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SHORT COMMUNICATION

A NEW PROTEROCHAMPSID *CHANARESUCHUS ISCHIGUALASTENSIS* (DIAPSIDA, ARCHOSAURIFORMES) IN THE EARLY LATE TRIASSIC ISCHIGUALASTO FORMATION, ARGENTINA

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The proterochampsids are a group of crocodile-like archosauriforms usually considered as one of the potential successive sister taxa of the crown group Archosauria (e.g., Sereno and Arcucci, 1990; Sereno, 1991; Dilkes and Sues, 2009; Ezcurra et al., 2010). The clade is currently endemic to the late Middle and early Late Triassic of South America. The best-known proterochampsids come from the Chañares and Ischigualasto formations, which belong to the Ischigualasto-Villa Unión Basin (Fig. 1), which formed during the breakup of Gondwana (Uliana and Biddle, 1988; Ramos and Kay, 1991). The tetrapod assemblage from the Chañares Formation (Anisian–early Carnian; Desojo et al., 2011) has been usually interpreted to differ from that of the Ischigualasto Formation (late Carnian–earliest Norian; Martínez et al., 2011), and this traditional view also applies for proterochampsids. In the Chañares Formation, the proterochampsid genera *Chanaresuchus*, *Gualosuchus*, and *Tropidosuchus* (Romer, 1971, 1972; Arcucci, 1990) are documented, whereas in the Ischigualasto Formation only the genus *Proterochampsa* has been reported (Reig, 1959). The latter highlighted a complete replacement at a generic level among these proterochampsid assemblages in southwestern Pangaea. However, an almost complete proterochampsid skeleton from the Late Triassic Ischigualasto Formation is given a preliminarily description here and assigned to the traditionally Middle Triassic genus *Chanaresuchus* (cf. Sill et al., 1994). Accordingly, the new proterochampsid record reported here changes the pattern of macroevolutionary history of the group during the Middle to Late Triassic in southwestern Pangaea.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAUROMORPHA von Huene, 1946
ARCHOSAURIFORMES Gauthier, 1986
PROTEROCHAMPSIDAE Sill, 1967
CHANARESUCHUS Romer, 1971

Emended Diagnosis—Proterochampsid archosauriform with the following combination of characters: skull ornamented by longitudinal crests and depressions on the dorsal surfaces of the premaxillae, maxillae, and nasals; lateral fossa in the centra of presacral vertebrae; low deltopectoral crest on the humerus; and absence of phalanges on pedal digit V.

CHANARESUCHUS ISCHIGUALASTENSIS, sp. nov.
(Figs. 2–4)

Etymology—The specific epithet refers to the Ischigualasto Formation, the stratigraphic unit producing the new specimen.

Holotype—PVSJ 567, an articulated incomplete skeleton including skull with lower jaws, vertebral series lacking the distalmost caudals, pectoral girdle, both partial humeri, partial pelvic girdle, both femora, tibiae, fibulae, and pes, and some gastralia (Figs. 2–4).

Diagnosis—*Chanaresuchus* species characterized by the following autapomorphies: basal tubera wide (basal tubera width/parabasisphenoidal complex axial length ratio of 0.31) with rostrolateral contour transversely oriented; paroccipital processes distally expanded; articular surface of caudal prezygapophyses elliptical and notably anteriorly developed; astragalus lacking perforations in the posterior sulcus; and ornamentation of dermal plates consisting of only a longitudinal sulcus.

Type Locality and Horizon—Valle Pintado, Hoyada de Ischigualasto, Ischigualasto Provincial Park, San Juan Province, Argentina (Fig. 1). Cancha de Bochas Member (Currie et al., 2009), Ischigualasto Formation (late Carnian–earliest Norian; Martínez et al., 2011), Ischigualasto-Villa Union Basin (Romer and Jensen, 1966).

DESCRIPTION

Skull

The skull of PVSJ 567 is comparable to that of *Proterochampsa barrionuevoi* (Sill, 1967) and *Chanaresuchus bonapartei* (Romer, 1971), in being dorsoventrally compressed, subtriangular in outline, and with an anteriorly elongated snout (Fig. 2). The skull is strongly ornamented by several longitudinal crests and depressions present on the dorsal surfaces of the premaxillae, maxillae, and nasals. These crests and depressions acquire a radial pattern of ornamentation on the dorsal surfaces of the parietals and frontals. This ornamentation is very similar to *Chanaresuchus bonapartei*, but different from the rounded crests on the skull of *Proterochampsa*. The orbits are placed dorsally, similar to the condition in *Chanaresuchus bonapartei* (Romer, 1971) and *Proterochampsa*. The external nares are located near to the midline of the snout, and nearly on the top of the snout, as in the majority of proterochampsids. As in other proterochampsids, the small supratemporal fenestrae are dorsally oriented, the infratemporal fenestrae are exposed laterally, and the teeth are labiolingually compressed, similar to *Chanaresuchus bonapartei*. The teeth of *Chanaresuchus ischigualastensis* lack striated enamel and wear facets. There are six premaxillary, and eight maxillary, teeth. The maxillary teeth are the longest, as in *Chanaresuchus bonapartei* and *Proterochampsa*. In ventral view, the skull has a secondary bony palate composed of the premaxillae, maxillae, and palatines (Fig. 3), similar to *Chanaresuchus bonapartei* and *Proterochampsa*. In this view, the posterolateral development of the pterygoid of *Chanaresuchus ischigualastensis* contacts the ectopterygoid laterally, similar to *Chanaresuchus bonapartei*. The complete braincase is ventrally exposed; it is axially short and horizontally oriented, thereby differing from the axially longer braincase of *Chanaresuchus bonapartei* and *Proterochampsa.* The basal tubera are wide, with a basal tubera width/parabasisphenoidal complex axial length ratio of 0.31,

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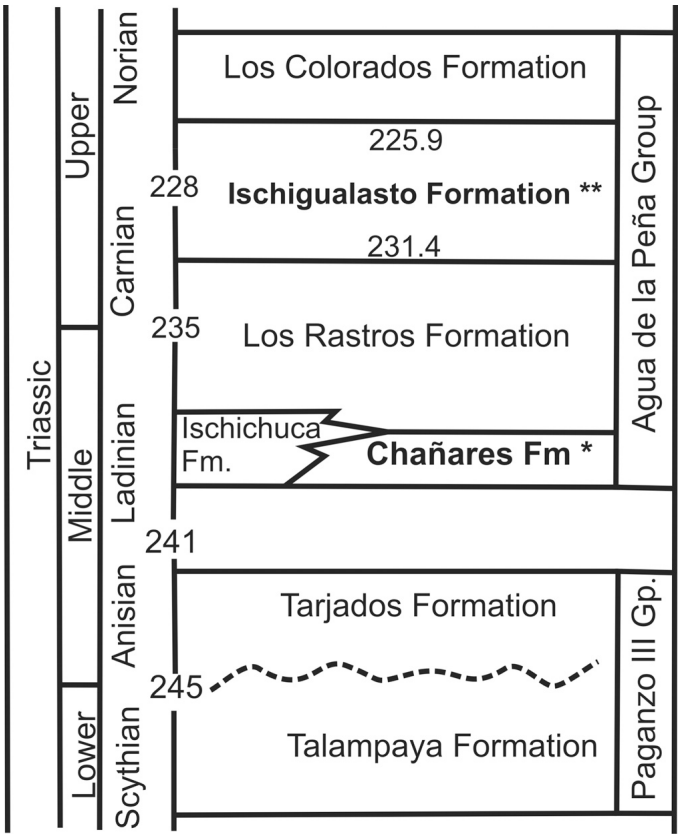

FIGURE 1. Scheme of the Triassic lithostratigraphy and chronostratigraphy in the Ischigualasto-Villa Unión Basin. The Triassic time scale is based on Geological Survey from EEUU. Modified from Rogers et al. (2001), scale time from Martínez et al. (2011). *Formation of origin of *Chanaresuchus bonapartei*; **formation of origin of *Chanaresuchus ischigualastensis*.

which is wider than in *Chanaresuchus bonapartei* (0.22) .The paroccipital processes are distally expanded, differing from the unexpanded processes of *Chanaresuchus bonapartei*.

Axial Skeleton

The postcranial axial skeleton is well preserved and most of its elements are articulated, but suffered strong post-mortem deformation. There are 21 articulated vertebrae, corresponding to nine cervicals, 12 dorsals, two sacrals, and the 18 proximal-most caudals (the distal-most caudal vertebrae are not preserved). The presacral vertebrae of *Chanaresuchus ischigualastensis* are anteroposteriorly short, dorsoventrally tall, amphicoelous, and have a transverse depression at the middle of centrum. The neural spines are rectangular in lateral view (Fig. 4D), differing from the rectangular neural spines of *Chanaresuchus bonapartei*. The anterior cervical ribs are gracile, bicephalous, and ventrally have a posterior sulcus, similar to *Chanaresuchus bonapartei*. The posterior cervical ribs are similar to the anterior ones, but they are remarkably more robust and anteroposteriorly compressed. The dorsal ribs exhibit proximal ends that are more transversely expanded, and shafts that are longer, than those of the cervicals, as occurs in *Chanaresuchus bonapartei*. The prezygapophyses of the caudal vertebrae are elliptical and notably anteriorly developed, differing from the circular and less anteriorly developed prezygapophyses of *Chanaresuchus bonapartei*. The gastral ribs are small, cylindrical bones distributed in a roughly parallel pattern. These bones represent the first record of a gastral series for the genus *Chanaresuchus*. These elements are smaller than the dorsal and cervicals ribs and have a constant width along their length (Fig. 4).

Appendicular Skeleton

Pectoral Girdle—The preserved pectoral girdle is composed of the right scapula, right coracoid, both clavicles, and three fragments that may belong to the interclavicle. These three fragments are situated between the two clavicles, and the lateral elements confer a 'T'-shape to this bone. The scapula and coracoid are fused to each other, and the scapular blade is tall and relatively narrow. A small elliptical tubercle, near to the scapular lip, probably corresponds to the attachment area for the triceps muscle. The glenoid cavity is elliptical and posterolaterally oriented, similar to those of other proterochampsids. The clavicle is not fused to the scapula. The coracoid of *Chanaresuchus ischigualastensis* is elliptical, similar to *Proterochampsa* (Trotteyn, 2012), but different from the subcircular coracoid of *Chanaresuchus bonapartei* (Romer, 1972). The medial surface of the coracoid is convex, its anterior edge is rounded and thin, and the posterior edge is thick. The coracoid has two surfaces, one posteroventrally oriented that forms the glenoid cavity and another anteroventrally oriented, which is the largest and has the coracoid foramen. The coracoid foramen is small and located anteromedial to the glenoid cavity.

Forelimb—The proximal ends of both humeri are preserved. They are graceful and transversely expanded, as in *Proterochampsa* and *Chanaresuchus bonapartei* (Romer, 1972). The deltopectoral crest is slight and extends parallel to the main axis of the bone, as in *Chanaresuchus bonapartei*. The preserved portion of the humeral shaft is narrow and presents an oval cross-section.

Pelvic Girdle—The pelvic girdle of PVSJ 567 is severely affected by post-mortem deformation. The acetabulum may be formed by the three pelvic bones, but it is not possible to determine if this structure is closed or open, because the heads of both femora are obscuring the region. The ilium is vertically oriented and presents a well-developed postacetabular process. The lateral surface of the iliac blade has a faint process located above the acetabulum, which forms together with the posterior process a laterodorsally concave structure (Fig. 4). The posterior process of the ilium is posteriorly long. As in the rest of the proterochampsids, the preacetabular process is very short. This process does not extend beyond the anterior edge of the acetabulum, and has a slight medial depression that should have articulated with the first sacral rib. The deformation of the pelvic region prevents us from determining if the ischia are missing or covered by other bones. Both pubes are almost complete, lacking their symphyses and obturator foramina. The pubis has a dorsoventrally extensive contact with the ilium, and forms the anteroventral portion of the acetabulum. The medial shaft of the pubis is laminar, as in *Chanaresuchus bonapartei*. The lateral edge of the pubic shaft is columnar in shape, anteriorly oriented, and posteriorly curved. The pubic tubercle is small, rough, and anterolaterally oriented.

Hind Limb—Both femora are preserved, but their proximal and distal ends are strongly compressed by post-mortem deformation, precluding detailed observation. As in all proterochampsids, the femora are sigmoid in anterior view, both ends are axially expanded, and the shafts have an oval cross-section. The femoral head is rounded and continuous with the shaft in anterior view, differing from the more angular head present in *Chanaresuchus bonapartei*. The intertrochanteric fossa is shallow and located along the proximal two-thirds of the anterior surface of the bone. The anterior trochanter and trochanteric shelf are absent. The fourth trochanter is aliform, posteromedially oriented, and located on the proximal one-third of the bone. Distal

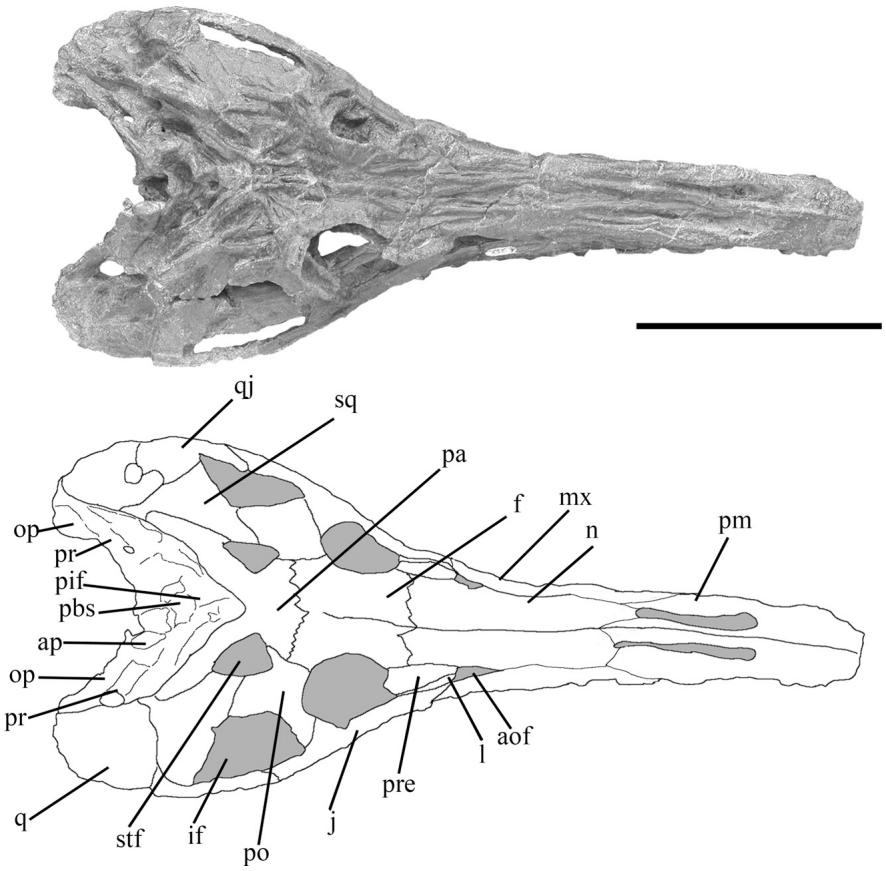

FIGURE 2. Skull of *Chanaresuchus ischigualastensis* (PVSJ 567) in dorsal view. **Abbreviations**: **aof**, antorbital fenestra; **ap**, alar process; **f**, frontal; **if**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **op**, opisthotic; **pa**, parietal; **pbs**, parabasisphenoid**; pif**, pituitary fossa; **pm**, premaxilla; **po**, postorbital; **pr**, prootic; **pre**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal; **stf**, supratemporal fenestra. Scale bar equals 5 cm.

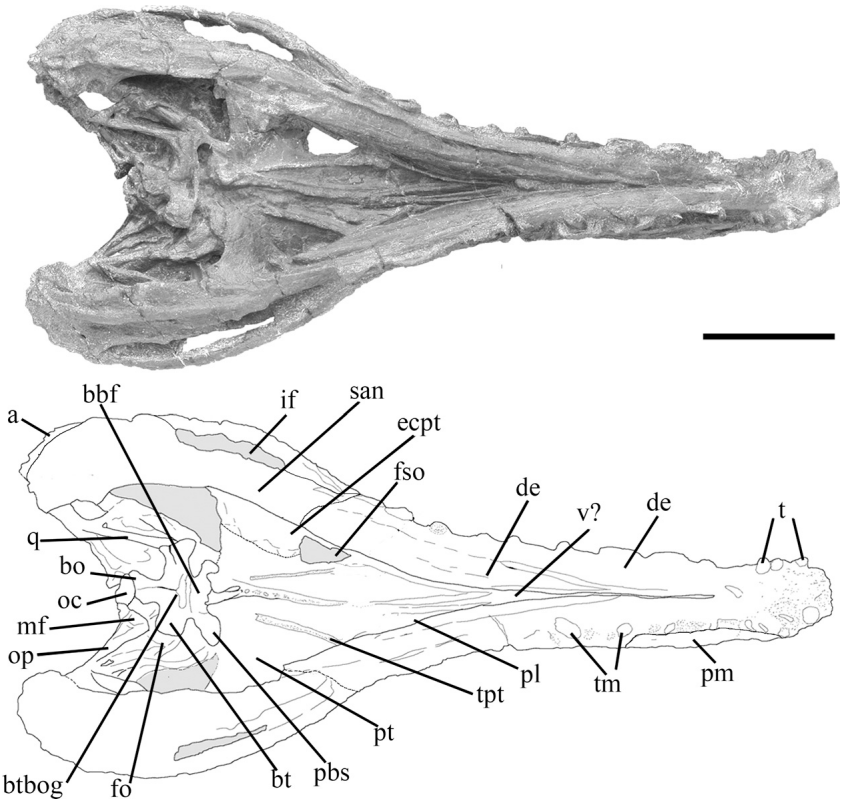

FIGURE 3. Skull of *Chanaresuchus ischigualastensis* (PVSJ 567) in ventral view. **Abbreviations**: **a**, angular; **bbf**, basioccipital-basisphenoid fossa; **bo**, basioccipital; **bt**, basal tubera; **btbog**, groove between basioccipital parts of the basal tubera; **de**, dentary; **fm**, maxillar fenestra; **ecpt**, ectopterygoid; **fo**, fenestra ovalis; **fso**, suborbital fenestra; **mf**, metotic foramen; **oc**, occipital condyle; **op**, opisthotic, **pm**, premaxilar; **pl**, palatine; **pbs**, basipterygoid process; **pt**, pterygoid; **q**, quadrate; **san**, surangular; **t**, tooth; **tm**, maxillary tooth; **tpt**, pterygoid tooth; **v?**, vomer?. Scale bar equals 5 cm.

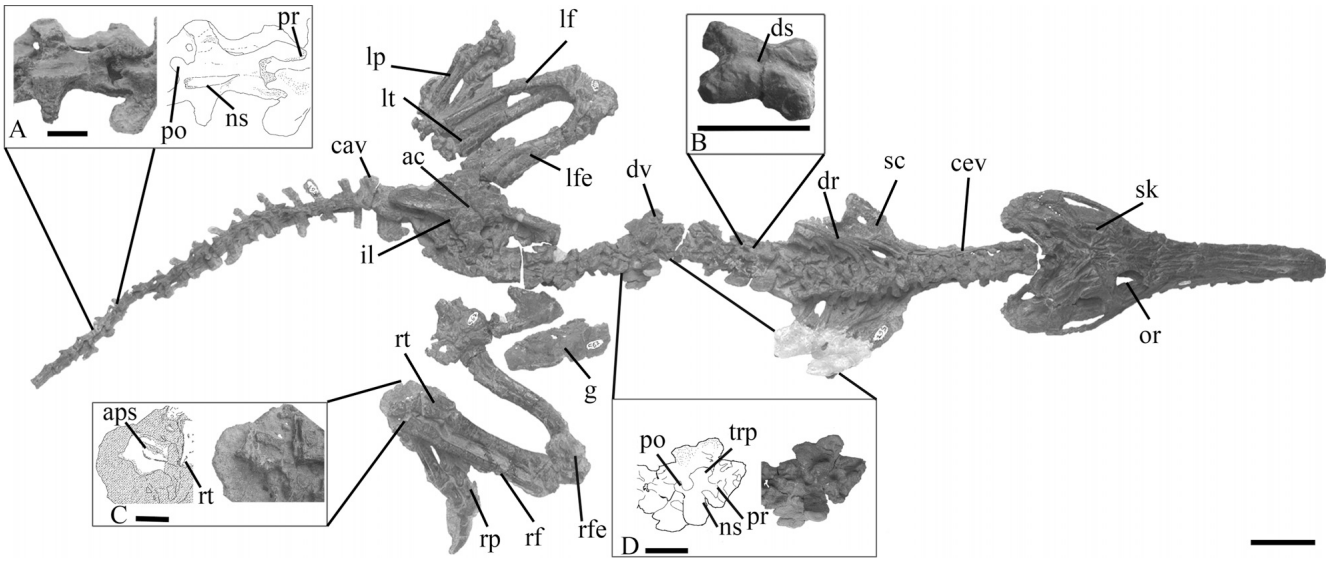

FIGURE 4. Photography of the specimen *Chanaresuchus ischigualastensis* (PVSJ 567) positioned as it was found in the field. **A**, Caudal vertebrae in dorsal view. Scale bar equals 1 cm. **B**, Dorsal osteoderm in dorsal view. Scale bar equals 1 cm. **C**, Right astragalus in posterior view. Scale bar equals 1 cm. **D**, Dorsal vertebrae in laterodorsal view. Scale bar equals 3 cm. **Abbreviations**: **ac**, acetabulum; **aps**, astragalar posterior sulcus; **cav**, caudal vertebra; **cev**, cervical vertebra; **dr**, dorsal rib; **ds**, dorsal sulcus of osteordem; **dv**, dorsal vertebra; **g**, gastral ribs; **il**, ilium; **lf**, left fibula; **lfe**, left femur; **lp**, left pes; **lt**, left tibia; **ns**, neural spine; **or**, orbit; **po**, postzygapophysis; **pr**, prezygapophysis; **rf**, right fibula; **rfe**, right femur; **rp**, right pes; **rt**, right tibia; **sc**, scapulocoracoid; **sk**, skull; **trp**, transverse processes. Scale bar equals 5 cm.

to the fourth trochanter, the femur has a shallow 'Y'-shaped sulcus, identified as the adductor ridge (sensu Romer, 1956).

Both tibiae are completely preserved, but dorsoventrally distorted by post-mortem deformation. The tibia is shorter than the femur, representing 90% of the femoral length. The tibial shaft is oval at midlength and both ends are anteroposteriorly expanded, presenting a slight torsion between them. A low cnemial crest is present in *Chanaresuchus ischigualastensis*. As in all archosaurs in the traditional sense, there is a shallow longitudinal sulcus on the lateral surface of the distal end of the tibia (Romer, 1956). The fibulae are the same length as the tibiae, but slimmer. Both ends are expanded and twisted with respect to each other. The fibula lacks a fibular anterior trochanter.

The astragalus is divided into three parts in dorsal view: a tibial facet, a fibular facet, and a non-articular groove. The tibial facet is sub-quadrangular and articulates with the tibia. In *Chanaresuchus ischigualastensis* the tibial facet is more expanded than the fibular facet, as in *Proterochampsa* and *Chanaresuchus bonapartei*. In medial view, this facet has a laterally oriented crest that divides it into two surfaces, resulting in a saddle-shaped structure. The tibial facet is concave in anterior view and this articular surface is flat. The rounded fibular facet is quadrangular, dorsally oriented, and different from the flat and dorsolaterally oriented facet of *Chanaresuchus bonapartei.* The anterior surface of the astragalus presents a concave surface (homologous to the anterior hollow sensu Sereno [1991] and Nesbitt et al. [2009]) that has a slight depression. The presence of this hollow is shared by *Proterochampsa* and *Chanaresuchus bonapartei*. In posterior view, the astragalus has two crests that limit a mediolaterally oriented concavity (posterior groove sensu Sereno, 1991). *Chanaresuchus ischigualastensis* lacks the foramina in the sulcus on the posterior surface of the astragalus that are present in *Chanaresuchus bonapartei*. The condyle that articulates with the calcaneum has a rounded surface and is ventrolaterally oriented.

The calcaneum is strongly deformed and fractured, so no fine details can be assessed. This bone is smaller than the astragalus and bears a sub-rectangular calcaneal tuber. The medial side of the calcaneum is articulated with the astragalus and the dorsal surface articulates with the fibula.

Both pedes are almost complete, lacking only some phalanges. The metatarsals and the proximal tarsals are articulated with a series of poorly preserved small bones that may be distal tarsals. The metatarsals overlap each other at their proximal ends and diverge from the ankle. Digit I is the smallest and all phalanges are twisted and have gynglimoid facets. In overall aspect, the pes of *Chanaresuchus ischigualastensis* is similar to that of other proterochampsids, including the absence of phalanges on pedal digit V. Metatarsal IV is the most gracile of all the metatarsals, as in *Chanaresuchus bonapartei.*

Osteoderms

Alongside the dorsal and sacral vertebrae of PVSJ 567 there are a series of disarticulated osteoderms, with their dorsal surfaces exposed. These dermal elements are sub-rectangular, with both edges concave in dorsal view, similar to those in *Chanaresuchus bonapartei*. The ornamentation of the osteoderms of *Chanaresuchus ischigualastensis* consists of a deep longitudinal dorsal sulcus. This ornamentation is different from the radiate pattern present in *Chanaresuchus bonapartei* and most other proterochampsids. The presence of osteoderms in *Chanaresuchus ischigualastensis* differs from the absence of these dermal structures in *Proterochampsa*.

DISCUSSION

PVSJ 567 is assignable to *Chanaresuchus* on the basis of diagnostic characters shared with *Chanaresuchus bonapartei* (e.g., skull ornamented by longitudinal crests and depressions on the dorsal surfaces of the premaxillae, maxillae, and nasals; lateral fossa in the centra of presacral vertebrae; low deltopectoral crest on the humerus; absence of phalanges on pedal digit V). PVSJ 567 exhibits several differences from *Chanaresuchus bonapartei* and can be assigned to a new species, *C. ischigualastensis* (e.g., basal tubera wide with rostrolateral contour transversely

oriented; paroccipital processes distally expanded; articular surface of caudal prezygapophyses elliptical and notably anteriorly developed; astragalus lacking perforations in the posterior sulcus; osteoderms with longitudinal dorsal sulcus).

The new specimen provides new information about *Chanaresuchus*. Until now, *Chanaresuchus* was restricted to the Chañares Formation (Ladinian–late Carnian; Desojo et al., 2011), but the new specimen described here from the Ischigualasto Formation (late Carnian; Martínez et al., 2011) changes our view about the biochron of this taxon and for proterochampsids. The macroevolutionary pattern of taxonomic replacement from the Middle to the Late Triassic is not at the genus level in proterochampsids. Rather, the replacement is at the specific level, as shown by the presence of *Chanaresuchus* in both the Middle and Late Triassic. Moreover, the persistence in the Late Triassic Ischigualasto Formation of several genera from the Middle Triassic Chañares Formation (e.g., *Chanaresuchus*, *Probelesodon*, and probably *Probainognathus*; Bonaparte and Crompton, 1994; Martínez and Forster, 1996) shows that this macroevolutionary replacement pattern was more common at the species level than previously supposed.

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