Unique near isometric ontogeny in the pterosaur *Rhamphorhynchus* suggests hatchlings could fly

DAVID W. E. HONE*, JOHN M. RATCLIFFE*, DANIEL K. RISKIN, JOHN W. HERMANSON AND ROBERT R. REISZ

LETHAIA

Rhamphorhynchus muensteri is one of the best-known flying reptiles, represented by >130 well-preserved fossil specimens, from hatchlings to full adults. The life history of this pterosaur remains controversial as to when in ontogeny they took flight. Here, we assess the growth of these animals based on the lengths of numerous key elements. We show that changes in the skeletal anatomy of this reptile across its post-hatch size range reveal that *R. muensteri* exhibited overall near isometric growth in the wings, with slightly negative allometry in the humerus, radius and stronger negative allometry in the fourth metacarpal compared to body length, and slightly positive allometry in the second and third phalanges compared to body length. This pattern is near unique among flying vertebrates and suggests *R. muensteri* flew soon after hatching. In bats and birds, offspring do not typically fly until nearly adult sized. Conversely, near isometric growth in *Rhamphorhynchus* suggests it was a precocial flier and that individuals may have inhabited several sequential foraging niches over their lifespan, as some terrestrial and aquatic vertebrates do today. □ *Bats, birds, ontogeny, precocial flight, pterosaurs.*

David W. E. Hone✉ *[d.hone@qmul.ac.uk], School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, UK; John M. Ratcliffe*✉ *[j.ratcliffe@utoronto.ca], and Daniel K. Riskin [dan.riskin@utoronto.ca], Robert R. Reisz [robert.reisz@utoronto.ca], Department of Biology, University of Toronto Mississauga, Mississauga, Ontario, Canada; John W. Hermanson [jwh6@cornell.edu], Department of Biomedical Sciences, Cornell University, Ithaca, NY, USA;* manuscript received on 12/08/2019; manuscript accepted on 20/04/2020.

Pterosaurs were flying reptiles that persisted from the late Triassic to the end Cretaceous. They spanned a wide range of body sizes as adults from <1 m to over 10 m in wingspan (Wellnhofer 1975; Bennett 1995; Witton 2013), but due to physical constraints on egg size from the soft shell and size of the pelvic opening, all began life as small hatchlings (Witton 2013). One unanswered question in pterosaur biology is when during ontogeny they gained the ability to fly. In birds and bats, the transition from non-volant juveniles to volant adults is reflected by changes in the relative proportions of body segments (Norberg 1990; Starck & Ricklefs 1998; Cooper *et al.* 2012). Here, we compare morphological data from the pterosaur *Rhamphorhynchus muensteri* (ESM1, ESM2) to new data from predatory bats and existing data on birds. We test whether pterosaurs show a similar pattern of rapid forelimb growth during post-hatching/ontogeny to that of bats and birds, and thus infer when in ontogeny *R. muensteri* would have become volant.

Rhamphorhynchus muensteri was a piscivorous pterosaur that lived ~160–140 mya and is especially

well represented in the fossil record (Wellnhofer 1975; Bennett, 1995). All *Rhamphorhynchus* specimens from Bavaria are now considered a single species (Bennett 1995). Four lines of evidence suggest that the smallest *R. muensteri* specimens were very young animals and potentially hatchlings. Histology reveals incomplete ossification of long bones in the smallest specimens tested (Prondvai *et al.* 2012), a disproportionate number of known specimens are small, consistent with high juvenile mortality (Bennett 1995; Hone & Henderson 2014), late-stage embryos of pterosaurs had well-developed, ossified wings (Wang & Zhou 2004; Codorniú *et al.* 2018), and finally while few fossilized pterosaur embryos are known, the ratio by which adults are larger than embryos (Lü *et al.* 2011; Wang *et al.* 2017) is similar to the size ratio between the largest *R. muensteri* specimens and the smallest.

What is not known is whether the smallest individuals of *R. muensteri* flew, and if not, when flight would have become possible for a growing pterosaur. Bats (Powers *et al.* 1991; Cooper *et al.* 2012) and most birds (Starck & Ricklefs 1998) begin life as non-volant animals with relatively small wings. Over ontogeny, wing area increases more quickly than

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*Joint lead authors.

predicted under isometry (i.e. show positive allometric growth), until wings become large enough for flight. In altricial birds (e.g. *Larus* (Carrier & Leon 1990) and *Coturnix* (Ren *et al.* 2016)), juveniles have disproportionally small wing bones compared to other elements, and the legs are much larger and better developed. Wing area (including feathers) grows dramatically very late during development (implying strong positive allometry). In contrast, precocial birds show a pattern of skeletal growth in the wings (which may be less closely tied to wing shape than in pterosaurs) close to isometry (Starck & Sutter 2000). If *R. muensteri* exhibited a similar pattern of positive allometry in wing area versus span, we would interpret this as evidence of late-onset volancy. If, however, wings exhibited isometric growth, we would infer they were sufficient for flight throughout ontogeny and that *R. muensteri* flew soon after hatching.

We tested for isometric versus allometric growth across 135 specimens of *R. muensteri* using bone length and composite measures (e.g. total wing length and total leg length) relative to: (1) total body length, from rostrum tip to the end of the tail; (2) skull length; and (3) humerus length. We estimated wingspan and body mass (Witton 2008) to estimate each individual animal's flight speed and manoeuvrability (Norberg 1990). We thus compare our pterosaur results to those from newborn through to adult predatory vespertilionid and molossid bats (Hermanson & Wilkins 2008) and to adult specimens of predatory molossid species spanning an order of magnitude in size (Norberg & Rayner 1987).

Methods

Taxon sampling

We follow Bennett (1995) and consider all specimens of *Rhamphorhynchus* currently known from the Solnhofen to belong to a single species – *R. muensteri*. The data for our analyses were primarily derived from those generated by Wellnhofer (1975). These comprised 108 specimens, including some now lost or in private hands. New specimens have continued to be excavated or rediscovered in collections, and we collected additional data with calliper measurements from specimens in 16 museums in six countries and, when necessary, from scaled photographs and the literature. In total, we added 27 specimens, making this the largest data set of complete or near-complete measurements on a single pterosaur species (ESM1). We estimated wingspan, mass and wing loading for specimens of sufficient material ($N = 78$) based on (Witton 2008).

Determining the exact ontogenetic stage of the smallest of *Rhamphorhynchus* specimens is difficult as no eggs or embryos are known. The smallest specimens are certainly very young animals as indicated by the lack of fusion of numerous major elements (e.g. carpus and pelvis) seen in adults and a distinct grainy bone texture only usually present in the youngest individuals (Bennett 1995). Comparisons to the very limited number of well-described pterosaur embryos and egg–adult associations do allow us to infer that the smallest *Rhamphorhynchus* may be hatchlings or at least very close to this size. *Pterodaustro* has a confirmed embryo with a humerus (Codorniú *et al.* 2018) of 18.6 mm compared to an adult one of length 112 mm (Codorniú *et al.* 2013) for a ratio of 6:1. *Hamipterus* (Wang *et al.* 2017) has hatchlings with humeral lengths of 18.8 mm compared to adults with humeri from 132 to 170 mm, (~7:1 to 9:1). In a Chinese Wukongopterid (Lü *et al.* 2011), with an adult–egg association, the adult humerus is ~2.6 times the length of the egg. In the near-term embryo tentatively referred to as *Haopterus* (Wang & Zhou 2004), the humerus is 23 mm long inside an egg with greatest width of 57 mm. Assuming similar proportions across pterosaurs, this indicates a humerus ~6.4 times longer in adults than hatchlings. The largest *Rhamphorhynchus* specimens have a humeral length ~5.8 times that of the smallest (ESM1), suggesting the latter were hatchling size or at least very young.

Bat data assembly

As mammals, bats are very phylogenetically distinct from pterosaurs and would likely grow and mature rather differently. However, bats also provide a very useful comparison to pterosaurs because members of both groups are quadrupedal walkers and launchers (Habib 2008), which fly with membranous wings that span from the shoulders to the outstretched forelimbs to the ankles, have leading edges supported by bony spars (Witton 2013) and occupy similar morphospace (McGowan & Dyke 2007). We used ontogenetic data for the slow-hawking vespertilionid, *Myotis austroriparius*, and the fast-hawking molossid, *Tadarida brasiliensis*. Specimens were collected, fixed and preserved as described in Hermanson & Wilkins (2008). We confirmed measurements from Hermanson & Wilkins (2008) and took additional measures of the metacarpal and first and second phalanges of the third finger (the digit that extends to the wingtip and is thus representative of span). To compare wingspan and wing loading estimates from *R. muensteri* specimens across their size range to those of fast-hawking open-space adult bats of

different size but similar morphology, we used 16 species, and used wing loading and wingspan data for free-tailed bats (Molossidae) available in Norberg & Rayner (1987).

Tests for ontogenetic isometry and allometry

We performed linear regressions of log-transformed length measurements of elements, using two-tailed *t*-tests, and determined whether slopes were significantly >1.0 (positive allometry), significantly <1.0 (negative allometry), or not significantly different from 1.0 (isometry) ($\alpha = 0.05$; 95% confidence intervals).

Results and discussion

Overall, *Rhamphorhynchus muensteri* specimens of all sizes (estimated wingspan: 0.29–1.72 m) had almost identical proportions (Figs 1, 2; ESM4) and total body length (rostrum tip to tip of tail) and wing length were isometrically related or nearly so (Figs 1–3). Linear relationships between any two bony elements were consistently strong and significant ((Bennett 1995); Figs 1, 2; ESM4), and different to those in both *Myotis austroriparius* and *Tadarida brasiliensis* (Figs 1, 2; ESM4). In the bats, more distal elements of the wing started out relatively short but grew quickly as they matured (Fig. 1; ESM4). At birth, the bats had disproportionately long legs relative to their wings, a situation that reversed over time (ESM4). Conversely, in *R. muensteri* the relationship between the lengths of any two bones or composite wing elements was either isometric or much closer to isometry than observed in bats (Figs 1–3; ESM4) or birds (Starck & Ricklefs 1998). Bones measured and reported include appendicular bones considered significant in understanding flight properties in bats (Norberg & Rayner 1987). While the skull is disproportionately large in newborn and juvenile *M. austroriparius* (Fig. 1; see ESM4), relative skull size showed the opposite trend in *R. muensteri*, increasing slightly with body size (ESM3, ESM4). For the pterosaur, there are only two markedly negative allometric measures. First, smaller animals had relatively larger orbits than larger ones (Fig. 1), which is the typical pattern for developing vertebrates. The second is the wing metacarpal (the shortest bone in the wing) also shows negative allometry (Fig. 2), which is also often seen in tetrapods (where newborns have proportionately large feet) and thus may represent a primitive condition, despite the derived isometry of other elements.

Our results suggest that even the smallest *Rhamphorhynchus* had adult skeletal proportions and thus wings sufficient for flight. This is corroborated by comparative osteological data (Figs 1, 2; ESM4). In non-flying newborn and juvenile bats, leg bones exhibit greater ossification than wing bones (Hermanson & Wilkins 2008) corroborating observations that juvenile bats first climb and only later fly (Norberg & Rayner 1987). Similarly, in gulls, hindlimb bones ossify earlier than do forelimb bones (Starck & Ricklefs 1998). In *Rhamphorhynchus*, there is a similar degree of ossification in the wing and leg bones in the smallest individuals and is comparable to that of wing bones in young, flight-capable bats (Hermanson & Wilkins 2008; Cooper *et al*. 2012). We interpret this lack of forelimb and hindlimb disparity (Fig. 3, ESM3, ESM4) in pterosaurs as evidence that terrestrial locomotion and flight were acquired early and simultaneously during ontogenetic development.

Further, for adult bats, terrestrial locomotion is more energetically expensive per unit distance travelled than flight (Voigt *et al*. 2012). If this was also true for *Rhamphornyhchus*, it seems unlikely that proficient terrestrial locomotion would have preceded flight. Depositional evidence also supports the idea that the smallest individuals could fly as specimens come from localities sometimes far from ancient shorelines (Bennett 1995), and a lack of decay and disarticulation in some of these would indicate that they had not been floating in the water column for extended periods prior to sinking and burial (Beardmore *et al.,* 2017).

Our statistical analyses demonstrate isometric or near-isometric skeletal growth for multiple metrics in *R. muensteri* (Figs 1, 2; ESM4), and a pattern fundamentally different from the ontogenetic trajectories of both birds (Starck & Ricklefs 1998) and bats ((Cooper *et al.* 2012); Figs 1, 2; ESM4). However, we contend that constancy of bauplan over ontogeny would not translate to constancy of realized foraging niche. All other factors being equal, juveniles would have lower wing loading than that of adults (ESM3) as mass increases faster than area as size increases under isometric growth. Isometric growth of most wing and hind limb element lengths would mean *Rhamphorhynchus* adults would have had similar wing shape to juveniles, but greater mass, giving them giving them a similar wing efficiency but at a higher wing loading. A pterosaur with higher wing loading while maintaining wing shape would equate to increased high speed soaring performance by increasing glide speed without negatively impacting glide ratio (Pennycuick, 2008). High wing loading also improves wind penetration and overall performance in high wind conditions, and living gust soaring specialists possess high wing loadings (Pennycuick, 2002). However, these differences may have been at least partially offset by lower levels of
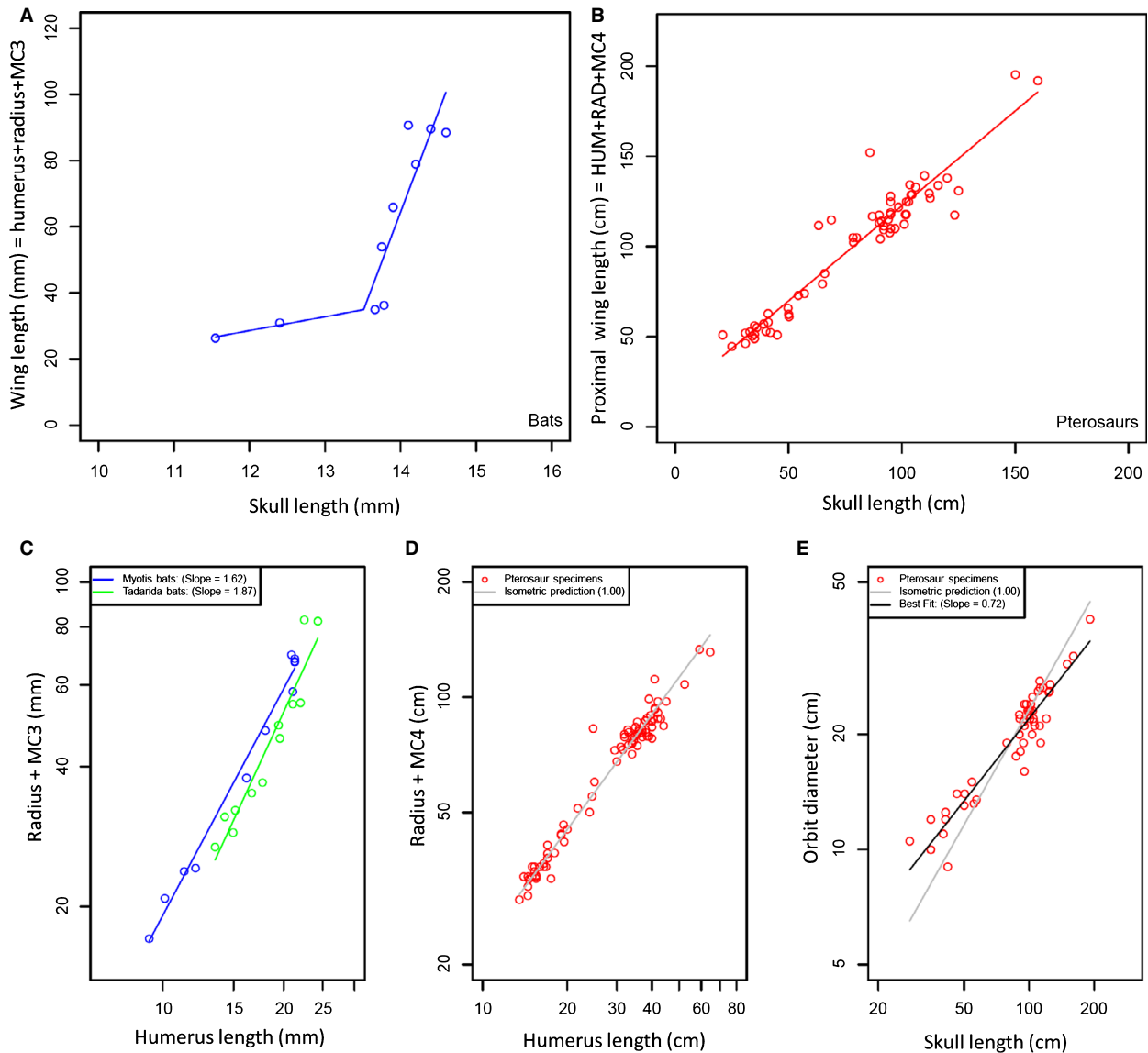
Fig. 1. Log–log plots of skeletal structures in bats and pterosaurs. The ontogenetic relationship between proximal wing (humerus, ulna and metacarpal) and skull is non-linear in *Myotis* (A) but linear for *Rhamphorhynchus* (B). In bats, wing growth is initially slow then increases to meet flight requirements (3,4,14). The lack of change for *Rhamphorhynchus* suggests no such transition. The relationship between proximal and distal elements of the proximal wing is positively allometric in bats (C) but isometric in *Rhamphorhynchus* (D). Orbit diameter alone deviated markedly from isometry in *Rhamphorhynchus*, exhibiting negatively allometric growth versus skull length (E).

ossification in juveniles and/or higher levels of pneumaticity in adults, as seen in other ornithodires (Schepelmann 1990; Wedel, 2003; Benson *et al.* 2012). Even so, we would expect juvenile and adult *Rhamphorhynchus* to have had different flight performance. We infer that juveniles would have been capable of lower minimum flight speeds and greater manoeuvrability than adults ((Riskin *et al.* 2012); Fig. 2), impacting foraging behaviour and diet selection.

While wing aspect ratio would remain stable due to isometric two-dimensional growth (Witton 2008),

differently sized *Rhamphorhynchus* would have occupied different foraging niches. This is true of many extant vertebrates (Dodson 1975; Feder & Burggren 1992; Humphries & Walker 2013), and this was also likely true of other pterosaurs (Bennett 2017). Minimum and maximum viable prey size alone will be determined by the size of the predator.

Isometric ontogeny is known from some amphibians, fishes and terrestrial reptiles, but not from extant flying vertebrates (Dodson 1975; Feder & Burggren 1992; Humphries & Walker 2013). Although hatchling flight is known from a few birds
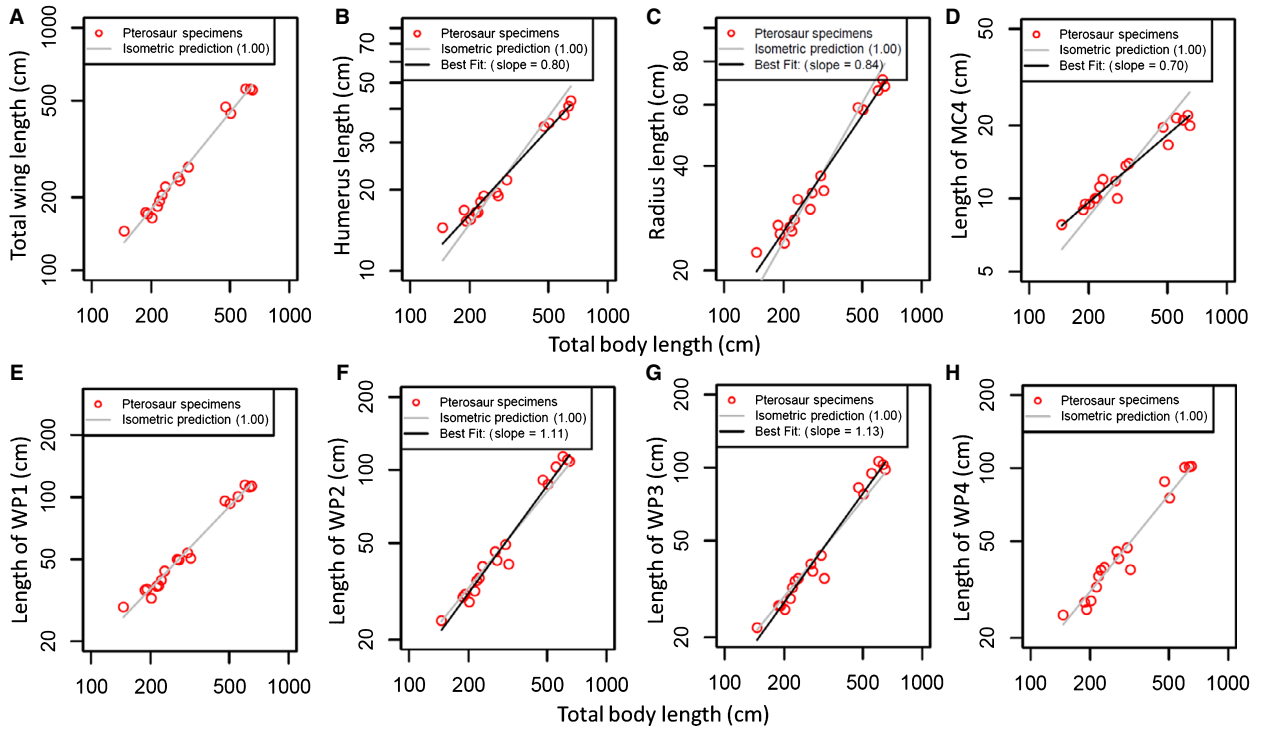
Fig. 2. Log–log plots of wing and wing elements versus body length. Although wing length is isometric with body length (sum of skull and vertebral column, A), more proximal wing elements grew with slight negative allometry (B, D), the first and fourth phalanges isometrically (E, H), and the two middle phalanges with slight positive allometry (F, G). As a result, in smaller individuals the more proximal elements would have been relatively longer and relatively heavier than in larger individuals, and thus, juveniles may have experienced lower inertial costs of flapping flight (Norberg & Rayner 1987).
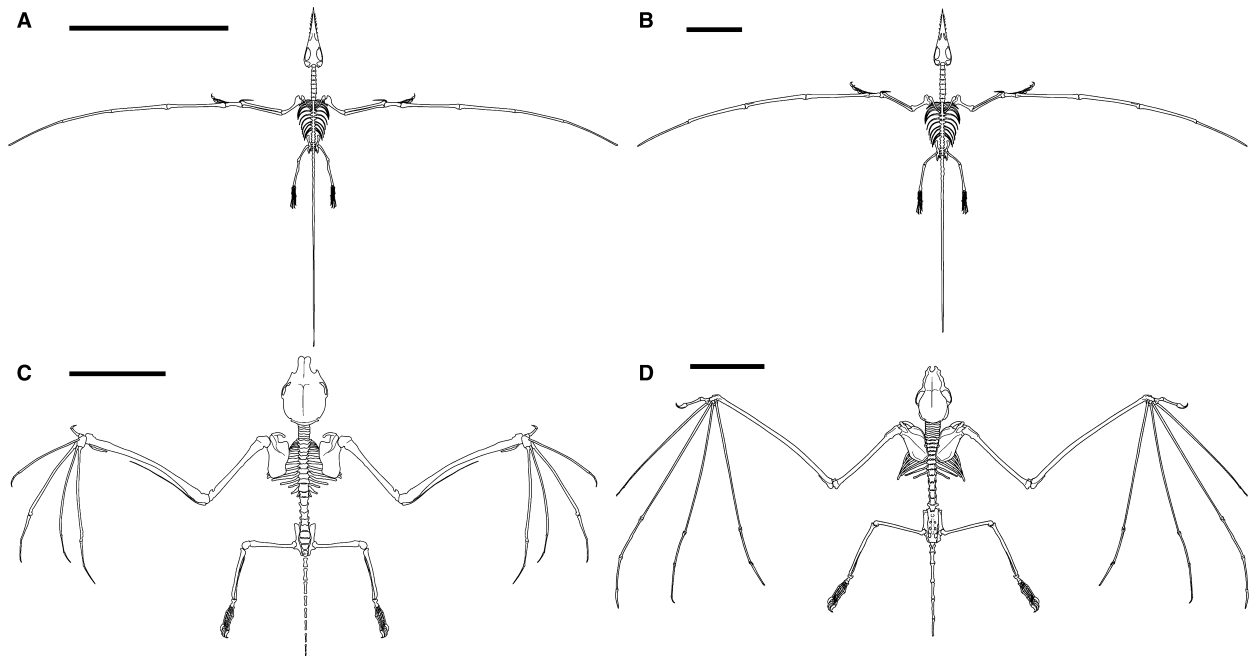

Fig. 3. Illustrations of pterosaur isometry and bat allometry. Scientific illustration of two specimens of *Rhamphorhynchus muensteri*. A, small, BSP 1938 I 503. B, large, SMF R 4128 – both scale bars 100 mm). C, adult, UF18885 and D, juvenile KTW774 – both scale bars 20 mm and *Myotis austroriparius*. The pterosaurs are near identical in proportions to one another while the juvenile bat has a disproportionately large head and small wings compared to the adult despite being much closer in size to each other than the two pterosaurs. Images by Rebecca Gelernter and used with permission.

(Starck & Ricklefs 1998), *R. muensteri* – and potentially other pterosaurs – were apparently unique among vertebrates, extant and extinct, in that they both flew soon after hatching and exhibited near isometric growth from hatchling through to full adult across a wide range of functional traits.

It has been proposed that the smallest *Rhamphorynchus* were non-volant based on the changes in growth rates and the nature of the bones of the youngest animals (Prondvai *et al.* 2012). However, this is challenged by their near isometry, the similarities in forelimb and hindlimb ossification, and the presence of so many small animals found out to sea. Work on the development of embryonic pterosaurs from China also suggests they were capable of aerial locomotion very soon after hatching (Unwin & Deeming, 2019) and supports this contention here for *Rhamphorhynchus*. This is not necessarily universal for pterosaurs, however. Wang *et al.* (2017) noted that in embryos of the pterodactyloid *Hamipterus*, although there was greater ossification of the limbs and vertebrae than the head, including of the shafts of longbones, there was limited ossification of some other parts of the skeleton that may have related to flight. They hypothesize in this case that hatchlings may have been able to walk before they could fly, though still imply relatively early flight for these animals.

One aspect that requires further attention is the role parental care might have played for vertebrates able to fly at such a young age. It has been suggested that young pterosaurs if precocial must have lacked parental care (Prondvai *et al.* 2012) but this is not necessarily so. Animals may be highly precocial in terms of their ability to move and follow their parents while also reliant on them for protection and especially food (e.g. many artiodactyls and equids can run within hours of birth but rely on sucking from their mothers for months – Grubb 1981). Pterosaurs, like almost all other archosaurs, probably provided parental care (Witton 2013), and precocial flight need not preclude this possibility. Bats typically attain flight in 4–5 weeks, and for many species, this point also marks juvenile dispersal; however, in others, months of mother–pup hunting still lie ahead (Geipel *et al.* 2013). Thus, while *Rhamphorhynchus* apparently flew at a young age, such volant offspring may have plausibly received parental care, including provisioned food, as they became independent foragers.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. ESM 1: Dataset.

Appendix S2. ESM 2: Photographs of two specimens of *Rhamphorhynchus* of different sizes. ESM 3: Wing loading versus wingspan for *Rhamphorhynchus* (red) and various bats (see Methods) from the Molossidae (purple). ESM 4: Regression analyses, excluding those presented in figures 1 and 2 from the main document.