First juvenile *Rhamphorhynchus* recovered by phylogenetic analysis

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ABSTRACT— Standing seven to 44 centimeters in height, a growing list of 120+ specimens assigned to the pterosaur genus *Rhamphorhynchus* are known chiefly from the Solnhofen Limestone (Late Jurassic, southern Germany). An early study recognized five species and only one juvenile. A later study recognized only one species and more than 100 immature specimens. Phylogenetic analyses were not employed in either study. Workers have avoided adding small Solnhofen pterosaurs to phylogenetic analyses concerned that these morphologically distinct specimens were juveniles that would confound results. Here a large phylogenetic analysis that includes tiny Solnhofen pterosaurs tests that concern and seeks an understanding of relationships and ontogeny within the Pterosauria with a focus on *Rhamphorhynchus*. 195 pterosaurs were compiled with 185 traits in phylogenetic analysis. *Campylognathoides* + *Nesodactylus* were recovered as the proximal outgroups to the 25 *Rhamphorhynchus* specimens. The ten smallest of these nested at the clade base demonstrating phylogenetic miniaturization. Two *Rhamphorhynchus* had identical phylogenetic scores, the mid-sized NHMW 1998z0077/0001, and the much larger, BMNH 37002. These scores document a juvenile/adult relationship and demonstrate isometry during pterosaur ontogeny, as in the azhdarchid, *Zhejiangopterus,* and other pterosaurs. Rather than confounding results, tiny Solnhofen pterosaurs illuminate relationships. All descended from larger long-tailed forms and nested as transitional taxa at the bases of the four clades that produced all of the larger Late Jurassic and Cretaceous pterodactyloids. No long-tailed pterosaurs survived into the Cretaceous, so miniaturization was the key to pterosaur survival beyond the Jurassic.

INTRODUCTION

Many pterosaur genera are known from single specimens. By contrast, the genus *Rhamphorhynchus* (Late Jurassic, Solnhofen formation, southern Germany, Figs. 1–3) includes a growing list of over 120 specimens. These have been studied over the last few decades in attempts at splitting and lumping the many members of this genus. These studies began when Koh (1937) examined the relative proportions of the skull and humerus and recovered two species: *R. muensteri* and *R. gemmingi*.

Wellnhofer (1975) divided 108 *Rhamphorhynchus* specimens into five species in order of increasing size. These also differed in cranial morphology, bone fusion patterns, and long bone proportions. Variations in the pelvis and tail vane were noted. Wellnhofer reported the 23 smallest ones with the shortest rostra were not juveniles due to the marked discontinuity in size between species. He assigned them to *R. longicaudus*. The eight larger *R. intermedius* specimens had a longer rostrum. Forty larger specimens with an even longer rostrum were assigned to *R. muensteri.* Six others were assigned to *R. gemmingi*. The two of the largest and most robust specimens (GPIT/RE/7321 and BMNH 37002), were assigned to *R. longiceps*. A third specimen half their size (CM 11428) was also assigned to that species. Wellnhofer considered BMNH 37012 a unique juvenile of uncertain affinity, despite the fact that it was slightly larger than some *R. longicaudus* specimens (Fig. 2). Twenty-two specimens were not assigned to a species. Many of these lack a skull, but most include forelimb and wing finger elements in the size range of *R. muensteri* and *R. gemmingi*.

Twenty years later, Bennett (1995) employed skull, humerus, radius and first wing phalanx length data from dozens of *Rhamphorhynchus* specimens gleaned from Wellnhofer (1975) for use in statistical analyses. Bennett's size-frequency histograms produced bimodal distribution graphs. Bennett concluded that two size-classes were present in moderate numbers (*R. longicaudus* and *R. muensteri* + *R. gemmingi*), along with a small number of large specimens (*R. longiceps*). He reported that his principal component analysis indicated that size accounted for 98 percent of observed variation in the skull, neck and wing skeleton and that suggested only one species was present. Bennett reported his results reflected the normal phylogenetic variation found within any population. Bennett further noted the gradual increase in pelvic fusion in larger specimens based on Wellnhofer's (1975) drawings. Bennett (1995) considered the bimodal distribution recovered by his analyses the result of seasonal mortality, likely due to weather changes biased against immature individuals. Bennett concluded that all Solnhofen *Rhamphorhynchus* specimens were conspecific and that the skull shape changed during ontogeny. Bennett noted that relative tooth sizes were longest in mid-sized subadults, but the tooth number did not change. He reported that sexual dimorphism was insignificant, if present at all. Bennett considered only the largest two specimens adults. They stood twice the height of members in the majority size class (Fig. 2). That 2/108 ratio of adults vs. immature specimens stands out as atypical in the fossil record where juveniles are relatively rare.

Bennett (1996) duplicated his earlier statistical methods in a study of the remainder of the Solnhofen taxa, all short-tailed pterodactyloids with data gleaned from Wellnhofer (1970). Results were once again bimodal. Bennett determined that nominal species had been over split taxonomically because earlier workers had ignored the juvenile status of the smaller ones. Bennett reported his size-frequency histograms were strongly skewed toward the small size. He reported that bone fusion patterns often associated with non-pterosaur juvenile archosaurs were also found in small pterodactyloids, with two exceptions: the type specimens of *Cycnorhamphus suevicus* and *C. canjuerensis*, both among the largest specimens in his study. Bennett rejected the hypothesis that the first pterodactyloids were descended from small 'rhamphorhynchoids' or that they had grown smaller as, or after, they evolved pterodactyloid characters, because the small, seemingly primitive taxa had typically juvenile traits.

Proceeding under the conventional hypothesis of allometry during ontogeny in pterosaurs, Bennett (2006) visually matched two tiny short-snouted pterosaurs, JME SoS 4593 and JME SoS 4006, to the much larger, long-snouted *Germanodactylus* holotype, BSP 1892.IV.1, in a juvenile/adult pairing. Bennett did not employ phylogenetic analysis in any of his three studies.

Cai and Wei (1994) reported on several *Zhejiangopterus* specimens in a wide range of sizes (Fig. 4), all isometrically identical. This ontogenetic series has been largely overlooked.

Pterodaustro hatchlings (Codorniú and Chiappe, 2004), an embryo (Chiappe, et al., 2004) and a complete ontogenetic series for this genus are known (Chinsamy et al., 2008). They reported juveniles grew rapidly for two years until they reached 53% of their mature body size, whereupon they attained sexual maturity. Relatively little allometry was reported for this ontogenetic series.

A juvenile/subadult/small adult *Tapejara* (Eck, et al., 2011) is known, virtually identical to its larger counterparts. Even at half size, crests were well developed. This was unexpected because Bennett (1991, 1992, 1993, 2001) had earlier determined that small crested *Pteranodon* specimens were juveniles and/or females. Larger, large-crested forms were considered males.

Peters (2011) reported that tiny Solnhofen pterosaurs had pedal proportions distinct from those of purported adults. Wellnhofer (1970) considered one of the tiniest of all pterosaurs, B St 1967 I 276, a juvenile based on its size and its lack of three ossified, disc-like, pedal phalanges (p3.2, p4.2 and p4.3), but Peters (2011) observed those tiny pedal phalanges were simply displaced during taphonomy. Peters (2011:fig. 2) also illustrated several *Rhamphorhynchus* pedes (more added here in Fig. 3) noting the variety in their morphologies. This was an unexpected dataset if these taxa were indeed conspecific, as Bennett (1995) had reported.

Pterosaurs with an unfused scapulocoracoid or sacral series are typically considered immature (e.g., Bennett, 1993, 1995, 1996; Kellner and Tomida, 2000), despite the fact that some of these specimens are among the largest of all non-azhdarchid pterosaurs. Scapulocoracoid fusion among pterosaurs has not been tested as a trait in phylogenetic analysis due to this paradigm.

Hone, et al. (2013) reidentified the third specimen (CM 11428) attributed to *R. longiceps* by Wellnhofer (1975) as another *R. muensteri*. Indeed, the specimen is similar in size to other *R. muensteri* specimens and shares many of their traits.

Prior Phylogenetic Analyses

No prior phylogenetic analyses of the Pterosauria (Kellner 2003, Unwin 2003, Andres 2010 and all works derived from them) have included tiny Solnhofen pterosaurs or more than two *Rhamphorhynchus* specimens. The nesting of *Rhamphorhynchus* has differed slightly in each study. Kellner (2003) nested *Rhamphorhynchus* between *Campylognathoides* + *Eudimorphodon* and the Pterodactyloidea. Unwin (2003) nested *Rhamphorhynchus longiceps* and *R. muensteri* with *Rhamphocephalus*, *Nesodactylus, Dorygnathus* and *Angustinaripterus* all within the Rhamphorhynchinae. This clade nested with *Scaphognathus* + *Sordes* and together these formed the proximal outgroup to the Pterodactyloidea. Andres (2010) nested *Rhamphorhynchus* with *Nesodactylus*, *Cacibupteryx*, *Dorygnathus* and *Scaphognathus* in order of increasing distance, then nested anurognathids as the proximal outgroup to the Pterodactyloidea.

The Addition of *Darwinopterus*

Lü, et al. (2010) and Unwin and Lü (2010) compiled 56 pterosaur taxa with 117 characters and recovered *Darwinopterus* as a transitional taxon bridging the former gap between long-tailed basal forms and short-tailed derived forms, members of the Pterodactyloidea. They also erected the clade Monofenestrata to include *Darwinopterus* + Pterodactyloidea. Unfortunately, 500,000+ most parsimonious trees were produced in their study with loss of resolution chiefly surrounding *Darwinopterus*. No single taxon, whether more primitive or more derived, was recovered proximal to *Darwinopterus*, so a specific transitional series of three or more generic taxa that includes *Darwinopterus* was not recovered.

Qinglongopterus* and *Bellubrunnus

Lü et al. (2012) reported that *Qinglongopterus guoi* was strikingly similar to *Rhamphorhynchus* and nested it between *Nesodactylus* and *Rhamphorhynchus*. Reflecting traditional concerns, the authors reported the juvenile status of *Qinglongopterus* could potentially confound their phylogenetic analysis, but concluded their dataset was not compromised by its inclusion.

Bellubrunnus rothgaengeri (Hone et al., 2012; Fig. 2) was likewise considered a juvenile specimen with a close affinity with *Rhamphorhynchus* based on a large, but unlisted, number of shared characteristics. It was considered distinct by virtue of its discovery in strata predating the classic Solnhofen Limestone, and unlike all other known pterosaurs by having anteriorly concave wingtip phalanges. The latter autapomorphy is a misinterpretation due to axial wing twisting during taphonomy, a common occurrence in pterosaur fossils. Hone et al. followed Bennett (1995) in their listing of the purported juvenile traits of *Bellubrunnus*: (1) orbits large; (2) skull short and broad; (3) edentulous mandible with blunt tip; (4) bone texture rough-porous and grainy-granulated; (5) some of the shafts of wing elements fluoresce less; (6) many bones not fused together. Contradicting that hypothesis, Hone, et al. (2012) also noted several traits that would argue against a juvenile status: (1) no epiphyses present; (2) sternum and small tarsals fully ossified. Hone et al. acknowledged that skeletal measurements place *Bellubrunnus* among the very smallest pterosaur specimens known. They did not provide a phylogenetic analysis, but briefly compared *Qinglongopterus* to *Bellubrunnus* noting, some skeletal proportions differ between the two. These were not specified.

The Present Study

In a break with paradigm and tradition, sparrow-to-hummingbird-sized Solnhofen pterosaurs were added to a genus- and specimen-based phylogenetic analyis of 195 pterosaurs and 20 outgroups (Fig. 1) compiled with 185 character traits. Three pterosaur embryos were also included. Morphological variation within several genera prompted the inclusion of as many as 25 taxa within a single genus. This was done to test prior phylogenetic and ontogenetic hypotheses of relationships within *Rhamphorhynchus* (Wellnhofer 1975, Bennett 1995), other pterosaur genera, and more broadly, within the Pterosauria.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; **BMMS (BMM)**, Burgermeister-Müller Museum, Solnhofen, Germany; **BMNH**, British Museum of Natural History, London, England; **BES SC**, Museo Civico di Storia Naturale di Milano, Italy; **BSp (BSPG, B St)**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; **CAGS IG,** China Academy of Geological Sciences, Institute of Geology, Beijing, China; **CM**, Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.; **CMC**, Cincinnati Museum Center, Cincinnati, Ohio, U.S.A.; **CYGB**, Chaoyang Geological Park, Chaoyang City, China; **D**, Dalian Natural History Museum, Shahekou, Dalian, Liaoning, China; **FHSM (SMM)**, Fort Hays State Museum, Fort Hays, Kansas, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **GPIH**, Geologisch-Paläontologisches Institut (Geomatikum) der Universität Hamburg, Germany; **GPIT**, Geologisch-Paläontologisches Institut, Tübingen, Germany; **IVPP**, Institute of Vertebrate

Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; **GLGMV**, Guilin Longshan Geological Museum, Gulin City, China; **G mu**, Institut für Geowissenschaften Christian-Albrechts-Universität, Kiel, Germany; **GMV**, National Geological Museum of China, Beijing, China; **HGM**, Henan Geological Museum, Zhengzhou, Henan Province, China; **JZMP**, Jinzhou Museum of Paleontology, Jinzhou City, Liaoning Province, China; **JME SoS**, Jura Museum, Eichstätt, Germany; **KUVP**, Natural History Museum, University of Kansas, Lawrence, Kansas, U.S.A.; **LPM**, Liaoning Paleontological Museum, Shenyang Normal University, China; **MB. AM (MB.R.)**, Museum für Naturkunde, Berlin, Germany; **MBH**, Museum Berger, Harthof, Eichstatt, Germany; **MCSNB**, Museo Civico di Scienze Naturali, Bergamo, Italy; **MHIN-UNSL-GEO-V**, Museo de Historia Natural de la Universidad Nacional de San Luis, San Luis, Argentina; **MNHN**, Museum National d'Historie Naturelle, Paleontologie, Paris, France; **MPUM**, Museo di Paleontologia, Universitá di Milano, Milan, Italy; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy; **MTM**, Gyn-Magyar Természettudományi Múzeum (Hungarian National History Museum), Budapest, Hungary; **NHMW**, Naturhistorisches Museum Wien, Vienna, Austria; **NMC**, National Museum of Canada (Canadian Museum of Nature), Ottawa, Canada; **PMOL**, Paleontological Museum of Liaoning, Shenyang Normal University, Liaoning Province, China; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **SC**, Museo Geologico della Carnia, Ampezzo, Italy; **SMF**, Senckenberg-Museum Frankfurt, Germany; **SMNK-PAL**, Staatliches Museum für Naturkunde, Karlsruhe, Germany; **SMNS**, Paläontologische Abteilung, Staatliches Museum für Naturkunde, Stuttgart, Germany; **St/Ei** = Stadt/Eichstätt Jura Museum, Eichstätt, Germany (see JME); **T**, Universität Zürich Paläontologisches Institut und

Museum, Zurich, Switzerland; **TM**, Teyler's Museum, Haarlem, The Netherlands; **UUPM R (UU)**, Institute and Museum of theUniversity of Uppsala, Uppsala, Sweden; **WU**, Washington University, St. Louis, Missouri, U.S.A.; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska, U.S.A.; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.; **YH**, Yizhou Museum, Yixian, Liaoning Province, China; **ZMNH**, Zhejiang Museum of Natural History, Zhejiang, China.

Anatomical Abbreviations—Manual and pedal phalanges are abbreviated in this pattern: **p3.2** refers to pedal digit three, second phalanx.

MATERIALS AND METHODS

The present study provides a phylogenetic analysis of 195 large and small pterosaurs plus 20 outgroup taxa compiled with 185 traits (Supplementary Data). Outgroup taxa were recovered by a large phylogenetic analysis of the Amniota (Peters, unpubl. data) that expanded on an earlier study (Peters, 2000b). Data were compiled in MacClade 4.08 (Maddison and Maddison, 2000) then imported into PAUP* 4.0b (Swofford, 2002) and analyzed using parsimony analysis with the heuristic search algorithm. All characters were treated as unordered and no character weighting was used. Bootstrap scores were computed (Fig. 1).

Distinct from prior studies, tiny Solnhofen pterosaurs were included along with several specimens within *Eudimorphodon*, *Campylognathoides*, *Rhamphorhynchus*, *Dorygnathus*, *Ctenochasma*, *Darwinopterus*, *Scaphognathus*, *Pterodactylus*, *Germanodactylus*, *Nyctosaurus*, *Pteranodon* and others. Many of the 215 inclusion set taxa were studied first hand, but due to the great size and breadth of this study, data from others were gleaned from photographs and the literature. Due to their crushed and scattered preservation, scaled reconstructions of all included *Rhamphorhynchus* fossils were produced for ready comparison (Fig. 2). Reconstructions of other included taxa can be viewed at http://www.reptileevolution.com. [note to editor: these can be uploaded as supplementary material or wherever else is appropriate, perhaps deleted].

Expanding on the Peters (2011) study of pterosaur pedes, a separate phylogenetic analysis was produced restricted to *Rhamphorhynchus* manual and pedal traits. Taxa that did not preserve these traits were deleted.

RESULTS

The phylogenetic analysis of the Pterosauria recovered a single optimal tree (Fig. 1) with a length of 2621 steps, a Consistency Index (CI) of 0.153, a Retention Index (RI) of 0.772, and a Rescaled Consistency Index (RC) of 0.118. The Homoplasy Index (HI) was very high at 0.847. Homoplasy was rampant with four clades convergently evolving a complete set of pterodactyloid traits. Two other clades evolved incomplete sets (see below). Subsets of the large tree had much higher Consistency Index scores and much lower Homoplasy Index scores. For example, scores for the *Rhamphorhynchus* clade plus two outgroup taxa were: CI = 0.494, RI = 0.721 RC = 0.357, HI = 0.506 with a length of 269 steps.

Rather than confounding results (contra Lü, et al., 2012), the addition of tiny Solnhofen pterosaurs clarified relationships, bringing new insights to the evolution of pterosaur clades and increasing the resolution of the tree topology. The present analysis recovered four pterosaur clades that independently attained the pterodactyloid grade (contra Kellner, 2003; Unwin, 2003; Lü et al., 2006; Andres, 2010). Nesting at the base of each clade was a series of tiny Solnhofen pterosaurs. Each series was miniaturized from larger taxa with longer tails and shorter metacarpals, and each series was basal to larger taxa with shorter tails, longer rostra, longer metacarpals and other pterodactyloid-grade traits.

Two of these pterodactyloid-grade clades arose from distinct lineages within the nine specimens that nested within the genus *Dorygnathus* (Fig. 1). One lineage ultimately produced giant azhdarchids after evolving through tiny transitional taxa. The other lineage produced ctenochasmatids from tiny transitional taxa. The remaining two pterodactyloid-grade clades arose from small *Scaphognathus* specimens. One produced cycnorhamphids and ornithocheirids from tiny transitional taxa. The other clade produced *Pterodactylus*, *Germanodactylus* and their tiny ancestors. A sister to one mid-sized *Germanodactylus* (B St 1892 IV 1) gave rise to larger dsungaripeterids and tapejarids. A sister to another mid-sized *Germanodactylus* (SMNK-PAL 6592) gave rise to larger elanodactylids, eopteranodontids, pteranodontids and nyctosaurids.

In the present analysis the last common ancestor of all pterodactyloid-grade pterosaurs was *Sordes pilosus* (Fig. 1), despite the fact that it had no pterodactyloid-grade traits. Given these results, the clades ‘Pterodactyloidea’ and ‘Monofenestrata’ can no longer be considered monophyletic unless they both include *Sordes* at their base along with all intervening pterosaurs.

Two other clades evolved only a few pterodactyloid traits. The clade Anurognathidae lost cervical ribs and greatly reduced the tail, but did not reduce the naris and pedal digit five, nor elongate the neck, metacarpus and rostrum. The Wukongopteridae (including *Darwinopterus*) elongated the neck and rostrum, and reduced the naris to absence, but did not elongate the metacarpus, reduce the tail or reduce pedal digit five. The Wukongopteridae produced no Cretaceous descendants according to the present analysis and inclusion set.

A series of ten, small-to-tiny taxa was recovered at the base of the clade *Rhamphorhynchus* (Fig. 2). A single miniaturized Solnhofen pterosaur, B St 1878 VI 1, nests at the base of the clade that includes *Nyctosaurus*, *Pteranodon* and the eopteranodontids. Yet another single tiny taxon, *Nemicolopterus*, nests at the base of the clade *Shenzhoupterus* plus Tapejaridae. Two tiny pterosaurs, CM11426 and B St 1911, were recovered between larger huanhepterids and larger azhdarchids. Though tiny, both had a long rostrum and small orbit. Tiny taxa also preceded *Dorygnathus* and *Campylognathoides.* Miniaturization likewise occurred at the base of the Fenestrasauria (Peters 2000b), represented here (Fig. 1) by *Cosesaurus,* a small taxon derived from a sister to the larger *Macrocnmeus* and *Jesairosaurus.*

When tested in phylogenetic analysis, tiny JME-SoS 4593 and JME-SoS 4006 nested with other tiny pterosaurs of similar morphology (Fig. 1, contra Bennett, 2006). These included *Ornithocephalus* (BSPG 1971 I 17, von Sömmerring, 1812, 1817) and SMNS 81775. Together these four nested in a distinct clade at the base of the

Pterodactylus and proto-*Germanodactylus* clades. In all of these examples of tiny pterosaurs in phylogenetic series, it is clear that miniaturization accompanied, or was the cause of, the substantial morphological changes that were retained by subsequent clades of larger genera.

Precursors to the Genus *Rhamphorhynchus*

Following the evolution of pterosaurs from their nonvolant fenestrasaur and lepidosaur precursors, the present phylogenetic analysis of the Pterosauria (Fig. 1) recovered a Triassic split between dimorphodontids and eudimorphodontids. The latter produced the small B St 1994 specimen, which nested as the proximal outgroup to *Campylognathoides. Nesodactylus* (AMNH FR 2000) nested within the genus *Campylognathoides*. The Pittsburgh specimen of *Campylognathoides* (CM1124) nested as the proximal outgroup to the genus *Rhamphorhynchus*. 50 million years separated *Campylognathoides* in the Hettangian (Earliest Jurassic), from *Rhamphorhynchus intermedius* in the Tithonian (Latest Jurassic).

Clades within the Genus *Rhamphorhynchus*

Here (Fig. 1) the five nominal species of *Rhamphorhynchus* reported by Wellnhofer (1975) were recovered in a new order: 1) *R. intermedius; 2) R. longicaudus*; 3) *R. longiceps*; 4) *R. muensteri*; 5) *R. gemmingi*. Not five, but eight clades were recovered. Most of the traits used to lump and split these clades, such as pedal proportions (Fig. 3), would have been absent from the dataset in Bennett's (1995) long bone length statistical analyses.

Clade number 1 includes small *R. intermedius* (St/Ei 8209, Tithonian) and tiny B St 1960 I 470A. Less than half the size of *Campylognathoides*, *R. intermedius* represents the first known stage in the phylogenetic miniaturization of basal *Rhamphorhynchus*. It retained a relatively long skull, but had a narrower sternal complex and reduced both the prepubis and deltopectoral crest. The naris remained relatively long, but the antorbital fenestra was reduced. The wings and hind limbs were relatively shorter. The teeth were anteriorly oriented and the hooked mandible was more pronounced.

Half the size of *R. intermedius*, BSPG 1960 I 470A had a shorter and more gracile tail. The ventral pelvis was not as deep. BSPG 1960 I 470A could have been a juvenile or a tiny adult because clade number 2 includes taxa similar in size.

Clade number 2 includes three tiny specimens, *Qinglongopterus* (Lü et al. 2012), *Bellubrunnus* (Hone et al. 2010) and the unnumbered MBH specimen (number 20 in the Wellnhofer 1975 catalog). Completing the process of phylogenetic miniaturization, these three were half the size of *R. intermedius* and all had a very short rostrum. They establish a lower limit to adult size that generally matches that of other tiny Solnhofen pterosaurs at 7 cm tall. In this clade the premaxilla was not pointed, but was wider than tall. The naris was further reduced relative to the antorbital fenestra.

Qinglongopterus was the tallest clade member and had the longest antebrachium. Relative to *R. intermedius*, the sternal complex was shorter and wider. The torso was more gracile. The wing finger was relatively longer. The prepubis was shorter.

Relative to *Qinglongopterus,* the unnumbered MBH specimen had a shorter torso and a more gracile wing, but also a more robust tail. The sternal complex was greatly reduced.

Of these three, *Bellubrunnus* had the shortest neck, torso, humerus and antebrachium. Relative to *R. intermedius, Bellubrunnus* was found in earlier highest Kimmeridigian strata. *Qinglongopterus* was found in even earlier Oxfordian strata, supporting their basal nesting with their chronological appearance. By contrast, the more primitive *R. intermedius* was a relic taxon surviving into the later Tithonian.

Clade number 3 includes three small, short-snouted specimens previously assigned to *R. longicaudus* (BSPG 1938 I 503a, TM 6924, and BSPG 1889XI 1), plus the only juvenile identified by Wellnhofer (1975), BMNH 37012. These three were slightly taller than clade number 2 members. Nesting at the base of clade number 3 and distinct from *Qinglongopterus*, BMNH 37012 had a larger sclerotic ring, smaller naris, and larger teeth. The dentary teeth were oriented anteriorly on either side of a toothless dentary process that did not extend beyond the anterior tooth tips. The upper temporal fenestra opened more laterally. The sternal complex was smaller and triangular. The other three specimens of clade number 3 had a longer rostrum and a longer anterior dentary that extended beyond the anterior teeth. The forelimbs were more gracile.

Clade number 4 includes two longer-snouted specimens. One (BSPG 1938 I 503a) was only as tall as clade number 3 members. The other (ROM 55352) was twice as tall.

Relative to clade number 3 specimens, BSPG 1938 I 503a had a longer rostrum and a more gracile dentary. The upper temporal arch was lower relative to the orbit. The scapulocoracoid was more gracile.

Relative to its clade sister, the ROM 55352 specimen had a relatively longer rostrum and dentary. The deltopectoral crest was hatchet-shaped. Manual 4.1 extended beyond the elbow when folded. The hind limb was relatively longer. The pedal digits were relatively shorter. Rather than a juvenile/adult pairing, these two appear to document an evolutionary progression in size and morphology that continues through the more derived clades.

Clade number 5 includes two of the largest *Rhamphorhynchus* specimens (GPIT/RE/7321 and BMNH 37002), along with a likely juvenile, the Vienna specimen (NHMW 1998z0077/0001). In phylogenetic scoring the Vienna specimen was identical to BMNH 37002 in all tested traits, only much smaller.

Relative to the mid-sized ROM 55352 specimen of clade number 4, the larger GPIT/RE/7321 specimen of clade number 5 was more robust overall with smaller antorbital and upper temporal fenestrae, a deeper dentary, and more robust wings. The upper temporal arch was aligned with the dorsal orbit rim. The jugal and jawline descended posteriorly. The tail was more robust. Fingers 1–3 were longer. The femur was shorter relative to the tibia.

Relative to GPIT/RE/7321, BMNH 37002 was even larger with a distinct tooth pattern. The antorbital fenestra was twice as large. The lateral temporal fenestra was more open. The tail was not so robust. The sternal complex was squared off caudally. The distal humerus and pedal unguals were more robust.

Compared to BMNH 37002, the Vienna specimen had a slightly shorter rostrum and sternal complex, but not short enough to affect its score. So, if it was indeed a juvenile of the larger BMNH 37002, then a measure of allometry was present. It is also possible that the Vienna specimen was a juvenile to a shorter-snouted, undiscovered adult. The third possibility, that the Vienna specimen was a smaller adult sister taxon that ultimately gave rise to the giant BMNH 37002 also remains a possibility, but the many examples of other closely related *Rhamphorhynchus* specimens that do not have identical character scores weighs against that idea. Despite their great size, none of these three clade number 5 members had a fused scapulocoracoid.

Clade number 6 includes three mid-sized specimens not cataloged by Wellnhofer (1975), JME SOS 4785, MTM V2008.33.1, and WU 970001 (Fig. 2). Relative to the ROM 55352 specimen of clade number 4, these three were 15% shorter. The sacrum was incompletely fused. The tail was shorter. The sternal complex was longer and squared off posteriorly, as in clade number 5. The scapulocoracoid was fused. The pubis was as deep as the ischium. The tibia was relatively longer than in clade number 5 members. The deeper prepubis created a deeper torso. The wing was longer. The MTM V2008.33.1 specimen had a relatively shorter metacarpus and tibia. The WU 970001 specimen had a smaller mandible and humerus.

Clade number 7 includes three additional *R. muensteri* specimens (CM 11427, YPM 1778, and JME-SOS 4009; all cataloged by Wellnhofer (1975; Figs. 1, 2). Here the quadratojugal process of the jugal was absent. The upper jawline was not ventrally concave, but straight. The dentary was shorter than the rostrum.

Relative to the JME SOS 4785 specimen of clade number 6, CM 11427 had a longer, more robust rostrum and cervical series. The teeth were relatively shorter. The sternal complex was larger and wider.

YPM 1778 was more gracile overall. All three clade members had pedal digits 2–4 aligned distally due to the elongation of digit 4. No pedal phalanges were disc-like. Pedal digit 5 was also relatively longer.

JME-SOS 4009 had a more dorsally placed naris, a more laterally open upper temporal fenestra and a more inclined quadrate along with a broader sternal complex.

Clade number 8 includes five medium-to-large specimens, three of which (TM 6920/21, SMF R 4128, and B St 1929 I 69) were assigned to *R. muensteri* by Wellnhofer (1975). Two others (TM 6922/6923 and GPIH MYE 13) were assigned to *R. gemmingi.* All clade members had a shorter nasal and longer frontal. All reduced the premaxillary teeth. All extended manual 4.1 far beyond the elbow of the folded wing. GPIH MYE 135 and BSPG 1929 I 69 shared a shorter neck and a longer antebrachium, convergent with five other *Rhamphorhynchus* clades. Together with TM 6922/6923, these three also shared a fused scapulocoracoid. BSPG 1929 I 69 was the largest clade number 8 member and the third largest tested specimen in this genus.

Rhamphorhynchus **Manus and Pes Phylogenetic Analysis**

A phylogenetic analysis of the clade *Rhamphorhynchus* restricted to manus and pes traits recovered an identical tree topology—until the three most derived taxa (all from clade number 8) were added. Their pedal proportions were most similar to those of basal *Rhamphorhynchus* specimens (Fig. 3), which attracted clade number 1 taxa to clade number 8. Even so, the variety in pedal morphologies in this clade, and for that matter across the Pterosauria (Peters, 2011), indicates a range of variation that cannot be attributed to ontogeny. In tested *Rhamphorhynchus* taxa, no two pedes were identical. Even in the juvenile/adult pairing of the Vienna specimen with BMNH 37002 the larger of the two had more gracile bones, pedal digit 5 was relatively reduced as if it had stopped growing, and the joints appear to have been more fully ossified, all possible ontogenetic differences.

DISCUSSION

Based on the present phylogenetic analysis of 195 pterosaurs and their 20 outgroup taxa: 1) the genus *Rhamphorhynchus* can be divided into eight distinct clades, but not in order of increasing size; 2) in *Rhamphorhynchus* and other pterosaur clades, phylogenetic miniaturization and rostral shortening preceded phylogenetic size increase with rostral lengthening and other morphological changes that subsequently produced derived clades; 3) *Rhamphorhynchus* was not a sister taxon to *Dorygnathus*, but was derived from *Campylognathoides*; 4) *Rhamphorhynchus* left no descendants and was not a transitional taxon related to pterodactyloids; 5) no matter their ontogenetic age, all tiny Solnhofen pterosaurs, including those nesting at the base of the *Rhamphorhynchus* clade, can be scored as sparrow-to-hummingbird-sized adults; 6) no long-tailed pterosaurs survived into the Cretaceous, so miniaturization and the development of pterodactyloid-grade traits during miniaturization was the key to lineage survival; 7) most tiny *Rhamphorhynchus* specimens were not juveniles, but at least one mid-sized specimen (the Vienna specimen, NHMW 1998z0077/000) was a likely juvenile of the largest known *Rhamphorhynchus* specimen; 8) *Qinglongopterus* and *Bellubrunnus* nest within the genus *Rhamphorhynchus*; 9) the morphological variety within all tested pterosaur genera and the new tree topology indicate that current pterosaur nomenclature and systematics are in need of revision; 10) there is a continuity in the present tree topology that presents no large gaps in the evolutionary record of the Pterosauria; 11) the origin and evolution of pterosaurs from lepidosaurs like *Huehuecuetzpalli*, *Macrocnemus* and members of the Fenestrasauria is likewise continuous and well documented; 12) *Darwinopterus* did not represent a transitional form between long-tailed and short-tailed pterosaurs, but was a terminal taxon (contra Lü, et al., 2010; Unwin, and Lü, 2010); 13) the tree topology of the genus clade *Pteranodon* demonstrates that large specimens with large crests evolved from smaller specimens with smaller crests and that no discernable gender or ontogenic traits can be discerned (contra Bennett, 1991, 1992, 1993, 1994, 2001); 14) several pterosaur juvenile/adult phylogenetic pairings document isometry during ontogeny, not allometry (contra Bennett, 1995, 1996); 15) scapulocoracoid fusion patterns in pterosaurs are phylogenetic, not ontogenic; 16) juvenile pterosaurs are very rare in the Solnhofen limestones, so they must have hatched and developed in areas not conducive to fossilization; 17) there is a lower size limit for fossilized, presumeably volant pterosaurs (approximately 7 cm in standing height), that is half again taller than hypothetical hatchlings of the largest *Rhamphorhynchus* specimens (Fig. 1); 17) based on pelvic opening size and the size relationship of *Pterodaustro* to its embryo (Chiappe, et al., 2004) and hatchlings (Codorniú and Chiappe, 2004), hatchling pterosaurs were one-eighth the size of the adult, so the hatchlings of the smallest adult pterosaurs would have been less than 1 cm tall; and 18) phylogenetic analysis identifies the three currently known embryo pterosaurs as a derived ctenochasmatid (*Pterodaustro*, MHIN-UNSL-GEO-V 246), a basal ornithocheirid (JZMP 03-03-2; Ji, et al., 2004) and a large basal anurognathid (IVPP V 13758; Wang and Zhou, 2004). The latter two genera do not have known adult counterparts, only adult sister taxa.

Confirmed hatchling, juvenile or subadult pterosaurs are known for *Tapejara* (Eck, et al., 2011), *Pterodaustro* (Codorniú, and Chiappe, 2004), *Zhejiangopterus* (Cai, and Wei, 1994, Fig. 4), and now *Rhamphorhynchus* (Fig. 2, 5). For the first time (Fig. 1) a juvenile *Rhamphorhynchus* and an embryo *Pterodaustro* nest with adult taxa in phylogenetic analysis. There is little doubt that the juveniles of the other two would do the same, as they are virtually identical to their much larger adult counterparts. The embryo *Pterodaustro* did not share as many character traits with its adult counterpart as did the juvenile *Rhamphorhynchus*, but then it was an embryo, one-eighth the size of the adult, rather than one-third as tall. These pairings demonstrate isometry during ontogeny, falsifying the present paradigm of allometry during ontogeny (contra Bennett, 1991, 1993, 1995, 1996, 2001, 2006, 2014). These four all represent mid-sized to large pterosaurs with 7+ cm tall hatchlings that likely were volant shortly after hatching (Deeming, and Unwin, 2007; Grellet-Tinner, et al., 2007). Exceptionally tiny hatchlings (less than 1 cm in standing height) of the smallest adult pterosaurs have not been discovered.

Rather than ‘confounding’ phylogenetic analyses (contra Lü et al. 2012), the addition of tiny Solnhofen pterosaurs, along with the addition of more specimens within several genera, illuminated relationships. The complete resolution of the present tree and the morphological similarity of all sister taxa therein provides great confidence that the present tree topology (Fig. 1) more parsimoniously echoes actual evolutionary events and relationships. Now there are four well-documented tiny pterosaur transitions to the pterodactyloid grade and several other examples of tiny pterosaurs at other clade bases. The final extinction of pterosaurs at the end of the Cretaceous might reflect the fact that there were no mid-size, small or tiny pterosaurs to pull them through as they did at the end of the Jurassic. With this in mind, it is surprising that no *Rhamphorhynchus* descendants are known from the Cretaceous. Perhaps all tiny basal species had already become extinct or had evolved to become mid-sized-to-large forms by the Jurassic/Cretaceous boundary.

Despite the fact that *Qinlongopterus* and *Bellubrunnus* nested within the genus *Rhamphorhynchus*, they will not be renamed here, as they appear to be sufficiently distinct from the holotype (BSP Inv. Nr. 1964 XXIV 121) and from each other to merit their current status if workers agree to split up the remainder of the genus *Rhamphorhynchus* generically. If not, these two should be absorbed under the genus *Rhamphorhynchus*. Nomenclature problems with other specimens and other clades are beyond the scope of the present study.

Regarding Wellnhofer (1975)

The present phylogenetic analysis supports the division of *Rhamphorhynchus* into several clades represented by adults in several size classes. That the clades were reordered and modified in the present tree is a product of computational abilities unavailable to Wellnhofer in 1975.

Regarding Bennett (1995)

The present phylogenetic analysis does not support the hypothesis of a single *Rhamphorhynchus* species, of allometry during ontogeny, nor the contention that most specimens represent immature individuals. Late Jurassic weather patterns do not appear to be biased against juvenile individuals. Instead, what we do see in the fossil record is a community of gull- and heron-sized to hummingbird-sized pterosaurs cohabitating in the Solnhofen lagoon area, each to their own niche.

Long Rostrum Tiny Pterosaurs

Prior systematic studies (Kellner, 2003; Unwin, 2003; Andres, 2010; and all works derived from them) did not include tiny Solnhofen pterosaurs in their matrices. This exclusion was based on the untested assumption that tiny pterosaurs represented morphologically distinct juvenile archosaurs with a short rostrum and large orbit. Unfortunately, this assumption ignores the many tiny pterosaurs that had a long rostrum and small orbit. These include SMF a. M. No. 4072, B St 1968 XV 132, B St 1911 I 31, MB. Am 3530.1, TM10341, B St 1936 I 50, and two embryos: the basal ornithocheirid, JZMP-03-03-2, and the *Pterodaustro* embryo, MHIN-UNSL-GEO-V 246. The third embryo, V13758, was originally identified as a short rostrum ornithocheirid, but nests here (Fig. 1) with anurognathids, which all have a very short rostrum as adults. The juvenile *Zhejiangopterus* M 1330 (Fig. 4) also had a very long rostrum and a very tiny orbit.

The Perils of Fly-Sized Hatchling Pterosaurs

Let us consider the ecology of 1 cm tall hatchlings of 7 cm tall adult pterosaurs. Hedges and Thomas (2001) report that the smallest living lepidosaur (*Sphaerodactylus ariasae*, < 2cm snout/vent length) must remain in a damp leaf litter environment or risk death by desiccation if removed. They suggest this is likely due to the high surface area/volume ratio of this tiny gecko. Hatchling tiny pterosaurs would have been at a similar, but multiplied risk with their wing membranes and uropatagia raising their surface area/volume ratio. Though mid-sized-to-large pterosaurs (those with hatchlings standing at least 7cm in height) were apparently able to fly shortly after hatching (Deeming and Unwin, 2007; Grellet-Tinner, et al., 2007), smaller hatchlings were relegated to clambering over and through damp leaf litter until growing to that minimum height. Flapping their wings in dry open air would have been risky at such small sizes. This humid and terrestrial common niche for tiny pterosaurs was likely a major factor in the appearance of convergent pterodactyloid-grade traits.

A pelage would have helped insulate tiny pterosaurs against water loss. Such a dermal covering has been preserved in several exceptionally preserved pterosaur fossils (e.g. *Jeholopterus*–Wang, et al. 2002; *Sordes*–Sharov, 1971). Perhaps the absence of smaller pterosaur hatchlings in the fossil record can be explained both by their exceptionally tiny and fragile bones along with their damp leaf litter niche, an environment not typically conducive to fossil preservation.

Fusion and Bone Texture as Ontogenetic Markers

Tiny pterosaurs are known for their lack of scapulocoracoid fusion and the presence of granular bone texture (Bennett, 1991, 1992, 1993, 1995, 1996, 2001, 2006, 2014), both widely and traditionally considered juvenile traits. If pterosaurs were archosaurs following typical archosaur growth patterns these hypotheses would be valid. Recent studies (Peters, 2000a, b, 2011, unpubl. data) and the present phylogenetic analysis (Fig. 1) demonstrate that pterosaurs evolved from fenstrasaur lepidosaurs, not archosaurs or protorosaurs (= prolacertiformes).

Other lepidosaur traits exhibited by pterosaurs include: (1) extreme eggshell thinness (Deeming and Unwin, 2007; Grellet-Tinner, et al., 2007); (2) absence of deep chevrons; (3) the retention of a large ossified sternum (as part of the sternal complex, Wild, 1993); (4) the quadrant-shaped coracoid of basal pterosaurs, which is straighter in derived taxa, is the result of extreme fenestratration of the anterior coracoid, leaving only the posterior rim ossified; (5) the pteroid and preaxial carpal are homologs of the two centralia found in *Sphenodon*, having migrated to the medial rim of the wrist (Peters, 2001, 2009); (6) the retention of a long and robust fourth metacarpal and digit on the manus; (7) the retention of a large lateral digit on the pes. The antorbital fenestra without a fossa of pterosaurs is a trait shared with lepidosaur fenestrasaurs (Peters, 2000b), convergent with archosauriformes and chroniosuchids.

The present study demonstrates that scapulocoracoid fusion patterns are strongly correlated to phylogeny. Basal pterosaurs and their fenestrasaur ancestors do not fuse the scapula and coracoid. Fusion occurs in basal dimorphodontids, but not in anurognathids. Fusion occurs in *Eudimorphodon* and *Campylognathoides*, but not in basal *Rhamphorhynchus*. Fusion returns in *Rhamphorhynchus* clades number 6 and number 8, which do not include the largest specimens. Only five basal dorygnathids fuse the scapulocoracoid. No protoazhdarchids and azhdarchids fuse the scapula and coracoid with the exception of the largest, most derived tested taxon, *Quetzalcoatlus*. No proto-ctenochasmatids and ctenochasmatids fuse the scapula and coracoid. All wukongopterids fuse these bones. No scaphognathids, including cycnorhamphids and basal ornithocheirids fuse the scapula and coracoid. Most derived ornithocheirids fuse these elements (*Arthurdactylus* and *Istiodactylu*s are exceptions). *Wenupteryx* and *Germanodactylus cristatus* fuse the scapulocoracoid. Most other germanodactylids, pterodactylids and their descendants do not. *Tupuxuara* and *Elanodactylus* are exceptions. *Pteranodon* fuses the scapulocoracoid, but eopteranodontids and all institutionalized specimens of *Nyctosaurus* do not. In sum, scapulocoracoid fusion can only be documented in only one-quarter of all tested taxa. Unfortunately we know of no juveniles or embryos of taxa in which the scapulocoracoid is fused in the adult, so we don't know how early in ontogeny this occurs. The acceptance of non-fusion of the scapulocoracoid in adult pterosaurs greatly reduces the number of recognized juvenile and subadult pterosaurs in the fossil record (contra Bennett, 1995, 1996). This reduced number puts pterosaurs more in accord with other fossil reptiles in which juveniles are also relatively rare. Maisano (2002) observed the retention of unfused bones in large and mature extant squamates. She also observed continued growth in squamates after bone fusion. Reynoso (1998) noted isometry in the ontogeny of the basal lepidosaur, *Huehuecuetzpalli*, a basal taxon in the lineage of pterosaurs. As lepidosaurs, pterosaurs followed these growth patterns.

With regard to the retention of granular bone texture in tiny to mid-size adults, tiny pterosaurs likely matured quickly, within a year, like tiny extant birds and mammals do. Bone histology often reveals annular rings in larger specimens that have a multi-year lifespan, but in smaller, presumably short-lived pterosaurs, this has not been possible to demonstrate (Padian, et al., 2004; Chinsamy, et al. 2008). Short-lived tiny pterosaurs may not have lived long enough, or have grown large enough, to develop cortical bone tissue or annular rings. With such hollow bones, they resorbed any such rings.

Because juvenile and subadult pterosaurs were virtual copies of their adult counterparts and were sexually mature at half their maximum size (Chinsamy, et al., 2008), it is difficult to ascertain the ontogenetic status of a specimen without; 1) the presence of associated eggshell, as in the three known embryos; 2) a physical proximity to larger identical specimens, as in *Zhejiangopterus* (Fig. 4); or 3) a phylogenetic nesting of a small specimen surrounded by larger taxa (Fig. 1), as in the case of the Vienna specimen of *Rhamphorhynchus*.

Rapid Phylogenetic Miniaturization

A biological mechanism for rapid phylogenetic size reduction has been reported. Chinsamy et al. (2008) observed that *Pterodaustro* hatchlings grew rapidly for two years until they reached 53% of their mature body size, whereupon they attained sexual maturity. If half-sized *Pterodaustro* laid half-sized eggs through a half-sized pelvic opening, they likely would have produced half-sized hatchlings. This reduction process could continue over several generations ultimately producing hatchling-sized adults and housefly-sized hatchlings. Reversing this process by postponing egg production could phylogenetically increase the size of the pelvic opening, egg, embryo, and adult over several generations.

Morphological changes require allometry, but with pterosaurs maturing isometrically, most of their allometric changes must have occurred prior to hatching. During a generational size reduction series with ever-smaller eggs that likely hatched sooner, at least in some cases the rostrum would not have had time to lengthen as the orbit remained enlarged, retaining the traits of all early-stage tetrapod embryos. During a generational size enlargement series, the embryo rostrum would have had more time to lengthen prior to hatching. An extreme version of this can be found in the embryo *Pterodaustro*, in which the jaws extend for much of the length of the elongated egg (personal observation).

Gender Differences

Wellnhofer (1975) reported that certain *Rhamphorhynchus muensteri* specimens had a relatively larger skull and longer wing. Wellnhofer's males include YPM 1778, TM 6920/21, and SMF R 4128 from the present taxon list (Figs. 1, 2). His females include CM 11427 and JME-SOS 4009. Wellnhofer's purported gender defining traits are not readily apparent here, but his females are both in clade number 7. His males populate clades number 7 and number 8.

Allometery and Isometry during Ontogeny in the Pterosauria

At present the *Pterodaustro* embryo (MHIN-UNSL-GEO-V 246) and adult (PVL 3860) pairing offers the best current opportunity to recover embryo/adult similarities and differences. At least in this pairing the embryo had a relatively shorter neck than the adult. The deltopectoral crest was wider than deep. The ulna/humerus ratio was shorter. The wing finger was shorter relative to the standing height. Metatarsal 2 was shorter and metatarsal 3 was longer relative to metatarsal 1. Noted differences might be the result of individual variation in a population or a splinter of that population because the two specimens were not found in close association. These embryo/adult differences could also represent a measure of allometry during early ontogeny, as differences between quarter- to half-sized juveniles, as in *Tapejara*, *Zhejiangopterus* and *Rhamphorhynchus*, are less apparent.

CONCLUSIONS

The present phylogenetic analysis of the Pterosauria presents a new tree topology in which pterosaurs were derived from lepidosaur fenestrasaurs and four lineages achieved the pterodactyloid grade. At least eight clades can be identified within the genus *Rhamphorhynchus*. They were derived from *Campylognathoides* and produced no descendants in the Cretaceous. *Qinglongopterus* and *Bellubrunnus* both nest with similar tiny taxa at the base of the *Rhamphorhynchus* clade. The mid-sized Vienna specimen of *Rhamphorhynchus* is a juvenile recovered by a phylogenetic nesting with a virtually identical *Rhamphorhynchus* three times taller. The *Pterodaustro* adult and embryo were similarly nested as sister taxa. Distinct pedal proportions lump and split all but the most derived *Rhamphorhynchus* taxa in a topological tree identical to the more inclusive study. Embryo and juvenile pterosaur specimens can be scored as adults because pterosaurs developed isometrically during ontogeny. There should be no further concerns that juvenile pterosaurs have the potential to confound analyses because this traditional concern has been tested and falsified. Phylogenetic patterns indicate that size reduction in pterosaurs was a survival mechanism enabling tiny lineages to continue evolving while larger pterosaurs became extinct throughout the Mesozoic. Bone fusion in pterosaurs can no longer be considered a valid ontogenetic marker due to the phylogenetic patterns of its appearance. Cortical bone and annular rings do not appear on tiny adults that lived and bred in less than a year. The number of known pterosaur juveniles has been greatly reduced and replaced by an equally large number of tiny to small adults providing new insight into pterosaur evolution, extinction and survival.

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LITERATURE CITED

Andres, B. 2010. A new rhamphorhynchoid pterosaur from the Upper Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs. Journal of Vertebrate Paleontology 30:163–187.

Bennett, S. C. 1991. Morphology of the Late Cretaceous pterosaur *Pteranodon* and systematics of the Pterodactyloidea. [Volumes I & II]. Ph.D. thesis, University of Kansas, Lawrence, Kansas, University Microfilms International/ProQuest.

Bennett, S. C. 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. Journal of Vertebrate Paleontology 12:422–434.

Bennett, S. C. 1993. The ontogeny of *Pteranodon* and other pterosaurs. Paleobiology 19:92–106.

Bennett, S. C. 1994. Taxonomy and systematics of the Late Cretaceous pterosaur *Pteranodon* (Pterosauria, Pterodactyloidea). Occassional Papers of the Natural History Museum University of Kansas 169:1–70.

Bennett, S. C. 1995. A statistical study of *Rhamphorhynchus* from the southern limestone of Germany: year classes of a single large species. Journal of Paleontology 69: 569–580.

Bennett, S. C. 1996. Year-classes of pterosaurs from the Solnhofen limestone of Germany: Taxonomic and systematic implications. Journal of Vertebrate Paleontology 16:432–444.

Bennett, S. C. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description of osteology. Palaeontographica, Abteilung A, 260:1–112. Part II. Functional morphology. Palaeontographica, Abteilung A, 260:113–153:92–106.

Bennett, S. C. 2006. Juvenile specimens of the pterosaur *Germanodactylus cristatus*, with a review of the genus. Journal of Vertebrate Paleontology 26:872–878.

Bennett, S. C. 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, 271:327–348.

Cai, Z., and F. Wei. 1994. On a new pterosaur (*Zhejiangopterus linhaiensis* gen. et sp. nov.) from Upper Cretaceous in Linhai, Zhejiang, China. Vertebrata Palasiatica, 32:181–194.

Chiappe, L. M., L. Codorniú, G. Grellet-Tinner, and D. Rivarola. 2004. Argentinian unhatched pterosaur fossil. Nature, 432:571.

Chinsamy, A., L. Codorniú, and L. Chiappe 2008. Developmental growth patterns of the filter-feeder pterosaur, *Pterodaustro guinazui*. Biology Letters 2008:282–285.

Codorniú, L., and L. M. Chiappe. 2004. Early juvenile pterosaurs (Pterodactyloidea: Pterodaustro guinazui) from the Lower Cretaceous of central Argentina. Canadian Journal of Earth Science 41:9–18.

Deeming, C., and D. M. Unwin. 2007. Eggshell structure and its implications for pterosaur reproductive biology and physiology. Flugsaurier, the Wellnhofer pterosaur meeting, Munich, 12.

Eck, K., Elgin, R. A., and E. Frey. 2011. On the osteology of *Tapejara wellnhoferi* Kellner 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. Swiss Journal of Palaeontology, 130:277–296.

Grellet-Tinner, G., S. Wroe, S. B. Thompson, and Q. Ji. 2007. A note on pterosaur nesting behavior. Historical Biology 19:273–277.

Hedges, S. B., and R. Thomas. 2001. At the lower size limit in amniote vertebrates: a new diminutive lizard from the West Indies. Caribbean Journal of Science 37:168–173.

Hone, D. W. E., H. Tischlinger, E. Frey, M. Röper 2012. A new non-pterodactyloid pterosaur from the Late Jurassic of southern Germany. PLoS ONE 7(7): e39312. doi:10.1371/journal.pone.0039312.

Hone, D. W. E., M. Habib, and M. C. Lamanna. 2013. An annotated and illustrated catalogue of Solnhofen (Upper Jurassic, Germany) pterosaur specimens at Carnegie Museum of Natural History. Annals of Carnegie Museum 82:165–191.

Ji, Q., S.-A. Ji, Y.-N. Cheng, H. L. You, J.-C. Lü, Y.-Q. Liu, and C. X. Yuan 2004. Pterosaur egg with leathery shell. Nature 432:572.

Kellner, A. W. A., and Y. Tomida. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with Comments on the pterosaur fauna from the Santana formation (Aptian–Albian), Northeastern Brazil. National Science Museum, Tokyo, Monographs, 17:1–135.

Kellner, A. W. A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group; pp. 105–137 in E. Buffetaut, and J. M. Mazin (eds.) Evolution and palaeobiology of pterosaurs: Geological Society Special Publication 217.

Koh, T.-P. 1937. Untersuchungen über die Gattung *Rhamphorhynchus*. Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie, Beilage-Band 77:455–506.

Lü, J., D. M. Unwin, X. Jin, Y. Liu, and Q. Ji. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. Proceedings of the Royal Society B, 277(1680):383–389. doi:10.1098/rspb.2009.1603 PMID 19828548

Lü, J., D. M. Unwin, B. Zhao, C. Gao, and C. Shen 2012. A new rhamphorhynchid (Pterosauria: Rhamphorhynchidae) from the Middle/Upper Jurassic of Qinglong, Hebei Province, China. Zootaxa 3158:1–19.

Maddison, D.R., and W. P. Maddison. 2000 MacClade 4: Analysis of phylogeny and character evolution. Sinauer Associates, Inc., Sunderland, Massachusetts.

Maisano, J. A. 2002. Terminal fusions of skeletal elements as indicators of maturity in squamates. Journal of Vertebrate Paleontology 22:268–275.

Padian, K., J. R. Horner, J. R., and A. de Ricqles. 2004. Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. Journal of Vertebrate Paleontology 24(3):555–571.

Peters, D. 2000a. Description and interpretation of interphalangeal lines in tetrapods. Ichnos 7:11–41.

Peters, D. 2000b. A redescription of four prolacertiform genera and implications for pterosaur phylogenesis. Rivista Italiana di Paleontologia e Stratigrafia 106 (3):293–336.

Peters, D. 2001. A new model for the evolution of the pterosaur wing—with a twist. Historical Biology 15:277–301.

Peters, D. 2009. A reinterpretation of pteroid articulation in pterosaurs. Journal of Vertebrate Paleontology 29:1327–1330.

Peters, D. 2011. A catalog of pterosaur pedes for trackmaker identification. Ichnos 18(2):114–141.

Reynoso, V. -H. 1998. *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México. Philosophical Transactions of the Royal Society, London B 353:477–500.

Sharov, A. G. 1971. New flying reptiles from the Mesozoic of Kazakhstan and Kirghizia. Transactions of the Paleontological Institute, Akademia Nauk, USSR, Moscow, 130:104–113 [in Russian].

Swofford, D. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*And Other Methods). Version 4.0b10. Sinauer Associates, Inc., Sunderland, MA.

Unwin, D. M., and J.-C. Lü 2010. *Darwinopterus* and its implications for pterosaur phylogeny. Acta Geoscientica Sinica 31(Supplement 1):68–69.

Unwin, D. M. 2003. On the phylogeny and evolutionary history of pterosaurs; pp. 139–190 in E. Buffetaut, and J. M. Mazin (eds.) Evolution and palaeobiology of pterosaurs: Geological Society Special Publication 217.

von Soemmering, S. T. 1812. Über einen *Ornithocephalus.* —Denkschriften der Akademie der Wissenschaften München, Mathematischen-physikalischen Classe 3:89–158.

von Soemmering S. T. 1817. Über einer *Ornithocephalus brevirostris* der Vorwelt. Denkschriften der Akademie der Wissenschaften München, Mathematischen-physikalischen Classe 6:89–104.

Wang, X.-L., Z. Zhou, F. Zhang, and X. Xu. 2002. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and ‘hairs’ from Inner Mongolia, northeast China. Chinese Science Bulletin 47(3):226–230.

Wang, X.-L., and Z. Zhou. 2004. Palaeontology: pterosaur embryo from the Early Cretaceous. Nature 429:623.

Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. Abhandlungen der Bayerischen Akademie d Wissenschaften, N.F., Munich 141:1–133.

Wellnhofer, P. 1975. Teil I. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. Allgemeine Skelettmorphologie. Paleontographica A 148:1–33. 1975b. Teil II. Systematische Beschreibung. Paleontographica A 148:132–186. 1975c. Teil III. Paläokolgie und Stammesgeschichte. Palaeontographica 149:1–30.

Wild, R. 1993. A juvenile specimen of *Eudimorphodon ranzii* Zambelli (Reptilia, Pterosauria) from the upper Triassic (Norian) of Bergamo. Rivisita Museo Civico di Scienze Naturali “E. Caffi” Bergamo 16:95–120.

FIGURE CAPTIONS

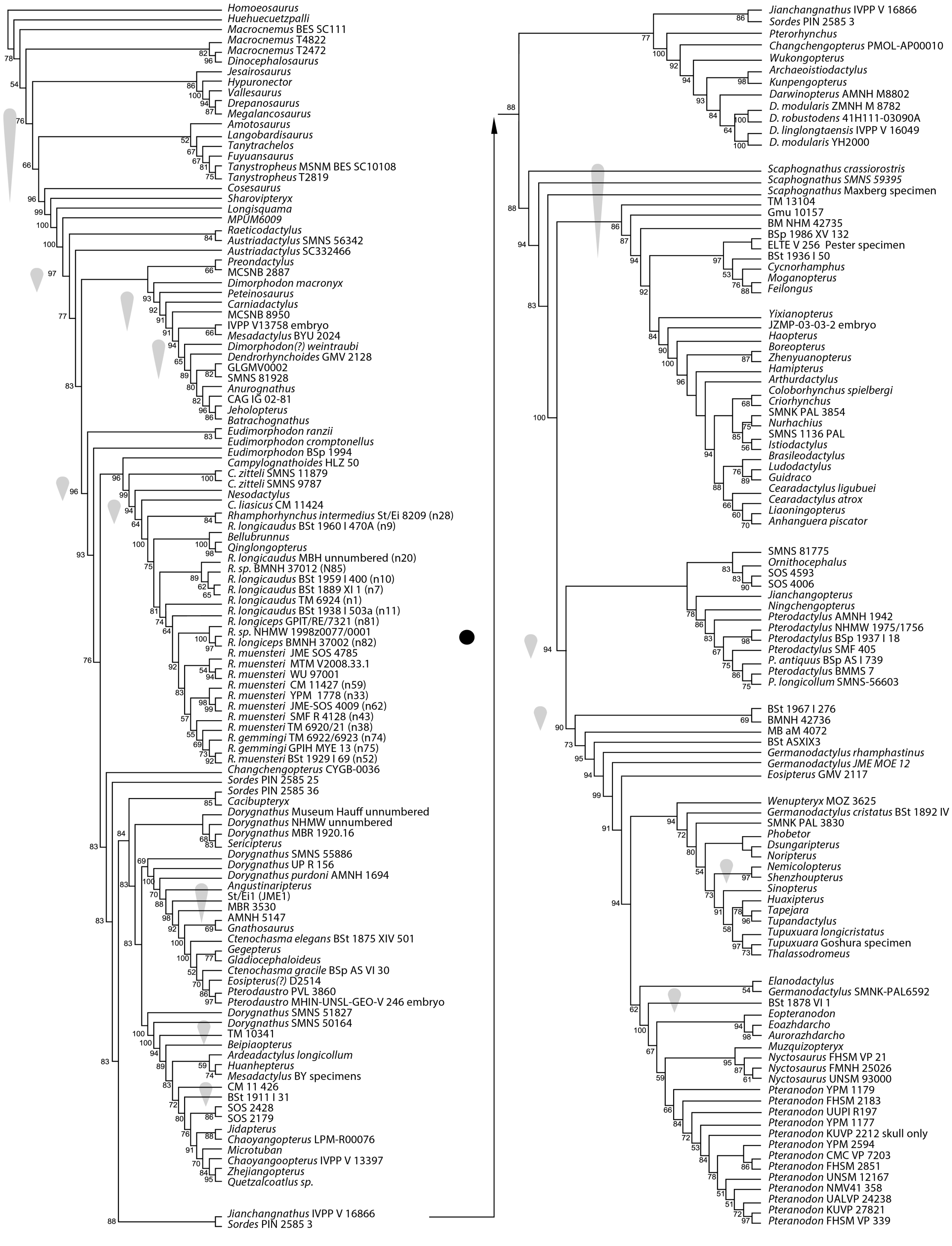

FIGURE 1. Phylogenetic analysis of the Pterosauria. Outgroups were recovered from Peters (2000b) and recent work (unpubl. data). Rather than confounding analyses, the addition of tiny Solnhofen pterosaurs illuminates relationships and increases tree resolution. Here *Rhamphorhynchus* is descended from *Campylognathoides* and leaves no descendants. *Bellubrunnus* and *Qinglongopterus* nest within eight clades of small, mid-sized and large *Rhamphorhynchus*. Tiny pterosaurs nest at the base of most major clades, including the genus clade *Rhamphorhynchus*. Four clades attain the "pterodactyloid" grade by convergence. Wellnhofer (1975) catalog numbers for *Rhamphorhynchus* are in gray. Black dot identifies the juvenile *Rhamphorhynchus*. Inverted teardrop shapes indicate nodes of phylogenetic miniaturization. Bootstrap scores are shown. Scores less than 50 occur when skull only taxa are nested with skull-less taxa. [planned for page width]

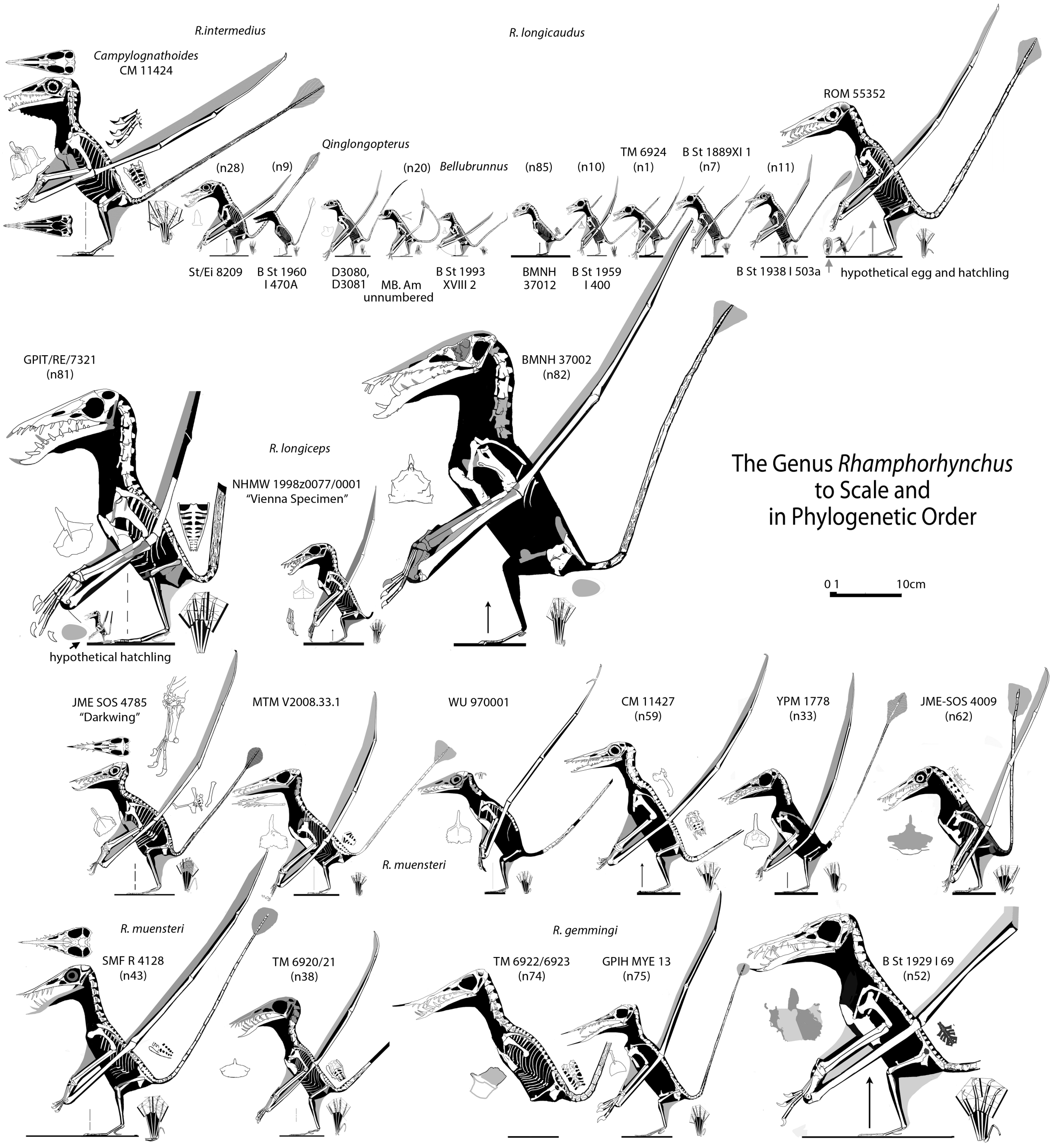

FIGURE 2. *Rhamphorhynchus* reconstructions to scale in phylogenetic order. At the base of the clade, phylogenetic miniaturization followed by an increase in size is readily apparent here. Despite generic similarities, no two specimens are phylogenetically identical, except the juvenile/adult pairing of the Vienna specimen (NHMW

1998z0007/0001) and three times larger BMNH 37002 specimen. Scale bar equals 10 cm.

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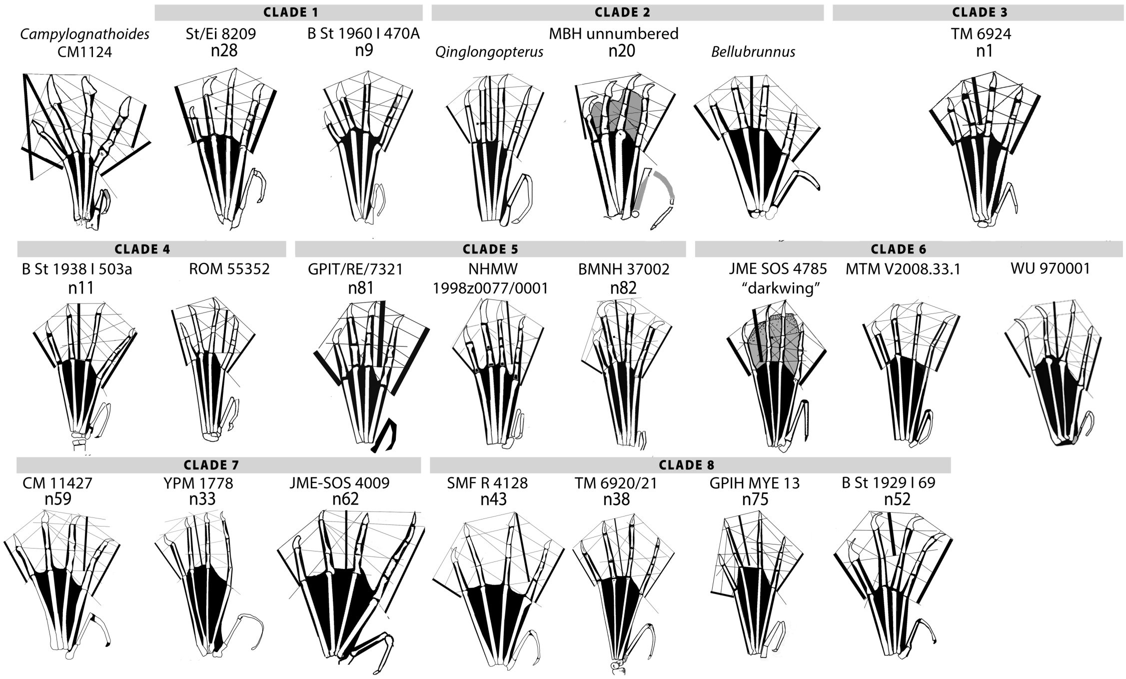

FIGURE 3. A selection of *Rhamphorhynchus* pedes in phylogenetic order, not to scale. *Rhamphorhynchus* pedes demonstrate their variety and evolutionary continuity. Such differences argue against the single species hypothesis of Bennett (1995). [planned for page width]

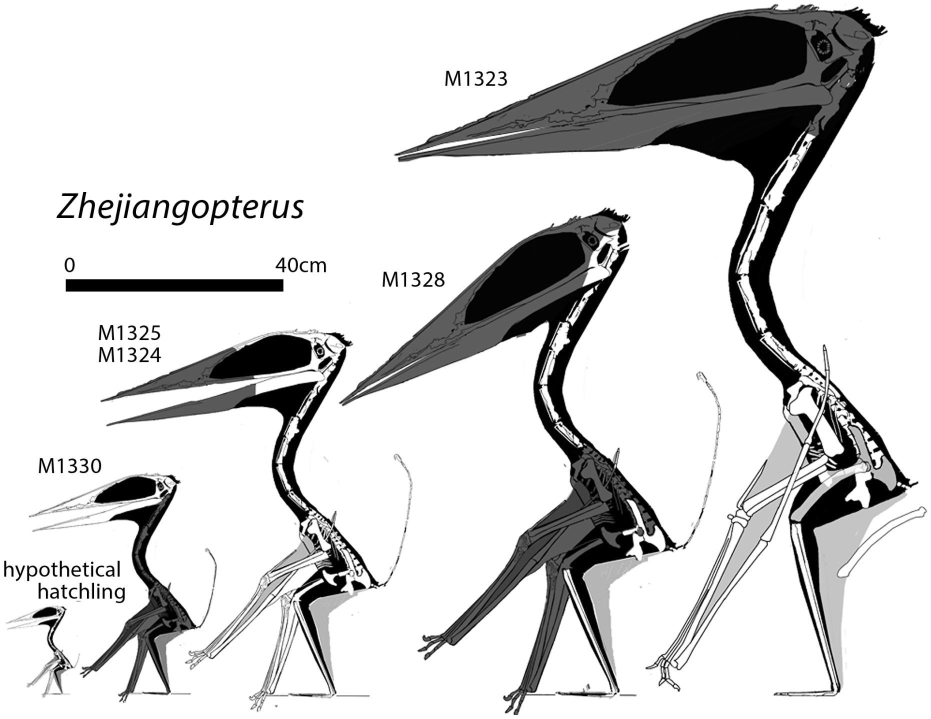

FIGURE 4. Ontogenetic series of the azhdarchid pterosaur, *Zhejiangopterus* to scale. This graphic is based on known specimens (Cai and Wei, 1994) plus a hypothetical hatchling one-eighth the size of the largest specimen, which was presumed to be a full-sized adult. White areas indicate preserved bone. Even the smallest specimen (ZMNH-M1330) has a long rostrum and small orbit, contra the current paradigm supported by Bennett (1995, 1996). This ontogenetic series demonstrates isometry. Scale bar equals 40 cm. [planned for column width]

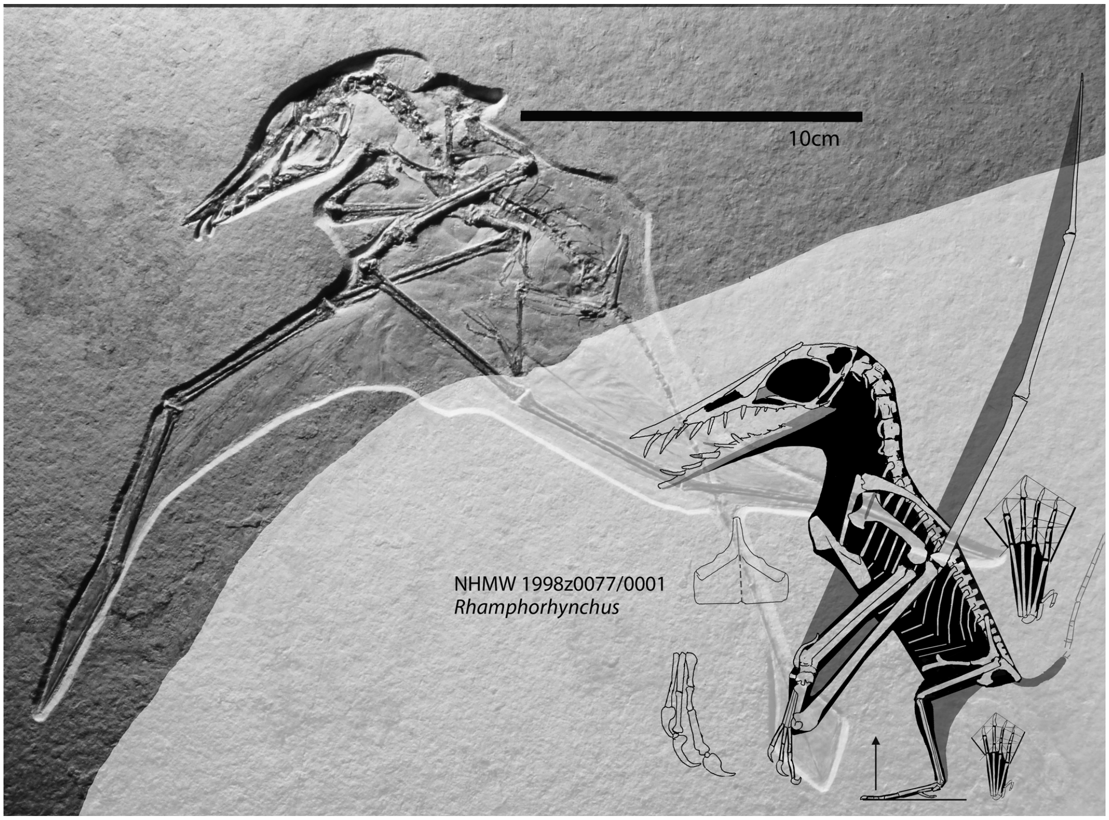

FIGURE 5. The Vienna specimen of *Rhamphorhynchus* (NHMW 1998z0077/0001). The ghosted area indicates the restored portion of the fossil on top of which is a standing reconstruction. This specimen phylogenetically nested with the three times larger BMNH 37002 specimen (Fig. 2). Along with the *Pterodaustro* embryo and adult, these are the first juvenile/adult pterosaur relationships recovered by phylogenetic analysis. Scale bar equals 10 cm. [planned for column width]

Supplementary Data
APPENDIX 1.

Description of characters used in the phylogenetic analysis. All characters are treated as unordered. Ectopalatine = ectopterygoid fused to palatine.

Note: Several "toothless" taxa actually have a single tooth tipping the sharp mandible and premaxilla. In *Scaphognathus* and derived taxa a secondary naris is present, smaller and anterior to the original naris, which can become confluent with the antorbital fenestra. The secondary ascending process of the maxilla extends anterior to the naris. A maxilla wrap is a taller, broader version of this that can contact dorsomedially.

Abbreviations: m4.3 = fourth manual digit, third phalanx; p2.1 = second pedal digit, proximal phalanx. Mc = metacarpal. Mt = metatatarsal.

(1) Skull length to height ratio: less than 4.4 (0); 4.4 to 6.9 (1); 7 or more (2).
(2) Skull vs. occiput-vent length: shorter than occiput-vent (0); not shorter (1).
(3) Rostral profile: straight (0); concave (1); convex (2); squared off (3); posterior convex (4).
(4) Hard rostral crest: absent (0); present (1).
(5) Premaxilla orientation: U- or V-shape (0); reduced to transverse (1); widened to transverse (2);
(6) Premaxilla width: not wider than tall (0); wider than tall (1).
(7) Premaxilla spoonbill: no (0); yes (1).
(8) Ventral premaxilla orientation: straight (0); curved dorsally (1); angled ventrally (2).
(9) Premaxilla ascending process extent: anterior to orbit (0); to anterior orbit (1); to mid or back orbit (2); beyond the orbit (3).
(10) Premaxilla < 20% jaw: no (0); yes (1).
(11) Premaxilla pointed: no (0); yes (1); tooth-tipped (2); square (3).
(12) Premaxilla-maxilla suture: ventral to naris (0); anterior or dorsal to naris (1); posterior to naris (2).
(13) Maxilla wrap: no wrap (0); maxilla contact dorsally (1); anterior maxilla rises but no contact (2).
(14) Secondary ascending process of maxilla: absent (0); present (1).
(15) Maxilla-lacrimal contact: present (0); absent (1).
(16) Maxilla posterior extent ventrally: to orbit (0); to posterior antorbital fenestra (1); to mid antorbital fenestra (2).
(17) Naris from tip: beyond a naris length (0); within a naris length (1).
(18) Naris in rostrum: first quarter (0); second quarter (1); beyond the second quarter (2).
(19) Naris size shape: narrow to oval (0); huge (1); rotated dorsally (2); secondary naris present 3).
(20) Naris dorsal to antorbital fenestra: not dorsal (0); at least one tenth dorsal (1).
(21) Antorbital fenestra vs. naris: no antorbital fenestra (0); not smaller than naris (1); smaller than naris (2); confluent (3).

(22) Antorbital fenestra size: closer to a third of rostrum (0); closer to a half (1); less than a third (2); no antorbital fenestra (3).

(23) Antorbital fenestra length: not twice as long as deep (0); twice as long as deep (1); no antorbital fenestra (2).

(24) Antorbital fenestra majority of rostrum: no (0); yes (1); yes, sans rostral crest (2).

(25) Antorbital fenestra vs orbit: no antorbital fenestra (0); > orbit (1); not > orbit (2).

(26) Orbit size at least two times antorbital fenestra: present (0); absent (1).

(27) Antorbital fenestra higher than orbit: not higher (0); higher (1).

(28) Orbit in anterior half of skull: absent (0); present (1).

(29) Orbit shape/jugal orientation: does not lean posteriorly (0); leans posteriorly (1); four corners (2); keyhole (3).

(30) Orbit depth: < 0.75 skull height (0); 0.75 or more (1).

(31) Orbital invasion: absent (0); from lacrimal (1); from postorbital (2); from vent lacrimal (3); from prefrontal (4).

(32) Nasals contact medially: contact posterior to premaxilla (0); no contact (1); anterior contact (2); [not used] (3); long contact (4).

(33) Nasal median process: absent (0); strut (1); nub (2); keel (3).

(34) Nasal posterior extent: mid orbit (0); anterior orbit (1); anterior to orbit (2); posterior orbit (3).

(35) Antorbital fenestra bridge: gracile (0); robust or deep (1); no antorbital fenestra (2); gracile but crested (3).

(36) Lacrimal fenestra: small or not present (0); large (1).

(37) Postorbital skull length: not > than orbit length (0); > orbit length (1).

(38) Top of postorbital position: not top third of orbit (0); top third of orbit (1).

(39) Upper temporal arch: robust (0); not robust (1).

(40) Jugal anterior extent: suborbital (0); posterior antorbital fenestra or equivalent (1); mid antorbital fenestra (2); anterior antorbital fenestra or equivalent (3); naris (4); beyond primary naris (5).

(41) Jugal lacrimal: long contact (0); lacrimal stem exposed (1); horizontal contact, broad lacrimal (2).

(42) Jugal postorbital process angle: obtuse (0); nearly a right angle (1); right angle to depressed jugal (2); short and strong curve (3).

(43) Jugal quadratojugal process: present (0); not present (1).

(44) Jugal ventral shape: mostly straight (0); ventrally convex (1); concave, then convex (2); depressed posteriorly (3).

(45) Jugal depth below orbit: no deeper than maxilla (0); deeper (1).

(46) Quadratojugal: absent (0); small spur (1); extended up quadrate (2); extended up quadrate, but very short quadrate (3).

(47) Quadrate inclination: not more than 160 degrees (0); more than 160 degrees (1); almost vertical (2).

(48) Vomer ridge/dentary sulcus: absent 0); ridge and sulcus (1); ridge (2).

(49) Lateral process of ectopterygoid/ectopalatine: posterior to vomer process of palatine (0); processes fairly even (1); anterior to vomer process of palatine (2).

(50) Ectopterygoid/ectopalatine anterior extent: posterior half of palate (0); anterior half (1).

(51) Maxilla palatal shelf: absent (0); present as rods (1); present as shelves (2).

(52) Anterior ectopalatine process (anterior palatine) contact with maxillary shelf: ectopterygoid and palatine not fused (0); contact on ectopalatine process (1); to maxilla wall (2); contacts both maxilla and premaxilla (3).
(53) Lateral pterygoid contact with maxilla: no contact (0); contact (1); lateral pterygoid transverse process contacts maxilla (2).
(54) Pterygoid shape: robust sine shape (0); short sine (1); slender stem-block head (2); anterior process reduced (3); lateral process large (4); sine with lateral process (5); short with lateral bud large (6); slender with spear head (7).
(55) Basisphenoids: separate (0); fused broad Y-shape (1); fused narrow (2); appressed medially (3).
(56) Paroccipital process: not prominent (0); laterally expanded (1); ear-like (2).
(57) Cranial crest: absent, soft or small; (0) > orbit (1); rostral and cranial crest (2).
(58) Nasal-frontal crest shape: no nasal-frontal crest (0); not anterior to orbit (1); anterior to orbit (2); premaxilla nasal crest anterior to orbit (3).
(59) Frontal-parietal crest: not present (0); present (1); frontal crest only (2).
(60) Parietal crest cantilever: no crest (0); crest present, no cantilever (1); crest cantilever present (2).
(61) Frontal parietal crest margin: no crest (0); above dorsal margin (1); chiefly below dorsal margin (2); above margin and posterior extent beyond occiput (3).
(62) Crest above orbit: not present (0); < twice orbits height (1); ≥ twice orbit height (2); deep nasals (3).
(63) Maxilla ventral shape: straight (0); convex (1); concave (2); notched (3).
(64) Jaw articulation: dorsal to mandible (0); posterior corner or ledge (1).
(65) Mandible: not gracile or robust (0); gracile (1); robust (2).
(66) Mandible ventral view: Gothic arch (0); Roman arch (1); sharp wedge (2); parallel or pinched rami (3); round tip wedge (4).
(67) Dentary tip: Gothic tip (0); keratin extension (1); doubletooth (2); square (3); singletooth (4); rounded (5).
(68) Dentary length: same as rostrum (0); shorter (1); longer (2).
(69) Dentary spatulate: no (0); yes (1).
(70) Anterior dentary bend: not bent/straight (0); down or down and up (1); only up (2).
(71) Dentary keel or skid: absent (0); present (1); deep symphysis (2).
(72) Dentary symphysis: short (0); longer than a quarter of the mandible (1).
(73) Articular/angular tab: absent (0); present (1).
(74) Posterior mandible: does not rise and deepen (0); rises and deepens (1).
(75) Tooth type: simple stabbers (0); swollen alveoli (1); some multicusped (2); toothless (3); slenderized, needle-like teeth (4); tiny (5).
(76) Tooth pattern: full arcade (0); edentulous (1); anterior toothless (2); posterior toothless (3).
(77) Number of premaxilla teeth: four (0); more than four (1); one (2); three (3); none (4); two (5).
(78) Premaxilla teeth rakelike: not (0); rakelike (1).
(79) Premaxilla dentition size: homodont (0); > maxilla (1); < maxilla (2); three post premaxilla teeth absent (3).
(80) Premaxilla tooth set: unreduced (0); reduced or absent (1); elongated (2).

(81) Medial premaxilla tooth: tiny, not like the others (0); tiny, like the others (1); absent (2); unreduced (3); snout spike (4).
(82) Medial premaxilla tooth inclination: ventral (0); inclined (1); absent (2); emerge anteriorly, curve ventrally (3); nub (4).
(83) Maxilla tooth inclination: vertical (0); anterior (1); posterior (2); absent (3).
(84) Dentary teeth deeper than dentary: absent (0); present (1).
(85) Anterior dentary teeth: larger than the others (0); smaller than the others (1); homodont (2); anterior dentary spike, but otherwise toothless (3).
(86) Dentary tooth-to-tooth contact: some contact (0); no contact (1).
(87) Anterior dentary teeth inclination: vertical (0); anterior (1).
(88) Anterior dentary fangs: no fangs (0); two fangs (1); more than two fangs (2); needle-like teeth (3).
(89) Dentary tooth number: one (0); 5-13 (1); 14-20 (2); 21-30 (3); 31 or more (4); zero (5).
(90) Cervicals one–five shorter than six-eight: absent (0); present (1).
(91) Cervical/torso ratio: half to one (0); about one (1); more than one (2); less than half (3).
(92) Cervicals: not gracile or robust (0); gracile (1); robust (2).
(93) Midcervical neural spines: lower than centrum depth (0); not lower (1).
(94) Cervical rib length: longer than centra (0); subequal to centra (1); tiny (2); absent (3).
(95) Notarium: absent (0); present (1).
(96) Robust ribs (counted from skull): none robust (0); 9 and 10 (1); 9–11 (2); four or more robust ribs attach to sternal complex (3); just #10 (4).
(97) Dorsal vertebral number: 12 to 16 (0); 10 to 11 (1); 9 or fewer (2); 17 or more (3).
(98) Sacral number: two (0); three (1); four (2); five (3); more than five (4).
(99) Sacrum: not co-ossified (0); mostly fused (1).
(100) Caudals: longer than occiput to vent length (0); not longer (1).
(101) Caudals: ≥ torso (0); < torso (1).
(102) Caudal transverse processes: large to the eighth caudal (0); tiny to the third caudal (1); absent (2).
(103) Tail hairs: present (0); absent (1); vane (2); tassel (3).
(104) Mid-caudal centrum length: < twice height (0); two to three times height (1); > thrice height (2).
(105) Mid-caudal hemals: shorter than caudals (0); subequal to caudals (1); no longer than two caudals (2); much longer than two caudals (3); absent (4); deep chevrons (5).
(106) Tail hook: absent (0); present (1).
(107) Humerus vs. sternal complex: humerus longer (0); subequal to sternal complex (1); humerus twice as long (2); no sternum (3); humerus shorter (4).
(108) Sternal complex: absent (0); present (1).
(109) Coracoid shape: disc-like (0); strut ventrally expanded (1); strut not expanded (2).
(110) Scapula shape: short (0); strap-like (1); tall (2); short with constricted middle (3).
(111) Scapula: attached to spine (0); not (1).
(112) Scapula vs. coracoid: scapula longer (0); coracoid longer (1); subequal (2); scapula longer, but coracoid transverse (bottom-decker) (3).

(113) Scapulocoracoid fusion: absent (0); present (1).
(114) Humerus shape: straight (0); concave anteriorly (1); expanded distally (2).
(115) Humerus robust: width: length ratio < 1: 10 (0); not < (1).
(116) Deltopectoral crest size: low (0); large (1).
(117) Deltopectoral crest warp: not warped (0); warped (1).
(118) Deltopectoral crest waisted: absent (0); present (1); present and flat anteriorly (2).
(119) Deltopectoral crest depth: wider than deep (0); not (1).
(120) Scapula: not > half humerus (0); > half humerus (1).
(121) Coracoid length: half or less of humerus (0); > half (1).
(122) Humerus vs. anterior ilium: > two vertebrae distinct in lateral view (0); not > (1).
(123) Humerus vs. femur: humerus longer (0); subequal (1); humerus shorter (2).
(124) Ulna/humerus ratio: < 1.2 (0); 1.2–.29 (1); 1.3–1.49 (2); 1.5–1.75 (3); > 1.75 (4).
(125) Ulna vs. tibia: ulna shorter (0); subequal (1); ulna longer (2).
(126) Forelimb vs. torso ratio: < 3.8 (0); 3.8–6.6 (1); > 6.6 (2).
(127) Radius/ulna diameter ratio: > 0.8 (0); 0.8–0.5 (1); < 0.5 (2).
(128) Pteroid: centralia within carpus (0); short pteroid (1); long pteroid (2); at least half the radius length pteroid (3); pteroid absent, no centrale (4).
(129) Carpals: small elements (0); syncarpals (1); block-like proximally, small distally (2).
(130) Metacarpal 4/ulna ratio: < .33 (0); .33–.60 (1); .61–.90 (2); .91–1.4 (3); > 1.4 (4).
(131) Metacarpal 4 vs. tibia: mc4 < half tibia (0); mc4 < tibia (1); subequal (2); mc4 > tibia (3); mc4 > 2x tibia (4).
(132) Metacarpals 1–3 medial extent: to the carpus (0); not all reach the carpus (1).
(133) Metacarpal lengths: 1<2<3 (0); 1<2=3 (1); all subequal (2); 1>2>3 (3).
(134) Manual digit lengths: 1<2<3<4 (0); 1<2=3<4 (1); 1=2=3<4 (2); 1<2<3=4 (3); 1<2=3=4 (4); 1<2=3=4 (5); 1=2<3<4 (6).
(135) Manual 1.1 vs. m2.1: (0) m1.1 not > 1.7x m2.1; (1); m1.1 > 1.7x m2.1 (2).
(136) Manual 1.1 vs. m2.1 alignment: (0) m1.1 is short; (1) joints align; (2) m1.1 is long; 3) m1.1 and m2.2 align
(137) Manual 2.1: subequal (0); m2.1 < m3.1 (1); m2.1 > m3.1 (2).
(138) Manual 2.2: not > m2.1 (0); > m2.1 (1).
(139) Manual 3.3: not the longest phalanx (0); longer than m3.1 or m3.2 (1).
(140) Manual digit 3 proportions: m3.3 < m3.1 (0); m3.3 ≥ m3.1 (1); m3.3 ≥ m3.1 + m3.2 (2).
(141) Manual 3.2: not a disc (0); disc (1).
(142) Manual digit 3 vs. mc4: > mc4 (0) ; subequal (1); > mc4 (2); > half mc4 (3).
(143) Manual digit 3 vs. pes: manual digit 3 > half of pes (0); half or less (1).
(144) Manual 3.4 (ungual): not > phalanges (0); < 2x deeper (1); not < 2x deeper (2).
(145) Manual digit 4 hyperelongate: no (0); yes (1).
(146) Manual 4.1 vs. ulna: m4.1 does not rotate posteriorly (0); m4.1 extends to distal ulna (1); m4.1 extends to prox ulna (2); halfpoint (3); extends to elbow (4); extends beyond elbow (5).
(147) Manual 4.1 vs. elbow joint: shorter (0) ; not shorter than elbow (1).
(148) Manual 4.1 + m4.2 vs. elbow: shorter (0); longer (1); subequal (2).
(149) Manual 4.2 vs m4.1: < m4.1 (0); not < m4.1 (1).
(150) Manual 4.3 vs m4.2: < m4.2 (0); not < m4.2 (1).

(151) Manual 4.4 vs m4.3: ≥ m4.3 (0); > half m4.3 (1); half or less of m4.3 (2).
(152) Manual 4.4 distal tip when quadrupedal: about as high as skull top (0); lower (1); higher (2).
(153) Anterior ilium extent: not longer than posterior ilium (0); longer (1).
(154) Post ilium ant process: absent (0); present (1).
(155) Ilial process radiation: obtuse (0); nearly right angles (1); virtually no posterior ilium (2).
(156) Pubis orientation: anteroventral (0); ventral; (1).
(157) Pubis depth: not shorter than ischium (0); shorter (1).
(158) Pubis ischium division: open split (0); fused (1); slight split (2).
(159) Posterior ischium process: not high (0); high post process (1).
(160) Ischium shape: broad basin (0); narrow with recess (1); broad with recess (2); broad but smaller than pubis (3).
(161) Prepubis: absent (0); dogleg anterior (1); ventral process longer (2); fan or excavated fan (3); putter shape (4); almost straight (5).
(162) Prepubis depth: no prepubis (0); not deeper than pelvis (1); deeper than pelvis (2).
(163) Prepubis perforation: no prepubis (0); no perforation (1); small perforation (2); ragged anterior (3); fused medially (4); perforation breaks anterior margin (5).
(164) Femoral head: not developed (0); inturned but no neck present (1); neck present (2).
(165) Tibia vs. ilium length: tibia ≥ twice ilium (0); tibia < twice ilium (1).
(166) Glenoid to acetabulum distance vs. tibia length: > tibia (0); not > tibia (1).
(167) Tibia vs. pes ratio: < 1.1 (0); 1.1–1.5 (1); 1.51–2.0 (2); 2.01–2.6 (3); > 2.61 (4).
(168) Fibula: narrow splintlike with distal trochlea (0); > half fused; (2) not narrow (1).
(169) Astragalus and calcaneum: fused (0); not fused (1).
(170) Metatarsal radiation: appressed and laterally increasing (0); parallel, not laterally increasing (1); spreading (2).
(171) Longest metatarsal(s): four (0); two and three (1); one and two (2); one (3); one–three (4); two (5); three (6); three and four (7); one–four 8).
(172) Metatarsal three vs. mt1: mt3 > (0); mt3 not > (1).
(173) Longest digit from heel: four (0); one (1); two (2); two and three (3); three (3); three and four (4); one or two thru four (5).
(174) Pedal phalangeal patterns: no phalanges reduced (0); p3.2, p4.2, p4.3 reduced (1); p4.3 disc-like (2); p4.2 and p4.3 disc-like (3); only p3.2 reduced (4); only p4.3 reduced (5); p4.2 and p4.3; (6) reduced.
(175) Pedal 1.1: not longer than p2.1 (0); > p2.1 (1).
(176) Pedal 2.2 vs. p2.1: p2.2 not > (0); p2.2 > (1).
(177) Pedal 2.1 vs. p3.1: < p3.1 (0); not < p3.1 (1).
(178) Pedal 3.2 vs. p3.3: p3.2 not < (0); p3.2 < (1).
(179) Pedal digit 4 vs. mt4: > mt4 (0); not > (1).
(180) Pedal 4.4 vs p4.1: < p4.1 (0); not < (1).
(181) Penultimate pedal phalanx: not the longest in series (0); p3.3 and p4.4 longest (1); p3.3 is the longest, p4.4 is not (2); p4.4 is the longest, p3.3 is not (3).
(182) Number of pedal digit 5 phallanges, sans ungual: three (0); two (1); one (2).
(183) Pedal 5.1 extent vs. mt4: not > mt4 (0); > mt4 (1).
(184) Pedal ungual depth: not > (0); > 0.3 deeper than penultimate phalanx (1).

(185) Pedal unguals 2–4 aligned at base; no (0); yes, digit 4 is the longest from the heel (1); yes, but digit 4 not the longest from the heel (2).

APPENDIX 2.

Character-taxon matrix used for phylogenetic analysis.

```
Homoeosaurus
00001100010000001000032000010104?1200000200?012????????000?0
0000010000000000?00?1000?0?0?0300000300000100010000202100000
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00001
Huehuecuetzpalli
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00001
Macrocnemus BES SC111
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