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

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 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 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, 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 and 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 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 Tujiangosaurus 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 (Fig. 1), and two referred teeth (Maidment et al., 2008). Additionally, there is a partial vertebra that was 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

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 of Stegasauria located on the teeth, they are referred to as indeterminate thyreophoran herein.

**Diagnosis:** The only identifiable autapomorphy of this genus within Stegasauria 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 Stegasauria 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 Stegasauria, 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 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 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 2). 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); *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 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 *Anodontosaurus* (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 (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 and 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 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 *Anodontosaurus* (NHMUK R4947), *Gastonia* (Kinneer, Carpenter and Shaw, 2016), *Edmontonia* (NHMUK R36851), *Pawpawsaurus* (Kinneer, Carpenter and Shaw, 2016), *Panoplosaurus* (Kirkland et al., 2013) and *Silvisaurus* (NHMUK R1107). In *Stegosaurus* (NHMUK R36730) and *Huayangosaurus* (Sereno and 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* (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), *Anodontosaurus* (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. 3). 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 Tuojangosaurus 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 Tuojangosaurus, 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), *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 and 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 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 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* (Carpenter, 2004; 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 R36730). In contrast, the prezygapophyses of other stegosaurs face dorsomedially (Maidment, Brassey and Barrett, 2015) similarly to the condition observed in the basal
ornithischian *Heterodontosaurus* (Santa Luca, 1980), the ornithopod *Tenontosaurus* (Sues and Norman, 1990), the hadrosauroid *Zhanghenglong* (Xing et al., 2014) and the ankylosaurs *Ankylosaurus* (Carpenter, 2004; Kinneer, Carpenter and Shaw, 2016) and *Euoplocephalus* (Arbour and Currie, 2013).

**Referred Teeth**

There are two isolated teeth (Fig. 5) that are the previously 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. Details on CT-scanning methodology can be found in the Online Supplementary Material.

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 phylogenies of Arbour, Gates and Zanno (2016) and 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. 6). 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* (Online 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 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.

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 A1). 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 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, Gates and Zanno 2016**

The Arbour, Gates and Zanno (2016) dataset is essentially the same as that of Arbour and 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 and Currie (2016), a ‘Traditional’ search was used, with 1000 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 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 C1 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 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.

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 and Maidment, 2017**

In Analysis E1, 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 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 Online 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 and Currie, 2016

The original strict consensus tree of Arbour and Currie (2016; figure 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 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 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 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 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 *Parathodon* 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 and Gates 2016

The original settings of Arbour, Zanno and 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 and 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 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 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 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 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 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 E1). *Isaberrysaura*, the Argentinian dinosaur found as a neornithischian by Salgado et al. (2017), was then found in a sister-taxon relationship with *Gigantospinosaurus* (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 Eurypoda. 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 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 ramachandranii*. *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 and 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 and 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 and 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 and 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 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 supermatrices (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 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 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. 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 euryodans. 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 synaplesiomorphies 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 and 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 and 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 dangerochoeki*, 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 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 stegosaurs 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.,
(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 (Apesteguía 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 A2). 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. A similar result occurred when running the dataset of Arbour, Zanno and 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 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.

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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).

*Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*
Figure 2

Premaxilla and maxilla of *Paranthodon africanus* NHMUKR47338

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.
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.
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.
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.
Figure 6

Simplified phylogenies from original datasets used in this study.

Ankylosaurian phylogenies by (A) Thompson et al. (2012) and (B) Arbour, Zanno and Gates (2016); (C) basal ornithischian phylogeny by Boyd (2015); (D) basal ornithischian phylogeny by Baron, Norman and Barrett (2017); (E) stegosaurian phylogeny by Raven and Maidment (2017); (F) ankylosaurid phylogeny by Arbour and Currie (2016)
Figure 7

Analyses of Arbour, Zanno and Gates (2016) (A, B) and Baron, Norman and 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 and Gates (2016) and Baron, Norman and Barrett (2017), respectively. Analysis B4 of Arbour, Zanno and Gates (2016) uses *Stegosaurus* as stegosaurian exemplifier, and Analysis C3 of Baron, Norman and 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 thyreophoran in B4 and in a monophyletic Stegosauria in C3. Resolution of analyses increases when derived taxonomic exemplifiers are used.

*Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*
Figure 8

Strict consensus tree from Analysis D6; inclusion of *Paranthodon*, *Huayangosaurus*, *Stegosaurus* and *Isaberrysaura* as OTUs into the Boyd (2015) dataset.

Red bar indicates group of basal thyreophorans, blue bar indicates stegosaurs. 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.*
Table 1 (on next page)

Measurements of the elements of *Paranthodon africanus* NHMUK R47338 and previously referred specimen NHMUK R4992
| Measurement                                      | Specimen   |
|-------------------------------------------------|------------|
| Nasal, anteroposterior length                  | NHMUK R47338 | NHMUK R4992 |
| Nasal, width                                   | 134mm      | 63mm        |
| Nasal, dorsoventral height                     | 33mm       |             |
| Premaxilla and maxilla, anteroposterior length | 178mm      |             |
| Premaxilla and maxilla, width                  | 67mm       |             |
| Premaxilla and maxilla, dorsoventral height    | 82mm       |             |
| Mean tooth crown height                        | 3.04mm     | 4.25mm      |
| Mean tooth crown anteroposterior length        | 6.20mm     | 5.25mm      |
| Mean tooth cingula height                      | 2.92mm     | 1.75mm      |
| Mean tooth cingula anteroposterior length      | 7.52mm     | 7.50mm      |
| Mean tooth crown width                         | 1.89mm     | 1.25mm      |
| Mean tooth cingula width                       | 5.05mm     | 4.25mm      |
Table 2 (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 3 (on next page)

All analyses performed, including original dataset and changes applied to each iteration.
| Analysis | Source of Original | Settings |
|----------|--------------------|----------|
| Analysis A1 | Arbour and Currie (2016) | Lesothosaurus used as outgroup. All characters unordered and of equal weight. Bissektipelta, Minmi paravertebræ and Tianchisaurus removed. Huayangosaurus used as exemplifier for Stegosauria. 'Traditional' search performed with original settings of Arbour and Currie (2016). |
| Analysis A2 | Arbour and Currie (2016) | Same as Analysis A1, except a 'New Technology' search was performed. |
| Analysis A3 | Arbour and Currie (2016) | Same as Analysis A2, except Paranthodon was added as an Operational Taxonomic Unit. |
| Analysis A4 | Arbour and Currie (2016) | Same as Analysis A2, except Paranthodon and Stegosaurus were added as OTUs, and Huayangosaurus removed. |
| Analysis A5 | Arbour and Currie (2016) | Same as Analysis A2, except Paranthodon and Stegosaurus were added as OTUs, in addition to Huayangosaurus. |
| Analysis A6 | Arbour and Currie (2016) | Same as Analysis A5, except Paranthodon was constrained to fall within Ankylosauria. |
| Analysis B1 | Arbour, Zanno and Gates (2016) | Lesothosaurus used as outgroup. All characters unordered and of equal weight. Huayangosaurus used as exemplifier for Stegosauria. 'Traditional' search performed with original settings of Arbour, Zanno and Gates (2016). |
| Analysis B2 | Arbour, Zanno and Gates (2016) | Same as Analysis B1, except a 'New Technology' search was performed. |
| Analysis B3 | Arbour, Zanno and Gates (2016) | Same as Analysis B2, except Paranthodon was added as an Operational Taxonomic Unit. |
| Analysis B4 | Arbour, Zanno and Gates (2016) | Same as Analysis B2, except Paranthodon and Stegosaurus were added as OTUs, and Huayangosaurus removed. |
| Analysis B5 | Arbour, Zanno and Gates (2016) | Same as Analysis B2, except Paranthodon and Stegosaurus were added as OTUs, in addition to Huayangosaurus. |
| Analysis B6 | Arbour, Zanno and Gates (2016) | Same as Analysis B5, except Paranthodon was constrained to fall within Ankylosauria. |
| Analysis C1 | Baron, Norman | Euparkeria used as outgroup. Characters 112, 135, 137, 138, 174 ordered. Anabisetia, Echinodon, Koreanosaurus, Yandosaurus and |
| Analysis  | Authors          | Details                                                                                                                                 |
|----------|------------------|----------------------------------------------------------------------------------------------------------------------------------------|
| C2       | Baron, Norman and Barrett (2017) | Same as Analysis C1, except *Paranthodon* was added as an OTU.                                                                         |
| C3       | Baron, Norman and Barrett (2017) | Same as Analysis C2, except *Stegosaurus* replaced *Huayangosaurus* as the exemplifier for Stegosauria.                                 |
| C4       | Baron, Norman and Barrett (2017) | Same as Analysis C2, except *Stegosaurus* was added as an OTU, as well as *Huayangosaurus*.                                           |
| C5       | Baron, Norman and Barrett (2017) | Same as Analysis C4, except *Isaberrysaura* was added as an OTU.                                                                       |
| C6       | Baron, Norman and Barrett (2017) | Same as Analysis C4, except *Paranthodon* was constrained to fall within Ornithopoda.                                                   |
| D1       | Boyd (2015)      | *Marasuchus* used as outgroup. All characters unordered. 'New Technology' search performed with original settings of Boyd (2015).    |
| D2       | Boyd (2015)      | Same as Analysis D1, except *Paranthodon* was added as an OTU.                                                                        |
| D3       | Boyd (2015)      | Same as Analysis D2, except *Huayangosaurus* was added as an OTU.                                                                      |
| D4       | Boyd (2015)      | Same as Analysis D2, except *Stegosaurus* was added as an OTU.                                                                        |
| D5       | Boyd (2015)      | Same as Analysis D2, except *Huayangosaurus* and *Stegosaurus* were added as OTUs.                                                    |
| D6       | Boyd (2015)      | Same as Analysis D5, except *Isaberrysaura* added as an OTU.                                                                          |
| D7       | Boyd (2015)      | Same as Analysis D5, except *Paranthodon* was constrained to fall within Ornithopoda.                                                  |
| D8       | Boyd (2015)      | Same as Analysis D5, except *Paranthodon* was constrained to fall within Thyreophora.                                                   |
| E1       | 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). |
| E2       | Raven and Maidment (2017) | Same as Analysis E1, except *Isaberrysaura* added as an OTU                                                                         |
| E3       | Raven and Maidment | Same as Analysis E1, except *Paranthodon* was constrained to fall within Ankylosauria.                                                 |
| Analysis | Thompson et al. (2012) | Description |
|----------|------------------------|-------------|
| F1       | Lesothosaurus used as outgroup. Bissektilpelta 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). |
| F2       | Same as Analysis F1, except that a 'New Technology' search was performed and Paranthodon was included as an OTU. |
| F3       | Same as Analysis F2, except that Paranthodon was constrained to fall within Stegosauria. |
Table 4 (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.
| Analysis | Source of Original | Stegosaurian Exemplifier | Placement of *Paranthodon* | Other results |
|----------|-------------------|--------------------------|-----------------------------|--------------|
| Analysis A1 | Arbour and Currie (2016) | *Huayangosaurus* | n/a | Same as Arbour and Currie (2016) |
| Analysis A2 | Arbour and Currie (2016) | *Huayangosaurus* | n/a | Higher resolution in strict consensus than Arbour and Currie (2016) |
| Analysis A3 | Arbour and Currie (2016) | *Huayangosaurus* | Ankylosaur | 9 MPTs |
| Analysis A4 | Arbour and Currie (2016) | *Stegosaurus* | Base of Thyreophora | 8 MPTs and increased resolution |
| Analysis A5 | Arbour and Currie (2016) | *Huayangosaurus* and *Stegosaurus* | Stegosaur | 9 MPTs and increased resolution |
| Analysis A6 | Arbour and Currie (2016) | *Huayangosaurus* and *Stegosaurus* | Ankylosaur (constrained) | 9 MPTs and reduced resolution |
| Analysis B1 | Arbour, Zanno and Gates (2016) | *Huayangosaurus* | n/a | Same as Arbour, Zanno and Gates (2016) |
| Analysis B2 | Arbour, Zanno and Gates (2016) | *Huayangosaurus* | n/a | Higher resolution in strict consensus than Arbour, Zanno and Gates (2016) |
| Analysis B3 | Arbour, Zanno and Gates (2016) | *Huayangosaurus* | Nodosaur | 3 MPTs and increased resolution in Nodosauridae |
| Analysis B4 | Arbour, Zanno and Gates (2016) | *Stegosaurus* | Base of Thyreophora | 5 MPTs and increased resolution in Ankylosauridae |
| Analysis B5 | Arbour, Zanno and Gates (2016) | *Huayangosaurus* and *Stegosaurus* | Stegosaur | 2 MPTs and similar resolution |
| Analysis B6 | Arbour, Zanno and Gates (2016) | *Huayangosaurus* and *Stegosaurus* | Ankylosaur (constrained) | 3 MPTs and similar resolution |
| Analysis C1 | Baron, Norman and Barrett (2017) | *Huayangosaurus* | n/a | Same as Baron, Norman and Barrett (2017) |
| Analysis C2 | Baron, Norman and Barrett (2017) | *Huayangosaurus* | Ankylosaur | Little resolution |
| Analysis C3 | Baron, Norman and Barrett (2017) | *Stegosaurus* | Stegosaur | Higher resolution |
| Analysis C4 | Baron, Norman and Barrett (2017) | *Huayangosaurus* and *Stegosaurus* | Stegosaur | Very high resolution |
| Analysis C5 | Baron, Norman and | *Huayangosaurus* and *Stegosaurus* | Stegosaur | Little resolution and *Isaberrysaura* = ornithopod |
| Analysis  | Reference                  | Species                  | Resolution                        | Note                                                                 |
|----------|----------------------------|--------------------------|-----------------------------------|----------------------------------------------------------------------|
| C6       | Baron, Norman and Barrett (2017) | *Huayangosaurus* and *Stegosaurus* | Ornithopod (constrained)          | Severely reduced resolution in Ornithopoda                            |
| D1       | Boyd (2015)                 | n/a - *Scelidosaurus* most derived thyreophoran | n/a                              | Same as Boyd (2015)                                                  |
| D2       | Boyd (2015)                 | n/a - *Scelidosaurus* most derived thyreophoran | Base of Ornithischia             | Thyreophora basal to Heterodontosauridae, Marginocephalia basal to Ornithopoda |
| D3       | Boyd (2015)                 | *Huayangosaurus*          | Ornithopod, sister-taxon to *Huayangosaurus* | *Huayangosaurus* = ornithopod and reduced resolution in Ornithopoda |
| D4       | Boyd (2015)                 | *Stegosaurus*             | Ornithopod, sister-taxon to *Stegosaurus* | *Stegosaurus* = ornithopod and increased resolution                   |
| D5       | Boyd (2015)                 | *Huayangosaurus* and *Stegosaurus* | Ornithopod, sister-taxon to *Huayangosaurus* and *Stegosaurus* | *Huayangosaurus* and *Stegosaurus* = ornithopod and little resolution |
| D6       | Boyd (2015)                 | *Huayangosaurus* and *Stegosaurus* | Ornithopod, sister-taxon to *Huayangosaurus* and *Stegosaurus* | *Huayangosaurus* and *Stegosaurus* = ornithopod and little resolution. *Isaberrysaura* = ornithopod |
| D7       | Boyd (2015)                 | *Huayangosaurus* and *Stegosaurus* | Ornithopod (constrained)          | *Huayangosaurus* and *Stegosaurus* outside of Ornithischia and increased resolution in Ornithopoda. |
| D8       | Boyd (2015)                 | *Huayangosaurus* and *Stegosaurus* | Thyreophoran                      | Ornithopoda resolution increased, Thyreophora resolution decrease    |
| E1       | Raven and Maidment (2017)   | n/a                      | Stegosaur                         | Similar to Raven and Maidment (2017)                                 |
| E2       | Raven and Maidment (2017)   | n/a                      | Eurypod                           | *Isaberrysaura* = basal stegosaur. Reduced resolution in Eurypoda     |
| E3       | Raven and Maidment (2017)   | n/a                      | Ankylosaur (constrained)          | Reduced resolution in Ankylosauria                                    |
| F1       | Thompson et al. (2012)      | *Huayangosaurus* and *Stegosaurus* | n/a                              | Same as Thompson et al. (2012)                                       |
| F2       | Thompson et al. (2012)      | *Huayangosaurus* and *Stegosaurus* | Ankylosaur                        | Higher resolution in strict consensus than Thompson et al. (2012)    |
| Analysis | Thompson et al. (2012) | *Huayangosaurus* and *Stegosaurus* (constrained) | Resolution of Nodosauridae increased |
|----------|-------------------------|-----------------------------------------------|-------------------------------------|
| 1        |                         |                                               |                                     |
| 2        |                         |                                               |                                     |