A NEW TILLODONT FROM THE EOCENE UPPER WILLWOOD FORMATION OF WYOMING

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ABSTRACT

A left mandible of a new tillodont from the Upper Willwood, Early Eocene of Buffalo Basin, Wyoming, is described. It represents a new genus and species, *Megalesthonyx hopsoni*. Included as parts of the type specimen are an upper incisor and several bones of the forefeet. Also referred to this species are a lower premolar, an upper premolar and two upper molars.

The new specimen is intermediate between *Esthonyx* and *Trogosus* in time and in many morphologic characters. Sufficient evidence is lacking to prove that *Megalesthonyx* was ancestral to *Trogosus*, but most features now known suggest that it was. The transitional state of this form supports the recognition of a single family, Esthonychidae, for these strange mammals. Two subfamilies are observed. The Tillodontia are regarded as a distinct order, contra Van Valen (1963), on the basis of extreme dental specializations.

INTRODUCTION

Tillodonts have long been known as a small but distinctive mammalian group with enigmatic affinities. Yale expeditions to the Early Eocene deposits of the Bighorn Basin of Wyoming during the past decade have resulted in the discovery of many new and significant specimens. Among these are a lower jaw and three upper teeth representing a new kind of tillodont, found associated with remains of the perissodactyl *Lambdotherium*. Study indicates that the new form is in many ways intermediate between the Early Eocene genus *Esthonyx* and the Middle Eocene trogosines.

Our understanding of the taxonomic relationships of the tillodonts is still somewhat confused. The new genus described here helps to bridge the fairly wide anatomical gap between the dental and mandibular structures of *Esthonyx* and *Trogosus*. Nevertheless, certain dental features discussed below still justify the placement of these two genera in separate subfamilies.

ABBREVIATIONS

Abbreviations used in this paper are as follows:

AMNH	American Museum of Natural History, New York, New York
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut

SYSTEMATICS

ORDER TILLODONTIA Marsh, 1875
FAMILY ESTHONYCHIDAE Cope, 1883
SUBFAMILY ESTHONYCHINAE Zittel and Schlosser, 1911

Megalesthonyx,[1] new genus

TYPE. *Megalesthonyx hopsoni*, new species.

KNOWN DISTRIBUTION. Early Eocene, Upper Willwood Formation, Bighorn Basin, Wyoming.

DIAGNOSIS. Considerably larger than species of *Esthonyx* (about 40 to 50% larger than *E. grangeri*, largest known species of *Esthonyx*), but slightly smaller than species of *Trogosus*. Lower dental formula 3.1.3.3. Incisors of

[1]Referring to the large size and the resemblance to *Esthonyx*.

same morphology and relative proportions as those in *Esthonyx*. Canine much reduced relative to that of *Esthonyx*. P_2 small, unicuspid, but double-rooted. Short diastemata separating I_3 from C, C from P_2, and P_2 from P_3; the last-mentioned diastema is the longest. Talonid of P_4 reduced relative to that of *Esthonyx*. Metastylids on the lower molars somewhat reduced relative to those of *Esthonyx*. Cristid obliqua originates from protocristid (see Szalay, 1969) more lingually (closer to metaconid) than in *Esthonyx;* in this feature the molars resemble those of *Trogosus*. Jaw deepest beneath M_3. Robustness of mandible comparable to the condition in *Esthonyx*, but not so robust as in *Trogosus*. Symphysis fused, robust, but relatively short, extending posteriorly to a point beneath the midpoint of P_3. Upper molars characterized by presence of prominent mesostyle, pronounced antero-internal cingulum, and small beads or fold of enamel in trigon basin.

Megalesthonyx hopsoni,[2] new species

TYPE. YPM 18767. Collected by James Meade and Joseph Alpert in June, 1962. Left mandible (lacking ascending ramus) with I_{1-2}, C, P_{2-4}, M_{1-3}, and alveolus for I_3; with symphysial region including right I_{1-2} and alveoli for right I_3 and C (see Figs. 1 and 2 and Table 1). Associated upper left I^2. Associated bones of the forefeet including left metacarpal I, right metacarpal IV, proximal ends of two more metacarpals and distal ends of four additional metacarpals, two complete proximal phalanges, fragments of three more proximal phalanges, proximal end of one medial phalanx, one complete distal phalanx, proximal end of another distal phalanx, and several indeterminate fragments.

HYPODIGM. Type specimen (YPM 18767); right P_3 (YPM 27334); two upper cheek teeth (YPM 17594); and an upper molar (YPM 27333).

LOCALITY AND HORIZON. YPM Locality 33, NE ¼, SE ¼ Sec. 22, T.49 N., R.98 W., Buffalo Basin of the Bighorn Basin, Wyoming. Early Eocene, Upper Willwood Formation.

DIAGNOSIS. Only known species of the genus.

DESCRIPTION. This is the largest esthonychine known, considerably larger than *Esthonyx grangeri* Simpson, 1937, a Clark Fork form, or *E. acutidens* Cope, 1881, a contemporary of *Megalesthonyx*.

The three incisors in each ramus are of the same morphology as those of *Esthonyx*. They are only slightly curved and not so laterally compressed as

[2]Named for Dr. James A. Hopson who, while at Yale, studied the type specimen and kindly forwarded his notes to me.

in *Trogosus*. They are not gliriform and show no indication of growing from persistent pulp. The root of I_2 extends to a point below the anterior part of P_3. This compares favorably with *Esthonyx*, but contrasts with *Trogosus*, in which the rootless I_2 extends at least to a point below P_4 and possibly further. The extent of the enamel approximates an intermediate condition between *Esthonyx*, in which enamel covers most of the mesial and distal sides of the incisors, as well as the labial face, and *Trogosus*, in which enamel extends only slightly beyond the labial side onto the mesial and distal sides. As in *Esthonyx*, the enamel extends slightly further distally than medially. The relative size of I_1 to I_2 is close to that in *Esthonyx*, not displaying the much greater size difference seen in *Trogosus*. Although I_3 is not present in the type of *M. hopsoni*, its alveolus indicates that it was somewhat smaller than I_1.

A short diastema separates the canine from I_3. Contrary to the condition in *Esthonyx*, the canine and most anterior premolar are greatly reduced. The canine is still relatively high but not so procumbent as in *Esthonyx*, inclining forward only about 15° from the vertical. The enamel is confined to the crown portion and is worn away on the lingual wear facet. In *Esthonyx*, C is about the same size or even larger than I_2. The condition in *Megalesthonyx* appears to be approaching that in *Trogosus*, where the canine has effectively lost its significance.

P_2 is separated from C by a short diastema. Although the tooth is greatly reduced, as in *Trogosus*, it remains two-rooted, as in *Esthonyx*. This feature is fairly clear from external examination of the type, but was confirmed in X rays of the specimen. Both roots of P_2 are almost directly in line with the tooth row, contrary to the condition in *Esthonyx*, where the anterior root may be situated labially up to 45° from the line of the tooth row. P_2 bears a single anteroposteriorly extended cusp.

The largest diastema separates P_3 from P_2. (P_3-M_3 are closely packed.) Although the mandible is fractured at this point, it is still possible to discern a slight rise in the level of the tooth row at the anterior root of P_3, as in *Trogosus*. P_3 is little different from that in *Esthonyx*. A prominent anterior cusp is followed by a low talonid basin; the talonid cusps cannot easily be distinguished on the talonid crest.

P_4 differs from P_4 of *Esthonyx* in the somewhat reduced talonid (approaching the condition in *Trogosus*), but this tooth is still nearly molariform. A short, low fold of enamel extends posteriorly from the metaconid but does not bear a distinct metastylid cusp.

The molar series does not vary greatly, except in size, among tillodonts. A consistent character is the presence of a metastylid lower than and posterior to the metaconid. In *Megalesthonyx*, the metastylid is distinct only on M_1, and is represented only by a short crest posterior to the metaconid on M_2 and M_3. In M_3 this is no more distinct than the similar development on P_4. The talonid cusps are joined by a continuous crest extending from the protocristid through to the entoconid. In all the molariform teeth, the cristid

obliqua portion of the crest originates more lingually than in *Esthonyx*, from a point nearing the metaconid.

The ramus is rather shallower and less robust than in *Trogosus*, resembling *Esthonyx* in this respect. The symphysis, though well fused and robust, is the shortest in any tillodont observed, extending back only to a point below the middle of P_3. In *Esthonyx* the symphysis usually extends to a point below the contact of P_3 and P_4, whereas in *Trogosus* it extends back to a point beneath the anterior part of M_1. In the later Bridger Eocene genus *Tillodon* the symphysis may extend posteriorly slightly farther. The mental foramen in the type of *Megalesthonyx* is a single opening situated beneath P_2, but this character is very variable in tillodonts.

TABLE 1. MEASUREMENTS (IN MILLIMETERS) OF TYPE SPECIMEN OF *Megalesthonyx hopsoni*, YPM 18767

I_1,	greatest diameter at alveolus	6.2
I_2,	greatest diameter at alveolus	11.0
I_3,	diameter of alveolus	4.0
C,	greatest diameter at alveolus	5.8
P_2,	anteroposterior (mesiodistal) diameter	5.0
	labiolingual diameter	3.2
P_3,	anteroposterior diameter	10.4
	labiolingual diameter	6.3
P_4,	anteroposterior diameter	12.5
	greatest labiolingual diameter	9.0
M_1,	anteroposterior diameter	12.5
	greatest labiolingual diameter	10.0
M_2,	anteroposterior diameter	16.2
	greatest labiolingual diameter	11.2
M_3,	anteroposterior diameter	21.5a
	greatest labiolingual diameter	10.4
Depth of mandible at posterior root of M_3		31.0
Depth of mandible at posterior root of P_4		29.3
Left I^2:	buccolingual diameter at base of crown	12.6
	mesiodistal diameter at base of crown	10.4

a = approximate

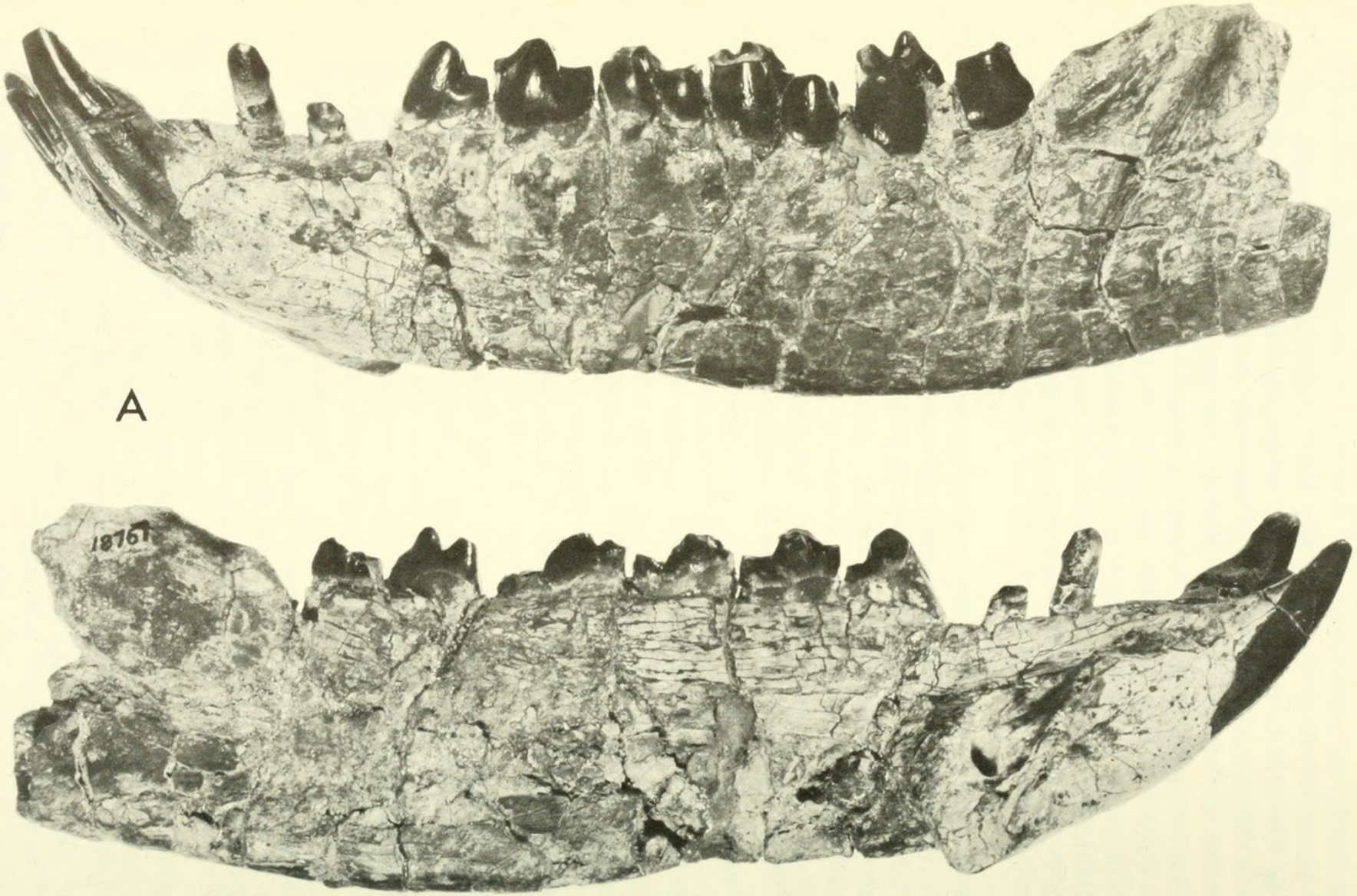

FIG. 1. *Megalesthonyx hopsoni*, n. sp., type, YPM 18767, left mandible (×1). A. Buccal view. B. Lingual view.

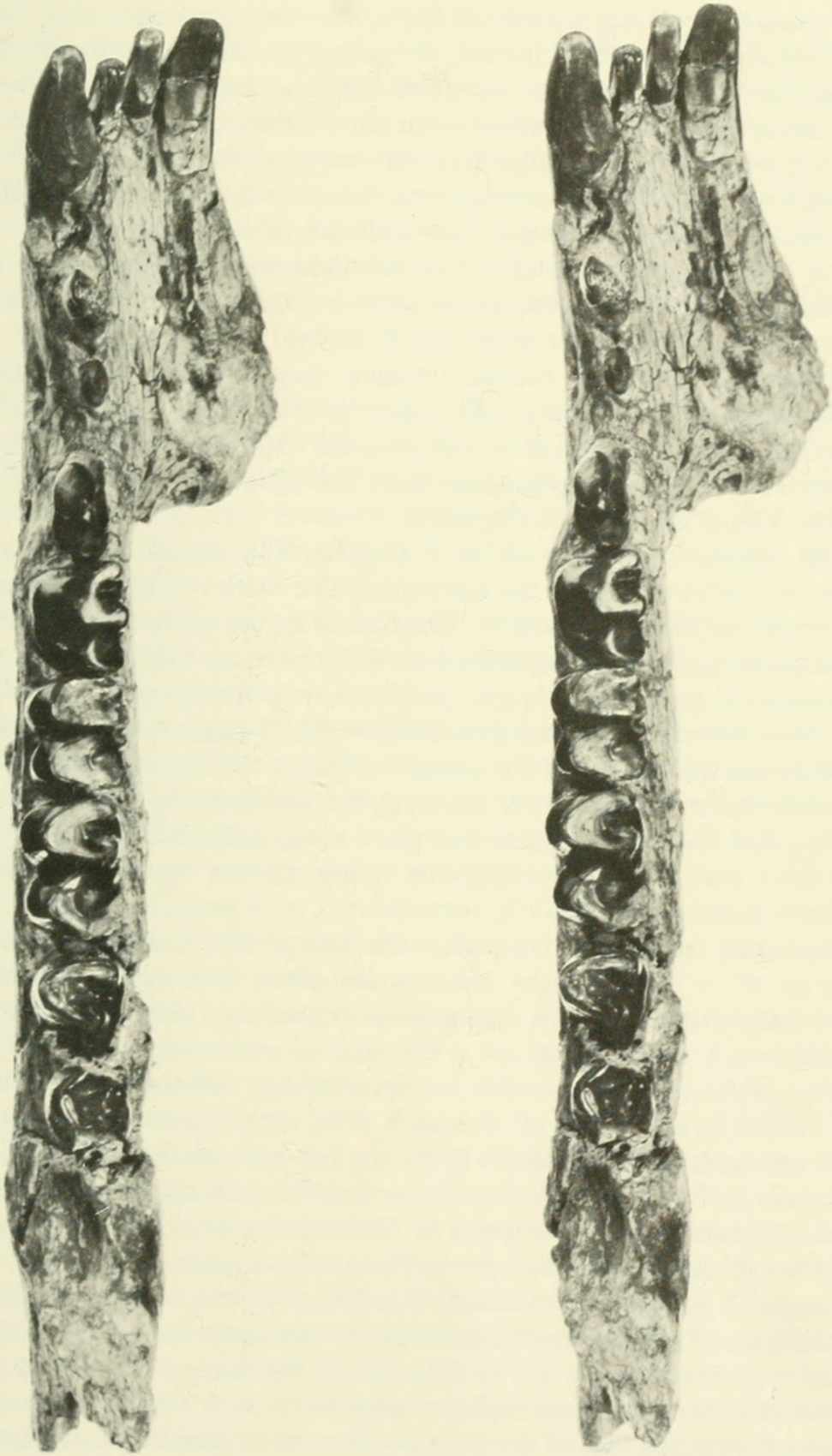

FIG. 2. *Megalesthonyx hopsoni*, n. sp., type, YPM 18767, occlusal view (stereophotograph, ×1).

Only a single upper tooth is preserved in the type; it is left I^2. The structure, relative size, and extent of enamel in this tooth resemble more closely I^2 of *Esthonyx* than that of *Trogosus*, but in many details the tooth is intermediate between the two. The tooth (and root) curves through an arc of nearly 90° and is therefore more curved than in *Esthonyx*, though not to such a degree as in *Trogosus*. In cross-section at the base of the crown it is roughly triangular, broad and flattened, or even slightly concave lingually, but rather laterally compressed and rounded labially. The root is not tapered but remains approximately the same diameter as at the base of the crown. Enamel is confined to the crown of the tooth, as in *Esthonyx* (but unlike *Trogosus*), covering the entire distal (lateral) side and most of the labial surface. On the labial surface, enamel may have extended slightly below the gum line. The enamel on the lingual face of I^2 has been completely worn off in this specimen. Enamel extends only onto the labial half of the mesial side. A longitudinal bulge runs from the tip of the root to a point about halfway up the crown of the tooth.

Although the end of the root of this I^2 is not totally closed, this condition may be due to the young age of the individual. The tooth was not persistently growing in the sense that it was in *Trogosus*. On the other hand, this I^2 may represent a transitional condition in which the tooth kept growing, and the root remained open, for a longer period of time than in *Esthonyx*. The fact that *Trogosus* evolved a persistently growing I^2 suggests that selection favored those individuals in which enamel extended far down on the labial surface of the incisors (eventually covering the whole tooth, which became "rootless"), and in which the incisors grew continually through life. The tendency for a shift toward the trogosine condition may have been present in *Megalesthonyx*.

Also belonging to the type specimen are several bones of the forefeet, consisting of all or part of eight metacarpals, all or part of five proximal phalanges, the proximal end of a medial phalanx, and two terminal phalanges (claws). Although the detail of these elements is obscured by a fine ironstone veneer, their general structure is approximately intermediate between those of *Esthonyx* and those of *Trogosus*. The metacarpals and proximal phalanges are more robust than in *Esthonyx* but still relatively longer and narrower than in *Trogosus*. The constriction of the shaft of the metacarpals just distal to the base (proximal end) is not as pronounced as in *Trogosus* but is more evident than in *Esthonyx*. The two complete metapodials are left metacarpal I and right metacarpal IV. The proximal ends are close in structure to those of previously known tillodont specimens, especially AMNH 17008, the type of *Trogosus grangeri* Gazin. In metacarpal I the base is a broad, transversely concave surface for articulation with the trapezium. As in *Trogosus*, the medial side of the proximal extremity projects much further proximally than does the lateral side. In metacarpal IV, the proximal end is somewhat convex dorsoventrally and very slightly concave transversely. A proximal end of a metacarpal, exhibiting a deep transverse concavity, is

probably left metacarpal II. Another specimen reveals a gently convex proximal facet of trapezoidal shape; it most likely represents left metacarpal III.

The proximal phalanges are like those in previously known tillodont specimens. The length is about the same is in *Trogosus,* but the diameter of the shaft and dimensions of the proximal end are smaller than in *Trogosus.*

The claws are long, curved, and laterally compressed. They are nearly as long as in some specimens of *Trogosus* but seem to be slightly more gracile than the majority of *Trogosus* claws. The proximal articulation is narrower dorsally than ventrally, but the transverse diameter varies considerably in the two claws preserved in the type. The bulbous palmar process for attachment of the tendon of the flexor profundus digitorum is quite prominent.

Three upper cheek teeth in the Yale collection are here referred to *Megalesthonyx hopsoni* (Table 2). The teeth [a molar and premolar, YPM 17594, and a molar, YPM 27333 (Fig. 3)] are not associated with the type specimen but are from a nearby locality, YPM locality 3, NE ¼, NW ¼ Sec. 26, T.49 N., R.98 W., which is of the same stratigraphic level as the site of the type.

In size and morphology these three teeth could readily occlude with the lower jaw of *M. hopsoni,* but in detail are unlike upper teeth of any other known tillodont species.

The premolar (right P^3) exhibits a prominent primary cusp followed posteriorly by a smaller crestlike cusp (tritocone of Gazin and others). The enamel at the base of the primary cusp is somewhat crenulated. A basal anteroexternal cingulum gives rise to a strong parastyle, and a somewhat weaker but longer posteroexternal cingulum terminates at a well-developed metastyle. The lingual cusp (deuterocone of Gazin and others) is prominent, but the specimen is damaged and it is impossible to determine if an internal cingulum or hypocone was present.

The molars are quadrate, characterized by a widely flaring hypoconal crest and a prominent mesostyle. This hypoconal crest is as wide as that observed in any other tillodont molars. The mesostyle, on the other hand, is totally unknown in any other tillodont. In the molar of YPM 17594 (a left M^1 or M^2), metastyle and parastyle are both well developed, the former perhaps slightly more so. The external cingulum in this tooth bears several smaller, lower cuspules, subsidiary to the parastyle and metastyle. A short, low anterior cingulum is present lingually. The trigon basin exhibits small beads of enamel, resembling the enamel folds seen in some *Trogosus* molars, though not so well developed. This feature has not been found in any specimen of *Esthonyx.* In YPM 27333 (left M^3?), the external cingulum is less apparent and there is no metastyle, which suggest that this may be M^3. The anteroexternal region of the tooth is missing, so the parastylar development cannot be determined; however, there are indications that the parastyle was prominent. The anterointernal cingulum is long and pronounced, considerably more so than in YPM 17594. A small fold of enamel present in the

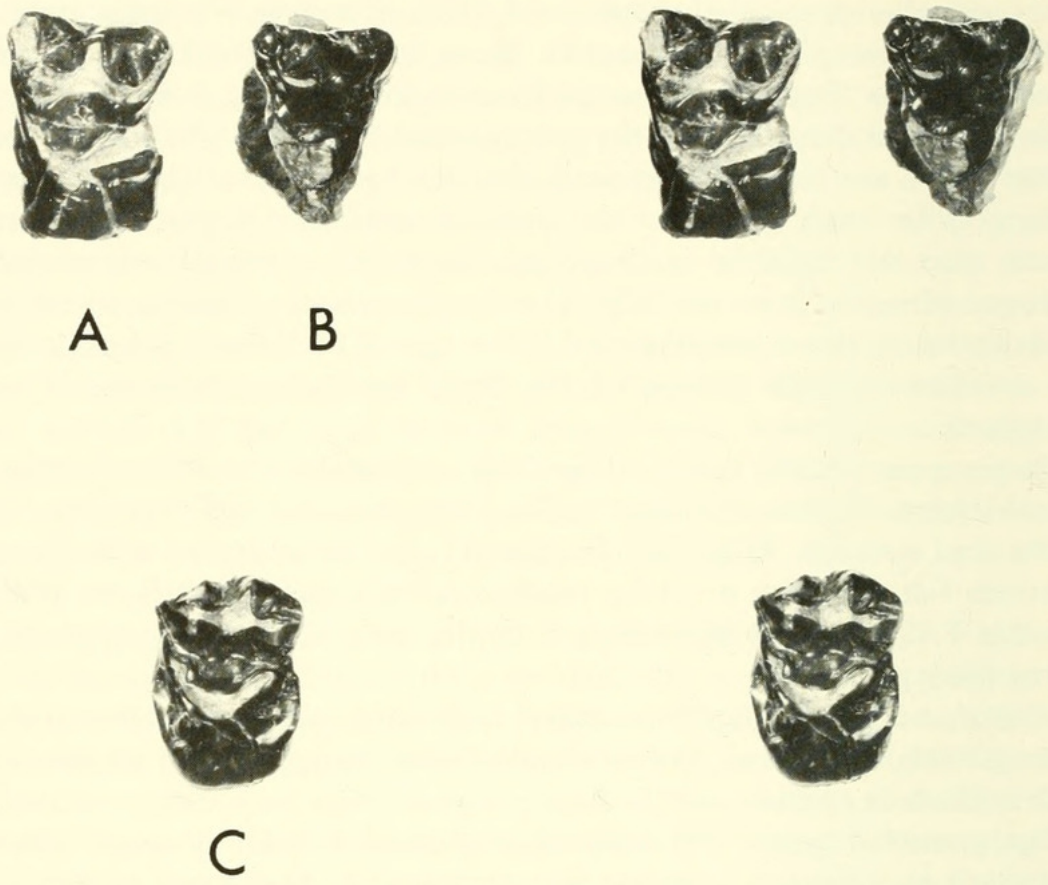

FIG. 3. Upper teeth of *Megalesthonyx hopsoni,* n. sp. (stereophotographs, ×1). A. YPM 17594, left molar. B. YPM 17594, right P^3. C. YPM 27333, left molar (M^3?).

trigon basin approximates more closely than does YPM 17594 the condition found in *Trogosus.*

PHYLETIC POSITION OF *Megalesthonyx hopsoni*

Megalesthonyx hopsoni is assigned to the subfamily Esthonychinae primarily on the basis of the morphology of the incisors. It is contemporary with the latest species of *Esthonyx* and just precedes the first known occurrence of *Trogosus.*

It is generally accepted that *Trogosus* was derived from *Esthonyx,* and there is as yet no evidence to contradict this view. Intermediates have not previously been known, however, but *Megalesthonyx* is intermediate stratigraphically and morphologically. The most significant morphologic features are the extent of enamel on I_2 and I^2, the open root of this tooth (possibly due to the age of the individual, as noted above), reduction of the canine and P_2 (while P_2 remains two-rooted) and of the talonid of P_4, and the presence of enamel folds in the trigon basin of the upper molars. The ab-

TABLE 2. MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH

YPM 17594,	premolar: right P^3	
	gratest anteroposterior (mesiodistal) diameter	14.2
	greatest labiolingual diameter	15.5
YPM 17594,	molar: left M^2 or M^1	
	greatest anteroposterior diameter	15.6
	greatest labiolingual diameter	21.2
YPM 27333,	molar: left M^3?	
	greatest anteroposterior diameter	14.5
	greatest labiolingual diameter	21.4a

a = approximate

solute size is intermediate. The degree of reduction of C and P_2 and the presence of diastemata closely approximate *Trogosus*.

There are, however, at least two problems in regarding *Megalesthonyx hopsoni* as a transitional form between *Esthonyx* and *Trogosus*. The incisors still basically reflect the plan seen in *Esthonyx*, with only subtle hints of a shift to the trogosine condition. The second and more important point concerns the prominent mesostyle present in the upper molars of *Megalesthonyx hopsoni*, but absent in its ancestor *Esthonyx* and supposed descendant *Trogosus*. It seems most unlikely, though not impossible, that this structure would develop to such an extent in a rather short time and be lost completely in an equally brief period. Also notable is the prominence of the anterointernal cingulum in the upper molars. In YPM 27333, this cingulum is as fully developed as in any *Esthonyx* specimen known to me. On the other hand, this structure is greatly reduced or absent in *Trogosus*.

These considerations suggest that *Megalesthonyx hopsoni* itself may not be the intermediate species, but that some as yet unknown species of the genus, or perhaps some other closely related form, was directly ancestral to the trogosines. In any event, it is highly probable that *Megalesthonyx* is very close to the ancestor-descendant line between *Esthonyx* and *Trogosus*.

A Note on Tillodont Taxonomy

The tillodonts have frequently been accorded ordinal rank. Van Valen (1963) revised their status to suborder and transferred them to the Condylarthra. I hesitate to follow this allocation, for it overburdens the already diverse order Condylarthra, while obscuring the extreme specialization achieved by Middle Eocene tillodonts. Thus it seems more useful at present to retain ordinal status for the Tillodontia. On the other hand, I agree with Van Valen's conclusion that the order was derived from the Arctocyonidae.

Most authors have distinguished at least two subgroups of tillodonts. In the most recent study of the order, Gazin (1953) grouped all tillodonts in a single family, Esthonychidae Cope, 1883, which he divided into two subfamilies, Esthonychinae and Trogosinae. This classification has been reexamined during the course of this study and it seems appropriate to maintain it here. The subfamily Esthonychinae, including *Esthonyx* and *Megalesthonyx,* is characterized by the presence of large but rooted second incisors. The Trogosinae have large gliriform second incisors which grow from persistent pulp. Included in this subfamily are *Trogosus, Tillodon,* and *Kuanchanius,* the last from the Middle Eocene of Shantung Province, China (Chow, 1963). *Adapidium* (Young, 1937) also from China, is known from posterior dentition only and cannot at present be assigned definitely to either subfamily.

There has been some dispute as to which family name should be applied. Esthonychidae, observed by Gazin (1953), is the most appropriate name, for the other two family names should be regarded as invalid. Anchippodontidae Gill, 1872, is undoubtedly the earliest named tillodont family, but it is based on a genus of indeterminate type *(nomen dubium), Anchippodus,* which is probably a trogosine. The family name Tillotheriidae should likewise be rejected, in the interest of stability, as it is based on the invalid genus *Tillotherium. (Tillotherium hyracoides* Marsh has since been referred to the genus *Trogosus.* Marsh later named *Tillotherium fodiens,* which is clearly of different generic affinities; Gazin (1953) proposed the genus *Tillodon* for this form. *Tillotherium,* therefore, has been used for animals of two different genera and must be regarded as invalid). Although the International Commission of Zoological Nomenclature has not issued an opinion for this case (i.e., family names based on totally invalid genera, not genera merely reduced to junior synonymy), it seems in the interest of stability to use the name Esthonychidae rather than any other proposed name.

The view that the tillodonts represent a single family is strengthened by *Megalesthonyx hopsoni,* which has been shown to be roughly intermediate between *Esthonyx* and *Trogosus.* Although future evidence may prove otherwise, it still seems appropriate to maintain two subfamilies, in recognition of the adaptive shift evident in the gliriform incisors of the trogosines.

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