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Stegosauria: a historical review of the body fossil record and phylogenetic relationships

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Abstract The first partial skeleton of a stegosaurian dinosaur was discovered in a brick pit in Swindon, UK in 1874. Since then, numerous stegosaurian remains have been discovered from Europe, North America, Africa and Asia, and continue to be discovered regularly. Stegosaurs are known from the Middle Jurassic to the Early Cretaceous; no definitive evidence of the clade is known from younger deposits. New discoveries are improving our understanding of stegosaur biology and showing that stegosaurs were more morphologically diverse than was previously realized. A new phylogeny, which includes all valid stegosaurian taxa, largely agrees with previous studies and shows the European Dacentrurinae was sister taxon to *Stegosaurus*. Poor resolution at the base of Stegosauria is probably due to the fragmentary nature of many of the Chinese taxa.

Keywords Dinosauria · Ornithischia · Stegosauria · Phylogeny

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Institutional abbreviations

CAMSM	The Sedgwick Museum, University of Cambridge, UK
CV	Chongqing Museum of Natural History, P. R. China
HMNH	Hayashibara Museum of Natural History, Okayama, Japan
IGB	Institute of Geology, National Academy of Sciences of Kyrgyz Republic, Biskek, Kyrgyzstan
IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, P. R. China
LHNB(CN)	Laboratório de História Natural da Batalha, Portugal
MHBR	Muséum d'Histoire Naturelle du Havre, Brun Collection, Le Havre, France
ML	Museum of Lourinhã, Portugal
NHMUK	The Natural History Museum, London, UK
OUMNH	Oxford University Museum of Natural History, UK
SGP	Sino-German Project, material currently housed in Museum of Palaeontology, Tübingen, Germany
SMA	Sauriermuseum, Aathal, Switzerland
TuvIKOPR	Tuvinian Institute of Complex Development of Natural Resources, Siberian branch of the Russian Academy of Sciences, Kyzyl, Russia
USNM	United States National Museum, Washington DC, USA
YORYM	Yorkshire Museum, UK
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA
ZDM	Zigong Dinosaur Museum, Sichuan, P. R. China

Introduction

Stegosauria is a clade of ornithischian armoured dinosaurs characterised by the presence of two rows of dorsally projecting dermal plates and spines that extended from the neck to the end of the tail. First discovered in Europe and North America in the latter part of the nineteenth century (e.g. Owen 1875; Marsh 1877), stegosaurs have achieved an iconic status and these quadrupedal, herbivorous dinosaurs are instantly recognisable to specialists and non-specialists alike.

Stegosaurs are known from all continents except South America, Australia and Antarctica (Galton and Upchurch 2004). The first stegosaurs are known from the Middle Jurassic of Europe and China [*Loricatosaurus priscus*: Middle Callovian Lower Oxford Clay, Cambridgeshire, UK, and Early Callovian Marnes à *Belemnopsis latesulcata* Formation, Calvados, France; *Huayangosaurus taibaii*: Bathonian–Callovian Lower Shaximiao Formation, Sichuan Province, China (Weishampel et al. 2004)] but they radiated during the Late Jurassic when they were an important component of the terrestrial fauna globally (Galton and Upchurch 2004). Stegosaurian diversity appears to have decreased after the Jurassic, and only a few, poorly preserved Early Cretaceous specimens are known [*'Craterosaurus pottonensis'*: Early Cretaceous Potton Sands, Bedfordshire, UK; *Stegosaurus homheni*: Valanginian–Albian Tugulu Group, Xinjiang, China (Weishampel et al. 2004)]. They appear to have been extinct by the Middle Cretaceous.

Despite their longevity and the fact that they were geographically widespread, little is known about the biology of these animals, and few well-preserved specimens have been found (Galton and Upchurch 2004). The aim of this paper is to give a historical review of the known stegosaurian body fossil record and present the most up-to-date phylogenetic analysis of the clade.

Historical review of the stegosaurian body fossil record

Stegosaurs from North America

In 1877, O. C. Marsh announced the discovery of a new 'order' of dinosaurs, which he named Stegosauria. The type specimen (YPM 1850) was named *Stegosaurus armatus*, and was discovered from the Late Jurassic Morrison Formation at Quarry 5, Morrison, Colorado (Ostrom and McIntosh 1999). In 1878, E. D. Cope described a new dinosaur from Colorado, noting that its neural arches were greatly elevated, but that it had a femur and teeth very similar to those of *Megalosaurus*, and so was probably closely related to the latter. He named his new dinosaur *Hypsirophus discursus*. The specimen is a composite of stegosaurian vertebrae and theropod limb bones and teeth. Cope (1879) named a new species of *Hypsirophus, H. seeleyanus* in a short note. Neither specimen was ever illustrated or fully described by Cope, but *H. discursus* was figured by Carpenter (1998a) who considered it a valid species, and Maidment et al. (2008), who considered it a junior synonym of *Stegosaurus armatus*. Marsh named *Stegosaurus ungulatus* two years after the initial note of the discovery of the 'order' (Marsh 1879). He outlined few details about its anatomy and never explained why the new specimen was given a new species name. *Stegosaurus ungulatus* was based on two specimens from the Morrison Formation (YPM 1853 and 1858) that Marsh later designated as cotypes (Gilmore 1914), one of which was found in Reed's Quarry 11, and one in Reed's Quarry 12, Como Bluff, near Como Station, Wyoming (Ostrom and McIntosh 1999). In 1880, Marsh published more details of Stegosauria. The description of the postcrania must have been based on *S. ungulatus* rather than the type specimen, *S. armatus*, since the type specimen (YPM 1850) is fragmentary (Carpenter and Galton 2001; Galton 2010). Several postcranial bones were figured for the first time, all belonging to *S. ungulatus*. A maxilla and teeth were also figured and these were the original teeth described as part of the holotype of *S. armatus*. It is clear that these teeth are referable to a sauropod, but in 1880 Marsh still considered them to belong to a stegosaur. He corrected himself in 1883, when he referred them to *Diplodocus*. Marsh (1880) created the 'family' name Stegosauridae, to which he referred *Stegosaurus* and the European genus *Omosaurus*. Marsh continued to publish prolifically on *Stegosaurus.* In 1881(a) he described further details of the anatomy of *S. ungulatus* and in the same paper noted that a new, smaller species, which he named *S. affinis*, had been found in Reed's Quarry 13, Como Bluff, Wyoming (Ostrom and McIntosh 1999). Also in 1881(b), Marsh named a new species of dinosaur, *Diracodon laticeps* (YPM 1885), found in Reed's Quarry 13, Como Bluff, Wyoming (Ostrom and McIntosh 1999). The new species was based upon a pair of maxillae with teeth, and while Marsh noted the similarity of the teeth with those of *Echinodon*, he still believed that the *Diplodocus* maxilla found with *S. armatus* was part of the stegosaurian skeleton, and so failed to recognise that *D. laticeps* shared close affinities with the stegosaurs (Marsh 1881b). Having amassed a significant amount of material, Marsh attempted to classify the dinosaurs of North America and of the world (Marsh 1882). In Stegosauridae, Marsh now recognised three genera: *Stegosaurus*, *Diracodon,* and *Omosaurus*. He considered Cope's genus *Hypsirophus* to be a junior synonym of *Stegosaurus,* and also now recognised that *Diracodon* bore teeth similar to those of *Stegosaurus* (Marsh 1882), although no explanation for this reassignment was given. *Stegosaurus stenops* (USNM 4934) was named by Marsh (1887) for a new, small, and in Marsh's opinion, distinct, species of *Stegosaurus*. The specimen (USNM 4934), from Felch's Quarry 1, Garden Park, Colorado (Ostrom and McIntosh 1999) was nearly complete, with dermal armour in place, allowing Marsh to comment more fully on the armour of the genus. It is in this paper that Marsh first stated that *S. ungulatus* bore four pairs of spines on its tail—a myth that was to confuse the taxonomy of the genus until it was proven false by Carpenter and Galton (2001). Marsh also informally named another new species, *S. sulcatus,* found in Reed's Quarry 13, Como Bluff, Wyoming (Ostrom and McIntosh 1999). Marsh (1887) created another species, *Stegosaurus duplex* (YPM 1853). The holotype of *S. duplex* was originally one of the cotypes of *S. ungulatus*, but was removed by Marsh (1887) to a new species because of differences in the articulation of the sacral ribs to the sacral vertebrae. However, as noted by Lull (1910a), no sacrum is preserved in YPM 1853, so the contrast made was based on an individual (YPM 1857) apparently arbitrarily referred to *S. duplex*. The first restoration of *Stegosaurus* was published by Marsh (1891) three years after the quarries at Como Bluff were closed. Despite having more than 20 partial skeletons of *Stegosaurus*, the exact way in which the plates were held on the back of the genus was unknown. Marsh, in his reconstruction, showed one row of plates extending down the back, with four pairs of caudal spines on the distal part of the tail. He also noted that there was a pair of small plates in the cervical region directly behind the skull.

Over the following century, much of the work carried out on *Stegosaurus* focused on the arrangement of its dermal armour, and Marsh's reconstruction resulted in a series of exchanges between Lucas (1910), Lull (1910a, b) and Gilmore (1912, 1914, 1915a, b), with Lucas and Gilmore arguing for two rows of plates in an alternating arrangement, while Lull maintained that the plates were arranged in pairs. Gilmore's (1914) monograph on *Stegosaurus*, based largely on USNM 4934 (*S. stenops*), remains the most detailed and complete description of *Stegosaurus,* and in it he named a new species, *S. longispinus*. The question of plate arrangement seemed to have been answered by this paper, with Gilmore providing evidence that in USNM 4934 the plates had been found more or less in life position, and it could clearly be seen that they alternated. Despite this clear evidence, the argument was to resurface in the 1980s–1990s until new specimens proved Gilmore's original evidence correct (Czerkas 1987; Bilbey and Hamblin 1992; Carpenter and Small 1993; Carpenter 1998b).

After Gilmore's (1914) monograph, little further was published on North American stegosaurs until the 1970s, when focus began to shift to the function of the plates of *Stegosaurus*. While Gilmore (1914) had suggested that the plates were used to ward off predators by making the animal look larger and well defended, Farlow et al. (1976) suggested that the plates had a primarily thermoregulatory function. Spassov (1982) noted that while this may have been the case for *Stegosaurus*, it could not have been the reason the plates originally evolved since other members of the group possessed simple spines, and not broad, plate-like structures, and he instead suggested that they acted as lateral display structures for intraspecific recognition. Buffrénil et al. (1986) investigated plate histology and related it to function. They showed that the plates were held vertically on the back, refuting the beliefs of some workers who suggested a recumbent position for the plates (see discussion in Buffrénil et al. 1986). They also suggested that the plates were too weak and lightly built to have been used defensively, and that the thermoregulatory model seemed to fit with evidence from bone histology. Carpenter (1998b) again raised Spassov's (1982) original objections, noting that other stegosaurs lived in similar environments and were similar sizes, but did not possess plates. Instead, he suggested that the plates were probably used for lateral display, and that the vascularisation of the plates may have allowed the animal to pump blood into them, allowing them to 'blush'. McWhinney et al. (1998, 2001) studied a stegosaurian tail spine that had been damaged in life, and proposed that it showed evidence of post-traumatic osteomyelitis, suggesting that tail spines were used as active defence structures. This was later confirmed when function of stegosaurian tail spikes was modelled, and this work showed that they were capable of being swung from side to side to inflict damage on predators (Sanders et al. 2002). Carpenter et al. (2005) presented an *Allosaurus* vertebra apparently pierced by a *Stegosaurus* tail spine: further evidence that stegosaurs used their fearsome caudal armour not just for display.

During the 1980s and 1990s, new *Stegosaurus* specimens began to come to light. Galton (1982b) described juveniles from Como Bluff, Wyoming, and Dinosaur National Monument, Utah, whilst Berman and McIntosh (1986) described a lower jaw of *Stegosaurus* among material collected by the Carnegie Museum in the 1920s. Bilbey and Hamblin (1992), Carpenter and Small (1993) and Carpenter (1998b) reported the finding of two new specimens, one from Utah, and one from Colorado; both supported the alternating plate arrangement of Gilmore (1914), and refuting the newly proposed single row model of Czerkas (1987). Carpenter et al. (2001) described a new genus of stegosaurian dinosaur from the Morrison Formation of Wyoming, and named it *Hesperosaurus mjosi*. The type specimen (HMNH 001) comprises a skull and axial skeleton. Carpenter et al. (2001) considered the specimen to represent a primitive stegosaur, closely related to *Dacentrurus armatus* from the Late Jurassic of England.

Maidment et al. (2008) reviewed the known *Stegosaurus* material and concluded that all of the differences between specimens could be accounted for by intraspecific variation. All specimens previously described as *Stegosaurus* were therefore either referred to *Stegosaurus armatus* or considered to be indeterminate. *Hesperosaurus* was considered by Maidment et al. (2008) to be synonymous with *Stegosaurus*, but was recognised as a distinct species, renamed *Stegosaurus mjosi*.

Stegosaurs from Europe

Regnosaurus northamptoni is a small portion of a dentary (NHMUK 2422) from the Berriasian–Valanginian Hastings beds (lower Wealden Group; Weishampel et al. 2004) of Sussex, UK, that has undergone numerous referrals since its original description by Mantell in 1848. It has been referred to *Hylaeosaurus* (Owen 1842), *Vectisaurus* (Lydekker 1888) and *Chondrosteosaurus* (McIntosh 1990). Barrett and Upchurch (1995) regarded NHMUK 2422 as an indeterminate stegosaur because of its apparent similarity to the lower jaw of the Chinese taxon *Huayangosaurus* (see below). Maidment et al. (2008), however, could identify no stegosaurian synapomorphies and considered it Thyreophora indet.

Craterosaurus pottonensis (CAMSM B.28814) was the first definitive stegosaurian dinosaur described anywhere in the world. From the Aptian–Early Albian Potton Sands of Bedfordshire, UK, and thought to have been reworked from Early Cretaceous deposits (Weishampel et al. 2004), it was originally described by Seeley (1874) as a partial skull. Nopcsa (1912) correctly identified it as the neural arch of a dorsal vertebra and Galton (1981a) referred it to Stegosauria based upon the elongation of the neural arch above the neural canal, considering it to be a valid taxon. However, Maidment et al. (2008) could not identify any autapomorphies.

In the same year as the original description of *Craterosaurus*, a partial postcranial skeleton of a new dinosaur was discovered in Swindon Great Quarry, a brick pit near Swindon, Wiltshire, UK. The bones were found in the Late Jurassic Kimmeridge Clay (Davis 1876). Owen described and figured the remains in his 'Monograph on the fossil reptilia of the Mesozoic formations' in 1875 (Owen 1875; Galton 1985). He called the new dinosaur *Omosaurus armatus* (NHMUK 46013). Ten years later, Hulke (1887) reported on a new stegosaur, *Omosaurus durobrivensis* (NHMUK R1989), in the collections of A. N. Leeds, a prolific collector of fossil reptile material from the Callovian Oxford Clay. Dermal plates described by Hulke (1887) were re-identified as belonging to the skull of the fish *Leedsichthys problematicus* by Woodward (1889), and dermal elements of this stegosaur would continue to be confused with the bones of *Leedsichthys* for some time. A large number of other fragmentary remains ascribed to various stegosaur genera were found or identified in existing collections in the UK periodically during the early decades of the twentieth century (Huene 1901, 1910; Nopcsa 1911a; Nopcsa 1912; Reynolds 1939). In 1902, Lucas noted that the name *Omosaurus* was occupied, and he introduced the new generic name *Dacentrurus* for the British material. However, few workers seemed aware of the changes proposed by Lucas, and the generic name *Omosaurus* continued to be used by some until the middle of the twentieth century.

The first stegosaurian specimen to be discovered in France was a partial skeleton from the Early Kimmeridgian of Octeville, Cap de La Hève, Normandy. It was excavated in 1899 and described by Nopcsa (1911b) as a new species of *Omosaurus, O. lennieri* (Galton 1991). Since this skeleton was destroyed during bombing in the Second World War, it is fortunate that it was well illustrated by Nopcsa (1911b) and Galton (1991, figs. 1–4C–E).

Numerous dinosaurian remains were discovered in Portugal during the 1940s (Zbyszewski 1946; Lapparent and Zbyszewski 1957). The bones were found at several locations, and represented fragmentary and disarticulated remains. Lapparent and Zbyszewski (1957) referred the remains to either *Omosaurus armatus* or *Omosaurus lennieri* based on the size of the bones (Galton 1991, figs. 4, 5, 8; pls. 1–3).

Hoffstetter (1957) reported on the discovery of a partial postcranial skeleton (MHBR 001) of a stegosaurian dinosaur from the Middle Callovian of Argences, Normandy and also reviewed the known stegosaurian material. He recognised that a large amount of material from the Callovian Lower Oxford Clay was distinct from both *Stegosaurus* and *Omosaurus* and more similar to the African genus *Kentrosaurus* than to any other known stegosaur remains. He therefore created a new genus, *Lexovisaurus* for *Omosaurus durobrivensis* Hulke 1887, the type specimen of which is NHMUK R1989. To this new genus, Hoffstetter referred *Stegosaurus priscus* (NHMUK R3167), and the newly discovered Argences specimen (MHBR 001), as well as the fragmentary material from Fletton, near Peterborough, UK.

During the 1980s, a complete review of all European stegosaur material then known was undertaken by Galton and Boiné (1980), Galton et al. (1980), Galton (1981a, b, 1983, 1985, 1990, 1991), and Galton and Powell (1983). Galton et al. (1980) redescribed and figured for the first time the material named by Hoffstetter (1957) as *Lexovisaurus durobrivensis*, which they agreed represented a valid genus. Galton and Powell (1983) suggested that a partial femur described as *Omosaurus vetustus* (Huene 1910) should be maintained as the holotype of a distinct species of *Lexovisaurus, L. vetustus*, because it represented the earliest record of stegosaurian remains from Europe.

Other material from the Bathonian, including plates found at New Park Quarry (Reynolds 1939) and a dorsal vertebra (OUMNH J.29770) and a cervical centrum (OUMNH J.29827) found in the 1900s in the Sharp's Hill Formation of Oxfordshire, were also referred to *L. vetustus* based upon their age. Galton (1985) proposed that *D. armatus* was the only valid species of *Dacentrurus,* and referred all known *Dacentrurus* and *Omosaurus* material from Europe to this species, with the sole exception of YORYM 498, *D. phillipsi,* which was considered a *nomen dubium*. Galton (1985) referred much of the material from the Oxford Clay of Fletton to *Lexovisaurus,* following Hoffstetter (1957), although it was noted that elements in the Woodwardian Museum, Cambridge, described as the dermal armour of *Omosaurus* by Huene (1901), were actually elements from the fish *Leedsichthys*, and Galton (1985) described them as gill rakers, but they are far too large, and are probably dorsal fin spines (J. Liston, pers. comm.).

In 1995, the first stegosaurian dinosaur material from Spain was reported by Casanovas-Cladellas et al. (1995a, b, c, 1999). Fragmentary material assigned to *Dacentrurus* was originally reported to have been found in the Arenas y Arcillas del Collado Formation and was described from two localities (Casanovas-Cladellas et al. 1995c, pls. 1–3). It was later reported that the material was actually from the Villar del Arzobispo Formation (Tithonian–Berriasian in age; Casanovas-Cladellas et al. 1999; Luque et al. 2005).

Escaso et al. (2007) reported on the remarkable discovery of a specimen (LHNB(CN)1) bearing *Stegosaurus* synapomorphies from the Late Jurassic of Portugal. The material was referred to *Stegosaurus* cf. *ungulatus,* and represents the first reported occurrence of *Stegosaurus* outside of North America.

In the first complete cladistic review of known stegosaurian material, Maidment et al. (2008) recognised only those taxa that could be diagnosed based on autapomorphies or unique character combinations. *Dacentrurus armatus* was considered a valid taxon based on the holotype specimen NHMUK 46013, but all other material previously referred to that taxon from the UK was considered indeterminate. Portuguese and Spanish material previously referred to *Dacentrurus* was considered to be referable to that genus, although small differences between the Iberian material and the British material indicated that it may be a different species. A species name was not given, however, because of the fragmentary nature of the material. *Lexovisaurus durobrivensis* and *L. vetustus* were both considered *nomina dubia* by Maidment et al. (2008), being based on indeterminate material. NHMUK R3167, the holotype of '*Stegosaurus priscus*' did bear autapomorphies, however, and this was made the type species of a new genus, *Loricatosaurus* Maidment, Norman, Barrett and Upchurch 2008. The specimen from Argences (MHBR 001) was referred to *Loricatosaurus*, while all other British material was considered indeterminate.

A further discovery from the Late Jurassic of Portugal was another new stegosaur, *Miragaia longicollum* (ML 433; Mateus et al. 2009). Closely related to *Dacentrurus armatus*, the species has 17 cervical vertebrae, more than any other non-avian archosaur. Recently, Buffetaut and Morel (2009) reported on the finding of a stegosaurian vertebra from the Middle Callovian of Sarthe, Pays-de-la-Loire, France, increasing the relatively poor fossil record of stegosaurs from that country.

Stegosaurs from Africa

Paranthodon africanus (NHMUK 47338) was the first dinosaur found in South Africa (Klerk 2000). Discovered in 1845 by W. G. Atherstone and A. G. Bain from the Valanginian Kirkwood Formation on the Bushman's River, Dassieklip, near Grahamstown, South Africa, the specimen underwent numerous referrals until its final identification as a stegosaur by Galton and Coombs (1981). According to Atherstone (1857) a number of large limb bones, as well as a fragmentary skull were collected. Although Atherstone and Bain were able to identify them as reptilian, they felt unqualified to further identify the animal, and so sent it to R. Owen at the British Museum (Natural History), London, in 1849 or 1853 (Klerk 2000), for further investigation. Owen eventually published on the fossils in 1876, although he only listed the fragmentary skull. The whereabouts of the limb bones recovered by Atherstone and Bain is now unknown. Unfortunately, Owen mixed up the fragmentary skull with Permian pariesaur material, now known to be from Styl-Kranz, Sneewburg Range, South Africa. Owen described all of the material as dinosaurian, calling it '*Anthodon serrarius*', and attributing all to the Dassieklip locality (Klerk 2000).

In 1890, Lydekker recognised that Owen had made a mistake in listing all '*Anthodon*' material as coming from the Dassieklip locality. He corrected this mistake, and catalogued all the '*Anthodon'* material as belonging to a Permian pariesaur. In 1910, R. Broom re-examined the fossil and noted that it was definitely dinosaurian and not referable to the pariesaur '*Anthodon*'. He suggested that it be placed in the ankylosaurian genus '*Palaeoscincus*' under the new species name '*africanus*'. Nopcsa (1929) also re-examined the fossil and was the first to suggest that it was a stegosaur. He named it '*Paranthodon oweni*', being apparently unaware of Broom's earlier species name (Klerk 2000).

Galton and Coombs (1981), realising that the fossil was not ankylosaurian, retained the genus name of Nopcsa (1929), and the species name of Broom (1910), which took precedence. They therefore recognised *Paranthodon africanus* as a valid genus based on features of the teeth that they considered to be diagnostic. Maidment et al. (2008) considered that, although the material did not bear any stegosaurian synapomorphies, it clearly belonged to a stegosaur, and that the material bore a single autapomorphy, making it a valid genus.

Kentrosaurus aethiopicus, represented by numerous specimens, was discovered in the first decade of the twentieth century in the Tendaguru beds (late Kimmeridgian–Tithonian; Weishampel et al. 2004) of Tanzania (then German East Africa). The material was discovered in several bone-beds and the majority was completely disarticulated; it is unclear how many animals are represented by the remains, and only a single partial associated skeleton exists (Mallinson 2010). The material was sent to the Museum für Naturkunde, Berlin, and it was described and figured by Hennig (1915, 1916, 1924, 1936; Janensch 1925).

Galton (1982a, 1988) and Maidment et al. (2008) agreed with the original conclusions drawn by Hennig (1915, 1924); all of the *Kentrosaurus* material was referable to one species, despite a number of differences among individuals. Galton (1982a) considered these to be either ontogenetic or sexual dimorphisms.

Stegosaurs from Asia

The first stegosaurian dinosaur discovered in China was collected in 1957 from Pinganxiang, Yongxing District, Quxian. It was named *Chialingosaurus kuani* and described by Young (1959). The specimen is from the Late Jurassic Upper Shaximiao Formation (Dong et al. 1983). A further specimen was excavated from the same locality as the type specimen in 1978, and included in the remains was a partial skull, as well as limb bones and limb girdle elements (CV 202). At the same time another specimen was excavated from a location 100 m west of the original quarry (CV 203). Dong et al. (1983) assigned this as the paratype; Maidment and Wei (2006) considered the specimen to be invalid and the genus *Chialingosaurus* to be a *nomen dubium* because it does not bear any autapomorphies or unique character combinations.

Wuerhosaurus homheni (Dong 1973) was found in the Valanginian–Albian Tugulu Group (Weishampel et al. 2004) of the Lianmuging Formation, Wuerho, Xinjiang, and comprised an incomplete skeleton (IVPP V4006). A second specimen, comprising three caudal vertebrae, was erected as the paratype (IVPP V4007; Dong 1990). In 1988, another specimen was found in the Early Cretaceous Ejinhoro Formation of Yang-Paul, in the Ordos Basin of Inner Mongolia (Dong 1993). Dong created a new species for this specimen, calling it *Wuerhosaurus ordosensis*. IVPP V6877 is the holotype, and IVPP V6878 and 6879 are referred specimens from the same locality. Maidment et al. (2008) considered that *Wuerhosaurus* was referable to the genus *Stegosaurus*, and referred the material originally described as *Wuerhosaurus ordosensis* to the new combination *Stegosaurus homheni*.

Tuojiangosaurus multispinus was discovered in 1974 in the Late Jurassic Upper Shaximiao Formation of Zigong City, Sichuan Province, and was collected along with other dinosaurian fossils (Dong et al. 1977). The holotype (CV 209) comprised a partial skeleton, and a second partial skeleton (CV 210) was erected as the paratype (Glut 1997). These were briefly described by Dong et al. (1977), and then in more detail by Dong et al. (1983) and Dong (1990). Maidment and Wei (2006) could locate little of the holotype and paratype material, but concluded that *Tuojiangosaurus* was a valid species nonetheless.

Chungkingosaurus jiangbeiensis was found at Mai-eisni, Jiangbei, near Chongqing in 1977 from the Late Jurassic Upper Shaximiao Formation. First described by Dong et al. (1983), the holotype, CV 206, is a partial skeleton including the anterior part of the skull. Three further specimens (CV 207, CV 205 and CV 208) were collected from various parts of Chongqing City, and Dong et al. (1983) and Dong (1990) regarded each as a different species of *Chungkingosaurus*. Maidment and Wei (2006) could locate little of the *Chungkingosaurus* material but considered that it was a valid species.

Huayangosaurus taibaii is perhaps the best known of the Chinese stegosaurs. The first specimen was found at Dashanpu in Zigong City, Sichuan Province in 1979–1980. Found in the lower part of the Upper Shaximiao Formation, which is Bathonian–Callovian in age, *Huayangosaurus* represents one of the earliest known stegosaurs from anywhere in the world. The specimen was described by Dong et al. (1982) and comprised a complete skull plus fragmentary postcrania (IVPP V6728). Zhou (1984) re-described and figured *Huayangosaurus* based on new specimens from the same locality, including a complete skeleton (ZDM T7001) and several other partial skeletons (ZDM T7002, T7004, T7008, T7010, CV 00720, and CV 00721). Sereno and Dong (1992) re-described the skull in great detail, noting several new features not described in earlier works, and Maidment et al. (2006) re-described the postcrania and noted that it shared a number of plesiomorphies with basal thyreophorans like *Scutellosaurus*.

The name '*Monkonosaurus*' was first published by Zhao (1983) in a faunal list, but the specimen was not described until Dong (1990) wrote a brief note on it in his paper on the stegosaurs of Asia, in which he added the species name *M. lawulacus*. The specimen was collected in 1976–1977 from the Early Cretaceous Loe-ein Formation (Weishampel et al. 2004) of Monkon, Qamdo, Tibet. Maidment and

Wei (2006) considered the species to be a *nomen dubium* because the holotype bears no autapomorphies or unique character combinations. Named for the enormous parascapular spines found in place alongside the specimen, *Gigantspinosaurus sichuanensis* was first mentioned in a short article by Gao et al. (1986). Ouyang (1992) described the specimen in more detail and Peng et al. (2005) published a diagnosis and figured a referred specimen (ZDM 0156). The holotype (ZDM 0019) is currently mounted at the Zigong Dinosaur Museum. Maidment and Wei (2006) considered *Gigantspinosaurus* to be a valid species.

Buffetaut et al. (2001) described a dorsal vertebra from the Late Jurassic of Thailand that has a moderately elongated neural arch, indicating affinities with Stegosauridae. The material is currently too fragmentary to name, however. Kurzanov et al. (2001, 2003) described teeth from the Late Jurassic of Siberia that they referred to *Stegosaurus* sp., however, the large denticles that are confluent with striations extending from the base of the crown to the tip are unlike those seen on other stegosaurian dinosaurs (e.g. *Huayangosaurus*, ZDM T7001; *Stegosaurus*, SMA 0018; *Paranthodon*, NHMUK 47338) and are more similar to ankylosaur teeth (Vickaryous et al. 2004). Maidment et al. (2008) considered them to be indeterminate ankylosaurian. Several new expeditions have led to the discovery of more material. Wings et al. (2007) reported on a stegosaurian dorsal vertebra (SGP 2002/001) from the Oxfordian Qigu Formation of the Junggar Basin, while Averianov et al. (2007a, b) reported on a stegosaurian braincase from the Late Jurassic Saldan Formation of Tuva, Russia (TuvIKOPR K-248), and some stegosaurian dorsal vertebrae from the Middle Jurassic of Kyrgyzstan (IGB 001).

A new stegosaur, *Jiangjunosaurus junggarensis* (IVPP V 14724), from the Late Jurassic Shishugou Formation of Xingjiang was reported by Jia et al. (2007). The articulated specimen includes a partial skull and cervical vertebrae with dermal armour.

Stegosauria from other locations

Bones and scutes of Cenomanian to Aptian age were found in the Lameta beds of Jubbalpore in 1917 (Matley 1923). The bones included a sacrum, pair of ilia and a tibia, plus many small dermal ossifications. Matley (1923) considered the specimen to be an armoured dinosaur (thyreophoran) and called it *Lametasaurus indicus.* Charkravarti (1933) refuted the claim that the bones were thyreophoran and instead proposed that the bones were referable to a theropod and the osteoderms to a sauropod. Huene and Matley (1933) described further bones indicating that *L. indicus* was club-tailed. Chatterjee and Rudra (1996) concluded that the holotype comprised theropod bones and dermal ossifications from sauropods and possibly ankylosaurs. The latter authors re-excavated the original site and found possible ankylosaurian material. *Lametasaurus indicus* is therefore considered here as an ankylosaur.

Piveteau (1926) described two teeth discovered in the Cenomanian–Turonian of NW Madagascar and referred them to *Stegosaurus.* Piveteau also re-assigned small osteoderms—that had been previously identified as belonging to a sauropod—to *Stegosaurus madagascariensis*. Russell et al. (1976) stated that the teeth found by Piveteau were similar to those of nodosaurid ankylosaurs. In 2000, Buckley et al. excavated a crocodyliform skull, *Simosuchus clarki*, of Middle or Late Cretaceous age. Naish and Martill (2001) noted that the teeth preserved in the skull were similar to those of stegosaurs and ankylosaurs, and they suggested that the teeth found by Piveteau (1926) were referable to this taxon. However, the teeth of *Simosuchus* are rather different from those originally illustrated by Piveteau (1926, fig. 1), and they were found lower down in the section (C.A. Forster, pers. comm. 2007). The teeth illustrated by Piveteau (1926) bear striations on the crown that extend to the tip of the tooth, where they are confluent with marginal denticles. This morphology is unlike that of stegosaur teeth, which have striations on the crown that are not confluent with the marginal denticles, which are very small (e.g. SMA S01; NHMUK 47338; MB wj 60; ZDM T7001; pers. obs. 2004–2006). The morphology of the Malagasy teeth is more similar to ankylosaur teeth (Vickaryous et al. 2004). It seems likely, therefore, that *Stegosaurus madagascariensis* is an indeterminate ankylosaur.

Dravidosaurus blanfordi was discovered in 1978 (Yadagiri and Ayyasami 1979) in the Trichinopoly group of southern India (Coniacian). Chatterjee and Rudra (1996, 518) viewed the material and could see no resemblance to the originally described stegosaurian. They described the material as "highly weathered limb and girdle elements and may belong to a plesiosaur". Chatterjee and Rudra (1996) also excavated further plesiosaur material when they visited the original site in 1996. *Dravidosaurus blanfordi* is considered a *nomen dubium* here as independent assessment and re-description of the material is needed. This is particularly important since *Dravidosaurus* is the only stegosaur so far reported from the Late Cretaceous.

Bonaparte (1996) described and illustrated cervical vertebrae from Argentina, the only record of a South American stegosaur. However, the material is fragmentary and bears no synapomorphies that allow it to be referred to Stegosauria; it was considered indeterminate by Maidment et al. (2008).

New discoveries are continuing to increase our knowledge of stegosaurian diversity and longevity. Specimens like that of *Miragaia longicollum* also add to our understanding of stegosaurian morphology, which appears to be far more diverse than was previously appreciated.

Stegosaurian phylogeny

Jiangjunosaurus (Late Jurassic, Shishugou Formation of Xingjiang, China; Jia et al. 2007) was added to the character-taxon matrix of Mateus et al. (2009; see Appendix in the electronic supplementary material). The matrix included all stegosaurian taxa currently considered to be valid (Maidment and Wei 2006; Jia et al. 2007; Maidment et al. 2008; Mateus et al. 2009). Since taxon sampling has been shown to have a large effect on cladistic topology (e.g. Ketchum and Benson 2010) the addition of newly described taxa tests previously proposed hypotheses of taxon relationships and the results are therefore able to indicate which relationships are robust and stable, and those that are less robust and likely to change as a result of new data. This analysis is the first to include *Jiangjunosaurus* and therefore represents the most up-to-date phylogenetic analysis of Stegosauria. Scoring of stegosaurian taxa and basal thyreophorans was based on first-hand observation of all of the specimens with the exception of *Jiangjunosaurus*, which was scored from the description in Jia et al. (2007). Scoring of ankylosaur specimens was based on first-hand observation and supplemented with data from the literature. Analyses were carried out following the methodology outlined in Maidment et al. (2008).

A branch and bound search in PAUP* 4.10b (Swofford 2002) recovered 41 most parsimonious trees (MPTs) with length 3739. *Lesothosaurus* was fixed as the outgroup. A consistency index of 0.63, a retention index of 0.71 and a rescaled consistency index of 0.45 were obtained. These statistics are comparable to those of Mateus et al. (2009). The strict component consensus tree (SCC) is shown in Fig. 1a. The tree is similar to that of Mateus et al. (2009), except that *Huayangosaurus* and *Chungkingosaurus* are not recovered as sister taxa. This suggests that the hypothesis of relationships proposed by Mateus et al. (2009) is robust to the addition of new taxa, lending support to relationships recovered, but that the relationship between *Huayangosaurus* and *Chungkingosaurus* is weakly supported by the data and is identified as an area that requires further investigation. There is a polytomy at the base of Stegosauria that contains several Chinese taxa including *Jiangjunosaurus*. This lack of resolution is likely to be due to the large amount of missing data for the taxa forming the basal polytomy. In order to test which taxa were unstable and generating the polytomy, a strict reduced consensus (SRC) profile was generated from the MPTs in RadCon (Thorley and Page 2000). The profile contains four trees, the first of which is the SCC tree. The SRC trees, which are mutually exclusive, successively prune unstable taxa to give more resolution. In tree SRC 2, *Jiangjunosaurus* was pruned to give a tree identical to the strict consensus tree in Mateus et al. (2009). In SRC 3, *Gigantspinosaurus* was also pruned, which resulted in a sister–taxon relationship between *Tuojiangosaurus* and *Paranthodon*, and in SRC 4, *Gigantspinosaurus* was included but *Tuojiangosaurus, Paranthodon* and *Jiangjunosaurus* were all pruned, resulting in a fully resolved

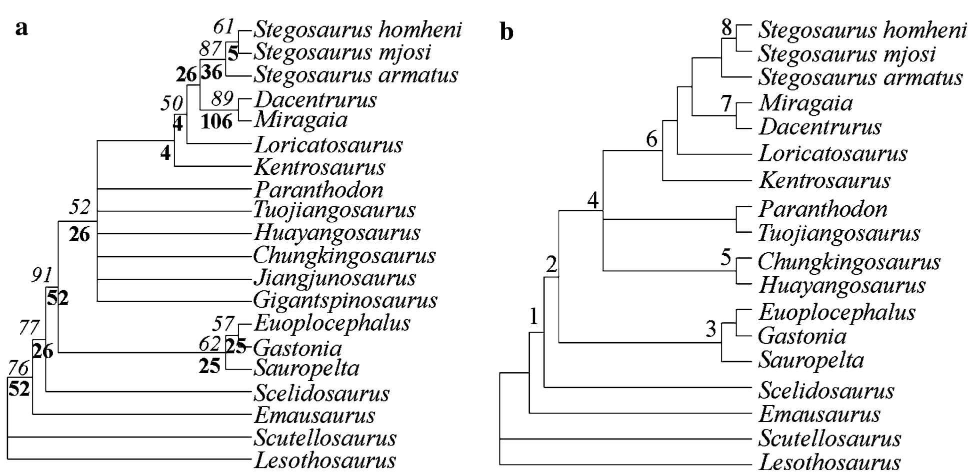

Fig. 1 **a** Strict component consensus of 41 most parsimonious trees of length 3739. *Numbers in italic* are bootstrap values. A bootstrap analysis with 5,000 replicates was carried out. Only values greater than 50% are shown. *Numbers in bold* are decay indices. A decay index PAUP file was written in MacClade (Maddison and Maddison 2003) and implemented in PAUP 4.10b (Swofford 2002). The cladistic analysis was carried out using the gap weighting methodology (see Maidment et al. 2008 for details), which involves weighting all characters to a value of 26. Decay indices are therefore 26 times greater than would be expected in a normally weighted analysis. A decay index of 26 in this analysis is equivalent to a decay index of 1 in a normally weighted analysis; all decay indices lower than 26 indicate the clade is supported by continuous data only. **b** Strict reduced consensus tree 3 (CIC = 55.83 bits) in which two unstable taxa, *Jiangjunosaurus* and *Gigantspinosaurus*, have been pruned, resulting in improved resolution. Numbers above clades indicate named clades as follows: *1* Thyreophoroidea, *2* Eurypoda, *3* Ankylosauria, *4* Stegosauria, *5* Huayangosauridae, *6* Stegosauridae, *7* Dacentrurinae, *8 Stegosaurus*

tree with *Gigantspinosaurus* as the most basal stegosaur and Huayangosauridae being the sister taxon to the other stegosaurs.

The Cladistic Information Content (CIC) of the SRC trees was calculated. This is a measure of the amount of information given in each SRC tree. SRC 3 was found to have the greatest CIC, and is shown in Fig. 1b.

Conclusions

Stegosaurian dinosaurs have been recovered from all northern hemisphere continents and Africa. They are temporally restricted, having been recovered in sediments dated from the Middle Jurassic to Early Cretaceous, with no definitive stegosaurian material known in younger sediments from anywhere in the world. Recent reviews and new material are increasing our understanding of the morphological, ecological and spatial diversity of stegosaurs. The most up-to-date phylogeny supports the results of other recent analyses and this suggests that our understanding of stegosaurian relationships is stabilizing. Further work should focus on the detailed description of newly discovered material, which is fundamental to palaeobiological hypotheses, as well as continued study of stegosaurian biology.

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