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 Preondactyliya. Some
analyses also support the existence of a clade that falls as sister-taxon to the zambellisaurus, 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.
Testing pterosaur ingroup relationships through broader sampling of avemetatarsalian taxa and characters and a range of phylogenetic analysis techniques

Matthew G. Baron¹

1. BPP University, London, Aldine Place, 142-144 Uxbridge Road, London W12 8AW, UK
2. Christ’s College, Cambridge, St Andrew’s Street, CB2 3BU

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

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 Preondactyli.
Some analyses also support the existence of a clade that falls as sister-taxon to the
zambellisaurids, 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 Dinosauria 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.

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

Pterosaurs were a diverse, disparate and highly specialised group of terrestrial reptiles that represent the oldest set of vertebrates currently understood to have achieved powered flight (Benton, 1985; Unwin, 2003; Andres, 2006; Barrett et al., 2008; Andres, Clark and Xu, 2014; Britt et al., 2018). Originating at some time in either the Early or Middle Triassic (Nesbitt et al., 2017), and first appearing in the fossil record in the middle of the Late Triassic (Barrett et al., 2008; Bennet, 2013), the pterosaurs went on to thrive throughout the Mesozoic Era as one of the dominant groups of land animals, lasting right up until the very end of the Cretaceous Period and achieving a global distribution (Unwin, 2003; Dalla Vecchia, 2004; Unwin and Martill, 2007; Barrett et al., 2008; Kellner et al., 2019).

The earliest pterosaurs were generally small bodied animals, with toothed upper and lower jaws and usually an elongated tail (e.g., Padian, 1984; Hone and Benton 2007; Padian, 2008a; Padian, 2008b; Bennett, 2007; Bennet, 2014; Kellner, 2015; Britt et al., 2018; Dalla Vecchia, 2010 Dalla Vecchia, 2013; Dalla Vecchia, 2019). In addition, all known early pterosaurs appear to be fully capable of powered flight and, as yet, no transitional non-flying pterosaur taxa are known (though some specimens have been suggested to be exactly that – e.g., Huene,
1914). Later pterosaurs went on to achieve a broader, truly global, geographic range, as well as much larger body sizes and much more unusual and often unique features of anatomy (e.g., Unwin and Bakhurina, 1994; Unwin and Bakhurina, 1995; Unwin, 2001; Unwin, 2003; Dalla Vecchia et al., 2002; Barrett et al., 2008; Hone et al., 2012; Upchurch et al., 2015; Kellner et al., 2019).

Within Pterosauria, which currently comprises the same set of taxa as the clade Pterosauromorpha (see, Nesbitt et al., 2013), there exists a number of distinct subgroups, many of which were already present in the Late Triassic. The many proposed subgroups within Pterosauria include the Eopterosauria, which is believed to comprise Preondactylia and Eudimorphodontoidea (e.g., Andres, Clark and Xu, 2014), and Macronychoptera, which comprises, *inter alia*, Dimorphodontidae, Anurognathidae and Pterodactyloidea (e.g., Britt et al., 2018; Dalla Vecchia, 2019)(Figure 1A-C).

The recent phylogenetic analysis by Dalla Vecchia (2019) suggested that the earliest diverging members of Pterosauria that were considered by that study were the Preondactylia – comprising *Preondactylus buffarinii* and *Austriadactylus cristatus*. This pairing of *Preondactylus buffarinii* and *Austriadactylus cristatus* concurs with the findings of Andres, Clark and Xu (2014). However, the results of these two analyses differ in that in the trees produced by Andres, Clark and Xu (2014), the Preondactylia form the sister-taxon to the clade comprising *Peteinosaurus zambellii* and Eudimorphodontoidea, a topology also supported by Upchurch et al. (2015). These clades together form Eopterosauria, a group not supported in the analysis by Britt et al. (2018) or Dalla Vecchia (2019). Equally, in the analysis by Dalla Vecchia (2019) no support was found for the clade Eudimorphodontidae (*sensu* Dalla, Vecchia 2014). In this respect, the
analyses of Dalla Vecchia (2019) and Britt et al. (2018) also differ from each other, despite using
the same dataset and having only a very small number of differences in terms of the
operational taxa included (see Figure 1). This just highlights the relative instability of some of
the early branching pterosaur taxa in phylogenetic analyses. Dalla Vecchia (2019) even admits
that Bremer support values for many of the clades in his analysis were low.

A monophyletic Macronychoptera was found to be in a sister-taxon relationship with
Peteinosaurus zambellii in the analysis of Dalla Vecchia (2019), and this unnamed clade was
found as sister-taxon to another unnamed group of pterosaurs containing a number of other
Late Triassic forms (Figure 1B). Unlike in the analysis by Andres, Clark and Xu (2014), Dalla
Vecchia recovers Eudimorphodon ranzii within Lonchognatha, and finds no evidence for a close
relationship between Eudimorphodon ranzii, Carniadactylus rosenfeldi and Arctcodactylus
cromptonellus (contra Andres, Clark and Xu, 2014) (Fig 1A-B). Similarly, a close affinity between
Eudimorphodon ranzii and Raeticodactylidae – which comprises Raeticodactylus filisuresensis and
Caviramus schesaplanensis according to Andres, Clark and Xu (2014) – was found by Britt et al.
(2018) but not Dalla Vecchia (2019) (Fig 1A-C). In the reduced strict consensus tree produced in
the analysis by Britt et al. (2018), the earliest diverging pterosaur clade contained a pair of taxa
- Austriadraco dallavecchiai and Arctcodactylus cromptonellus - a similar result to that obtained
by Kellner (2015), who named this clade Austriadraconidae (see also, Dalla Vecchia, 2009a;
Dalla Vecchia, 2009b). But again, this result differs from the analysis of both Upchurch et al.
(2015) and Dalla Vecchia (2019). In an analysis by Codorniú et al. (2016), the results vary even
more dramatically at the base of Pterosauira, with Anurognathidae diverging earlier within the
trees recovered than either Eudimorphodon ranzii or Austriadactylus cristatus. Codorniú et al.
(2016) also found evidence for a possible a *Dimorphodon macronyx* + *Peteinosaurus zambelli* sister-taxon relationship, which was not recovered in any of the other analyses discussed above.

It is clear from all of the differences observed between the various analyses discussed above that much work still needs to be done to resolve the interrelationships between the many early pterosaur taxa currently known. The ingroup relationships of the various early pterosaur clades are unstable, as are the interrelationships between clades. However, in all the studies discussed above, there is a potential problem with the analyses in that they perhaps do not include adequate sampling from without Pterosauria – i.e., the lack of informative anatomical information from certain key outgroup taxa could be causing the poor resolution within Pterosauria.

In the analysis of Britt et al. (2018), and of other studies that utilised the same data (e.g., Codorniú et al., 2016; Dalla Vecchia, 2019), the only other ornithodiran taxa to be included in the analysis as an outgroup taxon is the unusual hypercarnivore *Herrerasaurus ischigualastensis*. The taxon was presumably chosen as a representative of the Dinosauria, a clade supposedly closely related to Pterosauria. However, *H. ischigualastensis* is not necessarily the best representative of the ‘basal’ dinosaurian condition, being a very large predator that is quite distinct in terms of its anatomy to many, if not most, of the earliest dinosaurs (see, Brusatte et al., 2010; Baron, Norman and Barrett, 2017a). In fact, the position of this taxon has proved to be highly unstable in recent times (see, Baron, Norman and Barrett, 2017b; Langer et al., 2017; Lee et al., 2019; Pacheco et al., 2019) and belongs to a wider clade of Triassic hypercarnivores that may or may not fall within Dinosauria at all (see, Baron and Williams,
Moreover, in the analyses by Britt et al. (2018) and Dalla Vecchia (2019), *H. ischigualastensis* is recovered as the sister taxon to the rauisuchid paracrocodylomorph *Postosuchus kirkpatricki*, which might suggest that character optimisation outside of the pterosaurian lineage is somewhat confused and misleading. If the character distribution among taxa in this analysis was fairly reflective of the topology expected to be found for these taxa, *H. ischigualastensis* should, according to almost all modern phylogenetic hypotheses, fall closer to the pterosaurs than to *P. kirkpatricki*. This result, while not the key focus of any of the studies that recovered it, perhaps should have raised alarm bells in terms of what the data for taxa immediately at the base of and just outside of Pterosauria was like. The purpose of outgroup taxa is to reflect, as best as is possible, the ‘basal’ condition for the ingroup clade being studied – it is arguable that this is not the case in the analyses by Britt et al. (2018) and Dalla Vecchia (2019) and that these analyses fall short in this key respect. This omission of important anatomical data may, in turn, be having a substantial adverse effect on the resolution of the ingroup relationships among the numerous pterosaur taxa included in the studies.

Also missing from the datasets is a range of other close pterosaur relatives, the anatomical characteristics of which are potentially even more helpful in determining the ancestral state of Pterosauria than *H. ischigualastensis* is when considered alone. Silesaurids, who along with dinosaurs form the dinosauromorph clade Dracohors (Cau, 2018) are omitted, as are the dinosauriforms known as the lagerpetids. Similarly, looking the other way along this particular branch of the archosaur group, the aphanosaurs, a group believed to form the sister-taxon to the ornithodirans (see Nesbitt et al., 2017), are also not included. All of the anatomical
Other studies of early pterosaur interrelationships have similar shortcomings in terms of the outgroup taxa sampling. The analysis of Unwin (2003), for example, only used a single outgroup taxon in the form of the non-archosaurian archosauriform *Euparkeria capensis*. The analyses of Kellner (2003) had three outgroup taxa - *Ornithosuchus longidens*, *Herrerasaurus ischigualastensis* and *Scleromochlus taylori*. Of these, only one, *H. ischigualastensis*, is an ornithodiran. While *Scleromochlus taylori* was considered as a possible close relative of pterosaurs at the time Kellner (2003) was published, subsequent work on this taxon has demonstrated that it is more likely an archosauriform belonging to the clade Doswelliidae (see, Bennett, 2020). Finally, in the analyses of Andres, Clark and Xu (2014), the chosen outgroups were the non-avemetatarsalian archosauromorphs *Euparkeria capensis* and *Ornithosuchus longidens*, and the putative dinosaur *Herrerasaurus ischigualastensis*.

This study aims to test what effect, if any, the omission of such close pterosaur relatives from analyses has had on the overall topology within Pterosauria by using a modified version of the recent dataset of Britt et al. (2018). Many of the disagreements between the recent results of Andres, Clark and Xu (2014), Upchurch et al. (2015), Kellner (2015), Britt et al. (2018) and Dalla Vecchia (2014, 2019) could be resolved through a simple addition of better and more appropriate outgroup taxa, and this is what this study attempts to do. By also incorporating new anatomical characters, taken from recent early dinosaur and archosaur studies, this study aims to better anchor the base of Pterosauria to a position within Avemetatarsalia and
Ornithodira, so as to allow the ‘basal’ condition of pterosaurs to be better expressed in the data.

MATERIAL AND METHODS

The dataset of Britt et al. (2018), as modified by Dalla Vecchia (2019), was expanded through the addition of the following taxa: Aphanosauria, Lagerpetidae, *Marasuchus lilloensis*, Silesauridae, Ornithischia, Theropoda and Sauropodomorpha.

Full details of each new operational taxonomic unit, which specimens were studied, and which other sources of anatomical information were used are given in Table 1.

In addition to the new taxa, 27 new anatomical characters were incorporated into the dataset of Britt et al. (2018) – five were taken from the early dinosaur dataset of Baron et al. (2017a, b), which had built upon previous works (e.g., Langer and Benton, 2006; Nesbitt, 2011), and a further nine from the archosaur dataset of Nesbitt et al. (2017). Some other characters that were added were taken from both of these studies, as they had been used in each and either entirely or partially overlapped in terms of the features that they described (chars 111-116). These characters were conflated or otherwise adjusted so as to prevent repetition or over-scoring of each feature. A further three additional characters were added based upon the range of anatomical features observed in the various taxa in the study, including a simple absent/present statement for the pteroid (char. 94) to supplement character 71 of Britt et al. (2018), itself a modification from character 132 in the data of Bennett (2012). In addition, a character describing the radius to humerus ratio was added (char. 110), and a character describing the shape of the distal end of the scapula (char. 95). Four more ‘classic pterosaur characteristics’ were accounted for with new characters, each modified from the datasets of Vidovic and Martill (2014) and Lü et al. (2009) and were included in this study as characters 117-120. Character 99 in this analysis is a modified form of character 301 of Baron et al. (2017a)
– Dorsal margin of the ilium in lateral view: 0, sinusoidal; 1, concave (saddle-shaped), pre and preacetabular and postacetabular processes upturned relative to craniocaudal centre; 2, relatively straight or convex – state 0 has been added to describe the condition seen in *Macrocnemus bassanii*, *Postosuchus kirkpatricki* and aphanosaurs. State (2) is present in theropods and ornithischians, whereas state (1) describes the condition in ‘basal’ pterosaurs, herrerasaurs, sauropodomorphs, silesaurids, lagerpetids and *Marasuchus lilloensis*. The full list of characters added to the data matrix is given in the supplementary file.

Of the additional characters, 108 and 109 were treated as ordered, following Nesbitt (2011) and Baron et al. (2017a, b) in addition to characters 62, 74 and 91, which were also treated as ordered in the analyses of Britt et al. (2018) and Dalla Vecchia (2019).

Trees were searched for using equal weights implementation of parsimony, using TNT 1.5-beta (Goloboff et al., 2008), through the New technology search method. Following the protocol of Baron et al. (2017a, b) and Nesbitt et al. (2017), memory was first set at its maximum of 99,999, and trees were then searched for under equal weights parsimony through a New Technology (Goloboff et al., 2008) search, with ratchet and drift set at their default values and with 100 random additional sequences. A second search, following the protocol of Ezcurra (2016) was then done, in which trees were searched for using a New Technology Search (Goloboff et al., 2008) with ratchet set to 20 iterations, with five rounds of tree fusing and 100 additional sequences. The MPTs produced in this second type of analysis were then subjected to a second round of TBR branch swapping, with a change probability of 33 and 100 additional sequences as the default search settings. Finally, a search was carried out using implied weights parsimony, with implied weights (k-values) set to 3, 5, and 10 (see Parry, Baron and Vinther, 2017; Goloboff, 2018).
RESULTS

An initial analysis was run that excluded the additional 27 characters that were to be added to the dataset of Britt et al. (2018). This was done using equal weights and a simple New technology search. This analysis was carried out to test the effect of an expanded set of outgroup taxa alone, without the effect of added characters. The analysis produced 31 most parsimonious trees (MPTs) each of length 305 steps (Figure 2). In spite of the lack of additional characters that could help to resolve the relationships within Ornithodira and Avemetatarsalia, this analysis still recovered a monophyletic Pterosauria and generated fairly good resolution within this clade. The resolution among outgroup taxa is poor, with most outgroup taxa forming a polytomy outside of Pterosauria. Within Pterosauria there exists a ‘basal’ trichotomy. *Austriadactylus cristatus* and *Preondactylus bufarinii* are recovered in a sister taxon relationship; a second ‘basal’ clade comprises *Arcticodactylus cromptonellus, Austriadraco dallaveccchiai, Seazzadactylus venieri, Carniadactylus rosenfeldi, ‘Raeticodactylus’ filisurensis, Caviramus schesaplanensis* and unnamed specimen MCSNB 8950; the third of the ‘basal’ clades in the trichotomy contains *Peteinosaurus zambelli*, Dimorphodontidae and Lonchognatha. This result is more similar to the results of the analysis carried out by Dalla Vecchia (2019) than those of Britt et al. (2018), though this analysis has poorer resolution at the base of the pterosaur tree. The addition of new outgroups has, without the addition of new characters,
generated more uncertainty about the fundamental interrelationships between the earliest diverging pterosaur groups. Furthermore, the resolution between taxa in the second clade produced in this analysis – the one containing *Arcticodactylus cromptonellus*, *Austriadraco dallavecchiai*, *Seazzadactylus venieri*, *Carniadactylus rosenfeldi*, ‘Raeticodactylus’ *filisurensis*, *Caviramus schesaplanensis* and specimen MCSNB 8950 – is poorer with the addition of the new outgroups. In this analysis *Arcticodactylus cromptonellus* and *Austriadraco dallavecchiai* from a grade leading to a polytomy containing all other taxa in this group. In the results of Dalla Vecchia, on the other hand, found *Seazzadactylus venieri* and *Carniadactylus rosenfeldi* to also for part of this grade leading to a smaller polytomy of ‘Raeticodactylus’ *filisurensis*, *Caviramus schesaplanensis* and specimen MCSNB 8950. Within the other clades the recovered topology is the same as in the analyses of Dalla Vecchia (2019) (Figure 1B). The addition of new outgroup taxa alone did not result in the recovery of a monophyletic Austriadraconidae or Eopterosauria, as in other previous studies (e.g. Andres, Clark and Xu (2014; Britt et al. 2018) (Figure 1A, C). By adding in new characters that better resolve the relationships within Ornithodira and the character optimisation at the base of Pterosauria, this uncertainty at the base of the pterosaur tree was resolved and a different topology within certain constituent pterosaurian clades was recovered (Figure 3).

In this first full analysis that included both the added taxa and added characters, and using equal weights and a simple New technology search, two MPTs were recovered, each of length 390 steps. In the strict consensus rule tree produced from the two MPTs recovered in the analysis, a monophyletic Pterosauria was found (Figure 3). This clade contains all the taxa analysed in this analysis that are traditionally considered to be pterosaurs, and together this
clade forms a sister-taxon to a clade containing almost all of the newly added avemetatarsalian taxa, except for Aphanosauria and Lagerpetidae. Dinosauria is recovered, as is Dracohors and Dinosauriformes. Lagerpetidae is recovered without the clade containing Dinosauriformes and Pterosauria. *Herrerasaurus ischigualastensis*, which was the only non-pterosaurian ornithodiran outgroup included in the analyses of Britt et al. (2018) and Dalla Vecchia (2019), is found nested within Dracohors, in a position closer to Dinosauria than to Silesauridae, as is more consistent with some recent analyses of early dinosaurs (e.g., Baron and Williams, 2018).

In this full analysis, with all of the additional taxa and characters being active, the base of the pterosaurian clade no longer contained a trichotomy. Instead, *Austriadactylus cristatus* and *Preondactylus bufarini* are recovered as sister-taxa, forming their own small monophyletic group at the base of the pterosaur tree, falling outside of the clade that contains all other pterosaurs *sensu* Dalla Vecchia (2019). This clade - named Preondactylia by Andres, Clark and Xu (2014) - has also been found in a number of other studies (e.g., Upchurch et al., 2015; Britt et al., 2018; Dalla Vecchia, 2019). Preondactylia forms the sister taxon to a clade containing two distinct monophyletic groups: one group contains *Arcticodactylus cromptonellus, Austriadraco dallavecchiae, Seazzadactylus venieri, Carniadactylus rosenfeldi, 'Raeticodactylus' filisurensis, Cuviramus schesaplanensis* and specimen MCSNB 8950; the other contains *Peteinosaurus zambelli* and all other pterosaurs. This too largely agrees with the results obtained by Dalla Vecchia (2019) – however, the topology within the first of the two clades differs. As discussed above, in the results presented by Dalla Vecchia (2019), *Arcticodactylus cromptonellus, Austriadraco dallavecchiae, Seazzadactylus venieri* and *Carniadactylus rosenfeldi* formed a grade leading to a clade containing *'Raeticodactylus' filisurensis, Cuviramus schesaplanensis* and
specimen MCSNB 8950. This expanded analysis did not find such a topology within this clade. Instead, the results recover *Arcticodactylus cromptonellus, Austriadraco dallavecchiai* and *Seazzadactylus venieri* in their own clade, which is sister-taxon to a clade containing the others. This first clade is akin to Austriadraconidae, as named by Kellner (2015). Austriadraconidae, in this form, is not supported in the results presented by Dalla Vecchia, but was recovered, albeit in a different position by Britt et al. (2018). The placement and composition of Austriadraconidae in the results of this analysis are novel and appear to be the result of the combination of wider outgroup sampling and anatomical character choice. Within other major pterosaurian sub-clades, such as Macronychoptera, Dimorphodontidae, Anurognathidae, and Pterodactyloidea, the topology recovered in this analysis agrees with the topology recovered in the analysis by Dalla Vecchia (2019). Moreover, this analysis found no support for the placement of *Arcticodactylus cromptonellus* and *Austriadraco dallavecchiai* in their own exclusive clade placed as sister-taxon to all other pterosaurs, as had been found by Britt et al. (2018), *sensu* Dalla Vecchia (2019).

**Further Comparisons with Previous Studies.**

While the placement of Preodactylia as the earliest diverging of the pterosaur subclades agrees with the analysis by Dalla Vecchia (2019), the result differs from Britt et al. (2018). Whereas in the taxon-reduced analyses of Britt et al. (2018), a clade containing *Austriadraco dallavecchiai* and *Arcticodactylus cromptonellus* – termed Austriadraconidae by Kellner (2015) – was found as the earliest diverging pterosaur clade, the results of Dalla Vecchia (2019) and those of the first
analysis of this study do not provide support for such a position, but rather place the austriadraconids in a more deeply nested position. This result also differs substantially from that found by Codorniú et al. (2016) who did not find a sister-taxon relationship between *Austriadactylus cristatus* and *Preondactylus bufarinii* at all.

As stated above, the results of this first analysis support a monophyletic Austriadraconidae, *sensu* Kellner (2015), but, for the first time, also places *Seazzadactylus venieri* within it (Figure 2). In this analysis, the austriadraconids form a sister-taxon to a clade containing *Carniadactylus rosenfeldi* + ‘*Raeticodactylus’ filisurensis’, *Caviramus schesaplanensis* and unnamed specimen MCSNB 8950. Dalla Vecchia (2019) also recovered all of these taxa together into a monophyletic group, but his analysis did not recover the same interrelationships between them; *Arcticodactylus cromptonellus*, *Austriadraco dallavecchiai* and *Seazzadactylus venieri* form a grade leading into the clade containing *Carniadactylus rosenfeldi* and a trichotomy of ‘*Raeticodactylus’ filisurensis’, *Caviramus schesaplanensis* and MCSNB 8950 in the analysis of Dalla Vecchia (2019) (see, Figure 1A).

No close relationship is found between this group of pterosaurs and *Eudimorphodon ranzii*, *contra* the findings of Andres, Clark and Xu (2014), Upchurch et al. (2015) and Britt et al. (2018). Similarly, no support is found for the clade Eudimorphodontidae. Instead, *Eudimorphodon ranzii* is found within Macronychoptera and Lonchognatha, *sensu* Dalla Vecchia (2019).

Also consistent with the analysis of Britt et al. (2018) and of Dalla Vecchia (2019), *Dimorphodon macronyx* and *Caelestiventus hansenii* are found to be sister-taxon, forming their
own clade Dimorphodontidae. This stands in contrast to the results of Codorniú et al. (2016), who recovered *Peteinosaurus zambelli* as the sister-taxon to *Dimorphodon macrónyx*.

Both the analyses by Britt et al. (2018) and Dalla Vecchia (2019) found a Macronychoptera containing Dimorphodontidae and Lonchognatha, *sensu* Unwin 2003, and with *Peteinosaurus zambelli* forming the sister-taxon to Macronychoptera. This again differed from the results of Codorniú et al. (2016) who found a different position for *Peteinosaurus zambelli* (see above). However, despite the agreement between Britt et al. (2018) and Dalla Vecchia (2019) on the subgroups comprising Macronychoptera, the constituent taxa of Lonchognatha differed between these two analyses, with Britt et al. (2018) finding taxa such as ‘*Raeticodactylus* filisurensis’ and *Caviramus schesaplanensis* to be members of this more ‘derived’ clade (see also, Kellner, 2003). This study has not found such a construction of Lonchognatha, and instead has found a more reduced clade, *sensu* Dalla Vecchia (2019).

Further, within Lonchognatha is a clade containing Campylognathoides and all other pterosaurs analysed in this study - i.e. a monophyletic Novialoidea *sensu* Kellner 2003 - and this result largely agrees with the analyses of Kellner (2003), Andres and Myers (2013), Andres, Clark and Xu (2014), Upchurch et al. (2015), Britt et al. (2018) and Dalla Vecchia (2019).

Also consistent with each of the above studies is the recovery of a monophyletic Caelidracones. However, a sister-taxon relationship between Anurognathidae and Pterodactyloidea, as recovered by Andres and Myers (2013) is not supported in this analysis. As in the analyses by Britt et al. (2018) and Dall Vecchia (2019), Caelidracones contains two clades: one containing a trichotomy of *Sordes pilosus*, ‘ramphorynchids’, and Monofenestrata, and the other containing taxa that could be loosely termed ‘anurognathid types’. Again, a contrast can
be drawn with the results of this analysis and the results of the analysis by Codorníu et al. (2016), who placed Anurognathidae in a much more stem-ward position within Pterosauria.

Anurognathidae is also recovered in this analysis, but the interrelationships between the taxa in this clade differ from the analyses of Britt et al. (2018) and Dall Vecchia (2019) in that *Jeholopterus* and *Anurognathus* form sister taxa, with *Dendrocrinoides* and *Batrachognathus* forming successive sister-taxa. The taxon provisionally named ‘*Dimorphodon*’ *weintraubi* then forms the sister taxon to Anurognathidae, and this is consistent with the results of Dalla Vecchia (2019). These ‘anurognathid types’ together form the sister-taxon to the grouping of *Sordes pilosus*, the ‘ramphorynchids’ and monofenestratans, which is, as yet, also unnamed (see Dalla Vecchia, 2019).

One interesting aspect of this analysis is that it would appear, when applying current definitions, that Pterosauria falls within Dinosauria *sensu* Benton (1985) and not as its sister-taxon, *sensu* Gauthier (1986) and Nesbitt et al. (2017). Because Lagerpetidae falls outside of the clade containing Pterosauria and the grade leading into dinosaurs in this analysis, under the current definition of Dinosauria - the last common ancestor of *Lagerpeton chanarensis*, *Marasuchus lilloensis*, Dinosauria and all its descendants (Benton, 1985) – Pterosauria and, by definition, Ornithodira, would fall within Dinosauria. Ornithodira would comprise Pterosauria and Dinosauriformes, rather than Pterosauria and Dinosauria, as suggested in previous analyses (e.g., Langer and Benton, 2004; Nesbitt, 2011; Baron, Norman and Barrett, 2017a; Nesbitt et al., 2017). However, this position is only relatively weakly supported for now, and such interaltionships within the higher Ornithodira was not the focus of this analysis. Subsequent studies may recover more traditional topologies.
within Avemetatarsalia and composition of Ornithodira, so this study refrains from revising any
definitions based upon this result alone. Within Dinosauriformes are *Marasuchus lilloensis* and
Dracohors, *sensu* Cau (2018). Silesaurids form the sister-taxon to dinosaurs + herrerasaurs,
sensu Baron and Williams (2018). Dinosauria in this analysis contains Ornithoscelida (see Baron,
Norman and Barrett, 2017a) and Sauropodomorpha (see Baron, Norman and Barrett, 2017b).

The following is a list some of the notable nodes recovered from the base of the
pterosaur tree and including Pterosauria, with all synapomorphies listed for each (Node
numbers refer to numbering in Figure 3):

**Node 4. Pterosauria, sensu** Kellner (2003) ([*Preondactylus bufarini* + *Austriadactylus cristatus*]/Preondactylia + [Caviramidae + Zambellisauria])

Definition: Node-based - the most recent common ancestor of the Anurognathidae,
*Preondactylus bufarini* and *Quetzalcoatlus northropi* and all their descendants (Kellner, 2003).

Character support: 7 (1-->3), 9 (0-->1), 16 (1-->2), 22 (0-->1), 39 (0-->1), 40 (0-->1), 58 (0-->1), 60 (0-->1), 70 (0-->1), 74 (0-->1), 75 (0-->1), 91 (0-->1), 94 (0-->1), 117 (0-->1), 120 (2-->0).

Remarks: The definition given by Kellner (2003) is sufficient to contain all taxa found in this
analysis to be contained within the pterosaur group. As *Preondactylus bufarini*, together with
*Austriadactylus cristatus*, forms the earliest diverging clade within Pterosauria – a monophyletic
Preondactylia – this definition for Pterosauria encompasses the same set of taxa as
Pterosaurophora, sensu Padian (1997). Pterosauria would, in this hypothesis, take precedence over Pterosaurophora. However, it should be worth noting that, in results that do not find Preondactylia to be the earliest diverging pterosaur clade (e.g., Britt et al. 2018), Pterosauria would encompass fewer taxa than Pterosaurophora, as certain clades would fall outside of the taxa encompassed by the definition for Pterosauria given by Kellner (2003). In the example of Britt et al. (2018), Austriadraconidae would not be within Pterosauria but rather would be non-pterosaurian pterosaurophors, under such a regime (see below).

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

Definition: The least inclusive clade that includes Preondactylus bufarinii and Austriadactylus cristatus.

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

Remarks: Often found to be the earliest diverging members of Pterosauria (e.g., Dalla Vecchia 2019), or early diverging members of ‘Eopterosauria’ (e.g., Andres, Clark and Xu, 2014; Upchurch et al., 2015), this small clade is fairly consistently recovered among early pterosaur cladistic studies, with the notable exception of Codorniu et al. (2016).

Unnamed clade (Caviramidae + Zambellisauria)

Character support: 45 (1-->0), 47 (1-->0), 77 (0-->1), 95 (0-->1).
Remarks: This clade contains all pterosaur taxa except for the clade containing Preondactylus bufarinii. All pterosaurs more ‘derived’ than Preondactyli have consistently been found among studies (e.g., Codorniú et al., 2016; Britt et al., 2018; Dalla Vecchia, 2019), although the placement of certain taxa within this clade varies, for example in the results of Britt et al. (2018), this clade does not contain Arcticodactylus cromptonellus and Austriadraco dallavecchiai (see Figure 1C). It may prove necessary in the future to erect a stem-based clade to contain all taxa more closely related to, as an example, Quetzalcoatlus northropi than to Preondactylus bufarinii.

Node 7: Caviramidae (new clade)

Definition: Node-based – the least inclusive clade that includes Arcticodactylus cromptonellus and Caviramus schesaplanensis (new).

Etymology: For Caviramus schesaplanensis – one of two anchoring member taxa used in the node-based definition for the clade, as outlined above.

Character support: 3 (0-->1), a skull that is curved down caudally; 12 (0-->1), a jugal process of the maxilla that is subtrapezoidal, tapering to a point only distally, and a proximal part with parallel dorsal and ventral margins; 43 (0-->1), a dentition that has tri- to quinticuspid tooth crowns; 81 (0-->1), a wing phalanx two that is as long as the ulna.

Remarks: This clade has been recovered in the recent analysis of Dalla Vecchia (2019) and is also supported in the first analysis of this study by a number of shared anatomical character
states, or synapomorphies (see above). The topology within the clade varies between the
analyses of Dalla Vecchia (2019) and this study, but both find the same set of taxa and
specimens to fall within it. This early diverging subgroup contains within it the austriadraconids
of Kellner (2015) and a handful of other Triassic taxa and specimens, including the as yet
unnamed MCSNB 8950, which has previously been the source of phylogenetic uncertainty in
other studies (see Britt et al., 2018). This clade is the least consistently supported among the
various analyses of this study and this is discussed further below. However, it is worth noting
that the clade was found in both the analysis that used only new outgroup taxa but no new
characters and the analysis that used both. The internal topology differed between these two
analyses, as did the position of the clade within Pterosauria, but the constituent taxa was
consistent, and consistent with the results of Dalla Vecchia (2019).

Node 6. Austriadraconidea, sensu Kellner (2015) (Arcticodactylus cromptonellus + Austriadraco
dallavecchiai + Seazzadactylus venieri)

Definition: The least inclusive clade that includes Arcticodactylus cromptonellus and
Austriadraco dallavecchiai, sensu Kellner (2015).

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

Remarks: This clade was named by Kellner (2015), but was not supported in a number of other
recent analyses of early pterosaurs (e.g., Andres, Clark and Xu, 2014; Upchurch et al., 2015).
However, this close relationship was found in the more recent analyses of Britt et al. (2018),
who recovered the clade as the earliest diverging within Pterosauria, and then Dalla Vecchia
(2019), who, like this study, found the clade to be slightly more ‘derived’. Unlike either of the
aforementioned studies, this study has found that the clade also contains *Seazzadactylus
venieri*; as in the analysis of Dalla Vecchia (2019) this grouping of taxa fall within a larger clade
of early-diverging pterosaur taxa (here named as Caviramiidae, clade nov.).

### Unnamed clade (*Carniadactylus rosenfeldi* + *Raeticodactylus* filisurensis, *Caviramus
schesaplanensis* + MCSNB 8950)

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

Remarks: This clade was also recovered in the analysis by Dalla Vecchia (2019) and contained
the same taxa and the same internal topology.

### Node 8. Zambellisauria (new clade) (*Peteinosaurus zambelli* + Macranychoptera)

Definition: Node-based – the least inclusive clade that includes *Peteinosaurus zambelli*,
*Dimorphodon macranyx, Pterodactylus antiquus* and *Quetzalcoatlus northropi* (new).

Etymology: The clade name honours Rocco Zambelli, curator of the Bergamo natural history
museum, for whom *Peteinosaurus zambelli* was named; *P. zambelli* being one of the two taxa
chosen as an anchor in this cladistic definition. Zambelli (1973) also named *Eudimorphodon
ranzii*, a well-known and important early pterosaur and putative member of Zambellisauria (see
Andres, Clark and Xu, 2014; Britt et al., 2018; Dalla Vecchia, 2019).
Character support: 56 (0→1), more than three sacral vertebrae; 59 (0→1), filiform processes of the caudal zygapophyses present in caudal vertebrae.

Remarks: This clade is consistently recovered by most modern analyses (e.g., Britt et al. 2018, Dalla Vecchia, 2019) and in all of the analyses in this study, regardless of the optimality criteria used in searching for trees in the analyses, and both with and without the inclusion of the new anatomical characters. Such a clade was not found in the analysis of Andres, Clark and Xu (2014), who instead placed Peteinosaurus zambelli as sister-taxon to Eudimorphodontidae, within a monophyletic Eopterosauria – a hypothesis that has fallen out favour in more recent studies and is not supported in any of the analyses carried out in this study.

Node 9. Macronychoptera (Dimorphodontidae + Lonchognatha)

Character support: 63 (1→2), 64 (0→1), 65 (0→1)

Node 10. Dimorphodontidae (Dimorphodon macronyx + Caelestiventus hanseni)

Character support: 7 (3→2), 8 (0→1), 10 (0→1), 12 (0→2), 20 (0→1), 26 (0→1), 35 (0→1), 41 (0→1), 48 (0→1), 52 (0→1), 96 (1→0), 118 (1→2).

Remarks: As in the analyses of Britt et al. (2018) and Dalla Vecchia (2019), this study finds a close relationship between Dimorphodon macronyx and Caelestiventus hanseni.
Node 11. Lonchognatha

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

Remarks: The composition of Lonchognatha and its possible sister-taxon relationship with Dimorphodontidae has been fairly consistently recovered in recent analyses (Britt et al., 2018; Dalla Vecchia, 2019), although other studies have placed Lonchognatha within Novialoidae (e.g., Andres, Clark and Xu, 2014). This second hypothesis is not recovered in all but one of the analyses of this study. That is to say, in only one analysis does this study find Campylognathoides to be ‘less derived’ than Eudimorphodon species (see below).

In the second full analysis, utilising both the new taxa and new anatomical characters, TBR branch swapping after a differently configured New Technology search produced 2 MPTs, each also of length 390 steps. However, in this analysis, the resolution in this tree was greatly reduced (Figure 4A). While Aphanosauria and Lagerpetidae were still found outside of Ornithodira, and the monophyly of and interrelationships within Dinosauriformes remained consistent with previous analyses, in this second full analysis, the interrelationships between the groups within Pteorsauria was not clearly resolved – although monophyletic Austriadraconidae and Novialoidea were both found again. The large polytomy at the base of Pterosauria is more reminiscent of the full-taxon-sample analysis carried out using TNT by Britt et al. (2018). As in Britt et al. (2018), the specimen MCSNB 8950 was removed as a wildcard taxon and the analysis re-run. In this reduced analysis, a single tree was recovered (Figure 4B). In this tree, Austriadraconidae is once again recovered as monophyletic, as in the first analysis.
of this study and the second full-taxon-range analysis with TBR. However, in the reduced second analysis, but unlike in the full second analysis, Austriadraconidae contains Seazzadactylus venieri. This is similar to the result obtained in the first analysis, although the position of Austriadraconidae is different in both the reduced and full second analyses (compare Figure 3 and Figure 4B).

Finally, in the implied weights analyses, the topology within Pterosauria differed from the first and second analyses (Figure 5A-B). Only one tree was produced in each of three analyses, with lengths of 37.03690, 27.65440, and 17.04634 for k = 3, 5 and 10 respectively. In the first two of these analyses (k = 3 and 5), the earliest diverging clade of pterosaurs are the Austriadraconidae – however, this clade was not found to contain Seazzadactylus venieri in this analysis. The clade made up of Austriadactylus cristatus and Preondactylus buffarini, named above as Preondactylidae, then forms the sister-taxon of the clade of Peteinosaurus zambelli + Macronychoptera, named above as Zambellisauria. In searches with k at or above 10 however, the structure of the tree once again changes, with the preondactylids once again falling out as the most stem-ward of the clades in Pterosauria and, as in some of the previous analyses of this study, Austriadraconidae was found to contain Seazzadactylus venieri (Figure 5B). Caviramidae was not supported in any of these analyses, whereas Zambellisauria was consistently recovered in each. Likewise, clades such as Dimorphodontidae, Lonchognatha, Novialoidea, Caelidracones, Monofenestrata, Pterodactyloidea, and Anurognathidae were all found to be largely consistent through the various implied weights parsimony analyses. The taxon referred to as ‘Dimorphodon’ weintraubi was recovered closer to Sordes pilosus and the monofenestratans than to Anurognathidae in the lower weighted implied weights analyses, but closer to
Anurognathidae in analyses with a k value = 10 or more. In all the implied weights analyses, the ‘ramphorynchids’ we found to be more closely related to Monofenestrata than to Sordes pilosus, which was recovered as the sister-taxon to the clade of Monofenestrata + the ‘ramphorynchids’ (Figure 5A-B).

The largest difference in the arrangement of taxa between the implied weights analyses for k < 10 and for k = 10 or more is the composition of Zambellisauria. In all the analyses Zambellisauria is recovered as monophyletic, but in the lower k value analyses, contains, inter alia, Seazzadactylus venieri, Carniadactylus rosenfeldi, ‘Raeticodactylus’ filisurensis, Caviramus schesaplanensis and the specimen MCSNB 8950, whereas in analyses with k = 10 or more, these five operational taxonomic unites were recovered outside of Zambellisauria (see Figure 5A-B).

These differences in topology between the results of the various implied weights parsimony analyses suggests that certain anatomical characters in the dataset are broadly distributed across the taxa whilst also being important for uniting certain clades – as the implied weighting factor is increased, the weight of characters that could support the monophyly of clades such as Caviramidae (see above), or support a ‘basal’ position for Austriadraconidae, are being reduced by the search programme because these characters appear to be more homoplastic. However, these effects may be reduced by the further addition of anatomical characters as the dataset is expanded upon in subsequent studies.

DISCUSSION
It is clear from the variability in the results of the analyses in this study alone that the phylogenetic position of certain early pterosaur clades is still highly unstable, even with better taxon and character sampling. When analysed using certain methods, the addition of more avemetatarsalian taxa and new characters provided further support for certain clades and helped to revolve interrelationships between genera within some subclades. In addition, this expanded analysis changed the composition of some recognised clades, for example Austriadraconidae, which was, in analysis one, found to also include the recently described *Seazzadactylus venieri* for the first time. Choice of taxa and anatomical characters clearly has had some effect on the interrelationships of the ingroup pterosaur taxa, as has also been demonstrated to be the case in early studies of dinosaur (e.g., Müller and Dias-da-Silva, 2019).

This study has taken steps to address the under-sampling from closely related ornithdiran clades in previous pterosaur studies, but much work needs to be done to further broaden the datasets used in phylogenetic analyses, in terms of both the operational taxa and anatomical characters and character states.

What this study has also demonstrated is how using different approaches to phylogenetic analysis can produce substantially different results when it comes to the interrelationships within Pterosauria. The earliest diverging clade of pterosaurs has been found to be either the Preondactylia (in analysis one and in implied weights analyses for \(k = 10\) or more), or Austriadraconidae (when using TBR branch swapping or implied weights with \(k < 10\)).

However, in spite of this uncertainty, some clades have been consistently recovered throughout the various analyses of this study, and many too have been supported in previous analyses (Andres, Clark and Xu, 2014; Britt et al., 2018; Dalla Vecchia, 2019). This would suggest
that the evidence is increasingly supporting the validity of such monophyletic subsets within
Pterosauria, and these should, for the sake of stability and clarity in future research, be defined
and, if not already so, named. This study has erected two clades for these purposes.
Zambellisauria is erected to contain all pterosaur taxa descended from the most recent
common ancestor of *Peteinosaurus zambellii* and the various members of Macronychoptera.
This clade is now consistently recovered in most phylogenetic analyses and is strongly
supported in the results of these analyses. Should *Peteinosaurus zambellii* be recovered in a
much more stem-ward position in the future, for example if future analyses resurrect
Eopterosauria, with *Peteinosaurus zambellii* contained within it, the definition for
Zambelliasauria would then encompass the same set of taxa as Pterosauria and, as a result,
would become obsolete. However, in the emerging consensus on early pterosaur relationships
in this part of the tree, the clade Zambellisauria remains well-supported and distinct for now.
Under the definition given for Caviramidae, as also given above, in scenarios in which a
distinct monophyletic group is found to be more ‘derived’ than Preondactylyia but outside of the
clad containing all other, more ‘derived’ pterosaurs (see Figure 3), the name would be distinct
and valid. However, in scenarios such as presented in the results of the second and third
analyses, or in other studies (e.g., Britt et al., 2018) the clade Caviramidae would contain the
same taxa as Pterosauria and therefore become obsolete. However, the validity of Caviramidae
is not dependent on the position taxa such as *Peteinosaurus zambellii* and *Eudimorphodon
ranzii*, which have a tendency to ‘bounce around’ the tree, so long as the Autriadraconids are
not found to be either more or less ‘derived’ than the small clade containing *Carniadactylus
rosenfeldi*, *Raeticodactylus filisurensis*, and *Caviramus schesaplanensi*. It is only in hypotheses
in which Austriadraconids fall as the earliest diverging members of Pterosauria (e.g., analysis two of this study; Britt et al., 2018), or are paraphyletic (e.g., Codorniú et al., 2016), that Caviramidae would be invalid as a distinct clade.

It would also appear from the results of these analyses, and other recent works, that the higher-level interrelationships between pterosaur taxa are becoming more stabilised. Clades such as Dimorphodontidae, Lonchognatha, Novialoidea, Caelidracones, Monofenestrata, Pterodactyloidea, and Anurognathidae are all consistently found in these analyses, and only the composition of each varies a little between them. In particular *Eudimorphodon ranzii* is a particularly difficult taxon in terms of its position, having been recovered in a range of ‘derived’ and more ‘basal’ positions within the tree, in the both the analyses of this study and previous recent studies. With the addition of more taxa and more characters, and as more phylogenetic analysis techniques are turned on the question of pterosaur systematics, such problems of placing difficult to classify taxa may yet be resolved.

**CONCLUSIONS**

Pterosaur interrelationships have been shown to vary between analyses, with the fundamental interrelationships that are recovered being dependant upon the method of analysis, the character choice and taxon choice. The addition of more appropriate avemetatarsalian outgroup taxa to the early pterosaur dataset of Britt et al. (2018) made a difference in the overall topologies recovered within the various pterosaur clades, and to the fundamental structure of the pterosaur tree. However, a more dramatic change in result could be achieved
through the use of different phylogenetic analysis techniques, such as implied weights parsimony. While some pterosaur clades have proven to be stable throughout the various analyses, others have not, particularly those that fall most stem-ward on the tree. More needs to be done to resolve this issue, but wider character and taxon sampling in the future would be an important first step. Additional, utilisation of a wider range of phylogenetic analysis techniques should be adopted to test the strength of hypotheses of early pterosaur interrelationships as more taxa and character states are added.

REFERENCES

Andres BB. 2006. The earliest pterosaurs. Journal of Vertebrate Paleontology 26(3):37A.
Andres BB, Clark J, Xu X. 2014. The Earliest Pterodactyloid and the Origin of the Group. Current Biology. 24 (9): 1011–6. doi:10.1016/j.cub.2014.03.030.
Baron MG, Williams ME. 2018. A re-evaluation of the enigmatic dinosauriform Caseosaurus crosbyensis from the Late Triassic of Texas, USA and its implications for early dinosaur evolution. Acta Palaeontologica Polonica. 63 (1): 129-145 doi:10.4202/app.00372.2017
Baron MG, Norman DB, and Barrett PM. 2017a. A new hypothesis of dinosaur relationships and early dinosaur evolution. Nature, 543: 501–506. doi:10.1038/nature21700
Baron MG, Norman DB, Barrett PM. 2017b. Untangling the dinosaur family tree: a rebuttal. Nature. 551:E4–E5.
Baron MG, Norman DB, Barrett PM. 2017c. Postcranial anatomy of Lesothosaurus diagnosticus (Dinosauria: Ornithischia) from the Lower Jurassic of southern Africa: implications for basal ornithischian taxonomy and systematics. Zoological Journal of the Linnean Society 179(1):125-168
Barrett PM, Butler RJ, Yates AM, Baron MG, Choiniere JN. 2016. New specimens of the basal ornithischian dinosaur Lesothosaurus diagnosticus Galton, 1978 from the Early Jurassic of South Africa. Palaeontologia Africana 50:48-63.
Barrett PM, Butler RJ, Edwards NP, Milner AR. 2008. Pterosaur distribution in time and space: an atlas. Zitteliana B28:61-107.
Bennett SC. 2007. A second specimen of the pterosaur Anurognathus ammoni. Paläontologische Zeitschrift 81(4):376-398.

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

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

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

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

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

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

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

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

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

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

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

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

Dalla Vecchia FM. 2004 A review of the Triassic pterosaur record. Rivista del Museo Civico di Scienze Naturali “E. Caffi”, Bergamo 22(2003):13-29.
Dalla Vecchia FM. 2009a. Anatomy and systematics of the pterosaur Carniadactylus gen. n. rosenfeldi (Dalla Vecchia, 1995) Rivista Italiana di Paleontologia e Stratigrafia 115(2):159-186.

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

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

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

Dalla Vecchia FM. 2014. Gli pterosauri triassici. Udine: Museo Friulano di Storia Naturale.

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

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

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

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

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

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

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

Hone DWE, Benton MJ. 2007. An evaluation of the phylogenetic relationships of the pterosaurs among archosauromorph reptiles. Journal of Systematic Palaeontology, 5, 465–469.
Hone DWE, Tischlinger H, Frey E, Röper M. 2012. A new non-pterodactyloid pterosaur from the Late Jurassic of Southern Germany. PLOS ONE 7(7):e39312.

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

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

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

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

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

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

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

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

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

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

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

Langer MC, Ezcurra MD, Rauhut OWM, Benton MJ, Knoll F, McPhee BW, Novas FE, Pol D, Brusatte SL. 2017. Untangling the dinosaur family tree. Nature 551 (7678): E1–E3. doi:10.1038/nature24011.Müller RT, Dias-da-Silva S. 2019. Taxon sample and character coding
deeply impact unstable branches in phylogenetic trees of dinosaurs, Historical Biology, 31:8, 1089-1092, doi:10.1080/08912963.2017.1418341.

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

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

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

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

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

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

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

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

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

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

Nesbitt SJ, Desojo JB, Irmis RB. 2013. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin. Geological Society of London.
Nesbitt SJ, Butler RJ, Ezcurra MD, Barrett PM, Stocker MR, Angielczyk KD, Smith RMH, Sidor CA, Niedźwiedzki G, Sennikov AG, Charig AJ. 2017. The earliest bird-line archosaurs and the assembly of the dinosaur body plan. Nature. 544 (7651): 484–487 doi:10.1038/nature22037.

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

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

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

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

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

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

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

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

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

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

Unwin DM. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. Mitteilungen aus dem Museum fur Naturkunde in Berlin, Geowissenschaftliche Reihe 4: 189–221.
Unwin DM. 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut E, Mazin J-M, eds. Evolution and Palaeobiology of Pterosaurs. London: Geological Society London, Special Publication. 217:139-190.

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

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

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

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

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

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

Figures

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, Caveramidae (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, Preondactyla; 6, Austriadraconidae; 7, Caviromorpha (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.

Tables

Table 1. Sources of anatomical information for taxa added to the phylogenetic analyses.
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, Cavisramidae (*clade novo*); 3, Zambellisauria (*clade novo*).
Figure 3

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

Nodes: 1, Dino.sauro.morpha; 2, Dinosaurif.ormes; 3, Dinosauria; 4, Pterosauria; 5, Preon.dacty lia; 6, Austri.adora.nidae; 7, Cavi.rami.dae (clade novo); 8, Zambellisauria (clade novo); 9, Macronychoptera; 10, Dimorpho.dontidae; 11, Lonchognatha; 12, Novialoidea; 13, Anuro.gnathidae; 14, Caelidraconi.es; 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.
Table 1 (on next page)

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 |
|                           | Multiple - NHMUK; SAM; BP | | Butler et al. 2008; Norman et al. 2011; Galton 2014 |
| Ornithischia              | Hetero | Multiple - NHMUK; BP | Knoll 2002a, b, c; Porro et al. 2015; Barrett et al. 2016; Baron et al. 2017c |
|                           | Lesothosaurus diagnosticus | Multiple - AMNH FR 7224 | Butler 2010 |
|                           | Eocursor parvus | AMNH-PK-K8025 | specimens only |
| Theropoda                 | Tawa hallae | Multiple - GR | Nesbitt et al. 2009b |
|                           | Coelophysis bauri | AMNH FR 7224 | specimens only |
|                           | Eodromaeus murphi | Multiple - PVSJ | Martínez et al. 2011 |
| Sauropodomorpha           | Buriolestes schultzi | CAPPA/UFSM 0035 | Cabreira et al. 2016 |
|                           | Pampadromaeus barbarenai | 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 engelhardtii | Multiple - AMNH; SMNS | Nesbitt 2011 |