

Reconsidering the status and affinities of the ornithischian dinosaur *Tatisaurus oehleri* Simmons, 1965

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The early Mesozoic fossil fauna collected from the Lower Lufeng Formation of Yunnan Province, China, has attracted considerable interest and attention since its discovery in the late 1930s. Its importance reflected a combination of its comparatively remote geographical position and, more particularly, the similarities of its fauna compared with approximately contemporary discoveries from Europe, North and South America, and southern Africa. The fragmentary and poorly preserved Lufeng ornithischian dinosaur *Tatisaurus oehleri* was described in 1965 and proved taxonomically and systematically enigmatic from the start. Originally assigned, with some noted ambivalence, to the basal ('primitive') group of ornithischians known as hypsilophodontids, since 1965 *Tatisaurus* has been variously ignored, assigned to a more rigorously defined Hypsilophodontidae, referred to both of the armoured (thyreophoran) ornithischian dinosaur clades (Stegosauria and Ankylosauria), or referred to a more basal position within the thyreophoran lineage. In 1996 the holotype of *Tatisaurus* was renamed *Scelidosaurus oehleri*, and the genus *Scelidosaurus* was proposed as an index fossil of the '*Scelidosaurus* biochron' with the potential to be used for the global stratigraphic correlation of Early Jurassic (early Sinemurian) rocks. Because of this chequered history *Tatisaurus oehleri* Simmons, 1965 has been re-examined and is redescribed so that its taxonomic status and systematic position could be reassessed. *Tatisaurus* is identified as a basal thyreophoran (armoured ornithischian dinosaur); there is no basis for amalgamating it in synonymy with the genus *Scelidosaurus*, and the proposed creation of a '*Scelidosaurus* biochron' for the purposes of biostratigraphic correlation of Lower Jurassic outcrops has no utility whatever. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 150, 865–874.

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INTRODUCTION

ORNITHISCHIAN IN THE LUFENG FORMATION

The Lower Lufeng Formation of Yunnan Province, China, has yielded an important and diverse early Mesozoic vertebrate fauna (Young, 1940, 1946, 1951; Simmons, 1965; Sun *et al.*, 1985; Luo & Wu, 1994). The sequence, reviewed in some detail by Simmons (1965), is dominated by sandstones, siltstones, and clays that were deposited in a range of fluvial, overbank, and lacustrine environments. It is divided into two mappable units: the 'Dull Purplish Beds' and the overlying 'Dark Red Beds'; these units have been formally designated as the Shawan Member and the

Zhangjiawa Member (Fang *et al.*, 2000), respectively, although we retain the informal (and more widely known) terminology. The fauna associated with the 'Dull Purplish Beds' is recorded as being dominated by prosauropod saurischian dinosaurs and the tritylodontid synapsid *Bienotherium*; the 'Dark Red Beds' has yielded a more diverse fauna that includes ubiquitous tritylodontids and prosauropod saurischians, as well as early mammals, sphenodontian lepidosaurs, basal crocodylomorphs, theropod saurischian dinosaurs, and ornithischian dinosaurs (Simmons, 1965; Luo & Wu, 1994). Dating of the Lower Lufeng Formation has proved problematic because it is based upon similarity with faunas elsewhere. It has been proposed that some or all of the Lower Lufeng is Late Triassic in age (e.g. Simmons, 1965). However, other reviews support an Early Jurassic age for the whole of

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the Lower Lufeng (e.g. Sigogneau-Russell & Sun, 1981; Olsen & Galton, 1984; Luo & Wu, 1994; Lucas, 1996; Irmis, 2004).

Remains of ornithischian dinosaurs are rare in the Lower Lufeng, nevertheless four taxa have been named on the basis of fragmentary material collected from the 'Dark Red Beds': *Tawasaurus minor* Young, 1982a, *Dianchungosaurus lufengensis* Young, 1982b, *Bienosaurus lufengensis* Dong, 2001, and *Tatisaurus oehleri* Simmons, 1965. All of these taxa have proved to be taxonomically problematic since their initial descriptions. The holotype of *Tawasaurus*, originally described as a basal or 'fabrosaurid' ornithischian, pertains to a juvenile prosauropod saurischian (Serenó, 1991); similarly the holotype of *Dianchungosaurus*, initially referred to the ornithischian family Heterodontosauridae by Young (1982b), has been demonstrated to be represented by an assemblage of remains that can be assigned to two distinct groups: a prosauropod saurischian and a mesoeucrocodylian (Barrett & Xu, 2005). *Bienosaurus* was referred to the ornithischian clade Ankylosauria by Dong (2001); however, Jolyon Parish in his review of the Ankylosauria (Parish, 2005) indicated that the validity and ankylosaurian affinities of this taxon are doubtful, although its ornithischian affinities have not been questioned.

Of the Lower Lufeng material attributed to the Ornithischia, only *Tatisaurus* can still be considered taxonomically valid. Given this decidedly chequered past, there are some undoubtedly ornithischian postcranial remains among the 'Dark Red Beds' collection at the Field Museum, Chicago; these include fragmentary hindlimb material (Irmis, 2002) as well as pelvic elements.

THE AFFINITIES AND GENERAL SIGNIFICANCE OF *TATISAURUS OEHLERI*

Tatisaurus oehleri Simmons, 1965, was established on the basis of a left dentary (FMNH CUP 2088) collected from the 'Dark Red Beds' of the Lower Lufeng Formation, in the vicinity of Ta Ti village, Lufeng County, Yunnan Province, China. Simmons (1965) assigned *Tatisaurus* to the ornithischian ornithopod family Hypsilophodontidae (which was then regarded as a primitive and rather generalized group of small-bodied ornithischians that were ancestral to the later and more clearly defined ornithischian groups of the Late Jurassic and Cretaceous); in his comparative discussion Simmons hinted that *Tatisaurus* shared some anatomical features (presumed to be 'primitive') with armoured or ankylosaurian ornithischians. In a general review of the Ornithischia, Steel (1969) assigned *Tatisaurus* to the basal ornithischian family Heterodontosauridae on the basis of its stratigraphical age

and possession of a similarly robust dentary. Thulborn (1971, 1972) followed Simmons' original interpretation by including *Tatisaurus* within a similarly broadly conceived bipedal and cursorial Hypsilophodontidae; this referral was supported (although considered questionable) by Galton (1972) in his review of ornithopod evolution. Colbert (1981) reaffirmed its position as a hypsilophodontid ornithischian, but noted that it was poorly preserved and consequently difficult to analyse systematically. Attridge, Crompton & Jenkins (1985) resuscitated the idea that *Tatisaurus* was a heterodontosaur in a tabulation of early Jurassic taxa. Later authors have suggested alternative placements, but these have been exclusively within the dermally armoured ornithischian clade Thyreophora: Coombs, Weishampel & Witmer (1990) and Norman, Witmer & Weishampel (2004) considered *Tatisaurus* to be a basal thyreophoran; Dong (1990) proposed that *Tatisaurus* was a primitive stegosaur, referable to the family Huayangosaurinae; and Lucas (1996) synonymised *Tatisaurus* with the basal thyreophoran *Scelidosaurus* as *Scelidosaurus oehleri*.

Referral of *Tatisaurus* to the clade Stegosauria (Dong, 1990) has important implications for early thyreophoran evolution. The earliest reported stegosaur specimens are two isolated shafts of limb bones (probably femora; BRSMG Cb3869, Cb3870) described by Galton (2005). They were collected from the Westbury Formation (Late Triassic: Rhaetian) of England, but are extremely poorly preserved. Both bones lack articular ends and much of the outer bone surface is missing. The shafts are straight in lateral view, as seen in both sauropod saurischians and stegosaurs, but any trace of the fourth trochanter (assuming that these shafts represent femora) has been completely eroded. Galton proposed that the fourth trochanter was a low ridge (as in stegosaurs) rather than being more prominent (as seen in sauropods); self-evidently this character cannot be confirmed and although probably dinosaurian we cannot identify these elements beyond Reptilia indet. (see also Butler, Porro & Heckert, 2006).

Given the indeterminate nature of the Westbury Formation material, the earliest and most basal member of the clade Stegosauria currently recognized is Middle Jurassic, *Huayangosaurus taibaii*, from the Lower Shaximiao Formation (?Bajocian, Chen *et al.*, 1982; ?Bathonian–Callovian, Dong & Tang, 1984) of Sichuan Province, China (Dong, Tang & Zhou, 1982; Sereno & Dong, 1992; Maidment, Wei & Norman, 2006). It is an approximate contemporary of a more derived European form, *Lexovisaurus durobrivensis*, known from the Lower Oxford Clay (middle Callovian) of England, and the Marnes à *Belemnopsis latesulcata* Formation (early Callovian) of France (Galton, 1985, 1990).

The thyreophoran *Scelidosaurus harrisonii* Owen, 1861 from the Lower Lias (Sinemurian) of England has been variously interpreted as a primitive stegosaur (Romer, 1956), an ornithopod (Thulborn, 1977), a basal thyreophoran (Serenó, 1986), or as the most basal ankylosaur (Norman, 1984; Carpenter, 2001). Recent cladistic analyses consistently suggest that *Scelidosaurus* is a basal thyreophoran and the sister taxon to Ankylosauria + Stegosauria (Serenó, 1999; Norman *et al.*, 2004; Maidment, Wei & Norman, 2006; Butler *et al.* 2006). Nath, Yadagiri & Moitra (2002) briefly described material, which they referred to Ankylosauria, from the Kota Formation (Lower Jurassic) of India; however, they did not specify the synapomorphies that justified this referral and Ayyasami & Yadagiri (personal communication – cited in Wilson & Mohabey, 2006) indicate that these specimens represent a crocodylomorph. Pending a more detailed description of this material, we consider it as referable to Thyreophora *incertae sedis*. The earliest unambiguous members of the clade Ankylosauria are Middle Jurassic: *Sarcolestes leedsi* from the Lower Oxford Clay (middle Callovian) of England (Lydekker, 1893) and *Tianchiasaurus nedegoaperferima* from the Toutunhe Formation (Bathonian–Callovian) of China (Dong, 1993).

The earliest definite stegosaurs and ankylosaurs are either Bajocian or Bathonian in age, suggesting that the minimum date by which the two clades must have diverged is the earliest Bajocian. If *Tatisaurus* were referable to Stegosauria (as suggested by Dong, 1990), this would indicate that stegosaurs and ankylosaurs were present by the Early Jurassic (Sinemurian) and implies significant (minimum 25 million years) ghost lineages for both clades.

Lucas (1996) posited a radical reinterpretation of *Tatisaurus*; he synonymized it with the basal thyreophoran *Scelidosaurus* and created the new binomen *S. oehlerii* (Simmons, 1965) – although this taxonomic reassignment has not gained wide acceptance (e.g. Irmis, 2004; Norman *et al.*, 2004). This taxonomic reassignment allowed Lucas to propose an early Sinemurian date for the Lower Lufeng Formation because *Scelidosaurus* remains are reliably dated as early Sinemurian in England (Newman, 1968; Ensom, 1987, 1989). Padian (1989) had also described isolated dermal scutes from the Kayenta Formation (Glen Canyon Group) of Arizona, USA, which seemed comparable with those seen in the genus *Scelidosaurus* (see also Tykoski, 2005). This taxonomic adjustment, linked to its wide geographical distribution, led Lucas (1996: 84) to propose *Scelidosaurus* as an international index taxon that merited the establishment of a biostratigraphic ‘*Scelidosaurus* biochron’ for the early Sinemurian stage of the Lower Jurassic Period. The proposed synonymy of *Tatisaurus* and *Scelidosau-*

rus (if valid) has significant implications for Lower Jurassic terrestrial stratigraphic correlation.

The taxonomic status of *T. oehlerii* is reassessed below, as are the various phylogenetic positions to which it has been assigned, their implications for thyreophoran evolution, and the dating of the Lower Lufeng Formation of China.

Institutional abbreviations: BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; FMNH CUP, Field Museum of Natural History (Catholic University of Peking collection), Chicago, IL, USA; OUM, Oxford University Museum of Natural History, Oxford, UK.

SYSTEMATIC PALAEOLOGY

SYSTEMATIC HIERARCHY

ORNITHISCHIA SEELEY, 1887

THYREOPHORA NOPCSA, 1915 (*SENSU* NORMAN, 1984)

GENUS *TATISAURUS* SIMMONS, 1965

SPECIES *T. OEHLERII* SIMMONS, 1965 (*NOMEN DUBIUM*)

Synonymy: *T. oehlerii* Simmons (1965): 65; *S. oehlerii* Lucas, 1996: 82.

Holotype: FMNH CUP 2088. Partial left dentary, with fragments of the quadrate and surangular-articular adhering to its medial surface.

Description: The holotype of *T. oehlerii* Simmons, 1965 (Fig. 1) comprises a partial (relatively small) left lower jaw measuring just less than 60 mm in length. Fragments of a broken quadrate and of two postdentary bones: the surangular (sa) and what appears to be a portion of the articular (ar) are preserved and firmly attached to the medial surface of the dentary (Fig. 1A). Previous descriptions (Simmons, 1965: fig. 11; Dong, 1990: fig. 19.2; Lucas, 1996: figs 1–3) have identified many of the salient features of the holotype but have been at variance with respect to the identity of the attached bones. Dong, for example, concluded that the bone was a quadratojugal, whereas Simmons and Lucas interpreted it as a rib fragment.

Dentary: Figure 1 illustrates, in lateral and medial views, the holotype specimen. The dentary ramus is transversely thick and deep posteriorly at the point where its surface is abruptly truncated. The anterior one third of the dorsal edge of the dentary ramus slopes quite markedly toward the symphyseal region; the external (buccal) surface of the ramus has a pronounced, but diminishing, longitudinal bulge that would have formed a ledge, flooring a buccal (cheek) recess, with the posterior cheek teeth positioned along the medial edge of the dentary. At its midpoint along the length of the jaw the dentary ramus appears to be distorted by crushing (many minor fractures and evidence of post-mortem crushing are visible). Toward the symphysis, as the dentary continues to taper, the

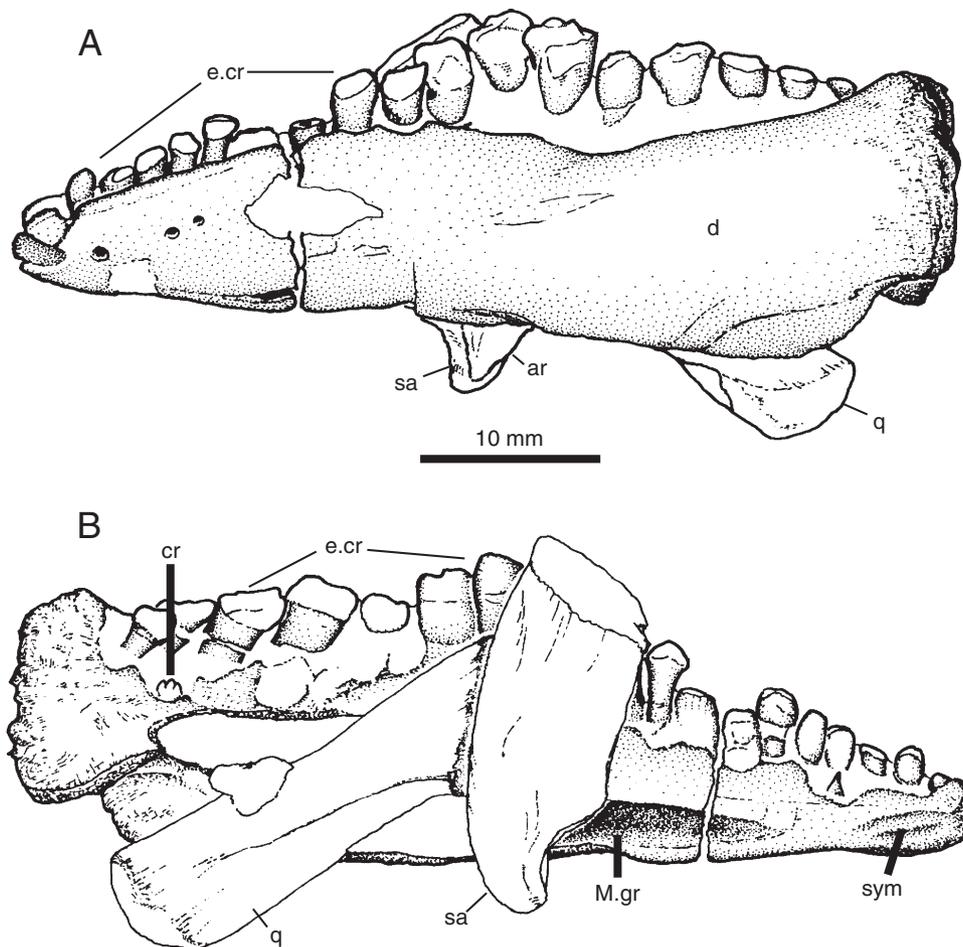


Figure 1. *Tatisaurus oehleri* Simmons, 1965. Holotype, FMNH CUP 2088. A, Lower jaw in lateral view. All the tooth crowns are heavily eroded and the jaw itself is poorly preserved. B, FMNH CUP 2088. Lower jaw in medial view; fragments of postdentary bones and a ?quadrate are firmly attached. Abbreviations: ar, articular/prearticular splint; cr, tip of crown of replacement tooth showing denticulate margin; d, dentary; e.cr, eroded crowns of functional teeth; M.gr, Meckel's groove; q, quadrate; sa, surangular; sym, dentary symphysis. The adherent bones are untextured, as is the matrix that surrounds the tooth roots and fills the alveoli.

ramus becomes generally narrower and develops a slight lateral overhang as the lower edge of the dentary twists medially toward its neighbour. The external surface of the ramus is marked by several foramina but, in general, the surface of the dentary is not well preserved and shows few of these more minor anatomical details.

Medially the dentary is partially obscured by the overlying bones (Fig. 1B) and, contrary to the description of Simmons, there is no indication of a splenial bone (which also appears to be the situation as illustrated by Simmons 1965: fig. 11B). A deeply incised Meckelian groove is clearly present (again contradicting Simmons' original description) and extends almost to the dentary symphysis, but is obscured by a combination of the overlying bones and infilling matrix more posteriorly. The dentary symphysis, which is only sep-

arated by a short section of dentary ramus from Meckel's groove, is marked by horizontal ridges and grooves, and, in the adjacent area near the tip of the jaw and in advance of the first alveolus, there is very little evidence for, or indeed room for, an ornithischian predentary [a broadly similar configuration is also found in the basal thyreophoran *Scelidosaurus* (D. B. Norman, pers. observ.) and in *Emausaurus* (SCRM & RJB, pers. observ.)]. The ventral edge of the dentary is twisted medially in the proximity of the symphysis, creating a very slightly spout-shaped region to the dentary adjacent to the symphyseal region, as observed in ornithischians generally. The lingual wall of the dentary above the Meckelian groove slopes buccally (dorsolaterally) toward the base of the alveolar trough. There is no evidence of an alveolar parapet that supported the lower and medial portions of the

dentition (Fig. 2B), but this specimen is poorly preserved and this part of the jaw may easily have been either removed accidentally or eroded away post-mortem. The posterior part of the dentary is clearly thick and deep, and hints at the presence of an at least modest coronoid eminence, but there is no clear evidence of sutures for the attachment of the postdentary bones.

Dorsally the relative transverse thickness of the dentary is evident at its posterior end and a pronounced cheek recess is clearly shown. The anterior tapering of the dentary might be expected to be accompanied by a degree of sinuosity of the dentition; however, the teeth appear to be arranged in a more or less linear pattern, but this may also be a post-mortem artefact as the alveolae themselves do seem to indicate some degree of medial curvature as the symphysis is approached.

Dentition: The dentition of *Tatisaurus* has been described in some detail by both Simmons (1965) and Lucas (1996); however, it must be emphasized that the dentition, as preserved, is heavily eroded and almost completely lacking in detail. The alveolar count of 18

is confirmed, as is the general cadence in tooth size: smaller anteriorly, increasing in size posteriorly before decreasing again in size at the extreme posterior end of the series. The teeth have subcylindrical roots that clearly expand (mesio-distally) into the base of the crown; it is clear from the close packing of the roots of the teeth that the crowns would have been arranged in an overlapping 'en echelon' pattern as reported by Simmons. The crowns themselves are heavily eroded and their structure and pattern of wear are not discernible (despite the description provided by both Simmons and Lucas). A single replacement crown tip is visible on the medial surface of alveolus 17 and reveals the presence of coarse denticulations along the mesio-distal margin of the crown; a fragment of replacement crown is present medially in alveolus 1, and a splinter of enamel lies medial to the root of the tooth in alveolus 4 (and might therefore represent the position of the replacement crown). A considerable amount of matrix is still present in the alveoli and around the bases of the much-eroded functional teeth, so the specimen might benefit from either further skilled preparation or non-invasive (computerized tomography, CT) scanning.

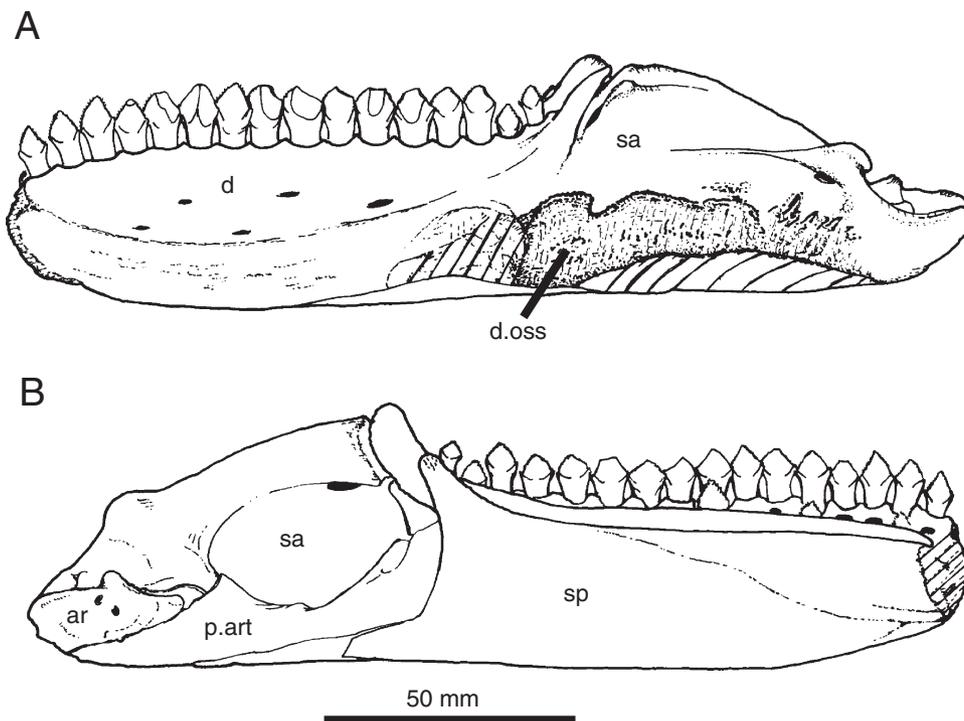


Figure 2. *Scelidosaurus harrisonii* Owen, 1861. Lectotype BMNH R.1111. A, Left lower jaw in lateral view. Distal tip of the dentary was lost during excavation of the original specimen. Parts of the lower surface of the postdentary bones have been chiselled off (probably also during original excavation in the late 1850s). B, BMNH R.1111. Left lower jaw in medial view. Abbreviations: ar, articular; d, dentary; d.oss, dermal ossification; p.art, prearticular; sa, surangular; sp, splenial. Cross-hatching indicates cut/broken surfaces.

Additional bony elements: The bones attached to the medial surface of the dentary are poorly preserved and their identification is necessarily tentative. There appear to be two bones: one oblique and somewhat slender, which is crushed up against a vertically orientated somewhat more 'blocky' element. The former element has a slightly convex distal articular surface and a rounded shaft that has a sinuous ridge and is tentatively identified as a partial quadrate (Fig. 1, q). The latter element (Fig. 1, sa) resembles that of an ornithischian surangular in some respects: notably the lipped concave facet, which may well represent the lateral portion of the jaw articulation. The medial side of this element (visible when the jaw is viewed laterally) seems to show the presence of a small posterior portion of the articular or splint of prearticular (Fig. 1, ar). It should be noted that there is no evidence of external foramina (which might be expected to be visible adjacent to the glenoidal part of the surangular), and the cross section in the region of fracture (dorsally) does not appear to show a hollowed interior as might be expected.

COMPARATIVE OBSERVATIONS

Lucas (1996: 32) claimed that '*Tatisaurus* shows remarkable similarities to *Scelidosaurus* in the structure of the dentary and lower dentition'. The basis for this claim is that the teeth of *Scelidosaurus* show a similar gradient of size along the length of the jaw, and that '...the tooth shapes of the two taxa are essentially identical as are their thick, robust dentaries'. The dentary and dentition of the lectotype of *S. harrisoni* BMNH R.1111 (Fig. 2; D. B. Norman, pers. observ.) cannot be compared in detail with those of *Tatisaurus* because of the extremely poor preservation of the latter (Fig. 1). The dentary of *Scelidosaurus* is considerably more robust and deeper along most of its length than that of *Tatisaurus*, and the ramus does not slope toward the symphyseal region from its mid-point in similar fashion; there is a pronounced cheek recess in *Scelidosaurus* that is bounded ventrally by a distinct ridge (Fig. 2) that follows a concave upward course along the lateral surface of the body of the dentary. There is a gradient in size along the dentition of *Scelidosaurus*, but the size difference is far more modest than that seen in *Tatisaurus*, and the gradient in size in dentary teeth, with the largest representatives occurring in the region of the rear third of the dentition, is plesiomorphic for Ornithischia (Serenó, 1991, 1999). The medial surface of the dentary of *Scelidosaurus* is covered by a deep sheet of bone formed by the splenial, and the medial wall of the alveoli adjacent to roots and replacement crowns is formed of a shallow alveolar parapet and a long splint-like coronoid bone; *Scelidosaurus* shows that Meckel's groove

extends anteriorly as far as the dentary symphysis (Fig. 2B). The dentition of *Scelidosaurus* has been illustrated, in part, by Barrett (2001), and it is clear that although in overall terms the dentition of *Tatisaurus* exhibits some of the features common to all basal ornithischians no details of its anatomy permit a closer affinity to be drawn, and certainly not specifically with *Scelidosaurus*.

Given the absence of genuine synapomorphies and comparative detail in the taxonomic revision proposed by Lucas (1996), there was no legitimate basis for reassigning *Tatisaurus* to the genus *Scelidosaurus*. It is also evident that, notwithstanding the poor preservation of the holotype of *Tatisaurus*, there are very few features that allow *Tatisaurus* to be diagnosed as anything more than a basal, possibly thyreophoran, ornithischian.

PHYLOGENETIC REASSESSMENT OF *TATISAURUS*

PHYLOGENETIC POSITION OF *T. OEHLERI*

Available material of *Tatisaurus* is fragmentary and poorly preserved, thereby limiting discussion of its phylogenetic position. That *Tatisaurus* is an ornithischian is confirmed by two characters: a spout-shaped symphyseal region and overlapping tooth crowns that increase in size towards the posterior of the row (Serenó, 1999; Butler, 2005; Butler *et al.* 2006). However, these characters are plesiomorphic for Ornithischia, and cannot be used to position *Tatisaurus* in a less inclusive clade within Ornithischia.

Only one unambiguous character supports referral of *Tatisaurus* to Thyreophora: the ventral deflection of the mesial end of the dentary tooth row (character 4 of Serenó, 1999: dataset 2; character 16 of Norman *et al.*, 2004; character 36 of Butler, 2005; character 104 of Butler *et al.* 2006; see also Coombs *et al.* 1990). The derived state of this character is absent in basal ornithischians (e.g. *Lesothosaurus*, Serenó, 1991), but is present in the thyreophorans *Scutellosaurus* (MNA P1.175; RJB & SCRM, pers. observ.), *Emausaurus* (Haubold, 1990: fig. 2), *Scelidosaurus* (Fig. 2), stegosaurs (e.g. Galton & Upchurch, 2004), and ankylosaurs (e.g. Vickaryous, Maryánska & Weishampel, 2004). Within Thyreophora, the dentary of *Tatisaurus* is more robust than that of *Scutellosaurus* and has a well-developed, posterior buccal emargination (weakly developed in *Scutellosaurus*, basal ornithischians, and ornithischian outgroups); however, a robust dentary and a well-developed buccal emargination also occurs in many neornithischians. These characters provide some evidence to suggest that *Tatisaurus* is more derived within Thyreophora than *Scutellosaurus*. There is little evidence to indicate a more accurate

phylogenetic position, and no evidence to suggest that *Tatisaurus* is either an early stegosaur, as first suggested by Dong (1990) and discussed further below, or that it shares affinities with more derived ankylosaurs as discussed by Simmons (1965).

IS THE HOLOTYPE OF *TATISAURUS* DIAGNOSABLE?

Despite being based upon extremely fragmentary material, recent reviews (Coombs *et al.*, 1990; Norman *et al.*, 2004) have retained *T. oehleri* as a valid taxon. Simmons (1965) provided the only diagnosis of this taxon to date, based upon the following characters: (1) small size; (2) mandible low anteriorly, slender and tapered; (3) anterior ventral border bends medially toward the symphysis; (4) jaw higher and more convex posteriorly; (5) teeth thecodont, overlapping, relatively simple and increasing in size from front to rear; (6) dentary–pre-dentary junction edentulous.

Characters 1, 3, 4, 5, and 6 represent ornithischian plesiomorphies (Serenó, 1986, 1991, 1999; Butler *et al.* 2006), whereas character 2 is widespread within thyreophorans and has been used to support referral of *Tatisaurus* to this clade (see above). None of these characters are apomorphic for *Tatisaurus*. The fragmentary nature of the holotype specimen prevents the identification of apomorphies and, as it is additionally not possible to develop a differential diagnosis for the genus, we therefore consider *Tatisaurus* a *nomen dubium*.

IS *TATISAURUS* A STEGOSAUR?

Dong (1990) suggested that *Tatisaurus* is a primitive member of the clade Stegosauria, and referred it to the family Huayangosaurinae. He did not provide explicit synapomorphies as a basis for this assignment, but suggested that the general features of the teeth were ‘similar’ in *Tatisaurus* and *Huayangosaurus*. As discussed above, the general morphology of the dentary teeth of *Tatisaurus* is not known (despite statements to the contrary): only the most general of features are apparent and these are widespread within basal ornithischians. Any supposed similarity between the teeth of *Tatisaurus* and *Huayangosaurus* would, at best, be the result of retained plesiomorphies, rather than shared derived characters. Some features can be identified that distinguish *Tatisaurus* and *Huayangosaurus*: the ventral margin of the mesial end of the dentary is inturned to a much greater degree in *Huayangosaurus* (Serenó & Dong, 1992: fig. 5D) than in *Tatisaurus*; the pre-dentary of *Huayangosaurus* has a narrow and elongate ventral process, whereas there is little evidence for the presence of a pre-dentary with an extensive ventral process in *Tatisaurus* (see above); and the dentary tooth count is considerably higher in

Huayangosaurus than in *Tatisaurus*. No synapomorphies can be identified that unite *Tatisaurus* with either *Huayangosaurus* or other stegosaurs, to the exclusion of other ornithischians. We therefore consider that the assignment of *Tatisaurus* to Stegosauria (Dong, 1990) is unsupported.

DISCUSSION

Tatisaurus cannot be referred to Stegosauria (*contra* Dong, 1990). As a result, the earliest known stegosaur remains are from the Middle Jurassic (either Bajocian or earliest Bathonian), and are approximately contemporaneous with the earliest definite ankylosaurs. This implies a minimum divergence date for Stegosauria and Ankylosauria of earliest Bajocian. However, if either *Scelidosaurus* or the thyreophoran material described by Nath *et al.* (2002) prove to be referable to the clade Ankylosauria, ghost lineages would imply the existence of stegosaurs in the early Sinemurian.

Cox (1974) noted that Late Triassic and Early Jurassic faunas were relatively uniform, with few differences between taxa occupying different continental areas, and that subsequent Mesozoic dinosaur evolution was dominated by the increasingly provincial faunas. Serenó (1999) noted that although Late Triassic and Jurassic genera might be expected, on purely palaeogeographical grounds, to have more widespread distributions than Cretaceous genera, this did not appear to be the case, with dinosaur genera being only rarely recorded beyond a single geographical region; this may, however, simply represent a taxonomic artefact, the coelophysoid genus *Megapnosaurus* (= *Syntarsus*) has been reported from the Lower Lufeng (Irmis, 2004), southern Africa (Raath, 1969, 1980), North America (Rowe, 1989), and Europe (Rauhut & Hungerbühler, 1998; although Irmis, 2004 considered this referral doubtful); similarly, the prosauropod genus *Massospondylus* has been reported from southern Africa (Cooper, 1981), North America (Attridge *et al.*, 1985), and Argentina (Martinez, 1999). If *Scelidosaurus* and *Tatisaurus* were synonymous, as proposed by Lucas (1996), this would compound the view of widespread early dinosaur genera and might support hypotheses concerning dinosaurian biogeography and faunal exchange.

Scelidosaurus and *Tatisaurus* are not synonyms. *Scelidosaurus* can only be recognized with certainty from the Lower Jurassic of England, and reports of this genus from the Kayenta Formation of Arizona (Padian, 1989; Tykoski, 2005) are based on isolated thyreophoran scutes that, although suggestive, cannot be confirmed until further diagnostic material emerges. Contrary to the views of Lucas (1996), although the Lower Lufeng Formation may well be of earliest Jurassic age *Tatisaurus* cannot be used

to support a Sinemurian age; similarly the proposal for a 'Scelidosaurus biochron' is untenable because unequivocal *Scelidosaurus* remains are recognized only from England. Index fossils for use in biostratigraphic correlation must be diagnosable, temporally restricted, abundant, and widespread (e.g. Holland, Audley-Charles & Bassett, 1978; Rawson, 2001; Rayfield *et al.*, 2005). *Scelidosaurus*, although being diagnosable and temporally restricted in England, is currently neither common nor widespread at a global level, and thus completely unsuitable for the purposes of biostratigraphic correlation.

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