Alcheringa: An Australasian Journal of Palaeontology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/talc20

A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation

Xabier Pereda-Suberbiola [a] , Peter M. Galton [b e f] , Heinrich Mallison [c] & Fernando Novas [d]

[a] Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencia y Tecnología, Departamento de Estratigrafía y Paleontología, Apartado 644, Bilbao, 48080, Spain

[b] 1065 Vintage Drive, Rio Vista, CA, 94571-9775, USA E-mail:

[c] Museum für Naturkunde, Leibniz-Institute für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Germany E-mail:

[d] CONICET, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Avenida Ángel Gallardo 470, Buenos Aires, 1405, Argentina E-mail:

[e] College of Naturopathic Medicine, University of Bridgeport, CT, 06604, USA

[f] Peabody Museum of Natural History, Yale University, New Haven, CT, 06520, USA

Version of record first published: 31 Aug 2012

To cite this article: Xabier Pereda-Suberbiola, Peter M. Galton, Heinrich Mallison & Fernando Novas (2012): A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation, Alcheringa: An Australasian Journal of Palaeontology, DOI:10.1080/03115518.2012.702531

To link to this article: http://dx.doi.org/10.1080/03115518.2012.702531

A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation

XABIER PEREDA-SUBERBIOLA, PETER M. GALTON, HEINRICH MALLISON and FERNANDO NOVAS

PEREDA-SUBERBIOLA, X., GALTON, P.M., MALLISON, H. & NOVAS, F. i*First* article. A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation. *Alcheringa*, 1–14. ISSN 0311-5518.

A re-evaluation of several vertebrae and dermal plates from the Lower Cretaceous (La Amarga Formation, Puesto Antigual Member; Barremian–lower Aptian) of Neuquén in Argentina, originally described as a stegosaurian dinosaur and recently referred to an indeterminate ornithischian, confirms the former identification. The Neuquén remains have a combination of features that is only known among stegosaurs: cervical vertebrae with a proportionally large cross-section of the neural canal, the anterior height and width of which are half the height of the anterior centrum, as in the cervical vertebrae of *Kentrosaurus*, *Dacentrurus* and *Stegosaurus*; prominent lateral depressions on the cervical centra, as in the presacral vertebrae of *Dacentrurus*; and cervical dermal plates that are subtriangular, longer than high and reminiscent of those of *Miragaia*. Moreover, a small bone here interpreted to be an anterior supraorbital (= first palpebral) is similar to that of *Stegosaurus* and other stegosaurs in having an elongate form and a dorsal rugose surface. The remains from Argentina exhibit some differences relative to other stegosaurs, suggesting that it is potentially a distinct taxon, but their incompleteness advises against the erection of a new genus and species. Interestingly, it is the only known skeletal record of Stegosauria in South America. It provides the second conclusive evidence of the presence of this clade in the Early Cretaceous of the Gondwanan landmasses.

X. Pereda-Suberbiola [xabier.pereda@ehu.es], Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencia y Tecnología, Departamento de Estratigrafía y Paleontología, Apartado 644, 48080 Bilbao, Spain; P.M. Galton[pgalton@bridgeport.edu], 1065 Vintage Drive, Rio Vista, CA 94571-9775, USA; H. Mallison [heinrich.mallison@googlemail.com], Museum für Naturkunde, Leibniz-Institute für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Germany; F. Novas [fernovas@yahoo.com.ar], CONICET, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Avenida Ángel Gallardo 470, Buenos Aires 1405, Argentina. *Also affiliated with Peabody Museum of Natural History, Yale University, New Haven, CT 06520, USA; College of Naturopathic Medicine, University of Bridgeport, CT 06604, USA.* *Received 5.3.2012; revised 7.6.2012; accepted 11.6.2012.*

Key words: Stegosauria, Lower Cretaceous, La Amarga Formation, Neuquén, Argentina, Gondwana, biogeography, vertebrae, dermal plates.

THE FOSSIL RECORD of thyreophoran dinosaurs from South America includes fragmentary skeletal remains of ankylosaurs and stegosaurs from Argentina (Coria & Cambiaso 2007, Novas 2009). Ankylosaurs are represented by postcranial elements from the Upper Cretaceous Allen Formation of Río Negro (Coria & Salgado 2001 and references therein). Other putative ankylosaurian remains from Patagonia were discussed by Novas (2009). In addition, ankylosaurian footprints have been described from the Late Jurassic–Early Cretaceous and the Late Cretaceous of Bolivia (Leonardi 1984, McCrea *et al*. 2001, Apesteguía & Gallina 2011) and, with reservations, from the Early Cretaceous of Brazil (Thulborn 1990). Stegosaurs are only represented by a set of bones from the Early Cretaceous of Argentina (Bonaparte 1996a, b) and by trackways from the Jurassic–Cretaceous boundary of Bolivia (Apesteguía & Gallina 2011).

Bonaparte (1995) first noted the presence of stegosaurs in the Early Cretaceous of Argentina. Bonaparte (1996a) mentioned the discovery of two incomplete cervical vertebrae and a caudal centrum (MACN N-43) from the La Amarga Formation, Neuquén. In another paper, Bonaparte (1996b) listed three vertebrae, including a posterior cervical with features typical of Stegosauria, and a probable small osteoderm, 'only 45 mm long, of triangular section, with a concave facet at its base' (Bonaparte 1996b, p. 110). Bonaparte (1996b) assigned the La Amarga remains to Stegosauria indet. and noted that the taxon was related to *Kentrosaurus* from Tanzania. This identification has been followed in synthetic works on Patagonian dinosaurs (Coria & Cambiaso 2007, Novas 2009). Recently, Ezcurra & Agnolín (2012, app. 1, 2) have included the Neuquén taxon as a basal stegosaur in a supertree of late Mesozoic archosaurs. However, Maidment *et al*. (2008) regarded the material as belonging to

ISSN 0311-5518 (print)/ISSN 1752-0754 (online)

http://dx.doi.org/10.1080/03115518.2012.702531

an indeterminate ornithischian because it does not bear any autapomorphies that allow it to be referred to Stegosauria (also Maidment 2010).

The aim of this paper is to revise and illustrate the presumed stegosaurian specimen from the La Amarga Formation of Argentina and to evaluate its affinities.

Institutional abbreviations. DMNH, Denver Museum of Nature and Science (formerly Denver Museum of Natural History), Colorado, USA; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MfN, Museum für Naturkunde—Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Germany; YPM, Peabody Museum of Natural History, Yale University, New Haven, CT, USA.

Geological setting

The fossils described below derive from the basal member (Puesto Antigual Member) of the La Amarga Formation (Leanza & Hugo 1995), which is well exposed in the southern part of the Neuquén Basin. According to Leanza *et al*. (2004), the La Amarga Formation unconformably overlies the transitional interval of the marine Agrio Formation (Lower Cretaceous, Hauterivian) and is overlain by the continental Lohan Cura Formation (Lower Cretaceous, upper Aptian–Albian). Based on basin analysis, stratigraphical relationships and tectonosedimentary interpretations, the La Amarga Formation is considered to be Barremian to early Aptian in age (Leanza *et al.* 2004). The basal Puesto Antigual Member (about 30 m in thickness, Barremian–lower Aptian) consists mainly of fluvial channel sandstones of a braided river system with well-developed palaeosols on top (Leanza *et al.* 2004).

Most of the vertebrate remains found in the La Amarga Formation come from the basal Puesto Antigual Member (Leanza *et al*. 2004). They have been recovered from several stratigraphical levels exposed on the northern slope of the China Muerta Hill, approximately 2.5 km southeast of the bridge over the La Amarga Creek, near the National Road 40, and about 70 km south of Zapala, in Neuquén Province, Argentina (Fig. 1; see also Apesteguía 2007, fig. 1, Novas 2009, figs 4.7, 7.1). The assemblage includes theropods (the abelisauroid *Ligabueino andesi*, a carcharodontosaurid-like basal tetanuran), sauropods (the dicraeosaurid *Amargasaurus cazaui*, the titanosaurian *Amargatitanis macni*, indeterminate titanosauriforms and rebbachisauroids), pterosaurs (an indeterminate pterodactyloid), mesoeucrocodylians (*Amargasuchus minor*) and the cladotherian mammal *Vincelestes neuquenianus* (Bonaparte 1996b, Leanza *et al*. 2004, Apesteguía 2007, Novas 2009, Fuente *et al*. 2007 and references therein). The stegosaurian remains described by Bonaparte (1996a, b) constitute the only ornithischian dinosaur from the La Amarga Formation.

The stegosaurian fossils were found in 1985 by José Bonaparte, Martín Vince and assistants (Bonaparte 1996a). According to J.F. Bonaparte (pers. comm. 2012), all the remains but one were found near the type locality of the mammal *Vincelestes neuquenianus*. The less complete cervical vertebra, which has a lighter colour than the other remains, was recovered at about 100 m from the type locality of *Amargasaurus cazaui*. It is possible that this vertebra comes from a stratigraphically older bed than the remainder of the material (J.F. Bonaparte, pers. comm.).

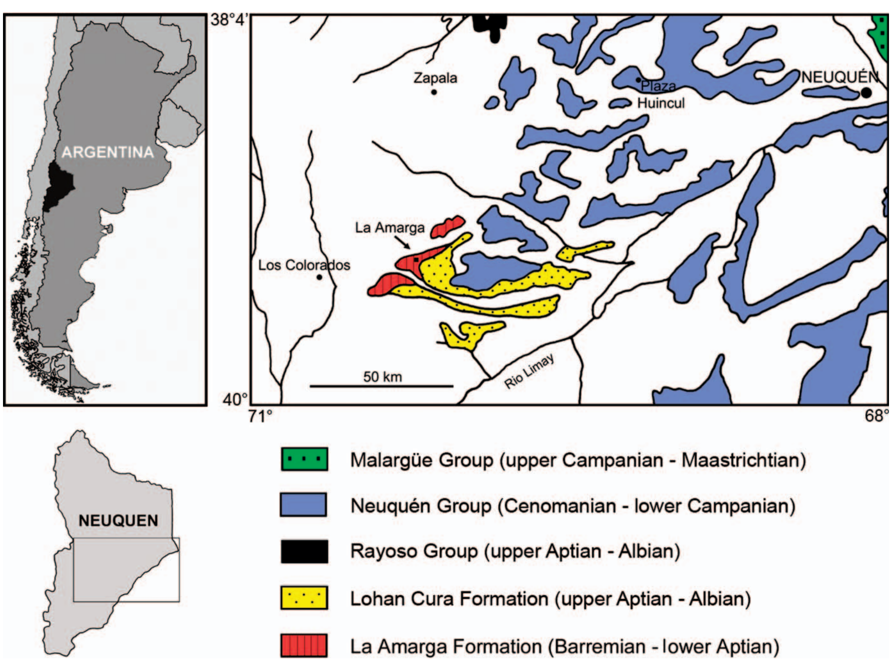

Fig. 1. Location map of the La Amarga Creek (Neuquén province, Argentina) where the stegosaurian remains were found. Geological sketch modified from Leanza *et al*. (2004, fig. 1).

Systematic palaeontology

ORNITHISCHIA Seeley, 1887
THYREOPHORA Nopcsa, 1915 *sensu* Norman, 1984
STEGOSAURIA Marsh, 1877

Stegosauria gen. et sp. indet.

Material. MACN N-43, a possible right anterior supraorbital, two cervical vertebrae, an isolated cervical prezygapophysis, part of the shaft of a rib, an anterior caudal centrum, a cervical plate and a possible second element from the dermal skeleton (Table 1); casts as YPM 058055.

Locality, unit and age. About 2.5 km southeast of the bridge at the La Amarga Creek, Catan Lil Department, Neuquén Province, Argentina; basal Puesto Antigual Member, La Amarga Formation, Lower Cretaceous, Barremian–lower Aptian (Leanza *et al*. 2004).

Skull

Supraorbital (?). The small osteoderm described by Bonaparte (1996b) bears no resemblance to those of any thyreophoran, be it the scutes of the Early Jurassic *Scelidosaurus* (Owen, 1863) and *Scutellosaurus* (Colbert, 1981), the lateral scutes of the stegosaur *Huayangosaurus* (Zhou, 1984), the paired dermal plates of any stegosaur (Gilmore 1914, Dong *et al*. 1983, Dong 1990, Galton & Upchurch 2004), the gular ossicles of *Stegosaurus* (Gilmore 1914), or the dermal armour of ankylosaurs (Ford 2000, Blows 2001b). However, comparisons with a partial skull roof of *Stegosaurus stenops* (Fig. 2F–L, for complete skull roof see Galton & Upchurch 2004, figs 16.2A, B, Sereno & Dong 1992, figs 10A, B) indicate that this bone (Fig. 2A–E) may be an isolated complete right anterior supraorbital (= first palpebral) of a stegosaur. The concave articulation on the wide end of the bone (l, Fig. 2C) fitted against the angular part of the lacrimal (cf. Fig. 2K, L), the largest subtriangular rugose area is the dorsal surface (Fig. 2A, I), and the gently rounded rugose orbital edge forms a gentle arch in lateral view (o, Fig. 2B; cf. Fig. 2G). The ventral surface (Fig. 2D) is bisected by a ridge, with the orbital margin (orb) lateral to it (cf. Fig. 2K), whereas medial to it are the sutural surfaces that overlapped the prefrontal (pf) more anteriorly and the middle supraorbital (ms) more posteriorly (this ventral surface is hidden by the prefrontal and the middle supraorbital in the skull roof of *Stegosaurus*, Fig. 2G). The obliquely truncated rugose posterior edge is the sutural surface for the posterior supraorbital (ps, Fig. 2A, D, E; cf. Figs 2G, I, K).

Axial skeleton

This portion of the skeleton consists of three incomplete vertebrae, two cervicals and a caudal (Fig. 3), plus an isolated cervical prezygapophysis. In addition, a fragmentary bone could be part of a dorsal rib.

Cervical vertebrae. The best-preserved cervical vertebra consists of the centrum and most of the neural arch, including the neural pedicles and the postzygapophyses (Fig. 3A–E; see also Bonaparte 1996b, fig. 44, Coria & Cambiaso 2007, fig. 7.2A–B, Novas 2009, fig. 7.3A–D). The massive centrum is amphiplatyan to slightly amphicoelous. The articular surfaces are roughly hemispherical to a dorsoventrally compressed oval. Both are mostly eroded, although anteriorly the central part has a slight dorsoventral concavity that is transversely flat. The transverse width of the centrum is greater than its height or length (Table 1). Laterally, most of the centrum and the adjacent part of the neural arch have a pair of deep elliptical depressions, with the

Skeletal elements	Measurements													
?Skull	L	W												
Possible anterior supraorbital	44	19												
Vertebrae			D_a	D_p	H	H_a	H_p	L'	W_a	W_p				
8th cervical			34	34	102*	41	42	41	58	52				
10th cervical			–	–	–	36*	–	42	57	–				
First caudal			–	–	–	35*	38*	34	52	52				
Dermal armour											H	L	W'	W''
Cervical plate											80	85	19	7
?Cervical plate											64*	90	22	3

Table 1. Measurements (mm) of MACN N-43. Abbreviations: D_a = anterior diameter of neural canal; D_p = posterior diameter of neural canal; H = maximum height; H_a = anterior height of centrum; H_p = posterior height of centrum; L = maximum length; L' = centrum length; W = maximum width; W_a = anterior width of centrum; W_p = posterior width of centrum; W' = anterior transverse width; W'' = posterior transverse width; *as preserved.

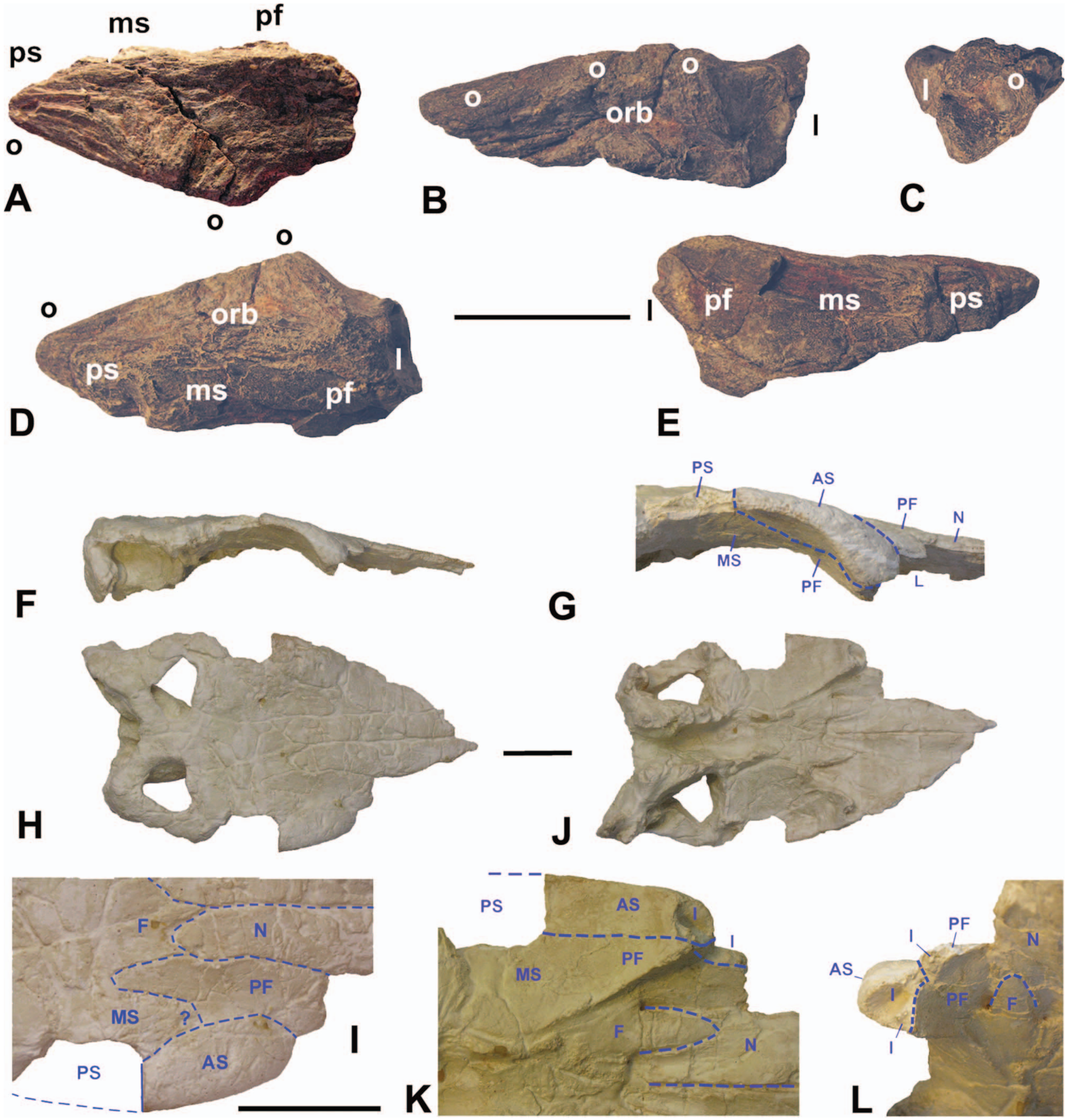

Fig. 2. **A–E**, Stegosauria indet., La Amarga Formation (Barremian), Argentina. MACN N-43, possible right anterior supraorbital in dorsal (**A**), lateral (**B**), anterior (**C**), ventral (**D**) and medial (**E**) views. **F–L**, *Stegosaurus stenops*, DMNH 1483, from Morrison Formation (Upper Jurassic) of Garden Park near Cañon City, Colorado, USA, most of skull roof (**F, H, J**) and detail of the right anterior supraorbital and adjacent bones (**G, I, K, L**) in right lateral (**F, G**), dorsal (**H, I**), ventral (**J, K**), and anteroventral (**L**) views. Abbreviations: bones—AS, anterior supraorbital; F, frontal; L, lacrimal; MS, medial supraorbital; N, nasal; PF, prefrontal; PS, posterior supraorbital; structures—o, orbital rim; orb, orbital margin; sutural surfaces indicated by bone abbreviation in lower case. Scale bars = 20 mm (A–E) and 50 mm (short bar for F, H, J; large bar for G, I, K, L).

ventral one being slightly wider and deeper than the dorsal one (Fig. 3C). The parapophysis is located close to the anterior edge of the centrum, slightly below the floor of the neural canal and approximately level with the dorsal depression. It projects laterally and the articular surface is gently concave and posterolaterally directed. The broad ventral surface of the centrum is mostly flat transversely and slightly concave anteroposteriorly. Posterolaterally, the ventral rim is thickened to form a large triangular area with an apex that projects anteriorly; the less thickened anterolateral area has a corresponding posteriorly projecting process (Fig. 3E). The neural canal is very large; its maximum diameter is greater than half the width or height of the centrum. Its outline is roughly circular with a flat floor in

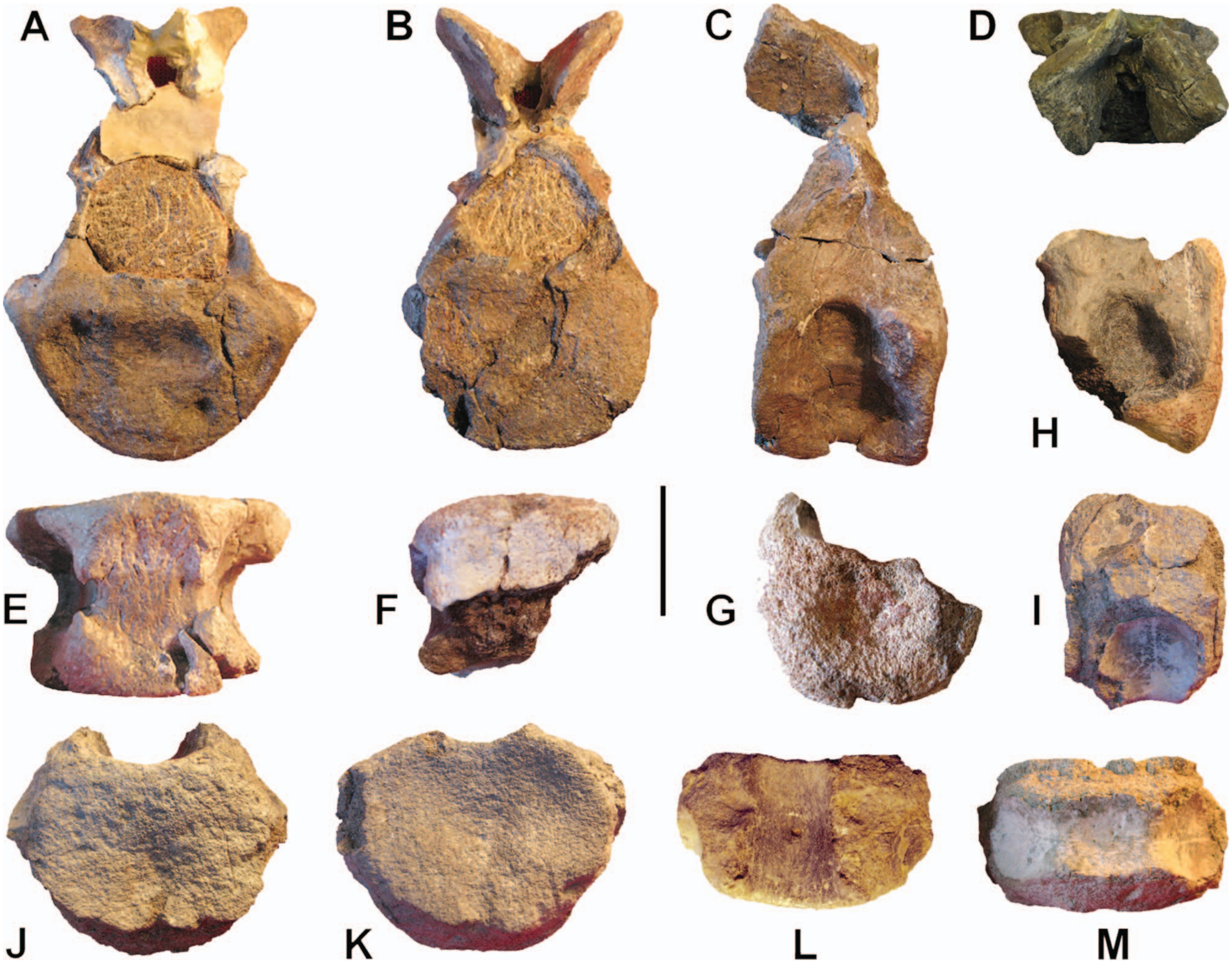

Fig. 3. Stegosauria indet., La Amarga Formation (Barremian), Argentina. MACN N-43, vertebrae. **A–E**, 8th cervical vertebra in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**) and ventral (**E**) views; **F–H**, 10th cervical vertebra in ventral (**F**), posterior (**G**) and right lateral (**H**) views; **I–M**, first caudal vertebra in left lateral (**I**), anterior (**J**), posterior (**K**), dorsal (**L**) and ventral (**M**) views. Scale bar = 30 mm.

anterior view and roughly pear-shaped in posterior view (Fig. 3A, B). One of the diapophyses (probably the right one) was originally complete (Bonaparte 1996b, fig. 44B), but only the most proximal parts of both are now preserved. They are located at the level of the top of the neural canal. The triangular and flat articular surfaces of the postzygapophyses are not ventrally continuous with each other and are oriented ventrolaterally, forming an angle of about 50° to the vertical (Fig. 3B, D). The postzygapophysis does not project beyond the posterior articular surface of the centrum.

Bonaparte (1996b) regarded this vertebra as a posterior cervical, possibly the seventh, and comparisons with figures of the cervical series of the MfN mounted skeleton of *Kentrosaurus aethiopicus* (MB.R.4777-4843) in lateral, ventral and posterior views indicate that it is probably the eighth (Fig. 4G–I). It must be noted that Hennig's restoration of *Kentrosaurus* was mostly based on disarticulated material (Hennig 1925, Janensch 1925). Cervical and dorsal vertebral formulae and the position of the individual specimens were determined based on comparison with *Stegosaurus* (Marsh 1880, 1891, 1896, Gilmore 1914). In contrast, the German Tendaguru Expedition found four articulated nearly complete tails, so that the positions of the individual caudal vertebrae are known with certainty (Hennig 1925).

A second cervical vertebra, which was found separately from the rest of the material, only preserves part of the centrum, including the anterior articular surface, the right parapophysis and most of the right lateral side plus the base of the adjacent part of the neural arch (Fig. 3F–H). The centrum is wider than long and high, its length being about the same as that of the other cervical. The anterior articular surface is flat to slightly concave. The parapophysis does not project laterally and the articular facet is larger than that of cervical 8. Laterally, the single depression is as deep as those of the preceding cervical, but its dorsoventral height is smaller (Fig. 3H). The floor of the large neural canal is incomplete on the left side of the centrum. Ventrally, the preserved flat anterior part of the centrum is much wider than in the more complete cervical. This vertebra is regarded as a more

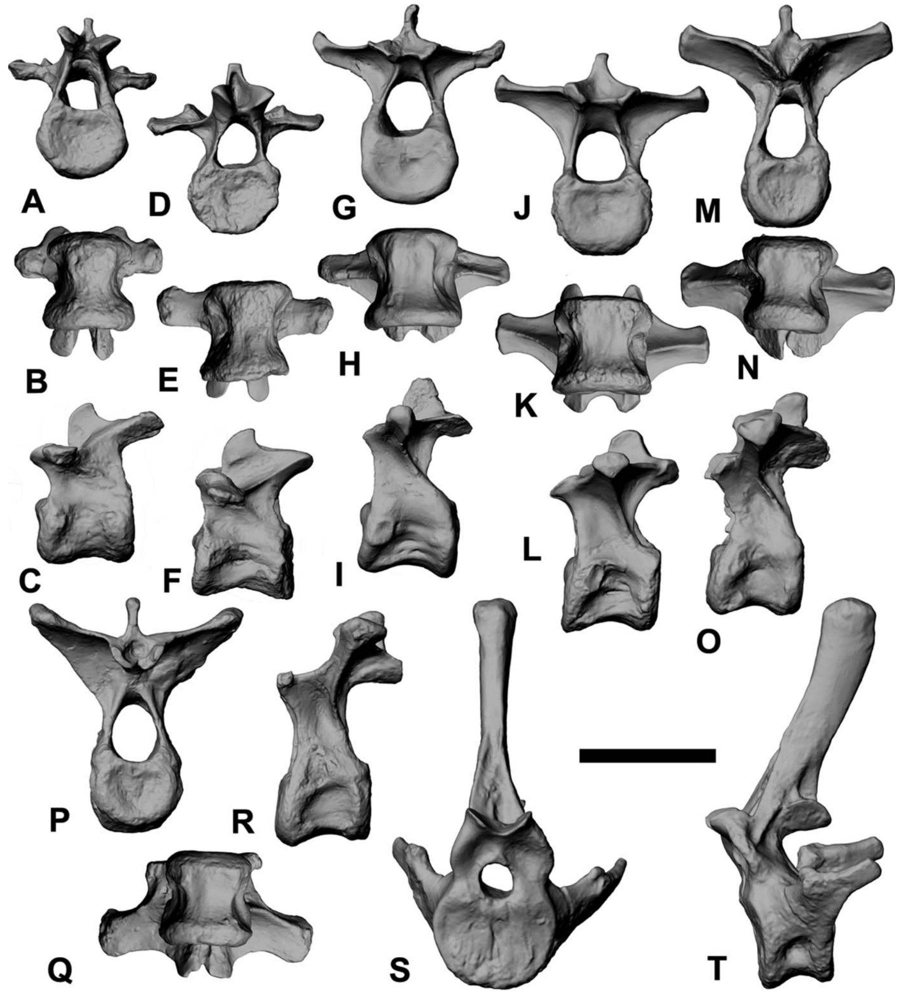

Fig. 4. HR digital scans of *Kentrosaurus aethiopicus*, Tendaguru Formation (Upper Jurassic), quarry St. Kindope, Tanzania. MfN mounted skeleton. **A–C**, presacral (cervical) vertebra 6 (**A–C**, MB.R.4783), 7 (**D–F**, MB.R.4784), 8 (**G–I**, MB.R.4785), 9 (**J–L**, MB.R.4786), 10 (**M–O**, MB.R.4787), and 11 (?dorsal 1) (**P–R**, MB.R.4788) in posterior (**A, D, G, J, M**), ventral (**B, E, H, K, N, Q**) and left lateral (**C, F, I, L, O, R**) views; **S–T**, second caudal (first free caudal) vertebra (MB.R.4800.6) in anterior (**S**) and left lateral (**T**) views. Scale bar = 100 mm.

posterior cervical and, based on comparisons with *Kentrosaurus* (Fig. 4M–O), it is probably cervical 10.

The articular surface of an isolated right prezygapophysis is roughly oval and smaller than those of the postzygapophysis of the more complete cervical 8. Laterally, the broken base of the lamina of the diapophysis extends from the anterior end across the middle of the prezygapophysis, so it is probably from a mid-cervical vertebra.

Caudal vertebra. A caudal vertebra preserves the centrum and the basal region of the neural arch (Fig. 3I–M). The centrum is short, wider than high, and the articular end surfaces are roughly oval in outline (Fig. 3J, K). The surface identified as the anterior one (see below) is asymmetrical. The dorsal half is gently convex dorsoventrally and transversely. The lower half is gently concave dorsoventrally and for the most part gently convex transversely except for the central part, which is gently concave. The posterior surface is uniformly gently concave. Both articular surfaces are damaged in the ventral region, so the presence or absence of chevron facets can not be determined (Fig. 3M). The broken bases of the transverse processes are on the dorsal half of the lateral side of the centrum. In lateral view, each process is preserved as an oblique prominence, with a small concavity anterodorsal to it (Fig. 3I). The neural canal is wider anteriorly than posteriorly (Fig. 3L).

Bonaparte (1996b) identified this centrum as that of a proximal caudal vertebra, here considered as the first caudal. This vertebra is missing in the MfN mounted skeleton of *Kentrosaurus aethiopicus*, but in other specimens it is incorporated into the sacrum as a caudosacral (Hennig 1925, Mallison 2010, caption to fig. 5). The tapering of the neural canal represents the posterior end of the sacral enlargement, the irregular form of the anterior articular surface indicating that it keyed in against the free end surface of the last fused sacral centrum, and the uniformly concave posterior surface was the first freely movable joint for the tail. The form of these articular surfaces agrees with those of the first caudal vertebra of *Chialingosaurus kuani* (Late Jurassic, China; Dong *et al*. 1983, fig. 70). In caudals 2–8 of the MfN mounted skeleton, the anterior and posterior articular surfaces are uniformly concave (Fig. 4S–T). This is also the case for the anterior caudals of the YPM mounted skeleton of *Stegosaurus ungulatus*, in which the caudosacral is incorporated into the sacrum (Ostrom & McIntosh

1999, pls 21, 25, 26, 31 for sacrum, caudals 3, 5, 1 and 2, respectively). However, the Argentinian centrum is not as anteroposteriorly short relative to its height or width as are the most anterior caudals in *Huayangosaurus* (Zhou 1984), *Chialingosaurus*, *Chungkingosaurus* (Dong *et al*. 1983), *Dacentrurus*, *Loricatosaurus* (Galton 1985) and especially *Stegosaurus* (Ostrom & McIntosh 1999).

Rib (?). A fragmentary bone looks like part of a damaged dermal plate. The bone is thin, but all surfaces are eroded except for the smooth inferior surface, which is gently concave longitudinally and gently convex transversely. It is tentatively identified as the inferior part of the mid-length of the shaft of a dorsal rib.

Dermal skeleton

Cervical plate. An incomplete dermal plate was first described by Novas (2009, p. 345, fig. 7.3E, F). It is subtriangular in shape and longer than high (Fig. 5A–D, Table 1). The anterior edge and the proximal part of the ventral edge are unbroken but, apart from the missing posterodorsal apex, the remaining edges are only slightly incomplete (Fig. 5A, D). In side view, the thin anterior edge is gently convex. The plate is transversely thin and tapers posteriorly (Fig. 5A). The presumed medial surface is gently convex vertically and anteroposteriorly but the prominent depression on the anterodorsal part is an artefact of erosion (Fig. 5C). The thick anterior basal portion, which is triangular in outline, is continued posterodorsally as a thickened area, which laterally is undercut more ventrally to form a prominent depression (Fig. 5D). In armour of the stegosaur *Miragaia* (Late Jurassic, Portugal) the posterior half of the thickened area forms a more prominent edge that extends ventrolaterally, so the undercut region forms the ventral depression of the plate (see Mateus *et al*. 2009, fig. S6 in supplementary information). In the MfN mounted skeleton of *Kentrosaurus*, the thickened area forms an

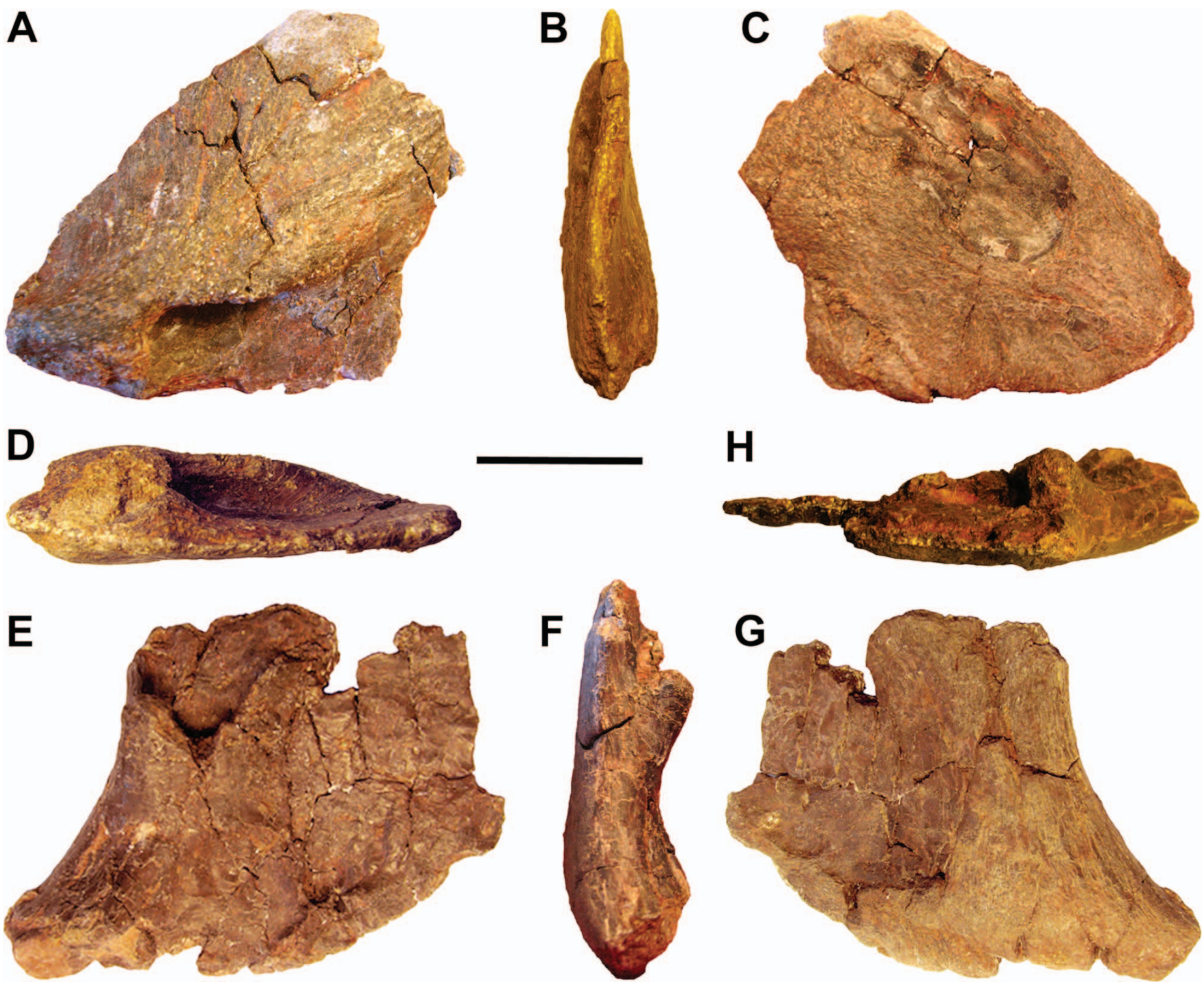

Fig. 5. Stegosauria indet., La Amarga Formation (Barremian), Argentina. MACN N-43, dermal armour. **A–D**, cervical plate in lateral (**A**), anterior (**B**), medial (**C**) and ventral (**D**) views; **E–H**, ?cervical plate in lateral (**E**), anterior (**F**), medial (**G**) and dorsal (**H**) views. Scale bar = 30 mm.

extremely prominent laterally directed horizontal flange above the depression in the sixth dermal plate (Hennig 1925, fig. 55, Galton 1982, pl. 5, figs 19–21). The rest of the ventral edge and the posterior edges are thin, so the plate is probably missing only a little bone in these regions. The sides are ornamented by a fine network of small grooves (canaliculi of Novas 2009). This plate was found associated with cervical remains and presumably comes from the neck (see below).

Dermal plate (?). A second piece is similar in size to the preceding plate (Table 1) and the ventral edge seems to be almost complete (Fig. 5E–G). The anterior half of the medial surface is gently convex but the posterior half is gently concave. The anterior edge has a concave outline. In lateral view (Fig. 5E), the anterior thick, triangular, rugose area is slightly smaller than in the other plate. However, the thick rounded anterior edge arises directly from it, with no thin anterior edge, and there is only a slight depression posteroventrally, so there is no overhang (Fig. 5E). In anterior view, the thick rounded edge becomes slightly thinner and thickens again before reaching the broken thick anterodorsal part of the plate (Fig. 5F). Despite this anterodorsal thickening, which is very unusual for a dermal plate, and the apparent absence of an evident ornamentation by small grooves (canaliculi), the similarities to the other plate, including the shape, the thickened triangular rugose area anteriorly and the presence of a depression anteroventrally (very strongly developed in the first plate), support the current anatomical identification.

Discussion

With the exception of the cervical vertebra of Fig. 3F–H, the bones from the La Amarga Creek were closely associated and presumably belong to a single individual. The cervical vertebra, here regarded as the eighth (Fig. 3A–E), indicates that it was probably a subadult or adult individual because the neural arches are fused to the centra (Irmis 2007). The lack of incorporation of the first caudal vertebra into the sacrum indicates that the individual was probably not fully grown. The size of the vertebrae and dermal plates indicates a small animal. The vertebrae are similar in size to those of *Kentrosaurus*, which has an estimated body length of about 4–5 m (Galton & Upchurch 2004).

Bonaparte (1996b) identified the material as stegosaurian on the basis of the large neural canal of the cervical vertebrae. He compared the vertebrae with those of *Stegosaurus* from the Late Jurassic of North America and noted that the morphology of the ventral and lateral sides of the centra and of the neural arch agrees well with the anterior cervicals figured by Marsh (1880) and in the Marsh lithographic plates reproduced by Ostrom & McIntosh (1966, pls 7–9, also in 1999). In addition, Bonaparte (1996b) noted that the cervical vertebrae from Patagonia are similar in size to those of *Kentrosaurus* from the Late Jurassic of Tanzania, but the centra are anteroposteriorly shorter. Bonaparte's interpretation (1996a, b), followed by Coria & Cambiaso (2007) and Novas (2009), was recently challenged by Maidment *et al*. (2008), who regarded the material as belonging to an indeterminate ornithischian due to the lack of autapomorphies that allow it to be referred to Stegosauria (see also Maidment 2010).

Cervical vertebra 8 from Neuquén was found in association with dermal elements, as typically occurs in thyreophorans (Sereno 1999, supplement, Maidment *et al*. 2008). Cortical remodelling of some bones of the skull roof (Figs 2A, F, G) is an unambiguous synapomorphy for Thyreophora, as is the presence of three supraorbitals forming the dorsal rim of the orbit for the Thyreophoroidea (*Scelidosaurus* + Stegosauria + Ankylosauria) (Maidment *et al*. 2008, p. 40, also Maidment 2010, Maidment & Porro 2010). The elongate form of the bone here regarded as an anterior supraorbital (Figs 2A–E) resembles those of *Stegosaurus stenops* (Fig. 2F–L; Galton & Upchurch 2004, fig. 16.2A, B), *Huayangosaurus taibaii* (Middle Jurassic, China) and *Hesperosaurus mjosi* (Late Jurassic, USA; see Galton & Upchurch 2004, fig. 16.3.A, B, D–F). In most ankylosaurs, the sutures of the skull roof are not visible, being obliterated or completely embossed over by extensive osseous ornamentation. The sutures are only visible in *Cedarpelta* (Early Cretaceous, USA, Carpenter *et al*. 2001), *Minmi* (Early Cretaceous, Australia, Molnar 1996) and *Pinacosaurus* (Late Cretaceous, China and Mongolia, Maryańska 1977, Hill *et al*. 2003). However, in these genera, the form of the supraorbitals does not resemble that of the Argentinian element (see Vickaryous *et al*. 2004, fig. 17.1, 2).

Maidment *et al*. (2008) noted that the cervical vertebrae lack the synapomorphic characters they considered to be diagnostic for Stegosauria. However, the cervical vertebrae show a combination of features that is known only in stegosaurs, *viz*., a proportionally large cross-section to the neural canal and the presence of prominent lateral depressions on the centra.

The anterior dorsal vertebrae of stegosaurs are characterized by neural canals that have a maximum diameter greater than half that of the centra (Galton & Upchurch 2004). Similarly, the cervical vertebrae of some stegosaurs have neural canals that are proportionally even larger. Lull (1917, p. 476) drew attention to the brachial enlargement in the anterior dorsal vertebrae of the YPM mounted skeleton of *Stegosaurus ungulatus* (see Lull 1910). There is an increase in width of the neural canal in vertebrae 8 to 13 from the average of 25 mm to the maximum width of

38 mm in vertebra 11. This condition is absent in other non-stegosaurian thyreophorans, including ankylosaurs (e.g., Carpenter & Kirkland 1998, Carpenter 2004).

The cervical vertebrae from Neuquén resemble those of *Kentrosaurus* (Fig. 4; Hennig 1925, figs 10–11, Mallison 2010, fig. 4), *Stegosaurus* (Ostrom & McIntosh 1999, pls 7–9) and *Dacentrurus* (Late Jurassic, western Europe; Galton 1991, fig. 2) in having a proportionally large neural canal, with an anterior height and width that are half or greater than half the anterior height and width of the centrum. Moreover, the cervical centra from Neuquén are massive and bear prominent lateral depressions, as in the presacral vertebrae and especially the dorsals of *Dacentrurus* (Galton 1985, 1991). However, the former are proportionally less massive and have proportionally deeper depressions than in *Dacentrurus*. The cervical centra from Neuquén are transversely wider than anteroposteriorly long, as in *Dacentrurus*, whereas the contrary condition is evident in the dacentrurine *Miragaia* (Mateus *et al*. 2009). In MACN N-43, the cervical ribs are not fused to the vertebrae, in contrast to dacentrurines (Mateus *et al*. 2009). Although less prominently developed, the presence of a pair of elliptical depressions in cervical vertebra 8 is matched in a cervical vertebra (?fourth, Ostrom & McIntosh 1999, pl. 8, fig. 1) of *Stegosaurus*. They are not present on the more posterior cervicals of *Stegosaurus* (Ostrom & McIntosh 1999, pl. 8, fig. 6, pl. 9, figs 1, 6, 10), but are weakly developed on cervical 9 of *Kentrosaurus* (Fig. 4L).

The best preserved dermal plate from Neuquén (Fig. 5A–D) differs from the nuchal plates of the Late Jurassic stegosaurs *Stegosaurus* and *Kentrosaurus*, which are subrhomboidal to oval and higher than long (Gilmore 1914, fig. 57, pls 14, 23, Galton 1982, pl. 1, Ostrom & McIntosh 1999, pls 59–60). In the Chinese stegosaurs *Huayangosaurus* (Middle Jurassic, Zhou 1984, fig. 35, pl. 11) and *Tuojiangosaurus* (Late Jurassic, Dong *et al*. 1983, fig. 86.1), the cervical plates are oval to subspherical and vertically elongated, whereas in *Jiangjunosaurus* (Middle–Late Jurassic, Jia *et al*. 2007) both preserved cervical plates are low, one being subtriangular and the other almost square in outline. The Neuquén plate is especially reminiscent of the cervical armour of *Miragaia* (Mateus *et al*. 2009, fig. S6 in supplementary information, see also Araújo *et al*. 2009). In both taxa, the plates are subtriangular and longer than high. However, the Neuquén plate differs from those of *Miragaia* in several respects. In the latter, the cervical plates taper distally instead of posteriorly, so they do not have a flattened spike shape and the whole basal surface is subequal in width and gently sinusoidal without any rugose area anteriorly. Moreover, the Patagonian plate lacks a notch and a projection on the anterodorsal margin, which is regarded as a diagnostic character of *Miragaia* by Mateus *et al*. (2009).

At first sight, the Neuquén plate resembles the caudal armour of some 'polacanthid' ankylosaurs (Ford 2000, Blows 2001b). In both cases, the plates are subtriangular, with a rounded convex anterior edge and much more acute posterior edges separated by a concave surface posteriorly. However, the lateral caudal plates of *Mymoorapelta* (Late Jurassic, western USA), *Gastonia* (Early Cretaceous, western USA) and *Polacanthus* (Early Cretaceous, Europe and, tentatively, western USA) are more laterally compressed, biconvex in cross-section and bear a nearly symmetrical hollow base (Blows 1987, fig. 7, Pereda Suberbiola 1994, pl. 4, Kirkland 1998, fig. 7, Kirkland *et al*. 1998, fig. 7, Pereda-Suberbiola *et al*. 2007, fig. 7). Differences are also evident relative to the presacral armour of these ankylosaurs. For instance, the cervical plates of *Gastonia* have a ventral projection for attachment (Kirkland 1998, fig. 7) and the shoulder or pectoral spines of *Mymoorapelta* possess a prominent groove seen in posterior and ventral views (Kirkland & Carpenter 1994, fig. 9). These characters are also known in *Polacanthus* (Blows 1987, Pereda Suberbiola 1994), but are absent in the Neuquén remains and do not support its assignment to an ankylosaur.

In conclusion, the material from the La Amarga Formation has stegosaurian affinities, as claimed by Bonaparte (1996a, b) and subsequent Argentinian authors. Minor differences in the cervical vertebrae and dermal armour relative to other known stegosaurs suggest that the Neuquén specimen is a new taxon. However, additional more complete material is needed to justify the erection of a new genus and species.

Cretaceous record of stegosaurs

Late Jurassic stegosaurs were abundant, very diverse, and occurred on all continents except South America, Australia and Antarctica. However, only a few species (or specimens) are currently recognized from the Early Cretaceous (Fig. 6). The incomplete edentulous dentary with only the tooth roots preserved of *Regnosaurus northamptoni* from England, regarded by Barrett & Upchurch (1995, also Galton & Upchurch 2004) as a basal stegosaur, is Stegosauria indet. (Barrett & Maidment 2011; note that Maidment *et al*. 2008 and Maidment 2010 considered it as Thyreophora indet.). *Craterosaurus pottoniensis* is based on an incomplete dorsal neural arch (Galton 1981) that is a nomen dubium but Stegosauria indet. (Maidment *et al*. 2008). Other possible records from the Wealden formations of Europe include indeterminate remains from England and Spain (Blows 2001a, Pereda-Suberbiola *et al*. 2003, 2005, Barrett & Maidment 2011). *Wuerhosaurus homheni* is based on

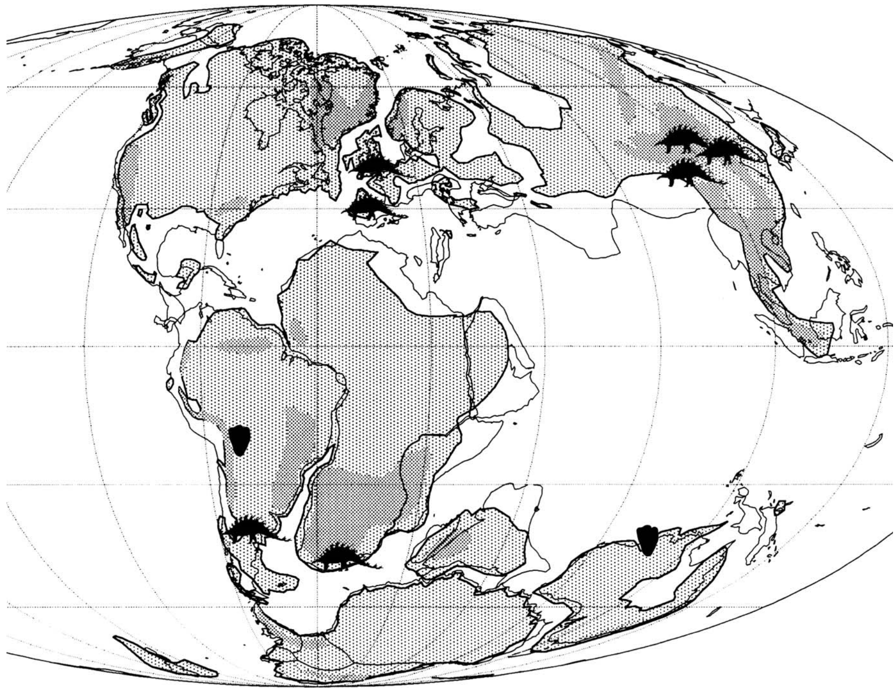

Fig. 6. Stegosaurian record from the Early Cretaceous, including both skeletal remains and footprints. Palaeocoastlines after Smith *et al.* (1994). See text for more details.

a few associated postcranial elements from China (Dong 1973, 1990). This species was referred to *Stegosaurus homheni* by Maidment *et al.* (2008), but this is regarded as incorrect by Carpenter (2010). The most complete stegosaurian postcranial skeleton from the Early Cretaceous, which consists of an articulated vertebral series (with ribs) from the posterior three cervicals to caudal 5 plus several appendicular bones, is the holotype of *W. ordosensis* from Inner Mongolia (Dong 1993), a taxon considered to be a nomen dubium by Maidment *et al.* (2008). *Monkonosaurus lawulacus* from Tibet is based on a complete sacrum with ilia, two partial vertebrae and three dermal plates (Dong 1990). Maidment & Wei (2006) considered the species to be a nomen dubium. Its age is uncertain: Dong (1990) regarded the Loe-ein Formation to be of Late Jurassic to Early Cretaceous age. According to Weishampel *et al.* (2004, p. 565), *M. lawulacus* comes from the Lura Formation (? = Loe-ein Formation), which is Early Cretaceous in age.

In the Gondwanan landmasses, the partial skull of *Paranthodon africanus* is known from the Late Jurassic–Valanginian of South Africa (Galton 1981, Galton & Coombs 1981, Maidment *et al.* 2008). However, the two teeth of *Stegosaurus madagascariensis* from the Late Cretaceous (Cenomanian–Turonian) of Madagascar are probably from an indeterminate ankylosaur (see Maidment *et al.* 2008, Maidment, 2010 for full discussion).

A supposed large stegosaur manus print from the Early Cretaceous Broome Sandstone of Broome, Western Australia, was re-identified as the manus print of a sauropod dinosaur by Page (1998). Incidentally, a small manus print with four toes (Hill *et al.* 1966, pl. 15, fig. 5, Thulborn 1990, fig. 3.39a), which came from the Middle Jurassic Walloon Coal Measures of Queensland, could be from a stegosaur, a group not represented in Australia by skeletal remains. However, it equally well might have originated from an early ankylosaur (Thulborn 1990, p. 209), a group represented by skeletons of *Minmi* from the Early Cretaceous of Queensland (Molnar 1980, 1996), so it is Thyreophora indet.

There are smaller five-toed manus prints (see Long 1998, p. 130 for colour photograph), occurring with incomplete pes prints (Thulborn 1997, fig. p. 15, photograph Dayton 1991), from the Early Cretaceous of Broome. Thulborn (1997, p. 8) noted that these footprints 'do not correspond at all closely with what is known of the hand and foot structure in ankylosaurs'. He identified them as thyreophoran (?stegosaur). However, given similarities to manus and pes prints of *Deltapodus*, a Middle and Late Jurassic footprint taxon from Europe (and Late Jurassic, USA and northern Africa) that has been referred to the Stegosauria (see Whyte & Romano 1994, 2001, Milàn & Chiappe 2009, Belvedere & Mietto 2010, Cobos *et al.* 2010, Mateus *et al.* 2011), these Broome prints probably represent a stegosaur.

Stegosaurs may have survived into the Late Cretaceous in southern India. A partial skeleton from the Coniacian (mid-Late Cretaceous) was described by Yadagiri & Ayyasami (1979) as *Dravidosaurus blanfordi* and some of the bones of the skull were re-identified by Galton (1981). Chatterjee & Rudra (1996, p. 518) concluded that this taxon is a nomen dubium because they 'could not see anything related to the stegosaurian plates and skull claimed by these authors. Instead, the bones are highly weathered limb and girdle elements and may belong to plesiosaurs', fragmentary remains of which they found at the holotype site. However, this important material needs to be independently re-examined and re-assessed because the original description included two photographs of a small tooth similar to that of *Kentrosaurus* and 10 photographs of bones and dermal armor (Yadagiri & Ayyasami 1979, pls 1–4) that do not resemble elements of plesiosaurs. Stegosaurian material was also reported from the latest Cretaceous (Maastrichtian) of India (Yadagiri & Ayyasami 1979, p. 529). However, to date only a photograph of a single plate, roughly symmetrical and subtriangular in side view (*ca* 17.4 cm wide close to base, *ca* 19 cm high), has been published (Yadagiri & Ayyasami 1978). In addition, Mateus *et al*. (2011) re-identified a 'sauropod' manus print from the latest Maastrichtian of India (Mohabey 1986) as a pes print resembling those of *Deltapodus* that was made by a stegosaur (see above).

In South America, footprints called *Caririchnium magnificum* from the Antenor Navarro Formation (Lower Cretaceous) of Paraiba in Brazil were described as possibly made by a stegosaur (Leonardi 1984, 1989). However, these footprints have been reinterpreted as those of a large quadrupedal ornithopod (Lockley 1987, Lockley & Wright 2001). Recently, Apesteguía & Gallina (2011) have described the only ichnological evidence of the presence of stegosaurs in South America. Trackways with tetradactyl manus and pes impresssions are known in the La Puerta Formation (Late Jurassic to Early Cretaceous) of Tunasniyoj, Chuquisaca Department, in Bolivia. They are the oldest stegosaurian footprints from the Southern Hemisphere (Apesteguía & Gallina 2011). Consequently, the material described in this paper from the La Amarga Creek area of Argentina is the only conclusive skeletal evidence for the occurrence of stegosaurs in South America.

Palaeobiogeographical comments

The presence of a stegosaur in the Barremian–early Aptian of Patagonia has interesting biogeographical implications because this is the second known record in the Early Cretaceous of the Gondwanan continents, the other being *Paranthodon* from South Africa. Is the Argentinian stegosaur the result of an Early Cretaceous dispersal event from the Laurasian continents or a relictual component of an older East Gondwanan fauna? The material recovered from the La Amarga Creek seems too fragmentary to provide useful information about its phylogenetic affinities and this prevents an accurate assessment of the palaeobiogeographical significance of this discovery.

Leanza *et al*. (2004) characterized the Amargan tetrapod assemblage (Barremian–early Aptian) from the Neuquén Basin of Argentina by the co-occurrence of late Pangaean dinosaurs, i.e., elements of lineages distributed throughout Pangaea during the Jurassic. The La Amarga dinosaur association includes basal abelisauroids and basal tetanurans among theropods, dicraeosaurids and rebbachisaurid diplodocoids, basal titanosauriforms and titanosaurians among sauropods (Leanza *et al*. 2004, Apesteguía 2007); stegosaurs are the only known ornithischians. The Amargan assemblage has been used to suggest certain similarities with the faunas from the Late Jurassic of East Africa, supporting a Gondwanan signature (Apesteguía 2007). According to Novas (2009), the association of stegosaurs with diplodocoid sauropods in the Early Cretaceous of Patagonia is consistent with the record of these groups in other parts of the world, especially in southern Africa. Several of the above-mentioned taxa are not recorded in the Lower Cretaceous formations of the Northern Hemisphere, suggesting that the separation between Laurasia and Gondwana was already achieved (Leanza *et al*. 2004, Novas 2009).

Finally, the distribution of Early Cretaceous stegosaurs seems to restrict them to the mid-latitude belts in both hemispheres (Fig. 6). All the stegosaur sites are located between 30° and 50°N and S palaeolatitude; the only low-latitude record (at about 20°S) is that from the Late Jurassic to Early Cretaceous of Bolivia (Apesteguía & Gallina, 2011). So, was the stegosaur distribution climatically influenced or is there a major sampling bias against the palaeotropics? If the map of Fig. 6 is predictive for palaeobiogeography, then we might expect that other stegosaur remains, either bones or tracks, will be found in mid-latitude areas.

Acknowledgements

We are indebted to Dr J.F. Bonaparte (Museo Municipal de Ciencias Naturales 'Carlos Ameghino', Mercedes, Buenos Aires, Argentina) for locality information on the bones, Dr Alejandro Kramarz (MACN, Buenos Aires) for the preparation of casts of the fossils, and to Ignacio Díaz Martínez (Logroño, La Rioja, Spain) for providing us with some photographs. PMG thanks Dr Ken Carpenter (then DMNH, now USU-CEU Prehistoric Museum, Price, Utah) for the cast of the skull roof of *Stegosaurus* (DMNH 1483). The paper benefited from the useful comments of the reviewers Dr Ralph E. Molnar (Museum of Northern Arizona, Flagstaff, USA) and Dr José Ignacio Ruiz-Omeñaca (Museo del Jurásico de Asturias, MUJA, Colunga, Spain). We also thank Dr S.C.R. Maidment (Natural History Museum, London, UK) for her comments on an earlier version of the MS. Financial support for XPS was provided by the projects

CGL2007-64061/BTE and CGL2010-18851/BTE of the Ministerio de Ciencia e Innovación (currently Ministerio de Economía y Competitividad, MINECO) of Spain, and by the research groups GIC 07/14-361 and IT-320-10 of the Gobierno Vasco/EJ.

References

Apesteguía, S., 2007. The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina). *Gondwana Research 12*, 533–546.

Apesteguía, S. & Gallina, P.A., 2011. Tunasniyoj, a dinosaur tracksite from the Jurassic–Cretaceous boundary of Bolivia. *Anais da Academia Brasileira de Ciências 83*, 267–277.

Araújo, R., Mateus, O., Walen, A. & Christiansen, N., 2009. Preparation techniques applied to a stegosaurian dinosaur from Portugal. *Journal of Paleontological Techniques 5*, 1–23.

Barrett, P.M. & Maidment, S.C.R., 2011. Armoured dinosaurs. In *English Wealden Fossils*. Batten, D.J., ed., Palaeontological Association, London, *Field Guides to Fossils 14*, 391–406.

Barrett, P.M. & Upchurch, P., 1995. *Regnosaurus northamptoni*, a stegosaurian dinosaur from the Lower Cretaceous of southern England. *Geological Magazine 132*, 213–222.

Belvedere, M. & Mietto, P., 2010. First evidence of stegosaurian *Deltapodus* footprints in North Africa (Iouaridène Formation, Upper Jurassic, Morocco). *Palaeontology 53*, 233–240.

Blows, W.T., 1987. The armoured dinosaur *Polacanthus foxi* from the Lower Cretaceous of the Isle of Wight. *Palaeontology 30*, 557–580.

Blows, W.T., 2001a. Possible stegosaur dermal armor from the Lower Cretaceous of southern England. In *The Armored Dinosaurs*. Carpenter, K., ed., Indiana University Press, Bloomington, 130–140.

Blows, W.T., 2001b. Dermal armor of the polacanthine dinosaurs. In *The Armored Dinosaurs*. Carpenter, K., ed., Indiana University Press, Bloomington, 363–384.

Bonaparte, J.F., 1995. Mesozoic vertebrates of South America. In *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. Sun, A. & Wang, Y., eds, China Ocean Press, Beijing, 89–90.

Bonaparte, J.F., 1996a. *Dinosaurios de América del Sur*. Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, 174 pp.

Bonaparte, J.F., 1996b. Cretaceous tetrapods of Argentina. In *Contributions of Southern South America to Vertebrate Paleontology*. Arratia, G., ed., *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie 30*, 73–130.

Carpenter, K., 2004. Redescription of *Ankylosaurus magniventris* Brown 1908 (Ankylosauridae) from the Upper Cretaceous of the Western Interior of North America. *Canadian Journal of Earth Sciences 41*, 961–986.

Carpenter, K., 2010. Species concept in North American stegosaurs. *Swiss Journal of Geosciences 103*, 155–162.

Carpenter, K. & Kirkland, J.I., 1998. Review of Lower and Middle Cretaceous ankylosaurs from North America. In *Lower and Middle Cretaceous Ecosystems*. Lucas, S.G., Kirkland, J.I. & Estep, J.W., eds, *New Mexico Museum of Natural History and Science Bulletin 14*, 249–270.

Carpenter, K., Kirkland, J.I., Burge, D. & Bird, J., 2001. Disarticulated skull of a new primitive ankylosaurid from the Lower Cretaceous of eastern Utah. In *The Armored Dinosaurs*. Carpenter, K., ed., Indiana University Press, Bloomington, 211–238.

Chatterjee, S. & Rudra, D.K., 1996. KT events in India: impact, rifting, volcanism and dinosaur extinction. In *Proceedings of the Gondwanan Dinosaur Symposium*. Novas, F. & Molnar, R.E., eds, *Memoirs of Queensland Museum 39*, 489–532.

Cobos, A., Royo-Torres, R., Luque, L., Alcalá, L. & Mampel, L., 2010. An Iberian stegosaurs paradise: the Villar del Arzobispo Formation (Tithonian–Berriasian) in Teruel (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology 293*, 223–236.

Colbert, E.H., 1981. A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. *Museum of Northern Arizona Press Bulletin Series 53*, 1–61.

Coria, R.A. & Cambiaso, A.V., 2007. Ornithischia. In *Patagonian Mesozoic Reptiles*. Gasparini, Z., Salgado, L. & Coria, R.A., eds, Indiana University Press, Bloomington, 167–187.

Coria, R.A. & Salgado, L., 2001. South American ankylosaurs. In *The Armored Dinosaurs*. Carpenter, K., ed., Indiana University Press, Bloomington, 159–168.

Dayton, L., 1991. Missing dinosaurs turn up in Australia. *New Scientist 131* (No. 1783), 14.

Dong, Z.-M., 1973. Dinosaurs from Wuerho. *Institute of Paleontology and Paleoanthropology Memoir 11*, 45–52. (Chinese)

Dong, Z.-M., 1990. Stegosaurs of Asia. In *Dinosaur Systematics. Approaches and Perspectives*. Carpenter, K. & Currie, P.J., eds, Cambridge University Press, Cambridge, 255–268.

Dong, Z.-M., 1994 (for 1993). A new species of stegosaur (Dinosauria) from the Ordos Basin, Inner Mongolia, People's Republic of China. In *Results from the Sino-Canadian Dinosaur Project*. Currie, P.J., ed., *Canadian Journal of Earth Sciences 30*, 2174–2176.

Dong, Z.-M., Zhou, S.-W. & Zhang, X., 1983. Dinosaurs from the Jurassic of Sichuan. *Palaeontologica Sinica 162* (C23), 1–151. (in Chinese with English summary)

Ezcurra, M.D. & Agnolín, F.L., 2012. A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. *Systematic Biology 61*, 553–566.

Ford, T.L., 2000. A review of ankylosaur osteoderms from New Mexico and a preliminary review of ankylosaur armor. In *Dinosaurs of New Mexico*. Lucas, S.G. & Heckert, A.B., eds, *New Mexico Museum of Natural History and Science Bulletin 17*, 157–176.

Fuente, M. de la, Salgado, L., Albino, A., Báez, A.M., Bonaparte, J.F., Calvo, J.O., Chiappe, L.M., Codorniú, L.S., Coria, R.A., Gasparini, Z., González Riga, B.J., Novas, F.E. & Pol, D., 2007. Tetrápodos continentales del Cretácico de la Argentina: una síntesis actualizada. In *Asociación Paleontológica Argentina, Publicación Especial 11*. Archangelsky, S., Sánchez, T. & Tonni, E.P., eds, *Ameghiniana 50° aniversario*, 137–153.

Galton, P.M., 1981. *Craterosaurus pottonensis* Seeley, a stegosaurian dinosaur from the Lower Cretaceous of England, and a review of Cretaceous stegosaurs. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 161*, 28–46.

Galton, P.M., 1982. The postcranial anatomy of stegosaurian dinosaur *Kentrosaurus* from the Upper Jurassic of Tanzania, East Africa. *Geologica et Palaeontologica 15*, 139–160.

Galton, P.M., 1985. British plated dinosaurs (Ornithischia, Stegosauridae). *Journal of Vertebrate Paleontology 5*, 211–254.

Galton, P.M., 1991. Postcranial remains of the stegosaurian dinosaur *Dacentrurus* from the Upper Jurassic of France and Portugal. *Geologica et Palaeontologica 25*, 299–327.

Galton, P.M. & Coombs, W.P., 1981. *Paranthodon africanus* (Broom): A stegosaurian dinosaur from the Lower Cretaceous of South Africa. *Géobios 14*, 299–309.

Galton, P.M. & Upchurch, P., 2004. Stegosauria. In *The Dinosauria,* 2nd edition. Weishampel, D.B., Dodson, P. & Osmólska, H., eds, University of California Press, Berkeley, 343–362.

Gilmore, C.W., 1914. Osteology of the armoured Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. *United States National Museum Bulletin 89*, 1–143.

Hennig, E., 1925. *Kentrurosaurus aethiopicus*, die Stegosaurierfunde vom Tendaguru, Deutsch-Ostafrika. *Palaeontographica Supplement 7*(1, 1), 101–254.

Hill, D., Playford, G. & Woods, J.T., 1966. *Jurassic Fossils of Queensland*. Queensland Palaeontographical Society, Brisbane, 32 pp.

Hill, R.V., Witmer, L.M. & Norell, M.A., 2003. A new specimen of *Pinacosaurus grangeri* (Dinosauria: Ornithischia) from the Late Cretaceous of Mongolia: Ontogeny and phylogeny of ankylosaurs. *American Museum Novitates 3395*, 1–29.

IRMIS, R.B., 2007. Axial skeletal ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology 27*, 350–361.

JANENSCH, W., 1925. Ein aufgestelltes Skelett des Stegosauriers *Kentrurosaurus aethiopicus* Hennig 1915 aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica Supplement 7*(1, 1), 255–276.

JIA, C., FOSTER, C.A., XU, X. & CLARK, J.M., 2007. The first stegosaur (Dinosauria, Ornithischia) from the Upper Jurassic Shishugou Formation of Xianjiang, China. *Acta Geologica Sinica 81*, 351–356.

KIRKLAND, J.I., 1998. A polacanthine ankylosaur (Ornithischia: Dinosauria) from the Early Cretaceous (Barremian) of eastern Utah. In *Lower and Middle Cretaceous Terrestrial Ecosystems*. LUCAS, S.G., KIRKLAND, J.I. & ESTEP, J.W., eds, *New Mexico Museum of Natural History and Science Bulletin 14*, 105–124.

KIRKLAND, J.I. & CARPENTER, K., 1994. North America's first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of western Colorado. *Brigham Young University Geology Studies 40*, 25–42.

KIRKLAND, J.I., CARPENTER, K., HUNT, A.P. & SCHEETZ, R.D., 1998. Ankylosaur (Dinosauria) specimens from the Upper Jurassic Morrison Formation. *Modern Geology 23*, 145–177.

LEANZA, H.A. & HUGO, C.A., 1995. Revisión estratigráfica del Cretácico inferior continental en el ámbito sudoriental de la Cuenca Neuquina. *Revista de la Asociación Geológica Argentina 50*, 30–32.

LEANZA, H.A., APESTEGUÍA, S., NOVAS, F.E. & DE LA FUENTE, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research 25*, 61–87.

LEONARDI, G., 1984. Le impronte fossili di dinosauri. In *Sulle orme dei Dinosauri*. BONAPARTE, J.F., COLBERT, E.H., CURRIE, P.J., DE RICQLÈS, A., KIELAN-JAWOROWSKA, Z., LEONARDI, G., MORELLO, N. & TAQUET, P., eds, Erizzo Editrice, Venice, 165–186.

LEONARDI, G., 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological significance. In *Dinosaur Tracks and Traces*. GILLETTTE, D.D. & LOCKLEY, M.G., eds, Cambridge University Press, Cambridge, 165–178.

LOCKLEY, M.G., 1987. Dinosaur footprints from the Dakota Group of eastern Colorado. *The Mountain Geologist 24*, 107–122.

LOCKLEY, M.G. & WRIGHT, J.L., 2001. Trackways of large quadrupedal ornithopods from the Cretaceous: a review. In *Mesozoic Vertebrate Life*. CARPENTER, K. & TANKE, D., eds, Indiana University Press, Bloomington, 428–442.

LONG, J.A., 1998. *Dinosaurs of Australia and New Zealand and other Animals of the Mesozoic Era*. Harvard University Press, Cambridge, 192 pp.

LULL, R.S., 1910. *Stegosaurus ungulatus* Marsh, recently mounted at the Peabody Museum of Yale University. *American Journal of Science 30* (series 4), 361–376.

LULL, R.S., 1917. On the functions of the 'Sacral Brain' in dinosaurs. *American Journal of Science 44* (series 4), 471–477.

MAIDMENT, S.C.R., 2010. Stegosauria: a historical review of the body fossil record and phylogenetic relationships. *Swiss Journal of Geosciences 103*, 199–210.

MAIDMENT, S.C.R. & PORRO, L.B., 2010. Homology of the palpebral and origin of supraorbital ossifications in ornithischian dinosaurs. *Lethaia 43*, 95–111.

MAIDMENT, S.C.R. & WEI, G.-B., 2006. A review of Late Jurassic stegosaurs from the People's Republic of China. *Geological Magazine 143*, 621–634.

MAIDMENT, S.C.R., NORMAN, D.B., BARRETT, P.M. & UPCHURCH, P., 2008. Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). *Journal of Systematic Palaeontology 6*, 367–407.

MALLISON, H., 2010. CAD assessment of the posture and range of motion of *Kentrosaurus aethiopicus* Hennig 1915. *Swiss Journal of Geosciences 103*, 211–233.

MARSH, O.C., 1877. A new order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. *American Journal of Science 14* (series 3), 34–35.

MARSH, O.C., 1880. Principal characters of American Jurassic dinosaurs. Part III. *American Journal of Science 19* (series 3), 253–259.

MARSH, O.C., 1891. Restoration of *Stegosaurus*. *American Journal of Science 42* (series 3), 179–181.

MARSH, O.C., 1896. The dinosaurs of North America. *United States Geological Survey, Annual Report 16* (1894–95), 133–244.

MARYAŃSKA, T., 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologica Polonica 37*, 85–151.

MATEUS, O., MAIDMENT, S.C.R. & CHRISTIANSEN, N.A., 2009. A new long-necked 'sauropod-mimic' stegosaur and the evolution of the plated dinosaurs. *Proceedings of the Royal Society of London B 276*, 1815–1821.

MATEUS, O., MILÀN, J., ROMANO, M. & WHYTE, M.A., 2011. New finds of stegosaur tracks from the Upper Jurassic Lourinhã Formation, Portugal. *Acta Palaeontologica Polonica 56*, 651–658.

MCCREA, R.T., LOCKLEY, M.G. & MEYER, C.A., 2001. Global distribution of purported Ankylosaur track occurrences. In *The Armored Dinosaurs*. CARPENTER, K., ed., Indiana University Press, Bloomington, 413–454.

MILÀN, J. & CHIAPPE, L.M., 2009. First American record of the Jurassic ichnospecies *Deltapodus brodkricki* and a review of the fossil record of stegosaurian footprints. *Journal of Geology 117*, 343–348.

MOHABEY, D.M., 1986. Note on dinosaur foot print from Kheda District, Gujarat. *Journal of the Geological Society of India 27*, 456–459.

MOLNAR, R.E., 1980. An ankylosaur (Ornithischia) from the Lower Cretaceous of southern Queensland. *Memoirs of the Queensland Museum 20*, 77–87.

MOLNAR, R.E., 1996. Preliminary report on a new ankylosaur from the Early Cretaceous of Queensland, Australia. In *Proceedings of the Gondwanan Dinosaur Symposium*. NOVAS, F. & MOLNAR, R.E., eds, *Memoirs of the Queensland Museum* 39, 653–668.

NOPCSA, F., 1915. Die Dinosaurier der Siebenbürgischen Landesteile Ungarns. *Mitteilungen aus dem Jahrbuche der Königlich Ungarischen Geologischen Reichsanstalt 23*, 1–26.

NORMAN, D.B., 1984. A systematic reappraisal of the reptile order Ornithischia. In *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. REIF, W.E. & WESTPHAL, F., eds, Attempto Verlag, Tübingen, 157–162.

NOVAS, F.E., 2009. *The Age of Dinosaurs in South America*. Indiana University Press, Bloomington, 454 pp.

OSTROM, J.H. & MCINTOSH, J.S., 1966. *Marsh's Dinosaurs. The Collections from Como Bluff*. Yale University Press, New Haven, xiv + 388 pp.

OSTROM, J.H. & MCINTOSH, J.S., 1999. *Marsh's Dinosaurs. The Collections from Como Bluff*. With a New Forward by Peter Dodson and a Historical Update by Clifford A. Miles and David W. Hamblin. Yale University Press, New Haven, xxiv + 388 pp.

OWEN, R., 1863. A monograph of the fossil Reptilia of the Liassic Formations. Part 2. A monograph of a fossil dinosaur (*Scelidosaurus harrisonii* Owen) of the Lower Lias. *Palaeontographical Society Monographs 14*, 1–26.

PAGE, D., 1998. Stegosaur tracks and the persistence of facies—the Lower Cretaceous of Western Australia. *Geology Today 14*, 75–77.

PEREDA SUBERBIOLA, J., 1994. *Polacanthus* (Ornithischia, Ankylosauria), a transatlantic armoured dinosaur from the Early Cretaceous of Europe and North America. *Palaeontographica A 232*, 133–159.

PEREDA-SUBERBIOLA, X., GALTON, P.M., TORCIDA, F., HUERTA, P., IZQUIERDO, L.A., MONTERO, D., PÉREZ, G. & URIÉN, V., 2003. First stegosaurian dinosaur remains from the Early Cretaceous of Burgos (Spain), with a review of Cretaceous stegosaurs. *Revista Española de Paleontología 18*, 143–150.

PEREDA-SUBERBIOLA, X., GALTON, P.M., RUIZ-OMEÑACA, J.I. & CANUDO, J.I., 2005. Dermal spines of stegosaurian dinosaurs from the Lower Cretacous (Hauterivian–Barremian) of Galve (Teruel, Aragon, Spain). *Geogaceta 38*, 35–38.

PEREDA-SUBERBIOLA, X., FUENTES, C., MEIJIDE, M., MEIJIDE-FUENTES, F. & MEIJIDE-FUENTES, M., JR, 2007. New remains of the ankylosaurian dinosaur *Polacanthus* from the Lower Cretaceous of Soria, Spain. *Cretaceous Research 28*, 583–596.

SEELEY, H.G., 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London 43* (printed 1888), 165–171.

SERENO, P.C., 1999. The evolution of dinosaurs. *Science 284*, 2137–2146.

SERENO, P.C. & DONG, Z., 1992. The skull of the basal stegosaur *Huayangosaurus taibaii* and a cladistic diagnosis of Stegosauria. *Journal of Vertebrate Paleontology 12*, 318–342.

SMITH, A.G., SMITH, D.G. & FUNNELL, B.M., 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, Cambridge, 99 pp.

THULBORN, T., 1990. *Dinosaur Tracks*. Chapman & Hall, London, 410 pp.

THULBORN, T., 1997. Dinosaur Tracks of the Broome Sandstone. In *Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*, Notes for Field Excursion 28–29th June 1997, 16 pp.

VICKARYOUS, M.K., MARYAŃSKA, T. & WEISHAMPEL, D.B., 2004. Ankylosauria. In *The Dinosauria,* 2nd edition. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 363–392.

WEISHAMPEL, D.B., BARRETT, P.M., CORIA, R.A., LE LOEUFF, J., XU, X., ZHAO, X., SAHNI, A., GOMANI, E.M.P. & NOTO, C.R., 2004. Dinosaur distribution. In *The Dinosauria,* 2nd edition. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 517–606.

WHYTE, M.A. & ROMANO, M., 1995 (for 1994). Probable sauropod footprints from the Middle Jurassic of Yorkshire, England. In *Aspects of Sauropod Paleobiology*. LOCKLEY, M.G., DOS SANTOS, V.F., MEYER, C.A. & HUNT, A.P., eds, *Gaia 10*, 15–26.

WHYTE, M.A. & ROMANO, M., 2001. Probable stegosaurian dinosaur tracks from the Saltwick Formation (Middle Jurassic) of Yorkshire, England. *Proceedings of the Geological Association 112*, 45–54.

YADAGIRI, P. & AYYASAMI, K., 1978. New dinosaurian remains. *Geological Survey of India News 9*(5), 4.

YADAGIRI, P. & AYYASAMI, K., 1979. A new stegosaurian dinosaur from Upper Cretaceous sediments of south India. *Journal of the Geological Society of India 20*, 521–530.

ZHOU, S., 1984. *The Middle Jurassic dinosaurian fauna from Dashanpu, Zigong, Sichuan. Volume 2: Stegosaurs*. Sichuan Scientific and Technological Publishing House, Sichuan, 52 pp. (in Chinese with English summary)