



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

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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, meaning it is one of the youngest and southernmost stegosaurs.

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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 & 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 parasagittal 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 & 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 & 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, in that it is an olive-grey medium sandstone, 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 & Christiansen, 2009), although Han et al. (2017) also found the Argentinian dinosaur *Isaberrysaura* to be a stegosaur.

The first phylogeny focusing on Stegosauria was produced by Galton & 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 & 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 & 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 (Fig. 1), and two referred teeth (Maidment et al., 2008). Additionally, there is a partial vertebra that was not described by Galton & 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 & 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

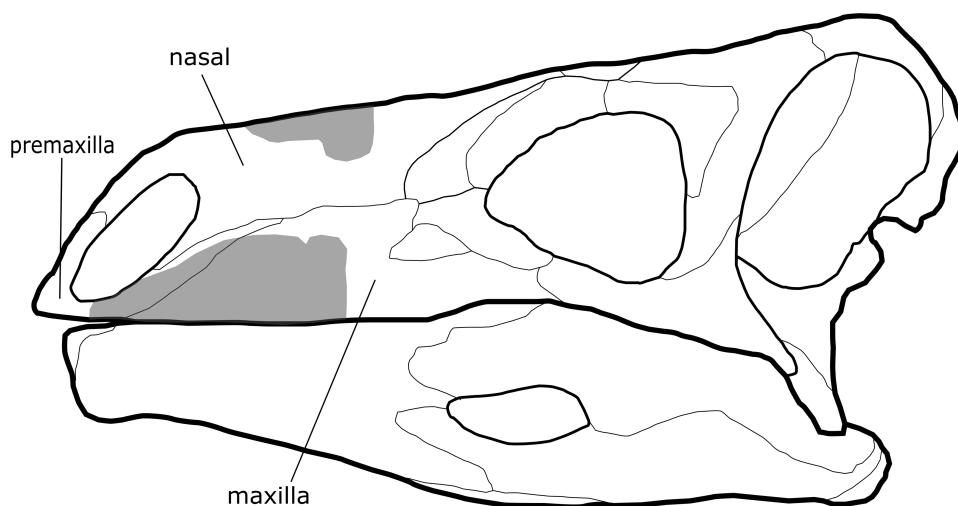


Figure 1 Comparison of cranial material of *Paranthodon africanus* NHMUK R47338 with that of *Stegosaurus*. Grey section, material of *Paranthodon*, including partial premaxilla, maxilla and nasal. *Stegosaurus* skull is a reconstruction from *Stegosaurus stenops* USNM 4934 (United States National Museum) and DMNH 2818 (Denver Museum of Nature and Science).

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utilises numerous phylogenetic hypotheses to constrain the evolutionary relationships of *Paranthodon*, including the first analysis of the taxon in an ankylosaurian phylogeny.

SYSTEMATIC PALAEOLOGY

DINOSAURIA Owen, 1841

ORNITHISCHIA Seeley, 1887

THYREOPHORA Nopcsa, 1915 (sensu Norman, 1984)

STEGOSAURIA Marsh, 1877

Paranthodon Nopcsa, 1929

Paranthodon africanus Broom, 1910

Synonymy

Anthodon serrarius Owen, 1876

Palaeoscincus africanus Broom, 1910

Paranthodon oweni Nopcsa, 1929

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

Table 1 Measurements of the elements of *Paranthodon africanus* NHMUK R47338 and previously referred specimen NHMUK R4992.

Measurement	Specimen	
	NHMUK R47338	NHMUK R4992
Nasal, anteroposterior length	134 mm	
Nasal, width	63 mm	
Nasal, dorsoventral height	33 mm	
Premaxilla and maxilla, anteroposterior length	178 mm	
Premaxilla and maxilla, width	67 mm	
Premaxilla and maxilla, dorsoventral height	82 mm	
Mean tooth crown height	3.04 mm	4.25 mm
Mean tooth crown anteroposterior length	6.20 mm	5.25 mm
Mean tooth cingula height	2.92 mm	1.75 mm
Mean tooth cingula anteroposterior length	7.52 mm	7.50 mm
Mean tooth crown width	1.89 mm	1.25 mm
Mean tooth cingula width	5.05 mm	4.25 mm

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 & 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 & Coombs \(1981\)](#), but the discovery of new thyreophoran material means a re-description is warranted. The previous study misidentified part of 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. Measurements are found in [Table 1](#).

Premaxilla

The left premaxilla consists of an anteriorly-projecting anterior process and a posterior process that projects posterodorsally ([Fig. 2](#)). The anterior end of the premaxilla is

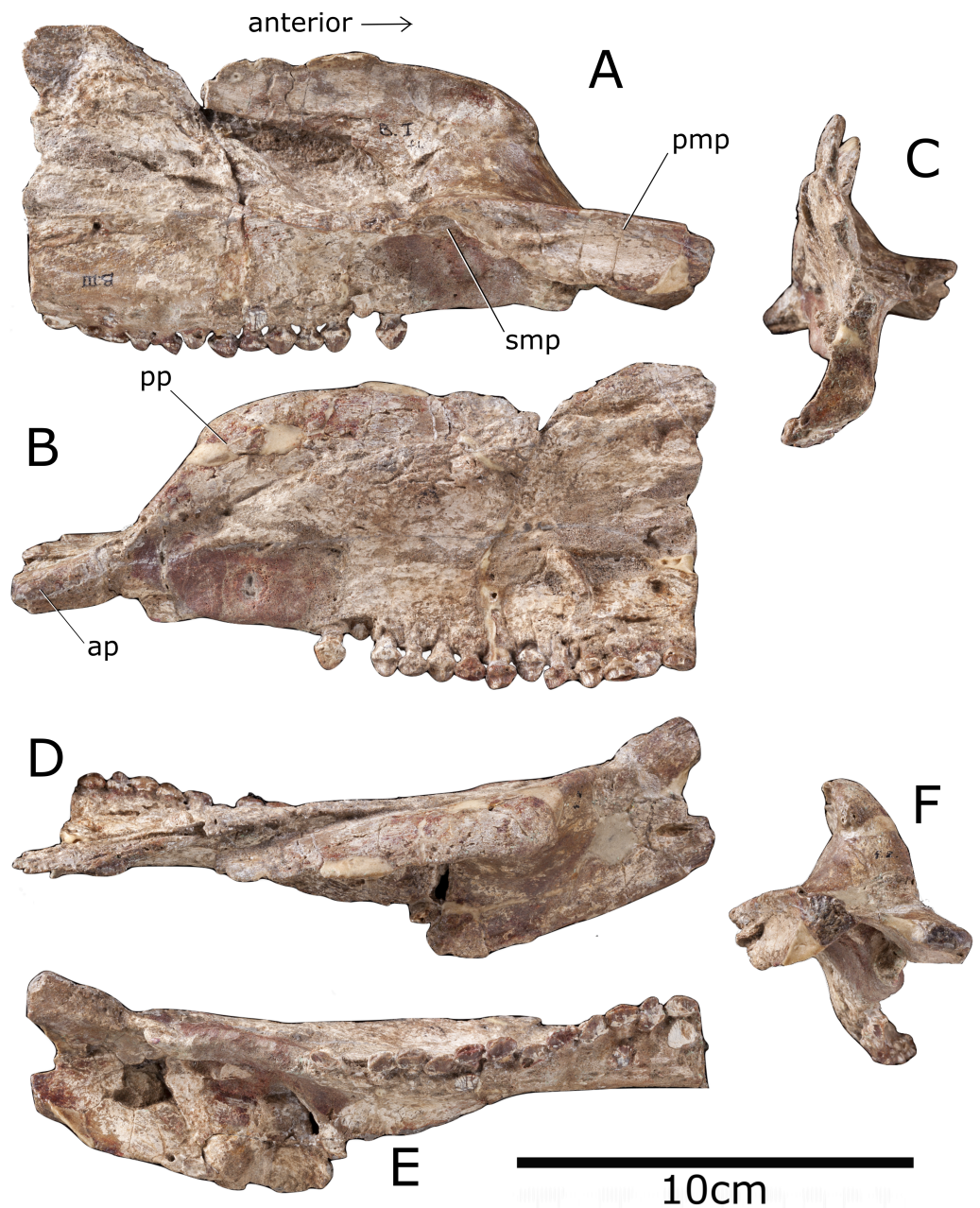


Figure 2 Premaxilla and maxilla of *Paranthodon africanus* NHMUK R47338. (A) Medial; (B) lateral; (C) posterior; (D) dorsal; (E) ventral; (F) anterior views. pmp, premaxillary process; smp, secondary maxillary process; pp, posterior process; ap, anterior process. Images copyright The Natural History Museum. Full-size [DOI: 10.7717/peerj.4529/fig-2](https://doi.org/10.7717/peerj.4529/fig-2)

incomplete, but the anterior process is sinuous in lateral view and curves ventrally, as in the stegosaurs *Miragaia* (Mateus, Maidment & Christiansen, 2009) and *Huayangosaurus* (Serenó & Dong, 1992), the ankylosaur *Silvisaurus* (NHMUK R1107) and the basal ornithischian *Heterodontosaurus* (Butler, Porro & Norman, 2008). This, however, contrasts to the horizontally-projecting process of the stegosaurs *Chungkingosaurus* (Maidment

& 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 & Norman, 2008) and the ornithopods *Camptosaurus* (NHMUK R1608) and *Jinzhouosaurus* (Wang & 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 2). The premaxilla is edentulous, as in every other stegosaur with cranial material preserved other than *Huayangosaurus* (Sereno & 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 *Gargoyleosaurus*, *Pawpawsaurus* and *Cedarpelta* (Kinneer, Carpenter & 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); *Anodontosaurus* (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 & 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 & Shaw, 2016) and *Anodontosaurus* (NHMUK R4947) and the ornithopods *Camptosaurus* (NHMUK R1608) and *Jinzhouosaurus* (Wang & Xu, 2001). This feature is, however, variable in stegosaurs; the same condition is seen in *Huayangosaurus* (Sereno & Dong, 1992), yet in *Stegosaurus* (NHMUK R36730) and *Hesperosaurus* (Carpenter, Miles & 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 & Wei, 2006), and ornithopods such as *Camptosaurus* (NHMUK R1608) and *Hypsilophodon* (NHMUK R197). 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 *Anodontosaurus* (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 (Witmer & Ridgely, 2008).

Maxilla

The maxilla is triangular in lateral view, with the tooth row forming an elongate base of the triangle (Fig. 2). This is similar to the condition in most other thyreophorans (e.g., *Stegosaurus* (NHMUK R36730), *Hesperosaurus* (Carpenter, Miles & Cloward, 2001), *Silvisaurus* (NHMUK R1107) and *Edmontonia* (NHMUK R36851)). However, the maxilla

Table 2 Premaxillary posterior process angle across a range of ornithischians.

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

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 & 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* (Serenó & 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 & 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 & Wei, 2006) and the basal ornithischian *Lesothosaurus* (Serenó, 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 *Anodontosaurus* (NHMUK R4947), *Gastonia* (Kinneer, Carpenter & Shaw, 2016), *Edmontonia* (NHMUK R36851), *Pawpawsaurus* (Kinneer, Carpenter & Shaw, 2016), *Panoplosaurus* (Kirkland et al., 2013) and *Silvisaurus* (NHMUK R1107). In *Stegosaurus* (NHMUK R36730) and *Huayangosaurus* (Serenó & Dong, 1992) the tooth row is straight in ventral view. 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* (Serenó & Dong, 1992). The contact angle between the maxilla and premaxilla in dorsal view is 30 degrees, similar to that of the stegosaurs *Tuojiangosaurus* (Maidment & Wei, 2006) and *Huayangosaurus* (Serenó & Dong, 1992). The ankylosaurs *Ankylosaurus* (Kinneer, Carpenter & Shaw, 2016) and *Pinacosaurus* (Maryńska, 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 & 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 & 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), *Anodontosaurus* (NHMUK R4947) and *Gastonia* (*Kinneer, Carpenter & 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. 3*). It is an anteroposteriorly elongate element, as in the stegosaurs *Stegosaurus* (NHMUK R36730), *Hesperosaurus* (*Carpenter, Miles & Cloward, 2001*) and *Huayangosaurus* (*Sereno & 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 & Wei, 2006*) and in the ornithomimid *Jinzhouosaurus* it tapers anteriorly (*Wang & 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 & 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 & Christiansen, 2009*). In the stegosaur *Tuojiangosaurus*, the nasal is gently concave transversely (*Maidment & Wei, 2006*), as it is in the basal ornithischian *Heterodontosaurus* (*Butler, Porro & 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 & Cloward, 2001*). As in the basal ornithischian *Heterodontosaurus*, the lateral margins are thickened into nasal ridges (*Butler, Porro & 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 & Cloward, 2001*). In the basal thyreophoran *Scelidosaurus* (NHMUK R1111) the sutures are not obvious and in the stegosaur *Tuojiangosaurus* the nasals are fused together (*Maidment & Wei, 2006*), although the fusion of skull sutures is likely ontogenetic in nature (*Currie, Langston & Tanke, 2008*). The nasal is not seen in contact with the premaxilla or maxilla, *contra Galton & Coombs (1981; Fig. 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

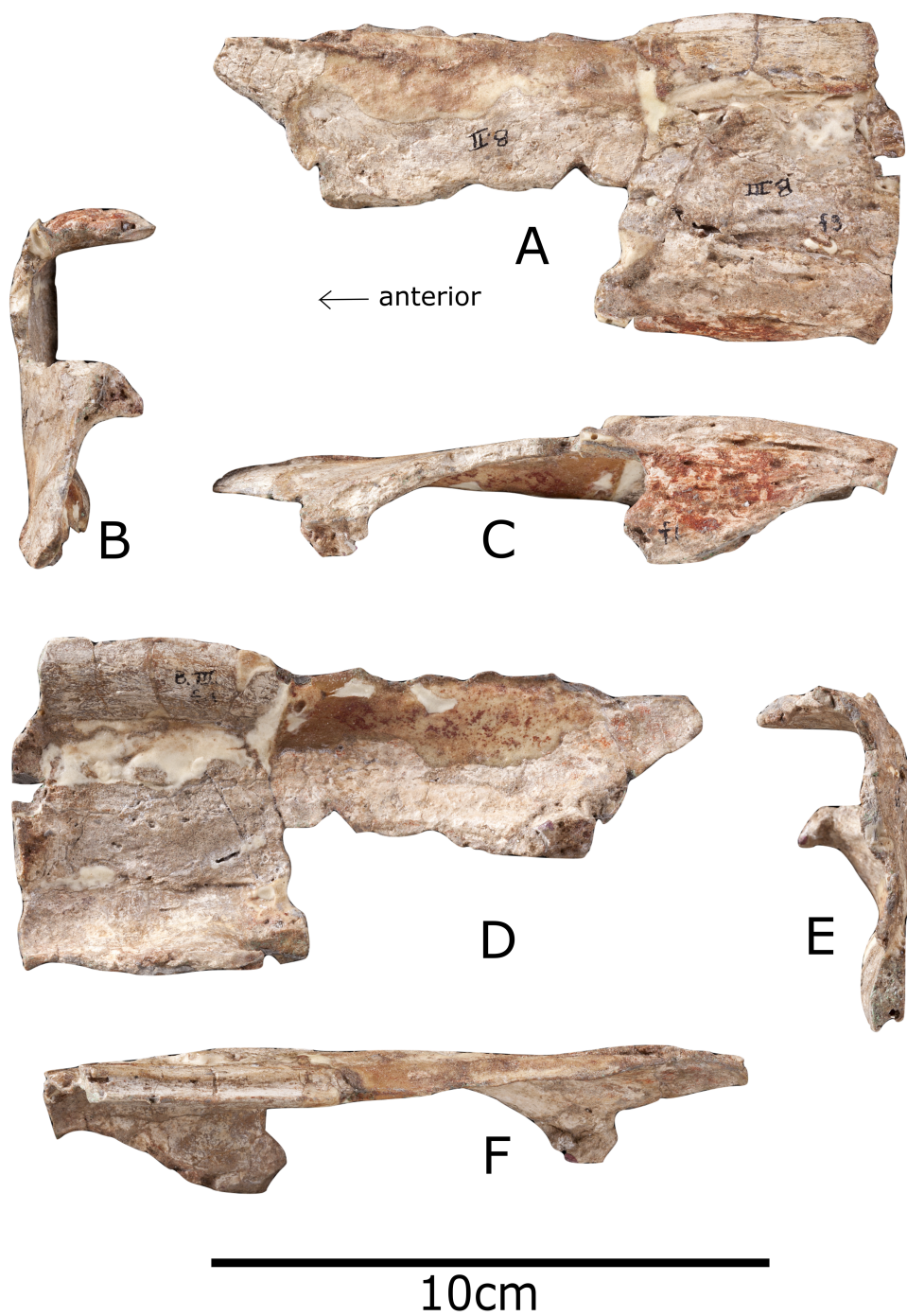


Figure 3 Nasal of *Paranthodon africanus* NHMUK R47338. (A) Dorsal; (B) posterior; (C) lateral; (D) ventral; (E) anterior; (F) medial. Images copyright The Natural History Museum.

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among ornithischians is widely variable, ranging from 10 in the ornithopod *Camptosaurus* (NHMUK R1608) to as many as 35 in *Ankylosaurus* (Kinneer, Carpenter & Shaw, 2016); tooth count also varies intraspecifically and was likely ontogenetically controlled (Butler, Porro & 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 & Christiansen, 2009), *Hesperosaurus* (Carpenter, Miles & Cloward, 2001), *Tuojiangosaurus* (Maidment & Wei, 2006), and *Jiangjunosaurus* (Jia et al., 2007) and the ankylosaur *Gastonia* (Kinneer, Carpenter & Shaw, 2016). The stegosaur *Chungkingosaurus* has a sharp, asymmetric tooth crown (Maidment & 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 & 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 & Wei, 2006), *Hesperosaurus* (Carpenter, Miles & Cloward, 2001), *Jiangjunosaurus* (Jia et al., 2007), *Miragaia* (Mateus, Maidment & Christiansen, 2009)) except *Huayangosaurus*, where a reduced swelling is present but not as a ring (Sereno & 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 & 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 & 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 & Wei, 2006); in contrast, it is very common in ankylosaur teeth (e.g., *Edmontonia* (NHMUK R36851), *Silvisaurus* (NHMUK R1107), *Gastonia* (Kinneer, Carpenter & Shaw, 2016), *Anodontosaurus* (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 & Cloward, 2001), whereas the root of *Kentrosaurus* tapers to a point (Galton, 1988).

Vertebra

The vertebra is extremely fragmentary; only the right transverse process and prezygapophysis are identifiable (Fig. 4). The anterior edge of the prezygapophysis is broken off and so the intraprezygapophyseal shelf is not preserved. The left transverse

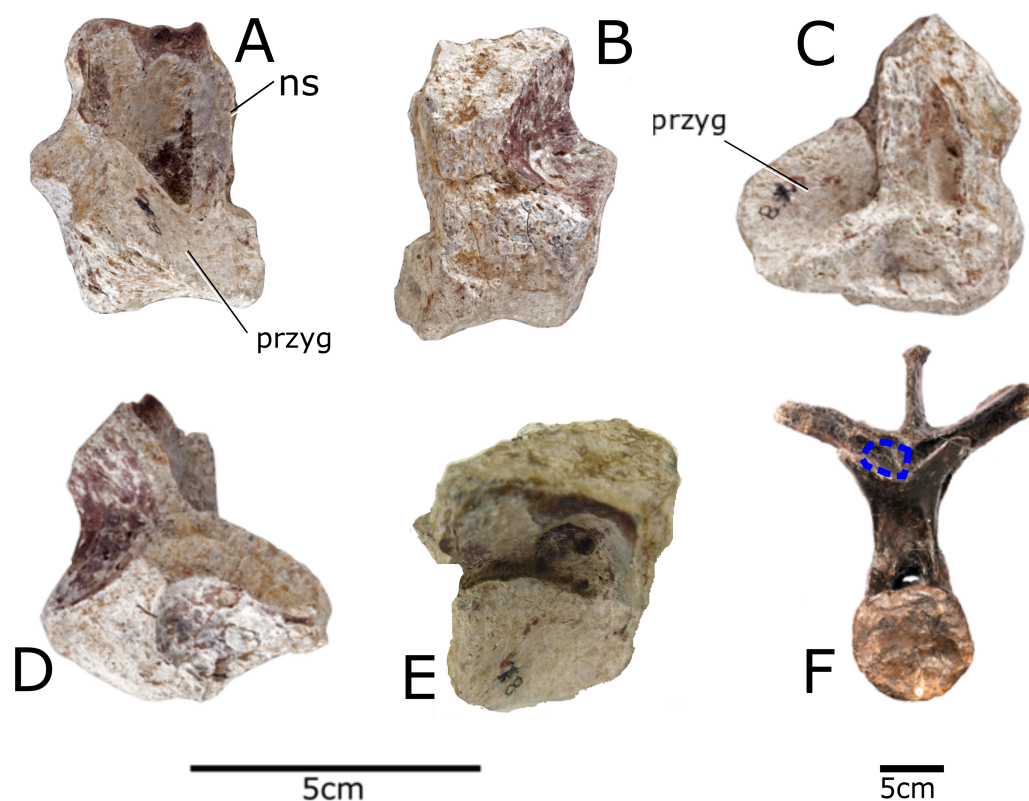


Figure 4 Vertebra of *Paranthodon africanus* NHMUK R47338. (A) Anterior; (B) posterior; (C) left lateral; (D) right lateral; (E) dorsal; (F) comparison with dorsal vertebra five of NHMUK R36730 showing location of fragmentary vertebra of *Paranthodon*. ns, neural spine; przyg, prezygapophysis. Scale bar on left is for (A), (B), (C), (D), and (E). Scale bar on right applies to (F) only. Images copyright The Natural History Museum.

Full-size DOI: [10.7717/peerj.4529/fig-4](https://doi.org/10.7717/peerj.4529/fig-4)

process is not present, nor are the posterior end of the vertebra or the centrum. The top of the right transverse process is not preserved, and part of the midline ridge has split so that it tapers to a 3 mm 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 & Wei, 2006). The dorsal vertebrae of the stegosaur *Gigantospinosaurus* (Maidment & Wei, 2006) have transverse processes that project laterally, whereas they project dorsolaterally in the ankylosaurs *Ankylosaurus* (Carpenter, 2004; Kinneer, Carpenter & Shaw, 2016), *Euoplocephalus* (Arbour & 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 & 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

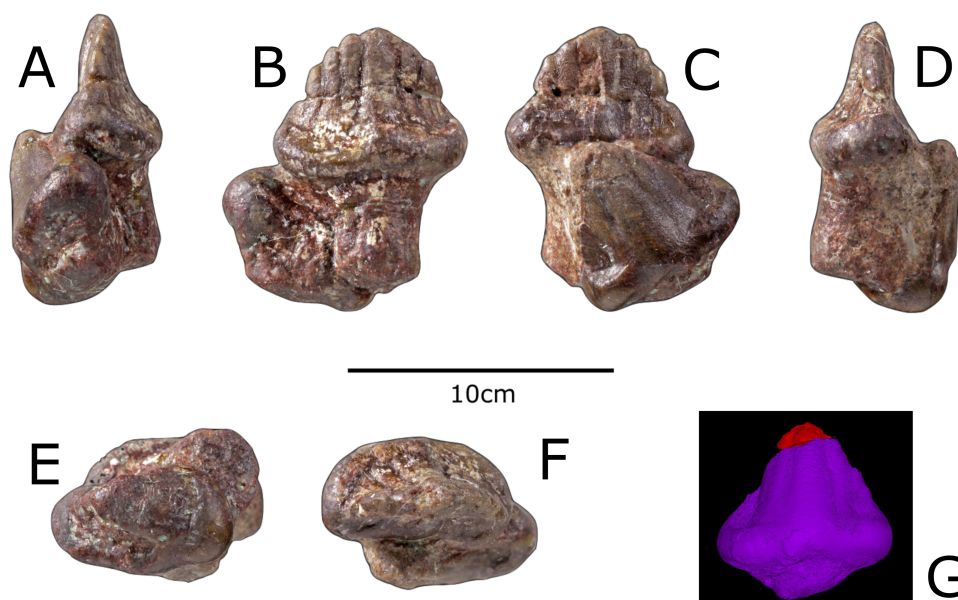


Figure 5 Previously referred teeth of *Paranthodon africanus* NHMUK R4992. (A) Posterior; (B) lingual; (C) buccal; (D) anterior; (E) ventral; (F) dorsal; (G) screenshot of digital model derived from a CT-scan of one of the referred teeth, with uncertain material above crack in red. Images copyright The Natural History Museum.

Full-size DOI: [10.7717/peerj.4529/fig-5](https://doi.org/10.7717/peerj.4529/fig-5)

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 & 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 & Barrett, 2017) and the stegosaur *Stegosaurus* (NHMUK R36730). In contrast, the prezygapophyses of other stegosaurs face dorsomedially (Maidment, Brassey & Barrett, 2015) similarly to the condition observed in the basal ornithischian *Heterodontosaurus* (Santa Luca, 1980), the ornithopod *Tenontosaurus* (Sues & Norman, 1990), the hadrosauroid *Zhanghenglong* (Xing et al., 2014) and the ankylosaurs *Ankylosaurus* (Carpenter, 2004; Kinner, Carpenter & Shaw, 2016) and *Euoplocephalus* (Arbour & Currie, 2013).

Referred teeth

There are two isolated teeth (Fig. 5) that are the previously referred specimen NHMUK R4992 (Galton & 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. Details on CT-scanning methodology can be found in the [Supplementary Material](#).

[Galton & 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 & Currie \(2016\)](#), the ankylosaurian phylogenies of [Arbour, Zanno & Gates \(2016\)](#) and [Thompson et al. \(2012\)](#) and the basal ornithischian phylogenies of [Boyd \(2015\)](#) and [Baron, Norman & Barrett \(2017\)](#) were updated to include *Paranthodon* as an Operational Taxonomic Unit (OTU) ([Fig. 6](#)). The most recent phylogeny of Stegosauria by [Raven & Maidment \(2017\)](#) was updated with new characters and character-scores based on a more thorough description of *Paranthodon* ([Supplementary Data](#)). These phylogenies were chosen as there is not currently a species-level matrix for the entirety of Thyreophora, and creating one is outside the scope of this project. All analyses were carried out in TNT ([Goloboff, Farris & 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. 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 1,000 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 1,000 replicates on a 'New Technology' search of existing trees.

[Arbour & Currie \(2016\)](#)

In all analyses of [Arbour & 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

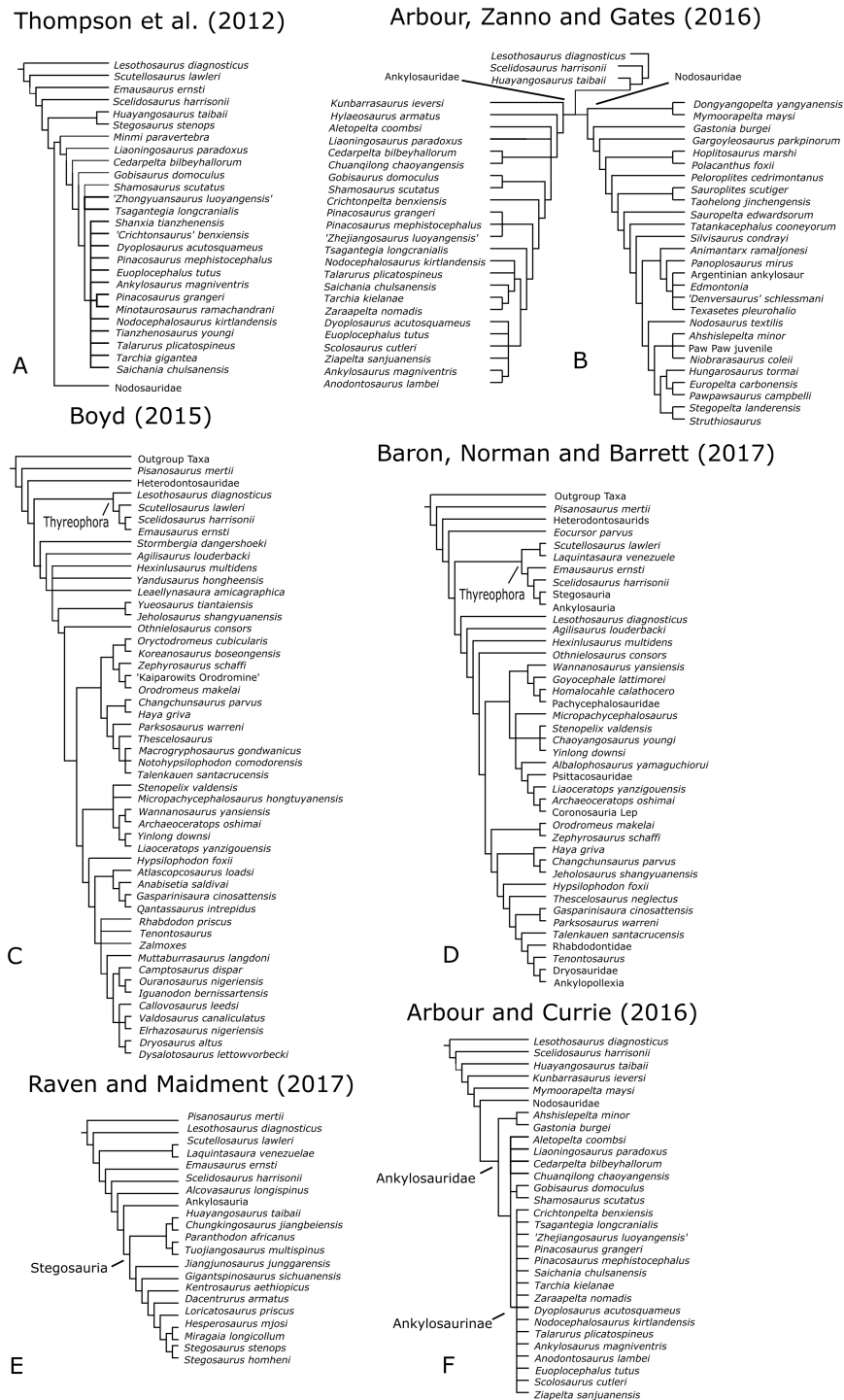


Figure 6 Simplified phylogenies from original datasets used in this study. Ankylosaurian phylogenies by (A) *Thompson et al. (2012)* and (B) *Arbour, Zanno & Gates (2016)*; (C) basal ornithischian phylogeny by *Boyd (2015)*; (D) basal ornithischian phylogeny by *Baron, Norman & Barrett (2017)*; (E) stegosaurian phylogeny by *Raven & Maidment (2017)*; (F) ankylosaurid phylogeny by *Arbour & Currie (2016)*.

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the original topology could be replicated (Analysis A1). The original analysis of *Arbour & Currie (2016)* used a ‘Traditional’ search, however, more common recent approaches used ‘New Technology’ searches in TNT (see *Ezcurra (2016)*; *Baron, Norman & Barrett (2017)*; *Raven & 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 A2).

In Analysis A3, *Paranthodon* was added as an OTU, and *Huayangosaurus* was kept as the stegosaurian exemplifier, as in the original analysis. In Analysis A4, *Paranthodon* was again included as an OTU, but *Huayangosaurus* was replaced as the stegosaurian exemplifier by the more derived *Stegosaurus*. Analysis A5 included *Paranthodon*, *Huayangosaurus* and *Stegosaurus* as Operational Taxonomic Units.

In Analysis A6, *Paranthodon* 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 3](#).

Arbour, Zanno & Gates (2016)

The *Arbour, Zanno & Gates (2016)* dataset is essentially the same as that of *Arbour & Currie (2016)* but with increased taxon sampling in Nodosauridae. In all analyses, *Lesothosaurus diagnosticus* was used as the outgroup and all characters were unordered and of equal weight. The original analytical settings were repeated here, in order to repeat the original results (Analysis B1). As with the original analysis of *Arbour & Currie (2016)*, a ‘Traditional’ search was used, with 1,000 random addition sequences holding 10 trees per replicate. The unedited dataset was then re-run with the more common ‘New Technology’ search (Analysis B2).

Paranthodon was then added as an OTU to the dataset, with *Huayangosaurus* acting as the stegosaurian exemplifier (Analysis B3). In Analysis B4, *Paranthodon* was again included as an OTU, but *Huayangosaurus* was replaced as the stegosaurian exemplifier by the more derived *Stegosaurus*. In Analysis B5, as well as *Paranthodon* and *Huayangosaurus*, *Stegosaurus* was included as an OTU. *Paranthodon* was then constrained to fall within Ankylosauria (Analysis B6).

Baron, Norman & Barrett (2017)

The updated analyses of *Baron, Norman & 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 C1 was produced with the same settings as the original *Baron, Norman & Barrett (2017)* analysis to make sure the original topology could be replicated. The original analysis used *Huayangosaurus* as the taxonomic exemplifier for Stegosauria.

Analysis C2 included *Paranthodon* as an OTU into the original analysis. In Analysis C3, *Paranthodon* was again included but *Stegosaurus* replaced *Huayangosaurus* as the stegosaurian exemplifier. Analysis C4 included *Paranthodon*, *Huayangosaurus* and *Stegosaurus* as OTUs, with the latter two acting as exemplifiers for Stegosauria.

Table 3 All analyses performed, including original dataset and changes applied to each iteration.

Analysis	Source of original	Settings
Analysis A1	<i>Arbour & Currie (2016)</i>	<i>Lesothosaurus</i> used as outgroup. All characters unordered and of equal weight. <i>Bissektipelta</i> , <i>Minmi paravertebrata</i> and <i>Tianchisaurus</i> removed. <i>Huayangosaurus</i> used as exemplifier for Stegosauria. ‘Traditional’ search performed with original settings of <i>Arbour & Currie (2016)</i> .
Analysis A2	<i>Arbour & Currie (2016)</i>	Same as Analysis A1, except a ‘New Technology’ search was performed.
Analysis A3	<i>Arbour & Currie (2016)</i>	Same as Analysis A2, except <i>Paranthodon</i> was added as an Operational Taxonomic Unit.
Analysis A4	<i>Arbour & Currie (2016)</i>	Same as Analysis A2, except <i>Paranthodon</i> and <i>Stegosaurus</i> were added as OTUs, and <i>Huayangosaurus</i> removed.
Analysis A5	<i>Arbour & Currie (2016)</i>	Same as Analysis A2, except <i>Paranthodon</i> and <i>Stegosaurus</i> were added as OTUs, in addition to <i>Huayangosaurus</i> .
Analysis A6	<i>Arbour & Currie (2016)</i>	Same as Analysis A5, except <i>Paranthodon</i> was constrained to fall within Ankylosauria.
Analysis B1	<i>Arbour, Zanno & Gates (2016)</i>	<i>Lesothosaurus</i> used as outgroup. All characters unordered and of equal weight. <i>Huayangosaurus</i> used as exemplifier for Stegosauria. ‘Traditional’ search performed with original settings of <i>Arbour, Zanno & Gates (2016)</i> .
Analysis B2	<i>Arbour, Zanno & Gates (2016)</i>	Same as Analysis B1, except a ‘New Technology’ search was performed.
Analysis B3	<i>Arbour, Zanno & Gates (2016)</i>	Same as Analysis B2, except <i>Paranthodon</i> was added as an Operational Taxonomic Unit.
Analysis B4	<i>Arbour, Zanno & Gates (2016)</i>	Same as Analysis B2, except <i>Paranthodon</i> and <i>Stegosaurus</i> were added as OTUs, and <i>Huayangosaurus</i> removed.
Analysis B5	<i>Arbour, Zanno & Gates (2016)</i>	Same as Analysis B2, except <i>Paranthodon</i> and <i>Stegosaurus</i> were added as OTUs, in addition to <i>Huayangosaurus</i> .
Analysis B6	<i>Arbour, Zanno & Gates (2016)</i>	Same as Analysis B5, except <i>Paranthodon</i> was constrained to fall within Ankylosauria.
Analysis C1	<i>Baron, Norman & Barrett (2017)</i>	<i>Euparkeria</i> used as outgroup. Characters 112, 135, 137, 138, 174 ordered. <i>Anabisetia</i> , <i>Echinodon</i> , <i>Koreanosaurus</i> , <i>Yanosaurus</i> and <i>Yueosaurus</i> removed. ‘New Technology’ search performed with original settings.
Analysis C2	<i>Baron, Norman & Barrett (2017)</i>	Same as Analysis C1, except <i>Paranthodon</i> was added as an OTU.
Analysis C3	<i>Baron, Norman & Barrett (2017)</i>	Same as Analysis C2, except <i>Stegosaurus</i> replaced <i>Huayangosaurus</i> as the exemplifier for Stegosauria.
Analysis C4	<i>Baron, Norman & Barrett (2017)</i>	Same as Analysis C2, except <i>Stegosaurus</i> was added as an OTU, as well as <i>Huayangosaurus</i> .
Analysis C5	<i>Baron, Norman & Barrett (2017)</i>	Same as Analysis C4, except <i>Isaberrysaura</i> was added as an OTU.
Analysis C6	<i>Baron, Norman & Barrett (2017)</i>	Same as Analysis C4, except <i>Paranthodon</i> was constrained to fall within Ornithopoda.
Analysis D1	<i>Boyd (2015)</i>	<i>Marasuchus</i> used as outgroup. All characters unordered. ‘New Technology’ search performed with original settings of <i>Boyd (2015)</i> .

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Table 3 (continued)

Analysis	Source of original	Settings
Analysis D2	<i>Boyd (2015)</i>	Same as Analysis D1, except <i>Paranthodon</i> was added as an OTU.
Analysis D3	<i>Boyd (2015)</i>	Same as Analysis D2, except <i>Huayangosaurus</i> was added as an OTU.
Analysis D4	<i>Boyd (2015)</i>	Same as Analysis D2, except <i>Stegosaurus</i> was added as an OTU.
Analysis D5	<i>Boyd (2015)</i>	Same as Analysis D2, except <i>Huayangosaurus</i> and <i>Stegosaurus</i> were added as OTUs.
Analysis D6	<i>Boyd (2015)</i>	Same as Analysis D5, except <i>Isaberrysaura</i> added as an OTU.
Analysis D7	<i>Boyd (2015)</i>	Same as Analysis D5, except <i>Paranthodon</i> was constrained to fall within Ornithopoda.
Analysis D8	<i>Boyd (2015)</i>	Same as Analysis D5, except <i>Paranthodon</i> was constrained to fall within Thyreophora.
Analysis E1	<i>Raven & Maidment (2017)</i>	<i>Pisanosaurus</i> 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 <i>Raven & Maidment (2017)</i> .
Analysis E2	<i>Raven & Maidment (2017)</i>	Same as Analysis E1, except <i>Isaberrysaura</i> added as an OTU
Analysis E3	<i>Raven & Maidment (2017)</i>	Same as Analysis E1, except <i>Paranthodon</i> was constrained to fall within Ankylosauria.
Analysis F1	<i>Thompson et al. (2012)</i>	<i>Lesothosaurus</i> used as outgroup. <i>Bissektipelta</i> 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 <i>Thompson et al. (2012)</i> .
Analysis F2	<i>Thompson et al. (2012)</i>	Same as Analysis F1, except that a 'New Technology' search was performed and <i>Paranthodon</i> was included as an OTU.
Analysis F3	<i>Thompson et al. (2012)</i>	Same as Analysis F2, except that <i>Paranthodon</i> was constrained to fall within Stegosauria.

In Analysis C5, 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 C6), using Analysis C4 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 D1 was performed, with no additional taxa included, to make sure the original analysis could be replicated.

In Analysis D2 *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 D3). *Huayangosaurus* was then replaced as the exemplifier for Stegosauria by the derived stegosaur *Stegosaurus*, with *Paranthodon* also included as an OTU, in Analysis D4.

In Analysis D5, 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 D6), along with *Paranthodon*, *Huayangosaurus* and *Stegosaurus*.

Constraint trees were again written to test the lability of *Paranthodon*, using Analysis D5 as a starting point. Analysis D7 constrained *Paranthodon* to be within Ornithopoda, and Analysis D8 constrained *Paranthodon* to be within Thyreophora.

Raven & Maidment (2017)

In Analysis E1, the character list of [Raven & 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 E2, *Isaberrysaura mollensis* was also added as an OTU. The full character list and justifications to changes to the original character list can be found in the [Supplementary Material](#).

A constraint tree was then produced with *Paranthodon* being enforced to fall within Ankylosauria (Analysis E3).

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 F1 was performed to ensure the original results could be replicated.

Paranthodon was included as an OTU in Analysis F2, 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 F3).

RESULTS

Arbour & Currie (2016)

The original strict consensus tree of [Arbour & Currie \(2016\)](#); Fig. 11) was replicated in Analysis A1, using the same settings as the original analysis, although this found a tree length of 421 rather than the reported 420; a full list of the results of all analyses can be found in [Table 4](#). Running the analysis of [Arbour & Currie \(2016\)](#) with a ‘New Technology’ search reduced the number of most parsimonious trees (MPTs) from 3,030 in the original

Table 4 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.

Analysis	Source of original	Stegosaurian exemplifier	Placement of <i>Paranthodon</i>	Other results
Analysis A1	<i>Arbour & Currie (2016)</i>	<i>Huayangosaurus</i>	n/a	Same as <i>Arbour & Currie (2016)</i>
Analysis A2	<i>Arbour & Currie (2016)</i>	<i>Huayangosaurus</i>	n/a	Higher resolution in strict consensus than <i>Arbour & Currie (2016)</i>
Analysis A3	<i>Arbour & Currie (2016)</i>	<i>Huayangosaurus</i>	Ankylosaur	9 MPTs
Analysis A4	<i>Arbour & Currie (2016)</i>	<i>Stegosaurus</i>	Base of Thyreophora	8 MPTs and increased resolution
Analysis A5	<i>Arbour & Currie (2016)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Stegosaur	9 MPTs and increased resolution
Analysis A6	<i>Arbour & Currie (2016)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ankylosaur (constrained)	9 MPTs and reduced resolution.
Analysis B1	<i>Arbour, Zanno & Gates (2016)</i>	<i>Huayangosaurus</i>	n/a	Same as <i>Arbour, Zanno & Gates (2016)</i>
Analysis B2	<i>Arbour, Zanno & Gates (2016)</i>	<i>Huayangosaurus</i>	n/a	Higher resolution in strict consensus than <i>Arbour, Zanno & Gates (2016)</i>
Analysis B3	<i>Arbour, Zanno & Gates (2016)</i>	<i>Huayangosaurus</i>	Nodosaur	3 MPTs and increased resolution in Nodosauridae
Analysis B4	<i>Arbour, Zanno & Gates (2016)</i>	<i>Stegosaurus</i>	Base of Thyreophora	5 MPTs and increased resolution in Ankylosauridae
Analysis B5	<i>Arbour, Zanno & Gates (2016)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Stegosaur	2 MPTs and similar resolution
Analysis B6	<i>Arbour, Zanno & Gates (2016)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ankylosaur (constrained)	3 MPTs and similar resolution
Analysis C1	<i>Baron, Norman & Barrett (2017)</i>	<i>Huayangosaurus</i>	n/a	Same as <i>Baron, Norman & Barrett (2017)</i>
Analysis C2	<i>Baron, Norman & Barrett (2017)</i>	<i>Huayangosaurus</i>	Ankylosaur	Little resolution
Analysis C3	<i>Baron, Norman & Barrett (2017)</i>	<i>Stegosaurus</i>	Stegosaur	Higher resolution
Analysis C4	<i>Baron, Norman & Barrett (2017)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Stegosaur	Very high resolution
Analysis C5	<i>Baron, Norman & Barrett (2017)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Stegosaur	Little resolution and <i>Isaberrysaura</i> = ornithopod
Analysis C6	<i>Baron, Norman & Barrett (2017)</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ornithopod (constrained)	Severely reduced resolution in Ornithopoda
Analysis D1	<i>Boyd (2015)</i>	n/a— <i>Scelidosaurus</i> most derived thyreophoran	n/a	Same as <i>Boyd (2015)</i>
Analysis D2	<i>Boyd (2015)</i>	n/a— <i>Scelidosaurus</i> most derived thyreophoran	Base of Ornithischia	Thyreophora basal to Heterodontosauridae, Marginocephalia basal to Ornithopoda
Analysis D3	<i>Boyd (2015)</i>	<i>Huayangosaurus</i>	Ornithopod, sister-taxon to <i>Huayangosaurus</i>	<i>Huayangosaurus</i> = ornithopod and reduced resolution in Ornithopoda

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Table 4 (continued)

Analysis	Source of original	Stegosaurian exemplifier	Placement of <i>Paranthodon</i>	Other results
Analysis D4	Boyd (2015)	<i>Stegosaurus</i>	Ornithopod, sister-taxon to <i>Stegosaurus</i>	<i>Stegosaurus</i> = ornithopod and increased resolution
Analysis D5	Boyd (2015)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ornithopod, sister-taxon to <i>Huayangosaurus</i> and <i>Stegosaurus</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i> = ornithopod and little resolution
Analysis D6	Boyd (2015)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ornithopod, sister-taxon to <i>Huayangosaurus</i> and <i>Stegosaurus</i>	<i>Huayangosaurus</i> and <i>Stegosaurus</i> = ornithopod and little resolution. <i>Isaberrysaura</i> = ornithopod
Analysis D7	Boyd (2015)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ornithopod (constrained)	<i>Huayangosaurus</i> and <i>Stegosaurus</i> outside of Ornithischia and increased resolution in Ornithopoda.
Analysis D8	Boyd (2015)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Thyreophoran	Ornithopoda resolution increased, Thyreophora resolution decrease
Analysis E1	Raven & Maidment (2017)	n/a	Stegosaur	Similar to Raven & Maidment (2017)
Analysis E2	Raven & Maidment (2017)	n/a	Eurypodan	<i>Isaberrysaura</i> = basal stegosaur. Reduced resolution in Eurypoda
Analysis E3	Raven & Maidment (2017)	n/a	Ankylosaur (constrained)	Reduced resolution in Ankylosauria
Analysis F1	Thompson et al. (2012)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	n/a	Same as Thompson et al. (2012)
Analysis F2	Thompson et al. (2012)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Ankylosaur	Higher resolution in strict consensus than Thompson et al. (2012)
Analysis F3	Thompson et al. (2012)	<i>Huayangosaurus</i> and <i>Stegosaurus</i>	Stegosaur (constrained)	Resolution of Nodosauridae increased

analysis to 11 (Analysis A2), 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 & 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 & Currie \(2016\)](#), with *Dyoplosaurus* found outside of Ankylosaurini. The resolution was as high as that of the 50% majority rule tree of [Arbour & Currie \(2016\)](#).

When *Paranthodon* was added as an OTU and *Huayangosaurus* was used as the only stegosaurian exemplifier, as in the original analysis, (Analysis A3), 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 A4), eight MPTs were recovered with a length of 425. The strict consensus tree had a similar topology to Analysis A2, however

Paranthodon was found in a polytomy with *Stegosaurus* and *Kunbarrasaurus* near the base of Thyreophora.

In Analysis A5, 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 *Paranthodon* and *Stegosaurus*. *Kunbarrasaurus* was found at the base of Ankylosauria again.

Analysis A6 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 A5. *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 were non-significant.

Arbour, Zanno & Gates (2016)

The original settings of *Arbour, Zanno & Gates (2016)* were replicated in Analysis B1 and the same results were found. Running the analysis with a 'New Technology' search (Analysis B2) produced three MPTs of length 551. 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 & Nixon, 2008*). The strict consensus had higher resolution than that of the original analysis, approaching that of the 50% majority rule tree, particularly within Ankylosauridae.

When *Paranthodon* was added as an OTU and *Huayangosaurus* was used as the only stegosaurian exemplifier, as in the original analysis (Analysis B3), three MPTs were found, of length 555. *Paranthodon* was recovered as a basal nodosaur and there was reduced resolution in Ankylosauridae relative to Analysis B2, but increased resolution within Nodosauridae, including a monophyletic *Struthiosaurus*.

In Analysis B4, the more derived stegosaur *Stegosaurus* was used as the stegosaurian exemplifier and *Huayangosaurus* was excluded as an OTU. This resulted in five MPTs of length 554. The strict consensus had a similar resolution within Nodosauridae to Analysis B3 but there was increased resolution in Ankylosauridae. *Paranthodon* was found as a sister-taxon to *Stegosaurus* as the base of Thyreophora.

When *Paranthodon* was added as an OTU and both *Huayangosaurus* and *Stegosaurus* were used as the stegosaurian exemplifiers (Analysis B5), two MPTs of length 557 were found. Stegosauria was monophyletic, with *Huayangosaurus* basal to a sister-taxon relationship between *Paranthodon* and *Stegosaurus*. There was similar high resolution in Ankylosauridae relative to Analysis B4 but there was reduced resolution within Nodosauridae.

Analysis B6 constrained *Paranthodon* to be an ankylosaur. This produced three MPTs, of length 558, with similar resolution in both Ankylosauridae and Nodosauridae relative to Analysis B5. *Paranthodon* was found as a sister-taxon to *Shamosaurus* and *Gobisaurus* within Ankylosauridae. The constraint tree was analysed using the Templeton Test, which

indicated the length differences between the unconstrained tree and the constrained tree were non-significant.

Baron, Norman & Barrett (2017)

The original settings of the basal ornithischian analysis of *Baron, Norman & Barrett (2017)* were replicated and the same topology was found (Analysis C1).

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 C2). 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 C3). This produced 96 most parsimonious trees of length 583 and the strict consensus provided much higher resolution throughout the tree than in Analysis C2. *Paranthodon* was found as sister-taxon to *Stegosaurus*, with Ankylosauria a separate lineage within Thyreophora.

In Analysis C4, 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 C5 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 C4. *Isaberrysaura* was found in a large polytomy within Ornithopoda.

Analysis C6 constrained *Paranthodon* to Ornithopoda. This resulted in 10 most parsimonious trees of length 595. Relative to the unconstrained Analysis C4, 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 D1).

The dataset was then updated to include *Paranthodon* as an OTU (Analysis D2), 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 & 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 Ornithopoda.

In Analysis D3, *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 D4). This produced three most parsimonious trees, of length 928. The strict consensus tree had increased resolution relative to Analysis D3, and *Paranthodon* and *Stegosaurus* were found as sister-taxa within Ornithopoda, again distant from Thyreophora.

In Analysis D5, 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 D6. 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 D7 constrained *Paranthodon* within Ornithopoda. This produced six most parsimonious trees of length 964, and increased resolution in Ornithopoda relative to the unconstrained Analysis D5. 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 D8 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 & 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 & Maidment (2017)

The most recent phylogeny of Stegosauria by [Raven & 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 E1). *Isaberrysaura*, the Argentinian dinosaur found as a neornithischian by [Salgado et al. \(2017\)](#), was then found in a sister-taxon relationship with *Gigantspinosaurs* (Analysis E2). However, the strict consensus of the four most parsimonious trees of length 285.38 had a lack of resolution at the base of

Euryopoda. Analysis E3 was produced to constrain *Paranthodon* to within Ankylosauria, using Analysis E1 as a starting point. This produced one most parsimonious tree of length 280.43, 0.78 steps longer than Analysis E1. The Templeton Test showed that there were no significant difference 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 F1).

The dataset was then updated to include *Paranthodon* as an OTU (Analysis F2), 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 & Nixon, 2008*). The results vastly improved on the 4,248 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 *Dyoplosaurus 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 F3 constrained *Paranthodon* to Stegosauria. This produced three most parsimonious trees of length 531, two steps longer than the unconstrained Analysis F1. 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 & Currie (2016)* and *Huayangosaurus* used as the stegosaurian exemplifier (Analysis A3), *Paranthodon* was found as an ankylosaur. However, when the exemplifier was changed to *Stegosaurus* (Analysis A4), *Paranthodon* was found at the base of Thyreophora. When both *Huayangosaurus* and *Stegosaurus* were included in the analysis, Stegosauria became monophyletic with *Huayangosaurus* basal to *Paranthodon* + *Stegosaurus* (Analysis A5).

Similarly, when *Huayangosaurus* was used as the stegosaurian exemplifier and *Paranthodon* was added as an OTU into the dataset of *Arbour, Zanno & Gates (2016)*, *Paranthodon* was found as a basal nodosaur (Analysis B3). However, *Paranthodon* was found at the base of Thyreophora when the stegosaurian exemplifier was changed to *Stegosaurus* (Analysis B4). *Paranthodon* was then found in a monophyletic Stegosauria

when both *Huayangosaurus* and *Stegosaurus* were included in the analysis (Analysis B5). The inclusion of *Paranthodon* into the [Baron, Norman & Barrett \(2017\)](#) dataset reduced the resolution of the tree, but a 50% majority rule tree found *Paranthodon* as an ankylosaur (Analysis C2). When *Stegosaurus* replaced *Huayangosaurus* as the stegosaurian exemplifier (Analysis C3), the resolution in the tree increased and *Paranthodon* was sister-taxon to *Stegosaurus*. When both *Huayangosaurus* and *Stegosaurus* were included in the analysis (Analysis C4), there was again increased resolution and a monophyletic Stegosauria, including *Paranthodon*.

The inclusion of *Paranthodon* to the [Boyd \(2015\)](#) dataset (Analysis D2) 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 (Analysis D3), *Paranthodon* and *Huayangosaurus* were sister-taxa within Ornithopoda. Replacing *Huayangosaurus* as the stegosaurian exemplifier with *Stegosaurus* (Analysis D4) 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 ([Fig. 7](#)). 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 & Russell, 1998](#)), even the use of multiple exemplifiers. While the use of exemplifiers can produce accurate tree topologies that are subsequently and independently found in later analyses (for example, [Butler, Upchurch & 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 & 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](#))

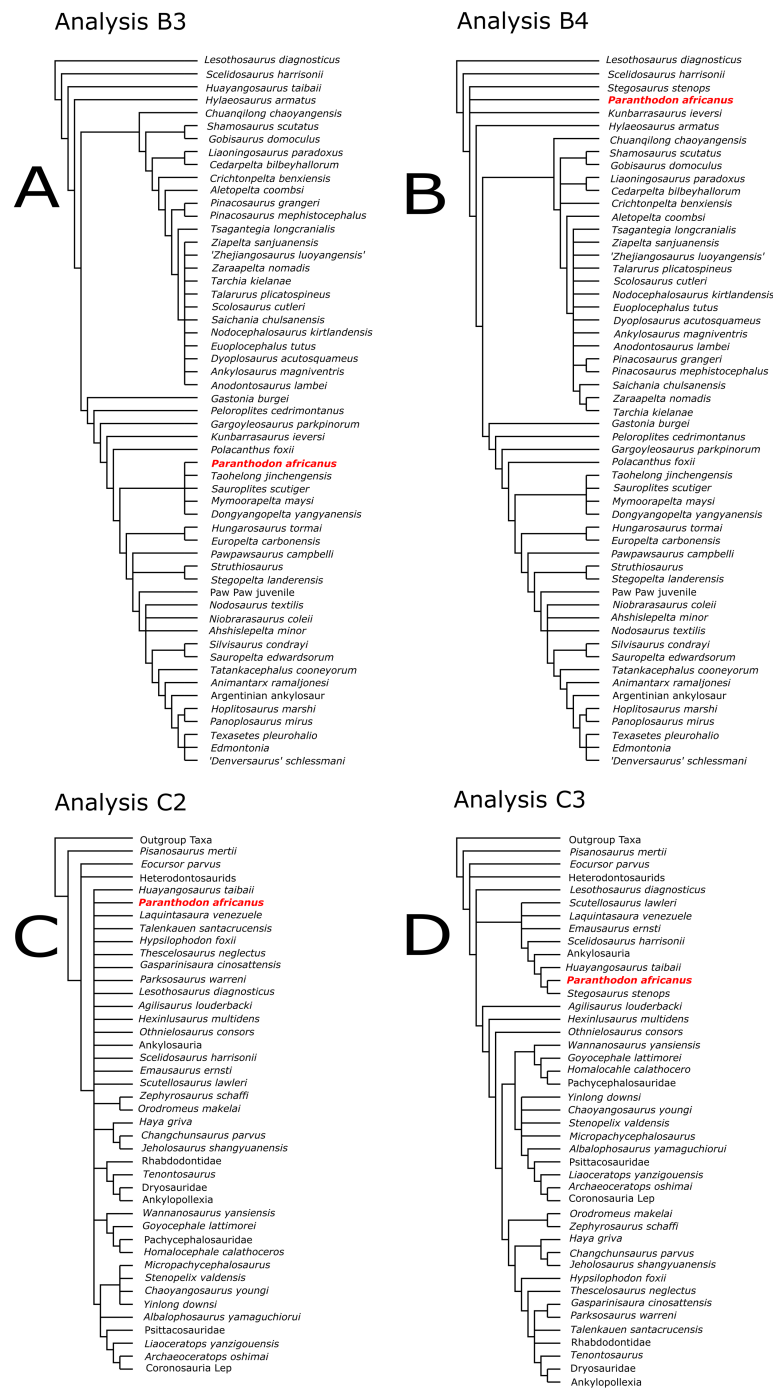


Figure 7 Analyses of [Arbour, Zanno & Gates \(2016\)](#) (A, B) and [Baron, Norman & Barrett \(2017\)](#) (C, D) showing labile positioning of *Paranthodon* depending on stegosaurian exemplifier used. Analysis B3 and C2 use *Huayangosaurus* as stegosaurian exemplifier for analyses of [Arbour, Zanno & Gates \(2016\)](#) and [Baron, Norman & Barrett \(2017\)](#), respectively. Analysis B4 of [Arbour, Zanno & Gates \(2016\)](#) uses *Stegosaurus* as stegosaurian exemplifier, and Analysis C3 of [Baron, Norman & Barrett \(2017\)](#) uses both *Huayangosaurus* and *Stegosaurus*. *Paranthodon* is found as a basal nodosaurid in B3, in a large polytomy in C2, as a basal thyrophoran in B4 and in a monophyletic Stegosauria in C3. Resolution of analyses increases when derived taxonomic exemplifiers are used.

Full-size DOI: [10.7717/peerj.4529/fig-7](https://doi.org/10.7717/peerj.4529/fig-7)

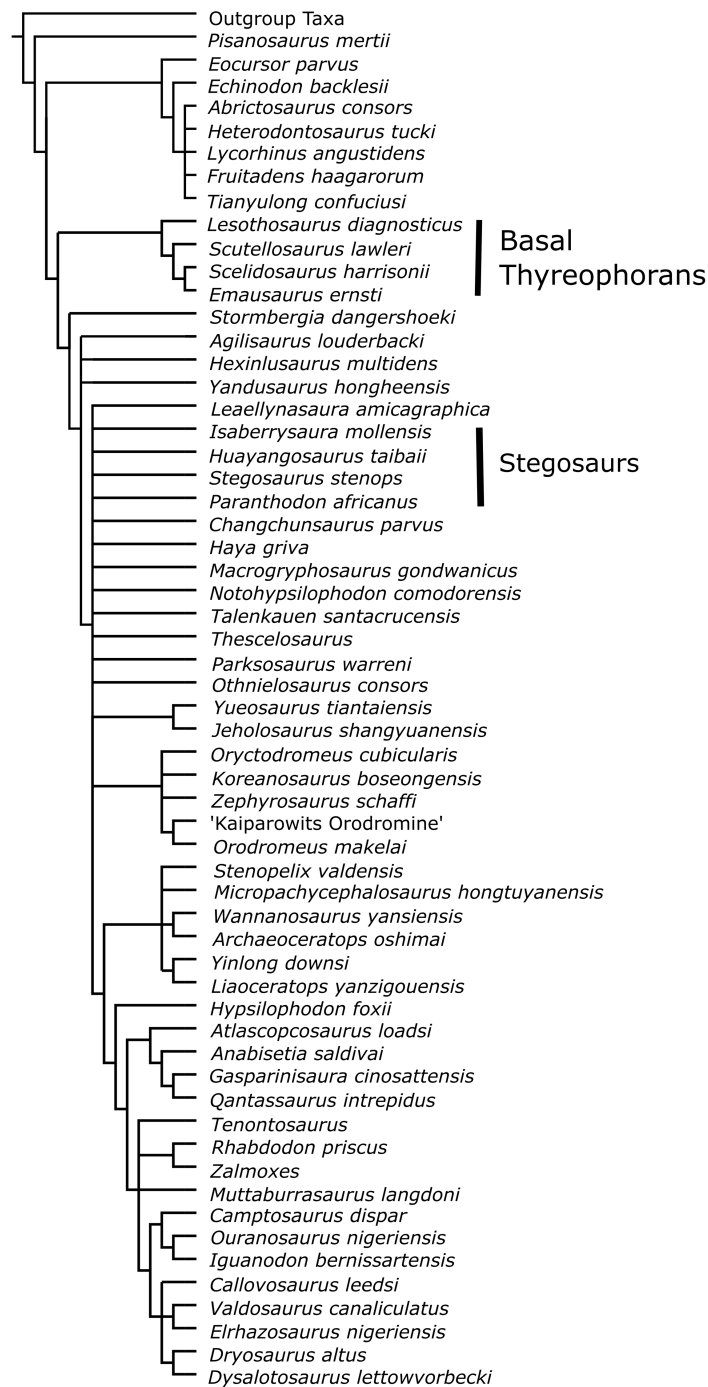


Figure 8 Strict consensus tree from Analysis D6; inclusion of *Paranthodon*, *Huayangosaurus*, *Stegosaurus* and *Isaberrysaura* as OTUs into the [Boyd \(2015\)](#) dataset. Only two synapomorphies characterise the group of basal thyreophorans; a ridge on the lateral surface of surangular, which is not 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. \(2017\)](#).

Full-size DOI: [10.7717/peerj.4529/fig-8](https://doi.org/10.7717/peerj.4529/fig-8)

was included as an OTU in Analysis D6, as well as *Huayangosaurus*, *Stegosaurus* and *Paranthodon* (Fig. 8). 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 D6 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 Euryopoda, Euryopoda + *Alcovasaurus*, or Stegosauria in the *Raven & Maidment (2017)* dataset that are found in the *Boyd (2015)* dataset, equating to 2.7% of the total number of characters. 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 euryopodans. 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 & 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 & Upchurch (2004)*, and this condition is present in *Paranthodon*. The discovery of a well-preserved specimen of *Stegosaurus* (*Maidment, Brassey & 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 *Gigantospinosaurus*.

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 A6 of [Arbour & Currie \(2016\)](#) reduced the resolution in Ankylosauridae and increased the number of steps in the tree. Similarly, constraining *Paranthodon* to within Ankylosauria in Analysis B6 of [Arbour, Zanno & Gates \(2016\)](#) increased the number of steps in the tree and the number of most parsimonious trees found. In Analysis C6, 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 D7 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 D8) 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 & Barrett \(2017\)](#), moved into Thyreophora. Constraining *Paranthodon* to be an ankylosaur in the updated dataset of [Raven & Maidment \(2017\)](#) (Analysis E3) increased the tree length of the one most parsimonious tree. In Analysis F3, 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 results presented here suggest that *Paranthodon* is most robustly recovered as a stegosaur and this 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 & 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 & Ayyasami, 2017](#)), and Bolivia ([Apesteguía & 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 & 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 & Currie \(2016\)](#) was re-analysed herein with a ‘New Technology’ search in TNT (Analysis A2). This has improved the resolution of the analysis, especially the relationships of derived ankylosaurids, and reduced the number of MPTs from 3,030 to 11, relative to the original analysis by [Arbour & Currie \(2016\)](#). The resolution of the strict consensus tree in this study is similar to that of the 50% majority rule tree in [Arbour & Currie \(2016\)](#), but *Crichtonpelta* has moved outside of Ankylosaurinae, meaning it is not the oldest known ankylosaurine. A similar result occurred when running the dataset of [Arbour, Zanno & Gates \(2016\)](#) with a ‘New Technology’ search (Analysis B2); the resolution of Ankylosauridae in the strict consensus improved such that it approached that of the 50% majority rule tree in the original analysis. Additionally, running the ankylosaurian dataset of [Thompson et al. \(2012\)](#) with a ‘New Technology’ search (Analysis F2) 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 & 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.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Thomas J. Raven conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Susannah C.R. Maidment conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

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