

GEOMETRIC MORPHOMETRIC APPROACH TO ESTABLISH PHYLOGENETIC AFFINITIES OF ENIGMATIC PTEROSAUR SPECIMENS FROM THE LOWER CRETACEOUS OF SOUTH KOREA

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Received: 23 August 2023 / Accepted: 27 January 2024 / Published online: 11 February 2024

Abstract. Fragmentary but scientifically important pterosaur fossils have been reported in Lower Cretaceous strata such as the Jinju and Hasandong formations of South Korea. Recently, several large teeth and a second wing phalanx found in these strata have been suggested to have affinities with Boreopteridae, a clade in which has so far been reported only in the Yixian Formation of China. Here, the phylogenetic affinities of these proposed boreopterid specimens are reassessed, using two-dimensional geometric morphometric shape analyses. The morphometric analyses found the South Korean pterosaur teeth in different morphospaces from the Yixian Fm. boreopterids, and plot them closer to anhanguerians. An isolated second wing phalanx does plot close to a boreopterid *Zhenyuanopterus longirostris* in a morphospace defined by first two principal component axes, but taxa from different lineages are also plotted as closely, or even closer. Thus, there seems to be no clear evidence that these specimens belong to Boreopteridae, and the tooth fossils appear to be very different from those of established members of this clade. Therefore, the hypothesis that some South Korean pterosaur fossils can be referred to boreopterids, is here tentatively rejected

Keywords: Pterosauria, Boreopteridae, Fossil, Tooth, Wing phalanx, South Korea.

INTRODUCTION

Pterosaurs were the first vertebrate group to have employed powered flight (e.g., Unwin, 2005; Witton, 2013; Jagielska & Brusatte, 2021). This specialized archosaurian clade has evolved and thrived in the Mesozoic, and their fossil record is cosmopolitan and spans from the Late Triassic to the end of the Cretaceous (e.g., Bestwick et al., 2018; Jagielska & Brusatte, 2021). The clade also had a high diversity in body size and overall bauplan, including long-tailed, early-diverging taxa with elongated, pointed snout that is filled with curved, needle-like teeth (e.g., Rhamphorhynchidae), small-bodied taxa with broad, rounded skull possessing unusually large orbits (e.g., Anurognathidae), moderate to large-bodied taxa with short tail, yet possessing elongated jaws that were usually filled with small to large teeth (i.e., many pterodactyloid taxa that lived in the Early Cretaceous), and colossal taxa (e.g., Azhdarchidae) exhibiting large skulls with long, edentulous snout, elongated to hyper-elongated cervical vertebrae and lengthened hindlimbs (e.g., Witton & Naish, 2008; Witton, 2013; Bestwick et al., 2018; Jagielska & Brusatte, 2021). Such a broad range of their fossil record as well as their wide morphological disparity suggest that pterosaurs were one of the most successfully diversified vertebrate clades in the history of life. Despite their successful evolutionary history, however, the body fossil record of pterosaurs is rather patchy, and is represented by fragmented materials in most localities, mainly due to their hollow bones with extremely thin cortices, making them hard to get fossilized (e.g., Jagielska & Brusatte, 2021).

An ideal example of this gap between high diversity and poor body fossil record is the case of Lower Cretaceous terrestrial sediments of South Korea. A rich amount of pterosaur ichnofossils has been reported from these South Korean sediments (e.g., Huh et al., 1996; Hwang et al., 2002; Kim et al., 2006; Yang, 2015; Kim & Huh, 2018), but body fossils of pterosaur have been very poorly documented. Only five isolated teeth, as well as fragmentary wing phalanges, have been described so far (Yun & Yang, 2001; Lim et al., 2001; Yun et al., 2007; Choi & Lee, 2017; Park et al., 2020). One of the wing phalanges (SNU 1001) was assigned to a dsungaripterid, mainly due to its relatively thick cortex (Lim et al., 2001). One tooth specimen (YCS 2005) recovered from the Hasandong Formation (Aptian-Albian), is too fragmentary to establish its phylogenetic affinity (Yun et al., 2007).

Other pterosaurian body fossils recovered from South Korea are controversial. Yun & Yang (2001) reported three large pterosaur teeth (KPE 40001-03) from the Jinju Formation (Albian), in which the largest and the most complete specimen (KPE 40001) is approximately 68.9 mm in length. Yun et al. (2007) described another large pterosaur tooth (YCS 2001; Fig. 1A) from the Hasandong Formation; its overall morphology as well as size (approximately 70 mm in length) were largely consistent with those of KPE 40001. Based on these observations, Yun et al. (2007) considered that KPE 40001 and YCS 2001 might represent the same pterosaurian taxon, or at least very closely related taxa. Both Yun & Yang (2001) and Yun et al. (2007) noted similarities between these specimens and rhamphorhynchid pterosaur teeth (e.g.,



Fig. 1. Map showing the localities where the analyzed South Korean pterosaur fossils were discovered. A, fossil locality yielding pterosaur teeth KPE 40001 and YCS 2001 (with YCS 2001 as an example); B, fossil locality where the second wing phalanx SNUVP 201901 was excavated. Images of YCS 2001 and SNUVP 201901 are modified from Yun et al. (2007) and Park et al. (2020), respectively, and the pterosaur silhouette is from phylopic.org (courtesy of FunkMonk, CC BY-SA 3.0).

Rhamphorhynchus), but, on the basis of their stratigraphic position as well as their size, these authors remarked that it is more parsimonious to consider that these teeth belonged instead to Cretaceous pterodactyloid taxa with enlarged teeth, citing *Cearadactylus* as an example. While this was a reasonable approach, it later turned out that most teeth of the holotype specimen (MN 7019-V) of *Cearadactylus atrox*, to which Yun & Yang (2001) and Yun et al. (2007) referred to in their comparisons, were in fact broken and have been substantially reconstructed (Unwin, 2002; Vila Nova et al., 2014).

In contrast, Choi & Lee (2017) stated that these teeth appear to be more similar to those of boreopterid pterosaurs like *Zhenyuanopterus* in their morphology, and reclassified them as Boreopteridae? (Choi & Lee, 2017: 869). While Choi & Lee (2017) did not provide details about how the Korean teeth are similar to boreopterid teeth, it is likely that their conclusions were drawn from the long, slender and striated morphology of the teeth (e.g., Yun, 2021), as well as from the geographic and stratigraphic proximity of the previously documented boreopterid remains. Park et al. (2020) accepted this reclassification, and even referred one isolated, fragmentary pterodactyloid second wing phalanx (SNUVP 201901; Fig. 1B) from the Hasandong Formation to cf. Boreopteridae. The main basis of Park et al. (2020) to assign this specimen to the clade

Boreopteridae is that, among the Asian pterosaurs known from Aptian strata, *Zhenyuanopterus longirostris* appears to have the most similar proximal condyle of the second wing phalanx. Accepting this taxonomic referral, Park et al. (2020) went on to consider SNUVP 201901 as the first unequivocal occurrence of boreopterid pterosaur outside the Yixian Formation (Aptian) of China, and assessed that the geographical range of the clade extended farther to the southeast than previously thought. Furthermore, based on the reconstructed sedimentary environment of the Hasandong Formation, Park et al. (2020) considered SNUVP 201901 as evidence that boreopterids dwelled in riparian environments as well as lacustrine ones. While Park et al. (2020) did note some differences between *Zhenyuanopterus longirostris* and SNUVP 201901, such as the larger size as well as greater curvature of the posterior edge of the proximal condyle in the latter, they interpreted these as possible intraspecific or interspecific variations within members of the Boreopteridae. These conclusions were challenged by Yun (2021), who suggested that the morphology of specimens KPE 40001-03 and YCS 2001 is in fact very different from that of the teeth of the known boreopterid taxa by their robust and more recurved nature. Instead, Yun (2021) argued that such tooth morphology is more consistent with that of anhanguerian pterosaurs, and referred the Korean teeth to probable anhanguerians. Additionally, Yun (2021) pointed out that pterodactyloid wing phalanges are

generally uniform in shape, citing the claim of Averianov (2010: 306) that there is not much variation in the structure of the proximal wing phalanges in pterodactyloids, and that thus it is doubtful whether boreopterid pterosaurs can be confidently identified based on an isolated, fragmentary wing phalanx. Unfortunately, all the comparisons reviewed above are based mostly on subjective observations made by different authors, and which can be greatly influenced by individual preconceptions. Indeed, none of the literature on the aforementioned Korean fossils provided quantitative or otherwise solid evidence for their classification other than a mention of their assumed similarity to some specific taxa (Yun & Yang, 2001; Yun et al., 2007; Choi & Lee, 2017; Park et al., 2020; Yun, 2021).

Geometric morphometric analysis, a technique of quantifying and visualizing morphological diversity through tracking homologous landmarks across specimens, in which the landmark point keeps the morphological information in the form of Cartesian coordinate (e.g., O'Higgins & Johnson, 1998; Bookstein, 1991; Polly, 2018), has begun to be used extensively in the field of vertebrate paleontology due to its efficacy to investigate shape patterns of lineages through deep time or life cycle (e.g., Hedrick, 2023). While geometric morphometric analysis is commonly used in studies that evaluate macroevolutionary pattern, growth changes or sexual dimorphism (e.g., Brusatte et al., 2012; Foth & Rauhut, 2013; Maiorino et al., 2013; Hedrick, 2023), the method has also been demonstrated to be useful in establishing the taxonomic affinities/identities of fragmentary vertebrate fossils as it allows for a more objective characterization and comparison (e.g., Gray et al., 2017; Cullen et al., 2021), and there is even a case where an isolated fragment of a pterosaur was correctly identified using this technique (Duque et al., 2022). Duque et al. (2022) applied two-dimensional geometric morphometrics to test the relevance of size and position of alveoli in the anterior part of the upper jaw in the characterization of different anhanguerian taxa, and successfully assigned an isolated pterosaur rostrum (DGEO-CTG-UFPE 8283) to *Anhanguera* sp. through this technique.

In this work, two-dimensional geometric morphometric analyses are applied to these contentious pterosaur fossils from South Korea. The main goals are as follows: (1) to investigate the main differences between boreopterid teeth and those of other contemporaneous pterosaur lineages with elongated teeth (e.g., *Anhangueria*); (2) to test whether the South Korean teeth plot closer to boreopterids than to any other pterosaurs or not; (3) to test whether the morphology of the proximal end of the second wing phalanx in boreopterids is distinctive among Early Cretaceous pterosaurs; and (4) to test whether SNUVP201901 plots in morphospace closer to boreopterids than to other pterosaur taxa.

Institutional abbreviations: BPMC, Beipiao Pterosaur Museum of China, China; DGEO-CTG-UFPE, Departamento de Geologia, Centro de Tecnologia and Geociências, Universidade Federal de Pernambuco, Recife, Brazil; D, Dalian Natural history Museum, Dalian, China; KPE, Department of Earth Science Education, Kyungpook National University, South Korea; MN, Museu Nacional/UFRJ, Rio de Janeiro, Brazil; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SNU, Seoul National University, South Korea; YCS, Paleontological collections of Dr. Cheol-Soo Yun, South Korea; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

MATERIAL AND METHODS

Photographs or figures of various elongated pterosaur teeth in labial/lingual views, originating from different lineages, were mainly retrieved from the literature, including the Korean teeth KPE 40001 and YCS 2001, with an assumption that the labial and lingual outlines were the same (File S1). To make the comparison more robust, only teeth of species belonging to a lineage that existed during the Early Cretaceous were examined, and therefore clades from earlier periods (e.g., Rhamphorhynchidae) were not used in the analysis, and taxa with relatively short teeth (e.g., Istiodactylidae) were also not included. Of note, even in pterosaurs with long teeth, the elongated teeth only appear at the anterior portion of the snout and the ones at the back are relatively much shorter. Therefore, only teeth from the anterior part of the snout were used for geometric morphometric analyses. Three landmarks were placed at the following points of each tooth: (1) the mesial point of the cervix of the crown; (2) the crown apex, and (3) the distal point of the cervix of the crown (Fig. 2A). In addition, six equally-spaced semi-landmarks were placed along the mesial and distal edges of the crown, respectively. Semi-landmarks assume curves or contours are homologous among specimens, and are useful in capturing the morphology of complex outlines when there are no homologous anatomical points (Maiorino et al., 2013). For the second wing phalanx, figures and photographs of the corresponding parts of various pterosaur species belonging to lineages that lived through the Early Cretaceous were collected from the literature, including SNUVP 201901, provisionally accepting that the identification of this material as a proximal part of the second wing phalanx is correct (File S1). Note, however, that much of the proximal end of SNUVP 201901 is eroded and damaged, therefore a rigorous reconstruction produced by Park et al. (2020) was used for the analysis in this work. Additionally, while Park et al. (2020) only made comparisons with lineages that lived in Asia, it is more appropriate to make a broader comparison given that pterosaurs were volant animals and cases of

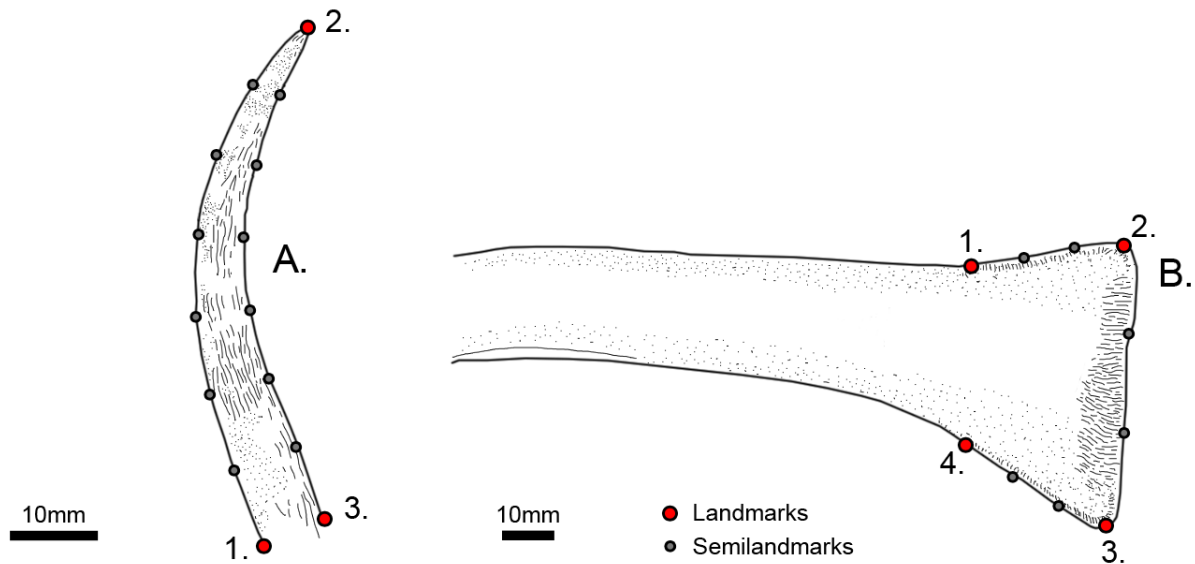


Fig. 2. Landmarks and semilandmark configurations for geometric morphometrics, with YCS 2001 and SNUVP 201901 (restored) as examples. A, Landmark and semilandmark positions used for teeth; B, Landmark and semilandmark positions for the proximal part of the second wing phalanx. Illustrations of YCS 2001 and SNUVP 201901 are after Yun et al. (2007) and Park et al. (2020), respectively.

cosmopolitan distribution of certain taxa are common (e.g., Witton, 2013). Thus, the specimens used for analysis in this study were not confined to Asian ones. SNUVP 201901 possesses a thin cortex, which strikingly differs from the thick cortex seen in dsungaripterids (e.g., Lim et al., 2001; Park et al., 2020) and therefore the members of the latter clade were omitted from the analysis. Azhdarchids were also not included in the analysis due to their characteristic T-shaped cross-section of the wing phalanx, which strikingly differs from the oval cross-sectional shape of SNUVP 201901 (Park et al., 2020). Wing phalanx images used in the analysis were dorsal/ventral views, assuming that outlines of these views are similar. The landmarks were placed at each of the following points at the proximal portion of the second wing phalanx: (1) distal base of the anterior part of the proximal condyle; (2) anteriormost point of the proximal condyle; (3) posteriormost point of the proximal condyle, and (4) distal base of the posterior part of the proximal condyle (Fig. 2B). Additionally, two equally-spaced semilandmarks were placed along the anterior, proximal and posterior edges, respectively. All landmarks and semilandmarks were placed through the programs tpsDIG and tpsUtil (Rohlf, 2015, 2017a, b), and scale bars were used to scale each digitized specimen. Plotting the semilandmarks followed the protocol of Ma et al. (2020), which involves drawing of the curve between the landmarks and resampling this curve into points through tpsDIG, and changing them into landmarks by tpsUtil. Corresponding TPS files are provided as supplementary data (Supplementary Files S2, S3), which will allow subsequent workers to reanalyze the data in light of any potential new discoveries. The coordinates of landmarks

and semilandmarks were then superimposed using Procrustes fit function in the program MorphoJ (Klingenberg, 2011) to generate the covariance matrix. Then, the generated covariance matrix was subjected to principal component analysis (PCA, Supplementary Files S4, S5), also using MorphoJ (Klingenberg, 2011). As many pterosaur skeletons, including those of the Yixian Fm. boreopterids (Lü & Ji, 2005; Lü, 2010; Jiang et al., 2014; Yun, 2021) are almost flattened into two dimensions, a simplified approach of two-dimensional geometric morphometric analysis is valid and appropriate. MorphoJ files including all shapes and analyses used in this work are provided in Supplementary File S6.

RESULTS

Teeth: The first four principal component (PC) axes (49.7%, 24.6%, 18.2%, and 2.7%, respectively) explain collectively 95.1% of the main tooth shape variations within the samples (Supplementary File S4). Negative PC1 values are associated with teeth with a thick, robust crown that is moderately recurved distally, whereas at positive PC1 values the tooth crown is extremely slender and nearly straight apicobasally (Fig. 3A). Negative PC2 values are associated with teeth having apicobasally straight, moderately thick crowns, with their thickness comparable to that of the mean shape (Fig. 3B). Additionally, they are associated with mesio basal shifting of the mesial point of the cervix, as well as the apicomeral shifting of the distal point of the cervix. Positive PC2 values are associated with teeth that are recurved distally, with convex mesial edge and concave

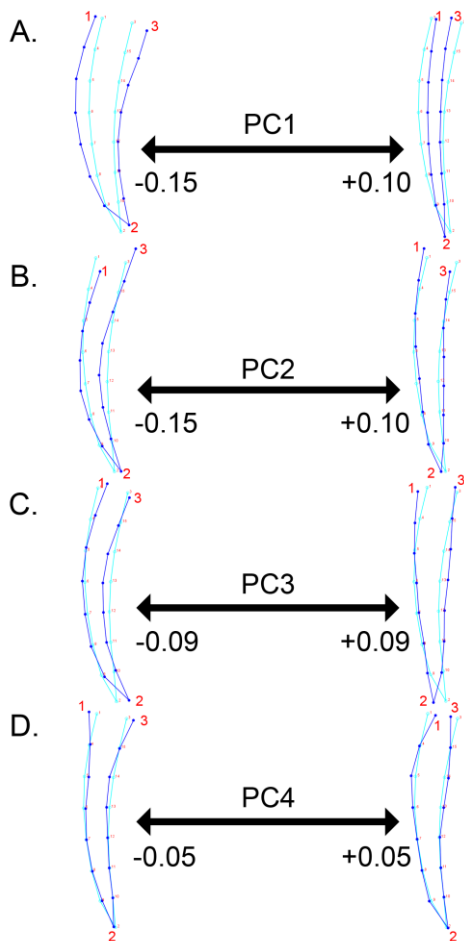


Fig. 3. Pterodactyloid tooth shape analyzed using geometric morphometrics. A, major changes in tooth shape on PC1; B, major changes in tooth shape on PC2; C, major changes in tooth shape on PC3; D, major changes in tooth shape on PC4. Red numbers indicate landmark positions.

distal edge (Fig. 3B). Furthermore, the mesial point of the cervix is positioned apicodistally, whereas its distal point is basodistally located at positive PC2 values. Thus, in life, such a tooth would have been procumbent. Positive PC3 values are associated with apicobasally straight tooth crowns, with a moderate mesiodistal expansion at the mid-basal part (Fig. 3C). Negative PC3 values, in contrast, are associated with distally recurved tooth crowns, with a basodistally located mesial part of the cervix (Fig. 3C). Positive PC4 values are associated with teeth displaying mesiodistal expansion at the basal third of the crown, and a narrow cervix region (Fig. 3D), whereas negative PC4 values are associated with mesiodistally narrow basal third of the tooth crowns, in which the cervix region is expanded (Fig. 3D).

The analyses found that the teeth of all three boreopterid taxa from the Yixian Formation (*Boreopterus cuiiae*, *Boreopterus giganticus*, *Zhenyuanopterus longirostris*) are differentiated from those of other pterosaurian clades used for the analysis (i.e., Anhangueria, Ctenochasmatoidea, Istiodactyliformes) by their highly positive PC1 values, clustering at the right extremity of the horizontal axis of the PC1 versus PC2 morphospace

(Fig. 4A; Supplementary Fig. S1A). Other clades are found to have broader distribution within the PC1 versus PC2 morphospace, and the 95% ellipse of anhanguerian shape space broadly overlaps with that of ctenochasmatooids.

In this morphospace (PC1 versus PC2), none of the South Korean teeth (KPE 40001, YCS 2001) plots close to those of boreopterids (Fig. 4A; Supplementary Fig. S1A). YCS 2001 had scores for both PC1 and PC2 that were most similar to those found in *Brasileodactylus* sp. (MN 4797-V), an anhanguerian pterosaur (Veldmeijer et al., 2005). Additionally, it was recovered deeply within the 95% ellipses of anhanguerians and ctenochasmatooids. Specimen KPE 40001 did not plot close to any other pterosaur taxa that were analyzed, but was found to fall within the 95% ellipses of anhanguerians and ctenochasmatooids. With respect to PC1, KPE 40001 had scores similar to those of ctenochasmatooid *Moganopterus zhuiana* (41HIII0419), whereas for PC2 it had similar scores to the anhanguerian cf. *Tropeognathus mesembrinus* (SMNS 56994).

In the PC3 versus PC4 morphospace, the three boreopterid taxa from the Yixian Formation are found to cluster together, and to fall within the 95% ellipses of Anhangueria and Ctenochasmatoidea (Fig. 4B; Supplementary Fig. S1B). In this morphospace, Yixian Fm. boreopterids are found to have similar PC3 and PC4 values with the ctenochasmatooids *Ctenochasma* sp., *Liaodactylus primus*, as well as with the anhanguerians *Anhanguera robustus* and cf. *Tropeognathus mesembrinus*. Regarding their PC3 and PC4 values, South Korean teeth are found to be significantly different from those of the Yixian Fm. boreopterids (Fig. 4B; Supplementary Fig. S1B). Specimen KPE 40001 is found to fall within the 95% ellipse of Anhangueria in the PC3 versus PC4 morphospace, and it plots close to *Guidraco venator*. Tooth YCS 2001 is found to have the lowest PC3 value among all pterosaur teeth that were analyzed, and in the PC3 versus PC4 morphospace did not fall within the 95% ellipses of any of the major clades analyzed.

Second wing phalanx: The first four PCs contain significant shape variation of the proximal part of the second wing phalanx (Supplementary File S5), and account together for 86.6% of the total variation (54.2%, 17.1%, 9.9%, and 5.4%, respectively). Positive PC1 values are associated with a squared end of the proximal condyle that is nearly symmetrical, proximodistally short, having straight anterior and posterior edges of the proximal condyle, and a broad shaft of the phalanx so that its width is comparable to that of the proximal condyle (Fig. 5A). Negative PC1 values, in contrast, are associated with an asymmetrical proximal condyle in which the posterior part is pointed as well as expanded posteriorly and proximally (Fig. 5A). Additionally, the anterior and posterior edges of the proximal condyle are elongated, and the phalanx shaft is considerably narrower

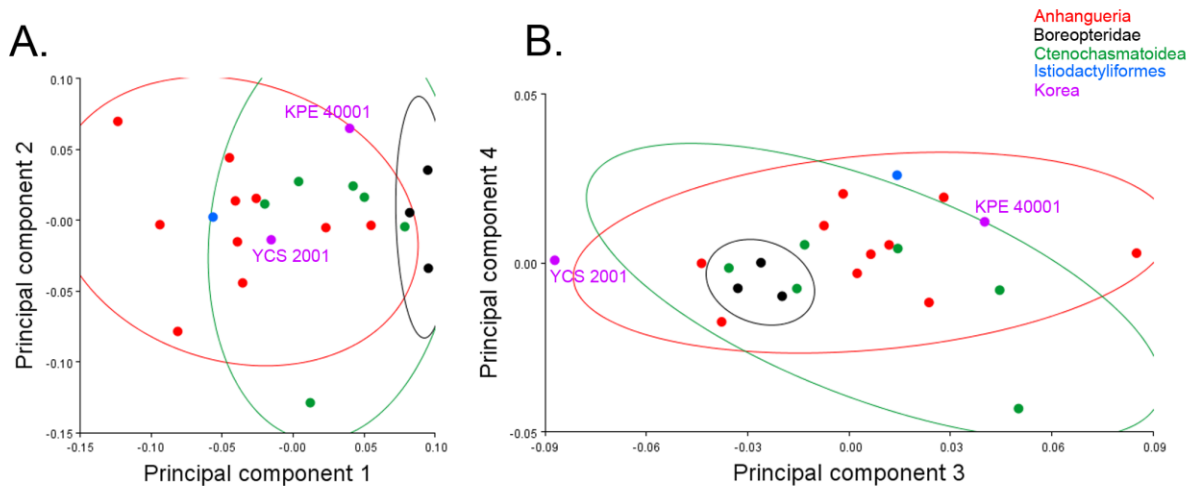


Fig. 4. Principal component analysis (PCA) of morphometric data collected from a variety of pterodactyloid teeth, with the South Korean specimens highlighted. A, PC1 versus PC2; B, PC3 versus PC4.

compared to the proximal condyle. Positive PC2 values are associated with a pointed, proximodistally narrow posterior part and a posteriodistally located anteroproximal point of the proximal condyle (Fig. 5B). For negative PC2 values, the anterior point of the proximal condyle is more anteroproximally located, whereas its posterior point is more anteriorly positioned (Fig. 5B). Positive PC3 values are associated with the convex proximal edge of the proximal condyle, and a slightly widened proximal condyle that is clearly set out from the narrowed diaphysis of the phalanx (Fig. 5C). Negative PC3 values, in contrast, are associated with a concave proximal edge of the proximal condyle, and a relatively thick shaft of the phalanx whose thickness is comparable to that of the proximal condyle (Fig. 5C). For positive PC4 values, the proximal edge of the proximal condyle is slightly convex, and the condyle is slightly narrowed. In contrast, the shaft of the phalanx is slightly thickened (Fig. 5D). Conversely, for negative PC4 values the proximal edge of the proximal condyle is concave, and its anterior and posterior parts are expanded. Furthermore, the diaphysis of the phalanx is narrowed (Fig. 5D).

No apparent separation in the morphospace (PC1 versus PC2) is found for the different pterosaur clades used for the analysis, as there was a large overlap between these groups (e.g., Anhangueria, Azhdarchoidea, Ctenochasmatoidea, Istiodactyliformes; Fig. 6A; Supplementary Fig. S2A). This appears to support previous suggestions according to which the structure of the proximal wing phalanx in pterodactyloids is uniform, without high degree of dissimilarity between the different clades (Averianov, 2010). The boreopterids *Boreopteris cuiaie* and *Zhenyuanopterus longirostris* are found to have PC2 values that are very slightly lower than 0, but these taxa are distinguished from each other by their PC1 values (greater than 0 in *Z. longirostris*, lower than 0 in *B. cuiaie*). Both of them are found to fall within the 90%

ellipses of all major pterosaurian clades that were analyzed (i.e., Anhangueria, Azhdarchoidea, Ctenochasmatoidea, Istiodactyliformes).

In the PC1 versus PC2 morphospace, SNUVP 201901 did not plot close to the boreopterid *Zhenyuanopterus longirostris*, but at least one other pterosaur taxon from a different clade (*Eosipterus yangi*) is found in an even closer position (Fig. 6A; Supplementary Fig. S2A). Additionally, several other pterosaur taxa (e.g., the anhanguerian *Brasileodactylus* sp., the ctenochasmatoid *Elanodactylus prolatus*, and the istiodactyliform *Mimodactylus libanensis*) were also found not to be significantly separated from SNUVP 201901 within the PC1 and PC2 morphospace.

As is the case for the PC1 versus PC2 morphospace, Anhangueria, Azhdarchoidea, Ctenochasmatoidea and Istiodactyliformes overlap significantly with each other in the morphospace generated by PC3 and PC4 (Fig. 6B; Supplementary Fig. S2B). The boreopterids *Boreopteris cuiaie* and *Zhenyuanopterus longirostris* are found to plot close to each other, and fall within the 90% ellipses of Anhangueria, Azhdarchoidea and Ctenochasmatoidea. SNUVP 201901 did not plot close to *Boreopteris cuiaie* or to *Zhenyuanopterus longirostris* in this morphospace, being found to have higher PC3 and lower PC4 values compared to these (Fig. 6B; Supplementary Fig. S2B). Instead, it plots close to some azhdarchoid and ctenochasmatoid taxa (e.g., *Balaenognathus maeuseri*, *Huaxiadraco corollatus* – BPMC 103, *Sinopterus* sp.), and was found to fall within the 90% ellipses of Azhdarchoidea and Ctenochasmatoidea.

DISCUSSION

The analyses performed in this study show that the pterosaur teeth from South Korea do not have shapes consistent with those of boreopterids, as the latter taxa are characterized by their extremely thin tooth morphology.

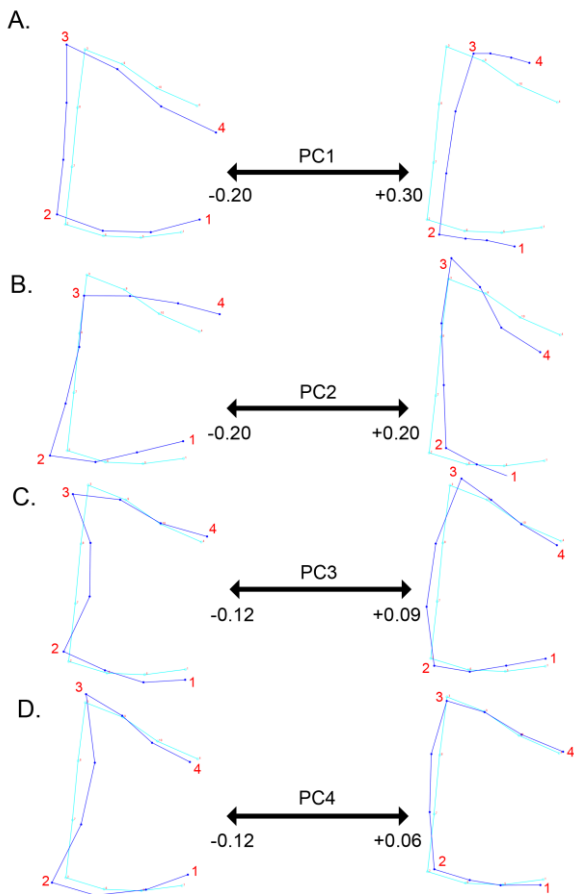


Fig. 5. Shape of the proximal part of the pterosaur second wing phalanx, analyzed using geometric morphometrics. A, major changes in shape on PC1; B, major changes in shape on PC2; C, major changes in shape on PC3; D, major changes in shape on PC4. Red numbers indicate landmark positions.

Instead, one of the specimens (YCS 2001) is found to closely resemble the tooth of the anhanguerian *Brasileodactylus* sp. (MN 4797-V) in the morphospace generated by PC1 and PC2, whereas the other specimen, KPE 40001, is found to have PC3 and PC4 values that are comparable to those of the anhanguerian *Guidraco venator*. These results potentially support anhanguerian affinities of these teeth, as suggested by Yun (2021). Regarding the taxonomic affinity of SNUVP 201901, a fragmentary second wing phalanx from the Hasandong Formation, it did plot near the boreopterid *Zhenyuanopterus longirostris* on the first two main axes of variation, but at least one other pterosaur taxon from a different clade (the ctenochasmatoid *Eosipterus yangi*) plotted even closer. Considering that all major clades that have been analyzed (Anhangueria, Azhdarchoidea, Ctenochasmatoidea, and Istiodactyliformes) overlap broadly with each other in the morphospaces generated by the four main PCs, it appears that the contours of the proximal part of the second phalanx of the fourth manual digit did not differ greatly from each other among the pterosaur lineages that existed in the Early Cretaceous epoch. Such results support and confirm the claims of Averianov (2010) and Yun (2021), who noted that

pterodactyloid wing phalanges are generally uniform in shape. Given that the Yixian Fm. boreopterids fall within the second wing phalanx morphospaces of other pterosaur clades on all the four main axes of variation, boreopterids also do not appear to have differed significantly from other pterosaurs of the same period. Lastly, SNUVP 201901 did not plot near any of the Yixian Fm. boreopterids on the PC3 and PC4 axes of variation. Although adequately restored, the fact that the outline of SNUVP 201901 used in the analysis (Park et al., 2020: fig. 2) is in fact a reconstruction, and the actual fossil is far more incomplete, also adds to the uncertainty about comparing or referring this specimen to any taxon in itself.

In summary, none of the purported evidences for the occurrence of boreopterid pterosaurs in the Early Cretaceous faunas of South Korea is in fact such an indicator. Geometric morphometric analyses reported here suggest that purported boreopterid tooth fossils from South Korea differ significantly from definite boreopterid teeth, but do provisionally indicate potential anhanguerian affinities of them.

Of note, while it might be argued that the relatively thick or strongly recurved nature of the South Korean teeth compared to those of Yixian Fm. boreopterids is simply the result of allometry or that of heterodonty between positions, these explications are highly unlikely for several reasons. Firstly, both the smaller *Boreopteris* spp. and the larger *Zhenyuanopterus longirostris* (which may even represent different growth stages of the same taxon; Witton, 2013) had very thin, straight teeth (Lü & Ji, 2005; Lü, 2010; Jiang et al., 2014), suggesting that the shape of the teeth did not change significantly with increasing body size in this clade. Secondly, the elongated nature of the South Korean teeth suggest that they are derived from the anterior part of the jaw, and in the Yixian Fm. boreopterids there are very thin and straight teeth at the front of the jaw that differ greatly from the South Korean teeth, whereas the more posterior teeth are much shorter and blunt (Lü & Ji, 2005; Lü, 2010; Jiang et al., 2014). Therefore, it is best to interpret these differences as of phylogenetic significance.

An isolated wing phalanx referred to cf. Boreopteridae does seem to be similar to that of *Zhenyuanopterus longirostris*, although it is not particularly more similar to this taxon as compared to other taxa. In fact, pterosaurs of the Early Cretaceous epoch seem to have quite similar shapes of this skeletal element. For more general concerns, Park et al. (2020) seem to have compared SNUVP 201901 with other pterosaurs based on published figures, and the analyses in this work are also based on them. However, the second wing phalanx of pterosaurs has been considered previously as systematically insignificant, and as such, in many cases only the overall shape was simply figured in previous literature, and any comparison based on such figures may imply potential risks of misinterpretation or overinterpretation. It is also noteworthy that many of the Chinese pterosaur skeletons,

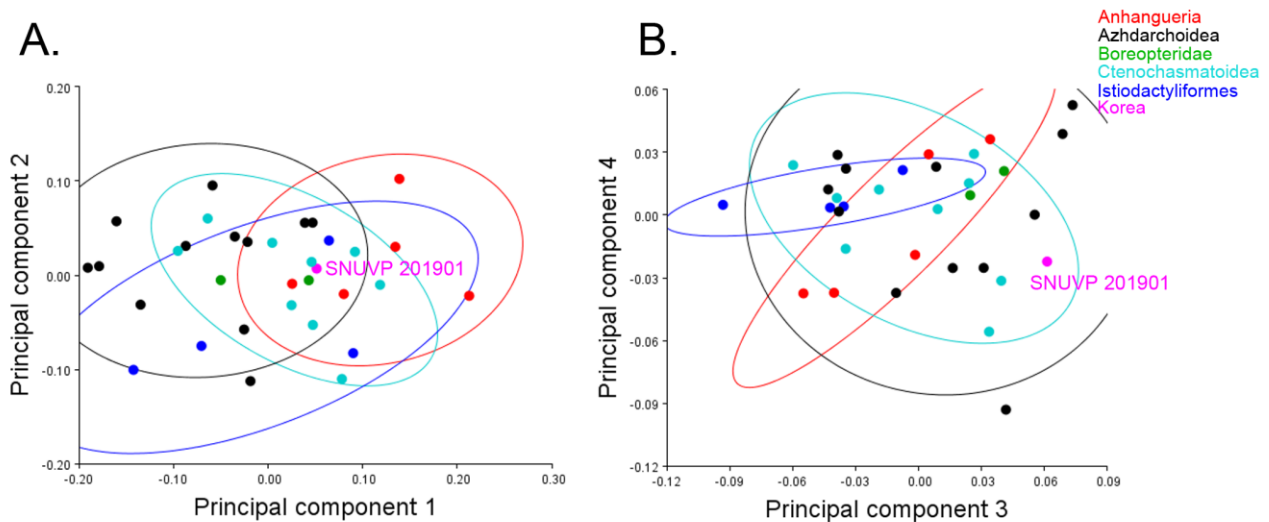


Fig. 6. Principal component analysis (PCA) of the morphometric data collected from the proximal part of second wing phalanges of various pterosaurs, with the South Korean specimen (SNUVP 201901) highlighted. A, PC1 versus PC2; B, PC3 versus PC4.

including the Yixian Fm. boreopterids, are laterally flattened, so the possibility of distortion cannot be ruled out for at least some of them (Lü & Ji, 2005; Lü, 2010; Jiang et al., 2014; Yun, 2021).

One notable point arising from the present study is that specimens referred to a single taxon – *Huaxiadraco corollatus* – by Pêgas et al. (2023; i.e., BPMC 103, 104, D2525, ZMNH M813), do not plot close to each other in the PCA morphospaces for the second wing phalanx. This suggests that even within a single pterosaur taxon, the proximal end of the second wing phalanx varied greatly depending on the individual, or else that this part was prone to severe post-mortem deformation especially considering that all these specimens were recovered in a very flattened state (Pêgas et al., 2023). In any case, this observation would suggest that it is unreasonable to use the shape of the proximal end of the second wing phalanx for classification or identification of pterosaur fossils.

As such, the hypothesis of the presence of boreopterid pterosaurs in the faunas of the Hasandong Formation and the Jinju Formation is provisionally rejected here, and consequently, evidences for a southeastern extension of the boreopterid distribution, as well as the occurrence of the clade in riparian environments, are also rejected. Of course, given the geographical proximity and the fact that boreopterids were probably piscivorous (e.g., Witton, 2013), it would not be surprising if this clade existed both in both riparian environments and in the Early Cretaceous paleoenvironments of South Korea, and additional lines of evidence may indeed support the presence of them in the faunas of the Hasandong Formation as well as those of the Jinju Formation. Until such time, however, there is no solid evidence to support this hypothesis.

While the occurrences of boreopterids in the Hasandong and Jinju formations are disputed, the possibility of the presence of anhanguerian pterosaurs raised through

geometric morphometric analyses bears some important implications.

Firstly, it lends some support to the hypothesis of Wang et al. (2012) that the Early Cretaceous pterosaur faunas of eastern Asia had a strong resemblance to those of Brazil, which is suggestive of strong paleobiogeographic ties between these regions. This hypothesis is based on close phylogenetic relationship between the Chinese taxon *Guidraco venator* and the Brazilian taxon *Ludodactylus sibbicki* (Wang et al., 2012), although it should also be considered that Anhangueria was a cosmopolitan clade (Kellner & Tomida, 2000; Wang et al., 2012).

Indeed, YCS 2001 is found to be close to the Brazilian *Brasileodactylus* sp. in the PC1 x PC2 analysis, and the PC3 x PC4 analysis suggests that KPE 40001 is close to *Guidraco venator* itself. Additionally, the pterosaur ichnotaxon *Pteraichnus koreanensis* occurs in the Hasandong Formation, and Park et al. (2020) already commented that such tracks are unlikely to be made by boreopterids, as manus and pedal tracks of *Pteraichnus koreanensis* are nearly equal in size (Lee et al., 2008), whereas in boreopterids the pedes are extremely small (Lü & Ji, 2005; Lü, 2010; Witton, 2013).

While the pedal anatomy of anhanguerians is admittedly poorly understood, available material suggests that their pedes were not as small as those of the boreopterids, and that their length is at least comparable to the manus length (Kellner & Tomida, 2000; Witton, 2013; Jung et al., 2022).

Thus, it is possible that the trackmaker of *Pteraichnus koreanensis* was an anhanguerian pterosaur, though members of other pterodactyloid clades from the same time and space (e.g., Azhdarchoidea, Ctenochasmatoidea, Dsungaripteroidea, Istiodactyliformes) are equally possible candidates in our current state of knowledge.

ACKNOWLEDGEMENTS

The author thanks Mark P. Witton (School of Earth and Environmental Sciences, University of Portsmouth, United Kingdom) for sharing a picture of dentition of *Zhenyuanopterus longirostris*, which was used for geometric morphometric analysis. Special thanks go to Denise Crampton and Christian Foth, for the detailed guidance about geometric morphometrics and related software. Lastly, the author's hat is off to all paleontologists who have previously suggested boreopterid affinities of the South Korean fossils that are analyzed here. Although our interpretations on them may differ, their valuable ideas started a new round of investigations that would be ultimately helpful in understanding the Cretaceous terrestrial ecosystem of the Korean Peninsula. This manuscript is benefited by insightful comments from reviewer David Hone (Queen Mary University of London), an anonymous reviewer, and by the editor Zoltan Csiki-Sava (University of Bucharest, Bucharest).

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SUPPLEMENTARY INFORMATION

Additional supplementary information, unedited from the format provided by the Author(s), can be found online at:

https://actapalrom.geo-paleontologica.org/Online_first/Yun_supplem_files.7z

Supplementary File S1. Table of data used in the analyses presented in Figures 3–6.

Supplementary File S2. TPS file of landmark coordinates of the tooth shape analysis.

Supplementary File S3. TPS file of landmark coordinates of the second wing phalanx shape analysis.

Supplementary File S4. PCA results of the tooth shape analysis.

Supplementary File S5. PCA results of the second wing phalanx shape analysis.

Supplementary File S6. MorphoJ files including all shapes and analyses.

Supplementary Figure S1. Principal component analysis (PCA) of morphometric data collected from a variety of pterodactyloid teeth, including purported boreopterid specimens from South Korea. A, PC1 versus PC2; B, PC3 versus PC4.

Supplementary Figure S2. Principal component analysis (PCA) of morphometric data collected from the proximal part of second wing phalanges of various pterosaurs, including the putative boreopterid specimen (SNUVP 201901) from South Korea. A, PC1 versus PC2; B, PC3 versus PC4.