

**Pre-natal development in pterosaurs and its implications for their
post-natal locomotory ability**

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21 **Abstract**

22 Recent fossil finds in China and Argentina have provided startling new insights
23 into the reproductive biology and embryology of pterosaurs, Mesozoic flying
24 reptiles. Nineteen embryos distributed among four species representing three
25 distinct clades have been described and all are assumed to be at, or near, term.
26 We show here how the application of four contrasting quantitative approaches
27 allows a more precise identification of the developmental status of embryos
28 revealing, for the first time, the presence of middle and late developmental stages
29 as well as individuals that were at term. We also identify a predicted relationship
30 between egg size and shape and the developmental stage of embryos contained
31 within. Small elongate eggs contain embryos at an earlier stage of development
32 than larger rounder eggs which contain more fully developed embryos. Changes
33 in egg shape and size likely reflect the uptake of water, consistent with a pliable
34 shell reported for several pterosaurs. Early ossification of the vertebral column,
35 limb girdles and principal limb bones involved some heterochronic shifts in
36 appearance times, most notably of manus digit IV, and facilitated full development
37 of the flight apparatus prior to hatching. This is consistent with a super-precocial
38 flight ability and, while not excluding the possibility of parental care in pterosaurs,
39 suggests that it was not an absolute requirement.

40

41 **1. Introduction**

42 Pterosaurs, Mesozoic flying reptiles, have been known since the late 1700s, but
43 fossil evidence for their prenatal development only dates back to 2004. To date
44 embryos and/or eggs have been reported in four species of pterosaur
45 representing three distinct Late Jurassic-Early Cretaceous clades ([1–8];

electronic supplementary material, table S1) These finds have provided critical insights into the reproductive biology of pterosaurs which, as in basal amniotes, seems to have involved paired ovaries, relatively small, ovoidal, pliable-shelled eggs and incubation via burial in substrate rather than bodily contact [4, 5, 7]. It has generally been assumed that hatchlings were altricial and required extended parental care before achieving flight, as in extant species of bats and many birds [8–13]. By contrast, we have argued that pterosaurs were capable of flight soon after hatching and likely did not require parental care [4, 14, 15] implying a profoundly different life history mode for pterosaurs, compared to that of extant fliers. Correct identification of the developmental stage of embryos is critical to resolving this debate [16] but, so far, has relied on informal, ad-hoc assertions that lack rigour [17]. A new approach, that combines four complementary quantitative methods allows refinement, and in some critical cases re-identification, of the stage of development reached by pterosaur eggs and embryos. This analysis reveals a more extensive record of pterosaur prenatal development that includes size and shape changes to eggs that reflect uptake of water during incubation and the early ontogenetic appearance of unique skeletal features, such as elongate fore and hind limbs that foreshadow fully developed flight capable hatchlings.

2. Materials and methods

(a) Egg shape and size

Changes in egg shape and size were investigated by plotting predicted egg mass against egg elongation ratio (EER), which is length of egg along major axis/length of egg along minor axis, for 37 eggs of *Hamipterus tianshanensis* [6, 8], including

three with embryos, and two eggs each containing a complete, near term embryo of an ornithocheirid from the Lower Cretaceous Yixian Formation of China [1, 2] (electronic supplementary material, table S2). We included data for a relatively small egg (IVPP V18938) also from the Hami locality [6], that likely represents a species of pterosaur distinct from that of *Hamipterus tianshanensis* (figure 1, electronic supplementary material, table S2) See electronic supplementary material for further discussion of the identity of this fossil.

(b) Predicting egg mass

Egg mass was predicted using the same data set (electronic supplementary material, table S2) as that used to calculate the egg elongation ratio. Egg mass (EM) was predicted from egg length (L) and egg breadth (B) using the methodology of Hoyt [18] where: $EM = 0.56 L^2 B$. The constant K (0.56) is derived from symmetrical crocodilian eggs [19] which provide a better model for pterosaur eggs than asymmetric bird eggs [4, 5, 14]. Wang et al. [7] applied a correction factor to their estimate of egg mass based on experimentation with an egg of the extant ratsnake *Elaphe taeniura*. Such approaches have merit, but in this case, required further development to avoid a number of potential pitfalls. For example, it is not clear whether the eggshell of *E. taeniura* has comparable biomechanical properties (elasticity, compliance) compared to the eggshell of pterosaurs. Moreover, experimental conditions for the egg of *E. taeniura*, including residence time in an aquatic regime, the chemical composition of the fluid in which the egg was immersed, and key aspects of compressional regimes including speed of and geometry of compression and the compliance of surrounding sediment (or absence of it) are likely to have differed dramatically

from those experienced by pterosaur eggs. In the absence of more comprehensive studies it is simpler to apply a standardized method of predicting egg mass to all pterosaur eggs [5, 15] and avoid complications stemming from the introduction of arbitrary correction factors.

(c) Morphometric analyses

Data was compiled from the literature (see sources listed in electronic supplementary material, tables S1, S3 and S4) and personal examination (by DMU) of fossil material. The entry for the composite of *Hamipterus tianshanensis* was based on an aggregation of data for embryos 11, 12 and 13 of this pterosaur. These are closely comparable in size and thought to represent the same developmental stage [8]. Missing values were estimated by multiplying the length of the relevant element of IVPP V13758, a similarly sized embryo of a closely related taxon, by 1.05. This value was generated by calculating the mean for seven cases where the length of the element in IVPP V13758 could be directly compared to that for the composite: $(\sum(\text{element length IVPP V13758} / \text{element length composite})) / 7 = 1.05$. Similarly, forelimb lengths for IVPP V18943, embryo 7 and IVPP V18942 hatchling, were estimated on the basis of the humerus/forelimb index for IVPP V13758. Note that this relationship shows near isometry in ornithocheirids (figure 2 and electronic supplementary material, table S3).

(d) Determining prenatal patterns of ossification

Anatomical comparison of skeletogenesis within Pterosauria. Cross comparison of the degree of ossification of skeletal structures of four pterosaur

embryos, calibrated against a range of hatchling and immature individuals (electronic supplementary material, table S1) was used to capture data on developmental patterns of skeletogenesis that reflect the unique skeletal morphology of pterosaurs including manus digit IV, the 'wing-finger'. The pterosaur skeleton was divided into a series of discrete structural units (see figure 3 for listing). Units were assigned to one of three categories of ossification. To qualify as a 'well ossified' unit (figure 3b, c: dark grey cells) required ossification of the entire diaphysis as, for example, is the case with long bones of IVPP V18941 (*Hamipterus tianshanensis* embryo 11) and IVPP V13758 (figure 3a). Units that were present, but in which only part of the diaphysis (generally the mid-region) appears to be ossified, e.g. IVPP V18942, (*Hamipterus tianshanensis* embryo 12; figure 3a) were categorised as poorly ossified (figure 3b, c: light grey cells). Data for *Hamipterus* embryos 11-13, was combined into a single composite entry to maximize completeness for this growth stage and reduce the impact of any taphonomic modifications to the embryonic skeletons. Finally, skeletal units were ordered according to the incidence of their occurrence in specimens (figure 3b): highest rates, in which the unit (e.g. humerus) occurred in all specimens examined, to the left, lowest rates (e.g. tarsals) to the right.

Developmental patterns of skeletogenesis: comparisons with extant taxa. A second approach to the analysis of developmental patterns of skeletogenesis involved comparison with sequential (temporal) growth stages for taxa that form the extant phylogenetic bracket for pterosaurs. Pterosaurs are generally (although not universally) accepted to be archosaurs and bracketed by crocodilians and birds [9, 14]. We compared staged developmental sequences for *Alligator*

mississippiensis (figure 3c) [20, 21] and a precocial bird, *Coturnix coturnix* (electronic supplementary material, table S5) [22-24] with data for four pterosaur embryos. To facilitate cross-comparison data for individual ossifications that contribute to composite structures (cranium, mandible, pelvis, manus and pes) in *A. mississippiensis* and *C. coturnix*, was combined into structural units that matched those defined for pterosaurs (see above). For extant taxa the appearance of a skeletal unit (figure 3c: dark grey cell) was coded at the earliest onset of ossification for that element (see electronic supplementary material for further details).

Absence of ossification versus missing data Skeletal structures that appear to be absent (figure 3b, c: cells with no fill) may reflect several different circumstances. It may be, as is commonly the case in embryos, that mineralization of the structure had not yet begun at the point at which the individual died. Alternatively, the structure may have been partially or well mineralized, but partly, or wholly, obscured by other skeletal elements, or buried in matrix. Another possibility is that a skeletal structure may have originally been present, but lost due to postmortem decay and/or damage to the fossil. This is common for postnatal ‘free living’ individuals (e.g. *Pterodaustro guinazui*, MIC V 241 [25]), but less likely in the case of embryos enclosed within eggs, as finds from the Yixian Formation [2] and Lagarcito Formation [3] show.

The absence in *Hamipterus* embryos 11-13 of a series of skeletal structures and teeth (figure 3) is argued here to reflect a lack of ossification/eruption, rather than their loss due to taphonomic processes. This argument is supported by the observation that, originally, many eggs including those containing embryos

appear to have been complete [8] with embryonic bones that are now visible having been exposed by collection and preparation. Computed tomography scanning reveals, in the case of *Hamipterus* embryo No. 13, a seemingly intact skeleton [8]. In the case of embryo No. 12 skeletal elements appear to be in articulation [8] suggesting that the taphonomic process that led to their burial and preservation did not lead to the mechanical disaggregation of the skeleton.

Finally, the pattern of presence/absence of structures is also revealing. Almost all elements that ossify at an early stage in pterosaurs (figure 3b) or by stage 22 in *Alligator* (figure 3c) are present in embryo numbers 11-13, whereas almost all elements that ossify at later stages of development are absent. It seems much more probable that this pattern reflects lack of ossification of a particular set of elements that mineralise relatively late (*i.e.*, sacral and caudal vertebrae, ribs, gastralia, pelvis, carpals and tarsals), rather than taphonomic processes that are likely to have resulted in a random assortment of elements.

3. Results

(a) Egg size and morphology

More than 300 eggs have been reported for *Hamipterus tianshanensis*, an ornithocheirid pterosaur from the Lower Cretaceous of China ([6, 8]; electronic supplementary material, table S1). The eggs exhibit a relatively large size range, the largest reaching 151% the length and four times the predicted mass of the smallest (electronic supplementary material, table S2). The most elongated eggs are those with the smallest predicted mass and as size increases the eggs become less elongated, with the heaviest examples showing the lowest egg elongation ratios. This change in shape is primarily achieved by a

disproportionate increase in width (168%) compared to length (151%). The eggs containing the three smallest embryos (IVPP V 18941-3 embryos 5, 11, 12) and thought to represent the same developmental stage [8], are closely comparable in size to each other and have EERs (1.91–2.21) that fall within the middle of the range (1.70–2.63). Eggs of a closely related ornithocheirid from the Yixian Formation of China [1, 2], exhibit low EERs (1.29–1.75), comparable to, or lower than that for, *Hamipterus* eggs (figure 1).

The parchment-like shell structure of the eggs of extant lizards and snakes allows them to absorb water during incubation [26]. In lizards, this results in an increase in mass, over incubation, of 150–200%, accommodated by an increase in egg length and breadth of 23–60% depending on species [27–29], with breadth tending to increase more rapidly leading to a decrease in the EER. The presence of the same pattern in *Hamipterus*, in which the largest eggs show the lowest EERs, suggests that the range of egg sizes and egg elongation exhibited by this pterosaur [6, 8] reflects a sample from differing stages of incubation: the smallest eggs with highest EERs having died at an early stage of incubation while the largest eggs with the lowest EERs had been incubated for longer and were likely near term when they died.

(b) Size distribution and morphometrics

Reported lengths for the humerus of embryos and a hatchling of *Hamipterus tianshanensis* exhibit a relatively large size range: 13.3 mm in the three smallest embryos (numbers 11–13), 20% longer in embryo No. 7 and 40% longer in a hatchling ([8] electronic supplementary material, table S3). This corresponds to estimated forelimb lengths of between 124–175 mm and wingspans of 0.26–0.36

m (figure 2). Based on regression analyses of recent mass estimates for pterosaurs [30, 31] the mass of the *Hamipterus* hatchling is likely to have been at least double that of the smallest embryos (numbers 11–13). The relatively large size range subtended by the embryos and hatchling of *Hamipterus* is further emphasised by comparison with data for prenatal and early postnatal growth stages in other pterosaurs (figure 2; electronic supplementary material, tables S1, S4). In species such as *Aurorazhdarcho micronyx*, immature individuals of which span the exact same size range as individuals of *Hamipterus* [32], there is a significant change in skeletal proportions. The humerus, for example, exhibits negative allometry with regard to forelimb length, a relationship that is common within pterosaurs, although ornithocheirids are exceptional in that the humerus-forelimb index shows a near isometric relationship over a large range of sizes (electronic supplementary material, table S3). The key point here is that the smallest individual of *Aurorazhdarcho micronyx*, which corresponds in size to embryos 11–13 of *Hamipterus*, represents a distinctly different, younger growth stage from that of the largest and presumably oldest individual, which corresponds in size to the *Hamipterus* hatchling (figure 2).

(c) Ossification sequences in prenatal pterosaurs.

The single known embryo of *Pterodaustro guinazui* (figure 3a; electronic supplementary material, table S1) [3, 33], generally thought to be near term, or full term [3, 4, 15, 24, 33], is closely comparable in terms of degree of ossification to hatchlings of the same species (MIC V241, MMP 1168; [25]) and immature individuals of *Pterodactylus kochi* [32] and *Rhamphorhynchus muensteri* [34], although the phalanges of manus digits I–III are seemingly unossified in the

embryo (figure 3b). The same elements, and the metacarpals, tarsals and pedal phalanges, are unossified in embryos of an ornithocheirid pterosaur from the Yixian Formation ([1, 2]; electronic supplementary material, table S1) suggesting a slightly earlier developmental stage. The skeletons of *Hamipterus* embryos 11–13 are markedly less well ossified (figure 3a), with no evidence for a series of elements including the rostrum, teeth, sacral and caudal vertebrae, ribs, gastralia, carpals, manus digits I–III, the pelvis, tarsals or pes digits I–IV. Those elements that are present (cervical and possibly dorsal vertebrae, coracoid, metacarpals I–III, distal wing-phalanges, metatarsals), appear more poorly ossified compared to the same structures in IVPP V13758 or MIC V246. This is also true for some limb elements such as the humerus which, in embryo 13, seems less clearly defined than that of the *Hamipterus* hatchling or other embryos (figure 2).

(d) Comparison with embryological development in extant archosaurs.

Comparison with the well-established prenatal developmental sequence for *Alligator mississippiensis* [20, 21] shows that the Yixian Formation ornithocheirid embryos correspond most closely to developmental stages 23/24 of *A. mississippiensis*, while the *Pterodaustro* embryo corresponds to stages 24/25 (figure 3c). *Hamipterus* embryos 11–13 show closest congruence with developmental stages 21/22 of *A. mississippiensis*: the teeth have not yet erupted and elements which ossify at later stages of development in *A. mississippiensis* (sacral and caudal vertebrae, ribs, gastralia, pelvis, carpals, manus digits I–III, tarsals and pedal phalanges) are seemingly unossified in these embryos. Notably, the tibia/fibula, which ossifies at stage 18 in *A. mississippiensis* also appears to be absent. By contrast, metacarpal IV and proximal phalanges of manus digit IV

(i.e., the wing-finger) are ossified in the *Hamipterus* embryos. This might suggest a slightly later stage of development as, in *A. mississippiensis*, the homologous elements ossify in stages 22 and 23 respectively. However, an equivalency to *A. mississippiensis* stages 22/23 for the *Hamipterus* embryos is less congruent than for stages 21/22 and likely reflects a pattern of ossification that is heterochronic relative to that of *A. mississippiensis* and interpreted here (see below) as flight related. Irrespective of whether embryos 11–13 correlate to stages 21, 22 or 23, it is clear that within a developmental framework based on *A. mississippiensis* these embryos represent an earlier developmental stage than the *Pterodaustro* or ornithocheirid embryos.

Comparison with the ossification sequence for the quail, *Coturnix coturnix*, (table S5) [22–24] yielded the same pattern as those for *A. mississippiensis* with regard to the differing stages of development reached by the pterosaur embryos included in this analysis. *Hamipterus* embryos 11–13 conform most closely to day 8/9 of embryonic development in *C. coturnix*, the Yixian ornithocheirid embryos to day 12, or possibly later, and the *Pterodaustro* embryo to day 16 (term).

Sequence incongruencies reflect the relatively late stage of mineralisation of the vertebral column in *Coturnix* [23], and a shift to an earlier stage of ossification of manus digit four in pterosaurs.

4. Discussion

(a) Extending the fossil record of prenatal development in pterosaurs

Current interpretations of the fossil record of early development in pterosaurs, heavily reliant upon qualitative assertions [17], identify almost all finds as perinatal – either near-term embryos and eggs, or hatchlings [1–4, 6–8, 14, 15,

33]. Multiple lines of evidence used in this study provide a much firmer basis for, and greater precision in, the assignment of records to particular growth stages and show that some eggs and embryos should be reassigned to earlier stages. This extends our knowledge of prenatal development in pterosaurs (figure 4) and has important consequences for understanding the conditions under which eggs were incubated and how they developed, prenatal ossification sequences in pterosaurs and how they compare to those of other tetrapods, and the implications of those sequences for the locomotory ability of pterosaur hatchlings.

(b) A new map of pre- and peri-natal development in pterosaurs

Two eggs preserved in association with a specimen of *Darwinopterus modularis* (ZMNH M8802) provide direct evidence for egg size and morphology at oviposition [5, 7]. The EER for these eggs (1.45–1.56) is relatively low, but may reflect a species-specific morphology or taphonomic compression of the fossil. The most elongate, relatively low predicted mass eggs of *Hamipterus* (figures 1, 4) likely represent the earliest stages of incubation prior to any significant skeletogenesis.

Embryos 11–13 of *Hamipterus* appear to represent a ‘mid-term’ stage of development in which skeletogenesis had begun, but was relatively incomplete (figure 4). This is consistent with the mid-range degree of elongation and masses of eggs containing these embryos (figure 1), the relatively small size of the embryos (figure 2) and the lower degree of ossification, compared to late term embryos (figure 3b). This roughly corresponds to developmental stages 21/22 in *A. mississippiensis* (figure 3c) and day 8/9 in *Coturnix* (electronic supplementary material, table S5) which is approximately 50% of the incubation period for these

taxa [21, 23, 35]. *Hamipterus* embryo 5, enclosed in an egg with a relatively high EER (2.1) and with a seemingly very poorly ossified skeleton [8], may represent a slightly earlier stage of development compared to embryos 11–13.

Compared to *Hamipterus* embryo 13, the scapula of embryo 4 and the humerus of embryo 7 are approximately 20% longer ([8]; electronic supplementary material, table S2). The latter two specimens likely represent late term embryos that were accommodated in a larger, less elongate egg, comparable to those of the Yixian ornithocheirid (IVPP V13753; JZMP 03-03-2) that exhibit a relatively low EER (figure 1). *Hamipterus* eggs with comparable EERs exhibit cracking and crazing of the outer surface of the eggshell (electronic supplementary material, figure S1; [6]) that likely reflects the accommodation of volumetric changes following water uptake.

Comparison with hatchling and immature pterosaurs and prenatal developmental sequences for *A. mississippiensis* and *C. coturnix* confirm the conclusions of earlier studies that the Yixian ornithocheirid embryos were at a late developmental stage when they died [1, 2, 4, 14, 15] but, seemingly, not quite as advanced as the *Pterodaustro* embryo. The latter has been recognized as well developed [3, 4, 14, 15, 33, 36, 37] and is more specifically identified here as very near term or at the point of hatching when it died.

Many of the *Hamipterus* eggs described by Wang et al. [6, 8] lack evidence of embryonic skeletal remains and seem to be collapsed. Dimpling of the shell may reflect dehydration post mortem [6], but might also represent empty egg shells after hatching, particularly for shells that are crumpled [8], or seem to have been slit open [8], as observed in hatched eggshells of extant lizards [38]. One example (figure 4J [8]), exhibits an EER (1.83) typical of late term eggs.

Two individuals of *Pterodaustro guinazui* (MIC V241, MMP 1168) closely comparable in size and skeletal development to MIC V246, and interpreted as 'at a very early stage of postnatal development' [25] are confirmed here as highly immature and probably hatchlings. A small humerus preserved on block IVPP V 18942 has been identified as belonging to a hatchling of *Hamipterus* [8]. This is consistent with its size, degree of ossification and relative proportions (the length of the deltopectoral crest compared to the length of the humerus is only slightly greater than in the *Hamipterus* embryos [8]), although the possibility that it represents an isolated element from a pre-hatching individual cannot be entirely excluded.

(c) Implications of prenatal development for postnatal flight ability in pterosaurs

Precise identification of the developmental stage of embryos is critical for inferring the locomotory ability of hatchlings [17, 39]. It has been argued, primarily on the basis of embryos 11-13, that the more advanced state of ossification of hind limb compared to forelimb elements and the incomplete ossification of key flight muscle attachment sites, such as the *processus scapularis* of the scapula and deltopectoral crest of the humerus, means that hatchlings of *Hamipterus* would not have been able to fly [8, 13]. However, as shown here, embryos 11-13 likely represent a mid-term stage of development, consequently the relatively poor ossification of forelimb bones and muscle attachment sites almost certainly reflects initial stages in the mineralization of the skeleton, and not the skeletal morphology of near-term embryos, as for example, *Pterodaustro* (MIC V246). Indeed, patterns of ossification evident in the prenatal pterosaur fossil record

described here (figure 4) provide new support for the idea of super-precocial flight ability in pterosaurs.

Hamipterus embryos 11–13 show two key features. First, a relatively greater degree of ossification of the principal fore and hind limb long bones, which form the main wing spars, compared to the rest of the skeleton (figure 3b). With the exception of the tibia-fibula, all the principal wing-spar elements are at least partially ossified including the metacarpus and proximal phalanges of manus digit four which, in *A. mississippiensis* and *C. coturnix* ossify at later stages of development (figure 3; electronic supplementary material, table S5), as is typical for amniotes [40]. This pattern seems to have been underpinned by a developmental heterochrony unique to pterosaurs that involved a shift in the timing of ossification of metacarpal and digit IV to a much earlier stage of development (figure 3b). Second, embryos 11–13 exhibit relatively elongate fore limbs, the estimated length of which is more than nine times the length of the humerus. Principally, this was achieved through hyper-elongation of metacarpal IV and manus digit IV which reach 114% and 165% of humerus length respectively (electronic supplementary material, table S3). The early ossification, and elongation, of flight-related skeletal elements, as demonstrated by the mid-term growth stages of *Hamipterus*, show that unique components of the pterosaur bauplan were present at the earliest stages of skeletal formation and acted as anatomical precursors to the final stages of prenatal development.

Terminal stages of embryonic development, represented by MIC V246 [3, 33, 36, 37], IVPP V 13758 [2, 4, 15], JZMP 03-03-2 [1, 4, 15], and the humeri of a near term embryo (No. 7) [8] and a hatchling of *Hamipterus* (figure 2) have multiple features that point toward flight ability in hatchlings. First, extensive

ossification of all elongate structures contributing to the flight apparatus that are likely to have experienced significant loads in bending during flight. These include dorsal and sacral vertebrae, the limb girdles and diaphyses of long bones that form the wing spars. This stiffening of the skeletal components of the flight module is analogous to ossification sequences in *A. mississippiensis* [21], the hatchlings of which are also highly precocial locomotors, but is in sharp contrast to most extant birds where, prior to hatching, only the central region of the diaphysis of long bones is ossified [41].

Second, inferences regarding the implied lack of development of key flight muscles, based on the absence or poor development of osteological features, are insecure for two reasons: (1) Muscle attachment sites do not need to be ossified in order to function effectively [42]. In tension, cartilage can accommodate loads comparable to those for bone [43], consequently it cannot be assumed, a priori, that an incomplete deltopectoral crest directly implies a relatively small *m. pectoralis*, the principal wing depressor. (2) The relative size and shape of the deltopectoral crest of embryos 7, 11-13 and the hatchling (figure 2) is smaller than that of adult *Hamipterus*, but it is directly comparable in terms of shape and relative size to the deltopectoral crest of other pterosaurs including individuals of *Anurognathus* and *Aurorazhdarcho* that are widely considered to have been flight capable [9, 14, 30-32, 44].

Third, the relative elongation of long bones contributing to the wing spars, their relative proportions to each other and the relative elongation of the fore limb of mid and late term embryos compare closely to the same indices for mature, flight capable individuals of ornithocheirids (electronic supplementary material, table S2). This is in sharp contrast to most birds and all bats where fore limb

proportions comparable to those of adults, and flight ability, are only achieved at a relatively late stage of postnatal development [45, 46].

(d) Parental care in pterosaurs

Parental care in pterosaurs has been proposed by several authors [3, 8-13, 47, 48], although the particular modes of care (e.g. defending nest, protecting young) are rarely specified. The requirement for postnatal care has often been directly related to the idea that hatchling pterosaurs were not flight capable, as suggested for *Hamipterus* [8]. However, as shown here, available evidence favours the idea that the hatchlings of *Hamipterus* and other pterosaurs were flight capable at a very early stage in their postnatal development. It may be that early postnatal growth stages received parental care, in the form of protection from predators, as for example in crocodylians [49], but such a behaviour is difficult to demonstrate and, for the present, there is no direct evidence to suggest that pterosaur hatchlings required parental care.

The fossil accumulation at Hami, comprising eggs, embryos, hatchlings, juveniles and adults, has been interpreted as evidence for gregariousness in pterosaurs, a component of which might have involved care of young [8]. Alternatively, however, the nesting site of Hami, may have attracted *Hamipterus* and seemingly another pterosaur, because it provided a suitable substrate within which to deposit clutches and the persistence of this sedimentary environment through time encouraged multiple nesting events. Gregariousness (in the sense of individuals interacting with each other) is not a required outcome of such locations and a better analogy might be turtle nesting sites [50].

Data accessibility. Supporting data are accessible in electronic supplementary material, figure S1 and tables S1–5.

Author contributions. DMU and DCD conceived the project, conducted the research, constructed the figures and tables and wrote the paper.

Competing interests

The authors declare no competing interests.

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Figure legends

Figure 1.

Predicted egg mass plotted against egg elongation for eggs of *Hamipterus* *tianshanensis* without (open circles) and with embryos (filled circles: embryos 5, 11 and 12 of Wang *et al.* [8]), a second pterosaur from the Lower Cretaceous of Hami (triangle), and two ornithocheirid pterosaurs (grey diamonds) from the Yixian Formation [1, 2]. Outlines of *Hamipterus* eggs illustrate relationship between shape and mass. See electronic supplementary material for data (table S1, S2).

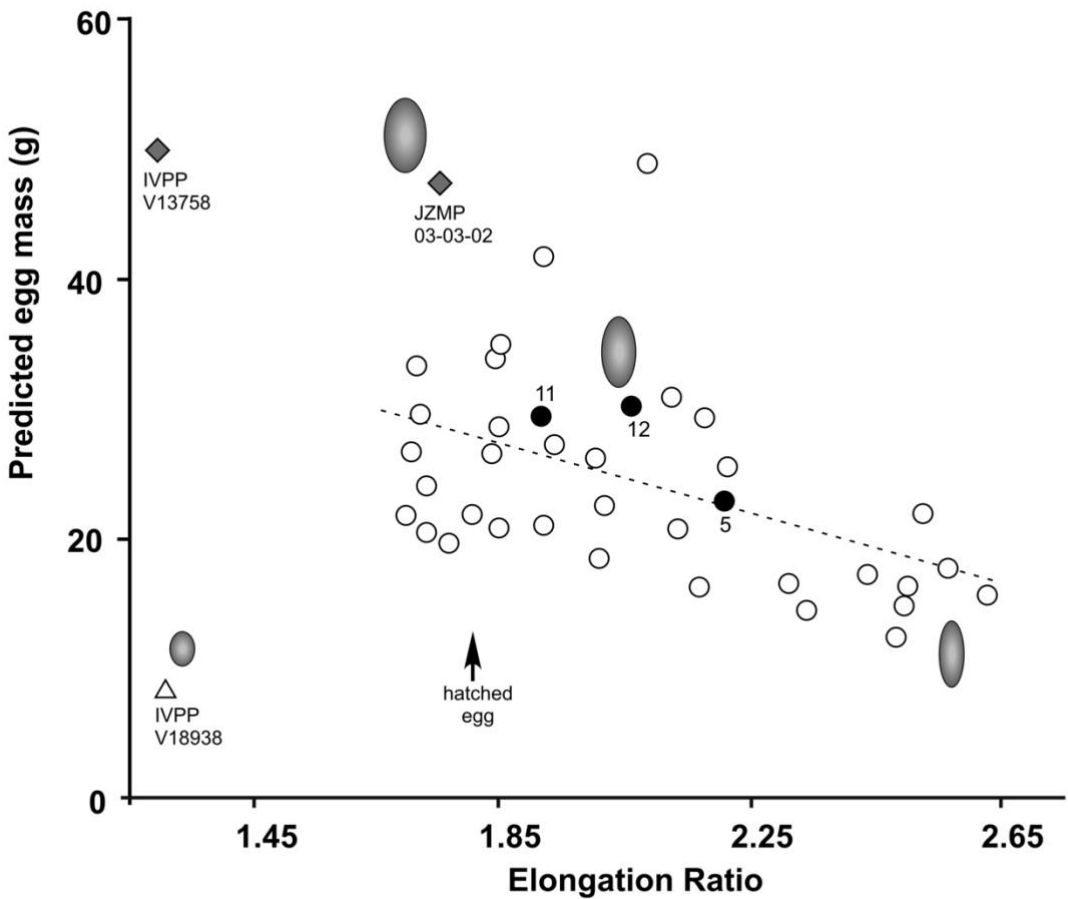


Figure 2.

Humerus length as a proportion of forelimb length plotted against forelimb length (mm) for a sample of pterosaur embryos, hatchlings and immature individuals with humeri ranging from 12-20 mm in length. Solid symbol = embryo, open symbol = hatchling or immature individual. (a) SMNS 81928 (cast); (b) IVPP V13758; (c) IVPP V18943, embryo 13; (d) BSP 1964 XXIII 100; (e) MIC V246; (f) IVPP V18942. Humeri drawn to scale and shown in lateral view. Scale bar = 5mm. (a) redrawn from [44]; (b) modified from [2]; (c) and (f) redrawn from [8]; (d) redrawn from [32]; (e) modified from [33]. (See electronic supplementary material, table S4 for complete data set). Trend lines are least square regressions generated by Excel (see table S4).

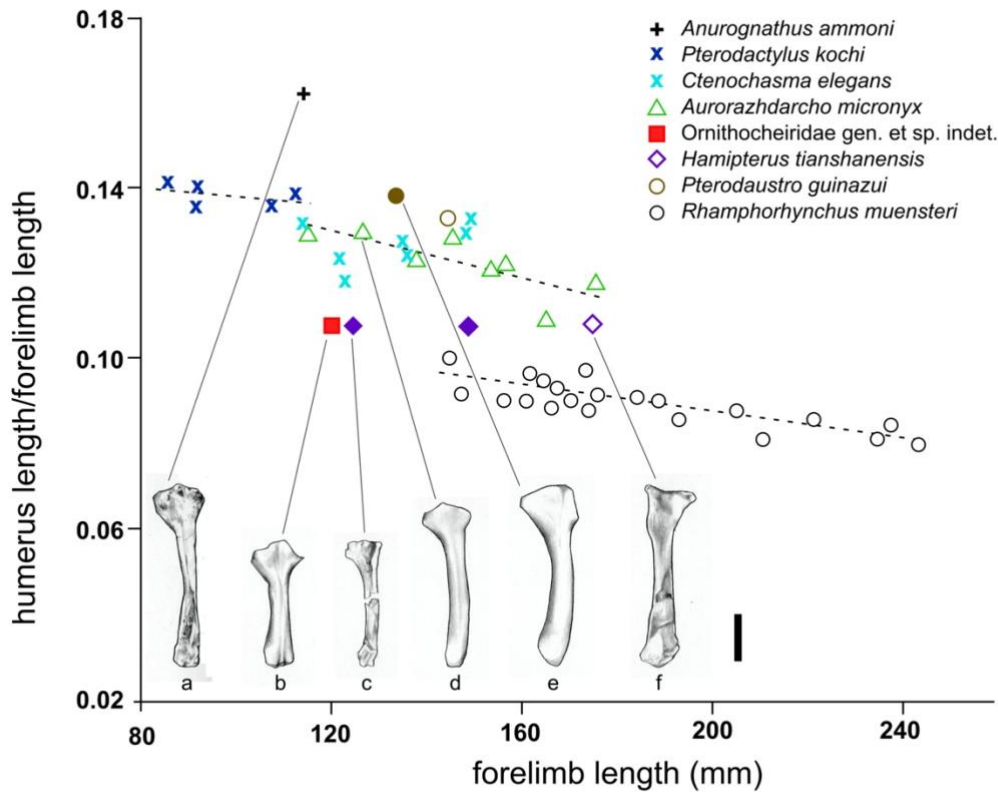


Figure 3.

Ossification of the skeleton in pterosaur embryos. **(a)** Comparison of mid-term embryos (left) and near-term embryos (right). Scale bar = 5mm. Redrawn from [2, 8, 33]. **(b)** Degree of ossification of principal skeletal elements in four pterosaur embryos, calibrated against a hatchling and two immature individuals. **(c)** Comparison of developmental stages in *Alligator mississippiensis* with four pterosaur embryos. Symbols: dark grey fill = skeletal structure well ossified/teeth erupted or, in *A. mississippiensis*, any degree of ossification; light grey fill = skeletal structure poorly ossified; no fill = absence of element inferred to be due to lack of ossification; **X** = ossified element inferred to have originally been present, but now obscured by overlying elements, buried, or lost due to postmortem damage; **?** = uncertain identification of element. Abbreviations: Em, embryo; Ha, hatchling; Im, Immature, OS, Ontogenetic status. Taxonomic abbreviations: Am, *Alligator mississippiensis*, Ht, *Hamipterus tianshanensis*; Or, Ornithocheiridae gen et sp. indet., Pg, *Pterodaustro guinazui*; Pk, *Pterodactylus kochi*; Rm, *Rhamphorhynchus muensteri*. Anatomical abbreviations: Ca, carpals; Cd, caudal vertebrae; Co, coracoid; Cr, cranium; Cv cervical vertebrae; De, dentition; Do, dorsal vertebrae; Fe, femur; Ga, gastralia; Hu, humerus; Ma, mandibles; MI–III, manual digits I–III; MIV, manual digit IV; Mcl–III, metacarpals I–III; MclV, metacarpal IV; Mt, metatarsals; Pe, pelvis, Pd, pedal digits; Ri, ribs, Ro, rostrum; R/U, radius/ulna; Sa, sacral vertebrae; Sc, scapula, Sk, skull; St, Sternum; Ta, tarsals; T/F tibia/fibula; W1, 2, 3, 4, wing-finger phalanges 1, 2, 3, 4. See electronic supplementary material, table S1 for sources of data.

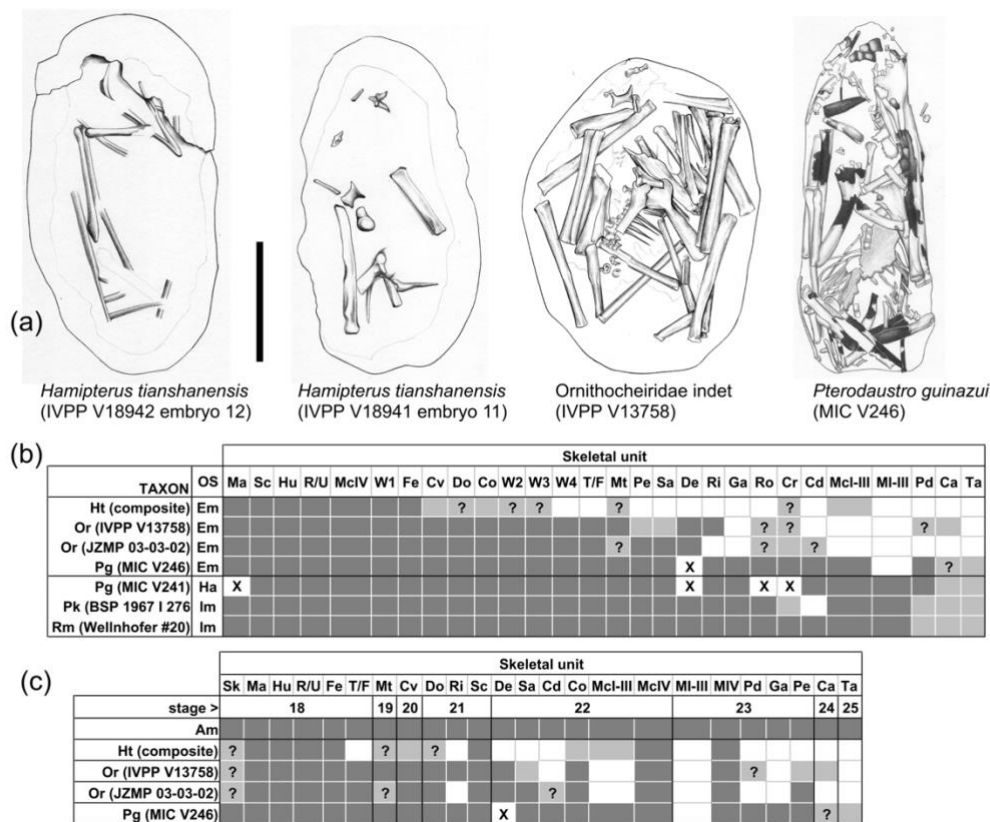


Figure 4.

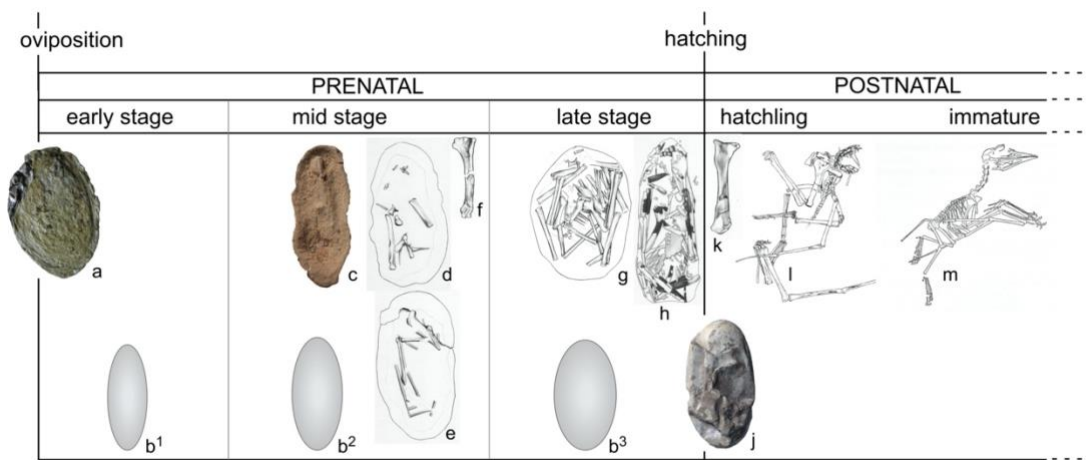
Fossil record of prenatal and early postnatal development in pterosaurs.

Darwinopterus modularis (a) ZMNH M8802. *Hamipterus tianshanensis* (b1-3) outlines of egg shape illustrating changes in size and shape; (c) IVPP V18942 embryo 5; (d) IVPP V18941 embryo 11; (e) IVPP V18942 embryo 12; (f) IVPP V18943 humerus of embryo 13; (j) IVPP V18942 hatched? egg; (k) IVPP V18942 humerus. Ornithocheiridae genus et sp. indet. (g) IVPP V13758 embryo.

Pterodaustro guinazui (h) MIC V246, embryo; (i) MIC V241 hatchling.

Pterodactylus kochi (m) BSP 1967 I 276. Not to scale. (c-f, j, k) redrawn from [8],

(g) redrawn from [2], (h) redrawn from [33], (l) redrawn from [25]; (m) redrawn from [32].



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Pre-natal development in pterosaurs and its implications for their post-natal locomotory ability

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Supplementary information

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689

690 **Supplementary notes on methodology: comparison with ossification**
691 **sequence patterns in extant taxa**

692 Extensive data has been published on prenatal patterns of ossification for a broad
693 range of tetrapods (e.g., papers cited by Fröbisch [40], Maxwell et al. [S1] and
694 Mitgutsch et al. [S2]). Selecting the most appropriate taxa that might be used to
695 establish the stage of development of pterosaur embryos faces three challenges:
696 disagreement regarding the extant phylogenetic bracket for pterosaurs;
697 anatomical similarity, and dissimilarity; and heterochrony.

698

699 **1. The extant phylogenetic bracket.** While most recent studies have concluded
700 that pterosaurs belong within Ornithodira [S3, S4] some analyses have located
701 them outside this clade, although still within Archosauromorpha [S5, S6]. Here,
702 we accept the majority view, that pterosaurs are ornithodirans, with an extant
703 phylogenetic bracket consisting of crocodiles and birds. *Alligator mississippiensis*
704 was selected as representative of Crocodylia because of the availability of
705 detailed descriptions of the prenatal ossification pattern for this species [20, 21].
706 Such patterns are often highly conserved [40] and divergences, in other
707 crocodylians, from the pattern seen in *A. mississippiensis* are likely to be minor
708 and of little consequence for the outcome of this study.

709 Prenatal ossification sequences have been reported for a wide range of
710 birds. Choosing a comparator in this case is more complex as there is significant
711 interspecific variation [22]. The quail, *Coturnix coturnix*, was selected as it is
712 highly precocial, there are detailed descriptions of the ossification sequences for
713 this species [22-24], and it conforms closely to the general model of prenatal
714 ossification for birds proposed by Maxwell et al. [S1].

715 If pterosaurs are considered to belong within Archosauromorpha, but lie
716 outside Ornithodira [S5, S6] then the extant phylogenetic bracket would shift to
717 Crocodylia and Squamata or possibly even, depending on the phylogeny
718 adopted, Testudines. This is beyond the bounds of this study although we note

that in *Lacerta*, for example [S7], the pattern of ossification compares closely to that seen in *Alligator*.

2. Anatomical similarity and dissimilarity. Pterosaurs are highly derived in some regards, for example with respect to the forelimb, but much of their skeletal anatomy can be relatively easily homologised with that of many other diapsids [9, 14]. Consequently, identification in *Alligator* of the skeletal units defined in this study for pterosaurs (figure 3c) is relatively simple. By contrast, extant birds are highly derived and the loss of structures, such as teeth, manus digit one and distal phalanges in manus digits II-IV, complicate comparisons (electronic supplementary material, table S5). Despite these drawbacks our results show that prenatal ossification sequences in crocodylians and birds are of some utility for understanding such sequences in pterosaurs, although much still remains to be explored in this regard.

3. Heterochrony. It would be surprising if the ossification sequence in pterosaurs showed perfect congruence with that of *Alligator* or *Coturnix* and that is not the case as we show. However, there is a sufficiently high degree of congruence in both cases that data for the extant taxa can be used effectively to distinguish three different prenatal stages of ossification among the 19 pterosaur embryos described to date (figure 4). Examples of non-congruence such as the early ossification of manus digit IV in pterosaurs (figure 3b, c) and comparatively late ossification of the vertebral column in *Coturnix* [23] compared to other amniotes [40], can be attributed to heterochronic shifts.

Reassessment of the identity of IVPP V13938

Wang et al. [6] assigned a small relatively spherical egg (IVPP V13938) from Lower Cretaceous deposits at Hami, Xinjiang, China to *Hamipterus tianshanensis* arguing that it represented an earlier stage of development than other eggs assigned to the same taxon. The analysis of egg shape and mass, presented here (figure 1) clearly shows that IVPP V13938 does not lie within the cloud of points that define the size/shape relationship for *Hamipterus tianshanensis*. There are three possible explanations.

First, IVPP V18938 is correctly assigned, but represents a malformed egg. It does not, however, exhibit any clear signs of malformation. The malformation might be restricted to its relatively small size, but this is inconsistent with the low EER (1.3). By contrast, low mass eggs of *H. tianshanensis* have a relatively high EER (2.5).

Secondly, and more likely, IVPP V13983 pertains to a second, presumably smaller, species of pterosaur. The apparent absence of evidence, so far, of any taxa other than *H. tianshanensis* in the deposits at Hami is not necessarily problematic since the rarity of the IVPP V13983 egg type (<0.33% of all egg finds reported to date) may reflect the rarity of a second species of pterosaur at Hami. Several species of ornithocheirid have already been reported from the Lower Cretaceous of China and non-ornithocheirids from contemporaneous deposits include ctenochasmatoids, lonchodectids, dsungaripterids and tapejarids [S8].

Thirdly, IVPP V13938 might pertain to a non-pterosaurian oviparous vertebrate, although not one has yet been reported from the fluviolacustrine sequence at Hami.

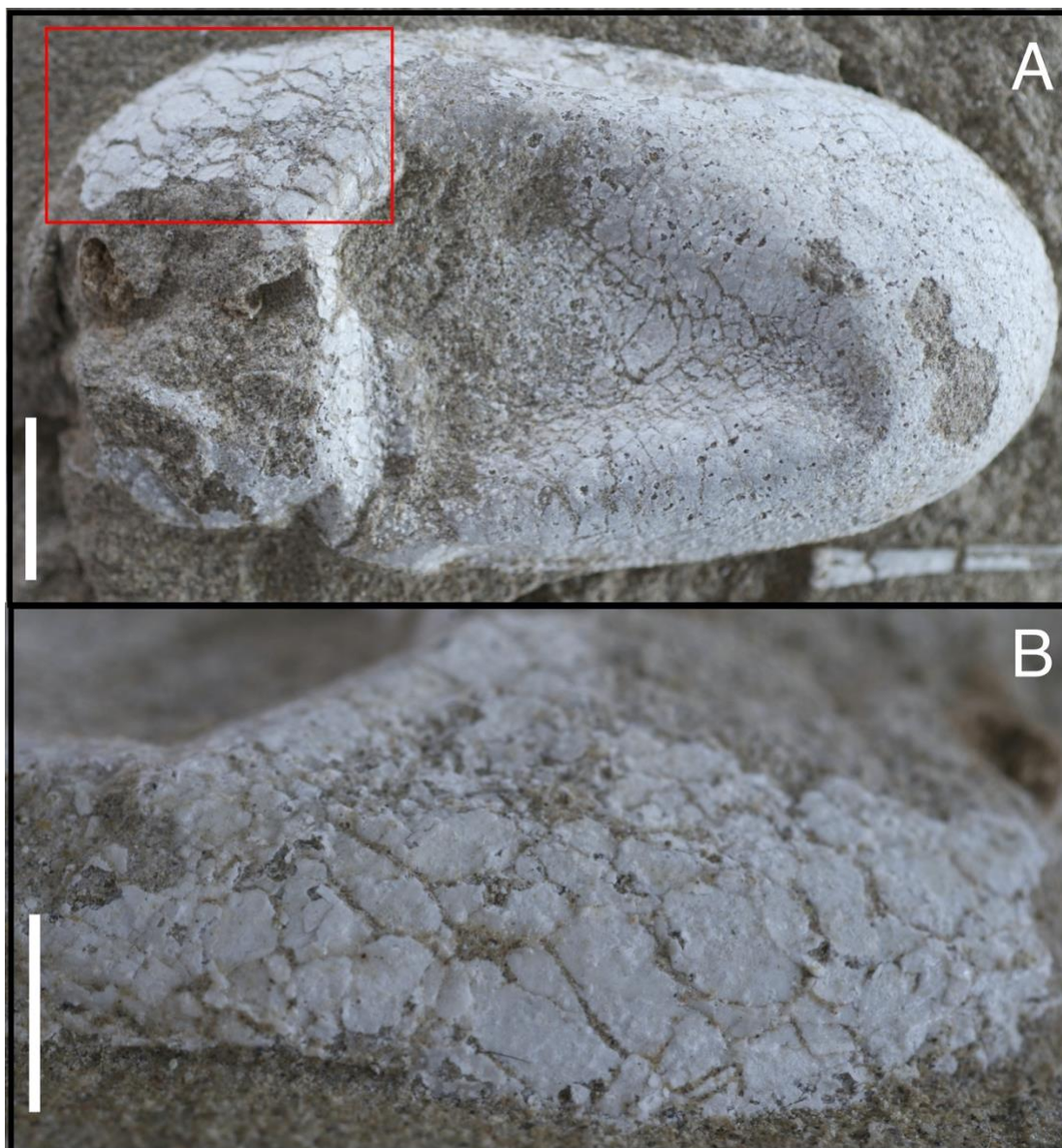
In summary, while the second explanation, that IVPP V13938 pertains to a second species of pterosaur, is the most likely, the other two cannot be entirely excluded. Further finds may help to resolve this issue.

772 **Museum acronyms**

773 **BMNH**, Natural History Museum, London, United Kingdom; **BSP**, Bayerische
 774 Staatssammlung für Paläontologie und Geologie, München, Germany; **CM**,
 775 Carnegie Museum, Pittsburgh, USA; **ELTE**, Natural History Museum of Eötvös
 776 University, Budapest, Hungary; **GIE**, Geologisches Institut der Universität,
 777 Erlangen, Germany; **GLGMV**, Guilin Longshan Geological Museum, Guilin City,
 778 China; **IVPP**, Institute for Vertebrate Palaeontology and Palaeoanthropology,
 779 Beijing, China; **JS**, Sammlung Jürgen Schmidt, Frankfurt, Germany; **JZMP**,
 780 Jinzhou Paleontological Museum, Liaoning Province, China; **MBH**, Museum
 781 Bergèr, Harthof bei Eichstätt, Germany; **MIC**, Museo Interactivo de Ciencias,
 782 Universidad Nacional de San Luis, San Luis, Argentina; **MM**, Museum Friedrich
 783 Müller, Solnhofen, Germany; **MCZ**, Museum of Comparative Zoology, Harvard,
 784 USA; **NMW**, Naturhistorisches Museum, Wien, Austria; **NSM**, National Science
 785 Museum, Tokyo, Japan; **PMZ**, Paläontologisches Institut und Museum der
 786 Universität Zürich, Switzerland; **PTH**, Philosophisch-Theologische Hochschule,
 787 Eichstätt, Germany; **RGM**, Rijksmuseum van Geologie en Mineralogie, Leiden,
 788 Netherlands; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Germany;
 789 **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Germany; **TM**, Teyler
 790 Museum, Haarlem, Netherlands; **UB**, Universität Brno, Brno, Czech Republic;
 791 **ZMNH**, Zhejiang Museum of Natural History, Hangzhou, China.

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Supplementary Figure S1

Eggshell texture in *Hamipterus tianshansensis* (IVPP V18937). **A**, complete, slightly collapsed egg. **B**, detail (indicated by red box in **A**) showing cracking and crazing of eggshell. Scale bar: = 10mm in **A** and 5 mm in **B**. (Photo: DMU).

800 **Supplementary Table S1:** Summary of pre-, peri-natal and selected examples of
801 immature and mature pterosaurs included in this study.

Taxon	Species	Specimen	material	Locality	Formation	Age	Reported ontogenetic status	Ontogenetic status this paper	Sources
Anurognathidae	<i>Anurognathus ammoni</i>	SMNS 81928 (cast)	complete skeleton	Eichstätt, Bavaria	Solnhofen Beds	Upper Jurassic (Tithonian)	immature	immature	[39]
Rhamphorhynchidae	<i>Rhamphorhynchus muensteri</i>	MMK V. 45/1 (Wellnhofer 22)	complete postcranial ske	Bavaria					[27]
		MM (Solnhofen) (Wellnhofer 14)	incomplete skeleton	?					[27]
		MM (Solnhofen) (Wellnhofer 13)	complete skeleton	?					[27]
		MBH unnumbered (Wellnhofer 20)	complete skeleton	Bavaria					[27]
		BSP 1877 X 1 (Wellnhofer 5)	complete postcranial ske	Eichstätt, Bavaria					[27]
		lost							[27]
		SL (Bochum) 010 (Wellnhofer 15)	incomplete skeleton	Schemfeld, Bavaria					[27]
		BSP 1889 XI i (Wellnhofer 7)	near complete skeleton	Eichstätt, Bavaria					[27]
		JS (Frankfurt) (Wellnhofer 18)	disarticulated, incomplete	Eichstätt, Bavaria					[27]
		MMK 1891. 740 (Wellnhofer 23)	Isolated forelimb	Solnhofen, Bavaria					[27]
		MB unnumbered (Wellnhofer 19)	incomplete skeleton	Eichstätt, Bavaria					[27]
		TM 6924 (Wellnhofer 1)	near complete skeleton	Solnhofen, Bavaria	Solnhofen Beds	Upper Jurassic (Tithonian)	immature [10]	immature	[27]
		CM 11433 (Wellnhofer 21)	complete skeleton	'Solnhofen' Bavaria					[27]
		PTH 1966.6 (Wellnhofer 12)	disarticulated, incomplete	Solnhofen, Bavaria					[27]
		MB unnumbered (Wellnhofer 4)	complete skeleton	Eichstätt, Bavaria					[27]
		BSP 1938 I 503 (Wellnhofer 11)	complete skeleton	Eichstätt, Bavaria					[27]
		MBH unnumbered (Wellnhofer 17)	near complete skeleton	Bavaria					[27]
		BSP 1959 I 400 (Wellnhofer 10)	complete skeleton	Zandt, Bavaria					[27]
		JS (Frankfurt) (Wellnhofer 29)	incomplete skeleton	Langenaltheim, Bavaria					[27]
		BSP 1943 I 36 JS (Wellnhofer 24)	near complete skeleton	Langenaltheim, Bavaria					[27]
		31)	Isolated forelimb	Zandt, Bavaria					[27]
Basal Monofenestrata	<i>Darwinopterus modularis</i>	ZMNH M8802	near complete skeleton associated with two eggs	Linglongta, Liaoning Prov. China	Tiaojishan Formation	Upper Jurassic (Oxfordian)	mature female with eggs ready for oviposition	mature female with eggs ready for oviposition	[5]
Ornithocheiridae	<i>Hampterus tianshanensis</i>	IVPP V18943 embryo 13	skeleton preserved within an egg				late stage embryo	mid-stage embryo	[8]
		IVPP V18942 embryo 12	partially articulated skeleton preserved within an egg				late stage embryo	mid-stage embryo	[8]
		IVPP V18941 embryo 11	skeletal remains preserved within an egg	Turpan-Hami Basin, Xinjiang, China	Tugulu Group	Lower Cretaceous	late stage embryo	mid-stage embryo	[8]
		IVPP V18942 embryo 4	skeletal remains preserved within an egg				late stage embryo	late stage embryo	[8]
		IVPP V18942 embryo 7	skeletal remains preserved within an egg				late stage embryo	late stage embryo	[8]
		IVPP V18942 'hatchling'	humerus				hatchling	peri-natal individual	[8]
	Ornithocheiridae gen et sp. indet		skeleton preserved within an egg	Jingangshan, Liaoning, China	Yixian Formation	Lower Cretaceous (Barremian)	late stage embryo	late stage embryo	[2]
	JZMP-03-03-02		skeleton preserved within an egg				late stage embryo	late stage embryo	(DMU), [1]
	<i>Boreopteris cuiae</i>	JZMT 04-07-03	near complete skeleton	Yixian County Jinzhou, Liaoning Prov. China	Yixian Formation	Lower Cretaceous (Barremian)		immature	(DMU), [S3]
	<i>Zhenyuanopterus longirostris</i>	GLGMV 0001	complete skeleton	Shangyuan, Liaoning Prov. China	Yixian Formation	Lower Cretaceous (Barremian)		mature	(DMU), [S4]
Ctenochasmatoidea	<i>Arthurdactylus conadoylei</i>	SMK 1132 PAL	near complete postcranial skeleton	Chapada do Araripe, Brazil	Crato Formation	Lower Cretaceous (Aptian)		mature	(DMU), [S5]
	<i>Anhangura santanae</i>	NSM PV19892	near complete skeleton	Chapada do Araripe, Brazil	Santana Formation	Lower Cretaceous (Aptian)	sub adult	mature	(DMU), [S6]
	<i>Pterodactylus antiquus</i>	TM 10 341	complete skeleton	Eichstätt, Bavaria			juvenile	immature	[26]
	<i>Pterodactylus kochi</i>	BMNH 42736	almost complete skeleton	Kelheim, Bavaria			juvenile	immature	[26]
	<i>Pterodactylus kochi</i>	BSt 1967 I 276	complete skeleton	Schemfeld, Bavaria	Solnhofen Beds	Upper Jurassic (Tithonian)	juvenile	immature	[26]
Ctenochasmidae	<i>Pterodactylus kochi</i>	TM 13 105	complete skeleton	Schemfeld, Bavaria			juvenile	immature	[26]
	<i>Pterodactylus kochi</i>	BSt 1924 V 1	complete skeleton	Eichstätt, Bavaria			juvenile	immature	[26]
	<i>Ctenochasma elegans</i>	lost	complete skeleton	Lithographic Beds, Bavaria			adult	immature	[26]
	<i>Ctenochasma elegans</i>	BSP 1875 XIV 501	complete skeleton	Eichstätt, Bavaria			adult	immature	[26]
	<i>Ctenochasma elegans</i>	BSP 1867 II 1	complete skeleton	Eichstätt, Bavaria			adult	immature	[26]
	<i>Ctenochasma elegans</i>	MBH unnumbered; Wellnhofer 49	complete skeleton	Eichstätt, Bavaria	Solnhofen Beds	Upper Jurassic (Tithonian)	adult	immature	[26]
	<i>Ctenochasma elegans</i>	PMZ A/III 100	complete skeleton	Eichstätt, Bavaria			adult	immature	[26]
	<i>Ctenochasma elegans</i>	PTH 1950.33	complete skeleton	Eichstätt, Bavaria			adult	immature	[26]
	<i>Ctenochasma elegans</i>	MBH unnumbered; Wellnhofer 51	complete skeleton	Eichstätt, Bavaria			adult	immature	[26]
	<i>Pterodaustro guinazui</i>	MHNI-UNSL-GEO-V241	complete postcranial skeleton	Loma del Pterodaustro, San Luis Prov. Argentina	Lagarcito Formation	Lower Cretaceous (Albian)	juvenile	hatchling	[32]
Azhdarchoidea	<i>Pterodaustro guinazui</i>	MIC V246	skeleton preserved within an egg				late stage embryo	late stage embryo	[3, 25]
	<i>Aurorazhdarcho micronyx</i>	BSP 1936 I 50	near complete skeleton	Eichstätt, Bavaria			juvenile	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	BSP 1964 XXIII 100	complete skeleton	Schemfeld, Bavaria			juvenile	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	UB E552	complete skeleton	?Eichstätt, Bavaria			juvenile	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	CM 11 425	near complete skeleton	Solnhofen, Bavaria			?adult	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	TM 13 104	complete skeleton	Schemfeld, Bavaria	Solnhofen Beds	Upper Jurassic (Tithonian)	juvenile	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	NMW R405	complete skeleton	?Eichstätt, Bavaria			?adult	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	RGM Leiden St. 18 183	complete skeleton	Eichstätt, Bavaria			juvenile	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	NHM (BMNH) 42 735	complete skeleton	Eichstätt, Bavaria			juvenile	immature	[26]
	<i>Aurorazhdarcho micronyx</i>	ELTE V 256	complete postcranial skeleton	Eichstätt, Bavaria			immature	immature	[S7]

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Supplementary Table S2: Principal dimensions, degree of elongation and mass estimates for fossil eggs of *Hamipterus* and Ornithocheiridae gen. et sp. indet. from the Lower Cretaceous of China. See Methodology for details of mass estimate calculations.

Taxon	Material	Specimen nb.	Major axis (mm)	Minor axis (mm)	Elongation ratio	K	Predicted egg mass (g)	Source
Ornithocheiridae indet	Egg/embryo	IVPP V13758	53	41	1.29	0.56	49.9	[2]
Ornithocheiridae indet	Egg/embryo	JZMP 03-03-02	63.7	36.4	1.75	0.56	47.3	[1]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	47.84	27.14	1.76	0.56	19.7	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	47.88	27.7	1.73	0.56	20.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	48.28	28.46	1.70	0.56	21.9	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	50.28	27.93	1.80	0.56	22.0	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	50.31	27.3	1.84	0.56	21.0	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	50.52	29.26	1.73	0.56	24.2	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	51.04	25.48	2.00	0.56	18.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	51.39	23.72	2.17	0.56	16.2	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	51.43	20.73	2.48	0.56	12.4	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	51.71	30.34	1.70	0.56	26.7	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	51.82	27.04	1.92	0.56	21.2	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	52.21	22.35	2.34	0.56	14.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	53.88	31.32	1.72	0.56	29.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	54	23.37	2.31	0.56	16.5	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	54.18	29.61	1.83	0.56	26.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	54.65	27.16	2.01	0.56	22.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	54.99	22.02	2.50	0.56	14.9	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	55.27	25.92	2.13	0.56	20.8	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	55.76	30.24	1.84	0.56	28.6	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	55.85	32.63	1.71	0.56	33.3	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	56.73	29.34	1.93	0.56	27.3	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	56.73	22.66	2.50	0.56	16.3	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	56.79	23.27	2.44	0.56	17.2	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	57.19	28.61	2.00	0.56	26.2	[8]
<i>Hamipterus tianshanensis</i>	Egg/embryo (#11)	IVPP V 18941	57.54	30.12	1.91	0.56	29.2	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	57.98	22.06	2.63	0.56	15.8	[8]
<i>Hamipterus tianshanensis</i>	Egg/embryo (#5)	IVPP V 18942	58.39	26.46	2.21	0.56	22.9	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	58.98	32.08	1.84	0.56	34.0	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18939	59.3	23.1	2.57	0.56	17.7	[6, 8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	59.55	32.29	1.84	0.56	34.8	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	60.55	27.36	2.21	0.56	25.4	[8]
<i>Hamipterus tianshanensis</i>	Egg/embryo (#12)	IVPP V 18942	61.14	29.74	2.06	0.56	30.3	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	62.77	29.62	2.12	0.56	30.8	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	62.81	28.89	2.17	0.56	29.4	[8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18932.2	63.1	25	2.52	0.56	22.1	[6, 8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18937	64.9	33.9	1.91	0.56	41.8	[6, 8]
<i>Hamipterus tianshanensis</i>	Egg	IVPP V 18941-3	72.32	34.73	2.08	0.56	48.8	[8]
Pterosaur	Egg	IVPP V18938	29.6	22.8	1.30	0.56	8.6	[6, 8]

Supplementary Table S3: Lengths (in mm) and comparative indices for the shoulder girdle and selected fore and hind limb elements of embryos of *Hamipterus tianshansensis* and Ornithocheiridae gen. et sp. indet., and postnatal individuals of four additional ornithocheirid genera. ‘Composite’ based on data for *Hamipterus tianshanensis* embryos 11-13 (see Methods for further details). Actual measurements shown in bold, estimated values shown in grey. Abbreviations: Co, coracoid; E, embryo; Fe, Femur; FL forelimb length; H, hatchling; Hu, humerus; I, immature; M, mature; MIV, metacarpal IV; OS, ontogenetic status; Sc, scapula; UI, ulna; W1-4, wing-finger phalanges 1-4.

Taxon	Specimen	Sc	Co	Hu	UI	M4	W1	W2	W3	W4	Fe	FL	Hu/FL	UI/Hu	M4/Hu	W1/Hu	W1/W2	Fe/Hu	Source
<i>Hamipterus tianshanensis</i>	embryo 13	8.3	8.2	13.3	12.2+		21.9	13.4+			13.6					1.65		1.02	[8]
	embryo 12			13.3	20	12.6+		20						1.50					[8]
	embryo 11	9.2				15.1	22												[8]
	composite	8.3	8.2	13.3	20	15.1	21.9	20	18.8	14.6	13.6	124	0.11	1.50	1.14	1.65	1.10	1.02	
	embryo 4	9.9																	[8]
	embryo 7			16								149							[8]
	hatchling			18.8								175							[8]
Ornithocheiridae gen et sp. indet	IVPP V13758	8.8		13	19	13	23	21	18	14	11	121	0.11	1.46	1.00	1.77	1.10	0.85	[2]
	JZMP-03-03-02	11		16.3	24.2	15.2	27.2	24.5			12.8			1.48	0.93	1.67	1.11	0.79	DU [1]
<i>Boreopteris cuiiae</i>	JZMT 04-07-03			79	110	94	137	122	98	87	82	727	0.11	1.39	1.19	1.73	1.12	1.04	DU [S2]
<i>Zhenyuanopterus longirostris</i>	GLGMV 0001	80	60	210	262	230	360	275	210	190	210	1737	0.12	1.25	1.10	1.71	1.31	1.00	DU [S3]
<i>Arthurdactylus conandoylei</i>	SMK 1132 PAL	80	115	230	312	227	445	402	312	275	190	2203	0.10	1.36	0.99	1.93	1.11	0.83	DU [S4]
<i>Anhanguera santanae</i>	NSM PV19892	112	145	257	384	257	462	387	270	225	236	2242	0.11	1.49	1.00	1.80	1.19	0.92	DU [S5]

Supplementary Table S4: Humerus lengths (mm) and forelimb lengths (mm) for nine species of pterosaur with a humerus length < 21mm. Estimates shown in bold. Abbreviations: Hu, humerus; FL, Forelimb. See electronic supplementary material, for museum acronyms. Linear regression data relates to regression estimates shown in figure 2.

Taxon	Ontogenetic status	Specimen	Hu	FL	Hu/FL	Source
<i>Hamipterus tianshanensis</i>	embryo	composite (11, 12, 13)	13.3	124	0.11	This paper Table S2
<i>Hamipterus tianshanensis</i>	embryo	IVPP V18942 (embryo 7)	16	149	0.11	[8]
<i>Hamipterus tianshanensis</i>	hatchling	IVPP V18942	18.8	175	0.11	[8]
<i>Ornithocheiridae</i> gen et sp. indet.	embryo	IVPP 13758	13	121	0.11	[2]
<i>Aurorazhdarcho micronyx</i>		BSP 1936 I 50	15	115	0.13	[26]
<i>Aurorazhdarcho micronyx</i>		BSP 1964 XXIII 100	16.5	127	0.13	[26]
<i>Aurorazhdarcho micronyx</i>		UB E552	16.9	137	0.12	[26]
<i>Aurorazhdarcho micronyx</i>		CM 11 425	18	165	0.11	[26]
<i>Aurorazhdarcho micronyx</i>		TM 13 104	18.5	154	0.12	[26]
<i>Aurorazhdarcho micronyx</i>		NMW R405	18.5	154	0.12	[26]
<i>Aurorazhdarcho micronyx</i>		RGM Leiden St. 18 183	18.8	146	0.13	[26]
<i>Aurorazhdarcho micronyx</i>		NHM (BMNH) 42 735	19	156	0.12	[26]
<i>Aurorazhdarcho micronyx</i>		ELTE V 256	20.7	176	0.12	[S7]
<i>Anurognathus ammoni</i>		SMNS 81928 (cast)	18.5	114	0.16	[38]
<i>Ctenochasma elegans</i>		lost	14.5	123	0.12	[26]
<i>Ctenochasma elegans</i>		BSP 1875 XIV 501	15	122	0.12	[26]
<i>Ctenochasma elegans</i>		BSP 1867 II 1	15	114	0.13	[26]
<i>Ctenochasma elegans</i>		lost	16.9	136	0.12	[26]
<i>Ctenochasma elegans</i>		PMZ A/III 100	17	136	0.13	[26]
<i>Ctenochasma elegans</i>		PTH 1950.33	19.2	148	0.13	[26]
<i>Ctenochasma elegans</i>		MBH unnumbered; Wellnhofer 51	19.5	149	0.13	[26]
<i>Pterodaustro guinazui</i>	hatchling	V241	19.23	145	0.13	[25]
<i>Pterodaustro guinazui</i>	embryo	MIC V246	18.45	134	0.14	[3, 24]
<i>Pterodactylus antiquus</i>		TM 10 341	15	116	0.13	[26]
<i>Pterodactylus kochi</i>		BMNH 42736	12	85	0.14	[26]
<i>Pterodactylus kochi</i>		BSt 1967 I 276	12.3	91	0.14	[26]
<i>Pterodactylus kochi</i>		TM 13 105	12.8	92	0.14	[26]
<i>Pterodactylus kochi</i>		BSt 1924 V 1	14.5	107	0.14	[26]
<i>Pterodactylus kochi</i>		MCZ 1503	15.5	112	0.14	[26]
<i>Rhamphorhynchus muensteri</i>		MMK V. 45/1 (Wellnhofer 22)	13.5	147	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		MM (Solnhofen) (Wellnhofer 14)	14	157	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		MM (Solnhofen) (Wellnhofer 13)	14.5	161	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		MBH unnumbered (Wellnhofer 20)	14.5	145	0.10	[27]
<i>Rhamphorhynchus muensteri</i>		BSP 1877 X 1 (Wellnhofer 5)	14.6	166	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		lost	15.3	174	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		SL (Bochum) 010 (Wellnhofer 15)	15.3	170	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		BSP 1889 XI i (Wellnhofer 7)	15.5	164	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		JS (Frankfurt) (Wellnhofer 18)	15.5	163	0.10	[27]
<i>Rhamphorhynchus muensteri</i>		MMK 1891. 740 (Wellnhofer 23)	15.5	168	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		MB unnumbered (Wellnhofer 19)	16	176	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		TM 6924 (Wellnhofer 1)	16.5	183	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		CM 11433 (Wellnhofer 21)	16.5	193	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		PTH 1966.6 (Wellnhofer 12)	16.8	173	0.10	[27]
<i>Rhamphorhynchus muensteri</i>		MB unnumbered (Wellnhofer 4)	17	189	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		BSP 1938 I 503 (Wellnhofer 11)	17	211	0.08	[27]
<i>Rhamphorhynchus muensteri</i>		MBH unnumbered (Wellnhofer 17)	18	205	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		BSP 1959 I 400 (Wellnhofer 10)	19	221	0.09	[27]
<i>Rhamphorhynchus muensteri</i>		JS (Frankfurt) (Wellnhofer 29)	19	235	0.08	[27]
<i>Rhamphorhynchus muensteri</i>		BSP 1943 I 36 JS (Wellnhofer 24)	19.5	243	0.08	[27]
<i>Rhamphorhynchus muensteri</i>		GIE (Erlangen) unnumbered (Wellnhofer 31)	20	237	0.08	[27]

Supplementary Table S5: Comparison of developmental stages in *Coturnix coturnix* [23] with four pterosaur embryos. Symbols and abbreviations as for figure 3, except: Cc, *Coturnix coturnix*; St, Sternum.

element >	Hu	R/U	Fe	T/F	Ro	Cr	Ma	Sc	Mc	Mt	Ri	Co	M1-3	Pe	Pd	Cv	Do	Sa	St	Cd	M4
day >	7				8						9					11	12		14	15	16
Cc																					
Ht (comp)						?											?				
Or (IVPP V13758)										?					?						
Or (JZMP 03-03-02)					?					?										?	
Pg (MIC V246)										?											

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