



# North Africa's first stegosaur: Implications for Gondwanan thyreophoran dinosaur diversity

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## ABSTRACT

Eurypoda, the major radiation of armoured dinosaurs, comprises the ankylosaurs and their sister group, the stegosaurs. As the earliest-branching major clade of ornithischian dinosaurs, the evolutionary history of Eurypoda is significant for understanding both the palaeobiology of bird-hipped dinosaurs and the composition of middle Mesozoic ecosystems. Eurypodans were diverse and abundant throughout the Late Jurassic and Cretaceous in Laurasia; in contrast, their remains are extremely rare in Gondwana. Herein, we describe a new genus and species of stegosaur from the Middle Jurassic of Morocco, *Adratiklit boulahfa*. *Adratiklit* is the first eurypodan from north Africa and the oldest definitive stegosaur from anywhere in the world. The genus is more closely related to the European stegosaurs *Dacentrurus* and *Miragaia* than it is to the southern African taxa *Kentrosaurus* and *Paranthodon*. Statistically significant correlations between the number of dinosaur-bearing formations, dinosaur-bearing collections, and eurypodan occurrences in Gondwana indicates that their fossil record is biased by both geological and anthropogenic factors. Tantalizing but fragmentary remains and trackways suggest that eurypodan diversity in Gondwana may have been as rich as that of Laurasia, and the prospects for future discoveries of new genera across Gondwana are therefore very good.

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## 1. Introduction

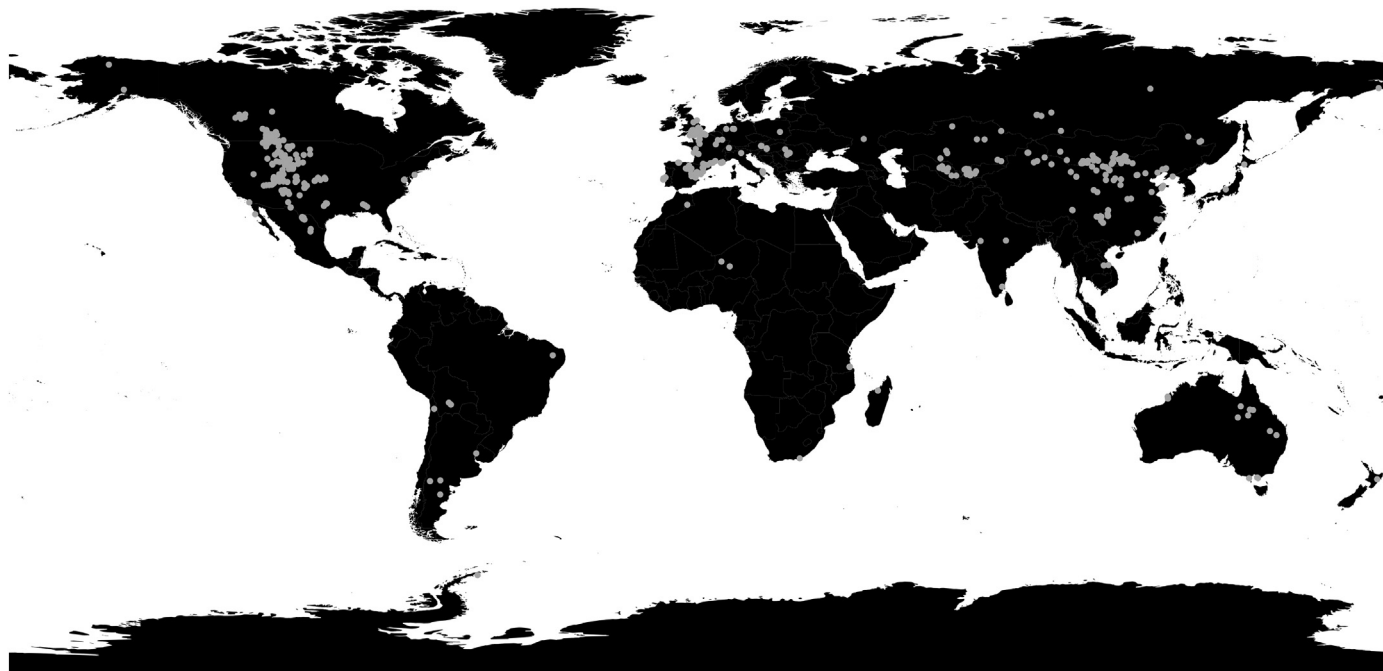
Stegosauria is a clade of ornithischian ('bird-hipped') dinosaurs characterized by a series of plates and spines extending from the neck to the end of the tail in two parasagittal rows. Known from the Middle Jurassic to the Early Cretaceous (but see Galton and Ayyasami, 2017 for possible evidence of a Late Cretaceous taxon), their remains have been found across Laurasia, where 11 valid genera are recognized (Raven and Maidment, 2017). Currently, only two valid genera are known from former Gondwanan continents: *Kentrosaurus aethiopicus*, represented by numerous disarticulated remains from the Upper Jurassic Tendaguru Beds of Tanzania (Hennig, 1915; Galton, 1982, 1988), and *Paranthodon africanus*, based on a partial premaxilla and maxilla from the lowermost Cretaceous part of the Kirkwood Formation of South Africa (Fig. 1; Galton and Coombs, 1981; Raven and Maidment, 2018). Stegosauria and its sister taxon, Ankylosauria, together form the clade Eurypoda. Ankylosaurs are known from rare Jurassic forms (Galton, 1980a, 1980b; Kirkland and Carpenter, 1994; Carpenter et al., 1998), but increased rapidly in diversity during the Cretaceous coincident with a decline in stegosaur species richness. Ankylosaurs were an

important constituent of Cretaceous Laurasian ecosystems, but their fossil record is sparse in Gondwana (Fig. 1). One valid ankylosaur taxon is known from the Early Cretaceous of Australia, *Kunbarrasaurus* (Leahey et al., 2016) and *Antarctopelta* is known from the Late Cretaceous of Antarctica (Salgado and Gasparini, 2006; Arbour and Currie, 2016 consider the taxon to be a *nomen dubium*, although it clearly is ankylosaurian).

It remains unclear whether eurypodans were genuinely rare in Gondwanan Mesozoic ecosystems, or whether their poor fossil record on southern continents (Fig. 1) is the result of sampling bias. Tantalizing but extremely fragmentary discoveries of possible eurypodans have been made in Argentina (Coria and Salgado, 2001; De Valais et al., 2003; Pereda-Superbiola et al., 2013), Australia (Barrett et al., 2010; Leahey and Salisbury, 2013; Leahey et al., 2016), New Zealand (Molnar and Wiffen, 1994), India (Chatterjee and Rudra, 1996; Nath et al., 2002; Galton and Ayyasami, 2017; Galton, 2019), and Madagascar (Maidment, 2010), while eurypodan trackways have been identified from Morocco (Belvedere and Mietto, 2010), Australia (Salisbury et al., 2016), Bolivia (McCrea et al., 2001; Apestaguía and Gallina, 2011), and Brazil (Leonardi and Carvalho, 2002). Furthermore, it has been suggested that a recently described ornithischian from Patagonia, *Isaberrysaura* (Salgado et al., 2017), might be a stegosaur (Han et al., 2018; Raven and Maidment, 2018). These discoveries seem to

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**Fig. 1.** Global distribution of Eurypoda. Eurypodan occurrences are shown in the grey dots. Data derived from the Paleobiology Database ([www.paleobiodb.org](http://www.paleobiodb.org)). Map by Tom Patterson, Nathaniel Vaughn Kelso and others from [naturalearthdata.com](http://naturalearthdata.com), Bjørn Sandvik [CC0], via Wikimedia Commons.

indicate that eurypodans may have been as widely distributed across Gondwana as they were across Laurasia.

As the earliest diverging major clade of ornithischian dinosaurs, the palaeobiogeography of Thyreophora has important implications for our understanding of the origin and subsequent radiation of the ornithischian dinosaurs as a whole. The poor fossil record of the clade in Gondwana currently hinders our understanding of the evolution and radiation of armoured dinosaurs.

Here, we report the first stegosaurian body fossils from North Africa. The remains are fragmentary and, on the basis of preservation style, likely represent more than one individual. Found in Middle Jurassic strata in the Middle Atlas Mountains of Morocco, these fossils represent an extremely important data point for understanding thyreophoran (armoured) dinosaur diversity and palaeobiogeography, as they represent some of the oldest body fossils of Eurypoda from anywhere in the world, and the first evidence of this dinosaur group from northern Africa.

### 1.1. Institutional abbreviations

**MB**, Museum für Naturkunde, Berlin, Germany; **MHBR**, Muséum d'Histoire Naturelle du Havre, Brun Collection, Le Havre, France; **ML**, Museu da Lourinhá, Portugal; **NHMUK**, Natural History Museum, London, UK; **ZDM**, Zigong Dinosaur Museum, Sichuan Province, People's Republic of China.

### 1.2. Data availability

The specimens described herein are housed at the NHMUK and are available for study by qualified researchers. The character–taxon matrix and character list for the phylogenetic analysis are included as Online Supplementary Material to this paper. Eurypodan occurrence data is available from the Paleobiology Database ([www.paleobiodb.org](http://www.paleobiodb.org)) and is freely available.

## 2. Geological setting

The material described herein was found south of Boulemane in the Middle Atlas Mountains, Morocco (Fig. 2). The Middle Atlas Mountains

are a series of basins and ranges comprising folded Mesozoic strata that were deformed during the Alpine Orogeny (Charrière, 1990; Pratt et al., 2015). During the Triassic, the area was an active rift basin (Ouarhache, 2002), but cessation of rifting occurred during the Early (Pratt et al., 2015) or Middle Jurassic (Ouarhache et al., 2012). Early stages of rifting were accompanied by the deposition of evaporites and continental strata, followed in the Early Jurassic by a thick sequence of shallow marine marls, carbonates and shales. During the Middle Jurassic (Bathonian and Callovian), shallow marine and continental mixed clastic, evaporitic and carbonate sediments of the El Mers Group were deposited (Charrière et al., 2011; Pratt et al., 2015; Oukassou et al., 2015, 2018), following which the area was emergent until the Cretaceous, leading to an unconformity between these Middle Jurassic sediments and the overlying Barremian sequence (Charrière et al., 1994; Pratt et al., 2015). The El Mers Group, which is dated as Bathonian–Callovian based on echinoderm, brachiopod and ammonite biostratigraphy (Charrière et al., 1994), is divided into three formations known as El Mers I–III (Oukassou et al., 2015).

The El Mers I Formation comprises varicoloured mudstones and interbedded, laterally restricted sandstones and is interpreted as predominantly terrestrial. It is dated as middle Bathonian on the basis of ammonite biostratigraphy of the surrounding marine intervals (Oukassou et al., 2015). Dinosaur bones have previously been reported from the El Mers I Formation of the region (Termier et al., 1940; Lapparent, de A. F., 1955) and from the El Mers Group at a location SW of Boulemane (Charroud and Fedan, 1992), which we believe to be the same location as that yielding the specimens described herein, based on descriptions of the site provided in Charroud and Fedan (1992).

At the dinosaur locality, the El Mers Group crops out in a series of badlands, and is ~110 m thick, although the base and top is not exposed. The outcrops comprise greyish green silts and thin sandy limestones with shell fragments near the base of the exposure. Upwards, sandy limestones are replaced by yellowish green, ripple cross-laminated very fine sandstones with bioturbated top surfaces, which become increasingly rare and are replaced by structureless green siltstones. A distinctive, dark red siltstone with elongate greenish rootlets occurs about halfway up the section, and is interpreted as a well-developed palaeosol. The fossiliferous horizon appears to be a green siltstone

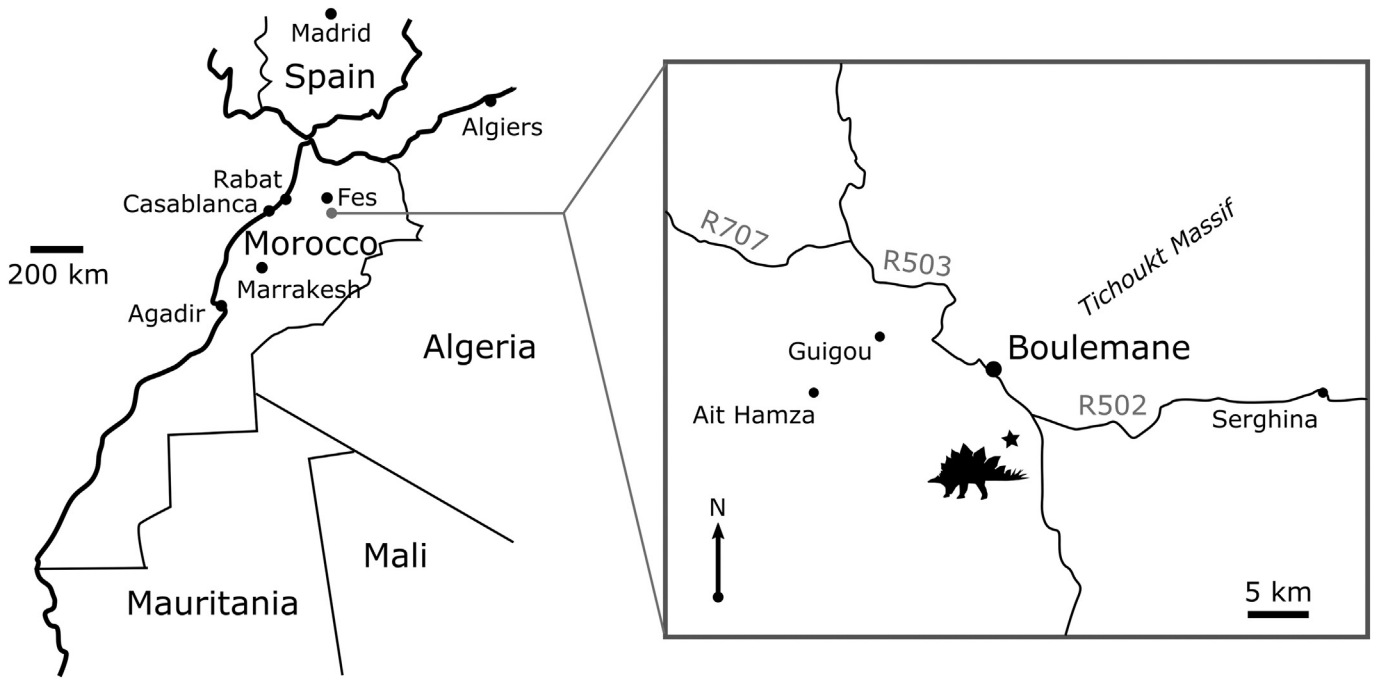


Fig. 2. Map showing the type locality for *Adratiklit boulahfa*, within the Middle Atlas of Morocco.

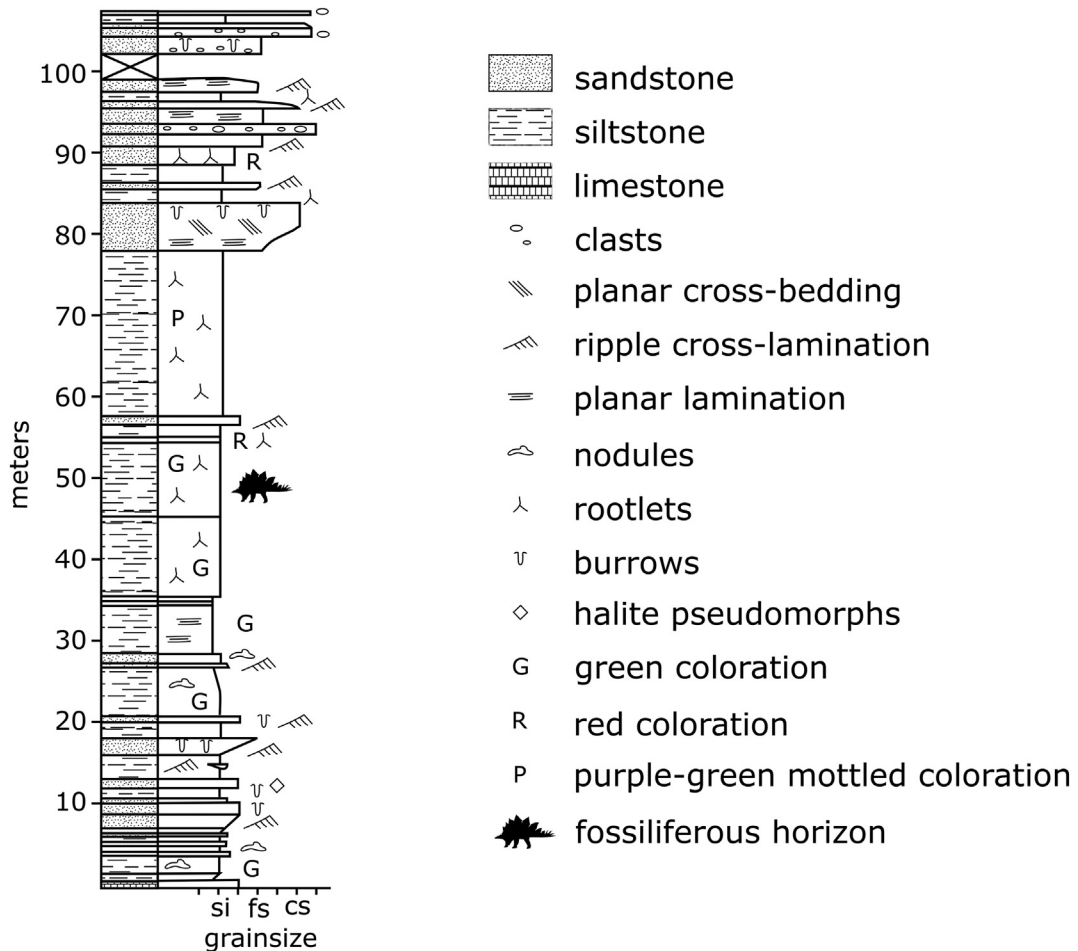


Fig. 3. Sedimentological log of the El Mers Group measured at the stegosaur locality showing the location of the fossiliferous horizon. Si, silt; fs, fine sand; cs, coarse sand.

with orange mottles and abundant charcoal fragments immediately below this palaeosol. Above the palaeosol, purple and green varicoloured silts are present, and the top of the section is marked by the presence of several laterally discontinuous, coarse sandstones to conglomerates with planar cross-bedding and bioturbated top surfaces (Fig. 3). The outcrops may correspond to the El Mers II Formation of the nearby Skoura syncline (D.O., pers. obs.). Fig. S1 of Online Supplementary Data shows a geological map of the region.

### 3. Systematic palaeontology

#### Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Stegosauria Marsh, 1877

*Adratiklit* gen. nov.

*Adratiklit boulahfa* gen. et sp. nov.

Holotype

A dorsal vertebra, NHMUK PV R37366 (Fig. 8).

Referred specimens

Three cervical vertebrae (NHMUK PV R37367; R37368; Figs. 4–6), a dorsal vertebra (NHMUK PV R37365; Fig. 8), and a left humerus

(NHMUK PV R37007; Fig. 11). NHMUK PV R37365 shares a single autapomorphy (5, see Diagnosis, below) with the holotype. The other referred specimens share no autapomorphies with the holotype; however, we consider the referral of NHMUK PV R37367, R37368 and R37007 likely because they are clearly stegosaurian and there is insufficient evidence to regard them as a second distinct taxon. The humerus bears one unambiguous stegosaurian synapomorphy, while the cervicals are anatomically similar to those of other stegosaurs (see Description, below). Moreover, they were found in the same locality as the holotype, although it is unclear if the specimens were found in association, and their differing preservation styles suggests they may have been found in different horizons and/or depths with respect to the weathered surface of the silts.

#### 3.1. Locality and horizon

El Mers Group, probably El Mers II Formation (Bathonian), Boulahfa, south of Boulemane, Fès-Meknes, Morocco.

#### 3.2. Etymology

Generic name *Adratiklit* from 'Adras', Berber for 'mountain', and 'tiklit', a Berber word for lizard. The specific name, *boulahfa*, refers to the location where the specimen was found.

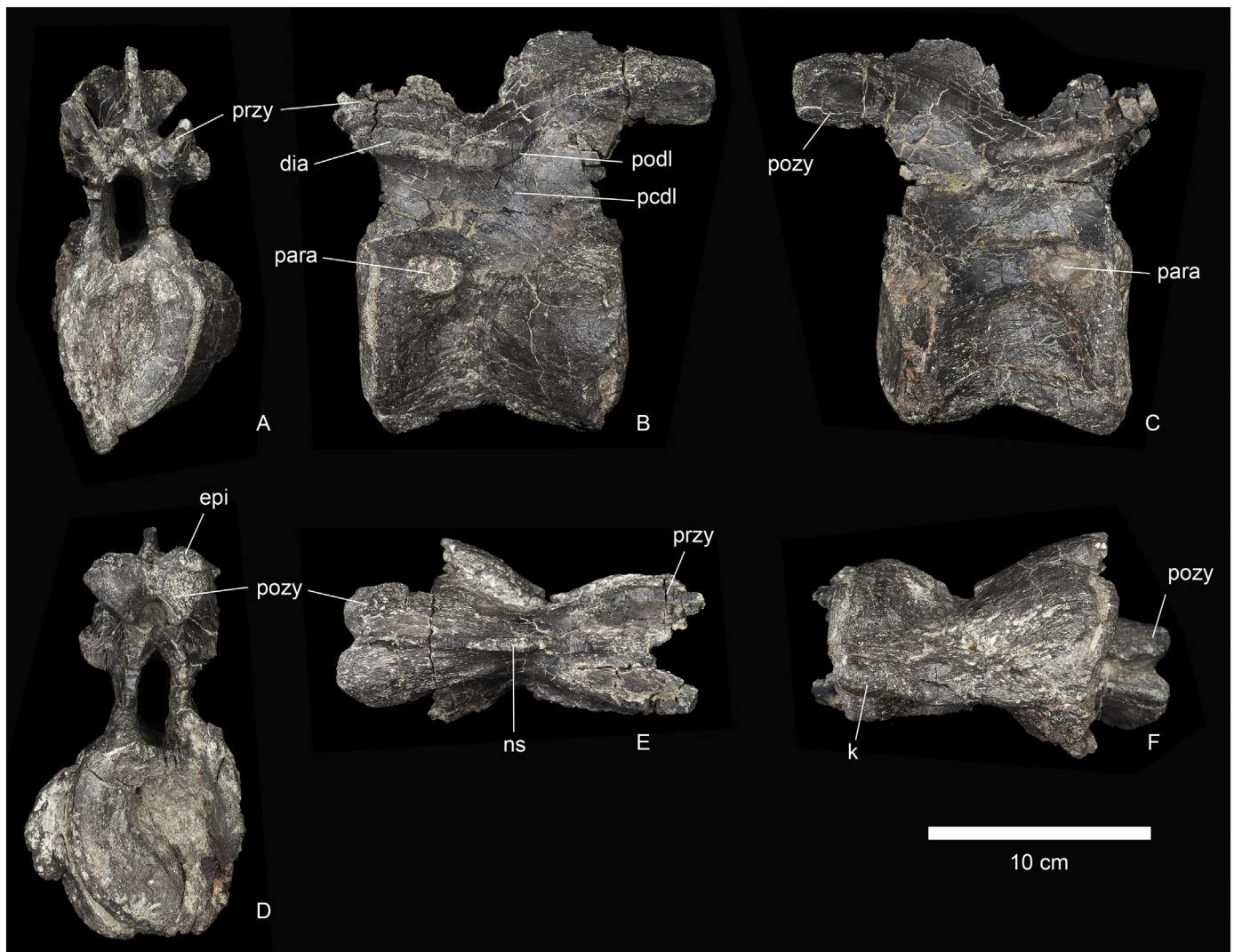
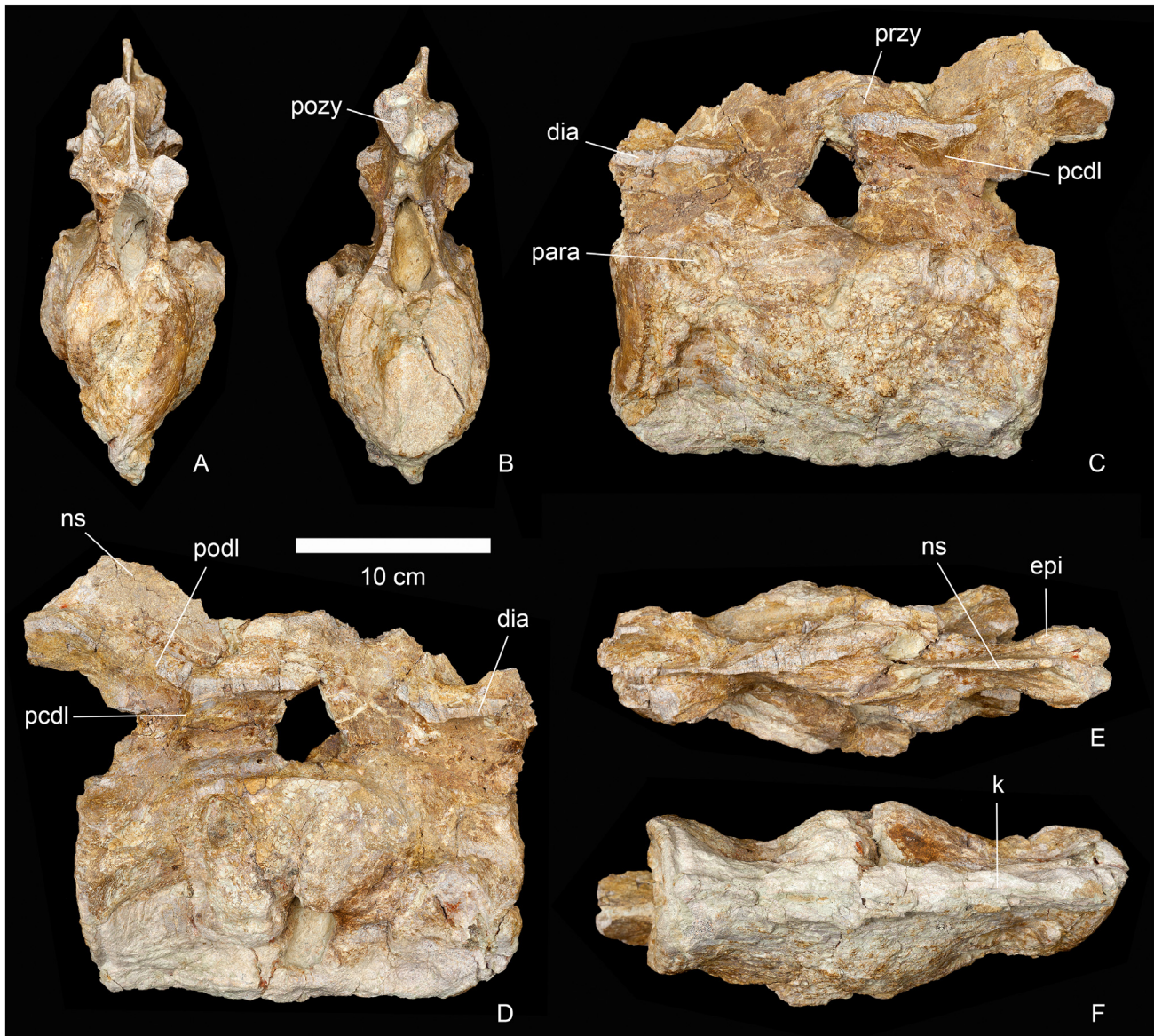
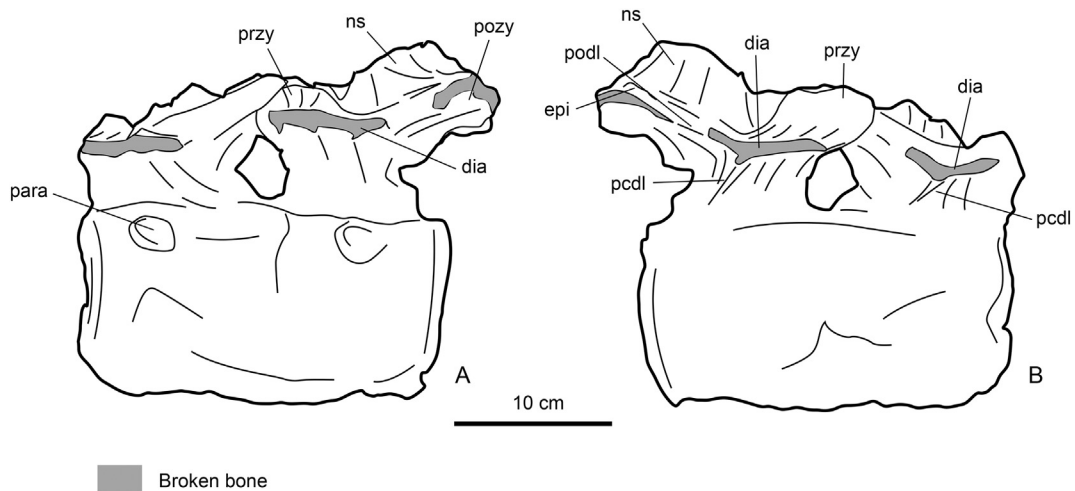


Fig. 4. NHMUK PV R37367, isolated cervical vertebra referred to *Adratiklit boulahfa* in A, anterior, B, left lateral, C, right lateral, D, posterior, E, dorsal and F, ventral views. **Dia**, diapophysis; **epi**, epipophysis; **k**, keel; **para**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **podl**, postzygodiapophyseal lamina; **pozy**, postzygapophysis; **przy**, prezygapophysis.



**Fig. 5.** NHMUK PV R37368, articulated pair of cervical vertebrae referred to *Adratiklit boulahfa* in **A**, anterior, **B**, posterior, **C**, left lateral, **D**, right lateral, **E**, dorsal and **F**, ventral views. **Dia**, diapophysis; **epi**, epipophysis; **k**, keel; **ns**, neural spine; **para**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **podl**, postzygodiapophyseal lamina; **pozy**, postzygapophysis; **przy**, prezygapophysis.



**Fig. 6.** Interpretive drawing of NHMUK PV R37368, articulated pair of cervical vertebrae referred to *Adratiklit boulahfa* in **A**, right lateral and **B**, left lateral views. **Dia**, diapophysis; **epi**, epipophysis; **ns**, neural spine; **para**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **podl**, postzygodiapophyseal lamina; **pozy**, postzygapophysis; **przy**, prezygapophysis.

### 3.3. Diagnosis

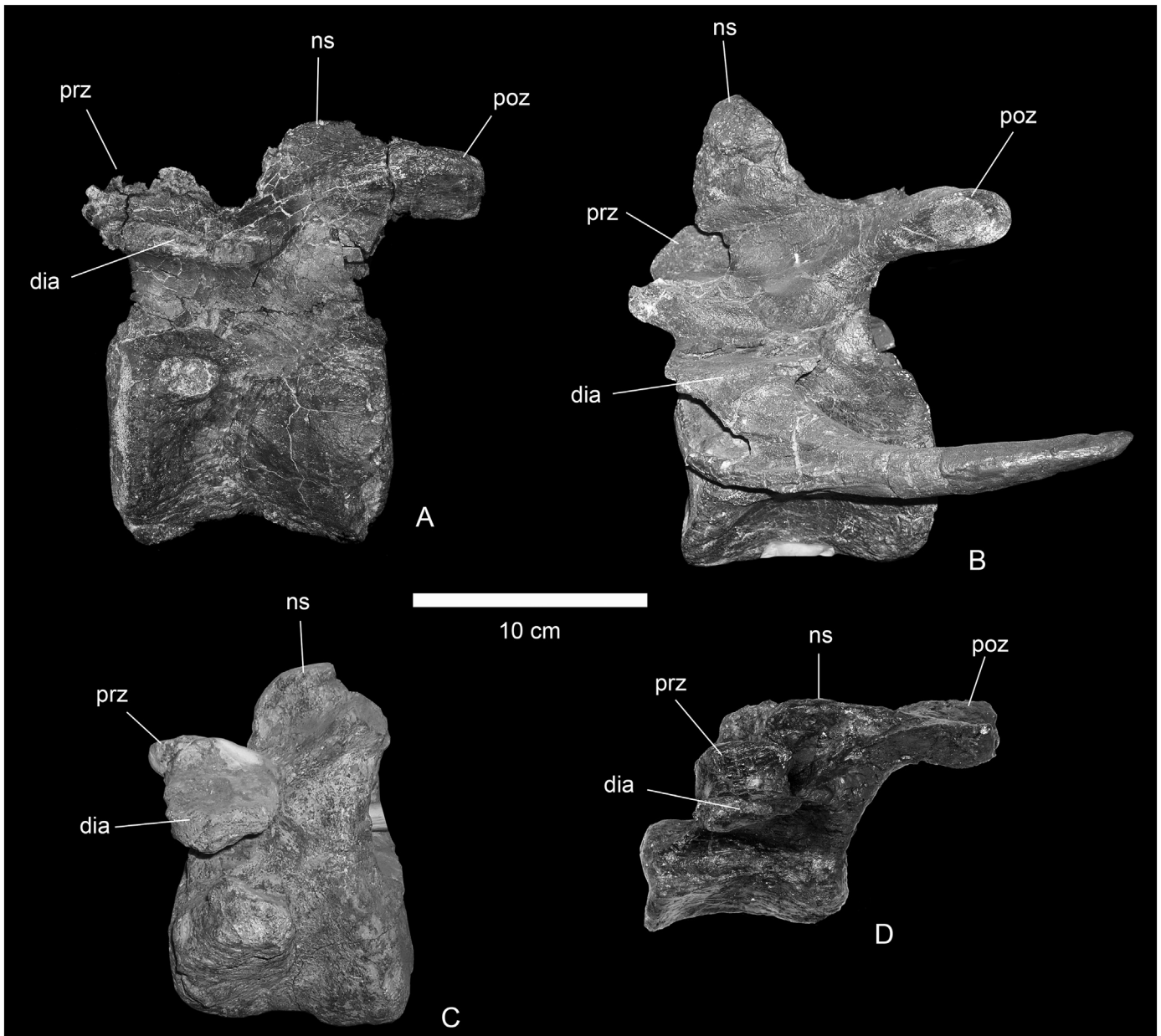
*Adratiklit boulahfa* differs from all other stegosaurs by possession of the following autapomorphies: (1) a small, triangular, rugose protuberance situated dorsally on the prezygapophysis posterior to the articular facet of dorsal vertebrae; (2) anterior centroparapophyseal laminae drawn into anteriorly-projecting rugosities either side of the neural canal in dorsal vertebrae. In addition, the following features appear to be unique to *Adratiklit*, but are only present on the referred cervical vertebrae, and not on the holotype. Due to uncertainty about association of the material, we do not include them in the diagnosis of the taxon, but flag their presence here because further discoveries may indicate that they are indeed autapomorphies: (1) anteroposteriorly elongate prezygapophyses on cervical vertebrae; (2) anteroposteriorly elongate and blade-like neural spine that extends posteriorly to the distal end of the postzygapophyses on cervical vertebrae; (3) epipophyses, in the form of rugose ridges, present on the postzygapophyses of posterior cervical vertebrae;

### 4. Description

The specimens described herein were acquired by the Natural History Museum, London, from Moussa Direct, Cambridge, UK. In the below description, comparative observations supported by a specimen number are based on the first-hand observations of SCRM.

#### 4.1. Cervical vertebrae (NHMUK PV R37367, NHMUK PV R37368)

Three cervical vertebrae are available. One is dark grey in colour (Fig. 4; NHMUK PV R37367), while the other two are preserved in articulation and are pale yellow (Figs. 5, 6; NHMUK PV R37368). This difference in preservation style suggests they were not collected from the same bed and cannot be closely associated, although they are morphologically similar and comparable in size. Comparison with *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) suggests that all are posterior cervical vertebrae. The isolated vertebra (Fig. 4) preserves the centrum (which is transversely crushed) and the neural arch, which



**Fig. 7.** Comparison of cervical vertebrae of stegosaurian dinosaurs in right lateral view. **A**, *Adratiklit*, NHMUK PV R37367; **B**, *Mirigaia*, ML 433; **C**, *Loricatosaurus*, MHBR 001; **D**, *Stegosaurus*, NHMUK PV R36730. **dia**, diapophysis; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis.

includes parts of the prezygapophyses, the postzygapophyses and the base of the neural spine, as well as the bases of the diapophyses. The two articulating vertebrae (Figs. 5, 6) preserve transversely crushed centra and neural arches; in the anterior vertebra, almost all of the processes have broken off, except for partial postzygapophyses, while in the posterior vertebra, the prezygapophyses, postzygapophyses and a partial neural spine are preserved.

The centra of all three vertebrae are longer anteroposteriorly than they are wide transversely. This is similar to the condition in other stegosaurs (Fig. 7; e.g. *Stegosaurus* NHMUK PV R36730, Maidment et al., 2015; *Miragaia* ML 433, Mateus et al., 2009; *Loricatosaurus* MHBR 001, Galton, 1990; *Kentrosaurus* MB.R.4786, Hennig, 1915; *Huayangosaurus* ZDM T7001, Zhou, 1984) except for *Dacentrurus armatus* (NHMUK OR 46013, Galton, 1985), where the cervical centra are wider than long. The anterior articular facets of the centra are flat to shallowly concave, while the posterior articular facets are gently concave (as in other stegosaurs, including *Stegosaurus* NHMUK PV R36730, Maidment et al., 2015; *Miragaia* ML 433, Mateus et al., 2009; *Loricatosaurus* MHBR 001, Galton, 1990; *Kentrosaurus* MB.R.4786, Hennig, 1915; *Huayangosaurus* ZDM T7001, Zhou, 1984 and *Dacentrurus armatus* NHMUK OR 46013, Galton, 1985), although the degree of concavity appears to have been accentuated by crushing, especially on the isolated cervical (Fig. 4A, D). Laterally, the centra are deeply excavated, being anteroposteriorly concave. In lateral view the ventral margin of the centrum of the isolated cervical, which is the best preserved of the three, is upwardly concave, while those of the articulating centra are flat. All three bear a ventral keel (Fig. 4F; 5F), as in *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) and *Dacentrurus armatus* (NHMUK OR 46013; Galton, 1985). Parapophyses are located dorsally on the anterolateral surfaces of the centra; they are offset posteriorly from the anterior articular facet, and located immediately below the presumed location of the neurocentral suture, which cannot be observed in any of the specimens (Figs. 4B, C; 5C, 6). The parapophyses are oval, with their long axes orientated anteroposteriorly, and they are shallowly concave. A low ridge extends posteriorly from the posterior margin of the parapophyses, separating a shallow fossa dorsally from the lateral surface of the centrum below; this is similar to the condition seen in other stegosaurs, such as *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) and *Jiangjunosaurus* (Jia et al., 2007).

In all three cervicals the neural arch is anteroposteriorly elongate, extending for the entire length of the centrum, in contrast to *Stegosaurus* (NHMUK PV R36730, Maidment et al., 2015) where the neural arches are displaced posteriorly from the anterior articular facet (Fig. 7). Neural canals are transversely crushed, and are oval to teardrop-shaped in all three vertebrae. In the isolated cervical, the prezygapophyses are incomplete anteriorly and dorsally; in the anterior of the articulated cervical pair, only the bases of the prezygapophyses are preserved, while in the posterior vertebra the prezygapophyses are preserved in articulation with the postzygapophyses of the former (Figs. 5C, 6). The prezygapophyses are anteroposteriorly elongate (Fig. 4B), much more so than in *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015), *Kentrosaurus* (MB.R.4787; Hennig, 1915) and *Miragaia* (ML 433; Mateus et al., 2009), and they overhang the centrum anterior surface, as in *Miragaia* (ML 433; Mateus et al., 2009) and *Huayangosaurus* (Zhou, 1984; Fig. 11) but contrasting with the condition in *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015), *Loricatosaurus* (MHBR 001; Galton, 1990), and *Kentrosaurus* (MB.R.4787; Hennig, 1915; Fig. 7). Their articular surfaces face medially and slightly dorsally, forming an angle of around 60 degrees with the horizontal (Fig. 4A), similar to the condition in the posterior cervicals of other stegosaurs (e.g. *Stegosaurus* NHMUK PV R36730, Maidment et al., 2015; *Miragaia* ML 433, Mateus et al., 2009; *Loricatosaurus* MHBR 001, Galton, 1990, and *Huayangosaurus*, Zhou, 1984; Fig. 9). In dorsal view, the articular surfaces of the prezygapophyses are separated along their entire length by a 'V'-shaped notch (Fig. 5E), similar to the condition in *Huayangosaurus* (Zhou, 1984; fig. 9), but in contrast to *Stegosaurus*

**Table 1**Measurements of the cervical and dorsal vertebrae and humerus of *Adratiklit boulahfa*.

Element	Measurement	Dimensions (cm)
Cervical vertebra NHMUK PV R37367	Centrum length	12
Cervical vertebra NHMUK PV R37367	Anterior articular facet height	9
Cervical vertebra NHMUK PV R37367	Anterior articular facet width	9.5
Cervical vertebra NHMUK PV R37368	Centrum length	11.4
Cervical vertebra NHMUK PV R37368	Anterior articular facet height	9
Cervical vertebra NHMUK PV R37368	Anterior articular facet width	6.4
Cervical vertebra NHMUK PV R37368	Centrum length	11.5
Cervical vertebra NHMUK PV R37368	Posterior articular facet height	10.6
Cervical vertebra NHMUK PV R37368	Posterior articular facet width	7.4
Dorsal vertebra NHMUK PV R37365	Centrum length	5.5
Dorsal vertebra NHMUK PV R37365	Anterior articular facet height	8.2
Dorsal vertebra NHMUK PV R37365	Anterior articular facet width	6.2
Dorsal vertebra NHMUK PV R37365	Neural arch height (top of centrum to base of postzygapophyses)	13.1
Dorsal vertebra NHMUK PV R37366	Centrum length	6.1
Dorsal vertebra NHMUK PV R37366	Posterior articular facet height	7.9
Dorsal vertebra NHMUK PV R37366	Posterior articular facet width	9
Dorsal vertebra NHMUK PV R37366	Neural arch height	12
Left humerus NHMUK PV R37007	Length	61
Left humerus NHMUK PV R37007	Minimum shaft circumference	26.4

(NHMUK PV R36730; Maidment et al., 2015) and *Miragaia* (ML 433; Mateus et al., 2009), where the articular surfaces of the prezygapophyses are joined ventrally throughout their length. The neural spine appears to have arisen immediately posterior to the 'V'-shaped notch separating the prezygapophyses, so there was no intraprezygapophysial shelf, in contrast with the condition in *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) and *Miragaia* (ML 433; Mateus et al., 2009), but similar to *Huayangosaurus* (Zhou, 1984: Figs. 9, 11). The elongate prezygapophyses appear to be unique to this taxon among stegosaurs and are regarded as an autapomorphy (Fig. 7).

Diapophyses are broken in all three cervicals, but their bases are preserved (Fig. 5B, C, 6). They appear to have been dorsoventrally compressed and anteroposteriorly elongate, arising on the lateral surfaces of the prezygapophyses and extending posteriorly to a point level with the centrum midlength (Figs. 5C, D, 6). The diapophyses of *Huayangosaurus* (Zhou, 1984: Fig. 11), *Kentrosaurus* (MB.R.4783; Hennig, 1915) and *Loricatosaurus* (MHBR 001; Galton, 1990) also arise on the lateral surfaces of the prezygapophyses, but those of *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) and *Miragaia* (ML 433; Mateus et al., 2009) arise from the neural arch ventral to the prezygapophyses (Fig. 7). A subtle ridge (the posterior centrodiapophyseal lamina [PCDL] of Wilson, 1999) extends from the posterior margin of the diapophysis posteroventrally towards the posterior articular facet of the centrum; in the isolated cervical it fades before the presumed position of the neurocentral suture (Fig. 4B, C), but in the articulated cervicals it extends further, reaching the neurocentral suture just anterior to the posterior edge of the neural arch (Fig. 5C, D, 6). A PCDL is present in the posterior cervicals of

*Stegosaurus* (Maidment et al., 2015) and *Huayangosaurus* (Zhou, 1984: Fig. 11). A second lamina is visible extending from the posterior margin of the diapophysis posterodorsally towards the postzygapophyses (the postzygodiapophyseal lamina [PODL] of Wilson, 1999); on the articulated cervicals, this lamina is confluent with the epipophyses (see below; Figs. 4D; 6). These laminae define the margins of a shallowly concave fossa on the posterodorsal surface of the neural arch. A PODL appears to be present in the posterior cervicals of *Stegosaurus* (Maidment et al., 2015) but in the latter taxon it extends to the dorsolateral margin of the postzygapophyses, rather than epipophyses, which are absent in *Stegosaurus*.

Neural spines are broken in all three vertebrae and only the bases remain. The neural spine appears to have been transversely compressed, at least basally. The spine base is blade-like, anteroposteriorly elongate, and extends posteriorly to the distal end of the postzygapophyses (Figs. 4E, 5C–E, 6). Such an extremely elongate, blade-like neural spine is unknown in other stegosaurs, such as *Huayangosaurus* (Zhou, 1984: Fig. 11), *Kentrosaurus* (MB.R.4783; Hennig, 1915), and *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015), and this feature appears to be unique to this taxon (Fig. 7).

In dorsal view, the postzygapophyses are joined for almost their entire length, and separated by only a very short 'V'-shaped notch at their distal ends (Fig. 4E), as in the most posterior cervical vertebrae of *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015), but in contrast to the condition in *Miragaia* (ML 433; Mateus et al., 2009) where the postzygapophyses are separated for about one-third of their length. Pronounced rugosities on the dorsal surfaces of the postzygapophyses form

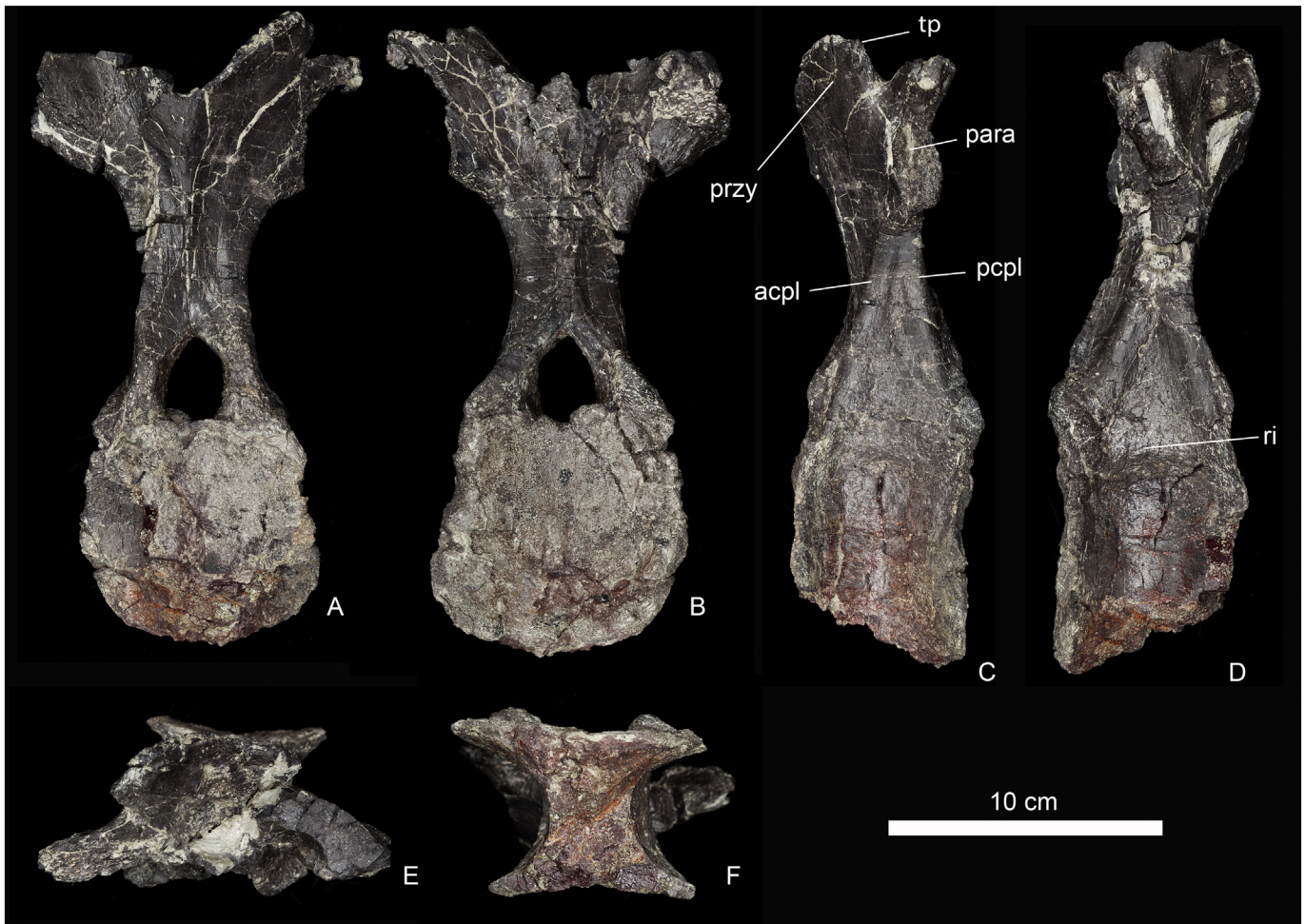


Fig. 8. NHMUK PV R37366, holotype specimen of *Adratiklit boulahfa*. Dorsal vertebra in A, anterior, B, posterior, C, left lateral, D, right lateral, E, dorsal and F, ventral view. acpl, anterior centroparapophyseal lamina; para, parapophysis; pcpl, posterior centroparapophyseal lamina; przy, prezygapophysis; ri, ridge; tp, triangular process posterior to prezygapophysis.



small, but distinct, epiphyses (Figs. 4D, E, 5E, 6); the presence of epiphyses on posterior cervical vertebrae is a unique character of this taxon among stegosaurs, and among ornithischians in general, where epiphyses, if present, are confined to cervicals 3 and 4. In lateral view, the postzygapophyses extend posterior to the posterior articular facet of the centrum to about the same degree as they do in cervical 12 of *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015); the postzygapophyses also overhang the posterior centrum surface in *Miragaia* (ML 433; Mateus et al., 2009; Fig. 7) but not in *Huayangosaurus* (Zhou, 1984; Fig. 11). The postzygapophyseal articular facets are flat, smooth, and face ventrolaterally (Fig. 5B). They are oval, with the long axis orientated anteroposteriorly, and anteroposteriorly elongate. The articular facets are not joined ventrally and a deep cleft separates them in ventral view (Fig. 5F). This separation is more pronounced than in the posterior cervicals of *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015). Measurements can be found in Table 1.

The morphology of the cervicals of ankylosaurs and stegosaurs are similar, and thus it is possible that these cervicals pertain to an ankylosaur. However, there is no other evidence of ankylosaurian dinosaur remains at the type locality or indeed in the El Mers Group. In contrast, the dorsal vertebrae and humerus bear clear stegosaurian synapomorphies (see below) and the cervicals were found in the same location as this

material. We therefore consider it most likely that these cervicals pertain to *Adratiklit* and not an otherwise unknown ankylosaur. More complete discoveries in the future will allow this association to be tested.

#### 4.2. Dorsal vertebrae (NHMUK PV 37365; NHMUK PV R37366)

Two dorsal vertebrae are preserved. NHMUK PV R37366 is dark grey in colour (Fig. 8), similar to the isolated cervical, and is designated the holotype specimen; the other dorsal, NHMUK PV R37365, is pale brown-pink (Fig. 9), and is more similar in colour to the articulated cervicals. There is no information, however, on whether these vertebrae were found in the same horizons as the cervicals. The centrum and neural arches of the dorsal vertebrae are preserved but most of the processes are broken: one preserves a left prezygapophysis, while the other preserves partial postzygapophyses.

The centrum is slightly wider transversely than it is long anteroposteriorly, as in *Hesperosaurus* (DMNH 29431) and *Dacentrurus armatus* (NHMUK OR 46013; Galton, 1990), but in contrast to *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015), *Loricatosaurus* (NHMUK PV R3167; Galton, 1985), *Kentrosaurus* (MB.R.1930; Hennig, 1915) and *Huayangosaurus* (ZDM T7001; Zhou, 1984), in which the centra are equidimensional or slightly longer than wide. Both articular

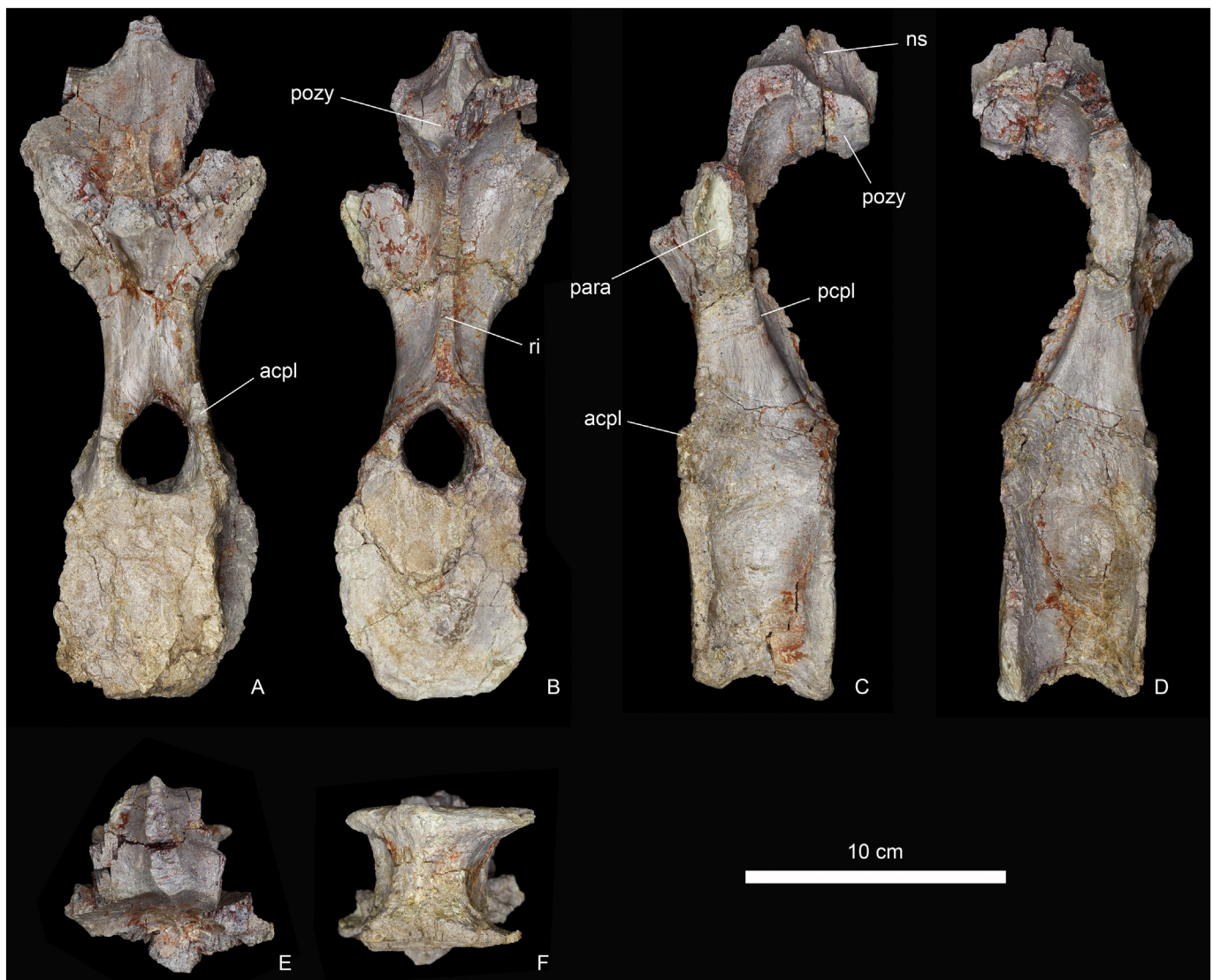


Fig. 9. NHMUK PV R37365, a dorsal vertebra referred to *Adratiklit bouldhfa*, in A, anterior, B, posterior, C, left lateral, D, right lateral, E, dorsal and F, ventral view. **acpl**, anterior centroparapophyseal lamina; **ns**, neural spine; **para**, parapophysis; **pcpl**, posterior centroparapophyseal lamina; **pozy**, postzygapophysis; **ri**, ridge.

facets are flat. The centrum is very strongly constricted laterally and strongly spool-shaped in ventral view (Figs. 8F, 9F). The lateral surfaces of the centrum are flat anteroposteriorly and dorsoventrally; a slight groove is present ventrally but this is likely due to crushing. The neurocentral suture is obliterated but its location is marked by a strong, anteroposteriorly-extending ridge (Fig. 8D). The lateral constriction of the centrum and prominence of the anteroposterior ridge are more pronounced than in other stegosaurs, although these features may have been accentuated by crushing.

The neural canal is teardrop-shaped with the apex pointing dorsally. The neural arch pedicle is dorsoventrally tall and is flat anteriorly dorsal to the neural canal. Anterior centroparapophyseal laminae (ACPL; Wilson, 1999) extend posterodorsally from the anterodorsal corners of the centrum to merge with the bases of the parapophyses, and these laminae form the lateral margins of the neural arch in anterior view (Fig. 8A, C). ACPL are also present in *Stegosaurus* (Maidment et al., 2015; Fig. 10). Adjacent to the neural canal, ACPLs are extended slightly anteriorly into rugose processes; this feature appears to be unique to *Adratiklit* among stegosaurs.

The prezygapophyses were fused ventrally, as in other stegosaurs, except for the anterior-most dorsals of *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) in which they are separated. Their articular facets are elongate and oval in outline with their long axes trending dorsoventrally, and they face dorsomedially, as in most other stegosaurs, except for the anterior-most dorsals of *Stegosaurus* (Maidment et al., 2015), in which the articular facets face dorsally. Posterior to the articular facet a small triangular protuberance is situated dorsally on the prezygapophysis (Fig. 8). This is strongly rugose, and appears to be a unique feature of this taxon among stegosaurs, so is regarded as an autapomorphy of *Adratiklit*.

Posterior to the prezygapophyses, the intraprezygapophyseal shelf is extremely narrow, and a dorsally extending plate of bone that supports the postzygapophyses and the neural spine arises from this region. A ridge extends up the midline of this shelf, bifurcates at a point level with the top of the prezygapophyses, and then these ridges merge again a short distance dorsally, similar to the condition in *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015), *Kentrosaurus* (MB.R.1930; Hennig, 1915) and *Huayangosaurus* (Zhou, 1984; Fig. 13).

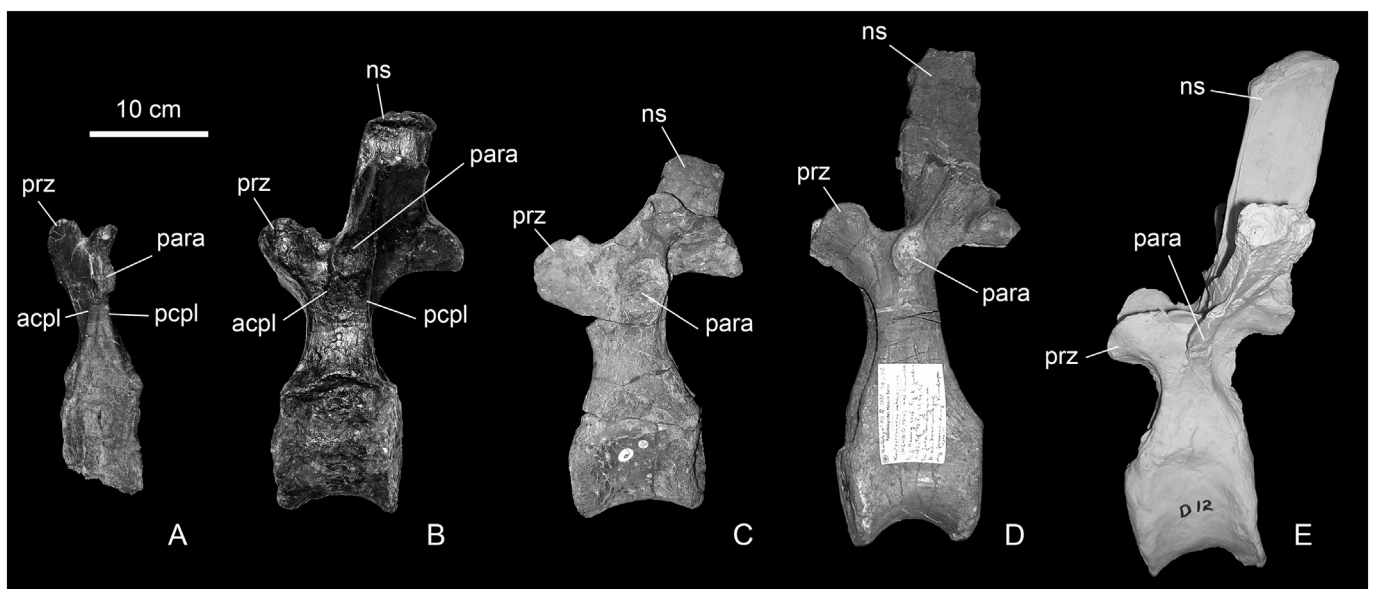
In lateral view, a lamina extends from the posterior margin of the parapophysis posteroventrally towards the posterodorsal corner of the

centrum (the posterior centroparapophyseal lamina [PCPL] of Wilson, 1999; Figs. 8C, 9C, 10). The parapophyses are deeply concave and were presumably situated at the base of the diapophyses, which have broken off (Fig. 9C). The postzygapophyses extend posteriorly to about the same level as the posterior centrum surface (Fig. 9C), as in *Huayangosaurus* (Zhou, 1984; Fig. 14) and *Kentrosaurus* (MB.R.1930; Hennig, 1915); in *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015) the postzygapophyses overhang the centrum posteriorly. The articular surfaces of the postzygapophyses face ventrolaterally and are rounded in outline (Fig. 9B, C). The base of the neural spine is supported by the postzygapophyses, but the spine itself is not preserved (Fig. 8C, D).

In posterior view, a ridge extends along the midline of the neural arch from the top of the neural canal to the base of the postzygapophyses. It is broken along its length but appears to have been prominent. Either side of this ridge, two shallow fossae occupy the neural arch (Fig. 9B), as in other stegosaurs. Measurements can be found in Table 1.

#### 4.3. Left humerus (NHMUK PV R37007)

The humerus is pale pink-grey in colour (Fig. 11). It is dumbbell-shaped in outline, although the dorsal end is broader transversely than the ventral end. The small head is semicircular and restricted to the posterior surface of the humerus (Fig. 11B). A prominent descending ridge and well-developed triceps tubercle are present, which together represent a synapomorphy of Stegosauria (Raven and Maidment, 2017; Fig. 11A, B). The ridge extends ventrally along the posterior margin of the deltopectoral crest. The triceps tubercle is located about two-thirds of the way down the descending ridge, and the ridge extends to the base of the deltopectoral crest, as in other stegosaurs, including *Kentrosaurus* (MB.R.4804; Hennig, 1915), *Loricatosaurus* (NHMUK PV R3167; Galton, 1985), *Dacentrurus armatus* (NHMUK OR 46013; Galton, 1985) and *Stegosaurus* (NHMUK PV R36730; Maidment et al., 2015). A scar for the *m. latissimus dorsi* (Maidment and Barrett, 2012) is present ventral to the head and medial to the lower part of the ridge ventral to the triceps tubercle. It is oval, longer anteroposteriorly than high dorsoventrally, and rugose (Fig. 11B). The distal condyles are well preserved; the medial condyle extends further ventrally than the lateral condyle, and a shallow fossa separates them on the posterior surface. Ventrally the condyles are saddle-shaped, as in other stegosaurs.



**Fig. 10.** Comparison of dorsal vertebrae of stegosaurian dinosaurs in right lateral view. **A**, *Adratiklit*, NHMUK PV R37366; **B**, *Stegosaurus*, NHMUK PV R36730; **C**, *Loricatosaurus*, NHMUK PV R3167; **D**, *Kentrosaurus*, MB.R.1931; **E**, cast of *Hesperosaurus*, DMNH 29431. **acpl**, anterior centroparapophyseal lamina; **ns**, neural spine; **para**, parapophysis; **pcpl**, posterior centroparapophyseal lamina; **prz**, prezygapophysis.

In anterior view, the medial tuberosity is eroded but very rugose (Fig. 11C). The dorsal margin of the humerus has been compressed and folded ventrally so that it overhangs the anterior surface. The dorsal margin of the humerus in the region of the head is very strongly rugose and covered in calcified cartilage (Fig. 11E). The anterior margin of the deltopectoral crest is also strongly rugose. The medial condyle is characterized by a flat, medially-facing surface that is also rugose. Measurements can be found in Table 1.

## 5. Phylogenetic analysis

*Adratiklit boulahfa* was added into the data matrix of Raven and Maidment (2017), which was compiled to investigate stegosaurian interrelationships, along with the recently described probable stegosaurian *Isaberrysaura* (Raven and Maidment, 2018). The data matrix consists of 25 taxa scored for 115 morphological characters. The character list and data matrix can be found in online supplementary data, and further details are available in Raven and Maidment (2017). The matrix was analysed in TNT v1.5 (Goloboff et al., 2008) using the same analytical settings as the original study. A New Technology search was performed

using sectorial, ratchet, drift and tree fusing options and 10 random addition sequences. *Pisanosaurus mertii* was used as the outgroup. The New Technology search option in TNT finds all of the most parsimonious trees (MPTs) needed to produce a strict consensus tree, but it does not recover all MPTs. Thus, the MPTs recovered from the New Technology search were used as the starting point for a round of tree bisection–reconnection (TBR) using the Traditional Search option, as this more fully explores treespace for additional most parsimonious topologies. The search was carried out with one random addition seed and 1000 replicates. Multistate characters 105 and 106 were ordered, as were the continuous characters (1–24). Support for the relationships obtained was evaluated using symmetric resampling and bootstrap analysis. Symmetric resampling was applied to matrix using 5000 replicates and a New Technology search, and 1000 pseudoreplicate datasets were produced for bootstrap analysis.

Two most parsimonious trees (MPTs) with lengths of 265.76 steps were recovered. In both MPTs, *Adratiklit* is recovered as the sister-taxon to a clade containing the European stegosaurs *Dacentrurus armatus* and *Miragaia longicollum*; the MPTs differ only in their placement of *Alcovasaurus* in relation to *Paranthodon* and *Tuojiangosaurus*,

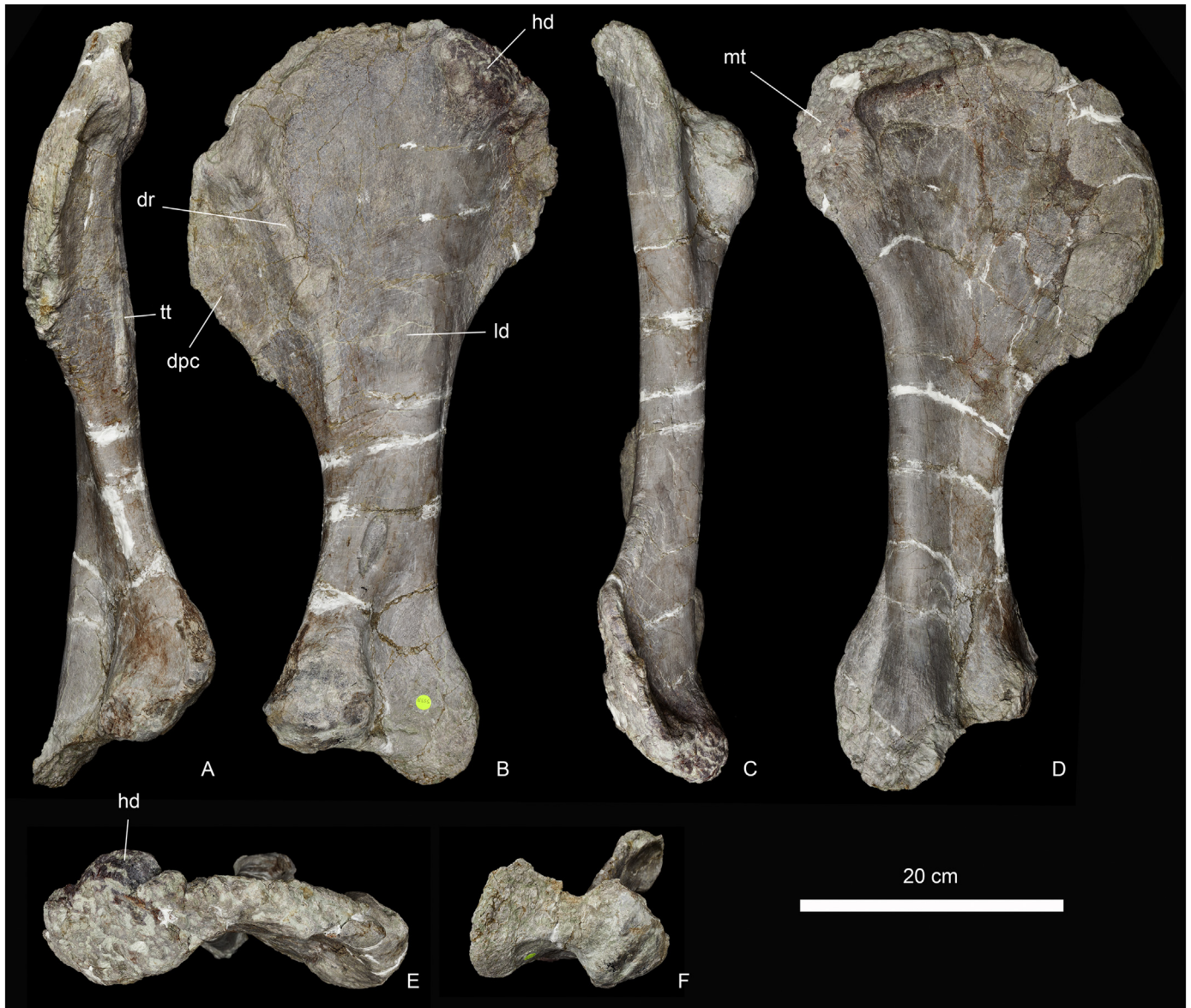


Fig. 11. NHMUK PV R37007, left humerus referred to *Adratiklit boulahfa* in A, lateral, B, posterior, C, medial, D, anterior, E, dorsal and F, ventral views. **dpc**, deltopectoral crest; **dr**, descending ridge; **hd**, head; **ld**, muscle scar for the insertion of the *m. latissimus dorsi*; **mt**, medial tuberosity; **tt**, triceps tubercle.

and *Jiangjunosaurus* in relation to *Hesperosaurus*. We resolve the Patagonian ornithischian *Isaberrysaura* as a basal stegosaur, a result also found by Han et al. (2018) and Raven and Maidment (2018). A strict consensus of the MPTs, showing measures of support for clades, is shown in Fig. 12.

**6. Discussion**

Haddoumi et al. (2016) reported a possible stegosaurian tooth from the Bathonian Anoual Formation of the High Atlas Mountains, Morocco. This tooth (Haddoumi et al., 2016: Fig. 14D) is damaged, missing its apex, so its overall shape cannot be determined, and features like marginal denticles cannot be seen. The reasons for its referral to c.f. *Stegosauria* are unclear. Therefore, as it bears no particular resemblance to stegosaurian teeth over those present in other ornithischians, or indeed other herbivorous archosaurs, it is regarded as non-ornithischian (*Archosauria* indet.). However, *Adratiklit* is clearly referable to *Stegosauria* on the basis of unequivocal stegosaurian synapomorphies, including an elongate neural arch pedicel in dorsal vertebrae and a tri-caps tubercle with descending ridge of the humerus, and thus represents the earliest record not only of stegosaurs, but also of the clade

Eurypoda, from Africa. It is also the first eurypodan body fossil from northern Africa.

Non-eurypodan ('basal') thyreophorans are known from the Early Jurassic and have a worldwide distribution, including Europe (*Scelidosaurus*: Sinemurian–Pliensbachian of the UK [Owen, 1861; Page, 2009]; *Emausaurus*: Toarcian, Germany [Haubold, 1990]), North America (*Scutellosaurus*: Pliensbachian, USA [Colbert, 1981; Steiner and Tanner, 2014]), South America (*Laquintasaura*: Hettangian, Venezuela [Barrett et al., 2014]), southern Africa (*Lesothosaurus*: Hettangian–Sinemurian, South Africa and Lesotho [Porro et al., 2015; Baron et al., 2017]) and Asia ('*Bienosaurus*' and '*Tatisaurus*': Hettangian–Sinemurian, China [Norman et al., 2007; Raven et al., 2019]). The earliest record of the clade Eurypoda, which is also the earliest stegosaur, *Isaberrysaura*, is known from the Bajocian part of the Los Molles Formation of Patagonia (Salgado et al., 2017). This indicates that Eurypoda had already diverged by the Early or earliest Middle Jurassic. The relatively derived phylogenetic position of *Adratiklit* suggests that stegosaurs diversified rapidly in the Middle Jurassic, although the fossil record of the clade is extremely poor at this time: *Loricatosaurus priscus*, from the Oxford Clay of the UK and France, is Callovian in age (Cox et al., 1992; Maidment et al., 2008) and is the only other valid Middle Jurassic taxon, although other

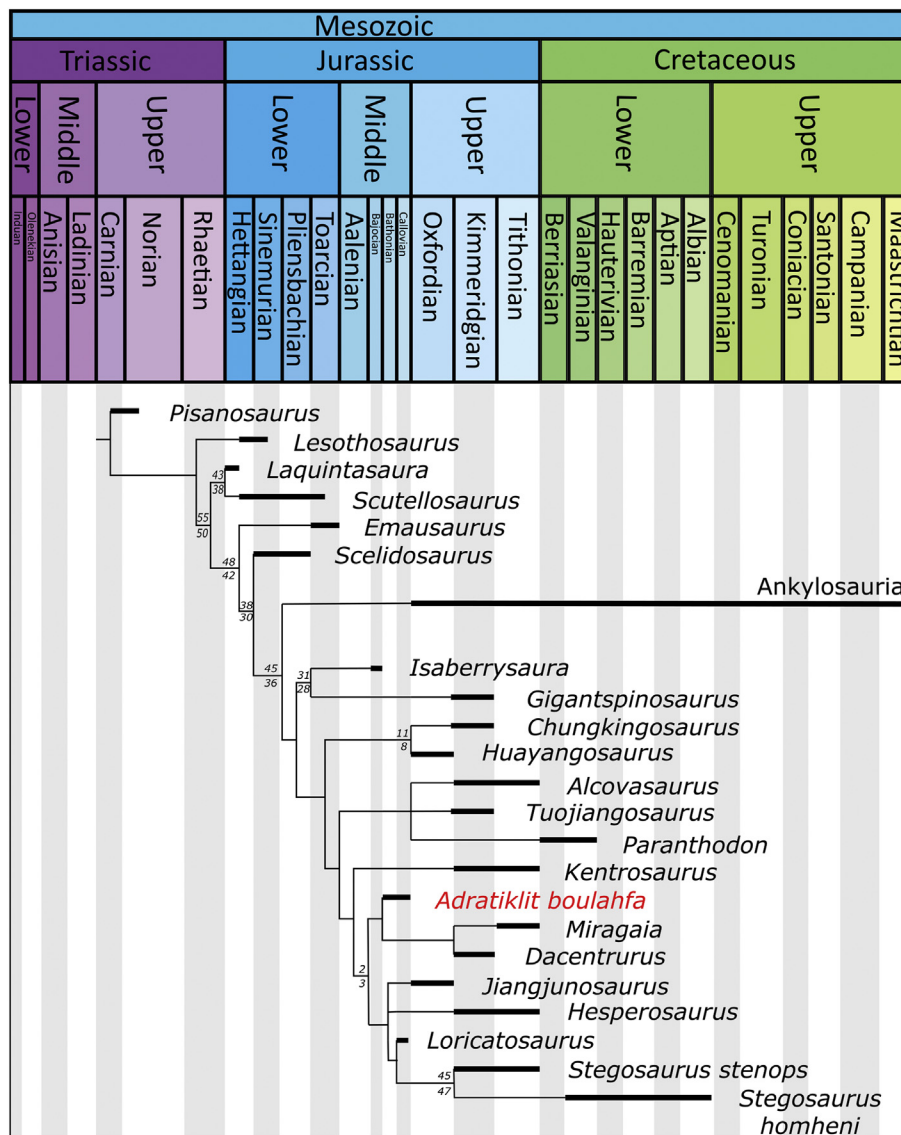
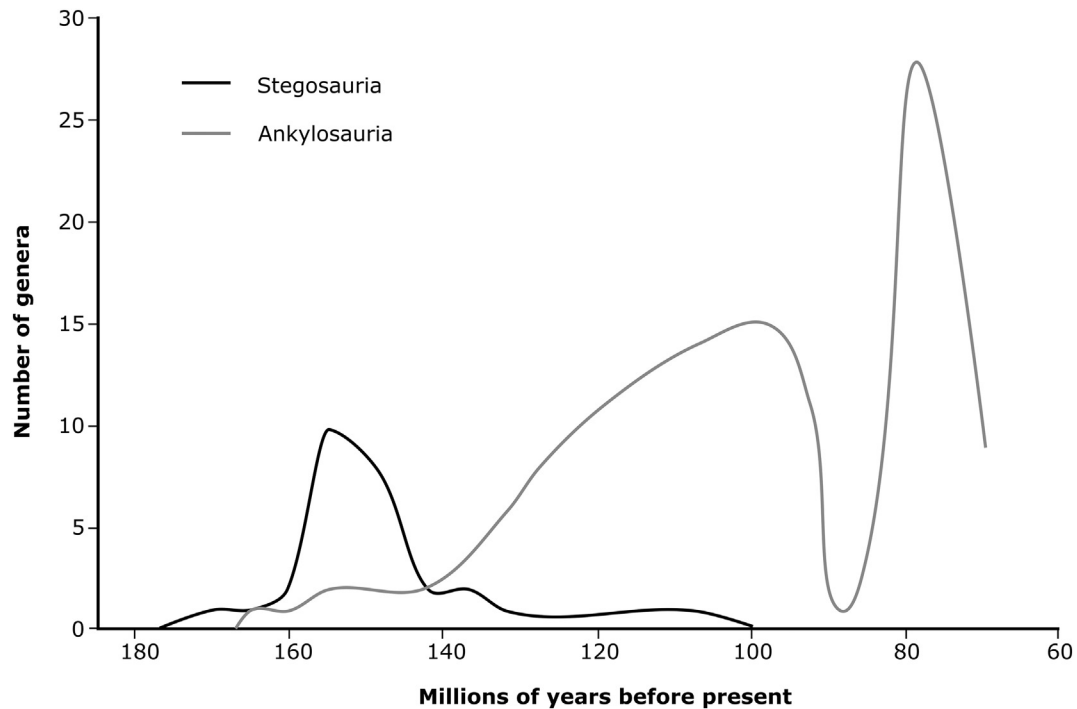


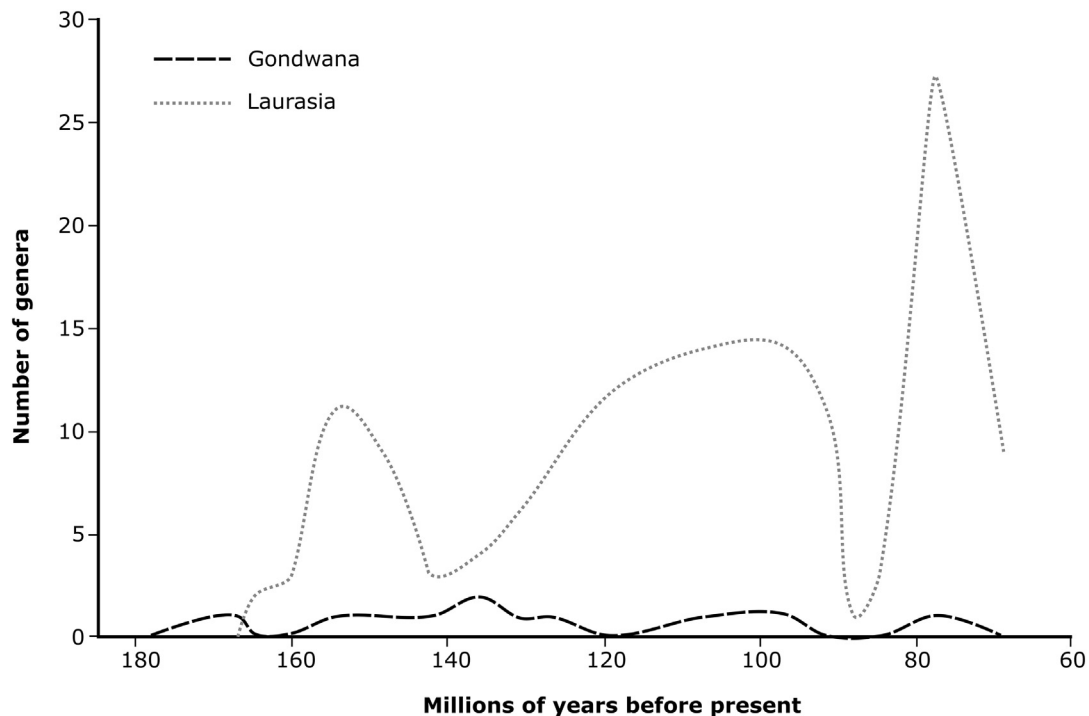
Fig. 12. Strict consensus of the two most parsimonious trees recovered by the phylogenetic analysis. Numbers above clades are symmetric resampling frequencies and numbers below clades are bootstrap support percentages.



**Fig. 13.** Raw generic diversity of eurypodan thyreophoran clades Stegosauria (black line) and Ankylosauria (grey line) through the Jurassic and Cretaceous. Data modified from the Paleobiology Database (PBDB).

indeterminate material is known from the Bathonian of Europe (see review in [Maidment et al., 2008](#)). The oldest definitive ankylosaurs, *Sarcolestes leedsi* ([Galton, 1983](#)) and '*Cryptosaurus emerus*' ([Naish and Martill, 2008](#)) are from the Callovian Oxford Clay Formation and the Oxfordian Amphill Clay Formation, respectively. Other thyreophoran taxa that were previously considered to be Middle Jurassic in age (e.g. *Huayangosaurus* from the Lower Shaximiao Formation of China) are now thought to date from the Late Jurassic ([Wang et al., 2018](#)).

In Late Jurassic terrestrial deposits, the remains of stegosaurs are widespread (e.g. Morrison Formation of the USA ([Gilmore, 1914](#); [Maidment et al., 2015](#)); Lourinhá Formation of Portugal ([Mateus et al., 2009](#)); Villar del Arzobispo Formation of Spain ([Cobos et al., 2010](#); [Company et al., 2010](#)); Tendaguru Beds of Tanzania ([Hennig, 1915](#)); Lower & Upper Shaximiao formations of the Sichuan Basin, China ([Dong et al., 1983](#); [Zhou, 1984](#); [Maidment et al., 2006](#); [Maidment et al., 2006](#); [Wang et al., 2018](#)), and they appear to have been relatively



**Fig. 14.** Raw generic eurypodan diversity in Laurasia (grey dotted line) and Gondwana (black dashed line) through the Jurassic and Cretaceous. Data modified from the PBDB.

abundant worldwide at this time. In contrast, ankylosaurs seem to have been rare, and are represented by just a handful of taxa, including *Mymooropelta* and *Gargoyleosaurus* from the Morrison Formation (Kirkland and Carpenter, 1994; Carpenter et al., 1998), and *Dracopelta* from the Lourinhá Formation (Galton, 1980a), as well as other taxonomically indeterminate fragments. Ankylosaurs diversified in the Early Cretaceous, coincident with the decline of stegosaurs (Fig. 13), and became important constituents of Late Cretaceous ecosystems (e.g. Dinosaur Park Formation, Hell Creek Formation). Whether ankylosaurs competitively replaced stegosaurs, or whether they opportunistically exploited vacant ecological space as the result of a purported extinction event at the end of the Jurassic (Raup and Sepkoski, 1982), remains unexplored (Butler et al., 2010).

The vast majority of eurypodan taxa so far recognized have been described from Laurasia, with just three stegosaurs (*Isaberrysaura*, *Kentrosaurus*, *Paranthodon*) and two ankylosaurs (*Antarctopelta*, *Kunbarrasaurus*) being known from Gondwanan continents throughout the entire Mesozoic (Fig. 14). The discovery of *Adratiklit* in Africa therefore adds significantly to the known diversity of Gondwanan eurypodans.

The absence of eurypodans from Gondwana is puzzling in the light of their abundance and diversity in Laurasia. Four possible scenarios can be envisaged to explain this lack of diversity: (1) eurypodans were genuinely rare faunal constituents in Gondwana; (2) terrestrial rocks of the right age are not present in Gondwana and thus eurypodan fossils are not preserved (a geological sampling bias); (3) Gondwanan continents have not been intensively sampled (an anthropogenic sampling bias); and (4) the fossil record of eurypodans in Gondwana might have been affected by both geological and anthropogenic sampling biases. In order to examine these four scenarios, all occurrences of Gondwanan eurypodans, all Gondwanan formations in which dinosaurs have previously been found (dinosaur-bearing formations, DBFs), and all collections containing Gondwanan dinosaurs (dinosaur-bearing collections, DBCs) were obtained from the Paleobiology Database ([www.paleobiodb.org](http://www.paleobiodb.org); downloaded April 2019) for the time period from 190 to 66 Ma, covering the known temporal range of the clade (Fig. 15). DBFs and DBCs are strongly correlated with each other

(Kendall's tau = 0.740,  $p < 0.001$ ; Spearman's rho = 0.89,  $p < 0.001$ ), suggesting that, as might be expected, greater rock availability allows more opportunities for fossil recovery. DBCs and DBFs are both correlated with the number of eurypodan occurrences throughout the time interval (DBFs vs. occurrences: Kendall's tau = 0.49,  $p = 0.004$ ; Spearman's rho = 0.61,  $p = 0.003$ ; DBCs vs. occurrences: Kendall's tau = 0.55,  $p = 0.001$ ; Spearman's rho = 0.68,  $p = 0.001$ ), indicating that scenario (4) is likely to be correct: the fossil record of Gondwana is biased by both geological and anthropogenic sampling biases. Gondwanan eurypodans may have been as diverse and abundant as their Laurasian relatives, but their fossil record has yet to be fully exploited. This means that prospects for the discovery of further eurypodan material from new sites in the Jurassic and Cretaceous of the former Gondwanan continents are more promising than usually assumed.

## 7. Conclusions

*Adratiklit boulahfa* is the first eurypodan thyreophoran dinosaur from North Africa, and represents one of the earliest records of this clade from anywhere in the world. Based on currently available data, it is more closely related to a clade of European stegosaurs that it is to either of the known African genera, *Kentrosaurus* or *Paranthodon*. The paucity of eurypodan dinosaur material in Gondwana during the Jurassic and Cretaceous probably results from anthropogenic and geological sampling biases, and it is possible that eurypodans might have been as diverse and abundant in Gondwana as they were in Laurasia. The prospects for finding new thyreophorans on the continents that made up Gondwana are therefore stronger than previously supposed.

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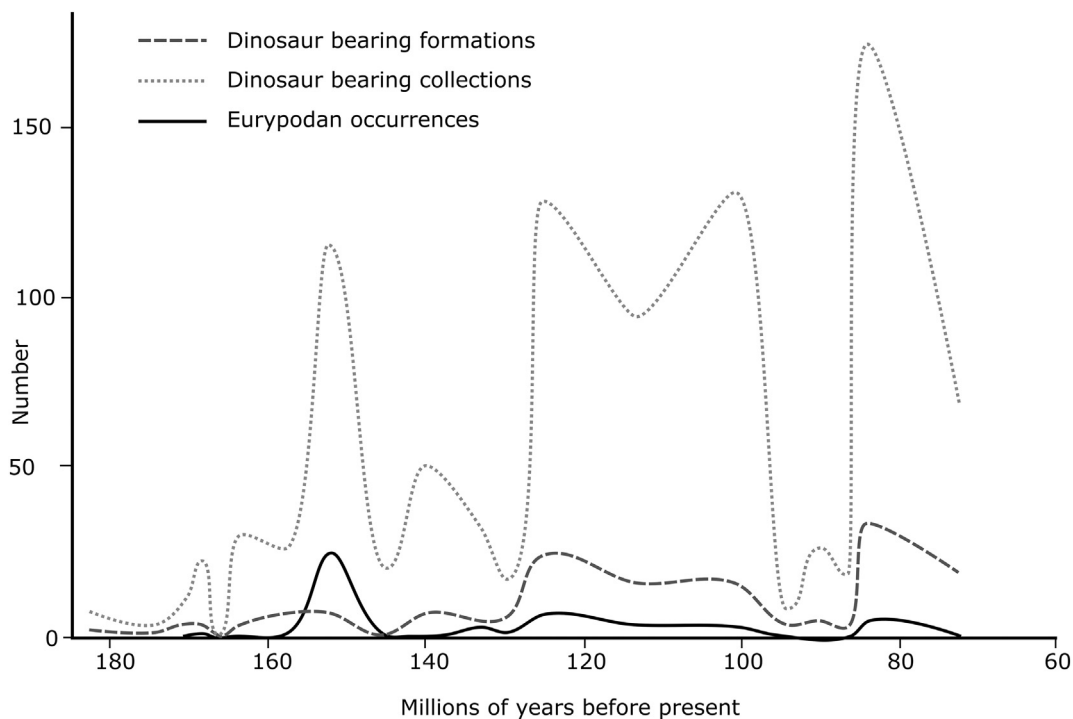


Fig. 15. Gondwanan eurypodan occurrences, Gondwanan dinosaur-bearing formations and Gondwanan dinosaur-bearing collections through the Jurassic and Cretaceous. Data from the PBDB.

Photography Unit) for photography of the specimens. André Charrière provided his unpublished geological map of the area for Fig. S1. Martin Munt made us aware of the material and helped to arrange for its acquisition, supported by the Earth Sciences DIF (Natural History Museum). TJR is supported by a Science Scholarship from the University of Brighton. Eurypodan diversity data was obtained from the Paleobiology Database, and we thank all data inputters who contributed. Thanks to Mark Graham (NHMUK) for preparation of the specimen.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gr.2019.07.007>.

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