

## Osteological profile of new Mesosauridae from the Irati Formation (Paraná Basin)

### *Perfil osteológico de novos Mesosauridae provenientes da Formação Irati (Bacia do Paraná)*

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#### ABSTRACT

Mesosaurids represent one of the oldest known groups of semi-aquatic amniotes. In Brazil, they occur in the 275 Ma Irati Formation (Paraná Basin), where three monotypic genera (*Mesosaurus*, *Stereosternum*, and *Brazilosaurus*) were originally described. However, recent studies propose synonymizing these under *Mesosaurus* Gervais, 1865. In this context, we provide osteological data based on 30 samples from the LABPALEO/UFPR and IGc/USP collections, constructing detailed profiles through morphometric analysis while accounting for ontogeny and taphonomy. While our data clarify key anatomical features, preservation artifacts in many specimens introduce ambiguity when applying traditional taxonomic characters. Comparative analysis with historical descriptions reveals both consistencies and contradictions, highlighting the need for revised diagnostic criteria in mesosaurid systematics.

**Keywords:** Osteology; Marine vertebrates; Morphometric analysis; Taphonomy; Ontogeny.

#### RESUMO

Os mesossaurídeos representam um dos grupos mais antigos conhecidos de amniotas semiaquáticos. No Brasil, ocorrem na Formação Irati (Bacia do Paraná) datada de 275 Ma, onde três gêneros monotípicos (*Mesosaurus*, *Stereosternum* e *Brazilosaurus*) foram originalmente descritos. Contudo, estudos recentes propõem a sinonímia destes sob *Mesosaurus* Gervais, 1865. Neste contexto, fornecemos dados osteológicos baseados em 30 amostras das coleções LABPALEO/UFPR e IGc/USP, construindo perfis detalhados através de análise morfométrica, considerando ontogenia e tafonomia. Embora nossos dados esclareçam características anatômicas-chave, artefatos de preservação em muitos espécimes introduzem ambiguidade na aplicação de caracteres taxonômicos tradicionais. Análises comparativas com descrições históricas revelam tanto consistências quanto contradições, destacando a necessidade de critérios diagnósticos revisados para a sistemática dos mesossaurídeos.

**Palavras-chave:** Osteologia; Vertebrados marinhos; Análise morfométrica; Tafonomia; Ontogenia.

## INTRODUCTION

Mesosaurids are a fossil group of viviparous or ovoviviparous amniotes (Piñeiro et al., 2012a) that possibly had its origin in the Carboniferous-Permian transition (Bastos et al., 2021; Calisto and Piñeiro, 2019; Nuñez Demarco et al., 2022). They are considered as one of the first amniotes with semi-aquatic lifestyle, and these adaptations are associated with morphological and anatomical features, such as interdigital webbing, a long laterally flattened tail and nostrils close to the eyes (Houssaye, 2013; Nuñez Demarco et al., 2018; Romer, 1956). However, the phylogenetic position of the group is still uncertain to date. While some authors placed mesosaurids in the sister group of Parareptilia (MacDougall et al., 2018; Modesto, 1999; Modesto et al., 2015), others considered the group as basalmost sauropsids (Laurin and Piñeiro, 2017, 2018; Laurin and Reisz, 1995). In the literature, there are records of three monotypic genera of mesosaurids in Brazil — *Mesosaurus brasiliensis* McGregor, 1908; *Stereosternum tumidum* Cope, 1885; and *Brazilosaurus sanpauloensis* Shikama and Ozaki, 1966. Nonetheless, according to recent analyses including comparative morphometrics and ontogenetic studies, some authors implied a synonymy, stating that all mesosaurids belong to the genus *Mesosaurus tenuidens* Gervais, 1865 (Piñeiro et al., 2021).

Regarding the feeding behavioral patterns of these animals, some studies indicate that their diet was mainly composed of predation on pygocephalomorph crustaceans, based on associated fauna (Oelofsen and Araújo, 1983; Piñeiro et al., 2012b; Xavier et al., 2018) and by the presence of remains of these invertebrates in the gastric contents of mesosaurids, as well as in coprolites (Silva et al., 2017a). Dietary shifts across ontogenetic stages are further documented by Carlisbino et al. (2024) through tooth microanatomical studies. The authors report that juveniles possess shorter, sturdier teeth unsuitable for actively piercing prey skin, whereas adults develop elongated but more fragile dentition. Another interesting behavior of the group, which was described through *Mesosaurichnium natans* trace fossil, is associated with the habit of diving close to the bottom of the sea in which they lived in order to get momentum or change direction while swimming (Da Silva and Sedor, 2017; Sedor and Da Silva, 2004). This swimming behavior was attributed to the fact that mesosaurids could not reach high speeds below water due to environmental factors, such as extreme saline conditions (Villamil et al., 2016). This environmental condition probably selected evolutionary adaptations related to buoyancy control in the water column, through the development of pachyosteosclerosis in bones (Houssaye, 2013; Nuñez Demarco et al., 2018).

The taphonomic grades of mesosaurid samples are varied, ranging from complete skeletons to pavements with thousands of disarticulated bones. For such differences, Soares (2003) proposed three taphofacies to explain mass mortality caused by storm events, followed by reworking of

biogenic and sedimentary materials on Irati-Whitehill sea deposition. Xavier et al. (2018) also verified the assemblage of storms before transgressive system tracks (TST) sequences, through analysis of outcrops and boreholes from the Irati Formation in Rio Grande do Sul state. Differently, Piñeiro et al. (2012c) described the Mangrullo Formation of Uruguay as a low-energy environment, according to the deposition of this *Konservat-Lagerstätte*. Instead of mass mortality induced by storms events, the authors proposed gradual environmental changes that were possibly caused by scarce rainfall periods and volcanic eruptions (Piñeiro et al., 2012c). The Kungurian anoxic events and Choiyoi magmatism identified by Cagliari et al. (2022) may represent an additional factor contributing to climatic changes, triggering mesosaurid mass mortality in the Irati-Whitehill sea. This is further supported by the presence of bentonite layers within the Irati Formation, which record synchronous volcanic ashfall accumulations (Silva et al., 2017b). The deposition occurred during late Artinskian to early Kungurian (Bastos et al., 2021; Cagliari et al., 2022; Holz et al., 2010; Rocha-Campos et al., 2019; Santos et al., 2006), maintaining an epeiric sea that was characterized by shallow waters with a pronounced oxygen gradient between surface and bottom (Oelofsen and Araújo, 1983). Thus, five different stages of evolution were described with changes in salinity, increasing input of terrestrial matter and algal bloom, leading to widespread anoxia and abrupt ecological changes until its demise (Bastos et al., 2021). Thereby, distinct sedimentary depositional facies in the Paraná and Karoo basins correlate with similar preservation modes of these taxa, as evidenced by comparable biostratigraphic distributions (Lavina et al., 1991; Oelofsen and Araújo, 1983; Piñeiro et al., 2012c; Soares, 2003).

In South America, samples of mesosaurids are found along a large part of the margins of the Paraná Basin, from the south, southeast, and central-west regions of Brazil to some areas of Uruguay and Paraguay (Filippi, 2001; Oelofsen and Araújo, 1983; Piñeiro et al., 2021). However, many fossil samples are also found in South Africa and Namibia, in correlated geological units of the Karoo Basin. This distribution is important evidence for the physical connection between South America and Africa during the Paleozoic (Oelofsen and Araújo, 1983).

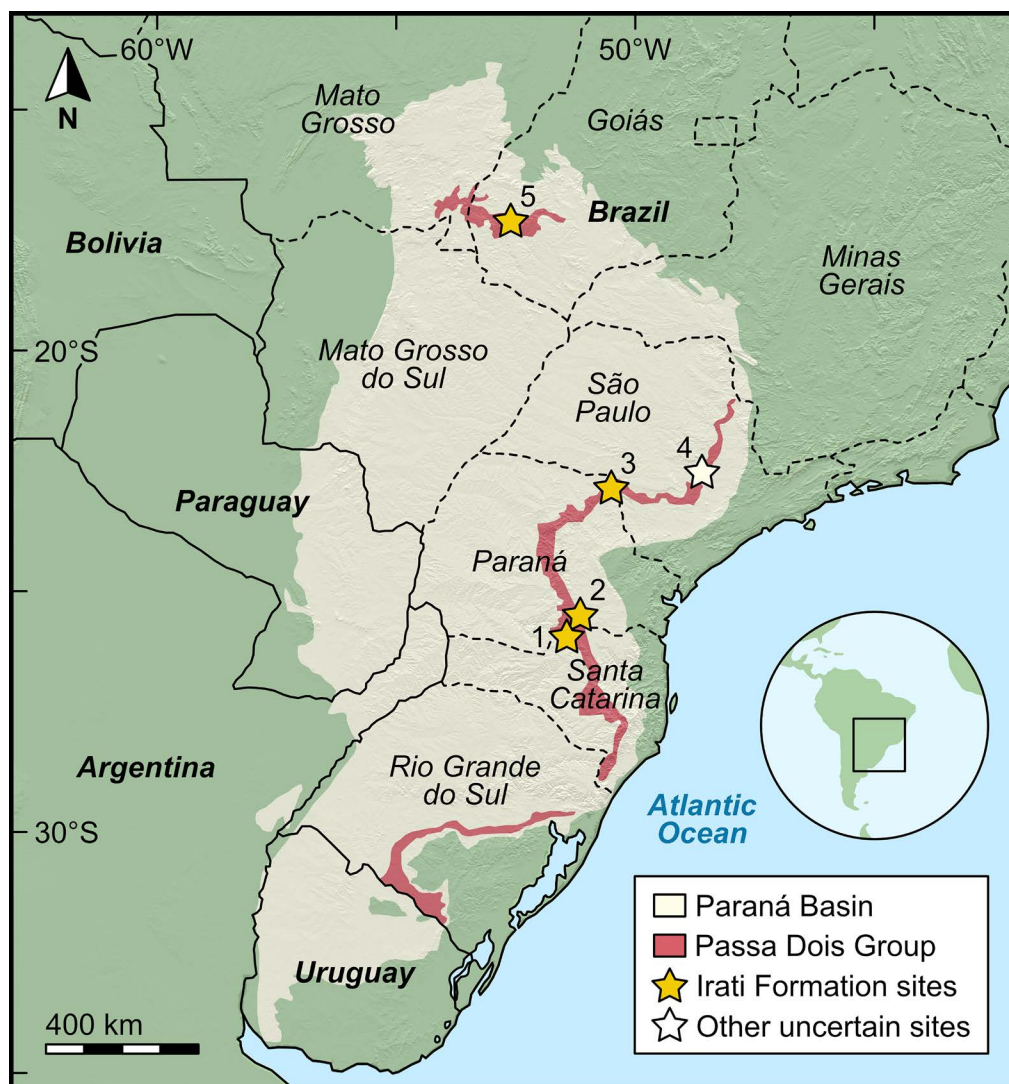
Despite the paleontological significance of this group, many questions remain unresolved and could benefit from the description of new material. Here, we describe additional mesosaurid specimens housed in the collections of Laboratório de Paleontologia of Universidade Federal do Paraná (LABPALEO/UFPR) and Museu de Geociências of Universidade de São Paulo (IGc/USP) analyzing them through established morphometric, taphonomic and ontogenetic frameworks. By constructing osteological profiles for these specimens, we compare our observations with prior descriptions of Brazilian material. Therefore, this work provides a qualitative reappraisal of newly examined mesosaurid specimens, grounded in published criteria.

## GEOLOGICAL SETTING

The samples described in the present study were collected from rock exposures along the southeast and northwest edges of the Paraná Basin, in Brazil (Figure 1). These regions correspond to the Irati Formation, a Permian lithostratigraphic unit at the base of Passa Dois Group, which is characterized by the fossiliferous intercalation of shales and carbonates. The formation is historically divided into the Taquaral and Assistência members, which preserve evidence of an ancient epeiric sea, the Irati-Whitehill Sea, which covered the western edge of the supercontinent Pangea, during the transition between marine influence and continentalization of the Paraná Basin (Barbosa and Gomes, 1958; Holz et al., 2010; Milani et al., 2007). Such strata are dated to the early Kungurian (Rocha-Campos

et al., 2019; Santos et al., 2006) and are coeval to the Huab Formation in Namibia, the Mangrullo Formation in Uruguay, the San Miguel Formation in Paraguay, and the Whitehill Formation in South Africa (Oelofsen and Araújo, 1983; Padula, 1968; Stollhofen et al., 2000).

In the basal portion of the Irati Formation, the Taquaral Member groups mainly silty shales with subordinate intercalations of sandstones, which include some records of algae, acritarchs, crustaceans, and disarticulated remains of vertebrates (Chahud and Petri, 2013, 2016). In turn, the Assistência Member, at the top of the formation, is characterized by a richly fossiliferous succession of black bituminous shales and dolomitic limestones, which are well known for their abundance of mesosaurid remains (Araujo, 2001; Hachiro, 1991).



**Figure 1.** Geological map of the Passa Dois Group in the Paraná Basin. The yellow stars (1, 2, 3 and 5) indicate the provenance of the studied mesosaurid samples from known sites of the Irati Formation in the states of Goiás, Paraná, and Santa Catarina. The white star indicates an estimated geographical position for some studied mesosaurid samples from the Irati Formation in the state of São Paulo.

## MATERIAL AND METHODS

The study analyzed 30 mesosaurid specimens collected from distinct localities within the Irati Formation (Figure 1). 28 specimens are housed in the scientific collection of the Laboratório de Paleontologia at Universidade Federal do Paraná (UFPR), under catalog numbers UFPR 0369 PV, UFPR 0379 PV to UFPR 0404 PV, and UFPR 0409 PV. Additionally, 2 specimens from the Museu de Geociências collection at Universidade de São Paulo (USP) were included in the analysis: GP/2E - 296 and GP/2E - 8972.

Complete morphological measurements, descriptions, and additional data for all specimens are provided in the Supplementary Document. However, due to preservation quality and anatomical completeness, only 10 specimens were selected for detailed analysis and illustration in this text (Table 1).

An osteological study of these specimens (Figure 2) was conducted using a binocular stereomicroscope at 20×–40× magnification for bone analysis. Bone measurements were obtained with a pachymeter and cross-verified following Mariani and Romano (2017), using high-definition images processed in ImageJ software. Taxonomic interpretations were based on (1) the original descriptions of mesosaurids that recognized three genera in Brazil (Araújo, 1977; Cope, 1885; McGregor, 1908; Oelofsen, 1981; Shikama and Ozaki, 1966) and (2) recent morphometric and ontogenetic studies proposing taxonomic revisions (Nuñez Demarco et al., 2022; Piñeiro et al., 2021; Verrière and Fröbisch, 2022). All specimen illustrations were created using Procreate on iPadOS 17.2.

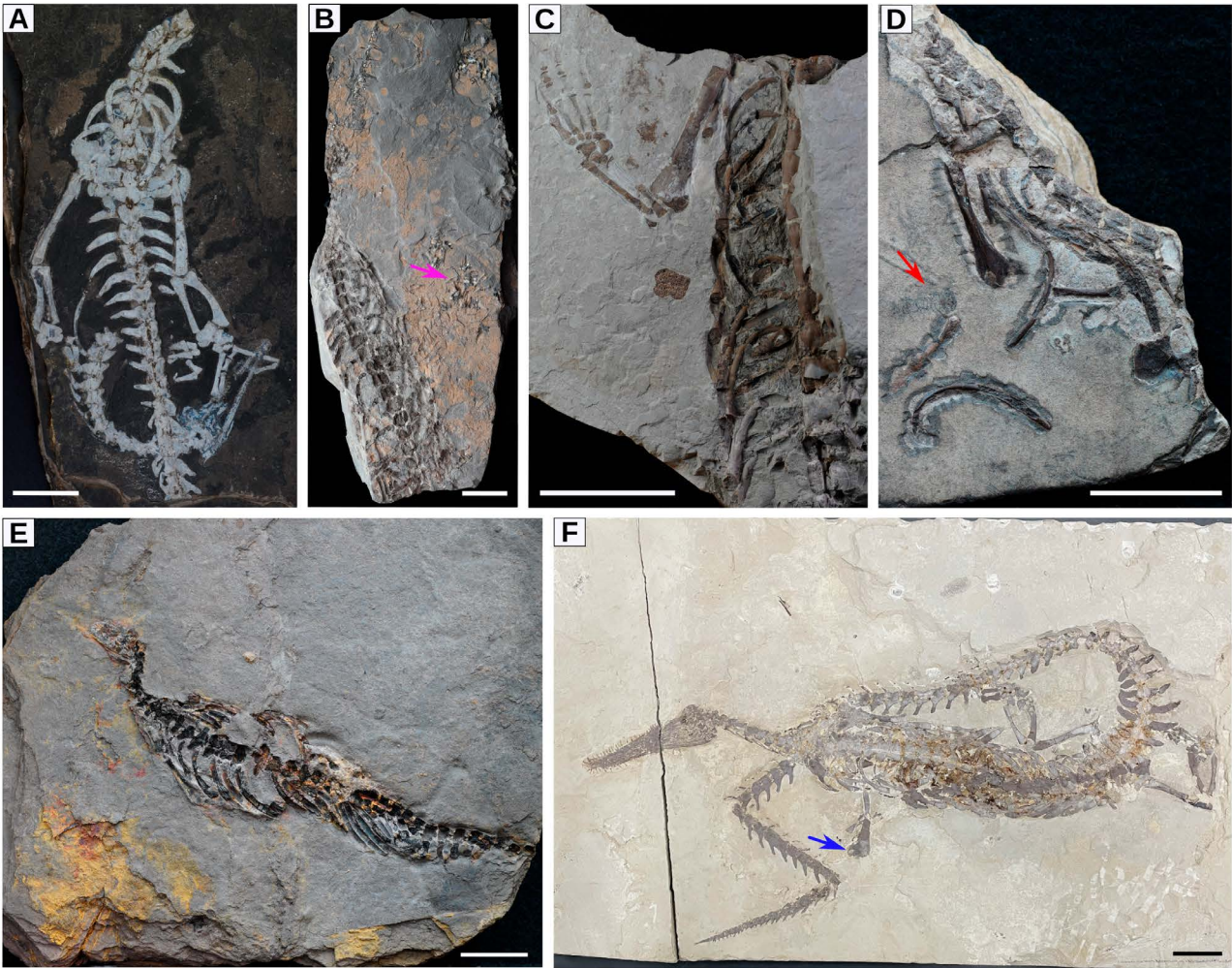
## SYSTEMATIC PALEONTOLOGY

Clade Amniota Haeckel, 1866

Family Mesosauridae Baur, 1889

**Table 1.** Summary of the analyzed samples, their origin, and fossilized remains.

Sample Number	Collection Site and Coordinates	Rock Type and Matrix Composition	Fossilized Remains
UFPR 0382 PV	Perolândia (Goiás), Sucas Quarry (17°29'02"S 52°03'14"W)	Marlstone with intercalations of shale and limestone	Presacral vertebrae, dorsal ribs, fragments of pectoral girdle, and forelimbs.
UFPR 0379 PV	São Paulo State (unknown outcrop)	Limestone with intercalated levels of black shale	Parts of mandible, presacral, sacral, and caudal vertebrae, pelvic girdle, and hind limbs.
UFPR 0384 PV	São Paulo State (unknown outcrop)	Mudstone	Presacral, sacral, and caudal vertebrae, left hind limbs (preserved in bone fragments and mold).
UFPR 0388 PV	São Paulo State (unknown outcrop)	Limestone intercalated with brownish mudstone	Presacral vertebrae, forelimbs, pubis, disarticulated ribs (fragmented). A 20 mm pygocephalomorph crustacean near ulna.
UFPR 0409 PV	São Mateus do Sul (PR) (25°53'43.0"S, 50°21'58.0"W)	Mudstone	Cranial and mandibular elements, complete cervical region, presacral and sacral regions, partial caudal region, pectoral girdle, and forelimb elements (weathered).
UFPR 0393 PV	Santa Catarina State (unknown outcrop)	Gray mudstone	Presacral vertebrae with some associated ribs, disarticulated pelvic girdle, and hind limbs (low preservation).
UFPR 0399 PV	Unknown	Dark mudstone	Mold with fragments of presacral vertebrae and ribs, right hind limb elements (low preservation).
UFPR 0401 PV	Unknown	Dark mudstone	Jaw fragment with dentary bone, disarticulated teeth, dorsal vertebrae (mold), forelimb elements, disarticulated hemal arches.
UFPR 0404 PV	Unknown	Dark limestone intercalated with mudstone	Disarticulated ribs, caudal vertebrae, neural arches, teeth, fragmented presacral vertebrae, pectoral girdle elements (fragmented), fragmented femur with epiphysis.
GP/2E - 8972	Unknown	Limestone intercalated with mudstone	Mandibular, axial skeleton nearly complete, both humeri (left occluded), femur, tibia and fibula, disarticulated and fragmented carpals.



Scale bars: 30 mm.

**Figure 2.** Studied specimens. (A) UFPR 0379 PV: weathered, disarticulated bones. (B) UFPR 0401 PV: most bones in mold and fragments; violet arrow indicates a disarticulated V-shaped hemal arch (sensu Piñeiro et al., 2021). (C) UFPR 0382 PV: articulated, well-preserved bones. (D) UFPR 0388 PV: completely disarticulated, with weathering signs; red arrow marks an unidentified pygocephalomorph crustacean (~20 mm) near the ulna. (E) UFPR 0409 PV: majority of bones in mold and fragments. (F) GP/2E-8972: nearly complete skeleton, with weathering and fragmentation; blue arrow shows the entepicondylar foramen in the right humerus (ventral view).

## Skull and mandible

Among preserved skull elements, only UFPR 0409 PV exhibits visible cranial material, though all elements are poorly preserved with taphonomic artifacts that obscure bone contacts. The skull is fragmented in lateral view, lacking rostral portions. A large but incomplete prefrontal forms the anterior orbital margin, displaying weathering-induced fragmentation. The frontal cannot be delineated; instead, a crescent-shaped prefrontal occupies the postero-dorsal orbital corner, widest posteroventrally. Beneath it, a fragmentary postorbital precludes definitive morphological assessment. Disarticulated elements in this region obscure the lower temporal fenestra (sensu Piñeiro et al., 2012b). A spatulate jugal with slight concavity lies below the orbit. Above it, possible squamosal fragments appear loosely as-

sociated with the jugal but lack sutural clarity (cf. Modesto, 2005). The inferred parietal, positioned dorsal to the squamosal, is too weathered for detailed interpretation.

The mandible is near-complete in UFPR 0379 PV (45 mm) and UFPR 0401 PV (61.2 mm). In UFPR 0409 PV, fragmentation precludes measurements of the surangular, angular, splenial, and dentary (Figures 3A – 3B). The dentary in UFPR 0379 PV shows subtle curvature (Figure 3C), whereas UFPR 0401 PV exhibits an elongated, thin, and strongly curved dentary (Figure 3D). Both specimens display faint symphyseal sutures and poorly preserved alveoli. Teeth vary between specimens: UFPR 0379 PV has small, thick-based teeth, while UFPR 0401 PV bears conical, elongated teeth. Caudally, the articular's processes are visible in UFPR 0379 PV (Figure 2A), but splenial and surangular traces are absent.

## Axial skeleton

Seventeen specimens preserve dorsal vertebrae and ribs; fragile cervical elements are typically disarticulated. Cervicals (3.5 – 5 mm) articulate with dorsals in rare cases (e.g., UFPR 0409 PV retains 11 visible fragmented cervicals). Dorsals (4.7 – 8.7 mm) occur in 21 specimens, often articulated, with ribs attached to centra in 15 specimens. Neural spines are taller than cervicals; some dorsals show transverse process relief. Ribs are thin proximally and thick distally (Figure 4), except in two specimens with uniformly thin ribs. First dorsal ribs in some specimens (e.g., UFPR 0379 PV; Figure 4B) exhibit truncated ends. Muscle-attachment ridges are prominent in UFPR 0404 PV (Figure 5A).

Six specimens preserve sacrals (6 – 8 mm), five with articulated vertebrae. Sacral ribs fuse to diapophyses, flattening mid-shaft and widening terminally. In UFPR 0379 PV, the first sacral rib is broader than the second's and appears ankylosed to the centrum (Figure 4A).

Twelve specimens show variable segments. In GP/2E – 8972, 57 caudals were counted. Anterior caudals (6.9 – 8 mm) bear transverse processes decreasing in size poste-

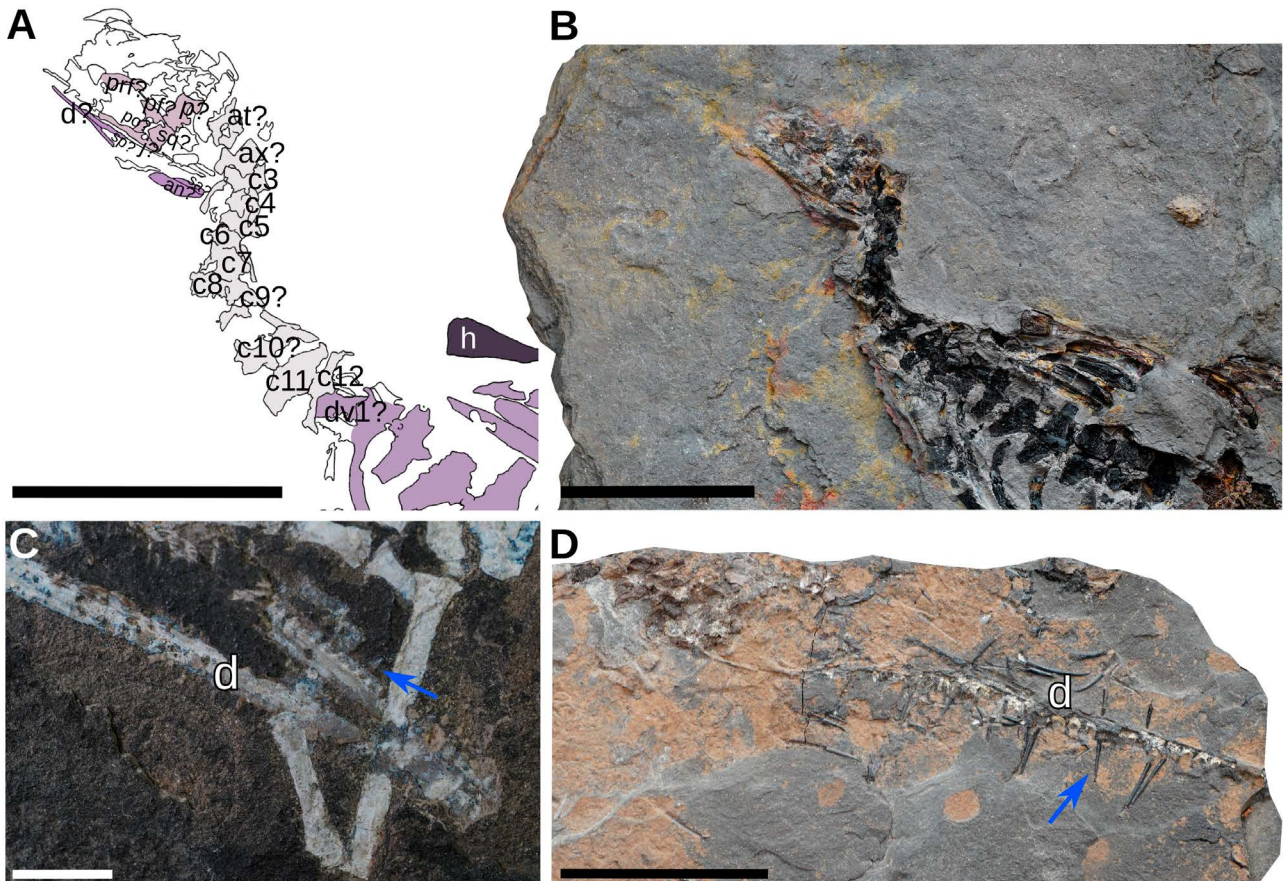
riorly (to cd6 in UFPR 0379 PV; Figure 4B). Ribs of cd7 – cd11 project anteriorly; largest ribs associate with cd3 – cd4. Hemal arches in five specimens range from articulated to fragmented, including expanded (U-shaped) and slender (V-shaped) (*sensu* Piñeiro et al., 2021) types in UFPR 0401 PV and UFPR 0404 PV.

## Pectoral girdle

Only UFPR 0404 PV preserves pectoral elements (Figures 5A – 5C): a fragmented scapulo-coracoid (articulation indeterminate) and a 28.6 mm interclavicle (diamond-shaped head, long stem, minor central ornamentation; *sensu* Piñeiro et al., 2021).

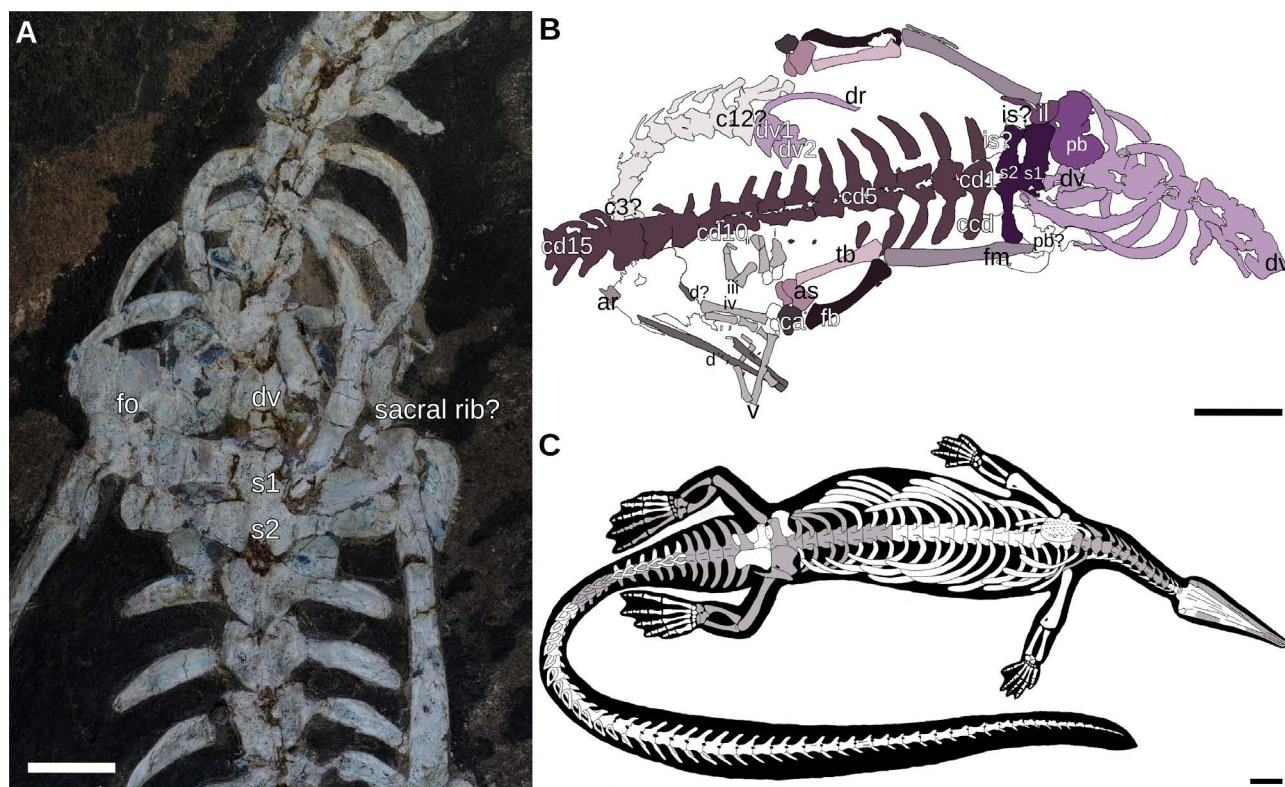
## Forelimbs

Nine specimens preserve forelimbs with variable completeness. Seven retain humerus (24 – 42.9 mm), which are slender with truncated proximal ends and distally thickened supinator processes (entepicondylar foramen visible in two specimens; Figures 2F, 5A). Radius and ulna (1:1 length



Acronyms – an: angular; at: atlas; ax: axis; c: cervical vertebrae; d: dentary; j: jugal; p: parietal; pf: postfrontal; po: postorbital; prf: prefrontal; sa: surangular; sp: splenial; sq: squamosal. Scale bars: 5 mm (C); 30 mm (A, B, D).

**Figure 3.** Cranial and mandible elements of UFPR 0379 PV, UFPR 0401 PV and UFPR 0409 PV. (A) Interpretative illustration of UFPR 0409 PV with legends of possible cranial elements identified; (B) UFPR 0409 PV presacral region; (C) a close up view of UFPR 0379 PV mandible, highlighting dentary and teeth (blue arrow); (D) a close up view of UFPR 0401 PV fragmented mandible and many articulated teeth to their alveoli (blue arrow);



Acronyms – ar: articular; as: astragalus; c: cervical vertebrae; ca: calcaneous; cd: caudal vertebrae; ccd: caudal ribs; d: dentary; dr: dorsal ribs; dv: dorsal vertebrae; fb: fibula; fm: femur; fo: obturator foramen; il: ilium; is: ischium; na: navicular; pb: pubis; s: sacral vertebrae; tb: tibia. Scale bars: 10 mm (A); 30 mm (B-C).

**Figure 4.** Osteological profile of UFPR 0379 PV. (A) close up view of pelvic girdle with dorsal, sacral and caudal vertebrae preserved, as well as both femurs; (B) Interpretative illustration of UFPR 0379 PV, displaying the entire specimen with identified bones; (C) Skeletal diagram showing recovered bones (grey) in ventral view, modified from Osborn (1903).

ratio) occur together; the ulna is slightly curved with expanded ends, while the radius is rod-like. UFPR 0382 PV (Figure 6) preserves the most complete forelimb, including carpals: intermedium, centrale, vestigial radiale, ulnare, and four distal carpals (I – IV; V disarticulated). Phalanges are mostly external molds; metacarpal I is best preserved.

## Pelvic girdle

Four specimens retain fragmentary pelvic bones. In UFPR 0379 PV, pubis and ilium (right side, ventral view) are overlain by bone fragments; the ischium is obscured by caudals (Figure 4A). The obturator foramen occurs well preserved near pelvic junctions in UFPR 0379 PV (Figures 4A) and as vestigial mold in UFPR 0404 PV (Figure 5C). The ilium's posterior projection is clearest in UFPR 0379 PV; ischial plates are incomplete in all specimens.

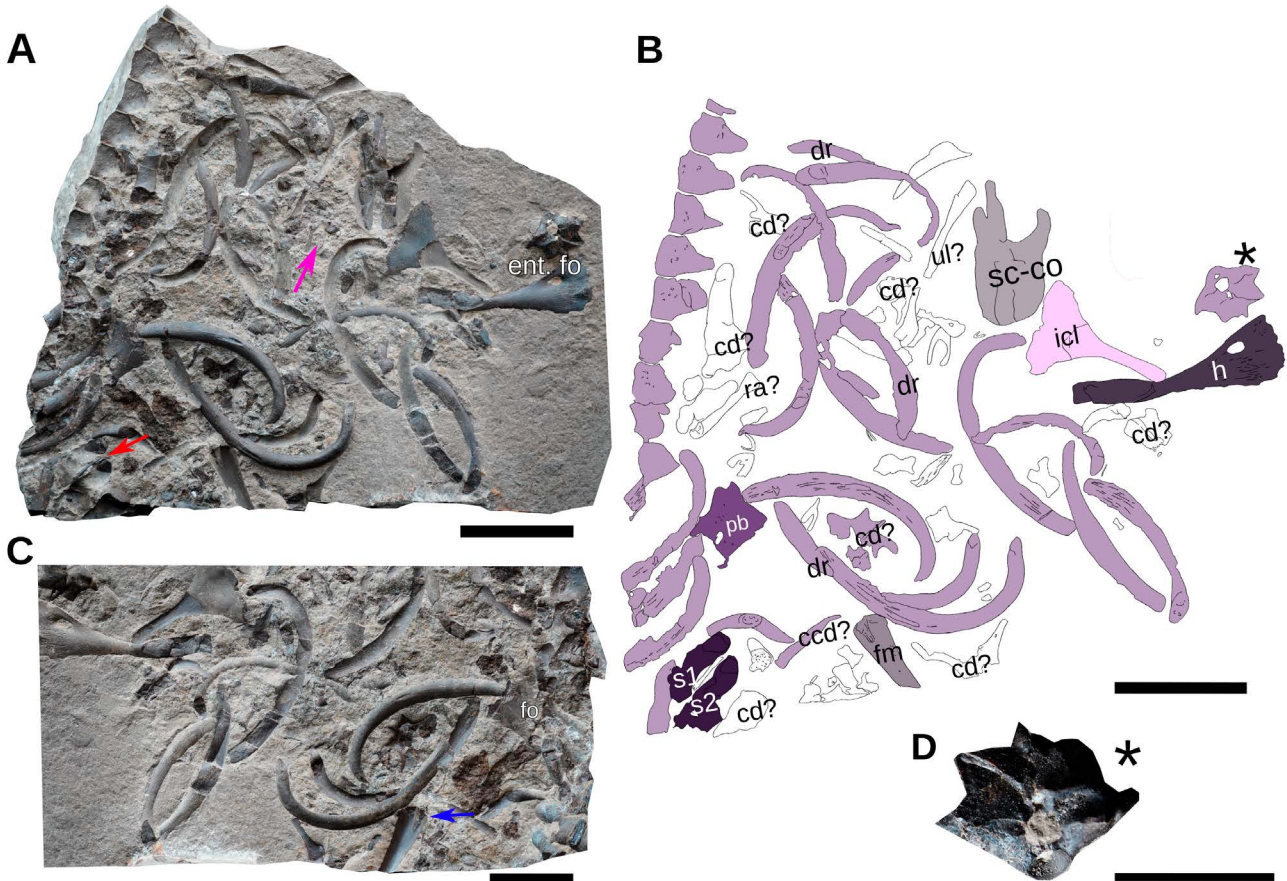
## Hind limbs

Five specimens preserve hind limbs. Femur (26 – 37.5 mm) are slender with internal trochanters (UFPR 0404 PV; Figure 5C) or flattened epiphyses (UFPR 0379 PV; Figure 4A). Tibiae (15 – 25 mm) and fibulae (16 – 24.3 mm) show a 2:1 ratio to femur. The fibula curves with

thickened epiphyses; the tibia widens proximally, tapering distally with outward expansion (Figure 7). Tarsal elements include calcaneous (three specimens) with a lateral prominence and astragalus (four specimens); broad with nearly fused navicular (Figure 7C; sensu Piñeiro et al., 2016). Five distal tarsals occur (tarsal V diminutive). A prominent foramen separates calcaneus and astragalus. Metatarsals (complete in UFPR 0379 PV and UFPR 0399 PV) accompany disarticulated phalanges; no complete phalangeal formula is preserved.

## DISCUSSION

The Irati Formation outcrops have historically yielded three recognized genera of mesosaurids (Cope, 1885; Osborn, 1903; McGregor, 1908; Shikama and Ozaki, 1966; Araújo, 1977; Oelofsen, 1981). However, recent studies have questioned the reliability of osteological characters used in these original taxonomic descriptions for differentiating taxa. This has led some authors to propose synonymizing all mesosaur taxa under a single genus, *Mesosaurus* (Piñeiro et al., 2021). Importantly, alternative explanations for the observed morphological variation have been proposed, with several studies suggesting these differences may reflect ontogenetic changes rather than taxonomic distinctions (e.g., Nuñez Demarco et al.,



Acronyms – ccd: caudal ribs; cd: caudal vertebrae; dr: dorsal ribs; ent. fo: entepicondylar foramen; fm: femur; fo: obturator foramen; h: humerus; icl: interclavicle; pb: pubis; s: sacral vertebrae; sc-co: scapulo-coracoid; ul: ulna. Scale bars: 30 mm (A - D); 10 mm (E).

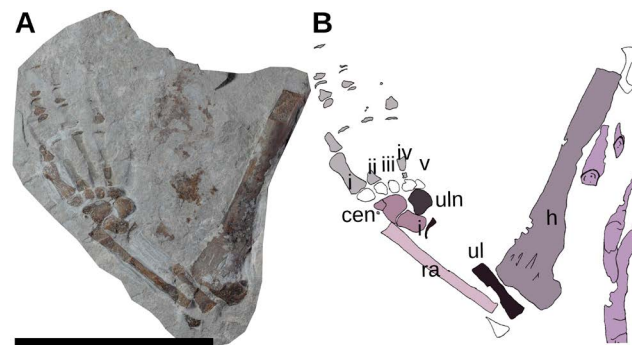
**Figure 5.** Osteological profile of UFPR 0404 PV. (A) and (C) represents part and counterpart of the specimen, respectively; (B) represents an interpretative illustration of UFPR 0404 PV; and (D) a caudal vertebra in transverse view, displaying the neural arch preserved in the middle, the vertebral foramen and transverse processes preserved in both sides. The red arrow in A is pointing to disarticulated phalanx; violet arrow in A is pointing to disarticulated U-shaped hemal arch (sensu Piñeiro et al., 2021) and blue arrow in C is pointing to the internal trochanter.

2022; Verrière and Fröbisch, 2022). Consequently, these revised interpretations must be carefully considered when conducting taxonomic assessments of new material.

### Cranial and mandibular elements:

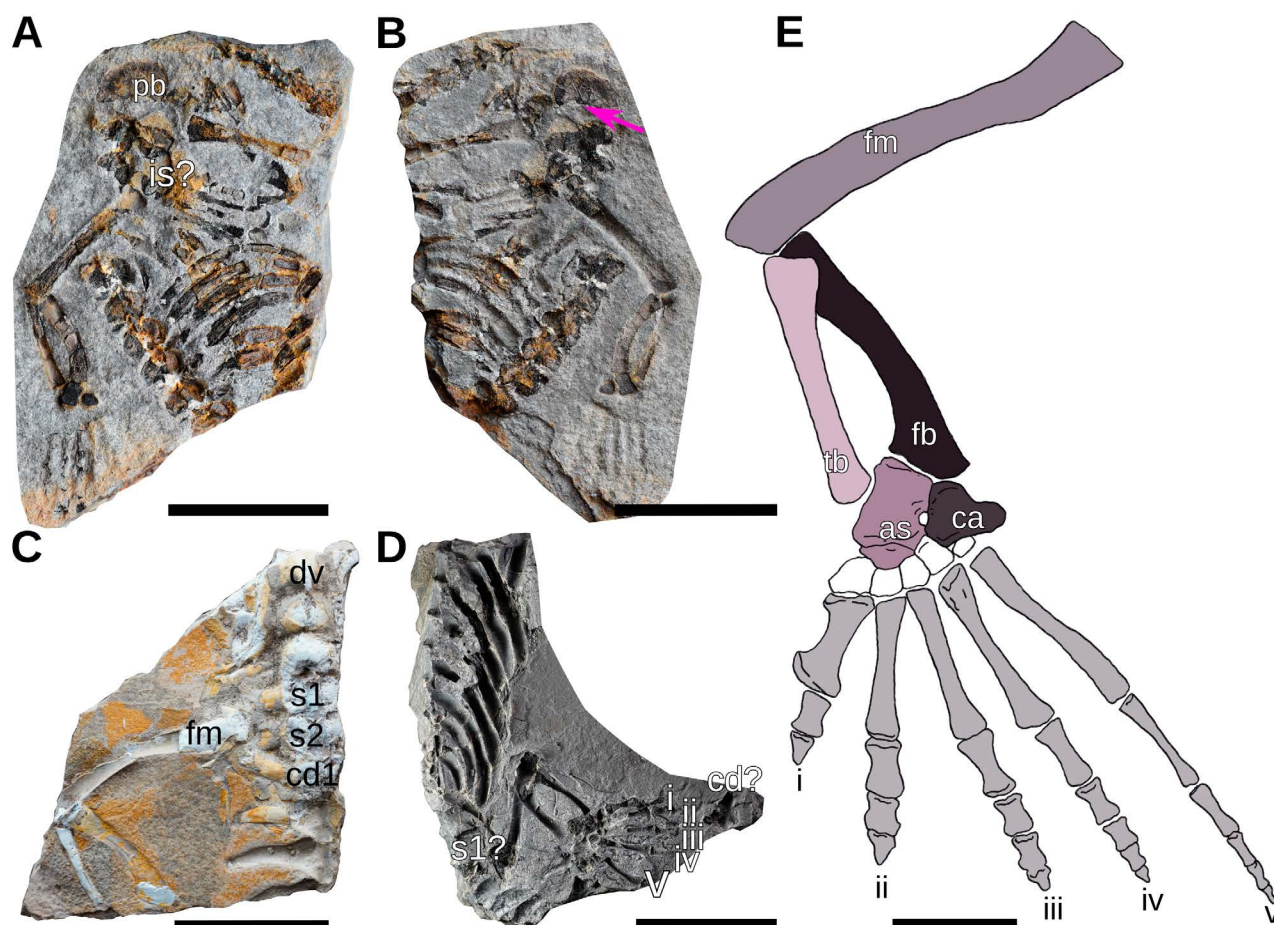
Despite efforts to characterize cranial elements in UFPR 0409 PV, preservation quality precludes definitive conclusions. Mandibular analysis reveals morphological divergence between two specimens: UFPR 0379 PV exhibits an elongated dentary with subtle curvature, while UFPR 0401 PV demonstrates pronounced elongation and curvature (Figures 3C – 3D; Romer, 1956). These differences may reflect taphonomic distortion or ontogenetic variation. The dentary symphysis, though exhibiting an extensive sagittal suture, cannot be precisely delimited or measured against the two-fifths mandibular extension ratio established for *Mesosaurus* (McGregor, 1908; Oelofsen, 1981). UFPR 0379 PV displays a shorter, triangular rostral morphology aligning with *Stereosternum* and *Brazilosaurus* (Araújo, 1977), including a spatulate snout tip resembling *Stereosternum* (Modesto, 1999). Conversely, UFPR 0401 PV pre-

sents an elongated, slender mandible consistent with *Mesosaurus* (McGregor, 1908; Araújo, 1977; Modesto, 2005). Dental morphology further differentiates the specimens: UFPR 0401 PV bears conical teeth typical of *Mesosaurus*, whereas UFPR 0379 PV has smaller, laterally compressed teeth resembling *Stereosternum* (Araújo, 1977; Oelo-



Acronyms – cen: lateral centrale; h: humerus; i: intermedium; ra: radius; ul: ulna; uln: ulnare. Scale bar: 30 mm.

**Figure 6.** Forelimb preserved on UFPR 0382 PV. (A) The entire right arm and hand preserved; (B) interpretative illustration of UFPR 0382 PV forelimb.



Acronyms – as: astragalus; ca: calcaneus; cd: caudal vertebrae; dv: dorsal vertebrae; fb: fibula; fm: femur; is: ischium; na: navicular; pb: pubis; s: sacral vertebrae; tb: tibia. Scale bars: 30 mm (A - D); 10 mm (E).

**Figure 7.** Specimens with preservation of hind limbs. (A) fossilized part of UFPR 0393 PV; (B) counterpart of UFPR 0393 PV; (C) preservation of right hind limb of UFPR 0384 PV displaying surface weathering of bones; (D) preservation of UFPR 0399 PV hind limb in mold. (E) reconstruction of hind limb modified from Piñeiro et al., 2016. The violet arrow in B is pointing to a taphonomic artifact close to the obturator foramen on the pubic margin.

fsen, 1981; Modesto, 1999, 2005). However, taphonomic and ontogenetic factors complicate taxonomic assignment (Piñeiro et al., 2021), rendering definitive distinctions unreliable given preservation limitations. Since tooth variance morphology may reflect an ontogeny stage regarding dietary shift (Verrière and Fröbisch, 2022; Carlisbino et al., 2024). The fragile and needle-like teeth attributed to adults are described as adaptations to catch slippery prey, like the pygocephalomorphs found alongside disarticulated bones (Carlisbino et al., 2024; Figure 2D). In contrast, positive allometry in skull, mandible, and tooth size (Verrière and Fröbisch, 2022) could not be assessed in these samples due to taphonomic alteration.

### Axial skeleton:

Presacral vertebrae counts vary historically: 29 – 34 for mesosaurids (Romer, 1956), with *Mesosaurus* reportedly exhibiting 29 (Araújo, 1977) or 33 – 34 vertebrae (Modesto, 1999), and *Stereosternum/Brazilosaurus* displaying 33

– 35 (Araújo, 1977; Modesto, 1999; Sedor and Ferigolo, 2001). UFPR 0409 PV preserves 33 presacrals (12 cervical, 21 dorsal) and GP/2E – 8972 preserves 32 presacrals (9 cervical visible and 23 dorsal; see Supplementary Document). Dorsal ribs exhibit pachyostosis (thinner proximally, wider distally), a trait documented in *Mesosaurus* and *Stereosternum* (Osborn, 1903; McGregor, 1908; Romer, 1956; Araújo, 1977), though *Brazilosaurus* specimens show reduced pachyostosis (Piñeiro et al., 2021). Two specimens exhibit atypically thin ribs (Figures 2D, 7A – 7B), contrasting with the banana-shaped ribs of others (Figures 2A, 2C – 2E, 5A, 7D). Sacral vertebrae (n=6 specimens) are fused and ankylosed to ribs (Sedor and Ferigolo, 2001; Piñeiro et al., 2021), with the first sacral rib consistently wider than the second (McGregor, 1908; Oelofsen, 1981; Sedor and Ferigolo, 2001). A gap for ilium accommodation (Oelofsen, 1981) is visible in UFPR 0379 PV (Figure 4A). We found no support for sexual dimorphism in sacral rib morphology (Piñeiro et al., 2021); preserved ribs in UFPR 0379 PV and GP/2E – 8972 display linear/columnar forms, not the distally expanded shape proposed as dimorphic. Caudal

vertebrae estimates exceed 60 across all genera (Osborn, 1903; McGregor, 1908; Oelofsen, 1981; Sedor and Ferigolo, 2001; Piñeiro et al., 2021). GP/2E – 8972 preserves 57 caudals, though few are occluded by dorsals and ribs. Vertebral size decreases posteriorly, with caudal ribs anteriorly oriented from the sixth vertebrae (Oelofsen, 1981; Modesto, 1999; Sedor and Ferigolo, 2001). Hemal arches (observed from fifth caudal onwards; Romer, 1956) include V- and U-shaped disarticulated morphotypes (Figures 2B, 5A, respectively), likely taphonomic variants (Piñeiro et al., 2021).

### Appendicular skeleton:

The diamond-shaped interclavicle head in UFPR 0404 PV (Figure 5A) matches adult descriptions of *Mesosaurus* (Piñeiro et al., 2021), contrasting with triangular juvenile forms. This feature's taxonomic utility is debated due to ontogenetic influences (Modesto, 1996; Piñeiro et al., 2021). The entepicondylar foramen, absent in some *Stereosternum* reports (Modesto, 1999), may reflect taphonomic loss (Piñeiro et al., 2021); it is confirmed in two of seven humerus here (Figures 2F, 5A). On forelimbs, radius/ulna ratios (2:1) are consistent across taxa (McGregor, 1908; Romer, 1956; Araújo, 1977; Oelofsen, 1981). Carpal counts in UFPR 0382 PV (three proximal, five distal; Figure 6A) suggest a young adult stage observed in *Mesosaurus* (Nuñez Demarco et al., 2022). Puboischiatic plates and ilia morphology are also conserved among the three genera (Osborn, 1903; McGregor, 1908; Romer, 1956; Araújo, 1977). Obturator foramen development correlates with ontogeny in *Mesosaurus*: deep notches indicate juveniles, while fully formed foramen suggests adults (Piñeiro et al., 2021). Two of four specimens preserve foramen in the pubis (Figures 4A, 5C), though taphonomic artifacts resembling a well-developed foramen are present in UFPR 0393 PV (Figure 7B). As for hind limbs, the 1:2 tibia/femur ratio (Nuñez Demarco et al., 2018, 2022) aligns with semi-aquatic adaptations and is consistent in our samples (Supplementary Document). Tarsal ontogeny is evidenced by navicular-as-tragalus sutures in UFPR 0393 PV (Figure 7A; Piñeiro et al., 2016; Nuñez Demarco et al., 2022). Lastly, the reduced size of the fifth distal tarsal in UFPR 0379 PV may reflect late-stage isometric growth patterns in *Mesosaurus* (Nuñez Demarco et al., 2022), potentially indicating a young-adult ontogenetic stage for this specimen. This interpretation aligns with teeth and mandibular morphologies described herein, though the assessment remains uncertain given preservation constraints affecting other diagnostic characters.

### CONCLUSIONS

Our osteological analysis of 30 mesosaurid specimens from the LABPALEO/UFPR and IGc/USP collections compared morphological characters across the three historically recognized genera. The results reveal significant inconsistencies when applying traditional diagnostic

criteria, as recent morphometric and ontogenetic studies (Piñeiro et al., 2021; Nuñez Demarco et al., 2022; Verrière and Fröbisch, 2022) have challenged their reliability. Main issues include: (1) overlapping morphological variation between putative genera that may reflect ontogenetic stages rather than taxonomic distinctions; (2) diagnostic characters frequently obscured by preservation (e.g., external molds, loss of fragile structures and surface weathering prior to fossilization); and (3) insufficient consideration of taphonomic biases in original descriptions, potentially compromising morphological interpretations.

While recent studies advocate for synonymizing all mesosaurids under *Mesosaurus* Gervais, 1865 (Piñeiro et al., 2021), our analysis reveals persistent ambiguities in genus-level diagnostics. The examined specimens display morphological variation that could support either as taxonomic distinctions or ontogenetic variation. Given these unresolved controversies and preservation limitations, we retain all specimens at the family level (Mesosauridae Baur, 1889), as a comprehensive taxonomic revision falls beyond the scope of this study.

Conversely, this work underscores the need for revised diagnostic criteria in mesosaurid systematics. By documenting osteological variation across our sample, we identify key challenges in their taxonomic interpretation due to taphonomic artifacts and ontogenetic factors.

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