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A new phylogeny of Stegosauria (Dinosauria, Ornithischia)

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ABSTRACT

The stegosaurs are some of the most easily recognisable dinosaurs, but they are surprisingly rare as fossils. Consequently much remains unknown about their palaeobiology, and every new stegosaurian find contributes to understanding the evolution of the clade. Since the last attempt to examine the evolutionary relationships of Stegosauria, new specimens have come to light, including the most complete individual of *Stegosaurus* ever found, new taxa have been described and, perhaps most importantly, new methods for analysis of cladistic datasets have been produced. In the light of these new data and technological advances, the phylogenetic relationships of the stegosaurs and basal armoured dinosaurs are investigated. The inclusion of continuous data results in much better resolution than was previously obtained, and the resulting single most parsimonious tree supports re-erection of the genera *Miragaia* and *Hesperosaurus*, which had previously been synonymized with *Dacentrurus* and *Stegosaurus* respectively. The recently described genus *Alcovasaurus* is resolved as a basal thyreophoran, but this is likely to be due to a combination of a very high degree of missing data and the questionable ontogenetic stage of the specimen. Examination of the effects of continuous data on the analysis suggest that while it contains a phylogenetic signal congruent with that of discrete data and provides better resolution than discrete data alone, it can affect topologies in unpredictable ways, particularly in areas of the tree where there are large amounts of missing data. The phylogeny presented here will form the basis for future work on the palaeobiology of the plated dinosaurs.

KEY WORDS: Dinosauria, Stegosauria, Ornithischia, Phylogeny, Continuous Data

Stegosauria is a clade of thyreophoran ‘armoured’ ornithischian dinosaurs known from Middle Jurassic to Lower Cretaceous strata worldwide. They are characterized by the possession of two parasagittal rows of plates and spines that extend from the neck to the end of the tail, and are one of the most easily recognisable dinosaurs. Their iconic status among the general public belies their rarity as fossils: although large amounts of fragmentary material for the best-known genus, *Stegosaurus*, is known, other stegosaur genera are generally represented by single partial skeletons and highly incomplete material (Table 1). Consequently, much remains unknown about the palaeobiology and palaeoecology of the clade (Galton & Upchurch 2004; Maidment *et al.* 2008).

In particular, fragmentary fossil material has hindered attempts to explore interrelationships between members of Stegosauria, and the taxonomy of various species and genera remains in flux (Carpenter & Galton 2001; Galton & Upchurch 2004; Maidment *et al.* 2008; Carpenter 2010; Cobos *et al.* 2010; Galton & Carpenter 2016). Galton & Upchurch (2004) produced the first phylogeny of Stegosauria, but achieved very little resolution in this morphologically conservative clade where skull material is rare. Maidment *et al*. (2008; later updated for new taxa in Mateus *et al.* 2009 and Maidment 2010) achieved significantly better resolution by examining all taxa first-hand, adding new characters, and including continuous data, which was analysed using gap weighting (Thiele 1993).

In the eight years since the phylogeny of Maidment *et al.* (2008) was published, new material of *Stegosaurus* has come to light, including a virtually complete, fully articulated specimen of *S. stenops* (Maidment *et al.* 2015), and a new specimen of the very rare species *S. mjosi* (Maidment *et al.* in review). Discoveries in the Iberian Peninsula have led to the synonymization of *Miragaia longicollum* with *Dacentrurus armatus* (Cobos *et al.* 2010), and a new genus, *Alcovasaurus longispinus*, has been described (Galton & Carpenter 2016).

Furthermore, character transitions in the stegosaurian ‘stem lineage’ are now better understood, thanks to the recognition that the basal ornithischian *Lesothosaurus diagnosticus* may well be a thyreophoran (Butler *et al.* 2008; Boyd 2015), and the discovery of a probable new basal thyreophoran taxon, *Laquintasaura venezuelae* (Barrett *et al*. 2014; Baron *et al.* 2016).

New algorithms for the analysis of phylogenetic data, such as the New Technology searches in TNT (Goloboff *et al.* 2008), have become available since the last exploration of stegosaur phylogenetic relationships. Perhaps most importantly, continuous characters can now be directly analysed in TNT without the need to discretize character states (Goloboff *et al.* 2006). This advance is particularly important in a morphologically conservative clade such as Stegosauria, where many characters are related to changes in proportions of different elements.

Herein, we re-examine the phylogenetic relationships of Stegosauria in the light of these new data and technological advances. We add newly described taxa, new characters discovered from the detailed study of new specimens, revise and recode existing characters, and analyse continuous characters as such. The phylogeny we present will form the basis for future studies on basal thyreophoran and stegosaurian evolution and paleobiology.

METHODS

Taxon selection

All taxonomically valid basal thyreophoran and stegosaurian taxa were included, along with three ankylosaur taxa. *Pisanosaurus mertii,* a taxon generally considered to be the most basal ornithischian (e.g. Butler *et al.* 2008; Boyd 2015; Baron *et al.* 2016) was used as the outgroup. In the analysis of Maidment *et al.* (2008), *Lesothosaurus diagnosticus* was used as the outgroup; however, several subsequent analyses have found *Lesothosaurus* as a basal thyreophoran (Butler *et al.* 2008; Boyd 2015), so we included it within the ingroup to allow its phylogenetic position to vary with respect to other basal thyreophorans. *Laquintasaura venezuelae*, although originally described as a basal ornithischian (Barrett *et al.* 2014) has recently been recovered as a basal thyreophoran (Baron *et al.* 2016), so we also included this taxon.

All stegosaurs considered valid by Maidment *et al.* (2008) were included. The taxonomy of *Stegosaurus* has recently been stabilized by replacement of the former type species, *Stegosaurus armatus*, with the better-known species *Stegosaurus stenops* (Galton 2010; ICZN 2013). Maidment *et al.* (2008) considered the species synonymous, and character states for *S. armatus* in that analysis were largely based on the holotype of *S. stenops* in any case. *Miragaia longicollum* (Mateus *et al.* 2009) and *Jiangjunosaurus junggarensis* (Jia *et al.* 2007) were described after publication of Maidment *et al.* (2008) but were added in subsequent iterations of the matrix (Mateus *et al.* 2009 and Maidment 2010 respectively). *Miragaia longicollum* has subsequently been synonymized with *Dacentrurus armatus* (Cobos *et al.* 2010). There are significant differences between *Dacentrurus armatus* from the United Kingdom and isolated stegosaur material from the Iberian Peninsula (SCRM pers. obs. 2004–2016), and to test the synonymy of *Miragaia* with the genus *Dacentrurus* we retain the holotype and referred specimen of *Miragaia* as a separate operational taxonomic unit (OTU) that we refer to as *Dacentrurus longicollum.* Furthermore, because of the specifically indeterminate nature and unresolved taxonomy of much of the isolated stegosaur material from the Iberian Peninsula, we code *Dacentrurus armatus* based only on the type specimen, and *Dacentrurus longicollum* based only on the holotype and referred specimens that were described by Mateus *et al.* (2009). Finally, we add the recently described genus *Alcovasaurus longispinus* (Galton & Carpenter 2016), which was originally described as *Stegosaurus longispinus* (Gilmore 1914). The holotype and only known specimen was destroyed in the 1920s, and Maidment *et al.* (2008) considered it a *nomen dubium*. However, based on newly analysed archival photographs, Galton & Carpenter (2016) described the specimen as a new genus of stegosaur, a conclusion followed herein.

Character selection

The character list of Maidment (2010) was used as a starting point and updated. In total, 10 characters were revised from the original character list. Characters 30, 33, 50 and 76 from Maidment (2010) were reworded to make them clearer, and characters 21, 24, 42, 49, 57 and 72 were removed because new data indicates that the character states vary with ontogeny or intraspecifically. Full justification for these updates can be found in the Online Supporting Information (OSI). Thirty-one new characters were identified from recent publications describing new specimens (Maidment *et al.* 2015; Baron *et al.* 2016; Maidment *et al.* in review) and personal observations, and added to the character list. The final character list contains 114 characters, of which 24 are continuous. The full character list and description can be found in the OSI.

Multistate characters 105 and 106 were ordered, as in Maidment *et al.* (2008), as these refer to the successive loss of pedal phalanges, although when the dataset was analysed with these characters unordered there was no effect on the results. All the continuous characters (1-24) were ordered, as is necessary for the analysis of continuous data, under the assumption that elements progressively change dimensions (Goloboff *et al.* 2006). In this analysis, all discrete characters were weighted equally throughout, and continuous characters were automatically rescaled in TNT so that the total range of their values was equivalent to the 0-1 character state change of discrete characters (Goloboff & Catalano 2016). This insures that each continuous character has the same weight as each discrete character, and also mitigates to some extent the effects of changes on topology generated by arbitrarily choosing numerator and denominator in ratio characters (Mongiardino Koch *et al.* 2015).

Cladistic analysis

A character-taxon matrix of 114 characters, scored for 23 stegosaur, ankylosaur, basal thyreophoran and basal ornithischian taxa was built in Mesquite (Maddison & Maddison 2016; http://dx.doi.org/10.5061/dryad.ds543). Due to the constraints of Mesquite, the character-taxon matrix was built as two matrices, one for continuous data and one for discrete data, and then subsequently concatenated in a text file for use in TNT.

A New Technology search was performed in TNT 1.5 (Goloboff *et al.* 2008). The search was carried out using sectorial search, ratchet, drift and tree fusing options and 10 random addition sequences for the combined character-taxon matrix. In all searches performed *Pisanosaurus mertii* was used as the outgroup. The New Technology search option in TNT finds all MPTs needed to produce a strict consensus tree, but does not recover all MPTs. Thus, the MPTs recovered from the New Technology search were used as the starting point for a round of tree bisection-reconnection (TBR) using the Traditional Search option, as this more fully explores treespace for additional most parsimonious topologies (Barrett *et al.* 2014). The search was carried out with one random addition seed and 1000 replicates.

The effects of continuous data on the dataset were then investigated by excluding the 24 continuous characters *a priori*. All remaining characters were unordered except for 105 and 106, which were ordered. A New Technology search and then a Traditional search with TBR were performed as before.

Support for the relationships obtained was evaluated by using symmetric resampling and bootstrap analysis. Symmetric resampling was applied to the combined matrices using 5000 replicates and a New Technology search in TNT, and a bootstrap analysis was performed using 1000 pseudoreplicates.

The genus *Alcovasaurus longispinus* was originally described as *Stegosaurus longispinus* (Gilmore 1914) and to test the phylogenetic positioning relative to *Stegosaurus*, a constraint tree was written where *Alcovasaurus longispinus* was sister taxon to *Stegosaurus stenops*. The constraint tree was written in TNT using the 'Force' command.

RESULTS

The New Technology search followed by the Traditional Search with TBR, performed in TNT with the full dataset, produced one most parsimonious tree (MPT) with a length of 255.6 steps (Fig. 1). A consistency index (CI) of 0.626, a retention index (RI) of 0.677 and a rescaled consistency index (RC) of 0.424 were obtained.

Stegosaurus stenops and *Stegosaurus homheni* form a clade, which is sister-taxon to a clade containing *Stegosaurus mjosi* and *Dacentrurus longicollum*. *Loricatosaurus priscus, Dacentrurus armatus, Kentrosaurus aethiopicus, Gigantspinosaurus sichuanensis* and *Jiangjunosaurus junggarensis* are successive sister taxa to this clade. A second stegosaurian clade containing *Huayangosaurus taibaii, Chungkingosaurus jiangbeiensis, Tuojiangosaurus* *multispinus* and *Paranthodon africanus* is resolved. *Alcovasaurus longispinus* is not resolved as a stegosaur in this analysis, and lies basal to Eurypoda (Ankylosauria + Stegosauria). At the base of Thyreophora, *Laquintasaura venezuelae* and *Scutellosaurus lawleri* are sister-taxa (Fig. 1).

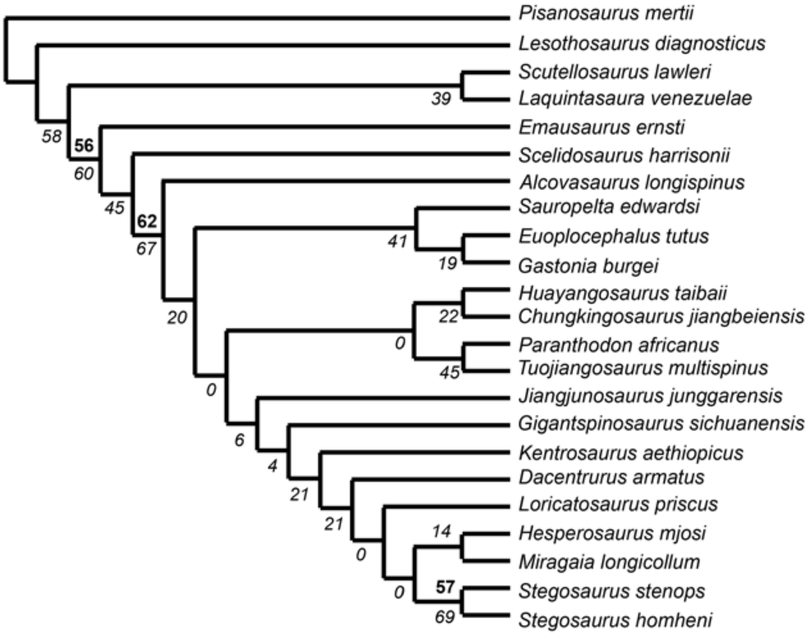

Figure one. Single most parsimonious tree obtained from an analysis of discrete and continuous characters. Numbers in bold above clades are bootstrap support percentages; only those over 50% are shown. Numbers in italics below clades are symmetric resampling frequencies. Symmetric resampling was carried out with a probability of 33 and using 5000 replicates on a New Technology search of existing trees, subsequent to the analysis being carried out.

The support for the groupings was tested using symmetric resampling and bootstrap analysis (Fig. 1). These metrics suggest support for most clades is weak, as the values are relatively low, but they indicate good support for Thyreophoroidea (*Scelidosaurus harrisonii* + *Alcovasaurus longispinus* + Eurypoda), *Stegosaurus stenops* + *Stegosaurus homheni*, and

Eurypoda + *Alcovasaurus longispinus*. The clades with the poorest support are Stegosauria, and the clade containing the most recent common ancestor of *Jiangojunosaurus junggarensis* and *Stegosaurus stenops* and all of its descendants.

When the analysis was re-run with continuous characters excluded, 36 MPTs were recovered with a length of 159 steps, and a strict consensus calculated (Fig. 2). The tree has a CI of 0.597, a RI of 0.697 and a RC of 0.416. The topology of Ankylosauria and the base of Stegosauria was identical to that obtained in the original analysis. The relationships of the basal thyreophorans and the derived stegosaurs, however, were not resolved. An agreement subtree produced in TNT pruned *Jiangjunosaurus junggarensis, Laquintasaura venezuelae, Scutellosaurus lawleri* and *Stegosaurus homheni,* indicating they are unstable taxa. This provided higher resolution in the previously unresolved areas; *Dacentrurus* is found to be monophyletic, *Loricatosaurus priscus* is found just outside *Stegosaurus* and *Lesothosaurus diagnosticus*, *Emausaurus ernsti* and *Scelidosaurus harrisonii* are found as successive sister-taxa at the base of Thyreophora. In the analysis where *Alcovasaurus longispinus* was constrained as the sister-taxon to *Stegosaurus stenops*, a tree length of 259.41 was obtained; this is 3.81 steps longer than the original tree.

DISCUSSION

The most recent previous phylogenetic analysis of Stegosauria (Maidment 2010) produced 41 MPTs, and a strict consensus showed little resolution at the base of Stegosauria. The improved resolution and single MPT obtained in this new analysis indicates new data, but most particularly new methods for analysing continuous characters, have significantly improved resolution. The strict reduced consensus (SRC) tree of Maidment

(2010) produced results congruent to those obtained here. *Gigantspinosaurus sichuanensis* and *Jiangjunosaurus junggarensis* were pruned to produce the SRC tree, while *Paranthodon africanus* + *Tujiangosaurus multispinus* and *Chungkingosaurus jiangbeiensis* + *Huayangosaurus taibaii* were collapsed into a polytomy with a clade containing the remaining stegosaurs (Stegosauridae of that analysis). The main difference between the SRC tree in Maidment (2010) and the single MPT produced by this analysis, other than improved resolution, is the placement of taxa referred to the genus *Dacentrurus*.

Placement of Dacentrurus longicollom

The synonymisation of *Miragaia longicollom* to the genus *Dacentrurus* by Cobos *et al.* (2010) is not supported herein, at least in the full analysis, as *Dacentrurus* is paraphyletic. *'Dacentrurus' longicollum* is found to be in a clade of taxa considered as *Stegosaurus* by Maidment *et al.* (2008), sister-taxon to *Stegosaurus mjosi*. The clade containing *Stegosaurus* and *'Dacentrurus' longicollum* is supported by nine synapomorphies; however the characters states in all but two characters (74, the quadrilateral shape of the acromial process of the scapula in lateral view and 77, the sub-circular outline of the coracoid) are unknown in *'Dacentrurus' longicollum*. The character states for characters 74 and 77 are unknown in *Dacentrurus armatus* and *Loricatosaurus priscus*, meaning that the positioning of *'Dacentrurus' longicollum* with *Stegosaurus* in this analysis is influenced by its own missing data and that of the taxa surrounding it, and may well change if future discoveries allow these characters to be scored.

The results of this analysis suggest two possible taxonomic alternatives: (1) that *'Dacentrurus' longicollum* should be synonymised with *Stegosaurus* as a new combination, or (2), that *Stegosaurus mjosi* should be removed from *Stegosaurus* and both it and *'Dacentrurus' longicollum* should be considered as genera distinct from *Stegosaurus.*

The genus *Stegosaurus* has been reported from the Iberian Peninsula previously (Escaso *et al.* 2007), so it is possible that *'Dacentrurus' longicollum* does indeed represent an Iberian species of *Stegosaurus*, although lack of overlapping material between the holotype of *'Dacentrurus' longicollum* and the material described as *Stegosaurus* by Escaso *et al.* (2007), which is fragmentary and specifically indeterminate (and thus not included as a separate OTU herein) makes referral unsafe.

Stegosaurus mjosi was originally considered a separate genus, *Hesperosaurus,* but was synonymized by Maidment *et al.* (2008). An alternative to referring *'Dacentrurus' longicollum* to *Stegosaurus* would be to remove *Stegosaurus mjosi* from *Stegosaurus*, re-instating it as the separate genus *Hesperosaurus*, and re-erecting the genus *Miragaia* for *'Dacentrurus' longicollum*. Here, we take this second approach, and recognise both *Miragaia* and *Hesperosaurus* as genera distinct from *Stegosaurus*. This is a more conservative approach, given that future discoveries are likely to impact on phylogenetic relationships in this part of the tree.

Placement of Alcovasaurus

Alcovasaurus longispinus, a specimen previously considered referable to *Stegosaurus* (Gilmore 1914; Maidment *et al.* 2008; Galton & Carpenter 2016) is found to lie outside of Eurypoda (Ankylosauria + Stegosauria) in this analysis. In order to investigate the robustness of this positioning, we constrained *Alcovasaurus longispinus* to be sister-taxon to *Stegosaurus stenops*. The single MPT recovered from the constrained analysis was just 3.81 steps longer than the MPT from the unconstrained analysis, suggesting its placement outside of Eurypoda is not strongly supported by the available data. Eurypoda is united by 11 synapomorphies (see OSI) but all except one are equivocal in *Alcovasaurus longispinus*, because 100 characters out of 114, representing 87.7% of the data, are missing from this OTU. A single synapomorphy of Eurypoda is absent in *Alcovasaurus longispinus*, resulting in its position outside of the clade: the fusion of the anterior and greater trochanters in adults (character 102). The anterior and greater trochanters fuse with ontogeny in Eurypoda, and it is possible that *Alcovasaurus longispinus* represents a sub-adult individual. However, because the holotype was destroyed, it is impossible to investigate its ontogenetic stage. Only a new discovery referable to *Alcovasaurus longispinus* will allow the taxon's phylogenetic position to be better resolved, but we strongly suspect that it is a stegosaur and its placement in this analysis is the result of missing data and the possibility that it was sub-adult at time of death. The anomalous placement of *Alcovasaurus longispinus* in this analysis demonstrates how missing data can affect topology, because for an OTU in which most characters cannot be scored, those that are scored have an overwhelming effect on placement.

Laquintasaura venezuelae + Scutellosaurus lawleri

The sister-taxon relationship of *Laquintasaura venezuelae* and *Scutellosaurus lawleri* at the base of Thyreophora is the same as that obtained by Baron *et al*. (2016), using an entirely different set of characters. This sister-taxon relationship is only supported by a single character in this analysis: the triangular shape of the axis neural spine in lateral view (character 54). However, the fact that this relationship has been resolved in two separate analyses, focusing on different groups, and using different character sets, offers strong support for the hypothesis that *Laquintasaura venezuelae* is a thyreophoran closely related to *Scutellosaurus lawleri.*

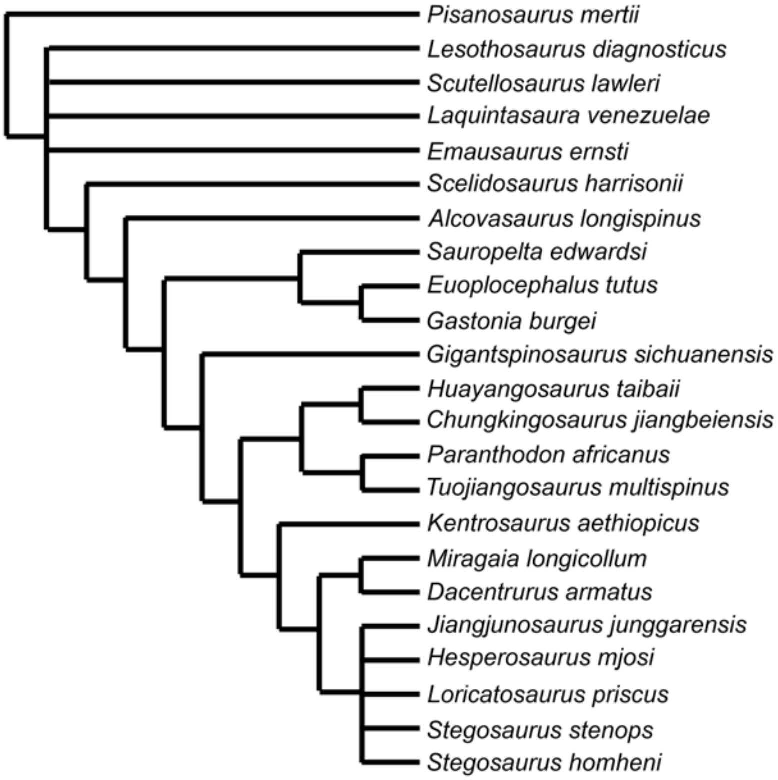

Figure two. Strict consensus of six most parsimonious trees obtained when continuous data was excluded from the analysis.

Effect of continuous data on resolution and topology

When continuous data were excluded from the phylogenetic analysis, 36 MPTs were produced, the strict consensus of which generally retained a similar topology to the full analysis, but with poorer resolution (Fig. 2). Resolution at the base of Thyreophora was lost, with *Laquintasaura venezuelae, Emausaurus ernsti, Scutellosaurus lawleri* and *Lesothosaurus diagnosticus* forming a basal polytomy. Thyreophora is supported by a single discrete synapomorphy (character 54: a sub-rectangular neural spine of the axis in lateral view), which is reversed in *Scutellosaurus lawleri* + *Laquintasaura venezuelae*. Two continuous characters lend support to the clade, however. Character 2, the number of dentary teeth, increases in thyreophorans, while character 24, the length to width ratio of metatarsal IV, decreases in thyreophorans with respect to *Pisanosaurus mertii*. In contrast, the clade containing all thyreophorans except *Lesothosaurus diagnosticus* is well supported by the data, with six discrete synapomorphies (see OSI), so it is not immediately obvious why this clade is not recovered in the analysis with continuous data excluded.

Within Stegosauria, membership of the two clades resolved by the full analysis remained the same, except that *Gigantspinosaurus sichuanensis* was recovered basal to that split. The clade which includes the most recent common ancestor of *Gigantspinosaurus sichuanensis* and *Stegosaurus stenops* in the full analysis is supported by two discrete synapomorphies, both of which are equivocal in *Jiangjunosaurus junggarensis*. There are no continuous characters that obviously lend support to this grouping, so once again it is not clear why *Gigantspinosaurus sichuanensis* collapses to the base of Stegosauria when continuous data are excluded.

The topology within the clade containing the most recent common ancestor of *Jiangjunosaurus junggarensis* and *Stegosaurus* in the full analysis differed in the analysis in which continuous data were excluded: *Jiangjunosaurus junggarensis* was recovered in a polytomy with the three species of *Stegosaurus* and *Loricatosaurus priscus*, while *Dacentrurus* was found to be monophyletic. It is unsurprising that relationships within this clade collapsed without support from continuous data, because neither *S. homheni* + *S. stenops* nor *S. mjosi* + *D. longicollum* are supported by discrete synapomorphies. The grouping of *D. longicollum* + *S. mjosi* is supported by two continuous characters, however: character 6, the neural arch to neural canal height ratio of dorsal vertebrae is lower in these two taxa than in other closely related stegosaurs, while character 7: the dorsal centrum height to neural arch height ratio is higher than in closely related taxa. Without these data, the grouping collapses, and *D. longicollum* is allied to *D. armatus*.

The continuous data included in this analysis have an effect both on the resolution and topology of the results, in ways that are not always predictable. Because each continuous character comprises as many character states as there are taxa, far fewer MPTs can be expected in analyses that contain continuous data coded as such. If the MPTs are more-or-less congruent, as we would hope if continuous data contains phylogenetic information, the result will be better resolution. A reduction in number of MPTs was also observed in Mannion *et al*. (2013), when coding continuous data as such, and was noted by Mongiardino Koch *et al.* (2015), who observed that analyses comprising continuous data often produce one MPT. Previous phylogenetic analyses that have investigated the effects of continuous characters have also concluded that continuous data improves resolution (Maidment *et al.* 2008; Ketchum and Benson 2010), although it is worth noting that in both of these studies, continuous data was coded using gap weighting, rather than treated as such.

In this analysis, a single MPT was obtained, suggesting that the continuous data were broadly congruent with the discrete data. Despite this, unpredictable changes in topology were observed when the continuous data were excluded from the analysis. Mongiardino Koch *et al.* (2015) found that the influence of continuous data on combined datasets was dependent not just upon the characters themselves, but their treatment and their proportion relative to discrete data. The changes in topology we recovered were focused around taxa for which large proportions of the data are missing. Whether the continuous data are stabilizing topologies, or leading to spurious relationships, in parts of the tree most greatly affected by missing data, warrants further investigation. Mannion *et al.* (2013) also found minor topological changes when they treated continuous data as such, but in general concluded that continuous data had little influence on overall relationships, a similar conclusion to that of Ketchum and Benson (2010). Both of those studies contained many more taxa than were used in this analysis, and so minor changes in topology appear less profound than they might do here.

An important area of incongruence between the discrete-only and complete analyses is in the relationships of *Dacentrurus.* In the complete analysis, *Dacentrurus* is found to be paraphyletic, while in the discrete-only analysis, it is found to be monophyletic, a result reinforced by the agreement subtree. The relationships of *Dacentrurus armatus, Miragaia/Dacentrurus longicollum,* and the large amounts of isolated stegosaur material known from the Iberian Peninsula will probably only be satisfactorily resolved once overlapping material between the holotypes of *Dacentrurus armatus* and *Miragaia longicollum* comes to light.

CONCLUSION

A new phylogenetic analysis of Stegosauria incorporating new thyreophoran taxa, new data on existing taxa, and using new methods of analysis has produced a much clearer picture of the relationships of basal thyreophorans and plated dinosaurs than has been achieved before. We find the recently described basal ornithischian *Laquintasaura venezuelae* as a sister-taxon to *Scutellosaurus lawleri*, a result also found in an analysis focusing on a different set of hypotheses and using a different character set (Baron *et al.* 2016). Stegosauria is divided into two clades, one containing some Middle Jurassic Chinese taxa and the poorly known South African taxon *Paranthodon africanus*, and the other containing *Gigantspinosaurus sichuanensis, Jiangjunosaurus junggarensis*, and the remaining stegosaurs, including European, African and North American Upper Jurassic forms. The genus *Dacentrurus* is paraphyletic, and *'Dacentrurus' longicollum* is more closely related to *'Stegosaurus' mjosi* than to any other stegosaur, warranting the re-erection of the generic names *Miragaia longicollum* and *Hesperosaurus mjosi* for these taxa. However, phylogenetic relationships in this part of the tree are poorly supported by available data, and future discoveries will result in more changes in topology. We obtained a single MPT, indicating that continuous data are congruent with discrete data in this analysis, and therefore contain important phylogenetic information. Unpredictable changes in topology as a result of the inclusion of continuous data are particularly focused on taxa in which a large proportion of the data is missing, and simulations are required to obtain a better understanding of the interactions between continuous and missing data.

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DATA ARCHIVING STATEMENT

The character-taxon matrix and character list for this study are available in the following data repository: http://dx.doi.org/10.5061/dryad.ds543

SUPPORTING INFORMATION

Additional supporting information can be found in the online version of this article:

Appendix S1 – Character list

Appendix S2 – Justification of changes to the character list of Maidment (2010)

Appendix S3 – Synapomorphies