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A new long-necked 'sauropod-mimic' stegosaur and the evolution of the plated dinosaurs

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Stegosaurian dinosaurs have a quadrupedal stance, short forelimbs, short necks, and are generally considered to be low browsers. A new stegosaur, *Miragaia longicollum* gen. et sp. nov., from the Late Jurassic of Portugal, has a neck comprising at least 17 cervical vertebrae. This is eight additional cervical vertebrae when compared with the ancestral condition seen in basal ornithischians such as *Scutellosaurus*. *Miragaia* has a higher cervical count than most of the iconically long-necked sauropod dinosaurs. Long neck length has been achieved by 'cervicalization' of anterior dorsal vertebrae and probable lengthening of centra. All these anatomical features are evolutionarily convergent with those exhibited in the necks of sauropod dinosaurs. *Miragaia longicollum* is based upon a partial articulated skeleton, and includes the only known cranial remains from any European stegosaur. A well-resolved phylogeny supports a new clade that unites *Miragaia* and *Dacentrurus* as the sister group to *Stegosaurus*; this new topology challenges the common view of *Dacentrurus* as a basal stegosaur.

Keywords: Stegosaurian dinosaurs; *Miragaia longicollum*; *Dacentrurus*; neck elongation; niche partitioning; sexual selection

Institution abbreviations: AMNH, American Museum of Natural History, New York, USA; BYU, Brigham Young University Museum, Salt Lake City, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; DMNH, Denver Museum of Nature and Science, Denver, USA; ML, Museum of Lourinhã, Portugal; USNM, United States National Museum, Washington DC, USA; VAL, Museo de Ciencias Naturales, Valencia, Spain; YPM, Peabody Museum of Natural History, Yale University, New Haven, USA

1. INTRODUCTION

Stegosauria is a clade of ornithischian dinosaurs characterized by an array of elaborate postcranial osteoderms (Galton & Upchurch 2004; Maidment & Wei 2006; Maidment *et al*. 2008). Stegosauria achieved a wide distribution during the Late Jurassic and members of the clade are abundant in faunas of this age (Europe, North America, Africa and Asia; see Galton & Upchurch 2004; Maidment *et al*. 2008 and references therein). Stegosauria and its sister taxon Ankylosauria are united in the clade Thyreophora, the armoured dinosaurs, along with a number of basal forms, including *Scutellosaurus* and *Scelidosaurus* from the Lower Jurassic (Owen 1861, 1863; Colbert 1981). Recent cladistic analyses suggest that Thyreophora is one of the most basal clades of ornithischian dinosaurs (Sereno 1999; Butler *et al*. 2008).

The European stegosaur *Dacentrurus armatus* was named in 1875, preceding *Stegosaurus* as the first stegosaur known to science, and for the following 125 years the holotype specimen has been unrivalled as the most complete stegosaur skeleton from Europe. The new find presented here is approximately as complete, but has a number of new and previously unknown anatomical features, including cranial material, dorsal plates and an almost complete neck.

Stegosaurs are traditionally reconstructed as feeding on low vegetation because of their small heads, short necks and short forelimbs (Weishampel 1984; Barrett & Willis 2001; Galton & Upchurch 2004; Fastovsky & Weishampel 2005; Parrish 2006). We describe a new stegosaurian dinosaur from the Upper Jurassic of Portugal that challenges this traditional view. *Miragaia longicollum* gen. et sp. nov. possessed at least 17 cervical vertebrae, eight more than basal ornithischians such as *Scutellosaurus* (Colbert 1981), and more cervical vertebrae than possessed by most sauropod dinosaurs, famed for their long necks (Upchurch *et al*. 2004). This new discovery indicates a previously unsuspected level of morphological and ecological diversity among stegosaurs.

2. SYSTEMATIC PALAEONTOLOGY

Dinosauria (Owen 1842)
Ornithischia (Seeley 1887)
Stegosauria (Marsh 1877)
Stegosauridae (Marsh 1880)
Dacentrurinae new clade

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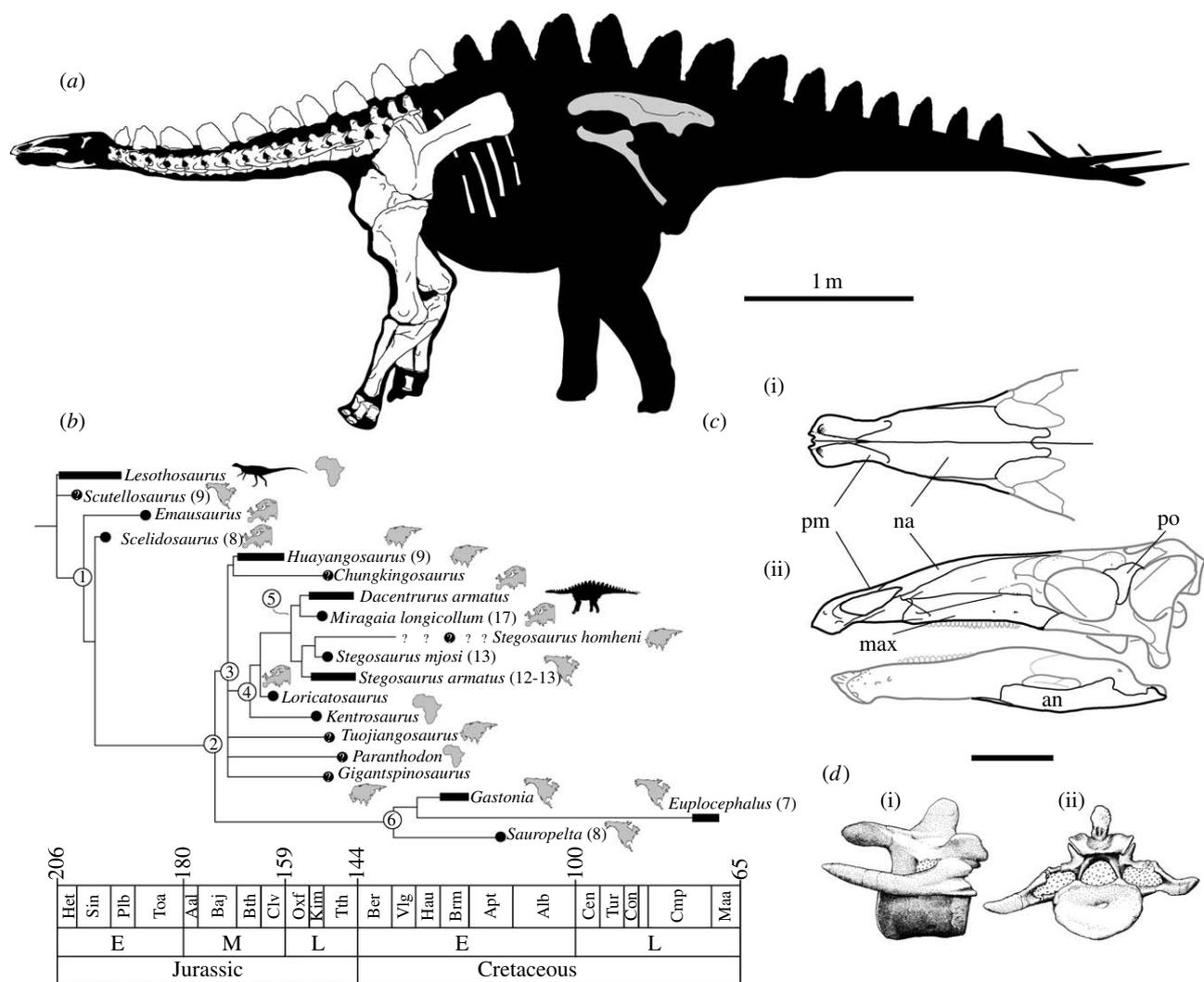
Figure 1. (*a*) Skeletal reconstruction of *M. longicollum* based on type specimen ML433, except the ilium and pubis (in grey), which are based upon the referred specimen (ML433-A), and have been scaled up. (*b*) Phylogeny and chronostratigraphy of Stegosauria. Strict consensus of five MPTs obtained from a branch-and-bound search (CI=0.617; RI=0.718; RC=0.458) Aal, Aalenian; Alb, Albian; Ans, Anisian; Apt, Aptian; Baj, Bajocian; Brm, Barremian; Bth, Bathonian; Ber, Berriasian; Clv, Callovian; Cmp, Campanian; Crn, Carnian; Cen, Cenomanian; Con, Coniacian; Hau, Hauterivian; Het, Hettangian; Kim, Kimmeridgian; Lad, Ladinian; Maa, Maastrichtian; Nor, Norian; Oxf, Oxfordian; Plb, Pliensbachian; Rht, Rhaetian; Sin, Sinemurian; Tth, Tithonian; Toa, Toarcian; Tur, Turanian; Vlg, Valanginian. E, Early; M, Middle; L, Late. Nodes: 1, Thyreophora; 2, Eurypoda; 3, Stegosauria; 4, Stegosauridae; 5, Dacentrurinae, n. clade; 6, Ankylosauria; the values in parenthesis show the number of cervical vertebrae; question marks represent insufficient stratigraphic resolution. (*c*) Skull in (i) dorsal and (ii) lateral views. (*d*) Sixteenth cervical vertebrae of *M. longicollum* ML433, in (i) right lateral and (ii) posterior views (for more details see the electronic supplementary material). an, angular; max, maxilla; na, nasal; pm, premaxilla; po, postorbital. Scale bar corresponds to 10 cm for the skull and vertebrae, and to 1 m for the skeletal reconstruction.

Definition. All stegosaurs more closely related to *D. armatus* (Owen 1875) than *Stegosaurus armatus* (Marsh 1877).

Unambiguous synapomorphies: cervical ribs fused to para- and diapophyses of cervical vertebrae; centra of dorsal vertebrae wider than long; olecranon horn present on ulna; and anterior end of anterior pubic process expanded dorsally.

Miragaia longicollum gen. et sp. nov.

(a) *Etymology*

Miragaia, after the locality and geological unit of the same name; *longicollum*, after the Latin *longus* (long) and *collum* (neck), in reference to its long neck. In addition, the stem *Mira-* can be read as the feminine form of Latin *mirus*, meaning wonderful, while *Gaia* is the Greek goddess of the Earth, so the name also means 'wonderful goddess of the Earth'.

(b) *Holotype*

Nearly complete anterior half of a skeleton (ML 433; see figure 1 and the electronic supplementary material) with partial cranium (right premaxilla, partial left maxilla, left nasal, right postorbital, and right and left angulars), 15 cervical vertebrae (atlas and axis are absent) with associated ribs, two dorsal vertebrae, both coracoids, scapulae, humeri, radii and ulnae, one metacarpal, three phalanges, 12 rib fragments, one chevron, one dermal spine and 13 dermal plates.

(c) *Referred specimen*

ML 433-A, a juvenile specimen found at the type locality, consisting of two dorsal centra, three dorsal neural arches,

a right pubis and a left ilium. Although this individual possesses none of the autapomorphies of *M. longicollum* (see §2*e*, below), its skeletal remains were found in close proximity to those of the holotype. Further discoveries may establish that ML 433-A is a different taxon; however, lacking evidence to the contrary, we regard it as referable to *M. longicollum*.

(d) *Locality and horizon*

Close to Miragaia at the municipality of Lourinhã (Portugal) in the Late Jurassic (Upper Kimmeridgian–Lower Tithonian) Miragaia Unit of the Sobral Formation (Lourinhã Group). Details on stratigraphy, fieldmap and location are available in Araújo *et al.* (in press).

(e) *Diagnosis*

Differs from other stegosaurs in the presence of the following autapomorphies: (i) anterior tip of the premaxilla is drawn into a point, (ii) anterolateral rim of the premaxilla projects ventrally, (iii) at least 17 cervical vertebrae, (iv) mid-cervical neural spines possess a notch at their base with an anterior projection dorsal to it, (v) mid and posterior cervical and anterior dorsal neural spines with transversely expanded apices, and (vi) paired, slightly outwardly convex, triangular cervical dermal plates with a notch and projection on the anterodorsal margin.

(f) *Description*

Several elements of the skull of ML 433 were found, representing the first skull material recovered from a European stegosaur. The right premaxilla is incomplete posteriorly and edentulous, similar to the same element in *Stegosaurus* (USNM 4934). Anteriorly, the lateral margin of the palate is deflected ventrally in lateral view, but posteriorly it is deflected dorsally, so that the side of the palate curves upwards in lateral view. The premaxilla is drawn into a point anteromedially in dorsal view where the two premaxillae joined, unlike in *Stegosaurus* (USNM 4934, BYU 12290), where there is a U-shaped notch in this area.

In the partial left maxilla, 16 tooth sockets are preserved, and the posterior ventral margin is edentulous. The anterior part of the maxilla is transversely thin and the element thickens posteriorly. Along the preserved dorsal margin of the bone, a prominent step is present in anterior or posterior view, so that the dorsal margin is offset medially relative to the tooth row.

The left nasal is an anteroposteriorly elongate, dorsally convex element, but the degree of convexity appears to have been accentuated by post-mortem deformation. The bone is sculpted on its dorsal surface, similar to *Stegosaurus* (USNM 4934, CM 106). Laterally, the element bears a prominent ridge that may be the facet for articulation with the maxilla.

Seventeen vertebrae are preserved intact and with little distortion. Fifteen of the vertebrae are cervicals, but the atlas and axis were not found, indicating that *Miragaia* possessed at least 17 cervical vertebrae. The two most anterior dorsal vertebrae were also recovered. A full description of all vertebrae is beyond the scope of this paper, so general trends will be described.

Cervical centra are amphiplatyan and are anteroposteriorly longer than transversely wide. Centra get larger and relatively less elongate through the vertebral series. A prominent ventral keel is present on mid and posterior centra. The cervical rib is fused to the parapophysis, which is located ventral to the neurocentral suture on the anterolateral part of the centrum. The rib projects posteriorly, as in specimen VAL Co-1 referred to *Dacentrurus* (Maidment *et al.* 2008). The capitulum possesses an additional process, not seen in VAL Co-1, which projects anteriorly to a point level with the anterior centrum face. The apicies of mid-cervical through anterior dorsal neural spines are transversely expanded owing to the presence of prominent interspinal scars that project anteriorly beyond the base of the neural spine, producing a marked notch. Neural spines are transversely compressed and bear two ridges projecting posteriorly and extending to lie dorsal to the postzygapophyses posteriorly. The postzygapophyses project beyond the posterior centrum face, as in *Stegosaurus* (AMNH 5752, USNM 4936). Prezygapophyses on mid and posterior cervical vertebrae bear a notch on the anterodorsal border in lateral view.

The anterior plate of the scapula is larger than the coracoid, and has a rectangular anterodorsal corner, as in *Stegosaurus* (DMNH 1483). The scapular blade is parallel sided. The coracoid is rounded, laterally convex and medially concave.

Both humeri are well preserved. The humerus is similar to *Stegosaurus* (e.g. YPM 1853). The deltopectoral crest projects strongly anteromedially. Posteriorly there is a prominent triceps tubercle, but the posterior vertical descending ridge is not as strong as in other stegosaurs (Galton & Upchurch 2004; Maidment *et al.* 2008).

In both ulnae, the olecranon process is prominent mainly because it bears an additional cup-like structure proximally. The surface of the bone in this area is more fibrous than the adjacent bone, which is regular smooth periosteon. We hypothesize that this lamina is evolutionarily incorporated into the ulna by a natural non-pathological enthesio process. Although from human perspective, the enthesio reaction is considered an abnormality, it represents a natural reaction to physical stress in the bone and tendons (see Rothschild 1987; Shaibani *et al.* 1991, 1993; Dar *et al.* 2007). As expected with this hypothesis, the enthesio reaction is absent in juveniles; as a result, the olecranon process is less prominent (Galton & Upchurch 2004, p. 354).

Both radii are present and similar to the same element in *Stegosaurus* (YPM 1856). The proximal articular surface is slightly concave at its midpoint and rugose along its rim. The shaft is round in cross section and slightly bowed posteriorly in lateral view.

Four manual elements were collected: a possible intermedium, right metacarpal I, and phalanges I-1, II-1 and III-1. The proximal articular surface of right metacarpal I is triangular with the long axis anteroposteriorly orientated (in contrast to *Stegosaurus*, see Gilmore 1914, fig. 39). The shaft is subtriangular in cross-sectional outline. In distal view, the element is trapezoidal.

The anterior pubic process is dorsoventrally deep and bears a dorsal projection at its anterior tip in lateral view, as in *Dacentrurus* (N. A. Christiansen 2008, personal observations; NHM 46013). The distal end of the posterior pubis process is weakly expanded dorsoventrally.

Cervical osteoderms are subtriangular. Laterally, they are convex and medially they are concave, with a transversely unexpanded base. The last pair of plates, probably from the anterior dorsal region, is uniformly thin, except at the base, similar to the dorsal plates of

Stegosaurus (e.g. USNM 4934). All of the plates are paired (arranged symmetrically) and bear a hook anteriorly.

3. DISCUSSION

The most notable feature of *M. longicollum* is its long neck, with at least 17 cervical vertebrae. Cervical vertebrae were identified as those which bear a rib facet, the parapophysis, on the lateral side of the centrum (Romer 1956); in dorsal vertebrae, this facet migrates onto the neural arch. The primitive number of cervical vertebrae for Ornithischia appears to be nine (Sereno 1999; Butler *et al.* 2008). *Heterodontosaurus* and *Scutellosaurus* retained this primitive condition (Santa Luca 1980; Colbert 1981; S. C. R. Maidment 2005, personal observations) while *Scelidosaurus* had eight cervical vertebrae (S. C. R. Maidment 2005, personal observations, see the electronic supplementary material). The basal stegosaur *Huayangosaurus* had nine cervical vertebrae (Maidment *et al.* 2006), there are 12–13 cervicals in *S. armatus* (USNM 4934), and *Stegosaurus* (=*Hesperosaurus*) *mjosi* also appears to have had 13 cervicals (DMNH 29431). Elongation of the neck of stegosaurs therefore appears to have been a trend that occurred throughout their evolution (figure 1*b*), culminating in the long-necked *Miragaia*, which possessed four more cervicals than any other stegosaur, and eight more than basal ornithischians and the basal stegosaur *Huayangosaurus*. Indeed, *Miragaia* possessed more cervical vertebrae than any other non-avian archosaur, except the Chinese sauropods *Mamenchisaurus*, *Omeisaurus* and *Euhelopus*, also with 17 (Upchurch *et al.* 2004). Most Upper Jurassic sauropods have just 12–15 cervical vertebrae (Upchurch *et al.* 2004).

(a) *Anatomical changes responsible for neck elongation*

Neck elongation in any taxon may occur via three processes: cervicalization of dorsal vertebrae (incorporation of dorsal vertebrae into the neck); the addition of new cervical elements to the vertebral column; and elongation of individual cervical vertebrae. All three of these processes are thought to have occurred to form the long necks of the sauropod dinosaurs (Wilson & Sereno 1998; Rauhut *et al.* 2005).

In order to assess which of these processes was most important for neck elongation in stegosaurs, three scenarios can be proposed and tested.

(i) If cervicalization of dorsal vertebrae were important in neck elongation, the number of dorsal vertebrae would decrease, while number of cervical vertebrae would increase and a more or less constant presacral vertebral count would be maintained. Table 1 summarizes the number of presacral vertebrae in all stegosaurs for which the region is known. Presacral vertebral count increases slightly from 25 in the basal stegosaur *Huayangosaurus* to 26 or 27 in *S. armatus*. Dorsal vertebral counts decrease from 16 in *Huayangosaurus* to 13 in *Stegosaurus mjosi* as neck length increases. This suggests that cervicalization of dorsal vertebrae played a significant role in stegosaurian neck elongation.

(ii) If addition of new cervical elements is the major process in neck elongation, the number of dorsal

Table 1. Presacral vertebrae numbers for thyreophorans. (?, insufficient information.)

taxon	presacral	cervical	dorsal
Scutellosaurus	23	9	14
Scelidosaurus	24	8	16
Huayangosaurus	25	9	16
Stegosaurus armatus	26–27	12–13	13–14
Stegosaurus mjosi	26	13	13
Miragaia	?	17	?

vertebrae would remain constant, while the number of cervical (and presacral) vertebrae would increase through stegosaur evolution. As seen in table 1, the number of dorsals actually decreases through stegosaur phylogeny. This suggests that the addition of new cervical elements played a minor role, but this cannot be confirmed for *Miragaia* because the dorsal vertebral column is not known.

(iii) If elongation of individual cervical vertebrae is important for neck elongation, then the length to width ratios of cervical vertebrae from specific locations on the cervical vertebral column should increase through stegosaur phylogeny. Cervical vertebrae 5, 6, 8 and 9 of *Huayangosaurus* are all wider than long, whereas all of the cervical vertebrae of *Miragaia*, and those of *Stegosaurus* for which we have measurements, are longer than wide (see the electronic supplementary material). This may suggest that some degree of elongation of the individual cervical vertebrae took place throughout stegosaur evolution. However, these ratios should be viewed with caution since they are likely to be strongly influenced by post-mortem deformation, and more data are needed to adequately assess the influence of individual cervical elongation on neck length in stegosaurs. See the electronic supplementary material for vertebrae measurements.

In contrast to mammals, for whom the cervical vertebral count is almost always seven, the number of cervical vertebrae is highly variable in reptiles. *Hox* genes control anteroposterior differentiation and patterning of the axial skeleton in all vertebrates, and specification of cervical vertebrae is associated with certain *Hox* genes (Galis 1999). In *Gallus* embryos, the *Hoxb5* is responsible for the development of cervical vertebrae (Cohn & Tickle 1999). In mice, at least four *Hox* genes knock out production of cervical ribs and the seventh cervical vertebra is partially or wholly transformed into a copy of the first thoracic vertebra (Galis 1999). Given that cervicalization of dorsal vertebrae is the major method for neck elongation, homeogenes must have played a role in the evolution of the neck of *Miragaia* by controlling the cervicalization and segment addition processes. This provides evidence for shifts in *Hox* gene expression in the fossil record and is another example of the high evolutionary plasticity of dinosaurs.

(b) *Evolutionary mechanisms driving neck elongation*

The giraffid mammals are the only extant vertebrates with extremely elongated necks relative to their ancestors, and

there is now a significant body of evidence to suggest that the selective pressure for neck elongation in these mammals was sexual selection (Simmons & Scheepers 1996), but see also Cameron & du Toit (2007) showing the relevance of resource partitioning driven by competition in giraffes. The long necks of the saurischian sauropod dinosaurs were commonly thought to have evolved through niche partitioning and interspecific competition (see Parrish (2006) and references therein); however, recent work has questioned that hypothesis (Stevens & Parrish 1999, 2005; Parrish 2006) and it has been suggested that the long neck of the sauropods may have arisen through sexual selection instead (Senter 2006).

Two hypotheses can be proposed regarding the selective pressures that lead to the elongation of the stegosaurian neck, culminating in the extremely long neck of *Miragaia*:

(i) the long neck allowed *Miragaia* to browse for foliage at a height not occupied by other taxa in the fauna, and
(ii) the long neck of *Miragaia* arose owing to sexual selection.

The fossil record of Iberian herbivores in the Upper Jurassic comprises small ornithopods (Antunes & Mateus 2003; Ruiz-Omeñaca *et al.* 2004; Mateus 2006; Sánchez-Hernández *et al.* 2007), and the thyreophorans *Dracopelta* (Galton 1980), *Dacentrurus* and *Stegosaurus* (Escaso *et al.* 2007). Also present are large-bodied sauropods, which achieved large body proportions at this particular time and in this geographical setting; *Lusotitan*, *Dinheirosaurus* and *Turiasaurus* are examples (Bonaparte & Mateus 1999; Antunes & Mateus 2003; Royo-Torres *et al.* 2006). There is no record, however, of small or medium-sized sauropods. Browsing height estimations were calculated for herbivores in the Lourinhã Formation (for methodology see the electronic supplementary material), and show that the browsing ranges of *Stegosaurus*, *Miragaia* and *Draconyx* would have overlapped. Therefore, we cannot accept without doubt the hypothesis that the long neck of *Miragaia* reflected niche partitioning, even though the longer neck and forelimbs of *Miragaia* did allow it to feed at a slightly greater height than *Stegosaurus* when the neck was maximally dorsiflexed. Although the browsing ranges of *Draconyx* and the stegosaurs in the Lourinhã Formation overlapped, niche partitioning due to preference for a particular food source may have existed. A dental macro- and microwear study could examine differentiation in food source and warrants further investigation. Conversely, niche partitioning has been hypothesized as the selective pressure responsible for neck shortening in the shorted-necked Argentinean dicraeosaurid sauropod *Brachytrachelopan* (Rauhut *et al.* 2005), which is suggested to have occupied a niche normally held by ornithischians.

Senter (2006, p. 45) proposed six indicators that could be used to determine whether a character had arisen via sexual selection. Two of these can be tested for in *Miragaia*: (i) the feature provides no immediate survival benefit, and (ii) the feature incurs a survival cost. The long neck of *Miragaia* may have incurred both benefit and cost for survival: it would have allowed a wider browsing radius, which may have been energy efficient and therefore

beneficial; however, energy usage studies of neck musculature are beyond the scope of this paper and this generalized observation requires more data and more detailed investigation. By contrast, the long neck of *Miragaia* incurred a survival cost because it presented a greater predation target for medium to large-sized theropods (for body-size calculations see the electronic supplementary material).

More data are required to distinguish which selective pressure provided the driving force for neck elongation in *Miragaia*. Larger sample sizes would allow examination of scaling of body size to neck length, and a larger number of complete skeletons would allow possible distinction between a long-necked and short-necked morph. An ontogenetic series would allow identification of features that develop with sexual maturity and dental micro- and macrowear and isotopic studies would allow a better understanding of niche partitioning in the Lourinhã Formation.

(c) Systematic observations

Four additional characters and *Miragaia* were added to the data matrix of Maidment *et al.* (2008; see details at electronic supplementary material; figure 1). *Miragaia* is resolved as the sister taxon to *D. armatus* and they are united in the new stem-based clade Dacentrurinae, defined as all stegosaurs more closely related to *D. armatus* (Owen 1875) than to *S. armatus* Marsh 1877. Dacentrurinae is the sister group to *Stegosaurus*. This result is in contrast to some other cladistic analyses of Stegosauria (Sereno & Dong 1992; Sereno 1999; Galton & Upchurch 2004; Escaso *et al.* 2007; Maidment *et al.* 2008) in which *Dacentrurus* is considered to be a basal stegosaur, but accords with the findings of Carpenter *et al.* (2001) who recovered *Dacentrurus* as the sister taxon to '*Hesperosaurus*' (= *Stegosaurus*) *mjosi*. In this analysis, the clade *Stegosaurus* + Dacentrurinae is supported by a single unambiguous synapomorphy: the presence of postzygapophyses on cervical vertebrae that are elongate and project posterior to the posterior centrum facet (see the electronic supplementary material). Postzygapophyses of cervical vertebrae are unknown in *Dacentrurus*, so it appears to be this character and the obviously close relationship between *Miragaia* and *Dacentrurus* that has resulted in the derived location of the latter, in contrast to its location as the most basal stegosaurid in the analysis of Maidment *et al.* (2008).

4. CONCLUSION

With at least 17 cervical vertebrae, a new Late Jurassic stegosaur *M. longicollum* from Portugal has a neck longer than any other stegosaur and more cervical vertebrae than most sauropod dinosaurs. Elongation of the neck occurred via cervicalization of dorsal vertebrae, and this suggests a shift in *Hox* gene expression preserved in the fossil record. Elongation of cervical centra and the addition of new cervical elements also seem to have taken place, but to a smaller degree. The long neck and fusion of ribs to vertebrae are convergent with sauropods. The specimen here described represents one of the most complete stegosaurs in Europe and the first that includes cranial material. *Miragaia* is found to be closely related to *Dacentrurus*, which is more derived than previously

thought, and together they constitute the new clade Dacentrurinae, sister group to *Stegosaurus*.

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SUPPLEMENTARY INFORMATION

A new long-necked 'sauropod-mimic' stegosaur and the evolution of the plated dinosaurs

Mateus, O., Maidment, S.C.R. & Christiansen, N.A. 2009. Proceeding of the Royal Society B

Supplementary Information Contents:

Figure S1. Skull reconstructions of *Miragaia longicollum* ML433. Abbreviations: an, angular; max, maxillary; na, nasal; pm, premaxillary; po, postorbital. Scale bar corresponds to 10 cm for the skull, and to 1 m for the skeletal reconstruction.
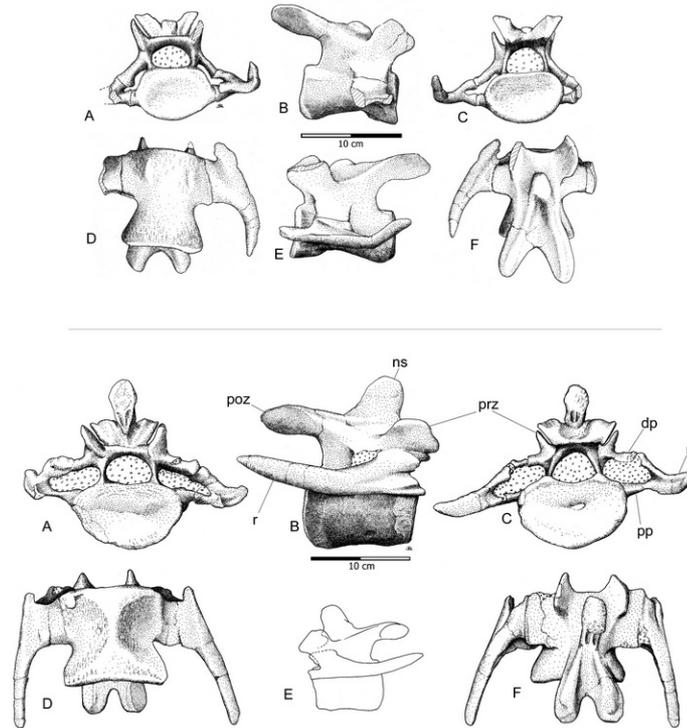
Figure S2. Thirteenth (upper set) and sixteenth (lower set) cervical vertebrae of *Miragaia longicollum* ML433, in A, anterior, B, right lateral, C, posterior, D, anterior, E, left lateral, and F, dorsal views. Abbreviations: dp, diapophysis; ns, neural spine; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; r, rib. Stippled areas represent sediment.
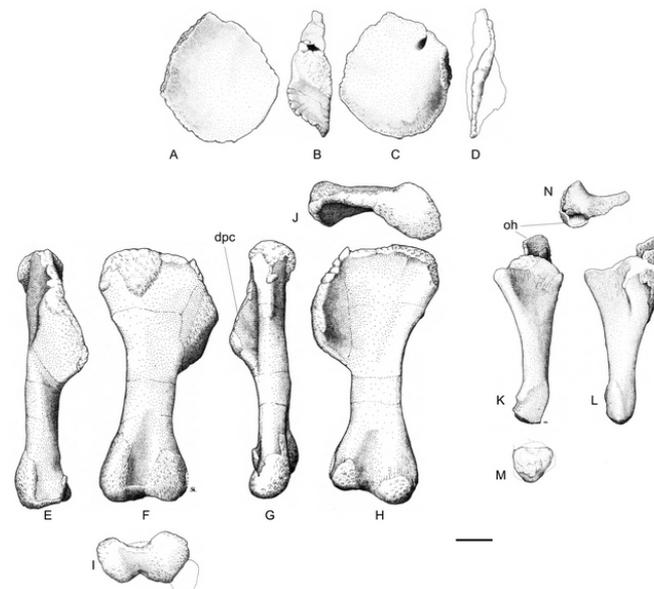
Figure S3. Forelimb of *Miragaia longicollum* ML433. A-C, left coracoid in medial (A), proximal (B), lateral (C), and distal (D) views; E-J, right humerus in lateral (E), posterior (F), medial (G), anterior (H), distal (I), and proximal (J) views; K-N, right ulna in anterior (K), lateral (L), distal (M) and proximal (N) views. Abbreviations: dpc, deltopectoral crest; oh, olecranon horn. Scale bar: 10 cm.
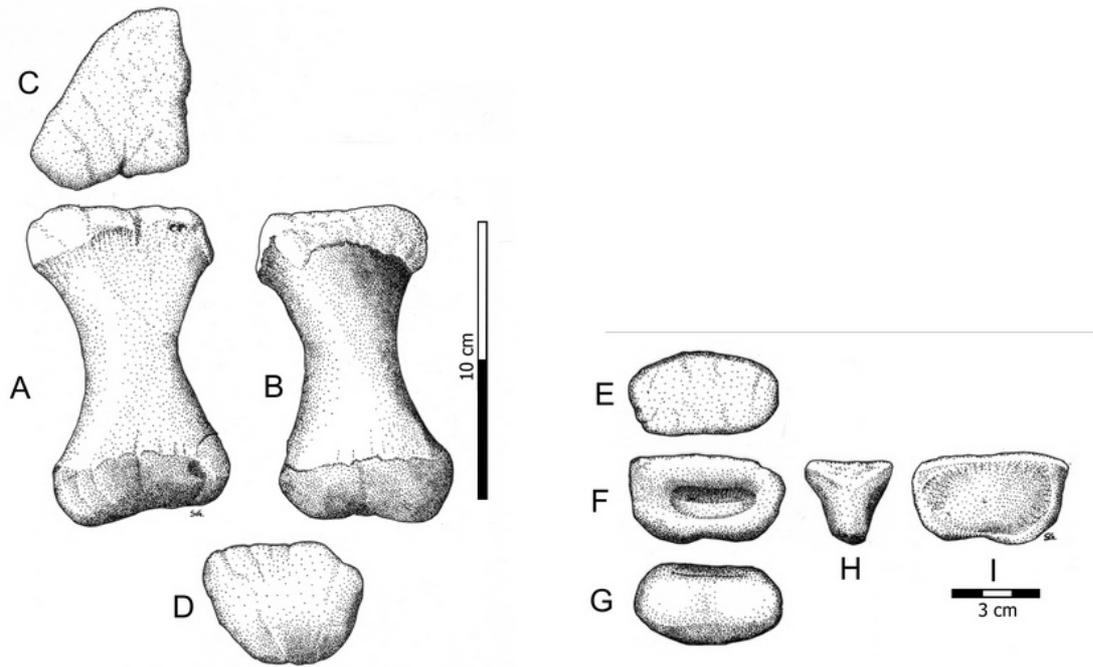
Figure S4. Manus elements of *Miragaia longicollum* ML433. A-D, right metacarpal I in dorsal (A), palmar (B), proximal (C), and distal (D) views; E-I, manual phalanx II-1 in proximal (E), dorsal (F), distal (G), lateral (H), and palmar (I) views.
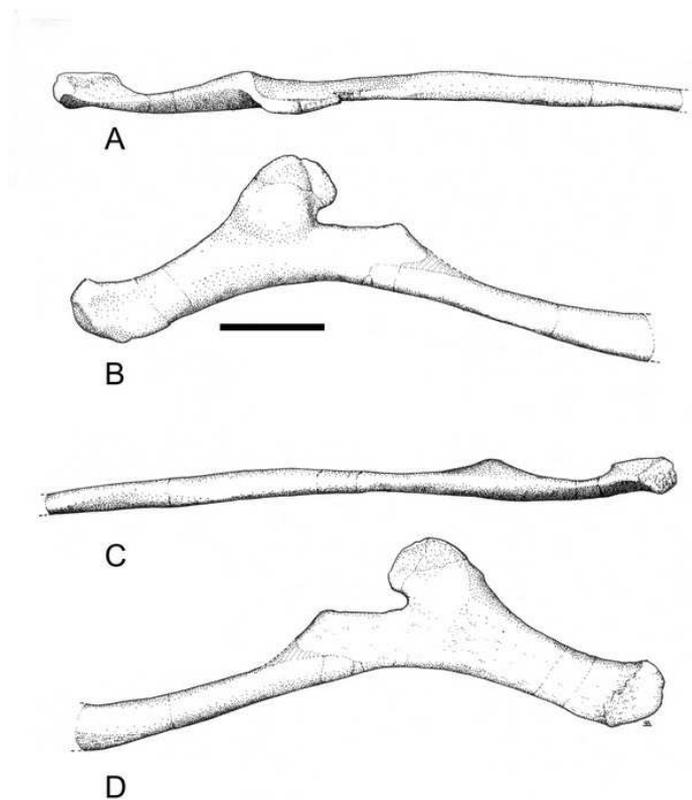
Figure S5. Right pubis of *Miragaia longicollum* in dorsal (A), lateral (B), ventral (C), and medial (D) views.
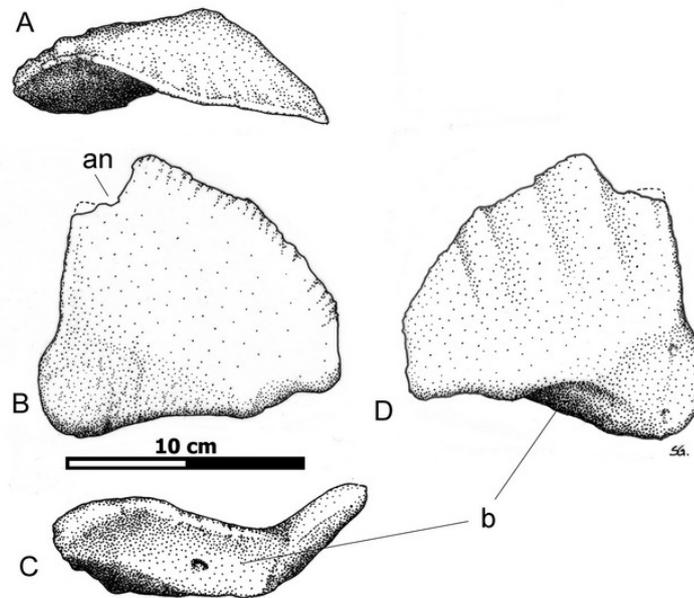
Figure S6. Osteoderm of *Miragaia longicollum* ML433 in dorsal (A), medial (B), ventral (C), and lateral (D) views.

2. NUMBER OF CERVICAL VERTEBRAE IN THYREOPHORANS

Colbert (1981: 12) stated that there were 24 presacral vertebrae in the basal thyreophoran *Scutellosaurus lawleri*. Examination by one of us (SCRM) suggests that the first presacral vertebra, as figured by Colbert, is actually the basioccipital, making the total number of presacral vertebrae 23 instead, although it is not clear whether all presacral vertebrae are present, and one or two may be missing.

In *Scutellosaurus,* neural arches are not fused to centra in the presacral series, and parapophyses are unclear: where visible they appear to be located on the neurocentral suture on all anterior presacral vertebrae (SCRM, pers. obs.). This makes determination of the number of cervical vertebrae problematic. Colbert (1981) suggested that there were nine cervical vertebrae on the basis that the sides of the first nine vertebrae were pinched for attachment of muscles to the occiput. The primitive number of cervical vertebrae for Ornithischia also appears to be nine (Santa Luca, 1980; Sereno 1999; Butler *et al.* 2008). Norman *et al.* (2004a) suggested that there were six or seven cervical vertebrae in *Scutellosaurus,* but gave no evidence for this observation and did not discuss their disagreement with Colbert (1981). Given the evidence available, it is most parsimonious to assume that *Scutellosaurus* retained the primitive nine cervical vertebrae.

Owen (1863) considered that the basal thyreophoran *Scelidosaurus* had a minimum of 22 presacral vertebrae, with perhaps one or two missing. Owen (1863) and Norman et al. (2004b) noted the presence of six cervical vertebrae on the holotype specimen (BMNH R1111) but both thought that at least one vertebra was missing from this region. An undescribed specimen (CAMSM X.39256) preserves a complete presacral series of 24 vertebrae, eight of which are cervical vertebrae, based upon the location of the parapophyseal facet (SCRM, pers. obs.). *Scelidosaurus* therefore had eight cervical and 16 dorsal vertebrae.

3. OSTEOLOGICAL MEASUREMENTS

Supplementary table 1. Vertebral measurements based upon the holotype of *Miragaia longicollum* (ML433). All measurements are in cm.

Vertebrae #	Length	Total height	Centrum height	Centrum width
3rd cerv.	7.5	10.3	4.6	6.5
4	8.6	10.0	4.9	6.9
5	9.3	10.2	5.7	7.2
6	9.5	11.9	5.5	8.2
7	10.6	12.1	6.3	8.0
8	10.6	13.0	6.7	8.4
9	11.0	13.5	7.0	9.3
10	11.1	14.8	7.0	9.8
11	10.8	15.5	7.5	9.4
12	10.5	17.5	7.6	10.6
13	10.9	17.9	7.6	11.7
14	11.0	20.1	9.0	10.8
15	10.0	23.8	9.0	11.4
16	9.5	26.9	9.4	11.4
17	8.5	28.8	9.2	11.4
1st dorsal vertebra	7.6	31.2	8.8	11.6
2nd dorsal vertebra	7.8	31.5	9.0	11.4
1st osteoderm	8.0	8.1	-	-
4th osteoderm	17.3	14.4	-	-
6th osteoderm	18.2	17.8	-	-

Supplementary table 2. Appendicular measurements based upon the holotype of *Miragaia longicollum* (ML433). All measurements are in cm

	Length	Proximal end transverse width	Distal end transverse width	Diaphyseal minimum perimeter
Left Humerus	71.5	34.4	23.8	36.9
Right Humerus	65,4	31.5	23.5	35.6

Left Ulna	56.1	19.8		
Right Ulna	57.6	20	9.8	21.7
Left Radius	45.8	13.6	13	20.5
Right Radius	46.0	13.7	15	20
Left Scapula	75*	46.5	-	-

* Estimated

4. METHODOLOGY FOR BROWSE HEIGHT ESTIMATION

Browse heights were estimated for all herbivores known from the Lourinhã Formation that are complete enough for acetabular height estimates to be made. These included *Lourinhasaurus alenquerensis, Lusotitan atalaiensis, Stegosaurus* sp*., Miragaia longicollum, Dryosaurus* sp*., Hypsilophodon* sp*.,* and *Draconyx loureiroi.* The methodology for browse height estimation was based upon acetabular height (femur length + tibia length; see Senter 2006 for imformation about neutral head height estimation) for sauropods and ornithopods, and forelimb (humerus + ulna) lengths for thyreophorans (Supplementary table 3). Although the sauropod *Dinheirosaurus* (Bonaparte & Mateus 1999) and the thyreophorans *Dracopelta* (Galton 1980) and specimens attributed to *Dacentrurus* (Lapparent & Zbyszewski 1957; Maidment *et al.* 2008) are known from the Lourinhã Formation, they are too incomplete to warrant browse height estimations. *Lusotitan atalaiensis* is a brachiosaurid known from postcranial elements, including limbs (Antunes & Mateus 2003). The humerus is estimated to be 2 m long, a similar size to that of *Brachiosaurus brancai*. Stevens & Parrish (2005) have calculated the maximum browse height of *Brachiosaurus* based upon reconstructions of maximum neck dorsi- and ventriflexion, and suggested that its maximum browse height was upwards of 6 m. We assume a similar maximum browse height for *Lusotitan*. The browse height of basal eusauropods such as *Lourinhasaurus* has not been calculated quantitatively, and they lack the conspicuous browsing specializations of diplodocoids and brachiosaurids (as ground-level and canopy browsers, respectively). Browse height estimations for *Lourinhasaurus* are therefore difficult to make. Here, we assume that *Lourinhasaurus* could have lifted its head up to six metres; three metres higher than acetabular height, and in accordance with the maximum browse heights of non-brachiosaurid sauropods found by Stevens & Parrish (1999, 2005).

Senter (2006) showed that acetabular height is a good estimator of the height at which the head was held when the neck was neither ventri- nor dorsiflexed (neutral head height) in sauropod dinosaurs. However, as shown by the reconstructions of Carpenter (1982: fig. 2a, 1984: fig. 2a) for ankylosaurs and Galton & Upchurch (2004: fig 16.1) for stegosaurs, forelimb length is a better estimator of neutral head height in thyreophorans because the hind limbs are so much longer than the forelimbs in these taxa, leading to a steep downward curvature of the vertebral column.

Estimates of browse heights in the bipedal ornithopods were carried out using reconstructions of *Hypsilophodon* and *Dryosaurus* from Norman *et al.* (2004a: fig. 18.8b) and Norman (2004b: fig. 19.13b) respectively. The total length of the presacral vertebral column, the length of the tail, and the height above ground of the acetabulum, as reconstructed, were measured for these two taxa. For these simple models, it was assumed that the vertebral column was kept more or less straight and that the acetabulum acted as a simple pivot. It was assumed that 50% of the tail would be able to flex to lie horizontally on the ground. Using this model, the maximum height to which the head was able to reach was therefore constrained by the point at which 50% of the tail was lying on the ground, with the vertebral column remaining straight and the

acetabulum acting as the point of rotation. The relationship between acetabular height and maximum head height was calculated and this relationship was used to estimate maximum browse heights of the Lourinhã Formation ornithopods. Maximum head height was found to be 2.2 times the height of the acetabulum in *Hypsilophodon*, and 2.6 times the height of acetabulum in *Dryosaurus*. The relationship was also 2.6 in *Camptosaurus*, and this ratio was used to reconstruct the maximum browse height in *Draconyx*. These are, of course, very simplified models, but serve to estimate approximate browse heights in these ornithischians.

In order to estimate browse heights in the stegosaurs *Stegosaurus* and *Miragaia*, the reconstruction of *Stegosaurus* in Galton & Upchurch (2004: fig. 16.1a) was used. *Stegosaurus* is the most closely related taxon to *Miragaia* for which we have a relatively complete skeleton. However, this requires the assumption that *Miragaia* and *Stegosaurus* had the same forelimb to hind limb ratio and the same length of the dorsal vertebral column. Further discoveries may prove these assumptions to be incorrect; but they do allow the comparison of browse heights based upon differing neck length and forelimb length alone. It was assumed that the maximum angle of flexure of the neck from the dorsal vertebral column was 90 degrees in both taxa. At this degree of flexure, the cervical and dorsal plates would have come into close contact, preventing further dorsiflexion. Total neck length was calculated by adding the total lengths of cervical vertebral centra 3 through 13 in *Stegosaurus* (USNM 4934) and 3 through 17 in *Miragaia*. The axis and atlas were excluded, as they are unknown in *Miragaia*. Total forelimb length was calculated by adding the humerus and ulna lengths for both specimens. The curvature of the dorsal vertebral column and distance between glenoid and acetabulum was kept constant and the reconstruction in Galton & Upchurch (2004: fig. 16.1a) was used to estimate this. The neck was extended at a 90 degree angle from the dorsal vertebral column measured at the glenoid. The maximum height above the ground could then be measured. Once again, these models are very simple, but serve for comparison, and detailed computational modelling is beyond the scope of this paper.

Browse heights (Supplementary table 3) indicate that the small basal ornithopods *Hypsilophodon* and *Dryosaurus* would have browsed or grazed no higher than 1 m on low growing vegetation such as lycopsids, bryophytes and ferns (Stevens & Parrish 2005). The ornithopod *Draconyx* and the stegosaurs *Stegosaurus* and *Miragaia* had similar neutral head heights of 1 - 1.5 m, and the stegosaurs may have been able to browse up to 2 - 2.5 m when their necks were in maximum dorsiflexion. This would allow these taxa to feed on the tallest sphenophytes and tree ferns (Stevens & Parrish 2005). The potential for *Draconyx* to rear onto its hind legs would allow for it to browse at a height of up to 4 m in height, allowing it to reach the tallest cycads (Stevens & Parrish 2005). The sauropods would have been able to browse on the tallest ginkgos and conifers (Stevens & Parrish 2005), and had browse heights in excess of 6 m.

The browse heights estimated for *Stegosaurus* and *Miragaia* are based upon a quadrupedal stance. However, it has been suggested that it may have been possible for stegosaurs to rear up onto their hind legs (Bakker 1986). The arguments put forward in favour of this centre around a suggestion that the centre of gravity would have been above the hips, the evidence for strong musculature but maximum flexibility in the tail, and the presence of T-shaped chevrons (Bakker 1986: 187–190). However, mathematical modelling of the centre of gravity in *Stegosaurus* has shown that it was anterior to the acetabulum (Henderson 1999: fig. 10b), and the presence of strong dorsal and lateral musculature and a flexible tail is unsurprising given the weight of the large dermal spines at the end of the tail, which would have been held above the ground by dorsal musculature. Furthermore, mathematical modelling has shown that tail spines of *Stegosaurus*, when swung from side to side, would have been a formidable weapon (Carpenter *et al.* 2005) and flexibility and strong lateral musculature would have been needed to deliver a damaging blow. Finally, T-shaped chevrons are not present in stegosaurs (Gilmore 1914: fig. 29). The chevrons of *Stegosaurus* are laterally compressed and posteriorly expanded distally, a shape that is sub-optimal for even weight distribution if the animal was resting on its tail. Therefore, although it is possible that, like most extant quadrupeds, *Stegosaurus* could have reared onto its hind limbs, there is no osteological evidence to suggest this was a habitual posture.

Supplementary table 3. Browse heights of Lourinhã Formation herbivores.

Taxon	Acetabular height above ground (m)	Forelimb length (m)	Maximum browse height (m)
Lourinhasaurus alenquerensis	3	-	6
Lusotitan atalaiensis	3.5	-	>6
Stegosaurus sp.	-	1.2	2.2
Miragaia longicollum	-	1.2	2.5
Dryosaurus sp.	< 0.5		1.1
Hypsilophodon sp.	< 0.5		1.1
Draconyx loureiroi	1.5		4

Supplementary table 4. Comparison of the width to length ratio of specific cervical vertebrae in stegosaurs.

Cervical number	*Huayangosaurus* (ZDM T7001)	*Stegosaurus armatus* (from Gilmore, 1914)	*Miragaia longicollum*
3	2.3	1.3	1.2
4	1.3	1.6	1.2
5	0.9	1.2	1.3
6	0.9	?	1.2
7	1.3	?	1.3
8	0.6	?	1.3
9	0.8	?	1.2

5. CLADISTIC ANALYSIS

Miragaia longicollum was added to an altered version of the data matrix of Maidment *et al.* (2008). Four additional characters were included (22, 24, 49 and 74 in the new analysis) and scored for all stegosaurian and basal thyreophoran taxa based upon first-hand observation by S.C.R.M. Information for ankylosaurian taxa was obtained from the literature. Analyses were carried out following the methodology outlined in Maidment *et al.* (2008). A branch-and-bound search resulted in five MPTs of length 3713, with tree statistics as follows: CI = 0.617; RI = 0.718; RC = 0.458. Strict, Adams and 50% Majority-Rule consensus trees were calculated and are shown in Fig. S7. A decay index PAUP file was written in MacClade and analysed in PAUP, and the results are shown on Fig. S7a (see below). A bootstrap analysis with 10000 replicates using the heuristic search method was carried out, and the results are shown on Fig. S7a.

The addition of *Miragaia* to the analysis of Maidment *et al.* (2008) resulted in the collapse

of *Tuojiangosaurus* and *Paranthodon*, found to be derived in the latter analysis, into a polytomy at the base of Stegosauria. This is probably due to the fragmentary nature of both specimens: 96.5% of the data is missing for *Paranthodon* and 76.5% is missing for *Tuojiangosaurus*, making them the least complete taxa in the analysis and therefore vulnerable to topological changes as additional operational taxonomic units (OTUs) are added. More complete specimens of these taxa are required to resolve their taxonomic positions.

6. RESULTS OF THE CLADISTIC ANALYSIS
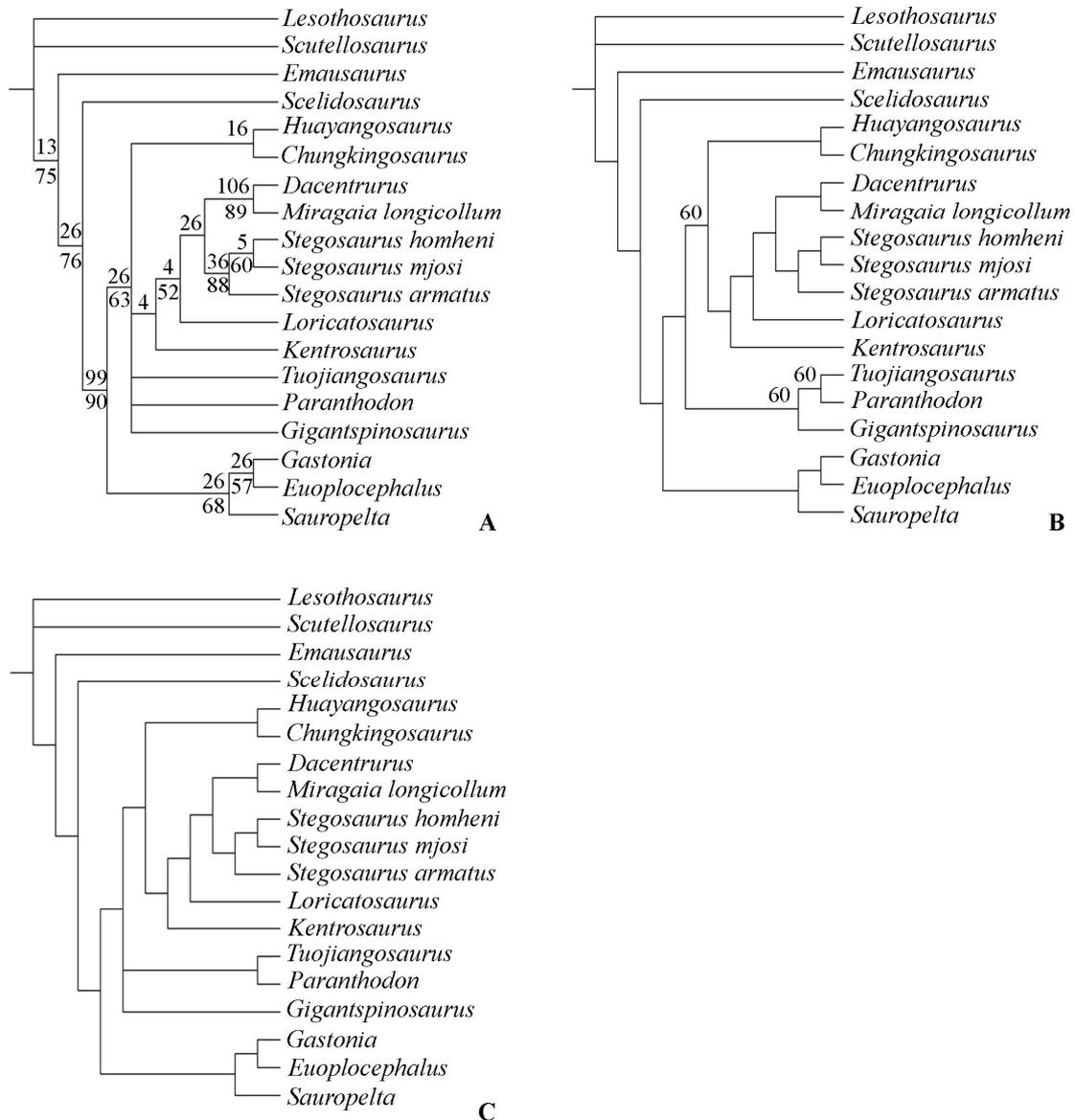
Figure S7. **A,** strict consensus of five MPTs obtained by a branch-and-bound search. Figures above nodes are decay indices. Because of the constraints of the gap weighting methodology, all characters were weighted to a value of 26 in this analysis. Therefore, a decay index of 26 in this analysis is equal to a decay index of 1 in an analysis where all characters are given a weighting of 1. Figures below nodes are bootstrap percentages. Only those bootstrap percentages greater than 50% are shown. **B,** 50% Majority-Rule consensus tree. Values above nodes represent the percentage of MPTs in which the grouping was obtained; nodes without values were obtained in 100% of MPTs. **C,** Adams consensus tree. A clade containing *Paranthodon* and *Tuojiangosaurus* has been collapsed to the base of Stegosauria, suggesting that these taxa are unstable, fitting into several places in the tree and causing multiplication of MPTs.

10

7. CHARACTER LIST

The following characters were used in the cladistic analysis. A full description of these characters can be found in Maidment *et al*. (2008). Four characters (22, 24 , 49 and 74) not used by Maidment *et al.* (2008) have been added and are described below.

1. Skull, overall shape in posterior view: deeper than wide (0); wider than deep (1).
2. Snout, depth: depth to length ratio of maxilla coded using Gap Weighting.
3. Premaxilla: Broad 'V' or 'U' shaped notch between premaxillae on the midline absent (0); present (1).
4. Premaxilla: Height to length ratio of subnarial portion coded using Gap Weighting.
5. Maxilla: tooth row inset medially from the lateral surface of the maxilla absent (0); present (1).
6. Frontals: form the dorsal rim of the orbit (0); supraorbital elements form the dorsal rim of the orbit (1).
7. Parietals, dorsal surface: convex (0); flat (1).
8. Quadrate: fossa/fenestra absent (0); present (1).
9. Quadrate: proximal head strongly transversely compressed, absent (0); present (1).
10. Quadrate: head is strongly arched posteriorly relative to the shaft, absent (0); present (1).
11. Quadrate: axis extending through condyles in posterior view orientated transversely (0); orientated strongly ventromedially (1).
12. Quadrate: contact with paroccipital process unfused (0); fused (1).
13. Quadrate: lateral ramus present (0); absent (1).
14. Dentary: tooth row in lateral view visible (0); not visible (1).
15. Dentary: tooth alveoli face dorsally (0); dorsomedially (1).
16. Dentary: tooth row in lateral view straight (0); sinuous (1).
17. Premaxillary teeth: present (0); absent (1).
18. Maxillary teeth: cingulum absent (0); present (1).
19. Skull roof: cortical remodelling absent (0); present (1).
20. Skull roof: cortical remodelling present in only some bones (0); present in all bones, along with the fusion of dermal ossifications, so that the antorbital and supratemporal fenestrae are closed (1).
21. Atlas: neural arch, contact with intercentrum in adults, not fused (0); fused (1).
22. Cervical vertebrae: number coded using Gap Weighting. Cervical vertebrae are those that bear parapophyses on the sides of the centrum rather than on the neural arch. The number of cervical vertebrae varies throughout Thyreophora, although few taxa are complete enough for the complete number of cervical vertebrae to be known.
23. Posterior cervical vertebrae: postzygapophyses not greatly elongated (0); greatly elongated and project over the back of the posterior centrum facet (1).
24. Cervical ribs: contact with para- and diapophyses of cervical vertebrae: unfused (0); fused (1). Cervical vertebrae are those that bear parapophyses on the sides of the centrum rather than on the neural arch. In most thyreophoran taxa, cervical ribs remain unfused to the cervical vertebrae. However, in some taxa the cervical ribs are fused to both the para- and diapophyses.
25. Dorsal vertebrae: all centra longer than wide (0); wider than long (1).
26. Dorsal vertebrae: neural arch to neural canal height ratio coded using Gap Weighting.
27. Dorsal vertebrae: centrum height to neural arch height ratio coded using Gap Weighting.
28. Dorsal vertebrae: centrum height to neural canal height ratio coded using Gap Weighting.
29. Dorsal vertebrae: fusion of prezygapophyses absent (0); present (1).
30. Dorsal vertebrae: prezygapophyses are fused only in middle and posterior dorsals (0); fused on all dorsals (1).
31. Dorsal vertebrae: transverse processes project approximately horizontally (0); at a high angle to the horizontal (1).

32. Anterior caudal vertebrae: transverse processes on cd3 posteriorly are directed laterally (0); directed strongly ventrally (1).

33. Anterior caudal vertebrae: dorsal process on transverse process absent (0); present (1).

34. Anterior caudal vertebrae: neural spine height less than or equal to the height of the centrum (0); greater than the height of the centrum (1).

35. Anterior caudal vertebrae: bulbous swelling at tops of neural spines absent (0); present (1).

36. Posterior caudal vertebrae: centra are elongate (0); equidimensional (1).

37. Caudal vertebrae: transverse processes on distal half of tail present (0); absent (1).

38. Scapula: proximal plate area to coracoid area ratio coded using Gap Weighting.

39. Scapula: acromial process in lateral view, convex upwards dorsally (0); quadrilateral with a posterordorsal corner (1).

40. Scapula: acromial process projects dorsally (0); projects laterally (1).

41. Scapula: blade, distally expanded (0); parallel sided (1).

42. Scapula and coracoid: unfused (0); fused (1).

43. Coracoid: in lateral view, foramen present (0); notch present (1).

44. Humerus: ratio of width of distal end to minimum shaft width coded using Gap Weighting.

45. Humerus: triceps tubercle and descending ridge posterolateral to the deltopectoral crest absent (0); present (1).

46. Humerus: ratio of transverse width of distal end to length coded using Gap Weighting.

47. Humerus: anterior iliac process length to humerus length coded using Gap Weighting.

48. Ulna: proximal width to length ratio coded using Gap Weighting.

49. Ulna: olecranon horn absent (0); present (1). The olecranon horn is an ossification that appears to be fused to the top of the olecranon process. Posteriorly, it is convex and in anterior view it is concave and hollow.

50. Ratio of humerus length to ulna length coded using Gap Weighting.

51. Ungual phalanges: Manual and pedal unguals claw-shaped (0); hoof-shaped (1).

52. Ilium: anterior iliac process to acetabular length ratio coded using Gap Weighting.

53. Ilium: anterior iliac process lies approximately horizontally (0); strongly angled ventrally (1).

54. Ilium: anterior iliac process projects roughly parallel to the parasagittal plane (0); diverges widely from the parasagittal plane (1).

55. Ilium: horizontal lateral enlargement absent (0); present (1).

56. Ilium: horizontal lateral enlargement incipient (small) (0); large (1).

57. Ilium: supra-acetabular flange present (0); absent (1).

58. Ilium: supra-acetabular flange projects at 90 degrees from the anterior iliac process absent (0); present (1).

59. Ilium: ratio of acetabular length to dorsoventral height of pubic peduncle of ilium coded using Gap Weighting.

60. Ilium: posterior iliac process, distal shape tapers (0); blunt (1).

61. Ilium: medial processes on posterior iliac processes absent (0); present (1).

62. Ilium: ventromedial flange backing the acetabulum absent (0); present (1).

63. Ilio-sacral block: Five or more sacral vertebrae (0); four or fewer sacral vertebrae (1).

64. Ilio-sacral block: Posterior sacral rib angled laterally (0); posterolaterally (1).

65. Ilio-sacral block: dorsal shield of sacrum is perforated by foramina in between ribs (0); is solid with no foramina (1).

66. Ischium: convex proximal margin within the acetabulum absent (0); present (1).

67. Ischium: dorsal surface of shaft is straight (0); has a distinct angle at approximately midlength (1).

68. Ischium: posterior end of ischium, expanded relative to the shaft (0); not expanded and tapers (1).

69. Pubis: obturator notch is backed by posterior pubic process absent (0); present (1).

70. Pubis: prepubis to postpubis length ratio coded using Gap Weighting.

71. Pubis: postpubis to acetabular length ratio coded using Gap Weighting.

72. Pubis: posterior end of postpubis relative to shaft, not expanded (0); expanded (1).

73. Pubis: acetabular portion faces laterally, posteriorly and dorsally (0); faces wholly laterally (1).

74. Pubis: anterior end of prepubis expanded dorsally absent (0); present (1). The anterior end of the prepubis of some taxa is expanded dorsally so that in lateral view, the anterior end of the prepubis possesses a knob-like process projecting dorsally.

75. Femur: Fourth trochanter prominent and pendant (0); present as a rugose ridge (1); absent (2).

76. Femur: anterior trochanter fused to greater trochanter in adults absent (0); present (1).

77. Femur: length to humerus length ratio coded using Gap Weighting.

78. Femur: length to tibia length ratio using Gap Weighting.

79. Pedal digit I: present (0); absent (1).

80. Pedal digit III: has 4 or more phalanges (0); has 3 phalanges (1); has 2 or fewer phalanges (2).

81. Pedal digit IV: has 5 phalanges (0); has 4 phalanges (1); has 3 or fewer phalanges (2).

82. Dermal armour: including scutes, and/or spines and/or plates absent (0); present (1).

83. Plates and spines: two parasagittal rows of plates and/or spines absent (0); present (1).

84. Cervical collars: U-shaped cervical collars composed of keeled scutes absent (0); present (1).

85. Osteoderms: mosaic of small osteoderms between larger osteoderms on the ventral surfaces of the neck, trunk, and proximal portions of the limbs absent (0); present (1).

86. Parascapular spine: absent (0); present (1).

87. Dorsal plates: have a thick central portion like a modified spine (0); have a generally transversely thin structure, except at the base (1).

88. Parasagittal rows of dermal armour: paired (0); alternating either side of the midline (1).

89. Ossified epaxial tendons: present (0); absent (1).

8. CHARACTER-TAXON MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Lesothosaurus	0	A	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	?	0	?	0	0
Scutellosaurus	?	?	0	0	1	0	0	?	?	?	?	?	0	0	0	1	0	0	1	0	0	0	?	0
Emausaurus	0	F	?	R	1	0	?	?	?	?	?	?	?	?	0	0	1	0	0	?	?	0	?	0
Scelidosaurus	?	A	0	D	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	3	0	0
Huayangosaurus	0	R	0	H	1	1	0	1	1	0	1	0	1	0	0	1	0	0	1	0	1	3	0	0
D. armatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Miragaia	?	?	1	4	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	?	R	1	1
Loricatosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
Kentrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	?	?	1	?	0	0
Paranthodon	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?
Chungkingosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tuojiangosaurus	?	?	?	?	0	?	0	?	?	?	?	?	?	1	1	?	?	1	?	?	?	?	?	?
Gigantspinosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	1	?	?	?	?	?	0
S. homheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. armatus	0	0	1	8	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0	1	A	1	0
S. mjosi	0	?	?	?	1	1	1	1	1	1	1	0	1	?	?	?	1	?	1	0	0	F	1	0
Gastonia	1	?	1	?	1	1	1	0	?	0	?	1	1	?	?	?	1	0	1	1	?	3	0	0
Sauropelta	1	?	?	?	1	1	0	0	?	0	1	1	1	0	0	1	1	1	1	1	1	3	0	0
Euoplocephalus	1	?	1	?	1	1	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	3	0	0

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Lesothosaurus	0	0	R	N	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	P	0	0	0	0
Scutellosaurus	0	0	P	L	0	?	0	0	0	?	?	0	1	7	0	0	0	0	0	3	0	0	3	?
Emausaurus	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Scelidosaurus	0	1	K	H	0	?	1	0	0	1	0	0	0	2	0	0	0	0	0	L	0	H	?	?
Huayangosaurus	0	?	?	8	1	0	1	?	?	?	0	0	0	0	0	0	1	1	?	L	1	H	8	?
D. armatus	1	G	3	D	?	?	1	0	1	1	1	?	?	?	?	?	?	?	?	0	1	8	3	6
Miragaia	1	?	?	?	?	?	1	?	?	?	?	?	?	J	1	0	?	?	?	3	1	H	?	K
Loricatosaurus	0	9	5	B	1	1	1	0	1	1	?	?	1	?	?	?	?	?	?	5	1	H	?	6
Kentrosaurus	0	3	0	0	1	0	1	0	1	1	1	1	0	E	0	0	1	1	0	F	1	R	B	6
Paranthodon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chungkingosaurus	0	N	6	R	?	?	1	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Tuojiangosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gigantspinosaurus	0	?	?	?	1	0	0	0	0	1	0	?	0	?	0	0	0	1	0	?	1	H	?	?
S. homheni	0	1	4	J	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. armatus	0	R	3	1	1	1	1	1	1	1	1	1	1	R	1	0	1	0/1	0/1	5	1	H	E	D
S. mjosi	0	4	B	G	1	1	1	1	1	1	1	1	1	?	?	?	1	?	?	A	1	R	E	D
Gastonia	0	0	Q	M	1	1	1	0	0	1	0	0	1	?	?	1	0	1	0	F	0	R	H	R
Sauropelta	0	0	D	B	1	1	1	0	0	0	0	0	1	B	?	1	1	1	0	R	0	8	?	K
Euoplocephalus	0	0	M	J	1	1	1	0	1	?	?	0	1	9	?	1	0	1	1	F	0	8	R	D

	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Lesothosaurus	0	R	0	0	0	0	0	?	1	0	0	?	0	1	?	?	?	0	0	0	0	?	R	0
Scutellosaurus	?	?	?	?	0	0	1	0	1	0	?	?	0	1	0	?	?	0	0	0	0	?	?	?
Emausaurus	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Scelidosaurus	?	?	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0	0	1	0	H	0
Huayangosaurus	0	?	1	E	1	0	1	1	0	0	0	0	0	0	1	0	0	0	?	?	1	?	J	1
D. armatus	1	7	?	D	0	1	1	1	0	0	?	1	0	?	1	0	?	0	0	1	0	5	K	1
Miragaia	1	E	1	B	0	1	1	1	0	0	?	1	0	?	?	?	?	?	0	?	0	?	?	1
Loricatosaurus	0	0	?	?	?	?	1	1	0	?	?	?	?	?	?	?	?	0	1	1	0	?	?	1
Kentrosaurus	0	0	1	D	0	1	1	1	0	0	9	0	0	1	1	1	1	0	1	1	0	9	E	1
Paranthodon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chungkingosaurus	?	?	?	9	1	0	1	1	0	0	7	0	0	?	1	1	0	?	?	?	?	?	?	?
Tuojiangosaurus	?	?	?	P	1	1	1	1	0	0	5	0	0	?	1	0	0	?	?	?	?	?	?	?
Gigantspinosaurus	0	?	?	?	0	1	1	1	0	0	?	0	0	?	1	0	0	?	?	?	?	?	?	0
S. homheni	?	?	1	B	1	1	1	1	0	1	R	1	1	0	1	0	1	?	?	?	?	?	?	?
S. armatus	0	0	1	G	1	1	1	1	0	1	E	1	1	0	1	0	1	0	1	1	0	5	K	0
S. mjosi	0	0	1	B	1	1	1	1	0	1	8	1	1	0	1	0	1	0	1	1	0	5	G	1
Gastonia	0	4	?	8	0	1	1	1	1	0	?	0	0	?	1	0	0	1	1	1	?	?	?	?
Sauropelta	0	7	1	?	0	?	1	1	1	0	?	0	0	0	1	0	0	0	1	1	1	?	?	?
Euoplocephalus	0	4	1	R	1	1	1	1	1	0	2	0	0	0	1	0	0	1	0	?	0	R	0	0

	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Lesothosaurus	0	?	0	0	E	0	0	?	?	0	0	0	0	0	?	?	?
Scutellosaurus	0	?	?	0	0	3	?	?	?	1	0	0	0	0	?	?	0
Emausaurus	?	?	?	?	?	?	?	?	?	1	0	0	0	0	?	?	?
Scelidosaurus	0	0	0	0	?	8	0	0	0	1	0	1	0	0	?	?	0
Huayangosaurus	1	0	1	1	4	?	1	?	?	1	1	0	0	?	0	0	0
D. armatus	1	1	2	1	7	?	?	?	?	1	1	0	?	?	0	?	1
Miragaia	1	1	?	?	?	?	?	?	?	1	1	0	0	?	1	0	?
Loricatosaurus	1	0	2	1	J	?	?	?	?	1	1	?	?	1	1	?	?
Kentrosaurus	1	0	2	1	J	J	1	2	2	1	1	0	0	1	0	0	1
Paranthodon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chungkingosaurus	?	?	?	?	?	?	?	?	?	1	1	?	0	?	0	0	?
Tuojiangosaurus	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?
Gigantspinosaurus	?	?	2	1	E	L	?	?	?	1	1	0	0	1	0	0	0
S. homheni	?	?	?	?	?	?	?	?	?	1	1	?	?	?	1	?	?
S. armatus	1	0	2	1	R	P	1	2	2	1	1	0	0	0	1	1	1
S. mjosi	1	0	2	1	M	R	1	?	?	1	1	0	0	0	1	?	0
Gastonia	?	?	1	1	R	?	?	?	?	1	0	1	1	0	?	?	?
Sauropelta	0	?	0	1	B	D	0	0	1	1	0	1	1	0	?	?	0
Euoplocephalus	1	0	?	1	?	?	1	0	2	1	0	1	1	0	?	?	?

Letters A-R (excluding I) represent numbers 10-25 and are used for Gap-Weighted characters.

9. SYNAPOMORPHIES AND CLADE DEFINITIONS

THYREOPHORA Nopcsa, 1915

All genasaurs more closely related to *Ankylosaurus* than to *Triceratops* (Sereno 1998)

Unambiguous synapomorphies:

- Maxillary tooth row inset medially from the lateral surface of the maxilla (reversed in *Tuojiangosaurus* and *Paranthodon*)
- Dentary tooth row sinuous in lateral view (reversed in *Stegosaurus armatus*)
- Cortical remodelling of the skull roof present
- Horizontal lateral enlargement of the ilium present
- Dermal armour, including scutes, and/or spines, and/or plates present

Additional synapomorphy under ACCTRAN:

- Axis extending through quadrate condyles in posterior view angled strongly ventromedially (equivocal in *Scutellosaurus* and *Emausaurus*)

THYREOPHOROIDEA Nopsca, 1915

Scelidosaurus, Ankylosaurus, their most recent common ancestor and all of its descendants (Sereno, 1986; Maidment *et al.* 2008)

Unambiguous synapomorphies:

- Supraorbital elements form the dorsal rim of the orbit
- Anterior caudal neural spine height is greater than the height of the centrum (reversed in *Sauropelta*)

Additional synapomorphy under ACCTRAN:

- U-shaped cervical collars composed of keeled scutes present (lost in Stegosauria)
- Transverse processes present on caudal vertebrae in the distal half of the tail (assumes basal state is 1, reversed in Ankylosauria and *Loricatosaurus* + *Stegosaurus* + Dacentrurinae)

Additional synapomorphies under DELTRAN:

- Axis extending through quadrate condyles in posterior view angled strongly ventromedially (equivocal in *Scutellosaurus* and *Emausaurus*)
- Transverse processes of dorsal vertebrae project at a high angle to the horizontal (reversed in *Gigantspinosaurus*; equivocal in *Emausaurus*)
- Four or fewer sacral vertebrae with ribs that contact the acetabulum (equivocal in *Emausaurus*)
- Horizontal lateral enlargement of the ilium well developed (equivocal in *Emausaurus*)

EURYPODA Sereno, 1986

Stegosaurus, Ankylosaurus, their most recent common ancestor and all of their descendants (Sereno 1998)

Unambiguous synapomorphies:

- Quadrate lateral ramus absent
- Premaxillary teeth absent (reversed in *Huayangosaurus*)
- Maxillary teeth have crowns that have a prominent and ring-like cingulum (reversed in *Gastonia* and *Huayangosaurus*)
- Atlas neural arch fused to intercentrum (reversed in *Stegosaurus mjosi*)
- Prezygapophyses fused on some dorsal vertebrae
- Scapula and coracoid fused (reversed in some members of *Stegosaurus armatus*)
- Manual and pedal unguals hoof-shaped
- Anterior iliac process projects at an angle that diverges widely from the parasagittal plane (reversed in Huayangosauridae)
- Ventromedial flange backing the acetabulum present (reversed in *Kentrosaurus*)
- Dorsal surface of distal ischial shaft has a distinct angle at approximately midway along the shaft (reversed in *Euoplocephalus* and *Dacentrurus*)
- Posterior end of ischium is not expanded relative to the shaft
- Anterior trochanter of femur is completely fused to the greater trochanter in adults

Additional synapomorphies under ACCTRAN

- Broad 'V' or 'U' shaped notch present on the premaxillae where they meet on the midline (reversed in *Huayangosaurus*)

- Posterior iliac process tapers distally (assumes state 1 is basal; reversed in *Loricatosaurus* + *Stegosaurus* + Dacentrurinae, equivocal in *Loricatosaurus*)
- Acetabular portion of the pubis faces wholly laterally (reversed in *Sauropelta*)
- Pedal digit I absent (reversed in *Sauropelta*)
- Pedal digit IV has three or fewer phalanges (reversed to state 1 in *Sauropelta*)

There are no additional synapomorphies under DELTRAN

STEGOSAURIA Marsh, 1877

All eurypods more closely related to *Stegosaurus* than to *Ankylosaurus* (Sereno 1998)

Unambiguous synapomorphies:

- Triceps tubercle and descending ridge posterolateral to the deltopectoral crest of the humerus present
- Fourth trochanter absent or indistinct (reversed to be present as a rugose ridge in *Huayangosaurus*)
- Two parasagittal rows of plates and/or spines present
- Parascapular spine present (reversed in *Stegosaurus*)

Additional synapomorphies under ACCTRAN:

- Quadrate fossa/fenestra present (equivocal in *Gigantspinosaurus, Paranthodon* and *Tuojiangosaurus*)

- Quadrate proximal head strongly transversely compressed (equivocal in *Gigantspinosaurus, Paranthodon* and *Tuojiangosaurus*)

- Prezygapophyses fused in middle and posterior dorsal vertebrae only (assumes basal state is 1, reversed in *Loricatosaurus* + *Stegosaurus* + Dacentrurinae)
- Scapular blade parallel-sided (reversed in *Gigantspinosaurus*, convergent in *Sauropelta*)
- Pedal digit III has two or fewer phalanges (equivocal in non-stegosaurid stegosaurs)
- Cervical collars of keeled scutes lost

Additional synapomorphies under DELTRAN:

- Supra-acetabular flange present (convergent in *Scelidosaurus*)
- Acetabular portion of pubis faces laterally (convergent in *Euoplocephalus*)
- Pedal digit I absent (convergent in *Euoplocephalus*)

HUAYANGOSAURIDAE Dong, Tang & Zhou, 1982

All stegosaurs more closely related to *Huayangosaurus* than to *Stegosaurus* (Maidment *et al.* 2008)

Unambiguous synapomorphies

- Anterior iliac process projects at an angle roughly parallel to the parasagittal plane
- Anterior iliac process is strongly angled ventrally in lateral view (convergent in *Stegosaurus, Tuojiangosaurus* and *Euoplocephalus*)
- Posterior end of postpubis expanded relative to the shaft (convergent in Stegosauridae)

Additional synapomorphies under DELTRAN:

- Quadrate fossa/fenestra present (equivocal in Gigantspinosaurus, Paranthodon and Tuojiangosaurus)

- Quadrate proximal head strongly transversely compressed (equivocal in Gigantspinosaurus,

Paranthodon and Tuojiangosaurus)

- Scapular blade parallel-sided (convergent in Stegosauridae)

STEGOSAURIDAE Marsh, 1880

All stegosaurs more closely related to *Stegosaurus* than to *Huayangosaurus* (Sereno 1998)

Unambiguous synapomorphies:

- Alveoli of dentary tooth row not visible in lateral view (convergent in *Tuojiangosaurus*)
- Dorsal process on transverse process of caudal vertebrae present (convergent in *Euoplocephalus*)
- Anterior caudal vertebrae with bulbous swellings at the top of neural spines
- Posterior caudal vertebrae equidimensional
- Sacral shield solid with no foramina in between sacral ribs of adults in dorsal view
- Posterior end of postpubis expanded relative to the shaft (convergent in Huayangosauridae, reversed in *Stegosaurus armatus*)
- Ossified epaxial tendons absent (reversed in *Stegosaurus mjosi*)

Additional synapomorphies under ACCTRAN:

- Dorsal surface of parietals flat (equivocal in Stegosauridae other than *Stegosaurus*)
- Quadrate head strongly arched posteriorly (equivocal in Stegosauridae other than *Stegosaurus*)
- Obturator notch of pubis not backed by shaft of postpubis (convergent in *Euoplocephalus*)

Additional synapomorphies under DELTRAN:

• Quadrate fossa/fenestra present (equivocal in *Gigantspinosaurus*, *Paranthodon* and *Tuojiangosaurus*)

• Quadrate proximal head strongly transversely compressed (equivocal in *Gigantspinosaurus*, *Paranthodon* and *Tuojiangosaurus*)

- Scapular blade parallel-sided (convergent in Huayangosauridae and *Sauropelta*)
- Pedal digit III has two or fewer phalanges (equivocal in non-stegosaurid stegosaurs)
- Pedal digit IV has three or fewer phalanges (convergent in *Euoplocephalus*)

LORICATOSAURUS + *STEGOSAURUS* + **DACENTRURINAE (unnamed clade)**

Unambiguous synapomorphy:

- Dorsal dermal plates have a transversely thin structure (reversed in *Dacentrurus armatus*)

Additional synapomorphy under ACCTRAN:

- Acromial process of scapula quadrilateral with a posterodorsal corner (equivocal in *Loricatosaurus*)

Additional synapomorphies under DELTRAN:

- Prezygapophyses fused on all dorsals (assumes basal state is 0, convergent in Ankylosauria)
- Transverse processes on distal half of tail absent (assumes basal state is 0, convergent in Ankylosauria and *Scutellosaurus*)

STEGOSAURUS + **DACENTRURINAE (unnamed clade)**

Unambiguous synapomorphy:

- Postzygapophyses of cervical vertebrae elongated and project posterior to the posterior centrum facet

Additional synapomorphies under DELTRAN:

- Broad 'U' or 'V' shaped notch in dorsal view between the premaxillae where they meet on the midline anteriorly (convergent in ankylosaurids)
- Acromial process of scapula quadrilateral with a posterodorsal corner (equivocal in *Loricatosaurus*)
- Posterior iliac process blunt distally (assumes basal state is 0, convergent in *Scelidosaurus*, equivocal in *Loricatosaurus*)

STEGOSAURUS Marsh, 1877

Stegosaurinae, as defined by Sereno (1998), is synonymous with the genus *Stegosaurus* in this analysis, as *Stegosaurus* and *Dacentrurinae* are sister taxa.

Unambiguous synapomorphies:

- Transverse processes on caudal vertebra three are directed strongly ventrally
- Anterior iliac process angled strongly ventrally in lateral view (convergent in Huayangosauridae, *Tuojiangosaurus* and *Euoplocephalus*)
- Supra-acetabular flange of ilium projects at 90 degrees from the anterior iliac process
- Medial process on posterior iliac process present

Additional synapomorphies under DELTRAN:

- Dorsal surface of parietals flat (equivocal in Stegosauridae other than *Stegosaurus*, convergent in *Gastonia*)
- Quadrate proximal head strongly arched posteriorly (equivocal in Stegosauridae other than *Stegosaurus*)

DACENTRURINAE n. clade

All stegosaurs more closely related to *Dacentrurus armatus* (Owen, 1875) than to *Stegosaurus armatus* Marsh, 1877.

Unambiguous synapomorphies:

- Cervical ribs fused to para- and diapophyses of cervical vertebrae
- Dorsal vertebral central wider than long
- Olecranon horn present
- Anterior end of prepubis expanded dorsally

10. INSTITUTIONAL ABBREVIATIONS:

BMNH: The Natural History Museum, London, U.K; **CAMSM**: The Sedgwick Museum, University Of Cambridge, U.K.; **ML**: Museum of Lourinhã, Portugal; **USNM**: United States National Museum, Washington D. C., U.S.A; **ZDM**: Zigong Dinosaur Museum, Sichuan Province, People's Republic of China.

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