SKELETON OF EARLY EOCENE *HOMOGALAX* AND THE ORIGIN OF PERISSODACTYLA

by

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ABSTRACT

The first good skeletal remains of *Homogalax protapirinus* from the Wasatchian of the Bighorn Basin, Wyoming, indicate that this primitive tapiromorph was more plesiomorphic in many features than primitive equoids including *Hyracotherium*. Compared to *Hyracotherium*, *Homogalax* more closely resembles Phenacodonta (the closest outgroup of Perissodactyla for which postcrania are known) in various details of articular surfaces, muscle attachments, and proportions of the humerus, manus, and pes. Among known taxa, *Homogalax* most nearly approximates the plesiomorphic postcranial skeletal anatomy of Perissodactyla.

RESUME

Les premiers restes squelettiques valables d'*Homogalax protapirinus* du Wasatchien du Bassin de Bighorn, Wyoming, indiquent que ce tapiromorphe primitif était plus plésiomorphe par de nombreux caractères que les équoïdés primitifs, y-compris *Hyracotherium*. Comparé à *Hyracotherium*, *Homogalax* ressemble plus aux Phenacodonta (le groupe le plus proche des Perissodactyla pour lequel les os des membres soient connus) par des détails variés des surfaces articulaires, des attaches musculaires, et des proportions de l'humérus, de la main et du pied. Parmi tous les taxa connus, *Homogalax* est celui qui se rappoche le plus de l'anatomie postcrânienne plésiomorphe des Perissodactyla.

INTRODUCTION

Although teeth and jaws of primitive perissodactyls are among the most abundant fossils in early Eocene Holarctic faunas, knowledge of their postcranial skeletons has been remarkably limited. The principal sources of information on basal perissodactyl postcranial anatomy have been three partial skeletons and numerous isolated elements of the oldest equid, Wasatchian *Hyracotherium* (Cope 1884, Kitts 1956, Hussain 1975), and two partial skeletons of the late Wasatchian ceratomorph *Heptodon* (Osborn & Wortman 1892, Radinsky 1965). Though somewhat younger (middle Eocene-early Oligocene), European Palaeotheriidae provide additional information on plesiomorphic perissodactyl anatomy. They resemble phenacodontids, and are therefore considered more primitive than *Hyracotherium*, in certain dental traits and in having a convex iliac crest and a less elevated greater trochanter (Franzen 1989). They are autapomorphous, however, in various other features, such as having metacarpals that are longer than the metatarsals. When better known, middle Eocene *Hallensia*, another primitive equoid from Europe (Franzen 1990), may also prove to shed light on the primitive perissodactyl skeleton.

The basal tapiromorph *Homogalax* (including many specimens long known as *Systemodon*) is a common component of many early Wasatchian faunas from western North America (Savage & Russell 1983) and has been well known from dentitions for a century. Two North American species are recognized, *H. protapirinus* and *H. aureus*

(Radinsky 1963, Gingerich 1991); the former one is better known. Despite the widespread occurrence and relative abundance of primitive tapiromorph dentitions in Holarctic early Eocene faunas (e.g., Radinsky 1963, Chow & Li 1965, Savage *et al.* 1966, Savage & Russell 1983, Russell & Zhai 1987, Prothero & Schoch 1989), little or nothing has been known of the postcranial skeleton in the oldest representatives — *Homogalax*, and recently named *Cardiolophus* and *Orientolophus* — except for brief comments on *Homogalax* by Wortman (1896), Kitts (1956), and Gingerich (1991), and mention of a single tarsal specimen of *Cardiolophus* (Gingerich 1991). *Orientolophus* is known solely from teeth (Ting 1993). *Cymbalophus*, initially proposed as a primitive ceratomorph (Hooker 1984), has subsequently been regarded by Hooker (1989) as the most primitive equoid; in any case it, too, is still known only from teeth (Hooker, pers. comm. 1994). Several recently collected partial skeletons of *Homogalax protapirinus*, however, preserve much of the limb skeleton (Rose 1990, Gingerich 1991), and they are the focus of this report. *Homogalax*, *Hyracotherium*, and *Cardiolophus* were present in part or all of the Wasatchian Willwood Formation, and briefly coexisted in early Wasatchian time (Gingerich 1991).

Homogalax and *Cardiolophus* are the most primitive members of Isectolophidae, variously regarded as the most primitive family of the superfamily Tapiroidea (Radinsky 1963, Gingerich 1991) or of the suborder or infraorder Tapiromorpha (Hooker 1989; = Moropomorpha of Prothero & Schoch 1989). Despite disagreements on how to classify these animals, there is universal agreement that *Homogalax* is one of the most primitive known perissodactyls.

As will be shown here, the postcranial skeleton of *Homogalax* is very similar to that of other primitive perissodactyls such as *Hyracotherium* and *Heptodon*, making positive identification very difficult in the absence of associated teeth (the condition of most postcrania). Nevertheless, comparisons among postcrania reliably associated with teeth reveal a number of more or less consistent differences, pertaining particularly to the humerus, the manus, and the pes. The description here, restricted to the limb skeleton, is based on such associated material unless otherwise indicated. These new skeletons allow a test of the hypothesis that *Homogalax* was more primitive than equoids including *Hyracotherium* (e.g., MacFadden 1976, 1988).

Abbreviations: UM, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; USGS, U.S. Geological Survey, Paleontology & Stratigraphy Branch, Denver, Colorado.

MATERIALS

The most important postcranial specimens of *Homogalax protapirinus* are:

USGS 25032: mandible with complete dentition, maxillae and premaxillae with almost complete dentition; several vertebrae, complete left humerus, partial right humerus, partial left pelvis, nearly complete left femur and tibia, patella, left distal fibula, nearly complete left tarsus, metatarsals II-IV, three phalanges; from USGS locality D-1838, approximately 400-500 meter interval of the Willwood Formation (see Bown *et al.* 1994).

USGS 21843: jaw fragments indicating at least two individuals, vertebrae, parts of scapula, humeri, ulna, radii, femur, tibia, astragalus, calcanei, metapodials, and phalanges; from USGS locality D-1415, 354 meter level in Willwood Formation.

UM 87027: palate and jaw fragments, several articulated vertebrae, parts of both humeri, proximal right ulna, proximal and distal radius fragments, most of right manus, left femur, proximal and distal tibial fragments, parts of pes; from UM locality FG-091, Willwood Formation, stratigraphic level uncertain.

More fragmentary postcrania (associated with teeth of *Homogalax*) are included with USGS 1931, USGS 25006, UM 92584 (at least two individuals), and UM 95068. Specimens without teeth that are believed to represent *Homogalax* because of close resemblance to the previous specimens are USGS 21913 (distal humerus, proximal radius and ulna, distal radius), USGS 21958 (tibia, calcaneus, astragalus), USGS 38040 (proximal tibia, astragalus, cuboid, distal metapodials), and UM 90987 (fragments of humerus, ulna, radius, femur, calcaneus, astragalus). Problematic specimens compared include USGS 25284 (*Homogalax* or *Heptodon*), USGS 38041 (?tapiromorph), and UM 91257 (*Homogalax* or *Hyracotherium*).

A single postcranial specimen lacking associated teeth has been attributed to *Cardiolophus radinskyi* (Gingerich 1991): UM 80318 includes a distal tibia, calcaneus, astragalus, and three phalanges.

The following comparative postcrania also were studied:

Phenacodus vortmani: USGS 5022, 7159, 21855, 21878, 25299.

Phenacodus trilobatus: USGS 7146, 7162, 16477, 21838, 25127.

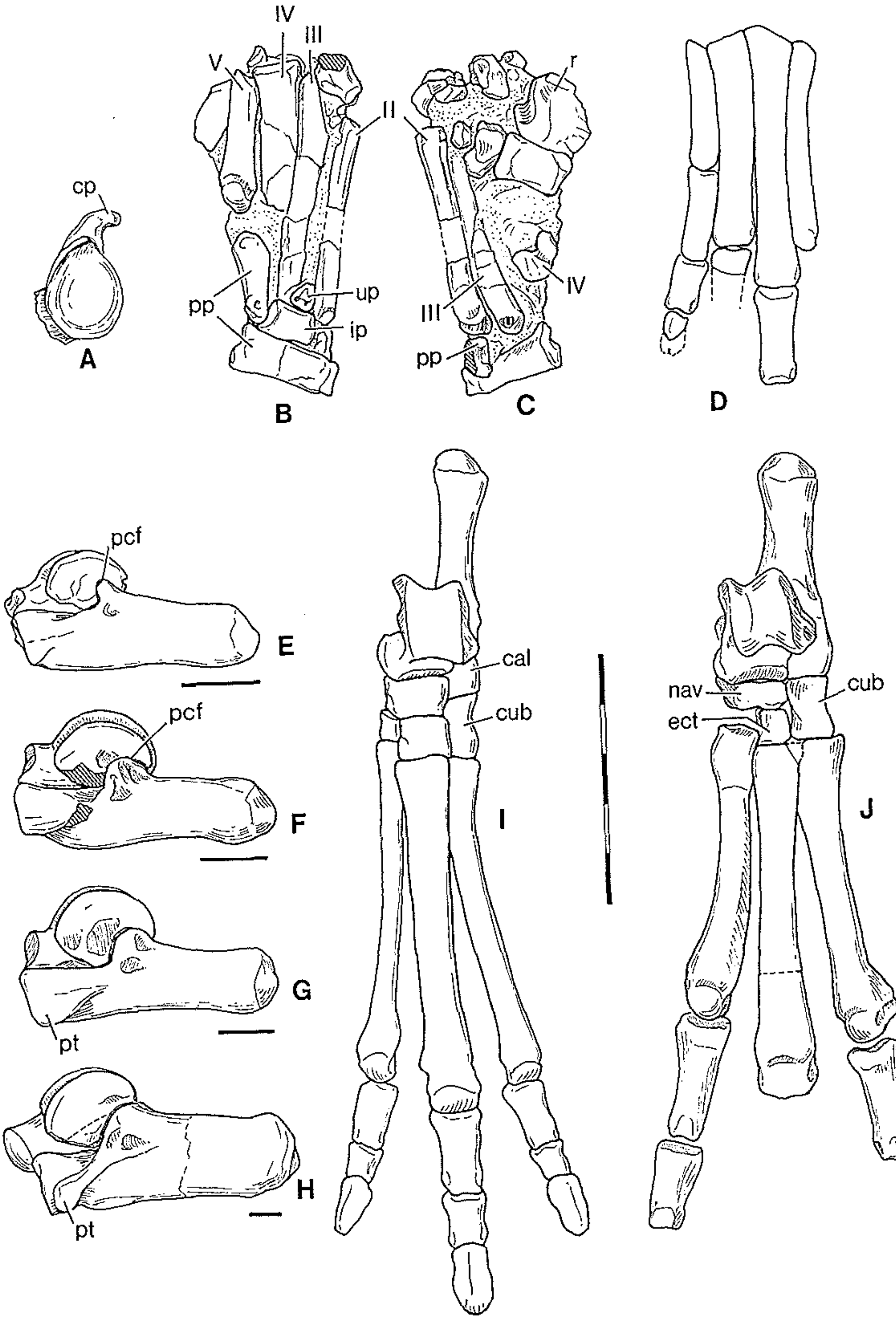
Copecion brachypternus? (formerly placed in *Phenacodus*): USGS 25302.

Hyracotherium species (with associated teeth): USGS 4723, 5907, 6110, 21858, 21877, 21924, 25255, 38044; (without teeth): USGS 5901, 5904, 5905, 6097, 16479, 21860, 21911, 21977, 25003, 25089, 25105, 25150, 25209, 25226, 25234, 25329, 25336, 38039, 38042, 38043, and several uncatalogued specimens.

Hyracotherium or small tapiromorph (without associated teeth): USGS 25016, 25092, 25119, 25157, 25167, 25198, 25327, and uncatalogued specimens.

Heptodon sp. (with teeth): USGS 21861; (without associated teeth): USGS 21921, 21923, 21961, 25252, 25308, 25333, 38045.

Figure 1.— A-D, Forelimb elements of *Homogalax protapirinus*. A, Glenoid fossa of right scapula, USGS 21843. B-D, Right manus, UM 87027; B and C, dorsal and ventral views of partly articulated manus as preserved; D, restored manus. E-H, Left calcaneus and astragalus in lateral view; E, *Hyracotherium*, USGS 38039; F, *Cardiolophus radinskyi*?, UM 80318; G, *Homogalax protapirinus*, UM 95068 (reversed), supplemented by UM 87027 and USGS 21958; H, *Phenacodus trilobatus*, USGS 7146 (partly restored from opposite side). I, Left pes of *Hyracotherium "angustidens,"* after Kitts 1956; J, Left pes of *Homogalax protapirinus*, USGS 25032. 5 cm scale applies to A-D, I-J; scales for E-H are 1 cm. Abbreviations: cal, calcaneus; cp, coracoid process; cub, cuboid; ect, ectocuneiform; ip, intermediate phalanx; nav, navicular; pcf, proximal calcaneal facet; pp, proximal phalanx; pt, peroneal tubercle; r, radius; up, ungual phalanx; Roman numerals identify metacarpals.



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Comparisons to *Meniscotherium* are based on descriptions and illustrations by Gazin (1965) and Williamson & Lucas (1992).

COMPARATIVE ANATOMY OF APPENDICULAR SKELETON

SCAPULA

(Figure 1A)

Only the glenoid portion is preserved (USGS 21843). As in other primitive perissodactyls, *Phenacodus*, and *Meniscotherium*, it is broadly ovoid and distinctive in having a prominent, pointed supraglenoid tubercle. The medially projecting coracoid process is particularly high and prominent but otherwise resembles that of *Heptodon* (USGS 25333) and *Hyracotherium* (USGS 25003) and differs from the lower, bilobed coracoid of *Phenacodus* (USGS 7159, 21878) and some *Meniscotherium*.

HUMERUS

(Plate 1, fig. 3)

The humerus of *Homogalax* closely resembles that of other early perissodactyls in being slender and elongate (more so than in *Phenacodus* or *Meniscotherium*) and having a prominent, high greater tuberosity, weakly developed deltopectoral crest, and relatively narrow distal articulation with reduced epicondyles, no entepicondylar foramen, constricted capitulum, and a large supratrochlear foramen — characters associated with cursoriality. In USGS 25032 the humerus measures 123.8 mm in articular length, 132.5 mm in total length, and 11.7 mm in midshaft anteroposterior diameter. The distal end is relatively wider than in *Hyracotherium* and *Heptodon*, however, and has more pronounced epicondyles (especially the entepicondyle), at the expense of the articular surface (Fig. 2). The narrow articular shelf lateral to the capitulum, typical of early perissodactyls, projects more proximally than in *Hyracotherium*. The supinator crest (lateral supracondylar ridge) is sharp and projects posterolaterad. It is better developed than in these genera, although some specimens of *Heptodon* approach *Homogalax* in this regard (Radinsky 1965). The distal end in *Homogalax* is also less anteroposteriorly expanded than in *Hyracotherium* and *Heptodon* (UM 87027 even less so than USGS 25032), with a less caudally projecting entepicondyle than in the other Wasatchian perissodactyls. In all these features, *Homogalax* more closely approximates the character states present in *Phenacodus* and *Meniscotherium*.

The distal end is also similar to that of the primitive artiodactyl *Bunophorus* (USGS 16470, probably *B. etsagicus*) in size and general form, including the moderately prominent medial epicondyle. *Bunophorus* can be readily distinguished by its more central capitulum (=intercondylar ridge) and, consequently, relatively narrower trochlea and more extensive articular surface lateral to the capitulum.

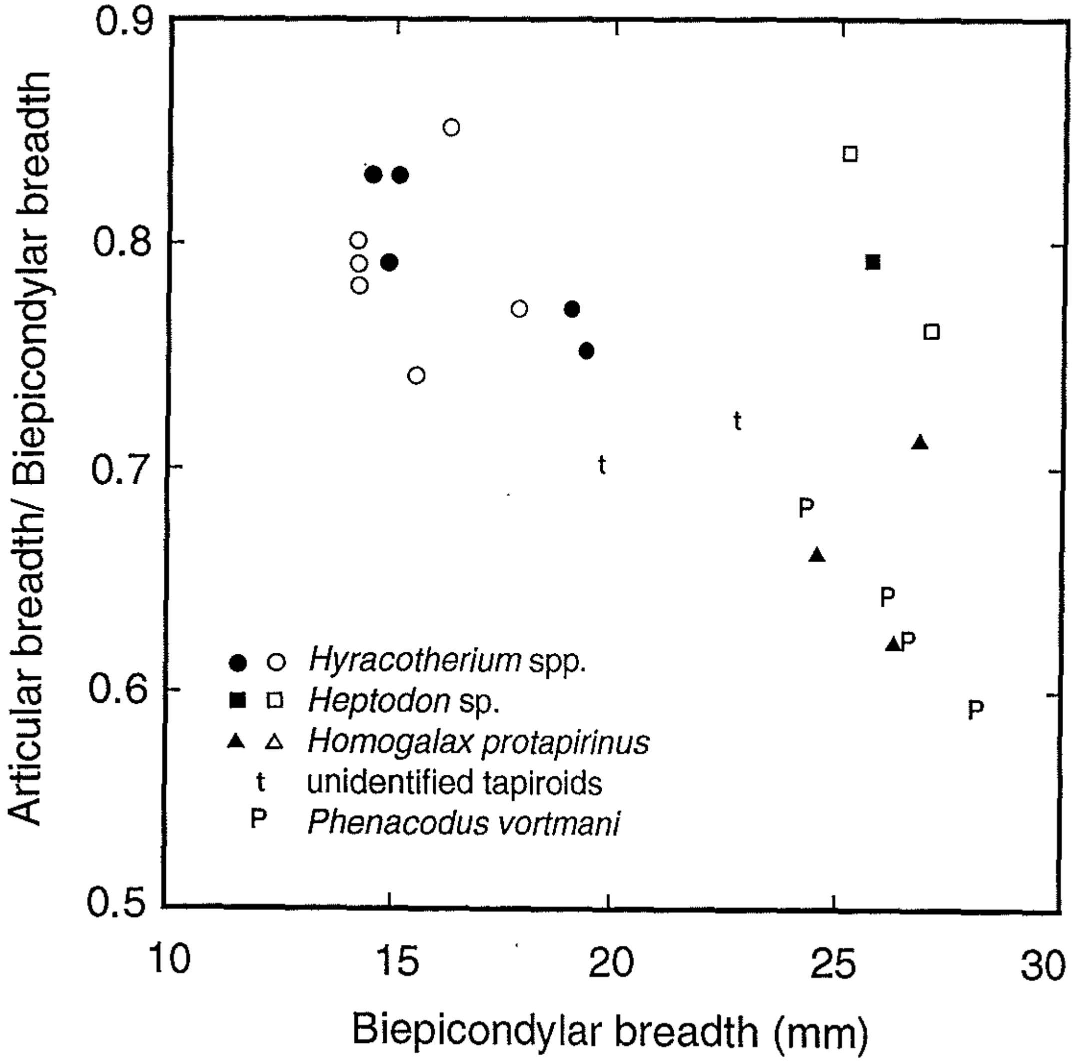

Figure 2.— Scatterplot of distal humeral dimensions in primitive perissodactyls and *Phenacodus* from the Willwood Formation, to illustrate relatively narrower articular surface in *Homogalax*. Solid symbols indicate specimens with associated teeth; open symbols are specimens lacking associated teeth and assigned by morphology alone.

The greater tuberosity in USGS 25032 is oriented as in *Hyracotherium* but extends higher above the head than in other primitive perissodactyls or *Phenacodus*. This is possibly an apomorphous trait of *Homogalax*, but in USGS 21843 and UM 87027, which are less well-preserved in this region, the greater tuberosity appears to be somewhat less elevated. The intertubercular groove is relatively a little wider than in *Hyracotherium* but not as broad as in *Phenacodus*.

ULNA

Only fragments of the ulna are preserved in available specimens. The proximal end exhibits a more robust olecranon, relatively deeper anteroposteriorly than in *Hyracotherium* but less so than in *Heptodon* (Radinsky 1965: fig. 8). The olecranon resembles that of other early perissodactyls in being more mediolaterally compressed and less medially inflected than in *Phenacodus* or *Meniscotherium* and in having an anteroposterior groove, associated with triceps insertion, on its proximal end.

RADIUS

The proximal and distal articulations of the incomplete radius do not appear to be significantly different from those of *Hyracotherium*. The humeral articulation is mediolaterally broad with an irregular concavoconvex surface that interlocked with the humerus to prevent radial rotation. The trochlear facet is broader and the capitular articulation deeper than in *Phenacodus*, consequently that part of the surface that articulated with the shelf lateral to the capitulum is better discriminated than in *Phenacodus*. As in *Hyracotherium* and *Phenacodus*, the distal articulation consists of two concavities, for lunar and scaphoid. The latter facet is distinctly convex on its posterior border, as in *Hyracotherium*, but in contrast to *Phenacodus*, in which both facets have more nearly concave articular surfaces (see also Kitts 1956). The posteriorly expanded scaphoid facet implies the presence of a larger scaphoid tubercle, which reflects more powerful carpal flexors than in *Phenacodus* (Radinsky 1966).

MANUS
(Figure 1B-D)

UM 82027 includes a partly articulated, though damaged, right manus. Most of the carpal elements in this specimen are poorly preserved or obscured by hematitic matrix and will not be further considered here. Four metacarpals are present, but due to breakage and matrix only approximate measurements are possible: Mc III is the longest (about 51 mm long), Mc II and IV somewhat shorter (41 mm and 42 mm, respectively), and Mc V much shorter (28 mm). Thus the manus appears to indicate greater relative reduction of lateral digits than in *Hyracotherium* (Kitts 1956) or *Heptodon* (Radinsky 1965). At the same time, the length of Mc III relative to humeral length (about 42%) is intermediate between *Phenacodus* (31%) or *Meniscotherium* (27-31%) and *Hyracotherium* (53-55%) (Kitts 1956, Radinsky 1966, Williamson & Lucas 1992). The second metacarpal is beveled proximomedially, suggesting that a vestigial first metacarpal may have been present; unfortunately, this surface is not adequately preserved to demonstrate this conclusively.

The phalanges are similar in form to those in other primitive perissodactyls but are relatively longer compared to the metacarpus. The proximal phalanx of digit III is 19 mm long, or 37% as long as Mc III. In *Hyracotherium* and *Heptodon*, this phalanx is approximately 25% as long as Mc III.

PELVIS

As far as can be determined from available fragments, *Homogalax* does not differ significantly from *Hyracotherium* in the bony pelvis. The iliac crest is concave dorsally, rather than straight or convex as in *Phenacodus* and palaeotheres (Kitts 1956, Franzen 1989).

FEMUR

(Figure 3A)

Like most other early perissodactyls, *Homogalax* has a very prominent, proximally projecting greater trochanter associated with attachment of gluteus medius, a powerful hip extensor (Hussain 1975, Getty 1975). A high greater trochanter is typical of, but not restricted to, cursorial mammals, and is especially characteristic of perissodactyls (Howell 1944, Lessertisseur & Saban 1967). Palaeotheres have a lower greater trochanter, as in *Phenacodus*, and may be more primitive in this regard (Franzen 1989). The tuberosity of the third trochanter in *Homogalax* is slightly higher on the shaft than in *Hyracotherium*, being situated just proximal to the distal end of the lesser trochanteric flange rather than distal to it as in *Hyracotherium* (USGS 5904, 5907, 21858, 21860; see also Kitts 1956). Both *Heptodon* (Radinsky 1965) and phenacodontids (Kitts 1956, Thewissen 1990, Otts 1991) resemble *Hyracotherium* in having more distal third trochanters. Whether this represents a real difference between *Homogalax* and the other genera or was variable intraspecifically is uncertain based on the small samples available for this study.

The distal femur is not well preserved in any of the *Homogalax* specimens at hand but does not appear to differ significantly from that of *Hyracotherium*: its anteroposterior dimension exceeds the mediolateral breadth, and the patellar trochlea is raised, well defined, and has a slightly sharper, more elevated medial rim. There is also very close similarity to the distal femur of *Phenacodus vortmani* (e.g., USGS 5022).

The estimated articular length of the femur in USGS 25032 is 142 mm, and estimated total length (including greater trochanter) is 150 mm.; the total length in UM 87027 is also 150 mm. Midshaft anteroposterior diameter is 13.1 mm in USGS 25032 and 14.0 mm in UM 87027.

TIBIA AND FIBULA

(Figure 3B)

A complete but somewhat crushed tibia is present in USGS 21958 (total articular length = 154 mm; midshaft anteroposterior diameter = 12.8 mm). USGS 25032 has a somewhat better preserved and more gracile tibia, missing part of the proximal diaphysis (midshaft anteroposterior diameter = 9.0 mm), and the distal end of the fibula. These elements do not differ significantly from their counterparts in *Hyracotherium*. As in the latter, the tibia is gently sinuous in lateral profile, the distal half being slightly concave anteriorly. The tibial crest extends slightly more than one-third the length of the bone (about 55 mm in USGS 21958), about as in *Hyracotherium* and *Phenacodus*, but is more distinct.

PES

(Figure 1G, J; Plate 1, fig. 8)

All the tarsal elements are known except the meso- and entocuneiforms. Because there are relatively few specimens of well-preserved tarsals associated with identifiable teeth of early perissodactyls, it is difficult to determine with certainty characters that differ among the various genera. A survey of more than 40 tarsal specimens available for this study indicates that *Homogalax* often differs from *Hyracotherium*, especially in traits of the calcaneus and astragalus, as follows:

(1) The ectal (proximal calcaneal) facet of the astragalus is more gently concave proximodistally (somewhat oblique to the sagittal plane), conforming to the more smoothly rounded proximal facet of the calcaneus. This can be seen in lateral perspective (Fig. 1G). In *Hyracotherium* the ectal facet is often much more tightly curved (e.g., USGS 4723, 6097, 21858, 38039, 38044; see Fig. 1E and Plate 1, fig. 6), corresponding to the pointed, angular proximal calcaneal facet (a consequence of the two principal parts of the joint surface being arranged at an acute angle). The latter morphology does not occur in any *Homogalax* known to me. Not all *Hyracotherium* specimens show this configuration, however; some resemble *Homogalax* in having a rounder ectal facet on the astragalus (e.g., USGS 6110, 430 m level of Willwood Formation), and some show an intermediate condition (USGS 21877). Whether these differences represent inter- or intraspecific variation is not known; however, USGS 25234, a small calcaneus (28.6 mm long, from the 5 meter level of the Willwood Formation, Wa-0 zone of Gingerich 1989) with smoothly rounded proximal facet, probably represents the very primitive *Hyracotherium sandrae*. The calcaneus of USGS 21877 (438 meter level) also has a rounded proximal facet, so this trait does not correlate with low stratigraphic position. Several larger isolated astragali from the upper Willwood Formation (USGS 21921, 21923, 21961, 25252), probably referable to *Heptodon*, also resemble *Homogalax* in this regard, as does *Palaeotherium* (see also Radinsky 1965: fig. 19; MacFadden 1976: fig. 3). It may be that the rounded ectal astragalar facet in some *Hyracotherium* is a primitive trait that was retained in tapiromorphs.

(2) The sustentaculum tali is relatively wider and rounder than in *Hyracotherium*, projecting medially farther from the calcaneal shaft (compare Plate 1, figs. 6 and 8).

(3) The cuboid facet of the calcaneus is mediolaterally broader, in contrast to the typically more compressed semicircular facet of *Hyracotherium* (compare Plate 1, figs. 6 and 8). Correspondingly, the cuboid is relatively a little broader than in *Hyracotherium*.

(4) The peroneal tubercle in *Homogalax*, though reduced compared to its condition in *Phenacodus* (Fig. 1H and Plate 1, fig. 9) and *Meniscotherium*, is conspicuously larger than in *Hyracotherium*. It is not absent in these taxa, as was reported by Thewissen & Domning (1992).

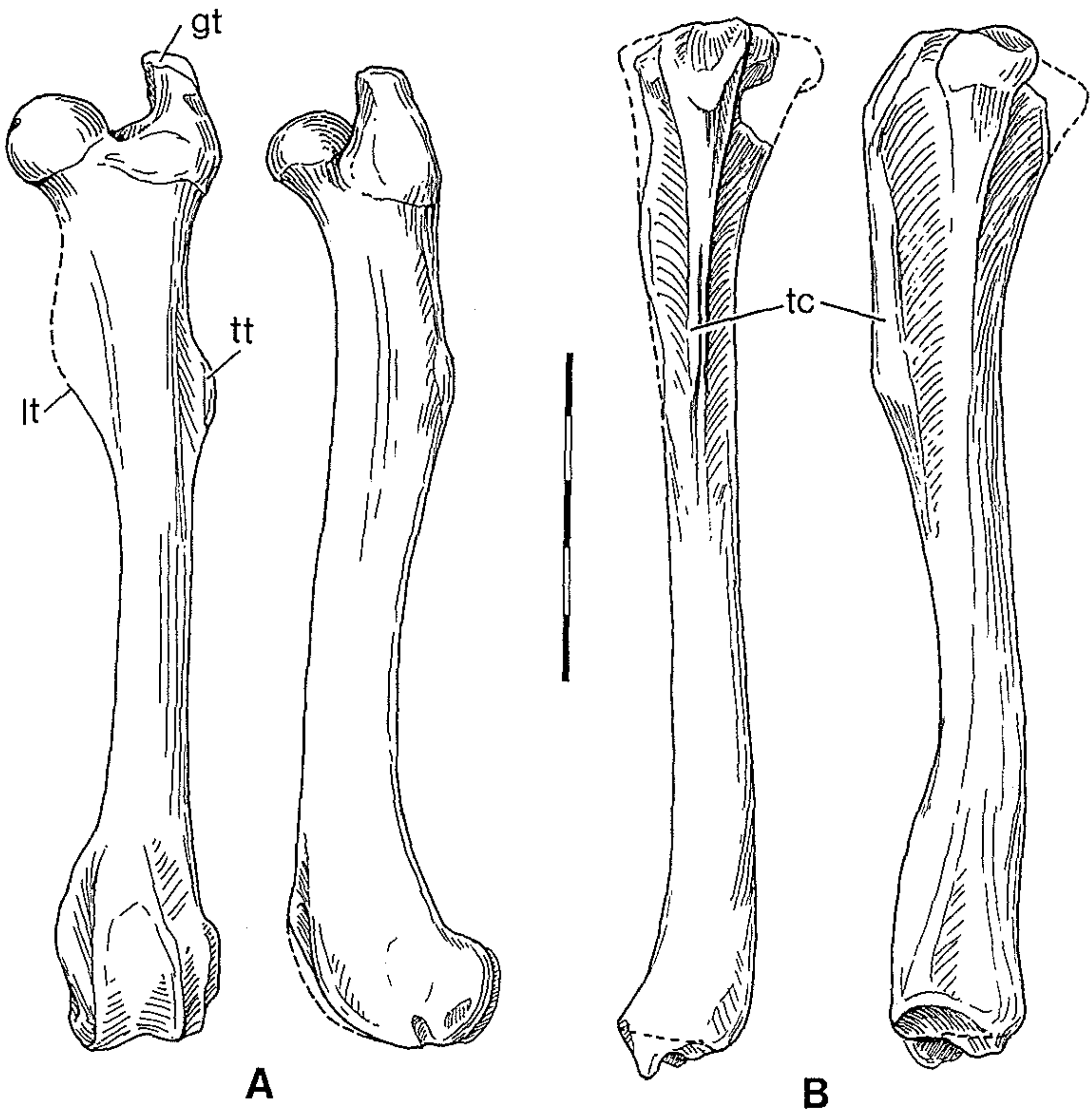

Figure 3.— Femur and tibia of *Homogalax protapirinus*. A, Left femur in anterior and lateral views, UM 87027, supplemented by UM 90987 and USGS 25032. B, Left tibia, USGS 21958, supplemented by USGS 25032. Scale = 5 cm. Abbreviations: gt, greater trochanter; lt, lesser trochanter; tc, tibial crest; tt, third trochanter.

(5) The navicular is relatively wider and proximodistally more compressed, and the ectocuneiform relatively smaller, than in *Hyracotherium* (compare Fig. 1I and J). These elements are known only in USGS 25032, hence these comparisons should be regarded as tentative.

In addition, the calcaneal shaft in *Homogalax* tends to be more robust, and the astragalar neck slightly longer, than in *Hyracotherium* (compare Fig. 1 I and J, and Plate 1, figs. 6 and 8), but there is considerable variation in these traits. It is particularly difficult to substantiate these differences because of the frequent lack of associated teeth and consequent uncertainty of allocation.

Homogalax resembles *Phenacodus* in all of these characteristics more closely than *Hyracotherium* does, confirming Kitts' observation (see also Radinsky 1966) that the astragalus and calcaneus of *Homogalax* and *Heptodon* are "more condylarth-like" than those of *Hyracotherium*.

In all *Homogalax* specimens where it can be assessed (except UM 91257, which may in fact represent *Hyracotherium*), the astragalus extends distally as far as or beyond the calcaneus. Thus contact between the calcaneus and navicular is insignificant or nonexistent, as in *Hyracotherium sandrae* (Gingerich 1991) and some *Hyracotherium* studied here (e.g., USGS 5901, 6097, 38039). In other *Hyracotherium* (Kitts 1956; see Fig. 1I), however, as in *Heptodon* (Radinsky 1965), the calcaneus extends distally slightly beyond the astragalar head, allowing a small calcaneonavicular contact. Such a contact is missing in phenacodontids (Thewissen 1990).

UM 80318 has been ascribed to *Cardiolophus* (Gingerich 1991), presumably on the basis of size and stratigraphic position; no teeth are associated. It shows a curious combination of features: a gracile calcaneal shaft and relatively narrow sustentacular and cuboid facets (more typical of *Hyracotherium*), coupled with a gently concave ectal facet on the astragalus and smoothly convex proximal astragalar facet on the calcaneus, and a peroneal tubercle of intermediate size (Fig. 1F and Plate 1, fig. 7). As Gingerich (1991) observed, there was apparently no contact between calcaneus and navicular (as for *Homogalax*).

Wortman (1896) noted that the pes of *Systemodon* is very similar to that of *Heptodon*, with relatively longer, more slender phalanges than in *Hyracotherium*. The material reported here corroborates these observations. Wortman reported the presence of a vestigial fifth digit in *Homogalax*, which is not evident in USGS 25032. Kitts (1956) also reported a reduced Mt V in *Hyracotherium* (but figured the pes without it), whereas Radinsky (1965) reported a vestigial Mt I but no evidence of Mt V in *Heptodon*. *Homogalax* seems to conform with *Heptodon* in this regard: Mt II in USGS 25032 is beveled proximally, like its metacarpal counterpart, suggesting the presence of a vestigial Mt I; but there is no evidence of Mt V.

Metatarsals II, III, IV are 30-40% longer than the metacarpals but relatively shorter than in comparably sized *Hyracotherium* (Fig. 1I,J). The length of Mt III (about 67 mm) compared to estimated femur length is approximately 45-48%; the same ratio is 51-56% in *Hyracotherium*, 35-37% in *Phenacodus*, and 32% in *Meniscotherium* (Kitts 1956, Radinsky 1966, Williamson & Lucas 1992). Metatarsals II and IV are about 10% shorter than Mt III (59 and 62 mm, respectively). The metatarsals of USGS 25032 are slender, barely any greater in girth than the metacarpals of UM 87027, and roughly equal in caliber (midshaft minimum and maximum diameters: Mt II, 5.0 x 7.0 mm; Mt III, 5.3 x 7.2 mm; Mt IV, 4.9 x 6.6 mm); but fragmentary metatarsals with USGS 21843 are more robust. In *Hyracotherium* Mt II and IV are somewhat reduced in diameter but only very slightly in length relative to Mt III. As in the manus, the proximal phalanges are about 35-40% as long as the metatarsals (preserved ones measure 23.2 and 23.5 mm long; middle phalanx is 14.9 mm long), comparatively much longer than in *Hyracotherium* (25%; Kitts 1956).

BODY SIZE OF *HOMOGALAX*

Regressions for prediction of body mass based on tooth size are not available for primitive perissodactyls, but several such regressions have been derived from long bone dimensions. The latter, particularly regressions based on long bone cross-sectional dimensions, are probably more reliable than tooth-based estimates because they are directly related to support of body weight (e.g., Ruff 1989). Owing to small sample size and the fragmentary nature of the fossils, the estimates provided here should be regarded as tentative, but they can provide a general idea of the size of *Homogalax*. Gingerich's BODYMASS program (1990, developed from a diversity of mammals) applied to available lengths and anteroposterior diameters of humerus, femur, and tibia in USGS 25032 and 21958, yields estimates ranging from 5.7 to 13.4 kg (95% prediction limits: 2.2-37.1 kg), with a mean estimate of 9.5 kg (95% prediction limits: 7.0-14.4 kg). Based on metacarpal length and femur dimensions of UM 87027, Gingerich (1991) estimated the mass of *Homogalax* to be 10.4-13.8 kg. Somewhat higher estimates are generated using Scott's (1990) all-ungulate regressions: 7.2 to 22.3 kg (mean = 15.1 kg). These estimates indicate that *Homogalax* was slightly larger than the paca *Agouti* and a little smaller than the collared peccary, *Tayassu tajacu*.

DISCUSSION

Late Paleocene *Radinskya yupingae* (?Phenacolophidae) is probably the closest outgroup to Perissodactyla, but it is known only from a single palatal dentition (McKenna *et al.* 1989). Therefore, postcranial character polarities of *Homogalax* are assessed here by comparison with the next closest outgroup, Phenacodonta (phenacodontid and meniscotheriid "condylarths"; Gazin 1965, Radinsky 1966, Thewissen 1990, Otts 1991, Williamson & Lucas 1992, Thewissen & Domning 1992), as well as with the more distantly related arctocyonid "condylarths" (e.g., Matthew 1937, Russell 1964, Rose 1987) and with other early perissodactyls, particularly *Hyracotherium* and *Heptodon* (Kitts 1956, Radinsky 1965). Phenacodonta are the most primitive members of Paenungulata, which includes the order Perissodactyla (Thewissen & Domning 1992; see also Prothero *et al.* 1988).

In most postcranial features *Homogalax* is very similar to *Hyracotherium*. The sharper tibial crest, relatively more reduced fifth metacarpal, and more proximal third trochanter of *Homogalax*, however, may be more derived than in *Hyracotherium*. (It is also possible that the last trait is primitive for Perissodactyla, since a more distal third trochanter would increase the leverage of the superficial gluteal muscle.) But there are many more characters in which *Homogalax* is clearly more primitive than *Hyracotherium*.

Characters of *Homogalax* that approximate the conditions found in phenacodontids, meniscotheriids, and more generalized arctocyonids — and, on this basis, are regarded to be plesiomorphic relative to *Hyracotherium* — include: relatively broad distal humerus with narrow articular surface, prominent entepicondyle and low, sharp supinator crest; wider intertubercular groove than in *Hyracotherium*; in both manus and pes, metapodials shorter and phalanges longer relative to proximal limb segments; manual first digit possibly present; tibial crest stronger; proximal calcaneoastragalar joint more smoothly rounded, thus allowing more mobility; calcaneus more robust, with broader sustentacular and cuboid facets and larger peroneal process; astragalus extending distad at least as far as calcaneus; navicular and cuboid somewhat broader (mediolaterally) and shorter, and lateral metatarsals less reduced in caliber, than in *Hyracotherium*. For the most part these are rather subtle distinctions, not substantial differences. Nonetheless, they indicate that in several osteological features relating to cursorial specialization (e.g., Howell 1944, Jenkins 1973, Van Valkenburgh 1987), *Homogalax* was less progressive than the contemporary equoid *Hyracotherium*. *Homogalax* was intermediate between phenacodontids and *Hyracotherium* in relative elongation of distal limb segments and concomitant reduction of distal muscle mass. Furthermore, joints and muscle attachment areas suggest that the radius and the tarsus were somewhat more flexible than in *Hyracotherium*.

Absence of calcaneonavicular contact in *Homogalax* and some *Hyracotherium* also characterizes phenacodontids and arctocyonids (Matthew 1937, Russell 1964, Thewissen 1990) and may reflect the primitive phylogenetic position of these taxa. Presence of an astragalocuboid contact is also considered primitive (Thewissen & Domning 1992). Contact between these two tarsal bones occurs in arctocyonids and primitive perissodactyls including *Homogalax*, but not in phenacodontids (Thewissen 1990) or meniscotheriids (Williamson & Lucas 1992). However, the joint in perissodactyls is located posteriorly, not anteriorly as in arctocyonids and may not be homologous. Establishment of minor contacts between astragalus and cuboid posteriorly and calcaneus and navicular anteriorly in some early perissodactyls, in addition to the saddle-shaped astragalonavicular joint, may be cursorial specializations associated with stabilizing the tarsus and restricting its mediolateral mobility.

In addition to these postcranial characters, *Homogalax* and *Cardiolophus* were more primitive than *Hyracotherium*, and like palaeotheres, in having a shorter postcanine (C_1–P_1) diastema and a less molarized P^2 (Franzen 1989, Gingerich 1991).

To summarize, *Homogalax* is more primitive than *Hyracotherium* in several characters, and possibly more derived than primitive equoids in only a couple of features. The postcranial evidence supports recent conclusions that tapiromorphs (or ceratomorphs) are the stem group of Perissodactyla (MacFadden 1976, 1988, Hooker 1984, Ting 1993). *Homogalax* was nonetheless one of the most cursorially adapted mammals of the Wasatchian.

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LEGEND OF THE PLATE

PLATE 1

Figures 1-5: Left humeri, in anterior and distal views; scale = 5 cm.

Fig. 1.— *Heptodon* sp., USGS 25333.

Fig. 2.— *Hyracotherium* sp., USGS 25105.

Fig. 3.— *Homogalax protapirinus*, USGS 25032: anterior, posterior, and distal views.

Fig. 4.— *Phenacodus vortmani*, USGS 7159.

Fig. 5.— *Chriacus* sp., USGS 2353, supplemented by USGS 15404 and USGS 21907.

Figures. 6-9: Left calcanei in anterior and distal views; scales = 1 cm.

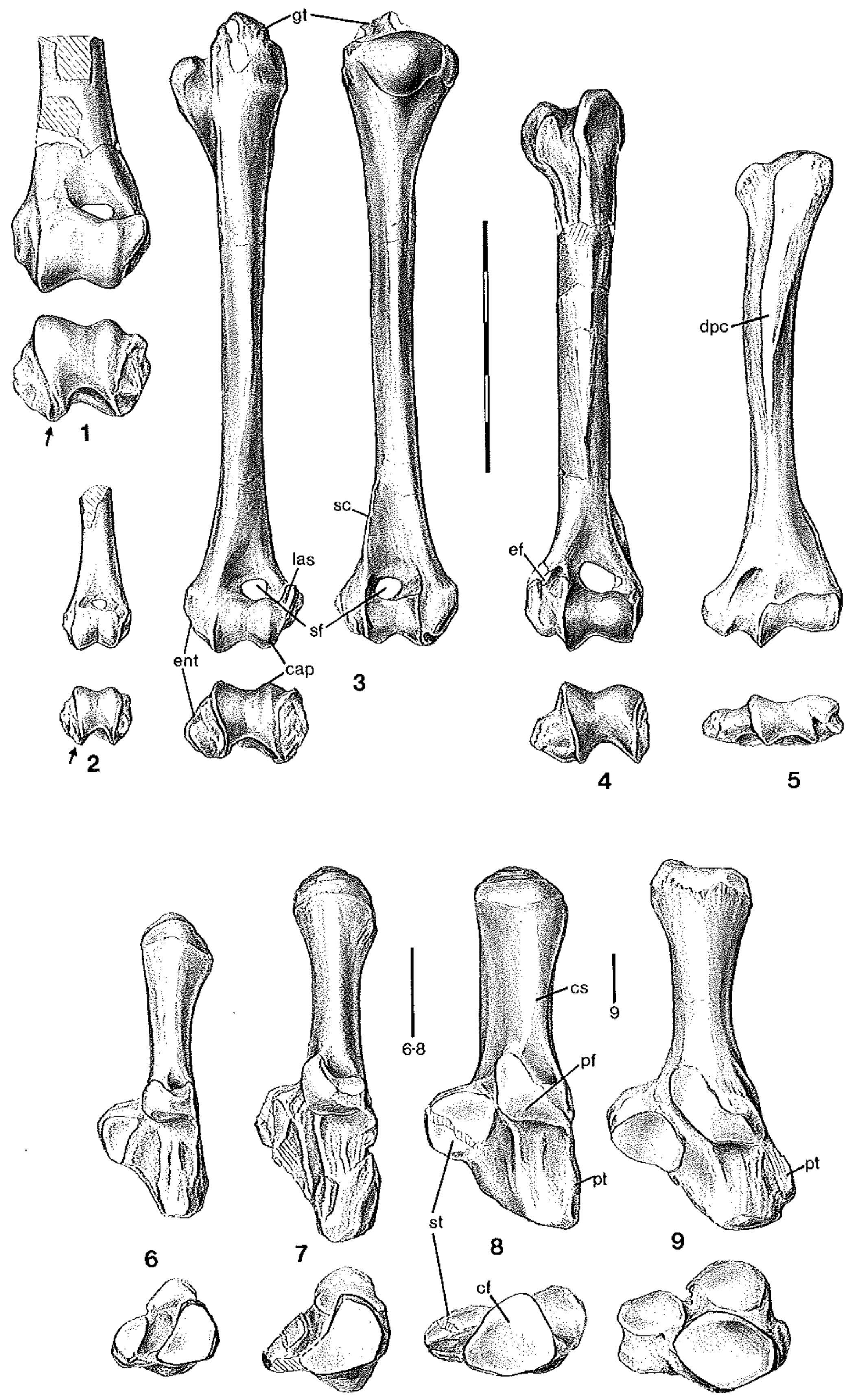
Fig. 6.— *Hyracotherium* sp., USGS 38039.

Fig. 7.— *Cardiolophus radinskyi*?, UM 80318.

Fig. 8.— *Homogalax protapirinus*, UM 87027 (reversed), supplemented by UM 95068 and USGS 21843.

Fig. 9.— *Phenacodus trilobatus*, USGS 7146.

Abbreviations: cap, capitulum; cf, cuboid facet; cs, calcaneal shaft; dpc, deltopectoral crest; ef, entepicondylar foramen; ent, entepicondyle; gt, greater tuberosity; las, lateral articular shelf; pf, proximal facet of calcaneus; pt, peroneal tubercle; sc, supinator crest; sf, supratrochlear foramen; st, sustentaculum tali. Arrows point to caudally projecting entepicondyle in *Hyracotherium* and *Heptodon*.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