

New smallest specimen of the pterosaur *Pteranodon* and ontogenetic niches in pterosaurs

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Abstract.—A new juvenile specimen of *Pteranodon* from the Smoky Hill Chalk Member of the Niobrara Formation of western Kansas had an estimated wingspan in life of 1.76 m, ~45% smaller than the smallest previously known specimens, but does not differ in morphology from larger specimens. Its presence indicates that juveniles were capable of flying long distances, so it falsifies the interpretation of *Pteranodon* as growing rapidly to adult size under parental care before flying. Instead juveniles were precocial, growing more slowly to adult size while flying and feeding independently for several years before going to sea. Because juveniles are otherwise unknown in the Smoky Hill Chalk Member, they must have occupied different environments and ecological niches than adults; thus *Pteranodon* exhibited ontogenetic niches. Evidence is presented that most other pterosaurs (e.g., *Rhamphorhynchus*, *Pterodactylus*, *Anhanguera*) also exhibited various ontogenetic niches, which, along with their large body size, suggests that pterosaur taxonomic diversity was rather low, like that of crocodilians.

Introduction

The first specimens of the pterosaur *Pteranodon*, two isolated distal ends of wing metacarpals, were found in 1870 by O.C. Marsh and the Yale College Scientific Expedition in the Smoky Hill Chalk Member of the Niobrara Formation of western Kansas (Marsh, 1871). Over the next ten years, hundreds of additional specimens of *Pteranodon* plus ten or so specimens of the smaller *Nyctosaurus* were collected in the Smoky Hill Chalk Member by Marsh and various parties working for him. Less-intensive collecting has continued to the present day such that there are over 1000 specimens of *Pteranodon* in museum collections.

Bennett (1992, 1994a, 2001) studied all available *Pteranodon* specimens from the Smoky Hill Chalk Member and found two species, *P. longiceps* Marsh, 1876 and *P. sternbergi* Harksen, 1966, which differed in jaw and cranial crest shape, but no evidence that more than one species was present at any time, so they seem to have formed a single anagenetically evolving lineage with *P. sternbergi* from the lower parts of the Smoky Hill Chalk Member evolving into *P. longiceps* from the upper parts of the Smoky Hill Chalk Member and the Sharon Springs Member of the Pierre Shale. Specimens were bimodally distributed with the small size-class with estimated wingspans in life of 3.0–4.8 m roughly twice as abundant as the large size-class with wingspans of 4.8–6.7 m. The ontogenetic ages of specimens were determined using size-independent criteria reflecting the extent of ossification and fusion of bones, and immature individuals were found to make up ~15% of the sample and to be present in both size-classes such that the size-classes could not be age-classes (Bennett, 1993). The size-classes differed only in cranial crest size and pelvic morphology, and were interpreted as dimorphic

sexes: the small class consisting of females with small crests and large pelvic canals to allow the passage of relatively large eggs and the large class consisting of males with small pelvic canals and large crests to attract mates and/or intimidate rivals in a polygynous mating system (Bennett, 1992). The absence of specimens of *Pteranodon* with wingspans of <3 m from the Smoky Hill Chalk Member was not attributed to a bias against the preservation of small specimens because the Smoky Hill Chalk Member also preserves specimens of the pterosaur *Nyctosaurus* with wingspans of 1.6–3.3 m. Therefore, based on the absence of small individuals and the presence of large subadults with immature skeletons, it was argued that *Pteranodon* exhibited rapid growth to adult size while under parental care before flying and feeding independently (Bennett, 1993). Similarly, based on the absence of small juveniles from the collections of *Nyctosaurus* from the Smoky Hill Chalk Member and ornithocheiroids from the Cambridge Greensand of England and the Romualdo Formation of Brazil, it was argued that the pattern of rapid growth while under parental care was shared with other large pterodactyls.

A new juvenile specimen of *Pteranodon* collected from the Smoky Hill Chalk Member is so small that it challenges the interpretation of rapid growth to large size before flying and feeding (Bennett, 2014a). This paper describes the specimen and discusses its implications for *Pteranodon*'s growth and behavior. The interpretation of rapid growth while under parental care is rejected and it is concluded that *Pteranodon* exhibited ontogenetic niches, flying and feeding independently from hatching and growing to adult size over several years while occupying different environments and ecological niches at different stages of its life history. Evidence is also presented that most other pterosaurs exhibited ontogenetic niches.

Repositories and institutional abbreviations.—AMNH, American Museum of Natural History, New York, New York; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; FHSM, Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas; FMNH, Field Museum of Natural History, Chicago, Illinois; GPIT, Paläontologische Forschungs-, Lehr- und Schausammlung, Institut für Geowissenschaften (formerly the Geologische-Paläontologische Institut), Universität Tübingen, Tübingen, Germany; JME-SOS, JuraMuseum (Solnhofen Sammlung), Eichstätt, Germany; KUVP, Natural History Museum, University of Kansas, Lawrence, Kansas; LACM, Los Angeles County Museum of Natural History, Los Angeles, California; MTM, Hungarian Natural History Museum, Budapest, Hungary; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NSM, National Science Museum, Tokyo, Japan; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California; SM, Senckenberg Museum, Frankfurt, Germany; TM, Teyler Museum, Haarlem, Netherlands; and YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Material and methods

The new specimen, FHSM 17956, was examined with stereo microscope, measured, and photographed. A small piece of cortical bone that was removed from the posterior side of the neck of metacarpal (Mc) IV, just proximal to the distal condyles, was sectioned, ground, and polished, and the resulting thin sections were examined and photographed with optical and polarizing microscopes. Measurements of other specimens of *Pteranodon* and *Nyctosaurus* were taken from Bennett (2001, and unpublished data). Wingspans in life were estimated using the method of Bennett (2001), in which span equals two times the summed lengths of the humerus, antibrachium, McIV, and wing phalanges (WP) 1–4; the omission of the pectoral girdle and carpus compensates for flexures of the elbow, wrist, and metacarpophalangeal joints and the curvature of the wingfinger. In addition, where elements were missing or incomplete, their lengths were calculated from linear regression equations calculated from available samples (Bennett, 2001, 2007a, 2013a).

Ontogenetic ages of specimens were determined using size-independent criteria reflecting the extent of ossification and

fusion of the skeleton (Bennett, 1993, 1995), and unless otherwise stated all discussion of immaturity and maturity refers to osteological rather than sexual maturity. The ontogeny of pterosaurs is divided into six stages: eggs; hatchlings and young-of-the-year; small juveniles; large juveniles that are significantly smaller than mature adults; subadults with immature skeletons, but not significantly smaller than mature adults; and adults with mature skeletons.

Kellner (2010) revised *Pteranodon* and split it into four species in three genera, but that interpretation has not been generally accepted (e.g., Witton, 2013; Martin-Silverstone et al., 2017). Several errors in the revision have been identified and will be addressed elsewhere, therefore Bennett's (1994a) taxonomic scheme is accepted here.

A privately held fragmentary pterosaur specimen from the Smoky Hill Chalk Member referred to as Tweety or Ptweety has been reconstructed and interpreted as a very small *Pteranodon*, even though it is within the size range of *Nyctosaurus* specimens. Based on my examinations of the specimen, the morphology of its notarium, humeri, and McIV is consistent with that of *Nyctosaurus*, but inconsistent with that of *Pteranodon*, so the specimen provides no evidence of a *Pteranodon* smaller than FHSM 17956. Unfortunately, the reconstruction so misused the specimen that it is of no scientific value whatsoever.

Description

The new specimen, FHSM 17956, is an incomplete right wing preserved in dorsal view on a roughly pentagonal slab of pale yellow chalk ~ 54 x 19 x 4 cm (Fig. 1). It was collected from the Smoky Hill Chalk Member of the Niobrara Formation in the SE¼, NE¼, SE¼ of Sec. 29, T11S, R23W of Trego County, Kansas by Mr. Glenn Rockers of Hays, Kansas, who prepared the specimen and donated it to the FHSM. Exposures in the E½, SE¼ of Sec. 29 have gray chalk at the base, ~2 m of pale yellow chalk with a series of five very fine-grained bentonite seams spaced 25, 32, 20, and 27 cm apart, and ~3.5 m of massive bioturbated chalk caprock at the top, and preserve abundant *Platyceramus platinus* (up to 1.2 m diameter) and *Pseudoperma congesta*. The caprock is Hattin's (1982) Marker Unit 10 and the sequence of bentonite seams beneath it

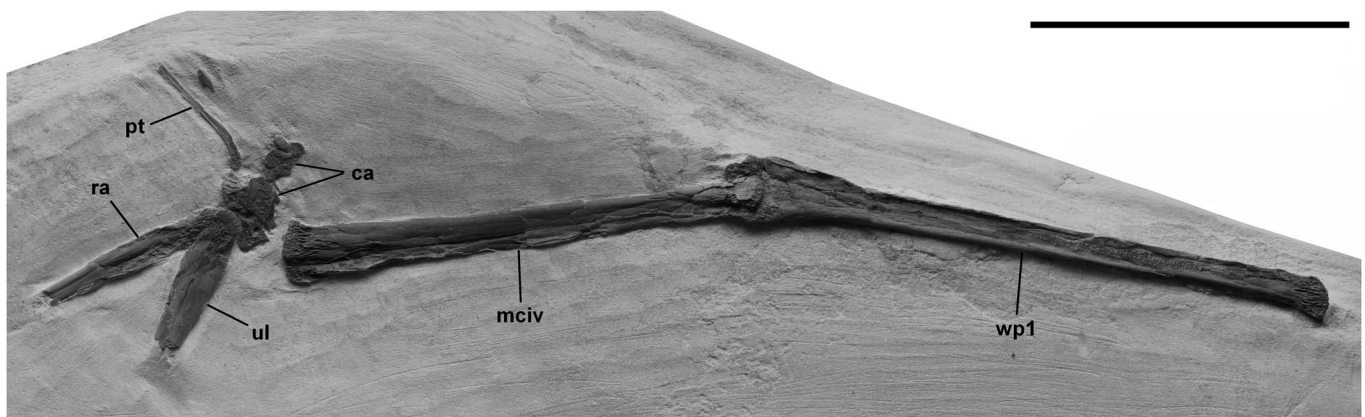


Figure 1. *Pteranodon* sp. indet. (FHSM 17956). Photograph of incomplete right wing in dorsal view. Abbreviations: ca, carpus; mciv, metacarpal IV; pt, pteroid; ra, radius; ul, ulna; and wp1, wing phalanx 1. Scale bar is 10 cm.

compares well with what he described immediately below the caprock, as does the abundance of bivalve fossils. Based on the specific locality information, the specimen was collected from the fossiliferous chalk no more than 1.5 m below Marker Unit 10, and is of upper middle Santonian age.

The specimen consists of the distal halves of the radius (61 mm) and ulna (50 mm), the carpus, and complete McIV (160 mm) and WP1 (194 mm). The bones were flattened by compression, as is typical of Smoky Hill Chalk Member pterosaur specimens, and some of the bone of WP1 in an area ~7.5 cm x ~5 mm near the distal end was lost and reconstructed with plaster painted to resemble the adjacent bone. The bones of the specimen are largely articulated and were presumably held in articulation by ligaments until arriving on the sea floor, but there are minor dislocations that probably resulted from gravity or currents after the ligaments decomposed. Thus, the radius, ulna, and carpus are preserved in close association, but are separated from McIV by ~6 mm, and the individual carpal elements exhibit dislocations. McIV and WP1 are articulated with the metacarpophalangeal joint extended as in flight.

The radius and ulna halves exhibit irregular breaks with no impressions of the missing portions in the chalk, and they are splayed apart proximally even though the distal ends are preserved nearly in contact with the proximal syncarpal. This indicates that the bones were broken or perhaps bitten off before preservation of the specimen.

The carpus is shown in Figure 2. All carpal elements are severely deformed by compression such that they preserve little of their original morphology, and all exhibit pitted surfaces indicative of incomplete ossification. The radiale and ulnare that would have fused to form the proximal syncarpal are preserved slightly disarticulated from one another and close to the distal radius and ulna and the distal row of carpals. Few details of the

radiale are discernable other than its wedge-shaped dorsal aspect and part of the intersyncarpal articular surface. The ulnare exhibits the articular surface for the dorsal articular facet of the ulna and its slender-waist dorsal aspect is pierced by an oval pneumatic foramen. Its intersyncarpal articular surface is not exposed. The three distal carpals that would have fused to form a distal syncarpal are preserved slightly disarticulated from one another and close to the proximal carpals, but well separated from the proximal end of McIV. Most prominent is the sub-rectangular dorsal aspect of distal carpal 3, which is pierced by an oval pneumatic foramen. Most of distal carpal 2 is hidden behind distal carpal 3, but its prominent preaxial carpal process is visible anterior to distal carpal 3, and distal carpal 4 is largely hidden behind distal carpal 3. The preaxial carpal is still articulated with the preaxial carpal process of distal carpal 2, and its fovea is directed upward with the pisiform (= Sesamoid A of Bennett, 2001, 2008) articulated in it. The pteroid is preserved in dorsal view a short distance away from the carpals. It is shaped like an ice hockey stick and is ~42 mm long as preserved, although its non-articular end is missing. The articular end of the pteroid has a pitted articular surface indicative of incomplete ossification. There is a more or less straight section ~11 mm long and ~4 mm wide, a gentle bend of ~25°, and then the bone narrows to 2 mm to form a long straight shaft extending proximally. A small bone fragment that does not seem to be related to the carpus lies ~8 mm from the shaft of the pteroid.

Metacarpal IV is crushed such that it seems to present a posterolateral view, whereas WP1 is crushed such that it seems to present a fully dorsal view. The posterior margin of McIV is broken and some fragments presumably were lost. The extensor tendon process is articulated with the rest of WP1, but is unfused. The articular ends of both bones were poorly ossified

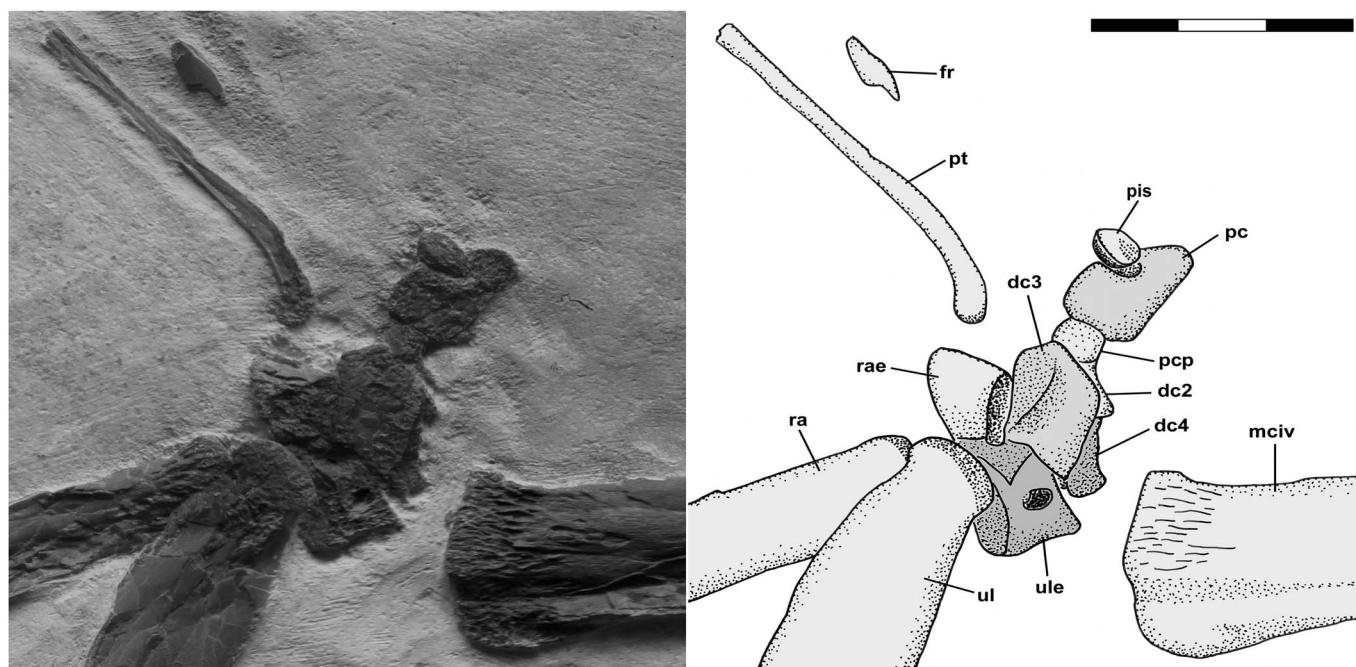


Figure 2. *Pteranodon* sp. indet. (FHSM 17956). Detailed photograph and interpretive drawing of right carpus in dorsal view. Individual carpal elements are indicated with different shades of gray. Abbreviations: dc, distal carpal; fr, indeterminate bone fragment; mcv, metacarpal IV; pc, preaxial carpal; pcp, preaxial carpal process of distal carpal 2; pis, pisiform; pt, pteroid; ra, radius; rae, radiale; ul, ulna; and ule, ulnare. Scale bar is 3 cm.

and their fragile cortical bone was lost when prepared with a rotating wire brush, revealing the internal septate bone. The bones are otherwise unremarkable.

Ontogenetic status.—The articular surfaces of the radius, ulna, pteroid, McIV, and WP1 are pitted and rough, indicating incomplete ossification, and similar pitting is visible on the carpal elements as well. The diaphyses of the radius, ulna, pteroid, McIV, and WP1 exhibit immature grain with many vascular canals opening onto the external surface of the bone. The proximal and distal rows of carpals are not fused into proximal and distal syncarpals, and the extensor tendon process is not fused to WP1. Thus, the specimen exhibits immature states of all three size-independent criteria that Bennett (1993) used to identify immature specimens of *Pteranodon* and does not exhibit any evidence of osteological maturity, so it is immature.

Thin section.—Cortical bone was sampled from the posterior side of the neck of McIV, just proximal to the distal condyles where it was thought that the bone would be thickest and provide the best chance of finding a line of arrested growth (LAG), if present. The resulting thin section (Fig. 3.1) is 540 μm thick, and exhibits well-vascularized plexiform bone (sensu Francillon-Vieillot et al., 1990) with vascular canals opening onto the external surface. The internal surface is uneven and appears to be resorptive. No LAG is evident, but a second section ground much thinner exhibits multiple discontinuous narrow circumferential bands of blue against a background of magenta when examined under polarized light with a first-order retardation ($=\lambda$) plate (Fig. 3.2). The spacing of the bands ($\sim 80 \mu\text{m}$) suggests some sort of regular variation in fiber orientation. The pattern of bone and vascularization is similar to that previously found in the immature bone of a subadult *Pteranodon* (Bennett, 1993, fig. 2C), although the bone is thinner and the spacing between vascular canals is somewhat less than in the subadult.

Discussion

Only two pterosaur genera, *Pteranodon* and *Nyctosaurus*, are known from the Smoky Hill Chalk Member (Bennett, 1994a). FHSM 17956 is referred to *Pteranodon* because the morphology of its distal syncarpal with prominent preaxial carpal process and ice hockey-stick-shaped pteroid (Bennett, 2001, and unpublished data) are as found in *Pteranodon* and unlike *Nyctosaurus*, in which the syncarpal has a short preaxial carpal process and the pteroid has a pointed lateral end extending distally beyond the articulation (Williston, 1903; Bennett, 2003). In addition, the proportions of FHSM 17956 (i.e., ratio of lengths of McIV and WP1, ratios of proximal width and diameters of distal condyles to McIV length, and ratios of proximal, midshaft, and distal widths to WP1 length, Bennett, 2001, and unpublished data) are consistent with those of *Pteranodon* and inconsistent with those of *Nyctosaurus* (Fig. 4). There is no evidence that the specimen represents a new species, but it is not clear which *Pteranodon* species it does represent. Bennett (1994a) thought that the transition between *P. sternbergi* and *P. longiceps* occurred in the middle of the

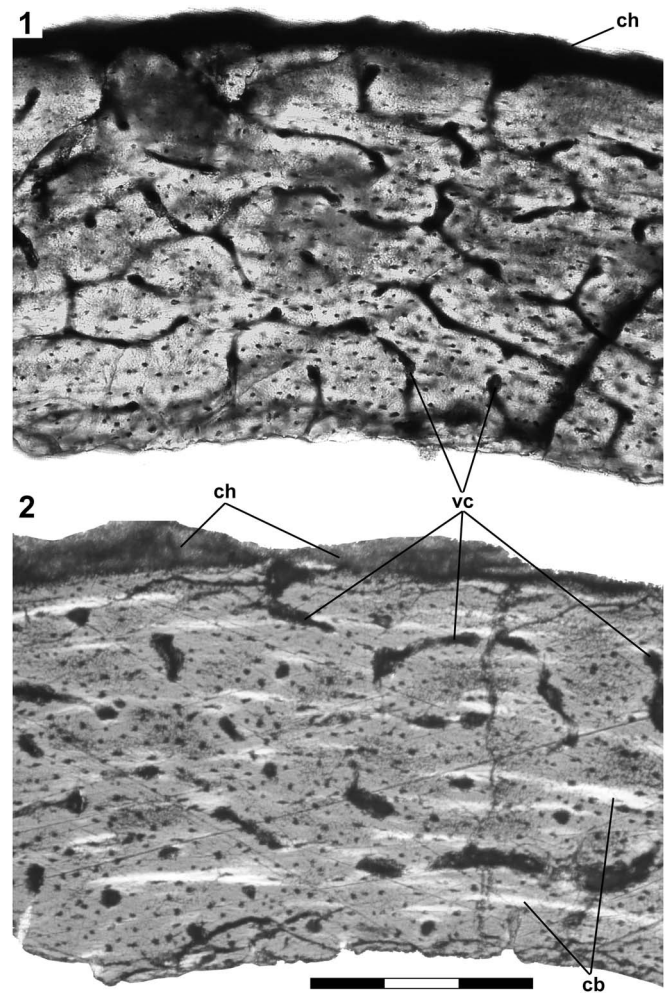


Figure 3. *Pteranodon* sp. indet. (FHSM 17956). (1) Thin section of cortical bone from the distal end of metacarpal IV photographed under visible light; (2) thinner section photographed under polarized light and first order retardation ($=\lambda$) plate showing narrow discontinuous circumferential bands of blue (light gray) against a background of magenta (medium gray); dark band at top is chalk residue on external surface of bone. Abbreviations: cb, circumferential band; ch, chalk; and vc, vascular canal. Scale bar is 300 μm .

Smoky Hill Chalk Member and arbitrarily chose the non-fossiliferous caprock (Marker Unit 10, Hattin, 1982) as the dividing line between the species. Because the specimen was collected from just below the caprock and does not exhibit any characters used to differentiate the species of *Pteranodon*, it is considered to be *Pteranodon* sp. indet.

The lengths of the missing elements of FHSM 17956 were calculated using Bennett's (2001) regression equations, and the wingspan in life estimated as 1.76 m (Table 1). The smallest relatively complete previously known specimen of *Pteranodon*, AMNH 4908, consists of a partial trunk skeleton and tail, scapulocoracoid, humerus through WP2, both femora and tibiae, and a disarticulated foot (Bennett, 2001; Table 1), had an estimated wingspan in life of 3.33 m. Just slightly larger is YPM VP 2345, an incomplete wing of an immature individual, and YPM VP 2350, an isolated WP1 (352 mm long). The greatest diameters of the dorsal condyles of McIV of AMNH 4908 and YPM VP 2345 are 20 and 19.9 mm, respectively. There are eight fragmentary specimens with greatest dorsal condyle

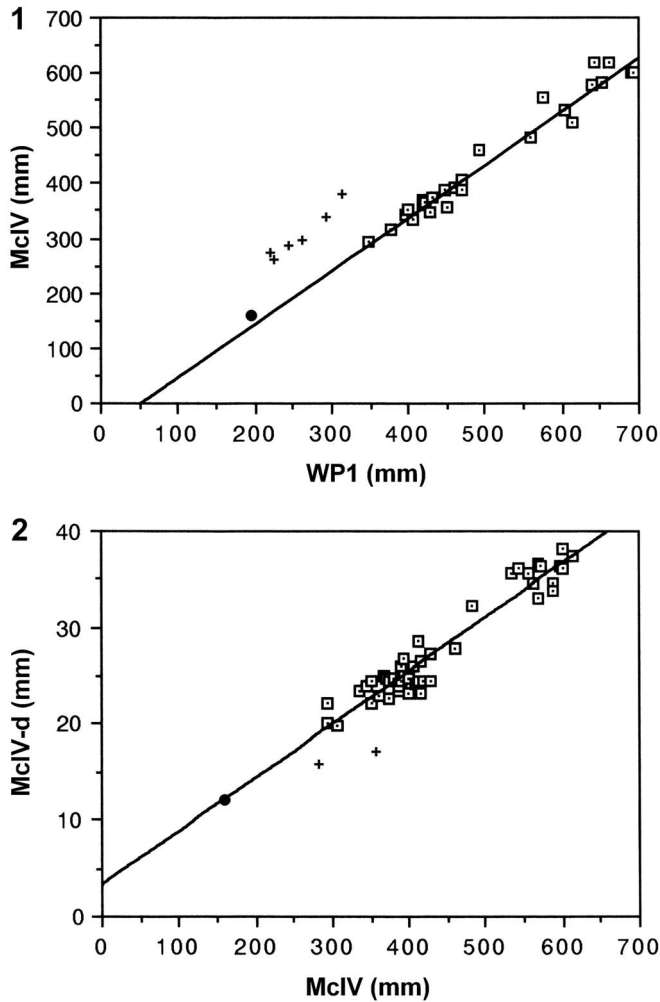


Figure 4. Scatter plots of limb element measurements of *Pteranodon* and *Nyctosaurus* from the Smoky Hill Chalk Member, Niobrara Formation. (1) Metacarpal (Mc) IV length plotted against wing phalanx (WP) 1 length. (2) Greatest diameter of dorsal condyle of distal wing metacarpal (McIV-d) against McIV length. *Pteranodon* data from Bennett (2001, fig. 119D, I) indicated by dotted squares, *Nyctosaurus* data from Bennett (2003, and unpublished data) indicated by plus signs, and FHSM 17956 indicated by the large dot. FHSM 17956 was not included in the samples from which the regression equations were calculated.

Table 1. Length measurements (in mm except as noted) of limb elements and the greatest diameter of the dorsal distal condyle of the wing metacarpal of small specimens of *Pteranodon* from the Smoky Hill Chalk Member. Wingspans in life estimated by the method of Bennett (2001).

	FHSM 17956	FMNH P27476	AMNH 4908	YPM VP 2345
Humerus	74*	—	134	140*
Ulna	117*	—	198	207*
Metacarpal IV (McIV)	160	—	294	308
McIV dorsal condyle	12.0	18	20	19.9
Wing phalanx 1	194	—	348	380*
Wing phalanx 2	154*	—	328	306
Wing phalanx 3	120*	—	234*	220*
Wing phalanx 4	63*	—	129*	108
Femur	72*	—	139	139*
Tibia	148*	—	215	218*
Estimated span (m)	1.76	3.0**	3.33	3.34

*length of incomplete or missing limb bone calculated with linear regression equations (Bennett, 2001)

**wingspan estimated based on comparison to AMNH 4908

diameters of 18–20 mm (FMNH P27476, YPM VP 2454, KUVB 85401, YPM VP 2755, LACM 51136 “B”, YPM VP 2444, 2490, and 2710, arranged in order of increasing diameter), although it should be noted that abrasion of the poorly ossified condyles may have reduced their diameters somewhat. The smallest of the eight specimens is 10% smaller than AMNH 4908, so presumably would have had an estimated wingspan in life of 3.0 m. Thus, FHSM 17956 is much smaller than the smallest previously known specimens; only ~53% the size of AMNH 4908 and ~59% the size of FMNH P27476. There is no information as to the sex of FHSM 17956, but if it was female it would have been ~53% the size of the smallest previously known female, whereas if it was male it would have been only ~37% the size of the smallest previously known male.

FHSM 17956 exhibits immature states of the size independent criteria Bennett (1993) used to assess maturity of specimens, i.e., incomplete ossification of epiphyses, immature grain on limb bone shafts, and no fusion of bones, and so is immature. Though much smaller than the smallest previously known specimens, it is otherwise indistinguishable from the immature subadults present throughout the sample of *Pteranodon*; thus no more immature morphologically than the most immature previously known specimens. However, because it is much smaller than the subadults, it is considered to be a juvenile. As such, it was presumably significantly younger than all previously known specimens.

Although FHSM 17956 is much smaller than previously known specimens, its morphology provides no evidence to suggest that it was incapable of flying out into the Western Interior Seaway where it was found (~200 km from the nearest shore). It is unlikely that it died elsewhere and floated out to sea before sinking to the bottom and becoming preserved; large dinosaurs (e.g., *Claosaurus*, *Niobrarasaurus*) occasionally floated to sea, but the Smoky Hill Chalk Member preserves no evidence that small terrestrial vertebrates (e.g., lizards, immature crocodylians) did so. One reviewer argued that there is no evidence that FHSM 17956 flew to its resting place, an isolated wing ripped off a carcass onshore could conceivably have floated to sea. That is true, but following that line of reasoning there is no evidence that any of the >1000 specimens of *Pteranodon* flew out to sea and no evidence that any pterosaur actually could fly. Despite that, all pterosaur workers find it most parsimonious to interpret pterosaurs as having flown. It is also most parsimonious to interpret FHSM 17956, smaller than but otherwise indistinguishable from the ~150 immature subadults in the sample of *Pteranodon*, as having flown out to sea, though it may not have done so intentionally and might have been blown by a storm.

The thin section (Fig. 3) demonstrates that the bone histology is similar to that of immature subadult *Pteranodon* (Bennett, 1993, fig. 2C), so is consistent with the interpretation of the specimen as immature. No LAG was found in the thin section, just as none was found in the thin section of the subadult, although LAGs do occur in *Pteranodon* bones (L.E. Wilson, personal communication, 2016). Chinsamy et al. (2008, 2009) documented rapid growth without LAGs in *Pterodaustro* for the first 2–3 years until ~50% of full size was attained. Four LAGs were found in a tibia ~91% of full size, with the

inter-LAG spacing decreasing outward demonstrating that the growth rate decreased progressively until full size was attained in ~7 years. If *Pteranodon* grew as *Pterodaustro* did, then LAGs would not be expected in FHSM 17956 because it is only ~46% the size of a fully grown modal female with ~3.8 m wingspan.

Bennett (1992) proposed that *Pteranodon*'s marked sexual dimorphism and female biased sex ratio was indicative of a lek-type mating system with large males competing for access to more abundant females. In addition, the presence of immature specimens with poorly ossified epiphyses and limb bone shafts with virtually all bones unfused combined with the absence of specimens of <3 m wingspan was interpreted as evidence of rapid growth to adult size. I assumed that juveniles could not have sustained rapid growth while flying and feeding independently, and so thought that *Pteranodon* hatchlings would have required parental feeding before flying and feeding independently, much as many extant seabirds do (Bennett, 1993). The discovery of FHSM 17956 does not affect the interpretation of sexual dimorphism, but falsifies the assumption of rapid growth and parental feeding before flying and feeding independently.

If small juveniles were capable of flying out to sea, then why are they so rare in the Smoky Hill Chalk Member? It is conceivable that there was a bias against the preservation of small specimens. The sample of *Nyctosaurus* from the Smoky Hill Chalk Member consists of 30 specimens, most of which have estimated wingspans of 1.6–2.0 m. If one were to assume that *Pteranodon* and *Nyctosaurus* were equally abundant in the Western Interior Seaway, then the relative rarity of small *Nyctosaurus* specimens (30 *Nyctosaurus* versus >1000 *Pteranodon*) might suggest a bias against the preservation of small individuals, but if that were the case then small juveniles of *Pteranodon* would still be ~30 times rarer than similarly sized specimens of *Nyctosaurus*. However, there is no evidence that *Nyctosaurus* was as abundant as *Pteranodon* and no evidence of a bias against the preservation of small pterosaurs. Therefore, the extreme rarity of small juveniles of *Pteranodon* in the Smoky Hill Chalk Member is interpreted as reflecting an extreme rarity in life because they did not normally go to sea until their wingspans were ~3 m. Juveniles between ~1.5 and ~3 m wingspan must have been occupying different environments and ecological niches than adults did. Thus, *Pteranodon* exhibited ontogenetic niches.

Ontogenetic niches have been defined as varying patterns of resource use as individuals increase in size from hatching or birth to adulthood and beyond (Werner and Gilliam, 1984), such that individuals in different stages of their life history occupy different environments and/or ecological niches in sequence. Ontogenetic niches are found in a wide variety of animals. Most fishes exhibit several shifts of food type and often habitat as they grow; most amphibians transition from aquatic, often herbivorous larvae to carnivorous terrestrial adults, and newts return to water after a terrestrial eft stage with associated shifts in food type (Tomašević Kolarov et al., 2011); and many reptiles switch from carnivory to herbivory with increasing size. There can also be morphological changes associated with habitat and dietary changes; for example, hatchling *Alligator mississippiensis* (Daudin, 1802) occupy well-vegetated swamps and marshes, have short blunt snouts and needle-like teeth suited

to piercing, and feed primarily on insects; juvenile *A. mississippiensis* have longer snouts and transition to crustaceans and small vertebrates; and adults prefer deeper open waters of rivers and lakes, have long and broad snouts and robust blunt teeth suited to crushing, and feed on turtles and large mammals (Subaluskus et al., 2009; Gignac and Erickson, 2015). However, many birds and mammals do not exhibit ontogenetic niches other than a period of parental feeding before transitioning to feeding independently in the same environment and niche as their parents.

Ontogenetic niches are often simply a necessary consequence of the great increases in body length and mass that some organisms exhibit, e.g., a few mm to 2.5 m body length in Atlantic Goliath Grouper *Epinephelus itajara* (Lichtenstein, 1822) (Artero et al., 2015) or a 7000-fold increase in body mass in *Alligator* (Gignac and Erickson, 2015), with the animal switching to larger and larger foods and the environments where those foods can be obtained as it grows. However, selection will favor those environments and niches that provide an optimum balance of predation risk and growth rate (Dahlgren and Eggleston, 2000).

Ontogenetic niches have been recently described in dinosaurs (Codron et al., 2012, 2013; Fowler et al., 2013), which exhibited great increases in body length and mass as they grew to adulthood. Therefore, it should not be surprising that *Pteranodon* exhibited ontogenetic niches as hatchlings with wingspans of ≤1 m that grew into adults with wingspans up to ~6 m. With the exception of FHSM 17956, the sample of *Pteranodon* from the Smoky Hill Chalk Member consists of ~85% mature adults and ~15% immature subadults of similar size (Bennett, 1993). The fossils are so abundant in the Smoky Hill Chalk Member of the Niobrara Formation and the Sharon Springs Member of the Pierre Shale Formation, making up ~10% of tetrapod fossils in both the Smoky Hill Chalk Member (SCB, personal observation) and the Sharon Springs Member (Nicholls and Russell, 1990), that adults and subadults must have spent much time in the Western Interior Seaway. *Pteranodon* may also have been long-lived because a thin section of wing bone of an adult (Bennett, 1993, fig. 2D; Fig. 5) exhibits three closely spaced circumferential bands ~22 μm apart, which compare well to the closely spaced LAGs in the peripheral cortex of the dinosaur *Syntarsus* (Chinsamy, 1990, fig. 1C). Spaced ~22 μm apart and ~480 μm below the external surface, if interpreted as LAGs and annual lines, the thickness of bone between the first LAG and the external surface would represent ~22 years if the growth rate was constant. Thus some individuals may have survived many years after reaching skeletal maturity, which would be similar to long-lived albatrosses that can live 40 years or more (Bird Banding Laboratory, 2016).

The Smoky Hill Chalk Member in western Kansas consists of ~180 m of impure chalk deposited in open sea 150–300 m deep in the middle of the Western Interior Seaway (Hattin, 1982), which supported a diverse and abundant planktonic and pelagic biota, but had a depauperate benthos because of poorly oxygenated bottom waters (Stewart, 1990; Everhart, 2005). *Pteranodon* at sea fed on fish and perhaps invertebrates as well. An isolated mandible of a female *Pteranodon*, AMNH 5098, is preserved in dorsal view with ~3 cm diameter mass of fish

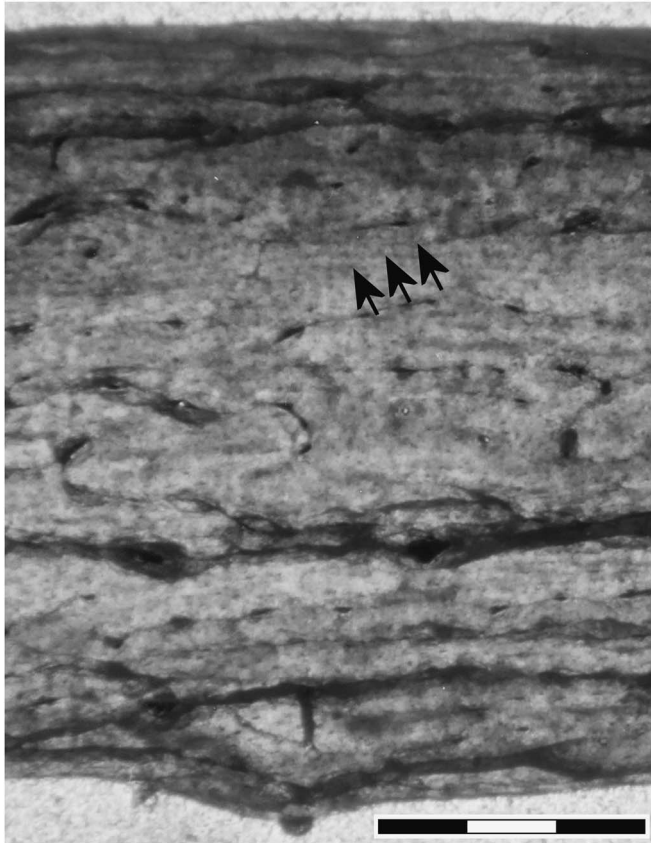


Figure 5. *Pteranodon* sp. indet. Thin section of cortical bone of limb bone shaft of a mature adult after Bennett (1993, fig. 2C). Arrows point to closely spaced circumferential bands interpreted as lines of arrested growth of a very slow growing fully mature adult individual. Scale bar is 500 μ m.

vertebrae just behind the posterior margin of the symphyseal shelf of the mandible (Fig. 6.1), and another female specimen consisting of an articulated cranium and mandible was preserved in left lateral view with a small mass of fish remains in a similar position immediately behind the posteroventral end of the symphysis (G. Rockers, personal communication, 2015). In both specimens, the masses were presumably ejected from the gut perimortem. Brown (1943, p. 106) commented on AMNH 5098 and stated that the mass included “the joint of a crustacean,” but my examinations failed to find any such evidence. Most of the vertebrae are 3.5–4.0 mm long, but the largest vertebra is 8.8 mm long. It is not clear what fish species the vertebrae pertain to, but they are consistent with those of *Enchodus*, which is common in the Smoky Hill Chalk Member. The smaller vertebrae are comparable to those of an *Enchodus* ~23–27 cm long, whereas the largest vertebra is comparable to those of an *Enchodus* ~53 cm long, a fish that was quite large relative to the head and body of *Pteranodon* (Fig. 6.2). Thus, the Smoky Hill Chalk Member represents a pelagic feeding habitat in the middle of the Western Interior Seaway where adult and subadult *Pteranodon* spent much of their time feeding on relatively large fishes, and FHSM 17956 is a one-in-a-thousand occurrence of a small juvenile that apparently strayed from its normal habitat and flew out to sea.

The Sharon Springs Member in western Kansas, South Dakota, and Wyoming consists of ~15 m of gray claystone and

shale deposited in the Western Interior Seaway as the seaway regressed, narrowed, and received more terrigenous sediment (Gill et al., 1972). Like the Smoky Hill Chalk Member, on which it often lies conformably, it supported a diverse and abundant pelagic biota that was simply the continuation of the Smoky Hill Chalk Member’s fauna (Carpenter, 1990, 2008). The sample of *Pteranodon* from the Sharon Springs Member is much smaller than that from the Smoky Hill Chalk Member, but like that of the Smoky Hill Chalk Member it consists primarily of mature adults with a small percentage of immature subadults of virtually adult size (Bennett, 2001). Thus the Sharon Springs Member also represents a pelagic feeding habitat in the middle of the Western Interior Seaway where adult and subadult *Pteranodon* fed on relatively large fishes.

The absence of hatchlings and juveniles in the Western Interior Seaway poses three questions. At what age did *Pteranodon* subadults go to sea? What were *Pteranodon* hatchlings and juveniles doing before they went to sea? Where were *Pteranodon* hatchlings and juveniles?

At what age did Pteranodon subadults go to sea?—Relatively little is known about pterosaur growth rates. Bennett (1995; Fig. 7.1) studied the sample of *Rhamphorhynchus muensteri* Goldfuss, 1831 from the Solnhofen Limestone monographed by Wellnhofer (1975) and found it to consist of two distinct size-classes plus a few larger individuals that might represent more size-classes. Specimens in the small size-class were most immature, specimens in the medium size-class were older but still immature, and only the largest specimens could be considered fully mature adults. I argued that the size-classes represent year-classes resulting from seasonal sampling of a population of individuals growing at a more or less uniform rate, and that the growth rate was comparable to that of extant *Alligator*. If *Rhamphorhynchus* maintained a constant growth rate, it would have taken ~3 years for hatchlings to grow to the size of the largest specimen (~1.8 m wingspan); however, it is likely that the growth rate declined with increasing size and age and it took somewhat longer. Similarly, Bennett (1996, 2013a; Fig. 7.2) studied the sample of *Pterodactylus antiquus* (Sömmerring, 1812) from the Solnhofen Limestone monographed by Wellnhofer (1970) and found it to consist of two distinct year-classes plus a few larger individuals that might represent more year-classes, which again suggested it would have taken at least three years to reach adult size (~1.1 m wingspan). The patterns of growth of *Rhamphorhynchus* and *Pterodactylus* compare well to that of *Pterodaustro* (Chinsamy et al., 2008, 2009), which grew rapidly for 2–3 years until half grown and then grew progressively more slowly for another ~4 years until reaching full size (~2.5–3 m wingspan, Witton, 2013; L. Codorniu, personal communication, 2015), except that *Pterodaustro* took longer to reach its greater full size. There is no evidence that juvenile *Pterodaustro* grew faster than juvenile *Rhamphorhynchus* in order to reach the larger size of adults, so *Pterodaustro* presumably prolonged the period of rapid growth.

Prondvai et al. (2012) examined the bone histology of selected elements of five specimens of *Rhamphorhynchus*. Two specimens in the first year-class exhibited fibrolamellar bone with occasional laminar endosteal bone, and on that basis they were interpreted as early juveniles. Two specimens in the

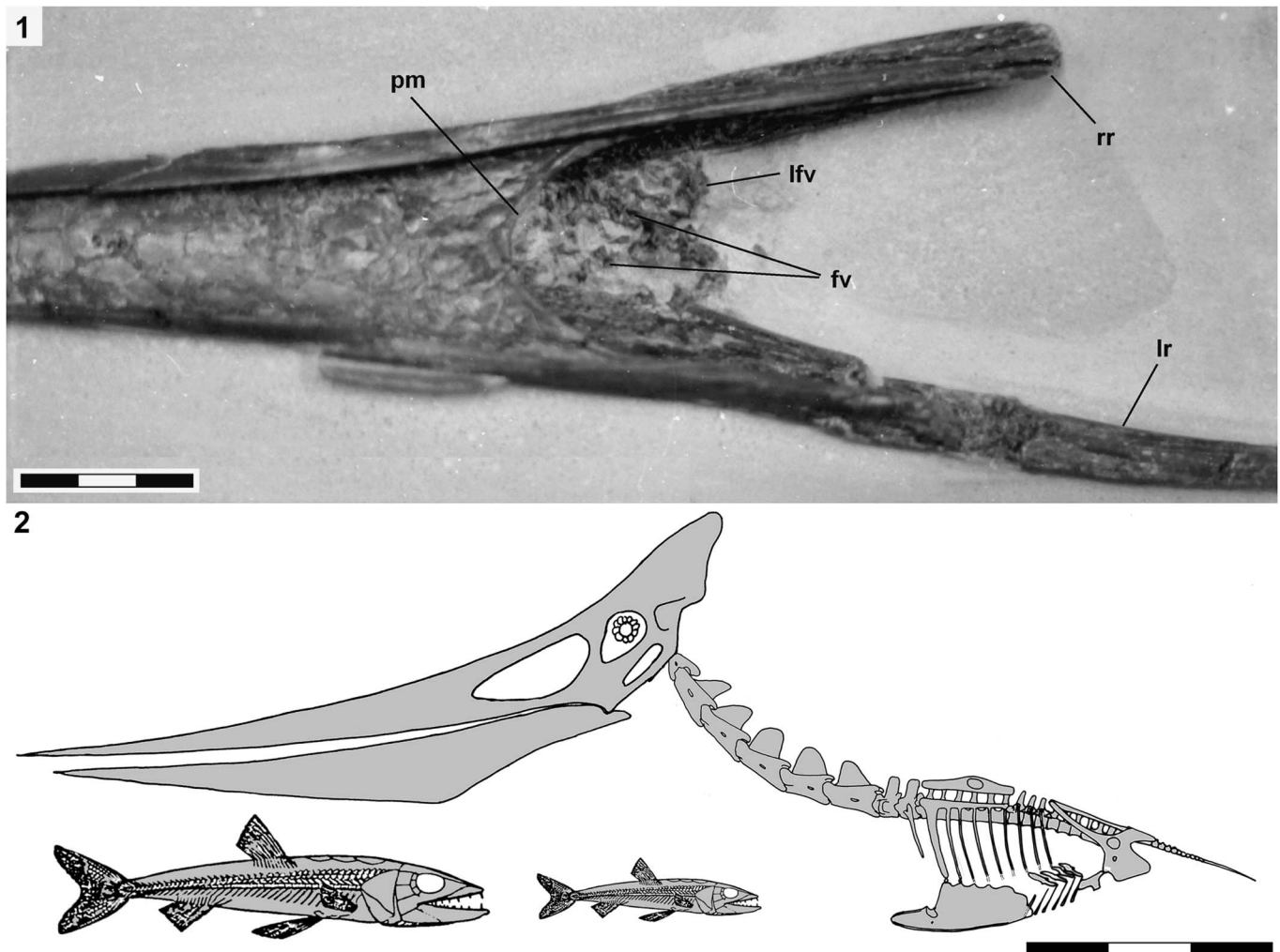


Figure 6. *Pteranodon* and prey. (1) AMNH 5098, incomplete mandible of *Pteranodon* in dorsal view with mass of fish vertebrae preserved just behind symphysis. (2) Reconstruction of *Pteranodon* axial skeleton in left lateral view modified from Bennett (2001) and scaled to size of AMNH 5098 with skeletal reconstructions of fish (after Woodward, 1902–1912, fig. 12) scaled to sizes of the typical and largest fish vertebrae in the mass. Abbreviations: fv, mass of fish vertebrae, rr, right ramus of mandible; lr, left ramus of mandible; lfv, largest fish vertebra; and pm, posterior margin of symphyseal shelf. Scale bars are 3 and 15 cm, respectively.

second year-class exhibited parallel-fibered bone and lamellar bone with LAGs. The smaller of the two exhibited two closely spaced LAGs in the inner half of the cortex and a thick layer of parallel-fibered bone in the outer half of the cortex with a few primary osteons but lacking LAGs, and was interpreted as a late juvenile. The larger specimen in the second year-class, MTM V 2008.33.1, exhibited both primary and secondary osteons and three LAGs in the outer half of the cortex of the ulna, but only one in the femur, and was interpreted as an adult exhibiting skeletal maturity. The closely spaced LAGs in these specimens make it unlikely that every LAG is an annual line, but they may record successive stops and starts during a season of slowed growth. The largest specimen, BSP 1929.I.69, which exhibited parallel-fibered bone with primary osteons and 5–6 LAGs, was also interpreted as an adult. Prondvai et al. (2012) also discussed two specimens described by Padian et al. (2004), one similar in size and histology to the specimens in the small year-class, and RAM V97017/258, similar in size to MTM V 2008.33.1, which exhibited two widely spaced LAGs and fibrolamellar bone transitioning to lamellar bone with reduced vascularity in its

ulna, three LAGs in its femur, and four LAGs in its tibia. Prondvai et al. (2012) interpreted RAM V97017/258 as an adult.

Based on their interpretation that MTM V 2008.33.1, RAM V97017/258, and the larger BSP 1929.I.69 were all mature adults, Prondvai et al. (2012) concluded Bennett's (1995) medium year-class was not a real ontogenetic stage because some mature adults occurred in it. However, Prondvai et al. (2012) did not use the terms juvenile and adult as Bennett (1995) did. Whereas Prondvai et al. (2012) interpreted MTM V 2008.33.1 as adult because of its histology and the fusion of bones, Bennett (1995) applied that term only to the largest most mature specimens and would have viewed the presence of an external fundamental system as the definitive indicator of histological adulthood just as Woodward et al. (2011) did in *Alligator*. Despite exhibiting relatively mature histology, MTM V 2008.33.1 is less mature than BSP 1929.I.69 because its jaws and teeth are less robust than those of BSP 1929.I.69, just as BSP 1929.I.69 is less mature than GPIT RE 7321 because its jaws and teeth are less robust than those of GPIT RE 7321. In the end, Prondvai et al.'s (2012) histological information is consistent with and supports Bennett's (1995, 1996) interpretation that the small

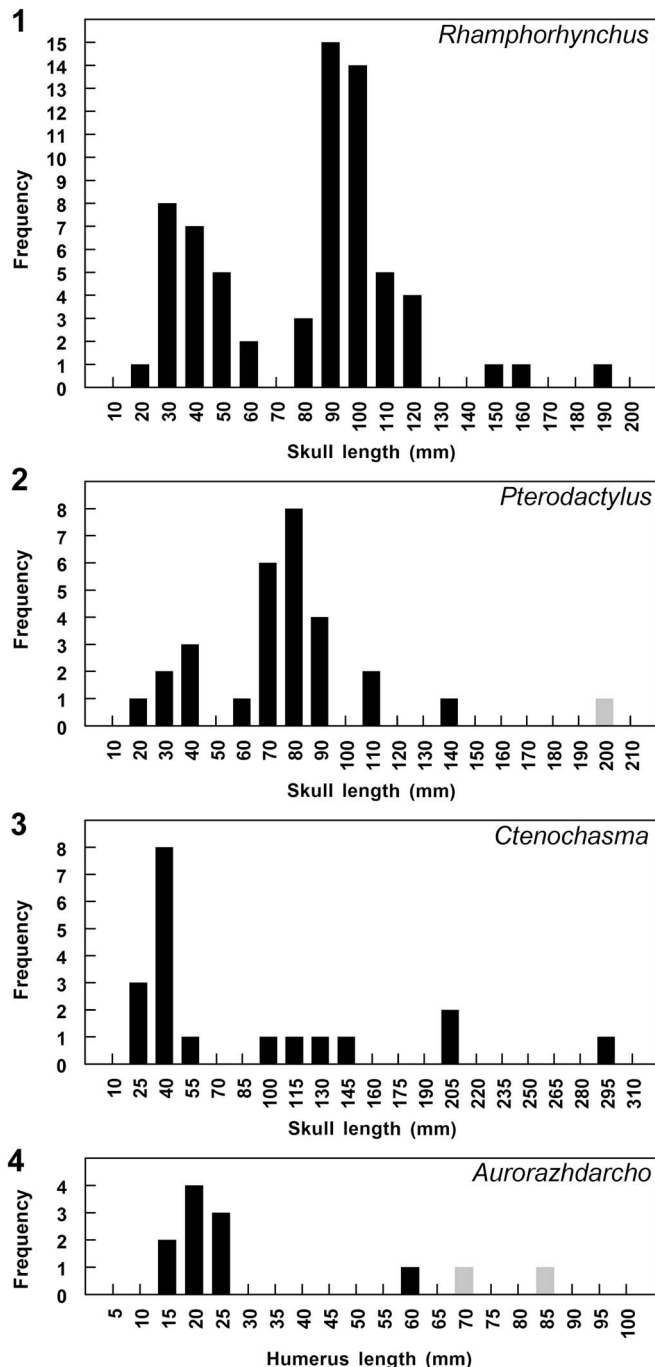


Figure 7. Size-frequency histograms of samples of pterosaurs from the Solnhofen Limestone. (1) *Rhamphorhynchus muensteri* skull length (data from Wellnhofer, 1975; Bennett, 1995). (2) *Pterodactylus antiquus* skull length (data from Wellnhofer, 1970; Bennett, 2006, 2103a), gray bar at right is the adult from the Hienheim Beds. (3) *Ctenochasma elegans* skull length (data from Wellnhofer, 1970; Bennett, 2007a, 2013a). (4) *Aurorazhdarcho micronyx* humerus length (data from Wellnhofer, 1970; Bennett, 2006, 2013a), gray bars at right represent approximate size of *Gnathosaurus subulatus* Meyer, 1834 specimens known only from skulls. See text for explanation.

and medium year-classes of *Rhamphorhynchus* consist of small immature and larger more-mature specimens, respectively, and the finding that the upper end of the medium year-class includes specimens with relatively mature histology and fused bones refines the interpretation.

Prondvai et al. (2012) interpreted the transition to lamellar bone with primary and secondary osteons in *Rhamphorhynchus* as resulting from the onset of flight based on comparisons to enantiornithine birds, and it was stated that juveniles would have been restricted to the ground and/or trees and would have received parental feedings or somehow fed themselves. There are several problems with that interpretation. It is not clear that the histological transition necessarily reflects anything other than a decrease in growth rate with increasing size, and there is no reason to think that pterosaur ontogeny would be comparable to that of enantiornithines (assuming that the relationship between ontogeny and histology in enantiornithines is correctly understood) because pterosaurs were not closely related to birds and are as different from birds and bats as birds and bats are different from each other. More importantly, the smallest, most immature specimens of *Rhamphorhynchus* were no more than a few weeks old, yet had skeletal anatomy and proportions similar to those of adults (Unwin, 2006; Lü et al., 2011). The long, well-ossified, although actively growing forelimb bones that would be subjected to bending loads in flight, extensive patagia (e.g., BSP 1938 I 503), and low wing loadings because of their small size indicate they were capable of powered flight. Prondvai et al. (2012) mischaracterized that interpretation as superprecociality (i.e., active locomotion within minutes of hatching), and argued against it and presumably precociality (i.e., relatively mature and mobile from hatching in contrast to the relative helplessness at hatching of altriciality) as well on the grounds that pterosaur eggs represented only a small investment of nutrients relative to maternal body size. Pterosaur eggs were not particularly small relative to maternal trunk volume (Unwin and Deeming, 2008; Lü et al., 2011), but it is the absolute rather than relative size that is important for precociality and some diapsids with relatively much smaller eggs produce super-precocial hatchlings (e.g., baby sea turtles dig out of the nest and sprint for the safety of the sea immediately after hatching, and baby crocodylians swim well immediately). Pterosaur hatchlings seem to have been precocial, but it is unlikely that they were superprecocial because of the tight folding of the wingfinger within the egg (Unwin and Deeming, 2008). In most pterosaurs, the wingfinger's interphalangeal joints allowed only slight flexion and extension (Bennett, 2007b, 2013b), and so it probably took hours to days for the wingfinger and patagium to attain flight configuration. Prondvai et al. (2012) also suggested that hatchlings' flight muscles would not have been powerful enough for flight, but there is no evidence of that because hatchlings of the superprecocial Australian Brush-Turkey, *Alectura lathami* Gray, 1831, can fly within 24 hours of hatching (Starck and Ricklefs, 1998; Dial and Jackson, 2011). Hatchling diapsids usually have residual yolk constituting ~10% of hatching mass that can sustain the individual for some weeks (Allsteadt and Lang, 1995; Tucker et al., 1998; Radder et al., 2007; Wolanski et al., 2007; Van Dyke et al., 2011), and it is conceivable that hatchling pterosaurs used such residual yolk for some days of grounded flapping so as to attain the wing's flight configuration, to exercise the pectoral musculature, and to train the neural control mechanisms needed for flight.

The large fully formed wings of hatchling *Rhamphorhynchus* and *Pterodactylus* are in marked contrast to the wings of neonate bats and most hatchling birds. The wings of Indian Pygmy Bat,

Pipistrellus mimus (Wroughton, 1899), neonates are small and there is a linear increase in wing length and area and decrease in wing loading until sustained flight is attained at ~29 days (first flight ~22 days; Isaac and Marimuthu, 1997). Those of larger fruit bats *Cynopterus sphinx* (Vahl, 1797) and *Rousettus leschenaulti* (Desmarest, 1820) similarly exhibit a linear increase in wing length and area until attaining wingspans of 70–80% that of adults and first flight at ~50 days (sustained flight ~60 days) whereas wing loading decreases linearly for ~35 and ~50 days, respectively, before beginning to increase with increasing body mass (Elangovan et al., 2004, 2007). Birds are more variable than bats in this regard, but many hatchling birds lack flight feathers and grow considerably before flying, increasing wing span and area (Starck and Ricklefs, 1998). In addition, the long bones of wings of hatchling California Gulls, *Larus californicus* (Lawrence, 1854), remain relatively weak as they grow to flight size and only attain the necessary strength for flight when wing flapping begins shortly before fledging at ~35 days (Pugesek, 1983; Carrier and Leon, 1990). If pterosaurs delayed the onset of flight until they were half grown, then they probably would have hatched with small wings that only reached the necessary length, strength, area, and wing loading for flight as the individual approached half size and the onset of flight, but that is not the case.

One last problem is that Prondvai et al. (2012, p. 2) did not discuss how long *Rhamphorhynchus* would have been restricted to the ground and/or trees, receiving parental feedings or feeding themselves, and stated only that the presence of fibrolamellar bone suggested that “growth did not protract over several years.” The fact that fibrolamellar bone is correlated with ‘rapid’ deposition in extant endotherms has been used to argue that the presence of fibrolamellar bone in extinct organisms indicates ‘rapid’ growth; however, just as with the argument that flying vertebrates must be endothermic because extant vertebrate fliers are endotherms, correlation does not imply causation, and ‘rapid’ in pterosaurs may not be the same as ‘rapid’ in extant birds. Fibrolamellar bone has been reported in free living *Alligator* (Tumarkin-Deratzian, 2007) and in temnospondyls (Woodward et al., 2014), so the presence of fibrolamellar bone in *Rhamphorhynchus* is not necessarily inconsistent with an *Alligator*-like growth rate, and any bone tissue will be deposited more slowly in an animal that allows its metabolic rate and body temperature to decrease significantly at rest and at night resulting in a low mean body temperature (e.g., endotherms exhibiting torpor, ectotherms) than in an animal that maintains a constant high metabolic rate and body temperature. Without temporal information to support it, Prondvai et al.’s (2012) suggestion that fibrolamellar bone in *Rhamphorhynchus* indicates that growth did not take several years is unreliable. Bennett’s (1995, 1996) interpretation that the discontinuous distribution of small, medium, and large size-classes in the samples of *Rhamphorhynchus* and other pterosaurs and fishes from the Solnhofen Limestone are year-classes resulting from seasonal mortality and/or preservation of specimens provides the needed temporal information to evaluate the growth rate of *Rhamphorhynchus*. The time represented by the gap between the small and medium size-classes is ~1 year, which contradicts Prondvai et al.’s (2012) suggestion that growth did not take several years. Prondvai et al. (2012) made no attempt to counter the interpretation of year-classes or explain away the discontinuous distributions.

The histological transition to slower-growing bone in *Rhamphorhynchus* seems to have occurred in the larger individuals in the medium year-class, so if juveniles delayed the onset of flight until the histological transition, then they would have delayed flight for ~1 year. That would be a long time to be grounded and receiving parental feedings, and the abundance of fossils of hatchlings and juveniles in the Solnhofen Limestones, significantly greater than that of non-flying lizards (Barthel et al., 1990), suggests that they spent much time in the lagoons, which would be unlikely if they received parental feeding. It is also unlikely that juveniles could have fed themselves adequately on the ground or in the trees with their fish-grab dentition and their very long wingfingers and very short hindlimbs hampering both walking and climbing. If the onset of flight was correlated with the histological transition to a slower-growing bone in other pterosaurs, then *Pterodaustro* would not have flown for 2–3 years until half grown. Similarly, *Pteranodon* subadults that were not significantly smaller than mature adults would not have attained flight until after they arrived in the Western Interior Seaway because they exhibit well-vascularized plexiform bone without evidence of lamellar bone or LAGs (Bennett, 1993). FHSM 17956 with 1.76 m of well-developed wings are no different structurally or histologically from those of subadults, and would not have been able to fly until it almost doubled its size. In short, there is no evidence that *Rhamphorhynchus* and *Pterodaustro* could not have flown and sustained growth to half-size over the course of ~1 and 3–4 years, respectively, and the well-developed wings of hatchling *Rhamphorhynchus* and *Pterodactylus*, plus the fact that FHSM 17956 must have flown to the middle of the Western Interior Seaway, demonstrate that hatchlings and juveniles with plexiform and fibrolamellar bone were capable of flight. Therefore, Prondvai et al.’s (2012) interpretation of delayed onset of flight must be rejected.

In the end, we cannot know how old *Pteranodon* subadults were when they went to sea. However, if their growth rate was comparable to that of *Rhamphorhynchus*, *Pterodactylus*, and *Pterodaustro*, then it would have taken at least three years to reach the size of FHSM 17956 and another 3–4 years to reach ~3 m wingspan. In growing to modal wingspans of 3.8 and 5.6 m for females and males (Bennett, 1992), respectively, *Pteranodon* presumably prolonged the period of rapid growth even further than *Pterodaustro* did by delaying the transition from plexiform to lamellar bone until their wingspan was 3.0 m or more. Indeed, based on the assumption that a 3 m wingspan subadult would grow into a modal 3.8 m mature adult female, the transition would occur at ~80% of maximum size rather than the ~50% seen in *Pterodaustro*. *Pteranodon* also seems to have delayed the development of large cranial crests by males until after they went to sea (Bennett and Penkalski, 2017), which suggests that sexual maturation in both sexes was roughly coincident with skeletal maturation, as indicated by well-ossified epiphyses, mature grain on limb bone shafts, and fusion of bones some time after going to sea. That would be consistent with the interpretation of Chinsamy et al. (2008, 2009) that the histological transition from fast- to slower-growing bone reflects the onset of sexual maturation and the diversion of nutrients and energy from rapid growth to reproduction.

What were Pteranodon hatchlings and juveniles doing before they went to sea?—*Pteranodon* hatchlings and juveniles presumably were flying and feeding independently like those of *Rhamphorhynchus*, *Pterodactylus*, and *Pterodaustro*. They would have resembled females in having pointed edentulous, roughly equilateral jaws comparable to those of herons, storks, and many other extant birds, which would have been well suited to feeding on all manner of small animals. The more conservative interpretation is that *Pteranodon* hatchlings and juveniles fed on suitably sized aquatic prey (e.g., crustaceans, small fishes) in shallow waters and progressed to larger and larger prey as they grew. However, they also could have fed on suitably sized prey in terrestrial environments (e.g., arthropods, small tetrapods), much as extant storks do.

Where were Pteranodon hatchlings and juveniles?—At present, there is no evidence to suggest where *Pteranodon* hatchlings and juveniles were, but if they fed on suitably sized aquatic prey, then they could have lived around lakes, rivers, wetlands, and estuaries, or along beaches and coastlines, wherever small aquatic prey was available, whereas if they fed on suitably sized terrestrial prey, then they could have lived in varied terrestrial environments. Bennett (1994b) envisioned *Pteranodon* laying eggs and rearing young in crowded colonies on islands free of terrestrial predators, much as do many extant seabirds. However, whereas pterosaurs do seem to have aggregated to lay their eggs in colonies (Bell and Padian, 1995; Wang et al., 2014), there is no evidence that they did so on islands and they probably laid their eggs near those environments that provided suitable niches for hatchlings so that hatchlings would not need to travel far to find food and relative safety.

The sample of *Nyctosaurus gracilis* (Marsh, 1876) from the Smoky Hill Chalk Member, though numerically smaller than that of *Pteranodon*, is similar to it in most respects. It consists of 30 specimens with wingspans of 1.6–3.3 m (Bennett, 1994a, 2003, and unpublished data), 11 of which are immature, but do not differ significantly in size from mature individuals and are considered to be subadults, whereas the other 19 are considered to be adults. There is size variation in the sample, but bimodality reflecting sexual dimorphism has not been demonstrated. As with *Pteranodon*, the sample of *Nyctosaurus* consists of mature adults and immature subadults of similar size that were feeding in the middle of the Western Interior Seaway and there is no evidence of hatchlings or juveniles. Although the absence of hatchling and juvenile *Nyctosaurus* is less significant statistically than the one in 1000 occurrence of a juvenile *Pteranodon*, the absence indicates that hatchlings and juveniles occupied different environment(s) and ecological niche(s) than adults such that *Nyctosaurus* exhibited ontogenetic niches.

The pattern of ontogenetic niches exhibited by *Pteranodon* and *Nyctosaurus* would have permitted hatchlings and juveniles to occupy environments that provided suitably sized prey and an optimal balance between prey availability and predation risk, yet permitted large adults to access the abundant supply of large fishes in the Western Interior Seaway that would not have been available if adults stayed around their breeding grounds and continental or coastal environments with hatchlings and juveniles. At sea, the marked size dimorphism of *Pteranodon* with modal males of 5.6 m wingspan, ~50% larger than modal

females of 3.8 m wingspan (Bennett, 1992), would have enabled males to feed on significantly larger fishes than females. This suggests that the available food resources of the Western Interior Seaway were partitioned between *Pteranodon* sexes by size, and *Nyctosaurus* with wingspans of 1.6–3.3 m and more lightly built jaws than *Pteranodon* presumably fed on even smaller prey that represented a third partition of the Seaway's food resources. Thus, *Pteranodon* sexes and *Nyctosaurus* seem to have occupied three different niches at sea so as to reduce competition.

Other pterosaurs

Having found evidence of ontogenetic niches in the size and age distributions of samples of *Pteranodon* and *Nyctosaurus* from the Smoky Hill Chalk Member and Sharon Springs Member, the size and age distributions of samples of other pterosaurs from selected well-studied Konservat-Lagerstätten were surveyed for evidence of ontogenetic niches (Table 2). Whereas the complete absence of eggs, hatchlings, small juveniles, and large juveniles save FMNH 17956 provides evidence of ontogenetic niches in *Pteranodon*, in other pterosaurs the presence of eggs, hatchlings, and small juveniles or the absence of subadults and adults can provide evidence of ontogenetic niches. Eggs are unlikely to travel far, so their presence indicates proximity to nesting grounds. Similarly, hatchlings are unlikely to travel great distances, so it is reasonable to assume that localities where hatchlings have been found are relatively close to nesting grounds. Subadults and adults probably could travel great distances, so their absence or unexpected rarity will suggest that they were not normally present or abundant in the depositional environment.

Solnhofen Limestone.—The Solnhofen Limestone consists of well-bedded lithographic limestones deposited in shallow hypersaline lagoons connected with open-marine environments (Barthel et al., 1990). Anoxic bottom waters provided conditions favorable to the preservation of vertebrate skeletons, and Unwin (2006) reported >1000 pterosaur specimens have been found. Small fishes (e.g., *Leptolepides*) were a significant component in the fauna, and demonstrate that the lagoons and/or nearby waters would have provided abundant food for piscivorous pterosaurs.

The pterosaurs of the Solnhofen Limestone of southern Germany were monographed by Wellnhofer (1970, 1975) and restudied by Bennett (1995, 1996, 2006, 2007a, 2007b, 2013a, 2013c, 2014b). Bennett (1995) determined the ontogenetic ages of *Rhamphorhynchus muensteri* specimens, and noted that the sample of 109 specimens monographed by Wellnhofer (1975) consists of two distinct size-classes interpreted as year-classes resulting from seasonal sampling of a population of individuals growing at a more or less uniform rate over the course of several years, plus a few larger individuals that might represent additional year-classes (Fig. 7.1). The first year-class consists of 33 hatchlings and young-of-the-year with wingspans of 29–59 cm, the second year-class consists of 73 yearlings with wingspans of 86–132 cm, there are two larger more mature specimens with wingspans of ~1.5 m, and there is one large fully

Table 2. Ontogenetic composition of samples of selected taxa from selected Konservat-Lagerstätten and corresponding interpretations of the Lagerstätte's habitat in stratigraphic order. Data include N, number of individuals in taxon sample, and percentages (rounded to the nearest non-zero integer) of: E, eggs; H, hatchlings; SJ, small juveniles; LJ, large juveniles; SA, subadults; and A, adults. See text for discussion.

Lagerstätte	Taxon	N	E	H	SJ	LJ	SA	A	Habitat
Smoky Hill Chalk Mbr., Niobrara Formation	<i>Pteranodon</i>	710	—	—	—	1	15	85	Pelagic adult feeding
	<i>Nyctosaurus</i>	30	—	—	—	—	37	63	
Bissegby Formation	<i>Azhdarcho lancicollis</i> ¹	13	—	8	38	31	15	8	Riverine multi-age feeding
	<i>Pterodactylo gaimazi</i> ²	>28	7	7	—	43	7	36	Lacustrine multi-age feeding near nesting grounds
Romualdo Member, Santana Formation	<i>Anhangueira</i> s.s.	21	—	—	—	—	19	81	Pelagic adult feeding
	<i>Anhangueira</i> s.l. (including <i>Brasileodactylus</i> , <i>Maaradactylus</i> , and <i>Tropeognathus</i>)	31	—	—	—	16	13	71	Pelagic large juvenile through adult feeding
Solnhofen Limestone	<i>Rhamphorhynchus muensteri</i>	109	—	30	67	2	—	1	Lagoonal hatchling and juvenile feeding
	<i>Pterodactylus antiquus</i>	28	—	21	71	7	—	—	
	<i>Aurorazhdarcho micronyx</i>	10	—	90	—	10	—	—	
	<i>Germanodactylus cristatus</i>	4	—	50	—	—	25	25	Lagoonal hatchling feeding near nesting grounds
	<i>Ctenochasma elegans</i>	19	—	63	21	11	—	5	Lagoonal multi-age feeding

¹Data based on proximal humeral fragments, from A. Averianov (personal communication, 2015). ²Data from L. Codorniu (personal communication, 2015).

mature adult specimen with a wingspan of 1.8 m (Wellnhofer, 1975; Bennett, 1995).

Bennett (1996) noted year-classes in samples of the pterodactyloids monographed by Wellnhofer (1970). The sample of *Pterodactylus antiquus* consists of 28 specimens based on Wellnhofer's data, Bennett's (1996) study, and Jouve's (2004, see also Bennett, 2013a) synonymization of *P. kochi* (Wagner, 1837) with *P. antiquus* after the addition of the Vienna specimen (NHMW 1975/1756/0000, Wellnhofer, 1987) and the exclusion of JME-SOS 4593 that Bennett (2006) referred to *Germanodactylus cristatus* (Wiman, 1925). Note that Vidovic and Martill (2014) erected the genus *Aerodactylus* for the species *Pterodactylus scolopaciceps* (Meyer, 1860), which Wellnhofer (1970) considered a junior synonym of *P. kochi*. They referred several *Pterodactylus* specimens to *Aerodactylus*, which they considered to differ from *Pterodactylus* in possessing a unique combination of features, but did not cite any features that did not fall within the range of variation of the hypodigm of *P. antiquus*. Five scatter plots of length measures were presented to support their interpretation, but: (1) all reflect only minor differences in skull depth, (2) slopes of regression lines of their Morphotype 1 (= *Aerodactylus*) in two plots (Vidovic and Martill, 2014, figs. 9, 10) differed markedly from those of other Solnhofen pterodactyloids such that the morphotype probably is an unnatural assemblage, and (3) no evidence was presented to suggest that the differences do not merely reflect preservational (e.g., orientation, compression) or individual variation. In the end, despite arguing that the specimens differed, they did not present evidence or arguments that the differences are taxonomically significant, and therefore *Aerodactylus scolopaciceps* is considered a junior synonym of *Pterodactylus antiquus*.

The sample of *P. antiquus* consists of two distinct year-classes plus a few larger individuals that might represent more year-classes (Fig. 7.2). The first year-class consists of six hatchlings and young-of-the-year with wingspans of 17–23 cm, the second year-class consists of 20 yearlings with wingspans of 33–54 cm, and there are two larger more mature specimens with wingspans of 64 and 71 cm, respectively. Note that the largest known specimen of *P. antiquus* is a large isolated skull of an adult with a wingspan of 1.06 m (Bennett, 2013a) from the Hienheim Beds that are stratigraphically equivalent to the Mörnsheimer Limestone.

The sample of *Ctenochasma elegans* (Wagner, 1861) consists of 19 specimens based on the 15 listed in Bennett's (2007a) revision plus the four specimens that Wellnhofer (1970) had referred to *Pterodactylus micronyx* Meyer, 1856 (his Ex. 29 at Neuberg, Ex. 33 at Brno, Ex. 34 [TM 13104], and Ex. 37 [SM 405/NHMW 2012/0118/0001]), which Bennett (2013a) referred to *Ctenochasma* on the basis of skeletal proportions. The sample consists of two distinct year-classes plus a few larger individuals that might represent more year-classes (Fig. 7.3). All specimens of >125 mm skull length and >83 cm wingspan consist of isolated skulls. The first year-class consists of 12 hatchlings and young-of-the-year with wingspans of 23–36 cm, the second year-class consists of four yearlings with wingspans of 75–97 cm, there are two larger more mature specimens with wingspans of ~1.3 m, and one large fully mature adult specimen with a wingspan of 1.9 m.

The sample of *Aurorazhdarcho micronyx* (Meyer, 1856) consists of 12 specimens after the holotype of *A. primordius* Frey et al., 2011 was synonymized with *Pterodactylus micronyx* and the four specimens mentioned above that were referred to *Ctenochasma elegans* (Bennett, 2013a) are excluded, but only ten specimens after the two specimens that have different skeletal proportions and may represent a distinct taxon (Bennett, 2013a) are excluded. All of them, except the holotype of *Aurorazhdarcho primordius*, form what is interpreted as a single year-class of hatchlings and young-of-the-year with wingspans of 23–46 cm (Fig. 7.4). The single large specimen had a wingspan of 1.06 m.

The sample of *Germanodactylus cristatus* (Wiman, 1925) is too small to reveal the presence or absence of year-classes, but consists of two hatchlings with wingspans of 21 and 22 cm, one subadult, and one adult with a wingspan of 96 cm. Bennett (2006) noted that the two hatchlings came from a single quarry, Workerszell near Eichstätt, that seems not to have produced any other pterosaur specimens, which suggests that that part of the basin was near the *Germanodactylus* nesting grounds and provided conditions preferred by the hatchlings, and that juveniles occupied other habitats.

Comparison of the ontogenetic compositions of the samples of Solnhofen pterosaurs reveals three different patterns of abundance. *Rhamphorhynchus* and *Pterodactylus* share a pattern with two year-classes, the second more than twice as abundant as the first, and subadults and adults rare to absent. It is surprising that yearlings are more abundant than hatchlings. The abundance of hatchlings suggests that the nesting grounds were close to the Solnhofen lagoons, and the abundance of juveniles indicates that they remained near the lagoons feeding and growing for up to two years. If one assumes that hatchlings and yearlings had equivalent mortality and preservation rates, this could have resulted if hatchlings were present near the lagoons for only part of the depositional season whereas yearlings were present for the entire season. Alternatively, yearlings might have had a higher mortality rate than hatchlings because they were transitioning to a different food source. If the histological transition that occurred in the larger individuals in the medium year-class correlates with the onset of sexual maturity, then *Rhamphorhynchus* probably would have first bred at two years old. Although specimens of ~1.8 m wingspan are expected to be rare, the relative rarity of specimens between the upper limit of the medium year-class and the largest specimens, which would represent two or more additional year-classes, suggests that sexually mature breeding individuals spent most of their time elsewhere. Comparable histological information is not available for *Pterodactylus*, but it is possible that *Pterodactylus* was similar to *Rhamphorhynchus* in age at first breeding and preferred habitat of adults.

Ctenochasma exhibits a second pattern with a single year-class of hatchlings and young-of-the-year and low numbers of older juveniles through adults. This suggests that *Ctenochasma* individuals remained near the lagoons feeding on small aquatic prey throughout their life, and is consistent with a high hatchling mortality followed by reduced mortality of juveniles through adults well adapted to their environment.

Aurorazhdarcho exhibits a third pattern with a single year-class of hatchlings and young-of-the-year and a few large adults,

whereas yearlings and larger juveniles are absent. This suggests that the nesting grounds were close to the Solnhofen lagoons and that hatchlings spent only their first year near the lagoons, whereas older juveniles and adults left the lagoons and fed elsewhere, perhaps returning to the area only to lay their eggs. This might have been because the dentition of *Aurorazhdarcho* was suited to feeding on considerably larger prey than *Ctenochasma*, such that the preferred foods of older juveniles and adults were not available in the Solnhofen lagoons.

Bissekty Formation.—The Bissekty Formation consists of ~67 m of medium- to coarse-grained sands with occasional cross-bedding and abundant fossils reflecting a fluvial environment with a very diverse vertebrate fauna, including the pterosaur *Azhdarcho lancicollis* Nesov, 1984 (Archibald et al., 1998; Averianov, 2010). The sample of *Azhdarcho* consists of one hatchling, five small juveniles, four large juveniles, two immature subadults, and one mature adult based on a count of proximal humeral fragments (A. Averianov, personal communication, 2015). That pattern of abundance is consistent with progressively decreasing mortality of small juveniles through adults occupying the same riverine habitat. If not attributable to a preservational bias, the relative rarity of hatchlings may suggest that the depositional area of the Bissekty Formation was some distance from the nesting grounds and protected habitats where hatchlings presumably spent their first months.

Lagarcito Formation.—The “Loma del *Pterodaustro*” Lagerstätte within the Lagarcito Formation consists of ~8 m of laminated claystones and massive siltstones with a few sandstone beds deposited in the middle of a large, shallow perennial freshwater lake that supported abundant algae and invertebrates, a somewhat restricted fish fauna, and the pterosaur *Pterodaustro guinazi* Bonaparte, 1970 (Chiappe et al., 1998; Prámparo et al., 2005, Arcucci et al., 2015). The vast majority of *Pterodaustro* specimens came from ~1 m of laminated claystones and the sample consists of one egg with embryo, an incomplete eggshell, two hatchlings little bigger than the embryo, no small juveniles, two catalogued and many other large juveniles, two immature subadults, and many mature adults (L. Codorníu, personal communication, 2015). The data in Table 2 are based on the arbitrary assumption that ‘many’ equates to 10. The pattern of abundance suggests that large juveniles through adults occupied the same lacustrine habitat, whereas the rarity of small juveniles suggests that they occupied other habitats.

Pterodaustro has been interpreted as feeding while standing in shallow waters, dipping its curving jaws into the water to sieve out small organisms (Wellnhofer, 1991a; Chiappe et al., 1998); however, it does not exhibit any wading adaptations such as elongate limbs. Whereas sieving on the wing is precluded because of the excessive drag the mandible would have produced, it is possible that *Pterodaustro* fed while floating, duck-like and sieving surface waters where prey might congregate to feed on phytoplankton. If that were the case, they could have fed on a much greater proportion of the lake’s surface area and the lake could have supported much larger populations of *Pterodaustro* than if they were restricted to shallow waters. In addition, if small juveniles remained in shallow protected waters near shore and large juveniles and

adults ventured onto deeper waters, which would explain the absence of small juveniles in the sample.

One reviewer suggested that the large feet of ctenochasmatooids could be interpreted as a wading adaptation, and questioned whether *Pterodaustro* could have floated in a posture that would have permitted it to sieve given that computational analyses of floating postures have suggested that pterosaurs were nose heavy (Hone and Henderson, 2013). Those analyses and similar computational analyses of pterosaur body masses (Henderson, 2010), like the apocryphal mathematical proof that bumblebees (*Bombus* spp.) cannot fly, are based on questionable assumptions, in this case assumptions as to the volume and density of pterosaur body parts. In particular, the floating posture analyses ignored the probability that there were extraskelatal pneumatic spaces within the wings, such as the retrophalangeal wedge in *Rhamphorhynchus* (Bennett, 2016), which would have significantly increased buoyancy anteriorly and presumably resulted in a stable floating posture. As for feet, if *Pterodaustro* sieved while floating, then their enlargement could be interpreted as for paddling rather than wading.

The presence of eggs indicates that the area of deposition of the “Loma del *Pterodaustro*” was close to the nesting grounds of *Pterodaustro*. Grellet-Tinner et al. (2014) compared *Pterodaustro* to grebes and flamingoes and suggested that it deposited and brooded its eggs in floating nests; however, there is no evidence of active incubation of eggs in pterosaurs (Unwin and Deeming, 2008). The presence of the eggs in sediments deposited in the middle of the lake could be explained by flooding events washing eggs deposited on land into the lake. The presence of eggs and hatchlings in the middle of the lake might seem at variance with the absence of small juveniles in the same sediments, but floods that could have washed eggs into the lake probably would have overwhelmed non- and poorly flying hatchlings as well, but could have been escaped by better-flying small juveniles.

Romualdo Member of the Santana Formation.—The Romualdo Member of the Santana Formation consists of shales to sandstones deposited in a large lake or inland sea (Maisey, 1991), and its vertebrate fossils preserved in abundant calcareous concretions represent a diverse fauna of fishes, turtles, crocodilians, and pterosaurs. The concretions seem to have formed in thin horizons (Saraiva et al., 2007), such that the temporal range of the fauna is restricted.

Anhanguerids dominate the Romualdo Member pterosaur fauna, and are oversplit taxonomically because authors have considered minor morphological differences to be taxonomically significant such that many species are represented by single specimens. Authors have often not presented evidence or argumentation to suggest that the differences do not merely reflect ontogenetic or individual variation (but see Pinheiro and Rodrigues, 2017), and I find most characters used to differentiate species of *Anhanguera* of doubtful significance. In my opinion, there are at least two distinct species of anhanguerid in that the holotypes of *Tropeognathus mesembrinus* Wellnhofer, 1987 and *T. robustus* Wellnhofer, 1987 exhibit multiple differences, but I concur with Rodrigues and Kellner (2013) in viewing *T. robustus* as referable to *Anhanguera* and I find no evidence to view any *Anhanguera* specimens represented by skull materials as not conspecific.

I assembled a broad sample of 31 anhanguerid specimens, including 21 referred to the most abundant anhanguerid genus, *Anhanguera*, or synonymous genera described and/or illustrated by Buissonjé (1980), Campos and Kellner (1985), Wellnhofer (1985, 1991b), Kellner and Tomida (2000), and Veldmeijer (2002), four specimens assigned to *Tropeognathus* or *Coloborhynchus* (Wellnhofer, 1987; Veldmeijer, 2003a; Kellner et al., 2013), the holotype of *Maaradactylus kellneri* (Bantim et al., 2014), four specimens assigned to *Brasileodactylus* (Kellner, 1984; Veldmeijer, 2003b; Veldmeijer et al., 2005, 2009), and the holotype of *Araripesaurus castilhoi* (Price, 1971). All specimens were evaluated for size and evidence of ontogenetic age using Bennett’s (1993) size-independent criteria. Sixteen *Anhanguera* specimens are of a size corresponding to skull lengths of ~50 cm, whereas five specimens are of a size corresponding to skull lengths of ~62 cm. Four *Anhanguera* specimens exhibit evidence of immaturity, whereas the other 17 seem to be mature adults. All *Anhanguera* skulls exhibit low rostral crests, which is considered a diagnostic character of *Anhanguera*. The five specimens assigned to *Tropeognathus*, *Coloborhynchus*, and *Maaradactylus* are mature adults, larger and more robust than is typical of *Anhanguera*, but most only slightly larger than the largest specimens of *Anhanguera*, and all have large and tall rostral crests and/or deep symphyseal keels on their mandibles. The four specimens of *Brasileodactylus* resemble *Anhanguera* specimens, but lack rostral crests and symphyseal keels, and some are somewhat smaller than *Anhanguera* specimens. Two *Brasileodactylus* specimens are isolated incomplete jaws and their ontogenetic age cannot be assessed, but AMNH 24444 (skull length = 43 cm, Veldmeijer, 2003b; thus ~15% smaller than the more abundant smaller specimens of *Anhanguera* with skull lengths of ~50 cm) and BSP 1991 I 27 (slightly larger than the smallest specimens of *Anhanguera*) exhibit size-independent indicators of skeletal immaturity. Lastly, the holotype of *Araripesaurus castilhoi* is an even smaller specimen, ~33% smaller than the more abundant smaller specimens of *Anhanguera*, consisting of a partial right wing that exhibits unfused carpal elements indicating immaturity, but is otherwise indistinguishable from *Anhanguera* specimens.

The anhanguerid sample exhibits three size-classes. The large size-class consists of 10 specimens, the *Tropeognathus*, *Coloborhynchus*, and *Maaradactylus* specimens and the five largest *Anhanguera* specimens, which have skull lengths of ~65 cm or more and, with the exception of NSM-PV 19892, all have large and tall rostral crests and/or deep symphyseal keels on their mandibles. NSM-PV 19892 was referred to *Anhanguera* because its rostral crest was small and low, but that probably is a result of its immaturity. Presumably, if the specimen had grown to maturity, the crest would have been larger and taller and the skull would have resembled that of specimens assigned to *Tropeognathus*. The medium size-class consists of the 16 smaller *Anhanguera* specimens with skull lengths of ~50 cm and low rostral crests. The smaller specimens assigned to *Brasileodactylus* and the even smaller the holotype of *Araripesaurus castilhoi* form a third, small size-class. All specimens in the small size-class that can be evaluated for ontogenetic age exhibit evidence of immaturity, whereas the medium and large size-classes consist primarily of mature

individuals, but immature individuals are present in both size-classes. The presence of immatures in the medium and large size-classes indicates that those size-classes cannot be age-classes, and because those immature specimens seem not to be significantly smaller than mature adults, they are considered to be subadults. The medium and large size-classes are dimorphic in rostral crest size, and, based on comparison to the dimorphic size-classes of *Pteranodon*, they are tentatively interpreted as sexes, small females with small and low crests, and large males with large and tall crests.

The pelvis of AMNH 22555, a specimen in the medium size-class that has deep pubes and ischia that would have resulted in a relatively large pelvic canal like that seen in female *Pteranodon*, provides further support for the interpretation of sexual dimorphism. The *Brasileodactylus* and *Araripesaurus* specimens in the small size-class seem to be immature and differ from specimens assigned to *Anhanguera* only in the lack of rostral crests and symphyseal keels, and because they are smaller than mature adults in the medium and large size-classes they are considered to be large juveniles. Presumably if the specimens had grown to maturity they would have developed rostral crests and mandibular keels and their skulls would have resembled those of presumed females assigned to *Anhanguera* or presumed males assigned to *Tropeognathus*, *Coloborhynchus*, and *Maaradactylus*.

According to the above interpretation, the anhanguerid sample consists of large males with large and tall rostral crests and symphyseal keels, small females with small rostral crests, and immature large juveniles lacking crests. Females are ~60% more abundant than males, males are ~30% larger than females, and large immature juveniles make up ~16% of the sample. The sample is similar to that of *Pteranodon* from the Smoky Hill Chalk Member in exhibiting sexual dimorphism, although the sex ratio and size dimorphism are not as marked as in *Pteranodon*. If those differences are real and do not result from collection and publication biases, they might reflect the fact that the Romualdo Member anhanguerids are ~20 my older than *Pteranodon*. Based on that interpretation, the Romualdo Member would represent a littoral multi-age feeding habitat of large juveniles through adults, and hatchlings and small juveniles were absent because they occupied other habitats.

Patterns and implications of ontogenetic niches.—The best evidence for ontogenetic niches in pterosaurs comes from the samples of pterosaurs in which one or more ontogenetic stages are absent or markedly rarer than expected: (1) *Pteranodon* and *Nyctosaurus* in which juveniles are absent or virtually so, (2) *Rhamphorhynchus* in which mature presumably breeding adults are much rarer than expected given the abundance of yearlings, and (3) *Aurorazhdarcho* in which yearlings and older juveniles are much rarer than expected given the abundance of hatchlings and young-of-the-year. One reviewer suggested that there are many possible explanations other than particular ontogenetic stages of those taxa being somewhere other than the Western Interior Seaway or the Solnhofen lagoons, but they offered no specific explanations, and none that I can devise seems as plausible. In addition, the fact that samples of other pterosaurs are consistent with the interpretations of ontogenetic niches and do not provide evidence of parental care and/or

delayed onset of flight until half grown supports the view that pterosaurs exhibited ontogenetic niches.

There seems to be variation in the patterns of ontogenetic niches in different pterosaurs. *Ctenochasma* and *Azhdarcho* have the simplest patterns. *Ctenochasma*'s pattern of abundance is consistent with hatchlings through adults occupying the same habitat and feeding on the same items throughout their life with no change of niche other than that hatchlings presumably fed on individuals of prey species, whereas juveniles and adults sieved to catch multiples. *Azhdarcho*'s pattern of abundance suggests that juveniles through adults occupied the same riverine habitat, probably feeding on differently sized prey, although hatchlings may have spent some time elsewhere. Other pterosaurs exhibit more complex patterns of ontogenetic niches. *Pterodaustro*'s pattern of abundance is similar to that of *Ctenochasma* except that large juveniles through adults probably fed on open lake waters, whereas hatchlings and small juveniles were elsewhere, probably in protected nearshore habitats. *Rhamphorhynchus* and *Pterodactylus* hatchlings and small juveniles remained in or around the Solnhofen lagoons that were presumably close to the nesting grounds, and large juveniles through adults presumably were elsewhere except when nesting. Large juveniles through adults of *Anhanguera* and subadults and adults of *Pteranodon* and *Nyctosaurus* were at sea and hatchlings and small juveniles were elsewhere. Note that one reviewer suggested that the recently described *Hamipterus* (Wang et al., 2014) and *Caiuajara* (Manzig et al., 2014), both of which are represented by samples with broad size ranges including juveniles through adults, should have been included in the survey of pterosaurs. However, the ontogenetic compositions of the samples have not been documented sufficiently for them to be considered here.

The occurrence of ontogenetic niches in most pterosaurs probably had a significant impact on pterosaur diversity. The pattern of ontogenetic niches and food resources partitioned by size in *Pteranodon*, *Nyctosaurus*, and *Anhanguera* would have resulted in greater overall abundance of the species than if they had been limited to continental or coastal environments, but also resulted in a less-diverse pterosaur fauna than if each different ontogenetic niche occupied by *Pteranodon*, *Nyctosaurus*, and *Anhanguera* was occupied by a distinct species. In addition, pterosaur faunas would have been biased toward large species because hatchlings and juveniles of large species such as *Pteranodon* and *Anhanguera* would have competed with any small species that lived in the continental or coastal environments. Therefore, the presence of ontogenetic niches would have meant that pterosaur diversity was like that of crocodylians, with relatively few large species and each having broad ecological roles in which they preyed on a wide variety of foods of different sizes while growing to ~10 times their size at hatching, filling what might have been many different niches. Thus, pterosaurs were not like speciose passerines with many similar small species filling many narrow ecological roles.

Andres et al. (2010, 2014) suggested that there was a dichotomy between terrestrial (e.g., *Sericipterus* and *Kryptodrakon*) and aquatic pterosaurs. Whereas it is reasonable to accept that a particular species of pterosaur lived in the depositional environment in which its fossils are found, there is often no reason to think that the species was limited to that environment. Ctenochasmatooids with jaws specialized as fish traps and sieves were probably limited to

feeding in aquatic environments, and the same may have been true of *Rhamphorhynchus* with jaws and teeth suited to spearing fishes. But many other pterosaurs had skulls, dentitions, and other features that would not have prevented them from succeeding in terrestrial environments, particularly as juveniles with usually somewhat more generalized morphologies (e.g., *Dimorphodon*, *Scaphognathus*, *Anhanguera*, *Pteranodon*). Therefore, it is not unreasonable to think that some pterosaurs may have exhibited ontogenetic niches such that they lived in terrestrial and aquatic environments at different times in their lives. There is nothing in the morphology of *Sericipterus* and *Kryptodrakon* (Andres et al., 2010, 2014) to distinguish them from pterosaurs found in aquatic environments; indeed, the dentition of *Sericipterus* has long slender teeth like those of its relatives *Scaphognathus* and *Rhamphorhynchus* found in aquatic environments. Thus, there is insufficient evidence to conclude that there was a dichotomy between terrestrial and aquatic pterosaurs.

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