

A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary bone

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Abstract

The South American Late Triassic offers the most comprehensive window to the early radiation of dinosaurs. This is enhanced by the discovery of *Sacisaurus agudoensis*, a new dinosauriform from the Caturrita Formation of Brazil. Various morphological features suggest its close phylogenetic affinity to *Silesaurus*, and both may be basal ornithischian dinosaurs. *Sacisaurus* has a pair of elements forming the tip of its lower jaw, hypothesized to be equivalent to the ornithischian predentary. This suggests that during an initial stage of their evolution, those dinosaurs had a paired predentary, which later fused into a single structure. As an originally paired bone, the predentary is comparable to elements that more often form the vertebrate mandible, such as the mentomeckelian bone. Although synapomorphic for ornithischians, the predentary does not seem neomorphic for the group, but primarily homologous to parts of the symphyseal region of the lower jaw of other vertebrates.

Keywords: *Sacisaurus*, Late Triassic, ornithischia, predentary, Brazil, Caturrita Formation

Introduction

The presence of a separate ossification at the tip of the lower jaw, the predentary bone, is as typical of ornithischian dinosaurs as their opisthopic pelvis. Some consider the junior synonym *Predentata* Marsh 1894, to more “properly” designate the taxon, given that various maniraptorans are obviously “bird-hipped” (Ostrom 1976; Barsbold 1979; Hutchinson and Chiappe 1998), but no other major dinosaur group possesses a predentary. Despite its ambiguous presence in the putative basal-most member of the group, *Pisanosaurus mertii* from the Late Triassic of Argentina (Casamiquela 1967; Bonaparte 1976; Sereno 1991), the predentary is often considered synapomorphic for Ornithischia as a whole (Norman 1984; Sereno 1984, 1986; Maryanska and Osmólska 1985; Cooper 1985; Norman et al. 2004). Otherwise, a homonymous bone has only been referred to some

teleosts and fossil birds (Regan 1909; Gregory and Conrad 1937; Bardack and Sprinkle 1969; Martin 1987, 1991; Brito 1997). The origin of the ornithischian predentary is not comprehensively known, but new material from southern Brazil provides information that can help to understand the acquisition of this unique element.

The new taxon described here comes from a bone accumulation horizon within the Caturrita Formation, Rio Grande do Sul, Brazil (Figure 1). This stratigraphic unit is of Late Triassic age (Rubert and Schultz 2004; Langer 2005a), suggesting that the new form is one of the oldest known putative ornithischians. The first members of the Ornithischia are of Ischigualastian age (early-mid Carnian), including *Pisanosaurus* and possible isolated remains from the North American Atlantic coast (Galton 1983; Hunt and Lucas 1994; Weishampel and Young 1996) and Morocco (Galton 1985a; Gauffre 1993; but see Jalil and Knoll 2002).

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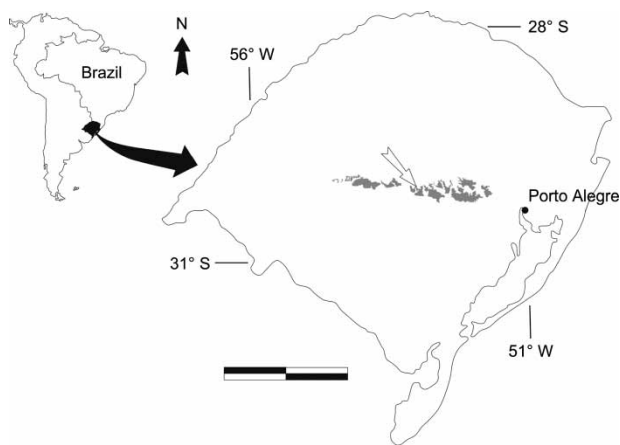


Figure 1. Sketch map of Rio Grande do Sul showing the outcrop areas of the Santa Maria sequence (shaded) and approximate location of the type-locality of *Sacisaurus agudoensis* gen. et sp. nov. (arrowed). Scale bar represents 200 km.

Other alleged Triassic ornithischians include an heterodontosaurid from Patagonia (Baez and Marsicano 2001), an undescribed basal neornithischian from southern Africa (Butler 2005), and fragmentary material from Western USA (Chatterjee 1984; Hunt and Lucas 1994; Heckert 2004; Irmis et al. 2006), Europe (Godefroit and Cuny 1997; Cuny et al. 2000), and India (Weishampel et al. 2005). The ornithischian affinity of most of these remains was based on often criticized (Serenio 1991; Knoll 2002) characters of tooth morphology. More recently, Parker et al. (2005; see also Irmis et al. 2006) demonstrated that the putative ornithischian *Revueltosaurus callenderi* represents a pseudosuchian archosaur with herbivorously-adapted teeth, showing that several of the alleged ornithischian dental apomorphies are not unique to that dinosaur group among Late Triassic archosaurs. Following this conservative approach, it is the mainly South American Late Triassic records that are referable to Ornithischia (Casamiquela 1967; Baez and Marsicano 2001), emphasizing that, as with saurischians (Langer 2004), this continent played a pivotal role in the origin and early radiation of those dinosaurs (Parker et al. 2005).

Systematic palaeontology

Archosauria Cope, 1869
 Ornithosuchia Gauthier, 1986
 Dinosauriformes Novas, 1992
 cf. Dinosauria Owen, 1842
 cf. Ornithischia Seeley, 1887
Sacisaurus agudoensis, gen. and sp. nov. (Figures 2–4)

Derivation of name

The genus name is formed from the Portuguese derivation of the indigenous—Tupi—name *Saci* (= a fabled entity of Brazilian lore that possesses a single leg) and the Greek word *sauros* (= lizard), in an anecdotal

allusion to the fact that only right femora of the new taxon have been found. The species name refers to Agudo, the town where the material was found.

Locality and horizon

All specimens referred to *Sacisaurus agudoensis* were collected in a single locality (Figure 1) inside the urban area of Agudo, Rio Grande do Sul, Brazil (19°43'12" S; 47°45'04" W). The type stratum is composed of fine grained sandstones full of mudstone rip-up clasts and isolated fossil remains within the “highstand systems tract” of the Santa Maria 2 sequence (Zerfass et al. 2003). This corresponds to the top of the Alemoa Member (Santa Maria Formation) and to the Caturrita Formation (Andreis et al. 1980), from the base of which the new material was excavated. In biostratigraphic terms, isolated teeth of stem-mammals (Bonaparte et al. 2003, 2005), the tritheletondid *Riograndia* (Bonaparte et al. 2001), and a large traversodontid, possibly *Exaeretodon* (Abdala et al. 2002), suggest a correlation to the “Ictidosaur Assemblage Zone” (Rubert and Schultz 2004), which is typically considered post-Ischigualastian and can be given a late Carnian to early Norian age (Langer 2005a,b).

Holotype (Figures 2C, 3B)

Partial left mandible (MCN PV10041) housed at the Museu de Ciências Naturais (MCN), Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; this includes most of the dentary, with three preserved herbivorously-adapted teeth, and an edentulous rostral portion that might represent a separate paired ossification.

Diagnosis

Dinosauriform differing from other known basal members of the group, except *Silesaurus opolensis* and ornithischians, for the presence of an edentulous rostral portion of the mandible. This jaw segment differs from that of *S. opolensis* (Dzik 2003) because its front tip is not dorsally curved, and from that of ornithischians because it does not form a single (unpaired) predentary, but articulates to its counterpart in the midline.

Referred material (Figures 2–4)

Most of the partial lower-jaws collected in the type-locality (MCN PV10042, PV10043, PV10044, PV10061) share with the holotype of *Sacisaurus agudoensis* a similar edentulous rostral portion, and are clearly referable to that taxon. A mandible fragment lacking the rostral part (MCN PV10048), as well as the single recovered maxilla (MCN PV10050), bear similar ornithischian-like dentition, and are also tentatively assigned to *S. agudoensis*. This is also the

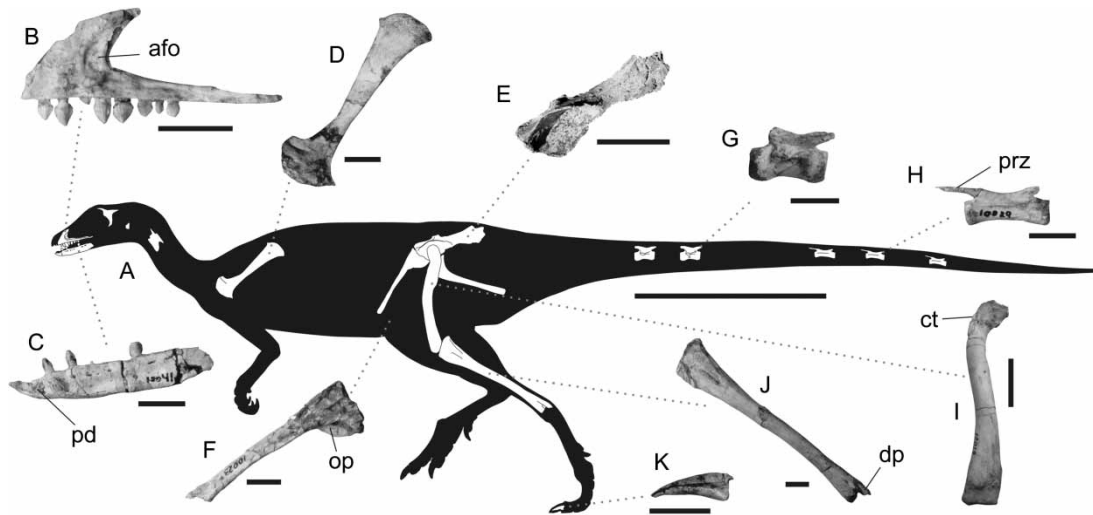


Figure 2. (A), skeletal reconstruction of *Sacisaurus agudoensis* gen. et sp. nov., with preserved bones on black outline based on *Lesothosaurus diognisticus*. Scale bar = 20 mm. Individual bones referred to *S. agudoensis* in lateral (G–G, J–K) and cranial (I) aspects: (B), right maxilla (MCN PV10050, reversed); (C), partial left hemi-mandible (MCN PV10041, holotype); (D), right scapula (MCN PV10033, reversed); (E), left ilium (MCN PV10100); (F), left pubes (MCN PV10023); (G), mid-caudal vertebra (MCN PV10 097); (H), distal caudal vertebra (MCN PV10029); (I), right femur (MCN PV10019); (J), right tibia (MCN PV10020, reversed); (K), indeterminate ungual phalanx (MCN PV10096). Scale bars = 10 mm. Abbreviations: afo, antorbital fossa; ct, cranial trochanter; dp, descending process; op, obturator process; pd, prementary; prz, prezygapophysis.

case of numerous isolated teeth, whereas no other kind of archosaur teeth has been recorded in the bone-bed. Other isolated remains are also tentatively assigned to *S. agudoensis*, namely: postorbital (MCN PV10051); ectopterygoid (MCN PV10049), vertebrae (MCN PV10028, PV10029, PV10032, PV10090, PV10097), scapula (MCN PV10033), ilium (MCN PV10100), pubes (MCN PV10023, PV10024), ischium (MCN PV10025), femora (MCN PV10009, PV10010, PV10011, PV10013, PV10014, PV10015, PV10016, PV10018, PV10019, PV10063, PV10075), tibia (MCN PV10020), and phalanges. These are of similar relative sizes and have the morphology expected for a basal dinosauriform. Two femora (MCN PV10007, PV10008) and one ilium (MCN PV10026) from the type-locality do not seem to be referable to *S. agudoensis*. These differ in morphology from the ilium and femora attributed to that taxon and apparently represent a much larger basal dinosaur.

Comparative description

The ascending process of the maxilla of *Sacisaurus* (Figures 2B, 3A) extends from the rostral margin of the bone, and is not caudally inset as in basal eusaurischians (Langer 2004). The internal and external antorbital fenestrae are more extensive than usual for basal ornithischians (Sereno 1991; Haubold 1991), defining a narrow antorbital fossa. *Sacisaurus* also differs from those dinosaurs because it possesses a thinner caudal maxillary ramus, the outer surface of which lacks large nutrient foramina and has an oblique dorsal margin. The referred postorbital

(MCN PV10051) is triradiate, forming a slightly convex dorsocaudal orbital margin, as typical of basal dinosaurs in general (Sereno 1991; Langer 2004; Haubold 1991; Tykoski and Rowe 2004), while the ectopterygoid (MCN PV10049) is composed of a caudally curved lateral ramus and a ventrally excavated medial body. The front portion of the mandible (Figure 3B–I) includes an edentulous rostral tip and a broad tooth bearing section. Except for its nearly straight dorsal margin, the tip of the lower jaw is remarkably similar to that of *Silesaurus opolensis* (Dzik 2003). It is laterally striated and depressed in relation to the rest of the mandible (Figure 3B–C, E–G), implying that a typical ornithischian corneous beak (Norman et al. 2004) was present. Its neural and vascular supply was provided through a mental foramen (Figure 3B), hypothesized to be equivalent to the “anterior dentary foramen” that pierces the jaw at the caudal margin of the depressed area and leads cranially to a bifurcating furrow, as seen in the prementary of *Lesothosaurus* (Sereno 1991). In two specimens (Figure 3C–F), it is possible to recognize that the depressed mandibular rostral portion is formed by a subtriangular separate ossification, the caudal margin of which extends obliquely below and above the mental foramen. This demarcation is not visible in other mandibles (Figure 3B, G, I), in which the bone is apparently fused to the dentary. This ossification is considered homologous to the prementary bone of ornithischians and its implications are discussed below. The rest of the lateral surface of the mandible is formed by the dentary, which bears an irregular row of nutrient

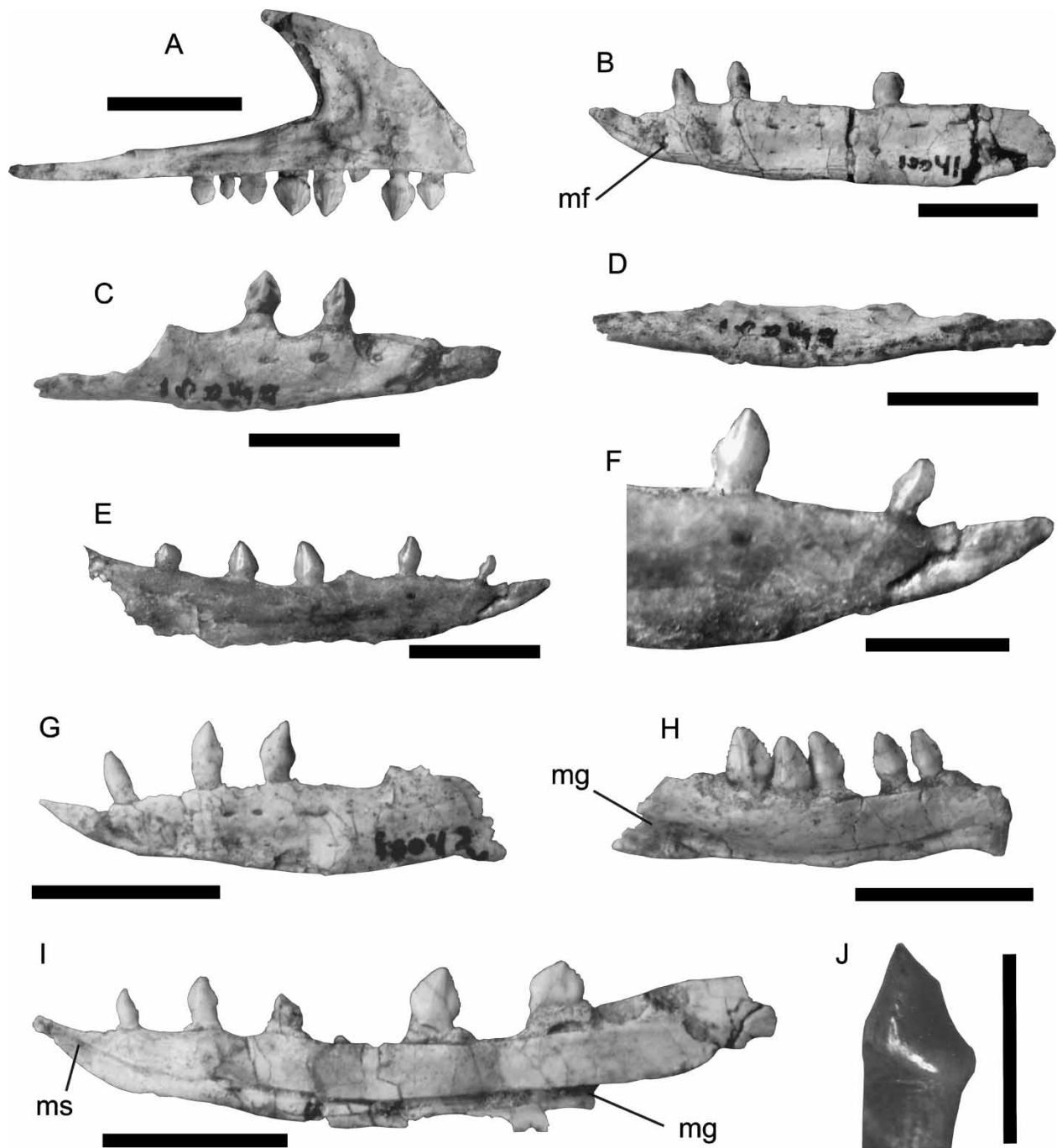


Figure 3. Jaw/dental elements referred to *Sacisaurus agudoensis* gen. et sp. nov. in lateral (A–C, E–G), ventral (D), medial (H–I), and distal/mesial (J) aspects. (A), right maxilla (MCN PV10050); (B–I), partial left (B, G–H) and right (C–E, G), mandibles, and rostral portion of partial right mandible (F); (B), MCN PV10041 (holotype); (C–D), MCN PV10040; (E–F), MCN PV10061; (G), MCN PV10042; (H), MCN PV10048 (rostral part not preserved); (I), MCN PV10043; (J), isolated cheek tooth (MCN PV10060). Scale bars: (A–E, G–I) = 10 mm, (F), (J) = 5 mm. Abbreviation: mf, mental foramen; mg, meckelian groove; ms, mandible symphyseal area.

foramina (Figure 3B–C, E–G). Medially, the meckelian groove leads cranially to a sharp ridge, that forms part of the striated symphyseal area of the jaw (Figure 3I).

The maxilla and most complete dentaries (MCN PV-10043, PV-10061) referred to *Sacisaurus* have about ten and 15 tooth positions, respectively. This count is smaller than that of most basal dinosaurs (Colbert 1989; Sereno and Novas 1993; Sereno et al.

1993; Benton et al. 2000), including most ornithischians (Colbert 1981; Sereno 1991; Haubold 1991; Peng 1992), and closer to the condition of *Pisanosaurus* (Casamiquela 1967; Bonaparte 1976) and *Silesaurus* (Dzik 2003). Also unlike ornithischians, the teeth of *Sacisaurus* are not markedly inset from the lateral margin of the bearing bones, and the upper series does not reach the caudal end of the maxilla (Figure 3A). On the other hand, elements from

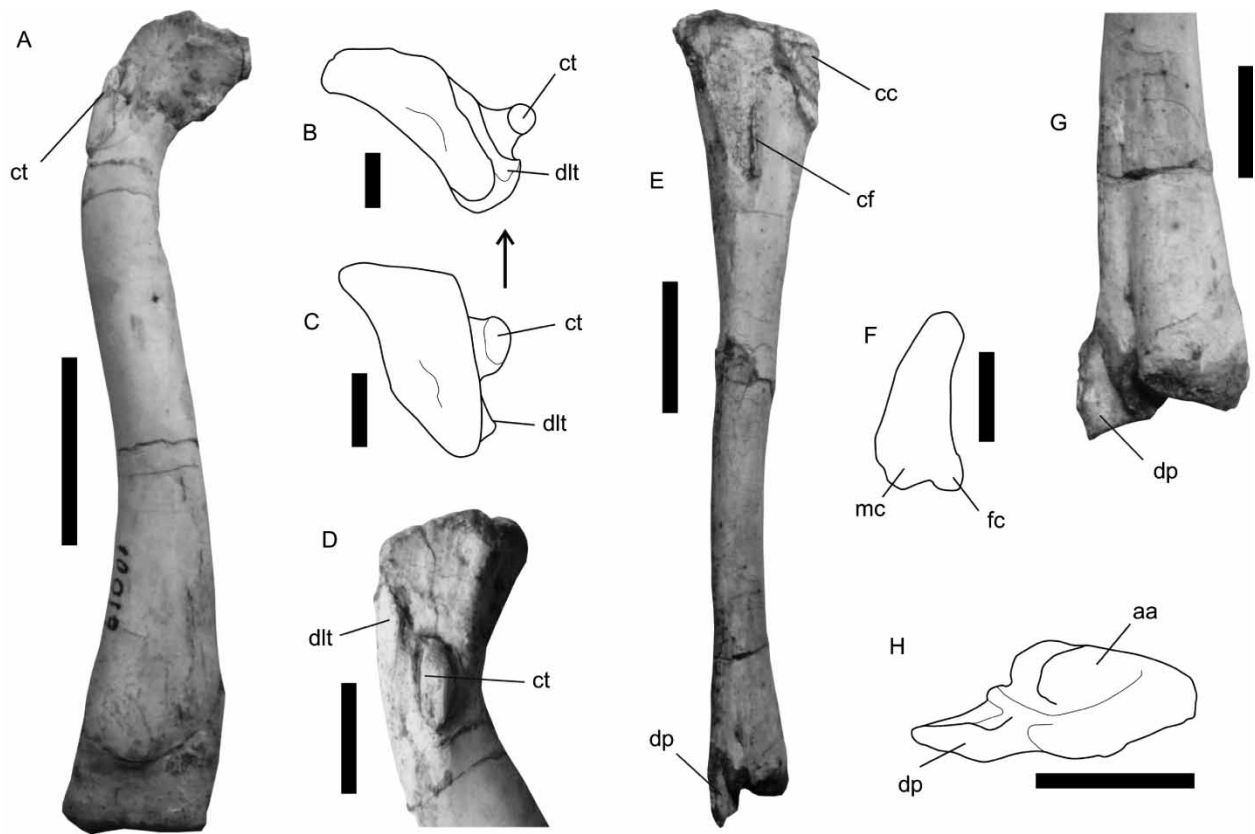


Figure 4. Right femora (A–D) and tibia (E–H) referred to *Sacisaurus agudoensis* gen. et sp. nov. (A–B, D), MCN PV10019 in (A), cranial; (B), proximal; and (D), craniolateral (proximal portion) aspects; (C), MCN PV10018 in proximal aspect; (E–G), MCN PV10020 in (E), lateral; (F), proximal; (G), craniolateral (distal portion), and (H), distal aspects. Scale bars: (A, E) = 20 mm; (B–C) = 5 mm; (D, F–H) = 10 mm. Arrow in (B–C) points cranially. Abbreviations: aa, articulation of astragalar ascending process; cc, cnemial crest; cf, fibular crest; ct, cranial trochanter; dlt, dorsolateral trochanter; dp, descending process, fc, fibular condyle; mc, medial condyle.

the central to caudocentral part of the series are the largest (Figure 3A, H–I), a condition regarded as typical for those dinosaurs (Sereno 1991, 1999; but see Yates 2003). Maxillary and dentary teeth are similar in most aspects; no crown has the longitudinal striations present in *Silesaurus* (Dzik 2003), but some bear a rounded eminence extending apically along the centre of its labial surface (Figure 3H) that is common to ornithischians (Colbert 1981; Norman et al. 2004). This is continuous with the cingulum (Figure 3J) that occurs at the base of the lingual surface (MCN PV10048, PV10060; Figure 3J), in the position where a semi-lunar pit might develop due to wear (MCN PV10053). The tooth crowns are mesiodistally expanded, so that the distal margin of each element laterally overlaps the mesial portion of the one behind (Figure 3H). This gives the impression that the crowns are constricted by a neck, separating them from the long (twice the crown length) subcylindrical root, a condition often considered to diagnose Ornithischia (Heckert 2004; but see Parker et al. 2005). Teeth on the rostral part of both maxilla and dentary are more slender, and have fainter denticles (possibly due to wearing) forming oblique angles to the long axis of the tooth (Figure 3A–I). Their mesial margin is evenly

convex, whereas the distal margin is convex at the base and concave apically. As a result, their acute (less than 45°) apex is slightly curved caudally. More caudal teeth are stouter, with prominent cinguli. Their mesial and distal margins are more expanded at the base and straight apically, so that the apex forms an angle of about 90°. The denticles are more apparent, and subparallel to the long axis of the tooth (Figure 3A–I).

From the vertebral column were recovered an atlantal intercentrum (MCN PV10032) and various caudal vertebrae (Figure 2G–H). Proximal tail vertebrae (MCN PV10028) have broad centra as long as high, with a concave ventral margin in lateral aspect. The transverse processes are elongated, each bearing a deep ventral pit along its base, while the postzygapophyses are raised on the neural spine, as in various ornithischians (Janensch 1955; He and Cai 1984). Mid-tail vertebrae (MCN PV10097) are lateromedially compressed, with an axially elongated fossa below each transverse process, as seen in ornithischians in general (Galton 1974; Santa Luca 1980). The most remarkable feature of the distal tail vertebrae (MCN PV10029, PV10090) are their prezygapophyses, which extend over one third of the proximally adjacent centrum. The scapular blade

(Figure 2D) broadens gradually towards its rim, and forms an angle of more than 90° to the acromion. The more robust ventrocaudal portion of the bone supports the glenoid, which forms an angle of 45° to the long axis of the blade.

If the pelvic bones assembled from the type-locality (Figure 2) belong to *Sacisaurus*, the new taxon represents one of the three putatively propubic ornithischians, the others being *Pisanosaurus* (Sereno 1991) and *Silesaurus* (Dzik 2003). Its acetabulum is almost fully closed, with the iliac inner wall forming a convex ventral margin as in *Silesaurus* and other basal dinosauriforms (Novas 1996). The ilium (Figure 2E) is incomplete, but approaches the morphology of *Silesaurus* (Dzik 2003), “*Caseosaurus*” (Long and Murry 1995), and poposaurid pseudosuchians (Galton 1985b; Galton and Walker 1996). It bears a short preacetabular ala buttressed by a robust ridge that extends towards the acetabulum. The acetabular craniodorsal margin is laterally expanded to form a well-developed crest. The postacetabular ala is much longer, accounting for nearly half the length of the bone, and expands distally. The pubis (Figure 2F) bears well-developed obturator plate and ambiens process, and the shaft is laminar medially and thicker at the lateral margin. The ischium (MCN PV10025) meets its pair for most of the plate-like shaft and its proximal portion is not ventrally concave as in basal ornithischians (Sereno 1991; Norman et al. 2004).

Two femoral types with size disparity were excavated in the type-locality: the larger one is known from two (left and right) nearly complete bones (MCN PV10007, PV10008) about 150 mm long, whereas 15 right femora of the smaller kind were recovered, nine of which are almost complete (see referred material). These morphotypes are believed to represent different taxa, and the smaller ones are tentatively assigned to *Sacisaurus*, based on their matching size to other skeletal parts. They range from 88 to 103 mm long, and are typical of basal dinosauriforms (Figures 2I, 4A–D), as given by their sigmoid shape and head not well set from the shaft, the long axis of which forms an angle of about 40° to the intercondylar line. The flat proximal surface of the head has a subtriangular outline, with nearly straight cranial, craniolateral, and caudomedial surfaces, and bears a longitudinal groove. This morphology approaches that of forms such as in *Pseudolagosuchus* (Novas 1996), *Silesaurus* (Dzik 2003), and *Eucoelophysis* (Sullivan and Lucas 1999). Some femora (Figure 4C) have a prominent medial tuberosity, as in some basal dinosauriforms and dinosaurs (Padian 1986; Novas 1996), whereas this structure is lacking in other specimens (Figure 4B). The ridge-like dorsolateral (= “greater”) trochanter overhangs slightly cranially, as seen in basal saurischians (Langer and Benton 2006), and ornithischians (Sereno 1991). The small “spike-like” cranial trochanter is separated from the shaft by a cleft, and a “trochanteric shelf” is

lacking, whereas the small fourth trochanter is symmetrical and non-pendant. This set of features resembles the most those seen in the femora of *Guaibasaurus* (Bonaparte et al. 1999) and basal theropods (Welles 1984; Rauhut 2003).

The straight tibia (Figures 2J, 4E–H) has a subtriangular proximal articulation, with fibular and medial condyles nearly aligned at the caudal margin. This is seen in *Lagerpeton*, *Silesaurus*, *Pisanosaurus*, and other basal dinosaurs (Langer 2004), but not in *Marasuchus* (Sereno and Arcucci 1994) or *Lesothosaurus* (Thulborn 1972). The cnemial crest is not well-developed and proximally projected as in most dinosauriforms (Novas 1996), but resembles those of basal ornithischians (Thulborn 1972; Bonaparte 1976). A well-developed fibular crest is also present proximally on the tibia, as seen in *Silesaurus* (Dzik 2003) and basal theropods (Padian 1986; Rauhut 2003). The distal articulation of the tibia has a typically dinosaurian descending process, as described by Novas (1996), but also seen in *Silesaurus* (Dzik 2003). In addition, that process expands laterally to partially overlap the distal portion of the fibula, as seen in various theropods (Welles 1984; Raath 1990), but more markedly in ornithischians, in which it forms the “outer malleolus” (Thulborn 1972; Colbert 1981). All recovered ungual phalanges are non-trenchant (Figure 2K).

Discussion

Phylogenetic relationships of sacisaurus agudoensis

Previous phylogenetic studies (Norman 1984; Sereno 1984, 1986, 1999; Maryanska and Osmólska 1985; Cooper 1985; Norman et al. 2004) established the presence of a predeontary bone as one of the most conspicuous synapomorphic features of Ornithischia. Although dissimilar to the unpaired element of those dinosaurs, we hypothesize that the pair of bones that form the mandibular tip of *Sacisaurus* is its homologue. This suggests the nesting of the new taxon within the stem of “all dinosaurs closer to *Iguanodon* than to *Cetiosaurus*” (Norman et al. 2004). Additionally, the “anterior dentary foramen” leading cranially to a bifurcated furrow is otherwise known in *Lesothosaurus* (Sereno 1991) and might be another basis for referring *Sacisaurus* to Ornithischia. Ornithischian dental synapomorphies are harder to define (Gauffre 1993; Heckert 2004), but typical traits are seen in *Sacisaurus*. These include: 1—larger teeth on the caudocentral part of the series (Sereno 1986; Gauffre 1993); 2—low triangular crowns in lateral profile (Sereno 1986; Hunt and Lucas 1994); 3—basal cingulum more expanded lingually, so that the tooth is asymmetrical in mesial and distal views (Hunt and Lucas 1994; Norman et al. 2004); 4—carinae composed of large denticles (Sereno 1986; Hunt and Lucas 1994). More recently, Parker et al. (2005)

showed that most of the putative ornithischian synapomorphies based on tooth morphology are not unique to those dinosaurs among Late Triassic archosaurs. Of these, only the basal cingulum might be diagnostic for the group (Parker et al. 2005), a trait seen in most specimens of *Sacisaurus*. Other features reminiscent of the ornithischian condition are seen in the tibia of *Sacisaurus*. It shares with *Lesothosaurus* and *Pisanosaurus* a non-proximally expanded cnemial crest, and an “outer malleolus” that projects laterally and distally to cover most of the caudal margin of the fibula. The latter feature is seen in most members of the group (Galton 1974; Colbert 1981), as well as, but to a lesser degree, in basal theropods and some sauropodomorphs (Novas 1989; Langer and Benton 2006).

If *Sacisaurus* is an ornithischian, its basal position is clear based on various plesiomorphic traits otherwise unknown in typical members of that dinosaur group, namely: large antorbital fenestrae, narrow caudal ramus of maxilla with oblique dorsal margin, small number of teeth, propubic pelvis, closed acetabulum, short preacetabular ala of ilium, medially laminated pubic shaft, knob-like cranial trochanter, and non-pendant fourth trochanter. The ischium attributed to *Sacisaurus* also lacks a typically saurischian rod-like shaft (Langer 2003, 2004), but other referred material possesses theropod features such as a ventrally excavated ectopterygoid with a strongly curved jugal process, long prezygapophyses on the distal caudal vertebrae, and a well-developed fibular flange in the tibia (Serenó 1999; Rauhut 2003). However, a theropod-like ectopterygoid was described for the sauropodomorph *Thecodontosaurus* (Yates 2003), and a fibular crest is also seen in *Silesaurus* (Dzik 2003). Indeed, the distribution of these characters casts doubts upon their validity as theropod synapomorphies, alluding to a broader distribution among basal dinosaurs. Alternatively, the mosaic of characters seen in *Sacisaurus* might point against the association of its skeletal remains as seen in Figure 2. Accordingly, its inclusion as such into a numerical phylogenetic analysis is potentially misleading and was not attempted here.

Regardless of their phylogenetic position, the resemblance and probable affinity of *Sacisaurus* and *Silesaurus* is clear. This is based on morphological similarities of not only the front portion of the mandible and teeth, but also the pelvic and hind limb bones. The peculiar edentulous and depressed mandibular tip of both taxa is remarkably similar, and its equivalence to the predentary may support their ornithischian affinity, as hinted in the original description of *Silesaurus* (Dzik 2003). The morphology of that structure might unite those two taxa into a clade, but could also represent a preliminary step towards the acquisition of a typical predentary, shared as a plesiomorphy by very basal members of the ornithischian lineage. Other features that could

suggest the affinity of both *Sacisaurus* and *Silesaurus* with the Ornithischia include a large mental foramen in the rostral portion of the dentary (possibly related to neural and vascular supply for the corneous beak), and a well developed “outer malleolus” in the tibia. Yet, the distal tibia of *Silesaurus* is more rounded, whereas those of *Sacisaurus* and basal ornithischians are more axially compressed (Langer and Benton 2006). Likewise, in the evolutionary context of dinosauriforms with herbivorously-adapted teeth, those of *Sacisaurus* seem more coarsely denticulated, and closer to the ornithischian condition than those of *Silesaurus*. The femur of *Sacisaurus* lacks a “trochanteric shelf” but otherwise resembles that of *Silesaurus* (Dzik 2003) for its proximally flat and subtriangular head, which is not well set from the shaft. This is also seen in *Pseudolagosuchus* (Novas 1996), implying a non-dinosaur affinity. The ilia of *Sacisaurus* and *Silesaurus* are also atypical for dinosaurs, but resemble those of poposaurid rauisuchians (Galton and Walker 1996). Although their ornithosuchian affinity is not in question, the iliac anatomy might also be a hint to the basal phylogenetic position of *Sacisaurus* and *Silesaurus* (Langer and Benton 1996) among dinosauriforms.

Origins of the predentary bone

The predentary is usually considered a neomorphic feature of ornithischians; i.e. a structure with no evident equivalence to ordinary organismal traits from which it could have arisen. In fact, because the bone was never homologized with skeletal parts of the outgroups to Ornithischia, its presence has been regarded as synapomorphic for the group. A homonymous bone was, however, reported to some fossil birds (Martin 1987, 1991) and both fossil and extant teleosts—e.g., aspidorhynchids (Brito 1997), ichthyodectids (Bardack and Sprinkle 1969), and istiophorid sailfishes (Regan 1909; Gregory and Conrad 1937). Albeit non-homologous in phylogenetic terms, it is plausible that these bones have a similar ontogenetic origin, representing the expression of developmental patterns common to these groups, and therefore to most vertebrates.

The most peculiar attribute of the predentary is its unpaired condition. This is very unusual for lower jaw bones, which are as a rule directly or indirectly connected to the development of the pair of Meckel’s cartilages (De Beer 1937). Indeed, if the predentary origin is linked to the mandibular arch, it almost certainly derives from the fusion of formerly paired ossification centres. At least for ornithischians, the recognition of a paired bone in the rostral tip of some mandibles attributed to *Sacisaurus* strengthens that hypothesis. It is noteworthy that this taxon lived during the time interval of the early radiation of dinosaurs and has a suite of plesiomorphic features

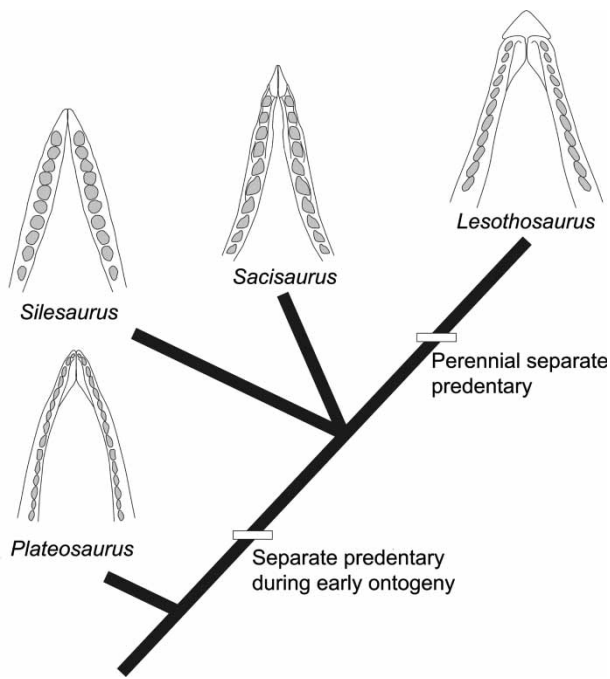


Figure 5. Graphic representation of the two-phase paedomorphocline suggested for the early evolution of ornithischians. Lower jaw reconstructions (in occlusal aspect) based on Galton (1984) for *Plateosaurus*, Sereno (1991) for *Lesothosaurus*, Dzik (2003) for *Silesaurus*, and MCN PV10044 for *Sacisaurus*.

indicating its basal phylogenetic position. Hence, it is possible to envisage an initial stage of ornithischian evolution in which the prementary was a paired bone. In this scenario, the single prementary of derived ornithischians was acquired latter, by the fusion of those two ossifications. In *Sacisaurus*, the prementaries tended to coossify caudally, rather than to its counterpart at the midline. Of the recovered partial mandibles, the larger (MNC PV10041) has the prementary fused to the dentary, but this varies within the smaller specimens. On the contrary, the single prementary of ornithischians is never caudally fused, even in juveniles (Carpenter 1994; Horner and Currie 1994; Hill et al. 2003) and this seems important for the bone to act as a lower jaw stabilizer during occlusion (Crompton and Attridge 1986). It is possible, therefore, to recognize a paedomorphic component in the early evolution of ornithischians (Figure 5), regarding the caudal fusion of the prementary. This would be characterized by its retention as a separate rostral mandibular ossification along the life of more derived forms. *Sacisaurus*, and perhaps *Silesaurus*, would represent an intermediary stage of this paedomorphocline, in which that ossification was separate in juvenile forms, but eventually fused to the rest of the jaw in adult individuals.

Various vertebrate groups possess a paired ossification at the rostral tip of the mandible. This is termed the mental, mentomandibular, or more often mentomeckelian bone, and is better known in some jawed

fishes (Schultze 1993; Grande and Bemis 1998; Adriaens and Verraes 1998) and lissamphibians (Trueb 1993; Sheil 1999; Yeh 2002). Less commonly, a similar element is found in the lower jaws of extant lizards (De Beer 1937; Jollie 1973) and birds (Baumel and Witmer 1993). This bone frequently fuses to its pair and/or to the dentary at the symphyseal area (Romanoff 1960; Trueb 1993), and is normally considered to be an ossification of the tip of Meckel's cartilage (De Beer 1937; Schultze 1993), although a different embryologic origin has been proposed for anurans (Trueb 1993). Mammals lack a mentomeckelian bone, but small bilateral ossification centres referred to as *ossicula mentalia* are involved in the formation of their mental-symphyseal region (Testut and Latarjet 1899; Spalteholz 1965; Radlanski et al. 2003), but rarely remain isolated from the rest of the jaw (Meckel 1832). These are currently believed to result from the ossification of either the rostral tip of Meckel's cartilage (Rodríguez-Vásquez et al. 1997) or other possibly secondary cartilages (Goret-Nicaise et al. 1984; Hinrichsen 1990; Bareggi et al. 1994).

As acknowledged by Presley (1993) "for any neomorphic feature some consideration of the developmental processes by which it could have arisen is obligatory before using the feature as a phylogenetic discriminant". In this context, the recognition of the ornithischian prementary as derived from the fusion of originally paired structures allows its comparison to similar rostral elements in the lower jaw of other vertebrates. This is particularly the case of the mentomeckelian, which fits to the topographic criteria for the definition of homology (Jardine 1969). Indeed, following the homology concept advocated by Panchen (1994), the lower jaw symphyseal bones of various vertebrate groups might represent equivalent evolutionary units, given that they share a common developmental origin; even if they are not present as separate elements in immediate sister taxa of those groups. Therefore, although synapomorphic for ornithischians the prementary does not seem to represent a neomorphic structure of these dinosaurs. Instead, its homology to the mentomeckelian bone, and possibly also to parts of the rostral portion of most vertebrate mandibles, is proposed here. In this case, it does not correspond to a dermal bone as most of the lower jaw, but to an ossification preceded by cartilage.

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