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The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs

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A new discovery of skeletons of *Revueltosaurus callenderi* from the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona clearly shows that *Revueltosaurus* is not an ornithischian dinosaur as previously supposed. Features such as the presence of a postfrontal, crocodile-normal ankle and paramedian osteoderms with anterior bars place *R. callenderi* within the Pseudosuchia, closer to crocodylomorphs than to dinosaurs. Therefore, dental characters previously used to place *Revueltosaurus* within the Ornithischia evolved convergently among other archosaur taxa, and cannot be used to diagnose ornithischian dinosaur teeth. As a result, all other putative North American Late Triassic ornithischians, which are all based exclusively on teeth, are cast into doubt. The only reasonably well-confirmed Late Triassic ornithischians worldwide are *Pisanosaurus mertii* and an unnamed heterodontosaurid from Argentina. This considerably changes the understanding of early dinosaur diversity, distribution and evolution in the Late Triassic.

Keywords: *Revueltosaurus*; Ornithischia; Pseudosuchia; Late Triassic; Petrified Forest National Park

1. INTRODUCTION

The record of Triassic ornithischian dinosaurs is poor; only a single taxon, *Pisanosaurus*, is known from cranial and postcranial material (Casimiquela 1967; Bonaparte 1976). Other proposed Triassic ornithischians (*Galtonia*, *Tecovasaurus*, *Lucianosaurus*, *Pekinosaurus*, *Technosaurus* and *Revueltosaurus*) are known from isolated jaw fragments or teeth (Chatterjee 1984; Hunt & Lucas 1994; Heckert 2002).

Hunt & Lucas (1994) and Heckert (2002) have argued that ornithischian teeth are capable of being diagnosed using autapomorphies, and therefore can be used to designate valid taxa. Hunt (1989) described *Revueltosaurus callenderi* as a probable ornithischian dinosaur from the Bull Canyon Formation of New Mexico on the basis of several isolated teeth, and later authors have followed this assignment (e.g. Padian 1990*a*; Long & Murry 1995; Heckert 2002). Sereno (1991*a*,*b*) argued that the characteristics and associations that Hunt (1989) provided were ambiguous and, therefore, *Revueltosaurus* represented a *nomen dubium*, but he did not dispute its ornithischian affinities. All known specimens of *Revueltosaurus* are isolated teeth except for an undescribed skull fragment collected by Hunt (Heckert 2002). Heckert (2002) reanalysed the genus and erected a second species, *Revueltosaurus hunti*, again based upon isolated teeth.

We have now discovered skeletal material of *R. callenderi* in the Petrified Forest National Park (AZ, USA), as the result of an ongoing palaeontological inventory of the park (Parker & Clements 2004), including hundreds of cranial and postcranial elements of at least six individuals from a single quarry. Apart from fragmentary material referable to a poposaurid similar to *Chatterjeea*, all of the material from the quarry belongs to a single taxon and includes individuals of varying size. The chatterjeeid material is considerably larger and was only recovered in a small area of float. The most important specimen (PEFO 33787) consists of a partial articulated skeleton, including the skull, vertebral column, osteoderms, forelimb and hindlimb material, which was collected *in situ*. In many cases, the *Revueltosaurus* material collected on the surface of the quarry was associated, providing further evidence that the material described here represents one taxon. All postcranial remains described here have been found in direct association with cranial remains identifiable as *Revueltosaurus*. The quarry is still being developed and is producing numerous additional *in situ* elements of the same taxon. Additionally, identical cranial and postcranial material has been found in collections from Dinosaur Hill in Petrified Forest National Park, where Padian (1990*a*) reported the presence of *R. callenderi* teeth. This further strengthens the association of the material.

Because much of the material is still being prepared, a full description of the material will not be given here. Our

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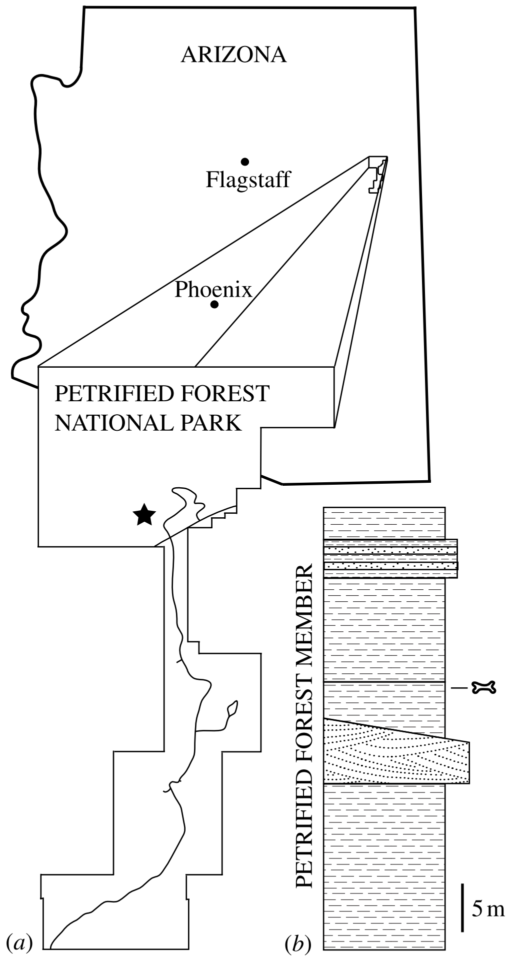

Figure 1. Location and stratigraphic position of the *Revueltosaurus* quarry. (*a*) Map of Petrified Forest National Park with star showing the location of the quarry; and (*b*) stratigraphy in the vicinity of the quarry with bone symbol showing the stratigraphic position of the *Revueltosaurus* material.

aim is to establish the revised systematic position of *Revueltosaurus*, and to discuss the implication of this for our understanding of early dinosaur evolution.

2. GEOLOGICAL SETTING

The '*Revueltosaurus* Quarry' (PFV 297) is located in the Painted Desert region of Petrified Forest National Park (AZ) in the vicinity of Lacey Point (figure 1*a*). The material is found in a moderately pedogenically modified mudstone (i.e. 'paleosol taphofacies' of Hunt *et al.* 1995) interpreted as proximal floodplain deposits associated with a levee deposit just lateral to one of the prominent local sandstones common in the region. This area is characterized by thick sequences of red mudstones traditionally assigned to the upper Petrified Forest Member of the Chinle Formation (Stewart *et al.* 1972). However, Heckert & Lucas (2002) and Woody (2003) have determined that the lower Petrified Forest and Sonsela Sandstone beds represent members that are lithologically distinct from the upper beds and accordingly have been removed from the Petrified Forest Member. Therefore, the quarry is located (figure 1*b*) in the middle portion of the Petrified Forest Member (equals Painted Desert Member of Lucas 1993) approximately 25 m below the Black Forest Bed of Ash (1992).

Palynomorphs (Litwin *et al.* 1991), invertebrates (Good 1998) and vertebrates (Long & Murry 1995; Lucas 1998) suggest a Norian age (equals Revueltian lvf of Lucas 1998) for these beds. Equivalent strata within a square kilometre of the quarry contain the remains of unionid bivalves, lungfish teeth and associated remains of the metoposaurid *Apachesaurus*, the diapsid *Vancleavea* (*sensu* Hunt *et al.* 2002), a fragmentary phytosaur, the aetosaur *Typothorax coccinarum*, the 'rauisuchian' *Postosuchus*, a chatterjeeid, *Chindesaurus*, a coelophysoid theropod and additional material of *Revueltosaurus*. An isotopic date for the Black Forest Bed (Riggs *et al.* 2003) provides an age of 209 Myr, thus supplying a relative minimum age (Norian) for the quarry.

Institutional abbreviations—NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; PEFO, Petrified Forest National Park, AZ.

3. SYSTEMATIC PALAEONTOLOGY

Archosauria Cope 1869, *sensu* Gauthier 1986. Pseudosuchia Zittel 1887–90, *sensu* Gauthier 1986. *Revueltosaurus* Hunt 1989. *R. callenderi* Hunt 1989.

(a) *Emended diagnosis*

Archosaur possessing the following unique combination of character states: ventral process of postorbital articulates with jugal medially; mediolaterally expanded anterior end of squamosal; posterior process of premaxilla fits into distinct slot of the nasal; jugal articulates with groove in quadratojugal; nasals, frontals, parietals and dentary covered by distinct pitted and grooved sculpturing; no mandibular fenestra; an articular foramen that completely pierces the medial flange of the articular; calcaneal tuber of calcaneum only expanded dorsally; and an armour carapace of sub-rectangular dermal osteoderms with anterior bars and subcircular pitting arranged in a random to weakly radial pattern.

(b) *Holotype*

NMMNH P-4957, a nearly complete premaxillary tooth.

(c) *Type locality and horizon*

Revuelto Creek (NMMNH locality 1), Quay County, NM, USA, Bull Canyon Formation, Dockum Group (Upper Triassic: Norian).

(d) *Referred material*

PEFO 33787, partial skeleton including skull; PEFO 33788, partial skull; PEFO 33789, scapulocoracoid; PEFO 33790, humerus; PEFO 33791, ilium; PEFO 33792, femur; PEFO 33793, calcaneum; PEFO 33794, astragalus; PEFO 33795, paramedian osteoderm.

4. NEW FEATURES OF *R. CALLENDERI*

The skull of *Revueltosaurus* is low and long (figure 2), and a fine sculpturing of pits and grooves (figure 2*a*,*c*) covers the nasals, frontals, parietals and dentary. The premaxilla contains at least five teeth that decrease in size posteriorly.

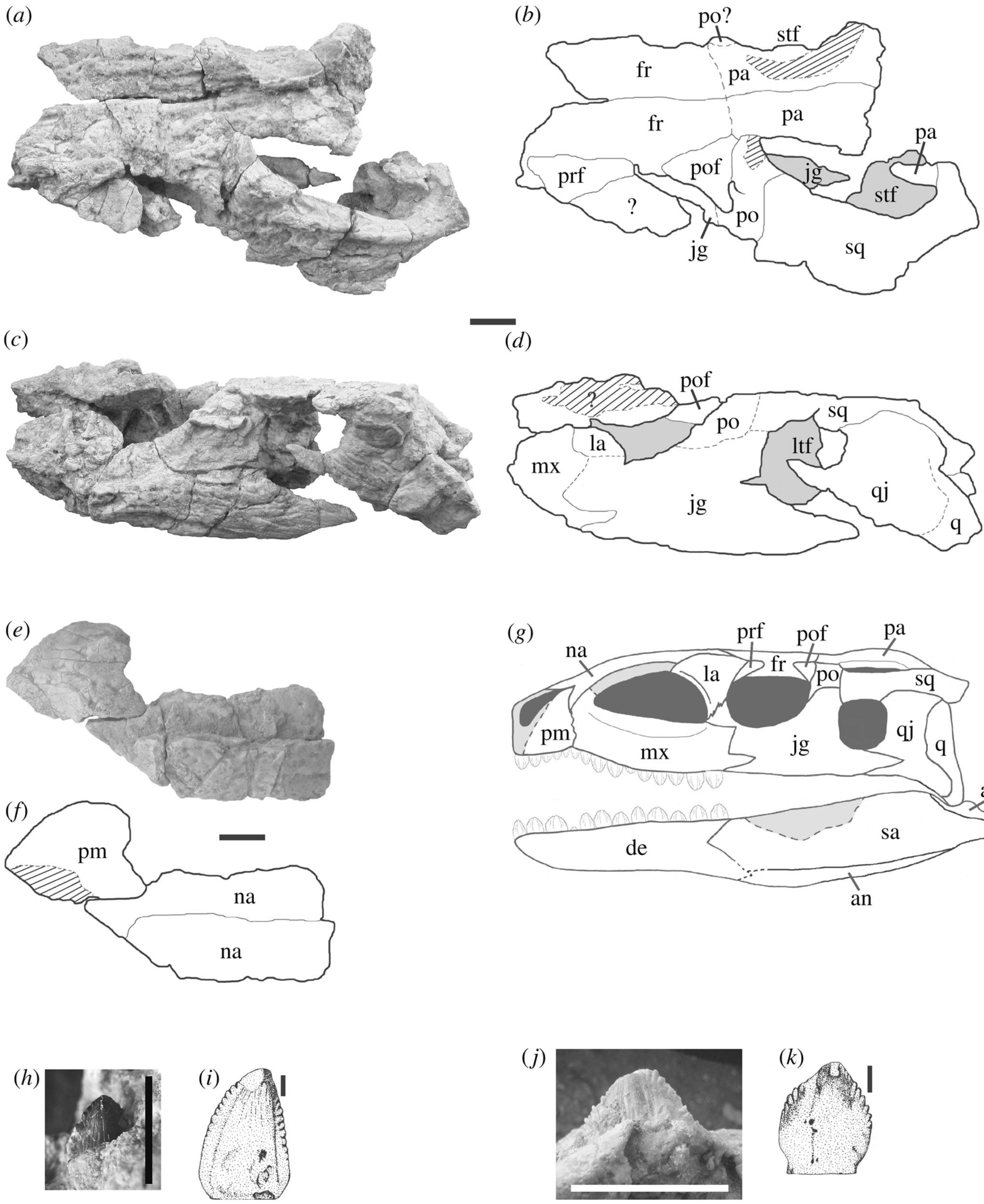

Figure 2. Cranial material of *Revueltosaurus callenderi*. (*a*) Posterior portion of the skull of PEFO 33787 in dorsal view; (*b*) drawing of PEFO 33787 in dorsal view; (*c*) posterior portion of the skull of PEFO 33787 in lateral view; (*d*) drawing of PEFO 33787 in lateral view; (*e*) nasals and right premaxilla of the skull of PEFO 33788 in dorsal view; (*f*) drawing of nasals and right premaxilla of the skull of PEFO 33788 in dorsal view; (*g*) reconstruction of the skull of *Revueltosaurus* in left lateral view; (*h*) *in situ* premaxilla tooth of PEFO 33787; (*i*) paratype premaxilla tooth (NMMNH P-4959) of *R. callenderi* (from Hunt & Lucas 1994); (*j*) *in situ* dentary tooth of PEFO 33787; and (*k*) paratype maxilla/dentary tooth (NMMNH P-4958) of *R. callenderi* (from Hunt & Lucas 1994). Abbreviations: an, angular; ar, articular; de, dentary; fr, frontal; jg, jugal; la, lacrimal; ltf, lateral temporal fenestra; mx, maxilla; na, nasal; pa, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; stf, supratemporal fenestra; ?, unidentified element crushed into orbit. Cross-hatching indicates broken surfaces and dashed lines indicate inferred sutures. Scale bars equal 1 cm for all except (*i*) and (*k*), where the scale bar equals 1 mm.

The posterior process of the premaxilla fits into a distinct slot in the anterior portion of the nasal (figure 2*e*,*f*). The maxilla contains nine or 10 alveoli, and articulates with the jugal both medially and laterally (figure 2*c*,*d*). Both the prefrontal and postfrontal are present (figure 2*a*,*b*), and the postfrontal is triangular in dorsal view. The frontals are robust and bear distinct bosses along the margin of the orbit (figure 2*a*). The parietals are unusually deep and also possess distinct bosses around the margin of the supratemporal fenestra (figure 2*a*). The ventral process of the postorbital articulates with the jugal medially, and the postorbital articulates with both a dorsal and ventral process of the squamosal (figure 2*b*, *d*). The squamosal itself is horizontal and its anterior end is mediolaterally expanded (figure 2*b*,*c*). The anterior portion of the quadratojugal possesses a groove that fits the posterior process of the jugal (figure 2*g*). The lower jaw lacks a mandibular fenestra, and a foramen completely pierces the medial flange of the articular. There is no evidence that a predentary bone articulated with the anterior end of the dentary.

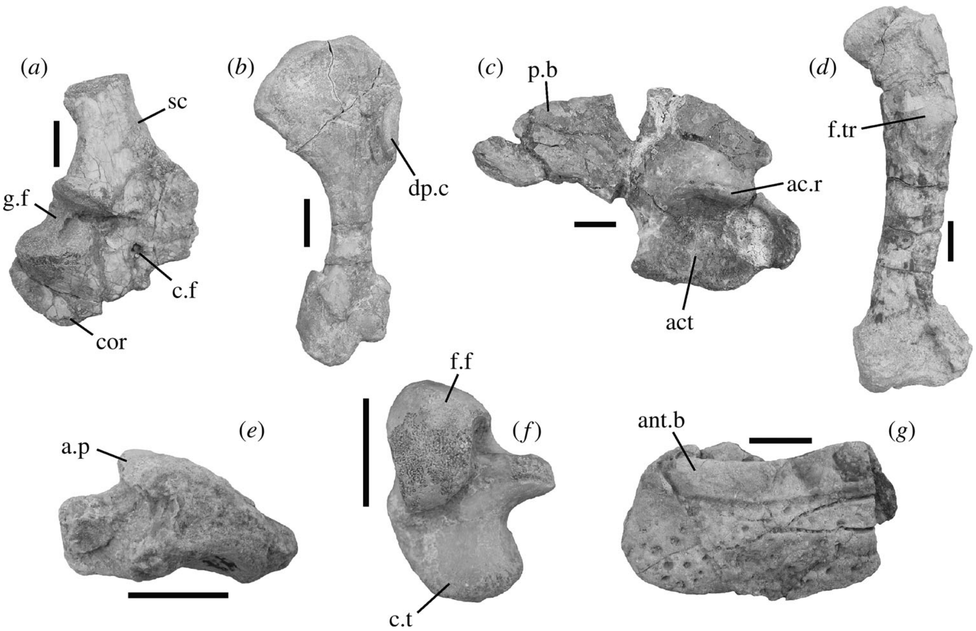

Figure 3. Postcranial material of *R. callenderi*. (*a*) PEFO 33789, right scapulocoracoid in lateral view; (*b*) PEFO 33790, left humerus in anteromedial view; (*c*) PEFO 33791, right ilium in lateral view; (*d*) PEFO 33792, right femur in medial view; (*e*) PEFO 33794, right astragalus in lateral view; (*f*) PEFO 33793, left calcaneum in dorsal view; and (*g*) PEFO 33795, paramedian osteoderm in dorsal view. Abbreviations: a.p, astragular process; ac.r, acetabular ridge; act, acetabulum; ant.b, anterior bar; c.f, coracoid foramen; c.t, calcaneal tuber; cor, coracoid; dp.c, deltopectoral crest; f.f, fibular facet; f.tr, fourth trochanter; g.f, glenoid fossa; p.b, posterior blade; and sc, scapula. Scale bars equal 1 cm.

The teeth of the new specimens (figure 2*h*,*j*) are identical to the holotype and paratype teeth of *R. callenderi* (figure 2*i*,*k*), which have been described in detail elsewhere (Heckert 2002). Hunt (1989) was correct in his assignments of isolated teeth to the premaxillary and maxillary/dentary regions.

The coracoid (figure 3*a*) is dorsoventrally short and possesses no postglenoid process. The humerus (figure 3*b*) is identical to one found with the partial skeleton and has a broad, proximally restricted deltopectoral crest. The ilium (figure 3*c*) is plesiomorphic and has only a short robust anterior process. The acetabular rim is strongly pronounced and two sacral rib articulations are present on the medial side. The femur (figure 3*d*) is remarkably similar to that of *Turfanosuchus* (Wu & Russell 2001), with a sizable fourth trochanter and a poorly defined rounded femoral head. The ankle is crocodile-normal. The calcaneum, which was associated with the partial skeleton, has a fibular facet (figure 3*f*) that is well-developed and resembles other pseudosuchians such as *Postosuchus*, aetosaurs and crocodylomorphs; however, the calcaneal tuber only extends dorsally, unlike the tubers of most pseudosuchians that generally project both dorsally and ventrally. The astragalus (figure 3*e*) is larger mediolaterally than in most pseudosuchians and the astragalar process (for insertion into the calcaneum) is well developed.

Revueltosaurus possesses four major shapes of osteoderms, but the exact placement on the body of each kind is uncertain. All osteoderms have some subcircular pitting arranged in a random to weakly radial pattern. Presumed paramedian osteoderms (figure 3*g*) are rectangular (wider than long), have an anterior bar like that of other suchians (*sensu* Krebs 1974: all taxa closer to Crocodylomorpha than to Phytosauria), no keel and surface pitting.

5. DISCUSSION

The Petrified Forest animal can clearly be assigned to *R. callenderi* because teeth from both the skull (PEFO 33787; figure 2*h*,*j*) and additional specimens are identical to the holotype and paratype teeth (figure 2*i*,*k*). Teeth referable to *R. callenderi* can be differentiated from all other known Triassic archosaur teeth by denticles that extend equally far along the anterior and posterior carinae, are very fine basally, coarser more apically, and fine again at the tip of the crown (see Heckert 2002 for a complete diagnosis of the teeth). *Contra* the arguments of Sereno (1991*a*,*b*), *Revueltosaurus* teeth are autapomorphic and can easily be recognized as a distinct taxon, so *R. callenderi* represents a valid species. Both Hunt & Lucas (1994) and Heckert (2002) carefully outlined the apomorphic nature of *Revueltosaurus* teeth, and we agree with their assessment. Heckert (2002) assigned a second species to *Revueltosaurus*, *R. hunti*. This taxon may be assignable to *Revueltosaurus*, as examination of other material collected from a referred locality of *R. hunti* has turned up a squamosal that is nearly identical to that seen in the Petrified Forest material.

The presence of an armour carapace and crocodile-normal ankle clearly precludes *R. callenderi* from being an ornithischian dinosaur. Furthermore, the presence of a postfrontal is a plesiomorphic state that places *R. callenderi* outside Dinosauriformes (Dzik 2003). Additional characters that place *Revueltosaurus* outside the Dinosauria and Dinosauriformes include a proximally restricted deltopectoral crest on the humerus and the lack of a subrectangular, offset femoral head (Novas 1993). A pseudosuchian (*sensu* Gauthier 1986: all taxa closer to Crocodylomorpha than to Aves) affinity for *Revueltosaurus* is supported by the presence of a fully formed crocodile-normal ankle and mediolaterally wide armour with

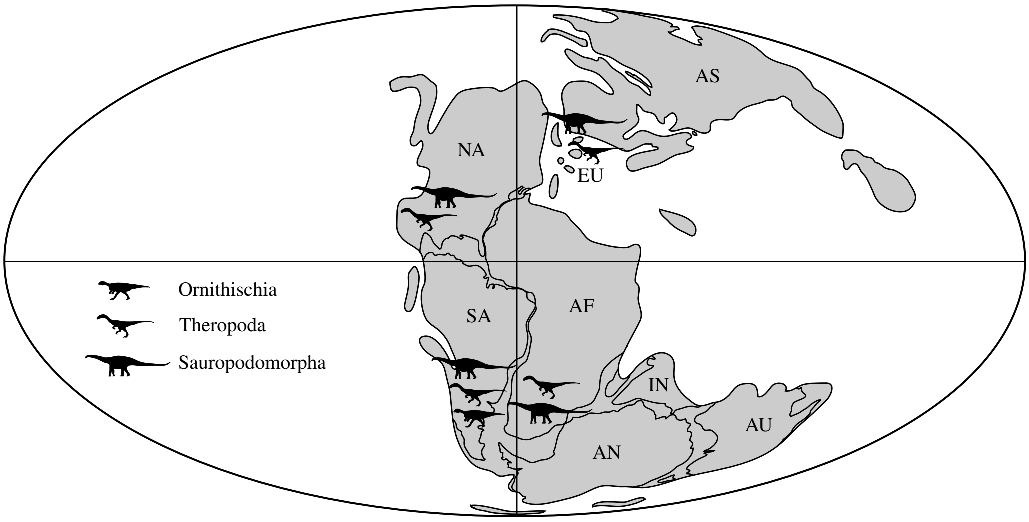

Figure 4. Global distribution of major dinosaur clades during the Late Triassic Period. Palaeogeographic map modified from Smith *et al.* (1994). Abbreviations: AF, Africa; AN, Antarctica; AS, Asia; AU, Australia; IN, India; NA, North America; SA, South America.

a distinct anterior bar. However, *R. callenderi* cannot currently be placed within any known monophyletic clade of pseudosuchians. It appears to be a stem pseudosuchian that combines a highly autapomorphic skull with plesiomorphic postcrania (e.g. coracoid and ilium). Interestingly, the squamosal of *Revueltosaurus* is most similar to aetosaurs (Walker 1961), although it is not rotated laterally as in that group. It is premature to conduct a phylogenetic analysis of the new material of *R. callenderi* given the confused state of basal archosaur relationships, notably 'Rauisuchia', and poor understanding of the polarity of basal archosaurian characters (Gower & Wilkinson 1996).

Sereno (1991*a*,*b*) and Hunt & Lucas (1994; cited in Heckert 2002) listed several characters of the teeth of *R. callenderi* that they considered ornithischian synapomorphies. These include: low triangular tooth crown in lateral view; recurvature absent from maxillary and dentary teeth; well-developed neck separating crown from root; prominent large denticles arranged at 45° or greater to the mesial and distal edges; premaxillary teeth distinct from the maxillary/dentary teeth; and maxillary and dentary teeth asymmetrical in mesial and distal views. Obviously, because *Revueltosaurus* is not an ornithischian or even a dinosaur, none of these character states can be considered synapomorphies of the Ornithischia. *Silesaurus*, a possible basal dinosauromorph from the Late Triassic of Poland, also has low asymmetrical triangular teeth with distinct necks (Dzik 2003). Teeth with well-developed necks are present in several non-ornithischian taxa, such as aetosaurs and therizinosaurid theropods. In fact, only one dental synapomorphy (the presence of a cingulum) is diagnostic of Ornithischia, but this character state is conspicuously absent in *Revueltosaurus*.

No purported Late Triassic ornithischian taxon based exclusively on teeth possesses a cingulum. Only *Pisanosaurus mertii* (Bonaparte 1976) from the Late Triassic of Argentina, which is also known from postcrania, possesses a cingulum (Sereno 1991*a*,*b*), and has been assigned to the Ornithischia based on dental morphology. Even *Pisanosaurus*, however, possesses few non-dental character states that place it within the Ornithischia (Sereno 1991*a*,*b*). We question the assignments of taxa such as *Galtonia*, *Tecovasaurus*, *Lucianosaurus*, *Pekinosaurus* and *Technosaurus* to the Ornithischia, because at present no synapomorphies support these referrals. This does not mean that future non-dental remains of such taxa cannot place them within the Ornithischia, only that phylogenetic support is lacking until additional material is found. Although phylogenetic placement of Triassic herbivore-like tooth taxa is hazardous at best, this does not mean they cannot be autapomorphic and diagnosable taxa (e.g. *R. callenderi*). Nevertheless, naming isolated herbivore-like teeth can be hazardous because future work may show that separate species possess identical dental morphologies (e.g. Lambe 1918; Coombs 1990).

R. callenderi and *Silesaurus* (Dzik 2003) are examples that show the danger of assigning isolated herbivore-like teeth to specific groups. Both animals hint at a poorly understood diversity of Triassic herbivorous archosaurs with similar tooth morphology. All herbivore-like archosaur teeth must have evolved from a laterally compressed, serrated and recurved plesiomorphic tooth form, so there is limited variability in the *Bauplan* of herbivore-like archosaur teeth. This can be seen in the similarity among teeth in a variety of archosaurs such as *Revueltosaurus*, aetosaurs, *Silesaurus*, ornithischians, prosauropods, therizinosaurs and some crocodylomorphs (Buckley *et al.* 2000; Harris *et al.* 2000).

Our reinterpretation of *Revueltosaurus* casts doubt upon the entire North American Late Triassic ornithischian dinosaur record and, consequently, the first confirmed occurrences of an ornithischian within North America are *Scutellosaurus lawleri* and *Scelidosaurus* sp., from the Lower Jurassic Kayenta Formation of northern Arizona (Colbert 1981; Padian 1990*b*). Globally, the only confirmed Late Triassic ornithischians are *Pisanosaurus* (Bonaparte 1976) and an unnamed heterodontosaurid (Báez & Marsicano 2001), both from Argentina. This radically alters the view of the initial origin and diversification of dinosaurs (Hunt *et al.* 1998), and suggests that at least in North America, theropods were well established much earlier than ornithischians were. Similar patterns are seen with theropods and sauropodomorphs in Africa and Europe, where they are clearly present (to the exclusion of ornithischians) in Late Triassic sediments (figure 4; Olsen & Galton 1984; Rauhut & Hungerbühler 2000; Yates 2003*a*,*b*). Interestingly, South America is the only continent where unambiguous ornithischians (Bonaparte 1976), sauropodomorphs (Bonaparte 1972; Langer *et al.* 1999), and theropods (Arcucci & Coria 2003) all occur within Late Triassic sediments (figure 4). This may be cited as support for a South American origin of dinosaurs, but the number of known specimens and localities is too small at present to establish clear patterns.

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