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NEW SPECIES OF *APHELISCUS*, *HAPLOMYLUS*, AND *HYOPSODUS* (MAMMALIA, CONDYLARTHRA) FROM THE LATE PALEOCENE OF SOUTHERN MONTANA AND EARLY EOCENE OF NORTHWESTERN WYOMING

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PHILIP D. GINGERICH

Abstract—The most common early Wasatchian *Apheliscus* in the Clarks Fork Basin of northwestern Wyoming is a new species, *A. chydaeus*, that is larger than contemporary *A. wapitiensis* (Van Valen) and smaller than both earlier Clarkforkian *A. nitidus* Simpson and later Wasatchian *A. insidiosus* (Cope). *Haplomylus* is now represented by large samples at many levels. These show a repeated pattern of size increase with small early Clarkforkian *H. palustris*, new species, giving rise to larger middle and late Clarkforkian *H. simpsoni* Rose, and then small early Wasatchian *H. speirianus* Cope giving rise to larger middle Wasatchian *H. scottianus*, new species. *Hyopsodus pauxillus*, new species, is a rare *Haplomylus*-sized middle Wasatchian species that is unusually small for North American *Hyopsodus*.

INTRODUCTION

The evolutionary history of mammalian lineages is often difficult to trace without a detailed stratigraphic record. This is a special problem whenever closely similar (and probably closely related) species are involved. Clarification of such examples is important for understanding the continuity and complexity of evolutionary history, and clarification is important for biostratigraphy because distinctive short-lived species are useful for local and broader correlation. Closely similar species, if they differ enough to recognize them at all, usually differ quantitatively in continuous size or shape variables, or they differ quantitatively in the proportional representation of discretely coded characteristics. This is the nature of species-level evolution.

One of the most readily-studied quantitative characteristics of mammals is their overall body size, which can be represented by tooth size. Tooth size and body size are highly correlated in mammals and one is generally a good proxy for the other. Tooth size can be measured in many different ways, and study of large samples requires simplification. One of the most useful simplifications when large samples of mammalian teeth are studied is concentration on central cheek teeth (here M^1 and M_1). These are usually available in greatest numbers, and they are usually less variable than other cheek teeth (Gingerich, 1974b). Other teeth can be measured as well, but much of the size information they provide is likely to be redundant.

The Clarks Fork Basin of northwestern Wyoming is a Laramide intermontane depositional basin that preserves an unusually complete and well exposed stratigraphic record of Tiffanian (late Paleocene), Clarkforkian (latest Paleocene), and Wasatchian (early Eocene) mammals spanning the Paleocene-Eocene boundary (Gingerich, 1989). As a result of nearly 20 years of intensive collecting, fossil remains of three problematic small condylarths, *Apheliscus*, *Haplomylus*, and *Hyopsodus*, are now known in sufficient abundance to indicate the main features of their evolution in this area. One new species of *Apheliscus*, two new species of *Haplomylus*, and one new species of *Hyopsodus* are described in this report.

INSTITUTIONAL ABBREVIATIONS

ACM	— Amherst College Museum, Amherst, Massachusetts
AMNH	— American Museum of Natural History, New York, New York
CM	— Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
UM	— University of Michigan Museum of Paleontology, Ann Arbor, Michigan
YPM	— Yale Peabody Museum, Yale University, New Haven, Connecticut
YPM-PU	— Princeton University collection at Yale Peabody Museum, New Haven, Connecticut

SYSTEMATIC PALEONTOLOGY

Order CONDYLARTHRA
Family HYOPSODONTIDAE
Subfamily APHELISCINAE

Apheliscus Cope, 1875

Apheliscus chydaeus, new species
Fig. 1

Apheliscus insidiosus? (in part), Matthew, 1918, p. 596, fig. 24 (dentary only).
Apheliscus nitidus (in part), McKenna, 1960, p. 110, fig. 60.
Apheliscus cf. *insidiosus*, Bown, 1979, p. 103, figs. 57d, 58a-d.
Apheliscus sp., Rose, 1981, p. 84, table 26.

Holotype.— UM 66875, right dentary with P_4-M_2.

Type locality.— UM locality SC-125, NE¼, Section 24, T55N, R102W (UTM zone 12T, 651250E, 4965050N; Clark quadrangle), Park County, Wyoming.

Age and distribution.— The holotype comes from the 1535 m level, early Wasatchian zone Wa-1 (Sandcouleean), in the Clarks Fork Basin, Wyoming. This species is widely distributed in early Wasatchian (early Eocene) strata of the Bighorn and Clarks Fork basins, Wyoming, and its total geographic range, if known, would probably be much larger.

Diagnosis.— Differs from earlier *A. nitidus* in being 12-25% smaller in linear dimensions and in having weaker postcingula and smaller hypocones on M^{1-2} (Rose, 1981, p. 84). Differs from contemporary *A. wapitiensis* in being 17-29% larger. Differs from later *A. insidiosus* in being 12-25% smaller. Size differences are documented in Table 1.

Etymology.— *chydaios* Gr., common, abundant, in reference to the relative abundance of this species in comparison to smaller contemporary *A. wapitiensis*.

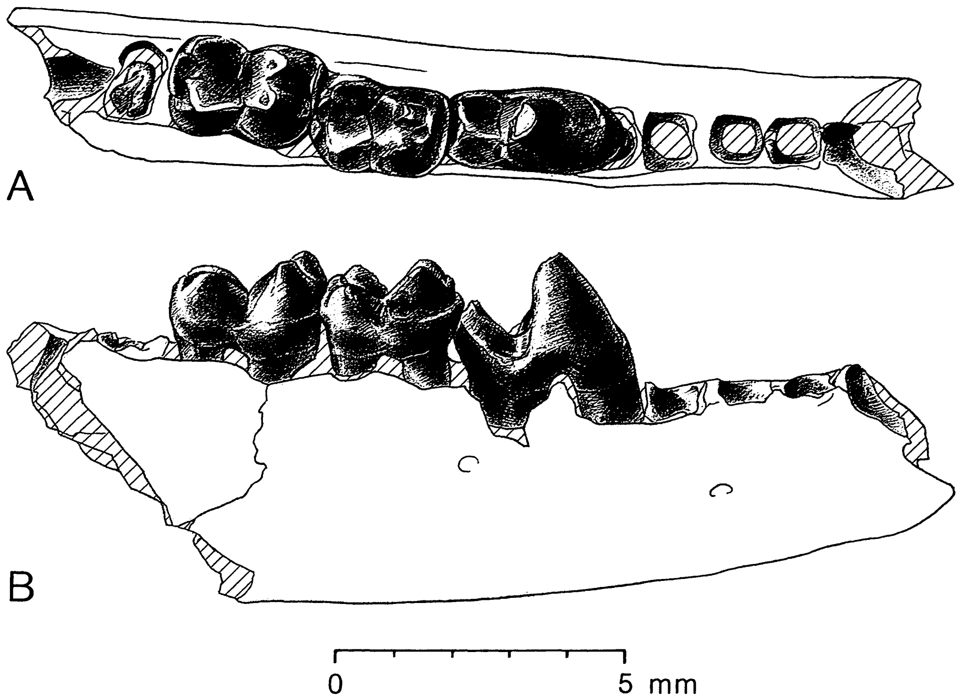

FIG. 1—Type specimen of early Wasatchian *Apheliscus chydaeus*, UM 66875, right dentary with P_4-M_2 from Clarks Fork Basin, Wyoming. A, occlusal view. B, lateral view. There is a mental foramen on the lateral surface of the dentary beneath alveoli for P_3, but the depression beneath the posterior root of P_4 is evidently a bite mark. Position of type relative to other Clarkforkian and Wasatchian *Apheliscus* is shown in Figure 2.

Hypodigm.— **SC-1**: UM 81973. **SC-2**: UM 64548, 68299, 71263, 76330, 76334, 76345, 80033, 82349, 85890, 90997. **SC-4**: UM 66492, 72871, 80832, 98235. **SC-6**: UM 79400, 85579. **SC-12**: UM 64800. **SC-17**: UM 73747. **SC-26**: UM 80772. **SC-31**: UM 65267, 85556, 85626. **SC-33**: UM 78978. **SC-44**: UM 65441. **SC-46**: UM 66419, 66420, 86300, 98020, 98024, 99026. **SC-47**: UM 66379, 66383, 86501. **SC-54**: UM 65589, 80064, 80089. **SC-64**: UM 65744, 72806. **SC-124**: UM 87533. **SC-125**: UM 66875 (holotype). **SC-133**: UM 68097, 68118, 75074, 79689, 82700, 82701, 82722, 86347. **SC-161**: UM 68195, 68654, 75166, 79023, 79134, 80697, 82316, 82479, 98354. **SC-192**: UM 69618, 85696. **SC-207**: UM 69477, 80002. **SC-210**: UM 72225, 72238, 72256. **SC-211**: UM 73859, 82341. **SC-213**: UM 69849, 79571, 79582, 84691, 85475. **SC-221**: UM 85813. **SC-232**: UM 71719. **SC-304**: UM 75748. **SC-305**: UM 76099. **SC-310**: UM 84704, 84736, 85609. **SC-311**: UM 76629. **SC-316**: UM 80177. **SC-317**: UM 77341. **SC-319**: UM 77402. **SC-326**: UM 85545.

Description.— *Apheliscus chydaeus* is a typical *Apheliscus* in terms of its known dental morphology. The most complete specimen of *Apheliscus* known to date is AMNH 15696, a partial skull with lower jaws and fragmentary postcranials of late Graybullian *A. insidiosus* described by Matthew (1918, p. 592) and Gazin (1959). *A. chydaeus* has the same enlarged and distinctively specialized P^4 in the maxilla occluding with an enlarged pointed P_4 in the dentary. The type specimen shown in Figure 1 has the relatively long, narrow lower cheek teeth characteristic of the genus. P_4 has a single high, sharply pointed trigonid cusp, and a narrow, basined talonid. Molars are quadrate in outline, with massive protoconid and meta-

TABLE 1— Statistical summary of central cheek tooth measurements for Clarkforkian and Wasatchian species of *Apheliscus*. *A. chydaeus* is compared to other species in right hand columns. Tooth measurements in mm.

Measurement	Species N	Species range	Species mean	Within-sample std. dev.	*A. chydaeus* differs by: SD units	%
A. insidiosus (middle Wasatchian levels 2050 - 2240 m)						
M^1 length	5	2.2 - 2.5	2.40	0.11*	−1.91	−8.8
M^1 width	5	2.6 - 2.8	2.68	0.11*	−2.00	−8.2
M_1 length	8	2.2 - 2.7	2.40	0.11*	−1.27	−5.8
M_1 width	8	1.6 - 2.0	1.81	0.11*	−1.55	−9.4
A. wapitiensis (early Wasatchian levels 1750 - 1760 m)						
M^1 length	1	1.7	1.70	0.11*	+4.45	+28.8
M^1 width	1	2.1	2.10	0.11*	+3.27	+17.1
M_1 length	3	1.9 - 2.0	1.93	0.11*	+3.00	+17.1
M_1 width	3	1.3 - 1.4	1.33	0.11*	+2.82	+23.3
A. chydaeus (early to middle Wasatchian levels 1530 - 1970 m)						
M^1 length	9	2.1 - 2.4	2.19	0.11*	--	--
M^1 width	9	2.3 - 2.8	2.46	0.11*	--	--
M_1 length	34	2.1 - 2.5	2.26	0.11*	--	--
M_1 width	34	1.5 - 1.9	1.64	0.11*	--	--
A. nitidus (early to late Clarkforkian levels 1015 - 1515)						
M^1 length	5	2.6 - 3.1	2.90	0.11*	−6.45	−24.5
M^1 width	5	2.8 - 3.4	3.12	0.11*	−6.00	−21.2
M_1 length	5	2.4 - 2.7	2.58	0.11*	−2.91	−12.4
M_1 width	4	1.9 - 2.0	1.95	0.11*	−2.82	−15.9

*Sample standard deviations [SD] are weighted values for samples within species as calculated in Fig. 2.

conid cusps. There is a distinct paraconid on M_1 but none on M_2. The talonid is narrow and rectangular on both molars, and both have a distinct hypoconulid between the hypoconid and entoconid at the posterior margin of the crown. There is a mental foramen beneath alveoli for P_3 on the type, and a depression, evidently a bite mark, beneath and just behind the posterior root of P_4.

Measurements (mm) of teeth in the type specimen, UM 66875, are as follows: $P_4 = 2.87 \times 1.43$; $M_1 = 2.29 \times 1.63$; $M_2 = 2.43 \times 1.84$. The mandibular ramus measures 4.5 mm in depth beneath M_1.

Discussion.— Matthew (1918, p. 596) illustrated a dentary of *Apheliscus chydaeus*, AMNH 16925, from a Sandcouleean interval in the Clarks Fork Basin, describing this as a possible "primitive mutant" of *A. insidiosus*. McKenna (1960) described several specimens of *Apheliscus* from the Four Mile faunas of northern Colorado. He stated that their size is as in the type of Clarkforkian *A. nitidus*, but gave few comparative measurements. Some or all of these Four Mile specimens may represent *A. chydaeus*. Specimens described by Bown (1979) are probably all *A. chydaeus*, and some described by Delson (1971) may be.

The stratigraphic distribution of Clarkforkian and early Wasatchian *Apheliscus* shown in Figure 2 illustrates the complexity of evolution of this genus as it is now known. The most important conclusion to be derived from Figure 2 is that *A. wapitiensis* and *A. chydaeus* coexisted during part of early Wasatchian time. The evolution of *Apheliscus*, while possibly dominated by a single lineage leading from *A. nitidus* to *A. chydaeus* and then *A. insidiosus*, involved at least one additional lineage.

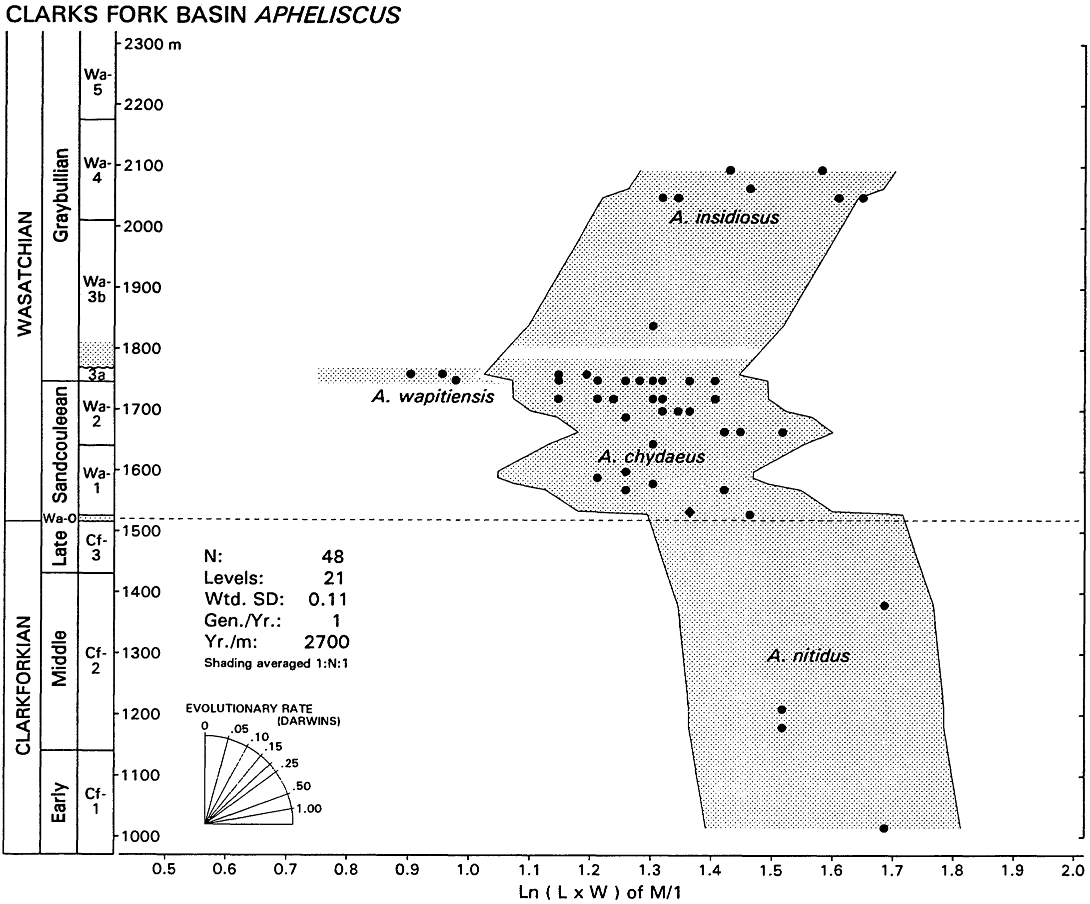

FIG. 2—Stratophenetic plot of Clarkforkian and early Wasatchian *Apheliscus* from the Clarks Fork Basin of northwestern Wyoming. Abscissa is tooth size (and by inference body size), and ordinate is meter level in measured stratigraphic section. Type specimen of *A. chydaeus* is shown by solid diamond.

There are many conflicting ideas about the systematic position of *Apheliscus* among early Cenozoic mammals (see, e.g., Gazin, 1959; Bown, 1979). Placement in Hyopsodontidae is conservative, following McKenna (1960) and Rose (1981), but evidence comes almost exclusively from teeth. Better knowledge of the skull or postcranial skeleton might eventually suggest closer relationship to a different order of mammals.

Subfamily HYOPSODONTINAE

Haplomylus Matthew, 1915

Haplomylus palustris, new species
Fig. 3A,F

Haplaletes-like form, Van Valen, 1967, p. 249.
Haplomylus simpsoni (in part), Rose, 1989, p. 78.
Haplomylus cf. *simpsoni*, Rose, 1989, p. 128.

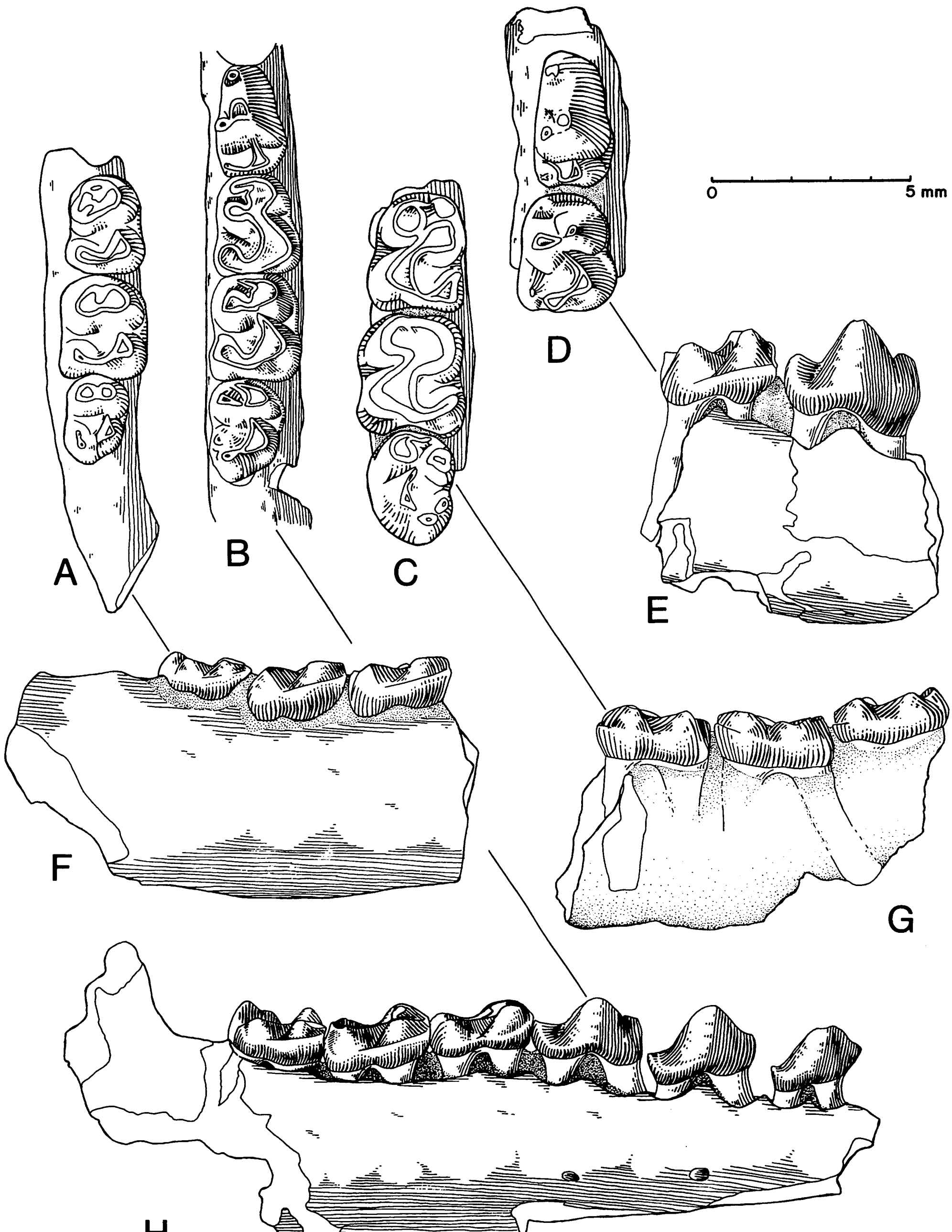

FIG. 3—Clarkforkian and Wasatchian *Haplomylus* from southern Montana and northwestern Wyoming. A, type specimen of early Clarkforkian *H. palustris*, YPM-PU 18347, right dentary with $M_{1\text{-}3}$ from Bear Creek, Montana, in occlusal view (F is lateral view). B, well preserved specimen of *H. speirianus* shown for comparison, YPM 31285 from Yale locality Y-363 in central Bighorn Basin, occlusal view ($P_{2\text{-}3}$ present in specimen are not drawn in B, H is lateral view). C, referred specimen of middle Wasatchian *H. scottianus*, UM 63123 from Yale-Michigan locality YM-419 in central Bighorn Basin, in occlusal view (G is lateral view). D, referred specimen of *H. simpsoni*, AMNH 16074 from Clarks Fork Basin, in occlusal view (E is lateral view).

TABLE 2— Statistical summary of central cheek tooth measurements for Clarkforkian and Wasatchian species of *Haplomylus*. *H scottianus* is compared to other species in right hand columns. Tooth measurements in mm.

Measurement	Species N	Species range	Species mean	Within-sample std. dev.	*H. scottianus* differs by: SD units	%
H. scottianus (middle Wasatchian levels 1815 - 2095 m)						
M^1 length	63	2.5 - 3.3	2.92	0.08*	–	–
M^1 width	63	3.0 - 3.9	3.54	0.08*	–	–
M_1 length	175	2.4 - 3.2	2.77	0.08*	–	–
M_1 width	175	2.0 - 2.6	2.30	0.08*	–	–
H. speirianus (early Wasatchian levels 1525 - 1760 m)						
M^1 length	173	2.2 - 3.1	2.67	0.08*	+3.13	+9.4
M^1 width	173	2.9 - 4.2	3.34	0.08*	+2.50	+6.0
M_1 length	487	2.2 - 2.9	2.56	0.08*	+2.63	+8.2
M_1 width	487	1.7 - 2.5	2.11	0.08*	+2.38	+9.0
H. simpsoni (middle to late Clarkforkian levels 1200 - 1515 m)						
M^1 length	1	2.9	2.90	0.08*	+0.25	+0.7
M^1 width	1	3.3	3.30	0.08*	+3.00	+18.0
M_1 length	18	2.6 - 3.2	2.89	0.08*	−1.50	−4.2
M_1 width	18	2.1 - 2.7	2.42	0.08*	−1.50	−5.0
H. palustris (early Clarkforkian Bear Creek locality)						
M^1 length	0	–	–	–	–	–
M^1 width	0	–	–	–	–	–
M_1 length	1	2.38	2.38	0.08*	+4.88	+16.4
M_1 width	1	2.03	2.03	0.08*	+3.38	+13.3

*Sample standard deviations [SD] are weighted values for samples within species as calculated in Fig. 5

Holotype.— YPM-PU 18347, right dentary with M_{1-3}.

Type locality.— Carbonaceous clay above Coal #3 in the Eagle Mine, Bear Creek, Carbon County, Montana.

Age and distribution.— *Haplomylus palustris* is known primarily from early Clarkforkian zone Cf-1 at Bear Creek in the northern Clarks Fork Basin of south central Montana. One specimen from the 1090 m level at SC-173, early Clarkforkian zone Cf-1, in the Clarks Fork Basin extends the geographic range to northwestern Wyoming.

Diagnosis.— Differs from all later *Haplomylus* in having paraconid and metaconid cusps on P_4 conspicuously less developed. Differs from later Clarkforkian *H. simpsoni* in being 16-17% smaller in linear dimensions. Similar in size to earliest Wasatchian *H. speirianus*, but differs in being 4-7% smaller than average for the species. Differs from middle Wasatchian *H. scottianus* in being 12-14% smaller. Size differences are calculated from means in Table 2.

Etymology.— *palustris* Gr., marshy, swampy, in reference to the environment this species probably inhabited, as evidenced from discovery at the top of a lignitic coal seam.

Hypodigm.— YPM-PU 18347 (holotype), and AMNH 22172, isolated left P_4 from Bear Creek (this is Van Valen's *Haplaletes*-like form). UM 68434 from early Clarkforkian SC-173, cited by Rose (1981, p. 79), includes a probable partial upper M^2 of this species. Rose (1981, p. 128) listed AMNH 22227I, part of AMNH 22218, and CM 11663 (not seen) as small *Haplomylus* from Bear Creek, and these probably belong to *H. palustris* as well.

Description.— This species is still poorly known. P_4 in AMNH 22172 (not illustrated) has the proportions typical of P_4 in *Haplomylus*, with the crown being much longer than it is wide, a high central protoconid, and a narrow basined talonid. There is a small cusp at the anterior edge of P_4 that represents the paraconid, and a swelling medial to the protoconid that represents the metaconid, but neither of these, especially the metaconid, is as well developed as the accessory talonid cusps in later *Haplomylus*. The talonid has a small hypoconid and entoconid, but no hypoconulid.

$M_{1\text{-}3}$ are present in the type specimen. These are small, but otherwise seemingly identical to lower molars in later *Haplomylus*. All have swollen crowns and bulbous cusps, and all are worn like typical *Haplomylus*. M_1 appears to retain a distinct paraconid, but this cusp is lost on M_2 and M_3 as it is in later *Haplomylus*.

Measurements (mm) of teeth in the type specimen, YPM-PU 18347, are as follows: $M_1 = 2.38 \times 2.03$; $M_2 = 2.42 \times 2.27$; $M_3 = 2.37 \times 1.59$; the mandibular ramus measures 4.4 mm in depth beneath M_1. P_4 in the referred specimen, AMNH 22172, measures 2.87×1.53.

Discussion.— E. Delson appears to have been the first to recognize that PU 18347 (now YPM-PU 18347) is a specimen of *Haplomylus*, as indicated by his annotation on the Princeton specimen label. Van Valen (1967) called AMNH 22172 "*Haplaletes*-like" because, probably, it lacks the well developed paraconid and metaconid of later *Haplomylus*. At the time, there was considerable confusion about the existence of a distinctive Clarkforkian land-mammal fauna and age (Wood, 1967), and comparison of Bear Creek specimens with Wasatchian *Haplomylus* may have seemed inappropriate. Now that the two specimens have been compared with each other, the Clarkforkian problem has been solved (Rose, 1981), and comparison has been made with later *Haplomylus*, both specimens appear to represent the same small species of early Clarkforkian *Haplomylus*.

Haplomylus scottianus, new species
Figs. 3C,G, 4

Haplomylus speirianus (all or part), Matthew, 1915, p. 313. Denison, 1937, p. 12. Simpson, 1937, p. 22. Gazin, 1962, p. 61. Bown et al., 1994, p. 55.
Haplomylus sp. B, Gingerich, 1976, p. 15.

Holotype.— UM 92489, left dentary with P_4-M_3.

Type locality.— UM locality MP-122, NE¼, Section 19, T53N, R98W (UTM zone 12T, 682800E, 4936800N; Gilmore Hill quadrangle), Park County, Wyoming.

Age and distribution.— The holotype comes from the 855 m level in the UM McCullough Peaks section, middle Wasatchian zone Wa-5 (earliest late Graybullian), in the northern Bighorn Basin, Wyoming. This species is widely distributed in middle Wasatchian (early Eocene) strata of the Bighorn and Clarks Fork basins, Wyoming, and its total geographic range, if known, would probably be much larger.

Diagnosis.— Differs from early Clarkforkian *H. palustris* in being 13-16% larger in linear dimensions and in having a more distinct paraconid and metaconid on P_4. Similar in size to middle and late Clarkforkian *H. simpsoni* but differs in having lower-crowned lower cheek teeth, which makes them appear more massive, and in having a relatively shorter M_3. Differs from early Wasatchian *H. speirianus* principally in being 6-9% larger on average (this corresponds to a size difference of 2-3 standard deviations). Size differences are documented in Table 2.

Etymology.— Named for William Berryman Scott, in memory of the hot June day in 1876 when Scott sat on a Princeton canal bank with Francis Speir and Henry Fairfield Osborn and proposed that they organize a paleontological expedition to the American West. Cope (1880)

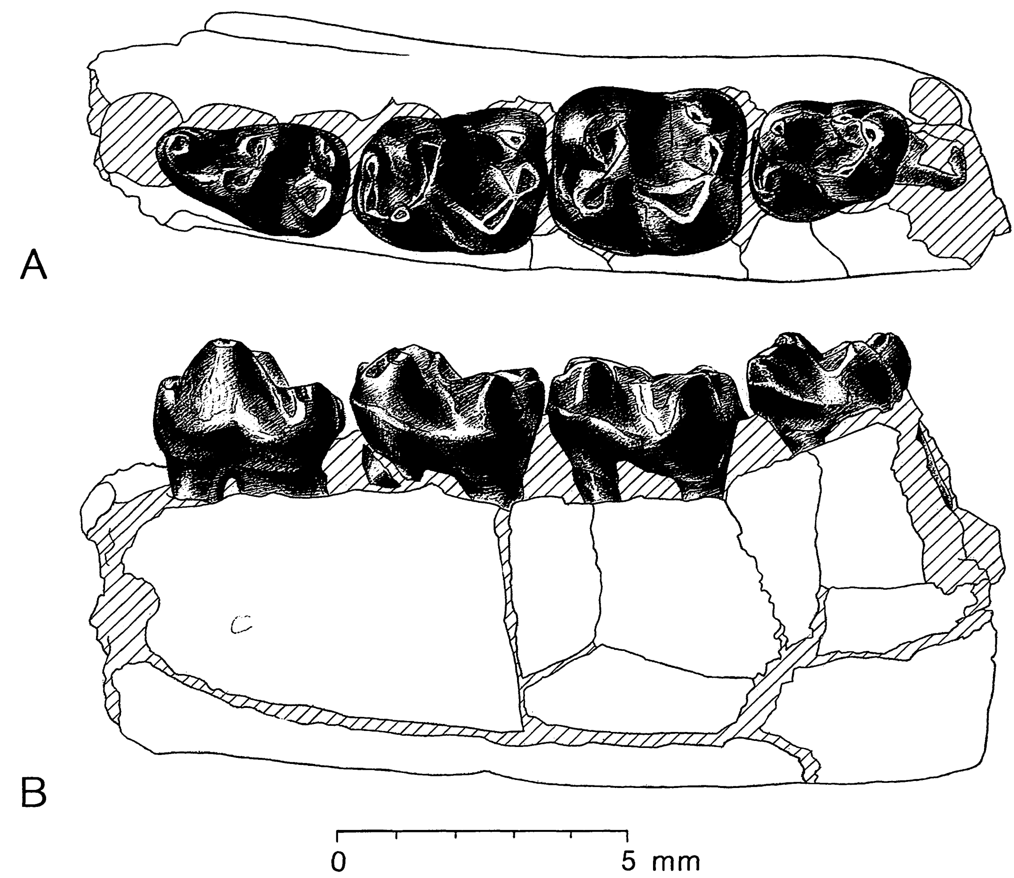

FIG. 4—Type specimen of middle Wasatchian *Haplomylus scottianus*, UM 92489, left dentary with P_4-M_3 from Clarks Fork Basin, Wyoming. A, occlusal view. B, lateral view. Position of type relative to other Clarkforkian and Wasatchian *Apheliscus* is shown in Figure 5.

named "*Hyopsodus*" [*Haplomylus*] *speirianus* for Speir, and it seems appropriate to name this species for Scott.

Hypodigm.— **MP-122** (type sample): UM 92430, 92433, 92436, 92438, 92439, 92441, 92446, 92448, 92453, 92459, 92466, 92468, 92469, 92471, 92472, 92473, 92475, 92478, 92481, 92482, 92484, 92488, 92489 (holotype), 92494, 92495, 92497, 92522, 92526, 92529, 92533, 92535, 92537, 92538, 92543, 92544, 92548, 92549, 92550, 92551, 92557, 92563, 92564, 92565, 92567, 92569, 92571, 92604, 92605, 92606, 92607, 92608, 92609, 92629, 92630, 92631, 92637, 92638. **MP-130**: UM 97302, 97303, 97305, 97317. **MP-143**: UM 93393, 93394. **MP-145**: UM 93490, 93504. **MP-148**: UM 93593. **MP-149**: UM 93630, 93646, 93648, 93649. **MP-157**: UM 93846, 93847, 93861. **MP-163**: UM 94011. **MP-167**: UM 94130. **MP-184**: UM 94623. **MP-210**: UM 95291. **MP-211**: UM 95815, 95837. **MP-226**: UM 96162. **SC-32**: UM 65293, 82957, 82964. **SC-33**: UM 71201, 73801, 73803, 82973. **SC-34**: UM 73894, 73897, 73899, 73912, 73917, 73920, 73921, 73922, 73923, 73930, 75004, 75008, 76769, 76770, 78991, 78992, 78994. **SC-35**: UM 65315, 73943, 73945, 73948. **SC-36**: UM 71692, 71728, 81876, 83042. **SC-63**: UM 73024. **SC-64**: UM 65732, 65743, 66649, 66653, 66665, 66669, 66674, 66675, 66776, 72805, 72813, 72814, 72817, 72820, 72828, 72830, 72838, 72839, 72840, 72841, 72920, 72924, 72926, 72930, 72934, 72935, 72945, 72949, 72953, 79420, 79423, 79425, 79434, 83148, 83153, 87615. **SC-111**: UM 66777, 66781, 66782, 66783, 66786, 72958, 72965, 79903, 87620, 87624. **SC-112**: UM 66803, 66812, 72989, 72995, 79908, 79910, 79915, 79922, 79925, 79931, 79933. **SC-113**: UM 66826, 73010, 73011, 79940, 79948, 79956, 79957, 79969, 79970, 79972, 79974, 79980. **SC-114**: UM 73027. **SC-145**: UM 67291, 69701, 69702. **SC-147**: UM 67135, 67311. **SC-148**: UM 67327, 67331, 67331, 67344, 67348, 69718, 87606, 87607. **SC-192**: UM 85695, 85699, 85702, 85705, 85714, 85715, 85722, 85726, 85728, 85739, 85741, 85751, 85753, 85755, 85757, 85758, 85764, 85765, 85766, 85767, 85768, 85769, 85770, 85771, 85780, 85781. **SC-224**: UM 71210, 71213, 71231, 78957. **SC-225**: UM 71225, 71227, 78962, 78964, 78966, 83542, 83547, 83552. **SC-232**: UM 71720, 81858. **SC-236**: UM 71592, 79014. **SC-237**: UM 71597, 76801, 83057, 83058, 83059. **SC-253**: UM 73032, 73035, 76431. **SC-255**: UM 73083, 73096, 73097, 73098, 73106, 73112, 73113, 73114, 73120, 73121, 73136, 73144, 73148, 73149, 73152, 73153, 73154, 73162, 73164, 73165, 73166, 73176, 73179, 73180, 73181, 73192, 73193, 73205, 73219, 73222, 73223, 73228, 73230, 73242, 73245, 73246, 73253, 73256, 73262, 73293, 73301, 73302, 73303, 73306, 73307, 73311, 73315, 75680, 75689, 75694, 75696, 75698, 75699, 77240, 77439, 77440, 80107, 80108, 80113, 80123, 80125, 80146, 80154, 80155. **SC-256**: UM 73321, 73535, 73543, 73555. **SC-265**: UM 73475, 73476, 83676, 83678, 83680, 83681, 83695, 83719. **SC-290**: UM 73826, 73827, 73830. **SC-324**: UM 79449, 79450. **SC-325**: UM 79461, 79462, 79468, 79473, 79474, 79477, 79484. **SC-353**: UM 88054, 88067, 88068, 88082. **YM-419**: UM UM 63121, 63122, 63123, 63124.

Description.— *Haplomylus* is abundantly represented by maxillary and mandibular fragments with cheek teeth, but it remains poorly known osteologically. Teeth of *H. scottianus* resemble closely those of Wasatchian *Haplomylus* described by Matthew (1915, p. 313) and Gazin (1962, p. 61). The most complete maxilla from the type locality is UM 92436, a left maxilla with P^4-M^3. This has the partially molarized P^4 and greatly reduced M^3 characteristic of the genus.

UM 92489 was chosen as the type specimen of *H. scottianus* because it includes intact crowns of P_4-M_3 showing little wear. P_4 has well developed trigonid cusps, with the paraconid and metaconid being large and well separated from the protoconid. The talonid is broad, with a distinct hypoconid and entoconid but no hypoconulid. Lower molars are bulbous. M_1 retains a distinct paraconid, but M_2 and M_3 lack this. All have the protoconid and metaconid well developed on the trigonid, and the hypoconid, hypoconulid, and entoconid well developed on the talonid.

Measurements (mm) of teeth in the type specimen, UM 92489, are as follows: $P_4 = 2.96 \times 1.87$; $M_1 = 2.99 \times 2.46$; $M_2 = 2.85 \times 2.75$; $M_3 = 2.54 \times 1.92$. The mandibular ramus measures 5.1 mm in depth beneath M_1.

Discussion.— The type specimen of the type species of *Haplomylus*, AMNH 4190, the type of *H. speirianus*, was first described by Cope (1880) as part of a small fauna including the types of *Esthonyx bisulcatus* and *Didymictis leptomylus* coming from the Wind River Basin, Wyoming. Cope later indicated that these came from the Bighorn Basin. Matthew (1915, p. 314), after discussion with the collector J. Wortman, confirmed that all three types came from the Bighorn Basin, which Wortman visited briefly in the summer of 1880. All three species are present in Sandcouleean-age beds of the southern Bighorn Basin, and *H. speirianus* is abundant (Bown, 1979, p. 131). This is the first area of badlands Wortman would have encountered entering the Bighorn Basin from the south (Bown et al., 1994, Pl. 2). These observations, as well as the small size of the type of *H. speirianus*, indicate that *H. speirianus* is the Sandcouleean early Wasatchian form of *Haplomylus*.

Simpson (1937, p. 22) anticipated separation of Sandcouleean *Haplomylus speirianus* and Graybullian *H. scottianus*, noting that:

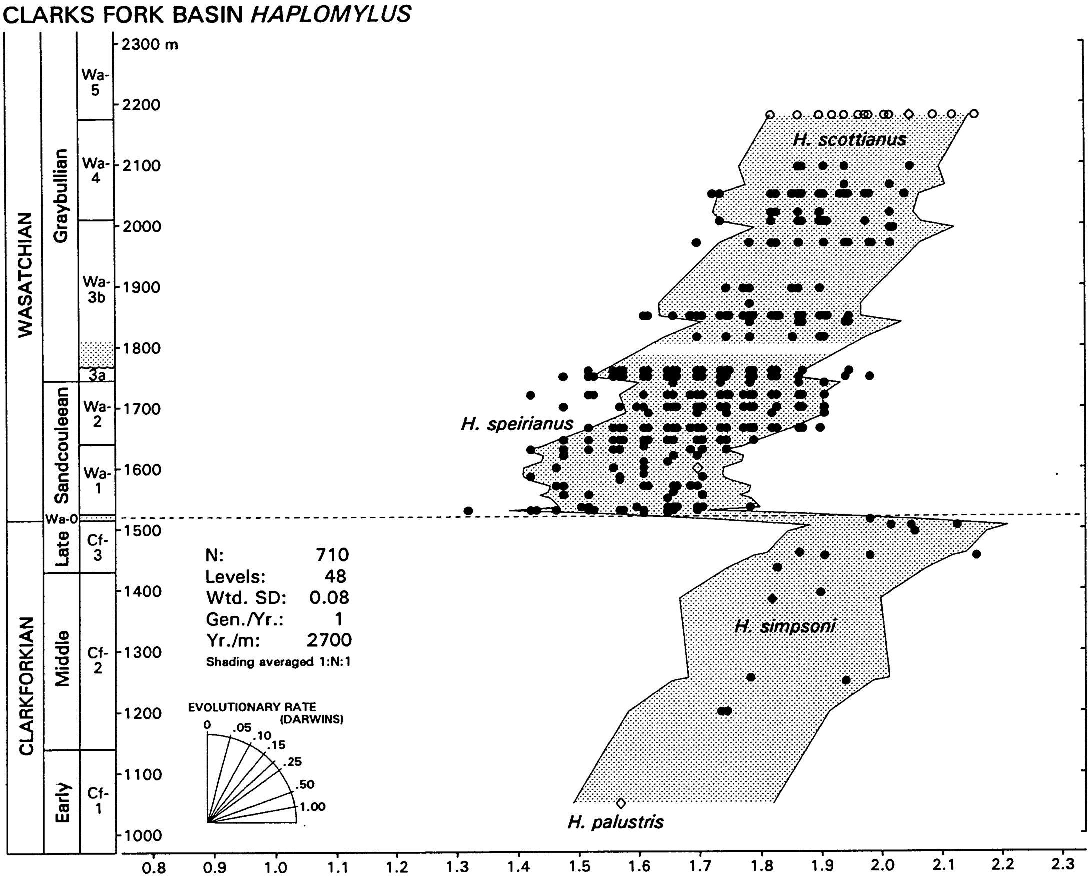

FIG. 5—Stratophenetic plot of Clarkforkian and early Wasatchian *Haplomylus* from the Clarks Fork Basin of northwestern Wyoming. Abscissa is tooth size (and by inference body size), and ordinate is meter level in measured stratigraphic section. Positions of all type specimens are shown by diamonds. Specimens from Bear Creek (type of *H. palustris*), the southern Bighorn Basin (type of *H. speirianus*), and the McCullough Peaks area of the northern Bighorn Basin (type sample of *H. scottianus*) are shown with open symbols.

> The Sand Coulee specimens, although their range overlaps (but is not entirely included in) that of the Gray Bull specimens, average smaller, and the difference in size is decisively significant (the chances that such a difference would be due to random sampling of the same race are considerably less than one in a hundred).

H. scottianus is the distinctly larger Graybullian middle Wasatchian form that intergrades continuously with *H. speirianus*. The boundary between the two species in the Clarks Fork Basin is drawn arbitrarily at the condensed interval separating zones Wa-3a and Wa-3b within the early Graybullian subage of the Wasatchian (see Fig. 5).

The type sample of *Haplomylus scottianus* is important because it is a large homogeneous sample coming from a single thin, dark, organic-rich mudstone exposed over a large area at MP-122. This sample is also important because the locality includes the stratigraphically-important guide fossil *Bunophorus etsagicus* (UM 92457, a right astragalus). The 855 m level marks the highest occurrence of *Haplomylus* and the lowest occurrence of *Bunophorus* in the McCullough Peaks area (cf. Clyde et al., 1994).

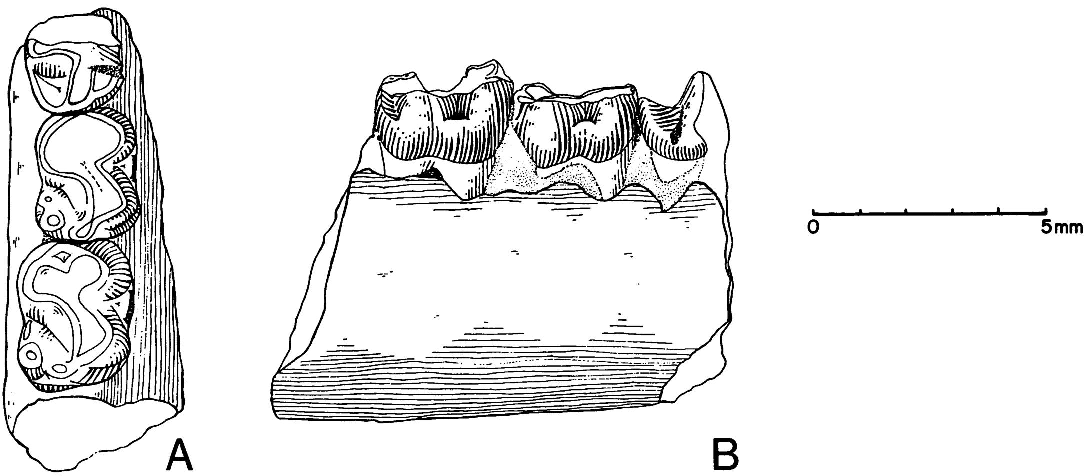

FIG. 6—Type specimen of middle Wasatchian *Hyopsodus pauxillus*, YPM 26344, right dentary with P_4-M_2 from central Bighorn Basin, Wyoming. A, occlusal view. B, lateral view. Position of type relative to other Wasatchian *Hyopsodus* is shown in Figure 7 here and in Figure 4 of Gingerich (1976).

Hyopsodus Leidy, 1870

Hyopsodus pauxillus, new species
Fig. 6

Hyopsodus simplex (in part), Gingerich, 1974a, p. 108; 1976, p. 12.
Hyopsodus new species, Gingerich, 1976, p. 12.

Holotype.— YPM 26344, right dentary with P_4-M_2.

Type locality.— YPM locality 219, in SW¼, NW¼, Section 30, T50N, R95W (UTM zone 12T, 713330E, 4905720N; Wardell Reservoir quadrangle), Big Horn County, Wyoming.

Age and distribution.— *Hyopsodus pauxillus* is known only from the type locality in middle Wasatchian strata of the Bighorn Basin, Wyoming. The locality is at the 860 foot level in the Meyer-Radinsky stratigraphic section of the central Bighorn Basin. According to Bown et al. (1994, p. 93), this locality is at the 397 meter level in their new composite section, which is 32 m above the first appearance of *Bunophorus* marking the beginning of Wasatchian zone Wa-5 (late Graybullian).

Diagnosis.—Smallest Wasatchian species of *Hyopsodus*. Differs from early Wasatchian *H. loomisi* in being 16-21% smaller in linear dimensions. Differs from middle Wasatchian *H. latidens* in being 23-28% smaller. Differs from contemporary middle Wasatchian *H. simplex* in being 18-21% or about 6 standard deviation units smaller. Size differences are documented in Table 3.

Etymology.— *paucus*, *pauxillus* L., few, little; in reference to the small size and rarity of this species.

Hypodigm.— Type specimen only.

Description.— The type specimen is a right dentary with P_4-M_2. The anterior half of P_4 is broken and lost, but the posterior part of the trigonid and short talonid are preserved intact. The talonid of P_4 lacks an entoconid. Shortness of the talonid and absence of an entoconid are characteristic of *Hyopsodus*. Crowns of M_1 and M_2 are well preserved and show the narrow-

TABLE 3— Statistical summary of central cheek tooth measurements for Wasatchian species of *Hyopsodus*. *H. pauxillus* is compared to other species in right hand columns. Tooth measurements in mm.

Measurement	Species N	Species range	Species mean	Within-sample std. dev.	*H. pauxillus* differs by: SD units	%
H. pauxillus (middle Wasatchian)						
M^1 length	–	–	–	–	–	–
M^1 width	–	–	–	–	–	–
M_1 length	1	2.84	2.84	0.10*	–	–
M_1 width	1	2.26	2.26	0.10*	–	–
H. simplex (middle Wasatchian level 2240 m)						
M^1 length	6	3.0 - 3.6	3.28	0.10*	–	–
M^1 width	6	4.1 - 4.7	4.33	0.10*	–	–
M_1 length	9	3.2 - 3.7	3.47	0.10*	−6.3	−18.2
M_1 width	9	2.6 - 3.2	2.86	0.10*	−6.0	−21.0
H. latidens (middle Wasatchian levels 1815 to 2110 m)						
M^1 length	132	3.1 - 4.2	3.59	0.10*	–	–
M^1 width	131	4.1 - 5.4	4.72	0.10*	–	–
M_1 length	308	3.1 - 4.4	3.67	0.10*	−8.3	−22.6
M_1 width	308	2.5 - 4.3	3.14	0.10*	−8.8	−28.0
H. loomisi (early to middle Wasatchian levels 1520 - 1780)						
M^1 length	312	2.7 - 3.9	3.30	0.10*	–	–
M^1 width	312	3.7 - 5.4	4.38	0.10*	–	–
M_1 length	847	2.8 - 4.2	3.37	0.10*	−5.3	−15.7
M_1 width	847	2.3 - 3.6	2.85	0.10*	−5.9	−20.7

*Sample standard deviations [SD] are weighted values for samples within species as calculated in Fig. 7.

ness, slight obliquity, and flat wear typical of *Hyopsodus*. M_1 is too heavily worn for determination of whether this had a distinct paraconid like that of earlier *Hyopsodus* and some *H. simplex*. M_2 is less worn and probably lacked a paraconid. Both M_1 and M_2 have a small tubercle in front of the entoconid mentioned by Loomis (1905) as being characteristic of *H. simplex*.

Measurements (mm) of teeth in the type specimen, YPM 26344, are as follows: P_4 = — × 2.15; M_1 = 2.84 × 2.26; M_2 = 3.00 × 2.52. The mandibular ramus measures 5.3 mm in depth beneath M_1.

Discussion.— Loomis (1905) named a small species of *Hyopsodus*, *H. simplex*, from the Bighorn Basin. The type of *H. simplex* was part of a collection from "upper and lower beds of the Wasatch on Gray Bull River" (Loomis, 1905, p. 420). The type specimen, ACM 2290, lacks a paraconid on M_1 (i.e., has the "simple" metaconid of Loomis, 1905, p. 424). This agrees closely with some specimens of late Graybullian *H. simplex* in the University of Michigan collection (e.g., UM 92572 from MP-122), while others (e.g., UM 92527 from MP-122) have a paraconid on M_1. A distinct paraconid is present on M_1 in most specimens and on M_2 in some specimens of *H. loomisi* (McKenna, 1960; Gingerich, 1989, p. 48), but a paraconid is never more than faintly developed on M_2 in *H. latidens* and most specimens lack it entirely (Denison, 1937; Gingerich, 1989, p. 48). A paraconid is sometimes faintly developed on M_1 of *H. simplex*, but most specimens lack it. These three species, *H. loomisi*, *H. latidens*, and *H. simplex* differ in size as well as paraconid development, with *H. loomisi* and *H. simplex* being smaller and *H. latidens* being larger (Fig. 7).

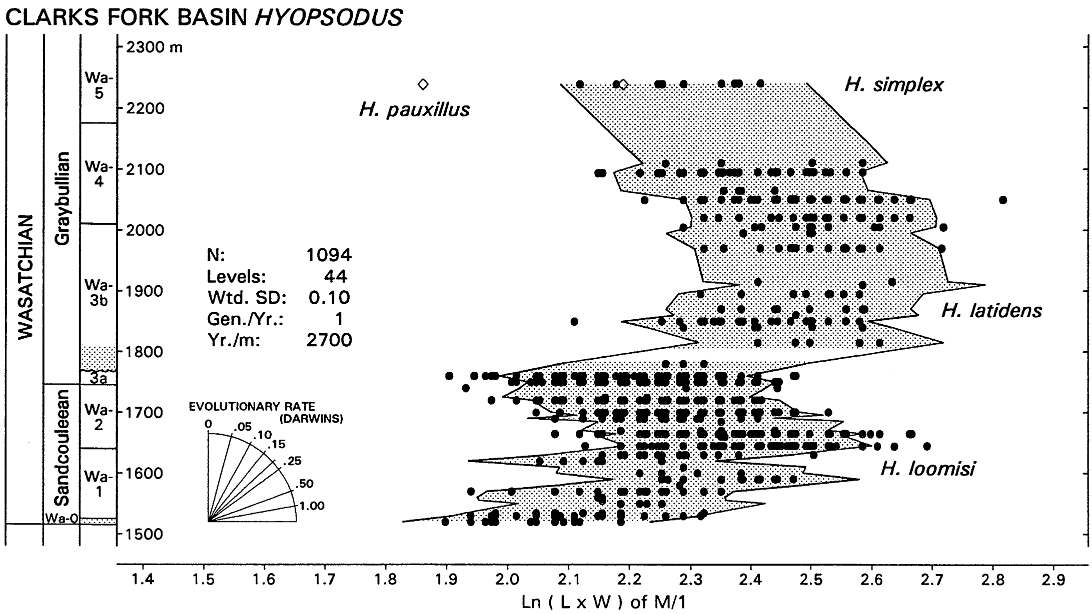

FIG. 7—Stratophenetic plot of Clarkforkian and early Wasatchian *Hyopsodus* from the Clarks Fork Basin of northwestern Wyoming. Abscissa is tooth size (and by inference body size), and ordinate is meter level in measured stratigraphic section. Positions of type specimens are shown by open diamonds where these preserve M_1. Both diamonds are open because type specimens come from the central Bighorn Basin. This figure duplicates pattern in lower part of Figures 4 and 5 in Gingerich (1976) and corrects systematic nomenclature. Sample of *H. simplex* shown here was inadvertently included with *H. latidens* by Gingerich and Gunnell (1994).

I first identified YPM 22344 as *H. simplex* (Gingerich, 1974a), but later recognized that it is new after studying the type specimen of *H. simplex* and finding that it is the size of typical *H. loomisi*, *H. latidens*, or *H. minor* (Gingerich, 1976, p. 12). With much larger samples now available in stratified context, I regard *H. simplex* as a valid species intermediate in time and form between early-to-middle Graybullian *H. loomisi* and Lysitean *H. minor*. The size and stratigraphic position of the type of *H. pauxillus* relative to other early and middle Wasatchian species of *Hyopsodus* is illustrated in Figure 7, which shows that *H. pauxillus* is smaller and clearly distinct from contemporary late Graybullian *H. simplex* (see also Table 3).

COMPLEXITY AND DIRECTIONALITY OF EVOLUTION IN *APHELISCUS*, *HAPLOMYLUS*, AND *HYOPSODUS*

Size change with time is shown in the stratigraphic distributions of *Apheliscus*, *Haplomylus*, and *Hyopsodus* shown in Figures 2, 5, and 7. All three have within-sample variability on the order of 0.10 tooth size units (here calculated as Ln L×W of M_1), which is characteristic of time-homogeneous samples of extinct and extant mammalian species (Gingerich, 1974b). All three stratigraphic distributions show change with time, which sometimes appears to involve substitution of one species for another but could also involve short intervals of high rates of change. This complexity of pattern could not be demonstrated without a detailed stratigraphic record.

Stippling in Figures 2, 5, and 7 illustrates the hypothesis of gradual change that most closely fits the observed stratigraphic and morphological distribution of fossils. Study of evolutionary rates in the *Haplomylus speirianus*-to-*H. scottianus* lineage shows that this lineage has a temporal scaling slope of rates significantly lower than −0.5. This means that tooth size (and, by inference, overall body size) increased nonrandomly and directionally through time in the lineage (Gingerich and Gunnell, 1994). In contrast, study of evolutionary rates in the *Hyopsodus loomisi*-to-*H. latidens* lineage as a whole, and evolution within each species considered individually, shows that each has a temporal scaling slope of rates significantly higher than −0.5. This means that tooth size (and body size) remained stable through time in the lineage as a whole and within each species (Gingerich and Gunnell, 1994). There is a random component of change in all of these examples, but, superimposed on this, *Haplomylus* shows a significantly nonrandom component of directional change and *Hyopsodus* shows a significantly nonrandom component of stasis.

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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. Memoirs of the Geological Survey of Wyoming, 2: 1-151.

———, K. D. ROSE, E. L. SIMONS, and S. L. WING. 1994. Distribution and stratigraphic correlation of upper Paleocene and lower Eocene fossil mammal and plant localities of the Fort Union, Willwood, and Tatman Formations, southern Bighorn Basin, Wyoming. U.S. Geological Survey Professional Paper, 1540: 1-103.

CLYDE, W. C., J. SAMATAKOS, and P. D. GINGERICH. 1994. Chronology of the Wasatchian land-mammal age (early Eocene): magnetostratigraphic results from the McCullough Peaks section, northern Bighorn Basin, Wyoming. Journal of Geology, 102: 367-377.

COPE, E. D. 1880. The northern Wasatch fauna. American Naturalist, 14: 908-909.

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

DENISON, R. H. 1937. Early lower Eocene mammals from the Wind River Basin, Wyoming. Proceedings of the New England Zoological Club, 16: 11-14.

GAZIN, C. L. 1959. Early Tertiary *Apheliscus* and *Phenacodaptes* as pantolestid insectivores. Smithsonian Miscellaneous Collections, 139(7): 1-7.

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

GINGERICH, P. D. 1974a. Stratigraphic record of early Eocene *Hyopsodus* and the geometry of mammalian phylogeny. Nature, London, 248, 107-109.

———. 1974b. Size variability of teeth in living mammals and the diagnosis of closely related sympatric fossil species. Journal of Paleontology, 48: 895-903.

———. 1976. Paleontology and phylogeny: patterns of evolution at the species level in early Tertiary mammals. American Journal of Science, 276: 1-28.

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

——— and G. F. GUNNELL. 1994. Rates of evolution in Paleocene-Eocene mammals of the Clarks Fork Basin, Wyoming, and a comparison with Neogene Siwalik lineages of Pakistan. Palaeogeography, Palaeoclimatology, Palaeoecology, in press.

LOOMIS, F. B. 1905. Hyopsodidae of the Wasatch and Wind River basins. American Journal of Science, Series 4, 19: 416-424.

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.

MATTHEW, W. D. 1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part II.— Order Condylarthra, family Hyopsodontidae. Bulletin of the American Museum of Natural History, 34: 311-328.

——— 1918. A revision of the lower Eocene Wasatch and Wind River faunas. Part V.— Insectivora (continued), Glires, Edentata. Bulletin of the American Museum of Natural History, 38: 565-657.

ROSE, K. D. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. University of Michigan Papers on Paleontology, 26: 1-196.

SIMPSON, G. G. 1937. Notes on the Clark Fork, upper Paleocene, fauna. American Museum Novitates, 954: 1-24.

VAN VALEN, L. 1967. New Paleocene insectivores and insectivore classification. Bulletin of the American Museum of Natural History, 135: 217-284.

WOOD, R. C. 1967. A review of the Clark Fork vertebrate fauna. Breviora, Harvard University Museum of Comparative Zoology, 257: 1-30.