

Hind limb osteology of *Gracilisuchus stipanicorum* (Archosauria: Pseudosuchia)

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ABSTRACT: *Gracilisuchus stipanicorum* Romer, 1972, from the Middle-Late Triassic of the Ischigualasto–Villa Unión Basin of Argentina, is an extinct pseudosuchian archosaur on the stem to Crocodylomorpha. The pelvic girdle and hind limb anatomy of a referred specimen of *Gracilisuchus stipanicorum* is described and compared with that from a broad range of archosauriform taxa, including basal members such as crurotarsans and basal ornithomirans. The description of this specimen reveals new information on the anatomy of the pelvic girdle and hind limb of *Gracilisuchus*, through a detailed examination of some anatomical regions barely or not previously described, as well as reinterpretations of previous features. The phylogenetic affinities of *Gracilisuchus* within the Archosauria remain to be tested, but *Gracilisuchus* shares two putative synapomorphies with some non-crocodyliform crocodylomorphs, providing tentative support for the monophyly of Sphenosuchia (e.g., Sereno & Wild 1992; Wu & Chatterjee 1993) and the close relationship of *Gracilisuchus* to that clade. These characteristics are: (i) the morphology and poor development of the femoral fourth trochanter, closely resembling the condition of *Pseudhesperosuchus* and *Trialestes*; and (ii) a poor anterior development of the femoral head, shared with *Pseudhesperosuchus*. On the other hand there are characters that reject the inclusion of *Gracilisuchus* within Crocodylomorpha (Nesbitt 2011), such as the absence of an imperforated acetabulum, and that rather suggests a sister-taxon position to Crocodylomorpha.

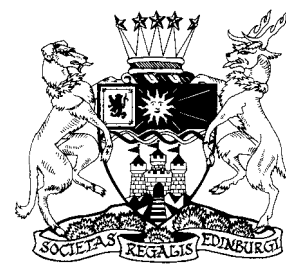
KEY WORDS: Appendicular anatomy, Argentina, Chañares Formation, pelvic girdle, Pseudosuchia, Triassic

In 1964, during a field trip headed by Dr A. S. Romer to the Ischigualasto–Villa Unión Basin (a continental Triassic succession outcropping in NW Argentina), a very rich fossil tetrapod assemblage was discovered in the Middle Triassic beds of the Chañares Formation (*sensu* Romer 1966; Romer & Jensen 1966). This assemblage records some of the earliest members of many of the major tetrapod lineages that subsequently dominated terrestrial vertebrate faunas during the rest of the Mesozoic. Among these fossils were the remains of several basal archosauriforms (i.e., *Tropidosuchus romeri* Arcucci, 1990; *Gualosuchus reigi* Romer, 1971a; *Chañaresuchus bonapartei* Romer, 1971a), the basal-most dinosauromorphs (i.e., *Lagerpeton chanarensis* Romer, 1971b (Sereno & Arcucci 1993); *Lagosuchus talampayensis* Romer, 1971b (Sereno & Arcucci 1994); *Marasuchus lilloensis* (Sereno & Arcucci), 1994; *Pseudolagosuchus major* Arcucci, 1987), a ‘rauisuchian’ archosaur (i.e., *Luperosuchus fractus* Romer, 1971c (Desojo & Arcucci 2009)), and another pseudosuchian archosaur, *Gracilisuchus stipanicorum* Romer, 1972, that may be closely related to Crocodylomorpha (e.g., Brusatte *et al.* 2010), but recently found to be a basal suchian (Nesbitt 2011).

The affinities of *Gracilisuchus* within Archosauria have been a longstanding debate in archosaur systematics. At first, Romer considered it a member of the poorly-understood Ornithosuchidae (*sensu* Bonaparte 1975a) when this group was a member of the dinosaurian lineage of archosaurs. However,

Brinkman (1981), based on the morphology and articulation of the proximal tarsals (i.e., astragalus and calcaneum) as well as some cranial and other postcranial characters, recognised *Gracilisuchus* as a member of the crocodylian lineage. This hypothesis was followed by several authors (e.g., Sereno & Arcucci 1990; Juul 1994; Brusatte *et al.* 2010). Nevertheless, the lack of consensus in this topic still persists and a variety of phylogenetic positions have been proposed for *Gracilisuchus*, ranging from very basal within Pseudosuchia (e.g., Li *et al.* 2006) to diverse placements within Suchia (e.g., Benton & Clark 1988; Sereno 1991; Parrish 1993). Despite its uncertain position, *Gracilisuchus* has acquired more relevance as an outgroup in a number of independent phylogenetic analyses of Crocodylomorpha and stem-crocodylomorphs (e.g., Clark 1994; Clark & Sues 2002; Benton & Walker 2002; Sues *et al.* 2003; Clark *et al.* 2004; Pol 2005; Pol & Gasparini 2009; Brusatte *et al.* 2010). Regardless of the importance of *Gracilisuchus* for understanding suchian diversification and as a putative sister taxon of Crocodylomorpha, the published anatomical information is very limited. The original publication (Romer 1972) provides a brief account of its general anatomy, and subsequent revisions are brief and limited to character scorings in phylogenetic datasets (e.g., Sereno 1991; Wu & Chatterjee 1993; Clark *et al.* 2000, 2004).

Because of the poorly known anatomy of *Gracilisuchus stipanicorum*, as well as the mostly accepted but still ambiguous



interpretation of its affinities (i.e., close relationship with Crocodylomorpha), a detailed study of *Gracilisuchus* is essential. In order to increase the anatomical knowledge of this relevant taxon and as a means to reassess its phylogenetic position, this paper presents a detailed description of the pelvic girdle and hind limb anatomy of the specimen PVL 4597 assigned to *Gracilisuchus stipanicorum*, along with comparisons to members of Archosauriformes, as part of the PhD project of A. Lecuona. This provides an accurate source of osteological information that can now be included in phylogenetic analyses, leading to more accurate character scorings. This will provide a stronger basis for phylogenetic interpretations of the affinities of *Gracilisuchus* and of the entire set of taxa, as well as bring a better supported base for understanding the evolution of characters in a systematic context.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, New York, USA; AZA, refer to locality designations for specimens of *Arganasuchus*; BSPG AS, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; GMPKU-P, Geological Museum, School of Earth and Space Sciences, Peking University, Beijing, People's Republic of China; ISI, Geological Studies Unit of the Indian Statistical Institute, Calcutta, India; MACN-Pv, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Paleontología de Vertebrados, Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina; MLP, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MPEF-AC, Museo Paleontológico Egidio Feruglio, Anatomía Comparada collection, Trelew, Chubut Province, Argentina; MUCPv, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; NHMUK, Natural History Museum, London, UK; PULR, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja Province, Argentina; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán Province, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan Province, Argentina; SAM, South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, Museum of Paleontology, University of California, Berkeley, USA; UNC, North Carolina Museum of Natural Sciences, Raleigh, NC, USA; UNLP, Universidad Nacional de La Plata, Buenos Aires, Argentina; USNM, National Museum of Natural History, Washington DC, USA; YPM, Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA.

1. Systematic palaeontology

Archosauria Cope, 1869 *sensu* Gauthier & Padian 1985
Pseudosuchia Zittel, 1887–1890 *sensu* Gauthier & Padian 1985
Suchia Krebs, 1974 *sensu* Benton & Clark 1988

Gracilisuchus stipanicorum Romer, 1972

Holotype. PULR 08, partially articulated cranium and mandible; presacral vertebral series; cervical and most dorsal paramedian osteoderm; many articulated ribs, most cervical and dorsal ribs from the right side and a few from the left side; incomplete scapula and humerus. This specimen was preserved in a slab mixed with other taxa, and some of these elements were later reinterpreted as pertaining to different taxa (*Tropi-*

dosuchus romeri, Sereno & Arcucci 1994). Due to this mixture of materials, the holotypic material of *G. stipanicorum* is here considered to be the elements articulated with the main part of the specimen. A left ilium, an articulated right femur, tibia, fibula and pes, and several series of vertebrae were elements originally assigned to the holotype specimen of *G. stipanicorum*, whereas none of those elements is now considered to be part of *Gracilisuchus stipanicorum*, but instead belong to other taxa (Sereno & Arcucci 1994) (see below).

Referred material. MCZ 4116A (in part), partial cranium, an incomplete articulated caudal vertebral series, and articulated ischia; MCZ 4117, almost complete and well preserved cranium; MCZ 4118, partial cranium, articulated cervical series (from axis to cervical 6) articulated with osteoderms, a series of three articulated cervicodorsal vertebrae, a series of six cervicodorsal vertebrae articulated with ribs, a dorsal series of at least nine elements; PVL 4597 (the 'Tucuman specimen' of Romer 1972, Bonaparte 1975a), nearly complete skull and mandible in articulation, an almost complete presacral vertebral series with articulated paramedian dorsal osteoderms, two sacral vertebrae, an incomplete caudal vertebral series, both ilia, left pubis, both ischia, an almost complete left hind limb, fragmentary right hind limb, and several undetermined fragments of bone; PVL 4612, nearly complete skull, articulated with the left mandibular ramus, exposing the palate.

Locality, horizon and age. Ischigualasto–Villa Unión Basin, La Rioja Province, 3 km north of the northern branch of Chañares River and 5 km southwest of the Puerta de Talampaya (Sereno & Arcucci 1994). Chañares Formation (~Ladinian age, Stipanovic 1983; Spalletti *et al.* 1999; Rogers *et al.* 2001), NW Argentina (Fig. 1).

Emended diagnosis. Lightly-built pseudosuchian with skull length of ~85 mm and ~28 cm of presacral length, diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): large antorbital fenestra occupying approximately 0.3 of the anteroposterior length of the skull table (measured from the anterior end of the premaxilla to the posterior end of the parietals); large antorbital fossa occupying 0.4 of the length of the skull table; presence of a postfrontal and a small postparietal; anterior ramus of squamosal laterally extended; interparietal suture partially obliterated; narrow occipital portion of the parietals; postzygapophyseal facet of the axis horizontal, posteriorly directed, and facing ventrally*; high and vertical anterior border of the axial neural spine*; presence of a ventral longitudinal median keel on axial centrum; poor development of ventral keel on the cervical vertebrae; circular depression on the mid-dorsal region of the neural arch of cervical vertebrae; spine table in posterior cervical vertebrae; lack of a well-defined acetabular surface on the pubis; L-shaped lamina on proximal pubic apron; ischiadic symphysis proximally located*; femur longer than tibia; knob-shaped iliofibular trochanter; two paramedian osteoderms per vertebra.

2. Materials and methods

The material of *Gracilisuchus stipanicorum* studied here is a well-preserved pelvic girdle and hind limb pertaining to the specimen PVL 4597, referred to *Gracilisuchus* by Romer (1972, p. 3) and Bonaparte (1975a), and supported by the present diagnosis. Measurements of the osteological elements are summarised in Tables 1 and 2 and are based on completely preserved elements.

The usage of taxonomic names is based on the definitions of the following authors: Reptilia (Gauthier *et al.* 1988); Archosauria (Gauthier 1986); Crurotarsi (Sereno & Arcucci 1990);

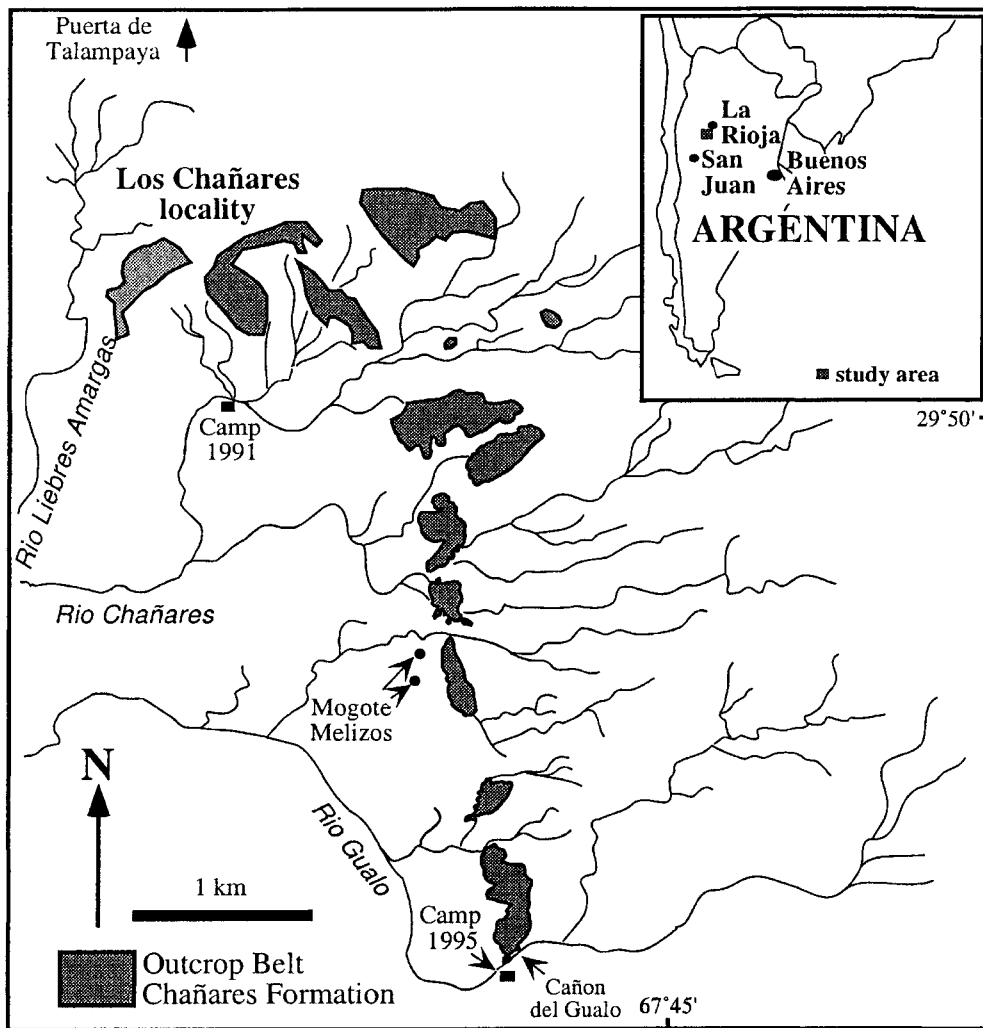


Figure 1 Geological map of the Ischigualasto–Villa Unión Basin (La Rioja and San Juan provinces) showing the location where *Gracilisuchus stipanicorum* was collected. Modified from Rogers *et al.* (2001).

Table 1 Measurements (in mm) of pelvic girdle elements of *Gracilisuchus stipanicorum* (PVL 4597). The * indicates partially preserved elements.

| | Anteroposterior (or proximodistal) length | | Lateromedial width | | Dorsoventral height | |
|---|---|--------|--------------------|-------------|---------------------|-------|
| | Right | Left | Right | Left | Right | Left |
| Ilium | 40.4 | 39.63 | – | – | 19.34 | 18.88 |
| Iliac blade | 35.7 | 34.12* | – | – | 11.66 | 11.54 |
| Anterior process | 4 | 2.66* | – | – | – | – |
| Posterior process | 19.40 | 15.50 | – | – | – | – |
| Acetabular portion | 19.4 | 22.45 | – | – | 8.05 | 6.59* |
| Pubis | – | 53.16 | – | – | – | – |
| Iliac pedicle | – | 12.82 | – | 3.53 | – | 10.29 |
| Pubic apron | – | 40.21 | – | 14.35 | – | – |
| Ischium | 45.79 | 44.64 | – | – | – | – |
| Ischiadic apron (from beginning of the symphysis) | 33.51 | – | 11.78 (max) | 13.71 (max) | – | – |
| Symphysis | 9.81* | – | – | – | – | – |

Nesbitt 2011); Pseudosuchia (Gauthier 1986); 'rauisuchians' (*sensu* Brusatte *et al.* 2010); Ornithodira (Hutchinson 2001a, b; Padian *et al.* 1999). This phylogenetic framework is summarised in a cladogram of the Archosauriformes (Fig. 2) modified from Brusatte *et al.* (2010, fig. 5).

3. Description and comparisons

The pelvic girdle and hind limb elements of PVL 4597 comprise both ilia, the left pubis, both ischia, the fragmentary right hind limb represented by the proximal end of the femur, the

Table 2 Measurements (in mm) of hind limb elements of *Gracilisuchus stipanivicorum* (PVL 4597). The * indicates incomplete elements. The ⁱ indicates element measured in the interpreted orientation given in the text.

| | Proximodistal length | Lateromedial width | Anteroposterior thickness |
|-------------------------------|----------------------|--|--|
| Left hind limb | | | |
| Femur | 79.93 | Proximal: 6.11 Distal: 6.81 | Proximal: 11.93 Distal: 12.01 |
| Tibia | 72.42 | Proximal: 10.95 Medial: 4.08 Distal: 8.90 | Proximal: 8.61* Medial: 6.26 Distal: 6.15 |
| Fibula | 68.26* | Proximal: 2.32* Medial: 3.42 Distal: 3.33* | Proximal: 5.57* Medial: 4.24 Distal: 6.57* |
| Astragalus | 6.18 | 11.10 | 7.51 |
| Calcaneum | 9.07 | 9.23 | 12.09 |
| Calcaneal condyle | 5.94 | 5.90 | 7.48 |
| Calcaneal tuber | 6.97 | 8.53 | 4.73 |
| Distal tarsal IV ⁱ | 7.47 | 9.11 | 4.35 |
| Metatarsal I | 24.5 | 3.2 | – |
| Metatarsal II | 28.6 | 2.7 | – |
| Metatarsal III | 31 | 2.2 | – |
| Metatarsal IV | 29.4 | 2.1 | – |
| Metatarsal V | 19.6 | Proximal: 6.5 Distal: 2.9 | |
| Digit I | | | |
| Phalanx I | 8.03 | | |
| Phalanx II | 6.94 | | |
| Digit II | | | |
| Phalanx I | 8.26 | | |
| Phalanx II | 5.76 | | |
| Phalanx III | – | | |
| Digit III | | | |
| Phalanx I | 8.29 | | |
| Phalanx II | 5.26 | | |
| Digit IV | | | |
| Phalanx I | 6.87 | | |
| Phalanx II | – | | |
| Digit V | | | |
| Phalanx I | 6.05 | | |
| Right hind limb | | | |
| Femur* | – | Proximal: 4.3 | Proximal: 12.26 |
| Astragalus | 8.32 | 11.61 | 7.80 |
| Calcaneum | 8.93 | 8.28 | 12.41 |
| Calcaneal condyle | 6.97 | 4.59 | 7.55 |
| Calcaneal tuber | 8.72 | 7.57 | 5.57 |
| Distal tarsal IV ⁱ | 7.52 | 7.02 | 4.86 |
| Metatarsal I | 24.70 | | |
| Metatarsal II | 29.29 | | |
| Metatarsal III | 29.88 | | |
| Metatarsal IV | 31.41 | | |
| Metatarsal V | 19.28 | | |

distal end of the tibia and fibula articulated, the astragalus, calcaneum, distal tarsal 4, metatarsals I to V, and three phalanges including an unequal phalanx, and the left hind limb represented by the femur, tibia, incomplete fibula, astragalus, calcaneum, distal tarsal 4, metatarsals I to V, complete digit I and incompletely preserved digits II to V including five complete and three incomplete phalanges (Figs 3–12). Taxonomic comparisons are made with the following archosauriform taxa based on the published literature and/or the listed specimens: *Euparkeria capensis* Broom, 1913 (Ewer 1965; “*Euparkeria*: An Image Library”); *Turfanosuchus dabanensis* Young, 1973 (Wu & Russell 2001); *Tropidosuchus romeri* (Arcucci 1990; PVL 4601, PVL 4603, PVL 4606); *Riojasuchus tenuisceps* Bonaparte,

1969 (Bonaparte 1972; PVL 3827); *Ornithosuchus longidens* Huxley, 1877 (Walker 1964); *Neoetosauroides engaeus* Bonaparte, 1969 (Desojo 2005; PVL 3525); *Aetosauroides scagliai* Casamiquela, 1960 (Desojo 2005; PVL 2073); *Saurosichus galilei* Reig, 1959 (Sill 1974; Trotteyn *et al.* 2011); *Fasolasuchus tenax* Bonaparte, 1978 (Bonaparte 1981; PVL 3850); *Postosuchus kirkpatricki* Chatterjee, 1985 (Long & Murry 1995; Weinbaum 2002; CM 73372); *Postosuchus alisonae* Peyer, Carter, Sues, Novak & Olsen, 2008 (Peyer *et al.* 2008; UNC 15575); *Batrachotomus kupferzellensis* Gower, 1999 (Gower & Schoch 2009; SMNS 52970); *Poposaurus gracilis* Mehl, 1915 (Weinbaum & Hungerbühler 2007); *Effigia okeeffeae* Nesbitt & Norell, 2006 (Nesbitt 2007);

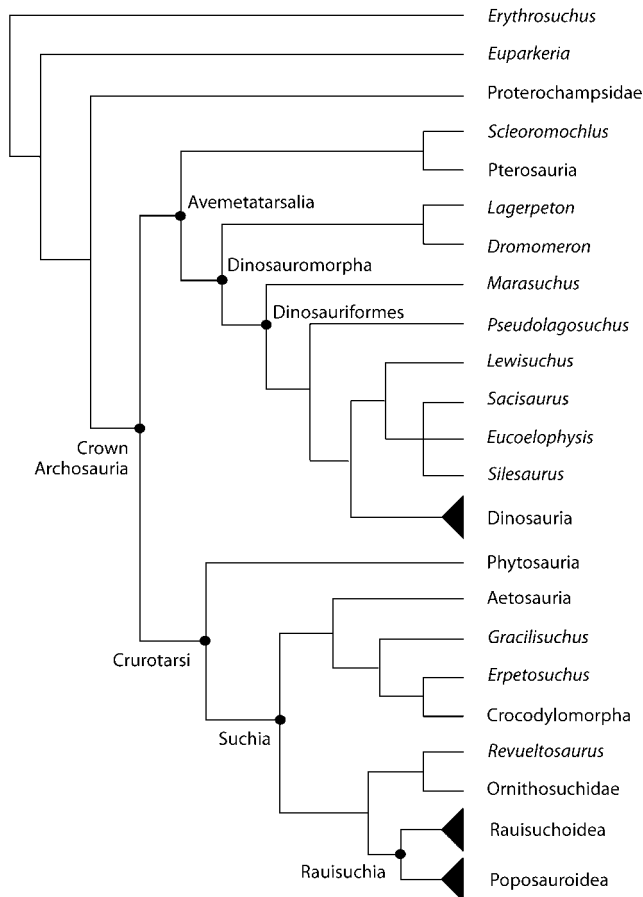


Figure 2 Cladogram of selected archosauriforms, modified from Brusatte *et al.* (2010).

Pseudhesperosuchus jachaleri Bonaparte, 1969 (Bonaparte 1972; PVL 3830); *Trialestes romeri* (Reig, 1963) (PVL 3889); *Hemiprotosuchus leali* Bonaparte, 1969 (Bonaparte 1972; PVL 3829); *Dromicosuchus grallator* Sues, Olsen, Carter & Scott, 2003 (Sues *et al.* 2003; UNC 15574); *Terrestrisuchus gracilis* Crush, 1984 (Crush 1984); *Hesperosuchus agilis* Colbert, 1952 (Colbert 1952); UCMP 129470, a large basal crocodylomorph referred to *Hesperosuchus agilis* by Sereno & Wild (1992), Clark *et al.* (2000), and Clark & Sues (2002); *Kayentasuchus walkeri* Clark & Sues, 2002 (Clark & Sues 2002; UCMP 131830); *Protosuchus richardsoni* (Brown, 1933) (Colbert & Mook 1951; AMNH 3024); *Orthosuchus stormbergi* Nash, 1968 (Nash 1975); *Marasuchus lilloensis* (Sereno & Arcucci 1994; PVL 3871, PVL 3870); *Lagerpeton chanarensis* (Sereno & Arcucci 1993; PVL 4619).

3.1. Pelvic girdle

3.1.1. Ilium (Fig. 3). Both ilia are preserved in articulation with the ribs of the two sacral vertebrae. The presence of two sacral vertebrae is primitive for Archosauriformes, being found in most representatives of this taxon, such as *Euparkeria* and *Tropidosuchus*. Among Crurotarsi it is present in Parasuchia (e.g., *Parasuchus hislopi* Lydekker, 1885; Chatterjee 1978), Aetosauria (e.g., *Aetosauroides scagliai*, PVL 2073; *Aetosaurus ferratus* Fraas, 1877; Schoch 2007), Crocodylomorpha (e.g., *Dromicosuchus grallator*, UNC 15574; *Terrestrisuchus agilis*, Crush 1984; *Kayentasuchus walkeri*, Clark & Sues 2002; *Protosuchus richardsoni*, Colbert & Mook 1951; *Orthosuchus stormbergi*, Nash 1975). Among Rausuchia, several taxa are found to have two sacral vertebrae (e.g., *Saurosuchus galilei*, Sill 1974, Trotteyn *et al.* 2011; *Postosuchus kirkpatricki*, Weinbaum, 2002, Long & Murry 1995, *contra* Chatterjee,

1985), whereas others have three or more (e.g., *Poposaurus gracilis*, Weinbaum & Hungerbühler 2007; *Arizonasaurus babbitti*, Nesbitt, 2005; *Sillosuchus longicervix* Alcober & Parrish, 1997). Among pseudosuchians, three sacral ribs are also found in the ornithosuchids *Riojasuchus tenuisiceps* (PVL 3827) and *Ornithosuchus longidens* (Walker, 1964). Basal forms within Ornithodira also exhibit two sacral vertebrae (e.g., *Marasuchus lilloensis*; *Lagerpeton chanarensis*; *Herrerasaurus ischigualastensis* Reig, 1963), but more than two sacral vertebrae are found in the non-dinosaur silesaurid *Silesaurus opolensis* Dzik, 2003 (Dzik 2003; Dzik & Sulej 2007) and several dinosaur taxa (Langer *et al.* 2010).

The iliac blades in *Gracilisuchus* are parallel to each other in anterior view (Fig. 3A) and slightly medially concave in dorsal view (Fig. 3D). The preacetabular process is short (10% of the total length of the iliac blade, Table 1) and has an anteriorly pointing triangular outline (Fig. 3C: pr p). Similar weak extensions of this process are found somewhat scattered among the taxa compared, such as *Euparkeria* (8%), *Turfanosuchus* (9%), *Postosuchus kirkpatricki* (10%), and *Caiman latirostris* (9%); slightly larger processes are present in *Saurosuchus* (14%) and *Dromicosuchus* (16%), whereas the largest are present in *Aetosauroides* (20%), *Lagerpeton* (23%), *Trialestes romeri* (25%, PVL 3889), *Neoaetosauroides* (26%), and *Terrestrisuchus* (30%). The anterior end of the process does not reach the anterior border of the pubic peduncle of the ilium, as in *Euparkeria*, *Turfanosuchus*, *Saurosuchus*, *Postosuchus kirkpatricki* (Weinbaum 2002, fig. 5.25) and *Lagerpeton*. Besides, in *Aetosauroides* the preacetabular process reaches anteriorly almost to the same level as the pubic peduncle of the ilium. Conversely, the preacetabular process passes over the anterior edge of the pubic peduncle in *Neoaetosauroides* and *Terrestrisuchus*, where an extremely long process is present. The postacetabular process of *Gracilisuchus* is a long structure (54% of the total iliac blade length, Table 1), comparable with that present in *Postosuchus kirkpatricki* (60% of the iliac blade, Weinbaum 2002, fig. 5.25) and *Turfanosuchus* (62%), whereas other taxa have this process between 40% and 45% of the iliac blade (e.g., *Euparkeria*, *Saurosuchus*, *Neoaetosauroides*, *Terrestrisuchus*, *Dromicosuchus*, *Trialestes*, *Caiman*, *Lagerpeton*), and the shortest process is present in *Aetosauroides* (18%). The postacetabular process bears a medially directed horizontal shelf along the entire ventral margin of the process, resulting in an L-shape iliac blade in posterior view, the brevis shelf (Fig. 3B: bs). The expanded second sacral rib articulates dorsal to this shelf. Structures referred as a 'brevis shelf' have been described for different taxa among pseudosuchian and avian lineages of archosaurs (e.g., Sill 1974; Novas 1996; Hutchinson 2001a). The dinosaurian brevis shelf was held to be a synapomorphy of Dinosauria, or more inclusive groups (e.g., Novas 1996; Benton 2004; Ezcurra 2006; Irmis *et al.* 2007). A 'brevis shelf' was described for *Saurosuchus galilei* (Sill 1974) being a medially located shelf situated at mid height on the postacetabular process and roofing a ventral fossa, the latter structure is absent in *Gracilisuchus*. Structures similar to the medial shelf observed in *Gracilisuchus* were described for *Terrestrisuchus* (Crush 1984), *Dromicosuchus* (Sues *et al.* 2003) and have been observed in *Marasuchus* (PVL 3870); in the latter two the second sacral rib also articulates dorsally. In *Trialestes*, a shelf is present along the complete length of the process, but it is less medially extended and somewhat ventromedially directed. In other taxa similar structures are present, such as in *Turfanosuchus*, which possess a prominent ridge along the ventral margin of the iliac blade, but in these the sacral rib articulations are dorsally located. In the ornithosuchid *Riojasuchus tenuisiceps* (PVL 3827; Bonaparte 1972; Hutchinson 2001a), the medial shelf structure is short and

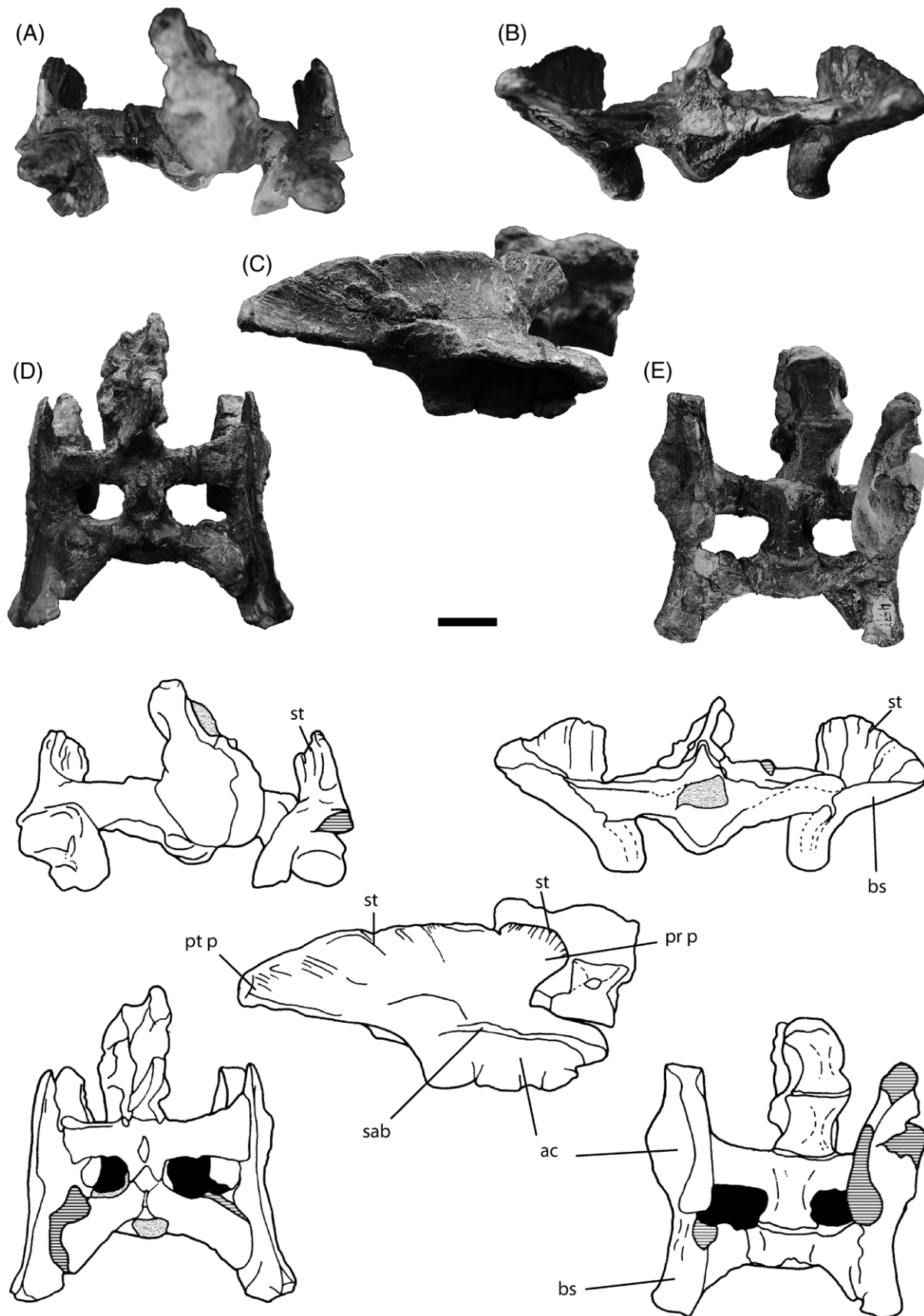


Figure 3 Photographs and equivalent line drawings (below) of ilia of *Gracilisuchus stipanicorum* (PVL 4597) in (A) anterior, (B) posterior, (C) right lateral, (D) dorsal and (E) ventral views. Abbreviations: ac=acetabulum; bs=brevis shelf; pr p=preacetabular process of the ilium; pt p=postacetabular process of the ilium; sab=supraacetabular buttress; st=striae. Scale bar=1 cm.

located in the anteriormost region of the postacetabular process. In other rauisuchians the posteromedial shelf is also present, for example in *Postosuchus kirkpatricki* (Weinbaum

2002), *Effigia okeeffeae* (Nesbitt 2007), *Batrachotomus kupferzellensis* (Gower & Schoch 2009), and *Poposaurus gracilis* (Weinbaum & Hungerbühler 2007).

A brevis shelf and fossa have been described from several groups within Dinosauria (e.g., Novas 1992, 1996), but there the shelf is a ventrolateral projection and the fossa is lateral to the iliac blade. The ventral and lateral surface of this shelf is part of the origin site of the *M. caudofemoralis brevis* in living crocodiles, and also inferred to be primitive for Archosauria (Romer 1927; Hutchinson 2001a), whereas in the dinosaurian line the brevis shelf was interpreted as a neomorphic feature related with the shift and development of this muscle (Novas 1996; Hutchinson 2001a). No shelf is present in several archosaurian taxa such as Aetosauria (e.g., *Neoaetosauroides*, *Aetosauroides*, *Stagonolepis robertsoni* Agassiz, 1844), the living crocodyliform *Caiman*, and some Dinosauria (e.g., Ornithischia, Dromaeosauridae; Romer 1927; Novas 1996; Hutchinson 2001a).

The contact between the ilium and the first sacral ribs occurs on the medial surface dorsal to the acetabular wall, slightly posterior to the mid-point of the acetabulum (Fig. 3D). Although these ribs are incomplete distally, they remain almost unexpanded at their contact with the ilium and do not contact with the preacetabular process. As mentioned above, the contact with the second sacral ribs occurs along almost all the dorsal surface of the posteromedial shelf. The second sacral ribs are markedly flared at their contact, and with the posterior expansion longer than the anterior one (Fig. 3D). This contact is present in almost all taxa (e.g., *Marasuchus*, *Saurosuchus*, *Postosuchus*, *Dromicosuchus* and *Poposaurus*). By contrast, in *Euparkeria*, the articulation is through the anterior region of the rib, and in *Turfanosuchus* the ridge is located above the articulation.

The lateral surface of the iliac blade is very finely striated (Fig. 3C: st), from the anterior to the posterior dorsal border. The anterior striae are the shortest and are oriented slightly posteriorly; the median ones are slightly longer and are anteriorly directed, whereas the posterior striae are the longest, with some extending along the entire length of the postacetabular process. In the anteroposteriorly short region between the acetabulum and the aforementioned striae, there is a shallow depression, probably for the hypothesised insertion of the *M. iliofemoralis* (Fig. 3C). The medial surface of iliac blade also has some striae (Fig. 3A, B: st), with almost the same orientation as the lateral ones, but these are more weakly developed.

The acetabular region, measured as the longest distance from the inner edges of the anterior and posterior borders of the acetabulum, represents slightly more than half of the anteroposterior length of the iliac blade (54%, Table 1). The length of the acetabulum of *Gracilisuchus*, like that of *Aetosauroides*, seems to be proportionally larger than that of other archosauriforms, which exhibit smaller acetabulae that are less than half of the length of the iliac blade. However, the length of the acetabulum based on this ratio has to be taken with caution, because among various taxa the iliac blade also shows notable changes in its anteroposterior length. The supraacetabular buttress is located at the mid dorsal margin of the acetabulum (Fig. 3C: sab), and forms a well-developed structure for articulation with the femur. This buttress is widely distributed among other taxa (e.g., *Turfanosuchus* (Wu & Russell 2001), *Saurosuchus* (PVSJ 615), *Marasuchus* (PVL 3870), *Lagerpeton* (PVL 4916), *Hallopus victor* (Marsh, 1877; Walker 1970), and *Dromicosuchus* (UNC 15574)). The ventral margins of both ilia are damaged, and thus the nature of the articulation with the pubes and ischia cannot be determined. Consequently, the differentiation of the articular margins between pubes and ischia is not possible (*contra* Romer 1972, fig. 8b). On the basis of the preserved region of the acetabulum, it can be inferred that it was not perforated, as occurs

in *Euparkeria*, *Turfanosuchus*, aetosauroids, rauisuchids, *Marasuchus* and *Lagerpeton*, but contrasting with the perforated condition present in *Ornithosuchus* (Walker 1964), *Riojasuchus* (PVL 3827), some Poposauridae (Brusatte *et al.* 2010), some crocodylomorphs such as *Orthosuchus* (Nash 1975) and dinosaurs (e.g., *Herrerasaurus*).

3.1.2. Pubis (Fig. 4). A single, nearly complete, left pubis is preserved, contrary to Romer (1972), who stated that this element was absent (see below). The iliac peduncle is lateromedially narrow and the articular surface for the ilium is flat, anteroposteriorly short, and lateromedially narrow (Fig. 4B, C: si). The anteroposteriorly short condition of the articular surface for the ilium is similar to that seen in the basal archosauriform *Tropidosuchus*, the basal crocodylomorph UCMP 129470 (Parrish 1991, fig. 8), and the basal Crocodyliformes *Protosuchus* and *Orthosuchus*. In contrast, an anteroposteriorly long articular surface is seen in most other taxa (e.g., *Euparkeria*, *Mystrisuchus planirostris* (SMNS 12986), *Neoaetosauroides*, *Ornithosuchus* (Walker 1964, fig. 11), *Postosuchus kirkpatricki* (Long & Murry 1995, fig. 135), *Batrachotomus* (Gower & Schoch 2009, fig. 5), *Terrestrisuchus* (Crush 1984, text-fig. 8), *Marasuchus* and *Lagerpeton*). On the proximal end of the pubis of *Gracilisuchus* the articular surface for the ilium is visible, and, although the proximal half of the obturator foramen is enclosed by real bone, no articular surface for the ischium can be seen. The absence of a discrete ischiatic surface contrasts with the ancestral condition of Archosauromorpha, although, as far as it can be seen, the preserved bone surface is a finished bone structure. Both contacts with ischium and pubis are present in basal archosauromorphs (e.g., *Euparkeria* (Ewer 1965), *Tropidosuchus*), basal Dinosauriomorpha (e.g., *Marasuchus*, *Lagerpeton*), basal non-dinosaurian crurotarsans (e.g., *Mystrisuchus planirostris* Meyer (SMNS 12986), *Riojasuchus*, *Neoaetosauroides*, *Fasolasuchus*), basal Crocodylomorpha (e.g., *Terrestrisuchus*, *Trialestes*), as well as Crocodyliformes (e.g., *Protosuchus*, *Orthosuchus*). On the other hand, the presence of an articular surface for the ilium is shared with most taxa, but in Crocodyliformes complete contact of the pubis with the ischium and exclusion of the pubis from the acetabulum occurs. In some basal crocodyliforms the contact between ilium and ischium is small (e.g., *Orthosuchus*, *Protosuchus* and *Gobiosuchus kielanae* Osmólska, 1972 (Osmólska *et al.* 1997)), whereas in more derived forms the pubis has lost contact with the ilium and instead contacts only the ischium (e.g., Buckley & Brochu 1999; Pol *et al.* 2004; Turner 2006), a character retained also in living crocodylians (e.g., Mook 1921).

The proximodistal length of this pedicle represents 24% of the total pubic length (Table 1). Along the lateroventral angle of the proximal end there is a small, ventrally extended, bony tongue (Fig. 4B, C: ptip) that forms a groove in its medial side, which is in turn lateral to a thin proximal bony portion of the obturator foramen (Fig. 4C). This structure, as far as can be seen, is present only in *Postosuchus kirkpatricki* (Long & Murry 1995, fig. 135), but because of the delicate morphology of this region and this structure in particular, it can be sometimes damaged and hard to recognise. No acetabular surface on the proximal pubis can be recognised, thus the contribution to the acetabulum cannot be determined. Extensive participation of the pubis in the acetabulum is seen in several taxa, such as *Euparkeria*, *Neoaetosauroides* and *Lagerpeton*, whereas others have a poor participation of the acetabulum, such as some aetosauroids (e.g., *Stagonolepis robertsoni*, Walker 1961; *Aetosaurus ferratus*, Schoch 2007), rauisuchians (e.g., *Saurosuchus*; *Postosuchus*, Long & Murry 1995, fig. 135; *Effigia okeeffeae*), *Parasuchus*, *Riojasuchus*, *Ornithosuchus* and *Marasuchus*. Among basal pseudosuchians, this feature is

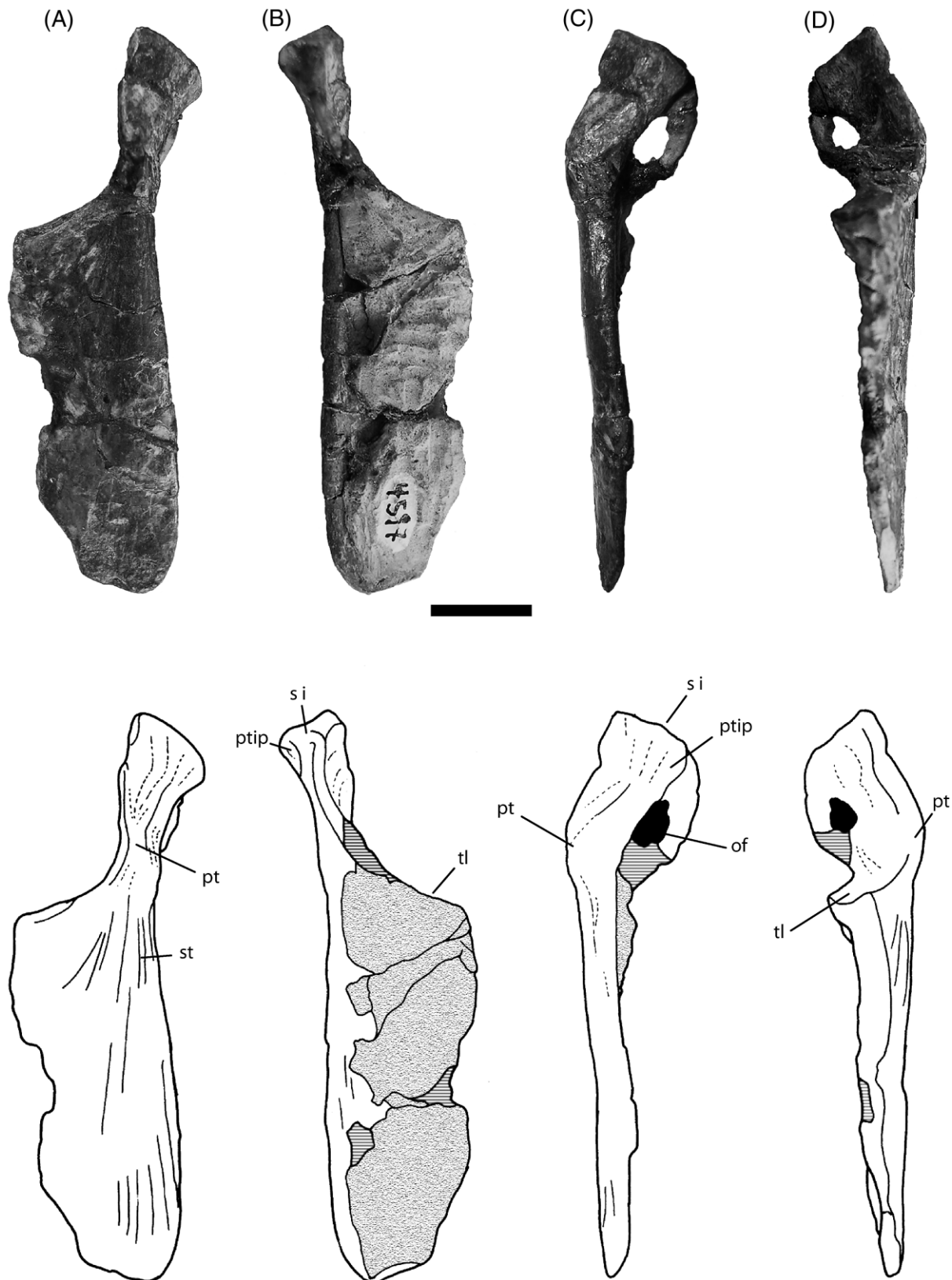


Figure 4 Photographs and equivalent line drawings (below) of left pubis of *Gracilisuchus stipanicorum* (PVL 4597) in (A) anterior, (B) posterior, (C) lateral and (D) medial views. Abbreviations: of=obturator foramen; pt=pubic tubercle; ptip=proximal bony tongue on iliac pedicle of the pubis; si=articular surface for ilium; st=striae; tl=thin L-shape lamina on proximal pubic apron. Scale bar=1 cm.

probably present in the poorly-preserved pubis of *Fasolasuchus*. The exclusion of the pubis from the acetabulum is present in basal crocodyliforms (e.g., *Orthosuchus*; GMPKU-P 200102 described in Pol *et al.* 2004), whereas pubic participation is retained in *Protosuchus richardsoni* (Colbert & Mook 1951). In contrast, in non-crocodyliform crocodylomorphs, a

small participation, if it exists, is present in UCMP 129470 (Parrish 1991, fig. 8); a small participation occurs in *Terrestri-suchus* (Crush 1984, text-fig. 8C), and also in *Sphenosuchus acutus* Haughton, 1915 (Walker 1990, p. 8).

The obturator foramen is limited proximally by a very thin bony rod that is incomplete distally. It was probably closed in

life with unossified bone tissue that seems to have bounded a large and oval foramen (Fig. 4C, D: of). The presence of an obturator foramen is the plesiomorphic condition present in *Euparkeria*, *Tropidosuchus*, Phytosauria (e.g., *Parasuchus hislopi* Chatterjee, 1978), Aetosauria and Rauisuchia. Among basal Crocodylomorpha, a large foramen is present in *Terrestrisuchus*, whereas none was inferred for the basal crocodylomorph UCMP 129470 (Parrish 1991), and it is absent in Crocodyliformes (e.g., *Protosuchus*, *Orthosuchus*) including Mesoeucrocodylia.

The anterior surface of the iliac pedicle has a slight concavity at its mid-region and distally has a well-developed tubercle, the pubic tubercle (Hutchinson 2001a; 'Processus lateralis pubis', sensu Walker 1977) (Fig. 4A, C, D: pt). The pubic tubercle is considered a plesiomorphic structure for Reptilia (Romer 1956; Hutchinson 2001a), located on the anterolateral surface of the proximal pubic region and associated with the union of different soft tissues, including the *M. ambiens* (Hutchinson 2001a). This tubercle is well developed in Archosauromorpha and reduced progressively until its strong reduction or absence in Crocodylia (Hutchinson 2001a). Although the different states of development of the pubic tubercle cannot be unequivocally correlated with the attachment of the *M. ambiens*, the presence of this structure has traditionally been related to the presence of this muscle (e.g., *Riojasuchus*, Bonaparte 1972; *Marasuchus*, Bonaparte 1975b, Sereno & Arcucci 1994). The pubic tubercle is present in Archosauriformes (e.g., *Tropidosuchus*, PVL 4601) and Pseudosuchia (e.g., *Ornithosuchus*, Walker 1964; *Postosuchus kirkpatricki*, Long & Murry 1995, fig. 135), but is absent in crocodylomorphs (e.g., *Terrestrisuchus*, Crush 1984; *Protosuchus*, AMNH 3024).

The pubic apron is a plate-like structure narrowing towards its medial border that forms the pubic symphysis; it is partly damaged. The proximodistal length of the apron, taken from the lateralmost proximal region at the contact with the pubic shaft to the distal end, constitutes 76% of the total pubic length, taken from the proximal articular surface to the distal end of pubic shaft (Table 1). The proximal border of the pubic apron has a narrow and very thin lamina, ventrally directed to the pubic apron surface, giving an L-shape configuration in medial view (Fig. 4D: tl). This structure has not been recorded in any other taxon, probably as a result of its fragile nature and thus poor preservation. The dorsal (anterior) has weak, radially oriented striae (Fig. 4A: st), and there are more lightly developed longitudinal striae located on the lateral border. This surface might mark the origin of *M. puboischiofemoralis externus 1* (Witmer 1995; Hutchinson 2001a), because the origin of the larger part in living crocodylians is present in this bone (Romer 1923). However, a different origin for that muscle is present in avians, where it originates mostly on the ischiatic surface (e.g., Hudson 1937; McGowan 1979).

3.1.3. Ischium (Fig. 5). Both ischia are preserved in articulation with each other; they have an overall plate-like shape in cross-section. The proximal articular surface of the iliac peduncle is triangular in outline and slightly concave (Fig. 5D: s i), the poor preservation of this region prevents precise determination of the articulation with the ilium. Moreover, an articular surface for the pubis cannot be seen anteriorly, as present in basal archosauriforms (e.g., *Euparkeria*, *Tropidosuchus*), Dinosauromorpha (e.g., *Lagerpeton*, *Marasuchus*), phytosaurs (e.g., *Parasuchus*), Pseudosuchia (e.g., *Neoaetosauroides*, *Stagonolepis*, *Postosuchus*), and basal members of Crocodylomorpha (e.g., *Terrestrisuchus*, *Trialestes*). In contrast, in Crocodyliformes two proximal processes are present for articulation with the ilium, a posterior and an anterior one both forming the ventral margin of the acetabulum (e.g.,

Protosuchus, *Orthosuchus*, Mesoeucrocodylia), and contact for the pubis is located in the anterior or ventral surface of the anterior process (e.g., Mook 1921; Wu & Sues 1996; Osmólska *et al.* 1997; Buckley & Brochu 1999). From the proximal articular surface, ischium width increases distally until a point at the beginning of the symphysis, and then narrows towards the distal end. Distal to the symphysis (Fig. 5B: is), the medial edge of the right ischium has a broken edge, but the left element is complete, thus the symphysis can be identified as located in the proximal region and being quite short (22% of the total length, Table 1). Plesiomorphically for Archosauriformes, the symphysis is located along the complete length of the ischial shaft (e.g., *Euparkeria*, *Tropidosuchus*), a condition retained in Dinosauromorpha (e.g., *Lagerpeton*) and several other crurotarsan taxa such as Parasuchia (e.g., *Leptosuchus*), Aetosauria (e.g., *Aetosauroides*) and Rauisuchia with their conjoined ischia (e.g., *Saurosuchus*, *Postosuchus*, *Prestosuchus chiniquensis* von Huene, 1938). An elongated ischiatic symphysis is also present in the basal crocodylomorph *Terrestrisuchus*. A similar condition to that observed in *Gracilisuchus* may also be present in *Ornithosuchus* (Walker 1964, fig. 11), but first-hand examination of this material is needed to confirm this. The ischia of *Gracilisuchus* have a lateral contact almost forming an angle of 180° in proximal view (Fig. 5D). In other taxa this angle is smaller, such as in the archosauriform *Euparkeria*, which has an angle of 68° (maybe less due to compression of the material; Ewer 1965). Among pseudosuchiids, a small angle is also present in *Ornithosuchus* (Walker 1964, fig. 11), *Aetosauroides*, *Saurosuchus* and the dinosauriform *Marasuchus* (PVL 3870). A lateral ischial contact similar to *Gracilisuchus* is found in the dinosauriform *Lagerpeton* (PVL 4619), but differs from the former in that the proximal half of the ischia are strongly bowed downwards.

3.2. Hind limb

3.2.1. Femur (Fig. 6). The left femur has been preserved somewhat deformed, thus our anatomical interpretations and comparisons are based on Hutchinson 2001b. The distal fibular and tibial femoral condyles are situated anteriorly with the axis that unites them transversely to the sagittal plane. Due to the preservation of the femur, the major axis of the femoral head is anteroposteriorly oriented. The femoral shaft has a sigmoidal curvature, primitively present in Archosauria and the successively more closely related *Euparkeria* and Proterochampsidae (Gauthier 1984; Gauthier *et al.* 1988; Sereno & Arcucci 1990; Sereno 1991). More specifically, the distal portion of the femoral diaphysis of *Gracilisuchus* is bowed anteriorly along approximately 55% of the total length (Sereno 1991). An anterior bowing of more than 80% of the total length is present in Ornithodira (e.g., *Lagerpeton*, *Marasuchus*, Dinosauria; Sereno 1991); by contrast the plesiomorphic character state (anterior curvature of 50–80%) is found in Ornithosuchidae (e.g., *Riojasuchus*, PVL 3827), Aetosauria (e.g., *Aetosauroides*), Rauisuchia (e.g., *Saurosuchus*), and in several basal crocodylomorphs (e.g., *Pseudhesperosuchus*, PVL 3830; *Kayentasuchus*, UCMP 131830; *Hesperosuchus*, Colbert 1952). An exception is present in the crocodylomorph *Terrestrisuchus*, which displays an anterior bowing of almost the entire length of the bone (Sereno 1991). The femoral shaft of *Gracilisuchus* is slightly mediolaterally compressed, maybe as an artefact of preservation.

The proximal end of the femur is somewhat damaged along the anterior and posterior edges, but the general features can be recognised. The femoral head has a slight medial expansion, giving it a triangular outline in proximal view (Fig. 6E). In anterior or posterior views, the femur has a medial expansion in its proximal end, developing a flat surface dorsomedially

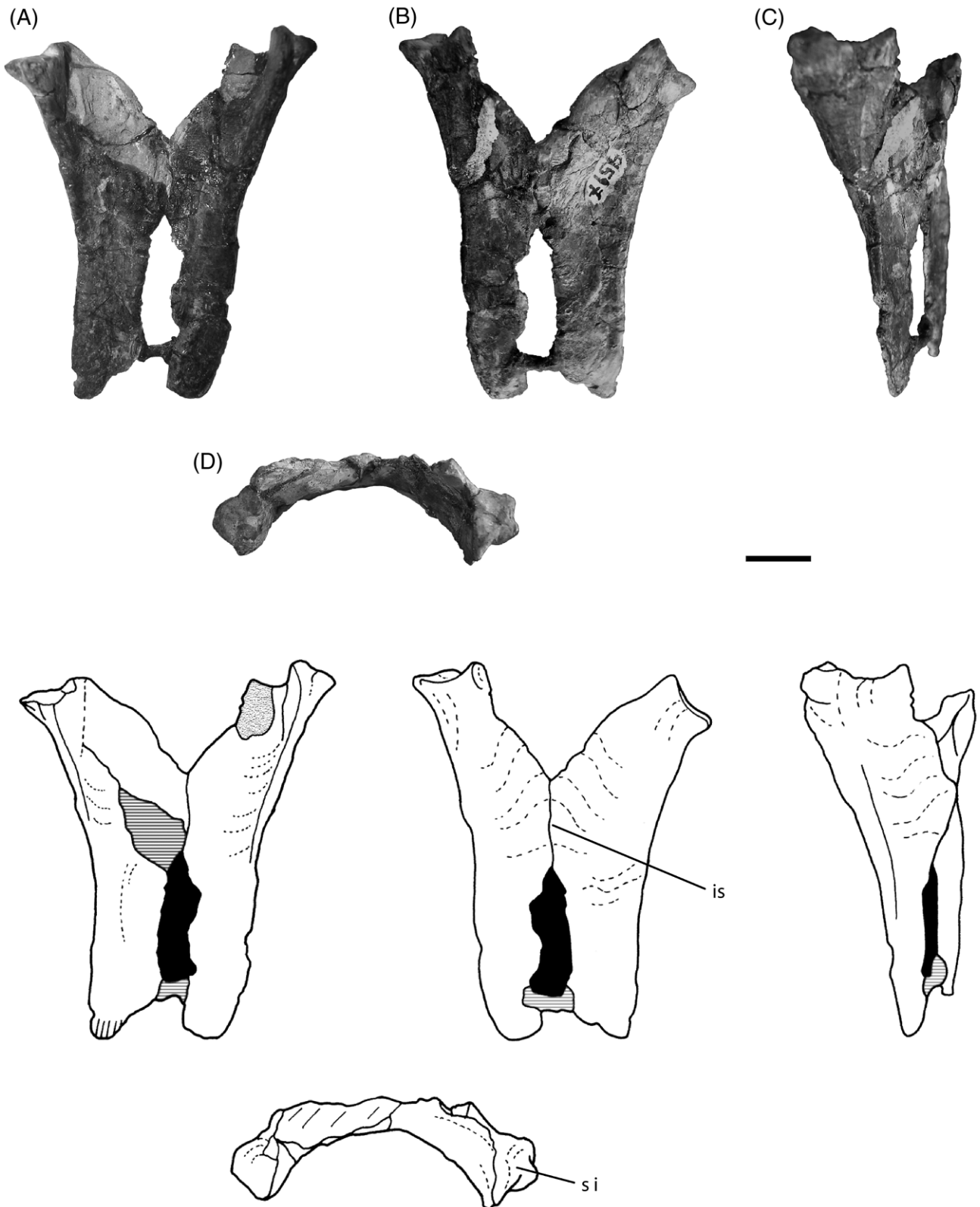


Figure 5 Photographs and equivalent line drawings (below) of ischia of *Gracilisuchus stipanivicorum* (PVL 4597) in (A) dorsal, (B) ventral, (C) right lateral and (D) proximal views. Abbreviations: is=ischial symphysis; si = articular surface for ilium. Scale bar=1 cm.

oriented that articulates with the acetabulum (Fig. 6A, B). In lateral or medial views, the femoral head has a round anterior profile and is continuously concave with the anterior edge of the shaft (Fig. 6C, D); it lacks an offset femoral head and a femoral neck. The slight medial and wide expansion of the proximal end is also observed in the phytosaur *Parasuchus*, the basal pseudosuchians *Fasolasuchus* and *Postosuchus kirk-*

patricki (Weinbaum 2007, fig. 5.21), and the dinosauriform *Marasuchus*. The expansion is more projected and has anterior and posterior constrictions in other pseudosuchians such as *Riojasuchus* and *Aetosauroides*, while a flat medial surface of the femoral head is present in the crocodylomorph *Pseudhesperosuchus* and two processes in the rauisuchian *Effigia*. *Gracilisuchus* also contrasts with a well-developed and

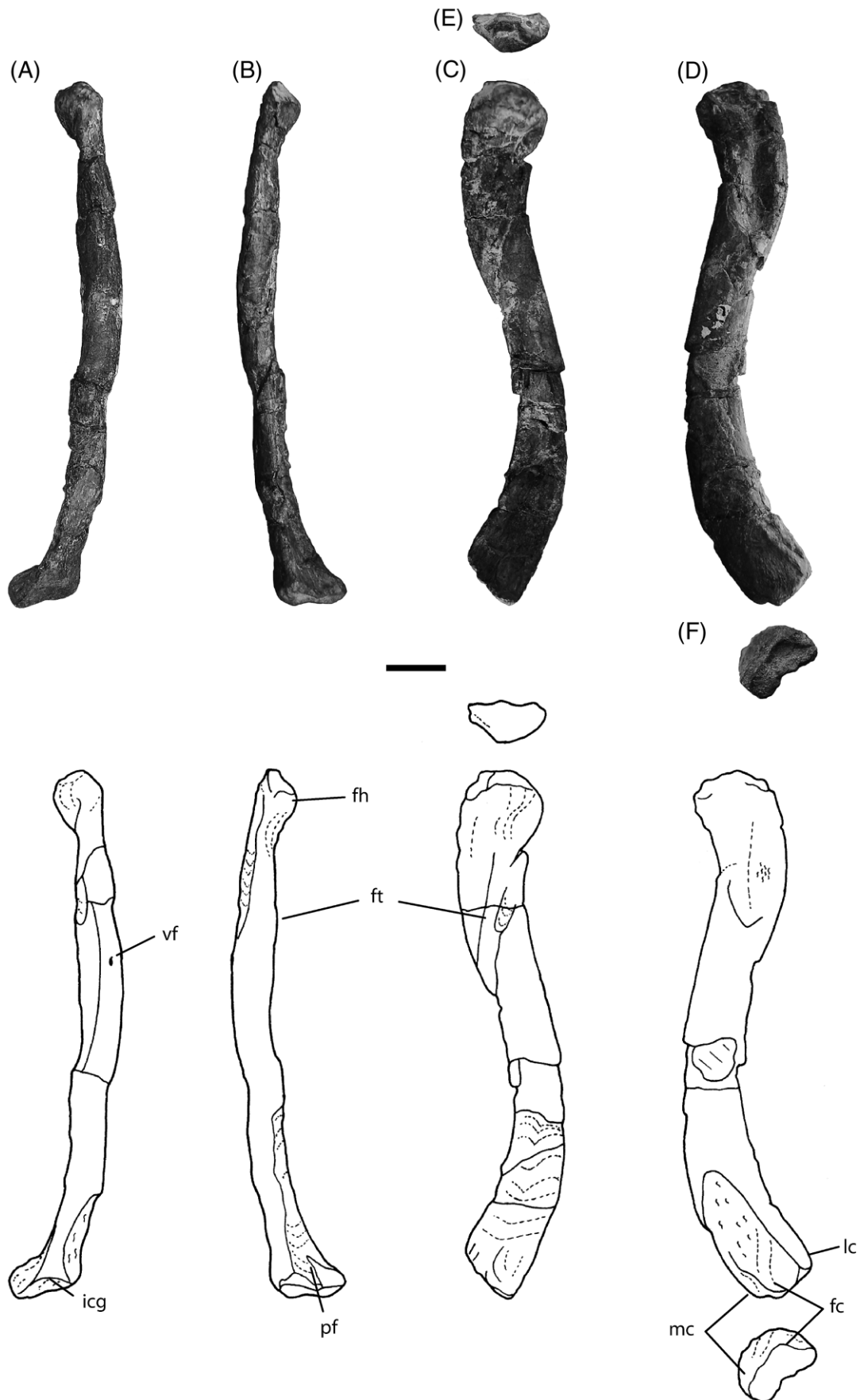


Figure 6 Photographs and equivalent line drawings (below) of left femur of *Gracilisuchus stipanicorum* (PVL 4597) in (A) anterior, (B) posterior, (C) medial, (D) lateral, (E) proximal and (F) distal views. Abbreviations: fc=fibular condyle; fh=femoral head; ft=fourth trochanter; icg=intercondylar groove; lc=lateral condyle; mc=medial condyle; pf=popliteal fossa; vf=vascular foramen. Scale bar=1 cm.

medially-projected femoral head present in the crocodylomorphs *Dromicosuchus*, *Kayentasuchus*, *Terrestrisuchus*, *Saltoposuchus* von Huene, 1921 (SMNS 12596), *Hallopus*, *Macelognathus vagans* Marsh, 1884 (Göhlich *et al.* 2005) and *Gobiosuchus* (Osmólska *et al.* 1997). On the other hand, the small anterior projection of the proximal end from the anterior surface of the shaft in lateral view is somewhat similar to that seen in the crocodylomorph *Pseudhesperosuchus*, but contrasts with the slightly more developed projection present in *Protosuchus* and *Caiman*, as well as with the well-developed anterior projection present in some pseudosuchians (e.g., *Riojasuchus*, *Fasolasuchus*, *Effigia*) and dinosauromorphs (e.g., *Marasuchus*, *Lagerpeton*).

On the medial surface of the femur there is a poorly-developed, shallow, fourth trochanter, which is located one-fourth distance of femur length from the proximal end, where it forms a short and somewhat elongated knob (Fig. 6C: ft). The presence of a fourth trochanter has been listed as a synapomorphic character of Archosauriformes (Gauthier 1984; Gauthier *et al.* 1988) or of less inclusive clades (e.g., Ezcurra *et al.* 2010). It is subsequently lost in Pterosauria and has different degrees of development in Dinosauria, including its absence in Maniraptora (Gatesy 1990). A well-defined ridge-like fourth trochanter is present in many archosauriforms (*Tropidosuchus* (PVL 4601), Phytosauria (e.g., *Parasuchus*, ISI R43), Aetosauria (e.g., *Aetosauroides*, PVL 2073), *Riojasuchus* (PVL 3827), *Batrachotomus kupferzellensis* (SMNS 52970), basal dinosauromorphs (e.g., *Lagerpeton*, PVL 4619; *Marasuchus*, PVL 3871), and some basal crocodylomorphs (e.g., *Dromicosuchus*, UNC 15574; *Kayentasuchus*, UCMP 131830; *Terrestrisuchus*, NHMUK PV OR10002)). A well-defined knob-like fourth trochanter is also seen in the basal pseudosuchians *Saurosuchus* (Sill 1974), Jalil & Peyer, 2007 (AZA 900), *Prestosuchus* (BSPG AS XXV10) and *Postosuchus* (Long & Murry 1995; Weinbaum 2007). A shallow fourth trochanter similar to *Gracilisuchus* is described for *Macelognathus* (Göhlich *et al.* 2005) as a weak axial crest, and in *Orthosuchus* (Nash 1975) as a thickening of the bone. In the basal crocodylomorphs *Pseudhesperosuchus* (PVL 3830) and *Trialestes* (PVL 3889) the fourth trochanter is also very shallow, as in *Gracilisuchus*. In the basal crocodyliforms *Gobiosuchus* (Osmólska *et al.* 1997) and GMPKU-P 200102 (Pol *et al.* 2004) the fourth trochanter is absent. This trochanter is a direct osteological correlate of the insertion of the *M. caudifemoralis longus*. Its anterior margin is limited in *Gracilisuchus* by a short and narrow groove of smooth texture, which is inferred to be the insertion point of *M. puboischiofemoralis internus 1*, and posteriorly there is a smooth surface where the *M. caudofemoralis brevis* may have inserted. Distal to the fourth trochanter, the shaft is mostly smooth. The anterior surface of the shaft is pierced by a small foramen located one-third from the proximal end, through which putative vessels for supply of the *M. femorotibialis internus* could pass, as is present in living crocodylians (Romer 1923).

The distal femoral condyles are seen in distal view (Fig. 6F), with a medial condyle (or inner tibial or tibial; Fig. 6D, F: mc) on the anteromedial angle, a fibular condyle (Fig. 6D, F: fc) on the anterolateral angle, and a lateral condyle (or outer tibial or tibiofibular crest; Fig. 6D, F: lc) posterolaterally. The distal articular surfaces of the condyles are almost flat. The fibular and medial condyles are separated on the anterior surface by a shallow intercondylar groove (or patellar groove; Fig. 6A: icg). A similar poorly-developed groove is also present in *Euparkeria*, *Tropidosuchus* (Arcucci 1990) and probably in *Turfanosuchus* (Wu & Russell 2001, fig. 10C, D). Among archosaurs, the poorly-developed groove is also seen in *Riojasuchus* (PVL 3827), *Marasuchus* (PVL 3870) and *Lagerpeton* (PVL 4619),

but in other taxa a deeper anterior groove is present (e.g., *Parasuchus*, *Aetosauroides* (PVL 2073), *Neo-aetosauroides* (PVL 3525), *Fasolasuchus* (PVL 3850), *Pseudhesperosuchus* (PVL 3830), *Hesperosuchus* (Colbert 1952, fig. 27), *Macelognathus* (Göhlich *et al.* 2005), *Orthosuchus* (Nash 1975, fig. 16A, C)).

The popliteal fossa (or flexor fossa) is located on the posterior surface, between the medial and the lateral condyles (Fig. 6B: pf), and is deeper than the anterior groove. This fossa is equally poorly developed in *Aetosauroides* (PVL 2073) and *Marasuchus* (PVL 3871), and comparatively much shallower than in most other taxa (e.g., *Tropidosuchus* (PVL 4601), *Lagerpeton* (PVL 4619), *Riojasuchus* (PVL 3827), *Neo-aetosauroides* (PVL 3525), *Fasolasuchus* (PVL 3850), *Pseudhesperosuchus* (PVL 3830), *Dromicosuchus* (Sues *et al.* 2003), and *Macelognathus* (Göhlich *et al.* 2005)). Finally, on the lateral surface, the fibular and the lateral condyles are separated by an almost flat surface (Fig. 6F), which is seen in a few taxa (e.g., *Aetosauroides* (PVL 3525), *Marasuchus* (PVL 3871)), in contrast to the variably developed groove seen in most taxa (e.g., *Lagerpeton* (PVL 4619), *Parasuchus* (Chatterjee 1978)), *Neo-aetosauroides* (PVL 3525), *Fasolasuchus* (PVL 3850), *Pseudhesperosuchus* (PVL 3830), *Dromicosuchus* (Sues *et al.* 2003)). The medial condyle is narrower than the fibular one, being more distally extended and with a sharper distal end, whereas the lateral condyle is barely developed and posteriorly directed.

3.2.2. Tibia (Fig. 7). The tibia is shorter than the femur (90% of the total femoral length, Table 2), a plesiomorphic character for Archosauria (Serenó 1991). Nevertheless, some exceptions are present within Pseudosuchia, such as the long limbed basal crocodylomorph *Terrestrisuchus* (Crush, 1984) and the protosuchian *Gobiosuchus* (Clark *et al.* 2004). The proximal end of the tibia is triangular in outline, with two flat articular surfaces for articulation with the distal end of the femur, which are posteriorly divided by a wide concavity (Fig. 7B, E: tpc). The medial proximal articular surface is antero-posteriorly longer and lateromedially wider than the lateral one, and both face slightly posteriorly. The proximal anterior surface exhibits a wide and deeply eroded hollow where the cnemial crest would have been located (nothing can be said about the morphology of the cnemial crest *contra* Romer (1972), see below).

The shaft of the tibia is straight, as in *Euparkeria* (SAM k 5867), *Aetosauroides* (PVL 2073), *Neo-aetosauroides* (PVL 3525), *Fasolasuchus* (PVL 3850), *Postosuchus* (Weinbaum 2007) and *Lagerpeton* (PVL 4619). By contrast, in some basal crocodylomorphs a slight posterior curvature to the distal end of the shaft is present, including *Sphenosuchus acutus* (Walker 1990), *Pseudhesperosuchus*, *Macelognathus vagans* (Göhlich *et al.* 2005) and *Dromicosuchus*, but absent in others such as *Terrestrisuchus*. The shaft has a mostly smooth surface and is mediolaterally compressed, with proximal and distal ends slightly mediolaterally expanded.

The distal end has a triangular outline, with a wide anterior surface and a tapered posterior one. On the anterior edge, the medial and lateral condyles are separated by a slight anterior depression. This end is lateromedially wider than antero-posteriorly long, as in *Dromicosuchus*, but contrasting with *Aetosauroides* and *Riojasuchus*. The distal articular surface articulates with the astragalus by two facets, which are slightly inclined in different directions, articulating with the astragalus in the so-called 'screw-joint' (Fig. 7B, F: s aa, s pa; Parrish 1986; Sereno & Arcucci 1990; Sereno 1991). The anterior region of the distal surface of the tibia is inclined posterodistally and contacts the anteroproximal surface of the astragalus, whereas the posterior surface of the distal tibia is inclined anterodistally with a lesser slope and articulates with the posteroproximal surfaces of the astragalus. The morphology of

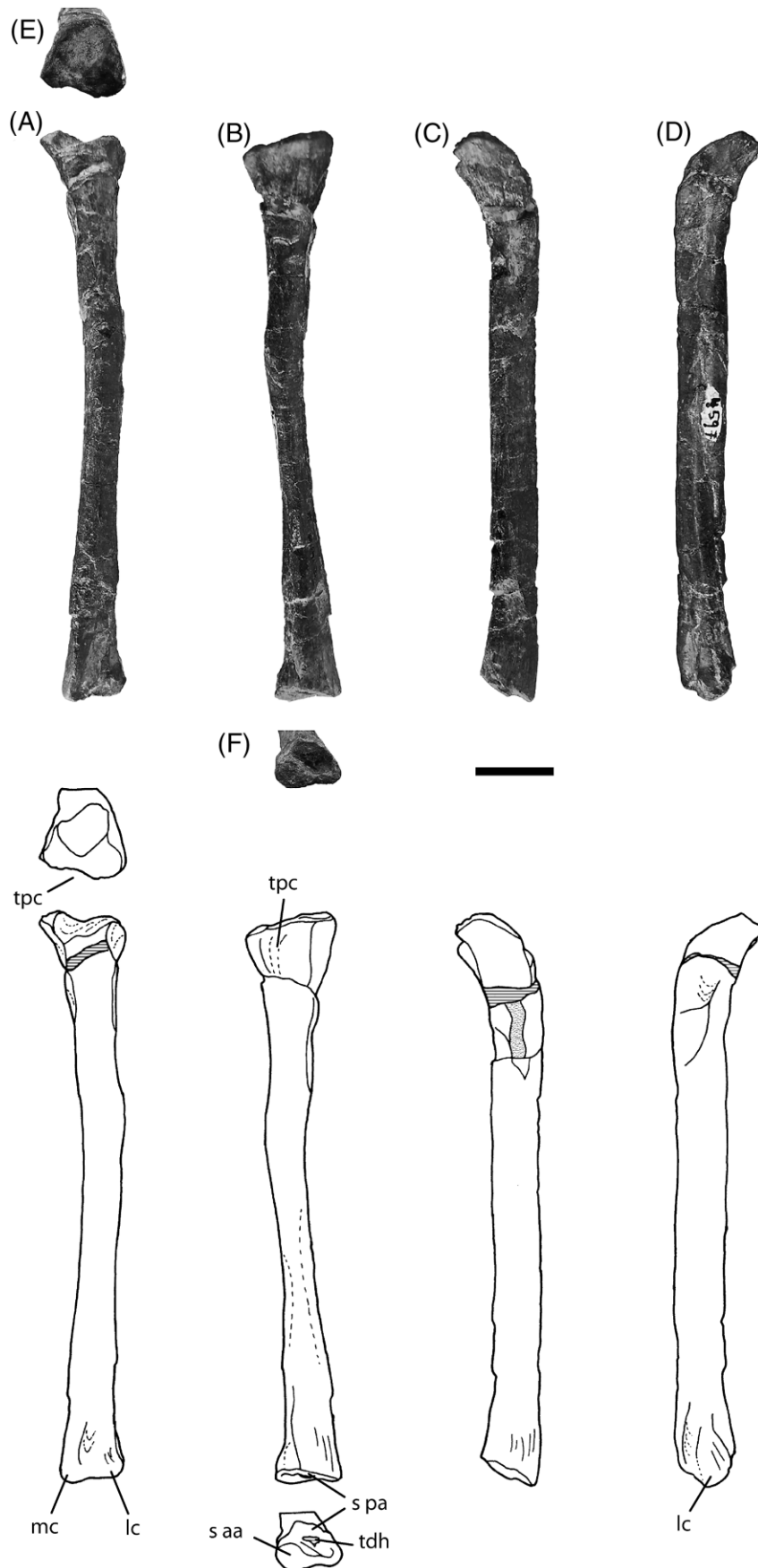


Figure 7 Photographs and equivalent line drawings (below) of left tibia of *Gracilisuchus stipanicorum* (PVL 4597) in (A) anterior, (B) posterior, (C) posteromedial, (D) anterolateral, (E) proximal and (F) distal views. Abbreviations: lc=lateral condyle; mc=medial condyle; s aa=anterior articular surface for astragalus; s pa=posterior articular surface for the astragalus; tdh=tibia distal hollow; tpc=tibial posterior concavity. Scale bar=1 cm.

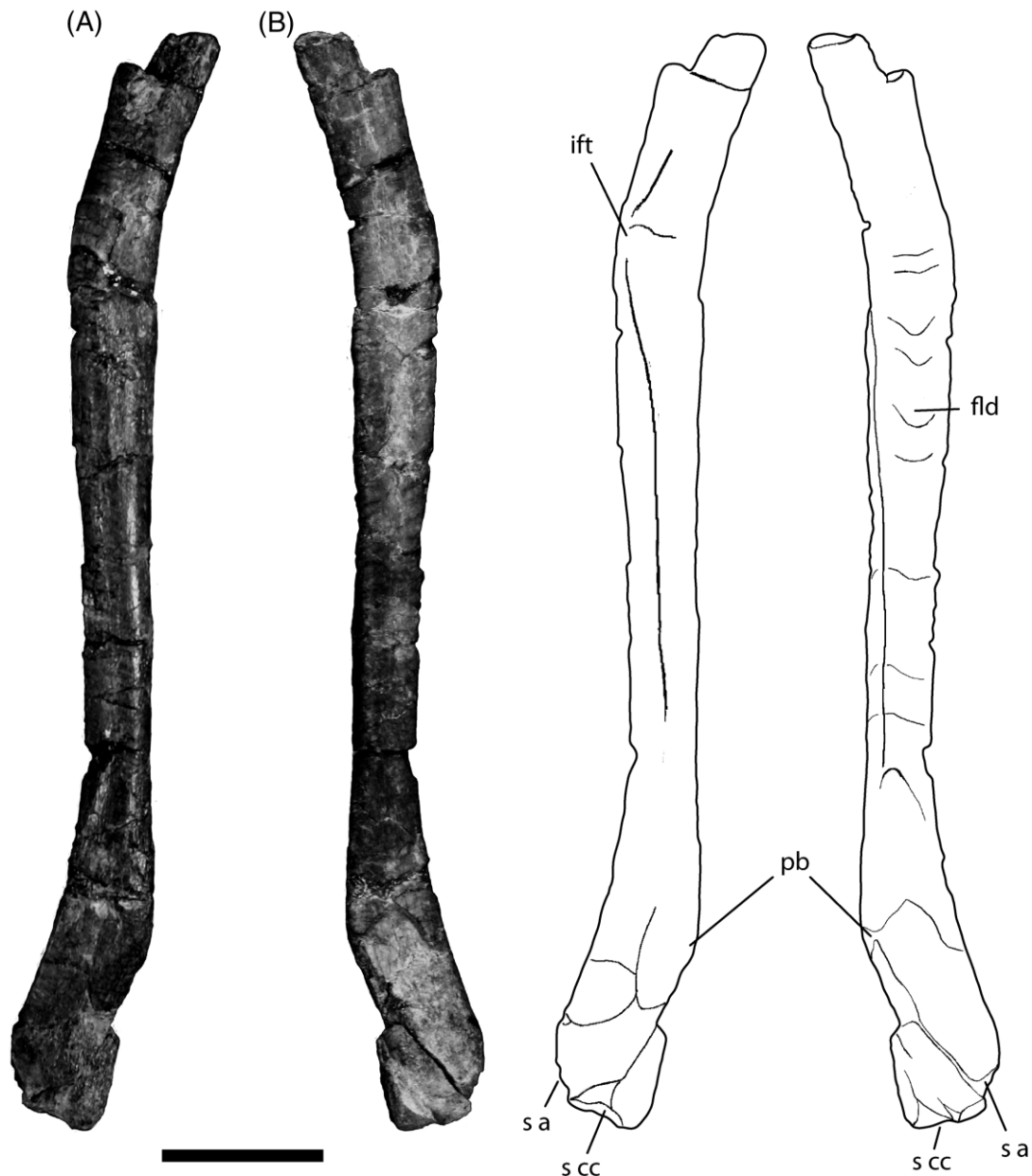


Figure 8 Photographs and equivalent line drawings (beside) of left fibula of *Gracilisuchus stipanicorum* (PVL 4597) in (A) anterior and (B) posterior views. Abbreviations: fld= fibular longitudinal depression; ift= iliofibular trochanter; pb= posterior bend; sa= articular surface for astragalus; scc= articular surface for the calcaneal condyle. Scale bar= 1 cm.

this end contrasts with that present in most basal archosauriforms, which possess a flat surface (e.g., *Euparkeria*, Sereno 1991; *Turfanosuchus*, Wu & Russell 2001). Pseudosuchia all show two diverging facets, with some variation amongst taxa. For example, *Neoacetosauroides* (PVL 3525) has the anterior surface flat and wide and the posterior one convex and elongated distally, whereas *Riojasuchus* (PVL 3827) shows an anterior surface anterodistally inclined and a posterior one posterodistally inclined. Besides, the latter two taxa have the posterior edge more distally extended than the anterior, similar to *Marasuchus*, but contrasting with *Gracilisuchus*, in which the anterior edge reaches a more distal position. It also contrasts with *Sphenosuchus* (Walker 1990), where the medial and lateral articular facets meet at a sharp angle, and with *Macelognathus* (Göhlich *et al.* 2005), which has an anterior convex facet and a posterior concave one. In the centre of the distal surface of *Gracilisuchus* there is a shallow hollow (Fig. 7F: tdh), which might be the insertion site for ligaments that hold the tarsal elements with the distal end of the crus.

3.2.3. Fibula (Fig. 8). The fibula is a gracile bone, antero-posteriorly compressed for most of its length. It is slightly thickened in the medial region and mediolaterally expanded at its proximal and distal ends. The fibula is almost complete, but lacks a small portion of its proximal end; the fibula length can be estimated on the basis of the tibial length. This element has some degree of *post-mortem* deformation, including compression and rotation on the longitudinal axis, and the exact position and contacts are difficult to determine, thus the description will be based on the orientation in which it was originally found.

From less than one-fourth of its length from the proximal preserved end, the fibula has an anteromedial bend on which a weakly developed iliofibular trochanter is situated (Fig. 8A: ift). This trochanter is located around 25% from the proximal based on the total length of the tibia. This very proximal position is also found in the living form *Caiman latirostris* (MPEF-AC 205) and possibly in the crocodylomorph *Terrestrisuchus*, but the exact location cannot be determined due

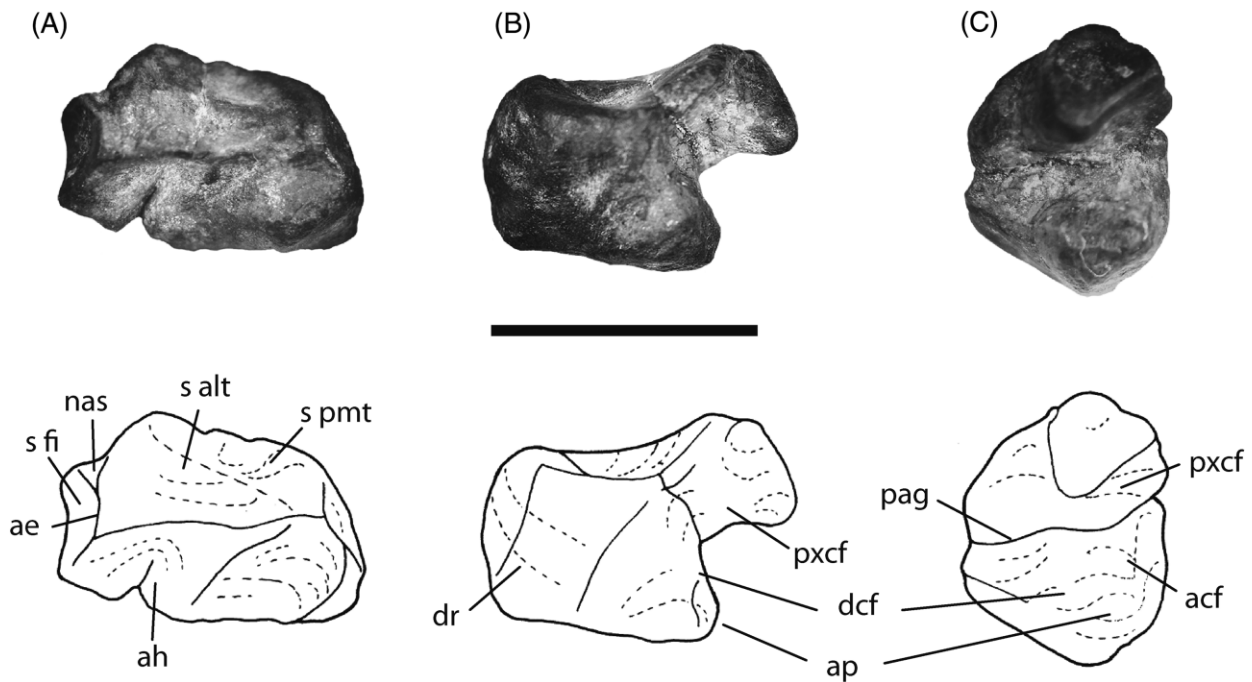


Figure 9 Photographs and equivalent line drawings (below) of right astragalus of *Gracilisuchus stipanicorum* (PVL 4597) in (A) proximoanterior, (B) distoposterior and (C) lateral views. Abbreviations: acf=anterior calcaneal facet; ae=anterior edge; ah=anterior astragalular hollow; ap=astragalular peg; dcf=distal calcaneal facet; dr=distal roller; nas=non articular surface; pag=posterior astragalular groove; pxcf=proximal calcaneal facet; s alt=anterolateral articular surface for the tibia; s fi=articular surface for the fibula; s pmt=posteromedial articular surface for the tibia. Scale bar=1 cm.

to incomplete preservation of its distal end (Crush 1984, text-fig. 9). Other taxa have a more distally positioned trochanter, at around one-third and one-half the length from the proximal end (*Myriosuchus planirostris* (41%), *Riojasuchus* (40%), *Neoaetosauroides* (48%), *Aetosauroides* (34%), *Fasolasuchus* (39%), *Postosuchus alisonae* (44%), and *P. kirkpatricki* (Weinbaum 2007)). A poorly developed trochanter is also present in the archosauriform *Euparkeria* (Serenó 1991, p.27), the dinosauriform *Marasuchus* (Serenó & Arcucci 1994), the rauisuchian *Effigia* and in the basal crocodylomorphs *Terrestriusuchus* and *Dromicosuchus*. A trochanter is absent in *Tropidosuchus* and the basal crocodyliform *Orthosuchus*. A well-developed trochanter is present in several taxa, such as dinosauromorphs (e.g., *Lagerpeton*), phytosaurs (e.g., *Parasuchus*), aetosauroids (e.g., *Neoaetosauroides*, *Aetosauroides*, *Aetosaurus*) and rauisuchians (e.g., *Saurosuchus*, *Prestosuchus*, *Postosuchus alisonae*). Distal to the iliofibular trochanter, the anterior surface of the bone in *Gracilisuchus* is smooth, with a poorly developed longitudinal muscular line along the medial margin, which could be the osteological correlate for the boundary between the origins of the *Mm. fibularis longus et brevis* (Romer 1923). The posterior surface is also smooth, with a shallow, longitudinal depression at the level of the trochanter (Fig. 8B: fld) that vanishes distally. Close to the distal end there is a posteriorly directed bend (Fig. 8: pb) and, distal to it, the posterior margin is broken. The distal articular surface has two facets for contact with the proximal tarsals. The lateral articular surface is slightly concave and contacts the lateral proximal surface of the calcaneal condyle (Fig. 8: s cc), whereas the medial articular surface is strongly mediolaterally directed and contacts the fibular surface (lateral) of the astragalus (Fig. 8: s a).

3.2.4. Proximal tarsals. The two proximal tarsals (i.e., astragalus and calcaneum) were recovered in both hind limbs of PVL 4597, which is the single specimen that preserves these elements (see below). The tarsus has a crurotarsal-type articu-

lation (Schaeffer 1941), in which the astragalus is firmly attached to the tibia and the calcaneum to the distal tarsals and pes. Thus part of the articulation goes between the tarsus and crus. This articulation contrasts with the mesotarsal type (Schaeffer 1941), characteristic of Ornithodira, in which both proximal tarsals are attached to the crus and thus the articulation goes between the proximal and distal tarsals. Two specific types of articulations have been described of the crurotarsal type. The commonest is the 'crocodile-normal' type (Chatterjee 1978) found in most crurotarsans, including *Gracilisuchus*, in which the astragalus has a lateral projection or peg that articulates into a medial hole or socket of the calcaneum. The second is the 'crocodile-reverse' type (Chatterjee 1978) only found in Ornithosuchidae (Serenó & Arcucci 1990; Serenó 1991), in which the calcaneum has the peg to articulate into the socket of the astragalus. The two proximal tarsals of *Gracilisuchus* are similar in size (Table 2); they articulate laterally and are located in the same horizontal plane.

3.2.5. Astragalus (Fig. 9). The proximal (dorsal) region has two articular surfaces for the tibia and fibula that are steeply angled, separated by a sharp edge anteriorly and by a non-articular surface posteriorly (Fig. 9A: ae, nas). The tibial facet is the larger, occupying around three-quarters of the medial side. It is somewhat concave, divided into two surfaces by a low ridge, a posteromedial surface and an anterolateral one (Fig. 9A: s alt, s pmt). The tibial facet as a whole is somewhat concave and proximoposteriorly oriented, but each of its facets are slightly divergent relative to each other, displaying a so-called screw-joint articulation with the tibia, as in other Crurotarsi (Parrish 1986; Serenó & Arcucci 1990; Serenó 1991; Fig. 9A). This morphology contrasts with the single tibial facet of basal archosauriformes, such as *Euparkeria* (Serenó 1991) and *Turfanosuchus* (Wu & Russell 2001), ornithodiran archosaurs (e.g., *Marasuchus*; Serenó 1991) and parasuchia (USNM 18313, Parrish 1993). Two diverging facets are present in other taxa such as Aetosauria (e.g., *Neoaetosauroides*, *Stagonolepis*

wellesi, Long & Murry 1995, fig. 82), and 'rauisuchians' (e.g., *Saurosuchus*, Sill 1974; *Fasolasuchus*, PVL 3850). In the basal crocodylomorph *Sphenosuchus*, the astragalus was not recovered, but based on the morphology of the distal tibia where two angled facets are seen, the presence of two surfaces in the tibial astragalal facet can be inferred. Conversely, the basal crocodyliform *Protosuchus* lacks the two facets, having a single groove (Hecht & Tarsitano 1984), similar to the living form *Caiman*, with a very concave and continuous facet. The fibular articular facet is flat, strongly proximolaterally oriented, and smaller than the tibial one.

On the anterior surface, the anterior astragalal hollow (Fig. 9A: ah; Sereno 1991; extensor hollow *sensu* Sullivan 2007) occupies 50% of the lateromedial width in the left astragalus, and more than 50% in the right one, reaching the proximal border in both astragali. This structure is larger than 50% of the anterior surface in non-archosaurian archosauriforms (e.g., *Euparkeria*, *Turfanosuchus*). It is also of this proportion in Phytosauria (e.g., USNM 18313, Sereno 1991, fig. 6), Aetosauria (e.g., *Stagonolepis*, Walker 1961), and many 'rauisuchians' (e.g., *Saurosuchus*, Sill 1974; *Postosuchus alisonae*, Peyer *et al.* 2008), except *Fasolasuchus* (PVL 3850), in which a small fossa is present. Conversely, in *Lagerpeton* and *Marasuchus* a smaller and proximally located hollow is present (Sereno & Arcucci 1994). In addition, *Gracilisuchus* has inside this fossa a thin and deeper pit located close to the proximolateral margin.

The articular surfaces with the distal tarsals and metatarsal elements are located in the distal region of the astragalus of *Gracilisuchus*, the distal roller (*sensu* Cruickshank 1979; Fig. 9B: dr). Although these articular facets are not clear, some deductions can be made concerning their structure. In the distal middle region there is a wide, slightly laterally-orientated facet that could be for articulation with the metatarsal II, or with it and the distal tarsal 3. Medial to this region, there is a narrower and more medially oriented facet, probably for articulation with the metatarsal I. On the medial side, the surface is flat, nearly vertical, and slightly posteromedially oriented, that could be the attachment site for the medial portion of the extensor retinaculum (Tarsitano 1981). The morphology of this region contrasts with that of basal archosauriforms with a flat distal surface larger than that of *Gracilisuchus* (e.g., *Euparkeria*, Ewer 1965, Sereno 1991; *Turfanosuchus*) and a lower medial one (e.g., *Euparkeria*, Ewer 1965, Sereno 1991), but similar to the flat distal surface of the phytosaur *Parasuchus*. Conversely, the high and anteromedially directed distal facet of *Gracilisuchus* resembles that of Aetosauria (e.g., *Aetosauroides*), Ornithosuchidae (e.g., *Riojasuchus*), 'rauisuchians' (e.g., *Prestosuchus*), basal Crocodylomorpha (e.g., *Terrestriusuchus*) and Crocodyliformes (e.g., *Orithosuchus*, *Protosuchus*), but contrasts with the strongly anteriorly-directed facet for the metatarsals present in *Fasolasuchus* (Bonaparte 1981).

Three distinct facets for contact with the calcaneum (Sullivan 2007) can be seen in lateral view (Fig. 9C). The proximal calcaneal facet (Fig. 9C: pxcf) is anterodistally oriented and slightly concave in an anteroposterior direction. This facet forms the sliding articulation with the proximal astragalal facet of the calcaneal condyle. The anterior calcaneal facet (Fig. 9C: acf; extensor calcaneal facet *sensu* Sullivan 2007) is somewhat flat and anterolaterally oriented. Posterior to the latter, is the distal calcaneal facet (Fig. 9C: dcf), which is long, low, somewhat convex and posterolaterally oriented. The two calcaneal facets form the laterally-directed astragalal peg (Fig. 9C: ap) that fits into the calcaneal socket, which in turn possesses a planar astragalal facet on the anterior region for contact with the former facet, and a posterior astragalal facet for contact with the latter. The anterior calcaneal facet of the

astragalus is larger and longer posteriorly than the proximal calcaneal facet of the astragalus, a characteristic feature of Crurotarsi (Sereno 1991), except in *Riojasuchus*, where both surfaces are fused (Sereno 1991, fig. 7). The contact for the calcaneum in *Gracilisuchus* is more complex than the simple and slightly curved astragalal surface of non-archosaur archosauriforms (e.g., *Euparkeria*, *Turfanosuchus*). The posterior astragalocalcaneal groove (Fig. 9C: pag; Sereno 1991) is situated posteriorly, proximal to the distal calcaneal facet, with an anteroposterior orientation.

3.2.6. Calcaneum (Fig. 10). The calcaneum is anteroposteriorly elongated, being almost twice as deep as it is wide. The calcaneal condyle (Fig. 10: cc), with a continuous, proximo-anterior, hemicylindrical articular facet, is located in the anterior region of the calcaneum. The sliding articulations with the fibula and astragalus occur on the proximal surface of the condyle. The contact with the fibula is in the lateral half of the proximal surface of the calcaneal condyle (Fig. 10A, C: s fi), and the contact with the astragalus is in the medial half. The latter is the proximal astragalal facet (Fig. 10A: pxaf) that contacts with the proximal calcaneal facet of the astragalus. The distal surface of the calcaneal condyle is flat and contacts with distal tarsal 4; it is ventrally directed and forms a sharp angle with the anterior surface (Fig. 10C: s dt4). A calcaneal condyle, and thus the sliding articulation with the fibula, is characteristic of phytosaurs and pseudosuchians (e.g., USNM 18313, Sereno 1991; *Aetosauroides*; *Fasolasuchus*; *Saurosuchus*; *Riojasuchus*; *Dromicosuchus*; *Macelognathus*), whereas it is absent in some basal archosauriforms such as *Euparkeria*, but not in *Turfanosuchus* (Wu & Russell 2001). Both articular facets of the proximal calcaneal condyle surface of *Gracilisuchus* are continuous, as in most pseudosuchians except *Riojasuchus*, which possesses both articular facets slightly angled laterally and medially.

The medial side of the condyle bears a deep calcaneal socket (Fig. 10A, B: cs) for articulation with the astragalal peg. This socket is absent in the archosauriform *Euparkeria*, but present in *Turfanosuchus* (Wu & Russell 2001), as well as in crurotarsan taxa with a crocodile normal tarsus (i.e., Phytosauria, Aetosauria, Rauisuchia, Crocodylomorpha). The anterior surface of this socket forms the anterior astragalal facet (Fig. 10B: aaf; extensor astragalal facet *sensu* Sullivan 2007), which is posteromedially oriented and contacts the anterior calcaneal facet of the astragalus. The posterior surface of the socket contacts the distal calcaneal facet of the astragalus and is thus called the distal astragalal facet (Fig. 10B: daf). The latter surface is located on the anterior surface of the medial flange (Brinkman 1981), being proximodistally low and mediolaterally long, reaching medially the level of the medial margin of the calcaneal tuber in proximal view (Fig. 10A). The distal astragalal facet has a posteromedial orientation, forming an angle with the calcaneal condyle that is slightly more than 90°, as in other pseudosuchians with similar angulations (e.g., *Aetosauroides*, *Effigia*) or with right angles (e.g., *Stagonolepis welllesi*, Long & Murry 1995; *Saurosuchus*; *Fasolasuchus*). Conversely, it differs from the basal Crocodyliformes *Hemiprotosuchus* and *Protosuchus*, where the posteromedial orientation forms a more obtuse angle with the calcaneal condyle. It also differs from the situation seen in phytosaurs (e.g., *Parasuchus*) where a medially developed facet is lacking. Posteriorly, between the distal astragalal facet and the calcaneal tuber, there is a marked notch (Figs. 10A, B: n), also seen in *Aetosauroides*, *Fasolasuchus*, *Dromicosuchus*, *Protosuchus*, *Caiman latirostris* (MPEF-AC 205), where it is fairly well developed and forms the neck of the tuber, and also probably in the archosauriform *Turfanosuchus*. The lateral surface of the calcaneal condyle is mostly flat with a slight median depression, probably for the

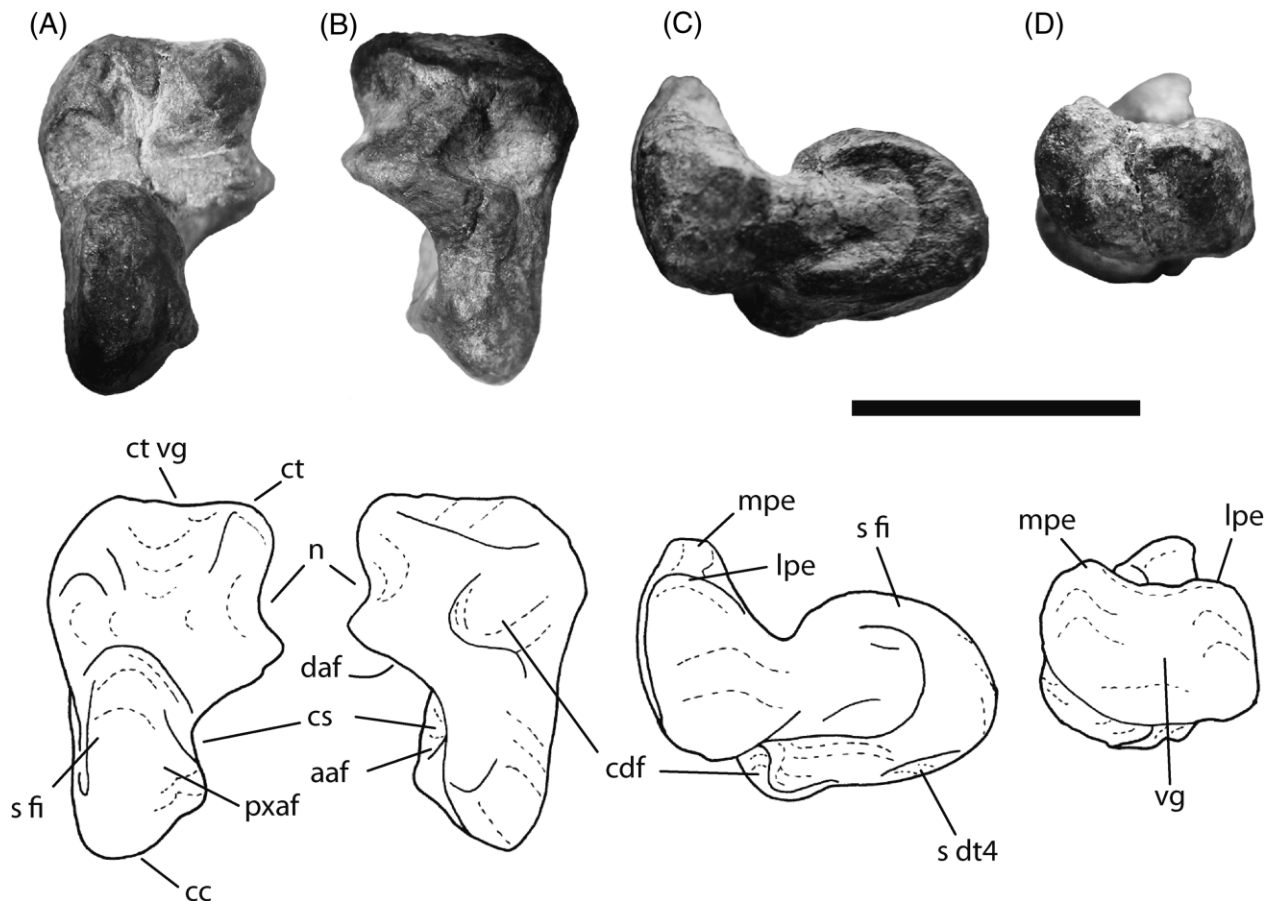


Figure 10 Photographs and equivalent line drawings (below) of right calcaneum of *Gracilisuchus stipanicorum* (PVL 4597) in (A) proximal, (B) distal, (C) lateral and (D) posterior views. Abbreviations: aaf=anterior astragalar facet; cc=calcaneal condyle; cdf=calcaneal distal (ventral) fossa; ct=calcaneal tuber; daf=distal astragalar facet; lpe=lateral proximal edge of calcaneal tuber; mpe=medial proximal edge of calcaneal tuber; n=notch; pxaf=proximal astragalar facet; s dt4=articular surface for the dt4; s fi=articular surface for the fibula; vg=posterior vertical groove of calcaneal tuber. Scale bar=1 cm.

attachment of the lateral portion of the extensor retinaculum (Tarsitano 1981).

The calcaneal tuber of *Gracilisuchus* is posteriorly directed and oriented in the same axis as the calcaneal condyle. This contrasts with basal archosauriformes (e.g., *Euparkeria*, *Tropidosuchus*) and Parasuchia (e.g., USNM 18313; *Parasuchus* (ISI R43)) that have a calcaneal tuber somewhat laterally directed. The posteriorly-directed condition of the tuber of *Gracilisuchus* is also present in *Turfanosuchus* and all non-crocodylian suchians, such as aetosauroids (e.g., *Neoaetosauroides*, PVL 3525), raiuisuchians (e.g., *Fasolasuchus*, PVL 3850; *Saurosuchus*, Sill 1974), crocodylomorphs (e.g., *Terrestriusuchus*, Crush 1984; *Dromicosuchus*, Sues *et al.* 2003) including crocodyliformes (e.g., *Protosuchus*); but living forms of the clade (e.g., *Caiman*) are similar to that of phytosaurs. In *Gracilisuchus* the calcaneal tuber is wider than high, a character present in phytosaurs (e.g., *Parasuchus*, USNM 18313, Sereno 1991), aetosauroids (e.g., *Stagonolepis*, *Aetosauroides*), and *Turfanosuchus*, but not in the archosauriform *Euparkeria*, which has a tuber as high as wide (SAM K 5867; Sereno 1991). Among Pseudosuchia, a tuber that is higher than wide is seen in some raiuisuchians (e.g., *Fasolasuchus*; *Saurosuchus*; *Postosuchus alisonae*, Peyer *et al.* 2008, fig. 9C), the crocodylomorph *Macelognathus*, and in some crocodyliforms (e.g., *Protosuchus*, AMNH 3024).

The posterior surface of the tuber of *Gracilisuchus* bears a very shallow median groove that is vertically aligned (Fig. 10A, B, D: vg) and which held the tendon of the *M. gastrocnemius externus* on its way to the plantar aponeurosis (Tarsitano 1981). This groove is present in most suchians,

including aetosauroids, raiuisuchians and crocodylomorphs. It divides the posterior surface into a lateral and a medial region, with the medial region having a proximal edge more proximally extended than the lateral one (Fig. 10C, D: mpe, lpe). This morphology is also found in *Hemiprotosuchus jachaleroi* (PVL 3829) and *Caiman latirostris* (MPEF-AC 205), while the converse condition (with the lateral region reaching a more proximal position than the medial one) is present in *Stagonolepis wellsi* (Long & Murry 1995, fig. 82), *Fasolasuchus tenax* (PVL 3850) and *Postosuchus kirkpatricki* (Long & Murry 1995).

On the distal surface of the calcaneal tuber is a distal calcaneal fossa (Fig. 10B, C: cdf), a deep and wide depression that occupies the major part of the lateromedial distal surface, and which is homologous to the lateral channel of Crocodylia (Hecht & Tarsitano 1984). It is anteriorly limited by a small posterior projection of the distal surface of the calcaneal condyle. This fossa is also present in aetosauroids (e.g., *Aetosauroides*, *Stagonolepis*), raiuisuchians (e.g., *Fasolasuchus*; *Saurosuchus*; *Postosuchus kirkpatricki*; *Prestosuchus chiniquensis*, BSPG XXV 11C) and the Crocodyliformes *Protosuchus* and *Hemiprotosuchus*; but is absent in the archosauriforms *Euparkeria* and the phytosaurs *Parasuchus* and USNM 18313.

3.2.7. Distal tarsal 4 (Fig. 11). The distal tarsal 4 is the single distal tarsal element preserved of *Gracilisuchus* (*contra* Romer 1972, Bonaparte 1975a; see below). The distal tarsal 4 of both feet are preserved, but not in life position. These elements are pyramidal in shape, with the right distal tarsal 4 (Fig. 11A, B) higher and narrower than the left one (Fig. 11C,

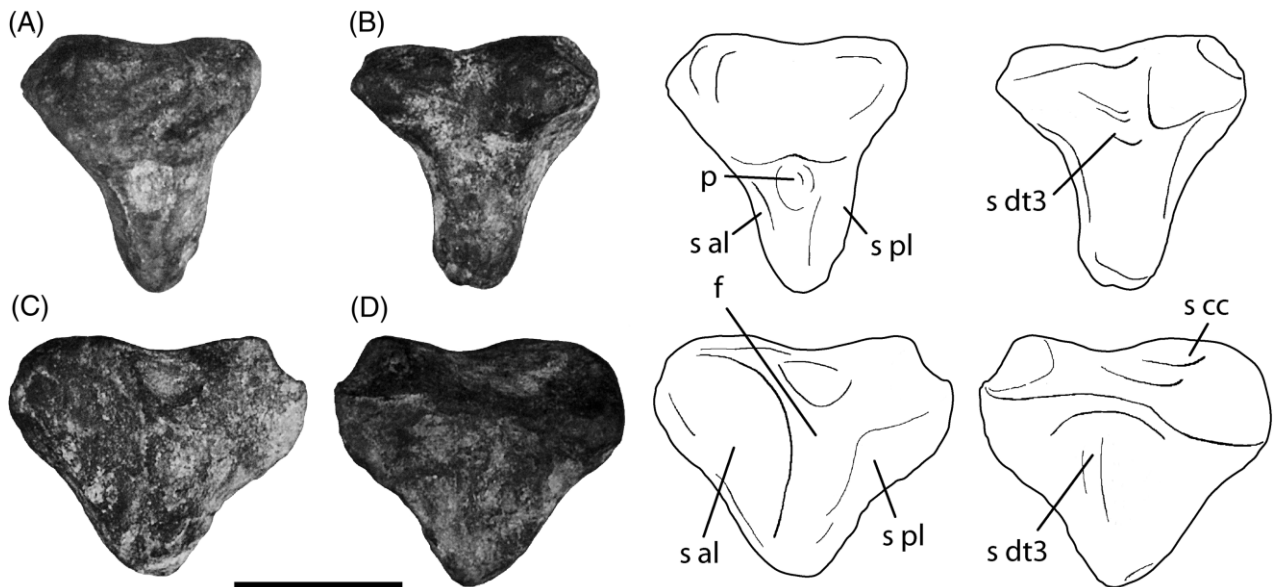


Figure 11 Photographs and equivalent line drawings of right (A, B) and left (C, D) distal tarsal 4 of *Gracilisuchus stipanicorum* (PVL 4597) in (A, C) ?dorsal and (B, D) ?ventral views. Abbreviations: f=flat small surface; p=pit; s al=anterolateral articular surface; s cc=articular surface for the calcaneal condyle; s dt3=probable articular surface for the dt3; s pl=posterolateral articular surface. Scale bar=1 cm.

D), which is more depressed and expanded. A pyramidal morphology is also seen in *Saurosuchus* (Sill 1974), but different morphologies of this element are found in *Euparkeria*, *Riojasuchus* (where the element is larger and square-shaped), *Aetosauroides* (more complex in shape) and in the crocodylomorph *Terrestriusuchus* (Crush 1984) and the crocodyliform *Hemiprotosuchus*, that have a lateromedial anterior expansion as wide as the posterior height. In *Gracilisuchus* the base of this pyramid has slightly concave edges, a concave surface that could be medially directed for contact with the distal tarsal 3 (Fig. 11B, D: s dt3). A concave facet for contact with distal tarsal 3 is also described for *Saurosuchus*, *Effigia* and *Riojasuchus*. The tip of the pyramid has a small, somewhat flat surface in the left element (Fig. 11C: f), but a small pit in the right one (Fig. 11A: p). The proximal surface has a somewhat asymmetric hour-glass shape with the posterior region narrower than the anterior, where the latter may have contacted with the distal surface of the calcaneal condyle (Fig. 11B, D: s cc). The anterolateral (Fig. 11A, C: s al) and posterolateral (Fig. 11A, C: s pl) surfaces are almost flat to slightly concave, where the former facet would have contacted with metatarsal V. The morphology of this facet contrasts with that of *Saurosuchus*, which was described as being saddle-shaped and convex.

3.2.8. Metatarsus (Fig. 12). The five metatarsals are preserved in both feet, with the left ones articulated and better preserved. They are proximally and partially overlapped, with metatarsal I on the dorsomedial proximal surface of metatarsal II and so on. This configuration is present in basal Archosauriformes (e.g., *Euparkeria*), Parasuchia (e.g., *Parasuchus*, ISI R 43), *Riojasuchus* (PVL 3827), Aetosauria (e.g., *Aetosauroides*, PVL 2073; *Neoetosauroides*, PVL 3525), some 'rauisuchians' (e.g., *Prestosuchus chiniquensis*) and Crocodylomorpha (e.g., *Macelognathus*, Göhlich *et al.* 2005; *Protosuchus*, Hecht & Tarsitano 1984; *Orthosuchus*, Nash 1975) including living forms (e.g., *Caiman*, MPEF-AC 205). By contrast, the proximal ends of the metatarsals are more vertically oriented and thus contact along the entire lateral surfaces of metatarsals in some other 'rauisuchians' (e.g., *Postosuchus alisonae* (UNC 15575), *Effigia* (Nesbitt 2007, fig. 47A), *Saurosuchus* (Sill 1974, p. 346)), as well as in Ornithodira (e.g., *Marasuchus*, *Lagerpeton*). Measurements of the shaft width have been taken from

the proximodistal middle of metatarsals (Table 2). In *Gracilisuchus*, the overall morphology of metatarsals I to IV are more gracile (measured as the width at the mid-shaft over the total length) than in *Euparkeria*, *Parasuchus*, aetosaurs, *Riojasuchus* and the preserved elements of the basal crocodylomorph *Sphenosuchus*, but are similar or slightly more robust than in *Marasuchus* (PVL 3870), the preserved elements of *Macelognathus*, *Terrestriusuchus* and *Protosuchus*.

The metatarsus of *Gracilisuchus* decreases in robustness from metatarsal I to IV, increase in length from metatarsal I to III, and decrease in width up to metatarsal IV. Metatarsal I is the shortest, as in *Euparkeria*, *Tropidosuchus*, *Neoetosauroides*, *Saurosuchus*, *Postosuchus*, *Riojasuchus* and *Marasuchus*, but contrasts with other forms in which metatarsal I is slightly longer than the metatarsal IV, as in *Effigia* (Nesbitt 2007, fig. 47B) and *Terrestriusuchus* (Crush 1984, text-fig. 10E). Metatarsal I has a triangular proximal articular surface and the lateral proximal edge slightly expanded laterally. Distally, this metatarsal expands to form the distal ginglymum (Fig. 12B: gy) for articulation with the proximal-most phalanx, in which the lateral and medial surfaces have shallow depressions for the collateral ligaments (Fig. 12B: cl) and the dorsal surface has a deep extensor pit (Fig. 12A: ep). Metatarsal II also has a triangular proximal surface with a lateral expansion overlapping metatarsal III. The distal end is higher dorsoventrally than metatarsal I; it has a larger and deeper fossa for the collateral ligament on the lateral side compared to the medial one. The proximal end of metatarsal III is very depressed and much more expanded both laterally and medially than the other metatarsals, with its lateral expansion the largest of all the digits. At the distal end, the dorsal extensor pit (Fig. 12A: ep) is the deepest and longest among metatarsals, and the fossae for the collateral ligaments are shallow on both sides. On the ventral surface, a deep longitudinal flexor groove is present, deeper than in other elements.

Metatarsal III is slightly longer than metatarsal IV, similar to the condition present in *Riojasuchus* (PVL 3827), *Stagonolepis* (Walker 1961), *Neoetosauroides* (PVL 3525), *Saurosuchus* (Sill 1974), *Hallopus* (Walker 1970), probably *Sphenosuchus* (Walker 1990), and *Marasuchus* (PVL 3870). Metatarsal IV is slightly shorter than metatarsal III and the narrowest of the

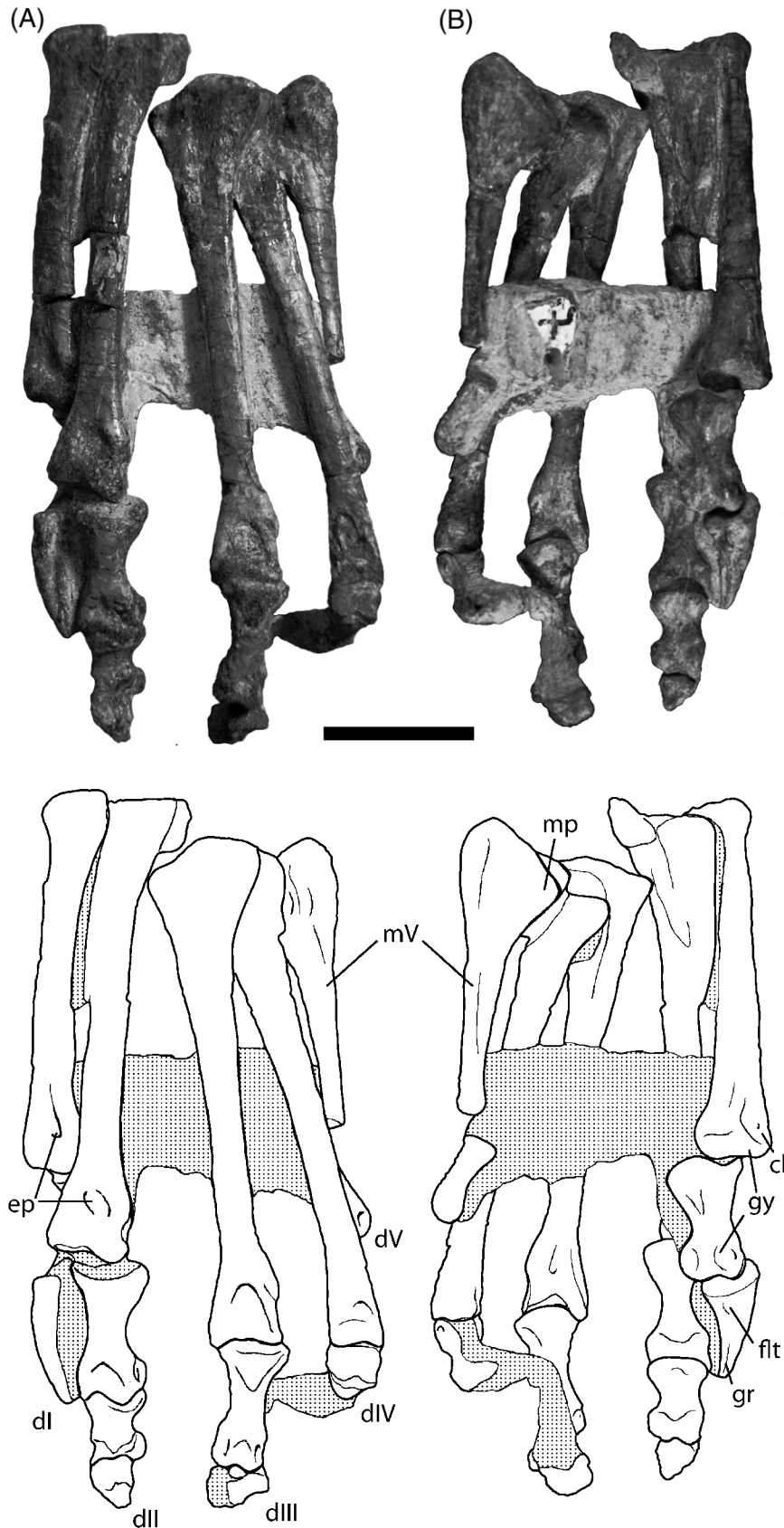


Figure 12 Photographs and equivalent line drawings (below) of left pes of *Gracilisuchus stipanicorum* (PVL 4597) in (A) dorsal and (B) ventral views. Abbreviations: cl=depression for the collateral ligament; ep=extensor pit; dI-dV=digits I to V; ft=flexor tubercle; gr=median ventral groove; gy=ginglymus; mp=medial projection; mV=metatarsal V. Scale bar=1 cm.

metatarsals. It is a straight bone, as in other archosaurs (e.g., *Neoaetosauroides*, PVL 3525; *Riojasuchus*, PVL 3827), unlike the slightly curved one present in *Saurosuchus* (Sill 1974) and Dinosauriformes (Novas 1996). The distal end is poorly pre-

served, being narrow with shallow dorsal and ventral depressions. Metatarsal V is the most distinct of the metatarsals. It has an elongated subtriangular shape in both dorsal and ventral views, where close to the proximal end it is expanded as

a medial projection (Fig. 12B: mp) with a short and straight proximomedial edge and a longer and somewhat concave edge distal to this projection. The proximal region has a triangular outline in proximal view, with a flat ventral (plantar) surface, a dorsomedial surface that contacts metatarsal IV, a lateral one distolaterally inclined, and a small facet in the proximomedial region that contacts distal tarsal 4. This morphology is similar to that found in *Riojasuchus* (PVL 3827), but contrasts with other taxa where there is a medial extension. In *Euparkeria* (Ewer 1965), *Parasuchus* (ISI R 43), *Aetosauroides* (PVL 2073), *Neoaetosauroides* (PVL 3525) and some rauisuchians (e.g., *Saurosuchus*, Sill 1974; *Batrachotomus*, Gower & Schoch 2009), the proximal end is medially enlarged into a hooked-shaped structure forming a nearly 90-degree proximomedial angle between the proximal edge and a long medial facet for distal tarsal 4. In other rauisuchians (e.g., *P. alisonae*, UNC 15575; *Effigia*, Nesbitt 2007), a smaller medial expansion is present, with the facet for distal tarsal 4 proximomedially directed.

Among Crocodylomorpha, two different morphologies are observed. In *Hemiprotosuchus* (PVL 3829) and probably *Terrestrisuchus* (Crush 1984) a triangular expansion similar but less developed than in *Gracilisuchus* is present, and in *Protosuchus* (AMNH 3024) and *Caiman* (MPEF-AC 205) the medial expansion is better developed and the contact for distal tarsal 4 is medial. Furthermore, compared to *Gracilisuchus*, the latter taxa have a reduced metatarsal V. Up to the end, this metatarsal becomes narrower and higher, with a subrectangular distal end lacking the typical ginglymus of other metatarsals. As preserved, the shaft of this metatarsal is oriented parallel to the remaining elements, as also occurs in *Parasuchus*, *Riojasuchus*, *Neoaetosauroides* and *Stagonolepis*, but the metatarsal diverges laterally in *Euparkeria*, *Ticinosuchus ferox* Krebs, 1965 (Krebs 1965: abb. 60) and *Saurosuchus*.

3.2.9. Phalanges (Fig. 12). Many phalanges have been preserved, some still in articulation. The first digit of the left foot has its two phalanges in partial articulation. The first phalanx is wide at its proximal and distal ends (Table 2). The proximal articular surface has a medial and a lateral shallow depression for contact with the distal articular end of metatarsal I. The distal ginglymus is strongly marked with a deep central groove (Fig. 12B: gy). On the medial side of the distal end there is a shallow fossa for insertion of the collateral ligament. The ungual phalanx has a minute flexor tubercle (Fig. 12B: flt) on the proximoverventral surface, probably for the insertion of the *M. flexor digitorum longus* (Dilkes 1999). Distal to the tubercle there is a slight medial depression on the ventral surface, and the distal one-third forms a flat surface with a median straight groove (Fig. 12B: gr). Phalanx 1 of digit II has a wide proximal end and a flat ventral surface. The distal ginglymus has a median groove that is wider than phalanx 1-I, a slightly defined fossae for collateral ligaments, and a marked dorsal extensor pit. The second phalanx of digit II has a shallow ventral proximal depression and a defined distal ginglymus. It articulates with a small fragment of phalanx 3-II. Digit III has two phalanges instead of three (*contra* Romer 1975; Bonaparte 1975a; see below). The first phalanx of this digit is not well preserved, but displays a similar overall morphology to that of the other digits, and the second phalanx is damaged and only its general morphology can be determined.

Digit IV has a completely preserved phalanx 1 with a poorly preserved dorsal extensor pit and fossae for collateral ligaments. A small fragment of the second phalanx is preserved (*contra* Romer 1975; Bonaparte 1975a; see below). The fifth digit preserves a complete first phalanx (*contra* Romer 1975; Bonaparte 1975a; see below) that is lateromedially narrow,

with a dorsoventrally deep proximal end. The distal end is depressed and the dorsal surface has a small, rounded pit. The ventral surface has a very shallow depression close to the distal end and ends distally with a flat surface. The absence of the typical phalanx morphology, including the lack of the distal ginglymal articulation present in other phalanges, suggests that this phalanx could be the last one of the fifth digit, thus lacking an ungual phalanx. If the presence of a single phalanx is assumed in digit V of *Gracilisuchus*, it contrasts with most other taxa, such as *Euparkeria*, *Parasuchus*, *Ticinosuchus* and *Postosuchus alisonae* that possess three phalanges, the aetosaur *Neoaetosauroides* that has two, *Stagonolepis* that has four, and the ornithosuchid *Riojasuchus* that may have two (Bonaparte 1972). This number also contrasts with the crocodyliform *Protosuchus* and *Orthosuchus* that lack phalanges on that digit. The phalangeal formula present in *Gracilisuchus* is thus 2-(3)-(2)-(2)-(1), where the brackets represent the maximum number preserved. Comparisons of the pes with other taxa are somewhat difficult due to the scarcity of preservation of this anatomical region.

4. Discussion

The comparisons of *Gracilisuchus* with other archosauriforms highlight similarities and differences with members of this clade that can provide phylogenetic information for future phylogenetic analyses. Here we focus on osteological characteristics shared with basal members of Suchia, Crocodylomorpha and non-crocodyliform Crocodylomorpha (i.e., 'Sphenosuchia'), as well as on autapomorphies.

Among the shared features with basal members of Suchia, the absence of a well-defined acetabular surface on the proximal pubis of *Gracilisuchus* is also seen in *Fasolasuchus tenax* (Bonaparte 1981) (although the actual contribution of the pubis to the acetabulum is unknown in *Gracilisuchus*). In other pseudosuchians, there is a clear and wide contribution of the pubis (*Neoaetosauroides* – Desojo (2005)), or a smaller but definite contribution (*Riojasuchus tenuisceps* (Bonaparte 1972), other aetosaurs (e.g., *Aetosauroides*, Desojo 2005; *Stagonolepis*, Walker 1961), 'rauisuchians' (e.g., *Saurosuchus galilei*, Sill 1974; *Postosuchus kirkpatricki*, Long & Murry 1995) and basal crocodylomorphs (e.g., *Terrestrisuchus gracilis*, Crush 1984; UCMP 129470, Parrish 1991; *Sphenosuchus*, Walker 1990, p. 8)). The lateroventral proximal angle of the peduncle of the pubis of *Gracilisuchus* has a short bony tongue (Fig. 4: ptip), only shared with *Postosuchus kirkpatricki* (Long & Murry 1995).

In *Gracilisuchus* the length of metatarsal I in relation to metatarsal III (Serenó 1991) is slightly more than 75%, similar to the range of 50–75% present in *Euparkeria* and some basal Suchia (e.g., *Riojasuchus*, *Neoaetosauroides*, *Stagonolepis*, *Postosuchus*). By contrast, this ratio is higher (more than 85%) in some Crocodylomorpha such as *Terrestrisuchus*, *Protosuchus* and living crocodylians. The orientation of the major axes of the calcaneal tuber and calcaneal condyle in the same direction but opposite sense is a common feature seen in many Suchia. This characteristic is not only present in *Gracilisuchus* but also in Aetosauria (e.g., *Neoaetosauroides* (PVL 3525)), 'rauisuchia' (e.g., *Fasolasuchus* (PVL 3850), *Saurosuchus* (Sill 1974)) and Crocodylomorpha including Crocodyliformes (e.g., *Terrestrisuchus* (Crush 1984), *Dromicosuchus* (Sues *et al.* 2003) and *Protosuchus* (AMNH 3024)). The ancestral condition, in which the calcaneal tuber is laterally directed, is present in basal archosauriforms such as *Euparkeria* and *Turfanosuchus*, but in the supposed basal form *Turfanosuchus dabanensis* a posteriorly aligned calcaneal tuber is present, suggesting that this

taxon is probably more derived (Ezcurra *et al.* 2010). The ancestral condition is also found in some phytosaurs (e.g., USNM 18313 and *Parasuchus*).

Gracilisuchus shares with crocodyliforms an anteroposteriorly short proximal iliac articular surface of the pubis, contrasting with the long condition found in basal forms (i.e., some aetosaurs, phytosaurs, rauisuchians and basal dinosauriformes). Among basal archosauriforms and basal crocodylomorphs, contrasting morphologies are present; long surfaces are present in *Euparkeria* and *Terrestrisuchus*, whereas smaller ones, as in *Gracilisuchus*, are seen in *Tropidosuchus* and UCMP 129470. It is not currently possible to say whether this character is a convergent or a more widely distributed feature that has been lost several times.

Gracilisuchus, however, lacks derived characters of Crocodylomorpha. For instance, it has an imperforated acetabular wall present primitively in Archosauriformes, and also present in Phytosauria (e.g., *Parasuchus*), Aetosauria (e.g., *Neoaetosauroides*, *Aetosauroides*, *Stagonolepis*) and some rauisuchians (e.g., *Saurosuchus*, PVSJ 615; *Postosuchus*, Long & Murry 1995). Ornithosuchids (e.g., *Ornithosuchus longidens*, Walker 1964; *Riojasuchus tenuisiceps*, Bonaparte 1972), basal crocodylomorphs (e.g., *Kayentasuchus walkeri*, *Terrestrisuchus gracilis*; *Dibothrosuchus elaphros* Simmons, 1965; Wu & Chatterjee 1993) and crocodyliforms (e.g., *Orthosuchus stormbergi*, *Protosuchus richardsoni*), all have perforated acetabula. The presence of a pubic tubercle at the anterior surface of the iliac pedicle of the pubis is shared with most basal taxa and has been taken as ancestral for Reptilia (Hutchinson 2001a), being well developed in basal Archosauriformes, Crurotarsi and basal dinosauriforms, but absent in basal crocodylomorphs, as well as crocodyliforms. *Gracilisuchus* also lacks derived characters of Crocodyliformes. In *Protosuchus* (AMNH 3024) and *Caiman* (MPEF-AC 205), the tibial astragalar facet is a continuous surface, contrasting with the two regions present in *Gracilisuchus*. On the calcaneum, the distal astragalar facet is posteromedially directed in *Hemiprotosuchus* (PVL 3829) and *Protosuchus* (AMNH 3024), forming an obtuse angle with the calcaneal condyle. Conversely, in *Gracilisuchus*, this facet is more medially directed, forming an almost right angle with the condyle.

Gracilisuchus shares some features with a few, but not all, basal taxa of non-crocodyliform Crocodylomorpha, and which are absent in more derived members of the clade and most basal suchians. The femur of *Gracilisuchus* has been generally described as lacking a fourth trochanter (e.g., Romer 1972; Juul 1994). However, as noted Bonaparte (1975a), the fourth trochanter is present as a very slightly elevated structure. Although poorly developed, this trochanter has the same topological position as in other Crurotarsi and the same function is inferred for it (i.e., insertion of the caudifemoral musculature), suggesting that they are homologous structures. The fourth trochanter of *Gracilisuchus* is a shallow knob-like structure with a short and slightly elongated shape, similar to that in the basal crocodylomorphs *Pseudhesperosuchus jachaleri* (PVL 3830; Bonaparte 1972) and *Trialestes romeri* (PVL 3889). Nevertheless, this has to be taken with caution, as the later two taxa are based on poorly-preserved individuals. Other taxa have a well-defined ridge-like fourth trochanter, including the basal archosauriform *Tropidosuchus* (PVL 4601), the crurotarsans *Parasuchus* (ISI R43), *Aetosauroides* (PVL 2073), *Riojasuchus* (PVL 3827) and *Batrachotomus* (SMNS 52970), and the basal dinosauromorphs *Marasuchus* (PVL 3871) and *Lagerpeton* (PVL 4619); or a well-defined knob-like structure such as most 'rauisuchians' (e.g., *Saurosuchus* (Sill 1974), *Arganasuchus* (AZA 900), *Prestosuchus* (BSPG AS XXV10), and *Postosuchus* (Long & Murry 1995; Weinbaum

2007)); or lack a fourth trochanter (e.g., *Gobiosuchus* (Osmólska *et al.* 1997); GMPKU-P 200102 (Pol *et al.* 2004)). Among Crocodylomorpha, the degree of development of the fourth trochanter is highly variable (shallow knob-like, well-defined ridge, and absent). A poor anterior development of the femoral head of *Gracilisuchus* is shared with *Pseudhesperosuchus*, whereas basal pseudosuchians, crocodylomorphs and dinosauromorphs have a more developed anteriorly extended femoral head.

Finally, some putative autapomorphies of *Gracilisuchus* have been recognised. A very thin, L-shaped, laminar ventral projection on the proximal edge of the pubic blade (Fig. 4B, D: tl) could represent an autapomorphy, although this is a weak bony region that could be missing or not preserved in other specimens. Another probable autapomorphic feature of *Gracilisuchus* is the location of the ischiadic symphysis, limited only to the proximal region of the ischia (Fig. 5B: is). This condition is observed not only in the specimen PVL 4597 but also in the ischium associated with the remains of the MCZ 4116. Nevertheless, a similar condition was shown to be present in *Ornithosuchus* (Walker 1964, fig. 11), suggesting, on the basis of the last phylogenetic analyses of Archosauriformes (e.g., Brusatte *et al.* 2010), that it was independently acquired.

5. New interpretations

Romer (1972) stated that the pubic and ischiadic facets of the ilium in *Gracilisuchus* were clearly differentiated, as figured in his illustration (Romer 1972, fig. 8b). This contrasts with the morphology observed in PVL 4597, where there are no definite facets for the contact with the pubis and ischium. The ilium originally interpreted as the ilium of the holotype of *Gracilisuchus* is mixed with many elements of different taxa (e.g., *Lagosuchus talamayensis* (Romer 1971b; Sereno & Arcucci 1994) and *Tropidosuchus romeri*, (Sereno & Arcucci 1994)), being similar to proterochampsids ilia (Martín D. Ezcurra pers. comm. 2009). The ilium associated with the MCZ specimen has contrasting morphology (e.g., long preacetabular process, straight dorsal edge of iliac blade) and the association with elements diagnostic of *Gracilisuchus* still has to be proved. Thus, the single ilium currently undoubtedly assigned to *Gracilisuchus* is of the PVL 4597 specimen and the ilium described by Romer is not considered to be conspecific.

The pubis of *Gracilisuchus* was originally not described, although a single pubis was later found among the material of PVL 4597 (Bonaparte 1975a). The tibia was described as having a well-developed cnemial crest, based on PVL 4597, PULR 08, MCZ 4116 and MCZ 4118 by Romer (1972). There are no tibia assigned to the holotype specimen, the tibia of PVL 4597 has a proximal end with a wide and deep hole, and the tibia in the MCZ specimen cannot be assigned to *Gracilisuchus* with certainty. Therefore, nothing can be said about this crest on the basis of the currently available specimens.

The proximal tarsals astragalus and calcaneum were briefly described based on the Tucuman specimen (i.e., PVL 4597), the two distal tarsals were only mentioned in the original description based mainly in the pes associated with the holotype (Romer 1972, p.21), and the remainder of the foot described from both specimens. The tarsus and pes were thus figured as a composite of the available material (Romer 1972, fig. 9d). Since the pes associated with the holotype has been reinterpreted as a different taxon, its features cannot be considered. Although later descriptions and figures of the foot of *Gracilisuchus* have been based on better preserved material (apparently on PVL 4597 but not clearly stated (Bonaparte 1975a; Brinkman 1981; Arcucci 1989)), some differences with

the present study remain. Among these discrepancies is the reported absence of the distal tarsal 3 (Bonaparte 1975a, fig. 11), being represented only by distal tarsal 4, probably due to taphonomic effects. Differences are also found in the elements of the pes of PVL 4597. The third digit was described with three phalanges, although only two have been found here. The fourth digit presents an additional small fragment of the second phalanx, and the fifth digit also has preserved the complete first phalanx (also in Bonaparte 1975a).

The longstanding idea that *Gracilisuchus* is closely related to Crocodylomorpha (e.g., Parrish 1993; Pol & Gasparini 2009; Brusatte *et al.* 2010) has recently been challenged by Nesbitt (2011). The present authors' revision found two features in *Gracilisuchus* shared with some non-crocodyliform crocodylomorphs, providing tentative support for the monophyly of Sphenosuchia (e.g., Sereno & Wild 1992; Wu & Chatterjee 1993) and the close relationship of *Gracilisuchus* to that clade. These characteristics are: (i) the morphology and poor development of the femoral fourth trochanter, closely resembling the condition of *Pseudhesperosuchus* and *Trialestes*; and (ii) a poor anterior development of the femoral head, shared with *Pseudhesperosuchus*. On the other hand, there are characters that reject the inclusion of *Gracilisuchus* within Crocodylomorpha (Nesbitt 2011), such as the absence of an imperforated acetabulum, and that rather suggests a sister-taxon position to Crocodylomorpha. The new interpretation of the available material from the PVL specimen clarifies several aspects of the previously known and published information of the anatomy of *Gracilisuchus*. In addition, some of the features identified are probably unique to this species (e.g. L-shaped laminar projection on the pubis, ischiadic symphysis proximally located), but deeper studies in other taxa and comparisons are needed. The phylogenetic affinities of *Gracilisuchus* among a wide range of archosauriforms remains to be tested.

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