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(MAMMALIA, TILLODONTIA) IN THE EARLY EOCENE OF NORTH AMERICA**

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SYSTEMATICS AND EVOLUTION OF THE GENUS *ESTHONYX*  
(MAMMALIA, TILLODONTIA) IN THE EARLY EOCENE OF NORTH AMERICA

By

Philip D. Gingerich and Gregg F. Gunnell

*Abstract.*— The systematics and stratigraphic ranges of early Eocene species of *Esthonyx* are revised with the aid of a large number of new specimens collected in recent years from the northern Big Horn Basin, Wyoming. The oldest species, *Esthonyx xenicus* n. sp., first appeared in North America at or near the beginning of the Clarkforkian. *Esthonyx xenicus* gave rise to *E. ancylion* n. sp., which was ancestral to *E. grangeri* Simpson. This lineage evolved rapidly toward larger body size. At the beginning of the Wasatchian, a second lineage of small *Esthonyx* appeared that increased in size relatively slowly through the remainder of the Wasatchian. Early Wasatchian *Esthonyx spatularius* Cope probably gave rise to *E. bisulcatus* Cope in the late Wasatchian (Lysitean and Lostcabinian), and *E. bisulcatus* probably gave rise to Lostcabinian *E. acutidens* Cope, but these transitions are not yet fully understood. *Esthonyx bisulcatus* appears to have survived until the end of the Wasatchian in southern North America. Esthonychine tillodonts became extinct in North America in the early Bridgerian when they were replaced by more advanced trogosine tillodonts. *Esthonyx* first appeared in North America as part of an immigrant fauna including Rodentia. Recent discoveries in the Paleocene of China suggest that both tillodonts and rodents originated in Asia. Tillodonts may have originated from Condylarthra, Anagalida, or Pantodonta, but until their origin is better known, they are best retained in a separate order, Tillodontia.

INTRODUCTION

The genus *Esthonyx* is a relatively common element in the early Eocene mammalian fauna of North America. Nevertheless, the systematics, phylogeny, and evolution of this genus have remained confusing. E. D. Cope named three species of *Esthonyx* from the San Juan Basin of New Mexico in 1874 when he first named the genus. Subsequently, Cope (1880, 1881) named a fourth species from an unknown locality in the Big Horn Basin of Wyoming and a fifth species from the Wind River Basin. Later, Simpson (1937) named two additional species from the late Clarkforkian of the northern Big Horn Basin, Wyoming. It has long been impossible to determine which of these species are valid and how they are related. In recent years University of Michigan field expeditions have made large collections of late Paleocene and early Eocene mammals from the northern Big Horn Basin, and these contribute to a substantially better understanding of the morphology, stratigraphic distribution, systematics, and evolution of *Esthonyx* in North America.

The new specimens described here are nearly all from measured stratigraphic sections in the Clark's Fork River and Shoshone River valleys of the northern Big Horn Basin. *Esthonyx* is found

through a total thickness of just under 1100 meters of sediment in our study area, spanning the Clarkforkian and early Wasatchian land mammal ages (about 55 to 51 million years before present; Berggren *et al.*, 1978). Descriptions of the measured stratigraphic sections, fossil localities, and reviews of other taxonomic groups of fossil vertebrates are in preparation.

The Clarkforkian land mammal 'age' has generally been recognized as a short interval of time corresponding to a single *Plesiadapis* zone (the *Ples. cookei* Zone, Gingerich, 1976b), but recent work has shown that it is a more substantial interval including strata above and below the *Ples. cookei* Zone. A detailed study of the Clarkforkian fauna and its subdivisions is in progress (Rose, in prep.). Subdivisions of the Wasatchian land mammal 'age' have never been adequately defined, and we have followed the *Pelycodus* zonation of Gingerich and Simons (1977). They provisionally equated Sandcouleean with the *Pelycodus ralstoni* Zone, lower Graybullian with the *P. mckennai* Zone, upper Graybullian with the *P. trigonodus* Zone, Lysitean with the *P. abditus* Zone, and Lostcabinian with the *P. jarrovii* Zone. This yields a five-part subdivision of the Wasatchian that conforms closely to previous usage and can be recognized throughout western North America.

In this paper we first describe dental variability in *Esthonyx*, review and revise the systematic nomenclature of *Esthonyx*, and then consider the evolution of the genus in North America. Tillodonts are known to have been present during the early Tertiary in Asia, North America, and (briefly) in Europe. Recent discoveries in Asia contribute to a new perspective on the origin and early evolution of the Tillodontia, and this is discussed in a concluding section of the paper. We have concentrated attention on Clarkforkian and early Wasatchian species of *Esthonyx* since these are most important for understanding the systematics of the genus. Mr. David Shankler, Yale University, is studying *Esthonyx* from the Wasatchian of the central Big Horn Basin, and he will further clarify details of the transition from *E. spatularius* to *E. bisulcatus* and to *E. acutidens*.

Institutional abbreviations used in this paper are as follows: ACM, Amherst College Museum (Amherst, Mass.); AMNH, American Museum of Natural History (New York); CM, Carnegie Museum of Natural History (Pittsburgh); MNHN AL, Muséum National d'Histoire Naturelle (Paris), Agéian collection of Lemoine; PU, Princeton University Museum of Natural History (Princeton, N. J.); UM, University of Michigan Museum of Paleontology (Ann Arbor); USNM, National Museum of Natural History (Washington, D. C.); and YPM, Yale Peabody Museum (New Haven, Conn.).

#### DENTAL VARIABILITY IN *ESTHONYX*

*Esthonyx* is a common genus in mammalian faunas of the North American early Eocene, but it is never abundant. Consequently, there are no large geographically and stratigraphically homogeneous samples that can be used to quantify dental variability in *Esthonyx*. The two largest samples available are (1) specimens of lower Graybullian *Esthonyx spatularius* from the restricted 30 m stratigraphic interval between levels 1675 m and 1705 m in University of Michigan collections from the Clark's Fork Basin, Wyoming, and (2) specimens of Lostcabinian *Esthonyx bisulcatus* from the San José Formation in the San Juan Basin, New Mexico. Statistical summaries of tooth size in these two samples are listed in Tables 1 and 2, respectively. The latter sample is particularly important since it contains the type specimens of Cope's three original species of *Esthonyx*.

Examination of Tables 1 and 2 indicates that there are not large enough samples of *Esthonyx* available at present to permit a definitive study of the dental variability of this genus. However, the larger of the available samples (Table 2) does at least suggest that variability in *Esthonyx* conformed to the general mammalian pattern, with  $M_1$  and  $M_2$  being the least variable cheek teeth (Gingerich, 1974). The first lower molar in *Esthonyx* is also usually the best represented in terms of number of specimens available for study. Therefore we have based much of our analysis of size

TABLE 1 — Summary of measurements of the lower and upper cheek teeth in a sample of *Esthonyx spatularius* from a 30 m stratigraphic interval in the lower Graybullian, Clark's Fork Basin. All specimens in University of Michigan collection, from localities between levels 1675 m and 1705 m of stratigraphic section shown in Text-fig. 3. Distribution of  $M_1$  size is compared to that of other Wasatchian species in Text-fig. 1. L is length; W, width; n, sample size; OR, observed range;  $\bar{x}$ , sample mean; s, standard deviation; V, coefficient of variation. Measurements in mm.

		n	OR	$\bar{x}$	s	V
$P_3$	L	2	5.4–5.7	5.55	.21	3.8
	W	2	3.5–3.7	3.60	.14	3.9
$P_4$	L	3	6.6–7.1	6.77	.29	4.3
	W	3	4.9–5.3	5.07	.21	4.1
$M_1$	L	8	6.5–7.8	7.18	.43	6.0
	W	8	5.5–6.2	5.90	.25	4.2
$M_2$	L	9	7.3–8.2	7.92	.27	3.4
	W	9	6.0–7.0	6.47	.38	5.8
$M_3$	L	3	9.6–10.3	9.97	.35	3.5
	W	4	5.1–5.7	5.40	.26	4.8
Log <sub>e</sub> (L x W) of $M_1$		8	3.65–3.83	3.74	.064	—
$P^3$	L	1	6.8	—	—	—
	W	1	5.5	—	—	—
$P^4$	L	0	—	—	—	—
	W	0	—	—	—	—
$M^1$	L	4	6.9–8.2	7.60	.54	7.0
	W	4	9.7–12.6	10.90	1.24	11.3
$M^2$	L	3	7.0–7.9	7.43	.45	6.1
	W	3	10.4–12.4	11.50	1.02	8.8
$M^3$	L	1	6.0	—	—	—
	W	1	10.2	—	—	—

trends in *Esthonyx* on changes observed in  $M_1$  size. The dentition of *Esthonyx* is typical of mammals in being diphyodont, with one set of molars that do not change in size ontogenetically. Tooth size is highly correlated with body size in mammals (Gould, 1975; Gingerich, 1976b), and changes in  $M_1$

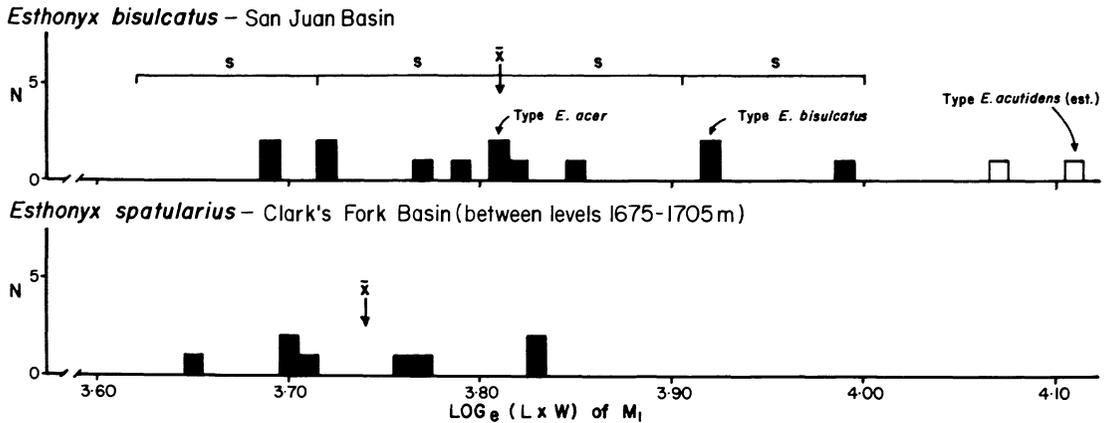
TABLE 2 — Summary of measurements of the lower cheek teeth of *Esthonyx bisulcatus* from the San Jose Formation, San Juan Basin, New Mexico. Sample is based on specimens in the American Museum of Natural History and National Museum of Natural History, and includes E. D. Cope's type specimens of *Esthonyx bisulcatus*, *E. acer*, and *E. burmeisteri*. Distribution of  $M_1$  size is compared to that of other Wasatchian species in Text-fig. 1. Abbreviations as in Table 1. Measurements in mm.

		n	OR	$\bar{x}$	s	V
$P_3$	L	1	6.7	—	—	—
	W	1	4.3	—	—	—
$P_4$	L	5	6.6–7.5	7.20	.37	5.1
	W	5	4.8–5.6	5.18	.36	6.9
$M_1$	L	13	7.1–8.3	7.57	.37	4.9
	W	13	5.5–6.7	5.97	.33	5.4
$M_2$	L	9	7.6–8.5	7.96	.34	4.2
	W	9	6.3–7.2	6.61	.29	4.4
$M_3$	L	6	9.0–11.2	10.33	.77	7.4
	W	6	4.8–6.0	5.65	.49	8.7
$\text{Log}_e(L \times W)$ of $M_1$		13	3.69–3.99	3.81	.095	—

size undoubtedly reflect changes in overall body size. Measurements of other teeth or measurements of osteological remains could be used to quantify size changes if they were better represented in collections, but the high degree of correlation and integration of skeletal parts in mammals dictates that study of other dental or skeletal characters would probably show a very similar pattern of change in body size to that documented here using  $M_1$  size.

A compound measure of crown cross-sectional area, length multiplied by width ( $L \times W$ ), is used to represent  $M_1$  size in order to take advantage of two independent measurements of each tooth. A logarithmic scale is used to make the variability of samples of large individuals comparable to that of samples of smaller individuals. The fact that large samples of *Esthonyx* are not available from single localities means that the expected range of variation in  $M_1$  size must be estimated statistically. The standard deviation of the  $\log_e$  of length multiplied by width ( $L \times W$ ) of  $M_1$  for the largest sample is .095 (Table 2). Hence, two standard deviation units on each side of the mean, encompassing 95% of the expected range of  $M_1$  size variation for the whole population, gives a total expected range of about .380 on a natural logarithmic scale. This is typical of the range of variation of large homogeneous samples of other living and fossil mammals studied.

Standard deviation units can be used to compare the means of small samples, and the value of .095 for  $\text{Ln}(L \times W)$  of  $M_1$  has been used in the diagnoses to quantify the amount of difference between type specimens. If a representative value for one sample exceeds a representative value for another sample by more than two standard deviation units, there is less than .05 probability that the two represent the same population. To illustrate this, tooth size is plotted graphically in text-



TEXT-FIG. 1 – Comparison of size distributions of Wasatchian species of *Esthonyx*, based on samples described in Tables 1, 2, and 9. Expected size range of 95% of San Juan Basin *E. bisulcatus* is shown above the actual distribution as the mean ( $\bar{x}$ )  $\pm$  two standard deviations (s). This range of .38 units on a natural logarithmic scale was used to construct the width of the shaded evolutionary pathways in text-figure 3. Early Wasatchian *E. spatularius* falls within the expected size range of late Wasatchian *E. bisulcatus*, but differs from it in premolar morphology (see text). Specimens of *E. acutidens* from the Wind River Basin are shown with open squares for comparison. Note that the holotype of *E. acutidens* falls well outside the range of San Juan Basin *E. bisulcatus*.

figure 1 for samples of the three species of Wasatchian *Esthonyx*. The mean and an expected range of four standard deviation units are shown for *E. bisulcatus* (total range = .38 on the  $\log_e$  scale). Note that the two specimens of *E. acutidens* shown in text-figure 1 fall well outside of the expected range of *E. bisulcatus*. They are approximately three standard deviations from the mean of *E. bisulcatus*, and the probability is less than .01 that they were sampled from the same population. The width of the shaded areas shown in text-figure 3 has been constructed to include a band width of four standard deviation units at any given stratigraphic level.

### SYSTEMATIC REVISION

The evolutionary patterns outlined in the following section of this paper were originally determined from a study of the fossils and stratigraphic framework before any species names were (or could be) applied to the patterns. Once the patterns were known, it was possible to search the literature, compare the various species types, and apply names to successive segments of the evolutionary lineages. Since use of the valid names will facilitate subsequent discussion, we present the systematic revision before the evolutionary patterns, although the latter formed the basis of the systematic revision.

All of the available species names for early Eocene *Esthonyx* and the closely related genus *Megalesthonyx* are listed in Table 3. The type locality, type specimen number, and size of  $M_1$  in the type specimen are also listed in Table 3 to facilitate comparisons. *Esthonyx* is not an abundant mammal in existing collections, and the type sample is in most cases still limited to the type specimen itself. Six early Eocene species of *Esthonyx* were generally recognized as valid before this study (Gazin, 1953), and we here recognize seven species. New collections from Clarkforkian sediments in the Clark's Fork Basin and surrounding area within the northern Big Horn Basin have yielded two new

TABLE 3 — Species of *Esthonyx* and its close relatives from the early Eocene of North America and Europe. Species of early Eocene Tillodontia recognized as valid in this revision are numbered in the order in which they were described. Locality, specimen number, and size of  $M_1$  are given for the type specimen of each species.

Species	Type Locality	Type Specimen	$\text{Log}_e(\text{LxW})$ of $M_1$	Additional References
(1) <i>Esthonyx bisulcatus</i> Cope, 1874 [Type species of <i>Esthonyx</i> ]	Arroyo Blanco, San Juan Basin New Mexico	USNM 1103	3.92	Simpson, 1951, p. 14
<i>Esthonyx burmeisteri</i> Cope, 1874 [Synonym of <i>E. bisulcatus</i> ]	Arroyo Blanco, San Juan Basin New Mexico	USNM 1105	—	Simpson, 1951, p. 14
<i>Esthonyx acer</i> Cope, 1874 [Synonym of <i>E. bisulcatus</i> ]	Arroyo Almagre, San Juan Basin New Mexico	USNM 1104	3.81	Simpson, 1951, p. 16
<i>Esthonyx miticulus</i> Cope, 1874 [Now placed in <i>Hyopsodus</i> ]	Arroyo Almagre, San Juan Basin New Mexico	Type lost	2.48	Cope, 1874, p. 8 Simpson, 1951, p. 16
(2) <i>Esthonyx spatularius</i> Cope, 1880	Gray Bull beds, Big Horn Basin Wyoming	AMNH 4809	—	Gazin, 1953, p. 23
(3) <i>Esthonyx acutidens</i> Cope, 1881	Lost Cabin beds, Wind River Basin, Wyoming	AMNH 4807	—	Gazin, 1953, p. 25
(4) <i>Esthonyx muniteri</i> (Lemoine, 1891) [Type species of <i>Plesiesthonyx</i> ]	Spamacia(?) , Paris Basin France	MNH 5174	—	Teilhard, 1922, p. 63
(5) <i>Esthonyx grangeri</i> Simpson, 1937	Clark Fork beds, Clark's Fork Basin, Wyoming	AMNH 16067	4.66	—
<i>Esthonyx latidens</i> Simpson, 1937 [Synonym of <i>E. grangeri</i> ]	Clark Fork beds, Clark's Fork Basin, Wyoming	AMNH 16066	4.43	—
(6) <i>Megalesthonyx hopsoni</i> Rose, 1972 [Type species of <i>Megalesthonyx</i> ]	Yale Loc. 33 (Lostcabinian), Big Horn Basin, Wyoming	YPM 18767	4.83	—
(7) <i>Esthonyx xenicus</i> , new species	Michigan Loc. SC-74 (Clark- forkian), northern Big Horn Basin, Wyoming	UM 66166	3.87	—
(8) <i>Esthonyx ancylion</i> , new species	Michigan Loc. SC-176 (Clark- forkian), Clark's Fork Basin, Wyoming	UM 68551	4.18	—

species, and our more complete understanding of stratigraphic relationships requires revision of several species previously proposed by others.

### Order TILLODONTIA Marsh, 1875

#### Family ESTHONYCHIDAE Cope, 1883

Anchippodontidae Gill, 1872, p. 11

Tillotheriidae Marsh, 1875, p. 221

Esthonychidae Cope, 1883, p. 80

*Included genera.*— Tillodonts are all placed in one family Esthonychidae, which is usually divided into two subfamilies: Esthonychinae including *Esthonyx* Cope and *Megalesthonyx* Rose, and Trogosinae including *Trogosus* Leidy, *Tillodon* Gazin, and *Anchippodus*(?) Leidy. Additional genera have been described from Asia that appear to be esthonychid, but these cannot yet be allocated confidently to subfamilies. The Asian genera are *Adapidium* Young, 1937; *Kuanchuanus* Chow, 1963; *Lofochaius* Chow *et al.*, 1973; *Meiostylodon* Wang, 1975; and probably *Basalina* Dehm and Oettingen-Spielberg, 1958.

*Stratigraphic and geographic distribution.*— Esthonychids are known from the middle(?) Paleocene through late Eocene of Asia, the early and middle Eocene of North America, and the early Eocene of Europe.

*Discussion.*— Gazin (1953) revised the family-group nomenclature of tillodonts and included all the known genera in the family Esthonychidae Cope, 1883. The two family-group names with priority over Esthonychidae (Anchippodontidae and Tillotheriidae) were rejected because *Anchippodus* is of indeterminate affinities, and *Tillotherium* is a junior synonym of *Trogosus*. By modern rules of nomenclature, Tillotheriidae would continue to be available for the name of the family group even though the genus on which it is based is a junior synonym of another genus. However, following Article 40(a) of the International Code of Zoological Nomenclature, Esthonychidae appears to be the valid name. Gazin's (1953) revision predates the year 1961, and this name has won general acceptance (cf. Lavocat, 1958; Romer, 1966; Rose, 1972).

#### *Esthonyx* Cope

*Esthonyx* Cope, 1874, p. 6. Type: *Esthonyx bisulcatus* Cope.

*Plesiesthonyx* Lemoine, 1891, p. 276. Type: *Plesiesthonyx munieri* Lemoine.

*North American species.*— *Esthonyx xenicus* nov., *E. ancylion* nov., *E. grangeri* Simpson, *E. spatularius* Cope, *E. bisulcatus* Cope, *E. acutidens* Cope.

*European species.*— *E. munieri* Lemoine.

*Known distribution.*— Early Eocene (Clarkforkian and Wasatchian) of the western interior of North America, and early Eocene (Sparnacian or Cuisian) of the Paris Basin in Europe. Morris (1966) reported cf. *Esthonyx* sp. from Baja California, but this specimen has never been described.

*Diagnosis.*— *Esthonyx* and *Megalesthonyx* differ from other Tillodontia in having relatively large rooted second incisors that are oval in cross-section with enamel limited to the anterior, lateral, and a narrow band of the medial surfaces of the crown. P<sub>2</sub><sup>2</sup> one- or two-rooted. *Esthonyx* has canines relatively large, anterior cheek teeth less reduced than in later genera, P<sub>3,4</sub> with well-developed talonid. M<sub>1,3</sub> with distinct metastylids. P<sup>4</sup>-M<sup>3</sup> with broad buccal cingulum and distinct anterior and posterior cingula. *Esthonyx* differs from *Megalesthonyx* in being smaller and in lacking mesostyles on the upper molars.

*Description.*— The dental formula of all species of *Esthonyx* is  $\frac{2}{3} \cdot \frac{1}{1} \cdot \frac{3}{3} \cdot \frac{3}{3}$ . Three upper incisors are not known in any specimen. The remaining incisors, interpreted as  $I^2$  and  $I^3$  by Gazin (1953), are both large and have projecting crowns.  $I^2$  is much larger than  $I^3$ . Slight wear removes the thin enamel on the posterolingual surfaces of the incisors at even a young age. The upper canine is single-rooted, with a relatively blunt crown that is oval in cross-section. Judging from alveoli,  $P^2$  was two-rooted in *E. spatularius* and had a simple narrow crown.  $P^2$  in *E. acutidens* is single-rooted and the crown reduced to a simple conical shape (Gazin, 1953, p. 25-26).  $P^3$  is triangular in outline, with a small protocone at the base of the medial apex of the crown. A single large buccal cusp is present on  $P^3$ . The crown of  $P^4$  is molariform, but differs from the true molars in being shorter anteroposteriorly, in having the paracone and metacone little separated, and in having a smaller hypocone shelf. The upper molars are tritubercular, with a broad buccal cingulum, a distinct anterolingual cingulum, and a prominent posterolingual cingulum. The latter occasionally supports a small distinct hypocone. The buccal cingulum on the upper molars lacks a mesostyle, but a strong parastylar crest extends out anterobuccally on  $M^2$  and  $M^3$ , giving these teeth a much less symmetrical appearance than is seen in  $M^1$ .

The lower central incisors are relatively small.  $I_2$  is the largest of the anterior lower teeth.  $I_3$  is very small, being only approximately half the size of  $I_1$ . All three lower incisors have very thin enamel on the posterior surface of the crown, and this wears away at an early age. They have a thick enamel covering on the anterior surfaces that extends onto the medial and lateral sides as well. The lower canines are approximately the same size as  $I_2$ , and they also have a thin covering of enamel on the posterolingual surface of the crown. This is often worn completely away, leaving enamel covering only the labial, medial, and distal surface of the tooth.  $P_2$  and  $P_3$  are two-rooted in the lineage leading to *E. grangeri*, but  $P_2$  is usually single-rooted in *E. spatularius* and its descendants. The crown of  $P_2$  is narrow with a single major cusp and no talonid, whereas  $P_3$  has a small but distinctly basined talonid.  $P_4$  is nearly molariform but it has a narrower crown and lacks the metastylid usually found on  $M_{1-3}$ . The lower molars have a distinct hypoconid and entoconid on the talonid. The hypoconid is not well developed except on  $M_3$ , where it forms an extended posterior lobe.

The mandibular rami are unfused in the lineage leading to *E. grangeri*, but they are always solidly fused in *E. spatularius* and its descendants. A nearly complete skull of *Esthonyx* is known from the Clarkforkian of the Clark's Fork Basin (Plate 2), but its structure has not yet been analyzed in detail.

*Discussion.*— There are clearly at least two lineages of *Esthonyx* represented in North America that do not differ greatly in structure. The first lineage, leading to *E. grangeri*, appeared at the beginning of the Clarkforkian and evolved rapidly, disappearing in the early Wasatchian. The second known lineage, comprising *E. spatularius* and its descendants, first appeared at the beginning of the Wasatchian and it evolved relatively slowly through the Wasatchian and into the early Bridgerian.

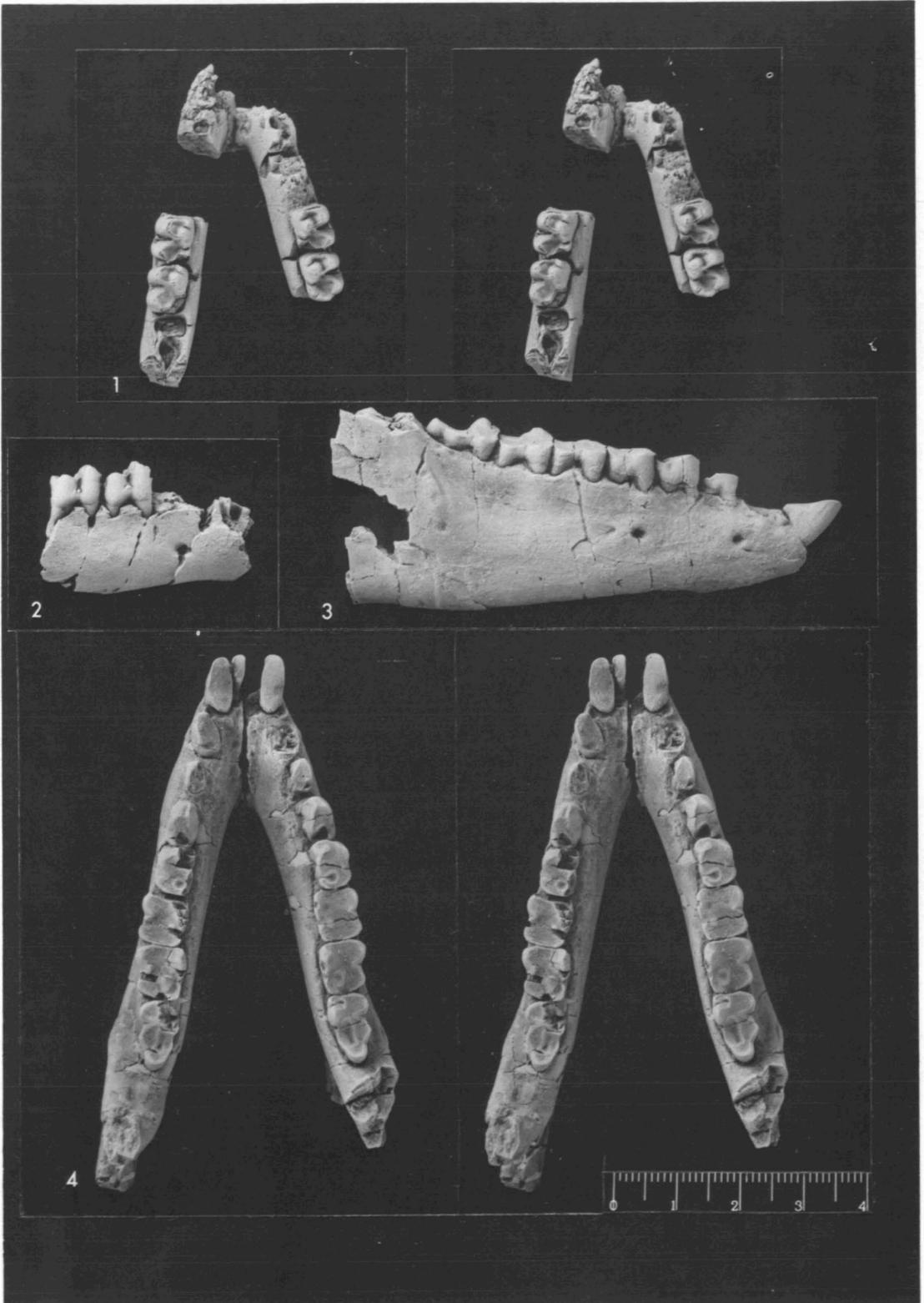
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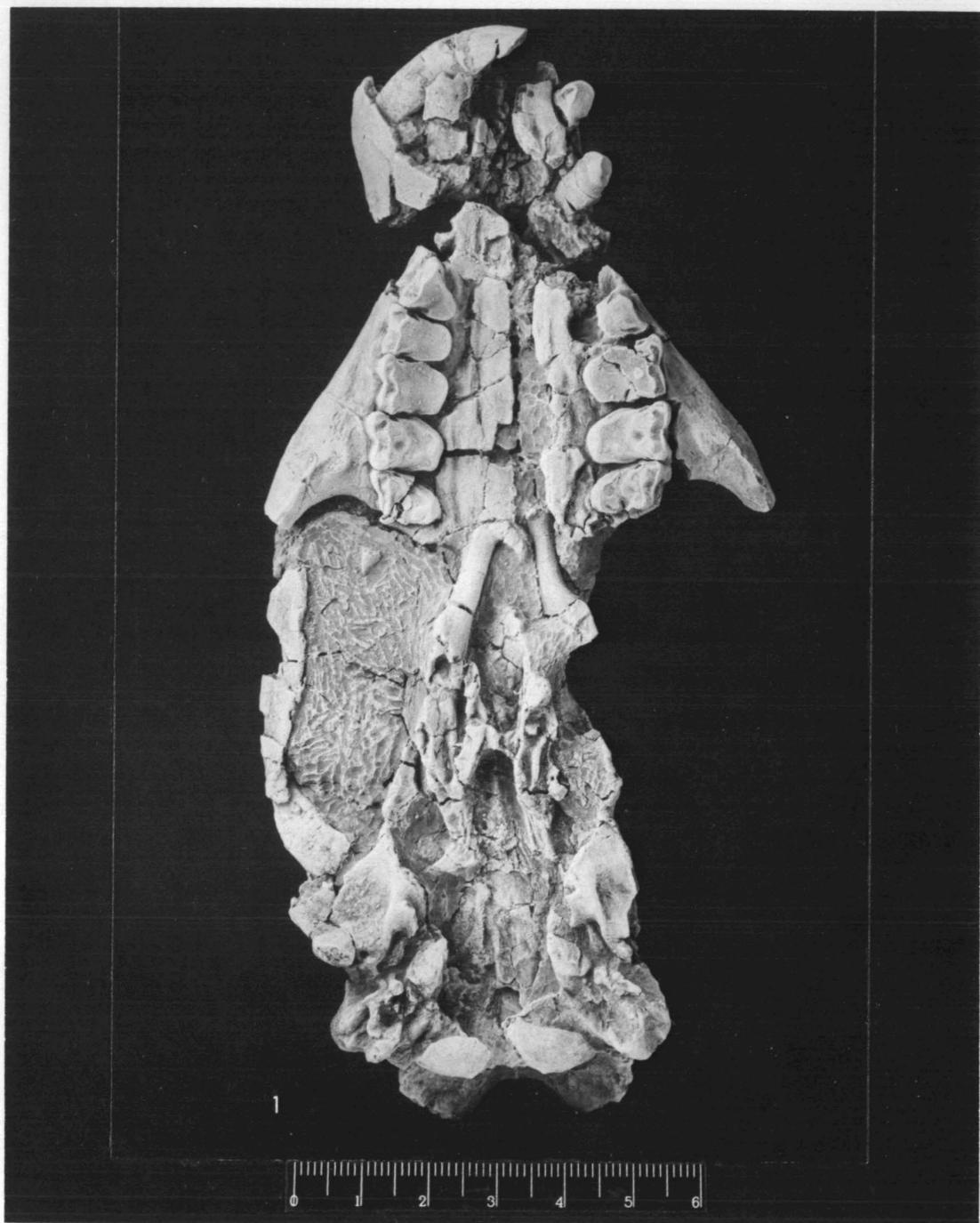
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EXPLANATION OF PLATE 1

(All figures natural size, scale in cm)

- Figure 1 — Type specimen of *Esthonyx xenicus*, UM 66166, left and right mandibles with  $M_{1-2}$  in occlusal view, stereophotograph.
- Figure 2 — Type specimen of *Esthonyx xenicus*, UM 66166, right mandible with  $M_{1-2}$  in lateral view.
- Figure 3 — Type specimen of *Esthonyx ancylion*, UM 68511, right mandible with  $I_2$  and  $P_{2-4}M_{1-3}$  in lateral view.
- Figure 4 — Type specimen of *Esthonyx ancylion*, UM 68511, left and right mandibles with nearly complete lower dentition in occlusal view, stereophotograph. Note heavy wear on all teeth, and unfused mandibular symphysis.





## EXPLANATION OF PLATE 2

(Figure natural size, scale in cm)

Figure 1 – Type specimen of *Esthonyx ancylion*, UM 68511, cranium with nearly complete upper dentition in palatal view.

The two lineages are most distinctive in the structure of the mandibular symphysis, with the symphysis being solidly fused in the later one. Since both lineages of *Esthonyx* did change significantly through time, they are potentially important biostratigraphically. This is especially true in the Clarkforkian. The following descriptions will consider each of the North American species in order of their appearance in the geological record. A brief discussion of the only European species of *Esthonyx* follows description of the North American forms.

*Esthonyx xenicus*, new species

Pl. 1, fig. 1, 2; Pl. 3, fig. 1, 4

*Esthonyx ?bisulcatus*, Simpson, 1937, p. 6, fig. 1.

*Esthonyx* cf. *spatularius*, Gazin, 1953, p. 21, fig. 5.

*Esthonyx spatularius* (in part), Van Valen, 1963, p. 367, Pl. 2, fig. 1, 4.

*Type*.— UM 66166, right and left mandibles and maxillae, with  $M_{1-2}$  on both sides, left  $dP^{3-4}M^1$  and right  $M^{1-2}$ . Collected in 1976 by G. F. Gunnell from UM locality SC-74 on the east side of Polecat Bench (E½, NW¼, S36, T56N, R100W, Park Co., Wyoming).

*Diagnosis*.— Differs from *E. ancylion* and *E. grangeri* in being significantly smaller ( $M_1$  sizes in the type specimens differ by 3.3 and 8.3 standard deviation units, respectively). *E. xenicus* also differs in having a relatively shallower mandible. Differs from *E. spatularius*, *E. bisulcatus*, and *E. acutidens* in lacking symphyseal fusion and in having a narrower  $P_2$  that is two-rooted rather than single-rooted. Differs from *E. munieri* in being smaller and having less inflated cheek teeth.

*Etymology*.— *xenikos*, Gr., of a stranger, foreign, with reference to the apparent immigration of *Esthonyx* into North America, this being the earliest North American species.

*Age and distribution*.— Lower part of the Clarkforkian, early Eocene, from beds below and in the lower part of the *Plesiadapis cookei* Zone. *E. xenicus* is at present known only from the northern Big Horn Basin, including the Clark's Fork Basin, Wyoming.

*Description*.— The dental morphology of *E. xenicus* conforms to that described above under the generic description. However, *E. xenicus*, like *E. ancylion* and *E. grangeri* but unlike *E. spatularius* and its descendants, lacks fusion of the mandibular rami. This is true even in old individuals with heavily worn teeth (e.g., PU 19988). The mandibular symphysis in *E. xenicus* ends at the level of the front edge of  $P_3$ , whereas in *E. spatularius* the symphysis ends at the front edge of  $P_4$ . *E. xenicus* is also distinguished from the similar species *E. spatularius* by having a longer, narrower two-rooted  $P_2$  and  $P_3$  (see discussion under *E. spatularius*). The deciduous upper fourth premolar is well preserved in the holotype, and it differs from the true molars principally in being narrower buccal-lingually (Pl. 3, fig. 1).

Measurements of the type and other specimens of *E. xenicus* from the type locality are given in Table 4.

*Discussion*.— Simpson (1937) described the first known specimen of *E. xenicus*, AMNH 16065, a well-preserved left mandible with all cheek teeth. He referred this specimen questionably to *E. bisulcatus* since it fell within the expected range of size variation of the Graybullian specimens he identified as *E. bisulcatus*. Simpson also included *E. spatularius* tentatively in *E. bisulcatus*. Gazin (1953) retained the name *E. spatularius* for early Graybullian specimens, and referred AMNH 16065 to this species. With a greater number of good specimens now available from carefully documented stratigraphic levels, it is clear that AMNH 16065 does not belong to either *E. bisulcatus* or *E. spatularius*.

Examination of the paleontological archives in the American Museum of Natural History indicates that AMNH 16065 was collected by William Stein on October 2, 1912, from the "Bluff N.E. of

TABLE 4 — Measurements of the teeth in the type and other specimens of *Esthonyx xenicus* from UM locality SC-74. Measurements in mm.

Tooth	UM 66166 (type)		UM 71234		AMNH 16065	
	Length	Width	Length	Width	Length	Width
P <sub>2</sub>	—	—	—	—	4.2	2.7
P <sub>3</sub>	—	—	—	—	6.0	4.1
P <sub>4</sub>	—	—	6.6	5.8*	7.4	5.3
M <sub>1</sub>	7.4	6.5	—	—	7.5	6.5
M <sub>2</sub>	7.9	6.7	7.5*	6.5*	7.7	6.6
M <sub>3</sub>	—	—	8.0*	5.8*	9.4	5.1
dp <sup>4</sup>	7.1	7.2	—	—	—	—
M <sup>1</sup>	8.0	10.1	—	—	—	—
M <sup>2</sup>	—	11.6	—	—	—	—

\*estimated

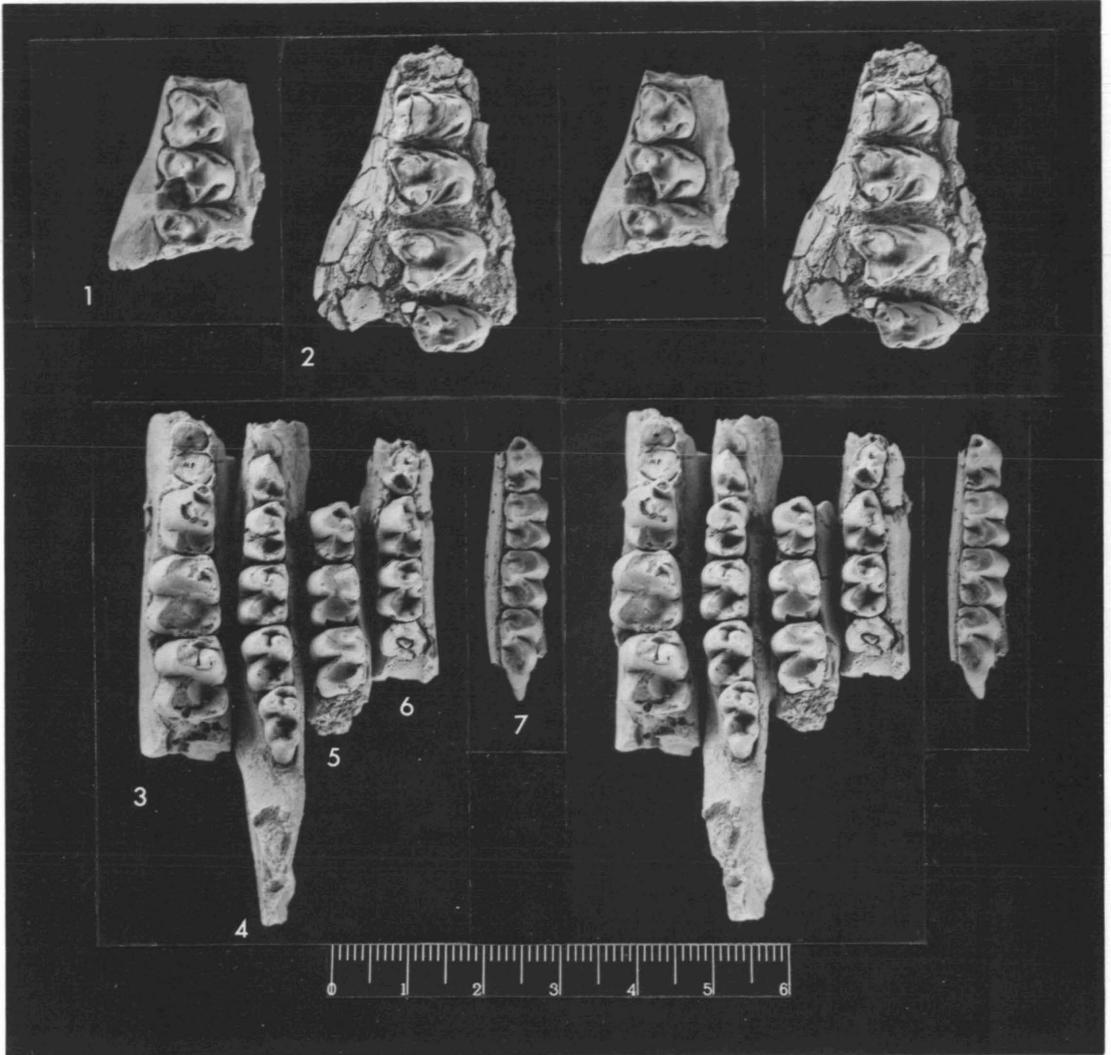
Ralston [Polecat Bench] — on Fisher's contact line." A note on the original specimen label indicates that this is "between Ralston and Powell," two towns on the south and east sides of Polecat Bench. "Fisher's contact line" refers to the "Laramie-Wasatch" (*i.e.*, Cretaceous-Tertiary) boundary shown by Fisher (1906, Pl. 3). This would place the locality where AMNH 16065 was found in section 36, T56N, R100W. In other words, AMNH 16065 probably came from very near what we now call locality SC-74, the type locality of *Esthonyx xenicus*. Fisher (1906) apparently mapped the beginning of the Tertiary as the first appearance of red beds in his stratigraphic section. Locality SC-74 is just below the lowest red beds on the east side of Polecat Bench.

It is interesting to note that according to a letter from W. Granger to W. D. Matthew, October 2, 1912 was followed by "three days of rain, sleet, and snow — over a foot of the latter." This bad weather undoubtedly curtailed the exploration Granger and Stein first began of Polecat Bench. Subsequently, G. L. Jepsen and others have documented a remarkably complete succession of Paleocene and early Eocene land mammal faunas in the vicinity of Polecat Bench.

Locality SC-74, the type locality of *Esthonyx xenicus*, is 1150 m above the Cretaceous-Tertiary boundary as exposed on Polecat Bench. Another specimen referred to *E. xenicus*, UM 71191 from locality SC-83, comes from level 915 m in the same section, which is at or near the base of the sedimentary sequence yielding Clarkforkian mammals.

*Esthonyx* is also represented in the small collection made by Jepsen from the Noble Site locality on the west side of the Clark's Fork Basin, west of the Clark's Fork River. The best specimen from this locality, PU 19988, is a left mandible with P<sub>2,4</sub> and M<sub>1</sub>. It is approximately the same size as UM 66166 and it has an unfused mandibular symphysis and a double-rooted P<sub>2</sub> with a narrow crown. This specimen and PU 19553 are clearly *E. xenicus* and help to date the Noble Site as lower Clarkforkian in age.

UM 71303, a left M<sub>2</sub> from locality SC-226 in the Badger Basin oil field, Clark's Fork Basin, also represents *E. xenicus*. Two specimens, UM 66320 and 67179 (both left mandibles), are tentatively referred to *E. xenicus* although they are slightly larger and from a higher stratigraphic level (localities SC-91 and SC-135, probably about level 1200 m on scale of text-fig. 3). They are clearly transitional between *E. xenicus* and its descendant *E. ancylion*.



## EXPLANATION OF PLATE 3

(All figures natural size, scale in cm)

- Figure 1 – Type specimen of *Esthonyx xenicus*, UM 66166, right maxilla with  $dP^4M^{1-2}$  in occlusal view, stereophotograph.
- Figure 2 – *Esthonyx ancylion*, UM 67189, right maxilla with  $P^4M^{1-3}$  in occlusal view, stereophotograph.
- Figure 3 – *Esthonyx grangeri*, UM 66154, left mandible with  $P_4M_{1-2}$  in occlusal view, stereophotograph.
- Figure 4 – *Esthonyx xenicus*, AMNH 16065, left mandible with  $P_{2-4}M_{1-3}$  in occlusal view, stereophotograph.
- Figure 5 – *Esthonyx spatularius*, UM 65465, left mandible with  $P_4M_{1-2}$  in occlusal view, stereophotograph.
- Figure 6 – *Esthonyx bisulcatus*, UM 65939 from Lysitean of central Big Horn Basin, left mandible with  $P_{3-4}M_1$  in occlusal view, stereophotograph. Note open trigonid on  $P_4$  distinguishing this species from otherwise similar *E. spatularius*.
- Figure 7 – *Esthonyx bisulcatus*, USNM 1104 from San Juan Basin (holotype of *E. acer*), right mandible with  $P_4M_{1-3}$  in occlusal view, stereophotograph. Note open trigonid on  $P_4$ .

*Typodigm.*— The type sample from SC-74 includes UM 66166 (holotype), 71234, and probably AMNH 16065. Other specimens referred to *E. xenicus* were all mentioned above.

*Esthonyx ancylion*, new species

Text-fig. 2; Pl. 1, fig. 3, 4; Pl. 2, fig. 1; Pl. 3, fig. 2

*Type.*— UM 68511, skull and both mandibles, with a nearly complete dentition. Collected in 1977 by Mr. M. Godinot from UM locality SC-176 on the west side of Polecat Bench, Clark's Fork Basin (NW¼, NW¼, S28, T56N, R100W).

*Diagnosis.*— Differs from *E. xenicus* in being significantly larger ( $M_1$  in type is 3.3 standard deviation units larger than type of *E. xenicus*) with a relatively deeper mandible. Differs from *E. grangeri* in being significantly smaller ( $M_1$  in type is 5.1 standard deviation units smaller than type of *E. grangeri*), with a shallower mandible. Differs from *E. spatularius*, *E. bisulcatus*, and *E. acutidens* in lacking symphyseal fusion of the mandibular rami and in retaining a two-rooted  $P_2$ . Approximately the same size as *E. munieri*, but differs from it in having a relatively higher paraconid and metaconid, a less open trigonid, and a less rounded heel on  $P_4$ . Also differs from *E. munieri* in having a relatively longer talonid lobe on  $M_3$ .

*Etymology.*— *ancylion*, Gr., ring or link in a chain, with reference to the intermediate position of this species in linking *E. xenicus* to *E. grangeri*.

*Age and distribution.*— Middle part of the Clarkforkian, early Eocene, from beds in the middle and upper part of the *Plesiadapis cookei* Zone and the lowest beds of the overlying *Phenacodus-Ectocion acme* Zone. *E. ancylion* is presently known only from the Clark's Fork Basin, Wyoming.

*Description.*— The dental morphology of this species is very similar to that of *E. xenicus* and *E. grangeri*, the principal difference from those species being its intermediate size. The type specimen is a skull with virtually the entire upper and lower dentition, and this can be described in greater detail than is possible for most other species of *Esthonyx*. Reference is made also to Plate 1, fig. 3, 4; and Plate 2, fig. 1. Measurements of the dentition of the type specimen, UM 68511, are given in Table 5.

The preserved upper incisors of *E. ancylion* are both large, stout teeth with a relatively short, simple crown. The roots are definitely closed, indicating that the incisors were not ever-growing. The enamel is completely worn off of the posterior surfaces of both incisors. The additional incisor usually present in generalized placental mammals appears to have been lost even in early species of *Esthonyx*, but it is not possible to determine with certainty if the tooth now missing was  $I^1$ ,  $I^2$ , or  $I^3$ . We follow Gazin (1953) in identifying the remaining teeth as  $I^2$  and  $I^3$ , but emphasize that the true homologies cannot be determined with certainty.

The upper canine is oval in cross-section, with a short crown and long root. The canine is emplaced entirely in the maxillary bone some 3 mm behind the premaxilla-maxilla suture.  $P^1$  is not present in any *Esthonyx*. The crown of  $P^2$  is not preserved in UM 68511 but alveoli on the right side of the skull show it to have been two-rooted, unlike the condition in *E. acutidens* where  $P^2$  is clearly single-rooted (Gazin, 1953, fig. 8). The remainder of the upper molars have the structure of typical *Esthonyx*, as described above under the generic description.

The lower dentition includes three incisors, of which only  $I_2$  is enlarged.  $I_1$  is much smaller but clearly functioned with  $I_2$ , occluding against  $I^1$  above. The crown of  $I_3$  is not preserved, but judging from the size of the root the crown was very small. The lower canine is a stout tooth like the upper canine, with a large root and short blunt crown.  $P_2$  is a small tooth with a narrow crown and two distinct roots.  $P_{3,4}$  and  $M_{1,3}$  are typical of these teeth in other *Esthonyx*, as described above.  $P_4$  has a relatively closed trigonid as is typical of primitive *Esthonyx*. UM 68511 clearly represents an adult animal with all teeth heavily worn, yet there is no sign of symphyseal fusion of the mandibular rami. A mandible with little dental wear, UM 71455, is illustrated in text-figure 2.

TABLE 5 — Measurements of the teeth in the type specimen of *Esthonyx ancylion*, UM 68511, from UM locality SC-176. Measurements in mm.

Mandibular Dentition			Maxillary Dentition		
<u>Tooth</u>	<u>Length</u> (Anteroposterior)	<u>Width</u> (Transverse)	<u>Tooth</u>	<u>Length</u> (Anteroposterior)	<u>Width</u> (Transverse)
I <sub>1</sub>	4.0	2.2	I <sup>1</sup>	—	—
I <sub>2</sub>	7.3	4.1	I <sup>2</sup>	7.0	5.2
I <sub>3</sub>	2.2*	1.0*	I <sup>3</sup>	6.1	4.5
C	6.0	4.2	C	5.8	3.7
P <sub>2</sub>	5.0	3.5	P <sup>2</sup>	—	—
P <sub>3</sub>	7.2	5.0	P <sup>3</sup>	8.5	8.4
P <sub>4</sub>	7.5	5.9	P <sup>4</sup>	7.7	10.7
M <sub>1</sub>	8.5	7.7	M <sup>1</sup>	8.8	10.8
M <sub>2</sub>	8.5	8.2	M <sup>2</sup>	8.5	12.4
M <sub>3</sub>	11.2	7.2	M <sup>3</sup>	6.9	10.8

\*estimated

Some details can be added here concerning the structure of the skull in *Esthonyx ancylion*. Cranial length measured from the upper central incisors to the occipital condyles appears to have been approximately 150 mm. The skull was approximately 80 mm wide across the zygomatic arches. Strong sagittal and nuchal crests are present and the preserved posterior portions (angle and ascending ramus) of each mandible are very large, indicating that the masticatory muscles were also large and powerful. By comparison with modern mammals, the brain appears to have been very small. Cranial proportions resemble those of the living opossum *Didelphis*, but the snout was relatively shorter and the angular portion of each mandible was much larger in *Esthonyx*. More detailed study and a graphic reconstruction of the skull of *E. ancylion* are in progress.

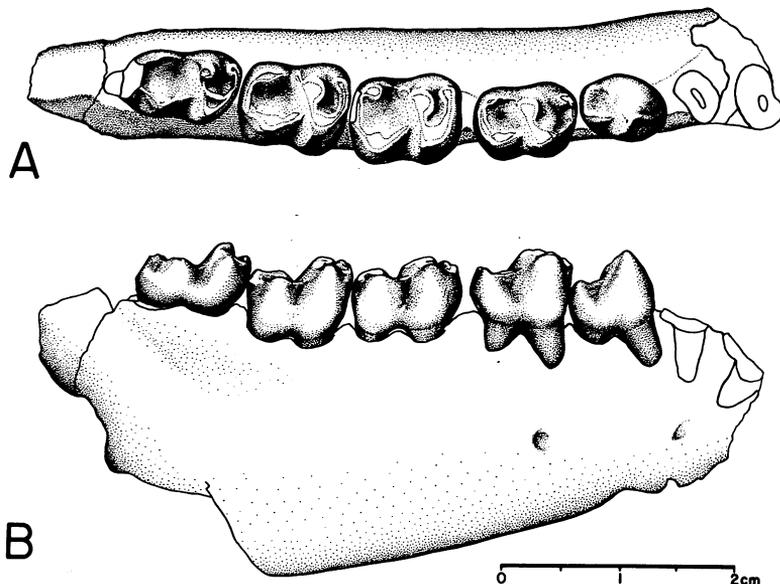
*Discussion.*— Discovery of this species is a welcome addition to knowledge of *Esthonyx* since it connects *E. xenicus* with the much larger *E. grangeri* by a graded series of intermediate specimens. A total of some twenty specimens of *E. ancylion* are now known, all from a restricted stratigraphic interval about 200 m thick in the middle part of the Clarkforkian. *E. ancylion* is one of an increasing number of Clarkforkian species known to be restricted to a narrow stratigraphic range, making it potentially useful for detailed biostratigraphic correlation.

*Typodigm.*— The type specimen, UM 68511, is the only specimen from the type locality. Other specimens in the hypodigm from the Clark's Fork Basin include: UM 65010, 65051, 65774, 65780, 66732, 66912, 67189, 68225, 68236, 68245, 68874, 69264, 69298, 69309, 71455, 71464, 71474; PU 18176, 19622, 20987, and 21513.

*Esthonyx grangeri* Simpson, 1937

Pl. 3, fig. 3

*Esthonyx grangeri* Simpson, 1937, p. 9, fig. 2, 3. Gazin, 1953, p. 28, fig. 9, 10.*Esthonyx latidens* Simpson, 1937, p. 10, fig. 4. Gazin, 1953, p. 30, fig. 11.*Esthonyx* sp., Gazin, 1953, p. 62, fig. 21.



TEXT-FIG. 2 – Right mandible of *Esthonyx ancylion*, UM 71455, with  $P_{3-4}M_{1-3}$  in occlusal (A) and lateral view (B). Roots of the lower canine and  $P_2$  are preserved but the crowns are missing. Reproduced 1.5 x natural size.

*Type.*— AMNH 16067, a left mandible with  $P_4M_{1-3}$ . Collected by W. Granger in 1912 from the “Head of Big Sand Coulee,” Clark’s Fork Basin, Wyoming.

*Type of synonym.*— *Esthonyx latidens*: AMNH 16066, left maxilla with  $dP^3-M^1$ ; left  $dP_3-M_1$ , and associated teeth. Collected by W. Granger in 1912 from “3 miles east of mouth of Pat O’Hara Creek,” Clark’s Fork Basin, Wyoming. The fauna from this locality is very nearly the same age as that from the head of Big Sand Coulee where the type specimen of *E. grangeri* was found.

*Diagnosis.*— Largest known species of *Esthonyx*. Differs from *E. xenicus* and *E. ancylion* also in having a relatively deeper mandibular ramus. Differs from *E. spatularius*, *E. bisulcatus*, and *E. acutidens* also in lacking symphyseal fusion of the mandibular rami. Differs from *E. munieri* in having a less open trigonid on  $P_4$ , relatively longer  $M_3$ , and less inflated molar cusps.

*Age and distribution.*— Upper Clarkforkian and lowermost Wasatchian (all but the lowest beds of the *Phenacodus-Ectocion* acme Zone of the Clarkforkian and the overlying *Pelycodus ralstoni* Zone of the Wasatchian), early Eocene. *E. grangeri* is presently known only from the Big Horn Basin, including the Clark’s Fork Basin, northwestern Wyoming.

*Description.*— The dentition of *Esthonyx grangeri* is very similar to that of *E. ancylion*, but larger. New specimens collected in recent years from the Clark’s Fork Basin document the stratigraphic range of *E. grangeri* but do not add any anatomical information to that previously published by Simpson (1937) and Gazin (1953). Measurements of the teeth of representative specimens are listed in Table 6.

*Discussion.*— The transition from *Esthonyx ancylion* to *E. grangeri* was a continuous one, and some intermediate specimens have to be arbitrarily allocated to one species or the other depending on their relative stratigraphic position. The boundary between successive species of a single evolving lineage is always arbitrary to some degree. The more complete the record documenting such a transition, the more arbitrary the boundary between successive species must be. To accurately represent

TABLE 6 — Selected measurements of teeth in the type and other specimens of *Esthonyx grangeri*. Additional measurements are given by Simpson (1937). Abbreviations as in Table 1. Measurements in mm. C.F. = Clarkforkian, W. = Wasatchian.

LOWER DENTITION										
Tooth	AMNH 16067 (type)		AMNH 16066 (type <i>E.</i> <i>latidens</i> )		UM 66154 (SC-72, C.F.)		UM 67351 (SC-149, C.F.)		UM 67471 (SC-26, W.)	
	L	W	L	W	L	W	L	W	L	W
P <sub>4</sub>	—	—	—	—	8.9	6.7	9.2	6.5	—	—
M <sub>1</sub>	10.7	9.9	9.9	8.5	10.2	9.3	10.0	8.0	—	—
M <sub>2</sub>	—	—	—	—	10.3	9.5	10.3	8.5	11.0	9.3
M <sub>3</sub>	—	—	—	—	—	—	—	—	15.2	9.0

UPPER DENTITION										
Tooth	AMNH 16066 (type <i>E.</i> <i>latidens</i> )		UM 66187 (SC-80, C.F.)		UM 66289 (SC-90, C.F.)		UM 65170 (SC-7, W.)			
	L	W	L	W	L	W	L	W		
P <sup>3</sup>	—	—	—	—	9.4	9.9	—	—		
P <sup>4</sup>	—	—	10.3	15.2	10.2	13.4	9.6	13.1		
M <sup>1</sup>	10.4	13.0	10.6*	—	10.5	16.1	9.1*	15.1*		
M <sup>2</sup>	—	—	10.8	—	—	—	9.1	17.0		

\*estimated

species diversity at any given time, the boundary between successive species must be a temporal one rather than a purely morphological one. Dividing *E. ancylion* and *E. grangeri* as shown in text-figure 3 conforms to this requirement.

The persistence of *Esthonyx grangeri* into the earliest Wasatchian contributes one of a number of primitive elements that make the Sand Coulee beds of Granger (1914) distinctive from the overlying Gray Bull beds. Primitive species of a number of Wasatchian lineages, *Pelycodus ralstoni* for example, also give the Sand Coulee fauna a less advanced character (Gingerich and Simons, 1977). The transitions from Sand Coulee to lower Gray Bull, and lower Gray Bull to upper Gray Bull beds are well documented in the Clark's Fork Basin, and the differences between these successive subdivisions of the Wasatchian are clearly not of the same magnitude as those distinguishing land mammal ages like the Tiffanian, Clarkforkian, and Wasatchian from each other. Jepsen (1930, p. 119) argued that the Sand Coulee beds were faunally indistinguishable from the lower Gray Bull beds. However, our recent field work supports Granger's (1914) and Simpson's (1937, p. 1 fn.) observations that the basal Wasatchian Sand Coulee fauna is distinctly more primitive than the lower Gray Bull fauna. *Esthonyx grangeri* is an element of the Sand Coulee fauna only rarely found in the latter.

*Typodigm.*— The exact locality where the type specimen, AMNH 16067, was found in the head of Big Sand Coulee is not known. Three additional specimens, UM 65261, 65644, and 68780 have also

been found in the head of Big Sand Coulee, but these are all fragmentary and add little to the type sample.

In addition, the following specimens of *E. grangeri* are known from the Clark's Fork Basin and northern Big Horn Basin: AMNH 16066; UM 64830, 64846, 64970, 65072, 65099, 65170, 65372, 66154, 66158, 66187, 66289, 66316, 66344, 66878, 67227, 67351, 67454, 67456, 67471, 68204, 69353; PU 13239, 13341, 14727, and 20995.

*Esthonyx spatularius* Cope, 1880

Pl. 3, fig. 5

*Esthonyx spatularius* Cope, 1880, p. 908. Cope, 1881, p. 186. Cope, 1885, p. 211, Pl. 24a, fig. 22-25.

*Esthonyx burmeisteri* (in part), Cope, 1885, p. 204.

*Esthonyx* sp. indet., Dorr, 1952, p. 91, Pl. 7, fig. 7. Dorr, 1978, p. 83.

*Esthonyx spatularius* (in part), Gazin, 1953, p. 21, fig. 4.

*Esthonyx bisulcatus* (in part), Denison, 1937, p. 14. Gazin, 1953, p. 17, fig. 3, 34. McKenna, 1960, p. 85, fig. 43. Delson, 1971, p. 353.

*Esthonyx* cf. *bisulcatus*, Gazin, 1962, p. 42.

*Type.*— AMNH 4809, eight associated teeth including a left  $P_3$ , left  $M_3$ , and posterior portion of right  $M_1$  or  $M_2$ . Collected by J. L. Wortman in 1880 from the Big Horn Basin, Gray Bull beds (see Gazin, 1953, p. 21-23 for discussion).

*Diagnosis.*— Close to *E. xenicus*, *E. bisulcatus*, and *E. munieri* in size. Differs from *E. xenicus* in having mandibular rami fused at the symphysis, a shorter, broader  $P_3$ , and smaller, less basined heels on  $P_3$  and  $P_4$ . Differs from *E. bisulcatus* in having a more closed trigonid on  $P_4$ , with the protoconid, paraconid, and metaconid positioned approximately at the apices of an equilateral triangle. Differs from *E. munieri* in the latter characteristic, and also in having less inflated cheek teeth. Differs from *E. ancylion* and *E. grangeri* in being smaller and having a fused mandibular symphysis. Differs from *E. acutidens* in being significantly smaller (text-fig. 1).

*Age and distribution.*— *Esthonyx spatularius* is known principally from the early Wasatchian, especially from the Sand Coulee and lower Gray Bull beds (*Pelycodus ralstoni* and *Pelycodus mckennai* Zones of Gingerich and Simons, 1977). Specimens from the upper Graybullian (*Pelycodus trigonodus* Zone) tend to be somewhat larger. Upper Graybullian specimens of *Esthonyx* are here provisionally referred to *E. spatularius*, but they may ultimately prove to be sufficiently distinct to warrant description of a new species. *Esthonyx spatularius* is known from the Clark's Fork, Big Horn, Hoback, and Powder River Basins, Wyoming. According to Gazin (1962), it is also known from several localities in southwestern Wyoming.

*Description.*— The upper and lower dentition of *Esthonyx spatularius* is relatively well known, and morphologically it conforms closely to that of other *Esthonyx*. The mandibular rami were solidly fused at the symphysis in the specimens preserving this region (e.g., UM 65336, 66839). The incisors and canines are preserved in UM 65336, and these appear to be virtually identical to the anterior dentition of Clarkforkian *Esthonyx xenicus* (e.g., UM 66633), in which the symphysis was unfused.  $P_2$  was clearly two-rooted in UM 66839. The talonids of  $P_3$  and  $P_4$  are relatively smaller in *E. spatularius* than in earlier *Esthonyx* but no other differences were noted from the dentition of typical *Esthonyx*.

Measurements of the teeth of an early Graybullian sample of *E. spatularius* are given in Tables 1 and 7.

*Discussion.*— The type specimen of *E. spatularius* is an association of isolated teeth. Much confusion about the relationships of this species has been caused by the poor condition of the type specimen. However, with the excellent comparative material now available it is possible to state with little

TABLE 7 — Measurements of the preserved cheek teeth in the type specimen of *Esthonyx spatularius*, AMNH 4809. Measurements in mm. Values in parentheses are two standard deviations less than the mean for the larger sample of this species described in Table 1. The holotype of *E. spatularius* is within two standard deviations of the early Graybullian sample mean in all measurements except M<sub>3</sub> length.

Tooth	Length		Width	
P <sub>3</sub>	5.2	(5.13)	3.7	(3.32)
M <sub>1</sub> or M <sub>2</sub>	—	(6.32 or 7.38)	5.9*	(5.40 or 5.71)
M <sub>3</sub>	8.6	(9.27)	4.9	(4.88)

\*estimated

doubt that *E. spatularius* is the correct name for the early Wasatchian material that has generally been identified as *E. bisulcatus*.

The type specimen of *E. spatularius* was found by J. L. Wortman in 1880 during a brief reconnaissance trip through the Big Horn Basin. It was apparently found with the type specimens of *Haplomylus speirianus* and *Didymictis leptomylyus*, and it was described with these by Cope (1880). The associated forms are important in determining the age of the type specimen of *E. spatularius* as lower Graybullian (Gazin, 1953, p. 21-23). Comparing the type specimen, AMNH 4809, with other early Graybullian *Esthonyx* further supports this age assignment. The type is smaller than most early Graybullian *Esthonyx*, but specimens as small as AMNH 4809 in most dimensions are known. The Clarkforkian specimen AMNH 16065 was considered to represent *E. spatularius* (Gazin, 1953) but its greater age indicates that it belongs to *E. xenicus*. The morphology of M<sub>3</sub> in AMNH 16065 is closely comparable to that in AMNH 4809, but the structure of P<sub>3</sub> is different. AMNH 4809 resembles early Graybullian *Esthonyx* in having a short, broad P<sub>3</sub> with a very small talonid (cf. especially UM 63668, 64616, and 68165). Measurements of the cheek teeth in the type specimen of *E. spatularius* are given in Table 7, where they are also compared to the larger sample described in Table 1. The type specimen of *E. spatularius* is within two standard deviations of the mean given in Table 1 for all tooth measurements except M<sub>3</sub> length. This comparison is by no means a definitive test, but it does indicate that AMNH 4809 can reasonably be included with the early Graybullian sample of *Esthonyx*. Early Graybullian specimens of *Esthonyx* are the smallest known, and these are closest to the type specimen of *E. spatularius* in size and morphology of P<sub>3</sub>. Considering the circumstantial evidence that the type was found in lower Graybullian strata, there is little doubt that *E. spatularius* is the correct name for early Wasatchian *Esthonyx*.

Upper Graybullian specimens of *Esthonyx* are somewhat larger than those from the lower Graybullian and may represent a new species distinct from *E. spatularius*. We have conservatively referred these to *E. spatularius* until the transition from *E. spatularius* to *E. bisulcatus* is better known. One broken upper molar, with UM 65730, is so large that it could possibly represent a late survival of a small *E. grangeri* into the upper Graybullian. However it is not outside the extreme upper limit expected for the size of M<sup>1</sup> and M<sup>2</sup> in late Graybullian *E. spatularius*, and we have retained it in this species rather than proposing a major range extension of *E. grangeri* based on so little evidence.

*Typodigm.*— The type sample of *E. spatularius* consists of the type specimen only. There are numerous additional specimens of early Wasatchian *E. spatularius* in the AMNH, PU, YPM, and other museum collections. The sample actually studied and forming the basis for our inferences about the

characteristics of this species includes: UM 27244 from the Hoback Basin; UM 61756, 61757, 63668, 63773, 63799, 63896, 63899, and 65791-65799 from the central Big Horn Basin; and UM 64616, 64763, 64773, 65336, 65338, 65465, 65595, 65801-65803, 66414, 66416, 66464, 67080, 67085, 67147, 67375, 67472, 67484, 67509, 68086, 68165, 68463, 69125, 69134, 69143, 69371, 69451, 69523, 69541, 69578, 69588, 69591, 69732, and 69988 from the Clark's Fork Basin and vicinity. Also, upper Graybullian specimens tentatively referred to *E. spatularius* include UM 65730, 65739, 65742, 66825, 66839, 67057, 67156, and 67167 from the Clark's Fork Basin and vicinity, and UM 64378 and 65800 from the central Big Horn Basin.

*Esthonyx bisulcatus* Cope, 1874

Pl. 3, fig. 6, 7

*Esthonyx bisulcatus* Cope, 1874, p. 6. Cope, 1875, p. 24. Cope, 1877, p. 154, Pl. 40, fig. 27-33. Kelley and Wood, 1954, p. 340, fig. 3a, b. Guthrie, 1967, p. 33.

*Esthonyx burmeisterii* Cope, 1874, p. 7. Cope, 1875, p. 24. Cope, 1877, p. 156, Pl. 40, fig. 26.

*Esthonyx acer* Cope, 1874, p. 7.

*Esthonyx burmeisteri* (in part), Cope, 1884, p. 479, fig. 23, 24. Cope, 1885, p. 204, Pl. 24c, fig. 1-10.

*Esthonyx bisulcatus* (in part), Gazin, 1953, p. 17, fig. 1, 2.

*Type*.— USNM 1103, left mandible with  $P_3$ ,  $M_{1-3}$ . Collected by E. D. Cope in 1874 from Arroyo Blanco, San Juan Basin, New Mexico.

*Types of synonyms*.— *Esthonyx burmeisterii*: USNM 1105, a mandibular fragment with  $M_3$  collected by Cope in 1874 from Arroyo Blanco, San Juan Basin, New Mexico. *Esthonyx acer*: USNM 1104, a right mandible with  $P_4M_{1-3}$  collected by Cope in 1874 from Arroyo Almagre, San Juan Basin, New Mexico (these localities were determined by Simpson, 1951, from Cope's diary of the 1874 expedition).

*Diagnosis*.— Differs from *E. xenicus*, *E. ancylion*, and *E. grangeri* in having a solidly fused mandibular symphysis. Similar to *E. spatularius*, but differs from it in having a more open trigonid on  $P_4$  and broader, more basined talonids on  $P_3$  and  $P_4$ . Differs from *E. acutidens* in being smaller (text-fig. 1). Differs from *E. munieri* in having a more symmetrical trigonid on  $P_4$  and in having relatively narrower cheek teeth.

*Age and distribution*.— Late Wasatchian (Lysitean and Lostcabinian), early Eocene. *Esthonyx bisulcatus* is known from the central Big Horn Basin and the Wind River Basin, Wyoming, and from the San Juan Basin, New Mexico.

*Description*.— This species has been adequately described by Cope, Gazin, and others. It is sufficient to emphasize here the distinctive open trigonid of  $P_4$  and the more rounded and basined talonids of  $P_3$  and  $P_4$  that distinguish *E. bisulcatus* from *E. spatularius* (compare Plate 3, figs. 6 and 7 with fig. 5 on the same plate).

Measurements of the type and other specimens from the San Juan Basin are given in Table 8.

*Discussion*.— The evolutionary transition from *Esthonyx spatularius* in the early Wasatchian to *E. bisulcatus* in the late Wasatchian appears to be a continuous one. Intermediate forms from the middle Wasatchian (late Graybullian) are at present difficult to classify because they resemble both species. For the present these have been referred to *E. spatularius*, but when late Graybullian *Esthonyx* is better known it may be necessary to erect a new species or to transfer these specimens to *E. bisulcatus*. Similarly, the transition from *E. bisulcatus* to *E. acutidens* requires more study. It is not yet clear if *E. acutidens* is simply a continuation of the *E. bisulcatus* lineage, or if these two species were contemporaneous, with the former being found in Colorado and Wyoming at the same time as the latter inhabited the San Juan Basin of New Mexico. Mr. David Shankler is analyzing the transitions between Wasatchian species of *Esthonyx*, based on the YPM collection, and his work will undoubtedly clarify these problems.

TABLE 8 — Measurements of the lower dentition of the type and other specimens of *Esthonyx bisulcatus* from the San José Formation, San Juan Basin, New Mexico. A statistical summary of the entire sample from this Formation is given in Table 2. Abbreviations as in Table 1. Measurements in mm.

Tooth	USNM 1103 (type)	USNM 1104	USNM 1105	USNM 17153	AMNH 16241	AMNH 48325
P <sub>3</sub>	L	6.7	—	—	—	—
	W	4.3	—	—	—	—
P <sub>4</sub>	L	6.6	7.4	—	7.4	7.5
	W	4.8	4.9	—	5.1	5.6
M <sub>1</sub>	L	8.0	7.4	—	7.5	7.7
	W	6.3	6.1	—	6.1	6.1
M <sub>2</sub>	L	8.2	7.7	—	7.9	7.8
	W	6.5	6.4	—	6.5	6.4
M <sub>3</sub>	L	11.2	10.6	10.4	—	10.8
	W	5.9	5.9	5.3	—	6.0

*Typodigm.*— In a narrow sense the type sample of *E. bisulcatus* includes only USNM 1103 (holotype) and 1105, both known to have been collected by E. D. Cope from Arroyo Blanco. In a broader sense, the type sample can be extended to include all of the following specimens from the San José Formation of New Mexico: USNM 1103 (holotype), 1104, 1105, 1130, 17153, 17154, 17155, 17156, and AMNH 4648a, 16241, 48325, 48328, 48500, 48502, 92904. Together these form a homogeneous sample that appears to have been collected from a relatively restricted temporal interval.

In addition to the sample from the San Juan Basin, there is a large collection of *E. bisulcatus* from the Big Horn Basin. This is principally in the AMNH and YPM collections, but UM 65939, 65973, 66074, and 66119 are included here. UM 64081, 64106, 64140, 64147, and 64154 are intermediate between *E. spatularius* and *E. bisulcatus* but appear to be closer to the latter. Wind River Basin specimens are principally in the ACM, AMNH, CM and PU collections.

#### *Esthonyx acutidens* Cope, 1881

*Esthonyx acutidens* Cope, 1881, p. 185. Cope, 1885, p. 210, Pl. 24a, fig. 17, 18, 20, 21. White, 1952, p. 192. Gazin, 1953, p. 24, fig. 6-8. Robinson, 1966, p. 43, Pl. 5, fig. 8. Guthrie, 1971, p. 79. West, 1973, p. 125, Pl. 11, fig. a, b. McKenna, 1976, p. 354, fig. 1.

*Esthonyx cf. acutidens*, Gazin, 1952, p. 21. Gazin, 1962, p. 42, Pl. 1, fig. 3.

*Type.*— AMNH 4807, left M<sub>1</sub> and M<sub>2</sub>, collected by J. L. Wortman in 1880 from the Wind River Basin (Lost Cabin beds), Wyoming.

*Diagnosis.*— Differs from *E. xenicus*, *E. ancylion*, and *E. grangeri* in having fused mandibular rami and narrower, more sharply crested cheek teeth. Differs from *E. spatularius* and *E. bisulcatus*

TABLE 9 — Measurements of the lower dentition of the type and other specimens of *Esthonyx acutidens* from the Wind River Basin, Wyoming, and Huerfano Park, Colorado. Abbreviations as in Table 1. Measurements in mm.

Tooth	Wind River Basin			Huerfano Park		
	AMNH 4807 (type)	AMNH 4808	AMNH 14738	AMNH 17531	AMNH 55294	AMNH 98215
P <sub>3</sub>	L	—	—	6.4	—	—
	W	—	—	3.9	—	—
P <sub>4</sub>	L	—	8.5	8.6	—	—
	W	—	5.9	5.5	—	—
M <sub>1</sub>	L	—	8.6	8.2	8.5	—
	W	—	6.8	6.0	6.2	—
M <sub>2</sub>	L	9.4	9.6	9.2	8.7	9.7
	W	7.4	7.1	7.3	6.9	6.7
M <sub>3</sub>	L	13.1	—	12.2	11.9	12.4
	W	6.5	—	6.6	6.0	6.2

principally in being larger (text-fig. 1), but also in having P<sub>2</sub><sup>2</sup> single-rooted with reduced crowns. Differs from *E. munieri* in being larger, having a more symmetrical trigonid on P<sub>4</sub>, and having relatively narrower lower cheek teeth.

*Age and distribution.*— Latest Wasatchian (Lost Cabin beds and equivalents) and earliest Bridgerian (Bridger A equivalent), early and middle Eocene. *Esthonyx acutidens* is known principally from the Wind River Basin and Green River Basin, Wyoming, and Huerfano Park, Colorado.

*Description.*— *Esthonyx acutidens* has been adequately described by Gazin (1953). *E. acutidens* resembles *E. bisulcatus* in most details, but it is significantly larger. This is shown graphically in text-figure 1. Measurements of the type and other specimens are given in Table 9.

*Discussion.*— *Esthonyx acutidens* is very similar to *E. bisulcatus* and it occurs later in time than most *E. bisulcatus*, raising the possibility that it is a direct descendant of the latter. However, the adapid primates from both Almagre and Largo facies of the San José Formation of New Mexico appear to be the same as those found in Lostcabinian age strata in Wyoming (Gingerich and Simons, 1977), and the distribution of *Hyracotherium* species suggests the same Almagre-Largo correlation with Lost Cabin beds (Gingerich, in prep.). This raises the possibility that *E. acutidens* and *E. bisulcatus* were closely related contemporaneous sister species inhabiting adjacent northern and southern ranges.

McKenna (1976) published the first record of *E. acutidens* in the upper part of the Huerfano Formation. The adapid primate fauna from the upper Huerfano appears to be equivalent to that from the lower Bridgerian (Bridger A, see Gingerich, 1979), and this is thus the first record of *Esthonyx acutidens* in the middle Eocene of North America. The fauna from the lower Bridgerian is still relatively poorly known, and it is possible that *E. acutidens* will eventually be found in Bridger A equivalent beds elsewhere as well.

*Typodigm.*— The type specimen, AMNH 4807, is from an unknown locality in the Wind River Basin and no other specimens can be referred to the type sample with certainty, although AMNH 4808 was also collected by J. L. Wortman from the Wind River Basin in 1880. Additional specimens include AMNH 14738, 14740, and USNM 18202 from the Wind River Basin; AMNH 98215, and probably 17531 and 55294 from the Huerfano Basin; and USNM 22124 and FMNH 15567 and 15574 from southwestern Wyoming. Guthrie (1971) gives statistics for a sample of Wind River specimens without giving numbers for these — the sample presumably includes specimens he found that are now in the CM collection.

*Esthonyx munieri* (Lemoine, 1891)

*Esthonyx*, Lemoine, 1889, p. 269, fig. 7.

*Plesthonyx munieri* Lemoine, 1891, p. 276, Pl. 10, fig. 32.

*Esthonyx munieri*, Teilhard, 1922, p. 63, fig. 30, Pl. 3, fig. 18, 19, 26. Gazin, 1953, p. 31.

*Type.*— MNHN AL-5174, a right  $M_3$  collected by V. Lemoine from the Argiles à Lignites or the Sables à Unios et Térédines in the vicinity of Epernay, Paris Basin, France.

*Diagnosis.*— Differs from all North American species in having inflated cheek teeth with more bulbous cusps, an asymmetrical trigonid on  $P_4$ , and a short, broad hypoconulid on  $M_3$ .

*Age and distribution.*— *E. munieri* is known only from the early Eocene of the Paris Basin, France. As part of Lemoine's "Ageian" collection, the three known specimens may have come from either a Sparnacian or a Cuisian fauna.

*Description.*— Three specimens of *E. munieri* are known, a right  $M_3$  (type), a left  $P_4$ , and a left  $M^1$  or  $M^2$ . The following description is based on sharp plaster casts kindly provided by Dr. D. E. Russell, Muséum National d'Histoire Naturelle, Paris.

The type specimen,  $M_3$ , measures approximately 9.6 mm in length and 6.3 mm in width (measured on cast). It is a relatively short and broad tooth for  $M_3$  in *Esthonyx*, with a relatively short hypoconulid lobe. Also, the trigonid is constructed differently from that in North American specimens. The paraconid is closely appressed to the metaconid, nearly closing the trigonid. A small metastylid is present on the posterointernal side of the metaconid.  $P_4$  measures approximately 8.6 mm in length and 5.9 mm in width (measured on cast). It has a markedly asymmetrical trigonid construction, with the paraconid set below and well forward of the protoconid. The metaconid is also below the protoconid, but it is much closer and directly lingual from the protoconid. The talonid on  $P_4$  is a broad basin with a rounded crest marking the perimeter. The enamel on  $P_4$  is slightly crenulated. The upper molar MNHN AL-5175, is broken and somewhat waterworn, with the external cingulum missing. This tooth,  $M^1$  or  $M^2$ , measures approximately 8.2 mm in length and it is estimated to have been about 12.5 mm in width (measured on cast). It closely resembles upper molars of *Esthonyx spatularius* and *E. bisulcatus*.

*Discussion.*— Judging from the three known teeth, *E. munieri* appears to be the most distinctive species of *Esthonyx*. *E. munieri* is clearly closely related to North American species of *Esthonyx*, but more complete material might well indicate that a separate genus is represented.

*Typodigm.*— The type, MNHN AL-5174, a second specimen under the same number, and MNHN AL-5175 are the only known specimens of *E. munieri*. They are probably all from the same type sample, but this is not known for certain.

PHYLOGENY AND EVOLUTION OF *ESTHONYX*

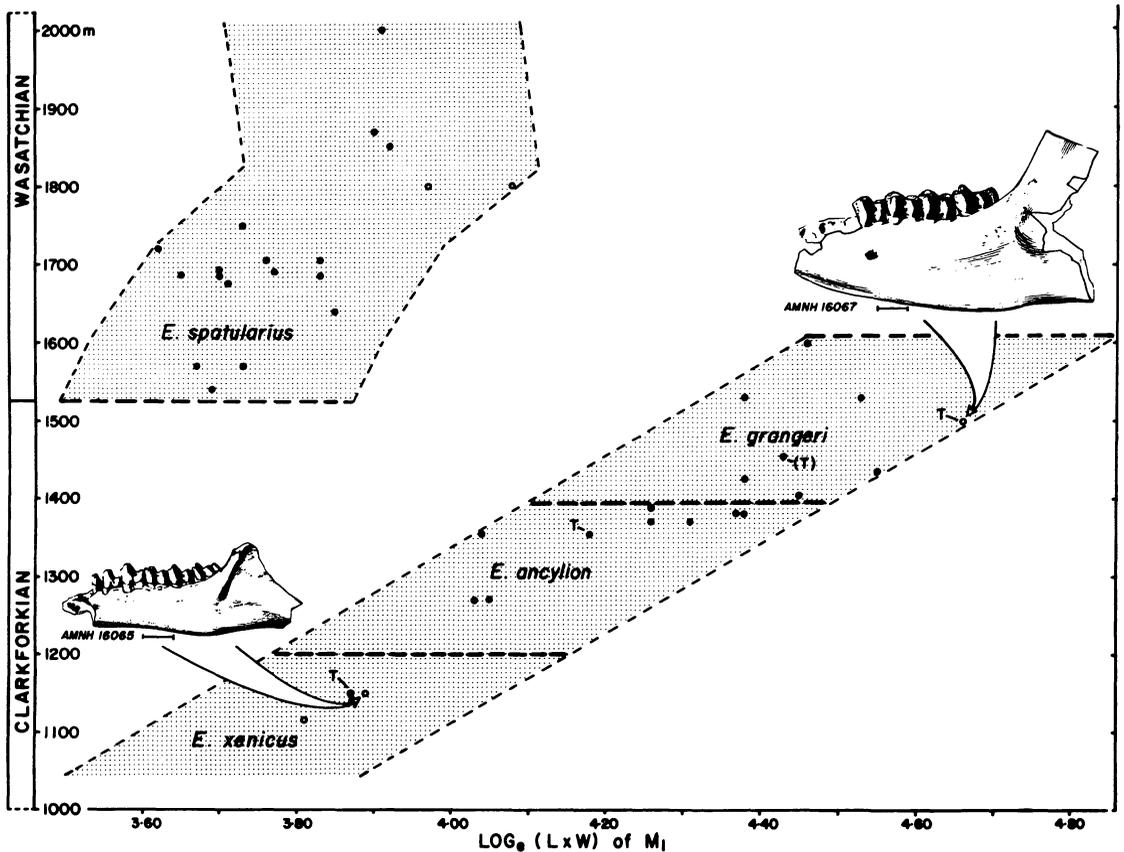
Early Eocene tillodonts have been known for over 100 years, but the phylogenetic relationships of described species of *Esthonyx* have never been very clear. As a result of recent detailed stratigraphic collecting in the Clark's Fork Basin, a reasonably large number of specimens are available that are dated precisely relative to each other. The size of the first lower molar is plotted in text-figure 3 for all specimens with adequate locality and stratigraphic data. Most of these are in the new University of Michigan collections, but several important American Museum of Natural History and Princeton University specimens are plotted as well. The relative stratigraphic positions of the latter were clarified by our recent work in the Clark's Fork Basin.

The pattern of phylogeny that emerges from stratophenetic linking of Clarkforkian and early Wasatchian *Esthonyx* (text-fig. 3) indicates that two evolutionary lineages are clearly represented. The first lineage consists of the three species of *E. xenicus*, *E. ancylion*, and *E. grangeri*. This lineage first appeared at the beginning of the Clarkforkian and persisted into the early Wasatchian. The second lineage consists of *E. spatularius*, *E. bisulcatus*, and *E. acutidens*. This lineage first appeared at the beginning of the Wasatchian and persisted into the early Bridgerian. The most evident characteristic separating the two lineages is their disjunct distribution in the morphology-time plot shown in text-figure 3. Another characteristic that distinguishes the two lineages is symphyseal fusion. *E. xenicus* and its direct descendants lacked symphyseal fusion, while *E. spatularius* and its descendants all had fused mandibular symphyses. Placing the two lineages in separate genera, the one characterized by symphyseal fusion and the other lacking it, was considered but the two lineages are very similar in all other known dental characteristics. Generic separation does not seem warranted, nor would the use of named subgenera contribute any more to understanding evolutionary relationships than does a diagram like that shown in text-figure 3. A classification should be consistent with phylogenetic relationships but it need not express them in full detail. The use of subgeneric names requires use of a trinomial each time a name is mentioned, whereas relationships can usually be expressed and discussed more economically and explicitly in a simple diagram with accompanying text.

Given the stratigraphic relationships shown in text-figure 3, what is the origin of Wasatchian *E. spatularius* and how is it related to the *E. xenicus* lineage? Morphologically the two are very similar. They differ chiefly in having fused and unfused mandibular symphyses, respectively. Separation of the *E. spatularius* and *E. xenicus* lineages might possibly be considered an example of speciation by the "punctuated equilibria" model of Gould and Eldredge (1977), although neither lineage could really be considered to be in "equilibrium." Also, judging by the rate of evolutionary change from *E. xenicus* to *E. grangeri*, the gap of one to two million years between *E. xenicus* and *E. spatularius* would be sufficient to permit one to evolve gradually into the other. Such a transition, gradual or "punctuated," clearly happened somewhere, but there is no evidence that it happened instantaneously in geological time. The appearance of *E. spatularius* in the Big Horn Basin and Clark's Fork Basin is part of a major faunal immigration at the beginning of the Wasatchian. Connecting forms linking *E. spatularius* to the *E. xenicus* lineage are not preserved, and this speciation probably happened outside the range of presently known early Eocene *Esthonyx*. Nothing is known to indicate whether the transition was "punctuated" or gradual like those linking other Tertiary mammalian species (Gingerich, 1976a).

The principal evolutionary change documented here is in tooth size and, by inference, body size. The rate of size increase in the lineage *E. xenicus* — *E. ancylion* — *E. grangeri* is greater than that documented in other early Tertiary mammals. The change is shown in text-figure 3, where lower molar size increased from about 3.80 to about 4.60 on a natural logarithmic scale in an interval of about 2 million years. This is a change of .40 units per million years, or a rate of .40 darwins (Hal-

## CLARK'S FORK BASIN ESTHONYX



TEXT-FIG. 3 – Evolutionary pathways of early Eocene *Esthonyx* in the Clark's Fork Basin, Wyoming. Stratophenetic plot shows continuity between species of the *E. xenicus* – *E. grangeri* lineage, and discontinuity at the immigration of *E. spatularius*. Elevations on the vertical axis are levels in the Polecat Bench and Willwood Formations, as measured above the Mantua coal seam (Cretaceous-Tertiary boundary) on Polecat Bench. *E. xenicus* is recorded from as low as level 915 m on the east side of Polecat Bench (locality SC-83), which is very near the beginning of the Clarkforkian land mammal age. Width of shaded areas calculated as shown in text-figure 1. Scaled inset figures from Simpson (1937) show change in mandible size in the transition from *E. xenicus* to *E. grangeri*. Solid circles are specimens from University of Michigan localities actually in measured sections. Open circles represent specimens for which precise locality or stratigraphic data are lacking. T indicates the position of type specimens of species named from the Clark's Fork Basin and east side of Polecat Bench (T in parentheses is type of *E. latidens*, a synonym of *E. grangeri*). This figure includes approximately the lower one half of Wasatchian time (*Pelycodus ralstoni*, *P. mckennai*, and lower part of *P. trigonodus* Zones of Gingerich and Simons, 1977). Upper Wasatchian strata are not represented in the Clark's Fork Basin. Shaded area of *E. spatularius* pathway is drawn to include the ranges of specimens from correlative Yale-Michigan localities in the central Big Horn Basin but these specimens are not actually plotted in the figure.

dane, 1949). This rate is nearly twice the maximum rate of evolution of molar size in the Paleocene primate family Plesiadapidae, and it exceeds that observed in *Hyopsodus* and *Pelycodus* by an almost equal amount (Gingerich, 1976b, p. 68).

The skull and dentition of *Esthonyx* apparently changed relatively little during the early Eocene

except for the changes in size discussed above. Comparison of the palate of *Esthonyx acutidens* figured by Gazin (1953, fig. 8) with that of *E. ancylicion* (Pl. 2, fig. 1) indicates that the snout in *E. acutidens* was relatively larger than that of more primitive *Esthonyx*. Thus the more open trigonid of P<sub>4</sub> characteristic of *E. bisulcatus* and *E. acutidens* may possibly be explained as a change correlated with snout elongation in the transition from *E. spatularius* to *E. acutidens*.

Judging from tooth wear, primarily in UM 68511, we envision *Esthonyx* as having been rhizophagous, with its enlarged tusk-like incisors and canines being used to unearth roots and tubers. The wear on these teeth was clearly not caused by tooth-to-tooth occlusion, but rather by the abrasion of food grasped between the teeth. Grooved wear against the sides of the enlarged lower incisors indicates that the incisors were probably used to pull vegetation out of the earth or to strip leaves off of stems of vegetation. Very heavy wear on the entire dentition is a distinctive characteristic of *Esthonyx*, and this suggests that it was feeding on the ground and ingesting a considerable amount of soil and grit along with its food. *Esthonyx* was probably pig-like in dietary adaptations. Extensive rooting for rhizomes and tubers would certainly have favored the development of the ever-growing incisor tusks found in middle Eocene trogosine tillodonts. There is, however, no indication in *Esthonyx* itself of the development of ever-growing incisors. A careful functional analysis of the available postcranial remains of *Esthonyx* and other tillodonts has never been attempted. This would greatly increase our understanding of their general adaptations and their role in Eocene mammalian communities.

#### ORIGIN OF TILLODONTIA

Early Eocene *Esthonyx* was for a long time the oldest tillodont known, and it is thus natural that the origin of this group of mammals was sought among North American Paleocene mammals. Cope (1874) apparently first regarded *Esthonyx* as a North American member of the Toxodontia, but he later included it in the order Insectivora because of similarities shared with *Erinaceus*, while also noting resemblances to Creodonta and Primates. Other authors subsequently suggested affinities with rodents and pantodonts. Gregory (1910), Gazin (1953), and most recently Van Valen (1963) have advanced the hypothesis that tillodonts were derived from arctocyonid condylarths, and Van Valen went so far as to include Tillodontia as a suborder of Condylarthra. There are resemblances in the dentition of *Esthonyx* and "*Claenodon*" *procyonoides*, as Van Valen (1963) demonstrated. It is not inconceivable that early Eocene *Esthonyx* evolved from a middle Paleocene "*Claenodon*"-like ancestor, but intermediate forms are lacking. Recent discoveries of what appear to be primitive tillodonts in the Paleocene of China add new information that must be included in any analysis of tillodont origins.

Tillodonts have been known from the late Eocene of Asia since Gazin (1953) first recognized *Adapidium huanghoense* Young, 1937, as an esthonychid. Subsequently, Chow (1963) added a *Trogosus*-like tillodont, *Kuanchuanius shantunensis*, to the middle Eocene fauna of China. Dehm and Oettingen-Spielberg (1958) described a new form, *Basalina basalensis*, from the middle Eocene of Pakistan as a taeniodont, but its morphology more closely resembles that of tillodonts. On biogeographical evidence *Basalina* is also more likely to represent a tillodont than a taeniodont.

The most important specimens for understanding tillodont origins were described in recent years by Chow *et al.* (1973, 1977) and Wang (1975). Chow *et al.* (1973) described a new genus and species, *Lofochaius brachyodus*, as an esthonychid tillodont from the middle Paleocene. Wang (1975) described another Paleocene tillodont, *Meiostylodon zaoshiensis*, from the Chaling Basin, Hunan. This form is mentioned by Chow *et al.* (1977, p. 91) as possessing "nearly all the essential structures necessary to fill the gaps between *Lofochaius* and *Esthonyx*. It is more advanced, but near to the

former, from a high stratigraphic horizon (probably late Paleocene), and with chisel-like incisors typically of the tillodont type." Thus it appears that the ancestry of tillodonts is to be found in the Paleocene of Asia, not North America.

*Esthonyx* first appeared in North America at the beginning of the Clarkforkian as part of an immigration including the earliest rodents found in North America. Rodents, too, are most plausibly derived from Paleocene ancestors in Asia, with *Heomys orientalis* described by Li (1977) appearing closely related to rodent origins. Thus, some of the important immigrants marking the beginning of the Clarkforkian in the Clark's Fork Basin are probably of Asian origin. What other orders of mammals tillodonts are most closely related to remains an open question. *Esthonyx* and its allies may have originated from Condylarthra, Anagalida, or Pantodonta, but until this question is resolved they are appropriately retained in a separate order, Tillodontia.

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