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SYSTEMATICS AND EVOLUTION OF EARLY EOCENE PERISSODACTYLA (MAMMALIA) IN THE CLARKS FORK BASIN, WYOMING

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Abstract.— Four genera and eight species of Perissodactyla are known from the Willwood Formation, early Eocene, of the Clarks Fork Basin, Wyoming. The equid *Hyracotherium* Owen, represented by five species (one new), is the most diverse. A new tapiroid genus, *Cardiolophus*, is represented by one new species (and "*Homogalax*" *semihians* from the Bighorn Basin is referred to this genus). *Homogalax* Hay and *Paleomoropus* Radinsky are each represented by a single species in the Clarks Fork Basin (one new species of *Homogalax* is described from North Dakota). First appearances of *Hyracotherium* spp. and *Homogalax protapirinus* are important stratigraphically in marking the beginning of the Sandcouleean and Graybullian subdivisions of the Wasatchian land-mammal age. Tooth size and long bone measurements yield compatible estimates of body mass in *Hyracotherium*. Two species of *Hyracotherium* retain a distinct foramen ovale in the basicranium. Two genera and species of early and middle Wasatchian perissodactyls are present through most of the Clarks Fork Basin stratigraphic section, but three genera are present during two brief intervals.

INTRODUCTION

University of Michigan field parties have systematically surveyed Eocene badlands in northwestern Wyoming since the summer of 1974. Work has been concentrated in the northern Bighorn Basin and in the Clarks Fork Basin, where a continuous stratigraphic section spans much of the Paleocene and early Eocene. The Clarks Fork Basin is the type area of the Sandcouleean subage of the Wasatchian land-mammal age. Biostratigraphic subdivision of the Eocene has long been based on perissodactyls, and the Clarks Fork Basin section is important for understanding the earliest perissodactyl zones. Field work carried out to date has produced more than three thousand catalogued perissodactyl specimens, including many representatives of the new genus and two of the new species described below.

Early Eocene Perissodactyla are difficult to study because species, genera, and even higher taxa differ little from each other. Good specimens with associated anterior teeth and cheek teeth, quantitative study of variation, stratigraphic superposition of sample intervals, and a long period of comparative study have been required to reach conclusions presented here regarding the number of species present and the patterns of their evolution in the Clarks Fork Basin. An initial study carried out in the 1970s lead to publication of a diagram showing evolutionary patterns based on specimens known at that time (Gingerich, 1980: fig. 6). Study then continued, with modifications incorporated and documented here: (1) *Hyracotherium sandrae* is now recognized as being different from *H. grangeri.* (2) Ancestral-descendant relationship of *Hyracotherium grangeri* and *H. aemulor* is less clear than it first appeared to be. (3) *Hyracotherium aemulor*, previously employed as a nomen nudum, is a new species different from later *H. cristatum.* (4) "*Homogalax planeticus*" (nomen nudum) is distinct from *Homogalax* at the generic level and is here published as the new genus and species *Cardiolophus radinskyi.* (5) *Homogalax protapirinus*, formerly regarded as a junior synonym of *H. semihians*, appears to be valid, while the latter species belongs in *Cardiolophus*.

Study of a large sample of *Hyracotherium* from one quarry, Castillo Pocket in the Huerfano Basin of Colorado (Gingerich, 1981), while outside the basin and temporal interval studied here, was helpful in providing standards for intraspecific variability and sexual dimorphism. This is a species-level study that does not deal in any way with higher-level evolutionary relationships, although it is obviously important for higher-level systematics to know the generic and species-level diversity and the morphological disparity of forms appearing early in the perissodactyl diversification. Cladistic relationships of early perissodactyls are thoroughly explored by MacFadden (1976), Hooker (1984), and many authors in Prothero and Schoch (1989).

Dental nomenclature follows Radinsky (1963, 1969) and Savage et al. (1965, 1966). New observations are provided on the distribution of an important basicranial foramen, the foramen ovale, in early Eocene *Hyracotherium* and close relatives. Significant postcranial remains are known for some of the species described here, and long bone measurements are given when possible. The reader is referred to Kitts (1956), Hussain (1975), and Rose (1990) for more information on the postcranial skeleton of early North American perissodactyls.

The Wasatchian land-mammal age has long been subdivided into subages, zones, or biochrons, based largely on the distribution of perissodactyl genera and species. Eight zones of the Wasatchian are recognized, numbered Wa-0 through Wa-7. The first three, Wa-0 through Wa-2, belong to the Sandcouleean subage regarded as early Wasatchian; the second three, Wa-3 through Wa-5, belong to the Graybullian subage, regarded as middle Wasatchian; and the last two zones, Wa-6 and Wa-7, belong to the Lysitean and Lostcabinian subages, respectively, regarded as late Wasatchian. Recognition and composition of zones are discussed at greater length near the end of this paper.

This overview of Clarks Fork Basin specimens represents about the first half of the Wasatchian land-mammal age in one depositional basin of the Western Interior. Systematic relationships of middle and late Wasatchian perissodactyls in the continguous Bighorn Basin, the San Juan Basin, and elsewhere remain to be clarified.

ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

AMNH	– American Museum of Natural History, New York
UM	– University of Michigan, Museum of Paleontology, Ann Arbor
USGS	– U. S. Geological Survey, Denver
USNM	– U. S. National Museum of Natural History, Washington
UW	– University of Wyoming, Laramie
YPM	– Yale University Peabody Museum of Natural History, New Haven
YPM-PU	– Princeton collection at Yale Peabody Museum, New Haven

University of Michigan localities in the Sand Coulee area of the Clarks Fork Basin are prefaced SC. Localities in the Foster Gulch and McCullough Peaks areas of the northern Bighorn Basin are prefaced FG and MP, respectively. Yale-Michigan localities, Michigan localities in the Graybull River area, and Michigan localities in the Red Butte area of the central Bighorn Basin are prefaced YM, GB, and RB, respectively.

HISTORY OF STUDY

The history of study of Wasatchian Perissodactyla of the North American early Eocene is complicated, but some background is useful for understanding the complexity of systematic problems involved in this group. The first reports were published in 1872 and 1873 when E. D. Cope named two species, *Lophiotherium vasacciense* and *Orotherium index*, from the Bear River valley near Evanston, Wyoming (specimens in AMNH). This area has yielded *Heptodon* and is regarded as Lysitean (Granger, 1914; Gazin, 1962), or late Wasatchian in age.

Between 1874 and 1877, Cope named seven species (including *Orohippus tapirinus*), and O. C. Marsh named one from the San Juan Basin, New Mexico. San Juan Basin localities are also regarded as Lysitean (Lucas et al., 1981), or late Wasatchian. The Cope and Marsh collections from the San Juan Basin (at USNM and YPM, respectively) sort into three size groups (Fig. 1), meaning that at least three of the ten species are valid. The oldest available name for the small species is *Hyracotherium index* (Cope, 1873). The oldest available name for the middle-sized species is *Hyracotherium vasacciense* (Cope, 1872). The oldest available name for the large species is *Hyracotherium tapirinum* (Cope, 1875; or *Systemodon tapirinus*, see below).

In 1876, Marsh described the genus *Eohippus* with two species, *E. validus* and *E. pernix*. The former, type of the genus, is from the late Wasatchian of New Mexico and a synonym of *Hyracotherium vasacciense*. The latter is from older Graybullian (middle Wasatchian) strata near Bitter Creek Station in southwestern Wyoming (Gazin, 1962). *H. pernix* is the first species named from the middle Wasatchian, and it is used here for medium-sized specimens from the middle and late Graybullian upper part of the Clarks Fork Basin section.

In 1880 and 1881, Cope named two species, *Hyracotherium craspedotum* and *H. venticolum*, from the late Wasatchian (Lostcabinian subage) of the Wind River Basin, Wyoming. The first good specimens from the Bighorn Basin were collected in 1881. Seeing these and mistaking them for *Hyracotherium tapirinum*, Cope (1881b) transferred *H. tapirinum* to a new genus *Systemodon*. New Bighorn Basin perissodactyls were named by Cope (1882, 1885), Wortman (1896), Granger (1908), and finally Kitts (1956).

Kitts (1956) is the most recent author to review Wasatchian *Hyracotherium*, and the species and subspecies he recognized are as follows:

Hyracotherium angustidens [small to large]
- *Hyracotherium angustidens angustidens* (Cope, 1875)
- *Hyracotherium angustidens etsagicum* (Cope, 1885)
- *Hyracotherium angustidens grangeri* Kitts (new)

Hyracotherium vasacciense [medium to large]
- *Hyracotherium vasacciense vasacciense* (Cope, 1872)
- *Hyracotherium vasacciense venticolum* (Cope, 1881)

Hyracotherium craspedotum [large]
- *Hyracotherium craspedotum* Cope, 1880 (no subspecies)

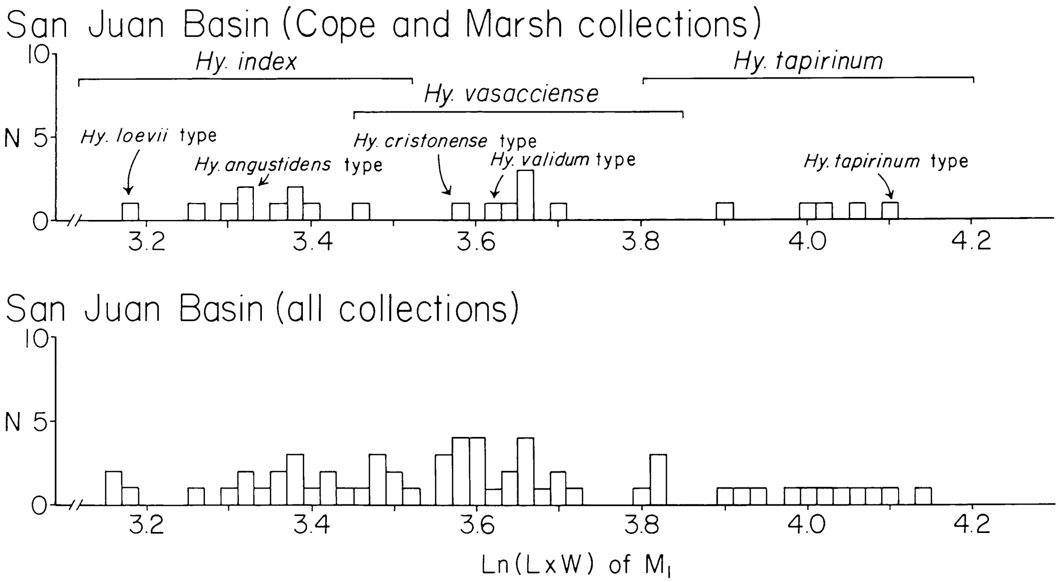

FIG. 1—Histograms of tooth size for *Hyracotherium* from the San Juan Basin, New Mexico. Abscissa is the natural logarithm of length multiplied by width for the lower first molar (M_1): mammalian species almost always have a range of 0.4 units on this scale. Histogram at top shows three size groups present in early E. D. Cope and O. C. Marsh collections. Arrows indicate positions of type specimens when these preserve M_1. Type specimen of *Hyracotherium index* (Cope) from Bear River has Ln (LxW) of M_1 = 3.18, indicating that it falls in the small-species group (with *H. sulcatum*, *H. angustidens*, *H. cuspidatum*, and *H. loevii* as probable synonyms). *Hyracotherium vasacciense* is a middle sized species but the type lacks M_1 (*H. singularis*, *H. validum*, and *H. cristonense* are probable synonyms). *Hyracotherium* (or *Systemodon*) *tapirinum* is a large species with no synonyms from the San Juan Basin. Lower histogram shows how subsequent collecting has obscured separation between the three San Juan Basin species, possibly because a wider stratigraphic interval has been sampled spanning more evolutionary time. This interpretation of San Juan Basin perissodactyls was first summarized as a personal communication in Lucas et al. (1981).

Differences proposed here result largely from a better understanding of the temporal sequence of localities within sedimentary basins, and a better understanding of temporal correlations between basins. There is little practical or theoretical justification for use of temporal subspecies because trinomials convey so little more information than binomials, and postulated relationships must be shown in a diagram in any case.

Kitts (1956) regarded *Hyracotherium index* as a synonym of *H. vasacciense*, and regarded *H. angustidens* as the valid name for small middle-to-late Wasatchian *Hyracotherium*. However, considering that the San Juan Basin and Bear River collections are both Lysitean in subage (Granger, 1914; Lucas et al., 1981), and considering the close similarity of *Hyracotherium* from each, I think *H. index* must be regarded as a senior synonym of *H. angustidens*. In the time since Kitts' (1956) report was published, *Hyracotherium angustidens* has been applied indiscriminately to virtually all North American *Hyracotherium*. One positive consequence of synonymy of *H. angustidens* with *H. index* is suppression of a name so widely applied that it has become virtually meaningless.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA
Superfamily EQUOIDEA Gray, 1821
Family EQUIDAE Gray, 1821

Hyracotherium Owen, 1841

Hyracotherium Owen, 1841, p. 205.
Pliolophus Owen, 1858, p. 54.
Eohippus Marsh, 1876, p. 402.
?*Systemodon* Cope, 1881, p. 1018.
Protorohippus Wortman, 1896, p. 104.

Type species.—*Hyracotherium leporinum* Owen, 1841.

Included species.—Type species and *H. vulpiceps* (Owen, 1858) in Europe. *H. sandrae* Gingerich, 1989; *H. grangeri* Kitts, 1956; *H. aemulor*, new; *H. pernix* (Marsh, 1876); *H. cristatum* Wortman, 1896; *H. index* (Cope, 1873); *H. vasacciense* (Cope, 1872); possibly *H. tapirinum* (Cope, 1875); *H. venticolum* Cope, 1881; *H. craspedotum* Cope, 1880; possibly *H. seekinsi* Morris, 1968; and possibly others from North America. *H. gabuniai* Dashzeveg, 1979, from Asia.

Age and distribution.—Early Eocene in Europe, North America, and Asia.

Discussion.—*Cymbalophus cuniculus* (Owen, 1842) and *C. hookeri* Godinot, 1987, may belong here.

I formerly regarded the large late Wasatchian perissodactyl from Castillo Pocket in the Huerfano Basin as *Hyracotherium tapirinum*, but some specimens clearly have the enlarged premolars characteristic of *Xenicohippus* described by Bown and Kihm (1981). Synonymy of *Systemodon* with *Hyracotherium* is questionable because there is a good chance *Systemodon* is a senior synonym of *Xenicohippus*, in which case *Systemodon* would not be a synonym of *Hyracotherium*. Problems like this can only be solved with further quantitative analysis of middle and late Wasatchian perissodactyls.

Hyracotherium sandrae Gingerich, 1989

Hyracotherium sandrae Gingerich, 1989, p. 58, figs. 38, 39a, 40.

Holotype.—UM 83567, right dentary with M_{1-3}.

Type locality.—University of Michigan locality SC-139, Clarks Fork Basin, Wyoming.

Age and distribution.—Early Sandcouleean subage (zone Wa-0) of Wasatchian land-mammal age, early Eocene. Species is known only from the northern Bighorn Basin and Clarks Fork Basin, northwestern Wyoming.

Diagnosis.—Differs from most species of *Hyracotherium* in being significantly smaller (*H. sandrae* is 15-20% smaller in linear dimensions than contemporary *H. grangeri*). Similar in size to *H. index*, but differs in having the paracristid on dP_4 and M_{1-2} curving up the front of the metaconid and usually enclosing a distinct anterior fovea on the trigonid. Also differs in having a less elongated M_3. Differs from similar-sized *H. seekinsi* in having narrow upper molars with a weaker lingual cingulum, in having narrower labial cingulids and weaker protolophids on lower molars, and in having the paracristid on M_{1-2} curving up the front of the metaconid.

Referred specimens.—**FG061:** UM 85291; **SC067:** UM 66139, 74078, 79883, 79888, 79889, 82385, 83473, 83615, 86229, 87336, 87858, 92352, 93382, 94837, 94908, 95105, 95793; **SC121:** UM 83459, 85667, 86138; **SC139:** UM 83567. All are from the 1520 m level stratigraphically, at the base of the Wasatchian land-mammal age.

Description.—The dentition and partial postcranial skeleton of this species were described and illustrated by Gingerich (1989), which includes measurements of the dentition and long bones (see also discussion of body mass below). In addition, it is worth noting that UM 79889 includes an articulated tibia, astragalus, and calcaneum. The astragalus measures 13.6 mm in maximum length, and 10.4 mm in breadth across the body (including the lateral fibular process). As articulated, the distal extremity of the calcaneum extends only to the distal edge of the astragalus (navicular facet), precluding significant contact between the calcaneum and navicular in this early species.

Discussion.—This species is contemporary with early *Hyracotherium grangeri*, and disappeared with the first appearance of *Cardiolophus*.

Hyracotherium grangeri Kitts, 1956
Figs. 2, 9B

Hyracotherium angustidens grangeri Kitts, 1956, p. 42.
Hyracotherium angustidens (in part), McKenna, 1960, p. 116. Delson, 1971, p. 355.
Hyracotherium cf. *H. angustidens*, Jepsen and Woodburne, 1969, p. 543, fig. 1.
Hyracotherium cf. *angustidens*, Bown, 1979, p. 105, fig. 59a.
Hyracotherium grangeri, Gingerich, 1989, p. 62.

Holotype.—AMNH 16134, fragment of maxilla with P^3-M^3. Collected by W. Granger, September 20, 1912.

Type locality.—Three miles SE of mouth of Pat O'Hara Creek, Clarks Fork Basin, Wyoming.

Age and distribution.—Species is known from the early Sandcouleean (zone Wa-0) through earliest Graybullian (zone Wa-3a) subdivisions of the Wasatchian land-mammal age. It is best known in the type area, the Clarks Fork Basin, but it is also known from the central and southern Bighorn Basin and from the Power River Basin, Wyoming, and Sand Wash Basin, Colorado.

Original diagnosis.—Size small, but larger than *H. angustidens*, length of M_3 (14 specimens), mode 10.0-10.5, mean 10.02 (Kitts, 1956).

Revised diagnosis.—Differs from contemporary *H. sandrae* in being 18-25% larger in linear dimensions. Differs from *H. aemulor* in averaging about 14% smaller. Similar in size to *H. pernix* but differs from the latter in having more rounded upper and lower molars and molar cusps, with weaker crests connecting cusps into lophs. Hypoconid and entoconid often separated completely with no connecting crest.

Referred specimens.—Holotype and AMNH 16135, 16136, 16138 are known from the type locality. Specimens from known levels in the Clarks Fork Basin stratigraphic section include **SC001:** UM 64427, 64428, 64429, 64440, 64442, 68157, 68163, 68167, 75964, 75978, 75983, 75990, 81959, 81976; **SC002:** UM 64532, 64539, 64540, 64543, 64544, 64728, 64738, 64740, 64753, 64754, 64756, 66558, 66572, 67485, 67514, 67515, 67516, 68295, 68310, 68312, 68322, 69442, 69990, 69990, 71244, 71248, 71253, 71257, 71258, 71271, 71272, 71280, 75146, 75158, 75159, 75160, 76328, 76343, 78916, 78917, 78920, 78928, 80020, 80034, 80038, 80467, 80468, 80478, 80486, 80498, 82207, 82216, 82348, 83407, 83412, 85845, 85847, 85848, 85886, 85888, 85903, 85904, 87355, 87357, 87358, 87359, 87374, 87387, 87397, 87399, 87400, 87401, 87402, 87405; **SC004:** UM 61605, 64582, 64598, 64602, 64612, 64615, 64618, 64641, 64647, 64648, 64649, 64660, 64661, 65043, 65045, 65046, 65132, 65136, 65138, 65146, 65147, 65148, 65149, 65325, 65714, 65766, 65783, 66487, 66489, 67470, 68005, 72843, 72846, 72849, 72856, 72876, 72878, 72880, 72887, 74639, 80829, 80830, 81917, 81918, 81919, 81920, 82018, 85570; **SC005:** UM 64622, 64624, 64629, 64631, 76410, 76411, 76416, 76418, 83390, 83391, 83392, 83393, 83398; **SC006:** UM 64664, 64826, 64827, 64831, 64833, 64834, 64835, 64838, 64840, 64843, 64848, 64851, 64859, 64860, 66339, 66341, 66345, 68007, 68013, 68014, 68023, 69858, 69859, 69862, 72898, 72902, 72908, 72913, 72915, 78909, 78911, 79380, 79381, 79391, 79398, 79408, 79409, 80606, 80607, 80614, 80618, 82402, 83448, 83453, 83454, 83456, 87831, 87833, 87837, 87843, 87848; **SC007:** UM 64666, 64673, 64679, 64682, 64683, 64691, 65154, 65155, 65163, 65166, 65174, 65182, 67541, 67548, 76562, 80171, 82954, 83286, 83292, 83294, 83296, 83297, 83298, 90976; **SC012:** UM 64762, 64767,

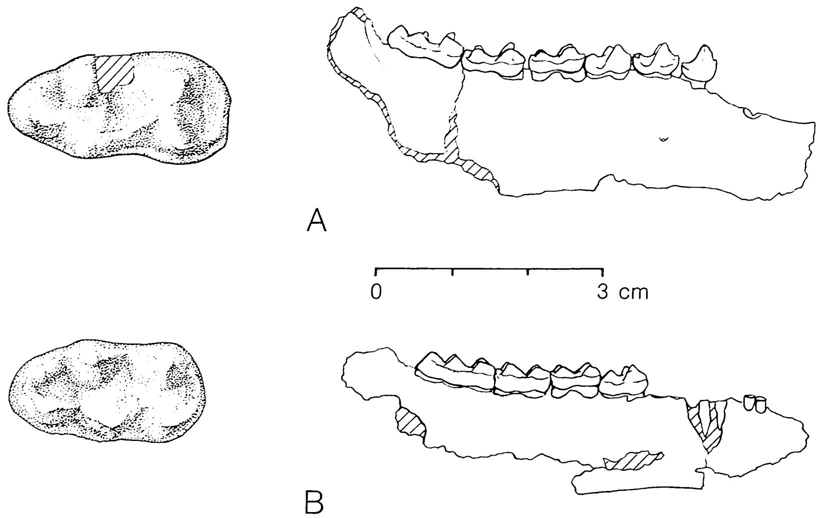

FIG. 2—Right lower third molars (M_3) and dentaries of *Hyracotherium grangeri* from the Clarks Fork Basin, Wyoming. A, UM 64785 (rev.) from locality SC-12. B, UM 68312 from locality SC-2. Note relatively short diastemata between C_1 and P_1, and single-rooted P_1 in UM 69785 but double-rooted P_1 in UM 68312. Both specimens come from same narrow stratigraphic interval.

64770, 64776, 64779, 64781, 64785, 64789, 64790, 64793, 64802, 64804, 64811, 64813, 64815, 69587, 69590; **SC013:** UM 64869, 64873, 69580, 69583; **SC014:** UM 64887, 64892; **SC015:** UM 64899, 64902, 64909, 75216, 75218, 75231, 75232, 75244, 75302, 75325, 75326, 75338, 75340; **SC016:** UM 64914, 64917, 64918, 64922, 64923, 75344, 75348, 75351, 76307, 76320; **SC017:** UM 64936, 64945, 64961, 64981, 73733, 73737, 73745, 73752; **SC018:** UM 69390, 69391, 69393, 69394, 69399, 69401, 69405, 76013, 76028, 76032, 76038, 76039, 76040, 76041, 76042, 76043, 76048, 76049, 76050; **SC026:** UM 65184, 65190, 65195, 65197, 65200, 65202, 65206, 65207, 65213, 67387, 67388, 67390, 67392, 74049, 80773, 80778; **SC027:** UM 65227, 65228, 80787, 83826, 83827; **SC030:** UM 76746, 76748, [below] 81879; **SC031:** UM 65264, 65265, 65271, 65274, 65279, 76489, 76491, 76499, 84807, 84897; **SC037:** UM 69409, 69430, 69433, 69435; **SC038:** UM 65362, 65363, 65365, 65367, 71165, 75401, 75402, 75403, 75410, 75411, 75412, 75413, 75414, 75415, 75416, 75417, 75418, 75589, 75590, 75611, 75612, 75613, 75614, 75768, 75777, 75795, 75943, 76115, 76116, 76118, 79837, 79838, 79839, 79840, 79844; **SC039:** UM 65380, 65385; **SC040:** UM 65389, 65390, 65392, 65395, 69369, 69370, 69373, 69374, 69375, 69376, 69377, 69379, 69384, 73757, 73761, 73762, 73763, 80371, 80373, 80374, 80375, 80376, 80382, 80395, 87556, 87558, 87559, 87561, 87566, 87567, 87568, 87577, 87584, 87587; **SC041:** UM 65399, 76215, 76217, 76231; **SC042:** UM 65403, 65406, 65415, 65416, 65418, 65422, 65424; **SC043:** UM 65431, 65437; **SC044:** UM 65440, 65442, 76473, 76475, 76476, 76480, 76481; **SC045:** UM 65334, 65335, 80837;**SC046:** UM 65457, 65515, 65517, 66399, 66401, 66402, 66405, 66418, 66428, 66429, 66438, 66439, 66441, 67405, 76590, 83356, 83358, 83360, 83362, 86278, 86294, 86298, 86351, 86355, 86358, 86359, 86360, 86362, 86418, 86420, 86421, 86425, 86426, 86442, 86455; **SC047:** UM 65460, 65461, 65463, 65468, 65468, 65468, 65468, 65510, 65511, 65512, 66373, 66380, 66384, 66385, 83370, 83372, 83373, 86308, 86321, 86323, 86482, 86484, 86512, 86515, 86516, 86527, 86534; **SC054:** UM 65559, 65561, 65563, 65570, 65574, 65583, 65586, 65592, 65597, 65607, 65609, 65610, 65614, 65616, 65620, 65624, 65627, 65629, 65681, 65684, 65685, 65688, 65690, 65699, 65701, 65705, 66939, 66943, 66946, 66957, 66965, 66989, 66990, 66994, 67000, 67003, 67011, 67014, 67521, 67526, 67538, 68560, 68566, 68569, 68573, 68578, 68580, 68582, 68585, 71402, 75251, 75253, 75999, 76003, 80052, 80056, 80070, 80079, 80080, 80081, 80083, 80084, 80087, 80091, 80100, 82193, 82198, 82228, 82235, 82236, 82238, 82240, 82242, 85907; **SC067:** UM 66615, **SC067/308:** UM 83637; **SC079:** UM 83642; **SC087:** UM 66232, 66248, 66266, 66267, 66515, 66516, 66519, 66522, 66529, 66530, 68539, 68545, 76513, 76525, 76533, 79820, 79822, 81881, 81882, 82116, 82131; **SC088:** UM 76541, 76542, 76543, 76546, 84867, 84871, 84876, 86192; **SC089:** UM 66282; **SC094:** UM 66360, 66606; **SC095:** UM 66451, 76643, 76647, 76648, 82545; **SC096:** UM 66453, 66465, 66480, 77325, 77327, 77356, 77366, 77371; **SC097:** UM 66482; **SC104:** UM 66588; **SC122:** UM 66857; **SC124:** UM 66864, 66865, 87526, 87527; **SC125:** UM 66876, 66881, 66886, 66889, 83771; **SC126:** UM 66896, 66898, 66901, 66902, 83775; **SC129:** UM 67073, 67074, 67075, 67078; **SC130:** UM 67079; **SC131:** UM 67082, 67361, 76723, 76724, 76726, 76728, 76729; **SC133:** UM 67091, 67104, 67106, 67114, 67115, 67118, 67127, 67140, 67142, 67145, 67146, 67370, 68048, 68049, 68055, 68069, 68073, 68077, 68084, 68098, 68112, 68119, 68454, 68457, 68464, 68473, 68474, 68479, 68480, 68488, 71759, 71759, 75048, 75049, 75050, 75055, 75056, 75060, 75075, 75083, 75087, 79677, 79690, 79696, 79697, 79711, 79720, 79731, 79740, 79766, 79769, 82699, 82705, 82709, 82716, 82717, 82731, 82734, 82737, 82744, 82745, 82750, 82755, 82756, 82777, 82779, 82781, 82784, 82786, 82789, 83329, 83332, 83342, 83344, 83500, 83512, 83521, 83575, 83580, 83597, 83601, 83603, 83604, 83608, 85827, 85829; **SC142:** UM 67260, 69351, 83810;**SC151:** UM

67418, 67420, 67426, 67431, 72803; **SC160:** UM 68144, 68146, 68148, 68149, 68496, 68503, 68504, 75099, 77531, 77532, 77540; **SC161:** UM 68177, 68183, 68184, 68187, 68188, 68200, 68397, 68398, 68399, 68402, 68604, 68609, 68610, 68612, 68613, 68614, 68625, 68626, 68640, 68646, 68648, 68668, 68674, 68681, 68685, 68689, 68692, 68717, 68800, 68801, 68811, 68816, 68819, 68820, 68825, 68827, 68849, 75171, 75178, 75182, 77458, 77479, 77490, 79025, 79026, 79040, 79052, 79057, 79060, 79062, 79064, 79068, 79076, 79085, 79086, 79087, 79100, 79104, 79105, 79117, 79131, 79148, 80521, 80534, 80539, 80549, 80678, 80679, 80680, 82251, 82253, 82276, 82277, 82281, 82296, 82465, 86028, 86029, 86039, 86053, 86054, 86060, 86073, 86083, 86095, 86096, 86103, 86105, 86118; **SC206:** UM 69422, 69424, 69426; **SC207:** UM 69447, 69449, 69471, 69478, 69494, 69495, 69504, 69522, 69524, 69525, 69533, 79987, 79994, 80005, 80009, 82808, 82809, 82819, 82829, 83487, 83489, 83490, 83498, 86329, 86332, 86334, 86336; **SC210:** UM 72079, 72123, 72126, 72139, 72155, 72165, 72170, 72180, 72181, 72185, 72187, 72190, 72200, 72210, 72216, 72219, 72220, 72234, 72235, 72237, 72246, 72250, 72252, 72254, 72255, 73194, 76867, 83091, 83094, 83096, 83107, 87418, 87420, 87422, 87436, 87457, 87458; **SC211:** UM 69723, 69729, 69730, 69739, 73841, 73846, 73851, 73861, 82320, 82345, 82346; **SC212:** UM 69755, 69768, 75396, 75625, 75626; **SC213:** UM 69785, 69832, 69835, 69839, 69841, 71062, 71063, 71113, 71114, 71117, 71136, 71139, 75375, 75380, 75387, 79544, 79581, 79584, 79586, 79664, 79665, 79771, 82134, 82141, 82148, 82170, 82171, 84637, 85496, 85501; **SC221:** UM 71161, 79786, 79791, 79799, 84835, 84863, 84864, 85812; **SC287:** UM 80367; **SC288:** UM 73776, 73781; **SC293:** UM 73870; **SC300:** UM 75109, 75118, 75119, 77545, 77552, 83325; **SC304:** UM 75745, 75746, 75747, 75753, 75755, 76061, 76067, 76077, 76090; **SC305:** UM 76091, 76093, 76095; **SC306:** UM 76196, 76200, 76208; **SC309:** UM 76552, 76557; **SC310:** UM 76578, 76586, 76587, 84747, 84751, 85600, 85603, 85604, 85619, 86005, 86009, 86010, 86022, 86217, 86218, 86551, 86554; **SC311:** UM 76628, 76632, 83380; **SC312:** UM 76655, 76661, 76670, 82553, 82555; **SC315:** UM 76845; **SC316:** UM 80176, 80178, 80180, 80182, 80183, 80184, 80188, 80191, 80210, 80211, 80219, 80220, 80221, 80222, 80285, 80286, 80309, 80310, 80315, 80320, 80323, 80403, 80406, 80411, 80414; **SC318:** UM 77377, 77380, 77387; **SC319:** UM 77393, 77395; **SC341:** UM 84887, 84888. These range from the 1520 through 1760 meter levels. YPM-PU 18316 belongs here, and there are undoubtedly other YPM-PU specimens of this species. Specimens described by Bown (1979) from the southern Bighorn Basin are in the UW collection.

Description.—One skull is known, UM 82954 from locality SC-7, with upper and lower cheek teeth. It is poorly preserved, but retains the right maxilla with P^2-M^3 attached to the skull, identifying it unquestionably as *H. grangeri*. The left maxilla, parts of both dentaries, and fragmentary postcranial remains were found in association. The basicranium is intact on the right side, and it shows clearly that this early species had a distinct foramen ovale (see below).

Upper cheek teeth of *H. grangeri* are illustrated in Figure 9B. Lower cheek teeth are illustrated in Figures 2A and 2B, which show long diastemata separating the lower canine from P_1, and short diastemata separating this tooth from P_2. P_1 is usually single-rooted, but some specimens of *H. grangeri* retain two roots. Sexual dimorphism in canine size in *H. grangeri* was documented by Gingerich (1981).

Several partial skeletons of this species are known, but only one preserves a complete long bone: UM 82242 from locality SC-54 has a femur measuring 134 mm in total length and 12.2 mm in anteroposterior midshaft diameter (see discussion of body mass below). Astragali typically measure about 16.5 mm in maximum length and 13.0 mm in breadth across the body (including the lateral fibular process).

Discussion.—*Hyracotherium grangeri* is a very common element in early Wasatchian faunas of the Clarks Fork Basin and elsewhere. It was originally proposed with little comment as a subspecies of *H. angustidens* (Kitts, 1956), but this important form deserves full species rank. Some or possibly all specimens of *Hyracotherium* described by McKenna (1960) from the Sand Wash Basin, Colorado, and by Delson (1971) from the Powder River Basin, Wyoming, belong to this species.

Jepsen and Woodburne (1969) recorded *Hyracotherium* from Paleocene-age Tiffanian or Clarkforkian strata in the Clarks Fork Basin. The one specimen reported, YPM-PU 18316, was identified in the laboratory with no accompanying record of collector or field number. It is indistinguishable from specimens of *H. grangeri*, which is abundant elsewhere in the Clarks Fork Basin. *Hyracotherium* has not been found in Paleocene strata of the Clarks Fork Basin subsequently, in spite of an intensive collecting effort at the purported locality where YPM-PU 18316 was found, and the locality record for this specimen is almost certainly in error. This and other dubious records of *Hyracotherium* in the Paleocene are discussed at greater length in Gingerich (1989). There is no credible evidence of *Hyracotherium* in the Paleocene of North America.

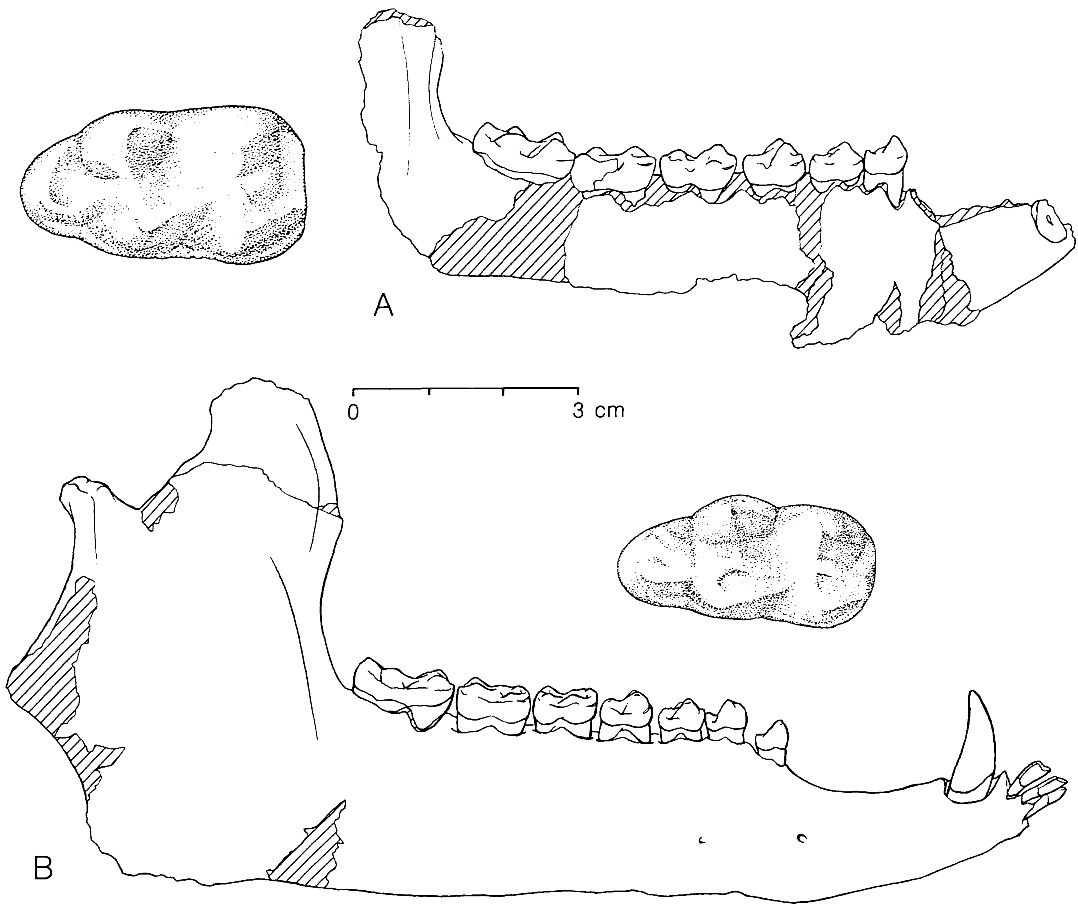

FIG. 3—Right lower third molars (M_3) and dentaries of *Hyracotherium cristatum* and *Hyracotherium aemulor* from the Clarks Fork Basin, Wyoming. A, UM 73452, *H. cristatum* from locality SC-265. B, UM 71523 (holotype) *H. aemulor* from locality SC-34. Note moderate development of crest connecting the hypoconid and entoconid on M_3 of *H. cristatum* and absence of this crest on M_3 of *H. aemulor*. Note also long diastema separating C_1 and P_1 in *H. aemulor*.

Hyracotherium aemulor, new species
Fig. 3B

Holotype.—UM 71523, left and right dentaries with all teeth except left I_1, collected by W. S. Bartels.

Type locality.—University of Michigan locality SC-34, Clarks Fork Basin, Wyoming.

Age and distribution.—Ranges through much of the early Graybullian (zone Wa-3b) subdivision of the Wasatchian land-mammal age in the northern Bighorn and Clarks Fork basins, Wyoming.

Diagnosis.—Differs from earlier *Hyracotherium grangeri* in averaging about 16% larger in linear dimensions and in having a longer C_1-P_1 diastema. Differs from later *H. pernix* in having more rounded upper and lower molars and molar cusps, with weaker crests connecting cusps into lophs. Differs from later *H. cristatum* in being about 18% smaller in linear dimensions. Hypoconid and entoconid often separated completely with no connecting crest.

TABLE 1—Measurements of type specimens of *Hyracotherium aemulor* and *Homogalax aureus*

	Hyracotherium aemulor UM 71523 SC-34 (holotype)			*Homogalax aureus* YPM-PU 17359 Golden Valley (holotype)	
	L	W	H	L	W
Lower dentition					
I_1	2.8	2.3	--	--	--
I_2	3.3	2.3	--	--	--
I_3	3.3	2.2	--	--	--
C_1	5.5	4.4	12.5	--	--
P_1	4.1	2.5	--	--	--
P_2	5.6	3.0	--	6.4	4.0
P_3	6.6	4.3	--	7.9	5.0
P_4	6.7	4.9	--	7.8	5.3
M_1	8.1	5.6	--	8.9	5.7
M_2	9.4	7.0	--	9.2	6.1
M_3	13.0	6.4	--	13.4	6.4
Mandibular depth beneath M_1		20.8		--	

Etymology.—Latin *aemulus*, emulating. Name is given because of close resemblance of fragmentary and worn specimens of this species to worn specimens of earlier *Cardiolophus radinskyi* and contemporary *Homogalax protapirinus.*

Referred specimens.—Specimens from locality MP-201 include UM 95080, 95334, 95338, and 95663. Specimens from known levels in the Clarks Fork Basin stratigraphic section include **SC003:** UM 66647, 76737; **SC032:** UM 65284, 65285, 65292, 73791, 78947, 78952, 82958, 82962, 82963; **SC033:** UM 73795, 73796, 73798, 82970; **SC034:** UM 65312, 71511, 71519, 71521, 71523, 71524, 71529,73809, 73895, 73896, 73901, 73904, 73924, 73925 73926, 73928, 73933, 75003, 78995, 78997; **SC035:** UM 65316, 65357, 71362, 71739, 71748, 73936, 73939, 73949, 73957; **SC036:** UM 65345, 65346, 65347, 65352,71668, 71670, 71672, 71725, 71726, 83024, 83034, 83046; **SC063:** UM 73022, 74631, 76741, 76742; **SC064:** UM 65733, 65745, 65747, 65747, 65752, 66678, 66681, 67666, 72939, 74638, 79424; **SC087/above/:** UM 85539, 85540(m); **SC111:** UM 74632, 79897; **SC114:** UM 66706, 66842, 66843, 66844, 76776; **SC224:** UM 71205, 71206, 71207, 71208, 71209, 71294, 78955, 82977, 82981, 83530, 83533, 83537; **SC225:** UM 83543, 83546, 83553, 83554, 83555; **SC232:** UM 71369, 76778, 76779, 76784, 76786, 81864; **SC236:** UM 71540, 71544; **SC237:** UM 71595, 71596,76803, 76805, 76809, 76811, 76816, 79018, 83060, 83076; **SC254:** UM 73057, 73061; **SC290:** UM 73817,73820, 82831, 82984, 82985, 82987; **SC313:** UM 82568, 82569; **SC314:** UM 76822, 76823; **SC321:** UM82990, 83525; **SC322:** UM 79007, 79009, 79011; **SC324:** UM 79436, 79438, 79439, 79441, 79442, 79443, 79444; **SC325:** UM 79478, 79479; **SC326:** UM 79659, 79807, 85539, 85540, 85541. These range from the 1770 through 2005 meter levels.

Description.—UM 95080 is a partial skull of this species from locality MP-201 in the northern Bighorn Basin. Upper premolars and molars and a good left dentary are preserved, indicating without question that the genus represented is *Hyracotherium.* This specimen and others from the locality match the size of *H. aemulor*, and the associated fauna indicates an early Graybullian age. Much of the skull is damaged, but the basicranium is well preserved on the left side, and it shows clear evidence that a foramen ovale was retained (see discussion below).

The holotype dentary (Fig. 3B) preserves an almost entire lower dentition, with left I_1 being the only missing tooth. Incisors are small, spatulate, and procumbent. Canines are large, indicating by comparison with male and female specimens of *H. grangeri* that the type is a male. The diastema between C_1 and P_1 is about 21 mm long, which is long for *Hyracotherium* (even a species this size). P_1 is single-rooted and positioned close to P_2. Cheek teeth are typical of *Hyracotherium.* M_3 has only the slightest suggestion of a crest connecting the hypoconid and entoconid (this crest is stronger in some referred specimens). Measurements of the holotype are listed in Table 1.

Notable postcranial remains of this species are lacking.

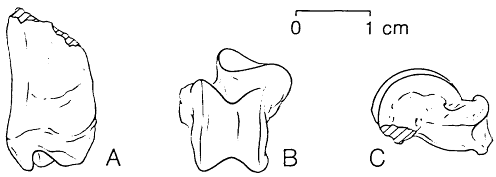

FIG. 4—Lectotype of *Hyracotherium pernix*, YPM 11304, from middle Wasatchian of Bitter Creek, Washakie Basin, Wyoming. A, left distal tibia in anterior view. B and C, left astragalus in dorsal and right medial view. Note smoothly concave navicular facet typical of *Hyracotherium* on the astragalus.

Discussion.—Broken and worn specimens of this species are easy to confuse with worn *Cardiolophus* and *Homogalax*, and it was only with discovery of well preserved specimens like the holotype that it became clear there is a medium-sized *Hyracotherium* in early Graybullian sediments of the Clarks Fork Basin.

Hyracotherium aemulor has some of the distinctive characteristics of earlier and smaller *H. grangeri*, like the common absence of a crest connecting the hypoconid and entoconid on M_3, and it may possibly be a direct descendant of *H. grangeri*. *Hyracotherium aemulor* has teeth about the same size as those of *Cardiolophus radinskyi* and, for ecological or environmental reasons, these species appear not to occur together.

Hyracotherium pernix (Marsh, 1876)
Figs. 4, 5B

Eohippus pernix Marsh, 1876, p. 402. Granger, 1908, p. 224.
Hyracotherium vasacciense vasacciense (in part), Kitts, 1956, p. 46.
Hyracotherium, cf. *angustidens*, Gazin, 1962, p. 72.

Lectotype.—YPM 11304, distal left tibia and articulating left astragalus (Fig. 4), collected by J. Heisey on July 11, 1876. Granger (1908, p. 224) is responsible for restricting the type to the distal tibia and accompanying astragalus.

Type locality.—Marsh (1876) gives the locality as "*Coryphodon* beds, or lowest Eocene, of Wyoming." Granger (1908, p. 224) gives this as "Bitter Creek, Wyo." Gazin (1962, p. 12) clarifies this as $1\frac{1}{4}$ miles south of Bitter Creek Station on the Union Pacific railroad, Washakie Basin, Wyoming.

Age and distribution.—Graybullian (middle Wasatchian), early Eocene, of the Washakie Basin, southwestern Wyoming, and Bighorn and Clarks Fork basins, northwestern Wyoming.

Diagnosis.—Similar in size to *H. grangeri*. Averages about 14-15% smaller than *H. aemulor*. Differs from both in having slightly more squared upper and lower molars, with a tendency for stronger hypoconid-entoconid crests on lower molars (especially M_3). Differs from *H. cristatum* in averaging about 40% smaller in linear dimensions and in having the hypoconulid crest typically join the hypoconid rather than joining the hypoconid-entoconid crest. Intermediate in size between *H. index* and *H. vasacciense*.

Referred specimens.—Holotype, YPM 11307, and YPM 11308 from the type locality. Gazin (1962) indicates that additional specimens from the type locality are at the USNM. Specimens from known levels in the Clarks Fork Basin stratigraphic section include **SC112**: UM 66797, 66802, 66820, 79913; **SC113**: UM 73595, 73638; **SC145**: UM 67269, 67277, 67278, 67279, 67280, 67281, 67283, 67284, 67285, 67299, 67300, 67301, 69705; **SC148**: UM 67332, 67334, 67339, 67341, 67347, 69715, 87608, 87609; **SC253**: UM 73033, 73046, 73047, 73048, 73049, 73052, 74633, 76425, 76426, 76437; **SC255**: UM 73067, 73090, 73104, 73191, 73207, 73248, 73254, 73267, 73272, 73275, 73286, 73290, 73295, 74525, 74636, 75693, 75700, 75701, 77441, 80121, 80144; **SC256**: UM 73320, 73322, 73536; **SC265**: UM 73455, 73464, 73467, 73468, 73469, 75641, 80734, 83671, 83684, 83693, 83694, 83697, 83732, 87710; **SC295**: UM 74019, 74020, 82589; **SC297**: UM 75023; **SC299**: UM 75032, 75033, 75035; **SC303**: UM 75719, 75726, 75729, 75731. These range from the 2020 through 2240 meter levels.

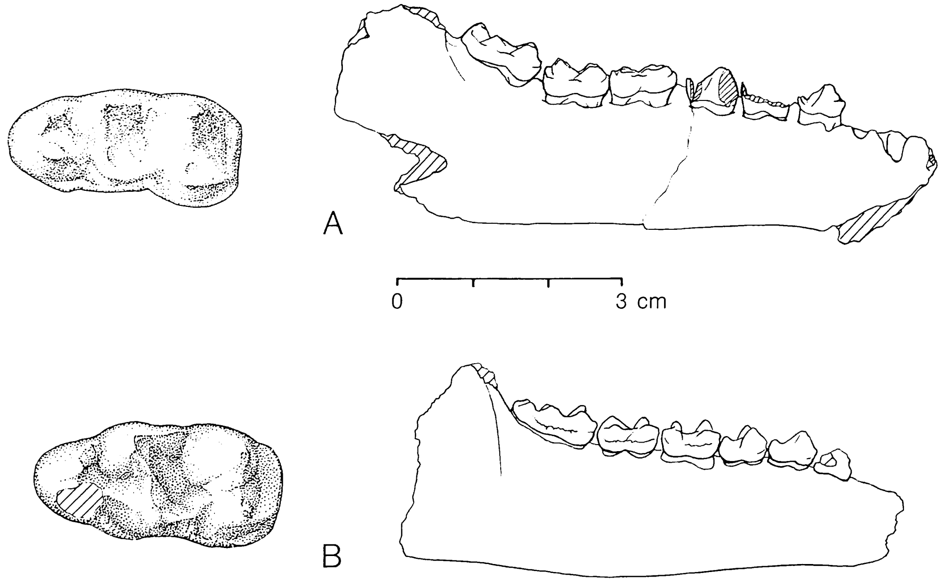

FIG. 5—Right lower third molars (M_3) and dentaries of *Cardiolophus semihians* and *Hyracotherium pernix* from the central Bighorn Basin, Wyoming. A, UM 64202, *C. semihians* from locality YM-45. B, UM 64168, *H. pernix* from locality YM-421 (= GR-3). Note crowded anterior alveoli with canine close to P_1 and P_2 in *C. semihians*, and long narrow M_3 crown with strong hypolophid. Note distinct crest connecting the hypoconid and entoconid on M_3 of *H. pernix*, although this is not a fully developed hypolophid like those seen on M_3 of *Cardiolophus* and *Homogalax*.

Description.—The original type sample presently includes foot bones (now numbered YPM 11304, Fig. 4), a left dentary with M_{1-2} (YPM 11307), a left maxilla with M^{1-2} (YPM 11308), and two isolated upper molars (unnumbered). The left astragalus of the type is typical of *Hyracotherium* (and Perissodactyla) in having a deeply grooved trochlea, and smoothly concave saddle-shaped navicular articulation on the head (which also has a small but distinct cuboid facet). The astragalus measures 17.2 mm in maximum length and 12.6 mm transversely across the body (including the lateral fibular process), and the head measures 11.0 mm transversely and 7.6 mm dorsoventrally. The head is short, with the navicular articulation starting only 3.3 mm in front of the articular ridge bounding the trochlea medially. The distal tibia too is typical of *Hyracotherium* in having a small medial malleolus, complex surface for articulation with the astragalus, and roughened lateral surface for articulation with the distal fibula. The tibia measures 10.4 mm anteroposteriorly and 12.8 mm transversely.

Skulls and significant other postcrania are still unknown for this species. UM 69715 includes a distal tibia that is slightly larger but otherwise closely comparable to the type. The most notable characteristics of *H. pernix* are its slightly more squared upper and lower molars, and its tendency to have crests connecting the hypoconid and entoconid on lower molars.

Discussion.—Marsh's (1876) measurements suggest that he had at least one dentary with M_{1-3} intact when he described the species, but none of this material was ever illustrated (Marsh's 1892 fig. 15 may not be based on *H. pernix* at all).

Wortman (1896, p. 82) states that Marsh's measurements and description of *H. pernix* correspond exactly to those of *H. index* of Cope *from the same locality* [my emphasis]. Both types are from Wyoming, but they are not from the same locality and they are probably not the same age. *H. pernix* could be a synonym of *H. vasacciense* (as Kitts, 1956, proposed), but it is just as likely to be the common ancestor of both *H. index* and *H. vasacciense*.

Granger (1908, p. 224) stated that Marsh's sample of *H. pernix* includes several individuals and at least two species, and restricted the type to the left distal tibia and accompanying astragalus. Restriction to postcranial elements for a cursorial species like this is consistent with the etymology of its name (*pernix*, L., swift), but it does not facilitate comparison with other species. With the type restricted, Granger regarded the species as indeterminate or possibly a synonym of *H. index*. One of Marsh's unnumbered molars appears to be deciduous and a little smaller than the other uppers, but comparison of Marsh's other specimens with teeth and postcranial remains of small *Hyracotherium grangeri* indicates these all represent a *Hyracotherium* of about the same size, which is consistent with presence of one species (and most could possibly represent one individual).

Gazin (1962) regarded the Bitter Creek type locality as Graybullian, which is substantiated by the joint occurrence of *Haplomylus* sp. and "*Homogalax*" (or a *Homogalax*-sized *Hyracotherium*). Gazin described Bitter Creek *Hyracotherium* as "comparatively advanced" and as having possibly given rise to typical *H. vasacciense*, but he disagreed with Kitts' synonymy of *H. pernix* with *H. vasacciense*. These observations are consistent with my interpretations here.

M_1 and M_2 in YPM 11307, the surviving dentary in Marsh's original type material, both have small but distinct crests connecting the hypoconid directly to the entoconid, as is seen commonly in Clarks Fork Basin specimens of the same size here referred to *H. pernix*.

Hyracotherium cristatum Wortman, 1896
Fig. 3A

Hyracotherium cristatum Wortman, 1896, p. 96, fig. 6.
Hyracotherium tapirinum (in part), Wortman, 1896, p. 94, figs. 4-5.
Eohippus cristatus, Granger, 1908, p. 239.
Eohippus resartus Granger, 1908, p. 240, figs. 1-2.
Hyracotherium angustidens etsagicum (in part), Kitts, 1956, p. 40, fig. 4, Pl. 3:5, 4:2, 5:2, 6:2, 7:1.

Lectotype.—AMNH 258b, right dentary with $P_{3\text{-}4}$ and $M_{1\text{-}2}$ (designated by Granger, 1908, p. 239), collected in 1891.

Type locality.—Graybull River, Bighorn Basin.

Age and distribution.—Species makes its first appearance in middle Graybullian zone Wa-4 (middle Wasatchian). Upper limit of age presently unknown. It is recorded only from the Bighorn and Clarks Fork Basins.

Diagnosis.—Large species of *Hyracotherium* with broad molars and a moderate to strong crest connecting the hypoconid and entoconid on M_3. Wortman's (1896) cotype, AMNH 240, has a fully developed hypolophid on M_3.

Referred specimens.—Specimens from known levels in the Clarks Fork Basin stratigraphic section include SC-146: UM 67303; SC-265: UM 73452. These range from the 2065 through 2095 meter levels. Many specimens are known from the Bighorn Basin, including AMNH 15428 and 15820 described by Kitts (1956) and UM 91257 (from MP-62).

Description.—UM 73452 (Fig. 3A) includes much of both left and right dentaries. It has a moderate diastema separating the root of C_1 from that of P_1. P_1 appears to have been single-rooted. P_2 is double-rooted like the following cheek teeth, but it has a narrow crown with no metaconid. P_3 and P_4, like M_1 and M_2, are broad. M_3 has a crest connecting the hypoconid and entoconid. This is not as well developed as illustrated by Wortman (1896), but resembles the hypoconid-entoconid crest on M_3 referred to *H. resartum* by Granger (1908; AMNH 143a). The hypoconulid lobe of M_3 is similarly short. UM 67303 is a right dentary preserving $M_{2\text{-}3}$. Although first identified as *Homogalax*, it is clearly not as lophodont as that genus and represents this large *Hyracotherium*.

AMNH 15428 and 15820 include good postcranial skeletons of this species (Kitts, 1956; see Table 4 here). UM 91257 includes most of one articulating tarsus. The astragalus in this specimen measures 21.5 mm in maximum length and 17.3 mm in breadth across the body (including the lateral fibular process).

Discussion.—*Hyracotherium resartum* may prove to be different from *H. cristatum* when middle and late Wasatchian *Hyracotherium* are better studied, in which case *H. resartum* is probably be the correct name for the large Clarks Fork Basin species.

Superfamily TAPIROIDEA Gill, 1872
Family ISECTOLOPHIDAE Peterson, 1919

Cardiolophus, new genus

Systemodon (in part), Cope, 1882, p. 184.
Homogalax (in part), Hay, 1899, p. 593.
Cf. *Homogalax*, McKenna, 1960, p. 119.
Hyracotherium (in part), Bown, 1979, p. 106.

Type species.—*Cardiolophus radinskyi*, new species.

Included species.—Type species and *C. semihians* (Cope, 1882).

Age and distribution.—Wasatchian land-mammal age, early Eocene, Bighorn Basin and Clarks Fork Basin, Wyoming.

Diagnosis.—Tapiroid with short diastemata in front and back of P^1 and P_1. Cheek teeth only moderately lophodont and easily confused with *Hyracotherium*. Differs from *Homogalax* and other isectolophids in having lower-crowned and consequently less lophodont upper and lower cheek teeth, differs in having narrow double-rooted P^{1-2} like those of *Hyracotherium*, differs in having narrower upper molars (making them relatively square like those of *Hyracotherium*), and differs in having less molarized P_4.

Etymology.—Greek *kardia*, heart, and *lophos*, crest. Named for Heart Mountain, a prominent landmark overlooking the type locality and much of the Clarks Fork Basin.

Discussion.—McKenna described several teeth that are here placed in *Cardiolophus*, noting that these are intermediate in size and morphological detail between *Hyracotherium* and *Homogalax*, and suggested that this form might be "essentially ancestral" to *Homogalax*. The dense stratigraphic record in the Clarks Fork Basin seems to indicate a separate origin for *Homogalax*, rather than direct descent from *Cardiolophus*, but *Cardiolophus* is important, with *Hyracotherium* and *Homogalax* in consideration of the origin of Perissodactyla.

Cardiolophus radinskyi, new species
Figs. 6, 7, 9A, 11B

Undescribed species cf. *Homogalax primaevus* (in part), McKenna, 1960, p. 119, fig. 63a, b, e.
Homogalax sp. (in part), Radinsky, 1963, p. 16.
Hyracotherium sp., Bown, 1979, p. 106, fig. 59b.

Holotype.—UM 78915, skull and lower jaws, atlas and axis vertebrae, collected by S. J. Carlson.

Type locality.—University of Michigan locality SC-2, Clarks Fork Basin, Wyoming.

Age and distribution.—Middle and late Sandcouleean, and earliest Graybullian subages of Wasatchian land-mammal age. Species is known from Bighorn Basin and Clarks Fork Basin, northwestern Wyoming.

Diagnosis.—Similar to middle and late Wasatchian *Cardiolophus semihians*, but differs in having less molarized P^2, in having a narrower mandibular symphysis, and in having a shorter and relatively broader M_3

Etymology.—Named for the late Professor Leonard Radinsky of the University of Chicago, in recognition of his many contributions to knowledge of Eocene Perissodactyla and in appreciation of his interest in fine-scale evolutionary study of Eocene mammals.

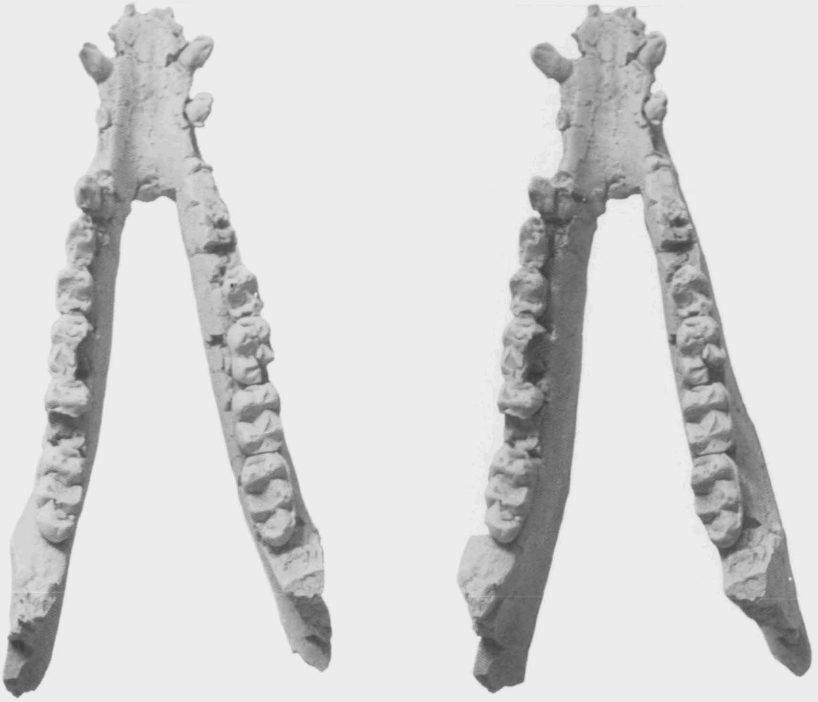

FIG. 6—Left and right dentaries of *Cardiolophus radinskyi*, UM 78915 (holotype), from locality SC-2 in the Clarks Fork Basin, Wyoming. Stereophotograph in occlusal view.

Referred specimens.—Specimens from known levels in the Clarks Fork Basin stratigraphic section include **SC001:** UM 81977; **SC002:** UM 66564, 78915, 87396; **SC004:** UM 64592, 64634, 65141; **SC006:** UM 72901, 79396; **SC007:** UM 90971; **SC012:** UM 64771, 64775, 64780, 69586; **SC016:** UM 64913, 64931, 76311; **SC017:** UM 64937, 64982, 73736; **SC018:** UM 69362; **SC037:** UM 75940; **SC038:** UM 75772; **SC040:** UM 69361, 69387, 73754, 73755, 73756, 80394, 87572; **SC044:** UM 66868; **SC054:** UM 66966, 67522, 67523, 68555, 71403, 76005, 80073; **SC087:** UM 66231, 66239, 68523, 68548; **SC129:** UM 67077; **SC133:** UM 68070, 68087, 68122, 79728, 82704; **SC142:** UM 69354; **SC160:** UM 77530, 82800; **SC161:** UM 79097, 82313; **SC207:** UM 83482, 83483; **SC210:** UM 72172, 87415; **SC213:** UM 69816, 71064, 79515, 79772, 82168, 84641; **SC300:** UM 83321; **SC310:** UM 84709, 84786; **SC316:** UM 80318, 80409, 80412; **SC318:** UM 77379. These range from the 1530 through 1760 meter levels. The specimen described by Bown (1979) is UW 8201.

Description.—The most complete specimen is the holotype, UM 78915, which is a nearly complete skull with lower jaws. It was found in mudstone, and is surprisingly little deformed or distorted compared to most skulls from the Clarks Fork Basin. The cranium measures 144 mm in condylobasal length, and about 2 × 34.5 = 69 mm in bizygomatic breadth. It resembles the skull of female *Hyracotherium* (or *Systemodon*) *tapirinum*, AMNH 55267, in having robust nasals projecting forward over the premaxillae, in having a narrowed or waisted rostrum (viewed dorsally), and in having a modestly inflated frontal region (Gingerich, 1981). This probably represents the general form of female skulls of primitive perissodactyls. The postorbital process is small. Much of the dorsal surface of the brain case is missing, so the relative size of sagittal and nuchal crests cannot be determined. Foramina of the medial orbital wall are not well preserved, and the aperture of the infraorbital canal is not preserved either. The bony palate extends posteriorly to end at the level of M_3. The basicranium is well preserved, with the foramen ovale on each side clearly distinct from the middle lacerate foramen. The braincase is filled with sediment. The foramen magnum is slightly deformed, but it appears to measure about 13.2 mm in breadth and 9.2 mm in height.

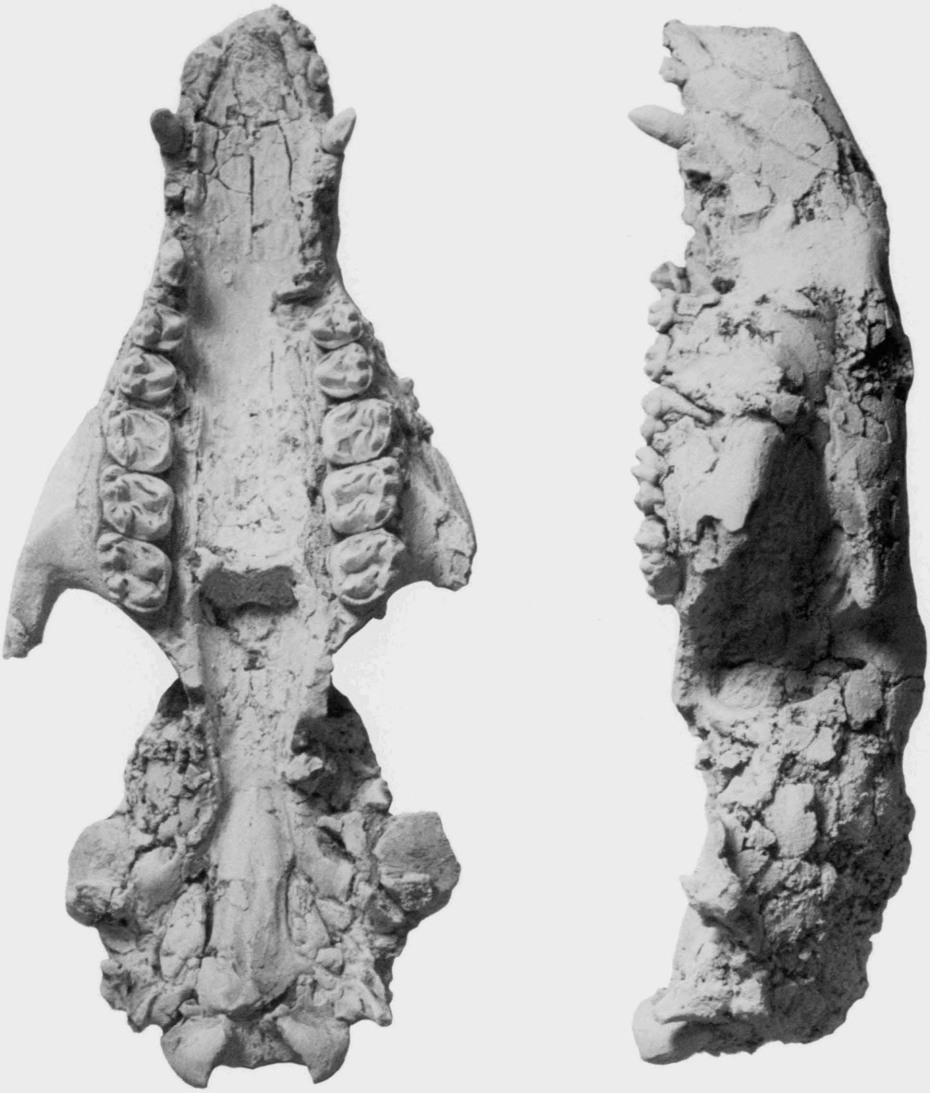

FIG. 7—Skull of *Cardiolophus radinskyi*, UM 78915 (holotype) from locality SC-2 in the Clarks Fork Basin, Wyoming. A, ventral view. B, left lateral view.

Roots and/or partial crowns are present for I^{1-3}, and these increase in size from front to back. C^1 is preserved intact on both sides, and the crown is small and bluntly pointed. It does not project very far, indicating that this individual was probably a female. Alveoli indicate that P^1 was double-rooted. P^2 is also double-rooted, with a narrow crown, a single

FIG. 8—Skull of *Cardiolophus semihians*, UM 78915 from locality RB-14 in the central Bighorn Basin, Wyoming. A, ventral view. B, left lateral view.

apical cusp, and very little posterolingual expansion of the crown. P^{3-4} are small relative to molar size and, if worn or found in isolation, they and M^{1-2} could easily be mistaken for cheek teeth of *Hyracotherium*. M^3 has a slightly stronger metaloph and the trapezoidal outline more typical of *Homogalax*.

TABLE 2—Measurements of teeth of *Cardiolophus*.

	Cardiolophus radinskyi					*Cardiolophus semihians*		
	UM 78915 (female) SC-2 (holotype)			UM 68548 (male) SC-87		UM 71839 (female) RB-14		
	L	W	H	L	W	L	W	H
Upper dentition								
I^3	4.0	2.7		--	--	4.0	2.6	
C^1	4.6	3.9	6.3	--	--	4.7	3.5	6.4
P^1	5.1	2.5		--	--	4.9	2.5	
P^2	6.2	4.1		6.3	4.5	6.1	4.3	
P^3	6.3	6.9		6.9	7.2	6.6	7.4	
P^4	6.6	7.6		7.0	8.2	6.8	8.6	
M^1	9.0	9.9		8.0	9.9	8.1	10.2	
M^2	9.0	10.4		10.0	11.0	8.9	11.3	
M^3	8.8	10.0		8.8	11.1	8.6	10.3	
Lower dentition								
C_1	4.7	3.0	4.9	4.9	5.4	--	--	
P_1	4.4	2.5		3.4	2.7	--	--	
P_2	--	3.5		6.6	3.5	--	--	
P_3	6.6	4.3		7.1	4.0	--	--	
P_4	6.9	5.1		--	4.9	--	--	
M_1	8.8	6.4		8.3	6.0	--	--	
M_2	9.1	6.7		9.6	6.8	--	--	
M_3	12.4	6.8		13.6	7.5	--	--	

The dentary preserves roots for I_{1-3}. These are procumbent and increase in size from front to back. None of the incisor crowns are preserved. The lower canine in UM 78915 is very small and blunt, again indicating a female individual. In contrast, C_1 in UM 68548 is a much larger tooth that is both longer anteroposteriorly and much broader. The crown is broken, but this specimen is almost certainly a male. P_1 in the holotype is similar to the canine in being single-rooted and in its bluntness, but it is even smaller and it differs from the canine in having a distinct cuspule at the posterior base of the crown. I_3 and C_1, and C_1 and P_1 are each separated by short diastemata (2.0 mm and 3.8 mm, respectively), but P_1 and P_2 are separated by a longer diastema (7.0 mm). P_2 through P_4 increase in complexity posteriorly, with larger metaconids and broader talonids. M_{1-3} are all lophodont, and each has a moderately developed hypolophid. In UM 78915 (holotype) the hypoconulid crest joins the hypolophid near the hypoconid, however in UM 68548 the hypoconulid crest joins the hypoconid directly.

Measurements of upper and lower teeth of *Cardiolophus radinskyi* are listed in Table 2.

The postcranial skeleton of this species is as yet very poorly known. UM 80318 has a number of associated tarsal elements, including a left astragalus and calcaneum. The astragalus measures 21.2 mm in maximum length and 14.7 mm transversely across the body (including the lateral fibular process), and the head measures 13.1 mm transversely and 8.3 mm dorsoventrally. The calcaneum measures 40.0 mm in total length, with a relatively short distal extremity. The most interesting feature, clear when astragalus and calcaneum are articulated, is absence of contact between the calcaneum and navicular. This is possibly a primitive characteristic in Perissodactyla (achieved again independently later): *Hyracotherium* typically has substantial contact between the calcaneum and navicular (Kitts, 1956: fig. 4), while phenacodontid condylarths lack this (Thewissen, 1990).

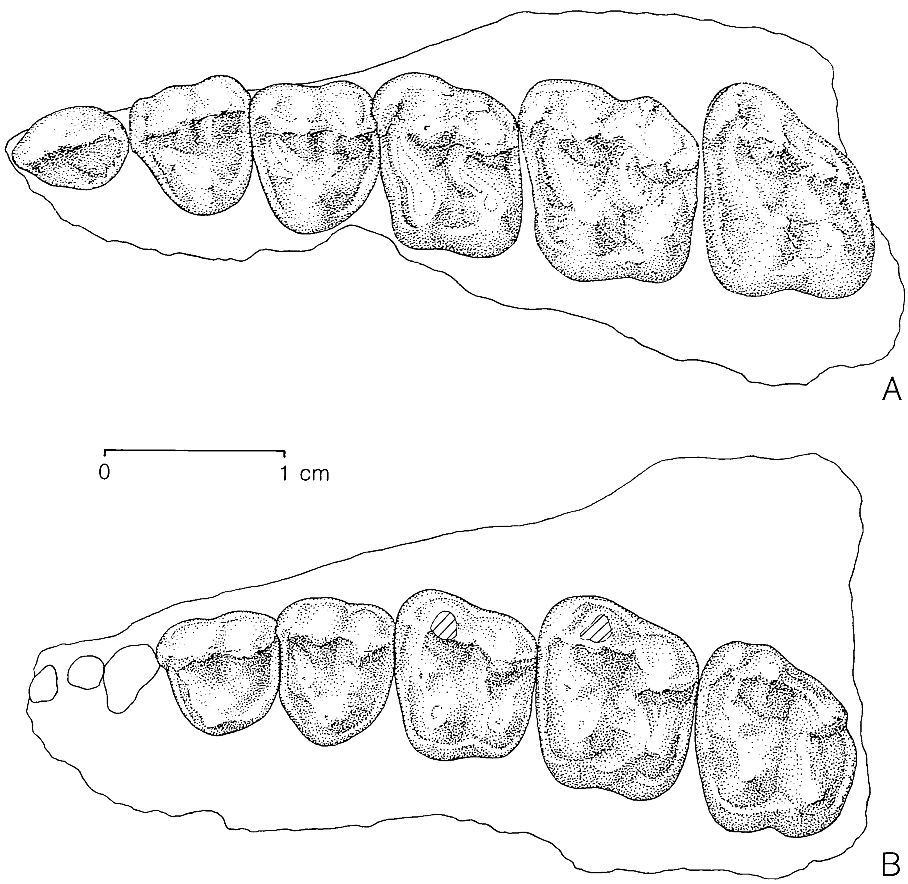

FIG. 9—Comparison of maxillary cheek teeth of *Cardiolophus radinskyi* with those of *Hyracotherium grangeri*. A, left maxilla of *C. radinskyi* with P^2-M^3, UM 68548 from locality SC-87. B, left maxilla of *H. grangeri* with P^3-M^3, UM 74639 from locality SC-4. Note general similarity, but better development of protoloph and slightly more trapezoidal outline of M^3 in *C. radinskyi*.

Discussion.—McKenna (1960) was the first to recognize that specimens here called *Cardiolophus radinskyi* represent a perissodactyl intermediate in size between *Hyracotherium* and *Homogalax* but different from both. Radinsky (1963, p. 17) regarded the intermediate size and cusp configurations of McKenna's specimens as ideal transitional forms linking *Hyracotherium* and *Homogalax.*

Cardiolophus semihians (Cope, 1882)
Figs. 5A, 8, 10

Systemodon semihians Cope, 1882, p. 184.
Systemodon semihians, Cope, 1885, p. 622, Pl. 56, fig. 3. Wortman, 1898, p. 89.
Homogalax semihians, Hay, 1899, p. 593.

Holotype.—AMNH 4485, left premaxilla and maxilla with alveoli for I^3, C^1, P^1, and worn crowns of $P^{2\text{-}3}$ and $M^{1\text{-}3}$.

Type locality.—Bighorn Basin, Wyoming (holotype was collected by J. Wortman in 1881, probably somewhere south of the Graybull River.

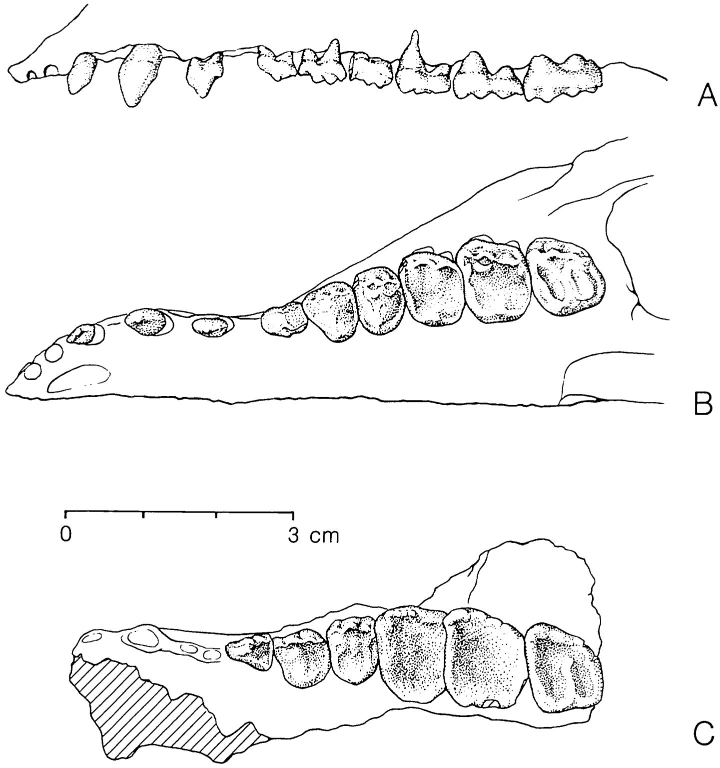

FIG. 10—Comparison of maxillary dentition of referred skull of *Cardiolophus semihians*, UM 78915 from locality RB-14 in the central Bighorn Basin, Wyoming (A, left lateral view; B, occlusal view) with holotype specimen of *C. semihians*, AMNH 4485, from unknown locality in Bighorn Basin (C, occlusal view). Note similar overall size, similar placement and conformation of alveoli I^3, C^1, and P^1, and similar trapezoidal outline of M^3. Breadth of M^{1-2} in type specimen is exaggerated by heavy wear and microfracturing of enamel.

Age and distribution.—Middle and late Wasatchian, early Eocene. This species is presently known only from the Bighorn Basin.

Diagnosis.—Similar in size to early Wasatchian *Cardiolophus radinskyi*, but differs in having a more molarized P^2, a broader mandibular symphysis, and a longer and narrower M_3.

Referred specimens.—Holotype from an unknown locality in the central Bighorn Basin. UM 64202 is from locality YM-45. UM 71839 is from locality RB-14. USGS 22408 from locality D-1660 is a well preserved right dentary of this species with crowns of I_2-M_3 intact. There are many additional specimens of this species in AMNH, UM, USGS, and YPM collections from the central Bighorn Basin.

Description.—The type specimen, AMNH 4485 (Fig. 10C), exhibits two important characteristics of *Cardiolophus*, a short diastema between the upper canine and two-rooted P^1, and relatively small premolars. The root of the upper canine is preserved, and it has a small cross section indicating that it the type is probably female. Molars in the type are very heavily worn, and as Radinsky (1963) observed, have been distorted and enlarged somewhat by deformation.

The referred skull, UM 71839 (Figs. 8, 10A,B), was found in sandstone, and it is very well preserved. It is distorted in having the frontals, palate, and rostrum compressed dorsoventrally, and the rostrum slightly sheared laterally. The cranium measures 140 mm in condylobasal length, and 67 mm in bizygomatic breadth. In dorsal view, the skull is seen to have a very small sagittal crest but a large nuchal crest projecting caudally and dorsally. Large emissary foramina leave the brain case dorsally and project toward the nuchal crest. There is a distinct postorbital process. In lateral view, the infraorbital foramen opens above the posterior border of P^2. It is moderate in size, measuring about 3.9 mm high and 2.4 mm wide. Foramina of the medial orbital wall are not well preserved. In ventral view, there is a long narrow palatine fissure separating the premaxilla and maxilla anteriorly, and the bony palate extends posteriorly to end at the level of M^3. The basicranium is well preserved, with the foramen ovale clearly distinct from the middle lacerate foramen. The braincase is filled with sediment, but the foramen magnum measures about 10 mm in breadth and in height.

Alveoli are present for I^{1-2}, but these teeth are missing. I^3 is intact on the left side, with a simple pointed crown. C^1 is present on both sides. The canines are very small, with a simple conical crown that does not project very far, indicating that this individual was probably female. P^1 is double-rooted and has a simple crown that is elongated anteroposteriorly, with a small posterior basal cuspule. P^2 is triangular in outline with a single buccal cusp and a substantial posterolingual expansion of the crown. P^3-M^3 are worn but still show that the premolars were small relative to molar size by comparison with *Homogalax*, while the molars (especially M^3) have the lophodont wear pattern and M_3 has the slightly trapezoidal outline typical of *Homogalax*. Tooth measurements are given in Table 2.

Discussion.—UM 71839, the skull illustrated in Figures 8 and 10A,B, was found by Mr. Carl Godwin of Ann Arbor while prospecting for fossils in the central Bighorn Basin during a family vacation trip to Wyoming. It is important in showing that a species with the distinctive characteristics shown in Cope's type specimen of *Systemodon semihians* is present in the central Bighorn Basin where the type was collected, and in showing that this species differs significantly from *Homogalax protapirinus*. Lacking good comparative material, Radinsky (1963) concluded that Cope's type is indeterminate and suggested that the species *semihians* should be suppressed in systematic nomenclature. Figure 10 shows a comparison of AMNH 4485, type of *C. semihians*, with the skull UM 71839.

Cardiolophus semihians is still not well known in terms of either morphological variability or stratigraphic range, and it is possible that it may prove indistinguishable from *C. radinskyi*. *Cardiolophus* as a genus has *C. radinskyi* as its type species rather than *C. semihians* because *C. radinskyi* is based on a much more complete type specimen than *C. semihians* and it is presently the better known of the two included species.

Homogalax Hay, 1899

Systemodon (in part), Cope, 1885, p. 618. Wortman, 1896, p. 87.
Homogalax (in part) Hay, 1899, p. 593. Radinsky, 1963, p. 10.

Type species.—*Systemodon primaevus* Wortman, 1896.

Included species.—Type species and *H. aureus*, new species.

Age and distribution.—Wasatchian land-mammal age, early Eocene, of Wyoming and North Dakota.

Diagnosis.—Differs from *Cardiolophus* in having smaller diastemata separating canines from first premolars, in having higher crowned and consequently more lophodont cheek teeth, and in having upper premolar and molar crowns broader transversely.

Discussion.—Hay (1899) referred three species, *Systemodon semihians*, *S. protapirinus*, and *S. primaevus*, to *Homogalax* when he first described this genus. *H. semihians* is here placed in *Cardiolophus*, and Radinsky (1963, p. 14) synonymized *H. primaevus* with *H. protapirinus*.

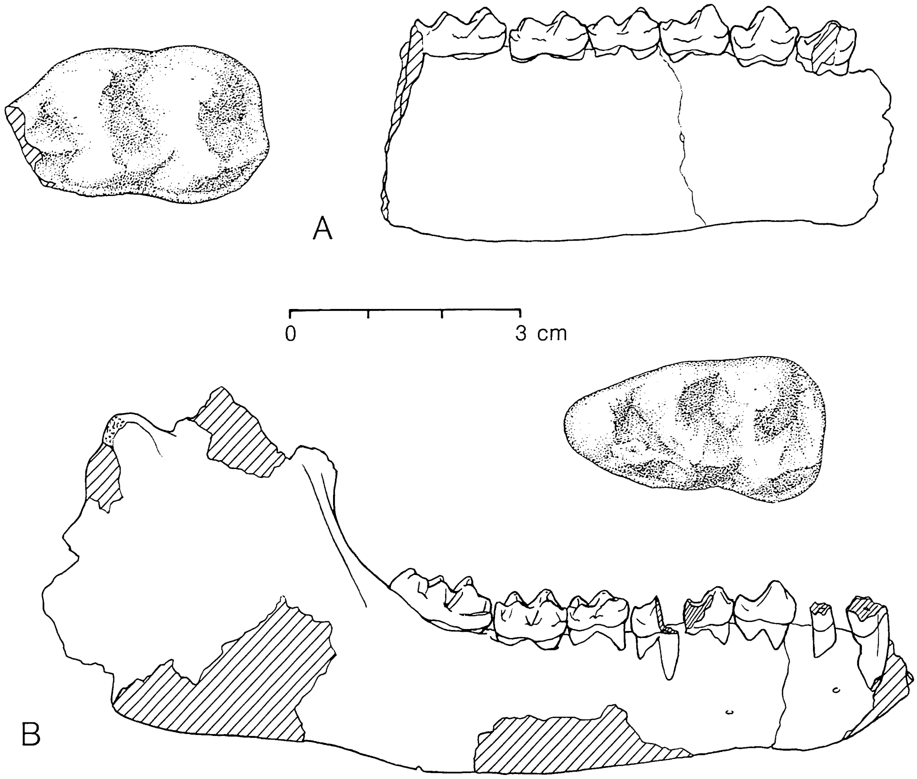

FIG. 11—Right lower third molars (M_3) and dentaries of *Homogalax protapirinus* and *Cardiolophus radinskyi* from the Clarks Fork Basin, Wyoming. A, UM 66650, *H. protapirinus*, from locality SC-64 ($P_{2\text{-}3}$ and M_3 rev.). B, UM 68548, *H. radinskyi*, from locality SC-87. Note well developed hypolophid on M^3 in both specimens, but both protolophid and hypolophid are conspicuously stronger in *Homogalax*.

Homogalax protapirinus (Wortman, 1896)
Fig. 11A

Systemodon protapirinus Wortman, 1896, p. 89, figs. 1-2.
Systemodon primaevus Wortman, 1896, p. 89, fig. 3.
Homogalax protapirinus, Hay, 1899, p. 593.
Homogalax primaevus, Hay, 1899, p. 593.
Homogalax protapirinus (in part), Radinsky, 1963, p. 13, Pl. 1, figs. 1, 5.

Holotype.—AMNH 4460, right maxilla with left and right dentaries.

Type locality.—Bighorn Valley, Wyoming. Collected by J. L. Wortman, 1891.

Age and distribution.—Species is known primarily from sediments of middle Wasatchian age (early Eocene), but it may be present in some early late Wasatchian localities. Known primarily from Bighorn Basin and Clarks Fork Basin, northwestern Wyoming.

Diagnosis.—Differs from *H. aureus* in being 8-12% larger in linear dimensions and in having relatively broader lower molars.

Referred specimens.—Specimens from known levels in the Clarks Fork Basin stratigraphic section include **SC003:** UM 65725; **SC005:** UM 64621, 64623; **SC032:** UM 78951; **SC033:** UM 71195, 82968; **SC034:** UM 65309, 71510, 73918; **SC035:** UM 65356; **SC036:** UM 71673, 71727, 71730; **SC063:** UM 73019; **SC064:** UM 65754, 66650, 72922; **SC087:** UM 66227, 66254, 66509, 66525, 76534, 72961, 66793, 66819; **SC112:** UM 79919, 79935, 79936; **SC113:** UM 66823, 73630; **SC114:** UM 66838; **SC133:** UM 67109, 68088; **SC145:** UM 69704, 69707; **SC148:** UM 67325; **SC213:** UM 69811, 71127, 75391, 75395, 79556, 79585; **SC221:** UM 71163, 79798; **SC224:** UM 82976; **SC225:** UM 71220, 78959; **SC232:** UM 71714, 71715, 76787; **SC237:** UM 76794, 76817, 83054, 83061, 83074; **SC255:** UM 80120; **SC256:** UM 73557; **SC265:** UM 73458, 75649, 83710; **SC291:** UM 73832; **SC303:** UM 83733; **SC309:** UM 76556; **SC310:** UM 84707, 86216; **SC312:** UM 82554. These range from the 1750 through 2110 meter levels.

Description.—Dental remains of *Homogalax protapirinus* are adequately described by Wortman (1896) and Radinsky (1963). Good skulls are not yet known, and little has been written about the postcranial skeleton. UM 87027 is a good partial skeleton of *H. protapirinus*, including a palate, good series of thoracic and lumbar vertebrae, much of the forelimb including a nearly complete carpus, and some elements of the hind limb (Table 5). UM 92584 includes articular ends of many long bones, but none with complete shafts.

UM 90987 from locality SC-192 and UM 95068 from MP-200 each include an associated right astragalus and calcaneum. When articulated these show, as in *Cardiolophus*, that the distal calcaneum in *Homogalax* was too short to have articulated with the navicular. UM 90987 measures 21.8 mm in maximum length, and 18.1 mm in breadth across the body (including the lateral fibular process). These measurements in UM 95068 are 22.4 and 17.1 mm, respectively.

Discussion.—Specimens from the San Juan Basin described as *Homogalax protapirinus* and cf. *Homogalax* sp. by Froehlich and Reser (1981) are, I think, *Heptodon* and large *Hyracotherium*, respectively. Gazin (1962, p. 77) reported *Homogalax primaevus* from Bitter Creek in the Washakie Basin of southwestern Wyoming, but the specimens he illustrated (Pl. 12, figs. 5, 6) look more like *Hyracotherium cristatum* than they do *Homogalax protapirinus* (= *primaevus*).

Homogalax aureus, new species

Homogalax cf. *H. protapirinus*, Jepsen, 1963, p. 679. Radinsky, 1963, p. 16.

Holotype.—YPM-PU 17359, left dentary with P_2-M_3.

Type locality.—White Butte Site, SW$\frac{1}{4}$, Section 29, T139N, R97W, Stark County, North Dakota. Collected by G. L. Jepsen field party.

Age and distribution.—Wasatchian, early Eocene. Species is presently known only from the type locality in southwestern North Dakota.

Diagnosis.—Differs from *H. protapirinus* in being 7-11% smaller in linear dimensions and in having relatively narrower lower molars.

Etymology.—Latin *aureus*, golden, in reference to the Golden Valley of North Dakota and the color of the specimens.

Referred specimens.—Holotype and YPM-PU 17157, 17161, 17164, 17165, 17229, 17230, 17284, 17285, 17358, 17360-17362, 17364, 17373, and 17399.

Description.—Upper and lower dentition is indistinguishable from that of *Homogalax protapirinus*, as described by Wortman (1896) and Radinsky (1963), except that cheek teeth are smaller and lower cheek teeth are narrower relative to tooth length. The skull and postcranial skeleton are unknown.

Measurements of the holotype are listed in Table 1.

Discussion.—Radinsky (1963) recognized that specimens described here are *Homogalax* but almost certainly a significantly smaller species than *H. protapirinus*. The fauna from the type locality has never been fully studied and its age is not precisely known. Jepsen (1963) reported *Cantius ralstoni* from the Golden Valley fauna and suggested an early Wasatchian age, but this identification was altered to *Cantius trigonodus* by Gingerich and Simons (1977), implying a middle Wasatchian age consistent with the distribution of *Homogalax* known elsewhere. Better documentation of possible size change in Bighorn Basin *Homogalax protapirinus* and further study of the Golden Valley mammalian fauna will be necessary to determine whether *H. aureus* is a contemporary sister species or a descendent of *H. protapirinus*.

Superfamily CHALICOTHEROIDEA Gill, 1872
Family CHALICOTHERIIDAE Gill 1872

Paleomoropus Radinsky, 1964

Paleomoropus Radinsky, 1964, p. 2.

Type species.—*Paleomoropus jepseni* Radinsky, 1964.
Included species.—Type species only.
Age and distribution.—Middle Wasatchian, early Eocene, of Clarks Fork Basin, Wyoming.
Diagnosis.—*Paleomoropus* is distinguished from all other North American early Eocene perissodactyls in having highly lophodont molars with a distinct protoconule on the protoloph. Similar to *Heptodon* in having a high uninterrupted metaloph. This genus and *Lophiaspis* are distinctive among chalicotheroids in having low-crowned cheek teeth and in lacking mesostyles on upper molars.
Discussion.—Classification in Chalicotheriidae follows Savage et al.'s (1966) placement of European *Lophiaspis* in this family. *Paleomoropus* is very similar dentally to *Lophiaspis*. Fischer (1977) considered both to be lophiodontid tapiroids.

Paleomoropus jepseni Radinsky, 1964

Paleomoropus jepseni Radinsky, 1964, p. 2, fig. 1.

Holotype.—The type and only specimen of this species is YPM-PU 13254, left M^{1-3}, collected by J. Page of Princeton on July 12, 1928.
Type locality.—T55N, R102W, Park County, Clarks Fork Basin, Wyoming. Precise locality is uncertain (see below).
Age and distribution.—*Paleomoropus jepseni* is known only from the middle Wasatchian, early Eocene, of the Clarks Fork Basin, Wyoming.
Diagnosis.—As for the genus.
Referred specimens.—Holotype is only known specimen.
Description.—Radinsky (1964) provides a full description and good illustrations.
Discussion.—Two specimen labels accompany the type of *Paleomoropus jepseni*. The first says "2½ miles S. of Camp #1" and the second "Section 9, T55N, R102W," Park County, Wyoming. These places are different, and the latter (the one published by Radinsky, 1964) cannot be correct because Section 9 is a sagebrush-covered plain with no Eocene outcrops. A July 12 entry in Jepsen's 1928 field notebook records finding the corner marker between Sections 11, 12, 13, and 14. July 12 is the day the type was collected, and this section corner is near UM locality SC-265. Locality SC-265 is about three miles south of Jepsen's Camp #1, and, considering that he had no detailed maps, this is very possibly the locality where PU 13254 was found. SC-265 is at the 2095 meter level in the Clarks Fork Basin stratigraphic section. Whatever the precise locality and level of the holotype, Jepsen's Camp #1 was on strata of middle Wasatchian age and all outcrops within walking distance to the south are middle Wasatchian as well.

Upward revision of the age of *Paleomoropus* (here) and downward revision of the age of *Lophiaspis maurettei* from Palette in France (Godinot et al., 1987) means that early Ypresian *Lophiaspis* rather than middle Wasatchian *Paleomoropus* is likely to be the oldest of known chalicotheroids.

BIOSTRATIGRAPHIC SUBDIVISION OF WASATCHIAN LAND-MAMMAL AGE

Walter Granger led an American Museum field party exploring the Wind River Basin in 1909, and found evidence of a new faunal zone intermediate between the standard *Lambdotherium* zone of the Wind River Basin and the so-called *Coryphodon* zone of the Bighorn Basin (Granger, 1910). Following up on this, Sinclair and Granger (1911) proposed that the new Wind River zone be called Lysite "formation" and the *Lambdotherium* zone be called Lost Cabin "formation." Sinclair and Granger also recognized three faunal horizons, numbered 1-3, underlying beds yielding *Lambdotherium* in the Bighorn Wasatchian. Further work in the Bighorn Basin led Sinclair and Granger (1912) to place the Bighorn "*Coryphodon* zone" in what they called Knight formation, characterized by the presence of *Eohippus* and *Systemodon*. They also reported Lysite formation with *Heptodon* overlying the Knight, and Lost Cabin formation with *Lambdotherium* overlying the Lysite. Granger (1914) proposed Gray Bull to replace "Knight" in the Bighorn Basin (after *Heptodon* was recognized in collections from the type Knight), again characterizing this interval as being the interval of *Systemodon*. Granger further recognized a zone beneath the Graybullian in the Clarks Fork Basin that has *Eohippus* but lacks *Systemodon*. This he called Sand Coulee. Thus, by 1914, Wasatchian time in the Bighorn and Clarks Fork basins was divided into Sand Coulee or Sandcouleean with *Eohippus*, Gray Bull or Graybullian with the addition of *Systemodon*, Lysite or Lysitean with the addition of *Heptodon*, and Lost Cabin or Lostcabinian with the addition of *Lambdotherium*. Granger's "*Eohippus*" is the genus here called *Hyracotherium*, and his "*Systemodon*" is the genus here called *Homogalax*.

Jepsen (1930, p. 119) caused some confusion for Granger's subdivision of the Wasatchian when he reported finding "typical *Homogalax*" in Sand Coulee beds, claiming that the distinction between Sand Coulee and Gray Bull was no longer valid. Jepsen mentioned having found "only one good specimen" of *Homogalax* in Sand Coulee beds, but declined to list the specimen's number or to give the locality where this had been found. If the specimen came from Sandcouleean beds (which is an open question), then it was almost certainly *Cardiolophus radinskyi* rather than *Homogalax protapirinus*. As far as I am aware, *Homogalax* has never been found in beds here regarded as Sandcouleean.

Granger's sequence of four Wasatchian faunal zones, Sandcouleean, Graybullian, Lysitean, and Lostcabinian, established almost eighty years ago, is still in general use (Krishtalka et al., 1987), but several attempts have been made to refine or replace this in recent years. In 1980 I subdivided the Wasatchian land-mammal age into five zones, numbered Wa-1 through Wa-5 (Gingerich, 1980), based on successive stages of evolution of *Pelycodus* (now *Cantius*). These corresponded approximately to Sandcouleean, early Graybullian, late Graybullian, Lysitean, and Lostcabinian, but correlations were not well enough established at the time to be very sure about the correspondence.

At about the same time, Schankler (1980) completed study of Wasatchian faunas from the central Bighorn Basin and criticized my *Pelycodus* zones as being problematic because the species boundaries are often arbitrary (a justifiable criticism), and because he claimed data exist showing isochronous populations of the same species to differ in size within the Bighorn Basin (which would be difficult to show and remains to be documented). Schankler proposed a sequence of six zones: (1) lower *Haplomylus-Ectocion* range zone, (2) upper *Haplomylus-Ectocion* range zone, (3) *Bunophorus* interval zone, (4) lower *Heptodon* range zone, (5) middle *Heptodon* range zone, and (6) upper *Heptodon* range zone. The first three correspond to early, middle, and late Graybullian, the fourth and fifth to the Lysitean, and the sixth to the Lostcabinian. Schankler (1980) omitted any discussion of the Sandcouleean interval, and abandoned *Homogalax* as an index fossil for the Graybullian because of its virtual absence in the No Water area studied by Bown (1979) and because of its range overlap with *Heptodon*. Absence of *Homogalax* in Wasatchian faunas of the No Water area is almost certainly because faunas

Table 3—Biostratigraphic zonation of Wasatchian land-mammal age based on Perissodactyla

	Zone	Principal taxon making first appearance at beginning of zone	Auxiliary taxa making first appearance at beginning of zone	Alternative name for zone	Interval in CFB strat. section (m)
Late	Wa-7	***Lambdotherium primaevum***		Lostcabinian	--
	Wa-6	***Heptodon calciculus***		Lysitean	--
	Wa-5	⇑	***Bunophorus etsagicus***	Late Graybullian	2240
Middle	Wa-4	⇑	***Hyracotherium pernix***	Middle Graybullian	2020-2110
	Wa-3b	⇑	***Hyracotherium aemulor***	Early Graybullian	1770-2005
	Wa-3a	***Homogalax protapirinus***	--	"	1750-1760
	Wa-2	⇑	***Arfia shoshoniensis***	Late Sandcouleean	1645-1740
Early	Wa-1	⇑	***Cardiolophus radinskyi***	Middle Sandcouleean	1525-1635
	Wa-0	***Hyracotherium grangeri***	*Hyracotherium sandrae*	Early Sandcouleean	1520

there are Sandcouleean in age and predate appearance of *Homogalax*. Range overlap with *Heptodon* is not a problem because, as Schankler himself recognized, the first appearance of each genus (e.g., *Heptodon*) is what is important, not its last appearance.

In 1983 I expanded Schankler's zonation by adding two pre-*Homogalax* zones in the Sandcouleean, numbering all Wa-1 through Wa-7 (Gingerich, 1983). Recently it has been necessary to add Wa-0 at the base of the sequence (Gingerich, 1989). The complete zonation is listed in Table 3. This is basically Granger's system, clarified by separation of Sandcouleean *Cardiolophus* from Graybullian *Homogalax* and clarified by a clear understanding of the stratigraphic ranges of *Hyracotherium* species within the Graybullian. It includes, in addition, the first appearance of large *Arfia* (Gingerich and Deutsch, 1989), and the first appearance of large *Bunophorus* (Schankler, 1980) as stratigraphic markers. This zonation describes the sequence of appearance of faunally important taxa in the Clarks Fork Basin and northern Bighorn Basin. Thicknesses of faunal intervals corresponding to these zones in the Clarks Fork Basin range from a few meters to 235 meters. The utility of these zones will, of course, be tested as faunal sequences are described from the central Bighorn Basin and elsewhere.

BODY MASS OF *HYRACOTHERIUM* AND *HOMOGALAX*

Tooth size is commonly used to predict body mass in mammals. An equation relating body mass to tooth size for generalized ungulates is $\text{Ln } Y = 1.5133 \cdot \text{Ln } X + 3.6515$ (Legendre, 1989, p. 24), where X is length multiplied by width of M_1 in mm^2, and Y is body mass in g. This yields predicted body masses ranging from 3,900 to 7,100 g for *Hyracotherium sandrae*, 6,600 to 12,100 g for *Hyracotherium grangeri*, and 15,200 to 27,800 g for *Homogalax protapirinus*.

For comparison, postcranial elements of *Hyracotherium* and *Homogalax* can be used to predict body mass (Gingerich, 1990). The most complete skeletons of *Hyracotherium* are those described by Kitts (1956): Late Wasatchian (Lostcabinian) AMNH 4832 attributed to *H. vasacciense*, and middle Wasatchian (Graybullian) AMNH 15428 attributed to *H. angustidens* (here *H. cristatum*). The former has a body mass predicted from long bone length of about 8,000 to 9,000 g, while the latter has a body mass predicted from long bone length of about 15,000-16,000 g (Table 4). There is considerable variation in predictions based on single bones, depending on which element is used, and there is considerable breadth in the prediction limits. The best single predictor appears, in both cases, to be femur length. Applying this to Clarks Fork Basin species, the femur of *Hyracotherium sandrae*, UM 79889 with a length of 113.5 mm, yields a predicted body mass of 5,000 g. The femur of *H. grangeri*, UM 82242 with a length of 134 mm, yields a predicted body mass of 7,900 g. Both fall near the middle

TABLE 4—Body size determination for Eocene perissodactyl *Hyracotherium cristatum* based on associated partial skeleton AMNH 15428 (Kitts, 1956). Predictions computed using program in Gingerich (1990).

Hyracotherium cristatum AMNH 15428	Measurement (mm)	Predicted body mass(g)	95% Prediction limits Min(g)	Max(g)
Humerus length	130	12,512	3,704	42,258
Ulna length	141	9,813	3,109	30,976
Metacarpal length	61 (est.)	22,614	3,528	144,940
Femur length	174	15,711	4,299	57,418
Tibia length	166.5	12,674	3,440	46,696
Metatarsal length	82.5	32,279	4,748	219,457
N, geom. mean, max, min	(6)	16,026	4,748	30,976
Multiple regression	All species: (Artio.rem.):	11 L&D-	6 L-	14,950 (11,740)

TABLE 5—Body size determination for Eocene perissodactyl *Homogalax protapirinus* based on associated partial skeleton UM 87027. Predictions computed using program in Gingerich (1990).

Homogalax protapirinus UM 87027	Measurement (mm)	Predicted body mass(g)	95% Prediction limits Min(g)	Max(g)
Humerus length		---		
Ulna length		---		
Metacarpal length	50	13,825	2,176	87,830
Femur length	149	10,409	2,852	37,983
Tibia length		---		
Metatarsal length		---		
Humerus diameter		---		
Ulna diameter		---		
Metacarpal diameter		---		
Femur diameter	13.2	13,664	7,182	25,997
Tibia diameter		---		
Metatarsal diameter		---		
N, geom. mean, max, min	(3)	12,518	7,182	25,997

of the range predicted from tooth size, corroborating use of tooth size and femur length for prediction of body mass in *Hyracotherium*.

The humerus, ulna, and tibia of *Hyracotherium* all yield body mass predictions below the average for long bones taken together (Table 4), indicating that these elements are shorter than average for mammals of that mass living today. Metacarpal length yields a prediction 44% higher than femur length in *Hyracotherium cristatum* (Table 4) and 105% higher than femur length in *H. vasacciense*. Metatarsal length yields a prediction 105% higher than femur length in *H. cristatum* (Table 4) and 115% higher than femur length in *H. vasacciense*. These values indicate that *Hyracotherium* had longer metapodials than are seen typically in mammals today, which is consistent with common interpretation that it was a cursor. These values also suggest that smaller *Hyracotherium* had relatively longer metapodials (or that metapodial length increased from middle to late Wasatchian time).

Postcranial remains of *Homogalax protapirinus* are limited, but these are nonetheless interesting in yielding an estimate of 13,000 g (Table 5), well below the range predicted from tooth size. Femur length alone yields a predicted body mass of only 10,400 g. If the femur available for study is representative, then *Homogalax* had either relatively short femora or relatively large molars for its body mass. It is interesting too to note that metacarpal length yields a prediction 33% higher than femur length (Table 5), which indicates that *Homogalax* had elongated metacarpals, but these were relatively short by comparison with those of *Hyracotherium*.

FORAMEN OVALE IN EARLY PERISSODACTYLA

The foramen ovale is a foramen at the base of the skull enclosing the root of the mandibular nerve. This foramen is typically present as a distinct foramen in extant Artiodactyla while it is absent in being confluent with the foramen lacerum medium in extant Perissodactyla. The foramen ovale has evidently been lost independently in many groups of mammals (Edinger and Kitts, 1954). Edinger and Kitts (1954) reported the foramen ovale absent in one skull of late Wasatchian *Hyracotherium* (AMNH 4832), partially within the foramen lacerum medium in another skull of late Wasatchian *Hyracotherium* (AMNH 4831), and present in a third specimen (YPM 11694; Radinsky, 1976, later identified this as a skull of the condylarth *Meniscotherium*). Kitts (1956) further reported the foramen ovale to be missing in a late middle Wasatchian skull of *Hyracotherium* (AMNH 15428, discussed above as *H. cristatum*). MacFadden (1976) regarded confluence of the foramen ovale with the foramen lacerum medium, that is, loss of the foramen ovale, as a diagnostic characteristic supporting inclusion of *Hyracotherium* in a holophyletic family Equidae.

Six new skulls of *Hyracotherium* or *Hyracotherium*-like perissodactyls have been examined in the course of this study, and all have a distinct foramen ovale. The first is a skull of early Wasatchian *Hyracotherium grangeri*, UM 82954, which has the left maxilla with P^2-M^3 attached. The basicranium is well preserved on the right side, with a relatively large foramen ovale (measuring 1.5 × 4.0 mm) present anterior to the foramen lacerum medium. The second is a skull of early middle Wasatchian *Hyracotherium aemulor*, UM 95080, which has much of the dentition associated (although no teeth are attached to the piece bearing the braincase and basicranium). The basicranium is well preserved on the left side, with a sizable foramen ovale (measuring ca. 1.0 × 3.0 mm) present anterior to the foramen lacerum medium. The foramen ovale here is divided by a break running through it and displacing the medial part anteriorly and the lateral part posteriorly.

The type skull of early Wasatchian *Cardiolophus radinskyi* illustrated in Figure 7, UM 78915, has a distinct foramen ovale present in front of the foramen lacerum medium on both left and right sides. The referred skull of middle or late Wasatchian *Cardiolophus semihians* illustrated in Figure 8, UM 71839, also has a distinct foramen ovale present on both sides. One late Wasatchian skull referred to *Hyracotherium tapirinum* by Gingerich (1981), AMNH 55267 (male), has the thin bone separating the foramen ovale and foramen lacerum medium broken away on both sides, but this bone is still present on the right side showing that the two foramina were separate. A second skull from the same locality referred to *Hyracotherium tapirinum* by Gingerich (1981), AMNH 55266 (female) has a separate foramen ovale preserved in front of the foramen lacerum medium on both left and right sides. If *H. tapirinum* belongs in *Systemodon* or *Xenicohippus*, then this species is not directly relevant in assessing the presence or absence of a foramen ovale in *Hyracotherium*.

Damage to AMNH 55267 is instructive in showing how easily evidence of a foramen ovale may be obliterated through breakage. This suggests that it might be worth comparing *Hyracotherium* skulls that are said to lack the foramen with those that clearly retain it as a way of assessing breakage. At the same time, the foramen ovale has to have been lost at some time in the history of Equidae, and it is to be expected that an early genus like *Hyracotherium* might include species with and without the foramen. It appears from present evidence that the foramen ovale was lost in *Hyracotherium* during early or middle Wasatchian time.

EVOLUTIONARY PATTERNS

Evolutionary patterns in early Eocene Perissodactyla are illustrated in Figures 12 and 13. These show the abrupt appearance of two species of *Hyracotherium* at the beginning of the Wasatchian land-mammal age, with near synchronous appearance of *Cardiolophus* as well. Abrupt appearance of these (and many other) taxa suggests that Perissodactyla evolved elsewhere and dispersed into the study area at the beginning of the Wasatchian time. *Hyracotherium* has long been regarded as the most primitive perissodactyl, but it is specialized in having a long C_1-P_1 diastema and possibly in other ways as well. *Cardiolophus* appeared at almost the same time. It is intermediate between *Hyracotherium* and later *Homogalax*, and it is the most generalized and hence, possibly, the most primitive of known perissodactyls. Perissodactyla have long been thought to have evolved from phenacodontid Condylarthra (see Radinsky, 1969, for review), and this is possible. However, the profound break between Clarkforkian (late Paleocene) and Wasatchian (early Eocene) mammalian faunas in North America (Gingerich, 1989), with Perissodactyla appearing in the Wasatchian, makes it unlikely that the transition occurred in the Western Interior of North America.

Two lineages of perissodactyls are the maximum number present during any interval of early Wasatchian (Sandcoulcean) time. *Hyracotherium grangeri* is present through this entire interval, but the only other perissodactyls known are *Hyracotherium sandrae* and *Cardiolophus radinskyi*. Stratigraphic ranges of the latter two species do not overlap. Three genera (*Hyracotherium*, *Cardiolophus*, and *Homogalax*) and three species are present for a brief time in the interval from 1750 through 1760 m, at the beginning of the middle Wasatchian (Graybullian), but there is then a long interval again with only two species present. Finally, at about level 2065, two additional lineages appear (but *Paleomoropus* is known from a single specimen and it cannot have been an important faunal element). Standing species richness was fairly constant through the whole interval, with two species present most of the time and three or four species present only for brief intervals.

The only species-level evolutionary transition in the whole sequence is the possible transition from *Hyracotherium grangeri* to *H. aemulor* in the interval between 1760 and 1780 m. This 20 meter thick interval is filled almost entirely with a multistory sheet sandstone that probably represents more time than most other 20-meter intervals in the Clarks Fork Basin stratigraphic section. It represents a condensed interval, with an indeterminate amount of sediment and time missing. A reworked soil-nodule conglomerate appears at the base of the sandstone in places, and this has yielded two specimens of *H. aemulor* (those marked as coming from above locality SC-87), indicating that any possible evolutionary transition took place during an erosional phase between deposition of the last remaining mudstone and emplacement of the overlying sandstone. The direction of change of late *H. grangeri* and the rounded and little-crested molars of both species are consistent with ancestor-descendant relationship, but this will have to be tested elsewhere. Interestingly, whatever its origin, *H. aemulor* did not appear until the same-sized *Cardiolophus radinskyi* had disappeared.

Some species, like *Homogalax protapirinus*, did not change significantly through their whole long record in the Clarks Fork Basin ($N = 15$, $F = 0.09$, and $p \leq 0.78$ for regression of M_1 size on stratigraphic level). *Cardiolophus radinskyi*, with a shorter record, did change significantly ($N = 37$, $F = 9.98$, $p \leq 0.003$ for regression of M_1 size on stratigraphic level). *Hyracotherium grangeri* first became smaller and then became larger. Rates of change range from virtually zero (stasis) to as much as 0.2 or 0.4 darwins when measured on a scale of a hundred thousand years or so (Figs. 12 and 13), although rates would be much greater if measured on finer scales of time (long-scale rates, by themselves, are not very informative).

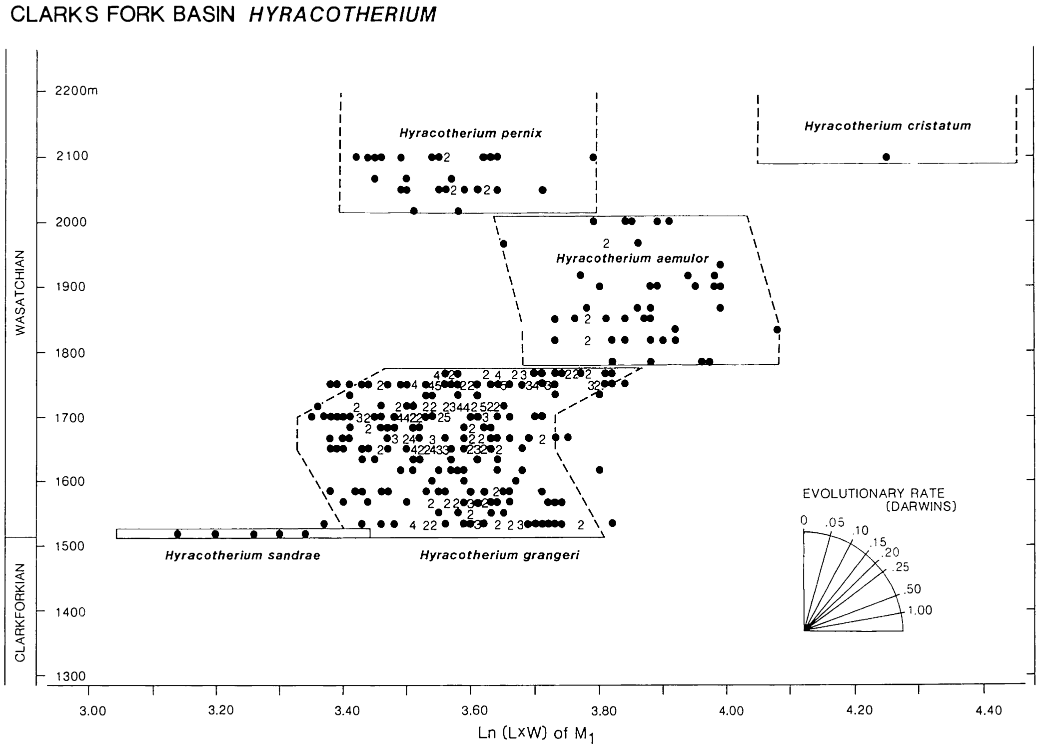

FIG. 12—Stratigraphic distribution of early Wasatchian *Hyracotherium* in the Clarks Fork Basin, Wyoming. Abscissa is natural logarithm of crown area of first lower molar (M_1). Ordinate is stratigraphic level in Clarks Fork Basin stratigraphic section (m). Solid circles are individual specimens, numerals represent multiple specimens falling at same point. Interval from 1520 through 2270 m represents about 2 million years of evolutionary time.

This study covers the first one-half or so of Wasatchian time as represented in the Clarks Fork Basin and vicinity. Our understanding of early Eocene perissodactyl evolution will not be complete until the rest of the Wasatchian is studied in the Bighorn Basin and other basins that have good stratigraphic records.

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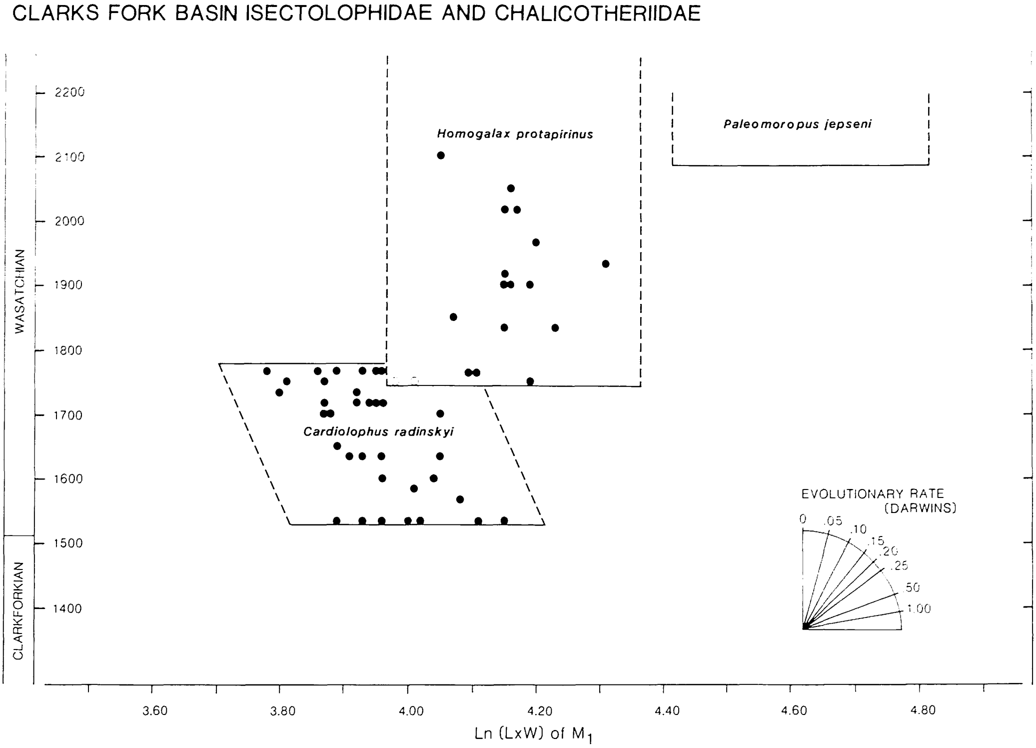

FIG. 13—Stratigraphic distribution of early Wasatchian *Cardiolophus*, *Homogalax*, and *Paleomoropus* in the Clarks Fork Basin, Wyoming. Abscissa is natural logarithm of crown area of first lower molar (M_1). Ordinate is stratigraphic level in Clarks Fork Basin stratigraphic section (m). Solid circles are individual specimens, numerals represent multiple specimens falling at same point. Interval from 1520 through 2270 m represents about 2 million years of evolutionary time.

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LITERATURE CITED

BOWN, T. M. 1979. Geology and mammalian paleontology of the Sand Creek Facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming. Geological Survey of Wyoming Memoir, 2: 1-151.

———, and A. J. KIHM. 1981. *Xenicohippus*, an unusual new hyracotheriine (Mammalia, Perissodactyla) from lower Eocene rocks of Wyoming, Colorado and New Mexico. Journal of Paleontology, 55: 257-270.

COPE, E. D. 1872. On a new genus of Pleurodira from the Eocene of Wyoming. Proceedings of the American Philosophical Society, 12: 472-477.

———. 1873. Fourth notice of extinct Vertebrata from the Bridger and the Green River Tertiaries. Palaeontological Bulletin, 17: 1-4.

———. 1875. Systematic catalogue of the Vertebrata of the Eocene of New Mexico collected in 1874. Report to the Engineer Department, U. S. Army, G. M. Wheeler in Charge, Washington, pp. 5-37.

———. 1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Geographical Surveys West of the One Hundredth Meridian, G. M. Wheeler, in charge, Washington, pp. 1-370.

———. 1880. The badlands of the Wind River and their fauna. American Naturalist, 14: 745-748.

———. 1881a. On the Vertebrata of the Wind River Eocene beds of Wyoming. Bulletin of the U. S. Geological and Geographical Survey of the Territories, 6: 183-202.

———. 1881b. A new genus of Perissodactyla diplarthra. American Naturalist, 15: 1018.

———. 1882. Contributions to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. I. The fauna of the Wasatch beds of the basin of the Big Horn River. Proceedings of the American Philosophical Society, 20: 139-191.

———. 1885. The Vertebrata of the Tertiary formations of the West. Book I. Report of the U. S. Geological Survey of the Territories, F. V. Hayden, U. S. Geologist in Charge, Washington, 3: 1-1009.

DASHZEVEG, D. 1979. Discovery of *Hyracotherium* in Mongolia. Paleontologicheskiy Zhurnal, Akademiya Nauk S.S.S.R., Moscow, 3:108-113. [Translated from Russian by B. Kushner]

DELSON, E. 1971. Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming. Bulletin of the American Museum of Natural History, 146: 305-364.

EDINGER, T., and D. B. KITTS. 1954. The foramen ovale. Evolution, 8: 389-404.

FISCHER, K. 1977. Neue Funde von *Rhinocerolophiodon* (n. gen.), *Lophiodon* und *Hyrachyus* (Ceratomorpha, Perissodactyla, Mammalia) aus dem Eozän des Geiseltals bei Halle (DDR). Zeitschrift für Geologische Wissenschaften, Berlin, 5: 909-919.

FROEHLICH, J. W., and P. K. RESER. 1981. First occurrence of *Homogalax* (Mammalia, Perissodactyla, Tapiroidea) in the Regina Member of the San Jose Formation, San Juan Basin, New Mexico. In S. Lucas, K. Rigby, and B. Kues (eds.), Advances in San Juan Basin Paleontology. University of New Mexico Press, Albuquerque, pp. 293-303.

GAZIN, C. L. 1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. Smithsonian Miscellaneous Collections, 144(1): 1-98.

GINGERICH, P. D. 1980. Evolutionary patterns in early Cenozoic mammals. Annual Reviews of Earth and Planetary Sciences, 8: 407-424.

———. 1981. Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). Paleobiology, 7: 443-455.

———. 1983. Paleocene-Eocene faunal zones and a preliminary analysis of Laramide structural deformation in the Clarks Fork Basin, Wyoming. Wyoming Geological Association Guidebook, Thirty-Fourth Annual Field Conference, 34: 185-195.

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

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

——— and H. A. DEUTSCH. 1989. Systematics and evolution of early Eocene Hyaenodontidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. Contributions from the Museum of Paleontology, University of Michigan, 27: 327-391.

——— and E. L. SIMONS. 1977. Systematics, phylogeny, and evolution of early Eocene Adapidae (Mammalia, Primates) in North America. Contributions from the Museum of Paleontology, University of Michigan, 24: 245-279.

GODINOT, M., J-Y. CROCHET, J.-L. HARTENBERGER, B. LANGE-BADRÉ, D. E. RUSSELL, and B. SIGÉ. 1987. Nouvelles données sur les mammifères de Palette (Eocène inférieur, Provence). Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie, 10: 273-288.

GRANGER, W. 1908. A revision of the American Eocene horses. Bulletin of the American Museum of Natural History, 24:221-264.

———. 1910. Tertiary faunal horizons in the Wind River Basin, Wyoming, with descriptions of new Eocene mammals. Bulletin of the American Museum of Natural History, 28: 235-251.

———. 1914. On the names of lower Eocene faunal horizons of Wyoming and New Mexico. Bulletin of the American Museum of Natural History, 33: 201-207.

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

HOOKER, J. J. 1984. A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe. Zoological Journal of the Linnean Society, 82: 229-244.

HUSSAIN, S. T. 1975. Evolutionary and functional anatomy of the pelvic limb in fossil and Recent Equidae (Perissodactyla, Mammalia). Anatomy, Histology, and Embryology, Berlin, 4: 179-222.

JEPSEN, G. L. 1930. New vertebrate fossils from the lower Eocene of the Bighorn Basin, Wyoming. Proceedings of the American Philosophical Society, 69: 117-131.

———. 1963. Eocene vertebrates, coprolites, and plants in the Golden Valley Formation of western North Dakota. Geological Society of America Bulletin, 74: 673-684.

——— and M. O. WOODBURNE. 1969. Paleocene hyracothere from Polecat Bench Formation, Wyoming. Science, 164: 543-547.

KITTS, D. B. 1956. American *Hyracotherium* (Perissodactyla, Equidae). Bulletin of the American Museum of Natural History, 110: 1-60.

KRISHTALKA, L., R. M. WEST, C. C. BLACK, M. R. DAWSON, J. J. FLYNN, W. D. TURNBULL, R. K. STUCKY, M. C. McKENNA, T. M. BOWN, D. J. GOLZ, and J. A. LILLEGRAVEN. 1987. Eocene (Wasatchian through Duchesnean) biochronology of North America. In M. O. Woodburne (ed.), Cenozoic Mammals of North America, Geochronology and Biostratigraphy. University of California Press, Berkeley, 77-117.

LEGENDRE, S. 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie, 16: 1-110.

LUCAS, S. G., R. M. SCHOCH, E. MANNING, and C. TSENTAS. 1981. The Eocene biostratigraphy of New Mexico. Geological Society of America Bulletin, 92: 2268-2307.

MARSH, O. C. 1876. Notice of new Tertiary mammals. V. American Journal of Science, Series 3, 12: 401-404.

———. 1892. Recent polydactyle horses. American Journal of Science, 43: 339-355.

MacFADDEN, B. J. 1976. Cladistic analysis of primitive equids, with notes on other perissodactyls. Systematic Zoology, 25: 1-14.

McKENNA, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. University of California Publications in Geological Sciences, 37:1-130.

MORRIS, W. J. 1968. A new early tertiary perissodactyl, *Hyracotherium seekinsi*, from Baja California. Los Angeles County Museum Contributions in Science, 151: 1-11.

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

———. 1842. Description of some molar teeth from the Eocene sand at Kyson in Suffolk, indicative of a new species of *Hyracotherium* (*Hyr. cuniculus*). Annals and Magazine of Natural History, London, 8: 1-2.

———. 1858. Description of a small lophiodont mammal (*Pliolophus vulpiceps*, Owen), from the London Clay, near Harwich. Quarterly Journal of the Geological Society, 14: 54-71.

PROTHERO, D. R., and R. M. SCHOCH (eds.). 1989. The Evolution of Perissodactyls. Oxford Monographs on Geology and Geophysics 15. Oxford University Press, New York, 537 pp.

RADINSKY, L. 1963. Origin and early evolution of North American Tapiroidea. Peabody Museum of Natural History, Yale University, Bulletin 17: 1-106.

———. 1964. *Paleomoropus*, a new early Eocene chalicothere (Mammalia, Perissodactyla), and a revision of Eocene chalicotheres. American Museum Novitates, 2179: 1-28.

———. 1969. The early evolution of the Perissodactyla. Evolution, 23: 308-328.

———. 1976. Oldest horse brains: more advanced than previously realized. Science, 194: 626-627.

ROSE, K. D. 1990. Postcranial skeletal remains and adaptations in early Eocene mammals from the Willwood Formation, Bighorn Basin, Wyoming. Geological Society of America Special Paper, 243: 107-133.

SAVAGE, D. E., D. E. RUSSELL, and P. LOUIS. 1965. European Eocene Equidae (Perissodactyla). University of California Publications in Geological Sciences, 56: 1-94.

———. 1966. Ceratomorpha and Ancyclopoda (Perissodactyla) from the lower Eocene, Paris Basin, France. University of California Publications in Geological Sciences, 66: 1-38.

SCHANKLER, D. M. 1980. Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming. University of Michigan Papers on Paleontology, 24: 99-114.

SINCLAIR, W. J., and W. GRANGER. 1911. Eocene and Oligocene of the Wind River and Bighorn basins. Bulletin of the American Museum of Natural History, 30: 83-117.

———. 1912. Notes on the Tertiary deposits of the Bighorn Basin. Bulletin of the American Museum of Natural History, 31: 57-67.

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

WORTMAN, J. L. 1896. Species of *Hyracotherium* and allied perissodactyls from the Wahsatch and Wind River beds of North America. Bulletin of the American Museum of Natural History, 8: 81-110.