



The anatomy and phylogenetic position of the Triassic dinosaur *Staurikosaurus pricei* Colbert, 1970

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Table of contents

Abstract	1
Introduction	2
Geological and Taphonomic notes	3
Systematic Palaeontology	3
Description and comparisons	4
Mandible and dentition	4
Vertebral column	10
Pectoral girdle	25
Forelimb	26
Pelvic girdle	27
Hindlimbs	36
Discussion	44
Acknowledgments	49
References	50

Abstract

We redescribe the holotype of the saurischian dinosaur *Staurikosaurus pricei* Colbert, 1970 from Late Triassic Santa Maria Formation (southern Brazil), following additional preparation that revealed new anatomical features. A revised diagnosis is proposed and the published synapomorphies for Dinosauria and less inclusive clades (e.g. Saurischia) are evaluated for this species. Some characters previously identified as present in the holotype, including the intramandibular joint, hyposphene-hypantrum articulations in dorsal vertebrae, and a cranial trochanter and trochanteric shelf on the femur, cannot be confirmed due to poor preservation or are absent in the available material. In addition, postcranial characters support a close relationship between *S. pricei* and *Herrerasaurus ischigualastensis* Reig, 1963 (Late Triassic, Argentina), forming the clade Herrerasauridae. Several pelvic and vertebral characters support the placement of *S. pricei* as a saurischian dinosaur. Within Saurischia, characters observed in the holotype, including the anatomy of the dentition and caudal vertebrae, support theropod affinities. However, the absence of some characters observed in the clades Theropoda and Sauropodomorpha suggests that *S. pricei* is not a member of Eusaurischia. Most morphological characters discussed in previous phylogenetic studies cannot be assessed for *S. pricei* because of the incompleteness of the holotype and only known specimen. The phylogenetic position of *S. pricei* is constrained by that of its sister taxon *H. ischigualastensis*, which is known from much more complete material.

Key words: Dinosauria, Saurischia, Santa Maria Formation, Late Triassic, Brazil

Introduction

Since the description of *Staurikosaurus pricei* Colbert, 1970, the anatomy and phylogenetic position of this taxon have been extensively debated (Galton 1973, 1977, 2000a; Brinkman & Sues 1987; Sues 1990; Novas 1993; Sereno 1999; Kellner & Campos 2000; Rauhut 2003; Yates 2003a, 2007a, b; Bittencourt 2004; Bittencourt & Kellner 2004; Langer & Benton 2006). Colbert (1970) presented an initial description of the holotype, and Galton (1973, 1977, 2000a) published further comments and figures, but some morphological features were not discussed in detail due to lack of preparation. Although several phylogenetic positions have been proposed, *S. pricei* is generally thought to be closely related to *Herrerasaurus ischigualastensis* Reig, 1963 (Late Triassic, Argentina), comprising the clade Herrerasauridae Benedetto, 1973. The monophyly of this taxon is widely accepted in the literature (e.g. Novas 1992, 1993, 1997; Sereno & Novas 1992, 1993; Sereno 1999; Langer & Benton 2006; *contra* Galton 1977; Brinkman & Sues 1987; Sues 1990), but its taxonomic composition is controversial (Galton 1985a; Chatterjee 1987; Novas 1992, 1997; Chatterjee & Creisler 1994; Long & Murry 1995; Hunt *et al.* 1998; Irmis *et al.* 2007a; Nesbitt *et al.* 2007; Yates 2007a, b).

Several alternative phylogenetic positions have been proposed for *S. pricei*, including: a saurischian with prosauropod affinities (Colbert 1970; Kischlat 2002); Saurischia *incertae sedis* (Bonaparte 1970; Galton 1977); a basal dinosauriform lying outside the clade of Ornithischia + Saurischia (Gauthier 1986; Brinkman & Sues 1987; Benton 1990; Novas 1992; Padian & May 1993; Holtz 1994, 1995, 2000); a primitive theropod (Galton 1973; Novas 1993, 1996, 1997; Sereno 1993, 1997, 1999; Sereno & Novas 1993; Long & Murry 1995; Kellner & Campos 2000; Rauhut 2003; Bittencourt & Kellner 2004); or, more recently, a basal saurischian excluded from the sauropodomorph and theropod lineages (Langer *et al.* 1999; Yates 2003a, 2007a; Langer 2004; Ezcurra 2006; Langer & Benton 2006). The conflict between these hypotheses is largely the result of disagreement over the definition of taxa, characters and character states used in cladistic analyses. Moreover, the scarcity of anatomical data for the immediate outgroups of Dinosauria has hampered a more accurate diagnosis of this clade (Fraser *et al.* 2002; Nesbitt *et al.* 2005, 2007), and complicated attempts to understand the interrelationships of basal dinosaurs.

Despite the fact that new dinosauriform material has recently been found in the Triassic strata of Rio Grande do Sul (e.g. Langer *et al.* 1999; Leal *et al.* 2004; Bonaparte *et al.* 2007; Cabreira *et al.* 2007; Ferigolo & Langer 2007), at present no additional material of *S. pricei* has been identified. Therefore, the holotype provides the only anatomical information available for this taxon. One incomplete specimen recovered in the stratigraphically correlated Ischigualasto Formation (Late Triassic, Argentina) attributed to cf. *Staurikosaurus* sp. does not possess any diagnostic features that would justify such an assignment (Brinkman & Sues 1987; Sues 1990; Novas 1992), and was later referred to *H. ischigualastensis* (Novas 1993; Sereno 1993). Although previous descriptions of *S. pricei* have contributed significant anatomical data (Colbert 1970; Galton 1977, 2000a), here we provide a detailed redescription of this Brazilian Triassic dinosaur, including a revised diagnosis and several new morphological details revealed by additional preparation of the holotype. In addition, we discuss the phylogenetic position of *S. pricei* based on published phylogenetic analyses of basal dinosaurs, including recent analyses that place *S. pricei* as a non-theropod basal saurischian (e.g. Yates 2003a, 2007a, b; Langer 2004; Ezcurra 2006; Langer & Benton 2006).

Institutional abbreviations: MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Cambridge, USA; PVL, Fundación “Miguel Lillo”, San Miguel de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, San Juan, Argentina; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Geological and Taphonomic notes

The type material of *S. pricei* is housed at the Museum of Comparative Zoology (MCZ), Harvard University, under the catalogue number MCZ 1669. The specimen was collected from the locality Sanga Grande, an outcrop of the Alemoa Member of the Santa Maria Formation (Carnian; see Langer *et al.* 2007b). The Alemoa Member is lithologically composed of red, laminated to massive mudstones and fine to conglomerated sandstones, possibly deposited in a fluvial environment (Bortoluzzi 1974; Andreis *et al.* 1980; Barberena *et al.* 2002; Scherer *et al.* 2002; Zeffass *et al.* 2003). The associated tetrapod fauna includes cynodonts, proterochampsids, rhynchosaurs and the early dinosaur *Saturnalia tupiniquim* Langer, Abdala, Richter & Benton, 1999 (Barberena *et al.* 1985a, b; Kellner & Campos 1999; Langer *et al.* 1999, 2007a; Barberena & Dornelles 2002; Barberena *et al.* 2002; Kischlat 2002; Langer & Schultz 2002).

Taphonomic features of MCZ 1669 include bones that are mostly broken, distorted or deformed and coloration varying from white to grey, with several possessing a crust of red hematite (Colbert 1970). They are neither completely flattened as occurs frequently in some fossil Lagerstätten such as the Jehol Group of China (e.g. Chang *et al.* 2003; Wang *et al.* 2007), nor do they show the excellent three dimensional preservation with little or no deformation seen in material from the Santana Formation (e.g. Fara *et al.* 2005). They also do not show the common deformation observed in some fossil specimens from the Santa Maria Formation, in which the internal spaces of the bones are infilled with sediment, causing a considerable increase in the size of individual elements (Holz & Schultz 1998). The presence of both mandibular rami and the partial articulation of the vertebral column suggest limited post-mortem transportation of the specimen. The preservation of MCZ 1669 required both mechanical and chemical preparation, a combination of techniques that has been previously applied to fragile fossil vertebrates (e.g. Kellner 2004; Oliveira & Kellner 2007). Mechanical preparation was performed using an air scribe (Model Micro-Jack 4, 100–120 psi; 40,000 cpm; 1.5 mm), and chemical preparation involved the local application of dilute formic acid, which facilitated disaggregation of the matrix.

Systematic Palaeontology

Dinosauria Owen, 1842 *sensu* Padian & May 1993

Saurischia Seeley, 1887 *sensu* Gauthier 1986

Herrerasauridae Benedetto, 1973 *sensu* Novas 1997

Staurikosaurus pricei Colbert, 1970

Figures 1–32

Holotype. Incomplete skeleton (MCZ 1669, Figs 1–32), housed in the Museum of Comparative Zoology, Harvard University, comprising: both mandibular rami with fragments of teeth *in situ*; six cervical, 15 dorsal, three sacral, and 34 caudal vertebrae; rib fragments; distal left scapula; ilia, ischia, and pubes; femora, tibiae, and fibulae; several unidentified fragments. A cast (MN 6104-V) is housed at the Museu Nacional/UFRJ, in Rio de Janeiro, Brazil.

Type locality. An outcrop of the Alemoa Member, Santa Maria Formation (Carnian), locality Sanga Grande, city of Santa Maria, Rio Grande do Sul, Brazil.

Revised diagnosis. Saurischian dinosaur distinguished by the following autapomorphies: 1) craniomedial region of the distal pubis is distinctly beveled (Novas 1993; Figs 22–23); 2) femoral cranial trochanter reduced in size (Fig. 27); 3) distal end of tibia is subcircular in distal view (modified from Rauhut 2003; Fig. 28g); 4) dorsoventrally oriented sulcus present on the medial surface of the proximal third of fibula (Fig. 30c–d).

Comments. Rauhut (2003) proposed two additional autapomorphies for *S. pricei*: postacetabular process of ilium abbreviated and caudally straight; pubic boot confluent with pubic shafts caudally. These proposed autapomorphies are problematic because the postacetabular iliac process is also short in several primitive dinosaurs, including *H. ischigualastensis*; moreover, in *S. pricei* the process is rounded rather than straight caudally. The configuration of the pubic boot identified as autapomorphic by Rauhut (2003) is also present in *H. ischigualastensis* (Langer & Benton 2006).



FIGURE 1. *Staurikosaurus pricei*, skeletal reconstruction, (based upon MCZ 1669, holotype), depicting the preserved bones. After Novas (1997). Scale bar = 20 cm.

Description and comparisons

Mandible and dentition. Both mandibles are preserved but are broken in the cranial region of the dentary in such a way that the symphysis is not preserved (Figs 2–4). There is some deformation in the region of the mandibular fossa in both mandibles; the presence of this deformation means that it is not possible to identify the coronoid. Some fragments of teeth are preserved *in situ*, but few of them are sufficiently well-preserved to merit description (Fig. 4c).

Dentary. The dentary is elongate and forms half of the length of the mandible (Figs 2a–d, 3a–d). The rostralmost border of the left ramus forms an obtuse angle (approximately 135°) with its ventral margin. Laterally, the rostral quarter of the left dentary is dorsoventrally shallower than its caudal part, and bears a number of faint vascular foramina (Fig. 2a–b). The rostralmost foramina are positioned at the mid-height of the dentary; more caudally, the foramina are positioned nearer to the tooth row than to the ventral margin of the bone. In the dorsomedial region of the dentary, immediately below the tooth row, there is a rostrocaudally oriented furrow that extends from the level of the second to the ninth preserved tooth positions (Fig. 2c–d). In ventral view, the dentary and the splenial of the left mandibular ramus have been separated from one another by the infilling of the mandibular canal with sediment (Fig. 3c–d). In the right ramus, the dentary is closely articulated with the splenial bone in such a way that these bones can only be distinguished from each other by a ventromedial sulcus (Fig. 4a). This latter extends from a faint medioventral excavation close to the rostral tip of the mandible to the caudal extremity of the splenial and dentary. The rostral contact between these bones is not clear. The caudal region of the dentary is not well-preserved in either of the mandibles and the nature of the articulation between the dentary and surangular cannot be clearly recognised because the material is badly distorted (Figs 2a–b, 3a–b).

Splenial. The splenials are completely exposed on the medial surface of both mandibular rami (Figs 2c–d, 3a–d, 4a). Their dorsoventral height is slightly less than that of the dentary, but ventrally they are similar to the dentary in transverse width. The splenial is closely articulated with the dentary along its rostrocaudal length (Figs 3c–d, 4a). The mylohyoid foramen reported in other dinosaurs (Rauhut 2003) is not seen in the splenials

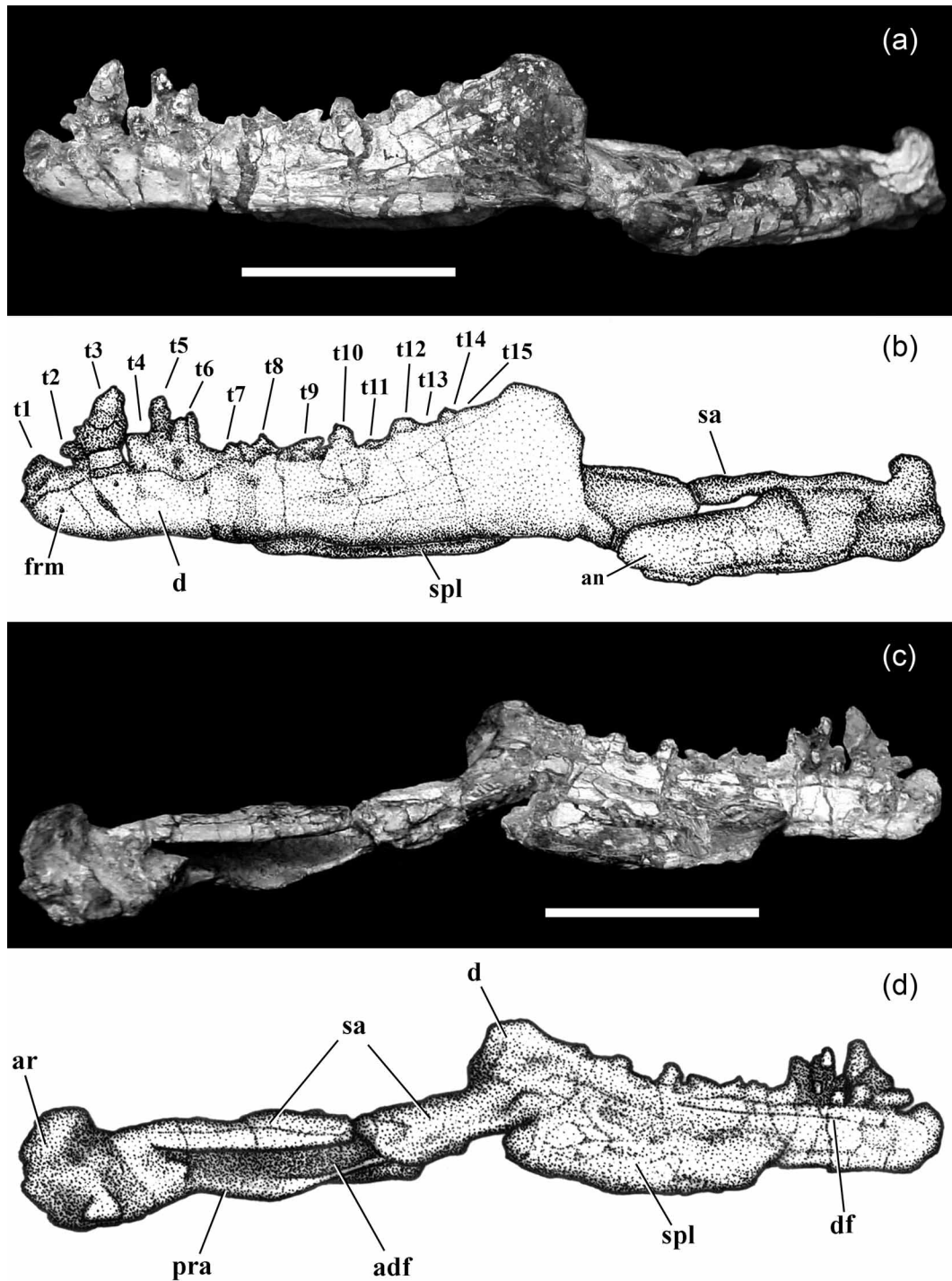


FIGURE 2. Photographs and drawings of the left mandibular ramus in lateral (a, b) and medial (c, d) views. Abbreviations: **adf**, adductor fossa; **an**, angular; **ar**, articular; **d**, dentary; **df**, dentary furrow; **frm**, foramen; **pra**, prearticular; **sa**, surangular; **spl**, splenial; **t1–t15**, preserved teeth or fragments of teeth numbered sequentially beginning at the rostral end of the dentary. Scale bar = 4 cm.

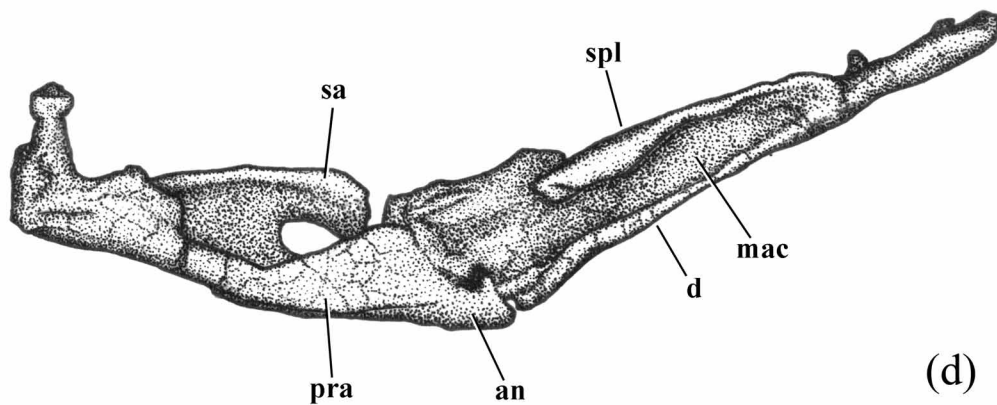
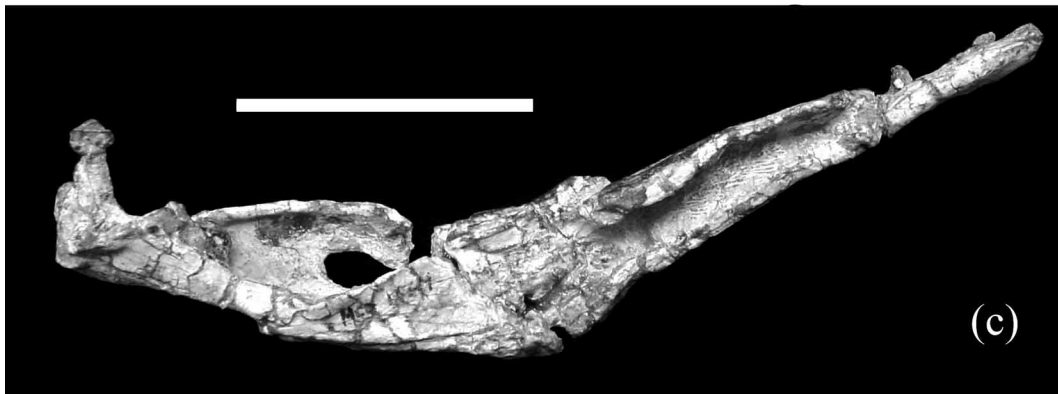
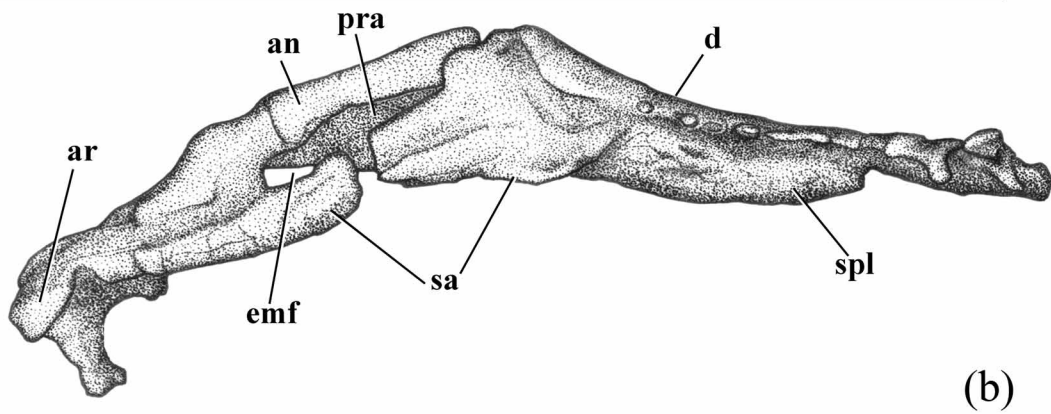


FIGURE 3. Photographs and drawings of the left mandibular ramus in dorsal (a, b) and ventral (c, d) views. Abbreviations: **an**, angular; **ar**, articular; **d**, dentary; **emf**, external mandibular fenestra; **mac**, mandibular canal; **pra**, prearticular; **sa**, surangular; **spl**, splenial. Scale bar = 6 cm.

of *S. pricei*, as preserved. The caudalmost portion of the right splenial possesses a caudal projection that forms the rostroventral wall of the mandibular foramen (Fig. 4a). Moreover, caudally this bone is offset from the dislocated angular by a break that prevents an accurate examination of the articulation between these two elements (Figs 2a–b; 4a). In summary, it is not possible with the material at hand to confirm whether the caudal end of the splenial is straight, concave or convex, or if it forms a sliding joint with the angular.

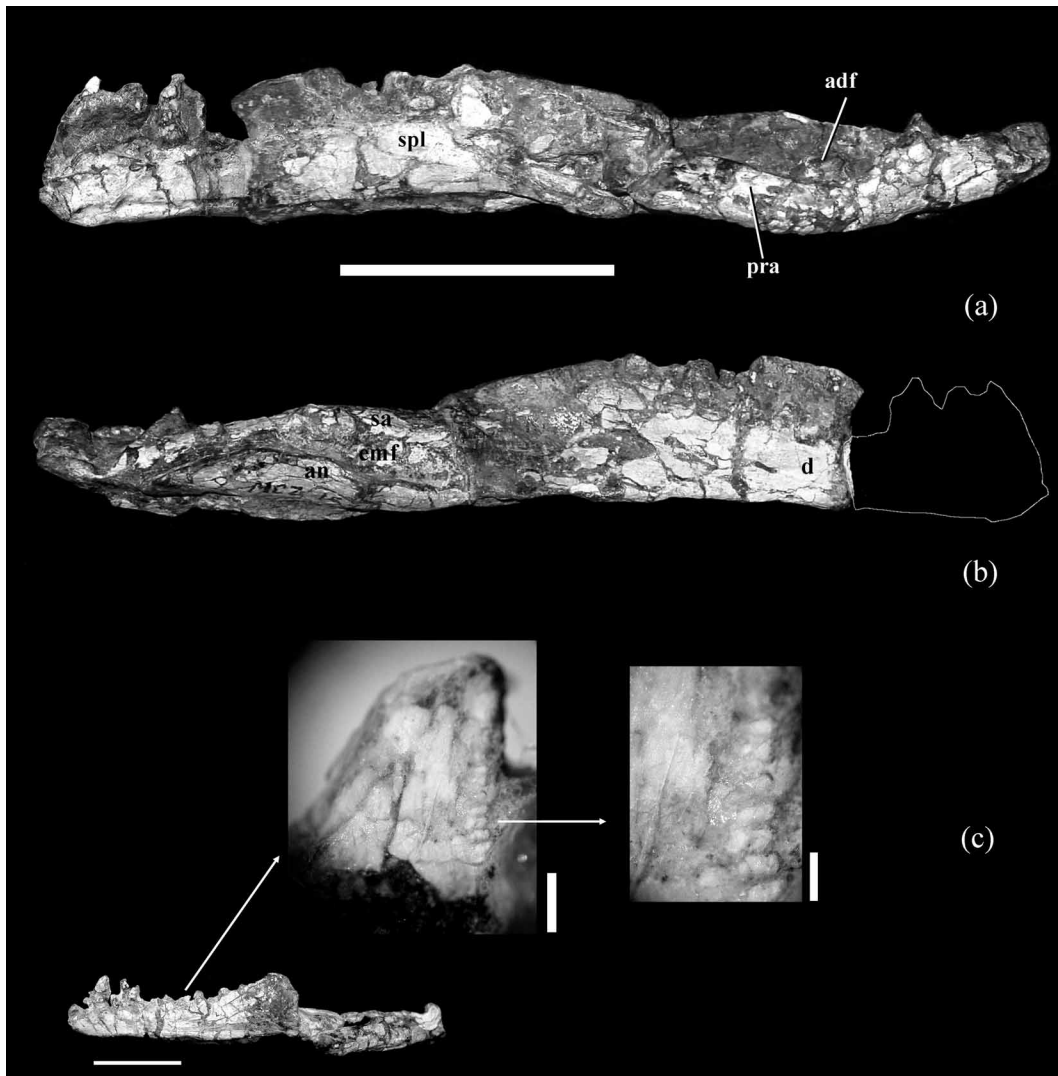


FIGURE 4. Photographs of the right mandibular ramus in medial (a) and lateral (b) views. Photographs of the left mandibular ramus in lateral view (c) demonstrating the morphology of the 8th tooth and details of the serrated carina. Abbreviations: **adf**, adductor fossa; **an**, angular; **d**, dentary; **emf**, external mandibular fenestra; **pra**, prearticular; **sa**, surangular; **spl**, splenial. Scale bar for (a–b) = 6 cm. Scale bars for (c) = 4 cm for mandible, 5 mm for the tooth, and 1 mm for the details of tooth serrations.

Surangular. As a result of post-mortem deformation, the caudal region of the left mandible is rotated inwards approximately 90° along its rostrocaudal axis, in such a way that the lateral and medial surfaces of the surangular are twisted to face dorsally and ventrally, respectively (Figs 2a–d, 3a–b). Despite such deformation, it is clear that the surangular is elongated and dorsoventrally deeper at its rostral end than in its middle portion, although the depth of the surangular at its rostral end may have been enhanced by the presence of an indistinguishable coronoid element (Fig. 3a–b). The rostral end of the surangular presumably articulated with the caudal portion of the dentary, but the form of the articulation between them cannot be accurately described because of the distortion of the material (Figs 2–3, 4b). The caudal extremity of the surangular bears a strong upward curvature; together with the articular, this forms the glenoid fossa for articulation with the

quadrate (Figs 3a–b, 4b). The surangular also forms the entire dorsal wall of the external mandibular fenestra, which is elliptical (with the long-axis of the ellipse oriented rostrocaudally) and extends for half of the postdentary length of the jaw (Fig. 3a–b). In the right mandible, the external mandibular fossa has been obliterated by the downward dislocation of the surangular, which, as a result, is in close contact with the dorsal margin of the angular (Fig. 4b).

Angular. In the right mandible, the angular has rotated outwards as a result of post-depositional deformation in such a way that its lateral surface is somewhat ventrally oriented, and in close contact with the ventral margin of the surangular (Fig. 4b). In the left ramus, as mentioned above, the angular has been rotated inwards. Rostrally, the angular is presumed to have articulated with the caudal ends of the splenial and dentary. However, due to the aforementioned post-depositional deformation the rostral and caudal ends of the angular, including the articulations with other mandibular bones, cannot be accurately described (Figs 2a–b, 4a–b). The angular is elongated, higher caudally than rostrally and mediolaterally compressed (Figs 2a–b, 3a–b, 4b), but in the left ramus its shaft is more rounded in dorsal view (Fig. 3a–b).

Prearticular. The right and left prearticular bones are very prominent and elongate, and extend along the entire postdentary region of the mandible (Figs 2c–d, 3c–d, 4a). In the left ramus, the prearticular has also been rotated inwards, resulting in the rostrolateral surface of the bone facing ventrally (Fig. 3c–d). The main axis of the prearticular is curved along its length, with the rostral and caudal extremities positioned more dorsally and being deeper than the central part of the bone (Fig. 3c–d, 4a). In the left prearticular, the rostral end is dorsoventrally expanded, but the anatomy of its articulation with other elements cannot be assessed. The caudal end is less broad mediolaterally than the rostral end, and articulates with the ventral surface of the articular.

Articular. This bone is not clearly distinguishable in either mandibular ramus because of post-depositional deformation. Colbert (1970) noted that the only characteristics that can be inferred from the preserved material are the presence of a prominent retroarticular process and a broad glenoid fossa (Figs 2–3). In the left mandible, a stout “process” projects from the medial region of the articular-surangular articulation (Fig. 3). This is probably an artifact, and the configuration of the caudal extremity of the mandible is not different to that seen in *H. ischigualastensis* (Serenó & Novas 1993)

Dentition. The left dentary bears evidence of at least fifteen teeth (Fig. 2a–b). The tooth row begins at the rostral extremity of the dentary and ends near to its caudal margin. The rostrocaudally oriented base of the crown of the first tooth is 7 mm long and 4 mm wide, resulting in an elliptical cross-section. As in the more caudal preserved teeth, the crown is labiolingually compressed and the labial and lingual surfaces are equally convex. The third tooth is broken into two pieces that are separated by a layer of sediment. The base of the crown (beneath the break) is 6.5 mm long and 4 mm high. The apex of the crown is positioned 8 mm above the break, so the exposed part of this tooth should be 12 mm high. The crown is slightly recurved, pointed apically, and transversely compressed. The eighth tooth bears serrations (Figs 2a–b, 4c), which compare well with the general pattern of serrations seen amongst theropod dinosaurs. The chisel-like serrations are located on the distal carina and spaced at approximately 2 serrations per millimetre (Fig. 4c). There is no evidence of blood grooves or striated enamel.

Comments. The dentary of *H. ischigualastensis*, generally considered the sister taxon of *S. pricei*, is elongate, deeper at its caudal end than at its rostral end, with several foramina at the mid-height of the bone, and is slightly upturned in the rostradorsal region (Serenó & Novas 1993). This morphology is similar to that seen in some basal theropods, including *Coelophysis bauri* Cope, 1889, *Dilophosaurus wetherilli* (Welles, 1954), *Syntarsus rhodesiensis* Raath, 1969, and *Ceratosaurus nasicornis* Marsh, 1884 (Gilmore 1920; Welles 1984; Colbert 1989; Rowe & Gauthier 1990; Tykoski & Rowe 2004). By contrast, in *S. pricei* foramina are only visible on the rostral quarter of the dentary, which is not upturned (Fig. 2a–b). Additionally, the mandible of *S. pricei* differs from those of basal sauropodomorphs and *Saturnalia tupiniquim* because in those taxa the mandibular length is less than 50% of the length of the femur (Benton *et al.* 2000), the dentary is downturned at its rostral end (Galton 1990; Galton & Upchurch 2004), and a longitudinal crest is present on its lateral surface (Yates 2003a). An additional character observed in neotheropods and in some sauropodomorphs

(Yates 2003a) is the presence of a foramen near the ventral margin of the splenial, the mylohyoid foramen of Currie & Zhao (1993; see also Rauhut 2003; Yates 2003a, 2007a, b; Langer & Benton 2006). An equivalent foramen is absent in *S. pricei* (Figs 2c–d, 4a), *Eoraptor lunensis* Sereno, Forster, Rogers & Monetta, 1993 (PVSJ 512; Rauhut 2003), and basal ornithischians (Langer & Benton 2006). The holotype of *Ischisaurus cattoi* Reig, 1963 (MACN 18.060), a species considered a junior synonym of *H. ischigualastensis* (Novas 1992, 1993), also lacks this foramen, suggesting that its presence is a eusaurischian feature. However, in basal sauropodomorphs, e.g. *Saturnalia tupiniquim*, *Thecodontosaurus antiquus* Morris, 1843, and *Pantydraco caducus* (Yates, 2003a) (Langer *et al.* 1999; Benton *et al.* 2000; Yates 2003a), the poor preservation of the mandibles does not allow the assessment of this character. In addition, comparisons with *Eoraptor lunensis* should be treated with caution, because the holotype of this species may represent a juvenile individual (Bonaparte *et al.* 2007; but see Sereno *et al.* 1993).

Gauthier (1986) proposed two synapomorphies of Theropoda based on the anatomy of the mandible: 1) reduction of the overlap area between the dentary and postdentary bones, resulting in an increased degree of mobility between them; 2) rostrocaudal shortening of the mandibular symphysis. In *S. pricei*, although the caudal region of the dentary is not well preserved, there is no evidence of a caudal extension of the dentary as apparently occurs in *H. ischigualastensis* (Sereno & Novas 1993). Therefore, the first of these proposed synapomorphies appears to be present in the species described here. (Figs 2a–b, 4a). The second cannot be evaluated since the symphyseal region is not preserved. Sereno & Novas (1993: 471) redefined the former character as the ‘presence of a well-developed intramandibular joint’, focusing on the anatomy of the articulations between the dentary and surangular above the external mandibular fenestra and between the splenial and angular below the fenestra (‘The splenial-angular articulation is developed between a tongue-shaped posterior process of the splenial and a hook-shaped anterior process of the angular’; Sereno & Novas 1993: 471), which were both presumed to be sliding joints. Sereno & Novas (1993) suggested that this character is present in *H. ischigualastensis*, in some ceratosaurs including *Ceratops nasicornis* and *Carnotaurus sastrei* Bonaparte, 1985, and in *S. pricei*. However, in *S. pricei* reexamination of the material demonstrates that the articulations between the dentary and surangular and between the dentary and articular are not sufficiently well-preserved (Figs 2a–b, 4b) to confirm with confidence whether the morphology of these articulations is similar to that of *H. ischigualastensis*. Moreover, Sereno & Novas (1993) and Sereno (1999) have claimed that the intramandibular joints of Neotheropoda (*sensu* Sereno 1998) and Herrerasauridae are distinctly constructed, because in the former the splenial is concave and the angular convex while in the latter the opposite condition is observed. This difference has led some authors to consider the presence of the intramandibular joint found in these two clades as possibly non-homologous (Holtz 2000; Fraser *et al.* 2002; Langer 2004). However, exact morphological similarity between two structures is not a prerequisite for the erection of an *a priori* hypothesis of homology (Stevens 1984; de Pinna 1991). If the most parsimonious cladogram(s) derived from cladistic analysis supports the hypothesis that neotheropods and herrerasaurids are closely related, there is no convincing reason to consider that the intramandibular joint did not appear once and was subsequently modified independently in each clade. In any case, the condition observed in *H. ischigualastensis* cannot be recognized as the general condition for all herrerasaurids, because this morphology cannot be confirmed for *S. pricei*.

With regard to the dentition, 16 dentary teeth were reported for *H. ischigualastensis* (Sereno & Novas 1993), with the rostralmost tooth being somewhat procumbent. Both conditions are very similar to that of *S. pricei*, in which the total estimated number of teeth is 15 (Fig. 2a–b). The dentary of *Pisanosaurus mertii* Casamiquela, 1967 (PVL 2577) has 15 preserved teeth (Norman *et al.* 2004a; Irmis *et al.* 2007b). In *Saturnalia tupiniquim* there are 17 mandibular tooth positions (Langer & Benton 2006). In other basal sauropodomorphs the number of dentary teeth is greater with 22 in *Plateosaurus engelhardti* (Meyer, 1837), 22–27 in *Plateosaurus longiceps* Jaekel, 1914, and 20 or 21 in *Thecodontosaurus antiquus* (Galton 1984, 1990, 2001a; Benton *et al.* 2000; Galton & Upchurch 2004). Moreover, in several sauropodomorphs the first dentary tooth is inset caudal to the rostral tip of the mandible by the space of one tooth (Yates & Kitching 2003; Upchurch *et al.* 2007); this differs from the condition in *S. pricei* and other dinosaurs. In neotheropods,

the number of dentary teeth varies amongst coelophysoids: *Coelophysis bauri* has 27 while *Dilophosaurus wetherilli* has 17–18 (Tykoski & Rowe 2004). Basal tetanurans have 14–18 dentary teeth (Holtz *et al.* 2004). However, intraspecific and ontogenetic variation occurs in the tooth count of several archosaur taxa, including dinosaurs (Madsen 1976; Colbert 1989; Varrichio 1997; Rauhut & Fehner 2005). Within dinosaurs, the general dental morphology seen in *S. pricei* (Figs 2, 4) is typical of theropods (Currie *et al.* 1990; Farlow *et al.* 1991; Sander 1997), also occurring in *H. ischigualastensis* (Sereno & Novas 1993) and *Eoraptor lunensis* (PVSJ 512; Sereno *et al.* 1993). However, it is quite different from those of the herbivorous/omnivorous taxa (i.e. Sauropodomorpha and Ornithischia), in which the tooth crown is not recurved and the denticles are relatively larger and set at an angle of 45° to the tooth margin (Galton 1985b; Benton *et al.* 2000; Yates 2003a, 2007a, b; Yates & Kitching 2003; Galton & Upchurch 2004). It is generally thought that the carnivorous dental morphology is plesiomorphic for dinosaurs, so that it cannot be used as an indication of phylogenetic relationships within the clade (Sander 1997; Ray & Chinsamy 2002). However, the dental morphology of the taxa presumed to represent immediate outgroups to Dinosauria is not well known (Arcucci 1987, 1997; Sereno & Arcucci 1993, 1994; Abler 1997). In addition, recent phylogenetic schemes have positioned *Silesaurus opolensis* Dzik, 2003 (Late Triassic, Poland) as a basal dinosauriform close to Dinosauria (Ezcurra 2006; Langer & Benton 2006; Irmis *et al.* 2007a). The dentary of this species contains approximately 12 omnivorous/herbivorous teeth (Dzik 2003). Thus, the hypothesis that a carnivorous dentition is apomorphic within dinosaurs cannot be dismissed on the basis of available evidence (see also Barrett 2000).

Vertebral column

Cervical series. The holotype of *S. pricei* has 21 presacral vertebrae preserved, the last 18 of which are articulated, comprising the entire dorsal series and part of the cervical column. Although some basal dinosaurs, such as *Syntarsus rhodesiensis* (see Tykoski & Rowe 2004) and *Plateosaurus longiceps* (Galton 2001a; Galton & Upchurch 2004), are thought to have possessed 25 presacrals (10 cervical and 15 dorsal vertebrae), we follow Galton (1977) in assuming 24 as the original number of presacrals for *S. pricei* (9 cervical and 15 dorsal vertebrae), as Novas (1993) did for *H. ischigualastensis*. However, this count must be regarded as tentative because the point of transition from cervical to dorsal vertebrae is not clear. Because the presumed 15 dorsal vertebrae are articulated, the remaining six presacrals are regarded as cervical vertebrae. The atlas and axis are not preserved; it appears that only one postaxial vertebra is missing from the presacral column. Galton (1977) suggested that the six preserved cervical vertebrae (Figs 5–8) should be identified as 3–5 and 7–9. However the vertebra identified by Galton (1977) as the third cervical is here identified as the fourth cervical (Figs 5–7), because it is more similar to the fourth cervical of *H. ischigualastensis* (Sereno & Novas 1993) in possessing both pre- and postzygodiapophyseal laminae (*sensu* Wilson 1999). Therefore, the six preserved cervicals of the *S. pricei* holotype are here identified as the fourth to ninth. Only the presumed fourth cervical is isolated (Figs 5–7), and the remaining cervicals are located in a block that also contains most of the dorsal series and a proximal piece of the right femur (Fig. 8).

The spool-shaped and amphicoelous fourth centrum is longer and lower than the dorsal centra, lacks pleurocoels, and bears a ventral keel along its craniocaudal midline (Figs 5–6). The parapophyses are short and rounded processes placed in the ventrolateral right and left margins of the cranial articular surface (Figs 5, 6a–b), which in cranial view has a subrectangular outline and is slightly concave (Fig. 7a–b). The caudal articular facet is obliquely oriented (Fig. 5), rounded, and more strongly concave than the cranial surface (Fig. 7). The preserved neural arch is approximately twice as high as the centrum (Figs 5, 7). The right transverse process is triangular in dorsal view (the process has a craniocaudally broad base and the cranial and caudal margins of the process converge upon one another distally: Fig. 6) and is positioned more ventrally than the pre- and postzygapophyses, covering part of the centrum in left lateral view (Fig. 5a–b). The cranial margin of the transverse process forms a bony blade that merges with the laterodistal portion of the prezygapophysis (the prezygodiapophyseal lamina, Figs 5a–b, 6c–d, 7a–b). The postzygodiapophyseal lamina emerges from the

midlength of the base of the transverse process, reaching the dorsolateral margin of the postzygapophysis (Fig. 5a–b). On the left side, the postzygodiapophyseal lamina delimits two shallow fossae (Fig. 5a–b: caf, crf): one caudally located, on the dorsoproximal region of the transverse process and below the postzygapophysis; and another more cranially positioned, behind the prezygapophysis in lateral view. The neural spine is proximally short in lateral view and vertically oriented, but the determination of its exact height is not possible (Fig. 5). The prezygapophysis is elongate and projects far beyond the cranial articular facet. Its distal end is rounded and the articular face is dorsomedially oriented (Figs 5–6). In the ventral region of the prezygapophysis, there is a fossa medially delimited by the ventromedial margin of the prezygapophysis and laterally by the prezygodiapophyseal lamina (Fig. 7a–b). The bases of the right and left prezygapophyses define the margins of a median sulcus positioned immediately cranial to the neural spine (Figs 6c–d, 7a–b). The postzygapophyses are broad processes, the articular facets of which are tall, wide and ventrolaterally oriented (Figs 6c–d, 7c–d). They are set apart by a deep median sulcus, the interpostzygapophyseal sulcus, which is positioned on the caudal margin of the neural spine (Fig. 7d). The caudodorsal margin of the postzygapophysis forms a bony blade that ends dorsally in a short but thick process here interpreted as the epiphysis (Figs 6c–d, 7c–d: ep). Cranially, the subcircular neural canal has a height that is half of that of the centrum (Fig. 7a–b).

The more caudal cervicals are encased within a block bounded by matrix obscuring details of their anatomy (Fig. 8). The centra do not seem to be significantly shorter than that of the fourth cervical, and cranial and caudal centrodiapophyseal laminae are present. The parapophyses cannot be identified. The transverse processes are distally short and slightly dorsally directed. Because of the fragmentary condition of the material, the presence of epiphyses on the caudal cervical vertebrae cannot be confirmed.

Dorsal vertebrae. Galton (1977) identified 14 dorsal vertebrae plus a fragment of a neural arch of a 15th element (Figs 8, 9, 10a–b). Eight of these vertebrae are articulated (Fig. 8), three are isolated from the remaining vertebrae but are articulated with one another (Fig. 9a), and four are associated with the ilium (Fig. 10a–b).

The amphicoelous centra are craniocaudally short relative to the height of the vertebra (centrum length is approximately one third of the vertebra height) and laterally compressed (Figs 8–10), with the cranial and caudal articular facets parallel to one another in lateral view (Fig. 10a). The prominent transverse processes are broader at their bases than at their apices, dorsocaudally directed, and subtriangular in cross-section (Figs 8, 10a–b). Ventral to the transverse process, there are two bony buttresses diverging towards the centrum that delimit three adjacent fossae (see Welles 1984; Fig. 10a–b). The cranialmost buttress is the cranial centrodiapophyseal lamina that forms the cranial margin of the infradiapophyseal fossa and the caudal margin of the infraprezygapophyseal fossa (Makovicky 1997). The caudalmost buttress is the caudal centrodiapophyseal lamina, which delimits the caudal margin of the infradiapophyseal fossa and the cranial margin of the infrapostzygapophyseal fossa. The neural spines of the dorsal vertebrae are tall with slightly concave cranial and caudal margins, in such a way that the extremities of the spines appear to be broader than the intermediate region (Fig. 10a–b). Pre- and postzygapophyses are not sufficiently well-preserved to present a detailed description. Novas (1993: 415) mentioned the presence of a ‘dorsoventrally deep (5 mm) and transversely robust (7 mm)’ process divided into dorsal and ventral parts by a craniocaudal crest at the level of the postzygapophysis in the eighth preserved dorsal vertebrae, and interpreted this structure as a hyposphene (Fig. 10c–d). It is difficult to state with certainty if this structure represents part of a hyposphene associated with a postzygapophysis, because the bony plate positioned ventral to the ‘robust process’ may represent the postzygapophysis itself. The lack of additional evidence from the remaining dorsal vertebrae makes the identification of a hyposphene doubtful.

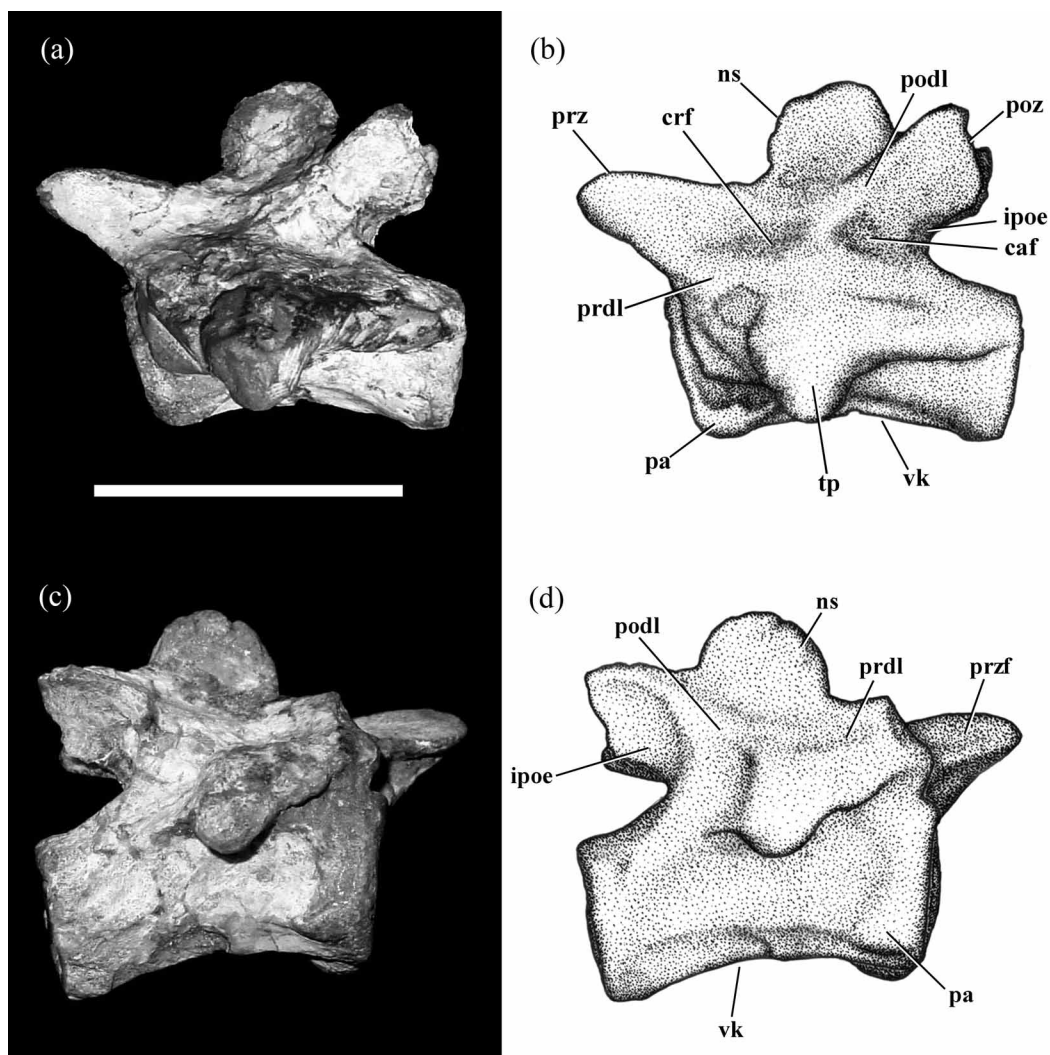


FIGURE 5. Photographs and drawings of the fourth cervical vertebra in left (a–b) and right (c–d) lateral views. Abbreviations: **caf**, caudal fossa; **crf**, cranial fossa; **ipoe**, infrapostzygapophyseal excavation; **ns**, neural spine; **pa**, parapophysis; **podl**, postzygodiapophyseal lamina; **poz**, postzygapophysis; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **przf**, prezygapophysis articular facet; **tp**, transverse process; **vk**, median ventral keel. Scale bar = 3 cm.

Sacral and caudal vertebrae. The first sacral vertebra is tightly attached to the inner caudal surface of the left ilium, although dislocated from its original position (Fig. 10a–b). The centrum is about 60% longer than that of the last dorsal vertebra, and the cranial articular facet of the first sacral is more strongly concave, higher, and broader than the caudal articular facet. The sacral rib emerges from the dorsal region of the centrum and fuses with the transverse process. The transverse process expands laterally from the neural arch, above the sacral rib (for additional figures, see Colbert 1970; Galton 1977, 1999, 2000a). Both the sacral rib and the transverse process form a robust lateral process, which is transversely wider cranially than caudally, and occupies most of the medial surface of the iliac blade. The neural arch is twice as high as the centrum when measured in the region of the caudal articular facet.

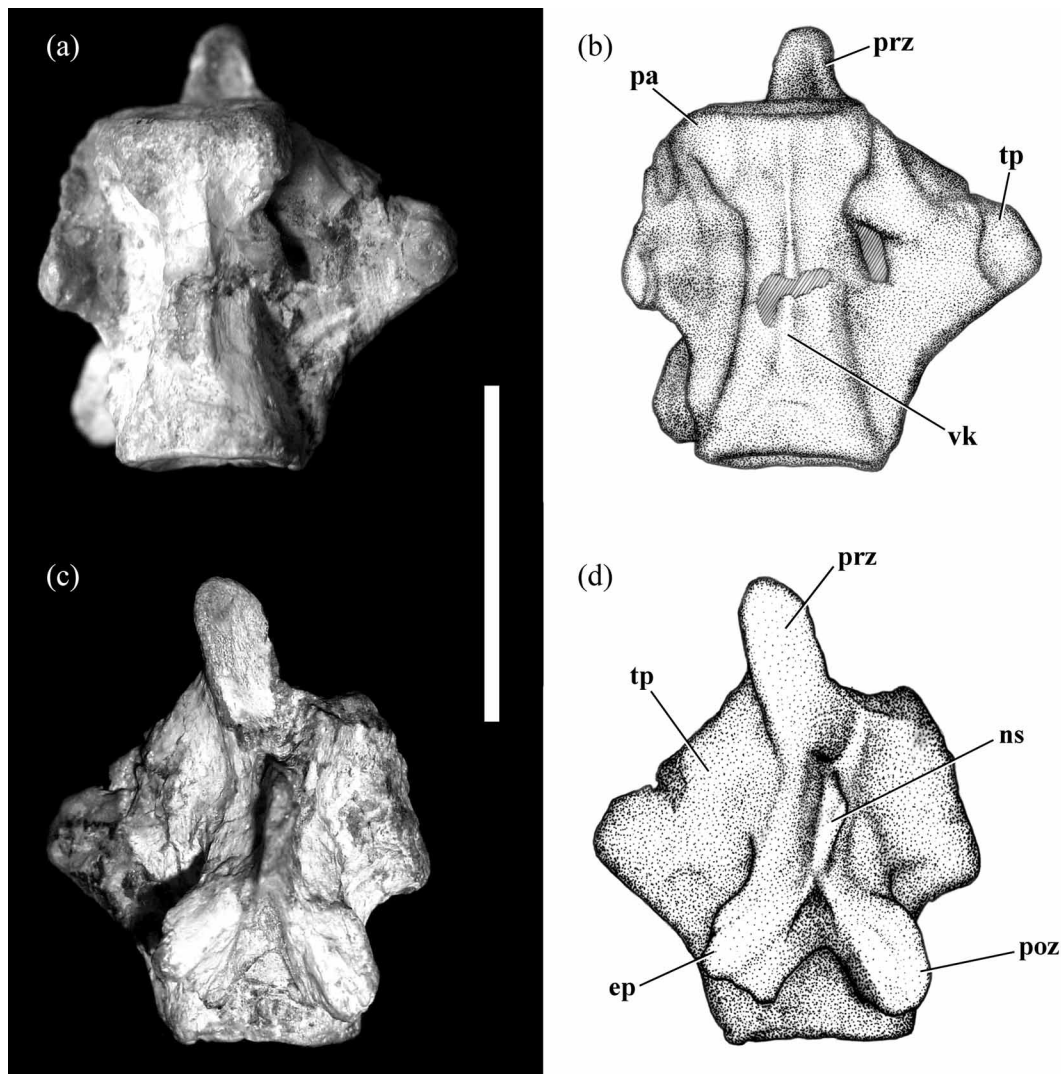


FIGURE 6. Photographs and drawings of the presumed fourth cervical vertebra in ventral (a–b) and dorsal (c–d) views. Abbreviations: **ep**, epiphysis; **ns**, neural spine; **pa**, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process; **vk**, median ventral keel. Scale bar = 3 cm.

The second sacral is nearly complete and isolated (Fig. 11). Its centrum is shorter than that of the preceding vertebra and the cranial and caudal articular facets are similar to each other in size. The lateral process is broader caudally than cranially, the opposite of the preceding vertebra. The distal end of the lateral process bears a subtriangular articular surface for the ilium. The craniodorsal portion of the lateral process has two conspicuous concavities: a deep and more distally positioned one and a shallower more proximally located one (Fig. 11a–b: *lcpl*, *mclp*). The medial concavity is positioned immediately above the lateral concavity and cranial to the cranial margin of the transverse process. The lateral margin of the cranial articular facet of the centrum is set apart from the craniomedial margin of the lateral process by a shallow sulcus (Fig. 11a–b: *crls*). The neural spine is shorter than that of the preceding vertebra and possesses a dorsoventrally extending sulcus on both cranial and caudal surfaces (Fig. 11). The lateral margins of the neural spine extend cranially and caudally to form the spinoprezygapophyseal and spinopostzygapophyseal laminae, respectively. The prezygapophyses are short and their articular faces are dorsomedially oriented. The postzygapophyses are badly damaged and the only observable characteristics are their shortness and the ventrolateral orientation of the articular faces.

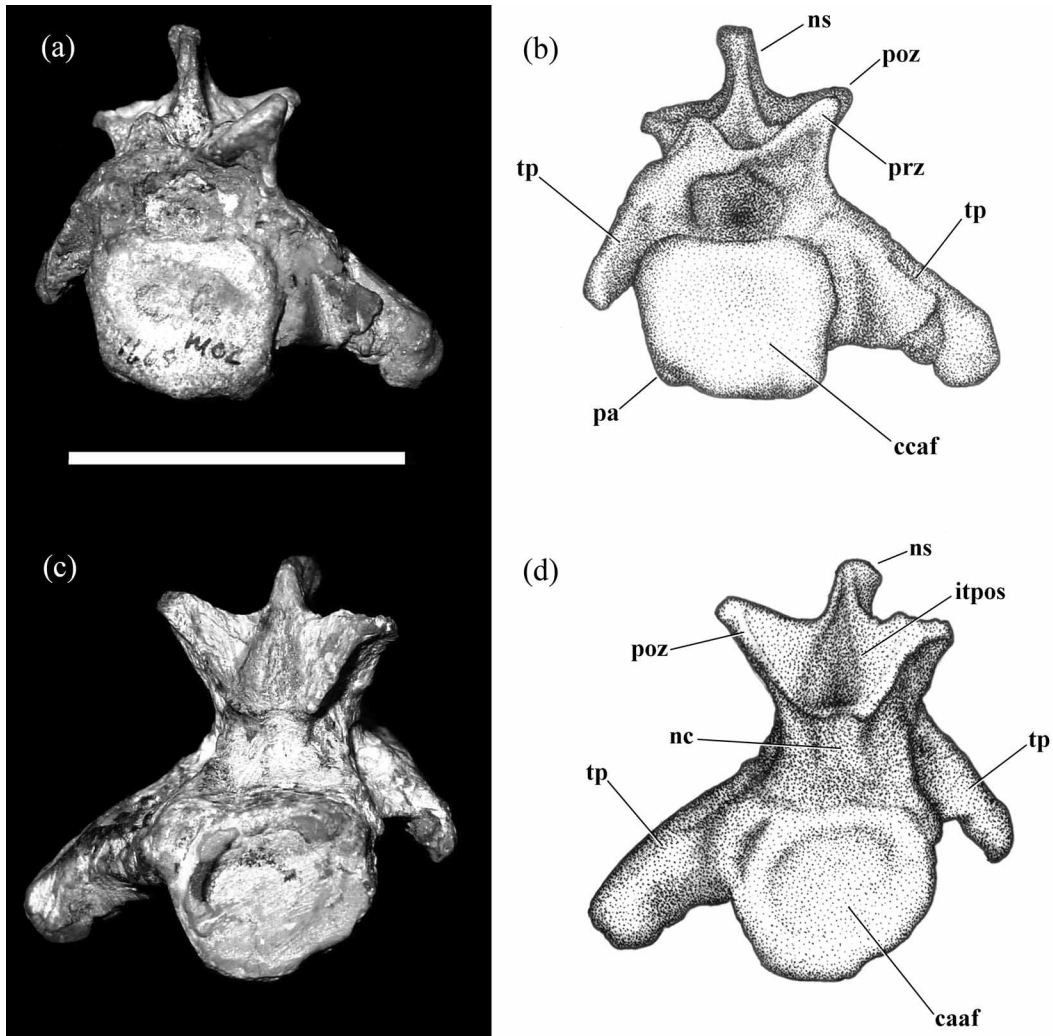


FIGURE 7. Photographs and drawings of the presumed fourth cervical vertebra in cranial (a–b) and caudal (c–d) views. Abbreviations: **caaf**, caudal articular facet of centrum; **ccaf**, cranial articular facet of centrum; **itpos**, interpostzygapophyseal sulcus; **nc**, neural canal; **ns**, neural spine; **pa**, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process. Scale bar = 3 cm.

The subsequent vertebra is subject of controversy in the literature (Colbert 1970; Galton 1977, 2000a), because its identification as either a sacral or a caudal vertebra is debatable. In this work, we identify this bone as the third sacral vertebra (Figs 12–14a), based on the presence of a stout lateral process, absent in caudal vertebrae. The centrum has a caudal articular facet that projects ventrally relative to the cranial articular facet; as a result, this vertebra is probably a caudosacral element. No keel or groove is present on the ventral surface (Fig. 12e–f). On the left side a broad lateral expansion is observable: this expansion is not composed only of sediment as has been previously suggested (see Galton 2000a), although some sediment is encrusted on the bone surface (Figs 12–13). On the right side of this vertebra the lateral expansion is not present but there is a fragment of a dorsoventrally narrow process that derives from the neural arch, which probably represents a remnant of a transverse process (Fig. 14a). Only a piece of the prezygapophysis is preserved, and is distally broad and rounded (Fig. 12a–d).

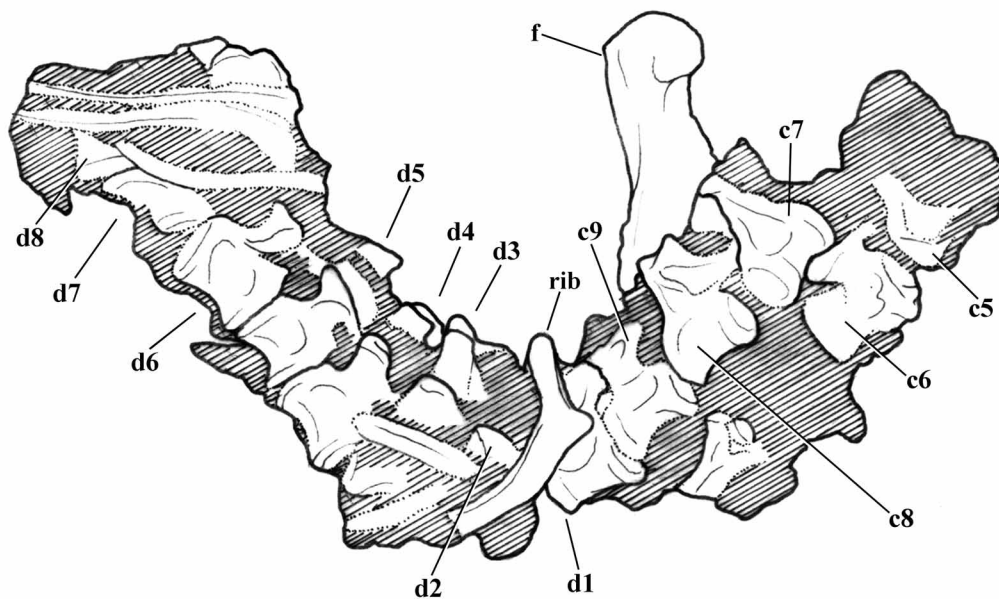
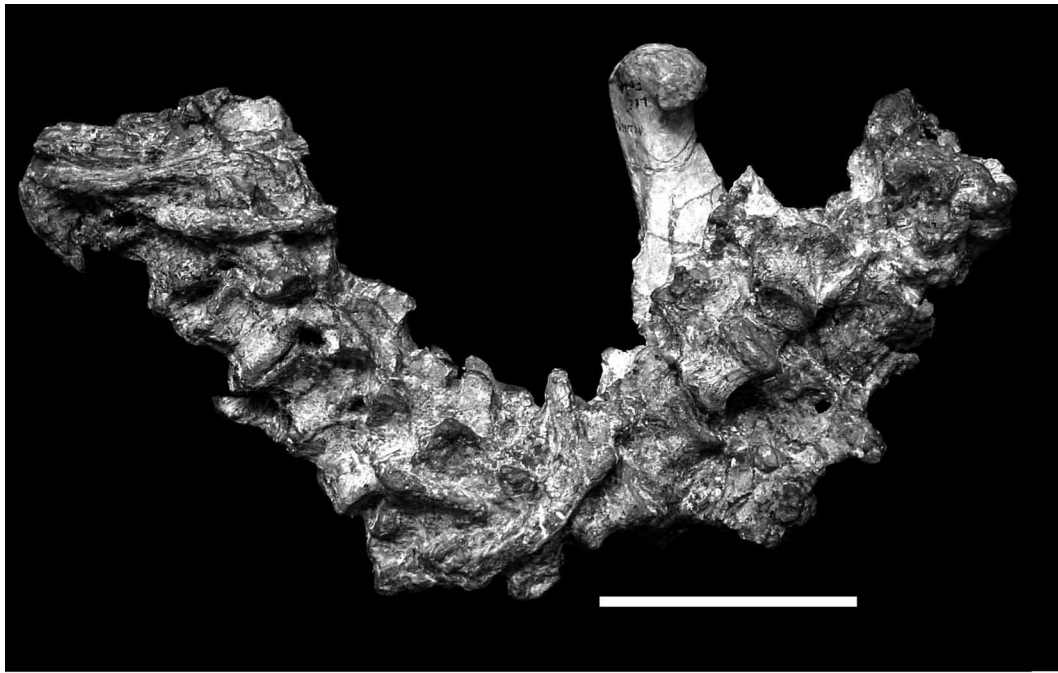


FIGURE 8. Photograph and drawing of cervical and dorsal vertebrae embedded within sediment along with the left femur, in right lateral view. Abbreviations: **c5–c9**, presumed cervical vertebrae 5 to 9; **d1–d8**, dorsal vertebrae 1 to 8; **f**, femur. Scale bar = 8 cm.

The subsequent preserved vertebra was identified as the second caudal by Galton (2000a), but it is here considered the first caudal (Fig. 14b): its centrum is broader than those of the caudal dorsal vertebrae and the neural arch is tall, particularly in the part that comprises the pedicels of the neural canal. As in more distal caudal vertebrae, no keel or groove is observed on the ventral surface of the centrum. The neural spine is broken distally but is clearly dorsally oriented. The prezygapophysis is elongate and subtriangular in lateral view and the postzygapophysis is preserved as a caudally directed process oriented perpendicular to the neural spine, with its articular face directed ventrolaterally. The second to fourth caudals (Figs 15–16a) are morphologically similar to one another with the exception of decreases in their dimensions: in more distal

vertebrae, the centra are shorter and lower and the neural spines tend to be more caudally oriented. Another isolated caudal centrum is preserved (not figured here), and judging from its dimensions, it probably belongs to the proximal region of the caudal series.

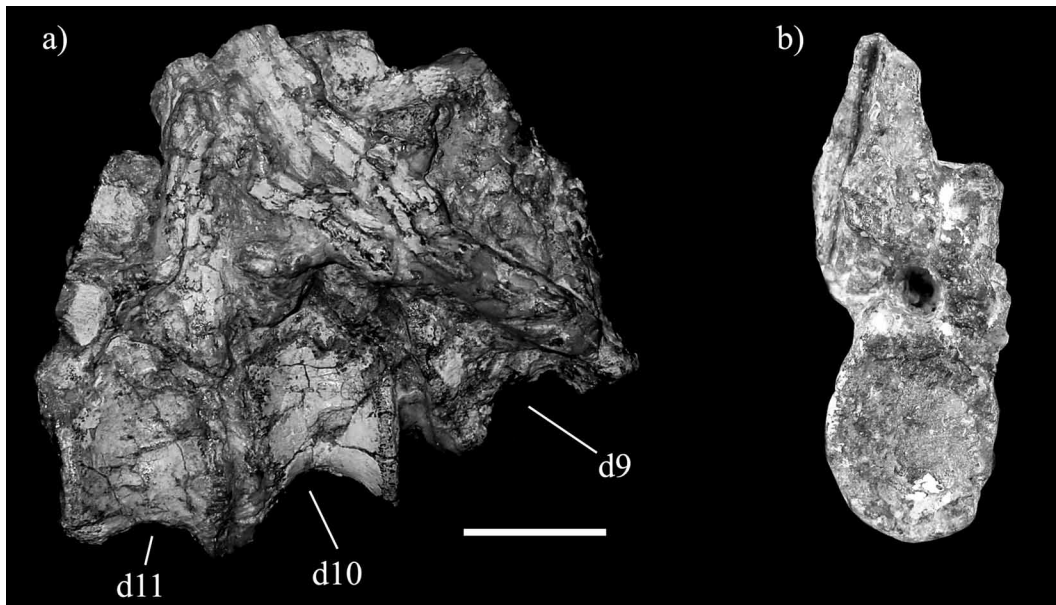


FIGURE 9. Photographs of dorsal vertebrae 9–11 in right lateral view (a) and the centrum of the 12th dorsal vertebra (b) in cranial view. Abbreviations: **d9–d11**, dorsal vertebrae 9 to 11. Scale bar = 2.5 cm.

More caudally, there are six sequences of articulated caudal vertebrae; however, the sequences do not directly articulate with one another (with the exception of the last two sequences). Sequence one (Fig. 16b) comprises two vertebrae, the sixth to seventh preserved caudals; sequence two (Fig. 16c) comprises two vertebrae, the eighth to ninth preserved caudals; sequence three (Fig. 17a–b) includes six vertebrae, the 10th to 15th preserved caudals; sequence four (Fig. 17c–d) contains seven vertebrae, the 16th to 22nd preserved caudals; sequence five (Fig. 18a–b) comprises nine vertebrae (the last one is a fragment that continues in the next sequence), the 23rd to 31st preserved caudals; and sequence six (Fig. 18c–d) contains three vertebrae, the 32nd to 34th preserved caudals.

The vertebrae of the first to third sequences are different from the fourth preserved caudal in that they are longer, much lower, narrower and have a reduced neural arch (Figs 16, 17a–b). In the third sequence, the transverse processes are represented by short lateral expansions located near the cranial articular facet and are only observable until the fifth vertebra of this sequence (Fig. 17a–b). The pre- and postzygapophyses are elongated and overlap slightly more than 30% of the adjacent vertebrae. In the fourth sequence, the centra are somewhat longer and lower than those of sequence three (Fig. 17c–d). The neural arches are even more strongly reduced, both pre- and postzygapophyses are relatively longer (overlapping 50% of the adjacent vertebrae), and transverse processes are absent. The vertebrae of the fifth and sixth sequences are strongly compressed laterally (Fig. 18–19), and have prezygapophyses that are connected to the postzygapophyses of the preceding vertebra by a lamina, resulting in a convex dorsal margin in lateral view.

Comments. The anatomy of the cervical vertebrae is important in the assessment of the phylogenetic position of basal dinosaurs, because this region can contain several potential saurischian synapomorphies. The presence of epipophyses on the postzygapophyses of cranial cervical vertebrae, for instance, was regarded as a synapomorphy of Saurischia by Gauthier (1986), although this structure is also present in basal ornithischians (Santa Luca 1980; Sereno 1991a; Langer & Benton 2006), and in some non-dinosaur archosaurs (Langer & Benton 2006; Nesbitt *et al.* 2007). Sereno *et al.* (1993) and Langer & Benton (2006) considered the presence of epipophyses on mid-caudal cervical vertebrae as a saurischian synapomorphy. The

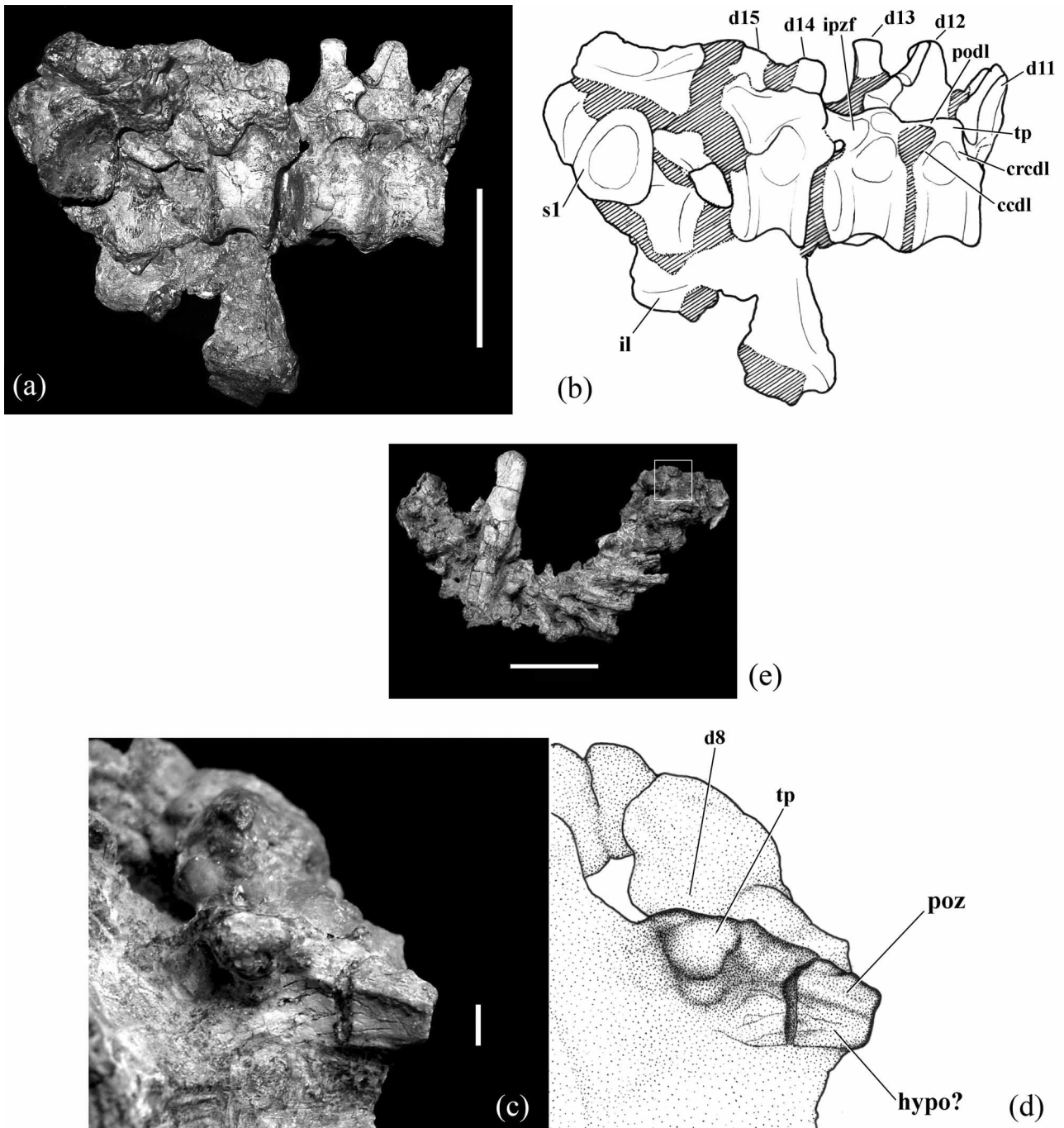


FIGURE 10. Photographs and drawings of the caudal dorsal vertebrae in right lateral view, associated with the first sacral and the left ilium (a–b), and detail of the 8th dorsal vertebra in left lateral view (c–d). The miniature photo (e) marks the region of the block detailed in (c–d) (see also Fig. 8). Abbreviations: **ccdl**, caudal centrodiapophyseal lamina; **crccd**, cranial centrodiapophyseal lamina; **d8**, 8th dorsal vertebra; **d11–d15**, dorsal vertebrae 11 to 15; **hypo?**, doubtful hyposphene; **il**, ilium; **ipzf**, infrapostzygapophyseal fossa; **podl**, postzygodiapophyseal lamina; **poz**, postzygapophysis; **tp**, transverse process; **s1**, first sacral vertebra. Scale bar for (a–b) = 6 cm; (c–d) = 5 mm; miniature = 8 cm.

presence of this character in *S. pricei* is problematic, because although the fourth cervical vertebra of *S. pricei* bears unambiguous epiphyses (Fig. 6c–d), cervical vertebrae 5–9 are not well-preserved and the presence of epiphyses on these vertebrae cannot be confirmed. Some other proposed saurischian synapomorphies, including the presence of pleurocoels in the cervical centra (Gauthier 1986), centra of cervicals 3–6 being longer than the centrum of the axis (Yates 2003a), and the presence of mid-cervical ribs elongated and parallel

to the vertebral column (Sereno 1999) are either not present (the former character) or cannot be verified (the two latter characters) in *S. pricei*. In addition, some of the proposed synapomorphies of Eusaurischia *sensu* Langer 2004 (Sauropodomorpha + Theropoda, excluding Herrerasauridae and *Eoraptor lunensis*) are based on the anatomy of the cervical region. These characters are: 1) the neck comprises more than 40% of the

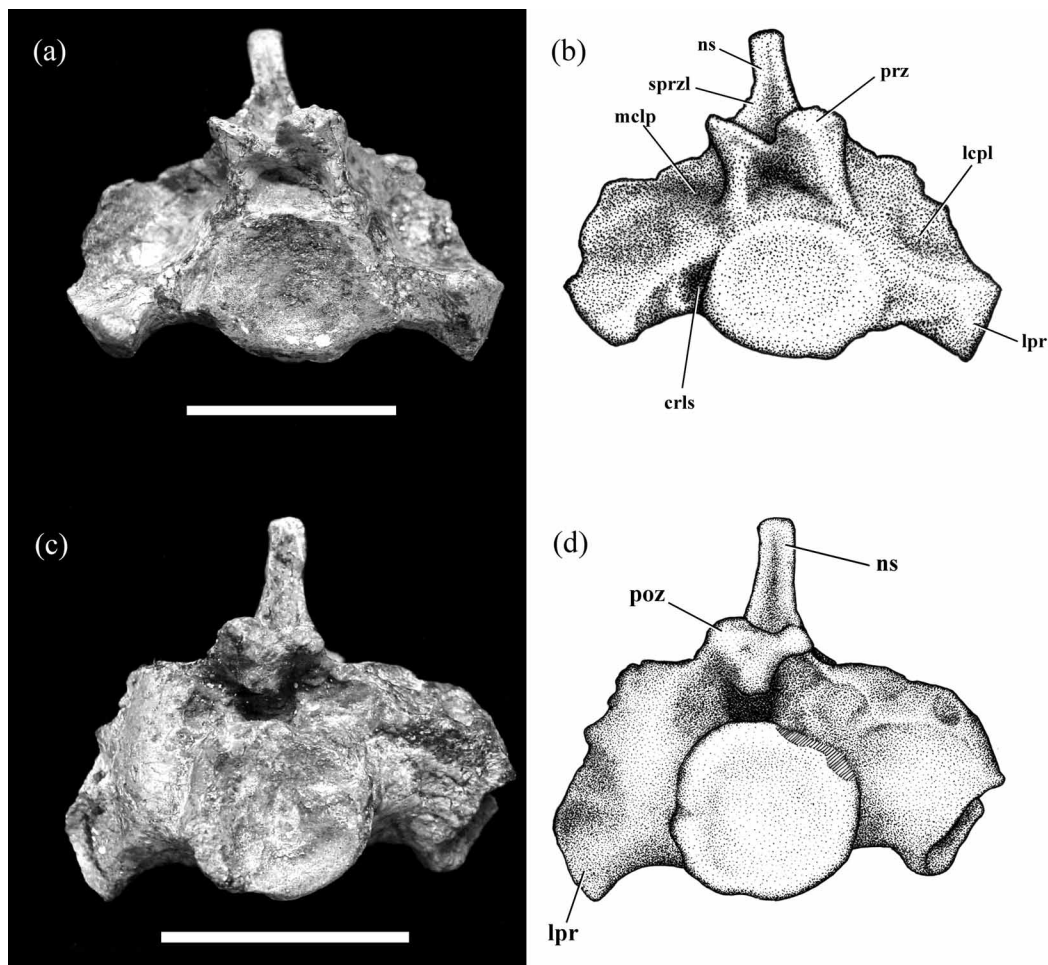


FIGURE 11. Photographs and drawings of the second sacral vertebra in cranial (a–b) and caudal (c–d) views. Abbreviations: **crls**, craniolateral sulcus; **lcpl**, lateral concavity on the lateral process; **lpr**, lateral process; **mclp**, medial concavity on the lateral process; **ns**, neural spine; **prz**, prezygapophysis; **poz**, postzygapophysis; **sprzl**, spinoprezygapophyseal lamina. Scale bars = 4 cm.

presacral segment of the vertebral column (Langer *et al.* 1999); 2) the caudal cervical vertebrae are approximately 35% longer than the cranial dorsal vertebrae (Langer *et al.* 1999); 3) the centra of cervicals 7–9 are longer than the centrum of the axis (Yates 2003a). The first and third characters cannot be scored for *S. pricei*, and the second is absent. These characters are absent in *H. ischigualastensis* (Sereno & Novas 1993).

Several characters of the dorsal vertebrae have been proposed in phylogenetic analyses of basal dinosaurs. Gauthier (1986) considered the presence of an accessory articulation (hyposphene-hypantrum articulation) in the dorsal vertebrae as synapomorphic of Saurischia, and Welles (1984) regarded the presence of the infradiapophyseal laminae as unique for that clade (see also Yates 2003a). The former character (hyposphene-hypantrum articulation) is doubtful in *S. pricei*, but the latter (infradiapophyseal laminae) is present. However, the identification of dinosaur material based on those characters is problematic, since several non-dinosaur archosaurs possess equivalent features (Benton 2004; Nesbitt *et al.* 2007). Novas (1992) proposed two synapomorphies of Herrerasauridae based on the dorsal vertebrae: caudal dorsal centra craniocaudally shortened with a square shape in lateral view, and caudal dorsal and first sacral vertebrae possess robust neural

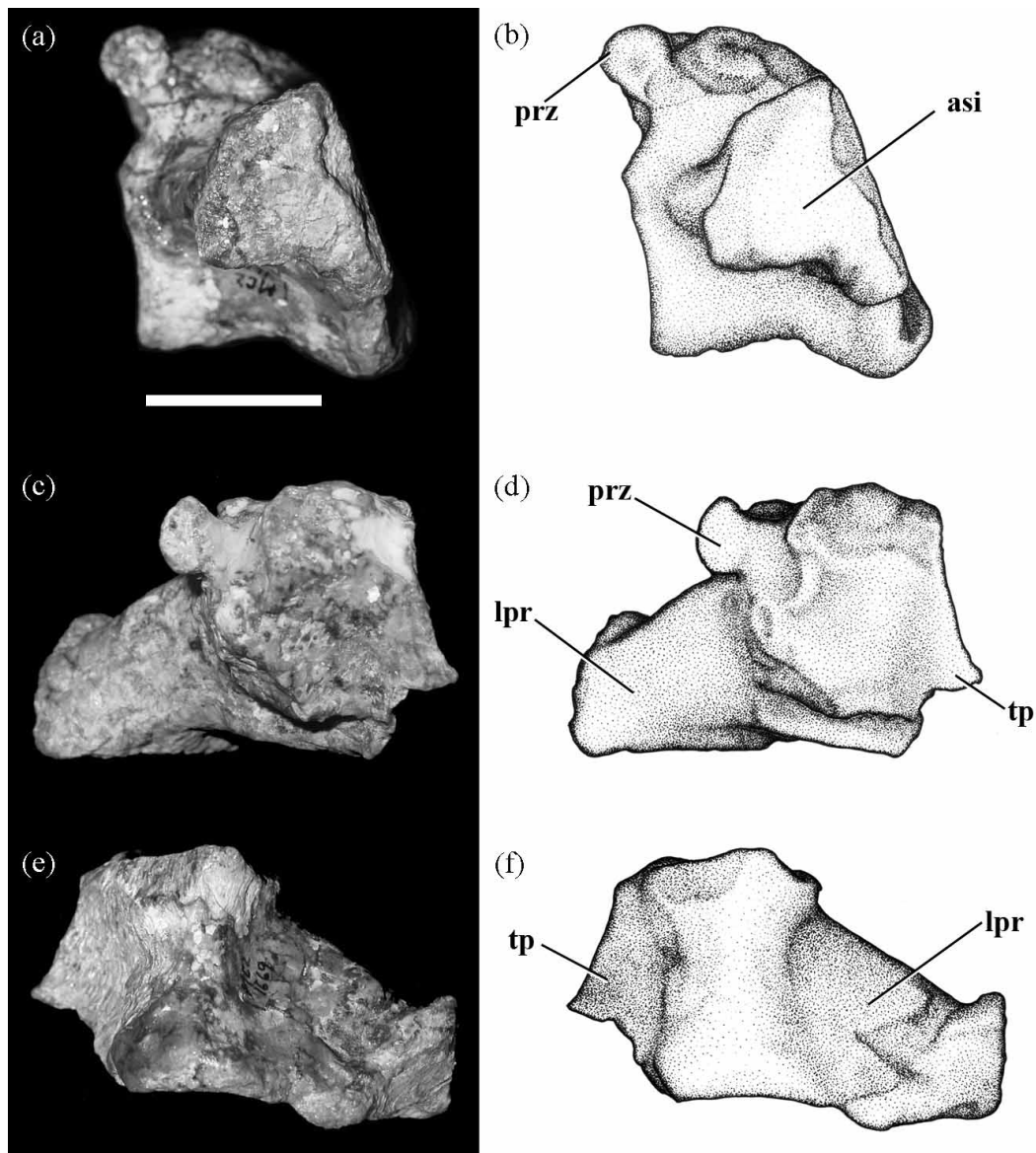


FIGURE 12. Photographs and drawings of the third sacral vertebra in left lateral (a–b), dorsal (c–d) and ventral (e–f) views. Abbreviations: **asi**, articular surface for ilium; **lpr**, lateral process; **prz**, prezygapophysis; **tp**, transverse process. Scale bar = 2 cm.

spines that are axially shortened with a squared shape in cross-section. The former character has been confirmed as an unambiguous synapomorphy of Herrerasauridae by recent phylogenetic studies (Yates 2003a, 2007a, b; Langer & Benton 2006). The neural spines of the caudal dorsal vertebrae are also axially shortened in herrerasaurids, a condition absent in *Eoraptor lunensis* (PVSJ 512), *Saturnalia tupiniquim* (MCP 3844-PV), basal theropods (Tykoski & Rowe 2004) and basal ornithischians (Norman *et al.* 2004a; also *Heterodontosaurus tucki* Crompton & Charig, 1962; see Santa Luca 1980). This supports the suggestion that this character is a synapomorphy of Herrerasauridae (Yates 2003a). The neural spines of the sacral vertebrae of *H. ischigualastensis* (PVL 2566), however, are axially elongate, and not square-shaped in cross section.

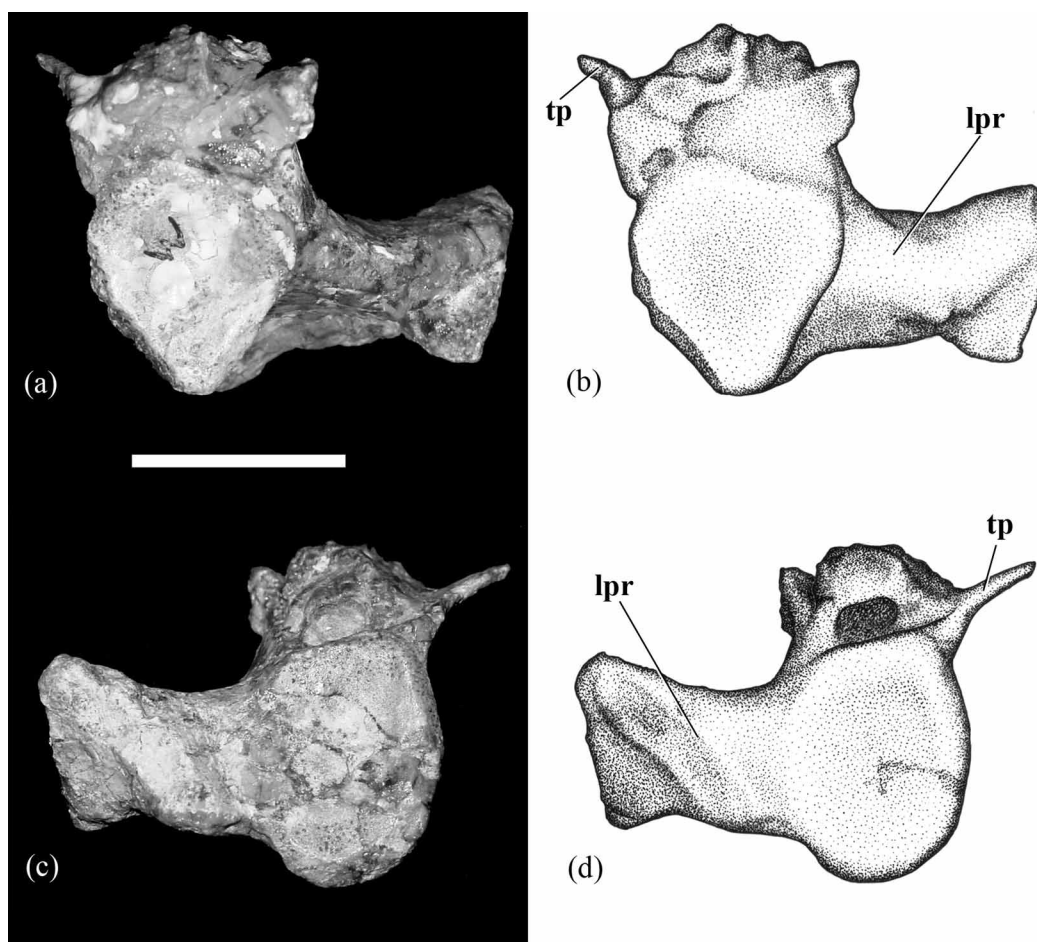


FIGURE 13. Photographs and drawings of the third sacral vertebra in cranial (a–b) and caudal (c–d) views. Abbreviations: **lpr**, lateral process; **tp**, transverse process. Scale bar = 2 cm.

Similarities between *S. pricei* and *H. ischigualastensis* also occur within the sacral series, including the presence of deep sacral ribs, in which the distal expansion of the sacral rib covers more than half of the medial surface of ilium (Langer & Benton 2006). This condition is different from that of dinosauromorphs, including basal dinosaurs, and it has been correctly regarded as a synapomorphy of Herrerasauridae (Novas 1992; Langer & Benton 2006).

Contra to previous studies (Galton 1977, 2000a), *S. pricei* is here regarded as having three sacral vertebrae (Colbert 1970). This assignment is based on the presence of a robust sacral rib on the vertebra previously considered the first caudal (Galton 2000a). Three sacrals are also present in *Eoraptor lunensis* (Sereno *et al.* 1993; Sereno 2007), *Saturnalia tupiniquim* (Langer & Benton 2006), and most basal sauropodomorphs (Sereno 1999; Yates 2003a; Galton & Upchurch 2004). Some of the closest outgroups to Dinosauria, such as *Lagerpeton chanarensis* Romer, 1971, *Marasuchus lilloensis* Sereno & Arcucci, 1994, and *Pseudolagosuchus major* Arcucci, 1987, possess two sacrals (Novas 1993, 1996; Yates 2003a, 2007a, b). In *H. ischigualastensis*, the number of sacrals is disputed: Novas (1993) considered this species to possess two sacral vertebrae, but we agree with Sereno (2007), who suggested that it possesses three sacrals (PVL 461). However, the three sacrals of *H. ischigualastensis* appear to be the result of the incorporation of a dorsal vertebra into the sacrum (Sereno 2007), while in *S. pricei* it is a caudal element that has been added. This indicates a non-homologous relationship between the conditions seen in these two taxa, also implying that simply coding the number of sacrals as a character in phylogenetic analyses of basal dinosaurs is problematic (Sereno 1999; Yates 2003a; Langer & Benton 2006). The number of sacrals should be analysed in terms of the origin of the sacral vertebrae from distinct segments of the vertebral column (Yates 2007a, b). In *Eoraptor lunensis*, there is a

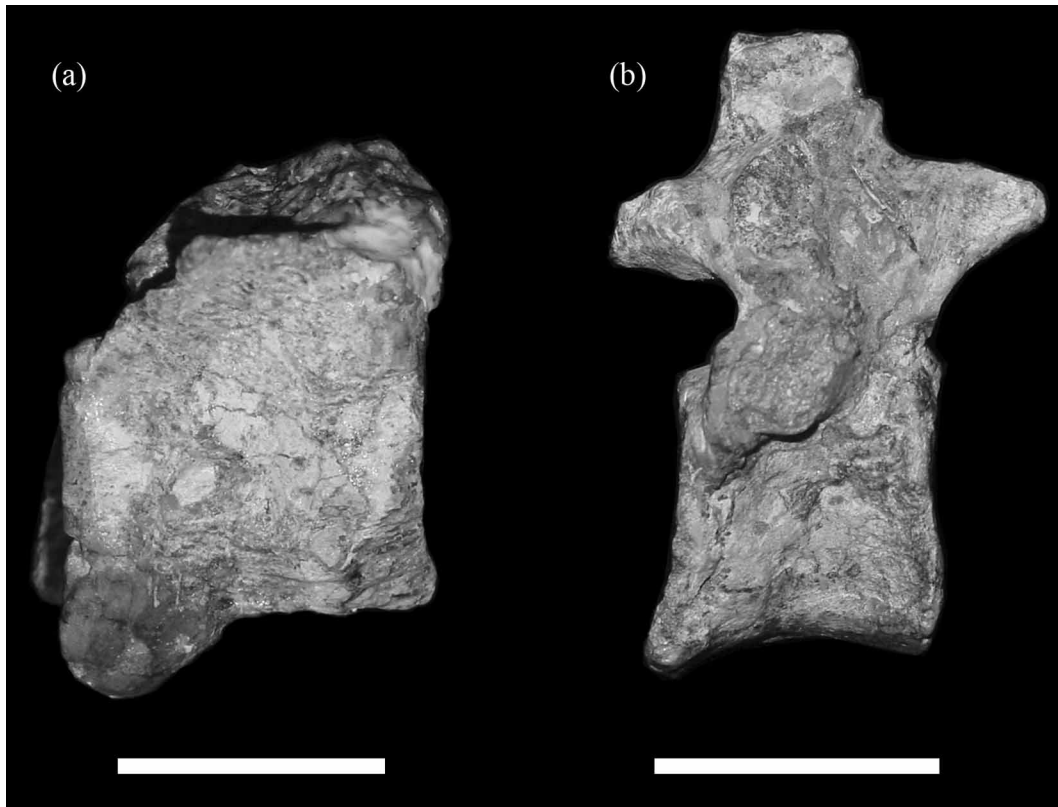


FIGURE 14. Photographs of the third sacral (a) and the first caudal vertebrae (b) in right lateral view. Scale bar for (a) = 2 cm; (b) = 2.5 cm.

dorsosacral (Sereno 2007), while in *Saturnalia tupiniquim* a caudosacral is seen (Langer & Benton 2006). In other basal sauropodomorphs with three sacrals (see Yates 2003a), both dorsal and caudal incorporations of additional vertebrae to the primitive sacral series have occurred (Galton 1999, 2001b; Yates 2003b, 2007a, b; Galton & Upchurch 2004). Basal neotheropods and ornithischians generally bear more than three vertebrae in the sacrum (Colbert 1989; Holtz 2000; Holtz *et al.* 2004; Norman *et al.* 2004a, b, c; Tykoski & Rowe 2004) and both dorsal and caudal additions occurred (Langer & Benton 2006; Yates 2007a, b). A recent study suggests that *Silesaurus opolensis* has three sacrals (Dzik & Sulej 2007), possibly with a dorsal vertebra incorporated into the primitive series. If this observation is confirmed, as well as the proposed phylogenetic position of *Silesaurus opolensis* as a non-dinosaurian dinosauriform, the presence of at least three sacral vertebrae (here understood as two primitive sacrals plus a dorsosacral) may represent a dinosauriform synapomorphy rather than a dinosaurian synapomorphy. In light of this character distribution, *S. pricei* and *Saturnalia tupiniquim* are primitive (or derived by reversal) within Dinosauria with regard to the absence of a dorsosacral. The caudosacral vertebra seen in these species, as well as in basal ornithischians, some sauropodomorphs (e.g. *Plateosaurus gracilis* [Huene, 1908]; Yates [2003b])), and theropods, are not recorded in most non-dinosaurian dinosauriforms. However, the absence of this character in *Eoraptor lunensis*, *Guaibasaurus candelariensis* Bonaparte, Ferigolo & Ribeiro, 1999, a putative basal theropod from south Brazil which bears only two sacral vertebrae (Bonaparte *et al.* 1999, 2007; Langer & Benton 2006; Langer *et al.* 2007a; Yates 2007a, b), and basal sauropodomorphs (Yates 2007b), also prevents recognition of this character as an unambiguous synapomorphy of Dinosauria.

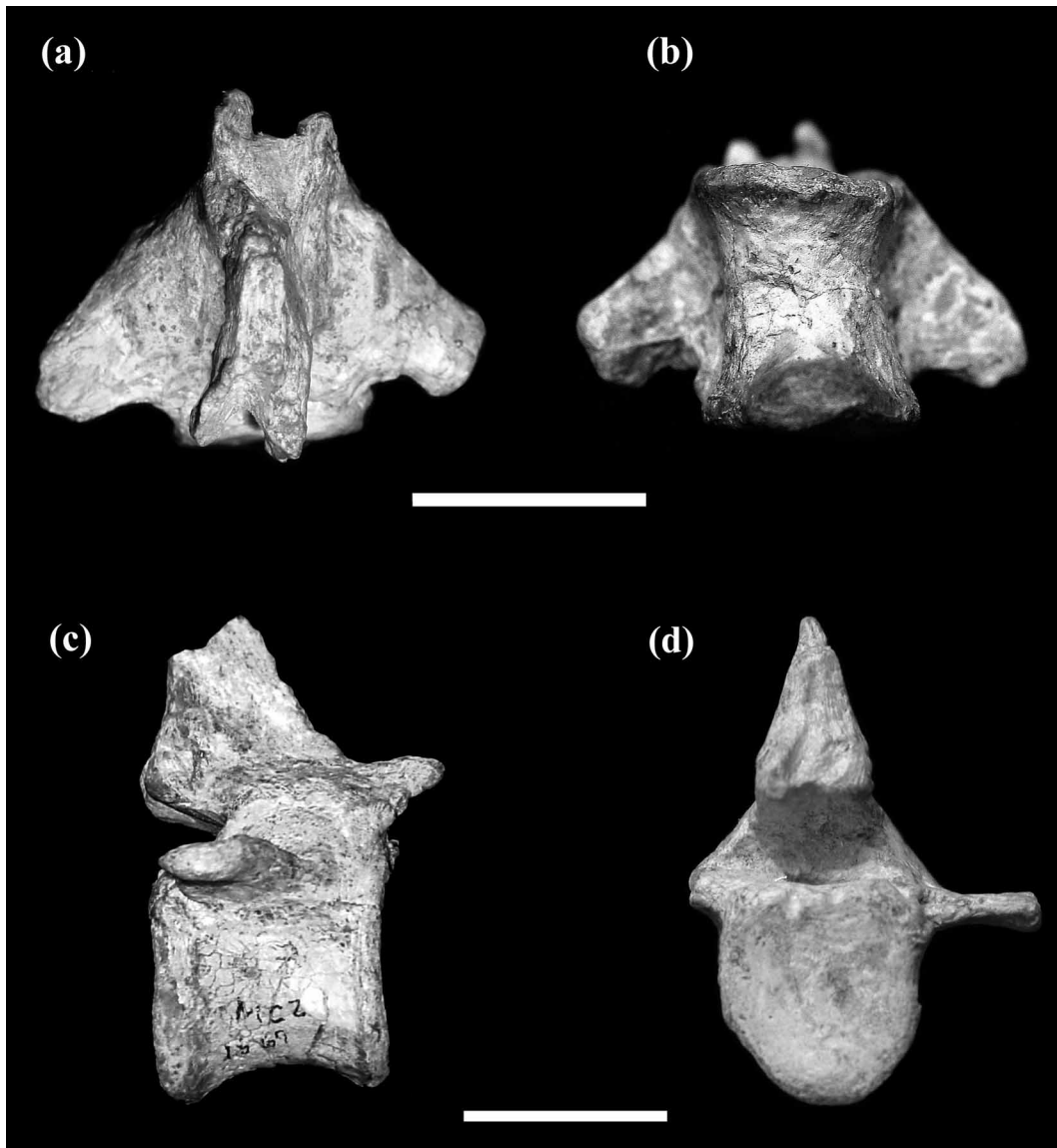


FIGURE 15. Photographs of the second caudal vertebra in dorsal (a) and ventral (b) views, and the third caudal vertebra in right lateral (c) and caudal views (d). Scale bars = 2 cm.

With regard to the caudal vertebrae, the presence of vertical neural spines on the proximal caudals was also considered a unique derived trait for *S. pricei* and *H. ischigualastensis* (Novas 1992). This character is not present in *Marasuchus lilloensis* (PVL 4671; Sereno & Arcucci 1994) or basal dinosaurs (Langer *et al.* 1999; Galton & Upchurch 2004; Norman *et al.* 2004a; Tykoski & Rowe 2004), including *Eoraptor lunensis* (PVL 512), and *Guaibasaurus candelariensis* (MCN-PV 2355; UFRGS PV 0725T); as a result, this character appears to be apomorphic for herrerasaurids.

Caudal anatomy has been used to support a close relationship between theropods and herrerasaurids (Sereno 1999). One character that potentially supports such a relationship is the presence of a ‘transition point’ in the tail (Russell 1972; Gauthier 1986). In recent matrices, this character has been replaced by the presence of elongated prezygapophyses in the distal caudal vertebrae (Rauhut 2003; Yates 2003a, 2007a, b; Langer 2004; Langer & Benton 2006). However, the transition point as discussed by Gauthier (1986: 19–20) is more complex, and includes at least one other feature: the absence of transverse processes and neural spines beyond the middle caudals. This character is present in *S. pricei*, *H. ischigualastensis* (Novas 1993), *Dilophosaurus wetherilli* (Welles 1984), and *Allosaurus fragilis* Marsh, 1877 (Madsen 1976), and is absent in

Marasuchus lilloensis (Serenó & Arcucci 1994), *Plateosaurus longiceps* (Galton 2001a; Galton & Upchurch 2004), and *Heterodontosaurus tucki* (Santa Luca 1980). However, several basal dinosauriforms and dinosaurs, including *Silesaurus opolensis* (Dzik 2003), *Saturnalia tupiniquim* (Langer *et al.* 1999), *Eoraptor lunensis* (PVSJ 512; Sereno *et al.* 1993), and *Guaibasaurus candelariensis* (Bonaparte *et al.* 1999, 2007) lack well-preserved and complete caudal series, hampering more accurate comparisons. Elongated prezygapophyses are present in the distal caudal vertebrae of several theropods (Rauhut 2003) and the suchian *Effigia okeeffeae* Nesbitt & Norell, 2006, but are absent in *Coelophysis bauri* and *Dilophosaurus wetherilli* (Welles 1984; Rauhut 2003; Langer & Benton 2006).

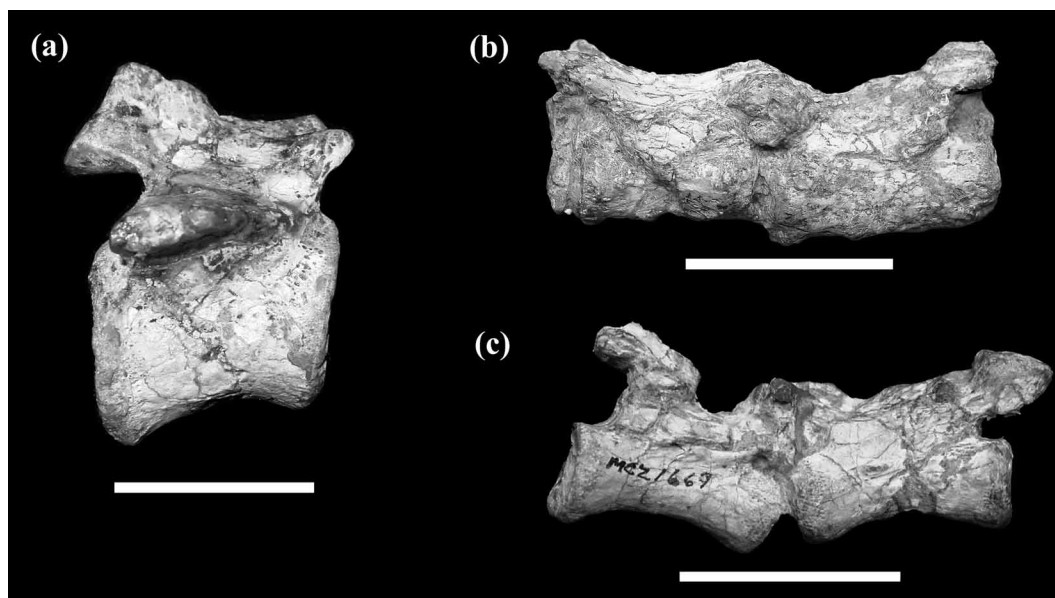


FIGURE 16. Photographs of the fourth caudal vertebra in right lateral (a), caudal vertebrae, sequence 1 (b) in left lateral view, and caudal vertebrae, sequence 2 (c) in right lateral view. Scale bar for (a) = 2 cm; (b–c) = 3 cm.

Yates (2003a) identified some similarities between the caudal vertebrae of herrerasaurids and sauropodomorphs: in both clades the first caudal centrum is taller than long and the middle caudal centra are less than twice as long as their maximum height. However, these characters are absent in *S. pricei* (see Figs 14, 17). In addition, Yates (2003a) reported the presence of a median furrow on the ventral surface of the proximal caudals of ornithischians, neotheropods and derived sauropodomorphs, stating that the presence of this character in herrerasaurids is dubious. By contrast, Rauhut (2003) claimed that this character is present in the majority of theropods, but correctly scored it as absent in herrerasaurids. The ventral groove is also absent in *Guaibasaurus candelariensis* (Bonaparte *et al.* 1999, 2007), and the character state for *Eoraptor lunensis* is uncertain (PVSJ 512; Rauhut 2003).

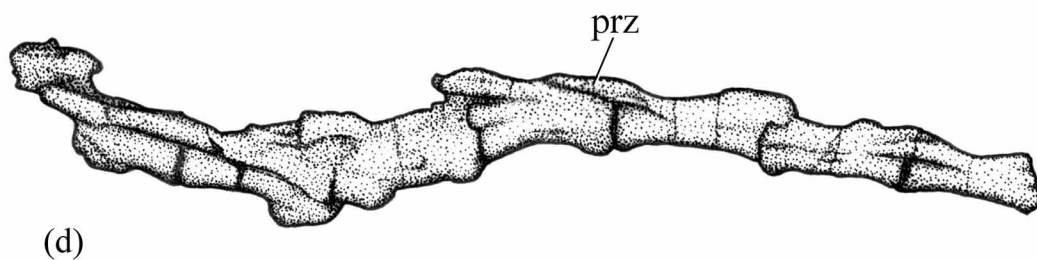
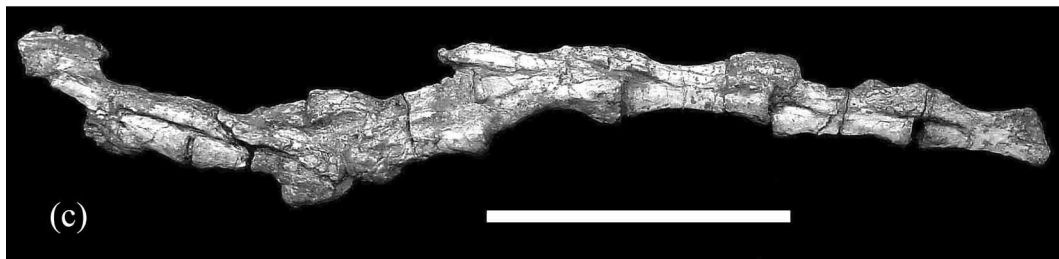
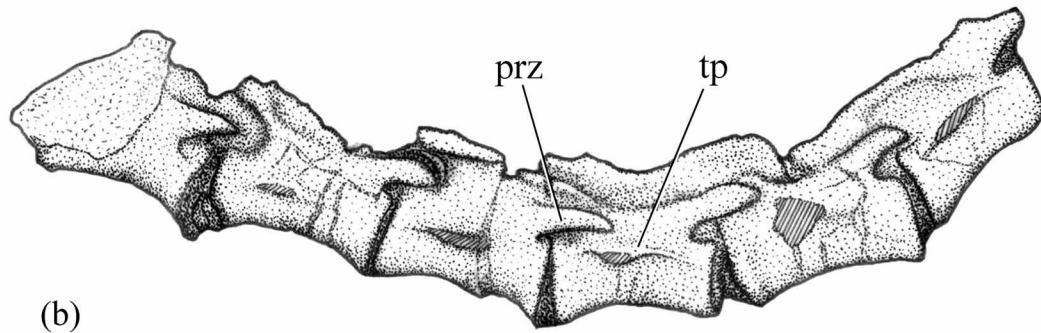
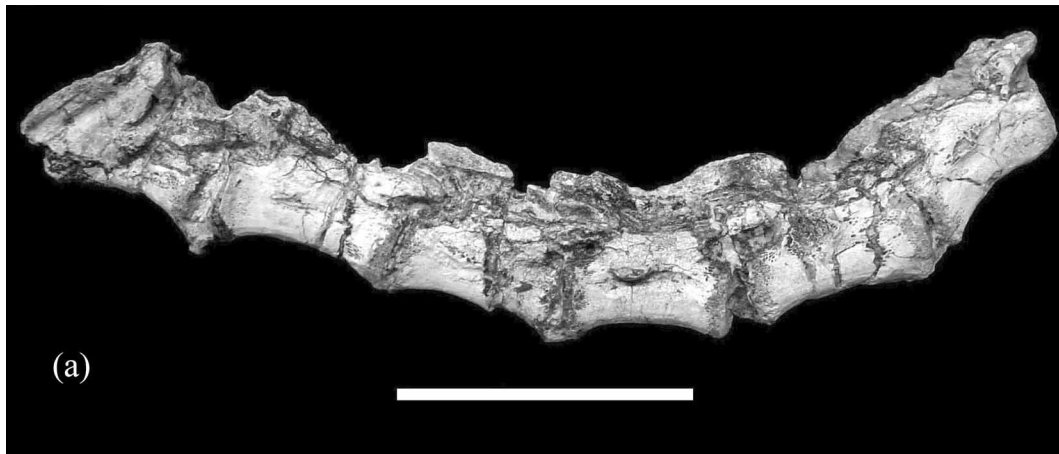


FIGURE 17. Photographs and drawings of six distal caudal vertebrae, sequence 3, in right lateral view (a–b), and seven distal caudal vertebrae, sequence 4, in left lateral view (c–d). Abbreviations: **prz**, prezygapophysis; **tp**, transverse process. Scale bar for (a–b) = 5 cm; (c–d) = 6 cm.

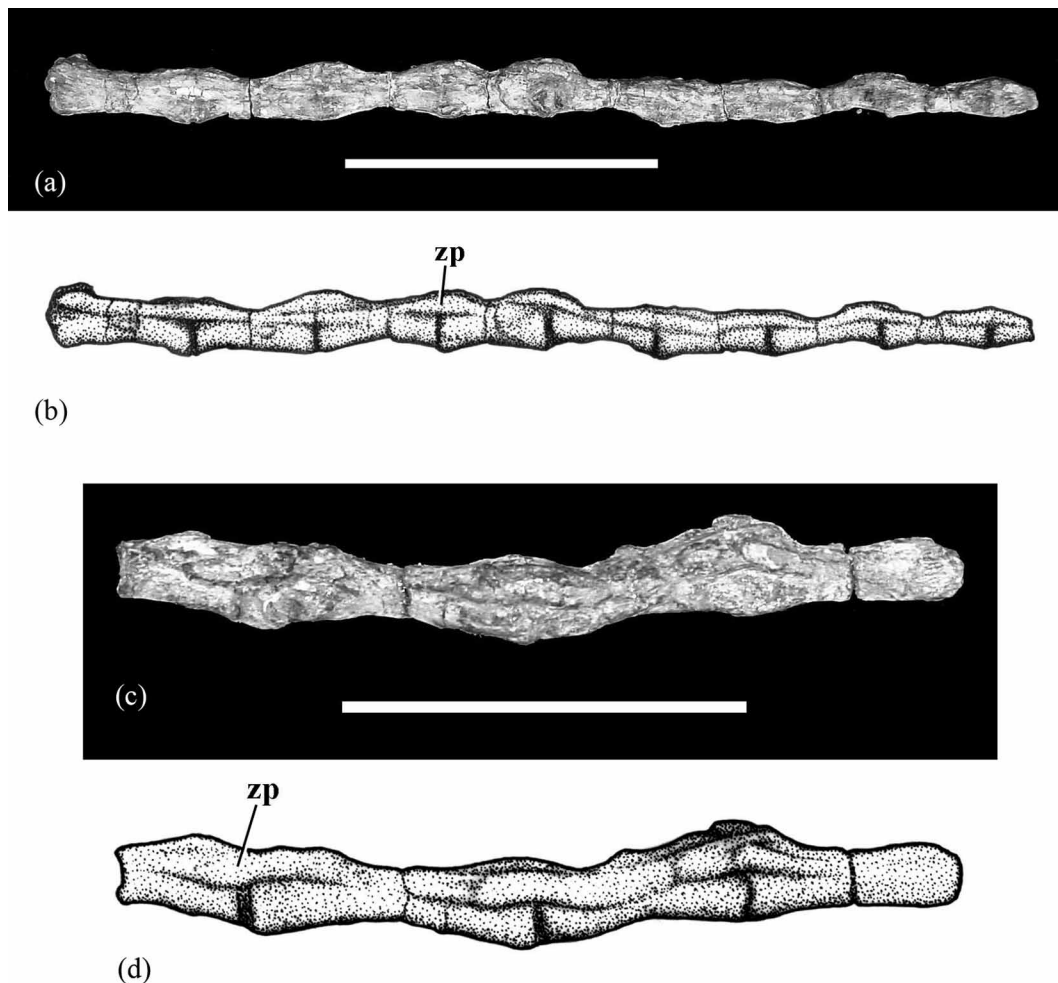


FIGURE 18. Photographs and drawings of the distal caudal vertebrae, sequence 5 (a–b) and sequence 6 (c–d), in right lateral view. Abbreviation: **zp**, zygapophysis. Scale bar = 6 cm.

Pectoral girdle

The only preserved bone of the pectoral girdle is the dorsal fragment of a scapula (Fig. 20). The bone identified as the right scapula by Novas (1992), Sereno (1993), and Galton (2000a) is here interpreted as the right ischium (Fig. 24e–f), because its form and dimensions are identical to those observed in the left ischium (Fig. 24a–d), which is more complete.

Scapula. The dorsal fragment of the left scapula is 24.5 mm long at the ventralmost preserved region and 27.5 mm long dorsally (Fig. 20). The maximal width of the blade is 6.5 mm measured at the dorsal margin. In dorsal view, the thickness of the blade increases from the cranial margin to the caudal margin. The dorsocranial and dorsocaudal corners are slightly rounded in lateral view.

Comments. Novas (1992) proposed two synapomorphies of Herrerasauridae in the pectoral girdle: reduction of the dorsal length of the scapular blade, and the presence of an acromial process extending distally with respect to the scapular glenoid lip, forming a right angle with the scapular blade. Because only the distal part of the scapula is preserved, the distal expansion relative to the shaft cannot be evaluated. Nevertheless, the distal end of the scapula of *S. pricei* has slightly rounded dorsocranial and dorsocaudal corners, more similar to that of *H. ischigualastensis* than to any other basal dinosaur scapula. The anatomy of the acromial process cannot be determined due to the poor preservation of the specimen.

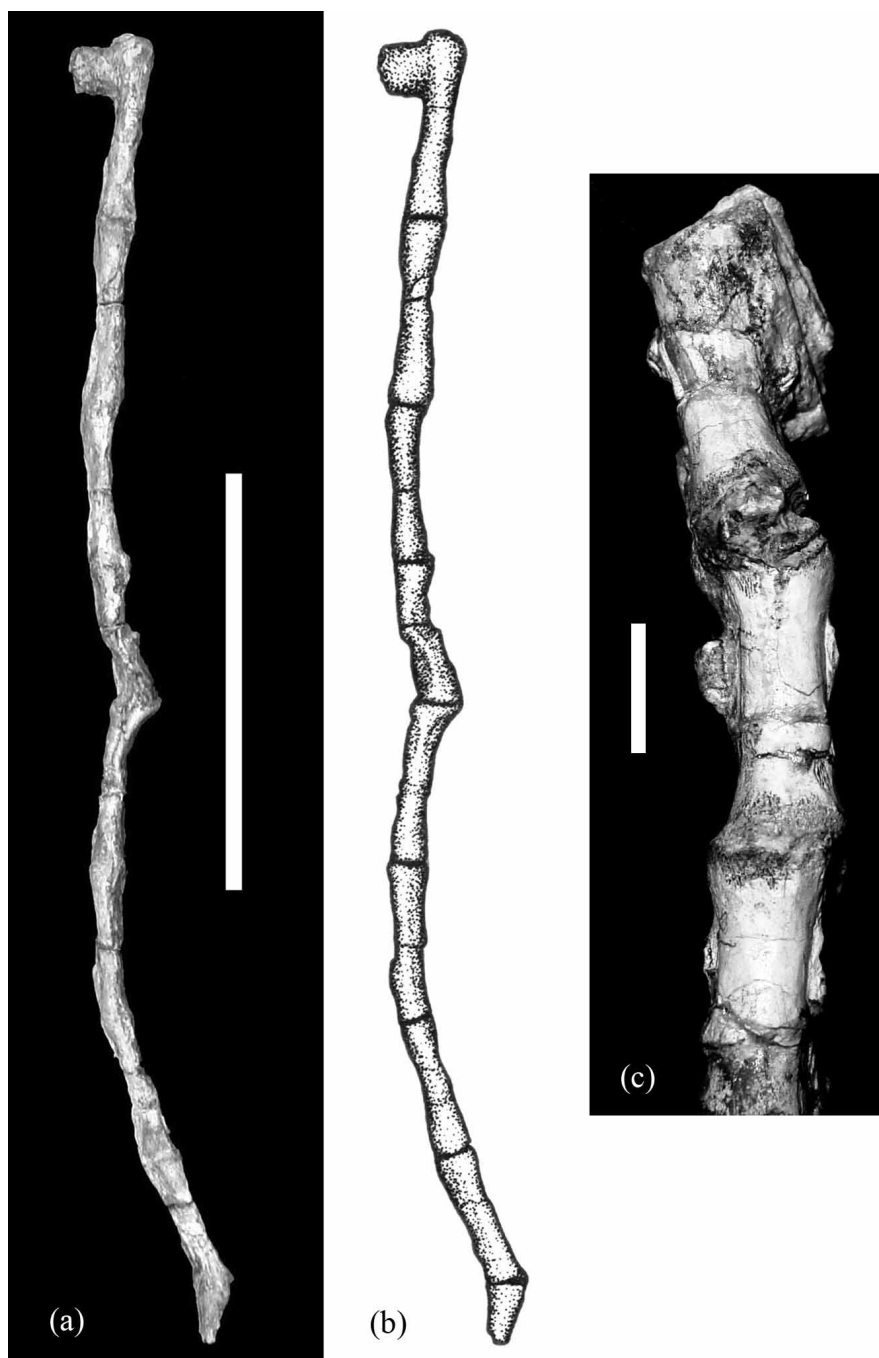


FIGURE 19. Photographs and drawings of distal caudal vertebrae in ventral view, sequence 5 (a–b) and detail of the caudal vertebrae of sequence 3 (c). Scale bar for (a–b) = 6 cm; (c) = 2 cm.

Forelimb

Colbert (1970) reported the presence of a proximal fragment of the right humerus in the holotype of *S. pricei*, but Galton (1977, 2000a) and Sereno (1993) contested this assignment. Some of the characteristics of this element (Fig. 31), including the short axis and the abrupt expansion of the extremity (resulting in a fan shape), are quite distinct from those observed in dinosaur humerus. We therefore agree that this bone is not a humerus, but rather an unidentifiable element.

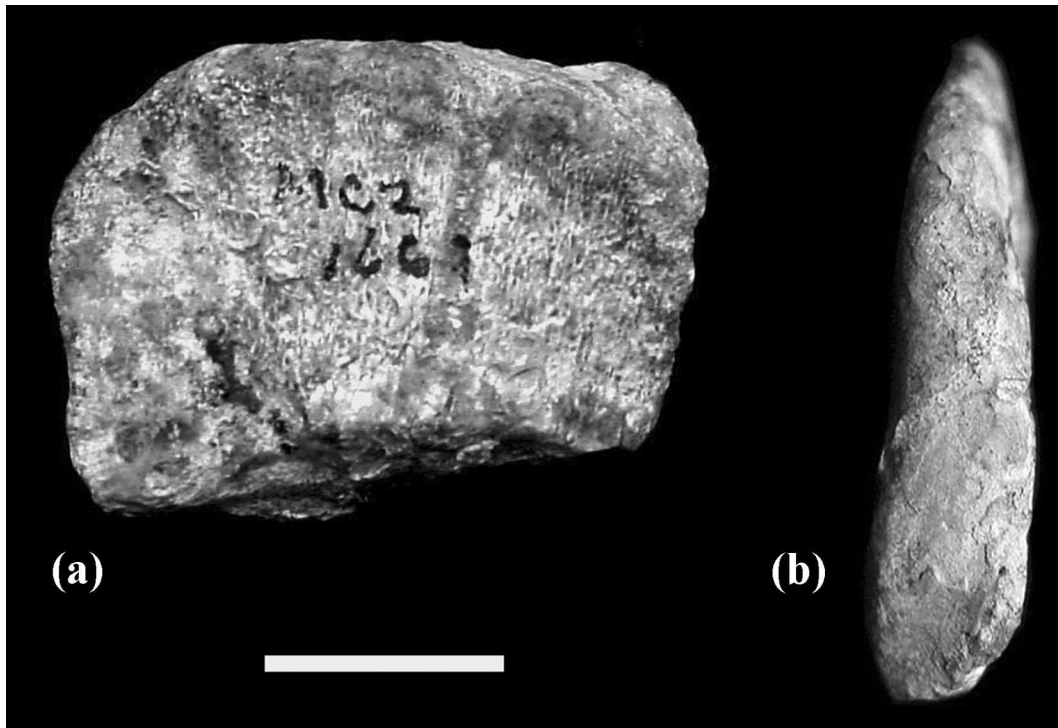


FIGURE 20. Photographs of the left scapula in lateral (a) and distal (b) views. Scale bar = 1 cm.

Pelvic girdle

The bones of the pelvic girdle of *S. pricei* are well preserved although somewhat distorted by taphonomic effects. Both ilia are preserved: the left is complete but part of the iliac blade of the right ilium is missing (Fig. 21). The pubes are preserved but are broken along the medial margin (Figs 22–23). The ischia are also present, but the distal end of the left ischium is missing as well as the cranioproximal region of the right ischium (Fig. 24). The bones of the pelvic girdle have been the subject of more detailed descriptions, comparisons, and discussion than any other part of the anatomy of *S. pricei*, beginning with the original description by Colbert (1970) and continued by subsequent revisions (Galton 1977, 2000a; Sues 1990; Novas 1992, 1996, 1997).

Ilium. The ilium is high and short (Fig. 21), similar to the brachyliac morphotype of Colbert (1970). The preacetabular process is cranially rounded and bears an obliquely oriented, robust bony crest, which runs from the proximal end of the pubic peduncle to the tip of the preacetabular process (Fig. 21a–b: *prac*). The cranialmost extremity of the preacetabular process does not extend as far cranially as the cranialmost limit of the pubic peduncle (Fig. 21). On its lateral surface, the iliac blade bears two well-defined concavities: a cranial concavity, which extends over most of the supraacetabular region, and a shallow caudal concavity, positioned immediately above the ischial peduncle (Fig. 21a–b: *cric*, *caic*). The cranial concavity is delimited at its cranial margin by the preacetabular crest (Fig. 21a–d) and at its caudal margin by a postacetabular elevation (Fig. 21a–b: *poae*). The caudal concavity is delimited at its dorsal and caudal margins by the caudal margin of the postacetabular process and at its cranial margin by the postacetabular elevation. The acetabulum is dorsoventrally deep and partially perforated: its dorsal margin is delimited by the robust supraacetabular crest, its cranial margin by the pubic peduncle, and its caudal margin by the ischial peduncle (Fig. 21). The inner wall of the acetabulum is broad, mediolaterally and dorsoventrally concave, and medially projected. The pubic peduncle is higher than wide and bears a laterocaudal crest that is confluent with the supraacetabular crest. The ischial peduncle is short and triangular in lateral view. A smooth surface in this region could be

interpreted as the antitrochanter, but it is quite different from the antitrochanter of *H. ischigualastensis* (Novas 1993). Colbert (1970) reconstructed the caudoventral margin of the left ilium with two gently concave notches: one between the ischial peduncle and a short caudal process and another between this caudal process and the dorsocaudal extremity of the postacetabular process (Fig. 21a–b). Although this condition is more marked in the left ilium, which is somewhat crushed, the right ilium also bears two notches on the caudoventral margin of the postacetabular process. Medially, a broad concavity is observed between the dorsal and caudal portions of the iliac blade, where the lateral process of the first sacral vertebra contacted the ilium. The medial articular surfaces seen in the ilium of *H. ischigualastensis* (Novas 1993) are not observed in *S. pricei*.

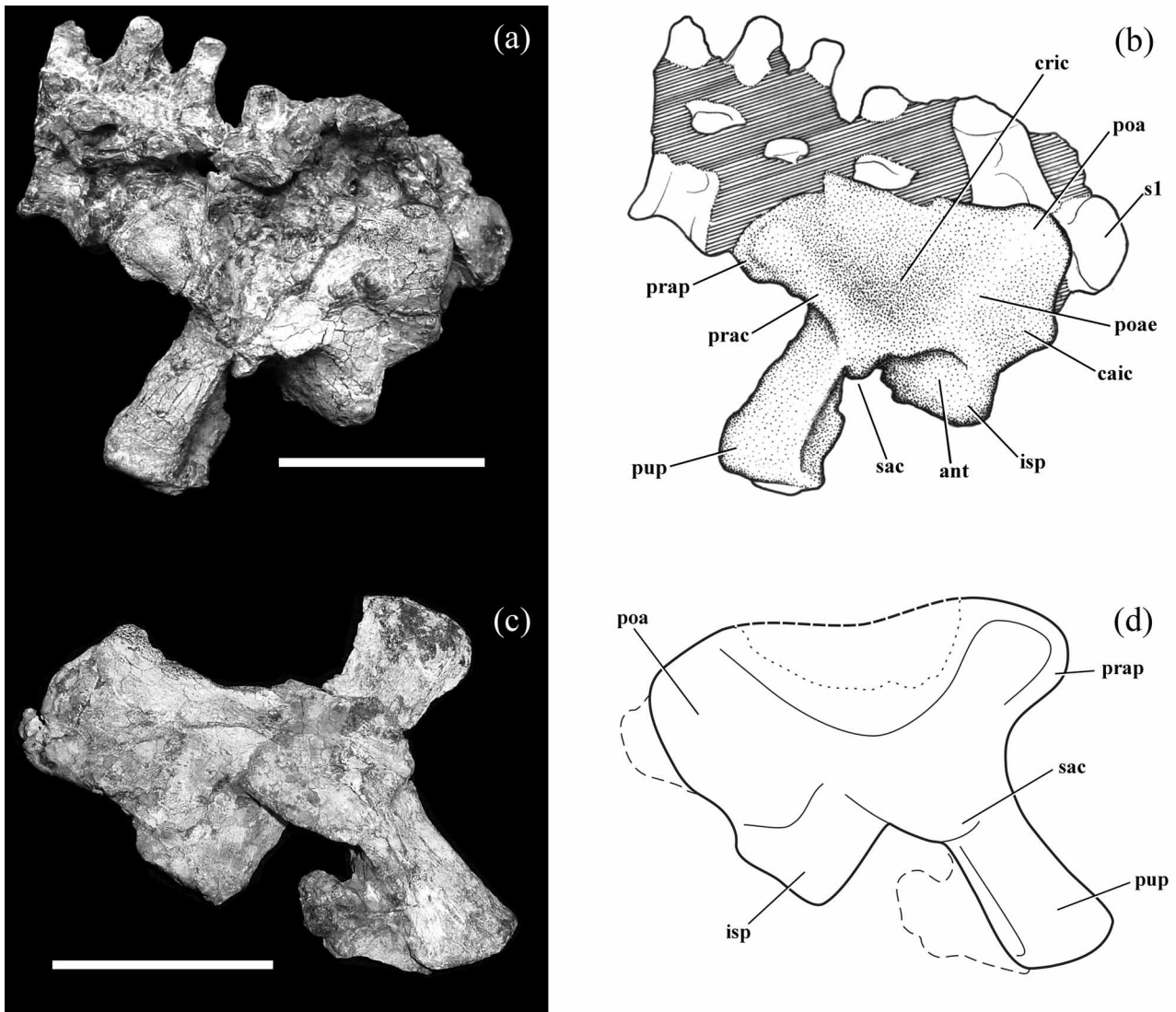


FIGURE 21. Photograph and drawing of the left ilium associated with the vertebral column, in lateral view (a–b), and the right ilium in lateral view (c–d). Abbreviations: **ant**, antitrochanter; **caic**, caudal iliac concavity; **cric**, cranial iliac concavity; **isp**, ischial peduncle; **prap**, preacetabular process; **prac**, preacetabular crest; **pup**, pubic peduncle; **poa**, postacetabular process; **poae**, postacetabular elevation; **s1**, first sacral vertebra; **sac**, supraacetabular crest. Scale bar for (a–b) = 6 cm; for (c–d) = 5 cm.

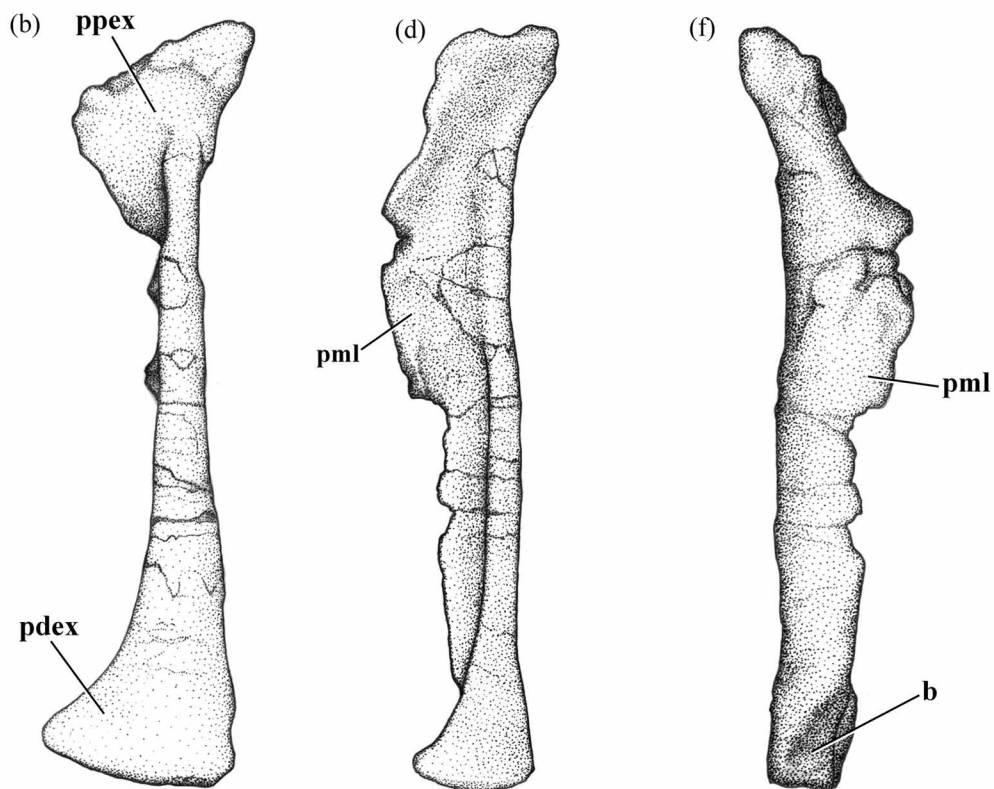


FIGURE 22. Photographs and drawings of the right pubis in lateral (a–b), caudal (c–d) and cranial (e–f) views. Abbreviations: **b**, distinct bevel on distal end of pubis; **pdex**, distal expansion of pubis; **pml**, medial lamina of pubis; **ppex**, proximal expansion of pubis. Scale bar = 6 cm.

Pubis. The pubis is expanded at both proximal and distal ends (Fig. 22), and the medial margin of the element is drawn out to form a long symphyseal region (Fig. 22c–f). In the right pubis, the proximal region is medially expanded and counterclockwise rotated outwards in such a way that the medial region projects caudally and the lateral surface is cranially oriented (Fig. 22a–d). This region forms the articulation area for the iliac pubic peduncle. The ischio-acetabular groove found in other dinosauriforms (Langer 2003; Ezcurra 2006; Nesbitt *et al.* 2007) is not seen in *S. pricei*. The left pubis has suffered post-mortem compression at its proximal end (Fig. 23). The obturator notch and the ambiens process cannot be recognized, perhaps as a result of taphonomic damage. The anatomy of the distal end of the bone is the opposite of that seen at the proximal end: it is mediolaterally expanded with the lateral region distally oriented and the medial region facing cranially (Fig. 22a–d). This forms the pubic ‘boot’; in the right pubis the craniocaudal expansion of the ‘boot’ is about five times the craniocaudal width of the pubic shaft and approximately equal to the proximal expansion (Fig. 22a–b). In the craniomedial region of the pubic ‘boot’ there is a small elevation that is confluent ventrally with a smooth surface that forms the caudal wall of a beveled area. This beveled area can be clearly observed in medial and lateral views (Figs 22e–f, 23b).

Ischium. Both ischia are craniocaudally expanded at their proximal ends (Fig. 24). The cranial region comprises the plate of the obturator process. Although the entire extent of this process cannot be determined because of breakage, there is no evidence that it extends beyond the proximal third of the bone. The caudoproximal portion forms a triangular-shaped process in lateral view, with a thickened caudal end. In the left ischium, immediately beneath the caudal end of the aforementioned caudoproximal process, a shallow excavation is present (Fig. 24a–b). This excavation does not appear to be the result of post-mortem distortion or overpreparation; however, an equivalent feature is absent from the left ischium (Fig. 24e–f). The ischium is laterally convex (Fig. 24a–b) and medially concave in the region of the obturator plate (Fig. 24c–d). The cranial and caudal margins of the proximal portion of the bone converge upon one another ventrally, resulting in a craniocaudally short shaft which is slightly curved caudally (Fig. 24) and has a triangular cross section. The extent of the ischial symphysis cannot be evaluated due to the incompleteness of the craniomedial surface of the ischia. No sulci or crests are present on the shaft. The distal extremities of the ischia are not preserved and the total length of this bone cannot be determined.

Comments. The general morphology of the herrerasaurid ilium is more similar to that of the basal dinosauiromorphs *Lagerpeton chanarensis* (PVL 4619; Sereno & Arcucci 1993) and *Marasuchus lilloensis* (PVL 3870; Sereno & Arcucci 1994) than to those of basal dinosaurs, with the exception of the acetabular region. The basal dinosauriform *Silesaurus opolensis* bears a large brevis fossa on the ilium, a closed acetabulum, and an elongate postacetabular process (Dzik 2003). These conditions are very distinct from those seen in herrerasaurids. Comparisons with *Chindesaurus bryansmalli* Long & Murry, 1995, a putative herrerasaurid from the Chinle Group (Late Triassic, USA), are problematic, since the better preserved ilium referred to this taxon subsequently became the holotype of another species, *Caseosaurus crosbyensis* Hunt, Lucas, Heckert, Sullivan & Lockley, 1998. Nesbitt *et al.* (2007), in a recent review of this material, considered the distinction between *Chindesaurus bryansmalli* and *Caseosaurus crosbyensis* dubious, and questioned the presence of a brevis fossa on the ilium of the former. Similarly, the ilia of *S. pricei* and *H. ischigualastensis* also lack a brevis fossa. Sereno (1999) suggested that the ilium attributed to *Chindesaurus bryansmalli* (possibly that which became the holotype of *Caseosaurus crosbyensis*) is more similar to the ilium of *S. pricei* in possessing an iliac blade that is caudoventrally inclined and an everted ventral margin of the preacetabular process. These characters were used to support a closer relationship between *Chindesaurus bryansmalli* and *S. pricei* than between either taxon and *H. ischigualastensis* (see Murry & Long 1989; Long & Murry 1995; *contra* Novas 1997). However, the ilium of *Caseosaurus crosbyensis* is broken in the dorsal region of the blade, and appears not to be inclined to a significant degree (Nesbitt *et al.* 2007), and the ventral margins of the preacetabular processes of the ilia of *H. ischigualastensis* and *S. pricei* are not significantly different. In addition, the preacetabular process of the ilium of *Caseosaurus crosbyensis* is subtriangular in lateral view and the postacetabular process is deep and elongate; a corresponding morphology is absent in the South American herrerasaurids (Novas 1993; Long & Murry 1995; Hunt *et al.* 1998; Nesbitt *et al.* 2007). Moreover,

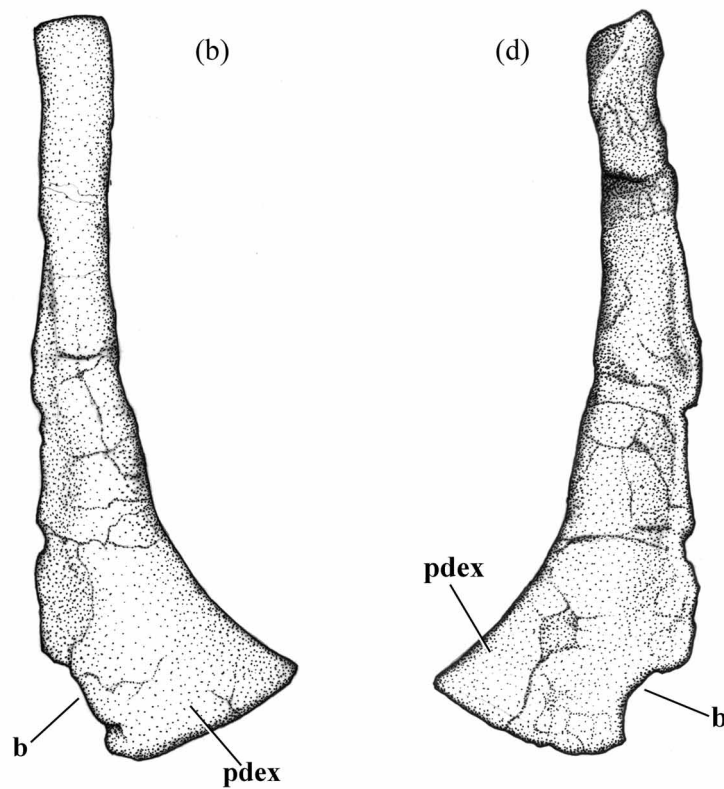
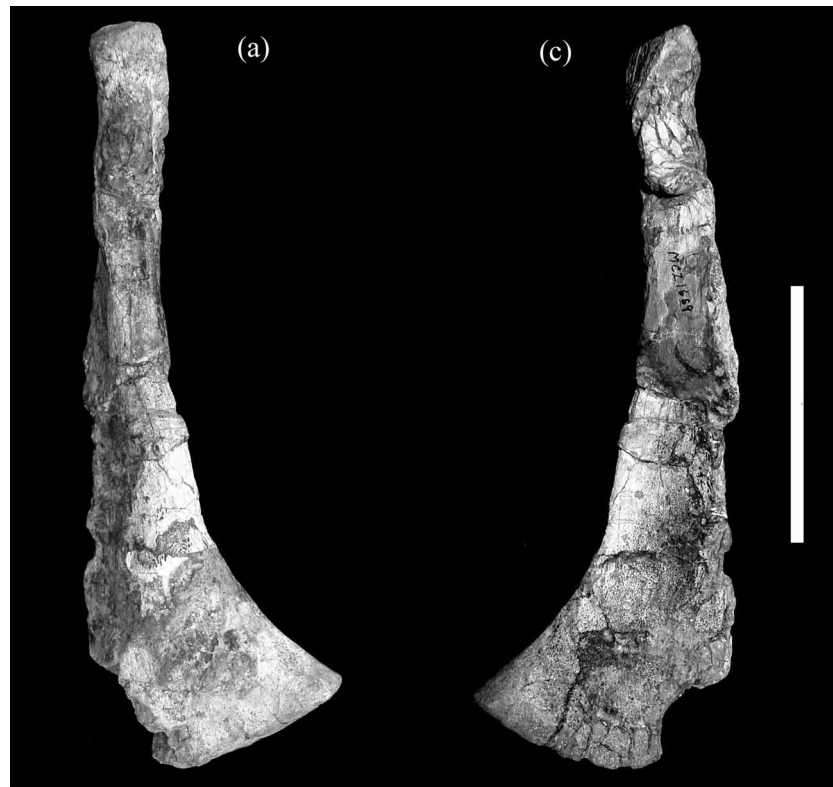


FIGURE 23. Photographs and drawings of the left pubis in lateral (a–b) and medial (c–d) views. Abbreviations: **b**, distinct bevel on distal end of pubic; **pdex**, distal expansion of pubis. Scale bar = 6 cm.

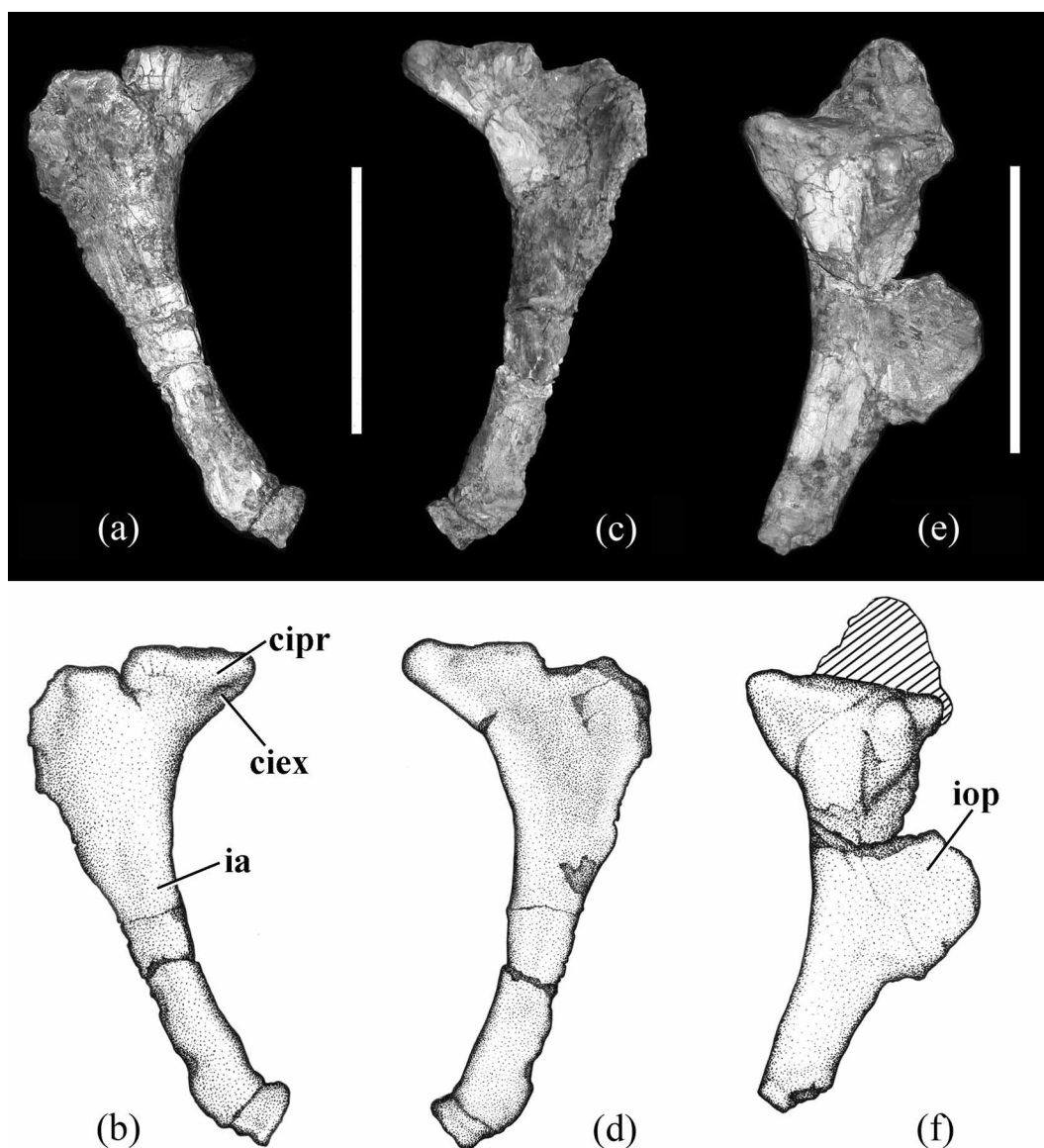


FIGURE 24. Photographs and drawings of the left ischium in lateral (a–b) and medial (c–d) views and the right ischium (e–f) in lateral view. Abbreviations: **ciex**, caudal ischial excavation; **cipr**, caudal ischial process; **ia**, ischial axis; **iop**, ischial obturator plate. Scale bar = 6 cm.

both *Chindesaurus bryansmalli* and *Caseosaurus crosbyensis* bear a triangular rugosity on the lateral surface of the postacetabular process, a feature absent in *S. pricei* and *H. ischigualastensis*.

In neotheropods, the preacetabular process is a cranially rounded blade that projects far beyond the cranialmost limit of the pubic peduncle, while the postacetabular process is caudally straight with a square shape in lateral view (Madsen 1976; Holtz *et al.* 2004; Tykoski & Rowe 2004). Both conditions are different from those seen in herrerasaurids. In basal sauropodomorphs, such as *Pantydraco caducus* (Yates 2003a; Galton *et al.* 2007), *Plateosaurus engelhardti* (Galton & Upchurch 2004) and *Riojasaurus incertus* Bonaparte, 1969 (PVL 3808; Bonaparte 1972), the preacetabular process is subtriangular in lateral view, not cranially rounded as in *S. pricei* and *H. ischigualastensis*. The postacetabular process of herrerasaurids is also different from that of sauropodomorphs. In *Saturnalia tupiniquim* (Langer 2003) and *Riojasaurus incertus* (PVL 3808; Bonaparte 1972), the postacetabular process is very elongated; in *Pantydraco caducus* (Yates 2003a; Galton *et al.* 2007) it is deeper and shorter than that of *Saturnalia tupiniquim*, and caudally rounded; in *Efraasia minor*

(Huene, 1908) (Yates 2003b) the dorsal surface of the postacetabular process slopes ventrally and forms a pointed caudoventral corner, which continues cranially to form a straight ventral margin.

The anatomy of the caudoventral margin of the ilium in *S. pricei* and *H. ischigualastensis* is similar to that of *Agnosphitys cromhallensis* Fraser, Padian, Walkden & Davis, 2002 (Fraser *et al.* 2002) and *Marasuchus lilloensis* (Sereno & Arcucci 1994), although the postacetabular process of the latter is subtriangular in lateral view and more strongly compressed (Sereno & Arcucci 1994). In most saurischians, the caudoventral margin is markedly concave (Galton & Upchurch 2004; Holtz *et al.* 2004; Tykoski & Rowe 2004). This modification of the caudal part of the ilium is associated with the development of two structures: the brevis shelf and the brevis fossa. Novas (1996: 734) defined the brevis shelf as a ‘distinct and prominent shelf on the caudolateral margin of the iliac blade, placed external to the caudoventral iliac margin, which runs from the ischial peduncle to the posterior extremity of the blade’. In *H. ischigualastensis*, Novas (1993) noted that ventral to the caudal margin of the postacetabular process there is a horizontal furrow just ventral to a laterally thickened surface in the caudoventral margin of the ilium. On the lateral surface of the ilium of *S. pricei* this ‘thickened surface’ is present as an elevation of the caudal portion of the iliac blade (Fig. 21: poae) that delimits the two concavities described above (Fig. 21: cric, caic). We here suggest that the thickened surfaces observed in the ilia of *S. pricei* and *H. ischigualastensis* are homologous and represent a very weakly-developed brevis shelf. The brevis fossa is represented in *S. pricei* by the caudal concavity dorsal to the ischial peduncle (Fig. 21: caic). The reduced condition of the brevis shelf and fossa is regarded as unique to Herrerasauridae amongst dinosaurs (Novas 1993, 1996; Sereno 1999; Hutchinson 2001a; Langer & Benton 2006). In this sense, *Chindesaurus bryansmalli* and *Caseosaurus crosbyensis*, which do not bear brevis fossae, could be regarded as herrerasaurid representatives in northern latitudes (Novas 1997; Irmis *et al.* 2007a). In *Silesaurus opolensis* and *Guaibasaurus candelariensis*, a more robust brevis shelf appears to be present (Dzik 2003; Bonaparte *et al.* 1999, 2007). The origin of these structures in dinosaurian lineages is debatable. Langer and Benton (2006) suggest independent origins of the brevis shelf in ornithischians and saurischians. Other authors support the hypothesis of a single origin of this structure in dinosaurs, but suggest it derives either from a ventrolateral expansion of the postacetabular iliac blade (Welles 1984; Novas 1996), or from a medial extension of the iliac blade (Charig & Milner 1997; Hutchinson 2001a). Which of these alternatives is correct cannot be answered with data from Herrerasauridae, because the morphology seen in herrerasaurids is probably apomorphic and not representative of the ancestral condition for Dinosauria.

The acetabular region of the archosaur ilium has been subject of discussion, since the presence of a partially to totally perforate acetabulum was accepted as a diagnostic character for Dinosauria (Bakker & Galton 1974; Gauthier 1986; Novas 1996; Benton 1999; Fraser *et al.* 2002). A more recent definition of this character deals with the ventral margin of the acetabular wall, which is regarded as concave in most dinosaurs, and more commonly convex to straight in non-dinosaur archosaurs (see Langer & Benton 2006). Although the concave condition is not well-marked in some basal dinosaurs (e.g. *Saturnalia tupiniquim*, *Guaibasaurus candelariensis*: Langer 2003; Bonaparte *et al.* 1999, 2007), and is also found in some crurotarsans (Gauthier 1986; Langer & Benton 2006; Irmis *et al.* 2007a), this feature is often cited as a synapomorphy of Dinosauria (Irmis *et al.* 2007a; Yates 2007a, b). The presence of this character in *S. pricei*, along with other features, supports its placement within dinosaurs.

Another feature that is noteworthy for dinosaurs is the presence of an antitrochanter. Novas (1993: 404) reported the presence of an antitrochanter in *H. ischigualastensis* as a ‘raised, kidney-shaped surface, which faces craniolaterally and slightly dorsally and extends over the ischial peduncle of the ilium and the postacetabular portion of the ischium’. In *S. pricei* no such structure is found, but in both ilia the caudal portion of the acetabular wall is more ventrally projected than the cranial portion (Fig. 21), and its caudoventral part, which is confluent with the ischial peduncle, can be interpreted as homologous to the antitrochanter of other basal dinosaurs (Langer 2003; Langer & Benton 2006). Although the antitrochanter of several basal dinosaurs is not a well-marked structure (Langer & Benton 2006), its complete absence is generally seen in some basal tetanurans and more advanced theropods (Smith *et al.* 2007).

Rauhut (2003: character 177) suggested that the pubic peduncle of *S. pricei* is more similar to that of some

tetanurans by being significantly longer than the ischial peduncle, and that the latter tapers ventrally and bears no clearly defined articular facet. This character can be also understood as three different transformations: 1) the lengthening of the pubic peduncle with regard to the ischial peduncle; 2) the tapering form of the ischial peduncle; 3) the presence of a distinct articular facet. These three features are also present in *Caseosaurus crosbyensis* (Long & Murry 1995; Nesbitt *et al.* 2007) and basal ornithischians (*Lesothosaurus diagnosticus* Galton, 1978 and *Heterodontosaurus tucki*; Norman *et al.* 2004a, b). A long pubic peduncle is also present in sauropodomorphs [e.g. *Ammosaurus major* (Marsh, 1889); Galton & Upchurch 2004], and the tapering ischial peduncle was also described for *Pantydraco caducus* (Yates 2003a; Galton *et al.* 2007), showing that those characters are homoplastic within dinosaurs.

With regard to the pubis, *S. pricei* shares with *H. ischigualastensis* a derived characteristic in that the expansion of its distal end comprises more than 25% of the length of the pubis (Novas 1992). This character has also been coded in an imprecise qualitative fashion as the presence of a pubic ‘boot’, or the presence of a distally expanded pubis, and has been regarded as an unequivocal synapomorphy of Herrerasauridae plus Neotheropoda (Novas 1997; Sereno 1999). However, the absence of a distal expansion in some primitive theropods, such as *Coelophysis bauri* (Colbert 1989) and *Syntarsus rhodesiensis* (Raath 1990), as well the anatomical difference between the distal expansion of herrerasaurids and neotheropods, have led some authors to reject the hypothesis of primary homology between the distal pubic expansions of herrerasaurids and neotheropods (Langer 2004). This conclusion is based upon the interpretation that the distal pubic expansion seen in herrerasaurids is a result of a caudally directed folding of the laterodistal margin of the pubis and not a craniocaudal expansion of the distal portion as observed in some theropods (Langer 2004; Langer & Benton 2006). This condition is more evident in *S. pricei*, which is more lightly built than *H. ischigualastensis*, but in the latter taxon there is clearly a craniocaudal expansion of the distal pubis (PVL 2566), with which the laterocaudal margin of the pubic blade is confluent. In the basal tetanuran *Piatnitzkysaurus floresii* Bonaparte, 1979 (PVL 4073; Rauhut 2003; Smith *et al.* 2007), the condition is very similar to that observed in *H. ischigualastensis*. This suggests that a putative homoplastic relationship between the pubic boot in herrerasaurids and in neotheropods is the result of the proposed phylogenetic position of herrerasaurids as non-theropods rather than true morphological incongruence.

Based on the reconstruction of Novas (1993), the pubis of *H. ischigualastensis* projects caudoventrally, a condition also acquired convergently by ornithischians and coelurosaurian theropods. The orientation of the pubis in *S. pricei* is quite difficult to evaluate, because the proximal regions of the pubes appear to be damaged. In the right pubis, the proximal surface forms an angle of approximately 65° with the pubic shaft, a similar angle to that observed between the distal surface of the pubic peduncle and the dorsoventral axis of the ilium. Therefore, if both the right ilium and right pubis are assumed to be complete, it seems likely that the pubis of *S. pricei* was nearly vertically oriented, more similar to *H. ischigualastensis* than to other basal saurischians. The proximal surface of the left pubis does not form such an angle with the pubic shaft, which would instead suggest a cranioventral orientation, but the proximal region of this element is clearly deformed. Here, *S. pricei* is reconstructed as possessing a slightly cranioventrally orientated pubis (Fig. 1), but it should be noted that the evidence for the orientation is ambiguous.

Another peculiarity of the pubis of *S. pricei* is the presence of a distinct bevel on the craniomedial portion of the distal end. This feature was proposed as an autapomorphy of this species by Novas (1993), and his proposal is followed here. Nesbitt & Chatterjee (2008) reported the presence of a pubis from the Upper Triassic of the Dockum Group of Texas which was referred to as a ‘Saurischia similar to *Staurikosaurus*’. Indeed, the pubis described by Nesbitt & Chatterjee (2008) is similar to that of *S. pricei* with regard to the presence of a craniomedial bevel on the distal pubis and the presence of a pubic boot in which the laterocaudal margin of the pubic blade is confluent with caudodistal expansion of the pubis. The main difference between those specimens is that both the distal bevel and the pubic boot are more marked in *S. pricei* than in the Dockum pubis. Specimens similar to *S. pricei* in Upper Triassic strata of North America have been described in the literature (Murry & Long 1989; Long & Murry 1995). However, more material is needed to confirm the possibility that taxa closely related to *S. pricei* are present in North American deposits of that age.

Novas (1997) suggested that *Chindesaurus bryansmalli* shares with *H. ischigualastensis* a transversely narrow pubic apron, a character supposedly absent in *S. pricei*. However, based on the reconstruction of the pelvis of *H. ischigualastensis* provided by Novas (1993) and on our own observations of the material referred to this species (e.g. PVL 2566), we noted that the dimensions of the pubic apron are not significantly different in *H. ischigualastensis* and *S. pricei*. The pubic blade of *Chindesaurus bryansmalli* appears to be transversely narrower than in *S. pricei* and *H. ischigualastensis*, but the material is too incomplete to yield more conclusive data (Nesbitt *et al.* 2007).

The ischium of *S. pricei* displays some dinosaurian and saurischian synapomorphies including the narrowness of the distal shaft and the restriction of the obturator process to the proximal third of the bone (Novas 1996; Langer & Benton 2006). Furthermore, two other synapomorphies were proposed to be present in other saurischians to the exclusion of Herrerasauridae (Sereno 1999; Yates 2003a): the presence of a sulcus on the dorsolateral margin of the ischium and expansion of the distal end of the ischium. The first character is absent in Herrerasauridae, and the second character is observed in *H. ischigualastensis*, but the condition of these characters for *S. pricei* cannot be assessed due to the incompleteness of the holotype specimen.

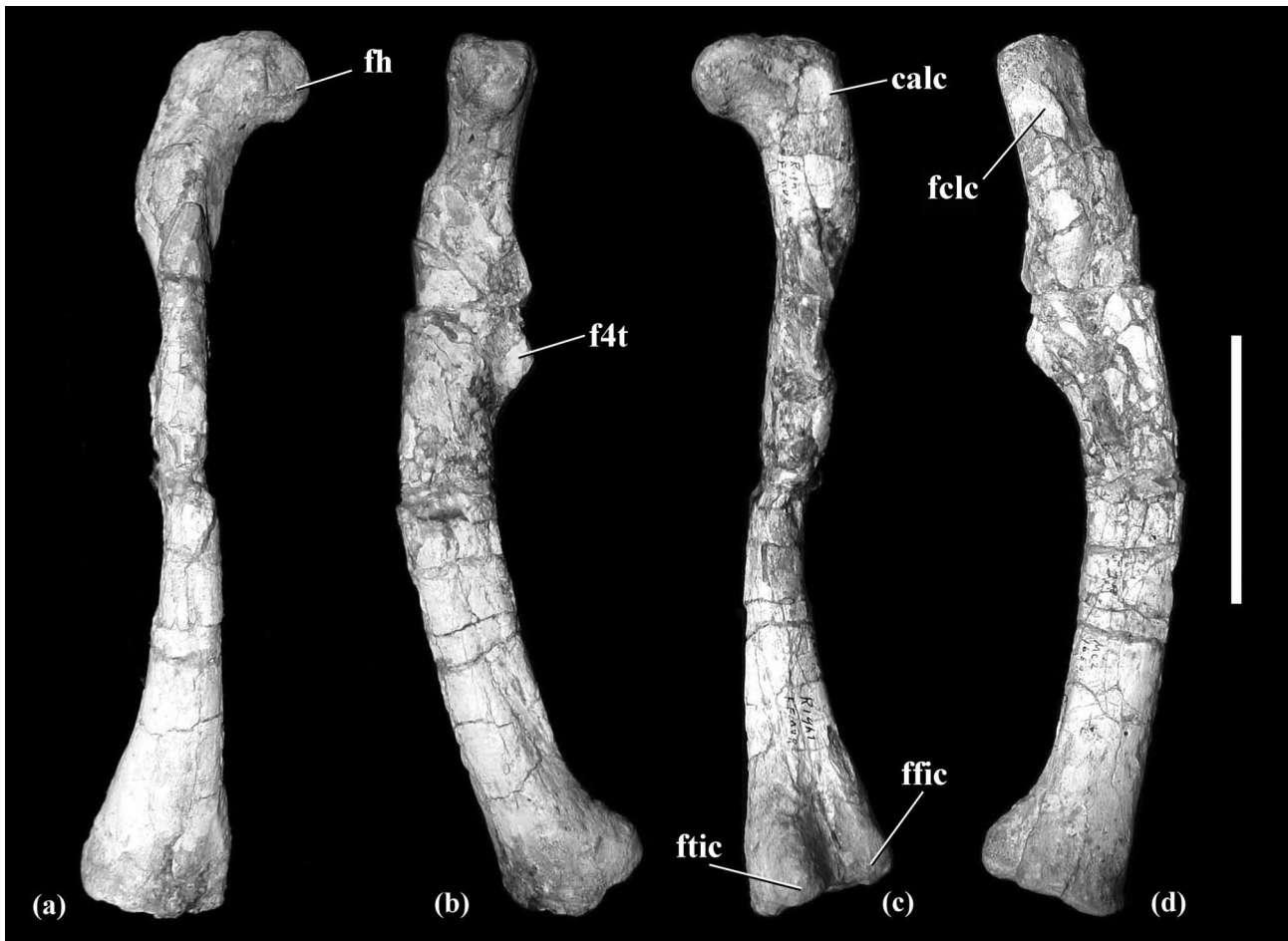


FIGURE 25. Photographs of the right femur in cranial (a), medial (b), caudal (c), and lateral views (d). Abbreviations: **calc**, caudolateral crest; **f4t**, femoral fourth trochanter; **ffic**, femoral fibular condyle; **fclc**, femoral craniolateral crest; **fh**, femoral head; **ftic**, femoral tibial condyle. Scale bar = 7 cm.

Hindlimbs

Of the hindlimbs, the femora, tibiae, and fibulae are preserved (Figs 25–30). They are in a good state of preservation but some deformation caused by post-depositional processes is evident. Colbert (1970) and Galton (1977, 2000a) described these bones in detail; however, a review of the material revealed the need for further discussion of some structures in order to resolve several issues of homology and to more precisely diagnose the species.

Femur. The right femur is better preserved than the left femur, but there is evidence of lateral flattening at the level of the fourth trochanter (Fig. 25a–c). The left femur is broken in two parts: the proximal part is attached via sediment to the block that contains the cranial region of the vertebral column, whereas the distal end is isolated but tightly bounded to a rib fragment along the caudal margin of the shaft (Fig. 26c–d).

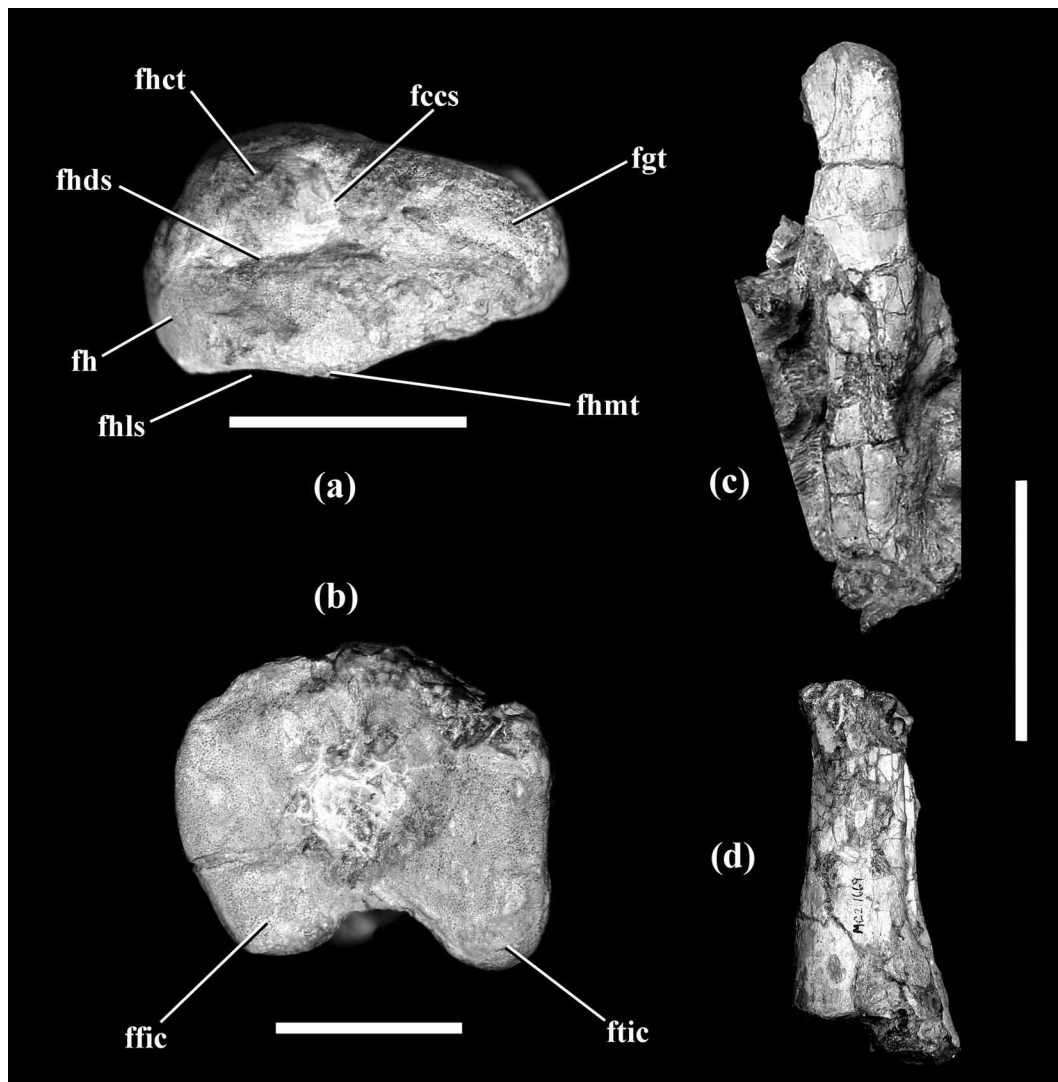


FIGURE 26. Photographs of the right femur in proximal (a) and distal (b) views, the proximal part of the left femur that is attached to vertebral column (see Fig. 8) in laterocaudal view (c), and the isolated distal part of the left femur in lateral view (d). Abbreviations: **fcs**, craniocaudal sulcus on the dorsal surface of the femoral head; **ffc**, femoral fibular condyle; **fgt**, femoral “greater” trochanter; **fh**, femoral head; **fhct**, craniomedial tuberosity of the femoral head; **fhds**, mediolateral dorsal sulcus of the femoral head; **fhls**, sulcus for *ligamentum captis femoris*; **fhmt**, caudomedial tuberosity of the femoral head; **ftic**, femoral tibial condyle. Scale bar for (a–b) = 2 cm; (c–d) = 8 cm.

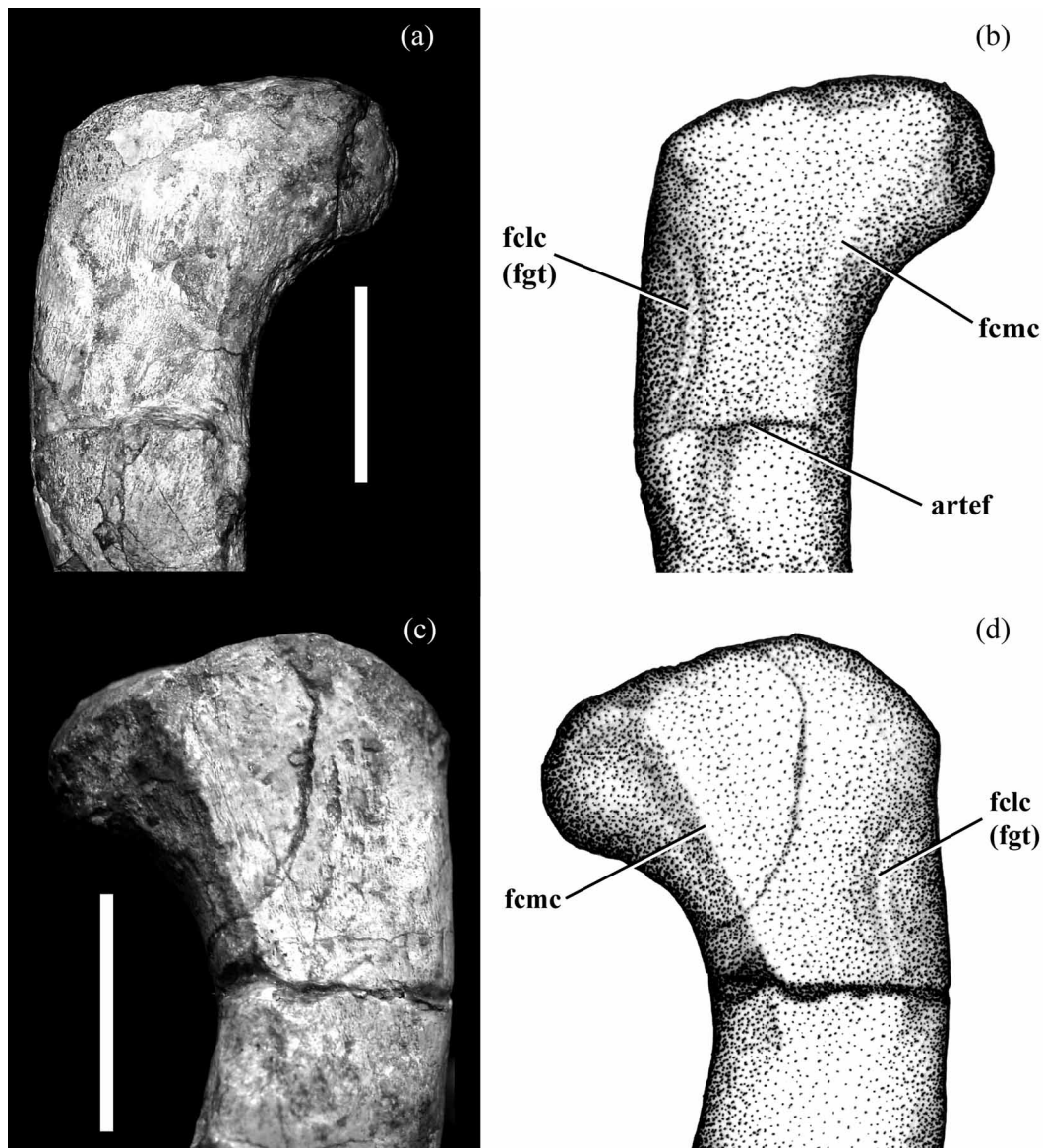


FIGURE 27. Photographs and drawings of the right (a–b) and left (c–d) proximal femora in cranial view. Abbreviations: **artef**, artefactual shelf; **fclc (fgt)**, femoral craniolateral crest, part of the “greater” trochanter; **fcme**, femoral craniomedial crest. Scale bars = 2 cm.

The femoral head is distinctly set off from the shaft, and possesses a medial expansion for articulation with the acetabulum (Figs 25–26a). The ventral edge of the head is not craniolaterally emarginated. In dorsal view, the caudomedial region of the femoral head bears a shallow sulcus for the *ligamentum captis femoris* and a faint medial tuberosity (Fig. 26a); the craniomedial portion is formed by a more prominent tuberosity. Between those tuberosities, in dorsal view, there are two well marked sulci: one extending mediolaterally, separating the craniomedial and caudomedial tuberosities; and another craniocaudally oriented, laterally delimiting the craniomedial tuberosity. The lateral portion of the femoral head is formed by the ‘greater’ trochanter. It begins on the dorsolateral surface and extends ventrally to continue in an S-shape crest on the craniolateral region of the proximal region of the femur (Figs 26a, 27: fclc). This crest was treated as the cranial trochanter (= anterior or lesser trochanter) by Galton (1977, 2000a), but it is here regarded as the dorsolateral trochanter (see ‘Comments’, below). A shallow *fossa articular antitrochanterica* occurs on the caudomedial region of the femoral head. The cranial face of the proximal femur also bears an obliquely

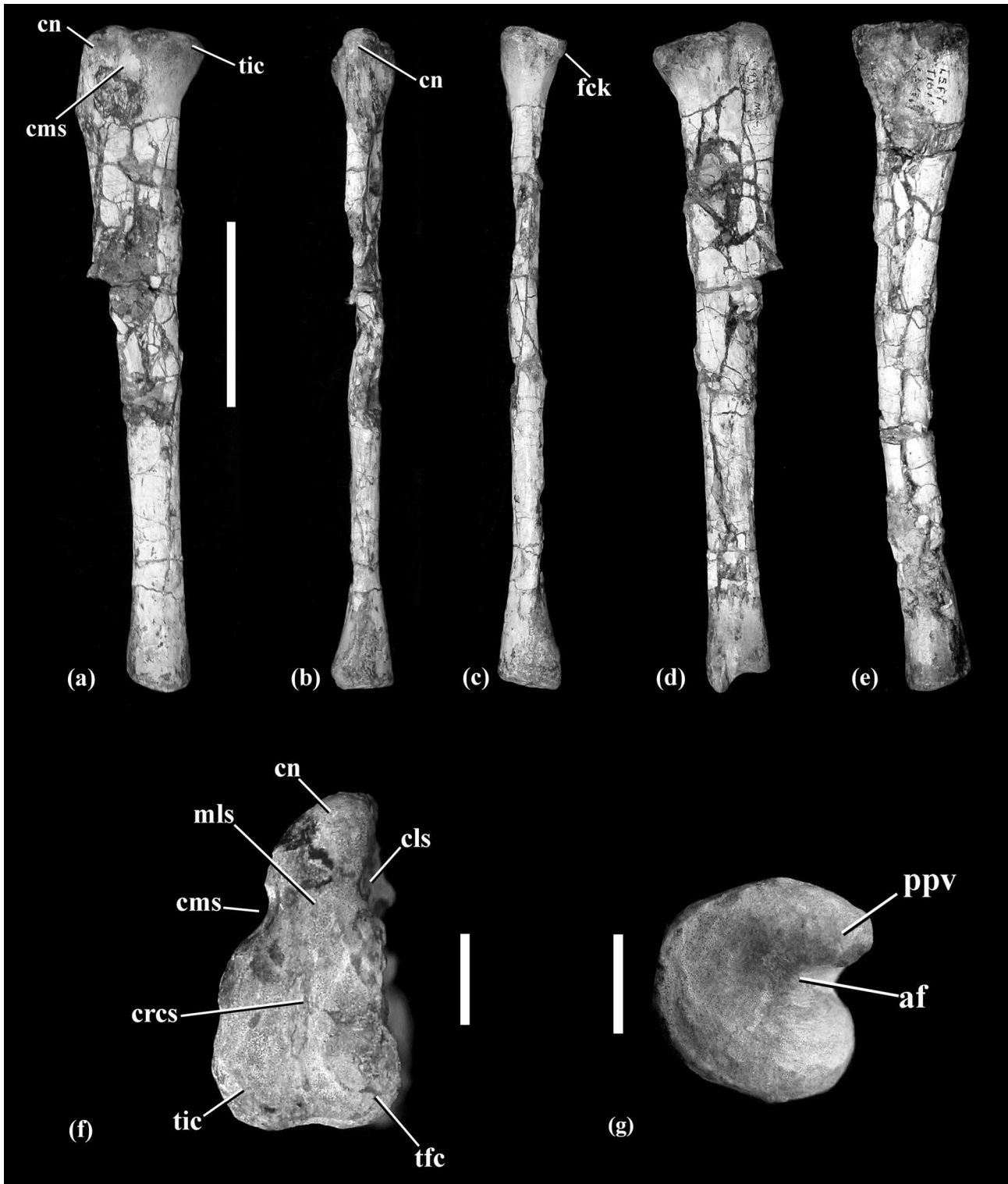


FIGURE 28. Photographs of the right tibia in medial (a), cranial (b), caudal (c) and lateral (d) views; the left tibia in medial view (e), and the right tibia in proximal (f) and distal (g) views. Abbreviations: **af**, articular facet for the ascending process of the astragalus; **cls**, craniolateral sulcus; **cms**, craniomedial sulcus; **cn**, cnemial crest; **crcs**, craniocaudal dorsal sulcus; **fck**, fibular condyle keel; **mls**, mediolateral sulcus; **ppv**, caudoventral process; **tfc**, tibial condyle for fibula; **tic**, tibial inner condyle. Scale bar for (a–e) = 7 cm; (f–g) = 1 cm.

dorsoventrally extended crest on its medial portion (Fig. 27: fcmc). Lateral to this crest, in the region homologous to the cranial trochanter and the trochanteric shelf, a distinct elevated surface is observed on the

right femur, but it appears to be a taphonomic artifact (Fig. 27a–b). In the same region of the left femur, this elevation does not occur; but a rugose surface is present (Fig. 27c–d), suggesting that both the cranial trochanter and trochanteric shelf are reduced. A proximodistally extended and narrow crest for insertion of the *m. puboischiofemoralis internus II* is present in the caudolateral region of the proximal femur (Fig. 25c: calc). The fourth trochanter of *S. pricei* is a prominent process located on the proximal third of the caudal surface of the femur (Fig. 25b). It is damaged in both femora, so it cannot be confirmed whether or not it had a symmetrical outline.

The cranial surface of the shaft is medially convex (Fig. 25a, d). In its distal half, a dorsoventrally extending scar on the medial surface is observed (Fig. 25b). Distally, the cranial margin of the femur is convex, the ventral surface is flat, and the caudal margin is divided into two condyles separated by an intercondylar fossa (Figs 25c, 26b). The medial or tibial condyle is more prominent and caudally rounded than the lateral or fibular condyle (Fig. 26b).

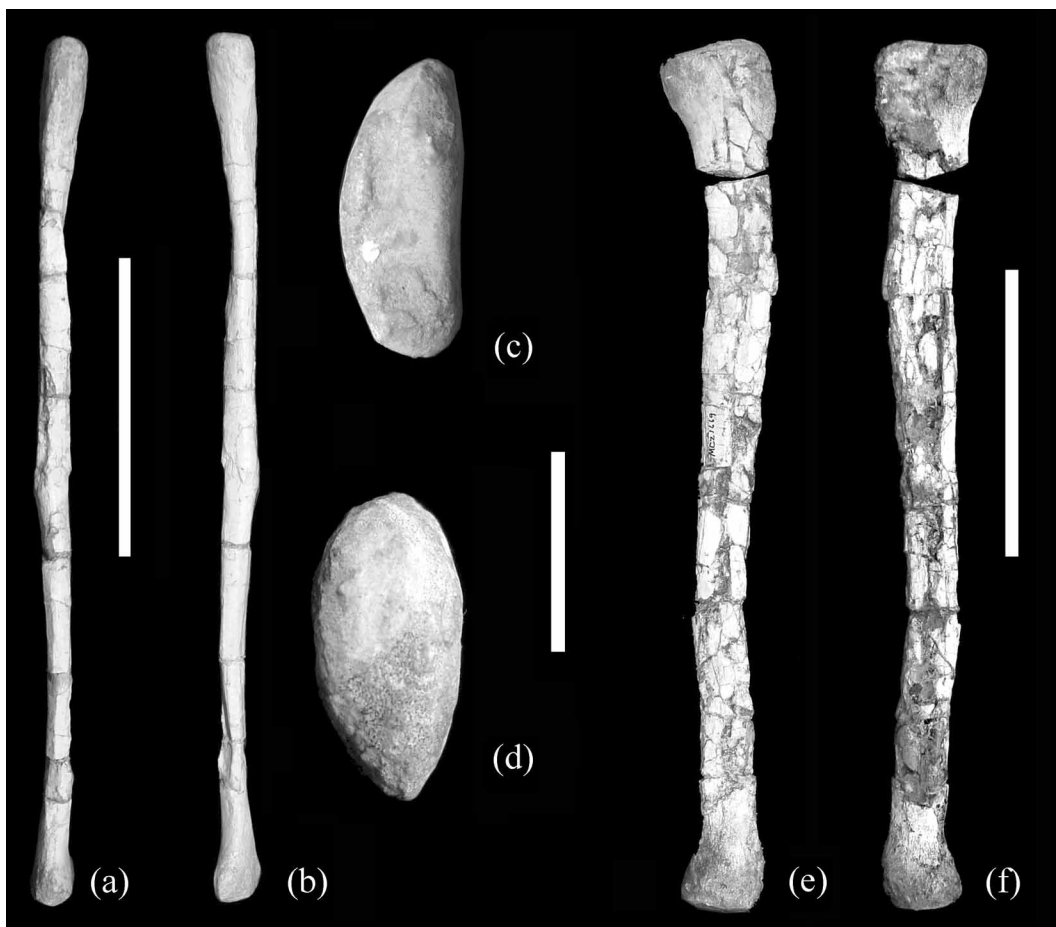


FIGURE 29. Photographs of the left fibula in cranial (a), caudal (b), proximal (e) and distal (f) views, and the right fibula in lateral (c) and medial (f) views. Scale bar for (a–d) = 8 cm; (e–f) = 2 cm.

Tibia. The tibiae are somewhat longer (approximately 107% of the length of) and narrower than the femur (Fig. 28). The right tibia is straight (Fig. 28a–d), while the left one is slightly curved caudally along its length (Fig. 28e). In the cranioproximal region of the right tibia, a prominent cnemial crest is present (Fig. 28a–b, d). Caudal to the cnemial crest, two prominent condyles are present (Fig. 28a, c, f): one laterally positioned (the fibular condyle) and the second medially placed (the inner condyle). The caudal margins of both condyles are equally positioned with regard to the craniocaudal plane of the bone (Fig. 28f). The fibular condyle has a more rounded outline and is shorter craniocaudally than the inner condyle. A small keel that is observed on the caudomedial region of the proximal tibia is the result of the expansion of the fibular condyle (Fig. 28c: fck). The condyles are divided from one another caudally by a slight notch and dorsally by a

shallow median sulcus (Fig. 28f: *crcs*). In addition to this sulcus, another sulcus is present on the dorsal surface of the tibia but is mediolaterally oriented and separates the caudal condyles from the cnemial crest (Fig. 28f: *mls*). In medial view, a proximodistally extending sulcus separates the cnemial crest from the inner condyle (Figs. 28d, f: *cms*), and in lateral view a proximodistally extending sulcus is present between the cnemial crest and the fibular condyle (Fig. 28f: *crls*).

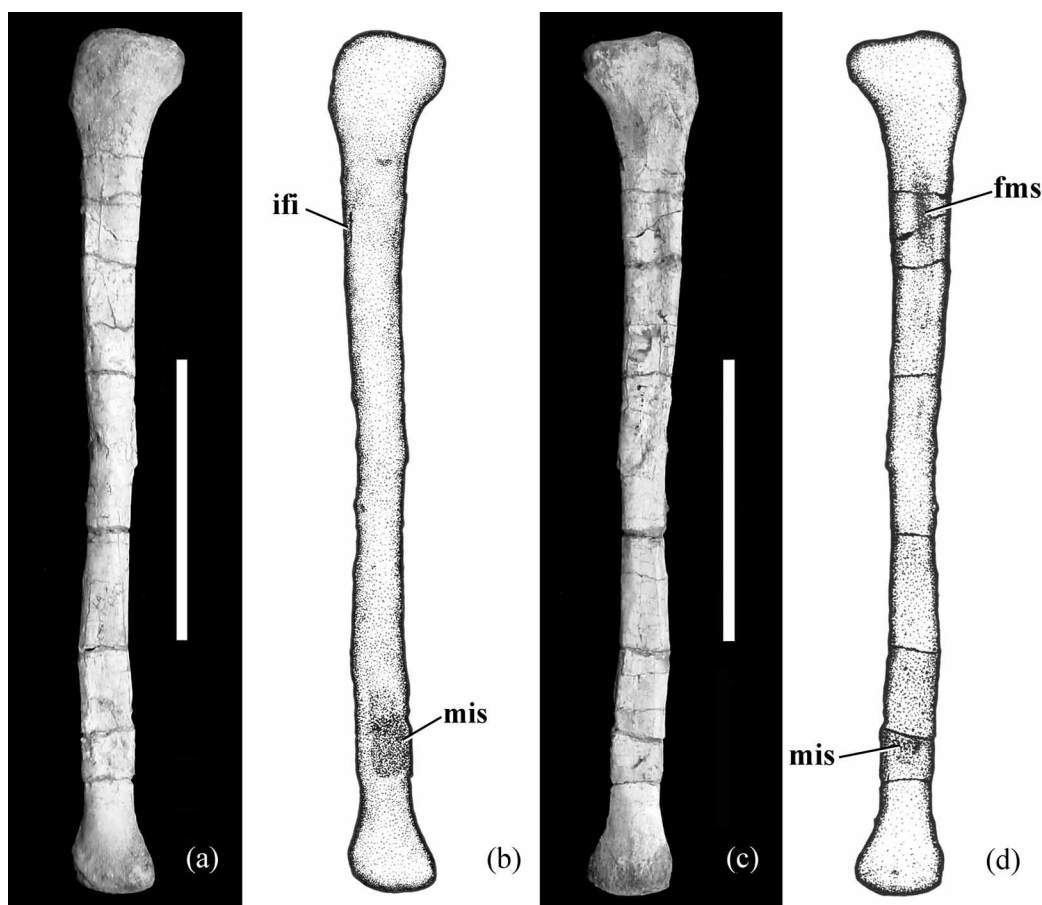


FIGURE 30. Photographs and drawings of the left fibula in lateral (a–b) and medial (c–d) views. Abbreviations: **fms**, fibular medial sulcus; **ifi**, insertion of the iliofibularis muscle; **mis**, scar for muscular insertion. Scale bar = 8 cm.

The shaft of the tibia is transversely compressed and not rounded in cross section. The ridge for fibular attachment seen in several theropods (Rauhut 2003; Smith *et al.* 2007) is absent. A foramen on the lateral surface of the proximal third of the bone is present in *H. ischigualastensis* (Novas 1993), but has not been identified in *S. pricei*. The distal end of the tibia of *S. pricei* (Fig. 28g) has rounded craniomedial, craniolateral, caudomedial, and caudolateral margins. The cranialmost portion of the distal surface is the surface for the articulation with the astragalus, and the caudalmost portion projects ventrally (the ‘posteroventral process’ of Novas [1989]). The articular surface for the astragalus is smooth, laterally rounded and separated proximally from the caudoventral process by a lateral sulcus (Fig. 28g). The tibial caudal flange is weakly developed, and the caudomedial notch observed in the distal tibia of some dinosaurs (see Ezcurra 2006; Langer & Benton 2006; Yates 2007a) is absent in *S. pricei*.

Fibula. Both fibulae are elongate and transversely compressed (Fig. 29a–d). The inner surface of the fibula is flattened at its proximal end, whereas the outer surface is convex, resulting in the proximal part of the fibulae having a sickle shape in proximal view (Fig. 29c). In the left fibula, a broad caudal prominence is present that articulated with the fibular condyle of the tibia (Fig. 29e–f). More distally, on the lateral surface, a narrow proximodistally extending crest is observed in an equivalent position to that present on the fibula of *H. ischigualastensis* (Novas 1993) and is regarded as the tubercle for the insertion of the *iliofibularis*

musculature (Fig. 30a–b). On the medial surface of the proximal third of the fibula, a unique proximodistally extending sulcus is present (Fig. 31c–d). The shaft is transversely compressed at its proximal and distal extremities but more rounded at midlength, as observed by Galton (1977), and the cranial margin of the shaft is consistently wider transversely than the caudal margin. On the lateral and medial surfaces of the distal shaft there is a rounded surface cranioventrally delimited by a narrow bony crest that possibly represents an area of muscle insertion (Fig. 30). The cranial margin of the distal end is transversely broader than the tapering caudal margin and the plane formed by the craniocaudal axis of the distal surface is slightly offset in lateral view with respect to the plane formed by the craniocaudal axis of the proximal surface of the proximal end (Fig. 29b).

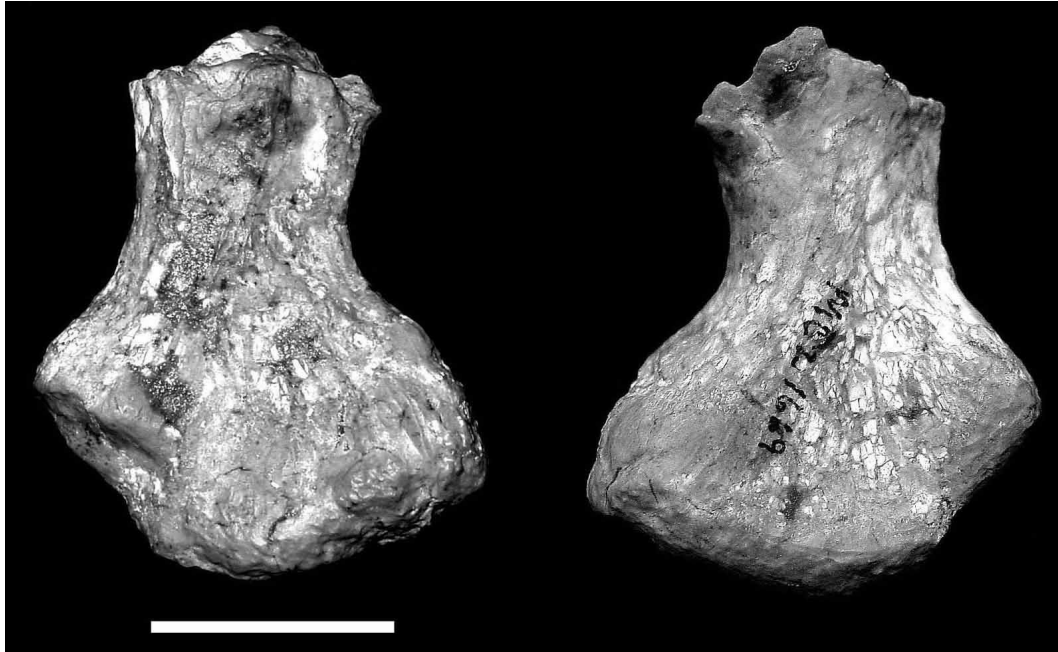


FIGURE 31. Photographs of an undetermined bone, initially described as the right humerus by Colbert (1970). Undetermined orientations. Scale bar = 2 cm.

Comments. The establishment of hypotheses of primary homology for the areas of muscular attachment upon the dinosaurian femur is the cause of many controversies in the literature, and these controversies result mainly from the lack of robust definitions about the presence and position of the femoral trochanters (Hutchinson 2001b). As mentioned above, the cranioproximal region of the femoral head in *S. pricei* displays two distinctive prominences: the craniomedial and craniolateral crests (Fig. 26). The craniomedial crest was previously regarded as autapomorphic for *S. pricei* (Bittencourt & Kellner 2005). However, the specimen PVSJ 373 attributed to *H. ischigualastensis* bears a craniomedial crest (not described by Novas 1993) which is quite similar to that seen on the right femur of *S. pricei*. Based on this observation, the presence of such a crest cannot be regarded as autapomorphic for this species. Other dinosaurs as *Saturnalia tupiniquim* (MCP 3846-PV) and *Syntarsus rhodesiensis* (Raath 1990) also bear this crest, although it is not as thin as in herrerasaurids. It is also noteworthy that not all specimens of *H. ischigualastensis* (e.g. PVL 2566) and *Saturnalia tupiniquim* (e.g. MCP 3844-PV; Langer 2003) have this crest, suggesting some degree of intraspecific variation for this character.

The craniolateral crest was regarded by previous authors as the cranial trochanter (= anterior or lesser trochanter), based on the similarities that this structure displays with the femora of basal sauropodomorphs (Galton 1977, 1985a, 2000a). In contrast, in *H. ischigualastensis* the cranial trochanter is a short process positioned on the craniomedial region of the proximal femur that extends distally as a prominent trochanteric shelf. This configuration is quite similar to that observed in *Saturnalia tupiniquim* (Langer 2003) and the basal theropod *Syntarsus rhodesiensis* (Raath 1969, 1990). Bonaparte *et al.* (1999) reported in *Guaibasaurus*

candelariensis the presence of a cranial trochanter with a similar morphology and topological position to that of *H. ischigualastensis* and *Saturnalia tupiniquim*, the absence of the trochanteric shelf, and the presence of a dorsolateral trochanter, located on the craniolateral region of the femoral head. An additional specimen of *Guaibasaurus candelariensis* (UFRGS PV 0725T) supports such a configuration. Hutchinson (2001b) interpreted the dorsolateral trochanter of *Guaibasaurus candelariensis* as the insertion scar of the *m. puboischiofemoralis externus* (PIFE), and therefore part of the “greater” trochanter. This interpretation can be applied to the craniolateral crest of *S. pricei* and to homologous structures found in *Saturnalia tupiniquim* (Langer 2003), *H. ischigualastensis* (Novas 1993), *Chindesaurus bryansmalli* (Long & Murry 1995), *Eoraptor lunensis* (PVL 521) and some sauropodomorphs, such as *Massospondylus carinatus* Owen, 1854 (Hutchinson 2001b). In addition, the cranial trochanter is reduced and the trochanteric shelf is absent on the femur of *S. pricei*. The presence of these structures was interpreted as synapomorphic for Dinosauriformes by Novas (1996). However, intraspecific variation of these characters occurs among basal dinosauriforms and dinosaurs (e.g. *Silesaurus opolensis*, *Saturnalia tupiniquim*, *Syntarsus rhodesiensis* (Raath 1990; R. Irmis personal communication)).

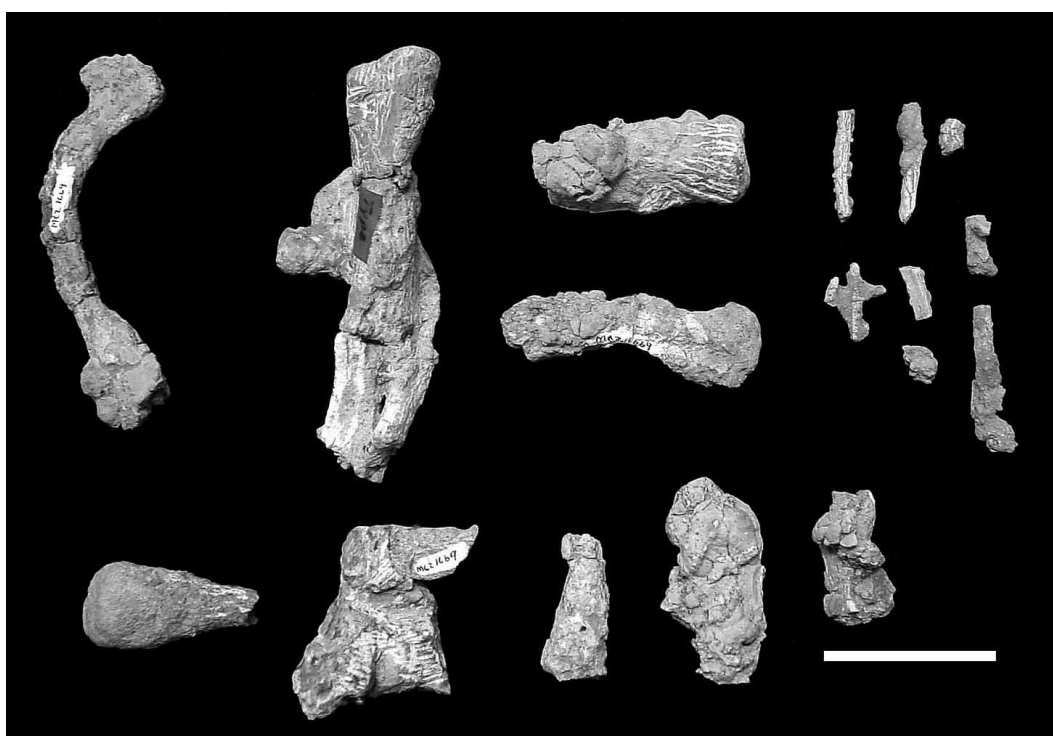


FIGURE 32. Undetermined bone fragments. Scale bar = 5 cm.

The femur of *S. pricei* also possesses a femoral head that is distinctly set off from the shaft, as well as the reduction of the tuberosity that laterally bounds the *ligamentum captis femoris*; both of these characters have been considered dinosaur synapomorphies (Novas 1992, 1993, 1996; Langer *et al.* 1999). Irmis *et al.* (2007a) confirmed the former as a synapomorphy of dinosaurs, apparently acquired convergently with *Effigia okeeffeae*, *Lagerpeton chanarensis*, and *Dromomeron romeri* Irmis *et al.*, 2007a. However, we agree with these authors that the reduced mediolateral tuberosity is present in several archosaurs (Irmis *et al.* 2007a), including basal dinosauriforms (e.g. *Marasuchus lilloensis*: PVL 3870; Sereno & Arcucci 1994) and cannot be used to diagnose Dinosauria. The femoral head of *S. pricei* also bears a ventral ligament sulcus on the caudal surface of the femoral head, a possible dinosaurian synapomorphy (Irmis *et al.* 2007a). A feature commonly found in dinosauriforms is the femoral head articular surface extending underneath the head (Irmis *et al.* 2007a). This character is present in *S. pricei*, but not to the extent observed in *Marasuchus lilloensis* (Sereno & Arcucci 1994; Novas 1996). The craniomedial sulcus on the femoral head observed in *S.*

pricei is also seen in basal dinosauriforms (e.g. *Eucoelophysis baldwini*, Sullivan & Lucas, 1999, Ezcurra 2006; *Silesaurus opolensis*, Dzik 2003) and saurischians (e.g. *Coelophysis bauri*, Padian 1986; *Saturnalia tupiniquim*, Langer 2003), but not in *H. ischigualastensis* (PVL 2566; PVSJ 373; Novas 1993). The sulcus observed in the saurischians cited above is more medially restricted than that seen in basal dinosauriforms.

The size difference between the distal condyles of the femur evolved in different ways in the various early dinosaur lineages. In *S. pricei*, *H. ischigualastensis*, and *Saturnalia tupiniquim* the medial condyle is more prominent than the lateral condyle, whereas in *Guaibasaurus candelariensis*, Sauropodomorpha (e.g. *Plateosaurus engelhardti*; Galton 2000b), Neotheropoda (e.g. *Syntarsus rhodesiensis*; Raath 1990), and basal Ornithischia (e.g. *Lesothosaurus diagnosticus*, *Pisanosaurus mertii*; Weishampel & Witmer 1990) the lateral condyle is more pronounced. The plesiomorphic condition for Dinosauria is ambiguous because in *Marasuchus lilloensis* the distal region of the femur is damaged, although a reconstruction showed both condyles equally expanded (Serenó & Arcucci 1994). Equally expanded distal condyles are also seen in MCZ 7064 (Brinkman & Sues 1987), a fragmentary postcranium recovered from the Ischigualasto Formation and referred to *H. ischigualastensis* (Novas 1993). In *Pseudolagosuchus major*, the medial condyle was described as more expanded than the lateral condyle (Arcucci 1987), the opposite condition to that seen in *Lagerpeton chanarensis* (PVL 4619; Sereno & Arcucci 1993) and *Dromomeron romeri* (Irmis *et al.* 2007a).

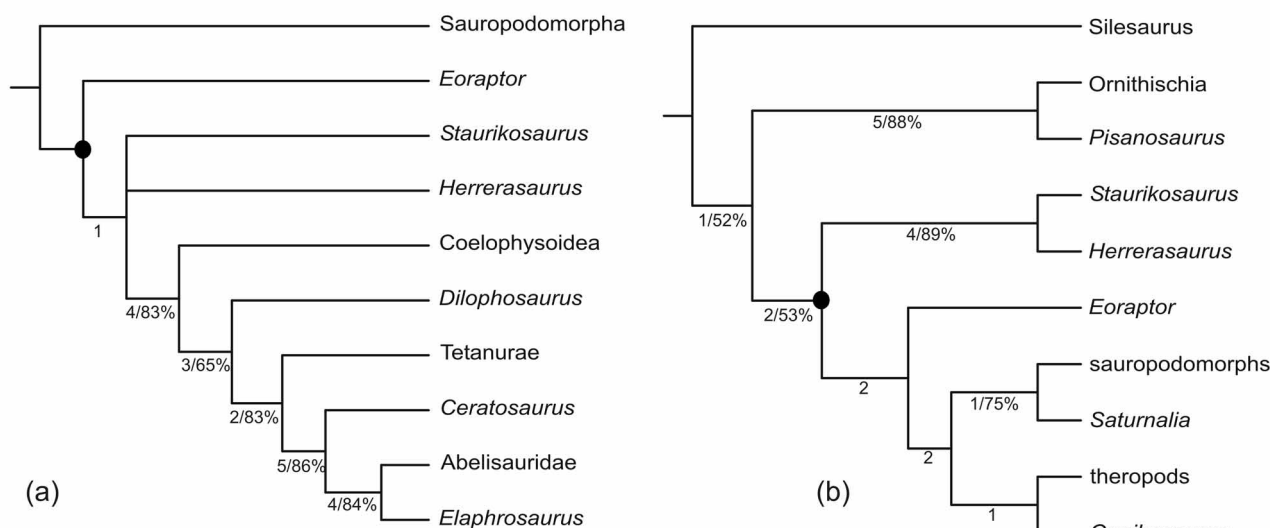


FIGURE 33. Cladograms showing the alternative phylogenetic positions of *Staurikosaurus pricei* and Herrerasauridae: (a) based upon reanalysis of the dataset of Rauhut (2003), showing *S. pricei* as a theropod; (b) based upon reanalysis of the dataset of Langer & Benton (2006), showing *S. pricei* as a basal saurischian. The black circle on cladogram (a) represents the Theropoda node, and on (b), the Saurischia node. Numbers at the branches represent Bremer support (before slash) and bootstrap support above 50% (percentages after slash). Both values were calculated with TNT software following Goloboff *et al.* (2008). The tree generated for the Rauhut (2003) dataset represents the strict consensus of 1488 MPTs, with tree length of 643 steps (CI = 0.426; RI = 0.740). Coelophysoids and tetanurans are represented as a single clade. Only a single MPT was recovered during reanalysis of the Langer & Benton (2006) dataset, with a tree length of 183 steps (CI = 0.574; RI = 0.549). In both cladograms the outgroups were omitted.

The tibia is longer than the femur in *S. pricei*, and Sereno (1991b) proposed this condition as a synapomorphy of Ornithodira. Working at a less inclusive taxonomic level, Benton *et al.* (2000) suggested that this state is a synapomorphy of Sauropodomorpha; however their data matrix scored this state incorrectly for *H. ischigualastensis* – the tibia is shorter than the femur in this taxon (Novas 1993). In *Saturnalia tupiniquim* the tibia and femur are subequal in length. In MCZ 7064 (Brinkman & Sues 1987), proximal

fragments of the articulated right tibia and fibula and the left distal tibia are preserved. The proximal surface of the right tibia is wider than long, which differs from the condition in the holotype of *S. pricei*; moreover, the cnemial crest is more prominent in MCZ 7064 than in *S. pricei*. With regard to the distal end of the tibia, Novas (1992, 1993, 1996) proposed two synapomorphies for Dinosauriformes: 1) presence of a longitudinally extended lateral groove; 2) quadrangular shape of the distal end, in which the medial and caudal surfaces form an obtuse angle in distal view. He furthermore proposed a synapomorphy for Dinosauria: 3) distal end of the tibia overlaps cranioproximally and caudally the ascending process of the astragalus; consequently, the caudal process of the tibia projects ventrally. The first and third of these characters are present in *S. pricei*, but the distal outline of the tibia is rounded and is autapomorphic for this species. Irmis *et al.* (2007a) have recently stated that a rounded distal tibia is present in several non-dinosauriform archosaurs. However, the mediolateral shortening of the cranial surface of the distal tibia of *S. pricei*, associated with rounded acute angles of the craniolateral and caudolateral corners, is unique among dinosauriforms, and is absent in other taxa including *Lagerpeton chanarensis* (PVL 4619), *Dromomeron romeri* (Irmis *et al.* 2007a), *Silesaurus opolensis* (Dzik 2003), and basal dinosaurs (Novas 1989).

Few characters used in the phylogenetic reconstruction of basal dinosaurs pertain to the fibula - the morphology of this bone is considerably less variable than that of other elements, such as the pelvis (Rauhut 2003; Yates 2003a, 2007a, b; Smith *et al.* 2007). The craniodistally extending crest on the medial surface of the proximal fibula seen in several basal theropods (Smith *et al.* 2007) is not present in *S. pricei*. A peculiarity of the fibula of *S. pricei* is the presence of a short proximodistally extending sulcus on the medial surface of the proximal third of the bone (Fig. 30c–d). A similar feature has not been reported in other basal dinosaurs or in immediate outgroups to Dinosauria (Novas 1993, 1996; Sereno & Arcucci 1993, 1994; Bonaparte *et al.* 1999; Dzik 2003). In *Saturnalia tupiniquim*, the medioproximal region is excavated, but the concavity is broader and extends more proximally than that of *S. pricei*. Several theropods also have the medioproximal portion of the fibula concave or with a marked fossa (Rauhut 2003; Smith *et al.* 2007). The structure observed in *S. pricei* is different to that of theropods, because the medioproximal region of the fibula is mostly flat in *S. pricei* and the sulcus is restricted to the proximalmost section of the shaft. Therefore, the condition seen in *S. pricei* is proposed as an autapomorphy of this species.

Both distal and proximal ends of the fibulae are preserved in MCZ 7064. As figured by Brinkman & Sues (1987), the right fibula is articulated with the tibia at its proximal end; the medial surface of the fibula is slightly concave and the cranial portion is narrow and fits into the lateral sulcus of the tibia, differing from the condition in *S. pricei* in which the medial surface is flat. This configuration gives the fibula of MCZ 7064 a more strongly developed sickle shape in proximal view than seen in *S. pricei*.

Discussion

In order to assess the phylogenetic position of *S. pricei*, we reran two cladistic analyses dealing with basal dinosaurs (Rauhut 2003; Langer & Benton 2006). These datasets were selected for different reasons. The matrix of Rauhut (2003) is focused on Theropoda, and allows an assessment of the characters that allegedly support the inclusion of herrerasaurids within that clade. The matrix of Langer & Benton (2006) includes several characters previously proposed as synapomorphic for herrerasaurids, thus allowing the assessment of a diagnosis for this clade. In addition, this matrix samples characters regarded as synapomorphic for the main dinosaur lineages, and the proposed alternative positions of *S. pricei* within dinosaurs (as either a theropod or a basal saurischian) can be evaluated. The results of the analyses conducted here are compared with other published phylogenetic analyses (i.e. Sereno 1999; Yates 2003a, 2007a, b; Ezcurra 2006; Ezcurra & Novas 2007; Irmis *et al.* 2007a; Smith *et al.* 2007).

The matrices were analysed with the software TNT for Windows (Goloboff *et al.* 2008), by implementing the option 'traditional search', with the 'tree bisection and reconnection' algorithm for branch-swapping (1000 random addition sequence replicates). The most parsimonious trees (MPTs) found on the first analysis

were submitted to a second branch swapping procedure, in order to check for possible additional MPTs. This procedure was especially important for the reanalysis of the matrix of Rauhut (2003), which encompasses a large number of taxa and characters. The original characteristics of the matrices regarding character weighting and ordering, outgroups, and excluded taxa were maintained, resulting in a matrix of 51 taxa and 224 characters for the dataset of Rauhut (2003) and 11 taxa with 98 characters for the dataset of Langer & Benton (2006). In the case of the Rauhut (2003) dataset, the original analysis used three outgroups (*Euparkeria capensis* Broom, 1913, *Marasuchus lilloensis*, and *Ornithischia*). However, TNT only employs one taxon as the outgroup and so *Euparkeria capensis* was chosen; a constraint was created to enforce the monophyly of Saurischia, and force both *Ornithischia* and *Marasuchus lilloensis* as successive outgroups to Saurischia. In addition, the scorings for *S. pricei* were reevaluated in the matrices of Rauhut (2003) and Langer & Benton (2006), based upon the anatomical redescription presented here (Table 1). The data scored for the remaining taxa in the original matrices was in general left unchanged for the analyses conducted here. However, according to M. Langer (personal communication), the matrix published in the final version of Langer & Benton (2006) includes a typographical error for character 78 of *Guaibasaurus candelariensis*, which was incorrectly scored as 0/1 instead of 1/2 (see also Sereno 2007). Here, we used the corrected version of the matrix.

In this section we briefly comment the general results regarding the topology of the trees, with emphasis on the phylogenetic position of *S. pricei*. The dataset of Rauhut (2003) resulted in 1488 MPTs of 643 steps, the consensus of which is shown in Figure 34a. The herrerasaurids (*S. pricei*, *H. ischigualastensis*) were not recovered as a clade, but they fall well within Theropoda, with *Eoraptor lunensis* positioned more basally. These results differ mainly from the analysis of Rauhut (2003) in the smaller number and shorter length of MPTs and in the non-monophyly of *S. pricei* with *H. ischigualastensis*. The positioning of the herrerasaurids (or, at least, *H. ischigualastensis*) as theropods agrees with other phylogenetic analyses (Sereno *et al.* 1993; Novas 1996; Benton 1999; Sereno 1999; Rauhut 2003; Bittencourt & Kellner 2004; Ezcurra & Cuny 2007; Ezcurra & Novas 2007). The reanalysis of the Langer & Benton (2006) dataset resulted in a single MPT (Fig. 34b), the topology of which is not different from that recovered by Langer & Benton (2006), although it is shorter in length (184 steps rather than 203 steps). Dinosaurs are monophyletic, and Herrerasauridae (*S. pricei*, *H. ischigualastensis*) is positioned at the base of Saurischia, outside of Eusaurischia. This result is similar to that found by other authors (Yates 2003a, 2007a, b; Ezcurra 2006; Irmis *et al.* 2007a; Smith *et al.* 2007). Below, we discuss alternative phylogenetic positions of *S. pricei* based on the analyses conducted here, as well as comparisons with other phylogenetic studies.

TABLE 1. Character scoring for the datasets used in this paper, applied to *Staurikosaurus pricei*. For list of characters and character states, see original references.

Rauhut (2003)
????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?0?0?0?0?? ?00?0000?? ???0?0000 00?000010 0010020000 01?0000?? ?????????? ?????????? ?????????? ?????00000 00000?100? ?001101?00 ?0?00000?0 0000000?00 00????????? ????
Langer & Benton (2006)
0????????? ?????????00? 0000000?? 1?1?00??10 01111111?? ?????????? ??????????021 010000101? ?01?1000?0 0?????????

The dinosaurian affinity of *Staurikosaurus pricei*

Although only a very few authors doubt the monophyly of Dinosauria (e.g. Thulborn 1975; Thulborn 2006), there is little consensus as to how this clade can be diagnosed. Previous studies have proposed a set of dinosaurian synapomorphies (Bakker & Galton 1974; Gauthier 1986; Novas 1989, 1992, 1996; Sereno 1999), and recent reviews have regarded some of these characters as valid (Benton 1990, 1999, 2004; Langer 2004; Langer & Benton 2006; Irmis *et al.* 2007a; Nesbitt *et al.* 2007). However, Fraser *et al.* (2002: 87) claimed that

several synapomorphies present in ‘true dinosaurs’ are not observed in herrerasaurids; they therefore suggested that herrerasaurids could not be considered as dinosaurs (i.e. they considered herrerasaurids to fall outside the Ornithischia + Saurischia split; see also Padian & May 1993). Nevertheless, this hypothesis has not received support from most subsequent studies which assessed all available evidence: i.e. the majority of character evidence supports the position of herrerasaurids within Dinosauria (Novas 1996; Rauhut 2003; Yates 2003a; Langer 2004). Langer and Benton (2006: 316–317) listed 15 putative synapomorphies of Dinosauria (not included in their matrix), of which eight were considered unambiguous: 1) transversely reduced ischiadic medioventral lamina; 2) inturned femoral head; 3) tibial descending process fits caudal to astragalar ascending process; 4) astragalus with a straight caudal margin; 5) flat to concave proximal calcaneum; 6) distal tarsal IV proximodistally flat; 7) broad weight-bearing portion of metatarsus; 8) metatarsals II and IV subequal in length. Only the first three of these characters can be confirmed in *S. pricei*; the remaining characters pertain to elements not preserved in the holotype. These three characters suggest that *S. pricei* is indeed a dinosaur. In addition to these characters proposed as synapomorphic for Dinosauria, reanalysis of the matrix of Langer & Benton (2006) suggests the following additional unambiguous synapomorphies: 1) post-temporal opening is a fissure between the skull roof and braincase; 2) epiphyses present in post-axial cranial cervical vertebrae; 3) first primordial sacral rib dorsally expanded on its cranial margin; 4) distal apex of the deltopectoral crest distal to the proximal 30% of the humeral shaft; 5) ventral margin of iliac acetabulum concave; 6) ‘trochanteric shelf’ absent on the lateral surface of the proximal femur; 7) fourth trochanter asymmetrical, with distal margin forming a steeper angle to the shaft; 8) articular facet for fibula occupies less than 0.3 of the transverse width of the astragalus. Of these, characters 2, 3, 5, and 6 are present in *S. pricei* (the remaining characters deal with non-preserved parts of the skeleton), yielding additional support for its position within dinosaurs. The analysis of Irmis *et al.* (2007a) yields other potential synapomorphies for Dinosauria: pubic process of the ischium waisted and separated from the ilial peduncle; presence of a ventral ligament sulcus on the caudal side of the femoral head; *fossa articularis antitrochanterica* on femoral head expanded asymmetrically onto caudomedial surface. The latter two characters are present in *S. pricei*, while the former character cannot be evaluated due to missing information.

***Staurikosaurus pricei* as a herrerasaurid**

Prior to the work of Novas (1992), who identified several characters thought to unite *S. pricei* and *H. ischigualastensis* in a single clade (Fig. 34b), the hypothesis of a close relationship between both species forming the clade Herrerasauridae was contested by several authors (Galton 1977; van Heerden 1978; Brinkman & Sues 1987; Sues 1990). Herrerasauridae is nowadays widely accepted as monophyletic and well-supported by a suite of postcranial characters (Novas 1993, 1996, 1997; Sereno & Novas 1993; Sereno 1999; Kellner & Campos 2000; Rauhut 2003; Bittencourt & Kellner 2004; Langer 2004; Langer & Benton 2006). Reanalysis of the matrix of Langer & Benton (2006) resulted in the following synapomorphies for Herrerasauridae: 1) centra and neural spines of caudal dorsal vertebrae axially shortened; 2) ribs of the first primordial sacral vertebra are deeper than half the depth of the ilium; 3) neural spines of proximal caudal vertebrae dorsally directed; 4) prezygapophyses of distal caudal vertebrae overlap more than a quarter of the adjacent centrum; 5) ventral portion of the postacetabular process does not bear a deep fossa in its caudal portion for the origin of *M. caudofemoralis brevis* (= reduction of the brevis fossa); 6) lateral margin of the pubis caudally folded at its distal portion, with the pubic pair showing a U-shaped transverse section; 7) caudolateral flange of distal tibia short and does not project to the fibula. Characters 1–3 are seen only in herrerasaurids, but character 4 is also observed in theropods (Gauthier 1986; Novas 1992), and was formerly used to support a phylogenetic position of herrerasaurids within Theropoda (e.g. Sereno 1999). In the phylogenetic hypothesis of Langer & Benton (2006) this character is interpreted as independently acquired in theropods and herrerasaurids. Characters 5 and 7 are reversals to the ancestral state for Dinosauria; usage of these characters to diagnose Herrerasauridae is unproblematic because the position of this clade within dinosaurs is well-supported (see above). The presence of plesiomorphic character states in taxa of a given in-group should not be surprising, because evolution is prolific in every kind of homoplasy, i.e. convergences,

parallelisms and reversals (Amorim 1997). In the reanalyses of the dataset of Rauhut (2003) conducted here, herrerasaurids do not appear as a clade in the strict consensus tree, possibly due to the non-inclusion of characters considered synapomorphic for *H. ischigualastensis* and *S. pricei* (Langer & Benton 2006).

Among the characters presented above, *Chindesaurus bryansmalli* and *Caseosaurus crosbyensis* only definitely possess the reduction of the brevis fossa, but the materials attributed to these taxa are too incomplete to yield accurate conclusions as to their phylogenetic position. The shortening of the caudal dorsal vertebrae reported for *Chindesaurus bryansmalli* (Novas 1997) was contested by Nesbitt *et al.* (2007). According to Irmis *et al.* (2007a), the presence of two sacral vertebrae unites *H. ischigualastensis* and *Chindesaurus bryansmalli*. However, as stated by Sereno (2007), *H. ischigualastensis* bears three sacral vertebrae (two sacrals plus one dorsosacral), as does the basal dinosauriform *Silesaurus opolensis* (Dzik & Sulej 2007). In *S. pricei*, there are also three sacrals, although this differs from *H. ischigualastensis* by the incorporation of a caudal element, rather than a dorsal element, into the sacrum. Therefore the presence of two sacral vertebrae is not a synapomorphy of Herrerasauridae, and *Chindesaurus bryansmalli* and *Caseosaurus crosbyensis* cannot be unequivocally assigned to Herrerasauridae on the basis of available evidence.

The saurischian affinities of *Staurikosaurus pricei*

The reanalysis of the matrix of Langer & Benton (2006) identified the following unambiguous synapomorphies for Saurischia: 1) narial fossa expanded in the rostroventral corner of the naris; 2) lacrimal folds over the caudal/dorsocaudal part of antorbital fenestra; 3) ventral ramus of squamosal forms less than half of the caudal border of the lower temporal fenestra; 4) atlantal articulation facet in axial intercentrum concave, with upturned lateral borders; 5) centra of postaxial cranial cervical vertebrae longer than the axis centrum; 6) epiphyses present in caudal cervical vertebrae (6-9); 7) hyposphene-hypantrum articulations present in trunk vertebrae; 8) humerus shorter than 0.6 of the length of the femur; 9) manual length (measured as the average length of digits I-III) accounts for more than 0.4 of the total length of humerus plus radius; 10) distal carpal V absent; 11) extensor pits in metacarpals I-III deep and asymmetrical; 12) first phalanx of manual digit I is the longest non-ungual phalanx of the manus; 13) twisted first phalanx present in manual digit I; 14) shaft of metacarpal IV significantly narrower than that of metacarpals I-III; 15) manual digit V lacks phalanges; 16) ischiadic medioventral lamina is restricted to its proximal third. Only character 16 is present in *S. pricei*, and the remaining characters cannot be evaluated for *S. pricei* due to the incomplete preservation of the holotype. Irmis *et al.* (2007a) suggested the following additional synapomorphies of Saurischia: 1) presence of a caudal recess between the postzygapophysis and the neural arch in the cranial cervical vertebrae; 2) distal portion of the pubis at least slightly expanded craniocaudally; 3) medioventral lamina of the ischium restricted to the proximal third of the bone. All of these features are present in the holotype of *S. pricei*. However, Langer & Benton (2006) have interpreted the presence of a caudal recess between the postzygapophysis and the neural arch in the cranial cervical vertebrae as a dinosaurian synapomorphy, and the distal bulging of the pubis as a saurischian symplesiomorphy. Therefore, concerning the synapomorphies of Saurischia, the data presented by Irmis *et al.* (2007a) and Langer & Benton (2006) agree only in the medioventral restriction of the ischial lamina as a derived character for this clade. The presence of this feature in *S. pricei* suggests that this species is a saurischian, although such an assignment is weakly supported.

Theropoda or basal Saurischia?

One of the main points of disagreement regarding the phylogenetic position of herrerasaurids within Dinosauria is whether they are theropods (Fig. 34a; Sereno & Novas 1992; Novas 1993, 1997; Sereno 1999; Kellner & Campos 2000; Rauhut 2003; Bittencourt & Kellner 2004; Ezcurra & Cuny 2007; Ezcurra & Novas 2007) or basal saurischians excluded from Eusaurischia *sensu* Langer 2004, i.e. Sauropodomorpha + Theropoda (Fig. 34b; Langer *et al.* 1999; Padian *et al.* 1999; Yates 2003a, 2005, 2007a, b; Yates & Kitching 2003; Langer 2004; Ezcurra 2006; Langer & Benton 2006; Irmis *et al.* 2007a). Our analyses of the dataset of Rauhut (2003) resulted in the following unambiguous synapomorphies for Theropoda: 1) fifth manual digit

present and fourth manual digit reduced to a metacarpal with only one phalanx; 2) well-developed extensor pits on the dorsal surface of the distal end of metacarpals; 3) penultimate phalanx of the third finger longer than the first phalanx. In addition, the herrerasaurids share the following characters with other theropods excluding *Eoraptor lunensis*: 4) neural spines of caudal dorsal vertebrae are significantly higher than long (characters 2–4 are also cited in Ezcurra & Novas [2007]). Characters 1–3 cannot be assessed in *S. pricei* due to poor preservation, and the derived state for character 4 is absent in coelophysoids (Rauhut 2003). The analysis of Ezcurra & Novas (2007) yields additional characters supporting the theropod affinity of *H. ischigualastensis*, but none can be evaluated in *S. pricei* due to poor preservation. In addition, the datasets of Rauhut (2003) and Ezcurra & Novas (2007) poorly sample sauropodomorph taxa and characters supposedly synapomorphic for Eusaurischia (Yates 2003a, 2007a, b; Langer & Benton 2006). Other matrices available in the literature which are focused on theropods (i.e. which include a more complete sampling of theropod taxa than of other dinosaurs) find herrerasaurids to be basal saurischians excluded from Eusaurischia (Yates 2005; Ezcurra 2006; Smith *et al.* 2007). A number of characters cited by Sereno (1999) support a close relationship between herrerasaurids and neotheropods. However, several of them cannot be evaluated in *S. pricei* due to poor preservation: the ectopterygoid fossa; the intramandibular joint; axial intercentrum width more than maximum width of axial centrum; and additional characters associated with the manus. Other proposed characters (Sereno 1999) are absent or cannot be assessed in the available material of *S. pricei*: cervical epiphyses prong-shaped; distal width of the pubic blade narrower than the proximal width; arched iliac brevis fossa; and cranial attachment depression on the distal end of the femur. The presence of the ischial obturator process and the extreme hollowing of centra and long bones, characters proposed as uniquely shared by herrerasaurids and neotheropods (Sereno 1999), require more precise definition in order to be accurately assessed in basal dinosaurs (Langer & Benton 2006). Two characters discussed by Sereno (1999) are indeed shared by neotheropods and the herrerasaurids, including *S. pricei*: the reduced width of the distal scapular with regard to its length and the elongated prezygapophyses of the distal caudal vertebrae. However, the matrix of Sereno (1999) has been criticized due to poor character sampling (Rauhut 2003), problematic definitions of some characters and character states (Langer & Benton 2006), and the inclusion of taxa with questionable monophyly, such as Prosauropoda and Ceratosauria (Carrano *et al.* 2002, 2005; Rauhut 2003; Yates 2003a), or with problematic taxonomy, such as *Chindesaurus bryansmalli* (Nesbitt *et al.* 2007). Although these studies clearly show that a number of characters are shared by herrerasaurids and neotheropods, a more extensive phylogenetic analysis encompassing a larger number of species-level sauropodomorph and ornithischian taxa is needed to test whether the characters cited above support the placement of herrerasaurids within Theropoda.

The analysis of Langer & Benton (2006) resulted in herrerasaurids being positioned as basal saurischians, outside Eusaurischia. The synapomorphies that support the clade *Eoraptor lunensis* + Eusaurischia are: 1) maxilla approaches or enters the external naris; 2) rostral margin of the maxilla and its ascending process concave, with the base of the ascending process continuous with the rostral margin of the bone, or markedly offset from it; 3) nasal forms part of the dorsal border of the antorbital fossa; 4) nasal possesses a caudolateral process that envelops part of the rostral ramus of the lacrimal; 5) ventral ramus of the lacrimal long, forming about 0.75 or more of the maximum preorbital skull height, and mainly vertical; 6) width of metacarpal I at the middle of the shaft accounts for more than 0.35 of the total length of the bone; 7) lateral condyle of the metacarpal I is more expanded distally than the medial one. Additionally, the following characters support Eusaurischia: 8) caudoventral premaxillary process is restricted to the ventral border of the external naris; 9) centra of caudal cervical vertebrae longer than those of cranial trunk vertebrae; 10) radius shorter than 0.8 of the length of the humerus; 11) digit I with metacarpal subequal or shorter than the ungual; 12) metacarpal II subequal or longer than metacarpal III; 13) distal end of ischium is dorsoventrally expanded. Only character 9 can be evaluated for *S. pricei*, and it is indeed absent in this species, while other characters deal with non-preserved parts of the holotype. Yates (2007a) proposed additional characters that support a close affinity between Sauropodomorpha and Theropoda to the exclusion of herrerasaurids (see also Yates 2003a, 2007b). These characters include: a large subnarial foramen, located on the rim of the narial fossa or inside it; pointed

caudolateral process of the nasal overlapping the lacrimal; rostral profile of the maxilla with a strong inflection at the base of the ascending ramus, creating a rostral ramus with parallel dorsal and ventral margins; length of the ungual of manual digit two is 75–100% of that of the ungual of manual digit one. None of these characters can be evaluated for *S. pricei* due to poor preservation. Smith *et al.* (2007) also cited several characters for Eusaurischia, to the exclusion of herrerasaurids and *Eoraptor lunensis*. Three of these proposed synapomorphies can be assessed for *S. pricei*: iliac supraacetabular crest hook-like, extending laterally and also curving ventrally to cover the dorsal portion of the acetabulum in lateral view; ridge on lateral surface of tibia for connection with fibula; craniocaudal breadth of the medial margin of the distal tibia is broader than the lateral margin. These character states are absent in the holotype of *S. pricei*, yielding additional support for its placement as a non-eusaurischian.

A complete review of the characters and character states scored for basal dinosaurs in all of the abovementioned matrices is beyond the scope of this paper. Nevertheless, based on published data, a position of herrerasaurids as basal saurischians outside of Theropoda + Sauropodomorpha appears to be better supported than the placement of Herrerasauridae within Theropoda. However, it is also true that most synapomorphies of Eusaurischia cannot be assessed in *S. pricei* due to poor preservation. Accordingly, the phylogenetic position of *S. pricei* is constrained by the strongly supported sister-group relationship between *S. pricei* and the well-known *H. ischigualastensis* within Herrerasauridae.

Comparisons of cladistic analyses dealing with basal dinosaurs is a complicated task, since most analyses oversample taxa and characters regarding a single dinosaurian clade with respect to other groups. This is the case for the published analyses of basal theropods (Rauhut 2003; Yates 2005; Ezcurra 2006; Ezcurra & Novas 2007; Smith *et al.* 2007), sauropodomorphs (Yates 2003a; 2007a, b), and ornithischians (Butler 2005; Butler *et al.* 2007, 2008). Other datasets use a large number of supraspecific taxa as operational taxonomic units (Sereno 1999; Langer 2004, Langer & Benton 2006). Both procedures may lead to erroneous assignment of highly homoplastic characters as synapomorphies. In addition, each matrix uses a different set of characters, preventing an accurate reevaluation of earlier proposed synapomorphies. Further analyses with better sampling of species and characters related to the main dinosaur lineages (Ornithischia, Herrerasauridae, Sauropodomorpha, Theropoda), including recent discoveries from Late Triassic deposits of South America (Ezcurra 2008; Martinez *et al.* 2008), might help to clarify phylogenetic relationships among basal dinosaurs.

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