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The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil)

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Three partial skeletons allow a nearly complete description of the sacrum, pelvic girdle, and hind limb of the stem-sauropodomorph *Saturnalia tupiniquim*, from the Late Triassic Santa Maria Formation, South Brazil. The new morphological data gathered from these specimens considerably improves our knowledge of the anatomy of basal dinosaurs, providing the basis for a reassessment of various morphological transformations that occurred in the early evolution of these reptiles. These include an increase in the number of sacral vertebrae, the development of a brevis fossa, the perforation of the acetabulum, the inturning of the femoral head, as well as various modifications in the insertion of the iliofemoral musculature and the tibio-tarsal articulation. In addition, the reconstruction of the pelvic musculature of *Saturnalia*, along with a study of its locomotion pattern, indicates that the hind limb of early dinosaurs did not perform only a fore-and-aft stiff rotation in the parasagittal plane, but that lateral and medial movements of the leg were also present and important.

INTRODUCTION

Saturnalia tupiniquim was described in a preliminary fashion by Langer et al. (1999) as the basal-most sauropodomorph dinosaur, an assignment generally accepted (Galton 2000a, Kellner and Campos 2000). Further work by the author (Langer 2001a, b, 2002) has confirmed the position of this dinosaur as the most basal member of the sauropodomorph lineage. Yet, Sauropodomorpha Huene, 1932 is currently defined as a node-based taxon including Prosauropoda Huene, 1920 and Sauropoda Marsh, 1878 (Salgado et al. 1997, Sereno 1998, Yates 2003a, Langer 2002), and *Saturnalia* does not belong to either of these groups. Instead, it is clearly more basal in the dinosaur phylogenetic tree than any sauropod or "prosauropod." Accordingly, *Saturnalia* cannot be regarded as a sauropodomorph *sensu stricto*, and is better considered a taxon in the stem-lineage (Jefferies 1979) to that group.

The three known skeletons of *Saturnalia* come from the same locality (Langer et al. 1999) in the Upper Santa Maria Formation, Rio Grande do Sul state, south Brazil (Barberena et al. 1985, Langer 2001a). These beds encompass, together with the Ischigualasto Formation of North-western Argentina, the Ischigualastian "reptile-age" of Bonaparte (1982), which is usually dated as Carnian (Rogers et al. 1993, Lucas 1998). Accordingly, *Saturnalia* is equivalent in age to the more famous Argentinean "oldest-known dinosaurs," *Herrerasaurus ischigualastensis* Reig, 1963 and *Eoraptor lunensis* Sereno et al., 1993.

MATERIALS AND METHODS

Saturnalia tupiniquim is based on its syntypical series (Langer et al. 1999) housed at the Museu de Ciências e Tecnologia PUCS, Porto Alegre (**MCP**). This includes the holotype (MCP 3844-PV), a well preserved skeleton consisting of most of the presacral vertebral series, both sides of the pectoral girdle, right humerus, partial right ulna, right radius, both sides of the pelvic girdle with the sacral series, left femur and most of the right limb; and two paratypes: MCP 3845-PV, a partial skeleton including the caudal part of the skull with braincase, the natural cast of a mandibular ramus bearing teeth, presacral series including caudal cervical and cranial trunk vertebrae, both sides of the pectoral girdle, right humerus, right side of the pelvic girdle and most of the right hind limb; and MCP 3846-PV, an incompletely prepared skeleton, from which a partial tibia and foot, as well as some trunk vertebrae, are visible. All these specimens are semi-articulated (taphonomic class I of Holz and Barberena 1994), and show good to excellent preservation (taphonomic class I of Holz and Schultz 1998).

The distinctive preservation of the skeletal remains of *Saturnalia tupiniquim* allows the recognition of various osteological traces (trochanters, scars, etc.) left by the attachments of major groups of muscles. Accordingly, some insights on its pelvic limb myology are presented here. The tentative identifications of the musculature corresponding to each of these traces are inferences based on a "phylogenetic bracket" approach (Witmer 1995, Hutchinson 2001a). Obviously, birds and crocodiles are used as the main elements of comparison, because they are the only extant archosaur groups, and the closest living "relatives" of *Saturnalia*.

The following anatomical account is based mainly on MCP 3844PV, except where explicitly stated otherwise. Relevant information was also obtained from the paratypes, especially MCP 3845PV. Measurements of all available pelvic skeletal elements of the three specimens of *Saturnalia* are presented in Tables 1–5 (see Appendix). Anatomical nomenclature follows the conventions of the compendium "The Dinosauria"

(Weishampel et al. 1990, p. 6–7) and the "Nomina Anatomica Avium" (Baumel 1993).

Unless noted to the contrary, the term "basal dinosaurs" is used herein to broadly include basal saurischians such as *Herrerasaurus*, *Staurikosaurus*, *Guaibasaurus*, and *Eoraptor* (Langer 2003), as well as basal theropods such as *Liliensternus*, *Megapnosaurus*, and *Dilophosaurus* (Carrano et al. 2002); basal "prosauropods" as *Thecodontosaurus*, *Efraasia*, and *Plateosaurus* (Yates 2003a); and basal ornithischians such as *Lesothosaurus*, *Scelidosaurus*, and *Heterodontosaurus.* Additionally, the sauropodomorph dinosaurs from the Stubensandstein of Germany are treated according to the alpha-taxonomy proposed by Yates (2003b).

Additional institutional abbreviations: **BMNH**, Natural History Museum, London; **BRSUG**, Department of Earth Sciences, University of Bristol; **GPIT**, Instutut für Geologie und Paläontologie, Tübingen; **MB**, Museum für Naturkunde, Berlin; **MCZ**, Museum of Comparative Zoology, Cambridge; **MCN**, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; **PVL**, Fundacíon Miguel Lillo, Tucumán; **PVSJ**, Museo de Ciencias Naturales, San Juan; **QVM**, Queen Victoria Museum, Harare; **SMNS**, Staatlisches Museum für Naturkunde, Stuttgart.

COMPARATIVE DESCRIPTION

Sacral Vertebrae and Ribs

The sacrum of *Saturnalia* (Figs. 1A–B) includes two main vertebrae, which represent the plesiomorphic archosaur elements (Romer 1956, Ewer 1965, Cruickshank 1972, Sereno and Arcucci 1994). Their platycoelic centra are not fused to one another, or to any other centrum, and lack ventral keels. Both vertebrae are firmly attached, but not fused, to the ilia by means of massive ribs and transverse processes. The last trunk vertebra is placed cranial to the iliac preacetabular alae, and differs from that of *Herrerasaurus* (Novas 1994) because its transverse processes do not touch either the ilia or the ribs of the first sacral. Accordingly, as also seen in *Staurikosaurus* (Galton 1977), and some basal "prosauropods" (Galton 1976, 1999, 2000b), *Saturnalia* does not present trunk vertebrae added to the sacrum. In this respect it differs from *Eoraptor* (Sereno et al. 1993), theropods (Welles 1984, Cuny and Galton 1993), ornithischians (Janensch 1955, Galton 1974, *Scelidosaurus*—BMNH 6704) and most sauropodomorphs (Young 1941a, 1942, Cooper 1981, Galton 1999, *Riojasaurus*—PVL 3808), all of which bear at least one dorsosacral vertebra.

The two vertebrae caudal to the two main sacrals of *Saturnalia* are placed within the boundaries of the iliac postacetabular alae. The transverse processes of the caudalmost of these do not reach either the ilia or the transverse processes of the second sacral, while the cranial element has uncertain relations to the sacrum (see discussion below). Accordingly, in contrast to most other archosaurs, dinosaurs always have more than two vertebrae placed within the limits of the iliac alae (Novas 1994). This condition seems to have been achieved in two ways: the craniocaudal compression of the vertebrae, as seen in *Herrerasaurus* (Novas 1994), and to a lesser degree also *Staurikosaurus* (Galton 1977), or the elongation of the preacetabular and/or postacetabular iliac alae. *Saturnalia* does not have constricted vertebrae in the sacral area, and is similar to most dinosaurs in this respect. Accordingly, the presence of four vertebrae within the limits of its ilia is due to the elongation of the postacetabular alae.

The centra of the two main sacral vertebrae of *Saturnalia* are more slender towards the central part of the sacrum. The cranial articulation of the first of these, as well as the caudal articulation of the second, is broader and more robust. This is distinct from the general morphology of the sacral vertebrae of dinosaurs, as discussed by Welles (1984), and seen in most basal members of the group (Galton 1999; *Scelidosaurus*—BMNH 6704). Yet, this is by no means an unknown feature among dinosaurs, and is particularly common in "ceratosaurs" (Gilmore 1920, Raath 1969, Bonaparte et al. 1990).

First Sacral Vertebra—The centrum is broader than high, as is its neural canal, resembling *Staurikosaurus* (Galton 1977), theropods (Huene 1934, Welles 1984), sauropodomorphs (Galton 1999, *Riojasaurus*—PVL 3808), and some ornithischians (*Dryosaurus*—MB dy II), but differing from *Herrerasaurus* (Novas 1994), which has more laterally compressed sacral vertebrae. Its neural spine is not entirely preserved, but it is clearly not as transversely broad as that of *Herrerasaurus* (Novas 1994) or *Staurikosaurus* (Galton 1977). Instead, it is narrow and craniocaudally elongated as in most other basal dinosaurs (Raath 1969, Galton 1976, Cooper 1981; *Scelidosaurus*—BMNH 6704). There are also no indications of a "spine table" and/or dorsal broadening, which have been recognized in *Herrerasaurus* (Novas 1994), *Eoraptor*, as well as in more derived dinosaurs (Bonaparte et al. 1990, Galton 2000b).

The first sacral vertebra has each of its ribs and corresponding transverse processes fused into a single structure with an expanding (both craniocaudally and dorsoventrally) lateral portion. Laterally expanding transverse processes/ribs are also present in basal dinosauromorphs (Sereno and Arcucci 1993, 1994), as well as in *Herrerasaurus* (Novas 1994) and some "prosauropods" (Galton 1999). On the contrary, the "primordial" first sacral vertebra of most other basal dinosaurs (Raath 1969, Galton 1981, Welles 1984) has derived transverse processes/ribs, which are much narrower in dorsal aspect.

Although fused, the sacral ribs and transverse processes of *Saturnalia* can be distinguished from one another by their position and morphology. This is based on comparison with some specimens of *Plateosaurus* (SMNS F65), in which both elements are not completely fused together. In these forms (*contra* Galton 2000b), as in *Saturnalia*, the craniodorsal margin of the structure is not formed by the cranial margin of the transverse process, but by the dorsal-

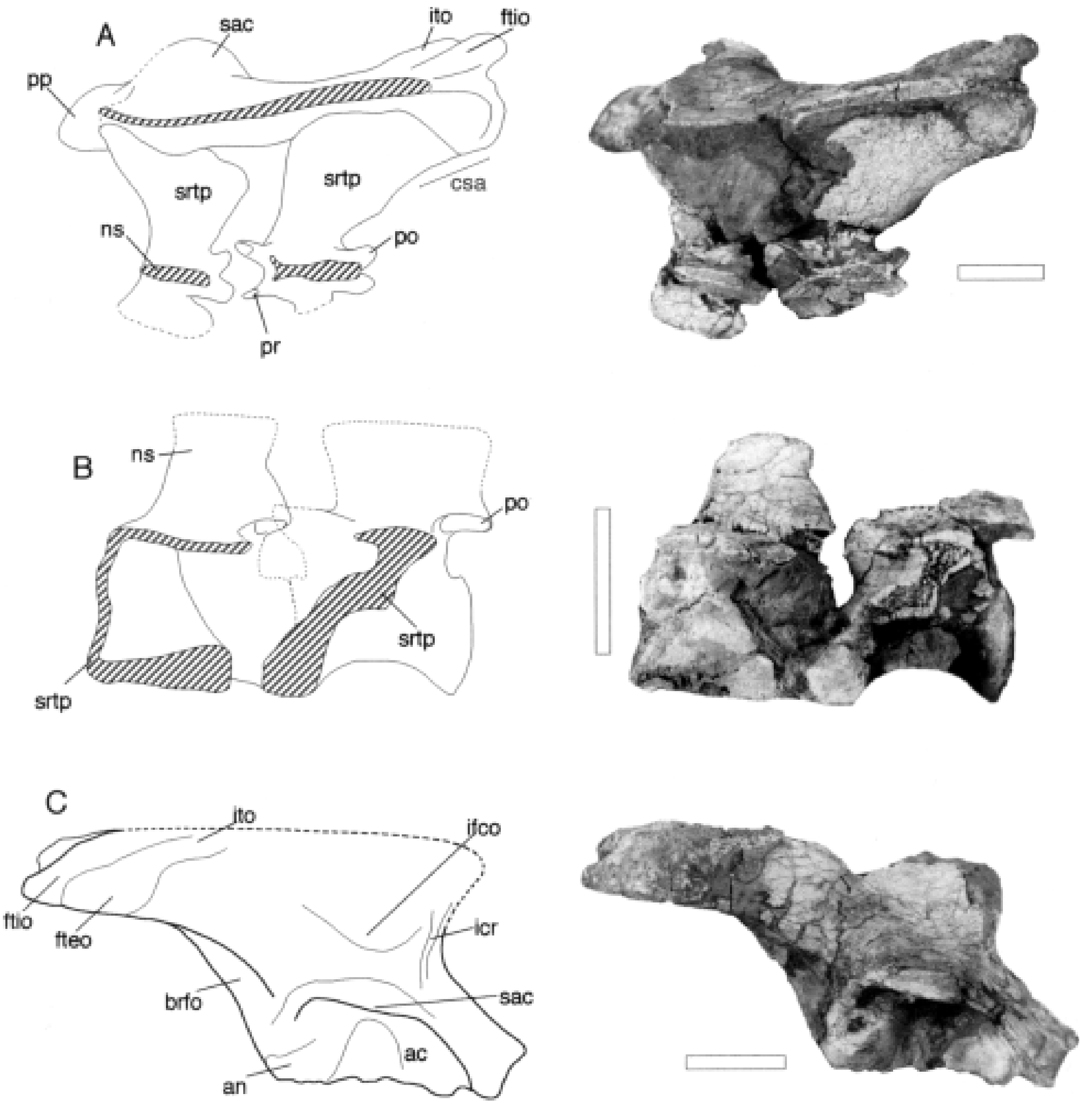

Fig. 1. Sacrum and ilium of *Saturnalia tupinquim* (MCP 3944-PV). Scale bar = 2 cm. **A.** Dorsal aspect of sacral vertebrae and right ilium. **B.** Left lateral aspect of sacral vertebrae. **C.** Lateral aspect of right ilium. Abbreviations: **ac**, acetabulum; **an**, antitrochanter; **brfo**, brevis fossa; **csa**, articulation area for the "caudosacral" vertebra; **fteo**, flexor tibialis externus origin; **ftio**, flexor tibialis internus origin; **icr**, iliac preacetabular ridge; **ifco**, iliofemoralis cranialis origin; **ito**, iliotibialis origin; **ns**, neural spine; **po**, postzygapophysis; **pp**, pubic peduncle; **pr**, prezygapophysis; **sac**, supracetabular crest; **srtp**, sacral rib and transverse process.

most portion of the rib, which contacts the cranial-most tip of the iliac ala. Caudal to this, each transverse process arises from the lateral surface of the respective neural arch to form a horizontal platform. Like in other basal saurischians (Huene 1926, Raath 1969, Novas 1994), the space between the ilia and the first sacral vertebra is "roofed" by the transverse processes. However, unlike *Herrerasaurus* and theropods, but similarly to some "prosauropods" (Cooper 1981, fig. 12b, "tp"; *Plateosaurus*—SMNS F65), the bony part of the transverse process does not contact the ilium, and the lateral-most part of the "roofing" was probably completed by cartilage. These structures together (craniodorsal margin of the rib plus transverse process) are fan-shaped in dorsal aspect, articulating with the dorsomedial margin of the ilium, from its cranial tip as far as the level of the ischial peduncle.

The rib of the first sacral vertebra expands from the craniodorsal corner of the centrum, and is composed of two main parts: an inclined ventral platform, and a cranial vertical wall. These give the rib an "L-shaped" lateral outline, which is apomorphic for Dinosauria, because the sacral ribs of basal dinosauromorphs (Sereno and Arcucci 1993, 1994, Novas 1996) and most basal archosaurs (Ewer 1965, Romer 1972, Chatterjee 1978) are simple plate-like structures. The ventral platform of the first sacral vertebra of *Saturnalia* is fan-shaped, expanding lateroventrally and caudally to form the "floor" of the space between the ilium and the first sacral vertebra (see Novas 1994 for a similar condition in *Herrerasaurus*). It articulates with the internal surface of the ilium, from the caudal margin of the preacetabular embayment to the cranial part of the ischial peduncle, at a level corresponding to the supracetabular crest on the external surface of the bone. The vertical wall, on the other hand, bridges the gap between the cranial margins of the transverse process and the ventral platform of the rib, forming the entire cranial portion of the vertebral articulation to the ilium. It inserts along the cranial and ventral parts of the medial surface of the preacetabular ala. The depth of this vertical wall (representing the depth of the entire rib/transverse process) distinguishes *Saturnalia* from forms such as *Staurikosaurus* (Galton 1977) and *Herrerasaurus* (Novas 1994), the first sacral of which has a much deeper rib.

The transverse process/rib of the first sacral of *Saturnalia* has a "C-shaped" lateral outline. This is formed by the ventral platform and the cranial wall of the rib and the "roofing" transverse process. This configuration is also seen in *Herrerasaurus* (Novas 1994), as well as in some "prosauropods" (Benton et al. 2000, Galton 2000b, fig. 6a). A transverse process that "roofs" the space between the ilium and the fist sacral vertebra is also present in the primordial first sacral of several theropods (Gilmore 1920, pl. 8, "d" of s3, Raath 1969) and in "prosauropods" with a sacral added from the trunk series (Young 1941a, Cooper 1981). The vertical wall and ventral platform of the rib are, on the other hand, also known in *Staurikosaurus* (Galton 1977) and ornithischians (Janensch 1955, abb. 23, "sw3").

Second Sacral Vertebra—Its centrum is almost identical to that of the first sacral vertebra, and the dimorphism seen in *Herrerasaurus* (Novas 1994) and *Staurikosaurus* (Galton 1977) is not present. The neural arches are also similar, but the two vertebrae differ significantly in the morphology of their transverse processes/ribs. As is also seen in *Herrerasaurus* (Novas 1994), these have an "inverted C-shaped" lateral outline, composed of dorsal and ventral horizontal platforms, and a cranioventrally to caudodorsally inclined caudal wall.

Each dorsal platform is fan-shaped in dorsal aspect and, based on the comparison to some "prosauropods" (*Plateosaurus*—SMNS F65; *Riojasaurus*—PVL 3805), it seems to be composed mainly of the transverse process. It expands laterally from the lateral border of the neural arch, forming an extensive articulation with most of the mediodorsal surface of the iliac postacetabular ala, closely resembling the condition in *Herrerasaurus* (Novas 1994). The dorsal platform of the second sacral vertebra of *Saturnalia* is, however, more craniocaudally elongated, correlating with its much longer iliac postacetabular ala. In addition, it "roofs" the space between the cranial part of the second sacral vertebra and the ilium, as seen in *Herrerasaurus* and some theropods (Gilmore 1920, Raath 1969). Unlike these forms, however, its cranial margin is not in contact with the transverse process of the first sacral. This "roofing" seems to represent a derived feature among dinosaurs, since only the caudal wall and ventral platform are recognizable in the second sacral of basal dinosauromorphs (Sereno and Arcucci 1994).

In *Saturnalia*, the caudal wall and ventral platform of each pelvic articulation of the second sacral vertebra is formed only by the rib, which circumscribes ventrally and caudally the space between the cranial part of that vertebra and the ilium. The caudal wall extends from the mid-cranial portion of the centrum, where it contacts the caudal-most part of the dorsal platform attachment, to insert along the medioventral surface of the cranial part of the iliac postacetabular ala, medial to the insertion area for the M. caudofemoralis brevis (M. caudofem. brevis; see below). The ventral platform, on the other hand, bridges the cranial-most part of the centrum to the medial surface of the iliac body, just cranial to the postacetabular embayment. As in most dinosaurs (Huene 1926, Janensch 1955, Novas 1994, Galton 2000b), its craniolateral margin contacts the caudolateral part of the ventral platform of the first sacral rib, and an open space is left medial to this articulation.

The articulation between the ilium and the second primordial sacral of most other dinosaurs, including *Staurikosaurus* (Galton 1977), *Herrerasaurus* (Novas 1994), "prosauropods" (Galton 1973, Cooper 1981, fig. 13, Benton et al. 2000), theropods (Gilmore 1920), and ornithischians (Forster 1990, fig. 4, third sacral), also present a caudal wall and ventral platform. In various forms that show caudal vertebrae added to the sacrum, however, the caudal wall is less developed and often perforated (Gilmore 1920, Janensch 1955, Galton 1976, 2000b).

?Caudosacral Vertebra—The vertebral element caudal to the second main sacral of *Saturnalia* is not completely preserved, but it seems to represent a sacral vertebra added from the caudal series. Its centrum is about the same length as that of sacral vertebrae 1 and 2, but only slightly narrower. The transverse processes/ribs are fused to the middle part of the centrum and neural arches, at the level of the neurocentral joint. In dorsal aspect, the transverse possesses seem to extend perpendicularly to the column, and to expand laterally. Their distal-most portions are, however, obliterated. Yet, a striated area is seen in the mediocaudal margins of the right iliac ala and second sacral transverse process (Fig. 1A), where signals of osseous attachments are present. Most probably, this indicates the articulation area of the caudosacral transverse process.

Most dinosaurs possess at least one caudosacral vertebra. These are present in all theropods (Raath 1969, Welles 1984) and ornithischians (Galton 1999, *Scelidosaurus*—BMNH 6704), and apparently also in *Staurikosaurus* (Langer 2003). On the contrary, *Herrerasaurus* (Novas 1994) and *Eoraptor* (Sereno et al. 1993) do not have caudosacral vertebrae. This condition is apparently also present in most basal sauropodomorphs with a three-vertebrae sacrum, such as *Massospondylus* (Cooper 1981), *Riojasaurus* (PVL 3808), *Yunnanosaurus* (Young 1942), and *Lufengosaurus* (Young 1941a). *Plateosaurus*, on the contrary, does present a caudosacral vertebra (Galton 1999, 2000b, Yates 2003a), a condition that it might be also present in *Thecodontosaurus* (Benton et al. 2000), and *Ammosaurus* (Galton 1999).

The "caudosacral" vertebra of *Saturnalia* differs from the cranial-most caudal vertebra of *Herrerasaurus* (Novas 1994) in that its centrum is not axially shortened, and the transverse processes not so caudally directed. Indeed, the latter condition seems to be related to the peculiar compression seen in the vertebrae of the sacral area of *Herrerasaurus*, which cranially displaced the caudal centra. Moreover, the transverse processes/ribs of the second sacral vertebra of *Herrerasaurus* entirely occupy its short postacetabular iliac alae, leaving no space for the articulation of a caudosacral vertebra. The caudosacral vertebra of *Staurikosaurus* (Galton 2000a) more closely resembles that of *Saturnalia*. Compared to the first caudal vertebra of *Herrerasaurus*, it is not so axially shortened, and the transverse processes/ribs not so caudally projected. Yet, the iliac articulations of both the second sacral and the caudosacral vertebrae are not as craniocaudally expanded as in *Saturnalia*, fitting the short postacetabular alae of that dinosaur.

Among basal sauropodomorphs, the "caudosacral" vertebra of *Saturnalia* is not comparable to the putative one of *Ammosaurus* (Galton 1976), which presents a bulged centrum and much thinner transverse processes, but resembles more those of *Plateosaurus* (Galton 1999, 2000b, Yates 2003b, SMNS 5715). However, the transverse processes of the second sacral vertebra are not so distally expanded (fan-shaped) in these forms as in *Saturnalia*, while those of the caudosacral vertebra articulate to a larger area on the medial surface of the ilium. In *Saturnalia*, on the other hand, they only directly contact the ilia in a very short area, which might correspond to an equally short free space (caudal to the articulation of the second sacral transverse process) seen on the iliac alae of *Efraasia* specimens with putative two-vertebrae sacrum (Galton 1999; fig. 1F). In fact, the lateral articulation of the caudosacral of *Saturnalia* is very peculiar. The cranial part of the transverse processes articulate to the mediocaudal margin of the second sacral vertebra transverse processes, and not only to their caudal margin as in *Plateosaurus*.

In some aspects, the sacrum of *Saturnalia* is intermediary between those of *Herrerasaurus* and "prosauropods" with a caudosacral. As in *Herrerasaurus*, the transverse processes of the second sacral are large and fan shaped, but those of the caudosacral also articulates to the expanded postacetabular iliac alae (as in *Plateosaurus*). A caudosacral that articulates to the transverse processes of the second sacral and to the mediocaudal margin of the ilia might also be present in *Thecodontosaurus* (Benton et al. 2000), and represent the ancestral condition among sauropodomorphs.

Pelvic Girdle

Ilium (Figs. 1A, C)—Both alae are strongly developed, but the postacetabular ala is much more elongated. The dorsal iliac crest forms a continuous line in dorsal aspect, the cranial half of which is concave laterally. This is formed by a marked depression on the lateral surface of the bone (see below), and is supposed to represent a primitive feature among dinosaurs, since similar structures are present in *Marasuchus* (Sereno and Arcucci 1994), *Herrerasaurus* (Novas 1994), "*Caseosaurus*" (Long and Murry 1995), and *Thecodontosaurus* (Benton et al. 2000). The dorsal iliac crest of other dinosaurs is also laterally concave, but the concavity is usually not as strong (Raath 1969, Thulborn 1972; *Scelidosaurus*—BMNH 6704; *Liliensternus*—MB.R. 2175), or it is placed more caudally (Galton 1973, 1976, 2000b).

The preacetabular ala of *Saturnalia* (PVL 3845PV) is very short, and does not extend cranial to the pubic peduncle as in basal theropods (Huene 1934, Raath 1969, Welles 1984) and basal ornithischians (Thulborn 1972, Charig 1972, Santa Luca 1980). Moreover, it presents a truncated cranial margin that, among dinosaurs with a short preacetabular ala, is more similar to that of *Herrerasaurus* (Novas 1994), *Staurikosaurus* (Colbert 1970), "*Caseosaurus*" (Long and Murry 1995, Hunt et al. 1998), and *Thecodontosaurus* (Benton et al. 2000, fig 15c), than to those of most "prosauropods" (Bonaparte 1972, Galton 1976, Cooper 1981), which are pointed and more elongated. Accordingly, there is no evidence for a cranial cartilaginous extension, as suggested for *Massospondylus* (Cooper 1981), and the rugose area on the craniodorsal surface of the preacetabular ala seems to be related to muscle attachments. In fact, this rugosity is continuous with the rest of the dorsal iliac crest, although significantly wider. A similar wider area is seen in *Herrerasaurus* (Novas 1994), "*Caseosaurus*" (Long and Murry 1995), and "prosauropods" (*Riojasaurus*—PVL unnumbered; *Plateosaurus*—SMNS 13200b), as well as in ornithischians (Romer 1927), sauropods (Romer 1923a), and theropods (Perle 1985). As suggested for ornithischians (Romer 1927, Thulborn 1972), this area possibly marks the origin of the M. iliotibialis cranialis (M. iliotib. cran. = avian M. sartorius, Vanden Berge and Zweers 1993), indicating a division in the iliotibialis musculature (Fig. 8). From that muscle insertion area, a robust lateral ridge extends caudoventrally, bordering the caudal margin of the preacetabular embayment, to reach the craniodorsal border of the acetabulum. A similar ridge is seen in various dinosaurs (Romer 1923a, Thulborn 1972, Novas 1994, Long and Murry 1995, Benton et al 2000; *Liliensternus* - MB.R. 2175), as well as in more basal archosaurs such as *Ornithosuchus* (Walker 1977) and poposaurids (Galton 1977). However, in *Saturnalia* this ridge is more robust than that of basal ornithischians (Thulborn 1972) and "prosauropods" (Cooper 1981), approaching the condition of *Staurikosaurus* (MCZ 1669), *Herrerasaurus* (PVL 2566), and some theropods (*Liliensternus* MB.R. 2175, Romer 1923a).

Caudal to the aforementioned rugose area and ridge, the lateral surface of the ilium of *Saturnalia* presents a marked sub-triangular concavity. This area is most probably related to the origin of part of the iliofemoral musculature, based on topographic correlation with crocodiles (Romer 1923b). Differing from those reptiles, however, but resembling birds (Rowe 1986), *Saturnalia* might have had two branches of the M. iliofemorale (M. iliofem.), judging from their distinct insertions on the femur (see below). This concavity appears to mark the origin of the largest branch, i.e. the avian M. iliofemoralis cranialis (M. iliofem. cran. = M. iliotrochantericus posterius, McGowan 1979). A similar concavity can also be seen in "prosauropods" (Cooper 1981; fig. 85 "ife"), theropods (Huene 1934, Welles 1984), and ornithischians (Thulborn 1972, Santa Luca 1980). As in birds, the origin of this branch is cranially expanded in all dinosaurs compared to the condition in crocodiles (Romer 1923b; fig. 2), as is the preacetabular ala. This modification seems to be related to the increase in the importance of this muscle in medial rotation of the femur, together with a small role in the protraction of the bone (Vanden Berge 1975, McGowan 1979). This trend is particularly clear in theropods, in which the origin of the M. iliofem. cran. occupies most of the lateral surface of their extremely enlarged preacetabular ala (Romer 1923a, Padian 1986).

It has been suggested (Russell 1972) that a vertical ridge extending through the lateral surface of the ilium of some theropods (Osborn 1916, Osmólska et al. 1972, Galton and Jensen 1979, Bonaparte 1986, Barsbold and Maryanska 1990, Cuny and Galton 1993) marks the division between the origins of the two branches of the M. iliofem. Such a ridge is not clearly seen in most dinosaurs, but *Saturnalia* presents a faint elongated convexity extending caudodorsally from the caudal half of the acetabulum. *Contra* Russell (1972), it is here proposed that this ridge separates the origin areas of the M. iliofem. (most probably the M. iliofem. cran. alone), cranially, and M. iliofibularis (M. iliofib.), caudally, as suggested by Walker (1977). The very similar ridge of some birds (McGowan 1979, fig. 2) also separates the origins of these two groups of muscles (Vanden Berge 1975).

The second branch of the avian M. iliofem., the M. iliofemoralis externus (M. iliofem. ext. = M. gluteus medius et minimus), originates immediately dorsal to the antitrochanter, either at the dorsal margin of the ilium (McGowan 1979), or at the sulcus antitrochantericus (Vanden Berge and Zweers 1993). Various authors (Romer 1927, Coombs 1979) have suggested that this muscle originated from the so-called "antitrochanter" of some ornithischians. In fact, there has always been a discussion of whether the M. iliofem. ext. of ornithischians originated at the mid-cranial lateral surface of the dorsal iliac crest (Walker 1977) or at the "antitrochanter," while the M. iliotrochantericus caudalis originated at the aforementioned part of the dorsal iliac crest (Galton 1969, Norman 1986). Rowe (1986) proposed that these two muscles are derived from the reptilian M. iliofemoralis. Based on this assumption, it is clear that, as in birds, the M. iliofem. cran. (= avian M. iliotrochantericus caudalis) of dinosaurs originated on the mid-cranial lateral surface of the dorsal iliac crest, while the M. iliofem. ext. originated somewhere caudal to it, but cranial to the M. iliofib. No clear origin area for the M. iliofem. ext. is seen on the ilium of *Saturnalia*, and it might have been fleshy as suggested for *Thescelosaurus* (Romer 1927, p. 264). A possible origin, however, is the dorsal border of the acetabulum, just caudal to the supraacetabular crest. This area bears clear indications of muscle insertion, and it is both dorsal to the antitrochanter and caudal to the origin of the M. iliofem. cran., as expected for the origin of the M. iliofem. ext. Likewise, no sign of the origin of the M. iliotrochanterici (M. iliotroc.), *sensu* Rowe 1986, is seen on the pelvis of *Saturnalia*. This might indicate that this muscle had its origins on the caudalmost presacral vertebrae, as is the case in crocodiles (= M. puboischiofemoralis internus pars dorsalis; Walker 1977).

The postacetabular ala of *Saturnalia* is longer than the space between the preacetabular and postacetabular embayments of the ilium, a condition shared by most eusaurischians (Huene 1934, Raath 1969, Welles 1984, Padian 1986, Benton et al. 2000; *Guaibasaurus*—MCN PV 2355) and two marked ridges extend through its ventral portion. The medial one ("pv" in Novas 1996; fig. 8) extends caudodorsally from the caudal border of the ischial peduncle, where its ventral margin is more ventrally projected than that of the second (lateral) ridge. More caudally, the ventral portion of this ridge deflects medially to form a horizontal platform, which extends to the end of the ala. The lateral ridge, on the other hand, extends caudally from near the caudodorsal margin of the acetabulum, and its caudal two thirds ("bs" in Novas, 1996; fig. 8) overhangs the medial ridge/platform laterally and ventrally. At the cranial portion of the postacetabular ala, the lateral and medial ridges define a ventrally concave surface - the brevis fossa (see Novas 1996)—that corresponds to the large origin area of the M. caudofem. brevis (Gatesy 1990). More caudally, the origin of this muscle expands into the much broader ventral surface of the platform formed by the caudal part of the medial ridge, which is laterally bound by the lateral ridge.

Several muscle scars are seen in the dorsal and lateral surfaces of the postacetabular iliac ala of *Saturnalia*. The most marked of these is a craniocaudally elongated rugose area, which is continuous with the dorsal iliac crest. Accordingly, its craniodorsal portion is thought to mark the origin of part of the M. iliotibialis, which also extends cranially along the dorsal iliac crest (Romer 1923b). More caudally, the rugose area enters the lateral surface of the ala, expanding ventrally and occupying most of its caudal portion. Based on the comparison with the crocodile (Romer 1923b, 1927), it is suggested that this ventrally expanded area represents the origin of the M. flexor tibialis externus (M. flex. tib. ext.), while the M. flexor tibialis internus (M. flex. tib. int.) had its origin at the caudal-most part of the lateral surface of the ala (fig. 1C). Birds also present a similar arrangement, with the M. flexor cruris lateralis (= semitendinosus) originating caudal to the origin of the M. iliotibialis (Vanden Berge 1975, McGowan 1979). A similar rugose area is found in several dinosaurs, including "*Caseosaurus*" (Long and Murry 1995), *Herrerasaurus* (Novas 1994), basal ornithischians (Janensch 1955, Abb. 3, Santa Luca 1980, fig. 17, 1984, fig. 12), and "prosauropods" (Galton 1976, fig. 26e, *Plateosaurus*—GPIT skeleton 1; *Efraasia*—SMNS 12389). In theropods, on the other hand, this rugose area is restricted to a more caudal portion of the ala (Gilmore 1920, pl. 10.2, Raath 1969; *Liliensternus*—MB.R. 2175).

As already discussed, the smooth area between the rugose origin of the M. flex. tib. ext. and the ridge that marks the caudal margin of the M. iliofem. cran. origin probably corresponds to the origin area of the M. iliofib. This is corroborated by the fact that in birds, the origin of this muscle is also between the origins of the M. caudofem. brevis (= M. piriformis) and M. iliotibialis (Vanden Berge 1975, McGowan 1979). As reconstructed for various other dinosaurs (Gregory 1923, Romer 1923a, Galton 1969, Russell 1972, Coombs 1979, Norman 1986, Dilkes 2000), the origin of the reptilian M. iliocaudalis (Romer 1923b) was probably at the caudal surface of the postacetabular ala and its medial platform.

The dorsalmost part of the internal surface of the postacetabular ala of *Saturnalia* bears strong striations, which are also present on the dorsal surface of the transverse process of the second sacral vertebrae. As discussed by Dilkes (2000), this probably corresponds to the origin of the M. longissimus, or of less differentiated dorsal muscles (Romer 1923b). Ventral to this, the rib/transverse process of the second sacral vertebra articulates with the medial border of the platform that forms the caudal part of the brevis fossa. Further cranially, this vertebral articulation is bounded ventrally by a ridge, which extends cranially along the internal surface of the ilium. This ridge is continuous with the platform itself, and it is also seen in several other dinosaurs (Long and Murry 1995, fig. 181b, Galton 2000b; *Liliensternus*—MB.R. 2175; *Efraasia*—SMNS 12389). Needless to say, this ridge has nothing to do with either of the two ridges mentioned above, which mark the medial and lateral boundaries of the brevis fossa.

The body of the ilium of *Saturnalia* is slightly longer than deep, proportions also seen in basal theropods (Huene 1934, Raath 1969, Padian 1986), basal ornithischians (Thulborn 1972), and some "prosauropods" (Galton 1973, Benton et al. 2000). This differs from the iliac body of robust "prosauropods" (Bonaparte 1972, Cooper 1981) and *Herrerasaurus* (Novas 1994), which are deeper than long.

The pubic peduncle of *Saturnalia* bears a straight dorsal margin at about 45° to the horizontal plane, and a subtriangular robust pubic articulation, which is broader medially and tapers laterally. This differs from the pubic peduncle of basal ornithischians, which is shorter and tapers ventrally (Thulborn 1972, Charig 1972), and is also distinct from those of basal theropods, which are much shorter and broader (Raath 1990, Cuny and Galton 1993; *Liliensternus*—MB.R. 2175). Right on the laterodorsal part of its articulation area, the pubic peduncle of *Saturnalia* presents a series of striations. Thulborn (1972) suggested that similar scars in *Lesothosaurus* indicate the presence of cartilaginous tissues binding the ilium to the pubis. However, as seen in *Maiasaura* (Dilkes 2000), it is likely that such scarring corresponds to the origin of either the M. ambiens (see below) or the M. puboischiofemoralis internus pars medialis (M. pub. isch. fem. int. med. = avian M. iliofemoralis internus; Walker 1977). Indeed, the medial surface of the pubic peduncle of *Saturnalia* presents faint muscular scars leading ventrally, which most probably are not associated with the origin of a crocodilian-like M. ambiens and/or M. pub. isch. fem. int. med. (see Romer 1923b, Walker 1977).

The iliac acetabulum of *Saturnalia* is longer than high, and deeper in its caudal part. It is almost fully closed, with the ventral border of the well-developed medial acetabular wall preserved as an almost straight margin. This suggests that the acetabular aperture, if present, would be rather reduced, and restricted to a small craniocaudally elongated gap between the ventral part of the iliac medial wall and the acetabular incisure of the pubis and ischium. Such a well-developed iliac medial wall approaches that of *Marasuchus* (Sereno and Arcucci 1994, Novas 1996), and the only other basal dinosaurs known to have such a closed acetabulum are *Guaibasaurus* (Bonaparte et al. 1999) and *Scelidosaurus* (BMNH 6704). In addition, as in most dinosaurs, *Saturnalia* has a well-developed supraacetabular crest.

The medial acetabular wall of *Saturnalia* shows a different texture in its central area, which is almost exactly in the position of the acetabular aperture of various basal dinosaurs (Bonaparte 1972, Novas 1994). It is suggested that this area, which is perforated in more derived dinosaurs, represents one of the articulation surfaces of the femoral head. A second main articulation area for the femoral head in the acetabulum is the antitrochanter (see Fraser et al. 2002), which occupies its caudoventral portion. It most closely resembles the antitrochanter of *Marasuchus* (Sereno and Arcucci 1994), *Herrerasaurus* (Novas 1994), "*Caseosaurus*" (Long and Murry 1995), and basal theropods (Raath 1969, Padian 1986; *Liliensternus*—MB.R. 2175). "Prosauropods" such as *Efraasia* (SMNS 12667) and *Plateosaurus* (GPIT skeleton 1), also have the antitrochanter in a similar position, but it is not so prominent as in the forms mentioned above. The antitrochanter of ornithischians, on the other hand, is usually more dorsally placed (Thulborn 1972, Maryanska and Osmólska 1974, Charig 1972), also facing more ventrally in some forms (Santa Luca 1980). Obviously, the so-called "antitrochanter" of several derived ornithischians (Romer 1927, Weishampel and Horner 1990, Dodson 1996) is not homologous to the articular area discussed here.

The short and robust ischial peduncle of *Saturnalia* is divided into two portions: the acetabular area, which is mainly occupied by the antitrochanter; and a caudal portion, the lateral surface of which is somewhat continuous with the brevis fossa. In lateral aspect, the caudal portion tapers ventrally, and does not contribute significantly to the ischial articulation, which is almost entirely below the area of the antitrochanter. This seems to represent a plesiomorphic feature for dinosaurs, since it is present in *Marasuchus* (PVL 3870), *Staurikosaurus* (Colbert 1970), *Guaibasaurus* (Bonaparte et al. 1999), basal ornithischians (Charig 1972, Santa Luca 1984), and some "prosauropods" (*Efraasia*—SMNS 12667). Robust basal dinosaurs, such as *Herrerasaurus* (PVL 2566) and various "prosauropods" (Bonaparte 1972, Van Heerden 1979), also retain this character, but the caudal part of the peduncle is much broader. In theropods, on the other hand, the ischial articulation faces caudoventrally, rather than ventrally, and the caudal part of the pubic peduncle is expanded (Raath 1990; *Liliensternus*—MB.R. 2175).

The articular facet of the ischial peduncle of *Saturnalia* is sub-rectangular, rounded laterally, but more angled medially. This contrasts with the sub-triangular and narrower articulation of *Lesothosaurus* (BMNH RUB17), *Staurikosaurus* (MCZ 1669), and *Herrerasaurus* (Novas 1994), but approaches the more derived condition seen in "prosauropods" (Young 1942, Galton 1973), theropods (*Liliensternus*—MB.R. 2175), and most ornithischians (Maryanska and Osmólska 1974, Galton 1981; *Scelidosaurus*—BMNH 6704).

Pubis (Fig. 2)—It is composed of a robust proximal body and an elongated shaft. The main axis is about 70° to the horizontal plane, a much higher angle than that of basal Dinosauriformes (Arcucci 1987, Sereno and Arcucci 1993, 1994), basal theropods (Huene 1934, Raath 1990), and "prosauropods" (Bonaparte 1972, Galton 1976, 1990, but see Galton 1984, fig.1e). Together with that of *Staurikosaurus* (Galton 1977), the pelvis of *Saturnalia* approaches a derived opisthopubic condition, as seen in *Herrerasaurus* (Novas 1994), but especially ornithischians (Seeley 1887) and some derived theropods (Perle 1979, 1985). Like *Pseudolagosuchus* (PVL 4629) and all basal dinosaurs, but different from more basal dinosauriforms (Sereno and Arcucci 1993, 1994), the pubis of *Saturnalia* is also much longer than half the length of the femur.

The body of the pubis in *Saturnalia* is composed of a robust cranial portion, a small caudal process, and the obturator plate. The boundaries between these three areas are clearly seen in lateral aspect. The ischio-acetabular groove (Sullivan and Lucas 1999) marks the separation between the cranial portion and the caudal process, which are clearly distinguished from the obturator plate because of their more robust construction. Their medial surfaces, on the other hand, are less differentiated, and are continuous with those of the pubic peduncle and the medial acetabular wall of the ilium.

The portion of the pubic body craniodorsoal to the ischio-acetabular groove is very robust, bearing a large and flat dorsocaudally facing proximal surface, the cranial two thirds of which is entirely in articulation with the pubic peduncle of the ilium. A flat acetabular incisure occupies the caudal third of that surface, forming the cranial-most part of the acetabular floor. Its medial margin is bounded cranially by the cranialmost part of the iliac medial acetabular wall, and caudally by the ischio-acetabular groove.

The ischio-acetabular groove was first described for the basal theropod *Eucoelophysis* (Sullivan and Lucas 1999), but it also constitutes a peculiar feature on the pubis of *Saturnalia*. It consists of a strong elongated concavity that excavates the proximal surface of the bone, and is entirely open towards the acetabulum. It also opens externally, piercing the lateral surface of the bone at its proximal margin. From that point it extends craniomedially, separating the pubic acetabular floor (craniolaterally) from the short contribution of the bone to the medial acetabular wall (caudomedially). Its medial end is, however, difficult to determine. It does not directly pierce the medial acetabular wall, but it might be connected to the inner part of the body by the main acetabular aperture. A much fainter ischio-acetabular groove is also seen on the pubis of some "prosauropods" such as *Plateosaurus* (Huene 1926, tafel V, fig. 3a,c) and *Efraasia* (SMNS 12354).

The function of this structure is uncertain, and it might represent only an incisure derived from the rearrangement of the proximal pubic articulation. It seems more likely, however, that it marks the position of a particular soft-tissue element, or represents the pathway of a vascular structure crossing the pelvis through the acetabular aperture. Sullivan and Lucas (1999) suggested that it might correspond to a branch of the ischial artery, but I am unaware of any living diapsid with a major blood vessel penetrating the acetabular aperture (O'Donoghue 1920, Baumel 1975). Some basal theropods (Camp 1936, Raath 1969, Rowe and Gauthier 1990, Carpenter 1997), as well as some basal archosaurs (Walker 1961, Ewer 1965), have two pubic apertures, which have been related to the obturator foramen and the "thyroid fenestra" (Romer 1956, Walker 1961, Raath 1969). Yet, these are placed on the obturator plate and neither seems to be homologous to the ischio-acetabular groove. The obturator foramen of basal theropods is in an absolutely corresponding position to that of *Saturnalia*. The extra aperture is, however, placed ventral to the ridge that marks the dorsal border of the main branch of the M. puboischiofemoralis externus (M. pub. isch. fem. ext.), whereas the ischio-acetabular groove is dorsal to it.

Caudal to the ischio-acetabular groove lies the caudal process of the proximal pubis. Its caudal margin forms a mediocaudally facing subtriangular convex articulation facet, which fits into a corresponding concavity on the craniolateral corner of the ischium. Laterally, the process has two inclined surfaces converging to an elongated raised central area. The dorsal surface forms the mediocaudal border of the ischio-acetabular groove, and also a small part of the cranioventral portion of the medial acetabular wall, where it is connected to the iliac part of the wall. The ventral surface of the process is continuous with the obturator plate.

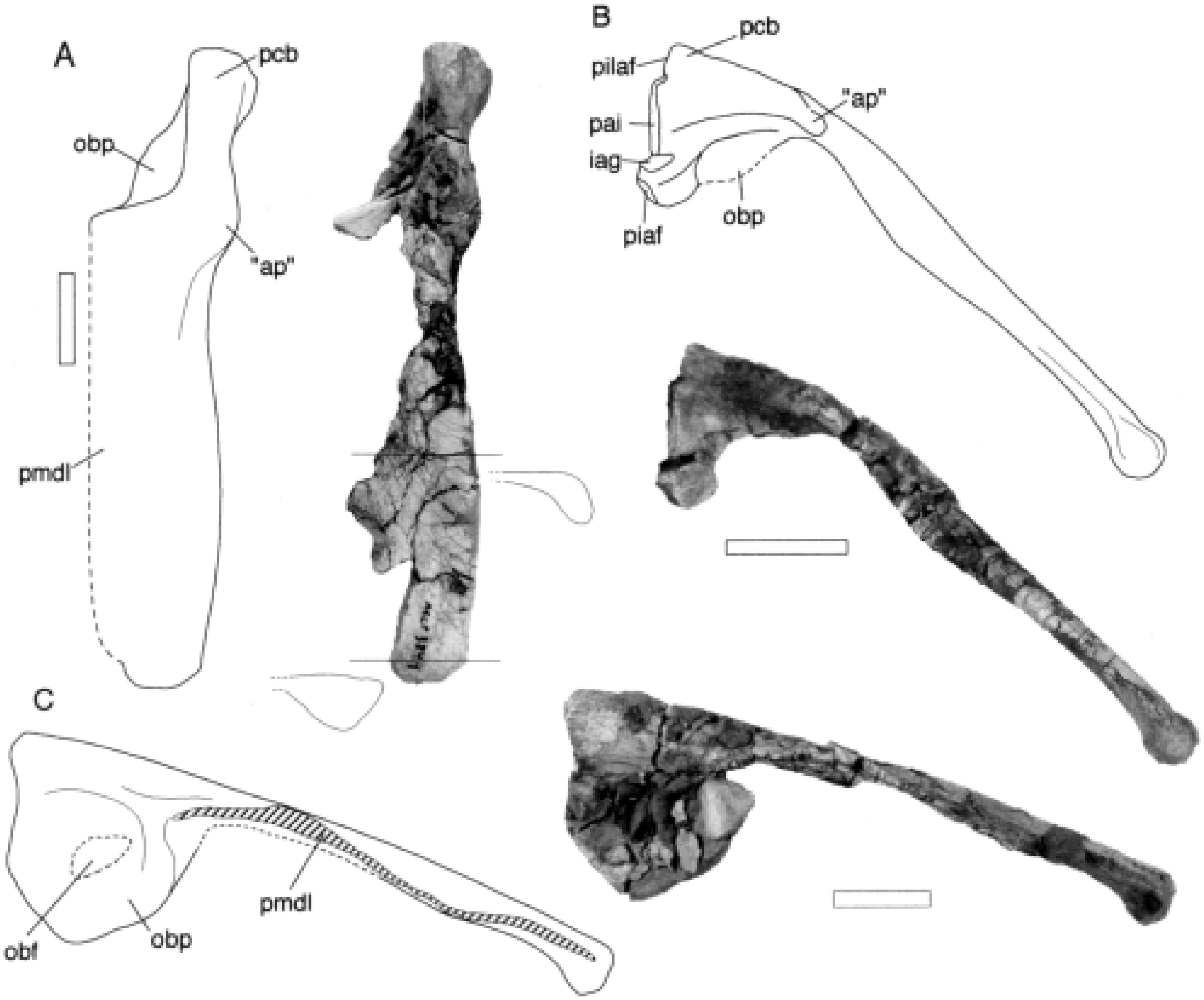

Fig. 2. Pubis of *Saturnalia tupinquim* (MCP 3944-PV). Scale bar = 2 cm. Right pubis in (**A.**) cranial, including cross section at the middle of the shaft and distal outline, and (**B.**) lateral aspects. **C.** Medial aspect of left pubis. Abbreviations: **"ap,"** "ambiens" process; **iag**, ischio-acetabular groove; **obf**, obturator fenestra; **obp**, obturator plate; **pai**, pubic acetabular incisure; **pcb**, pubic cranial butress; **piaf**, ischiadic articular facet on pubis; **pilaf**, iliac articular facet on pubis; **pmdl**, pubic mediodistal lamina.

The obturator plate forms the thin ventral part of the pubic body, expanding from the medial margin of its more robust proximal portion. It extends distally as a medially concave flange for about one quarter of the length of the pubis. At this point its ventral border is mediodorsally deflected to form the thin medial part of the pubic shaft, which composes the entire symphyseal area of the bone. Differing from basal theropods (Rowe and Gauthier 1990) a single aperture is present in the obturator plate, which is the obturator foramen. Its size is comparable to that of most basal dinosaurs, though it is smaller than that of some "prosauropods" (Huene 1926, Cooper 1981).

The body of the pubis possesses several indications of muscle attachments. Its craniodorsal rim forms a broad striated ridge that is continuous with the similarly striated dorsal margin of the pubic peduncle of the ilium. In the lateral surface of the bone, a series of strong striations radiate from the cranial margin of the acetabulum, at the pubis-ilium contact. More ventrally, two longitudinal ridges are seen. The first ridge extends from the caudal part of the acetabular incisure, entering the pubic shaft to form the ventrolateral corner of its proximal portion. Dorsally to the middle of this ridge, a very strong protuberance is seen, which is somewhat continuous with the broad ridge on the dorsal part of the bone. The second ridge is fainter and extends sub-parallel and ventral to the previous one. It originates from the striated caudal process of the iliac body, and also extends cranially.

As in *Saturnalia*, the dorsal rim of the pubis of most dinosaurs is somewhat salient, a feature much more marked in certain sauropods (Gillette 1991). In an arrangement similar to that of the crocodile (Romer 1923b), several authors reconstructed the origin of the M. ambiens in this area, both in sauropods (Romer 1923a, Borsuk-Bialynicka 1977) and other dinosaurs (Romer 1927, Perle 1985, Dilkes 2000). This might also have been the case in *Saturnalia*, but the more distal "pubic tubercle" (Hutchinson 2001b) also seems to represent a suitable origin area for that muscle, as suggested for several other dinosauromorphs (Galton 1973, 1984, Bonaparte 1986, Arcucci 1987, Novas 1994, Sereno and Arcucci 1993, 1994, Bonaparte et al. 1999, Sullivan and Lucas 1999). Although the M. ambiens has a single head in birds (McGowan 1979), it is suggestive that crocodiles have a second head, which originates on the internal surface of the pubic body (Romer 1923b). Accordingly, it is possible that basal dinosaurs had a double-headed M. ambiens (Fig. 8), originating on the dorsal rim of the pubis and on the more distal lateroventral protuberance. Indeed, both areas are nearly continuous in some basal dinosaurs (Galton 1984, Sereno and Wild 1992).

In conclusion, the well-developed bump on the dorsal rim of the pubis of some derived sauropodomorphs and theropods (Romer 1923a, Perle 1985, Gillette 1991) is not homologous to the more distal lateroventral protuberance of basal dinosauromorphs, and other basal archosaurs (Walker 1961, 1964). Accordingly, this last structure seems to have been progressively lost in various dinosaur lineages (Gilmore 1920, Cooper 1981, 1984, Welles 1984). If basal dinosaurs had a single-headed M. ambiens, the dorsal rim of the pubis could mark the insertion of a branch of the abdominal muscles, or the origin of the M. pub. isch. fem. int. med. (Romer 1923b, Walker 1977, Dilkes 2000). Alternatively, as discussed by Hutchinson (2001b), the "pubic tubercle" might be related to pelvic ligaments or the abdominal musculature.

As in most saurischians (Cooper 1981, 1984, Sereno and Wild 1992, Novas 1994), the proximal portion of the pubic symphysis of *Saturnalia* is formed by the dorsomedially deflected ventral margin of the distal part of the obturator plate. From that point, the symphysis continues distally along almost the entire medial margin of the shaft. This situation is distinct from that of ornithischians, the pubic symphysis of which is restricted to the distal end of the bone, as is that of their ischium (Ostrom and McIntosh 1966). In addition, the shaft of the highly derived ornithischian pubis is narrow and rod-like, usually lacking a medial lamina (but see Thulborn 1972). The pubic shaft of *Saturnalia*, on the other hand, presents an extensive medial lamina, which expands from the mediodorsal corner of the more robust lateral border to form the pubic symphysis. This condition is thought to be primitive for dinosaurs, because it occurs in basal dinosauriforms (Sereno and Arcucci 1993, 1994; *Pseudolagosuchus* - PVL 4629) as well as in *Herrerasaurus* (Novas 1994), *Staurikosaurus* (MCZ 1669), *Guaibasaurus* (Bonaparte et al. 1999), "prosauropods" (Huene 1926, Galton 1973), and basal theropods (Huene 1934, Raath 1969, Carpenter 1997). In addition, in *Saturnalia*, *Guaibasaurus*, and basal theropods, the lateral margin of the pubis extends ventrally, giving the shaft a transversely concave ventral surface.

The pubis of *Saturnalia* is swollen at its distal end, a feature unknown in basal ornithischians (Thulborn 1972, Charig 1972). *Herrerasaurus* (PVSJ 373), *Staurikosaurus* (MCZ 1669), basal theropods (Huene 1926, Welles 1984, Padian 1986, Carpenter 1997), and "prosauropods" (Huene 1926, Bonaparte 1972, Galton 1973), also present a swollen distal end of the pubis, a feature considered plesiomorphic for dinosaurs because it is also present in *Pseudolagosuchus* (PVL 4629). Besides, in all non-ornithischian basal dinosaurs, and possibly also in *Pseudolagosuchus* (PVL 4629), the thin medial flange that composes most of the pubic symphysis is slightly proximally deflected, and does not contact its counterpart at the distal end of the bone. In "prosauropods" this space is occupied by the distal bulging of the bone, which is medially extended and meets its counterpart in the symphyseal area. Their symphysis, therefore, reached the distal end of the pubis, which shows an "apron-like" shape (Huene 1926, Galton 1973, 1990) that is characteristic of the group. On the contrary, the swollen area of the distal pubis of *Saturnalia* is not medially extended, and a small gap appears between the distal end of the pubic shafts, which is also seen in basal theropods (Padian 1986, Carpenter 1997), *Pseudolagosuchus* (PVL 4629), and *Herrerasaurus* (PVSJ 373), but is particularly marked in *Staurikosaurus* (Novas 1994). Yet, in the last two forms the distal bulging of the pubis is much more transversely extensive, approaching the condition of "prosauropods," and differing from that of the other taxa mentioned above, which are narrow in distal outline. However, they still do not contact the counterpart (*Staurikosaurus*—Novas 1994), or this contact is cranially restricted (*Herrerasaurus*—PVSJ 373). This last arrangement seems to be also present in some basal theropods such as *Coelophysis* (Padian 1986) and *Gojirasaurus* (Carpenter 1997). Other members of the group (Huene 1934, Sereno and Wild 1992), however, present an arrangement more similar to that of *Saturnalia* and *Staurikosaurus*, and their pubic symphysis is restricted to the medial thin flange of the bone.

The main muscle attached to the pubic shaft of *Saturnalia* is the M. pub. isch. fem. ext. (Fig. 8). Its part 1 (Romer 1923b) originated on the cranial surface of the distal half of the bone, and extended proximally, bounded dorsally by a lateroventral protuberance ("ambiens process") and the dorsalmost longitudinal ridge of the lateroventral part of the pubic body. The origin of part 2 of the muscle was on the caudal surface of the pubic shaft. Its proximal part extended ventral to part 1, covering the obturator plate, bounded dorsally by the ventral-most ridge of the lateroventral part of the pubic body. The caudal process of the pubic body was also covered by part 1 of the M. pub. isch. fem. ext., and its striated lateral surface might have marked a separated branch of this muscle, as seen in the crocodile (Romer 1923b). In the modified pubis of *Herrerasaurus*, the lateral surface of the distal half is equivalent to the cranial surface of that of *Saturnalia*. Accordingly, the extensive longitudinal ridge seen on that surface marks the dorsomedial border of the origin of puboischiofemoralis part 1. A similar muscle arrangement on the pubis was probably present not only in *Marasuchus* and *Staurikosaurus*, but also in more derived theropods with a marked distal "boot" (*contra* Romer 1923a).

The pubic shaft of *Saturnalia* and "prosauropods" (Bonaparte 1972, Galton 1973) presents a lateral expansion in the distal half of its lateral border. The proximal margin of this expansion probably marks the passage of the part 1 of M. pub. isch. fem. ext., extending proximally from its origin at the cranial surface of the pubis. A similar concavity is seen in *Herrerasaurus* (Novas 1994) but not in basal theropods (Gilmore 1920, Colbert 1989, Sereno and Wild 1992, Carpenter 1997), which present a mainly straight lateral margin of the pubis that converges medially towards the distal end. This arrangement might indicate that part 1 of their M. pub. isch. fem. ext. originated from a more restricted area on the distal pubis and extended more ventral to the shaft, a condition likely to have been also present in *Guaibasaurus* (Bonaparte et al. 1999).

Ischium (Fig. 3)—Its body is composed of a robust dorsal portion and the thin obturator plate. The medial surface of the dorsal portion is flat to slightly convex, whereas the lateral surface is markedly convex. The obturator plate is a sigmoid flange, convex laterally and concave medially in its proximal portion, but convex medially and concave laterally in its distal portion. The proximal surface of the ischium is almost flat, lacking an excavated acetabular incisure as seen in most basal dinosaurs (Santa Luca 1984, Raath 1990). The caudomedial portion of that surface is occupied by the

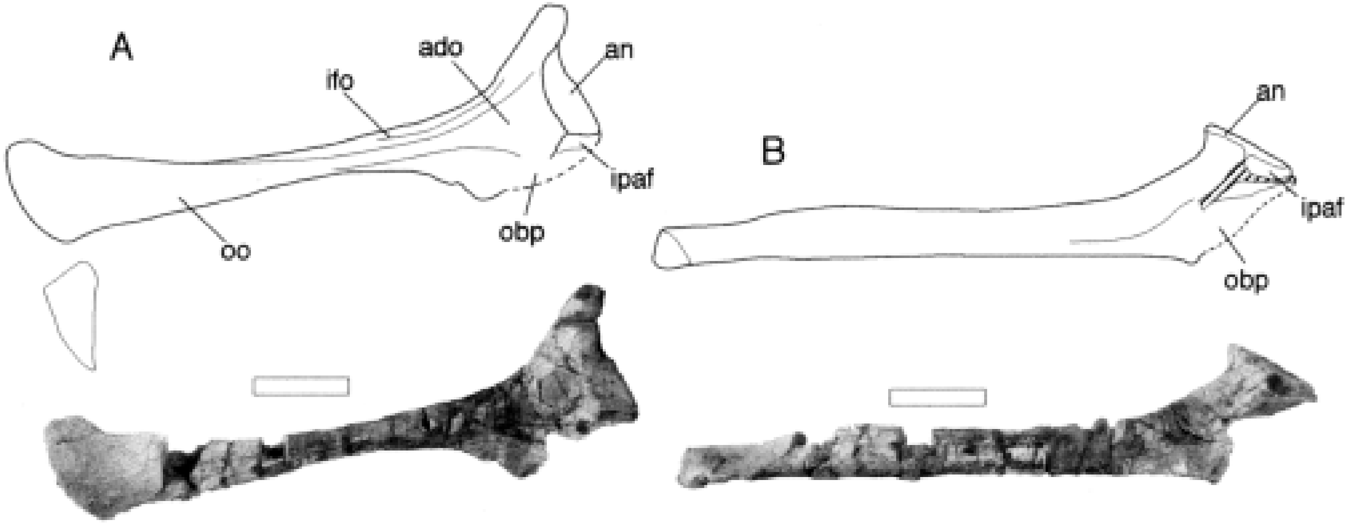

Fig. 3. Left ischium of *Saturnalia tupinquim* (MCP 3944-PV) in (**A.**) lateral, including distal outline, and (**B.**) ventral aspects. Scale bar = 2 cm. Abbreviations (see also Figs. 1 and 2): **ado**, abductor dorsalis origin; **ifo**, ischifemoralis origin; **ipaf**, ischiadic articular facet for pubis; **oo**, obturatorius origin.

articulation with the ischial peduncle of the ilium, the ventrocaudal corner of which is covered by the upturned caudal margin of the ischial body. Cranial to this, the antitrochanter of *Saturnalia* occupies the entire acetabular incisure. It presents strongly expanded lateral borders, and reaches the pubic articulation at its cranial end. This differs from the condition in *Marasuchus* (Novas 1996), *Herrerasaurus* (Novas 1994), "prosauropods" (*Plateosaurus*—IGPT skeleton 1; SMNS F-07), and basal theropods (Huene 1934, Welles 1984, Raath 1990), the ischial antitrochanter of which is restricted to the caudal part of the acetabular incisure. The condition in theropods is even more distinct from that of *Saturnalia*, because their ischium bears a strong concavity at the cranial part of the acetabular incisure. Ornithischians, on the other hand, have a distinct antitrochanter, which does not enter the ischium (Maryanska and Osmólska 1974, Charig 1972, Santa Luca 1980, Sereno 1991a).

No other basal dinosaur presents an ischial antitrochanter as large as that of *Saturnalia*. Such a well-developed structure is thought to represent an autapomorphic reversal in this taxon, since it is otherwise known only in more basal archosaurs (Walker 1964, Ewer 1965, Chatterjee 1978), including the dinosauromorph *Lagerpeton* (Sereno and Arcucci 1993). Moreover, the ischial antitrochanter of *Saturnalia* is craniomedially bounded by the medial acetabular wall of the ilium, though the ischium itself does not contribute to that wall. This arrangement is also plesiomorphic, since it is unknown in dinosaurs with a partially closed acetabulum (Novas 1994), but it is present in *Lagerpeton* (Sereno and Arcucci 1993) and *Marasuchus* (Novas 1994).

In the ischium of *Saturnalia*, the pubic articulation is placed cranioventral to the antitrochanter. Its main part is formed by a laterocranially facing concavity, which receives the caudal process of the pubis. The thin sheet of bone that forms its medial surface is continuous with the obturator plate, and overlaps the caudal process of the pubis medially. The obturator plate itself is incompletely preserved but, contrary to the condition in some other dinosaurs (Huene 1926, Novas 1994), it does not seem to contribute significantly to the pubo-ischial articulation. However, it was certainly ventrally extensive, occupying the entire cranioventral margin of the ischial body. This condition seems to be apomorphic within dinosaurs, since the cranial margin of the ischium of *Marasuchus* (Sereno and Arcucci 1994) apparently does not have such a well-developed thin ventral expansion. This condition seems to have been retained in ornithischians, because the pubic peduncle of their ischium either lacks (Ostrom and McIntosh 1966, Colbert 1981; *Scelidosaurus*—BMNH 6704) or presents a very reduced obturator plate (Santa Luca 1980, Forster 1990, Sereno 1991a). In *Herrerasaurus* (Novas 1994), *Staurikosaurus* (Colbert 1970), "prosauropods" (Bonaparte 1972, Galton 1984), and basal theropods (Janensch 1925, Huene 1934, Welles 1984, Raath 1990), on the other hand, a thin ventral flange forms at least half of the depth of the pubic peduncle, corresponding to a well-developed obturator plate. In various theropods, this plate is caudally displaced (Osborn 1916, Ostrom 1969, Barsbold et al. 1990, Barsbold and Maryanska 1990) to a position similar to that of the so-called "obturator process" of ornithopods (Galton 1974, 1981, Forster 1990), which is not homologous to the structure dealt with here (see below).

Each obturator plate of *Saturnalia* meets its counterpart on its caudoventral margin, where it forms the short cranial-most portion of the ischial symphysis. Caudal to that, as in all basal saurischians, the obturator plate merges into the shaft, and the rest of the symphysis is formed by the rod-like distal part of the bone (Gilmore 1920, Janensch 1925, Huene 1926, 1934, Young 1941a, b, Raath 1969, Bonaparte 1972, 1982, Galton and Jensen 1979, Van Heerden 1979, Cooper 1981, 1984, Welles 1984, Galton 1984 Novas 1994, 1996, Bonaparte et al. 1999; *Eoraptor*—PVSJ 512; *Staurikosaurus*—MCZ 1669). That portion of the symphysis marks the caudal border of the pubo-ischial fenestra, the ischial part of which is well-developed in *Saturnalia*, as it is in most basal dinosauriforms, except *Lagerpeton* (Sereno and Arcucci 1993). Yet, this part of the fenestra seems to be apomorphically less extensive in forms that, like *Saturnalia*, present an enlarged obturator plate (Huene 1926, Raath 1969, Novas 1994). On the contrary, the ischial symphysis of *Marasuchus* (Bonaparte 1975) is restricted to the caudal part of the shaft, and the ventromedial lamina of the bone forms the caudal margin of a larger pubo-ischial fenestra. Similarly, a major excavation forming the caudolateral margin of the pubo-ischial fenestra is seen in the craniomedial surface of the ischium of *Lesothosaurus* (Thulborn 1972). Indeed, a distally restricted ischial symphysis seems to be a general ornithischian feature (Ostrom and McIntosh 1966). In addition, the ischium of *Lesothosaurus* (Thulborn 1972; BMNH RUB17) presents a ventromedial lamina expanding from the lateral border of its caudal half. This is probably homologous to the so-called "obturator process" of some derived ornithopods (Romer 1927, Galton 1974), which seems to represent a remnant of it.

The caudal two thirds of the rod-like ischial shaft of *Saturnalia* is sub-triangular in cross section. Such an arrangement is given by its flat medial, dorsal, and lateroventral margins. In fact, the medial margin is not completely flat, but bears a longitudinal groove, as seen in some theropods (Gilmore 1920, Raath 1969). The dorsal margin, on the other hand, is slightly inclined, giving the dorsal surface of the joined ischia a concave outline, and joins the lateroventral margin to form a marked lateral ridge. This ridge is one of the major features of the ischial shaft of *Saturnalia*, and a similar structure has been recognized in most other basal dinosaurs, including *Guaibasaurus* (MCN 2355), *Herrerasaurus* (PVL 2566; PVSJ 373), "prosauropods" (Bonaparte 1972, Galton 1984), basal theropods (Gilmore

1920, Janensch 1925, Huene 1926, Raath 1969), and basal ornithischians (Thulborn 1972, Charig 1972, Santa Luca 1984; *Dryosaurus*—MB mounted skeleton). In *Saturnalia*, the cranial part of the ridge enters the lateral surface of the ischial body, where it is dorsally deflected, extending as far as the caudal part of the antitrochanter. This arrangement is different from that of dinosaurs with a strong acetabular incisure (Raath 1969, Santa Luca 1980, 1984, Cooper 1984, Bonaparte 1986; *Liliensternus*—MB.R. 2175), in which this ridge usually bifurcates along the body of the ischium. In *Saturnalia*, such a bifurcation can only be hinted at by the presence of a feeble secondary ridge, extending cranially and ventral to the main ridge. Caudally, the main lateral ridge forms the dorsolateral corner of the ischial shaft. This condition is similar to that of *Herrerasaurus* (PVSJ 373), *Guaibasaurus* (MCN 2355), and "prosauropods" (Huene 1926, Cooper 1981). In basal theropods, on the other hand, the lateral ridge is more ventrally placed. As a result, the cross section of the ischial shaft is semicircular rather than sub-triangular (Raath 1969, Padian 1986; *Liliensternus*—MB.R. 2175), a condition apparently also present in *Staurikosaurus* (MCZ 1669). In *Saturnalia*, the lateral ridge is dorsally deflected in the distal third of the ischium. In addition, it meets its counterpart medially, defining the caudal border of the concave dorsal surface of the conjoined ischial shafts.

As in all basal eusaurischians (Huene 1926, 1934, Young 1942, Galton and Jensen 1979, Bonaparte 1972, 1982, Jain et al. 1975, Van Heerden 1979, Welles 1984, Padian 1986, Bonaparte et al. 1990, 1999, Raath 1990), but distinct from other basal dinosauromorphs (Ostrom and McIntosh 1966, Colbert 1970, Santa Luca 1980, Novas 1994, Sereno and Arcucci 1993, 1994, Sereno et al. 1993; *Scelidosaurus*—BMNH 6704; *Lesothosaurus*—BMNH RUB17), the distal end on the ischium of *Saturnalia* is dorsoventrally expanded. In addition, the dorsal end of the shaft is slightly upturned and more distally projected than the ventral end. A similar form of the distal end of the ischium is seen in "prosauropods" (Huene 1926, Bonaparte 1972), basal theropods (Huene 1926, Padian 1986), *Guaibasaurus* (MCN 2355), and also *Herrerasaurus* (PVL 373). The ischium of basal ornithischians, on the contrary, has its distal surface forming straight angles to the dorsal and ventral margins (Charig 1972, Galton 1974, Sereno 1991a, Peng 1997).

The distal aspect of the ischium of *Saturnalia* is incompletely known, because its dorsolateral corner is not well preserved in any of the available specimens. It seems, however, that the lateral ridge reaches the distal border of the bone at its dorsal-most portion. This condition is also seen in "prosauropods" (Buffetaut et al. 1995), *Guaibasaurus* (MCN 2355), *Herrerasaurus* (Novas 1994), and most basal ornithischians (Thulborn 1972, Galton 1981, Colbert 1981), but not in basal theropods (Gilmore 1920, Padian 1986) and some other ornithischians (*Scelidosaurus*—BMNH 6704), in which the distal part of the crest is more ventrally placed. Yet, the caudodorsal surface of the ischium of *Saturnalia* is not as broad and flat as that of some "prosauropods" (Young 1941a, 1942, Van Heerden 1979, Buffetaut et al. 1995). Instead, it approaches more the condition of other members of the group (Huene 1926, Galton 1976; ?*Massospondylus*—BPI 4693), as well as that of basal theropods (Padian 1986), *Herrerasaurus* (PVSJ 373) and *Guaibasaurus* (MCN 2355), in which the dorsocaudal surface of the ischium is narrower and dorsally convex.

The lateral ridge of the ischium is the main muscle-related feature of this bone in *Saturnalia*. It marks the separation between the areas of origin of the M. ischiofemoralis (M. ischiofem. = M. ischiotrocantericus; Romer 1923b, Dilkes 2000) mediodorsally, and those of the M. pub. isch. fem. ext. part 3 (= avian M. obturatorius) and dorsal branch of the M. adductor (M. add. = avian M. puboischiofemorale), lateroventrally. This ridge apparently corresponds with the entire dorsal surface of the ischium of non-dinosaurian archosaurs (Romer 1956, Walker 1964, Chatterjee 1978, Sereno and Arcucci 1993, 1994), which separates the origin area of the aforementioned muscles. In birds, like in dinosaurs, this separation is placed on the lateral surface of the ischium, rather than at its dorsal border (Feduccia 1975, McGowan 1979).

The striations related to the origin of the M. obturatorius (M. obt.) occupy all the lateroventral surface of the ischial shaft of *Saturnalia*. Therefore, different from the reconstructions of Romer (1923a) for saurischians, it is suggested that the origin of this muscle was not restricted to the obturator plate, but extended along almost the entire ischial shaft (see also Gregory 1923, Russell 1972, Borsuk-Bialynicka 1977). From that area the muscle extended proximally, lateral to the obturator plate, in the direction of the femoral head (Fig. 8). Similar relations for the M. obt. were also reconstructed by Romer (1927) for *Thescelosaurus*, and probably represent the condition for most basal dinosaurs. As already discussed, the lateral ridge has a faint side branch extending cranially along the ventral portion of the ischial body, dorsal to the obturator plate. This possibly marks the ventral edge of the origin area of the dorsal branch of the M. add., which has been reconstructed in approximately the same position in various other dinosaurs (Romer 1923a, 1927, Dilkes 2000).

In the crocodile (Romer 1923b), two other muscles originate at the lateral surface of the cranioventral portion of the ischium: the M. puboischiotibialis and the ventral branch of the M. add. The presence of such muscle attachment areas in *Saturnalia* is unclear, due to incomplete preservation of the obturator plate. However, a rugose sub-triangular scar is seen at the ventral margin of the caudal part of the plate, just dorsal to the area where it forms the cranial part of the ischial symphysis. Such a rugose area is also seen in other basal dinosaurs such as *Megapnosaurus* (QVM QG1) and *Efraasia* (SMNS 12354), and it might be related to the origin of the ventral branch of the M. add.

The ischium of *Saturnalia* bears a marked laterodorsally-facing groove, which extends along the dorsal surface of the cranial part of the bone, and is continuous with the dorsal platform that occupies most of the shaft. This is the main muscle attachment area medial to the lateral ridge of the ischium, and it surely corresponds to the origin of the M. ischiofem. (Fig. 3A). A similar groove is known in various basal dinosaurs including *Guaibasaurus* (MCN 2355), basal sauropodomorphs (Huene 1926, Cooper 1981, 1984), basal theropods (Gilmore 1920, Janensch 1925—*Liliensternus*—MB.R. 2175), and basal ornithischians (Thulborn 1972, Santa Luca 1984; *Dryosaurus*—MB mounted skeleton). In all these forms, the marked dorsomedial border of the ischium, the cranial portion of which rises above the lateral ridge itself, borders the groove medially. This seems to represent a neomorphic structure of dinosaurs, since it is absent in other archosaurs, in which the origin of the M. ischiofem. is restricted to the medial surface of the bone (Romer 1923b). On the contrary, in dinosaurs, as in birds (McGowan 1979), the origin of this muscle is partially on the lateral surface of the ischium. In some derived ornithischians (Romer 1927, Galton 1969, Santa Luca 1980, Norman 1986), the caudal portion of the lateral ridge is lateroventrally deflected, entering the lateral surface of the shaft. In these forms, the entire laterodorsal surface of the bone is occupied by the M. ischiofem. An analogous situation is also seen in basal theropods (Raath 1969, Padian 1986), the lateral ridge of which is placed more ventrally on the lateral surface of the shaft. In *Saturnalia*, in particular, the M. ischiofem. does not occupy only the dorsal groove, but also spreads onto the flat dorsomedial surface of the caudal part of the bone.

In the crocodile (Romer 1923b), two branches of the M. flex. tib. int. (= avian M. flexor cruris medialis) have their origins on the ischium. The more caudal origin has been recognized in *Piatnitzkysaurus* (Bonaparte 1986), and different authors have also associated it with different structures on the lateral surface of the ischium of ornithischians (Romer 1927, Thulborn 1972, Coombs 1979, Dilkes 2000). In *Saturnalia*, a small rugose area is seen on the caudal part of the lateral ridge, between the areas of origin of M. obt. and M. ischiofem. Its position is almost the same as that of the “knob-like” structure described by Novas (1994) on the ischium of *Herrerasaurus.* This probably corresponds to the origin of the caudal part of the M. flex. tib. int., the caudal position of which is thought to be primitive amongst dinosaurs.

The origin of the dorsal part of the M. flex. tib. int., has been related to a rugose area on the caudal part of the ischial body of some saurischians (Romer 1923a, Borsuk-Bialynicka 1977). Indeed, the M. flexor cruris medialis has its origins in a very similar position on the avian pelvis (Vanden Berge 1975, Dilkes 2000). In *Saturnalia*, the caudal part of the ischial body has a striated caudal surface, which is continuous with the protuberant caudomedial margin of the bone. Various basal saurischians (Gilmore 1920, Bonaparte 1986; *Herrerasaurus*—PVL 2566; *Efraasia*—SMNS 12354) have a concavity just cranial to that caudal border, while the caudal border itself is particularly well developed in *Riojasaurus* (Bonaparte 1972). Both the concavity and/or the border could be associated with the origins of the M. flex. tib. int.

The poor preservation of the distal end of the ischium of *Saturnalia* does not allow the recognition of muscle scars, but their position can be partially inferred based on the general shape of that area. Norman (1986) reconstructed the insertion of the M. rectus abdominis on the cranial surface of the distal end of the ischial shaft of *Iguanodon.* It is likely that such an insertion was also present on the ventrocranial corner of the expanded distal ischium of various basal dinosaurs (Huene 1926, 1934, Bonaparte 1972, Padian 1986; *Herrerasaurus*—PVSJ 373), including *Saturnalia.* Similarly, the distally expanded caudodorsal part of the end of the ischium of these forms (Galton 1984, Padian 1986, Raath 1990, Bonaparte et al. 1999) probably corresponds with the origin of the reptilian M. ischiocaudalis (Romer 1923b), as also reconstructed for other members of the group (Romer 1923a, Russell 1972, Dilkes 2000). According to Dilkes (2000), both the M. ischiocaudalis and M. iliocaudalis of reptiles correspond to the avian M. pubocaudalis (Vanden Berge and Zweers 1993).

Pelvic Limb

The hind limb of *Saturnalia* is more than twice the estimated length of the forelimb. A similar proportion is also found in theropods (Huene 1926, Raath 1969, Welles 1984), bipedal ornithischians (Thulborn 1972, Santa Luca 1980), and it was also estimated for *Herrerasaurus* (Novas 1994, Sereno 1994). Most “prosauropods,” on the other hand, have relatively long forelimbs (Cooper 1981, Galton 1976, Bonaparte and Pumares 1995), which are more than half the hind limb length. Various authors (Romer 1966, Cooper 1981) have used these ratios as indicative of bipedal or quadrupedal gait in dinosaurs. Based solely on this approach, *Saturnalia* would be placed within the bipedal group.

Femur (Fig. 4)—It shows a “sigmoid” aspect both in cranial and lateral views. As discussed by Hutchinson (2001b), however, the dinosaur “sigmoid” femur results from the combination of an inturned head and a bowed shaft. In the case of *Saturnalia*, the femoral shaft is bowed both cranially and medially. The cranial bowing is a common feature of the archosaur femur, which is retained plesiomorphically in most early dinosaurs (Hutchinson 2001b). The medial bowing is also plesiomorphic for dinosaurs, since it is present in *Lagerpeton* (PVL 4619) and *Pseudolagosuchus* (PVL 4629).

The proximal surface of the femoral head of *Saturnalia* is flat, and articulates entirely with the acetabulum. It bears a distinct groove, which extends along its long axis. This groove fits into a faint ridge in the dorsal part of the acetabulum, and divides the femoral head into mediocaudal and laterocranial areas, which articulated respectively with the body of the ilium and the supracetabular buttress (see also Cooper 1981, fig. 64). A similar groove is present in various basal dinosaurs, including *Staurikosaurus* (Galton 1977), *Herrerasaurus* (PVL 2558), *Scelidosaurus* (BMNH 6704), *Coelophysis* (Padian 1986; fig. 5.4c, "gr1"), *Liliensternus* (MB.R. 2175), *Anchisaurus* (Galton 1976), and *Massospondylus* (Cooper 1981). In ornithopods and advanced theropods (Galton 1981, Forster 1990, Barsbold

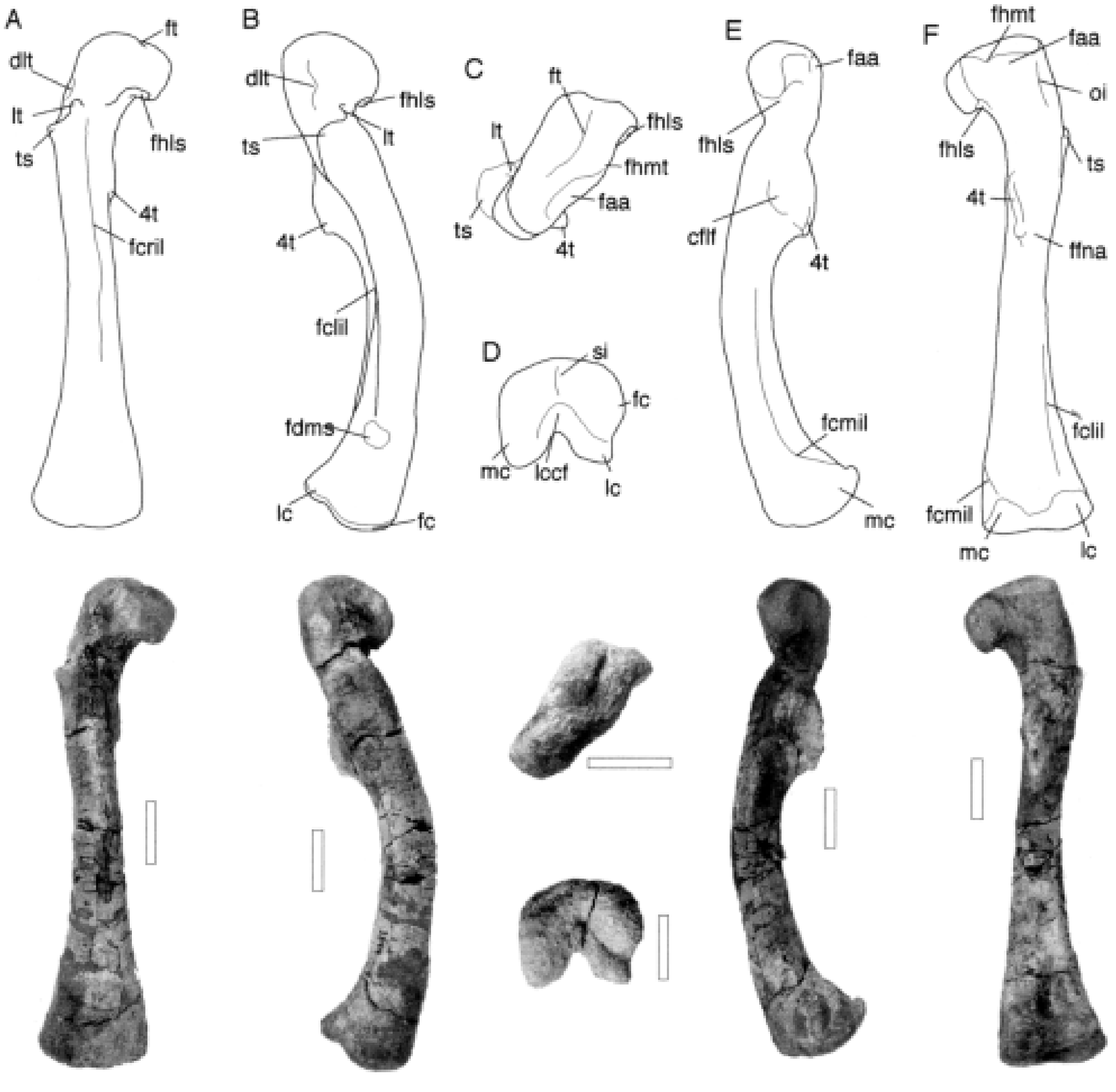

Fig. 4. Right femur of *Saturnalia tupinquim* (MCP 3944-PV) in (**A.**) cranial, (**B.**) lateral, (**C.**) proximal, (**D.**) distal, (**E.**) medial, and (**F.**) caudal aspects Scale bar = 2 cm. Abbreviations: **cflf**, fossa for caudofemoralis longus; **dlt**, dorsolateral trochanter; **faa**, facies articularis antitrochanterica; **fc**, fibular condyle; **fclil**, femoral caudolateral intermuscular line; **fcmil**, femoral caudomedial intermuscular line; **fcril**, femoral cranial intermuscular line; **fdms**, muscle scar on laterocranial distal femur; **ffna**, foramen for nutritive artery on femur; **fhls**, ligament sulcus on femoral head; **fhmt**, medial tuber on femoral head; **ft**, fossa trochanteris; **lc**, lateral condyle; **lccf**, facet for Lig. cruciatum craniale; **lt**, lesser trochanter; **mc**, medial condyle; **oi**, obtutarorius insertion; **si**, sulcus intercondilaris; **ts**, trochanteric shelf; **4t**, fourth trochanter.

et al. 1990, Russell and Dong 1993), on the other hand, this groove is highly modified into the well-developed constricted area that separates their elevated "greater trochanter" from the inturned medial part of the head. This arrangement is also seen in birds (Baumel and Witmer 1993), which have a trochanteric fossa (fossa trochanteris) separating the greater trochanter (trochanter femoris) from the inturned head (collum and caput femoris). Accordingly, the "greater trochanter" of early dinosaurs is not restricted to the laterocaudal corner of the femoral head, as often suggested (Welles 1984, Padian 1986, Rowe 1989, Novas 1994). Instead, it encompasses the entire lateral surface extending from that corner to the craniolateral ridge ("r" in Padian 1986, fig. 5.4c).

In birds (McGowan 1979), the lateral surface of the greater trochanter bears the insertion area of the M. iliotroc. (*sensu* Rowe 1986). This was probably also the case in *Saturnalia*, in which an array of cavities and bumps are seen on the lateral surface of the head, in an arrangement very similar to that of *Herrerasaurus* (Novas 1994). Among these muscle scars, one deserves special attention for its widespread distribution among dinosaurs. In *Saturnalia*, it represents a crescent structure situated on the laterocaudal corner of the femoral head, as also seen in *Staurikosaurus* (Galton 1977, Fig 5c), *Guaibasaurus* ("dlt" in Bonaparte et al. 1999, fig. 8), ornithischians (Galton 1974, fig 54a, Galton and Jensen 1973, fig. 5a, Norman 1986, fig 79d), "prosauropods" (Galton 1984, pl. 4), and basal theropods ("Tg" in Raath 1990, fig. 7.7k; *Liliensternus*—MB.R. 2175). As suggested by Galton (1969) and Norman (1986), this is an insertion point for a branch of the M. iliotroc. that, judging by the orientation of the muscle scars and structure of the ridge, extended cranially.

An obturator ridge, like that of coelophysoid theropods (Raath 1990), is not present in the femur of *Saturnalia*. However, the caudal part of the medial surface of the femoral head bears a small proximodistally oriented ridge that seems to represent the insertion area for the external puboischiofemoral musculature, including its part 3 (= avian M. obt.; see Romer 1923b, Walker 1977, Dilkes 2000). As in birds, in which the impreciones obturatorae (Baumel and Witmer 1993) mark the mediocaudal border of the greater trochanter, the "greater trochanter" of *Saturnalia* is also limited caudally by the aforementioned ridge. Cranial to this, a longitudinal groove extends through the mediocaudal part of the head, entering the proximal surface of the bone as a faint concavity. In some dinosaurs, this groove is continuous with the trochanteric fossa. Yet, it clearly served for the articulation of the antitrochanter, and is considered here as homologous to the avian facies articularis antitrochanterica (Baumel and Witmer 1993).

Novas (1996; fig. 3c, "pd") erroneously considered the proximal part of the facies articularis antitrochanterica of *Herrerasaurus* as its single correlate to the avian trochanteric fossa. This is probably because in some specimens of that taxon (PVSJ 373) this articular area is so enlarged that it merges with the trochanteric fossa itself, and is not clearly distinguishable from it. In addition, Novas (1996) also claimed that such a structure was not for the articulation with the antitrochanter, because *Lagerpeton*, which has an antitrochanter, lacks a corresponding element. However, *Lagerpeton* has a facies articularis antitrochanterica, but because the antitrochanter of this dinosauromorph is placed more ventrally (Sereno and Arcucci 1993), it does not extend onto the proximal femur, but is restricted to the medial surface of the bone (see Novas 1996; fig. 3a,d).

The femoral head of *Saturnalia* has a medially projected portion, which is bounded caudally by the facies articularis antitrochanterica, and laterally and cranially by the trochanteric fossa. This is homologous to the collum end caput femoris of birds (Baumel and Witmer 1993), and a longitudinal ridge on its mediocaudal part leads proximally to the so-called medial tuber (see Novas 1996). More cranially, the femoral head forms a rounded articulation, which projects further medially. It articulates dorsally and medially with the cranial part of the iliac acetabulum, and cranially, distally, and laterally to the pubic acetabulum. This area is not as projected in basal dinosauromorphs (*Marasuchus*—PVL 3870; *Pseudolagosuchus*—PVL 4629) as it is in *Saturnalia* and other dinosaurs, and its further development seems to represent a derived feature of the group. Strong cavities, which border this projection distally and mediocaudally, are probably for the insertion of ligaments of the caput femoris—Lig. iliofemorale and pubofemorale (see Baumel and Raikow 1993). In various dinosaurs (Galton 1981, Barsbold et al. 1990, *Scelidosaurus*—BMNH 6704), these ligaments insert smoothly onto proximally expanded concavities, both cranial and caudal to the medial projection. In *Saturnalia*, and in a series of other basal dinosaurs (Colbert 1970, Galton 1976, Cooper 1981, Bonaparte et al. 1990, Raath 1990, Novas 1994, Madsen and Welles 2000; *Liliensternus*—MB.R. 2175), the insertion area of the cranial ligament is restricted to the distal part of the head, and lateroproximally bordered by a step border.

Based on the homology hypothesis for the femoral structures presented here, the achievement of a fully inturned femoral head within dinosaurs must be reviewed. In *Saturnalia*, as well as in most basal dinosaurs (Huene 1926, Galton 1977, Welles 1984, Raath 1990, Sereno 1991a, Novas 1994), the femoral head is slightly inturned and the "greater trochanter" faces laterocranially. This is a derived condition if compared to the femoral head of basal dinosauriforms such as *Marasuchus* (Sereno and Arcucci 1994) and *Pseudolagosuchus* (Arcucci 1987), in which it is almost not inturned, and possesses a laterally facing "greater trochanter." A fully inturned head, on the other hand, is derived for dinosaurs, and most previous studies argued that this condition was acquired via the medial rotation of the proximal elements of the bone (Gauthier 1986, Carrano 2000, Hutchinson 2001b). In some dinosaur groups this seems to have been the case, as in various tetanuran theropods (Osmólska et al. 1972, Madsen 1976, Currie and Zhao 1993) and derived "prosauropods"—*Melanorosaurus* (Van Heerden and Galton 1997) and *Ruehleia* (Galton 2001a, b)—which have a mainly cranially facing "greater trochanter." In ornithopods (Galton 1981, Norman 1986, Forster 1990) and more derived tetanurans (*Ingenia*—Barsbold et al. 1990; *Alxasaurus*—Russell and Dong 1993; *Saurornithoides*—Currie and Peng 1993), on the other hand, the "greater trochanter" faces laterally, a condition that seems to have been retained in birds (McGowan 1979). These forms seem to have acquired an inturned femoral head via the extreme elongation of its medial part, rather than via its medial rotation.

Distal to the insertion area for the M. iliotroc., the lateral surface of the femur of *Saturnalia* presents a "S-shaped" insertion area for the iliofemoral musculature (*sensu* Rowe 1986). It begins in the laterocranial corner of the bone, as a proximally projecting, but not strongly developed trochanter ("lesser trochanter"). From the base of that trochanter, a protuberant ventrally arched shelf ("trochanteric shelf") extends caudally along the entire lateral surface of the bone. At the caudolateral corner of the femur, it curves distally and merges into the shaft. Similar structures are described for *Herrerasaurus* (Novas 1994) and basal theropods (Andrews 1921, Padian 1986, Rowe 1989, Raath 1990, Madsen and Welles 2000), and it is here suggested that the "trochanteric shelf" and "lesser trochanter" correspond respectively to the insertion of the M. iliofem. ext. (M. gluteus medius et minimus, in McGowan 1979) and M. iliofem. cran. (see Walker 1977). *Marasuchus* (Sereno and Arcucci 1994) and *Staurikosaurus* (MCZ 1669) also show similar insertions for the iliofemoral musculature. However, their trochanter and shelf are not protuberant, and only a "S-shaped" scar is present. A different version of this muscle insertion is seen in other dinosaurs such as *Thecodontosaurus* (BRSUG various specimens), *Liliensternus* (MB.R. 2175), and various ornithischians (Galton 1974, Novas 1996; *Scelidosaurus*—BMNH 6704; *Lesothosaurus*—BMNH BUB17). Most of these forms present a more expanded "lesser trochanter," while the shelf is reduced to a caudal scar and/or faint bump. Birds, on the other hand, differ from most dinosaurs because the lesser trochanter is fused to the femoral head to form a "true" trochanter femoris ("lesser" plus "greater trochanter"). This is a structure that, therefore, receives the insertion not only of part of the M. iliofem., but also of the M. iliotroc. In conclusion, the presence of a protuberant insertion for the iliofemoral musculature seems to represent a dinosaur apomorphy.

The fourth trochanter of *Saturnalia* is a pronounced element whose midpoint is located at one third of the way along the femur from its proximal end. It starts as a faint ridge on the caudal surface of the femur, distal to the insertion area for the M. obt., and extends medially to the posteromedial corner of the bone. At this point, it curves distally, extending in that same direction as a vaguely "S-shaped," pronounced crest. The fourth trochanter is sub-rectangular in outline, resembling that of *Herrerasaurus* (Novas 1994) and "prosauropods" (Galton 1990). Extensive scarring is seen in its mediocaudal surface, where the M. caudofem. brevis inserted. Romer (1927) suggested that distally extending muscles—a proximal branch of the M. gastrocnemius (M. gastroc.), according to Galton (1969)—also attached to that element, which accounted for its pendant shape in ornithischians. Such a musculature might have also been present in *Saturnalia*, *Herrerasaurus*, and "prosauropods," the fourth trochanters of which show a sharply angled distal margin. This hypothesis is corroborated by the presence of somewhat distinct scars on the distal inflection of the fourth trochanter of *Saturnalia*, and by its pendant shape in some specimens of *Massospondylus* (Cooper 1981, fig. 59).

The femur of *Saturnalia* has a marked oval concavity cranial to the fourth trochanter, which corresponds to the insertion of the M. caudofemoralis longus (M. caudofem. long.). It is craniodistally bounded by a ridge, which extends cranioproximally from the distal end of the fourth trochanter. This ridge, based on a topographic comparison with the crocodile (Romer 1923b), is for the insertion of a branch of the M. pub. isch. fem. int. med. (= avian M. iliofemoralis internus; Walker 1977, Rowe 1986). An osteological correlate of the M. ischiofem. is not found in the femur of *Saturnalia*. It is suggested, however, that it inserted somewhere between the proximal end of the fourth trochanter and the caudal part of the trochanteric shelf.

Several longitudinal intermuscular lines are seen on the femoral shaft of *Saturnalia*. The most pronounced of them extends through its cranial surface, from the lesser trochanter to the distal third of the bone. This line (termed here "cranial line") is probably homologous with the avian linea intermuscularis cranialis (Baumel and Witmer 1993), and was also described for other dinosaurs, such as *Hypsilophodon* (Galton 1969, fig 10), *Massospondylus* (Cooper 1981, fig 84), *Iguanodon* (Norman 1986, fig 70a), and *Herrerasaurus* (Novas 1994, fig. 7 "q"). A second intermuscular line is seen on the caudolateral corner of the femur. It extends distally from the caudal part of the "trochanteric shelf," and bifurcates into two branches on the distal half of the bone. The cranial branch extends onto the lateral surface of the distal femur, while the caudal branch enters the popliteal fossa. This line (termed here "caudolateral line") is approximately in the same position as the avian linea intermuscularis caudalis (Baumel and Witmer 1993), and might be homologous to it. A similar intermuscular line was described for *Massospondylus* (Cooper 1981, fig. 84), *Hypsilophodon* (Galton 1969, fig. 10), and *Iguanodon* (Norman 1986, fig. 70a). A third and fainter line is seen on the caudomedial part of the femur. It extends from distal of the insertion area for the M. caudofem. long. to the lateral part of the medial condyle. This line (termed here "caudomedial line") was also described for *Hypsilophodon* (Galton 1969, fig. 10).

Based on the position of the intermuscular lines, it is possible to reconstruct the musculature extending along the femoral shaft of *Saturnalia*. Regarding the M. femorotibialis, crocodiles have only two branches of this muscle—M. femorotibialis internus and externus (Romer 1923b). Birds, on the other hand, have three branches—M. femorotibialis lateralis, intermedius and medialis (Vanden Berge and Zweers 1993). In addition, both crocodiles (Romer 1923b) and birds (McGowan 1979) have the M. adductor femoris (= avian M. puboischiofemoralis; Vanden Berge and Zweers 1993) inserting along the femoral shaft, usually on its caudal surface. *Saturnalia* shows four potential areas for these muscles: the first area occupies most of the medial surface of the shaft, between the cranial and the caudomedial lines; while the other three are on the lateral surface of the shaft, the larger of them between the cranial and the caudolateral lines, and smaller areas between the caudolateral line and the fourth trochanter, and between the two diverging branches of the caudolateral line. Most of these areas were also described for other dinosaurs (Galton 1969, Cooper 1981, Norman 1986; see table 5.1), but their relation to the bird and crocodile muscles is not clear.

Given the homology between the cranial intermuscular line of *Saturnalia* and the linea internus cranialis of birds, it follows that the musculature extending medial to this structure along the femur of *Saturnalia* corresponds to both the avian M. femorotibialis intermedius and M. femorotibialis medialis. Indeed, a faint line extends proximally from the medial condyle along the medial surface of the femur of *Saturnalia*, which might represent the incipient division between these two muscles. These correspond to the M. femorotibialis internus of crocodiles (*contra* Hutchinson 2001b; but see Norman 1986, p. 344), which is the single branch of the femorotibial musculature that extends through the dorsal and cranial surfaces of the femur (Romer 1923b). Accordingly, the M. femorotibialis externus (M. fem. tib. ext. = avian M. femorotibialis lateralis) and the M. add. are associated with the three areas on the lateral part of the femur of *Saturnalia*. It is suggested that the distal head of the M. fem. tib. ext. (Vanden Berge 1975, McGowan 1979) inserted in the area between the two diverging branches of the caudolateral line, while its main body extended proximally along the large lateral surface of the bone. This arrangement also accounts for the modifications involving the insertion of the iliofemoral musculature in dinosaurs, which shifted from a more distal position on the femoral shaft, as in crocodiles (Romer 1923b), to a more proximal position, as in birds. As a result, the laterocranial surface of the femur was abandoned by the M. iliofem., and occupied by the lateral shift of the M. fem. tib. ext. In this scenario, the space between the caudolateral line and the fourth trochanter is most probably related to the insertion of the M. add. This is also the area where the nutritive artery of the proximal femur, a branch of the ischial artery (Baumel 1975), becomes interosseous, perforating the femur.

Other muscle scars are seen on the distal part of the femur of *Saturnalia*. The clearest of them is circular in shape and placed craniodistal to the scar for the distal head of the M. femorotibialis lateralis. A similar scar was described for *Herrerasaurus* (Novas 1994, fig. 7, "ms"), and is probably associated with the origin of the proximal arm of the ansa M. iliofib. (Vanden Berge and Zweers 1993). Further down the shaft, the M. flexor digitorum longus probably originated on the truncated caudoproximal part of the tibiofibular crest, while the accessory part of the M. flexor cruris lateralis originated on the ridge proximal to it.

The medial condyle occupies the entire medial surface of the distal femur, and articulates with the internal condyle of the proximal tibia. It is pinched caudally, and its flat medial surface might have hosted various muscle insertions (see Dilkes 2000). The cnemial crest of the tibia articulates with the sulcus intercondilaris, a faint craniocaudally-oriented groove that laterocranially bounds the medial condyle. Yet, contrary to the condition in most dinosaurs (Galton 1976, fig. 8, Forster 1990, fig. 19, Currie and Zhao 1993, fig. 22d), this groove is not proximally extended, and does not excavate the cranial surface of the distal femur. Instead, *Saturnalia* retains a primitive flat craniodistal femoral margin, as also seen in basal dinosaurs such as *Herrerasaurus* (Novas 1994), *Staurikosaurus* (Galton 1977), *Liliensternus* (MB.R. 2175), and *Lesothosaurus* (Thulborn 1972). Caudal to the sulcus intercondilaris, a strong concavity is present on the distal surface of the femur. It differs from that of basal theropods (Padian 1986, fig. 5.4 "inc"; *Liliensternus*—MB.R. 2175) because it is separated from the strong caudal incision of the bone by a caudal elevation. This concavity might have hosted the insertion of the Lig. cruciatum caudalis, whereas the caudal incision represents the pathway of the Lig. cruciatum cranialis, also forming the caudalmost separation between the lateral and medial condyles (Baumel and Raikow 1993). The laterocranial part of the distal femur is occupied by the broad fibular condyle (Novas 1994), which articulates with the proximal fibula. Caudal to this surface a groove extends caudolaterally from the medial concavity, cranially bordering the small lateral condyle. Its lateral expression forms the trochlea fibularis, onto which the caudoproximal part of the fibula articulates. The lateral condyle is parallelogram-shaped, and the medial part of its distal area articulates with the fibular condyle of the tibia.

Tibia (Figs. 5A–D, G–H)—It is a straight bone, with a craniocaudally elongated proximal end, and a sub-quadrangular distal end. It is subequal in length to the femur, as seen in *Eoraptor* (PVSJ 512), *Staurikosaurus* (MCZ 1669), *Guaibasaurus* (Bonaparte et al. 1999), and most basal theropods (Gilmore 1920, Camp 1936, Huene 1934, Welles 1984, Padian 1986, Colbert 1989). This condition is also present in *Pseudolagosuchus* (Arcucci 1987), and considered primitive for dinosaurs in general. Most basal sauropodomorphs (Galton 1976, 1984, Cooper 1981, 1984, Bonaparte and Pumares 1995), on the other hand, have a tibia that is significantly shorter than the femur, as also seen in *Herrerasaurus* (Novas 1994).

The proximal articulation of the tibia of *Saturnalia* shows well-developed internal and fibular condyles, as well as a pronounced cnemial crest. The internal condyle occupies most of the mediocaudal part of that articulation, and its medial and caudal surfaces present indication of muscle attachments. These might correspond to the origin for the M. plantaris, or the insertion of the M. puboischiotibialis and/or M. flex. tib. ext. (McGowan 1979, Dilkes 2000). The fibular condyle of *Saturnalia* does not extend as far caudally as the internal condyle, as seen in most basal dino-

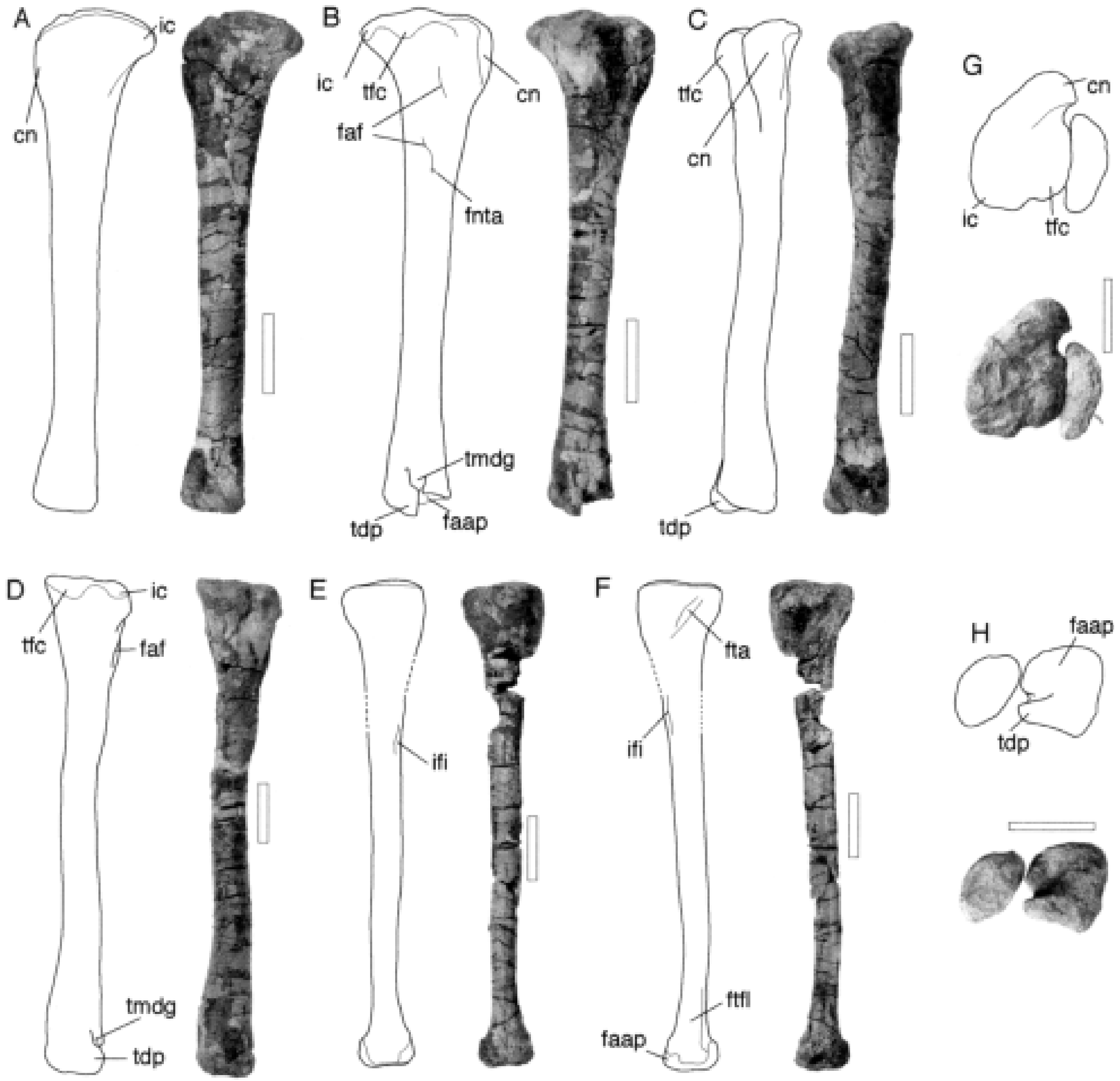

Fig. 5. Right tibia and fibula of *Saturnalia tupinquim* (MCP 3944-PV). Scale bar = 2 cm. Tibia in (**A.**) medial, (**B.**) lateral, (**C.**) cranial and (**D.**) caudal aspects. Fibula in (**E.**) lateral and (**F.**) medial aspects. Tibia and fibula in (**G.**) proximal and (**H.**) distal aspects. Abbreviations: **cn**, cnemial crest; **faap**, articular facet for the astragalar ascending process; **faf**, fibular articular facet; **fnta**, foramen for the nutritive tibial artery; **fta**, tibial articulation on fibula; **ftfl**, facet for the tibiofibular ligament; **ic**, internal condyle; **ifi**, iliofibularis insertion; **tdp**, tibial descending process; **tfc**, fibular condyle of tibia; **tmdg**, tibial mediodistal groove.

saurs (Novas 1994, Galton 1977; *Pisanosaurus*—PVL 2577; *Eoraptor*—PVSJ 512), and most basal theropods (Huene 1934, Welles 1984, Padian 1986, Carpenter 1997; *Megapnosaurus rhodesiensis*—QVM QG 691, 792). Instead, it is placed at the center of the lateroproximal corner of the bone, as in most basal sauropodomorphs (Bonaparte 1972, Galton 1976, Cooper 1984, Benton et al. 2000), and ornithischians (Thulborn 1972, Santa Luca 1980; *Scelidosaurus*—BMNH 1111). In addition, a clear cleft separates the caudal margins of the fibular and internal condyles, a condition shared with most dinosaurs, but apparently absent in *Staurikosaurus* (Galton 1977) and *Herrerasaurus* (Novas 1994).

A faint transverse groove on the proximal surface of the tibia of *Saturnalia* marks the caudal limit of the cnemial crest. This groove is somewhat continuous with the insisura tibialis (Currie and Zhao 1993), which extends distally to separate the cnemial crest from the fibular condyle. The cnemial crest itself projects laterocranially from the shaft, but not dorsally, and it is almost level with the caudal surface of the proximal tibia. In this respect *Saturnalia* resembles forms such as *Heterodontosaurus* (Santa Luca 1980) and *Herrerasaurus* (Novas 1994), differing from most basal saurischians, in which the cnemial crest is well projected dorsally (Huene 1934, Raath 1969, Galton 1976, Cooper 1981). It also differs from *Staurikosaurus* (Galton 1977), *Pisanosaurus* (Bonaparte 1975), and *Lesothosaurus* (Thulborn 1972), in which the proximal projection of the crest is even more restricted. In addition, as in *Herrerasaurus* (Novas 1994) and "prosauropods" (Cooper 1981, Benton et al. 2000), the cnemial crest of *Saturnalia* is not very elongated, and does not extend for more than one third of the tibial length. In basal theropods (*Liliensternus*—MB.R. 2175; *Megapnosaurus*—QVM QG1), some ornithischians (Thulborn 1972, Galton 1981), and *Guaibasaurus* (MCN PV2355), on the other hand, the faint excavation that extends lateral to the cnemial crest can be traced for the entire proximal half of the bone. Scars for muscle attachments are seen both lateral and medial to the cnemial crest. The medial scars might correspond to the origin of the tibial head of the M. gastroc., while the lateral scars possibly hosted the origin of the M. tibialis cranialis (M. tib. cran.) more proximally and the M. extensor digitorum longus (M. ext. dig. long.) more distally (McGowan 1979, Dilkes 2000).

The lateral surface of the tibia of *Saturnalia* bears a strong rugosity extending distally from the cranial part of the fibular condyle. This is for the articulation of the fibula and the attachment of the Lig. tibiofibularis, representing a feeble version of the fibular crest of theropods. Indeed, as in those dinosaurs, the tibial rugosity fits into a corresponding ridge on the medial surface of the fibula. When articulated, the distal part of the fibular ridge joins the proximal end of the tibial rugosity, to form a "single" connected structure. Other sauropodomorphs (*Plateosaurus*—SMNS F65; *Massospondylus*—Cooper 1981) show an oval scar on the lateral tibia, distal to the fibular condyle, which might represent a modified version of the rugosity seen in *Saturnalia*. Caudal to the distal end of this rugosity, the lateral surface of the tibia of *Saturnalia* presents a vascular related structure. It starts proximally as a canal, leading distally to a foramen that penetrates the bone. A similar foramen was described for other dinosaurs (Cooper 1981, Novas 1994, Currie and Zhao 1993), and it is probably related to the nutritive tibial artery, which represents a branch of the A. tibialis cranialis (Baumel 1993).

Two intermuscular lines extend along the tibial shaft. The first of them starts at the cnemial crest and extends distally to the mediocranial border of the bone. The second crest starts cranial to the foramen for the nutritive tibial artery, and extends distally to the laterocranial part of the tibia. These lines probably mark the lateral and medial boundaries of the origin of the M. ext. dig. long. (Vanden Berge and Zweers 1993).

While the lateral border of the tibia remains approximately the same width throughout the shaft, its medial border becomes more robust towards its distal end, which bears strongly marked mediocranial and mediocaudal corners. This is clearly seen in the distal aspect of the bone, which is wider medially than laterally, as seen in most basal dinosaurs (Thulborn 1972, Padian 1986, Bonaparte et al. 1999, Benton et al. 2000; *Liliensternus*—MB.R. 1275; *Megapnosaurus rhodesiensis*—QVM QG 691, 792; *Pisanosaurus*—PVL 2577 *Scelidosaurus*—BMNH 1111) but not in *Herrerasaurus* (Novas 1994), *Staurikosaurus* (Novas 1989), and *Eoraptor* (PVSJ 512). In addition, as in *Herrerasaurus* (Novas 1994) and *Staurikosaurus* (Galton 1977), the mediocaudal corner of the distal tibia of *Saturnalia* forms a right angle, differing from other basal dinosaurs—*Pisanosaurus* (PVL 2577), *Guaibasaurus* (Bonaparte et al. 1999), *Lesothosaurus* (Thulborn 1972), *Megapnosaurus* (QVM QG792), *Liliensternus* (MB.R. 2175), and "prosauropods" (Novas 1989)—in which that corner forms an obtuse angle.

Similar to *Herrerasaurus* (Novas 1994), *Staurikosaurus* (MCZ 1669), and "prosauropods" (Novas 1989), the distal surface of the tibia of *Saturnalia* has a flat medial articulation for the astragalus. Laterally, this articulation is more complex. It bears a large cranial surface which is lateroproximally inclined to receive the astragalar ascending process. In addition, the laterocranial corner of the tibia is slightly projected laterally in its distal part. This feature is also present in most other basal dinosaurs (Padian 1986, Novas 1994, Bonaparte et al. 1999, Benton et al. 2000), but absent in ornithischians (Thulborn 1972, Galton 1981, Colbert 1981), including *Pisanosaurus* (PVL 2577).

The laterocaudal part of the distal tibia of *Saturnalia* forms a wall-like descending process. It overlaps the caudal surface of the astragalar ascending process and fits into a concavity caudal to it. Indeed, the presence of tibial articulation caudal to the astragalar ascending process is a dinosaur apomorphy. The descending process of *Saturnalia* is slightly more distally projected than the rest of the distal tibia. It also projects laterally from the shaft, as in most basal dinosaurs (*Pisanosaurus*—PVL 2577; *Eoraptor*—PVSJ 512; *Guaibasaurus*—MCN PV 2355), including most basal sauropodomorphs (Galton 1976; *Thecodontosaurus*—BRSUG 23623, 23624) and some basal theropods (Padian 1986, Carpenter 1997; *Liliensternus*—MB.R. 1275), but not as much as in basal ornithischians (Thulborn 1972, Colbert 1981; *Scelidosaurus*—BMNH 1111), and in various theropods (Gilmore 1920, Bonaparte 1986, Raath 1990).

A faint groove on the distal surface of the tibia of *Saturnalia* separates its descending process from the articular surface for the ascending process of the astragalus, and it leads into a cleft on the laterodistal corner of the bone. This cleft expands proximally along the lateral surface of the tibia, forming a groove with steep borders. This divides the laterally projecting laterocranial and laterocaudal (descending process) corners of the bone, and was suggested as an apomorphic feature of Dinosauriformes (Novas 1996).

Fibula (Figs. 5E–H)—It is long and thin, flat medially, and with a rounded lateral border. The proximal end is craniocaudally expanded, and its central portion articulates medially with the fibular condyle of the tibia. Its cranial part overhangs the insisura tibialis laterally, but does not articulate with it. The caudal part, on the other hand, bears an internal ridge extending craniodistally from its caudoproximal corner. Similar scarring for the articulation with the tibia was described for other dinosaurs (Cooper 1981, Novas 1994), and it is a common feature of the group. Distal to this area, despite their close position, no direct contact between tibia and fibula is seen.

At about one third of its length from the proximal end of the fibula, a marked rugosity is present in the laterocranial border of the bone. This structure was also observed in several other dinosaurs such as *Herrerasaurus* (Novas 1994), *Dilophosaurus* (Welles 1984), *Sinraptor* (Currie and Zhao 1993), *Plateosaurus* (GPIT skeleton 1), *Massospondylus* (Cooper 1981), and *Maiasaura* (Dilkes 2000), and corresponds to the insertion of the M. iliofib. In *Saturnalia*, however, a second rugosity is seen proximal to that, on the mediocranial corner of the bone. The fibular shaft is kinked between these two structures, so that its distal part is laterally displaced, as seen in modern birds (McGowan 1979). A similarly kinked fibula is seen in *Guaibasaurus* (Bonaparte et al. 1999).

A closer contact between tibia and fibula is present at their distal ends, where abundant scarring indicates the presence of a strong ligamentous attachment between the two bones. The flat medial surface of the distal fibula faces slightly mediocaudally, matching the also slightly cranially inclined lateral surface of the distal tibia. The cranial and caudal borders of that surface are marked by a pair of ridges, which match the laterally expanded laterocaudal and laterocranial corners of the tibia, as also described for *Herrerasaurus* (Novas 1994).

The fibula extends slightly more distally than the tibia. Its distal end is swollen and mediocranially to laterocaudally expanded. As a result, its long axis forms an angle of approximately 40° with that of the proximal end of the bone. Its cranial part articulates medially with the lateral surface of the astragalar ascending process, while the laterocaudally extended part matches the shape of the calcaneal tuber, as described for *Herrerasaurus* (Novas 1994). Differently from this form, however, the distal surface of the fibula of *Saturnalia* in not inclined, but mainly horizontal with a slightly more distally expanded laterocaudal corner. The lateral part of its distal surface articulates with the calcaneum, while its mediocranial expansion and medial border articulate distally with the laterocranial and laterocaudal processes of the astragalus.

Astragalus (Figs. 6A–F)—It is a robust and transversely elongated bone. The medial part is more craniocaudally expanded than the lateral, and it has a broad faint concavity extending craniocaudally through its proximal surface. The medial part of the distal tibia fits onto this surface, the cranial part of which extends laterally to form the flat proximal articulation of the ascending process. The ascending process itself is a wedge-shaped element, low medially, but higher laterally and caudally. It is also wider towards its lateral portion, where it forms a broad table-like structure, with a flat proximal surface and steep cranial, medial, and caudal borders. In its general shape, it resembles the ascending process of *Herrerasaurus* (Novas 1989) and "prosauropods" (Cooper 1981, Novas 1989), differing markedly from those of theropods (*Liliensternus*—MB.R. 2175, *Megapnosaurus*—QVM QG792) and most ornithischians (Galton 1981, Colbert 1981), whose astragali are much narrower, and lack a well-developed flat proximal surface.

The astragalar ascending process of *Saturnalia* is bounded cranially by a feeble platform, which separates it from the main cranial margin of the bone as seen in basal theropods (Huene 1934, Welles and Long 1974, Raath 1990, Britt 1991, Madsen and Welles 2000), and "prosauropods" (Huene 1926, Cruickshank 1980, Novas 1989, Galton and Van Heerden 1998), but not in basal dinosauriforms (Novas 1996) and ornithischians (Galton 1974, 1981, Colbert 1981; *Scelidosaurus*—BMNH 1111; *Pisanosaurus*—PVL 2577). Caudally, the ascending process is bordered by a well-developed concavity—the dorsal basin of Novas (1989), which articulates with the descending process of the tibia. This concavity is separated from the ascending process by a nearly vertical steep border, the lateral portion of which forms a strong column-like corner. At the medial end of the ascending process, the border extends caudally, and separates the dorsal basin from the medial articular surface of the astragalus. This characterizes the "interlocking" tibial-astragalar articulation that is typical of *Herrerasaurus* (Novas 1989) and "prosauropods" (Young 1951, pl. V, Cooper 1981, fig. 71, Novas 1989). On the contrary, in other basal dinosaurs (Gilmore 1920, Colbert 1981, Welles 1984, Britt

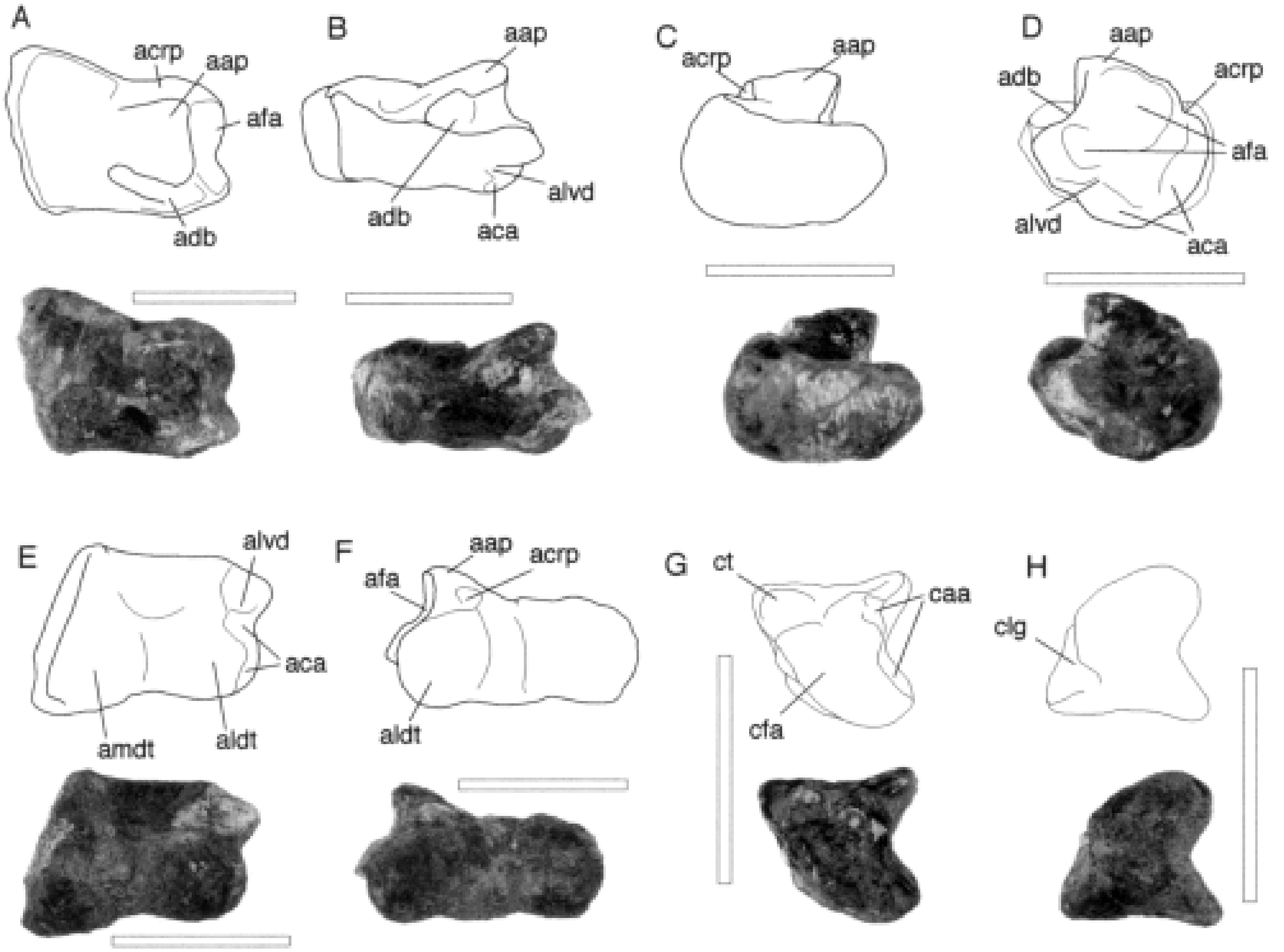

Fig. 6. Right proximal tarsals of *Saturnalia tupinquim* (MCP 3944-PV). Scale bar = 2 cm. Astragalus in (**A.**) proximal, (**B.**) caudal, (**C.**) medial, (**D.**) lateral, (**E.**) distal and (**F.**) cranial aspects. Calcaneum in (**G.**) proximal and (**H.**) distal aspects. Abbreviations: **aap**, astragalar ascending process; **aca**, calcaneum articulation on astragalus; **acrp**, astragalar cranial platform; **adb**, astragalar dorsal basin; **afa**, fibular articulation on astragalus; **aldt**, articulation for the lateral distal tarsal; **alvd**, lateroventral depression on astragalus; **amdt**, articulation for the medial distal tarsal; **caa**, astragalar articulation on calcaneum; **cfa**, fibular articulation on calcaneum; **clg**, lateral groove on calcaneum; **ct**, calcaneal tuber.

1991; *Guaibasaurus*—MCN PV 2356; *Liliensternus*—MB.R. 2175; *Pisanosaurus*—PVL 2577; *Scelidosaurus*—BMNH 1111; *Megapnosaurus rhodesiensis*—QVM QG 174, 786, 792, CT6), the articular area caudal to the ascending process is continuous with that on the medial part of the astragalus.

The fibula articulates with the concave proximal surface of the lateral part of the astragalus, as well as with the lateral surface of the ascending process. In this respect *Saturnalia* differs from most ornithischians (Galton 1974, Colbert 1981), except *Pisanosaurus* (PVL 2577), the astragalus of which bears no articular facet for the fibula. *Saturnalia* is also plesiomorphic in relation to most basal sauropodomorphs, in which the lateral part of the astragalus is very reduced, and the fibula articulates mainly to the lateral surface of the ascending process (Huene 1926, Sereno 1999).

In the astragalus of *Saturnalia*, the base of the fibular articulation is formed by its laterocranial and laterocaudal processes. The former receives the calcaneum at its laterodistal surface, which includes two flat articulation areas corresponding to the two medial processes of that bone. The caudal articulation area is more medially expanded, and cranially borders an articulation-free groove—the "posterior groove" of Sereno (1991b). These two structures together form a concavity on the ventral part of the astragalus termed the "lateroventral depression" by Novas (1989). A third articular facet, for the calcaneum, is seen caudal to the "posterior groove," in the craniodistal surface of the laterocaudal process of the astragalus, and it fits into the proximal surface of the mediocaudal calcaneal process. This astragalocalcanar articulation is plesiomorphic in comparison to that of most dinosaurs. The astragalus retains well-developed lateral processes, as well as the "lateroventral depression," elements common to basal dinosauriforms (Novas 1989, Sereno and Arcucci 1994), and basal dinosaurs such as *Herrerasaurus* (Novas 1989), *Guaibasaurus* (MCN PV 2356), and *Alwalkeria* (Chatterjee 1987), but reduced or absent in most members of the group.

Medial to the laterocaudal process, the central part of the astragalus is thin, and its smooth distal surface probably corresponds to a pathway for the M. gastroc. Cranially and medially, however, the bone is more robust, and its craniodistal surface bears three large articulation areas, separated from each other by faint grooves. The medialmost of them forms a flat area, which probably served for the articulation of the metatarsal II. Proximally, the borders of the mediocranial corner rises steeply, forming an acute and articulation-free proximal surface. The articulation for the medial distal tarsal lies medially to that of metatarsal II. It is sub-circular in shape, and does not enter the cranial surface of the astragalus. More laterally, the rounded articulation facet for the medial portion of the lateral distal tarsal bounds the calcaneal articulation medially on the laterocranial astragalar process, and extends onto the cranial surface of the bone. The robust medial margin of the astragalus bears strong striations, which might correspond to the insertion of joint ligaments to the medial surface of the tibia.

Calcaneum (Figs. 6G–H)—It is a proximodistally flat, triradiate bone, with well-developed mediocranial and mediocaudal processes, and a laterocaudally oriented tuber. This format is similar to that of basal dinosauromorphs (Novas 1989, Sereno and Arcucci 1994), and *Herrerasaurus* (Novas 1989), but is primitive among dinosaurs in general, the calcaneal projections of which are less marked (Huene 1926, Galton 1974, Cooper 1981, Welles 1984, Novas 1989; *Dryosaurus*—HNN mounted skeleton; *Liliensternus*—MB.R. 2175, *Scelidosaurus*—BMNH 1111; *Megapnosaurus rhodesiensis*—QVM QG174). The fibular articulation occupies most of the proximal surface of the bone, except that of its mediocaudal process. Its cranial part forms a shallow obliquely elongated concavity, the curved shape of which accompanies the laterocranial border of the bone. Caudally, on the proximal surface of the tuber, there is a depressed facet, which articulates with the slightly more distally expanded laterocaudal corner of the distal fibula.

The medial border of the calcaneum articulates entirely with the laterodistal part of the astragalar laterocranial process. Its concave surface is composed of two inclined articular facets on the internal part of its medial processes, and a vertical facet between them. In addition, the proximal surface of its mediocaudal process articulates with the craniocaudal surface of the astragalar laterocaudal process. This articulation facet is broader at its lateral portion, where it articulates with the tip of the astragalar laterocaudal process. Medially, it extends along the process as a much thinner articulation area. Cranial to it, a small knob-like element fits between the lateral astragalar processes when articulated.

Unlike its proximal surface, the distal part of the calcaneal tuber of *Saturnalia* bears no articular facets. It seems to correspond to the insertion area for the M. peroneus longus (Dilkes 2000), and forms, together with the caudal surface of the bone, an articulation-free area on the flexor aspect of the tarsus. The distal and cranial surfaces of the mediocranial process, on the other hand, bear a clear articular facet for the lateral part of the lateral distal tarsal. Caudal to it, a small concavity is seen in the center of the bone, which might represent the articulation of the lateroproximal tip of the metatarsal V. An elongated groove extends along the lateral and cranial surfaces of the bone, which separates the tuber and the fibular articular area from the distal articular facets for the lateral distal tarsal and metatarsal V. A similar groove was described for *Herrerasaurus* (Novas 1989), and "prosauropods" (Cooper 1981, Novas 1989), but seems to be absent from the highly modified calcaneum of ornithischians and theropods. Its function is unknown, and it might represent the pathway of a vascular element, or even the separation between the calcaneum and a incompletely fused distal tarsal.

Distal Tarsals (Figs. 7A–D)—Only two ossified distal tarsals are observed in *Saturnalia* (MCP 3845-PV). This same count is known in basal dinosauromorphs (Novas 1996), *Herrerasaurus* (Novas 1994), "prosauropods" (Huene 1926), most ornithischians (Galton 1974, Forster 1990), and most theropods (Ostrom 1969, Welles 1984), and seems to represent the primitive condition for dinosaurs. However, a third ossified distal tarsal, medial to these two elements, is known in some basal theropods (Rowe 1989, Colbert 1989) and ornithischians (Santa Luca 1980).

The medial distal tarsal of *Saturnalia* (MCP 3845-PV) is proximodistally flat, parallelogram-shaped, with rounded corners. It articulates with the lateral distal tarsal via the deeper caudal part of its lateral border, the cranial part of which bears a socket-like articular facet. Its proximal surface is slightly convex, and articulates with the astragalus. On the opposite side, the bone has a concave distal surface, which covers the entire proximal surface of the metatarsal III. Its caudal end is deeper than the rest of the bone, and expands distally to accommodate the caudoproximal corner of that metatarsal. Most basal dinosaurs (Huene 1926, Novas 1996) have a medial distal tarsal of similar proportions, but theropods (Padian 1986, Raath 1990) and ornithischians (Galton 1974, Forster 1990), show a much larger element. Also different from some theropods and ornithischians, the medial distal tarsal of *Saturnalia* is not fused to metatarsal III, and does not cover part of metatarsal II.

The lateral distal tarsal of *Saturnalia* is an elongated bone, the long axis of which forms an angle of about 35° to the transverse line of the metatarsals. As in basal dinosauromorphs (Sereno and Arcucci 1993, Novas 1996), it is markedly constricted in its midline, formed by strong laterocaudal and medial concavities, which divide the bone into a laterocranial portion and a mediocaudally pointed

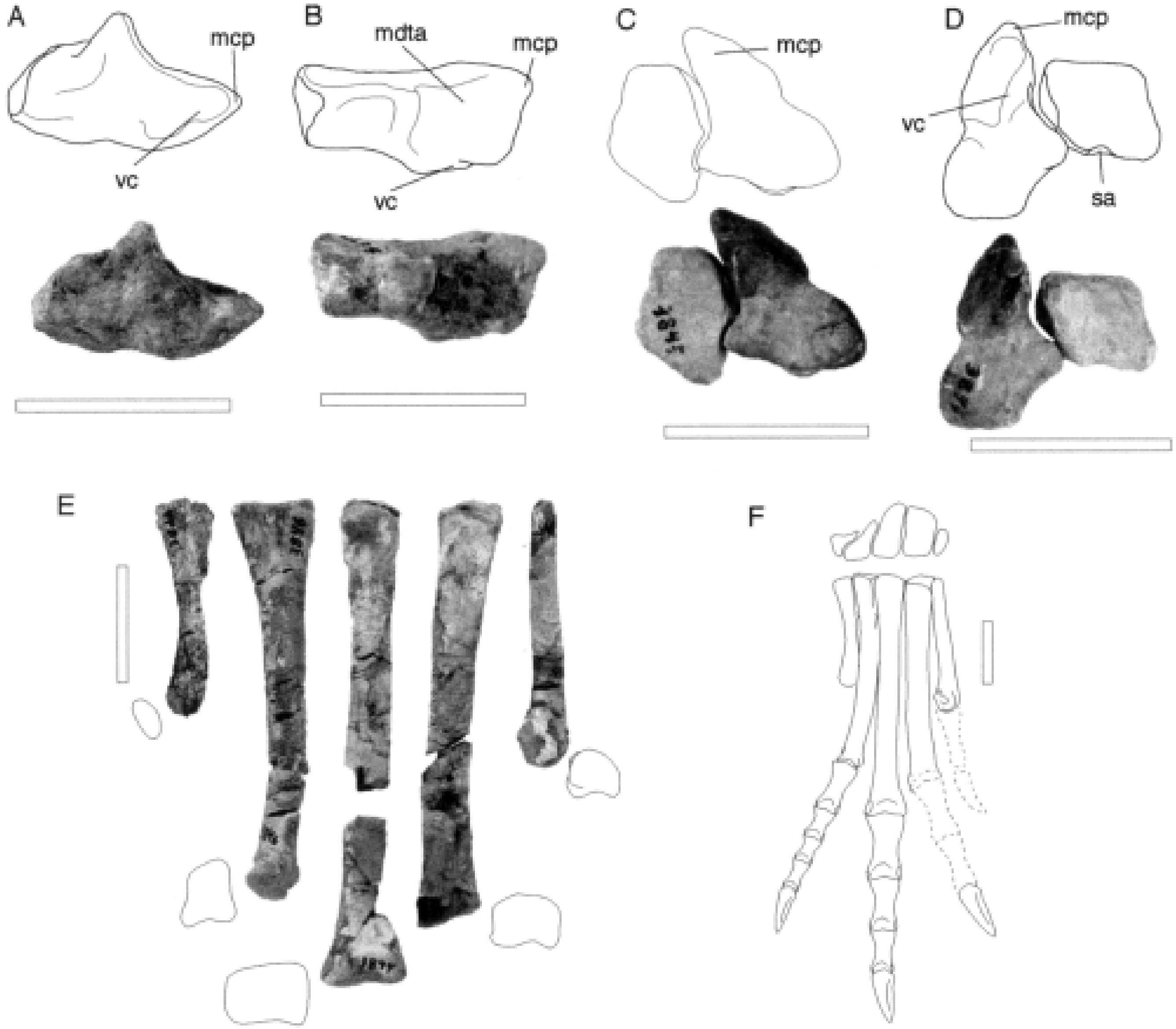

Fig. 7. Distal tarsals and pes of *Saturnalia tupinquim*. Scale bar = 2 cm. Right lateral distal tarsal of MCP 3944-PV in (**A.**) ventral and (**B.**) medial aspects. Left medial and lateral distal tarsals of MCP 3945-PV in (**C.**) proximal and (**D.**) distal aspects. **E.** Right metatarsals I, II, III, and V of MCP 3944-PV, and metatarsal IV of MCP 3946-PV in cranial aspect, with respective distal outline. **F.** Composite reconstruction of the right foot of *Saturnalia* in flexor aspect, with proximal outline of the metatarsals. Abbreviations: **mcp**, mediocaudal process of lateral distal tarsal; **mdta**, medial distal tarsal articulation on lateral distal tarsal; **msa**, medial distal tarsal socket articulation; **vc**, ventral crest of lateral distal tarsal.

projection. The medial concavity occupies the entire medial surface of the bone, and its cranial two thirds articulate with the medial distal tarsal. The laterocaudal concavity, on the other hand, is smaller, and forms a proximodistally-elongated groove. This groove articulates with the mediocaudal ridge of metatarsal V, while the surface cranial to it receives the mediocranial ridge of that metatarsal. The laterocaudal portion of the medial distal tarsal is subrectangular and flatter than the mediocaudal projection. Its distal surface presents a hemicylindrical articular facet, with a concave middle part and expanded lateral and medial borders. This articulation extends proximally, and forms the cranial border of the bone, which articulates with the upturned cranioproximal corner of the metatarsal IV. The lateral border of this articulation is strong and scarred, possibly representing the insertion area for a joint ligament to the proximal tarsus.

The proximal surface of the lateral distal tarsal is slightly concave, and its lateral portion articulates with the calcaneum. The medial part, on the other hand, forms a crescentic facet, which extends along all the proximal surface of the mediocaudal projection, and articulates with the base of the laterocranial process of the astragalus. As in other dinosaurs (Huene 1926, Padian 1986, Novas 1989), the mediocaudal projection presents a slightly upturned caudal margin, which caudally bounds its articulation with the astragalus.

Extending distally from its upturned margin, the mediocaudal projection bears a large and smooth laterocaudal border, which forms a somewhat continuous surface with the caudodistal part of the astragalus. Distally, the mediocaudal projection forms a strong crest, which is also present in basal dinosauromorphs (Sereno and Arcucci 1993, Novas 1996), but is reduced or absent in most other basal dinosaurs (Huene 1926, Padian 1986, Novas 1994). Its lateral tip articulates with the upturned caudoproximal corner of metatarsal IV. From that point, a faint ridge expands cranially, and articulates with the medial part of the proximal surface of metatarsal IV. It is uncertain, based on the available specimens, whether this element also articulated with the caudal-most part of metatarsal III.

The general morphology of the lateral distal tarsal of *Saturnalia* is intermediate between those of basal dinosauromorphs and other dinosaurs. As in *Lagerpeton* (Sereno and Arcucci 1993) and *Marasuchus* (Novas 1996), it is elongated and strongly constricted, but also somewhat sub-triangular like those of *Herrerasaurus* (Novas 1994) and "prosauropods" (Huene 1926, Cooper 1981). This subtriangular shape is given by the combined enlargement of the cranial border of the bone and the shift in the orientation of its mediocaudal projection. In basal dinosauromorphs, this projection is proximally convex, forming a caudally directed articulation-free heel on the flexor aspect of the tarsus (Sereno and Arcucci 1994, Novas 1996). In *Saturnalia* and other dinosaurs, on the other hand, it is proximally concave, mediocaudally directed, and articulates cranially with other elements of the tarsus. In particular, *Saturnalia* presents a long mediocaudal projection, if compared to those of *Herrerasaurus* (Novas 1989) and "prosauropods" (Huene 1926). In theropods (Padian 1986, Raath 1990) and ornithischians (Galton 1974, Forster 1990), this projection is even more reduced; a condition probably related to the increase in size of the medial distal tarsal. The lateral margin of the laterocranial portion is also more elongated in the lateral distal tarsal of *Saturnalia*, "prosauropods" (Huene 1926), and *Herrerasaurus* (Novas 1989), than in that of theropods (Padian 1986, Raath 1990) and ornithischians (Galton 1974, Santa Luca 1980, Forster 1990) that, probably due to the reduction of the calcaneum, also reduced the lateral expansion of this bone.

Metatarsals (Figs. 7E-F)—The pes of *Saturnalia* is composed of five metatarsals, of which metatarsals I and V are the shortest and narrowest. Accordingly, as suggested for most dinosauromorphs, only the three central pedal digits acted as weight-supporting structures. The three central metatarsals of *Saturnalia* form a more slender unit (width about 40% of its length) than those of most "prosauropods" (Bonaparte 1972, Galton 1976; *Thecodontosaurus*—BMNH P24) and *Herrerasaurus* (Novas 1994). This resembles the condition in *Guaibasaurus* (Bonaparte et al. 1999), the metatarsus of which is also not as gracile as that of basal dinosauromorphs (Sereno and Arcucci 1993, 1994), basal theropods (Huene 1934, Raath 1969) and basal ornithischians (Thulborn 1972, Santa Luca 1980). In addition, the maximum length of the metatarsus of *Saturnalia* is about 50% of its tibial length, a condition only significantly surpassed by *Pisanosaurus* (Bonaparte 1976) and coelophysoids (Raath 1969, Colbert 1989) among basal dinosaurs.

The shafts of metatarsals I-IV of *Saturnalia* are "twisted," so that the long axis of their proximal end angles about 40° to the plantar surface of their distal articulations. As a result, there is an overlapping of the proximal part of these elements, with the articulation facets for the medially adjacent element facing mediocranially and those for the lateral elements facing laterocaudally. This arrangement was suggested to be apomorphic for saurischians (Sereno 1999), because it is present in *Herrerasaurus* (Novas 1994), "prosauropods" (*Thecodontosaurus*—BMNH P24, Huene 1926, Cooper 1981), *Guaibasaurus* (MCN PV 2355), and theropods (Huene 1934, Welles 1984), but absent in basal ornithischians (Santa Luca 1980, 1984, Galton 1981, Forster 1990; *Scelidosaurus*—BMNH 1111). However, a similar condition also seems to be present in basal dinosauromorphs (Bonaparte 1975).

Metatarsal I of *Saturnalia* is about 60% of the length of metatarsal II, and 55% of that of metatarsal III. This relative length is greater than that of basal dinosauromorphs (Sereno and Arcucci 1994) and theropods (Raath 1969, Welles 1984), but less than that of *Herrerasaurus* (Novas 1994), *Guaibasaurus* (MCN PV 2355), and most "prosauropods" (Huene 1926, Galton 1976; *Thecodontosaurus*—BMNH P24).

The proximal part of the bone is elliptical in outline, lateromedially compressed, and craniocaudally expanded. It is slightly concave medially, and laterally flat, where it articulates with metatarsal II. Proximally, the bone reaches the same level as metatarsals II-IV, and apparently articulates with the tarsus. This articulation is, however, not very extensive. It does not occupy the entire proximal surface of the bone, and leaves no clear scar on the astragalus. A similarly restricted proximal articulation is seen in *Herrerasaurus* (Novas 1994), and seems to represent a derived condition among dinosaurs, because those of basal dinosauromorphs (Bonaparte 1975), and "prosauropods" (*Thecodontosaurus*—BMNH P24; *Riojasaurus*—PVL skeleton no. 6; *Plateosaurus*—SMNS 13200), are clearly larger. Among ornithischians, although some basal forms have a proximally compressed metatarsal I (Thulborn 1972, Galton and Jensen 1973), a relatively broad tarsal articulation (Forster 1990; *Scelidosaurus*—BMNH 1111) seems to represent the primitive condition for the group (Sereno 1991a). The very derived metatarsal I of theropods, on the other hand, is proximally pinched and fails to reach the tarsus (Raath 1969, Welles 1984).

Unlike *Herrerasaurus* (Novas 1994), no clear scars for muscle attachments are seen on the shaft of metatarsal I of *Saturnalia*. Its distal articulation is composed of two condyles, which are separated by a groove on the plantar surface of the bone. The lateral condyle is, however, much larger in all dimensions, as is the respective pit for the collateral ligaments. Accordingly, the further distal projection of the medial condyle promotes the medial displacement of the phalanges of the first digit. This condition is also seen in *Herrerasaurus* (Novas 1994), *Guaibasaurus* (MCN PV 2355), "prosauropods" (Galton 1976; fig. 29), and theropods (Currie and Zhao 1993), but apparently not in ornithischians (Forster 1990; *Lesothosaurus*—BMNH RUB17; *Scelidosaurus*—BMNH 1111). Instead, the latter group presents a medially curved distal part of the metatarsal, which produces an analogous medial projection of the digit (Santa Luca 1980, Sereno 1991a).

In *Saturnalia*, the proximal articulation of metatarsal II is flat and parallelogram-shaped. Its cranial border is straight, bearing marked lateral and medial corners, whereas the caudal border is narrower and bears rounded corners. Its lateral border is flat, for the reception of metatarsal III, while the smaller medial articulation for metatarsal I is slightly concave. This proximal outline resembles that of *Herrerasaurus* (Novas 1994) and some ornithischians (Galton and Jensen 1973), but differs from that of "prosauropods," which are typically "hourglass-shaped" (Young 1941a, Cooper 1981), as well as from that of theropods (Huene 1934, Welles 1984), which are medially rounded because of reduction of the proximal part of metatarsal I. Furthermore, because the proximal articulation of metatarsal II of *Saturnalia* is subequal to that of the metatarsal III, it is primitive in comparison to that of some ornithischians (Galton and Jensen 1973, Galton 1981; *Scelidosaurus*—BMNH 1111) and "prosauropods" (Huene, 1926, Cooper, 1981), in which the proximal metatarsal II is much larger.

The proximal part of the shaft of metatarsal II matches the shape of its proximal surface, and is flatter cranially and more rounded caudally. A strong concavity is seen at the proximal end of its dorsal surface, as well as in that of metatarsal III (MCP 3845-PV), probably corresponding to insertion areas for the M. ext. dig. long. (Dilkes 2000). More distally, in the laterocranial corner of the shaft, another muscle scar is seen. It faces a similar but stronger scar on the mediocranial surface of metatarsal III (MCP 3845-PV), and both are thought to represent the insertion of the M. tib. cran. (Dilkes 2000). Distally, metatarsal II expands to form an articulation with two condyles. These are subequal in size, but the lateral condyle is slightly more distally extended. Like those of metatarsal I, the condyles are separated by a groove on their plantar surface, and clear collateral ligament pits are present. From the lateral pit, however, a strong ridge extends proximally through the lateral part of the plantar surface of the bone, which is probably related to a ligamentous attachment.

Metatarsal III is the longest in the series. Similar to metatarsal II, its proximal articulation is flatter cranially, but tapers caudally in a rounded border. The distal articulation is also like that of metatarsal II, but the condyles are equally projected distally. The muscle-related features of the bone were discussed together with those of metatarsal II.

Metatarsal IV of *Saturnalia* is about 90% the length of metatarsal III. This relative length is roughly the same in all basal dinosaurs, but metatarsal IV is significantly longer in basal dinosauromorphs (Sereno and Arcucci 1993, 1994). In *Saturnalia*, its proximal articulation is cranially flat, but proximally projected in its caudal portion. It is sub-triangular in outline, with marked mediocaudal and lateral projections. The mediocranial border of the mediocaudal projection forms a flat articular surface for metatarsal III, while the cranial border of the lateral projection forms a rugose free edge on the extensor surface of the pes. Laterocaudally, the proximal part of the bone bears a slightly concave surface, which articulates with metatarsal V.

In most basal dinosaurs, the proximal surface of metatarsal IV is sub-triangular. However, its mediocaudal process is reduced in ornithischians (Galton and Jensen 1973, Galton 1981; *Lesothosaurus*—BMNH RUB17; *Scelidosaurus*—BMNH 1111), the proximal metatarsal IV of which have the mediocaudal and mediocranial corners equally projected medially. In this respect, *Saturnalia* resembles more *Herrerasaurus* (Novas 1994), "prosauropods" (Huene 1926, Cooper 1981), and basal theropods (Huene 1934, Welles 1984), in which the mediocaudal process is well developed. Differing from these forms, the lateral projection of the proximal metatarsal IV is truncated in theropods.

The proximal two thirds of the lateral surface of metatarsal IV articulates with metatarsal III. This portion of the bone is flat and bears articulation scars. Distal to this, the shaft is sub-circular in cross section, and laterally kinked as in most basal dinosaurs. Further distally, a muscle scar is seen on the lateral border of its plantar surface, which is probably for the insertion of a branch of the M. gastroc. Dilkes (2000) noted that metatarsals II and III of *Maiasaura* bear similar scarred areas for the insertion of other branches of the M. gastroc. These are, however, not visible in *Saturnalia*. In addition, the distal articulation of metatarsal IV of *Saturnalia* is both deeper than wide and asymmetrical, with the medial condyle larger and more distally projected than the lateral.

Metatarsal V of *Saturnalia* is about 45% of the length of metatarsal III. This proportion matches that of *Guaibasaurus* (MCN PV 2355) and some basal "prosauropods" (Galton 1976; *Thecodontosaurus*—BMNH P24), but it is greater than that of most ornithischians (Galton and Jensen 1973, Galton 1974; *Scelidosaurus*—BMNH 1111) and basal theropods (Camp 1936, Raath 1969), and less than that of *Herrerasaurus* (Novas 1994). In proximal aspect the metatarsal is “L-shaped,” bearing a long mediocaudal process and marked lateral and mediocranial corners. This outline is similar to that of *Marasuchus* (Bonaparte 1975), *Herrerasaurus* (Novas 1994), and “prosauropods” (Huene 1926, Cooper 1981), although the mediocaudal process is much more developed in the latter group. On the contrary, in theropods (Welles 1984, Currie and Zhao 1993) and ornithischians (Galton and Jensen 1973), the mediocaudal process is absent, and the proximal outline of the bone is rounded to sub-triangular.

Metatarsal V articulates proximally with the calcaneum, via the margin between its lateral and mediocranial corners. It is, therefore, placed further proximally in relation to the other metatarsals. Both corners, together with the mediocaudal process, extend as ridges down the shaft of the bone, the proximal half of which is sub-triangular in cross section. At that point, the medial articulation of the bone is formed between its two medial ridges, which articulate with the lateral margin of the lateral distal tarsal, more proximally, and to the laterocaudal surface of metatarsal IV, more distally. The bone is, therefore, also slightly displaced caudally in relation to the other metatarsals. Moreover, the mediocaudal process projects distally as a plate-like articulation area, which extends through half the length of the bone, and fits into the laterocaudal concavity of the lateral distal tarsal. More distally, it extends as a ridge along the entire bone, forming, together with the lateral ridge, the borders of the elliptical cross section of the distal half. The mediocranial ridge, on the other hand, does not enter the distal half of the metatarsal.

At its distal third the metatarsal is “twisted,” deflecting the lateral ridge caudally and the medial ridge cranially. Its distal end is a simple rounded articulation, elliptical in cross section. It is surrounded by muscle scars, which extend further onto the cranial surface of the bone and for most of its lateral ridge. These scars could be related to the insertion of either the M. peroneus brevis, or a branch of the M. gastroc. (Dilkes 2000).

Pedal Digits (Fig.7F)—The pedal phalangeal formula of *Saturnalia* is ?-3-4-5-0 (MCN PV 2355), and the presence of two phalanges in its digit 1 can be suggested as a “level 1′” inference under a phylogenetic bracket approach (see Witmer 1995, Hutchinson 2001a), based on comparison with other basal dinosaurs. Digits 2–4 bear the number of phalanges common to all basal dinosaurs, but the absence of these elements in the fifth digit is curious. Pedal digit 5 of both the holotype and MCP 3845-PV were carefully extracted from the bearing rocks in order to recognize small elements, which might represent vestigial phalanges. Despite the overall fine and articulated preservation, nothing was recovered, and the lack of phalanges in pedal digit 5 is not believed to represent a taphonomic artifact. Indeed, because *Herrerasaurus* and most “prosauropods” have phalanges in that digit (Huene 1926, Galton 1976, Novas 1994), this condition was suggested to be plesiomorphic for saurischians (Gauthier 1986, Benton 1990). Yet, considering that *Saturnalia*, together with basal dinosauromorphs (Sereno and Arcucci 1993, 1994), ornithischians (Galton 1974, Galton and Jensen 1973, Forster 1990), and theropods (Raath 1969, Welles 1984, Colbert 1989), lack such elements, it is more parsimonious to consider that they were ancestrally lost in dinosaurs, and reacquired in *Herrerasaurus* and derived sauropodomorphs.

As in most basal dinosaurs (Huene 1926, Galton 1976, Santa Luca 1980), the first phalanx is the longest in the pedal digits of *Saturnalia.* In addition, caudal to their distal articulation, the dorsal surfaces of most phalanges bear well-developed pits for the extensor ligaments. Pits for the collateral ligaments are also present on all the recovered non-ungual phalanges, and are approximately of the same depth on both sides of the bones. As reported for *Sinraptor* (Currie and Zhao 1993), these pits are more dorsally placed in the penultimate phalanges of the digits. Collateral scars for the insertion of the collateral ligaments are also present on the plantar-proximal corner of all recovered phalanges, including the unguals. The plantar insertions of the M. flexor digitorum brevis (Dilkes 2000) are, however, not visible in the available material.

The unguals are sub-triangular in cross-section and slightly curved, but elongated and non-raptorial. Their proximal articulations are biconcave, and present a dorsoproximal prong, the dorsal surface of which bears scars for the attachment of a possibly combined M. extensor digitorum longus and brevis. Clear scars for the M. flexor digitorum longus (see Dilkes 2000) are seen on the proximal part of the plantar surface of all unguals.

HIND LIMB FUNCTION

The hind limb and pelvic girdle anatomy of *Saturnalia* is representative of a general construction shared by basal dinosauriforms such as *Marasuchus* and *Pseudolagosuchus*, basal dinosaurs, including *Herrerasaurus*, *Staurikosaurus*, and *Guaibasaurus*, as well as basal sauropodomorphs, and some basal theropods and ornithischians (Carrano 2000; Hutchinson 2001b, c). Accordingly, various of the considerations presented here regarding the hind limb function of *Saturnalia* are believed to be applicable to most basal dinosaurs, and to represent the locomotion model involved in the origin and early diversification of the group.

As asserted by Gatesy (1990) for other dinosaurs, the femur of *Saturnalia* was mainly vertically oriented, not showing a bird-like more horizontal position. This is evident by its hip and knee articulation, because the maximum angle of femoral protraction is about 55° to the vertical, while the epipodium did not reach a flexion of much more than 90°. In addition, it is suggested that, despite the lack of a fully open acetabulum and an inturned femoral head, the hind limb of *Saturnalia*, like those of several other dinosauromorphs bearing similar morphological features (Arcucci 1989, Carrano 2000), was fully erect during locomotion. This inference is partially based on the very deep acetabulum (see Bonaparte 1984, Parrish 1986) and the presence of a marked supracetabular crest, which indicates that the pelvis of *Saturnalia* was constructed to support a strictly dorsally directed pressure derived from the weight of the animal (Charig, 1972; fig. 8). Indeed, the flat proximal articulation of the femoral head reflects this arrangement, fitting perfectly below the dorsal roof of the acetabulum.

It is clear that the femoral articulation to the dorsal roof of the acetabulum defines the axis for the fore-and-aft swing of the limb. As discussed by Walker (1977; fig. 7), this is different from the condition of various dinosaurs with both a well-developed *collum* and *caput femoris* and a fully opened acetabulum (Galton 1981, Norman 1986, Forster 1990, Barsbold et al. 1990, Currie and Peng 1993). In these forms, the axis of femoral rotation was at the center of the head, rather than at its proximal margin. In addition, the femoral abduction was severely restricted in these dinosaurs, because of the close articulation of their hip joint. In *Saturnalia*, on the contrary, a significant degree of abduction was possible, which was indeed an integral part of the proposed hind limb movement. However, the hip-joint construction of *Saturnalia* did not allow a full sprawling position to be adopted. Accordingly, the complete resting position of the animal would most probably have involved lying on the lateral surface of the body.

Before further analyzing the limb movements in *Saturnalia*, it is necessary to examine the structure of its knee and ankle joints. The knee mainly operated with a simple fore-and-aft movement, as few possibilities of rotation and/or lateral movements are present. Yet, the main axis of the proximal surface of the tibia forms an angle of about 60° to the femoral intercondylar line. Accordingly, its cranial part is laterally displaced, and the cnemial crest protrudes cranially at the level of the lateral femoral condyle. Because of a slight “twisting” along the tibial shaft, however, the transverse axis of the distal epipodium is almost parallel to the femoral intercondylar line. In addition, the articular surface of the distal femur and that of the proximal tibia are inclined. The medial femoral condyle is more distally projected than the lateral, while that of the tibia projects more proximally. As a result, the long axis of the epipodium of *Saturnalia* is inclined (about 20°) in relation to that of the femur, and its distal part shows a markedly lateral displacement.

As in other dinosaurs, the ankle-joint movements of *Saturnalia* were mainly related to those between the proximal tarsals and the distal tarsals-metatarsals. As with the knee, the main ankle movement was simply that of a fore-and-aft flexion-extension, although some rotation and lateral movement seems to have also taken place. Interestingly enough, the axis of the main fore-and-aft movement does not seem to have been parallel to a sagittal section through the epipodium. Instead, in its preferential angle of articulation, the metatarsus was slightly inturned, so that its cranial surface was more medially directed than that of the epipodium.

The step cycle of *Saturnalia*

As a starting point for the discussion of the step cycle of *Saturnalia*, a resting position for its hind limb is defined, with the femur conformably set into the acetabulum. Accordingly, the proximal surface of the femoral head sits at the dorsal roof of the acetabulum, with its longitudinal groove (fossa trochanteris) fitting into the corresponding ridge on the acetabular roof, and the articulation between the antitrochanter and the trochanteric fossa at its maximal. In this position, the femoral shaft bows both laterally and cranially, so that the flexor surface of the knee is inturned, forming an angle of about 45° to the sagittal line. This implies that, when articulated, the epipodium would extend both medially and caudally, with the extensor surface of the ankle facing caudomedially. In this arrangement, the pes would naturally extend craniolaterally. However, because of its inwards rotation, it extends almost cranially. As a result, the propodium plus epipodium form a craniolaterally-inflected arch, whereas the epipodium plus metapodium inflect caudomedially.

It is unclear whether *Saturnalia* would have abducted the hind limb during motionless periods or not, as the hip-joint articulation would allow the femoral head to form an angle of some 35° to the vertical (see Van Heerden 1979). Yet, the advantage of a more vertical limb posture is obvious (Charig 1972), and it was most probably adopted by a “quietly-standing” *Saturnalia*. Such an “improved” position seems to have been possible despite the fact that the distinct functional parts of its hind limb (femur, tibiotarsus, and pes) do not align in a parasagittal plane. This is because of the relative slope of each of those parts, with the hind limb experiencing a perfect counterbalance of the medially and laterally directed transverse forces. This condition, rather than the parasagittal alignment of each limb part, is the fundamental characteristic of a fully erect gait (Charig 1972; p.132). Accordingly, during a preferential “fore-and-aft” movement, the long axis of the leg of *Saturnalia* would travel in a parasagittal plane, although that of each of its parts would not.

During the propulsive phase (Fig. 8), the femur of *Saturnalia* was retracted, while its knee and ankle were extended, and the metatarsal-phalangeal joints flexed. A large array of muscles appears to have helped in the retraction of the femur, including: M. caudofem. brevis, M. ischiofem., M. add., and the caudal part of the M. obt. (= M. pub. isch. fem. ext. part 3). As suggested by Gatesy (1990) for other non-avian dinosaurs, however, the M. caudofem. long. is believed to represent the main femoral retractor of *Saturnalia*. Galton (1969, see also Romer 1923b) proposed that the forward pull given by the contraction of the M. iliotroc. also promoted femoral retraction. However, as dis-

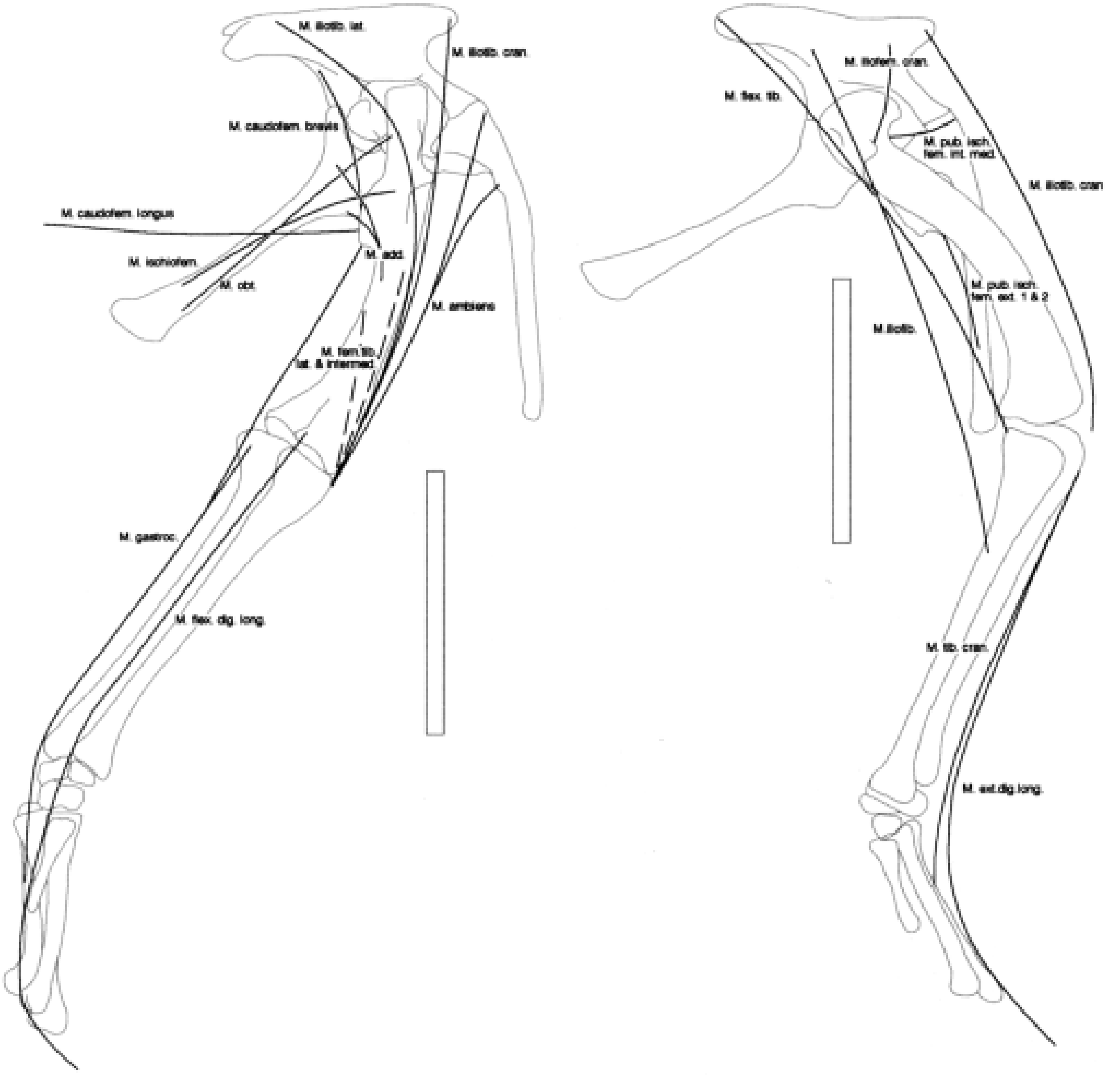

Fig. 8. Pelvic girdle, and partial hindlimb of the holotype of *Saturnalia tupiniquim* (MCP-3844PV) articulated as in (**A.**) the final stages of the propulsive phase (depicting main muscles acting on the femoral retraction, knee and ankle extension, and flexion of the metatarsal-phalangeal joints) and as in (**B.**) the final stages of the protractive phase (depicting main muscles acting on the femoral protraction, leg elevation, knee and ankle flexion, and extension of the metatarsal-phalangeal joints). Scale bar = 10 cm. Abbreviations: **M. add.**, M. adductor; **M. ambiens**, M. ambiens; **M. caudofem. brevis**, M. caudofemoralis brevis; **M. caudofem. long.**, M. caudofemoralis longus; **M. ext. dig. long.**, M. extensor digitorum longus; **M. fem. tib. intermed.**, M. femorotibialis intermedius; **M. fem. tib. lat.**, M. femorotibialis lateralis; **M. flex. dig. long.**, M. flexor digitorum longus; **M. flex. tib.**, M. flexor tibiale; **M. gastroc.**, M. gastrocnemius; **M. iliofem. cran.**, M. iliofemoralis cranialis; **M. iliofib.**, M. iliofibularis; **M. iliotib. cran.**, M. iliotibialis cranialis; **M. iliotib. lat.**, M. iliotibialis lateralis; **M. ischiofem.**, M. ischiofemoralis; **M. obt.**, M. obturatorius; **M. pub. isch. fem. int. med.**, M. puboischiofemoralis internus pars medialis; **M. tib. cran.**, M. tibialis cranialis.

cussed by Walker (1977; fig. 7), since the femur of *Saturnalia* was mainly held against the upper part of the acetabulum, the forward pull of any muscle placed distal to that articulation (as is the case of the M. iliotroc.) played no role in femoral retraction (see also Coombs 1979), and was not significant in promoting the forward stroke of the leg. In addition, knee extension in *Saturnalia* seems to have been mainly promoted by the contraction of the M. ambiens, M. iliotibiale, and M. femorotibialis lateralis, and intermedius, all of which probably inserted on the cnemial crest via the patellar ligament. The M. gastroc., on the other hand, was probably the main ankle extensor, whereas the flexion of the pedal articulations was promoted by the M. flexor digitori.

Because the insertion point of the M. caudofem. long. is on the medial surface of the femur, the contraction of this muscle, while promoting the retraction of that bone, also medially rotated the hind limb, so that the surface that was cranially directed would be medially directed. In this context, the primary action of the M. iliotroc. is clarified, since its contraction was surely also related to femoral medial rotation. Accordingly, this medial rotation lead to a complete change in the position of the limb, in relation to its resting position. At maximal retraction, the insertion point of the M. caudofem. long. would be shifted caudally to face its origin area, which is on the lateral surface of the caudal vertebrae. As a result, the long axis of the femoral head would then be perpendicular to the sagittal line, and the shaft of the bone bowed cranially and medially. Moreover, the caudal surface of the epipodium would face laterocaudally, the propodium plus epipodium forming a mediocranial arch, and the epipodium plus metapodium arching laterocaudally. As a result, the distal part would be more laterally placed than the proximal part, the knee joint being placed slightly medially to the acetabulum, and the ankle slightly lateral to it. This arrangement would lead to a medial to craniomedial orientation of the extensor surface of the inturned pes, making evident the importance of some rotational movement of the ankle joint to turn the foot outward, in order for a more cranial orientation to be achieved. In this context, the overlapping pattern of the metatarsals of *Saturnalia* and other basal dinosaurs is also of importance. In these forms, distal parts of the more medial metatarsals are displaced cranially, so that even were the cranial surface of the proximal part of the metatarsus to face more medially, the flexor surface of the pes itself would be more cranially directed.

The protractive phase (Fig. 8) is believed to resemble that of other tetrapods (Brinkman 1980) with an initial flexion of knee and ankle joints, and the lift and forward movement of the limb, followed by its lowering and the extension of those joints. The scarring associated with the insertion of the M. pub. isch. fem. int. med. (= avian M. iliofemoralis internus) and M. pub. isch. fem. ext. (parts 1 and 2) indicate that these were probably the main femoral protractors, and responsible for the forward movement of the limb. In dinosaurs with a large iliac preacetabular ala, the M. iliofem. cran. seems also to represent an important femoral protractor (Russell 1972, Carrano 2000; see also Coombs 1979). Similarly, in forms such as ornithopods (Walker 1977, Norman 1986) with well-developed *collum* and *caput femoris* and fully opened acetabulum, the contraction of the M. iliofem. cran. seems to have promoted some femoral protraction. However, in the case of *Saturnalia*, and other basal dinosaurs with a short iliac preacetabular ala and a less derived hip joint, the action of the M. iliofem. cran. in femoral protraction was much less significant (see Carrano 2000). In addition, some knee extensors such as the M. iliotib. cran. probably helped the final stages of the femoral protraction, by promoting the elevation of the bone. The flexion of the knee and ankle were, on the other hand, mainly promoted by the contraction of M. iliofib. and M. flexor tibiale, and M. tib. cran., respectively. Moreover, the forward travel of the leg was also accompanied by the extension of the pedal articulations promoted mainly by the M. extensor digitori.

As discussed by Charig (1972) for the crocodile, the M. iliofem. cran. of *Saturnalia* seems to have acted mainly in a transverse plane, having been primarily involved in femoral abduction. Yet, because of the cranial position of the "lesser trochanter," the contraction of that muscle would also have had secondary importance in femoral protraction. Indeed, this conjoined action was probably important in the final stages of femoral protraction, when the abduction promoted by the M. iliofem. cran. would alleviate the "femur-knocking-on-the-pubis" problem (Charig 1972), allowing that bone to pass forward of the level of the pubis, and reach its maximum protraction of about 60° to the vertical plane. As in birds (Vanden Berge 1975), the M. iliofem. ext., on the other hand, was probably a postural muscle related to the rotation of the femur on the acetabulum.

During the initial stages of the protractive phase, the hind limb was also laterally rotated, coming back from the maximum medial rotation achieved at the end of its retraction. This is because the main muscles responsible for femoral protraction were inserted on the medial surface of the bone, and their contraction turned the cranial surface of the bone laterally. Due to this lateral rotation, the knee performed an inward arching movement during protraction, while the foot was displaced laterally. At maximum protraction, the long axis of the femoral head would approach a parasagittal plane. This is just slightly more medially rotated than that of the resting position, and the foot would touch the ground with its extensor surface cranially directed.

Osteological evidence for these hind-limb movements is scarce. Yet, a few signs of some of the particular phases are observed in the skeleton of *Saturnalia.* In particular, a very distinct and rugose texture is seen at the ventral portion of its iliac medial acetabular wall, cranial to the antitrochanter. This is a topological correlate of the portion of the acetabulum that is perforated in several basal dinosaurs, including most "prosauropods" (Huene 1926, Galton 1984), basal theropods (Huene 1934, Welles 1984, Raath 1990), and basal ornithischians (Thulborn 1972, Santa Luca 1984), and it is believed to represent the part of the medial acetabular surface in which the medial tip of the femoral head swung during its lateral-medial rotation, also rotating due to its protraction-retraction. Accordingly, at the beginning of the propulsive phase, while the femoral head was almost aligned to the parasagittal plane, its medial tip articulated with the cranial portion of the rugose area. During retraction/medial rotation, this part of the head would move backwards along the rugose area, to the cranial margin of the antitrochanter, where the medial "tip" of the perpendicularly oriented head would articulate with the caudal part of the rugose area.

In addition, the shape of the proximal surface of the femur also provides some hints regarding its movements in the acetabulum. Its articular area is more distally expanded in its cranial portion, especially between the laterocranial ridge ("r" in Padian 1986; fig. 5.4) and the mediocranial tip of the head. This area is thought to face the cranial surface of the acetabulum during the resting period, but to articulate to its "roof" at maximum protraction. In this position, only the mediocranial part of the head was in contact with the acetabulum, with the proximal extension of the laterocranial ridge articulating with the top of the acetabular roof, just below the central part of the supracetabular ridge.

According to the model proposed above, it is clear that movements at the hip joint of *Saturnalia* were not simply a rotation in the parasagittal plane as suggested for various dinosaurs (Wade 1989, Padian and Olsen 1989, Carrano 2000). Instead, it is more likely that, similar to the proposition of Christian et al. (1996; see also Van Heerden 1979) for *Plateosaurus*, lateral movements of the hind limb played an important role in the locomotion of *Saturnalia*.

Ichnological evidence and final considerations

Some of the inferences regarding the limb movements of *Saturnalia* listed above are interestingly supported by studies of dinosaur footprints in general. The positive—inwards—rotation of the pes, for instance, is a well-known feature of various dinosaur trackways, especially those of bipedal forms (Padian and Olsen 1989, Thulborn 1990). This indicates that the foot was inturned during the kick-off phase (see Thulborn and Wade 1989). Indeed, this phase corresponds to the final part of hind-limb retraction in the step cycle of a dinosaur. In the case of *Saturnalia*, as already discussed, because of the medial rotation associated with the retraction of the leg, this phase is characterized by a marked inturning of the pes.

Thulborn (1989) observed that, in semibipedal basal ornithischians (see Ellenberger 1974, Thulborn 1990; p. 187, fig. 9.14), locomotion tended to be faster when the animals shifted from a quadrupedal to a bipedal gait. Accordingly, as is typical of faster locomotion, the pace angulation and the stride length increased, while the imprints of the more proximal parts of the pes became less marked. More importantly, the positive rotation of the pes was also more pronounced. Again, this change can be explained based on the functional analysis of the hind limb of *Saturnalia*. Indeed, as proposed by various authors (Alexander 1976, Demathieu 1984), an increase in speed is partially related to a higher gait angle. As discussed above, the more retracted the femur of *Saturnalia* is, the more medially rotated it is. Therefore, during the kick-off phase, the pes is expected to have been more inturned in a faster than in a slower pace. This condition is highlighted by the fact that, during fast locomotion, the durations of footfalls are reduced (Brown and Yalden 1973). Accordingly, the touch-down and weight-bearing phases (Thulborn and Wade 1989) are abbreviated, whereas the kick-off phase becomes more prominent. Indeed, it is exactly during the kick-off phase that the leg of *Saturnalia* was more medially rotated, and its foot more inturned.

During a slower pace, because of the smaller gait angle involved, the protraction and retraction of the leg in *Saturnalia* were reduced. Accordingly, the inwards rotation of its pes was less marked. Indeed, in most quadrupedal trackways—including those attributed to "prosauropods" (Thulborn 1990; fig. 6.22)—the pes usually shows a negative (outwards) rotation. The pes of *Saturnalia* would have shown an equivalent position during the final phases of limb protraction, and initial phases of its retraction, when the femur was maximally rotated laterally. Indeed, during a slower pace, the fore-and-aft movement of the leg would have been much more restricted, and the inturning of the foot much less marked.

Thulborn (1990) related footprint rotation to the different gaits of dinosaurs, either quadrupedal or bipedal. However, it seems that, at least when it comes to basal dinosaurs, the footprint rotation might also have been related to the higher gait angle of fast locomotion. Further ichnological evidence of the proposed locomotory strategy of *Saturnalia* comes from the craniolaterally extended scrape-marks commonly found in some dinosaur footprints—including some possibly related to a "prosauropod" walking bipedally (Thulborn 1990; p. 261, fig. 6.23). These have previously been related to an arc-like outwards movement of the limb (Thulborn 1990). These marks might instead be related to the outwards rotation of the foot during the initial phase of leg protraction, as in the reconstructed gait of *Saturnalia*.

Basal dinosauromorphs, as well as basal ornithischians and theropods, were all primarily or obligatorily bipeds (Padian 1997), while all sauropods were quadrupeds (McIntosh 1990). The gaits of "prosauropods" are, however, more controversial. Very large forms, such as the melanorosaurids, are usually accepted as quadrupeds (Weishampel and Westphal 1986, Galton 1990, Upchurch 1997). Typical "prosauropods," on the other hand, have alternatively been considered fully bipedal (Cooper 1981) or obligately quadrupedal (Van Heerden 1979, Wellnhofer 1994). More commonly, these forms are presented as having possessed an intermediate mode of locomotion (Galton 1976, 1990, Galton and Cluver 1976, Upchurch 1997). It is evident, therefore, that regardless of the exact moment at which it occurred, a trend towards a locomotion more dependent on the forelimb action was present during the early evolution of sauropodomorphs. Accordingly, the study of the locomotion of basal members of the group, such as *Saturnalia* and *Thecodontosaurus*, is relevant to understanding this transition.

Several skeletal features of *Saturnalia*, such as its long distal limb elements and short muscle lever arms in the hind limb, indicate that it was more cursorial than any typical sauropodomorph (Coombs 1978, Carrano 1999), with the possible exception of *Thecodontosaurus* (see Benton et al. 2000). In addition, *Saturnalia* has the hind limb elongation necessary to achieve bipedal locomotion (see Christian et al. 1994). As discussed by those authors, modern reptiles switch to a bipedal gait when the advantages of faster locomotion compensate for higher instability. Yet, as already discussed, *Saturnalia* possesses an "improved" hind limb construction in comparison to that of "sprawling" forms such as lizards (Charig 1972). This would probably alleviate the problems related to instability. It is very likely, therefore, that *Saturnalia* adopted a bipedal posture more often than modern lizards do, most probably for fast locomotion.

Given that *Saturnalia* was capable of bipedal locomotion, would it have been an obligatory biped, or would it sometimes have walked on all fours? It has often been proposed (Galton 1990, Upchurch 1997) that *Thecodontosaurus*, and "thecodontosaurids," were bipeds. Indeed, Galton (1990) considered *Thecodontosaurus* a full biped, because its trunk to hind limb ratio is equivalent to that of other bipedal dinosaurs. Yet, most of the relevant anatomical data available for *Thecodontosaurus* is misleading, and figures on the trunk to hind limb proportion are highly uncertain. The only nearly complete skeleton of the taxon (Kermack 1984) lacks its trunk series (Benton et al. 2000), and the cranial part of that specimen (skull, cervical vertebrae, and partial humerus) may not belong with the caudal part (most pelvic girdle, hind limb, and caudal vertebrae). Kermack (1984) believed that this was the case and scaled the caudal part, producing the reconstruction used by Galton (1990) in support of his hypothesis of a bipedal *Thecodontosaurus.*

It is possible to calculate a confident estimate of the trunk to hind limb ratio of *Saturnalia*, and this is of the order of 1.0 to 1.1. This ratio is less than that of obligatorily bipedal dinosaurs, but higher than that of typical quadrupeds (see Galton 1970). In fact, it is also higher than that of most "prosauropods," a possible exception being *Massospondylus* (Galton 1976, Cooper 1981). In fact, the gait of *Saturnalia* was probably somewhere between that of a fully bipedal dinosaur like *Coelophysis* and that of forms such as *Plateosaurus*, which were mainly quadrupedal, becoming bipedal only at high speeds (see Christian and Preuschoft 1996). *Saturnalia* would have used a bipedal gait more often than other "prosauropods," probably to escape from predators, but also for active hunting of small prey, when relatively fast locomotion was advantageous. However, it was probably not an obligatory biped. During a slower pace—perhaps while moving through areas with vegetation that could be eaten (Upchurch 1997)—it is likely that *Saturnalia* walked on all fours, a position possibly also adopted during resting periods.

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APPENDIX

Table 1. Measurements (mm) of the sacral vertebrae of the holotype of *Saturnalia tupiniquim* (MCP 3844-PV).

First sacral vertebra	
Length of the centrum	23
Cranial width of the centrum	22
Cranial height of the centrum	14
Cranial width of the neural canal	8
Cranial height of the neural canal	4
Length of the neural spine	25
Length of the right transverse process	22
Height of the left rib	21
Second sacral vertebra	
Length of the centrum	25
Caudal width of the centrum	19
Caudal height of the centrum	19
Length of the neural spine	19
Length of the right transverse process	20
Height of the left rib	11
Third sacral/first caudal vertebra	
Length of the centrum	26
Cranial width of the centrum	17
Cranial height of the centrum	19
Caudal width of the centrum	18
Caudal height of the centrum	23

Table 2. Measurements (mm) of the pelvic girdle of *Saturnalia tupiniquim*. Abbreviation: ( ) = estimated.

	MCP 3844-PV		MCP 3845-PV
	Right	Left	Left
Ilium			
Maximum depth	–	49	60
Maximum length	–	(90)	83
Depth of the acetabulum	–	25	–
Maximum length of the acetabulum	–	37	–
Width of the supracetabular crest	–	14	–
Length of the preacetabular ala	–	–	7
Length of the postacetabular ala	–	45	60
Maximum width of the postacetabular ala			–
Inter-embayment length	–	40	–
Length of the pubic peduncle	–	24	27
Pubis			
Maximum length	121	127	(102)
Distal extension of the obturator plate	42	–	–
Proximal depth	41	35	–
Distal depth	11	10	–
Ischium			
Maximum length	132	121	(96)
Length of the antitrochanter	–	22	–
Distal depth	–	22	–
Distal extension of the obturator plate	32	33	–

Table 3. Measurements (mm) of the propodium and epipodium of *Saturnalia tupiniquim*. Abbreviation: ( ) = estimated.

	MCP 3844-PV		MCP 3845-PV	
	Right	Left	Right	Left
Femur				
Maximum length	157	152	—	156
Maximum width of the head	36	35	—	—
Maximum width middle of the shaft	17	17	16	17
Width of medullary canal in the middle of the shaft	—	8	10	12
Lateromedial width of the distal end	35	34	28	29
Tibia				
Maximum length	—	158	—	155
Craniocaudal width of the proximal end	—	41	—	—
Lateromedial width of the proximal end	—	27	—	21
Maximum width at middle of the shaft	—	12	14	12
Width of medullary canal at the middle of the shaft	—	—	7	6
Maximum craniocaudal width of the distal end	—	21	—	19
Maximum lateromedial width of the distal end	—	18	—	20
Fibula				
Maximum length	—	154	—	154
Maximum proximal width	—	27	—	24
Maximum width at middle of the shaft	—	10	9	8
Width of medullary canal at the middle of the shaft	—	3	—	4
Maximum caudal width	—	19	—	19
Astragalus				
Craniocaudal length on lateral border	—	16	15	—
Craniocaudal length on medial border	—	20	20	—
Width at caudal border	—	24	15	—

MCP 3844-PV	
Maximum craniocaudal width of the distal end of the right tibia	15
Maximum lateromedial width of the distal end of the right tibia	21
Maximum width of the distal fibula	18

Table 4. Measurements (mm) of the metatarsals of *Saturnalia tupiniquim*.

	MCP 3844-PV	MCP 3845-PV		MCP 3846-PV
	Right	Right	Left	Right
Length of metatarsal I	46	–	–	–
Proximal depth of metatarsal I	10	–	8-	–
Distal depth of metatarsal I	8	–	–	–
Distal width of metatarsal I	9	–	–	–
Length of metatarsal II	70	–	–	–
Proximal depth of metatarsal II	17	–	15	–
Distal depth of metatarsal II	10	–	–	–
Distal width of metatarsal II	12	11	–	–
Length of metatarsal III	84	–	–	–
Proximal depth of metatarsal III	20	–	15	–
Distal depth of metatarsal III	10	–	–	–
Distal width of metatarsal III	14	–	–	–
Length of metatarsal IV	74	–	–	73
Proximal depth of metatarsal VI	(21)	–	15	16
Distal depth of metatarsal VI	11	10	–	12
Distal width of metatarsal VI	10	9	–	8
Length of metatarsal V	38	40	–	–

Table 5. Measurements (mm) of the phalanges of *Saturnalia tupiniquim* (MCP 3845-PV).

Length of ungual of digit II	22
Length of phalanx 1 of digit III	24
Length of phalanx 2 of digit III	19
Length of phalanx 3 of digit III	15
Length of ungual phalanx of digit III	(20)
Length of phalanx 1 of digit IV	14
Length of phalanx 2 of digit IV	10
Length of phalanx 3 of digit IV	9
Length of phalanx 4 of digit IV	11
Length of ungual phalanx of digit IV	(17)