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Osteology and functional morphology of the hind limb of the marine sloth *Thalassocnus* (Mammalia, Tardigrada)

by

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## ABSTRACT

The anatomy of the skeletal elements of the hind limb of *Thalassocnus* is described. This genus of “ground sloth” comprises five species represented by Neogene specimens from the coast of Peru and Chile, mostly found in the Pisco Formation. The hind limb of the genus *Thalassocnus* as a whole is characterized by a small iliac wing, a gracile femur with well-formed femoral neck, teardrop shaped patella, long and slender tibia, triangular tuber calcis, and proximal development of the lateral process of the Mt V. The comparison of the species of *Thalassocnus* with each other suggests a progressive shift to a particular ecology from the earliest to the latest species of the genus, a conclusion in agreement with those of the studies of craniomandibular, dental, and forelimb gross morphology, and bone internal microstructure. The pedolateral stance, which involves the bearing of the weight on the lateral side of the foot, was practiced by the earliest species of *Thalassocnus*, as was the case for other Megatheria. This stance was apparently forsaken by the late species of the genus in favor of the acquisition of a secondary plantigrady. A plantigrade hind limb may have been more efficient for paddling and for bottom-walking. Additionally, the late species of *Thalassocnus* differ from the early ones in the morphology of the pelvis and the slight overall reduction of the hind limb. This suggests the decrease of the support function of the hind limb of these species when compared to that of the early species of *Thalassocnus*.

Keywords: Aquatic adaptation; hind limb; functional anatomy; marine mammal; Pisco Formation;

*Thalassocnus*; Xenarthra

## INTRODUCTION

Among Tardigrada (Folivora, Phyllophaga, or more commonly sloths), the critical systematic and functional importance of the pes, and more particularly the astragalus, is noteworthy. This is well exemplified by the literature that concerns *Thalassocnus* Muizon and McDonald, 1995. The first mention of *Thalassocnus* material (decades before naming of the genus and first species) attributed it to an undescribed megatheriid (Hoffstetter 1968), mainly based on the morphology of the astragalus. Later systematic studies (including the first formal description) considered *Thalassocnus* as a member of the Nothrotheriidae (Muizon and McDonald 1995; McDonald and Muizon 2002; Muizon et al. 2003, 2004a).

The first morphofunctional analysis of *Thalassocnus* focused on the cranial, mandibular, and dental material (Muizon et al. 2004b). The reconstruction of the feeding habits of *Thalassocnus* concluded that the early species of the genus (*T. antiquus* Muizon et al., 2003, *T. natans* Muizon and McDonald, 1995, and *T. littoralis* McDonald and Muizon, 2002) were partial grazers and that the late ones (*T. carolomartini* McDonald and Muizon, 2002, and *T. yaucensis* Muizon et al., 2004) were more specialized grazers. The second morphofunctional analysis focused on the knee joint, and recognized a sesamoid bone and an ossified meniscus in a sub-complete specimen referred to *Thalassocnus* (Salas et al. 2005). These anatomical features are also found in other sloths, and the presence of these bones is apparently related to the adoption of a particular stance (the pedolateral stance, see below). The study of the internal microstructure of the ribs and long bones revealed an increasing degree of osteosclerosis (and to a lesser extent pachyostosis) in *Thalassocnus*, from its earliest to its latest species (Amson et al. 2014). This was interpreted as an adaptation to buoyancy and trim control, paralleling that of sirenians for instance. Finally, study of the gross anatomy of the forelimb concluded that it was most likely involved in underwater stabilization, bottom-walking, and digging in order to feed on marine vegetation (Amson et al. in press).

The postcranial anatomy of sloths is peculiar in many of its aspects. As was true for the previous morphofunctional analyses, considering these peculiarities is crucial for the recognition of the adaptations of *Thalassocnus*. The present study examines the gross anatomy of the hind limb, which has been, in sloths, a subject of particular interest. This is mainly due to the stance supposedly adopted by most terrestrial sloths (all families except one, megalonychids), which is not one of the classical plantigrade, digitigrade or unguligrade postures. Mylodontids, nothrotheriids, and megatheriids are unique among mammals in using the so-called pedolateral stance (McDonald 2007, 2012). This stance apparently affects the biomechanics of the

whole hind limb, and, as we will see, is of major importance in the functional interpretation of the hind limb of *Thalassocnus* and associated evolutionary changes.

The extremely rich Neogene deposits of the Pisco Formation (Peru) allowed a thorough characterization of the hind limb anatomy of *Thalassocnus*, and the recognition of both inter- and intraspecific variations. This work is part of a series of three publications that endeavors to thoroughly describe and interpret functionally the postcranium of the five species of *Thalassocnus*. The forelimb was treated in a previous publication (Amson et al. in press), and the axial postcranium will be the subject of a subsequent study.

Institutional abbreviations:

**BMNH**, British Museum of Natural History, London, United Kingdom; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **MCL**, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MPC**, Museo Paleontológico de Caldera, Chile; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; **YPM**, Yale Peabody Museum, New Haven, Connecticut, USA.

## MATERIAL AND METHODS

Differences among the five species of *Thalassocnus*, namely *T. antiquus*, *T. natans*, *T. littoralis*, *T. carolomartini*, and *T. yaucensis*, will be discussed only when they are distinctive. Otherwise, and unless indicated, the anatomical descriptions will be applicable to all species. Each species comes from a distinct horizon of the Pisco Formation, each of which has been dated respectively at ca. 8, 7, 6, 5, and 4 Ma (Muizon et al. 2004a; Ehret et al. 2012). For each specimen, all of the sufficiently complete bones were measured. The measurements are presented in a separate table for each bone (except for the pes for which all measurements are gathered in a single common table). An exhaustive list of the material for each species of *Thalassocnus* and each element of the hind limb is given in Online Resource 1. The definitions of the tardigradan clades follow those of Gaudin (2004), except that of the Nothrotheriini, which follows the definition of De Iuliis et al. (2011), and which only comprises *Nothrotheriops* Hoffstetter, 1954, and *Nothrotherium* Lydekker, 1889. Comparisons were made with *Nothrotheriops shastensis* (Sinclair, 1905) (personal observations; Stock 1925;

Lull 1929), *Nothrotherium maquinense* (Lund, 1839) from caves of the Bahia region, Brazil (personal observations; Cartelle and Fonseca, 1983), *Nothrotherium escrivanense* (Reinhardt, 1878) and *Mionothropus cartellei* De Iuliis et al., 2011 (LACM 4609/117533) from the Rio Acre, Brazil (personal observations; De Iuliis et al. 2011). Comparisons with *Hapalops* Ameghino, 1887 (personal observations; Scott 1903-1904) and *Planops martini* Hoffstetter, 1961 (personal observation of casts; Hoffstetter 1961) were also made because these taxa are likely to feature for a good number of their characters the plesiomorphic condition for Megatherioidea. *Megatherium americanum* Cuvier, 1796, is also included in the comparison. More sporadically, the extant giant anteater *Myrmecophaga* Linnaeus, 1758, megalonychids, and mylodontids are mentioned. Myological inferences are based on dissections of various mammals (Miller et al. 1965; Barone 1968).

The five species of *Thalassocnus* were initially described for the most part based on cranial, mandibular, and dental material. They are found in five successive levels of the Pisco Formation. The postcranial material is consistent with this stratigraphic distribution, i.e., the observed variation suggests only one morphotype in each level, which allows referring to early and late species of the genus.

## COMPARATIVE DESCRIPTION

### General size

The specimens comprising the most complete hind limbs are the holotype of *T. natans* (MNHN.F.SAS734) and MUSM 1995, which is referred to *T. carolomartini*. The proximodistal length of the sub-complete, articulated hind limb of the holotype of *T. natans* is roughly 85 cm. A great size range is represented by the specimens of *Thalassocnus*, both inter- and intraspecifically. The larger sample of specimens interpreted as adults is based on the femora (see Table 1). We will hence use the greatest length of this bone, and neglect the possible variation of proportions to compare *Thalassocnus* to other Megatheria. The smallest femur of *Thalassocnus* on which the length can be measured (265 mm) is referred to *T. littoralis*. It is slightly larger than those of the two species of *Nothrotherium*, *N. maquinense* (mean value = 233 mm) or *N. escrivanense* (246 mm; Reinhardt 1878), although in the latter case it should be noted that the specimen corresponds to a young individual and may not have achieved full size. The largest femur of *Thalassocnus* (401 mm) is referred to *T. yaucensis* and is much larger than that of *Planops* Ameghino, 1887 (315 mm; Hoffstetter 1961) or *Mionothropus* De Iuliis et al., 2011 (320 mm), and even larger than some specimens of *Nothrotheriops*. Larger sizes are found in megatheriines.

As suggested by a study of the humeral length (Amson et al. in press), the number of specimens including a femur and referred to *T. littoralis* suggests intraspecific variation, but is too low to document it with statistical significance. A wide range in proximodistal length is observed, from 265 to 401 mm (N=9; Table 1). As with the humerus, three groups seem to be recognized in the sample currently available: over 300 mm long – putatively males; around 280 mm long – putatively females; and specimens that show incomplete epiphyseal closure – immature specimens. This large size range and the possibility of sexual dimorphism make it difficult to evaluate the possibility of size trends from the earliest to the latest species, given the small sample sizes of the other species currently available. However, it can be mentioned that the femur of the holotype of *T. antiquus* is one of the smallest (based on measurements other than proximodistal length, which is unavailable for this specimen; Table 3), and that the largest specimen, an isolated femur found in the Yauca locality (MUSM 434), is referred to *T. yaucensis*. The femur from the Yauca locality (MUSM 434) is roughly 40% larger than that of the holotype of *T. antiquus*. Moreover, the femur of the holotype of *T. yaucensis*, which represents one of the smallest individuals of the genus, was already interpreted as a female by Muizon et al. (2004). A larger sample is needed to document sexual size dimorphism, but the data currently available are compatible with an increase in size when the early species are compared to the late ones, which corroborates the same hypothesis based on humeral length (Amson et al. in press). Moreover, great intraspecific variation is observed, with putatively a small female morphotype and a large male one, which once again was a hypothesis suggested by humeral dimensions.

#### Pelvis

The pelvis is known by sub-complete specimens in *T. littoralis* (Fig. 1a, b). Both *T. antiquus* and *T. carolomartini* are known by one specimen, each of which is limited to an iliac wing with the acetabulum. The pelvis is unknown in *T. natans* and *T. yaucensis*. The ilium differs conspicuously in *Thalassocnus* from that of other extinct sloths in the small size of the wing (Figs. 1a, 2a-c; Table 2). This is especially true when compared to the Nothrotheriini and megatheriids. In *Thalassocnus*, the reduction of the ilium is mostly the result of its weak lateral extension, even when compared to *Hapalops*. Consequently, the (cranial) ventral iliac spine barely protrudes laterally from the level of the lateral border of the acetabulum. Moreover, the wing is clearly reduced on the specimen referred to *T. carolomartini* (MNHN.F.SAO201; Fig. 2c) when compared to that of specimens of earlier species (Fig. 2a, b). This is conspicuous when one compares the dimensions of the acetabulum to the width of the iliac wing. In *Thalassocnus* the angle formed by the anteroposterior axis of the ilium and the vertebral axis (of the sacral vertebra)

is low (Fig. 1b), less than 40°. In other Megatheria, a similar condition is found in *Nothrotherium* (Fig. 3a). In *Nothrotheriops*, this angle is higher (over 45°), and *M. americanum* features an almost right angle (Fig. 3b). In other words, the ilium faces anteroventrally in *Nothrotheriops* and almost only anteriorly in *M. americanum*. A roughly right angle is also present in the Mylodontidae. The ventral surface of the ilium is gently concave on the whole, but has a deep concavity approximately at mid-width, at the level of the centrum of the third sacral vertebra, forming a large area of muscle attachment, probably the origin of the iliacus muscle. The dorsal surface features a faint gluteal line extending posteriorly from the medial edge of the ilium at the level of the caudal edge of the third sacral vertebra, to the level of the fourth, and then turns anteriorly and laterally, demarcating the area of origin of the gluteus medius muscle.

Just anterior to the acetabulum, on the lateral edge of the ilium, is a tuberosity, probably homologous to the iliopectineal eminence. This structure probably received the origin of the rectus femoris muscle (Fig. 2a-c). This tuberosity is larger in *T. carolomartini* (MNHN.F.SAO201; Figs. 2c, 4) than in the earlier species, *T. antiquus* and *T. littoralis* (Fig. 2a, b). In the Nothrotheriini, this tuberosity is less conspicuous and positioned more anteriorly, i.e., anterior to the midlength of the wing.

The acetabulum is ovoid in outline in lateral view, the major axis being anteroposterior (Fig. 4). The acetabular notch is wide and forms the ventral edge of a well-elevated ischiatic cornu. The acetabulum of *Thalassocnus* differs from that of *M. americanum*, *Planops*, and *Nothrotherium* (and probably most other Megatheria) in having a reduced pubic cornu, i.e., its posterior edge reaches just posterior to the midlength (anteroposterior) of the whole acetabulum. Therefore, in *Thalassocnus* there is no deep notch between the posterior edges of the two cornua visible in posterior view of the acetabulum as there is in the Nothrotheriini. *Thalassocnus carolomartini* differs from the earlier species (*T. antiquus* and *T. littoralis*; Fig. 2a, b) in featuring, in dorsal view, a more (medially) concave dorsal border of the acetabulum. In *T. carolomartini*, the ventral border of the acetabulum is therefore visible in anterodorsal view, i.e., a view normal to the plane formed by the iliac wing (MNHN.F.SAO201, Fig. 2c).

The sacro-ischiatic fossa is subcircular. The ischiatic tuberosity is robust, triangular, located on the posterodorsal end of the pelvis, and appears relatively more developed than that of other Megatheria. Although it is known only from fragmentary specimens, it can be mentioned that the ischium is anteroposteriorly short, being only slightly longer than the acetabulum.



## Femur

The femur of all species of *Thalassocnus* is known by complete specimens, except for *T. antiquus* for which it is known only by a partial left femur (lacking the proximal epiphysis and the lateral epicondyle) and the right head of the same specimen (the holotype, MUSM 228). A femur supposedly of *T. natans* was briefly described in Muizon and McDonald (1995), but the specimen on which this description is based (MNHN.F.SAS40) is here referred to *T. littoralis*. One of the major and most obvious characteristics of the femur is its relative slenderness and narrowness when compared to that of the other Megatheria (Tables 3, 4; Figs. 5-9). The femur of *Thalassocnus* is even slightly narrower (relative to its length) and less flattened anteroposteriorly than that of *Hapalops*. As in *Hapalops*, *Nothrotherium*, and *Mionothropus*, the mediolateral widths of the proximal and distal ends are about equal. This condition differs from that of *Nothrotheriops*, in which the distal extremity of the bone is much wider than the proximal one (which reflects the greater development of the lateral epicondyle). The proximal end is rotated relative to the long axis of the femur so that the head is positioned anterior to the greater trochanter and the diaphysis is bent, i.e., strongly concave anteriorly and convex posteriorly. While a similar proximal torsion occurs in *Hapalops*, *M. americanum*, the Nothrotheriini, and *Mionothropus* (although less conspicuously in *Hapalops*), it is never associated with the marked anteroposterior bending of the femur observed in *Thalassocnus* in medial (Fig. 8) or lateral (Fig. 9) view.

The head is hemispherical but, correlatively to the acetabular morphology, it is slightly elongated anteroposteriorly. In *M. americanum*, it is less markedly elongated. In *Hapalops* and other nothrotheriids, it is almost perfectly hemispherical. The fovea capitis is a deep notch interrupting the posteromedial edge of the head (Figs. 7, 8). Within the foveal notch there may be a variable number of foramina present. The fovea is triangular, because it widens posteriorly and distally. In all other nothrotheriids and non-megatheriid megatherioids, the fovea is a depression much smaller and shallower than in *Thalassocnus*, located posteromedially within the articular surface of the head and not open posterodistally. This is the general mammalian condition (Lessertisseur and Saban 1967: 879). In *M. americanum* the fovea is similarly located but relatively much shallower (Owen 1858). In this respect *Thalassocnus* more closely resembles mylodontids (Owen 1842) than any other more closely related taxa. In *T. natans* and *T. littoralis* (no data for *T. antiquus*; Fig. 5b, c), the proximal apex of the head is located slightly more proximal than that of the greater trochanter. In *T. carolomartini* and *T. yaucensis* both have approximately the same proximal extension (Figs. 5d, 6).

The femur of *Thalassocnus* differs from that of other extinct sloths in featuring a well-developed and distinct neck. An approaching condition is found, although less pronounced, in *Myrmecophaga*. In *Thalassocnus* the head and greater trochanter are separated by a deep U-shaped notch (Fig. 5). A somewhat similar notch is found in *Megalocnus* Leidy, 1868 (Matthew and Paula Couto 1959), but no neck is present as in *Thalassocnus*. The distinct constriction occurring between the head and the shaft emphasizes the presence of the neck. The proximolateral side of the neck is deeply excavated and the lateral edge of the articular surface of the head is at a marked angle with the lateral side of the neck.

The greater trochanter is slightly shallower (anteroposteriorly) than the head (Fig. 9). This condition resembles that of *Hapalops* and *Nothrotherium* but differs from that of *Nothrotheriops* and *Mionothropus*, in which the greater trochanter is markedly shallower than the head. In *M. americanum* the greater trochanter is deeper than the head. In *Thalassocnus*, the greater trochanter is somewhat pointed proximally.

One of the main features of *Thalassocnus* that distinguishes this genus from *Hapalops* and other Megatheria is the third trochanter. In *Thalassocnus* the third trochanter proximally forms a continuous ridge with the greater trochanter (Figs. 5, 7). The joining of the third trochanter and greater trochanter into a single crest resembles to the condition found in the Cuban megalonychid *Megalocnus*. However, in *Thalassocnus* the junction of the two trochanters is still perceivable due to a concavity that is especially conspicuous in anterior view (Fig. 5). In *Hapalops* and *Nothrotherium*, the third trochanter remains distinct, while in *Nothrotheriops* and *Planops* it forms distally a continuous ridge with the lateral epicondyle. A somewhat intermediate condition is found in *Mionothropus*. In *M. americanum* and myrmecophagids the whole proximodistal length of the femur is marked by a crest continuous from the greater trochanter to the lateral epicondyle. In *Thalassocnus*, the combined third trochanter and greater trochanter ridge is thickened anteroposteriorly, with the anterior margin expanded to form a narrow crest. This crest extends proximomedially onto the anterior edge of the greater trochanter. Additionally, the lateral side of the ridge formed by the third trochanter and greater trochanter is marked on all specimens by conspicuous muscle scars.

The trochanteric fossa is large and deep (Fig. 7), as is generally the case in extinct sloths, but differing from the shallow fossa of *M. americanum*. The lesser trochanter is a small process on the medial side of the diaphysis (Fig. 8). As in other Megatheria, it is positioned a short distance distal to the head. This condition differs from that of *Hapalops* in which the lesser trochanter is positioned more proximally. In *Thalassocnus* this trochanter does not protrude medially as much as in *Hapalops* and (to a lesser extent) *Nothrotherium*, and resembles that of *Nothrotheriops* and *Mionothropus*.

Although narrower anteroposteriorly than mediolaterally, the diaphysis does not show the anteroposterior compression present in other Megatheria but instead is oval in cross-section. The anterior surface of the diaphysis medial to the crest formed by the greater and third trochanters is marked by a large fossa (probably for the origin of the vastus lateralis muscle; Fig. 5). The proximomedial border of this fossa is limited medially by a rugose ridge. This ridge is salient and extends approximately up to the level of the lesser trochanter (except for one specimen, MNHN.F.SAS42, on which it extends up to the third trochanter). On some specimens, medial to this second line, another ridge is present (probably the origin of the vastus medialis muscle). This ridge runs distally on the diaphysis from the notch separating the head from the greater trochanter. The crest formed by the greater and third trochanters and the two ridges probably delimit three elements of the quadriceps femoris muscle (vastus lateralis, vastus intermedius, and vastus medialis muscles). In *Nothrotherium*, these lines are inconspicuous, even on mature specimens. In *Thalassocnus*, because of the proximal position of the third trochanter and the mediolateral narrowing of the distal part of the diaphysis, there is a proximal restriction of the origin of the vastus lateralis and intermedius muscles.

As usual in gravigrades the distal end is widest across the epicondyles and then narrows distally. Both epicondyles conspicuously protrude medially and laterally. The holotype of *T. natans* differs from all other specimens of *Thalassocnus* in the great development of the lateral epicondyle (Fig. 10; no data for *T. antiquus*). From each epicondyle a narrow and sharp crest extends proximally on the edges of the diaphysis, probably for the origin of the gastrocnemius lateralis and medialis muscles. The posterior side of each crest is excavated and forms a distinct fossa just proximal to each condyle (Fig. 7). The medial fossa is deeper in all specimens and may have been the location of the origin of the semimembranosus muscle. The medial crest is a very fine lamina in *T. natans* and *T. littoralis*, hence often not preserved. This condition differs from that of *T. carolomartini* in which this crest is much more robust (no data for *T. antiquus* and *T. yaucensis*). Both crests are developed to a lesser extent than in *Hapalops* and other Megatheria (and may even be absent). Distal to the lateral epicondyle, two fossae are positioned anteroposteriorly to one another on the lateral side of the distal epiphysis, and probably reflect the origins of the popliteus and extensor digitorum longus muscles.

The femoral trochlea forms a continuous articular surface with both condyles (Figs. 10, 11), contrary to the condition of the Nothrotheriini and *Pronothrotherium* Ameghino, 1907, in which the three articular surfaces are distinct, or that of *Mionothropus* in which the lateral condyle is separated from the patellar surface but the medial condyle abuts anteriorly the patellar surface (De Iuliis et al. 2011: text-fig. 17). In this respect *Thalassocnus*

approaches the condition of *Hapalops* (contra Stock 1925) and *Planops*, but differs from that found in *M. americanum* in which the patellar surface is reduced to the anterior continuation of the lateral condyle. In *T. carolomartini* and *T. yaucensis* (Fig. 10d, e), the junction between the patellar surface and the medial condyle is narrower than that of the earlier species, due to a notch extending medially from the intercondylar fossa onto the articular surface, probably indicating a large medial (posterior) cruciate ligament. A similar morphology is found in *Planops*. In *T. antiquus* and *T. natans* (Figs. 10a, b, 11), the medial edge of the patellar surface forms an elevated crest (medial trochlear ridge), more elevated than that of *Hapalops*, and approaching the condition of *Mionothropus* or *Planops*. It is less elevated in the Nothrotheriini (however in *Nothrotherium* the whole patellar facet is inclined laterally). The patellar surface is therefore, in the two earliest species of *Thalassocnus*, clearly asymmetrical and more strongly concave than in *Hapalops* and the Nothrotheriini. The medial trochlear ridge is lower and the patellar surface shallower in *T. littoralis* (Fig. 10c). It is even lower in *T. carolomartini* and *T. yaucensis* (Fig. 10d, e), in which the medial and lateral edges have almost the same degree of anterior extension, forming an almost symmetrical patellar surface, especially in the latest species. To quantify the development of the medial trochlear ridge, we can compare the anteroposterior depth of its part located anterior to the level of the lateral trochlear ridge to the depth of the distal epiphysis at the level of the lateral trochlear ridge (Fig. 11). In *T. antiquus*, this ratio is lower than that of *Mionothropus* (Table 5). The ratio of *T. natans* is slightly lower, being intermediate between that of *Nothrotherium* and that of *Nothrotheriops*. That of *T. littoralis* is lower than those of the taxa just mentioned, and is close to the condition of *Hapalops*. *Thalassocnus carolomartini* features a ratio that is even slightly lower. Finally, *T. yaucensis* features the lowest ratio. The medial condyle is slightly wider than the lateral and its articular surface is regularly convex posteriorly. In *T. antiquus* and *T. natans*, in anterior view, the lateral condyle reaches further distally than the medial. In *T. littoralis*, the condyles either extend to the same distance, or the lateral extends slightly distally. In *T. carolomartini* and *T. yaucensis*, the condyles extend distally to the same distance. This results in a modification of the bicondylar angle among the species of *Thalassocnus* (see Discussion). The medial condyle projects further posteriorly than the lateral. A medial condyle positioned well posteriorly is found in *Hapalops*, *Mionothropus*, and the Nothrotheriini, while condyles aligned almost transversally are found in *M. americanum*; an intermediate condition is present in *Planops*. The intercondylar notch is deeper and narrower than in the other Megatheria, more resembling that of *Hapalops*. As in *Hapalops*, *M. americanum*, *Nothrotheriops*, *Mionothropus*, and *Choloepus* Illiger, 1811 (and probably present in most sloths), a small articular facet lies proximolateral to the posterior side of the lateral condyle. In *Nothrotherium*, it appears to be present but is located more laterally. This probably articulates

with the cyamo-fabella (fusion of knee sesamoids cyamella and lateral fabella, see Salas et al. 2005 and hereafter) when the knee joint is flexed.

The proportions of the femur to the rest of the skeleton are of interest in *Thalassocnus*. In *T. natans* the proximodistal length of the femur is more than 20% greater than that of the humerus (Table 6). On the only specimen referred to *T. carolomartini* that includes both complete femur and humerus (MUSM 1995), the femur is only slightly longer (9%) than the humerus. *Thalassocnus littoralis* is represented by specimens in which the ratio between the two bones ranges from 1.09 to 1.19. Other Megatheria show various ratio values. When comparing the width at the epicondyles of the femur to the width at the proximal tuberosities of the humerus (Table 7), we find that *T. littoralis* features a slightly lower ratio than that of *T. natans*, while the ratio of *T. carolomartini* is lower than that of *T. littoralis* and that of *T. yaucensis* is in turn lower than that of *T. carolomartini*. Other Megatheria feature ratios that are similar to or greater than that of *T. natans*. The comparison of the greatest proximodistal length of the femur to the skull (length from anterior side of M1 to posterior side of M4) or mandible (maximal depth of the horizontal ramus) reveals similar observations: the relative length of the femur is slightly smaller in *T. littoralis* when compared to *T. natans*; it is even smaller in *T. carolomartini* and *T. yaucensis* (Table 8). Other nothrotheres feature ratios that are either close to those of the early species of *Thalassocnus* or slightly lower, but they never reach the lowest ratios found in *T. carolomartini* and *T. yaucensis*, which indicates the relatively smaller femur found in these late species of *Thalassocnus* (even though the overall body size is probably greater in these species, see above).

#### Patella

The patella is known in all species of *Thalassocnus* except for *T. carolomartini* (Table 9). The patella of *Thalassocnus* is readily distinguishable from that of *Hapalops* and other Megatheria by the distal tapering of the apex. This gives to the bone a teardrop shape in anterior or posterior view with a mediolaterally-expanded proximal end (Fig. 12). In posterior (femoral) view (Fig. 12e-h), the proximal width of the apex is narrower than the distal width of the femoral facet. In *Hapalops* and other Megatheria, these widths are approximately of the same size. While in most Megatheria and *Hapalops* the proximodistal length of the apex is approximately equal to that of the femoral facet (roughly two-thirds the size in the Nothrotheriini) or even longer in *Mionothropus* (undescribed left patella of the holotype), it is shorter in *Thalassocnus*. Although the length of the apex seems subject to intraspecific variation, it appears to be reduced in the species of the genus later than *T. antiquus* (Table 10). Moreover the apex is

conspicuously bent posteriorly in *T. antiquus*, its distal tip being located well posterior to the level of the femoral facet (Fig. 12i). This is not the case in the other species, in which the apex is rectilinear (Fig. 12j-l).

The proximal end of the patella features a rounded tuberosity occupying the lateral half of the bone. A similarly-located tuberosity is found in the mylodontid *Lestodon* Gervais, 1855, and other nothrotheriids. This morphology differs from that of *Hapalops* in which a lateral and a medial groove are present (De Iuliis et al. 2011).

Correlated with the patellar surface of the femur, the articular surface for the femur is convex mediolaterally, and only slightly concave proximodistally. This facet can therefore be divided into a medial and a lateral surface that are at an angle to each other and slope anteriorly from a median ridge (Fig. 12e-h). The medial surface is mediolaterally wider but proximodistally shorter than the lateral. Therefore, the proximal edge of the lateral surface of the facet is more extended proximally, which is the opposite condition to that of *Nothrotheriops* and *Mionothropus*. In *Nothrotherium*, the facet is subcircular. In *T. yaucensis* (no data for *T. carolomartini*, but probably the same morphology, based on the similarity of the femur in the two species), the medial surface is reduced medially, corresponding to the different morphology of the femur described in the later species. A similar observation can be made concerning the angle between the medial and lateral surfaces, which is reduced in the late species of *Thalassocnus*, corresponding to the reduction of the medial trochlear ridge of the femur. The femoral facet of the later species is therefore more symmetrical than that of the early species.

In *T. natans* and *T. littoralis*, the length of the facet for the femur represents roughly 80% of the maximum depth of the horizontal ramus of the mandible (Table 11). In *T. yaucensis*, the patella is relatively smaller, this percentage being close to 70%. A relatively smaller patella is hence found in the latest species of *Thalassocnus* when they are compared to the early ones (no data for *T. carolomartini*). *Thalassocnus antiquus* features a slightly lower percentage than that of *T. natans* and *T. littoralis*, which is not in agreement with the previous statement. However, the ratio of the width of the facet for the femur to the same mandibular measurement is almost identical for *T. antiquus* and *T. natans*, and lower in *T. yaucensis*. This suggests that the patella is indeed relatively smaller in the latest species of *Thalassocnus*, and that *T. antiquus* features a facet for the femur that is wider than long.

## Tibia

The tibia is known for all species of *Thalassocnus* (Table 12). Compared to other Megatheria, the tibia of *Thalassocnus* is unusual in its slenderness and its relatively greater length, being almost as long as the femur. The general shape more closely resembles that of *Hapalops* than that of any other Megatheria (Figs. 13, 14). In *Hapalops*

and other Megatheria, the tibia is approximately three-fourths as long as the femur (proximodistal length taken at the greater trochanter; Table 13). Such a proportion was already found as common in “ground sloths” by Muizon and McDonald (1995). In *Thalassocnus*, the length of the tibia is roughly 0.9 that of the femur. Such a proportion can be found in *Myrmecophaga* for instance. The proximal end is mediolaterally wider than the distal end, with the shaft in between the two ends narrower both mediolaterally and anteroposteriorly.

The proximal medial articular surface is oval in outline (Fig. 15b-d), being longer anteroposteriorly than mediolaterally except in *T. antiquus* in which it is more circular (Fig. 15a). It is weakly concave in *T. antiquus*, being reminiscent of that of *Hapalops*, but is deeper in the later species of *Thalassocnus*. The intercondylar eminence is located at the anterolateral corner of the medial condyle so that part of the articular surface extends on to its medial side. In *T. antiquus* (Fig. 13a), as in *Hapalops* and *Nothrotherium* (and *Myrmecophaga*), it is high and forms a vertical continuation of the medial articular surface (in *Nothrotheriops*, the eminence is well developed but does not protrude much due to the proximal position of the lateral articular surface). This condition differs from that found in the later species of *Thalassocnus* (and other Megatheria), in which it is lower (Fig. 13b-d). The lateral side of the intercondylar eminence is convex and unusually smooth (Fig. 15). It appears to be an articular surface. A medial ossified meniscus hence may have been present, based on the facts that a medial one has already been described (see Salas et al. 2005 and below) and that both lateral and medial ossified menisci are present in *Choloepus* (Lessertisseur and Saban 1967: fig. 667). If this facet is indeed for the medial meniscus, it would have an unusual lateral location. As in *Hapalops* or *Planops*, there is in *Thalassocnus* only a narrow groove separating the two condylar surfaces (Fig. 15) in contrast to the wide gap between the two surfaces present in the Nothrotheriini, *Mionothropus*, or *M. americanum*. Unlike most sloths, in which the lateral condyle is shifted laterally and not positioned directly over the shaft of the tibia, the lateral condyle in *Thalassocnus* is positioned closer to the midline of the bone and is supported by the shaft almost to the same extent as the medial condyle. The proximal lateral articular surface is flat anteroposteriorly. In *T. antiquus* and *T. natans*, this surface is slightly concave mediolaterally, due to an elevation on the anteromedial corner of the surface. In the other species of the genus, this elevation is weakly developed, which causes the lateral articular surface to be roughly flat. The lateral articular surface differs from that of *Hapalops* and other Megatheria (except for *M. americanum*) in being positioned more anteriorly, i.e., its anterior edge is at the same level as that of the proximal medial facet. Moreover, the anterior end of this facet is set at a slight angle from the rest of it, facing more anteriorly. This reflects the articular surface for the lateral ossified meniscus (Fig. 15; see Salas et al. 2005). In anterior view (Fig. 13), the lateral condyle is positioned slightly more proximally than the medial. It is

triangular in outline with the posterior margin much wider than the anterior. Extending obliquely from the posterolateral margin of the lateral condyle is the articular surface for the cyamo-fabella (Fig. 15). Its articular surface is convex and continuous with that of the lateral condyle. The proximal articular surface for the fibula is an elongate oval along the posterodistal edge of the lateral condyle. It meets the articular surface for the cyamo-fabella at an acute angle, but the two facets do not connect. Anterior to the proximal articular surfaces, the bone has an irregular surface for the tendinous attachment of the patella (Fig. 13). The tibial tuberosity is very different from that of *Hapalops* in being not prominent, short proximodistally, but wide mediolaterally. Moreover, the tibial tuberosity has a more medial location, being approximately at mid-width of the bone, which also departs from that of *Hapalops* and other nothrotheriids. Moreover, in *T. carolomartini* and *T. yaucensis*, the tibial tuberosity does not overhang laterally, and hence does not form a small tibial fossa for the origin for the tibialis anterior muscle as in *T. natans* and *T. littoralis* (no data for *T. antiquus*). In *T. natans* (no data for *T. antiquus*), a small tuberosity marks the posterior margin of this fossa. This tuberosity is reduced or absent in the later species of the genus. In all species of *Thalassocnus*, the tibial fossa is much shorter proximodistally, anteroposteriorly narrower and shallower than that of *Hapalops*. In *Thalassocnus*, as in *Hapalops*, the tibial tuberosity is more developed than in the other Megatheria, which gives to the proximal extremity of the bone a more triangular outline than in the latter. The epiphysis hence appears less compressed anteroposteriorly than in the other Megatheria.

The diaphysis differs conspicuously from that of most Megatheria in being subcircular in cross-section, and not well-flattened anteroposteriorly as in the latter. In *Thalassocnus* it is even more rod-like than in *Hapalops* and *Mionthropus*, the shaft being only slightly compressed anteroposteriorly in its distal third. This compression is stronger in *T. littoralis* and *T. carolomartini* than in *T. natans*, and is associated with a flattening of the anterior side of the distal shaft. This is even more conspicuous in *T. yaucensis*. A subcircular diaphysis is also found in *Planops*, but this genus lacks the proximodistal elongation, which is responsible for the characteristic slenderness of the tibia of *Thalassocnus*. The anteromedial border of the shaft is marked by a rugose line reflecting muscular attachment. At approximately the proximal third of its length, this line forms a small tuberosity (Fig. 14). A similar tuberosity is found in *Hapalops* but is located more posteriorly. In *Planops* and *Mionthropus*, this tuberosity is more proximal. De Iuliis et al. (2011) inferred that this tuberosity was for the semimembranosus muscle. In *Nothrotheriops* and *M. americanum* (and to a lesser extent *Nothrotherium*), the whole proximodistal length of the anteromedial border of the shaft is marked by a strong rugose line. Just distal to the proximal epiphysis, on the posterior side of the shaft, a shallow fossa is present, probably for the insertion of the popliteal muscle (Fig. 14). Much less excavated than that of



*Hapalops* and the Nothrotheriini, it is even shallower in the species of *Thalassocnus* later than *T. natans* (no data for *T. antiquus*), approaching the condition of *Planops*.

The distal epiphysis is slightly wider mediolaterally than deep anteroposteriorly. The medial side bears three tendinal grooves that extend obliquely from posteroproximal to anterodistal (Fig. 14). The central groove is on a raised tuberosity in *T. antiquus*. This is reminiscent of *Hapalops* and the Nothrotheriini, but this tuberosity is reduced in the later species of *Thalassocnus*. The grooves positioned anterior and posterior to the tuberosity are less pronounced. A third ridge, very low, is located anterior to the others. In some specimens referred to *T. littoralis*, a roughened strip extends proximally from the posterior ridge. The anteriormost groove is probably for the tendon of the tibialis caudalis muscle, the middle groove is for the tendon of the flexor digitorum longus muscle, and the tendon of the flexor hallucis longus muscle passes through the posterior groove. This last groove is bounded laterally by a distal protrusion of the posterodistal edge of the epiphysis. While a similar arrangement of the tendinal grooves is present in *Hapalops* and other Megatheria (except for Megatheriinae), in these taxa the two most posterior grooves are much deeper, due to the size of the two most posterior ridges being clearly larger than in *Thalassocnus*. In *Thalassocnus*, the posterior ridge is low and rectilinear, while in *Hapalops* and other Megatheria (except for Megatheriinae) this ridge usually forms a prominent process and extends posteromedially from the diaphysis to form a hook around the groove for the flexor hallucis longus muscle.

The articular surface for the astragalus is composed of two concavities separated by a median ridge (Fig. 16). In all species of *Thalassocnus* except *T. yaucensis* (Fig. 16a-d), this median ridge is well elevated along the entire anteroposterior depth of the epiphysis, as in *M. americanum*. This condition conspicuously differs from that of *Hapalops*, *Planops*, and the other nothrotheriids, in which this ridge is restricted to the anterior half or two-thirds of the bone. However, the astragalar facet of *T. yaucensis* clearly differs from that of the earlier species in featuring a lower median ridge (Fig. 16e). The medial articular surface, for the odontoid facet of the astragalus, is smaller than the other one, roughly circular, and markedly concave. The lateral surface, for the discoid facet of the astragalus, is an elongate crescent with the posterior part curving medially. It partially extends posterior to the medial facet. A similar condition is found in *Nothrotheriops* and the Megatheriidae, and differs from that of *Hapalops* and *Nothrotherium* in which the surfaces are less separated and the medial one is less circular and less concave. Another important feature of the medial facet is its orientation relative to the shaft, which reflects the orientation of the odontoid process of the astragalus relative to the tibia. In *Hapalops* (in which the astragalar facets are weakly separated), the medial facet is directed medially, and only slightly proximally. A very similar condition is found in the

Nothrotheriini. In *Planops*, the facet is directed more proximally, but the main direction is still the mediolateral one. In the species of *Thalassocnus* earlier than *T. yaucensis* and in *M. americanum*, the medial facet is directed more proximally, forming an angle less than 45° with the long axis of the shaft. The most extreme condition is seen in mylodontids such as *Lestodon*, in which this facet is almost completely directed proximally. In *T. yaucensis* the facet is directed more medially, this angle reaching 60°. The lateral astragalar facet forms a continuous articular surface with the facet for the fibula, but both facets are separated from each other by a low ridge. The distal articular surface for the fibula is small, semi-elliptical, and confined to the anterior half or two-thirds of the distal epiphysis. In *T. antiquus*, *T. natans*, *Hapalops*, and the Nothrotheriini (no data for other Nothrotheriinae), the fibular facet faces mainly distally, and only slightly laterally. On the other hand, in *T. littoralis* and *T. carolomartini*, as in *Planops*, it faces more laterally. In *T. yaucensis*, the orientation of the bone is similar to that of *T. littoralis* and *T. carolomartini*, but the facet is either reduced or absent, and the whole area features a roughened surface with small fossae.

Just proximal to the surface for the odontoid facet, on the anteromedial side of the bone, some specimens of *Thalassocnus* show a small smooth surface. This convex surface is apparently of articular nature, and may have been for an undescribed sesamoid.

As for the femur and patella, the tibia is smaller in *T. yaucensis* than in *T. natans* (as evidenced by the width at the distal epiphysis compared to the depth of the horizontal ramus of the mandible, which were not available for the other species; Table 14). *Nothrotherium* features a relatively larger tibia than *T. natans*.

As already mentioned by Muizon et al. (2004b), two fractured tibiae and fibulae featuring bony callus (therefore healed) were recovered.

#### Cyamo-fabella

The cyamo-fabella is preserved in the holotype of *T. natans* (MNHN.F.SAS734) and several specimens referred to *T. littoralis* (Table 15). This sesamoid of the knee was described by Salas et al. (2005). Because additional specimens were available for this study, some details will be added. We acknowledge the articular position described by the previous authors (see Figs. 1 and 3 of Salas et al. 2005). However, we have chosen different terms of orientation, for clarity's sake. We will refer to the side bearing the facet for the tibia as anterior (and not ventral), and the side bearing the posterior sulcus described by Salas et al. (2005) as distal. It has been observed that this element is subject to intraspecific variation in shape (such variation is well exemplified by the specimens of *Nothrotheriops* in the LACM collection), as well as intra-individual variation (as shown by the different size of the right and left cyamo-

fabellae of the specimen MNHN.F.SAS53). In the holotype of *T. natans*, the body features two sulci (Fig. 17a). The first, described by Salas et al. (2005), extends from the anterodorsal side to the middle of the distal side of the bone. It is bounded medially and laterally by two distinct processes. These processes are fused on two specimens referred to *T. littoralis* (MNHN.F.SAS53, MNHN.F.SAS800), this first sulcus hence being almost absent (Fig. 17b). This morphology is more reminiscent of that of *Megatherium urbinai* Pujos and Salas, 2004 (Salas et al. 2005), which lacks this sulcus. The second sulcus extends mediolaterally on the distal side, just posterior to the tibial facet. In the holotype of *T. natans*, it is very narrow anteroposteriorly, and interrupted by the first sulcus. In the specimens referred to *T. littoralis*, it is much wider and uninterrupted. While in *T. natans* the facet for the tibia is regularly and gently concave, that of *T. littoralis* (MNHN.F.SAS53) is flatter, and its medial third is offset, being directed anteromedially. A pyramidal cyamo-fabella is found in the Nothrotheriini and *Megalonyx* (McDonald 1977).

#### Ossified meniscus

The only ossified meniscus recovered is described by Salas et al. (2005) and pertains to the specimen MUSM 223 (Table 15). Referred by these authors to *T. natans*, it is here referred to *T. littoralis*. It was articulating with the anterior part of the proximal lateral articular surface of the tibia. A meniscus of similar shape is found in *Nothrotheriops*.

#### Fibula

The fibula is known by complete specimens of *T. natans* and *T. littoralis* and by fragmentary material for the other species of the genus (Table 15). The fibula is never found fused to the tibia (except in the case of fractured and healed specimens), as in *Hapalops*, *Planops*, and other nothrotheriids, and differs from *M. americanum* in which the two are fused. Like the tibia, the fibula is more slender and elongate than in other sloths (Figs. 18, 19). The expansion of the proximal end anteroposteriorly is not as great as the distal end but both ends are wider in this dimension than the shaft.

The anterolateral margin of the proximal end is an enlarged tuberosity, probably for the fibularis longus muscle (Fig. 18). There is a smaller tuberosity on the posterolateral margin, probably for the flexor hallucis longus muscle. The posterior edge of the bone just distal to the proximal articular surface is marked by a third tuberosity, smaller than the others. While it is clearly isolated from the proximal facet on the holotype of *T. natans*, this tuberosity is more proximal in *T. littoralis*, almost abutting the facet. The last two tuberosities are reduced on a

specimen referred to *T. carolomartini* (MNHN.F.SAO201) and the three tuberosities appear as reduced on the holotype of *T. yaucensis* (no data for *T. antiquus*). The proximal articular surface for the tibia is flat and oval in outline. It is set at an angle to the long axis of the tibia, being, in *T. natans* and *T. littoralis*, oriented proximally, medially and slightly posteriorly. In *T. carolomartini* and *T. yaucensis* (no data for *T. antiquus*) this facet faces only proximally and medially. It occupies the posterior two-thirds or slightly more of the anteroposterior depth of the epiphysis. There is no facet for the cyamo-fabella, departing from the condition of *Mionothropus* (facet for cyamella sensu De Iuliis et al. 2011). Just distal to the tibial facet on the medial side of the proximal end is a marked fossa for the origin of the tibialis caudalis muscle. This fossa is deeper than in the Nothrotheriini, *Mionothropus*, and megatheriids, suggesting that the tibialis caudalis muscle was well developed in *Thalassocnus*. However, mature specimens of Nothrotheriini show marked ridges for muscular attachment on the medial side of the proximal end. This fossa is reduced in *T. carolomartini* and *T. yaucensis* when compared to the earlier species of the genus (no data for *T. antiquus*).

The shaft is roughly circular in cross-section except for its mediolaterally-flattened proximal and distal ends, which differs from the condition of the Nothrotheriini in which it is roughly triangular in cross-section for all its length. However, the anterior edge of the bone presents a pronounced ridge, which extends along the distal two-thirds of the fibula. The shaft differs from that of *Hapalops* and other Megatheria in featuring a medial bending, located at its proximal third. The only two specimens referred to *T. littoralis* that are complete enough to preserve this feature show a slightly more pronounced bending than that of the holotype of *T. natans*, but this feature seems to be subject to intraspecific variation.

The distal end has a strongly-protruding tuberosity (lateral malleolus) on the lateral side for the fibular collateral ligament (Fig. 18). This tuberosity is however relatively much smaller than that of *Nothrotheriops*. Medially the distal articular surfaces for the tibia and the astragalus are set at an angle to each other (Figs. 18, 19). Correspondingly to the different distal fibular facet of the tibia, the tibial articular surface is oriented more medially in *T. littoralis* (Figs. 18c, 19c and putatively *T. carolomartini*, based on the distal tibia) than in *T. antiquus* and *T. natans* (Figs. 18a, b, 19a, b; no data for *T. yaucensis*). A similarly obtuse angle between the astragalus and tibial facets is found in *Planops*, which departs from the right angle observed in the Nothrotheriini. The distal tibial facet is triangular, being wider anteriorly than posteriorly, and slopes anterodistally. The astragalus facet also slopes anterodistally; it is strongly concave anteroposteriorly in *T. antiquus* but flatter in the later species of the genus (no data for *T. yaucensis*). The lateral malleolus firmly locks the astragalus in place and restricts its movement to

plantarflexion-dorsiflexion without any lateral movement. There is a small eminence, just proximal to the tibial facet, on the anterodistal edge of the shaft. It inserts into a shallow depression on the tibia. This shallow depression is often reduced to a surface pierced by foramina that probably reflects a tendinous attachment.

The interosseous space (formed with the tibia) is much reduced when compared to that of *Hapalops* and other Megatheria, due, at least partially, to the medial bending of the proximal shaft found in *T. natans*. Both the more transversally-oriented distal tibio-fibular articulation and the more medially-bent shaft of the fibula result in an even smaller interosseous space in *T. littoralis* (no data for the other species).

Macroscopic observations of fractured specimens reveal details of the internal microstructure similar to those observed in the other long bones (Amson et al. 2014): a large medullar cavity is found in *T. antiquus* (holotype, MUSM 228; no data for *T. natans*), a small one is found in *T. littoralis* (MNHN.F.SAS1605), a few small discontinuous cavities are found in *T. carolomartini* (MUSM 1995), and no porosity at all is found in *T. yaucensis* (MUSM 2068). The osteosclerosis found in *Thalassocnus* hence also affects the fibula (bone not sampled in Amson et al. 2014).

#### Pes as a whole

The most complete pes known in *Thalassocnus* pertains to the holotype of *T. natans* (MNHN.F.SAS734; Figs. 20a, 21a). Each bone will be described independently (see Table 17 for measurements) but some general remarks can be given beforehand.

Like other Megatheria (for which the pes is known), *Thalassocnus* features a type of pedolaterality, i.e., the pes is rotated so that the morphological sole faces medially and the weight of the animal is transmitted mainly to the fifth metatarsal and the tuber calcis of the calcaneum. Nevertheless, the orientations will be given as in the ‘classical’ plantigrade disposition. Moreover, the tip of the tuber calcis will be referred to as the proximal-most end of the pes, and the tip of the digits as the distal end.

As pointed out by McDonald (2007, 2012), pedolateral sloths display two major variations of this stance, i.e., the ‘low-arched’ megatheriines and mylodontines (Fig. 22a) and the ‘high-arched’ nothrotheriids and scelidotheriids (Fig. 22b). *Thalassocnus* features a somewhat intermediate condition (Figs. 20, 21). As in the ‘high-arched’ pes taxa, only the proximal margin of the tuber calcis contacts the ground (McDonald 2007). However, in *Thalassocnus* the distal extension of this ground-contacting surface is greater than that of other nothrotheriids, but does not reach that of the ‘low-arched’ taxa, in which most of the proximodistal length of the bone contacts the

ground. Moreover, the mediolateral width of the Mt V is slight, which contrasts with the broad Mt V of the ‘high-arched’ taxa. In the latter, the arched appearance is enhanced by this feature. In this respect the pes of *Thalassocnus* more closely resembles that of megatheriids. In *Thalassocnus*, when they are articulated, the metatarsals are positioned not only mediolaterally to one another but also dorsoplantarly, which differs from the ‘classical’ horizontal disposition of *Hapalops* and the vertical one of *Nothrotheriops*; this is another common feature of *Thalassocnus* and megatheriids.

The first metatarsal and the phalanges of the first digit are unknown in *Thalassocnus* and were probably absent. The second metatarsal is much reduced. The third to fifth metatarsals are decidedly shorter in the late species when compared to those of the early species. These metatarsals are parallel (i.e., not diverging distally), and feature scars of syndesmosis. There are claws only on digits II to IV. Conversely, in *Hapalops*, digits I to IV are clawed. In the Nothrotheriini the first metatarsal is retained, fused to the entocuneiform; digit I is lost or vestigial (possibly co-ossified with the Mt I and entocuneiform) and claws are present on digits II to IV. In *M. americanum* metatarsals I and II and their phalanges are lost, the two medial-most cuneiforms are fused to form the mesocuneiform-entocuneiform complex (MEC, sensu Pujos and Salas 2004), and only digit III is clawed. In the earliest species of *Thalassocnus*, the tibio-astragalar articulation more closely resembles that of *M. americanum*. In *T. natans*, the angle between the shaft of the tibia and that of the fifth metatarsal ranges, in lateral view, ranges from approximately 70° (maximal dorsiflexion) to 110° (maximal plantarflexion). In *M. americanum*, this angle ranges from 90° to 110°; the dorsal component of the lateral rotation was therefore of less importance.

As will be described hereafter for each individual bone, the pes of *T. carolomartini* and *T. yaucensis* departs markedly from that of the earlier species of the genus, but each species in its own way. *Thalassocnus carolomartini* conspicuously differs from the condition of the other species of the genus in the torsion of the distal calcaneum, implying a different orientation of the tarsals and metatarsals relative to one another. This torsion brings the ectal facet more dorsally and hence causes an arched appearance of the pes (somewhat reminiscent of that of the Nothrotheriini). When the metatarsals of *T. carolomartini* are articulated with one another (Figs. 20b, 21b), they are all on the same plane, and when articulated with the tarsus, they are aligned mediolaterally and lack the dorsoplantar disposition found in the earlier species (e.g., *T. natans*, Figs. 20a, 21a).

*T. yaucensis* also appears to feature a more plantigrade condition. However, this is not a consequence of the reorientation of the elements of the pes, but rather the result of a modification of the tibio-astragalar articulation, because its morphology is more reminiscent of that of non-pedolateral mammals.

When compared to earlier species, *T. yaucensis* features smaller pedal elements relative to those of the forelimb and to the mandible. This is exemplified by the ratio of the dorsoplantar depth of the astragalus to the width at the proximal tuberosities of the humerus, and also of the dorsoplantar depth of the astragalus to the maximal depth of the horizontal ramus of the mandible (Table 18). *Nothrotherium* displays a relatively deeper astragalus than any species of *Thalassocnus*.

#### Astragalus

In *Thalassocnus*, the plesiomorphic condition of the astragalus, found in the three earliest species of the genus, resembles that of megatheriids in having the medial portion of the trochlea modified into a prominent and well-individualized odontoid process (Figs. 23, 24a-c). In this respect, *Thalassocnus* clearly differs from *Hapalops*, which lacks an enlarged and distinct odontoid process. McDonald (2007, 2012) describes the variation of the angle between the medial and lateral trochleae among the different families of extinct sloths. The 0° of this author (found in taxa in which the odontoid process is absent) corresponds to an angle of 180° between the discoid (lateral trochlea) and odontoid (medial trochlea) facets of Pujos and Salas (2004). The latter convention will be used for this study. In the holotype of *T. antiquus*, this angle reaches 90° (Figs. 23d, 24a-d), which is sensibly less (i.e., more acute) than that of the Nothrotheriini, and highly reminiscent of that of *M. americanum*. In the holotype of *T. natans*, the angle is 95°. Eleven specimens referred to *T. littoralis* display a variation of this angle from 100° to 105° (with the exception of one specimen that scores 110°; see Table 17). In *T. carolomartini*, this angle ranges from 100° to 115° (Fig. 24d). As already pointed out by Salas et al. (2005), MUSM 347, a specimen referred to *T. yaucensis*, differs from the earlier species in featuring a wider angle (approximately of 135°) between the tibial facets (Fig. 24e). An angle of at least 110° was also observed on another specimen referred to *T. yaucensis* (MUSM 2072), but its lack of a proximal fragment precludes a precise assessment. This reflects the different morphology of the distal articular surface of the tibia of *T. yaucensis* (see above). On the odontoid process, the odontoid facet features a regular proximodistal convexity. In all species except *T. yaucensis*, the angle between the odontoid and discoid facets of *Thalassocnus* is well defined along all its proximodistal extension (Fig. 23a). Among megatherioids, a similar condition is only found in megatheriids (e.g., *M. americanum*) because, in all other taxa that feature an odontoid process, this angle progressively becomes more obtuse proximally and finally disappears (i.e., the facets are not distinct anymore). This is not the case in *T. yaucensis*, in which this angle is more poorly defined, especially proximally, being in this respect reminiscent of that of *Hapalops*. The discoid facet curves medially and its proximal part extends well proximal to the

odontoid process (Fig. 23a; no data for this feature for *T. yaucensis*). A similar condition is not found in Megatheria but rather in mylodontines (McDonald 2012). In dorsal view (Fig. 23a), in all species except *T. yaucensis*, the discoid facet is expanded laterally, its lateral margin being well curved. This feature, described by De Iuliis (1994) as the ‘semicircular dorsolateral trochanter,’ is present in *Pronothrotherium* and *M. americanum*, intermediate in the Nothrotheriini, but absent (i.e., ‘straight-sided’) in *Hapalops* and *Planops*. In *T. carolomartini* and *T. yaucensis*, the lateral expansion of the discoid facet is reduced (as already mentioned by Salas et al. 2005 for *T. yaucensis*), but its lateral edge is rounded. The distal margin of the tibial trochleae is separated from the navicular process by a fossa, whose depth is variable. This fossa is where the anterior edge of the median ridge of the distal epiphysis of the tibia is located during extreme lateral rotation (dorsiflexion) of the pes. This fossa is well developed in *Hapalops*, *Planops*, and the Nothrotheriini, but reduced in *M. americanum*.

The articular surface for the fibula is at an acute angle (slightly less than 90°) to the discoid facet (Fig. 23d). It is triangular with its widest part at the distal margin and it narrows proximally, being strongly recurved plantarly. Its distal edge reaches the level of that of the odontoid process, as in *Hapalops*, *Planops*, the Nothrotheriini, and *Pronothrotherium*. In *M. americanum* this facet is more proximally positioned. In *Thalassocnus*, this facet is flat or slightly concavo-convex.

The navicular process (or head) is short so that its distal margin projects only a short distance distal to the discoid facet (Fig. 23a). As in all sloths the navicular facet is concavo-convex. This facet is formed by a dorsal area, which is concave to receive the mammillary process of the navicular, and a plantar area, which is a convex continuation of the surface articulating with the rest of the surface of the navicular. However, this surface shows some interspecific variation among *Thalassocnus*: in *T. antiquus* the concavity is marked, and the medioplantar continuation well developed; that of *T. natans* (holotype, MNHN.F.SAS734) is also concave distally, but its incomplete preservation precludes describing a definite difference from that of the earlier species (however, the morphology of the navicular suggests a condition closer to that of *T. littoralis*); that of *T. littoralis* is also concave, but the medioplantar continuation less developed; finally, that of *T. yaucensis* features a conspicuously less concave distal part and a reduced medioplantar continuation. That of *T. carolomartini* is subject to intraspecific variation. In all species of *Thalassocnus*, the concave surface is oval, with the major axis being oriented mediolaterally. A similar condition is found in *Hapalops* and the Nothrotheriini; in *Planops* it is more developed laterally, while in *M. americanum* it is circular. The dorsal edge of the navicular process slightly protrudes dorsally from the plane formed by the discoid facet (Fig. 23d). This is an intermediary position between the plantar one of *M. americanum*, in which



the process does not protrude dorsally from the level of the discoid facet, and the dorsal one of *Hapalops* (and *Myrmecophaga*), in which the navicular process protrudes dorsally from the medial tip of the odontoid process. In this respect the astragalus of *Thalassocnus* is more reminiscent of that of the Nothrotheriini and *Planops*. Moreover, the navicular facet faces only distally, a condition only found, among megatherioids, in *M. americanum*. Consequently, in fibular (or lateral) view (Fig. 23c), the navicular process is barely visible (and not visible in *M. americanum*), which contrasts with the more laterally oriented process found in *Hapalops* and other Megatheria. In distal view (Fig. 23d) the navicular process of *Thalassocnus* is at the level of the odontoid process, as in *Hapalops* and the Nothrotheriini. It is located more laterally in *M. americanum*, being at the level of the discoid facet. The medial and plantar borders of the navicular process of *Thalassocnus* form a single continuous articular surface. The medial surface articulates with the navicular, and the articular surface of the plantar and lateral border contacts the cuboid (Fig. 23b, d). The articular surface for the cuboid is extended by a small facet on the distal side of the discoid process. The two parts of the cuboid articular surface (that of the discoid process and that of the navicular process) are set at an obtuse angle. The discoid portion of the cuboid facet is for a proximal continuation of the astragalar surface of the cuboid. The sustentacular surface connects distally with the cuboid facet, and is separated from the ectal facet by a deep sulcus (sulcus tali) (Fig. 23b). The sustentacular surface is prolonged proximally by a small facet on the medial end of the discoid facet, directed plantarly and set at an obtuse angle to the rest of the surface. It articulates with a similar facet of the calcaneum. The ectal facet faces plantarly and is positioned directly plantar to the discoid facet. This contrasts with the more proximally-oriented ectal facet of the Nothrotheriini and *Scelidotherium* Owen, 1839 (which reflects the ‘high-arched’ morphology sensu McDonald 2007, 2012). The distance between the ectal and discoid facets is subject to intraspecific and even intra-individual variation. Nevertheless, it is always very small (Fig. 23c), even smaller than in *M. americanum*, which is the taxon included in the comparison of De Iuliis (1994) that displays the shortest distance. That allows the facet of *Thalassocnus* to be more concave and longer proximodistally. Moreover, the ectal facet is only slightly convex mediolaterally, being almost flat in that direction, which also differs from the condition of *M. americanum*. Small movements of dorsoplantar flexion-extension of the calcaneum on the astragalus seem to have been possible in *Thalassocnus*, which was not the case in *M. americanum*. The medial side of the odontoid process is separated from the navicular process by a tubercle.

Calcaneum

The general morphology of the calcaneum of *Thalassocnus* more closely resembles that of mylodontines and megatheriids than that of *Hapalops* and other nothrotheriids (Figs. 25-27). The tuber calcis of sloths displays a distinctive variety of forms and, before the description of the calcaneum of *Thalassocnus*, some considerations on the homology of its components are necessary. In *Hapalops*, the tuber calcis is a mediolaterally-expanded tuberosity, narrow dorsoplantarly, except for two plantar thickenings. The lateral one, the smallest, will be herein called the lateroproximal process, and the second one, located at the medial end of the bone and proximal to the level of the former, will be called the medioproximal process. A similar morphology is seen in Nothrotheriini (and in megalonychids and scelidotheriines), and can be described as ‘fan-like’ (Stock 1925) or ‘axe-head shaped’ (Hoffstetter 1961); however, in the latter the lateroproximal process is displaced proximally, reaching the level of the medioproximal process. Consequently, in the Nothrotheriini only the proximal margin of the tuber calcis contacts the ground, with the distal part of the calcaneum raised well off the ground. This arrangement gives to the pes the ‘high-arched’ appearance described by McDonald (2007, 2012). An interesting condition is found in *Planops*, in which the general morphology found in *Hapalops* is easily recognizable. But *Planops* differs from the latter in featuring a lateroproximal process extending more plantarly, and a medioproximal process much more developed and knob-like. Keeping this pattern in mind allows us to understand the morphology of *Thalassocnus* and other pedolateral sloths. In *Thalassocnus* the medioproximal process differs from that of *Planops* in being developed distally, reaching the level of the lateroproximal process (Figs. 25b, 26b, 27a). The distal edge of the tuber calcis is marked by a notch, which separates the medioproximal and lateroproximal processes. Moreover, the medioproximal process of *Thalassocnus* has shifted distally when compared to that of *Hapalops*. In *M. americanum* and *Mylodon* for instance, the two processes can also be recognized and are also separated by a notch, but differ in being much more developed distally. As a consequence, in the latter taxa almost all of the plantar side of the calcaneum contacts the ground, which reflects the ‘low-arched’ morphology mentioned above. This disposition gives a generally triangular shape to the tuber calcis, with one apex of the triangle directed proximally (“shell-shaped” as described in Megatheriinae; Pujos and Salas 2004).

*Thalassocnus* differs from other megatherioids in featuring a well-developed tuberosity on the dorsal side of the tuber calcis. This tuberosity is present in *M. americanum*, but is proportionally much smaller. Usually in plantigrade mammals the insertion of the gastrocnemius muscle (and other pedal extensors) is on the proximal tip of the calcaneum and the dorsal surface. In *Myrmecophaga* a round scar on the dorsal half of the proximal side of the bone marks this insertion (Gambaryan et al. 2009: 10). In *Hapalops*, this insertion is probably at the level of the

medioproximal process. Taking into account the positional shift of the mediodorsal process of the tuber calcis in *Thalassocnus* and *M. americanum*, it is here inferred that the tuberosity dorsal to the tuber calcis is for the gastrocnemius muscle (Fig. 26c).

The neck of *T. natans* has a roughly circular cross-section (Fig. 26a-c) in contrast to *Hapalops* and the Nothrotheriini in which the neck is dorsoplantarly compressed. While the neck is narrower than the tuber calcis and the articular parts as in other nothrotheriids and megalonychids, it is proportionately shorter in *Thalassocnus* than in these other sloths. Due to the great distal extension of the tuber calcis, the neck is virtually absent in mylodontids and megatheriines. When compared to that of *T. antiquus* (Fig. 25c), *T. natans* (Fig. 26d), and *T. littoralis*, the whole distal end of the calcaneum (bearing all the articular surfaces) of *T. carolomartini* seems to have undergone, when viewed distally, a torsion (clockwise when on the left side), bringing the ectal facet lateral to the other facets (Fig. 27c). The ectal facet for the astragalus is the largest of the three articular surfaces (Figs. 25c, 26d, 27c). Correspondingly to that of the astragalus, the ectal facet of the calcaneum is long, proximodistally convex, and only slightly concave mediolaterally. In distal view, in all species of *Thalassocnus* except *T. carolomartini*, as in *Hapalops*, *Nothrotherium*, and *M. americanum*, the long axis of this facet is at an angle of about 45° to the ground (which is perpendicular to the surface formed by the tuber calcis; Figs. 25c, 26d) while in *T. carolomartini* this angle is about 75° and the proximal third of the facet faces dorsally rather than medially (Fig. 27c). In *Nothrotheriops*, the ectal facet departs from the conditions just mentioned in being somewhat curled around the sustentacular facet. The ectal facet is separated from the sustentacular facet and the cuboid articular surface by a well-developed sulcus (which underwent the torsion in *T. carolomartini* as well). On the only specimen referred to *T. yaucensis* that preserves this area, the ectal facet is prolonged on its laterodorsal edge by a lip-like facet, directed laterally. This putatively articulates with the fibula (the lack of a specimen preserving the distal fibula precludes the observation of the corresponding facet). The sustentacular and cuboid facets are widely confluent (Figs. 25c, 26d, 27c) as in megatheriids, and not separated as in *Hapalops* and the Nothrotheriini. In all *Thalassocnus* species except *T. carolomartini*, as in megatheriids and the Nothrotheriini, the sustentacular facet is positioned slightly dorsal to the cuboid facet, whereas in *Hapalops* they are positioned lateromedially. The sustentacular process lies close to the body of the calcaneum and extends distally. The dorsal end of the sustentacular facet is offset dorsally from the rest, articulating with the small articular facet on the medial end of the discoid facet of the astragalus (see above). As already mentioned, both sustentacular and cuboid facets of *T. carolomartini* underwent the lateral torsion: the

sustentacular facet is positioned more dorsally relative to the cuboid facet (Fig. 27c). Furthermore, in distal view, the dorsal edge of the sustentacular facet reaches the level of the dorsal edge of the ectal facet in *T. carolomartini*.

Along the lateral side of the distal part of the calcaneum is a large process that supports a prominent tendinal groove (Figs. 26b, c, 27a, b). This groove provides a channel for tendons, probably of the fibularis muscles and extensor digiti lateralis muscle. The depth of this groove is affected by intraspecific, possibly ontogenetic variations: MNHN.F.SAS490, a specimen referred to *T. littoralis* representing a young individual, shows a very shallow groove; MNHN.F.SAS176, referred to the same species but representing an even younger individual with unfused proximal epiphysis, even lacks it; mature specimens also show either a deep groove or none at all. However, the groove seems to have been reduced in *T. carolomartini* and *T. yaucensis* when compared to the earlier species (no data for *T. antiquus*). This groove is present in *Hapalops* (but shallower) and *M. americanum* (in which the proximal wall is much reduced) but is absent in Nothrotheriini. Another interspecific variation is seen in its orientation: in *T. natans* (no data for *T. antiquus*) the groove extends proximodorsally from the plantar margin at an oblique angle, while in the later species of the genus it is more curved, its proximal end pointing only dorsally.

#### Navicular

The general shape of the navicular is oval in proximal or distal view, being more elongated dorsoplantarly than mediolaterally (Figs. 28, 29). As in other sloths there is a raised mammillary process dorsal to a concave surface that fits over the medioplantar side of the navicular process of the astragalus. Correspondingly to the morphology of the astragalus (see earlier in the text), the astragalar facet is less concavo-convex in the late species of *Thalassocnus*: while the plantar part (covering the medioplantar side of the navicular process of the astragalus) clearly extends more proximally than the mammillary process in *T. antiquus* (Fig. 28a, b), it is reduced in the later species (Fig. 29c, d; no data for *T. yaucensis*), having approximately the same proximal extension as the mammillary process. This concave part is less extended plantarly and is narrower in the species of the genus later than *T. natans* (no data for *T. yaucensis*). Except for the holotype of *T. antiquus* (Fig. 28b), the navicular of *Thalassocnus* presents a distinct sulcus between the lateroplantar corner of the bone and the facet for the cuboid (Fig. 29d; no data for *T. yaucensis*). The cuboid facet lies on the lateral margin and is confluent with the astragalar surface and, in its dorsal half, with that for the ectocuneiform. Most of the distal surface is covered by the articular surface for the ectocuneiform and is gently concavo-convex (Fig. 28d). This surface is formed by two facets, the larger being dorsal to the other, and the smaller being subcircular (data only available for the holotype of *T. antiquus*). There is a small articular facet for the

mesocuneiform, facing mainly distally but also medially, which is medial to the surface for the ectocuneiform and less than one-fourth its size. Such a reduction of the mesocuneiform facet is found in *M. americanum*, and contrasts with that of *Hapalops* in which the surfaces for the ectocuneiform and mesocuneiform are about equal in size, or the slightly smaller mesocuneiform facet in the case of the Nothrotheriini.

#### Cuboid

The cuboid is wedge shaped with the proximal part narrower than the distal (Fig. 30). The medial face of the bone has two articular facets, for the astragalus and for the calcaneum (Fig. 30a). The former is concave and triangular in outline. A small facet, which is the continuation of the surface for the astragalus, is found on the dorsal side of the surface, and is set at a right angle (it articulates with the small facet found on the distal side of the lateral trochlea of the astragalus). The surface for the astragalus is broadly confluent with the facet for the navicular on its distal edge (Fig. 30d). In medial view, the astragalar facet contacts at an acute angle the facet for the calcaneum, which is slightly convex. The entire lateral surface is formed by the common flat articular surface for the fourth and fifth metatarsals (Fig. 30b). The articular surfaces for the two metatarsals are not distinct from each other, which differs from the condition of *Nothrotherium* and *Nothrotheriops* in which the facets are set at an obtuse angle (the angulation is very weak in the latter genus). In *T. natans* the distal edge of the articular surface for Mt IV is marked by a median notch (no data for *T. antiquus* but putatively the same, given the morphology of the ectocuneiform; see below). A similar condition is present in *Nothrotherium* and *Nothrotheriops*, but the notch is located more plantarly in the latter. This notch is reduced or absent in the later species of *Thalassocnus*. The distal edges of the surfaces for Mt IV and for the navicular are confluent (or on one specimen separated by a small gap) on their dorsal third, with a distally facing facet for the ectocuneiform (Fig. 30d). A very narrow lateral strip of this surface contacts the lateroproximal tip of the third metacarpal. This forms a ‘tripoint articulation’ between the cuboid, ectocuneiform and Mt III on the lateral sides of these bones (Fig. 21a). A similar condition is found in *M. americanum* (and *Scelidotherium*). This condition differs from that of the Nothrotheriini in which Mt III does not contact the cuboid.

#### Entocuneiform

Unknown; probably absent, because the navicular lacks a facet for it.

#### Mesocuneiform

While not yet recovered, its presence is indicated by a well-developed articular facet on the navicular. In addition to the navicular, the mesocuneiform articulated with the ectocuneiform and the second metatarsal, and possibly with a remnant of the entocuneiform, if the latter was present. Considering the morphology of the bones articulating with it, the mesocuneiform was lenticular and relatively smaller than those of *Hapalops* and the Nothrotheriini (although, at least in *Nothrotheriops*, it is fused with Mt II).

#### Ectocuneiform

The ectocuneiform is a lenticular bone, proximodistally thick dorsally, that becomes thinner plantarly (Figs. 29, 31). The proximal surface is slightly excavated for the navicular, divided into a dorsal and a plantar part (Fig. 31b; data only available for the holotype of *T. antiquus*). The distal surface is dome shaped for the articulation with the third metatarsal (Figs. 29f, 31c). The dorsal third of the lateral side features on all its proximodistal length a facet for the cuboid (Fig. 29d, 31a). In distal view, the lateral edge of the bone is shallowly notched at mid-depth in *T. antiquus* and *T. natans*, which appears to be correlated with the notch found on the distal edge of the corresponding articular surface of the cuboid. This edge is roughly rectilinear in the other species (no data for *T. yaucensis*, but in this species the condition is inferred from the morphology of the cuboid).

#### Second Metatarsal

The first metatarsal is lost in *Thalassocnus*. Therefore, the medial-most metatarsal of *Thalassocnus* is the second metatarsal. It is never found co-ossified with the mesocuneiform, as is the case in *Nothrotheriops*. The second metatarsal is small, shortened proximodistally, and irregularly shaped (Fig. 32). The bone is much shorter in proportion to the other metatarsals compared to *Hapalops* and the Nothrotheriini, the shaft being virtually nonexistent. The medial side of the shaft bears a conspicuous tubercle, which is absent in the Nothrotheriini. Another, distinctly larger tubercle occupies the proximal half of the plantar side. In *Nothrotheriops*, this tubercle bears the facet for the entocuneiform-Mt I complex. The dorsal two-thirds of the proximal end are covered by two confluent facets, for the mesocuneiform and the Mt III, which are set at roughly a right angle. The mesocuneiform facet is concave (Fig. 32c). One specimen referred to *T. carolomartini* (no data for *T. antiquus* and *T. yaucensis*) differs from the others in displaying a surface for the mesocuneiform divided into two dorsoplantarily-disposed facets, the plantar one being smaller and subcircular. The facet for the third metatarsal is smaller and continuous with the dorsal half of the mesocuneiform facet. It is a flat semicircular surface that sits on a slightly raised prominence. The distal end is not

distinct from the shaft. It has a low carina occupying its entire dorsoplantar length. The surface lateral to the carina is distal to the surface medial to it, which implies that the digit was slightly deviated medially.

#### Digit Two

One specimen referred to *T. littoralis* (MUSM 438; Fig. 33a, b) and one referred to *T. carolomartini* (MUSM 1995) feature co-ossified first and second phalanges of digit II. The condition in the other species is unknown. These phalanges are small. Proximally the articular surface reflects the distal one of Mt II; the distal end bears two condyles of intermediate development, much shallower dorsoplantarly than the proximal end. Small fossae are found on both plantar and dorsal sides, just proximal to the condyles.

The ungual phalanx is much smaller, relative to the size of the pes, than the same bone in *Hapalops* and the Nothrotheriini (Fig. 33c, d). The proximal articular surface is, on the holotype of *T. natans*, a single small concavity. An additional one, lateral to the other, is present on specimens referred to *T. littoralis*, *T. carolomartini*, and *T. yaucensis*. There is a well-developed overhanging process that is slightly deviated laterally. As in all the pedal ungual phalanges there is a large subungual process on the distal margin of the plantar surface for the insertion of the flexor digitorum profundus muscle. This tubercle very reduced in *Nothrotheriops*, but well developed on the pedal ungual phalanx of *Nothrotherium* and *M. americanum*. As in the manual ungual phalanges, the base of the ungual crest is often perforated by two large foramina. The ungual process is short and triangular in cross section, its plantar edge being rectilinear and its dorsal edge being weakly convex. It differs from that of the other digits in being conspicuously flattened mediolaterally; its distal tip is slightly expanded and also features a roughened surface, hence being reminiscent of that of the first digit of the manus (Amson et al. in press).

#### Third Metatarsal

The third metatarsal in *Thalassocnus* is shortened proximodistally, as is generally the case in sloths. However, in *T. antiquus* and *T. natans* it is less shortened than that of most sloths in that it has an elongate appearance, being longer proximodistally than it is wide (Figs. 34, 35a, b, f, g, 36a). In *T. littoralis*, the shortening is more pronounced, reaching proportions approaching that of *Hapalops* (Figs. 35c, h, 36b); Mt III of *T. carolomartini* (Figs. 35d, i, 36c) and *T. yaucensis* (Figs. 35e, j, 36d) approach the even more shortened condition found in *M. americanum* (Table 19). In *Nothrotheriops* and *Nothrotherium*, Mt III appears still more shortened, the bone being wider than long. However, the shortness found in the latter can be attributed to the absence of a well-developed

lateroproximal process (see below). Mt III of *Thalassocnus* is never found co-ossified with the ectocuneiform, contrary to the condition often observed in *Nothrotheriops*.

The proximal end of the bone is much deeper dorsoplantarly than wide mediolaterally (Figs. 34c). The plantar side of the proximal end presents a tubercle, probably weight-supporting. The relative size of this tubercle is subject to intraspecific variation, as is observed in a sample of four Mt III of *T. littoralis*. This tubercle is small but present in *M. americanum* and the Nothrotheriini. The rest of the proximal end is completely covered by the well-excavated articular surface for the ectocuneiform. On nearly all specimens of *Thalassocnus*, this surface presents in its center a small fossa, probably for the attachment of a tarsometatarsal ligament. The surface for the ectocuneiform and the facet for Mt IV are expanded proximally by what will be called herein the lateroproximal process. In the species of *Thalassocnus* earlier than *T. yaucensis*, this process has a proximal extension comparable to that of *Hapalops* (Fig. 35f-i). In the latest species of the genus (Fig. 35j), this process is more developed proximally and laterally, and forms a fine and sharp crest. The morphology of *T. yaucensis* in this respect is highly reminiscent of that of *M. americanum*. As stated in the description of the cuboid, a very slight contact exists between the cuboid and Mt III, via the proximal extension of the lateroproximal process. On two specimens (referred to *T. littoralis* and *T. carolomartini*), this contact is slightly more extensive than on the other specimens, the proximal tip of the process being flattened and forming a dorsoplantarly-elongated facet. The articular surface for the second metatarsal is smaller than that for the fourth metatarsal. The facet for Mt IV is flat or slightly convex dorsoplantarly (Fig. 34b); in *T. yaucensis* it is directed more distally than in the earlier species.

Distal to the facet for Mt IV, the shaft shows a roughened surface, which is probably a scar of syndesmosis, reminiscent of the condition observed on the metacarpals (Fig. 34b; Amson et al. in press). This feature was described in *M. americanum* as a ‘honeycombed’ surface (Owen 1859: 817).

The distal end features a greater mediolateral width but lesser dorsoplantar depth than the proximal end (Fig. 34d). The distal carina is well developed on all the dorsoplantar depth of the bone, and extends, as in *Hapalops* and the Nothrotheriini, on the plantar side of the shaft. On either side of the plantar end of the carina a shallow concavity is present, which probably reflects the location of sesamoids. This differs from the much reduced carina found in *M. americanum*. The carina is slightly oblique, because its dorsal edge is positioned slightly more laterally than the plantar one. This results in a slightly-medially deviated third digit. In lateral view, the carina is roughly straight and does not have the curvature seen in *Hapalops* and the Nothrotheriini. In all species of *Thalassocnus*, the shelf for the phalanx on the medial side is wider than the lateral one and flattened mediolaterally. Due to this flattening, very little



or no mediolateral deviation (in the mediolateral plane) was possible at this metatarsophalangeal articulation. In *T. natans* and *T. littoralis* (no data for *T. antiquus*) the medial shelf shows a slight dorsoplantar curvature, which allows some degree of flexion-extension at this metatarsophalangeal joint, but it appears that these movements were less extensive in *T. natans* and *T. littoralis* than in *Hapalops* and Nothrotheriini. In *T. carolomartini* and *T. yaucensis*, the median shelf is distinctly flattened. Two specimens referred to these species comprise Mt III and the corresponding co-ossified proximal and second phalanges (see below; MNHN.F.SAO201 and MNHN.F.PPI271 respectively). Articulation of both elements of these specimens shows that the flexion-extension movements at this joint were extremely reduced, if not absent, in *T. carolomartini* and *T. yaucensis*.

### Digit Three

The proximal and second phalanges of this digit are co-ossified in *Thalassocnus*, as in the Nothrotheriini and *M. americanum* (Fig. 37a, b). On some specimens, minute dorsal and plantar fissures mark the fusion of the bones. The two bones are separate in *Hapalops* and *Pronothrotherium*; both conditions are found within the genus *Megalonyx* (McDonald 1977). The composite bone is roughly cubic. The proximal end has a deep median groove for the carina of the metatarsal with the complementary symmetrical development of the medial and lateral articular surfaces. As a consequence, the proximoplantar edge of the bone is distinctly cleft. Two small facets for sesamoids are present on either side of the groove. A shallow fossa on the dorsal surface of the shaft is present and receives the overhanging process of the ungual phalanx. Complete extension of the distal interphalangeal joint is impossible: during maximal extension (i.e., when the overhanging process of the ungual phalanx is placed in the dorsal fossa of the co-ossified phalanges), there remains an angle of 55° between the plantar surfaces the co-ossified phalanges and of the ungual phalanx. This condition is not found in *Nothrotherium* (and probably not in other nothrotheriids either), in which this angle approaches 0°. A plantar fossa is also present on the co-ossified proximal and second phalanges. It is shallower than the dorsal fossa in *T. natans*, and deeper in *T. littoralis*, *T. carolomartini*, and *T. yaucensis* (no data for *T. antiquus*). Thanks to the presence of this fossa, the flexion was considerable (more in the late species than in the early ones) and the angle just mentioned exceeds 90°. This angle is close to 90° in the Nothrotheriini. Medial and lateral to the distal trochlea, a tuberosity is present, which probably marks the insertion of lumbricales muscles. The distal end has two well-developed condyles; the medial one is slightly wider than the lateral.

The ungual phalanx of digit III of the pes is by far the largest of the pedal ungual phalanges, those of the second and fourth digits being much smaller (Fig. 37c, d). The articular surfaces for the condyles of the co-ossified

proximal and second phalanges are deep and separated by a well-developed ridge. The medial articular surface is deeper and slightly wider than the lateral one. This causes a medial deviation for the unguis phalanx when flexed. This phalanx is easily distinguishable from the others (manual or pedal) by the great size of its overhanging process. Because its width is not reduced relative to that of the plantar side of the phalanx (as is the case on other digits), this process is somewhat rectangular. It protrudes well proximal to the level of the proximal articular surface and displays proximally a well-marked insertion of the extensor digitorum longus and interosseous muscles. This insertion is so deep on the holotype of *T. natans* that the proximal end of the overhanging process is bifid. A similar morphology is found in the Nothrotheriini. Such an insertion is not present in *M. americanum*. This unguis phalanx also has an enlarged subunguis process for the flexor digitorum profundus muscle. A nearly similar condition is found in *Nothrotherium*, but this process is relatively smaller in *Nothrotheriops*. As usual, the plantar side of the unguis crest is perforated by two large foramina. The unguis process is asymmetrical and has a slight medial curvature. The dorsal edge of the process is sharp and not rounded as on the other digits. The process is triangular in cross-section; the lateral side is slightly convex while the medial side is slightly concave.

#### Fourth Metatarsal

The general morphology of the fourth metatarsal is more reminiscent of an ancestral plantigrade state, because it is less shortened proximodistally than the other metatarsals (Fig. 38). However, Mt IV of *T. littoralis* and *T. carolomartini* are clearly shortened (relative to their width) when compared to the earlier species of the genus (Table 20). Mt IV of *T. yaucensis* is even shorter: the length of the bone is less than four times its width at mid-shaft. As a consequence, the bone is stouter, being proportionally wider and deeper in the later species of *Thalassocnus* (Fig. 39), a condition that differs from other ‘pedolateral sloths’ in which it is mainly the medial metatarsals and digits that are reduced. The proximal and distal ends of Mt IV of *Thalassocnus* are expanded dorsoplantarly relative to the shaft. The proximal end is roughly rectangular in proximal view, with the dorsal and plantar edges having about the same width. The plantar side of the proximal end presents a large flattened tubercle that was probably weight-supporting (as in *Nothrotheriops* and *M. americanum* and to a lesser extent in *Nothrotherium*). The articular surface for the cuboid covers most of the proximal surface and faces medioproximally. It contacts the slightly concave articular surface for the third metatarsal, as in *M. americanum*, and differing from the condition of *Hapalops* and the Nothrotheriini (Fig. 38a, c). The former surface also broadly connects laterally with the facet for Mt V, as is more common among sloths (Fig. 38c). The articular surface for the third metatarsal appears more deeply concave in

the species later than *T. natans*. The surface for the fifth metatarsal is flat, semicircular and confined to the dorsal two-thirds of the lateral side of the proximal end (Fig. 38b). At the level of the cuboid facet, the shaft is depressed on both its dorsal and plantar sides. This dorsal depression is slightly deeper in *T. antiquus* and *T. natans* than in the later species. Distal to the facet for the adjacent metatarsals the shaft is rugose, which probably marks a syndesmosis between the bones.

On the laterodorsal side of the distal end is a raised tuberosity, probably weight-supporting. This tuberosity is also present in *Nothrotherium* and, much more developed, in *M. americanum*. In *Nothrotheriops*, in place of this tuberosity is a small facet. The carina of the distal end is straight in profile (Fig. 38a, b). Viewed distally it is broadly rounded mediolaterally. It has a slight medial curve and a single additional articular surface for the proximal phalanx on the plantar corner of the medial side. This latter surface is confluent plantarly with a relatively large facet for a large sesamoid. Preserved on the holotype of *T. antiquus*, this medial (plantar) sesamoid is dorsoplantarly flattened, and features a raised lamina directed plantarly and medially. The lateral (plantar) sesamoid was also recovered for this specimen; it displays a more ‘classical’ sesamoid shape.

#### Digit Four

The proximal phalanx is unknown. Given the morphology of Mt IV and the second phalanx, it most likely presented a proximal groove medially skewed, and two distal condyles, with the medial more developed than the lateral.

The second phalanx is short proximodistally (Fig. 40a). The proximal end is expanded dorsoplantarly and quickly narrows distally. The proximal articular surface has two articular surfaces for the condyles of the proximal phalanx. They are shallow and separated by a median ridge. The medial surface is deeper and slightly wider mediolaterally. The distal articular surface is composed of a relatively large medial condyle and a much reduced lateral one. Only minute flexion/extension movements seem to have been possible between the second and ungual phalanges.

The articular surface of the ungual phalanx is composed of one dorsoplantarly-elongated fossa and a small facet lateral to it. The overhanging process is well developed and slightly deviated medially (Fig. 40b). As in the other pedal ungual phalanges, a well-developed tubercle for the flexor digitorum profundus muscle marks the plantar side of the bone. The ungual process is short and triangular both in lateral profile and in cross-section, its dorsal and plantar edges being rectilinear.

### Fifth Metatarsal

The fifth metatarsal of *Thalassocnus* is easily distinguishable from that of other sloths by the shape of its lateral process sensu Stock (1925). The general condition, found in myrmecophagids and megalonychids, is a small process, directed laterally or lateroproximally. In some taxa in which the whole plantar surface of the metatarsal contacts the ground, such as *M. americanum* or *Lestodon*, this process is almost absent. In the Nothrotheriini, this process is expanded laterally and its distal end is displaced dorsally, to enlarge the surface of contact with the ground. *Thalassocnus* differs from all other taxa just mentioned, because the lateral process is directed proximally, its lateral expansion being almost absent (except on MUSM 1995, specimen referred to *T. carolomartini*), and the lateral border of the metatarsal being almost rectilinear (Figs. 41, 42). The area of contact with the substratum, which is marked by a rugose surface, covers the whole proximal end of the process. At the level of the articular surface, this area only covers the lateral and medial borders of the bone (Figs. 41b, 42b; this surface, bifurcated distally, is reminiscent of that of the tuber calcis). Moreover, in the species later than *T. natans* (see Fig. 42a, b for *T. carolomartini*, Fig. 42c for *T. yaucensis*; no data for *T. antiquus*), the process is conspicuously reduced when compared to the earlier species (see Fig. 41 for *T. natans*), because it is less extended proximally and narrower mediolaterally. A rugose area encompasses the whole lateral side of the metatarsal as well as a triangular area on the dorsal side of the bone, distal and lateral to the facet for Mt IV. This surface, probably for the insertion of the fibularis brevis and abductor digiti quinti muscles, is very similar to that seen in *M. americanum*. On several specimens referred to *T. littoralis*, this area is interrupted at the level of the facet for Mt IV. On one specimen referred to *T. carolomartini* (MNHN.F.SAO201; Fig. 42a), this dorsal and triangular area is more elevated dorsally, forming a knob that ends in a small and flat surface, which was probably in contact with Mt IV.

The articular surfaces for the fourth metatarsal and cuboid are semicircular. They are broadly confluent and meet at an angle of about 120°, approaching the condition of the Nothrotheriini. This contrasts with the almost flat angle of *M. americanum* and the approximately right angle of *Hapalops*. Moreover, in other megatherioids, the whole articular surface faces only laterally, while in *Thalassocnus* it faces also dorsally. The dorsal component of this orientation is greater in *T. carolomartini* (Fig. 42a) than in the other species (for instance *T. antiquus*, Fig. 43, and *T. natans*, Fig. 41a), because, in dorsal view, the articular surface in this species occupies more than a third of the total width of the bone at the same level. Moreover, *T. yaucensis* differs from the earlier species of the genus in displaying

a more rounded edge between the facets for the cuboid and Mt IV (Fig. 42c). In all species of *Thalassocnus*, the part of the fifth metatarsal that supports the articular surfaces is expanded both dorsally and medially.

In *T. natans*, *T. littoralis* and *T. carolomartini* (no data for *T. antiquus*), distal to the articular surfaces, the shaft is approximately oval in cross section, being slightly flattened dorsoplantarly. This differs from the much broader and dorsoplantarly-flattened shaft of the only specimen referred to *T. yaucensis* that preserves this area (MUSM 2065, Fig. 42d). This specimen approaches in this respect the condition of the Nothrotheriini. The shaft appears proximodistally shorter in *T. carolomartini* than in the earlier species of the genus (no data for *T. antiquus* and *T. yaucensis*). The distal end is slightly more expanded dorsoplantarly than the shaft. Its plantar side is marked by a fossa, probably the location of a sesamoid. There is a small and flat articular facet for the proximal phalanx.

#### Digit Five

No secure number of phalanges can be given for this digit but, judging from the articular surface on Mt V, it/they would have been vestigial (as is the case in all Megatheria and *Hapalops* where the phalanges are not lost). This is usual for “ground sloths,” because only *Pelecycodon* Ameghino, 1891, retains functional phalanges of digit V of the pes. Two specimens preserve what appears to be the only phalanx of this digit (Fig. 44). It is vestigial. Its proximal end is covered by a flat and rounded facet; its distal end terminates in a process of which the elongation is parallel to the plane of the articular facet.

#### Comments on the specimens of the AGL level of the Aguada de Lomas locality

An isolated patella and navicular were found at the Aguada de Lomas locality. They were found in the AGL level, in a horizon either equivalent or close to that of the holotype of *T. antiquus*. The patella (MNHN.F.PPI245) is reminiscent of that of *Thalassocnus*, because it is constricted at the base of the apex, and the femoral surface is highly asymmetrical, being strongly convex mediolaterally as in *T. antiquus*. However, it differs markedly from all other specimens: the apex is relatively long (hence more reminiscent of the proportions of that of *T. antiquus*; Table 10) but wider distally (i.e., less pointed), resembling more that of *Hapalops*, the Nothrotheriini or *Mionothropus*. Moreover, the apex is bent laterally. This suggests either intraspecific variation, or, because no other specimen displays such a different morphology, the presence of another species of *Thalassocnus* in this level.

The navicular (MNHN.F.PPI244) is also reminiscent of *Thalassocnus*. However, it shows a hemispherical concave part of the astragalar facet; whereas that of *Thalassocnus* (even *T. antiquus*) is dorsoplantarly compressed when compared to that specimen. Hence this is also consistent with the occurrence of another species of *Thalassocnus* in this level.

#### Comments on the specimens of the Bahía Inglesa Formation

Along with a fragmentary mandible (hardly referable to a particular species of *Thalassocnus*), a complete isolated femur (MPC 644) has been recovered from the Cerro Ballena locality of the Chilean Bahía Inglesa Formation (Pyenson et al. 2014). Based on the attribution of the femur to *T. natans*, the upper bound of the age of the unit of the Formation found at the Cerro Ballena locality would correlate to the age of the Montemar Horizon of the Pisco Formation. The unit is hence considered to be late Miocene in age by these authors. However, it must be pointed out the features that they considered diagnostic of *T. natans* are in fact found in the whole genus. Nevertheless, the great development of the medial trochlear ridge on MPC 644 agrees with an attribution to either *T. antiquus* or *T. natans*. It is hence possible that the unit of the Bahía Inglesa Formation found at the Cerro Ballena locality may be correlated to the AGL level of the Pisco Formation, and hence slightly older than previously thought.

#### DISCUSSION

Study of the skull, mandible, and dentition of *Thalassocnus* revealed an evolution in the feeding adaptations, from the early species practicing partial grazing to late species practicing specialized grazing (Muizon et al. 2004b). Previous studies of the postcranium of *Thalassocnus* have focused on the internal microstructure and gross morphology of the forelimb (Amson et al. in press). They have also suggested the gradual evolution of an array of adaptations from the early to the late species of the genus. Increasingly pronounced osteosclerosis and pachyostosis were also described in the genus. Allowing buoyancy and trim control (Domning and Buffrénil 1991), these adaptations indicate that a submerged position on the seafloor was preponderant, especially in the late species of *Thalassocnus*. Moreover, the forelimb was described as well adapted to grip fixed objects in the context of stabilization and bottom-walking. It was also thought to be implicated in fossorial activities, probably uprooting rhizomes of seagrasses.

The present study reveals, as the previous studies have done, some characteristics of the hind limb shared by all species of *Thalassocnus* as well as interspecific differences. Such comparative observations were interpreted in terms of function, as summed up in Table 21. The hind limb of *Thalassocnus* does not depart from the condition generally found in tetrapods, which is obviously implicated in the function of support of the rest of the body and in locomotion. However, the major differences found when a comparison is done with closely related terrestrial sloths suggest that a particular set of constraints applied to the hind limb of *Thalassocnus*.

#### General structure and size of the hind limb

A typical feature of graviportal mammals is the vertical orientation of the ilium (Polly 2007). Concerning sloths, Scott (1903-1904) and Stock (1925) pointed out that a great development of the iliac wing is associated with large animals that have large viscera that need to be supported. More specifically, Pujos et al. (2007) recognized two morphologies of the pelvis of sloths, one characterizing large terrestrial forms, in which “wings of the ilia protrude laterally and dorsally,” the other characterizing “small terrestrial and possibly climbing sloths,” in which the iliac wings are “weakly developed laterally, with ilia subparallel to the sacral vertebrae.” The positive correlation between body mass and angle between the ilium and sacrum appears well verified in Megatheria, and might be exaggerated by the possible upright posture (if not bipedal locomotion) often hypothesized in “ground sloths.” The largest forms (e.g., *M. americanum*) feature an almost upright iliac wing. *Nothrotheriops*, of intermediate size, features a wing that is roughly at 50° from a craniocaudal direction. *Nothrotherium*, of small size, features a weak wing angle, below 40°. Such a correlation is however not verified in *Thalassocnus*, in which the iliac wing displays an orientation closer to that of the small *Nothrotherium* (Fig. 1). Knowing the general size of the *Thalassocnus*, one would expect a more upright orientation of the wing, closer to the condition of *Nothrotheriops*. Moreover, the iliac wing is weakly developed in *Thalassocnus*, weakly protruding laterally from the level of the acetabulum. Even the smaller *Nothrotherium* features a better-developed wing. Additionally, the iliac wing is reduced in *T. carolomartini* when compared to the earlier species of the genus (Fig. 2; no data for *T. natans* and *T. yaucensis*). Such a horizontal orientation and weak development of the iliac wing may reflect the aquatic habits of the taxon, because water provides support (buoyant force). Similar conclusions were already drawn from the pelvic morphology of desmostylians (Domning 2002).

The femur of most “ground sloths” departs from the general mammalian condition in its general shape, being quadrate in anterior or posterior view and flattened anteroposteriorly. This is found to different degrees among taxa,

the most conspicuous condition being probably found in *M. americanum*, in which the mediolateral width is almost four times greater than the anteroposterior depth (Casinos 1996). This morphology was interpreted as indicative of a practice form of locomotion that produces high lateral stresses on the hind limb (more specifically a particular bipedalism). Even though this morphology is most conspicuous in large forms (e.g., *M. americanum*, *Nothrotheriops*) and is even subject to size allometry (Milne et al. 2011), it is found in forms smaller than *Thalassocnus* (e.g., *Nothrotherium*). The relative gracility of the femur of all species of *Thalassocnus* is hence clearly derived. According to the preceding interpretation, we can suppose that the stresses undergone by the hind limb of *Thalassocnus* were markedly different from those of other “ground sloths.”

The tibia of most “ground sloths” is also characterized by its shortness. As already mentioned by Muizon and McDonald (1995), *Thalassocnus* clearly departs from this condition, having a long and slender tibia (Table 13; Figs. 13, 14). As already argued by these authors, a long tibia relative to the femur is usually found in aquatic and semi-aquatic forms. However, in the case of sloths, it appears that it is the short tibia, found in most non-thalassocnine taxa, that is a specialization allowing a particular function. Blanco and Czerwonogora (2003) inferred for *M. americanum* a bipedal gate implying large compressive stresses that would explain the mediolaterally wide femur and tibia. Moreover, graviportal forms such as proboscideans illustrate well the shortened zeugopod segment required in a particular terrestrial context. It is hence probable that a short posterior zeugopod is part of the structural requirements shared by most “ground sloths.” Such a disposition is not found in *Thalassocnus*, which suggests, like the femoral morphology, that the constraints applied to the hind limb were drastically different from those of other sloths.

All *Thalassocnus* species feature a well-developed (i.e., not vestigial), tight crus and pes. However, comparison of several ratios among the species of *Thalassocnus* indicates that the hind limb was relatively smaller in the late species of the genus. This conclusion is drawn from comparison of the femoral length to humeral length (Table 6) and of the proximal width of the femur to that of the humerus (Table 7); it is also indicated by comparison of femoral length, patellar dimensions, tibial length or astragalar width to the depth of the mandible (or to the proximal width of the humerus) (Tables 8, 11, 14, 18 respectively). The reduced iliac wing found in *T. carolomartini* compared to the earlier species of the genus (no data for *T. natans* and *T. yaucensis*) agrees with this hypothesis.

Hip joint



A more medially located dorsal margin of the acetabulum characterizes taxa capable of more extensive femoral abduction (Jenkins and Camazine 1977). We can draw such a conclusion for *T. carolomartini*, which displays a more concave dorsal edge of the acetabulum than the earlier species of the genus (no data for *T. natans* and *T. yaucensis*).

The anteriorly-restricted pubic cornu of *Thalassocnus* (Figs. 4, 45a) departs from that of other Megatheria that were examined (Fig. 45b, c). This implies a different acetabulofemoral articulation. Movements of large amplitude of the femur on the pelvis were obviously possible in all directions. However, when the ligament scars of the acetabulum and the femoral head are superposed (i.e., in the estimated neutral position of the articulation: see Jenkins and Camazine 1977), the femur of *Thalassocnus* is extremely abducted and faces almost anteriorly. During maximal abduction, the femur could have reached a nearly horizontal position, i.e., its proximodistal axis forming an almost right angle with the sagittal plane (Fig. 46a). In *Nothrotherium*, the angle of the axis of the shaft to the vertical (i.e., a plane parallel to the sagittal and passing through the lateral border of the head) is around 20° when maximally adducted and 45° when maximally abducted (when the fovea capitis is superimposed on the acetabular notch). While a usually abducted position of the knee is inferred in some “ground sloths” (particularly those that adopt a pedolateral stance; White 1993, 1997; Fig. 46b), the acetabulofemoral articulation of *Thalassocnus* suggests a more extensive capability of abduction of the femur.

The presence of a femoral neck in *Thalassocnus* is a distinctive feature not seen in other “ground sloths.” The incipient femoral neck of *Acratocnus* Anthony, 1916 (when compared to the virtually absent one of non-thalassocnine “ground sloths”) was already suggested as indicative of great hip mobility (White 1993). The head of *Thalassocnus* is even more distinctive, as a result of the presence of a deep notch between the head and greater trochanter (Fig. 5). This notch is the location of the dorsal edge of the acetabulum during maximum abduction of the femur. This morphology of the femur hence concurs with the extensive femoral abduction ability inferred in *Thalassocnus*.

The femur of *Thalassocnus* departs from that of most sloths in the connection of the greater and third trochanters that forms a thick crest on the proximal half of the diaphysis (Fig. 5). The lateral side of this crest, marked by conspicuous muscular scars, probably provides a large area of insertion for the abductor(s) of the femur (the main one being probably homologous to the gluteus medius muscle). This emphasizes the strength of this movement in *Thalassocnus*.

Strong and frequent abductions of the femur were already inferred in *Thalassocnus* based on the depth of the fovea capitis femoris (Muizon and McDonald 1995). The morphology of other components of the hip joint, namely the acetabulum and femoral neck, corroborates this assumption. It is noteworthy that the late species of *Thalassocnus* (at least *T. carolomartini*) appear to have emphasized this specialization. It is noteworthy that very pronounced abduction of the hip is described in desmostylians (Domning 2002). In the latter, however, it is associated with a vertically oriented pelvis.

#### Evolution of morphofunctional complex related to pedolaterality in *Thalassocnus*

Sloths, or at least some of them, are unique in practicing a pedolateral stance (McDonald 2007). Even though it is found under different modalities among the diversity of sloths, this stance always implies that the side of the pes homologous to the plantar surface of plantigrade mammals faces more or less medially, which corresponds to the inversion of the pes to various degrees. The movements of the pes relative to the leg are hence extensively modified, and while they are homologous with plantarflexion-dorsiflexion of a plantigrade pes, they will be modified to produce a mediolateral rotation, i.e., rotation of the pes around the odontoid process of the astragalus. Depending on the taxon, the dorsoplantar component of the rotation is reduced to various degrees. Previous authors associated this stance with different morphological features of the pes: the astragalus (which probably displays the most significant degree of departure from the general mammalian condition) features a tibial articular surface that includes odontoid and discoid facets; the calcaneum is often elongated, with the expansion of the tuber calcis for a greater contact with the ground; the relative disposition of the tarsals of the distal row is modified; the medial metatarsals/digits are reduced/lost; and the fifth metatarsal is modified for its lateral side to be in contact with the ground (Stock 1917; Hirschfeld 1985; McDonald 2007, 2012). Other non-pedal features associated with the pedolateral stance include: the torsion of the shaft of the femur (McDonald 2007) and the enlarged medial condyle (White 1993, 1997), which are interpreted as suggestive of an abducted position of the knee; the presence of an ossified meniscus, a rounded medial condyle of the femur, and a deeply concave medial femoral facet of the tibia, which are interpreted as indicating the occurrence of rotational movement of the knee during locomotion (Salas et al. 2005); and the distal articular surface of the tibia, which obviously reflects the morphology of the astragalus, allows the shift from dorsoventral movements of the pes to mediolateral ones.

The morphology of the patellar surface was considered as indicative of terrestrial/arboreal preferences (White 1993; White 1997), with the inference that a high trochlear (or patellar) lip may serve to prevent displacement

of the patella. It appears that the morphology of the patellar surface was overlooked in the context of the pedolateral stance. Sloths recognized as practicing a pedolateral stance usually feature an over-developed medial trochlear ridge (or lip), which extends anterior to the level of the lateral one to various degrees depending on the taxon (see for instance the nothrotheriids and *Planops*, Table 5; Fig. 47). This results in an asymmetrical patellar surface. Some exceptions exist, such as megatheriines. However, the latter appear to feature another specialization at the knee joint, with the reduced patella and patellar surface restricted to an anterior continuation of the lateral condyle. This may be related to their large size, but other large forms (such as *Lestodon*) feature an asymmetrical patellar surface. On the contrary, taxa considered to be plantigrade usually have a low medial trochlear ridge, such as *Hapalops* (Table 5) or *Megalonyx*.

Interestingly and unexpectedly, modifications of the trochlear ridges (or patellar lips) have already been associated with a particular stance, but in another taxon, namely *Australopithecus sediba* Berger et al., 2010 (DeSilva et al. 2013). A distal view of the femur indeed reveals highly reminiscent structures, particularly the anterior development of one trochlear ridge. However, in *A. sediba* it is the lateral lip that is developed and not the medial one as in the sloths in question. A large bicondylar angle in sloths is associated with knee abduction, rotation, and pedolateral stance (White 1993; Salas et al. 2005). This angle, first used in human morphometrics, is defined as the angle between the diaphysis of the femur and a line perpendicular to the infracondylar plane (Shefelbine et al. 2002). The presence of this angle in humans is apparently indicative of bipedalism, in contrast with non-human apes (Shefelbine et al. 2002). However, one must bear in mind that the knee is adducted in bipedal apes (genu valgum), and abducted in sloths (genu varum). Therefore, while *A. sediba* features a bicondylar angle estimated to be around  $9^\circ$  (it ranges from  $8$  to  $11^\circ$  in modern humans, see *Homo sapiens* Linnaeus, 1758, in Fig. 48), sloths with pedolateral stance feature a negative angle, around  $-5^\circ$  (see *T. antiquus*, *T. natans*, and *T. littoralis* in Fig. 48). Both patellar surface and bicondylar angle of bipedal apes and pedolateral sloths are hence reminiscent to some degree, if the structures are mediolaterally inverted. Moreover, the double meniscus attachment, possibly present in *A. sediba* and definitively interpreted in *Homo* Linnaeus, 1758, as a control on the rotation of the knee (DeSilva et al. 2013), is reminiscent of the ossified meniscus of sloths that have a pedolateral stance (Salas et al. 2005).

DeSilva et al. (2013) inferred that the elevated lateral trochlear ridge of *A. sediba* is an adaptation to resist lateral translation of the patella, which occurs in concert with medial (internal) rotation of femur and tibia and pronatory torque, i.e., a medial weight transfer at the pes, which occurs during the stance phase within the context of the particular bipedal gait practiced by this taxon. The inverted position of the pes in those sloths that adopt

pedolateral stance is likely to have implied lateral translation of the body weight. This condition is in agreement with the resemblance of their structures, found when they are mediolaterally inverted, and suggests a similar inversion of the movements described for *A. sediba*. The pedolateral stance hence implies a stance phase marked by a medial translation of the patella, movements of lateral rotation of femur and tibia, and a supinatory torque, i.e., a lateral translation of the weight (Fig. 49) rather than medial as in *A. sediba*. Finally, DeSilva et al. (2013) predicted for *A. sediba* an increased robustness of the medial tarsals, metatarsals, and phalanges (no known material). This prediction is verified in pedolateral sloths when the structures are mediolaterally inverted, i.e., in sloths the lateral elements, and particularly Mt V, are more robust. Some features of sloths practicing pedolateral stance and bipedal apes are hence analogously departing from the quadrupedal plantigrade condition, with the acquisition of an asymmetrical knee, and the displacement of some elements away from a parasagittal plane passing through the acetabulum (although the structures are inverted mediolaterally). We do not consider these common features as necessarily indicative of obligatory bipedalism for the sloths practicing pedolateral stance. It rather suggests that pedolaterality implies drastic modifications of the forces applied to the different hind limb segments and of how body weight is supported during locomotion, as was apparently the case with the hyperpronation of *A. sediba*.

The five species of *Thalassocnus* are particularly interesting in this context, as they apparently document the shift from one posture to another. The lateral condyle of the femur is, in anterior view, distal to the level of the lateral one in *T. antiquus* and *T. natans* (Fig. 5a, b). In the late species of *Thalassocnus*, there is a reduction of the distal projection of the lateral condyle, bringing both condyles roughly to the same level. This has for consequence a modification of the bicondylar angle, which is around  $-5^\circ$  in *T. antiquus*, *T. natans*, and *T. littoralis* (negative angle relative to the angle of bipedal apes) and close to  $0^\circ$  in the later species of the genus (Fig. 48). This implies that in the early species of the genus, the knee was held abducted as in other sloths with pedolateral stance, and that in the late species of the genus, the knee was held below the acetabulum, acquiring a more classical parasagittal posture.

The medial trochlear ridge is very developed in the early species of *Thalassocnus*, and is gradually reduced in the late species (Figs. 10, 47c, d; Table 5). This suggests, considering the preceding analogy with bipedal apes, that the patella was subjected to medial translation forces in the early species of *Thalassocnus*, as in other sloths with pedolateral stance (except megatheriines; Fig. 47a, b), but that this was less so or no longer the case in the late species of the genus.

On the tibia, the intercondylar eminence is well developed in *T. antiquus*, but is reduced in the later species of the genus (Fig. 13). Similarly, the elevation found on the anteromedial border of the lateral articular surface of the

tibia (for the femoral condyle) is well developed in *T. antiquus* and *T. natans* but reduced in the later species of the genus. Elevated elements on the median part of the femorotibial articulation are probably related to the important rotation of the knee, which is purported in pedolateral sloths (Salas et al. 2005). The reduction of these structures in the late species of *Thalassocnus* hence possibly reflects the reduction of the rotation of the knee putatively associated with pedolateral stance.

Comparison of the ankle joints of the different species of *Thalassocnus* is of particular interest. On the distal epiphysis of the tibia, the median ridge, well elevated throughout the entire anteroposterior depth of the epiphysis, allows to all species of *Thalassocnus* (except *T. yaucensis*) and to *M. americanum* an extensive medial rotation (plantarflexion) of the inverted pes (Fig. 16). The low ridge of *T. yaucensis* that is restricted anteriorly is more reminiscent of that of plantigrade mammals. The angle of the plane in which the medial surface (for the odontoid process) lies to the shaft was pointed out as part of the “functional shift” accompanying the different modalities of the pedolateral stance (McDonald 2012). In all species of *Thalassocnus* except *T. yaucensis*, and in *M. americanum*, the plane in which the medial surface of the astragalar facet lies is directed proximomedially (Fig. 13; forming an angle less than 45° with the long axis of the shaft). In *T. yaucensis* it is less directed proximally, hence being more reminiscent of that of plantigrade mammals. These modifications of the tibia are reflected on the astragalus: the angle formed by the discoid and odontoid facets is well defined along its whole proximodistal extension and of 90° in *T. antiquus*, 95° in *T. natans*, and around 100° in *T. littoralis* (Fig. 24). This morphology is associated with the pedolateral stance. McDonald (2007, 2012) stated that a right angle between the discoid and odontoid facets implies that no dorsoplantar movement was possible, only mediolateral rotation. There is indeed a reduced dorsoplantar component to the rotation of the pes in *Thalassocnus* (i.e., reduced dorsiflexion when laterally rotated and plantarflexion when medially rotated). However, some degree of dorsoplantar movement is present, the reason being that even though the angle between the trochleae is close to 90°, the odontoid process is not directed proximally relative to the shaft of the tibia, but medioproximally. This condition differs from that seen, for instance, in *Lestodon*, in which the odontoid process is almost completely directed proximally, probably suppressing almost entirely the dorsoplantar movements. Furthermore, a discoid facet that extends proximally relative to the odontoid process, as in *Thalassocnus* for instance (no data for *T. yaucensis*), allows an extensive medial rotation of the pes. Finally, *T. yaucensis* (and some specimens referred to *T. carolomartini*) differs from the earlier species of the genus in featuring a less defined and more obtuse angle between the odontoid and discoid facets, being in this respect more reminiscent of plantigrade mammals. This was already pointed out by Salas et al. (2005).

It must also be pointed out that the tarsus of *T. carolomartini* features an autapomorphic character, namely the torsion of the distal calcaneum. Because of this torsion, the metatarsals are in a mediolateral position (Figs. 20b, 21b) rather than in a partly dorsoventral position as in the earlier species of the genus (Figs. 20a, 21a). This also contributes to the loss of pedolaterality and to the acquisition of a kind of secondary plantigrady.

Another feature apparently reflecting the use of the pedolateral stance is the articulation between the navicular and the astragalus. Firstly, in *Thalassocnus* and *M. americanum*, the navicular process faces only distally (Fig. 24) and not laterodistally as in other sloths. This causes a more medial position of Mt IV with respect to Mt V. In *M. americanum*, the process is even more plantarly positioned, which allows Mt III to be located medially as well. That is the reason why the pedes of *T. antiquus*, *T. natans*, *T. littoralis*, and *M. americanum* are more ‘spread’ medially than that of *Nothrotheriops* for instance, which features a completely vertical disposition of the metatarsals (and corresponding digits; see Lull 1929: plate VI). Secondly, a very concavo-convex and circular surface for the navicular as in *M. americanum* seems to allow great capability of inversion/eversion of the metatarsus and digits on the tarsus. These movements do not seem to have been particularly extensive in the early species of *Thalassocnus* and are even more reduced in the late species. This is seen when the astragalus of *T. antiquus* is compared to that of the later species of the genus, and when *T. yaucensis* is compared to the earlier species (Fig. 24; no data for the astragalus of the holotype of *T. natans* on which the surface for the navicular is slightly damaged). This feature varies in *T. carolomartini*, which displays a condition reminiscent of either *T. littoralis* or *T. yaucensis*. The facet for the astragalus of the navicular reflects such differences, because it is clearly more concavo-convex in *T. antiquus* than in the later species of the genus.

It must also be mentioned that the lateral process of Mt V is reduced in the late species of *Thalassocnus* (Fig. 42) relative to the early species (Fig. 41). Because robust lateral elements are apparently associated with the pedolateral stance (see above), the reduction of this process corroborates the shift to a plantigrade stance inferred for the late species of *Thalassocnus*.

Salas et al. (2005) argued that the cyamo-fabella of *T. natans* departs from that of other sloths in featuring a sulcus for the tendon of the gastrocnemius muscle. These authors concluded that this sesamoid bone apparently acted as a pulley to produce more powerful extension of the pes during swimming activity. However, observation of additional specimens seems to indicate that the presence of the sulcus in question is variable, and hence could not characterize any one species of *Thalassocnus*.

## Metatarsals and phalanges

In *Thalassocnus*, only metatarsals III to V are well developed, Mt I being absent and Mt II being very reduced (Fig. 32). This reduction of the medial elements is found to various degrees among sloths. The other metatarsals are long (when compared to their width at midshaft) in the early species of *Thalassocnus*, even relatively longer than those of other sloths sampled (Tables 19, 20; Figs. 35a, b, f, g, 36a, 39a, b). However, there is a distinct shortening of these metatarsals in the late species (Tables 19, 20, Figs. 35c-j, 36b-d, 39c-e) when compared to the early species of the genus. The shortening of the metatarsals in the late species of *Thalassocnus* is reminiscent of that of the metacarpals (Amson et al. in press). A ratio of shortening of the metapodials of *T. yaucensis* relative to *T. natans* can be defined by this equation:

$$\left( \left( \frac{D_{T. yaucensis}}{L_{T. natans}} - \frac{D_{T. natans}}{L_{T. yaucensis}} \right) \right) \cdot L_{T. yaucensis}$$

with  $D_T$  the width or depth of the metapodial for the taxon T and  $L_T$  the length of the metapodials for the taxon T. This ratio is around 0.3 for Mc IV and Mt IV, greater for the Mc II (0.38), and lesser for the Mc III (0.09). That of Mt III is greater than those of the other metapodials (for which there are data), because it scores 0.60. The shortening of Mt III is hence greater than those of other metapodials. A correlation of the shortening of this metatarsal (and to a lesser extent those of other metatarsals) in *Thalassocnus* with a function unique to this genus is hardly achievable, because a short Mt III is also found in other (terrestrial) Megatheria.

In all species of *Thalassocnus* the metatarsophalangeal articulation of the third digit has a small amplitude of flexion-extension. Furthermore, *T. carolomartini* and *T. yaucensis* were apparently nearly incapable of such movements. Additionally, in all species of *Thalassocnus* for which there are data (namely *T. natans* and *T. littoralis*), the distal interphalangeal articulation of the third digit is permanently flexed (see Figs. 20a, 21a, in which the articulation is positioned in maximum extension). Such morphology is hardly understandable from a functional standpoint if one considers the more plantigrade posture inferred for the late species of *Thalassocnus* (see above). In this context, one proposition would be that the strong ungual process of this digit might have acted as a crampon partly stuck into the substratum. The locked distal interphalangeal articulation found in *T. carolomartini* and *T. yaucensis* would have helped in this function.

## Hypothesis of functions of the hind limb

Most “ground sloths” are characterized by a large and everted wing of the ilium, a robust femur, and short tibia. The absence of such characteristics in *Thalassocnus* appears to be a derived condition related to different constraints applied to the hind limb. The plesiomorphic stance of *Thalassocnus*, represented in *T. antiquus*, is the pedolateral one. Like mylodontids and other Megatheria, the early species of *Thalassocnus* are characterized by an abducted knee, an asymmetrical patellar surface, and bearing of (at least a part of) the weight by the lateral side of the pes. This stance allows the development of large claws that are hence kept off the ground (in a sub-horizontal position), and is possibly related to bipedal stance (and/or locomotion). This stance was apparently associated with particular movements of the hind limb segments during stance phase, namely medial translation of the patella, lateral rotation of the femur and tibia, and a supinatory torque. However, the complex of characters associated with the pedolateral stance is modified in the late species of *Thalassocnus*. The two latest species, which show the greatest degree of departure from the plesiomorphic condition, are for these characters more reminiscent of plantigrade forms practicing parasagittal movement of the hind limb.

Quadrupedal paddling (‘dog-paddle’), practiced by most mammals, was probably part of the repertoire of swimming modes of *Thalassocnus* (see Amson et al. in press). As argued by Salas et al. (2005), the plantigrade position of the pes, postulated for one specimen (MUSM 347), may be considered as allowing more efficient paddling. The present study of the whole hind limb further substantiates the secondary plantigrady acquired by the late species of *Thalassocnus*, especially *T. carolomartini* and *T. yaucensis*. It is unlikely that *Thalassocnus* swam by pelvic rowing. Among mammals, pelvic rowing is used by *Ondatra* Link, 1795 (muskrat) when swimming underwater (Thewissen and Taylor 2007). The muskrat has an enlarged pes capable of great pronation (Howell 1930). Beside its long tibia and fibula (a feature seen in various semi-aquatic and aquatic mammals; see Muizon and McDonald 1995), *Thalassocnus* lacks the characteristics seen in mammals that swim by pelvic oscillation (phocids and the walrus, *Odobenus* Brisson, 1762; see Thewissen and Taylor 2007). The pes of mammals swimming by pelvic paddling is usually enlarged (Thewissen and Taylor 2007). Even *Hydromys* Geoffroy, 1804 (common water rat), which is considered by the latter authors to have poorly developed webbing, has a relatively enlarged pes (Howell 1930; Thewissen and Taylor 2007). Hence it is unlikely that the pes of *Thalassocnus*, with its relatively small surface, generated enough thrust to allow efficient pelvic paddling. However, the plantigrade position seen in the late species of *Thalassocnus* probably increased the thrust. Therefore, in addition to quadrupedal paddling, another swimming mode in which the hind limb of *Thalassocnus* is likely to have been actively used is bottom-walking. This is suggested by studies of the internal microstructure of various bones (Amson et al. 2014) ; see also subsequent study



of the axial postcranium). In this context, the plantigrade pes, with the strong third ungual phalanx that was permanently flexed, may have also helped for stabilizing purposes, anchored on the seafloor and/or helping in bottom-walking by increasing the surface of contact with the substratum. A similar function was suggested for the posterolaterally-directed pes of desmostylians (Domning 2002). Stabilization was apparently critical to bottom-walking putatively practiced by *Thalassocnus*, especially its late species, as it is also reflected in the forelimb morphology. Hildebrand (1985) argued that the fossorial activity of forelimb diggers is associated with bracing. According to Hildebrand, large (terrestrial) diggers have sufficient weight for this purpose. However, smaller forms usually need to grip the soil with pedal fingers and claws. One can suppose that an analogous need for bracing was found in *Thalassocnus* during underwater digging (see the study of the forelimb; Amson et al. in press), as the weight of the animal was partially nullified by the buoyant force. A great mobility of the hip is found in *Thalassocnus*, especially in femoral abduction. As a matter of fact, Hildebrand (1985) mentions unusual abduction capability for the hind limb of mammals that dig with the forelimb.

The iliac wing of *Thalassocnus* is not everted like that of other sloths of similar size. Moreover, it is reduced in the late species of *Thalassocnus*, along with the rest of the hind limb. These characters seem to suggest a decreased function of support for the hind limb, which putatively reflects habitual (at least partial) submergence for the late species of *Thalassocnus*.

## CONCLUSION

The hind limb of *Thalassocnus* is on the whole characterized by a small iliac wing, a gracile femur with well-formed femoral neck, a teardrop shaped patella, a long and slender tibia, the triangular shape of the tuber calcis, and proximal development of the lateral process of Mt V. All species of *Thalassocnus* feature a fully developed hind limb. The latest species of the genus, namely *T. carolomartini* and *T. yaucensis*, have nearly solid (amedullar) long bones (Amson et al. 2014), and it is most likely that all segments of their hind limb were functional and bore a part of the weight. Some characters showing interspecific variation are difficult to interpret from a functional standpoint. This is true for instance in the case of the shorter metatarsals, and particularly Mt III, which is also extremely shortened in other (terrestrial) Megatheria. But, as was the case for internal microstructure of various bones (Amson et al. 2014), craniomandibular and dental (Muizon et al. 2004b), and forelimb gross morphology (Amson et al. in press), comparison of the species of *Thalassocnus* with each other suggests a progressive shift to a particular ecology from the earliest to the latest species of the genus. Their adaptation to this ecology was apparently accompanied by a

gradual loss of osteological traits associated with the pedolateral stance, and hence the acquisition of a secondary plantigrady. The early species of *Thalassocnus* clearly show all morphological traits associated with the pedolateral stance, which is found in all families of Eutardigrada except megalonychids. These traits are lost in the late species of *Thalassocnus*, particularly *T. carolomartini* and *T. yaucensis*. A plantigrade hind limb may have indeed been more efficient for paddling (although no enlargement of the pes is observed) and for bottom-walking (increasing the surface of contact with the substratum). The pes may have also contributed to underwater stabilization, anchoring the body during foraging/fossorial activity with the forelimbs. Finally, the morphology of the pelvis and the slight overall reduction of the hind limb in the late species of *Thalassocnus* suggest for these species more habitual (at least partial) submergence.

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## Figure legends

**Fig. 1** Pelvis of *Thalassocnus littoralis*: **a**, dorsal view (MUSM 223); and **b**, lateral view

(MNHN.F.MNHN.F.SAS251). Abbreviation: S4, fourth sacral vertebra

[Intended for double column width]

**Fig. 2** Iliac wing and acetabulum of *Thalassocnus* in laterodorsal view (normal to plane of the iliac wing): **a**, *T.*

*antiquus* (holotype, MUSM 228, left inverted); **b**, *T. littoralis* (MUSM 223, right); and **c**, *T. carolomartini*

(MNHN.F.SAO201, left inverted)

[Intended for double column width]

**Fig. 3** Different orientations of the iliac wing in Megatheria other than *Thalassocnus*: Left lateral view of the pelvis

of **a**, *Nothrotherium*; and **b**, *Megatherium americanum*. Not to scale

[Intended for single column width]

**Fig. 4** Iliac wing and acetabulum of *T. carolomartini* (MNHN.F.SAO201, left inverted) in lateral view

[Intended for single column width]

**Fig. 5** Femur of *Thalassocnus* in anterior view: **a**, *T. antiquus* (holotype, MUSM 228, left inverted); **b**, *T.*

*natans* (holotype, MNHN.F.SAS734, right); **c**, *T. littoralis* (MUSM 223, right); and **d**, *T. carolomartini*,

(MUSM 1995, right)

[Intended for double column width]

**Fig. 6** Right femur of *Thalassocnus yaucensis* (MUSM 434) in anterior view

[Intended for single column width]

**Fig. 7** Femur of *Thalassocnus* in posterior view: **a**, *T. antiquus* (holotype, MUSM 228, left inverted); **b**, *T.*

*natans* (holotype, MNHN.F.SAS734, left inverted); **c**, *T. littoralis* (MUSM 223, right); **d**, *T.*

*carolomartini*, (MUSM 1995, right); and **e**, *T. yaucensis* (MUSM 434, left inverted)



[Intended for double column width]

**Fig. 8** Right femur of *Thalassocnus* in medial view: **a**, *T. natans* (holotype, MNHN.F.SAS734); **b**, *T. littoralis* (MUSM 223); and **c**, *T. carolomartini*, (MUSM 1995)

[Intended for single column width]

**Fig. 9** Right femur of *Thalassocnus* in lateral view: **a**, *T. natans* (holotype, MNHN.F.SAS734); **b**, *T. littoralis* (MUSM 223); and **c**, *T. carolomartini*, (MUSM 1995)

[Intended for single column width]

**Fig. 10** Femur of *Thalassocnus* in distal view: **a**, *T. antiquus* (holotype, MUSM 228, left inverted); **b**, *T. natans* (holotype, MNHN.F.SAS734, right); **c**, *T. littoralis* (MUSM 223, right); **d**, *T. carolomartini*, (MNHN.F.SAO201, right); and **e**, *T. yaucensis* (MUSM 434, left inverted)

[Intended for single column width]

**Fig. 11** Femur of *Thalassocnus antiquus* (holotype, MUSM 228, left inverted) in distal view with explanatory drawing. Abbreviations: MTR, anteroposterior depth of medial trochlear ridge located anterior to the level of the lateral trochlear ridge; LTR, depth of the distal epiphysis at the level of the lateral trochlear ridge

[Intended for single column width]

**Fig. 12** Patella of *Thalassocnus*: anterior (**a-d**), posterior (**e-h**) and lateral (**i-l**) views of *T. antiquus* (**a, e, i**; holotype, MUSM 228, left inverted); *T. natans* (**b, f, j**; holotype, MNHN.F.SAS734, right); *T. littoralis* (**c, k, h**; MUSM 223, right); and *T. yaucensis* (**d, h, l**; MUSM 347, right)

[Intended for double column width]

**Fig. 13** Tibia of *Thalassocnus* in anterior view: **a**, *T. antiquus* (holotype, MUSM 228, left proximal epiphysis inverted and right distal epiphysis); **b**, *T. natans* (holotype, MNHN.F.SAS734, right); **c**, *T. littoralis* (MNHN.F.SAS53, left inverted); **d**, *T. carolomartini*, (MNHN.F.SAO201, right); and **e**, *T. yaucensis* (MUSM 347, left proximal epiphysis inverted)

[Intended for double column width]

**Fig. 14** Tibia of *Thalassocnus* in posterior view: **a**, *T. antiquus* (holotype, MUSM 228, right distal epiphysis); **b**, *T. natans* (holotype, MNHN.F.SAS734, right); **c**, *T. littoralis* (MNHN.F.SAS53, left inverted); and **d**, *T. carolomartini*, (MNHN.F.SAO201, right)

[Intended for double column width]

**Fig. 15** Tibia of *Thalassocnus* in proximal view: **a**, *T. antiquus* (holotype, MUSM 228, left inverted); **b**, *T. natans* (holotype, MNHN.F.SAS734, right); **c**, *T. littoralis* (MNHN.F.SAS53, left inverted); and **d**, *T. carolomartini*, (MNHN.F.SAO201, right) Abbreviation: f., facet.

[Intended for double column width]

**Fig. 16** Tibia of *Thalassocnus* in distal view: **a**, *T. antiquus* (holotype, MUSM 228, right); **b**, *T. natans* (holotype, MNHN.F.SAS734, right); **c**, *T. littoralis* (MNHN.F.SAS53, left inverted); **d**, *T. carolomartini*, (MNHN.F.SAO201, right); and **e**, *T. yaucensis* (MUSM 347, left inverted). Abbreviation: f., facet

[Intended for double column width]

**Fig. 17** Cyamo-fabella of *Thalassocnus* in distal view: **a**, *T. natans* (holotype, MNHN.F.SAS734, right); and **b**, *T. littoralis* (MNHN.F.SAS53, left inverted)

[Intended for single column width]

**Fig. 18** Left fibula of *Thalassocnus* in anterior view: **a**, *T. antiquus* (holotype, MUSM 228); **b**, *T. natans* (holotype, MNHN.F.SAS734); **c**, *T. littoralis* (MNHN.F.SAS761)

[Intended for single column width]

**Fig. 19** Left fibula of *Thalassocnus* in medial view: **a**, *T. antiquus* (holotype, MUSM 228); **b**, *T. natans* (holotype, MNHN.F.SAS734); **c**, *T. littoralis* (MNHN.F.SAS761)

[Intended for single column width]

**Fig. 20** Pes of *Thalassocnus* in dorsal view: **a**, *T. natans* (holotype, MNHN.F.SAS734, left); **b**, *T. carolomartini* (MUSM 1995, right inverted, phalanges not shown). Abbreviations: D., digit; Mt, metatarsal; ph., phalanx

[Intended for double column width]

**Fig. 21** Pes of *Thalassocnus* in lateral view: **a**, *T. natans* (holotype, MNHN.F.SAS734, left); **b**, *T. carolomartini* (MUSM 1995, right inverted, phalanges not shown). Abbreviations: D., digit; Mt, metatarsal; ph., phalanx

[Intended for double column width]

**Fig. 22** The two main morphologies of the pes of sloths: lateral view of left pes of **a**, the ‘low-arched’ pes of *Megatherium americanum*; and **b**, the ‘high-arched’ pes of *Scelidotherium leptocephalum* Owen, 1839. Not to scale

[Intended for single column width]

**Fig. 23** Left astragalus of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, dorsal view; **b**, plantar; **c**, fibular (roughly identical to lateral); and **d**, distal views. Abbreviation: f. (fs for plural), facet

[Intended for double column width]

**Fig. 24** Astragalus of *Thalassocnus* in distal view: **a**, *T. antiquus* (holotype, MUSM 228, right inverted); **b**, *T. natans* (holotype, MNHN.F.SAS734, left); **c**, *T. littoralis* (MNHN.F.SAS163, left); **d**, *T. carolomartini*, (MUSM 1995, right inverted); and **e**, *T. yaucensis* (MUSM 347, left)

[Intended for single column width]

**Fig. 25** Right calcaneum of *Thalassocnus antiquus* (holotype, MUSM 228): **a**, dorsal view; **b**, plantar; and **c**, distal views. Abbreviation: f., facet

[Intended for single column width]

**Fig. 26** Left calcaneum of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, dorsal view; **b**, plantar; **c**, lateral; and **d**, distal views. Abbreviation: f. (fs for plural), facet

[Intended for double column width]

**Fig. 27** Left calcaneum of *Thalassocnus carolomartini* (MNHN.F.SAO16): **a**, plantar; **b**, lateral; and **c**, distal views. Abbreviation: f., facet

[Intended for single column width]

**Fig. 28** Right navicular of *Thalassocnus antiquus* (holotype, MUSM 228): **a**, medial; **b**, lateral; **c**, proximal; and **d**, distal views. Abbreviation: f. (fs for plural), facet

[Intended for single column width]

**Fig. 29** Articulated left navicular and ectocuneiform of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, dorsal; **b**, plantar; **c**, medial; **d**, lateral; **e**, proximal and **f**, distal views.

Abbreviations: Ecc., ectocuneiform; f., facet; Na., navicular

[Intended for single column width]

**Fig. 30** Left cuboid of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, medial; **b**, lateral; **c**, proximal; and **d**, distal views. Abbreviation: f. (fs for plural), facet

[Intended for single column width]

**Fig. 31** Right ectocuneiform of *Thalassocnus antiquus* (holotype, MUSM 228): **a**, lateral; **b**, proximal; and **c**, distal views. Abbreviation: f. (fs for plural), facet

[Intended for single column width]

**Fig. 32** Left second metatarsal of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, dorsal; **b**, lateral; **c**, proximal; and **d**, distal views. Abbreviation: f., facet.

[Intended for single column width]

**Fig. 33** Right second digit of *Thalassocnus littoralis* (MUSM 438). Co-ossified proximal and second phalanges in **a**, dorsal; and **b**, medial views. Ungual phalanx in **c**, dorsal; and **d**, medial views

[Intended for single column width]

**Fig. 34** Left third metatarsal of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, dorsal; **b**, lateral; **c**, proximal; and **d**, distal views. Abbreviation: f., facet

[Intended for single column width]

**Fig. 35** Third metatarsal of *Thalassocnus*: lateral (**a-e**) and dorsal (**f-j**) views of *T. antiquus* (**a, f**; holotype, MUSM 228, right inverted); *T. natans* (**b, g**; holotype, MNHN.F.SAS734, left); *T. littoralis* (**c, h**; MUSM 438, right inverted); *T. carolomartini*, (**d, i**; MUSM 1995, right inverted); and *T. yaucensis* (**e, j**; MNHN.F.PPI278, left)

[Intended for single column width]

**Fig. 36** Outlines of the third metatarsal of *Thalassocnus*. The size of each specimen was modified in order to bring the mediolateral width at midshaft to a common value. **a**, *T. natans* (holotype, MNHN.F.SAS734, left); **b**, *T. littoralis* (MUSM 438, right inverted); **c**, *T. carolomartini*, (MUSM 1995, right inverted); and **d**, *T. yaucensis* (MNHN.F.PPI278, left)

[Intended for double column width]

**Fig. 37** Left third digit of *Thalassocnus natans* (holotype, MNHN.F.SAS734). Co-ossified proximal and second phalanges in **a**, dorsal; and **b**, medial views. Ungual phalanx in **c**, dorsal; and **d**, medial views

[Intended for single column width]

**Fig. 38** Left fourth metatarsal of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, medial; **b**, lateral; and **c**, proximal views. Abbreviation: f., facet

[Intended for single column width]

**Fig. 39** Fourth metatarsal of *Thalassocnus* in medial view: **a**, *T. antiquus* (holotype, MUSM 228, right inverted); **b**, *T. natans* (holotype, MNHN.F.SAS734, left); **c**, *T. littoralis* (MNHN.F.SAS1605, right inverted); **d**, *T. carolomartini*, (MUSM 1995, right inverted); and **e**, *T. yaucensis* (MUSM 2065, left)  
[Intended for double column width]

**Fig. 40** Left second (**a**) and ungual (**b**) phalanges of the fourth digit of *Thalassocnus natans* (holotype, MNHN.F.SAS734) in dorsal view  
[Intended for single column width]

**Fig. 41** Left fifth metatarsal of *Thalassocnus natans* (holotype, MNHN.F.SAS734): **a**, dorsal; **b**, plantar; and **c**, medial views. Abbreviation: f., facet  
[Intended for double column width]

**Fig. 42** Fifth metatarsal of *Thalassocnus*: *T. carolomartini* (MNHN.F.SASO201) in **a**, dorsal; and **b**, plantar views; *T. yaucensis* in **c**, dorsal (MUSM 347, right); and **d**, plantar (MUSM 2065, right) views. For MNHN.F.SASO201, the proximal portion is that of the right metatarsal and is inverted; the distal portion is that of the left metatarsal. A complete hybrid image is obtained thanks to the presence of an overlap between the two fragments. Abbreviation: f., facet  
[Intended for single column width]

**Fig. 43** Right fifth metatarsal of *Thalassocnus antiquus* (holotype, MUSM 228) in dorsal view.  
Abbreviation: f., facet  
[Intended for single column width]

**Fig. 44** Phalanx of fifth digit of *Thalassocnus littoralis* (MUSM 438): **a**, lateral or medial; **b**, proximal; and **c**, distal views. Abbreviation: f., facet  
[Intended for single column width]

**Fig. 45** Comparison of right acetabula in lateral view: **a**, *Thalassocnus*; **b**, *Nothrotherium*; and **c**, *Megatherium americanum*. Not to scale

[Intended for single column width]

**Fig. 46** Articulated right hind limb of *Thalassocnus* and *Nothrotherium*. **a**, *Thalassocnus* during maximum abduction of the femur; and **b**, *Nothrotherium* with femur in neutral position (i.e., slight abduction of the knee). Not to scale

[Intended for single column width]

**Fig. 47** Comparison of the femora of nothrotheriids in distal view: **a**, *Nothrotherium* (MCL 21937, right inverted); **b**, *Nothrotheriops* (LACM 21618); **c**, *T. antiquus* (holotype, MUSM 228, right inverted); and **d**, *T. yaucensis* (MUSM 347, left).

[Intended for single column width]

**Fig. 48** Bicondylar angle in *Homo sapiens* and *Thalassocnus*. Femur in anterior view of *H. sapiens* (not to scale); *T. antiquus* (holotype, MUSM 228, left inverted); *T. natans* (holotype, MNHN.F.SAS734, right); *T. littoralis* (MNHN.F.SAS1621, right); *T. carolomartini*, (MUSM 1995, right); and *T. yaucensis* (holotype, MUSM 434, left inverted). The infracondylar plane is aligned with the horizontal

[Intended for double column width]

**Fig. 49** Articulated right hind limb of a *Paramylodon harlani* (Owen, 1840) in anterior view. The grey arrows indicate the inferred rotatory movements implicated by the pedolateral stance. The posture is exemplified as bipedal (hence the very horizontal orientation of the femur)

[Intended for single column width]

## Tables

Table 1. General size (based on femur) in *Thalassocnus* and other megatherioids. Proximodistal length of femur is given in millimeters and taken at the level of the greater trochanter.

Taxon	Specimen number	PD length
<i>T. natans</i>	MNHN.F.SAS734	312.8
<i>T. littoralis</i>	MNHN.F.SAS40	305.1
	MNHN.F.SAS41	283.7
	MNHN.F.SAS42	264.6
	MNHN.F.SAS53	288.4
	MNHN.F.SAS158	273.0
	MNHN.F.SAS1611	317.1
	MNHN.F.SAS1621	290.8
	MUSM 223	310.0
<i>T. carolomartini</i>	MUSM 1995	323.5
<i>T. yaucensis</i>	MUSM 38	276*
	MUSM 434	401*
<i>Nothrotheriops</i>	LACM 21618	387.3
<i>N. maquinense</i>	MCL 1020	221.2
	MCL 2819	242.4
	MCL 21937	234.7
	MCL 21978	232.6
<i>Mionothropus</i>	LACM 4609/117533	300.5
<i>Hapalops</i>	MNHN.F.1902-6	178.6
<i>Planops</i>	BMNH M.9211	315

Footnotes: \*, estimate; PD, proximodistal.

Table 2. Measurements (in millimeters) of the pelvis of *Thalassocnus*.

	<i>T. antiquus</i>	<i>T. natans</i>	<i>T. littoralis</i>	<i>T. carolomartini</i>	<i>T. yaucensis</i>
ilium, AP length of lateral border (from iliac crest to anterior edge of acetabulum)	174*	-	186* (MUSM 223)	156* (MNHN.F.SAO201)	-
ilium, greatest width (just posterior to ventral iliac spine, perpendicular to dorsal surface of wing)	-	-	178.5 (MNHN.F.SAS251)	171.7 (MNHN.F.SAO201)	-
acetabulum, AP diameter (at level of posteroventral edge of ischiatic cornu)	59.8	-	58.4 (MNHN.F.SAS8); 63.1 (MNHN.F.SAS251); 63* (MUSM 223)	64.8 (MNHN.F.SAO201)	-
acetabulum, DV diameter	53.7	-	48.5 (MNHN.F.SAS8); 56.8 (MNHN.F.SAS251); 62.2 (MUSM 223)	61.2 (MNHN.F.SAO201)	-
acetabulum, depth in dorsal view	18.4	-	12.2 (MNHN.F.SAS8); 18* (MNHN.F.SAS251); 13.7 (MUSM 223)	20.9 (MNHN.F.SAO201)	-



ischium, AP length (from ischiatic cornu of acetabulum to posterior edge of ischiatric tuberosity)	-	-	130.5 (MUSM 223)	-	-
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Footnotes: If no specimen number is given after a measurement, it is that of the holotype of the species. \*, estimate; AP, anteroposterior; DV, dorsoventral.

Table 3. Measurements (in millimeters) of the femur of *Thalassocnus*.

	<i>T. antiquus</i>	<i>T. natans</i>	<i>T. littoralis</i>	<i>T. carolomartini</i>	<i>T. yaucensis</i>
			305.1 (MNHN.F.SAS40); 283.7 (MNHN.F.SAS41); 264.6 (MNHN.F.SAS42); 288.4 (MNHN.F.SAS53); 273.0 (MNHN.F.SAS158); 317.1 (MNHN.F.SAS1611);		
greatest PD length (from proximal tip of greater trochanter to distal surface of lateral condyle)	-	312.8; 339.5 (MUSM 1916)	290.8 (MNHN.F.SAS1621); 310.0 (MUSM 223); 304.5 (2062)	324* (MNHN.F.SAO201); 257.8 (MNHN.F.SAO203); 323.5 (MUSM 1995)	276*; 401* (MUSM 434)
			31* (MNHN.F.SAS40); 33.7 (MNHN.F.SAS41); 31.1 (MNHN.F.SAS42); 28.4 (MNHN.F.SAS53); 30* (MNHN.F.SAS158); 32.3 (MNHN.F.SAS492); 34* (MNHN.F.SAS1611);		
head, PD radius (normal to the base of the head, anterior view)	31.9	33.7; 37.8 (MUSM 1916)	31.9 (MNHN.F.SAS1621); 33.4 (MUSM 223);	27.5 (MNHN.F.SAO203); 32* (MUSM 1995)	32.0; 43.9 (MUSM 434)
			54.5 (MNHN.F.SAS40); 50.5 (MNHN.F.SAS41); 51* (MNHN.F.SAS42); 49.7 (MNHN.F.SAS492); 55* (MNHN.F.SAS1611);		
head, ML diameter (normal to the base of the head)	52.3	54*; 65.2 (MUSM 1916)	51.6 (MNHN.F.SAS1621); 56.9 (MUSM 223);	48* (MNHN.F.SAO203); 63.7 (MUSM 1995)	47.9; 71.9 (MUSM 434)

			54.1 (MNHN.F.SAS40); 49.6 (MNHN.F.SAS41); 52.8 (MNHN.F.SAS42); 51.5 (MNHN.F.SAS53); 53.5 (MNHN.F.SAS158); 50.1 (MNHN.F.SAS492); 57* (MNHN.F.SAS1611); 51.9 (MNHN.F.SAS1621); 58.6 (MUSM 223)	47.9 (MNHN.F.SAO203); 60* (MUSM 1995)	48.1; 68.6 (MUSM 434)
head, AP diameter (normal to the base of the head)	46.8	55.5; 61.7 (MUSM 1916)	89* (MNHN.F.SAS9); 107.6 (MNHN.F.SAS40); 93.1 (MNHN.F.SAS41); 87* (MNHN.F.SAS42); 99.0 (MNHN.F.SAS53); 93.6 (MNHN.F.SAS55); 100* (MNHN.F.SAS158); 91.7 (MNHN.F.SAS492); 107.8 (MNHN.F.SAS1611); 101.5 (MNHN.F.SAS1621); 110.3 (MUSM 223)	101* (MNHN.F.SAO201); 88.6 (MNHN.F.SAO203); 132.1 (MUSM 1995)	98.9; 162* (MUSM 434)
proximal end, greatest ML width (from medial edge of head to lateral edge of greater trochanter)	-	109.1; 122.9 (MUSM 1916)	49.1 (MNHN.F.SAS40); 54.5 (MNHN.F.SAS41); 38.7 (MNHN.F.SAS42); 41.5 (MNHN.F.SAS53); 50.0 (MNHN.F.SAS158); 33.4** (MNHN.F.SAS493); 50.8 (MNHN.F.SAS1611); 46.5 (MNHN.F.SAS1621); 51.8 (MUSM 223); 59.4 (1995)		73.2 (MUSM 434)
midshaft, ML width	46.0**	57.8; 55.7 (MUSM 1916)		59.4 (MUSM 1995)	

			32.0 (MNHN.F.SAS40); 30.8 (MNHN.F.SAS41); 25.7 (MNHN.F.SAS42); 30.0 (MNHN.F.SAS53); 29.5 (MNHN.F.SAS158); 21.2** (MNHN.F.SAS493); 31.4 (MNHN.F.SAS1611); 30.8 (MNHN.F.SAS1621); 34.0 (MUSM 223)			
midshaft, AP depth	27.4**	34.2; 35.1 (MUSM 1916);	37.0 (MUSM 1995)		45.4 (MUSM 434)	
epicondyles, ML width (oblique to shaft)	-	116*; 110.9 (MUSM 1916);	97.6 (MNHN.F.SAS40); 89.1 (MNHN.F.SAS42); 90.8 (MNHN.F.SAS737); 106.0 (MNHN.F.SAS1611); 101.4 (MNHN.F.SAS1621)	112.8 (MNHN.F.SAO12); 103.9 (MNHN.F.SAO201); 88.7 (MNHN.F.SAO203); 113.3 (MUSM 1995)	109* (MUSM 347); 135.9 (MUSM 434)	
AP depth of medial trochlear ridge anterior to lateral one (measured on photographs)	11.7	13.6	9.5 (MNHN.F.SAS1611); 9.0 (MNHN.F.SAS1621); 9.4 (MUSM 223)	9.1 (MNHN.F.SAO201)	6.6 (MUSM 434)	
AP depth at lateral trochlear ridge (measured on photographs)	42.2	56.3	46.1 (MNHN.F.SAS1611); 44.2 (MNHN.F.SAS1621); 50.8 (MUSM 223)	53.5 (MNHN.F.SAO201)	66.3 (MUSM 434)	

Footnotes: If no specimen number is given after a measurement, it is that of the holotype of the species; \*, estimate; \*\*, measurement at estimated midshaft; AP, anteroposterior; ML, mediolateral; PD, proximodistal.

Table 4. Proximodistal length of the femur compared to the width at midlength in *Thalassocnus* and other megatherioids.

Taxon	Specimen number	PD length (L)	ML width at midshaft (W)	L/W	Species value (mean if several specimens)
<i>T. natans</i>	MNHN.F.SAS734	312.8	57.8	5.41	5.75
	MUSM 1916	339.5	55.7	6.10	
<i>T. littoralis</i>	MNHN.F.SAS40	305.1	49.1	6.21	6.14
	MNHN.F.SAS41	283.7	54.5	5.21	
	MNHN.F.SAS42	264.6	38.7	6.84	
	MNHN.F.SAS53	288.4	41.5	6.95	
	MNHN.F.SAS158	273.0	50.0	5.46	
	MNHN.F.SAS1611	317.1	50.8	6.24	
	MNHN.F.SAS1621	290.8	46.5	6.25	
	MUSM 223	310.0	51.8	5.98	
<i>T. carolomartini</i>	MUSM 1995	323.5	59.4	5.45	5.45
<i>T. yaucensis</i>	MUSM 434	401*	73.2	5.48	5.48
<i>Hapalops</i>	MNHN.F.1902-6	178.6	51	3.50	3.50
<i>Nothrotheriops</i>	LACM 21618	387.3	114.1	3.39	3.39

<i>Nothrotherium</i>	MCL 1020	221.2	48.0	4.61	4.61
<i>Mionothropus</i>	LACM 4609/117533	300.5	92.4	3.25	3.25

Footnotes: \*, estimate; ML, mediolateral; PD, proximodistal.

Table 5. Development of medial trochlear ridge in *Thalassocnus* and other megatherioids.

Taxon	Specimen number	AP depth of medial trochlear ridge anterior to lateral one (Dm)	AP depth at lateral trochlear ridge (DI)	Dm/DI	Species value (mean if several specimens)
<i>T. antiquus</i>	MUSM 228	11.7	42.2	0.277	0.277
<i>T. natans</i>	MNHN.F.SAS734	13.6	56.3	0.242	0.242
<i>T. littoralis</i>	MNHN.F.SAS1611	9.5	46.1	0.206	0.198
	MNHN.F.SAS1621	9.0	44.2	0.204	
	MUSM 223	9.4	50.8	0.185	
<i>T. carolomartini</i>	MNHN.F.SAO201	9.1	53.5	0.170	0.170
<i>T. yaucensis</i>	MUSM 434	6.6	66.3	0.100	0.100
<i>Hapalops</i>	MNHN.F.1902-6	6.3	32.6	0.193	0.193
<i>Nothrotheriops</i>	LACM 21618	13.0	60.1	0.216	0.216
<i>Nothrotherium</i>	MCL 21937	8.9	32.6	0.273	0.273
<i>Mionothropus</i>	LACM 4609/117533	17.6	61.4	0.287	0.287
<i>Planops</i>	BMNH M.9207	12.8	50.0	0.256	0.256

Footnotes: AP, anteroposterior.

Table 6. Proximodistal length of femur compared to that of humerus in *Thalassocnus* and other Megatheria.

Taxon	Specimen number	PD length of femur (Lf)	PD length of humerus (Lh)	Lf/Lh	Species value (mean if several specimens)
<i>T. natans</i>	MNHN.F.SAS734	312.8	255.4	1.22	1.22
<i>T. littoralis</i>	MNHN.F.SAS53	288.4	243.2	1.19	1.14
	MUSM 223	310.0	284*	1.09	
<i>T. carolomartini</i>	MUSM 1995	323.5	297.0	0.96	1.09
<i>Nothrotheriops</i>	YPM 13198	332	387	0.86	0.86
<i>Nothrotherium</i>	MCL 1020	221.2	248.7	0.89	0.89
<i>Mionothropus</i>	LACM 4609/117533	300.5	319.5	0.94	0.94
<i>Planops</i>	BMNH M.9207	314.5	282	1.12	1.12
<i>M. americanum</i>	holotype; data from Casinos (1996)	678	678	1.00	1.00

Footnotes: PD, proximodistal.

Table 7. Mediolateral width of femur at epicondyles compared to that of humerus at proximal tuberosities in *Thalassocnus* and other nothrotheriids.

Taxon	Specimen number	ML width of femur at epicondyles (Wf)	ML width of humerus at proximal tuberosities (Wh)	Wf/Wh
<i>T. natans</i>	MNHN.F.SAS734	116*	83.3	1.39
<i>T. littoralis</i>	MUSM 223	110.3	84*	1.31
<i>T. carolomartini</i>	MUSM 1995	113.3	90.8	1.25
<i>T. yaucensis</i>	MUSM 347	109*	95.1	1.15
<i>Nothrotheriops</i>	YPM 13198	163.5	94.2	1.74
<i>Nothrotherium</i>	MCL 1020	92.9	57.2	1.62
<i>Mionothropus</i>	LACM 4609/117533	123.6	74.2	1.67

*Planops* BMNH M.9207 117 86 1.36

Footnotes: \*, estimate; ML, mediolateral.

Table 8. Proximodistal length of femur compared to mandible and skull measurements in *Thalassocnus* and other nothrotheriids.

Taxon	Specimen number	PD length of femur (Lf)	Maximum depth of horizontal ramus of mandible (Md)	Lf/Md	AP length from anterior of M1 to posterior of M4 (Ls)	Lf/Ls
<i>T. natans</i>	MNHN.F.SAS734	312.8	44.8	6.98	50.7	6.17
<i>T. littoralis</i>	MUSM 223	310.0	45.4	6.83	53.7	5.77
<i>T. carolomartini</i>	MNHN.F.SAO203	257.8	45.9	5.62	58.5	4.41
<i>T. yaucensis</i>	MUSM 37	276*	46.4	5.95	60.7	4.55
<i>Nothrotherium</i>	MCL 1020	221.2	32.4	6.83	43.7	5.06
<i>Mionothropus</i>	LACM 4609/117533	300.5	45.1	6.66	46.4	6.48

Footnotes: AP, anteroposterior; PD, proximodistal.

Table 9. Measurements (in millimeters) of the patella of *Thalassocnus*.

	<i>T. antiquus</i>	<i>T. natans</i>	<i>T. littoralis</i>	<i>T. yaucensis</i>
greatest PD length (from proximal border to distal tip of apex)	63*	68.3; 69.3 (MNHN.F.SAO?210)	65.5 (MNHN.F.SAS50); 65.3 (MNHN.F.SAS491); 49.0 (MNHN.F.SAS1622); 62.6 (MUSM 223)	68.5 (MUSM 347)
PD length of facet for femur at mid-width	31.9	36.4; 36.7 (MNHN.F.SAO?210)	33.5 (MNHN.F.SAS50); 33.1 (MNHN.F.SAS53); 37.3 (MUSM 223)	37.2 (MUSM 347)
PD length of apex	27*	22.3; 26.9 (MNHN.F.SAO?210)	25.3 (MNHN.F.SAS50); 22.9 (MNHN.F.SAS491); 21.8 (MUSM 223)	23.6 (MUSM 347)
ML width at mid-length of facet for femur	50.4	53.7; 57.3 (MNHN.F.SAO?210)	59.0 (MNHN.F.SAS50); 49.4 (MNHN.F.SAS53); 50.5 (MNHN.F.SAS491); 40.1 (MNHN.F.SAS1622);	50.9 (MUSM 347)

			21.0 (MNHN.F.SAS9);	
			25.4 (MNHN.F.SAS50);	
			23.0 (MNHN.F.SAS53);	
			22.3 (MNHN.F.SAS173);	
			22.7 (MNHN.F.SAS491);	
			22.9 (MNHN.F.SAS1605);	
AP depth at middle of facet for femur	23.6	27.2; 30.5 (MNHN.F.SAO?210)	19.3 (MNHN.F.SAS1622); 26.1 (MUSM 223)	25.5 (MUSM 347)

Footnotes: No data for *T. carolomartini*. If no specimen number is given after a measurement, it is that of the holotype of the species; \*, estimate; AP, anteroposterior; ML, mediolateral; PD, proximodistal.

Table 10. Development of apex of patella in *Thalassocnus* and nothrotheriids.

Taxon	Specimen number	PD length of apex (La)	PD length of facet for femur at mid-width (Lf)	La/Lf
<i>T. antiquus</i>	MUSM 228	27	31.9	0.85
<i>T. natans</i>	MNHN.F.SAS734	22.3	36.4	0.61
<i>T. littoralis</i>	MNHN.F.SAS50	25.3	33.5	0.76
	MUSM 223	21.8	37.3	0.58
<i>T. yaucensis</i>	MUSM 347	23.6	37.2	0.63
<i>Thalassocnus</i> sp.	MNHN.F.PPI245	25.2	28.5	0.88
<i>Nothrotheriops</i>	LACM 156609	33.3	55.7	0.60
<i>Nothrotherium</i>	MCL 1020	20.5	31.6	0.65
<i>Mionothropus</i>	LACM 4609/117533	32.1	27.7	1.16

Footnotes: PD, proximodistal.

Table 11. Size of patella compared to depth of mandible in *Thalassocnus* and other nothrotheriids.

Taxon	Specimen number	PD length of facet for femur of patella at mid- length (Lp)	Maximum depth of horizontal ramus of mandible (Md)	Lp/Md	ML width of facet for femur of patella at mid- length (Wp)	Wp/Md
<i>T. antiquus</i>	MUSM 228	31.9	42.5	0.75	50.4	1.19
<i>T. natans</i>	MNHN.F.SAS734	36.4	44.8	0.81	53.7	1.20
<i>T. littoralis</i>	MUSM 223	37.3	45.4	0.82	-	-
<i>T. yaucensis</i>	MUSM 347	37.2	51.5	0.72	50.9	0.99
<i>Nothrotherium</i>	MCL 1020	31.6	32.4	0.98	28.0	0.86
<i>Mionothropus</i>	LACM 4609/117533	27.7	45.1	0.61	46.3	1.03

Footnotes: ML, mediolateral; PD, proximodistal.

Table 12. Measurements (in millimeters) of the tibia of *Thalassocnus*.

<i>T. antiquus</i>	<i>T. natans</i>	<i>T. littoralis</i>	<i>T. carolomartini</i>	<i>T. yaucensis</i>
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			240.2 (MNHN.F.SAS6); 237.4 (MNHN.F.SAS43); 271* (MNHN.F.SAS53); 246* (MNHN.F.SAS494); 281* (MUSM 223); 240.3 (MUSM 2064)	276* (MUSM 1995)	244* (MUSM 2065)
greatest PD length (from intercondylar eminence to median process between astragalar facets)	-	274*		70.0 70.0 (MNHN.F.SAO75); 88.4 (MNHN.F.SAO201); 96* (MUSM 1995)	92.9 (MUSM 347); 85* (MUSM 2065)
proximal end, greatest ML width	73*	96*	82.6 (MNHN.F.SAS43); 87.3 (MNHN.F.SAS53); 85* (MNHN.F.SAS54); 78.9 (MUSM 2064)	52* (MNHN.F.SAO75); 59.3 (MNHN.F.SAO201); 65* (MUSM 1995)	57.4 (MUSM 2065)
proximal end, AP depth at tibial tuberosity	47.9	62.6	51* (MNHN.F.SAS43); 58.1 (MNHN.F.SAS53); 54* (MNHN.F.SAS54); 67.1 (MUSM 223); 49.0 (MUSM 2064)		
			29.5 (MNHN.F.SAS6); 28.4 (MNHN.F.SAS43); 32.6 (MNHN.F.SAS46); 29.3 (MNHN.F.SAS53); 34*** (MNHN.F.SAS60); 30.5 (MNHN.F.SAS494);	35.2 (MUSM 1995)	-
midshaft, ML width	28.3**	33.6	24.6 (MNHN.F.SAS6); 24* (MNHN.F.SAS43); 29.3 (MNHN.F.SAS46); 25.5 (MNHN.F.SAS53); 31.8** (MNHN.F.SAS60); 25.1 (MNHN.F.SAS494); 29.3 (MUSM 223);	32.0 (MUSM 1995)	27.0 (MUSM 2065)
midshaft, AP depth	23.9**	30.2	70.3 (MNHN.F.SAS6); 69.2 (MNHN.F.SAS43); 77.5 (MNHN.F.SAS46); 74.8 (MNHN.F.SAS53); 85.9 (MNHN.F.SAS60); 66.1 (MNHN.F.SAS494); 64.7 (MUSM 2064)	69.2 (MNHN.F.SAO201); 78.8 (MUSM 1995)	77.4 (MUSM 347); 73* (MUSM 2065)
distal end, greatest ML width	-	74.6	45.1 (MNHN.F.SAS6); 48* (MNHN.F.SAS46); 48.3 (MNHN.F.SAS53); 57.4 (MNHN.F.SAS60); 43.5 (MNHN.F.SAS494); 42.2 (MUSM 2064)	47.1 (MNHN.F.SAO201); 52.8 (MUSM 1995)	54.3 (MUSM 347); 45.4 (MUSM 2065)
distal end, greatest AP depth	-	47.1			

Footnotes: If no specimen number is given after a measurement, it is that of the holotype of the species; \*, estimate; \*\*, measurement at estimated midshaft; AP, anteroposterior; ML, mediolateral; PD, proximodistal.

Table 13. Length of tibia compared to that of femur in *Thalassocnus* and other megatherioids.

Taxon	Specimen number	PD length of femur (Lf)	PD length of tibia (Lt)	Lt/Lf
<i>T. natans</i>	MNHN.F.SAS734	312.8	274*	0.88
<i>T. littoralis</i>	MNHN.F.SAS53	288.4	271*	0.94
	MUSM 223	310.0	281*	0.91
<i>T. carolomartini</i>	MUSM 1995	323.5	276.0	0.85
<i>Nothrotheriops</i>	YPM 13198	332.0	253.0	0.76
<i>Nothrotherium</i>	MCL 1020	221.2	172.5	0.78
<i>Hapalops</i>	data from Scott (1903)	218	163	0.75
<i>Planops</i>	BMNH M.9207	314	237	0.75
<i>M. americanum</i>	holotype; data from Casinos (1996)	676.9	488.4	0.72
<i>Myrmecophaga</i>	MNHN.2005.269	216.5	184.2	0.85

Footnotes: \*, estimate; PD, proximodistal.

Table 14. Size of tibia compared to depth of mandible in *Thalassocnus* and *Nothrotherium*.

Taxon	Specimen number	ML width of distal end of tibia (Wt)	Maximum depth of horizontal ramus of mandible	Wt/Md
<i>T. natans</i>	MNHN.F.SAS734	74.6	44.8	1.67
<i>T. yaucensis</i>	MUSM 347	77.4	51.5	1.50
<i>Nothrotherium</i>	MCL 1020	62.7	32.4	1.94

Footnotes: ML, mediolateral.

Table 15. Measurements (in millimeters) of the cyamo-fabella and ossified meniscus of *Thalassocnus*.

	<i>T. natans</i>	<i>T. littoralis</i>
<u>cyamo-fabella</u>		
greatest PD length	22.0	16.2 (MNHN.F.SAS53); 19.5 (MUSM 223)
greatest ML width	28.3	18.4 (MNHN.F.SAS53); 21* (MUSM 223)
<u>ossified meniscus</u>		
greatest AP depth	22.7	18.2 (MNHN.F.SAS53); 17.5 (MNHN.F.SAS800); 19.5 (MUSM 223)

Footnotes: No data for *T. antiquus*, *T. carolomartini*, and *T. yaucensis*. If no specimen number is given after a measurement, it is that of the holotype of the species; \*, estimate; ML, mediolateral; PD, proximodistal.

Table 16. Measurements (in millimeters) of the fibula of *Thalassocnus*.

	<i>T. antiquus</i>	<i>T. natans</i>	<i>T. littoralis</i>	<i>T. carolomartini</i>	<i>T. yaucensis</i>
greatest PD length	-	264.2	257.7 (MNHN.F.SAS761); 267.5 (MUSM 223)	256.5* (MUSM 1995)	-
proximal end, greatest ML width (at anterior tuberosity)	-	24.3	19.8 (MNHN.F.SAS54); 20.9 (MNHN.F.SAS290); 21.2 (MNHN.F.SAS761); 20.7 (MNHN.F.SAS1604); 25.8 (MUSM 223)	24.7 (MUSM 1995)	21.0



proximal end, greatest AP depth	-	38.7	36.9 (MNHN.F.SAS54); 38.0 (MNHN.F.SAS290); 40.8 (MNHN.F.SAS761); 33.2 (MNHN.F.SAS1604); 45.3 (MUSM 223)	38.3 (MNHN.F.SAO201); 49.3 (MUSM 1995)	46.0
distal end, greatest ML width	25.7	38.5	33.7 (MNHN.F.SAS761); 24.1 (MNHN.F.SAS1604); 24* (MUSM 223)	33.4 (MUSM 1995)	-
distal end, greatest AP depth	33.5	41.1	35.2 (MNHN.F.SAS761); 34.9 (MNHN.F.SAS1604); 38.5 (MUSM 223)	47* (MUSM 1995)	-

Footnotes: If no specimen number is given after a measurement, it is that of the holotype of the species; \*, estimate; AP, anteroposterior; ML, mediolateral; PD, proximodistal.

Table 17. Measurements (in millimeters) of the bones of the pes of *Thalassocnus*.

	<i>T. antiquus</i>	<i>T. natans</i>	<i>T. littoralis</i>	<i>T. carolomartini</i>	<i>T. yaucensis</i>
astragalus			48.9 (MNHN.F.SAS13); 46.1 (MNHN.F.SAS52); 57.2 (MNHN.F.SAS53); 48.6 (MNHN.F.SAS163); 48.8 (MNHN.F.SAS740); 52.1 (MNHN.F.SAS744); 45.3 (MNHN.F.SAS745);	46.5 (MNHN.F.SAO15); 46.1 (MUSM 345); 59.5 (MUSM 1995)	-
greatest PD length (at level of junction between medial and lateral trochlea)	49.5	53.4; 60.5 (MNHN.F.SAO? 210)	47.9 (MNHN.F.SAS794); 61.7 (MUSM 438)	46.5 (MNHN.F.SAO15); 46.1 (MUSM 345); 59.5 (MUSM 1995)	-

			50.9 (MNHN.F.SAS13); 47.7 (MNHN.F.SAS52); 57.5 (MNHN.F.SAS53); 51.9 (MNHN.F.SAS163); 53.6 (MNHN.F.SAS740); 56.9 (MNHN.F.SAS744); 55.1 (MNHN.F.SAS745);	62.8 (MNHN.F.SAO14); 49.3 (MNHN.F.SAO15); 52.6 (MUSM 345)	
greatest ML width (between odontoid process and fibular facet)	53.4	54.9; 64.4 (MNHN.F.SAO? 210)	51.9 (MNHN.F.SAS794); 62.1 (MUSM 438)		60.0 (MUSM 347)
			43.8 (MNHN.F.SAS13); 49.3 (MNHN.F.SAS53); 43.9 (MNHN.F.SAS163); 43.6 (MNHN.F.SAS740); 49.0 (MNHN.F.SAS744); 44.2 (MNHN.F.SAS745);		
greatest DP depth (between dorsal edge of trochleae and level of plantar edge of navicular process)	43.6	47.8; 54.7 (MNHN.F.SAO? 210)	42.1 (MNHN.F.SAS794); 51.9 (MUSM 438)	41.0 (MNHN.F.SAO15); 40.5 (MUSM 345); 49.7 (MUSM 1995)	43.6 (MUSM 347)
			100° (MNHN.F.SAS13); 105° (MNHN.F.SAS52); 100° (MNHN.F.SAS53); 100° (MNHN.F.SAS63); 105° (MNHN.F.SAS148); 105° (MNHN.F.SAS163); 105° (MNHN.F.SAS740); 100° (MNHN.F.SAS744); 110° (MNHN.F.SAS745);		
angle between trochleae in distal view ( $\pm 5^\circ$ )	90°	95°; 95° (MNHN.F.SAO? 210)	105° (MNHN.F.SAS794); 100° (MUSM 438)	100° (MNHN.F.SAO14); 100° (MUSM 345); 115° (MUSM 1995)	135° (MUSM 347)
calcaneum					

greatest PD length (from proximal tip of tuber calcis to distal end of sustentaculum)	88*	105.0; 106.5 (MNHN.F.SAO? 210)	84.0 (MNHN.F.SAS490); 85.6 (MNHN.F.SAS1606)	114.4 (MUSM 1995)	-
proximal end, greatest ML width (at distal end of tuber calcis)	-	54.4; 53.6 (MNHN.F.SAO? 210)	40.1 (MNHN.F.SAS163); 37.5 (MNHN.F.SAS381); 38.5 (MNHN.F.SAS490); 49* (MNHN.F.SAS741); 39.5 (MNHN.F.SAS1606)	51.1 (MNHN.F.SAO16); 50.1 (MUSM 1995)	-
proximal end, greatest DP depth (at distal end of tuber calcis)	30.3	38.3; 45.8 (MNHN.F.SAO? 210)	43.9 (MNHN.F.SAS64); 29.3 (MNHN.F.SAS170); 29.0 (MNHN.F.SAS381); 27.6 (MNHN.F.SAS490); 37.0 (MNHN.F.SAS741); 26.1 (MNHN.F.SAS1606)	39.4 (MNHN.F.SAO16); 33* (MUSM 1995)	37.2 (MUSM 347); 35.0 (MUSM 2065); 39.8 (MUSM 2069)
neck, greatest ML width	21.0	26.5; 34.1 (MNHN.F.SAO? 210)	30.3 (MNHN.F.SAS64); 22.6 (MNHN.F.SAS163); 24.1 (MNHN.F.SAS170); 24* (MNHN.F.SAS381); 23.1 (MNHN.F.SAS490); 27.5 (MNHN.F.SAS741); 24.0 (MNHN.F.SAS1606)	31.5 (MNHN.F.SAO16); 34.6 (MUSM 1995)	23.7 (MUSM 2065); 25.7 (MUSM 2069)
neck, greatest DP depth	24.6	26.4; 35.0 (MNHN.F.SAO? 210)	26.2 (MNHN.F.SAS64); 22.2 (MNHN.F.SAS163); 21.4 (MNHN.F.SAS170); 20.6 (MNHN.F.SAS381); 20.7 (MNHN.F.SAS490); 25.8 (MNHN.F.SAS741); 23.5 (MNHN.F.SAS1606)	23.9 (MNHN.F.SAO16); 27.3 (MUSM 1995)	28.6 (MUSM 347); 22.8 (MUSM 2065); 26.5 (MUSM 2069)

navicular					
			13.2 (MNHN.F.SAS1603);		
greatest PD length	18.4	16.7	16.0 (MNHN.F.SAS1604); 19.3 (MUSM 438)	17* (MUSM 1995)	-
greatest ML width	31.6	35.1	31.8 (MNHN.F.SAS1604)	38.6 (MUSM 1995)	-
			37.8 (MNHN.F.SAS1604);		
greatest DP depth	38.9	40.6	38.4 (MNHN.F.SAS1604); 44.0 (MUSM 438)	44.1 (MUSM 1995)	-
cuboid					
			30.1 (MNHN.F.SAS163);		
greatest PD length	25*	26.7	32.1 (MNHN.F.SAS190); 25.6 (MNHN.F.SAS1603)	33.5 (MUSM 1995)	30* (MUSM 347)
			28.4 (MNHN.F.SAS163);		
greatest ML width	24.9	28.6	28.0 (MNHN.F.SAS190); 23.1 (MNHN.F.SAS1603); 24.7 (MNHN.F.SAS1608)	35.1 (MUSM 1995)	-
			37.5 (MNHN.F.SAS163);		
greatest DP depth	31.4	36.7	36.5 (MNHN.F.SAS190);	42.2 (MUSM 1995)	35.6 (MUSM 347)
ectocuneiform					
greatest PD length (at level of facet for the cuboid)	11.9	13.9; 14.9 (MNHN.F.SAO? 210)	13.7 (MNHN.F.SAS53)	18.6 (MUSM 1995)	-
greatest ML width	21.4	23.8; 24.8 (MNHN.F.SAO? 210)	-	26.2 (MUSM 1995)	-
		32.7; 38.9 (MNHN.F.SAO? 210)	36.8 (MNHN.F.SAS53)	39.4 (MUSM 1995)	-
greatest DP depth	32.6				
Mt II					
greatest PD length	-	31.8	32.1 (MNHN.F.SAS799); 30.3 (MUSM 438)	31.7 (MUSM 1995)	-
greatest ML width	-	22.1	21* (MNHN.F.SAS799); 22.4 (MUSM 438)	22.8 (MUSM 1995)	-

greatest DP depth	-	30.0	30.2 (MNHN.F.SAS799); 32.3 (MUSM 438)	32.1 (MUSM 1995)	-
<hr/> Ph. 1-2 D. II <hr/>					
greatest PD length	-	-	15.0 (MNHN.F.SAS53); 18.0(MNHN.F.SAS1605); 25.1 (MUSM 438)	20.9 (MUSM 1995)	-
greatest ML width	-	-	16.6 (MNHN.F.SAS53); 18.3 (MNHN.F.SAS1605)	21.0 (MUSM 1995)	-
greatest DP depth (at proximal end)	-	-	18.7 (MNHN.F.SAS53); 24.6 (MNHN.F.SAS1605); 26.2 (MUSM 438)	24.9 (MUSM 1995)	-
<hr/> Ph. 3 D. II <hr/>					
greatest PD length (N.B. the distal tip is rarely preserved)	-	62*; 64* (MNHN.F.SAO? 210)	49.3 (MUSM 438)	-	50* (MUSM 2065)
proximal end, ML width	-	16.9; 20.1 (MNHN.F.SAO? 210)	16.9 (MUSM 438)	20.9 (MUSM 1995)	-
proximal end, DP depth	-	22.8; 24.8 (MNHN.F.SAO? 210)	24.9 (MUSM 438)	27.0 (MUSM 1995)	21.1 (MUSM 2065)
<hr/> Mt III <hr/>					
greatest PD length (at dorsal border)	39.9	52.0	34* (MNHN.F.SAS189); 30* (MNHN.F.SAS491); 34* (MNHN.F.SAS1605); 42.4 (MUSM 438)	43.4 (MUSM 1995)	40.6 (MNHN.F.PP 1271)
midshaft, ML width	20*	19.5	18.3 (MNHN.F.SAS163); 18.3 (MNHN.F.SAS189); 20.4 (MNHN.F.SAS491); 20.0 (MNHN.F.SAS1602); 18.7 (MNHN.F.SAS1605); 20.1 (MUSM 438)	19.8 (MNHN.F.SAO201); 26.2 (MUSM 1995)	24.4 (MNHN.F.PP 1271)

			28.0 (MNHN.F.SAS189); 28.0 (MNHN.F.SAS491); 24.8 (MNHN.F.SAS1602); 27*	33.0	30.2
midshaft, DP depth	21*	26.9	(MNHN.F.SAS1605); 33.4 (MUSM 438)	(MNHN.F.SAO201); 34.1 (MUSM 1995)	(MNHN.F.PP I271)
<hr/> Ph. 1-2 D. III <hr/>					
			29.6 (MNHN.F.SAS53); 28.1 (MNHN.F.SAS163); 32.2 (MUSM 438)	33*	35.1 (MUSM 347)
PD length at midwidth	-	29.2	25.2 (MNHN.F.SAS53); 26.4 (MNHN.F.SAS163); 28.5 (MUSM 438)	(MNHN.F.SAO201)	
greatest ML width	-	27.7	25.4 (MNHN.F.SAS163); 30.5 (MUSM 438)	28.1 (MNHN.F.SAO201)	31.3 (MUSM 347)
greatest DP depth (at proximal end)	-	31.7	28.5 (MNHN.F.SAO201)	28.5 (MNHN.F.SAO201)	33.2 (MUSM 347)
<hr/> Ph. 3 D. III <hr/>					
greatest PD length (N.B. the distal tip is rarely preserved)	-	89* 26.3; 28.4 (MNHN.F.SAO? 210)	- 22.4 (MNHN.F.SAS163); 29.7 (MUSM 233)	-	29* (MUSM 347)
proximal end, ML width	-				
proximal end, DP depth	-	31.3; 38.1 (MNHN.F.SAO? 210)	28.9 (MNHN.F.SAS163); 35.4 (MUSM 233)	-	37.6 (MUSM 347)
<hr/> Mt IV <hr/>					
			73.1 (MNHN.F.SAS163); 72.4 (MNHN.F.SAS368); 76.3 (MNHN.F.SAS1605); 21.3 (MNHN.F.SAS10); 15.4 (MNHN.F.SAS368); 17.1 (MNHN.F.SAS1605); 18.0 (MUSM 438)	83* (MUSM 1995)	71* (MUSM 2065)
greatest PD length (at dorsal border)	75.4	86*; 86.0 (MNHN.F.SAO? 210)			
midshaft, ML width	15.1	17.2; 19.1 (MNHN.F.SAO? 210)		18.2 (MUSM 1995)	18.3 (MUSM 2065)

			20.1 (MNHN.F.SAS10); 16.9 (MNHN.F.SAS368); 16.6 (MNHN.F.SAS1605);			
midshaft, DP depth	15.2	16.5; 20.1 (MNHN.F.SAO? 210)	21.4 (MUSM 438)	19.5 (MUSM 1995)	18.2 (MUSM 2065)	
<hr/> Ph. 2 D. IV <hr/>						
greatest PD length	-	-	19.3 (MUSM 438)	16.3 (MUSM 1995)	-	
proximal end, ML width	-	16.7	19.9 (MUSM 438)	19.5 (MUSM 1995)	-	
proximal end, DP depth	-	24.7	21.5 (MUSM 438)	23.5 (MUSM 1995)	-	
<hr/> Ph. 3 D. IV <hr/>						
greatest PD length (N.B. the distal tip is rarely preserved)	-	61*	61* (MUSM 223)	-	-	
proximal end, ML width	-	16.0	19.6 (MUSM 223)	-	-	
proximal end, DP depth	-	19.9	22.8 (MUSM 223)	-	-	
<hr/> Mt V <hr/>						
greatest PD length	-	114.0	92.7 (MNHN.F.SAS1604); 33.1 (MNHN.F.SAS58); 38.4 (MNHN.F.SAS759); 34.3 (MNHN.F.SAS1604); 32.7 (MNHN.F.SAS58); 29.6 (MNHN.F.SAS388); 35.2 (MNHN.F.SAS759); 28.1 (MNHN.F.SAS1604);	106* (MNHN.F.SAO201); 114.7 (MUSM 1995)	-	
ML width at junction between facets for Mt IV and cuboid	-	41.9	32.7 (MNHN.F.SAS58); 29.6 (MNHN.F.SAS388); 35.2 (MNHN.F.SAS759); 28.1 (MNHN.F.SAS1604);	35.0 (MNHN.F.SAO201); 34.5 (MUSM 1995)	36.2 (MUSM 347)	
DP depth at junction between facets for Mt IV and cuboid	21.5	29.6	28.1 (MNHN.F.SAS1604);	28.3 (MNHN.F.SAO201); 31* (MUSM 1995)	26.2 (MUSM 347)	
greatest PD length	-	-	11,0 (MUSM 438)	12,7 (MUSM 1995)	-	

Footnotes: If no specimen number is given after a measurement, it is that of the holotype of the species; \*, estimate; DP, dorsoplantar; ML, mediolateral; PD, proximodistal.

Table 18. Depth of astragalus compared to that of mandible or proximal width of humerus in *Thalassocnus* and other megatherioids.

Taxon	Specimen number	greatest DP depth of astragalus (Da)	Maximum depth of horizontal ramus of mandible (Md)	ML width of humerus at proximal tuberosities (Wh)	Da/Md	Da/Wh
<i>T. antiquus</i>	MUSM 228	43.6	42.5	73.7	1.03	0.59
<i>T. natans</i>	MNHN.F.SAS734	47.8	44.8	83.3	1.07	0.57

<i>T. carolomartini</i>	MUSM 1995	49.7	-	90.8	-	0.55
<i>T. yaucensis</i>	MUSM 347	43.6	51.5	95.1	0.85	0.46
<i>Nothrotherium</i>	MCL 1020	37.5	32.4	57.2	1.16	0.66

Footnotes: DP, dorsoplantar; ML, mediolateral.

Table 19. Proportions of third metatarsal in *Thalassocnus* and other Megatheria.

Taxon	Specimen number	PD length (L)	ML width at midshaft (W)	L/W
<i>T. natans</i>	MNHN.F.SAS734	52.0	19.5	2.67
<i>T. littoralis</i>	MNHN.F.SAS189	34	18.3	1.86
	MUSM 438	42.4	20.1	2.11
<i>T. carolomartini</i>	MUSM 1995	43.4	26.2	1.66
<i>T. yaucensis</i>	MNHN.F.PPI278	40.6	24.4	1.66
<i>Nothrotheriops</i>	LACM 119730	46.3	61.0	0.76
<i>Nothrotherium</i>	MCL 1020	27.0	30.5	0.89
<i>M. americanum</i>	MNHN.F.PAM295	117.7	95.8	1.23

Footnotes: ML, mediolateral; PD, proximodistal.

Table 20. Proportions of fourth metatarsal in *Thalassocnus* and other Megatheria.

Taxon	Specimen number	PD length (L)	ML width at midshaft (W)	L/W
<i>T. antiquus</i>	MUSM 228	75.4	15.1	4.99
<i>T. natans</i>	MNHN.F.SAS734	86	17.2	5.00
<i>T. littoralis</i>	MNHN.F.SAS1605	76.3	17.1	4.46
<i>T. carolomartini</i>	MUSM 1995	83	18.2	4.56
<i>T. yaucensis</i>	MUSM 2065	71	18.3	3.88
<i>Nothrotheriops</i>	LACM 156608	110.6	24.4	4.53
<i>Nothrotherium</i>	MCL 1020	56.3	13.7	4.11
<i>M. americanum</i>	MNHN.F.PAM295	220.8	66.2	3.34

Footnotes: ML, mediolateral; PD, proximodistal.

Table 21. Summary of anatomical comparisons with functional significance.

Region and structure	Region and structure Inferred function	Comparison					
		other Megatheria	<i>T. a.</i>	<i>T. n.</i>	<i>T. l.</i>	<i>T. c.</i>	<i>T. y</i>
pelvis							
smallness of wing and horizontal orientation	reduced terrestrial occupation	∅	+	?	+	++	?
concave dorsal border of acetabulum	amplitude of abduction of femur	∅	∅	?	∅	+	?
femur							
general size	size of hind limb	∅	∅	∅	-	--	--
general slenderness, anteroposterior bending, oval cross-section	particular constraints	∅	+	+	+	+	+
notch between greater trochanter and head	abducted position of femur	∅	?	+	+	+	+
junction of greater and third trochanters, insertion of gluteus medius	abduction of the femur strength	∅	?	+	+	+	+



development of medial trochlear ridge	prevention of medial translation of patella (pedolaterality)	++++ (not in megatheriids)	++++	+++	++	+	∅
bicondylar angle	abducted position of the knee (pedolaterality)	++ (not in megatheriids)	++	++	+	∅	∅
reduction of general size when compared to that of other skeletal elements	reduction of hind limb	∅	?	∅	+	++	++
<hr/>							
patella							
general size	size of hind limb	±	∅	∅	∅	?	-
<hr/>							
tibia							
general size	size of hind limb	∅	?	-	?	?	--
slenderness of tibia (length and shape in cross-section)	particular constraints	∅	?	+	+	+	?
size of intercondylar eminence	rotation of the knee (pedolaterality)	∅	+	-	-	-	-
elevation on lateral articular surface for condyle	rotation of the knee (pedolaterality)	∅	+	+	-	-	-
tibio-astragalar articulation							
odontoid and discoid surfaces individualized and set at a right angle	pedolateral stance	±	+	-	--	--,---	-----
<hr/>							
astragalus							
general size	size of hind limb	∅	-	-	?	-	--
concavo-convexity of navicular facet	inversion/eversion of the metatarsus over the tarsus (pedolateral stance)	∅	-	?	-	--,---	--
<hr/>							
metatarsals							
Mt V, size of lateral process	robustness of the lateral elements (pedolaterality)	∅	?	∅	-	-	-
<hr/>							
digits							
digit III, metatarsophalangeal joint	locking of articulation	∅	-	-	-	--	--
obligated flexion of distal interphalangeal joint of digit III	anchoring?	∅	?	+	+	?	?

Footnotes: *T.a.*, *T. antiquus*; *T.n.*, *T. natans*; *T.l.*, *T. littoralis*; *T.c.*, *T. carolomartini*; *T.y.*, *T. yaucensis*; ∅, no conspicuous difference; ?, no data; ±, variable.

## Appendix

Online Resource 1. Specimen numbers of *Thalassocnus* hind limb material. Abbreviations: (R), right; (L), left; (R&L), right and left; (R or L), right or left (unknown laterality).