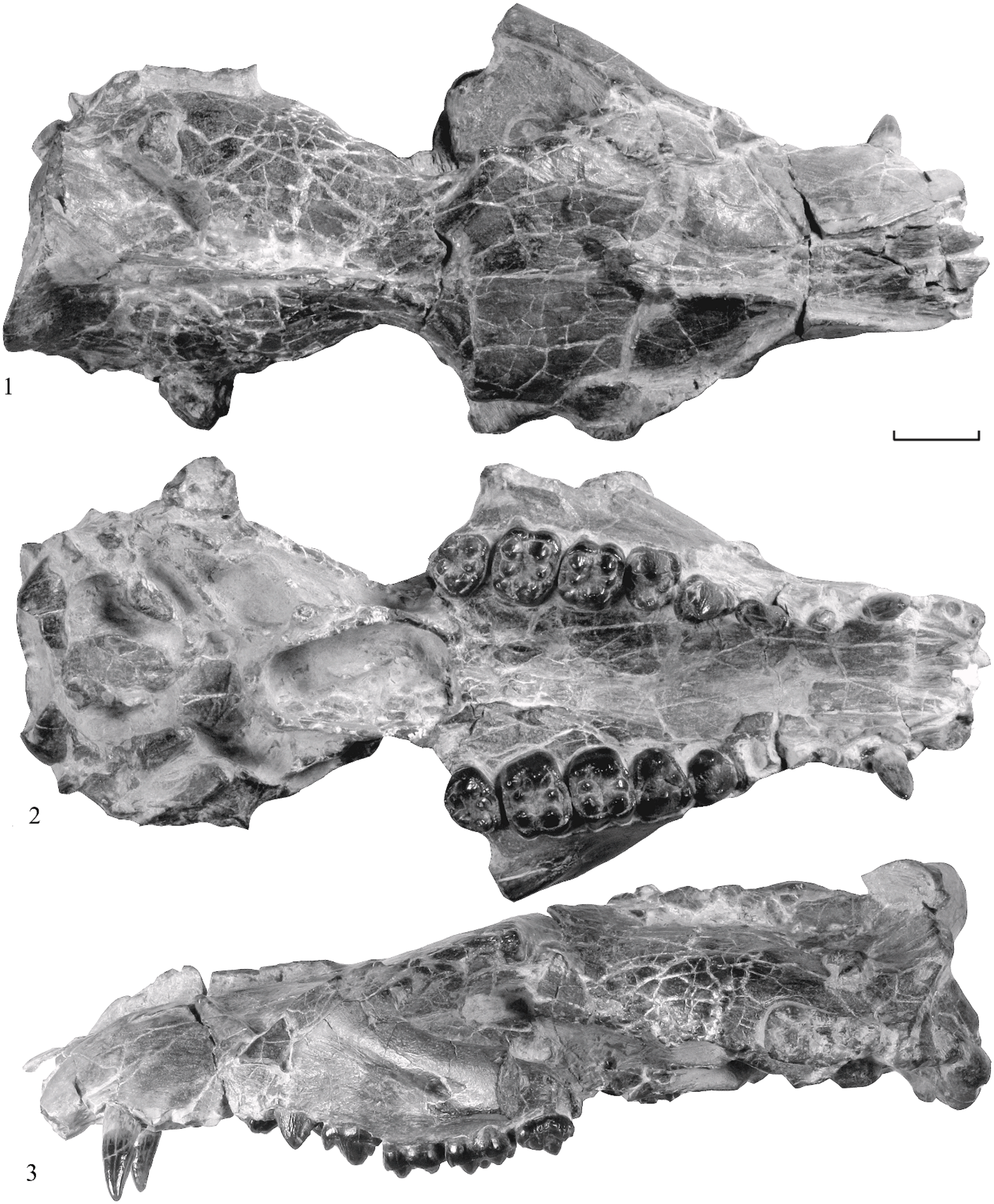

FIGURE *1*—Skull of *Tetraclaenodon puercensis* "*pliciferus*" (Cope, 1882b), NMMNH P-20949: *1*, dorsal view; *2*, ventral view; *3*, left lateral view. Scale bar=1 cm.

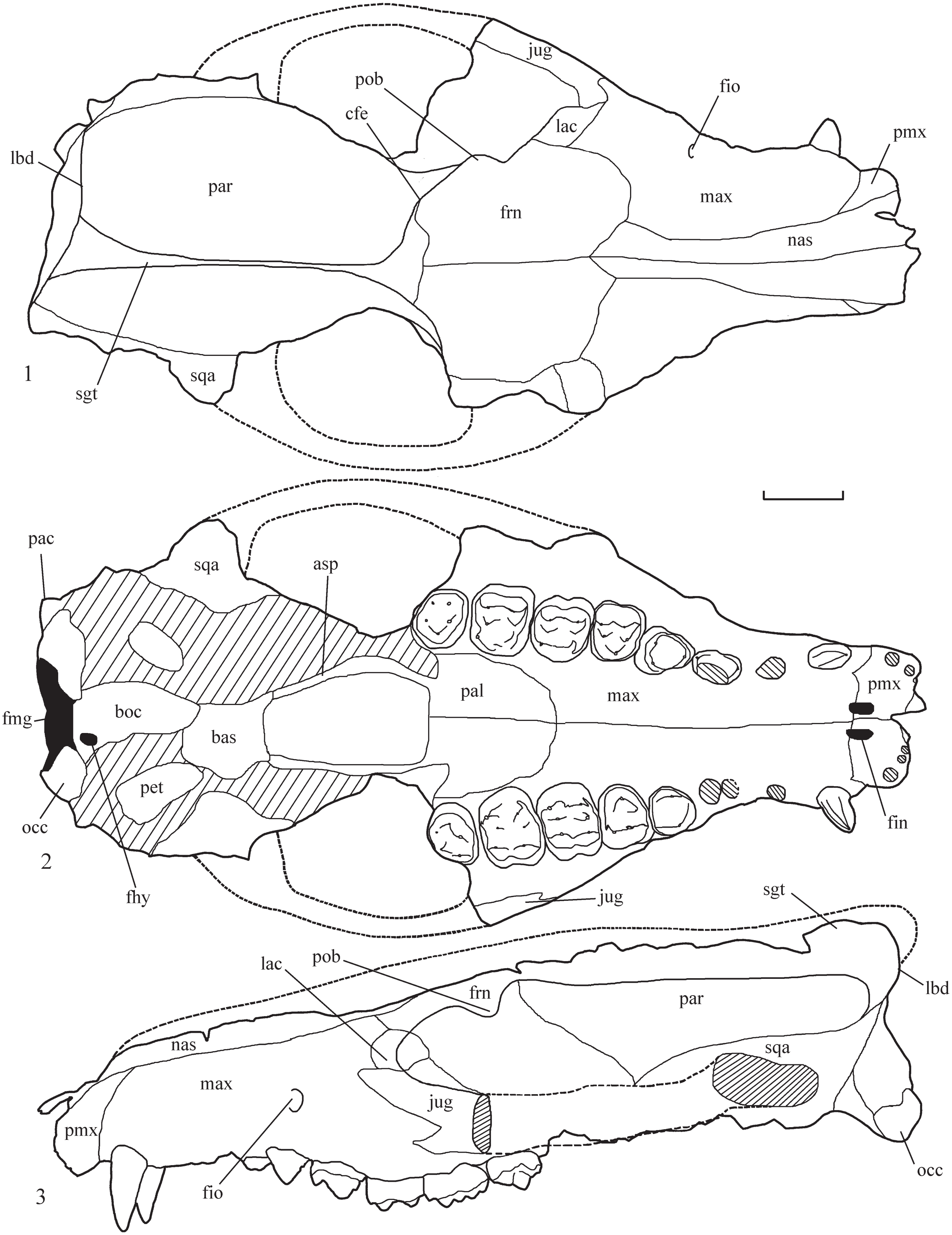

FIGURE 2—Reconstruction of the skull of *Tetraclaenodon puercensis* "*pliciferus*": *1*, dorsal view; *2*, ventral view; *3*, left lateral view. Abbreviations: asp=alisphenoid; bas=basisphenoid; boc=basioccipital; cfe=crista frontalis externa; fhy=foramen hypoglossi; fin=foramen incisivum; fio=foramen

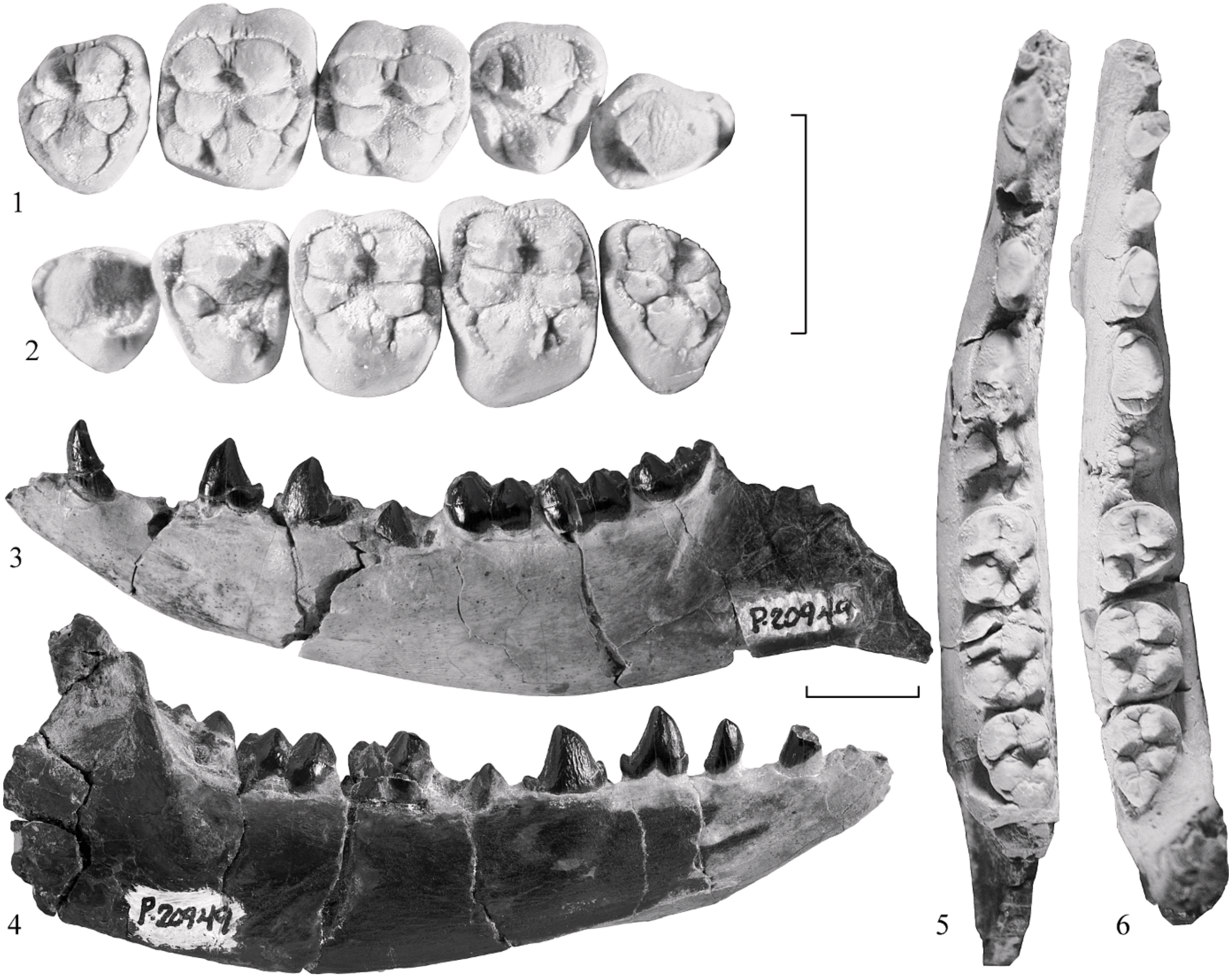

FIGURE *3*—Upper teeth and dentaries of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20949: *1*, right P3–M3, occlusal view; *2*, left P3–M3, occlusal view; *3*, left dentary with c1, p2–p3, m1–m3, labial view; *4*, right dentary with c1–m3, labial view; *5*, left dentary with c1, p2–p3, m1–m3, occlusal view; *6*, right dentary with c1–m3, occlusal view. Scale bars=1 cm.

two size groups of *Tetraclaenodon* are not likely to represent sexual dimorphism because the smaller specimens come from the lower levels within Torrejonian, while the larger specimens come from the upper levels of that interval (Libed et al., 2001). Although dental morphology has been described for both permanent and deciduous dentition of *Tetraclaenodon puercensis puercensis*, the dentition of the smaller subspecies has not been well characterized, so we include it here. Matthew (1937) briefly described the very fragmentary skull of *Tetraclaenodon puercensis*, while the very few postcranial elements known for this species have been only briefly mentioned (Radinsky, 1966) and not described formally.

Tetraclaenodon puercensis "*pliciferus*" Cope, 1882b
Figures 1–7

Tetraclaenodon pliciferus COPE, 1882b, p. 833; COPE, 1884b, p. 893, fig. 14; MATTHEW, 1937, p. 193; WEST, 1971, p. 8, fig. 3.

Type.—AMNH 3900, mandibular and maxillary fragments with left P4–M2 and p4–m2.

Skull, mandible, and dentition.—The skull is poorly preserved as it is crushed dorsoventrally and the ventral portion is displaced to the left side. Most of the bones are crushed into a mosaic of small pieces, which makes the identification of sutures very difficult or impossible. The orbit, basicranium, and palate are badly crushed and did not provide much information about the location of foramina and fissures. The rostral portion of the skull is longer than the cephalic portion (Figs. 1, 2). The narrowest point of the skull is at the postorbital constriction. The premaxilla does not contact the frontal; it wedges between the nasal and maxilla. The nasals are long and taper posteriorly. Anteriorly they are pointed and overhand the nares. The maxillary bone forms most of the rostral part of the skull and the palate. The infraorbital foramina are

---

←

infraorbitale; fmg=foramen magnum; frn=frontale; jug=jugale; lac=lacrimale; lbd=lambdoid crest; max=maxillare; nas=nasale; occ=occipital condyle; pac=paroccipital process; pal=palatinum; par=parietale; pet=petrosum; pmx=premaxillare; pob=postorbital process; sgt=sagittal crest; sqa=squamosum. Scale bar=1 cm.

FIGURE 4—Forelimb bones of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20949: *1*, right humerus, anterior view; *2*, right humerus, posterior view; *3*, right humerus, lateral view; *4*, right humerus, medial view; *5*, right humerus, proximal view; *6*, right radius, posterior view; *7*, right radius,

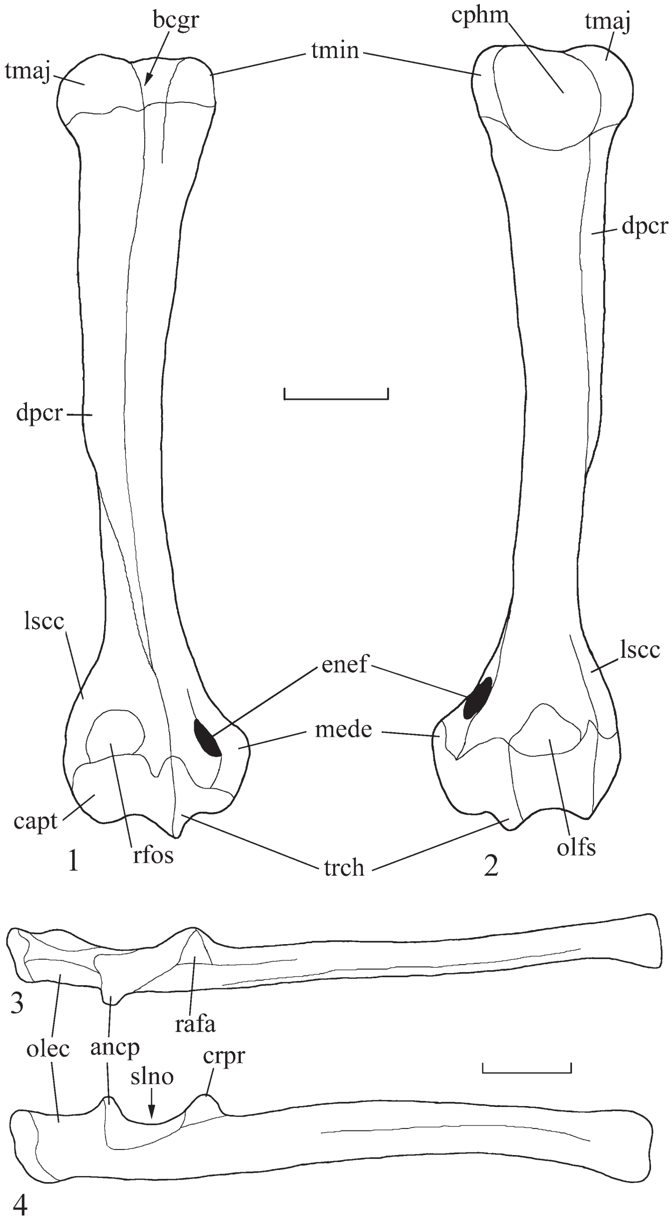

FIGURE 5—Reconstruction of the right humerus and ulna of *Tetraclaenodon puercensis* "*pliciferus*": *1*, humerus, anterior view; *2*, humerus, posterior view; *3*, ulna, anterior view; *4*, ulna, lateral view. Abbreviations: ancp=anconeal process; bcgr=bicipital groove; capt=capitulum; cphm=caput humeri; crpr=coronoid process; dpcr=deltopectoral crest; enef=entepicondylar foramen; lscc=lateral supracondylar crest; mede=medial epicondyle; olec=olecranon; olfs=olecranon fossa; rafa=radial facet; rfos=radial fossa; slno=semilunar notch; tmaj=tuberculum majus; tmin=tuberculum minor; trch=trochlea. Scale bar=1 cm.

situated above the P3. The maxilla does not contact the frontal within the orbital rim as there is a large lacrimal bone. A small lacrimal tubercle is present. The lacrimal canal opens within the orbit. The zygomatic arches were robust. The jugal (=os zygomaticum) is distinctly bifurcated anteriorly and almost reaches the anterior corner of the orbit dorsally. It contacts the lacrimal and maxillary bones anteriorly. The frontals are wide; the postorbital processes are well developed and form the roof of the orbit dorsally. The external frontal crests merge together at the postorbital constriction and form a well-expressed sagittal crest, which joins the rather tall lambdoid crest posteriorly. The occiput is narrow and triangular in outline; there are two low crests that extend from the sides of the foramen magnum dorsally. The occipital condyles have a rather complex shape: the medial part of the condyles is narrow, and the lateral part is much expanded. The paroccipital processes are well-expressed, but short; they are separated from the occipital condyles by shallow notches. Robust alisphenoid bones formed lateral walls of the posterior part of the choanae. The presence or absence of alisphenoid canal cannot be established for certain, although it looks like there was a lateral flange on either of the alisphenoid bones, which could have contained the alar canal. Badly crushed basioccipital fragment contains a hypoglossal foramen on the left side.

The dental formula is i3/3 c1/1 p4/4 m3/3, and the tooth rows are almost parallel to each other (see Tables 1 and 2 for tooth measurements). There are short diastemata between the C1/c1 and the P1/p1, and even shorter ones between the P1/p1 and P2/p2. The incisors are simple, round in cross-section, and of similar size. The upper canine is small, pointed, and slightly compressed laterally.

The P1 is single-rooted; the P2 is much larger and has two roots. The P3 has a well-expressed protocone that is less than a third of the size of the paracone. The cingulum is very well developed and is only interrupted on the labial side of the crown. It forms two additional cusps, very small parastyle and metastyle. A very small metacone is situated on the posterior slope of the paracone. The P4 is semi-molarized and has a large protocone that is only slightly smaller than the paracone; a parastyle, formed by the anterior cingulum; a metacone, which is adjacent to the posterior wall of the paracone; and a paraconule. The cingulum is nearly complete and only interrupted at the lingual base of the protocone.

The upper molars are bunodont. The M1 is square in outline and has six cusps. The protocone, paracone, and metacone are close in size and are larger than the paraconule, metaconule, and hypocone. The lingual cingulum is absent. There is a small cuspule on the posterior slope of the protocone. The M2 is similar to M1 in structure, but is larger and has a rectangular outline. The cuspule on the posterior slope of the protocone is better developed than on the M1. The M3 is significantly reduced and is nearly oval in outline. The hypocone is absent. The paracone and protocone are similar in size and are larger than the paraconule, metacone, and metaconule, which are close in size to each other. The cingulum is nearly complete.

The mandible is long and slender (Fig. 3). The mandible is similar in shape to that of other phenacodontids and early perissodactyls, in having a long horizontal ramus and a tall vertical ramus, which is almost perpendicular to the horizontal ramus (Radinsky, 1966). Although most of the angular portion of the mandible is missing in NMMNH P-20949, it is evident from the left ramus that the angular process projects ventrally, similar to other phenacodontids and early perissodactyls (Radinsky, 1966). The symphysis extends to the level of the posterior root of the p2. The symphysis is unfused. The anterior mental foramen is under the p1, and the posterior is under the p3.

←

anterior view; *8*, right radius lateral view; *9*, right ulna, anterior view; *10*, right ulna, lateral view; *11*, right ulna, medial view; *12*, right metacarpals II–IV embedded in matrix; *13*, left metacarpals I–V, proximal phalanges of digits III and IV, middle phalanx of digit III. Scale bar=1 cm.

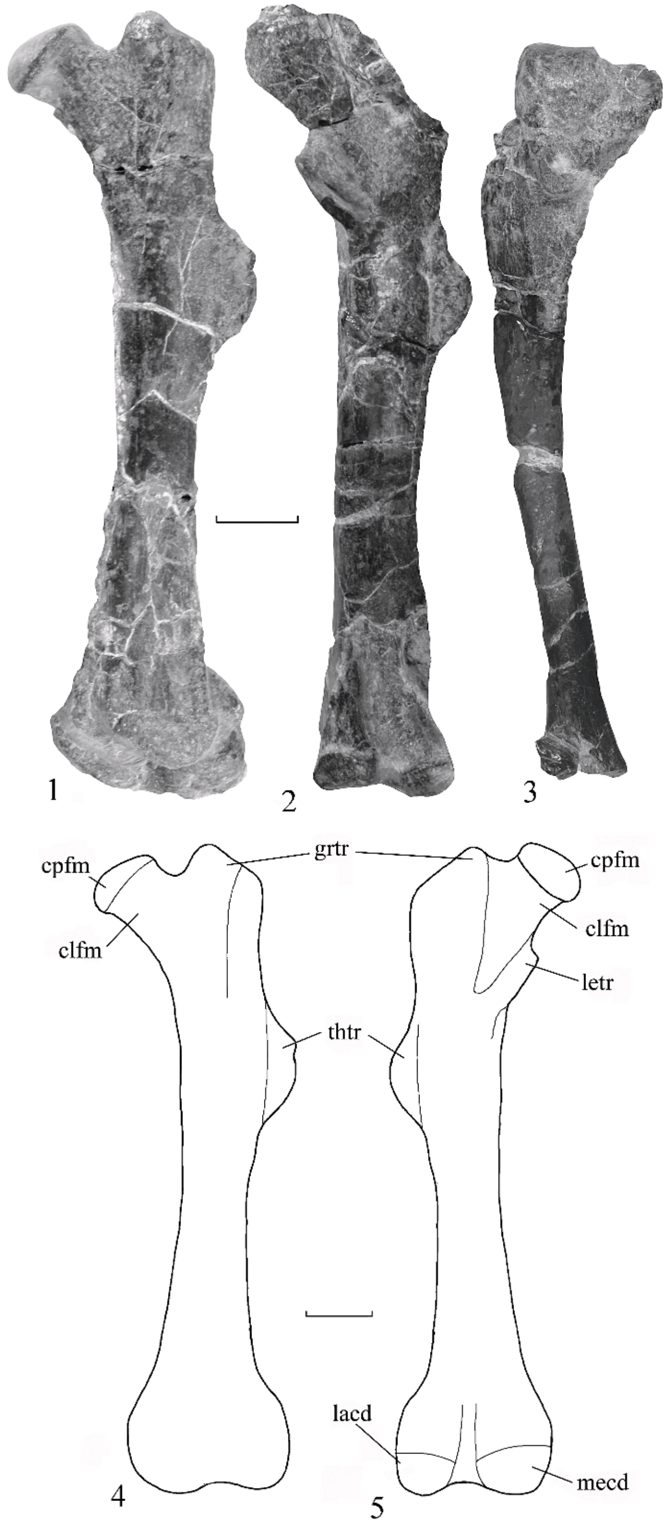

FIGURE 6—Hind limb bones of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20949: *1*, left femur, anterior view; *2*, right femur, posterior view; *3*, right tibia, medial view; *4*, reconstruction of the left femur, anterior view; *5*, reconstruction of the left femur, posterior view. Abbreviations: clfm=collum femoris; cpfm=caput femoris; grtr=greater trochanter; lacd=lateral condyle; letr=lesser trochanter; mecd=medial condyle; thtr=third trochanter. Scale bar=1 cm.

The lower canine is small and round in cross-section. The p1 is simple, single-cusped, and single-rooted. The p2 is larger, double-rooted and has an additional cuspid posterior to the protoconid. The p3 has a small talonid; the anterior cingulid forms a small cuspid. The erupting p4 has a tricuspid trigonid.

The m1 is rectangular in shape. The paraconid is fused to the metaconid. The paracristid is weak, but distinct. The cristid obliqua joins the posterolingual wall of the metaconid. The entoconid is large and equal in size to the hypoconid. The hypoconulid is small and median in position. The postcristid and entocristid are weak, and the talonid basin is open lingually. There is a small denticle on the anterior slope of the entoconid. The m2 is larger than m1, and the paraconid is greatly reduced but still discernible on the anterior slope of the metaconid. The paracristid is weak. The hypoconulid is slightly larger than on the m1. The m3 is laterally compressed; the paraconid is not as reduced as on the m1–m2 and is more centrally placed. The hypoconulid is large and close in size to the hypoconid.

Skull measurements (in mm).—Skull length, 110.2; skull width at the level of M2, 47.6; skull width between the tips of the postorbital processes, 29.2; width of the snout at the level of the canines, 19.7; length of the hard palate, 57.5; maximum width of the hard palate, 16.9; distance between the rostral corner of the orbit and the tip of the snout, 46.4; length of nasal bones, 18.7; maximum width of nasal bones, 10.8; maximum width of the braincase, 32.8; length of the sagittal crest, 41.7; height of the occiput (including the lambdoid crest), 28.5; distance between the tips of the paroccipital processes, 29.4; distance between tip of the postorbital process and the tip of the snout, 58.5; transverse diameter of the foramen magnum, 13.4; vertical diameter of the foramen magnum, 7.6; height of the left occipital condyle, 7.6; width of the left occipital condyle, 9.9; height of the right occipital condyle, 6.4; width of the right occipital condyle, 10.7; width of the palate between the M2s, 16.3; width of the palate between the P4s, 14.9; width of the choanae, 10.5.

Vertebral column.—Most of the thoracic and all of the lumbar and sacral vertebrae are almost completely covered by intractable matrix and thus are unavailable for description. The axis is preserved in a separate block with several other cervical vertebrae. It has a large odontoid process, and the articular facets for the atlas are rounded. Its spinous process is tall and robust. Ventrally, there is a prominent tubercle on the posterior part of the centrum and a sharp central crest. One of the middle cervicals (probably C3 or C4) shows morphology typical of cervical vertebrae, with a well-developed transverse foramen, laterally projecting transverse processes, and a tall spinous process. Several disarticulated caudal vertebrae have been found in association with the skeleton. They have cylindrical bodies that are constricted in the middle. Anterior articular processes are better developed than the posterior processes. The hemal arches are absent.

Humerus.—The right humerus of NMMNH P-20949 is complete, including the epiphyses (Figs. 4, 5), and the left lacks the distal end. The head of the humerus is hemispherical and projects to the same level as the tuberculum majus. In terrestrial taxa, the greater tubercle usually projects above the humeral head, restricting the mobility of the shoulder joint (Szalay and Sargis, 2001; Sargis, 2002a). The condition seen in *Tetraclaenodon* is intermediate between that of climbing mammals (Sargis, 2002a; Salton and Sargis, 2008) and typical terrestrial taxa in that the rather robust greater tubercle neither projects above the humeral head nor is located much below the head. There is a very shallow groove on the dorsal surface of the greater tubercle for the insertion of m. supraspinatus, which abducts and rotates the forelimb laterally. The lesser tubercle is very well developed and robust and projects

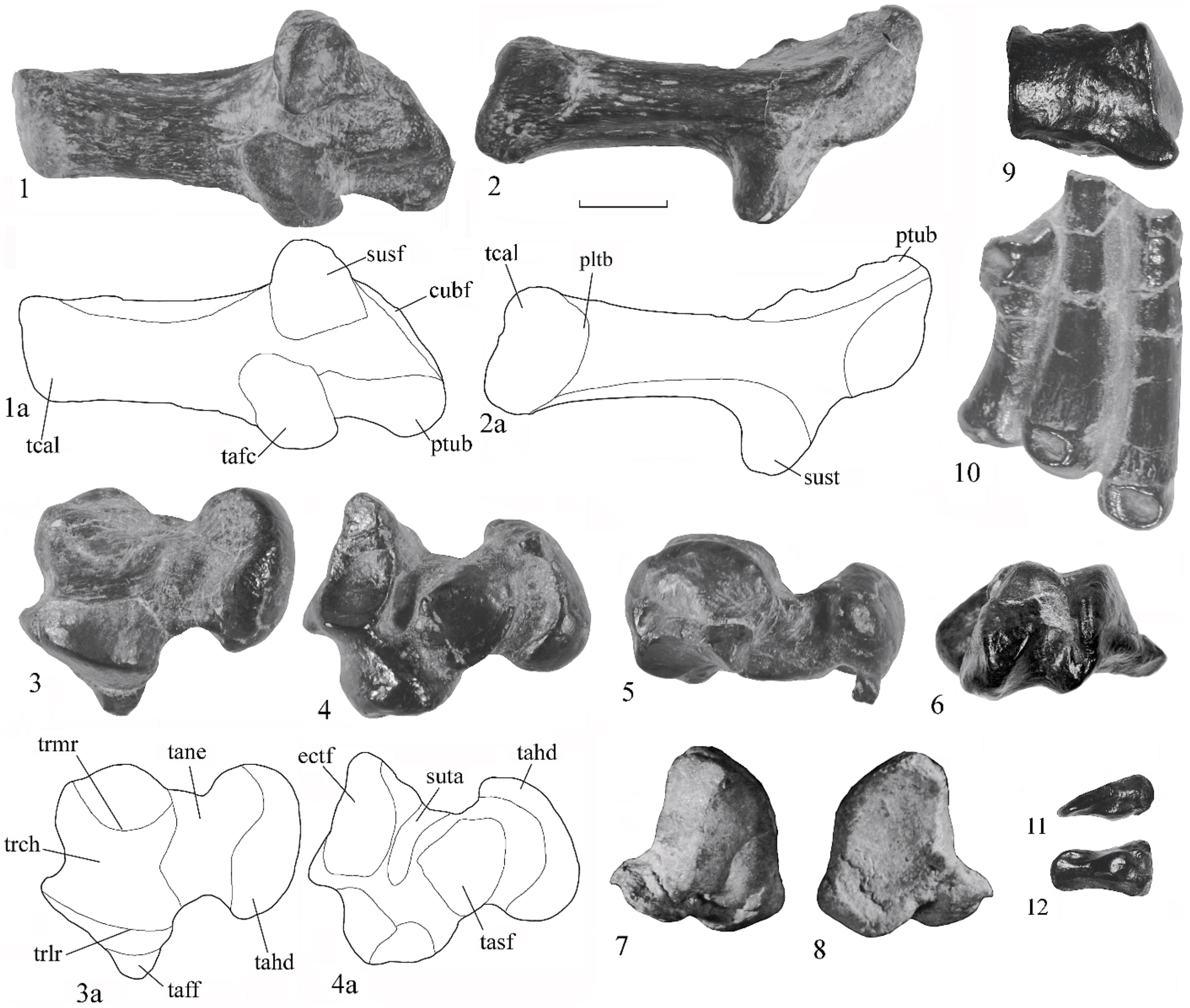

FIGURE 7—Foot bones of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20949: *1*, right calcaneus, dorsal view; *2*, right calcaneus, ventral view; *3*, right talus, dorsal view; *4*, right talus, ventral view; *5*, right talus, lateral view; *6*, right talus, proximal view; *7*, right navicular, distal view; *8*, right navicular, proximal view; *9*, right cuboid, dorsal view; *10*, metatarsals II–IV; *11*, ungual phalanx, lateral view; *12*, ungual phalanx, plantar view. Abbreviations: cubf=cuboid facet of calcaneus; ectf=ectal (=posterior calcaneoastragalar) facet; pltb=plantar tubercle; ptub=peroneal tubercle; susf=sustentacular facet of calcaneus; sust=sustentaculum; suta=sulcus tali; tafc=talar facet of calcaneus; taff=fibular facet of talus; tahd=head of talus; tane=neck of talus; tasf=sustentacular facet of talus; tcal=tuber of calcaneus; trch=trochlea of talus; trlr=lateral rim of the trochlea of talus; trmr=medial rim of the trochlea of talus. Scale bar=5 mm.

above the head of the humerus. The lesser tubercle provides an area for the insertion of m. subscapularis, which rotates the humerus medially, stabilizes the joint, and adducts the appendage. This muscle is very strong in climbing mammals, which have an enlarged lesser tubercle (Larson, 1988; Sargis, 2002a). The teres major tuberosity is not well expressed, and the bicipital groove is wide and shallow, different from climbing mammals (Taylor, 1974; Salton and Sargis, 2008). The shaft of the humerus is long and slender and is bowed anteriorly. There is a prominent deltopectoral crest that descends distally for more than 60 percent of the length of the bone, which was also noted by Radinsky (1966). A long deltopectoral crest is typical of climbing mammals (Gebo and Rose, 1993; Gebo and Sargis, 1994; Salton and Sargis, 2008) and is usually weak and short in terrestrial and cursorial taxa (Penkrot et al., 2008; Salton and Sargis, 2008). A different, much more robust type of deltopectoral crest is found in fossorial mammals, such as palaeanodonts, *Ernanodon*, and

TABLE *1*—Upper tooth measurements (in mm) of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20494.

	Tooth (Side)													
	C1		P2		P3		P4		M1		M2		M3	
	R	L	R	L	R	L	R	L	R	L	R	L	R	L
Length	4.0	4.1	—	6.0	5.9	6.1	6.0	6.1	6.6	6.9	7.1	7.1	5.5	5.7
Width	3.0	3.1	—	4.8	5.9	6.0	7.8	7.5	8.9	8.5	9.1	9.4	7.8	7.5

TABLE 2—Lower tooth measurements (in mm) of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20494.

Tooth	Length	Trigonid width	Talonid width
Rc1	3.2	2.9	—
Rp1	3.0	2.1	—
Rp2	5.7	3.0	—
Rp3	6.2	4.3	—
Rm1	7.0	6.5	—
Rm2	7.8	7.0	6.8
Rm3	8.2	4.8	4.0
Lc1	3.1	3.0	—
Lp2	5.7	3.1	—
Lp3	6.0	—	—
Lm1	8.0	6.2	6.4
Lm2	8.1	—	6.7
Lm3	7.3	6.0	5.1

large arctocyonids (Rose and Emry, 1983, 1993; Ding, 1985; Rose et al., 1992; Kondrashov and Agadjanian, 2005; personal observations).

The distal portion of the humerus is wider mediolaterally than in other phenacodontids (Cope, 1884a; Osborn, 1898; Thewissen, 1990; Rose, 1996a, 2001). The lateral supracondylar ridge is well pronounced, but short. It is weaker than in climbing mammals but more pronounced than in cursorial mammals in our collection and resembles that of terrestrial tenrecs (Salton and Sargis, 2008). The medial epicondyle is moderately developed and does not project as far medially as in most climbing mammals (Emry and Thorington, 1982; Argot, 2001; Sargis, 2002a; Salton and Sargis, 2008), but is larger than in *Phenacodus* and early perissodactyls (Radinsky, 1966). Although the entepicondylar foramen is partially filled with matrix, it is easy to trace it on both the anterior and posterior sides of the humerus. It is large and faces posterodorsally. The entepicondylar foramen is usually reduced in mammals with terrestrial and especially cursorial adaptations (Reed, 1951; Salton and Sargis, 2008; personal data). The capitulum is hemispherical in shape, providing more mobility in the joint by allowing the radius to rotate more freely (Szalay and Dagosto, 1980; Rose, 1988; Sargis, 2002a), which is more typical of mammals with climbing adaptations. In terrestrial and cursorial taxa, the capitulum is spool-shaped in order to restrict motion to the parasagittal plane. On the other hand, the trochlea is mediolaterally narrow and continuous with the capitulum, bringing the ulna and radius closer together and restricting the range of motion this way, more like in terrestrial taxa (Gebo and Sargis, 1994; Argot, 2001; Sargis, 2002a; Salton and Sargis, 2008). Both the radial and olecranon fossae are rather deep, but the presence or absence of the supratrochlear foramen cannot be established for certain. Usually the radial and olecranon fossae are shallow in mammals with adaptations for climbing (Salton and Sargis, 2008).

Humerus measurements (in mm).—Right humerus: length 75.6; maximum proximal width 17.0; diameter of the head (mediolateral) 11.4; diameter of the head (anteroposterior) 10.7; distal width 18.2; length of the deltopectoral crest 49.1; left humerus: maximum proximal width 18.6; diameter of the head (mediolateral) 11.5; diameter of the head (anteroposterior) 10.5; length of the deltopectoral crest 50.4.

Ulna.—The right ulna of NMMNH P-20949 is complete (Figs. 4, 5), and only part of the shaft of the left ulna was preserved in natural articulation with the left radius shaft. The ulna is laterally compressed and slightly bowed posteriorly. The olecranon is well developed, long, tall, straight, and slightly curved medially, but not inclined anteriorly, which is different from the condition seen in climbing mammals, where the olecranon is both reduced and inclined anteriorly, and corresponds closely to the condition seen in terrestrial taxa (Taylor, 1974; Van Valkenburg, 1987; Argot, 2001; Szalay and Sargis, 2001; Sargis, 2002a; Salton and Sargis, 2008). The olecranon/ulna index is 19%, which is typical for terrestrial mammals, but too high a value for climbing mammals (Verma, 1963; Sargis, 2002a; Salton and Sargis, 2008).

The olecranon is deeply excavated medially and bears a crest for the insertion of the triceps. There is a distinct crest on the lateral side of the olecranon, probably for the insertion of the m. tensor fasciae antebrachii, which apparently was very strong. The olecranon and proximal ulna are also important areas for the origin of the carpal and digital flexors, such as m. flexor carpi ulnaris, which originates on the medial olecranon and flexes the hand, and m. flexor digitorum profundus (ulnar head), which originates at the caudal proximal ulna. Both muscles are very important for providing a hand-grip in climbing mammals. Another interesting feature is the presence of a distinct groove on the lateral side of the ulna for the m. abductor pollicis longus, which manipulates the thumb, but there is no other evidence of the abducted pollex. The semilunar (or trochlear) notch is deep and long, but very narrow. The deeper semilunar notch is more typical of terrestrial rather than climbing mammals (Argot, 2001; Salton and Sargis, 2008). The long axis of the notch is 20–25° to the long axis of the bone, very similar to Eocene *Chriacus* (Rose, 1987). The anconeal process is taller than the coronoid process. The latter is not bifurcated and has a very small radial facet, which occupies the lateral surface of the coronoid process. The radial facet is smaller than in either climbing mammals (e.g., squirrels and *Bassariscus* Coues, 1887) or cursorial/terrestrial taxa (e.g., ungulates: personal data). The distal ulna is damaged, so the shape of the styloid process is difficult to judge.

Ulna measurements (in mm).—NMMNH P-20949, right ulna: length 71.9; mid-shaft diameter (mediolateral) 7.3; mid-shaft diameter (anteroposterior) 3.3; olecranon length 11.8.

Radius.—The distal two thirds of the right radius are preserved in natural articulation with the right ulna (Fig. 4), and half of the left distal radius, including the articular surface, is preserved. The radius is rather short compared to the humerus: the brachial index (radial length/humerus length) calculated based on the estimated radial length is ~0.7, which is almost identical to the brachial index in *Prolimnocyon* Matthew, 1915a (Gebo and Rose, 1993). Relatively shorter radii are typical of arboreal and scansorial taxa, whereas in cursorial mammals this index is much higher (Davis, 1964; Hildebrand and Goslow, 2002; Gebo and Rose, 1993), but short radii may also reflect the primitive condition. No radial head is preserved. The radius is slightly bowed posteriorly. The bone distinctly widens distally. The middle part of the shaft is round in cross-section, and the distal part is triangular in cross-section, keeled on the palmar surface. Having three prominent planes on the distal radius provides plenty of area for the attachment of m. pronator quadratus, similar to scansorial mammals (Gebo and Rose, 1993). The distal radius is not well preserved.

Radius measurements (in mm).—NMMNH P-20949, right radius: length (estimated) 53.0; mid-shaft diameter 4.1; NMMNH P-20949, left radius: mid-shaft diameter 4.3.

Manus.—Most of the elements of the right manus of NMMNH P-20949 are damaged and covered with matrix. Radinsky (1966) mentioned that the carpus of *Tetraclaenodon* is of 'alternating' type, which means that the scaphoid (os

TABLE *3*—Measurements (in mm) of the manus elements of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20494.

Bone of the manus	Length	Proximal width	Distal width
Right metacarpal II	28.0	—	—
Right metacarpal III	29.0	—	5.6
Right metacarpal IV	25.0	—	5.1
Left metacarpal IV	24.0	4.3	4.9
Left metacarpal V	—	3.9	—
Proximal phalanx of digit III	12.3	6.5	4.1
Proximal phalanx of digit II or IV	11.6	4.9	3.8
Middle phalanx of digit III	6.9	4.25	3.3

carpi radiale) partially rests on the capitatum (os carpi distale III), and the lunatum (os carpi intermedium) partially rests on the hamatum (os carpi distale IV). The carpus of later phenacodontids (e.g., large *Phenacodus*) is of serial type, which means that the scaphoid rests only on the trapezoid/ trapezium and the lunatum rests only on the capitatum (Radinsky, 1966). Metacarpals II–IV of NMMNH P-20949 are preserved in natural articulation, together with the broken and displaced distal portion of the fifth metacarpal (Fig. 4). Metacarpal III is most robust and is slightly longer than metacarpals II and IV (Table 3). The metacarpals slightly widen distally. The distal articular surfaces of the metacarpals expand onto dorsal and ventral sides. The metacarpals differ slightly in relative length from those in Eocene *Chriacus* (Rose, 1987). Metacarpal IV is relatively shorter in Eocene *Chriacus* (75% of the metacarpal III length) than in *Tetraclaenodon* (86% of the metacarpal III length). Both metacarpals I and V are smaller than metacarpals II–IV. The difference is not as drastic as in early perissodactyls, but the lateral elements of the forelimb still seem to be slightly reduced, possibly indicating terrestrial habits (Hopwood, 1947; Gambaryan, 1974).

A few isolated phalanges are associated with the skeleton. The proximal phalanx of the third digit has a concave proximal articular surface that is split ventrally by a deep fissure. The distal articular surface is saddle-shaped and mostly confined to the distal and ventral sides of the bone. The bone is excavated distally on both sides for ligament insertion. The middle phalanx of the third digit is more than half of the length of the proximal phalanx (Table 3). The proximal articular surface has two deep concavities; on the dorsal side there is a process overhanging the articular surface. The distal articular surface extends onto dorsal and ventral sides of the bone.

Pelvis.—The pelvis is heavily concreted, and the right innominate is almost completely covered by matrix. The left innominate is more exposed and allows some comparison. The iliac wing is wide and slightly concave laterally. The ischial spine is located anteriorly, dorsal to the posterior border of the acetabulum. The acetabular area is covered with intractable matrix and not available for study. The ischium is long and narrow and forms a flat tuberosity. The most caudal portion of the ischium is slightly curved ventrally. The pelvis is too fragmentary for detailed measurements.

Femur.—Both left and right femora of NMMNH P-20949 are preserved although partially concreted and crushed. The right femur is mostly exposed along its posterior side, and the left femur is mostly exposed along its anterior side (Fig. 6). The femur is long and robust with a rounded shaft and wide proximal and distal ends. The central axis of the head and neck of the femur is oriented at about 135° to the long axis of the shaft. The greater trochanter projects slightly more superiorly than the head, and it is wide and blunt. Because the skeleton belonged to a subadult individual, it is possible that the epiphysis of the greater trochanter has been lost, which could have contributed to its small size. The intertrochanteric fossa is deep, indicating strong development of the lateral rotators of the femur, such as mm. obturator externus et internus and mm. gemelli superior et inferior. The lesser trochanter is very well developed, triangular in shape, and projects more medially than posteriorly, indicating terrestrial or cursorial habits (Taylor, 1976; Gebo and Sargis, 1994; Heinrich and Rose, 1997; Szalay and Sargis, 2001; Sargis, 2002b). The extremely large, distally-placed third trochanter is located one third of the length of the bone from the proximal end, similar to *Phenacodus* and early perissodactyls. The enlarged third trochanter would increase the leverage of the attached muscles, including m. gluteus superficialis, which is a powerful extensor of the hip. Sargis (2002b) suggested that an enlarged third trochanter in some tupaiines could be an indication of powerful extension of the thigh during terrestrial running. The shaft is rounded in cross-section and slightly widens distally. The femur is straight and does not have the curvature seen in the femora of scansorial taxa (e.g., *Prolimnocyon* and *Thinocyon* Marsh, 1872) (Gebo and Rose, 1993; Morlo and Gunnell, 2003). Both femora are damaged distally, and articular surfaces are not preserved.

Femur measurements (in mm).—NMMNH P-20949, left femur: length 89.4; distance between the tip of the greater trochanter and middle of the third trochanter 32.6; maximum proximal diameter 23.2; diameter of the head (mediolateral) 11.0; diameter of the head (anteroposterior) 8.4; mid-shaft diameter 10; NMMNH P-20949, right femur: length 88.3; distance between the tip of the greater trochanter and middle of the third trochanter 34.3; maximum proximal diameter 24.0; diameter of the head (anteroposterior) 9.5; mid-shaft diameter 10.3.

Tibia.—Both tibiae are incompletely preserved in NMMNH P-20949. The left tibia is partially encased in a concretion and broken, and the right tibia is also partially covered with matrix, but most of its shaft is not in the concretion (Fig. 6). The tibia is rather long (the estimated crural index is ~101%), which is typical of terrestrial mammals (Gebo and Rose, 1993). The proximal articular surface is divided into two by a well-expressed intercondylar eminence. The lateral articular surface is slightly more elevated than the medial one, which indicates that the medial condyle of the femur projected farther distad than the lateral condyle and suggests that *Tetraclaenodon* possibly had knee valgus (was knock-kneed), although this cannot be confirmed by the femur morphology because both distal femora are badly damaged. The shaft of the bone is laterally compressed in its proximal part and becomes rounded in cross-section towards its distal end. The cnemial crest is well expressed and long. It extends to approximately 45 percent of the length of the bone. The distal portions of both tibiae are missing.

Tibia measurements (in mm).—NMMNH P-20949, left tibia: length (estimated) 90.0; maximum proximal diameter 18.9; cnemial crest length 41.0; NMMNH P-20949, right tibia: length (estimated) 89.0; maximum proximal diameter 19.0; cnemial crest length 39.0.

Fibula.—The partial left fibula, missing proximal and distal ends, was found associated with the tibia in the concretion. The right fibula is represented by a shaft fragment. The tibia and fibula are not fused. The shaft of the fibula is rounded in cross-section. The medial surface of the fibular shaft is flat, and the lateral surface is convex.

TABLE 4—Talus measurements (in mm) of *Tetraclaenodon puercensis* "*pliciferus*" (NMMNH P-20494) and *T. puercensis* "*puercensis*" (NMMNH P-48072, P-48360, and P-35059). Abbreviations: HD=head diameter (mediolateral); L=length; PCFL=length (anteroposterior) of the posterior calcaneus facet; PCFW=width (mediolateral) of the posterior calcaneus facet; SL=length (anteroposterior) of the sustentacular facet; SW=width (mediolateral) of the sustentacular facet; TW=trochlea width; W=width.

Specimen no.	Side	L	W	HD	TW	PCFW	PCFL	SW	SL
NMMNH P-20494	Right	14.9	12.7	9.3	7.9	8.3	4.6	5.1	5.8
NMMNH P-20494	Left	15.0	12.2	9.5	7.8	7.9	4.4	—	—
NMMNH P-48072	Right	17.7	14.5	—	9.3	9.2	4.5	6.1	6.8
NMMNH P-48360	Left	17.6	14.1	9.8	8.9	9.9	5.1	6.1	6.7
NMMNH P-35059	Left	16.8	15.8	9.2	9.3	9.7	5.0	5.9	7.1

Fibula measurements (in mm).—NMMNH P-20949, left fibula: mid-shaft diameter 4.7; NMMNH P-20949, right fibula: mid-shaft diameter 4.5.

Talus.—Both tali of NMMNH P-20949 are preserved: the right is complete (Fig. 7), and the left is incomplete. The overall shape of the talus (=astragalus) resembles that of terrestrial and scansorial mammals; it is not long-necked as in arboreal taxa (Polly, 2008). The overall shape corresponds to either a semidigitigrade or a digitigrade stance (Polly, 2008), as the astragalus has a short neck. The talus is very similar to the corresponding bone of other phenacodontids, even such specialized ones as *Meniscotherium* Cope, 1874 (Williamson and Lucas, 1992), in the shape of the fibular facet. It is also similar to the talus assigned by Szalay and Lucas (1996) to Paleocene *Chriacus*.

The trochlea is cylindrical and tall. It is deeper than in specialized scansorial and arboreal forms (except for specialized leapers), but shallower than in specialized cursors. The trochlea extends onto the posterior (proximal) surface of the talus, a feature associated with cursorial adaptations (Penkrot et al., 2008), although it also occurs in arboreal sciurids (personal observation). Both lateral and medial rims are about the same height and diverge slightly. The medial wall of the trochlea is rather steep, whereas the lateral wall slopes rather gently and forms a laterally-projecting flange—a feature also found in the talus of other phenacodontids (personal observations), *Meniscotherium* (Williamson and Lucas, 1992), and to a much lesser extent in *Protungulatum* Sloan and Van Valen, 1965 (Szalay, 1977). The flange has a distinct dorsal articular surface for articulation with the fibula. This feature was not observed in other archaic ungulates, such as *Arctocyon* Blainville, 1841 or Paleocene and Eocene *Chriacus*, or any of the studied scansorial, terrestrial, or cursorial carnivores or sciurids (personal data).

The curvature of the lateral rim is slightly greater than that of the medial rim. The head is ellipsoidal in shape and is slightly compressed dorsoventrally. It is much wider than the neck. There is a facet on the lateral side of the head for articulation with the cuboid. The neck is oriented at about 45° to the long axis of the trochlea. The articular surface of the head is rather convex, similar to the Paleocene and Eocene *Chriacus* (Rose, 1987; Szalay and Lucas, 1996). The sulcus tali is well expressed. The posterior calcaneoastragalar (ectal) facet is elongated transversely and concave, similar to *Meniscotherium* (Williamson and Lucas, 1992). It is separated from the sustentacular facet by a deep groove. The sustentacular facet is rather large, more like that of scansorial taxa (Polly, 2008) and has a rounded outline; it is very gently convex. The talar canal does not seem to be present, although the very hard nature of the matrix, which has the same color and consistency as the bone, could obscure the existing canal. If present, the canal is greatly reduced. The shape of the two calcaneal facets closely resembles the morphology described for other phenacodontids, *Meniscotherium*, and Paleocene *Chriacus* (Thewissen, 1990; Williamson and Lucas, 1992; Szalay and Lucas, 1996). See Table 4 for measurements.

Calcaneus.—The complete right calcaneus is preserved with NMMNH P-20949. The calcaneus is robust, and the tuber calcanei is rather long and slightly compressed laterally (Fig. 7), similar to terrestrial or cursorial taxa (Heinrich and Rose, 1997; Hildebrand and Goslow, 2002). The peroneal tubercle is very well pronounced and located farther distally than the cuboid facet, similar to other phenacodontids (Thewissen, 1990; Williamson and Lucas, 1992; Rose, 1996a). A distally placed peroneal tubercle is typically associated with terrestrial or cursorial locomotion, while in climbing mammals, such as *Potos* Geoffroy, Saint-Hilaire, and Cuvier, 1795, *Nasua* Storr, 1780, and *Nandinia* Gray, 1830, the peroneal tubercle is more proximally positioned (Heinrich and Rose, 1997). The cuboid facet is at a 45° angle to the rest of the bone. It is rectangular in shape and is very slightly concave dorsoventrally, as in *Ectocion* and *Phenacodus*. The posterior facet for the articulation with the body of the talus and distal fibula has a rounded outline. The sustentaculum is triangular in shape and projects far medially. The plantar tuberosity is very well expressed. Overall, the calcaneal morphology is very similar to that of other phenacodontids in the general shape, position of the peroneal tubercle, and shape of the sustentacular and talar facets. See Table 5 for measurements.

Cuboid.—The complete right cuboid is preserved with NMMNH P-20949. The cuboid is cylindrical in shape (Fig. 7). The calcaneal facet is oblique and very gently convex, similar to other phenacodontids. This facet is more strongly convex and helical in Eocene *Chriacus*. Overall, the calcaneocuboid joint was rather stable and allowed little mobility. The plantar groove for the m. peroneus longus is deep. The talar facet is very narrow and expands slightly towards the plantar side. There is a large, rounded plantar tubercle on the plantar side.

TABLE 5—Calcaneus measurements (in mm) of *Tetraclaenodon puercensis* "*pliciferus*" (NMMNH P-20494) and *T. puercensis* "*puercensis*" (NMMNH P-15742 and P-35059). Abbreviations: CFH=cuboid facet height; CFL=cuboid facet width; L=length; MDW=maximum distal width; SW=sustentaculum width; TH=tuber height; TL=tuber length; TW=tuber width.

Specimen no.	L	MDW	TL	TW	TH	SW	CFL	CFH
NMMNH P-20494	26.2	12.6	13.0	5.1	7.9	6.3	13.7	6.2
NMMNH P-15742	33.4	—	18.1	9.2	10.1	7.4	14.1	6.8
NMMNH P-35059	31.7	—	17.8	8.9	9.4	—	13.5	6.8

TABLE 6—Measurements (in mm) of the elements of the pes of *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20494.

Bone of the pes	Length	Proximal width	Distal width
Right metatarsal II	—	—	6.6
Right metatarsal III	—	—	6.9
Right metatarsal IV	—	—	5.8
Proximal phalanx of digit 3	16.5	7.0	5.8
Proximal phalanx of digit 4	13.9	5.9	4.1
Middle phalanx of digit 3	8.9	5.3	3.9
Ungual phalanx of digit ?4	6.4	3.5	2.6

TABLE 7—Body mass estimates for *Tetraclaenodon puercensis* "*pliciferus,*" NMMNH P-20494 in grams.

Bone	Body mass
Humerus (length)	2,931.2
Humerus (circumference)	4,009.7
Ulna	2,857.4
Radius	3,244.8
m1 area	14,244.5

Measurements (in mm).—NMMNH P-20949, right cuboid: length 9.6; width 7.1.

Navicular.—The bone is proximodistally compressed, concave proximally, and slightly convex distally (Fig. 7). The articular facet for the talar head is dorsoventrally elongated and distinctly concave. There is a large, triangular plantar process. The articular surfaces for the third and fourth metacarpals are separated by a sharp ridge but there is no depression between these two surfaces. Another more flattened ridge separates the facet for the fourth metacarpal from the facet for the fifth metacarpal.

Navicular measurements (in mm).—NMMNH P-20949, right navicular: width 11.9; NMMNH P-20949, left navicular: width 11.55; length 5.82; depth 9.7.

Metatarsals and phalanges.—Three metatarsals (II–IV) are preserved in one block with a proximal phalanx, middle phalanx, and an ungual phalanx (Fig. 7). Metatarsals II and IV are about the same size, while metatarsal III is larger (Table 6). Distal sagittal crests are well expressed. The metatarsals are larger and more robust than the metacarpals. The proximal phalanx of the third digit of the foot is larger than any phalanges of the forelimb. The morphology of the phalanges of the pes is very similar to that described for the manus. The only preserved ungual phalanx is rounded distally and flattened dorsoventrally in its distal part, but laterally compressed in its proximal part. The phalanx is sharply keeled ventrally, with a very large flexor tubercle on the plantar side. The ungual phalanx is intermediate in morphology between a claw-like and a hoof-like phalanx.

ESTIMATED BODY MASS

We estimated the body mass of NMMNH P-20949 *Tetraclaenodon* to be ~3.2 kg based on the humeral, radial, and ulnar measurements (Table 7) using equations by Roth (1990) and Scott (1990). This means that *Tetraclaenodon* was heavier than the average domestic cat, and intermediate in weight between a rock hyrax and a mouse-deer. The estimated body mass varied between 2.9 and 4.0 kg depending on the measurement taken, which is very close to the range calculated by Gingerich (1990) for *Copecion brachypternus* (Cope, 1882d), another phenacodontid, which was similar in size to *Tetraclaenodon* (humeral length 75.6 in *Tetraclaenodon puercensis* and 80.6 in *Copecion brachypternus*). The estimated body mass for *Copecion brachypternus* varied between 2.4–3.8 kg with an average of 3.15 kg (Gingerich, 1990). The prediction of body mass by using dental measurements gave a much higher estimate of ~14 kg for *Tetraclaenodon*, which was also the case for *Ectocion*, where the body mass estimated from tooth measurements was twice the body mass estimated from long bone dimensions, possibly indicating that these early ungulates had relatively large teeth for their body mass (Gingerich, 1990).

MORPHO-FUNCTIONAL ANALYSIS

Vertebral column.—The number of thoracic vertebrae has recently been discussed in placental mammal systematics (Sánchez-Villagra et al., 2007). Unfortunately, this character is difficult to assess in *Tetraclaenodon,* as thoracic portions of the vertebral columns of NMMNH P-20949 and AMNH 2468 are rather poorly preserved. AMNH 2468 provides some information about the caudal vertebrae, which indicate that *Tetraclaenodon* had a long tail. A long tail (18 caudals preserved in AMNH 2468, one through eight with neural arches; Osborn, 1898) is more typical of arboreal and scansorial mammals, where it is either used for balancing or as a prehensile organ (Jenkins and Krause, 1983; Rose, 1987) but could simply represent a plesiomorphic condition. Kielan-Jaworowska and Gambaryan (1994) argued that a long tail can be used for fast terrestrial locomotion.

Forelimb.—The humeral morphology of *Tetraclaenodon* on one hand resembles terrestrial taxa, but on the other shows adaptations found in climbing mammals, such as a strong deltopectoral crest, low greater tubercle, well-developed lesser tubercle, well-developed lateral supracondylar crest, and hemispherical capitulum. Adaptations for cursorial locomotion usually involve the opposite traits, such as a tall, superiorly-projecting greater tubercle, reduced lesser tubercle, short deltopectoral crest, distally narrow humerus with undeveloped medial epicondyle, weak lateral supracondylar crest, and a laterally compressed (crest-like) capitulum. The scansorial adaptations, though, are very weakly expressed in the *Tetraclaenodon* humerus. Judging from the humeral morphology, *Tetraclaenodon* was a terrestrial mammal that could climb trees to seek food or to avoid predators.

The ulna resembles that of terrestrial tenrecs, such as *Setifer* Froriep, 1806 and *Tenrec* Lacépède, 1799, in the overall shape and orientation of the olecranon (Salton and Sargis, 2008). The shape of the semilunar notch, the lateral position of the radial notch, and the presence of a sharp keel on the distal radius, though, resemble morphology seen in some scansorial carnivores. There is a slight reduction of the lateral metacarpals of the forelimb of *Tetraclaenodon*, which is more indicative of a terrestrial lifestyle, but it is much less expressed than in other phenacodontids and early perissodactyls.

Hind limb.—The hind limb of *Tetraclaenodon* resembles that of terrestrial mammals. The *Tetraclaenodon* femur has a very well-developed, distally-located third trochanter. The third trochanter is also well developed in all phenacodontids and in early perissodactyls (Radinsky, 1965, 1966; Rose, 1996a) and we consider it as one of the synapomorphies of these two groups. The third trochanter increases in size in the lineage *Tetraclaenodon–Phenacodus–Hyracotherium*, which helps to identify the polarity of this character (Radinsky, 1966). This means that a small third trochanter indicates the plesiomorphic condition. The third trochanter is also enlarged in some other archaic ungulates (e.g., *Hyopsodus* Leidy, 1870) and apheliscids (*Apheliscus* Cope, 1875 and *Haplomylus* Matthew, 1915b), but has a different shape. It is either lower or more proximally placed than in Phenacodontidae and Perissodactyla. The shape and size of the third trochanter vary significantly between different mammalian taxa with the same type of locomotion, which may indicate that it is a more meaningful character for phylogenetic analysis. The third trochanter is poorly developed in either cursorial or scansorial/arboreal carnivores, but is well developed in modern squirrels (Gebo and Rose, 1993; Heinrich and Rose, 1997; Rose and Chinnery, 2004; Heinrich and Houde, 2006). It is enlarged in early perissodactyls but weak in cursorial artiodactyls (Rose, 1985, 1996b). The enlarged lesser trochanter provides evidence of a well-developed m. iliopsoas, which is a powerful protractor of the hind limb (especially its m. iliacus portion). The high estimated crural index of *Tetraclaenodon* (~100%) is more typical of terrestrial mammals.

The talus has a primitive morphology, with a shallow trochlea and talar-cuboid contact (Schaeffer, 1947; Szalay and Decker, 1974). The talar trochlea of *Tetraclaenodon* is deeper than in typical scansorial mammals, but shallower than in specialized cursorial mammals. The talus of *Tetraclaenodon* is very similar to the corresponding bone of other phenacodontids and some other archaic ungulates in having a separate fibular facet. The calcaneus is very similar to other phenacodontids and exhibits some primitive characters, such as a distally-placed peroneal tubercle and oblique cuboid facet, found in other archaic ungulates (*Protungulatum*: Szalay and Decker, 1974). The calcanei of early perissodactyls differ from those of *Tetraclaenodon* in having a very weak and slightly more proximally placed peroneal tubercle (Rose, 1996a). Overall, the ankle contains a mixture of archaic features found in terrestrial mammals.

Tetraclaenodon shows some reduction in the size of lateral metatarsals and phalanges of the hind limb, but to a much lesser degree than in other phenacodontids and early perissodactyls. The ungual phalanges of *Tetraclaenodon* are different from either the claw-like ungual phalanges found, for example, in arctocyonids, such as *Chriacus* and *Arctocyon* (personal observations), or the flattened hoof-like phalanges of other phenacodontids or perissodactyls, and are more similar to the narrower hooves of early artiodactyls (Rose, 1985). The presence of hooves instead of claws in *Tetraclaenodon* is consistent with terrestrial habits.

COMPARISON WITH OTHER PHENACODONTIDS

The postcrania of *Tetraclaenodon* show multiple similarities to other phenacodontids, especially in the hind limb morphology, but differ somewhat in the forelimb morphology in lacking derived cursorial traits, which was also mentioned by Radinsky (1966).

Phenacodus.—Cope (1884a) gave detailed descriptions and illustrated postcrania of *Phenacodus primaevus* Cope, 1873. Rose (1996a, 2001) briefly discussed some postcranial features of *Phenacodus*. The humerus of *Phenacodus* exhibits distinct cursorial adaptations, such as a very tall greater tubercle that projects much farther superiorly than the humeral head. The deltoid tuberosity is not as strong as in *Tetraclaenodon*. The distal humerus is much narrower than in *Tetraclaenodon*, the lateral supracondylar crest is weakly developed, and the supratrochlear foramen is present, which are definitive cursorial traits. The manus and pes show more pronounced reduction of the side digits than in *Tetraclaenodon*.

The calcaneus of *Phenacodus* is similar to *Tetraclaenodon* in having an oblique cuboid facet and in the distal placement of the peroneal tubercle, although the latter is not as well developed as in *Tetraclaenodon*. The cuboid is more square in *Phenacodus*, and the navicular is more flattened. The ungual phalanges of *Phenacodus* are extremely wide and more hoof-like compared to the narrower ungual phalanges of *Tetraclaenodon*.

Copecion.—The postcranial anatomy of *Copecion* was briefly described by Thewissen (1990). The humerus of *Copecion* is slightly bowed, similar to *Tetraclaenodon*, but not as much as in the latter. The greater tubercle is better developed in *Copecion* than in *Tetraclaenodon*, reflecting more cursorial adaptations of the former. The distal humerus is narrower and has a supratrochlear foramen, which is also an indication of cursoriality in *Copecion*. The *Copecion* ulna is different from *Tetraclaenodon* in having a short and straight olecranon. The femoral morphology is similar in *Tetraclaenodon* and *Copecion*, but the latter has a much smaller lesser trochanter. The greater and third trochanters are similarly developed in these two genera. The *Copecion* talus is similar to that of *Tetraclaenodon* in general shape, in having the posterior facet oriented mediolaterally, and in having a rounded sustentacular facet. The calcanei of both forms are also similar in the shape of the sustentaculum, in the proximal placement of the peroneal tubercle, and in the oblique cuboid articular surface.

Meniscotherium.—The humerus of *Meniscotherium* is distinctly adapted for cursorial locomotion and is quite different from *Tetraclaenodon*; it has a very tall greater tubercle that projects much farther superiorly than the corresponding structure of *Tetraclaenodon* (Gazin, 1965; Williamson and Lucas, 1992). The distal humerus is much narrower with a well-expressed supratrochlear foramen. The hind limb morphology is more similar between the two genera, especially in the tarsus. The tali of the two genera are similar in the shape of the fibular and sustentacular facets and in the shape of the head and the angle of the neck. The calcanei of both forms are also similar in the shape of the sustentaculum, in the placement and shape of the peroneal tubercle, and in the oblique cuboid facet.

COMPARISON WITH EARLY PERISSODACTYLS

The postcrania of *Tetraclaenodon* differ from the postcranial skeleton of early perissodactyls in lacking the derived cursorial adaptations. Radinsky (1965) and Rose (1996) provided descriptions of early tapiroid postcranial material, which allows comparison with *Tetraclaenodon*.

Forelimb.—Tapiroid humeri are characterized by a very large greater tubercle that projects much farther superiorly than the head, a trait usually associated with cursoriality. Distally, the tapiroid humerus is rather narrow, with very weak lateral and medial epicondyles and a very weak lateral supracondylar crest. The supratrochlear foramen is present in all early tapiroids. Ulna has a posteriorly inflected olecranon, and the long axis of the semilunar notch is almost parallel to the long axis of the bone. The radius is very robust, with a well-expressed styloid process. According to Radinsky (1965), there is no evidence of the first metacarpal in *Heptodon* Cope, 1882c, although it may be present in *Homogalax* Hay, 1899 (Rose, 1996a). The fifth metacarpal is much reduced. The ungual phalanges are extremely wide and hoof-like. Most of these characters are in a plesiomorphic state in *Tetraclaenodon*.

Hind limb.—The femora of *Heptodon* and *Homogalax* are different from *Tetraclaenodon* in having a deeper patellar groove, large and posteriorly projecting condyles, very tall greater trochanter, and less obtuse angle between the neck and the body of the bone. The most distinctive similarity is the large third trochanter in all phenacodontids and early perissodactyls (Radinsky, 1965; Thewissen, 1990; Rose,

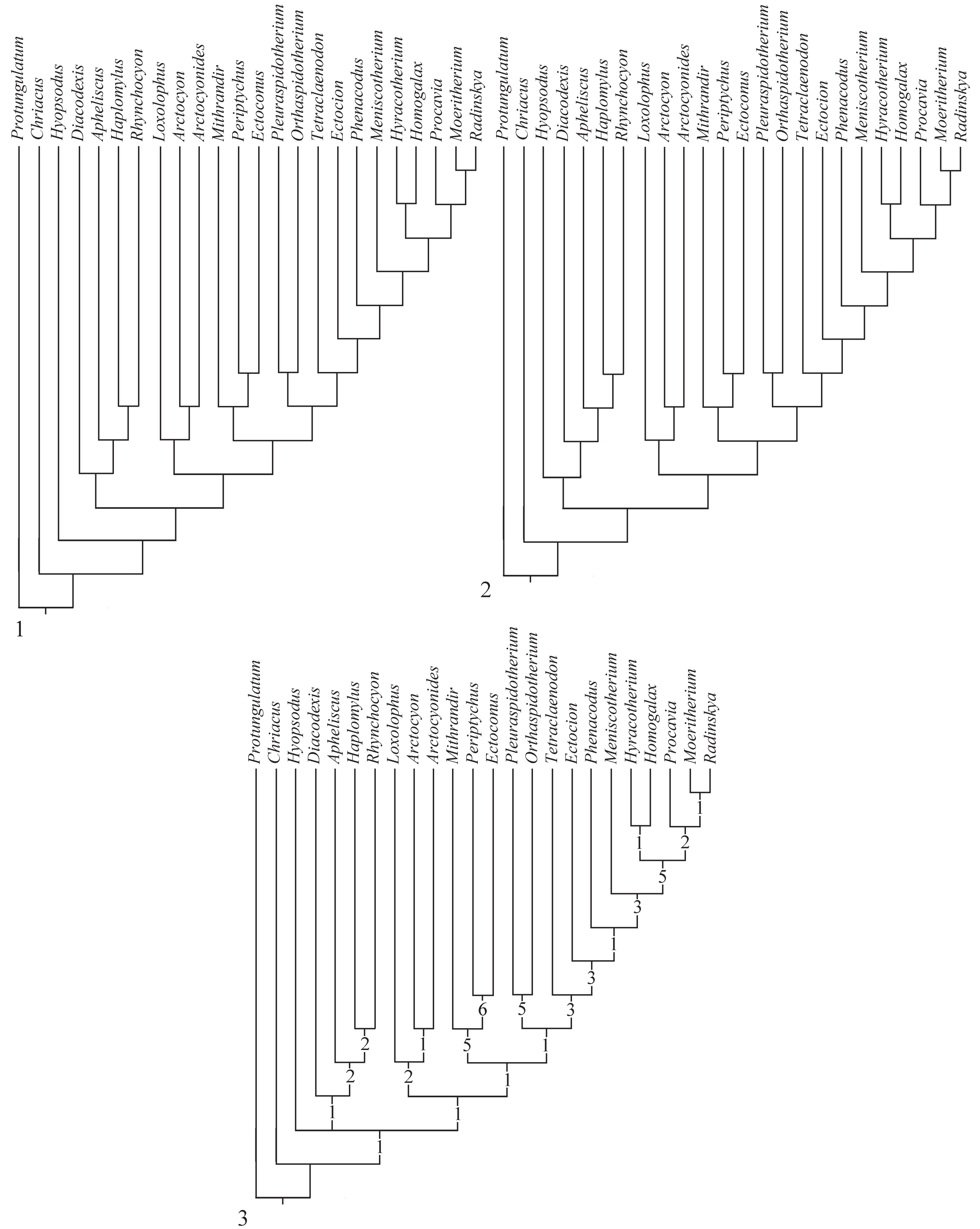

FIGURE 8—Results of the phylogenetic analysis of 86 characters in 24 taxa: *1*, *2*, two most parsimonious trees (tree length=323 steps); *3*, strict consensus of the two most parsimonious trees with branch support values.

1996a). The peroneal tubercle of *Tetraclaenodon* is much better developed than the corresponding structure in *Homogalax* and other early perissodactyls (Rose, 1996a). The ungual phalanges are wide and hoof-like in all early perissodactyls.

PHYLOGENETIC ANALYSIS

The importance of the family Phenacodontidae in the origin of modern groups of ungulates has been well recognized (Radinsky, 1966; Thewissen and Domning, 1992; Janis et al., 1998). *Tetraclaenodon*, as the most primitive and oldest member of Phenacodontidae, is very important for understanding the phylogenetic relationships both within the family and with other groups of ungulates. In our analysis, we focused on three main aspects of phenacodontid relationships: 1) within the family Phenacodontidae; 2) between phenacodontids and other archaic ungulates; and 3) between phenacodontids and early perissodactyls, artiodactyls, hyraxes, prosobscideans, and macroscelideans. Unfortunately, very few archaic ungulates are known from their postcranial skeleton, so our selection of 'condylarths' was rather limited. For this reason, many of the analyses of relationships of archaic ungulates are either limited to dental characters (Tabuce et al., 2001) or to dental and ankle characters (Zack et al., 2005; Tabuce et al., 2007). Despite the very scarce information about the postcrania of archaic ungulates, we were able to include representatives of five "condylarth" families in our analysis: Arctocyonidae, Periptychidae, Hyopsodontidae, Pleuraspidotheriidae, and Phenacodontidae. We chose *Homogalax* and *Hyracotherium* Owen, 1841 as examples of early perissodactyls, *Diacodexis* Cope, 1882c as an early artiodactyl, *Procavia* Storr, 1780 as a hyracoid, *Moeritheium* Andrews, 1901 as a representative of early proboscideans, and *Rhynchocyon* Peters, 1847 as an elephant shrew. We included *Radinskya* in our analysis as it was considered by some to be close to the perissodactyl ancestry (McKenna et al., 1989; Beard, 1998), although the dataset for this taxon is only limited to the upper dentition and few cranial characters. We used *Protungulatum* as an outgroup.

Cladistic analysis of 86 characters in 24 taxa produced two most parsimonious trees with the tree length of 323 steps. The two most parsimonious trees and a strict consensus tree are shown in Figure 8. The phylogenetic analysis strongly supported the concept of Altungulata Prothero and Schoch, 1989 (see also Fischer and Tassy, 1993; McKenna and Bell, 1998; Shoshani and McKenna, 1998; Gheerbrant et al., 2005; Rose, 2006), which in our analysis included Perissodactyla + Hyracoidea + Proboscidea + *Radinskya* (branch support=5). Phenacodontids formed a series of sister taxa to Altungulata with *Tetraclaenodon* being the basal-most member of the clade "Phenacodontidae" + Altungulata (branch support=3), which is very similar to the resulting cladogram from the analysis by Janis et al. (1998) and Archibald (1998), who termed the taxon "Phenacodontidae" + Altungulata as Paenungulata. Thus, our analysis did not support either Afrotheria or Laurasiatheria as defined by molecular studies but the results were consistent with other morphological analyses (Shoshani and McKenna, 1998; Springer et al., 2004; Zack et al., 2005; Penkrot et al., 2008).

Within Altungualta *Radinskya* showed closest affinities to *Moeritherium* and not to perissodactyls, which supports the idea that *Radinskya* is a phenacolophid embrithopod and thus a tethythere (Hooker and Dashzeveg, 2003; Hooker, 2005). *Procavia* showed close affinities to *Moeritherium* and *Radinskya* confirming the monophyletic Tethytheria, which is "the best supported monophyletic grouping among the ungulates" (Gheerbrant et al, 2005, p. 98). Tethytheria is supported by both molecular and morphological data (Kondrashov, 1998; Springer et al., 2004; Sánchez-Villagra et al., 2007; Tabuce et al., 2007; Asher and Lehman, 2008; Tabuce et al., 2008).

Pleuraspidotheriidae (*Pleuraspidotherium* Lemoine, 1878 and *Orthaspidotherium* Lemoine, 1885), Arctocyonidae (*Loxolophus* Cope, 1885, *Arctocyonides* Lemoine, 1891, and *Arctocyon*, but not *Chriacus*), and Periptychidae (*Ectoconus* Cope, 1884b, *Periptychus* Cope, 1881b, and *Mithrandir* Van Valen, 1978) each formed well-supported clades that are loosely associated (weak branch supports of 1) with the Altungulata + phenacodontids clade.

Rhynchocyon, Haplomylus, and *Apheliscus* formed a monophyletic group (branch support=2), which is consistent with the analyses presented by Zack et al. (2005), Penkrot et al. (2008), and Tabuce et al. (2007). This further supports the idea that *Haplomylus* and *Apheliscus* should be excluded from Hyopsodontidae, as *Hyopsodus* did not show close affinities to either of them. The analysis of early artiodactyl relationships is beyond the scope of this paper, although it is worth noting that *Diacodexis* did not show close affinities to Arctocyonidae as has been suggested by some researchers (e.g., Rose, 1996b) and formed a sister group to the macroscelidean clade.

CONCLUSIONS

The skeleton of *Tetraclaenodon* described here belonged to a lightly built animal with strong forelimbs and hind limbs and a body mass just over 3 kg. The postcranial anatomy of *Tetraclaenodon* includes a mixture of archaic characters that indicate a mostly terrestrial lifestyle. Some of the features of the forelimb do not exclude the possibility of *Tetraclaenodon* being able to climb trees. *Tetraclaenodon* probably spent most of the time on the ground but could use trees to avoid predators. The mixture of characters reflects the archaic nature of the taxon and its position as the oldest member of "Phenacodontidae." Such mixed adaptations, for example, were identified in an archaic erinaceomorph insectivore *Zinodon* Dunn and Rasmussen, 2009 from the early Eocene of Utah, which was reconstructed as a terrestrial mammal that could also climb and probably dig. Our cladistic analysis did not recover monophyletic "Phenacodontidae," instead phenacodontids formed a series of sister taxa to the Altungulata clade. *Tetraclaenodon* is the basal-most member of the well supported "Phenacodontidae" + Altungulata clade.

ACKNOWLEDGMENTS

The work of PK was partially supported by Russian Basic Research Foundation, project 08-04-00483-a, by the program "Historical Dynamics of Biological Resources and Importance of Their Conservation and Use," and by the program "Origin and Evolution of the Biosphere." We thank R. J. Asher, J. J. Hooker, L. T. Holbrook, K. D. Rose, and M. T. Silcox for comments and suggestions that helped to improve the manuscript and K. Rogers for help with photographs. P. Sealey discovered the skeleton of *Tetraclaenodon* described here.

REFERENCES

Andrews, C. W. 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt. Geological Magazine, 8:400–436.

Archibald, J. D. 1998. Archaic ungulates (Condylarthra), p. 292–331. *In* C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Vol. 1: Terrestrial Carnivores, Ungulates and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Argot, C. 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials

Mayulestes ferox and *Pucadelphys andinus*. Journal of Morphology, 247:51–79.

Argot, C. 2002. Functional-adaptive analysis of the hindlimb anatomy of extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. Journal of Morphology, 253:76–108.

Asher, R. J. 2007. A database of morphological characters and a combined-data reanalysis of placental mammal phylogeny. BMC (BioMed Central) Evolutionary Biology, 7:108.

Asher, R. J. and T. Lehmann. 2008. Dental eruption in Afrotherian mammals. BMC (BioMed Central) Evolutionary Biology, 6:14.

Asher, R. J., M. J. Novacek, and J. H. Geisler. 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. Journal of Mammalian Evolution, 10:131–194.

Barnosky, A. D. 1982. Locomotion in moles (Insectivora, Proscalopidae) from the middle Tertiary of North America. Science, 216:183–185.

Beard, K. C. 1991. Vertical postures and climbing in the morphotype of Primatomorpha: implications for locomotor evolution in primate history, p. 79–87. *In* Y. Coppens and B. Senut (eds.), Origines de la Bipédie chez les Hominidés. Editions du CNRS (Centre national de la recherche scientifique) (Cahiers de Paléoanthropologie), Paris.

Beard, K. C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. Bulletin of the Carnegie Museum of Natural History, 34:5–39.

Blainville, H. M. 1841. Ostéographie et description iconographique des Mammifères récentes et fossiles (Carnivores). Vol. I, II. Paris. 446 p.

Cifelli, R. L. 1983. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). American Museum Novitates, 2772:1–49.

Cope, E. D. 1873. On some Eocene mammals, obtained by Hayden's Geological survey of 1872. Paleontological Bulletin, 17:1–6.

Cope, E. D. 1874. Report upon vertebrate fossils, discovered in New Mexico, with description of new species, p. 588–606. *In* Appendix FF3, Annual Report of the Chief of Engineers, 1874. U.S. Government Printing Office, Washington, D.C.

Cope, E. D. 1875. Systematic catalogue of Vertebrata of the Eocene of New Mexico, collected in 1874. Geographic Explorations and Surveys west of the 100th meridian, G. M. Wheeler, Corps of Engineers, U.S. Army, Washington, 4:37–282.

Cope, E. D. 1881a. On some Mammalia from the lowest Eocene beds of New Mexico. Proceedings of the American Philosophic Society, 19:484–495.

Cope, E. D. 1881b. Mammalia of the lower Eocene beds. American Naturalist, 15:337–338.

Cope, E. D. 1882a. Notes of Eocene Mammalia. American Naturalist, 16:522.

Cope, E. D. 1882b. Some new forms of the Puerco Eocene. American Naturalist, 16:833–834.

Cope, E. D. 1882c. Two new genera of Mammalia from the Wasatch Eocene. American Naturalist, 16:1029.

Cope, E. D. 1882d. Contribution to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. Proceedings of the American Philosophic Society, 20:139–197.

Cope, E. D. 1884a. The Vertebrata of the Tertiary formations of the West. Report of the United States Geological Survey of the West, 1009 p.

Cope, E. D. 1884b. The Condylarthra. American Naturalist, 18:790–805; 892–906.

Cope, E. D. 1885. The oldest Tertiary Mammalia. American Naturalist, 19:385–387.

Coues, E. 1887. *Bassariscus*, a new generic name in mammalogy. Science, 9:516.

Court, N. 1995. A new species of *Numidotherium* (Mammalia, Proboscidea) from the Eocene of Libya and the early phylogeny of the Proboscidea. Journal of Vertebrate Paleontology, 15:650–671.

Davis, D. D. 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana Zoology Memoirs, 3:1–339.

Delmer, C., M. Mahboubi, R. Tabuce, and P. Tassy. 2006. A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: new perspectives on the ancestral morphotype of the genus. Palaeontology, 49:421–434.

Ding, S. 1985. A Paleocene edentate from Nanxiong basin, Guangdong. Paleontologia Sinica, 24:1–118.

Dunn, R. H. and D. T. Rasmussen. 2009. Skeletal Morphology of a new genus of Eocene insectivore (Mammalia, Erinaceomorpha) from Utah. Journal of Mammalogy, 90:321–331.

Earle, C. 1893. On the systematic position of the genus *Protogonodon*. American Naturalist, 27:377–379.

Emry, R. J. and R. W. Thorington. 1982. Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia, Sciuridae). Smithsonian Contributions to Paleobiology, 47:1–35.

Fischer, M. S. and P. Tassy. 1993. The interrelation between Proboscidea, Sirenia, Hyracoidea, and Mesaxonia, p. 217–234. *In* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny. Placentals. Springer-Verlag, New York.

Froehlich, D. J. 2002. Quo vadis eohippus? The systematics and taxonomy of the early Eocene equids (Perissodactyla). Zoological Journal of the Linnaean Society, 134:141–156.

Froriep, L. F. 1806. C. Dumeril's Analytische Zoologie. Aus dem Französischen mit Zusätzen. Landes-Industrie-Comptoir, Weimar, 344 p.

Gambaryan, P. P. 1960. Adaptive Features of Locomotion Organs in Burrowing Mammals. Academy of Sciences of Armenian Soviet Socialist Republic Press, Yerevan, 195 p. (In Russian)

Gambaryan, P. P. 1974. How Mammals Run. Anatomical Adaptations. John Wiley & Sons, New York, 367 p.

Gazin, C. L. 1941. The mammalian fauna of the Paleocene of central Utah. Proceedings of the United States National Museum, 91:1–53.

Gazin, C. L. 1965. A study of the early Tertairy condylarthran mammal *Meniscotherium.* Smithsonian Miscellaneous Collections, 149:1–98.

Gazin, C. L. 1968. A study of the Eocene condylarthran mammal *Hyopsodus.* Smithsonian Miscellaneous Collections, 153:1–89.

Gebo, D. L. and K. D. Rose. 1993. Skeletal morphology and locomotor adaptations in *Prolimnocyon atavus*, an early Eocene hyaenodontid creodont. Journal of Vertebrate Paleontology, 13:125–144.

Gebo, D. L. and E. J. Sargis. 1994. Terrestrial adaptations in the postcranial skeleton of guenons. American Journal of Physical Anthropology, 93:341–371.

Geisler, J. H. 2001. New morphological evidence for the phylogeny of Artiodactyla, Cetacea, and Mesonychidae. American Museum Novitates, 3344:1–53.

Geoffroy, E., É. Saint-Hilaire, and F. G. Cuvier. 1795. Mémoire sur une nouvelle division des mammifères, et les principes qui doivent servir de base dans cette sorte de travail, lu à la Société d'Histoire naturelle, Ie premier floréal de l'an troisième. Magazine Encyclopédique, 2:164–187.

Gheerbrant, E., D. P. Domning, and P. Tassy. 2005. Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives), p. 84–105. *In* K. D. Rose and J. D. Archibald (eds.), The Rise of Placental Mammals. Origin and Relationships of the Major Extant Clades. The John Hopkins University Press, Baltimore.

Gingerich, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). University of Michigan Papers on Paleontology, 15:1–141.

Gingerich, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. University of Michigan Papers on Paleontology, 28:1–97.

Gingerich, P. D. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. Contributions from the Museum of Paleontology, University of Michigan, 28:79–92.

Gray, J. E. 1830–1834. Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke. Treuttel, Wurtz, Treuttel, Jun and Richter, London. Vol. 1 and 2.

Hay, O. P. 1899. On the names of certain North American fossil vertebrates. Science, 9:593–594.

Heinrich, R. and P. Houde. 2006. Postcranial anatomy of *Viverravus* (Mammalia, Carnivora) and implications for substrate use in basal Carnivora. Journal of Vertebrate Paleontology, 26:422–435.

Heinrich, R. and K. D. Rose. 1997. Postcranial morphology and locomotor behaviour of two early Eocene miacoid carnivorans, *Vulpavus* and *Didymictis.* Palaeontology, 40:279–305.

Hildebrand, M. and G. Goslow. 2002. Analysis of Vertebrate Structure (fifth edition). John Wiley & Sons, New York, 660 p.

Holbrook, L. T. 2009. Osteology of *Lophiodon* Cuvier, 1822 (Mammalia, Perissodactyla) and its phylogenetic implications. Journal of Vertebrate Paleontology, 29:212–230.

Hooker, J. J. 1989. Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships, p. 79–101. *In* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.

Hooker, J. J. 2005. Perissodactyla, p. 199–214. *In* K. D. Rose and J. D. Archibald (eds.), The Rise of Placental Mammals. The John Hopkins University Press, Baltimore and London.

Hooker, J. J. and D. Dashzeveg. 2003. Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene–Eocene boundary, p. 479–500. *In* S. L. Wing, P. D. Gingerich, B. Schmitz, and E. Tomas (eds.), Causes and Consequences of Globally

Warm Climates in the Early Paleogene. Geological Society of America Special Paper 369.

Hopwood, A. T. 1947. Contributions to the study of some African mammals. III. Adaptations in the bones of the fore-limb of the lion, leopard and cheetah. Journal of the Linnean Society of London (Zoology), 41:259–271.

Howell, A. B. 1970. Aquatic Mammals: Their Adaptations to Life in the Water. Dover Press, New York, 338 p.

International Committee on Veterinary Gross Anatomical Nomenclature (I.C.V.G.A.N.). 2005. Nomina Anatomica Veterinaria. Available at www.wava-amav.org/Downloads/nav_2005.pdf. Accessed 10 November 2010.

Janis, C. M., J. D. Archibald, R. L. Cifelli, S. G. Lucas, C. R. Schaff, R. M. Schoch, and T. E. Williamson. 1998. Archaic ungulates and ungulate-like mammals, p. 247–259. *In* C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Vol. 1: Terrestrial Carnivores, Ungulates and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Jenkins, F. A. Jr. and D. W. Krause. 1983. Adaptation for climbing in North American multituberculates (Mammalia). Science, 220:712–714.

Kielan-Jawarowska, Z. and P. P. Gambaryan. 1994. Postcranial anatomy and habits of Asian multituberculate mammals. Fossils and Strata, 36:1–92.

Kondrashov, P. E. 1998. The taxonomic position and relationships of the order Hyracoidea (Mammalia, Eutheria) within the Ungulata sensu lato. Paleontological Journal, 32:418–428.

Kondrashov, P. and A. K. Agadjanian. 2005. A nearly complete skeleton of Ernanodon (Mammalia, Ernanodonta) from Mongolia: Functional analysis. Journal of Vertebrate Paleontology, 25:79A, Supplement.

Lacépède, B. G. E. de. 1799. Mémoire sur une nouvelle table méthodique des animaux à mamelles. Mémoires de l'Institut National des Sciences et des Arts. Sciences Mathématiques et Physiques, 3:469–502.

Ladevèze, S., P. Missiaen, and T. Smith. 2010. First skull of *Orthaspidotherium edwardsi* (Mammalia, "Condylarthra") from the late Paleocene of Berru (France) and phylogenetic affinities of the enigmatic European family Pleuraspidotheriidae. Journal of Vertebrate Paleontology, 30:1559–1578.

Larson, S. G. 1988. Subscapularis function in gibbons and chimpanzees: Implications for interpretation of humeral head torsion in hominoids. American Journal of Physical Anthropology, 76:449–462.

Leidy, J. 1870. Remarks on the collection of fossils from the western Territories. Proceedings of the Academy of Natural Sciences of Philadelphia, 22:109–110.

Lemoine, V. 1878. Recherches sur les Ossements fossils des terrains tertiares inférieurs des environs de Reims. Annales Des Sciences Naturelles, 3:1–56.

Lemoine, V. 1885. Etude sur quelques mammifères de petite taille de la faune cernaysienne des environs de Reims. Bulletin de la Société Géologique de France, 13:203–217.

Lemoine, V. 1891. Etude d'ensemble sur les dents des mammifères fossiles des environs de Reims. Bulletin de la Société Géologique de France, 19:263–291.

Libed, S. A., S. G. Lucas, and P. E. Kondrashov. 2001. Anagenetic evolution of *Tetraclaenodon*, a Paleocene "condylarth" from the San Juan Basin, New Mexico. Journal of Vertebrate Paleontology, 21:73A, Supplement.

Lopatin, A. V. 2006. Early Paleogene insectivore mammals from Asia and establishment of the major groups of Insectivora. Paleontological Journal, 40:205–405, Supplement.

Marsh, O. C. 1872. Preliminary description of new Tertiary mammals, Parts I–IV. American Journal of Science and Arts, 4:122–128, 202–224.

Matthew, W. D. 1897. A revision of the Puerco fauna. Bulletin of the American Museum of Natural History, 9:259–323.

Matthew, W. D. 1915a. A revision of the lower Eocene Wasatch and the Wind River faunas. Pt. 1. Order Ferae (Carnivora), Suborder Creodonta. Bulletin of the American Museum of Natural History, 34:4–103.

Matthew, W. D. 1915b. A revision of the lower Eocene Wasatch and the Wind River faunas. Pt. 2. Order Condylarthra, family Hyopsodontidae. Bulletin of the American Museum of Natural History, 34:311–328.

Matthew, W. D. 1937. Paleocene faunas of the San Juan Basin, New Mexico. Transactions of the American Philosophic Society, 30:1–510.

McKenna, M. C. and S. K. Bell. 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York, 631 p.

McKenna, M. C., M. Chow, S. Ting, and Z. Luo. 1989. *Radinskya yupingae*, a perissodactyl-like mammal from the late Paleocene of southern China, p. 24–36. *In* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.

Morlo, M. and G. F. Gunnell. 2003. Small Limnocyonines (Hyaenodontidae, Mammalia) from the Bridgerian middle Eocene of Wyoming: *Thinocyon*, *Prolimnocyon*, and *Iridonon*, new genus. Contributions from the Museum of Paleontology, University of Michigan, 31:43–78.

Osborn, H. F. 1898. Remounted skeleton of *Phenacodus primaevus*. Comparison with *Euprotogonia*. Bulletin of the American Museum Natural History, 10:159–164.

Owen, R. 1841. Descriptions of the fossil remains of a mammal (*Hyracotherium leporinum*) and of a bird (*Lithornis vulturinus*) from the London Clay. Transactions of the Geological Society of London, 6:203–208.

Penkrot, T. A., S. P. Zack, K. D. Rose, and J. I. Bloch. 2008. Postcranial morphology of *Apheliscus* and *Haplomylus* (Condylarthra, Apheliscidae): evidence for a Paleocene Holarctic origin of Macroscelidea, p. 73–106. *In* E. J. Sargis and M. Dagosto (eds.), Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer Science, Dordrecht.

Peters, W. C. H. 1847. Charakteristik die neuen Säugethiergatt *Rhynchocyon* u. d. Frucht eines Nilpferdes. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königl. Preuss. Akademie der Wissenschaften zu Berlin, 12:36.

Polly, P. D. 2008. Adaptive zones and the pinniped ankle: a three-dimensional quantitative analysis of carnivoran tarsal evolution, p. 167–196. *In* E. J. Sargis and M. Dagosto (eds.), Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer Science, Dordrecht.

Prothero, D. R. and R. M. Schoch. 1989. Classification of the Perissodactyla, p. 504–537. *In* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.

Radinsky, L. D. 1965. Evolution of tapiroid skeleton from *Heptodon* to *Tapirus*. Bulletin of the Museum of Comparative Zoology, 134:69–106.

Radinsky, L. D. 1966. The adaptive radiation of the phenacodontid condylarths and the origin of Perissodactyla. Evolution, 20:408–417.

Reed, C. A. 1951. Locomotion and appendicular anatomy in three soricoid insectivores. American Midland Naturalist, 45:513–671.

Rose, K. D. 1985. Comparative osteology of North American dichobunid artiodactyls. Journal of Paleontology, 59:1203–1226.

Rose, K. D. 1987. Climbing adaptations in the early Eocene mammal *Chriacus* and the origin of Artiodactyla. Science, 236:314–316.

Rose, K. D. 1996a. Skeleton of early Eocene *Homogalax* and the origin of Perissodactyla. Palaeovertebrata, 25:243–260.

Rose, K. D. 1996b. On the origin of the order Artiodactyla. Proceedings of the National Academy of Sciences of the United States of America, 93:1705–1709.

Rose, K. D. 2001. Compendium of Wasatchian mammal postcrania from the Willwood Formation of the Bighorn Basin. University of Michigan Papers on Paleontology, 33:157–181.

Rose, K. D. 2006. The Beginning of the Age of Mammals. The John Hopkins University Press, Baltimore, 428 p.

Rose, K. D. and B. J. Chinnery. 2004. The postcranial skeleton of early Eocene rodents. Bulletin of Carnegie Museum of Natural History, 36:211–244.

Rose, K. D. and R. J. Emry. 1983. Extraordinary fossorial adaptation in the Oligocene palaeanodonts *Epoicotherium* and *Xenocranium* (Mammalia). Journal of Morphology, 175:33–56.

Rose, K. D. and R. J. Emry. 1993. Relationships of Xenarthra, Pholidota, and fossil "Edentates": the morphological evidence, p. 81–102. *In* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny. Placentals. Springer-Verlag, New York.

Rose, K. D. and S. G. Lucas. 2000. An early Paleocene palaeanodont (Mammalia, ?Pholidota) from New Mexico, and the origin of Palaeanodonta. Journal of Vertebrate Paleontology, 20:139–156.

Rose, K. D., R. J. Emry, and P. D. Gingerich. 1992. Skeleton of *Alocodontulum atopum*, an early Eocene epoicotheriid (Mammalia, Palaeanodonta) from the Bighorn basin, Wyoming. Contributions from the Museum of Paleontology University of Michigan, 28:221–245.

Rose, M. D. 1988. Another look at the anthropoid elbow. Journal of Human Evolution, 17:193–224.

Roth, V. L. 1990. Insular dwarf elephants: a case study in body mass estimation and ecological inference, p. 151–179. *In* J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, New York.

Salton, J. A. and E. J. Sargis. 2008. Evolutionary morphology of the Tenrecoidea (Mammalia) forelimb skeleton, p. 51–71. *In* E. J. Sargis and M. Dagosto (eds.), Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer Science, Dordrecht.

Sánchez-Villagra, M. R., Y. Narita, and S. Kuratani. 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Systematics and Biodiversity, 5:1–7.

SARGIS, E. J. 2002a. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. Journal of Morphology, 253:10–42.

SARGIS, E. J. 2002b. Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. Journal of Morphology, 254:149–185.

SCHAEFFER, B. 1947. Notes on the origin and function of the artiodactyl tarsus. American Museum Novitates, 1356:1–21.

SCHLOSSER, M. 1911. Beiträge zur Kenntnis der Oligozänen Landsäugetiere dem Fayum (Ägypten). Beiträge zur Paläontologie und Geologie von Osterreich-Ungarns und des Orients, 24:51–167.

SCOTT, K. M. 1990. Postcranial dimensions of ungulates as predictors of body mass, p. 301–336. *In* J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, New York.

SCOTT, W. D. 1892. A revision of North American Creodonta with notes on some genera which have been referred to that group. Proceedings of the Academy of Natural Sciences of Philadelphia, 4:291–323.

SHOSHANI, J. AND M. C. MCKENNA. 1998. Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data. Molecular Phylogenetics and Evolution, 9:572–584.

SLOAN, R. E. 1970. Cretaceous and Paleocene terrestrial communities of western North America. Proceedings of the North American Paleontological Convention, Pt. E:427–453.

SLOAN, R. E. AND L. VAN VALEN. 1965. Cretaceous mammals from Montana. Science, 148:220–227.

SPRINGER, M. S., M. J. STANHOPE, O. MADSEN, AND W. W. DE JONG. 2004. Molecules consolidate the placental mammal tree. Trends in Ecology and Evolution, 19:430–438.

STEIN, B. 2000. Morphology of subterranean rodents, p. 19–61. *In* E. A. Lacey, J. L. Patton, and G. N. Cameron (eds.), Life Underground: The Biology of Subterranean Rodents. University of Chicago Press, Chicago.

STORR, G. C. C. 1780. Prodromus Methodi Mammalium. Ad Instituendam ex Decreto Gratiosæ Facultatis Medicæ pro Legitime Consequendo Doctoris Medicinæ Gradu Inauguralem Disputationem Propositus Præside. Tubingæ. (Dissertatio Medica). Reiss, 43 p.

SWOFFORD, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, Massachusetts.

SZALAY, F. S. 1977. Phylogenetic relationships and a classification of the eutherian Mammalia, p. 315–374. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. NATO Advanced Study Institute. Series A. Vol. 14. Plenum Publication Company, New York.

SZALAY, F. S. AND M. DAGOSTO. 1980. Locomotor adaptations as reflected on the humerus of Paleogene Primates. Folia Primatologia, 34:1–45.

SZALAY, F. S. AND R. L. DECKER. 1974. Origins, evolution, and function of the tarsus in late Cretaceous Eutheria and Paleocene Primates, p. 239–259. *In* F. A. Jenkins (ed.), Primate Locomotion. Academic Press, New York.

SZALAY, F. S. AND S. G. LUCAS. 1996. The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. New Mexico Museum of Natural History and Science Bulletin, 7:1–47.

SZALAY, F. S. AND E. J. SARGIS. 2001. Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. Geodiversitas, 23:139–302.

TABUCE, R., B. COIFFAIT, P.-E. COIFFAIT, M. MAHBOUBI, AND J.-J. JAEGER. 2001. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: A possible origin for elephant-shrews. Journal of Vertebrate Paleontology, 21:535–546.

TABUCE, R. L., R. J. ASHER, AND T. LEHMAN. 2008. Afrotherian mammals: A review of current data. Mammalia, 72:2–14.

TABUCE, R., L. MARIVAUX, M. ADACI, M. BENSALAH, J.-L. HARTENBERGER, M. MAHBOUDI, F. MEBROUK, P. TAFFOREAU, AND J.-J. JAEGER. 2007. Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. Proceedings of the Royal Society B, 274:1159–1166.

TAYLOR, B. K. 1978. The anatomy of the forelimb in the anteater (Tamandua) and its functional implications. Journal of Morphology, 157:347–368.

TAYLOR, M. E. 1974. The functional anatomy of the forelimb of some African Viverridae (Carnivora). Journal of Morphology, 143:307–336.

TAYLOR, M. E. 1976. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). Journal of Morphology, 148:227–254.

THEWISSEN, J. G. M. 1990. Evolution of Paleocene and Eocene Phenacodontidae (Mammalia, Condylarthra). University of Michigan Papers on Paleontology, 29:1–107.

THEWISSEN, J. G. M. AND D. P. DOMNING. 1992. The role of phenacodontids in the origin of the modern orders of ungulate mammals. Journal of Vertebrate Paleontology, 12:494–504.

VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. Bulletin of the American Museum of Natural History, 132:1–126.

VAN VALEN, L. 1978. The beginning of the age of mammals. Evolutionary Theory, 4:45–80.

VAN VALKENBURGH, V. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. Journal of Vertebrate Paleontology, 7:162–182.

VERMA, K. 1963. The appendicular skeleton of Indian hedgehogs. Mammalia, 27:564–580.

VINOGRADOV, B. S. AND P. P. GAMBARYAN. 1952. Oligocene cylindrodonts from Mongolia and Kazakhstan. Proceedings of the Paleontological Institute, 41:24–39. (In Russian)

WANG, J. AND Y. TONG. 1997. A new phenacodontid condylarth (Mammalia) from the Early Eocene of the Wutu basin, Shandong. Vertebrata Palasiatica, 35:283–289.

WEST, R. M. 1976. The North American Phenacodontidae (Mammalia, Condylarthra). Milwaukee Public Museum Contributions in Biology and Geology, 6:1–78.

WILLIAMSON, T. E. 1996. The beginning of the age of mammals in the San Juan Basin, New Mexico: Biostratigraphy and evolution of Paleocene mammals of the Nacimiento Formation. New Mexico Museum Natural History and Science Bulletin, 8:1–141.

WILLIAMSON, T. E. AND S. G. LUCAS. 1992. *Meniscotherium* (Mammalia, Condylarthra) from the Paleocene–Eocene of western North America. New Mexico Museum Natural History and Science Bulletin, 1:1–75.

WILSON, R. W. 1949. Preliminary report on a Torrejonian faunule from near Angel's Peak, San Juan Basin, New Mexico. Geological Society of America Bulletin, 60:1930–1931.

ZACK, S. P., T. A. PENKROT, J. J. BLOCH, AND K. D. ROSE. 2005. Affinities of 'hyopsodontids' to elephant shrews and a Holarctic origin of Afrotheria. Nature, 434:497–501.

ACCEPTED 19 AUGUST 2011