Ossified meniscus and cyamo-fabella in some fossil sloths: a morpho-functional interpretation

Ménisque ossifié et cyamo-fabella chez certains paresseux fossiles : une interprétation morpho-fonctionnelle

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Abstract

An articulated skeleton of *Thalassocnus natans* (Xenarthra : Nothrotheriidae) and a review of some other fossil sloths provide new information on sesamoid bones located at the knee joint. A sesamoid bone and an ossified meniscus have been identified at this joint. The cyamo-fabella (posterior sesamoid of the tibio-femoral articulation) of *T. natans* may act like a pulley through which the tendon of the *m. gastrocnemius* would have passed. The ossified meniscus, which is also present in Megatheriidae and Mylodontidae, could be related to the pedolateral stance and a large rotation of the knee joint during locomotion.

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Résumé

La découverte d’un squelette articulé de *Thalassocnus natans* (Xenarthra: Nothrotheriidae), ainsi que la révision de nombreux autres restes de paresseux fossiles, donnent de nouvelles informations sur les sésamoïdes du genou. Un sésamoïde et un ménisque ossifié ont été identifiés au niveau de cette articulation. Chez *T. natans*, la cyamo-fabella (sésamoïde postérieur à l’articulation tibio-fémorale), pouvait avoir le rôle d’une poulie par laquelle pouvait passer le tendon du *m. gastrocnemius*. Le ménisque ossifié, également présent chez les Megatheriidae et les Mylodontidae, pourrait être lié avec la condition pédiolatérale et l’importante rotation de l’articulation du genou durant la locomotion.

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Resumen

Un esqueleto articulado de *Thalassocnus natans* (Xenarthra: Nothrotheriidae), así como la revisión de varios otros restos de perezosos fósiles, dan nueva información acerca de los sesamoïdes ubicados en la articulación de la rodilla. Se ha identificado la presencia de un sesamoïde y un menisco osificado en esta articulación. La cyamo-fabella (sésamoïde posterior de la articulación tibio-femoral) en *T. natans*, podría cumplir el rol de una polea por el cual se deslizaría el tendón del *m. gastrocnemius*. El menisco osificado, también presente en Megatheriidae y Mylodontidae, podría estar relacionado con la condición pedolateral y una gran rotación al nivel de la articulación de la rodilla durante la locomoción.

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Abbreviations : MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos Lima Perú ; MNHN, Muséum national d’Histoire naturelle Paris France ; UF, Florida Museum of Natural History Florida USA.

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1. Introduction

Xenarthra constitutes an atypical group of mammals that evolved mainly in South America during the Cenozoic. In sloths the functional anatomy of the limbs has been widely documented, but not fully understood (Mendel, 1981; White, 1993, 1997). Most fossil forms are considered terrestrial, bipedal and/or quadrupedal (Mann de Toledo, 1996), although extant sloths are exclusively arboreal (Mendel, 1985). In some fossil sloth such as Nothrotheriidae, Mylodontidae, and Megatheriidae, the latero-plantar portion of the posterior digits IV–V and of the calcaneum contact the ground. This posture depends on 45° to 70° lateral torsion of the pes due to the development of an astragalar odontoid process. In megalonychids and some “nothrotheriids”, traditionally considered as morphologically basal among Phyllophaga (= Tardigrada; De Iuliis, 1996), the foot has a classical plantigrade position.

In sloths, as in other mammals, sesamoid bones are located in the knee joint, but their systematic identification and function are unclear. Sesamoid bones of the knee joint were identified in Mylodon (Stock, 1925), Scelidotheriinae (McDonald, 1987), Megatheriinae (De Iuliis, 1996) as well as in the treessloth Choloepus (Mendel, 1981, 1985). Previously, Pearson and Davin (1921) mentioned the existence of a cyamella in many xenarthrans (i.e., Bradypus, Tamandua) and observed that a “lunula” (ossified meniscus) is present in Megatherium cuvieri (= M. americanum). Lessertisseur and Saban (1967) indicate that Xenartha and Pholidota do not possess a fabella and that in Bradypus the only sesamoid of the knee joint corresponds to a fusion of the cyamella and fabella. An ossified meniscus was also identified by these authors in Choloepus.

In the marine deposits of the Pisco Formation (latest Miocene, Peru) a specimen of the aquatic sloth Thalassocnus natans (MUSM 223) was discovered in the Montemar Vertebrate Horizon (sensu De Muizon and DeVries, 1985) of the Aguada de Lomas locality. Megatheriid and mylodontid remains are from late Pleistocene deposits of the Peruvian coast.

2.1. Cyamo-fabella

In the articulated skeleton of T. natans (MUSM 223, Fig. 1A) the cyamo-fabella articulates with the posterior part of tibia’s lateral articular surface (Fig. 1B). This sesamoid bone is cubic in shape, slightly antero-posterily compressed and larger medially than laterally. The articular facet for the tibia is wide and only slightly concave. The cyamo-fabella bears a deep sulcus that connects its dorsal and posterior surfaces. This arrangement partially divides the bone into a large medial portion and a smaller lateral portion (Fig. 2A). Its peculiar morphology apparently reflects the

Fig. 1. T. natans (MUSM 223). A, knee region in lateral view (patella and fibula not shown, MUSM 223); B, proximal epiphysis of right tibia in dorsal view (MUSM 223). Abbreviations: cf, cyamo-fabella; caft, cyamo-fabella articular facet of the tibia; fe, femur; ifat, lateral femoral articulation of the tibia; mfat, medial femoral articulation of the tibia; om, ossified meniscus; omaft, ossified meniscus articular facet of the tibia; ti, tibia. Scale bars equal 2 cm.

2. Comparative description and discussion

Four species of Thalassocnus (T. antiquus, late Miocene; T. natans, latest Miocene; T. littoralis, Mio-Pliocene; T. carolomartini, early late Pliocene) are currently recognized in the Pisco Formation and probably represent a single evolutionary lineage, but is not fully confirm (Muizon and McDonald, 1995; McDonald and de Muizon, 2002; De Muizon et al., 2003). They are considered sloths adapted to an aquatic environment based on the abundance of articulated specimens in the near-shore marine deposits, as well as conspicuous changes in the morphology of the premaxilla, femur, caudal vertebrae and orientation of the occipital condyles (De Muizon and McDonald, 1995; McDonald and de Muizon, 2002). T. natans (MUSM 223) was discovered in the Montemar Vertebrate Horizon (sensu De Muizon and DeVries, 1985) of the Aguada de Lomas locality. Megatheriid and mylodontid remains are from late Pleistocene deposits of the Peruvian coast.
fusion of the cyamella with the external fabella (= cyamo-fabella), with the cyamella representing the smaller lateral portion. This arrangement was proposed for Bradypus (Pearson and Davin, 1921) and Choloepus (Lessertisseur and Saban, 1967). The internal fabella, never found in xenarthrans by Pearson and Davin (1921), is not present in MUSM 223.

Both cyamo-fabellae are preserved in a Megatherium specimen (M. urbinai, MUSM 15 holotype; Pujos and Salas, 2004) from the Pleistocene deposits of Sacaco area (southern Peru, Pujos and Salas, 2001; Pujos and Salas, 2004). The morphology of the cyamo-fabella of MUSM 15 is similar to that of T. natans, but lacks a sulcus (Fig. 2B).

In most mammals internal and external fabellae are located on the posterior portion of the femoral condyles. They are attached to the femur by the fabello-femoral ligament and to the tuber calcanei of the calcaneum by the tendon of the m. gastrocnemius. The m. popliteus originates on the cyamella and inserts on the crista tibiae. McDonald (1987) reported a cyamo-fabella articular facet in mylodontids (Proscelidodon, Scleridodon, Sclerotherium and Pseudopreotherium) and Pearson and Davin (1921); De Iuliis (1996) in megatheriids. Apparently, in all xenarthrans known, the cyamella and external fabella are fused. The cyamo-fabella is cubic in extant (Bradypus and Choloepus) and fossil sloths in which it is known (T. natans, M. americanum, and M. urbinai).

In the cyamo-fabella of T. natans the presence of the sulcus might indicate a distinct use of this sesamoid. It is possible that the tendon of the m. gastrocnemius passed through the sulcus. The medial side of the cyamo-fabella probably corresponds to the origin of the m. popliteus and the lateral side the attachment of the cyamo-femoral ligament (Fig. 3). The tibial articular facet of the cyamo-fabella is concave and permits little movement, thus restricting the orientation of the sulcus so that the cyamo-fabella could act like a pulley, imparting a mechanical advantage to the m. gastrocnemius and allowing a more powerful extension of the foot. In Thalassocnus this function could reflect the dynamic use of hind limbs during swimming activity (Muizon and McDonald, 1995). Conspicuous differences in Thalassocnus astragalus (MUSM 347) recovered from a more recent level (Yauca, late Pliocene) of the Pisco Formation may corroborate the previous statement. The astragalus of the Yauca specimen shows (1) a wider angle between the tibial facets and (2) decrease in the height of lateral tibial facets, compared with older species of the genus. These characters produce a more plantigrade position of the pes. A plantigrade condition may increase the foot surface for propulsion in an animal that spend most of the time in water. In this sense, the use of hind limbs in the Thalassocnus lineage would favor its peculiar cyamo-fabella morphology.

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**Fig. 2.** Cyamo-fabella in dorsal (A, C) and posterior (B, D) views. A, B, T. natans (MNHN SAS 734, holotype); C, D, M. urbinai (MUSM 15). Abbreviation: su, sulcus. Scale bar equals 1 cm.

**Fig. 3.** Posterior view of the knee region of T. natans where the dorsal-ventral arrow shows the passage of the m. gastrocnemius by way of the sulcus of the cyamo-fabella from the femur to the calcaneum. Abbreviations: cf, cyamo-fabella; cfl, cyamo-femoral ligament; po, m. popliteus. Scale bar equals 2 cm.
2.2. Ossified meniscus

This sesamoid is a crescentic, wedge-shaped element in *T. natans* (MUSM 223) and located on the anteriorly on the lateral femoro-tibial articular surface (Fig. 1B). The anterior side is convex, more prominent anterolaterally, and its posterior margin is concave (Fig. 4A). This sesamoid was referred to as a lunula by Pearson and Davin (1921); McDonald (1987);
De Iuliis (1996). According to Lessertisseur and Saban (1967), the lunula is a plantar sesamoid of the pes located under the astragalus. The sesamoid described here (and discussed by previously cited authors) corresponds to the ossification of the anterior portion of the external femoro-tibial meniscus.

The ossified menisci preserved in the Megatherium specimen from Sacaco (MUSM 15; Fig. 4B) and Scelidodon chilensis (MNHN CPN 16) from the Pleistocene–Holocene deposits of Pampa de los Fósiles (northern Peru; Fig. 4C) exhibit a similar morphology. We identified an ossified meniscus in Ereotherium eomigrans (UF 206880, Haile 7C) from the late Pliocene-early Pleistocene of Florida.

Lessertisseur and Saban (1967) proposed that the ossified meniscus may help in the rotation of the femur against the tibia. So far, an ossified meniscus has been only recovered in fossil sloths in which the pes is inverted. Such a pedolateral stance (see McDonald, 1987), directly related to the development of an odontoid process in the astragalus (Fig. 4J–L), produces a large rotatory movement of the knee during locomotion. The deep, concave, and round medial femoral facet of the tibia and the hemispherical medial condyle of the femur are characteristic of the “ground sloths” previously cited (Fig. 4D–I). Together, these characters constitute the “pivot joint” of Hildebrand (1988). This structure permits rotation of the femur in the axis of its medial condyle, while the flat articular facet of the ossified meniscus would allow an antero-posterior slipping of the lateral condyle of the femur during locomotion (Fig. 5). The antero-posteriorly convex and long lateral femoral facet of the tibia facilitates this extensive displacement. A similar condition was identified in glyptodonts by Shockey (2001).

Megatheriidae, Mylodontidae, and Nothrotheriidae present a more medially projected and enlarged internal condyle (Fig. 4D–F) than Megalonychids and Santacrucian “nothrotheriids” producing a substantial bicondylar angle (sensu White, 1993). Tardieu (1983) considers this condition as an indicator of extensive knee rotation. Furthermore, according to White (1993), this morphology could be related to lateral torsion of the pes for terrestrial locomotion, or for climbing. The small sized semi-arboreal anteater Tamandua also presents a substantial bicondylar angle and adopts a pedolateral stance while climbing (Hirschfeld, 1985).

The pedolateral stance and odontoid process might have been developed more than once in different taxa of the “ground sloths” (De Iuliis, 1994) due to climbing. During locomotion on ground, the rotation of the pes over the odontoid process axis was absorbed by the ossified meniscus at the knee joint (Fig. 6).
3. Conclusions

The sesamoid bone located on the posterior process of the lateral femoral articulation of the tibia in modern and fossil Phyllophaga, probably corresponds to the fusion of the cyamella and the external fabella (cyamo-fabella). It is possible to extend this proposal to all xenarthrans. It is cubic in extant (Bradyergus and Choloepus) and fossil sloths in which it is known (T. natans, M. americanum, and M. urbinai). Exclusively in the aquatic sloth T. natans the cyamo-fabella bears a proximo-distal sulcus extended in which the tendon of the m. gastrocnemius probably passed. This sesamoid bone apparently acted as a pulley to produce more powerful extension of the pes during swimming activity.

The crescent-shaped sesamoid bone found in the knee joint of some “ground sloths” with a pedolateral stance corresponds to the ossification of the anterior portion of the lateral meniscus. The ossified meniscus is involved in rotation of the femur against the tibia during locomotion. Other characters related to large knee rotation present in sloths with a pedolateral stance and ossified meniscus are: (1) a deep, concave, and round medial femoral facet of the tibia and hemispherical medial condyle of the femur (pivot joint), (2) a substantial bicondylar angle in the femur, and (3) a well developed astragalar odontoid process.

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