Testing pterosaur ingroup relationships through broader sampling of avemetatarsalian taxa and characters and a range of phylogenetic analysis techniques

Matthew G Baron Corresp. 1, 2

1 BPP University, London, United Kingdom

2 Christ's College, University of Cambridge, Cambridge, United Kingdom

Corresponding Author: Matthew G Baron
Email address: m.baron2@my.bpp.com

The pterosaurs first appear in the fossil record in the middle of the Late Triassic. Their earliest representatives are known from Northern Hemisphere localities but, by the end of the Jurassic Period, this clade of flying reptiles achieved a global distribution, as well as high levels of diversity and disparity. Our understanding of early pterosaur evolution and the fundamental interrelationships within Pterosauria has improved dramatically in recent decades. However, there is still debate about how the various pterosaur subgroups relate to one another and about which taxa comprise these. Many recent phylogenetic analyses, while sampling well from among the known Triassic and Early Jurassic pterosaurs, have not included many non-pterosaurian ornithodirans or other avemetatarsalians. Given the close relationship between these groups of archosaurs, the omission of other ornithodirans and avemetatarsalians has the potential to adversely affect the results of phylogenetic analyses, in terms of character optimisation and ingroup relationships recovered. This study has addressed this issue and tests the relationships between the early diverging pterosaur taxa following the addition of avemetatarsalian taxa and anatomical characters to an existing early pterosaur dataset. This study has, for the first time, included taxa that represent the aphanosaurs, lagerpetids, silesaurids and dinosaurs, in addition to early pterosaurs. Anatomical characters used in other recent studies of archosaurs and early dinosaurs have also been incorporated. By expanding the outgroup taxa and anatomical character coverage in this pterosaur dataset, better resolution between the taxa within certain early pterosaur subclades has been achieved and stronger support for some existing clades has been found; other purported clades of early pterosaurs have not been found in this analysis - for example there is no support for a monophyletic Eopterosauria or Eudimorphodontidae. Further support has been found for a sister-taxon relationship between *Peteinosaurus zambelli* and Macronychoptera, a clade here named Zambellisauria (clade nov.), as well as for a monophyletic and early diverging Preondactylia. Some

analyses also support the existence of a clade that falls as sister-taxon to the zambellisaurs, here named Caviramidae (clade nov.). Furthermore, some support has been found for a monophyletic Austriadraconidae at the base of Pterosauria. Somewhat surprisingly, Lagerpetidae is recovered outside of Ornithodira *sensu stricto*, meaning that, based upon current definitions at least, pterosaurs fall within Dinosauromorpha in this analysis. However, fundamental ornithodiran interrelationships weren't the focus of this study and this particular result should be treated with caution for now. However, these results do further highlight the need for broader taxon and character sampling in phylogenetic analyses, and the effects of outgroup choice on determining ingroup relationships.

1 **Testing pterosaur ingroup relationships through broader sampling of avemetatarsalian taxa**

2 **and characters and a range of phylogenetic analysis techniques**

4 Matthew G. Baron[1]

6 1. BPP University, London, Aldine Place, 142-144 Uxbridge Road, London W12 8AW, UK

7 2. Christ's College, Cambridge, St Andrew's Street, CB2 3BU

9 Corresponding author: m.baron2@my.bpp.com

21   **ABSTRACT**

22   The pterosaurs first appear in the fossil record in the middle of the Late Triassic. Their earliest

23   representatives are known from Northern Hemisphere localities but, by the end of the Jurassic

24   Period, this clade of flying reptiles achieved a global distribution, as well as high levels of

25   diversity and disparity. Our understanding of early pterosaur evolution and the fundamental

26   interrelationships within Pterosauria has improved dramatically in recent decades. However,

27   there is still debate about how the various pterosaur subgroups relate to one another and

28   about which taxa comprise these. Many recent phylogenetic analyses, while sampling well from

29   among the known Triassic and Early Jurassic pterosaurs, have not included many non-

30   pterosaurian ornithodirans or other avemetatarsalians. Given the close relationship between

31   these groups of archosaurs, the omission of other ornithodirans and avemetatarsalians has the

32   potential to adversely affect the results of phylogenetic analyses, in terms of character

33   optimisation and ingroup relationships recovered. This study has addressed this issue and tests

34   the relationships between the early diverging pterosaur taxa following the addition of

35   avemetatarsalian taxa and anatomical characters to an existing early pterosaur dataset. This

36   study has, for the first time, included taxa that represent the aphanosaurs, lagerpetids,

37   silesaurids and dinosaurs, in addition to early pterosaurs. Anatomical characters used in other

38   recent studies of archosaurs and early dinosaurs have also been incorporated. By expanding the

39   outgroup taxa and anatomical character coverage in this pterosaur dataset, better resolution

40 between the taxa within certain early pterosaur subclades has been achieved and stronger

41 support for some existing clades has been found; other purported clades of early pterosaurs

42 have not been found in this analysis - for example there is no support for a monophyletic

43 Eopterosauria or Eudimorphodontidae. Further support has been found for a sister-taxon

44 relationship between *Peteinosaurus zambelli* and Macronychoptera, a clade here named

45 Zambellisauria (clade nov.), as well as for a monophyletic and early diverging Preondactylia.

46 Some analyses also support the existence of a clade that falls as sister-taxon to the

47 zambellisaurs, here named Caviramidae (clade nov.). Furthermore, some support has been

48 found for a monophyletic Austriadraconidae at the base of Pterosauria. Somewhat surprisingly,

49 Lagerpetidae is recovered outside of Ornithodira *sensu stricto*, meaning that, based upon

50 current definitions at least, pterosaurs fall within Dinosauromorpha in this analysis. However,

51 fundamental ornithodiran interrelationships weren't the focus of this study and this particular

52 result should be treated with caution for now. However, these results do further highlight the

53 need for broader taxon and character sampling in phylogenetic analyses, and the effects of

54 outgroup choice on determining ingroup relationships.

55

56 Keywords: Ornithodira; Triassic; evolution; systematics; cladistics; powered flight

57

58

59

60

61

62

63

INTRODUCTION

65 Pterosaurs were a diverse, disparate and highly specialised group of terrestrial reptiles that

66 represent the oldest set of vertebrates currently understood to have achieved powered flight

67 (Benton, 1985; Unwin, 2003; Andres, 2006; Barrett et al., 2008; Andres, Clark and Xu, 2014;

68 Britt et al., 2018). Originating at some time in either the Early or Middle Triassic (Nesbitt et al.,

69 2017), and first appearing in the fossil record in the middle of the Late Triassic (Barrett et al.,

70 2008; Bennet, 2013), the pterosaurs went on to thrive throughout the Mesozoic Era as one of

71 the dominant groups of land animals, lasting right up until the very end of the Cretaceous

72 Period and achieving a global distribution (Unwin, 2003; Dalla Vecchia, 2004; Unwin and Martill,

73 2007; Barrett et al., 2008; Kellner et al., 2019).

74 The earliest pterosaurs were generally small bodied animals, with toothed upper and

75 lower jaws and usually an elongated tail (e.g., Padian, 1984; Hone and Benton 2007; Padian,

76 2008a; Padian, 2008b; Bennett, 2007; Bennet, 2014; Kellner, 2015; Britt et al., 2018; Dalla

77 Vecchia, 2010 Dalla Vecchia, 2013; Dalla Vecchia, 2019). In addition, all known early pterosaurs

78 appear to be fully capable of powered flight and, as yet, no transitional non-flying pterosaur

79 taxa are known (though some specimens have been suggested to be exactly that – e.g., Huene,

80   1914). Later pterosaurs went on to achieve a broader, truly global, geographic range, as well as

81   much larger body sizes and much more unusual and often unique features of anatomy (e.g.,

82   Unwin and Bakhurina, 1994; Unwin and Bakhurina, 1995; Unwin, 2001; Unwin, 2003; Dalla

83   Vecchia et al., 2002; Barrett et al., 2008; Hone et al., 2012; Upchurch et al., 2015; Kellner et al.,

84   2019).

85   Within Pterosauria, which currently comprises the same set of taxa as the clade

86   Pterosauromorpha (see, Nesbitt et al., 2013), there exists a number of distinct subgroups, many

87   of which were already present in the Late Triassic. The many proposed subgroups within

88   Pterosauria include the Eopterosauria, which is believed to comprise Preondactylia and

89   Eudimorphodontoidea (e.g., Andres, Clark and Xu, 2014), and Macronychoptera, which

90   comprises, *inter alia*, Dimorphodontidae, Anurognathidae and Pterodactyloidea (e.g., Britt et

91   al., 2018; Dalla Vecchia, 2019)(Figure 1A-C) .

92   The recent phylogenetic analysis by Dalla Vecchia (2019) suggested that the earliest

93   diverging members of Pterosauria that were considered by that study were the Preondactylia –

94   comprising *Preondactylus buffarinii* and *Austriadactylus cristatus*. This pairing of *Preondactylus*

95   *buffarinii* and *Austriadactylus cristatus* concurs with the findings of Andres, Clark and Xu (2014).

96   However, the results of these two analyses differ in that in the trees produced by Andres, Clark

97   and Xu (2014), the Preondactylia form the sister-taxon to the clade comprising *Peteinosaurus*

98   *zambellii* and Eudimorphodontoidea, a topology also supported by Upchurch et al. (2015).

99   These clades together form Eopterosauria, a group not supported in the analysis by Britt et al.

100   (2018) or Dalla Vecchia (2019). Equally, in the analysis by Dalla Vecchia (2019) no support was

101   found for the clade Eudimorphodontidae (*sensu* Dalla, Vecchia 2014). In this respect, the

102   analyses of Dalla Vecchia (2019) and Britt et al. (2018) also differ from each other, despite using

103   the same dataset and having only a very small number of differences in terms of the

104   operational taxa included (see Figure 1). This just highlights the relative instability of some of

105   the early branching pterosaur taxa in phylogenetic analyses. Dalla Vecchia (2019) even admits

106   that Bremer support values for many of the clades in his analysis were low.

107   A monophyletic Macronychoptera was found to be in a sister-taxa relationship with

108   *Peteinosaurus zambellii* in the analysis of Dalla Vecchia (2019), and this unnamed clade was

109   found as sister-taxon to another unnamed group of pterosaurs containing a number of other

110   Late Triassic forms (Figure 1B). Unlike in the analysis by Andres, Clark and Xu (2014), Dalla

111   Vecchia recovers *Eudimorphodon ranzii* within Lonchognatha, and finds no evidence for a close

112   relationship between *Eudimorphodon ranzii*, *Carniadactylus rosenfeldi* and *Arcticodactylus*

113   *cromptonellus* (*contra* Andres, Clark and Xu, 2014) (Fig 1A-B). Similarly, a close affinity between

114   *Eudimorphodon ranzii* and Raeticodactylidae – which comprises *Raeticodactylus filisurensis* and

115   *Caviramus schesaplanensis* according to Andres, Clark and Xu (2014) – was found by Britt et al.

116   (2018) but not Dalla Vecchia (2019) (Fig 1A-C). In the reduced strict consensus tree produced in

117   the analysis by Britt et al. (2018), the earliest diverging pterosaur clade contained a pair of taxa

118   - *Austriadraco dallavecchiai* and *Arcticodactylus cromptonellus* - a similar result to that obtained

119   by Kellner (2015), who named this clade Austriadraconidae (see also, Dalla Vecchia, 2009a;

120   Dalla Vecchia, 2009b). But again, this result differs from the analysis of both Upchurch et al.

121   (2015) and Dalla Vecchia (2019). In an analysis by Codorniú et al. (2016), the results vary even

122   more dramatically at the base of Pterosauira, with Anurognathidae diverging earlier within the

123   trees recovered than either *Eudimorphodon ranzii* or *Austriadactylus cristatus*. Codorniú et al.

124 (2016) also found evidence for a possible a *Dimorphodon macronyx + Peteinosaurus zambelli*

125 sister-taxon relationship, which was not recovered in any of the other analyses discussed

126 above.

127   It is clear from all of the differences observed between the various analyses discussed

128 above that much work still needs to be done to resolve the interrelationships between the

129 many early pterosaur taxa currently known. The ingroup relationships of the various early

130 pterosaur clades are unstable, as are the interrelationships between clades. However, in all the

131 studies discussed above, there is a potential problem with the analyses in that they perhaps do

132 not include adequate sampling from without Pterosauria – i.e., the lack of informative

133 anatomical information from certain key outgroup taxa could be causing the poor resolution

134 within Pterosauria.

135   In the analysis of Britt et al. (2018), and of other studies that utilised the same data (e.g.,

136 Codorniú et al., 2016; Dalla Vecchia, 2019), the only other ornithodiran taxa to be included in

137 the analysis as an outgroup taxon is the unusual hypercarnivore *Herrerasaurus*

138 *ischigualastensis*. The taxon was presumably chosen as a representative of the Dinosauria, a

139 clade supposedly closely related to Pterosauria. However, *H. ischigualastensis* is not necessarily

140 the best representative of the 'basal' dinosaurian condition, being a very large predator that is

141 quite distinct in terms of its anatomy to many, if not most, of the earliest dinosaurs (see,

142 Brusatte et al., 2010; Baron, Norman and Barrett, 2017a). In fact, the position of this taxon has

143 proved to be highly unstable in recent times (see, Baron, Norman and Barrett, 2017b; Langer et

144 al., 2017; Lee et al., 2019; Pacheco et al., 2019) and belongs to a wider clade of Triassic

145 hypercarnivores that may or may not fall within Dinosauria at all (see, Baron and Williams,

146   2018). Moreover, in the analyses by Britt et al. (2018) and Dalla Vecchia (2019), *H.*

147   *ischigualastensis* is recovered as the sister taxon to the rauisuchid paracrocodylomorph

148   *Postosuchus kirkpatricki*, which might suggest that character optimisation outside of the

149   pterosaurian lineage is somewhat confused and misleading. If the character distribution among

150   taxa in this analysis was fairly reflective of the topology expected to be found for these taxa, *H.*

151   *ischigualastensis* should, according to almost all modern phylogenetic hypotheses, fall closer to

152   the pterosaurs than to *P. kirkpatricki*. This result, while not the key focus of any of the studies

153   that recovered it, perhaps should have raised alarm bells in terms of what the data for taxa

154   immediately at the base of and just outside of Pterosauria was like. The purpose of outgroup

155   taxa is to reflect, as best as is possible, the 'basal' condition for the ingroup clade being studied

156   – it is arguable that this is not the case in the analyses by Britt et al. (2018) and Dalla Vecchia

157   (2019) and that these analyses fall short in this key respect. This omission of important

158   anatomical data may, in turn, be having a substantial adverse effect on the resolution of the

159   ingroup relationships among the numerous pterosaur taxa included in the studies.

160   Also missing from the datasets is a range of other close pterosaur relatives, the

161   anatomical characteristics of which are potentially even more helpful in determining the

162   ancestral state of Pterosauria than *H. ischigualastensis* is when considered alone. Silesaurids,

163   who along with dinosaurs form the dinosauromorph clade Dracohors (Cau, 2018) are omitted,

164   as are the dinosauriforms known as the lagerpetids. Similarly, looking the other way along this

165   particular branch of the archosaur group, the aphanosaurs, a group believed to form the sister-

166   taxon to the ornithodirans (see Nesbitt et al., 2017), are also not included. All of the anatomical

167   information that could be provided by the inclusion of these taxa is lost from the early

168   pterosaur phylogenetic analyses and ought to be corrected for.

169   Other studies of early pterosaur interrelationships have similar shortcomings in terms of

170   the outgroup taxa sampling. The analysis of Unwin (2003), for example, only used a single

171   outgroup taxon in the form of the non-archosaurian archosauriform *Euparkeria capensis.* The

172   analyses of Kellner (2003) had three outgroup taxa - *Ornithosuchus longidens*, *Herrerasaurus*

173   *ischigualastensis* and *Scleromochlus taylori*. Of these, only one, *H. ischigualastensis*, is an

174   ornithodiran. While *Scleromochlus taylori* was considered as a possible close relative of

175   pterosaurs at the time Kellner (2003) was published, subsequent work on this taxon has

176   demonstrated that it is more likely an archosauriform belonging to the clade Doswelliidae (see,

177   Bennett, 2020). Finally, in the analyses of Andres, Clark and Xu (2014), the chosen outgroups

178   were the non-avemetatarsalian archosauromorphs *Euparkeria capensis* and *Ornithosuchus*

179   *longidens,* and the putative dinosaur *Herrerasaurus ischigualastensis*.

180   This study aims to test what effect, if any, the omission of such close pterosaur relatives

181   from analyses has had on the overall topology within Pterosauria by using a modified version of

182   the recent dataset of Britt et al. (2018). Many of the disagreements between the recent results

183   of Andres, Clark and Xu (2014), Upchurch et al. (2015), Kellner (2015), Britt et al. (2018) and

184   Dalla Vecchia (2014, 2019) could be resolved through a simple addition of better and more

185   appropriate outgroup taxa, and this is what this study attempts to do. By also incorporating

186   new anatomical characters, taken from recent early dinosaur and archosaur studies, this study

187   aims to better anchor the base of Pterosauria to a position within Avemetatarsalia and

188   Ornithodira, so as to allow the 'basal' condition of pterosaurs to be better expressed in the

189   data.

190

191   **MATERIAL AND METHODS**

192   The dataset of Britt et al. (2018), as modified by Dalla Vecchia (2019), was expanded through

193   the addition of the following taxa: Aphanosauria, Lagerpetidae, *Marasuchus lilloensis*,

194   Silesauridae, Ornithischia, Theropoda and Sauropodomorpha.

195   Full details of each new operational taxonomic unit, which specimens were studied, and

196   which other sources of anatomical information were used are given in Table 1.

197   In addition to the new taxa, 27 new anatomical characters were incorporated into the

198   dataset of Britt et al. (2018) – five were taken from the early dinosaur dataset of Baron et al.

199   (2017a, b), which had built upon previous works (e.g., Langer and Benton, 2006; Nesbitt, 2011),

200   and a further nine from the archosaur dataset of Nesbitt et al. (2017). Some other characters

201   that were added were taken from both of these studies, as they had been used in each and

202   either entirely or partially overlapped in terms of the features that they described (chars 111-

203   116). These characters were conflated or otherwise adjusted so as to prevent repetition or

204   over-scoring of each feature. A further three additional characters were added based upon the

205   range of anatomical features observed in the various taxa in the study, including a simple

206   absent/present statement for the pteroid (char. 94) to supplement character 71 of Britt et al.

207   (2018), itself a modification from character 132 in the data of Bennett (2012). In addition, a

208   character describing the radius to humerus ratio was added (char. 110), and a character

209   describing the shape of the distal end of the scapula (char. 95). Four more 'classic pterosaur

210   characteristics' were accounted for with new characters, each modified from the datasets of

211   Vidovic and Martill (2014) and Lü et al. (2009) and were included in this study as characters

212   117-120. Character 99 in this analysis is a modified form of character 301 of Baron et al. (2017a)

213   – Dorsal margin of the ilium in lateral view: 0, sinusoidal; 1, concave (saddle-shaped), pre and

214   preacetabular and postacetabular processes upturned relative to craniocaudal centre; 2,

215   relatively straight or convex – state 0 has been added to describe the condition seen in

216   *Macrocnemus bassanii*, *Postosuchus kirkpatricki* and aphanosaurs. State (2) is present in

217   theropods and ornithischians, whereas state (1) describes the condition in 'basal' pterosaurs,

218   herrerasaurs, sauropodomorphs, silesaurids, lagerpetids and *Marasuchus lilloensis*. The full list

219   of characters added to the data matrix is given in the supplementary file.

220   Of the additional characters, 108 and 109 were treated as ordered, following Nesbitt

221   (2011) and Baron et al. (2017a, b) in addition to characters 62, 74 and 91, which were also

222   treated as ordered in the analyses of Britt et al. (2018) and Dalla Vecchia (2019).

223   Trees were searched for using equal weights implementation of parsimony, using TNT

224   1.5-beta (Goloboff et al., 2008), through the New technology search method. Following the

225   protocol of Baron et al. (2017a, b) and Nesbitt et al. (2017), memory was first set at its

226   maximum of 99,999, and trees were then searched for under equal weights parsimony through

227   a New Technology (Goloboff et al., 2008) search, with ratchet and drift set at their default

228   values and with 100 random additional sequences. A second search, following the protocol of

229   Ezcurra (2016) was then done, in which trees were searched for using a New Technology Search

230   (Goloboff et al., 2008) with ratchet set to 20 iterations, with five rounds of tree fusing and 100

231   additional sequences. The MPTs produced in this second type of analysis were then subjected

232   to a second round of TBR branch swapping, with a change probability of 33 and 100 additional

233   sequences as the default search settings. Finally, a search was carried out using implied weights

234   parsimony, with implied weights (k-values) set to 3, 5, and 10 (see Parry, Baron and Vinther,

235   2017; Goloboff, 2018).

236   This manuscript and the nomenclatural acts it contains was registered with ZooBank and the

237   manuscript assigned the following LSID: urn:lsid:zoobank.org:pub:BE350658-1D5C-456B-B129-

238   FFDE827E7DDF.

239

240   **RESULTS**

241   An initial analysis was run that excluded the additional 27 characters that were to be added to

242   the dataset of Britt et al. (2018). This was done using equal weights and a simple New

243   technology search. This analysis was carried out to test the effect of an expanded set of

244   outgroup taxa alone, without the effect of added characters. The analysis produced 31 most

245   parsimonious trees (MPTs) each of length 305 steps (Figure 2). In spite of the lack of additional

246   characters that could help to resolve the relationships within Ornithodira and Avemetatarsalia,

247   this analysis still recovered a monophyletic Pterosauria and generated fairly good resolution

248   within this clade. The resolution among outgroup taxa is poor, with most outgroup taxa forming

249   a polytomy outside of Pterosauria. Within Pterosauria there exists a 'basal' trichotomy.

250   *Austriadactylus cristatus* and *Preondactylus bufarinii* are recovered in a sister taxon

251   relationship; a second 'basal' clade comprises *Arcticodactylus cromptonellus*, *Austriadraco*

252   *dallavecchiai*, *Seazzadactylus venieri*, *Carniadactylus rosenfeldi*, *'Raeticodactylus' filisurensis*,

253   *Caviramus schesaplanensis* and unnamed specimen MCSNB 8950; the third of the 'basal' clades

254   in the trichotomy contains *Peteinosaurus zambelli*, Dimorphodontidae and Lonchognatha. This

255   result is more similar to the results of the analysis carried out by Dalla Vecchia (2019) than

256   those of Britt et al. (2018), though this analysis has poorer resolution at the base of the

257   pterosaur tree. The addition of new outgroups has, without the addition of new characters,

258   generated more uncertainty about the fundamental interrelationships between the earliest

259   diverging pterosaur groups. Furthermore, the resolution between taxa in the second clade

260   produced in this analysis – the one containing *Arcticodactylus cromptonellus*, *Austriadraco*

261   *dallavecchiai*, *Seazzadactylus venieri*, *Carniadactylus rosenfeldi*, 'Raeticodactylus' *filisurensis*,

262   *Caviramus schesaplanensis* and specimen MCSNB 8950 – is poorer with the addition of the new

263   outgroups. In this analysis *Arcticodactylus cromptonellus* and *Austriadraco dallavecchiai* from a

264   grade leading to a polytomy containing all other taxa in this group. In the results of Dalla

265   Vecchia, on the other hand, found *Seazzadactylus venieri* and *Carniadactylus rosenfeldi* to also

266   for part of this grade leading to a smaller polytomy of *Raeticodactylus' filisurensis*, *Caviramus*

267   *schesaplanensis* and specimen MCSNB 8950. Within the other clades the recovered topology is

268   the same as in the analyses of Dalla Vecchia (2019) (Figure 1B). The addition of new outgroup

269   taxa alone did not result in the recovery of a monophyletic Austriadraconidae or Eopterosauria,

270   as in other previous studies (e.g. Andres, Clark and Xu (2014; Britt et al. 2018) (Figure 1A, C). By

271   adding in new characters that better resolve the relationships within Ornithodira and the

272   character optimisation at the base of Pterosauria, this uncertainty at the base of the pterosaur

273   tree was resolved and a different topology within certain constituent pterosaurian clades was

274   recovered (Figure 3).

275   In this first full analysis that included both the added taxa and added characters, and

276   using equal weights and a simple New technology search, two MPTs were recovered, each of

277   length 390 steps. In the strict consensus rule tree produced from the two MPTs recovered in

278   the analysis, a monophyletic Pterosauria was found (Figure 3). This clade contains all the taxa

279   analysed in this analysis that are traditionally considered to be pterosaurs, and together this

280   clade forms a sister-taxon to a clade containing almost all of the newly added avemetatarsalian

281   taxa, except for Aphanosauria and Lagerpetidae. Dinosauria is recovered, as is Dracohors and

282   Dinosauriformes. Lagerpetidae is recovered without the clade containing Dinosauriformes and

283   Pterosauria. *Herrerasaurus ischigualastensis*, which was the only non-pterosaurian ornithodiran

284   outgroup included in the analyses of Britt et al. (2018) and Dalla Vecchia (2019), is found nested

285   within Dracohors, in a position closer to Dinosauria than to Silesauridae, as is more consistent

286   with some recent analyses of early dinosaurs (e.g., Baron and Williams, 2018).

287   In this full analysis, with all of the additional taxa and characters being active, the base

288   of the pterosaurian clade no longer contained a trichotomy. Instead, *Austriadactylus cristatus*

289   and *Preondactylus bufarinii* are recovered as sister-taxa, forming their own small monophyletic

290   group at the base of the pterosaur tree, falling outside of the clade that contains all other

291   pterosaurs *sensu* Dalla Vecchia (2019). This clade - named Preondactylia by Andres, Clark and

292   Xu (2014) - has also been found in a number of other studies (e.g., Upchurch et al., 2015; Britt

293   et al., 2018; Dalla Vecchia, 2019). Preondactylia forms the sister taxon to a clade containing two

294   distinct monophyletic groups: one group contains *Arcticodactylus cromptonellus*, *Austriadraco*

295   *dallavecchiai*, *Seazzadactylus venieri*, *Carniadactylus rosenfeldi,* '*Raeticodactylus*' *filisurensis*,

296   *Caviramus schesaplanensis* and specimen MCSNB 8950; the other contains *Peteinosaurus*

297   *zambelli* and all other pterosaurs. This too largely agrees with the results obtained by Dalla

298   Vecchia (2019) – however, the topology within the first of the two clades differs. As discussed

299   above, in the results presented by Dalla Vecchia (2019), *Arcticodactylus cromptonellus*,

300   *Austriadraco dallavecchiai*, *Seazzadactylus venieri* and *Carniadactylus rosenfeldi* formed a grade

301   leading to a clade containing '*Raeticodactylus*' *filisurensis*, *Caviramus schesaplanensis* and

302   specimen MCSNB 8950. This expanded analysis did not find such a topology within this clade.

303   Instead, the results recover *Arcticodactylus cromptonellus*, *Austriadraco dallavecchiai* and

304   *Seazzadactylus venieri* in their own clade, which is sister-taxon to a clade containing the others.

305   This first clade is akin to Austriadraconidae, as named by Kellner (2015). Austriadraconidae, in

306   this form, is not supported in the results presented by Dalla Vecchia, but was recovered, albeit

307   in a different position by Britt et al. (2018). The placement and composition of

308   Austriadraconidae in the results of this analysis are novel and appear to be the result of the

309   combination of wider outgroup sampling and anatomical character choice. Within other major

310   pterosaurian sub-clades, such as Macronychoptera, Dimorphodontidae, Anurognathidae, and

311   Pterodactyloidea, the topology recovered in this analysis agrees with the topology recovered in

312   the analysis by Dalla Vecchia (2019). Moreover, this analysis found no support for the

313   placement of *Arcticodactylus cromptonellus* and *Austriadraco dallavecchiai* in their own

314   exclusive clade placed as sister-taxon to all other pterosaurs, as had been found by Britt et all.

315   (2018), *sensu* Dalla Vecchia (2019).

316

317   **Further Comparisons with Previous Studies.**

318   While the placement of Preodactylia as the earliest diverging of the pterosaur subclades agrees

319   with the analysis by Dalla Vecchia (2019), the result differs from Britt et al. (2018). Whereas in

320   the taxon-reduced analyses of Britt et al. (2018), a clade containing *Austriadraco dallavecchiai*

321   and *Arcticodactylus cromptonellus* – termed Austriadraconidae by Kellner (2015) – was found as

322   the earliest diverging pterosaur clade, the results of Dalla Vecchia (2019) and those of the first

323   analysis of this study do not provide support for such a position, but rather place the

324   austriadraconids in a more deeply nested position. This result also differs substantially from that

325   found by Codorniú et al. (2016) who did not find a sister-taxon relationship between

326   *Austriadactylus cristatus* and *Preondactylus bufarinii* at all.

327   As stated above, the results of this first analysis support a monophyletic

328   Austriadraconidae, *sensu* Kellner (2015), but, for the first time, also places *Seazzadactylus*

329   *venieri* within it (Figure 2). In this analysis, the austriadraconids form a sister-taxon to a clade

330   containing *Carniadactylus rosenfeldi* + '*Raeticodactylus*' *filisurensis*, *Caviramus schesaplanensis*

331   and unnamed specimen MCSNB 8950. Dalla Vecchia (2019) also recovered all of these taxa

332   together into a monophyletic group, but his analysis did not recover the same interrelationships

333   between them; *Arcticodactylus cromptonellus*, *Austriadraco dallavecchiai* and *Seazzadactylus*

334   *venieri* form a grade leading into the clade containing *Carniadactylus rosenfeldi* and a

335   trichotomy of '*Raeticodactylus*' *filisurensis*, *Caviramus schesaplanensis* and MCSNB 8950 in the

336   analysis of Dalla Vecchia (2019) (see, Figure 1A).

337   No close relationship is found between this group of pterosaurs and *Eudimorphodon*

338   *ranzii*, *contra* the findings of Andres, Clark and Xu (2014), Upchurch et al. (2015) and Britt et al.

339   (2018). Similarly, no support is found for the clade Eudimorphodontidae. Instead,

340   *Eudimorphodon ranzii* is found within Macronychoptera and Lonchognatha, *sensu* Dalla Vecchia

341   (2019).

342   Also consistent with the analysis of Britt et al. (2018) and of Dalla Vecchia (2019),

343   *Dimorphodon macronyx* and *Caelestiventus hanseni* are found to be sister-taxa, forming their

344   own clade Dimorphodontidae. This stands in contrast to the results of Codorniú et al. (2016),

345   who recovered *Peteinosaurus zambelli* as the sister-taxon to *Dimorphodon macronyx*.

346   Both the analyses by Britt et al. (2018) and Dalla Vecchia (2019) found a

347   Macronychoptera containing Dimorphodontidae and Lonchognatha, *sensu* Unwin 2003, and

348   with *Peteinosaurus zambelli* forming the sister-taxon to Macronychoptera. This again differed

349   from the results of Codorniú et al. (2016) who found a different position for *Peteinosaurus*

350   *zambelli* (see above). However, despite the agreement between Britt et al. (2018) and Dalla

351   Vecchia (2019) on the subgroups comprising Macronychoptera, the constituent taxa of

352   Lonchognatha differed between these two analyses, with Britt et al. (2018) finding taxa such as

353   '*Raeticodactylus*' *filisurensis* and *Caviramus schesaplanensis* to be members of this more

354   'derived' clade (see also, Kellner, 2003). This study has not found such a construction of

355   Lonchognatha, and instead has found a more reduced clade, *sensu* Dalla Vecchia (2019).

356   Further, within Lonchognatha is a clade containing Campylognathoides and all other pterosaurs

357   analysed in this study - i.e. a monophyletic Novialoidea *sensu* Kellner 2003 - and this result

358   largely agrees with the analyses of Kellner (2003), Andres and Myers (2013), Andres, Clark and

359   Xu (2014), Upchurch et al. (2015), Britt et al. (2018) and Dalla Vecchia (2019).

360   Also consistent with each of the above studies is the recovery of a monophyletic

361   Caelidracones. However, a sister-taxon relationship between Anurognathidae and

362   Pterodactyloidea, as recovered by Andres and Myers (2013) is not supported in this analysis. As

363   in the analyses by Britt et al. (2018) and Dall Vecchia (2019), Caelidracones contains two clades:

364   one containing a trichotomy of *Sordes pilosus*, 'ramphorynchids', and Monofenestrata, and the

365   other containing taxa that could be loosely termed 'anurognathid types'. Again, a contrast can

366   be drawn with the results of this analysis and the results of the analysis by Codorniú et al.

367   (2016), who placed Anurognathidae in a much more stem-ward position within Pterosauria.

368   Anurognathidae is also recovered in this analysis, but the interrelationships between

369   the taxa in this clade differ from the analyses of Britt et al. (2018) and Dall Vecchia (2019) in

370   that *Jeholopterus* and *Anurognathus* form sister taxa, with *Dendrorynchoides* and

371   *Batrachognathus* forming successive sister-taxa. The taxon provisionally named '*Dimorphodon*'

372   *weintraubi* then forms the sister taxon to Anurognathidae, and this is consistent with the

373   results of Dalla Vecchia (2019). These 'anurognathid types' together form the sister-taxon to

374   the grouping of *Sordes pilosus*, the 'ramphorynchids' and monofenestratans, which is, as yet,

375   also unnamed (see Dalla Vecchia, 2019).

376   One interesting aspect of this analysis is that it would appear, when applying current

377   definitions, that Pterosauria falls within Dinosauromorpha *sensu* Benton (1985) and not as its

378   sister-taxon, *sensu* Gauthier (1986) and Nesbitt et al. (2017). Because Lagerpetidae falls outside

379   of the clade containing Pterosauria and the grade leading into dinosaurs in this analysis, under

380   the current definition of Dinosauromorpha - the last common ancestor of *Lagerpeton*

381   *chanarensis*, *Marasuchus lilloensis*, Dinosauria and all its descendants (Benton, 1985) –

382   Pterosauria and, by definition, Ornithodira, would fall within Dinosauromorpha. Ornithodira

383   would comprise Pterosauria and Dinosauriformes, rather than Pterosauria and

384   Dinosauromorpha, as suggested in previous analyses (e.g., Langer and Benton, 2004; Nesbitt,

385   2011; Baron, Norman and Barrett, 2017a; Nesbitt et al., 2017). However, this position is only

386   relatively weakly supported for now, and such interaltionships within the higher Ornithodira

387   was not the focus of this analysis. Subsequent studies may recover more traditional topologies

388   within Avemetatarsalia and composition of Ornithodira, so this study refrains from revising any

389   definitions based upon this result alone. Within Dinosauriformes are *Marasuchus lilloensis* and

390   Dracohors, *sensu* Cau (2018). Silesaurids form the sister-taxon to dinosaurs + herrerasaurs,

391   *sensu* Baron and Williams (2018). Dinosauria in this analysis contains Ornithoscelida (see Baron,

392   Norman and Barrett, 2017a) and Sauropodomorpha (see Baron, Norman and Barrett, 2017b).

393

394   The following is a list some of the notable nodes recovered from the base of the

395   pterosaur tree and including Pterosauria, with all synapomorphies listed for each (Node

396   numbers refer to numbering in Figure 3):

397

398   **Node 4. Pterosauria**, *sensu* Kellner (2003) ([*Preondactylus bufarinii + Austriadactylus*

399   *cristatus*]/Preondactylia + [Caviramidae + Zambellisauria])

400   Definition: Node-based - the most recent common ancestor of the Anurognathidae,

401   *Preondactylus bufarinii* and *Quetzalcoatlus northropi* and all their descendants (Kellner, 2003).

402   Character support: 7 (1-->3), 9 (0-->1), 16 (1-->2), 22 (0-->1), 39 (0-->1), 40 (0-->1), 58 (0-->1), 60

403   (0-->1), 70 (0-->1), 74 (0-->1), 75 (0-->1), 91 (0-->1), 94 (0-->1), 117 (0-->1), 120 (2-->0).

404   Remarks: The definition given by Kellner (2003) is sufficient to contain all taxa found in this

405   analysis to be contained within the pterosaur group. As *Preondactylus bufarinii*, together with

406   *Austriadactylus cristatus*, forms the earliest diverging clade within Pterosauria – a monophyletic

407   Preondactylia – this definition for Pterosauria encompasses the same set of taxa as

408 Pterosauromorpha, *sensu* Padian (1997). Pterosauria would, in this hypothesis, take precedence

409 over Pterosauromorpha. However, it should be worth noting that, in results that do not find

410 Preondactylia to be the earliest diverging pterosaur clade (e.g., Britt et al. 2018), Pterosauria

411 would encompass fewer taxa than Pterosauromorpha, as certain clades would fall outside of

412 the taxa encompassed by the definition for Pterosauria given by Kellner (2003). In the example

413 of Britt et al. (2018), Austriadraconidae would not be within Pterosauria but rather would be

414 non-pterosaurian pterosauromorphs, under such a regime (see below).

415

416 **Node 5. Preondactylia**, *sensu* Andres, Clark and Xu (2014) (*Preondactylus bufarinii* +

417 *Austriadactylus cristatus*)

418 Definition: The least inclusive clade that includes *Preondactylus bufarinii* and *Austriadactylus*

419 *cristatus*.

420 Character support: 11 (0-->1), 48 (0-->1), 49 (0-->1).

421 Remarks: Often found to be the earliest diverging members of Pterosauria (e.g., Dalla Vecchia

422 2019), or early diverging members of 'Eopterosauria' (e.g., Andres, Clark and Xu, 2014;

423 Upchurch et al., 2015), this small clade is fairly consistently recovered among early pterosaur

424 cladistic studies, with the notable exception of Codorniú et al. (2016).

425

426 **Unnamed clade** (Caviramidae + Zambellisauria)

427 Character support: 45 (1-->0), 47 (1-->0), 77 (0-->1), 95 (0-->1).

428   Remarks: This clade contains all pterosaur taxa except for the clade containing *Preondactylus*

429   *bufarinii + Austriadactylus cristatus* i.e., all pterosaurs more 'derived' than Preondactylia. This

430   clade has consistently been found among studies (e.g., Codorniú et al., 2016; Britt et al., 2018;

431   Dalla Vecchia, 2019), although the placement of certain taxa within this clade varies, for

432   example in the results of Britt et al. (2018), this clade does not contain *Arcticodactylus*

433   *cromptonellus* and *Austriadraco dallavecchiai* (see Figure 1C). It may prove necessary in the

434   future to erect a stem-based clade to contain all taxa more closely related to, as an example,

435   *Quetzalcoatlus northropi* than to *Preondactylus bufarinii*.

436

437   **Node 7: Caviramidae** (new clade)

438   Definition: Node-based – the least inclusive clade that includes *Arcticodactylus cromptonellus*

439   and *Caviramus schesaplanensis* (new).

440   Etymology: For *Caviramus schesaplanensis* – one of two anchoring member taxa used in the

441   node-based definition for the clade, as outlined above.

442   Character support: 3 (0-->1), a skull that is curved down caudally; 12 (0-->1), a jugal process of

443   the maxilla that is subtrapezoidal, tapering to a point only distally, and a proximal part with

444   parallel dorsal and ventral margins; 43 (0-->1), a dentition that has tri- to quinticuspid tooth

445   crowns; 81 (0-->1), a wing phalanx two that is as long as the ulna.

446   Remarks: This clade has been recovered in the recent analysis of Dalla Vecchia (2019) and is

447   also supported in the first analysis of this study by a number of shared anatomical character

448   states, or synapomorphies (see above). The topology within the clade varies between the

449   analyses of Dalla Vecchia (2019) and this study, but both find the same set of taxa and

450   specimens to fall within it. This early diverging subgroup contains within it the austriadraconids

451   of Kellner (2015) and a handful of other Triassic taxa and specimens, including the as yet

452   unnamed MCSNB 8950, which has previously been the source of phylogenetic uncertainty in

453   other studies (see Britt et al., 2018). This clade is the least consistently supported among the

454   various analyses of this study and this is discussed further below. However, it is worth noting

455   that the clade was found in both the analysis that used only new outgroup taxa but no new

456   characters and the analysis that used both. The internal topology differed between these two

457   analyses, as did the position of the clade within Pterosauria, but the constituent taxa was

458   consistent, and consistent with the results of Dalla Vecchia (2019).

459

460   **Node 6. Austriadraconidea**, *sensu* Kellner (2015) (*Arcticodactylus cromptonellus + Austriadraco*

461   *dallavecchiai + Seazzadactylus venieri*)

462   Definition: The least inclusive clade that includes *Arcticodactylus cromptonellus* and

463   *Austriadraco dallavecchiai*, *sensu* Kellner (2015).

464   Character support: 103 (1-->0), 120 (0-->1).

465   Remarks: This clade was named by Kellner (2015), but was not supported in a number of other

466   recent analyses of early pterosaurs (e.g., Andres, Clark and Xu, 2014; Upchurch et al., 2015).

467   However, this close relationship was found in the more recent analyses of Britt et al. (2018),

468   who recovered the clade as the earliest diverging within Pterosauria, and then Dalla Vecchia

469   (2019), who, like this study, found the clade to be slightly more 'derived'. Unlike either of the

470   aforementioned studies, this study has found that the clade also contains *Seazzadactylus*

471   *venieri*; as in the analysis of Dalla Vecchia (2019) this grouping of taxa fall within a larger clade

472   of early-diverging pterosaur taxa (here named as Caviramidae, clade nov.).

473

474   **Unnamed clade** (*Carniadactylus rosenfeldi* + '*Raeticodactylus*' *filisurensis*, *Caviramus*

475   *schesaplanensis* + MCSNB 8950)

476   Character support: 11 (0-->2), 21 (0-->1), 65 (0-->1), 76, (0-->1), 80 (0-->1).

477   Remarks: This clade was also recovered in the analysis by Dalla Vecchia (2019) and contained

478   the same taxa and the same internal topology.

479

480   **Node 8. Zambellisauria** (new clade) (*Peteinosaurus zambelli* + Macronychoptera)

481   Definition: Node-based – the least inclusive clade that includes *Peteinosaurus zambelli*,

482   *Dimorphodon macronyx*, *Pterodactylus antiquus* and *Quetzalcoatlus northropi* (new).

483   Etymology: The clade name honours Rocco Zambelli, curator of the Bergamo natural history

484   museum, for whom *Peteinosaurus zambelli* was named; *P. zambelli* being one of the two taxa

485   chosen as an anchor in this cladistic definition, . Zambelli (1973) also named *Eudimorphodon*

486   *ranzii*, a well-known and important early pterosaur and putative member of Zambellisauria (see

487   Andres, Clark and Xu, 2014; Britt et al., 2018; Dalla Vecchia, 2019).

488   Character support: 56 (0-->1), more than three sacral vertebrae; 59 (0-->1), filiform processes of

489   the caudal zygapophyses present in caudal vertebrae.

490   Remarks: This clade is consistently recovered by most modern analyses (e.g., Britt et al. 2018,

491   Dalla Vecchia, 2019) and in all of the analyses in this study, regardless of the optimality criteria

492   used in searching for trees in the analyses, and both with and without the inclusion of the new

493   anatomical characters. Such a clade was not found in the analysis of Andres, Clark and Xu

494   (2014), who instead placed Peteinosaurus zambelli as sister-taxon to Eudimorphodontoidae,

495   within a monophyletic Eopterosauria – a hypothesis that has fallen out favour in more recent

496   studies and is not supported in any of the analyses carried out in this study.

497

498   **Node 9. Macronychoptera** (Dimorphodontidae + Lonchognatha)

499   Character support: 63 (1->2), 64 (0->1), 65 (0->1)

500

501   **Node 10. Dimorphodontidae** (*Dimorphodon macronyx + Caelestiventus hanseni*)

502   Character support: 7 (3-->2), 8 (0-->1), 10 (0-->1), 12 (0-->2), 20 (0-->1), 26 (0-->1), 35 (0-->1), 41

503   (0-->1), 48 (0-->1), 52 (0-->1), 96 (1-->0), 118 (1-->2).

504   Remarks: As in the analyses of Britt et al. (2018) and Dalla Vecchia (2019), this study finds a

505   close relationship between *Dimorphodon macronyx* and *Caelestiventus hanseni*

506

507 **Node 11. Lonchognatha**

508 Character support: 70 (1-->2), 80 (0-->2), 88 (0-->1)

509 Remarks: The composition of Lonchognatha and its possible sister-taxon relationship with

510 Dimorphodontidae has been fairly consistently recovered in recent analyses (Britt et al., 2018;

511 Dalla Vecchia, 2019), although other studies have placed Lonchognatha within Novialoidae

512 (e.g., Andres, Clark and Xu, 2014). This second hypothesis is not recovered in all but one of the

513 analyses of this study. That is to say, in only one analysis does this study find

514 *Campylognathoides* to be 'less derived' than *Eudimorphodon* species (see below).

515

516   In the second full analysis, utilising both the new taxa and new anatomical characters,

517 TBR branch swapping after a differently configured New Technology search produced 2 MPTs,

518 each also of length 390 steps. However, in this analysis, the resolution in this tree was greatly

519 reduced (Figure 4A). While Aphanosauria and Lagerpetidae were still found outside of

520 Ornithodira, and the monophyly of and interrelationships within Dinosauriformes remained

521 consistent with previous analyses, in this second full analysis, the interrelationships between

522 the groups within Pteorsauria was not clearly resolved – although monophyletic

523 Austriadraconidae and Novialoidea were both found again. The large polytomy at the base of

524 Pterosauria is more reminiscent of the full-taxon-sample analysis carried out using TNT by Britt

525 et al. (2018). As in Britt et al. (2018), the specimen MCSNB 8950 was removed as a wildcard

526 taxon and the analysis re-run. In this reduced analysis, a single tree was recovered (Figure 4B).

527 In this tree, Austriadraconidae is once again recovered as monophyletic, as in the first analysis

528   of this study and the second full-taxon-range analysis with TBR. However, in the reduced

529   second analysis, but unlike in the full second analysis, Austriadraconidae contains

530   *Seazzadactylus venieri*. This is similar to the result obtained in the first analysis, although the

531   position of Austriadraconidae is different in both the reduced and full second analyses

532   (compare Figure 3 and Figure 4B).

533   Finally, in the implied weights analyses, the topology within Pterosauria differed from

534   the first and second analyses (Figure 5A-B). Only one tree was produced in each of three

535   analyses, with lengths of 37.03690, 27.65440, and 17.04634 for k = 3, 5 and 10 respectively. In

536   the first two of these analyses (k = 3 and 5), the earliest diverging clade of pterosaurs are the

537   Austriadraconidae – however, this clade was not found to contain *Seazzadactylus venieri* in this

538   analysis. The clade made up of *Austriadactylus cristatus* and *Preondactylus buffarini*, named

539   above as Preondactylidae, then forms the sister-taxon of the clade of *Peteinosaurus zambelli* +

540   Macronychoptera, named above as Zambellisauria. In searches with k at or above 10 however,

541   the structure of the tree once again changes, with the preondactylids once again falling out as

542   the most stem-ward of the clades in Pterosauria and, as in some of the previous analyses of this

543   study, Austriadraconidae was found to contain *Seazzadactylus venieri* (Figure 5B). Caviramidae

544   was not supported in any of these analyses, whereas Zambellisauria was consistently recovered

545   in each. Likewise, clades such as Dimorphodontidae, Lonchognatha, Novialoidea, Caelidracones,

546   Monofenestrata, Pterodactyloidea, and Anurognathidae were all found to be largely consistent

547   through the various implied weights parsimony analyses. The taxon referred to as

548   '*Dimorphodon*' *weintraubi* was recovered closer to *Sordes pilosus* and the monofenestratans

549   than to Anurognathidae in the lower weighted implied weights analyses, but closer to

550   Anurognathidae in analyses with a k value = 10 or more. In all the implied weights analyses, the

551   'ramphorynchids' we found to be more closely related to Monofenestrata than to *Sordes*

552   *pilosus*, which was recovered as the sister-taxon to the clade of Monofenestrata + the

553   'ramphorynchids' (Figure 5A-B).

554   The largest difference in the arrangement of taxa between the implied weights analyses

555   for k < 10 and for k = 10 or more is the composition of Zambellisauria. In all the analyses

556   Zambellisauria is recovered as monophyletic, but in the lower k value analyses, contains, *inter*

557   *alia*, *Seazzadactylus venieri, Carniadactylus rosenfeldi, 'Raeticodactylus' filisurensis, Caviramus*

558   *schesaplanensis* and the specimen MCSNB 8950, whereas in analyses with k = 10 or more, these

559   five operational taxonomic unites were recovered outside of Zambellisauria (see Figure 5A-B).

560   These differences in topology between the results of the various implied weights parsimony

561   analyses suggests that certain anatomical characters in the dataset are broadly distributed

562   across the taxa whilst also being important for uniting certain clades – as the implied weighting

563   factor is increased, the weight of characters that could support the monophyly of clades such as

564   Caviramidae (see above), or support a 'basal' position for Austriadraconidae, are being reduced

565   by the search programme because these characters appear to be more homoplastic. However,

566   these effects may be reduced by the further addition of anatomical characters as the dataset is

567   expanded upon in subsequent studies.

568

569   **DISCUSSION**

570   It is clear from the variability in the results of the analyses in this study alone that the

571   phylogenetic position of certain early pterosaur clades is still highly unstable, even with better

572   taxon and character sampling. When analysed using certain methods, the addition of more

573   avemetatarsalian taxa and new characters provided further support for certain clades and

574   helped to revolve interrelationships between genera within some subclades. In addition, this

575   expanded analysis changed the composition of some recognised clades, from example

576   Austriadraconidae, which was, in analysis one, found to also include the recently described

577   *Seazzadactylus venieri* for the first time. Choice of taxa and anatomical characters clearly has

578   had some effect on the interrelationships of the ingroup pterosaur taxa, as has also been

579   demonstrated to be the case in early studies of dinosaur (e.g., Müller and Dias-da-Silva, 2019).

580   This study has taken steps to address the under-sampling from closely related ornithdiran

581   clades in previous pterosaur studies, but much work needs to be done to further broaden the

582   datasets used in phylogenetic analyses, in terms of both the operational taxa and anatomical

583   characters and character states.

584   What this study has also demonstrated is how using different approaches to

585   phylogenetic analysis can produce substantially different results when it comes to the

586   interrelationships within Pterosauria. The earliest diverging clade of pterosaurs has been found

587   to be either the Preondactylia (in analysis one and in implied weights analyses for k = 10 or

588   more), or Austriadraconidae (when using TBR branch swapping or implied weights with k < 10).

589   However, in spite of this uncertainty, some clades have been consistently recovered

590   throughout the various analyses of this study, and many too have been supported in previous

591   analyses (Andres, Clark and Xu, 2014; Britt et al., 2018; Dalla Vecchia, 2019). This would suggest

592   that the evidence is increasingly supporting the validity of such monophyletic subsets within

593   Pterosauria, and these should, for the sake of stability and clarity in future research, be defined

594   and, if not already so, named. This study has erected two clades for these purposes.

595   Zambellisauria is erected to contain all pterosaur taxa descended from the most recent

596   common ancestor of *Peteinosaurus zambellii* and the various members of Macronychoptera.

597   This clade is now consistently recovered in most phylogenetic analyses and is strongly

598   supported in the results of these analyses. Should *Peteinosaurus zambellii* be recovered in a

599   much more stem-ward position in the future, for example if future analyses resurrect

600   Eopterosauria, with *Peteinosaurus zambellii* contained within it, the definition for

601   Zambelliasauria would then encompass the same set of taxa as Pterosauria and, as a result,

602   would become obsolete. However, in the emerging consensus on early pterosaur relationships

603   in this part of the tree, the clade Zambellisauria remains well-supported and distinct for now.

604   Under the definition given for Caviramidae, as also given above, in scenarios in which a

605   distinct monophyletic group is found to be more 'derived' than Preondactylia but outside of the

606   clade containing all other, more 'derived' pterosaurs (see Figure 3), the name would be distinct

607   and valid. However, in scenarios such as presented in the results of the second and third

608   analyses, or in other studies (e.g., Britt et al., 2018) the clade Caviramidae would contain the

609   same taxa as Pterosauria and therefore become obsolete. However, the validity of Caviramidae

610   is not dependent on the position taxa such as *Peteinosaurus zambellii* and *Eudimorphodon*

611   *ranzii*, which have a tendancy to 'bounce around' the tree, so long as the Autriadraconids are

612   not found to be either more or less 'derived' than the small clade containing *Carniadactylus*

613   *rosenfeldi*, '*Raeticodactylus*' *filisurensis*, and *Caviramus schesaplanensi*. It is only in hypotheses

614   in which Austriadraconids fall as the earliest diverging members of Pterosauria (e.g., analysis

615   two of this study; Britt et al., 2018), or are paraphyletic (e.g., Codorniú et al., 2016), that

616   Caviramidae would be invalid as a distinct clade.

617   It would also appear from the results of these analyses, and other recent works, that the

618   higher-level interrelationships between pterosaur taxa are becoming more stabilised. Clades

619   such as Dimorphodontidae, Lonchognatha, Novialoidea, Caelidracones, Monofenestrata,

620   Pterodactyloidea, and Anurognathidae are all consistently found in these analyses, and only the

621   composition of each varies a little between them. In particular *Eudimorphodon ranzii* is a

622   particularly difficult taxon in terms of its position, having been recovered in a range of 'derived'

623   and more 'basal' positions within the tree, in the both the analyses of this study and previous

624   recent studies. With the addition of more taxa and more characters, and as more phylogenetic

625   analysis techniques are turned on the question of pterosaur systematics, such problems of

626   placing difficult to classify taxa may yet be resolved.

627

628   **CONCLUSIONS**

629   Pterosaur interrelationships have been shown to vary between analyses, with the fundamental

630   interrelationships that are recovered being dependant upon the method of analysis, the

631   character choice and taxon choice. The addition of more appropriate avemetatarsalian

632   outgroup taxa to the early pterosaur dataset of Britt et al. (2018) made a difference in the

633   overall topologies recovered within the various pterosaur clades, and to the fundamental

634   structure of the pterosaur tree. However, a more dramatic change in result could be achieved

635   through the use of different phylogenetic analysis techniques, such and implied weights

636   parsimony. While some pterosaur clades have proven to be stable throughout the various

637   analyses, others have not, particularly those that fall most stem-ward on the tree. More needs

638   to be done to resolve this issue, but wider character and taxon sampling in the future would be

639   an important first step. Additional, utilisation of a wider range of phylogenetic analysis

640   techniques should be adopted to test the strength of hypotheses of early pterosaur

641   interrelationships as more taxa and character states are added.

REFERENCES

643

644   Andres BB. 2006. The earliest pterosaurs. Journal of Vertebrate Paleontology 26(3):37A.

645   Andres BB, Clark J, Xu X. 2014. The Earliest Pterodactyloid and the Origin of the Group. Current
646   Biology. 24 (9): 1011–6. doi:10.1016/j.cub.2014.03.030.

647   Baron MG, Williams ME. 2018. A re-evaluation of the enigmatic dinosauriform Caseosaurus
648   crosbyensis from the Late Triassic of Texas, USA and its implications for early dinosaur
649   evolution. Acta Palaeontologica Polonica. 63 (1): 129-145 doi:10.4202/app.00372.2017

650   Baron MG, Norman DB, and Barrett PM. 2017a. A new hypothesis of dinosaur relationships and
651   early dinosaur evolution. Nature, 543: 501–506. doi:10.1038/nature21700

652   Baron MG, Norman DB, Barrett PM. 2017b. Untangling the dinosaur family tree: a rebuttal.
653   Nature. 551:E4–E5.

654   Baron MG, Norman DB, Barrett PM. 2017c. Postcranial anatomy of Lesothosaurus diagnosticus
655   (Dinosauria: Ornithischia) from the Lower Jurassic of southern Africa: implications for basal
656   ornithischian taxonomy and systematics. Zoological Journal of the Linnean Society 179(1):125-
657   168

658   Barrett PM, Butler RJ, Yates AM, Baron MG, Choiniere JN. 2016. New specimens of the basal
659   ornithischian dinosaur Lesothosaurus diagnosticus Galton, 1978 from the Early Jurassic of South
660   Africa. Palaeontologia Africana 50:48-63.

661   Barrett PM, Butler RJ, Edwards NP, Milner AR. 2008. Pterosaur distribution in time and space:
662   an atlas. Zitteliana B28:61-107.

663   Bennett SC. 2007. A second specimen of the pterosaur Anurognathus ammoni.
664   Paläontologische Zeitschrift 81(4):376-398.

665   Bennett SC. 2013. The phylogenetic position of the Pterosauria within the Archosauromorpha
666   reexamined. Historical Biology 25(22), 545–563.

667   Bennett SC. 2014. A new specimen of the pterosaur Scaphognathus crassirostris, with
668   comments on constraint of cervical vertebrae number in pterosaurs. Neues Jahrbuch für
669   Geologie und Paläontologie Abhandlungen 271(3):327-348.

670   Bennett SC. 2020. Reassessment of the Triassic archosauriform Scleromochlus taylori: neither
671   runner nor biped, but hopper. PeerJ 8:e8418 https://doi.org/10.7717/peerj.8418.

672   Benton MJ. 1985. Classification and phylogeny of the diapsid reptiles. Zoological Journal of the
673   Linnean Society 84:97-164.

674   Butler RJ. 2005. The 'fabrosaurid' ornithischian dinosaurs of the Upper Elliot Formation (Lower
675   Jurassic) of South Africa. Zoological Journal of the Linnean Society 145:175-218.

676   Butler RJ. 2010. The anatomy of the basal ornithischian dinosaur Eocursor parvus from the
677   lower Elliot Formation (Late Triassic) of South Africa. Zoological Journal of the Linnean Society
678   160:648-684.

679   Butler RJ, Smith R, Norman DB. 2007. A primitive ornithischian dinosaur from the Late Triassic
680   of South Africa and the early evolution and diversification of Ornithischia. Proceedings of the
681   Royal Society B 274:2041-2046.

682   Butler RJ, Porro LB, Norman DB. 2008. A juvenile skull of the primitive ornithischian dinosaur
683   Heterodontosaurus tucki from the 'Stormberg' of southern Africa. Journal of Vertebrate
684   Paleontology 28:702-711.

685   Britt BB, Dalla Vecchia FM, Chure DJ, Engelmann GF, Whiting MF, Scheetz RD. 2018.
686   Caelestiventus hanseni gen. et sp. nov. extends the desert-dwelling pterosaur record back 65
687   million years. Nature Ecology & Evolution 2(9):1386-1392.

688   Brusatte SL, Nesbitt SJ, Irmis RB, Butler RJ, Benton MJ, Norell MA. 2010. The origin and early
689   radiation of dinosaurs. Earth-Science Reviews 101(1), 68-100.

690   Cau A. 2018. The assembly of the avian body plan: a 160-million-year long process. Bollettino
691   della Società Paleontologica Italiana. 57 (1): 1–25. doi:10.4435/BSPI.2018.01.

692   Codorniú L, Paulina Carabajal A, Pol D, Unwin D, Rauhut OW. 2016. A Jurassic pterosaur from
693   Patagonia and the origin of the pterodactyloid neurocranium. PeerJ. 2016;4:e2311.
694   doi:10.7717/peerj.2311.

695   Dalla Vecchia FM. 2004 A review of the Triassic pterosaur record. Rivista del Museo Civico di
696   Scienze Naturali "E. Caffi", Bergamo 22(2003):13-29.

697   Dalla Vecchia FM. 2009a. Anatomy and systematics of the pterosaur Carniadactylus gen. n.
698   rosenfeldi (Dalla Vecchia, 1995) Rivista Italiana di Paleontologia e Stratigrafia 115(2):159-186.

699   Dalla Vecchia FM. 2009b. The first Italian specimen of Austriadactylus cristatus (Diapsida,
700   Pterosauria) from the Norian (Upper Triassic) of the Carnic Prealps. Rivista Italiana di
701   Paleontologia e Stratigrafia 115(3):291-304.

702   Dalla Vecchia FM. 2010. A new pterosaur from the upper Triassic of northeastern Italy. Acta
703   Geoscientica Sinica 31(supp 1):17.

704   Dalla Vecchia FM. 2013. Triassic pterosaurs. In: Nesbitt SJ, Desojo JB, Irmis RB, eds. Anatomy,
705   Phylogeny and Palaeobiology of Early Archosaurs and their Kin. London: Geological Society
706   London, Special Publication. 379:119-155.

707   Dalla Vecchia FM. 2014. Gli pterosauri triassici. Udine: Museo Friulano di Storia Naturale.
708   54:319 Pubblicazione del Museo Friulano di Storia Naturale

709   Dalla Vecchia FM. 2019. Seazzadactylus venieri gen. et sp. nov., a new pterosaur (Diapsida:
710   Pterosauria) from the Upper Triassic (Norian) of northeastern Italy. PeerJ 7:e7363
711   https://doi.org/10.7717/peerj.7363.

712   Dalla Vecchia FM, Wild R, Hopf H, Reitner J. 2002. A crested rhamphorhynchoid pterosaur from
713   the Late Triassic of Austria. Journal of Vertebrate Paleontology 22(1):196-199.

714   Dzik J 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic
715   of Poland. Journal of Vertebrate Paleontology. 23 (3): 556–574. doi:10.1671/a1097.

716   Ezcurra MD. 2016. The phylogenetic relationships of basal archosauromorphs, with an
717   emphasis on the systematics of proterosuchian archosauriforms. PeerJ 4:e1778
718   doi.org/10.7717/peerj.1778.

719   Galton PM. 2014. Notes on the postcranial anatomy of the heterodontosaurid dinosaur
720   Heterodontosaurus tucki, a basal ornithischian from the Lower Jurassic of South Africa. Revue
721   de Paléobiologie, Genève. 1. 33: 97–141.

722   Gauthier JA. 1986. Saurischian monophyly and the origin of birds. The Origin of Birds and the
723   Evolution of Flight, K. Padian (ed.), Memoirs of the California Academy of Sciences 8:1–55.

724   Goloboff PA, Farris JS, Nixon K. 2008. TNT, a free program for phylogenetic analysis. Cladistics
725   24, 774–786. doi:10.1111/j.1096-0031.2008.00217.

726   Hone DWE, Benton MJ. 2007. An evaluation of the phylogenetic relationships of the pterosaurs
727   among archosauromorph reptiles. Journal of Systematic Palaeontology, 5,

728   465–469.

729   Hone DWE, Tischlinger H, Frey E, Röper M. 2012. A new non-pterodactyloid pterosaur from the
730   Late Jurassic of Southern Germany. PLOS ONE 7(7):e39312.

731   Huene Fv. 1914. Beiträge zur Geschichte der Archosaurier. Geologische und paläontologische
732   Abhandungen, NF 13:3-53.

733   Irmis, RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A. 2007. A Late Triassic
734   dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science. 317 (5836):
735   358–361. doi:10.1126/science.1143325.

736   Kellner AWA. 2003. Pterosaur phylogeny and comments on the evolutionary history of the
737   group. In: Buffetaut E, Mazin J-M, eds. Evolution and Palaeobiology of Pterosaurs. London:
738   Geological Society London, Special Publication. 217:105-137

739   Kellner AWA. 2015. Comments on Triassic pterosaurs with discussion about ontogeny and
740   description of new taxa. Anais da Academia Brasileira de Ciências 87(2):669-689.

741   Kellner AWA, Rodrigues T, Costa FR, Weinschütz LC, Figueiredo RG, Souza GA, Brum AS,
742   Eleutério LHS, Mueller CW, Sayão JM. 2019. Pterodactyloid pterosaur bones from Cretaceous
743   deposits of the Antarctic Peninsula. Anais da Academia Brasileira de Ciências 91: e20191300.
744   DOI 10.1590/0001-3765201920191300.

745   Knoll F. 2002a. Les fabrosauridae Galton, 1972. (Dinosauria: Ornithischia): répartition
746   géographique et stratigraphique; systématique et phylogénie. Paris: Muséum national
747   d'Histoire naturelle. (Vol. 1) Pp. 243 +(Vol. 2) 71 pl

748   Knoll F. 2002b. Nearly complete skull of Lesothosaurus (Dinosauria: Ornithischia) from the
749   Upper Elliot Formation (Lower Jurassic: Hettangian) of Lesotho. Journal of Vertebrate
750   Paleontology 22(2):238-243

751   Knoll F. 2002c. New skull of Lesothosaurus (Dinosauria: Ornithischia) from the Upper Elliot
752   Formation (Lower Jurassic) of southern Africa. Geobios 35:595-603.

753   Langer MC. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph Saturnalia
754   tupiniquim (Late Triassic, Brazil). PaleoBios, 23(2):1-40.

755   Langer MC, Benton MJ. 2006. Early dinosaurs: a phylogenetic study. Journal of Systematic
756   Palaeontology 4:309–358.

757   Langer MC, Abdala F, Richter M, Benton MJ. 1999. A sauropodomorph dinosaur from the Upper
758   Triassic (Carnian) of southern Brazil. Comptes Rendus de l'Académie des Sciences, 329: 511-
759   517.

760   Langer MC, Ezcurra MD, Rauhut OWM, Benton MJ, Knoll F, McPhee BW, Novas FE, Pol D,
761   Brusatte SL. 2017. Untangling the dinosaur family tree. Nature 551 (7678): E1–E3.
762   doi:10.1038/nature24011.Müller RT, Dias-da-Silva S. 2019. Taxon sample and character coding

763   deeply impact unstable branches in phylogenetic trees of dinosaurs, Historical Biology, 31:8,
764   1089-1092, doi:10.1080/08912963.2017.1418341.

765   Lee MSY, Baron MG, Norman DB, Barrett PM. 2019. Dynamic biogeographic models and
766   dinosaur origins. Earth Environmental Science Transactions of the Royal Society of Edinburgh
767   Vol. 109, Issue 1-2 (Fossils, Function and Phylogeny: Papers on Early Vertebrate Evolution in
768   Honour of Professor Jennifer A. Clack), 325-332 doi:10.1017/S1755691018000920.

769   Lü JC, Azuma Y, Dong ZM, Barsbold R, Kobayashi Y, Lee YN. 2009 New material of dsungaripterid
770   pterosaurs (Reptilia: Pterosauria) from western Mongolia and its paleoecological implications.
771   Geol. Mag. 146, 690–700. doi:10.1017/S0016756809006414.

772   Martínez RN, Sereno PC, Alcober OA, Colombi CE, Renne PR, Montañez IP, Currie BS. 2011. A
773   basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. Science 331:206-
774   210.

775   Martínez RN, Apaldetti C, Correa GA, Abelín D. 2016. A Norian lagerpetid dinosauromorph from
776   the Quebrada del Barro Formation, northwestern Argentina. Ameghiniana. 53 (1): 1–13.
777   doi:10.5710/AMGH.21.06.2015.2894

778   Martz JW, Small BJ. 2019. Non-dinosaurian dinosauromorphs from the Chinle Formation (Upper
779   Triassic) of the Eagle Basin, northern Colorado: Dromomeron romeri (Lagerpetidae) and a new
780   taxon, Kwanasaurus williamparkeri (Silesauridae) PeerJ 7:e7551
781   https://doi.org/10.7717/peerj.7551.

782   Müller RT, Dias-da-Silva S. 2019. Taxon sample and character coding deeply impact unstable
783   branches in phylogenetic trees of dinosaurs, Historical Biology, 31:8, 1089-1092, DOI:
784   10.1080/08912963.2017.1418341.

785   Nesbitt SJ. 2011. The Early Evolution of Archosaurs: Relationships and the Origin of Major
786   Clades. Bulletin of the American Museum of Natural History 352: 1–292.

787   Nesbitt SJ, Irmis RB, Parker WG, Smith ND, Turner AH, Rowe T. 2009a. Hindlimb osteology and
788   distribution of basal dinosauromorphs from the Late Triassic of North America. Journal of
789   Vertebrate Paleontology. 29 (2): 498–516. doi:10.1671/039.029.0218.

790   Nesbitt SJ, Smith ND, Irmis RB, Turner AH, Downs A, Norell MA. 2009b. A complete skeleton of a
791   Late Triassic saurischian and the early evolution of dinosaurs. Science, 326 (5959): 1530–1533,
792   doi:10.1126/science.1180350.

793   Nesbitt SJ, Sidor CA, Irmis RB, Angielczyk KD, Smith RMH, Tsuji LA. 2010 Ecologically distinct
794   dinosaurian sister group shows early diversification of Ornithodira. Nature 464(7285):95-8.

795   Nesbitt SJ, Desojo JB, Irmis RB. 2013. Anatomy, Phylogeny and Palaeobiology of Early
796   Archosaurs and Their Kin. Geological Society of London.

797   Nesbitt SJ, Butler RJ, Ezcurra MD, Barrett PM, Stocker MR, Angielczyk KD, Smith RMH, Sidor CA,
798   Niedźwiedzki G, Sennikov AG, Charig AJ. 2017. The earliest bird-line archosaurs and the
799   assembly of the dinosaur body plan. Nature. 544 (7651): 484–487 doi:10.1038/nature22037.

800   Nesbitt SJ, Butler RJ, Ezcurra MD, Charig AJ, Barrett PM. 2018 The anatomy of Teleocrater
801   rhadinus, an early avemetatarsalian from the lower portion of the Lifua Member of the Manda
802   Beds (Middle Triassic). J. Vertebr. Paleont. 37(Supp. 1), 142–177. doi:10.1080/
803   02724634.2017.1396539.

804   Norman DB, Crompton AW, Butler RJ, Porro LB, Charig AJ. 2011. The Lower Jurassic
805   ornithischian dinosaur Heterodontosaurus tucki Crompton & Charig, 1962: Cranial anatomy,
806   functional morphology, taxonomy, and relationships. Zoological Journal of the Linnean Society:
807   182–276. doi:10.1111/j.1096-3642.2011.00697.x.

808   Pacheco C, Müller RT, Langer MC, Pretto FA, Kerber L, Dias da Silva SD. 2019. Gnathovorax
809   cabreirai: a new early dinosaur and the origin and initial radiation of predatory dinosaurs. PeerJ.
810   doi:10.7717/peerj.7963.

811   Padian K. 1984. Pterosaur remains from the Kayenta Formation (Early Jurassic) of Arizona.
812   Palaeontology 27:407-413.

813   Padian K. 1997. Pterosauromorpha. In P.J. Currie and K. Padian (editors), Encyclopedia of
814   dinosaurs: 617–618. San Diego: Academic Press.

815   Padian K. 2008a. The Early Jurassic pterosaur Dorygnathus banthensis (Theodori, 1830) Special
816   Papers in Palaeontology 80:1-64

817   Padian K. 2008b. The Early Jurassic pterosaur Campylognathoides Strand, 1928. Special Papers
818   in Palaeontology 80:65-107

819   Parry LA, Baron MG, Vinther J. 2017. Multiple optimality criteria support Ornithoscelida. Royal
820   Society open science:4170833. doi.org/10.1098/rsos.170833.

821   Porro LB, Witmer LM, Barrett PM. 2015. Digital preparation and osteology of the skull of
822   Lesothosaurus diagnosticus (Ornithischia: Dinosauria) PeerJ 3:e1494.

823   Sereno PC, Martínez RN, Alcober OA. 2013. Osteology of Eoraptor lunensis (Dinosauria,
824   Sauropodomorpha). Basal sauropodomorphs and the vertebrate fossil record of the
825   Ischigualasto Formation (Late Triassic: Carnian-Norian) of Argentina. Journal of Vertebrate
826   Paleontology. Memoir. 12: 83–179. doi:10.1080/02724634.2013.820113.

827   Unwin DM. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand
828   (Cretaceous) of Eastern England. Mitteilungen aus dem Museum fur Naturkunde in Berlin,
829   Geowissenschaftliche Reihe 4: 189–221.

830   Unwin DM. 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut E,
831   Mazin J-M, eds. Evolution and Palaeobiology of Pterosaurs. London: Geological Society London,
832   Special Publication. 217:139-190.

833   Unwin DM, Bakhurina NN. 1994. Sordes pilosus and the nature of the pterosaur flight
834   apparatus. Nature 371, 62–64. https://doi.org/10.1038/371062a0.

835   Unwin DM, Bakhurina NN. 1995. Wing shape in pterosaurs. Nature 374: 315–316.

836   Unwin DM, Martill DM. 2007. Pterosaurs of the Crato Formation. In: D.M. Martill, G. Bechly,
837   and R.F. Loveridge (eds.), The Crato Fossil Beds of Brazil, 475–524. Cambridge University Press,
838   Cambridge.

839   Upchurch P, Andres B, Butler RJ, Barrett PM. 2015. An analysis of pterosaurian biogeography:
840   implications for the evolutionary history and fossil record quality of the first flying vertebrates.
841   Historical Biology 27, 697–717.

842   Vidovic SU, Martill DM. 2014. Pterodactylus scolopaciceps Meyer, 1860 (Pterosauria,
843   Pterodactyloidea) from the Upper Jurassic of Bavaria, Germany: The Problem of Cryptic
844   Pterosaur Taxa in Early Ontogeny. PLoS ONE 9(10): e110646.
845   doi.org/10.1371/journal.pone.0110646.

846   Zambelli R. 1973. Eudimorphodon ranzii gen. nov., sp. nov., uno pterosauro triassico. Istituto
847   Lombardo—Academia di Scienze e Lettere (Rendiconti di Scienze) B 107:27-32.

848

849

850

851

852

853   **Figures**

854

855   Figure 1. Previous recent hypotheses of early pterosaur relationships. A, the results of the
856   reduced taxon analysis by Britt et al. (2018); B, the results of the analysis by Dalla Vecchia
857   (2019); C, the results of the analysis by Andres, Clark and Xu (2014).

858   Figure 2. Strict consensus rule tree produced in the initial analysis that did not utilise any new
859   anatomical characters. Nodes: 1, Preondactylia; 2, Caviramidae (*clade novo*); 3, Zambellisauria
860   (*clade novo*).

861

862   Figure 3. Strict consensus rule tree produced in full analysis one, using equal weights
863   parsimony. Nodes: 1, Dinosauromorpha; 2, Dinosauriformes; 3, Dinosauria; 4, Pterosauria; 5,
864   Preondactylia; 6, Austriadraconidae; 7, Caviramidae (*clade novo*); 8, Zambellisauria (*clade*
865   *novo*); 9, Macronychoptera; 10, Dimorphodontidae; 11, Lonchognatha; 12, Novialoidea; 13,
866   Anurognathidae; 14, Caelidracones; 15, Monofenestrata; 16, Pterodactyloidea.

867

868   Figure 4. Strict consensus (A) and reduced strict consensus (B) trees produced when following
869   the analysis protocol of Ezcurra (2014) and using equal weights parsimony. White circle and
870   arrow indicate the position of Zambellisauria in this analysis.

871

872   Figure 5. Trees produced using implied weights implementation of parsimony for k values < 10
873   (A) and k values = 10 more (B). Coloured nodes and tips added to highlight the taxa whose
874   positions changed substantially between the implied weights parsimony analyses. White circles
875   and arrows indicate the position of Zambellisauria in each analysis.

876

877

878   **Tables**

879

880   Table 1. Sources of anatomical information for taxa added to the phylogenetic analyses.

881

Figure 1

Previous recent hypotheses of early pterosaur relationships.

A, the results of the reduced taxon analysis by Britt et al. (2018); B, the results of the analysis by Dalla Vecchia (2019); C, the results of the analysis by Andres, Clark and Xu (2014).

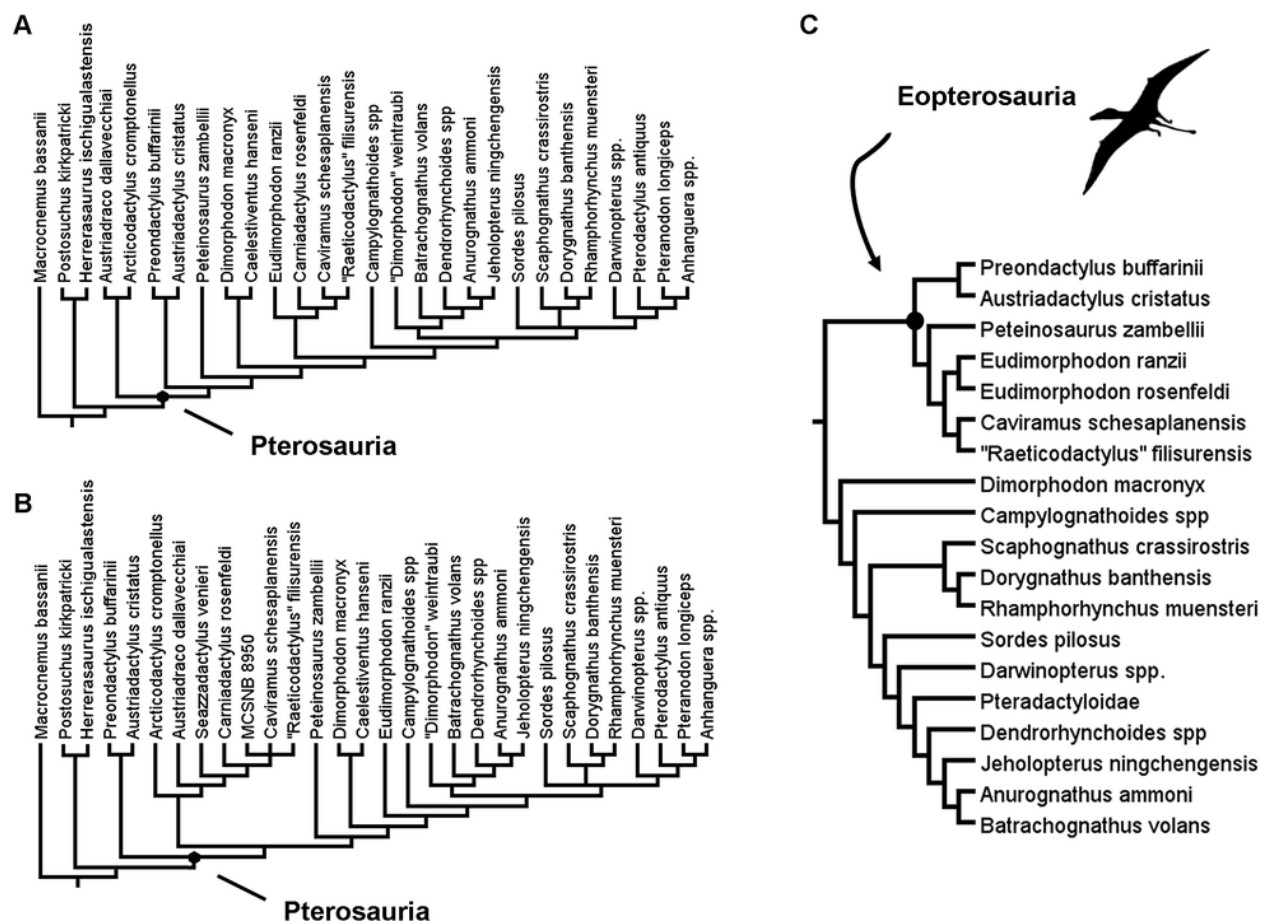



Figure 2

Strict consensus rule tree produced in the initial analysis that did not utilise any new anatomical characters.

Nodes: 1, Preondactylia; 2, Caviramidae (*clade novo*); 3, Zambellisauria (*clade novo*).

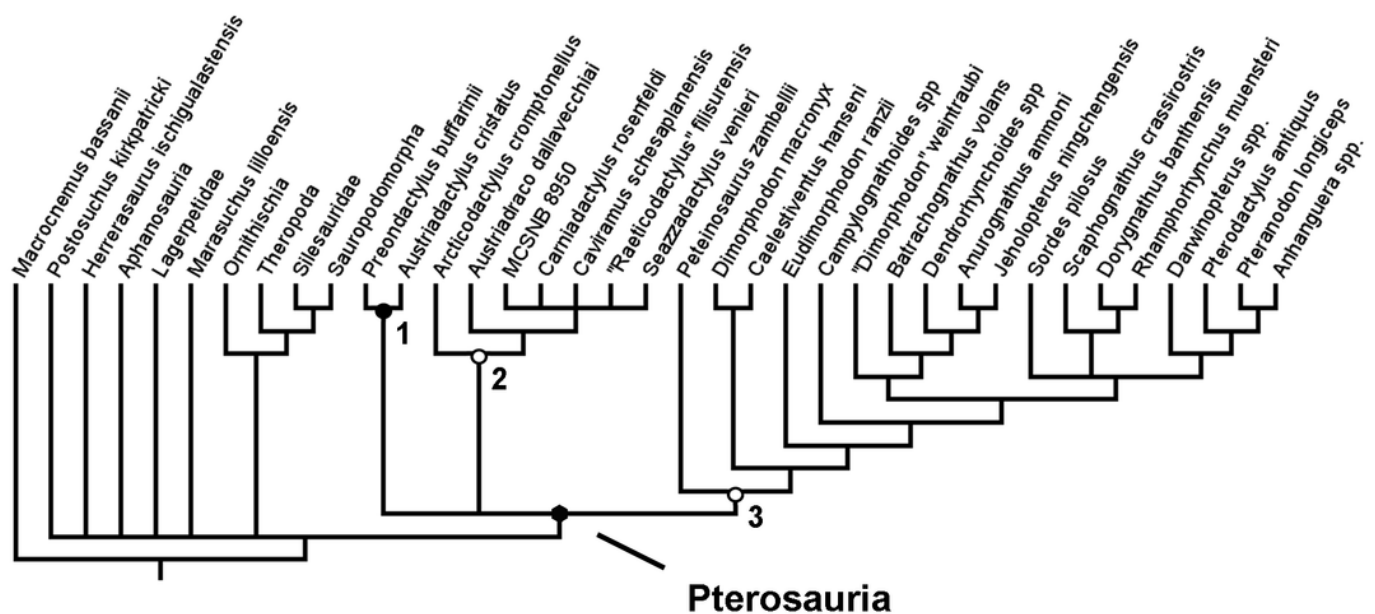



Figure 3

Strict consensus rule tree produced in full analysis one, using equal weights parsimony.

Nodes: 1, Dinosauromorpha; 2, Dinosauriformes; 3, Dinosauria; 4, Pterosauria; 5, Preondactylia; 6, Austriadraconidae; 7, Caviramidae (*clade novo*); 8, Zambellisauria (*clade novo*); 9, Macronychoptera; 10, Dimorphodontidae; 11, Lonchognatha; 12, Novialoidea; 13, Anurognathidae; 14, Caelidracones; 15, Monofenestrata ; 16, Pterodactyloidea.

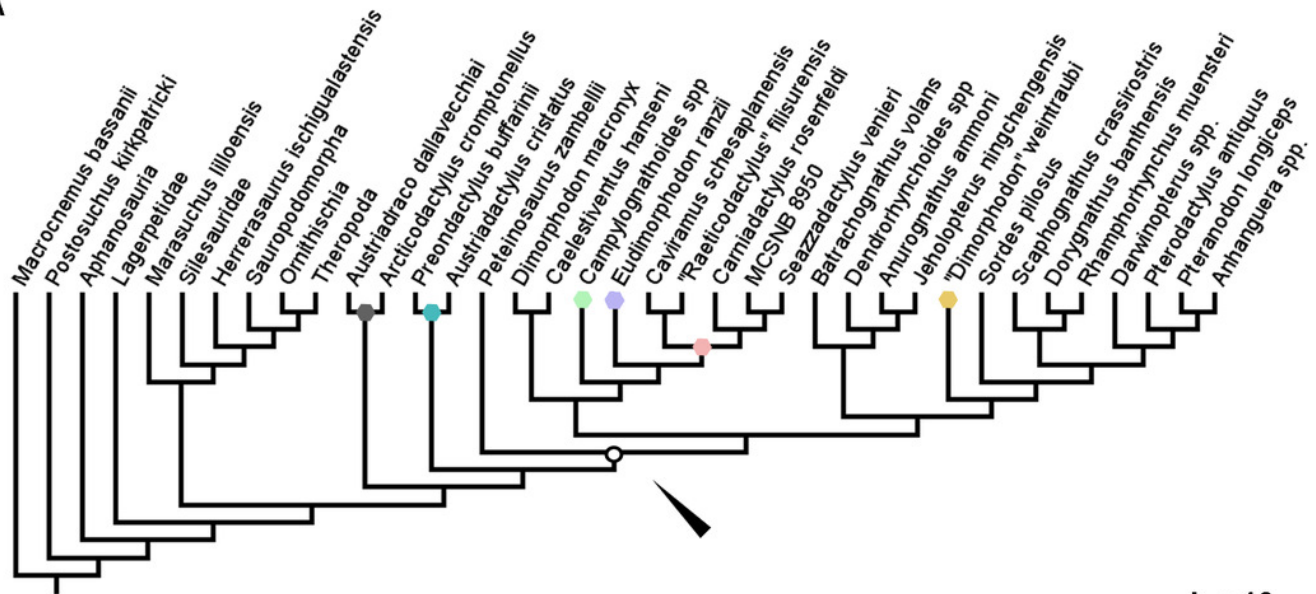
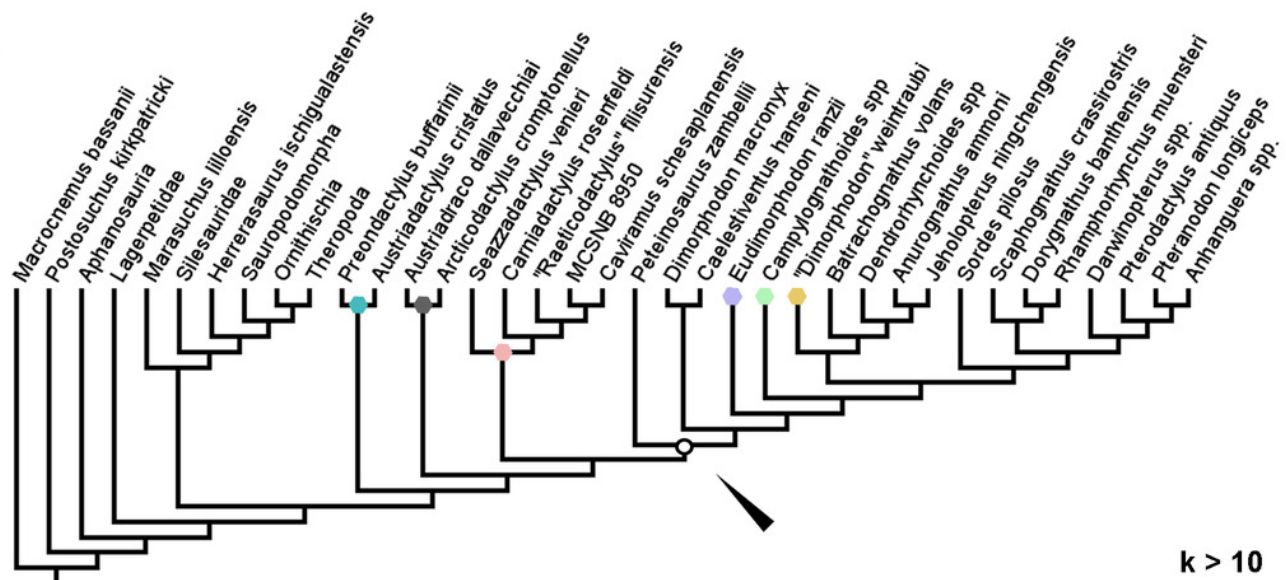
Figure 4

Strict consensus (A) and reduced strict consensus (B) trees produced when following the analysis protocol of Ezcurra (2014) and using equal weights parsimony.

White circle and arrow indicate the position of Zambellisauria in this analysis.

Figure 5

Trees produced using implied weights implementation of parsimony for k values < 10 (A) and k values = 10 more (B).

Coloured nodes and tips added to highlight the taxa whose positions changed substantially between the implied weights parsimony analyses. White circles and arrows indicate the position of Zambellisauria in each analysis.

Sources of anatomical information for taxa added to the phylogenetic analyses

Operational taxonomic unit	Based upon	Specimens	Sources
Aphanosauria	*Teleocrator rhadinus*	NHMUK PV R6795-6	Nesbitt et al. 2017, 2018
	Dongusuchus efremovi	Multiple - PIN	Nesbitt et al. 2017
	Yarasuchus deccanensis	Multiple - ISIR	Nesbitt et al. 2017
Lagerpetidae	*Lagerpeton chanarensis*	Multiple - **PVL**	*specimens only*
	D. gregorii	TMM 31100–1306	Nesbitt et al. 2009a
	D. romeri	GR 218; DMNH EPV.29956	Irmis et al. 2007; Martz & Small 2019
	D. gigas	PVSJ 898	Martínez et al., 2016
	Ixalerpeton polesinensis	ULBRA-PVT059	Cabreira et al. 2016
Marasuchus lilloensis	*Marasuchus lilloensis*	Multiple - **PVL**	*specimens only*
Silesauridae	*Silesaurus opolensis*	Multiple - ZPAL	Dzik 2003
	Kwanasaurus williamparkeri	Multiple - DMNH	Martz & Small 2019
	Asilisaurus kongwe	NHMUK R16303	Nesbitt et al. 2010
Ornithischia	*Hetero*	Multiple - **NHMUK; SAM; BP**	Butler et al. 2008; Norman et al. 2011; Galton 2014
	Lesothosauru diagnosticus	Multiple - **NHMUK; BP**	Knoll 2002a, b, c; Porro et al. 2015; Barrett et al. 2016; Baron et al. 2017c
	Eocursor parvus	**SAM-PK-K8025**	Butler 2010
Theropoda	*Tawa hallae*	Mutiple - GR	Nesbitt et al. 2009b
	Coelophysis bauri	**AMNH FR 7224**	*specimens only*
	Eodromaeus murphi	Multiple - **PVSJ**	Martinez et al. 2011
Sauropodomorpha	*Buriolestes schultzi*	CAPPA/UFSM 0035	Cabreira et al. 2016
	Pampadromaeus barberenai	ULBRA-PVT016	Cabreira et al. 2011
	Saturnalia tupiniquim	Multiple - MCP	Langer et al. 1999; Langer 2003
	Eoraptor lunensis	**PVSJ 512**	Sereno et al. 2011
	Plateosaurus engelhardti	Multiple - **AMNH**; SMNS	Nesbitt 2011