

Specialized knee joints in some extinct, endemic, South American herbivores

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Distal femora of some extinct, endemic, South American herbivores are shown to have modifications related to knee extension. *Toxodon* (Order Notoungulata) had an enlarged medial trochlear ridge (MTR) similar to those seen in horses. The MTR of horses serves to 'lock' the patella and ligaments in the proximal position and it likely function the same for *Toxodon*. The patella of *Toxodon* has a medial process that would have locked by wrapping around the MTR. Macraucheniid and proterotheriid litopterns may also have had knee locks, but with a different mechanism. The femora of these litopterns have deep suprapatellar fossae in which the patellae could have become lodged. Indeed, the distal end of the patella of cf. *Eoauchenia* (Proterotheriidae) conforms to and is supported within the suprapatellar fossa. Several glyptodontids (Order Xenarthra) have conical MTRs that would have impeded the medial patellar ligaments during the initiation of extension. This would have caused patellar rotation and resulted in a complex knee extension. These glyptodonts also had suprapatellar fossae, suggesting that the ligaments slid over the MTR and 'locked' during hyperextension. Locking knees in these diverse animals implies that they stood for long periods of time and did not engage in intermittent, 'bout feeding' as seen in modern ruminants.

Key words: Herbivores, Notoungulata, Litopterna, Glyptodontoidea, knee, passive stay.

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Introduction

A subtle, but major, difference in the behavior of carnivores and herbivores is that herbivores spend much more time on foot than do carnivores. This is a function of the herbivore's need to flee from carnivores, but it is also related to the fact that herbivores spend more time feeding than carnivores. Greater foraging time is required for herbivores because it is much more difficult to obtain usable energy and protein from plants than from meat (Janis 1976; Eisenberg 1981).

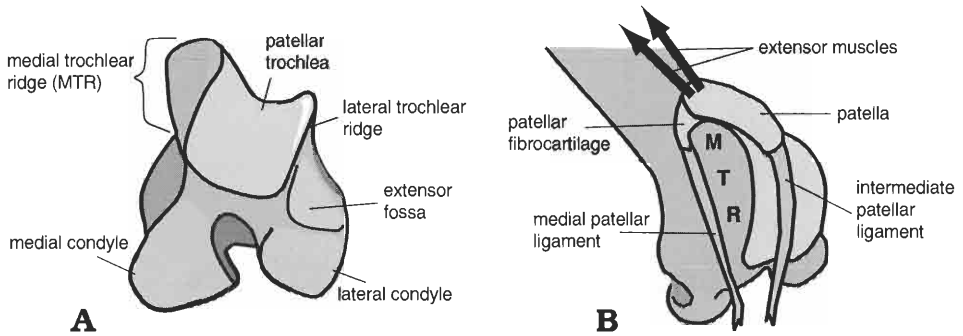


Fig. 1. Distal femur of the horse *Equus* showing morphological features discussed in the text. **A.** Distal view of left femur. **B.** Oblique-medial view of distal left femur showing location of patellar ligaments and extensor muscles. MTR, medial trochlear ridge. Drawing based upon specimen of *E. insulatus* of Tarija, MNHN-Bol-V-3164.

Horses and rhinos are known to have developed adaptations of the knee joint to reduce muscle fatigue while standing for long periods of time (Hermanson & MacFadden 1996). They accomplish this by way of a greatly hypertrophied medial trochlear ridge (MTR; Fig. 1) which serves to 'snag' the medial patellar ligament, or parapatellar cartilage, and the patella when the knee joint is hyperextended (Sack 1988). This secures the patella in its proximal position, where it rests upon the MTR, such that a 'resting' facet forms on the proximal surface of the MTR (Dyce *et al.* 1996). Thus, with the patella held in this proximal position, the patellar ligaments maintain tension at their attachments to the tibia, thereby preventing the lower limb from flexing passively under the force of gravity. In this 'locked' condition, the extensor muscles (the quadriceps and tensor fasciae latae) may exert considerably less force, presumably reducing the metabolic 'cost' of standing. Thus, the animal may remain on foot for long periods of time without fatigue. Horses, for example, may stand for over 20 hours a day (Ruckebusch 1972; Boyd *et al.* 1988), even while sleeping.

The knee-lock of the horse is the best known and provides a model of our understanding of possible knee-locks in other animals. Its essential feature is a mechanical means of securing the lower leg in the extended position with little or no work from the extensor muscles. Also, in horses, the extension of the knee joint prevents dorsoflexion of the ankle joint, because when the knee is extended tension is maintained on the superficial digital flexor muscle which, in turn, maintains ankle joint extension (see Hermanson & MacFadden 1996; fig 6).

It is often assumed that cows and other artiodactyls lack knee locks (Hermanson and MacFadden 1996; Shockey 1998). However, Dyce *et al.* (1996) report that, just as in the horse, the patella, medial fibrocartilage, and the medial patellar ligament of the domestic cow combine to loop around the MTR to maintain knee extension. They indicate that this mechanism is much less efficient than the knee lock of the horse, but note that it is 'relatively common (p. 759)' for bullocks of India to get their knees stuck in the extended position. Typically, however, muscular activity is required to maintain the patella in the 'locked' position, however, this appears to demand much less energy to maintain the knee joint extended without this specialized knee. There may be some

heuristic value in thinking of the cow as having an 'active stay' in the knee (one that requires energy) and the horse as having a 'passive stay'.

Kappelmann (1988) noted enlarged MTRs in several open-habitat bovids, however, the function of the MTR in these animals remains poorly understood (see Discussion section). Locking knees are currently unknown in other extant ungulates. Clearly, the function in extant ungulates needs to be improved before we can more fully appreciate modifications of the knees of those that are extinct.

The distal femora of a variety of extinct, endemic South American herbivores have unusual morphologies, suggestive of some specialized functions. Such derived knees from the orders Notoungulata (*Toxodontidae*), Litopterna (*Macraucheniiidae* and *Proterotheriidae*) and Xenarthra (*Glyptodontidae*) are described in this work. Their possible functional significance is also discussed.

Abbreviations. — Abbreviations used for specimen identifications include MLP, Museo de La Plata, La Plata Argentina; and MNHN-Bol-V, the vertebrate paleontology collection of the Museo Nacional de Historia Natural, La Paz, Bolivia; GB, the GEOBOL collection curated in the MNHN-Bol; PU, the Princeton University Collection at Yale Peabody Museum, Yale University, New Haven, Connecticut. MTR, medial trochlear ridge of the distal femur (see Fig. 1).

Extinct, endemic South American taxa with modified knees

Order Notoungulata Roth, 1903

Family Toxodontidae Gervais, 1847

Genus *Toxodon* Owen, 1840

***Toxodon* sp.**

Material examined. — MLP 41-XI-28-28, left distal femur of *Toxodon*, Pleistocene, Fig. 2 and femora and patellae of uncataloged cast of *Toxodon* skeleton of the PU collection at Yale Peabody Museum.

Description. — The distal femur of *Toxodon* is similar to that of *Equus* by having a greatly enlarged medial trochlear ridge (MTR) and a well-developed extensor fossa. As Scott noted (1912) the articular surface covers most of the MTR, including much of its medial surface. The most conspicuous difference in their distal femora is that this element in *Toxodon* is more robust; consistent with the generally graviportal condition of the massive notoungulate. The femur of *Toxodon* also differs by its relatively deeper condyles, shallower patellar trochlea, and the lack of a narrow groove at the proximal surface of the medial trochlear ridge. Instead of a groove at the proximal MTR, *Toxodon* has a broad, flattened, shelf-like surface in this region.

The flattened region of the proximal MTR could have served as a platform to support the medial patellar ligament whenever (or if) the *Toxodon* hyperextended the knee joint. If so, the joint would have become fixed in the extended position such that the forces of gravity would not have collapsed the joint, thus serving as a passive-stay, or knee-lock, structurally similar to those of horses and rhinos.

Whereas modern horses have parapatellar cartilage that wraps around the MTR during locking, this region is actually ossified in *Toxodon*, such that the transverse dimension of the kneecap is greater than the anteroposterior length (see Scott 1912: fig. 29). This bony 'hook' likely wrapped around the proximal surface of the MTR to hold the patella in the proximal position while standing.

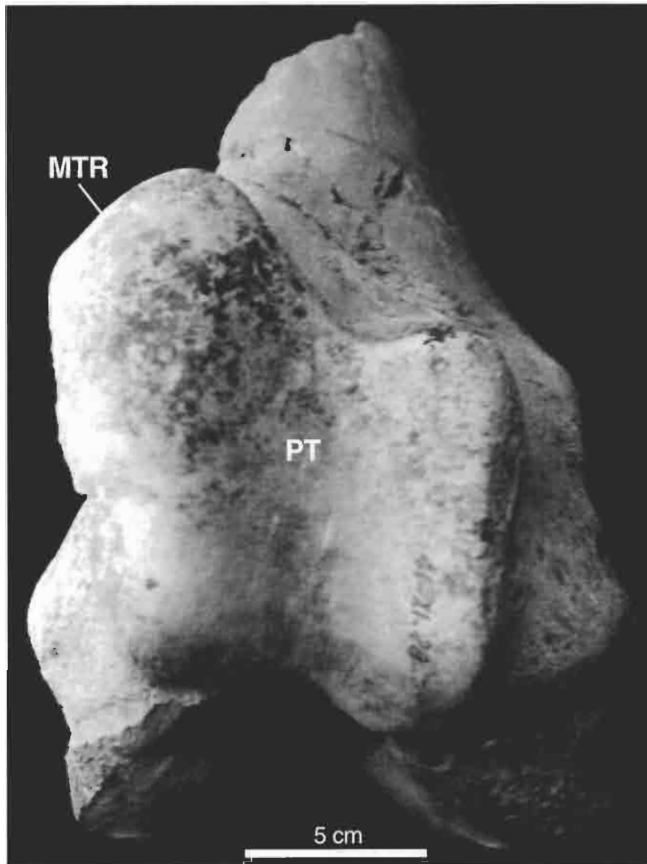


Fig. 2. Left distal femur of *Toxodon* (MLP 41-XI-28-28), showing patellar trochlea (PT) and enlarged medial trochlear ridge (MTR).

Discussion. — Where known in the Notohippidae (the presumed sister taxa of the Toxodontidae) the trochlear ridges of the femora are subequal (e.g., *Eurygenium pacegnum* Shockey, 1997b). The MTR is slightly enlarged in the femora of the earliest known toxodontids. These include Santacrucian (middle Miocene) toxodontids such as *Adinotherium* Ameghino, 1887 and *Nesodon* Owen, 1846 (see Scott 1912: pl XXVII.3 and pl. XXIII.2, respectively). It is also somewhat enlarged in late Miocene and Pliocene femora referred to *Adinotoxodon bolivarensis* Madden, 1990 (personal observations of GB-91 and MNHN-Bol-V-3293). Greatly enlarged MTRs in the Toxodontidae is first seen in the late Miocene *Hoffstetterius imperator* Saint-André, 1992 (see Saint-André 1994: pl. XXX.1), demonstrating that a diversification of locomotion occurred in the Toxodontidae by the late Miocene.

The suggestion that *Toxodon* had a knee-lock similar to that of horses challenges the usual reconstruction of the animal as being semiaquatic (e.g., Scott 1913; MacFadden & Shockey 1997). The same question was raised by Hermanson and MacFadden (1996) regarding the short-legged rhinoceros, *Teleoceros* Hatcher, 1894. They noted a knee-lock in this animal and wondered why an animal supported by the buoyancy of water would need such a specialized knee. Further doubt as to the semiaquatic biology of *Teleoceros* has been raised by MacFadden (1998) who found that the oxygen stable isotope signature of these animals is in conflict with what one would expect to find in an animal living in water. Similar questions and tests may be applied to *Toxodon*. One may note, however, that the extant river hippopotamus also has an enlarged MTR (observation of the mounted skeleton at MLP). Its function in the hippopotamus is unknown.

Order Litopterna Ameghino, 1889

Family Macraucheniidae Gervais, 1855

Genus *Coniopternium* Ameghino, 1895

?*Coniopternium primitivum* Cifelli & Soria, 1983

I have previously noted the suprapatellar fossa in the macraucheniid cf. ?*Coniopternium primitivum* from Salla, Bolivia and speculated that it functioned to lodge the patella in the distal position, thus providing a knee lock (Shockey 1999). Since a detailed description of the femur of *C. primitivum* is provided elsewhere (Shockey 1999), it is not repeated here.

Though similar in principle to the equid knee-lock, the putative macraucheniid locking mechanism is structurally different. In *Coniopternium*, the MTR is not greatly enlarged as in horses and *Toxodon*. Instead, the patella hypothetically became lodged in the deep suprapatellar fossa, or 'patellar pit', during hyperextension of the knee joint. This hypothesis was supported by a model patella that indeed became 'caught' in the 'pit' and was not dislodged by tension applied to the intermediate patellar ligament (Shockey 1997a, 1999).

Numerous macraucheniid genera have the distinctive suprapatellar fossa that varies depth. This 'pit' is distinctive in *Coniopternium* spp. (*C. primitivum*, MNHN-Bol-V-4502, and *C. andinum*, MLP 59-II-26-16). I have also observed this 'pit' in femora of *Cramauchenia* Ameghino, 1902, *Theosodon* Ameghino, 1887, *Promacrauchenia* Ameghino, 1904, and even *Macrauchenia* Owen, 1840. I have not encountered a macraucheniid in which it was lacking. Though this character appears to be universal in macraucheniids, it is not a synapomorphy for the family, since it is also present in protheriids (below).

Family Protheriidae Ameghino, 1887

Genus cf. *Eoauchenia* Cabrera, 1939

Material. — Referred to *Eoauchenia* sp.: MLP 48-XII-16-1, both tibiae, distal femora, patellae, and left pes; MLP 48-XII-16-3, left femur, and both tibiae; MLP 48-XII-16-2, left patella (which may be from the same individual as MLP 48-XII-16-3).

Description. — The femora of cf. *Eoauchenia* are comparable to those of the Santacrucian described by Scott (1910). They have the deep suprapatellar fossae noted by Scott for the Santacrucian

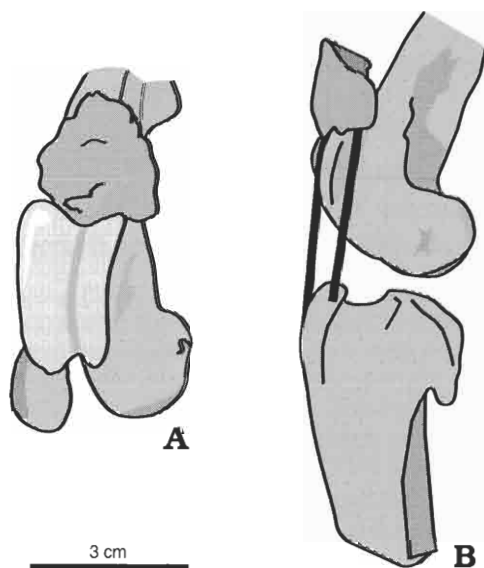


Fig. 3. Functional morphology of the knee joint of the protheriid cf. *Eoauchenia* sp. (based upon MLP 48-XII-16-3 and 2). **A.** Cranial view of tibia, patella, and femur. **B.** Lateral view of knee-joint with reconstruction of lateral and medial patellar ligaments.

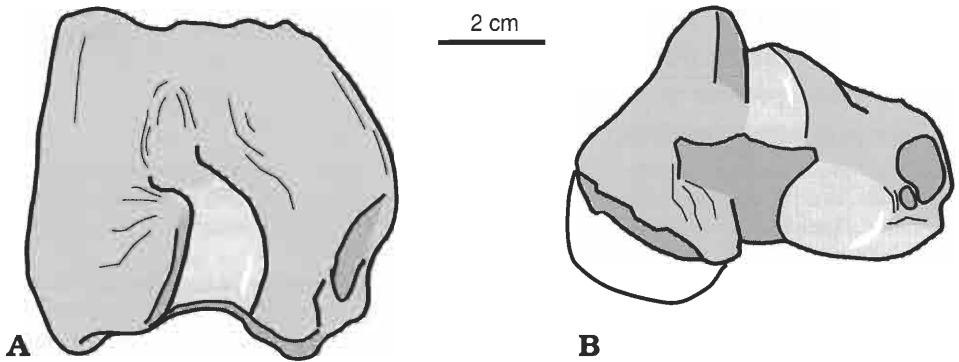


Fig. 4. Left distal femur of unnamed glyptodontid of Salla (MNHN-Bol-V-7003) in cranial (A) and distal (B) views.

proterotheriids, which are similar, though shallower, to the specimens of *Coniopternium* noted above. These proterotheriid femora are also smaller and more gracile than the *Coniopternium* femora and have patellar trochlea which are relatively longer and narrower.

The patella of cf. *Eoauchenia* is somewhat chevron-shaped, having three distal projections, presumably indicating attachment sites for the medial, intermediate and lateral patellar ligaments. The articular surface has a pronounced, longitudinal convexity that conforms to the concavity of the patellar groove of the femur and a longitudinal concavity, which conforms to the MTR of the femur. The most distal portion of the longitudinal convexity has a bulbous form whose shape is such that it fits snugly within the suprapatellar fossa of the femur.

Manipulation of the patella within the patellar groove demonstrates the gliding that would have occurred during flexion-extension of the lower limb. Placing the patella within the 'patellar pit' shows a remarkably good 'fit' which would have supported the patella in the proximal position during hyperextension. Locking could have occurred without 'snagging' the ligaments, though the ligaments may have aided the lock since they apparently would have wrapped around the proximal portion of the patellar ridges (Fig. 3).

Comments. — Scott (1910) noted the pronounced suprapatellar fossa in Santacrucian proterotheriids, but did not speculate as to its functional significance. The well-preserved hind-limb elements of cf. *Eoauchenia* from Monte Hermoso, Argentina (Early Pliocene) assist in developing a hypothesis similar to that proposed for *Coniopternium* and other macrauchenids. Indeed, the patellae of the *Eoauchenia* specimens fit so perfectly within the suprapatellar fossae that it is difficult to dismiss this proposed functional hypothesis.

Order Xenarthra Cope, 1889

Infraorder Cingulata Illiger, 1811

Superfamily Glyptodontoidea Burmeister, 1879

Material. — MNHN-Bol-V-7003, glyptodontoid (genus and species undetermined), left distal femur, from the Bransilla Level of Tapial Pampa West of Salla (Late Oligocene), Bolivia; MNHN-Bol-V-6480, left femur of a glyptodontid Propaleohoplophorinae (genus and species undetermined) from Rio Rosario (middle Miocene), Bolivia (Rio Rosario is believed to be stratigraphically equivalent to the nearby Quebrada Honda, MacFadden *et al.* 1990, which is temporally correlated with the La Ventan fauna of Colombia, see Flynn & Swisher 1995); MNHN-Bol-V-3346, glyptodontid, cf. *Trachycalypus* sp., left femur, patella, tibia, fibula and pes, from Achiri (late Miocene), Bolivia.

Description. — The femur of the Salla xenarthran is so highly derived that it is not readily recognizable as such (Figs. 4, 5, 7). Its oddities include a high, conically-shaped medial trochlear ridge, a sharply curved patellar groove, and a wedged-shaped lateral condyle. Comparison of this element with some-

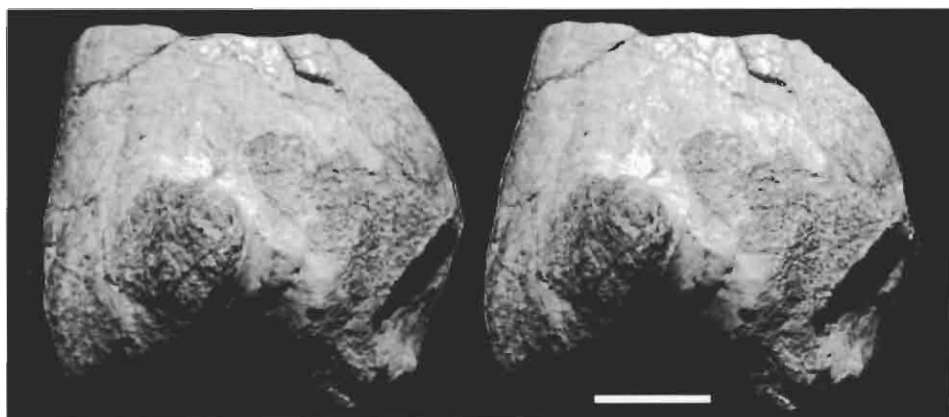


Fig. 5. Stereophoto of left, distal femur of a late Oligocene glyptodontid of Salla, Bolivia (MNHN-Bol-V-7003). Scale bar 2 cm.



Fig. 6. Left distal femur of a middle Miocene Propaleohoplophorinae glyptodontid of Rio Rosario, Bolivia (MNHN-Bol-V-6480). Stereophoto of cranial in aspect (A) and distal (B) views. Scale bar 2 cm.

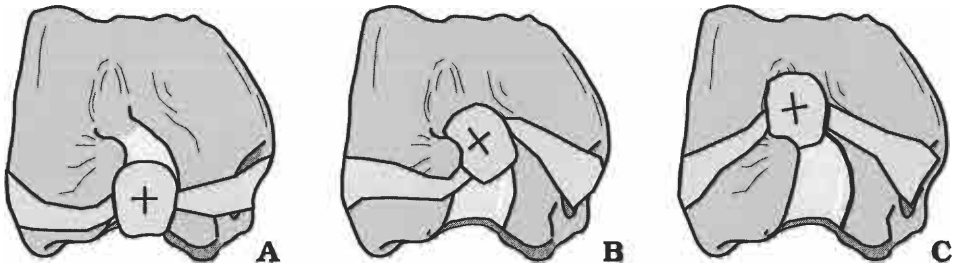


Fig. 7. Model of complex knee-extension of the Salla glyptodontid. **A.** Knee flexed. **B.** Knee partially extended with medial ligaments being retarded by the distinct, conical MTR, thus rotating the patella. **C.** Knee-joint hyperextended and 'locked'. A cross (+) is shown on the patella to illustrate the rotation that occurs during extension.

what less derived (though geologically younger) femora of various glyptodonts (cf. Propaleohoplophorinae, MNHN-Bol-V-6480, cf. *Trachycalyptus* Ameghino, 1908, MNHN-Bol-V-3346 and *Hoplophorus* Lund, 1838 see Paula Couto 1957) demonstrates that this element is indeed a femur (compare Figs. 4, 5, and 7 with Figs. 6 and 8; see also Paula Couto 1957: fig. 13) and most likely is that of a glyptodont (though the possibility that it is from the enigmatic sloth, *Pseudoglyptodon* Engelmann, 1987, should be considered).

This glyptodontoid femur of Salla is dorsoventrally compressed and is conspicuously wide in the transverse dimension. It is widest at the distal region of the element and becomes narrower proximally. This is in contrast to the comparative specimens (Propaleohoplophorinae, cf. *Trachycalyptus* sp. and *Hoplophorus*) which have femora that become wider on the lateral side until they grade into the third trochanter.

The patellar ridges of the glyptodont femur of Salla are asymmetric in regards to both size and orientation. The MTR is proximodistally shorter than the lateral patellar ridge, but its apex is much higher above the broad plane of the femoral shaft. The MTR is subconical in form and its long axis is directed perpendicular to both the long and transverse axes of the femur.

The patellar groove of the Salla femur makes a conspicuous medial turn proximal to the crest between the asymmetrically oriented medial and lateral trochlear ridges, whereas the patellar groove of the other glyptodonts form a more direct (but slightly curved) route for the patella. Also, the surface of the patellar trochlea has a lateral orientation suggesting that the anterior surface of the patella faced somewhat laterally during part of its route up the groove during extension. The Salla femur has a depression proximal to the patellar groove, as do the femora of the Propaleohoplophorinae and cf. *Trachycalyptus* specimens.

The medial condyle of the Salla specimen is missing. The lateral condyle is sharply convex, having distinct lateral and medial articular surfaces. It is essentially V-shaped when viewed distally. This form is similar to the Propaleohoplophorinae and cf. *Trachycalyptus* specimens.

Functional morphology. — Due to the greatly enlarged MTR, it is tempting to interpret these glyptodont femora as having served as knee-locks. However, the medial patellar ridge is so acute and high that it is difficult to see how the medial patellar and/or femoral-patellar ligaments could have easily passed over it. Perhaps the MTR retarded the medial ligaments associated with the patella thus immobilizing the medial side of the patella. This would have resulted in the lateral patella moving further than the medial, thus rotating the patella (Fig. 7). As a consequence, the lateral crus would move further than the medial, causing rotation of the lower leg during extension. This hypothesis would explain why the patellar groove of the Salla glyptodont is so distinctively curved.

Additional support for the hypothesis that the patella rotated about the 'spike-like' MTR is seen in the cf. *Trachycalyptus* specimen from the late Miocene locality of Achiri. (This specimen MNHN-Bol-V-3346 was designated as part of the hypodigm of *Trachycalyptoides achirensis* Saint-Andre, 1994, apparently a *nomen vanum*). MNHN-Bol-V-3346 preserves the femur, patella, crus, and pes. The femur has a pronounced, subconical MTR (Fig. 8) and the articular surface of the patella

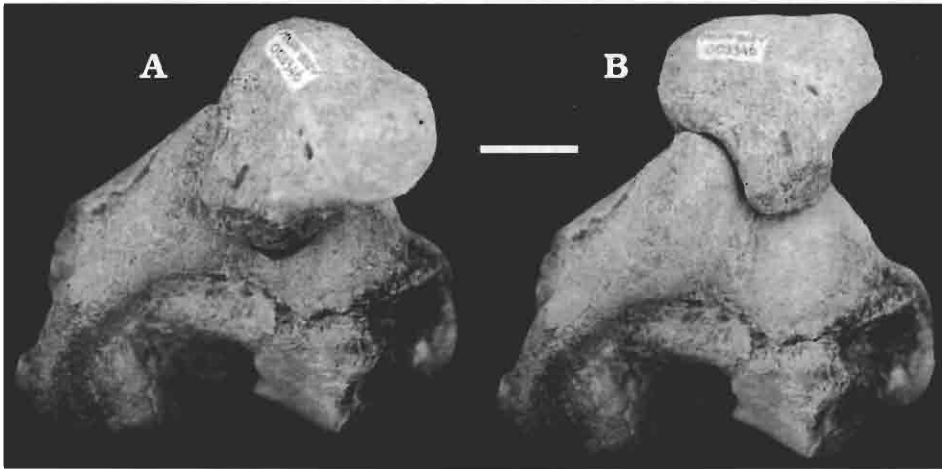


Fig. 8. Patellar rotation during extension in cf. *Trachycalyptus* sp. (MNHN-Bol-V-3346). Apparent position of patella when the knee was flexed (A) and extended (B). Scale bar 2 cm.

has a notch which articulated with the lateral surface of the MTR. The 'best fits' for the patella suggest that its long axis was subparallel with the long axis of the femur when it was in the distal portion of the patellar trochlea (knee flexed position), but was obliquely oriented when pulled to the proximal region of the patellar trochlea (knee extended position) (Fig. 8).

Therefore, it is hypothesized that the MTR of these diverse glyptodonts served to rotate the crus during extension. This finding is supported by morphology of the femoral facets of the tibia-fibula of cf. *Trachycalyptus*. The facet for the medial condyle for the femur is concave, supporting a ball-n-socket type articulation, whereas the lateral condyle of the tibia is flatter, slightly convex, supporting more of a gliding type joint.

Suprapatellar fossae are present in the glyptodont femora considered here. These fossae may have functioned as a site for the patella during hyperextension of the knee, suggesting the possibility that the medial ligaments of the patella ultimately passed over the medial patellar ridge (Fig. 7C). If so, the MTR would have permitted a stable hyperextension of the knee and functioned as a knee-lock.

Discussion

Medial Trochlear Ridge (MTR).— The enlarged MTR in horses and rhinos functions as the supportive structure for the locking mechanism. Hermanson & MacFadden (1996) documented the evolution of the enlarged MTR from the pleisiomorphic condition of subequal MTRs (e.g., *Mesohippus* Marsh, 1875) to slightly enlarged MTRs (e.g., *Parahippus* Leidy, 1858) to finally the fully developed MTRs that occurred about 12 million years ago in the common ancestor Hipparionini and Equini horses. They speculated that the enlarged MTR initially served some unknown function other than a stay mechanism, thus serving as a 'preadaptation' for the knee-lock.

Though enlarged MTRs are uncommon among artiodactyls, Kapplmann (1988) noted their presence in some open-habitat bovids (*Damaliscus* Sclater & Thomas, 1894, *Connochaetes* Lichtenstein, 1814, *Gazella* DeBlainville, 1816, and *Bos* Linnaeus, 1758). He speculated that the enlarged MTR provided a mechanical advantage for the knee extensor muscles. Hermanson & MacFadden (1996) were skeptical regarding

this functional interpretation, noting that the patella ‘tracks’ within the patellar groove, not over the MTR. However, this may be a case where thinking of the forces as an ideal line may not facilitate our understanding of the function. Indeed, the patella tracks within the patellar groove, but inspection of the articular surfaces of the patellae and MTRs in taxa with enlarged MTRs shows that the medial portion of the patella tracks over a portion of the MTR such that the medial side of the patella is raised relative to the lateral side during extension. This would increase the tension on the medial patellar ligament relative to the lateral and intermediate ligaments. This greater medial tension would be transferred to the medial side of the tibia, thus serving to secure the limb medially, below the body of the animal, restricting lateral movements of the crus. Thus, the primary function of an enlarged MTR may have been to aid in stable, forward locomotion. An enlarged MTR may also serve to resist the medial forces from the adductors (e.g., gracilis and vastus medialis) so that the patella is not pulled out of the patellar groove. These putative functions of an enlarged MTR could have served as a ‘preadaptation’ for the knee-lock of horses, rhinos, and possibly *Toxodon*.

The ‘preadaptation’ for the apparent knee-lock in some glyptodonts likely was quite different. The patellae of known glyptodonts do not track over the spike-like MTR, but appear to rotate around it. The enlarged MTR in glyptodonts likely served to retard the medial ligaments (collateral and/or patellar ligaments) and cause rotary movements of the patella, thus serving to rotate the crus during extension. Thus, it is proposed here that a complex extension of the crus of these glyptodonts was the primary function of the enlarged MTR in these taxa.

Feeding ecology. — Though a comprehensive study of knee-function in artiodactyls has not been accomplished, it appears that these ungulates have not evolved passive stay mechanisms to the extent as seen in horses and rhinos. Why not?

A possible explanation may be due to digestive physiology. Perissodactyls use cecal fermentation to aid digestion, whereas many artiodactyl families have ‘foregut’ or rumen digestion (Janis 1976). Ruminant artiodactyls feed, then cease feeding in order to ‘ruminate’; that is, remasticate food that has already been partially digested in the foregut. Thus, cows, for example, may spend much of the day sitting and ‘chewing their cud,’ whereas horses need to continue foraging for food while standing. There is less demand for ruminants to stand for extended periods of time, therefore little pressure for them to have evolved passive-stay mechanisms.

The presence of a knee-lock in extinct herbivores may provide clues regarding their behavior, feeding ecology, and even digestive physiology. For example, we may hypothesize that the extinct, endemic herbivores examined here spent considerable periods of time feeding while standing and that they did not feed intermittently as do ruminants.

Conclusions

A variety of modifications of the distal femora of extinct, South American, native herbivores are documented here. These include a near perfect analog of the horse knee-lock (*Toxodon*), a ‘patellar pit’ knee-lock (macraucheniiids and proterotheriids),

and a sub-conical MTR in glyptodonts that appears to be related to a complex knee-joint extension and possibly a knee lock. These specialized knees suggest that three lineages of native South American herbivores evolved knee-locks in order to facilitate standing for long periods of time. Previously, such adaptations had only been recorded in the Perissodactyla and to a lesser extent in the cow, giving the impression that such adaptations are rare. The hypothesis that knee-locks evolved three times in the Cenozoic of South America implies that knee-locks were not so uncommon. What may have been the exceptional adaptation was the evolution of ruminant digestive physiology that reduces the need for evolving specializations of the knees to aid in standing for long periods of time.

The preliminary findings here suggest that locking knees evolved independently at least five times (twice in perissodactyls and three times in extinct, native, South American herbivores). This indicates that economic standing may be more important for herbivores than our extant, predominately ruminant, ungulate fauna would suggest.

Acknowledgments

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