

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 (Serenó 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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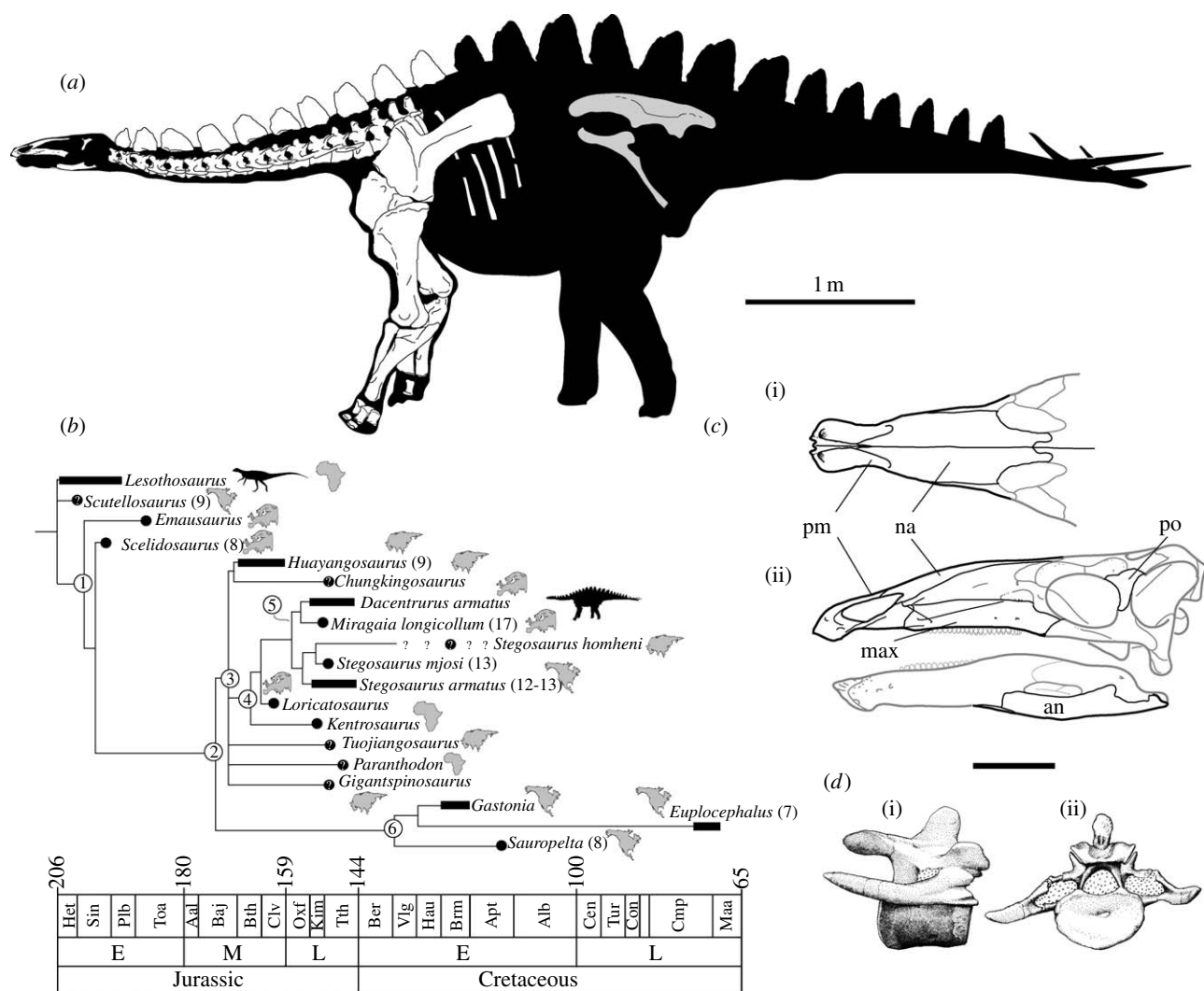


Figure 1. (a) Skeletal reconstruction of *M. longicollum* based on type specimen ML433, except the ilium and pubis (in grey), which are based upon the referred specimen (ML433-A), and have been scaled up. (b) Phylogeny and chronostratigraphy of Stegosauria. Strict consensus of five MPTs obtained from 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, Euryopoda; 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 §2e, 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 apices 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 periosteum. 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 (Serenio 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 & Serenio 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
<i>Scutellosaurus</i>	23	9	14
<i>Scelidosaurus</i>	24	8	16
<i>Huayangosaurus</i>	25	9	16
<i>Stegosaurus armatus</i>	26–27	12–13	13–14
<i>Stegosaurus mjosi</i>	26	13	13
<i>Miragaia</i>	?	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 short-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 (Serenó & 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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