The taxonomy and phylogeny of *Diopecephalus kochi* (Wagner, 1837) and "*Germanodactylus rhamphastinus*" (Wagner, 1851)

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Taxonomy of *Diopecephalus* and *Germanodactylus*

Abstract: The Solnhofen pterosaurs *Pterodactylus antiquus*, *Aerodactylus scolopaciceps*, *Diopecephalus kochi*, *Germanodactylus cristatus* and *Germanodactylus rhamphastinus* all have complicated taxonomic histories. Species originally placed in the genus *Pterodactylus*, such as *Aerodactylus scolopaciceps*, *Ardeadactylus longicollum*, *Cycnorhamphus suevicus* and *Germanodactylus cristatus* possess apomorphies not observed in the type species of *Pterodactylus*, and consequently have been placed in new genera. The affinities of another Solnhofen pterosaur previously placed in *Pterodactylus*, *Diopecephalus kochi*, are less clear. It has been proposed that *D. kochi* is a juvenile specimen of *Pterodactylus antiquus*, or perhaps "*Germanodactylus rhamphastinus*" specimens are mature examples of *D. kochi*. Furthermore, studies have suggested that "*Germanodactylus rhamphastinus*" is not congeneric with the type species of *Germanodactylus.* Geometric morphometric analysis of prepubes and a cladistic analysis of the Pterosauria elucidate plesiomorphic and apomorphic conditions for basal Jurassic pterodactyloids. *Germanodactylus* is found to be a monotypic genus and *Pterodactylus*, *Diopecephalus*, and *"G. rhamphastinus*" are found as distinct taxa belonging in individual genera, diagnosable using a combination of characters. Thus, *Diopecephalus kochi* is not demonstrated to be congeneric with *Germanodactylus* or *Pterodactylus* and is maintained as a valid taxon. "*G. rhamphastinus*" is readily distinguishable from other Solnhofen pterosaur taxa, and a new genus is erected for its reception.

Keywords: Solnhofen, *Pterodactylus*, *Germanodactylus*, Phylogeny, Taxonomy, Cladistic analysis, Geometric morphometrics

The Late Jurassic Franconia laminated limestone lagerstätten, typified by the Solnhofen Limestone, Bavaria yield exceptionally well preserved vertebrate fossils, including pterosaurs. The pterosaurs found in these laminated limestones are often fully articulated, with three-dimensional bones on two-dimensional slabs, and sometimes preserve soft-tissues (e.g. Frey and Martill 2003). Presently, there are eleven valid pterosaur genera, representing both monofenestratans and non-monofenestratans. However, the biodiversity of the Late Jurassic Franconia laminated limestones may be higher than previously thought, should those genera prove to be paraphyletic.

Until relatively recently, the genus *Pterodactylus* Cuvier, 1809 had been a wastebasket taxon that has included many diverse pterosaurs, including some that are now recognized as basal non-pterodactyloids. Throughout the 19th, 20th and 21st centuries, specimens were split from the type species *Pterodactylus antiquus* (Sömmerring 1812) (BSP AS I 739) and placed in different genera and families. Most recently, the wastebasket species *Pterodactylus kochi* (Wagner 1837) (BSP AS XIX 3 and SMF R 404) (Fig. 1) was reviewed and the majority of specimens assigned to the taxon were reallocated to the species "*Pterodactylus scolopaciceps*" Meyer, 1860, for which the replacement genus name *Aerodactylus* was erected (see Vidovic and Martill 2014). The remaining three specimens under the name *Pterodactylus kochi* require a review, to establish if they comprise a unique species in the genus, or if they are juveniles of *Pterodactylus antiquus*, or indeed, a juvenile of any other Tithonian pterosaur. Vidovic and Martill (2014) hypothesised that "*P. kochi*" was a juvenile of "*Germanodactylus rhamphastinus*" (Wagner 1851) (BSP AS I 745 a and b) (Fig. 2) and that both might belong to the genus *Diopecephalus* Seeley, 1871, for which *Diopecephalus kochi* is the type species. Indeed, the placement of "*G. rhamphastinus*" in the genus *Germanodactylus* Young, 1964 has been called into question in the past (Maisch et al. 2004; Wang et al. 2008), but no appropriate taxonomic action was taken. Here, a taxonomic review of "*Pterodactylus kochi*" and "*Germanodactylus rhamphastinus*" is presented. The specimens are placed in geological context, compared anatomically, a geometric morphometric analysis is used to test the validity of morphological observations, and a cladistic analysis is performed to test the monophyly of the genera *Pterodactylus* and *Germanodactylus*.

Institutional abbreviations

BMMS, Museum Solnhofen (formerly: Bürgermeister Müller Museum, Solnhofen); BSP, Bayerische Staatssamlung für Paläontologie Munich; JME, Jura Museum, Eichstätt; NHMUK, Natural History Museum, London; NMING, National Museum of Ireland, Dublin; OUMNH, Oxford University Museum of Natural History; PTH, Philosophisch-Theologische Hochschule, Eichstätt (Jura Museum); SMF,

Senckenberg Museum, Frankfurt; SMNK, Staatliches Museum für Naturkunde Karlsruhe; SMNS, Staatliches Museum für Naturkunde Stuttgart.

Taxonomic review

On "P. kochi": Diopecephalus *and* Aerodactylus

Using multiple lines of evidence, Vidovic and Martill (2014) demonstrated that "*P. kochi*" (*sensu* Wellnhofer 1968, 1970; Jouve 2004; Bennett 2013*a*) was a wastebasket taxon. Historically, sub-adult specimens were included in the taxon due to size criteria and convergent morphology in early ontogeny (Vidovic and Martill 2014). A subset of specimens referred to "*P. kochi*" shared common cranial, vertebral and pteroid characters that were distinct from the holotype of the species. The specimens belonging to this distinct morphotype consistently plot separately from specimens more similar to the holotype of "*P. kochi*" in morphometric bivariate plots (Vidovic and Martill 2014: Supporting Information S2.1). One specimen (BSP AS V 29 a/b) plotting as the distinct morphotype is a species name bearer with date priority, a new genus was erected for its reception (Vidovic and Martill 2014), producing the new combination *Aerodactylus scolopaciceps* (Meyer 1860). The detection of *Aerodactylus* specimens referred to "*P. kochi*" does not mean that the latter taxon is not a junior subjective synonym of *P. antiquus* (*sensu* Jouve 2004; Bennett 2013*a*). However, the two *Pterodactylus* species were demonstrated to be morphometrically distinct (Vidovic and Martill 2014: Supporting Information S2.1) and were found to be paraphyletic in cladistic analyses of the Pterodactyloidea (Howse 1986; Lü and Ji 2006; Lü et al. 2006; Lü 2009; Vidovic and Martill 2014). From this point forward, for clarity and to promote taxonomic stability, the full binomial *Diopecephalus kochi* is used rather than "*Pterodactylus kochi*", except in historical context.

Diopecephalus: *type species*

The holotype of "*Pterodactylus kochi*" was considered to belong to a distinct genus by Seeley (1871), which he unambiguously named *Diopecephalus* Seeley, 1871. Seeley (1871) also included "*Pterodactylus longicollum*" Meyer, 1854 and "*Pterodactylus rhamphastinus*" (Wagner, 1851) in the genus *Diopecephalus*. Bennett (2006, 2013*a*) discussed this at length, but perhaps due to a small grammatical error on Seeley's part, argued that Seeley did not designate a type species for *Diopecephalus* until 20 years later (Seeley 1901). However, Seeley (1871) did put the other two "*Pterodactylus* spp." 'under the name *P. kochi*' in the genus *Diopecephalus*, thus erecting a polytypic *Diopecephalus*:

'Another unnamed generic type is typified by *Pterodactylus longicollum*, *P. rhamphastinus*, and the two species' … are… 'included under the name *P. kochi*. In this genus the middle hole of the skull is entirely wanting. For it I suggest the name *Diopecephalus*.' Seeley 1871: p.35

On “P. longicollum”

It is noteworthy that Seeley (1871, 1901) was referring to the holotype of “*P. longicollum*”, which he would have seen a cast of in the Natural History Museum, London (NHMUK R 37990), not the original material that was later destroyed during WWII. Wellnhofer (1970) elected a neotype (SMNS 56603) for “*P. longicollum*” using a specimen originally described by Plieninger (1907) from a slightly older formation and different locality compared to the original. Finding SMNS 56603 to be distinct from *Pterodactylus*, Bennett (2013*a*) erected the new genus *Ardeadactylus* for its reception, an action with which we are in full agreement. Although we do not necessarily agree that SMNS 56603 is conspecific with Meyer's (1854) “*Pterodactylus longicollum*”. The ulnae and radii were not preserved in the holotype, thus it is impossible to interpret wing proportions and it may represent any aurorazhdarchian with the exception of *Cycnorhamphus* Seeley, 1870 which has unambiguous cranial autapomorphies.

On “G. rhamphastinus”

The remaining taxon within Seeley’s (1871) *Diopecephalus* hypodigm is “*Germanodactylus rhamphastinus*” (Fig. 2). There are currently three specimens identified as “*G. rhamphastinus*” (Wellnhofer 1968; Bennett 2002; Rodrigues et al. 2010). Each specimen possesses a straight rostrum terminating in a point. The skull is relatively deep when compared to other Jurassic pterodactyloids and the cervical vertebrae are shorter. “*Germanodactylus rhamphastinus*” has a complex taxonomic history which has been examined on several occasions recently (Bennett 1996, 2002, 2006; Maisch et al. 2004; Wang et al. 2008; Rodrigues et al. 2010; Vidovic and Martill 2014).

Many phylogenetic studies demonstrate that the two species of *Germanodactylus* nest together (Kellner 2003; Unwin 2003; Andres and Ji 2008; Lü et al. 2009; Wang et al. 2009; Andres et al. 2014) in a monophyletic clade, but a more focussed analysis by Maisch et al. (2004) demonstrates the genus to be paraphyletic. Maisch et al. (2004) created the *nomen nudum Daitingopterus,* intended for the reception of “*G. rhamphastinus*” by placing the name in a table with no specific reference to a specimen. Subsequently, Wang et al. (2008) noted that the tooth morphology of “*G. rhamphastinus*” (Fig. 2) differs from that of *Germanodactylus cristatus* (Wiman 1925) (BSP 1892 IV 1 and NMING F15005) (Fig. 3) and suggested that the former may be placed in a new genus, but still closely related to *Germanodactylus*. Rodrigues et al. (2010) reiterated that “*G. rhamphastinus*” might be generically distinct from *G. cristatus*. In a more comprehensive cladistic analysis of pterodactyloids Vidovic and Martill (2014) found Archaeopterodactyloidea of Kellner (2003) and Dsungaripteroidea of Unwin (2003) to be polyphyletic. Vidovic and Martill (2014) recovered *Germanodactylus cristatus* as a basal tapejaroid, while “*G*. *rhamphastinus*” was recovered as a basal

"transitional" taxon close to Aurorazhdarchidae. Furthermore, when the data of the Lü et al. (2009) analysis is re-run using TNT with *Noripterus* Young, 1973 included (as it was in the published matrix), a significantly shorter tree than the published tree (lacking *Noripterus*) also finds *Germanodactylus* to be paraphyletic.

The taxonomy of *Germanodactylus* and its present constituent species has most recently been reviewed in detail by Bennett (2006). The type specimen, *G. cristatus* (BSP 1892 IV 1) was originally described by Plieninger (1901) and identified as an example of "*P. kochi*". But Wiman (1925) considered BSP 1892 IV 1 distinct from "*P. kochi*" on account of its edentulous jaw tips and prominent sagittal crest, thus he named it *Pterodactylus cristatus* Wiman, 1925 (Fig. 3). Young (1964) considered BSP 1892 IV 1 to be generically distinct from *Pterodactylus* and erected the genus *Germanodactylus*, making the combination "*G. kochi*" (Wagner 1837). As Bennett (2006) noted, Young (1964) seemed unaware that this specimen had been renamed "*P. cristatus*" by Wiman (1925). Wellnhofer (1968), aware of Wiman's work, corrected Young's *lapsus*, creating the binomial *Germanodactylus cristatus* (Wiman 1925). Later, Bennett (2006) referred two specimens that had previously been referred to "*P. kochi*" (JME SoS 4593) and "*Pterodactylus micronyx*" Meyer, 1856 (JME SoS 4006) to *Germanodactylus cristatus*, considering them to represent juveniles of that taxon. In addition to these referrals, Bennett (2006) emended the diagnosis of *Germanodactylus* to accommodate perceived ontogenetic changes and maintained "*G. rhamphastinus*" within the genus contrary to Maisch et al. (2004).

Bennett's (2006) revised diagnosis of *Germanodactylus* lacks autapomorphies and distinguishes *Germanodactylus* from other pterosaurs by a combination of characters which are also possessed by more basal and derived taxa. However, *Germanodactylus cristatus* (Fig. 3), the type species of *Germanodactylus*, possesses autapomorphies not found in "*G. rhamphastinus*" (Fig. 2) such as edentulous jaw tips. Thus, *Germanodactylus* is rendered a metataxon. Here, "metataxon" is not used in the strict phylogenetic sense (Archibald 1994) because its use is not in reference to a cladogram, but because the taxon diagnosis cannot provide positive evidence of monophyly or paraphyly. Consequently, here the diagnosis of *Germanodactylus* is emended, and "*G. rhamphastinus*" is excluded from the genus.

Such an action, however, requires a reappraisal of the relationships of "*G. rhamphastinus*". It is difficult to distinguish "*G. rhamphastinus*" (Fig. 2) from the holotype of *Diopecephalus kochi* (Fig. 1) other than by using size related criteria. While it is difficult to distinguish sub-mature specimens from mature specimens, the only cladistic analyses known to include the holotype of *Diopecephalus kochi* (Howse 1986; Vidovic and Martill 2014) (i.e. not *Aerodactylus* specimens) find *Pterodactylus*

spp. (including *D. kochi*) and *Germanodactylus* spp. paraphyletic. Here, a rigorous and comprehensive cladistic analysis tests the relationship between "*G. rhamphastinus*", *D. kochi*, *P. antiquus* and *G. cristatus.* Appropriate taxonomic action is taken as a consequence of the outcome of the analysis.

Stratigraphic review

The traditional subdivisions of the Franconia laminated limestones represent short periods of geological time (<4 mya total duration: Late Kimmeridgian–Early Tithonian). Monofenestratan pterosaurs are known from Malm Zeta 1–3 (Kimmeridgian–Tithonian) (Table 1.) from quarries near Nusplingen, Solnhofen, Eichstätt, Schernfeld, Mörnsheim, Daiting, Schamhaupten, Painten, Kelheim and Zandt in southern Germany. With the exception of *Pterodactylus* and possibly *Cycnorhamphus* and *Ardeadactylus,* the vast majority of pterosaurs are restricted to single sub-divisions of the Franconia laminated limestones, even when they are represented by many specimens.

Specimens of *Pterodactylus antiquus* are known from the Lower Tithonian, Malm Zeta 2 and 3 (Bennett, 2013a). The taxon may also be present in the earliest Tithonian (Malm Zeta 1) cropping out at Zandt, Germany (SMF R 4072). *Diopecephalus kochi* and "*G. rhamphastinus*" are known only from Malm Zeta 3, Lower Tithonian of Kelheim and Daiting respectively according to Wellnhofer (1970). Exposures at Daiting are in the Moernsheimensis Horizon and Subzone of the Hybonotum Zone, making it the youngest pterosaur-bearing strata in the Franconia limestones (Schweigert 2007). Kelheim is reportedly in the Rueppelliansus Subzone of the Hybonotum Zone (Schweigert 2007), making it equivalent to Malm Zeta 2. The *Diopecephalus* locality is ~1 km North of Kelheim (Wellnhofer 1970), close to Painten (~6 km) which is Malm Zeta 1. Therefore, the age of *Diopecephalus* according to Wellnhofer (1970) (Malm Zeta 3) is in some doubt. Although the "Papiershiefer" has been considered contemporary with Mörnsheim Limestone (Meyer 1977), crushed *Gravesia gigas* (*riedlingensis* subzone) ammonites were misidentified as *G. gravesiana* resulting in a younger date being determined (Schweigert 2007). *Germanodactylus cristatus* is known from two juvenile and two mature specimens, of which the holotype (BSP 1892 IV 1 and NMING F15005) is from Eichstätt, Malm Zeta 2, Lower Tithonian.

The Painten pro-pterodactyloid (Tischlinger and Frey 2013) is from the Upper Kimmeridgian. The specimen seemingly represents a late surviving transitional morphology between wukongopterids and pterodactyloids. *Cycnorhamphus suevicus* (Quenstedt 1855) ranges from the Upper Kimmeridgian to Lower Tithonian. A specimen referred to *Cycnorhamphus,* the now lost "*Pterodactylus eurychirus*" Wagner, 1858 (Wellnhofer 1970) from Malm Zeta 2 is undiagnostic and

while it could represent *Cycnorhamphus* in Eichstätt, it could also represent an example of *Ardeadactylus* or *Aurorazhdarcho*. However, *Cycnorhamphus* is known from the Lower Tithonian of South-East France (Fabre 1976). The neotype of *Ardeadactylus longicollum* (Wellnhofer 1970) is from Malm Zeta 1, Upper Kimmeridgian. The lost holotype is from the Lower Tithonian, Malm Zeta 2, but as noted above it may not be conspecific with the neotype. Wellnhofer (1970) also referred other lost specimens to this species, but they also lack diagnostic features. Notably, a specimen referred to *Ardeadactylus*, "*Pterodactylus vulturinus*" Wagner, 1858 (Wellnhofer 1970) is an undiagnostic isolated wing-metacarpal from Malm Zeta 3.

Gnathosaurus subulatus Meyer, 1834 and its sister taxon *Ctenochasma elegans* (Wagner 1861*a*) are only known from Malm Zeta 2, Lower Tithonian. *Aurorazhdarcho micronyx* (Meyer 1856) is known from juvenile specimens and an adult missing its skull (Frey et al. 2011) which are all from Malm Zeta 2. *Aerodactylus scolopaciceps* (Meyer 1860) is also known only from Malm Zeta 2 of Solnhofen and Eichstätt, where the species is represented mostly by juvenile specimens. Additionally, a large wing of an adult *Aerodactylus* with ~2.5 meter wingspan (figured by Wellnhofer 1970: Exemplar Nr 78) (PTH 1963. 1 a) was found in Schernfeld, near Eichstätt (Malm Zeta 2).

Stratigraphy of putative Diopecephalus kochi *specimens*

A specimen referred to "*Pterodactylus kochi*" in the Oxford University Museum of Natural History (OUMNH JZ 1609) and its counterpart in the Natural History Museum, London (NHM) (NHM UK PV R 3949) are labeled as coming from Solnhofen, Kimmeridgian. However, it is likely that precise locality information was lost before the specimens were purchased for the museums (see supplementary material S.3.1.1.).

Another specimen referred to "*Pterodactylus kochi*" (Wellnhofer, 1970: Exemplar Nr. 12) (SMF R 4072) by von Huene (1951) is noted to be from Zandt, Germany. This locality is lesser known for its pterosaurs and is east of Kelheim and Painten, close to the Czech Republic. Stratigraphically, the Zandt lagerstätte is from the lower Hybonotum Zone, contemporaneous with the youngest lithographic limestone cropping out at Painten (Malm Zeta 1: earliest Tithonian) (Schweigert 2007). The specimen's juvenile state makes it difficult to refer it to any one of the Jurassic German pterosaurs that have a dentition extending from the jaw tips to a point under the nasoantorbital fenestra (Vidovic and Martill 2014, fig. 3). However, what is visible of the prepubis is elongate and narrow compared to *Diopecephalus* and "*G. rhamphastinus*". Additionally, the pedal and manual unguals of this specimen are more robust than those of *Diopecephalus kochi* and "*Germanodactylus rhamphastinus*", but similar to those of *Pterodactylus*.

Finally, An undescribed, privately owned specimen from Painten (Malm Zeta 1, Upper Kimmeridgian–Lower Tithonian) on display in the Museum Solnhofen is identified as "*Pterodactylus* c.f. *kochi*" (Arratia et al. 2015: p.468). The morphology of this specimen most closely matches *Diopecephalus kochi* and we agree with this assignation.

Materials and methods

Cladistic analysis and appraisal

A cladistic analysis of the Pterosauria, including all the taxa discussed here was performed. The analysis included 104 operational taxonomic units (OTUs) comprising 99 pterosaurs and 5 archosauriforms as an outgroup. The taxa were coded for 320 characters, of which 44 have continuous states and 276 have discrete states. Many of the characters are similar to those previously published, but 249 of the characters in this analysis were developed independent of the literature for an as of yet unpublished "distinct" analysis devised to test cladistic methods and clade recovery in the Pterosauria. The additional 71 characters were taken or modified from the literature. Great care was taken to avoid compound characters (Brazeau 2011) or combining multiple states into one. Martill et al. (2016) have demonstrated the benefits of this practice.

The analysis was performed in TNT using a "new technology search" (NT) (Goloboff et al. 2008*a*) and a "traditional search" was run, swapping from the saved NT trees, to find the maximum number of most parsimonious trees (MPTs). In the Vidovic and Martill (2014) analysis, four of the continuous characters required rescaling with the equation $i = \tan^{-1}a/b$, where i is the index number analysed and a/b is the quotient value of the elements being studied. Mongiardino Koch et al. (2015) subsequently suggested logarithmically transforming the quotient values for continuous states, to avoid the problems of researchers deciding to use either "top heavy" or "bottom heave" dividend/divisor relationships. However, both of these methods produce a continuum of weighted states that are an exponential function of the morphometric data. In this analysis, the characters were simply transformed using "top heavy" quotients. Where converse data was present in a character's coding, the equation was inverted to make it "top heavy" and made negative to differentiate it from those states that were not the product of an inverted equation. To ensure that the continuum of data was evenly spaced according to the morphological variation, the negative numbers had 1 added to them and positive numbers had 1 subtracted. A normalization equation was then used to transform negative numbers into positive numbers and place the data range between 0 and 3. Performing this data transformation rather than the trigonometric one (Vidovic and Martill 2014), or the logarithmic one (Mongiardino Koch et al. 2015), results in a continuum of

weighted states that are a direct function of the morphometric data, while resolving the problem of converse data and researcher decision. A manuscript detailing the advantages of this method of continuous data transformation over the previous one used by these authors (Vidovic and Martill 2014) is in preparation. Three (3.000) was chosen as the number of continuous states, rather than 1.000, as in Andres et al. (2014) and Vidovic and Martill (2014) or 2.000 as employed by (Pereyra and Mound 2009). The reason for choosing 3.000 states for continuous characters is that during trial and error experiments it produces a similar distribution of character reversals (plotted in a frequency histogram) compared to the discrete state characters, showing that the analysis was not biased towards any one type of character.

Implied weights were used during the analysis to weight against homoplasy (Goloboff et al. 2008*b*; Goloboff 2014). Using implied weighting means the researcher makes the least assumptions out of any weighting method – even using equal weights assumes that all characters are equally informative. However, the implied weighting method requires a concavity constant (K) and no consensus for which number should be used has been reached in the literature. It is possible to reverse the equation (W=[[-K]+[K+es]]/[K+es], where W is the weight and es is the extra steps) in order to calculate the K value required to transform a character with a designated fit into a predetermined weight. However, this method requires a researcher to decide *a priori* what character fit is excessively homoplastic and the weight this homoplastic character should receive. Experimentation with different K values, plotting fit against the implied weight demonstrates that the higher the number, the more linear the relationship becomes, whereas lower K values produce exponential curves. The TNT default K value of 3 approximates a logarithmic curve, meaning that poorer fitting characters are increasingly weighted against. Because of this “smooth” curvilinear relationship between fit and weight, 3 is selected as the optimal K value for this analysis.

The outgroup (*Erythrosuchus, Euparkeria, Scleromochlus, Lagerpeton, and Marasuchus*) is distinct among pterosaur analyses, but similar to the outgroups of some dinosaur analyses (Nesbitt et al. 2009). There were multiple reasons for altering the outgroup; 1) the combination of multiple taxa into a single hypothetical outgroup (Unwin 2003) is not a sound basis for polarizing characters or testing the ingroup’s monophyly; 2) the use of derived pseudosuchians and dinosaurs increased the opportunity for homoplasy, especially in the ankle (Bennett 2013*b*); 3) different authors use different outgroups, possibly polarizing characters differently. Polarizing characters biased towards the method of a single authorship could result in similar results due to shared methodology. Alternatively, multiple rooting methods could have been used, but it is difficult to estimate the composite outgroup of Unwin (2003) based on an almost entirely distinct character list.

The resulting tree was plotted on a geological time scale using the statistics program R and the packages phytools (Revell 2012) and strap (Bell and Lloyd 2014). The online Paleobiology Database (http://fossilworks.org) was used to place the taxa stratigraphically. Using the chronostratigraphic tree it is possible to calculate the gap excess ratio (GER) (Wills 1999) to correlate the phylogenetic results with the fossil record.

To compare the cladogram to key analyses (Maisch et al. 2004; Lü et al. 2009; Wang et al. 2009; Andres et al. 2014) the taxon lists were reduced to common taxa only, using CompPhy (Fiorini et al. 2014). The SPR distances (Goloboff 2008) and Robinson-Foulds distances (R-F) (Robinson and Foulds 1981) were calculated using TNT and CompPhy. A new index termed the clade retention index (CRI) was calculated using the Phytools package in R. An R script was written to implement the equation given below, and it is available in the supplementary material. Like the consistency fork index (CFI) (Colless 1980) the CRI uses a consensus of two trees to calculate tree similarity. Unlike the CFI, the CRI considers the polytomous taxa (not clades in polytomies) in the strict consensus, indicating how many monophyletic clades are shared between cladograms.

The CRI is calculated using the equation below, where nodes (N) on the consensus tree are indicators of agreement and individual taxa in polytomies (P) are an indicator of disagreement. To put the information about clade retention into context, the maximum possible agreement is calculated using the number of common taxa (T) minus one. The maximum index number (i) recoverable is 1 and the minimum is -1, so the result can be range scaled (normalized) to give a CRI between naught and one (X = 1), see equations below.

$$i = -\frac{P - N}{T - 1}$$

$$\therefore CRI = \frac{X}{(Rmax - Rmin) \times (i - Rmin)}$$

$$\therefore CRI = \frac{1}{(1 - -1) \times \left(-\frac{P - N}{T - 1}\right) - -1}$$

$$\therefore CRI = 0.5 \times \left(-\frac{P - N}{T - 1}\right) + 1$$

The reason for using three different tree comparison metrics is that no one metric represents all the information available. Additionally, tree comparison metrics can be confounded and should be used

313 in tandem. For example, the CRI will produce deflated similarity values if the trees being compared
314 already have polytomies. Also, the SPR metric can assign two different sets of trees with different
315 levels of agreement the same score.

316 Tanglegrams can be helpful for interpreting the results of tree comparison metrics. Dendextend
317 (Galili 2015) in R was used to produce tanglegrams of the reduced taxon trees produced by
318 CompPhy. In order to perform the analysis that produces a tanglegram in Dendextend, the
319 polytomies had to be randomly resolved. To provide as much information about tree similarity as
320 possible solid lines are used to represent branches that are agreed upon, dashed lines represent
321 unique branches, and the lines between the tree tips tangle to represent the disagreement after the
322 branches are rotated for maximum fit.

323 *Geometric morphometrics*

324 The prepubis of *Germanodactylus cristatus* is morphologically distinct from that of *G.*
325 *rhamphastinus*, which has a morphology more similar to that of *Diopecephalus* and *Darwinopterus.*
326 Descriptions and discussions of the prepubis morphology are lacking in the literature. Here, the
327 hypothesis that the morphology and proportions of this often overlooked bone are taxonomically
328 informative is tested using geometric morphometrics. Furthermore, it is hypothesised that *D. kochi*,
329 *D. modularis*, and "*G. rhamphastinus*" are more similar than any one is to *P*. *antiquus*.

330 The geometric morphometric analysis is compared with the phylogeny to establish if their
331 morphology can be used for taxonomic purposes. The analysis was performed on standardised
332 bitmap outline drawings of prepubes. The outlines were drawn from referred specimens of
333 *Dorygnathus* Wagner, 1860 (Wyoming Dinosaur Center specimen); *Scaphognathus* Wagner, 1861*b*
334 (SMNS 59395); *Darwinopterus* Lü et al., 2009 (41HIII-0309A); *Aerodactylus* Vidovic and Martill, 2014
335 (BSP 1883 XVI 1); *Ctenochasma* Meyer, 1852 (BSP 1935 I 24) and "*G. rhamphastinus*" (JME Moe 12 &
336 BSP 1977 XIX 1), and the holotypes of *Pterodactylus antiquus*; *Diopecephalus kochi*;
337 *Germanodactylus cristatus* and *Cycnorhamphus suevicus*. In some cases, it was necessary to use the
338 part and counterpart or moulds of the bone in the limestone to reconstruct the entire prepubis
339 morphology. In *Pterodactylus* a portion of the distal expansion is overlaid by the femur, so a
340 conservative estimate was made of the outline. The shapes were digitized by selecting a net of 100
341 landmarks in TSPdig 2 (Rohlf 2010). The TPS file was analysed in R using the package Geomorph
342 (Adams and Otárola-Castillo 2013). A generalized Procrustes analysis was performed, projecting the
343 landmark data into linear tangent space. The x-axis of the resulting principal component analysis was

converted into hierarchical clusters which were then plotted as a radial dendrogram (note the y-axis produces the same results).

Results

Cladistics

The cladogram presented here is a strict consensus of 2 most parsimonious trees (Fig. 4), which is highly congruent with the geological record (GER = 0.902). The cladogram demonstrates a paraphyletic "rhamphorhynchoidea" with a sister group of *Preondactylus* Wild, 1983 and *Austriadactylus* Dalla Vecchia et al., 2002 as the most basal branch of Pterosauria. This result is in broad agreement with Unwin (2003), Dalla Vecchia (2009), Lü et al. (2009) and Andres et al. (2014). Those Triassic pterosaurs possessing laterally compressed lanceolate or triangular teeth with coronal serrations are recovered in a monophyletic clade, distinct from those with multiple cusps. Multi-cusped taxa share a common ancestor with all remaining taxa with single-cusped teeth. Only the taxa with single-cusped teeth, lacking serrations survived the end-Triassic extinction. Although *Dorygnathus* and *Campylognathoides* are not found until the Toarcian, their shared common ancestor with *Dimorphodon* Owen, 1859 must have been a Triassic pterosaur.

Scaphognathidae contains an assortment of taxa with well-spaced, simple conical teeth, a convex dorsal margin to the skull, a slender dorsal process of the maxilla, a large round orbit, a low angle of the jaw symphysis to the ramus, a robust bowed pteroid bone, a reduced ventral crest of the wing metacarpal and distal phalanx of pedal digit 4 that is longer than the preceding phalanges. These uniting characters place anurognathids (reclassified here to Anurognathinae) in Scaphognathidae. Their deeply nested placement within Scaphognathidae is likely to be due to a lack of transitional-morphs combined with their paedomorphism. Thus, it is possible that anurognathines are far more basal members of Scaphognathidae and the analysis was confounded by their aberrant morphology. The paedomorphic characters exhibited by anurognathines (e.g. reduced rostrum length, large orbit, deep skull, shorter caudal vertebrae) might be the reason some researchers (e.g. Kellner 2003; Wang et al. 2009) find them as the most basal taxa in Pterosauria.

Parapsicephalus Arthaber, 1919 is closely related to scaphognathids, but it maintains some plesiomorphic characteristics which in the past have led to it being likened to *Dorygnathus* (Carpenter et al. 2003; Unwin 2003) and *Dimorphodon* (Andres et al. 2014). In this analysis, however, *Parapsicephalus* is the sister taxon to Monofenestrata (Lü et al. 2009).

Monofenestrata comprises two non-pterodactyloid clades and Pterodactyloidea. Wukongopteridae contains *Wukongopterus* Wang et al., 2009, *Darwinopterus* spp., and *Changchengopterus* Lü, 2009. It

may be that many wukongopterids comprise a single genus for which *Changchengopterus* has priority. The results of this analysis demonstrate that wukongopterids are in desperate need of a taxonomic review less than a decade after their discovery, in agreement with Sullivan et al. (2014). The next taxon stepwise is the as yet un-named German monofenestratan dubbed the Painten pro-pterodactyloid (Tischlinger and Frey 2013). The specimen exhibits a long 5th toe and a shortened tail with elongate chevrons, otherwise, it is *Pterodactylus*-like. *Eosipterus* and *Pterodactylus* are found to be the most basal members of Pterodactyloidea due to the extreme reduction of the 5th toe and reduced tail lacking elongate chevrons. Similar to Vidovic and Martill (2014), this analysis finds *Pterodactylus* to be a very basal member of Pterodactyloidea excluded from the monophyletic clade containing *Ctenochasma* and *Cycnorhamphus* where it has been found by many analyses (Kellner 2003; Unwin 2003; Andres et al. 2014). Despite the lack of consensus on the placement of *Pterodactylus*, its placement here is consistent with recent discoveries of non-pterodactyloid monofenestratans. Likewise, the paraphyly of Archaeopterodactyloidea and *Germanodactylus* is consistent with the discovery of the wukongopterids and *Hamipterus* Wang et al., 2014, meaning characters that were previously thought to be synapomorphies for these clades are in fact symplesiomorphies, and synapomorphies of Monofenestrata. The basal position of *Pterodactylus* excludes it from Lophocratia, which is divided into Euctenochasmatia and Eupterodactyloidea. The most recent definition of Eupterodactyloidea (Andres et al. 2014) does not define a clade similar to the one proposed by Bennett (1994) on this tree, so it is redefined here as the most inclusive clade containing *Nyctosaurus* Marsh, 1876*a*, *Pteranodon* Marsh, 1876*b, Dsungaripterus* Young, 1964 and *Azhdarcho* Nesov, 1984 (after Bennett 1994), but not *Pterodaustro* Bonaparte, 1970.

Diopecephalus is the most basal member of a monophyletic clade containing *Pterodaustro* and *Cycnorhamphus*, thus Euctenochasmatia contains Ctenochasmatoidea (Unwin 2003). Ctenochasmatoidea further contains Ctenochasmatidae and Aurorazhdarchia. Here, Aurorazhdarchidae is redefined as pterosaurs closer to *Aurorazhdarcho* than they are to *Cycnorhamphus*. The name Aurorazhdarchia is used as the unranked replacement name for the clade originally defined as Aurorazhdarchidae (Vidovic and Martill 2014), and it comprises *Aerodactylus*, Aurorazhdarchidae, and Gallodactylidae.

"*Germanodactylus rhamphastinus*" is found to be the most basal branch of Eupterodactyloidea, followed stepwise by *Germanodactylus cristatus* and *Elanodactylus* Andres and Ji, 2008. *Elanodactylus* is the sister taxon to Dsungaripteroidea *sensu* Kellner (2003), but Young (1964) considered Dsungaripteroidea to be defined as pterosaurs with a notarium, in which case *Germanodactylus cristatus* is the most basal dsungaripteroid. Indeed, in addition to other

409 synapomorphies, the presence of a notarium defines the clade (Dsungaripteroidea) comprising
410 *Germanodactylus*, *Quetzalcoatlus* Lawson, 1975 and *Nyctosaurus*.

411 The subjects of this study represent the most basal members of Pterodactyloidea and Lophocratia,
412 excluded from the derived monophyletic clade Ctenochasmatoidea. *Diopecephalus*, a basal most
413 member of Lophocratia is found to possess characters placing it in the monophyletic clade
414 Euctenochasmatia, while "*G. rhamphastinus*" and *G. cristatus* are found to possess characters of
415 Eupterodactyloidea. whereas, *Pterodactylus* is found more basal than any of the other Franconia
416 laminated limestone pterodactyloids. Given that the holotype of the type and only species is a
417 mature subadult and nearly complete, it is not expected to have suffered "rootward slippage" during
418 the analysis.

419 The taphonomic state of *Diopecephalus* may have caused "cladeward slippage" or "rootward
420 slippage", as modular evolution in pterosaurs has been demonstrated to cause both (Lü et al. 2009)
421 due to derived or plesiomorphic states being present in distinct morphological units which can be
422 lost during fossilisation. Two of the discrete state characters that place *Diopecephalus* in
423 Euctenochasmatia (characters 104 and 248) are difficult to code due to its small size and variable
424 state of preservation across the slabs. To test for "cladeward slippage" the two characters were
425 made inactive and the analysis was re-run. This analysis did result in *Diopecephalus* slipping
426 rootward by one branch, out of the monophyletic Euctenochasmatia, but it was still not found in a
427 monophyletic clade with *Pterodactylus* or "*G. rhamphastinus*".

428 The comparison metrics (Fig. 5–7) demonstrate good agreement between the three phylogenies
429 with a paraphyletic *Germanodactylus* (Maisch et al. 2004; Lü et al. 2009). Although the tanglegrams
430 (Fig. 8) demonstrate that similarity metrics (Fig. 5–7) are not independent of matrix dimensions.
431 Smaller trees have less opportunity to be incongruent, but fewer unique relationships are required
432 to lower the congruence metric significantly. To clarify the relationships of "*Germanodactylus*" spp.
433 the phylogeny presented here and the phylogeny of Lü et al. (2009) (Fig. 8 cii) were pruned to their
434 taxa common with Maisch et al. (2004) (Fig. 8 ci). The pruned trees compare favourably despite the
435 lack of topological congruence in the rest of the tree.

436 The CRI (Fig. 5) produces comparable results to the R-F distance metric (Fig. 6), demonstrating its
437 utility. However, the CRI has been affected by the polytomies already present in the source trees.
438 Most noticeably, values from the comparisons of the Lü et al. (2009) phylogeny are lowered by
439 polytomies that are already present in the source tree. By comparison, the SPR distances (Fig. 7)

provide a broad indication of similarity, but lack the resolution required to make fine-scale judgements.

Geometric morphometrics

The results of the geometric morphometric analysis (Fig. 9) compared to the result of the cladistic analysis demonstrate that a short and broad distal expansion of the prepubis is an apomorphy of Monofenestrata, shared by "*G. rhamphastinus*", *Diopecephalus* and *Darwinopterus*. *Germanodactylus,* a more derived eupterodactyloid has a deeper distal expansion, whereas the ctenochasmatoids and *Pterodactylus* have a more elongate/gracile diaphysis, but a plesiomorphic shape to the distal expansion. The basal non-monofenestratans *Dorygnathus* and *Scaphognathus* have a prominent bi-lobed distal expansion which distinguishes them from the monofenestratans. The separation of non-monofenestratans from the monofenestratans supports the hypothesis that the prepubis has a taxonomic utility, which has been overlooked in most previous analyses and descriptions.

Comparative anatomy

Pterodactylus *and* Diopecephalus

The genera *Pterodactylus* and *Diopecephalus* are remarkably similar. However, the only cladistic analyses to study both holotypes (Howse 1986; Vidovic and Martill 2014) find the two specimens in distinct monophyletic clades or in a paraphyletic genus respectively. Furthermore, some – but not all – morphometric bivariate plots (Vidovic and Martill 2014) demonstrate *Pterodactylus* to be more closely associated with *Aerodactylus* than *Diopecephalus*, while *Aerodactylus* is distinguishable from both species by its dentition, skull morphology and pteroid length.

Currently, there are just a few juvenile pterosaur specimens tentatively referred to *Diopecephalus* (three including the holotype and a possible specimen figured by Arratia et al. [2015]) (Vidovic and Martill 2014), rendering taxonomic work on a population impossible. However, using a typological approach, the holotype of *Diopecephalus* does differ from *Pterodactylus* in that the cervical vertebrae have a prominent spinous cranial hypapophysis (Howse 1986) and robust prominent zygapophyses. Additionally, the manual unguals are less robust in *Diopecephalus* compared to *Pterodactylus*, the diaphysis of the prepubis is more robust in *Diopecephalus* and the distal expansion is broader than in *Pterodactylus* (Fig. 9). It was noted that *Diopecephalus* and "*Pterodactylus elegans*" both lacked fusion of the atlas and axis and that the mid-cervical vertebrae were approximately the same size, which was considered a plesiomorphic condition for the Pterodactloidea by Howse (1986). However, due to their heterochrony, lack of fusion between

elements and those proportions of the mid-cervical vertebrae are common to juvenile pterodactyloids (pers. obs.) (e.g. BSP 1967 I 276; BSP 1971 I 17; BSP 1936 I 50).

Diopecephalus *and* "G. rhamphastinus"

No conditions have been identified that *Diopecephalus* shares with *Pterodactylus* that it does not also share with "*G. rhamphastinus*". Despite their similarity, the relationship of *Diopecephalus* and "*G. rhamphastinus*" has received little attention (Seeley 1871, 1901; Vidovic and Martill 2014). "*G. rhamphastinus*" has been considered congeneric with *D. kochi* (Seeley 1871, 1901) and the type species of *Germanodactylus* was originally referred to *"P. kochi*" (Plieninger 1901), but subsequent to the separation of *D. kochi* and *Germanodactylus* spp. (Wiman 1925; Young 1964; Wellnhofer 1968, 1970) the species have been considered distinct without further discussion.

"*G. rhamphastinus*" and *Diopecephalus* share yet more conditions, including a prepubis with a robust diaphysis and broad distal expansion, a more caudal extension of the dorsal process of the premaxilla and less robust manual unguals than *Pterodactylus.* Other possible uniting characters are tentative because they may be affected by ontogeny. For example, "*G. rhamphastinus*" has shorter cervical vertebrae with more robust zygapophyses than *Pterodactylus*, similar to the condition in *Diopecephalus* (Howse 1986).

"G. rhamphastinus" *and* Pterodactylus

"*G. rhamphastinus*" and *Pterodactylus* share conditions plesiomorphic to Monofenestrata and Pterodactyloidea as discussed above. They differ in that "*G. rhamphastinus*" has a straighter slope to the dorsal margin of the skull, pointed jaw tips, a steeper quadrate, fewer teeth in adult specimens, a piriform orbit and a prepubis more similar to that of *Diopecephalus*. Notably, the *Pterodactylus* specimen BMMS 7 was reconstructed using information available from *Aerodactylus* specimens (Bennett 2013*a*), resulting in an overestimate of rostrum length and tooth number. It is likely that the rostrum terminated shortly after the break in the rock and there were only 18 to 20 teeth in the mature specimen's jaws.

Although Bennett (1996) once suggested that the *Germanodactylus* spp. might represent more mature specimens of *Pterodactylus* he subsequently changed his view (Bennett 2002 p.45). We agree that some of the differences could be ontogenetically variable and perhaps vary between sexes, so in 1996 it seemed possible that the two species could be at least congeneric. However, more recent research has revealed more information on the ontogeny and phylogeny of pterodactyloids (Jouve 2004; Bennett 2006, 2013*a*; Lü et al. 2009) and common opinion is that the two are distinct genera.

Germanodactylus cristatus *and* "Germanodactylus rhamphastinus"

Germanodactylus cristatus differs from "*G. rhamphastinus*" and all other pterosaurs in that the dentition is absent from the rostrum tip, but still present in the premaxilla. Wang et al. (2008) also noted that the gestalt of the teeth differed between the two species. Also, the prepubis distal expansion is cranioventrally long, making it approach a reuleaux triangle in outline. Additionally, *Germanodactylus cristatus* has at least three fused dorsal vertebrae, which differs from the condition in similarly sized "*G. rhamphastinus*". These differences do not necessarily distinguish the two species at the generic level. Indeed, Bennett (2006) considered the differences observed between the two *Germanodactylus* species to diagnose the species within the genus. The two species are seemingly united by a similar skull shape and an extreme caudal extension of the premaxilla dorsal process, as well as some skeletal proportions (Bennett 2006 p.876). However, these similarities are also observed in more basal and derived branches of Pterodactyloidea, substantiating the claims that the genus is paraphyletic (Maisch et al. 2004; Vidovic and Martill 2014) which is supported by the phylogeny presented here.

Systematic palaeontology

DIOPECEPHALUS Seeley, 1871

Fig. 1

Type species: *Diopecephalus kochi* (Wagner 1837)

Synonymy:

*1837 *Ornithocephalus kochii* Wagner 1837, p.164, pl.1.

1860 *Pterodactylus kochi* Wagler bei A. Wagner, 1837; Meyer 1860, p.35.

1871 *Diopecephalus kochi* (no author attributed); Seeley 1871, p.35.

1888 *Pterodactylus kochi* Wagner, 1837; Lydekker 1888, p.6.

1901 *Diopecephalus kochi* (no author attributed); Seeley 1901, p.168.

1882 *Pterodactylus kochi* (Wagler); Zittel 1882, p.18, pl.13, fig. 1.

1967 *Pterodactylus kochi* (Wagler); Kuhn 1967, p.16.

1968 *Pterodactylus kochi* (Wagner, 1837); Wellnhofer 1968, p.99.

1970 *Pterodactylus kochi* (Wagner, 1837); Wellnhofer 1970, p.22.

2004 *Pterodactylus antiquus* (Soemmerring, 1812); Jouve 2004, p.549.

Jouve considered "*P. kochi*" synonymous with *P. antiquus*.

2013 *Pterodactylus antiquus* (Sömmerring, 1812); Bennett 2013*a*, p.283.

2014 *Pterodactylus kochi* (Wagner, 1837); Vidovic and Martill 2014 p.1.

2014 *Diopecephalus kochi* (Wagner, 1837); Vidovic and Martill 2014 p.15.

Holotype: Part and counterpart, BSP AS XIX 3 and SMF R 404 (Fig. 1). A nearly complete skeleton on a slab of limestone.

Referred material: An immature specimen represented by part and counterpart, NHM UK PV R 3949 and OUMNH JZ 1609. A privately owned specimen (Arratia et al. 2015: p.468, fig. 900) exhibited in Museum Solnhofen.

Locality and horizon: Kelheim, Germany, Malm Zeta 3 (Wellnhofer 1970), or Malm Zeta 2 (Schweigert 2007), Lower Tithonian.

Genus and species diagnosis: (None of the following are autapomorphic, but are a unique combination of characters) (1) A pterodactyloid pterosaur with an evenly sloping rostrum, leading caudally into a rounded parietal region of the skull, with the dorsal process of the premaxilla extending to the caudal region of a sub-rounded orbit. (2) Labiolingually compressed triangular teeth are present from the jaw tip continuing caudally beneath the nasoantorbital fenestra. (3) The longest cervical vertebra is 50% or less than the maximum skull depth, and no cervical vertebrae exceed a length/depth quotient of 2.5. The cervical vertebrae have robust zygapophyses and an enlarged spinous hypapophysis. (4) The prepubis flares abruptly to a broad distal expansion and its maximum length is approximately equal to its maximum width.

Note: Combination 1 differs from *G. cristatus* and "*G. rhamphastinus*" in the parietal region of the skull, and it differs from the condition in *Pterodactylus* in the caudal extent of the premaxilla. Combination 2 differs from "*G. rhamphastinus*" and *Pterodactylus* in the tooth morphology, and it also differs from *G. cristatus* in the distribution of that dentition. Combination 3 differs from *Pterodactylus* but is similar to the conditions seen in *G. cristatus* and "*G. rhamphastinus*". Condition 4 is different to the morphologies observed in *G. cristatus* and *Pterodactylus*, but similar to that of "*G. rhamphastinus*".

Remarks: Numerous examples of pterosaurs from the Solnhofen Limestone Formation have been referred to "*P. kochi*" (e.g. Wellnhofer 1984; Tischlinger 1993; Frey and Martill 1998). In a recent comparison of these examples and the holotype of *Diopecephalus,* they were excluded from the taxon (Vidovic and Martill 2014). A perception may have arisen that *Diopecephalus kochi* occurs frequently in the Tithonian limestones of Bavaria, Germany, but here it is regarded as a rare taxon.

Although technically the name "*Ornithocephalus kochii*" should be attributed to Wagner (1837), many subsequent authors attribute it to Wagler in Wagner (1837) (Wellnhofer 1968). In fact, although the name was devised by Wagler, and Wagner provided a reason to attribute it to Wagler when he stated:

'Wagler wollte dem neu aufgefudenen Exemplare, das der Gegenstand vorliegender Abhandlung ist, den Namen *Ornithocephalus Kochii* beilegen; ich behalte diese Benennung um so lieber bei, da mir hiedurch Gelegenheit gegeben ist, dem würdigen Manne, der mit zuvorkommender Güte mir das Original zur Publikation zukommen liess, ein geringes Denkmal meiner grossen Achtung und Anerkennung zu setzen'

'[Wagler wanted the newly found specimens, which are the subject of this treatise, to be given the name *Ornithocephalus kochii*. I keep this designation all the more gladly, because by doing so I am given the opportunity to honor the worthy man, who courteously allowed the publication of the original [material], a small monument of my great respect and recognition]'

… there is no reason to credit the published name to Wagler (Wellnhofer 1968).

ALTMUEHLOPTERUS gen. nov.

LSID: urn:lsid:zoobank.org:act:81B99AC3-0475-4FB2-A879-DE3D6D540465

Derivation of name: "Altmuehl" refers to the Altmühl river that flows through Solnhofen (close to M□rnsheim), Eichstätt and joins the river Danube at Kelheim. "Pterus" is a common suffix in pterosaur names referring to the wing. This name is presented as an alternative to the geographically significant name *Daitingopterus* (Maisch et al. 2004) which is a *nomen nudum*.

Type species: *Altmuehlopterus rhamphastinus* (Wagner 1851)

Fig. 2

Synonymy:

*1851 *Ornithocephalus ramphastinus* Wagner 1851, p.132, pl.1.

589 Note, here *ramphastinus* is spelled without the first letter 'h', named for its similarity to the
590 toucan *Ramphastos* (Bennett 2006).

591 1860 *Pterodactylus rhamphastinus* (Wagner, 1851); Meyer 1860, p.54.

592 Here Meyer makes the mistake of using an additional 'h' in the species name.

593 1861b *Pterodactylus rhamphastinus* no attribution; Wagner 1861*b*, p.531.

594 Wagner uses the emended spelling, seemingly accepting Meyer's *lapsus*.

595 1871 *Diopecephalus rhamphastinus* (Wagner, 1851); Seeley 1871, p.35.

596 1888 *Pterodactylus rhamphastinus* (Wagner); Lydekker 1888, p.8.

597 1927 *Pterodactylus rhamphatilus* (Wagner, 1851); Weigelt 1927, p.227, 28 Abb., Taf.37.

598 Lapsus. The 1989 English translation of Weigelt miscorrects this to *Germanodactylus*
599 *cristatus*.

600 1941 *Rhamphorhynchus kokeni* Plieninger, 1907; Edinger 1941, pp.671, 678.

601 1970 *Germanodactylus rhamphastinus* (Wagner, 1851); Wellnhofer 1970, p. 66.

602 1991 *Germanodactylus rhamphastinus* (Wagner, 1851); Wellnhofer 1991, p. 95.

603 1994 *Germanodactylus ramphastinus* (Wagner, 1851); Frickhinger 1994, p. 269.

604 Frickhinger returns to the original spelling of *ramphastinus*.

605 2004 *Daitingopterus rhamphastinus* no attribution; Maisch et al. 2004, p.631, table 1.

606 This name is a *nomen nudum* because the authors did not refer to a type specimen or state
607 that it was a new genus.

608 2006 *Germanodactylus rhamphastinus* (Wagner, 1851); Bennett 2006, p.877.

609 Bennett provides a detailed discussion of the synonymy.

610 2010 *Germanodactylus ramphastinus* (Wagner, 1851); Rodrigues et al. 2010, p.57.

611 These authors return to the original spelling of *ramphastinus*, but the emended spelling has
612 priority due to popular use.

613 Holotype: BSP AS I 745 a and counterpart BSP AS I 745 b (Fig. 2).

Referred material: MCZ 1886 adult specimen with dorsal soft tissue headcrest (Bennett 2002), JME Moe 12 and counterpart BSP 1977 XIX 1 (Rodrigues et al. 2010).

Horizon and locality: Mörnsheim Limestone Formation, Malm Zeta 3, Daiting, possibly Solnhofen Formation, Solnhofen (*see* Bennett 2002).

Genus and species diagnosis: (None of the following are autapomorphic, but together comprise a unique combination of characters) The dorsal process of the premaxilla supports a low, long crest, which extends back level with the caudal margin of a tall orbit. The premaxilla forms an approximately straight dorsal margin to the rostrum which terminates with a pointed rostrum tip. Simple cone teeth (taller and thinner than in *Germanodactylus* and *Diopecephalus*) present at the rostrum tip and below the nasoantorbital fenestra. There are ~16 widely spaced teeth in each jaw that grade up in size and back down mesiodistally.

Remarks: The emended spelling of the name *rhamphastinus* (with the 'h') is used, as it has priority through popular use (ICZN 33.3.1.). This seemed acceptable to Wagner (1861*b*).

The species is split from the genus *Germanodactylus* due to it only sharing conditions observed in both more basal and more derived pterosaurs. The similarities observed between *Germanodactylus cristatus* and *Altmuehlopterus rhamphastinus* are not considered to support their monophyly as a single genus. This is supported by the results of a cladistic analysis and a geometric morphometric analysis which indicate the condition of the prepubis in *Germanodactylus* is taxonomically significant.

GERMANODACTYLUS (Young 1964)

Fig. 3

Type species: *Germanodactylus cristatus* (Wiman 1925)

Synonymy:

1901 *Pterodactylus kochi* Wagler; Plieninger 1901, p.65.

*1925 *Pterodactylus cristatus* Wiman 1925, p.17.

1964 *Germanodactylus kochi* (Wagler); Young 1964, p.251.

1967 *Diopecephalus kochi* (Wagler); Kuhn 1967, p.34.

1970 *Germanodactylus cristatus* (Wiman, 1925); Wellnhofer 1970, p.64.

1991 *Germanodactylus cristatus* (Wiman, 1925); Wellnhofer 1991, p.96.

2006 *Germanodactylus cristatus* (Wiman, 1925); Bennett 2006, p.873, figs 1-2.

2010 *Germanodactylus cristatus* (Wiman, 1925); Hone 2010, p.263, fig. 3.

Holotype: BSP 1892 IV 1: disarticulated, but near complete skeleton on a slab of Solnhofen Limestone; Counterpart NMING F15005.

Referred material: JME SoS 4593, JME SoS 4006 (see Bennett 2006) and an undescribed specimen in Karlsruhe (SMNK PAL 6529).

Horizon and locality: Solnhofen Limestone, Malm Zeta 2, Solnhofen, Germany.

Genus and species diagnosis: (Those characters marked with * are unique autapomorphies) Pterodactyloid pterosaur with edentulous jaw tips but with short, triangular teeth present in the remaining premaxilla. Prepubis with a reuleaux triangle shaped distal expansion* (Fig. 3 & 9).

Description: See (Wellnhofer 1970).

Remarks: The holotype of *Germanodactylus cristatus* can also be distinguished from other pterosaurs by a unique suite of plesiomorphic and apomorphic characters including: approximately 50% of prenarial rostrum ventral surface is comprised of the premaxilla; teeth are short, robust with triangular outline in lateral view; tooth row extends beneath nasoantorbital fenestra; low, striated bony crest present on adult individuals (this may be sexually dimorphic [*see* Bennett 1992; Lü et al. 2011; Wang et al. 2014] as a large specimen (SMNK PAL 6529) lacks such a crest); straight and vertical orbit rostral margin; the wing-metacarpal is shorter than the ulna (Fig. 3); centra of dorsal vertebrae 1–3 fused forming a small notarium.

Discussion

The dendrogram demonstrating the morphospace of pterosaur prepubes (Fig. 9) is in general agreement with the phylogeny, suggesting that the prepubis morphology is of taxonomic value. Conversely, the prepubis of *Pterodactylus* is in disagreement with the phylogeny, appearing more similar to the ctenochasmatoid *Cycnorhamphus*, which is consistent with the results of other cladistic analyses (Lü et al. 2009; Wang et al. 2009; Andres et al. 2014). However, in the geometric morphometric analysis, the prepubis is only one anatomical unit expressing several characters across 10 specimens, compared to the 320 characters (including characters of the prepubis) and 99 OTUs of

671 the cladistic analysis. Furthermore, the dendrogram (Fig. 9) is constructed using hierarchical clusters,
672 akin to phenetics and is susceptible to the effects of homoplasy and reversibility (Camin and Sokal
673 1965). This methodology is far from a replacement for cladistic methods, but it does demonstrate
674 that the broad morphology of the prepubis can be used to understand the phylogenetic affinities of
675 pterosaurs (Fig. 9 and 10).

676 The cladistic analysis yields a strict consensus that places all four taxa with which this study is
677 concerned as basal pterodactyloid "transitional" taxa. *Pterodactylus* is the most basal branch of
678 these "transitional" taxa and the remaining three taxa are placed in Lophocratia (*Pterodaustro* +
679 *Quetzalcoatlus*). *Diopecephalus* is found in the monophyletic clade Euctenochasmatia
680 (*Diopecephalus* + *Pterodaustro*), while *Altmuehlopterus* and *Germanodactylus* are found as basal
681 members of the Eupterodactyloidea (closer to *Pteranodon* than *Pterodaustro*). *Altmuehlopterus*
682 occupies a more basal position than *Germanodactylus,* which is to be expected given the number of
683 plesiomorphic conditions it possesses by comparison. Some derived conditions of *Germanodactylus*
684 (i.e. presence of a notarium) are shared with other dsungaripteroids, including ornithocheiroids and
685 azhdarchoids. However, the restricted dentition absent from the rostrum tip is seemingly an
686 autapomorphy of *Germanodactylus,* and convergent with dsungaripterines.

687 Many similarities observed between Solnhofen pterosaur specimens are a product of their early
688 ontogeny, lacking peramorphic conditions (Vidovic and Martill 2014) and the presence of their
689 shared plesiomorphic conditions. *Pterodactylus*, *Diopecephalus*, *Germanodactylus* and
690 *Altmuehlopterus* all share characters in common with the Painten pro-pterodactyloid (Tischlinger
691 and Frey 2013) and wukongopterids. These characters include an approximately triangular, laterally
692 compressed skull with a dentition extending under the nasoantorbital fenestra (Fig. 10). In some
693 cases the plesiomorphic low, long, striated bony headcrest is present (e.g. *Darwinopterus*,
694 *Germanodactylus* and *Altmuehlopterus*). The headcrest is a confounding structure, given that it is
695 sexually dimorphic and might not develop until sexual maturity is achieved, although juvenile
696 pterosaurs with small crests have been identified (Dalla Vecchia 2009; Vidovic and Martill 2014).
697 *Pterodactylus* and *Diopecephalus* are most similar to the Painten pro-pterodactyloid and this is
698 reflected in their position in the phylogeny (Fig. 4). Likewise, *Altmuehlopterus* has a remarkably
699 similar skull to *Darwinopterus* and *Cuspicephalus* (Martill and Etches 2012), but the skull of
700 *Altmuehlopterus* can be distinguished as pterodactyloid (Witton et al. 2015).

701 Despite being maintained as a *Pterodactylus* species for over a century, *Diopecephalus kochi* shares a
702 similar list of common characters with *Altmuehlopterus rhamphastinus*. Disregarding *Diopecephalus*,
703 the taxa *Pterodactylus*, *Altmuehlopterus*, and *Germanodactylus* are distinct and readily diagnosable.

Thus, *Diopecephalus* is the most problematic of these taxa. *Diopecephalus* could potentially represent the juvenile condition of any of the other three genera discussed above, yet it is phylogenetically placed as the most basal branch of the Euctenochasmatia (Unwin 2003) which excludes these taxa. Vidovic and Martill (2014) demonstrated that *Pterodactylus* was more similar to *Aerodactylus* than *Diopecephalus* in its skull, nasoantorbital fenestra and cervical vertebra proportions. However, *Pterodactylus* is more similar to *Diopecephalus* in its dental distribution and PCRW proportions to the skull. Likewise, *Altmuehlopterus* has the same plesiomorphic prepubis condition and dental distribution as *Diopecephalus*, and both have a more caudal extension of the premaxilla dorsal process than *Pterodactylus*. There are subtle differences between the morphologies of *Altmuehlopterus* and *Diopecephalus* too. *Diopecephalus* has a more rounded parietal region of the skull and teeth similar to those of *Germanodactylus* (labiolingually compressed broad triangles) which differs from *Altmuehlopterus* (Wang et al. 2008). The mosaic of characters that each taxon has in common demonstrates a complex evolutionary and ontogenetic relationship. A privately owned specimen (Arratia et al. 2015) displayed in Museum Solnhofen demonstrates the prepubis morphology and short cervical vertebrae with robust zygapophyses that distinguishes the holotype of *Diopecephalus kochi* from *Pterodactylus* in a more mature individual. The specimen is approximately the same size as the holotype of *Pterodactylus antiquus*, thus, the morphological differences are unlikely to be ontogenetic in this specimen at least. Indeed, new examples may provide further support for the taxon's validity. This situation raises the debate of species and taxon concept, and how to deal with "transitional" taxa that demonstrate a mosaic of characters shared amongst multiple taxa.

The genera, *Pterodactylus*, *Diopecephalus*, *Altmuehlopterus* and *Germanodactylus* have been demonstrated to be valid monophyletic, monotypic taxa, despite their close similarities and mix of characters. However, when examples of *D. kochi* are included in *Pterodactylus* and *A. rhamphastinus* is included in *Germanodactylus* as has been asserted (Wellnhofer 1968, 1970; Jouve 2004; Bennett 2006, 2013*a*) (note, even taxonomic reviews that used empirical evidence [Jouve, 2004; Bennett 2013*a*] arguably suffered from the Texas sharpshooter fallacy and numerous explanations for the same data could be given) these two genera are paraphyletic. That is to say, the common ancestor of *P. antiquus* and *D. kochi* is also the common ancestor of higher taxa, including Ctenochasmatoidea and Eupterodactyloidea. Likewise, the common ancestor of *A. rhamphastinus* and *G. cristatus* is shared with the higher taxon Dsungaripteroidea. A monophyletic genus should comprise a natural group of species that share a most recent common ancestor that is not shared with any other higher taxa (Ebach and Williams 2010). Some proponents of Linnaean classification argue that it is a theoretical impossibility to not have paraphyletic taxa (Brummitt 1997; Hörandl and Stuessy 2010).

At an impossibly fine resolution, one taxon does evolve from a subset of the population of another taxon, rendering the progenitor taxon paraphyletic. However, to argue that one cannot artificially scrutinize between one population and another because they are part of an evolutionary continuum renders the use of both classification and cladification unsuitable. Indeed, if paraphyletic taxa were permissible in a cladistic model and only monophyletic, polytypic taxa were regarded as valid, the discovery of new fossil specimens would result in a continual reassessment of the taxonomy. This problematic situation is observed in the higher clades of Pterosauria in the absence of a formalized set of rules – for this purpose the PhyloCode has been proposed (Cantino and de Queiroz 2010). Therefore, to provide phyletic and nomenclatural (Queiroz 2006) stability to the four species with which this study is concerned they must occupy four distinct genera based on positive evidence of monophyly, not an assertion or negative evidence – recency of the common ancestor, not similarity.

Despite a taxonomic resolution the case remains that the four taxa with which this study is concerned are "transitional" monotypic taxa, which has proven especially problematic in the case of *Pterodactylus*, *Diopecephalus,* and *Altmuehlopterus*. Taxon concepts are based on a "snapshot" of organisms during a point in their evolution, either in the present day or in the fossil record. Thus, there is a general misconception that taxa are biologically distinct entities. We are fortunate that the Franconia laminated limestones provide a series of successive "snapshots" through a geologically short period (Fig. 10). This situation provides an unparalleled understanding of pterosaur evolution and ecological niche partitioning, but it also exposes the blurred lines of the taxon concept.

In the Franconia laminated limestones there is a succession of monofenestratan pterosaurs present, from the Painten pro-pterodactyloid (Tischlinger and Frey 2013) through to *Germanodactylus*. Pterosaurs from the Hybonotum Zone are numerous, by contrast with the Beckeri Zone. Clearly, by the start of the Tithonian, most of the non-dsungaripteroid pterosaur diversity had appeared. Further exploration of the laminated limestones in the Beckeri Zone could provide much more evidence for early pterodactyloid evolution and development.

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References

ADAMS, D. C. & OTÁROLA-CASTILLO, E. 2013. Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, **4**, 393–399.

ANDRES, B. & JI, Q. 2008. A new pterosaur from the Liaoning province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology*, **51**, 453–469.

ANDRES, B., CLARK, J. & XU, X. 2014. The earliest pterodactyloid and the origin of the group. *Current Biology*, **24**, 1011–1016.

ARCHIBALD, J. D. 1994. Metataxon concepts and assessing possible ancestry using phylogenetic systematics. *Systematic Biology*, **43**, 27–40.

ARRATIA, G., SCHULTZE, H.-P., TISCHLINGER, H. & VIOHL, G. 2015. *Solnhofen - Ein Fenster in die Jurazeit 1+2*. Pfeil, F.

ARTHABER, G. 1919. Studien über Flugsaurier auf grund der bearbeitung des Wiener exemplares von *Dorygnathus Banthensis* Theod. sp. *Denkschrift der Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse,* **97**, 391-464.

BELL, M. A. & LLOYD, G. T. 2014. *Strap: Stratigraphic Tree Analysis for Palaeontology*. R package version 1.4. https://CRAN.R-project.org/package=strap.

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. 1994. *Taxonomy and systematics of the Late Cretaceous pterosaur* Pteranodon *(Pterosauria, Pterodactyloida).* Occasional Papers of the Natural History Museum, University of Kansas, **169**, 1–70.

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. 2002. Soft tissue preservation of the cranial crest of the pterosaur *Germanodactylus* from Solnhofen. *Journal of Vertebrate Paleontology*, **22**, 43–48.

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. 2013a. New information on body size and cranial display structures of *Pterodactylus antiquus*, with a revision of the genus. *Paläontologische Zeitschrift*, **87**, 269–289.

BENNETT, S. C. 2013b. The phylogenetic position of the Pterosauria within the Archosauromorpha re-examined. *Historical Biology*, **25**, 545–563.

BONAPARTE, J. F. 1970. *Pterodaustro guinazui* gen. et sp. nov. Pterosaurio de la Formacion Lagarcito, Provincia de San Luis, Argentina y su significado en la geologia regional (Pterodactylidae). *Acta Geologica Lilloana*, **10**, 209–225.

BRAZEAU, M. D. 2011. Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society*, **104**, 489–498.

BRUMMITT, R. K. 1997. Taxonomy versus cladonomy, a fundamental controversy in biological systematics. *Taxon*, **46**, 723–734.

CAMIN, J. H. & SOKAL, R. R. 1965. A method for deducing branching sequences in phylogeny. *Evolution*, **19**, 311–326.

CANTINO, P. D. & DE QUEIROZ, K. 2010. International code of phylogenetic nomenclature. *Version 4c.[Online.] Available from: http://www. ohio. edu/phylocode/(accessed 30 May 2013)*.

CARPENTER, K., UNWIN, D., CLOWARD, K., MILES, C. & MILES, C. 2003. A new scaphognathine pterosaur from the Upper Jurassic Morrison Formation of Wyoming, USA. *Geological Society, London, Special Publications*, **217**, 45–54.

COLLESS, D. H. 1980. Congruence between morphometric and allozyme data for Menidia species: A reappraisal. *Systematic Zoology*, **29**, 288–299.

CUVIER, G. 1809. Mémoire sur le squelette fossile d'un reptile volant desenvirons d Aichstedt, que les naturalistes ont pris pour un oiseau, etdont nous formons un genre de sauriens, sous le nom de Ptero-Dactyle. *Annales du Muséum d'Histoire Naturelle*, **13**, 424–437.

824 DALLA VECCHIA, F. M. 2009. The first Italian specimen of *Austriadactylus cristatus* (Diapsida,
825 Pterosauria) from the Norian (Upper Triassic) of the Carnic Prealps. *Rivista Italiana di*
826 *Paleontologia e Stratigrafia [Research in Paleontology and Stratigraphy]*, **115**, 291–304.
827 DALLA VECCHIA, F. M., WILD, R., HOPF, H. & REITNER, J. 2002. A crested rhamphorhynchoid
828 pterosaur from the Late Triassic of Austria. *Journal of Vertebrate Paleontology*, **22**, 196–199.
829 EBACH, M. C. & WILLIAMS, D. M. 2010. Aphyly: a systematic designation for a taxonomic problem.
830 *Evolutionary biology*, **37**, 123–127.
831 EDINGER, T. 1941. The brain of *Pterodactylus*. *American Journal of Science*, **239**, 665–682.
832 FABRE, J. 1976. Un noveau Pterodactylidae sur le gisement '"Portlandian"'de Canjurs (Var):
833 *Gallodactylus canjuersensis* nov. gen., nov. sp. *Comptes Rendus de l'Academie des Science,*
834 *Paris*, **279**, 2011–2014.
835 FIORINI, N., LEFORT, V., CHEVENET, F., BERRY, V. & CHIFOLLEAU, A.-M. A. 2014. CompPhy: a web-
836 based collaborative platform for comparing phylogenies. *BMC evolutionary biology*, **14**, 253.
837 FREY, E. & MARTILL, D. M. 1998. Soft tissue preservation in a specimen of *Pterodactylus kochi*
838 (WAGNER) from the Upper Jurassic of Germany. *Neues Jahrbuch fur Geologie und*
839 *Palaontologie-Abhandlungen*, **210**, 421–441.
840 FREY, E., MEYER, C. A. & TISCHLINGER, H. 2011. The oldest azhdarchoid pterosaur from the Late
841 Jurassic Solnhofen Limestone (Early Tithonian) of Southern Germany. *Swiss Journal of*
842 *Geosciences*, **104**, 35–55.
843 FRICKHINGER, K. A. 1994. *Die Fossilien von Solnhofen: Dokumentation der aus den Plattenkalken*
844 *bekannten Tiere und Pflanzen*. Vol. 1. Goldschneck-Verlag.
845 GALILI, T. 2015. Dendextend: an R package for visualizing, adjusting and comparing trees of
846 hierarchical clustering. *Bioinformatics*: btv428.
847 GOLOBOFF, P. A. 2008. Calculating SPR distances between trees. *Cladistics*, **24**, 591–597.
848 GOLOBOFF, P. A. 2014. Extended implied weighting. *Cladistics*, **30**, 260–272.
849 GOLOBOFF, P. A., FARRIS, J. S. & NIXON, K. C. 2008a. TNT, a free program for phylogenetic analysis.
850 *Cladistics*, **24**, 774–786.
851 GOLOBOFF, P. A., CARPENTER, J. M., ARIAS, J. S. & ESQUIVEL, D. R. M. 2008b. Weighting against
852 homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, **24**, 758–
853 773.
854 HONE, D. W. 2010. A short note on modifications to nineteenth century pterosaur specimens held in
855 the National Museum of Ireland–Natural History, Dublin. *Geological Curator*, **9**, 261–265.
856 HÖRANDL, E. & STUESSY, T. F. 2010. Paraphyletic groups as natural units of biological classification.
857 *Taxon*, **59**, 1641–1653.
858 HOWSE, S. C. B. 1986. On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria).
859 *Zoological Journal of the Linnean Society*, **88**, 307–328.
860 HUENE, F. VON. 1951. Zwei ausgezeichnet erhaltene Exemplare von Pterodactylus im Natur-
861 Museum Senckenberg. *Senckenbergiana*, **32**, 1–7.
862 JOUVE, S. 2004. Description of the skull of a *Ctenochasma* (Pterosauria) from the latest Jurassic of
863 eastern France, with a taxonomic revision of European Tithonian Pterodactyloidea. *Journal*
864 *of Vertebrate Paleontology*, **24**, 542–554.
865 KELLNER, A. W. A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the
866 group. *Geological Society, London, Special Publications*, **217**, 105–137.
867 KUHN, O. 1967. *Die fossile Wirbeltierklasse Pterosauria*. Oeben, Krailling bei München, 52 pp.
868 LAWSON, D. A. 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest
869 flying creature. *Science*, **187**, 947–948.
870 LÜ, J. 2009. A new non-pterodactyloid pterosaur from Qinglong County, Hebei Province of China.
871 *Acta Geologica Sinica - English Edition,* **83**, 189–199.
872 LÜ, J. & JI, Q. 2006. Preliminary results of a phylogenetic analysis of the pterosaurs from western
873 Liaoning and surrounding areas. *Journal of Paleontological Society of Korea*, **22**, 239–261.

LÜ, J., JI, S., YUAN, C. & JI, Q. 2006. [Chapter 4: Phylogenetic analysis of the relationships of Chinese pterosaurs]. *In*: *[Pterosaurs from China]*, *Geological Publishing House, Beijing*.
LÜ, J., UNWIN, D. M., JIN, X., LIU, Y. & JI, Q. 2009. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society of London B: Biological Sciences*: rspb20091603.
LÜ, J., UNWIN, D. M., DEEMING, D. C., JIN, X., LIU, Y. & JI, Q. 2011. An egg-adult association, gender, and reproduction in pterosaurs. *Science*, **331**, 321–324.
LYDEKKER, R. 1888. *Catalogue of the fossil reptilia and amphibia in the British Museum (Natural History)*. Vol. 1. order of the Trustees, 309 pp.
MAISCH, M. W., MATZKE, A. T. & SUN, G. 2004. A new dsungaripteroid pterosaur from the Lower Cretaceous of the southern Junggar Basin, north-west China. *Cretaceous Research*, **25**, 625–634.
MARSH, O. C. 1876a. Principal characters of American pterodactyls. *American Journal of Science,* **72**, 479–480.
MARSH, O. C. 1876b. Notice of a new sub-order of Pterosauria. *American Journal of Science*, **11**, 507–509.
MARTILL, D. M. & ETCHES, S. 2012. A new monofenestratan pterosaur from the Kimmeridge Clay Formation (Kimmeridgian, Upper Jurassic) of Dorset, England. *Acta Palaeontologica Polonica*, **58**, 285–294.
MARTILL, D. M., VIDOVIC, S. U., HOWELLS, C. & NUDDS, J. R. 2016. The Oldest Jurassic Dinosaur: A Basal Neotheropod from the Hettangian of Great Britain. *PLoS ONE*, **11**, e0145713.
MEYER, H. 1834. *Gnathosaurus subulatus*, ein Saurus aus dem lithographischen Schiefer von Solnhofen. *Museum Senckenbergianum*, **1,** 5–7.
MEYER, H. 1852. *Ctenochasma römeri*. *Palaeontographica*, **2**, 82–84.
MEYER, H. 1854. *Pterodactylus longicollum* n. sp. *In: Solenhofener Schiefer. Neues Jahrburch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde. Briefwechsel Mittheilungen an Professor Bronn,* 51–56.
MEYER, H. 1856. *Pt. micronyx* n. sp. Neues Jahrburch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde. Briefwechsel Mittheilungen an Professor Bronn, 826–827.
MEYER, H. 1860. Zur Fauna der Vorwelt: Reptilien aus dem lithographischen Schiefer des Jura in Deutschland und Frankreich. Brieflichel Mitteilungen an Professor Bronn, 1–84.
MEYER, R. K. 1977. Stratigraphie und Fazies des Frankendolomits und der Massenkalke (Malm). *In: Südliche Frankenalb*. Erlanger geologische Abhandlungen, **104**.
MONGIARDINO KOCH, N., SOTO, I. M. & RAMÍREZ, M. J. 2015. Overcoming problems with the use of ratios as continuous characters for phylogenetic analyses. *Zoologica Scripta*, **44**, 463–474.
NESBITT, S. J., SMITH, N. D., IRMIS, R. B., TURNER, A. H., DOWNS, A. & NORELL, M. A. 2009. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science*, **326**, 1530–1533.
NESOV, L. A. 1984. [Pterosaurs and birds from the Late Cretaceous of Middle Asia]. *Paleontologicheskii Zhurnal*, **1984**, 45–57.
OWEN, R. 1859. On a new genus (*Dimorphodon*) of pterodactyle, with remarks on the geological distribution of flying reptiles. *Report for the British Association for the Advancement of Science*, **28**, 97–103.
PEREYRA, V. & MOUND, L. A. 2009. Phylogenetic relationships within the genus *Cranothrips* (Thysanoptera, Melanthripidae) with consideration of host associations and disjunct distributions within the family. *Systematic Entomology*, **34**, 151–161.
PLIENINGER, F. 1901. Beiträge zur Kenntnis der Flugsaurier. *Palaeontographica*, **48**, 65–90.
PLIENINGER, F. 1907. Die Pterosaurier der Juraformation Swabens. *Palaeontographica*, **53**, 209–313.
QUEIROZ, K. DE. 2006. The PhyloCode and the Distinction between Taxonomy and Nomenclature. *Systematic Biology*, **55**, 160–162.

QUENSTEDT, F. A. 1855. Über *Pterodactylus suevicus* im lithographischen Schiefer Württembergs. 1–52. Universität Tübingen, Tübingen.
REVELL, L. J. 2012. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
ROBINSON, D. F. & FOULDS, L. R. 1981. Comparison of phylogenetic trees. *Mathematical Biosciences*, **53**, 131–147.
RODRIGUES, T., KELLNER, A. W. A. & RAUHUT, O. 2010. A new specimen of the archaeopterodactyloid *Germanodactylus ramphastinus*. *Acta Geoscientica Sinica* **31** (Supp. 1), 57–58.
ROHLF, F. J. 2010. *TpsDig, digitize landmarks and outlines, ver. 2.16*.
SCHWEIGERT, G. 2007. Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany – first results and open questions. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen,* **245**, 117–125.
SEELEY, H. G. 1870. *The Ornithosauria: an elementary study of the bones of pterodactyles*. Deighton, Bell, and Co., Cambridge, 137 pp.
SEELEY, H. G. 1871. III.—Additional evidence of the structure of the head in Ornithosaurs from the Cambridge Upper Greensand; being a supplement to 'The Ornithosauria'. *Journal of Natural History*, **7**, 20–36.
SEELEY, H. G. 1901. *Dragons of the Air - An Account of Extinct Flying Reptiles*. Methuen and Co, 239 pp.
SÖMMERRING, S. 1812. Über einen *Ornithocephalus*. *Denkschrift der Königlichen Akademie Wissenschaften, München*, **3**, 89–120.
SULLIVAN, C., WANG, Y., HONE, D. W. E., WANG, Y., XU, X. & ZHANG, F. 2014. The Vertebrates of the Jurassic Daohugou Biota of Northeastern China. Journal of Vertebrate Paleontology, **34**, 243–80.
TISCHLINGER, H. 1993. Überlegungen zur Lebensweise der Pterosaurier anhand eines verheilten Obrschenkelbruches bei *Pterodactylus kochi* (Wagner). *Archaeopteryx*, **11**, 63–71.
TISCHLINGER, H. & FREY, E. 2013. Ein neuer Pterosaurier mit Mosaikmerkmalen basaler und pterodactyloider Pterosauria aus dem Ober-Kimmeridgium von Painten (Oberpfalz, Deutschland). *Archaeopteryx*, **31**, 1–13.
UNWIN, D. M. 2003. On the phylogeny and evolutionary history of pterosaurs. *Geological Society, London, Special Publications*, **217**, 139–190.
VIDOVIC, S. U. & MARTILL, D. M. 2014. *Pterodactylus scolopaciceps* Meyer, 1860 (Pterosauria, Pterodactyloidea) from the Upper Jurassic of Bavaria, Germany: the problem of cryptic pterosaur taxa in early ontogeny. *PLoS ONE*, **9**, e110646.
WAGNER, A. 1837. Beschreibung eines neu entdeckten *Ornithocephalus*: nebst allgemeinen Bemerkungen über die Organisation dieser Gattung. *Abhandlungen der Bayerische Akademie der Wissenschaften Mathematisch-Wissenschaftlichen Klasse*, **2**, 165-198.
WAGNER, A. 1851. Beschreibung einer neuen Art von *Ornithocephalus* etc. *Abhandlungen Bayerischen Akademie für Wissenschaften Mathematisch-Physikalische Klasse*, (1850), 127–192.
WAGNER, A. 1858. Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers. *Abteilung, Saurier. Abhandlungen der Bayerische Akademie der Wissenschaften Mathematisch-Wissenschaftlichen Klasse,* **8**, 417–528.
WAGNER, A. 1860. Bemerkungen über die Arten von Fische und Saurier, welche im untern wie im oberen Lias zugleich vorkommen sollen. *Sitzungsberichte der Konigliche Bayerischen Akademie der Wissenschaften Mathematisch-physik Klasse*, (1860), 36–52.
WAGNER, A. 1861a. Charakteristik einer neuen Flugeidechie, *Pterodactylus elegans*. *Sitzungsberichte der königlich bayerischen Akademie der Wissenschaften Mathematisch-physik Klasse*, (1861), 363 p.

WAGNER, A. 1861b. Übersicht über die fossilen Reptilen des lithographischen Schiefers in Bayern nach ihren Gattungen und Arten. *Sitzungsberichte der königlich bayerischen Akademie der Wissenschaften Mathematisch-physik Klasse*, (1861), 467–535.
WANG, X., CAMPOS, D. D. A., ZHOU, Z. & KELLNER, A. W. 2008. A primitive istiodactylid pterosaur (Pterodactyloidea) from the Jiufotang Formation (Early Cretaceous), northeast China. *Zootaxa*, (1813), 1–18.
WANG, X., KELLNER, A. W. A., JIANG, S. & MENG, X. 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. *Anais da Academia Brasileira de Ciências*, **81**, 793–812.
WANG, X., KELLNER, A. W. A., JIANG, S., WANG, Q., MA, Y., PAIDOULA, Y., CHENG, X., RODRIGUES, T., MENG, X., ZHANG, J., LI, N. & ZHOU, Z. 2014. Sexually Dimorphic Tridimensionally Preserved Pterosaurs and Their Eggs from China. *Current Biology*, **24**, 1323–1330.
WEIGELT, J. 1927. *Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung*. Leipzig, verlag Max Weg, 227 pp.
WELLNHOFER, P. 1968. Über *Pterodactylus kochi* (Wagner 1837). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **132**, 97–126.
WELLNHOFER, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Suddeutschlands. *Bayerische Akademie der Wissenschaften, Mathematisch-Wissenschaftlichen Klasse, Abhandlungen*, **141**, 1–133.
WELLNHOFER, P. 1984. Die Flughaut von *Pterodactylus* (Reptilia, Pterosauria) am Beispiel des Wiener Exemplares von *Pterodactylus kochi* (Wagner). *Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie*, **88**, 149–162.
WELLNHOFER, P. 1991. *The illustrated encyclopedia of pterosaurs*. Crescent Books.
WILD, R. 1983. A new pterosaur (Reptilia, Pterosauria) from the Upper Triassic (Norian) of Friuli, Italy. *Gortania - Atti del Museo Friulano di Storia Naturale*, **5**, 45–62.
WILLS, M. A. 1999. Congruence between phylogeny and stratigraphy: randomization tests and the Gap Excess Ratio. *Systematic Biology*, **48**, 559–580.
WIMAN, C. 1925. Über *Pterodactylus Westmani* und andere Flugsaurier. *Bulletin of the Geological Institution of the University of Uppsala*, **20**, 1–38.
WITTON, M. P., O'SULLIVAN, M. AND MARTILL, D. M. 2015. The relationships of *Cuspicephalus scarfi* Martill and Etches, 2013 and *Normannognathus wellnhoferi* Buffetaut et al., 1998 to other monofenestratan pterosaurs. *Contributions to Zoology*, **84**, 115–127.
YOUNG, C. C. 1964. On a new pterosaurian from Sinkiang, China. *Vertebrata PalAsiatica*, **8**, 221–255.
YOUNG, C. C. 1973. Reports of Paleontological Expedition to Sinkiang (II). Pterosaurian Fauna from Wuerho, Sinkiang. *Mem. Inst. Vert. Palaeont. Paleoanthr. Acad. Sin.* **11**, 18–35.
ZITTEL, K. A. 1882. Über Flugsaurier aus dem lithographischen Schiefer Bayerns. *Palaeontographica*, (1846-1933), 47–80.

1012

Table 1. *monofenestratans from Franconia laminated limestone localities*

Malm Zeta 1 **Upper Kimmeridgian**	**Malm Zeta 2** **Lower Tithonian**	**Malm Zeta 3** **Lower Tithonian**
Cycnorhamphus suevicus (Quenstedt 1855) (holotype) *Ardeadactylus longicollum* (Meyer 1854) (neotype) Painten pro-pterodactyloid (*sensu* Tischlinger and Frey 2013) *Pterodactylus c.f. antiquus* (SMF R 4072)	*Pterodactylus antiquus* (Sömmerring 1812) (holotype) *Gnathosaurus subulatus* Meyer 1834 *Aurorazhdarcho micronyx* (Meyer 1856) *Aerodactylus scolopaciceps* (Meyer 1860) *Ctenochasma elegans* (Wagner 1861*a*) *Germanodactylus cristatus* (Wiman 1925) *Ardeadactylus longicollum* (Meyer 1854) (lost holotype)*	*Diopecephalus kochi* (Wagner 1837)? "*Germanodactylus rhamphastinus*" (Wagner 1851) *Pterodactylus antiquus* (Sömmerring 1812) (Bennett 2013*a*) (BMMS 7)

1013 *Note that the lost holotype of "*Pterodactylus longicollum*" may represent another
1014 aurorazhdarchian

1015

1016

1017 **Fig. 1**. *Diopecephalus kochi* - photographs and interpretative drawings of the slabs (**a**) SMF R 404 and
1018 (**b**) BSP AS XIX 3. Abbreviations: a, articular; co, coracoid; cv, cervical vertebra; d, dentary; dv, dorsal
1019 vertebra; f, femur; fr, frontal; h, humerus; ip, ischiopubic plate; j, jugal; l, lacrimal; mt, metatarsal;
1020 mu, manual unguals; mx, maxilla; n, nasal; naof, nasoantorbital fenestra; o, orbit; p, parietal; pa,
1021 preacetabular process; pd, pedal digit; pd5, pedal digit 5; pmx, premaxilla; po, post-orbital; poa,
1022 postacetabular process; pp, prepubis; pt, pteroid; pu, pedal unguals; q, quadrate; qj, quadratojugal;
1023 ra, radius; ri, ribs; sc, scapula; sq, squamosal; sv, sacral vertebra; ti, tibia; u, ulna; wmc, wing
1024 metacarpal; wph1-4, wing phalanx 1-4.

1025

Fig. 2. "*Germanodactylus rhamphastinus*" - photographs and interpretative drawings of the slabs (**a**) BSP AS I 745 b and (**b**) BSP AS I 745 a. Abbreviations: pc, premaxillary crest; st, sternum.

Fig. 3. *Germanodactylus cristatus* - (**a**) a photograph of most of the skeleton on the slab and (**b**) a line drawing of the skull of the holotype BSP 1892 IV 1.

Fig. 4. Strict consensus cladogram of two trees found using a "new technology" search in TNT, analysing 104 taxa and 320 characters. The tree is plotted stratigraphically using Phytools and Strap, and the GER (Wills, 1999) is given on the top right. The four taxa with which this study is concerned are given in bold.

Fig. 5. Results of the CRI between the taxon reduced trees of Maisch et al. (2004), Lü et al. (2010), Wang et al. (2009), Andres et al. (2014) and the tree presented here. CRI values are reported on the upper right. Analyses with polytomies in their source trees are indicated by an asterisk. On the lower left there are pie charts indicating tree similarity (corresponding to diagonally symmetrical values); dark slices represent agreement; lighter slices represent disagreement.

Fig. 6. Robinson-Foulds (R-F) distances between the taxon reduced trees of Maisch et al. (2004), Lü et al. (2010), Wang et al. (2009), Andres et al. (2014) and the tree presented here. On the upper right the R-F distances from TNT are reported first, the colon is followed by the "proper" R-F distance calculated in CompPhy. On the lower left there are pie charts indicating tree similarity (corresponding to diagonally symmetrical values); dark slices represent agreement; lighter slices represent disagreement.

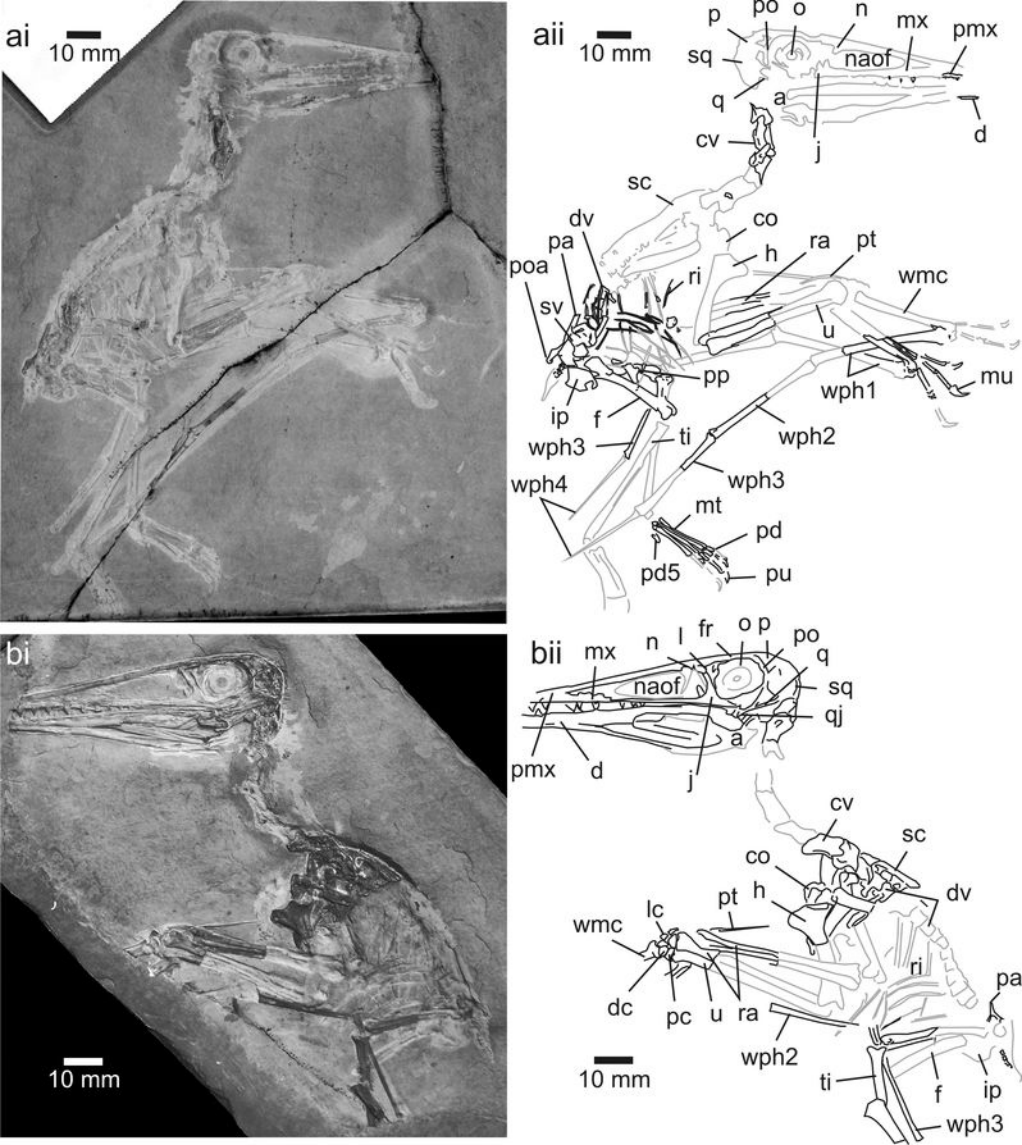
Fig. 7. SPR distances (Goloboff 2008) between the taxon reduced trees of Maisch et al. (2004), Lü et al. (2010), Wang et al. (2009), Andres et al. (2014) and the tree presented here. SPR distances are reported on the upper right. On the lower left are pie charts indicating the similarity (corresponding to diagonally symmetrical values); dark slices represent agreement; lighter slices represent disagreement.

Fig. 8. Tanglegrams of three cladograms that demonstrate a paraphyletic *Germanodactylus,* each recovered in a distinct cladistic analysis. (**a**) The cladogram of Maisch et al. (2004) and the cladogram presented here. It is possible that Maisch et al. (2004) coded a specimen of *Aerodactylus* previously

referred to "*P. kochi*". (**b**) The cladograms of Maisch et al. (2004) and Lü et al. (2010). Note that the Lü et al. (2010) cladogram is the most parsimonious tree from the matrix, not the suboptimal tree presented in the original publication. (**c**) The cladogram of Lü et al. (2010) in comparison to the cladogram presented in this paper. The analyses share 53 common taxa (**cii**), but have many unique branches. The trees are further pruned to only the taxa in common with Maisch et al. (2004) (**ci**), this subtree demonstrates complete agreement.

Fig. 9. Geometric morphometric dendrogram produced from a GPA of the prepubes figured. Note that a sister taxon relationship on the dendrogram means that those two species are closer to each other in prepubis morphospace than any other taxon, not that they are phyletically linked. Additionally, sister taxa in one phenetic group might be more or less morphometrically similar to each other than sister taxa in another clade. Despite the loss of information by extracting hierarchical clusters from a PCA this method is used to limit the subjectivity in interpreting the relationships observed in the PCA (see Supplementary Material). The phenetic group highlighted in dark grey consists of bi-lobed prepubes belonging to the basal-most taxa. The phenetic group highlighted in mid-grey is made up of a continuum of "transitional" taxa between the basal monofenestratans and *Germanodactylus*, typified by a robust diaphysis and broad distal expansion. The phenetic group highlighted in light grey contains the ctenochasmatoids and *Pterodactylus*, typified by a more gracile diaphysis and distal expansion.

Fig. 10. Cranial characters and prepubes of Franconia laminated limestone pterosaurs plotted onto a pruned tree. The tree is plotted against the "fine scale" dating criteria of the Franconia laminated limestones (Schweigert, 2007). The prepubes plotted on the branches demonstrate the apomorphic and plesiomorphic conditions of the respective taxa (Fig. 9) according to the topology recovered from the cladistics analysis. The red, light blue and dark blue colours filling the prepubes indicate the phenetic groups that were found in the geometric morphometric analysis. The skulls of each taxon have arrows pointing their ventral surfaces indicating the extent of the tooth row, and arrows pointing to their dorsal surfaces indicating the extent of the premaxilla. The dashed lines represent the uncertainty of the origin of the most recent common ancestor. The red line specifies the plesiomorphic condition of the prepubis and tooth row. The yellow line specifies the gracile prepubis morphology. The blue line specifies the gracile prepubis and a dentition restricted anteriorly. The black line specifies a deep prepubis distal expansion and an edentulous jaw tip.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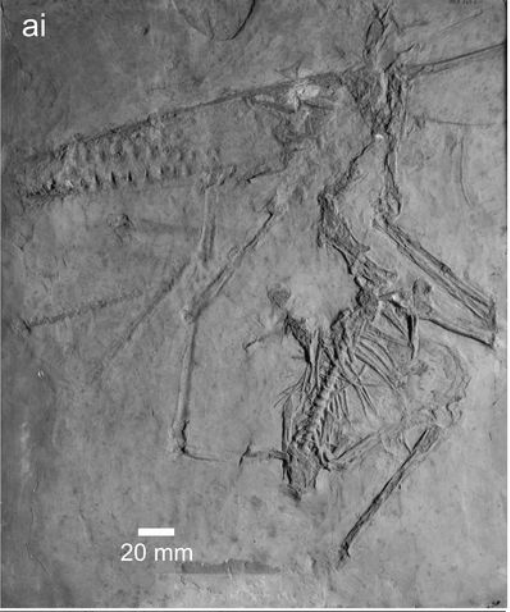
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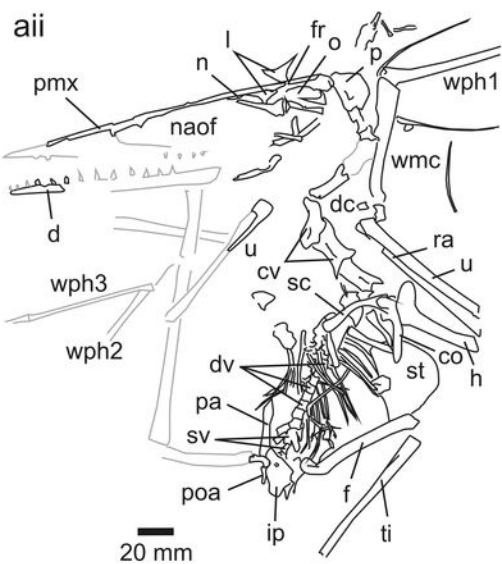
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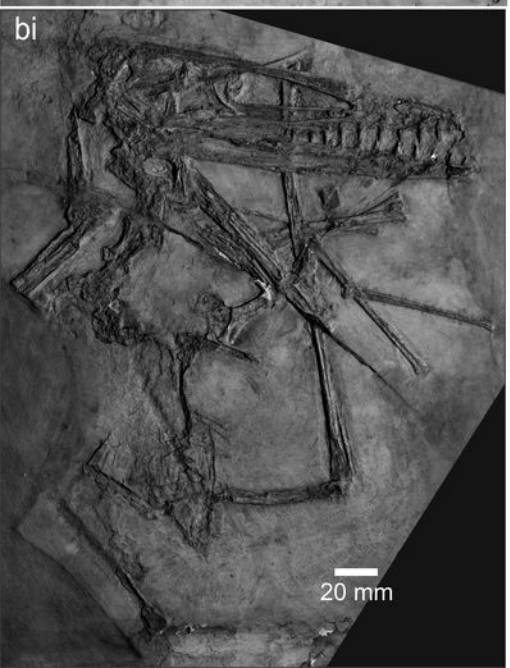
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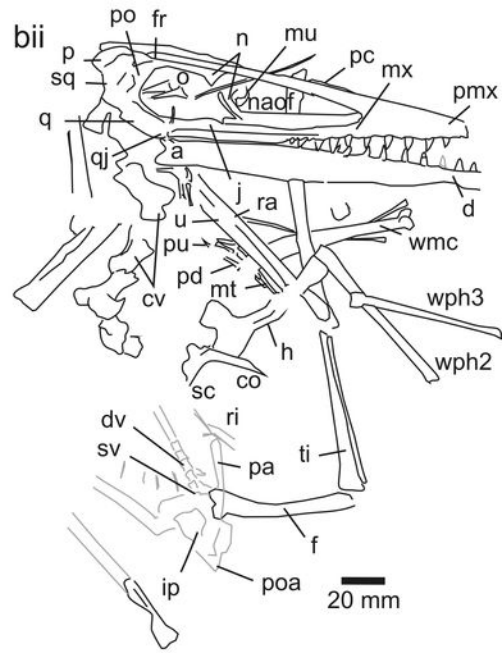
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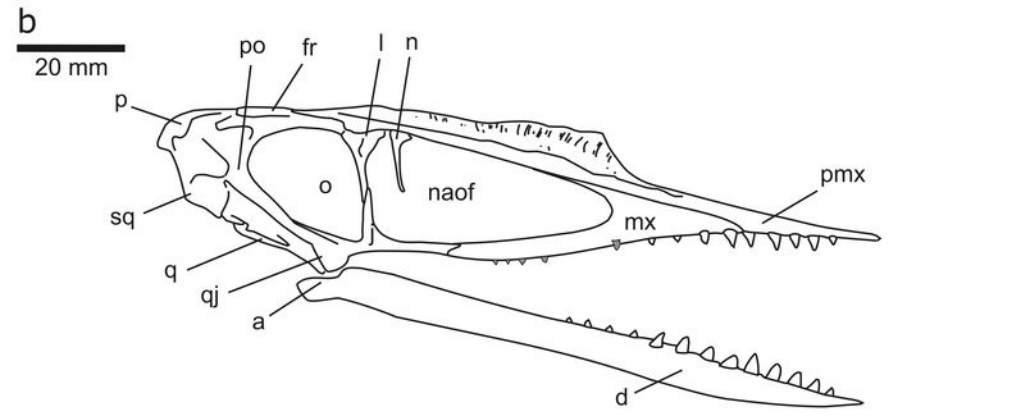
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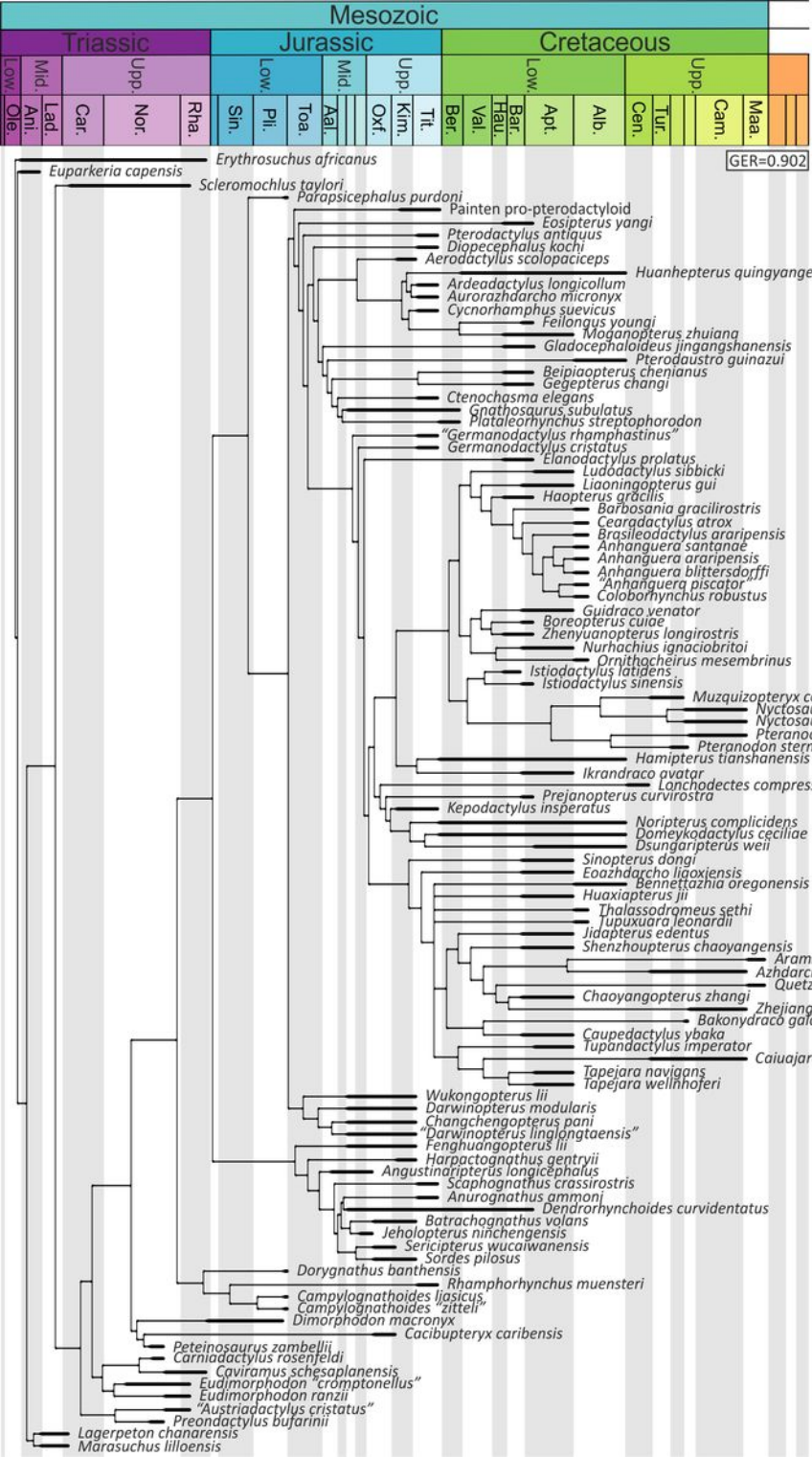
Mesozoic
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Tit.
Ber.
Val.
Hau.
Bar.
Apt.
Alb.
Cen.
Tur.
Cam.
Maa.
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Euparkeria capensis
Scleromochlus taylori
Parapsicephalus purdoni
Painten pro-pterodactyloid
Eosipterus yangi
Pterodactylus antiquus
Diopecephalus kochi
Aerodactylus scolopaciceps
Huanhepterus quingyangensis
Ardeadactylus longicollum
Aurorazhdarcho micronyx
Cycnorhamphus suevicus
Feilongus youngi
Moganopterus zhuiana
Gladocephaloideus jingangshanensis
Pterodaustro guinazui
Beipiaopterus chenianus
Gegepterus changi
Ctenochasma elegans
Gnathosaurus subulatus
Plataleorhynchus streptophorodon
"Germanodactylus rhamphastinus"
Germanodactylus cristatus
Elanodactylus prolatus
Ludodactylus sibbicki
Liaoningopterus gui
Haopterus gracilis
Barbosania gracilirostris
Cearadactylus atrox
Brasileodactylus araripensis
Anhanguera santanae
Anhanguera araripensis
Anhanguera blittersdorffi
"Anhanguera piscator"
Coloborhynchus robustus
Guidraco venator
Boreopterus cuiae
Zhenyuanopterus longirostris
Nurhachius ignaciobritoi
Ornithocheirus mesembrinus
Istiodactylus latidens
Istiodactylus sinensis
Muzquizopteryx coahuilensis
Nyctosaurus bonneri
Nyctosaurus gracilis
Pteranodon longiceps
Pteranodon sternbergi
Hamipterus tianshanensis
Ikrandraco avatar
Lanchodectes compressirostris
Prejanopterus curvirostra
Kepodactylus insperatus
Noripterus complicidens
Domeykodactylus ceciliae
Dsungaripterus weii
Sinopterus dongi
Eoazhdarcho liaoxiensis
Bennettazhia oregonensis
Huaxiapterus jii
Thalassodromeus sethi
Tupuxuara leonardii
Jidapterus edentus
Shenzhoupterus chaoyangensis
Arambourgiania philadelphiae
Azhdarcho lancicollis
Quetzalcoatlus sp.
Chaoyangopterus zhangi
Zhejiangopterus linhaiensis
Bakonydraco galaczi
Caupedactylus ybaka
Tupandactylus imperator
Caiuajara dobruskii
Tapejara navigans
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Wukongopterus lii
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Changchengopterus pani
"Darwinopterus linglongtaensis"
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Harpactognathus gentryii
Angustinaripterus longicephalus
Scaphognathus crassirostris
Anurognathus ammoni
Dendrorhynchoides curvidentatus
Batrachognathus volans
Jeholopterus ninchengensis
Sericipterus wucaiwanensis
Sordes pilosus
Dorygnathus banthensis
Rhamphorhynchus muensteri
Campylognathoides liasicus
Campylognathoides "zitteli"
Dimorphodon macronyx
Cacibupteryx caribensis
Peteinosaurus zambellii
Carniadactylus rosenfeldi
Caviramus schesaplanensis
Eudimorphodon "cromptonellus"
Eudimorphodon ranzii
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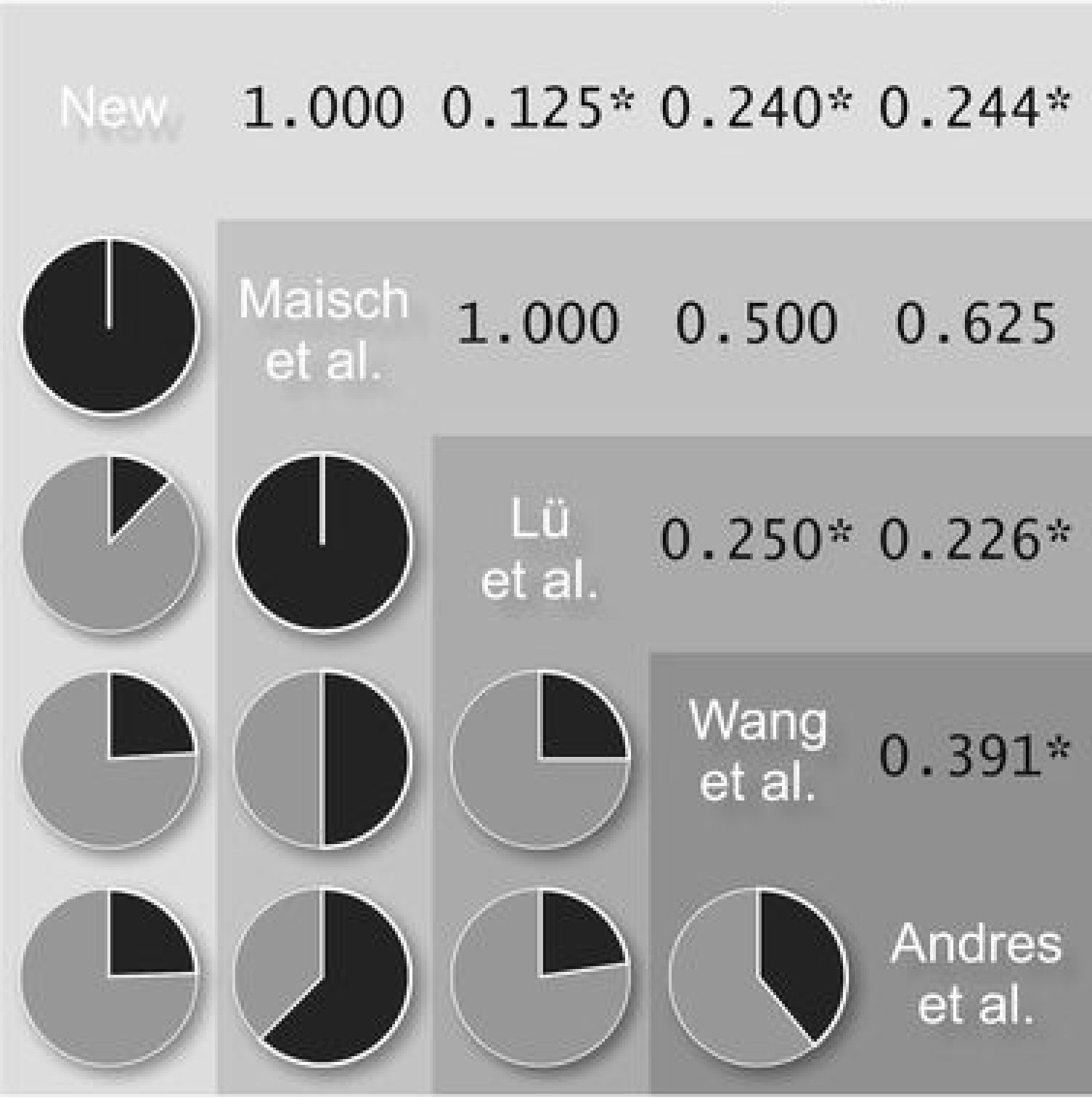
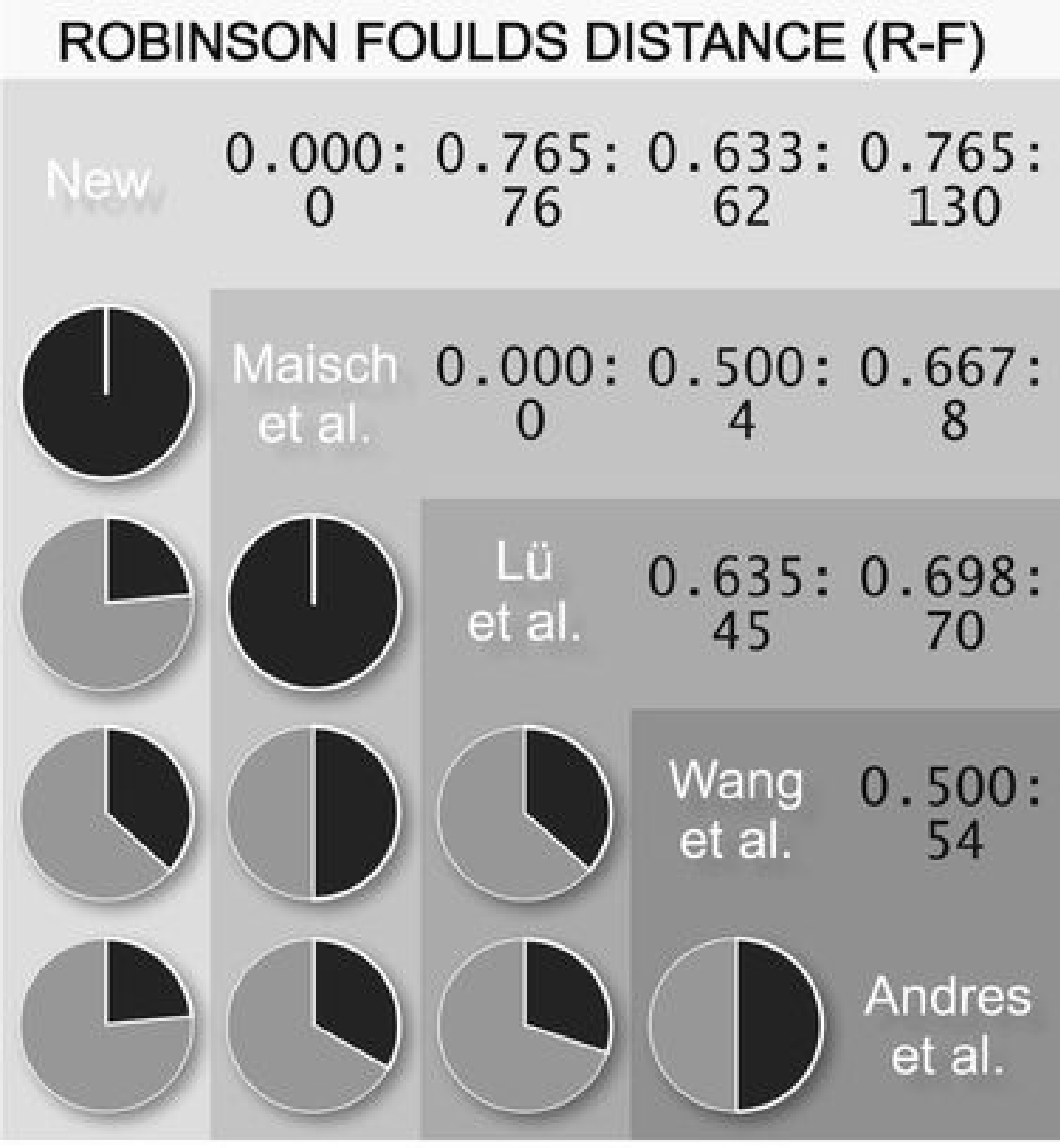
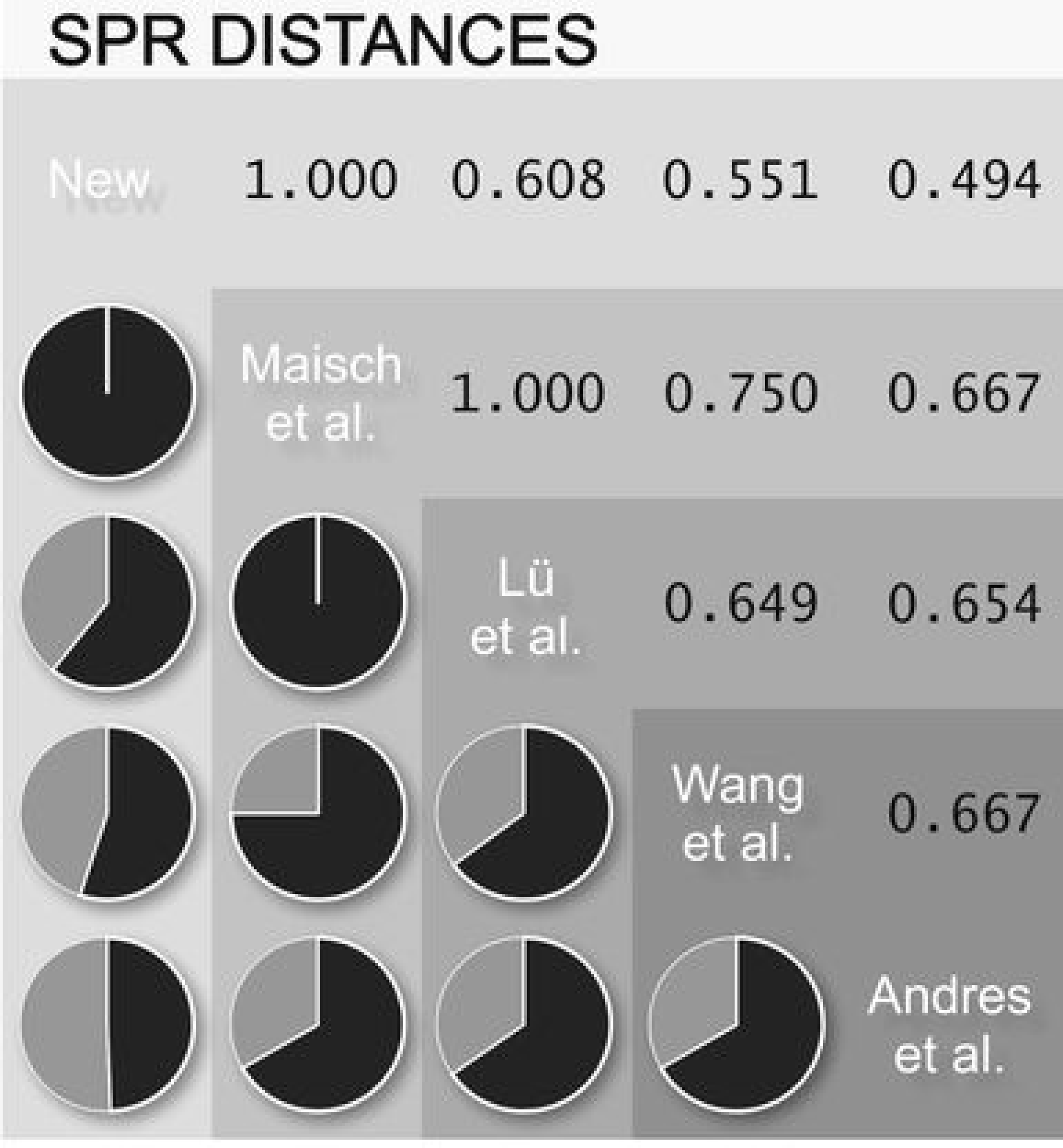
CLADE RETENTION INDEX (CRI)

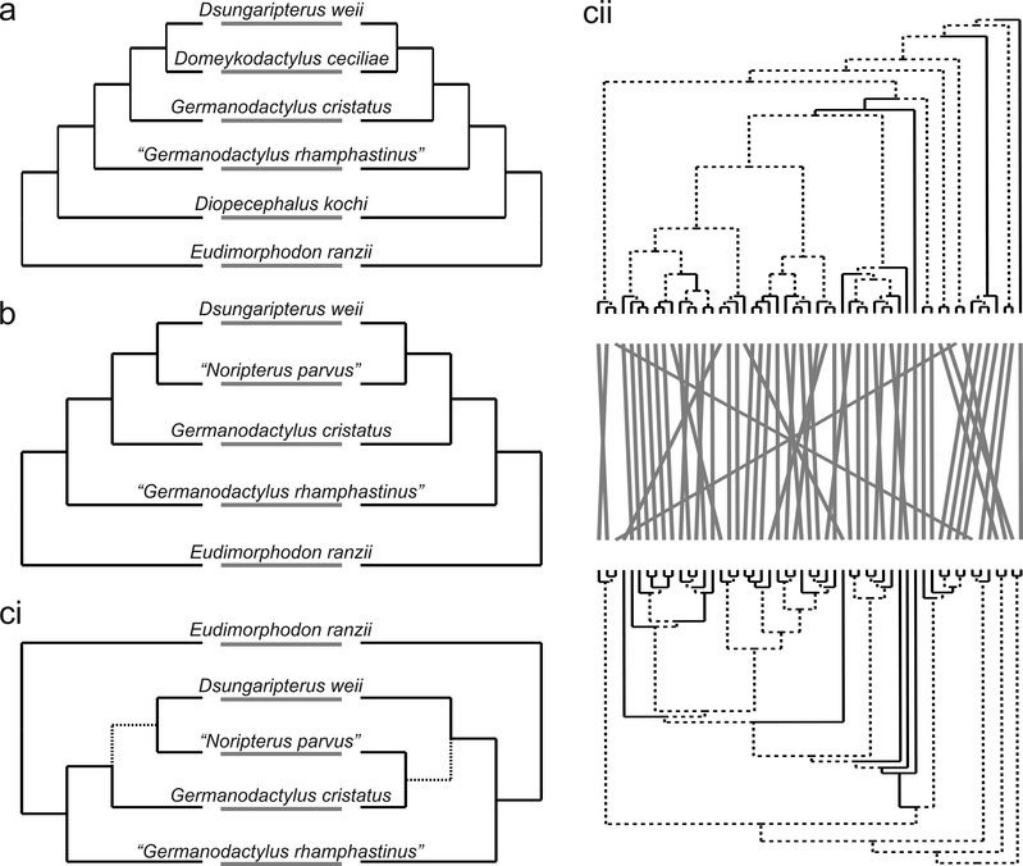


ROBINSON FOULDS DISTANCE (R-F)



SPR DISTANCES




a
Dsungaripterus weii
Domeykodactylus ceciliae
Germanodactylus cristatus
"Germanodactylus rhamphastinus"
Diopecephalus kochi
Eudimorphodon ranzii
b
Dsungaripterus weii
"Noripterus parvus"
Germanodactylus cristatus
"Germanodactylus rhamphastinus"
Eudimorphodon ranzii
ci
Eudimorphodon ranzii
Dsungaripterus weii
"Noripterus parvus"
Germanodactylus cristatus
"Germanodactylus rhamphastinus"
cii

Dorygnathus banthensis
Cycnorhamphus suevicus
Pterodactylus antiquus
Scaphognathus crassirostris
Aerodactylus scolopaciceps
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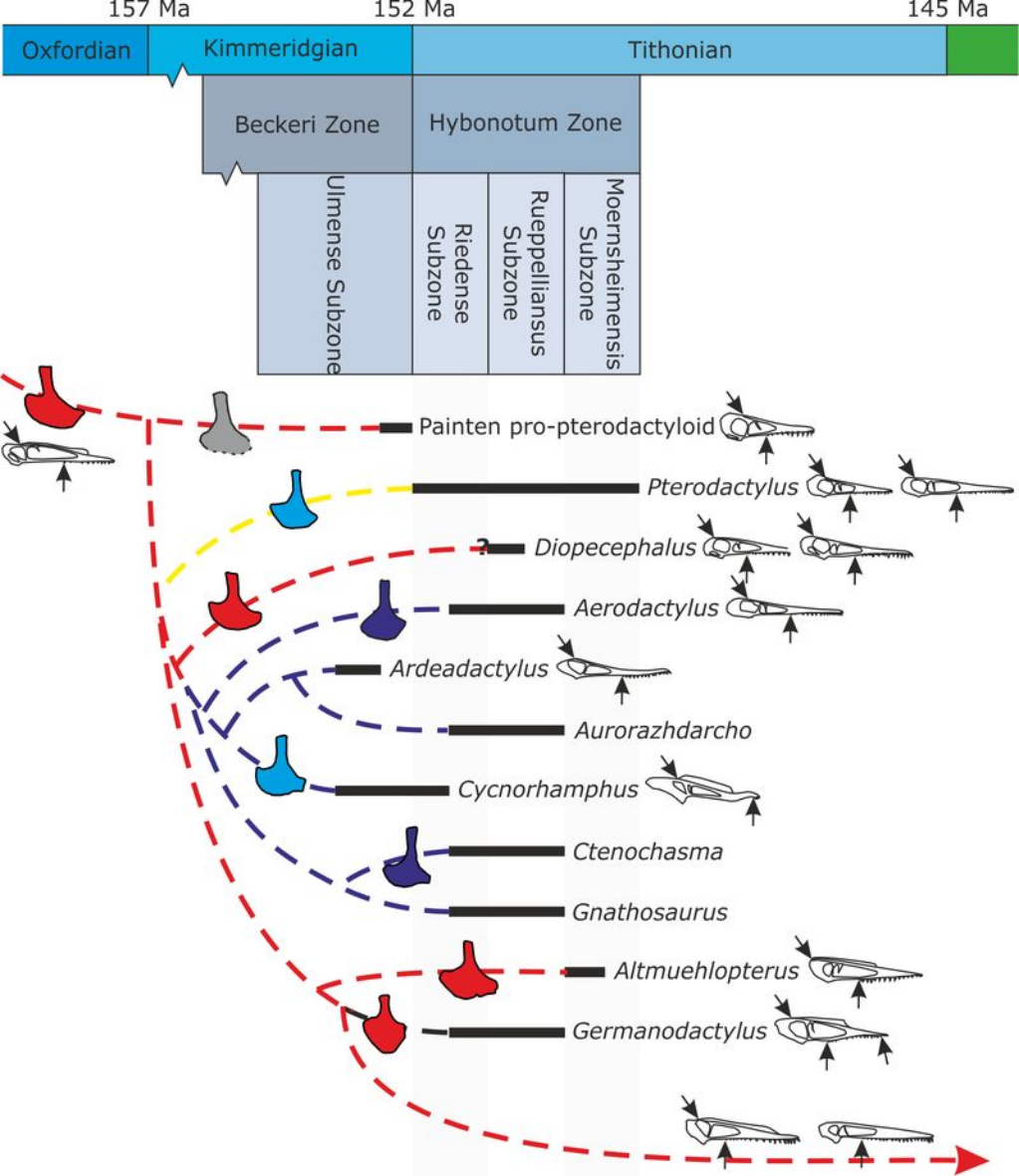
"Darwinopterus robustidens"
Diopecephalus kochi


157 Ma
152 Ma
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Oxfordian
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Beckeri Zone
Hybonotum Zone
Ulmense Subzone
Riedense Subzone
Rueppelliansus Subzone
Moernsheimensis Subzone
Painten pro-pterodactyloid
Pterodactylus
?
Diopecephalus
Aerodactylus
Ardeadactylus
Aurorazhdarcho
Cycnorhamphus
Ctenochasma
Gnathosaurus
Altmuehlopterus
Germanodactylus