

# THE PECTORAL GIRDLE AND FORELIMB ANATOMY OF THE STEM-SAUROPODOMORPH SATURNALIA TUPINIQUIM (UPPER TRIASSIC, BRAZIL)

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**Abstract:** Description of the pectoral girdle (scapulocoracoid) and forelimb (humerus, radius and ulna) elements of two specimens of *Saturnalia tupiniquim*, a stem-sauropodomorph from the Upper Triassic Santa Maria Formation, southern Brazil, reveals a distinctive set of plesiomorphic, derived and unique traits, which shed light on the function and phylogenetic significance of these skeletal elements within early dinosaurs. Autapomorphic features of *S. tupiniquim* include, among others, an unusually long olecranon process of the ulna. Its function is still unclear, but it might have helped to sustain a quadrupedal gait, as inferred from the structure of the entire forearm.

Although less clear than previously suggested, some traits of *S. tupiniquim*, such as a long deltopectoral crest and a broad distal humeral end, are indicative of its sauropodomorph affinity. The taxon also bears several features previously regarded as autapomorphic of *Herrerasaurus ischigualastensis*, alluding to their broader distribution among basal dinosaurs. Variations within *S. tupiniquim* are mainly robustness-related and do not necessarily imply taxonomic distinctions.

**Key words:** *Saturnalia tupiniquim*, Dinosauria, Brazil, Triassic, pectoral girdle, forelimb, anatomy.

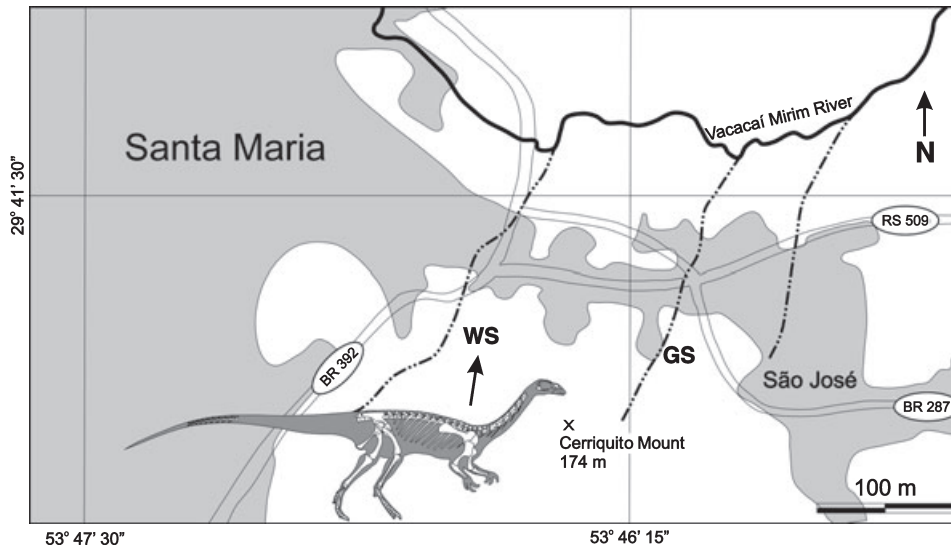
THE shoulder girdle and forelimb osteology of early dinosaurs is poorly known. Apart from the relatively abundant material referred to *Herrerasaurus ischigualastensis* (Reig 1963; Novas 1986; Brinkman and Sues 1987; Sereno 1993), and the still undescribed skeleton of *Eoraptor lunensis* (Sereno *et al.* 1993), most of the reported remains are incomplete. A nearly complete scapulocoracoid is part of the holotype of *Guaibasaurus candelariensis* (Bonaparte *et al.* 1999), but only scapula fragments and a dubious proximal humerus were assigned to *Staurikosaurus pricei* (Galton 2000; Bittencourt 2004). Within other putative Triassic dinosaurs, incomplete scapula and forelimb elements are among the material referred to *Saltopus elginensis* (von Huene 1910), *Spondylosoma absconditum* (Galton 2000) and *Agnosphitys cromhallensis* (Fraser *et al.* 2002).

In the austral summer of 1998, fieldwork conducted by the Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, collected three partial skeletons of a basal dinosaur in the red mudstone that typically crops out on the outskirts of Santa Maria (Text-fig. 1), in south Brazil (Langer *et al.* 1999; Langer 2005a). The material is only partially prepared, but a comprehensive description of the pelvis and hindlimb of *Saturnalia*

*tupiniquim* is available (Langer 2003). Among the other elements resulting from preparation of two of the skeletons are partial shoulder girdles and forelimbs, which are the subject of the present contribution.

Until now, because of the abundance of its material, *Herrerasaurus* has been the main basis on which the anatomy of the shoulder girdle and forelimb of basal dinosaurs was assessed. The constraint of using the condition in a single taxon, with its own set of derived and unique features, as almost the sole window on the plesiomorphic anatomy of a clade as diverse as the Dinosauria might lead to significant biases. The data available for *S. tupiniquim* is believed to alleviate this bias, adding morphological diversity to produce a better picture of the general anatomy of the shoulder girdle and forelimb of basal dinosaurs in general, and basal saurischians in particular.

*Institutional abbreviations.* BMNH, the Natural History Museum, London, UK; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MB, Museum für Naturkunde, Berlin, Germany; MCN, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia PUCRS, Porto Alegre, Brazil; PVL,



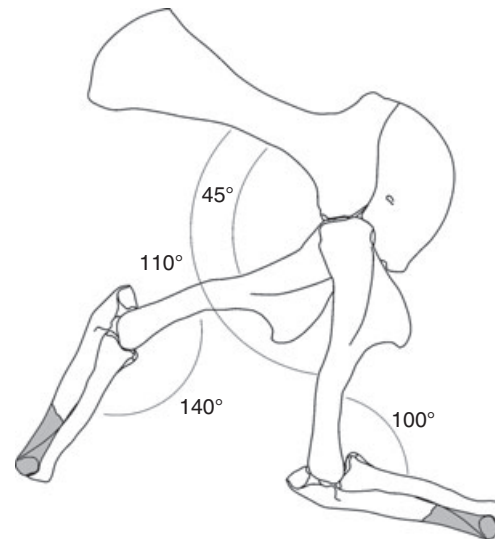
**TEXT-FIG. 1.** Map showing the fossil-bearing sites on the eastern outskirts of Santa Maria, Rio Grande do Sul, Brazil. Shaded parts indicate urban areas. GS: 'Grossesanga', type locality of *Staurikosaurus pricei* Colbert, 1970; WS: 'Waldsanga', type locality of *Saturnalia tupiniquim*.

Fundación Miguel Lillo, Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, San Juan, Argentina; QG, National Museum of Natural History, Harare, Zimbabwe; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

## MATERIAL AND METHODS

The shoulder girdle and forelimb elements of the holotype of *Saturnalia tupiniquim* (MCP 3844-PV) include a nearly complete right scapulocoracoid, humerus and radius, and a right ulna lacking its distal third. Additional material belongs to one of the paratypes (MCP 3845-PV), and includes two nearly complete scapulocoracoids, a partial right humerus and the proximal portion of the right ulna. No carpals, metacarpals or phalanges have been recovered, and there is also no trace of any of the dermal elements of the shoulder girdle. If not explicitly mentioned, the described features and elements are shared by both specimens.

Directional and positional terms used herein are those defined in Clark (1993) and the dinosaur compendium of Weishampel *et al.* (2004). Considering the rather uncertain, although most probably oblique (Colbert 1989), orientation of the shoulder girdle in basal dinosaurs (Text-fig. 2), it is treated as vertical for descriptive purposes (Nicholls and Russell 1985). Accordingly, the coracoid lies ventral to its articulation with the scapula, whereas the scapula blade expands dorsally. This orientation is chosen, rather than one that more closely reflects avian anatomy (Ostrom 1974), because it is plesiomorphic for archosaurs (Romer 1956) and also more traditional



**TEXT-FIG. 2.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil. Lateral view of the right pectoral girdle and partial forelimb reconstructed based mainly on MCP 3844-PV. Bones assembled in two different poses, corresponding to maximum angles of limb retraction and forearm extension, and limb protraction and forearm flexion. Shaded (see-through) area represents the missing distal part of the ulna, and scapulocoracoid long axis is at an angle of about 25 degrees to the horizontal.

(Romer 1966; Coombs 1978; Gauthier 1986). Regarding the forelimb, the arm and forearm are described with their long axes orientated vertically (Serenó 1993), and with the long axis of the elbow joint being orthogonal to the sagittal plane. This does not reflect their natural posi-

tion (see Text-fig. 2), but should render the description easier to follow. Hence, the deltopectoral crest expands cranially from the humerus and the forearm moves caudally during extension.

The remains of *S. tupiniquim* are well preserved (Langer 2003) and lack evidence of major taphonomic distortions. This allows the recognition of various osteological traces left by the attachments of major muscle groups, and some insights on pectoral girdle and limb myology are presented here (Text-fig. 3). The tentative identification of the musculature corresponding to these traces represents inferences based on a 'phylogenetic bracket' approach (Felsenstein 1985; Bryant and Russell 1992; Witmer 1995; Hutchinson 2001). Crocodiles and birds are evidently the main elements of comparison, because they are the only extant archosaurs and the closest living relatives of *S. tupiniquim*.

**SYSTEMATIC PALAEOLOGY**

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

EUSAURISCHIA Padian, Hutchinson and Holtz, 1999

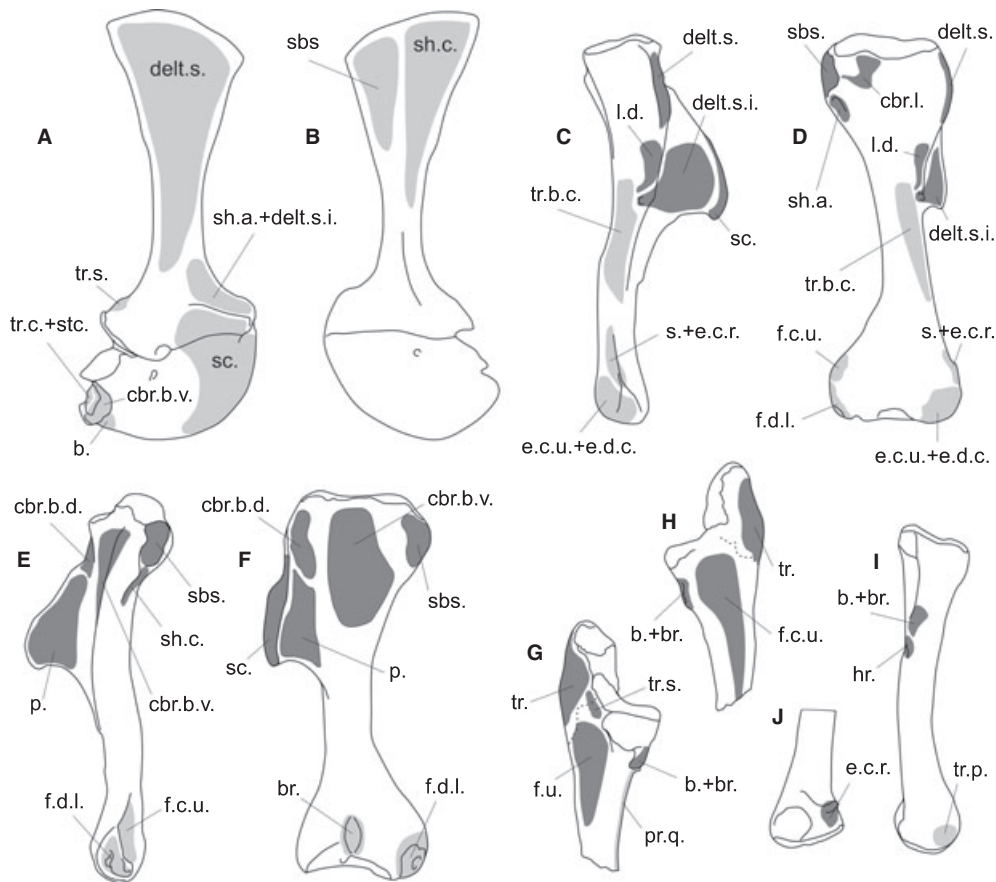
stem SAUROPODOMORPHA von Huene, 1932

Genus *SATURNALIA* Langer, Abdala, Richter and Benton, 1999

*Saturnalia tupiniquim* Langer, Abdala, Richter and Benton, 1999

Text-figures 2–9, Tables 1–3

*Referred specimens.* The type series is composed of the holotype (MCP 3844-PV) and two paratypes (MCP 3845-PV and 3846-PV) (Langer 2003).



**TEXT-FIG. 3.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil. Muscle attachment areas on A–B, right scapulocoracoid, C–F, humerus, G–H, partial ulna, I, radius, and J, distal part of radius, reconstructed based mainly on MCP 3844-PV, in lateral (A, C, G, J), medial (B, E, H–I), caudal (D), and cranial (F) views. Light shading indicates areas of muscle origin and dark shading their insertion areas. b., biceps; br., brachialis; cbr.b.d., coracobrachialis brevis pars dorsalis; cbr.b.v., coracobrachialis brevis pars ventralis; cbr.l., coracobrachialis longus; delt.s., deltoideus scapularis; delt.s.i., deltoideus scapularis inferior; e.c.r., extensor carpi radialis; e.c.u., extensor carpi ulnaris; e.d.c., extensor digitorum communis; f.c.u., flexor carpi ulnaris; f.d.l., flexor digitorum longus; f.u., flexor ulnaris; h., humeroradialis; l.d. latissimus dorsi; p. pectoralis; pr.q., pronator quadratus; s., supinator; sc., supracoracoideus; sbs., subscapularis; sh.a., scapulohumeralis anterior; sh.c., scapulohumeralis caudalis; stc., sternocoracoideus; tr., triceps tendon; tr.b.c., triceps brevis caudalis; tr.c., coracoidal head of triceps; tr.p., transvs. palmaris; tr.s., scapular head of triceps.

**TABLE 1.** Scapulocoracoid measurements of *Saturnalia tupiniquim* in millimetres. Brackets enclose approximate measurements, and inverted commas partial measurements taken from incomplete structures. Abbreviations: CGH, coracoidal glenoid dorsoventral height; CH, coracoid height on scapular axis; DSBB, distal scapula blade craniocaudal breadth; DSBT, distal scapula blade lateromedial thickness; MCGT, maximum coracoidal glenoid lateromedial thickness; MCL, maximum coracoid craniocaudal length; MCSB, maximum caput scapulae craniocaudal breadth; MSBB, minimum scapula blade craniocaudal breadth; MSBT, maximum scapula blade lateromedial thickness; MSGT, maximum scapula glenoid lateromedial thickness; MSL, maximum scapula length; SBL, scapula blade length; SGH, scapuloglenoid dorsoventral height; SPL, scapula prominence craniocaudal length.

	MCP 3844-PV (right)	MCP 3845-PV (right)	MCP 3845-PV (left)
MSL	111	98	99
SBL	92	78	79
DSBB	41·5	39	–
MSBB	(14)	12·5	12·5
MSBT	8	6	7
DSBT	5	2	2·5
MCSB	45·5	43·5	45
SPL	18	23	22
SGH	7	10	9·5
MSGT	‘12’	11·5	12
MCL	–	55	–
CH	33	23	‘27’
CGH	10·5	8	7
MCGT	12·5	11	11·3

*Type locality.* All of the type series comes from the same locality: a private piece of land, no. 1845, on road RS-509; outskirts of the city of Santa Maria, on the north-western slope of Cerriquito Mount (Text-fig. 1). This is presumably the locality known as ‘Waldsanga’ (von Huene and Stahlecker 1931; Langer 2005a).

*Horizon and age.* Alemoa Local Fauna, *Hyperodapedon* Biozone (Barberena 1977; Barberena *et al.* 1985; Langer 2005a); Santa Maria 2 sequence (Zerfass *et al.* 2003); Alemoa Member, Santa Maria Formation, Rosário do Sul Group (Andreis *et al.* 1980); Late Triassic of the Paraná Basin. Based on comparisons with the Ischigualasto Formation (Rogers *et al.* 1993), the Alemoa Local Fauna can be given an early–middle Carnian age (Langer 2005b).

*Revised diagnosis* (based on pectoral girdle and forelimb elements only). A dinosaur that differs from other basal members of the group in a series of features, namely: oval pit on the caudal margin of the scapula blade, immediately dorsal to the glenoid border; central pit on the subglenoid fossa of the coracoid; oval excavation on the caudodistal corner of the lateral surface of the deltopectoral crest; marked fossa olecrani on the caudal surface of

the distal humeral end; greatly enlarged but partially hollow olecranon process of the ulna, with a separate ossification forming its proximocranial portion; pointed tuber on the craniolateral corner of the distal radius.

*Comment.* Most of these traits have also been identified in a few other dinosaurs (see descriptive section below) and so cannot be strictly defined as autapomorphic prior to assessing their phylogenetic distribution. These features might subsequently be shown to reflect either convergence or, most probably, excellent preservation of structures that are rarely preserved in the fossil record.

## COMPARATIVE DESCRIPTION

### *Shoulder girdle*

As is typical for dinosaurs, the shoulder girdle of *Saturnalia tupiniquim* (Text-figs 2–5, Table 1), includes a scapula and coracoid that are attached to each other by an immobile joint. They form a pair of long, lateromedially-flattened scapulocoracoids, which, as they follow the contour of the rib cage, are medially concave. The holotype right scapulocoracoid (Text-fig. 4) is complete except for the middle portion of the scapula blade and the cranioventral portion of the coracoid. The right scapulocoracoid of MCP 3845-PV (Text-fig. 5) is missing only a small central portion of the coracoid, while the left lacks the craniodorsal edge of the scapula blade and the cranial half of the coracoid. Although not preserved, clavicles and sternal plates were probably present, considering their occurrence in most dinosaur lineages (Bryant and Russell 1993; Padian 1997; Tykoski *et al.* 2002; Galton and Upchurch 2004a; Yates and Vasconcelos 2005).

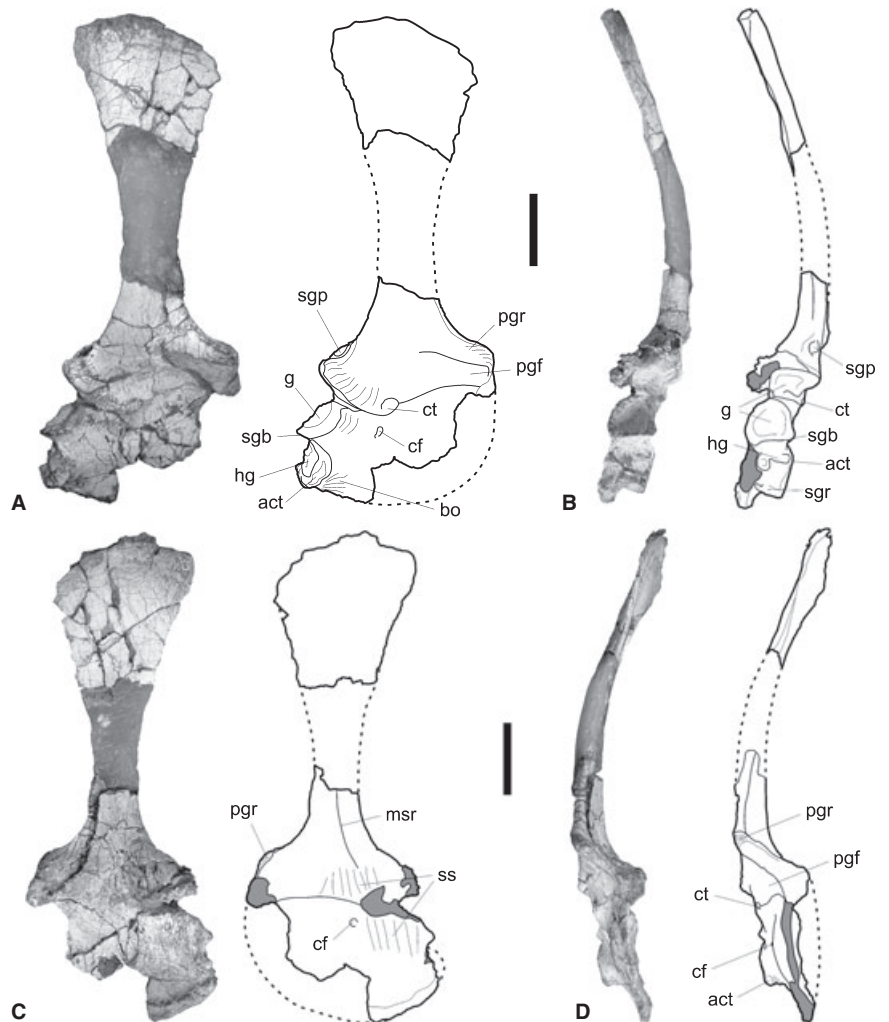
The degree of fusion between the scapula and coracoid is similar in both holotype and paratype. The suture is clear in its caudal part, near the glenoid, where the coracoid seems to overlap the scapula laterally. Although partially fused cranially, the articulation is traceable for its entire length. Its caudal third extends cranioventrally as a nearly straight line from the glenoid until the level of the coracoid foramen, but deflects dorsally to project cranially as a slightly dorsally arched line. This defines a scapula margin that is more ventrally projected in the caudal portion, as commonly seen in basal dinosaurs (Bonaparte 1972; Welles 1984; Colbert 1989; Butler 2005; *Eoraptor*, PVSJ 514; *Guaibasaurus*, MCN 3844-PV; *Liliensternus*, HB R.1275; *Efraasia*, SMNS 17928). Adjacent to the scapulocoracoid suture, just dorsal to the coracoid foramen, is a bulging area that forms a marked tubercle in the holotype (Text-figs 4–5, ct). A similar structure also occurs in other dinosaurs (Ostrom 1974; Brinkman and Sues 1987; Butler 2005; *Efraasia*, SMNS 17928; see also Walker 1961), and is enlarged in some of them (Galton 1981, fig. 6A; *Liliensternus*, HB R.1275). This resembles, in shape and position, the ratite ‘coracoid tuber’ (Cracraft 1974), as figured for the ostrich by McGowan (1982, fig. 4E; ‘acromial tuberosity’), which represents the origin of part of the deltoid musculature (Nicholls and Russell 1985). The whole scapulocoracoid junction of *S. tupiniquim* is bound by synchondral striations, more evident at the

medial surface and laterally between the glenoid and the coracoid foramen. The scapular and coracoidal portions of the glenoid are nearly of the same size, but the latter projects further caudally. The scapulocoracoid is excavated at the cranial end of the articulation between the two bones. This is clearer in MCP 3845-PV, whereas a subtler concavity is present in the holotype. The significance of this excavation has been explored in the context of theropod phylogeny (Currie and Carpenter 2000; Holtz 2000; Holtz *et al.* 2004). Among basal dinosaurs, an excavation similar to that of *S. tupiniquim* is widespread (Colbert 1981; *Efraasia*, SMNS 17928; *Eoraptor*, PVSJ 514), and does not seem to bear an important phylogenetic signal (but see Tykoski and Rowe 2004).

*Scapula.* The scapula of *S. tupiniquim* is elongated, lateromedially flattened and arched laterally. It is formed of a slender dorsal blade and a basal portion (= caput scapulae; Baumel and Witmer 1993), along the ventral margin of which the coracoid articulates. The basal portion is composed of a lateromedially broad caudal column that extends onto the glenoid, and a plate-like cranial extension, the scapular prominence (= 'acromial process'; Nicholls and Russell 1985). This is convex medially, while

its concave lateral surface forms the 'preglenoid fossa' (Welles 1984; Madsen and Welles 2000) or 'subacromial depression' (Currie and Zhao 1993), which may have located part of the origin of the supracoracoid musculature (Coombs 1978; Nicholls and Russell 1985; Norman 1986; Dilkes 2000; Meers 2003). Dorsal to that, the 'preglenoid ridge' (Madsen and Welles 2000) extends caudally, but does not deflect ventrally as in forms with a deeper 'subacromial depression' (Madsen and Welles 2000; *Liliensternus*, HB R.1275; see also Brinkman and Sues 1987). Instead, the depression has a smooth caudal margin as in most basal dinosauriforms. The 'preglenoid ridge' forms the entire dorsal margin of the acromion, which is thickened and striated, and was probably the origin of the *m. scapulohumeralis anterior* (Coombs 1978; Dilkes 2000). In addition, the acromial region represents the origin site for the avian *mm. deltoideus major* and *deltoideus minor* (George and Berger 1966; Vanden Berge 1975; McGowan 1982; Nicholls and Russell 1985), and the *m. deltoideus clavicularis* in crocodiles (Meers 2003; = *m. deltoideus scapularis inferior*; Nicholls and Russell 1985; Norman 1986) and some lizards (Romer 1922), and is probably also the origin for part of the deltoid musculature in *S. tupiniquim* (Text-fig. 3). The 'preglenoid ridge' is placed dorsal to the upper

**TEXT-FIG. 4.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil; MCP 3844-PV. Photographs and outline drawings of right scapulocoracoid in A, lateral, B, caudal, C, medial, and D, cranial views. act, acrocoracoid tubercle; bo, origin of *m. biceps*; cf, coracoid foramen; ct, coracoid tuber; g, glenoid; hg, horizontal groove; msr, medial scapular ridge; pgf, preglenoid fossa; pgr, preglenoid ridge; sgb, subglenoid buttress; sgp, supraglenoid pit; sgr, subglenoid ridge; ss, striation of scapulocoracoid synchondrosis. Shaded areas indicate missing parts. Scale bars represent 20 mm.



margin of the glenoid, a condition otherwise considered typical of herrerasaurs (Novas 1992), but also seen in other basal saurischians (Galton 1984; Rowe 1989; Raath 1990), although not in ornithischians (Owen 1863; Santa Luca 1980; Colbert 1981; Butler 2005).

Ventrally, the thickened caudal portion of the caput scapulae forms a subtriangular articulation with the coracoid and a broad glenoid. Dorsal to that, its caudal margin does not taper to a point, as does the majority of the scapula blade, but forms a flat caudomedially facing surface. The ridge that marks the lateral border of that surface is a ventral extension of the caudal margin of the blade, whereas the medial border is formed by a second ridge (Text-figs 4–5, msr) that extends along the medial surface of the blade, as seen also in *Herrerasaurus* (Serenó 1993). The distal part of this ridge may have separated the origins of the m. subscapularis cranially and the m. scapulohumeralis caudalis (= m. scapulohumeralis posterior, Dilkes 2000) caudally. Immediately dorsal to the glenoid border, an oval pit (Text-figs 4–5, sgp) lies at the end of the ridge extending from the caudal margin of the blade. A similar structure was reported for ornithomimosaurs (Nicholls and Russell 1985), *Heterodontosaurus* (Santa Luca 1980), and can be also seen in sauropods (e.g. *Barosaurus*: MB R.270.2 K34). This seems to represent the origin of a scapular branch of the m. triceps (Nicholls and Russell 1985; Brochu 2003), as this is usually immediately dorsal to the scapular part of the glenoid (George and Berger 1966; McGowan 1982) and often leaves a distinct scar (Meers 2003). Hence, in *S. tupiniquim* (Text-fig. 3), in contrast to the situation inferred for other dinosaurs (Borsuk-Bialynicka 1977; Coombs 1978; Norman 1986; Dilkes 2000), that muscle did not arise from the dorsal margin of the glenoid [i.e. the ‘supraglenoid buttress’ (Madsen and Welles 2000) or ‘glenoid tubercle’ (Norman 1986)]. Instead, the heavily striated surface, lateroventral to the oval pit, at the slightly projected laterodorsal border of the glenoid, is believed to represent an attachment area for ligaments of the shoulder joint. Indeed, this is the attachment site of the avian lig. scapulohumerale (Jenkins 1993) and the lepidosaurian caudodorsal ligament (Haines 1952). The scapular portion of the glenoid is ovoid in *S. tupiniquim* and meets the coracoid along its flat cranioventral margin, the medial part of which is more caudally projected. From that junction, its medial margin projects laterodorsally, and slightly caudally, while the lateral margin also projects caudodorsally, but diverges medially at its dorsal portion. As a consequence, the glenoid does not face strictly caudoventrally, but it is also directed somewhat laterally (MCP 3845-PV). This is typical of basal dinosaurs, although variants on the glenoid direction are seen in derived groups (Novas and Puerta 1997; Upchurch *et al.* 2004).

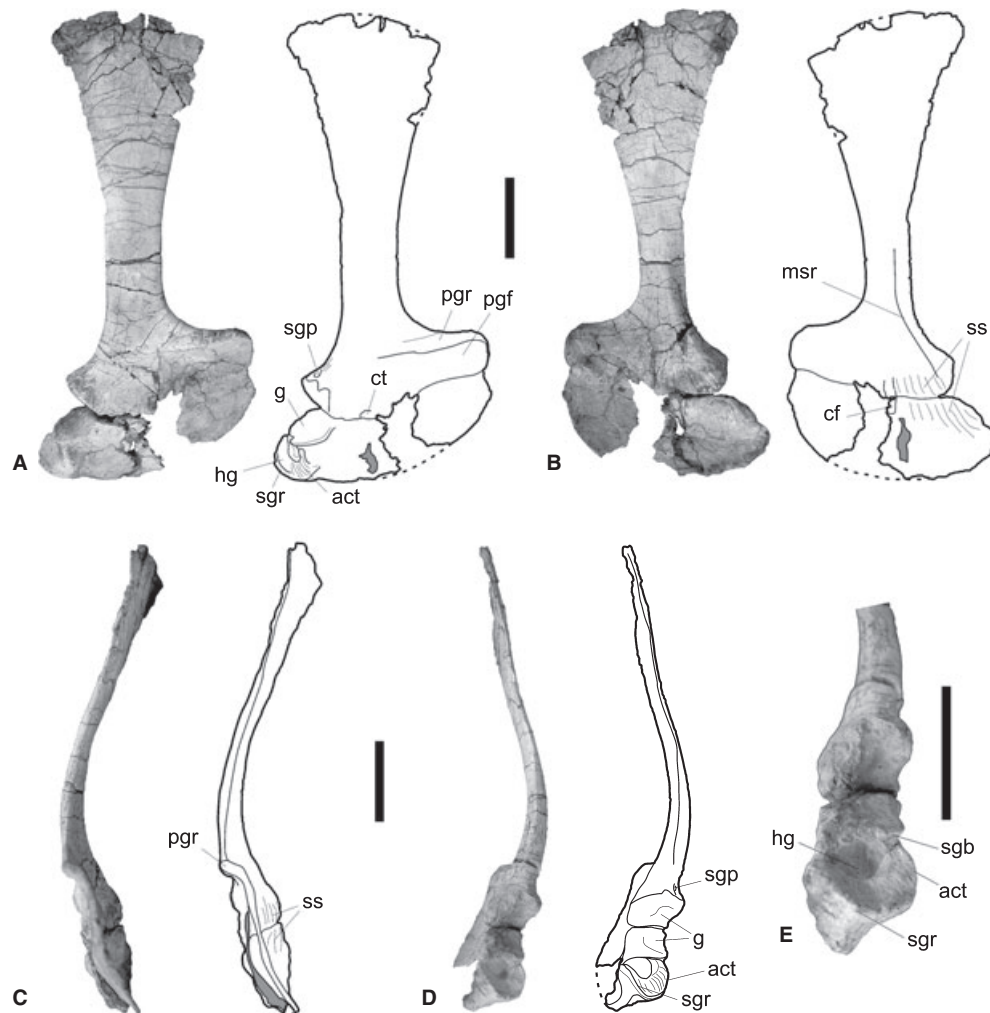
The scapula blade of the holotype lacks its middle portion, but has been safely reconstructed in length and shape based on the impression that the missing portion left in the matrix. It arches laterally, while the blade of MCP 3845-PV is more sinuous, with a straighter dorsal part, as seen in *Herrerasaurus* (Serenó 1993). Minor taphonomic distortions could, however, easily produce such a variation. In both specimens, the ventral portion of the blade is constricted to form the scapular neck, which is ovoid in cross-section. Dorsal to this, the bone becomes gradually thinner lateromedially, so that the distal end is plate-

like. The blade also expands craniocaudally, so that its minimal breadth is less than half that of the dorsal margin. As in most basal dinosaurs (but see Welles 1984; Raath 1990), this expansion is neither abrupt nor restricted to the dorsal summit. A similar condition is seen in basal ornithischians (Owen 1863; Thulborn 1972; Santa Luca 1980), theropods (von Huene 1934; Rowe 1989) and sauropodomorphs (von Huene 1926; Benton *et al.* 2000), but not in *Herrerasaurus* (Serenó 1993) and more derived theropods (Currie and Zhao 1993; Currie and Carpenter 2000; Madsen and Welles 2000), in which the scapula blade is strap-shaped and does not expand much distally. Large areas of the scapula blade bear subtle longitudinal striations, which might correspond to origin areas of the m. subscapularis medially and the m. deltoideus scapularis laterally (McGowan 1982; Jenkins and Goslow 1983; Nicholls and Russell 1985; Dilkes 2000; Meers 2003). The dorsal margin of the blade is convex with sharp edges, and its more porous surroundings might indicate that it supported a cartilaginous extension (see Butler 2005).

**Coracoid.** The coracoid is a craniocaudally elongated element that is concave medially and convex laterally. Its cranial two-thirds are plate-like, with a subcircular cranioventral margin. Subtle craniocaudally directed striations are seen on its lateral surface, which seem to correspond to the origin of part of the m. supracoracoideus (Ostrom 1974; Coombs 1978; Nicholls and Russell 1985; Dilkes 2000). The coracoid thickens towards its caudal margin, and caudodorsally towards the glenoid. The scapular articulation is also cranially thin, and widens caudally, forming a subtriangular surface caudal to the ‘coracoid tuber’. The coracoid foramen pierces the lateral surface of the bone well below the scapular articulation, and extends mediadorsally in an oblique fashion. In the holotype, the internal aperture is also below the scapular articulation (see also Santa Luca 1984; Serenó 1993), while in MCP 3845-PV it perforates the scapula-coracoid junction, forming a smooth excavation on the medioventral corner of the scapula (Text-fig. 5B), as reported for various basal dinosaurs (Norman 1986; Madsen and Welles 2000; Butler 2005).

The coracoidal portion of the glenoid is subrectangular and bears prominent lip-like lateral and caudal borders. The latter forms a delicate caudally projecting platform variously referred to as the ‘horizontal’ (Welles 1984), ‘infraglenoid’ (Kobayashi and Lü 2003) or ‘subglenoid’ (Madsen and Welles 2000) buttress (Text-figs 4–5, sgb). The flat to slightly concave humeral articulation faces almost entirely caudodorsally, and is not as laterally inclined as that of the scapula. Ventral to this, the coracoid bears a complex morphology. From near the lip-like caudolateral corner of the glenoid, but separated from it by a cleft, a short ridge extends cranioventrally along the lateral surface of the bone to meet a laterally extensive and craniodorsally to caudoventrally ‘elongated tuber’ (Text-figs 4–5, act). From the caudal end of that tuber, a blunt ridge projects medially forming a ‘loop’ (Text-figs 4–5, sgr) that reaches the medial margin of the bone. This supports a broad concave surface (= ‘horizontal groove’: Welles 1984, fig. 26b) with a deep pit at its centre, which is also seen in other archosaurs (Walker 1961; *Liliensternus*, HB R.1275).





**TEXT-FIG. 5.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil; MCP 3845-PV. A–D, photographs and outline drawings of right scapulocoracoid in A, lateral, B, medial, C, cranial, and D, caudal views. E, detail of glenoid area of right scapulocoracoid in caudal view. Abbreviations as in Text-figure 4. Shaded areas indicate missing parts. Scale bars represent 20 mm.

The above-mentioned ‘elongated tuber’ seems to be equivalent to a fainter ridge extending ventrally from the caudolateral corner of the glenoid of some archosaurs (Walker 1961, 1964; Long and Murry 1995; *Marasuchus*, PVL 3871), but a closer condition is shared by *Silesaurus* (Dzik 2003), *Guaibasaurus* (Bonaparte *et al.* 1999), *Eoraptor* (PVSJ 512) and basal sauropodomorphs (*Efraasia*, SMNS 17928), although the ‘tuber’ of the latter forms is often less expanded dorsally (Young 1941*a, b*, 1947; Moser 2003; Yates 2003; *Plateosaurus*, SMNS F65). This was referred to as the ‘biceps tubercle’ (Cooper 1981), whereas its ventral end was termed the ‘caudolateral process of the coracoid’ (Bonaparte 1972). The subglenoid part of the coracoid of basal theropods (Welles 1984; Madsen and Welles 2000; *Lilienstermus*, HB R.1275; *Coelophysis rhodesiensis*, QG 1) also compares to that of *S. tupiniquim*, despite the suggestion of Holtz (2000) that the ‘biceps tubercle’ is more developed in *Dilophosaurus* and *Coelophysidae* than in ‘prosauropods’. More derived theropods (Osmólska *et al.* 1972; Madsen 1976; Nicholls and Russell 1985; Makovicky and Sues 1998; Norell and Makovicky 1999; Brochu

2003) have a tuber placed further from the glenoid, and their dorsal ‘concave surface’ is more craniocaudally elongated. This follows an extension of the caudal process of the coracoid, as also seen in derived ornithischians (Gauthier 1986; Coria and Salgado 1996). Names applied to those structures vary: the tuber (= ‘diagonal buttress’: Welles 1984) has been termed ‘coracoid’ (Osmólska *et al.* 1972; Walker 1977; Norell and Makovicky 1999; Yates 2004) or ‘biceps’ (Ostrom 1974; Rowe 1989; Pérez-Moreno *et al.* 1994; Madsen and Welles 2000; Brochu 2003; Kobayashi and Lü 2003) tubercle, whereas the ‘subglenoid fossa’ (Norell and Makovicky 1999; Makovicky *et al.* 2005) seems to represent a caudally elongated version of the ‘horizontal groove’ (Welles 1984). In contrast, the coracoid of most ornithischians has a more plate-like subglenoid portion that apparently lacks those elements (Ostrom and McIntosh 1966; Colbert 1981; Forster 1990; Butler 2005; but see Janensch 1955; Santa Luca 1980).

The reconstruction of dinosaur coracoid musculature has been an issue of some debate (Ostrom 1974; Walker 1977), leading to the nomenclatural inconsistency seen above. In previous works,

the origins of the *m. biceps* and *m. coracobrachialis* have been reconstructed according to two different patterns. Some authors (Ostrom 1974; Nicholls and Russell 1985; Dilkes 2000) favoured origins restricted to the subglenoid portion of the bone, while in other reconstructions (Borsuk-Bialynicka 1977; Coombs 1978; Norman 1986; Bakker *et al.* 1992; Carpenter and Smith 2001) these spread along most of the ventral half of the coracoid. Comparisons to the myology of ratites and crocodiles seem to favour the first hypothesis, given that those two muscles originate on the caudal portion of their coracoid (McGowan 1982; Meers 2003), and that the origin of the *m. biceps* is consistently ventral to that of the *m. coracobrachialis*. Indeed, the 'elongated tuber' of *S. tupiniquim* is suggested to accommodate the origin of the latter (Text-fig. 3), most probably its cranial (= *brevis*) branch, which may extend onto the 'concave surface'. This corresponds to the 'depression on the dorsal edge of the posterior coracoid process' where Nicholls and Russell (1985, p. 669) also placed the origin of the *m. coracobrachialis brevis* in *Struthiomimus*. In such forms, a caudal (= *longus*) branch of the *m. coracobrachialis* might originate from their elongated caudal coracoid process. This is lacking in *S. tupiniquim*, but the oval pit and medial part of its 'concave surface' can be related to the origin of a coracoidal head of the *m. triceps* (Norman 1986; Dilkes 2000; Brochu 2003). In birds, the *impressio m. sternocoracoidei* lies in this region of the bone (George and Berger 1966; McGowan 1982; Baumel and Witmer 1993; Vanden Berge and Zweers 1993), so the 'concave surface' may also represent the insertion of the eponymous muscle (Vanden Berge and Zweers 1993; = *m. costocoracoideus*, Meers 2003). The *m. biceps*, on the other hand, might have originated from a rugose bump ventral to the 'elongated tuber' (Text-fig. 4, bo). Accordingly, this could be tentatively considered equivalent to the 'coracoid' or 'biceps' tubercle of theropods, which is inferred to accommodate the origin of the *m. biceps* (Nicholls and Russell 1985; Brochu 2003; contra Walker 1977; Norell and Makovicky 1999), but was also considered to represent an 'artefact' of bone growth, related to the convergence of three muscle masses (Carpenter 2002). In any case, the entire 'elongated tuber' of *S. tupiniquim* resembles, in shape and position, the 'acroracoid tuberosity' of ratites (Parker 1891; McGowan 1982), which is related to the origin of the *mm. coracobrachialis* and *biceps*. Indeed, the origin of these muscles is often so intimately associated (McGowan 1982; Nicholls and Russell 1985) that the search for their exact origin in dinosaurs might prove very difficult.

#### Forelimb

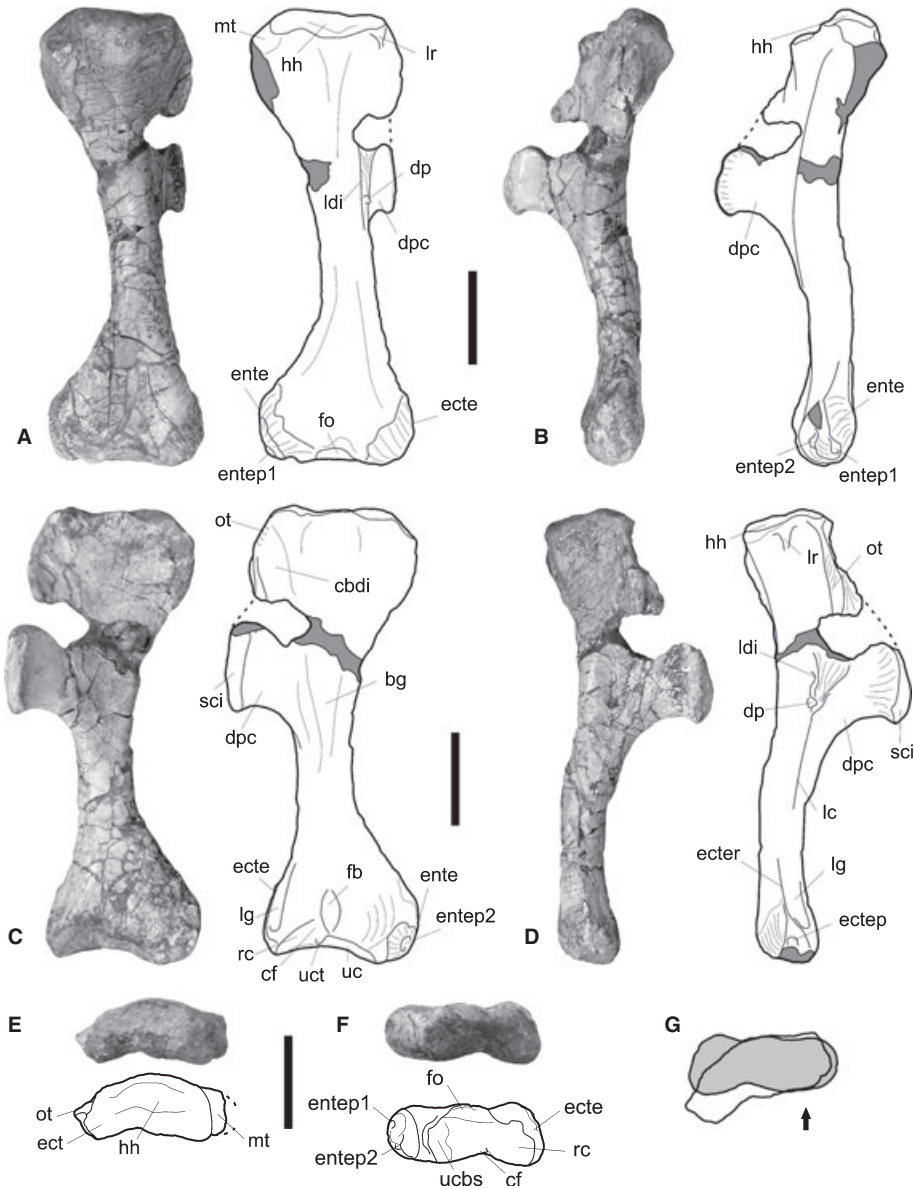
*Humerus.* The humerus of 3845-PV (Text-fig. 7) lacks most of the deltopectoral crest and the lateral half of the proximal articulation, whereas only the centre of the deltopectoral crest and part of the medial tuberosity is missing in the holotype (Text-fig. 6). Manipulation of the humerus on the caudolaterally facing glenoid of *S. tupiniquim* reveals a resting pose (with scapulo-coracoid positioned parasagittally) in which the bone is abducted about 20 degrees. It reaches maximal protraction and retraction of about 70 and 45 degrees relative to the long axis of the scapulo-coracoid, respectively (Text-fig. 2), allowing an arm rotational

movement of 65 degrees. The humerus of the holotype is bowed cranially along its proximal two-thirds and caudally in its distal half, while that of MCP 3845-PV is somewhat straighter with the proximal half bent caudally at an angle of 20 degrees, and the distal end curved cranially. Both arrangements give the bone a sigmoid outline, as is typical of basal dinosaurs (Rauhut 2003), resulting in a permanent minor retraction. The relatively short humeral shaft connects lateromedially expanded distal and proximal ends, the margins of which are also craniocaudally expanded. The bone is therefore markedly waisted in cranial-caudal view, with a medial excavation extending through the entire length of the shaft, and a lateral one distal to the deltopectoral crest.

The proximal surface of the humerus is almost entirely occupied, except for its caudolateral and medial corners (Text-fig. 6E), by the humeral head (= *caput articulare humeri*; Baumel and Witmer 1993). This includes a broad, lateromedially elongated medial body, and a narrower lateral portion (= 'ectotuberosity': Welles 1984) that projects cranio-laterally at an angle of about 35 degrees. As a result, the head has a 'bean-shaped' proximal outline that is caudolaterally rounded and excavated craniomedially. It articulated with the glenoid via a slightly caudally facing flat proximal surface, which is crossed by a shallow transverse groove and probably had a cartilaginous cover. Taken as a whole, the long axis of the humeral head forms an angle of approximately 30 degrees to that of the distal part of the bone, but the angle is merely 10 degrees if only the larger medial part of the head is considered. These account for the so called 'humeral torsion' (Raath 1969; Cooper 1981; Benton *et al.* 2000; Tykoski and Rowe 2004), which imposes a permanent 'supination' to the distal part of the bone. This is clearly seen in basal theropods (Welles 1984; *Coelophysis rhodesiensis*, QG 1; *Liliensternus*, HB R.1275) and 'prosauro-pods' (Moser 2003; Galton and Upchurch 2004a; *Riojasaurus*, PVL 3808), but is apparently more marked in the former group (Holtz 2000).

An indistinct trough separates the humeral head of *S. tupiniquim* from the medial/internal tuberosity (= *tuberculum ventrale*, Baumel and Witmer 1993; for alternative names, see Welles 1984; Nicholls and Russell 1985; Moser 2003). This corresponds to the *insicura capitis humeri* (Baumel and Witmer 1993), and is not as broad as in other basal dinosaurs (Raath 1969; Cooper 1981; Sereno 1993). The swollen and proximodistally elongated medial tuberosity (Text-fig. 7, mt) forms the medial margin of the proximal humerus (MCP 3845-PV), but does not rise proximally as in *Herrerasaurus* (Sereno 1993). It has a rugose texture that also enters the cranial surface of the bone, representing the insertion of the *m. subscapularis* (Ostrom 1969; Vanden Berge 1975; Coombs 1978; Meers 2003). The medial tuberosity gives rise to a sharp *crista bicipitalis* (Baumel and Witmer 1993; see Carpenter *et al.* 2005) extending distally along the medial corner of the humerus, the caudal surface of which might represent the insertion of the *m. scapulohumeralis caudalis* (Vanden Berge and Zweers 1993; Dilkes 2000). An oval pit is seen caudal to the crest (Text-fig. 7, ftp), which is comparable to the avian *fossa pneumotricipitalis* (Baumel and Witmer 1993). This was probably the origin of the medial head of the *m. humerotriceps* (= *m. triceps brevis caudalis*; Meers 2003) and the insertion of the *m. scapulohumeralis anterior* (Dilkes 2000; = *m. scapulohumer-*





**TEXT-FIG. 6.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil; MCP 3844-PV. A–F, photographs and outline drawings of right humerus in A, caudal, B, medial, C, cranial, D, lateral, E, proximal, and F, distal views. G, relative position of proximal and distal ends of the right humerus (arrow points caudally). bg, biceps gutter; cbdi, insertion of *m. coracobrachialis brevis dorsalis*; cf, cranial furrow; dp, deltoid pit; dpc, deltopectoral crest; ect, ectotuberosity; ecte, ectepicondyle; ectep, ectepicondyle pit; ecter, ectepicondyle ridge; ente, entepicondyle; entep1 and 2, entepicondyle pit 1 and 2; fb, fossa *m. brachialis*; fo, fossa *olecrani*; hh, humeral head; lc, lateral carina; ldi, insertion of *m. latissimus dorsi*; lg, ligament groove; lr, ligament ridge; mt, medial tuberosity; ot, outer tuberosity; rc, radial condyle; sci, insertion of *m. supracoracoideus*; uc, ulnar condyle; ucbs, ulnar condyle biconvex surface; uct; tubercle on ulnar condyle. Shaded areas indicate missing parts. Scale bars represent 20 mm.

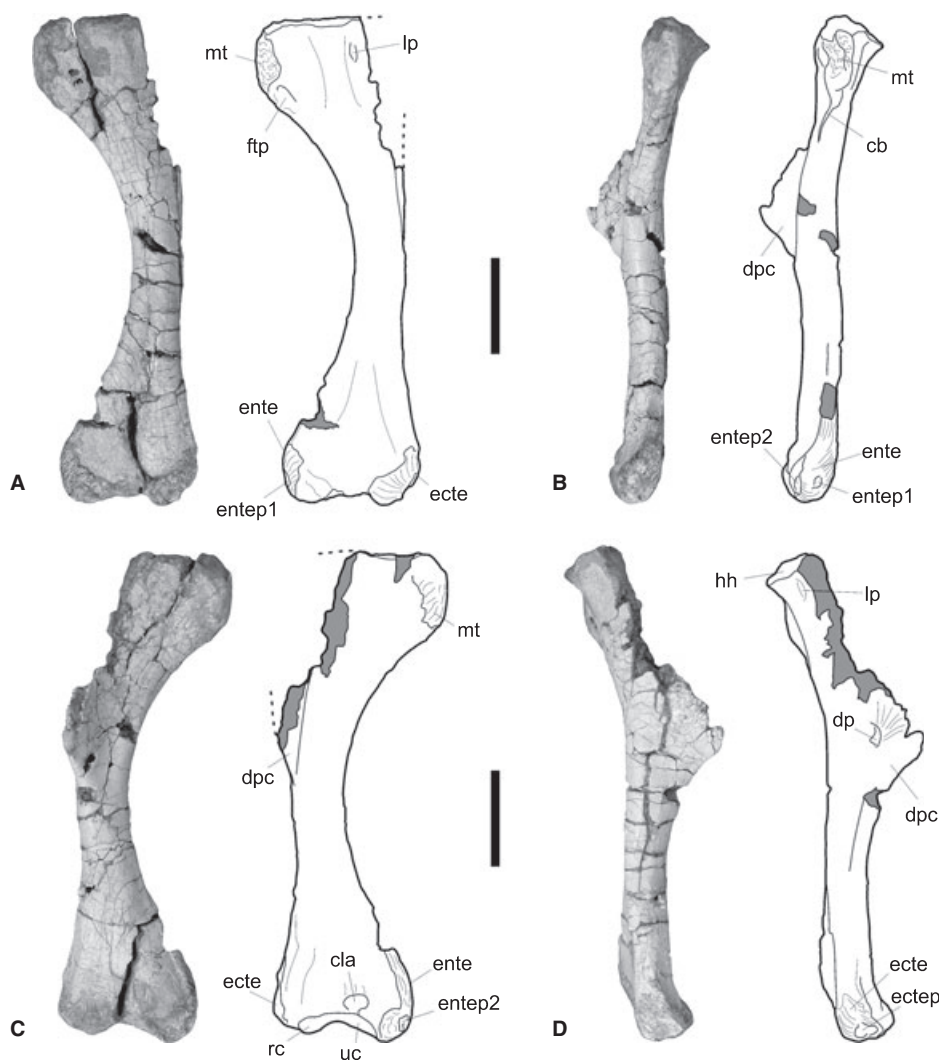
alis cranialis, Vanden Berge 1975; see also Ostrom 1969). Lateral to that, the caudal surface of the proximal humerus forms a slightly concave smooth surface that somewhat continues to the ‘capital groove’. This is laterally bound by a blunt ridge that defines a protruding lip-like border on the humeral head (MCP 3845-PV) and extends distally, in the direction of the ectepicondyle, as seen in *Scutellosaurus* (Colbert 1981, fig. 19a). The proximal part of the ridge is covered by a finely striated surface

(MCP 3844-PV) that forms a loop, extending medially until the base of the medial tuberosity (Text-fig. 3D), and possibly represents the insertion of *m. coracobrachialis longus* (Dilkes 2000; = caudalis, Vanden Berge 1975). More laterally, an ovoid depression (MCP 3845-PV) and a short, but rugose, ridge (MCP 3844-PV) mark the caudolateral margin of the humeral head and might be related to the caudodorsal ligaments of the shoulder joint (Haines 1952). On the cranial surface of the proximal

humerus, a shallow excavation projects distally from the concavity of the humeral head. Its smooth and longitudinally striated surface extends medially, approaching the margin of the bone, and probably accommodated the insertion of the *m. coracobrachialis brevis* (Dilkes 2000; = *cranialis*, Vanden Berge 1975) *pars ventralis* (Meers 2003).

The lateral border of the proximal humerus is formed by a sharp ridge that expands from the cranio-lateral corner of the humeral head, at an angle of 45 degrees to the long axis of the bone, and extends distally. Such a ridge is widespread among dinosaurs (Ostrom and McIntosh 1966; Cooper 1981; *Coelophysis rhodesiensis*, QG 1; *Liliensternus*, HB R.1275; *Plateosaurus*, SMNS F65; *Riojasaurus*, PVL 3808). Its rugose proximal portion ('outer tuberosity', Godefroit *et al.* 1998; 'greater tubercle', Madsen and Welles 2000; Carrano *et al.* 2002; *tuberculum majus sic*, Moser 2003) seems equivalent to the avian

*tuberculum dorsale* (Baumel and Witmer 1993), which receives the insertion of the *m. deltoideus minor* (Vanden Berge 1975; Vanden Berge and Zweers 1993). In 'reptiles', the *m. deltoideus scapularis* has a comparable insertion point lateral to the humeral head (Nicholls and Russell 1985; Dilkes 2000; Meers 2003), although it takes its origin from the scapula blade, while the *m. deltoideus minor* originates in the acromial area. Moreover, both the *m. deltoideus scapularis* and *m. deltoideus minor* lie deep to the *m. deltoideus clavicularis* and *m. deltoideus major* in crocodiles (Meers 2003) and birds (Vanden Berge 1975), respectively. In the case that they represent homologues, the shift of the origin of the *m. deltoideus minor* to a more proximal portion of the scapula might have been necessary if the muscle was to carry on acting as a forelimb abductor on the horizontally orientated avian scapulocoracoid. In *S. tupiniquim*, this ridge becomes less prominent distally and might correspond to the origin of the



**TEXT-FIG. 7.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil; MCP 3845-PV. Photographs and outline drawings of right humerus in A, caudal, B, medial, C, cranial, and D, lateral views. Abbreviations as in Text-figure 6 and: cb, crista bicipitalis; cla, attachment of collateral ligament; ftp, fossa tricipitalis; lp, ligament pit. Shaded areas indicate missing parts. Scale bars represent 20 mm.

m. triceps brevis cranialis, as described for crocodiles (Meers 2003). Its medial margin is heavily ornamented with pits and tubers, representing a likely insertion area for the m. latissimus dorsi (Borsuk-Bialynicka 1977; Dilkes 2000; Brochu 2003; Meers 2003). This portion of the ridge was described for tetanurans as related to the m. humeroradialis (Madsen 1976; Galton and Jensen 1979; Azuma and Currie 2000; Currie and Carpenter 2000; but see Carpenter and Smith 2001; Brochu 2003; Carpenter *et al.* 2005), but in *S. tupiniquim* that muscle probably had a more distal origin, near the margin of the deltopectoral crest. The distal end of the ridge under description is marked by an oval pit (Text-figs 6–7, dp) from which marked striae radiate proximocranially (MCP 3845-PV), partially representing the insertion of the deltoid musculature (see below). This is somewhat continuous (MCP 3844-PV) with an intermuscular line (= ‘lateral carina’; Cooper 1981, fig. 26) that extends along the lateral margin of the shaft. In certain reconstructions (Norman 1986), a similar line outlines the boundary between the m. brachialis laterally, and a humeral branch of the m. triceps medially.

The deltopectoral crest is the most prominent element of the proximal humerus, but it is not continuous with the humeral head. It rises from the proximal part of the previously described ridge at an angle of 90 degrees to the long axis of the distal end of the humerus, and arches medially, before flaring laterally. This is a muted version of the medial inflection of the crest defined by Yates (2003) for some ‘prosauropods’ and is also seen in other members of the group (Cooper 1981), but not in theropods (Welles 1984; Madsen and Welles 2000; *Coelophysis rhodesiensis*, QG 1; *Liliensternus*, HB R.1275) or *Herrerasaurus*

**TABLE 2.** Right humerus measurements of *Saturnalia tupiniquim* in millimetres. Brackets enclose approximate measurements, and inverted commas partial measurements taken from incomplete structures. Abbreviations: DCL, deltopectoral crest length; DW, distal width across condyles; ET, entepicondyle maximum craniocaudal thickness; LDC1, length from proximal margin to apex of deltopectoral crest; LDC2, length from distal margin to distal base of deltopectoral crest; ML, maximum length; MPW, maximum proximal lateromedial width; MPT, maximum proximal craniocaudal thickness; MWPA, maximum lateromedial width of proximal articulation; RCT, radial condyle maximum craniocaudal thickness; SB, craniocaudal shaft breadth; UCT, ulnar condyle maximum craniocaudal thickness.

	MCP 3844-PV	MCP 3845-PV
ML	97	98
MPW	‘32.5’	–
MWPA	28	–
MPT	14	11
DCL	33.5	–
LDC1	43	(47)
LDC2	50	51
SB	10.5	8.5
DW	33	28
ET	11.5	8
RCT	13	10
UCT	12	11

(MACN 18.060; but see Brinkman and Sues 1987). The crest in *S. tupiniquim* attains its maximum expansion and robustness near its distal margin, where it forms an angle of 60 degrees to the long axis of the distal end of the bone. In lateral view, it has a truncated distal end, with a hook-like cranial corner, but merges smoothly onto the shaft. Its flat to slightly bulging cranio-lateral margin is the inferred location of the insertion of the m. supracoracoideus (Vanden Berge 1975; Coombs 1978; Meers 2003), while its striated caudolateral surface (see also Charig and Milner 1997) represents the insertion of a muscle of the deltoid group that, judging by its position, seems to correspond to the avian m. deltoideus major (Vanden Berge 1975) and the m. deltoideus clavicularis (Meers 2003). The smooth distal portion of the craniomedial surface of the crest was occupied by the insertion of the m. pectoralis (Cooper 1981; Dilkes 2000; Meers 2003), while the m. coracobrachialis brevis dorsalis (Meers 2003) inserted proximally, on a shallow groove that extends onto the cranial margin of the ridge for the m. deltoideus minor (see above). Both insertion areas are medially separated from that of the m. coracobrachialis brevis ventralis by a faint ridge. Mediodistal to that, a well-developed ‘biceps gutter’ (Godefroit *et al.* 1998) crosses the cranial humeral surface longitudinally.

The humeral shaft has a subcircular cross-section, with a caudally flattened distal portion. This is continuous with the triceps fossae that extend distally as feeble excavations along the flat caudal surface of the distal end of the bone. The expanded distal humerus has well-developed and rugose epicondyles, although the ectepicondyle is not much expanded laterally, especially in MCP 3845-PV. It is barely separated from the radial condyle by a laterodistally facing cleft, and its more prominent element is a sharp longitudinal ridge that expands along the lateral corner of the bone. This is somewhat continuous with the ‘lateral carina’ (Cooper 1981), and might represent the origin area of the mm. supinator and extensor carpi radialis (McGowan 1982; Vanden Berge and Zweers 1993; Meers 2003). It forms the steep lateral margin of an elongated and distally deeper concavity that extends longitudinally on the cranial face of the ectepicondyle (Text-fig. 6, lg), and may represent the attachment area of dorsal collateral ligaments of the elbow joint (Baumel and Raikow 1993). Caudal to the lateral ridge, the caudolateral surface of the ectepicondyle has marked striations that surround a more distally placed pit (MCP 3845-PV), originally described as autapomorphic for *Herrerasaurus* (Sereno 1993). This whole area and pit are also probably related to the origin of extensor muscles such as the mm. extensor carpi ulnaris and extensor digitorum comunis (Dilkes 2000), and perhaps other elements (Meers 2003), including the m. ectepicondylo-ulnaris (Vanden Berge 1975; McGowan 1982). The entepicondyle corresponds mainly to a medially expanded rugose swelling, the caudolateral margin of which is separated from the ulnar condyle by a cleft. Its heavily striated caudal surface is continuous with a striated ridge (Text-fig. 7B) that extends proximally along the medial corner of the bone and probably corresponds to the origin of the m. flexor carpi ulnaris (Vanden Berge 1975; McGowan 1982; Meers 2003). The raised medial rim of that surface forms the caudal border of a longitudinally orientated ovoid pit that occupies the centre of a protruding area on the medial surface of the entepicondyle. This is paralleled by a similar depression placed cranial

and slightly proximal to it, on a craniomedial extension of that protruding area. Comparable elements were described as unique for *Herrerasaurus* (Serenó 1993; see also Brinkman and Sues 1987, fig. 3D), and might correspond to the origin of flexor muscles such as the m. flexor digitorum longus (Dilkes 2000; Meers 2003). A steep border separates the rugose medial margin of the entepicondyle from its smooth and slightly concave cranial surface, which might have received the origin of pronator muscles (Vanden Berge 1975; McGowan 1982; Meers 2003). Laterodistal to this, a small rugose area (MCP 3845-PV) probably corresponds to the attachment of the ventral collateral ligament of the elbow joint (Baumel and Raikow 1993). Between the inner limits of the epicondyles, a large eye-shaped depression occupies the centre of the cranial surface of the distal humerus (MCP 3844-PV). This compares to the fossa m. brachialis (Baumel and Witmer 1993) of birds, which is the site of the humeral origin of the eponymous muscle in this group (George and Berger 1966; McGowan 1986). An avian-like origin for the m. brachialis was inferred for some dinosaurs (Cooper 1981; Moser 2003), whereas a condition more similar to that of crocodiles, with the muscle originating from the distal margin of the deltopectoral crest (Meers 2003), was reconstructed for others (Borsuk-Bialynicka 1977; Coombs 1978; Norman 1986). The frequent occurrence of a similar fossa in basal dinosaurs (Yates 2004, p. 14) seems to favour the first hypothesis.

The distal humeral articulation is lateromedially expanded, occupying about 70 per cent of the distal margin of the bone. On the whole, it faces slightly cranially and is gently concave, with ulnar and radial condyles equally projected distally. The radial condyle occupies the lateral two-fifths of the articulation area, and is nearly continuous with the ulnar facet, except for faint cranial and caudal furrows. It has steep caudal, lateral and cranio-lateral rims, but lacks a caudal ridge as described for *Herrerasaurus* (Serenó 1993). Its craniomedial margin merges smoothly into the cranial surface of the bone, so that the condyle is craniocaudally convex (MCP 3844-PV). Its distally upturned medial border gives the radial condyle a barely concave transverse outline, so that it can be described as saddle-shaped, as in *Herrerasaurus* (Serenó 1993). The cranial extension of the condyle is medially bound by an enlarged expansion of the cranial furrow (Text-fig. 6C, cf) that separates it from the ulnar articulation facet and also surrounds that facet proximally (MCP 3844-PV). It leads into the 'brachial fossa' and may represent a feeble version of the incisura intercondylaris (Baumel and Witmer 1993). The lateromedially elongated ulnar condyle occupies the medial and central parts of the distal humeral articulation. It is crossed by a craniocaudal groove, medial to which the condyle has a craniocaudally elongated biconvex surface. This is surrounded by well-developed lip-like borders, and articulated with a groove on the 'medial process' of the ulna. The transversely flat lateral part of the ulnar condyle abuts the base of the olecranon region. This is not restricted to the distal margin of the bone, but extends onto its cranial surface, where the lip-like border of the articulation ends laterally in a small tuberosity. The ulnar articulation also enters the caudal surface of the humerus, forming a rounded facet with rugose margin, which corresponds to the avian fossa olecrani (Baumel and Witmer 1993). The whole ulnar articulation is therefore markedly convex craniocaudally,

forming a saddle-shaped facet, as also seen, and originally considered unique to *Herrerasaurus* (Serenó 1993). Manipulation of the radius and ulna on the humeral condyles reveal that the elbow joint performed a basically fore-and-aft hinge movement, but some degree of pronation occurred during flexion. The forearm could attain maximal flexion and extension of about 100 and 140 degrees to the humeral long axis, respectively (Text-fig. 2). Indeed, the cranial projections of the distal condyles form a shallow 'cuboid fossa', suggesting that a reasonable degree of forearm flexion was possible (Bonnar 2003; Bonnar and Yates 2007).

*Ulna.* The recovered portion (proximal end and partial shaft) of the most complete (MCP 3844-PV) ulna of *S. tupiniquim* (Text-fig. 8A–E) accounts for about 70 per cent of the total length of the bone, as estimated based on the length of the complete radius. Its proximal end is composed of a broad body, the caudal half of which expands proximally to form the base of the olecranon, and the main portion of that process, which projects further proximally. In its entirety, the olecranon corresponds to 23 per cent of the estimated ulnar length. Such a large process is unusual for basal dinosaurs, but typical of some derived members of the group (Galton and Upchurch 2004b; Vickaryous *et al.* 2004; Senter 2005). In fact, the olecranon of *S. tupiniquim* is formed of what seems to be three separately ossified, but firmly attached portions. The subpyramidal stout portion that forms the base of the process is continuous with the rest of the ulna, and distinguished from the other parts by its smoother outer surface. Its cranial margin is slightly proximally orientated, and articulated with the lateral part of the ulnar condyle of the humerus and to the fossa olecrani, whereas the caudolateral surface has a scarred cranial portion, just proximal to the 'lateral process' (see also Santa Luca 1980) that might represent a separate insertion for the scapular branch of the m. triceps (Baumel and Raikow 1993; Baumel and Witmer 1993). This basal portion seems to correspond to the entire olecranon of most basal dinosaurs (Young 1941a, b, 1947; Bonaparte 1972; Galton 1973, 1974, 1976, 1981, 1984; Van Heerden 1979; Cooper 1981; Welles 1984; Forster 1990; Benton *et al.* 2000; Yates and Kitching 2003; Butler 2005; *Liliensternus*, HB R.1275) that is usually much shorter than distally broad.

In the above-mentioned forms, the olecranon has an often broad and rugose caudoproximally orientated flat surface kinked from the caudal margin of the ulna, which sets the proximal tip of the process apart from its caudal margin. In *S. tupiniquim*, this is covered by a proximally projected sheet of bone (Text-fig. 8, aoo1) that seems to have ossified independently from the rest of the ulna. As a result, the rounded caudal margin of the olecranon is nearly continuous with that of the ulnar shaft and its tip is more caudally placed. The flat medial and bowed caudolateral surfaces of that ossification are heavily marked by longitudinal striations that represent the insertion of the m. triceps tendon (Coombs 1978; Norman 1986; Dilkes 2000). That element tapers proximally from its broad base, whilst thin palisades project cranially from its medial and lateral margins, enveloping the proximal portion of the humeral articulation, to form a shallow trench (Text-fig. 8, ob) proximal to it. The elongated olecranon of some other basal dinosaurs (Raath 1969, 1990;

**TABLE 3.** Right epipodium measurements of *Saturnalia tupiniquim* in millimetres. Inverted commas enclose partial measurements taken from incomplete structures. Abbreviations: MiRPB, minimum radius proximal breadth; MRPB, maximum radius proximal breadth; OPB, olecranon process craniocaudal breadth; OPL, olecranon process length; PUL, preserved ulna length; RAWU, width of ulnar articulation for radius; RDB, radius distal craniocaudal breadth; RDW, radius distal lateromedial width; RL, radius length; RSW, radius mid-shaft lateromedial width; UPB, ulna proximal craniocaudal breadth; UPW, ulna proximal lateromedial width; USB, ulnar shaft craniocaudal breadth; USW, ulnar shaft lateromedial width.

	MCP 3844-PV	MCP 3845-PV
PUL	55	33
UPB	22	18
RAWU	18	15
UPW	14	12
OPL	15	'12'
OPB	11	–
USW	5	–
USB	8	–
RL	61	–
MRPB	17	–
MiRPB	9	–
RSW	6.6	–
RDW	12.5	–
RDB	13	–

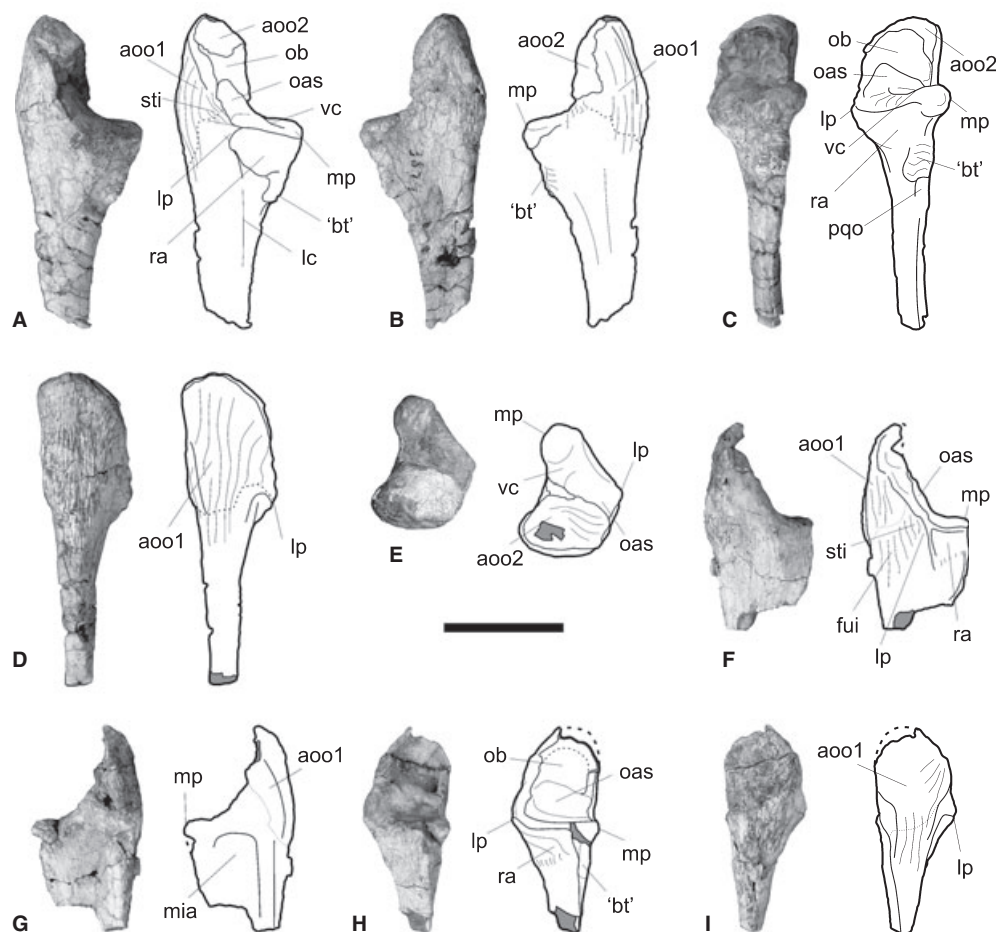
Santa Luca 1980; Sereno 1993) might encompass an equivalent ossification. In *S. tupiniquim*, this element does not contribute to the humeral articulation, but its cranial surface holds another separate ossification. This is not preserved in MCP 3845-PV, neither was it reported in any other basal dinosaur of which we are aware. It has the shape of a medially compressed half-hemisphere, forming the cranial half of the olecranon, proximal to the humeral articulation. It also does not take part in the humeral articulation, but roofs the basin formed by the former ossification, and defines a proximally hollow olecranon process. This peculiar construction is reminiscent of that of the ulnar epiphysis of *Agama agama* figured by Haines (1969, fig. 29), the cranial surface of which has a non-ossified gap, occupied by un-eroded cartilage.

The homology of the proximal elements of the olecranon of *S. tupiniquim* is hard to deduce. They could be tentatively interpreted as ossifications of the triceps tendon (see Haines 1969, fig. 39), such as sesamoids like the ulnar patella of some reptiles (Haines 1969) and birds (Baumel and Witmer 1993). Most probably, however, these represent ossifications of a separate epiphyseal centre that, often in conjunction with tendon ossifications, co-ossify to the ulnar shaft to form a long olecranon, as seen in lizards (Haines 1969). Crocodiles lack discrete epiphyseal ossifications (Haines 1969), and their olecranon remains mainly cartilaginous (Brochu 2003), as also inferred for some fossil archosaurs (Romer 1956; Cooper 1981). In any case, given that an expanded olecranon is known in both preserved ulnae of *S. tupiniquim*,

and also in other finely preserved basal dinosaurs (see above), this morphology is not considered pathological, but typical of the taxon. Interestingly, a similar process is seen emanating from the proximal margin of the left ulna of one specimen of *Plateosaurus* from Halberstadt, Germany (HNM C mounted skeleton; Galton 2001, fig. 27). In this case, even if considered abnormal (the right ulna is typical of 'prosauro-pods'); this might correspond to a rarely ossified or preserved anatomical feature of basal dinosaurs. In other tetrapods, a similarly large olecranon is associated with a strong, but not necessarily fast, forearm extension (Coombs 1978; Fariña and Blanco 1996; Vizcaíno *et al.* 1999). This could be related to digging abilities, even if not connected to fossorial habits (Senter 2005). In this scenario, however, the olecranon would experience a significant stress, which does not seem to match its rather fragile construction in *S. tupiniquim*. Accordingly, the function of the large but hollow and thin-walled olecranon of that dinosaur is unclear.

Craniodistal to the olecranon, the humeral articulation expands cranially to form the 'medial' and 'lateral' processes (Godefroit *et al.* 1998), both of which bear lip-like outer borders that might represent attachment areas for ligaments of the elbow joint (Baumel and Raikow 1993; Meers 2003). The 'medial process' probably represents the attachment site for the posterior radioulnar ligament whereas the anterior radioulnar ligament would have attached to the 'lateral process' (Landsmeer 1983). The 'medial process' is more cranially projected, and separated from the more caudal portion of the humeral articulation by a medially deeper subtle groove. This corresponds to the avian 'ventral cotyle' (Baumel and Witmer 1993), which articulates with the medial part of the ulnar condyle of the humerus. Between the 'medial' and 'lateral' processes, the straight to slightly concave margin of the humeral articulation forms the proximal border of the radial articulation. This extends distally along the cranial surface of the ulna, especially on its medial part, forming a subtriangular flat area for the reception of the proximal head of the radius. The ridge-like proximal part of its caudal margin is sharper in MCP 3845-PV (Text-fig. 8F), forming a steep border that cranially bounds a concave area, which may represent the insertion of the m. flexor ulnaris (Text-fig. 3H). The distal portion of the articulation is lined medially by a rugose buttress (Text-fig. 8, bt), which might accommodate an ulnar insertion of the m. biceps, possibly coupled to that of the m. brachialis inferior (Norman 1986; Dilkes 2000). At this point, the ulna is subtriangular in cross-section, with a flat radial articulation, a rounded caudolateral surface that formed part of the insertion of the m. flexor ulnaris (Meers 2003; = m. ectepicondylus-ulnaris, McGowan 1982), and a flat to slightly concave medial surface. The latter is more excavated in MCP 3845-PV (Text-fig. 8, mia) and might represent the insertion area of either the m. brachialis (Ostrom 1969; Baumel and Raikow 1993) or, most likely, a branch of the m. flexor carpi ulnaris (Borsuk-Bialynicka 1977; Dilkes 2000).

The proximal portion of the ulnar shaft has a hemispherical cross-section (flat medially and round laterally), marked by cranial and caudal margins and a 'lateral crest' (Cooper 1981, fig. 31). Its cranial margin is formed of a subtle flat area expanding distally from the insertion of the m. biceps. It tapers along the shaft, and might represent the origin area of the m. pronator



**TEXT-FIG. 8.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil. Photographs and outline drawings of partial right ulnae. A–E, MCP 3944-PV in A, lateral, B, medial, C, cranial, D, caudal, and E, proximal views. F–I, MCP 3945-PV in F, lateral, G, medial, H, cranial, and I, caudal views. aoo1 and 2, additional olecranon ossifications 1 and 2; 'bt', 'biceps tubercle'; fui, insertion of *m. flexor ulnaris*; lc, lateral crest; lp, lateral process; mia, muscle insertion area; mp, medial process; oas, olecranon articular surface; ob, olecranon 'basin'; pgo, origin of *m. pronator quadratus*; ra, radius articulation; sti, insertion of *m. triceps scapularis*; vc, ventral cotyle. Shaded areas indicate missing parts. Scale bar represents 20 mm.

quadratus (Meers 2003). The 'lateral crest' extends distally from the 'lateral process', diminishing distally, so that the ulnar shaft is elliptical at its most distally preserved portion. Its medullar channel, which is also elliptical, occupies one-quarter of the craniocaudal and one-fifth of the lateromedial width of the bone. From what is preserved of the ulna, it is not possible to determine the medial displacement (Serenó 1993) or distal twisting (Benton *et al.* 2000) of its distal portion, but the whole bone is not caudally arched as is seen in some sauropodomorphs (Van Heerden 1979).

*Radius.* The radius of *S. tupiniquim* (Text-fig. 9) is composed of an elongated body and expanded proximal and distal ends. The latter is craniolaterally placed relative to the ulna and articulates with it via a flat caudomedial surface. The opposite margin is rounded, and the proximal end as a whole has a caudolaterally to craniomedially elongated ovoid outline. The proximal articulation surface has a shallow oblique depression extending lateromedially throughout its centre, which receives the radial condyle

of the humerus. The caudolateral and craniomedial corners of the distal margin are slightly upturned, but neither is particularly projected proximally as in some other basal dinosaurs (Santa Luca 1980; Sereno 1993; *Plateosaurus*, SMNS F65). The articular facet for the ulna is broad at the proximal margin of the radius and tapers distally, forming a subtriangular surface that extends for almost one-fifth of the length of the bone. Its rugose summit (Text-fig. 9A–B, mt) lies caudal to the distal end of a ridge that marks the craniomedial margin of the articulation. This is somewhat distal to the suggested ulnar insertion of the *m. biceps*, and possibly the *m. brachialis inferior* (see above), and might represent the radial insertion of these same muscles. It extends distally as an elongated rugose tuber until the craniomedial corner of the shaft, forming the so-called 'biceps tubercle' (Serenó 1993), which might represent the insertion of the *m. humero-radialis* (Brochu 2003; Meers 2003), and continues as a short faint ridge until the middle of the bone. A comparable, but not necessarily equivalent arrangement of medial elements in the proximal radius has been figured for other dinosaurs (von



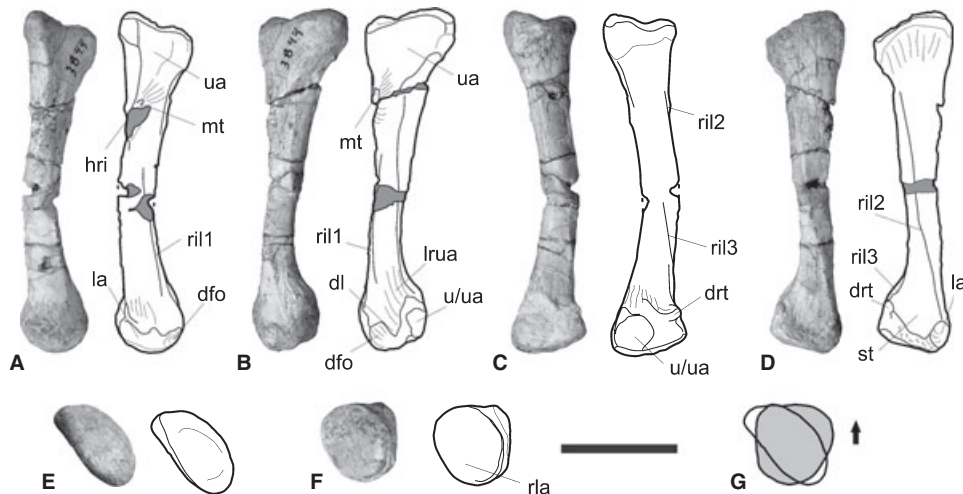
Huene 1926; Galton 1974), but in comparison to *Herrerasaurus* (Sereno 1993), the ‘biceps tubercle’ is not so well marked, and that part of the bone is not medially kinked.

The radius twists along its body, as if the distal end suffered a counter-clockwise rotation of 90 degrees (from a proximal standpoint on the right side). This is inferred from both comparison with other dinosaurs and tracing the intermuscular lines along the shaft. This indicates, for example, that the cranial surface of the proximal part of the bone is continuous with the medial surface at its distal part. The caudomedial surface of the proximal radial shaft is still flat distal to the ulnar articulation. A faint ridge (Text-fig. 9, ril1) emerges from that surface, entering the distal half of the bone as a marked intermuscular line. This forms the caudomedial corner of the distal portion of the shaft, which is subquadratic in cross-section. Another intermuscular line (Text-fig. 9, ril2), also seen in *Herrerasaurus* (Sereno 1993, figs 7B, 8A), arises from the craniolateral surface of the proximal radius, becomes more distinct at the middle of the bone, reaching the craniomedial corner of its distal end. A less obvious line (Text-fig. 9, ril3) marks the craniolateral corner of the distal shaft and is somewhat continuous to a faint ridge extending distally from the caudolateral margin of the proximal end of the bone (see also Sereno 1993, fig. 8B). The more rounded caudolateral corner of the distal shaft is aligned to the ventral margin of the flat caudolateral surface of the proximal radius. Distal to the ‘biceps tubercle’ the ulnar shaft is slightly bowed laterally, especially on its proximal part, but not to the extent seen in *Herrerasaurus* (Sereno 1993).

The radius has an expanded distal end, the perimeter of which is heavily ornate with tubers and grooves. Its cross-section is subtrapezoidal, formed by a broader cranial, a narrower caudal, and oblique lateral and medial surfaces. The cranial surface is flat, but slightly concave laterally, where an inverted extension of the radiale articulation bounds its distal margin. This excavation may correspond to the avian sulcus tendinosus (Baumel and Witmer

1993), which is occupied by tendons of the extensor muscles of the wrist joint. Medial to that, a bulging area occupies the craniomedial corner of the distal radius, stretching caudally along its medial surface (Text-fig. 9, la). A similar rugose element was figured for *Hypsilophodon* (Galton 1974, fig. 40, x), and its relative position seems to correspond to the attachment for the avian lig. radio-radiocarpale craniale (Baumel and Raikow 1993). Laterally, the distal end of the radius has a smooth cranial surface that distally and caudally surrounds a pointed tubercle, marking the craniolateral corner of the bone. A similar tubercle was reported for *Heterodontosaurus* (Santa Luca 1980) and related to the m. extensor carpi radialis. Alternatively, this might correspond to an insertion of the pronator musculature (Vanden Berge 1975; McGowan 1982; Meers 2003), which assists in flexing the forearm. Caudal to that, the ovoid articular facet for the ulna (Sereno 1993) and/or ulnare (Santa Luca 1980) occupies the lateral surface of the distal radius, and also expands into its caudolateral corner. That facet is proximally bound by marked longitudinal striations, possibly related to the lig. radioulnare. This may have also extended into a groove (= depressio ligamentosa: Baumel and Witmer 1993; Brochu 2003), on the rounded caudal surface of the distal radius, just medial to the aforementioned articulation. Medial to that, another rugose bulging area (Text-fig. 9, dfo) might correspond to the origin of a digit flexor (Carpenter and Smith 2001), perhaps the m. transv. palmaris (Meers 2003). All but the craniomedial corner of the distal surface of the radius is occupied by the articulation with the radiale. This has an ovoid shape, with the long axis nearly perpendicular to that of the proximal end of the bone. The articulation is almost flat, but dimly concave medially and convex laterally. The entire distal end of the radius is laterally kinked, so that the distal surface forms an angle of 70 degrees to the long axis of the shaft.

Given that the hand and distal ulna of *S. tupiniquim* are unknown, the orientation of its manus and the relative position



**TEXT-FIG. 9.** *Saturnalia tupiniquim*, Santa Maria Formation, Rio Grande do Sul, Brazil; MCP 3844-PV. A–F, photographs and outline drawings of right radius in A, medial, B, caudal, C, lateral, D, cranial, E, proximal, and F, distal views. G, relative position of proximal and distal ends of the right radius (arrow points cranially). dfo, origin of digit flexor muscle; dl, depressio ligamentosa; drt, distal radius tubercle; hri, insertion of m. humeroradialis; la, ligament attachment; lrua, attachment of lig. radioulnaris; mt, medial tuber; ril1, 2 and 3, radial intermuscular lines 1, 2 and 3; rla, radiale articulation; st, sulcus tendinosus; ua, ulna articulation; u/ua, ulna/ulnare articulation. Shaded areas indicate missing parts. Scale bar represents 20 mm.

of its radius and ulna cannot be positively established. However, it is possible to infer that, based on the position of the ulnar articulation facets on the radius and manipulation of the preserved parts of its epipodium, the twisting of the radius would allow it to cross over the ulna cranially, so that its distal end would be craniomedially placed relative to that bone. In this tentative scenario, the palmar surface of the manus would be directed caudomedially, and not medially to craniomedially as suggested for most saurischians (Sereno 1993; Carpenter 2002; Bonnan 2003; Senter and Robins 2005), although not for most sauropods (Bonnan 2003), which possess a pronated manus. Indeed, the twisting of the radius is not as clear in other basal saurischians (*Herrerasaurus*, PVSJ 373, 407; *Plateosaurus*, SMNS F65) as it is in *S. tupiniquim*, and their wrist joints seem only slightly pronated relative to the proximal radius and ulna. Yet, a radius-ulna crossing is seen in *Stormbergia* (Butler 2005), and a distal radius-ulna articulation similar to that inferred for *S. tupiniquim* was described for other taxa (Thulborn 1972, fig. 7J; Welles 1984, p. 129; Norman 1986, fig. 76C), indicating that the inferred arrangement is not unlikely for a basal dinosaur.

If the wrist was pronated in *S. tupiniquim*, as proposed here, that pronation must have been permanent, given that an active rotation of its radius relative to the ulna is prevented by their flat proximal articulation (see Carpenter 2002; Senter and Robins 2005). That pronation would enforce, at least partially, the caudal orientation of the palmar surface of the manus, which could be fully achieved by means of a minor abduction of the forelimb, as given by the regular articulation of the shoulder joint (see above). This implies that *S. tupiniquim* would be able to face its hand towards the ground, so that the forelimb could tentatively sustain a quadrupedal locomotion, as also inferred on the basis of hindlimb anatomy (Langer 2003). In this context, the enlarged olecranon of *S. tupiniquim* might have been needed to hold the body in a semierect (humerus abducted) position via forearm extension. Yet, this function also does not match its somewhat fragile construction, as previously discussed. Knowledge of manus anatomy is clearly necessary before fully establishing the role, if any, of the forelimb in the locomotion of *S. tupiniquim*. In any case, it would be important to determine whether its forearm construction represents the plesiomorphic saurischian condition, shared even by fully bipedal basal members of the group, or if it is linked to the reacquisition of a quadrupedal gait in an animal that is on the threshold between being an obligate biped and a facultative quadruped (Langer 2003). Indeed, as discussed by Bonnan (2003; see also Bonnan and Yates 2007), a shift in the position of the entire radius, not only of its distal portion, apparently characterizes the transition of facultative to obligatory quadrupedalism among sauropodomorphs.

## INFERENCES ON EARLY DINOSAUR PHYLOGENY

Except for the manus, which is particularly important in the characterization of Saurischia (Gauthier 1986; Langer 2004), the anatomy of the pectoral girdle and forelimb has been scarcely considered in phylogenetic studies of

basal dinosaurs. The latter elements represent the source of approximately 12 per cent of the characters used by Holtz (2000) and Yates (2004) in their phylogenies, 5 per cent of characters in Carrano *et al.* (2002), Rauhut (2003), Langer (2004), Tykoski and Rowe (2004) and Galton and Upchurch (2004a), and less than 2 per cent in the 'basal Dinosauria' section of Sereno's (1999) analysis. Yet, some of these characters are central to the definition of certain key hypotheses of relationships, such as herrerasaur-theropod affinity (Sereno *et al.* 1993), as well as dinosaur (Novas 1996) and 'prosauropod' monophyly (Sereno 1999). Various characters of phylogenetic significance have already been discussed in the descriptive section of this paper. Here, based on the pectoral girdle and forelimb elements described for *Saturnalia tupiniquim*, the status of various related morphological characters proposed in the literature is evaluated. A numerical phylogenetic study has not been carried out, but this reassessment of previously used characters can be incorporated into further studies.

Variations in the length and shape of the scapula blade have been coded differently in cladistic studies of basal dinosaurs. These attempted to define how elongate the scapula, or its blade, is (Holtz 2000, character 211; Carrano *et al.* 2002, character 97; Rauhut 2003, character 132; Yates 2004, character 113; Butler 2005, character 46), how distally expanded and/or constricted the middle of the blade is (Gauthier 1986; Novas 1992; Holtz 2000, character 212; Carrano *et al.* 2002, character 96; Rauhut 2003, character 133; Yates 2004, character 114; Tykoski and Rowe 2004, character 106), or a combination of these conditions (Sereno 1999). Even if somewhat shorter in *Eoraptor* (PVSJ 512), the scapula and/or scapula blade of most basal dinosaurs are equally long in comparison to the breadth of the caput scapulae, and that relation does not seem to bear an important phylogenetic signal. Regarding the second parameter, *S. tupiniquim* shares with most basal dinosaurs a clearly expanded distal blade. On the contrary, *Herrerasaurus* (Sereno 1993) and, to a lesser extent, *Eoraptor* (PVSJ 512) have less expanded blades. As stated by several authors (Holtz 2000; Carrano *et al.* 2002; Rauhut 2003; Langer 2004; contra Sereno *et al.* 1993; Sereno 1999), however, this is not considered to support a theropod-herrerasaur affinity, given that the scapula blade of most basal theropods is also expanded. Instead, it most probably represents an apomorphy of *Herrerasaurus*, and perhaps *Eoraptor*, which is convergently acquired by more derived theropods (Rauhut 2003; Tykoski and Rowe 2004). The condition in *Staurikosaurus* is ambiguous; its blade was either considered strap-like (Novas 1992) or distally expanded (Sereno 1993; Galton 2000; Langer 2004), but never with a strong basis. Considering that the identification of the putative proximal scapular (Bittencourt 2004) and humeral (Sereno 1993;

Galton 2000) fragments are disputed, there is no element of the pectoral girdle or forelimb left with which to compare its incomplete distal scapula. Yet, the craniocaudal length of that element is subequal to that of proximal trunk centra, while in other basal dinosaurs (Owen 1863; Galton 1973; Santa Luca 1980; Welles 1984; Colbert 1989), *Herrerasaurus* included (PVSJ 373; measurements in Novas 1993; Sereno 1993), the distal scapula blade is at least 1.5 times longer. Indeed, this suggests that the distal end of the scapula blade of *Staurikosaurus* is not expanded.

Somewhat related to the distal expansion of the scapula blade are characters dealing with the curvature of its caudal margin (Tykoski and Rowe 2004, character 107; Yates 2004, character 114). The holotype scapula blade of *S. tupiniquim* has an evenly curved caudal margin, whereas in MCP 3845-PV, especially on the left side, the proximal part of the blade is straighter. Indeed, this character has a somewhat erratic distribution: putatively distantly related forms (Owen 1863; Young 1942; Bonaparte 1972; Colbert 1981; Welles 1984; Butler 2005) have a curved caudal margin, whereas a straighter margin is more common among basal dinosaurs. This may be the case for the entire margin of the blade (Sereno 1993). Alternatively, it may be caudally curved only near its distal tip, which is typical of some coelophysoids (Tykoski and Rowe 2004), but is also seen in other basal forms (von Huene 1926; Young 1947; Thulborn 1972; Santa Luca 1980; Cooper 1981; Madsen and Welles 2000; *Efraasia*, SMNS 17928; *Eoraptor*, PVSJ 512; *Guaibasaurus*, MCN 3844-PV). Ultimately, we believe that such a highly variable character contributes only a poor phylogenetic signal to understanding the relationships of basal dinosaurs.

Forelimb length relations have been discussed in the context of theropod (Holtz 2000; Holtz *et al.* 2004), sauropodomorph (Yates 2003; Galton and Upchurch 2004a) and ornithischian (Butler 2005) evolution. The humerus plus radius length in *S. tupiniquim* is just over half that of the femur plus tibia, a condition typical of basal dinosaurs, including *Guaibasaurus* (Bonaparte *et al.* 2006), and dinosaur outgroups (Sereno and Arcucci 1994; Benton 1999; but see Dzik 2003). A longer arm plus forearm is commonly seen among sauropodomorphs (Cooper 1981), whereas the reverse is often the case for theropods (Raath 1969; Welles 1984) and ornithischians (Peng 1992; Butler 2005). On the contrary, the length of the humerus relative to the scapula does not vary greatly among basal dinosaurs. These are usually subequal, or the scapula is slightly longer (Owen 1863; Raath 1969; Galton 1973; Welles 1984; Colbert 1989; Butler 2005; *Eoraptor*, PVSJ 514), while a significantly longer humerus is seen in the outgroups to Dinosauria (Bonaparte 1975; Benton 1999; see also Dzik 2003). Moreover, the humerus of *S. tupiniquim* is approximately 60 per cent of the femoral length, a low ratio

compared to that of various 'prosauropods' (Yates 2004). This is, however, comparable to the condition of *Guaibasaurus* (Bonaparte *et al.* 2006) and dinosaur outgroups, while *Herrerasaurus* and *Eoraptor* share with basal theropods a humerus of about half the length of the femur (Novas 1993; Langer 2004; Langer and Benton 2006). The extension of the deltopectoral crest was used to define dinosaur and 'prosauropod' monophyly (Sereno 1999) and that of *S. tupiniquim* extends for about 45 per cent of the humeral length. Although typically dinosaurian, this length is over the usual proportional length seen in basal theropods (*Liliensternus*, HB R.1275; *Coelophysis rhodesiensis*, QG 1) and ornithischians (Santa Luca 1980; Colbert 1981; Butler 2005), but below that of most basal sauropodomorphs (Galton and Upchurch 2004a; Yates 2004). For this character, *S. tupiniquim* apparently possesses an intermediate condition in the basal dinosaur-sauropodomorph transition, as might also be the case for *Thecodontosaurus*. Fissure-fill deposits from the British Rhaetian have yielded many isolated humeri attributed to that taxon, including gracile and robust morphotypes that vary in the length of the deltopectoral crest (Galton 2005) between general dinosaur and sauropodomorph conditions. Other basal dinosaurs such as *Herrerasaurus* (MACN 18.060) and *Eoraptor* (PVSJ 514) have shorter crests (Langer and Benton 2006), but that of *Guaibasaurus* (Bonaparte *et al.* 2006) falls right into the typical 'prosauropod' range of lengths. Sereno (1999) also considered a deltopectoral crest forming an angle of 90 degrees to the long axis of the distal end of the bone as diagnostic of 'prosauropods'. Although we agree with Yates (2003) on the susceptibility of this character to taphonomic distortion, most 'prosauropods' show the derived condition (Galton and Upchurch 2004a), as is also the case for most basal theropods (Welles 1984; *Coelophysis rhodesiensis*, QG 1; *Liliensternus*, HB R.1275). On the contrary, *S. tupiniquim* shares with *Herrerasaurus* (MACN 18.060) and basal ornithischians (Santa Luca 1980; *Lesothosaurus*, BMNH RUB17), a crest forming a lower angle to the distal end of the bone.

Sereno (1993) defined four autapomorphies for *Herrerasaurus ischigualastensis* based on the humeral anatomy, namely: prominent medial tuberosity, separated by a groove from the head; circular pit on the ectepicondyle; prominent entepicondyle with cranial and caudal depressions; and a saddle-shaped ulnar condyle. It should be clear from the description of *S. tupiniquim* that the taxon possesses the three latter features, while the first is shared by some basal theropods (*Coelophysis rhodesiensis*, QG 1). Indeed, autapomorphies of fossil taxa that belong to poorly understood groups should be defined with caution. These might represent widespread conditions, unknown in putatively related forms given their poor preservation, and may not represent specific anatomical features of the taxon in question.

The forearm anatomy has been poorly explored in the literature dealing with basal dinosaur phylogeny. The reduction of the olecranon process of the ulna was considered in the context of sauropod (Upchurch 1998; Wilson and Sereno 1998) and theropod (Rauhut 2003) evolution, and its unusually large size in *S. tupiniquim* might bear a phylogenetic signal. Yet, it is unclear whether the proximal portion of its olecranon is homologous to that preserved in most basal dinosaurs, and so direct comparison may be misleading. It is likely that it corresponds to those of *Herrerasaurus*, *Heterodontosaurus* and one *Coelophysis rhodesiensis* morphotype, but if so, its significance is jeopardized by both the phylogenetic distance between these taxa and the variation within *C. rhodesiensis*. This suggests that the condition was independently acquired or, most probably, only preserved as such in those particular forms. In the latter case, the presence of a large olecranon among basal dinosaurs would be phylogenetically meaningless. Additionally, Holtz (2000) considered 'prosauropods' distinct from most basal theropods (*Herrerasaurus* included) for their more expanded and concave radial articular facet on the ulna. Yet, that articulation in *S. tupiniquim* is not markedly different from those of *Herrerasaurus* and other basal saurischians (*Plateosaurus*, SMNS F65; *C. rhodesiensis*, QG 1), whereas an excavated proximal ulna better characterizes more derived sauropodomorphs (Wilson and Sereno 1998; Bonnan 2003; Yates and Kitching 2003; Galton and Upchurch 2004a; Yates 2004; Bonnan and Yates 2007). The brachial-antebrachial length relation has also been discussed in the context of sauropodomorph (Yates 2004; Galton and Upchurch 2004a) and theropod (Sereno *et al.* 1998; Holtz 2000; Rauhut 2003; Tykoski and Rowe 2004) evolution. In basal dinosaurs, forearm reduction is apomorphic (Langer 2001, 2004; Yates 2003; Langer and Benton 2006), and *S. tupiniquim* shares with most forms, *Guaibasaurus* (Bonaparte *et al.* 2006) included, a derived condition in which the radius accounts for less than 70 per cent of the humeral length. On the contrary, a radius to humerus length ratio of more than 0.8 can be inferred for *Eoraptor* (PVSJ 514) and *Herrerasaurus* (PVSJ 373, 407; MACN 18.060), and also characterizes the outgroups to Dinosauria (Bonaparte 1975; Benton 1999; Dzik 2003).

## VARIATION IN SATURNALIA TUPINIQUIM

MCP 3845-PV and the holotype of *S. tupiniquim* differ in various details, the more significant of which are related to the greater robustness of the latter. The humeri (Table 2), femora, tibiae, fibulae and metatarsals (Langer 2003) of both specimens are nearly identical in length, suggesting that the animals were equivalent in size. The

long bones of MCP 3845-PV have, however, thinner walls and smaller articulation areas, and its scapulocoracoid is relatively smaller. Indeed, the humerus of the holotype has a shaft that is 12 per cent broader, a distal end that is 20 per cent wider, and a deltopectoral crest that is approximately 50 per cent broader at the base of its distal margin. Its proximal ulna is also broader, both transversely (10 per cent) and craniocaudally (20 per cent), although the olecranon process is equivalent in length to that of MCP 3845-PV. Similarly, although the femoral shafts of both specimens are almost equally thick, that of the holotype has a 65 per cent wider bone-wall (measured in absolute terms at the same portion of the shaft), and a 20 per cent broader distal end. Likewise, the tibial shaft of the holotype is only slightly wider than that of the paratype, but its bone-wall is about 60 per cent wider, and its maximal proximal breadth is 30 per cent greater. The proximal fibula of the holotype is also 10 per cent wider craniocaudally and its metatarsals II–IV are about 20 per cent wider proximally. In that context, variations on the distal width of the humerus are important because it has been used for phylogenetic inferences (Langer 2001, 2004; Yates 2003, 2004). In *S. tupiniquim*, the distal width represents 35 per cent of the length of the holotype humerus, but only 29 per cent of that of MCP 3845-PV. Such variation does not take place in any particular part of the distal humerus, but all parts (condyles and epicondyles) are involved. Those ratios are, respectively, above and below the threshold proposed to discriminate basal sauropodomorphs from other basal dinosaurs. Indeed, whereas almost no basal dinosaur has a humeral distal end corresponding to more than one-third of the length of the bone (Langer and Benton 2006), this is typical of basal sauropodomorphs, although it is reversed in various derived members of the group (Yates 2004). Indeed, the condition of *S. tupiniquim* might be intermediate between the plesiomorphic state and the distally broader humerus of sauropodomorphs, but the detected variation prevents a more precise definition. Similar ranges of variation, but below the one-third boundary, were reported for coelophysoids (Raath 1990; Tykoski and Rowe 2004), and may also apply to dinosaurs with ratios above that limit (see Bonaparte 1972).

In addition to the disparity in robustness, other morphological differences, especially regarding the pectoral girdle and forelimb, were recognized in the specimens of *S. tupiniquim* discussed. The scapular prominence, at the cranioventral part of the bone, is more expanded in MCP 3845-PV than in the holotype, representing, respectively, 44 and 33 per cent of the craniocaudal length of the caput scapulae. Also, the acromion forms a steeper angle to the main axis of the blade in MCP 3845-PV (nearly 90 vs. 65 degrees in the holotype), whereas the 'preglenoid ridge' of the holotype is broader, and its cranial tip

overhangs slightly laterally, as seen in *Stormbergia* (Butler 2005, fig. 10a). Yates (2004, character 112) codes *S. tupiniquim* as sharing a 'long acromion' with some sauropodomorphs and *Herrerasaurus*, but the variable length of its scapular prominence jeopardizes such an assumption. Furthermore, he considered that *S. tupiniquim* also shares with *Herrerasaurus* and some sauropodomorphs an acromion that forms an angle of 65 degrees or more to the scapula blade. Although this is true for both discussed specimens of *S. tupiniquim*, MCP 3845-PV approaches the atypical condition of *Herrerasaurus* more than that of any basal member of the sauropodomorph lineage, including the holotype of *S. tupiniquim*. Indeed, Novas (1992; see also Galton 2000) defined an acromion forming a right angle to the scapula blade as diagnostic for *Herrerasauridae*. Alternatively, more recent accounts have considered this condition to be either absent (Serenó 1993) or indeterminate (Bittencourt 2004) for *Staurikosaurus*, and hence 'autapomorphic' for *Herrerasaurus*. Yet, the record of a comparable morphology in the paratype of *S. tupiniquim* indicates that this condition is not unique to *Herrerasaurus*, but more widespread among basal dinosaurs. Furthermore, the variation in *S. tupiniquim* challenges the phylogenetic significance of this character.

The 'coracoid tuber' (Text-figs 4–5, ct) at the scapula-coracoid junction is more marked in the holotype, whereas the subglenoid part of the coracoid also varies between the two specimens of *S. tupiniquim*. In MCP 3845-PV the 'subglenoid buttress' (Text-figs 4–5, sgb) does not reach the medial margin of the bone but gives rise to a crest-like caudoventral projection of the caudo-medial corner of the glenoid, which expands as a ridge to bound medially the 'subglenoid fossa' (Text-fig. 5E). As a consequence, this fossa faces slightly laterally, and not strictly caudodorsally as in the holotype, and the lateral outline of the coracoid is not excavated ventral to the glenoid. On the contrary, the 'subglenoid buttress' of the holotype expands medially, and separates the caudomedial corner of the glenoid from the subglenoid part of the bone (Text-fig. 4A). The former lacks a well-developed ridge-like caudal expansion, and the caudal margin of the coracoid is excavated ventral to the glenoid. Yates (2004, character 116) suggested that a 'flat caudoventrally facing surface between the glenoid and the coracoid tubercle' was missing in theropods and some sauropodomorphs. This is the condition observed in MCP 3845-PV and apparently also in some ornithischians (Colbert 1981), theropods (Welles 1984; *Liliensternus*, HB R.1275), and *Thecodontosaurus* (Yates 2003), in which the caudal expansion of the glenoid disrupts the medial extension of that surface. In contrast, that surface roofs the entire cranial portion of the subglenoid fossa in MCP 3844-PV, some basal theropods (*Coelophysis rhodesiensis*, QG 1), ornithischians (Butler 2005), sauropodomorphs (Young

1941a; *Plateosaurus*, SMNS F65; *Riojasaurus*, PVL 3808), and possibly *Herrerasaurus* (Brinkman and Sues 1987). Accordingly, the variation in *S. tupiniquim* and the erratic distribution of this character among basal dinosaurs jeopardizes its phylogenetic informativeness.

Despite major differences in robustness, the humeri of MCP 3844-PV and 3845-PV are rather alike in other aspects. Some structures are better defined in the latter, such as most excavations on the cranial and caudal surfaces of both proximal and distal ends of the bone. Raath (1990) mentioned that the humeri of the robust morphotypes of *Coelophysis rhodesiensis* have distal condyles with more pronounced rims, but this is not clear in *S. tupiniquim*. Likewise, Raath (1990) noted variations in the development of the olecranon processes in ulnae attributed to *C. rhodesiensis*, but no relationship to either of the morphotypes was drawn. As discussed above, the process is equally elongated in both specimens of *S. tupiniquim*, while the absence of an extra ossification roofing of the proximal part of the olecranon in MCP 3845-PV is probably owing to lack of preservation. In the hind limb (Langer 2003), the external tibial condyle of the holotype of *S. tupiniquim* is placed cranial to the internal condyle, as in *Marasuchus*, *Pseudolagosuchus*, most 'prosauro-pods' and basal ornithischians. In MCP 3845-PV, on the other hand, this element lies in the caudolateral corner of the proximal tibia, as in *Herrerasaurus*, *Staurikosaurus*, *Pisanosaurus* and basal theropods, so that its morphology seems apomorphic among basal dinosaurs (Langer and Benton 2006). On the contrary, the distal tibia of MCP 3845-PV seems plesiomorphic for its almost subtriangular cross-section, which approaches the condition in *Marasuchus* (Bonaparte 1975) and basal ornithischians (Thulborn 1972). These lack the strong caudolateral corner seen in the holotype and most saurischians. Likewise, the non-vertical caudal border of the astragalar ascending process of the paratype represents a primitive feature for dinosaurs, because it is present in basal dinosauriforms and basal ornithischians (Novas 1989, 1996).

The robustness differences between the two specimens of *S. tupiniquim* can be related to sex, age or phylogeny, or some combination of these parameters. Horner *et al.* (2000) reported that older specimens of *Maiasaura* present relatively thinner bone-walls, because of the expansion of their medullary cavity. In this case, the endosteal margin spreads diffusely into the deep cortex, and the distinction between the medullary cavity and the bone-wall is not clear-cut. Such ageing signals are absent in *S. tupiniquim*, the long bones of which possess a discrete limit between these tissue layers. In this case, the thicker bone-walls of the holotype seem to be the result of more extensive appositional growth that, along with its broader articulations, would reflect an extended development, rather than the reverse. Sexual dimorphism, with a robust

more developed gender, could explain those differences. Yet, it is noteworthy that femora of both specimens of *S. tupiniquim* have a well-developed trochanteric shelf, the presence of which was regarded as sexually dimorphic in *Coelophysis rhodesiensis* (Raath 1990). On the other hand, if individual age is to be considered as the source of the robustness differences of *S. tupiniquim*, the similar size of the two specimens implies that the juvenile, or subadult, would already have virtually reached adult size. This suggests a quick growth in length during early ontogenetic stages (for a review of this subject, see Erickson 2005), with subsequent appositional growth increasing the thickness of the bone-walls and some skeletal parts.

If the variation identified in *S. tupiniquim* is at least partially driven by phylogeny, one has to admit the chance of taxonomic distinction between the two specimens in question, and search for morphological differences not associated *a priori* with developmental constraints. Indeed, some of their differences are putatively significant in the context of basal dinosaur evolution, standing for plesiomorphic or derived states (see above). Nevertheless, the two specimens share unique features, so that if future work defines *Saturnalia* as a congregation of different taxa, these will probably form a clade. As argued by Raath (1990) for *Coelophysis rhodesiensis*, the study of intraspecific variation is important to define whether states of a potential phylogenetically informative character fall within the range of variation of a single taxon. In this scenario, the paratype would simply not show certain features that define a fully developed individual of *S. tupiniquim*.

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## REFERENCES

ANDREIS, R. R., BOSSI, G. E. and MONTARDO, D. K. 1980. O Grupo Rosário do Sul, (Triássico) no Rio Grande do

- Sul. *Anais do XXXI Congresso Brasileiro de Geologia, Camboriú*, 2, 659–673.
- AZUMA, Y. and CURRIE, P. J. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences*, 37, 1735–1753.
- BAKKER, R. T., KRALLIS, D., SEIGWARTH, J. and FILLA, J. 1992. *Edmarka rex*, a new gigantic theropod dinosaur from the middle Morrison Formation, Late Triassic of the Como Bluff outcrop region, with comments on the evolution of the chest region and shoulder in theropods and birds, and a discussion of the five cycles of origin and extinction among giant dinosaurian predators. *Hunteria*, 2, 1–24.
- BARBERENA, M. C. 1977. Bioestratigrafia preliminar da Formação Santa Maria. *Pesquisas*, 7, 111–129.
- ARAÚJO, D. C. and LAVINA, E. L. 1985. Late Permian and Triassic tetrapods of southern Brazil. *National Geographic Research*, 1, 5–20.
- BAUMEL, J. J. and RAIKOW, R. J. 1993. Arthrologia. 133–187. In BAUMEL, J. J. (ed.). *Handbook of avian anatomy: nomina anatomica avium*. Publications of the Nuttall Ornithological Club, Cambridge, 779 pp.
- and WITMER, L. M. 1993. Osteologia. 45–132. In BAUMEL, J. J. (ed.). *Handbook of avian anatomy: nomina anatomica avium*. Publications of the Nuttall Ornithological Club, Cambridge, 779 pp.
- BENTON, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, 354, 1423–1446.
- JULL, L., STORRS, G. W. and GALTON, P. M. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwestern England. *Journal of Vertebrate Paleontology*, 20, 77–108.
- BITTENCOURT, J. S. 2004. Revisão descritiva e posicionamento filogenético de *Staurikosaurus pricei* Colbert 1970 (Dinosauria, Theropoda). Unpublished MSc Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 158 pp.
- BONAPARTE, J. F. 1972. Los tetrapodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triássico superior). *Opera Lilloana*, 22, 1–183.
- 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia – Pseudosuchia) y su significado en el origen de los Saurischia. Chañarense inferior, Triásico Medio de Argentina. *Acta Geologica Lilloana*, 13, 5–90.
- BREA, G., SCHULTZ, C. L. and MARTINELLI, A. G. 2006. A new specimen of *Guaibasaurus candelariensis* (basal Saurischia) from the Late Triassic Caturrita Formation of southern Brazil. *Historical Biology*, 18 (3), 1–10.
- FERIGOLO, J. and RIBEIRO, A. M. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul State, Brazil. 89–109. In TOMIDA, Y., RICH, T. H. and VICKERS-RICH, P. (eds). *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs, 15, 296 pp.
- BONNAN, M. F. 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. *Journal of Vertebrate Paleontology*, 23, 595–613.



- and YATES, A. M. 2007. A new description of the forelimb of the basal sauropodomorph *Melanorosaurus*: implications for the evolution of pronation, manus shape and quadrupedalism in sauropod dinosaurs. 157–168. In BARRETT, P. M. and BATTEN, D. J. (eds). *Evolution and palaeobiology of early sauropodomorph dinosaurs*. Special Papers in Palaeontology, **77**, 289 pp.
- BORSUK-BIALYNICKA, M. 1977. A new camarasaurid sauropod *Opisthocolicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica*, **37**, 5–63.
- BRINKMAN, D. B. and SUES, H.-D. 1987. A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. *Palaeontology*, **30**, 493–503.
- BROCHU, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Memoir of the Society of Vertebrate Paleontology*, **7**, 1–138.
- BRYANT, H. N. and RUSSELL, A. P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London, Series B*, **337**, 405–418.
- — 1993. The occurrence of clavicles within Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. *Journal of Vertebrate Paleontology*, **13**, 171–184.
- BUTLER, R. J. 2005. The ‘fabrosaurid’ ornithischian dinosaurs of the upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho. *Zoological Journal of the Linnean Society*, **145**, 175–218.
- CARPENTER, K. 2002. Forelimb biomechanics of nonavian theropod dinosaurs in predation. 59–76. In GUDO, M., GUTMANN, M. and SCHOLZ, J. (eds). *Concepts of functional engineering and constructional morphology*. Senckenbergiana Lethaea, **82**, 372 pp.
- and SMITH, M. 2001. Forelimb osteology and biomechanics of *Tyrannosaurus rex*. 90–116. In TANKE, D. H. and CARPENTER, K. (eds). *Mesozoic vertebrate life*. Indiana University Press, Bloomington, IN, 352 pp.
- MILES, C., OSTROM, J. H. and CLOWARD, K. 2005. Redescription of the small maniraptoran theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming. 49–71. In CARPENTER, K. (ed.). *The carnivorous dinosaurs*. Indiana University Press, Bloomington, IN, 371 pp.
- CARRANO, M. T., SAMPSON, S. D. and FORSTER, C. A. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, **22**, 510–534.
- CHARIG, A. J. and MILNER, A. C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum (Geology Series)*, **53**, 11–70.
- CLARK, A. C. Jr 1993. Termini situm et directionem partium corporis indicantes. 1–6. In BAUMEL, J. J. (ed.). *Handbook of avian anatomy: nomina anatomica avium*. Publications of the Nuttall Ornithological Club, Cambridge, 779 pp.
- COLBERT, E. H. 1970. A saurischian dinosaur from the Triassic of Brazil. *American Museum Novitates*, **2405**, 1–39.
- 1981. A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. *Bulletin of the Museum of Northern Arizona*, **53**, 1–61.
- 1989. The Triassic dinosaur *Coelophysus*. *Bulletin of the Museum of Northern Arizona*, **57**, 1–160.
- COOMBS, W. P. Jr 1978. Forelimb muscles of the Ankylosauria (Reptilia; Ornithischia). *Journal of Paleontology*, **52**, 642–657.
- COOPER, M. R. 1981. The prosauropod dinosaur *Mossospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums and Monuments of Rhodesia, Series B (Natural Sciences)*, **6**, 689–840.
- CORIA, R. A. and SALGADO, L. 1996. A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. *Journal of Vertebrate Paleontology*, **16**, 445–457.
- CRACRAFT, J. 1974. Phylogeny and evolution of the ratite birds. *Ibis*, **116**, 494–521.
- CURRIE, P. J. and CARPENTER, K. 2000. A new specimen of *Acrocantiosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, **22**, 207–246.
- and ZHAO, XI-JIN 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People’s Republic of China. *Canadian Journal of Earth Sciences*, **30**, 2037–2081.
- DILKES, D. W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **90**, 87–125.
- DZIK, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology*, **23**, 556–574.
- ERICKSON, G. M. 2005. Accessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology and Evolution*, **20**, 677–684.
- FARIÑA, R. A. and BLANCO, R. E. 1996. *Megatherium*, the stabber. *Proceedings of the Royal Society of London, Series B*, **263**, 1725–1729.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *The American Naturalist*, **125**, 1–15.
- FORSTER, C. A. 1990. The postcranial skeleton of the ornithopod dinosaur *Tenontosaurus tilletti*. *Journal of Vertebrate Paleontology*, **10**, 273–294.
- FRASER, N. C., PADIAN, K., WALKDEN, G. M. and DAVIS, A. L. 2002. Basal dinosauriform remains from Britain and the diagnosis of Dinosauria. *Palaeontology*, **45**, 79–95.
- GALTON, P. M. 1973. On the anatomy and relationships of *Efraasia diagnostica* (Huene) n. gen., a prosauropod dinosaur (Reptilia: Saurischia) from the Upper Triassic of Germany. *Paläontologische Zeitschrift*, **47**, 229–255.
- 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. *Bulletin of the British Museum of Natural History (Geology)*, **25**, 1–152.
- 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla*, **169**, 1–98.
- 1981. *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa. Postcranial skeleton. *Paläontologische Zeitschrift*, **55**, 271–312.

- 1984. An early prosauropod dinosaur from the Upper Triassic of Nordwürttemberg, West Germany. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, **106**, 1–25.
- 2000. Are *Spondylosoma* and *Staurikosaurus* (Santa Maria Formation, Middle–Upper Triassic, Brazil) the oldest known dinosaurs? *Paläontologische Zeitschrift*, **74**, 393–423.
- 2001. The prosauropod dinosaur *Plateosaurus* Meyer, 1837 (Saurischia: Sauropodomorpha; Upper Triassic). II. Notes on the referred species. *Revue de Paléobiologie*, **20**, 435–502.
- 2005. Basal sauropodomorph dinosaur taxa *Thecodontosaurus* Riley & Stutchbury, 1836, *T. antiquus* Morris, 1843 and *T. caducus* Yates, 2003: their status re humeral morphs from the 1834 Fissure Fill (Upper Triassic) in Clifton, Bristol, UK. *Journal of Vertebrate Paleontology*, **23** (Supplement to No. 3), 61A.
- and JENSEN, J. A. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University, Geological Studies*, **26**, 1–12.
- and UPCHURCH, P. 2004a. Prosauropoda. 232–258. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- and UPCHURCH, P. 2004b. Stegosauria. 343–362. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- GAUTHIER, J. A. 1986. Saurischian monophyly and the origin of birds. 1–55. In PADIAN, K. (ed.). *The origins of birds and the evolution of flight*. Memoirs of the Californian Academy of Sciences, **8**, 98 pp.
- GEORGE, J. C. and BERGER, A. J. 1966. *Avian myology*. Academic Press, New York, NY, and London, 500 pp.
- GODEFROIT, P., DONG ZHI-MING, BULTYNCK, P., LI HONG and FENG LU 1998. Sino-Belgian Cooperative Program. Cretaceous dinosaurs and mammals from Inner Mongolia: (1) New *Bactrosaurus* (Dinosauria: Hadrosauroida) material from Iren Dabasu (Inner Mongolia, P.R. China). *Bulletin de l'Institut Royal des Science Naturelles de Belgique, Sciences de la Terre*, **68** (Supplement), 3–70.
- HAINES, R. W. 1952. The shoulder joint of lizards and the primitive reptilian shoulder mechanism. *Journal of Anatomy*, **86**, 412–422.
- 1969. Epiphyses and sesamoids. 81–115. In GANS, C. BELLAIRS, A. d'A. and PARSONS, T. S. (eds). *Biology of the Reptilia, morphology A, volume 1*. Academic Press, New York, NY, 263 pp.
- HOLTZ, T. R. Jr 2000. A new phylogeny of the carnivorous dinosaurs. 5–61. In PÉREZ-MORENO, B. P., HOLTZ, T. R. Jr, SANZ, J. L. and MORATALLA, J. J. (eds). *Aspects of theropod paleobiology*. Gaia, **15**, 403 pp.
- MOLNAR, R. E. and CURRIE, P. J. 2004. Basal tetanurae. 71–110. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- HORNER, J. R., DE RICQLÈS, A. and PADIAN, K. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology*, **20**, 115–129.
- HUENE, F. VON 1910. Ein primitiver Dinosaurier aus der mittleren Trias von Elgin. *Geologische und Paläontologische Abhandlungen, Neue Folge*, **8**, 317–322.
- 1926. Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Keuper. *Geologische und Paläontologische Abhandlungen, Neue Folge*, **15**, 139–179.
- 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Paläontologie, Series 1*, **4**, 1–361.
- 1934. Ein neuer Coelurosaurier in der thüringischen Trias. *Paläontologische Zeitschrift*, **16**, 145–168.
- and STAHLLECKER, R. 1931. Geologische Beobachtungen in Rio Grande do Sul. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, B*, **65**, 1–82.
- HUTCHINSON, J. R. 2001. The evolution of hindlimb anatomy and function in theropod dinosaurs. Unpublished PhD thesis, University of California, Berkeley, CA, 415 pp.
- JANENSCH, W. 1955. Der Ornithopode *Dysalotosaurus* der Tendaguruschichten. *Paläontographica (Supplement 7)*, **3**, 105–176.
- JENKINS, F. A. Jr 1993. The evolution of the avian shoulder joint. *American Journal of Science*, **293A**, 253–267.
- and GOSLOW, G. E. Jr 1983. The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exanthematicus*). *Journal of Morphology*, **175**, 195–216.
- KOBAYASHI, Y. and LÜ JUN-CHANG 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica*, **48**, 235–259.
- LANDSMEER, J. M. F. 1983. The mechanism of forearm rotation in *Varanus exanthematicus*. *Journal of Morphology*, **175**, 119–130.
- LANGER, M. C. 2001. *Saturnalia Tupiniquim* and the early evolution of dinosaurs. Unpublished PhD thesis, University of Bristol, Bristol, 415 pp.
- 2003. The sacral and pelvic anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *Paleobios*, **23**, 1–40.
- 2004. Basal Saurischia. 25–46. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- 2005a. Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil. *Journal of South American Earth Sciences*, **19**, 205–218.
- 2005b. Studies on continental Late Triassic tetrapod biochronology. II. The Ischigualastian and a Carnian global correlation. *Journal of South American Earth Sciences*, **19**, 219–239.
- and BENTON, M. J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology*, **4**, 309–358.
- ABDALA, F., RICHTER, M. and BENTON, M. J. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes*, **329**, 511–517.
- LONG, J. A. and MURRY, P. A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *Bulletin of the New Mexico Museum of Natural History and Science*, **4**, 1–254.

- MADSEN, J. H. 1976. *Allosaurus fragilis*: a revised osteology. *Bulletin of the Utah Geology and Mineralogy Survey*, **109**, 3–163.
- and WELLES, S. P. 2000. *Ceratosaurus* (Dinosauria, Theropoda); a revised osteology. *Utah Geological Survey, Miscellaneous Publications*, **00–2**, 1–80.
- MAKOVICKY, P. J. and SUES, H.-D. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *American Museum Novitates*, **3240**, 1–27.
- APESTEGUÍA, S. and AGNOLÍN, F. L. 2005. The earliest dromaeosaurid theropod from South America. *Nature*, **437**, 1007–1011.
- McGOWAN, C. 1982. The wing musculature of the Brown Kiwi *Apteryx australis mantelli* and its bearing on ratite affinities. *Journal of Zoology*, **197**, 173–219.
- 1986. The wing musculature of the Weka (*Gallirallus australis*), a flightless rail endemic to New Zealand. *Journal of Zoology*, **210**, 305–346.
- MEERS, M. B. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. *Anatomical Record, Part A*, **274A**, 891–916.
- MOSER, M. 2003. *Plateosaurus engelhardti* Meyer, 1837 (Dinosauria: Sauropodomorpha) aus dem Feuerletten (Mittelkeuper; Obertrias) von Bayern. *Zitteliana*, **24**, 3–186.
- NICHOLLS, E. L. and RUSSELL, A. P. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). *Palaeontology*, **28**, 643–677.
- NORELL, M. A. and MAKOVICKY, P. J. 1999. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates*, **3282**, 1–45.
- NORMAN, D. B. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: Sciences de la Terre*, **56**, 281–372.
- NOVAS, F. E. 1986. Un probable terópodo (Saurischia) de la Formación Ischigualasto (Triásico superior), San Juan, Argentina. *Actas del IV Congreso Argentino de Paleontología y Estratigrafía. Mendoza*, **2**, 1–6.
- 1989. The tibia and tarsus in Herrerasauridae (Dinosauria, *incertae sedis*) and the origin and evolution of the dinosaurian tarsus. *Journal of Paleontology*, **63**, 677–690.
- 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology*, **35**, 51–62.
- 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology*, **13**, 400–423.
- 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology*, **16**, 723–741.
- and PUERTA, P. F. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature*, **387**, 390–392.
- OSMÓLSKA, H., MARYANSKA, T. and BARSBOLD, R. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica*, **27**, 103–143.
- OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History*, **30**, 1–165.
- 1974. The pectoral girdle and forelimb function of *Deinonychus* (Reptilia: Saurischia): a correction. *Postilla*, **165**, 1–11.
- and McINTOSH, J. S. 1966. *Marsh's dinosaurs*. Yale University Press, New Haven, CT, 388 pp.
- OWEN, R. 1842. Report on British fossil reptiles. Part II. *Reports of the British Association for the Advancement of Science*, **11**, 60–204.
- 1863. A monograph of the fossil Reptilia of the Liassic formations. Second part. *Scelidosaurus harrisonii* continued. *Palaeontographical Society Monographs*, **14**, 1–26.
- PADIAN, K. 1997. Pectoral girdle. 530–536. In CURRIE, P. J. and PADIAN, K. (eds). *Encyclopedia of dinosaurs*. Academic Press, San Diego, CA, 869 pp.
- HUTCHINSON, J. R. and HOLTZ, T. R. Jr 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *Journal of Vertebrate Paleontology*, **19**, 69–80.
- PARKER, T. J. 1891. Observations on the anatomy and development of *Apteryx*. *Philosophical Transactions of the Royal Society of London, Series B*, **182**, 25–134.
- PENG GUANG-ZHAO 1992. Jurassic ornithopod *Agilisaurus louderbacki* (Ornithopoda: Fabrosauridae) from Zigong, Sichuan, China. *Vertebrata Palasiatica*, **30**, 39–53. [In Chinese, English abstract].
- PÉREZ-MORENO, B. P., SANZ, J. L., BUSCALLONI, A. D., MORATALLA, J. J., ORTEGA, F. and RASSKIN-GUTMAN, D. 1994. A unique multi-toothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature*, **370**, 363–367.
- RAATH, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia*, **4** (28), 1–25.
- 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. 91–105. In CARPENTER, K. and CURRIE, P. J. (eds). *Dinosaur systematics. Approaches and perspectives*. Cambridge University Press, Cambridge, 334pp.
- RAUHUT, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, **69**, 1–213.
- REIG, O. A. 1963. La presencia de dinosaurios sauriscios en los 'Estrados de Ischigualasto' (Mesotriásico superior) de las Provincias de San Juan y La Rioja (Republica Argentina). *Ameghiniana*, **3**, 3–20.
- ROGERS, R. R., SWISHER, C. C. III, SERENO, P. C., MONETTA, A. M., FORSTER, C. A. and MARTÍNEZ, R. N. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of dinosaurs origins. *Science*, **260**, 794–797.
- ROMER, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History*, **46**, 517–606.
- 1956. *Osteology of the reptiles*. University of Chicago Press, Chicago, IL, 772 pp.

- 1966. *Vertebrate paleontology*. Third edition. University of Chicago Press, Chicago, IL, 468 pp.
- ROWE, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, **9**, 125–136.
- SANTA LUCA, A. P. 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. *Annals of the South African Museum*, **79**, 15–211.
- 1984. Postcranial remains of Fabrosauridae (Reptilia: Ornithischia) from the Stormberg of South Africa. *Palaentologia Africana*, **25**, 151–180.
- SEELEY, H. G. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, **43**, 165–171.
- SENER, P. 2005. Function in the stunted forelimbs of *Monykus olecranus* (Theropoda), a dinosaurian anteater. *Paleobiology*, **31**, 373–381.
- and ROBINS, J. H. 2005. Range of motion in the forelimb of the theropod dinosaur *Acrocanthosaurus atokensis*, and implications for predatory behaviour. *Journal of Zoology*, **266**, 307–318.
- SERENO, P. C. 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, **13**, 425–450.
- 1999. The evolution of dinosaurs. *Science*, **284**, 2137–2147.
- and ARCUCCI, A. B. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology*, **14**, 53–73.
- BECK, L., DUTHEIL, D. B., GADO, B., LARSSON, H. C. E., LYON, G. H., MARCOT, J. D., RAUHUT, O. W. M., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. D., WILSON, G. P. and WILSON, J. A. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, **282**, 1298–1302.
- FORSTER, C. A., ROGERS, R. R. and MONETTA, A. M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of the Dinosauria. *Nature*, **361**, 64–66.
- THULBORN, R. A. 1972. The post-cranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus australis*. *Palaentology*, **15**, 29–60.
- TYKOSKI, R. S. and ROWE, T. 2004. Ceratosauria. 47–70. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- FORSTER, C. A., ROWE, T., SAMPSON, S. D. and MUNYIKWA, D. 2002. A furcula in the coelophysid theropod *Syntarsus*. *Journal of Vertebrate Paleontology*, **22**, 728–733.
- UPCHURCH, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society*, **124**, 43–103.
- BARRETT, P. M. and DODSON, P. 2004. Sauropoda. 259–322. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- VAN HEERDEN, J. 1979. The morphology and taxonomy of *Euskelosaurus* (Reptilia: Saurischia; Late Triassic) from South Africa. *Navorsing van die Nasionale Museum*, **4**, 21–84.
- VANDEN BERGE, J. C. 1975. Aves myology. 1802–1848. In GETTY, R. (ed.). *Sisson and Grossman's The anatomy of the domestic animals. Volume 2*. Fifth edition. W.B. Saunders, Philadelphia, PA, 1881 pp.
- and ZWEERS, G. A. 1993. Myologia. 189–247. In BAUMEL, J. J. (ed.). *Handbook of avian anatomy: nomina anatomica avium*. Publications of the Nuttall Ornithological Club, Cambridge, 779 pp.
- VICKARYOUS, M. K., MARYANSKA, T. and WEISHAMPEL, D. B. 2004. Ankylosauria. 363–392. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- VIZCAÍNO, S. F., FARIÑA, R. A. and MAZZETTA, G. 1999. Ulnar dimensions and fossoriality in armadillos and other South American mammals. *Acta Theriologica*, **44**, 309–320.
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London, Series B*, **244**, 103–204.
- 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, **248**, 53–134.
- 1977. Evolution of the pelvis in birds and dinosaurs. 319–358. In ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds). *Problems in vertebrate evolution*. Linnean Society Symposia, **4**, 411 pp.
- WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. 2004. Introduction. 1–3. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, CA, 861 pp.
- WELLES, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaentographica A*, **185**, 85–180.
- WILSON, J. A. and SERENO, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoir of the Society of Vertebrate Paleontology*, **5**, 1–68.
- WITMER, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. 19–33. In THOMASON, J. J. (ed.). *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge, 293 pp.
- YATES, A. M. 2003. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Paleontology*, **1**, 1–42.
- 2004. *Anchisaurus polyzelus* (Hitchcock): the smallest known sauropod dinosaur and the evolution of gigantism among sauropodomorph dinosaurs. *Postilla*, **230**, 1–58.
- and KITCHING, J. W. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London, Series B*, **270**, 1753–1758.
- and VASCONCELOS, C. C. 2005. Furcula-like clavicles in the prosauropod dinosaur *Massospondylus*. *Journal of Vertebrate Paleontology*, **25**, 466–468.

- YOUNG CHUNG-CHIEN 1941a. A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.). *Palaeontologia Sinica, Series C*, 7, 1–53.
- 1941b. *Gyposaurus sinensis* Young (sp. nov.), a new Prosauropoda from the Upper Triassic beds at Lufeng, Yunnan. *Bulletin of the Geological Society of China*, 21, 205–252.
- 1942. *Yunnanosaurus huangi* Young (gen. et sp. nov.), a new Prosauropoda from the Red Beds at Lufeng, Yunnan. *Bulletin of the Geological Society of China*, 22, 63–104.
- 1947. On *Lufengosaurus magnus* (sp. nov.) and additional finds of *Lufengosaurus huenei* Young. *Palaeontologia Sinica, Series C*, 12, 1–53.
- ZERFASS, H., LAVINA, E. L., SCHULTZ, C. L., GARCIA, A. G. V., FACCINI, U. F. and CHEMALE, F. Jr 2003. Sequence stratigraphy of continental Triassic strata of southernmost Brazil: a contribution to southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology*, 161, 85–105.