The systematic position of the enigmatic thyreophoran dinosaur *Paranthodon africanus*, and the use of basal exemplifiers in phylogenetic analysis (#22703)

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The systematic position of the enigmatic thyreophoran dinosaur *Paranthodon africanus*, and the use of basal exemplifiers in phylogenetic analysis

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The first African dinosaur to be discovered, *Paranthodon africanus* was found in 1845 in the Lower Cretaceous of South Africa. Taxonomically assigned to numerous groups since discovery, in 1981 it was described as a stegosaur, a group of armoured ornithischian dinosaurs characterised by bizarre plates and spines extending from the neck to the tail. This assignment has been subsequently accepted. The type material consists of a premaxilla, maxilla, a nasal, and a vertebra, and contains no synapomorphies of Stegosauria. Several features of the maxilla and dentition are reminiscent of Ankylosauria, the sister-taxon to Stegosauria, and the premaxilla appears superficially similar to that of some ornithopods. The vertebral material has never been described, and since the last description of the specimen, there have been numerous discoveries of thyreophoran material potentially pertinent to establishing the taxonomic assignment of the specimen. An investigation of the taxonomic and systematic position of *Paranthodon* is therefore warranted. This study provides a detailed re-description, including the first description of the vertebra. Numerous phylogenetic analyses demonstrate that the systematic position of *Paranthodon* is highly labile and subject to change depending on which exemplifier for the clade Stegosauria is used. The results indicate that the use of a basal exemplifier may not result in the correct phylogenetic position of a taxon being recovered if the taxon displays character states more derived than those of the basal exemplifier, and we recommend the use, minimally, of one basal and one derived exemplifier per clade. *Paranthodon* is most robustly recovered as a stegosaur in our analyses.

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ABSTRACT

The first African dinosaur to be discovered, *Paranthodon africanus* was found in 1845 in the Lower Cretaceous of South Africa. Taxonomically assigned to numerous groups since discovery, in 1981 it was described as a stegosaur, a group of armoured ornithischian dinosaurs characterised by bizarre plates and spines extending from the neck to the tail. This assignment has been subsequently accepted. The type material consists of a premaxilla, maxilla, a nasal, and a vertebra, and contains no synapomorphies of Stegosauria. Several features of the maxilla and dentition are reminiscent of Ankylosauria, the sister-taxon to Stegosauria, and the premaxilla appears superficially similar to that of some ornithopods. The vertebral material has never been described, and since the last description of the specimen, there have been numerous discoveries of thyreophoran material potentially pertinent to establishing the taxonomic assignment of the specimen. An investigation of the taxonomic and systematic position of *Paranthodon* is therefore warranted. This study provides a detailed re-description, including the first description of the vertebra. Numerous phylogenetic analyses demonstrate that the systematic position of *Paranthodon* is highly labile and subject to change depending on which exemplifier for the clade Stegosauria is used. The results indicate that the use of a basal exemplifier may not result in the correct phylogenetic position of a taxon being recovered if the taxon displays character states more derived than those of the basal exemplifier, and we recommend the use, minimally, of one basal and one derived exemplifier per clade. *Paranthodon* is most robustly recovered as a stegosaur in our analyses.

INTRODUCTION

The first dinosaur to be found in Africa, *Paranthodon africanus* (NHMUK [Natural History Museum, London, UK] R47338), was discovered in 1845 in the Kirkwood Formation of South Africa. Originally identified as the pareiasaur *Anthodon serranius* (Owen, 1876), then the ankylosaurian *Palaeoscincus africanus* (Broom, 1910) and then the stegosaurian *Paranthodon oweni* (Nopsca, 1929), the specimen has had uncertain taxonomical affinities. Finally, Galton and Coombs (1981) settled the nomenclatural debate and coined *Paranthodon africanus*, agreeing with the assignment to Stegosauria. Stegosauria is a clade of thyreophoran ‘armoured’ ornithischian dinosaurs, characterized by the possession of two bizarre parasaggital rows of plates and spines that extend from the head to the end of their tail. They have a restricted temporal range, from the Middle Jurassic to the Lower Cretaceous, and are known from strata worldwide, with particularly high biodiversity in the Middle and Upper Jurassic of China (Maidment et al., 2008).

Dating the Kirkwood Formation, where *Paranthodon* was discovered, has proven problematic. However, recent consensus suggests the fossiliferous sections of the Upper Kirkwood Formation date to the early Early Cretaceous (e.g. Forster et al., 2009; Choiniere, Forster and de Klerk 2012; McPhee et al., 2016). This would make *Paranthodon* one of the youngest stegosaurs (Pereda Suberbiola et al., 2003), and stratigraphically close to the assumed extinction of the group. The Kirkwood Formation is part of the Uitenhage Group, found within the Algoa Basin of South Africa (Muir, Bordy and Prevec, 2015), and consists of three members; the Swartkops Member, the Colchester Member and an unnamed stratigraphically higher unit, which contains all of the vertebrate fossil material found in the Kirkwood Formation (McPhee et al., 2016). The lithologic description of the upper unit by McPhee et al. (2016) matches the matrix of NHMUK R47338, and thus it is likely that *Paranthodon* is derived from this unit. The geographic location of *Paranthodon* is particularly significant because it represents one of only two Gondwanan stegosaurs (Mateus, Maidment and Christiansen, 2009).

The first phylogeny of Stegosauria was produced by Galton and Upchurch (2004), but this provided little resolution in the morphologically conservative clade, and *Paranthodon* was deleted *a posteriori* from the analysis in order to achieve higher resolution. Maidment et al. (2008, later updated for new taxa in Mateus, Maidment and Christiansen (2009); Maidment (2010)) was the first phylogenetic analysis to include *Paranthodon*, but found it in a polytomy towards the base of Stegosaurinae with *Loricatosaurus priscus* and *Tuojiangosaurus multispinus*. The most recent phylogeny of Stegosauria by Raven and Maidment (2017) found *Paranthodon* in a sister-taxon relationship with *Tuojiangosaurus*, which together were sister-taxa to the clade Huayangosauridae (*Huayangosaurus taibaii* + *Chungkingosaurus jiangbeiensis*).

The material assigned to *Paranthodon* is a left partial maxilla, premaxilla and nasal (Maidment et al., 2008), and two referred teeth. Additionally, there is a partial vertebra that was mentioned but not described by Galton and Coombs (1981). Although classified as a stegosaurian, there are features that are reminiscent of the Ankylosauria, the sister clade to Stegosauria. These include tooth morphology and the presence of a secondary maxillary palate (Vickaryous, Maryańska and Weishampel, 2004). Furthermore, the dorsally elongate premaxilla is dissimilar to that of other thyreophorans (Galton & Upchurch 2004). This study provides a detailed re-description of the material referred to *Paranthodon*, including previously undescribed material, and provides comprehensive anatomical comparisons in order to evaluate the systematic position of the taxon. Furthermore, this study utilises numerous phylogenetic hypotheses to constrain the evolutionary relationships of *Paranthodon*, including the first analysis of the taxon in an ankylosaurian phylogeny.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1841

ORNITHISCHIA Seeley, 1887

THYREOPHORA Nopcsa, 1915 (sensu Norman, 1984)

STEGOSAURIA Marsh, 1877

Paranthodon Nopcsa, 1929

Paranthodon africanus Broom, 1910

1876 *Anthodon serrarius* Owen

1910 *Palaeoscincus africanus* Broom

1929 *Paranthodon oweni* Nopcsa

Holotype: NHMUK R47338. Left partial maxilla, premaxilla, nasal and a dorsal vertebra.

Referred specimens: NHMUK R4992. Two teeth. Locality and horizon unknown. Maidment et al. (2008) noted that while the teeth appear similar in morphology to *Paranthodon*, there are no autapomorphies of the genus located on the teeth, and so they were regarded as indeterminate stegosaurian. However, as there are no synapomorphies of Stegosauria located on the teeth, they are referred to as indeterminate thyreophoran herein.

Diagnosis: The only identifiable autapomorphy of this genus within Stegosauria is the possession of a medially extending maxillary palate.

Occurrence: Bushmans River, Algoa Basin, Eastern Cape Province, South Africa. Upper Kirkwood Formation, early Early Cretaceous (possibly Berriasian- Valanginian, Choiniere, Forster and de Klerk (2012); McPhee et al. (2016)).

Remarks: The placement of *Paranthodon* within Stegosauria herein is based on morphological similarities with stegosaurs, as well as numerous phylogenetic analyses in this study (see Discussion for further information). In stegosaurian, ankylosaurian and basal ornithischian cladograms, *Paranthodon* is found within Stegosauria or sister-taxon to the stegosaurian exemplifier used. Although *Paranthodon* contains no synapomorphies that place it unequivocally in Stegosauria, the use of phylogenetics allows this referral, and therefore *Paranthodon* can be considered a valid genus due to the presence of an autapomorphy within Stegosauria.

DESCRIPTION

The last description of *Paranthodon* (NHMUK R47338) was by Galton and Coombs (1981), but the discovery of new thyreophoran material means a re-description is warranted. The previous study misidentified the posterior process of the premaxilla as the nasal, and there was no description of the vertebra, which is described here for the first time.

Premaxilla

The left premaxilla consists of an anteriorly-projecting anterior process and a posterior process that projects posterodorsally (Fig. 1). The anterior end of the premaxilla is incomplete, but the anterior process is sinuous in lateral view and curves ventrally, as in the stegosaurs *Miragaia* (Mateus, Maidment and Christiansen, 2009) and *Huayangosaurus* (Sereno and Dong, 1992), the ankylosaur *Silvisaurus* (NHMUK R1107) and the basal ornithischian *Heterodontosaurus* (Butler, Porro and Norman, 2008). This, however, contrasts to the horizontally- projecting process of the stegosaurs *Chungkingosaurus* (Maidment and Wei, 2006) and *Stegosaurus stenops* (NHMUK R36730), the ankylosaur *Edmontonia* (NHMUK R36851), and the basal ornithischian *Lesothosaurus* (Sereno, 1991). The posterior process of the premaxilla is robust and similar to that of the basal ornithischian *Heterodontosaurus* (Butler, Upchurch and Norman, 2008) and the ornithopods *Camptosaurus* (NHMUK R1608) and *Jinzhousaurus* (Wang and Xu, 2001) in that it intervenes between the maxilla and nasal to stop them contacting each other. The angle of the posterior process in *Paranthodon* is 47 degrees relative to horizontal, although this varies widely in thyreophorans (Table 1). The premaxilla is edentulous, as in every other stegosaur with cranial material preserved other than *Huayangosaurus* (Sereno and Dong, 1992). The distribution of premaxillary teeth in other ornithischians varies; basal members of most ornithischian groups possess premaxillary teeth. For example, the basal ornithopod *Hypsilophodon* has five (Norman et al., 2004), and basal ankylosaurs, such as such as *Gargoyleosaurus*, *Pawpawsaurus* and *Cedarpelta* (Kinneer, Carpenter and Shaw, 2016) possess premaxillary teeth. More derived members of Ornithopoda and Ankylosauria, however, have edentulous premaxillae (e.g. most basal iguanodontids (Norman et al., 2004); *Edmontonia* (NHMUK R36851); *Euoplocephalus* (NHMUK R4947)). The premaxillae contacted each other along a dorsoventrally deep sutural surface and this forms a small premaxillary palate, similar to that of *Stegosaurus stenops* (NHMUK R36730) and in the ankylosaur *Gastonia* (Kinneer, Carpenter and Shaw, 2016), but not as robust as that of the basal thyreophoran *Scelidosaurus* (NHMUK R1111). The premaxillary palate of *Paranthodon* has a transversely concave dorsal surface. Despite poor preservation, the external naris appears to face anterolaterally, as in the ankylosaurs *Gastonia* (Kinneer, Carpenter and Shaw, 2016) and *Euoplocephalus* (NHMUK R4947) and the ornithopods *Camptosaurus* (NHMUK R1608) and *Jinzhousaurus* (Wang and Xu, 2001). This feature is, however, variable in stegosaurs; the same condition is seen in *Huayangosaurus* (Sereno and Dong, 1992), yet in *Stegosaurus* (NHMUK R36730) and *Hesperosaurus* (Carpenter, Miles and Cloward, 2001), the external nares face anteriorly. The external naris is longer anteroposteriorly than wide transversely in *Paranthodon*, similar to other stegosaurs such as *Stegosaurus stenops* (NHMUK R36730) and *Chungkingosaurus* (Maidment and Wei, 2006), and ornithopods such as *Camptosaurus* (NHMUK R1608) and *Hypsilophodon* (Butler, Porro and

Norman, 2008). The condition is the same in the ankylosaurs *Silvisaurus* (NHMUK R1107), *Europelta* (Kirkland et al., 2013) and *Kunbarrasaurus* (Leahey et al., 2015), in contrast, in the ankylosaurs *Euoplocephalus* (NHMUK R4947) and *Edmontonia* (NHMUK R36851) the naris is wider transversely than it is long anteroposteriorly. The internal surface of the naris is smooth, as in *Europelta* (Kirkland et al., 2013); this suggests the narial passage was simple, rather than convoluted as in ankylosaurids and derived nodosaurids.

Maxilla

The maxilla is triangular in lateral view, with the tooth row forming an elongate base of the triangle (Fig. 1). This is similar to the condition in most other thyreophorans (e.g. *Stegosaurus* (NHMUK R36730), *Hesperosaurus* (Carpenter, Miles and Cloward, 2001), *Silvisaurus* (NHMUK R1107) and *Edmontonia* (NHMUK R36851)). However, the maxilla of the basal ankylosaur *Kunbarrasaurus* is rectangular with the long axis orientated dorsoventrally (Leahey et al., 2015), and the element is rectangular in the ornithopods *Camptosaurus* (NHMUK R1608) and *Jinzhousaurus* (Wang and Xu, 2001), with the long axis anteroposterior. In lateral view, the maxillary tooth row is horizontal, as in the ornithopod *Camptosaurus* (NHMUK R1608), and the stegosaurs *Stegosaurus* (NHMUK R36730) and *Huayangosaurus* (Sereno and Dong, 1992). This contrasts with many ankylosaurs, such as *Silvisaurus* (NHMUK R1107), *Europelta* (Kirkland et al., 2013) and *Kunbarrasaurus* (Leahey et al., 2015), as well as the stegosaur *Hesperosaurus* (Carpenter, Miles and Cloward, 2001), where the tooth row arches ventrally. In ventral view, the tooth row is not inset from the lateral edge of the maxilla and is in line with the lateral edge of the premaxilla. This is similar to the condition in the stegosaur *Tuojiangosaurus* (Maidment and Wei, 2006) and the basal ornithischian *Lesothosaurus* (Sereno, 1991), but contrasts with all other members of Thyreophora, as well as ornithopods including *Hypsilophodon* (NHMUK R197), where there is a laterally-extending ridge dorsal to the tooth row. The tooth row is sinuous in ventral view, as in the basal thyreophoran *Scelidosaurus* (NHMUK R1111), the stegosaur *Jiangjunosaurus* (Jia et al., 2007) and the ankylosaurs *Euoplocephalus* NHMUK R4947), *Edmontonia* (NHMUK R36851) and *Silvisaurus* (NHMUK R1107). In *Stegosaurus* (NHMUK R36730) and *Huayangosaurus* (Sereno and Dong, 1992) the tooth row is straight in ventral view, and this condition is the same in the ankylosaurs *Gastonia* (Kinneer, Carpenter and Shaw, 2016), *Edmontonia* (NHMUK R36851), *Pawpawsaurus* (Kinneer, Carpenter and Shaw, 2016) and *Panoplosaurus* (Kirkland et al., 2013). There is a horizontal diastema between the maxillary teeth and the maxilla-premaxilla suture, similar to that of *Stegosaurus* (NHMUK R36730) and the ankylosaur *Silvisaurus* (NHMUK R1107). This is in the same location as the oval depression seen in the stegosaur *Huayangosaurus* (Sereno and Dong, 1992). The contact angle between the maxilla and premaxilla in dorsal view is 30 degrees, similar to that of the stegosaurs *Tuojiangosaurus* (Maidment and Wei, 2006) and *Huayangosaurus* (Sereno and Dong, 1992). The ankylosaurs *Ankylosaurus* (Kinneer, Carpenter and Shaw, 2016) and *Pinacosaurus* (Maryańska, 1977) have a contact with no deflection along the midline. The contact is perpendicular in ornithopods such as *Hypsilophodon* (NHMUK R197) and *Camptosaurus* (NHMUK R1608). *Contra* Galton and Coombs (1981), who said the posterior process of the premaxilla underlaps the maxilla, the posterior process of the premaxilla overlaps the maxilla, as in the stegosaur *Huayangosaurus* (Sereno and Dong, 1992). The posterior portion of the maxilla is incomplete, and so there is no evidence of contact with the lacrimal or the jugal.

In medial view, the maxilla bears a ridge extending from the premaxillary palate to form a secondary maxillary palate. This feature is unknown in other stegosaurs, and was considered the only identifiable autapomorphy of the genus by Maidment et al. (2008). However, it is common in ankylosaurs, including in *Edmontonia* (NHMUK R36851), *Euoplocephalus* (NHMUK R4947) and *Gastonia* (Kinneer, Carpenter and Shaw, 2016), although it is more pronounced than in *Paranthodon*. The basal thyreophorans *Scelidosaurus* (NHMUK R1111) and *Emausaurus* (Maidment, 2010) do not possess this feature.

Nasal

Only the anterior part of the left nasal is preserved (Fig. 2). It is an anteroposteriorly elongate element, as in the stegosaurs *Stegosaurus* (NHMUK R36730), *Hesperosaurus* (Carpenter, Miles and Cloward 2001) and *Huayangosaurus* (Sereno and Dong, 1992), and the basal thyreophoran *Scelidosaurus* (NHMUK R1111). In the ankylosaur *Europelta* the nasal is more equidimensional (Kirkland et al., 2013), in the stegosaur *Tuojiangosaurus* it is triangular in dorsal view (Maidment and Wei, 2006) and in the ornithopod *Jinzhousaurus* it tapers anteriorly (Wang and Xu, 2001). In *Paranthodon* the nasal is dorsally convex, to a greater degree than in the basal thyreophoran *Scelidosaurus* (NHMUK R1111) but not as much as in the stegosaurs *Stegosaurus* (NHMUK R36730) and *Hesperosaurus* (Carpenter, Miles and Cloward 2001). In the stegosaur *Miragaia*, this curvature is also seen, but the degree of curvature could have been affected by post-mortem deformation (Mateus, Maidment and Christiansen, 2009). In the stegosaur *Tuojiangosaurus*, the nasal is gently concave transversely (Maidment and Wei, 2006), as it is in the basal ornithischian *Heterodontosaurus* (Butler, Porro and Norman, 2008). The nasal of *Paranthodon* has variable dorsoventral thickness, from 2 mm to 7 mm. There are two subtle anteroposteriorly extending ridges on the dorsal surface, and it is possible these indicate the suture with the frontals, as in the stegosaur *Hesperosaurus* (Carpenter, Miles and Cloward 2001). As in the basal ornithischian *Heterodontosaurus*, the lateral margins are thickened into nasal ridges (Butler, Porro and Norman, 2008). There is a straight suture along the midline of the nasal that would have contacted its counterpart. This is a similar depth to that of *Stegosaurus* (NHMUK R36730) and *Hesperosaurus* (Carpenter, Miles and Cloward 2001). In the basal thyreophoran *Scelidosaurus* (NHMUKR1111) the sutures are not obvious and in the stegosaur *Tuojiangosaurus* the nasals are fused together (Maidment and Wei, 2006), although the fusion of skull sutures is likely ontogenetic in nature (Currie, Langston and Tanke, 2008). The nasal is not seen in contact with the premaxilla or maxilla, *contra* Galton and Coombs (1981; figure 1a), and is preserved separately.

Maxillary Teeth

There are 13 maxillary teeth preserved, although they extend to the incomplete posterior end of the maxilla and it is possible in life the animal had more. The number of maxillary teeth among ornithischians is widely variable, ranging from 10 in the ornithopod *Camptosaurus* (NHMUK R1608) to as many as 35 in *Ankylosaurus* (Kinneer, Carpenter and Shaw, 2016); tooth count also varies intraspecifically and was likely ontogenetically controlled (Butler, Porro and Norman, 2008). There are three teeth on the medial surface of the maxilla that are erupting, and the second tooth from the maxillary diastema is not fully erupted. The teeth of *Paranthodon* are symmetrical with a centrally located apex, as in the stegosaurs *Stegosaurus* (NHMUK R36730), *Miragaia* (Mateus, Maidment and Christiansen, 2009), *Hesperosaurus* (Carpenter, Miles and Cloward 2001), *Tuojiangosaurus* (Maidment and Wei, 2006), and *Jiangjunosaurus* (Jia et al., 2007) and the ankylosaur *Gastonia* (Kinneer, Carpenter and Shaw, 2016). The stegosaur *Chungkingosaurus* has a sharp, asymmetric tooth crown (Maidment and Wei, 2006) whereas the basal thyreophoran *Scelidosaurus* (NHMUK R1111) has distally offset crowns. The maxillary teeth of heterodontosaurids are chisel-shaped, with denticles restricted to the apical third of the crown (Norman et al., 2004), and in hadrosaurids they are arranged into a compact dental battery with elongate tooth crowns (Horner, Weishampel and Forster, 2004). A prominent ring-like cingulum is present on lingual and buccal sides of the teeth. This is the same in all other stegosaurs in which the teeth are known (e.g. *Stegosaurus* (NHMUK R36730), *Tuojiangosaurus* (Maidment and Wei, 2006), *Hesperosaurus* (Carpenter, Miles and Cloward 2001), *Jiangjunosaurus* (Jia et al., 2007), *Miragaia* (Mateus, Maidment and Christiansen, 2009)) except *Huayangosaurus*, where a reduced swelling is present but not as a ring (Sereno and Dong, 1992), and *Kentrosaurus* where the cingulum is restricted to one side (Galton, 1988). Within Ankylosauria, most ankylosaurs, including *Edmontonia* (NHMUK R36851), *Silvisaurus* (NHMUK R1107) and *Kunbarrasaurus* (Leahey et al., 2015) have a prominent cingulum, but it is not seen in *Gastonia* (Kinneer, Carpenter and Shaw, 2016). The cingulum of the basal thyreophoran *Scelidosaurus* (NHMUK R1111) is weak. The cingulum of *Paranthodon* varies in dorsoventral thickness along the width of each tooth in the tooth row. The best-preserved tooth is the sixth from the maxillary diastema, and is in the process of erupting. There are six denticles on the mesial side of the lingual surface, and this is seen on both the distal and mesial sides of all maxillary teeth, *contra* Galton and Coombs (1981). The denticles curve away from the central apex and thicken towards the tooth margins. The tooth crowns of *Paranthodon* bear striations, extending to the cingulum, and these are confluent with the marginal denticles. The only other occurrence of this within Stegosauria is in *Tuojiangosaurus* (Maidment and Wei, 2006); in contrast, it is very common in ankylosaur teeth (e.g. *Edmontonia* (NHMUK R36851), *Silvisaurus* (NHMUK R1107), *Gastonia* (Kinneer, Carpenter and Shaw, 2016), *Euoplocephalus* (NHMUK R4947)). *Stegosaurus* (NHMUK R36730) and *Kentrosaurus* (Galton, 1988) have striations that extend to the cingulum, but these are not confluent with marginal denticles. The tooth root is parallel-sided, as in the stegosaur *Hesperosaurus* (Carpenter, Miles and Cloward 2001), whereas the root of *Kentrosaurus* tapers to a point (Galton, 1988).

Vertebra

The vertebra is extremely fragmentary; only the left transverse process and prezygapophysis are identifiable (Fig. 3). The anterior edge of the prezygapophysis is broken off and so the intraprezygapophyseal shelf is not preserved. The right transverse process is not present, nor are the posterior end of the vertebra or the centrum. The top of the left transverse process is not preserved, and part of the midline ridge has split so that it tapers to a 3mm thick slice anteriorly. The vertebra is tentatively identified as mid-dorsal based on the angle of the transverse process and the orientation of the prezygapophysis. The transverse process is elevated dorsolaterally at an angle of 60 degrees, similar to the mid-dorsal vertebrae of the stegosaurs *Stegosaurus* (NHMUK R36730) and *Chungkingosaurus* (Maidment and Wei, 2006). The dorsal vertebrae of the stegosaur *Gigantspinosaurus* (Maidment and Wei, 2006) have transverse processes that project laterally, whereas they project dorsolaterally in the ankylosaurs *Ankylosaurus* (Kinneer, Carpenter and Shaw, 2016), *Euoplocephalus* (Arbour and Currie, 2013) and *Zhanghenglong* (Xing et al., 2014). The transverse processes of the posterior and mid-dorsal vertebrae of *Lesothosaurus* are laterally orientated (Baron, Norman and Barrett 2017), whereas on anterior dorsal vertebrae they project dorsolaterally; this shift to higher angles anteriorly is also seen in *Hypsilophodon* (NHMUK R197) and *Heterodontosaurus* (Santa Luca, 1980). In *Stegosaurus* (NHMUK R36730) the transverse processes are sub-horizontal in the anterior and posterior dorsal vertebrae but steeply angled in the mid-dorsal vertebrae. The parapophysis is located anteroventral to the base of the transverse process, as in the basal ornithischian *Lesothosaurus* (Baron, Norman and Barrett 2017), and the stegosaur *Kentrosaurus* (NHMUK R16874), and is adjacent to the prezygapophysis, as in *Stegosaurus* sp. (NHMUK R3216). The parapophysis is more concave than *Kentrosaurus* (NHMUK R16874) or *Stegosaurus* (NHMUK R36730; NHMUK R3216). The prezygapophysis faces dorsally in *Paranthodon*, as in the basal ornithischian *Lesothosaurus* (Baron, Norman and Barrett, 2017) and the stegosaur *Stegosaurus* (NHMUK R3216). In contrast, the prezygapophyses of other stegosaurs face dorsomedially (Maidment, Brassey and Barrett, 2015), similar to the condition observed in the basal ornithischian *Heterodontosaurus* (Santa Luca, 1980), the ornithopod *Tenontosaurus* (Sues and Norman, 1990), and the ankylosaurs *Ankylosaurus* (Kinneer, Carpenter and Shaw, 2016), *Euoplocephalus* (Arbour and Currie, 2013) and *Zhanghenglong* (Xing et al., 2014).

Referred Teeth

There are two isolated teeth (Fig. 4) that are the referred specimen NHMUK R4992 (Galton and Coombs, 1981). These differ from the maxillary teeth of the holotype in that they have four denticles on either side of the slightly asymmetrical apex. The cingula are 20% of the height of the crowns, which is less than the teeth of the holotype (58-80%), although the width of the teeth is 44% of the width of the cingula, which is similar to the maxillary teeth. Similarly to the maxillary teeth, the denticles are confluent with striations that extend to the cingula. CT-scanning shows no evidence of wear facets.

Galton and Coombs (1981) hypothesised that the two teeth were from the dentary, and, more specifically, one from the left dentary. They are possibly from the dentary, due to a slight difference in morphology to the maxillary teeth; however, as the only autapomorphy of *Paranthodon* is on the maxilla, they cannot be referred to this genus and thus are regarded as belonging to an indeterminate thyreophoran.

PHYLOGENETIC METHODOLOGY

Multiple phylogenetic analyses were performed to examine the phylogenetic affinities of *Paranthodon*.

The ankylosaurid phylogeny of Arbour and Currie (2016), the ankylosaurian phylogeny of Thompson et al. (2012) and the basal ornithischian phylogenies of Boyd (2015) and Baron, Norman and Barrett (2017) were updated to include *Paranthodon* as an Operational Taxonomic Unit (OTU) (Fig. 5). The most recent phylogeny of Stegosauria by Raven and Maidment (2017) was updated with new characters and character-scores based on a more thorough description of *Paranthodon*. All analyses were carried out in TNT (Goloboff, Farris and Nixon, 2008). The analyses were first performed on the original data matrices, using the original search settings and without including *Paranthodon* as an OTU, to make sure the original tree topologies could be replicated. The updated analyses were then performed using a ’New Technology’ search, with Sect Search, Ratchet, Drift and Tree Fusing algorithms, and 10 random addition sequences. ’Traditional’ TBR Branch-Swapping was then performed on trees held in RAM, as this provides a more complete exploration of tree space (Barrett et al., 2014). Taxonomic exemplifiers were varied to investigate the effect on tree topology; this was done by physically eliminating taxa from the character-taxon matrix, rather than making them inactive in TNT, as deactivating taxa does not reduce the size of the grid used for the initial phase of optimisation (Goloboff & Catalano, 2016). Constraint trees were then written using the 'Force' command in TNT to explore how labile the position of *Paranthodon* was in each phylogenetic analysis. The significance of the constraint trees was tested using 1000 replications of the Templeton Test (Salgado et al., 2017). Support for groupings was tested using symmetric resampling, which was carried out with a probability of 33% and 1000 replicates on a 'New Technology' search of existing trees.

Arbour and Currie, 2016

In all analyses of Arbour and Currie (2016) *Lesothosaurus diagnosticus* was used as the outgroup. All characters were unordered and of equal weight. The original analysis performed safe taxonomic reduction using TAXEQ3 (Wilkinson, 2001) to remove the taxa *Bissektipelta archibaldi*, *Minmi paravertebra* and *Tianchisaurus nedegoapeferima*, and so these taxa were also removed from all analyses here. The original analysis was repeated here, using the basal stegosaur *Huayangosaurus* as the exemplifier for Stegosauria, to ensure the original topology could be replicated (Analysis A). The original analysis of Arbour and Currie (2016) used a 'Traditional' search, however, more common recent approaches used 'New Technology' searches in TNT (see Ezcurra (2016); Baron, Norman and Barrett (2017); Raven and Maidment (2017)). To test the effect of this, the original dataset was re-run with a 'New Technology' search with settings as previously mentioned (Analysis B).

In Analysis C, *Paranthodon* was added as an OTU, and *Huayangosaurus* was kept as the stegosaurian exemplifier, as in the original analysis. In Analysis D, *Paranthodon* was again included as an OTU, but *Huayangosaurus* was replaced as the stegosaurian exemplifier by the more derived *Stegosaurus*. Analysis E included *Paranthodon, Huayangosaurus* and *Stegosaurus* as Operational Taxonomic Units.

In analysis F, *Paranthodo*n was constrained to fall within Ankylosauria due to the anatomical similarities between *Paranthodon* and ankylosaurs. A full list of analyses and taxa used can be seen in Table 2, and all trees produced can be found in the Online Supplementary Material.

Baron, Norman and Barrett 2017

The updated analyses of Baron, Norman and Barrett (2017) were performed with *Euparkeria capensis* as the outgroup, as in the original analysis. The characters 112, 135, 137, 138 and 174 were ordered and, as in the original analysis, the five unstable taxa *Anabisetia saldiviai, Echinodon becklesii, Koreanosaurus boseongensis, Yandosaurus hongheensis* and *Yueosaurus tiantaiensis* were excluded from the analyses. Analysis G was produced with the same settings as the original Baron, Norman and Barrett (2017) analysis to make sure the original topology could be replicated. The original analysis used *Huayangosaurus* as the taxonomic exemplifier for Stegosauria.

Analysis H included *Paranthodon* as an OTU into the original analysis. In Analysis I, *Paranthodon* was again included but *Stegosaurus* replaced *Huayangosaurus* as the stegosaurian exemplifier. Analysis J included *Paranthodon*, *Huayangosaurus* and *Stegosaurus* as OTUs, with the latter two acting as exemplifiers for Stegosauria.

In Analysis K, the recently described taxon *Isaberrysaura* (Salgado et al. 2017) was included along with *Paranthodon, Huayangosaurus* and *Stegosaurus*. This taxon was included here because although it was recovered as a basal neornithischian by Salgado et al. (2017), it possesses numerous anatomical features normally associated with thyreophorans, and was found to be a stegosaur in Han et al. (2017).

A constraint tree was then written (Analysis L), using Analysis J as a starting point, to test the hypothesis that *Paranthodon* could be an ornithopod, owing to the similarities of the posterior process of the premaxilla.

Boyd, 2015

Marasuchus lilloensis was used as the outgroup taxon for all analyses of Boyd (2015), and all characters were unordered, as in the original analysis. The original analysis did not include a taxonomic exemplifier for Stegosauria, instead including several basal thyreophorans. Analysis M was performed, with no additional taxa included, to make sure the original analysis could be replicated.

In Analysis N *Paranthodon* was added as an OTU to the original analysis. The basal stegosaur *Huayangosaurus* was then added to the dataset, as well as *Paranthodon*, so that it included a stegosaurian exemplifier (Analysis O). *Huayangosaurus* was then replaced as the exemplifier for Stegosauria by the derived stegosaur *Stegosaurus*, with *Paranthodon* also included as an OTU, in Analysis P.

In Analysis Q, both *Huayangosaurus* and *Stegosaurus* were included as exemplifiers for Stegosauria, with *Paranthodon* also as an OTU.

To again test the systematic positioning of *Isaberrysaura*, it was added as an OTU to the Boyd (2015) dataset (Analysis R), along with *Paranthodon, Huayangosaurus* and *Stegosaurus*. Constraint trees were again written to test the lability of *Paranthodon*, using Analysis Q as a starting point. Analysis S constrained *Paranthodon* to be within Ornithopoda, and Analysis T constrained *Paranthodon* to be within Thyreophora.

Raven and Maidment, 2017

In Analysis U, the character list of Raven and Maidment (2017) was updated following a more thorough description of *Paranthodon* and character scorings were updated to include the dorsal vertebra. *Pisanosaurus* was used as the outgroup taxon and, as in the original analysis, the 24 continuous characters were ordered, as were the discrete characters 34, 111 and 112. All discrete characters were weighted equally and the continuous characters were automatically rescaled in TNT. In Analysis V, *Isaberrysaura mollensis* was also added as an OTU. The full character list with new characters can be found in the Online Supplementary Material.

A constraint tree was then produced with *Paranthodon* being enforced to fall within Ankylosauria (Analysis W).

Thompson et al., 2012

As in the original analysis of Thompson et al. (2012), *Lesothosaurus* was used as the outgroup, *Bissektipelta* was excluded as an OTU, the characters 25, 27, 32, 133, 159 and 167 were removed from the analysis and all remaining characters were unordered and equally weighted. Analysis X was performed to ensure the original results could be replicated. *Paranthodon* was included as an OTU in Analysis Y, with the stegosaurian exemplifiers of *Huayangosaurus* and *Stegosaurus* already included in the dataset. A constraint tree with *Paranthodon* being enforced into Stegosauria was then produced (Analysis Z).

RESULTS

Arbour and Currie, 2016

The original findings of Arbour and Currie (2016; figure 11) were replicated in Analysis A, using the same settings as the original analysis; a full list of the results of all analyses can be found in Table 3. Running the analysis of Arbour and Currie (2016) with a 'New Technology' search reduced the number of most parsimonious trees (MPTs) from 3030 in the original analysis to 11 (Analysis B), with a length of 421. The use of a second, 'Traditional', search with TBR branch-swapping on RAM trees was not possible due to computational limits, although this would not change the topology of the strict consensus (Goloboff, Farris and Nixon, 2008). In the strict consensus tree, Nodosauridae had a similar lack of resolution to the original analysis. *Gastonia* and *Ahshislepelta* show the same sister taxon relationship basal to Ankylosauridae. Shamosaurinae was found outside of Ankylosaurinae. The rest of Ankylosaurinae had a higher resolution than the strict consensus tree of Arbour and Currie (2016), with *Dyoplosaurus* found outside of Ankylosaurini. The resolution was as high as that of the 50% majority rule tree of Arbour and Currie (2016).

When *Paranthodon* was added as an OTU and *Huayangosaurus* was used as the only stegosaurian exemplifier, as in the original analysis, (Analysis C), eight MPTs were recovered with a length of 424. *Paranthodon* was recovered as an ankylosaur, in a polytomy basal to Ankylosaurinae with *Gobisaurus* and *Shamosaurus*.

When the more derived stegosaur *Stegosaurus* was used as the stegosaurian exemplifier, and *Huayangosaurus* excluded as an OTU (Analysis D), eight MPTs were recovered with a length of 425. The strict consensus tree had a similar topology to Analysis B, however *Paranthodon* was found in a polytomy with *Stegosaurus* and *Kunbarrasaurus* near the base of Thyreophora.

In Analysis E, both *Huayangosaurus* and *Stegosaurus* were used as exemplifiers for Stegosauria, and *Paranthodon* was included as an OTU. This produced nine most parsimonious trees of length 427 and again had high resolution throughout the strict consensus tree. Stegosauria formed a monophyletic group, with *Huayangosaurus* basal to a sister-taxon relationship between *Parathodon* and *Stegosaurus*. *Kunbarrasaurus* was found at the base of Ankylosauria again.

Analysis F constrained *Paranthodon* to be an ankylosaur. This produced nine most parsimonious trees, of length 428, with slightly reduced resolution in Ankylosauridae, in comparison to the unconstrained tree of Analysis E. *Paranthodon* was found at the base of Ankylosauridae in a polytomy with *Shamosaurus scutatus* and *Gobisaurus domoculus*. The constraint tree was analysed using the Templeton Test, which indicated the length differences between the unconstrained tree and the constrained tree was non-significant.

Baron, Norman and Barrett 2017

The original settings of the basal ornithischian analysis of Baron, Norman and Barrett (2017) were replicated and the same topology was found (Analysis G).

The dataset was then updated to include *Paranthodon* as an OTU, and *Huayangosaurus* was used as the exemplifier for Stegosauria, as in the original analysis (Analysis H). The 'New Technology' search followed by TBR branch-swapping resulted in 144 most parsimonious trees of length 583; however, the strict consensus tree provided little resolution. A 50% majority rule tree suggested *Paranthodon* might be closer related to Ankylosauria than to *Huayangosaurus*.

The original exemplifier for Stegosauria, *Huayangosaurus,* was then replaced by *Stegosaurus*, and *Paranthodon* was included as an OTU (Analysis I). This produced 96 most parsimonious trees of length 583 and the strict consensus provided much higher resolution throughout the tree than in Analysis H. *Paranthodon* was found as sister-taxon to *Stegosaurus*, with Ankylosauria a separate lineage within Thyreophora.

In Analysis J, both *Huayangosaurus* and *Stegosaurus* were included as exemplifiers for Stegosauria, and *Paranthodon* was included as an OTU. This produced 84 most parsimonious trees of length 587 and very high resolution in the strict consensus. Stegosauria was found to be monophyletic, with *Paranthodon* more closely related to *Stegosaurus* than to *Huayangosaurus.*

Analysis K included the newly described *Isaberrysaura* as an OTU, in addition to *Paranthodon, Huayangosaurus* and *Stegosaurus*. This produced 340 most parsimonious trees of length 605, and little resolution in the strict consensus tree in Ornithopoda, but Thyreophora had the same topology as Analysis J. *Isaberrysaura* was found in a large polytomy within Ornithopoda.

Analysis L constrained *Paranthodon* to Ornithopoda. This resulted in 10 most parsimonious trees of length 595. Relative to the unconstrained Analysis J, this increased the resolution in Heterodontosauridae slightly but caused a severe reduction in resolution in Ornithopoda; *Paranthodon* was found in a polytomy at the base of the group with 11 other taxa. Again, the use of the Templeton Test showed that the differences between the unconstrained tree and the constrained tree were non-significant.

Boyd, 2015

The original results of the basal ornithischian phylogeny of Boyd (2015) were replicated here, using the same search settings (Analysis M).

The dataset was then updated to include *Paranthodon* as an OTU (Analysis N), with *Scelidosaurus* the most derived thyreophoran included from the original dataset. The use of a second, ‘Traditional’, search with TBR branch-swapping on RAM trees was not possible due to computational limits, although this would not change the topology of the strict consensus (Goloboff, Farris and Nixon, 2008). The ‘New Technology’ search produced two most parsimonious trees of length 884. In the strict consensus tree, *Paranthodon* was found to be in a sister-taxon relationship with *Pisanosaurus*. Interestingly, Thyreophora was basal to Heterodontosauridae, and Marginocephalia was basal to Cerapoda.

In Analysis O, *Huayangosaurus* was included to act as a stegosaur exemplifier, and *Paranthodon* was also added as an OTU. This produced five most parsimonious trees, of length 921, and there was reduced resolution in the strict consensus. *Paranthodon* and *Huayangosaurus* were found as sister-taxa at the base of Iguanodontia, distant from the other taxa that traditionally comprise Thyreophora.

Huayangosaurus was then replaced as the stegosaurian exemplifier by *Stegosaurus*, with *Paranthodon* again included as an OTU (Analysis P). This produced three most parsimonious trees, of length 928. The strict consensus tree had increased resolution relative to Analysis O, and *Paranthodon* and *Stegosaurus* were found as sister-taxa within Ornithopoda, again distant from Thyreophora.

In Analysis Q, both *Huayangosaurus* and *Stegosaurus* were used as the exemplifiers for Stegosauria, and *Paranthodon* was included as an OTU. This produced seven most parsimonious trees of length 955, but with a reduced resolution in most of the tree. *Paranthodon, Huayangosaurus* and *Stegosaurus* were found as sister-taxa, again separate from Thyreophora.

Isaberrysaura was then included, as well as *Huayangosaurus, Stegosaurus* and *Paranthodon*, into Analysis R. Five most parsimonious trees, of length 968, were produced. There was again little resolution in the strict consensus, particularly in Neornithischia, with *Isaberrysaura, Huayangosaurus, Stegosaurus* and *Paranthodon* forming part of a large polytomy at the base.

Analysis S constrained *Paranthodon* within Ornithopoda. This produced six most parsimonious trees of length 964, and increased resolution in Ornithopoda relative to the unconstrained Analysis Q. However, *Stegosaurus* and *Huayangosaurus* moved out of Ornithischia, as they were not constrained to be within Ornithopoda. *Paranthodon* was found in a large polytomy at the base of Ornithopoda with nine other taxa.

Analysis T constrained *Paranthodon, Huayangosaurus* and *Stegosaurus* to Thyreophora. This produced four most parsimonious trees of length 965. The strict consensus had higher resolution in Ornithopoda, but the resolution in Thyreophora was reduced. *Paranthodon, Huayangosaurus* and *Stegosaurus* formed a polytomy within Thyreophora. *Stormbergia dangershoeki*, a taxon that Baron, Norman and Barrett (2017) have recently synonymised with *Lesothosaurus*, moved to within Thyreophora in this analysis. The Templeton Test again showed that the differences between the unconstrained trees and the constrained trees were all non-significant.

Raven and Maidment, 2017

The most recent phylogeny of Stegosauria by Raven and Maidment (2017) showed *Paranthodon* and *Tuojiangosaurus* to clade together, a result that was found again here in the one most parsimonious tree of length 279.65 (Analysis U). *Isaberrysaura*, the Argentinian dinosaur found as a neornithischian by Salgado et al. (2017), was then found in a sister-taxon relationship with *Gigantspinosaurus* (Analysis V). However, the strict consensus of the four most parsimonious trees of length 285.38 had a lack of resolution at the base of Eurypoda. Analysis W was produced to constrain *Paranthodon* to within Ankylosauria, using Analysis U as a starting point. This produced one most parsimonious tree of length 280.43, 0.78 steps longer than Analysis U. The Templeton Test showed that there were no significance between the constrained and the unconstrained trees in all analyses.

Thompson et al., 2012

Using the original settings of Thompson et al. (2012), the original results were replicated (Analysis X).

The dataset was then updated to include *Paranthodon* as an OTU (Analysis Y), using both *Huayangosaurus* and *Stegosaurus* as the exemplifiers for Stegosauria, as in the original analysis. This analysis, using a 'New Technology' search, produced five MPTs with a length of 529, although the use of a second, 'Traditional', search with TBR branch-swapping on RAM trees was not possible due to computational limits, although this would not change the topology of the strict consensus (Goloboff, Farris and Nixon, 2008). The results vastly improved on the 4248 MPTs with a length of 527 produced in the 'Traditional' searches of the original analysis, and there was an improvement in the resolution of the strict consensus tree, especially within Ankylosauridae, where it approaches the resolution of the 50% majority rule tree of Thompson et al. (2012). *Pinacosaurus* was found to be paraphyletic; *Pinacosaurus mephistocephalus* and *Dyopolosaurus acutosquameus* are sister-taxa, as are *Pinacosaurus grangeri* and *Minotaurasaurus ramachandrani*. *Ankylosaurus magniventris* and *Euoplocephalus tutus* are also found as sister-taxa. *Stegosaurus* and *Huayangosaurus* clade together to form Stegosauria, which was sister taxon to Ankylosauria. *Paranthodon* was found in a large polytomy at the base of Ankylosauria.

Analysis Z constrained *Paranthodon* to Stegosauria. This produced three most parsimonious trees of length 531, two steps longer than the unconstrained Analysis X. The resolution of Ankylosauridae did not change but the resolution of Nodosauridae increased. *Paranthodon* had a closer relationship to *Stegosaurus* than to *Huayangosaurus*. Again, there were no significant differences between the constrained and the unconstrained trees according to the Templeton Test.

DISCUSSION

The use of basal exemplifiers in cladistic analysis

When *Paranthodon* was added as an OTU to the dataset of Arbour and Currie (2016) and *Huayangosaurus* used as the stegosaurian exemplifier (Analysis C), *Paranthodon* was found as an ankylosaur. However, when the exemplifier was changed to *Stegosaurus* (Analysis D), *Paranthodon* was found as a stegosaur. When both *Huayangosaurus* and *Stegosaurus* were included in the analysis, Stegosauria became monophyletic with *Huayangosaurus* basal to *Paranthodon* + *Stegosaurus* (Analysis E).

The inclusion of *Paranthodon* into the Baron, Norman and Barrett (2017) dataset reduced the resolution of the tree, but a 50% majority rule tree found *Paranthodon* as an ankylosaur (Analysis H). When *Stegosaurus* replaced *Huayangosaurus* as the stegosaurian exemplifier (Analysis I), the resolution in the tree increased and *Paranthodon* was sister-taxon to *Stegosaurus*. When both *Huayangosaurus* and *Stegosaurus* were included in the analysis (Analysis J), there was again increased resolution and a monophyletic Stegosauria, including *Paranthodon*.

The inclusion of *Paranthodon* to the Boyd (2015) dataset (Analysis N) found *Paranthodon* as a basal ornithischian, sister-taxon to *Pisanosaurus*, with large topological changes in the rest of the tree. When *Huayangosaurus* was included as an OTU, *Paranthodon* and *Huayangosaurus* were sister-taxa within Ornithopoda. Replacing *Huayangosaurus* as the stegosaurian exemplifier with *Stegosaurus* (Analysis P) improved the resolution of the tree but again both *Stegosaurus* and *Paranthodon* were found within Ornithopoda.

These results demonstrate that the systematic position of *Paranthodon* is highly dependent on the clade exemplifier used. When a basal exemplifier is used, *Paranthodon* is generally found to be an ankylosaur, but resolution is lost. When a more derived exemplifier (*Stegosaurus*) is used, *Paranthodon* is found as a stegosaur. When both a basal and a derived exemplifier is used, *Paranthodon* is found as a stegosaur, Stegosauria is found to be monophyletic, and resolution of the entire tree is generally increased. This indicates that the choice of exemplifier as a basal taxon within a clade may be inappropriate if the aim of the analysis is to test the phylogenetic position of a taxon that potentially shows more derived characteristics of a clade. This contrasts with most literature on the subject (e.g. Yeates 1995; Griswold et al. 1998; Prendini 2001; Brusatte 2010), which argues that an exemplifier species should be a basal taxon within its respective clade.

A more robust approach would be to use multiple exemplifiers, and this method has been argued previously (Prendini 2001; Brusatte 2010), but is not common practice. The use of supraspecific taxa to represent groups of species, in any method, can result in changes to topology of a phylogeny when compared to a complete species level analysis (Bininda-Emonds, Bryant and Russell, 1998), even the use of multiple exemplifiers. While the use of exemplifiers can produce accurate tree topologies (for example, Butler, Upchurch and Norman, 2008), caution should be applied when interpreting the phylogenies (Spinks et al., 2013), especially when including the use of fragmentary material. The ability of 'New Technology' searches in TNT to analyse large datasets in less time than 'Traditional' searches (Goloboff, Farris and Nixon, 2008) means more taxa can be included in the analysis, which would increase the accuracy dramatically (Prendini, 2001). This means it is not always impractical to include each species as a separate terminal. Phylogenetic super-matrices (Gatesy et al., 2002) therefore could and should be implemented to analyse evolutionary relationships, meaning the use of exemplifiers would be redundant.

That basal exemplifiers may be inappropriate is further supported by our analyses of the Boyd (2015) dataset. The recently described taxon *Isaberrysaura* (Salgado et al. 2017) was included as an OTU in Analysis R, as well as *Huayangosaurus, Stegosaurus* and *Paranthodon* (Fig. 6). This taxon was included here because although it was recovered as a basal neornithischian by Salgado et al. (2017), it possesses numerous anatomical features normally associated with thyreophorans, and was found to be a stegosaur in Han et al. (2017). Analysis R resulted in *Isaberrysaura* being found as a basal neornithischian, along with *Paranthodon* and the unambiguous stegosaurs *Huayangosaurus* and *Stegosaurus*. This surprising result is an artefact of the character distribution of the Boyd (2015) dataset; there are only seven characters that unite either Eurypoda, Eurypoda + *Alcovasaurus*, or Stegosauria in the Raven and Maidment (2017) dataset that are found in the Boyd (2015) dataset, equating to 2.7% of the total number of characters (Online Supplementary Material). Additionally, there are only two synapomorphies that unite the taxa used to represent Thyreophora (i.e. *Lesothosaurus, Scutellosaurus, Emausaurus* and *Scelidosaurus*) in the Boyd (2015) dataset; character 86: a strong, anteroposteriorly extending ridge present on the lateral surface of the surangular, and character 122: a concave lingual surface of maxillary teeth. These features, although synapomorphies for basal thyreophorans, are lost in stegosaurs and ankylosaurs, and this suggests the Boyd (2015) dataset cannot adequately test the relationships of eurypodans. The placement of *Isaberrysaura* as a basal neornithischian in Salgado et al. (2017) is almost certainly due to the fact that the dataset of Boyd (2015) does not contain the character data required to rigorously test the phylogenetic position of taxa which may be derived members of clades. It is therefore likely that, as found by Han et al. (2017), *Isaberrysaura* is a member of the Thyreophora.

The anatomy of *Paranthodon* is enigmatic, with features similar to many other members of Ornithischia. The tooth morphology and the presence of a secondary maxillary palate is reminiscent of ankylosaurs, and the cingulum is widely distributed among ornithischians, as is the sinuous curve of the anterior process of the premaxilla (Butler, Upchurch and Norman, 2008). The robust posterior process of the premaxilla is similar to that of ornithopods. The triangular maxilla in lateral view is a feature seen widely across Thyreophora, and an edentulous premaxilla is common to most stegosaurs but also many other derived ornithischians. There are no features of the skull that unite *Paranthodon* firmly within Stegosauria and *Paranthodon* contains no synapomorphies that place it unequivocally within Stegosauria. However, the orientation of the transverse processes of the mid-dorsal vertebra at higher than 50 degrees to the horizontal was considered a synapomorphy of the clade by Galton and Upchurch (2004), and this condition is present in *Paranthodon*. The discovery of a well-preserved specimen of *Stegosaurus* (Maidment, Brassey and Barrett, 2015) showed the transverse processes of the dorsal vertebrae vary in projection angle down the vertebral column. This character statement cannot, therefore, be used as a synapomorphy of the group; however, the condition is present in all stegosaurs with dorsal vertebrae known, other than *Gigantspinosaurus*.

On the available evidence, both anatomical and phylogenetic, it appears the most parsimonious solution is to refer *Paranthodon* to Stegosauria. The general anatomy appears most similar to the stegosaurs *Tuojiangosaurus* and *Stegosaurus*, and numerous phylogenetic analyses indicate, when both basal and derived exemplifiers are used, that there is a close relationship between *Paranthodon* and *Stegosaurus*. The increased resolution afforded by the use of *Stegosaurus* suggests some character conflict is being resolved, and the relative instability when *Huayangosaurus* is used could be because of symplesiomorphies between basal ankylosaurs and basal stegosaurs preventing a more derived taxon from 'finding a place' in the tree.

The use of constraint trees also provides evidence for *Paranthodon* as a stegosaur, although the use of the Templeton Test shows alternative hypotheses cannot be ruled out. Constraining *Paranthodon* to within Ankylosauria in Analysis F of Arbour and Currie (2016) reduced the resolution in Ankylosauridae and increased the number of steps in the tree. In Analysis L, where *Paranthodon* was constrained to within Ornithopoda, there was a reduced resolution within Ornithopoda and an increased number of steps in the tree. In Analysis S of the Boyd (2015) dataset, where *Paranthodon* was constrained within Ornithopoda, Stegosauria moved outside of Ornithischia and the number of steps in the tree increased, although there was increased resolution in Ornithopoda (as *Stegosaurus* and *Huayangosaurus* had moved out of the group). Constraining *Paranthodon* within Thyreophora using the Boyd (2015) dataset (Analysis T) increased the resolution in Ornithopoda, but reduced it in Thyreophora, and there were more steps in the tree. However, *Stormbergia dangershoeki,* a taxon that was synonymised with *Lesothosaurus diagnosticus* by Baron, Norman and Barrett (2017), moved into Thyreophora. Constraining *Paranthodon* to be an ankylosaur in the updated dataset of Raven and Maidment (2017) (Analysis W) increased the tree length of the one most parsimonious tree. In Analysis Z, where *Paranthodon* was constrained within Stegosauria using the Thompson et al. (2012) dataset, the resolution of Nodosauridae increased, although the tree length also increased. Although there is a lot of evidence from constraint trees for the positioning of *Paranthodon* within Stegosauria, it is also shown to be labile within Thyreophora. This labile positioning is likely to be due to both deep-rooted homology between Stegosauria and Ankylosauria, given the close evolutionary relationships of the two lineages of Thyreophora, as well as convergent evolution, given the similar ecology of the two groups of animals.

The placing of *Paranthodon* within Stegosauria means that the presence of the medial maxillary process is autapomorphic, and evolved independently in stegosaurs and ankylosaurs. *Paranthodon* is thus a valid genus. However, the systematic positioning of *Paranthodon* is likely to stay labile unless more material is found, and until a thyreophoran or ornithischian super-matrix can be utilised for phylogenetic analyses.

Importance of *Paranthodon*

The confirmation of *Paranthodon* as a stegosaur has important implications for this iconic yet surprisingly poorly understood group of dinosaurs. *Paranthodon* is one of the youngest stegosaurs and stratigraphically close to the assumed extinction event of the group (Pereda Suberbiola et al., 2003). There are few other pieces of evidence for Cretaceous stegosaurs; *Stegosaurus homheni* was found in the Lower Cretaceous of Inner Mongolia (Maidment et al., 2008) and the Burgos specimen of *Dacentrurus armatus* was found in the Lower Cretaceous of Spain (Pereda Suberbiola et al., 2003; Maidment et al., 2008). Additionally, indeterminate stegosaurians have been identified in the Lower Cretaceous of Inner Mongolia (previously known as *Wuerhosaurus ordosensis*; Maidment et al., 2008) and the Early Cretaceous of Portugal (Pereda Suberbiola et al., 2005). Stegosaurian ichnofacies have also reportedly been identified in the Early Cretaceous of China (Xing et al., 2013) (although these appear similar to sauropod footprints according to Salisbury et al. (2016)) and in the Lower Cretaceous Broome Sandstone of Western Australia (Salisbury et al., 2016), as well as in the Upper Cretaceous of Southern India (Galton and Ayyasami, 2017).

The biogeographical distribution of stegosaurs is also quite limited; other than *Paranthodon*, *Kentrosaurus* from Tanzania is the only other confirmed occurrence of Stegosauria in Gondwana. The aforementioned *Isaberrysaura* from Patagonia has characteristics of both basal thyreophorans and basal stegosaurs; however, further study and a postcranial description of the skeleton, are needed to elucidate the taxonomic status of the specimen. Stegosaurian ichnofacies are also reported throughout Gondwana, in Western Australia (Salisbury et al., 2016), Southern India (Galton and Ayyasami, 2017), and Bolivia (Apestequía and Gallina, 2011). Additionally, an indeterminate stegosaurian specimen was reported by Haddoumi et al. (2016) in Morocco, and there have been repeated reports to a taxon previously referred to as *Dravidosaurus* in Southern India (Galton and Ayyasami, 2017).

Paranthodon is therefore an important data point for future evaluations of both the stratigraphic and biogeographic evolution of the clade Stegosauria, as well as for total-group evaluations of Thyreophora.

Phylogeny of Ankylosauria

The recent phylogeny of the ankylosaurian dinosaurs by Arbour and Currie (2016) was re-analysed herein with a 'New Technology' search in TNT (Analysis B). This has improved the resolution of the analysis, especially the relationships of derived ankylosaurids, and reduced the number of MPTs from 3030 to 11, relative to the original analysis by Arbour and Currie (2016). The resolution of the strict consensus tree in this study is similar to that of the 50% majority rule tree in Arbour and Currie (2016), but *Crichtonpelta* has moved outside of Ankylosaurinae, meaning it is not the oldest known ankylosaurine. Additionally, running the ankylosaurian dataset of Thompson et al. (2012) with a 'New Technology' search (Analysis Y) improved the resolution of Ankylosauridae in the strict consensus so that it was approaching the resolution of the 50% majority rule tree in the original analysis, which was performed with a 'Traditional' search.

The results of these analyses are, therefore, more robust, as the use of strict consensus trees is a more rigorous method than majority rule trees for summarising the information found within the MPTs (Bryant, 2003). This improved resolution is due to the use of 'New Technology' searches, rather than the 'Traditional' search option used in the original analysis. 'Traditional' searches are heuristic, and can get stuck on local parsimony optimums within treespace, whereas 'New Technology' searches employ algorithms (Ratchet, Sectorial, Drift and Tree Fusing) that allow more rigorous searches for improved tree scores and a reduced number of optimal trees, within minimal time (Goloboff, Farris and Nixon, 2008). These are much more effective than branch-swapping methods, especially for datasets with hundreds of characters and a large number of taxa.

CONCLUSIONS

Our results demonstrate that the use of basal exemplifiers in cladistic analysis may prevent the correct phylogenetic position of derived taxa from being established. Instead, we recommend the use, minimally, of a basal and derived exemplifier for each clade. The phylogenetic position of *Paranthodon* is highly labile and is dramatically affected by the choice of taxonomic exemplifier, and further material of this enigmatic taxon is required to fully assess its affinities. However, based on the currently available data, it seems most likely that the taxon is a stegosaur.

ACKNOWLEDGEMENTS

Sandra Chapman and Paul Barrett (Natural History Museum) provided access to specimens in their care. Harry Taylor (Natural History Museum Photographic Unit) provided photographs of specimens. This work benefitted from discussion with members of the Imperial College Palaeobiology Research Group, and thanks to Paul Barrett, Richard Butler and Clint Boyd for discussions regarding *Isaberrysaura*. The Willi Hennig Society sponsored the development and free distribution of TNT. Alexander Schmidt-Lebuhn (Centre for Australian National Biodiversity Research) provided the script for running the Templeton Test in TNT.

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Figure 1

Premaxilla and maxilla of *Paranthodon africanus*

A: medial; B: lateral; C: posterior; D: dorsal; E: ventral; F: anterior views. pmp = premaxillary process. smp = secondary maxillary process. pp = posterior process. ap = anterior process.

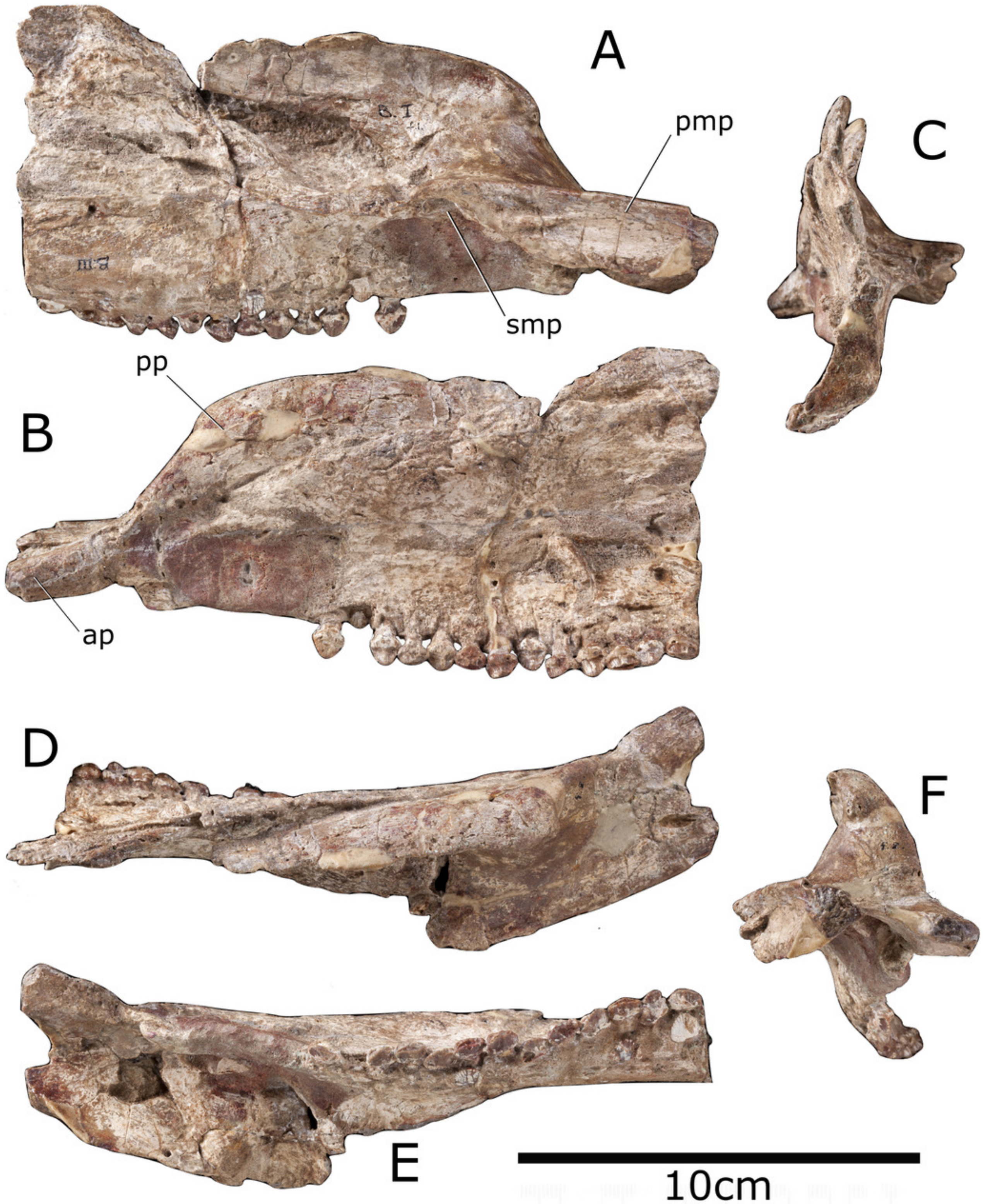

A
pmp
smp
C
pp
B
ap
D
F
E
10cm

Figure 2

Nasal of *Paranthodon africanus*

A: dorsal; B: posterior; C: lateral; D: ventral; E: anterior; F: medial.

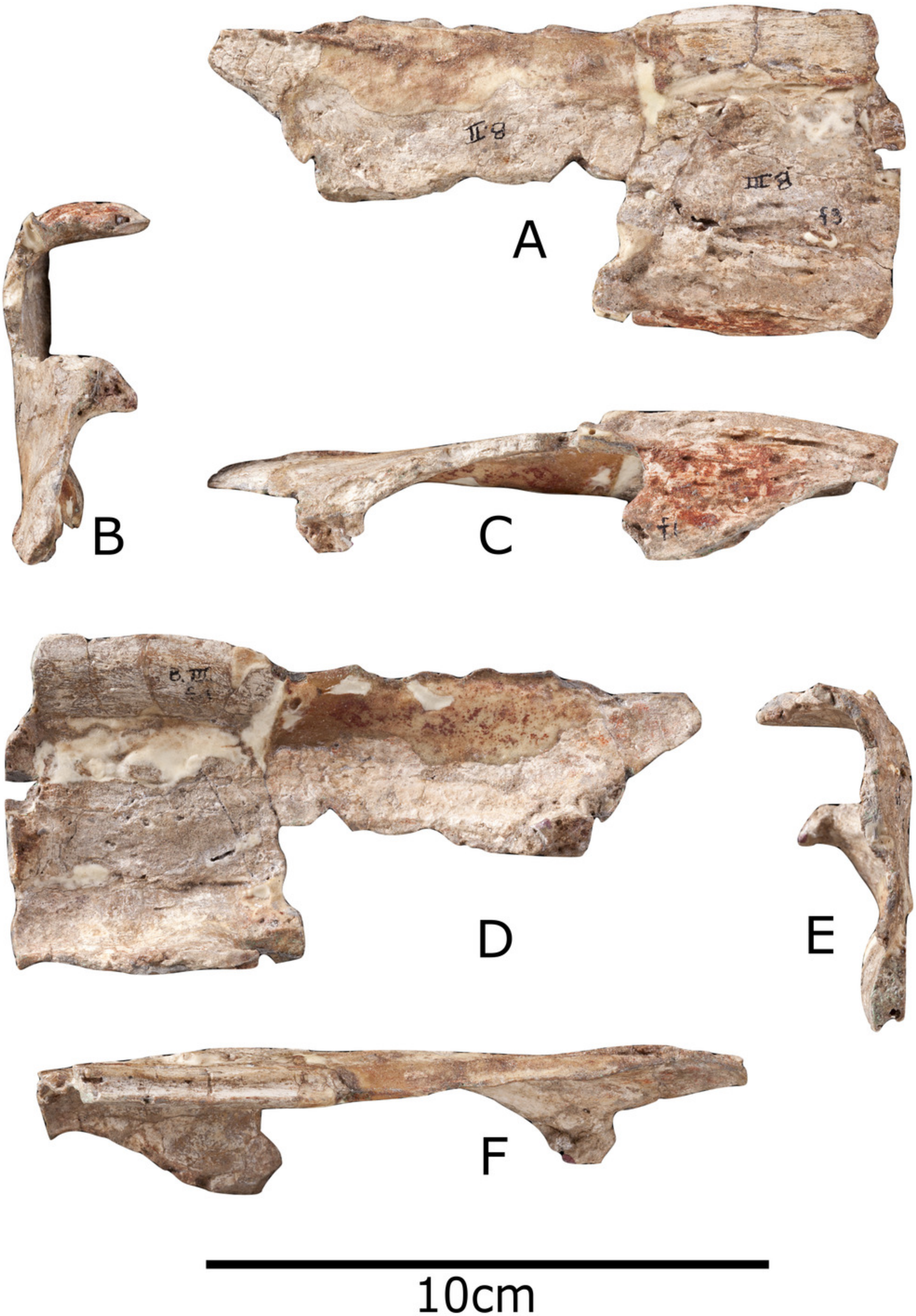

A
B
C
D
E
F
10cm

Figure 3

Vertebra of *Paranthodon africanus*

A: anterior; B: posterior; C: medial; D: lateral; E: dorsal; F: comparison with dorsal vertebra five of NHMUK R36730 showing location of fragmentary vertebra of *Paranthodon*. ns = neural spine. przyg = prezygapophysis. Scale bar on left is for A, B, C, D, and E. Scale bar on right applies to F only.

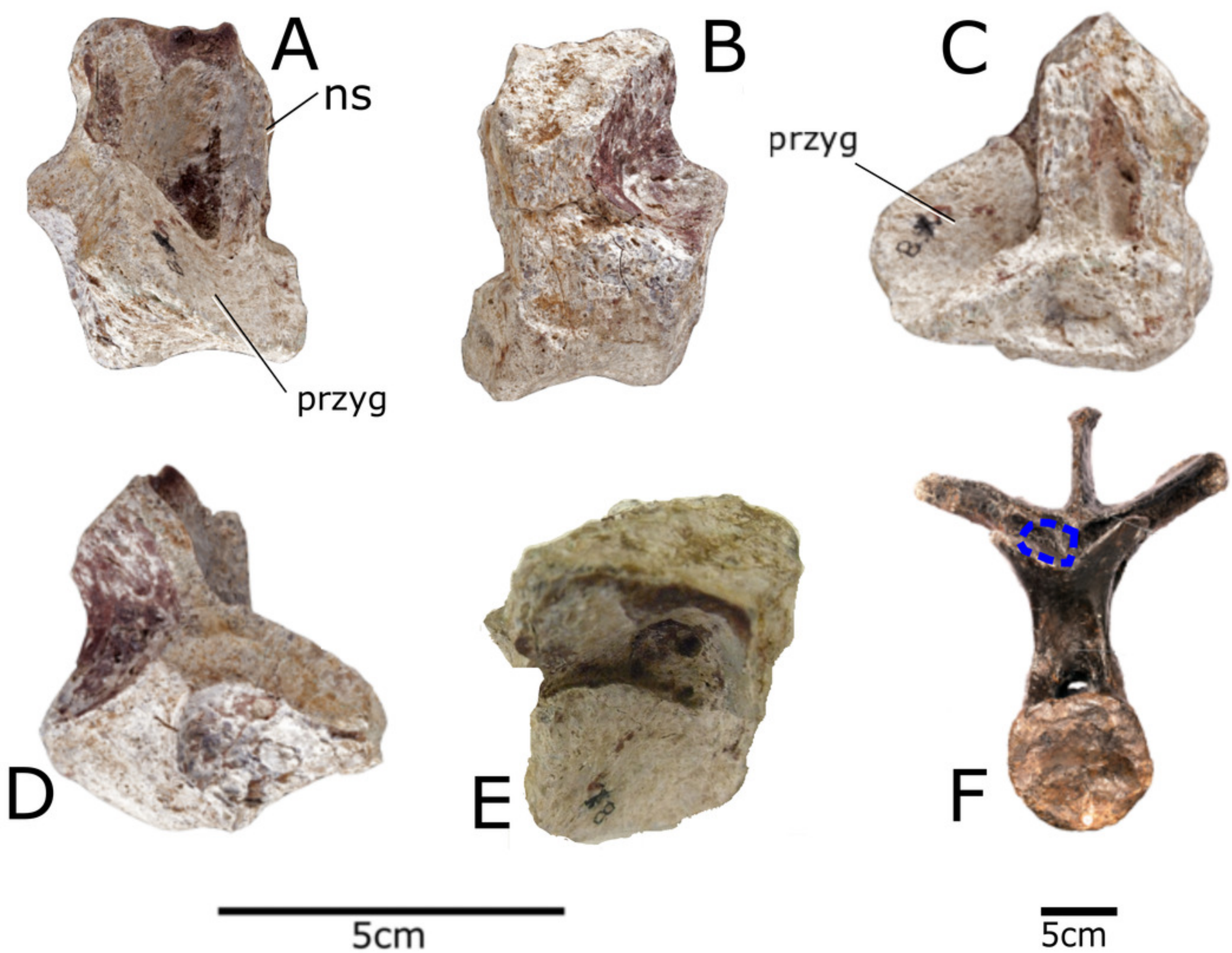


Figure 4

Previously referred teeth of *Paranthodon africanus*

A: posterior; B: lingual; C: buccal; D: anterior; E: ventral; F: dorsal. G: screenshot of CT-scan of one of the referred teeth, with uncertain material above crack in red.

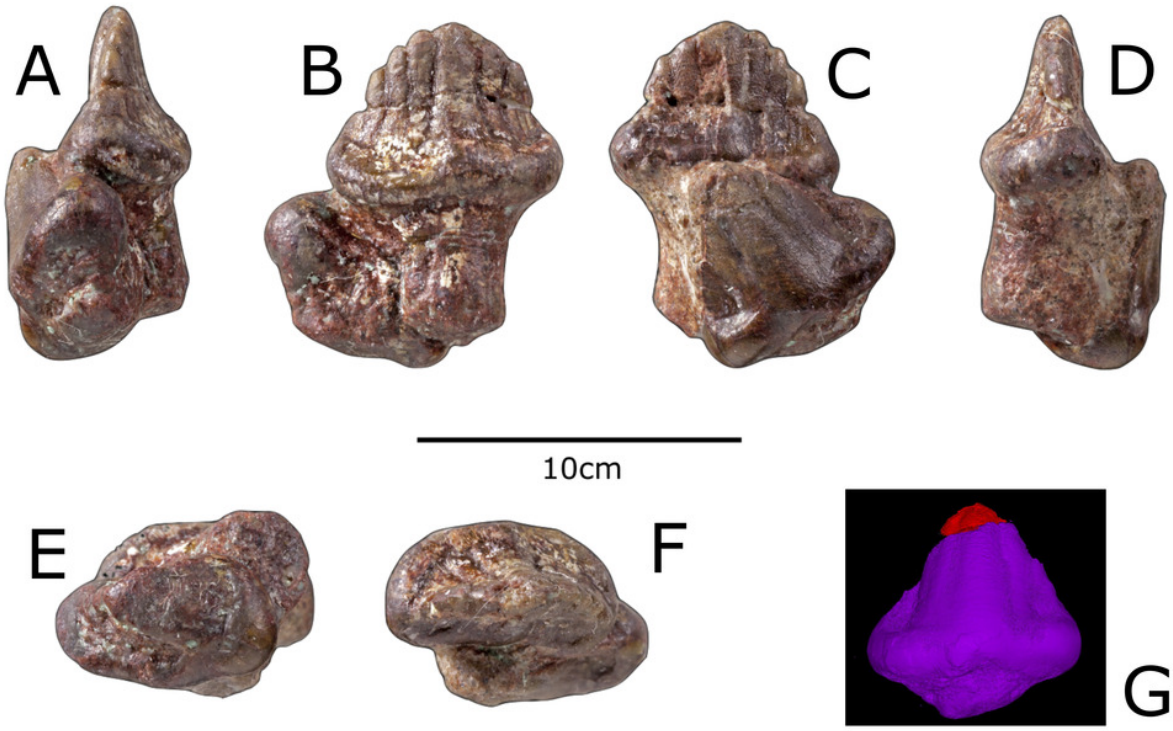
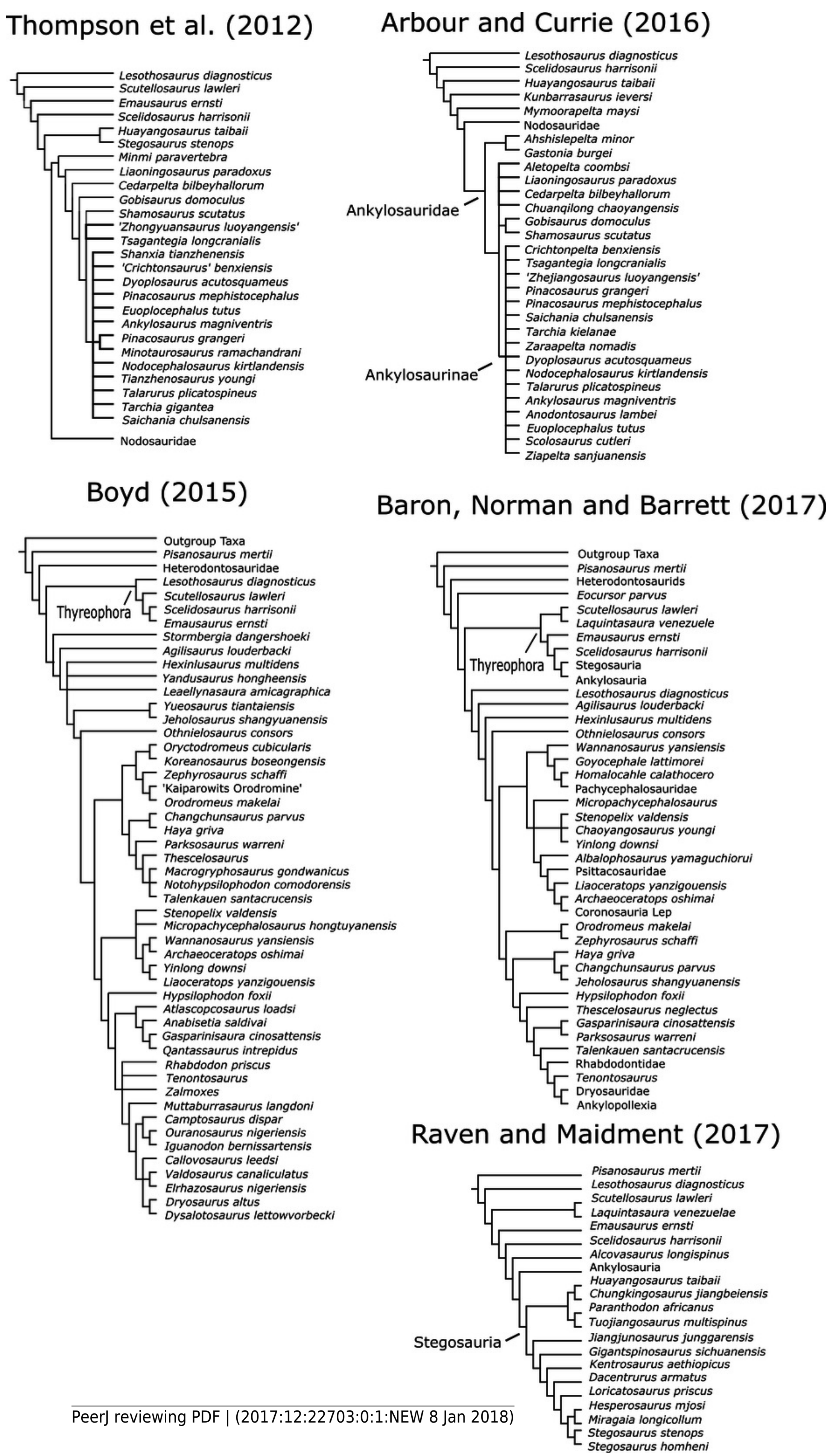

A
B
C
D
10cm
E
F
G

Figure 5

Simpliied phylogenies from original datasets used in this study.

Ankylosaurian phylogeny by Thompson et al. (2012); ankylosaurid phylogeny by Arbour and Currie (2016); stegosaurian phylogeny by Raven and Maidment (2017); basal ornithischian phylogeny by Baron, Norman and Barrett (2017); basal ornithischian phylogeny by Boyd (2015).



Thompson et al. (2012)
Lesothosaurus diagnosticus
Scutellosaurus lawleri
Emausaurus ernsti
Scelidosaurus harrisonii
Huayangosaurus taibaii
Stegosaurus stenops
Minmi paravertebra
Liaoningosaurus paradoxus
Cedarpelta bilbeyhallorum
Gobisaurus domoculus
Shamosaurus scutatus
'Zhongyuansaurus luoyangensis'
Tsagantegia longcranialis
Shanxia tianzhenensis
'Crichtonsaurus' benxiensis
Dyoplosaurus acutosquameus
Pinacosaurus mephistocephalus
Euoplocephalus tutus
Ankylosaurus magniventris
Pinacosaurus grangeri
Minotaurosaurus ramachandrani
Nodocephalosaurus kirtlandensis
Tianzhenosaurus youngi
Talarurus plicatospineus
Tarchia gigantea
Saichania chulsanensis
Nodosauridae
Arbour and Currie (2016)
Lesothosaurus diagnosticus
Scelidosaurus harrisonii
Huayangosaurus taibaii
Kunbarrasaurus ieversi
Mymoorapelta maysi
Nodosauridae
Ahshislepelta minor
Gastonia burgei
Aletopelta coombsi
Liaoningosaurus paradoxus
Cedarpelta bilbeyhallorum
Chuanqilong chaoyangensis
Gobisaurus domoculus
Shamosaurus scutatus
Crichtonpelta benxiensis
Tsagantegia longcranialis
'Zhejiangosaurus luoyangensis'
Pinacosaurus grangeri
Pinacosaurus mephistocephalus
Saichania chulsanensis
Tarchia kielanae
Zaraapelta nomadis
Dyoplosaurus acutosquameus
Nodocephalosaurus kirtlandensis
Talarurus plicatospineus
Ankylosaurus magniventris
Anodontosaurus lambei
Euoplocephalus tutus
Scolosaurus cutleri
Ziapelta sanjuanensis
Ankylosauridae
Ankylosaurinae
Boyd (2015)
Outgroup Taxa
Pisanosaurus mertii
Heterodontosauridae
Lesothosaurus diagnosticus
Scutellosaurus lawleri
Scelidosaurus harrisonii
Emausaurus ernsti
Thyreophora
Stormbergia dangershoeki
Agilisaurus louderbacki
Hexinlusaurus multidens
Yandusaurus hongheensis
Leaellynasaura amicagraphica
Yueosaurus tiantaiensis
Jeholosaurus shangyuanensis
Othnielosaurus consors
Oryctodromeus cubicularis
Koreanosaurus boseongensis
Zephyrosaurus schaffi
'Kaiparowits Orodromine'
Orodromeus makelai
Changchunsaurus parvus
Haya griva
Parksosaurus warreni
Thescelosaurus
Macrogryphosaurus gondwanicus
Notohypsilophodon comodorensis
Talenkauen santacrucensis
Stenopelix valdensis
Micropachycephalosaurus hongtuyanensis
Wannanosaurus yansiensis
Archaeoceratops oshimai
Yinlong downsi
Liaoceratops yanzigouensis
Hypsilophodon foxii
Atlascopcosaurus loadsi
Anabisetia saldivai
Gasparinisaura cinosattensis
Qantassaurus intrepidus
Rhabdodon priscus
Tenontosaurus
Zalmoxes
Muttaburrasaurus langdoni
Camptosaurus dispar
Ouranosaurus nigeriensis
Iguanodon bernissartensis
Callovosaurus leedsi
Valdosaurus canaliculatus
Elrhazosaurus nigeriensis
Dryosaurus altus
Dysalotosaurus lettowvorbecki
Baron, Norman and Barrett (2017)
Outgroup Taxa
Pisanosaurus mertii
Heterodontosaurids
Eocursor parvus
Scutellosaurus lawleri
Laquintasaura venezuele
Emausaurus ernsti
Scelidosaurus harrisonii
Stegosauria
Ankylosauria
Thyreophora
Lesothosaurus diagnosticus
Agilisaurus louderbacki
Hexinlusaurus multidens
Othnielosaurus consors
Wannanosaurus yansiensis
Goyocephale lattimorei
Homalocahle calathocero
Pachycephalosauridae
Micropachycephalosaurus
Stenopelix valdensis
Chaoyangosaurus youngi
Yinlong downsi
Albalophosaurus yamaguchiorui
Psittacosauridae
Liaoceratops yanzigouensis
Archaeoceratops oshimai
Coronosauria Lep
Orodromeus makelai
Zephyrosaurus schaffi
Haya griva
Changchunsaurus parvus
Jeholosaurus shangyuanensis
Hypsilophodon foxii
Thescelosaurus neglectus
Gasparinisaura cinosattensis
Parksosaurus warreni
Talenkauen santacrucensis
Rhabdodontidae
Tenontosaurus
Dryosauridae
Ankylopollexia
Raven and Maidment (2017)
Pisanosaurus mertii
Lesothosaurus diagnosticus
Scutellosaurus lawleri
Laquintasaura venezuelae
Emausaurus ernsti
Scelidosaurus harrisonii
Alcovasaurus longispinus
Ankylosauria
Huayangosaurus taibaii
Chungkingosaurus jiangbeiensis
Paranthodon africanus
Tuojiangosaurus multispinus
Jiangjunosaurus junggarensis
Gigantspinosaurus sichuanensis
Kentrosaurus aethiopicus
Dacentrurus armatus
Loricatosaurus priscus
Hesperosaurus mjosi
Miragaia longicollum
Stegosaurus stenops
Stegosaurus homheni
Stegosauria

Figure 6

Strict consensus tree from Analysis R; inclusion of *Paranthodon, Huayangosaurus, Stegosaurus* and *Isaberrysaura* as OTUs into the Boyd (2015) dataset.

Red bar = grouping of basal thyreophorans, blue bar = placement of *Paranthodon, Huayangosaurus, Stegosaurus* and *Isaberrysaura.* Only two synapomorphies characterise the group of basal thyreophorans; a ridge on the lateral surface of surangular, which is not present in stegosaurs, and a concave lingual surface of maxillary teeth, which is not a eurypodan character. This demonstrates that the Boyd (2015) dataset is inadequate for accurately testing the position of eurypodans, possibly explaining the positioning of *Isaberrysaura* as an ornithopod in Salgado et al. (2017).

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

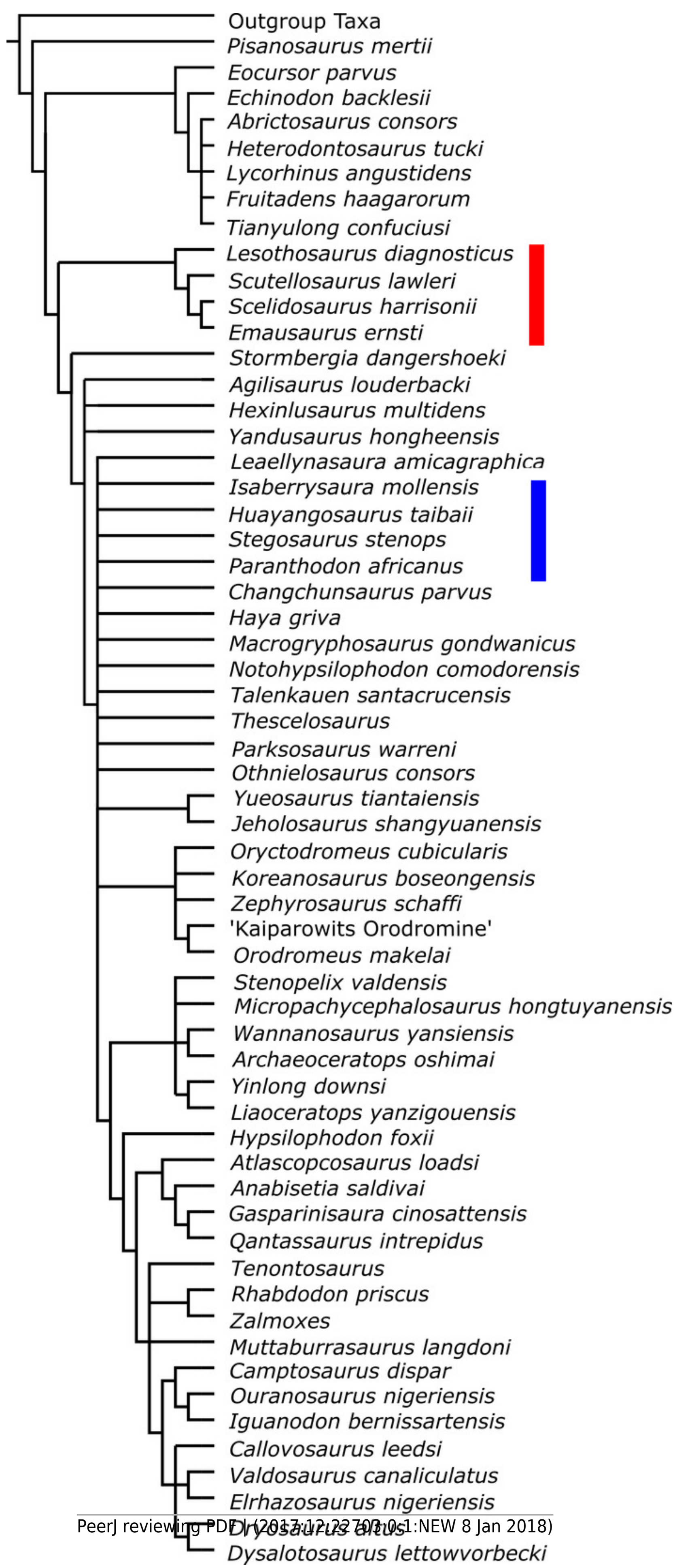

Outgroup Taxa
Pisanosaurus mertii
Eocursor parvus
Echinodon backlesii
Abrictosaurus consors
Heterodontosaurus tucki
Lycorhinus angustidens
Fruitadens haagarorum
Tianyulong confuciusi
Lesothosaurus diagnosticus
Scutellosaurus lawleri
Scelidosaurus harrisonii
Emausaurus ernsti
Stormbergia dangershoeki
Agilisaurus louderbacki
Hexinlusaurus multidens
Yandusaurus hongheensis
Leaellynasaura amicagraphica
Isaberrysaura mollensis
Huayangosaurus taibaii
Stegosaurus stenops
Paranthodon africanus
Changchunsaurus parvus
Haya griva
Macrogryphosaurus gondwanicus
Notohypsilophodon comodorensis
Talenkauen santacrucensis
Thescelosaurus
Parksosaurus warreni
Othnielosaurus consors
Yueosaurus tiantaiensis
Jeholosaurus shangyuanensis
Oryctodromeus cubicularis
Koreanosaurus boseongensis
Zephyrosaurus schaffi
'Kaiparowits Orodromine'
Orodromeus makelai
Stenopelix valdensis
Micropachycephalosaurus hongtuyanensis
Wannanosaurus yansiensis
Archaeoceratops oshimai
Yinlong downsi
Liaoceratops yanzigouensis
Hypsilophodon foxii
Atlascopcosaurus loadsi
Anabisetia saldivai
Gasparinisaura cinosattensis
Qantassaurus intrepidus
Tenontosaurus
Rhabdodon priscus
Zalmoxes
Muttaburrasaurus langdoni
Camptosaurus dispar
Ouranosaurus nigeriensis
Iguanodon bernissartensis
Callovosaurus leedsi
Valdosaurus canaliculatus
Elrhazosaurus nigeriensis
Dryosaurus altus
Dysalotosaurus lettowvorbecki

Table 1 (on next page)

Premaxillary posterior process angle across a range of ornithischians.

Taxon	Premaxilla posterior process angle, relative to horizontal (°)
Camptosaurus dispar	40
Gastonia burgei	60
Hesperosaurus mjosi	40
Heterodontosaurus tucki	40
Huayangosaurus taibaii	30
Hypsilophodon foxii	75
Jinzhousaurus yangi	60
Paranthodon africanus	47
Scelidosaurus harrisonii	60
Stegosaurus stenops	16
Tenontosaurus tilletii	50

Table 2 (on next page)

All analyses, including original dataset and changes applied to each iteration.

Analysis	Source of Original	Settings
Analysis A	Arbour and Currie (2016)	*Lesothosaurus* used as outgroup. All characters unordered and of equal weight. *Bissektipelta*, *Minmi paravertebra* and *Tianchisaurus* removed. *Huayangosaurus* used as exemplifier for Stegosauria. 'Traditional' search performed with original settings of Arbour and Currie (2016).
Analysis B	Arbour and Currie (2016)	Same as Analysis A, except a 'New Technology' search was performed.
Analysis C	Arbour and Currie (2016)	Same as Analysis B, except *Paranthodon* was added as an Operational Taxonomic Unit.
Analysis D	Arbour and Currie (2016)	Same as Analysis B, except *Paranthodon* and *Stegosaurus* were added as OTUs, and *Huayangosaurus* removed.
Analysis E	Arbour and Currie (2016)	Same as Analysis B, except *Paranthodon* and *Stegosaurus* were added as OTUs, in addition to *Huayangosaurus.*
Analysis F	Arbour and Currie (2016)	Same as Analysis E, except *Paranthodon* was constrained to fall within Ankylosauria.
Analysis G	Baron, Norman and Barrett (2017)	*Euparkeria* used as outgroup. Characters 112, 135, 137, 138, 174 ordered. *Anabisetia, Echinodon, Koreanosaurus, Yandosaurus* and *Yueosaurus* removed. 'New Technology' search performed with original settings.
Analysis H	Baron, Norman and Barrett (2017)	Same as Analysis G, except *Paranthodon* was added as an OTU.
Analysis I	Baron, Norman and Barrett (2017)	Same as Analysis H, except *Stegosaurus* replaced *Huayangosaurus* as the exemplifier for Stegosauria.
Analysis J	Baron, Norman and Barrett (2017)	Same as Analysis H, except *Stegosaurus* was added as an OTU, as well as *Huayangosaurus*.
Analysis K	Baron, Norman and Barrett (2017)	Same as Analysis J, except *Isaberrysaura* was added as an OTU.
Analysis L	Baron, Norman and Barrett (2017)	Same as Analysis J, except *Paranthodon* was constrained to fall within Ornithopoda.
Analysis M	Boyd (2015)	*Marasuchus* used as outgroup. All characters unordered. 'New Technology' search performed with original settings of Boyd (2015).

Analysis N	Boyd (2015)	Same as Analysis M, except *Paranthodon* was added as an OTU.
Analysis O	Boyd (2015)	Same as Analysis N, except *Huayangosaurus* was added as an OTU.
Analysis P	Boyd (2015)	Same as Analysis N, except *Stegosaurus* was added as an OTU.
Analysis Q	Boyd (2015)	Same as Analysis N, except *Huayangosaurus* and *Stegosaurus* were added as OTUs.
Analysis R	Boyd (2015)	Same as Analysis Q, except *Isaberrysaura* added as an OTU.
Analysis S	Boyd (2015)	Same as Analysis Q, except *Paranthodon* was constrained to fall within Ornithopoda.
Analysis T	Boyd (2015)	Same as Analysis Q, except *Paranthodon* was constrained to fall within Thyreophora.
Analysis U	Raven and Maidment (2017)	*Pisanosaurus* used as outgroup. The first 24 continuous characters were ordered, as were characters 34, 111 and 112. Discrete characters weighted equally. Character list and character scorings updated from Raven and Maidment (2017).
Analysis V	Raven and Maidment (2017)	Same as Analysis U, except *Isaberrysaura* added as an OTU
Analysis W	Raven and Maidment (2017)	Same as Analysis U, except *Paranthodon* was constrained to fall within Ankylosauria.
Analysis X	Thompson et al. (2012)	*Lesothosaurus* used as outgroup. *Bissektipelta* excluded as an OTU. Characters 25, 27, 32, 133, 159, 167 removed. All remaining characters unordered and equally weighted. 'Traditional' search performed with original settings of Thompson et al (2012).
Analysis Y	Thompson et al. (2012)	Same as Analysis W, except that a 'New Technology' search was performed and *Paranthodon* was included as an OTU.
Analysis Z	Thompson et al. (2012)	Same as Analysis X, except that *Paranthodon* was constrained to fall within Stegosauria.

1

Table 3(on next page)

Results of all phylogenetic analyses

Stegosaurian exemplifier for each analysis is stated, as is the placement of *Paranthodon africanus*, and any other results of importance.

Source of Original	Stegosaurian Exemplifier	Placement of *Paranthodon*	Other results
Arbour and Currie (2016)	*Huayangosaurus*	n/a	Same as Arbour and Currie (2016)
Arbour and Currie (2016)	*Huayangosaurus*	n/a	Higher resolution in strict consensus than Arbour and Currie (2016)
Arbour and Currie (2016)	*Huayangosaurus*	Ankylosaur	9 MPTs
Arbour and Currie (2016)	*Stegosaurus*	Base of Thyreophora	8 MPTs and increased resolution
Arbour and Currie (2016)	*Huayangosaurus* and *Stegosaurus*	Stegosaur	9 MPTs and increased resolution
Arbour and Currie (2016)	*Huayangosaurus* and *Stegosaurus*	Ankylosaur (constrained)	9 MPTs and reduced resolution
Baron, Norman and Barrett (2017)	*Huayangosaurus*	n/a	Same as Baron, Norman and Barrett (2017)
Baron, Norman and Barrett (2017)	*Huayangosaurus*	Ankylosaur	Little resolution
Baron, Norman and Barrett (2017)	*Stegosaurus*	Stegosaur	Higher resolution
Baron, Norman and Barrett (2017)	*Huayangosaurus* and *Stegosaurus*	Stegosaur	Very high resolution
Baron, Norman and Barrett (2017)	*Huayangosaurus* and *Stegosaurus*	Stegosaur	Little resolution and *Isaberrysaura* = ornithopod
Baron, Norman and Barrett (2017)	*Huayangosaurus* and *Stegosaurus*	Ornithopod (constrained)	Severely reduced resolution in Ornithopoda
Boyd (2015)	n/a - *Scelidosaurus* most derived	n/a	Same as Boyd (20150

	thyreophoran		
Boyd (2015)	n/a - *Scelidosaurus* most derived thyreophoran	Base of Ornithischia	Thyreophora basal to Heterodontosauridae, Marginocephalia basal to Cerapoda
Boyd (2015)	*Huayangosaurus*	Ornithopod, sister-taxon to *Huayangosaurus*	*Huayangosaurus* = ornithopod and reduced resolution in Ornithopoda
Boyd (2015)	*Stegosaurus*	Ornithopod, sister-taxon to *Stegosaurus*	*Stegosaurus* = ornithopod and increased resolution
Boyd (2015)	*Huayangosaurus* and *Stegosaurus*	Ornithopod, sister-taxon to *Huayangosaurus* and *Stegosaurus*	*Huayangosaurus* and *Stegosaurus* = ornithopod and little resolution
Boyd (2015)	*Huayangosaurus* and *Stegosaurus*	Ornithopod, sister-taxon to *Huayangosaurus* and *Stegosaurus*	*Huayangosaurus* and *Stegosaurus* = ornithopod and little resolution. *Isaberrysaura* = ornithopod
Boyd (2015)	*Huayangosaurus* and *Stegosaurus*	Ornithopod (constrained)	*Huayangosaurus* and *Stegosaurus* outside of Ornithischia and increased resolution in Ornithopoda.
Boyd (2015)	*Huayangosaurus* and *Stegosaurus*	Thyreophoran	Ornithopoda resolution increased, Thyreophora resolution decrease
Raven and Maidment (2017)	n/a	Stegosaur	Similar to Raven and Maidment (2017)
Raven and Maidment (2017)	n/a	Eurypodan	*Isaberrysaura* = basal stegosaur. Reduced resolution in Eurypoda
Raven and Maidment (2017)	n/a	Ankylosaur (constrained)	Reduced resolution in Ankylosauria
Thompson et al. (2012)	*Huayangosaurus* and *Stegosaurus*	n/a	Same as Thompson et al. (2012)
Thompson et al. (2012)	*Huayangosaurus* and *Stegosaurus*	Ankylosaur	Higher resolution in strict consensus than Thompson et al. (2012)
Thompson et al. (2012)	*Huayangosaurus* and *Stegosaurus*	Stegosaur (constrained)	Resolution of Nodosauridae increased