ISSN 0097-4463

ANNALS of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 52 7 DECEMBER 1983 ARTICLE 17

REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 4. THE TILLODONTIA

RICHARD K. STUCKY
Post-doctoral Fellow, Section of Vertebrate Fossils

LEONARD KRISHTALKA
Associate Curator, Section of Vertebrate Fossils

ABSTRACT

Two species of *Esthonyx*—*E. bisulcatus* and *E. acutidens*—are recorded from the Lysite Member, and the Red Creek Facies and Lost Cabin Member, respectively, of the Wind River Formation. *Trogosus,* hitherto unknown from this formation, has been recovered from two localities in the upper part of the Lost Cabin Member. The first occurrence of *Trogosus,* along with that of other typical Bridgerian mammals, marks the Wasatchian-Bridgerian boundary and, in part, defines the Gardnerbuttean (earliest Bridgerian) subage. A reconstruction of the phylogenetic relationships of North American and Asian tillodonts suggests that the North American genera *Esthonyx, Megalesthonyx,* and *Trogosus* may have had independent origins from among Asian tillodonts.

INTRODUCTION

Tillodonts were among the first fossil mammals reported from the Wind River Basin. Of the two species Cope (1880, 1881) named from the Wind River Formation—*Esthonyx acutidens* and *E. spatularius*—the type of the latter appears to have come from the Bighorn Basin (Gazin, 1953). Subsequently, excellent material of *E. acutidens* from the Boysen Reservoir area, Wind River Basin (White, 1952), was studied by Gazin (1953) in his major review of the Tillodontia. He formally recognized *E. bisulcatus* Cope, 1874 and *E. acutidens* from the "Lysite" and "Lost Cabin" beds, respectively, of the Wind River Formation—

Submitted 13 May 1983.

a conclusion corroborated in subsequent reviews (Kelley and Wood, 1954; Guthrie, 1967, 1971)—and suggested that *E. acutidens* may also occur in the Lysite Member. Gingerich and Gunnell (1979), in the last major treatment of tillodont systematics and evolution, did not specify the biostratigraphic occurrences of either species in particular basins. They reported *E. bisulcatus* from Lysitean and Lostcabinian aged horizons, and *E. acutidens* from "Lost Cabin beds and equivalents" (p. 146) and early Bridgerian horizons in western North America. Importantly, *Trogosus* has never been reported from the Wind River Formation.

Since Guthrie's (1967, 1971) work, 20 specimens from the Lysite Member (nine localities), 34 from the Lost Cabin Member (12 localities), and two from the Red Creek Facies (two localities; Stucky, 1983) have been added to the sample of tillodonts from the Wind River Formation. Two of the specimens—from the Lost Cabin Member—represent *Trogosus,* and the remainder, *Esthonyx.* Four of the localities (CM loc. 34; UCM locs. 80101, 81028, 79040), all in the upper part of the Lost Cabin Member, are earliest Bridgerian (=Gardnerbuttean, Robinson, 1966) rather than latest Wasatchian, according to biostratigraphic evidence presented here and elsewhere (Stucky, 1982, 1983; Krishtalka and Stucky, 1983). This conclusion is reflected in the "known occurrence" data in the systematic section below.

Abbreviations in text and tables are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, People's Republic of China; UCM, University of Colorado Museum; Loc., locality.

SYSTEMATICS

Order Tillodontia Marsh, 1875
Family Esthonychidae Cope, 1883

Gazin (1953) and Gingerich and Gunnell (1979) have reviewed the taxonomic history of tillodonts. Five North American genera are generally recognized—*Esthonyx* Cope, 1874; *Trogosus* Leidy, 1871; *Anchippodus* Leidy, 1868; *Tillodon* Gazin, 1953; *Megalesthonyx* Rose, 1972. *Esthonyx* has been reported from the Clarkforkian, Wasatchian, and earliest Bridgerian, *Trogosus* and *Tillodon* only from the Bridgerian, and *Megalesthonyx* from the late Wasatchian. The age of *Anchippodus,* although suggested to be Bridgerian (Gazin, 1953), cannot be determined from present evidence.

One esthonychid, *E. munieri* (Lemoine, 1889) is known from the Sparnacian or Cuisian of the Paris Basin, and four have been reported from the early Tertiary of China. Two of these, *Lofochaius* Chow et al., 1973, and *Meiostylodon* Wang, 1975, are early or middle Paleocene

in age, (Li and Ting, 1983), whereas *Kuanchuanius* Chow, 1963, and *Adapidium* Young, 1937, come from middle and late Eocene horizons, respectively. *Basalina* Dehm and Oettingen-Spielberg, 1958, from the middle Eocene of Pakistan, may be an esthonychid (Gingerich and Gunnell, 1979; Lucas and Schoch, 1981).

Esthonyx Cope, 1874

Gazin (1953) recognized five North American species of *Esthonyx,* which from stratigraphically oldest to youngest are: *E. grangeri* Simpson, 1937; *E. latidens* Simpson, 1937; *E. spatularius* Cope, 1880 (all Clarkforkian and Graybullian, Bighorn Basin); *E. bisulcatus* Cope, 1874 (Graybullian and Lysitean, Bighorn, Wind River, San Juan and Piceance basins); *E. acutidens* Cope, 1881 (?Lysitean and Lostcabinian, Bighorn, Wind River, Washakie and Piceance basins). He also identified *Esthonyx* sp. from the Lostcabinian part of the Huerfano Formation, the Cathedral Bluffs Tongue of the Wasatch Formation and the Lysitean of the Knight (=Wasatch) Formation.

Gingerich and Gunnell (1979) added two new species of *Esthonyx*—*E. xenicus* and *E. ancylion*—from the Clarkforkian of the Bighorn Basin, synonymized *E. latidens* with *E. grangeri,* and redefined the hypodigms of the other North American species. Part of the hypodigm of *E. xenicus* includes specimens previously referred to *E. spatularius* and *E. bisulcatus.* They posited two lineages of *Esthonyx* in Clarkforkian and Wasatchian strata of western North America. Species in the first lineage—*E. xenicus-E. ancylion-E. grangeri*—lack symphysial fusion, retain a double-rooted P_2, have non-overlapping stratigraphic ranges, and increase in size anagenetically. Species composing the second lineage—*E. spatularius-E. bisulcatus-E. acutidens*—have a fused mandibular symphysis, a single-rooted P_2, and show an anagenetic increase in size and hypsodonty. According to Gingerich and Gunnell (1979)—*E. spatularius* and *E. bisulcatus* do not overlap in range; specimens that are intermediate in age are also morphologically intermediate and tentatively referred to the former, with the provision that they may represent a new, intermediate species; and finally, the relationship between *E. bisulcatus* and *E. acutidens* is less clear, because they are contemporaneous in the middle and upper part of the *Heptodon* Range-Zone of the Bighorn Basin (Schankler, 1980).

The *E. xenicus* lineage begins in the early Clarkforkian, and the *E. spatularius* one at the onset of the Wasatchian. When the two lineages are compared, there is significant overlap in size between *E. spatularius* and *E. xenicus-E. ancylion,* and between *E. bisulcatus* and *E. ancylion.* Thus, it is difficult to identify specimens of similar size, unless they preserve the mandibular symphysis and/or anterior premolars. Accordingly, we suggest additional diagnostic features, given that the fig-

ures and descriptions in Gingerich and Gunnell (1979) accurately reflect the range of intraspecific morphologic variation. The *E. xenicus-ancylion-grangeri* group may be characterized by inflated metaconids, appressed paraconids and metaconids and low paracristids on M_{1-3}, and very narrow stylar shelves and salients on P^4–M^3. In contrast, the *E. spatularius-bisulcatus-acutidens* group has well-separated paraconids and metaconids, an unexpanded metaconid, and a high paracristid on M_{1-3}, and an expanded stylar shelf and salients on P^4–M^3. These characters may aid in identifying specimens that lack the diagnostic anterior portions of the lower dentition.

The *E. xenicus-ancylion-grangeri* lineage, known only from the northern part of the Bighorn Basin (including the Clark's Fork Basin), appears to be a chronospecies that increases in size. The divisions between the species are stratigraphic and necessarily arbitrary.

On the other hand, the *E. spatularius-bisulcatus-acutidens* clade is not necessarily one chronospecies. The first two species compose a morphocline of increasing size and hypsodonty through time, and individual specimens are indistinguishable except stratigraphically. In agreement with Bown (1979), they are here considered conspecific. *E. bisulcatus-E. acutidens* show similar anagenetic change, but their apparent co-occurrence at a number of horizons in the Bighorn Basin (Schankler, 1980) as well as non-overlapping ranges in size in the Wind River Basin (see below) imply that, for the present, they should be retained as separate species. Continued analyses of the Bighorn Basin material and denser samples from the Wind River Basin should clarify this issue.

Gingerich and Gunnell (1979) have attempted to define statistically the Clarkforkian and Wasatchian species of *Esthonyx*. They (1979:128) derive a 0.095 standard deviation value (for Ln [L × W] of M_1) from the "largest sample" of *Esthonyx* and use it to compute a diagnostic difference of 3.3 standard deviation units between the type specimens of *E. xenicus* and *E. ancylion,* and 5.1 standard deviation units between the types of the latter and *E. grangeri.* The three type specimens are compared to one another rather than to the descriptive statistics of any sample. In this light, these comparisons, although interesting, appear to violate principles of statistical analysis. The standard deviation of a sample is not applicable as a model to any other sample, population, or individual. Also, there are no statistical procedures that test for the significance of the difference between individual specimens, measurements of which can only be compared to the mean of a population or statistical sample (by means of a Z-test) (Simpson et al., 1960: 173; Sokal and Rohlf, 1969).

The assignment in Gingerich and Gunnell (1979) of a Lostcabinian age to the San Jose tillodont, *E. bisulcatus,* has been revised. Recent

analyses of the AMNH (Lucas et al., 1981) and CM (unpublished data) collections from the Regina and Tapicitos members of the San Jose Formation found evidence that the San Jose faunas are late Graybullian to Lysitean—the absence of the index fossil *Lambdotherium,* as well as *Shoshonius,* and the presence of a host of typical early to middle Wasatchian mammals (*Ambloctonus, Didymictis protenus, Ectoganus, Apheliscus, Pelycodus jarrovii, Navajovius, Chriacus, Anacodon, Homogalax*).

Esthonyx bisulcatus Cope, 1874
(Fig. 1; Tables 1, 3)

Referred specimens.—Partial dentary with P_4–M_2—CM 39205; P_3, dP_4—CM 37053; M_1—CM 39941, 39645, 39902, 37052; M_2—CM 39160, 37054, 22660 (2 teeth); M_3—CM 36117, 37056, 28722, 53785; lower molar fragments—CM 37055, 35929, 19902; partial maxilla with M^{1-3}—CM 39644; M^3—CM 54155; upper molar fragments—CM 35978, 35979, 35980.

Localities.—CM locs. 797, 799, 802, 806, 807, 927, 929, 931, 1091 (Lysitean, Lysite Member).

Known distribution.—early Wasatchian—Hoback and Powder River basins (Wasatch Fm.), Wyoming; early to late Wasatchian—Bighorn Basin (Willwood Fm.), Wyoming; middle Wasatchian—Wind River Basin (Wind River Fm.), Wyoming, San Juan Basin (San Jose Fm.), New Mexico.

Description and discussion.—The known morphology of *E. bisulcatus* is described in Gazin (1953) and Gingerich and Gunnell (1979). In the Wind River Basin this species is restricted to, but occurs through-

Table 1.—*Dimensions of lower teeth of* Esthonyx bisulcatus *from the Lysite Member, Wind River Formation, Wyoming.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 37053	807	6.1	3.8	8.7	5.3						
CM 39205	931			7.8	5.7	7.8	6.5	8.6	6.8		
CM 39941	797					7.5	6.1				
CM 39645	802					7.8	6.2				
CM 39902	797					7.8	6.2				
CM 37052	927					8.0	6.0				
CM 39160	806							8.5	6.5		
CM 22660	799							8.5	6.5		
CM 22660	799							8.5	6.5		
CM 53785	1091							8.4	6.1		
CM 37054	807								6.4		
CM 36117	929									10.0	5.2
CM 37056	929									10.0	
CM 28722	807										5.4

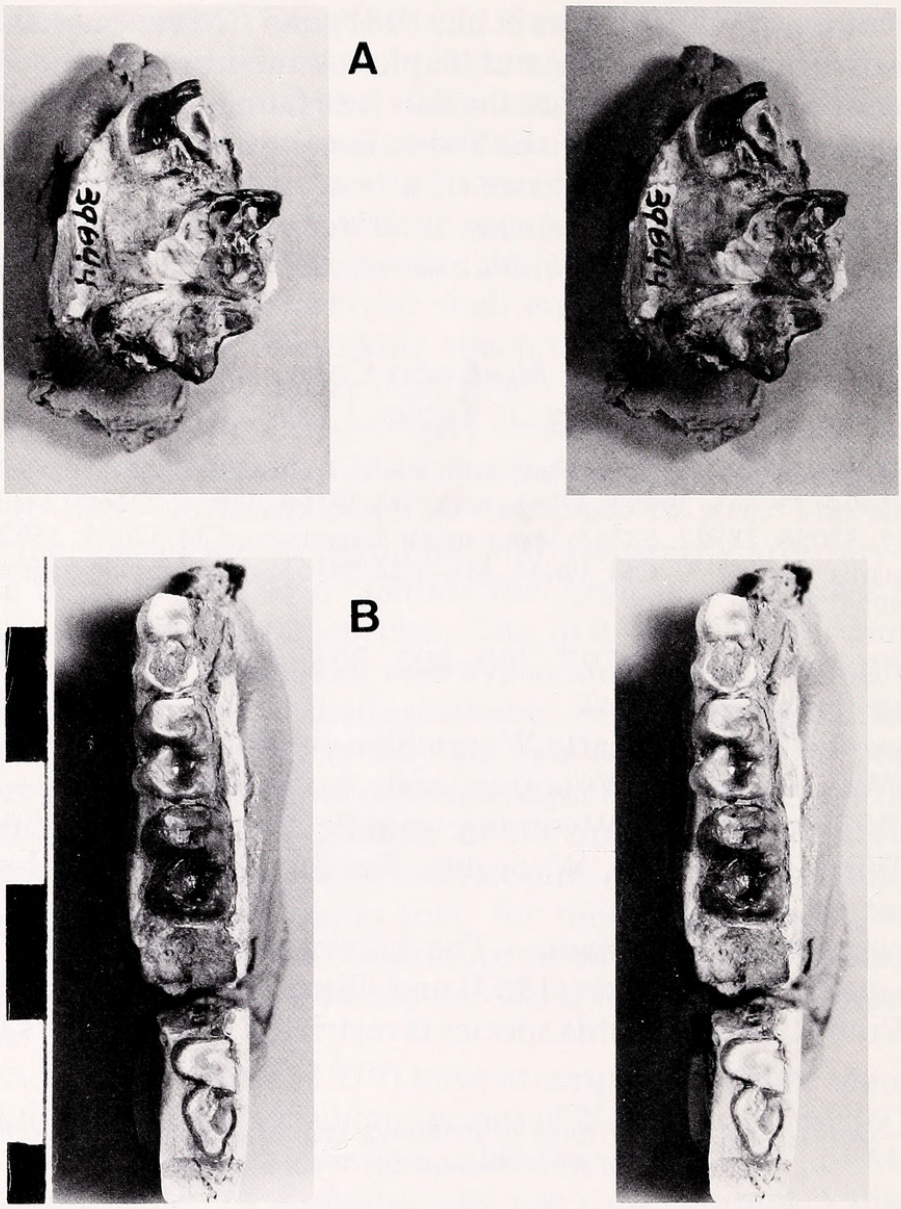

Fig. 1.—*Esthonyx bisulcatus.* A) CM 39644, LM^{1-3}; B) CM 39205, LP_4–M_2, and CM 36117, LM_3; all to same scale (1 cm).

out, the Lysite Member of the Wind River Formation. The absence of *E. bisulcatus* from localities in the Red Creek Facies (Stucky, 1983; Stucky and Krishtalka, 1982) of the Wind River Formation in the Red Creek-Deadman Butte area is coincident with the Lostcabinian age assigned to these sediments.

In *E. bisulcatus,* compared to Wind River *E. acutidens,* the teeth are significantly smaller (no overlap in range), P_4–M_3 are less hypsodont and bear a less robust metaconid, P_4 has a metastylid, M_{1-3} have a stronger metastylid, and P^4–M^3 have narrower stylar shelves with less expanded parastylar and metastylar salients.

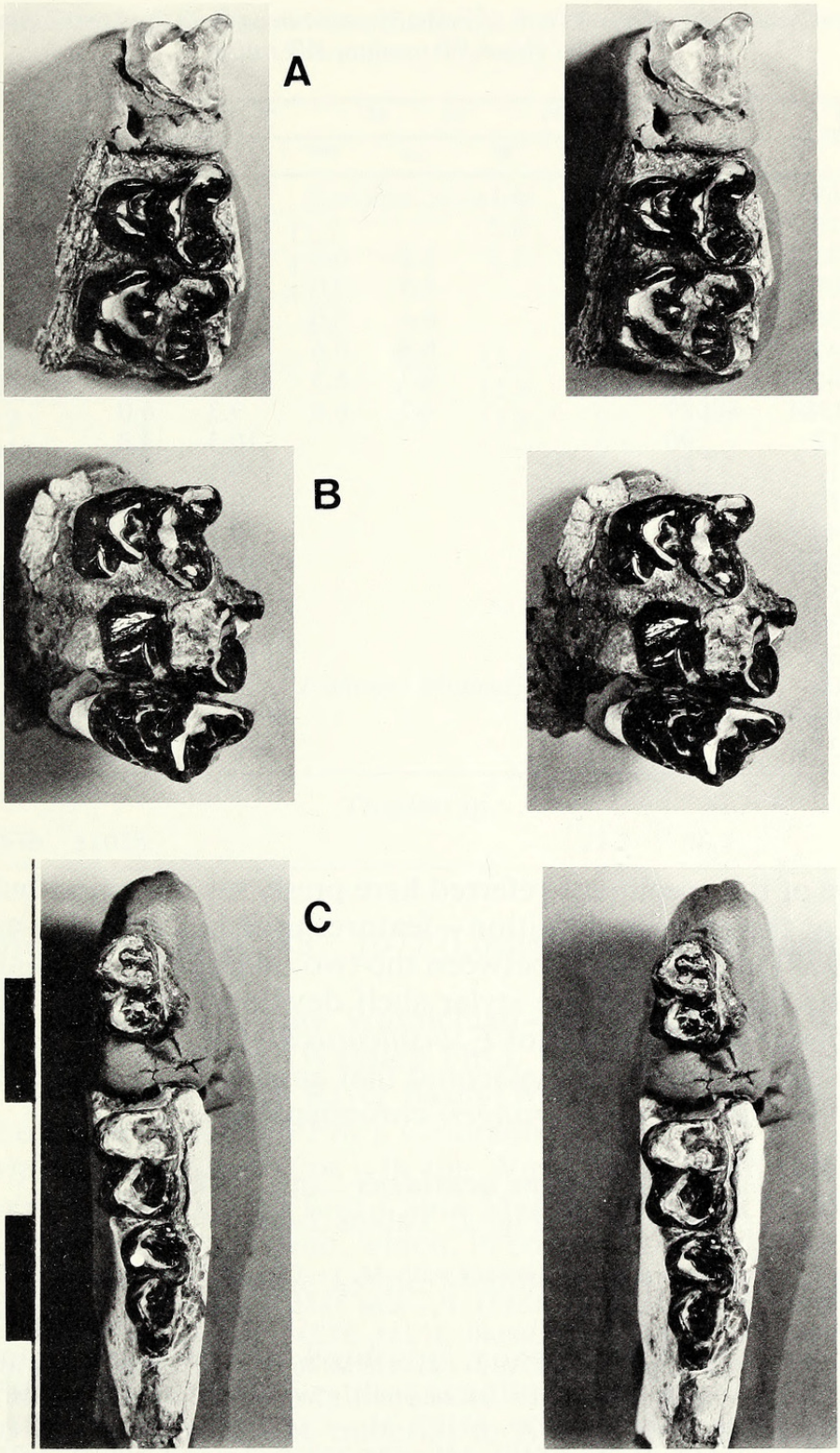

Fig. 2.—*Esthonyx acutidens.* A) CM 22311, RDP^4, and CM 42127, LP^4–M^1; B) CM 30943, LM$^{1-2}$, and CM 22310, LM^3; C) CM 35869, LP$_4$, and CM 22308, LM$_{2-3}$; all to same scale (1 cm).

Table 2.—*Dimensions of lower teeth of* Esthonyx acutidens *from the Lost Cabin Member, Wind River Formation, Wyoming.*

Specimen no.	Locality	P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W
CM 35869	34	8.8	6.1						
CM 35870	34	9.0	6.2						
CM 42131	34	8.1	5.2	8.8	6.6				
CM 22309	34			8.9	7.0				
CM 37236	34			8.6	7.0				
CM 30941	34			8.8	6.6				
CM 30942	34			8.7	6.5				
UCM 45384	80089			8.7	6.6	9.3	6.0		
CM 22312	90					10.3	7.2		
CM 22312	90					9.1	7.1		
CM 22312	90					9.8	7.5		
CM 30940	34					9.4	6.8		
CM 37235	34					10.0	7.0		
CM 36457	91					10.0	7.9		
CM 37238	34					9.5	8.0		
CM 42130	1077					10.9	7.5		
CM 22308	34					9.0	7.8	10.8	5.9
CM 55193	34							11.5	5.7
CM 37239	34								7.6

None of the specimens referred here preserves the mandibular symphysis or the anterior dentition—features used by Gingerich and Gunnell (1979) to distinguish between the two lineages of tillodonts. However, the teeth exhibit the stylar shelf development and lower molar hypsodonty that is typical of *E. bisulcatus* and *E. acutidens.* They lack the anteriorly expanded metaconid that appears to be characteristic of the *E. xenicus-ancylion-grangeri* chronospecies.

Esthonyx acutidens Cope, 1881
(Fig. 2; Tables 2–3)

Referred specimens.—Partial dentary with M_{1-2}—CM 21232; M_{2-3}—CM 22308; P_4–M_1—UCM 45384; P_4, M_1—CM 42131; P_4—CM 35869, 35870; M_1—CM 22309, 37236, 30941, 30942; M_2—CM 22312, 30940, 37235, 37238, 36457, 42130; M_3—CM 37239, 55193; lower molar fragments—CM 21131, UCM 46397; partial maxilla with P^4–M^1—CM 42127; M^{1-2}—CM 30943; M^{2-3}—CM 36477; ?associated dP^4, M^1—CM 22311; I/, M/—UCM 45528; P^4—CM 30939, 55192; M^1—CM 22312, 42128, 42133; M^2—CM 22312, 37237, 21113, 35841, 55191; M^3—CM 22310 (2 teeth), 30938, 22313, 55190, 55491; fragmentary upper molars—CM 42129, UCM 46368, 44321 (M/, /M).

Localities.—CM locs. 91, 98, 1048, UCM loc. 80063 (Lostcabinian, Lost Cabin Member); UCM locs. 80089, 81009 (Lostcabinian, Red Creek Facies); CM loc. 34, UCM loc. 80101 (Gardnerbuttean, Lost

Table 3.—*Dimensions of upper teeth of* Esthonyx *and* Trogosus *from the Wind River Formation, Wyoming.*

Specimen no.	Locality	P^4		M^1		M^2		M^3	
		L	W	L	W	L	W	L	W
				Esthonyx acutidens					
CM 55192	34	9.0	12.7						
CM 30939	34	9.0	11.3						
CM 42127	34	8.8	12.0						
CM 22311	34	8.4	8.6						
CM 42128	34			8.2	12.6				
CM 30943	34			8.5	12.3	8.9	13.4		
CM 22312	90			9.5	13.9	9.7	15.7		
CM 35841	34					9.7	14.2		
CM 55191	34					8.8	14.2		
CM 22313	91							8.0	15.6
CM 36477	34							7.6	12.9
CM 30938	34							7.5	13.4
CM 22310	34							7.3	13.5
CM 42131	34							7.2	13.0
				Esthonyx bisulcatus					
CM 39644	802					8.1	13.0	7.0	12.4
CM 54155	1091							7.2	12.7
				Trogosus sp.					
UCM 46536	81028					22.7	36.1		

Cabin Member); CM 90, 857, 1077 (Lostcabinian or Gardnerbuttean, Lost Cabin Member).

Known distribution.—Late Wasatchian—Bighorn Basin (Willwood Fm.), Green River Basin (Wasatch Fm.), Wyoming; late Wasatchian to early Bridgerian—Wind River Basin (Wind River Fm.), Wyoming, Huerfano Basin (Huerfano Fm.), Colorado.

Description and Discussion.—In the Wind River Basin this species is recovered only from the Lost Cabin Member and Red Creek Facies of the Wind River Formation, which, in combination with the restriction of *E. bisulcatus* to the Lysite Member, may be important biostratigraphically.

As was the case with *E. bisulcatus,* none of the material of *E. acutidens* referred here preserves the mandibular symphysis or teeth anterior to P_4. Referral of the material to *E. acutidens* is based on diagnostic criteria on $P^4/_4$–$M^1/_1$ outlined earlier. Compared to *E. bisulcatus,* the teeth of *E. acutidens* from the Wind River Formation are significantly larger, P_4 lacks a metastylid, M_{1-3} have weaker metastylids, and P_4–M_3 are more hypsodont with lingually robust metaconids; the stylar shelves on P^4–M^3, although variable in degree of

development, are more expanded, especially in the parastylar area on M^{2-3}.

E. acutidens, the youngest recorded species of the genus, has not been recovered from post-Gardnerbuttean horizons, and apparently became extinct sometime during the earliest Bridgerian (Stucky, 1983). It last appears at one locality (two horizons) in the upper part of the Lost Cabin Member, where it overlaps in range with *Trogosus,* and at Huerfano locality II (McKenna, 1976), where it co-occurs with *Trogosus.*

Trogosus Leidy, 1871

In his review of *Trogosus,* Gazin (1953) named two new species (*T. hillsi, T. grangeri*) from the Huerfano Basin, and cited five species that had previously been described from Bridger B horizons in the Bridger Basin. He recognized two of the latter as valid (*T. castoridens, T. hyracoides*), two as invalid (*T. minor, T. ? vetulus*), and one as questionable (*T. ? latidens*), but later (Gazin, 1976) included *T. latidens* in his comprehensive faunal list for the Bridger Formation.

Robinson (1966), impressed with the degree of variation in the *Trogosus* material from Huerfano, suggested that the differences between *T. hillsi* and *T. grangeri* were probably due to sexual dimorphism, and synonymized the two as *T. grangeri.*

This is the first record of *Trogosus* from the Wind River Basin.

***Trogosus* sp.**
(Table 3)

Referred specimens.—Partial M_1 or M_2, UCM 47717; M^2, UCM 46536.

Localities.—UCM locs. 79040, 81028 (Gardnerbuttean, Lost Cabin Member).

Known distribution.—Earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming; see text for occurrences of *Trogosus.*

Discussion.—These two teeth closely resemble comparable parts of the dentition of *Trogosus.* They are much larger than *Esthonyx* and *Megalesthonyx,* and M^2 (Stucky, 1982, Fig. 34) lacks the mesostyle that is characteristic of the latter. The two teeth are closest in size to *T. castoridens* and *T. hyracoides,* but, in the absence of diagnostic features of the skull and dentition (Gazin, 1953), the material cannot be referred to a species of *Trogosus.* Both of the localities at which *Trogosus* occurs are in the upper part of the Lost Cabin Member and are Gardnerbuttean (=early Bridgerian) in age (see below).

BIOSTRATIGRAPHIC IMPLICATIONS

Esthonyx and *Trogosus,* together with certain other taxa, have proven to be reliable indicators of biostratigraphic age. *Esthonyx* is common

in most Clarkforkian through Lostcabinian faunas. Its first appearance, along with that of other taxa, marks the onset of the Clarkforkian (Rose, 1981). The *E. xenicus-ancylion-grangeri* lineage is characteristic of the Clarkforkian in the Bighorn Basin (Gingerich and Gunnell, 1979) and becomes extinct in the early Wasatchian. The *E. spatularius-bisulcatus* chronospecies is characteristic of Graybullian and Lysitean horizons, and apparently extends into the Lostcabinian in the Bighorn Basin (Schankler, 1980). The first appearance of *E. acutidens* may mark the beginning of the Lostcabinian; this species is an index fossil of that subage, but it is also known from post-Lostcabinian (Gardnerbuttean) faunas at two localities—one in the Huerfano Formation (Huerfano II), and one in the Wind River Formation (CM. loc. 34, upper part of Lost Cabin Member). Its last appearance (contra McKenna, 1976) is not necessarily indicative of a late Wasatchian age.

Before the Bridgerian Land-Mammal Age was formally named, horizons in the Huerfano Formation (Huerfano B) that yielded *Trogosus,* as well as certain other taxa, were correlated with part of the Bridger Formation (Osborn, 1897, 1909, 1919, 1929; Matthew, 1899, 1909; Simpson, 1933). Subsequently, the Wood Committee (Wood et al., 1941) listed *Tillotherium* (=*Trogosus*) as an index fossil of the Bridgerian, and assigned this age to the fauna from Huerfano B. Robinson (1966), however, concluded that the Huerfano B fauna was representative of a new, latest Wasatchian subage, the Gardnerbuttean, which was younger than the Lostcabinian but older than the Bridgerian. Later, a new record of *E. acutidens* from Huerfano locality II (Huerfano B) led McKenna (1976) to question the utility of the Gardnerbuttean. Huerfano locality II is the only fossiliferous horizon that preserves the co-occurrence of *Esthonyx* and *Trogosus.*

Trogosus has also been recorded from the Aycross Formation (McKenna, 1980; Bown, 1982; CM collections), the Cathedral Bluffs Tongue of the Wasatch Formation (Morris, 1954; Gazin, 1962), Bridger A and B horizons in the Bridger Basin (McGrew and Sullivan, 1971; Gazin, 1976), the Green River Formation (CM collections, Powder Wash, Utah), and possibly from the Arkosic facies of the New Fork Tongue of the Wasatch Formation (Stucky, 1983). The record of *Trogosus* from the Wind River Basin comes from two localities in the upper part of the Lost Cabin Member, UCM locs. 79040 and 81028. The former also preserves *Palaeosyops* (=*Eotitanops,* see Wallace, 1980) *borealis, Hyrachyus* sp. cf. *H. eximius, Antiacodon pygmaeus,* and *Pantolestes* sp. cf. *P. longicaudus.* The M^2 of *Trogosus* is the only known specimen from UCM loc. 81028.

These taxa—*Trogosus, Palaeosyops, Hyrachyus, Antiacodon, Pantolestes*—and others, such as *Helohyus* and *Helaletes,* are restricted in the Wind River Formation to localities in the upper part of the Lost

Cabin Member. All of these taxa appear to be reliable index fossils of the Bridgerian. Most of them occur in faunas of unequivocal Bridgerian age (Gazin, 1976; Bown, 1982; McKenna, 1980; McGrew and Sullivan, 1971) and their first appearance can be used to mark the onset of the Bridgerian (Stucky, 1983). Some faunas—from Huerfano B, Cathedral Bluffs, upper part of the Lost Cabin Member—in which many of these Bridgerian taxa co-occur with typical late Wasatchian mammals, such as *Esthonyx, Shoshonius, Coryphodon, Bunophorus, Diacodexis, Hyracotherium,* and *Phenacodus,* have been assigned alternatively to either the latest Wasatchian (Robinson, 1966; Gazin, 1962; McKenna, 1976) or the earliest Bridgerian (Morris, 1954; West and Dawson, 1973; Gingerich, 1979; Bown, 1982; Stucky, 1982). We opt for the latter conclusion on the basis that the first appearances of the Bridgerian taxa, which apparently occur penecontemporaneously, are more reliable criteria of the Wasatchian-Bridgerian boundary than are the last appearances of the Wasatchian taxa, which are asynchronous and geographically disjunct. In short, the principle advocated here is that the first appearance of taxa through immigration or cladogenesis is a finer correlative tool and biostratigraphic measure than is the extinction and last appearance of taxa, or stage of evolution of taxa within an anagenetic lineage (Repenning, 1967; Savage, 1977; Woodburne, 1977; Rose, 1981).

Accordingly, the faunas from localities in the upper part of the Lost Cabin Member, as well as those from Huerfano B, Cathedral Bluffs, and the Arkosic facies of the New Fork Tongue of the Wasatch Formation (in part) are here considered Bridgerian. They preserve the first appearance of the Bridgerian taxa *Trogosus, Antiacodon, Palaeosyops,* and *Hyrachyus,* and the unique, earliest Bridgerian faunal assemblages that define the Gardnerbuttean (Stucky, 1983).

PHYLOGENETIC RELATIONSHIPS

All North American tillodonts appear to be united in having enlarged $I^2/_2$, strong, broad postcingula and stylar shelves on the upper molars, a talonid basin on P_{3-4}, high arcuate crests and metastylids on the lower molars, and in the loss of $P^1/_1$ and I^1 (Fig. 3, node 1). Two lineages of *Esthonyx,* the most primitive North American tillodont, appear to have diverged in the early Tertiary. One, the *E. xenicus-ancylion-grangeri* chronospecies, retains an unfused mandibular symphysis and a two-rooted P_2, but seems to be derived in having the paraconid on the lower molars close to an anteriorly inflated metaconid (Fig. 3, node 2). The second lineage of *Esthonyx* and all other North American tillodonts (Fig. 3, node 3) are advanced in having a fused mandibular symphysis (to at least below P_3), greatly reduced conules on M^{1-3}, and more hypsodont and deeply basined P_4–M_3, with higher, more arcuate

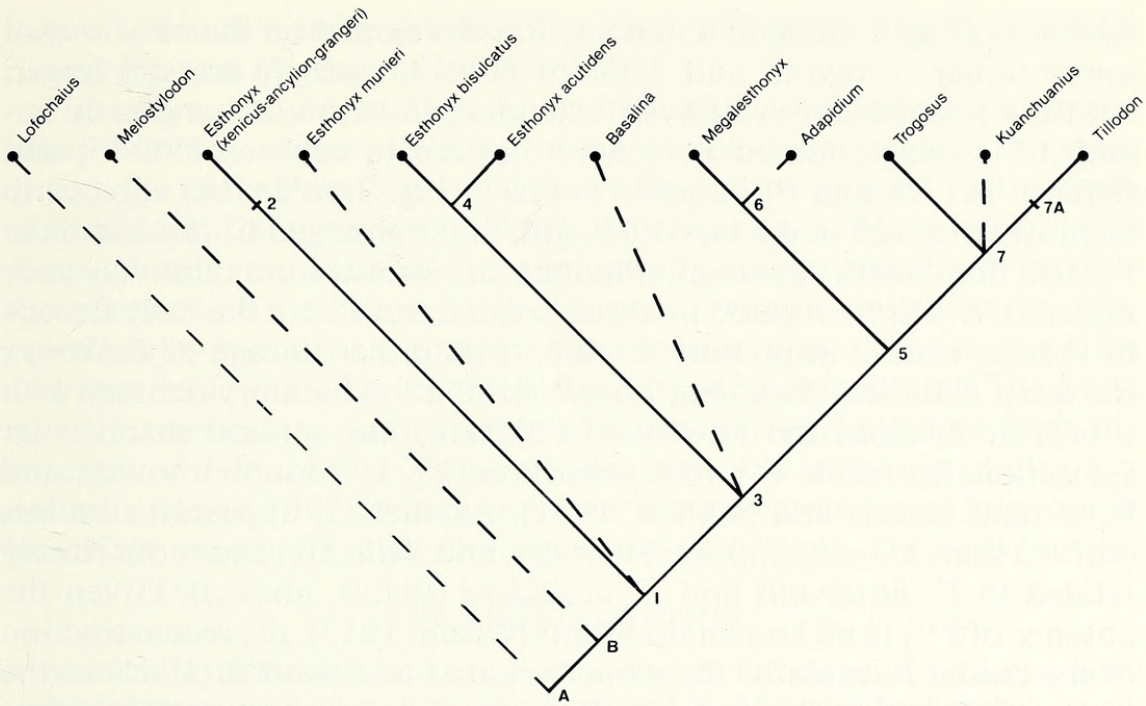

Fig. 3.—Proposed phylogenetic relationships among Tillodontia. *Node A*—P^4–M^3 with wing-like stylar salients, and postcingulum. *Node B*—I_2 enlarged; M^{1-2} with more expanded stylar shelf and postcingulum. *Node 1*—$I^2/_2$ more enlarged; M_{1-2} more hypsodont, with strong metastylid, arcuate paracristid and posthypocristid, reduced hypoconulid; M^{1-3} less transverse; I^1, $P^1/_1$ lost; P_{3-4} with talonid basin (?primitive). *Node 2*—M_{1-3} paraconid closer to anteriorly inflated metaconid; chronocline of increasing size from *E. xenicus-E. ancylion-E. grangeri*. *Node 3*—Mandibular symphysis fused to below P_3 or P_4; P_4–M_3 more hypsodont, with higher cristids, deeper basins and more U-shaped paracristid; M^{1-3} with reduced conules. *Node 4*—M^{1-3} with expanded stylar salients and deeper ectoflexi; P_2 single-rooted. *Node 5*—$I^2/_2$ enlarged, with restricted band of enamel; P_4–M_3 more hypsodont; M_{1-3} cristid obliqua more lingual, originating from below the metaconid; increase in size; reduction of C_1, P_2, P_4 talonid. *Node 6*—M^{1-2} with mesostyle. *Node 7*—Mandibular symphysis fused to below M_1; $I^2/_2$ greatly enlarged; increase in size; longer I^3-C-P^2 diastemata; P_2 single-rooted; $I^1/_1$, C, P_3 talonid reduced. *Node 7A*—I_3 lost; longer C–P_2 diastema.

cristids and stronger metastylids. *E. bisulcatus* (=*E. spatularius*) and *E. acutidens* (Fig. 3, node 4) have, in addition to these features, expanded stylar salients and deeper ectoflexi on M^{1-3}, and a single-rooted P_2. *E. bisulcatus* appears to be one Graybullian through Lysitean chronospecies; the lack of overlap in size between the latter and *E. acutidens*, and their apparent co-occurrence in Lostcabinian beds in the Bighorn Basin may imply specific distinction and a cladogenetic event.

Remaining tillodonts—*Megalesthonyx, Trogosus, Tillodon* (Fig. 3, node 5)—are much larger and more derived in having a restricted band of enamel on $I^2/_2$ (I^2 not known in *Megalesthonyx*), a cristid obliqua on the lower molars that originates lingually from the metaconid, more hypsodont cheek teeth, and reduced C_1, P_2, and P_4 talonid. In *Mega-*

lesthonyx (Fig. 3, node 6) a mesostyle is developed on the only known upper molar. *Trogosus* and *Tillodon* (Fig. 3, node 7) are still larger, with the mandibular symphysis extending to below M_1, a greatly enlarged $I^2/_2$, single-rooted P_2, longer diastemata between I^3-C-P^2, and reduced $I^1/_1$, C, and P_3 talonid. *Tillodon* (Fig. 3, node 7A) appears to be most advanced in the loss of $I^3/_3$ and in the enlarged C_1–P_2 diastema.

Most non-North American tillodonts are known from relatively poor material. *E. munieri,* based on three isolated teeth from the early Eocene of France, cannot at present be allied with either lineage of *Esthonyx* in North America. *Basalina,* known from a fragmentary dentary with a broken P_4 from the Eocene of Pakistan, has a fused mandibular symphysis (to below P_4), and unreduced C_1, P_2 (double rooted), and P_4 talonid (Lucas and Schoch, 1981). As such, it appears to be less derived than *Megalesthonyx, Trogosus,* and *Tillodon,* and more closely related to *E. bisulcatus* and *E. acutidens* (Fig. 3, node 3). Given the absence of $P^1/_1$ in all known tillodonts (Gazin, 1953), the reconstruction of the dental formula of *Basalina* by Lucas and Schoch (1981) in the diagnosis (p. 90) and their figure (Plate 15, Fig. 2) is questionable. More reasonable is the alternative interpretation (p. 91) of a two-rooted P_2 and the absence of P_1.

Lofochaius and *Meiostylodon,* from the early or middle Paleocene of China (Li and Ting, 1983), are known from P^4–M^3 and from M^{1-2} and I_2, respectively. They are tillodont-like in the enlargment of I_2 and in the wing-like stylar salients and expanded postcingula on the cheek teeth. In comparison to *Esthonyx, Lofochaius,* with transverse upper molars and narrower stylar shelves and postcingula, is the most primitive known tillodont (Fig. 3, node A). *Meiostylodon* retains transverse M^{1-2} and unreduced conules, but approaches *Esthonyx* in the development of the postcingula and stylar shelves, and appears to be intermediate morphologically between *Lofochaius* and *Esthonyx* (Fig. 3, node B). *Esthonyx* and all other tillodonts (Fig. 3, node 1) are more derived, in comparison, in having less transverse P^4–M^3. The other characters listed for this node are not preserved in *Lofochaius* and *Meiostylodon*; some or all may or may not have been present in these taxa.

Adapidium, from the late Eocene of China, has hypsodont lower molars with a lingual cristid obliqua that originates from below the metaconid (Fig. 3, node 5). It appears to be most closely related to *Megalesthonyx* (Fig. 3, node 6) in sharing the development of a mesostyle on at least M^1 (unpublished, unnumbered IVPP specimen), although this may have evolved independently.

Kuanchuanius (see Chow, 1963), from the middle Eocene of China, shares with *Trogosus* (Fig. 3, node 7) the derived features of very large size, a mandibular symphysis that extends to below M_1, a greatly en-

larged I_2 with a restricted band of enamel, reduced I_1 and C_1, a single-rooted P_2, and hypsodont lower molars.

The inferred phylogenetic relationships of the four Chinese Paleogene tillodonts may suggest that the origin of tillodonts occurred in Asia during the early Paleocene, and was followed by at least two periods of origin and immigration of North American taxa. *Meiostylodon* and *Kuanchuanius* are suitable morphologically and temporally to be near the ancestry of the larger *Esthonyx* and *Trogosus,* respectively. *Megalesthonyx* appears abruptly in the Lostcabinian of North America and may have shared a common ancestry with *Adapidium.* The presence of a mesostyle on M^2 seems to remove *Megalesthonyx* from the ancestry of *Trogosus* or *Tillodon.* Less plausible is the alternative hypothesis (Rose, 1972), which involves the appearance and subsequent loss of the mesostyle in an *Esthonyx-Megalesthonyx-Trogosus* lineage.

ACKNOWLEDGMENTS

We thank M. R. Dawson for reviewing the manuscript, P. Gingerich for his criticisms and information on Bighorn Basin tillodonts, and V. Abromitis for his photographic assistance. This work was supported, in part, by grants from the M. Graham Netting Research Fund of the Carnegie Museum of Natural History through a grant from the Cordelia S. May Charitable Trust, the Rea Postdoctoral Fellowship, Carnegie Museum of Natural History, and the Walker Van Riper Fund, University of Colorado Museum.

LITERATURE CITED

BOWN, T. M. 1979. Geology and mammalian paleontology of the Sand Creek facies, Lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. Mem. Geol. Survey Wyoming, 2:1–151.

———. 1982. Geology, paleontology, and correlation of Eocene volcaniclastic rocks, southeast Absaroka Range, Hot Springs County, Wyoming. Geol. Survey Prof. Papers, 1201–A:1–75.

CHOW, M. 1963. Tillodont materials from Eocene of Shantung and Honan. Vert. Palasiatica, 7:97–104.

CHOW, M., Y. CHANG, B. WANG, AND S. TING. 1973. New mammalian genera and species from the Paleocene of Nanhsiung, N. Kwangtung. Vert. Palasiatica, 11:31–35.

COPE, E. D. 1874. Report upon vertebrate fossils discovered in New Mexico, with description of new species. Annual Rept. Chief Engineers, U.S. Army, Appendix FF, p. 589–606 (Separatum, pp. 1–18).

———. 1880. The northern Wasatch fauna. Amer. Nat., 14:908–909.

———. 1881. On the Vertebrata of the Wind River Eocene beds of Wyoming. Bull. U.S. Geol. Geog. Surv. Terr., 6:183–202.

———. 1883. On the mutual relations of the bunotherian Mammalia. Proc. Acad. Nat. Sci., Philadelphia, pp. 77–83.

DEHM, R., AND T. OETTINGEN-SPIELBERG. 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. Abh. Bayer. Akad. Wiss., Math-Nat. Kl., 91: 1–54.

GAZIN, C. L. 1953. The Tillodontia: an early Tertiary order of mammals. Smithsonian Misc. Coll., 121:1–110.

———. 1962. A further study of the Lower Eocene mammal faunas of southwestern Wyoming. Smithsonian Misc. Coll., 144:1–98.

———. 1976. Mammalian faunal zones of the Bridger middle Eocene. Smithsonian Contrib. Paleobiol., 26:1–25.

GINGERICH, P. D. 1979. Phylogeny of middle Eocene Adapidae (Mammalia, Primates) in North America: *Smilodectes* and *Notharctus*. J. Paleont., 53:153–163.

GINGERICH, P. D., AND G. F. GUNNELL. 1979. Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. Contribs. Mus. Paleont., Univ. Michigan, 25:125–153.

GUTHRIE, D. A. 1967. The mammalian fauna of the Lysite Member, Wind River Formation, (early Eocene) of Wyoming. Mem. So. California Acad. Sci., 5:1–53.

———. 1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (Lower Eocene) of Wyoming. Ann. Carnegie Mus., 43:47–113.

KELLEY, D. R., AND A. E. WOOD. 1954. The Eocene mammals from the Lysite Member, Wind River Formation of Wyoming. J. Paleont., 28:337–366.

KRISHTALKA, L., AND R. K. STUCKY. 1983. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 3. Marsupialia. Ann. Carnegie Mus., 52:205–227.

LEIDY, J. 1968. Notice of some remains of extinct pachyderms. Proc. Nat. Acad. Sci., Philadelphia, 20:230–233.

———. 1871. Remarks on fossil vertebrates from Wyoming. Proc. Nat. Acad. Sci., Philadelphia, 23:228–229.

LEMOINE, V. 1889. Considérations générales sur les vertébrés fossiles des environs de Reims et spécialement sur les mammifères de la faune Cernaysienne. C. R. Congr. Internat. Zool., p. 233–279.

LI, CHUAN-KUEI, AND SU-YIN TING. 1983. The Paleogene mammals of China. Bull. Carnegie Mus. Nat. Hist., 21:1–98.

LUCAS, S. G., AND R. M. SCHOCH. 1981. *Basalina,* a tillodont from the Eocene of Pakistan. Mitt. Bayer. Staatslg. Palaont. hist. Geol., 21:89–95.

LUCAS, S. G., R. M. SCHOCH, E. MANNING, AND C. TSENTAS. 1981. The Eocene biostratigraphy of New Mexico. Bull. Geol. Soc. Amer., pt. 1, 92:951–967.

MARSH, O. C. 1875. New order of Eocene mammals. Amer. Jour. Sci., 9:221.

MATTHEW, W. D. 1899. A provisional classification of the freshwater Tertiary of the west. Bull. Amer. Mus. Nat. Hist., 12:19–75.

———. 1909. Faunal lists of the Tertiary Mammalia of the west. Bull. U.S. Geol. Surv., 361:91–138.

MCGREW, P. O., AND R. SULLIVAN. 1970. The stratigraphy and paleontology of Bridger A. Univ. Wyoming. Contribs. Geol., 9:66–85.

MCKENNA, M. C. 1976. *Esthonyx* in the upper faunal assemblage, Huerfano Formation, Eocene of Colorado. J. Paleont., 50:354–355.

———. 1980. Late Cretaceous and early Tertiary vertebrate paleontological reconnaissance, Togwotee Pass area, northwestern Wyoming. Pp. 321–343, *in* Aspects of vertebrate history (L. L. Jacobs, ed.), Museum of Northern Arizona Press, Flagstaff, xix + 407 pp.

MORRIS, W. J. 1954. An Eocene fauna from the Cathedral Bluffs Tongue of the Washakie Basin, Wyoming. J. Paleont. 28:195–203.

OSBORN, H. F. 1897. The Huerfano Lake Basin, southern Colorado and its Wind River and Bridger fauna. Bull. Amer. Mus. Nat. Hist., 9:247–258.

———. 1909. Cenozoic mammal horizons of western North America, with faunal lists of the Tertiary mammals of the west by William Diller Matthew. Bull. U.S. Geol. Surv., 361:1–138.

———. 1919. New titanotheres of the Huerfano. Bull. Amer. Mus. Nat. Hist., 41:557–569.

———. 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geol. Surv. Monograph 55.

REPENNING, C. A. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic. Pp. 288–311, *in* The Bering Land Bridge (D. M. Hopkins, ed.), Stanford Univ. Press, Stanford, California.

ROBINSON, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene of Colorado. Bull. Yale Peabody Mus. Nat. Hist., 21:1–95.

ROSE, K. D. 1972. A new tillodont from the Eocene upper Willwood Formation of Wyoming. Postilla, 155:1–13.

———. 1981. The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. Univ. Michigan Papers Paleont., 26: 1–197.

SAVAGE, D. E. 1977. Aspects of vertebrate paleontological stratigraphy and geochronology. Pp. 427–442, *in* Concepts and methods of biostratigraphy (E. G. Kaufmann and J. E. Hazel, eds.), Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

SCHANKLER, D. M. 1980. Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming. Pp. 99–114, *in* Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming (P. D. Gingerich, ed.), Univ. Michigan Papers Paleont., 24: vi + 1–146.

SIMPSON, G. G. 1933. Glossary and correlation charts of North American Tertiary mammal-bearing formations. Bull. Amer. Mus. Nat. Hist., 60:79–121.

———. 1937. Notes on the Clark Fork, upper Paleocene fauna. Amer. Mus. Novit., 954:1–24.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative Zoology. Revised ed., Harcourt, Brace and Co., New York.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

STUCKY, R. K. 1982. Mammalian faunas and biostratigraphy of the upper part of the Wind River Formation (early to middle Eocene), Natrona County, Wyoming, and the Wasatchian-Bridgerian boundary. Unpublished Ph.D. dissertation, Univ. Colorado, Boulder, 278 pp.

———. 1983. Geology and mammalian biostratigraphy of the upper part of the Wind River Formation (early to middle Eocene) of Wyoming, and the Wasatchian-Bridgerian boundary. Bull. Carnegie Mus. Nat. Hist., in press.

STUCKY, R. K., AND L. KRISHTALKA. 1982. Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 1. Introduction and Multituberculata. Ann. Carnegie Mus., 51:39–56.

WALLACE, S. M. 1980. A revision of North American early Eocene Brontotheriidae (Mammalia, Perissodactyla). Unpublished M.S. thesis, Univ. Colorado, Boulder, 157 pp.

WANG, B. 1975. Paleocene mammals of Chaling Basin, Hunan. Vert. Palasiatica, 13: 154–162. [Chinese]

WEST, R. M., AND M. R. DAWSON. 1973. Fossil mammals from the upper part of the Cathedral Bluffs Tongue of the Wasatch Formation (early Bridgerian), northern Green River Basin, Wyoming. Univ. Wyoming Contrib. Geol. 12:33–41.

WHITE, T. E. 1952. Preliminary analysis of the vertebrate fauna of the Boysen Reservoir area. Proc. U.S. Nat. Mus., 102:185–207.

WOOD, A. E., AND OTHERS. 1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Amer., 52(1):1–48.

WOODBURNE, M. O. 1977. Definition and characterization in mammalian chronostratigraphy. J. Paleont., 51:220–234.

YOUNG, C. C. 1937. An early Tertiary vertebrate fauna from Yuanchu. Bull. Geol. Soc. China, 17:413–438.