

A NEW EARLY SPECIES OF THE AQUATIC SLOTH *THALASSOCNUS* (MAMMALIA, XENARTHRA) FROM THE LATE MIOCENE OF PERU

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ABSTRACT—*Thalassocnus antiquus*, sp. nov., is a marine nothrothere from the late Miocene Aguada de Lomas vertebrate horizon (ca. 7 to 8 Ma) of the Pisco Formation in the Sacaco area of the southern coast of Peru. It is similar to the slightly younger latest Miocene *Thalassocnus natans*, but smaller and distinctly more gracile. The sloping morphology of the lateral border of the nares in *T. antiquus* differs from the probably plesiomorphic subvertical edge of the nares in *T. natans*. Parsimony analysis does not resolve the relative positions of *T. antiquus* and *T. natans*, and, therefore, does not fully confirm the possibility of a single *Thalassocnus* lineage, which spans over 4 Ma. However, *Thalassocnus* is an endemic genus and the stratigraphic distribution of its four species is well known. Furthermore, some characters indicate a continuous evolution from the oldest (*T. antiquus*) to the youngest species (*T. carolomartini*). Therefore, we prefer the hypothesis of a single *Thalassocnus* lineage, although a more complex evolutionary scenario is not discarded.

INTRODUCTION

Nothrotheres represent a relatively small group of ground sloths. Only four taxa are reasonably well known from South America, *Thalassocnus*, *Nothrotherium*, *Pronothrotherium*, and *Nothropus*. The latter three genera are best known from Argentina; *Nothrotherium* was also present in Brazil, and *Nothropus* also from Bolivia and Peru (but see below). Other nothrothere genera (*Xyophorus*, *Chasicobradys*, *Diheterocnus*, and ?*Synhapalops*) are known by isolated jaws, mostly from Argentina (Ameghino, 1887; Kraglievitch, 1928, 1930; Scillato-Yané et al., 1987). Excluding *Thalassocnus*, nothrotheres are rare in western South America (i.e., Chile, Peru, Bolivia, Ecuador, and Colombia) where records assigned to a genus consist of *Xyophorus* from the Huayquerian (late Miocene) of Achiri, Bolivia (Saint-André, 1996), and *Nothropus* from the Ensenadan (late early Pleistocene) of Tarija, Bolivia, (Marshall et al., 1984) and the Holocene of Rio Acre, Peru (Frailey, 1986). However, the Peruvian specimen was referred to *Pronothrotherium* by Webb and Rancy (1996) and assigned a Huayquerian age. Undetermined isolated bones of nothrotheres from La Venta, Colombia, were mentioned by Hirschfeld (1985) and McDonald (1997). Marshall et al. (1984) reported cf. *Nothropus* from the latest Pleistocene or Holocene of Cupisnique (Peru). However, the specimen is a partial skeleton referable to a new genus under study by F. Pujos.

Thalassocnus, the most diverse and best known nothrothere genus, was regarded by Muizon and McDonald (1995) and McDonald and Muizon (2002) as having aquatic or semi-aquatic habits. It is, so far, an endemic taxon from the Pisco Formation of the southern coast of Peru, which has yielded an abundant fauna of marine vertebrates (Muizon, 1981, 1984, 1988, 1993; Muizon and DeVries, 1985; Muizon et al., 1999). In the Sacaco area, the age of the formation ranges from the early late Miocene to the late Pliocene. Five vertebrate-bearing horizons in the Pisco Formation have produced distinct faunas: the Sacaco (**SAO**) Horizon (ca. 3 to 4 Ma), the Sud-Sacaco (**SAS**) Horizon (ca. 4 to 5 Ma), the Montemar (**MTM**) Horizon (ca. 6 Ma), the Aguada de Lomas (**AGL**) Horizon (ca. 7 to 8 Ma), and the El Jahuay (**ELJ**) Horizon (ca. 9 Ma) (Muizon and

Bellon 1980, 1986; Muizon and DeVries 1985). Fossils of ground sloths are well represented in the Pisco Formation of the Sacaco area and represent an unprecedented adaptation of the group to a marine habitat (Muizon, 1981). Three species of *Thalassocnus* have been described (Muizon and McDonald, 1995; McDonald and Muizon, 2002): *Thalassocnus natans*, MTM Horizon; *Thalassocnus littoralis*, SAS Horizon; and *Thalassocnus carolomartini*, SAO Horizon. They were regarded by McDonald and Muizon (2002) as segments of a single lineage representing the initial and progressively more aquatic adaptations. McDonald and Muizon (2002:350) mentioned a fourth, still older species of *Thalassocnus* from the AGL Horizon. The purpose of this study is to describe the skull and mandible of this older taxon and to reappraise the *Thalassocnus* lineage as presented by McDonald and Muizon (2002). The postcranial skeleton of *Thalassocnus* is currently under study by the authors. Although we provide a comparative figure of the radii of *Thalassocnus*, it will not be thoroughly described here. Reference is made to the radius because it possesses characters which are directly relevant to the discussion below on the problem of the *Thalassocnus* lineage.

Institutional Abbreviations—**MNHN**, Muséum national d'Histoire naturelle (Paris, France); **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima, Peru).

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope, 1889
Suborder PHYLLOPHAGA Owen, 1842
Family MEGALONYCHIDAE Gervais, 1855
Subfamily NOTHROTHERIINAE Ameghino, 1920
THALASSOCNUS Muizon and McDonald, 1995
THALASSOCNUS ANTIQUUS, sp. nov.

Holotype—MUSM 228, partial skeleton including the skull (Fig. 1), mandible (Fig. 2), and most of the postcranial skeleton. The latter is severely damaged and partly unprepared.

Type Locality—Aguada de Lomas, Sacaco Area, Arequipa Department, Peru.

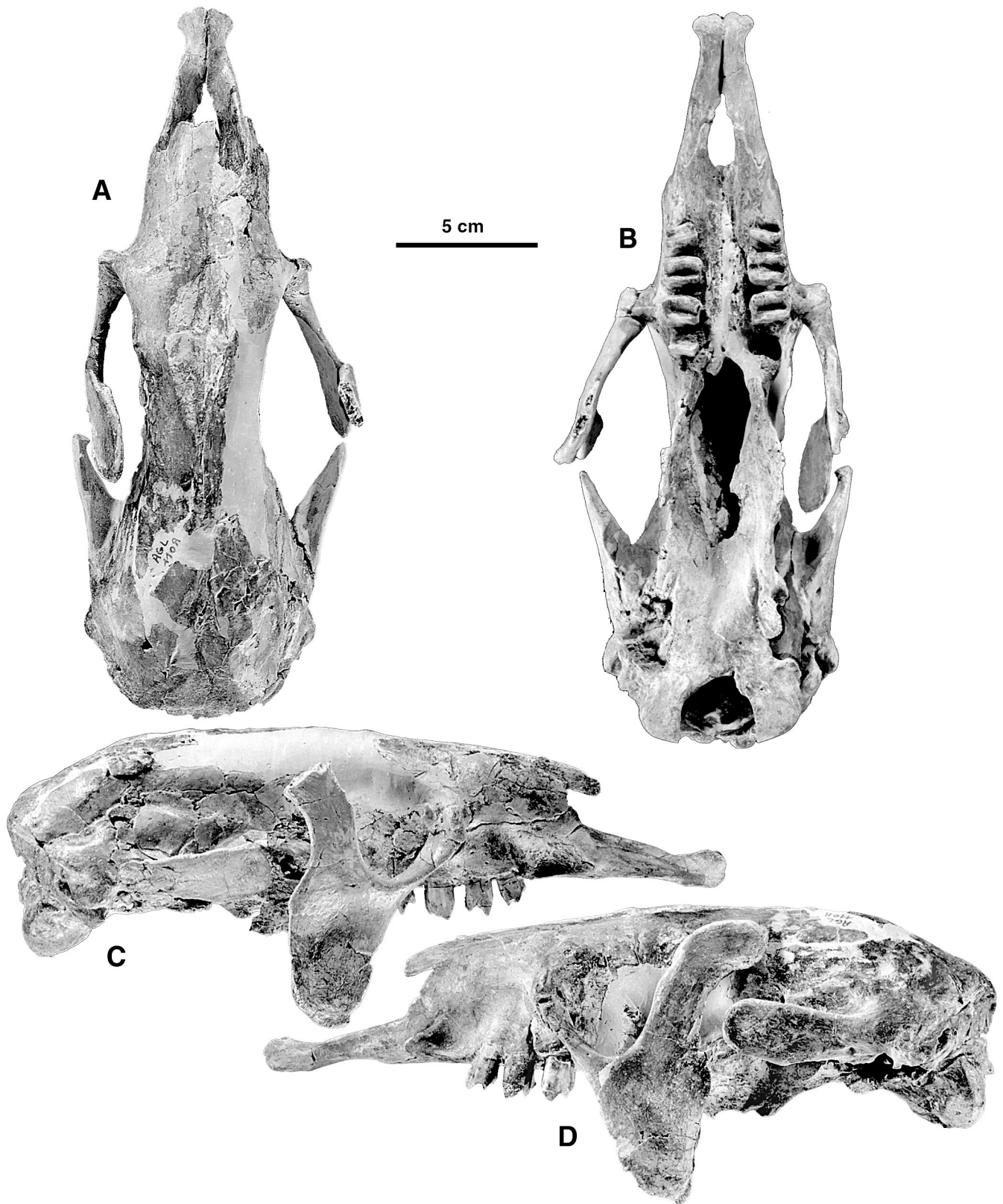


FIGURE 1. *Thalassocnus antiquus*, sp. nov.: Skull (holotype, MUSM 228) in dorsal (A), ventral (B), right lateral (C), and left lateral (D) views.

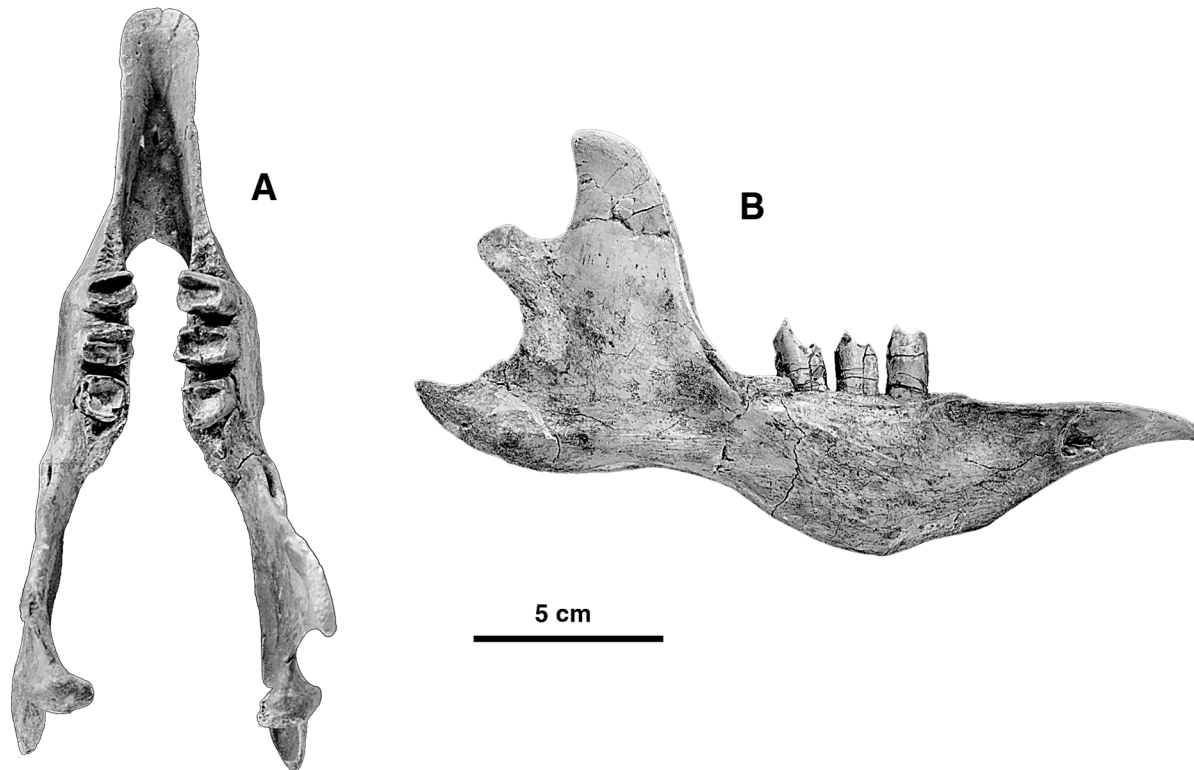


FIGURE 2. *Thalassocnus antiquus*, sp. nov.: Mandible (holotype, MUSM 228) in dorsal (A) and lateral (B) views.

Age and Formation—Pisco Formation, AGL vertebrate horizon, Huayquerian, ca. 8 Ma (Muizon and DeVries, 1985).

Diagnosis—Skull and mandible distinctly smaller and more gracile than in *Thalassocnus natans*; premaxillae proportionally shorter and narrower at base; narial opening narrower and, in dorsal view, anterior border of ascending process of the maxilla not salient laterally as in *T. natans*; nasal with an anteriorly projecting medial spine; teeth proportionally smaller and tooth rows anteroposteriorly shorter than in *T. natans*; mandibular spout not expanded apically, with thinner edges and much deeper dorsoventrally than in *Thalassocnus littoralis* and *Thalassocnus carolomartini*.

DESCRIPTION AND COMPARISONS

McDonald and Muizon (2002) provided detailed descriptions of the skull, mandible, and dentition of *Thalassocnus natans*, *Thalassocnus littoralis*, and *Thalassocnus carolomartini*. Because *Thalassocnus antiquus*, sp. nov. is most similar to *T. natans*, a detailed comparison of these two species is provided to support the creation of a new species and avoid redundancy with the previous description of *Thalassocnus*.

Skull

General Morphology—The skull of *T. antiquus* is slightly smaller than that of *T. natans* and more gracile (Fig. 1, Table 1). This characteristic is only slightly pronounced in the braincase, but especially evident in the rostrum. The ratio of the bizygomatic width/condylobasal length is 0.38 in *T. antiquus* and 0.42 in *T. natans*, while the ratio width of narial opening/length of rostrum from tip to anterior opening of infraorbital canal is 0.37 in *T. antiquus* and 0.51 in *T. natans*.

Premaxilla—The premaxilla of *Thalassocnus antiquus* (Fig. 1) generally resembles that of *T. natans* although more gracile

and narrower at the base. It is larger than in other nothrothere genera and has the splayed apex typical of the genus. The anterior tips of the premaxillae of *T. antiquus* are slightly less expanded than in *T. natans*. The lateral ramus increases in size posteriorly and the ascending process is longer and wider than in *T. natans*. The angle between the horizontal ramus of the premaxilla and the ascending process is more open (oblique) in *T. antiquus* (ca. 144° on the holotype) than in *T. natans* (ca. 126° on the holotype). In both of the former species it differs from the condition in the Pliocene species, *Thalassocnus littoralis* and *Thalassocnus carolomartini*. In the latter two species there is no angle between the horizontal and ascending rami of the premaxilla and the lateral border of the narial opening is regularly oblique from the apex of the premaxilla to the maxilla-nasal suture (Fig. 3; McDonald and Muizon, 2002:figs. 6 and 8). The horizontal part of the premaxillae (from the apex to the base of the ascending process) is shorter in *T. antiquus* (54.6 mm) than in the holotype of *T. natans* (62.5 mm) and more slender. Ventrally the palate at the base of the premaxillae is distinctly narrower in *T. antiquus* (25.8 mm) than in *T. natans* (30.1 mm).

Maxilla—At the anterior border of the buccinator fossa, the anterolateral process of the maxilla, which inserts between the dorsolateral and ventromedial rami of the premaxillae is longer and more slender than in *T. natans*. The pre dental region of the maxilla on the palate is longer in *T. antiquus* than in *T. natans* and approaches (although shorter than) the condition observed in *T. littoralis* and *T. carolomartini*. The distance between the posterior extremity of the incisive foramen and a line joining the anterior alveolar border of the first molariform is 19 mm in *T. antiquus* (a slightly smaller animal than *T. natans*), 13.5 mm on the holotype of *T. natans*, and 10.5 mm on a referred specimen MUSM 433. The anteroventral process of the maxilla, which borders the incisive foramen is narrower than in *T. na-*

TABLE 1. Measurements (mm) of the holotype skulls of *Thalassocnus antiquus* (MUSM 228) and *Thalassocnus natans* (MNHN SAS 734). **Abbreviations:** e, estimate.

	<i>Thalassocnus antiquus</i> MUSM 228	<i>Thalassocnus natans</i> MNHN SAS 734
Maximum length (in dorsal view)	260.4	262.9
Basicondylar length from anteroventral angle of ascending process of maxilla to posterior edge of occipital condyles	204.0	207.3
Length from anterior edge of M1 to posterior of occipital condyle	181.0	189.1
Length along midline from anterior edge of postpalatine notch to anterior edge of foramen magnum	107e	113.2
Length along midline of palate from medial base of anteroventral process of the maxilla to posterior edge	72e	69
Length from anterior of M1 to posterior of M4	46.8	50.7
Length from anterior of M1 to anterior edge of anteroventral process of maxilla	34.1	31.1
Maximum width between labial edges of M1	42.5	46.3
Maximum width between labial edges of M4	40.0	43.8
Length from posterior edge of M4 to posterior edge of occipital condyle	133.0	139.2
Maximum width between postorbital processes of frontal	26.5 × 2 = 53e	61.4
Least interorbital breadth	19.5 × 2 = 39e	48.2
Maximum width between mastoid processes	83.4	92.3
Maximum width between lateral margins of occipital condyles	56.7	61.6
Maximum height of occipital condyle	25.4	30.1
Width of foramen magnum between ventral edges of occipital condyles	25.5	20.7
Height of occiput in midline from dorsal edge of foramen magnum to nuchal crest	33.5	33.6
Maximum width between lacrimal foramina	70.2	83.2
Length from postorbital process of frontal to nuchal crest (measured horizontally)	126.5	130.0
Minimum width of palate between M1	18.6	19.6
Minimum width of palate between M4	18.1e	17.1

tans. The length of the process is similar to that of the holotype of *T. natans* but distinctly longer than in MUSM 433, which indicates that this feature presents some individual variation. It is, however, much longer and more developed in the four species of *Thalassocnus* than in other nothrotheres. The depth of the buccinator fossa and the width between the right and left fossae are similar to those of *T. natans*.

The region of the snout between the narial opening and the infraorbital foramen, and dorsal to the buccinator fossa, is distinctly wider (in ventral view) and slightly longer (in lateral view) than in *T. natans*. Furthermore, the edges of this region of the snout (the ascending processes of the maxillae) are slightly convergent anteriorly in *T. antiquus*, while they are parallel in *T. natans*.

The tooth rows of *T. antiquus* are subparallel and approximately 10 percent shorter than in *T. natans*, a difference which is probably related to the smaller size of *T. antiquus*. The ratio of length of the tooth row/mastoid width of the skull is 0.56 in *T. antiquus*, a value which is within the variation observed in *T. natans* (0.55 in MNHN SAS 734; 0.59 in MUSM 433).

The palate of *T. antiquus* is narrow as in *T. natans*. The infraorbital canal perforates the maxilla and the anterior opening is located dorsal to the space between M2 and M3.

On the dorsolateral surface of the rostrum, the anterodorsal edge of the ascending process of the maxilla is smoothly convex and resembles *T. carolomartini* and *T. littoralis*, but differs from the other nothrotheres (including *T. natans*), in which there is a pronounced angle at the anterior point of the nasal-maxilla suture (Fig. 3).

Nasal—The nasal is slightly longer than that of *T. natans*, but distinctly narrower. The anterior edge of each nasal is V-shaped and has subequal lateral and medial branches. Therefore, the dorsomedial region of the narial opening presents an anteriorly protruding process formed by the medial branches of both nasals as is observed in *Nothrotherium* and *Nothrotheriops*. This apparently plesiomorphic condition differs from that of *T. natans* and *T. carolomartini* in which the medial branch is absent and the lateral branch is small or absent in the former or larger and wider in the latter.

Jugal—As in *T. natans*, the jugal has a long dorsal process,

which almost reaches the level of the top of the skull. In lateral view, the anterior edge of the jugal at the level of the tooth row is lateral to the last molariform, as in *T. natans*.

Pterygoid—The pterygoid of *T. antiquus* is similar to that of *T. natans* in being thin and not thickened nor inflated at its posterior base, in contrast to the condition in *T. carolomartini* and *Nothrotheriops shastense*, respectively. The condition in *T. antiquus* and *T. natans* is plesiomorphic.

Except for the smaller size and gracility, the remainder of the skull is not significantly different from that of *T. natans*.

Mandible

The mandible of *T. antiquus* is very similar to that of *T. natans*, but also smaller and more gracile (Fig. 2, Table 2). The major differences between the two species are observed on the mandibular spout, which is narrower mediolaterally, deeper dorsoventrally, and has thinner edges than in *T. natans*. The ventral border of the symphysis is distinctly concave and short in lateral view as in *T. natans*, thus differing from the straight and elongated border of *T. carolomartini*. The horizontal ramus of *T. antiquus* is shallower and the dorsoventral constriction of the dentary posterior to m3 is more pronounced than in *T. natans*. It clearly differs from that of *T. carolomartini*, in which the concavoconvex morphology of the ventral edge of the horizontal ramus is strongly attenuated. The ratio length of tooth row/maximum depth of the horizontal ramus is slightly less than in *T. natans* (0.96 in *T. antiquus*; 1.01 in *T. natans*). However, this minor difference could be the result of individual variation and a larger sample is needed to determine its significance.

The ascending ramus of *T. antiquus* does not extend as far dorsally as in *T. natans*. The anterior border of the coronoid process slopes anteroventrally as in *T. natans*, but differs from the subvertical border observed in *T. carolomartini* (the slope of the anterior border in *T. littoralis* is intermediate between that present in *T. antiquus* and *T. natans* and that in *T. carolomartini*). The coronoid process is relatively flat and its apex is not bent medially, as is the case in *T. natans* (slightly) and *T. carolomartini* (strongly). The posterodorsal foramen of the

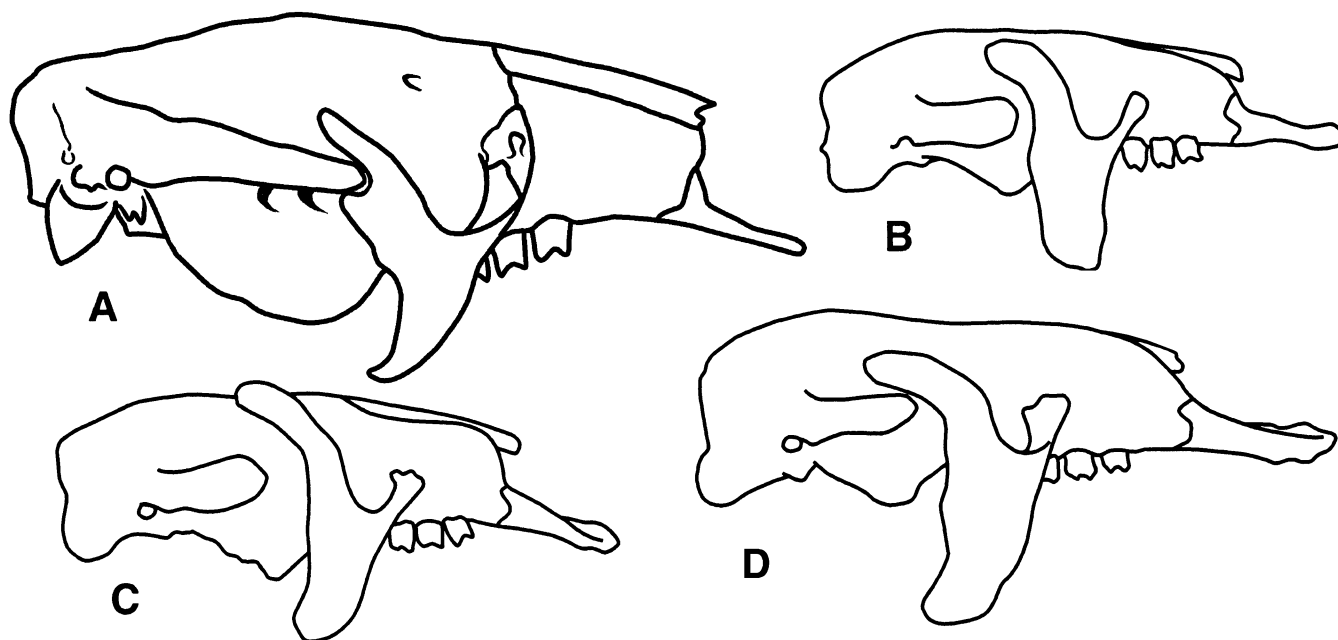


FIGURE 3. Lateral views of the skull of **A**, *Nothrotheriops shastense* (redrawn from Stock, 1925 and Paula Couto, 1959); **B**, *Thalassocnus antiquus* (holotype MUSM 228); **C**, *Thalassocnus natans* (holotype, MNHN SAS 734); and **D**, *Thalassocnus carolomartini* (MUSM 37) showing the vertical anterior edge of the narial opening in *N. shastense* and *T. natans*, while it is sloping in *T. antiquus* and *T. carolomartini*.

mandibular canal resembles that of *T. natans* in the dorsolateral orientation of its opening at the anterior base of the coronoid process, in its dorsoventral elongation, and in having a lateral border thinner than the medial. In *T. carolomartini*, the foramen is subcircular, opens anteriorly, and the medial and lateral ridges of the foramen are subequal in thickness.

The apex of the angular process of *T. antiquus* is located below the level of the alveolar border, while it is slightly above in *T. natans*. As a consequence, the concavity between the angular and condyloid processes is much more open in the former than in the latter. The condition seen in *T. antiquus* is also present in *Nothrotherium* (Cartelle and Fonseca, 1983) and *Hapalops*, and apparently plesiomorphic. This character state is even more pronounced in tree sloths (pers. obs.). The condition of *T. natans* is present in *Nothrotheriops* (Stock, 1925; Naples, 1987).

The condyloid process is shifted medially, as in *T. natans*. It is triangular in shape and transverse. It bears a laterally facing lateral facet and a smaller dorsoposteriorly facing medial facet. The shape of the condyloid process of *T. antiquus* is similar to that of the holotype of *T. natans*. However, the lateral facet of *T. natans* is oriented posteriorly and the medial facet medially. The neck is well developed and the condyle is oriented poster-

odorsally and, in lateral view, the dorsal component is approximately similar to the posterior, as in *T. natans*.

DISCUSSION

Although we consider them distinct species, the differences between *T. antiquus* and *T. natans* are subtle and could be regarded as individual variation because only one skull of the former species and two skulls of the latter are known (Tables 1–3; Fig. 3B–C). Furthermore, the postcranial skeleton of *T. littoralis* displays significant variation probably related to sexual dimorphism (Muizon and McDonald, pers. obs.). However, the morphology of the anterior part of the head (snout and mandibular symphysis) differs greatly in the two species and is not merely the result of differences in size. The fact that one of the major transformations of *Thalassocnus* through time (from AGL horizon, ca. 8 to 7 Ma, to SAO horizon, ca. 4 to 3 Ma) concerns the anterior part of the skull (premaxillae, premental portion of the maxillae, and mandibular symphysis) supports the validity of *T. antiquus*.

The more derived condition of later members of the *Thalassocnus* lineage compared to earlier members is also confirmed by the anatomy of some postcranial elements such as

TABLE 2. Measurements (mm) of the mandibles of the holotypes of *Thalassocnus antiquus* (MUSM 228) and *Thalassocnus natans* (MNHN SAS 734).

	<i>Thalassocnus antiquus</i> MUSM 228	<i>Thalassocnus natans</i> MNHN SAS 734
Length from anterior of spout to posterior edge of angular process	204.0	214.1
Length from anterior of spout to posterior edge of condyle	197.5	207.7
Length from anterior edge of spout to anterior edge of first molariform	75.0	72.5
Length from anterior edge of spout to posterior edge of last molariform	115.0	116.9
Length of spout from anterior edge to posterior edge of symphysis	59.5	62.4
Width of spout at anterior edge	21.5	24.1
Alveolar length of check teeth	41.5	44.5
Maximum depth of horizontal ramus	42.5	44.8
Depth of dentary below coronoid process	88.5	97.0

TABLE 3. Measurements (mm) of the teeth of the holotypes of *Thalassocnus antiquus* (MUSM 228) and *Thalassocnus natans* (MNHN SAS 734). **Abbreviations:** AP, anteroposterior; M, upper molariform; m, lower molariform; ML, mediolateral.

	<i>Thalassocnus antiquus</i> MUSM 228	<i>Thalassocnus natans</i> MNHN SAS 734
M1 AP length	8.1	9.8
M1 ML width	11.5	13.5
M2 AP length	10.4	11.0
M2 ML width	14.4	16.1
M3 AP length	10.0	10.2
M3 ML width	14.1	15.6
M4 AP length	7.1	7.2
M4 ML width	10.1	12.5
m1 AP length	10.8	12.6
m1 ML width	12.7	14.9
m2 AP length	11.6	12.3
m2 ML width	13.7	15.6
m3 AP length	10.0	13.6
m3 ML width	12.1	14.7

the radius, which has a less pronounced pronator ridge than in *T. natans*. Its anatomy in *T. antiquus* more closely resembles that of some terrestrial nothotheres such as *Nothrotheriops* and *Nothrotherium* than the other species of *Thalassocnus* (Fig. 4). Furthermore, the posterior offset of the proximal end is less pronounced than in *T. natans*, again resembling the condition of *Nothrotheriops* and *Nothrotherium*. Although they will be treated separately in the parsimony analysis below, it is noteworthy that the increase in size of the pronator ridge and the offset of the proximal end of the radius are probably linked and related to the improvement of locomotion in an aquatic environment. They occur jointly in the sloth taxa considered in Fig.

5 and in pinnipeds, in which they are always present, and are much more pronounced in the terminal members of the *Thalassocnus* lineage than in any other ground sloths.

Thalassocnus antiquus is currently the oldest species of the *Thalassocnus* lineage. In most of its characters, *T. antiquus* is clearly more similar to *T. natans* than to the two younger species. In the two older species, the premaxillae are more gracile, less elongated anteriorly, and narrower and less spatulate at their tip, the apex of the mandibular symphysis is not expanded transversely, the ventral border of the symphysis is markedly concave ventrally, and the ventral border of the dentary below the tooth row is strongly convex.

However, in one feature, *T. antiquus* more closely resembles *T. carolomartini* and *T. littoralis* than it does *T. natans*. In the latter, the lateral edge of the narial opening has a marked angle separating a subvertical posterodorsal portion formed by the anterior edge of the ascending processes of the maxilla and premaxilla and a horizontal anterior portion formed by the horizontal ramus of the premaxilla (Fig. 3B). In *T. antiquus*, *T. littoralis*, and *T. carolomartini*, the posterodorsal edge of the narial opening dips anteroventrally and the angle it forms with the horizontal processes of the premaxilla is either very open (*T. antiquus*; Fig. 3B) or absent (in *T. littoralis* and *T. carolomartini*; Fig. 3D). In the latter two species, the lateral edge of the narial opening gently and regularly slopes anteroventrally from the anterior point of the nasal-maxilla suture to the apex of the premaxillae. The condition of *T. natans* is present in all other sloths, which indicates that it probably represents the plesiomorphic condition. Therefore, the state of *T. antiquus* would seem to be more derived than that of *T. natans*, although the former is older than the latter.

Furthermore, the prepedal portion of the maxilla (excluding the anteroventral processes) of *T. natans* is distinctly shorter

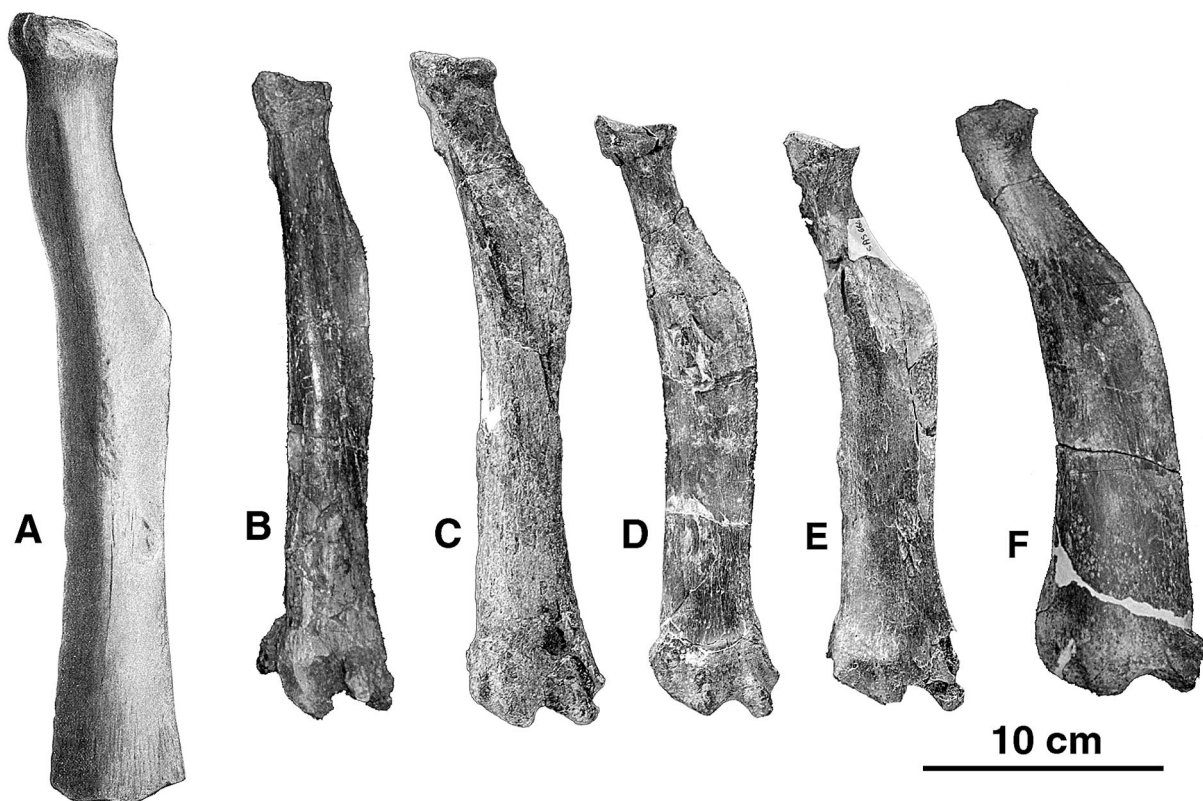


FIGURE 4. Lateral views of the radius of **A**, *Nothrotherium shastense* (from Stock, 1925, reversed); **B**, *Thalassocnus antiquus* (holotype, MUSM 228); **C**, *Thalassocnus natans* (holotype, MNHN SAS 734); **D**, *Thalassocnus littoralis* (MNHN SAS 801); **E**, *T. littoralis* (MUSM 443); and **F**, *Thalassocnus* cf. *carolomartini* (MUSM 37).

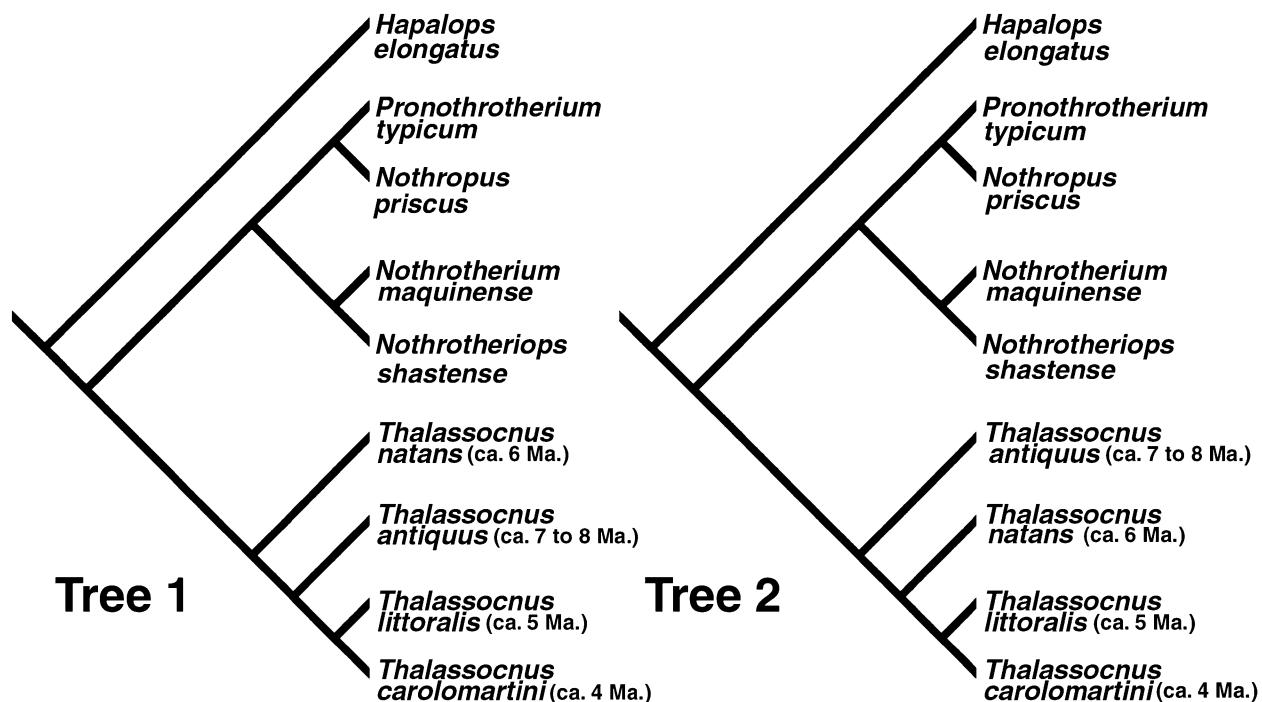


FIGURE 5. Two most parsimonious trees resulting from phylogenetic analysis of the Nothrotheriinae (Length: 46 steps; CI, 0.804; HI, 0.196; RI, 0.859; RC, 0.691) obtained by exhaustive analysis using PAUP 3.1.1 with *Hapalops* as outgroup. Characters and states listed in Appendices 1 and 2. As discussed in the text, although not discarded, the results of tree 1 are regarded as less likely, and we favor the hypothesis provided by tree 2 of a probable single *Thalassocnus* lineage from *Thalassocnus antiquus* to *T. carolomartini*.

than in the three other species of *Thalassocnus*. Because the clear evolutionary trend in the *Thalassocnus* group is to increase the length of the snout, the short rostrum of *Thalassocnus natans* probably represents the plesiomorphic condition.

These two rostral characters are probably related. The lengthening of the rostrum in *Thalassocnus* is achieved by an anterior extension of the anteroventral part of the skull (preidental portion of the maxillae and premaxillae). Dorsally, the maxillae are not significantly different in the four species. The ventral edges of the narial fossa extend anteriorly to a much greater extent than the dorsal edge and therefore, with the anterior extension of the preidental portion of the maxilla (on the palate), the lateral edges of the narial fossa tend to acquire an oblique position.

The characters described above seem to indicate that, if an ancestor-descendant relationship actually exists between the species of *Thalassocnus*, *T. natans*, which is more plesiomorphic for this character than the older *T. antiquus*, should probably be excluded from this lineage. The latter would therefore include *T. antiquus* (late Miocene), *T. littoralis* (earliest Pliocene), and *T. carolomartini* (early Pliocene).

A parsimony analysis using PAUP 3.1.1. determined the phylogenetic relationships of the four species of *Thalassocnus*. The character list presented by McDonald and Muizon (2002) has been modified according to the characters mentioned above (Appendices 1–2). Most of the characters deal with the cranium, but it is likely that study (in progress) of the postcranial skeleton of *Thalassocnus* will add more postcranial characters. ACCTRAN and DELTRAN character optimizations produced the same results. The outgroup is *Hapalops* (as in McDonald and Muizon, 2002), because it represents a generalized sloth. An exhaustive search resulted in two shortest trees (Fig. 5). The relationship of the genus *Thalassocnus* to other nothrotheres is clearly established and remains as determined by McDonald and Muizon (2002:fig. 9), but the relative positions of *T. antiq-*

uus and *T. natans* are unresolved. Tree 1 suggests that the *T. natans* clade diverged earlier than *T. antiquus*, therefore, before the AGL horizon (i.e., 7 to 8 Ma), while tree 2 supports the existence of a single *Thalassocnus* lineage.

CONCLUSIONS

The new parsimony analysis presented here indicates that the four species of *Thalassocnus* may not represent a single evolving lineage. *Thalassocnus natans* could be the earliest divergent taxon of the *Thalassocnus* clade. If this interpretation is correct, then two species of *Thalassocnus* should have existed at AGL time (ca. 7 to 8 Ma). So far, only one species has been found in the AGL Horizon. However, it is noteworthy that sloths are much less common in this horizon than in the Pliocene beds (SAS and SAO). Only one partial skull and skeleton is known from the AGL Horizon, while hundreds have been recorded in the SAS Horizon. A similar situation exists for the MTM Horizon, which has yielded two partial skeletons of *T. natans* and no intermediate species between *T. antiquus* and *T. littoralis*. However, this could be explained by the scarce record of the two Miocene species of *Thalassocnus*.

Although parsimony analysis indicates that the absence and existence of a single time-successive lineage including all four species of *Thalassocnus* are equally parsimonious, we are reluctant to accept the first interpretation. *Thalassocnus* is apparently an endemic genus and the stratigraphy of the Pisco Formation in the Sacaco area (where all the specimens were found) is reasonably well-established (Muizon and DeVries, 1985). Furthermore, many characters are clearly gradual from *T. antiquus* to *T. carolomartini*. The most distinct are: increase in length of the premaxillae; increase in the splaying of the apex of the premaxillae; increase in the width of the premaxillae posterior to their splayed apex; and acquisition of a splayed apex of the mandibular symphysis in the two younger species

(*T. littoralis* and *T. carolomartini*), while it is absent in the two older (*T. antiquus* and *T. natans*). As far as the postcranial skeleton is concerned, the most significant bone is certainly the radius (Fig. 4). This bone, from the oldest to the youngest species drastically increases the width of the shaft (which more resembles a sea lion than a sloth in *T. carolomartini*) and the posterior offset of the proximal end relatively to the distal one. Therefore, several characters favor a continuous *Thalassocnus* lineage from *T. antiquus* to *T. carolomartini*.

To conclude, a definitive decision is not easy to establish because reversals could explain the morphology of *T. natans* in the hypothesis of a lineage from *T. antiquus* to *T. carolomartini*. Moreover, the apparent contradiction of the snout morphology in *T. natans* (character 7) could possibly be the result of the small sample of each species. This character state is observable on one specimen of *T. antiquus*, two of *T. natans*, two of *T. littoralis*, and two of *T. carolomartini*. A larger sample of skulls would certainly provide a better evaluation of the range of individual variation and a better assessment of the validity of the character.

In spite of the result of the parsimony analysis, we believe that the exclusion of *T. natans* from a “*Thalassocnus* lineage” would be a surprising coincidence and that only a single *Thalassocnus* lineage is likely to have existed in the southeastern Pacific. The Peruvian coast was a desert during the Miocene and Pliocene (Sévrier et al., 1984; Todsál et al., 1984; Alpers and Brimhall, 1988). Therefore, given the limited biological resources available along the Peruvian coast to support herbivores, an adaptive radiation within the lineage does not seem biologically likely. However, we do not discard the possibility of a more complex evolutionary scenario for *Thalassocnus*.

Whether it represents a single lineage or not, *Thalassocnus* undoubtedly provides the best information on the Nothrotheriinae ever discovered. In fact, given the stratigraphic environment and the unique preservation (several partial skeletons) of the *Thalassocnus* specimens, the Pisco sloths represent the best known sloth lineage (or possible lineage) currently known.

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APPENDIX 1

List of Characters and Character States. All multistate characters treated as unordered in the phylogenetic analysis.

- Caniniform: closer to the anterior end of maxilla than to M1 (0); closer to M1 than to anterior end of the maxilla (1); absent (2).
- Molariforms: generally transversely oval-shaped (0); rectangular to square (1); molariforms tend to be circular (2).
- Molariform with labial and lingual longitudinal grooves: absent (0); present (1)
- Premaxillae length: short, length less than the alveolar length of upper molariforms (0); long, length greater than the alveolar length of upper molariforms (1).
- Premaxillae outline in ventral view: triangular (0); trapezoid to rectangular (1).
- Anteromedial process of maxilla: short (0); long (1); absent (2).
- Lateral edge of the narial opening: with a marked angle separating a subvertical posterior portion formed by the anterior edge of the ascending process of the maxilla and the ascending process of the premaxilla and a horizontal portion formed by the horizontal ramus of the premaxilla (the angle is either right or slightly obtuse) (0); gently and regularly sloping anteriorly from anterior point of the nasal-maxilla suture and angle, if present, widely open (1).
- Anteromedial process of nasal: present (0); absent (1)
- Buccinator fossa: shallow (0); deep (1).
- Dorsal profile of skull: domed over the parietals (0); domed over the frontals (1).
- Sagittal crest: continuous with dorsal margin of zygomatic process (0); does not connect with dorsal margin of zygomatic process (1).
- Attachment of base of jugal to skull: attaches more or less above M2 (0); attaches above M3 (1).
- Shape of ventral margin of descending ramus of jugal: pointed (0); rounded (1).
- Processes on anterior and posterior edge of lacrimal foramen: absent (0); present (1).
- Pterygoid pneumatic sinus: sinus absent (0); pterygoid hollowed out medially (1); sinus present (2). Data for *Nothropus* is from Gaudin and De Iuliis (1999).
- Posterior margin of pterygoid thickened and expanded mediolaterally: absent (0); present (1).
- Ectotympanic: narrow (0); wide, expanded medially (1).
- Shape of stylohyal fossa (character 54 of Gaudin, 1995): circular (0); oval (1).
- Occipital artery canal in mastoid process: absent (0); present (1).
- Orientation of the zygomatic process of the squamosal (character 85 of Gaudin, 1995, modified): anterolateral (0); anteroposterior (1).
- Fissura Glaseri (character 14 of Gaudin, 1995): lateral to entoglenoid process (0); opens into a groove medial to entoglenoid process.
- Vomerine keel (Gaudin and De Iuliis, 1999): small and not extending behind the choanae (0). Enormous and extended posteriorly (1).
- Shape of anterior margin of mandibular symphysis: tapered and narrow (0); expanded and spatulate (1).
- Internal trough of spout of mandible: reaches anterior edge of spout (0); does not reach anterior edge of spout (1).
- Femoral trochlea (Patellar surface) continuous with both condylar surfaces (0), separated from the condylar surfaces (1).
- Fusion of the proximal and second phalanges of digit III of pes: absent (0); present (1).
- Fusion of the proximal and second phalanges of digit III of manus: absent (0); present (1).
- Odontoid process of the astragalus: absent (0); present (1).
- Metatarsal V with mediolateral expansion: absent (0); present (1).
- Ungual phalanx of digit II of manus flattened: absent (0); present (1).
- Pronator ridge of the radius anteriorly expanded: absent (0); present (1).
- Position of the proximal epiphysis relatively to posterior edge of diaphysis of radius: axis of the posterior edge of the portion of diaphysis distal to pronator ridge reaches posterior half of proximal epiphysis (0); almost reaches, or reaches or is anterior to anterior edge of proximal epiphysis (1).
- Third trochanter of the femur: separated on mid-shaft (0); continuous with lateral epicondyle (1); connects with greater trochanter (2).

APPENDIX 2

Character matrix of 9 sloth taxa and 33 characters (Appendix 1) used in phylogenetic analysis (Fig. 5).

	12345	1 67890	1 12345	2 67890	2 12345	3 67890	3 123
<i>Hapalops elongatus</i>	00000	00010	00000	00000	00000	00000	110
<i>Pronothrotherium typicum</i>	11100	00?00	00000	00111	11001	00111	110
<i>Nothropus priscus</i>	111??	00?11	00001	???11	?1001	?01?1	??0
<i>Nothrotherium maquinense</i>	21100	00000	00002	00101	11001	10111	001
<i>Nothrotheriops shastense</i>	21100	00001	00012	00111	11001	10111	001
<i>Thalassocnus antiquus</i> , sp. nov.	21111	11000	01110	0??10	0?010	?1101	00?
<i>Thalassocnus natans</i>	21111	10100	01110	01010	00010	11101	112
<i>Thalassocnus littoralis</i>	21111	11100	01110	11010	00110	11101	112
<i>Thalassocnus carolomartini</i>	22111	11110	01110	11010	00110	11101	112