

THE AQUATIC SLOTH *THALASSOCNUS* (MAMMALIA, XENARTHRA) FROM THE LATE MIOCENE OF NORTH-CENTRAL CHILE: BIOGEOGRAPHIC AND ECOLOGICAL IMPLICATIONS

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Sloths are one of the most conspicuous groups of the mammalian fauna of South America. They were widely distributed and extremely diversified in terrestrial environments from the Oligocene to the Pleistocene (Hoffstetter, 1982). Modern sloths are restricted to an arboreal life style in neotropical forest (Mendel, 1981), but many different habits have been inferred for fossil ground sloths. These include arboreality (Pujos et al., 2007), fossoriality (Bargo et al., 2000), and scavenging (Fariña and Blanco, 1996). In addition to these terrestrial habits, an aquatic ecology has been suggested for the nothrotheriid *Thalassocnus* of the late Miocene-Pliocene Pisco Formation in the Sacaco area, Peru (Muizon and McDonald, 1995). *Thalassocnus* remains are found associated with whales, dolphins, seabirds, crocodiles, bony fishes, sharks and rays in sediments corresponding to a nearshore marine environment. (Muizon and DeVries, 1985). Five species of *Thalassocnus* are currently recognized (McDonald and Muizon, 2002; Muizon et al., 2003, 2004a). These include *T. antiquus* (late Miocene), *T. natans* (latest Miocene), *T. littoralis* (early Pliocene), *T. carolomartini* (early late Pliocene), and *T. yaucensis* (late Pliocene). Morphological analysis provides evidence of feeding and locomotor adaptations of the *Thalassocnus* 'lineage' to an aquatic environment (e.g., Muizon et al., 2003, 2004b).

In north-central Chile, the late Miocene marine deposits of the Bahía Inglesa Formation resemble the vertebrate faunal composition, to Pisco Formation (Walsh and Naish, 2002). In 2002, a partial mandible of *Thalassocnus* (SGO.PV 1093) was found in the Bahía Inglesa Formation from the Caldera area (Canto, Yáñez, and Cozzuol, 2002). This record is more than 1600 km south of Sacaco area. It represents the first non-Pisco Formation remains of *Thalassocnus* and provides evidence of a wider and more complex offsetting for the evolution of the genus. Biogeographical and ecological interpretations based on the new data are discussed below, and the discovery of *Thalassocnus* and associated fauna allow us to provide new supporting data for the late Miocene age of the Bahía Inglesa Formation.

The Chilean specimen of *Thalassocnus* sp. (SGO.PV 1093) is housed in the Museo Nacional de Historia Natural, Santiago, Chile. This specimen was compared with *Thalassocnus antiquus* (MUSM 228, holotype), *T. natans* (MNHN SAS 734, holotype; MUSM 433), *T. littoralis* (MUSM 1033; MUSM 223, formerly referred to *T. natans* in Salas et al., 2005), *T. carolomartini* (MNHN SAO 203), and *T. yaucensis* (MUSM 37, holotype;

MUSM 1034). Measurements of SGO-PV 1093 were made to a tenth of millimeter using analog calipers.

Institutional Abbreviations—**MNHN SAO**, Sacaco collection of the Muséum national d'Histoire naturelle, Paris, France; **MNHN SAS**, Sacaco Sur collection of the Muséum national d'Histoire naturelle, Paris, France; **MUSM**, Departamento de Paleontología de Vertebrados, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **SGO.PV**, Colección de Paleontología de Vertebrados del Museo Nacional de Historia Natural, Santiago, Chile.

GEOGRAPHIC SETTING, GEOLOGY, AND AGE

The Bahía Inglesa Formation, in the arid Caldera region, was described by Rojo (1985) and corresponds to a marine transgression on the northern-central coast of Chile (Fig. 1A) during the middle Miocene-early Pliocene (Marquardt et al., 2000). The type section is exposed in the inland of the Bahía Inglesa area and several outcrops dot the surrounding ravines that reach the sea (Fig. 1B). These fossiliferous deposits consist of 42 m of siltstones, fine sands, shelly coquinas, pebble beds, and a phosphatite (Walsh and Hume, 2001). Three stratigraphic sequences can be recognized of which the second is the well-known phosphatite bonebed (Unit 2, of Walsh and Hume, 2001) that bears a broad variety of marine fossil vertebrates (Walsh, 2002). The uppermost sequence is the sand and siltstone Lechero Member (Unit 3 of Walsh and Hume, 2001). SGO.PV 1093 was found in a small section of the Lechero Member located on private property 6 km northeast of the city of Caldera (Fig. 1B). The locality, known as 'Estanques de Copec' (EDC), includes at least one hectare of well exposed outcrops of this member with beds containing shark teeth and cetacean remains.

Different lines of evidence imply either an early Pliocene or late Miocene age for the Lechero Member. Planktonic foraminifera found in this sequence indicate an age of 4.5–2.6 Ma and 4.8 Ma (Ibaraki, 1995; Marchant et al., 2000) whereas the malaco-fauna generally suggests a late Miocene age (Guzman et al., 2000; DeVries, pers. comm., 2007). Based on the presence of the shark *Carcharodon carcharias*, but never *Cosmopolitodus* (= *Isurus*) *hastalis*, the Lechero Member had been constrained to the Pliocene (Long, 1993; Walsh and Hume, 2001; Walsh and Naish, 2002). However, during field work in EDC, one of us (JC) collected some shark teeth belonging to *C. (=I.) hastalis*, which had been shown to be an indication of Miocene horizons in the Pisco Formation (Muizon and DeVries, 1985). Additionally, anatomical characters of the *Thalassocnus* species from Chile

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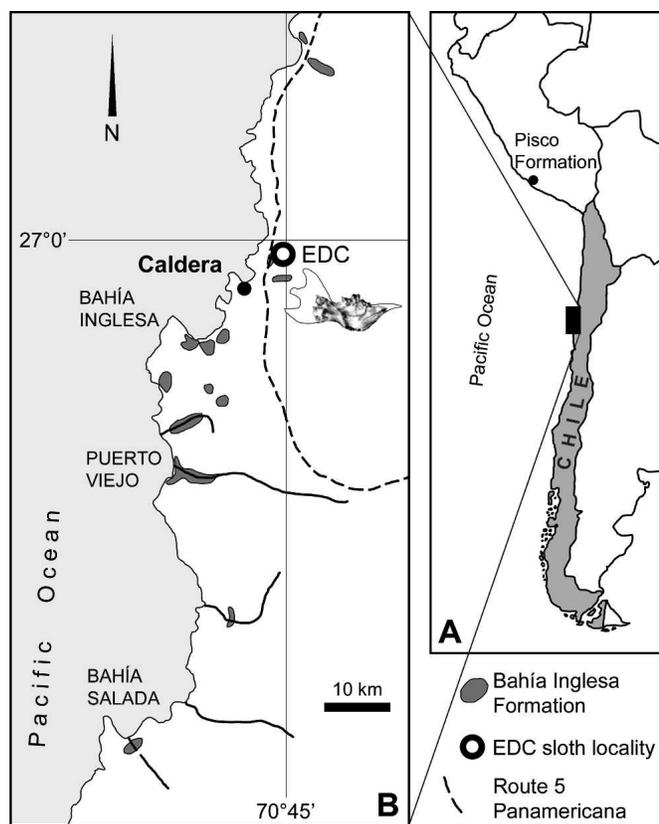


FIGURE 1. **A**, location of the study area in north-central Chile; and **B**, geographic map of the Caldera area showing the outcrops of the Bahía Inglesa Formation and the EDC (Estanques de Copec) sloth locality.

(SGO.PV 1093) fit with the morphology of either *T. antiquus* or *T. natans* (see below), two species known from the late Miocene and latest Miocene, respectively in the Pisco Formation (McDonald and Muizon, 2002; Muizon et al., 2003). Radiometric dates from an ash layer within the Lechero Member provides an $^{40}\text{K}/^{39}\text{Ar}$ age of 7.6 ± 1.3 Ma (late Miocene) (Marquardt et al., 2000) that is consistent with the new shark teeth data and evolutionary stage of the sloth taxon.

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope, 1889
 Suborder PHYLLOPHAGA Owen, 1842
 Superfamily MEGALONYCHOIDEA Simpson, 1931
 Family NOTHROTHERIIDAE Ameghino, 1920
 Subfamily THALASSOCNINAE Muizon et al., 2004a
THALASSOCNUS Muizon and McDonald, 1995
THALASSOCNUS sp.
 (Figs. 2, 4; Table)

Referred Specimen—SGO.PV 1093, partial right mandible with m1–m3 (Fig. 2) from ‘Estanques de Copec’ locality (EDC), coastal area next to N° 5 national route, 6 km northeast to Caldera city, III Region (27°02’S –70°48’W), Chile. The Lechero Member of the Bahía Inglesa Formation, late Miocene to latest Miocene.

Comparative Description—SGO.PV 1093 consists of a right mandibular portion, from the posterior symphysis to the base of the coronoid process. The complete molariform series (m1–m3) is preserved with the occlusal surface of m1 and m3 damaged.

TABLE. Measurements (mm) of the partial mandible of *Thalassocnus* sp. (SGO.PV 1093) from Bahía Inglesa Formation, north-central Chile.

	<i>Thalassocnus</i> sp. SGO.PV 1093
m1 AP length	14.0
m1 MD width	13.1
m2 AP length	11.6
m2 MD width	14.7
m3 AP length	12.6
m3 MD width	13.2
Alveolar length of cheek teeth	43.3
Maximum depth of the horizontal ramus	46.6e
Angle of ventral edge of spout relative to cheek tooth row	~45°

Abbreviations: AP, anteroposterior; e, estimate; m, lower molariform; MD, mesiodistal.

The size of the Chilean material is comparable to the size of *Thalassocnus antiquus* and *T. natans*.

The horizontal ramus is robust and particularly deep below the molariforms. In contrast, it presents an oblique ventral edge anterior to m1 (~45° to horizontal plane) and a pronounced dorsoventral constriction posterior to m3, therefore a marked concavoconvex ventral profile of the horizontal ramus as in *T. antiquus* and *T. natans* (Fig. 3; Muizon et al., 2003). In SGO.PV 1093 the ratio of length of tooth row to maximum depth of the horizontal ramus is ~0.93. In *T. antiquus* (MUSM 228) this ratio is 0.96, whereas in *T. natans* (MUSM 433; MNHN SAS 734) it ranges from 0.95 to 0.99. In *T. carolomartini* (MNHN SAO 203) and *T. yaucensis* (MUSM 37) it is 1.13 and 1.14, respectively (Fig. 3).

The molariforms are square to rectangular in cross section. The median molariform (m2) is clearly rectangular and wider than longer (Fig. 2; Table). Both anterior and posterior transverse crests (i.e., lophids) are high and almost straight. The lophids are separated by a transverse valley. These features are observed in *T. antiquus*, *T. natans*, and in lesser degree in *T. littoralis* (Muizon et al., 2004b).

The base of the coronoid process preserves the posteroexternal foramen of the mandibular canal. The foramen faces dorso-laterally as is observed in *T. antiquus* and *T. natans* (Muizon et al., 2003) while in *T. carolomartini* and *T. yaucensis* it faces anterodorsally (Muizon et al., 2004a).

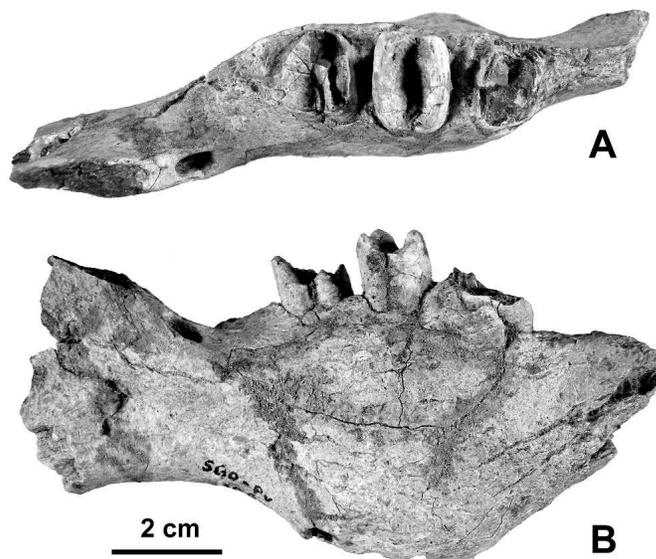


FIGURE 2. Partial right mandible of *Thalassocnus* sp. (SGO.PV 1093). **A**, occlusal view; and **B**, lateral view.

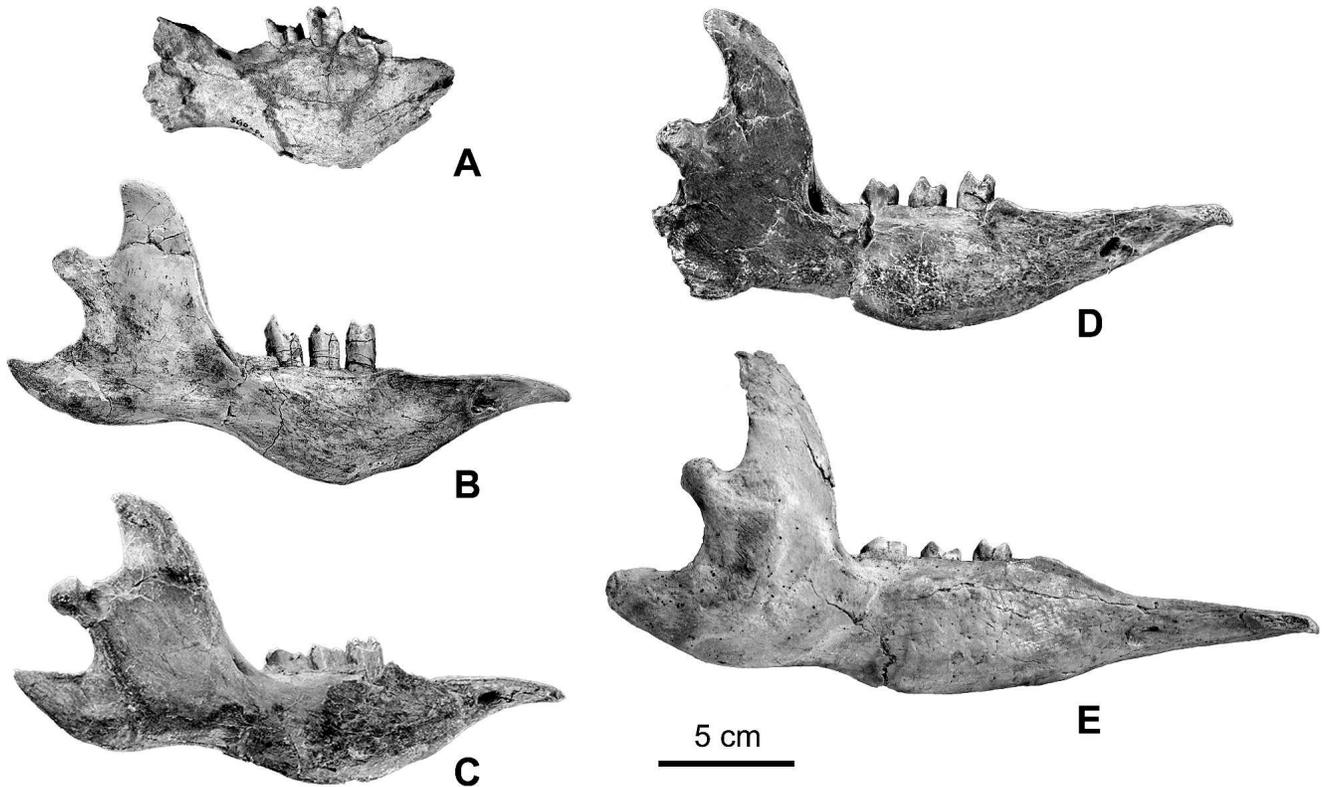


FIGURE 3. Comparative right lateral views of the mandible in *Thalassocnus* sp. from Bahía Inglesa Formation and species of *Thalassocnus* from Pisco Formation. **A**, *Thalassocnus* sp. (SGO.PV 1093); **B**, *T. antiquus* (holotype, MUSM 228); **C**, *T. natans* (holotype, MNHN SAS 734); **D**, *T. carolomartini* (MNHN SAO 203); and **E**, *T. yaucensis* (holotype, MUSM 37).

DISCUSSION

The fossil record of *Thalassocnus* provides unique evidence for the evolution and functional anatomy of a sloth lineage. The five species, recognized from well preserved skulls, mandibles, and postcranial elements from the Pisco Formation of the Sacaco area, had been considered endemic to the southern coast of Peru (e.g., Muizon et al., 2003) and as ranging from late Miocene to late Pliocene age (Muizon et al., 2004a).

The specimen from Bahía Inglesa increases the geographic distribution of *Thalassocnus* by more than 1600 km to the south of previous records. It may still be considered an endemic taxon, but on a more regional scale. Geologic and paleontologic evidence from Sacaco and Caldera indicate climatic and faunistic resemblance during the Miocene-Pliocene span. The forearc sedimentary succession is consistent with an arid to semiarid climate in southern Peru and northern Chile since the middle Miocene (Alpers and Brimhall, 1988) or considerably earlier (Hartley et al., 2005). Climate controls on the Peru-Chile desert (e.g., ancestral Humboldt Current) directly influenced coastal life in the whole area. During the late Miocene-Pliocene, the intertidal and subtidal molluscan fauna from southern Peru and northern Chile is mostly endemic and has a large proportion of species in common (DeVries and Frassinetti, 2003; DeVries, pers. comm., 2007). Among vertebrates, most of the genera of phocids (*Acrophoca*, *Piscophoca*), odontocetes (*Pliopontos*, *Brachydelphis*), marine birds (*Spheniscus*, *Phalacrocorax*, *Sula*), and now *Thalassocnus*, originally recorded in the Pisco deposits (e.g., Muizon, 1981, 1988; Cheneval, 1993; Muizon and McDonald, 1995; Canto, Crovetto, and Covacevich, 2002) have been identified in the Bahía Inglesa Formation (e.g., Walsh and Hume, 2001; Walsh and Naish, 2002). All this evidence suggests

that during the late Miocene-Pliocene in the southern Peru-northern Chile region, there existed a vast coastal area of stable ecological conditions, biogeographic continuity, and closely related evolutionary history.

Advanced anatomical features in *Thalassocnus* have been associated with an aquatic life style (e.g., Muizon et al., 2004b), though this ecological assumption is based mainly on the taphonomy of several articulated specimens found in the Pisco Formation (e.g., Muizon and McDonald, 1995). Sedimentologic data reveals that the Bahía Inglesa Formation corresponds to a shallow marine setting deposited within 10 km of the shore (Marquardt et al., 2000; Walsh 2002). The vertebrate assemblage including whales, dolphins, seals, crocodiles, seabirds, bony fish, sharks, and rays is present in both Pisco and Bahía Inglesa Formations. Taxa traditionally considered terrestrial (other than *Thalassocnus*) are very rare and fragmentary in the former (e.g., Muizon and DeVries, 1985; Salas et al., 2002) and completely absent in the latter formation (Walsh, 2002). Anatomical attributes related to the life style of the Chilean species of *Thalassocnus* cannot be inferred due to the scarcity of available material. However, the occurrence of this sloth in the Bahía Inglesa Formation is further taphonomic evidence of the aquatic affinities proposed for the *Thalassocnus* lineage.

The preserved mandible of *Thalassocnus* from Chile (SGO.PV 1093) is clearly more similar to *T. antiquus* and *T. natans* than any other later species of the genus. They share a marked concavoconvex ventral profile of the horizontal ramus, posteroexternal foramen of the mandibular canal facing dorsolaterally, and m2 rectangular and wider than long. Muizon et al. (2004b) show that the general cross section shape of the median molars (M2, M3, and m2) is useful in the recognition of *Thalassocnus* species. A scatter plot for m2 illustrates the position of SGO.PV

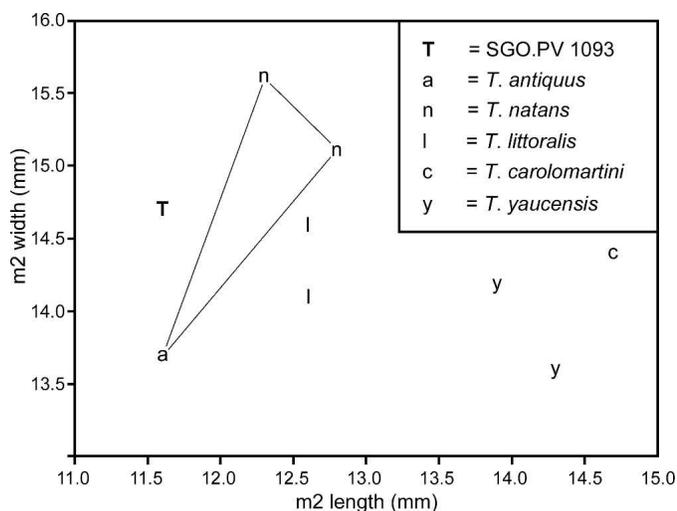


FIGURE 4. Length vs. width scatter plot of lower molar 2 (m2) samples of species of *Thalassocnus* relative to *Thalassocnus* sp. (SGO.PV 1093) from Bahía Inglesa Formation.

1093 relative to the species of *Thalassocnus* described from the Pisco Formation (Fig. 4). It is clearly observed that, from earlier to later species, the width/length ratio of m2 decreases to more equivalent dimensions. SGO.PV 1093 is located closer to the morphospace of *T. antiquus*-*T. natans* than to any other more derived species.

The phylogenetic analysis within the *Thalassocninae* presents two equally parsimonious hypotheses: one favors the existence of a single time-successive lineage, while the other excludes *T. natans* from the lineage due to the presence of some plesiomorphic characters relative to the earlier *T. antiquus* (Muizon et al, 2003) and implies an adaptive radiation of the *Thalassocninae*. Considering the small area of distribution known for *Thalassocnus* and the limited biological resources available along the arid coast of Peru during Late Miocene-Pliocene, Muizon et al. (2003) favored a single time-successive lineage. The Chilean material is insufficient to resolve the phylogeny, but indirectly supports the alternative hypothesis by offering a bigger geographic area with numerous opportunities for the adaptive radiation of the *Thalassocninae*.

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