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## Early ornithischian dinosaurs: the Triassic record

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### Abstract

Ornithischian dinosaurs are one of the most taxonomically diverse dinosaur clades during the Mesozoic, yet their origin and early diversification remain virtually unknown. In recent years, several new Triassic ornithischian taxa have been proposed, mostly based upon isolated teeth. New discoveries of skeletal material of some of these tooth taxa indicate that these teeth can no longer be assigned to the Ornithischia using unambiguous synapomorphies. The Triassic record of ornithischian dinosaurs now comprises only three probable occurrences: *Pisanosaurus* and an unnamed heterodontosaurid from Argentina, and an unnamed specimen from the uppermost Triassic of South Africa. This revised Triassic record suggests that ornithischians were not very diverse or abundant through the Triassic, and there are large gaps in the Triassic ornithischian fossil record. Moreover, traditional living analogues for interpreting the feeding ecology of early ornithischians from their tooth morphology are generally inappropriate, and “herbivorous” archosaur teeth such as those found in early ornithischians are not necessarily diagnostic of herbivorous feeding.

**Keywords:** *Ornithischia*, *Triassic*, *Pisanosaurus*, *Revueltosaurus*, *Dinosauria*, *Archosauria*

### Introduction

Despite their extensive fossil record and exceptional diversity during the later Mesozoic, the origin of the Ornithischia is poorly understood. Although all phylogenetic hypotheses in the past 20 years have placed ornithischians as the sister-group to the Saurischia (Sauropodomorpha + Theropoda), basal forms that actually support this phylogenetic relationship are scarce. Putative Late Triassic records are rare, representing a handful of occurrences scattered throughout Laurasia and Gondwana (Figure 1), most represented only by teeth (Serenó 1991; Hunt and Lucas 1994). The best-known Triassic ornithischian, *Pisanosaurus mertii* from Argentina (Casamiquela 1967; Bonaparte 1976), is the only specimen that includes appreciable post-cranial remains. Even the first well-known basal ornithischian, *Lesothosaurus diagnosticus* from the Lower Jurassic of South Africa, has already acquired

most ornithischian synapomorphies (Serenó 1991), and sheds little light on the initial stages of ornithischian evolution.

Recently, the record of Triassic ornithischians has been depleted further with the discovery that at least some isolated teeth previously assigned to the Ornithischia actually belong to other non-dinosaurian archosaurs (Parker et al. 2005). This complicates the identification of isolated ornithischian material in the Triassic, especially teeth. With this new view of criteria for recognizing Triassic ornithischians, what can we say about the origin, timing, and initial radiation of the Ornithischia? Here, we review worldwide records of putative Triassic ornithischians and discuss the implications of this revised record.

Identifying and assigning isolated and fragmentary remains to particular clades requires the recognition of phylogenetically informative character-states. In the context of a phylogenetic analysis, some character-states may provide in-group resolution and be

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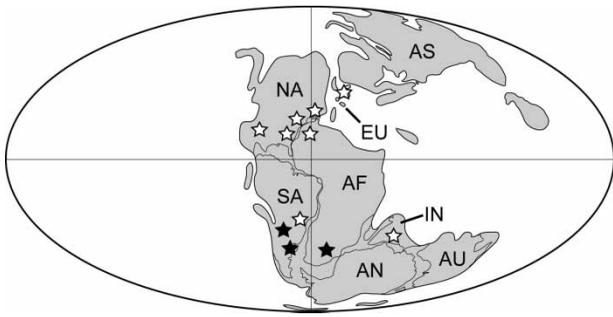


Figure 1. Global distribution of reported Late Triassic ornithischian dinosaur occurrences. Black stars indicate those occurrences confirmed in this study. Paleogeographic map modified from Smith et al. (1994). Abbreviations: AF, Africa; AN, Antarctica; AS, Asia; AU, Australia; IN, India; NA, North America; SA, South America.

synapomorphies of a clade; however, they may have a wider distribution among distantly related taxa or those not included in the analysis. If these other taxa are found in similarly aged strata, the character-states that diagnosed a clade in the phylogenetic analysis cannot be used alone to assign isolated remains to this clade. For example, several dental character-states may diagnose the Ornithischia in phylogenetic analyses of the Dinosauria, but they cannot be used alone to identify isolated Triassic ornithischian teeth, because these character-states are found in other Triassic non-dinosaur archosaurs (Parker et al. 2005). To be useful in identification of specimens, these character-states need to be used in association with unambiguous synapomorphies that can be recognized in the specimen of interest.

Given that this restricts the number of character-states available to diagnose fragmentary early ornithischian specimens, what unambiguous synapomorphies provide robust evidence for an ornithischian affinity? The monophyly of Ornithischia has not been questioned by any recent phylogenetic analysis, so synapomorphies diagnosing the clade Ornithischia provide a good starting point provided they are not found in other early Mesozoic archosaurs. The following character-states are unambiguous synapomorphies of the clade Ornithischia, and have been demonstrated as such by recent phylogenetic analyses (Sereno 1999; Butler 2005a). The status of some of these character-states, as well as other characters not included in this list but traditionally used to diagnose Ornithischia will be discussed later. This list of synapomorphies includes character-states not preserved or otherwise known in *Pisanosaurus*, because its status is explicitly re-assessed below without assuming *a priori* that *Pisanosaurus* is an ornithischian dinosaur. Cranial character-states include: buccal emargination of the maxilla separate from the margin of the antorbital fossa (modified from Butler 2005a); maxilla/dentary teeth with distinct asymmetric basal swelling (“cingulum”) of the crown (Sereno 1999;

Butler 2005a); presence of a separate predentary bone (Sereno 1999; Butler 2005a); and a coronoid process formed by a posterior process of the dentary (Sereno 1999; Butler 2005a). Postcranial character-states include: strap-like preacetabular process of the ilium that extends anteriorly beyond the pubic peduncle (Butler 2005a); posteroventrally rotated pubis with enlarged prepubic process (Butler 2005a); enlarged anterior trochanter of the femur that is anteroposteriorly wide and separated from the body of the femur by a distinct cleft (Butler 2005a); and posterolateral flange of the distal tibia extends posterolaterally behind entire distal end of fibula (Butler 2005a).

Institutional abbreviations: AMNH, American Museum of Natural History, New York; BRSMG, Bristol City Museum and Art Gallery, Bristol, England; CPBA, Cátedra de Paleontología de la Facultad de Ciencias Exactas de la Universidad de Buenos Aires, Argentina; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MNA, Museum of Northern Arizona, Flagstaff, Arizona; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; NSM, Nova Scotia Museum, Halifax, Nova Scotia; PVL, Instituto Miguel Lillo, Tucumán, Argentina; SAM, South African Museum, Cape Town, South Africa; UCMP, University of California Museum of Paleontology, Berkeley, California; YPM, Yale Peabody Museum, New Haven, Connecticut.

## Records of alleged Triassic ornithischians

### North America

Hunt and colleagues (e.g. Hunt 1989; Hunt and Lucas 1994; Hunt et al. 1998; Heckert 2002, 2004) identified a variety of Triassic ornithischian dinosaur taxa based on isolated teeth collected from Upper Triassic strata throughout North America, especially the south-western US. The first of these taxa published was *Revueltosaurus callenderi* (Hunt 1989) from the Norian-aged Bull Canyon Formation of New Mexico. Hunt (1989) referred this taxon to the Ornithischia because of the presence of several dental synapomorphies proposed by Sereno (1986) including low, triangular tooth crowns in lateral view, the absence of recurvature in maxillary and dentary teeth, and a well-developed neck separating crown from root. Hunt (1989) noted that *R. callenderi* lacked “cingula” and differed from other ornithischians in having incisiform premaxillary teeth.

Padian (1990) supported the referral of *Revueltosaurus* to the Ornithischia and referred to the taxon new material from the Chinle Formation of Arizona. Padian (1990) suggested that the lack of cingula and accessory cusps may be plesiomorphic for Ornithischia. He also cautioned that isolated teeth from different stratigraphic horizons in North America should not be referred to *Revueltosaurus* because

isolated archosaur teeth are generally “not diagnostic to lower taxonomic levels.”

Sereno (1991) argued that Hunt’s (1989) positional analysis for the isolated teeth was unfounded as a result of the lack of element association and, therefore, the diagnosis for the genus *Revueltosaurus* was not valid. Whereas Sereno (1991) considered *Revueltosaurus* to represent a *nomen dubium*, he did not dispute the proposed ornithischian affinities of the teeth. Although Kaye and Padian (1994) assigned an isolated tooth (MNA V3690) to *R. callenderi* from the *Placerias*/Downs quarry near St Johns, Arizona (later referred to *Tecovasaurus* by Heckert (2002)), they reiterated warnings regarding the taxonomic assignment of isolated teeth with accessory cusps or serrated denticles to specific clades. Long and Murry (1995) also assigned isolated teeth from the Blue Mesa Member of the Chinle Formation of Arizona to *R. callenderi*. Although they stated that this taxon represented an ornithischian in the systematic section of their paper, in their discussion they also questioned whether *Revueltosaurus* and *Technosaurus* could be confidently referred to the Ornithischia given the absence of associated skeletal elements.

Heckert (2002) provided a detailed redescription of *R. callenderi*, arguing that isolated teeth could indeed be referred with confidence to the Ornithischia because many of the synapomorphies of that clade were based on dental characters. Heckert referred numerous specimens to *Revueltosaurus* from both Arizona and New Mexico and referred the teeth described by Long and Murry (1995) to a new species, *Revueltosaurus hunti*. Heckert (2002) provided a revised diagnosis for both *Revueltosaurus* and *R. callenderi* based mainly on denticle morphology, which he suggested distinguished *Revueltosaurus* from the other North American Triassic “ornithischians” described by Hunt and Lucas (1994).

Parker et al. (2005) reported the discovery of the first tooth bearing and non-dental material that could unambiguously be assigned to *R. callenderi* (Figure 2). The presence of aetosaur-like osteoderms with an anterior bar (Figure 2D), a femur lacking an offset femoral head and anterior trochanter, an ilium with a closed acetabulum, a prefrontal bone, and a “crocodile-normal” ankle (Figure 2B, C) demonstrates that *R. callenderi* is a pseudosuchian, not a dinosaur (Parker et al. 2005). The exact relationships within the Pseudosuchia have yet to be determined, but the presence of rectangular paramedian osteoderms with a distinct anterior bar and a laterally oriented squamosal with an expanded distal end suggest a close relationship with aetosaurs. Numerous teeth were collected with this new material including many that are still in the jaw. These teeth are identical to the holotype teeth of *R. callenderi* and unlike other proposed “ornithischian” teeth from North America (Parker et al. 2005).

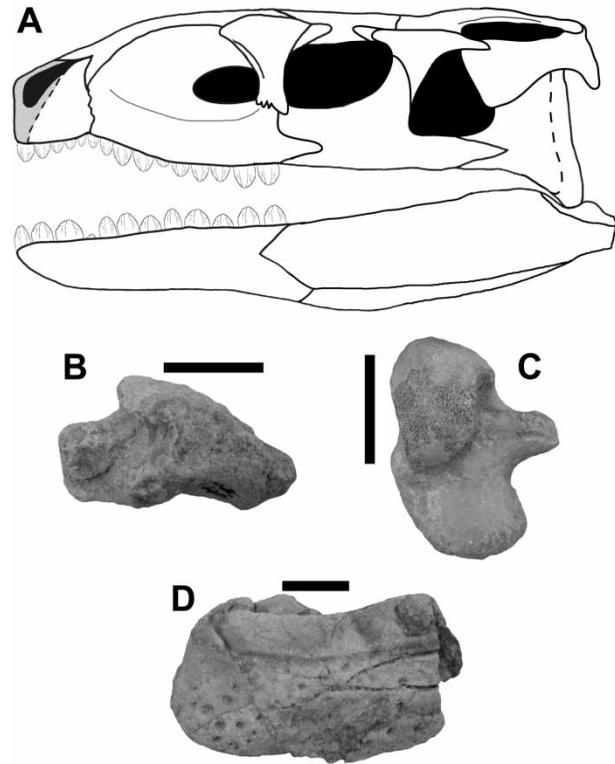


Figure 2. New material of the pseudosuchian archosaur *Revueltosaurus callenderi* from Petrified Forest National Park, Arizona, USA (modified from Parker et al. 2005). (A), skull reconstruction in left lateral view; (B), right astragalus (PEFO 33794) in lateral view; (C), left calcaneum (PEFO 33793) in dorsal view; (D), paramedian osteoderm (PEFO 33795) in dorsal view. Scale bars equal 1 cm.

More importantly, supposed ornithischian dental synapomorphies such as low, triangular tooth crowns, the separation of the crown and root by a distinct neck, and the presence of asymmetrical teeth with serrated denticles, also occur in other Late Triassic archosaurs, including aetosaurs (Walker 1961), *Silesaurus* (Dzik 2003) and now *R. callenderi* (Parker et al. 2005). Thus, these character-states cannot be used to assign isolated teeth to the Ornithischia (Parker et al. 2005; see discussion below). Only the presence of an asymmetrical basal swelling of the tooth crown (“cingulum”) remains as a potential unambiguous synapomorphy for identifying isolated Triassic ornithischian dental remains (Parker et al. 2005), but even this character-state is difficult to assess. Although this character is traditionally referred to as a cingulum, it is not morphologically homologous with the similarly named structure in mammalian teeth (a distinct ridge), and is better described as an asymmetrical labio-lingual swelling of the basal tooth crown. In unambiguous basal ornithischians such as *Lesothosaurus* (Sereno 1991), this basal swelling is poorly developed, and may simply be a result of basal expansion of the crown combined with a waisted root, two features also present in *Revueltosaurus*. If these characters influence the development of this

basal swelling, it may be difficult to determine whether teeth have a true asymmetrical basal swelling (“cingulum”) or simply an expanded basal crown. Galton (1984) suggested that labio-lingual asymmetry of the entire crown was also an ornithischian synapomorphy that separated ornithischian teeth from “prosauropods,” but the pseudosuchian *Revueltosaurus* also has labio-lingual asymmetry (e.g. Heckert 2002). We doubt that any known isolated teeth in Triassic strata can be confidently assigned to ornithischian dinosaurs, even with the presence of a basal swelling, because herbivorous-like teeth have developed many times in Archosauria to form similar tooth shapes (Parker et al. 2005). The morphology of teeth is highly correlated with both function and evolutionary history, complicating their use in taxonomic assignments. Nevertheless, the dental characters found in *Revueltosaurus* and ornithischian dinosaurs may be phylogenetically informative when combined with evidence from other parts of the skeleton.

Heckert (2002) assigned additional isolated tooth specimens to a new taxon, *R. hunti* (Figure 3). This material was recovered from the lower Chinle Formation of Arizona and lower Dockum Group of New Mexico (Heckert 2002). Heckert (2002) differentiated *R. hunti* from *R. callenderi* on the basis of coarser denticles and denticles that extend onto the labial and lingual faces of the teeth. This last feature is especially intriguing because the carinae appear to curve around the base of the crown to the labial and lingual sides of the tooth to form denticulated shelves (Figure 3A,C). In response to the report by Parker et al. (2005) that *R. callenderi* was not an ornithischian dinosaur, Heckert (2005) reiterated his belief that *R. hunti* was an ornithischian, and suggested that the denticulated shelf on the teeth represented a cingulum. He placed *R. hunti* in a new genus, *Krzyzanowskisaurus* (Heckert 2005) in support of this hypothesis. Nonetheless, this denticulated shelf is clearly not homologous to the ornithischian asymmetric swelling or a mammalian cingulum, but it may be an analogous structure. A similar convergent structure is found in teeth of the ankylosaurs *Priodontognathus* and *Texasetes*

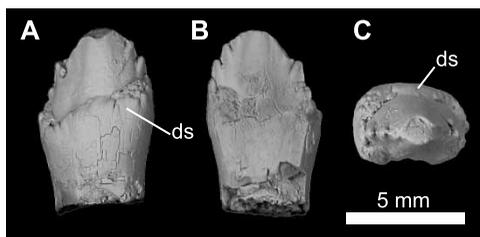


Figure 3. Referred isolated tooth of *Revueltosaurus hunti* (UCMP 139573) from the Upper Triassic Chinle Formation of Arizona. (A), labial view; (B), lingual view; (C), occlusal view. Note that the denticulated shelf (“cingulum”) discussed in the text is broken away from the lingual face of the crown in this specimen. Abbreviations: ds, denticulated shelf.

(Galton 1980; Coombs 1995; Barrett 2001). In these two dinosaurs, unlike *Revueltosaurus hunti*, the “cingula” do not originate from the carinae and wrap around the face of the tooth, and the denticulation of the ridge is less pronounced. This provides further evidence (beyond phylogenetic distance) that the two structures are not homologous. The function of these denticulated “cingula” is unknown and it is unclear if they occluded with teeth in the opposing dentition. Heckert (2005) placed *R. hunti* in a new genus because he believed it represented an ornithischian, and that the denticulated shelf was an autapomorphy. Although we agree that this feature is definitely autapomorphic, it does not justify placing the teeth in a new genus if *R. hunti* is more closely related to *R. callenderi* than any other taxon. We tentatively retain *R. hunti* in *Revueltosaurus* (as a probable pseudosuchian) based on the characters it shares with *R. callenderi* that Heckert (2002) outlined and that the teeth were found at the Blue Hills locality in Arizona (UCMP loc. 7308) in association with a squamosal (UCMP 165205), quadrate (UCMP 165206), and osteoderms that are identical to those of *R. callenderi*. These osteoderms were described by Heckert and Lucas (2002) as juvenile specimens of the aetosaur *Stagonolepis wellsi*, but they are indistinguishable from the osteoderms described by Parker et al. (2005) for *R. callenderi*. This evidence, combined with the fact that *R. hunti* lacks a true asymmetric basal swelling, prevents these teeth from being unambiguously assigned to the Ornithischia.

Responding to criticism from Padian (1990) and Sereno (1991) about whether isolated teeth could be apomorphic, Hunt and Lucas (1994) reiterated their opinion that ornithischian tooth taxa are diagnosable, and named several new genera from isolated Late Triassic teeth from North America (Figure 4). Hunt and Lucas (1994) assigned several teeth originally named *Thecodontosaurus gibbidens* by Cope (1877) from the Upper Triassic Newark Supergroup of Pennsylvania to a new genus *Galtonia* (Figure 4C), following Galton (1983) in recognizing that they did not belong to a sauropodomorph dinosaur. The diagnostic features of these teeth were based on their inferred position within the jaw and reexamination suggests that all of the specimens fall well within the range of variation observed for *R. callenderi*. The holotype tooth of *Galtonia* is nearly identical to the paratype tooth of *R. callenderi* figured by Hunt and Lucas (1994: compare figures 12.8A and C). Therefore, we consider *Galtonia gibbidens* specimens to be referable to *Revueltosaurus* sp.

Teeth named *Pekinosaurus olseni* (Figure 4D) by Hunt and Lucas (1994) are also very similar to the maxillary/posterior dentary teeth of *R. callenderi*. We tentatively also refer these teeth to *Revueltosaurus* sp. because they cannot be differentiated from that taxon and Hunt and Lucas (1994) did not provide a differential diagnosis, autapomorphies, or unique

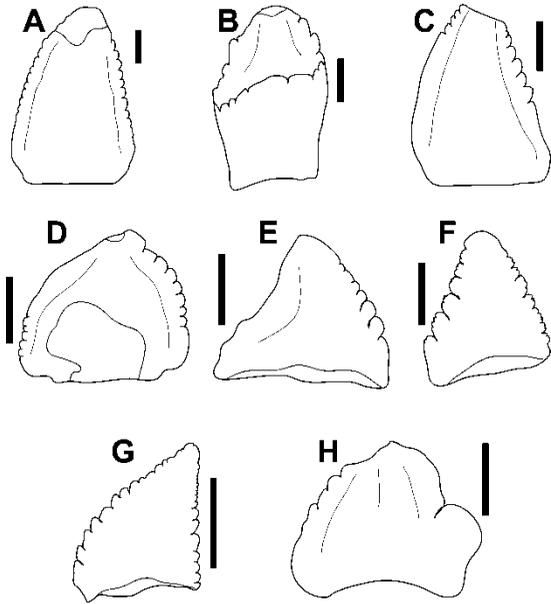


Figure 4. Purported ornithischian teeth from the Late Triassic of North America. (A), *Revueltosaurus callenderi* premaxillary tooth (NMMNH P-4959) in lingual view; (B), *Revueltosaurus hunti* (UCMP 139573) in presumed labial view; (C), holotype tooth of *Galtonia gibbidens* (AMNH 2339) in lingual view; (D), holotype tooth of *Pekinosaurus olsenii* (YPM 7666) in lingual view; (E), holotype tooth of *Tecovasaurus murryi* (NMMNH P-18192) in labial view; (F), paratype tooth of *Crosbysaurus harrisae* (NMMNH P-34201) in labial view; (G), holotype tooth of *Protecovasaurus lucasi* (NMMNH P-34196) in labial view; (H), holotype tooth of *Lucianosaurus wildi* (NMMNH P-18194) in labial view. Scale bars equal 2 mm (A–C) and 1 mm (D–H). (A), (C), (E), and H re-drawn from Hunt and Lucas (1994). F and G re-drawn from Heckert (2004).

combination of character-states for *Pekinosaurus*. Both of these taxa (*Galtonia* and *Pekinosaurus*) possess the following unique combination of dental character-states found only in *Revueltosaurus* that were outlined by Heckert (2002): denticles proportionally short and worn to the enamel by occlusion; denticles fine basally and coarse apically, fining again toward the tip; denticles offset lingually near the base; and denticle wear perpendicular to tooth height.

Hunt and Lucas (1994) also named two additional tooth taxa from the Dockum Group and Chinle Formation, *Tecovasaurus murryi* (Figure 4E) and *Lucianosaurus wildi* (Figure 4H). Although these teeth have diagnostic morphologies, they cannot be assigned to the Ornithischia using synapomorphies or even unique combinations of character-states. Both taxa lack a basal asymmetrical swelling of the tooth crown. *Tecovasaurus* was assigned to the Ornithischia on the basis of a sub-triangular crown and constricted root (Hunt and Lucas 1994). A sub-triangular crown is not unique to ornithischian or dinosaur teeth, and is found in other archosaurs such as *Revueltosaurus* (Parker et al. 2005) and basal sauropodomorph dinosaurs (Barrett 2000). Because no root is preserved, there is no evidence that *Tecovasaurus* had a

constricted root. We consider *Tecovasaurus* a valid taxon because it has the unique combination of the following character-states: mesio-distally asymmetric crown that is not recurved; mesial denticles that do not reach the base of the crown; and a much greater number of denticles on the mesial carina vs. the distal carina. Hunt and Lucas (1994) did not justify their assignment of *Lucianosaurus* to the Ornithischia, and it does not share any character-states with this clade. Specifically, although it has a sub-triangular crown, this morphology is also found in other archosaurs including *Revueltosaurus*, aetosaurs, and basal sauropodomorph dinosaurs. There also is no evidence for a constricted root (also found in the above archosaurs). Finally, *Lucianosaurus* lacks a basal asymmetrical swelling of the tooth crown, the only potential unambiguous synapomorphy of ornithischian teeth. We do consider *Lucianosaurus* a valid taxon because it possesses the autapomorphy of a single enlarged cusp on one carina with multiple smaller denticles on the other carina. Although we provisionally consider *Tecovasaurus* and *Lucianosaurus* valid taxa, they cannot be assigned to the Ornithischia or any other specific archosaur clade. We assign them to Archosauriformes *incertae sedis* because a variety of archosauriforms (e.g. aetosaurs, *Revueltosaurus*, some crocodylomorphs, *Silesaurus*, basal sauropodomorphs, ornithischians, and therizinosaurus) are the only Mesozoic vertebrates with teeth with sub-triangular crowns, enlarged denticles, and thecodont tooth implantation. Although all of the taxa listed above are archosaurs *sensu stricto*, herbivorous-like archosaur teeth could evolve from any laterally-compressed recurved tooth form (Parker et al. 2005), a morphology also found in basal archosauriforms. Given the uncertain phylogenetic affinities of these isolated teeth, we prefer to refer them to the more inclusive clade of Archosauriformes.

Using the criteria outlined by Hunt and Lucas (1994), Heckert (2004) named two new taxa, *Protecovasaurus lucasi* (Figure 4G) and *Crosbysaurus harrisae* (Figure 4F), for isolated “ornithischian” teeth from the Upper Triassic of Texas, New Mexico, and Arizona. Again, they do not display the basal asymmetrical swelling of the tooth crown that is the only unambiguous dental synapomorphy of the Ornithischia. Nor do they display the character of a constricted root that is also found in all ornithischian dinosaurs (and other herbivorous-like teeth). Both *Protecovasaurus* and *Crosbysaurus* are dramatically different in morphology from any known ornithischian or even any other archosauriform tooth. As described by Heckert (2004), *Protecovasaurus* is diagnosable by the following unique suite of character-states: recurved with apex of the crown overhanging the distal margin of the tooth; sharply acute apex of the tooth; and anterior margin strongly convex while the posterior margin is straight to slightly concave. *Crosbysaurus* is diagnosable by the autapomorphy of

large denticles that are compoundly divided so they are subdivided into smaller denticles (Heckert 2004). Both of these taxa are referred to Archosauriformes *incertae sedis* because the clade Archosauriformes is the only Mesozoic vertebrate group containing taxa with teeth that are recurved, have sub-triangular crowns, enlarged denticles, and thecodont tooth implantation.

In a brief publication, Chatterjee (1984) assigned a tooth-bearing premaxilla, partial dentary, posterior lower jaw, dorsal vertebra, and “astragalus” from the Post Quarry of the Bull Canyon Formation of the Dockum Group in Texas to a new taxon of ornithischian dinosaur, *Technosaurus smalli*. The Post Quarry represents a mixed assemblage of many different taxa, and association is often ambiguous. Chatterjee (1984) failed to describe the association of the holotype of *Technosaurus*; therefore, there has been much debate concerning what holotype elements can actually be attributed to *Technosaurus*. Sereno (1991) considered the premaxilla and posterior lower jaw to belong to a “prosauropod” dinosaur, the partial dentary to be ornithischian, the vertebrae indeterminate, and the “astragalus” to be an unidentifiable fragment. He also interpreted the tooth row of the dentary to be inset from the lateral margin, but this does not appear to be the case. Sereno (1991) used the size discrepancy between the preserved premaxilla and dentary of the holotype specimen to support his removal of the premaxilla from the type materials. We agree with Sereno (1991) in removing the “astragalus” and the dorsal vertebra from the holotype, but disagree with the splitting of the dentary and the premaxilla in the holotype. Our comparison of these elements with those of the ornithischian-like dinosauriform *Silesaurus* (Dzik 2003) demonstrates a similar size ratio. Moreover, the teeth in the premaxilla and dentary share the same morphology. The premaxilla of *Technosaurus* strongly resembles that of *Silesaurus* in lacking a rugose anterior margin, possessing alveoli that extend to the distal margin, a symphyseal facet that covers almost the entire medial surface, and teeth with straight lanceolate crowns. *Technosaurus* appears to possess five alveoli in the premaxilla; the same number of premaxilla teeth are found in *Silesaurus* (*contra* Dzik 2003). We also suggest (Nesbitt et al. in review) that the posterior portion of the mandible of *Technosaurus* actually belongs to the posterior portion of the mandible of *Shuvosaurus*, a suchian archosaur (Nesbitt and Norell 2006; Nesbitt et al. in review) that is common within the Post Quarry. Therefore, we restrict the holotype of *Technosaurus* to the premaxilla and the dentary.

Hunt and Lucas (1994) differentiated *Technosaurus* from other ornithischian dinosaurs on the basis of two tooth characters: accessory cusps on the dentary teeth and longitudinal striations at the base of the crown. Although *Silesaurus* lacks distinct accessory cusps, the striations are present (Dzik 2003). Regardless, it is not

clear if *Technosaurus* dentary teeth actually had accessory cusps because they are poorly preserved and often incomplete. Sereno (1991) recognized the following “ornithischian” dental characters in *Technosaurus*: sub-triangular crowns, well developed neck separating crown and root, and an increase in tooth size towards the posterior centre of the tooth row. All of these characters are present in *Silesaurus* (Dzik 2003) and at least the first two are present in the pseudosuchian *Revueltosaurus* (Parker et al. 2005). Furthermore, *Technosaurus* does not possess a distinct basal asymmetrical swelling of the tooth crown, an ornithischian tooth character-state. As a result, we argue that *Technosaurus* cannot be confidently assigned to the Ornithischia because it shares no unambiguous character-states with the clade, but instead may represent a *Silesaurus*-like taxon. This is a tentative hypothesis because it is based mainly on the characters of the teeth, which are already shown to be homoplastic, and needs to be supported by a formal phylogenetic analysis. We recognize that purported ornithischian-like resemblances of *Silesaurus* have led some workers to consider it to represent the sister taxon to Ornithischia (Dzik 2003; Ferigolo and Langer 2005; Langer and Ferigolo 2005); however, that these characters represent true homologues (e.g. the prementary beak) has not yet been demonstrated (see discussion below).

Romer (1968: p. 139) first mentioned ornithischian remains from the Upper Triassic Wolfville Formation of Nova Scotia. Galton (1983) was the first to describe the remains in a short abstract. He considered the isolated partial maxilla (NSM 004 GF 012.001) to belong to the Ornithischia on the basis of a tooth-row inset from the lateral margin of the maxilla, leaf-shaped teeth, and a well-developed neck between the crown and the root of the teeth. Unfortunately, this material has never been described in detail or figured.

The specimen consists of maxillary fragment that preserves one partial tooth missing the tip (Figure 5B–D). There is no evidence for an ascending process, and a portion of the antorbital fossa is preserved, indicating that the specimen preserves a portion of the maxilla posterior to the ascending process. The fragment preserves the last four alveoli in the maxilla (Figure 5C). The size of the alveoli decreases posteriorly. The medial side is broken exposing the alveoli in medial view. Much of the dorsal margin is broken, but the articular facet with the jugal is preserved on the posterodorsal surface. The ventral margin is complete. In lateral view, there is a sharp anteroposterior ridge well offset from the rest of the lateral surface that defines the ventral margin of the antorbital fossa (Figure 5B). Although the dorsal margin of the fossa (the edge of the antorbital fenestra) is broken away, it is clear that this represents part of the fossa because it is composed of finished bone. Ventral to the anteroposterior ridge, the surface is slightly concave.

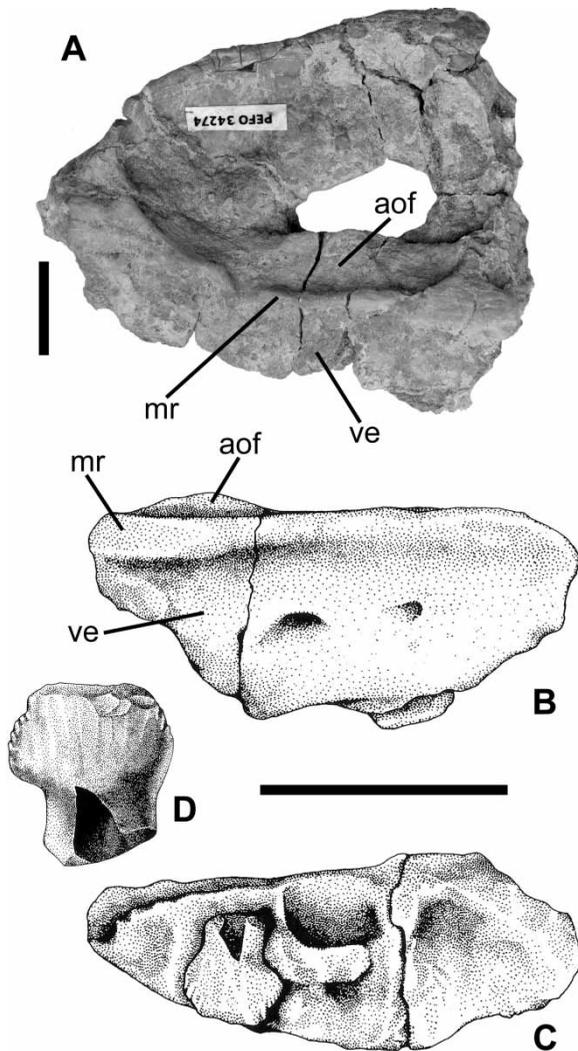


Figure 5. “Ornithischian” maxilla fragment (NSM 004 GF 012.001) from the Upper Triassic Wolfville Formation of Nova Scotia compared with the maxilla of *Revueltosaurus callenderi*. (A), left maxilla and lacrimal of *R. callenderi* (PEFO 34774) in lateral view; (B), NSM 004 GF 012.001 in lateral view; (C), NSM 004 GF 012.001 in medial view; (D), tooth of NSM 004 GF 012.001 in lingual view (not to scale). Scale bars equal 1 cm. Abbreviations: aof, antorbital fossa; mr, maxilla ridge; ve, ventral excavation.

Between the ridge and the ventral margin of the maxilla are two nutrient foramina (Figure 5B). The preserved tooth is missing its occlusal tip, clearly has a distinct neck at the junction of the root and crown, the denticles are aligned at an angle to the mesial and distal carinae, and lacks a basal asymmetrical swelling of the tooth crown (Figure 5D).

Before the discovery of the pseudosuchian phylogenetic placement of *R. callenderi* (Parker et al. 2005), this specimen would have been unambiguously considered an ornithischian dinosaur (e.g. Galton 1983; Hunt and Lucas 1994; Heckert 2002). However, these referrals were based exclusively upon dental character-states that can no longer be used as unambiguous synapomorphies of the Ornithischia. The absence of a basal asymmetrical swelling of the

tooth crown for NSM 004 GF 012.001 indicates it cannot be even tentatively assigned to an ornithischian dinosaur. The preserved portions of the tooth are very similar to maxillary teeth of *R. callenderi*; however, the characters that NSM 004 GF 012.001 and *R. callenderi* share are also present in *Silesaurus* and other ornithischian-like tooth taxa. Although basal ornithischians such as *Lesothosaurus* (Sereno 1991: Figure 5C,D) and *Scutellosaurus* (Colbert 1981: Figures 8,9) have a strong anteroposterior lateral maxillary ridge, a corresponding ventrolateral excavation, and nutrient foramina, all three of these features are also found in the maxilla of *R. callenderi* (Figure 5A). The lateral ridge of ornithischian maxillae is separated from the ventral margin of the antorbital fossa (P. Barrett, personal communication), whereas in the Wolfville specimen and *R. callenderi* the lateral ridge forms the ventral margin of the antorbital fossa. Although foramina on the lateral surface of the maxillae are not apparent in Figure 5A (they are obscured by matrix), these are definitely present in other specimens of *R. callenderi* (e.g. PEFO 33788a). Like other isolated fragments with ornithischian-like features, NSM 004 GF 012.001 does not have character-states exclusive to ornithischian dinosaurs. It is possible that NSM 004 GF 012.001 belongs to an ornithischian, but its incompleteness does not allow it to be unambiguously assigned to Ornithischia.

Kirby (1991) described several isolated teeth from the Owl Rock Member of the Upper Triassic Chinle Formation in northern Arizona. He tentatively assigned these teeth to the Dinosauria but was unsure of whether they belonged to the “Prosauropoda” or Ornithischia. Heckert (2001: pp. 279–282; Figure 11.8) re-examined and re-figured this material and suggested that some of the material represented juvenile phytosaur teeth, some was tentatively referable to the “Prosauropoda”, and one tooth was referable to the Ornithischia. Heckert’s (2001) “prosauropod” and ornithischian teeth are certainly distinct from phytosaur teeth, but they cannot be referred to either basal sauropodomorph or ornithischian dinosaurs using any synapomorphies. In particular, they lack a basal asymmetrical swelling of the crown that is a synapomorphy of ornithischian teeth. Thus, we consider this material to be referable to Archosauriformes *incertae sedis* because the clade Archosauriformes is the only Mesozoic vertebrate group containing taxa with teeth that have laterally-compressed triangular crowns, enlarged denticles, and thecodont tooth implantation.

Olsen and Baird (1986) named the new ichnogenus *Atreipus* for tridactyl footprints found in the Upper Triassic Newark Supergroup and the Middle Keuper of Germany. They considered this ichnotaxon to represent either an ornithischian dinosaur or a basal dinosauriform based on osteological correlations and the distribution of synapomorphies. Haubold (1986)

considered *Atreipus* an ornithischian, but later viewed it as a basal dinosauriform (Haubold and Klein 2000). Using a synapomorphy-based identification (Carrano and Wilson 2001) of the track-maker of *Atreipus* can only constrain *Atreipus* to Dinosauriformes, as originally pointed out by Olsen and Baird (1986). In particular, a functionally tridactyl pes is found in both saurischians and ornithischians, as well as the dinosauriform *Silesaurus* (Dzik 2003). As a result, *Atreipus* cannot be unambiguously assigned to an ornithischian track-maker.

In summary, there are no confirmed ornithischian records from the Triassic of North America (Parker et al. 2005). *Revueltosaurus* is a pseudosuchian archosaur, and some other isolated teeth such as *Pekinosaurus* and *Galtonia* may represent related forms. Other tooth taxa cannot be assigned to specific archosaur clades (e.g. *Lucianosaurus*, *Tecovasaurus*, *Protecovasaurus*, *Crosbysaurus*, and the Wolfville Fm. maxilla). *Technosaurus* may be similar to the basal dinosauriform *Silesaurus* from the Upper Triassic of Poland, and the ichnotaxon *Atreipus* can only be assigned to the clade Dinosauriformes. Because there are no confirmed North American Triassic ornithischians, the first such records in North America are *Scutellosaurus* and *Scelidosaurus* sp. from the Lower Jurassic Kayenta Formation (Parker et al. 2005).

### South America

Triassic ornithischian specimens from South America have played a critical role in the interpretation of the early evolution of the Ornithischia, even though only two published specimens exist to date. South American records are important for two reasons: *Pisanosaurus mertii* is the only Triassic ornithischian specimen preserving postcrania, and *Pisanosaurus* is coeval with other well-known basal dinosaurs, such as *Eoraptor* and *Herrerasaurus*, from one of the few Upper Triassic continental sequences that has been dated radiometrically (Rogers et al. 1993). These data have been used to suggest the appearance of all three major dinosaur lineages (Ornithischia, Sauropodomorpha, Theropoda) in South America by 228 ma. Therefore, the South American record is critical to our understanding of the origin of the Ornithischia.

The problem of *Pisanosaurus*—The specimen PVL 2577 from the middle portion of the Upper Triassic Ischigualasto Formation was described by Casamiquela (1967) as a new taxon of ornithischian dinosaur, *Pisanosaurus mertii*. Casamiquela (1967) considered *Pisanosaurus* a basal ornithopod, and placed it in a new family, Pisanosauridae. He recognized the general plesiomorphic form of the preserved material compared with all other known ornithischians, and suggested a possible affinity with *Poposaurus* based on the morphology of the vertebrae despite Colbert's (1961) evidence that *Poposaurus* did not belong in the

Ornithischia. Casamiquela (1967) rejected a relationship with known heterodontosaurids because *Pisanosaurus* lacks a caniniform tooth. Thulborn (1971, 1972) considered *Pisanosaurus* related to the “fabrosaur,” especially *Tatisaurus* from the Lower Jurassic Lufeng Formation of China. *Tatisaurus* is now known to be a basal thyreophoran (Coombs et al. 1990; Lucas 1996). Galton (1972) placed *Pisanosaurus* as the most basal hypsilophodontid because it has maxillary teeth that are inset from the lateral margin of the jaw.

Bonaparte (1976) redescribed and refigured *Pisanosaurus*. He also included the description of a block containing a partial impression of the pelvic region that was not described by Casamiquela (1967). After reviewing the available evidence, Bonaparte (1976) concluded that based upon the morphology of the teeth, *Pisanosaurus* was best placed in the Heterodontosauridae, although he noted that *Pisanosaurus* lacked the vertical striations present on the teeth of *Heterodontosaurus*. Cooper (1985) also placed *Pisanosaurus* as the sister group to the heterodontosaurids, but none of the characters he uses to diagnose this grouping are preserved in *Pisanosaurus*. Despite the recognition that *Pisanosaurus* could be critical to the origins and relationships of ornithischians, early phylogenetic studies of basal dinosaurs and ornithischian relationships (Norman 1984; Sereno 1984, 1986; Maryńska and Osmólska 1985; Gauthier 1986; Benton 1990) did not include *Pisanosaurus* in their analyses.

Novas (1989) was the first to include *Pisanosaurus* in a phylogenetic analysis. His result, based mainly on hindlimb characters and a modified version of Gauthier's (1986) matrix, was that *Pisanosaurus* was the sister group to all other ornithischians. Although they did not publish a matrix or tree, Weishampel and Witmer (1990) also considered *Pisanosaurus* in a phylogenetic context, and agreed with Novas (1989) that its position lay at the base of the ornithischian tree. In particular, they considered the emargination of the maxillary tooth row, systematic occlusion of the teeth (forming wear facets), loss of recurvature of the maxillary and dentary teeth, separation of the crown and root of the teeth by a neck, and dentary forming the anterior portion of the coronoid process as synapomorphies supporting the referral of *Pisanosaurus* to the Ornithischia (Weishampel and Witmer 1990: pp. 424–425). They also noted that *Pisanosaurus* lacked a number of features present in *Lesothosaurus* and other ornithischians. Although Weishampel and Witmer (1990) realized that some dental character-states were shared between *Pisanosaurus* and heterodontosaurids (mesio-distal contact between adjacent crowns and planar wear facets), they considered these convergences.

Sereno (1991) briefly redescribed *Pisanosaurus* in his review of early ornithischians. He suggested that the forelimb elements did not belong with the rest of

the specimen, because they were proportionally too small. Sereno also recognized that all of the ornithischian synapomorphies of *Pisanosaurus* are found in the maxilla, lower jaw, and teeth (some of which are more derived than *Lesothosaurus*), and combined with the plesiomorphies of the postcrania, this would make *Pisanosaurus* the most basal ornithischian. In his comprehensive phylogenetic analysis of dinosaur relationships, Sereno (1997, 1999) placed *Pisanosaurus* as the most basal ornithischian dinosaur. Three synapomorphies supported this placement: largest maxillary/dentary tooth in middle of tooth row; presence of a dentary coronoid process; and an external mandibular fenestra whose length is shorter than the maximum depth of the dentary ramus (Sereno 1999: supplementary information).

Langer (2004) included *Pisanosaurus* in his phylogenetic analysis of basal saurischians to test the hypothesis that it represented an ornithischian dinosaur. *Pisanosaurus* was found to be the sister group of all other ornithischians; it was constrained to this position because all other ornithischians were coded as a single operational taxonomic unit. In Langer's (2004) analysis, three unambiguous synapomorphies united *Pisanosaurus* and other ornithischians: a marked lateral ridge on the posterior portion of the dentary; expanded ventral border of the mandibular symphysis; and a low labio-lingual eminence on the maxillary and dentary tooth crowns (i.e. a "cingulum"). A similar result was found in an updated version of this dataset (Langer and Benton, in press). Norman et al. (2004) recognized the seemingly contradictory phylogenetic signals in the cranial and post-cranial remains, and questioned their association. The cranial remains alone suggested a placement within the Genasauria (Thyreophora + Cerapoda) or even Cerapoda (Marginocephalia + Ornithopoda) based mainly upon the dentition, but the postcrania lacks any dinosaurian synapomorphies (Norman et al. 2004). Conversely, if all the remains belong to one taxon, then Norman et al. (2004) suggested that *Pisanosaurus* should best be considered a genasaur of undetermined affinities. Butler (2005a) included *Pisanosaurus mertii* in a phylogenetic analysis of basal ornithischian dinosaurs. This study recovered *Pisanosaurus* as the sister group to all other ornithischians, but did not include any non-ornithischians in the analysis other than a composite-coded Saurischia and *Marasuchus* as outgroups.

We re-examined the only known specimen of *Pisanosaurus mertii* (PVL 2577) in an attempt to further elucidate its phylogenetic affinities. As noted by previous authors, the poor preservation of the specimen is the largest difficulty in interpreting its morphology. This results in ambiguous interpretations of character-states. There is no evidence to support claims (Sereno 1991; Norman et al. 2004) that the

holotype might be a chimaera of several individuals or taxa. All of the bones show similar preservation and colour. The field map published by Bonaparte (1976: Figure 1) suggests the material was semi-articulated, and neither Bonaparte (1976) nor Casamiquela (1967) reported the presence of any other vertebrate fossils in association with the holotype of *Pisanosaurus*. Sereno (1991) considered the forelimb material "too small" to be associated with the holotype, but gave no justification. We do not see any *a priori* reason to exclude this material from the holotype; regardless, the incomplete forelimb material is phylogenetically uninformative. Norman et al. (2004) suggested that the crania and post-crania might belong to separate taxa based upon their conflicting phylogenetic signal, but one cannot separate specimens based simply on character incongruence between different regions of the body.

The maxillary and dentary teeth are poorly preserved. It is clear that they have angled, nearly continuous wear facets (Figure 6A–F). The presence of cingula (Sereno 1991) could not be confirmed, although some of the maxillary and dentary teeth have clear constrictions between the crown and root (Figure 6A–B). Other teeth are closely packed together without spaces between the roots and crowns. At least one tooth (5th preserved maxillary tooth) preserves faint vertical ridges at the base of the crown. Both the maxillary and dentary tooth rows are distinctly inset from the lateral margins. In the dentary, the anterior tooth row curves laterally in occlusal view (Figure 6F). The dentary participates in a distinct coronoid process of the mandible (Figure 6D–E). A large mandibular fossa is developed on the medial side of the mandible, but it does not appear to be expressed laterally through a distinct fenestra (Figure 6E). The small lateral opening (Figure 6D) is irregular and has broken margins, making it unlikely that it is a natural fenestra (*contra* Sereno 1991). The dorsal margin of the posterior mandible is broken away, but there appears to be a distinct retro-articular process at the posteroventral end of the mandible (Figure 6D–E).

The vertebrae are very poorly preserved and add little phylogenetic information (Figure 6G). The vertebrae that Casamiquela (1967) assigned to caudals and Bonaparte (1976) assigned to cervicals are very difficult to interpret. The presence of a parapophysis on the centrum is equivocal because of preservation. As Bonaparte (1976) noted, if these vertebrae do pertain to the cervical region, they are unusual in having long prezygapophyses and no neural spine. However, this morphology would be more consistent with the caudal vertebral column. Nevertheless, we consider the position of these vertebrae indeterminate. The articulated dorsal vertebrae are also poorly preserved, and resemble the plesiomorphic condition of archosauriform dorsal vertebrae (Figure 6G). In contrast to all

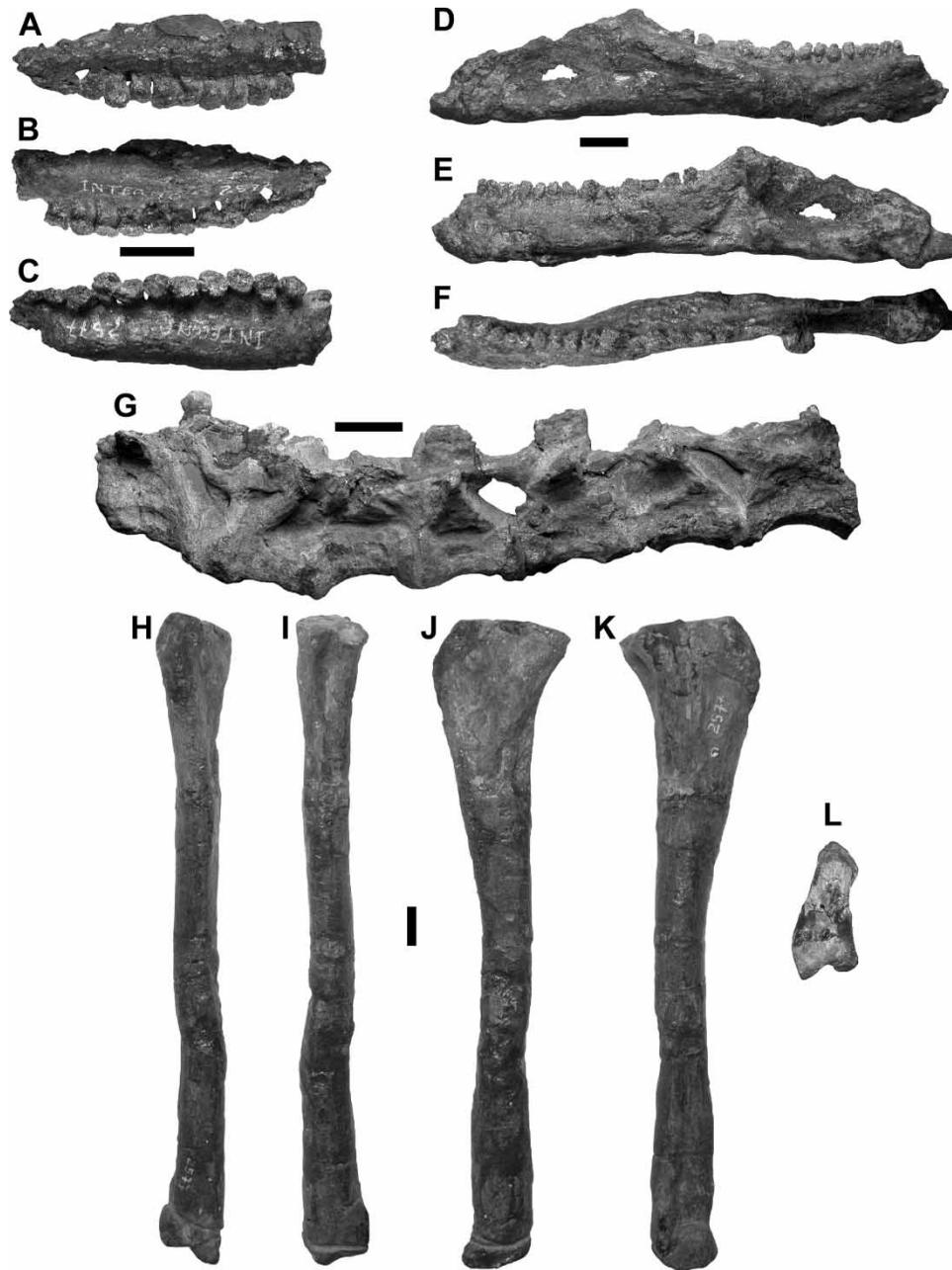


Figure 6. Selected elements of the holotype of *Pisanosaurus mertii* (PVL 2577) from the Upper Triassic Ischigualasto Formation of Argentina. (A), lateral view of maxilla; (B), medial view of maxilla; (C), occlusal view of maxilla; (D), lateral view of right lower jaw; (E), medial view of left lower jaw; (F), occlusal view of right lower jaw; (G), dorsal vertebrae in lateral view; (H), anterior view of right tibia and astragalus; (I), posterior view of right tibia and astragalus; (J), medial view of right tibia and astragalus; (K), lateral view of right tibia and astragalus; (L), proximal view of right tibia. Scale bars equal 1 cm.

previous authors, we can find no evidence that any of the vertebral impressions in the pelvic matrix block are of sacral vertebrae. Features that have previously been considered impressions of sacral ribs are actually cracks in the matrix, and there is not enough fidelity to determine if any of the centra are fused to each other. We agree with Sereno's (1991: Figure 14A) interpretation of the pelvic area, and cannot find any evidence for a posteriorly directed pubic shaft as reported by Bonaparte (1976). It is unclear what Bonaparte thought was evidence for a posteriorly directed pubis; in his figure of the area (Bonaparte 1976: Figure 4) the

pubic shaft is completely reconstructed with a dashed line. We did not observe the "beginning of the posterior process of the pubis suggested by the morphology of the impression" reported by Bonaparte (1976: p. 811).

The two partial distal femora are too incomplete to provide any phylogenetic information. The proximal head of the right tibia has a cnemial crest that curves gently laterally, with two symmetric posterior condyles that are not enlarged (Figure 6L). There is a small, but distinct posterolateral process of the distal tibia (Figure 6I). The distal tibia is obscured by the astragalus in distal view, but it is roughly equal in

dimensions with a convex posterolateral and postero-medial margin. There is a distinct anterior excavation for the reception of the ascending process of the astragalus (Figure 6H). The articulation between the tibia and astragalus is difficult to determine because it has been artificially incised. There is clear evidence for an ascending process of the astragalus, and there is an unusual anteromedial process of the astragalus that projects anteriorly. The astragalus and calcaneum are closely articulated, but there appears to be little or no fibular facet on the astragalus. The fibula is generally plesiomorphic, and was described accurately by Sereno (1991). The calcaneum appears to have a concave dorsal surface that articulates with the fibula, although this articulation is also artificially incised. Otherwise, the calcaneum is highly reduced and medio-laterally very narrow. The two preserved metatarsals were appressed proximally, but as Sereno (1991) noted, nothing can be said of their overlap (*contra* Weishampel and Witmer 1990). The other pedal elements are uninformative.

Our hypotheses about the phylogenetic position of *Pisanosaurus* are similar to those of Norman et al. (2004). The presence of a coronoid process formed in part by the dentary is an unambiguous synapomorphy of the Ornithischia (Sereno 1986, 1999; Weishampel and Witmer 1990). Although the presence of teeth with distinct necks between the crown and root cannot be used alone as a character for identifying ornithischian teeth, it does suggest ornithischian affinities in concert with the other unambiguous synapomorphies. The emarginated maxillary/dentary tooth row diagnoses the clade Genasauria (Norman et al. 2004). The character-state of *Lesothosaurus* (Sereno 1991) and *Scutellosaurus* (Colbert 1981) is a gradual and shallow beveling of the maxilla similar to the maxilla of the pseudosuchian *R. callenderi*, which differs from the sharp shelf found in heterodontosaurids (e.g. Thulborn 1970; Gow 1975), more derived ornithopods, and *Pisanosaurus*. Therefore, Butler (2005a) was incorrect in using the same coding for *Pisanosaurus* and all of Ornithischia. The presence of extensive wear facets led Norman et al. (2004) to suggest a phylogenetic position of *Pisanosaurus* within Cerapoda, because of the similarity with heterodontosaurids. Although this character supports such a placement, occlusal tooth wear is found in a variety of other ornithischians (e.g. Colbert 1981) as well as other dinosaurs (Barrett 2000; Upchurch and Barrett 2000; Schubert and Ungar 2005) and it is conceivable that occlusal patterns similar to those present in heterodontosaurids could have evolved several times within the Archosauria. Nevertheless, this hypothesis of homoplasy or homology cannot be tested without a formal phylogenetic analysis.

The postcrania preserve no synapomorphies of the Dinosauria. The proximal tibia is plesiomorphic and similar to those of basal dinosauriforms such as

*Silesaurus* (Dzik 2003: Figure 13B), *Pseudolagosuchus* (RBI, personal observation), and *Marasuchus* (Sereno and Arcucci 1994) in having a weakly curved cnemial crest in proximal view. Beyond the autapomorphic features of the distal tibia and astragalus described by Sereno (1991) and Norman et al. (2004), these elements are plesiomorphic for Dinosauriformes. The tibia is not distally expanded with a concave posterolateral margin in distal view as in *Lesothosaurus*, other ornithischians (Sereno 1991), basal sauropodomorphs, and theropods (Langer 2004), and the position and morphology of the ascending process of the astragalus is similar to those of basal dinosaurs (Norman et al. 2004) and basal dinosauriforms (e.g. Dzik 2003: Figure 13B). The presence of a posterolateral process on the distal tibia that touches, but does not overlap the medial edge of the fibula is a character-state found in *Herrerasaurus* (Novas 1993: Figure 8A) and *Silesaurus* (Dzik 2003: Figure 13B). Thus, it is not a synapomorphy of the Ornithischia as Butler (2005a) proposed. The metatarsals do not provide any additional phylogenetic information.

The combination of ornithischian cranio-dental features more derived than *Lesothosaurus* and plesiomorphic dinosauriform postcranial character-states makes it difficult to interpret the phylogenetic position of *Pisanosaurus* (Norman et al. 2004). Despite this apparent conflict, there is no evidence to suggest *Pisanosaurus* is a chimaera. Because the characters that place *Pisanosaurus* outside Ornithischia are plesiomorphies, we tentatively consider *Pisanosaurus* an ornithischian dinosaur. Nevertheless, because all of the ornithischian synapomorphies are related to feeding, the hypothesis that *Pisanosaurus* is a basal dinosauriform with jaw morphology convergent upon ornithischians cannot be eliminated, and is contingent upon a formal phylogenetic analysis. The problem with the few phylogenetic analyses that included *Pisanosaurus* (Sereno 1999; Langer 2004; Butler 2005a; Langer and Benton in press) is that they assumed *a priori* that it was a dinosaur. Although both Sereno (1999) and Langer (2004) recovered *Pisanosaurus* as sister group to all other ornithischian dinosaurs, they used a composite coded Ornithischia (Sereno coded the OTUs *Lesothosaurus*, Thyreophora, Ornithopoda, and Marginocephalia, and Langer (2004) used a single OTU, Ornithischia), so it was impossible to test the ornithischian in-group relationships of *Pisanosaurus* in these analyses. Conversely, although Butler (2005a) tested the ornithischian in-group relationships of *Pisanosaurus*, he did not test the hypothesis that it might not be an ornithischian dinosaur. Butler also did not include dental characters in his analysis that are shared between heterodontosaurid ornithischians and *Pisanosaurus*. There appears to be no evidence for an external mandibular fenestra, so Butler's (2005a) scoring of this character as "reduced" in *Pisanosaurus* artificially supported a

basal position within Ornithischia. Scoring it as absent might provide more support for a clade of *Pisanosaurus* with other neornithischians to the exclusion of *Lesothosaurus*. To determine the phylogenetic relationships of *Pisanosaurus*, it must be scored in an analysis that includes non-dinosaurian outgroups, basal dinosauromorphs, basal dinosaurs, and a variety of individual ornithischian taxa, without composite coded taxa. Only then will we have a robust phylogenetic hypothesis for the relationships of *Pisanosaurus*.

Recently, Báez and Marsicano (2001) assigned a tooth-bearing maxillary fragment and partial caniniform tooth from the Upper Triassic Laguna Colorada Formation of Argentina to cf. *Heterodontosaurus* sp. They conclusively documented character-states shared between the maxilla specimen (CPBA-V-14091) and heterodontosaurid dinosaurs, especially *Heterodontosaurus*. These include closely-packed, columnar teeth with basal vertical ridges that are curved lingually, and have wear facets. We agree with this assessment, although the extremely poor preservation of the specimen obfuscates whether or not the presumed wear facets are an original surface or just damage. We tentatively agree that CPBA-V-14091 represents a heterodontosaurid, but additional material is needed to confirm this assignment because the specimen is poorly preserved. The partial caniniform tooth (CPBA-V-14092) that Báez and Marsicano (2001) also referred to this taxon is laterally compressed, serrated, and recurved. It was found isolated in a separate concretion, and cannot be positively associated with the maxilla specimen or

diagnosed on its own; we refer it to Archosauriformes indeterminate.

New material from the Upper Triassic Caturrita Formation of southern Brazil has been recently reported as a new taxon of basal ornithischian dinosaur (Ferigolo and Langer 2005; Langer and Ferigolo 2005). This material is hypothesized to be the sister-taxon of *Silesaurus* from the Upper Triassic of Poland, and both of these taxa form the sister group to all other Ornithischia (Ferigolo and Langer 2005, this volume; Langer and Ferigolo 2005). Having briefly examined the material first-hand, we agree that this new taxon is closely related to *Silesaurus*, but cannot substantiate its placement as a basal ornithischian. This phylogenetic placement is based exclusively on dental character-states that are no longer diagnostic of only ornithischian teeth (Parker et al. 2005), plus a hypothesized homology between the ornithischian predentary and the beak-like anterior end of the dentary of *Silesaurus* and the new Brazilian form. We do not agree that these two structures are homologous because the suggested suture between the dentary and predentary in the Brazilian form appears to actually be a groove leading to a foramen, and is only visible in medial view. Additionally, the suggested suture is not present in the larger specimens. This leaves the ornithischian affinities of these two taxa hanging solely upon dental character-states that are phylogenetically ambiguous. Therefore, we prefer to consider the new Brazilian taxon and *Silesaurus* to represent autapomorphic basal dinosauriforms pending the rigorous phylogenetic analysis suggested above for *Pisanosaurus*.

In summary, the type and only known specimen of *Pisanosaurus mertii* from the Ischigualasto Formation and a partial maxilla from the Laguna Colorada Formation represent some of the only positively identifiable Late Triassic ornithischian material from anywhere in the world.

#### Europe

The published record of Triassic ornithischian dinosaurs from Europe is based almost exclusively on teeth (Figure 7). Tatarinov (1985) described, but did not figure a single tooth from the Latest Triassic deposits of Hallau, Switzerland and assigned it to ?*Abrictosaurus* sp. He described the tooth as triangular with 11–12 denticles, a central longitudinal ridge, and a neck separating the root and crown (Tatarinov 1985). None of these features are autapomorphies of *Abrictosaurus* (Thulborn 1974; Hopson 1975), nor are they unambiguous synapomorphies of the Ornithischia (Parker et al. 2005). For example, these features are found in many basal sauropodomorph dinosaurs (Galton 1985), although we do not imply a phylogenetic relationship with this group. Thus, this

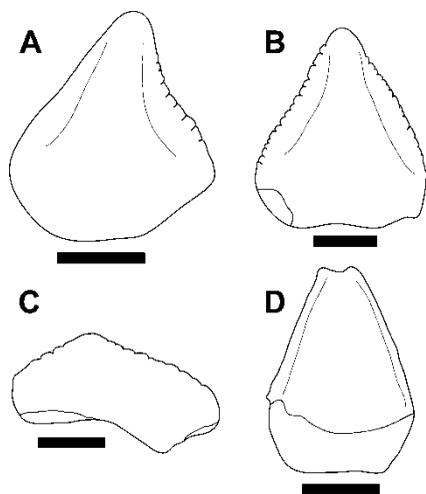


Figure 7. Purported ornithischian teeth from the Late Triassic of Europe. (A), isolated tooth IRSNB R185 from Saint-Nicolas-de-Port, France; (B), isolated tooth IRSNB R186 from Saint-Nicolas-de-Port, France; (C), isolated tooth IRSNB R202 from Saint-Nicolas-de-Port, France; (D), isolated tooth MALS 1998.2.39 from Lons-le-Saunier, France. Scale bars equal 1 mm (A–C) and .5 mm (D). (A–C) re-drawn from Godefroit and Cuny (1997) and (D) re-drawn from Cuny et al. (2000).

specimen cannot be assigned to the Ornithischia based upon Tatarinov's (1985) description.

Godefroit and Cuny (1997) allocated four isolated teeth from Upper Triassic fissure fills of France to three types of teeth that they referred to ?Ornithischia (Figure 7A–C). The referral of these teeth to ornithischian dinosaurs was based on the tooth characters set forth by Sereno (1986, 1991) and Hunt and Lucas (1994), that are no longer unambiguous synapomorphies of the Ornithischia (Parker et al. 2005). None of the teeth possesses a basal asymmetrical swelling of the tooth crown. The teeth described by Godefroit and Cuny (1997) cannot be assigned to the Ornithischia, and we refer them to Archosauriformes *incertae sedis* because Archosauriformes is the only Mesozoic vertebrate clade with laterally compressed sub-triangular tooth crowns, enlarged denticles, and thecodont tooth implantation. Although these teeth were not formally diagnosed as new taxa, they are distinct from all other early Mesozoic teeth. We agree with Heckert's (2002) assessment that Godefroit and Cuny's (1997) type I and type II teeth are the same taxon and not referable to *Tecovasaurus* (Godefroit and Cuny (1997) referred the type I teeth to aff. *Tecovasaurus*) because the teeth are not mesio-distally asymmetric and do not display a difference in size of mesial and distal denticles. The type III tooth (Godefroit and Cuny 1997) also appears to be a distinct morphotype (Heckert 2002), no other early Mesozoic tooth has such a low labio-lingual profile, is laterally-compressed, and has large but low rounded denticles that increase in size towards the base of the crown. The single tooth described by Cuny et al. (2000) from the uppermost Triassic of France lacks any ornithischian synapomorphies (Figure 7D) (e.g. asymmetrical swelling of the basal crown), and can only be assigned to Archosauriformes indeterminate. It is unique in being triangular, asymmetric, but lacks denticles on nearly the whole length of the carinae, although this feature could result from post-mortem wear.

Milàn and Gierlinski (2004) recently described an isolated tridactyl footprint from the Upper Triassic Höganäs Formation of Sweden as a thyreophoran ornithischian dinosaur track. This assignment was based upon overall similarity with supposed ornithischian tracks from the later Mesozoic. Using a synapomorphy-based method for the identification of trackway-makers (Carrano and Wilson 2001), there are no synapomorphies that allow the assignment of this footprint to the Ornithischia or any other dinosaurian group (Marsicano et al. 2005). *Silesaurus*, *Herrerasaurus*, other basal saurischians, ornithischians, and theropods all could potentially produce tridactyl footprints in the Late Triassic. The poor preservation of the footprint makes it impossible to discern any features which would allow referral of this specimen to any one of those taxa.

The basal dinosauriform *Silesaurus opolensis* is known from several skeletons from the Upper Triassic (Carnian) middle Keuper beds of Krasiejów, southern Poland (Dzik 2003). This taxon is peculiar in having herbivorous-like teeth as well as a presumed beak on the anterior end of the dentary. The taxon displays no other ornithischian synapomorphies, and features of the rest of the skeleton place it outside the Dinosauria (Dzik 2003; Langer and Benton in press). A recent phylogenetic analysis recovered *Silesaurus* as the sister group of the Dinosauria (Langer and Benton in press). The hypothesis that *Silesaurus* is a basal ornithischian (Ferigolo and Langer 2005; Langer and Ferigolo 2005) along with a new form from Brazil, as explained above, cannot be substantiated at present. Therefore, there appears to be no conclusive evidence for Triassic ornithischian dinosaurs from Europe.

Galton (2005) recently described several large vertebrate specimens from the Upper Triassic Penarth Group of south-west England. This group of specimens includes two large long-bone shafts (BRSMG Cb3869 and BRSMG Cb3870) that Galton (2005) described as partial femora and assigned to the Stegosauria, making them the earliest occurrences of this clade. Galton's referral of these specimens to the Stegosauria was based on cross-sectional asymmetry that relied upon an inferred anatomical orientation of the bones, and the presence of a thin cortex with extensive cancellous bone and/or trabeculae. These bone fragments are virtually featureless; they preserve no characters (e.g. processes, trochanters, etc.) that would support their identification as femora and allow anatomical orientation of the bones. Because these specimens cannot be identified as femora or oriented anatomically, the comparisons of asymmetry with other dinosaur femora made by Galton (2005) cannot be supported. Furthermore, the presence of extensive cancellous bone or trabeculae does not have a strong phylogenetic signal in tetrapods; it appears to be greatly influenced by biomechanics and life history (Laurin et al. 2004; Lee 2004; Cubo et al. 2005; A. Lee, personal communication). Therefore, these specimens cannot be assigned to the Stegosauria. Galton (2005) assigned these bones to the Dinosauria because of their large size; however, size alone is not a valid phylogenetic criterion. Until it can be demonstrated with confidence that these bones belong to a specific clade (e.g. using histological data), they can only be constrained to the Tetrapoda, and we consider them Tetrapoda indeterminate.

#### Africa

Dutuit (1972) originally described the taxon *Azendohsaurus laaroussii* from the Upper Triassic Argana Formation of Morocco from a tooth-bearing dentary and several isolated teeth. He considered it an ornithischian dinosaur based on the similarity of the

teeth with those of “*Fabrosaurus*” and *Lycorhinus* from the Lower Jurassic of southern Africa. Soon after, other authors (e.g. Thulborn 1974; Bonaparte 1976) realized that the teeth of *Azendohsaurus* displayed more similarities with basal sauropodomorph dinosaurs than ornithischians. Galton (1985: Figure 5N–O, 1986: Figure 16.3L–M) considered one tooth described by Dutuit (1972) as well as an additional undescribed tooth to belong to a “fabrosaurid” ornithischian, although he recognized the rest of the *Azendohsaurus* as belonging to a basal sauropodomorph dinosaur. This view was followed by Galton (1990) and Weishampel and Witmer (1990).

Gauffre (1993) redescribed *Azendohsaurus* and also referred additional material to the taxon. He concluded that *Azendohsaurus* pertained to a basal sauropodomorph, based upon characters of the dentition and maxilla. Gauffre (1993) also considered the “fabrosaurid” teeth of Galton (1985) to belong to *Azendohsaurus* based on their association with the other material and ascribed their different tooth morphology to heterodonty along the jaw and through ontogeny. The characters that Gauffre (1993) used to assign *Azendohsaurus* to the “Prosauropoda” are: the largest tooth is in the anterior third of the jaw and a “fully individualized” ascending process of the maxilla restricted to the anterior half of the element. It is not clear what Gauffre (1993) meant by a “fully individualized” ascending process of the maxilla. The presence of the largest tooth in the anterior third of the maxilla is found in a variety of non-dinosaurian archosaurs including *R. callenderi* (Parker et al. 2005). This is also true for an ascending process restricted to the anterior portion of the maxilla, which is a character-state that is plesiomorphic for Archosauria. Dental character-states previously used to assign *Azendohsaurus* material to either the Ornithischia or Sauropodomorpha are no longer restricted to the Dinosauria (Parker et al. 2005).

A non-dinosaurian phylogenetic placement for *Azendohsaurus* was supported by Jalil and Knoll (2002) who noted that disarticulated postcranial material found in direct association with tooth-bearing bones of *Azendohsaurus* at the type locality lacked any synapomorphies of the Dinosauria. This material displayed the plesiomorphic states of an imperforate acetabulum, absence of a brevis fossa, the lack of an offset femoral head of the femur, and a proximally located fourth trochanter of the femur (Jalil and Knoll 2002). Galton and Upchurch (2004) agreed that this suggested non-dinosaurian affinities for *Azendohsaurus* if the material belongs to the same taxon. Such a phylogenetic position seems likely because a nearly identical taxon from the Triassic of Madagascar that was originally described as the oldest “prosauropod” (Flynn et al. 1999) now appears to be a non-dinosaurian archosauriform based upon newly recovered material (Goswami et al. 2005).

Knoll (2004) reported an associated partial skeleton of an ornithischian dinosaur (SAM-PK-K8025; he incorrectly listed it as 8027) from the lower Elliot Formation of South Africa. There is considerable disagreement about the chronostratigraphic age of this specimen, as Knoll (2004) noted. The Elliot Formation is typically divided into upper and lower units; the boundary is defined by a biostratigraphic change from the “*Euskelosaurus* Range Zone” to the overlying “*Massospondylus* Range Zone” (Kitching and Raath 1984; Knoll 2004, 2005). This change has been interpreted as correlative to the Triassic–Jurassic boundary and has also been supported by data from the footprint record (Olsen and Galton 1984; Knoll 2004, 2005). SAM-PK-K8025 was recovered from five meters below a well-preserved sauropodomorph skeleton identified as “*Euskelosaurus*”, so this would seem to indicate that the specimen is from the lower Elliot Formation, and thus Triassic in age (Knoll 2004). To complicate matters, it appears that the taxonomy of “*Euskelosaurus*” is in need of revision; the holotype and much of the referred material used for biostratigraphic correlation may not be diagnostic (Yates 2003; Yates and Kitching 2003; Knoll 2004). Specimens used for biostratigraphy must represent monophyletic taxa and be identifiable using synapomorphies (Angielczyk and Kurkin 2003). The use of “*Euskelosaurus*” to determine the terminal Triassic boundary in the Elliot Formation may be unwise until the specimens assigned to this taxon are revised; the chronostratigraphic age of SAM-PK-K8025 is, therefore, unresolved. Butler (2005a) briefly mentioned some morphological features of SAM-PK-K8025 and included it in a phylogenetic analysis of basal ornithischians. Although it was recovered in a basal polytomy with *Lesothosaurus* and a clade containing the rest of Neornithischia, this position is most likely the result of missing data because SAM-PK-K8025 is coded exactly the same as *Lesothosaurus* for all preserved characters (Butler 2005a). Butler (2005a: p. 184) used a “relatively large manus” and intercondylar processes on the proximal phalanges to differentiate SAM-PK-K8025 from *Lesothosaurus*. This suggests SAM-PK-K8025 is a separate taxon from *Lesothosaurus*, but it is unclear how these features vary through ontogeny.

Following Haubold (1986) and Thulborn (1990), Knoll (2004) also considered the footprint taxon *Paratrisauropus* described by Ellenberger (1972) from the Upper Triassic Molteno Formation of southern Africa to have been made by an ornithischian dinosaur. Ellenberger (1972) assigned this taxon to the Ornithischia based upon overall similarity to ornithopod foot morphology and ornithischian tracks from the later Mesozoic. Neither Haubold (1986), Thulborn (1990), nor Knoll (2004) explained why they assigned *Paratrisauropus* to an ornithischian track-maker. Track-makers should be identified

Table I. Taxonomic assignment of purported Late Triassic ornithischian dinosaurs.

Taxon/specimen	Previous assignment	This study
North America		
<i>Reueltosaurus callenderi</i>	Ornithischia	Pseudosuchia
<i>Reueltosaurus hunti</i>	Ornithischia	?Pseudosuchia
<i>Galtonia gibbidens</i>	Ornithischia	<i>Reueltosaurus</i> sp.
<i>Pekinosaurus olseni</i>	Ornithischia	<i>Reueltosaurus</i> sp.
<i>Tecovasaurus murreyi</i>	Ornithischia	Archosauriformes <i>incertae sedis</i>
<i>Lucianosaurus wildi</i>	Ornithischia	Archosauriformes <i>incertae sedis</i>
<i>Protecovasaurus lucasi</i>	Ornithischia	Archosauriformes <i>incertae sedis</i>
<i>Crosbysaurus harrisae</i>	Ornithischia	Archosauriformes <i>incertae sedis</i>
<i>Technosaurus smalli</i>	Ornithischia	<i>Silesaurus</i> -like taxon?
Wolfville “ornithischian”	Ornithischia	Archosauriformes <i>incertae sedis</i>
Owl Rock Member teeth	“Prosauropoda”/Ornithischia	Archosauriformes <i>incertae sedis</i>
<i>Atreipus</i> spp.	Dinosauriformes/Ornithischia	Dinosauriformes
South America		
<i>Pisanosaurus mertii</i>	Ornithischia	Ornithischia
Laguna Colorada heterodontosaurid	Heterodontosauridae	Heterodontosauridae
Europe		
Hallau tooth	? <i>Abrectosaurus</i> sp.	Archosauriformes <i>incertae sedis</i>
Saint-Nicolas-de-Port teeth	Ornithischia; aff. <i>Tecovasaurus</i>	Archosauriformes <i>incertae sedis</i>
Lons-le-Saunier tooth	Ornithischia	Archosauriformes <i>incertae sedis</i>
Höganäs Fm footprint	Ornithischia	Dinosauriformes
<i>Silesaurus opolensis</i>	Dinosauriformes/Ornithischia	Dinosauriformes
Penarth Group material	Stegosauria	Tetrapoda indet.
Africa		
<i>Azendohsaurus laaroussii</i>	“Prosauropoda”/Ornithischia	Archosauriformes
SAM-PK-K8025	Ornithischia	Ornithischia
<i>Paratrisauropus</i>	Ornithischia	Dinosauriformes
India		
Dharmaram Fm material	Ornithischia	??

using synapomorphy-based identifications (Carrano and Wilson 2001), and there are no synapomorphies that allow the referral of tridactyl Triassic prints to the Ornithischia (Marsicano et al. 2005). Taxa such as *Silesaurus*, *Herrerasaurus*, ornithischians, and theropods all have functionally tridactyl pedes that can produce a tridactyl footprint. Therefore, *Paratrisauropus* cannot be used as evidence for Triassic ornithischian dinosaurs in the Late Triassic, and the only possible Triassic African record of ornithischian dinosaurs is SAM-PK-K8025, but even its chronostratigraphic provenance is ambiguous.

### India

Several authors (Kutty et al. 1987; Loyal et al. 1996; Heckert 2001) have mentioned the presence of an ornithischian from the upper Dharmaram Formation (Upper Triassic) of the Pranhita–Godavari Valley in central India. Unfortunately, the material has never been figured or described, so it cannot be evaluated here. The age of this formation is poorly constrained and is mainly based upon the presence of aetosaurs in the lower portion of the formation, the presence of undescribed “prosauropod” dinosaurs, the fact that it overlies the Upper Triassic Maleri Formation and underlies the Lower Jurassic Kota Formation, and comparisons with European vertebrate assemblages (Kutty et al. 1987). Therefore, it is also possible that

the top of the formation is earliest Jurassic in age (Kutty and Sengupta 1989).

## Discussion

### *Timing and divergence of the Ornithischia*

The revision of supposed Triassic ornithischians presented above markedly changes the known Triassic record for this clade (Table I), and has important implications for the early diversity of dinosaurs. Previously, Triassic ornithischians were considered to be fairly diverse in the Upper Triassic, especially in North America (Hunt and Lucas 1994; Hunt et al. 1998; Heckert 2004). Occurrences of ornithischians were known from the Late Triassic of both Laurasia and Gondwana, suggesting a relatively quick geographic dispersal of the clade. Now, possible Triassic ornithischian records are restricted to three specimens from Gondwana (Argentina and South Africa) and represent a maximum of three lineages. This is an incredibly low diversity, abundance and geographic distribution when compared with the records of Triassic theropods and sauropodomorphs (Parker et al. 2005).

The chronology of the few remaining Triassic ornithischian specimens suggests that we are missing most of the early evolutionary history of the Ornithischia (Figure 8). According to Rogers et al. (1993), the single specimen of *Pisanosaurus mertii* is from the middle Ischigualasto Formation,

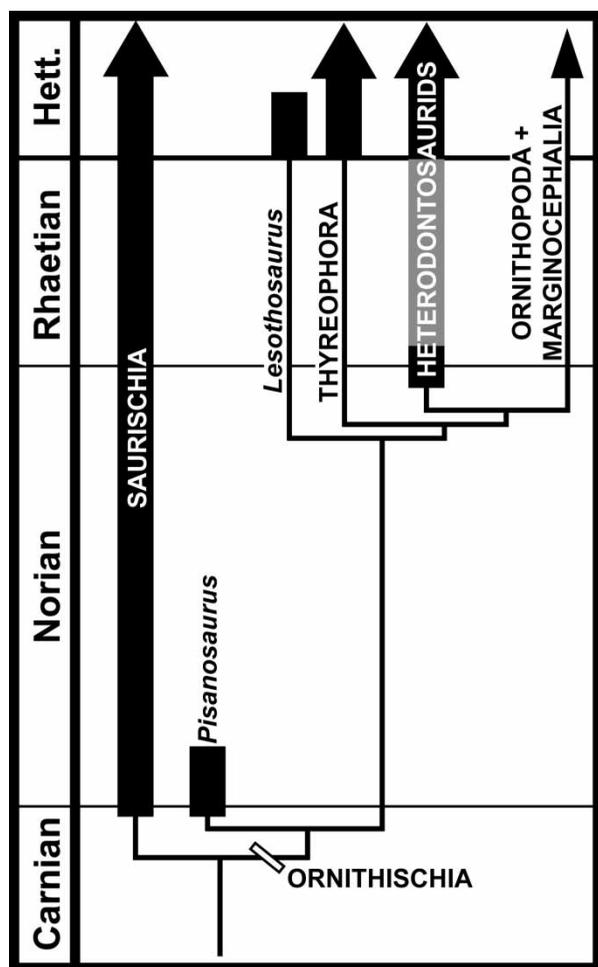


Figure 8. Time-calibrated cladogram of early ornithischians during the Late Triassic and Early Jurassic periods. Thick vertical black bars indicate confirmed occurrences; thin vertical lines indicate ghost lineages. The thick vertical grey bar indicates gap in heterodontosaurid record. Phylogeny based on Sereno (1986, 1999) and Butler (2005a); timescale based upon Muttoni et al. (2004).

approximately 150 m above the only radiometrically dated layer in the formation, which yielded a date of  $227.8 \pm 0.3$  ma. The most conservative calculation based on rift-basin sedimentation rates would suggest that *Pisanosaurus* is no more than five million years younger than this radiometric date (Rogers et al. 1993). Because the basal saurischians *Herrerasaurus* and *Eoraptor* are stratigraphically close to the radiometrically dated layer, it suggests that the two main dinosaur lineages Ornithischia and Saurischia were both present by 228 ma (Rogers et al. 1993) (Figure 8). The Laguna Colorado heterodontosaurid was assigned a broadly Norian age, based upon a Ladinian–Carnian age for underlying strata and granitoid intrusions into the Laguna Colorado Formation that provide a minimum age of  $203 \pm 2$  ma (Báez and Marsicano 2001). This is a relatively poorly constrained occurrence if the extreme length of the Norian (227–210 ma) reported by Muttoni et al. (2004) is confirmed. As discussed above, the dating

of the Elliot Formation ornithischian is ambiguous, but appears to be close to the Triassic–Jurassic boundary (200 ma).

If we accept the phylogenetic position of *Pisanosaurus* as the sister group to all other ornithischians (Sereno 1999; Langer 2004; Butler 2005a), and that the Laguna Colorado specimen is a heterodontosaurid, this implies substantial gaps in the Triassic ornithischian record. After *Pisanosaurus*, there is no record of the ornithischian stem lineage leading to the Genasauria until *Lesothosaurus* in the earliest Jurassic (Figure 8). This is a gap of at least 20 million years; although this is not unusual for the ornithischian dinosaur record (Weishampel 1996), it is still significant. A conservative age estimate for the Laguna Colorado heterodontosaurid would place it at 205 ma. This specimen suggests that the Cerapoda lineage existed by this time, and there is at least a five million year gap in its history until other cerapodans appear in the Early Jurassic of southern Africa (heterodontosaurids in the upper Elliot Formation (Knoll 2005)) (Figure 8). Because Cerapoda is the sister taxon of the Thyreophora, this implies a ghost lineage for the Thyreophora of at least five million years, because basal thyreophorans do not appear in the fossil record until the Early Jurassic of North America (Weishampel et al. 2004; Parker et al. 2005). The alternative topology of early ornithischian relationships proposed by Butler (2005a) does not change the length of these proposed ghost lineages. If heterodontosaurids are basal to the Genasauria as proposed by Butler (2005b), this would only shorten the ghost lineage leading to ornithopods, because SAM-PK-K8025 is from the Triassic and is a basal member of the Neornithischia (Butler 2005a). Quite possibly, the Laguna Colorado heterodontosaurid is even older than 205 ma, effectively increasing these gaps in the fossil record by several million years. If the cerapodan affinities of *Pisanosaurus* suggested by some (Bonaparte 1976; Norman et al. 2004) are correct, this would suggest a ghost lineage of over 20 million years for the Thyreophora, and imply an unrecorded diversification of the main ornithischian lineages by 225 ma. Alternatively, if *Pisanosaurus* and the Laguna Colorado specimen do not represent ornithischian dinosaurs, the ghost lineage for the whole of Ornithischia would be at least 25 million years long, because basal members of the Saurischia are present by 228 ma (Figure 8).

Regardless of which temporal hypothesis presented above is preferred, there are definitely large portions of the Triassic evolution of the Ornithischia that are missing from the fossil record. Where then are the Triassic ornithischians? Nearly all of the Late Triassic and Early Jurassic records of ornithischian dinosaurs are found in terrestrial fluvial-dominated sedimentary basins. It is possible that most Triassic ornithischians lived in paleoenvironments that did not preserve well in the geologic record, and then shifted during the

Early Jurassic to environments more conducive to fossilization. It is equally probable that Triassic ornithischians remained extremely depauperate in both taxonomic diversity and abundance, and only diversified into empty adaptive zones after the extinction(s) at end of the Triassic. At present, there is no positive evidence for either hypothesis. A third possibility is that the phylogenetic placement of the clade Ornithischia is incorrect, and it originated from one of the groups now nested within Saurischia (e.g. Paul 1984; Sereno 1984; Cooper 1985). Although we do not necessarily support this hypothesis given the strong consensus on the position of the Ornithischia (e.g. Sereno 1997, 1999; Butler 2005a), it must be evaluated in explanations for the virtual non-existence of Triassic ornithischians.

*Comments on the interpretation of herbivorous-like archosaur teeth*

The presence of teeth with sub-triangular crowns and enlarged denticles is commonly used to infer that archosaur taxa displaying these teeth are herbivorous, mainly based on modern analogues with iguanid lizards (Barrett 2000). In an extremely perceptive essay, Barrett (2000) pointed out that there are several problems with such an inference, not the least of which is that no iguanid lizard with similar teeth is fully herbivorous. Barrett (2000) suggested that taxa with these “herbivorous-like” teeth were more parsimoniously interpreted to have an omnivorous feeding ecology that lay somewhere on the spectrum between full carnivory and full herbivory. Although he focused on basal sauropodomorph teeth, the same could be said for basal ornithischians, *Revueltosaurus*, and the teeth we refer to Archosauriformes *incertae sedis*.

We agree with Barrett’s (2000) cautionary message, and wish to suggest caution when emphasizing the power of modern analogues in the study of archosaur paleoecology. The paleoecology of Mesozoic archosaurs is difficult to infer because the organisms were living in non-analogue environments and have no close living relatives. The two living archosaur lineages, Crocodylia and Neornithes, play specialized roles in their respective ecosystems that do not provide appropriate analogues for extinct terrestrial archosaurs. Using modern squamates as direct analogues for extinct archosaurs is possibly unwise given their phylogenetic and temporal distance from Mesozoic Archosauria. Even when a taxon can be phylogenetically bracketed, one or two broad morphological characteristics are difficult to use to infer function of teeth because morphology is a combination of phylogenetic history, material properties, and ecology/function (Seilacher 1970; Raup 1972). This is especially the case with “herbivorous-like” archosaur teeth, all of which evolved from the recurved, serrated, and laterally compressed plesiomorphic archosauriform tooth form (Parker et al. 2005). Finally,

tooth form may not always correlate with diet (e.g. Munk and Sues 1993), because an organism’s feeding apparatus only has to be “good enough” to obtain food, not optimally designed. Therefore, it is at present very difficult to say that certain archosaur tooth morphologies correlate with specific feeding ecologies (and this includes both “carnivorous-like” and “herbivorous-like” teeth). Micro-wear studies (e.g. Goswami et al. 2005) provide a limited frame of reference because there are no extant related archosaur taxa with similar jaw mechanics and tooth morphologies. Goswami et al. (2005) assumed that the archosaur teeth they studied pertained to an herbivorous animal, so their data do not address whether or not this taxon was herbivorous, only its jaw movement.

One way to test whether character-states in extinct taxa represent ecological shifts is to identify similar character-state changes through the phylogeny of an extant clade (e.g. Barrett 2000) that correlate with a shift in ecology. This method is especially powerful if functionally and morphologically similar character-states show the same ecological correlation in a variety of unrelated extant clades. Additional evidence for the correlation of a morphological character with ecology is if the character changes together with other morphological characters hypothesized to be related to the same ecological shift. This requires that the taxon of interest is placed in a phylogeny to test whether or not the multiple character-state changes are correlated (e.g. herbivorous teeth and modification of jaw movement). If they are not, it does not support the hypothesis that they all relate to the same ecological shift. Detailed studies of these types of correlated character transformations relating to hypothesized ecology are deficient for most Mesozoic archosaurs. Stable isotope studies may help address the ecology of extinct archosaurs, but there are several major problems that must first be addressed. First, the extremely thin enamel of non-mammalian teeth makes it difficult to sample (Thomas and Carlson 2004). More importantly, a thorough understanding of the isotopic landscape of the physical environment that the organism is living in is needed to reliably interpret ecological inferences from isotopic data (Feranec 2004; Thomas and Carlson 2004). This is difficult in non-analogue environments such as those in the Mesozoic. Finally, and most importantly, it is imperative to determine what effect diagenesis has had upon the isotopic signals in the fossils (Kolodny et al. 1996; Kohn 1999; Kohn and Cerling 2002; Thomas and Carlson 2004). There is ample opportunity to reset the isotopic signals present in vertebrate fossils, and it can often be difficult to determine conclusively whether or not a signal is biotic or diagenetic (Kohn and Cerling 2002). Thus, the null hypothesis should be that diagenesis has altered the sample. Nevertheless, when these pitfalls are addressed, stable isotope geochemistry has been

successfully used to interpret the diet of Mesozoic archosaurs (Thomas and Carlson 2004).

Why does all this matter for the early evolution of ornithischians? It has traditionally been assumed that all ornithischians were herbivorous. If we are to test hypotheses about why ornithischians diversified while other archosaur taxa with similar tooth forms did not, it is important to understand the ecology of these taxa. Unfortunately, the power of inference from modern analogues of ecologies of extinct taxa with no close extant relatives is over-stated; we must understand the limitations of this method and move on to other methods that provide explicit tests for hypotheses about the ecology of extinct organisms with no close living relatives. Once these tests are utilized, some of which are outlined above, we can start to test hypotheses about the origin and early evolution of the dinosaurs.

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