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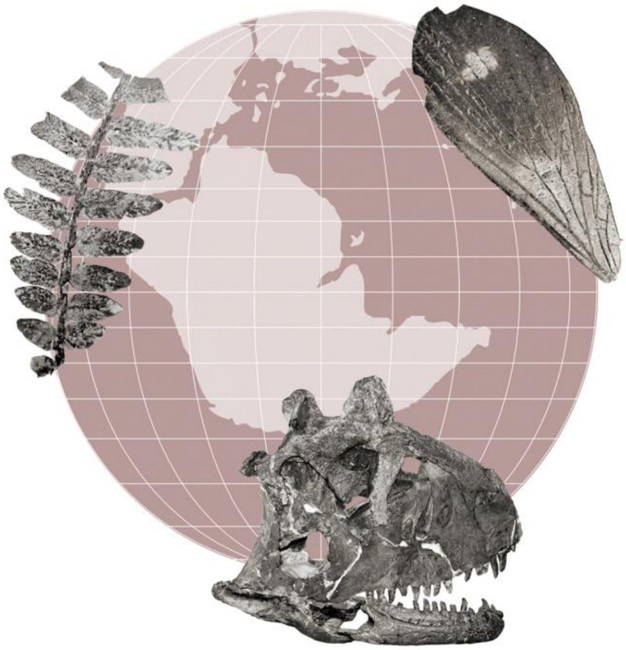

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MOST COMPLETE PRE-DESEADEN LITOPTERN POSTCRANIUM (GRAN HONDONADA, MIDDLE-LATE EOCENE, CHUBUT PROVINCE, ARGENTINA)

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Short Description:

El esqueleto parcial más antiguo conocido de un ungulado Litopterna, procedente del oeste de la Provincia del Chubut, Argentina.

The most ancient partial Litopterna ungulate skeleton yet discovered, from western Chubut Province, Argentina

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Abstract

Litopterna is an order of South American Native Ungulates, known for their cursorial adaptations. However, these features are only well documented in specimens from the late Oligocene (Deseadan Age) and Neogene. Here, we report a partial skeleton of a small litoptern from Gran Hondonada (middle-late Eocene). It consists of elements from both hind limbs of the same individual. Preliminary cladistic analyses (113 dental, cranial, and postcranial characters scored across 50 taxa) recovered the specimen (MLP-PV 67-II-27-375) as a branch of Lopholipterna that diverged before Macraucheniidae and Proterotheriidae, a position supported by two dental and four postcranial synapomorphies. It shares the following plesiomorphic traits with Protolipternidae: absence of the patellar groove on the tibia, a crest-like peroneal process, and the presence of a plantar process on the ectocuneiform bone. Like other lopholipterns, its tibia shows an anterior facet for the astragalus, a reduced medial malleolus, and more complex facets in the tarsal sinus. Various regression models were applied to associate MLP-PV 67-II-27-375 with a known taxon based on tooth size. An indeterminate Adianthidae was the only compatible match. However, MLP-PV 67-II-27-375 could also belong to a taxon not represented by dental remains. Regardless of its taxonomic identity, MLP-PV 67-II-27-375 suggests that many postcranial specializations characteristic of Macraucheniidae and Proterotheriidae were present in their shared ancestors since at least the late Eocene. Anisolambdidae and Adianthidae were recovered as a polyphyletic group of branches that diverged early. Future discoveries, especially of postcranial material, would help to better understand the evolution of Litopterna.

Keywords. Mustersan - South America - SANUs – Phylogeny – Paleobiology – Patagonia – Paleogene

Resumen. EL POSTCRANIO DE UN LITOPTERNA PRE-DESEADENSE MÁS COMPLETO CONOCIDO (GRAN HONDONADA, EOCENO MEDIO-TARDÍO, PROVINCIA DEL CHUBUT, ARGENTINA)

Los Litopterna son ungulados nativos sudamericanos caracterizados por presentar especializaciones relacionadas con hábitos cursoriales. Sin embargo, sólo están bien documentados para representantes neógenos y del Oligoceno tardío (Edad Deseadense). Aquí damos a conocer un esqueleto parcial de un pequeño Litopterna encontrado en la Gran Hondonada (Eoceno medio/tardío). Está conformado por elementos de ambos miembros posteriores del mismo individuo. Análisis cladísticos preliminares (113 caracteres dentarios, craneanos y poscraneanos escoreados en 50 taxones) recuperaron al MLP-PV 67-II-27-375 como una rama temprana de los litopterna lofolipterna que se diferenció antes de la divergencia entre Macraucheniidae y Proterotheridae. Comparte los siguientes caracteres pleisiomórficos con los Protolipternidae: la ausencia del surco patelar en la tibia, el proceso peroneal en forma de cresta y la presencia de un proceso plantar en el hueso ectocuneiforme. Como otros lopholipternas, la tibia tiene una faceta anterior para el astrágalo, el maléolo medial está reducido, y las facetas del seno del tarso son más complejas. Se aplicaron distintos modelos de regresión para asociar al MLP-PV 67-II-27-375 con algún taxón conocido por dientes, siendo un Adianthidae indet. el único con un tamaño esperado. También es posible que MLP-PV 67-II-27-375 corresponda a un taxón desconocido por los dientes. Cualquiera sea su asignación taxonómica, MLP-PV 67-II-27-375 indica que muchas de las especializaciones poscraneanas que caracterizan a los Macraucheniidae y Proterotheriidae ya habrían estado presentes en sus ancestros del Eoceno medio–tardío y que los Anisolambdidae y los Adianthidae serían un conjunto polifilético de ramas que divergieron tempranamente. Descubrimientos futuros, especialmente de huesos postcraneanos, ayudarán a comprender mejor la evolución de los Litopterna.

Palabras clave. Mustersense- América del Sur - SANUs – Filogenia – Paleobiología – Patagonia – Paleógeno

LITOPTERNA AMEGHINO, 1889 is the second most abundant and diverse order of South American native ungulates (SANU). Litopterna inhabited the continent since the late Paleocene, becoming extinct sometime during the Late Pleistocene–early Holocene (Lujanian South American Land Mammal "Age" or SALMA; Bonaparte & Morales, 1997; Bond *et al*., 2001; Soria, 2001; Ubilla *et al*., 2011; Gelfo *et al*., 2016). They were not exclusive to South America, as litopterns have also been found in the Eocene of West Antarctica (Bond *et al*., 2006; Gelfo *et al*., 2014). The extent and internal relationships of Litopterna remain uncertain, with authors holding differing views on the phylogenetic placement of certain Paleogene taxa such as Didolodontidae, Protolipternidae, Sparnotheriodontidae, Amilnedwardsiidae, Indaleciidae, and Anisolambdinae (Cifelli, 1983a,b; Soria, 1989; Lorente, 2015, 2016; Schmidt, 2015; Gelfo *et al*., 2016; McGrath *et al*., 2020; Püschel *et al*., 2022). Undisputed litoptern families include Adianthidae, Macraucheniidae and Proterotheriidae, grouped together as Lopholipterna (Cifelli, 1993). The term Lopholipterna has subsequently been used with different content and composition (e.g. Soria, 2001). For the sake of clarity, we use here Lopholipterna as the clade including the most recent common ancestor of *Adianthus*, *Macrauchenia*, and *Proterotherium*, and all its descendants, whether or not it includes taxa once classified in other families.

Proterotheriids are recorded from the late Oligocene up to the Late Pleistocene-Holocene (Soria, 2001; Muizon & Cifelli, 2000; Gelfo *et al*., 2016; Püschel *et al*., 2024), although several authors argued that some Eocene litopterns (i.e., *Anisolambda* and *Paranisolambda*) may belong to this family (Cifelli, 1983b; Bond *et al*., 2001; McGrath *et al*., 2020). Proterotheriids were small to medium size (15-70 kg) browsers that lived in a variety of environments (Bond *et al*., 2001; Ubilla *et al*., 2011; Corona *et al*., 2018). They are usually compared to equids because of their mesaxonic limbs, characterized by a functional third digit, with a tendency to reduce digits II and IV and the absence of digits I and V. This comparison has been called into question several times, with proterotheriids being considered functionally more similar to small artiodactyls than perissodactyls (Ameghino, 1905; Scott, 1910; Schaeffer, 1947; Soria, 2001; Lorente, 2017; Lorente *et al*., 2025).

Macraucheniids were present from the late Eocene (Mustersan) to the Pleistocene (Soria, 1982; Cifelli, 1983b, 1993; Dozo & Vera 2010; Schmidt & Ferrero 2014; but see Lobo *et al.*, 2024). They exhibit various evolutionary trends during their evolution such as increase in size, reduction of the nasal bones, development of a radial aliform expansion, and posterior migration of the external nares (Soria 1981, 1986; Bond, 1999; McGrath *et al.*, 2018; Püschel *et al.*, 2023). Fusion of the ulna and radius and of the tibia and fibula has also been mentioned (Püschel *et al.*, 2023) but this is absent in *Theosodon* and present in non-macraucheniids such as *Protheosodon* and *Adianthus* (Scott, 1910; Loomis, 1914; Cifelli, 1991). Macraucheniids are characterized by a relatively long neck, a complete dentition without any diastema, and functionally tridactyl feet. Macraucheniids may have had a plantar pad and subunguligrade locomotion (Vera & Krapovickas, 2022). Adianthidae is a poorly known assemblage of Paleogene and early Neogene litopterns, usually interpreted as related to the Macraucheniidae (Cifelli & Soria, 1983; Cifelli, 1993). *Adianthus godoyi*, the only Adianthidae with known postcranial elements, was a small cursorial herbivore from the Early Miocene of Chile (Cifelli, 1991).

Litopterns are well represented in the Paleogene record by cranial and mandibular remains with associated dentitions and many isolated teeth. Their cheek teeth are bunoselenodont, with a relatively conservative morphology, retaining many characters shared with South American and Laurasian archaic ungulates traditionally classified as “Condylarthra” (Kramarz *et al.*, 2021). In contrast, litopterns have a specialized appendicular morphology since very early in their evolution (Scott, 1910; Simpson, 1948; Lorente, 2015, 2016). Nevertheless, postcranial remains are much scarcer; the oldest known postcranial elements associated with dental remains are Late Oligocene (Deseadan SALMA; Loomis, 1914; Dunn *et al.*, 203; Shockey, 1999; Shockey et al 2023). Older remains are isolated bones from the early Eocene localities Itaboraí (east Brazil) and Paso del Sapo (central Patagonia; Cifelli, 1983a,b; Bergqvist, 1996; Soria, 2001; Lorente, 2015, 2016). These isolated litoptern-like postcranial remains can be easily distinguished from other mammals.

This work describes and analyzes two partial hindlimbs of the same individual (MLP-PV 67-II-27-375) with a clear litoptern morphology derived from Eocene sediments of the Sarmiento Formation. They were found together, semiarticulated, during a paleontological campaign of Museo de La Plata in 1967 at the Gran Hondonada locality, also known as El Pozón (Odreman Rivas, 1978; Cladera *et al.*, 2004: fig. 1) in central Patagonia (Chubut Province, Argentina). The Gran Hondonada locality bears a rich mammal assemblage, including didolodontids and litopterns, along with reptiles and birds. The mammal association suggests that the fossil-bearing levels are coeval with the Rosado and Lower Puesto Almendra members of the Sarmiento Formation at Gran Barranca Sur of Colhue Huapi Lake (see Figs. 1 and 2; Odreman Rivas, 1978; Cladera *et al.*, 2004), which is the type locality of the Mustersan SALMA (Bond & Deschamps, 2010), and dated between 38 and 37 Ma (middle–late Eocene) (Dunn *et al.*, 2013). Therefore, MLP-PV 67-II-27-375 is the most complete litoptern postcranium found in pre-Deseadan rocks. Here we describe MLP-PV 67-II-27-375, compare it to other Litopterna with known postcranial remains, discuss its mode of locomotion, analyze its phylogenetic relationships, and explore its possible attribution to dental taxa. Finally, we discuss the implications of this new specimen for the comprehension of the early appendicular evolution of Litopterna, especially in relation to the divergence between Macraucheniidae and Proterotheriidae.

Figure 1

Figure 2

Institutional abbreviations. **AMNH**, American Museum of Natural History, United States of America; **LIEB-PV** Paleovertebrate Collection Laboratorio de Investigaciones en Evolución y Biodiversidad, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia “San Juan Bosco”, Esquel, Chubut Province, Argentina; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina; **MLP-PV**, Division of Vertebrate Paleontology of Museo de La Plata, Argentina.

Anatomical abbreviations. Figures follow the anatomical style of Szalay (1994) for easier comparison. Abbreviations are in Supplementary Online Information 1 and through text. Directions follow the classical annotations for unguligrade mammals, where in the pes, dorsal is synonym to anterior, and plantar is synonym to posterior.

MATERIAL AND METHODS

Photographs were taken using two digital cameras: a Canon Powershot G15 and a Nikon d7200 with a Nikon 1:6.3 f= 12 cm macro lens.

Specimens of Proterotheriidae and Macraucheniidae used for comparison are listed in Supplementary Online Information 1. Observations in this paper are based on those specimens. “Later litopterns” refers to a temporal sense. “Protolipternidae from Brazil” refers to remains referred to *Protolipterna ellipsodontoides* and *Miguelsoria parayirunhor* (Cifelli, 1983a; Bergqvist, 1996; Bastos & Bergqvist, 2007). “Protolipternidae” (alone) also includes material referred to *Asmithwoodwardia* sp. from Patagonia (Lorente, 2015, 2016).

Osteological, arthrological and myological terminologies are based on veterinary anatomy (Getty, 1990; Schaller, 1996; ICVGAN, 2017), medical anatomy (Testut & Latarjet, 1978; Kelikian & Sarrafian, 2011; FIPAT, 2019), and others (Scott, 1910; Loomis, 1914; Davis, 1964; Szalay, 1994; Ercoli, 2015).

Specific terminology. “Referred” or “referred to” is used to describe associations based on linear regression models of dental and postcranial remains not found together, to avoid confusion when talking of partial skeletons. “Parasagittal” is used to encompass both cursorial and bounding locomotor modes, as both have adaptations to restrain movements to the sagittal plane and avoid bone displacement under great loads. Every time saltatorial or bounding is mentioned, we refer to quadrupedal mammals, not to bipedal hoppers.

Phylogenetic analyses

To test the phylogenetic position of MLP-PV 67-II-27-375, we used a modified version of the reduced matrix published by Carrillo *et al.* (2023), with several changes. We expanded the litoptern taxon sampling by adding *Adianthus godoyi*, *Coniopternium* sp. and *Macrauchenia patachonica*, the three species with known postcranial elements (see Supplementary Online Information 1). The terminal taxon *Asmithwoodwardia scotti* (Itaboraian SALMA) was replaced by *Asmithwoodwardia spp*, an operational unit encompassing the type species *A. subtrigona* and a closely related species reported as *Asmithwoodwardia* sp. nov. from Paso del Sapo Fauna in central Patagonia (Tejedor *et al.*, 2009). This change is because recent studies suggested that *A. scotti* is not congeneric with the type species (Gelfo, 2006; Püschel *et al.*, 2024), and because postcranial elements are known for the Patagonian species, but not for the Itaboraian species (Lorente, 2016). Consequently, we re-scored all characters for this taxon. We also added *Tricoelodus* to enlarge the adianthid sampling, and the notoungulate *Notostylops* sp. as the outgroup since it is one of the best-known Paleogene non-litoptern SANU with known postcranial elements (Lorente *et al.*, 2019; Vera *et al.*, 2023).

We re-defined character 49 (presence of mesostyle on upper molars) with three character states in order to capture the different degree of development and relationships of this structure observed within the taxon sampling. Moreover, Carrillo *et al.* (2023) scored as missing data several taxa where the occurrence of mesostyle on upper molars is well documented (*e.g.*, *Thoatherium minusculum*, *Lambdaconus lacerum*, *Neobrachytherium intermedium*, etc.; see Soria, 2001).

We included a new dental character that captures the presence of postmetaconule crista on M1-M2 (character 78), a feature of potential phylogenetic relevance not considered by Carrillo *et al.* (2023).

The scorings of some dental characters of several taxa were modified based on observations of the types and referred specimen; these are indicated and discussed in Supplementary Online Information 1.

The original data matrix by Carrillo *et al.* (2023) included 18 postcranial characters. The characters identified by the authors as 1C, 38Cm and 92MG are redundant as they capture the number of digits in manus and pes. We used only the character 92MG (character 80 in our matrix). Character 6C (navicular facet of astragalus) was deleted because no sampled taxon has state 0 and the same condition is partially captured by 5C (character 89 of our matrix). The character 47C (presence of medial collateral ligament facet) was deleted due to its morphological complexity. In some mammals (*e.g.*, Primates) the medial collateral ligaments pass over its own facet. In other animals, such as *Arctocyon*, there is a small sesamoid in the same place. In others, such as Notoungulata, *Phenacodus* and *Hyopsodus*, the navicular medial tuberosity is very large and articulates with a medial expansion in the navicular facet (character 8C) and there is no distinct facet for the medial collateral ligaments. These three structures may be embryologically homologous, but their configuration may be phylogenetically and morphofunctionally significant (Lewis, 1964; Hildenbrand, 1976; Lorente, 2015, Lorente *et al.*, 2019). Therefore, this character is not independent of character 47C, and it should be scored when both astragalus and navicular are known. Litopterns scored as lacking a medial collateral ligament facet have a medial sesamoid that articulates with the astragalus. This sesamoid has a composite facet between the astragalus and the navicular. This facet is harder to differentiate in the astragalus than in the navicular, particularly in the smaller litopterns.

The definition of other characters was modified in order to reflect current knowledge of appendicular anatomy. Additionally, we included new postcranial characters related to the femur, tibia, astragalus, calcaneus, navicular, and ectocuneiform. The pelvis was not included in the phylogenetic analysis due to its fragmentary state in MLP-PV 67-II-27-375 and because it is unknown in most of the remaining taxa. The postcranial characters were re-numbered following an anatomical ordering (*i.e.*, from proximal to distal).

It is worth mentioning that all postcranial characters of *Didolodus*, *Victorlemoinea*, *Lamegoia* and *Ricardocifellia* were re-scored as missing data following Soria (2001), Gelfo and Lorente (2012), and Lorente (2015, 2016). Postcranial characters of *Asmithwoodwardia, Tiuclaenus* and *Simoclaenus sylvaticus* were scored and/or re-scored following Muizon *et al.* (1998) and Lorente (2016). The scoring of postcranial characters for 12 litopterns species (*Anisolophus floweri*, *Diadiaphorus majusculus*, *Eoauchenia primitiva*, *Epitherium laternarium*, *Neobrachytherium* *intermedium*, *Neolicaphrium recens*, *Protheosodon coniferus*, *Tetramerorhinus cingulatum*, *Tetramerorhinus mixtum*, *Theosodon sp.*, *Thoatherium minusculum, Uruaguayodon alius*) were completed based on published remains (see Supplementary Online Information 1).

The complete matrix has 113 characters (numbered from 0 to 112) scored in 50 terminal taxa. The parsimony analyses were performed using the Traditional Search option of TNT program (version 1.5) with 1000 replications using the tree bisection-reconnection algorithm (TBR), followed by an extra TBR round on the optimal trees. The character matrix is available as Supplementary Online Information 2, and a second matrix with the combination of MLP-PV 67-II-27-375+MPEF 1101 is available as Supplementary Online Information 3.

Additional pictures are available at Morphobank, project id. 5001 (https://morphobank.org). The TNT file with the character matrix can also be download from Morphobank, but the character state of the file should be change to 32 (“nstates num 32”).

Body Mass

Body mass estimates were derived from previous works (Scott, 1990; Tsubamoto, 2014; Yapuncich *et al.*, 2015), applying quasi-maximum likelihood estimator as correction factor (Smith, 1993; Scarano *et al.*, 2011; see Supplementary Online Information 1). Models with the smallest percental prediction error (PE%) and percent standard error of the estimate (SEE%) were chosen as they better met the linear regression model assumptions (Ayinde *et al.*, 2012).

Postcranial association

A linear regression model for postcranial associations was performed to test the size relationship between teeth and postcranial remains.

$$\ln(\text{femoral interepicondylar transverse distance}) = (0.4709 \times \ln(\text{third molar area})) + 1.3194$$

This model was selected as the best fit model (Ayinde *et al.*, 2012) for these remains from Lorente (2015) based on a sample of 52 eutherian individuals with known postcrania. It has a correlation coefficient of 0.96, a percent prediction error (%PE) of 0.01%, a percent standard error of the estimate of 7.21% (%SEE; Van Valkenburgh, 1987) and a Shapiro-Wilk Test value of 0.42

(normal distribution of residuals). A 99% confidence interval was chosen to calculate the error of the estimations. The quasi-maximum likelihood estimator was applied as a correction factor (Smith, 1993; Scarano *et al.*, 2011).

RESULTS

Anatomical description and comparison

Studied material. MLP-PV 67-II-27-375, right partial pelvis, right and left femurs, right and left tibias, right calcaneus, right and left astragali, right navicular and right ectocuneiform (now lost) of the same individual. The bones of the right side are more complete and better preserved than those on the left side. All the remains were found together, with a tibia fully articulated with the corresponding astragalus. The bones on the left side (except the right femur) show some degree of erosion, rounded borders and some plastic deformation evident as transverse compression. Some of this can be explained by the skeleton being in a position that exposed the left side to natural erosion earlier than the right. The pelvis and long bones of both sides show transverse fractures.

Locality and age. La Gran Hondonada (44°20′49″S–69°46′57″W), Tehuelches Department, Chubut Province, Argentina; Sarmiento Formation, Mustersan SALMA (middle–late Eocene; Odreman Rivas, 1978: 36, figs. 1 and 2).

Pelvis (Fig. 3). Only part of the iliac region and the ischium and pubis are preserved from the right pelvis. Overall, it shows a very similar appearance to proterotheriids of the Santacrucian SALMA (*e.g., Tetramerorhinus mixtum*; Scott 1910).

The acetabulum (Ac) has a relatively high and prominent dorsal edge, its anterior end being rough, with no marked cotyloid edge. The acetabular fossa is relatively wide and elongated dorsoventrally to the posterior end of the cotyloid cavity, ischiopubic groove relatively short, not very defined. Dorsal to the lunate surface of the cotyloid cavity and separated from it by a small concavity of the cotyloid rim, there is a small rounded roughness tadicate the origin of the *Rectus femoris* muscle (knee extensor).

The ischium, especially the post-acetabular portion, is slender and thin, more reminiscent of that of Proterotheriidae than Macraucheniidae (*e.g.*, *Theosodon*; Scott, 1910) and *Adianthus* (Cifelli, 1991). The ischial spine (si) forms a sharp and linear crest that ends posteriorly at a 90°-degree angle, probably the medial insertion of the *Gemellus superior muscle* as in *Miguelsoria*, *Adianthus* and *Megadolodus* (Bergqvist, 1996; character 30). The ischium continues posteriorly, flattening at its end and directed externally; it preserves the beginning of the expansion of the tuberosity and the limiting edge of the posterior end of the obturator foramen (ob). From what is preserved, the latter was probably oval and elongated anteroposteriorly.

The pubis is poorly preserved, being crushed and compacted. It has a very well-marked ileopectineal tubercle (ipt) in the lateroventral part of the acetabular area. Then it thins out posteriorly in the form of a sheet, and the contact with the ischium cannot be observed due to breakage.

Figure 3

Femur (Fig. 4). The left femur is better preserved than the right femur, just lacking the plantar edge of the head and the proximal end of the lesser trochanter. The right femur lacks the head and it is broken in several parts of the diaphysis. The overall anatomy is similar in appearance to that of the Proterotheriidae and Macraucheniidae and also to postcranial remains referred to protolipternids (*Protolipterna* and *Miguelsoria*) and *Paranisolambda* from Itaboraí (Bergqvist, 1996).

The femoral neck (fn) is not very projected medially, it is relatively robust and directed anteriorly, as in the Proterotheriidae and unlike in the Macraucheniidae, in which it is more medial, with the upper end not very excavated. It has a rounded articular head (Fh). The greater trochanter (gt) is higher than the head, twisted inward, with the trochanteric eminences well-differentiated: a small anterior one (*pars cranialis*; gtpa) and a larger and more rounded posterior a one (*pars caudalis*; gtpp) for the abductor muscles of the femur. The greater trochanter of specimen MLP-PV 67-II-27-375 is lower than in the Proterotheriidae, although higher than in *Adianthus* (Cifelli, 1991) and Macraucheniidae. The trochanteric fossa (tf) is well marked, relatively deep and elongated. The intertrochanteric crest (itc) becomes smooth and less marked at the height of the Lesser trochanter (lt) and it continues distally beyond the trochanteric fossa and the lesser trochanter where it makes a wide round arch to join the lesser trochanter proximally.

The lesser trochanter is relatively small, elongated proximodistally and positioned posteromedially. Its appearance is not as laminar as in certain Proterotheriidae (*e.g.*, *Thoatherium*) and is a little more reminiscent of the Macraucheniidae (*e.g.*, *Theosodon;* Scott, 1910). Poor development of the lesser trochanter means a smaller insertion area for the flexor of the hip (Salton & Sargis 2009).

The third trochanter (3t) is the area of insertion of the *Gluteus superficialis* muscle (abductor of the femur and hip extensor). It is well developed, rectangular, starts proximally at the level of the distal end of the lesser trochanter and extends until to the middle part of the diaphysis distally. It is slightly concave on its anterior surface, its distal edge ending in a subtle crest, resembling more the condition observed in the Proterotheriidae than in the Macraucheniidae.

The transverse perimeter of the diaphysis is triangular, with its anterior face convex, and the posterior face slightly flattened, with the flattest portion corresponding to the area at the level of the third trochanter. There is no *linea or facies aspera i*n the posterior aspect of the diaphysis, which is mostly smooth, but a marked line (lateral labium of facies aspera; llfa) runs from the third trochanter to the supracondylar fossa (scf), where it divides in the lateral (lateral supracondylar tuberosity) and plantar borders of the fossa. The supracondylar fossa is the area of origin of *Flexor digitorum superficialis* (*Plantaris* after Terminologia Anatomica; FIPAT, 2019) muscle, that flexes the knee and extends the tarsus and is responsible for the stabilization and support of the digits. Distal to this fossa, a facet for the lateral femoral sesamoid bone can be observed.

The distal epiphysis of the femur has a long, transversely narrow trochlea (Ft), with parallel symmetrical crests (after Janis *et al.*, 2012). The medial condyle (Fmc) is slightly anteroposteriorly deeper than the lateral one (Flc), both with a convex semicircular shape although the medial one is flatter and more oblique in position. In the intercondylar cavity (fic), a soft oblique ridge in a proximomedial-ventrolateral direction is observed that connects both condyles. Below this ridge, a small foramen is observed. External to the lateral condyle, a small pit is observed, probably for the origin of the *Popliteus* muscle (inward rotation of the femur); a small rough area next to this pit could indicate the origin of the *Extensor digitorum longus muscle* (extensor of the phalanges). At the medial epicondyle (fmec), a longitudinal sulcus can be observed.

The distal femoral portion of MLP-PV 67-II-27-375 is different from that observed in the Proterotheriidae and Macraucheniidae of the Deseadan and Santacrucian SALMAs (Scott, 1910; Loomis, 1914). Unlike these, it lacks a well-developed and protruding trochlea without having the lateral ridges as marked. The supratrochlear fossa (sft) is very poorly defined, almost continuous with the patellar surface, and the fossa for the insertion of the gastrocnemius muscle is less deep. In these aspects, the specimen from La Gran Hondonada is a little more similar to a less specialized ungulate such as the condylarths Meniscotheriidae (i.e. *Meniscotherium*) or Hyopsodontidae (i.e. *Hyopsodus;* Gazin, 1965, 1968) from the early Eocene of North America than to later litopterns. This difference may be due to size, as smaller mammals often exhibit less defined trochleas (personal observation). The length and width of the trochlea are similar to protolipternids and *Paranisolambda* from Itaboraí (Cifelli, 1983a; Bergqvist, 1996), *Hyracotherium*, and lagomorphs.

Figure 4

Tibia (Fig. 5). The right tibia is the better preserved. The left tibia is eroded, particularly in the proximal end, with the proximal articulation compressed transversally and most features lost.

The two tibiae are long, thin and relatively straight, showing a slight twist toward the lateral direction in the proximal portion, similar to *Thoatherium* (Scott, 1910). In total length, they are almost as long as the femur, but longer if functional length of the femur is considered. They are longer and more gracile in appearance than litoptern tibiae known from the Deseadan, Santacrucian and Friasian SALMAs (Scott, 1910; Loomis, 1914; Cifelli, 1991), but when comparing diameter against length, they are proportionally equivalent.

The tibial plate is triangular in section and has separate medial and lateral condyles, with the lateral one being larger overall and more proximal. The lateral condyle has a small facet at the posterior end, for the *Popliteus* muscle (pmf). The intercondylar eminence (ice) is low, and the lateral intercondylar tubercle is higher than the medial one. The fibular facet (TiFi) for the proximal end of the fibula is located distal to the *Popliteus* facet (pmf). The tibial tuberosity (tt) is robust and presents a slightly concave surface. A defined groove for the middle patellar ligament is not observed, which is so well marked in later litopterns (*e.g.*, *Thoatherium*, *Theosodon*). Lateral to the tibial tuberosity, a very well-marked *Sulcus extensiorus* groove (gse) is observed. Through this groove slides the tendon of the extensor muscle of the fingers (forward direction of the foot) and *Fibularis tertius* muscle (also called *Peroneus tertius*, flexor of the joint).

The posterior tibial surface shows a well-defined muscular line (ml) below the proximal articular area. This line divides the posterior surface into two concavities, a lateral one, probably for the insertion of the *Popliteus* muscle (inward rotation of the femur), and a medial one, with a smoother secondary oblique line probably for the *Tibialis posterior* and *Flexor digitorum profundi* muscles. The lateral cavity for the insertion of the *Popliteus* muscle reaches the distal epiphysis at the medial border.

The tibial cnemial crest (cc; *Margo cranialis*) is well marked, reaching the middle of the tibia in a curved arc. From there, the diaphysis shows a subcircular section, until reaching an anteroposteriorly wider distal end.

The distal epiphysis has a deep cochlea (Ati), with an intermediate crest that ends in an anterior (tap) and a posterior (tpp) process. Of these two processes, the posterior one is more developed. The anterior process has a small anterior articular facet (ATia) for the astragalar neck fossa. This feature is shared with later litopterns; it is absent in *Asmithwoodwardia* (Lorente, 2015, 2016) and not described in *Protolipterna* (Bergqvist, 1996). The medial malleolus (mm) is relatively small and less developed than in the Protolipternidae but larger than later litopterns. Some works have mentioned a developed medial malleolus in partial tibiae of *Diadiaphorus* (Schmidt *et al.*, 2019) and *Neodolodus* (Carrillo *et al.*, 2023). However, the morphology of those specimens is similar to other better-preserved tibiae of proterotheriids (Scott, 1910; Soria, 2001), suggesting the proposed medial malleolus in those works is actually the posterior process.

The tibia does not present a clear distal fibular facet, but this may be a preservation issue.

Figure 5

Tarsus

The tarsus is reverse alternating after Cifelli (1993), with astragalonavicular articulation more proximal than the calcaneocuboid articulation (Lorente, 2019). No clear calcaneonavicular facets are observed.

Calcaneus (Fig. 6). Only the right calcaneus is preserved. It is similar to that described for the Proterotheriidae (Scott, 1910) and Protolipternidae (Cifelli, 1983a). It is elongated, with the calcaneal tuber or *Tuber calcanei* (tc) compressed transversally.

The *tuber calcanei* is rough, without division between different eminences, but this may be due to erosion in this area. There is a subtle transverse sulcus dividing the tuber calcanei into dorsal and plantar eminences.

The fibular facet (CaFi) is relatively small and less developed than in Proterotheriidae and Macraucheniidae, especially in the most recent genera. It is narrow and convex, proximally-distally elongated and oblique. Lateral to the fibular facet, there is a concavity similar to that observed in *Miguelsoria parayirunhor*, probably for one of the medial collateral ligaments. This concavity is limited plantarly by a well-defined peroneal crest (pp), related to *Fibularis longus* (*Peroneus longus*) muscle, which inserts distally into a small peroneal tubercle. The same condition is observed in *Miguelsoria parayirunhor* (Cifelli, 1983a), There is a well-defined anterior plantar tubercle (at) that ends distally around the proximal end of the cuboid facet (CaCu). The distal process (dp) is long and well developed, similar to other litopterns.

The ectal facet (CaA) is well developed, convex and extended proximally over half of the length of the calcaneal kneel, in a manner similar to that of Protolipternidae and Proterotheriidae (Lorente *et al.*, 2025). The ectal and sustentacular facets are separated by a narrow and shallow interarticular fossa. Distal to the ectal facet, the sinus tarsi has a well-marked crest that possibly served as the origin of the *Extensor digitorum brevis* muscle and the *Sinus tarsi* ligaments (Kelikian & Sarrafian, 2011; Ercoli, 2015). The sustentaculum tali is very well developed and expanded medially. The sustentacular facet (Su) is concave and elongated proximally-distally, nearly reaching the cuboid facet, as occurs in Proterotheriidae and Macraucheniidae and differing from Protolipternidae, which have a more triangular and smaller sustentacular facet (Bergqvist, 1996; Lorente, 2015, 2016). The plantar surface of the sustentaculum presents the sulcus for the tendon of the *Flexor hallucis longus* and/or *Flexor digitorum longus* muscles (this sulcus is independent of digit number). There is no apparent anterior calcaneal facet (x), but it must be considered that in larger litopterns, it is usually fused to the sustentacular facet and not very well differentiated (the x facet of Ameghino, 1905).

The cuboid facet is strongly oblique (angle from principal axis < 25°), extending antero-medially. It is concave both sagittaly and transversely, as in Protolipterna and Proterotheriidae.

Figure 6

Astragalus (Fig. 6). The right astragalus is better preserved than the left astragalus, which has rough borders and broken flexor groove. The astragalus is long and relatively narrow, as described for the Litopterna, and especially similar to that of the Proterotheriidae.

The astragalar body has a deep tibial trochlea (ATil), limited medially and laterally by very well-marked curved ridges. The flexor sulcus (dfs) of the tibial trochlea is more marked than in proterotheriids. There is no dorsal astragalar foramen. The trochlea extends to the neck as an anterior fossa (ATia) for the anterior process of the tibia. The trochlear ridges of the right astragalus have some asymmetry in length, with the lateral side longer than the medial side (after Mills, 2019).

The left astragalus is more symmetrical than the right one, but this difference is probably due to the erosion present in the former. The lateral ridge is more developed proximally-distally and also transversely than the medial ridge. There is no lateral projection of the astragalar body (“lateral process” in classical anatomy). The fibular facet (AFi) is flat and widens distally until it practically comes into contact with the latero-distal end of the ectal facet (CaA). However, it is still possible to observe a slightly rough area that diffusely marks the limit between both articular facets of the astragalus. The medial malleolar facet (ATim) is flat and limited to the edge of the ridge. The remainder of the medial astragalar surface is relatively rough and flat. There is no defined anterior plantar tubercle or insertion for the posterior component of medial tibioastragalar ligament.

The sustentacular facet (Su) of the astragalus is elongated in the proximal-distal direction, similar to that of the Proterotheriidae, but shorter than in the Macraucheniidae. It is convex, and gently oblique in a medio-lateral direction. It widens slightly at the latero-distal end where it contacts the medioplantar edge of the navicular facet. The limit between sustentacular and navicular facets is marked by a small crest.

The ectal facet is strongly concave, especially in its middle area, and is directed mostly laterally rather than plantarly. The distal end of this facet is convex and projected planto-laterally. The neck of the astragalus is relatively long, similar to that of the Proterotheriidae and longer than in the Macraucheniidae. On the medial surface there is a smooth groove that extends approximately in a dorso-plantar direction, from the distal end of the medial crest to the plantar edge.

The head of the astragalus is convex and elongated in a latero-medial direction. It is more convex than in *Miguelsoria*, similar to that of the Proterotheriidae and unlike the Macraucheniidae, where it is relatively flatter. The articular surface for the navicular (AN) extends towards the neck in its dorso-lateral portion and its planto-medial portion. The dorsolateral portion of the navicular facet is separated from the astragalar fossa by a very narrow groove that widens, obliquely, towards the medial edge.

Navicular (Fig. 7). Only the right navicular is preserved. It is extremely eroded, being hard to differentiate most facets. Because of this, to better understand the topology of the bone, it was whitened with ammonium chloride (NH4Cl; Parsley et al., 2018; dry method) and with neon-colored acrylic powder in an effort to better understand its morphology. Blue-colored powder, contrasted against the yellow color of the fossil, allowed us to observe more details than ammonium chloride.

The navicular is typically litoptern in morphology. Litopterns have a navicular unlike those of condylarths, notoungulates, or extant ungulates, presenting the following features: (a) proximodistally high; (b) two cuboid facets, one proximal (NaCup) and one distal (NaCud), the latter being continuous with the facet for the ectocuneiform (NaEc); (c) a entocuneiform facet plantarly placed; (d) medial tuberosity absent; and (e) very developed plantar hook-like process (npp). Scott (1910) pointed to the hook-like process in the navicular bone as characteristic of Litopterna.

The navicular of MLP-PV 67-II-27-375 is proximally-distally elongated. The astragalar facet (AN) is dorsoplantarly concave, with its long axis following a medio-lateral direction. The plantar edge is strongly raised, much more than the dorsal one. Plantarly, there is a strong hook-like process with a distally directed end. This plantar process is also present in later litoptern, and it is already present in the naviculars referred to protolipternids and *Paranisolambda* of Itaboraí and *Asmithwoodwardia* (Bergqvist, 1996; Lorente, 2015, 2016). A similar extended plantar process, although quite distinct in morphology, is present in parasagittal Hystricomorpha (García Esponda & Candela, 2016; Candela *et al.*, 2017).

The lateral edge end presents an elliptical area corresponding to the proximal facet for the cuboid, similar to other litopterns. A cuboid distal facet may be present, but the bone is too abraded for observing this feature.

Distally, the articular facet for the ectocuneiform (NaEn) is convex and extends along the entire length of the medial hook-like process, more than in other litopterns. This extension is not described for protolipternid naviculars of Itaboraí, and the hook-like process is broken in Paso del Sapo litoptern naviculars (Bergqvist, 1996; Lorente, 2015). At the dorso-medial end of the distal face of the navicular there is a concave articular facet for the mesocuneiform (NaMc), small but more developed than in the known Proterotheriidae and more similar in width to the ectocuneiform facet. The latter indicates that MLP-PV 67-II-27-375 had a well-developed mesocuneiform and, therefore, a functional metatarsal II as in Macraucheniidae and Deseadan *Protheosodon coniferus* and *Promylophis cifelli* (Shockey *et al.*, 2023). Modification of cuneiform facets, and consequently of toes, has been observed in early naviculars referred to Protolipternidae, with a larger ectocuneiform facet than meso- and entocuneiform facets (Bergqvist, 1996). A similar pattern is present in the indeterminate litoptern naviculars of Paso del Sapo (Lorente, 2015). The facet for the ectocuneiform of the specimen of Gran Hondonada is larger than in protolipternids.

Figure 7

Ectocuneiform (Lateral cuneiform; Fig. 8). This bone is currently lost, but information about it was gathered during previous years. It is narrow, extended in a dorso-plantar direction, and relatively elongated proximo-distally, almost as much as the navicular. The articular surface for the navicular (NaEc) occupies practically the entire proximal surface. Distally, the facet for metatarsal III (EcMt3) is elongated in a dorso-plantar direction, although it is shorter than the facet of the navicular and slightly concave. In these aspects, the ectocuneiform of the specimen MLP-PV 67-II-27-375 is reminiscent of that figured for the condylarth *Meniscotherium robustum* Thorpe, 1934, from the early Eocene of North America (Gazin, 1965, pl.10, fig. 5), although the proximal and distal articular facets of *M. robustum* do not extend as much. A striking difference with known Proterotheriidae and Machaucheniidae is the presence of a well-developed plantar process in the ectocuneiform bone (ch. 112). This process is present in most “archaic ungulates”, Carnivora and Notoungulata but smaller in Proterotheriidae + Macraucheniidae. It is also present in ectocuneiforms referred to protolipternids. Furthermore, the navicular facet of the ectocuneiform is extended over this plantar process, a state unknown in “archaic ungulates”, “protolipternids”, Carnivora and Notoungulata, where the plantar process is present, but the navicular facet is restricted to the ectocuneiform body.

Figure 8

Joints

All the joints have adaptations to restrain movements to the sagittal plane and avoid displacement under sagittal loads. Both the upper ankle and the transverse tarsal joints are very mobile hinge joints, a characteristic of parasagittal mammals. The lower ankle joint is also very mobile, and the astragalus would have been able to slide in the tuber portion of the ectal facet. This movement would position the astragalus perpendicular to longitudinal axis of the calcaneus, becoming the astragalus a functional part of the tibia, similarly to Artiodactyla (Ameghino, 1905; Schaeffer, 1947). Unlike artiodactyls, this movement would have also enlarged the calcaneal kneel, producing an extra pressure to recover the original position (Lorente *et al.*, 2025).

Upper ankle joint (UAJ). The articulation of the tibia and fibula with the astragalus and, in some orders, with the calcaneus. MLP-PV 67-II-27-375 would have extended plantarflexion and dorsiflexion. The development of anterior and posterior processes on the tibia would avoid displacement at great sagittal loads.

Lower ankle joint (LAJ). The lower ankle joint includes the articulations of the sinus tarsi, the ectal, sustentacular and anterior facets. In most eutherians this joint works as a gently ginglymoid joint that facilitates movements on inclined surfaces (Szalay, 1984, 1994). But in MLP-PV 67-II-27-375, Protolipternidae and Proterotheriidae, as in Artiodactyla and cursorial Hystricomorpha (García Esponda & Candela, 2016; Candela *et al.*, 2017), the movement is extended so, during dorsiflexion, the astragalus rotates over the calcaneus to become a functional part of the tibia. The calcaneal sustentacular facet is convex and round, longer in Protolipternidae and Proterotheriidae. The astragalar counterpart is long, contacting the navicular facet at the distal border, and has a gentle twist to the lateral side (an undifferentiated anterior facet). The calcaneal ectal extends proximally, having a concave anterior surface over the calcaneal kneel and convex slope in the sinus tarsi. MLP-PV 67-II-27-375 has a flat to concave proximal half, as in later litopterns but different to protolipternids.

Transverse tarsal joint (TTJ). This joint includes the astragalonavicular joint and the calcaneocuboid joint. In MLP-PV 67-II-27-375, as in protolipternids and proterotheriids, the astragalonavicular joint is more proximal than the calcaneocuboid joint (reverse alternating tarsus, Cifelli, 1993). This has been suggested to avoid dislocations in the transverse axis (Lorente, 2019). The TTJ of these families worked as a hinge joint, accentuating the movements in the sagittal plane.

Phylogenetic analysis

The parsimony analysis of the modified matrix (see Materials and Methods) yielded 352 most parsimonious trees (MPTs) of 446.259 steps. The strict consensus tree is shown in Fig. 9.1. In all the shortest trees, MLP-PV 67-II-27-375 is nested within the Lopholipterna clade (Node A), within an unresolved trichotomy encompassing *Proectocion* and the clade containing all the Proterotheriidae, all the Macraucheniidae, *Polymorphis*, *Protheosodon*, and *Tricoelodus* (Node B). Node B is supported by two dental characters (ch. 60 and 64), unknown in MLP-PV 67-II-27-375, and four postcranial characters:

- Presence of a facet on the anterior process of distal tibia/ distal extension of the astragalar neck (ch. 87).
- Absence of lateral process on the astragalar body (ch. 94).
- Astragalar ectal facet with complex C-shaped flat to convex borders and concave center (ch. 101).
- Calcaneal sustentacular facet ovoid with sagittal axis longer (ch. 103).

MLP-PV 67-II-27-375 shows no unambiguous autapomorphies and is excluded from the least inclusive clade encompassing all proterotheriids, macraucheniids, *Polymorphis*, *Protheosodon*, and *Tricoelodus* (Node C) by lacking the following postcranial apomorphies: well-developed fossa for the medial patellar ligament on proximal tibia (ch. 85), absence of calcaneal peroneal process (ch. 108), and absence of ectocuneiform plantar process (character 112).

Figure 9

In an additional analysis with implied weighting, using different K-values (3-15), MLP-PV 67-II-27-375 was recovered in the same position.

Associations with teeth

The best regression model for the association of teeth and hindlimb bones is between the area of the third lower molar and the femoral inter-epicondylar transverse distance. This model suggests a molar area size between 26 and 34 mm (~3-5 mm width and ~6-8 mm length) for the specimen of Gran Hondonada with a confidence interval of 99.7%. A test using other litopterns (*Diadiaphorus robustus*, *Epitherium laternarium*, *Macrauchenia patachonica*, *Megadolodus molariformis*, *Tetramerorhinus mixtum*, *Theosodon*, and *Thoatherium minusculum*) yield estimates with less than 0.001% error, for both m3 and femur of the same specimen and for different specimens of the same species or genus. This suggests a m3 area close to 27 mm^2.

Litopterns represented by dental materials at Gran Hondonada include *Didolodus* sp. (MLP 67-II-27-11) and others reported by Cladera *et al.* (2004): *Decaconus lanciformis, Polymorphis lechei* (=*Polyacrodon ligatus*), and an isolated m3 (MPEF-PV 1101) identified as Adianthidae indet. (see Supplementary Online Information1). The molars of all except the latter are much larger than the estimated molar size for MLP-PV 67-II-27-375, leaving the m3 MPEF-PV 1101 (m3 area = 33.33 mm^2) as the most probable association. This tooth (see Fig. 10) is bunolophodont, the paraconid is not evident, but the paralophid is very long reaching the lingual margin of the crown. The entoconid is very large and bunoid, connected to the hypolophid and the hypoconulid roughly in the center of the talonid. The hypoconulid is massive and well-extended distally, forming a well-defined third lobe. The hypoconulid is weakly connected to a small accessory cuspid on the distolingual corner of the talonid, which is associated to the distolingual cingulid. The mesiodistal cingulum is conspicuous. The labial and lingual cingulids are absent.

Figure 10

Body Mass

Body mass estimates were obtained based on previous works (Scott, 1990; Tsubamoto, 2014; Yapuncich *et al.*, 2015). The transverse diameter of the tibial plate (T2 of Scott, 1990) yields estimates of 2.381±1.04 kg for MLP-PV 67-II-27-375 when applying quasi-maximum likelihood estimator as a correction factor (Smith, 1993; Scarano *et al.*, 2011). The body mass is estimated at is 2.177±0.89 kg based on the astragalus (L1 with Cf, Tsubamoto, 2014). The body mass is 2.515±0.691 kg based on the surface area of the calcaneal cuboid facet (Yapuncich *et al.*, 2015) (see Supplementary Online Information 1).

Figure 11

DISCUSSION

Paleobiology

The litoptern represented by MLP-PV 67-II-27-375 was tiny, had at least three functional digits and a body mass around 2-3 kg (Fig. 11).

Shockey (1999, 2001) and Shockey *et al.* (2023) suggested that both macraucheniids and proterotheriids had evolved a knee-lock mechanism functionally similar to that of the modern horse (*Equus*). Specimen MLP-PV 67-II-27-375 has a poorly developed supratrochlear fossa (Fig. 4; "patellar pit" after Shockey, 2001) in the femur, and the trochlea is not as well defined and protruding as in later litopterns, which are features linked to the knee-lock mechanism according to Shockey *et al.* (2023). Also, the tibia lacks a groove for the passage of the middle patellar ligament (Fig. 5). At least in our sample, the supratrochlear fossa of the femur and the tibia groove for the passage of the middle patellar ligament seem to be interdependent. The small *Adianthus godoyi* also lacks both traits, the passage of the middle patellar ligament and a well-developed supratrochlear fossa. Janis *et al.* (2012) found evidence that the morphology of the knee joint of ungulates has a high allometric component and is affected secondarily by environmental preference (*i.e.*, closed, mixed, or open). Because both MLP-PV 67-II-27-375 and *Adianthus godoyi* (Cifelli, 1991) are small, it is probable that the absence (or poor development) of these traits is related to size and not to phylogenetic relationships. *Promylophis cifellii* (Shockey *et al.*, 2023), has a referred femur with a well-marked supratrochlear fossa. However, the size of the femur is almost double that of MLP-PV 67-II-27-375, more similar to *Thoatherium* (Shockey *et al.*, 2023).

Cifelli (1983a: 25) concludes that certain specializations in the calcaneus and astragalus indicate that the most primitive and smallest litopterns (referring to the Protolipternidae) could have been more saltatorial (quadrupedal bounding) in their locomotion. He considered that this would be preadaptive to the later radiations of larger and more strictly cursorial litopterns. The distal tarsus of the specimen analyzed here also indicates a more bounding type of locomotion. The navicular has a very developed plantar hook-like process (Fig. 7). Bergqvist (1996) described this process as the navicular medial tuberosity (Fig. 7: nmt) for the insertion of the tendons of the muscle *Tibialis posterior* and collateral ligaments, but this is unlikely. The insertion of these tendons is related to a medioplantar ossification center that shows great morphological variation in different mammals (see Material and Methods and Supplementary Online Information 1, ch. 92). In some Carnivora (*e.g., Ailuropoda melanoleuca,* Davis, 1964; Mustelidae, Ercoli, 2015), this ossification center does not develop into a navicular plantar tuberosity, but is instead a small sesamoid (Lewis, 1979). These carnivorans have also a small plantar process (Fig. 7: npp). Some exceptionally-preserved Litopterna (e.g., MACN-PV 8430 *Neobrachytherium intermedium*) have a medial plantar sesamoid, as occurs in mustelids. In litoptern specimens in which the sesamoid was not found, the astragalus and navicular have the corresponding facet for it (Fig. 7: NaS). Taking all this into account, the hook-like process is probably homologous to the small plantar process, and the sesamoid is the insertion of the tendons of the muscle *Tibialis posterior* and collateral ligaments (Fig. 12). Furthermore, Paleogene Notoungulata and Eulipotyphla, Artiodactyla, other Carnivora, and Perissodactyla (*Tapirus*) have both a small rounded plantar process and the navicular medial tuberosity in a medioplantar position, with the presence of both processes in the navicular probably basal for Laurasiatheria.

Figure 12

A similar extended (hook-like) navicular plantar process than Litopterna, although quite different in morphology (more triangular and less plantarly projected), is present in cursorial Hystricomorpha (García Esponda & Candela, 2016; Candela *et al.*, 2017). In rodents, *Tibialis posterior* and collateral ligaments insert in the medial tarsal (see Lewis, 1964, for homologies about this bone), and tendons of the flexor muscles run along the plantar process. This navicular plantar process along the cuboid plantar tuberosity and the plantar process of the third metatarsal, makes the distal tarsus of cursorial hystricomorphs a strong and rigid structure. This rigid distal tarsus allows the animal to resist the impact of each jump in uneven terrain (García Esponda & Candela, 2016; Candela *et al.*, 2017). Litopterns also have a similarly projected plantar process in the cuboid and the third metatarsal, and it probably worked functionally as in these rodents.

Although the protoliptern postcranium is specialized toward arasagittal movements, most probably bounding, as concluded by Cifelli (1983a: 25), early lopholipterns may have been further specialized toward jump than protolipternids (Lorente *et al.*, 2025). This is reflected in the modifications of the three principal tarsal joints of MLP-PV 67-II-27-375, Proterotheriidae and Macraucheniidae. These earliest lopholipterns would have an increased mobility in the astragalocalcaneal (LAJ) and astragalonavicular (TTJ) joints, indicated by the modifications in the distal tibia and the modified morphology of the articular facets, similar to artiodactyls and some hystricomorph rodents. This increased mobility would allow the astragalus to become a functional part of the tibia during the propulsive phase of the leaping gait. This produces a mechanical pressure to recover the original position transforming the tarsus in a powerful spring (Schaeffer, 1947; Lorente *et al.*, 2025). In litopterns, these astragalar movements would have also enlarged the calcaneal kneel, producing extra pressure to recover the original position (Lorente *et al.*, 2025). Some proterotheriids also developed an increased tibia:femur ratio that also suggests a bounding adaptation (Smith and Savage, 1956; Emerson, 1985; Chen and Wilson, 2015; Lorente *et al.*, 2025). Macraucheniidae shares these traits with proterotheriids, but the mobility is restricted (see below; Lorente *et al.*, 2025).

Considering the relatively small size of the La Gran Hondonada specimen, as well as the elongated tibia in relation to the femur, we can assume a cursorial-bounding (parasagittal) mode of locomotion instead of only cursorial. Considering the model of Chen and Wilson (2015) for small mammals, our specimen falls within terrestrial mammals. This category includes cursorial, ambulatory and quadrupedal bounding mammals. Also, small artiodactyls and cursorial rodents tend to have a more bounding gait than equids and ruminants (Smith & Savage, 1956; Emerson, 1985: Lorente *et al.*, 2025

Phylogenetic position and dental association

The results of the parsimony analysis (Fig. 9.1) indicate that MLP-PV 67-II-27-375 has a combination of plesiomorphic and derived character states, having diverged after protolipternids but before the differentiation between macraucheniids and proterotheriids. Consequently, MLP-PV 67-II-27-375 is retrieved as an early diverging Lopholipterna, as nearest (along with *Proectocion*) to the macraucheniid-proterotheriid divergence. Our phylogenetic reconstruction does not recover anisolambdines and adianthids as natural groups, but as separate branches basal to the main clade encompassing Macraucheniidae and Proterotheriidae and, therefore, they are also early diverging Lopholipterna. This scenario contrasts with the alleged proterotheriid affinities of anisolambdines (Soria, 2001) and the macraucheniid (or indaleciid) affinities of adianthids (Cifelli & Soria, 1983). *Tricoelodus* is an exception, being recovered in a politomy at the base of Macraucheniidae with *Polymorphis*. Our results also differ from those of Carrillo *et al.* (2023), which groups some of these taxa with Proterotheriidae and others with Macraucheniidae, as well as from those of Püschel *et al.* (2024), which uses a very different taxon and character sampling and does not include postcranial features. Lobo *et al.* (2024) recovered *Polymorphis* as the sister taxon of Macraucheniidae and Proterotheriidae. However, they used a smaller sample of early taxa and postcranial characters.

Certainly, the absence of associated dental elements limits the possible comparisons of MLP-PV 67-II-27-375 with the other known Paleogene Litopterna described based on teeth.

However, when MLP-PV 67-II-27-375 is removed from the analysis, the topology of the strict consensus tree remains the same, suggesting that our results are not influenced by the large amount of missing dental character states of MLP-PV 67-II-27-375 (see Supplementary Online Information 1).

The Proterotheriidae are sometimes considered more specialized than Macraucheniidae due to their functional monodactyly (MacFadden, 1992), with the third digit as the only fully functional one and a variable reduction of digits II and IV (ch. 80). This functional monodactyly is the only postcranial character (ch. 80) here recovered as an unambiguous synapomorphy of Proterotheriidae. However, the tarsus of Proterotheriidae appears more plesiomorphic compared to that of Macraucheniidae. As in protolipternids, proterotheriids have a long astragalus (ch. 89), with a pronounced gap between the astragalo-navicular and calcaneocuboid articulations (ch. 104), where the joints Macraucheniidae are closer together (Lorente, 2019). In contrast, the macraucheniid tarsus is wider, with closer joints, evidenced by the development of a small distal astragalocuboid articulation (ch. 91), and with the exception of *Theosodon*, a shortened calcaneal distal process (ch. 104). Ameghino (1905) and Shockey (1999) mentioned a lateral, instead of distal, astragalocuboid contact for *Thoatherium* and a Proterotheriidae indet. of Salla (Bolivia), but we could not confirm that in our available specimens. The changes that transformed the tarsus into a powerful spring (see Paleobiology above) in Protolipternidae and which allowed even more rapid movement in the Gran Hondonada specimen and Proterotheriidae, are present in Macraucheniidae. But these traits were not functional, because the closer joints would have worked as a stop (Lorente *et al.*, 2025). In particular, this is evidenced by the flat to convex astragalar head (ch. 90) and the smaller (round instead of with a longer sagittal axis) sustentacular facet of the calcaneus (ch. 103) in *Theosodon, Coniopternium, Promacrauchenia* (MLP-PV 12-1638, MLP-PV 29-X-10-63), *Macraucheniopsis* (MLP-PV 12-2460) and *Macrauchenia*. The astragalocuboid contact of Macraucheniidae is hidden by the convex articulation of the calcaneocuboid joint, which looks more distal than the astragalonavicular in anterior view (Supplementary Online Information 1), and it is described as absent by several authors (Scott, 1910; Cifelli, 1993); but as present by others, particularly in *Coniopternium* (Loomis, 1914; Bergqvist 1996; Shockey 1999).

As discussed above, the regression model for postcranial associations suggests that the isolated m3 MPEF-PV 1101 is the best candidate to be co-specific with MLP-PV 67-II-27-375 among the known litopterns of the Gran Hondonada locality. This tooth, listed as an adianthid by Cladera *et al.* (2004), has some resemblances with the corresponding tooth of the adianthids *Proectocion* and *Tricoelodus*, especially *T. boliviensis* (see Cifelli and Soria, 1983), for which their postcranium is not known. When MLP-PV 67-II-27-375 and MPEF-PV 1101 are scored as a single terminal taxon in our data matrix, it yields 60 most parsimonious trees (MPTs) of 449.074 steps. Specimen MLP-PV 67-II-27-375+MPEF-PV 1101 is recovered as the sister taxon of the clade encompassing Macraucheniidae (including *Polymorphis*) and Proterotheriidae in all MPTs (Fig. 9.2), a position similar to that of the previous analysis (see Fig. 9.1). *Tricoelodus* and *Proectocion* appear as the subsequent sister taxa, although none closely related to *Adianthus*. Consequently, MLP-PV 67-II-27-375 might be classified as an adianthid, while Adianthidae is conceived as a polyphyletic assemblage of early diverging Lopholipterna.

CONCLUSIONS

Thorough anatomical descriptions of postcranial elements are rare; however, they are essential for more robust phylogenetic analyses and for a better understanding of mammalian evolution. Specimen MLP-PV 67-II-27-375, the most complete litoptern skeleton predating the Deseadan SALMA, provides an improved understanding of Paleogene Litopterna postcranial anatomy. This specimen belongs to a small litoptern, around 2-3 kg, with a locomotion similar to a cursorial rodent or a small artiodactyl (*e.g.*, Tragulidae, Moschidae). It displays a mix of traits, including plesiomorphic features shared with Protolipternidae and apomorphies in common with Macraucheniidae and Proterotheriidae. Our phylogenetic reconstruction suggests that MLP-PV 67-II-27-375 represents an early branch of Lopholipterna that diverged before the divergence between Macraucheniidae and Proterotheriidae. The regression models show a possible association with the adianthid molar tooth MPEF-PV 1101, which is compatible with the phylogenetic position of MLP-PV 67-II-27-375, close to *Proectocion* and *Tricoelodus*. Nevertheless, the possibility persists that MLP-PV 67-II-27-375 corresponds to a taxon not known from teeth, and future findings may allow us to confirm or reject the association proposed here.

Anisolambdines, indaleciids, spanotheriodontids, and adianthids are still poorly understood groups, and their phylogenetic positions are uncertain or controversial. In our analysis, we recover them as a polyphyletic group of branches that diverged early, most of them before the differentiation of macrauchenids and proterotherids. Future discoveries, especially of postcranial material, should help determine the relationships among these groups and better understand the early evolution of Litopterna.

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Figure captions

Figure 1. Map of Chubut Province in central Patagonia showing the geographic location of the Gran Hondonada locality and others mentioned in the text. **CH**, Colhue Huapi Lake; **M**, Musters Lake; **Circle**, Gran Hondonada; **Star**, Gran Barranca, south of Colhue Huapi Lake.

Figure 2. Stratigraphic section of the Sarmiento Formation at Gran Hondonada (modified from Cladera *et al.*, 2004).

Figure 3. Photographs and line drawings of the right pelvis of **MLP-PV 67-II-27-375** in ventrolateral and dorsal views. Abbreviations: **Ac**, acetabulum; **ipt**, ileopectineal tubercle; **ob**, obturator foramen; **rf**, *Rectus femoris* muscle origin; **si**, ischial spine. Scale: 10 mm.

Figure 4. Illustration: right and left femurs of **MLP-PV 67-II-27-375** in dorsal and plantar views. Photographs and line drawings of left femur in anterior (1), posterior (2), lateral (3), medial (4),

proximal (5) and distal (6) views. Abbreviations: **3t**, third trochanter; **Fh**, femoral head; **fic**, intercondylar fossa; **Flc**, femoral lateral condyle; **flec**, femoral lateral epicondyle; **Fmc**, femoral medial condyle; **fmec**, femoral medial epicondyle; **fn**, femoral neck; **Ft**, femoral trochlea; **gt**, greater trochanter; **gtpa**, greater trochanter *pars cranialis eminence*; **gtpp**, greater trochanter *pars caudalis eminence*; **itc**, intertrochanteric crest; **lic**, linea intercondylaris; **llfa**, lateral labium of facies aspera; **lt**, Lesser trochanter; **scf**, supracondylar fossa; **sft**, supratrochlear fossa; **tf**, trochanteric fossa. Scale: 10 mm.

Figure 5. Right tibia of **MLP-PV 67-II-27-375** in anterior (1), posterior (2), lateral (3), medial (4), proximal (5) and distal (6) views. Abbreviations: **ATi**, astragalotibial facet (cochlea); **ATia**, anterior astragalotibial facet; **cc**, cnemial crest; **gse**, groove sulcus extensorius; **ice**, intercondylar eminence; **ml**, muscular lines; **mm**, medial malleolus; **pmf**, popliteus muscle facet; **tap**, tibial anterior process; **TiFi**, tibiofibular facet; **Tilc**, tibial lateral condyle; **Timc**, tibial medial condyle; **tpp**, tibial posterior process; **tt**, tibial tubercle. Scale: 10 mm.

Figure 6. Right calcaneus and right and left astragali of **MLP-PV 67-II-27-375**, in anterior (1), posterior (2), lateral (3), medial (4), proximal (5) and distal (6) views. Abbreviations: **AFi**, astragalofibular facet; **ampt**, astragalar medial plantar tuberosity; **AN**, astragalonavicular facet; **at**, anterior plantar tubercle; **ATia**, anterior astragalotibial facet; **ATil**, lateral astragalotibial facet (trochlea); **ATim**, medial astragalotibial facet; **CaA**, ectal facet (astragalocalcaneal); **CaCu**, calcaneocuboid facet; **CaFi**, calcaneofibular facet; **cp**, coronoid process; **dfs**, digitorum flexor sulcus; **dp**, distal process (“neck” in Cifelli, 1993); **pp**, peroneal process of calcaneus; **Su**, sustentacular facet; **tc**, tuber of calcaneus; **X**, x facet of Ameghino (1905) (anterior astragalocalcaneal facet). Scale: 10 mm.

Figure 7. Naviculars of **MLP-PV 67-II-27-375**, **LIEB-PV 4997** (Protolipternidae indet, Paso del Sapo fauna), **LIEB-PV 4999** (Notoungulata, Paso del Sapo fauna), Proterotheriidae indet. (Monte Hermoso, Early Pliocene, **MLP-PV 48-XII-16-1**) and *Macrauchenia patachonica* (**MLP-PV 12-1661**), in anterior (1), posterior (2), lateral (3), medial (4), proximal (5) and distal (6) views.

Abbreviations: **AN**, astragalonavicular facet; **CN**, calcaneonavicular facet; **NaCu**, naviculocuboid facet; **NaCud**, proximal naviculocuboid facet; **NaCup**, distal naviculocuboid facet; **NaEc**, naviculoectocuneiform facet; **NaEn**, naviculoentocuneiform facet; **NaMc**, naviculomesocuneiform facet; **NaS**, navicular sesamoid facet; **nmt**, navicular medial tuberosity; **npp**, navicular plantar process. Scale: 10 mm.

Figure 8. Right ectocuneiform of **MLP-PV 67-II-27-375**. Line drawings of left ectocuneiform (mirrored) of Proterotheriidae indet. (Monte Hermoso, early Pliocene, **MLP-PV 48-XII-16-1**) and right ectocuneiform of *Macrauchenia patachonica* (**MLP-PV 12-1661**), in anterior (1), posterior (2), lateral (3), medial (4), proximal (5) and distal (6) views. Abbreviations: **CuEc**, cuboidoectocuneiform facet; **CuEcd**, distal cuboidoectocuneiform facet; **CuEcp**, proximal cuboidoectocuneiform facet; **EcEn**, ectomesocuneiform facet; **EcM**, ectoentocuneiform facet; **EcMt2**, ectocuneiform-second metatarsal; **EcMt3**, ectocuneiform-third metatarsal; **EcMt4**, ectocuneiform-fourth metatarsal; **NaEc**, naviculoectocuneiform facet. Scale: 10 mm.

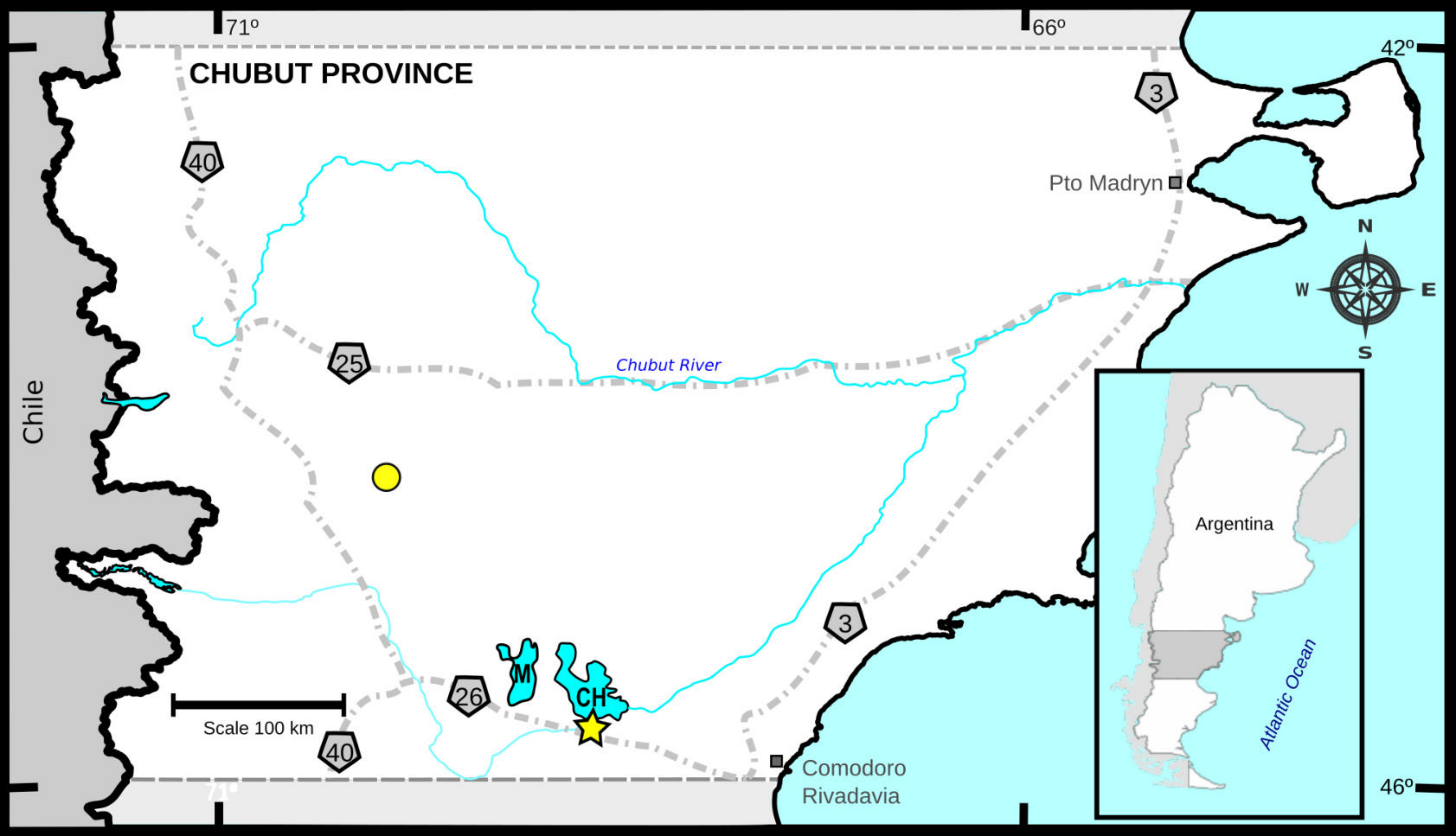
Figure 9. (1) Strict consensus from 352 most parsimonious trees produced from the parsimony analysis of the modified data matrix of Carrillo *et al.* (2023). (2), Strict consensus of 60 most parsimonious trees with MLP-PV 67-II-27-375 and MEF-PV 1101 (an isolated m3) scored as a single terminal taxon. **Node A**: Lopholipterna.

Figure 10. Isolated m3 of an **Adianthidae indet.** from Gran Hondonada in occlusal view, anterior to right. (MPEF-PV 1101). Scale: 10 mm.

Figure 11. Size comparison of Litopterna, excluding Macraucheniidae. Left side, Litopterna, from smallest to largest animal: ***Miguelsoria parayirunhor*** (1; black; modified from Michaud, 2019 CC0); **MLP-PV 67-II-27-375** specimen (2; purple); ***Lambdaconus suinus*** (3; light blue); ***Thoatherium minusculum*** (4; cyan); ***Diadiaphorus majusculus*** (5; dark blue). Right side, extant mammals from smallest to largest: ***Moschiola meminna*** (6; light green; Farke, 2015 CC0); ***Mazama govazoubira*** (7; green; Palomo-Munoz, 2021 CC-BY-NC); ***Homo sapiens*** (orange;

Lawler, 2023 CC BY). Approximate size estimated by the length of several bones. Images obtained from Phylopic (for Litopterna: Bayona, 2015 CC-BY-NC).

Figure 12. Alternative presentations of the medial ossification center for the insertion of the tendons of the muscle *Tibialis posterior* and collateral ligaments. (1 to 4) Ossification center fused to navicular forming the navicular medial tuberosity. (5 to 10) Ossification center as an independent sesamoid bone. (1) Posterior view of the tarsus of the notoungulate ***Eutypotherium lehmannnistchei*** (MLP-PV 12-1701); (2) Schematic representation of Notoungulata presentation in posterior view; (3) posterior and (4) medial views of the navicular LIEB-PV 4999 (Notoungulata); (5) posterior view of the tarsus of the litoptern ***Neobrachytherium intermedium*** (MACN-PV 8430); (6) Schematic representation of Litopterna presentation in posterior view. (7) posterior and (8) medial views of the navicular bone of MLP-PV 67-II-27-375; (9) posterior and (104) medial views of Proterotheriidae indet. (MLP-PV 48-XII-16-1). Abbreviations: **NaS**, navicular sesamoid facet; **nmt**, navicular medial tuberosity; **npp**, navicular plantar process.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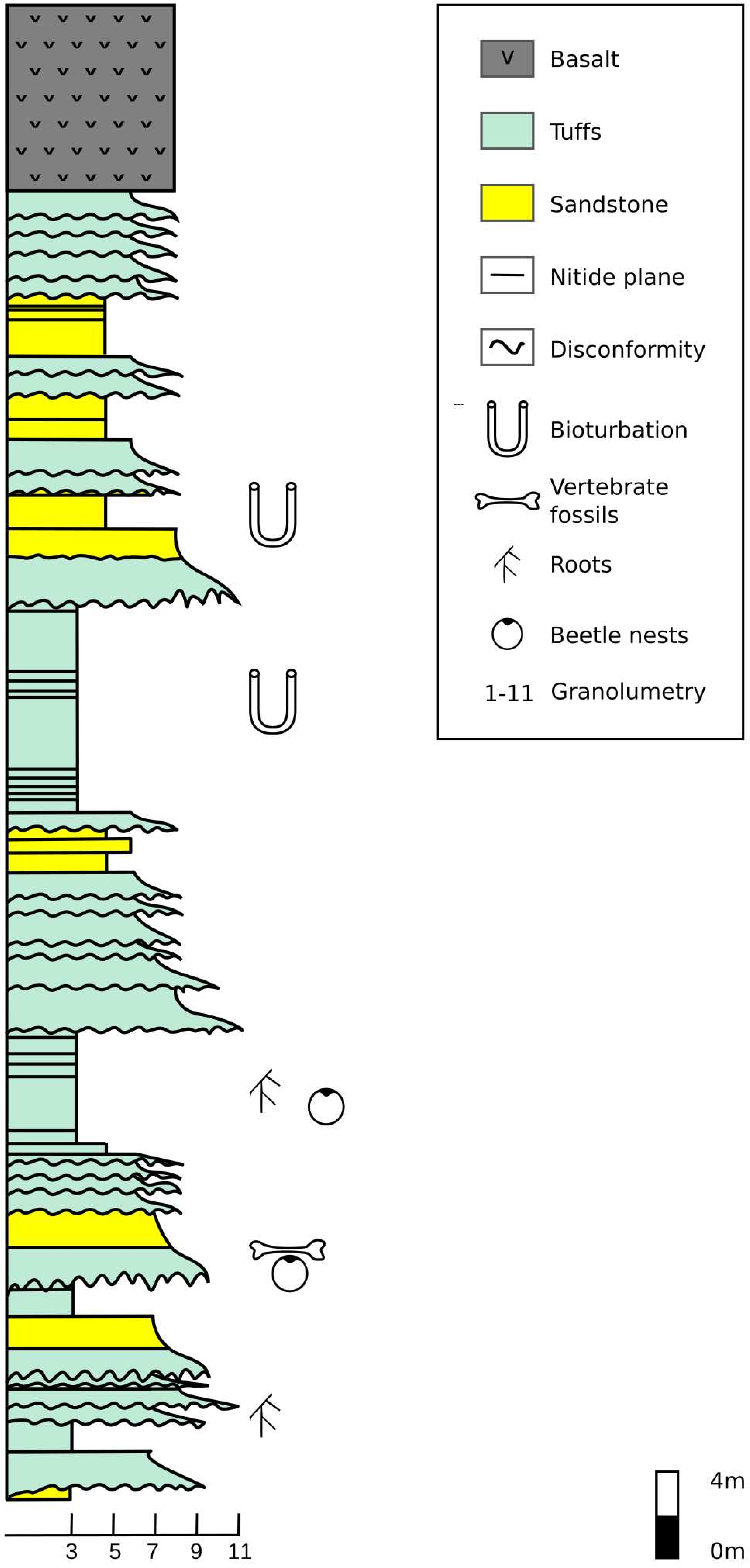
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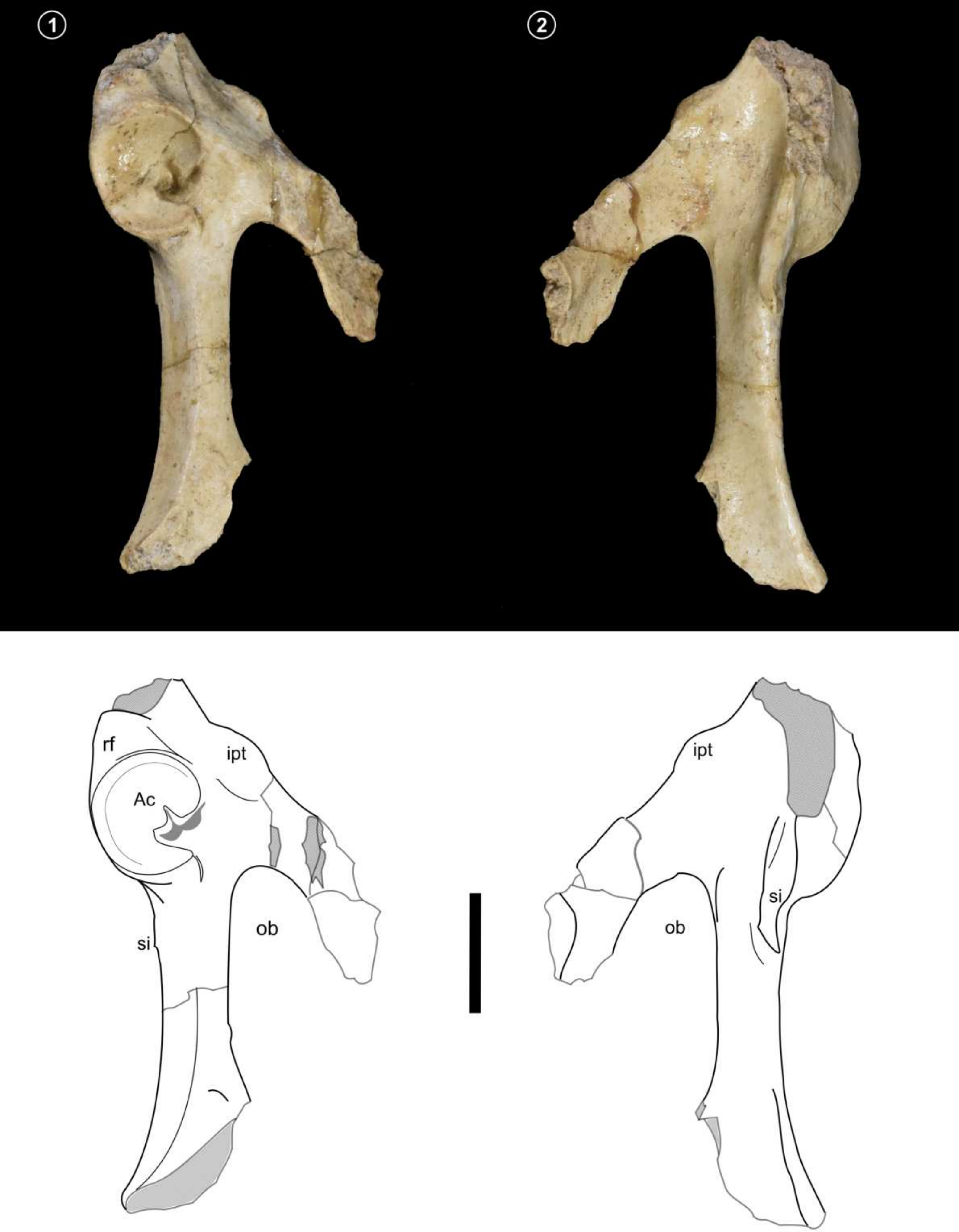
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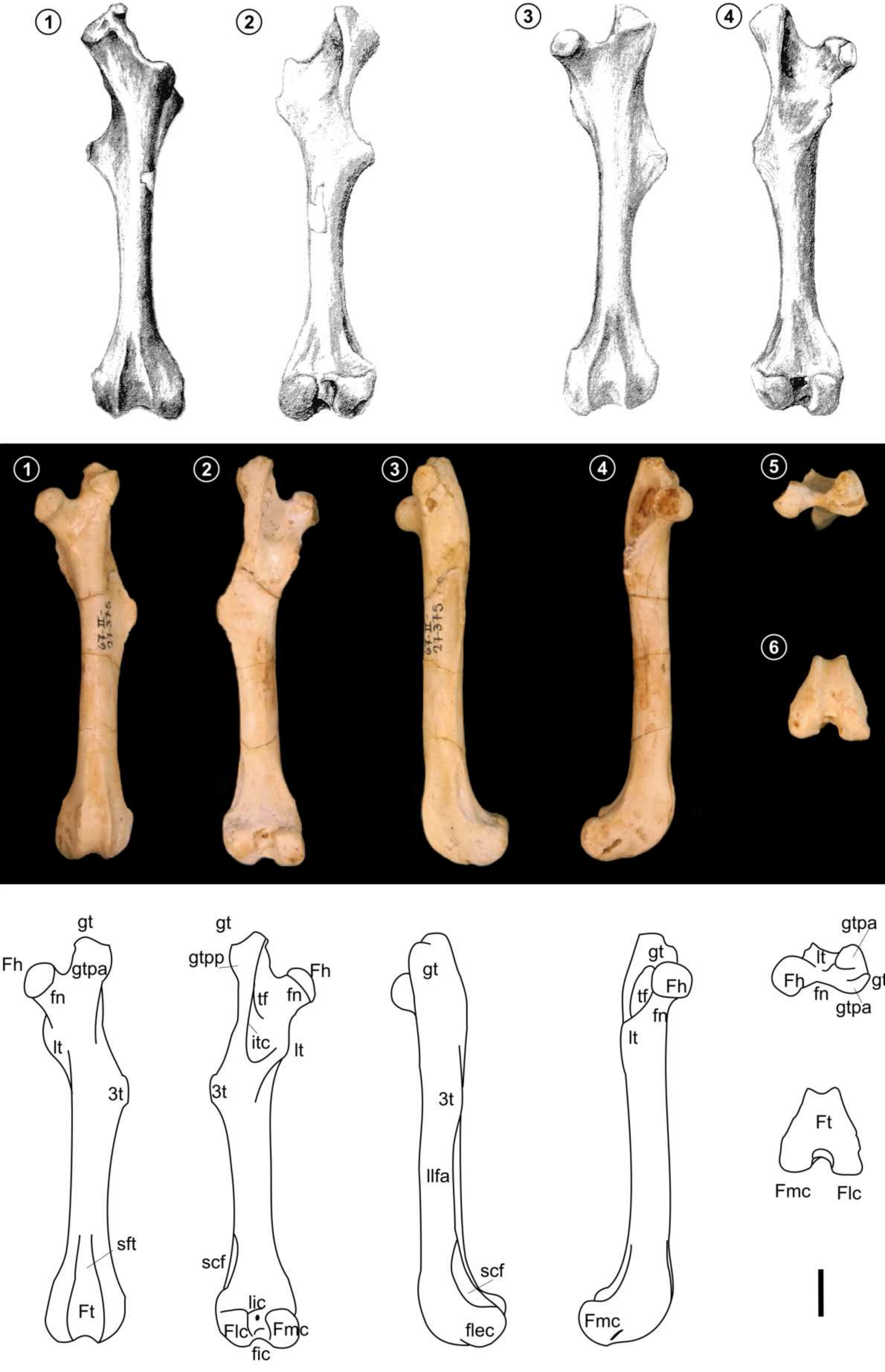
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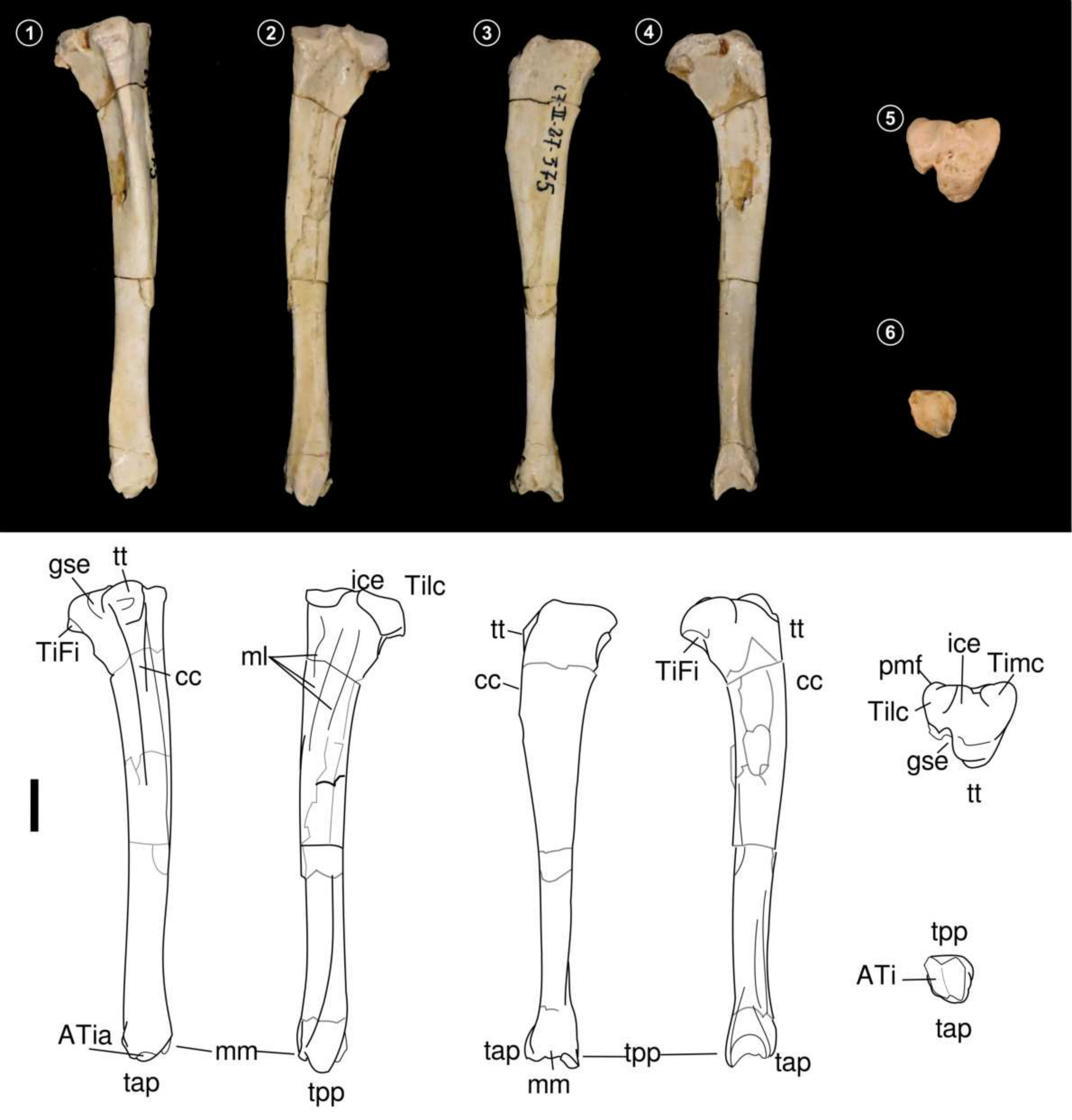
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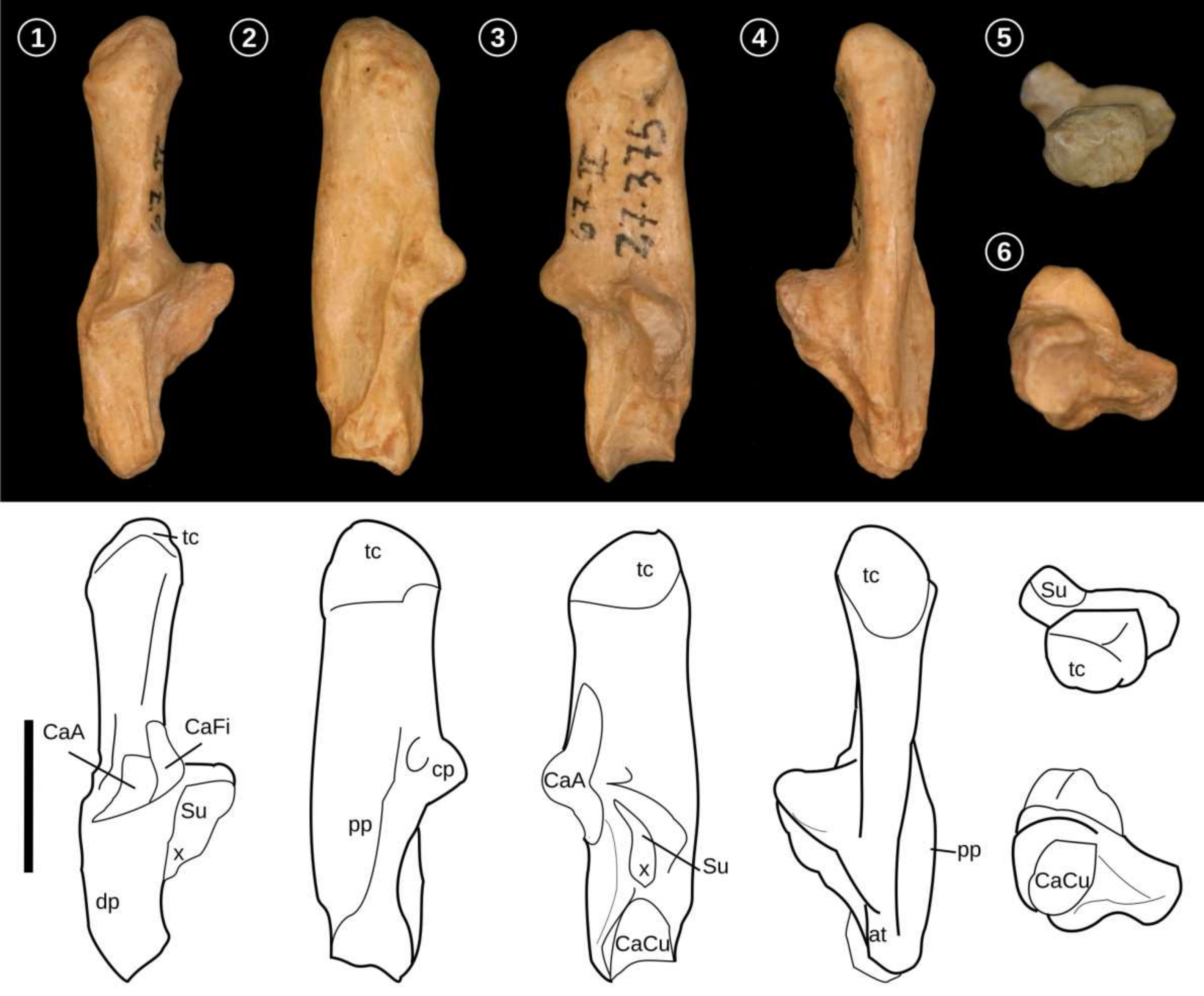
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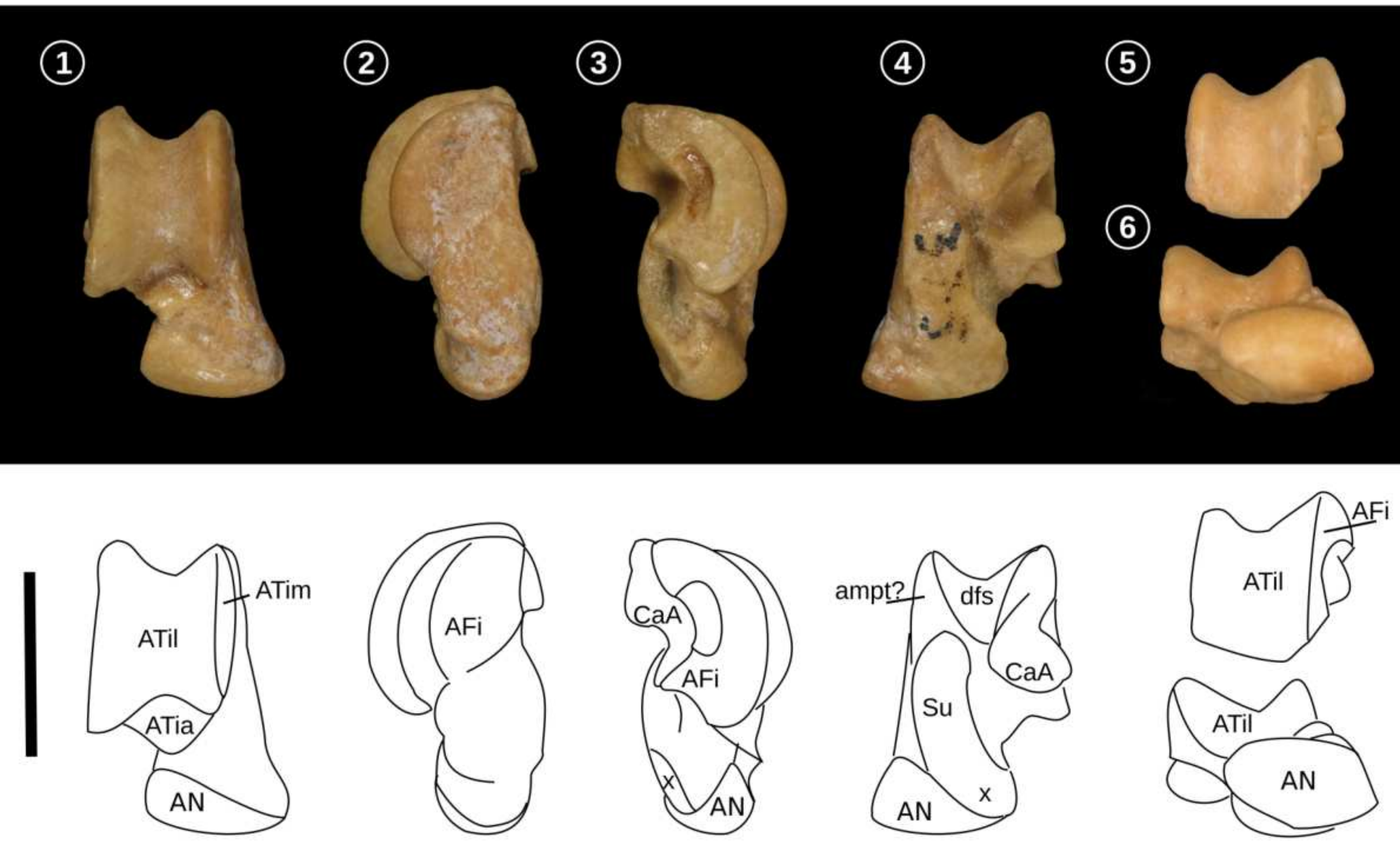
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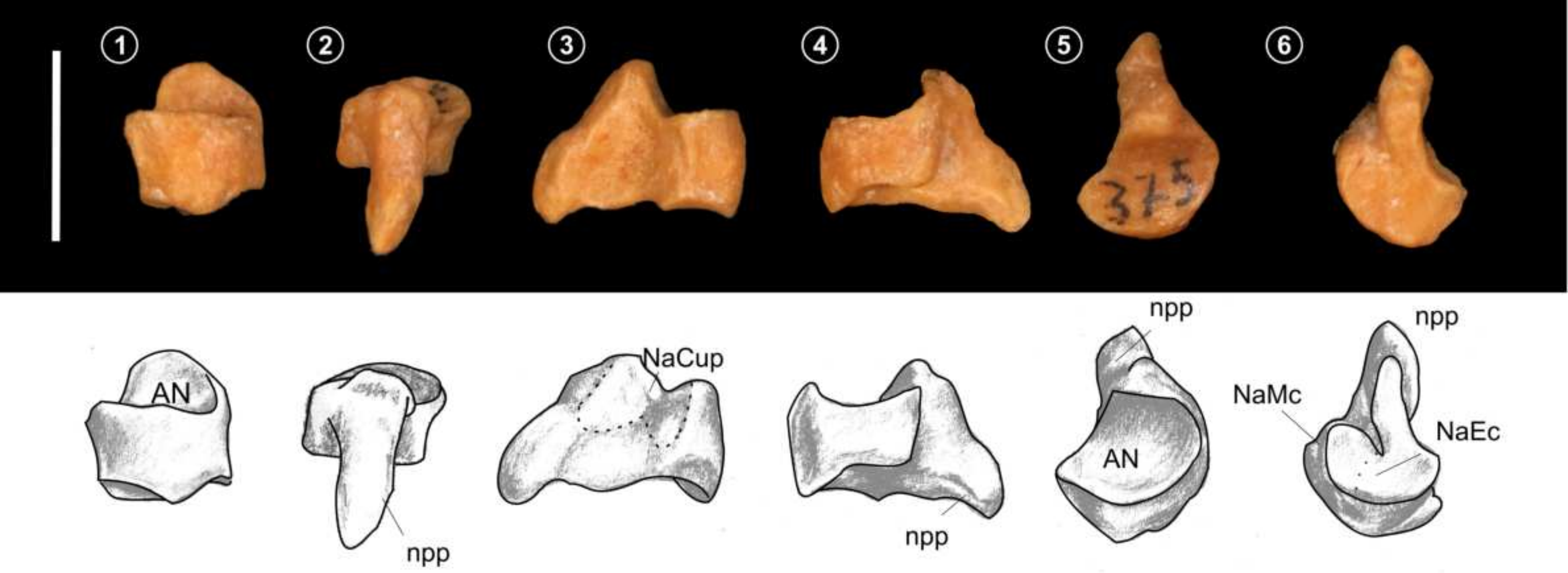

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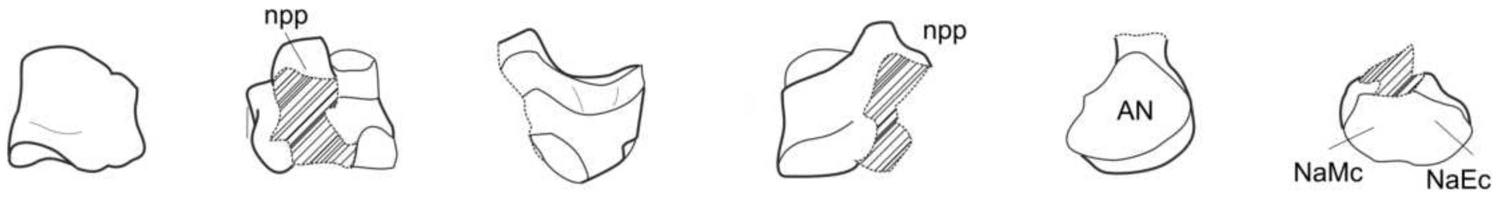

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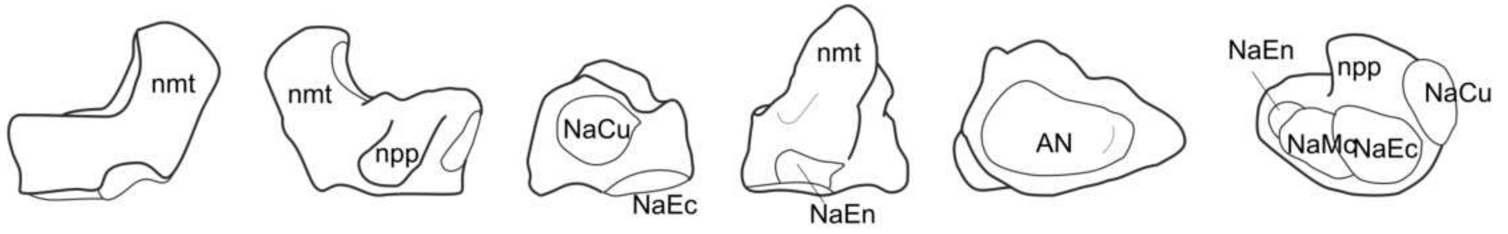

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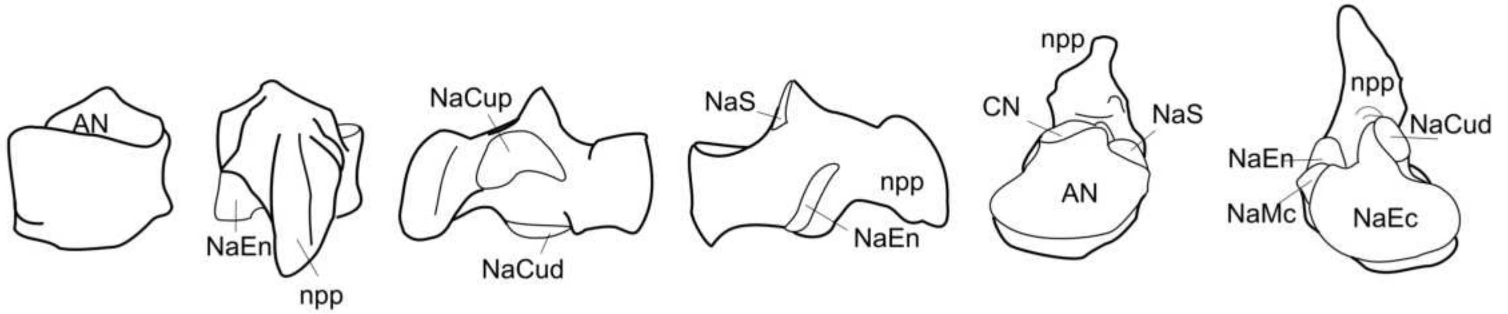

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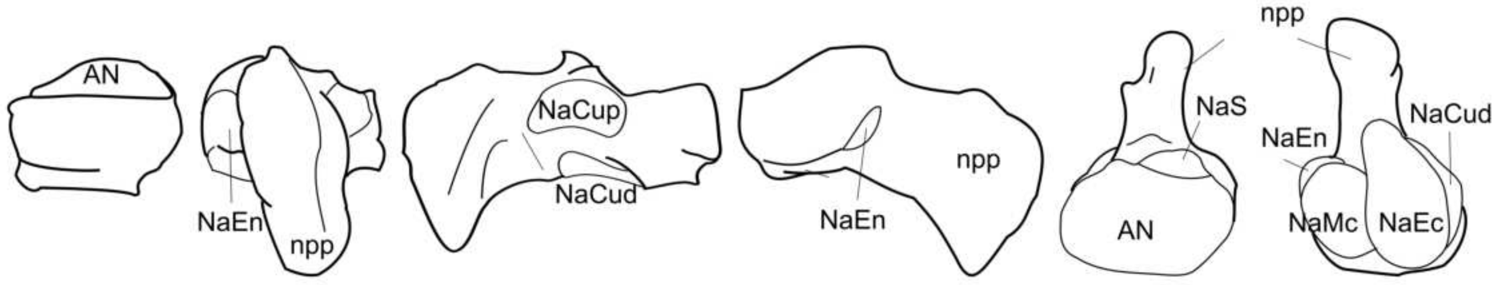

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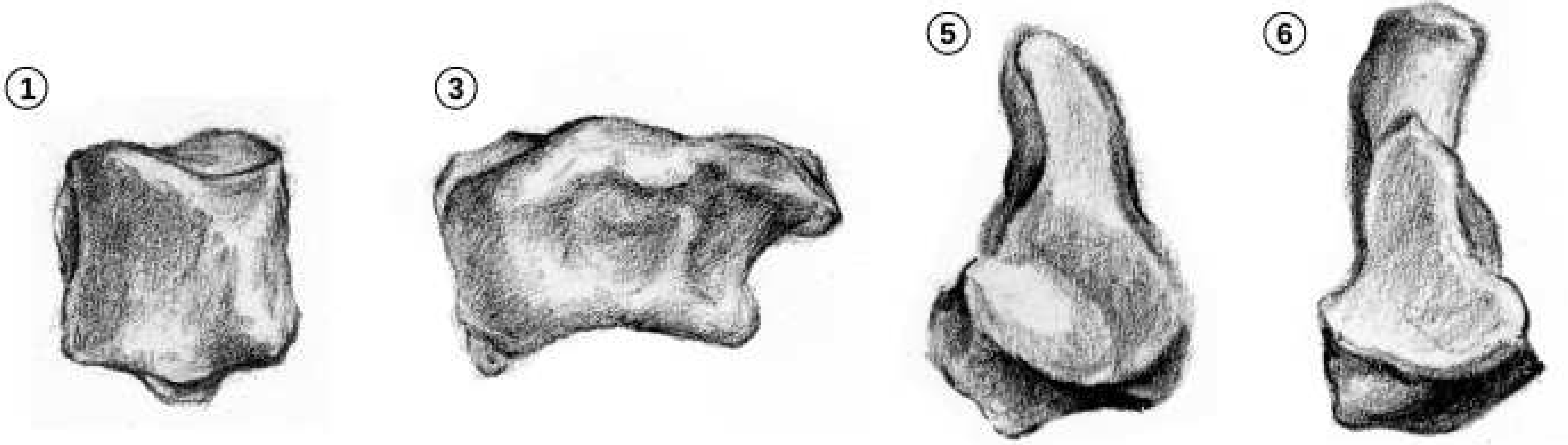

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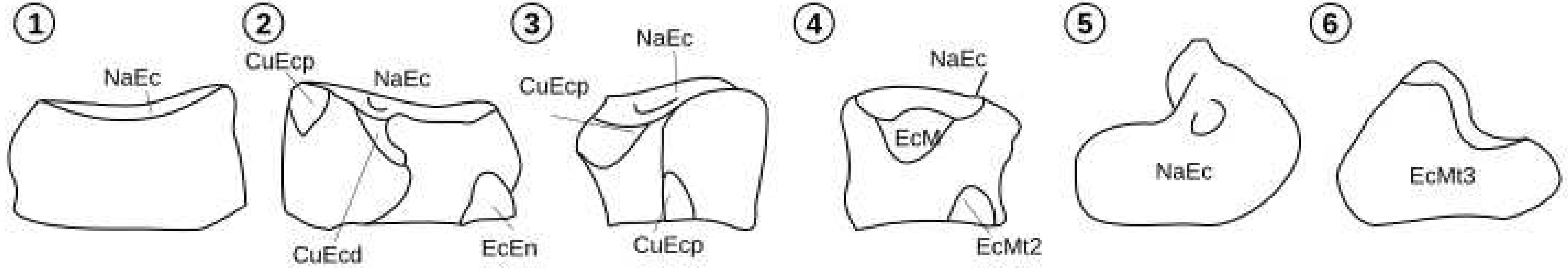

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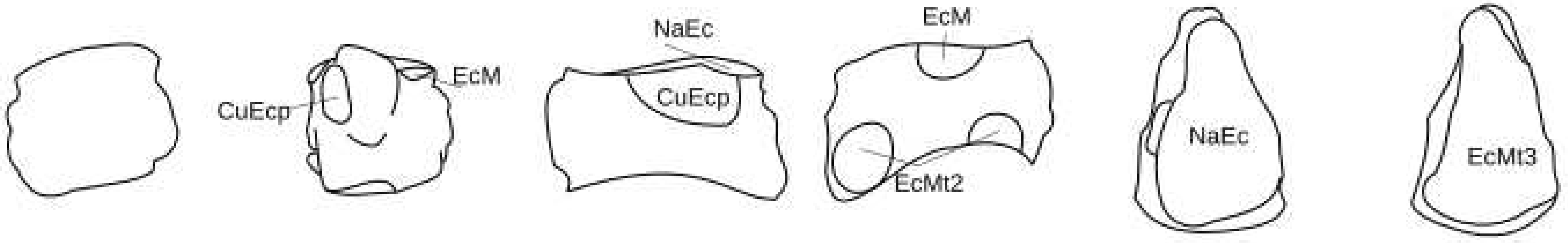

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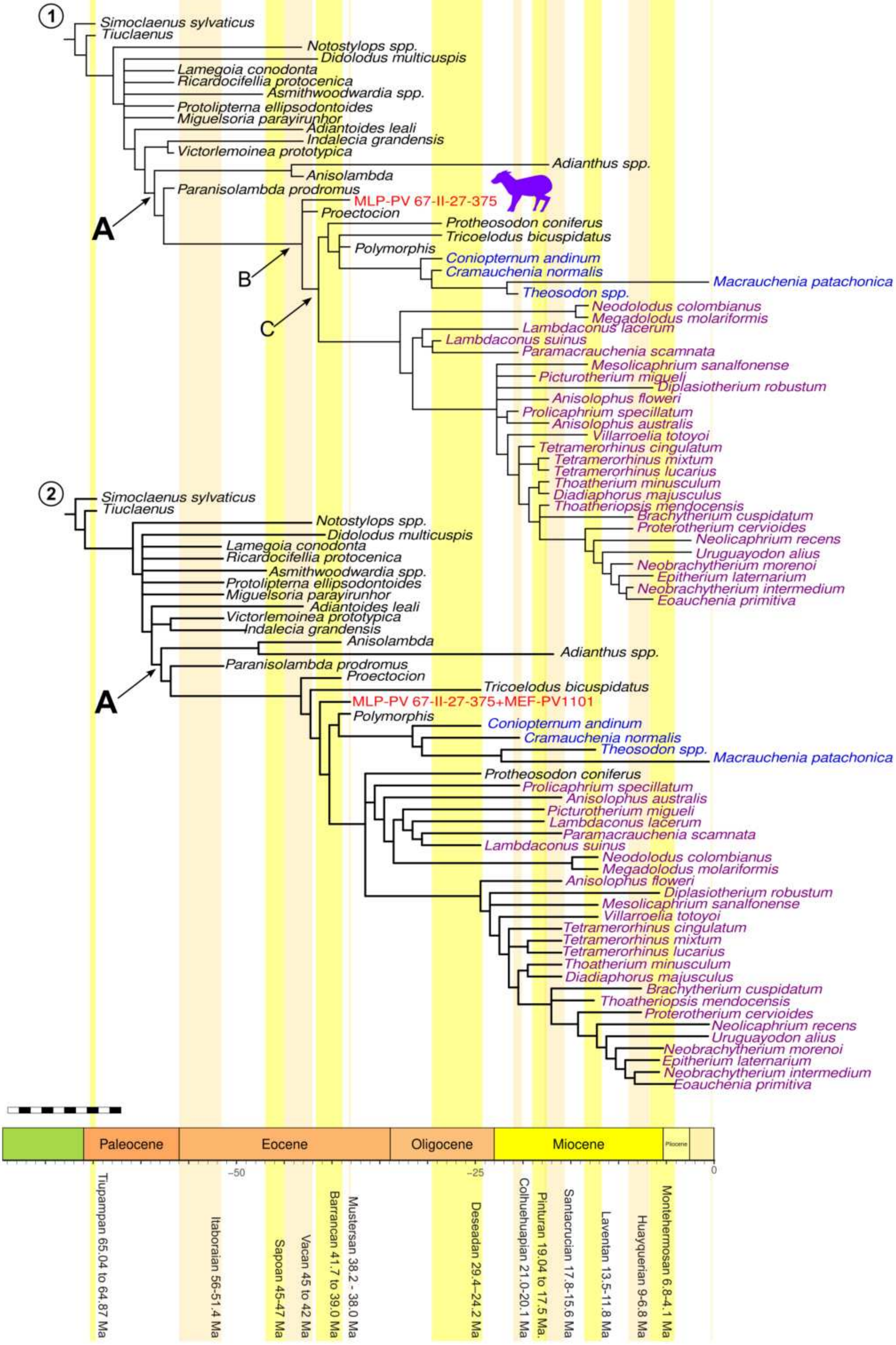
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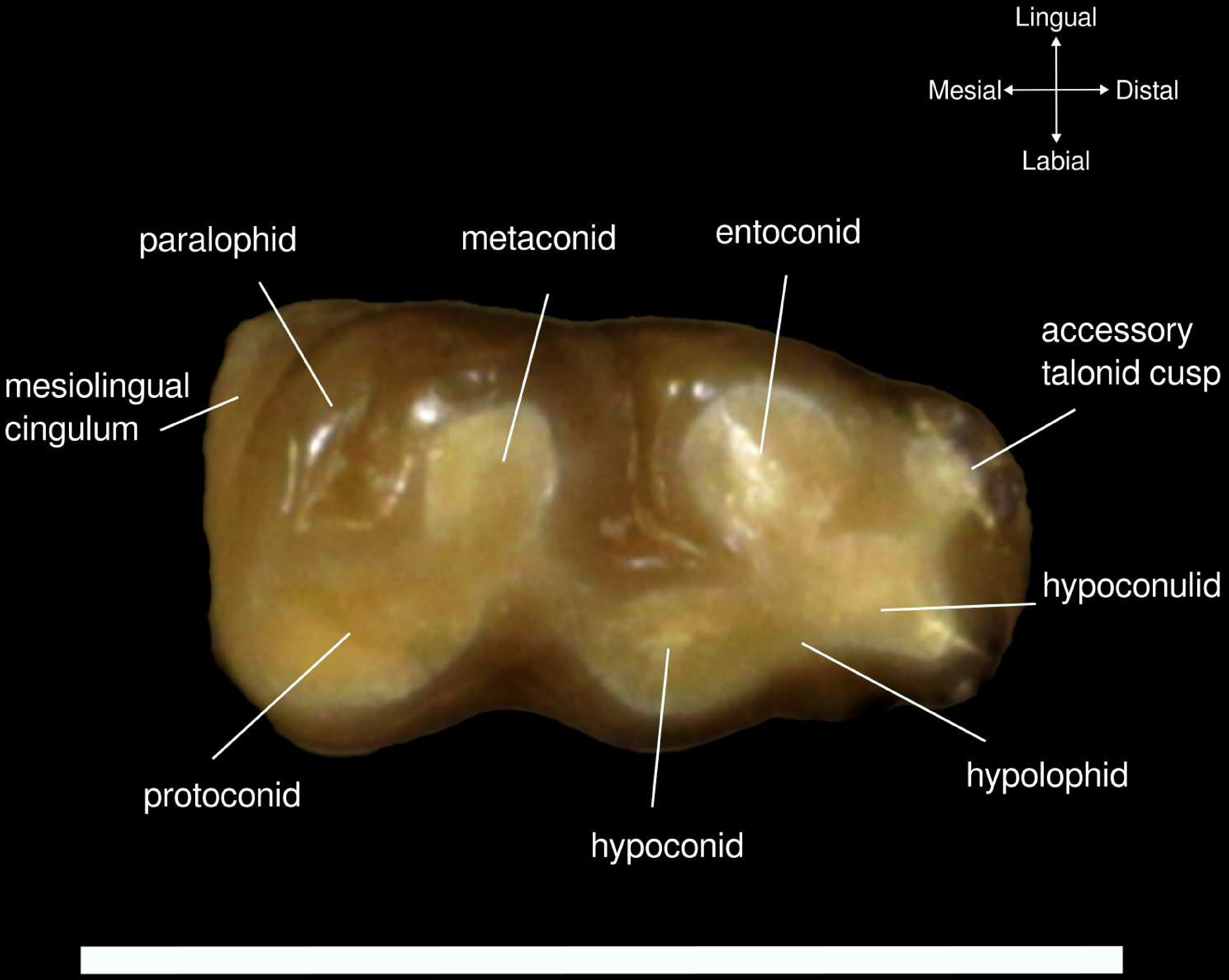
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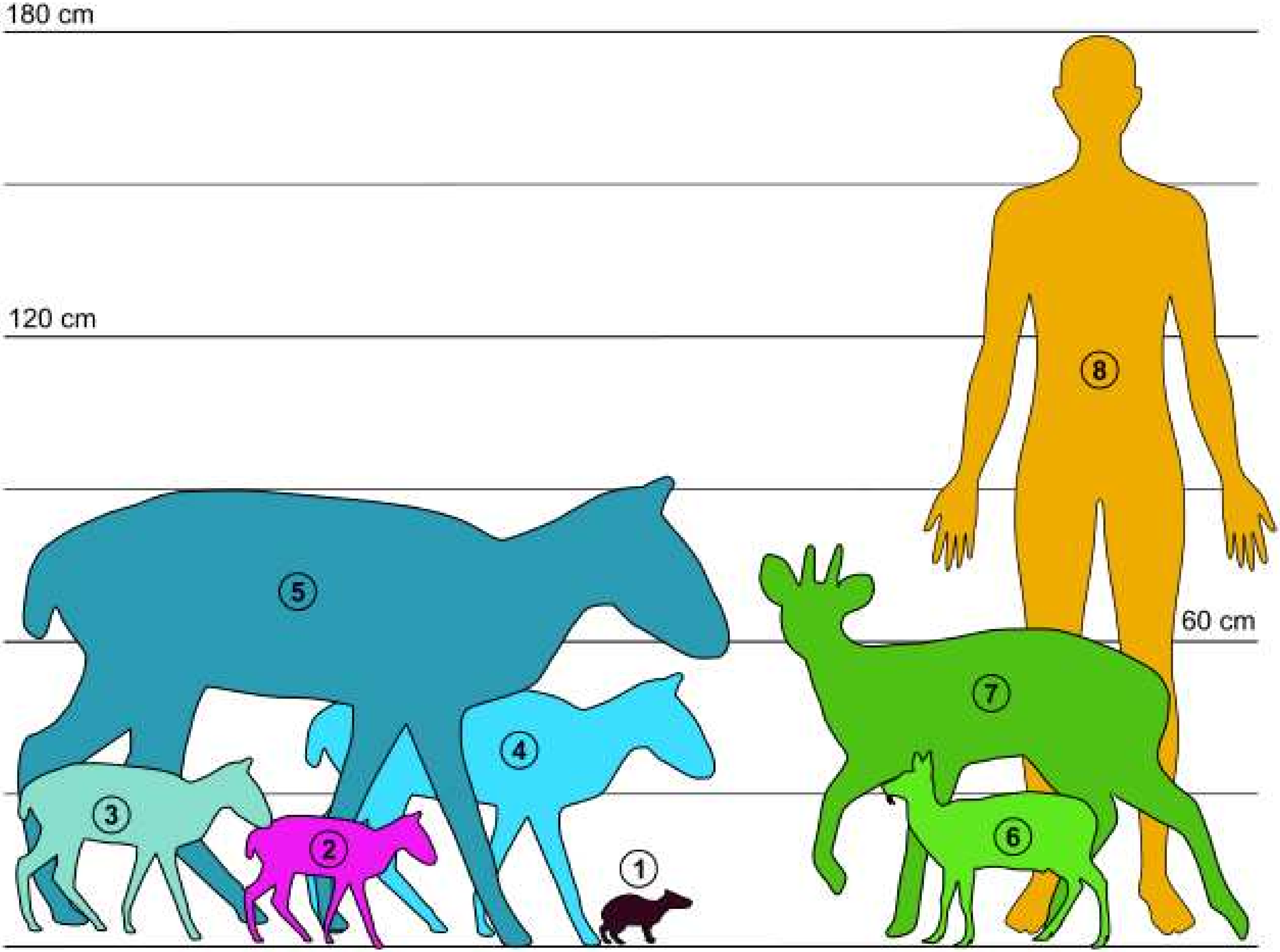
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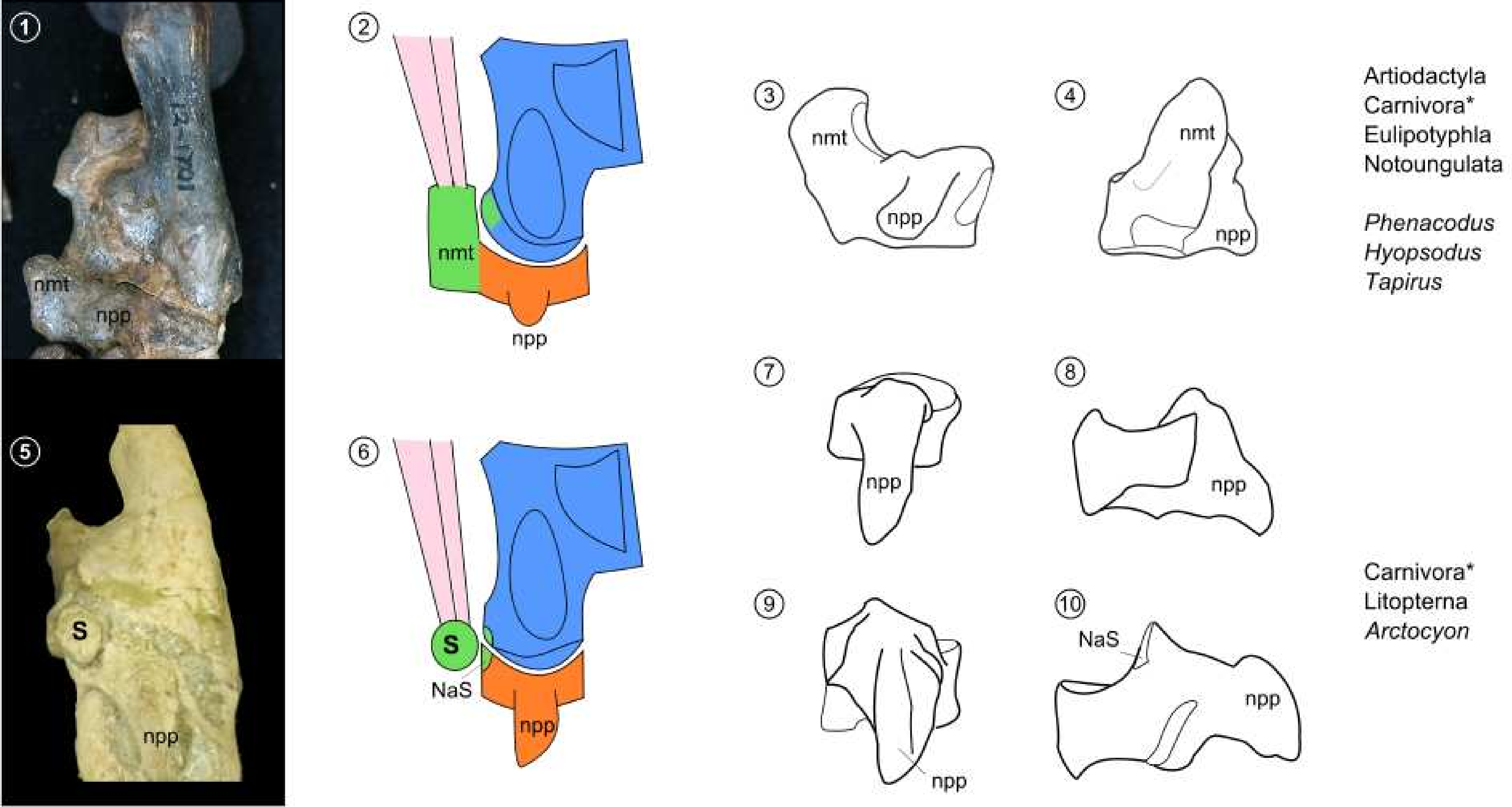
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