

THE YOUNGEST SPECIES OF THE AQUATIC SLOTH *THALASSOCNUS* AND A REASSESSMENT OF THE RELATIONSHIPS OF THE NOTHROTHERE SLOTHS (MAMMALIA: XENARTHRA)

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ABSTRACT—Two new specimens of the aquatic sloth *Thalassocnus* from the Pliocene of Peru are described, one of *T. carolomartini* McDonald and Muizon, 2002 and the other *T. yaucensis*, sp. nov. Comparisons with the type species of *Thalassocnus*, *T. natans*, demonstrates that *T. carolomartini* and *T. yaucensis* are more similar morphologically to each other than to other species of the genus and are more derived. For example, both have a more elongated rostrum (premaxillae and mandibular spout) and more robust, quadrate to circular molariform teeth. The aquatic sloth *Thalassocnus* is sufficiently distinct morphologically that it is placed in a new subfamily, the Thalassocninae, and the Nothotheriinae is raised to family rank. The morphological features shared by *T. carolomartini* and *T. yaucensis* indicate these species were better adapted to grazing on marine vegetation than earlier species of *Thalassocnus*.

INTRODUCTION

Two specimens recently discovered in the Pisco Formation of the Sacaco Region, Peru, provide additional insight into the evolutionary history of the *Thalassocnus* lineage of nothotheres sloths (Muizon and McDonald, 1995; McDonald and Muizon, 2002; Muizon et al., 2003). One is a partial skull and mandible along with associated hyoid elements, foot bones, and a femur. This specimen is from the locality of Sacaco and was discovered in the SAO (Sacaco) vertebrate-bearing horizon. It is, therefore, late early to early late Pliocene in age (Muizon and DeVries, 1985). Although slightly smaller and more gracile, it is otherwise very similar to the holotype of *Thalassocnus carolomartini* McDonald and Muizon, 2002, also from the SAO Horizon, and is referred to this species. The second specimen was discovered at Yauca, 10 km south of Sacaco, in a vertebrate-bearing horizon that was initially regarded as equivalent in age to the SAO Horizon. No geologic correlation has been established between the two localities and, so far, no biostratigraphic evidence indicates that the Yauca beds are the same age as the SAO Horizon. The Yauca specimen is a partial skeleton with an exceptionally well-preserved skull and mandible, much better than that of the holotype of *T. carolomartini* and one of the best-preserved specimens of the *Thalassocnus* lineage. Comparison of the Yauca specimen and those of *T. carolomartini* with the older species of Pisco sloths (*T. antiquus*, *T. natans*, *T. littoralis*) indicate that *T. carolomartini* and the Yauca specimen are more similar morphologically and are more derived. Despite the presence of numerous shared features, the morphology of the mandibular spout in the Yauca specimen differs significantly from that of the two specimens of *T. carolomartini* and, because of this feature, is referred here to a new species of *Thalassocnus*.

The purpose of this paper is to describe the skull and mandible of the new referred specimen of *T. carolomartini* and the Yauca specimen. They are compared to the holotypes of *T. carolomartini* and the genotypic species *T. natans*, which is the best preserved of the other three species in the genus. The Yauca specimen was closely associated with several bones of a second smaller individual indicating a fetal or newborn ontogenetic stage. This is regarded as an indication that the skeleton is probably that of a female.

GEOLOGY

The Pisco Formation is a Neogene marine unit present along the southern coast of Peru. It has yielded an abundant fauna of marine vertebrates including fishes, reptiles, birds and mammals. Hoffstetter (1968), Muizon (1981), Muizon and DeVries (1985), and Marocco and Muizon (1988) reported abundant remains of sloths, which were regarded by Muizon and McDonald (1995) as having semi-aquatic habits. This interpretation was initially based on the taphonomy of the specimens. The Peruvian coast was a desert during the late Neogene (Sévrier et al., 1984; Todsál et al., 1984; Alpers and Brimhall, 1988). These data, combined with the extreme abundance and excellent preservation (articulated skeletons) of the sloth remains and the fact that virtually no other land mammals have been found in the Pisco Formation, led to the conclusion that they regularly entered the ocean to feed on marine vegetation, either seaweed or sea grass. Many of the anatomical features of the Pisco nothotheres, *Thalassocnus natans*, are compatible with an interpretation of an aquatic or semi-aquatic life (Muizon and McDonald, 1995).

McDonald and Muizon (2002) and Muizon et al. (2003) described three additional species of *Thalassocnus* that were recovered from horizons above and below that in which the holotype of *T. natans* was found. The oldest species, *Thalassocnus antiquus*, is from the Aguada de Lomas Horizon (AGL), ca. 7 to 8 Ma; *T. natans* from the Montemar Horizon (MTM), ca. 6 Ma; *Thalassocnus littoralis* from the Sud-Sacaco (SAS) Horizon, ca. 5 Ma; and *T. carolomartini* from the Sacaco (SAO) Horizon, ca. 4 to 3 Ma. The stratigraphy of the Pisco Formation used here follows Muizon and DeVries (1985). Based on the above four species, McDonald and Muizon (2002) and Muizon et al. (2003) raised the hypothesis of the existence of a *Thalassocnus* lineage spanning four different vertebrate horizons and at least 4 Ma. However, Muizon et al. (2003) also admitted that *Thalassocnus* might have had a more complex evolutionary history.

Abbreviations—MNHN, Muséum national d'Histoire naturelle, Paris, France; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; SMNK, Staatliche Museum für Naturkunde, Karlsruhe, Ger-

many; **UPCH**, Universidad Peruana Cayetano Heredia, Lima, Peru.

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope, 1889

Suborder PHYLLOPHAGA Owen, 1842

Superfamily MEGALONYCHOIDEA Simpson, 1931

Family NOTHROTHERIIDAE Ameghino, 1920, new rank

Included subfamilies—Nothrotheriinae Ameghino, 1920; Thalassocninae, subfam. nov.

Revised Diagnosis—Skull elongated anterior to orbits and muzzle smaller than posterior part of skull; supraorbital foramen present; zygomatic arch incomplete with jugal separated from zygomatic process of squamosal; anteriorly directed zygomatic root; enormous vomerine keel in nasopharynx; mandibular symphysis elongated into a spout. Dentition either 5/4 or 4/3; when dentition is 5/4, anteriormost tooth in skull and mandible modified into a caniniform positioned midway between anterior of skull and molariform cheek teeth. Molariforms square in cross section with a well-developed transverse loph on the mesial and distal edges of occlusal surface; molariforms have a longitudinal groove on labial and lingual sides. Ungual on digit two of manus semicircular in cross section while all other unguals on the manus and pes are an isosceles triangle; third trochanter present on femur; patellar trochlea of femur separated from articular surfaces of distal condyles; tuber calcis of calcaneum expanded equally both anteroposteriorly and mediolaterally; astragalus with medial trochlea modified into an odontoid process and lateral trochlea anteroposteriorly curved; proximal and second phalanx of digit three of pes coossified in later members of family; fifth metatarsal with mediolaterally expanded insertion for the fibularis longus; unguals on digits 1–4 of pes.

History—The earliest nothrothere to be described was *Coelodon maguinense* Lund, 1838 (*Nothrotherium* Lydekker, 1889 is a replacement for *Coelodon* Lund, 1838, a preoccupied name). *Nothropus* was described by Burmeister in 1882, and *Pronothrotherium* by Ameghino in 1907. The North American nothrothere now referred to as *Nothrotheriops* was originally referred to *Nothrotherium* by Sinclair (1905). *Nothrotheriops* was initially described by Hoffstetter (1954) as a subgenus of *Nothrotherium*, but Paula Couto (1971) raised it to the level of genus.

Kraglievich (1923) placed the Nothrotheriinae within the Megalonychidae as one of four subfamilies. Other than *Nothrotherium*, the type genus of the subfamily, he did not refer any other genera to the subfamily. However, the provided geological and geographic distribution included the Oligocene to Pliocene of Argentina, Pliocene to Pleistocene of Brazil and Bolivia, and Pleistocene of North America (California and Texas), which suggests that Kraglievich (1923) was also including *Nothropus*, *Pronothrotherium*, and the North American nothrothere now known as *Nothrotheriops*. His diagnosis for the subfamily included the following characters: nasal region low and elongated; preorbital fossa of maxilla shallow; first upper molar absent; crown of the molars with grooves on the lateral face; pterygoid inflated, with air sinuses; femur wide and flattened anteroposteriorly; fovea captis of femur totally included within the articular surface of the head; and the three distal articular facets of the femur are independent.

Kraglievich's (1923) placement of the subfamily Nothrotheriinae within the Megalonychidae was followed by Simpson (1945). Patterson and Pascual (1968, 1972) were the first to suggest that the nothrotheres were more closely related to the megatheres. Paula Couto (1971) also placed the Nothrotheriinae within the Megatheriidae. Engelmann (1985) listed characters he felt united the Nothrotheriinae and Megatheriinae within the

Megatheriidae, but the validity of these characters was questioned by De Iuliis (1994). Patterson et al. (1992) included the Nothrotheriinae within the Megatheriidae using characters of the ear region and noted that the Megatheriinae and Nothrotheriinae shared a number of derived characters. McKenna and Bell (1997) altered this classification by creating the tribe Nothrotheriini, within the subfamily Megatheriinae, family Megatheriidae, thus eliminating the subfamily Nothrotheriinae altogether. Gaudin and De Iuliis (1999) used the designation Nothrotheriidae in their discussion of the relationship of *Nothropus priscus* and considered the group to be monophyletic based on three shared characters: separation of the patellar trochlea from the medial and lateral femoral condyles; an enormous vomerine keel in the nasopharynx; and an anteriorly directed zygomatic root.

It should be noted that the family Nothrotheriidae as used here does not include the Miocene genera *Hapalops*, *Synhapalops* and *Diheterocnus*, which have sometimes been included within the nothrotheres. These genera may be considered equivalent to the *Schismotherium* group identified by Patterson et al. (1992) and formally identified as the subfamily Schismotheriinae by McKenna and Bell (1997). While there may be a close relationship between these genera and the Nothrotheriidae (as defined here), and although McKenna and Bell (1997) included the genera *Synhapalops* and *Diheterocnus* in their Nothrotheriini, as of yet there is insufficient evidence to establish exactly what this relationship is. While further work will certainly elucidate these relationships, such an analysis is beyond the scope of this paper.

Recent research on the *Thalassocnus* lineage and its relationship to other nothrothere sloths has demonstrated that nothrotheres constitute a monophyletic group that has had an evolutionary history distinct from that of megalonychids and megatheres. As such, we propose the formal recognition of a family Nothrotheriidae. We also propose that they are more closely related to the megalonychids than to the megatheres, because they do not share any of the unique derived characters present in the Megatheriidae (McDonald and Muizon, 1995 and in prep.). As such they are placed in the superfamily Megalonychoidea. The closer relationship between nothrotheres and megalonychids was discussed briefly in Muizon and McDonald (1995). Therefore, the classification presented here differs from that of McKenna and Bell (1997).

Subfamily NOTHROTHERIIDAE Ameghino, 1920

Revised Diagnosis—Premaxillae primitive and triangular, shorter than length of molariform tooth row; post-palatine notch extends anteriorly to level of last molariform; caniniform may or may not be present; third trochanter of femur either positioned on midshaft or continuous with lateral epicondyle; length of tibia shorter than femur.

Type Genus—*Nothrotherium* Lydekker, 1889.

Included Genera—*Nothropus* Burmeister, 1882; *Xylophorus* Ameghino, 1887; *Pronothrotherium* Ameghino, 1907; *Nothrotheriops* Hoffstetter, 1954; *Chasicobradys* Scillato-Yané, Carlini, and Vizcaino, 1987; *Huilabradys* Villarroel, 1998; *Amphibradys* Scillato-Yané and Carlini, 1998.

Age Range—Middle Miocene to late Pleistocene (Colloncuran to Lujanian in South America, Irvingtonian and Rancholabrean in North America).

Subfamily THALASSOCNINAE, subfam. nov.

Diagnosis—Premaxilla large, robust, and greatly elongated with anterior edge expanded and spatulate with a correlative extension of mandibular symphysis in some taxa; anteroventral processes of maxillae much longer than in other nothrotheres; dentition 4/3, caniniform absent; in lateral view, dorsal profile

of frontal relatively straight as in *Nothrotherium* and *Pronothotherium*, not dorsally convex as in *Nothropus* and *Nothrotheriops*; sagittal crest not continuous with dorsal edge of zygomatic process of squamosal; infraorbital foramen short anteroposteriorly and located above M3. Ectotympanic wider than in *Pronothotherium* and *Nothrotherium*, expanded medially, and partially covering entotympanic; lateral edge of ectotympanic thickened at inferior edge of external auditory meatus; mastoid process of squamosal relatively stouter than in other nothrotheres; zygomatic process of squamosal anteroposteriorly short; proximal phalanx of digit 1 on manus absent; proximal and second phalanx of digit 3 of manus fused; third trochanter of femur continuous with greater trochanter, with distal end of femur narrower than proximal end; tibia relatively longer compared to length of the femur than in other nothrotheres; distal caudal vertebrae with bifurcate transverse processes or process perforated by a foramen.

Type and Only Genus—*Thalassocnus* Muizon and McDonald, 1995.

Age Range—Late Miocene to late Pliocene, Huayquerian to Chapadmalalan, possibly Uquian.

THALASSOCNUS Muizon and McDonald, 1995

Diagnosis—As for subfamily (see also McDonald and Muizon, 2002:350).

Type species—*Thalassocnus natans* Muizon and McDonald, 1995.

Included Species—*Thalassocnus littoralis* McDonald and Muizon, 2002; *Thalassocnus carolomartini* McDonald and Muizon, 2002; *Thalassocnus antiquus*, Muizon et al., 2003; *Thalassocnus yaucensis*, sp. nov.

THALASSOCNUS CAROLOMARTINI McDonald and Muizon, 2002

Holotype—SMNK PAL 3814, a nearly complete skull and mandible lacking part of the pterygoids, jugal, zygomatic processes of the squamosals, exoccipitals, condyloid and angular processes of the dentaries. Complete right and left manus (SMNK PAL 3815) are associated with the skull.

Referred Specimens—MNHN SAO 203, a partial skull (lacking basioccipital, right auditory region and most of the occipital) and mandible (lacking left condyle and angular processes), both stylohyals (lacking proximal extremity), right hypohyal and ceratohyal, basihyal, partial basihyal and fused right thyrohyal, the right femur, partial right calcaneum, right navicular, partial right cuboid, and partial right metatarsal 5; MNHN SAO 201, a partial postcranial skeleton including strongly weathered limbs and vertebral column; MNHN SAO 13, proximal right humerus; MNHN SAO 76, distal left humerus; SAO 204, distal left radius; MNHN SAO 77, right metacarpal 5; MNHN SAO 12, distal left femur; MNHN SAO 75, proximal right tibia; MNHN SAO 16, right calcaneum; MNHN SAO 14 right astragalus; MNHN SAO 51 co-ossified first and second phalanx of digit 3 of right foot.

Type Locality—The holotype and referred specimens of *T. carolomartini* are all from the locality of Sacaco, southern coast of Peru (McDonald and Muizon, 2002:fig. 1).

Horizon and Age—SAO Horizon, Pisco Formation (Muizon, 1981; Muizon and DeVries, 1985), Chapadmalalan, ca. 3 to 4 Ma (late early to early late Pliocene).

Description—Both skulls of *T. carolomartini* (holotype and MNHN SAO 203) are very similar. However, MNHN SAO 203 differs from SMNK PAL 3814 in its smaller size, the greater slenderness of its teeth and the slightly shorter premaxillae (Fig. 1A–D; Table 1). These differences could be related to a sexual dimorphism. For instance, the lesser development of the premaxillae could indicate a smaller upper lip in MNHN SAO 203.

In some recent mammals with a well-developed upper lip or a small proboscis such as elephant seals (Ling and Bryden, 1981) and saiga antelope (Sclater and Thomas, 1897), this feature is always more pronounced in the male. Therefore, this condition could be extrapolated to *T. carolomartini*. McDonald and Muizon (2002) already mentioned that the great individual variation observed in *T. littoralis* could be related to sexual dimorphism. It is noteworthy that the femur associated to MNHN SAO 203 is very small (22%) when compared to the femur of MNHN SAO 201 from the same locality and horizon. It resembles the size of the femur of the holotype of *Thalassocnus yaucensis*, sp. nov., which is interpreted as a female (see below).

The ascending ramus of the mandible is incomplete in the holotype, but is almost complete in MNHN SAO 203 (Fig. 1E; Table 2). The condylar process is small and its neck is short. It is located above the tooth row and the articular surface faces essentially dorsally. In fact, the orientation has a small posterior component, although much less developed than the dorsal. It is triangular (equilateral) in shape and its medial side is almost parallel to the axis of the tooth row. It is not transversely expanded as is observed in the earlier species of *Thalassocnus* (*T. antiquus*, *T. natans*, and *T. littoralis*) and in *Choloepus*. The masseteric fossa is relatively small when compared to the earlier species of *Thalassocnus* and the apex of the coronoid process is distinctly bent medially. On the lateral side of the process, a distinct posteroventrally curved ridge joins the posteroventral angle of the apex to the anterior base of the process. This ridge delimitates a medially bent anterodorsal surface, which received the anterior insertion of the temporalis muscle and could correspond to the M. temporalis superficialis pars zygomatica observed in *Choloepus* by Naples (1985). The process is long with a deeply concave posterior edge and appears strongly recurved posteriorly.

THALASSOCNUS YAUCENSIS, sp. nov.

Holotype—MUSM 37, partial skeleton including an almost complete skull (only lacking right jugal), mandible (lacking right angular process); stylohyals; cervical, dorsal, lumbar, and 3 proximal caudal vertebrae; 2 chevrons; ribs; both scapulae; right humerus, radius, and ulna; right trapezoid; left scaphoid; right metacarpals 1, 2, and proximal 3; first and second phalanges of right digit 2; distal left metacarpals 3, 4 and 5; phalanges 1–3 of left digit 2; right or left pisiform; right femur; and proximal left femur.

Referred Specimens—MUSM 434, isolated femur; and MUSM 347, partial skeleton including fragments of premaxilla, maxilla, and mandible, astragalus, partial humerus, radius, ulna, and tibia.

Etymology—From Yauca, a small village on the Peruvian coast, which is located close to the type locality.

Type Locality—The holotype was discovered on the southern side of the Panamerican Highway, approximately 3 km east of Yauca. This site is here called East Yauca. It is located approximately 30 km southeast of Sacaco.

Horizon and Age—Pisco Formation. Because the rostrum of *T. yaucensis* is distinctly more elongated (and therefore more derived) than in *T. carolomartini*, the horizon in which the new species was discovered is probably slightly younger than the SAO Horizon. The locality East Yauca is probably late Pliocene or early Uquian (1.5 to 3 Ma, Flynn and Swisher, 1995).

Diagnosis—Nasals longer than in *T. carolomartini*, extending posteriorly behind the maxilla-frontal suture and the transverse plane at the level of the lachrymal foramina; longer pre-dental portion of the maxillae; larger buccinator fossa; ventral edge of the choanae more posterior than in *T. carolomartini*; ventral process of the jugal larger and longer than dorsal process; mandibular symphysis longer than in *T. carolomartini*;

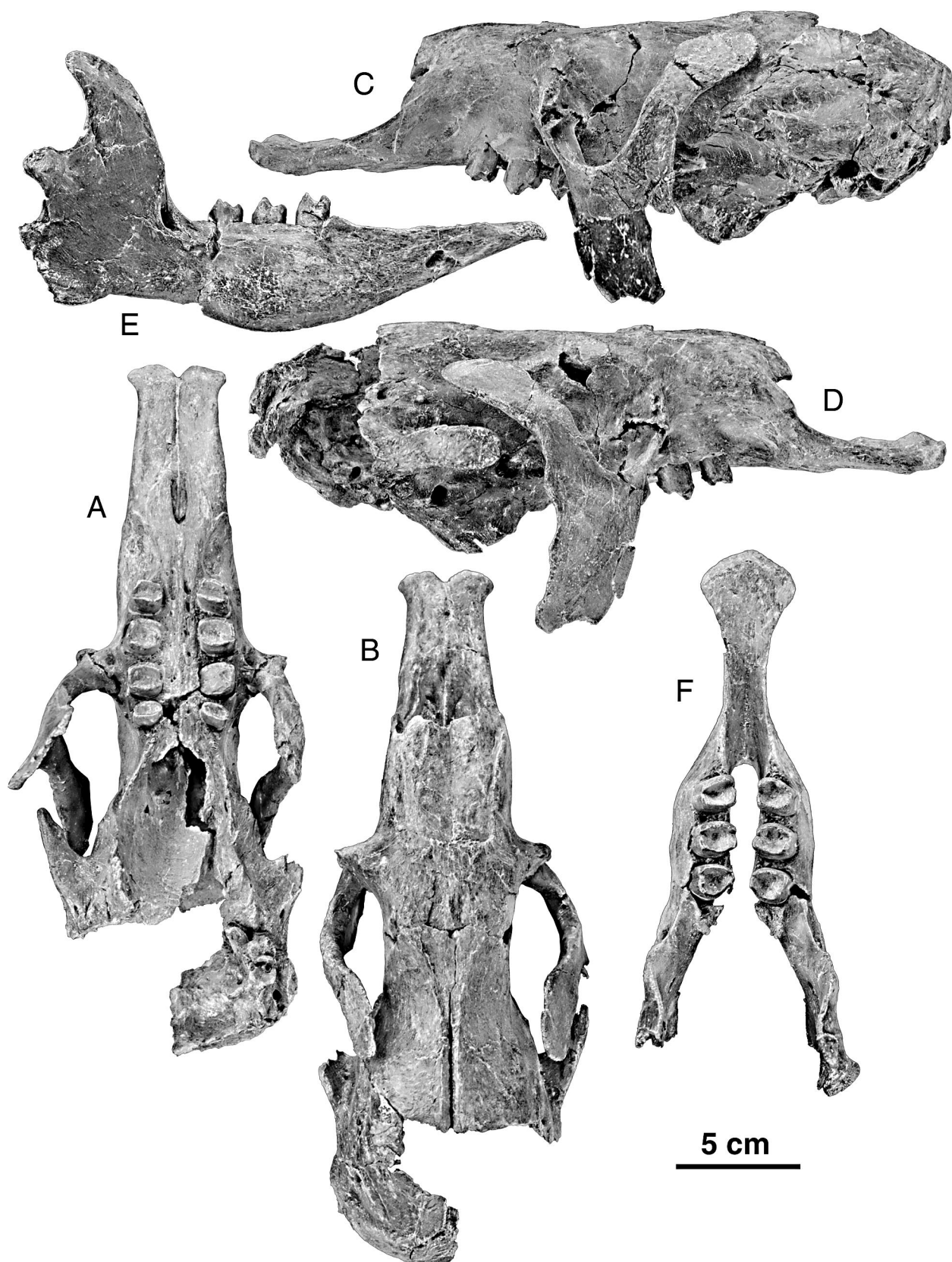


FIGURE 1. Skull of *Thalassocnus carolomartini*, referred specimen MNHN SAO 203, in ventral (A), dorsal (B), lateral left (C), and lateral right (D) views; mandible in lateral right (E) and dorsal (F) views.

TABLE 1. Comparative measurements of the new skulls of *Thalassocnus*. All measurements are in mm. Measurements followed by one decimal measured using digital calipers. Palatal measurements do not include the premaxillae. Abbreviations: AP, anteroposterior; e, estimate; L, length; MD, mesiodistal; W, width.

	<i>Thalassocnus carolomartini</i> MNHN SAO 203	<i>Thalassocnus yaucensis</i> MUSM 37 holotype
Maximum skull L (in dorsal view)	288e	299.4
Basicondylar L from anteroventral angle of ascending process of the maxilla to posterior edge of occipital condyles	—	215.8
L from anterior edge of M1 to posterior of occipital condyle	—	180.3
L along midline from anterior edge of postpalatine notch to anterior edge of foramen magnum	—	93.3
L along midline of palate from medial base of anteroventral process of the maxilla to posterior edge	90.1	96.5
L from anterior of M1 to posterior of M4	58.5	60.7
L from anterior of M1 to anterior edge of anteroventral process of maxilla	45.3	53.5
Maximum W between labial edges of M1	39.9	35.3
Maximum W between labial edges of M4	38.0	41.3
L from posterior edge of M4 to posterior edge of occipital condyle	—	119.5
Maximum W between postorbital processes of frontal	51.5	60.9
Least interorbital breadth	49.1	52.9
Maximum W between mastoid processes	—	100.9
Maximum W between lateral margins of occipital condyles	—	63.6
Maximum height of occipital condyle	—	27.1
W of foramen magnum between ventral edges of occipital condyles	—	16.0
Height of occiput in midline from dorsal edge of foramen magnum to nuchal crest	—	47.3
Maximum W between lacrimal foramina	67.2	72.3
L from postorbital process of frontal to nuchal crest (measured horizontally)	138.6	136.5
Least distance from posterolingual edge of M4 to postpalatine notch	14.6	10.4
Minimum W of palate between M1	14.0	10.4
Minimum W of palate between M4	15.1	15.2
M1 AP L	10.9	11.7
M1 MD W	12.7	12.3
M2 AP L	13.6	13.6
M2 MD W	14.4	13.6
M3 AP L	12.5	12.2
M3 MD W	14.6	14.3
M4 AP L	8.2	6.2
M4 MD W	11.9	12.5

mandibular spout horizontal with apex located below the alveolar border.

COMPARATIVE DESCRIPTION

The description below will focus on the major anatomical differences between *Thalassocnus carolomartini*, *T. yaucensis*, and the genotypic species, *T. natans*. In order to avoid redundancy with McDonald and Muizon (2002), the description will be comparative. The new specimen of *T. carolomartini*, which is extremely similar to the holotype, allows a better understand-

ing of the individual variation in this species and, therefore, a better definition of the new species.

The size of the skull of *T. yaucensis* is similar to that of the holotype of *T. carolomartini* in total length and mastoid width. The predental palate (i.e., distance between the anterior edge of M1 and the apex of the premaxillae) is slightly longer in *T. yaucensis* (107 mm) than in *T. carolomartini* (101.5 mm and 87.5 mm) (Fig. 2).

As in *T. carolomartini*, the premaxillae of *T. yaucensis* are distinctly longer than in *T. natans* and much wider at the apex. As a consequence, the lateral edges of the premaxillae are sub-

TABLE 2. Measurements of the mandibles of the new specimens of *Thalassocnus*. All measurements are in mm. Measurements followed by one decimal measured using digital calipers. Abbreviations as in Table 1.

	<i>Thalassocnus carolomartini</i> MNHN SAO 203	<i>Thalassocnus yaucensis</i> , sp. nov., MUSM 37
L from anterior of spout to posterior edge of angular process	—	250.8
L from anterior of spout to posterior edge of condyle	221.4	232.7
L from anterior edge of spout to anterior edge of m1	95.4	114.2
L from anterior edge of spout to posterior edge of m3	144.8	166.8
L of spout from anterior edge to posterior edge of symphysis	90.8	105
Alveolar L of cheek teeth	51.9	52.9
Maximum depth of horizontal ramus	45.9	46.4
W of spout at anterior edge	38.6	33e
Angle of ventral edge of spout relative to cheek tooth row	24°	12°
m1 AP L	14.1	14.0
m1 MD W	13.9	13.6
m2 AP L	14.7	14.3
m2 MD W	14.4	13.6
m 3 AP L	14.4	16.0
m 3 MD W	13.9	13.7

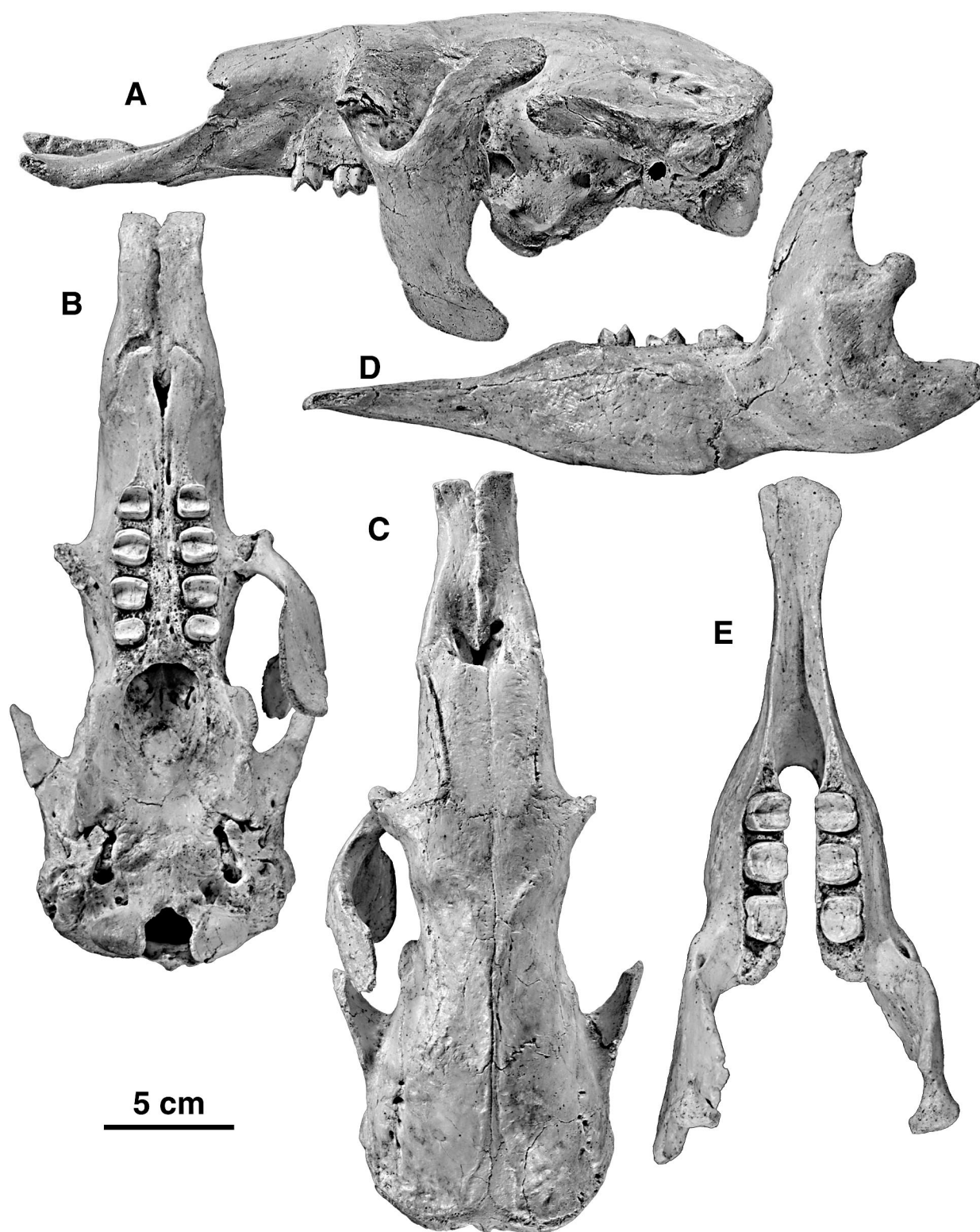


FIGURE 2. Skull of *Thalassocnus yaucensis*, sp. nov., holotype, MUSM 37 in lateral (A), ventral (B), dorsal (C), views; mandible in lateral left (D) and dorsal (E) views.

parallel in *T. carolomartini* and *T. yaucensis*, while they form a distinct 'V' in *T. natans* (Fig. 3). Furthermore, the premaxillae of *T. yaucensis* are also longer than in *T. carolomartini*.

The upper molariforms (essentially M2 and M3) of *T. yaucensis* are slightly more quadrate than in the *T. carolomartini*

and the anterior and posterior crests more pronounced and more transverse. However, they are conspicuously less compressed anteroposteriorly than in *T. natans* (Fig. 4).

The left jugal of the holotype of *T. yaucensis* is completely preserved (Fig. 2A). The dorsal process is stout and thick. Half-

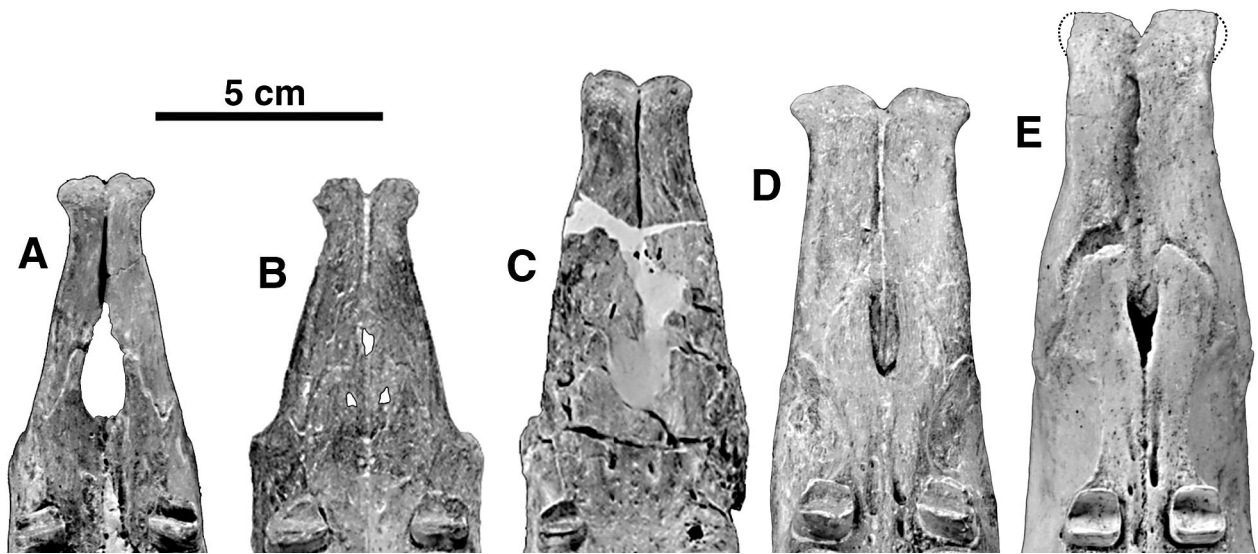


FIGURE 3. Outlines of the premaxillae in thalassocnines. *Thalassocnus antiquus* (holotype, MUSM 228) (A); *T. natans* (holotype, MNHN SAS 734) (B); *T. littoralis* (holotype, MNHN SAS 1615) (C); *T. carolomartini* (MNHN SAO 203) (D); *T. yaucensis* (holotype, MUSM 37, lateral sides of the apex reconstructed) (E). Not to scale.

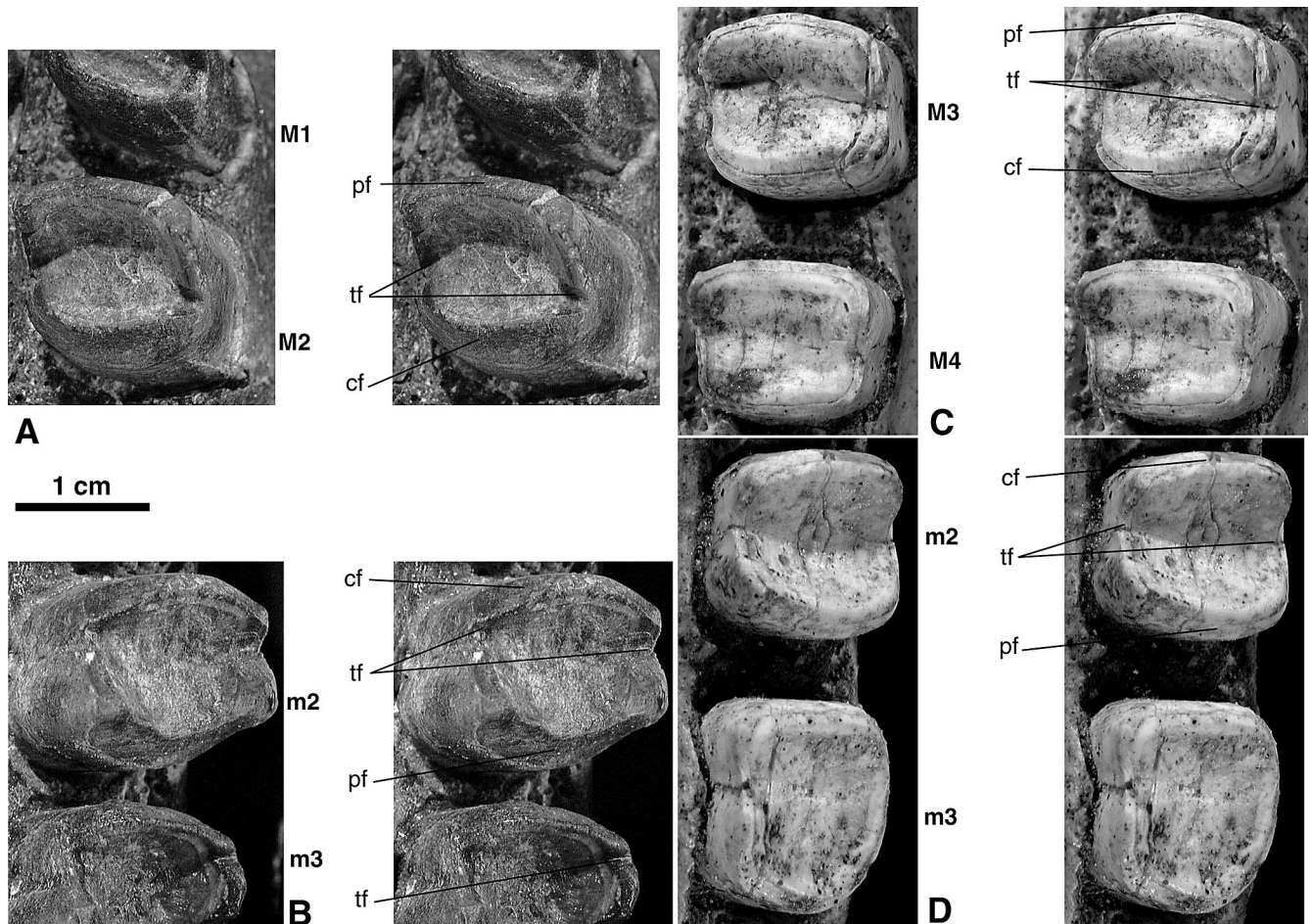


FIGURE 4. Dental morphology of advanced *Thalassocnus* in posterolabial view. *T. carolomartini* (MNHN SAO 203) left M2 and posterior edge of M1 (A) and m2 and anterior half of m3 (B). *T. yaucensis* (holotype, MUSM 37) left M2–M3 (C) and m2–m3 (D). Abbreviations: cf, convex wear facet; pf, planar wear facet; tf, facet indicating some transverse movement of the mandible.

way between its apex and the ventral border of the orbit its anterior edge bears a salient short crest (more a knob in the holotype), which probably corresponds to the ventral extension of the postorbital ligament. This ligament attached anteriorly on supraorbital process of the frontal, which is reduced to a small bump located posteroventral to the temporal crest at approximately 5 cm from the maxillary-jugal articulation. The medial face of the dorsal process of the jugal (its distal half) received part of the origin of the zygomaticomandibularis muscle. The posterior edge of the dorsal process of the jugal is distinctly concave as in *T. carolomartini*. However, it is not as notched as in *Nothrotheriops* and was not almost contacting the zygomatic process of the squamosal as in this genus. The jugal and squamosal processes are separated by 1.5 cm and the two bones are not imbricated as in *Nothrotheriops* (although never in contact, Naples, 1989). This condition is similar to that in *T. carolomartini*. The ventral process of the jugal is a long and wide plate, the apex of which is deflected posteriorly. On its lateral side attached the origin of the five portions of the masseter superficialis (Naples, 1989). Although the preservation of the specimen does not allow identification of the five heads of the masseter superficialis as in *Nothrotherium* (Naples, 1987), the size of the ventral process of the jugal indicates that this muscle was very powerful in both *T. carolomartini* and *T. yaucensis*. The posterior edge of the ventral process is also deeply concave. It is separated from the concave posterior edge of the dorsal process by a posteriorly expanded convex area, which is ca. 3 cm long (ca. 4 cm in the holotype of *T. carolomartini*). This condition however presents some variation because in the new specimen of *T. carolomartini* a second salient posterior spine is also present on the posterior border of the ventral process. This region of the jugal is similar to that of *Thalassocnus natans*, but does not form a true posterior process, ventral to the apex of the zygomatic process of the squamosal as in *Nothrotherium*. This convex part of the posterior edge of the jugal is approximately at the level of the inferior border of the orbit, while the posterior process of *Nothrotherium* is distinctly more dorsal than in the thalassocnine sloths.

Assuming that the condition of *T. yaucensis* was similar to that reconstructed in *Nothrotherium* (Naples, 1989), the masseter profundus originated on the medial side of the jugal, in a relatively central position (i.e., the ventral part of the dorsal process, the posterodorsal part of the ventral process and the apex of the zygomatic process of the squamosal). In *T. yaucensis*, the dorsal process of the jugal is distinctly shorter than the ventral process, contrary to the condition in *T. natans*. The ratio ventral process/dorsal process is 1.17 (81.7/69.5) in *T. yaucensis* (MUSM 37), 0.83 (65e/78) in *T. carolomartini* (MNHN SAO 203), and 0.76 (59.7/77.8) in *T. natans* (MNHN SAS 734) (the length of the processes is measured from the ventralmost point of the orbit to the apex of the process). In *T. yaucensis*, the dorsal edge of the jugal is distinctly lower than the sagittal crest.

The pterygoids of the holotype of *T. yaucensis* are remarkably well preserved. The pterygoid flanges are relatively small when compared to those of *Thalassocnus natans* and even smaller relatively to those of *Nothrotheriops* and *Glossotherium*. However, they are thickened and stout at their posterior base, as in *T. carolomartini* (Fig. 2B). The anteroventral edge of the flange is a thick crest, ca. 25 mm long and 5 mm wide. Dorsal to this crest is a conspicuous, shallow fossa for origin of the pterygoideus medialis. Dorsal to this fossa and posterior to the sphenoidal fissure and optical foramen is another, slightly larger fossa for the origin of the pterygoideus lateralis. It is not possible to identify separate origins for the upper and lower head of this muscle, although they could be distinguished on the right side of the skull by a very subtle division into two shallow fossae.

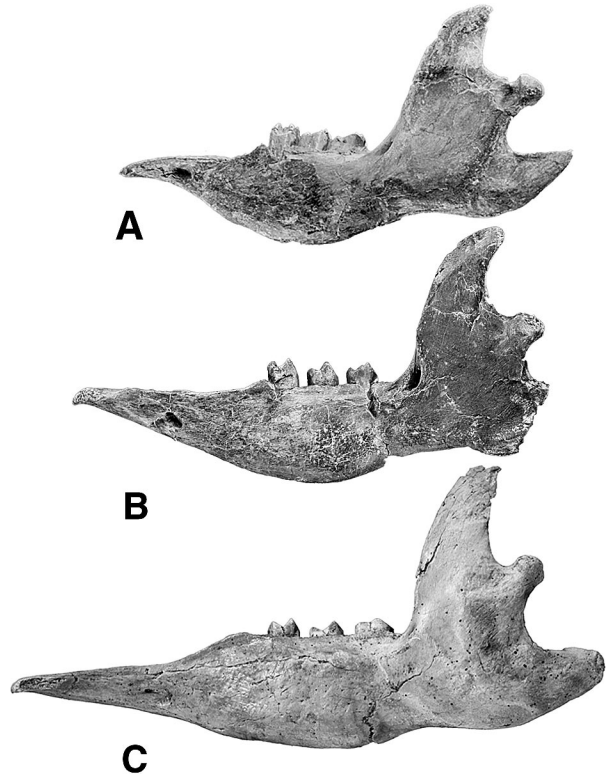


FIGURE 5. Comparative lateral views of the mandible in thalassocnines. *Thalassocnus natans* (holotype, MNHN SAS 734) (A); *Thalassocnus carolomartini* (MNHN SAO 203) (B); *Thalassocnus yaucensis* (MNHN SAO 203) (C). Not to scale.

On the lateral wall of the braincase of MUSM 37, the orbitosphenoid bears a distinct sphenorbital fissure and optical foramen. Separation of these foramina has not been observed in any of the other members of *Thalassocnus* and could represent individual variation. The remainder of the skull of the holotype of *T. yaucensis* does not present significant differences with the two known specimens of *T. carolomartini*.

The singular most obvious character of *T. yaucensis* is observed on the mandible. The mandibular spout is distinctly longer than in *T. carolomartini* (Figs. 5–6). The ratio of the length of the mandibular spout (from apex of the mandible to anterior edge of m1) to the foraminal length (from apex to anterior edge of the medial mandibular foramen) is 0.60 in *T. yaucensis*, 0.52 in *T. carolomartini* (average of SMNK 3814 and MNHN SAO 203), 0.49 in *T. natans* (one specimen), and 0.50 in *T. antiquus* (one specimen). The difference between *T. yaucensis* and *T. carolomartini* is almost 15% and is regarded here as too great to be the result of simple individual variation.

Another important difference of the mandible of *T. yaucensis* is the orientation of the mandibular spout (Fig. 5). In the holotype and only specimen for which a complete skull is known, it is oriented almost horizontally. Its dorsal and ventral edges form a similar angle with the tooth row and the apex is located distinctly below the alveolar border. The dorsal edge of the spout is concave and forms an angle of approximately 165° to 170° below the alveolar border. In *T. carolomartini*, the dorsal edge of the spout is straight and aligned with the alveolar border. This condition is also present in *T. natans*. Therefore, the mandibular spout of *T. yaucensis* is unique as far as its length and orientation are concerned.

The ascending ramus is short anteroposteriorly; the distance between the anterior base of the coronoid process and the pos-

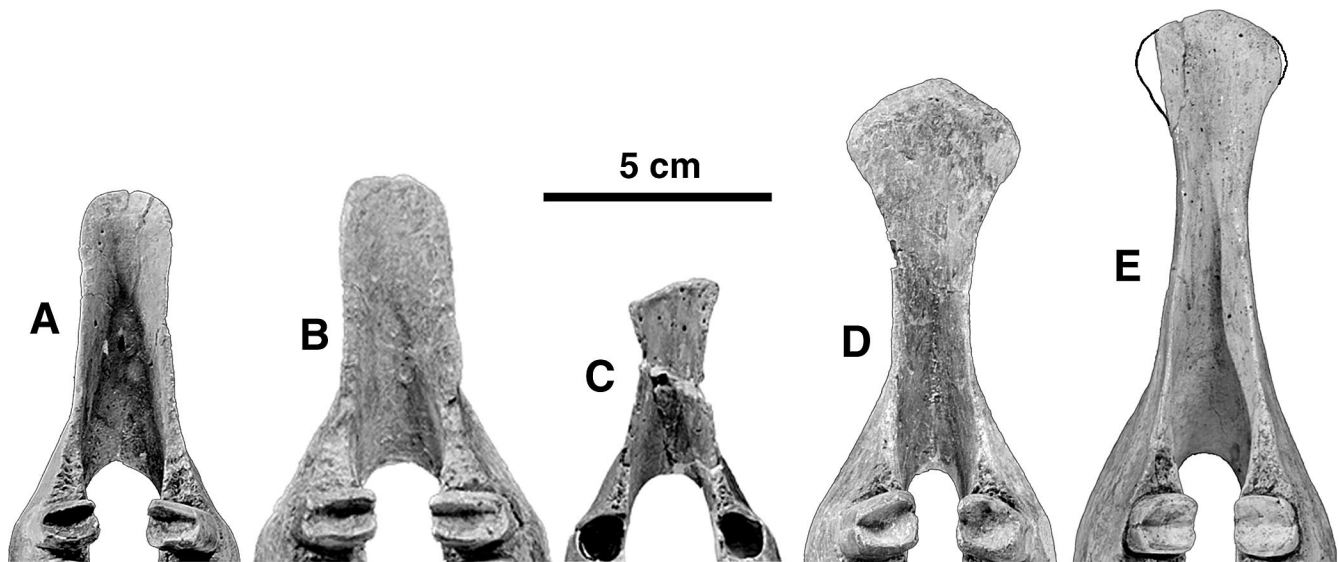


FIGURE 6. Outlines of the mandibular spout in *Thalassocnus*. *T. antiquus* (holotype, MUSM 228) (A); *T. natans* (holotype, MNHN SAS 734) (B); *T. littoralis* (MNHN SAS 736, juvenile) (C); *T. carolomartini* (MNHN SAO 203) (D); *T. yaucensis* (holotype, MUSM 37, restored) (E). Not to scale.

terior base of the condyloid process is shorter than in *T. natans* and *T. carolomartini* (Fig. 5). The condyloid process is small, its neck is short and it faces more dorsally than posteriorly. The condyle is triangular and its anterolateral edge is distinctly shorter than the anteromedial and the posterior, which is the longest. Therefore, the condyle is transversely expanded. Its medial portion is more slender than the lateral and projects medially. The condyloid process is located above the level of the tooth row.

The coronoid process is high and its posterior edge is deeply concave. It is recurved posteriorly and medially at its apex. Its anterior edge is strongly convex and reaches the horizontal ramus at an angle close to 90 degrees.

A portion of the hyoid apparatus is preserved in MUSM 37, but only the right stylohyal is complete (Table 3). It is short and massive relative to that of *T. natans*. Its proximal extremity is triangular-shaped and articulates in the tympanohyal fossa of the skull. The articular process is a rugose condyle. From this condyle the stylohyal extends anteroventrally in a long rod-like process. This process is proportionally shorter and thicker than in *T. natans*. Another small process extends posteroventrally and is approximately as developed as the condyle. The triangular proximal portion of the bone is gently concave laterally. Medially the bone is slightly rugose and do not present any fossa as in *T. natans*. The apex of the anterior process is expanded and bears the articulation for the epihyal.

CONCLUSIONS

As indicated by the features described above, both *T. carolomartini* and *T. yaucensis* have more advanced adaptations to an aquatic lifestyle relative to the other species of *Thalassocnus*. The newest species of aquatic sloth described here enlarges

the breadth of intrageneric variation of the genus *Thalassocnus*, currently represented by five species. The two youngest species of *Thalassocnus* differ significantly in their cranial and postcranial anatomy from the three earlier species, which could justify their placement in a separate genus. However, this would make *Thalassocnus* a paraphyletic taxon (see Muizon et al., 2003). Considering the fact that *Thalassocnus* is apparently an endemic taxon from the southern coast of Peru (and possibly northern Chile), we retain the five species in a single genus reflecting our argument that *Thalassocnus* represents a single evolutionary lineage, extending from the late Miocene (*T. antiquus*) to the late Pliocene (*T. yaucensis*) and illustrates the multiple stages of the adaptation of a terrestrial mammal to an aquatic environment.

On the skull, the most spectacular differences between the youngest two species of *Thalassocnus* and earlier species are in the anterior extension and widening of the premaxillae and in the splayed apex of the mandibular spout. These modifications are clearly related to feeding adaptations, including the development of strong lips. Muizon et al. (2004) provide a functional analysis of the evolution of feeding adaptations in *Thalassocnus*.

The aquatic specializations of the thalassocnines relative to other nothotheres are also present on the postcranial skeleton, although generally less spectacular than those of the skull. The most notable change is on the radius, which is distinctly transversely widened in *T. yaucensis* and approaches the condition of pinnipeds (the radius figured by Muizon et al., 2003:fig. 3E belongs to the holotype of *T. yaucensis*). This is an indication that, as mentioned by Muizon and McDonald (1995), the thalassocnines had some locomotor modifications adapted to facilitate feeding and/or locomotion in an aquatic environment. In

TABLE 3. Measurements of bones of the stylohyal in *Thalassocnus yaucensis*, sp. nov. (MUSM 37). All measurements are in mm. Measurements followed by one decimal measured using digital calipers. Abbreviations as in Table 1.

	Left	Right
L from articular facet for tympanohyal to articular facet for ceratohyal	—	56.2
AP L of proximal end	24.5	25.4

this respect, *T. yaucensis* is the most obviously derived relative to all other species of *Thalassocnus*. A study of the postcranial skeleton of the thalassocnines is currently in progress by the authors.

Despite the many aspects of the anatomy of *Thalassocnus* that are unique, the genus shares many features in common with other nothrotheres that distinguish the group as both monophyletic and distinct from other traditionally recognized families of sloths. The presence of both derived features unique to the nothrotheres and the group's taxonomic diversity including the highly derived thalassocnines justifies the recognition of the family Nothrotheriidae with two subfamilies, Nothrotheriinae and Thalassocniinae.

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LITERATURE CITED

- Alpers, C., and G. Brimhall. 1988. Middle Miocene climatic change in the Atacama Desert, northern Chile: evidence from supergene mineralization at La Escondida. *Bulletin of the Geological Society of America* 100:1640–1656.
- Ameghino, F. 1907. Notas sobre una pequeña colección de huesos de mamíferos procedentes de las grutas calcáreas de Iporanga del Estado de São Paulo-Brazil. *Revista del Museo Paulista* 7:59–124.
- Ameghino, F. 1920. Sur les édentés fossiles de l'Argentine. Examen critique, révision et correction de l'ouvrage de la M. R. Lydekker. *Obras Completas y Correspondencia Científica* 11:447–909.
- Burmeister, H. 1882. *Nothropus priscus*, ein bisher unbekanntes fossils. *Faust'sche Sitzungsberichte der (Königliche-preussischen) Akademie der Wissenschaften, Berlin* 1882(2):613–620.
- Cartelle, C., and G. A. Bohórquez. 1986. Descrição das pre-maxilas de *Nothotherium maquinense* (Lund) Lydekker, 1889. (Edentata, Megalonychidae) e de *Eremotherium laurillardi* (Lund) Cartelle & Bohórquez, 1982. (Edentata, Megatheriidae). *Iheringia Série Geologia* 11:9–14.
- De Iuliis, G. 1994. Relationships of the Megatheriinae, Nothrotheriinae, and Planopsinae: some skeletal characteristics and their importance for phylogeny. *Journal of Vertebrate Paleontology* 14:577–591.
- Engelmann, G. F. 1985. The phylogeny of the Xenarthra; pp. 51–64 in G. G. Montgomery (ed.), *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington, D.C.
- Flynn, J. J., and C. C. Swisher. 1995. Cenozoic South American land mammal ages: correlation to global geochronologies; pp. 317–333 in *Time Scales and Global Stratigraphic Correlation*. SEPM Special Publication 54, Tulsa.
- Gaudin, T. J., and G. De Iuliis. 1999. The Late Miocene sloth *Nothropus priscus*, with comments on the phylogeny of the Nothrotheriidae. *Journal of Vertebrate Paleontology* 19 (3,supplement):46A.
- Hoffstetter, R. 1954. Les gravigrades (Édentés Xénarthres) des cavernes de Lagoa Santa (Minas Gerais, Brésil). *Annales des Sciences Naturelles, Zoologie*, 11^{ème} Série, 16:741–764.
- Hoffstetter, R. 1968. Un gisement de vertébrés tertiaires à Sacaco (Sud-Pérou), témoin néogène d'une migration de faunes australes au long de la côte occidentale sudaméricaine. *Comptes Rendus de l'Académie des Sciences, Série D*, 267:1273–1276.
- Kraglievich, L. 1923. Descripción de dos cráneos y otros restos del género *Pliomorphus* Ameghino procedentes de la formación Enterriana de las barrancas del Río Paraná. *Anales del Museo Nacional de Historia natural de Buenos Aires* 33:1–56.
- Ling, J. K., and M. M. Bryden. 1981. Southern elephant seal—*Mirounga leonina*; pp. 297–327 in S. H. Ridgway and R. Harrison (eds.), *Handbook of Marine Mammals*, Vol. 2. Seals. Academic Press, London, 359 pp.
- Lund, P. W. 1838. Coup d'oeil sur les espèces éteintes de mammifères du Brésil. *Annales des Sciences Naturelles, série 2, (zoologie)* 11: 214–234.
- McDonald, H. G., and C. de Muizon. 2002. The cranial anatomy of *Thalassocnus* (Xenarthra, Mammalia), a derived nothrothere from the Neogene of the Pisco Formation (Peru). *Journal of Vertebrate Paleontology* 22:349–365.
- McKenna, M. C., and S. K. Bell. 1997. *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 631 pp.
- Marocco, R., and C. de Muizon. 1988. Los vertebrados del Neogeno de la costa sur del Perú: ambiente sedimentario y condiciones de fosilización. *Bulletin de l'Institut Français d'Études Andines* 17: 105–117.
- Muizon, C. de. 1981. Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie. Deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocène de Sud-Sacaco. *Travaux de l'Institut Français d'Études Andines*, 22:1–160.
- Muizon, C. de, and T. J. DeVries. 1985. Geology and paleontology of Late Cenozoic marine deposit in the Sacaco area (Peru). *Geologische Rundschau* 74:547–563.
- Muizon, C. de, and H. G. McDonald. 1995. An aquatic sloth from the Pliocene of Peru. *Nature* 375:224–227.
- Muizon, C. de, H. G. McDonald, R. Salas, and M. Urbina. 2003. An early species of the aquatic sloth *Thalassocnus* (Mammalia, Xenarthra) from the late Miocene of Peru. *Journal of Vertebrate Paleontology* 23:886–894.
- Muizon, C. de, H. G. McDonald, R. Salas, and M. Urbina. 2004. The evolution of feeding adaptations of the aquatic sloth *Thalassocnus*. *Journal of Vertebrate Paleontology*. 24:398–410.
- Naples, V. L. 1985. Form and function of the masticatory musculature in the tree sloths, *Bradypus* and *Choloepus*. *Journal of Morphology* 183:25–50.
- Naples, V. L. 1987. Reconstruction of cranial morphology and analysis of function in the Pleistocene ground sloth *Nothotheriops shastensis* (Mammalia, Megatheriidae). *Natural History Museum of Los Angeles County, Contributions to Science* 389:1–21.
- Naples, V. L. 1989. The feeding mechanism in the Pleistocene ground sloth, *Glossotherium*. *Natural History Museum of Los Angeles County, Contributions to Science* 415:1–23.
- Patterson, B., and R. Pascual. 1968. Evolution of mammals on southern continents. *Quarterly Review of Biology* 43:409–451.
- Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America; pp. 247–309 in A. Keast, F. C. Erk, and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*. State University of New York Press, Albany.
- Patterson, B., W. Segall, W. D. Turnbull, and T. J. Gaudin. 1992. The ear region in xenarthrans (=Edentata: Mammalia) Part II. Pilosa (Sloths, Anteaters), Palaeonodons, and a miscellany. *Fieldiana Geology new series* 24:1–79.
- Paula Couto, C. de. 1971. On two small Pleistocene ground-sloths. *Anais de Academia Brasileira de Ciências* 43:499–513.
- Paula Couto, C. de. 1976. The manus of *Nothotheriops shastense* (Sinclair, 1905). *Anais do XXVIII Congresso Brasileiro de Geologia* 2: 166–176.
- Phillips, R. C., S. Wyllie-Escheverria, and T. J. DeVries. 1996. Fossil *Heterozostera tasmanica* from south-central Peru; pp. 369 in J. Kuo, R. C. Phillips, D. J. Walker, and H. Kirkman (eds.), *Seagrass Biology. Proceedings of an International Workshop*, Rottneest, Island, Western Australia, 25–29 January 1996.
- Sclater, P. L., and O. Thomas. 1897. *The Book of Antelopes*, Volume III. R. H. Porter, London, 245 pp.
- Sévrier, M., R. Marocco, and J. Macharé. 1984. Evolution tectonique du piedmont pacifique et ses relations avec la cordillère des Andes du Pérou central et méridional; pp. 49–70 in *Montagnes et Piedmonts*, *Revue géographique des pyrénées et du Sud-Ouest*. Special Issue, Toulouse.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85:1–350.
- Sinclair, W. J. 1905. New mammalian from the Quaternary caves of California. *University of California Publications, Bulletin of the Department of Geology* 4:145–161.
- Stock, C. 1925. Cenozoic gravigrade edentates of western North Amer-

- ica with special reference to the Pleistocene Megalonychinae and Mylodontidae of Rancho La Brea. Carnegie Institution of Washington Publication 331:1–206.
- Todsar, R., A. Clark, and E. Farrar. 1984. Cenozoic polyphase landscape and tectonic evolution of the Cordillera Occidental, Southernmost Peru. *Bulletin of the Geological Society of America* 95:1318–1332.
- Received 14 January 2002; accepted 30 October 2003.