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SKELETAL REMAINS AND RESTORATION OF EOCENE ENTELONYCHIA FROM PATAGONIA[1]

BY GEORGE GAYLORD SIMPSON

The skeleton of South American ungulates has been practically unknown for any stage before the Deseado, and knowledge of the crucial early evolution of these groups has been derived from teeth and a very few skulls. The only exceptions are some isolated bones, a humerus ascribed to *Notopithecus* and several astragali ascribed to various genera, described by Ameghino. Even these exceptions, valuable as they are, are not very enlightening, being single unassociated bones of uncertain systematic position.

The Scarritt Expeditions were peculiarly fortunate in finding several partial skeletons in the Casamayor formation which reveal almost the entire structure in the Entelonychia of this very early stage, as well as limited parts of the skeleton in some other groups. Full description is deferred for a monograph of the whole fauna now well advanced, but it has become necessary to publish this preliminary and summary note in order not to impede the work of other students.

The accompanying reconstruction and restoration were drawn by Mrs. Mildred Clemans, 1935, under my direction.

The three principal specimens here briefly recorded are the following:

A.—Amer. Mus. No. 28905. Including most of the vertebrae from the atlas to the anterior caudals, nearly complete right fore-limb, left pelvis and femur, many ribs and other fragments. The genus is certainly *Thomashuxleya*. Fragments evidently of the skull of the same individual were found nearby. They were too extremely disintegrated to be worth restoration or even collecting, but permitted certain field identification as a species of *Thomashuxleya* of which several nearly complete skulls were found at the same horizon and locality. Furthermore this genus is there common and none other to which the skeleton could conceivably belong is known. Found by G. G. Simpson, 1930, in the Casamayor of the "Oficina del Diablo," Cañadón Vaca, Chubut.

B.—Amer. Mus. No. 28906. Fourteen vertebrae, sternum, clavicle, most of both fore-limbs, ribs, and other fragments. The generic ascription is uncertain, but may be possible later. The skeleton is smaller than A, but generally similar. It may belong to a small species of *Thomashuxleya*, or to one of the ill-known and as yet unre-

[1] Publications of the Scarritt Expeditions, No. 27.

vised genera of the same group which include species smaller than *Thomashuxleya* and larger than *Pleurostylodon*. In any event it is almost certainly an entelonychian. Found by C. S. Williams, 1931, in the Casamayor (slightly below the level of A but not appreciably different in age), Cañadón Vaca, Chubut.

C.—Amer. Mus. No. 28904. Left humerus, radius, and ulna, both femora and tibiae, numerous foot bones, one dorsal and several caudal vertebrae, ribs, and other fragments. The smallest skeleton of the three, almost surely of *Pleurostylodon*, as that is the commonest genus including species of this size and as the bones agree well with fragments found in actual association with *Pleurostylodon* skull and jaw fragments. Found by G. G. Simpson, 1931, in the Casamayor (same level as A), Cañadón Vaca, Chubut.

For brevity the three skeletons are described together and are referred to as A, B, and C. The structure is essentially the same in all, with differences apparently of not more than generic value.

Comparison is here made chiefly with *Homalodotherium* of the Santa Cruz, especially the skeleton found by the Field Museum party under Riggs and described by Scott (1930, see references). *Homalodotherium* represents the height of entelonychian specialization in the skeleton, as far as known,[1] and among the special points of interest of the Casamayor specimens are the demonstration of the origin of its peculiarities from a structure more normal, or more primitive, and indication of the degree of evolution in a single group from Casamayor to Santa Cruz time. Where the part is unknown in *Homalodotherium*, or to suggest special resemblances, some reference is also made to Santa Cruz typotheres as described by Sinclair (1909) and toxodonts as described by Scott (1912). More detailed comparisons are deferred.

VERTEBRAE.—The posterior dorsals, lumbars, sacrum, and anterior caudals were preserved in articulation in A, but breakage of the processes makes it uncertain exactly where the change from dorsal to lumbar occurs. There are certainly five and not more than seven lumbars, seven being the most probable number. There are preserved eleven to thirteen, probably eleven, dorsals, but as most of these were scattered a few may well be missing—judging from later notoungulates it is probable that there were about fifteen dorsals in the complete series. There are four sacrals in A. B and C do not contribute to knowledge of the vertebral formula.

Six cervicals are preserved in A, the missing vertebra probably being the fifth, or possibly the sixth. The atlas considerably resembles that of *Nesodon*, but is less depressed dorsoventrally and has the transverse processes relatively much smaller. The axis has a large, peglike odon-

[1] Only one later form, *Chasicotherium*, has been described and in it the skeleton is unknown.

toid process. The transverse processes, although imperfectly preserved, were clearly much smaller than in *Nesodon* and the canal through each is diminutive. The neural spine is much less expanded than in *Homalodotherium* (although relatively slightly more elongate than in *Nesodon*) and its expansion is less anteroposterior, more anteroinferior-posterosuperior so that it extends relatively farther above the postzygapophyses behind and in a more pronounced point above the odontoid before. A prominent vertebrarterial canal is present on all the four other preserved cervicals of A, but of the three cervicals of B (all posterior to the axis) one, probably the last, lacks the canal.[1] In both specimens, so far as shown, the neural arches of vertebrae C 3–7 are similar, simple, with large normal zygapophyses and weak, simple neurapophyses directed slightly backward. The transverse process on C 3 of A has a short anteroinferior reflection forward and a prominent, recurved production outward and backward. On C 6, or possibly C 5, the process is of similar shape but is less produced, and on C 7 it is longer but less expanded, simpler, and directed downward and outward. The process on C ?7 of B is similar but relatively shorter and directed less ventrally. On C ?6 of B, however, the process is unlike anything preserved in A (but the latter is incompletely preserved), forming a great, hatchet-like ventral plate produced into a posterior horn, recalling the process on the sixth cervical of *Nesodon* although of different exact outline. All the centra are short, the width in each case considerably exceeding the length.

The anterior dorsals have the ordinary scale-like zygapophyses and present no marked peculiarities aside from the slenderness and small size of the spines (noted also in *Homalodotherium* by Scott), and their marked posterior inclination. There is no anticlinal vertebra, even the lumbar (and indeed the sacral) spines being slightly inclined posteriorly, an unusual character probably associated with relative inflexibility of the posterior dorsal and lumbar region. On the posterior dorsals the spine is very low, relatively lower than in *Homalodotherium*, barely rising above the prezygapophyses, but expanded anteroposteriorly, squarely truncated, and only slightly inclined backward. Its position is wholly posterior, between the postzygapophyses. The metapophyses so strongly developed in *Homalodotherium* are absent or perhaps barely indicated by a slight blunt process directed upward and outward from the prezygapophysis. On the most posterior dorsal known in *Homalodotherium* the cylindrical toxodont lumbar type of articulation is not indi-

[1] The probable seventh of A is here poorly preserved and the apparent canal may be anomalous or spurious.

cated on the pre- and barely suggested on the postzygapophyses but in *Thomashuxleya* this type is fully developed at a corresponding part of the series, the articulation being there at least as fully cylindrical as on any lumbar in *Nesodon.*

The lumbar articulations are more complex and rigidly interlocking than in Santa Cruz toxodonts (or typotheres) and remarkably parallel the very specialized condition in some artiodactyl lumbars (e. g., in *Odocoileus*). In addition to the cylindrical primary articulation, another lamina is developed above this so that the articular surface is strongly S-shaped in transverse section. A low, non-articular, anteroposterior crest on the dorsal surface of the prezygapophysis represents the still poorly developed metapophysis. Anapophyses appear to be lacking. The neural spines and centra are as in the posterior dorsals save that the latter are somewhat more elongate and the former tend (at least in A) to be bifid posteriorly. The transverse processes are long, simple, dorsoventrally compressed blades.

The sacrum, known only in A and there rather poorly preserved, seems to consist of four coalesced vertebrae of which three articulate with the ilium. The general outline seems to be very much as in *Adinotherium* save that in the latter (and most later notoungulates) several caudals still free in *Thomashuxleya* have become fused into the sacral complex. The first sacral has somewhat larger metapophyses than are preserved on any of the lumbars. Posterior to this the articulations appear only as blunt, but quite distinct, processes in which the elements are not distinguishable. The first two neural spines are separate and prominent and posterior to these is only a low, sharp, nearly undifferentiated ridge.

The anterior caudals (A and C) are large, heavy, dorsoventrally compressed bones with semicylindrical zygapophyses. The neural spines are merely sharp longitudinal ridges barely rising into free processes. The transverse processes are strong, broad plates. In C this stout structure is seen to break down rapidly, probably by about the seventh or eighth and almost surely before the tenth caudal, and the more distal vertebrae are short, irregular centra with no neural arches or zygapophyses. The inference is that the tail in these forms was heavy but short.

Ribs.—The ribs with the three specimens are not remarkable in any way. None are strongly expanded or more than slightly slab-like.

Sternum.—Most of the sternum is preserved in B, and part of the presternum in A. The latter is like that of B, as far as preserved, except for being larger and proportionately stouter. The presternum (of B) has prominent first rib articulations at the widest part of the bone, and between and anterior to them is a deep dorsal concavity or pocket. The ventral surface of this part of the bone has a very high median keel. The anterior dorsal border is not preserved. After narrowing posterior to the rib articulations, the bone expands slightly at the posterior end. It is here much wider than deep. This bone is very unlike that of *Homalodotherium*, and somewhat more but not at all exactly like *Nesodon*. In B there follow five (or possibly six) quadrate mesosternal segments, much compressed dorsoventrally, with projections at the four corners but otherwise almost featureless. It cannot be determined whether the last of these is the xiphisternum or how many other segments may have been present.

Clavicle.—What is indubitably a clavicle is present in B. It is a well developed but simple, slender, curved bone very unlike the element considered as a clavicle in *Homalodotherium*.

Scapula.—The scapula is peculiar, very unlike later toxodonts and somewhat more like some typotheres, e. g., *Protypotherium*. This part is too poorly known in *Homalodotherium* to make very useful comparisons. The spine is very high in A, with a flattened free border. There is a single prominent metacromion at the posteroinferior end of the spine in both A and B, but no second metacromion above this. The acromion is incomplete in both these specimens, but clearly was unusually large and stout, although not wide. In Amer. Mus. No. 28878, *Pleurostylodon*, the acromion is completely preserved and is smaller and directed less anteriorly than is indicated in A and B, being very like this part in *Protypotherium*. The prespinous surface in B is much larger than the postspinous and the coracoid process is a stout hooklike projection.

Humerus.—The proximal end, completely preserved only in B, has a large projecting greater tuberosity which is, however, much less prominent than in *Nesodon*, and a smaller but distinct lesser tuberosity. The deltoid crest is prominent in all three individuals, but is less so than in *Homalodotherium*, does not extend so far distally, and does not form a free projection at the distal end. The supinator crest is strong, relatively about as marked as in *Homalodotherium* and longer proximodistally. The entepicondyle is of moderate development in A and B, about as in *Homalodotherium*. In C it is relatively larger. The entepicondylar foramen, absent in *Homalodotherium*, is present in all three of these earlier forms.

Radius and Ulna.—Radius and ulna are known in all three specimens and are essentially similar in all three save that those of B and C are somewhat lighter in build as well as smaller and have the ulnar shaft and side of the olecranon more excavated. They are heavy, separate bones, more elongate than in *Nesodon* but less so than in *Homalodotherium.* The ulna is nearly straight, not as bowed as in *Homalodotherium,* although the strong olecranon is somewhat deflected to the internal side. The distal end (in A, poorly preserved in B and C) is slightly less transverse than in *Homalodotherium.* Other characters agree rather closely with the latter or with notoungulates in general. The radius is markedly arched, apparently more than in *Homalodotherium.* The proximal end is considerably more transverse than in the latter and less circular, probably indicating less power of rotation. The distal end is likewise somewhat more transverse than in *Homalodotherium* and the scaphoid articulation, which is partly concave, seems to be relatively slightly smaller in A and B, but perhaps not in C. The dorsal notch between the two surfaces is present but somewhat less pronounced than in the later genus.

MANUS.—The left carpus is perfectly preserved in B except for some breakage of the cuneiform. Most of the right carpals of A are represented, but all but the pisiform and trapezium are fragmentary, and there are a few elements from C, but the differences are important only for generic distinctions and need not be pointed out here. The following remarks are all based on B. The eight usual mammalian elements are all present and separate. On the dorsal or lateral exposures, the cuneiform, unciform, and pisiform are large, the lunar, scaphoid, and trapezium moderate, and the magnum and trapezoid small. In the carpus of *Homalodotherium,* the magnum, trapezoid, and to a slight degree the lunar are relatively larger while the scaphoid is relatively smaller. In the later genus the proximal elements are relatively shorter, especially noticeable in the lunar, while the known distal elements are all relatively longer. The earlier carpus is distinctly less serial. In *Homalodotherium* the only distal articulation for the scaphoid is with the trapezoid, but in B it also has distinct facets for trapezium and magnum. The lunar-magnum articulation is much larger than the lunar-unciform in the later genus, but they are of nearly equal size in B. The facets for metacarpal II on the magnum and for III on the unciform also appear to be relatively larger in the earlier form. The pisiform of B is quite as large as any other carpal, and has a large facet for the ulna, with which it must have been constantly in contact (whereas in *Homalodotherium* the ulna has no facet for the pisiform). There is a small radial sesamoid, proximal to the trapezium.

The metacarpals are rather short and stout, not elongate as in *Homalodotherium.* The descending order of length is III–II–IV–V–I. In the articulated carpus II and IV are of nearly equal length and the foot is mesaxonic, although not markedly so. Unlike *Homalodotherium* V is decidedly shorter and not stouter than II to IV. In B, I is nearly as long as V but more slender, and in A it is relatively much shorter, but in both it is well developed and fully functional. Its proximal articulation is far removed from that of II and it diverges very markedly from the other metacarpals, although its articulation does not permit it to be definitely opposed to them. Each metacarpal (except possibly I, in contact with which they are not preserved) has a pair of large distal palmar sesamoids. Between these the articular surface is keeled, but even here the keel is very slight and there is none on the globular purely distal and dorsal part of the articulation which normally was all that came in contact with the proximal phalange. The pose can only have been digitigrade, with the main weight falling on and immediately anterior to the row of sesamoids. The phalanges had much freedom of motion on the metacarpals and, apparently, independent of each other. The whole structure is one of an animal which has not lost or which is secondarily acquiring a grasping manus, very unlike any typical ungulate development.

The proximal and medial phalanges are short and stout, but less so than in *Homalodotherium,* and the medial phalanges are all distinctly shorter and smaller than the proximal. The articulation between these two is about as oblique as in the later form, and that for the unguals permits a nearly equal freedom of motion. The unguals are much less claw-like than in *Homalodotherium,* although they show a possible structural beginning of such a specialization. The more medial unguals are long, depressed, and deeply fissured. The more lateral are less depressed and have the fissure much smaller or possibly absent.

PELVIS.—Aside from a few scraps of no interest, the pelvis is known only in A, in which the posterior and inferior parts of the ischium and the inferior part of the pubis are missing. The whole pelvis is rather like that of *Homalodotherium,* especially the ilium which is similarly expanded into a great crescentic, nearly horizontal plate, but the obturator foramen is distinctly more oval and anteroposterior and the ischial spine is more definite and more posterior. As far as preserved the ischium and pubis are more toxodont- or even typothere-like than in *Homalodotherium,* or in other words more generalized within the Notoungulata.

FEMUR.—The femora (A and C but imperfect in both cases) are much more primitive than in *Homalodotherium* and remarkably resemble those of *Hegetotherium* and *Protypotherium*, which may be assumed nearly to have retained the ancestral notoungulate structure in this part. The shaft is not notably flattened, the greater trochanter projects above the head, the notch between these is moderately pronounced. There is a lesser trochanter and it is prominent, the third trochanter is distinct, short proximodistally, and opposite or slightly distal to the lesser trochanter, and the patellar groove is relatively long and narrow—all features so fundamentally unlike *Homalodotherium* that, on this bone alone, the two types would hardly be supposed to be related at all.

TIBIA AND FIBULA.—The fibula is not known in A, B, or C, but is partly present in Amer. Mus. No. 28690, mentioned below, in which it is a slender, but complete and separate, bone of generally primitive character. The tibia, present in the specimen just mentioned and in C, is likewise primitive and altogether unlike that of *Homalodotherium*. It differs from the latter, among other ways, in being relatively longer and more slender, proximal and distal ends much less transverse, cnemial crest very prominent but less massive, extending farther distally, and ending more abruptly.

PES.—Of the pes, only the navicular and cuboid of C are preserved and surely identifiable in the three skeletons here chiefly considered. There is, however, another specimen, Amer. Mus. No. 28690, found by me at about the same level and locality as the three principal specimens, in which the tarsus, lacking only the distal end of the calcaneum, is well preserved and part of the metatarsus is present. The genus, or even family, is uncertain. The size is still smaller than C, but the morphology of the duplicated parts (including femur and tibia) is similar. The genus is probably not *Pleurostylodon*, but the family could well be the same (Isotemnidae) and in any event the tarsus is structurally primitive for the Notoungulata and probably also particularly for the Entelonychia. The following notes refer to this specimen.

The calcaneum is of normal proportions and the tuberosity is much less expanded than in *Homalodotherium*. The fibular facet is not preserved, but from the calcaneal facet on the fibula it must have been small. The trochlea of the astragalus is shallow and broad. There is a large astragalar foramen and a large, strongly differentiated groove for a flexor tendon. The neck is relatively long and the head spherical, somewhat transverse. There is no contact with the cuboid. The navicular is markedly transverse, although less so than in *Homalodotherium*, and the cuneiforms are all distinct, but the mesocuneiform is very small.

The first metatarsal is shorter than the second but is functional and was followed by phalanges. The third metatarsal is markedly larger than the second. Both second and third are much more slender than in *Homalodotherium* and the distal articulations are nearly spherical on the dorsal side and sharply keeled on the plantar side. The cuboid articulations do not suggest enlargement of the fifth metatarsal.

When articulated with the tibia and fibula, this foot tends to incline somewhat toward the tibial border when the crus is vertical. The flexibility of the tarsus permits it to assume a normal position, whether plantigrade or digitigrade, but it seems very unlikely that the foot could be brought to rest on the fibular border as in *Homalodotherium* (in the opinion of Scott and of Ameghino). The exact posture cannot be determined, but it seems probable that the foot was semi-digitigrade. The posture indicated by the pes of *Homalodotherium* is probably one of its many secondary specializations.

LIMB PROPORTIONS.—A few indices for various limb elements indicate the rather generalized proportions of the Casamayor skeletons as compared with those of later notoungulates:

Index	Casamayor Specimens A	B	C	28690	*Homalodotherium segoviae*	*Protypotherium australe*	*Nesodon imbricatus*
Radiohumeral	76	73	77	..	112	80	78
Metacarpohumeral	31	28	34	..	47	34	38
Humerofemoral	85	..	95	..	76	94	97
Tibiofemoral	..	..	88	..	60	113	87
Metatarsotibial	..	..	..	35	26	35	25

Some of these figures are approximate only, from various imperfections in the data, but they are adequate for broad comparisons. The figures for the Santa Cruz forms are calculated from measurements given by Scott and by Sinclair. More detailed consideration of proportions is deferred.

The Casamayor specimens agree rather closely with *Phenacodus*, save that the latter has the humerus slightly shorter relative to the three other elements with which these indices compare it, probably a reflection of the somewhat more cursorial habitus of *Phenacodus*. Even on this point the difference is not marked.

The Casamayor specimens differ little from the Santa Cruz typothere and toxodont save for the cursorial lengthening of the tibia in the former and graviportal shortening of the metatarsus in the latter. *Homalodo-*

therium differs markedly in each of these indices. The strong inference is that the proportions of the Casamayor forms are approximately those primitive for notoungulates in general and that these proportions were little changed in Santa Cruz toxodonts and typotheres but that *Homalodotherium* is profoundly modified in limb proportions.

Discussion.—It is not proposed to go into any detail at this time regarding the bearing of these skeletons on notoungulate morphology

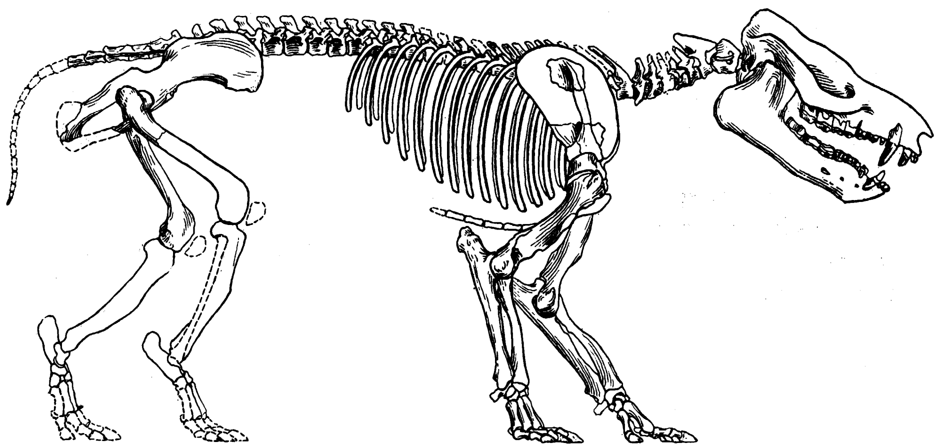

Fig. 1. *Thomashuxleya*. Reconstruction of skeleton. Skull and jaws are Amer. Mus. No. 28698, not associated with the skeleton but surely of the same genus and species, from the same horizon and locality, and of about the same individual age. Shaded parts of the skeleton are from Amer. Mus. No. 28905, a single individual. Unshaded parts in solid outline are from contemporaneous and closely related forms, scaled to the size of the individual skeleton. Parts in broken outline are restored from more distantly related notoungulates or in part hypothetical. (The ribs are shown in continuous outline, being in large part from a closely related form; they are partly present in this individual skeleton but it seemed unnecessary to indicate the exact outlines of fragments preserved). About one-twelfth natural size.

and phylogeny or to make many comparisons, but some broad conclusions stand out even in a brief review. *Thomashuxleya* is certainly a structural and possibly a direct ancestor of *Homalodotherium*. The several other Casamayor specimens examined are certainly no more specialized than *Thomashuxleya* and seem in some respects and to a slight degree to be less so. These facts together with the fairly complete series of dentitions, skulls, and jaws connecting *Thomashuxleya* with *Homalodotherium* suggest the hypothesis that the very marked difference in the

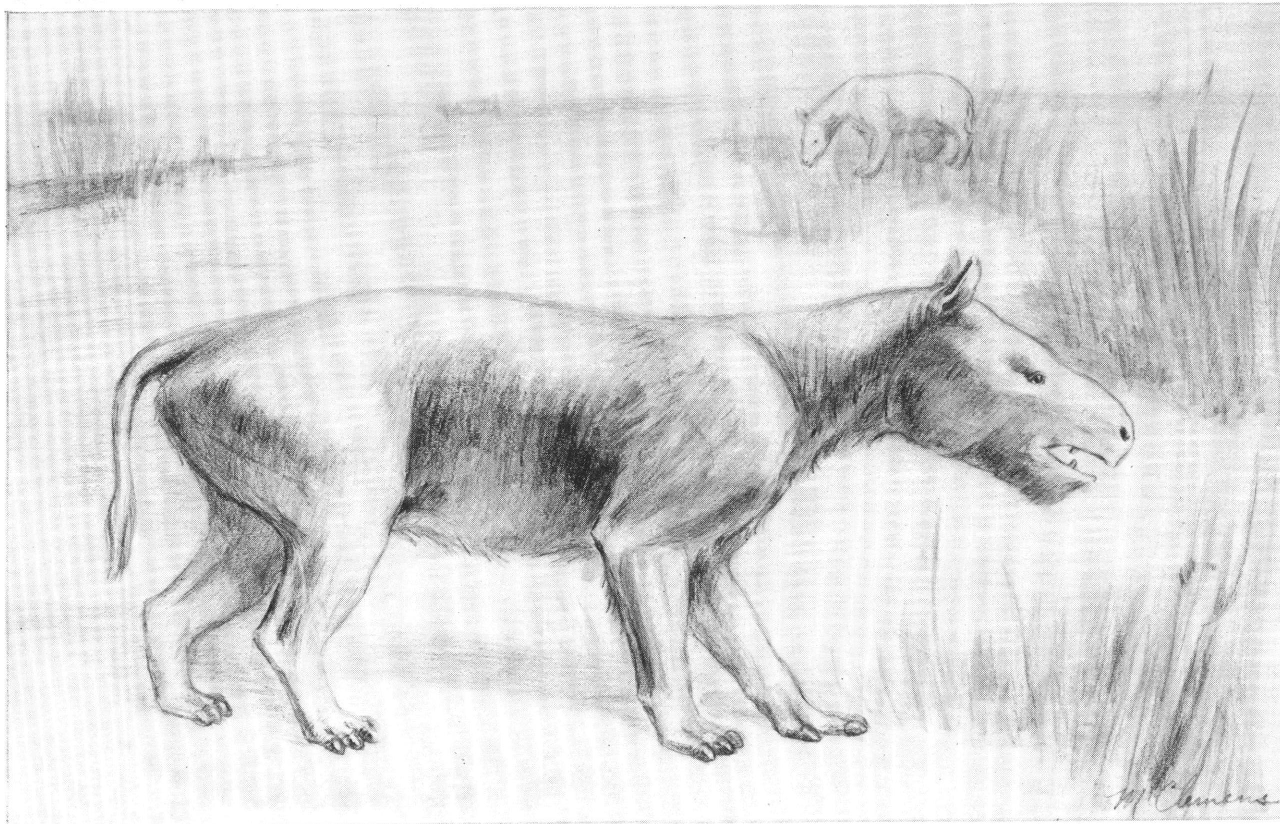

Fig. 2. *Thomashuxleya.* Restoration of living animal, based on the skeletal reconstruction (Fig. 1). The individual in the foreground is in exactly the same pose as the skeleton as figured, and is one-eleventh natural size. This is the largest animal known from the Casamayor, but is very primitive in most characters and nearly approaches the generalized ancestral notoungulate type.

limbs is caused by evolutionary advance and is not evidence that *Homalodotherium* is a descendant of an (unknown) more specialized Casamayor group.

If, as I believe, *Thomashuxleya* does represent a normal Casamayor entelonychian, it is striking that in structure it is on the whole such a generalized notoungulate, with only traces of incipient specialization recognizable as more particularly entelonychian. Among the possible inferences are:

1.—That *Homalodotherium*, despite its remarkable divergence in skeletal structure, was derived from the same general stock as the other notoungulates.

2.—That the entelonychian, or homalodothere, group had not long been separated from the toxodont and typothere stocks in Casamayor time.

3.—That the profound skeletal modification of *Homalodotherium* took place almost entirely in the span from Casamayor to Santa Cruz.

4.—That the Entelonychia are characterized by relative conservatism in dental structure and rapid skeletal evolution, whereas, on the whole, the reverse is true of typotheres and toxodonts.

NOTE ON *Periphragnis*.—*Periphragnis* Roth, 1899 (synonym, *Proasmodeus* Ameghino, 1902), from the Musters, represents the structural stage of homalodothere evolution immediately following *Thomashuxleya*. There are two manus of *Periphragnis* collected by Roth in the Museo de la Plata which I have studied, thanks to the courtesy of the officials of that Museum, and which I propose to describe later. It is worth noting here that these manus show very little advance over that of *Thomashuxleya*, suggesting that at least in this part, and by inference probably throughout,[1] the profound modification of the homalodotheres is not only post-Casamayor but also post-Musters.

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[1] The skull and dentition of *Periphragnis* are also very close to *Thomashuxleya*.