# A DESEADO HEGETOTHERE FROM PATAGONIA.[1]

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ABSTRACT. *Propachyrucos ameghinorum*, new species, is diagnosed and briefly described from a hitherto unrecorded Deseado (early Oligocene ?) deposit near Lat. 44-1/2° south, Long. 68-1/3° west, in central Chubut, Argentina. The type is a nearly complete skeleton, the oldest and one of the most perfect of known hegetothere skeletons. The mounted skeleton and a plastic restoration are figured.

## Introduction.

IN 1933-1934 the Second Scarritt Patagonian Expedition of The American Museum of Natural History found several rich Eogene faunules of unusual character in a hitherto scientifically unexplored region of central Chubut, in Argentine Patagonia. Monographic description of these has been unavoidably delayed but is in progress. In the meantime the present note is published in order to make known one of the most important specimens and to provide a name to be used in connection with exhibition and with distribution of copies of a plastic restoration.

This specimen is the virtually complete skeleton of a small hegetothere, representing a new species assignable, with sufficient probability, to the genus *Propachyrucos* Ameghino, 1897. As far as I know, this is the first hegetothere skeleton to be mounted, although several paper reconstructions have been published. Sinclair (1909) gave such a reconstruction of *Pachyrukhos*, from the Santa Cruz, a composite based on materials in The American Museum of Natural History. Loomis (1914) gave a paper reconstruction of *Prosotherium*, a Deseado form contemporaneous with *Propachyrucos*, but the specimen involved is very incomplete and the reconstruction correspondingly hypothetical. The best single hegetothere skeleton hitherto described belongs to a Chapadmalal species of *Paedotherium*, the last survivor among the hegetotheres. Kraglievich (1926) published a paper reconstruction of this skeleton.

The present specimen is also unusual in view of the great

[1] Contributions of the Scarritt Expeditions, No. 34.

rarity of adequate pre-Miocene mammal skeletons from South America. Besides *Prosotherium*, mentioned above, Loomis (1914) gave paper reconstructions of *Protheosodon* and *Rhynchippus* from the Deseado, but both were based on inadequate materials and there is some reason to suspect that the *Protheosodon* mandible is not of the same genus, or perhaps family, as the hind legs associated with it in the restoration. Several complete skeletons of *Scarrittia*, also a Deseado form, were found by us a few kilometers from the specimen described in the present paper and two of these have been prepared in the death pose, without reconstruction or mounting (see Simpson, 1935). The present specimen is thus the first mounted skeleton from the Deseado. Skeletal remains from pre-Deseado beds are still rarer and there is only one known specimen sufficiently perfect to permit skeletal reconstruction, a partial skeleton of *Thomashuxleya* from the Casamayor (paper reconstruction in Simpson, 1936; the skeleton has since been mounted).

The specimen here described was found by Justino Hernández, collected by me, and prepared and mounted by Albert Thomson. A life restoration was modeled by Miss France Baker, working at the American Museum as a student of Antioch College. John C. Germann drew the accompanying text-figures.

TAXONOMY.

Order Notoungulata Roth, 1903.
Family Hegetotheriidae Ameghino, 1894.
Subfamily Muñiziinae Kraglievich, 1931.
Genus *Propachyrucos* Ameghino, 1897.
*Propachyrucos ameghinorum*,[2] new species.

*Type.*—A. M. N. H. No. 29574, nearly complete skeleton.

*Horizon.*—Deseado, probably early Oligocene.

*Locality.*—About 1½ kilometers south of the sheepherder's hut called "Las Cascadas," on the northwest side of the Meseta Canquel, in a small valley tributary to the Cañadón de las Víboras, approximately in Lat. 44 1/2° south, Long. 68 1/3° west, central Chubut Territory, Argentina.

*Diagnosis.*—Lower cheek tooth series of type 32 per cent larger than in type of *P. smithwoodwardi* and at least 20 per

[2] Dedicated to the memory of Florentino and Carlos Ameghino.

cent smaller than in type of *P. crassus*. $I_3$ and probably $P_1$ more reduced than in *P. smithwoodwardi*, and larger diastemata on both sides of $P_1$. About the size of *P. aequilatus* (or slightly larger), but without the relatively large anterior (premolar and) molar lobes said by Ameghino to characterize that species.

DESCRIPTION.

The dental formula is complete but $I\frac{2-3}{3}$, $C\frac{1}{1}$, and $P_1$ are vestigial. $I^3$ and the upper canine are represented by tiny pits that do not contain roots in this specimen and it is probable that the teeth, themselves, were lost in life and that the upper formula in a senile individual would be 2.0.4.3. $I^2$ is closely appressed to the greatly enlarged $I^1$ and was probably functional although small. There are large diastemata be-

Fig. 1. *Propachyrucos ameghinorum*, new species. Type, American Museum of Natural History No. 29574. Crown views of right upper and left lower dentitions. Lower dentition in small part completed by reversal from right side. $I^{2-3}$ and $C^1$ are represented by alveoli. x 3/2.

tween $I^2$ and $I^3$ and between upper C and $P^1$, with a smaller diastema between $I^3$ and C. The premolars are obliquely triangular, increasing in width from $P^1$ to $P^4$. The internal faces are somewhat flattened but not grooved. Transition from $P^4$ to $M^1$ is abrupt. The molars have two distinct internal lobes, separated by a deep re-entrant fold, as in *Prosotherium* and the interatheres and markedly unlike *Pachyrukhos* and *Hegetotherium*. The outer wall is somewhat wavy, with poorly defined parastyle, paracone, and metacone convexities, but the groove between parastyle and paracone, often strong in interatheres and in some but perhaps not all species referred to *Prosotherium*, is vague and shallow. Cement is present, most definitely on the inner face, but is thin.

$I_1$ and $I_2$ are both enlarged, but $I_1$ is much larger, the longest diameter of a section being 5.1 mm. as against 3.0 mm. for $I_2$,

proportions about as in *Pachyrukhos*.[3] $I_3$, lower C, and $P_1$ are peg-like, tiny teeth but are present and functional. The canine is the smallest of the three, all of which are procumbent but decreasingly so from $I_3$ to $P_1$. There are short diastemata between $I_3$ and C, C and $P_1$, and $P_1$ and $P_2$. $P_2$ is unreduced and bilobed, differing little from $P_3$ except that the anterior lobe is relatively larger. $P_3$-$M_3$ have the usual hegetothere pattern, flattened lingually and bilobed labially except $M_3$, which is trilobed.

TABLE I.

Measurements in millimeters of dentition of *Propachyrucos ameghinorum*, type, A. M. N. H. No. 29574.

| | |
|---|---|
| $I^1$–$M^3$ | 55.4 |
| $P^1$–$M^3$ | 32.1 |
| $M^1$–$M^3$ | 16.2 |
| Maximum diameter of transverse section of $I^1$ | 6.9 |
| $I_1$–$M_3$ | 53.1 |
| $P_2$–$M_3$ | 30.9 |
| $M_1$–$M_3$ | 17.8 |
| Maximum diameter of transverse section of $I_1$ | 5.1 |
| Same, $I_2$ | 2.7 |

Upper cheek teeth, L=length of ectoloph, W=maximum transverse dimension (protoloph on molars):

| | $P^1$ | $P^2$ | $P^3$ | $P^4$ | $M^1$ | $M^2$ | $M^3$ |
|---|---|---|---|---|---|---|---|
| L | 3.3 | 4.7 | 4.8 | 4.7 | 5.6 | 5.4 | 6.0 |
| W | 2.7 | 3.9 | 3.9 | 4.0 | 4.6 | 4.1 | 3.4 |

Lower cheek teeth, L=maximum length, W. ant. =width of anterior lobe, W. post.=width of posterior lobe (2nd lobe on $M_3$):

| | $P_2$ | $P_3$ | $P_4$ | $M_1$ | $M_2$ | $M_3$ |
|---|---|---|---|---|---|---|
| L | 5.0 | 4.9 | 4.9 | 5.4 | 5.5 | 7.5 |
| W. ant. | 2.2 | 2.5 | 2.5 | 2.3 | 2.4 | 2.3 |
| W. post. | 2.5 | 2.6 | 2.6 | 2.9 | 2.8 | 2.5 |

| | |
|---|---|
| Width of 3rd lobe of $M_3$ | 1.9 |

The skull differs little from the later hegetothere type thoroughly described by Sinclair (1909) and details need not be discussed at this time. It is almost exactly like the skull of *Prosotherium* (see Loomis, 1914). It resembles *Pachyrukhos* more than it does *Hegetotherium*, but both skull and mandible are more nearly equal in depth anteriorly and posteriorly than in *Pachyrukhos*, so that the head, in lateral view, has a less triangular or wedge-shaped contour than in the latter genus.

[3] Loomis's figures (1914) suggest that $I_2$ is the larger in *Prosotherium* but this is probably an effect of perspective. Ameghino (1897) states that the first incisor is enlarged in this genus.

The cervical and dorsal vertebral series are complete and there appear to be only 12 dorsals although it is possible that the next vertebra, transitional morphologically, also carried a rib, giving 13 dorsals. 16 dorsolumbars are preserved and three more have been tentatively added in the reconstruction to give a total of 19 (probably d.12, l.7; possibly d.13, l.6). The formula is not completely known in any hegetothere, but Sinclair (1909) says that there are 8 lumbars in *Pachyrukhos*. The formula in *Interatherium* is d.15, l.7. Sinclair has reconstructed *Pachyrukhos* with d.15, l.8, and Loomis (1914) has reconstructed *Prosotherium* with the same formula. Because *Interatherium* is only quite distantly related to the hegetotheres and because our *Propachyrucos* surely has fewer than 15 dorsals, it is probable that these reconstructions have the column too long by at least two vertebrae. On the other hand it is possible that our reconstruction has too few lumbars and that the dorsolumbar total should be 20 or 21 rather than 19 as we have it. The neural spines of our specimen are strongly anticlinal as in *Pachyrukhos*. The anticlinal vertebrae is d.11, not d.13 as shown by Sinclair for *Pachyrukhos* or d.14 as shown by Loomis for *Prosotherium*, but neither of these reconstructions is reliable on this point. Sacrum and tail are missing in our specimen, but a short tail is probable in *Pachyrukhos* and we have restored the tail in the more primitive genus as slightly longer than in Sinclair's reconstructed *Pachyrukhos*.

The girdles and appendicular skeleton are so like *Pachyrukhos* that a detailed description of the minor differences that do exist is not necessary at this time. The resemblance to *Hegetotherium* is almost equally close, but the general build and proportions are more suggestive of *Pachyrukhos*. The one great difference from both Santa Cruz genera is that the tibia and fibula are unfused in the earlier genus, clearly a primitive character. These bones are more like *Hegetotherium* than like *Pachyrukhos*. The few elements in *Prosotherium* for which Loomis's data (1914) permit comparison are also generally similar, but with some apparent anomalies. The pelvis in *Prosotherium* seems to be relatively considerably larger. Loomis says that the third trochanter is on the posterior, not internal, side of the femoral shaft and so shows it in his figure, but this is so extraordinary that I suspect distortion or some peculiarity in orienting the bone. Loomis also shows the tibia as shorter than the femur in *Prosotherium*, whereas in all

TABLE II.

Skeletal dimensions in millimeters of *Propachyrucos ameghinorum* and compared species. (All measurements are maximum lengths.)

| | *Propachyrucos ameghinorum*, A.M.N.H. No. 29574 | *Pachyrukhos moyani*, A.M.N.H. No. 9481, from Sinclair | *Interatherium robustum*, A.M.N.H. No. 15401, from Sinclair |
|---|---|---|---|
| Skull | 101 | Ca. 76½* | 80 |
| Humerus | 68 | 56 | 60½ |
| Radius | 52 | 50 | 41½ |
| Metacarpals: | | | |
| II | 26 | 20 | 14 |
| III | 26½ | 22½ | 15½ |
| IV | 21 | 18½ | 13 |
| V | 15 | 14½ | 9 |
| Femur | Ca. 85 | Ca. 65* | 59 |
| Tibia | 92 | 82 | 64½ |
| Calcaneum | 29 | 21 | 19½ |
| Metatarsals: | | | |
| II | — | 26½ | 16½ |
| III | 33 | 30 | 21 |
| IV | 31 | 26½ | 22 |
| V | 25 | 21½ | 17½ |

* Calculated from proportions in other individuals of this species.

other known hegetotheres the tibia is definitely the longer of the two. The bones were incomplete in Loomis's specimen, however, and the reconstruction may be erroneous. In the hindfoot of *Prosotherium*, Loomis shows digits II and III subequal and large, IV and V subequal and small. This is very unlike *Propachyrucos* or *Pachyrukhos*, although it resembles the much later, collaterally allied *Paedotherium*. Whether these discrepancies represent generic differences between *Prosotherium* and *Propachyrucos* or have some other explanation is not clear.

Size and proportions of *Propachyrucos ameghinorum* are compared with some later forms in Tables II and III and Fig. 2. *Prosotherium garzoni* has been similarly compared, but the data are omitted here because observations are incomplete and, in part, anomalous. *P. ameghinorum* is larger than its Santa Cruz allies and analogues.[4] The skull is relatively smaller in *Pachyrukhos* than in *Propachyrucos* but relatively larger in *Interatherium*.

[4] Deseado forms tend to be larger than their later relatives, although more primitive, a peculiarity that merits further study.

TABLE III.

Ratios of lengths of skeletal elements in *Propachyrucos ameghinorum* and compared species. (Specimens the same as in Table II.)

| | *Propachyrucos ameghinorum* | *Pachyrukhos moyani* | *Interatherium robustum* |
|---|---|---|---|
| Humerus / Radius | 1.31 | 1.12 | 1.46 |
| Radius / MC III | 1.96 | 2.22 | 2.68 |
| MC III / MC II | 1.02 | 1.12 | 1.11 |
| MC III / MC IV | 1.26 | 1.22 | 1.19 |
| MC III / MC V | 1.77 | 1.55 | 1.72 |
| Femur / Tibia | Ca. .92 | Ca. .79 | .91 |
| Tibia / MT III | 2.79 | 2.73 | 3.07 |
| MT III / MT IV | 1.07 | 1.13 | .95 |
| MT III / MT V | 1.32 | 1.40 | 1.20 |

In *Propachyrucos ameghinorum* the radius is shorter relative to the femur and the tibia is shorter relative to the femur than in *Pachyrukhos*. The greater elongation of the distal segment in the later form apparently represents progressive cursorial or, probably, saltatory adaptation. In *Interatherium* the radius is less elongate, relatively, than in either of these hegetotheres, but the hind limb proportions are about as in *Propachyrucos*. The forefoot is more elongate relative to the radius in *Propachyrucos* than in *Pachyrukhos*, but this is a function of the shorter radius. Elongation of the foot relative to the forelimb as a whole is almost the same in the two genera and no evolutionary change is indicated. The forefoot in *Interatherium* is decidedly shorter than in hegetotheres.

The order of length of the metacarpals and of the corresponding toes is III>II>IV>V in *Propachyrucos*, *Pachyrukhos*, *Paedotherium*, and *Interatherium*, but there are distinct differences of proportion. In *Pachyrukhos* the manus is nearly mesaxonic, with digit III definitely longest, II and IV both stout and subequal, and V smaller but not clearly reduced. In *Prop-*

*achyrucos*, II and III are of almost equal length and stoutness, IV is distinctly smaller, and V is more reduced than in *Pachyrukhos*. The proportions in *Propachyrucos* are, in fact, more like those of the far later *Paedotherium* and it appears that *Propachyrucos* is more specialized in the manus than is *Pachyrukhos*. This is not too anomalous. *Propachyrucos* is not, I

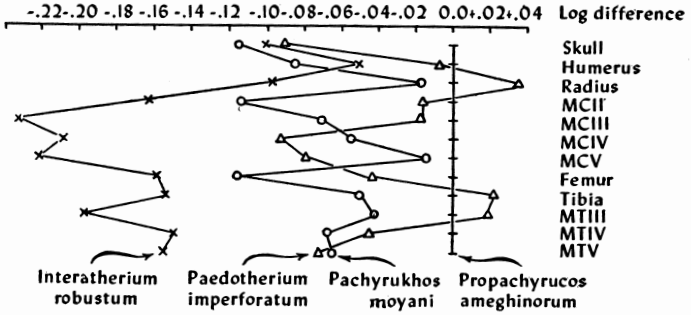



Fig. 2. Ratio (logarithm difference) diagram of lengths of skeletal elements, as labeled, in three hegetotheres and an interathere. Based on single specimens as in Table II.

think, ancestral to *Pachyrukhos* and there is no reason why the generally more primitive genus should not be precocious in some respects.

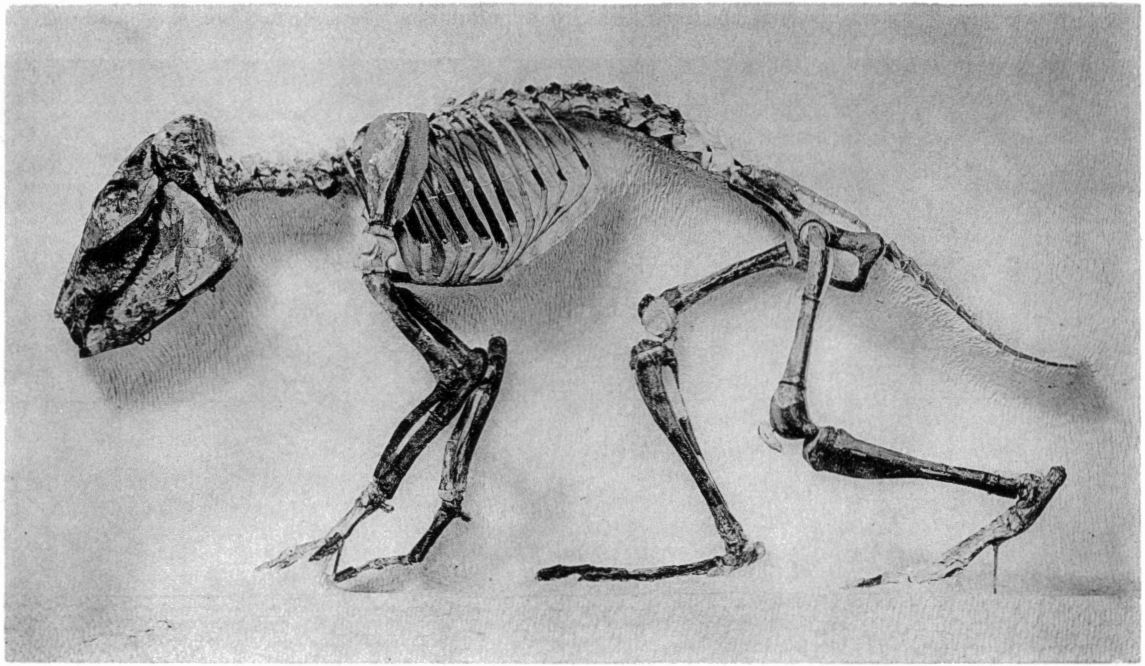
In all hegetotheres and typotheres, the hind-leg is much longer than the fore, and *Propachyrucos* is no exception. The length ratio of humerus plus radius plus third metacarpal to femur plus tibia plus third metatarsal is .70 in our specimen. In a specimen of *Pachyrukhos moyani* it is .73, showing a relatively less elongate hind-limb in the later species, but this is probably within the range of individual or specific variation. In Kraglievich's specimen of *Paedotherium imperforatum* the ratio is .70, the same as in our much older species. A specimen of *Interatherium robustum* has the ratio .81 and the fore and hind limbs are distinctly more nearly equal in that genus than in the hegetotheres.[5]

[5] Kraglievich (1926) has pointed out that in *Tragulus* the hind limb is even more elongate than in *Paedotherium*. The ratio that I use (not quite the same as Kraglievich's but bearing on the same characteristic) is .68 for Kraglievich's specimen of *Tragulus* and probably is not significantly different from *Propachyrucos*. However, this has little bearing on the pose of the animal (see below), because *Lepus*, so different in pose from *Tragulus* and so much more like *Propachyrucos* in habitus characters, has ratios in the same general range.

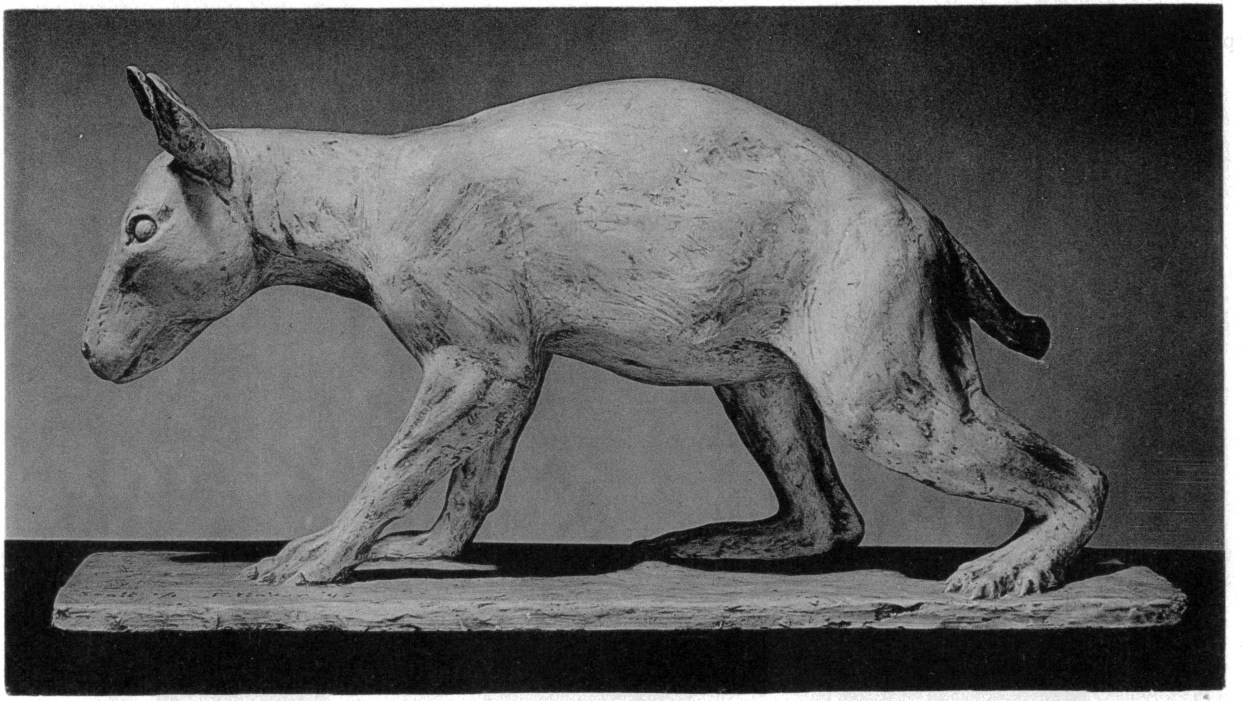
The second metatarsal is incomplete in our specimen of *Propachyrucos* but it was clearly more slender and probably shorter than IV. The size relationship for the metatarsals and the toes as a whole is III>IV>II>V. In *Pachyrukhos* II and IV are nearly equal in length. III is longer but no stouter and V is small but less reduced than in *Propachyrucos*. Thus *Pachyrukhos* has an essentially mesaxonic and, except for the loss of I, unreduced pes. In *Paedotherium*, however, II has become as stout and almost as long as III, IV is decidedly smaller than II, and V is much reduced, almost vestigial. *Paedotherium* is tending toward a pseudo-paraxonic type, with the weight borne by II and III, not by III and IV as in the true paraxonic pes. *Pachyrukhos* is mesaxonic, although it provides an appropriate base for the pseudo-paraxonic type. *Propachyrucos* belongs to neither type but more resembles, without belonging strictly to, the true paraxonic pattern. This complex of cross-specializations is further complicated by the fact that the forefoot of *Propachyrucos*, unlike the hindfoot, does approach the peculiar and specialized pseudo-paraxonic (II-III axis) type.

AFFINITIES.

*Propachyrucos smithwoodwardi* Ameghino, 1897, type of the genus, was based on a lower jaw with the dentition very like that of *Prosotherium*, *Pachyrukhos*, and *Hegetotherium* but differing from the first and second of these genera in the retention of the full dental formula and from the second and third in the unreduced, molariform $P_2$. Our specimen has these presumably generic characters of *P. smithwoodwardi* although it differs too much in size and in some other details to be placed in the same species. *P. crassus* Ameghino, 1897, was defined only on the basis of size, which is enough larger than the present specimen to make specific identity most improbable. The type, which has not been figured or described beyond a statement as to size, apparently included only $P_{2-3}$ and it is not clear that the genus can be recognized from these teeth alone or, consequently, that *P. crassus* does belong to *Propachyrucos*. The same doubt arises with regard to *P. aequilatus* Ameghino, 1901, also unfigured, apparently based on a jaw fragment with $P_4$-$M_3$, teeth that can with difficulty, or not at all, be distinguished generically among hegetotheres. The only morphological character given was that in *P. aequilatus* the



*Propachyrucos ameghinorum,* new species. Type, American Museum of Natural History No. 29574. Mounted skeleton, left side. X ⅓.



*Propachyrucos ameghinorum,* new species. Life restoration by France Baker, under the direction of John C. Germann and the author, based on the type skeleton as mounted (Plate 1). Original model X 1, this reproduction X ⅓.

anterior and posterior lobes of the cheek teeth are of equal size while in other species of *Propachyrucos* the anterior lobe is smaller. The anterior lobe is somewhat smaller in our specimen, but the difference is not marked, nor is it in Ameghino's figure of *P. smithwoodwardi* (1897, fig. 11, the only figure of *Propachyrucos* hitherto published). In *Prosotherium* the anterior lobe apparently tends to be somewhat larger, and it is not clear from the published data why *P. aequilatus* was not placed in *Prosotherium*, in which case it would probably be found synonymous with *P. garzoni*. Loomis (1914) described no material of *Propachyrucos*.

The only other species hitherto referred to *Propachyrucos*, as far as I know, is *P. schiaffinoi* Kraglievich, 1932, based on an upper jaw fragment from the Santa Lucía beds of Uruguay. This was not directly comparable with Ameghino's species, all based on lower jaws, but was tentatively placed in *Propachyrucos* because it retains $P^2$ and probably $P^1$ but otherwise is somewhat (not precisely) similar to *Pachyrukhos*. This specimen is however, radically unlike the upper jaw of *Propachyrucos ameghinorum*, for instance in the absence of internal folds on the molars, and certainly does not belong in the same or even a closely related genus. Since the reference of *P. ameghinorum* to *Propachyrucos* is fairly well established it follows that "*P.*" *schiaffinoi* almost surely does not belong to *Propachyrucos*.[6]

*Prosotherium* Ameghino, 1897, was described at the same time as *Propachyrucos*, based mainly on a complete palate although the lower dentition was briefly described, without illustrations. No direct contrast between *Prosotherium* and *Propachyrucos* was given by Ameghino, but his definitions involve the distinction that the lower canine and $P_1$ are absent in *Prosotherium*, a long diastema being present, while these teeth are present in *Propachyrucos* and there is, according to Ameghino, no diastema. Loomis (1914) had excellent material of *Prosotherium* but none of *Propachyrucos*, so that he could only add that $I_3$ is absent in *Prosotherium*, but that $P_1$ is present. Our specimen shows that *Prosotherium* and *Propachyrucos* are

[6] This also removes the basis for Kraglievich's correlation of the Santa Lucía beds with the Deseado. It is unlikely that "*P.*" *schiaffinoi* is pre-Deseado, but on present evidence it might belong almost anywhere from the Deseado to the Pleistocene.

very closely related and perhaps casts some doubt on whether they should be distinguished as separate genera.

Even in *Propachyrucos smithwoodwardi*, as figured by Ameghino, $I_3$, C, and $P_1$ are vestigial and there are small diastemata anterior and posterior to $P_1$. In the type of *P. ameghinorum* these teeth are still further reduced and the diastemata are larger. In the upper jaw $I^2$ is vestigial and C still more so, apparently lost in the adult. From Ameghino's querying $I_3$ in *Prosotherium* and saying that $P_1$ is absent, while Loomis says $I_3$ is absent and $P_1$ present, it is probable that these vestigial teeth vary in that genus, whether individually, ontogenetically, or inter-specifically. Apart from the presence or absence of these vestigial teeth, *Propachyrukhos* and *Prosotherium* are very similar. The other parts of the dentition and the skulls hardly seem to warrant generic separation. There are some apparent differences in the skeletons, as has been noted briefly above, but the significance of these is not altogether certain. There are also several species, or supposed species, of each genus in which the possible generic distinctions are poorly or not known. The separation is thus not clear-cut. There appears to be a complex of species, all closely allied, and whether division into *Propachyrucos* and *Prosotherium* is valid, sufficient, and natural is not as yet well established.

*Propachyrucos ameghinorum* has the skull and dentition of the same size as *Prosotherium garzoni*, but whatever the eventual disposition of the genera, it is sufficiently clear that these species are distinct.

*Prosotherium* and *Propachyrucos*, together, are distinguished from most other hegetotheres especially by the fact that the upper premolars are not molariform and that the upper molars have strong internal grooves, resembling interatheres (true typotheres) more than typical hegetotheres. *Prohegetotherium*, contemporaneous with *Prosotherium* and *Propachyrucos*, was more typically hegetothere in this respect.[7] Ameghino (1897) considered *Propachyrucos* the immediate ancestor of *Pachyrukhos* and Loomis (1914) assigned this position to *Prosotherium*.

[7] And so, perhaps, were earlier, Musters, forms. Ameghino named three genera of hegetotheres from the Musters, but their characters are dubious. His descriptions were brief, no figures were given, and the specimens could not be found in the Ameghino Collection when I made a search for them.

It is evident that *Propachyrucos*, *Prosotherium*, and *Pachyrukhos* are allies, but it is not clear that either (or both) of the first two is ancestral to the last. The upper cheek dentition of the named Deseado genera is sharply different from that of *Pachyrukhos*. The difference could readily be spanned by evolution, but the time lapse is not very great, intermediates are unknown and dentitions more like *Pachyrukhos* do occur in the Deseado.

The fate of the *Propachyrucos-Prosotherium* line may be revealed by *Muñizia*, and the origin of that puzzling genus may be explained by the comparison. *Muñizia* was described by Kraglievich in 1931 on the basis of a maxillary fragment from the Entrerrios beds of the Paraná. The molars are like those of interatheres, but the root of the zygoma is hegetothere-like. Kraglievich gave more weight to the molar structure and assigned this apparently synthetic type to the Interatheriidae but to a distinct subfamily, Muñiziinae. In a passing note (Simpson, 1932, p. 10), I expressed skepticism regarding so remarkable a reversion of the highly characteristic and specialized interathere jugal and suggested that *Muñizia* might be either a hegetothere with molars convergent toward interatheres, or a line distinct [from either] since the early Tertiary. Patterson (1934, p. 136) pointed out that the molars of *Muñizia* are similar to those of *Prosotherium* and concluded that *Muñizia* is probably a hegetothere that has preserved the primitive molar pattern, lost in *Pachyrukhos* and *Hegetotherium* (and in *Paedotherium*, the *Pachyrukhos*-like contemporary of *Muñizia*). The present restudy suggests that my two alternative suggestions and Patterson's third are all true, that *Muñizia* is a hegetothere, of a line distinct since the early Tertiary, with molar pattern departing from an earlier basis than the *Pachyrukhos* pattern, and to some extent convergent toward interatheres.

The evidence tends to show that two groups of hegetotheres can be distinguished at least from the Deseado to the Entrerrios, and perhaps earlier or later for one or both. One group, with less molariform premolars and interathere-like molars, includes *Propachyrucos*, *Prosotherium*, and *Muñizia*. The other, with molariform premolars and non-interathere-like molars, includes *Pachyrukhos*, *Hegetotherium*, and *Paedotherium*. Each group may contain other, at present dubious, genera, and each seems to have more than one line of precise descent, yet they

are probably phyletic units. This considerably lessens the probability that *Propachyrucos* is especially related or ancestral to *Pachyrukhos*, although it is clear that all the genera, of both groups, are quite closely similar despite their rather long separation.

If *Muñizia* is a descendent of the *Propachyrucos-Prosotherium* group, the advances visible in the single known fragment of the later genus indicate a considerable increase in size and the development of a small reëntrant enamel fold at the antero-internal edge of $P^{3-4}$. These premolars (the others are unknown) retain their triangular contour and are not molariform despite this slight complication. The zygomatic root may be somewhat more horizontal than in the Deseado genera and its posterior rim is more anterior, making the root relatively shorter, but the significance of these differences is questionable.

In the light of the evidence here summarized, I suggest that the subfamily Muñiziinae Kraglievich be retained, but in the family Hegetotheriidae, not Interatheriidae as proposed by Kraglievich. In addition to *Muñizia*, *Propachyrucos* and *Prosotherium* are referred to the Muñiziinae.

## RESTORATION.

The restored life-model by Miss Baker is of the natural size and is in the same pose as the skeleton. The animal is shown as alert but not in motion, just preparing to step away slowly, with both forefeet and the off hindfoot planted and the near hindfoot extended posteriorly, with the heel raised.

The forefeet are shown as digitigrade and the hindfeet as plantistat, rising to the digitigrade position in leaping or rapid progression. This question of foot posture is always a difficult one in mounting skeletons of animals without close allies or exact analogues in the recent fauna. The anatomical evidence is often equivocal and, as far as I know, no completely conclusive criterion has been found. Except in extreme cases, a habitually plantigrade foot can usually assume a digitigrade position and some digitigrade feet can easily be placed in either a plantigrade of an unguligrade position, especially when dealing only with the skeleton. In *Propachyrucos*, the hind feet could be mounted in the plantigrade, digitigrade, or unguligrade position, but when the articulation is placed in what seems the easiest, most relaxed way, with the tibia on the middle

of the astragalar trochlea, the foot tends naturally to be plantigrade. The terminal phalanges are more claw- than hoof-like. They are not fissured, but they are long, sharp, and compressed laterally, not dorso-ventrally. As far as analogy can be followed, the whole build of *Propachyrucos*, including the dentition, skull, and limbs, seems to me most like the leporids among recent mammals. There are, of course, striking differences also, but the resemblance in habitus seems to warrant the opinion that in *Propachyrucos*, as in most leporids, the forefoot was digitigrade and the hindfoot plantigrade at rest, i.e. plantistat,[8] but likewise digitigrade in locomotion, or in rapid locomotion.

This was nearly the opinion of Sinclair (1909) regarding *Pachyrukhos*, which he also considered analogous with leporids and called plantigrade as to pes and digitigrade as to manus. Kraglievich (1926) however, argued that *Pachyrukhos* was digitigrade, almost subunguligrade, and that its probable descendent *Paedotherium* was fully unguligrade. As evidence of unguligrady in *Paedotherium* he stressed the deep astragalar trochlea, the presence of strong metapodial keels, the hoof-like terminal phalanges, and the analogy with *Tragulus*. Whatever may be true of *Paedotherium*, these arguments do not apply to *Propachyrucos* or *Pachyrukhos*. The astragalar trochlea is shallower in them. The metapodial keels are weaker and ventral only; they are, in fact, like so many other habitus characters, almost exactly as in leporids. The terminal phalanges, especially in *Propachyrucos*, are more claw-like than hoof-like, although not fissured. Even for *Paedotherium* the analogy with *Lepus* seems to me much closer than the analogy with *Tragulus*, and this is still more obvious for the earlier genera. It is quite possible that Kraglievich is right, but the evidence does seem to incline somewhat to the view that *Propachyrucos* and *Pachyrukhos* were digitigrade with the pes plantistat, and that *Paedotherium* was more fully digitigrade, possibly subunguligrade, and digitistat.

The hypothetical external features have been treated con-

[8] This term, proposed by Virchow in discussing the penguins, means that the tarsus normally touches the ground when the animal is standing but relaxed. Plantigrade properly means that the tarsus touches the ground when the animal is walking, and this is not true of all plantistat animals. Man is plantistat, but optionally either plantigrade or digitigrade, depending mainly on speed of locomotion.

servatively in the restoration of *Propachyrucos*. The hair is shown as short and neither woolly nor fluffy, a supposition as reasonable as any other and making a more interesting restoration because the muscles are more visible and the modeling more plastic. The ears are shown as large. The sense of hearing was almost surely important and acute in this as in other small notoungulates. Rabbit-like ears have, however, been avoided in order not to exaggerate resemblance to the leporids and to keep clear in the minds of museum visitors the fact that this animal is not a sort of rabbit. For similar reasons the short tail is moderately tufted and not puffed.

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