TYLOCEPHALONYX, A NEW GENUS OF NORTH AMERICAN DOME-SKULLED CHALICOTHERES (MAMMALIA, PERISSODACTYLA)

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ABSTRACT

Tylocephalonyx, new genus, which includes a single species, *T. skinneri*, new species, is known from a quantity of material, including skulls and nearly complete postcranials from the Sheep Creek Formation (Nebraska) and the Split Rock vertebrate fauna (Wyoming). The most impressive morphological feature of *T. skinneri* is its domed skull; but dental, pedal, and other characters are also important in defining the species and determining its affinities and habits. Additional material of *Tylocephalonyx* from Oregon, Montana, Utah, and Colorado closely resembles *T. skinneri* but is too incomplete for definite reference. The morphology of *Tylocephalonyx* is compared with that of the well-known chalicothere species *Moropus elatus*, but similarities to *Moropus matthewi*, *Moropus merriami*, and *Ancylotherium* (*Ancylotherium*) *pentelicum*, are also noted.

Tylocephalonyx belongs to the chalicotheriid subfamily Schizotheriinae and shows special affinities to the genera *Moropus*, *Phyllotillon*, and *Ancylotherium*. A discussion of further relationships is inconclusive; *Tylocephalonyx* may have originated from near the common stem of *Moropus*, *Phyllotillon*, and *Ancylotherium*.

Floral/faunal associations suggest that *Tylocephalonyx* lived in moist temperate forests of northwestern North America but also had a significant distribution onto the Great Plains, perhaps associated with riparian communities. Its range appears to have differed from that of contemporary *Moropus*, which is rarely or never found in the same deposits and is found in more open woodland associations. The morphology of *Tylocephalonyx* is consistent with browsing habits and possibly for rearing up on the hindlimbs during feeding as was proposed for other schizotheriines by Borissiak (1945) and Schaub (1943). Many aspects of the habits of *Tylocephalonyx*, however, are still obscure.

INTRODUCTION

To many paleontologists, *Moropus elatus* from the Agate Spring Quarries of northwestern Nebraska is "the North American chalicothere." This species, by virtue of its prolific representation at Agate and the early publication of complete remains (Holland and Peterson, 1914), has come to be well known worldwide. North American chalicotheres later than *M. elatus* have in general been poorly known and described only from fragmentary remains. Skinner (1968) while describing a chalicothere metacarpal from the Valentine Formation (post-Barstovian) of Nebraska summarized additional North American Miocene occurrences. The temporal range of North American Chalicotheriidae, as affirmed by Skinner, is from early to medial Miocene (late Arikareean to Valentinian). Morphological study of all specimens gives further evidence that North American chalicotheriid evolution did not culminate in *M. elatus*. The present paper concerns an unusual branch of North American schizotheriine chalicotheriids, closely related to *Moropus* but sufficiently different to be placed in a separate genus, *Tylocephalonyx*.

The single species of *Tylocephalonyx* named in this paper is not among the species of *Moropus* listed by Holland and Peterson (1914). The first mention of material now referred to this species was by Matthew, who referred a phalanx from the Sheep Creek Formation to the Chalicotheriidae (1924, p. 152) and subsequently to *Macrotherium* sp. (1929, p. 519). The reference to "*Macrotherium*" [=*Chalicotherium*] was based on the notion that all "late Miocene" North American chalicotheres might belong to the Old World taxon. No comprehensive study of the specimens in question was made subsequently that could corroborate or disprove Matthew's idea. Taxonomy of these specimens has as a result been in an unstable state, with new (usually fragmentary) material being introduced as indeterminate chalicotheriids or even as *Macrotherium*. One of the most important conclusions of the study of which the present paper is a part is that *Chalicotherium* apparently never appeared in North America. All known North American chalicotheriids are referable either to *Moropus* or *Tylocephalonyx*.

Skinner, Skinner and Gooris (1977, p. 344) cited a personal communication from me (1973) concerning chalicotheres from the Sheep Creek Formation: "Although there are specimens from both the lower and middle parts of the Sheep Creek Formation, all evidence suggests that a single chalicothere species is represented. This species, a new one soon to be named, is clearly referable to *Moropus* and is most closely related to *Moropus matthewi* Holland and Peterson . . . from northeastern Colorado." The preceding statement was made before it became clear that the Sheep Creek chalicothere had a domed skull, for none of the chalicothere specimens known from the Sheep Creek Formation has a complete skull. The unique postcranial characters which caused me to place the Sheep Creek material in a separate species combine with newly discovered information on the domed skulls to suggest that the new Sheep Creek species belongs in a new genus, separate from *Moropus* but closely related to it. Other specimens, available for study since the paper by Skinner, Skinner and Gooris went to press, have caused me to question any close affinity between the Sheep Creek species and *Moropus matthewi*. *Moropus matthewi* is therefore not included in *Tylocephalonyx*.

The dome-skulled forms viewed in the context of chalicothere morphology, which by itself has provoked much functional speculation, present fascinating questions. The problem of dome function can be addressed by morphological comparisons of the skulls with those of other dome-skulled mammals. Such a comparison is the subject of a separate paper (Munthe and Coombs, in press). Probable functional differences between *Moropus* and *Tylocephalonyx* are treated generally in the present paper. The problem of the mode of life of *Moropus* and other schizotheriine chalicotheres will, however, be treated elsewhere.

ABBREVIATIONS

The following museum abbreviations are used with specimen numbers in the text, figures, and tables:

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York
CM, Carnegie Museum, Pittsburgh, Pennsylvania

DMNH, Denver Museum of Natural History, Denver, Colorado
F:AM, Frick American Mammals, American Museum of Natural History, New York
FMNH, Field Museum of Natural History, Chicago, Illinois
PU, Princeton University, Princeton, New Jersey
NMNH, National Museum of Natural History, Smithsonian Institution, Washington
UCM, University of Colorado Museum, Boulder, Colorado
UCMP, University of California Museum of Paleontology, Berkeley
UMMP, University of Michigan Museum of Paleontology, Ann Arbor
Other abbreviations used are Mc and Mt followed by a Roman numeral to indicate metacarpal and metatarsal, respectively.

TERMINOLOGY

Anatomical terminology closely follows that used by Butler (1965). Directional terminology as applied to the skeleton (such terms as radial/ulnar, dorsal/volar, labial/lingual follows that in general use and was further explained by Coombs (in press). Fused proximal and medial phalanges of digit II of the manus and pes are termed duplexes, following the usage of Holland and Peterson (1914).

ACKNOWLEDGMENTS

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SYSTEMATICS

CLASS MAMMALIA

ORDER PERISSODACTYLA

SUPERFAMILY CHALICOTHERIOIDEA GILL, 1872

FAMILY CHALICOTHERIIDAE GILL, 1872

SUBFAMILY SCHIZOTHERIINAE HOLLAND AND PETERSON, 1914

INCLUDED GENERA: *Schizotherium* Gervais, 1876; *Ancylotherium* Gaudry, 1862; *Moropus* Marsh, 1877; *Phyllotillon* Pilgrim, 1910; *Borissiakia* Butler, 1965; and *Tylocephalonyx*, new genus.

DISCUSSION: The subfamily Schizotheriinae was rediagnosed and compared with the Chalicotheriinae by Coombs (in press). A recent paper by Zapfe (1976) gave additional discussion of morphology, evolution, and function in the Chalicotheriinae.

Two new genera of schizotheriine chalicotheres were recently named from the Peoples' Republic of China: *Huanghotherium* Tung, Huang, and Qiu (1975) and *Gansuodon* Wu and Chen (1976). For reasons discussed elsewhere (Coombs, in press), it is questionable whether the upper teeth on which these new genera are based fall outside the range of variation of *Ancylotherium* (see, for example, figures of *Ancylotherium* in Thenius, 1953, and Bakalov and Nikolov, 1962). More information is necessary before *Huanghotherium* or *Gansuodon* can be accepted as separate from *Ancylotherium*.

TYLOCEPHALONYX, NEW GENUS

ETYMOLOGY: From Greek *Tylos* = knob + *Kephale* = head + *Onyx* = claw, hoof [masculine]. Refers to the domed skull of this genus and the clawed unguals common to chalicotheriids.

TYPE SPECIES: *Tylocephalonyx skinneri*, new species.

INCLUDED SPECIES: The type species only.

KNOWN DISTRIBUTION: Medial Hemingfordian—early Barstovian of western North America.

DIAGNOSIS: (1) Schizotheriine chalicotheres of medium size, similar to but slightly smaller than *Moropus elatus*; (2) dental formula $I^?_3$, $C^?_0$, P^3_3, M^3_3; (3) frontal and parietal bones of skull dorsally expanded to form a hollow, strutted dome; (4) upper molars higher crowned and more elongated than in *Schizotherium* but less than in *Ancylotherium*; (5) upper molars with prominent lingual cingulum opposite protocone and weak M^3 hypocone; (6) upper molars lacking (a) crista, (b) crochet, (c) labial rib on ectoloph between mesostyle and metastyle, and (d) accessory cuspules on M^3 posterolingual to hypocone; (7) no hypoconulid on M_3; (8) lower incisors, especially I_3, reduced; (9) Mc V present; (10) trapezium present in carpus; (11) scaphoid never contacting Mc II even during extreme carpal flexion; (12) volar process on lunate better developed than in *Ancylotherium*; (13) no dorsal flattening of metacarpals; (14) astragalus trochlea nearly symmetrical; (15) astragalus articulating distally only with navicular; (16) Mt III slightly longer than other metatarsals; (17) Mt IV not articulating with ectocuneiform; (18) metatarsals (especially Mt III) with flat to concave distal phalangeal facet and dorso-volar compression of distal shaft, and abrupt transverse broadening of distal ends; (19) proximal and medial phalanges of digit II of the manus fused to form a duplex in all except very young individuals.

DISCUSSION: *Tylocephalonyx* is known from almost complete skeletal remains. It can therefore be differentiated from other schizotheriine chalicotheres by a relatively large number of characters. Table 1 shows the diagnostic characters of *Tylocephalonyx* compared with characters of the other genera of the Schizotheriinae; probable plesiomorphic (P) and apomorphic (A) characters of *Tylocephalonyx* are marked.

Briefly, *Tylocephalonyx* is known to differ

TABLE 1
Comparison of Diagnostic Characters of *Tylocephalonyx* with Characters of Other Schizotheriinae

Capital letters at left refer to characters of *Tylocephalonyx* as: P (plesiomorphic within the Schizotheriinae), A (apomorphic), I (plesiomorphic compared with some, apomorphic compared to others), and ? (uncertain).

	Character	*Moropus*	*Schizotherium*	*Borissiakia*	*Phyllotillon*	*Ancylotherium*
I	1. Size	About the same[a]	Smaller	About the same	Same to slightly smaller	Same to larger
P	2. Dental formula	Same	Cheek teeth same, ? anterior teeth	? Same	? Same	Cheek teeth same, lower incisors reduced
A	3. Dome present	Absent	?	Absent	?	Absent
I	4. Crown height and elongation of upper molars	Same	Lower crowned, less elongated	Same	Same	Higher crowned, more elongated[b]
A	5. Strong lingual cingulum at protocone, weak hypocone on M³	Weaker cingulum, stronger hypocone	Weaker cingulum, stronger hypocone	Weaker cingulum, stronger hypocone	Weaker cingulum, stronger hypocone	Same
P	6. a. Crista absent[c]	Absent	Present	Present	Absent	Absent
P	b. Crochet absent	Absent	Absent	Absent	Occasionally present	Usually present
P	c. Labial ectoloph rib absent at metacone	Absent	Absent	Absent	Occasionally present	Usually present
P	d. M³ without posterolingual accessory cusps	Cusps absent	Cusps absent	Cusps present	Cusps absent	Cusps absent
A	7. M_3 hypoconulid absent	Absent	Present	Absent	Absent	Absent
A	8. Lower incisors reduced	Not reduced	?	Not reduced?	Not reduced	Strongly reduced
P	9. Mc V present	Present	Present	Present	?	Absent
P	10. Trapezium present	Present[d]	Present[d]	Absent or very small	?	Absent or fused to Mc II

TABLE 1 — (Continued)

Character	Moropus	Schizotherium	Borissiakia	Phyllotillon	Ancylotherium
P 11. Scaphoid never contacts Mc II	No contact	No contact	No contact	?	Contacts Mc II during extreme flexion
P 12. Volar process of lunate rather well developed	Well developed	?	Well developed	?	Weak
P 13. Dorsal flattening of metacarpals absent	Absent	Absent	Absent	?	Present
? 14. Astragalar trochlea fairly symmetrical	Less symmetrical	Less symmetrical	Fairly symmetrical	?	Fairly symmetrical
P 15. Astragalus articulating distally only with navicular	Only with navicular	Only with navicular	With both cuboid and navicular	?	Only with navicular
P 16. Mt III longest metatarsal	Mt III not longest metatarsal	? Mt III longest metatarsal	? Mt III longest metatarsal	?	Mt III longest metatarsal
?P 17. Articulation between Mt IV and ectocuneiform absent	Present	Absent (all species?)	?	?	Absent (all species?)
A 18. Well developed dorsal to volar compression of distal shaft and end of Mt III, distal facet flattening	No strong compression or flattening	No strong compression or flattening	No strong compression or flattening	?	Some dorsal to volar compression and some flattening
A 19. Duplex formed on digit II of manus	Fused	Not fused	Not fused	Fused	Fused

[a] M. distans and M. oregonensis smaller.
[b] Ancylotherium (Metaschizotherium) differs less from Tylocephalonyx.
[c] AMNH 7259, M³ referred to Moropus oregonensis, has a very small crista.
[d] Moropus hollandi and Schizotherium turgaicum appear to have lost the trapezium.

from *Schizotherium* in characters 1, 4, 5, 6a, 7, 14, 18, and 19; it is apomorphic compared with *Schizotherium* in all differing characters except 6a (absence of crista) and possibly 14 (symmetrical astragalus, polarity uncertain). *Tylocephalonyx* is known to differ from *Borissiakia* in characters 3, 5, 6a, 6d, 8, 10, 15, 18, and 19; of these differing characters, all are apomorphic compared with *Borissiakia* except 6a (absence of crista); 6d (absence of accessory cusps on M^3); 10 (trapezium present), and 15 (astragalus lacking cuboid facet). Neither *Schizotherium* nor *Borissiakia* is especially close morphologically to *Tylocephalonyx*.

Phyllotillon is known to differ from *Tylocephalonyx* only in a few dental characters (5, 8, and occasionally 6b and 6c); *Phyllotillon* is plesiomorphic in characters 5 and 8 but apomorphic in the occasional presence of crochet and labial ectoloph rib at the metacone of upper molars (6b, 6c). Skulls and postcranials other than phalanges are not known for *Phyllotillon*, so differences in these elements from *Tylocephalonyx* cannot be ascertained.

Moropus differs from *Tylocephalonyx* in characters 3, 5, 8, 14, 16, 17, and 18; *Tylocephalonyx* is apomorphic compared to *Moropus* in all these characters except the ones associated with the subequal lengths of Mt III and Mt IV in *Moropus* (16, ?14, ?17). *Moropus* and *Tylocephalonyx* share a large number of characters (1, 2, 4, 6a-d, 7, 9, 10, 11, 12, 13, 15, 19). These shared characters represent a similar "stage of evolution"—synapomorphic relative to *Schizotherium* and *Borissiakia*, symplesiomorphic relative to *Ancylotherium*.

Ancylotherium (including *Metaschizotherium*) differs from *Tylocephalonyx* in characters 1, 2, 3, 4, 6b, 6c, 9, 10, 11, 12, and 13; *Ancylotherium* is apomorphic compared with *Tylocephalonyx* in all these differing characters except for the presence of the dome (3). Several apomorphic characters (5, 8, ?18) are shared by *Tylocephalonyx* and *Ancylotherium* but not by *Moropus*. The significance of these apomorphies is unclear but will be discussed further in a separate section of this paper.

A number of characters of *Tylocephalonyx*, not included in the diagnosis, developed gradually and apparently independently in a number

of Schizotheriinae. These characters therefore occur in *Tylocephalonyx, Ancylotherium*, and late species of *Moropus* but not in early species of *Moropus, Schizotherium, Borissiakia*, or *Phyllotillon*. Among such characters are the reduction of the distal process on the scaphoid, the proportionate shortening of metatarsals (see table 8 and Coombs, 1974), and the increase of the distance between mesostyle and metacone on an unworn upper molar. Loss of the trapezium (retained in *Tylocephalonyx*) is another character which irregularly and/or progressively develops among various Schizotheriinae (see table 1).

The most unique diagnostic character of *Tylocephalonyx* is the domed skull.

Tylocephalonyx skinneri, new species

Chalicotheriidae: Matthew, 1924, p. 152.
Macrotherium sp.: Matthew, 1929, p. 519.
Chalicothere: Skinner, 1968, p. 6.

HOLOTYPE: F:AM 54915, a partial skeleton from Greenside Quarry, lower part of Sheep Creek Formation, Sioux County, Nebraska, including two rami with P_2-M_3 and two incisors, cervical vertebrae VI and VII, dorsal vertebrae III, IV, IX, X, XI, XX, sacrum, ribs, scapula, humerus, radius/ulna, trapezoid, unciform, innominate, femur, two tibiae, all tarsals, most from both sides, Mt II-IV from both sides, and most phalanges of the pes. See figures 4, 7, 8, 11, 13, 17, 19-23, 25-26.

HYPODIGM: A large quantity of material referable to *T. skinneri* comes from the lower part of the Sheep Creek Formation. Greenside Quarry: F:AM 54919a-c, P_2-M_3, P^2-M^3 from both sides and occipital region of skull (fig. 3, Munthe and Coombs, in press); F:AM 54942, left P^2-M^3 (figs. 3, 5C); F:AM 54940, right M^2-M^3; F:AM 54941, left and right P^3-M^3; F:AM 54929, M^1 and M^2; F:AM 54928, right P^3-M^1; F:AM 54916, right M_1; F:AM 54920, left and right P_2-M_3; F:AM 54923, left P_2-M_3; F:AM 54922, right P_3-M_2 and germinal M_3; F:AM 54924, right P_2-M_3; F:AM 54925, right P_4-M_3; F:AM 54917, left $?M_2$, $?M_3$; F:AM 54921, M_1-M_3; F:AM 54926, right M_2 and roots of other teeth; F:AM 54927, left dp^2-dp^4 (fig. 5B); F:AM 54918, right dp_2-dp_4 (fig. 5D);

F:AM 54943, occiput; F:AM 54978, cervical vertebra ?IV; F:AM 54990, left humerus; F:AM 54987, distal end of humerus, radius, ulna; F:AM 54984, damaged radius; F:AM 54970, radius (immature); F:AM 54986, radius; F:AM 54989, ulna; F:AM 54967, ulna; F:AM 54930, proximal end of ulna; F:AM 54931, scaphoid (fig. 9); F:AM 54946, cuneiform (fig. 10F-H); F:AM 101940, cuneiform; F:AM 54938, pisiform (fig. 10D); F:AM 54953, pisiform; F:AM 54977, unciform; F:AM 54932, unciform; F:AM 101938, unciform; F:AM 54933, magnum (fig. 12); F:AM 54960, Mc II; F:AM 54959, Mc II; F:AM 54971, Mc II (figs. 14B-D, 15A); F:AM 54954, Mc II; F:AM 54969, Mc III (figs. 15B, C, 16A); F:AM 54961, Mc IV; F:AM 54988, femur; F:AM 54991, tibia; F:AM 54962, patella (fig. 18); F:AM 54937, patella; F:AM 54976, astragalus; F:AM 54936, astragalus; F:AM 101934, astragalus; F:AM 54935, epiphysis of tibia; F:AM 54949, calcaneum; F:AM 54948a,b, two calcanea; F:AM 54950, calcaneum; F:AM 54966, calcaneum; F:AM 54979, cuboid; F:AM 54980, cuboid; F:AM 54939, ectocuneiform; F:AM 54957, Mt II; F:AM 54973a, Mt II and Mt III; F:AM 54973b-d, three ungual phalanges including large ungual of digit II of manus; F:AM 54964a,b, Mt II and Mt III; F:AM 54958, Mt III; F:AM 54944, Mt IV; F:AM 54974, Mt IV;F:AM 54975, Mt IV; F:AM 54945, left and right large duplexes of digit II of manus (fig. 25 left); F:AM 54951, duplex of digit II of pes; F:AM 54952, proximal phalanx; F:AM 54972, medial phalanx; F:AM 54968, large ungual phalanx of digit II of manus (fig. 27A); F:AM 54981, proximal phalanx of pes; F:AM 54982, proximal phalanx of pes; F:AM 54934, small ungual phalanx; F:AM 54947, ungual phalanx; F:AM 54955, two small ungual phalanges; F:AM 54965, ungual phalanx; F:AM 54956, small ungual phalanx; and F:AM 54983, three small ungual phalanges. Long Quarry: ?F:AM 54993, upper molar (fig. 28A); F:AM 54992, right P_2-M_3 and left P_2-P_4 with broken M_2; F:AM 54996, proximal end and shaft of ulna; F:AM 101937, lunate; F:AM 54994, patella; and F:AM 54995, ungual phalanx.

Several quarries from the middle part of the Sheep Creek Formation are also represented. Hilltop Quarry: F:AM 54861, left M^2 and M^3; F:AM 54862, left ?M^1; F:AM 54863, right M^1-M^3; ?F:AM 54998, right ?M^3 (fig. 28B); F:AM 54997, right P_4-M_1; F:AM 54869, right dp_2-dp_4; F:AM 101935, ectocuneiform; F:AM 54868, Mt III; F:AM 54867, proximal phalanx of pes; F:AM 54866, proximal phalanx; F:AM 54864, proximal phalanx; and F:AM 54865, small ungual phalanx. East Hilltop Quarry: F:AM 54870, ungual phalanx. Buck Quarry: F:AM 54880, right P^2-M^3; F:AM 54882, partial ulna; F:AM 54881a, b, Mc II and duplex of digit II of pes (fig. 25 right); F:AM 54883, tibia; and F:AM 101936, Mt III. East Ravine Quarry: F:AM 54874, right M^1-M^3; F:AM 54872, left P_3-M_3; and F:AM 54873, left M_1-M_3. Thomson Quarry: AMNH 20520, proximal phalanx of digit III of pes and medial phalanx; F:AM 54875, duplex of digit II of pes; and F:AM 54876, proximal end of Mc IV. Antelope Draw: F:AM 54871, left M^2-M^3. Rhino Quarry: F:AM 101939, Mt IV; and F:AM 54879, large duplex of digit II of manus. *Pliohippus* Draw 15 feet below Rhino Quarry zone: F:AM 54877, right P_4-M_3 with roots of P_2-P_3; and F:AM 54878, proximal phalanx. *Pliohippus* Draw: F:AM 101941, worn upper molar; F:AM 54885, left dp^2-M^1 (fig. 5A); F:AM 54886a, Mt II, Mt IV, and duplex of digit II of pes; F:AM 54886b, lunate (fig. 10A-C); F:AM 54887a, Mc II; F:AM 54887b, Mc IV (fig. 16B-D); and F:AM 54888, tibia. *Aphelops* Draw: F:AM 54884, humerus.

In Dawes County, specimens of *T. skinneri* occur in Sheep Creek equivalent beds at Ginn Quarry (F:AM 54912, right dp_3-dp_4) and in post-Runningwater, pre-Sheep Creek equivalent beds at Site 2 Prospect, Pepper Creek (F:AM 54910, proximal end of Mc II, fig. 14A).

Specimens of *T. skinneri* from the Split Rock vertebrate fauna in Fremont County, Wyoming, include: F:AM 54892, a scapula, humerus, radius/ulna, phalanges (one proximal, two medials, one ungual), ectocuneiform (fig. 28C, D), proximal end of Mt III (fig. 28E, F), two scaphoids, lunate, unciform, and sesamoids; UCMP 115867, a domed skull with jaws including P^2-M^3 (both sides, but most of the teeth are badly damaged; see figure 6 for

skull) and I , P -M ; UCMP 118295, a tibia fragment; UCMP 118296, an astragalus; UCMP 118298, a lunate; UCMP 118299, an unciform; and UCMP 118300, a medial phalanx.

DISCUSSION OF OCCURRENCES: Figure 1 is a map of the localities discussed in this section.

Skinner, Skinner and Gooris (1977) have recently made a monumental study of the Sheep Creek Formation and its complex relations with surrounding valley fill sediments. Chalicotheres in the Frick Collection from the Sheep Creek

Formation are the most completely known of those considered in the present paper. Material is known from the lower and middle parts of the Sheep Creek Formation as discussed by Skinner, Skinner and Gooris (1977); specimens from different parts of the formation do not differ appreciably from one another and are referred to a single species. AMNH 20520 and AMNH 20521, chalicothere specimens cited by Matthew (1924, pp. 152-153) from the "Lower Sheep Creek beds," are from "Stonehouse
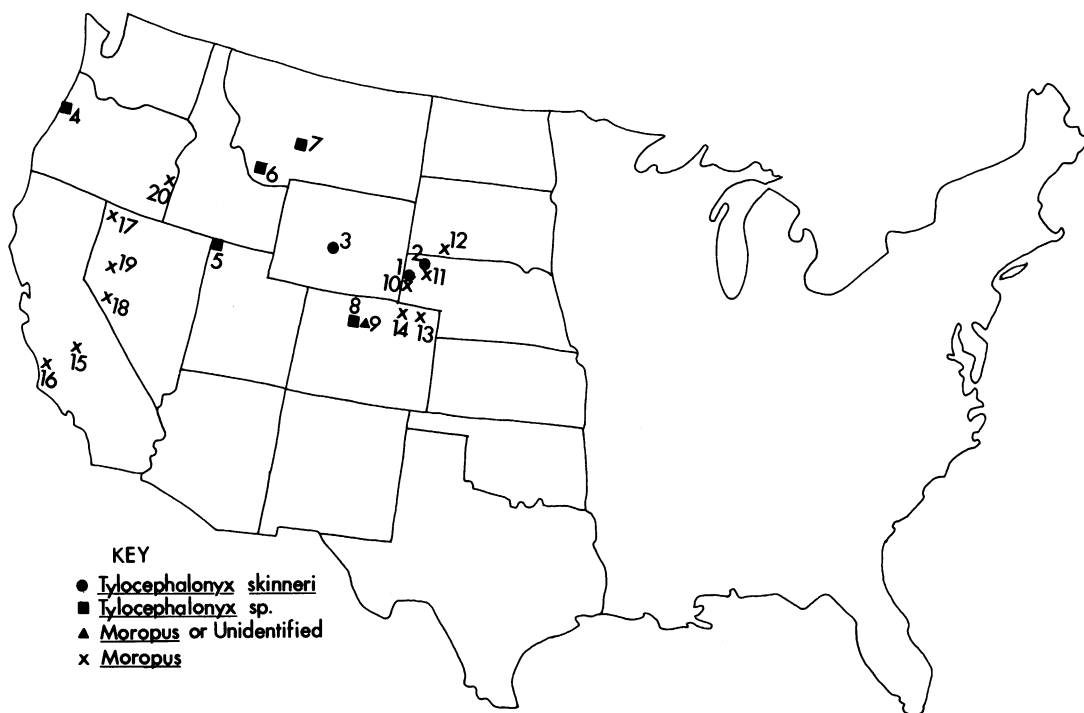

KEY
● Tylocephalonyx skinneri
■ Tylocephalonyx sp.
▲ Moropus or Unidentified
x Moropus

FIG. 1. Occurrences of Tylocephalonyx: (1) Sheep Creek Fm. (various quarries), Sioux Co., Nebraska; (2) Site 2 Prospect, Pepper Creek, and Ginn Quarry, Dawes Co., Nebraska; (3) Split Rock vertebrate fauna, Fremont Co., Wyoming; (4) "Iron Mountain Bed," Astoria Fm., Lincoln Co., Oregon; (5) UCMP Locality V77142, near Etna, Box Elder Co., Utah; (6) Dorr and Wheeler Locality 5, Madison Valley Fm., Madison Co., Montana; (7) Deep River Beds, Meagher Co., Montana; (8) Rickstrew Ranch locality, Eagle Co., Colorado. A phalanx from (9) the Troublesome Fm., Grand Co., Colorado, is discussed in the text as probably referable to Moropus. The following principal medial to late Hemingfordian and Barstovian occurrences of Moropus are included for comparison but are not discussed in the text: (10) Lower Snake Creek fauna, Olcott Fm. (various quarries), Sioux Co., Nebraska; (11) Runningwater Fm. (several localities), Dawes Co., Nebraska; (12) Flint Hill Quarry, Batesland Fm., Bennett Co., South Dakota; (13) Martin Canyon, Logan Co., Colorado; (14) near Pawnee Buttes, Weld Co., Colorado; (15) Phillips Ranch local fauna, Kinnick Fm., Kern Co., California; (16) Road Gap Canyon 2, Caliente Fm., San Luis Obispo Co., California, (17) Virgin Valley, High Rock Canyon, and Massacre Lake local faunas, Humboldt Co. and Washoe Co., Nevada; (18) Stewart Springs local fauna, Esmeralda Fm., Mineral Co., Nevada; (19) Monarch Mill Fm., near Eastgate, Churchill Co., Nevada; (20) Sucker Creek Fm., Malheur Co., Oregon.

Draw, Horizon A," which is the same as Thomson Quarry. According to Skinner, Skinner and Gooris (1977, p. 326), "Matthew (1924, p. 71) included the fossils from Thomson Quarry in his *Merychippus primus* zone that he considered as 'lower part of the Sheep Creek' formation . . . because he knew nothing of the stratigraphically lower Long and Greenside quarries discovered by Wilson in 1934 and 1935."

The Sheep Creek Ash, which lies just above the highest occurrence of the Sheep Creek Fauna, was dated at 14.7 m.y. (KA 891, glass) by Evernden et al. (1964). Skinner, Skinner and Gooris (1977) noted that fission-track dating of the same ash by Naeser and Izett at 16.1 ±3.7 m.y. (zircon) and 15.3 ±2.0 m.y. (glass) is more compatible with the inferred late Hemingfordian age of the Sheep Creek Fauna. Ginn Quarry in Dawes County, Nebraska, is interpreted by Galusha (personal commun.) as a biostratigraphic equivalent of the Sheep Creek Formation.

Moropus, but not *Tylocephalonyx*, is known from the Runningwater Formation of western Nebraska, but neither chalicothere genus is known from the overlying Box Butte Formation (Galusha, 1975). A Mc II of *Tylocephalonyx* (fig. 14A) was recovered from Site 2 Prospect, Pepper Creek, Dawes County, Nebraska. According to Galusha (personal commun.), the unnamed deposits from this locality contain a fauna later than that from the Runningwater Formation but earlier than that from the Sheep Creek Formation. Exact locations of all the Frick quarries discussed above can be found in Frick archives in the Department of Vertebrate Paleontology, the American Museum of Natural History.

Skinner (1968, p. 19) referred to chalicothere postcranials from Exposure 2-C, 7 miles (11.3 km.) west of Muddy Gap, Fremont County, Wyoming, and postulated a late Hemingfordian or early Barstovian age for the associated fauna. The chalicothere postcranials are part of the Split Rock vertebrate fauna, which also includes a domed chalicothere skull (fig. 6) collected by L.K. Munthe of the University of California, Berkeley (UCMP Locality V69190). According to Jens Munthe and Lander (1973), the Split Rock fauna is of medial Hemingford-

ian age, intermediate between older faunas from the Marsland Formation (*sensu* McKenna, 1965) of Nebraska and Martin Canyon in Colorado and the younger fauna of the Sheep Creek Formation of Nebraska. According to Jens Munthe (personal commun., 1977), a radiometric date of approximately 17 m.y. (KA 2649) was obtained from an ash 50 meters stratigraphically below the chalicothere skull. The Split Rock fauna is currently under study by Jens Munthe; detailed comparisons with faunas of the Runningwater and Box Butte formations are hampered by apparent differences in faunal composition.

ETYMOLOGY: Named for Morris F. Skinner, an expert in the geology of Sioux County, Nebraska, and on fossil perissodactyls, and a frequent advisor on this project.

KNOWN RANGE: Medial to late Hemingfordian of North American Great Plains.

DIAGNOSIS: Same as for genus. *T. skinneri* can also be differentiated by the following characters from various species of *Moropus*: (1) upper molars almost always lacking any ectoloph rib; (2) P^3 and P^4 with prominent anterolingual and posterolingual cingula and transverse lophs worn strongly before protocone; (3) rapidly worn lower molars with slightly curved lophids; (4) scaphoid with short distal process and elongated magnum facet which prevents contact between the distal lunate and trapezoid facets; (5) magnum with stronger volar hook than in *M. matthewi* and different width/depth proportions and scaphoid-trapezoid facet arrangements than in any species of *Moropus*; (6) cnemial crest on tibia and proximo-dorsal ridge on patella especially strongly rugose; (7) some transverse expansion of ectal facet between astragalus and calcaneum, and tuber calcis of calcaneum not strongly rugose; (8) facets among tarsals and metatarsals restrictive in shape to reduce lateral movement and torsion of the mesaxonic pes; (9) fusion of proximal and medial phalanges of digit II of pes common but not universal; and (10) ungual phalanges proportionally similar to those of *M. elatus*, broader than those of *M. matthewi* and *M. merriami* (table 12).

DESCRIPTION AND COMPARISON: This section compares *T. skinneri* with species of *Moropus* (especially *M. elatus*, *M. hollandi*, *M. mat-*

thewi, and *M. merriami*). The description format closely follows that used in the description of *M. elatus* and *M. hollandi* by Coombs (in press).

M³ (FIG. 5C): As is true in *Moropus elatus*, M³ is the least quadrate and least symmetrical of the three upper molar teeth. The generalization is particularly true for *T. skinneri*, for the posterior part of the tooth is unusually narrow and short. The primary reason for such narrowing is a decrease in the development of the hypocone and the metaloph. In all specimens the hypocone is very low, sometimes even depressed below the level of the metaloph. The whole of the metaloph is on a much lower plane than the ectoloph; the tallest point of the metaloph is usually at its labial origin from the ectoloph. At this point of origin of the metaloph there is in some specimens a hint of a possible metaconule (F:AM 54942). The labial origin of the metaloph on unworn specimens is farther from the mesostyle (15 to 20 mm.) than it is in *M. elatus*, and during wear the metacone and labial part of the metaloph appear to migrate farther posterolingually because of the absence of wear on the ectoloph posterior to the metacone. In the most worn specimens the metacone is quite far removed from the tip of the mesostyle. As it reaches the hypocone, the metaloph is continuous with a posterior crest, which in *M. elatus* forms part of the posterolingual cingulum. The thickened cingulum is nearly as tall as the low ectoloph and curves slightly posteriorly and labially to approach the metastyle. This cingulum, along with the metaloph and ectoloph, surrounds or nearly surrounds the postfossette, which because of the shortness of the metaloph has become merely a slit between ectoloph and metaloph.

The anterior blade of the ectoloph of M³ in *T. skinneri* is more strongly concave labially than in *M. elatus*, and the very pronounced mesostyle may have a noticeably posterior slant. No labial ectoloph rib is present at paracone or metacone. On the protoloph, a protoconule is present in the least worn specimens, but it is quickly worn away as is most of the protoloph. In most specimens the tip of the
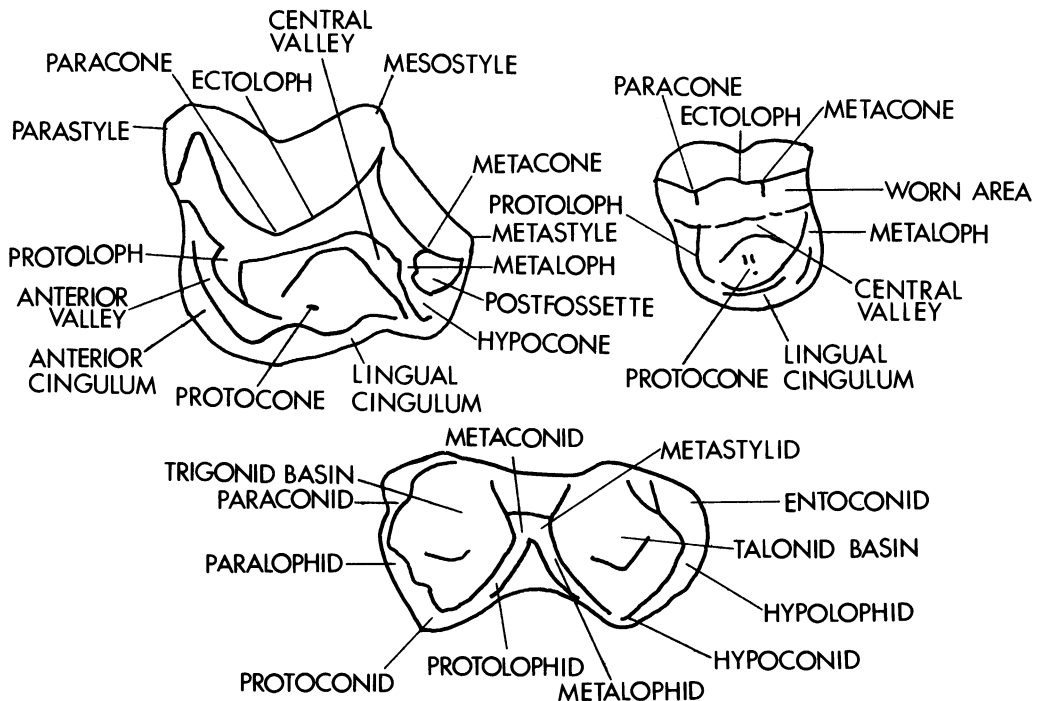

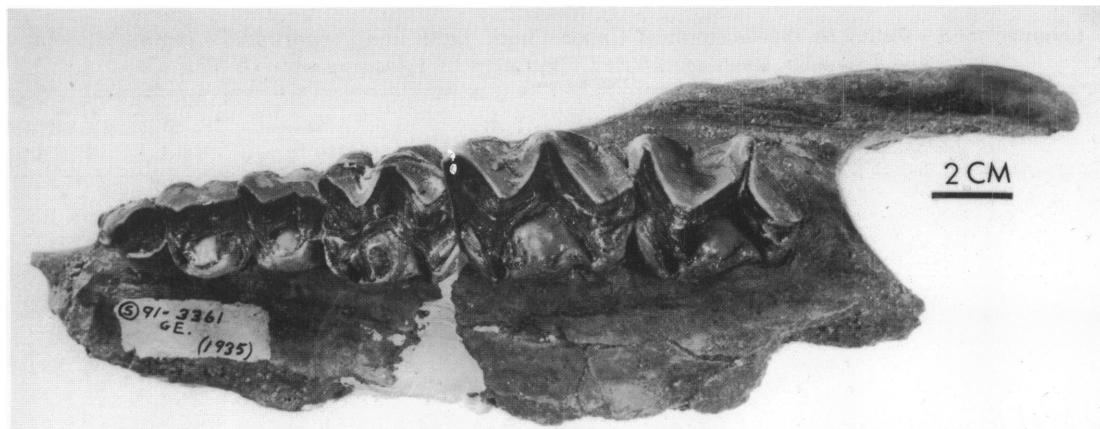FIG. 2. Diagrammatic drawings of occlusal views of left M³, P⁴, and M₃ of *T. skinneri*. Anterior at left.

FIG. 3. Maxilla with P²-M³ of F:AM 54942, *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. Occlusal view. X1/2.

protocone is blunter than in specimens of *M. elatus* and the base of the protocone is slightly more swelled, particularly in its labial part. The protoloph, where it remains, joins the protocone anteriorly.

Cingula are very similar to those described for *M. elatus*. The anterolingual cingulum very often sends a crest to join the protoloph at its junction with the protocone. Posterior to the point where it skirts the protocone lingually the cingulum becomes very prominent, forming a short crest separated by a distinct valley from the protocone. The thickness, prominence, and slightly oblique orientation of this ridge are very characteristic of M³ of *T. skinneri* and are, along with the weak hypocone and strong posterior cingulum closing the postfossette, convergent features to upper molars of *Ancylotherium (A.) pentelicum*. There is, however, a sharp and complete break in the cingulum posterior to the ridge at the lingual opening of the central valley.

M¹ AND M² (FIG. 3): In all specimens where M³ is present, M² has been strongly worn and M¹ almost effaced. Both teeth are more symmetrical and quadrate than M³, although M² is considerably larger and more elongated than M¹.

A reduction of the hypocone and shortening of the metaloph is to some degree characteristic of M¹ and M², but it is not so pronounced as

on M³. The apparent size of the hypocone is increased by wear, for the metaloph is obliterated and the postfossette broadened.

F:AM 54885 (on a maxilla with dp²-dp⁴; fig. 5A) shows the unworn condition for M¹, with the metaloph sharp and strongly curved and hypocone raised very slightly above it. As wear progresses on both M¹ and M² the postfossette increases in size and eventually becomes confluent with the central valley. Only in the newly erupted M¹ of F:AM 54885 and F:AM 54862 are protoconule present and protoloph complete. On M² of all specimens the protocone is blunt and broad-based, but on M¹ where the protocone is not worn it is pointed and more sharply conical. In both M¹ and M² the cingulum posterolingual to the protocone continues to form a distinct crest, but as on M³ it disappears at the opening of the central valley. M¹ has a variable lingual projection of its posterolingual angle; this eminence includes the root and is particularly visible in F:AM 54919b (right side). Neither M¹ nor M² has a labial ectoloph rib.

P²-P⁴ (FIG. 3): As in *Moropus elatus*, P³ and P⁴ of *T. skinneri* are very similar to each other in morphology but differ somewhat in size, though not so much as in *M. elatus*. The greater size uniformity results from the fact that in *T. skinneri* the difference in size between M¹ and P⁴ is greater than in *M. elatus*, that is, P⁴

TABLE 2
Lengths[a] and widths[b] (in Millimeters) of Upper Cheek Teeth and Proportional Lengths of Molar
and Premolar Rows of Selected Specimens of *Tylocephalonyx skinneri*

	F:AM 54942	F:AM 54919[b]	F:AM 54941	F:AM 54880	F:AM 54863	F:AM 54874
Length P^2	17.7	18.3	—	15.1	—	—
Width P^2	15.9	18.3	—	13.9	—	—
Length P^3	23.0	21.9	22.8	19.3	—	—
Width P^3	25.8	25.8	24.0	22.0	—	—
Length P^4	24.0	24.3	23.8	20.9	—	—
Width P^4	27.7	27.3	27.5	24.2	—	—
Length M^1	34.5	34.7[c]	37.8	31.0	35.0	37.0[c]
Width M^1	35.4	35.6	35.1	32.1	33.1	33.4
Length M^2	51.2	49.1	51.2	45.0	47.7	57.2[c]
Width M^2	39.1	42.6	40.4	37.1	40.1	41.8
Length M^3	49.2	53.8	51.0	49.6	49.0	55.2
Width M^3	40.1	40.7	41.2	38.6	39.2	42.7
Length Premolar Row	65.2	62.5	—	55.3	—	—
Length Molar Row	127.8	130.5	130.9	120.4	122.5	141.2
$\frac{\text{Premolar}}{\text{Molar}}$ Row	0.51	0.48	—	0.46	—	—

[a] Lengths are maximum anterior to posterior dimensions.

[b] Widths are maximum labial to lingual dimensions, including mesostyle on molars.

[c] Worn tooth or approximate measurement.

is less enlarged (see table 2). An exception to this generality is UCMP 115867 from the Split Rock vertebrate fauna whose P^4 is quite large. P^2, in the few specimens where it·is known, is much smaller than P^3 and relatively more reduced than in specimens of *M. elatus*.

Both P^3 and P^4 have slightly greater labiolingual width than anteroposterior length, but they are much closer to square-shaped than corresponding teeth of *M. elatus*, which have greater relative labiolingual width. On both P^3 and P^4 the ectoloph is weakly W-shaped, and P^4 has a more prominent parastyle than it does in *M. elatus*. The protocone is crescent-shaped with no distinct tip. Toward its base the protocone is swollen, on P^4 sometimes folded slightly. On even the least worn teeth both protoloph and metaloph have been obscured by wear directed in a lingual direction from the crest of the ectoloph. Only traces of protoloph and metaloph can be seen near ectoloph and protocone, and nothing of their original character can be determined. After further wear, the

ectoloph is flattened and the lingual wear edges on it become much less sharp. Eventually the protocone is worn flat also, so that only a small depression (valley) remains in the center of the tooth. The order of wear of tooth parts is different from that in *Moropus oregonensis* and *M. merriami*, in which the protocone is worn at least as soon as the transverse lophs. Posterior and anterior cingula, both strongly developed toward their lingual ends, help to give P^3 and P^4 a quadrate outline. These cingula are developed almost equally, but the lingual cingulum is often fused to the wall of the protocone and is only barely distinguishable from it (unlike *M. elatus*). The labial cingulum is very weak.

P^2 is rather worn in the specimens where it is preserved. It is very similar to P^2 of *M. elatus*, but its parastyle and anterolingual cingulum are in general not so strongly developed. P^2 is considerably smaller than P^3 and P^4.

M_1-M_3 (FIG. 4): Lower molars of *T. skinneri* are practically indistinguishable in relative size

and morphology from lower molars of *M. elatus*. M^3 can be distinguished from M_2 by its greater asymmetry, that is, by the greater posterior displacement of hypoconid and entoconid relative to the metastylid and consequent increase in size of the talonid basin. The labial cingula of M_3 are weaker than on M_1 and M_2 but are on the average heavier than on M_3 of *M. elatus*, though both extremes of development occur in both species.

In most specimens, M_1 is worn flat and M_2 only slightly less so (the entoconid is the last cuspid worn down, and wear spreading from the labial side rapidly reaches the level of the
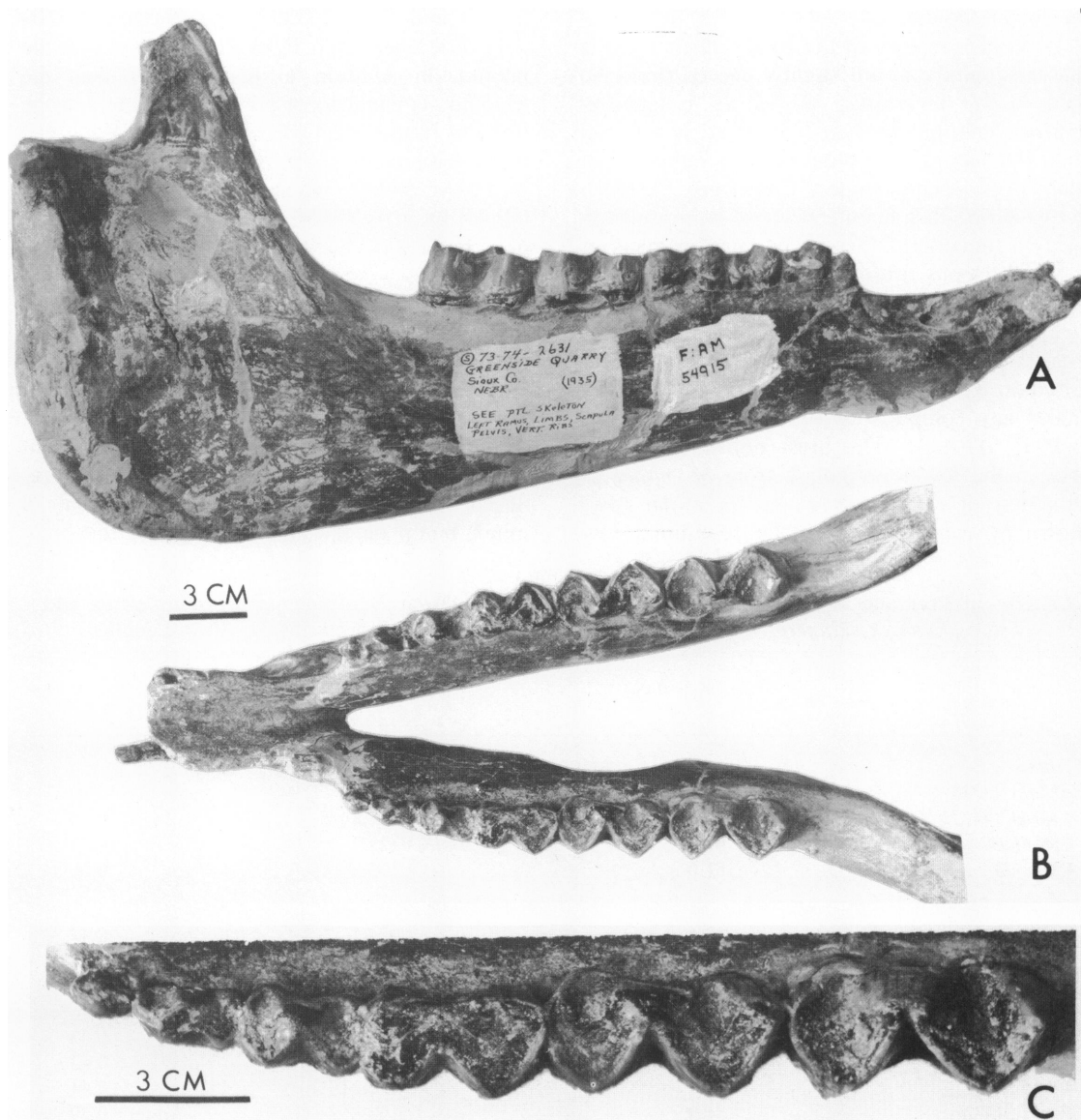

FIG. 4. A. Labial, and B, C. Occlusal views of mandible and lower teeth of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Left I^2, right I^3, and P^2-M^3; ×1/3. B. Left I^2, P^2-M^3, right I^3, P^2-M^3; × 1/3. C. Left P^2-M^3; × 2/3.

basins). In younger specimens where M_1 is less worn (F:AM 54922, M_3 only just erupting; and F:AM 54916), the metastylid can be seen to be barely distinct from and lower than the metaconid (less developed than in M_3 of *T. skinneri* or in any lower molar of *M. elatus*). The labial cingulum of M_1 is strongly visible. Lingual cingula are practically non-existent on any of the lower molars.

A notable feature of the lower molar teeth is that the lophids are all slightly curved (more so than in *M. merriami*; *M. elatus* is approximately intermediate) and join at protoconid and hypoconid in blunt-tipped rather than sharp-tipped acute angles. Care must be taken in evaluating this feature because it is probably partly a function of the strong wear on many of the teeth (lophs are more gently curved toward the bases of the teeth).

F:AM 54997 (P_4-M_1) from Hilltop Quarry is smaller than other lower tooth specimens referred to *T. skinneri*, but its heavy wear precludes any comparisons of morphology.

P_2-P_4 (FIG. 4): The most noticeable difference in the lower premolars from *M. elatus* is reduction of the length of the premolar row, shown by changes in premolar row/molar row

length ratios (table 3) and by premolar morphology. As the ratios suggest, reduction of premolars has occurred to varying degrees in *T. skinneri*, but over the time span for which specimens are known the variation seems constant with little or no tendency for one proportion to become established.

P^4 is seen in its least worn state in F:AM 54925 and F:AM 54922 (semi-erupted). Its only difference from P_4 of *M. elatus* is that the talonid, in addition to being lower than the trigonid, is equal to or slightly shorter than the trigonid (rather than slightly longer). P_3 is virtually indistinguishable from that of *M. elatus*. In F:AM 54922, where it is little worn, the talonid basin is slightly better defined, because of a more prominent entoconid, than in P_3 of *M. elatus*.

P_2 shows more than P_3 or P_4 the effects of the proportional shortening of the premolar row. Its general morphology and pattern of wear are similar to those in *M. elatus*, but some parts of the tooth are reduced. The protoconid continues to be the most prominent cuspid, but the paraconid is very much reduced. In *T. skinneri* the paraconid is only a minor bump on the anterior slope of the blunt

TABLE 3

Lengths of Premolar and Molar Rows (in Millimeters) of Lower Dentitions of *Moropus elatus* and *Tylocephalonyx skinneri*, with Proportions of Premolar Row Lengths/Molar Row Lengths

Specimen	Premolar Row Length	Molar Row Length	Premolar Row Molar Row
M. elatus			
AMNH 14378	67.4	134.2	0.50
AMNH 14427	65.6	142.8	0.46
CM 1750	67.5	128.3	0.53
CM 1754	61.0	109.0	0.56
T. skinneri			
F:AM 54915	52.6	124.1	0.42
F:AM 54919[a]	57.0	138.8	0.41
F:AM 54920	61.2	129.5	0.47
F:AM 54925	65.0[a]	140.0	0.46[a]
F:AM 54924	51.6	120.8	0.43
F:AM 54923	52.0	120.2	0.43
F:AM 54992	57.5	130.2	0.44
F:AM 54872	54.9[a]	140.8	0.39[a]
F:AM 54877	59.8[a]	126.3	0.47[a]
UCMP 115867	55.4[a]	134.4	0.41[a]

[a] Approximate measurement.

protoconid and on many specimens is barely visible. The talonid is also shortened. In several specimens (F:AM 54923, F:AM 54924, UCMP 115867, somewhat in F:AM 54915—fig. 4), P_2 is rotated slightly on its axis, so that the talonid is lingual to the paraconid of P_3 and only the small trigonid lies anterior to P_3. The rotation of P_2 compresses the length of the premolar row even farther; its effect is best seen in labial view.

INCISORS: The anterior part of the mandible is preserved only in F:AM 54915 (the holotype, fig. 4) and UCMP 115867. Three incisors (no canine) were present on each side, but neither specimen preserved all three complete. I_1 is a large, spatulate tooth which shows some wear at its tip in UCMP 115867. I_2 is spatulate and procumbent like its counterpart in *M. elatus* but is more symmetrical than I_2 in the earlier species and lacks an accessory labial cuspid. There is only slight wear on the tip of I_2 in F:AM 54915, despite well-worn premolars and molars. Compared with I_3 of *M. elatus*, I_3 in *T. skinneri* is strongly reduced, its crown only a small, rounded nubbin. There is no wear on the tooth, and it was probably vestigial. Reduction of lower incisors parallels that in *Ancylotherium* (*A.*) *pentelicum* (seen in Munich specimen AsII147), but is not so pronounced.

Premaxillae are not known for *T. skinneri*. A known premaxilla of *M. elatus* shows that *M. elatus* had no upper canine or incisors and presumably used a vegetation cropping mechanism not unlike that of modern ruminants (Coombs, 1978). Similarities of lower incisors of *T. skinneri* to those of *M. elatus* suggest that premaxillae of *T. skinneri* may also have been edentulous. However, the reduction of I_3 and the small degree of wear on I_1 and I_2 may suggest that ruminant-like cropping was of less importance in this species.

DECIDUOUS TEETH: Upper decidous teeth of *T. skinneri* (fig. 5A,B) are virtually indistinguishable from those of *M. elatus*; seemingly, many of the differentiating features developed by molars of *T. skinneri*, particularly M^3, are not shown by the deciduous premolars. On F:AM 54927 (fig. 5B) there is some suggestion of a metaconule on the labial part of the metaloph of both dp^3 and dp^4. On dp^3 and dp^4 there is a hint of a labial ectoloph rib

opposite the paracone, whereas on the same teeth of *M. elatus* the rib is strong and easily visible. On dp^2 the lingual and posterolingual cingula are slightly weaker than in *M. elatus* (in F:AM 54885 not distinct from the posterolingual base of the hypocone; in F:AM 54927 becoming elevated at one point just lingual to the hypocone to form a tiny cuspule).

The three known juvenile mandibles of *T. skinneri* differ little in morphology from specimens of *M. elatus*, but two differences are evident (fig. 5D): on dp_3 the paralophid is not so strongly elongated compared with the rest of the tooth, and on dp_2 the paraconid is not so distinct from the protoconid. Both differences reflect a decrease in the length of the premolar row compared with that of *M. elatus* and are reflected also in the length of the permanent premolars. On F:AM 54912, the least worn of the lower deciduous teeth, the metastylid on dp_4, though visible, is notably lower than the metaconid and is barely separate from the metaconid at its extreme tip. Such weak development is a continuation of the reduction of the metastylid already mentioned for M_1. Cingulum development on deciduous lower premolars is similar to that on the molars, with little or no lingual cingulum present.

SKULLS AND MANDIBLES: Despite the large quantity of dental and postcranial material of *T. skinneri*, there is only one complete skull (UCMP 115867 from the Split Rock vertebrate fauna; fig. 6). The relatively recent discovery of this skull and of another referred to *Tylocephalonyx* sp. (NMNH 187129) accounts for the belated recognition of the unusual nature of skulls of *Tylocephalonyx*. Two additional fragmentary skulls (F:AM 54919c and F:AM 54943 from the Sheep Creek Formation) add corroborative information. The detailed structure of the dome and speculations concerning its function are given elsewhere (Munthe and Coombs, in press).

Doming of the skull involves both the frontal and parietal bones and is most pronounced at the frontoparietal junction. The dome is hollow, and its walls are not especially thick, but there is some evidence of internal supporting strutwork. The interior of the dome forms a sinus dorsal to the braincase. F:AM 54919c, which preserves the posterior part of

TABLE 4

Comparison of Dental Features of *Moropus oregonensis*, *Moropus elatus*, *Tylocephalonyx skinneri*, and *Ancylotherium* (*A.*) *pentelicum*

Character	M. oregonensis	M. elatus	T. skinneri	A. (A.) pentelicum
Upper molars:				
1. Labial ectoloph origin on unworn M³	Very near mesostyle	Near mesostyle	Separated from mesostyle	Separated from mesostyle
2. Height of posterior cingulum at postfossette	Low	Variable, usually low	Well developed	Very well developed
3. Height of lingual cingulum just posterior to protocone	Medium	Low	Rather strong	Strong
4. Elongation	Medium	Rather strong	Rather strong	Strong
5. Crown height	Slightly increased	Moderately increased	Moderately increased	Notably increased
6. Unworn protocone relatively blunt or sharp	Sharp	Variable	Blunt	Rather blunt
7. Labial ectoloph rib?	Present at paracone	Present at paracone	Usually absent	Weak, but may be present at paracone and metacone
8. Crochet?	Absent	Absent	Absent	Present, strong
P³ and P⁴:				
9. Wear on transverse lophs compared to protocone	About same rate	Somewhat faster	Much faster	Somewhat faster
10. Development of antero-lingual cingula	Not strong	Medium to strong	Rather strong	Medium to rather strong
11. Protocone cusp-like or crescentic?	Cusplike	Cusplike to crescentic	Crescentic	Crescentic, may bear second cusp
Lower molars:				
12. Curvature of lophids	—	Straight to slightly curved	Curved	Slightly curved
13. Metastylid	—	Strongly separate	Separate, but not strong	Strongly separate

the parietals, shows an abrupt dorsal slant of the parietals and internal structure suggesting that this animal, like UCMP 115867, had a domed skull.

Paroccipital processes in *T. skinneri* are concave on their posterior sides and are curved much more strongly posteriorly than in *M. elatus*. Basicranial foramina show a basic resemblance to those in *M. elatus*, but this area of the skull has not been studied in detail in either species.

In those specimens where maxillae and palatines are preserved with dentitions, the internal nares open opposite M³, notably anterior to their position in *M. elatus*. The anterior part of the palate of UCMP 115867 is very narrow. The infraorbital foramen is consistently dorsal to the middle part of M¹, slightly anterior to its usual position in *M. elatus*.

Mandibles of *T. skinneri* differ slightly in proportions from specimens of *M. elatus*, but they vary so much among themselves that it is difficult to determine what the constant differences are. Study is further confused by the incompleteness of most of the specimens either in the anterior or posterior segments of the jaw and by variations in development at different stages of growth. The jaws seem to be shorter

in comparison to their height than are jaws of
M. elatus, particularly in the anterior part of
the jaw, but quantitative establishment of this
observation by means of proportions has not
been conclusive. In specimens where the poste-
rior part of the jaw is fully preserved the as-
cending ramus rises very abruptly above the

tooth row, becoming closer to vertical than oc-
curs in *M. elatus*. Because of the abrupt slant,
the coronoid process is relatively tall. The only
specimen where there is not such an abrupt
ascent is F:AM 54877, which is unusual also in
having a relatively large space along the tooth
row between M^3 and the beginning of the
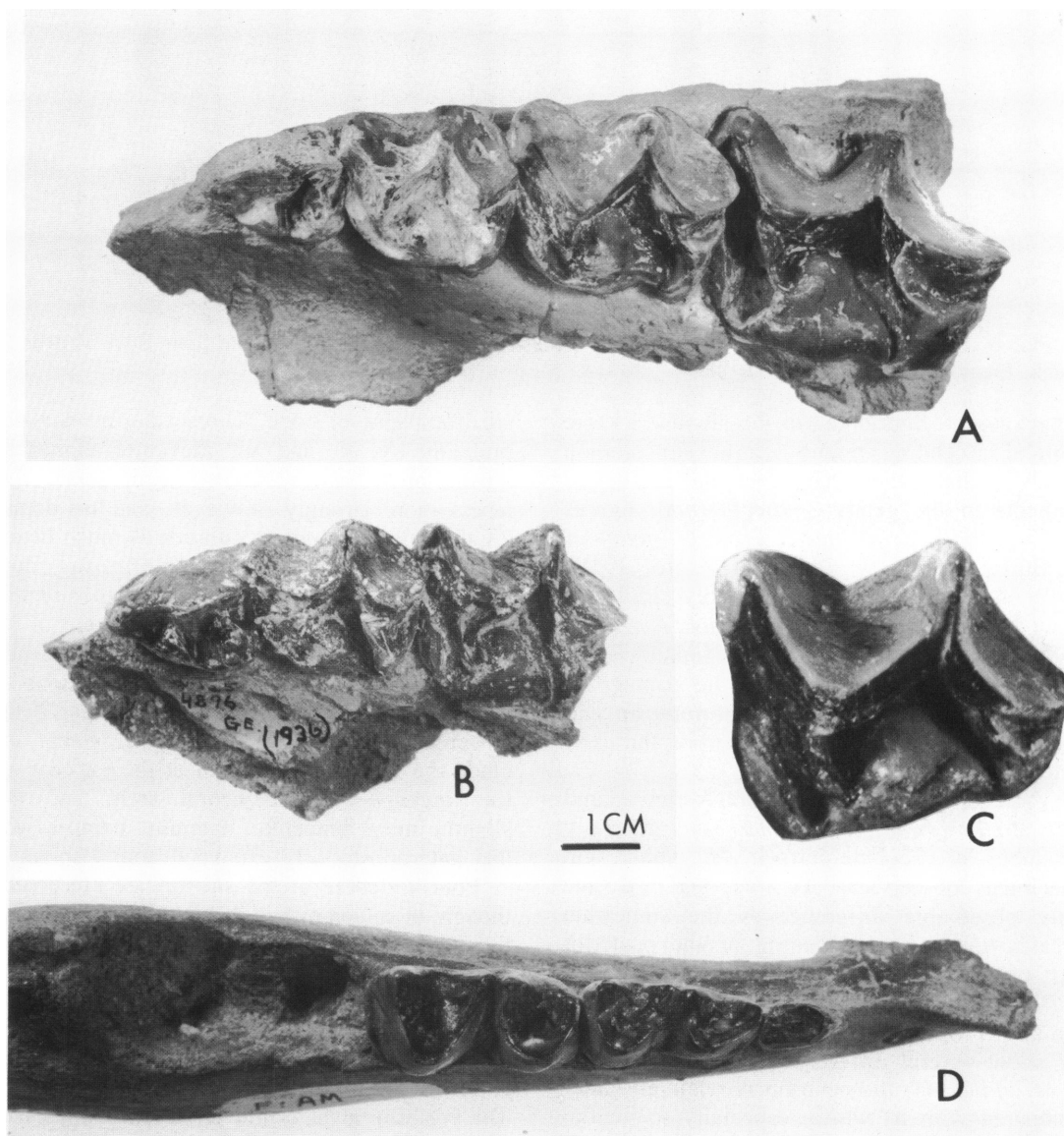

FIG. 5. Occlusal views of teeth of *T. skinneri* from the Sheep Creek Fm., Sioux Co., Nebraska. A. Left
dp^2-dp^4, M^1 of F:AM 54885. B. Left dp^2-dp^4 of F:AM 54927. C. M^3 of F:AM 54942. D. Right dp^2-dp^4 of
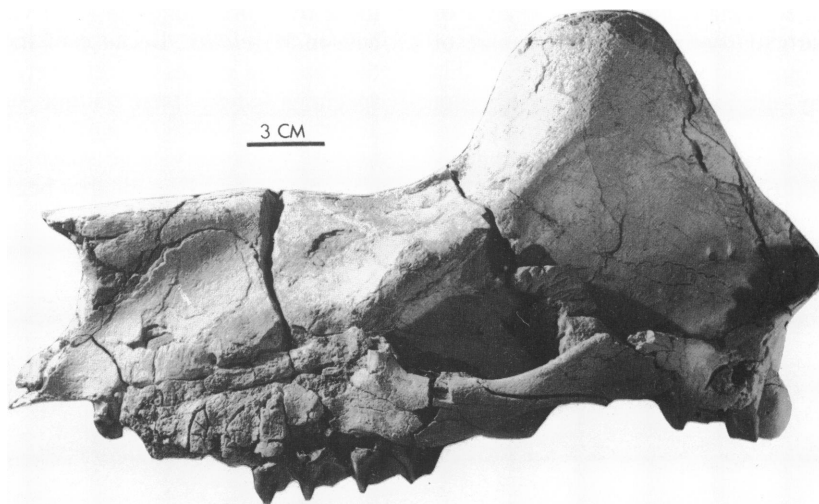F:AM 54918. × 1.

Fig. 6. Left lateral view of domed skull of UCMP 115867, *T. skinneri*, from the Split Rock vertebrate fauna, Fremont Co., Wyoming. × 1/3.

ramus ascent. Shortening of the jaw and a more vertical ascending ramus are not uncommon trends in chalicotheres (for example, see developments in the genus *Chalicotherium*: figures of *C. grande*, *C. rusingense*, and *C. goldfussi* in Butler, 1965; Schaefer and Zapfe, 1971). Jaws of *T. skinneri* are remarkably similar in other respects to those of *M. elatus*. A reasonably consistent difference in *T. skinneri* is the stronger lingual depression for the passage of blood vessels between the dental foramen and the notch in the posterior border of the jaw, below the articular condyle.

VERTEBRAE AND RIBS: Several vertebrae and ribs are known for *T. skinneri* and generally resemble their counterparts in *M. elatus*. On specimens of cervical ?IV, VI, and VII, the only observable difference is the somewhat greater transverse broadening of the posterior part of cervical VI.

The dorsal vertebrae (thoracics and lumbars) are known only in the holotype. Dorsals III and IV show several differences from counterparts in *M. elatus*: (1) the centrum is relatively taller compared with its width, especially so ventral to the facets for the rib capita; (2) the pre- and postzygapophyses are smaller and more circular; and (3) the caput articulations for ribs III and IV are not adjacent but separated by a

small expanse of bone. Three adjacent dorsals, probably IX, X, and XI, are quite similar to dorsals of *M. elatus*. The spine of dorsal ?IX tapers more strongly, however, and on dorsal ?X the anterior caput articulation is much better developed than the posterior. In *Moropus*, dorsals XVI-XXI are lumbars. The single lumbar known of *T. skinneri* appears, by virtue of its dorsoventrally compressed centrum and absence of flat zygapophyses for sacral articulation, to represent the penultimate lumbar (dorsal XX). Differences from dorsal XX of *M. elatus* include the larger neural canal at the expense of the thickness of the neural arch, and the slightly more bladelike, laterally compressed, and anteroposteriorly expanded neural spine.

Four vertebrae of the sacrum are preserved, though in a somewhat damaged condition, in the holotype of *T. skinneri*. These vertebrae are fused together strongly in the centra and at the tips of the neural spines, actually along most of the length of the neural spines (the neural spine of sacral I is broken and its degree of fusion cannot be satisfactorily determined). The posterior slant of the neural spine increases from the first through the fourth sacral, whereas the size of the centrum decreases. On all four sacrals the transverse processes are enlarged and apparently fused for articulation with the

ilium; that of sacral I is particularly broadened. Metapophyses are visible only on the anterior three sacrals and decrease in size from anterior to posterior. The metapophyses on sacral I bear flat articular surfaces for the posteriormost lumbar. Three dorsal foramina are visible between the sacral vertebrae; in the present state of preservation ventral foramina cannot be seen. As preserved, this sacrum shows no important differences from sacra of *M. elatus*, though what is preserved of the neural process of sacral I seems remarkably bladelike and transversely flattened; also there is a very high degree of fusion of the sacrals in this specimen. No caudal vertebrae are known for *T. skinneri*.

A few ribs are preserved for the holotype of *T. skinneri*, but no special differences from ribs of *M. elatus* are apparent.

SCAPULA (FIG. 7): The scapula was oriented in a living animal so that its anterior edge was medial to its posterior edge. As thus oriented, the scapular spine of *T. skinneri* slants posterolaterally from its base, whereas in *M. elatus* the spine is slanted anteromedially except at the tuber spinae, which is strongly reflected posterolaterally. Another difference is that the glenoid fossa in *T. skinneri* is truncated posterolaterally and thus has a subtriangular rather than oval outline, as well as a smaller area. The coracoid process, anteromedial to the glenoid fossa, is unusually prominent and rugose. The subscapular surface has a distinct posterior concave area, which is not so well defined on scapulae of *M. elatus*.

HUMERUS (FIG. 8A): The proximal end of the humerus is damaged or lost on all known specimens of *T. skinneri*. A few proportional differences from humeri of *M. elatus* are visible in the distal end. For example, the shaft does not narrow so much distally as it does in *M. elatus*. The entepicondyle remains as strongly developed as in *M. elatus*, and the ectocondylar ridge (supinator crest) and ectepicondyle are more strongly developed than in *M. elatus*. Increased development of the ectepicondyle in *T. skinneri* parallels a similar development in *Ancylotherium* (*A.*) *pentelicum*, but in neither species is the ectepicondyle so strongly developed as in other perissodactyls.

RADIUS/ULNA (FIG. 8B): Although a number

of radius and ulna specimens are available, there are few consistent differences from *Moropus* that can possibly be regarded as of any taxonomic value. The degree of fusion between radius and ulna is variable but usually involves the distal ends and sometimes much of the shafts (F:AM 54892 from the Split Rock vertebrate fauna shows an unusual degree of shaft fusion). Whether or not strong fusion occurred, it is unlikely that the radius was capable of any movement against the ulna. The anconeal process on the ulna is taller and more sharply de-
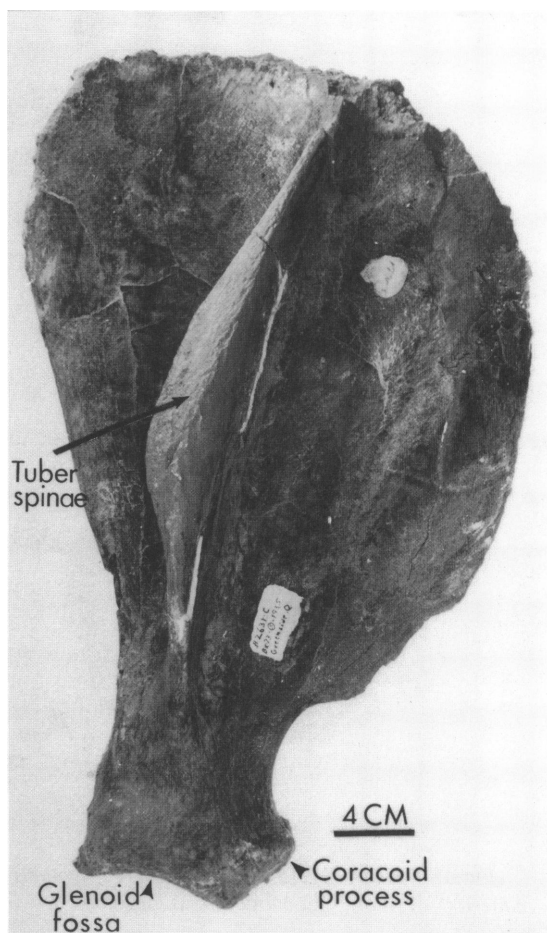
FIG. 7. Anterolateral view (anteromedial edge at right) of right scapula of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. × 1/4.
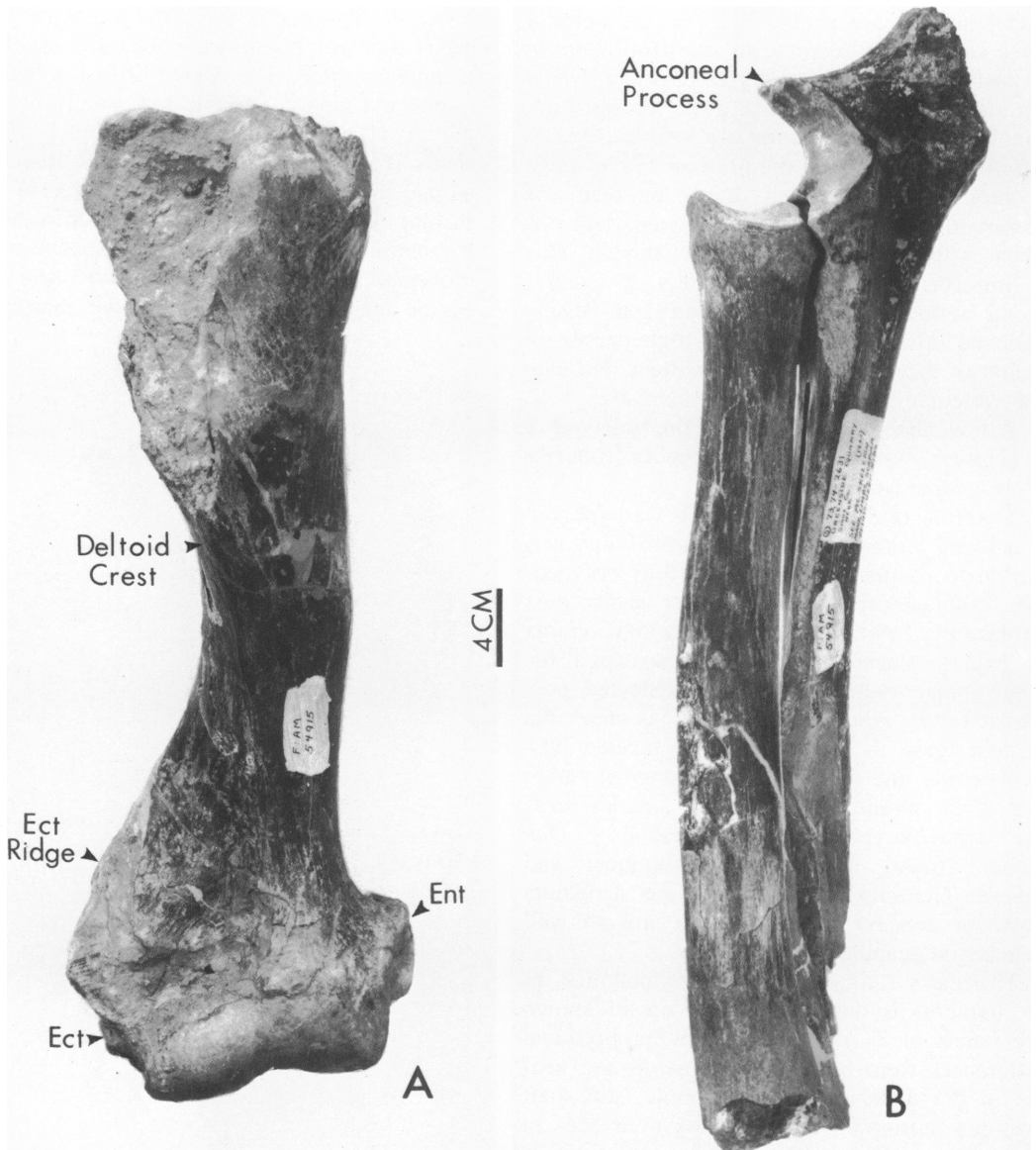
FIG. 8. F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Anterior view of right humerus. B. Radial view of right radius/ulna. × 1/4.

fined in *T. skinneri* than in *M. elatus*. The most lateral (ulnar) part of the proximal facet between radius and ulna is usually slightly smaller but more sharply delineated than in *M. elatus*.

CARPALS: The scaphoid of *T. skinneri* differs from its counterpart in all species of *Moropus*. The proximal surface, however, resembles quite closely that in *M. elatus* in that the articular surface for the radius is weakly convex and

lies on a platform, while the ulno-volar protuberance remains separate and free of any facet. On the radio-volar side of the bone (fig. 9D), a smooth trapezium facet is definitely present, separated from the trapezoid facet by only a blunt ridge. The saddle-shaped trapezoid facet differs from that in *M. elatus* only in being less concave in its volar part and not extending quite so far in the volar direction. On the ulnar side of the bone (fig. 9C), the proximal lunate facet is like that of *M. elatus*, but the distal one does not contact the trapezoid facet as it does in *M. elatus*. The difference is

not due so much to a change in the shape of the distal lunate facet as to one in the distal (centrale) process and the facet for the magnum. The magnum facet (fig. 9B,C) is quite elongated so that it comes between the distal lunate facet and trapezoid facet. In coordination with the elongation of the magnum facet, the distal end of the distal process is not squared as in *M. elatus* but elongated and slanted. The more elongated magnum facet and less squared distal process are the most obvious differences from the scaphoid of *M. elatus*.

Facets on the lunate are similar to those of
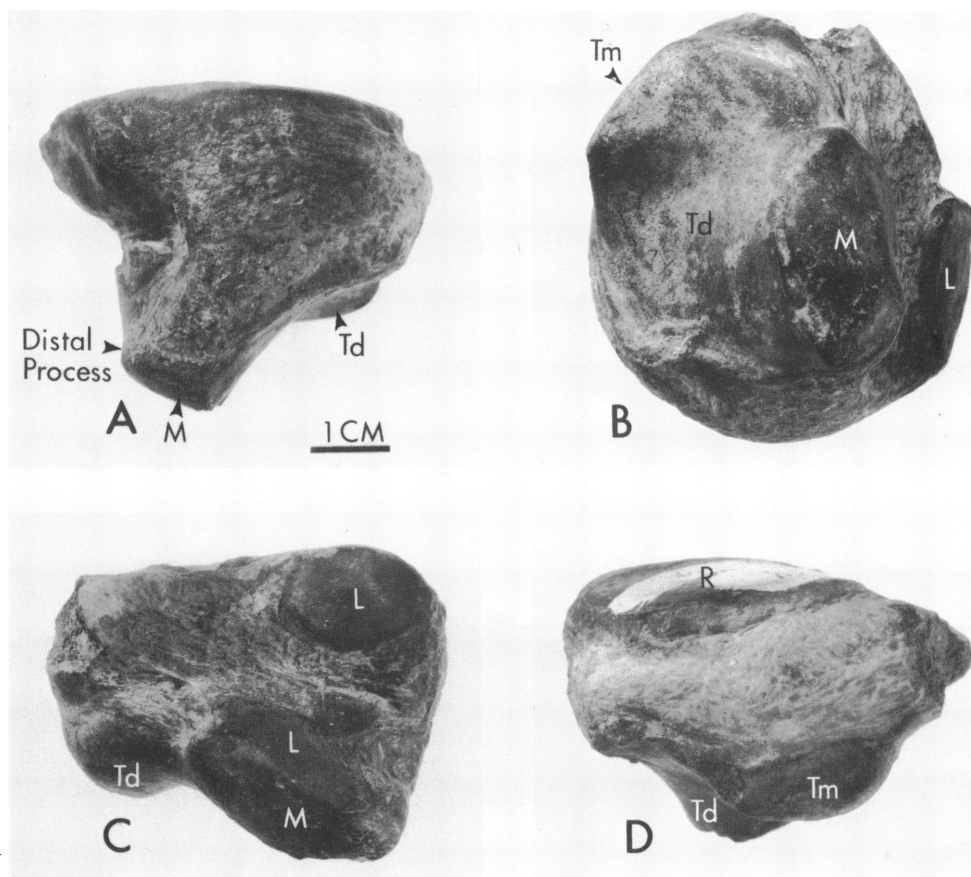
FIG. 9. Right scaphoid, F:AM 54931, *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Dorso-radial view. B. Distal view (dorsal edge at bottom). C. Ulnar view (dorsal edge at right). D. Radio-volar view. Abbreviations for facets in figs. 9-16; R = radius, U = ulna, S = scaphoid, L = lunate, Cn = cuneiform, Un = unciform, M = magnum, Td = trapezoid, Tm = trapezium, 2 = Mc II, 3 = Mc III, 4 = Mc IV, 5 = Mc V. × 1.

M. elatus. The shapes of the radius and proximal scaphoid facets (fig. 10A,C) suggest that the lunate was somewhat compressed in the dorsal to volar direction compared with that of
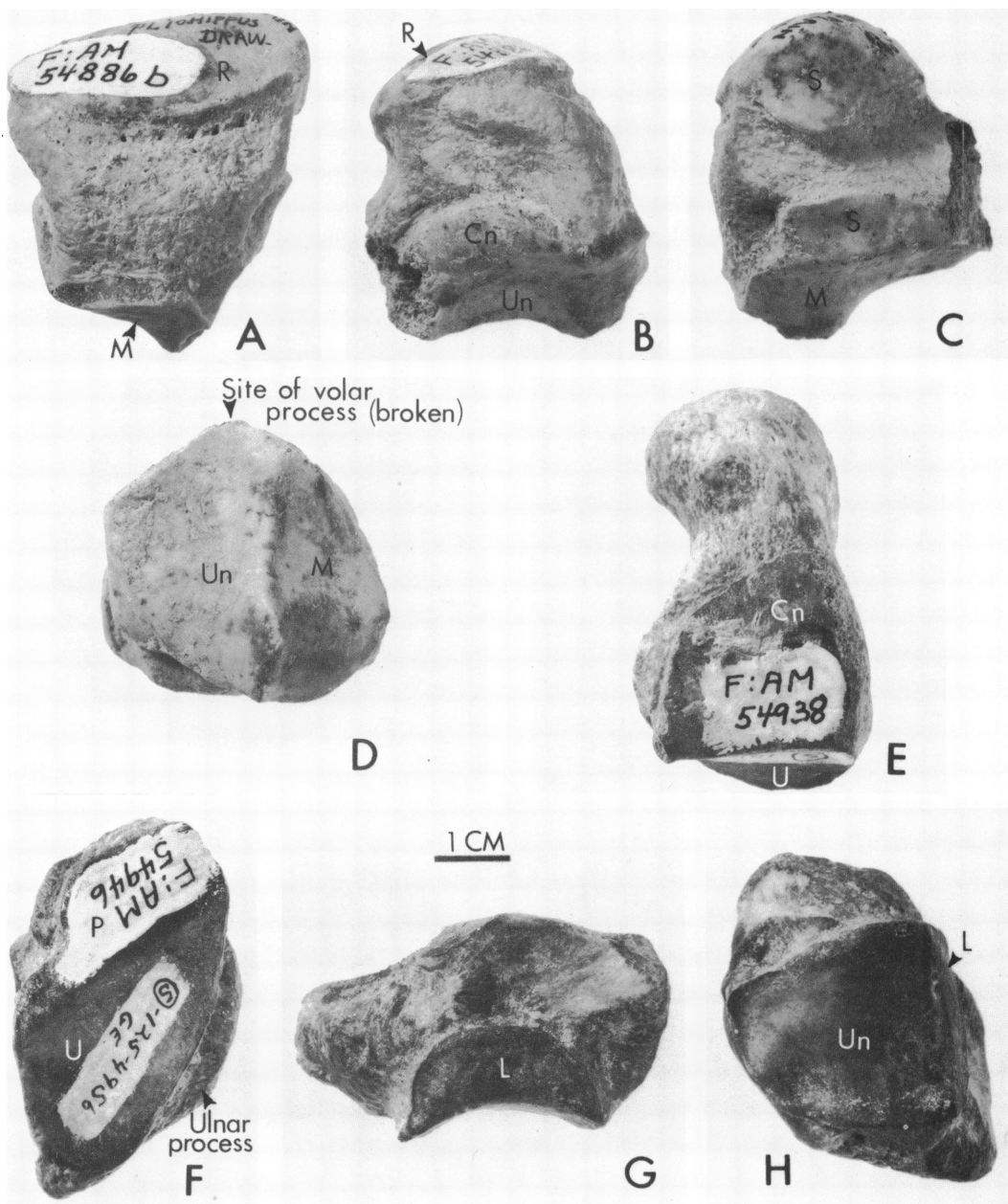
FIG. 10. Right lunate, F:AM 54886b, *T. skinneri*: A. Dorsal view. B. Ulnar view (dorsal edge at right). C. Radial view. D. Distal view (dorsal edge at bottom). Right pisiform, F:AM 54938, *T. skinneri*: E. Distal view. Left cuneiform, F:AM 54946, *T. skinneri*: F. Proximal view (dorsal edge at bottom). G. Radial view (dorsal edge at right). H. Distal view. All from the Sheep Creek Fm., Sioux Co., Nebraska. Abbreviations in figure 9. × 1.

M. elatus. However, the volar process is not especially shortened, unlike that in *Ancylotherium*. The elongated distal facet for the scaphoid (fig. 10C) is demarcated by a ridge from the magnum facet all along its length, but the dorsal and volar parts of the magnum facet, on the distal surface of the magnum with little or no curvature onto the dorsal surface, are nearly continuous with one another.

The cuneiform does not differ greatly from specimens of *M. elatus*. It is, however, broader in comparison to its dorsal to volar thickness and has a larger ulnar process (fig. 10F,H). The increase in width of the cuneiform in *T. skinneri* is primarily due to increase in size and rugosity of the ulnar process. As in *M. elatus*, the pisiform facet is only slightly elevated above the facet for the ulna. This latter facet is flat rather than concave and only slightly larger in area than the pisiform facet. On the distal surface of the cuneiform (fig. 10H) the unciform facet is especially wide, but otherwise unciform and lunate facets are not remarkable compared with those of *M. elatus*.

The two known pisiforms of *T. skinneri* differ considerably from one another in size but not in morphology. Facets for the cuneiform and ulna on these specimens are much the same as in *M. elatus* except that the cuneiform facet forms a larger, longer tongue than does the ulna facet; in *M. elatus* the two facets are subequal in size. The rugose volar end of the pisiform is curved more strongly in the radial direction than that in *M. elatus*, and the constriction in the middle part of the bone is greater (fig. 10E).

Unciforms of *T. skinneri* also are generally similar to those of *M. elatus*. In *T. skinneri*, however, the cuneiform facet (fig. 11C) has a slightly more ulnar orientation and is more strongly convex in its volar part. On the radial surface (fig. 11B) the weakly expressed junction between magnum and Mc III facets is oblique, the magnum facet extending less than halfway in the distal direction at its dorsal end but more than halfway at its volar end. As in *M. hollandi* and some specimens of *M. elatus*, a small strip of the magnum facet bordering the lunate facet extends for a short distance in the volar direction. The division between facets for Mc III and Mc IV is marked by a distinct ridge. Of these two facets, the former extends strongly
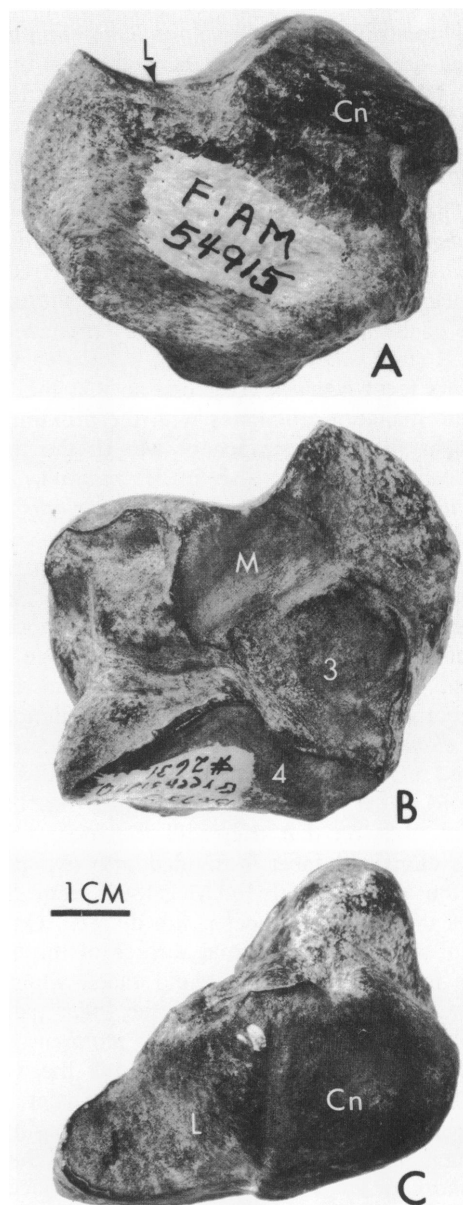

Fig. 11. Left unciform of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Dorso-ulnar view. B. Radio-volar view. C. Proximal view. Abbreviations in figure 9. × 1.

proximally but is restricted to the dorsal half of the bone. The latter, of irregular shape, is somewhat more convex than is the Mc IV facet

in *M. elatus*. No facet for Mc V is present. The unciforms from the Split Rock vertebrate fauna are unusual in that the volar part of the Mc IV facet curves slightly onto the radial surface of the bone and the Mc III facet is more deeply excavated than in other specimens of *T. skinneri*.

There is only one known magnum of *T. skinneri*; a second specimen from Utah resembles it in many respects and is referred to *Tylocephalonyx* sp. The distal half of the radial side of the magnum is occupied by the facet for Mc II (fig. 12B,C). There is a radial extension of this facet near its volar end so that this part of the magnum articulates with the proximal as well as the ulnar surface of Mc II; the radial extension is present also in *M. matthewi* and *M. merriami* but much less in *M. elatus* and *M. hollandi*. There is a small trapezoid facet on the proximal side of the extension. Separated from the small trapezoid facet by a depression is a more elongated, more proximal trapezoid facet, which borders at its proximal edge part of the scaphoid facet. The two trapezoid facets are completely different from the articulation in *M. elatus* and *M. matthewi*, but they correspond closely to magnum facets on the trapezoid of the holotype of *T. skinneri* (fig. 13C), except that on that trapezoid the more proximal, elongated facet is divided into two parts; on the trapezoid of F:AM 54892 from Split Rock the elongated facet is not divided. On the radial side of the proximal surface of the magnum is the elongated scaphoid facet, which in *T. skinneri* occupies more of the volar part of the bone than in *M. elatus* or *M. matthewi* (fig. 12A,B). The scaphoid facet shares the volar part of the magnum with the lunate facet. Lunate and unciform facets (fig. 12D) are similar to their counterparts in *Moropus*, except that in *T. skinneri* the volar part of the lunate facet is narrower, in correspondence with the increased width of the volar part of the scaphoid facet. On the distal surface of the magnum (fig. 12B,C,D) there is a well-developed volar hook curving in a distal and volar direction. This hook is somewhat stronger than the hook in *M. elatus* so that the Mc III facet is elongated. The Mc III facet is narrow transversely (fig. 12C)

and is not divided by a longitudinal ridge such as that of *M. matthewi*. The magnum of *T. skinneri* is deeper in proportion to its width than that of any species of *Moropus*.

The dorsoradial and volar surfaces of trapezoids of *T. skinneri* are very similar to those of *M. elatus* (fig. 13D). In both, the transversely convex scaphoid facet curves onto the volar surface to adjoin, without sharp delineation, the facet for the trapezium. The latter facet in turn contacts the facet for Mc II across a sharp ridge. The Mc II facet is not so transversely convex in *T. skinneri* as in *M. elatus* but nevertheless curves slightly onto the ulnar surface of the bone (fig. 13B). In correspondence with differences on the articulating surface of the magnum, the ulnar surface of the trapezoid (fig. 13C) differs most strongly from that of *M. elatus*. The scaphoid facet does not curve onto the ulnar side of the trapezoid but adjoins the single (F:AM 54892) or double (F:AM 54915) proximal facet(s) for the magnum. The other, more distal, magnum facet is separated from the Mc II facet by a sharp crest.

It is clear from the facets for a trapezium on scaphoid, trapezoid, and Mc II that a trapezium was present in *T. skinneri*, but no such specimen is known.

METACARPALS: Mc II differs in several important ways from that of *M. elatus*. The trapezium facet (fig. 14A,B) is of similar size and shape but is slightly more concave. The most important difference is in the shape of the trapezoid and magnum facets and in the relations between them (fig. 14A,B,D). As in *M. elatus*, the trapezoid facet is concavely V-shaped, forming the middle part of an M outlined by the radiodorsal edge of the proximal end (fig. 15A). The trapezoid facet is set off by sharp ridges from trapezium and magnum facets only in its dorsal part. The volar part of the trapezoid facet is, in contrast to that in *M. elatus*, flat or only weakly concave and is set off by only a weak ridge from the volar part of the magnum facet. Dorsal and volar parts of the trapezoid facet are demarcated from each other by a weak convexity. The magnum facet, almost completely on the ulnar side of the bone, is quite differently oriented in *T. skinneri* than
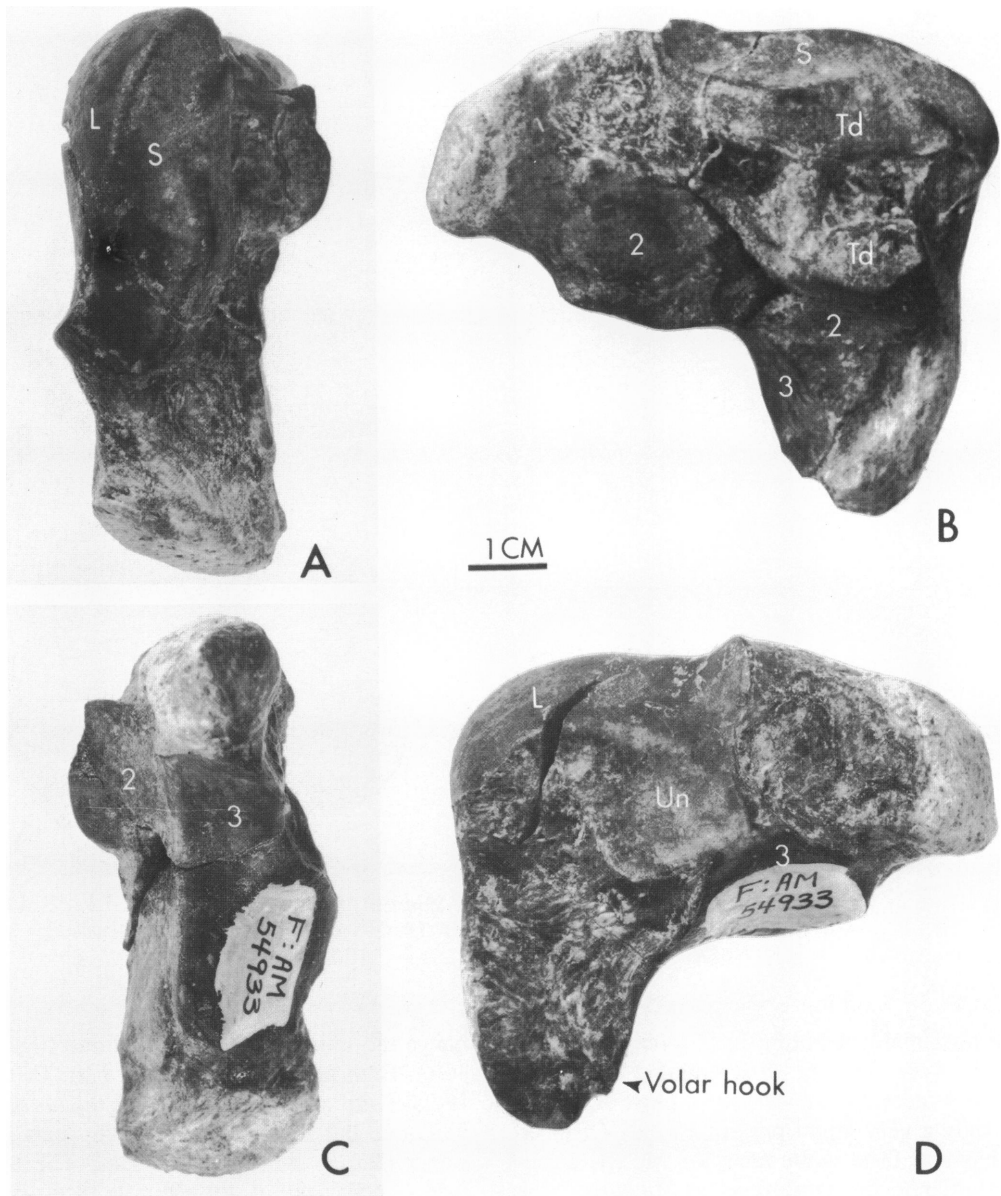
FIG. 12. Right magnum of F:AM 54933, *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Proximal view (dorsal edge at bottom). B. Radial view (dorsal edge at right). C. Distal view. D. Ulnar view. Abbreviations in figure 9. × 1.

in *M. elatus*. At its volar end the magnum facet faces almost entirely in the proximal direction and occupies the proximal surface of Mc II on both ulnar and volar sides of the trapezoid

facet. It is this extension of the magnum facet that causes the increased proportional depth of Mc II compared with that of *M. elatus*. The dorsal part of the magnum facet, which has
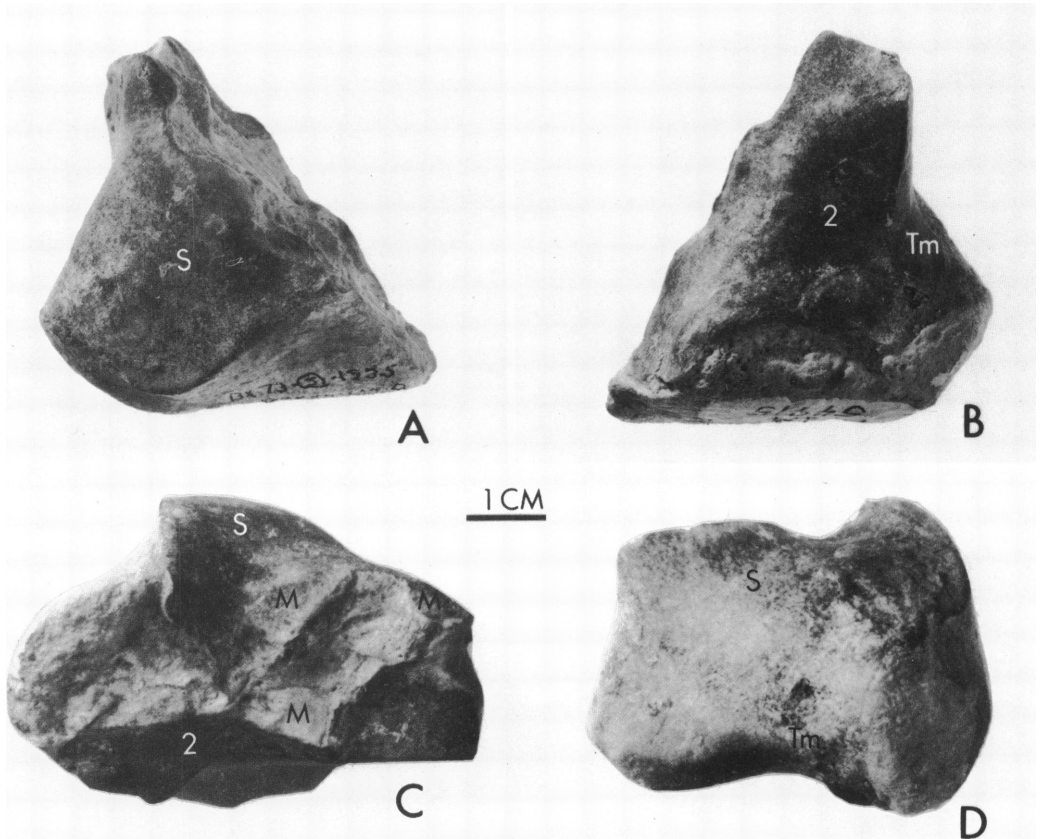
FIG. 13. Left trapezoid of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Proximal view (dorsoradial edge at bottom). B. Distal view. C. Ulnar view (dorsal edge at left). D. Radio-volar view. Abbreviations in figure 9. × 1.

some proximal orientation in *M. elatus*, is in *T. skinneri* very sharply differentiated from the trapezoid facet and faces in the ulnar direction with only a very slight proximal slant. Distal to the magnum facet is the facet for Mc III, basically similar to the same facet in *M. elatus*, but overhung by the magnum facet for less of its extent. At the distal end of Mc II the ridge between sesamoid facets may be more sharply defined than in *M. elatus*, but it is hard to tell whether the difference is consistent.

A single Mc III, F:AM 54969, is known for *T. skinneri*. The radial edge of the Mc II facet is in this specimen a sharp crest which over-

hangs the radial surface of the bone (figs. 15B, 16A). Both proximal and dorsal parts of the Mc II facet are continuous as in *M. elatus* and *M. hollandi*, but the proximal convex part is narrower than in the earlier species. The tongue-like dorsal part of the Mc II facet is more concave transversely. A pronounced ridge separates the Mc II facet from the magnum facet, which is strongly concave in its dorsal part (forming a depressed pit) and has a narrow, convex, volar part (fig. 16A). The dorsal part of the magnum facet is very sharply delineated from the adjoining unciform facet by a tall, sharp crest. However, this crest ends very

abruptly in the volar direction, so that the narrow volar part of the magnum facet is not bounded by an ulnar crest (where it has no contact with the unciform facet). At this point the volar part of the magnum facet curves strongly onto the proximal part of the ulnar
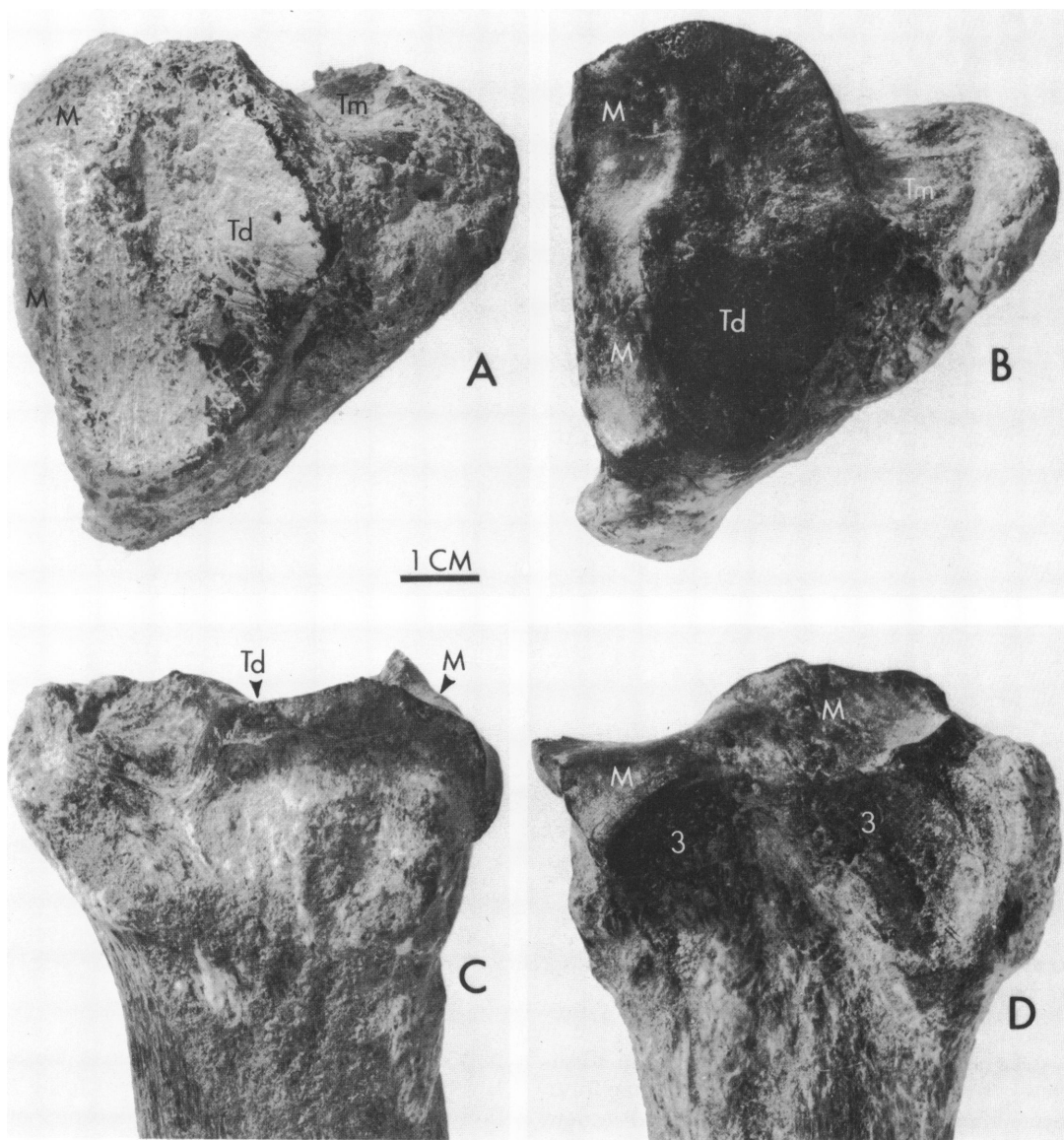
FIG. 14. Right Mc II, F:AM 54910, *T. skinneri*, from Site 2 Prospect, Pepper Creek, Dawes Co., Nebraska: A. Proximal view (dorsal edge at bottom). Right Mc II, F:AM 54971, *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska: B. Proximal view. C. Dorsal view (ulnar edge at right). D. Ulnar view. Abbreviations in figure 9. × 1.
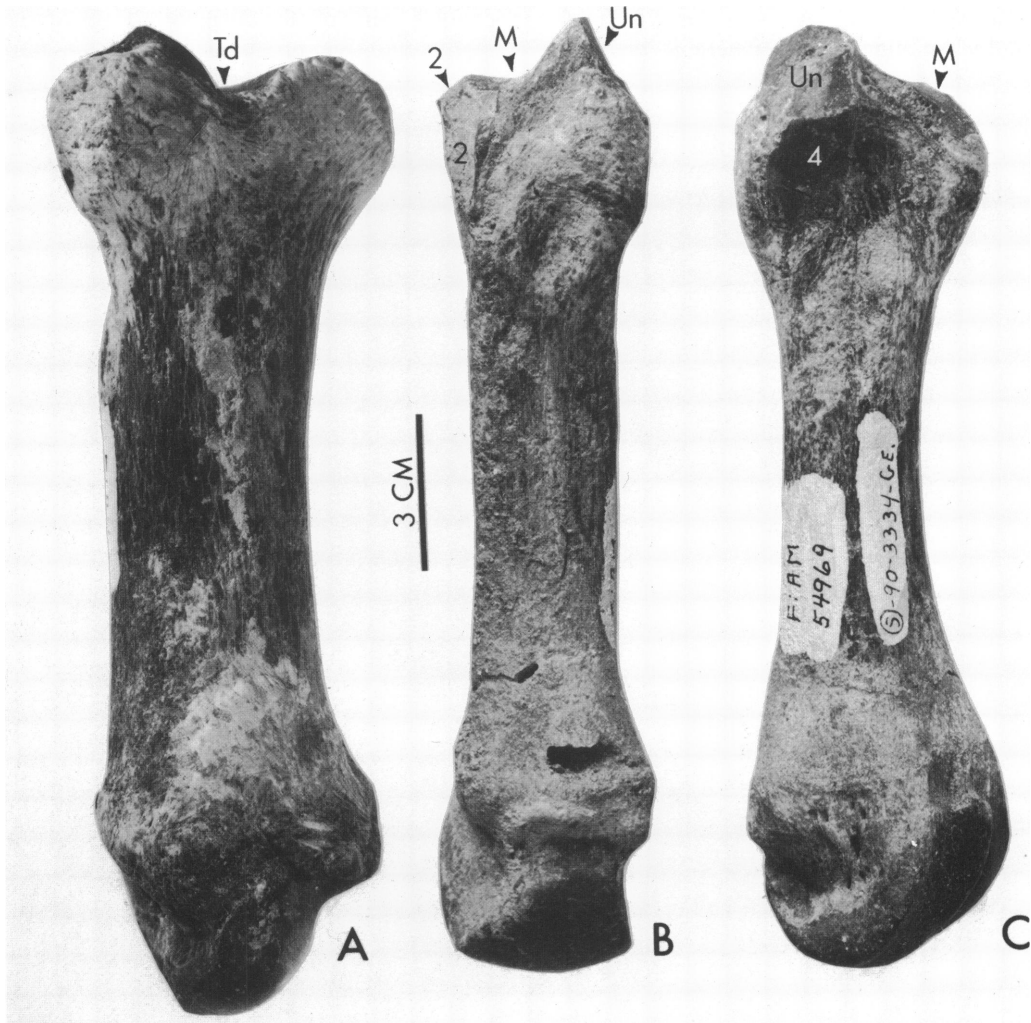
FIG. 15. Right Mc II, F:AM 54971, *T. skinneri*: A. Dorso-radial view. Left Mc III, F:AM 54969, *T. skinneri*: B. Dorsal view. C. Ulnar view. Both specimens from Sheep Creek Fm., Sioux Co., Nebraska. Abbreviations in figure 9. × 2/3.

surface so that it is easily visible in an ulnar view of the bone (fig. 15C). The unciform facet, abruptly truncated in the volar direction by a sinus, has an irregular surface, bounded proximally by the sharp junction with the magnum facet and distally by a weaker crest overhanging the facet for Mc IV. There is only a single facet for Mc IV, but this facet is different from that described in *M. elatus* and *M. hollandi*. The single Mc IV facet represents only the dorsal lobe or dorsal facet of the earlier species, the volar part (or facet) being entirely lost. The Mc IV facet thus occupies only the proximodorsal part of the concavity in the proximal part of the ulnar surface (fig. 15C). A dorsal rugosity is present on the shaft of Mc III just distal to the unciform facet, and there is a short volar longitudinal ridge onto the shaft from the magnum facet. The dorsal surface of the shaft is flat.

Only one specimen of Mc IV of *T. skinneri* is complete. The most important feature of the radial side of the proximal end is the complete absence of the volar facet for Mc III (fig. 16B,C). The single dorsal facet is more similar to the dorsal Mc III facet (or part of facet) in *M. elatus* than to that in *M. hollandi*. Even more than in *M. elatus* however, the Mc III facet passes onto some of the proximal part of the dorsal surface of Mc IV, where it sits on a strong, otherwise rugose, dorsoradial protuberance. The ridge separating the Mc III and unciform facets continues in the volar direction

beyond the Mc III facet; in this area the radial surface of Mc IV is rough. The unciform facet (fig. 16B), very similar to its counterpart in *M. elatus*, is cut at its ulno-volar edge by a notch, which is the most proximal edge of a large depression on the ulno-volar surface. The depression (fig. 16D) served as a facet for Mc V (of which no specimen is known) and differs from the facet in *M. elatus* in being uniformly concave and extending farther proximally. There are rugose protuberances both dorsal and volar to the Mc V facet. Specimens of Mc IV of *T. skinneri* have in general a greater proxi-
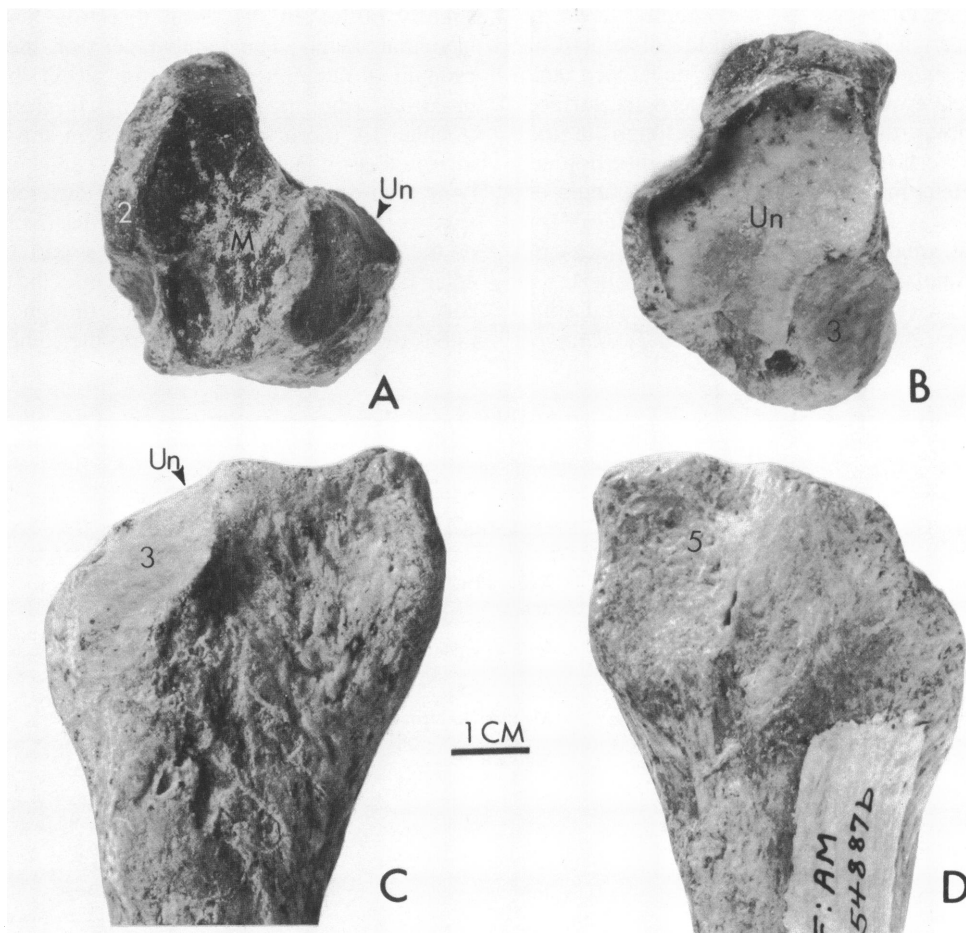

FIG. 16. Left Mc III, F:AM 54969, *T. skinneri*: A. Proximal view (dorsal edge at bottom). Right Mc IV, F:AM 54887b, *T. skinneri*: B. Proximal view (dorsal edge at bottom). C. Radial view. D. Ulno-volar view. Both specimens from Sheep Creek Fm., Sioux Co., Nebraska. Abbreviations in figure 9. × 1.

mal depth compared to width than do those of *M. elatus*.

Phalanges of the manus are discussed in a separate section along with those of the pes. Table 5 summarizes important differences of the manus among various chalicothere species.

INNOMINATE AND FEMUR: Both the innominate (the holotype only, fig. 17A) and femora (two specimens, fig. 17B) are known for *T. skinneri*. Neither differs in any important way from specimens of *M. elatus* or *M. hollandi*.

TIBIA (FIG. 17C): Tibiae of *T. skinneri* are similar in proportions and morphology to tibiae of *Moropus*. However, in *T. skinneri* the rugose proximal end of the cnemial crest is separated by a depression from the distal end of the crest and is more strongly developed and less concave. On the posterior (volar) surface of the tibia, the depression just opposite the cnemial crest (presumably for the insertion of the popliteus muscle) is very deep. No fibula of *T. skinneri* is known, but articular surfaces for the fibula are visible on the lateral surfaces of the proximal and distal ends of the tibia.

PATELLA (FIG. 18): Despite the general similarities in femur and tibia between *T. skinneri*

and *M. elatus*, the patella differs, on the average, in quite noticeable ways. These differences are summarized in table 6.

TARSALS: Astragali of *T. skinneri* differ in several ways from specimens of *M. elatus* and *M. hollandi*. There is some development of a distal neck, but this neck is smaller than in the earlier species. Unlike *Moropus*, the tibial and fibular sides of the astragalar trochlea are of approximately equal width and shape (slant), and the fibular side extends both farther proximally and farther distally than the tibial side (figs. 19A, 20A). The free distal extension of the fibular side of the trochlea hangs very slightly farther in the distal direction than the navicular facet. The ectal facet for the calcaneum is moderately deep (fig. 20A), but its proximal edge (ridge separating it from the trochlea) is more strongly slanted in the distal direction as it passes toward the center of the bone than occurs in *M. elatus*; the difference in slant is related to the equality of the two sides of the trochlea. The most concave part of the ectal facet is its proximal part, while the distal part is only gradually concave, though separated by a distinct ridge from the otherwise

TABLE 5

Summary of Known Characters of the Manus (excluding Phalanges) of *Moropus elatus*, *Moropus hollandi*, *Moropus matthewi*, and *Tylocephalonyx skinneri*

| Character	M. elatus	M. hollandi	M. matthewi	T. skinneri
1. Trapezium	Present	Reduced or absent	Probably present	Present
2. Distal process of scaphoid	Strong, squared	Strong, squared	Strong, oblique	Reduced, oblique
3. Volar process of lunate	Medium to strong	Medium to strong	—	Medium
4. Disto-volar hook on magnum	Medium	Medium	Reduced	Medium
5. Mc III facet on radial side of unciform	Small extent	Small extent	—	Extends halfway proximally
6. Facets between magnum and trapezoid	Two small	Two small	Two small	Three larger (sometimes fused to two)
7. Facet between Mc III and Mc IV	One or two (dorsal and volar)	One or two (dorsal and volar)	—	Single (dorsal only)
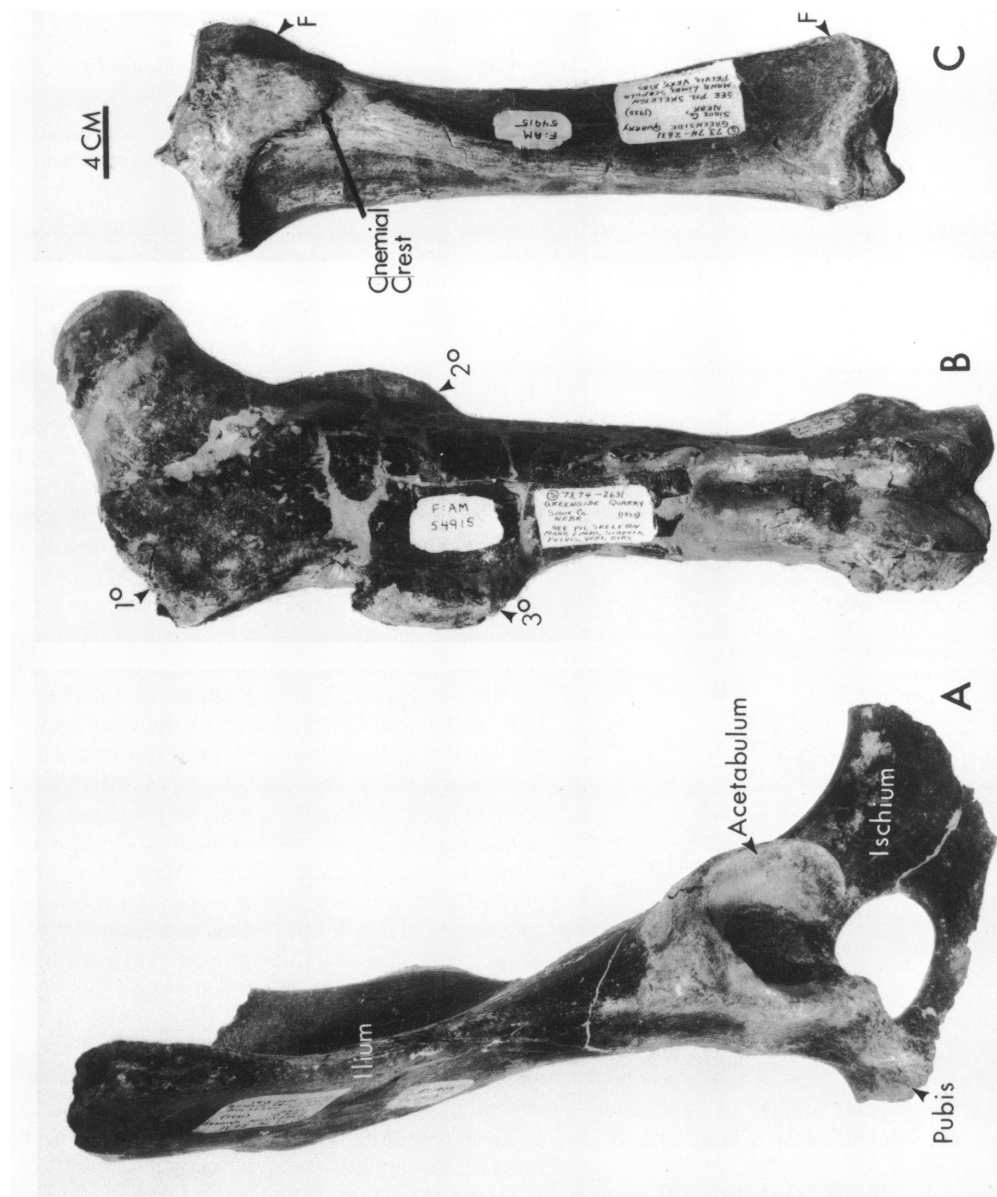
Fig. 17. Hindlimb bones of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Lateral view of left innominate. B. Anterior view of right femur. C. Anterior view of right tibia. Abbreviations: F = articulation for fibula, 1°, 2°, 3° = greater, lesser, and third trochanters.

TABLE 6
Comparison of Patellae of *Tylocephalonyx skinneri* with Those of *Moropus elatus*

Character	T. skinneri	M. elatus
1. Facet for femur	Broad, width about equal to height	Width less than height
2. Trochlear ridge between left and right sides of facet for femur	Sharp, curved sides of facet at right angles (or slightly obtuse) to each other	Blunt, curved sides of facet at obtuse angle to each other
3. Rugosity of anterior (dorsal) surface	Strong, large ridge present for insertion of knee extensors	Medium, some development of ridge for insertion of knee extensors
4. Distal tongue at patella apex	Absent (except in one known specimen)	Present (except in one known specimen)

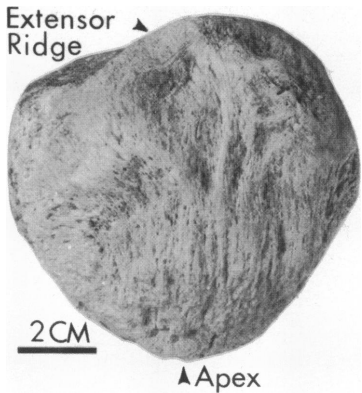FIG. 18. Anterior (= dorsal) view of patella, F:AM 54962, *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. × 1/2.

confluent calcaneal facet. There is a concave rather than convex sustentacular facet, and the single, pear-shaped, distal facet (for the navicular) does not extend so far tibially in its narrow part as it does in astragali of *M. elatus* and *M. hollandi*.

The tuber calcis of calcanea of *T. skinneri* (figs. 19B, 20B) is both shorter and broader than that in *M. elatus*; its section is only weakly triangular, and there is not so strong a rugose volar protuberance at the end of the tuber. Another difference from *M. elatus* is that

the ectal facet does not extend so far onto the tuber but is transversely very broad and strongly extended in the tibial direction at the base of the tuber calcis (fig. 20B). The degree of convexity of the ectal facet is not so great as in *M. elatus*; it varies among individuals, but in most is gently rather than abruptly curved throughout its surface. On most calcanea there is a facet for the tibia in continuation with that on the astragalus, but in contrast to *M. elatus* this facet is on the tibial side of the ectal facet, not on the part of the ectal facet farthest onto the tuber. When the calcaneum is articulated with the astragalus, the concave proximal end of the ectal facet on the astragalus (see above) forms a sort of hook which conforms to the gradually convex form of the ectal facet on the calcaneum. This "hook" does not occur in *M. elatus*. On the well-developed sustentacular process of the calcaneum, the sustentacular facet is more distally slanted than is that in *M. elatus*. The distal facet (for the cuboid) is flat and broadly pear-shaped but ends rather abruptly (and bluntly) in the tibial direction.

Despite some small individual variation in facet shape among the few known cuboids of *T. skinneri*, there is general resemblance to cuboids of *M. elatus*. In the holotype, the dorsal end of the facet for the calcaneum (proximal surface, fig. 22A) is concave and forms against the calcaneum an articulation in which little or no lateral slip was possible. The facet
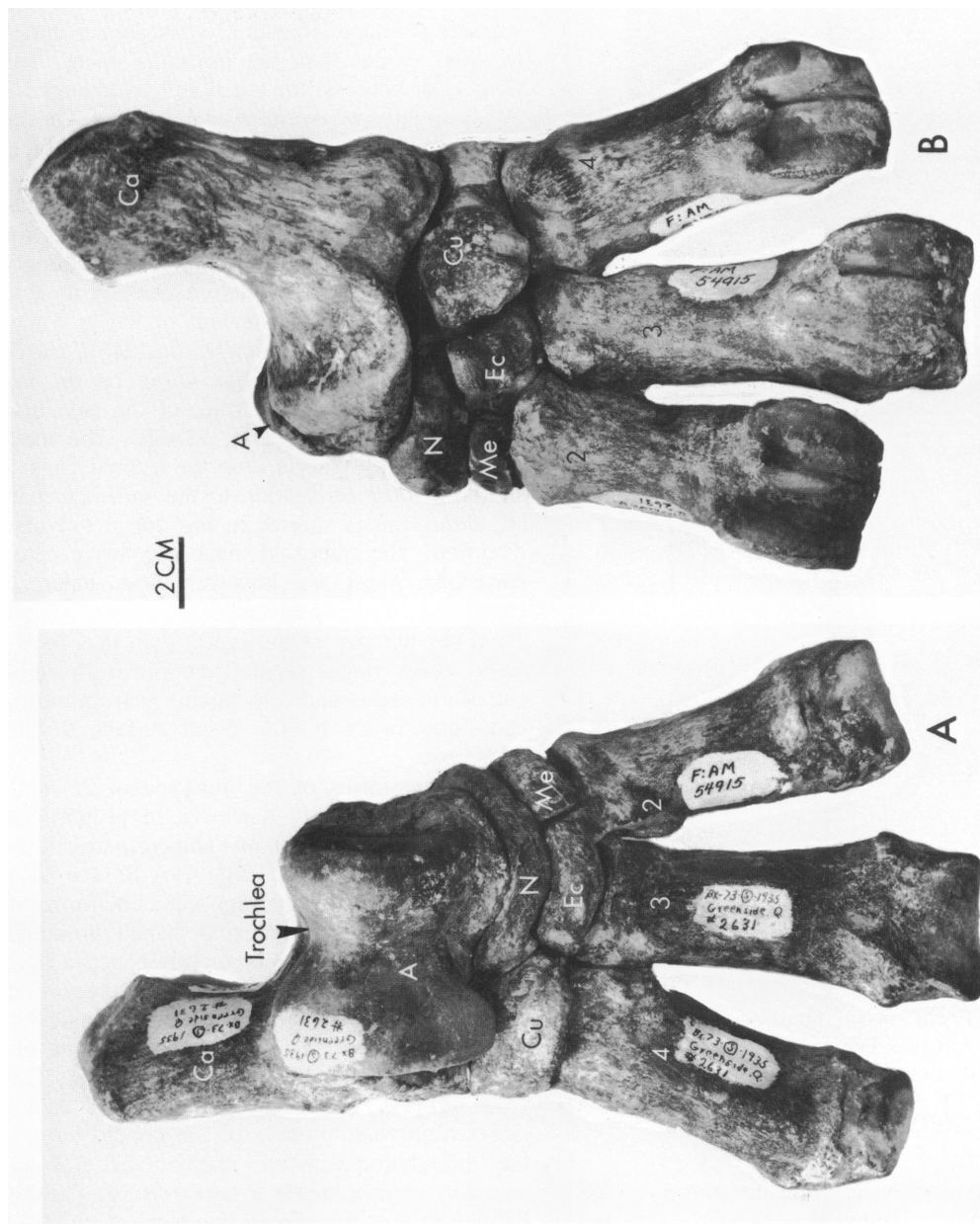
FIG. 19. A. Dorsal, and B. Volar views of right pes of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. Abbreviations of bones in this figure and of facets in figures 21-24, 28C-F, 29D-G: A = astragalus, C = calcaneum, N = navicular, Me = mesocuneiform, Ec = ectocuneiform, Cu = cuboid, 2 = Mt II, 3 = Mt III, 4 = Mt IV. Entocuneiform not available.
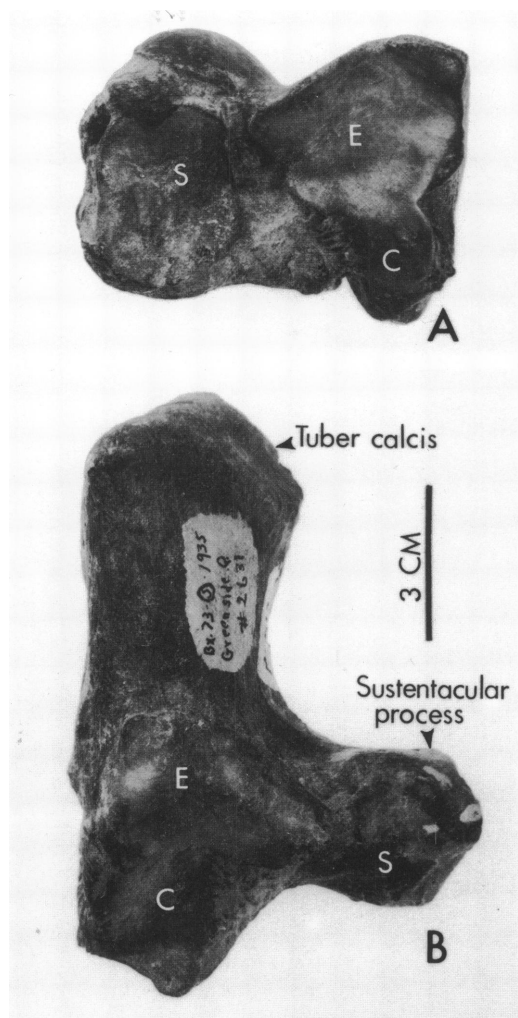
FIG. 20. F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Volar view of right astragalus. B. Dorsal view of right calcaneum. Facet abbreviations: E = ectal, S = sustentacular, C = calcaneal. × 2/3.

for the navicular on the tibial surface (fig. 23C) is more strongly slanted than in *M. elatus*, and therefore the ectocuneiform facet, still at a V-angle to the navicular facet, has almost a directly tibial orientation. Though the lobate navicular facet extends farther proximally than in *M. elatus*, it has less extent in the dorsal to volar direction. The ectocuneiform facet is not divided into two parts, and although somewhat variable in shape it generally has greater dorsal to volar extent than the navicular facet. The tibio-volar process, though it still overhangs Mt IV, is slightly weaker than in *M. elatus*. On the distal surface of the cuboid (fig. 22B), the facet for Mt IV is flatter than in *M. elatus*.

Two naviculars of the holotype of *T. skinneri* have only a very weakly concave facet for the astragalus, compared to the more strongly curved surface in *M. elatus*. Especially notable is the very weak development of the proximal curve at the tibio-volar angle (fig. 21C), corresponding to a similar weak curve on the astragalus. On the distal surface of the navicular are three facets (figs. 21D, 23A,B). The most fibular of these facets, for the cuboid, has a similar slanted orientation to the same facet in *M. elatus* but is shorter in the dorsal to volar direction. The trapezoid-shaped, concave ectocuneiform facet is, however, less enlarged compared to the mesocuneiform facet (about 1½ times the size of the latter) than it is in *M. elatus*. Low ridges separate cuboid from ectocuneiform facets and ectocuneiform from mesocuneiform facets on the distal surface of the navicular.

Ectocuneiforms of the holotype of *T. skinneri* are considerably narrower in proportions than ectocuneiforms of *M. elatus*, particularly so at the dorsal edge (fig. 21A,B; see also mention below of aberrant ectocuneiform of F:AM 54892). The trapezoid-shaped proximal facet (for the navicular) is slightly concave (fig. 21A). It does not occupy so large a proportion of the proximal surface as does the navicular facet in *M. elatus*, a result of the better developed, rugose volar process in *T. skinneri*. The volar process of the ectocuneiform and the larger tibio-volar process of the cuboid have a tiny articulation with one another (fig. 23B,C) and thus form a single rugose surface. On the fibular surface of the ectocuneiform (fig. 23B), the bandlike cuboid facet has a partial division into dorsal (flatter) and volar (more concave) moieties. Approximately the dorsal two-thirds of the fibular surface is occupied by the cuboid
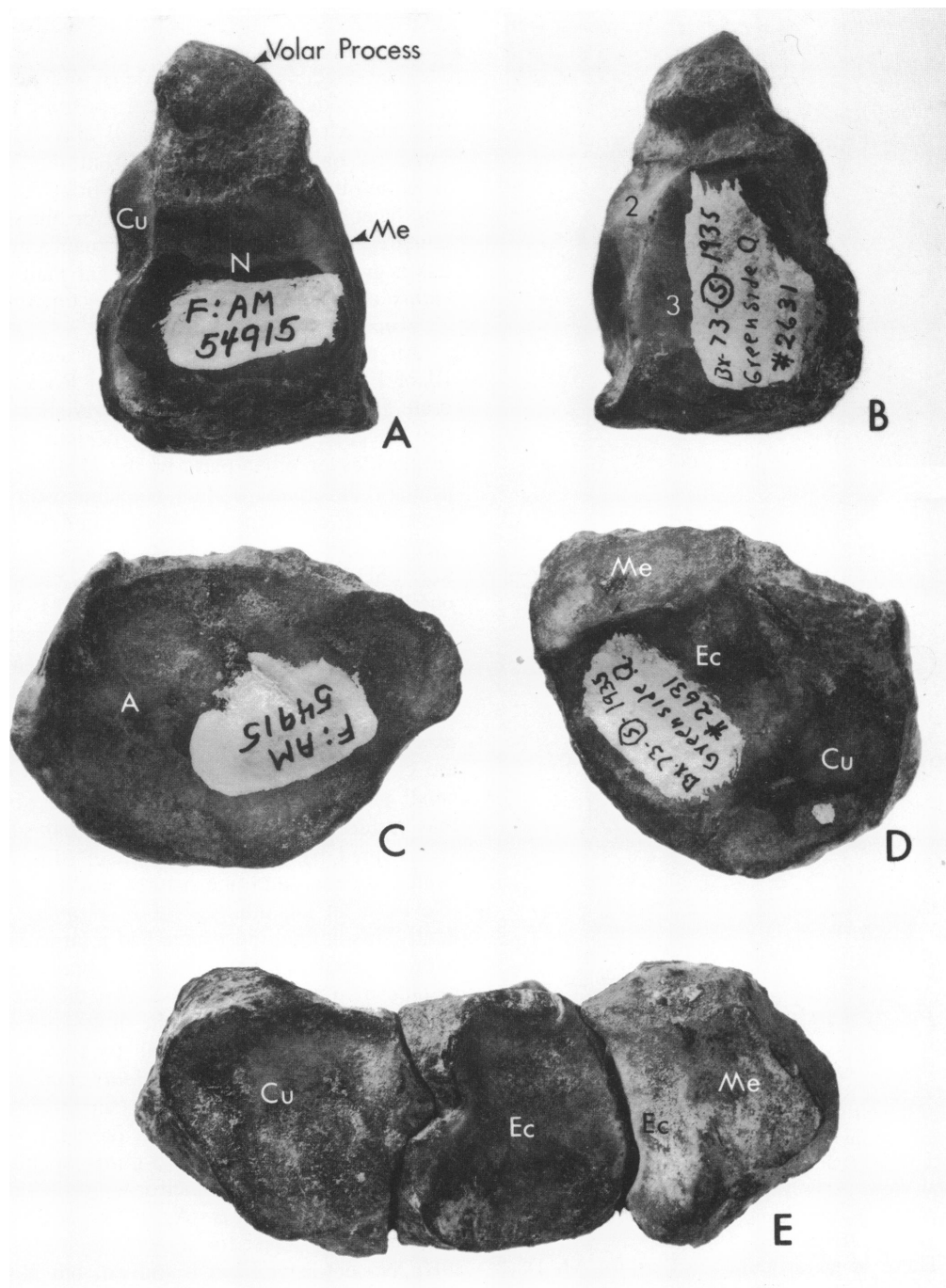
FIG. 21. F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. Right ectocuneiform: A. Proximal view (dorsal edge at bottom). B. Distal view. Right navicular: C. Proximal view (dorsal edge at bottom). D. Distal view. Right Mt IV (at left), Mt III, and Mt II: E. Proximal view. Abbreviations in figure 19. × 1.

FIG. 22. Left cuboid of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Proximal view (dorsal edge at bottom). B. Distal view. Abbreviations in figure 19. × 1.

facet. There is no articular surface for Mt IV, and the distal edge of the fibular surface forms a sharp ridge rather than a rounded facet. On the distal surface (fig. 21B), the Mt III facet does not extend onto the volar process. Division between the distal and tibial surfaces of

the ectocuneiform is made very indistinct by the intermediate (almost distal) position of the bandlike Mt II facet. The Mt II facet is separated by only a blunt ridge from the Mt III facet and by a somewhat sharper ridge from the flat facet on the tibial surface for the mesocuneiform (fig. 23A). The mesocuneiform facet has a greater dorsal to volar extent than in *M. elatus* and suggests that the mesocuneiform in *T. skinneri* was a deeper bone.

An ectocuneiform and proximal end of Mt III of F:AM 54892 from the Split Rock vertebrate fauna show an important variation from the Sheep Creek specimens, despite general similarities of other parts of the skeleton. The primary difference of this ectocuneiform from those of all other known North American specimens is the very large distal facet for Mt II (fig. 28D), which occupies slightly more than one-third of the width of the bone and is widest near its volar edge. The rest of the dorsal part of the distal surface is occupied by the Mt III facet. The facet for the cuboid on the fibular side has dorsal (smaller) and volar (larger and extending onto the volar process) lobes, which are connected only near the proximal edge. A small part of the cuboid facet is on the proximal surface, but most of the proximal surface is occupied by the navicular facet (fig. 28C). Both navicular and mesocuneiform facets are like those in the holotype of *T. skinneri*. Evidently this animal must have had a large cuboid with all tarsals shifted somewhat tibially on the metatarsals (see also discussion of the Mt III).

The mesocuneiform of the holotype of *T. skinneri* has a greater dorsal to volar depth compared with that of *M. elatus* and has a correspondingly longer facet for the ectocuneiform. The slightly convex facet for Mt II, which occupies the volar two-thirds of the distal surface of the mesocuneiform, resembles its counterpart in *M. elatus*. As in *M. elatus* there is a small tibial facet for an entocuneiform (fig. 19B). No entocuneiform is known, but it must have been a small bone that articulated only with the mesocuneiform.

METATARSALS: Metatarsal measurements and proportions are given in tables 7–9. These can be compared with measurements given for *M.*

elatus, *M. hollandi*, and other chalicotheriids (Coombs, 1974, in press). Metatarsal proportions of *T. skinneri* are generally similar to those known for *M. matthewi* and intermediate between those of *M. elatus* and *M. merriami* (metatarsals of *M. hollandi*, where known, fall roughly between those of *M. elatus* and *T. skinneri*). Decrease in proportional length over

time appears to be a general trend in all schizotheriine lineages and by itself provides no evidence of affinities. Metatarsals of *M. matthewi* resemble those of *T. skinneri* in a few respects other than proportions, but with the exception of Mt II (AMNH 9368) are poorly known. No special similarities of other parts of the skeleton occur. The longest metatarsal in *T. skinneri* is
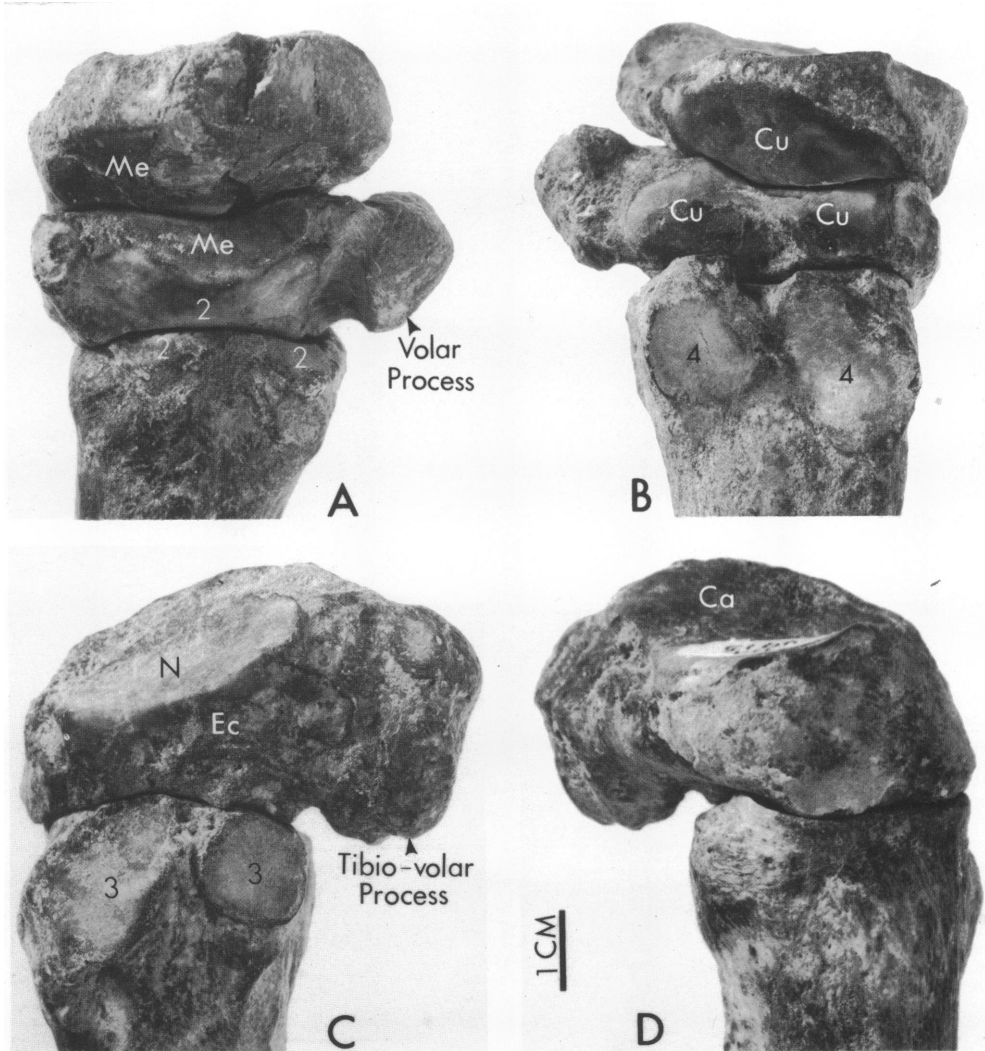
FIG. 23. F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. Right navicular, ectocuneiform, and Mt III: A. Tibial view. B. Fibular view. Right cuboid and Mt IV: C. Tibial view. D. Fibular view.
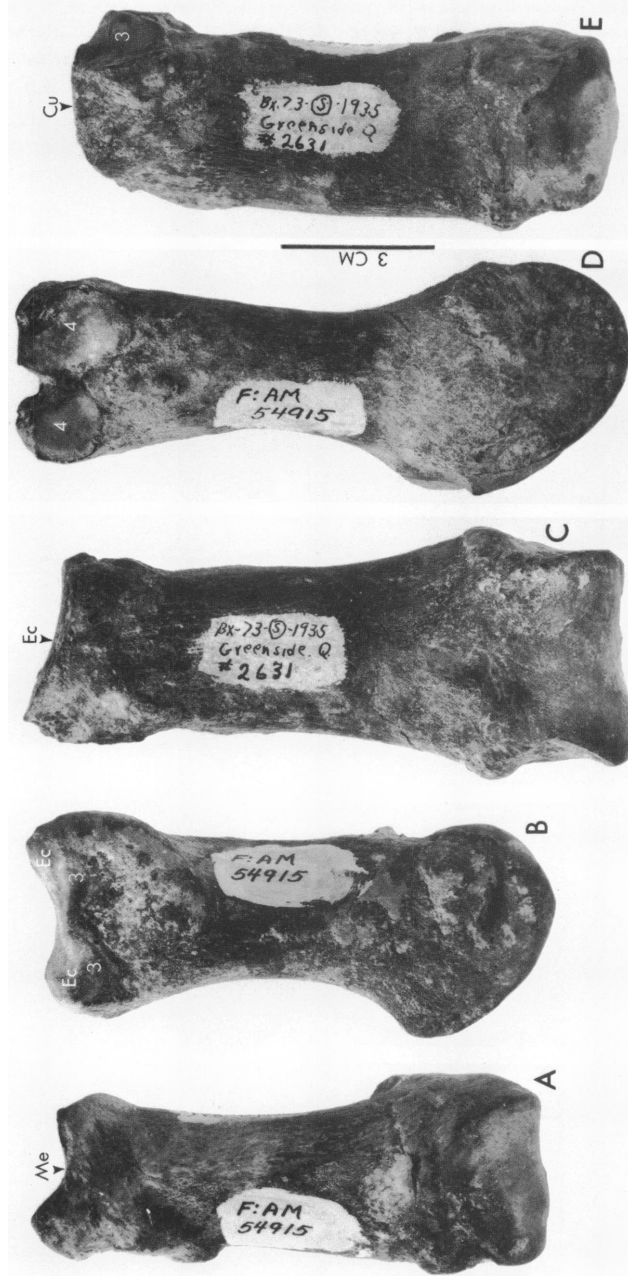
Fig. 24. F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. Right Mt II: A. Dorsal view. B. Fibular view. Right Mt III: C. Dorsal view. D. Fibular view. Right Mt IV: E. Dorsal view. Abbreviations in figure 19. × 2/3.

Mt III (table 7). *Ancylotherium* also shares this character, whereas *Moropus* has Mt III and Mt IV of subequal length. The relative lengths of Mt III and Mt IV in *Schizotherium* and *Borissiakia* are unclear, whereas *Chalicotherium* has Mt IV longer than Mt III. It is not clear whether subequal Mt III and Mt IV or Mt III as the longest metatarsal is primitive within the Schizotheriinae.

The proximal surface of Mt II is subtriangular as is that of *M. elatus* (fig. 21E), but in *T. skinneri* the triangular shape is closer to equilateral and an apex comes in the middle (rather than at one end) of the tibial side. Further, the ectocuneiform facet in *T. skinneri* has an orientation both proximal and fibular, rather than almost exclusively fibular as in *M. elatus*. In *T. skinneri* the ectocuneiform facet actually occupies some of the proximal surface of the bone, and the mesocuneiform facet is consequently slightly reduced. *Tylocephalonyx skinneri* and *M. matthewi* are similar in having some proximal orientation of the ectocuneiform facet on Mt II, though *M. matthewi* is to some extent intermediate between *M. elatus* and *T. skinneri* in the orientation of the facet. The shape of the facet for Mt III varies, but it is

only indistinctly differentiated from the distal edge of the ectocuneiform facet (fig. 24B). In general, the volar part of the Mt III facet extends farther distally than the dorsal part, and both parts are joined by a very narrow strip of facet, if at all. Distal to the Mt III facet, the fibular surface of Mt II is rugose. On the tibial side of the shaft there is no trace of the rugose ridge for muscle attachment often so prominent in *M. elatus*; there is, however, a different longitudinal ridge which runs almost the entire length of the tibial side of the dorsal surface of the shaft. The distal articular facet is more oblique than in *M. elatus*, and the keel between the sesamoid facets is stronger and sharper.

As in *M. elatus*, the proximal surface of Mt III of *T. skinneri* is rather flat, inclined slightly in the distal direction toward its tibial side, and of subtriangular shape (figs. 21C, 24C). However, on Mt III of *T. skinneri* the tibial apex is generally much flatter, and the base of the triangle along the fibular side shorter than in *M. elatus* because of less development of dorsal and volar processes on this side. On the fibular side of Mt III (figs. 23B, 24B) there is a more concave (in the dorsal to volar direction) Mt IV articulation, which interlocks very

TABLE 7

Maximum Lengths (in Millimeters) of the Three Metatarsals within Single Individuals of
Tylocephalonyx skinneri, Moropus elatus, Ancylotherium (A.) pentelicum, and *Chalicotherium grande*

Specimen	Length Mt II	Length Mt III	Length Mt IV	Length Mt II / Length Mt III	Length Mt IV / Length Mt III
F:AM 54915 *T. skinneri*	109.4	125.1	114.8	0.87	0.92
F:AM 54973a *T. skinneri*	112.1	131.7	—	0.85	—
F:AM 54886a *T. skinneri*	127.7	—	128.2	—	—
AMNH 14378 *M. elatus*	133.7	146.4	148.3	0.91	1.01
CM 1701 *M. elatus*	109.9	124.9	126.8	0.88	1.01
AMNH 10564 *A. (A.) pentelicum*[a]	127.0	171.3	147.2	0.74	0.86
CM 2299 *C. grande*[b]	65.8	77.7	107.7	0.85	1.39

[a] Cast of specimen from Pikermi in the Muséum National d'Histoire Naturelle, Paris, France.
[b] Cast of specimen from Sansan.

TABLE 8

Length and Width (In Millimeters) of Metatarsals of *Tylocephalonyx skinneri* (F:AM specimens), *Moropus matthewi* (AMNH specimens), and *Moropus elatus* (ranges only), With Proportions of Width Versus Length[a]

Specimen	Greatest Length	Greatest Distal Width	Minimum Shaft Width	Length / Distal Width	Length / Shaft Width
Mt II					
F:AM 54957	115.8	44.2	33.9	2.6	3.3
F:AM 54886a	122.7	50.5	—	2.4	—
F:AM 54973a	112.1	42.4	30.5	2.6	3.7
F:AM 54964a	99.7[b]	33.0[b]	22.3[b]	3.0[b]	4.5[b]
F:AM 54915	109.4	43.7	32.6	2.5	3.3
AMNH 9368	123.5	48.2	30.6	2.6	4.0
Moropus elatus	109.9-139.5	30.4-41.6	18.9-26.6	3.2-3.7	5.0-6.2
8 specimens				Median 3.6	Median 5.2
Mt. III					
F:AM 54973a	131.7	47.4	37.6	2.8	3.5
F:AM 54958	104.7	35.2	25.5	3.0	4.1
F:AM 54915	125.1	51.1	34.2	2.5	3.7
F:AM 54964b	114.5[c]	—	29.1	—	3.9[c]
UCM 39319 (?*Tylocephalonyx* sp.)	111.0	41.6	29.2	2.7	3.8
AMNH 9368[d]	97.3	34.9	26.2	2.8	3.7
AMNH 9077	123.2	47.9	34.7	2.6	3.6
Moropus elatus	124.9-156.0	38.7-45.0	24.5-30.4	3.2-3.5	5.2-5.6
4 specimens				Median 3.2	Median 5.5
Mt IV					
F:AM 54944	116.2	48.5	38.9	2.4	3.0
F:AM 54975	120.8	40.5[c]	36.2	3.0[c]	3.3
F:AM 54974	116.3	44.0	36.0	2.6	3.2
F:AM 54915	114.8	43.1	37.0	2.7	3.1
F:AM 54886a	128.2	44.9	39.7	2.9	3.2
Moropus elatus	126.8-164.8	34.9-49.0	23.9-31.9	3.2-3.8	4.8-5.5
8 specimens				Median 3.5	Median 5.3

[a] For comparisons with other schizotheriine metatarsal proportions see Coombs (in press).
[b] Measurement from immature specimen.
[c] Approximate measurement because of damage.
[d] Not same individual as Mt II of AMNH 9368.

tightly with Mt. IV. The two Mt IV facets are usually separated by a groove. As in *M. elatus*, the dorsal of the two Mt IV facets is approximately twice as large as the circular volar one. There is no sharp ridge dividing Mt IV facets from the proximal surface of Mt III, and in some cases there is a small strip of bone with no facet between the ectocuneiform and Mt IV facets. The facet for Mt II (fig. 23A) is variable but generally similar to that described for *M. elatus*, though not so large (on several bones there is some trace of a larger articulation). Dorsal and volar parts of the Mt II facet are connected only by a narrow proximal strip of articular platform. The shaft of Mt III is oval rather than circular in section, especially

so about two-thirds of the distance toward the distal end where the width of the bone is very obviously greater than the thickness. The articulation for the proximal phalanx is generally flat transversely but may be slightly concave (fig. 24C). An abrupt broadening of the distal end of Mt. III is characteristic of *Tylocephalonyx*.

The proximal end of Mt III of F:AM 54892 from the Split Rock vertebrate fauna, despite its general resemblance to Sheep Creek specimens of *T. skinneri*, differs in an important way from that material (fig. 28E,F; see also ectocuneiform above). Separating the ecto-

cuneiform facet from the Mt IV facet is a narrow strip of articular surface which apparently contacted the cuboid. This is a difference not only from Sheep Creek *T. skinneri* but also from all other schizotheriines, including *Ancylotherium* (*A.*) *pentelicum*, in which the cuboid is very broad and approaches Mt III. It is, however, a logical development from Sheep Creek *T. skinneri*, in which the ectocuneiform does not articulate with Mt IV as in *M. elatus* and the cuboid therefore comes close to Mt III. Apparently all of the tarsals (see ectocuneiform) were shifted slightly tibially relative to the metatarsals in this animal. Another dif-

TABLE 9

Proportions of Length/Distal Thickness (Depth) and Length/Minimum Shaft Thickness (Depth) of Mt III of *Tylocephalonyx skinneri* and Other Selected Schizotherine Specimens[a]

Specimens	Length (mm.)	Distal Depth (mm.)	Shaft Depth (mm.)	Length Distal Depth	Length Shaft Depth
T. skinneri					
F:AM 54973a	131.7	46.8	25.1	2.9	5.2
F:AM 54958	104.7	37.6	21.4	2.8	4.9
F:AM 54915	125.1	45.6	25.0	2.7	5.0
F:AM 54964b	114.5[b]	41.1[b]	22.2	2.8[b]	5.2[b]
?*Tylocephalonyx* sp.					
UCM 39319	111.0	39.9	21.1	2.8	5.3
Moropus elatus					
AMNH 14378	146.4	52.0	26.4	2.8	5.5
CM 1701	124.9	38.7	24.0	3.2	5.2
Moropus hollandi					
FMNH P13000	130.7	42.7	23.3	3.1	5.6
Moropus matthewi					
AMNH 9368	97.3	40.4	19.5	2.4	5.0
AMNH 9077	123.2	50.5[b]	26.5	2.4[b]	4.7
Moropus merriami					
UCMP 35582	97.6	41.6	23.4	2.3	4.2
UCMP 31417	128.7	53.0	31.3	2.4	4.1
Ancylotherium (*A.*) *pentelicum*					
AMNH 10564 (cast)	171.3	63.1	35.6	2.7	4.8

[a]Note that proportions of *T. skinneri* resemble those of *M. elatus* despite the broadening relative to length shown in table 8. Thus Mt III of *T. skinneri* is compressed in thickness compared to its width.

[b]Approximate measurement.

ference is that in F:AM 54892 dorsal and volar parts of the Mt IV facet are confluent.

The quadrilateral cuboid facet (fig. 21E) on Mt IV is separated by a sharp ridge from the Mt III facets on the tibial side. Dorsal and volar Mt III facets are separate and together form a strongly convex articular surface (fig. 23C), which must have prevented movement in the dorsal to volar direction between Mt III and Mt IV. Both Mt III facets have a tibial orientation, and there is no articulation for the ectocuneiform; because of this difference from *M. elatus*, the proximal surface of Mt IV appears narrow. The shaft of Mt IV is wider than deep and has a generally oval cross section. Curved slightly in the tibial direction, the distal end of

the bone is visibly asymmetrical. There is a lateral broadening of the sesamoid facets, and the facets therefore appear to be rather flat and the keel between them weak.

PROXIMAL PHALANGES: As in *Moropus* and other advanced schizotheriines, the proximal and medial phalanges of digit II of the manus are fused in *T. skinneri* to form a duplex bone (fig. 25A). However, these duplexes differ in several ways from their counterparts in *M. elatus* and articulate somewhat differently with Mc II. One of the most striking features of duplexes of *T. skinneri* is their asymmetry, visible in the crooked fusion between the proximal and medial phalanx as well as in the development of the proximo-volar tubercles and the Mc II

TABLE 10

A Summary of Known Pedal Characters (excluding Phalanges) of *Tylocephalonyx skinneri*, *Moropus elatus*, *Moropus hollandi*, and *Moropus matthewi*

(A dash means that character is not known.)

| Character	T. skinneri	M. elatus	M. hollandi	M. matthewi
1. Astragalus trochlea	Nearly symmetrical, reduced height	Asymmetrical, taller	Asymmetrical, taller	—
2. Astragalus distal neck	Reduced	Well developed	Well developed	—
3. Ectal facet on calcaneum	Broad, does not extend far onto tuber	Not broad, extends well onto tuber	Not broad, extends well onto tuber	—
4. Ectocuneiform articulates with Mt IV?	No	Yes	—	—
5. Orientation of ectocuneiform facet on Mt II	Proximofibular	Fibular	—	Proximofibular
6. Mesocuneiform deep in volar direction?	Yes	Not particularly	—	Not particularly?
7. Longest metatarsal	Mt III	Mt IV (III and IV subequal)	Mt IV?	—
8. Phalangeal facet on Mt III flattened?	Yes	No	No	Somewhat
9. Relative proportions of metatarsals	Medium vs. width	Longer vs. width	Medium vs. width	Medium vs. width
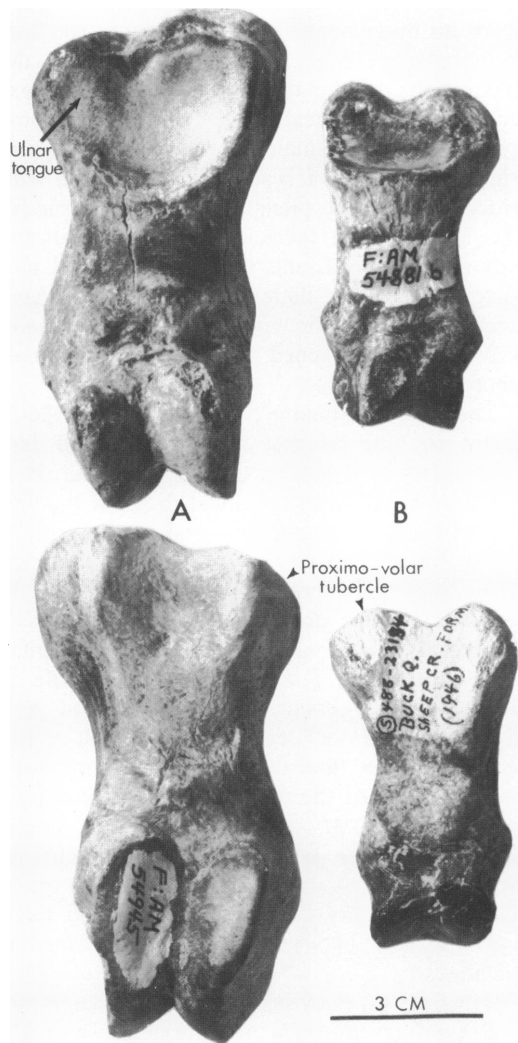
FIG. 25. Dorsal (above) and volar (below) views of duplexes of *T. skinneri* from the Sheep Creek Fm., Sioux Co., Nebraska. A. F:AM 54945, duplex of digit II of manus. B. F:AM 54881b, duplex of digit II of pes. × 2/3.

facet. The tubercle on the radial side is more strongly developed than the ulnar one, and there is an ulnar tongue on the Mc II facet that contacts the smaller ulnar side of the distal end of Mc II during movement of the duplex. In *M. elatus* the ulnar side of the distal end of Mc II has little or no contact with the duplex. The fused medial phalanx curves radially in respect

to the proximal part of the duplex, and the distal facet, deeply grooved, has very strongly flared edges on its volar side; these flanges are somewhat more sharply developed than in *M. elatus*.

Phalanges of *T. skinneri* referable to digits III or IV of the manus are very rare. Proximal phalanges of *M. elatus* belonging to digits III or IV of the manus are of two kinds, but it is unclear to which digit each kind belongs (Coombs, in press). No phalanx of the first kind described in *M. elatus* is known for *T. skinneri*, but three different specimens of the second kind are available. These resemble specimens of *M. elatus* in the pronounced asymmetrical flattening distal and adjacent to the metacarpal facet and in the torsion of the shaft. The distal facet in *T. skinneri* is slightly more asymmetrical than in *M. elatus*, and the shaft is thicker in the dorsal to volar direction.

Differentiation among the three proximal phalanges of the pes is stronger in *T. skinneri* than in *M. elatus*. Included in the holotype are the proximal phalanges of each digit with their respective metatarsals. It is therefore possible to discuss the morphology of each phalanx with the assurance that the identification of the digit it represents is correct.

Proximal phalanges of digit II of the pes have fused to the medial phalanx to form a duplex in all known specimens of *T. skinneri* except the holotype (figs. 25B, 26A). Thus it appears that although formation of a duplex is more common in *T. skinneri* than in *M. elatus*, it is not universal (such fusion in *M. elatus* occurs roughly in 10% of known individuals, but a higher percentage of fusion occurs in some other species of *Moropus*). In the holotype of *T. skinneri* little or no movement could have occurred between the proximal and medial phalanges, despite the lack of fusion, for the facet between them is very rough and irregular. Where fusion has occurred, it is variable in nature, but the duplex is generally short and thick with strongly rugose surfaces at the point of fusion (F:AM 54881b is somewhat longer than the average with less rugosity, fig. 25B). Duplexes of the pes of *T. skinneri* have a shallow, grooved distal facet with flat, unenlarged edges. Another difference of these phalanges from those of *M. elatus* is that the Mt II facet
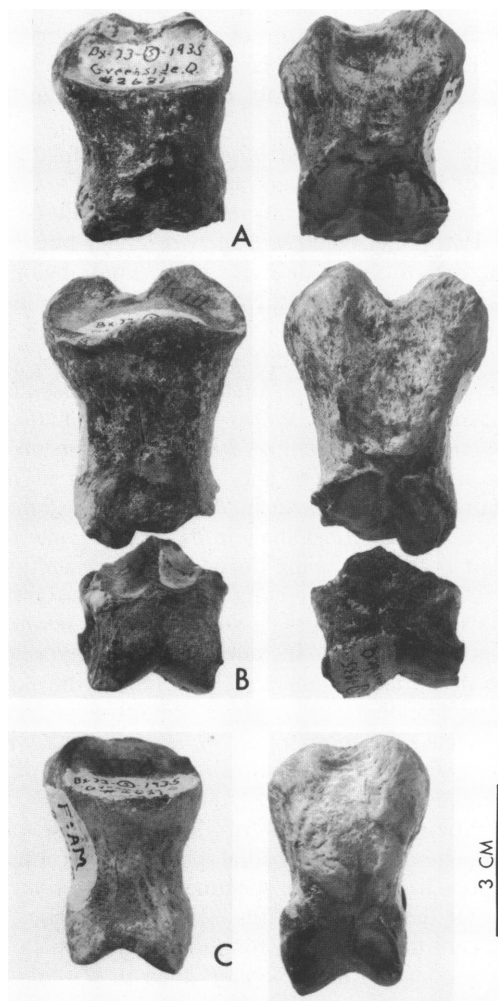
FIG. 26. Dorsal (left) and volar (right) views of proximal phalanges of pes of F:AM 54915, holotype of *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. A. Digit II. B. Digit III (with medial phalanx). C. Digit IV. × 2/3.

does not lie flat on the dorsal surface but is curved so that its distal part faces proximally. Such curvature is usual in proximal phalanges of the pes of *T. skinneri* and conforms to the flattened distal facet of the metatarsals. A very small degree of asymmetry distinguishes bones of the left and right side.

Digit III of the pes has a very asymmetrical

distal articulation which could have allowed little or no movement between proximal and medial phalanges (fig. 26B). In dorsal view the fibular lobe of the distal articular surface extends distal to the rest of the bone, and in some specimens other small lobes give the dorsal edge of the facet a scalloped appearance with which the medial phalanx articulates exactly. The Mt III facet faces rather strongly in the proximal direction, and its flattened dorsal part corresponds to the flattened or slightly concave facet on Mt III. The volar part of the phalanx is somewhat thickened and often bears small tubercles.

The proximal phalanx of digit IV (fig. 26C) is not so long as that for digit III and less transversely expanded at the proximal end. It is less asymmetrical in its distal facet in that no lobe of the facet extends beyond the rest of the bone. The Mt IV facet has a proximal to dorsal orientation. In its proximal part this phalanx is very thick in the dorsal to volar direction.

MEDIAL PHALANGES: In the few medial phalanges known for *T. skinneri*, it is possible to differentiate specimens of the manus and pes, for those from the pes are shorter and transversely broader than those of the manus. Medial phalanges of the manus are much like their counterparts in *M. elatus*. The short, broad phalanges of the pes have an asymmetrical, irregularly shaped, rather rugose proximal articular surface. Very little movement could have been possible between proximal and medial phalanges.

UNGUAL PHALANGES: Ungual phalanges of *T. skinneri* resemble in proportions those of *M. elatus*. The largest unguals belong to digit II of the manus (fig. 27A). These are quite broad at the base, particularly in the area of the subungual process, and are thus distinguishable from large unguals of *M. elatus*. They are also proportionally much broader than large unguals of *M. matthewi* and *M. merriami* (table 12). The subungual process is slightly less developed in *T. skinneri* than in *M. elatus* but is otherwise very similar. The sharp curvature of the concave facet for the duplex suggests that, just as in *M. elatus*, very little movement occurred between the duplex and ungual.

Unguals of intermediate size, apparently be-

longing to digit III or IV of the manus, resemble their counterparts in *M. elatus* but have longer dorsal processes. A number of small unguals of *T. skinneri* are also known, and none differs particularly from small unguals of *M. elatus*.

SESAMOIDS: Sesamoids were present on the volar parts of the distal articular facets of meta-

TABLE 11
Compared Features of Phalanges of Selected Schizotheriinae

Species	% Animals with Fusion of Duplex of Manus (Known Adults)	% Animals with Fusion of Duplex in Pes (Known Adults)	Proportions of Ungual Phalanx of Digit II of Manus
Tylocephalonyx skinneri	100	About 80	Relatively broad
Moropus elatus	100	About 10	Relatively broad
Moropus distans	Unknown	100	Unknown
Moropus matthewi	Unknown	Unknown	Relatively narrow
Moropus merriami	100	100	Relatively narrow
Phyllotillon naricus	100	Unknown	Unknown
Schizotherium priscum	0	0	Relatively broad, ? not enlarged
Borissiakia betpakdalensis	0	0	Relatively broad, large dorsal process
Ancylotherium (M.) fraasi	100	100	Relatively broad
Ancylotherium (A.) pentelicum	100	Uncertain	Relatively broad

TABLE 12
Measurements (in Millimeters) and Proportions of Large Ungual Phalanges (of Digit II of Manus) in
Tylocephalonyx and *Moropus*

Specimen	Basal Length (Subungual Process to Tip of Claw)	Maximum Transverse Width	Height perpendicular to Base of Claw at Subungual Process	$\dfrac{\text{Width}}{\text{Height}}$
F:AM 54968 *T. skinneri*	74.6	43.4	74.3	0.58
F:AM 54947 *T. skinneri*	—	42.5	71.4	0.60
F:AM 54973b *T. skinneri*	75.1	43.3	70.9	0.61
AMNH 21350 *Tylocephalonyx* sp.	77.4	43.3	65.8	0.66
AMNH 14378 *M. elatus*	63.1	37.3	58.4	0.64
AMNH 9076 *M. matthewi*	88.6	35.6	83.5	0.43
UCMP 19407 *M. merriami*	—	43.1[a]	98.6	0.44[a]

[a]Approximate, may be crushed.
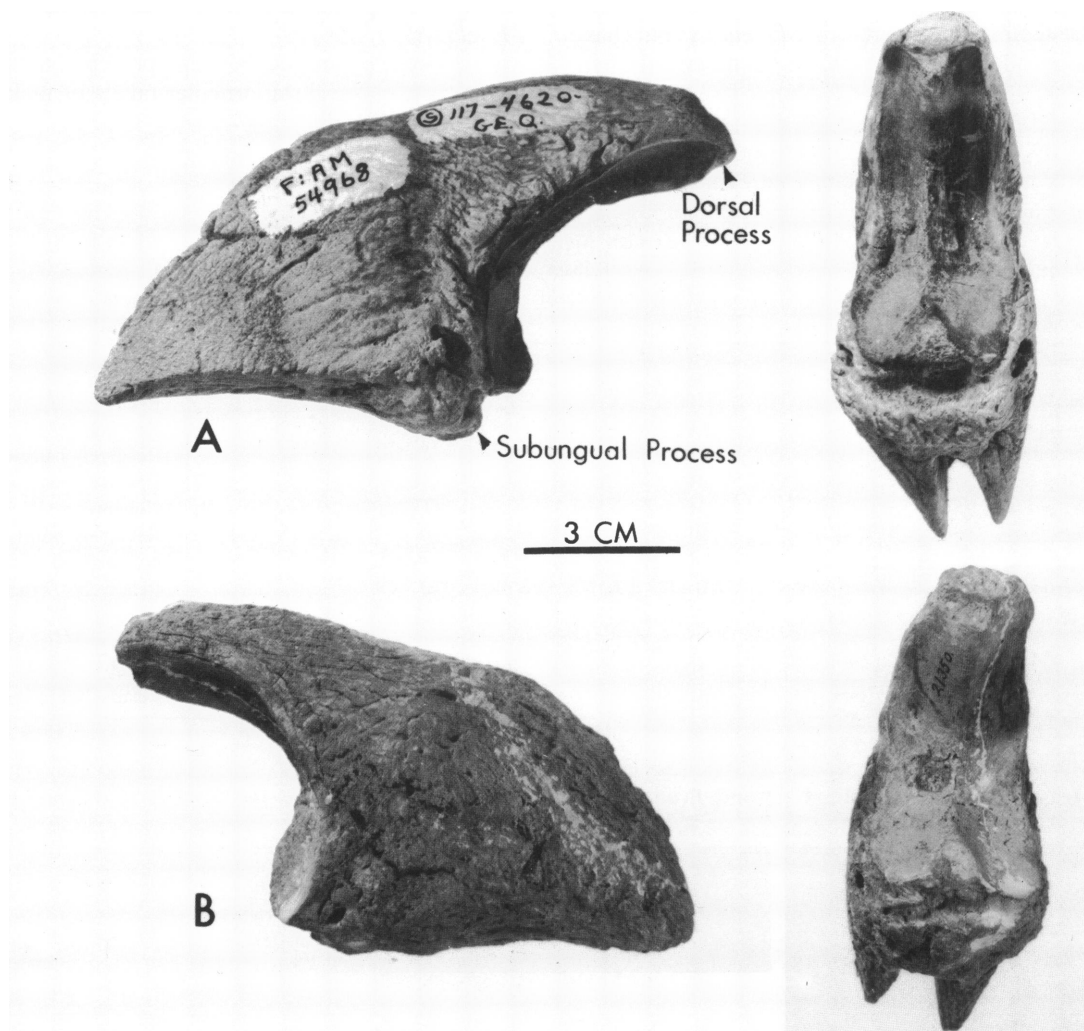
FIG. 27. Side (left) and volar (right) views of large ungual phalanges of digit II of manus. A. F:AM 54968, *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. B. AMNH 21350, *Tylocephalonyx* sp., from Deep River Beds, 7 miles south of Fort Logan, Meagher Co., Montana. × 2/3.

carpals and metatarsals and helped in the support of the animal. Some of the sesamoids belonging to the holotype of *T. skinneri* are more asymmetrical and irregular in shape than are their counterparts in *M. elatus*, but it is still difficult to assign them to digits. Some are broad and have more than one facet.

CHARACTER SUMMARY AND DISCUSSION: Tables 4, 5, 10, and 11 compare the morphology of *T. skinneri* with that of various species of

Moropus. A summary of important aspects of the anatomy of *T. skinneri* is given below.

The most prominent aspect of the structure of *T. skinneri* is the domed skull. However, no known specimen combines a skull with postcranial material; F:AM 54915, though it has no skull, was chosen as the holotype of *T. skinneri* because it preserves a large number of skeletal elements other than the skull. Several pieces of evidence link domed skulls with the

lower jaws and postcranials of the holotype. First, the few well-preserved upper molars and premolars of UCMP 115867, a domed skull from the Split Rock vertebrate fauna, are closely similar to those of specimens of *T. skinneri* from the Sheep Creek Formation. Second, lower jaws of UCMP 115867 are available, and these compare closely in tooth morphology, rotation of P_2, and apparent reduction of I_3 to the lower jaws of the holotype and other Sheep Creek specimens. Finally, F:AM 54919c preserves the broken posterior part of a domed skull (Munthe and Coombs, in press). F:AM 54919c is apparently part of the same individual as upper and lower dentitions (F:AM 54919a,b) which are closely comparable with teeth of the holotype of *T. skinneri* and other specimens of *T. skinneri*. Like the holotype, F:AM 54919c comes from Greenside Quarry.

Despite the slow evolution of chalicothere dentitions and difficulties of distinguishing teeth among different species of *Moropus* (Coombs, in press), the teeth of *T. skinneri* are unusual among North American chalicothere teeth and easily recognized. The strong asymmetry of M^3 is partly due to reduction of the hypocone and metaloph. On all upper molars the lingual cingulum near the protocone is an expanded ridge, and the posterior cingulum opposite the postfossette is also well developed. There is no labial rib on the ectoloph opposite the paracone. P^3 and P^4 have been squared by prominent development of anterolingual and posterolingual cingula. On lower molars the lophids are curved, and the metastylid is less prominent than in *M. elatus*. Upper and lower cheek teeth seem to be quite rapidly worn during the life of the animal, especially along the transverse lophs. Lengths of premolar rows, especially of P_2^2, are reduced in *T. skinneri* compared with those of *M. elatus* and *M. hollandi*. Lower incisors of *T. skinneri* show little wear, and I_3 is reduced.

Two isolated upper teeth from the Sheep Creek Formation, F:AM 54998 (?M^3, from Hilltop Quarry, fig. 28B) and F:AM 54993 (?M^2, from Long Quarry, fig. 28A), are smaller and more quadrate than other known upper molars of *T. skinneri*. In both specimens the protocone forms a point, and in F:AM
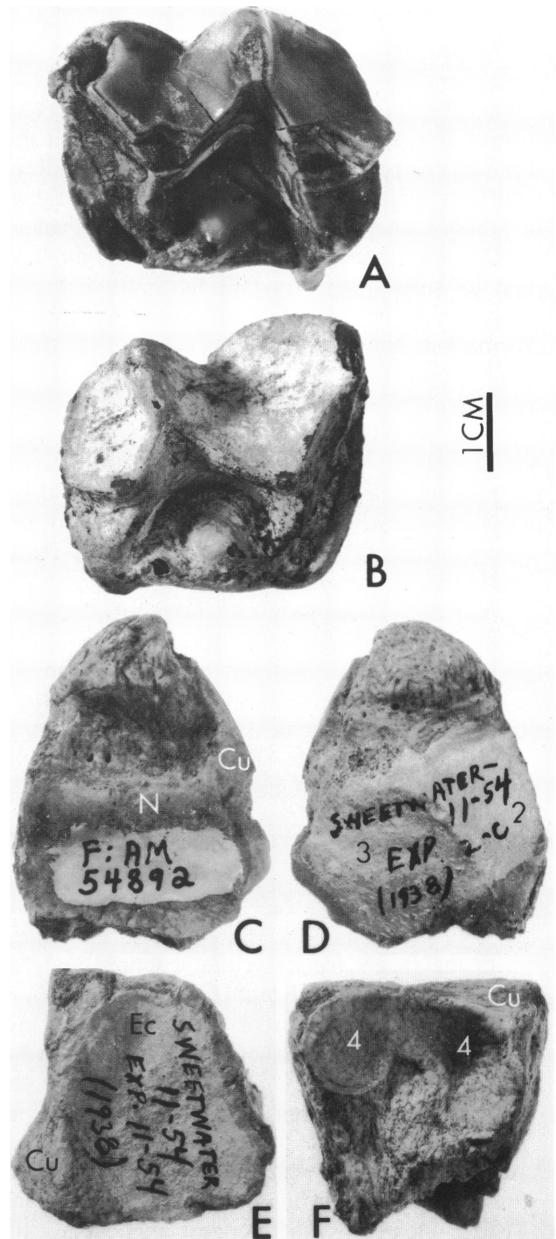
Fig. 28. A. F:AM 54993, left upper molar. B. F:AM 54998, right ?M^3. Both are unusual teeth, questionably referred to *T. skinneri*, from the Sheep Creek Fm., Sioux Co., Nebraska. C. Proximal, and D. Distal views of left ectocuneiform of F:AM 54892, *T. skinneri*, from the Split Rock vertebrate fauna, Fremont Co., Wyoming. E. Proximal, and F. Fibular views of right Mt III of F:AM 54892 (see C, D, above). Abbreviations in figure 19; see text for discussion. × 1.

54998 the metaloph is longer than in most M³ specimens of *T. skinneri*. Further, in F:AM 54993 the lingual cingulum near the protocone forms only a weak ridge, there is a fold at the base of the protocone within the central valley, and the postfossette looks like a pit rather than a groove. These characters are more prevalent in *Moropus* than in *T. skinneri* and might lead one to suspect that occasional individuals of *Moropus* were entombed in the Sheep Creek Formation. However, the unusual specimens resemble upper teeth of *T. skinneri* in some other respects, for example, the absence of a labial rib on the ectoloph. Postcranials of *Moropus* are completely unknown from the Sheep Creek Formation. The unusual upper molars could be aberrant representatives of *T. skinneri*. No answer concerning the correct reference of these specimens is presently possible.

Vertebrae and proximal parts of the forelimb, as presently known in *T. skinneri*, do not differ strongly from their counterparts in *M. elatus*. The manus also shows clear superficial resemblance to that of *Moropus* but differs in numerous details: the short distal process with elongated magnum facet on the scaphoid, the difference in the facets joining trapezoid and magnum, the more proximal extension of the Mc III articulation on the unciform, and the single (dorsal only) facet between Mc III and Mc IV. *T. skinneri* had a trapezium, as is clear from the facets for it on the scaphoid and Mc II, and thus differs from *M. hollandi*.

Although the femur of *T. skinneri* does not differ much from that of *M. elatus*, the tibia and patella have more prominent crests for the insertion of knee extensor musculature. The pes is more mesaxonic than that of *M. elatus*. Among characters which suggest a strong central axis for weight bearing on the hindfoot are: Mt III clearly is the longest metatarsal; the trochlea of the astragalus is more symmetrical than in *Moropus*; and there is no articulation between the ectocuneiform and Mt IV. The facets between pedal elements are quite restrictive in shape and presumably would have prevented most lateral movement, fore-aft excursion, and torsion of the hindfoot. Other pedal differences from *M. elatus* include the shorter neck on the astragalus, the transversely

broad ectal facet between astragalus and calcaneum which does not extend onto the calcaneal tuber, the more proximally oriented ectocuneiform facet on Mt II, the greater dorsal to volar depth of the mesocuneiform, the flatter phalangeal facets on the metatarsals, and the different proportions of the metatarsals (table 8). An entocuneiform was present in *T. skinneri* as in *Moropus*.

Postcranial specimens from the Split Rock vertebrate fauna appear to be referable to *T. skinneri* despite some minor differences from the Sheep Creek specimens. The most obvious difference, shown in the ectocuneiform and Mt III of F:AM 54892, is the tibial shift of weight so that the ectocuneiform contacts a large area on Mt II and the cuboid articulated with Mt III. Because only a small part of the pes is preserved in F:AM 54892, it is difficult to know what other compensatory pedal differences might have been present. The Split Rock specimens in general appear to represent a slightly different population of *T. skinneri*, possibly a separate subspecies.

Phalanges of the manus show a few differences from specimens of *M. elatus*. The duplex of digit II of the manus is more asymmetrical and articulated slightly differently with Mc II. The large ungual phalanx is proportionally broad and thus resembles the large ungual of *M. elatus* more than that of *M. matthewi* or *M. merriami*. In the pes, a large percentage of proximal and medial phalanges of digit II were fused, 80 percent as opposed to about 10 percent in *M. elatus*. However, the significance of the difference in fusion occurrence is not clear, for even when fusion did not occur very little movement between proximal and medial phalanges could have been possible. Movement between proximal and medial phalanges of digits III and IV of the pes seems unlikely in *T. skinneri*, based on the irregularly shaped distal facets of the proximal phalanges.

Tylocephalonyx sp.

The following specimens are referred to *Tylocephalonyx* but are too incomplete for specific assignment. All resemble *T. skinneri* fairly closely and may be referable to that species.

A spectacular domed skull, NMNH 187129, collected in 1971 by Douglas R. Emlong from the Astoria Formation of coastal Oregon and cited by Ray (1976), belongs to an aged individual whose upper teeth are badly worn. This skull, along with two others referred to *T. skinneri* (UCMP 115867 and F:AM 54919c), figures in the discussion of function of domed skulls (Munthe and Coombs, in press; see figs. 1-3). The upper teeth belonging to this skull are too damaged or worn to be of much taxonomic use. M^3 is the best-preserved tooth; its asymmetry, weak hypocone, ridgelike cingulum posterolingual to the protocone, and absence of labial ectoloph ribs are consistent with the morphology of known teeth of *T. skinneri*. The dome of NMNH 187129 is more gradual and slightly more anterior than that of UCMP 115867 from the Split Rock vertebrate fauna. Because so few domed skulls are known, the significance of such differences is unclear. The gradual slant of the dome and the poor preservation of the teeth are reasons for referring this skull to *Tylocephalonyx* sp. The basicranial region of NMNH 187129 is damaged. Anteriorly, there is a large depression on the left side of the skull near the expected position of the infraorbital foramen. Because nothing similar appears on the right side of the same specimen or on other maxillae, the depression probably resulted from post-mortem crushing. The internal nares open opposite the anterior part of M^3.

The skull from the Astoria Formation was found in place, "approximately 15 feet (4.6 m.) from base of bank at northern end of 'Iron Mountain Bed,' ¼ mile (0.4 km.) north of mouth of Schooner Creek," NW¼ NW¼ Sec. 20, T10S R11W, Lincoln County, Oregon. The "Iron Mountain Bed" is stratigraphically lower than the Depoe Bay Basalt (Clayton Ray, personal commun., 1975, *vide* Parke Snavely); the Depoe Bay Basalt has been KA dated at 16 ±0.65, 15.2 ±0.6, and 14.5 ±1.0 m.y. at different localities (see Snavely, MacLeod and Wagner, 1973, p. 404). According to these authors, the Astoria Formation at the type locality of the Depoe Bay Basalt a few miles north of the "Iron Mountain Bed" contains Foraminifera characteristic of Saucesian and Relizian Stages. Addicott (1976), using mol-

luscs, put the Astoria Formation low in his Newportian Stage, which he correlated with the upper Saucesian foraminiferal Stage. Most mammalian material from the Astoria Formation belongs to marine mammals, the chalicothere and several rhinoceros specimens from the "Iron Mountain Bed" being special exceptions. The rhinoceros specimens compare favorably with other late Hemingfordian or early Barstovian rhinoceroses from Texas, Nevada, and eastern Oregon (Jens Munthe, personal commun., 1977).

The distal end of a chalicothere Mt III (UMMP 24376 fig. 29C) was collected at Dorr and Wheeler Locality 5 (Dorr and Wheeler, 1964, pp. 298, 325-326; Skinner, 1968, p. 15) in the Madison Valley Formation of southwestern Montana. The fauna from which this specimen comes was considered to be early Barstovian. Dorr and Wheeler (1964, p. 325) referred to UMMP 24376 as *Moropus* sp. indet. The following characters suggest reference to *Tylocephalonyx* (fig. 29C): the flat dorsal surface of the shaft and phalangeal facet, the abrupt transverse broadening of the distal end compared to the shaft, and the dorsal to volar compression of both shaft and distal end. The general symmetry and flat dorsal surface suggest that this specimen is a left Mt III.

Scott (1895: p. 59) included *Chalicotherium* sp. among the species from the upper Deep River Beds (= "Loup Fork"). The specimen that prompted this notation was PU 10407, a proximal phalanx of digit III or IV of the pes of a chalicothere collected in 1891 from the Smith River valley of Montana (fig. 29a, b). Like phalanges of these digits in *T. skinneri*, PU 10407 has an asymmetrical distal facet, but it differs in the somewhat more dorsal orientation of the metapodial facet and greater transverse width compared to length. Despite its general resemblance to phalanges of *T. skinneri*, PU 10407 is too fragmentary a specimen even to be definitely referable to *Tylocephalonyx*.

AMNH 21350, a single large ungual phalanx from 7 miles (11.3 km.) south of Fort Logan (1 mile=1.6 km. east of Swarners Ranch), Montana, almost certainly belongs to digit II of the manus (fig. 27B). It is remarkably similar in
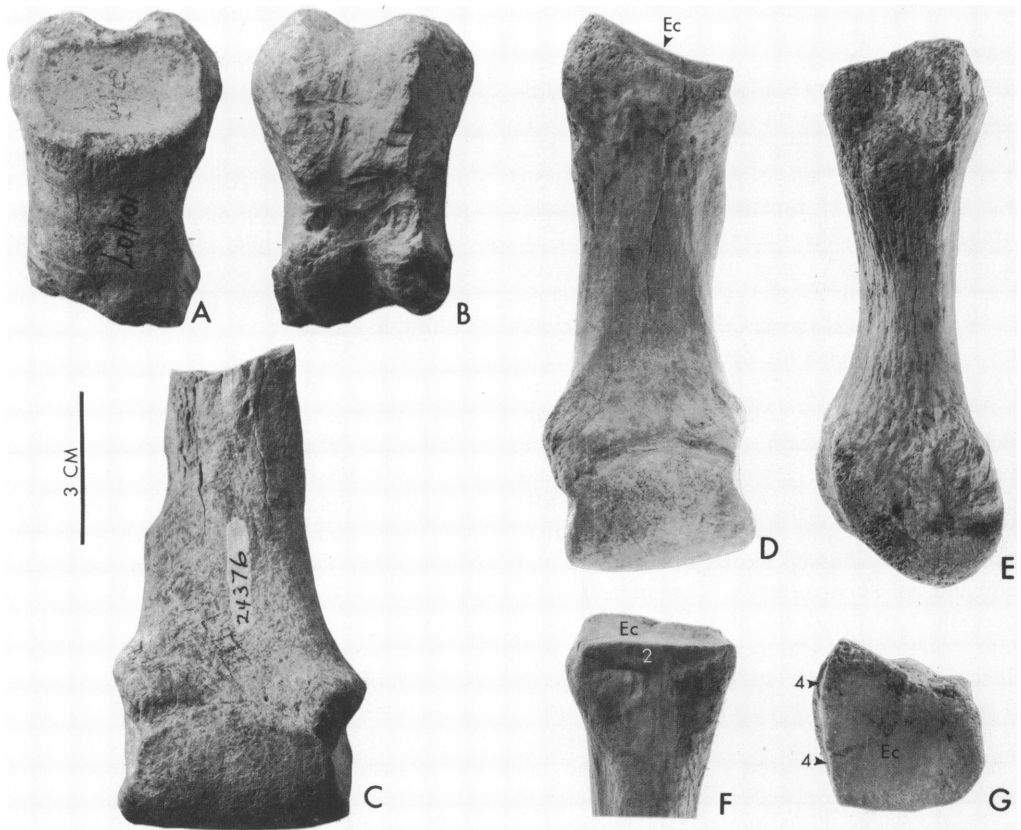
FIG. 29. A. Dorsal, and B. Volar views of proximal phalanx of digit III or IV of the pes, PU 10407, *Tylocephalonyx* sp., from the Deep River Beds, Smith River Valley, Meagher Co., Montana. C. Dorsal view of distal end of Mt III, UMMP 24376, *Tylocephalonyx* sp., from the Madison Valley Fm., Madison Co., Montana. D. Dorsal, E. Fibular, F. Tibial, and G. Proximal views of right Mt III, UCM 39319, *?Tylocephalonyx* sp., from the Rickstrew Ranch locality, Eagle Co., Colorado. Abbreviations in figure 19. × 2/3.

size and morphology to large unguals of *T. skinneri*. Aside from the similarity of proportions (table 12; no transverse compression, particularly in the area of the subungual process), there is an asymmetry of the two sides of the claw that especially resembles that in F:AM 54968 from the Sheep Creek Formation (fig. 27A). The proportions are clearly different from those of large unguals of *M. matthewi* or *M. merriami*.

AMNH 21350, like PU 10407 (above), comes from the Deep River Beds. The stratigraphy of the Deep River Beds is more complicated than it was considered to be by early

authors; most published determinations are therefore unreliable. No determination of the level from which PU 10407 came is possible on the basis of the data given. The American Museum of Natural History collected specimens from the same locality as AMNH 21350, including a horse, a cervid, and geomyoid rodents. The rodents, *Mookomys altifluminis* and a milk tooth of *Horatiomys montanus*, are not presently clearly correlative with other species and do not aid in dating. The genus *Mookomys* has a large Arikareean-Barstovian temporal range. Frick (1937, p. 241) referred the cervid (including AMNH 21356, AMNH 21357,

AMNH 21366) to *Blastomeryx gemmifer*, variant. In the same paper he named three subspecies of *B. gemmifer*. The Montana material resembles in tooth proportions the subspecies from the Sheep Creek Formation and from Pawnee Creek, northeastern Colorado, more than that from the Valentine Formation (see Frick, 1937, table 6, pp. 228-229). The horse remains from the same locality as AMNH 21350 include both upper and lower teeth (AMNH 21351, AMNH 21352, AMNH 21354) but have never been described. Skinner (personal commun., 1973) referred them to *Merychippus* and stated that while identification is uncertain on the basis of teeth alone these specimens seem closest to *Merychippus* in Sheep Creek and Lower Snake Creek faunas. On the basis of slightly larger size they are closer to Lower Snake Creek specimens; they certainly differ from Valentine *Merychippus*. The chalicothere ungual phalanx, by virtue of its reference to *Tylocephalonyx*, suggests that the local fauna from which it comes is medial Hemingfordian to early Barstovian in age. Such an age is consistent with the evidence provided by other elements from the same local fauna.

A chalicothere magnum (UCMP 119279), closely resembling that of *Tylocephalonyx* (F:AM 54933 from the Sheep Creek Formation), was recently recovered from UCMP Locality V77142, about 1 mile (1.6 km.) north of the settlement of Etna in Grouse Creek Valley and 1 mile south of Etna Reservoir on the Grouse Creek 7.5 ft. topographic quadrangle map (U.S. Geological Survey), northwestern Box Elder County, Utah. The local fauna to which the magnum belongs is from the Salt Lake Formation and is currently under study by Patrick McClellan of the University of California, Berkeley. Its exact age is yet to be determined. UCMP 119279 has been compared with magna of *T. skinneri* (F:AM 54933, fig. 12), *Moropus elatus*, *M. hollandi*, *M. matthewi*, and *M. merriami*. Its proportions and facets are extremely close to those of the magnum of *T. skinneri* with only a few slight differences in facet shapes. The specimen will be treated more fully in a paper by Patrick McClellan.

UCM 39319, a Mt III from northern Eagle County, Colorado, is questionably referred to *Tylocephalonyx* (fig. 29D-G). It easily fits within the range of proportions (tables 8,9) and morphologies known for *T. skinneri*: its ectocuneiform facet is blunt at the tibial apex as in the holotype of *T. skinneri*, the Mt II facet is a narrow dorsal to volar band slightly expanded near its volar edge, and the dorsal part of the Mt IV facet is much larger than the circular volar part. The dorsal surfaces of the phalangeal facet and distal end of the shaft are flat, and the shaft widens abruptly toward the distal articular surface. One reason for the questionable reference of this metatarsal is the close similarity in metatarsal proportions between *T. skinneri* and *M. matthewi*. Specimens of Mt III of *M. matthewi* are too badly damaged for detailed comparison, but reference of UCM 39319 to *M. matthewi* cannot be ruled out.

UCM 39319 is the same specimen that Skinner (1968, p. 17) mentioned as collected by Peter Robinson from "southwestern Park County, central Colorado." However, according to Robinson and G. Edward Lewis (personal commun., 1977) the specimen actually came from northern Eagle County, Colorado, more precisely from the Rickstrew Ranch locality (Vertebrate Locality No. D523 of the U.S. Geological Survey, Paleontology and Stratigraphy, Denver), on the Piney River 2½ miles (4 km.) south-southeast of the Colorado River. According to Izett (1975, pp. 191-192), these deposits are in the North Park Formation, overlie basaltic flows 24 to 21.5 m.y. old, and contain a fossil mammal assemblage 12 to 13 m.y. old. Lewis (personal commun., 1977) noted, however, that the outcrops more likely were in the Brown's Park Formation (as designated by Ogden Tweto in a recent geologic map of Colorado) or the Troublesome Formation (whose nearest outcrops are only 17 miles=27 km. away). According to Lewis, *Brachycrus* from Rickstrew Ranch is not far from *B. buwaldi* of the Barstow Formation.

Lovering (1930, p. 74), on the advice of Harold J. Cook, identified as *Moropus* cf. *M. elatus* a chalicothere specimen from the Troublesome Formation in Middle Park, Colorado. Further mention of chalicotheres in the Troublesome Formation was made by Izett and Lewis (1963, pp. B120-B121) and by Lewis

(1969, p. B54). The locality of Lovering's *Moropus* cf. *M. elatus* was listed as "near Granby, Colorado, about 20 miles (32 km.) east of Troublesome Creek." According to K. Don Lindsey of the Denver Museum of Natural History (personal commun., 1977), the only known chalicothere specimen identified by Cook was the proximal end of a large proximal phalanx, DMNH 1782, from Grand County, Colorado. This phalanx appears to be referable to *Moropus*, not *Tylocephalonyx*. Lewis (1969, p. B54), recognizing two faunal levels in the Troublesome Formation, included "*Macrotherium* sp." in the faunal assemblage equivalent to the "*Brachycrus* zone (Sheep Creek Formation and some younger rocks) of Nebraska." No further information concerning the material on which this reference was based is available. The Troublesome Formation is currently under study by Lewis, Izett, and others.

ECOLOGY AND AFFINITIES OF *TYLOCEPHALONYX*

The origin of the genus *Tylocephalonyx* is obscure. At its earliest known occurrences (Split Rock vertebrate fauna, Wyoming; Site 2 Prospect, Dawes County, Nebraska—both medial to late Hemingfordian), *Tylocephalonyx* is clearly different from all other chalicotheres. A time interval of some length, in which *Tylocephalonyx* evolved but is not preserved, must therefore be postulated. What is the closest relative of *Tylocephalonyx*? Matthew (1929) postulated the presence of representatives of the Chalicotheriinae in the Miocene of North America. No representatives of the Chalicotheriinae have, however, yet been found in North America. The teeth and foot elements of *T. skinneri* are clearly schizotheriine.

To postulate the closest relative(s) of *Tylocephalonyx* among the Schizotheriinae, it is necessary first briefly to discuss relationships among other schizotheriine genera. Figure 30A is a summary of proposed relationships and should be interpreted in the light of table 1 and the discussion of diagnostic characters of *Tylocephalonyx* (see Systematics). The cladogram omits the question of affinities of various genera of primitive chalicotheres (Eomoropidae); discussion of that question should be undertaken but is outside the scope of the present paper. Several points are unclear in the cladogram of figure 30A: the polarities of certain characters are debatable, and it is unclear in several cases whether derived characters are synapomorphic (due to common ancestry) or autapomorphic (convergent).

An example of a problematical polarity is the astragalus articulation with the cuboid, here considered apomorphic in *Borissiakia*. Known eomoropids have a small articulation between astragalus and cuboid; other primitive ungulates suggest that no articulation or a small articulation similar to that in *Eomoropus* may be primitive. *Borissiakia* has a large cuboid facet on the astragalus, as does *Chalicotherium*, a genus in other respects quite different from *Borissiakia*. The unusual nature of the astragalus of *Chalicotherium* suggests that a large astragalus articulation with the cuboid may be apomorphic, hence autapomorphic with respect to the facet in *Borissiakia*.

A similar problem besets the interpretation that subequal Mt III-Mt IV is an apomorphic character in *Moropus*. In most perissodactyls Mt III is the longest metatarsal. Unfortunately, most chalicotheres (among them *Schizotherium* and *Borissiakia*) do not preserve complete metatarsals all belonging to a single individual. *Chalicotherium* has a strongly elongated Mt IV, but this clearly is apomorphic. The dominance of Mt III, which I consider to be symplesiomorphic in *Ancylotherium* and *Tylocephalonyx*, is complicated by the presence in each genus of probably apomorphic pedal characters, for example the restriction of movement between certain tarsals in *Tylocephalonyx*.

The presence of a crista in both *Schizotherium* and *Borissiakia* is possible evidence that these two genera are sister groups. I have, however, considered the attainment of a crista in both genera to be autapomorphic and have linked *Borissiakia* to other schizotheriines on the basis of common loss of the hypoconulid on M^3. More evidence is necessary to ascertain
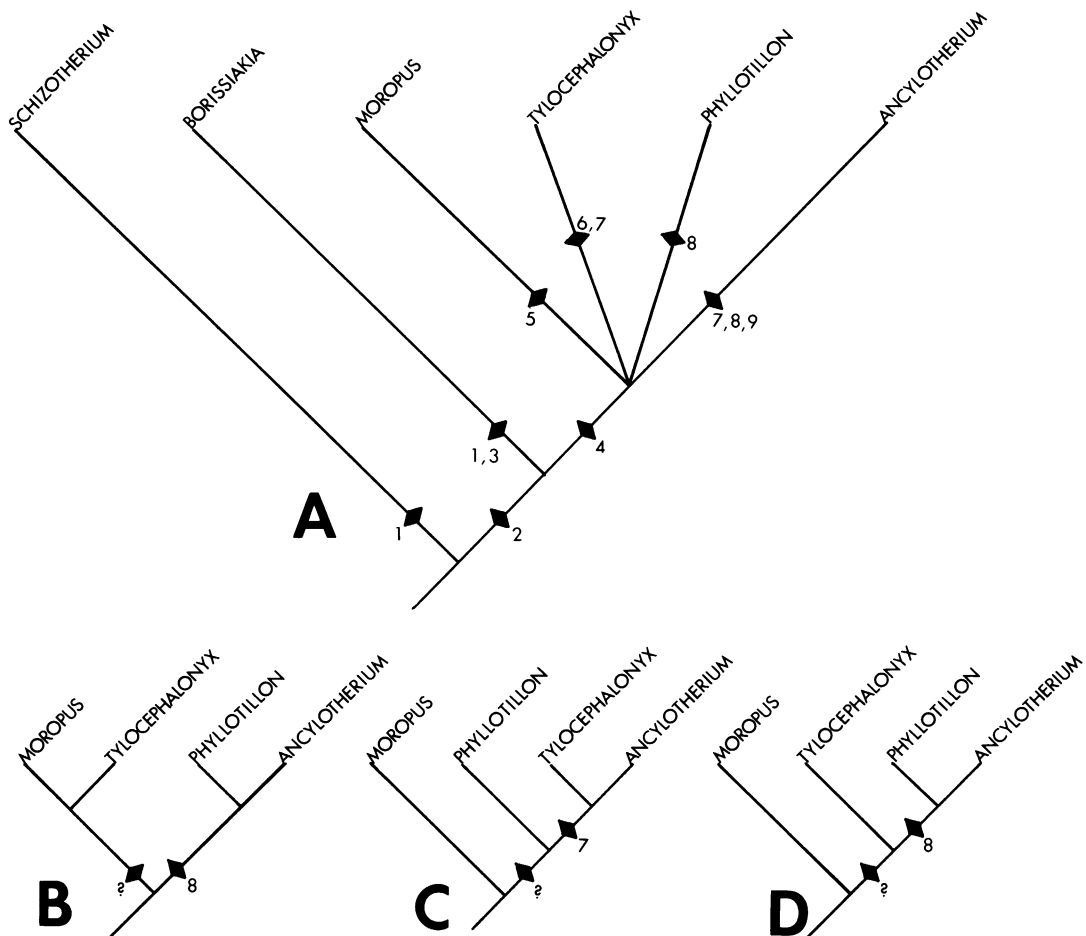
FIG. 30. Relationships among genera of the Schizotheriinae. A includes all schizotheriine genera. B represents a hypothesis of close relationship between *Tylocephalonyx* and *Moropus*, C between *Tylocephalonyx* and *Ancylotherium*, and D between *Phyllotillon* and *Ancylotherium*, with *Tylocephalonyx* as a sister group of both. Shared derived characters are (1) presence of crista; (2) more elongated molars, loss of M^3 hypoconulid; (3) extensive contact between astragalus and cuboid, extra posterolingual cuspules on M^3; (4) fusion of proximal and medial phalanges of digit II of manus; (5) Mt III and Mt IV of subequal length; (6) domed skull; (7) reduced lower incisors, low hypocone on M^3; (8) occasional or usual presence of crochet and of ectoloph rib opposite metacone on upper molars; (9) modified manus; and (?) uncertain. See text for discussion.

the relationships of *Schizotherium* and *Borissiakia* correctly.

Figure 30B-D represents conflicting hypotheses concerning precise affinities of *Tylocephalonyx*. *Tylocephalonyx* is close to *Moropus*, *Phyllotillon*, and *Ancylotherium* on the basis of fusion of proximal and medial phalanges of digit II of the manus—this shared character is clearly apomorphic.

The first hypothesis (fig. 30B) places *Tylocephalonyx* as a sister group of *Moropus*. There is little evidence for this hypothesis in terms of identified synapomorphies. The many shared characters between *Moropus* and *Tylocephalonyx* would place these two genera very near each other in any traditional estimation of morphological distance. However, all or most of the similarities appear to be sym-

plesiomorphic and are hence useless in a cladistic sense. On the other hand, some of the similarities extend to general facet shapes, and some of these may prove to be synapomorphic as detailed morphology of all schizotheriine species becomes better known.

Another hypothesis (fig. 30C) places *Tylocephalonyx* as a sister group of *Ancylotherium*. This hypothesis would be well supported by synapomorphy if it were not necessary to include *Phyllotillon* in the discussion. *Tylocephalonyx* and *Ancylotherium* both have reduced lower incisors, increased lingual cingulum on upper molars, and decreased hypocone and metaloph on M^3. There are also pedal similarities, some of which are probably apomorphic. However, *Ancylotherium* has a crochet on upper molars, a labial ectoloph rib between mesostyle and metastyle, dorsal flattening of the metacarpals, several adaptations for extreme flexion of the carpus, and other characters that are absent in *Tylocephalonyx*. There is at least some evidence (the occasional presence of a crochet and posterior labial ectoloph rib in *Phyllotillon*; fig. 30D) that certain of these divergent characters may have appeared early among Eurasian schizotheriines, even in animals that in other respects resemble *Moropus* more than *Ancylotherium*. *Phyllotillon* apparently had well-developed lower incisors and had no special modification of the upper molar lingual cingula or of the M^3 hypocone. None of the unusual characters of *Ancylotherium* mentioned above appears in any North American schizotheriine. The skull of *Ancylotherium* shows no signs of doming (Garevski, 1974).

A consideration of *Ancylotherium*, *Phyllotillon*, and *Tylocephalonyx* together leads to the conclusion that some autapomorphy must have occurred; development of crochet and posterior ectoloph rib in *Ancylotherium* and *Phyllotillon* on one hand or lingual cingulum development, hypocone reduction, and incisor reduction in *Tylocephalonyx* and *Ancylotherium* on the other. The analysis of precise relations among *Tylocephalonyx*, *Moropus*, *Phyllotillon*, and *Ancylotherium* is inconclusive. It is best at the present time to view *Tylpcephalonyx* as an offshoot near the common ancestry of *Moropus*, *Phyllotillon*, and *Ancylotherium*.

Little information is yet available concerning evolutionary radiation within *Tylocephalonyx*. Isolated, fragmentary finds, including a few thought to be early Barstovian, resemble *T. skinneri* fairly closely and are referred to *Tylocephalonyx* sp. *Tylocephalonyx* seems to have survived into the early Barstovian, but there is no definite evidence of survival subsequent to that time. The Mc III figured by Skinner (1968, F:AM 42982) from the Crookston Bridge Member of the Valentine Formation (post-Barstovian) resembles Mc III of *T. skinneri* in some respects (the single dorsal facet for Mc IV) but differs in others (for example, the double facet for the unciform). This specimen probably belongs either to *Moropus* or *Tylocephalonyx* but is generically indeterminate; despite its similar age it is clearly not referable to *Ancylotherium*.

What is known of occurrences of *Tylocephalonyx* suggests that *Tylocephalonyx* was ecologically separate from *Moropus*, living at the same time but rarely, if ever, entombed in the same deposits. The map in figure 1 shows geographical range of known occurrences of *Tylocephalonyx* and of medial Hemingfordian-Barstovian occurrences of *Moropus*. Although present in the Sheep Creek Formation, *Tylocephalonyx* is not known from early to medial Hemingfordian faunas of several well studied Great Plains formations (Upper Harrison, Runningwater, Batesland). Chalicotheres from these formations are referable to *Moropus*. Thus *Tylocephalonyx* seems to have replaced *Moropus* in known medial to late Hemingfordian faunas of the Great Plains.

At the same time *Moropus* is known from at least two Hemingfordian faunal localities in the far West (the Phillips Ranch local fauna, Kinnick Formation, California, Buwalda, 1916; the late Hemingfordian faunal assemblage of the Caliente Formation, California, undescribed). These fossils of *Moropus* show many resemblances to *Moropus merriami*, which is known from Barstovian faunas of Nevada. *Tylocephalonyx* appears to have been absent from known late Hemingfordian and Barstovian faunas of California, Nevada, and eastern Oregon, though it does appear in the Astoria Formation of northwest Oregon.

A chalicothere very similar to *M. merriami*

replaced *Tylocephalonyx* in the early Barstovian Lower Snake Creek fauna of Nebraska. At about the same time, *Tylocephalonyx*, but evidently not *Moropus*, occurred in Montana. Generally speaking then, *Tylocephalonyx* seems to have had a Great Plains and northwest distribution. It is not known from the warm, moist environments of the Gulf Coastal Plain, nor from the drier habitats of the American Southwest.

The apparent replacement of *Moropus* by *Tylocephalonyx* in medial Hemingfordian faunas (post-Runningwater) of the Great Plains and subsequent replacement of *Tylocephalonyx* by *Moropus* in the early Barstovian (Lower Snake Creek fauna) provide fascinating questions of faunal dynamics. The apparent replacements can be explained in two ways: (1) both *Moropus* and *Tylocephalonyx* lived for a long time in slightly different environments of the same area, but the known fossil faunas sampled only part of existing regional diversity at each time, and (2) there were real chalicothere replacements in the area in coordination with other faunal/floral changes. Existing evidence for either explanation is meager.

Only a few recent taxonomic works involving late Hemingfordian and/or early Barstovian mammals are available which outline range changes and faunal replacements among the taxa studied (among papers that do give such information are Woodburne, 1969; Patton and Taylor, 1971, 1973; Rich and Rich, 1971). In some cases mammalian faunal replacements seem to correspond generally to the replacements between *Tylocephalonyx* and *Moropus*. For example, the tayassuid *Dyseohyus* is present in the Lower Snake Creek fauna, replacing *Cynorca occidentale* from the Sheep Creek fauna. *Dyseohyus* is also known from southern California and from Texas and Colorado (Woodburne, 1969). Rich and Rich (1971) noted the presence of the erinaceid *Brachyerix macrotis* in (among other strata) the Sheep Creek Formation, the Split Rock Formation, and the Deep River Beds near Fort Logan, Montana, all deposits in which *Tylocephalonyx* is found. *Brachyerix incertis* is present in the Olcott Formation (Lower Snake Creek fauna), the Barstow Formation of California, and the Esmeralda Formation of Nevada. The finds of

B. macrotis versus *B. incertis* quite closely correspond to finds of *Tylocephalonyx* and *Moropus*. Galusha (1975) and Skinner, Skinner and Gooris (1977) gave up-to-date faunal lists for the Box Butte Formation, Sheep Creek Formation, and Olcott Formation. Their lists are of great value in evaluation of local changes and are of potential use in coordination with detailed lists from other areas (examples, Woodburne and Robinson, 1977; Rensberger, 1973; Lindsay, 1972) in understanding regional differences at various times. A comprehensive picture of broad faunal changes, involving diverse mammals over relatively short time spans and balancing temporal versus ecological considerations, is still emerging.

Much can be learned by comparison of ranges of fossil vertebrates with floral evidence. This approach was used successfully by Shotwell (1958, 1961), who correlated changes in range of aplodontids (Rodentia) and equids (Perissodactyla) with drying conditions in the late Miocene and Pliocene of the northern Great Basin. Recently Webb (1977) used a similar approach in a discussion of the history of North American savanna vertebrates.

Miocene floras from the Great Plains are rather sparse and not always correlated with vertebrate faunas, nor do they provide especially good temporal versus ecological resolution. MacGinitie (1962, p. 105) in his discussion of the Kilgore flora (75 ft. = 22.9 m. above the base of the Valentine Formation in north-central Nebraska) stated that "the fossil plants indicate an equable, warm-temperate climate with little or no frost. The area was occupied by a savanna type of vegetation with well-forested river bottoms and an open pine-oak forest of sub-humid aspect on the interfluves." Despite findings by Elias (1942) that some prairie grasses were present in Nebraska as early as the Hemingfordian, MacGinitie noted (p. 99) that the "Florissant, Ruby Basin, Kilgore, and Creede floras support the idea of savannas but not true prairies. The common combination of grazing and browsing animals in the interval from middle Miocene to middle Pliocene [early to late Miocene of current terminology, as utilized by Skinner, Skinner, and Gooris, 1977] also supports the idea of a savanna type of plant formation" (bracketed ma-

terial mine). MacGinitie's ideas are useful for a basic understanding of the long-term Great Plains biotope, but the Kilgore flora is later than the Hemingfordian/early Barstovian faunal changes involving *Tylocephalonyx* and *Moropus* and does not help to explain such relatively short-term occurrences.

Because both *Tylocephalonyx* and *Moropus* appear on the Great Plains (in different deposits), it is easier to understand the climatic and floral associations of each by noting their occurrences in other areas. This approach also has the merit that floral evidence from the far West and Great Basin is far better than that from the Great Plains. Outside Nebraska, *Tylocephalonyx* is known to occur in central Wyoming, western Montana, northwestern Utah, and western Oregon; the occurrence in north-central Colorado is too uncertain to be worthy of discussion here. The known occurrences are associated with mixed mesophytic forests often referred to as the Arcto-Tertiary Geoflora (Chaney, 1944; Chaney and Axelrod, 1959; Axelrod, 1964). This diverse flora was dominated by deciduous hardwoods and conifers and depended on a temperate climate with plentiful, year-round rainfall. The moistest, most heavily forested conditions obtained near the northwest coast, but the northern Great Basin (for example, northwestern Utah) had not yet undergone the drying conditions and floral/faunal replacements associated with the rising of the Cascades and other mountain ranges in the late Miocene and Pliocene (Chaney, 1944; Axelrod, 1950, 1976; Shotwell, 1958, 1961).

Late Hemingfordian and Barstovian occurrences of *Moropus*, outside Nebraska, are known from southeastern Oregon, Nevada, California, and northeastern Colorado. The occurrences in southern California are associated with the Madro-Tertiary Geoflora, composed of semi-arid woodland and chaparral floral elements (Axelrod, 1939; the Tehachapi flora, of semi-arid aspect, is found in near association with the Phillips Ranch local fauna). Barstovian occurrences of *Moropus* in west-central Nevada are in a region of intermixing of Arcto-Tertiary and Madro-Tertiary floral elements, with live-oaks of the latter often dominant (Axelrod, 1956). Although Arcto-Tertiary elements pre-

dominated in the Barstovian of northwestern Nevada and southeastern Oregon, the flora of this region was less rich and had somewhat lower rainfall than the highly diverse forests of farther north and coastal Oregon. The comparison of *Moropus* versus *Tylocephalonyx* distribution in Oregon is suggestive when compared to floral information.

Rainfall in northwestern Nebraska during late Hemingfordian time must have been lower than that over much of the northwestern range of *Tylocephalonyx*. The interchanges between *Moropus* and *Tylocephalonyx* on the Great Plains presumably involved a difference in habitat, with *Tylocephalonyx* preferring a moister, more forested environment possibly near streams. *Moropus*, at least in Barstovian Great Plains faunas, may have preferred somewhat more open country.

A functional discussion of schizotheriine chalicotheres (Coombs, in preparation) and a special study of the function of the domed skull in *Tylocephalonyx* (Munthe and Coombs, in press) make detailed treatment of function in the present paper undesirable. Certain morphological differences between *Moropus* and *Tylocephalonyx* are difficult to explain on a functional basis. Other characters, however, are useful in an attempt to reconstruct the environment of *Tylocephalonyx*.

The teeth of chalicotheres are generally recognized as indicating a browsing habit. The elongation of molars and greater loph development in schizotheriines than in chalicotheriines is generally taken to indicate a coarser diet for schizotheriines. Whereas *Tylocephalonyx* has not particularly elongated the molars or increased crown height compared with *Moropus elatus*, its teeth do appear to wear faster than those of *M. elatus*. Certain dental characters which occur in *T. skinneri* but not in *M. elatus* (the larger lingual cingulum near the protocone, the lower M^3 hypocone and metaloph, the reduction of lower incisors) occur in *Ancylotherium*. Because *Tylocephalonyx* lacks the unusually high-crowned molars and upper molar crochet of *Ancylotherium* it is uncertain whether the minor dental similarities between *Tylocephalonyx* and *Ancylotherium* reflect any special dietary similarities.

The manus of *Tylocephalonyx* differs little in basic structure from that of *Moropus elatus*. It lacks many of the special adaptations for exceptional flexion seen in the manus of *Ancylotherium* (Schaub, 1943). The pes resembles that of *Ancylotherium* in being distinctly mesaxonic: Mt III is the longest metatarsal, the astragalar trochlea is quite symmetrical, and Mt IV does not contact the ectocuneiform. However, pedal similarities between *Tylocephalonyx* and *Ancylotherium* are of uncertain functional significance because they seemingly involve a mixture of shared primitive and of derived characters. Borissiak (1945) and Schaub (1943) independently proposed that food gathering in schizotheriines might have required rearing up on the hindlimbs. A rigid hindlimb while maintaining an upright stance might explain certain hindlimb characters in *Tylocephalonyx*: the prominent cnemial crest on the tibia and proximodorsal crest on the patella, the shortening of the metatarsals relative to those in *M. elatus*, and the reduction of lateral movement and torsion of the pes by restrictive facets. The hypothesis of upright stance while feeding, of course, presumes the presence of enough trees sufficiently tall to make such an adaptation useful.

As was noted by Coombs (1975), *Moropus elatus* and other chalicotheriids show some evidence of being sexually dimorphic in body size, the males being notably larger than the females. *Tylocephalonyx* seems to have been no exception. Sexual dimorphism provides some evidence of social interaction, as may the domed skull of *Tylocephalonyx* (Munthe and Coombs, in press). Pronounced sexual dimorphism may be associated with open terrain herding behavior that promotes social interactions and vis-a-vis competition for mates, as Schaller (1977) has suggested for the Caprinae (Artiodactyla). On the other hand, the scarcity of chalicotheres in many deposits is sometimes interpreted as evidence of a solitary and/or relatively forested environment for these animals. It is difficult to know how *Tylocephalonyx* compared with other chalicotheriid genera in terms of social organization, but any interpretation of environment must take into account the morphological features which suggest some degree of social interaction.

SUMMARY

The domed skull of *Tylocephalonyx*, new genus, is unique among chalicotheres, but dental and postcranial characters provide clear evidence of affinities to the schizotheriine chalicotheriids. *Tylocephalonyx* is close to the schizotheriine genera *Moropus*, *Phyllotillon*, and *Ancylotherium* on the basis of shared loss of the hypoconulid on M^3 and fusion of the proximal and medial phalanges of digit II of the manus to form a duplex. It is not entirely clear which genus is closest to *Tylocephalonyx*. *Moropus* has the most similar morphology to *Tylocephalonyx*, but the major similarities are primitive. *Tylocephalonyx* and *Ancylotherium* share certain derived characters, such as the reduction of lower incisors, increase in upper molar lingual cingulum, and reduction of M^3 hypocone and metaloph; however, *Tylocephalonyx* lacks important derived characters of the dentition and manus of *Ancylotherium*. The morphology of *Phyllotillon* is a confusing factor in assessing the degree of relationship between *Tylocephalonyx* and *Ancylotherium*. *Tylocephalonyx* may be an offshoot near the common ancestry of *Moropus*, *Phyllotillon*, and *Ancylotherium*. The geographic origin of *Tylocephalonyx* is uncertain, but known distribution is confined to the medial Miocene of North America.

Knowledge of morphology of *Tylocephalonyx* is based primarily on *T. skinneri*, a new species based on quite complete skeletal material from the medial to late Hemingfordian of Nebraska and Wyoming. An aged domed-skull from the Astoria Formation of Oregon and various postcranials from Montana, Utah, and Colorado are referred to *Tylocephalonyx*, but they are too incomplete for specific assignment. Some of the material referred to *Tylocephalonyx* sp. is probably early Barstovian in age.

The distribution of *Tylocephalonyx* in the medial to late Hemingfordian and early Barstovian of North America is for the most part north of contemporary distribution of *Moropus*. Floral evidence suggests that *Tylocephalonyx* was associated with a moist, temperate, deciduous hardwood/conifer forest which covered northwestern North America, whereas *Moropus* at that time was associated with drier savanna or forest-woodland border situations. The above ecological preferences may help to explain replacement of *Moropus* by *Tylocephalonyx* in the Sheep Creek Formation of western Nebraska and of *Tylocephalonyx* by *Moropus* in the Olcott Formation.

Morphology of *Tylocephalonyx* is helpful in assessing general habits and habitats, but many aspects of the habits and ecological associations of this animal are still unexplained.

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