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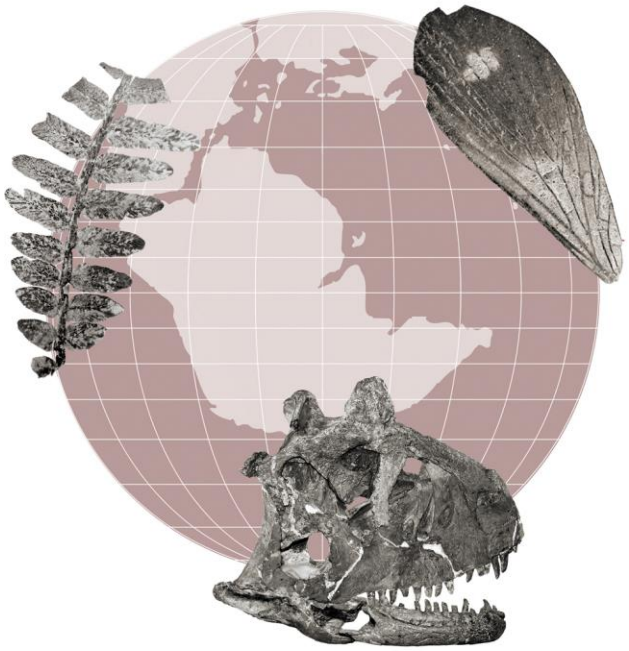

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AN ABELISAURID HUMERUS FROM THE BAJO DE LA CARPA FORMATION (UPPER CRETACEOUS, SANTONIAN), NORTHERN PATAGONIA, WITH COMMENTS ON MORPHOLOGICAL ASPECTS OF THE HUMERUS IN ABELISAURIDAE

ARIEL H. MÉNDEZ[1], E. EMANUEL SECULI-PEREYRA[1], JAVIER GONZÁLEZ-DIONIS[1], LUCÍA F. VETTORAZZI[2], ARIANA PAULINA-CARABAJAL[3,4], FEDERICO A. GIANECHINI[2], LEONARDO S. FILIPPI[5], ALBERTO C. GARRIDO[6], MAGALÍ CÁRDENAS[7], PENÉLOPE CRUZADO-CABALLERO[8,9], DO-KWON KIM[10], YUONG-NAM LEE[11]

[1]Instituto Patagónico de Geología y Paleontología (CCT CONICET-CENPAT), Bv. Brown 2915, U9120ACD, Puerto Madryn, Chubut, Argentina.
arielhmendez@yahoo.com.ar

[2]Instituto Multidisciplinario de Investigaciones Biológicas de San Luis (CONICET-UNSL), Ejército de Los Andes 950, D5700HHV, San Luis, San Luis, Argentina.

[3]Instituto de Investigaciones en Biodiversidad y Medioambiente (CONICET-INIBIOMA-UNCo), Quintral 1250, R8400FRF, S. C. de Bariloche, Río Negro, Argentina.

[4]Museo Paleontológico Bariloche. 12 de Octubre y Sarmiento, 8400, San Carlos de Bariloche, Río Negro, Argentina.

[5]Museo Municipal "Argentino Urquiza", Chos Malal 1277, Q8319AVY, Rincón de los Sauces, Neuquén, Argentina.

[6]Museo Provincial de Ciencias Naturales "Prof. Dr. Juan Olsacher", Dirección Provincial de Minería, Etcheluz y Ejército Argentino, Q8340AUB, Zapala, Neuquén, Argentina.

[7]Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470, C1405DJR, Ciudad de Buenos Aires, Argentina

[8]Área de Paleontología, Universidad de La Laguna, Av. Astrofísico Francisco Sánchez, s/n, La Laguna, Tenerife, España.

[9] Grupo Aragosaurus-IUCA, Facultad de Ciencias, Universidad de Zaragoza, C/ Pedro Cerbuna, 12, 50009 Zaragoza, Spain.

[10]Sicheong-ro, Namyang-eup, Hwaseong-si, Gyeonggi-do 18274, Republic of Korea.

[11]School of Earth and Environmental Sciences, Seoul National University, Seoul 08826, Republic of Korea.

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Running Header: MÉNDEZ *ET AL.*: ABELISAURID HUMERUS FROM PATAGONIA

Short Description: A new humerus of Abelisauridae is described. It displays morphological characteristics intermediate between noasaurids and derived abelisaurids.

Corresponding author: Ariel Hernán Méndez arielhmendez@yahoo.com.ar

Abstract. The Cerro Overo-La Invernada área (Bajo de la Carpa Formation, Upper Cretaceous, Santonian) in northern Patagonia has yielded abundant fossils of abelisaurid theropods, including cranial, vertebral, pectoral and pelvic remains. However, forelimb bones were unknown. Here, we describe a humerus that exhibits distinctive features that allow its assignment to Abelisauridae, for example, flattened distal condyles, greater tubercle distally located, and humeral head subspherical in proximal view. It also exhibits a noticeable torsion of the distal end. Morphofunctional analysis indicates a substantial capacity for protraction along with a limited capacity for lateromedial movement. In a general aspect, MAU-PV-LI-737 is morphologically intermediate between the more gracile humerus of noasaurids and the robust shape observed in Campanian-Maastrichtian abelisaurid forms.

Keywords. Humerus. Abelisauridae. Bajo de la Carpa Formation. Upper Cretaceous. Geometric morphometric.

Resumen. UN HÚMERO DE ABELISÁURIDO DE LA FORMACIÓN BAJO DE LA CARPA (CRETÁCICO SUPERIOR, SANTONIANO), PATAGONIA NORTE, CON COMENTARIOS SOBRE ASPECTOS MORFOLÓGICOS DEL HÚMERO EN ABELISAURIDAE. El área Cerro Overo-La Invernada (Formación Bajo de la Carpa, Cretácico Superior, Santoniano) en el norte de la Patagonia ha producido abundantes fósiles de terópodos abelisáuridos, incluyendo restos craneales, vertebrales, pectorales y pélvicos. Sin embargo, se desconocían huesos de las extremidades anteriores. Aquí describimos un húmero que exhibe características distintivas que permiten su asignación a Abelisauridae, por ejemplo, cóndilos distales aplanados, tubérculo mayor distalmente ubicado, cabeza humeral subesférica en vista proximal. También exhibe una notable torsión del extremo distal. El análisis morfofuncional indica una considerable capacidad de protracción junto con una limitada capacidad de movimiento lateromedial.

En aspecto general, MAU-PV-LI-737 es morfológicamente intermedio entre el húmero más grácil de los noasáuridos y la forma robusta observada en los abelisáuridos del Campaniano-Maastrichtiano.

Palabras clave. Húmero. Abelisauridae. Formación Bajo de la Carpa. Cretácico Superior. Morfometría geométrica.

CERRO OVERO – LA INVERNADA IS A PROLIFIC FOSSILIFEROUS AREA where Cretaceous sediments from the Bajo de la Carpa, Anacleto, and Allen formations emerge. Among these, the Bajo de la Carpa Formation stands out for the abundance and diversity of vertebrate fossils discovered, which include sauropod, theropod, and ornithopod dinosaurs, crocodiles, turtles, fish, as well as dinosaur footprints and eggs (Cruzado-Caballero *et al*., 2018, 2019; Filippi *et al*., 2016, 2018, 2024; Gianechini *et al*., 2021, 2022; Jiménez-Gomis *et al*., 2018; Méndez *et al*., 2018, 2022, 2024; Panzeri *et al*., 2022; Paulina-Carabajal *et al*., 2024). The remains of abelisauroid theropods, along with titanosaurid sauropods and chelid turtles, represent the largest number of specimens. To date, nine specimens belonging to the family Abelisauridae have been recovered, including two named taxa (*Viavenator* and *Llukalkan*, Filippi *et al*., 2016; Gianechini *et al*., 2021), four undetermined ones, and three others under study. All these forms can be nested within the clade Brachyrostra, except one (Gianechini *et al*., 2022) within Furileusauria. Among abelisaurid theropods from the Bajo de la Carpa Formation, forelimb elements are scarce, represented solely by the scapulocoracoid of *Viavenator*.

The humerus in Abelisauroidea is characterized by an anteroposterior expansion of the humeral head, a reduced development of the deltopectoral crest, the presence of a posterior or lateroposterior tuberosity, and a distal end with flattened radial and ulnar condyles. Noasaurids have a more slender humerus within this clade whereas abelisaurids tend to have a more robust and shorter humerus relative to body size (Novas *et al*., 2006; Méndez *et al*., 2010; Burch & Carrano, 2012).

Classical morphological studies are currently complemented by analysis using Geometric Morphometrics (GM), a tool that allows for evaluating shape changes (Zelditch *et al*., 2004; Benítez & Püschel, 2014). Combined with statistical analyses and descriptive graphics, GM enables effective quantification and a more appropriate

interpretation of morphological variation (Adams *et al*., 2013). In this work, we describe the tenth abelisaurid specimen for the Cerro Overo-La Invernada area (Figure 1), corresponding to a left humerus (Figure 2) exhibiting morphological features linked to the Abelisauridae family. We combined geometric morphometric techniques and statistical analyses to describe the shape variation and morphological affinities of this material. Additionally, we tested whether the differences in the humerus shape could be explained by taxonomical group and allometry.

Institutional abbreviations. FMNH, Field Museum of Natural History, Chicago, USA; **ISI,** Indian Statistical Institute, Kolkata, India; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MAU,** Museo Municipal "Argentino Urquiza", Rincón de los Sauces, Argentina; **MB,** Museum fur Naturkunde Berlin, Germany; **MCF,** Museo "Carmen Funes", Plaza Huincul, Argentina. **MPCN,** Museo Patagónico de Ciencias Naturales, General Roca, Argentina; **MPCO,** Museu de Paleontologia de Cruzeiro do Oeste, Cruzeiro do Oeste, Brazil

Anatomical abbreviations. dc, deltopectoral crest; **gt,** greater tubercle; **hh,** humeral head; **it,** internal tuberosity; **n,** notch; **pt,** posterior tuberosity; **rc,** radial condyle; **uc,** ulnar condyle

MATERIALS AND METHODS

Material

MAU-Pv-LI-737: complete left humerus.

Methods

Sample data and geometric morphometrics. Jointly with the humerus MAU-PV-LI-737, two-dimensional (2D) published left humeri images and photographs in anterior view were used. A total of four abelisaurids (*Carnotaurus* (personal image), *Eoabelisaurus* (personal image), *Majungasaurus* (Carrano, 2007; Burch & Carrano,

2012) and *Aucasaurus* (Coria *et al*., 2002), three noasaurids (*Elaphrosaurus*, Rauhut & Carrano, 2016; *Masiakasaurus*, Carrano *et al*., 2011; and *Vespersaurus*, Langer *et al*., 2019), one early diverging ceratosaurid (*Ceratosaurus*, Madsen & Welles, 2000) and one early diverging tetanuran (*Allosaurus*, Madsen, 1976) were used. When only the right element was available, we mirrored the image to allow landmarking. We designed a 2D configuration for the anterior view with five landmarks and 27 semilandmarks, digitized in tpsDig (2.6.4; Rohlf, 2004) (Figure 3-2 and Supplementary Online Information; Table 1). Likewise, we designed a 2D configuration to proximal view with two landmarks and 14 semilandmarks (Figure 4-2 and Supplementary Online Information, Table 2). Finally, a Generalized Procrustes Analysis was performed to eliminate the effects of rotation, translocation, and scale, obtaining the shape and size variables that were used for downstream analyses (gpagen, geomorph package; Adams & Otárola-Castillo, 2013) in both humeri views.

Ordination methods (Principal Component Analysis) and hypothesis testing. Ordination methods reduce the number of shape variables into a few principal components, which describe the significant shape changes across the morpho-space. We performed a Principal Component Analysis (PCA) (gm.prcomp function, geomorph package) to describe the significant shape changes across our humeri sample, emphasizing the shape changes of MAU-PV-LI-737.

We tested whether the differences in humeri shape could be explained by taxonomical group (Abelisauridae, Noasauridae, and early diverging taxa or outgroups), allometry (Centroid Size based), and the cross-factor (the interaction between these variables) using a Procustes ANOVA (procD.lm function, geomorph and RRPP package; Collyer & Adams, 2018) in the Procustes Coordinates (PC). Additionally, since Procustes Coordinates represents all the variation in humeri shape data, we also

used 90% of PC components in order to avoid more variables (numbers of landmarks) than species in the analysis.

Finally, since statistics based on the overconfidence in P-values has mainly been criticized (Benjamin *et al*., 2018; Amrhein *et al*., 2019; Yang *et al*., 2023), we used the variance explained (R-squared) and effect size (standardized differences (Z)) estimated in the Procustes ANOVA to discuss our results more compressively.

Osteological correlates and musculature. The osteological correlates and muscle nomenclature used in this study follow the work of Burch (2017), who performed a detailed myological reconstruction of the forelimb of the abelisaurid *Majungasaurus crenatissimus*. The abbreviations used for muscles (*e.g.*, *M. subscapularis* (SBS), *M. latissimus dorsi* (LD), *M. coracobrachialis* (CB)) are consistent with the standardized format proposed in that work, which integrates the extant phylogenetic bracket (EPB; Witmer, 1995) with osteological correlates to infer soft tissue anatomy in non-avian theropods.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881

CERATOSAURIA Marsh, 1884

ABELISAUROIDEA Bonaparte, 1991

ABELISAURIDAE Bonaparte & Novas, 1985

Abelisauridae indet.

Type material. MAU-Pv-LI-737 Left humerus

Geographic occurrence. La Invernada fossil site, 50 km south of Rincón de los Sauces city, Neuquén province, Argentina

Stratigraphic occurrence. Bajo de la Carpa Formation (Santonian, Upper Cretaceous)

Description. The humerus (MAU-Pv-LI-737) is complete and measures 18.5 cm. The humeral head is oval in proximal view, with the main axis in lateromedial direction, similar to *Eoabelisaurus* (Pol & Rauhut, 2012), *Elaphrosaurus* (Janensch, 1920), *Vespersaurus* (Langer *et al*., 2019) and the abelisauroid MCF-PVPH 53 (Novas *et al*., 2006), and unlike the rounded and globose shape observed in *Carnotaurus* (Bonaparte, 1985), *Majungasaurus* (Lavocat, 1955), *Aucasaurus* (Coria *et al*., 2002), *Rahiolisaurus* (Novas *et al*., 2010), and MPCN-PV 69 (Gianechini *et al*., 2015). In posterior view, the distal margin of the humeral head is located above the level of the internal tuberosity, as seen in *Eoabelisaurus*, *Elaphrosaurus*, *Masiakasaurus* (Sampson *et al*., 2001), *Vespersaurus*, *Majungasaurus*, *Aucasaurus* and MCF-PVPH 53, but unlike *Carnotaurus* and MPCN-PV 69, in which the distal margin is at the same level as the internal tuberosity. The deltopectoral crest and greater tubercle are less developed than in other abelisaurids and noasaurids. The internal tuberosity is separated from the humeral head by a poorly marked notch, similar to that observed in *Majungasaurus*, *Rahiolisaurus*, *Elaphrosaurus*, and MCF-PVPH-53. In contrast, *Aucasaurus*, *Carnotaurus*, and MPCN-PV 69 exhibit a more conspicuous notch. In MAU-Pv-LI-737, as in *Aucasaurus*, *Carnotaurus*, *Majungasaurus*, *Rahiolisaurus*, and MPCN-PV-69, the internal tuberosity is located above the level of the greater tubercle, whereas in the basal abelisauroid MCF-PVPH-53 is located at the same level. On the other hand, in *Elaphrosaurus* and *Vespersaurus*, the internal tuberosity is located below the level of the greater tubercle. The diaphysis is wide and arched, in anterior and posterior views, as in several abelisaurids such as *Carnotaurus*, *Aucasaurus*, and *Majungasaurus*, whereas in noasaurids such as *Elaphrosaurus*, *Vespersaurus*, and *Masiakasaurus*, the diaphysis is less arched and narrower. However, MAU-Pv-LI-737 differs because the

diaphysis in its distal third shows a rotation that makes the ulnar condyle remain in an anteromedial position instead of medial. Furthermore, a slight notch can be seen between the radial and ulnar condyles in the distal view, similar to that seen in *Majungasaurus*, *Vespersaurus*, and *Elaphrosaurus*. On the other hand, in *Aucasaurus*, this notch is much more noticeable whereas it is not observed in *Carnotaurus* and *Masiakasaurus*. In the anterior view, just below the edge of the humeral head, a slight depression is observed, possibly representing the insertion area for the *M. coracobrachialis* (Jasinoski *et al*., 2006; Carrano, 2007; Burch, 2017). This shallow condition is present in the abelisauroid MCF-PVPH 53 and *Vespersaurus*, which contrasts with the marked groove present in *Carnotaurus*, *Aucasaurus*, *Majungasaurus*, *Rahiolisaurus* and MPCN-PV 69, which is a product of the expansion of the humeral head in an anteroposterior direction. In the posterior view, a poorly developed posterior tuberosity is present at the level of the first proximal third. This bump is also present in *Aucasaurus*, *Carnotaurus*, *Majungasaurus*, *Rahiolisaurus*, MPCN-PV 69, MCF-PVPH 53, and probably in *Ceratosaurus* (Burch, 2017). The presence of this structure, possibly for the insertion of the *M. latissimus dorsi* and part of the *M. deltoideus* (Jasinoski *et al*., 2006; Carrano, 2007), is not documented in *Masiakasaurus*, *Vespersaurus*, and non-abelisauroid theropods (*e.g.*, the coelophysoids *Syntarsus* and *Liliensternus*, basal tetanurans as *Baryonyx*, *Allosaurus*, and in *Deinonychus*).

RESULTS

Ordination methods (Principal Component Analysis) and hypothesis testing

PCA in anterior view. The first two components of the PCA explained 64,69% of the total variance of the data (Figure 3-1). The PC1 was related to the humeral head and the internal tuberosity. This component distinguished Abelisauridae and early diverging taxa from Noasauridae in a pronounced well-developed internal tuberosity and rounded

humeral head (Figure 3-1). The PC2 was related to the width and length of the humerus (Figure 3-1). This component distinguished abelisaurids from early diverging taxa and noasaurids in a short and wide humeral shape for abelisaurids. MAU-PV-LI-737 was found close to Late Cretaceous abelisaurid forms, being more similar to *Majungasaurus* in shape (Figure 3-1).

We found that the humeral size (centroid size) had little effect on the shape of the humerus in both data sets (Table 1). Moreover, the interaction between factors (Taxonomy*Size) in all datasets explained around 15% of the total variation. However, the taxonomy variable explained more than 30% of the total variation of the humeral shape in both data sets (Table 1).

PCA in proximal view. The first two components of the PCA explained 65,76% of the total variance of the data in the proximal view (Figure 4-1). The PC1 component was related to the shape of the humeral head. This component distinguishes Late Cretaceous abelisaurids from Noasauridae, *Eoabelisaurus*, and MAU-PV-LI-737 in a circular-shaped humeral head. The PC 2 was related to the lower edge between the internal tuberosity and the deltopectoral crest. This component distinguished Noasauridae from *Eoabelisaurus* and upper Cretaceous abelisaurids, in a concave-shaped edge. MAU-PV-LI-737 was found more closely to MPCN-PV-69 and MCF-PVPH-53.

Hypothesis testing. The presence of allometry in humeral shape and its correlation with taxonomic groups were evaluated within a quantitative framework using Procrustes ANOVA on Procrustes coordinates and in the 90% shape variation in the principal component analysis for both humerus views. Our results indicate that humerus size (centroid size) had only a minor effect on shape variation in both datasets and views (Table 1). Additionally, in both views, the interaction between taxonomy and size accounted for approximately 15% of the total shape variation across datasets. In

contrast, taxonomy alone explained over 30% of the total variation in humeral shape in both datasets and humerus views (Table 1).

Osteological correlates and functional morphology

The degree of preservation of this material allows inferences to be drawn about the development of the musculature in the humerus thanks to the bone correlates found in MAU-Pv-LI-737 (Fig. 5). The bone correlates described by Burch (2017) have been taken as a reference. The internal tuberosity (IT), medially directed and moderately developed, would be unequivocally the insertion zone of the *M. subcoracoideus* (SBC) in the anteromedial surface and of the *M. subscapularis* (SBS) in the posteromedial surface of the IT. However, the division where these two muscles would be attached, which is defined in other abelisaurids by an intermediate ridge (Burch, 2017), is not observed in MAU-Pv-LI-737, so its arrangement could not be precisely defined. The rugosity that indicate the attachment area of the *M. scapulohumeralis posterior* (SHP) is not present, although in this area is observed a slight depression. This area is unequivocally located posteriorly under the insertion zone of *M. subscapularis* in the internal tuberosity. In anteromedial view, there is a slight depression which would be the origin of the *M. biceps brachii* (BB). The slight depression under the humeral head in the anterior view would be the insertion zone of the *M. coracobrachialis* (CB). Similarly, we can observe the slight development of the insertion zone of the *supracoracoideus complex*, which is formed by two muscles, the *M. supracoracoideus accessorius* (SCA), which inserts in the anterior zone of the greater tubercle, where a slight roughness is observed, and the *M. supracoracoideus* (SC) which attaches in the distal zone of the deltopectoral crest. In the posterior view, there is a roughness in the greater tubercle where the *M. deltoideus scapularis* (DS) would insert. Towards the medial area, there is an anterolateral thickening of the deltopectoral crest, where the *M.*

pectoralis (P) would attach. The *M. deltoideus clavicularis* (DC) would attach on the lateral surface of the deltopectoral crest, where a wide striated area extending dorsoventrally over a concave surface is observed. The arrangement of the *M. latissimus dorsi* (LD) would be more displaced towards the more posteromedial area, taking the more medial location of the posterior tuberosity as a reference, although it is impossible to identify any depression to confirm this. This position makes the area of origin of the *M. triceps brachii medialis* (TBM) smaller, which could affect the extension of the forearm. In the posterolateral view, a groove can be seen corresponding to the tentative area of origin of the lateral *M. triceps brachii lateralis* muscle. The *M. brachialis* (BR) does not have any defined scars, making it difficult to establish its area of origin with certainty. However, it should have been attached to the anterior surface next to the distal area of the deltopectoral crest. This suggests that it would have a more medial location, since the distal area of the deltopectoral crest is not very developed. Distal musculature related to antebrachium articulation is inferred to originate in association with the entepicondyle and ectepicondyle, but these structures are difficult to differentiate. It should be noted that due to the torsion of the shaft, a large groove is observed in the posterodistal area where the insertion zone of the *M. supinator* (SU) would be located. Furthermore, in the anterior view near the ulnar condyle, small depressions are observed, one towards the more medial side and the other more distal, which could be indicative of the origin of the *M. pronator teres* (PT) and *M. epitrocheloanconeus* (EA), *M. flexor carpi ulnaris* (FCU) and *M. flexor digitorum longus superficialis* (FDLS), respectively.

DISCUSSION

Humeral features. Although MAU-Pv-LI-737 consists solely of a humerus, the general morphology of this bone demonstrates similarities with theropods belonging to the

Abelisauridae clade (Figure 6). Characters associated with the humerus in the most recent phylogenetic analyses are discussed below.

Shape of the humeral head in proximal view (Rauhut, 2003). Rauhut (2003) identified two states for this character: those that were markedly oval (more than twice as wide as they were long anteroposteriorly) as in most theropods, and those that were more rounded or not so oval, a shape present in *Elaphrosaurus* and abelisaurids. In 2016, Rauhut and Carrano divided the latter state of the character into slightly oval (less than twice as wide as long) and globose. This differentiation groups MAU-Pv-LI-737 with the elaphrosaurins *Masiakasaurus* and *Elaphrosaurus,* as well as the basal abelisauroid MCF-PVPH-53 (and probably also *Eoabelisaurus*). On the other hand, the globose character is restricted to the majungasaurines *Majungasaurus* and *Rahiolisaurus* and the brachyrostrans *Carnotaurus*, *Aucasaurus,* and MPCN-PV-69. The globose morphology seems to be restricted to the abelisaurid taxa of the end of the Late Cretaceous (Campanian-Maastrichtian).

Shape of distal humeral condyles (Carrano *et al.*, 2002). Carrano and colleagues (2002) identified the distal shape of the humerus with two well-defined states, rounded or flattened condyles. The condyles, articulating with the radius and ulna, are rounded in most theropods. However, they become more flattened in Ceratosauria (including MAU-PV-LI-737), except in *Eoabelisaurus* and *Vespersaurus* (being less pronounced in the latter), which appear to retain the plesiomorphic condition.

Placement of humeral greater tubercle (Sereno *et al*., 2004). The greater tubercle is located approximately at the level of the humeral head in most theropods. In basal abelisauroids and noasaurids (*e.g.*, *Vespersaurus*, *Elaphrosaurus*, *Masiakasaurus*, MCF-PVPH-53), it is located just below the level of the distal margin of the humeral

head. The greater tubercle is located more distally in MAU-PV-LI-737 and the rest of the Abelisauridae.

Posterolateral tubercle on the proximal part of the humerus (Novas et al., 2006). Novas and colleagues (2006) identified a bulge in the posterior sector of the humerus MCF-PVPH-53. This feature is also present in MAU-PV-LI-737, the remaining abelisaurids, and *Elaphrosaurus*, being absent in coelophysoids and basal tetanurans (Novas *et al*., 2006).

Humerus in the anterior view (Rauhut & Carrano, 2016). Rauhut and Carrano (2016) describe a new character in which the medial and lateral margins of humeri of non-abelisauroid theropods would be concave or concave-straight, while in MAU-PV-LI-737 and Abelisauroidea, the lateral margin is moderately convex and the medial one markedly concave. This state of the character is not present in the noasaurin *Vespersaurus*, which presents a more plesiomorphic condition.

Longitudinal torsion of humeral shaft (Holtz, 2000). In basal theropods, the proximal and distal humeral articular surfaces are virtually in the same plane. A rotational axis shift is observed in more derived forms (*e.g.*, tetanurans, ceratosaurs; Carrano & Sampson, 2008), resulting in a longitudinal torsion. It is slightly noticeable in abelisaurids, while in MAU-PV-LI-737 and *Elaphrosaurus*, this rotation is more pronounced.

Size of deltopectoral crest (Paul, 1984). Most theropods (and dinosaurs generally, Benton, 1990; Sereno, 1999) have a well-developed deltopectoral crest. The development of this structure is markedly diminished in MAU-PV-LI-737 and all members of the Abelisauroidea.

Connection between the humeral head and the internal tuberosity, anterior view (Gianechini *et al*., 2015). In 2015, Gianechini and colleagues identified a new character

related to the connection between the humeral head and the internal tuberosity. Regardless of the morphology of the internal tuberosity (triangular or rectangular, Rauhut, 2003), in Theropoda, it is continuous with the humeral head. In *Ceratosaurus*, noasaurids, and majungasaurins (it also appears to be present in spinosaurids, Charig & Milner, 1997), this transition is observed as a slight concavity, while in late diverging furileusaurs such as *Carnotaurus* and *Aucasaurus*, a more pronounced step is seen. *Herrerasaurus* presents an autapomorphic condition with a deep groove separating the humeral head from an internal tuberosity.

Morphofunctional inferences. Based on the morphology of the osteological correlates observed, it is possible to suggest that MAU-Pv-LI-737 should not have a great capacity for protraction (muscles CB, DS, P, DC), being more similar to *Elaphrosaurus.* Similarly, the moderate development, as seen in *Aucasaurus*, and the lack of delimitation of the insertion area of SBS and SBC could indicate a low capacity for adduction and medial rotation in humeral retraction, compared to other abelisaurids such as *Majungasaurus* or *Carnotaurus*. The origin area of BR is similar to early diverging theropods, where its tentative location would be more medial than in other abelisaurids such as *Majungasaurus* or *Carnotaurus*, where it would be located slightly more distally (Burch, 2014, 2017). Similarly, the distal musculature correlates are poorly developed, which, combined with the flat morphology of the condyles, would suggest poor pronation and supination capacity. Finally, comparative evidence in other abelisaurids and theropods shows that humeral head morphology constrains shoulder range of motion. In abelisaurids with bulbous and hemispherical head (*e.g.*, *Carnotaurus*, *Majungasaurus*), greater mobility is inferred, notably wide humeral elevation in the transverse plane. In *Majungasaurus* this condition is explicitly associated with broad shoulder ranges of motion, and in *Carnotaurus* it has been linked

to expanded elevation relative to theropods lacking a hemispherical head (Senter & Parrish, 2006; Burch, 2017). By contrast, in theropods with non-hemispherical heads the range of motion can be more restricted or asymmetric. For example, in *Acrocanthosaurus* the head is more posteriorly extensive (non-hemispherical), which favours greater retraction than protaction (Senter & Robins, 2005). Alternatively, some clades achieve high elevation whit a head offset toward the deltopectoral crest (non-hemispherical), as in *Mononykus*, maintaining glenoid contact over a wider arc (Senter, 2023). In this way, the oval morphology of the humeral head of MAU-Pv-LI-737 suggests a limitation in lateromedial movements compared to other abelisaurids with a bulbous and hemispherical humeral head.

CONCLUSIONS

The humerus of abelisauroid theropods is well represented by the abelisaurids *Carnotaurus*, *Majungasaurus*, *Aucasaurus*, and the noasaurids *Masiakasaurus*, *Elaphrosaurus* and *Vespersaurus*. However, this bone is not entirely known for more basal abelisaurid forms. The humerus described here adds new data on the forelimb morphology of this group of ceratosaurian theropods.

This material is interpreted as belonging to an indeterminated abelisaurid theropod, an assignment supported by a moderately inflated humeral head, a reduced deltopectoral crest, and posterior tuberosity on the humeral shaft. The condition of the humeral head in MAU-PV-LI-737 seems to be more primitive than the globose shape of *Majungasaurus*, *Rahiolisaurus*, *Aucasaurus*, and *Carnotaurus*, but more derived than in non-abelisauroid theropods. The slightly concave transition between the humeral head and the internal tuberosity is shared with other non-furileusaurian abelisauroids. MAU-PV-LI-737 shares with other abelisaurids the general curvature of the shaft in the anterior or posterior view. The location of the greater tubercle to the humeral head is

another characteristic that groups it with the Abelisauridae. However, MAU-PV-LI-737 does not share a marked torsion of the distal part of the shaft with other abelisauroids.

The osteological correlates and associated musculature observed in MAU-Pv-LI-737 suggest a limited functionality of the humerus, primarily restricted in protraction, adduction, and medial rotation, being morphologically located between noasaurids and derived abelisaurids. In addition, the oval shape of the humeral head implies restrictions in lateromedial movements. Future studies, will allow a more precise exploration of the muscular arrangement and functional capabilities of this abelisauroid forelimb.

Regarding GM and statistical analysis, the shape, in the anterior view, of MAU-PV-LI-737 is more similar to Campanian-Maastrichtian abelisaurids, with a robust humeral shape. However, the shape in proximal view was morphologically more similar to the Jurassic abelisaurid *Eoabelisaurus* and noasaurids. Therefore, in general aspect, MAU-PV-LI-737 seems to be morphologically intermediate between the more gracile humerus of noasaurids (*e.g.*, *Vespersaurus*, *Elaphrosaurus*, *Masiakasaurus*) and the robust shape of derived abelisaurid forms (*e.g.*, *Majungasaurus*, *Carnotaurus*, *Aucasaurus*). On the other hand, the taxonomical classification of taxa explained better the shape of the humerus than size and the interaction between these factors (Taxonomy and Size). It means that abelisaurids, especially late diverging abelisaurids, exhibit a characteristic and conservative morphology, within the members of the family. It is interesting to note that the most robust form is present in those taxa or specimens originating from Campanian-Maastrichtian strata, regardless of the group to which they belong within Abelisauridae (Brachyrostra + Majungasaurinae). Whereas less robust forms are found among pre-Campanian abelisaurids, the most gracile ones appear within noasaurids.

However, the present analysis lacks a phylogenetic comparative approach to determine macroevolutionary patterns and trends in Abelisauridae humeral evolution. Future research must consider a phylogenetic approach to determine what patterns of evolution rates, selection strength, and constraint explain the conservative morphology of the abelisaurid humerus.

ACKNOWLEDGMENTS

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Appendices

Figure captions

Figure 1. (1) Map of the location of the La Invernada fossil area. (2) Detailed map showing the spatial provenance of the abelisaurid specimens of La Invernada. (3) Stratigraphic column with the location of the different finds (Modified from Méndez *et al*., 2022).

Figure 2. MAU-PV-LI-737 left humerus in (1) anterior, (2) lateral, (3) posterior, (4) medial, (5) proximal, and (6) distal views. Abbreviations: **dc,** deltopectoral crest; **gt,** greater tubercle; **hh,** humeral head; **it,** internal tuberosity; **n,** notch; **pt,** posterior tuberosity; **rc,** radial condyle; **uc,** ulnar condyle. Scale bar equals 20 mm.

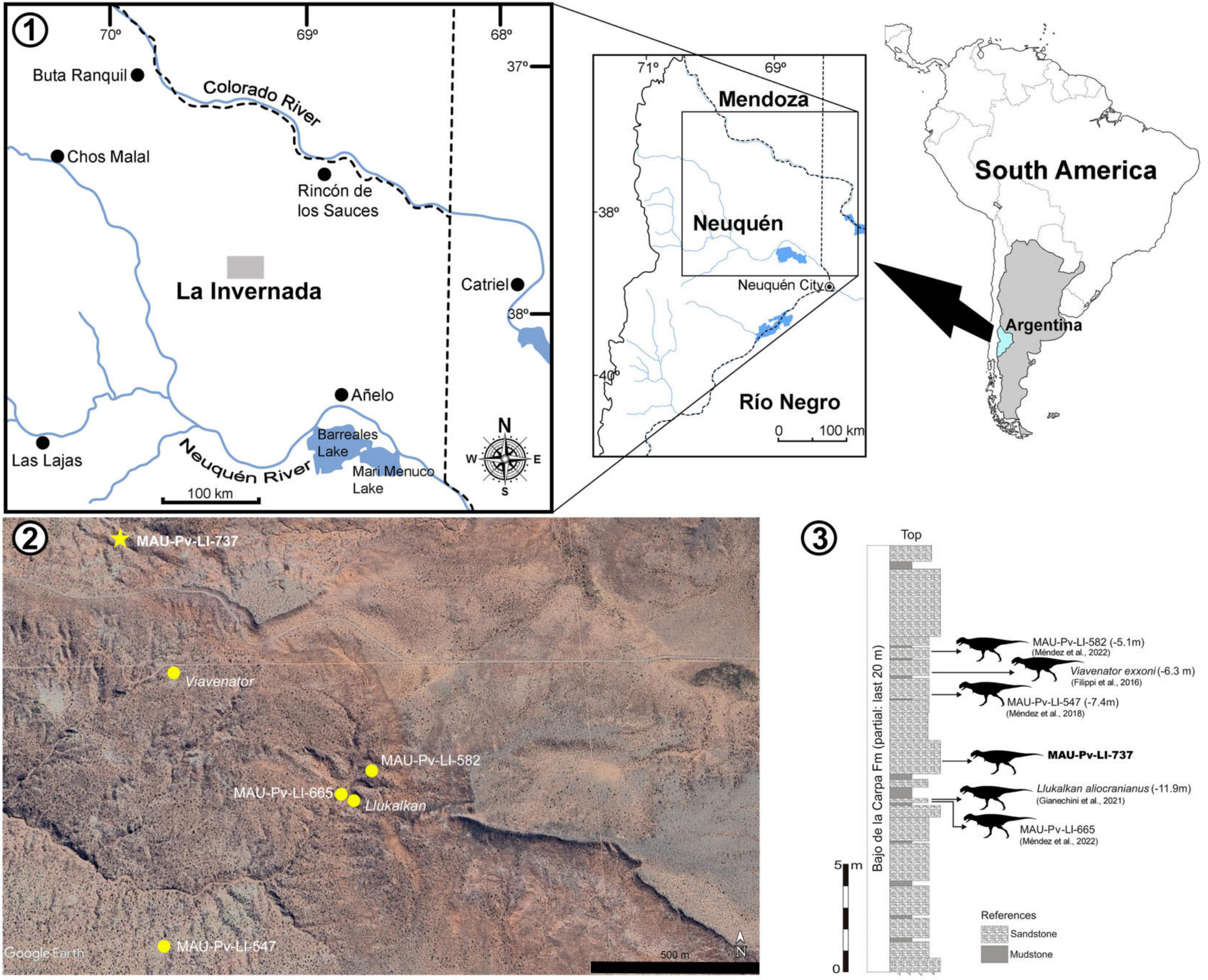
Figure 3: 1) PCA showing the first two Principal Components (PC) and deformation grids representing the shape of each extreme of the axis. The ratios represent the variance explained by each PC. Color areas delimits the morphospace occupied by Late Cretaceous abelisaurids (black), Abelisauridae (yellow), Jurassic taxa (green) and Noasauridae (red). 2) Landmark configuration over MAU-PV-LI-737 used in the analyses, in which landmarks are in red and semilandmarks are in blue.

Figure 4. 1) PCA showing the first two Principal Components (PC) and deformation grids representing the shape of each extreme of the axis. The ratios represent the variance explained by each PC. Color area delimits the morphospace occupied by abelisaurids (black). 2) Landmark configuration over MAU-PV-LI-737 used in the analyses, in which landmarks are in red and semilandmarks are in blue.

Figure 5. Myological reconstruction of the humerus of MAU-PV-LI-737 in anterior (1), lateral (2), posterior (3), and medial (4) views. Proposed muscle origins are indicated in red, proposed insertions in blue. Abbreviations: **AN**, *M. anconeus*; **AR**, *M, abductor radialis*; **BB**, *M. biceps brachii*; **BR**, *M. brachialis*; **CB**, *M. coracobrachialis*; **DC**, *M. deltoideus clavicularis*; **DS**, *M. deltoideus scapularis*; **EA**, *M. epitrocheloanconeus*; **ECR**, *M. extensor carpi radialis*; **ECU**, *M. extensor carpi ulnaris*; **EDL**, *M. extensor digitorum longus*; **FCU**, *M. flexor carpi ulnaris*; **FDLS**, *M. flexor digitorum longus superficialis*; **LD**, *M. latissimus dorsi*; **P**, *M. pectoralis*; **PT**, *M. pronator teres*; **SBC**, *M. subcoracoideus*; **SBS**, *M. subscapularis*; **SC**, *M. supracoracoideus*; **SCA**, *M. supracoracoideus accessorius*; **SHP**, *M, scapulohumeralis posterior*; **SU**, *M. supinator*; **TBL**, *M. triceps brachii longus*; **TBM**, *M. triceps brachii medialis*. Scale bar: 20mm.

Figure 6. Humeri of several abelisauroid theropods in anterior (1-9), lateral (10-18), and proximal (19-27) views. (1,10,19) *Masiakasaurus* (FMNH PR 2485 from Carrano *et al*., 2011); (2,11,20) *Elaphrosaurus* (MB R 4960 from Rauhut & Carrano, 2016); (3,12,21) *Vespersaurus* (MPCO.V 0006d from Langer *et al*., 2019); (4,13,22) MCF-PVPH 53 (from Novas *et al*., 2006); (5,14,23) MAU-PV-LI-737; (6,15,24) *Rahiolisaurus* (ISIR 657 from Méndez *et al*., 2010); (7,16,25) *Majungasaurus* (FMNH

PR 2423 from Carrano, 2007; FMNH PR 2836 from Burch & Carrano, 2012); (8,17,26) MPCN-PV-69; (9,18,27) *Carnotaurus* (MACN-CH 894). Not to scale.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Las Lajas
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Mendoza
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Neuquén
Neuquén City
40º
Río Negro
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100 km
South America
Argentina
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MAU-Pv-LI-737
Viavenator
MAU-Pv-LI-582
MAU-Pv-LI-665
Llukalkan
MAU-Pv-LI-547
Google Earth
500 m
N
3
Top
Bajo de la Carpa Fm (partial: last 20 m)
MAU-Pv-LI-582 (-5.1m)
(Méndez et al., 2022)
Viavenator exxoni (-6.3 m)
(Filippi et al., 2016)
MAU-Pv-LI-547 (-7.4m)
(Méndez et al., 2018)
MAU-Pv-LI-737
Llukalkan aliocranianus (-11.9m)
(Gianechini et al., 2021)
MAU-Pv-LI-665
(Méndez et al., 2022)
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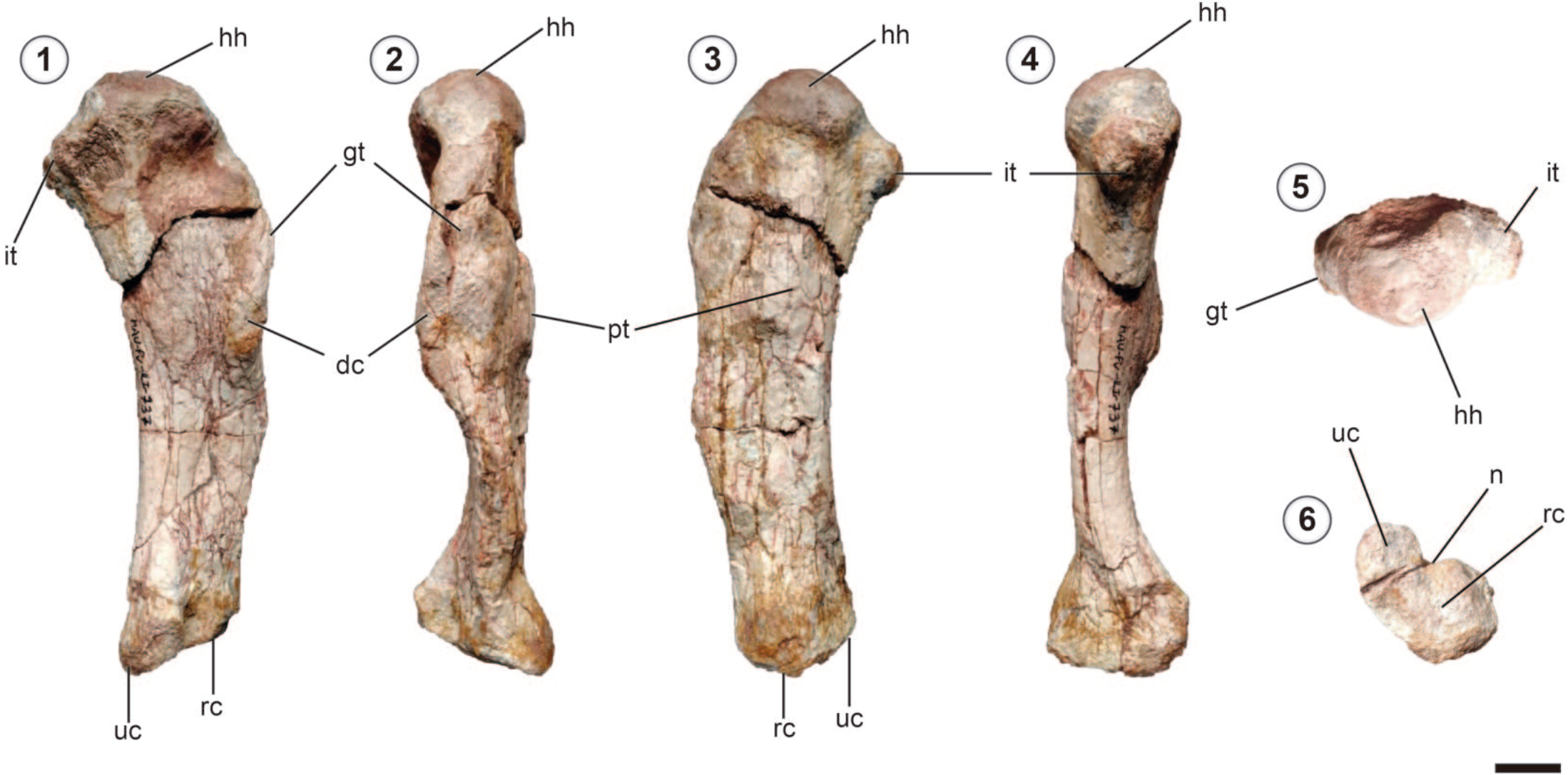
References
Sandstone
Mudstone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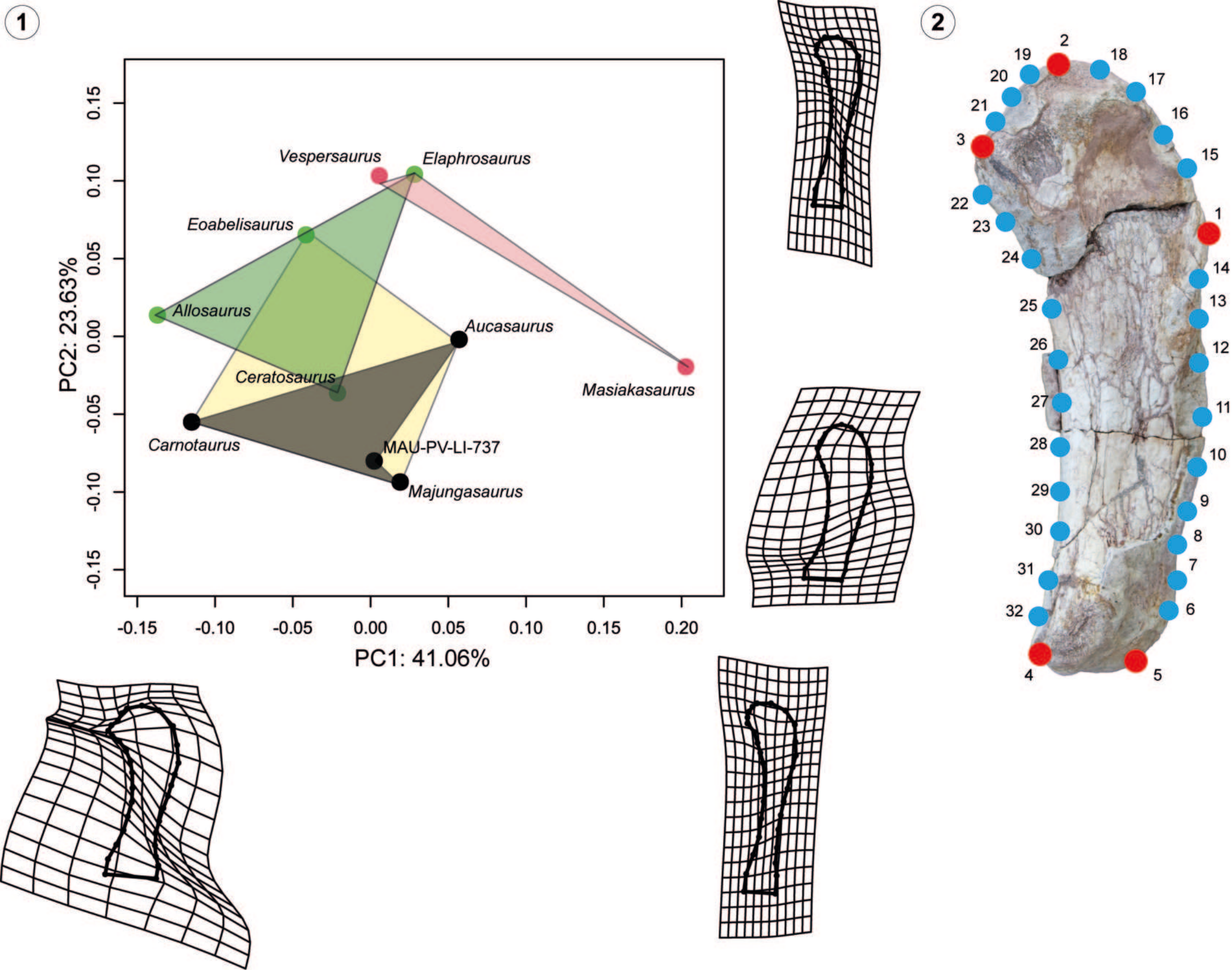
1
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Vespersaurus
Elaphrosaurus
Eoabelisaurus
Allosaurus
Aucasaurus
Ceratosaurus
Masiakasaurus
Carnotaurus
MAU-PV-LI-737
Majungasaurus
PC2: 23.63%
PC1: 41.06%
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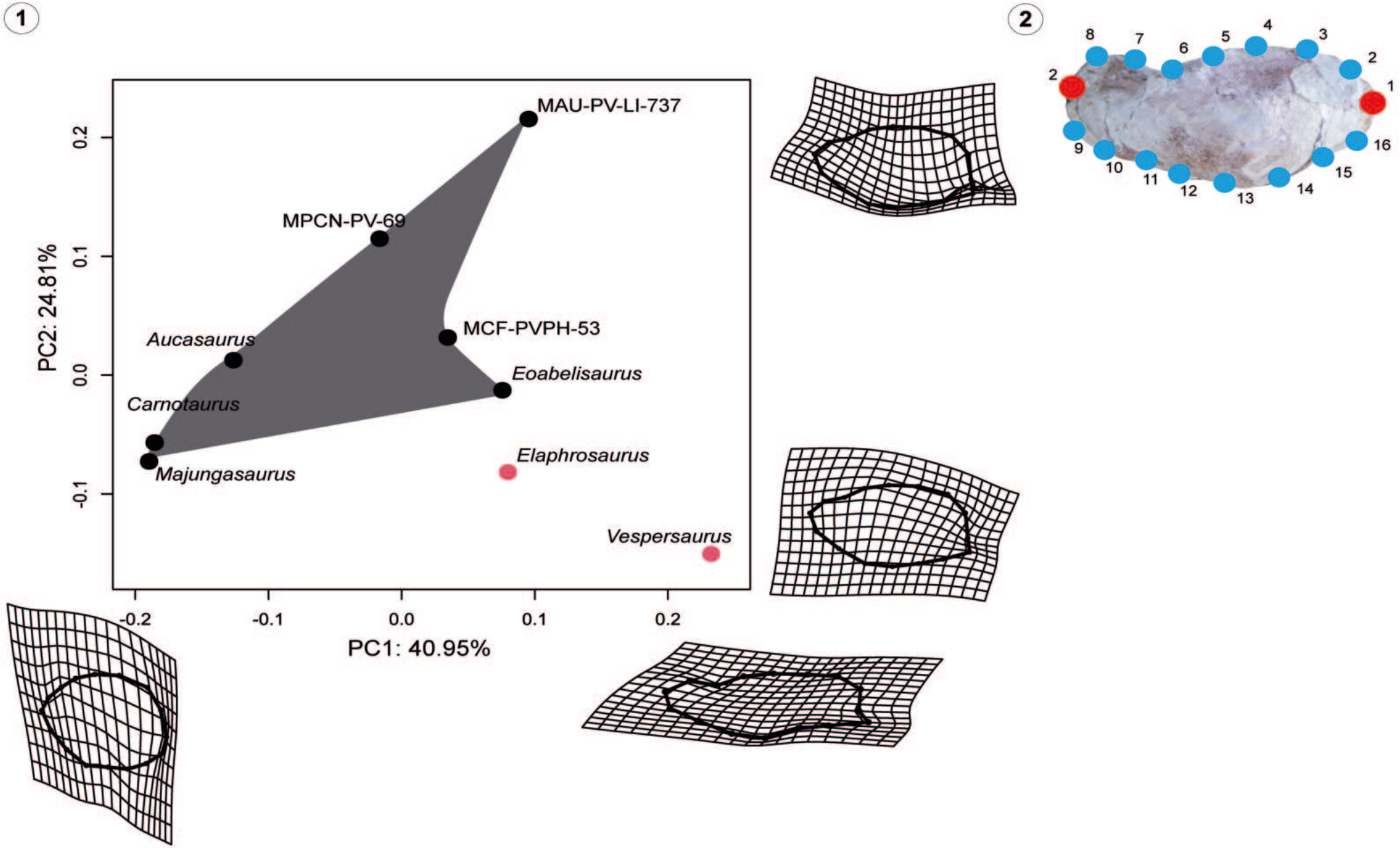
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MAU-PV-LI-737
MPCN-PV-69
MCF-PVPH-53
Aucasaurus
Eoabelisaurus
Carnotaurus
Elaphrosaurus
Majungasaurus
Vespersaurus
PC2: 24.81%
PC1: 40.95%
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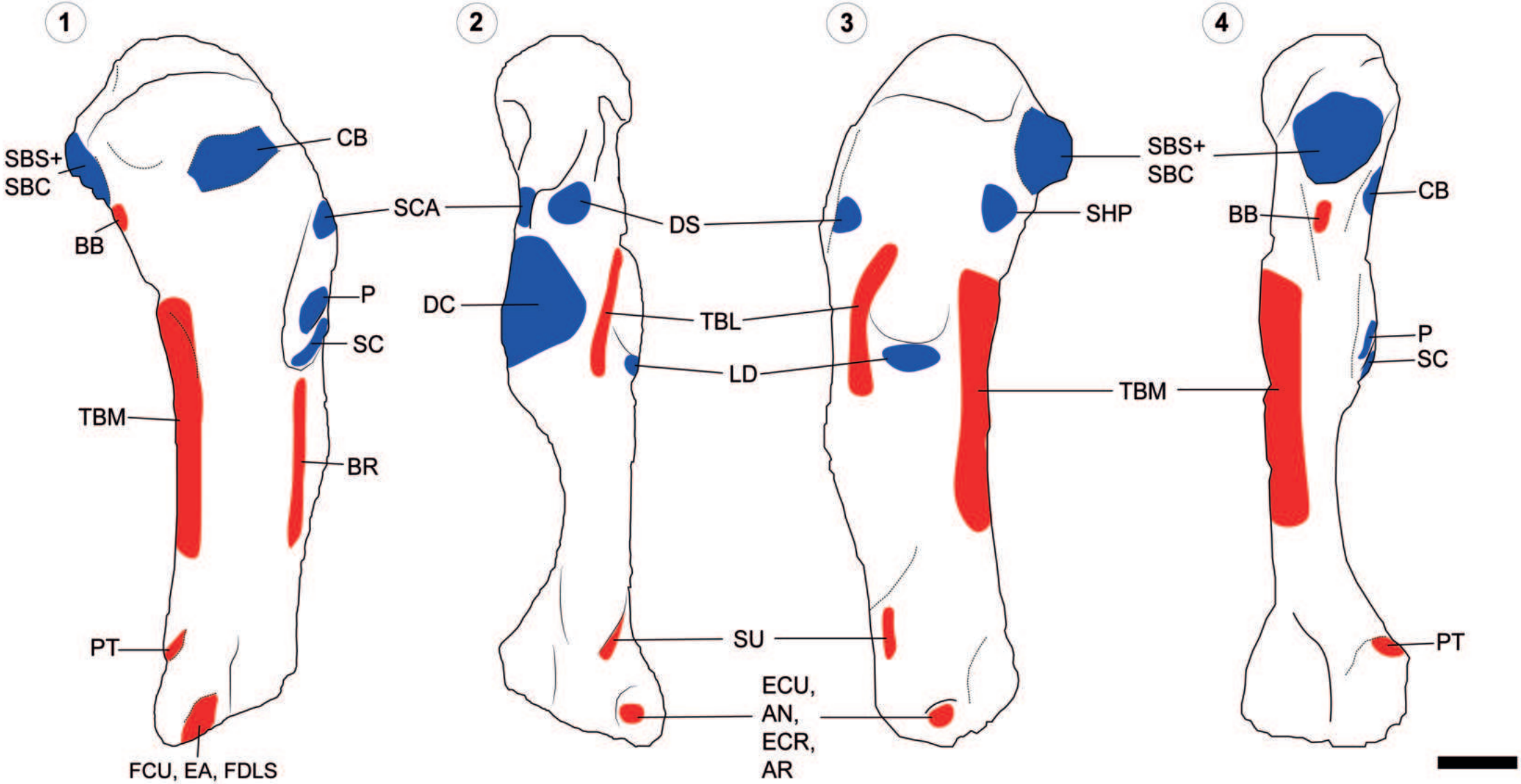
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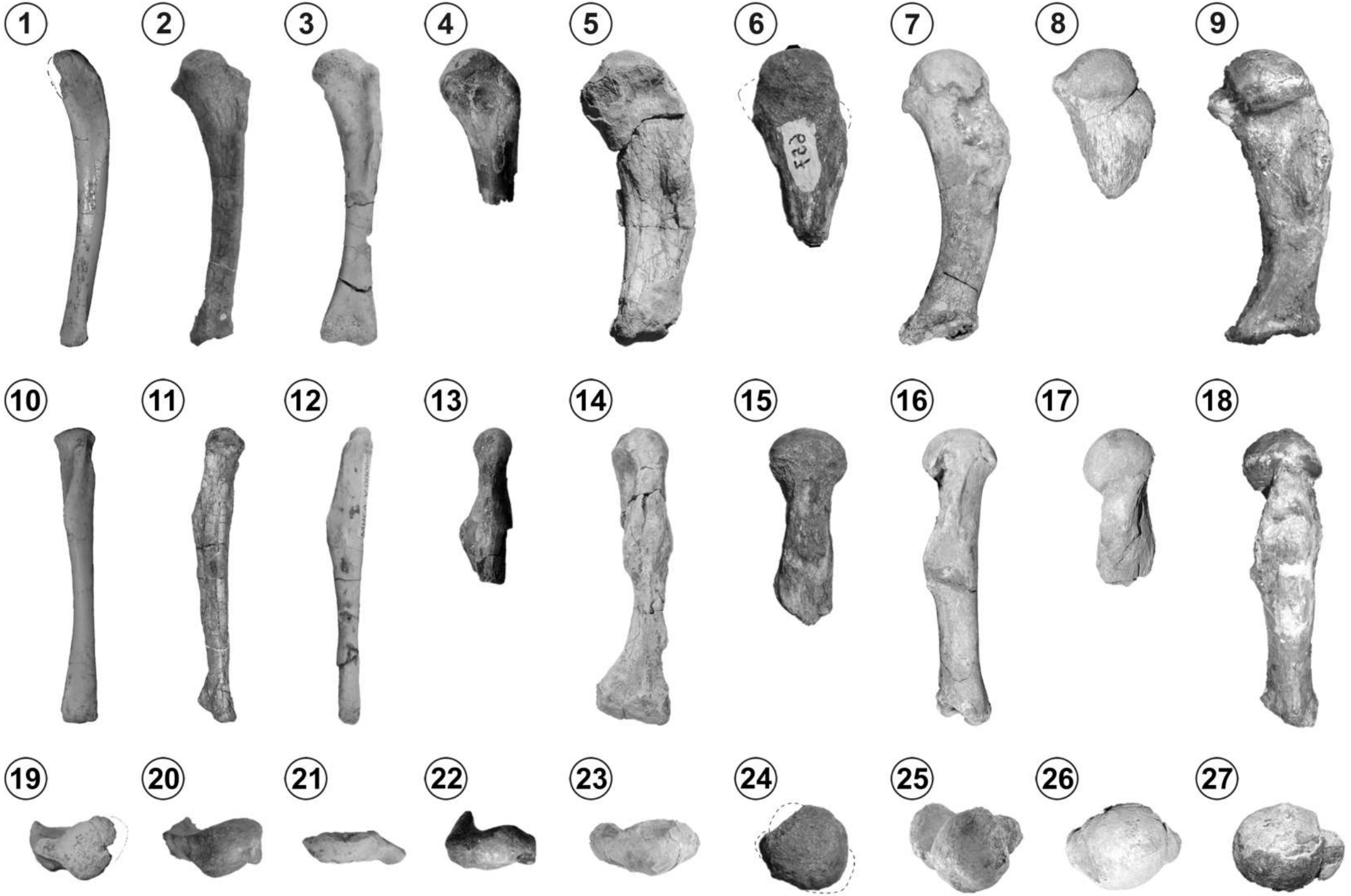
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TABLE 1. Procrustes ANOVA performed in Procrustes coordinates and 90% of PCA. Variables: Taxonomy (Abelisauridae, early diverging taxa and Noasauridae), Size of humeri and the interaction between the Taxonomy and size (Taxonomy*Size). SS: sum of square. R2: Variance explained by the factor in data. Z: effect of size.

	SS	R2	Z	SS	R2	Z
Taxonomy	0.06	0.30	1.06	0.04	0.31	0.59
Size	0.02	0.09	0.15	0.01	0.09	0.10
Taxonomy*Size	0.03	0.16	-0.23	0.01	0.15	-0.42
Residuals	0.07	0.38		0.05	0.36	
Total	0.19			0.13		