



Taylor & Francis
Taylor & Francis Group



Sexual Dimorphism of Pteranodon and Other Pterosaurs, with Comments on Cranial Crests

Author(s): S. Christopher Bennett

Source: *Journal of Vertebrate Paleontology*, Vol. 12, No. 4 (Dec. 15, 1992), pp. 422-434

Published by: Taylor & Francis, Ltd. on behalf of The Society of Vertebrate Paleontology

Stable URL: <https://www.jstor.org/stable/4523470>

Accessed: 09-03-2020 14:37 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Taylor & Francis, Ltd., The Society of Vertebrate Paleontology are collaborating with JSTOR to digitize, preserve and extend access to *Journal of Vertebrate Paleontology*

SEXUAL DIMORPHISM OF *PTERANODON* AND OTHER PTEROSAURS, WITH COMMENTS ON CRANIAL CRESTS

S. CHRISTOPHER BENNETT

Department of Systematics and Ecology and Museum of Natural History, University of Kansas, Lawrence, Kansas 66045

ABSTRACT—Metric data from the large collection of the Late Cretaceous pterosaur *Pteranodon* are bimodally distributed with a more numerous small size-class and a less numerous large size-class. The size-classes differ in cranial crest and pelvic structure. The small size-class has small cranial crests and deep puboischiadic plates that produce a large pelvic canal, while the large size-class has large cranial crests and shallow puboischiadic plates that produce a small pelvic canal. The difference in pelvic structure suggests that the small size-class is female. The various functions proposed for cranial crests are reviewed, and it is concluded that none can account for the difference in crest size. The conclusion is that the large crests of males are display structures.

INTRODUCTION

Studies of measurements of collections of small pterosaurs have examined growth and allometry (Wellnhofer, 1970, 1975; Mateer, 1976; Brower and Veinus, 1981), sexual dimorphism (Wellnhofer, 1970, 1975), and the utility of wing proportions in differentiating genera (Padian, 1980). To date, the main interest in measurements of large pterosaurs has been in the maximum size they attained. The collections of *Pteranodon* present a unique opportunity to examine allometry and variation in a large pterosaur because they include over 1,100 specimens, many more than collections of any other pterosaur. These large collections of *Pteranodon* allow statistical analyses, yet they cannot be considered an unbiased sample. All specimens were deposited at sea, some 200 km from the nearest shore, and therefore were old enough and large enough to fly that far. The collections cover a long temporal range because the Smoky Hill Chalk Member of the Niobrara Formation spans over four million years from the late Coniacian through the early Campanian (Hattin, 1982). In addition, the collections contain two species, *P. sternbergi* and *P. longiceps*, which appear to be chronospecies forming parts of a single anagenetic lineage. The postcranial skeletons of the two species are morphologically indistinguishable, and no evidence has been found to separate the two species by proportional differences of the postcranial skeleton (Bennett, 1991 and in prep.). It was not possible to separate the two species for this analysis because the vast majority of specimens do not include the skull and do not have sufficient locality data to determine the stratigraphic position. The results of the following study suggest that *Pteranodon* was sexually dimorphic in size and structure (Bennett, 1987).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; DMNH, Denver Museum of Natural History, Denver; FHSM, Fort

Hays State Museum (Sternberg Memorial Museum), Fort Hays State University, Hays, Kansas; KUV, Museum of Natural History, University of Kansas, Lawrence; UALVP, Geology Museum, University of Alberta, Edmonton; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven; and “UNC,” manuscript number from Bennett (1991) referring to uncatalogued specimens in the hands of private collectors.

MATERIALS AND METHODS

This analysis is based on examination and measurements of the over 1,100 available specimens of *Pteranodon* collected from the Smoky Hill Chalk Member of the Niobrara Formation of western Kansas, including nearly all such specimens in museum collections. The length of all limb bones, except the carpus, manual digits I–III, tarsus, and pes were measured, as well as the diameters of the distal condyles of metacarpal (mc) IV (see Bennett [1991 and in prep.] for specimen numbers, measurements, and data). Despite the large sample of *Pteranodon*, most specimens are so incomplete that only about 450 contributed measurements to this study. In addition, because most specimens are fragmentary, the numbers of associated skeletal elements are small. This limited statistical analysis to rather simple procedures. Multivariate analysis, such as was done by Mateer (1976) for *Pterodactylus*, was not possible because most specimens are fragmentary. About 10% of specimens included left and right elements. In this event, the measurements were averaged before analysis so that more complete individuals did not make a disproportionate contribution to the results. Length differences between right and left elements of an individual are generally minor (<2%). Size-frequency histograms of individual elements were produced, and statistical tests (G-tests; So-

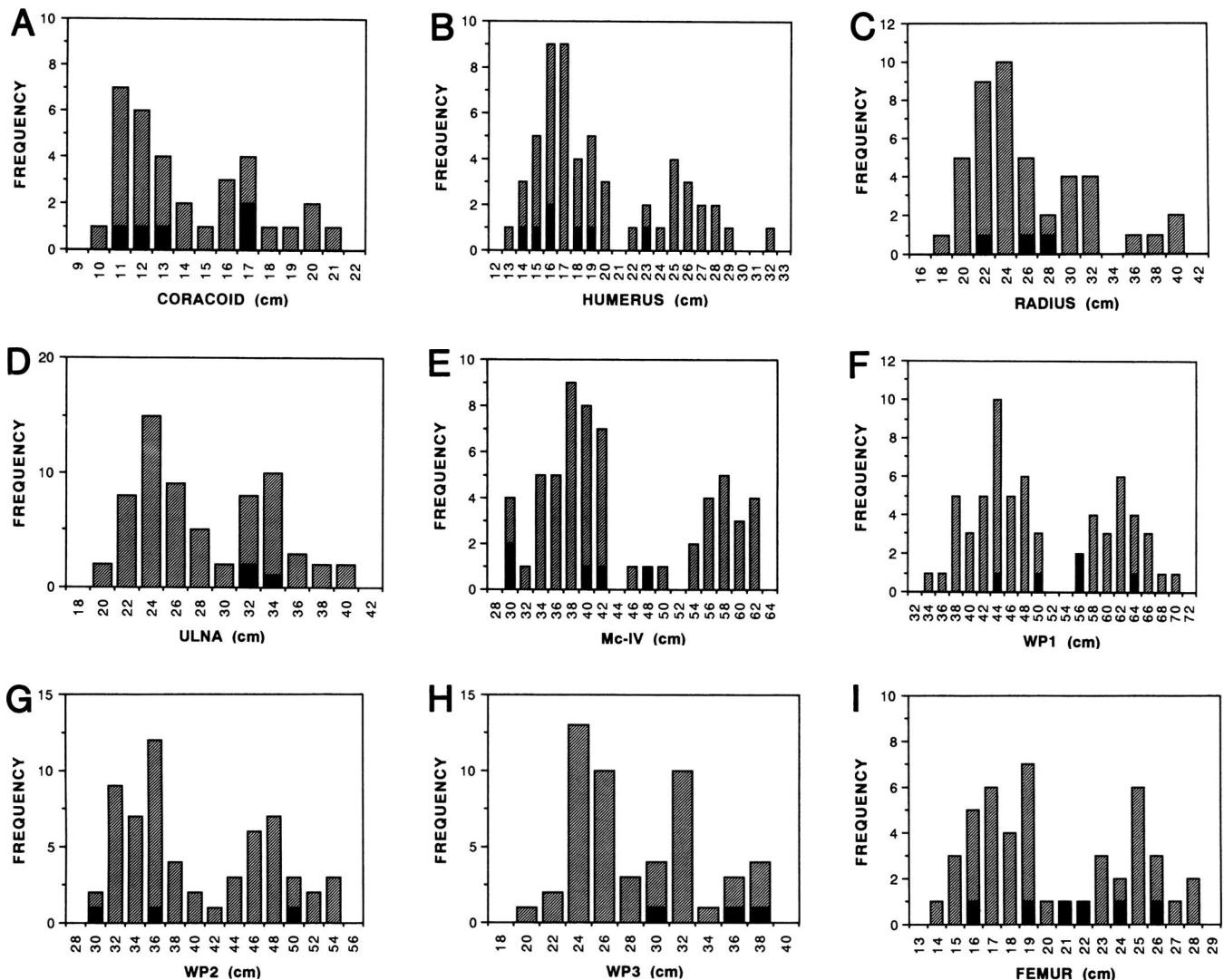


FIGURE 1. Size-frequency histograms of lengths of limb elements of *Pteranodon* (see Bennett [1991 and in prep.] for specimen numbers, measurements, and data). A, coracoid; B, humerus; C, radius; D, ulna; E, metacarpal IV; F, wing phalanx 1; G, wing phalanx 2; H, wing phalanx 3; I, femur. Immature specimens identified using size-independent criteria (Bennett, 1991) are shown in black, and mature and unrated specimens are hatched.

kal and Rohlf, 1981) were done on the measurements of the distal condyles of mc IV to compare the distributions to unimodal and bimodal distributions.

RESULTS

Size-frequency histograms of lengths of each element and the diameters of the dorsal and ventral distal condyles of mc IV are shown in Figures 1 and 2. Most of the size-frequency histograms show bimodal distributions, with a more numerous small size-class and a less numerous large size-class. Statistical tests for bimodality are available; however, Larkin (1979) showed that statistical tests for bimodality are significant at the 0.01 probability level when the bimodality is readily apparent in the graphed data. Because most of the

distributions in Figure 1 are visibly bimodal, tests for bimodality were not done on the data. A number of plots deviate to varying degrees from bimodality; however, these exceptions (scapula, coracoid, radius, wing phalanx [wp] 3, wp 4, and tibia) are those with small sample sizes.

Although the size-frequency distributions were not tested for bimodality, the data of the dorsal and ventral condyles of mc IV (Fig. 2) were tested against unimodal and bimodal distributions with the G-test. The distributions were split at the trough (mc IV-d = 30 mm; mc IV-v = 31.5 mm) and the sample size, mean, and standard deviation were determined for each size-class (Table 1). Three hypotheses were tested for each data set. The hypotheses are listed below, and the results of the tests are shown in Table 2.

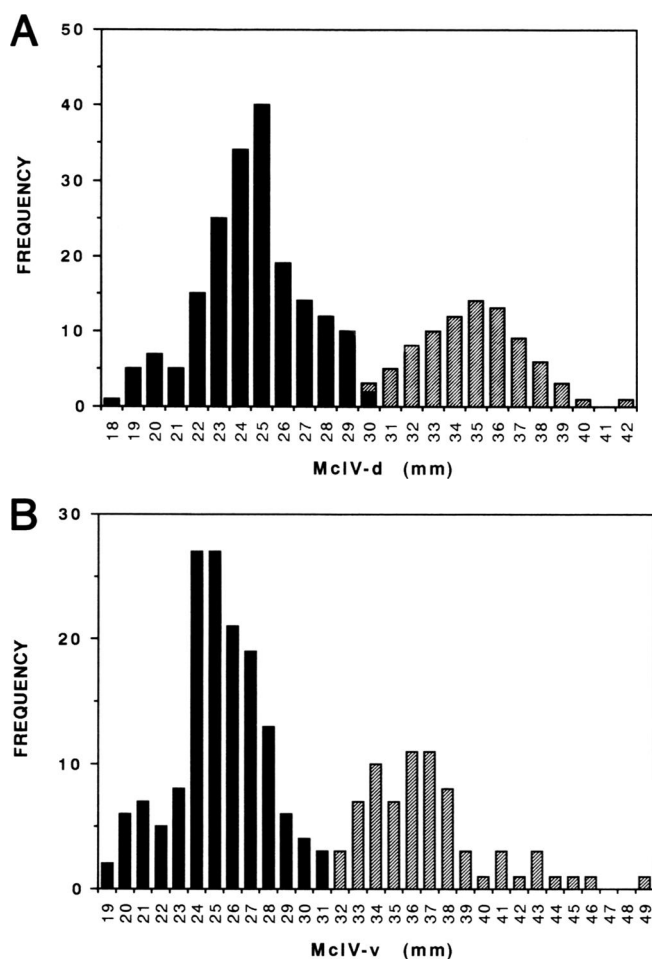


FIGURE 2. Size-frequency histograms of diameters of distal condyles of metacarpal IV of *Pteranodon* (see Bennett [1991 and in prep.] for specimen numbers, measurements, and data). A, dorsal and B, ventral condyle. Small size-class are in black and large class hatched.

Hypothesis 1: The data were sampled from a population with a unimodal normal distribution with mean and standard deviation equal to those of the whole sample. This hypothesis was rejected at the 0.001 probability level for both condyles.

Hypothesis 2: The data were sampled from a bimodally distributed population with a 1:1 ratio of two size-classes, each class normally distributed with a mean and standard deviation equal to those of the respective size-classes of the sample. This hypothesis was rejected at the 0.001 probability level for both condyles.

Hypothesis 3: The data were sampled from a bimodally distributed population with ratio of 2:1 of the two size-classes, each class normally distributed with a mean and standard deviation equal to those of the respective size-classes of the sample. This hypothesis was accepted at the 0.05 probability level for both condyles.

DISCUSSION

The data are bimodally distributed as shown by the size-frequency histograms, and in many of the histograms there is little overlap between the two size-classes. Each size-class has a somewhat restricted size range, with the smallest specimens in each class about 70% the size of the largest specimens. The two size-classes are not represented by equal numbers of specimens, and in all cases the small size-class is more numerous. The relative frequencies of the two size-classes of various elements range from 1.5:1 for the femur and wp 2 to about 2.4:1 for the radius (Table 3). The results of the G-tests (Table 2) show that the size-frequency distributions of the distal condyles of mc IV do not differ significantly from bimodal distributions in which the ratio of small to large is 2:1, but do differ significantly from bimodal distributions with 1:1 ratios. It is possible that preservation of *Pteranodon* was biased toward smaller individuals, but whether this difference in frequency of the size-classes is a result of preservation and collecting biases, or reflects real frequency biases in the populations of *Pteranodon* is not known.

Olson (1957) discussed the problems of interpreting size-frequency distributions among fossil organisms, and pointed out that bimodal and polymodal distributions usually result from sampling a population over a short period of time. One example of this is a single death assemblage, and repeated sampling in a particular season produces a similar result. In either situation, adults and young occur in the sample and represent growth stages or year classes. The polymodal distribution of the fossil catostomid fish *Amyzon* is an example of seasonal sampling producing year classes

TABLE 1. Summary of statistics of distributions of data on dorsal (mc IV-d) and ventral (mc IV-v) condyles of wing metacarpals of *Pteranodon* from the Niobrara Formation. Diameters (in mm) were measured as shown in the diagram below. Abbreviations: N, sample size; \bar{x} , sample mean; S, sample standard deviation.

	Size-class	N	\bar{x}	S
Mc IV-d	Small	188	24.56	2.379
	Large	83	34.96	2.354
	Both	271	27.75	5.355
Mc IV-v	Small	148	25.15	2.533
	Large	72	36.80	3.474
	Both	220	28.96	6.184

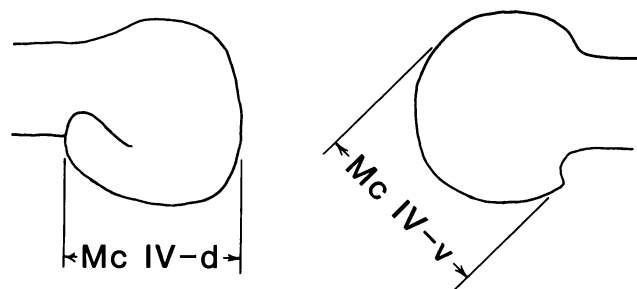


TABLE 2. Summary of statistical tests of data on dorsal and ventral condyles of wing metacarpals (mc IV) of *Pteranodon* from the Niobrara Formation. Critical value for mc IV-d is $G_{\alpha=0.05} = 26.30$; for mc IV-v is $G_{\alpha=0.05} = 31.41$.

Hypothesis	G test statistic	Result
Mc IV-d is unimodal	116.69	Reject
Mc IV-d is 1:1 bimodal	54.08	Reject
Mc IV-d is 2:1 bimodal	19.56	Accept
Mc IV-v is unimodal	95.73	Reject
Mc IV-v is 1:1 bimodal	50.18	Reject
Mc IV-v is 2:1 bimodal	28.22	Accept

(Wilson, 1984). However, neither of these situations can apply to *Pteranodon*. The fossil pterosaurs from the Niobrara Formation do not represent a single death assemblage, and although it is possible that most individuals of *Pteranodon* died during a particular season, the size-classes cannot be growth stages or adults and young. Subadult specimens of *Pteranodon* are readily identifiable on the basis of degree of skeletal maturity (Bennett, 1991), and subadults are present in both size-classes although adults predominate in each class (Fig. 1). In addition, the two size-classes occur together in the Smoky Hill Chalk Member of the Niobrara Formation and are not temporal isolates. Large and small specimens were collected throughout the exposure area of the Smoky Hill Chalk Member from the same horizons. Therefore, the populations of *Pteranodon* from which the collections were made were bimodally distributed in respect to body size.

The size-frequency distributions that deviate from bimodality need to be considered. As noted above, these deviations are seen only where the sample size is small (e.g., scapula, coracoid, radius, wing phalanges 3 and 4, and tibia). The deviations may be due to the large temporal span of the sample combined with a trend toward increased size in *Pteranodon*. The two species of *Pteranodon* appear to differ slightly in size, and the average size of small and large individuals from near the top of the Smoky Hill Chalk Member of the Niobrara Formation appears to be larger than the average size of such individuals from near the bottom of the member (pers. obs.). Unfortunately, it has not been possible to quantify this because of the lack of stratigraphic and locality data with most specimens. A second possibility is that the two species of *Pteranodon* differed slightly in proportions, which would not be surprising, but there is no evidence of that or evidence that the size-classes differ significantly in proportions (Bennett, 1991 and in prep.).

Sexual Dimorphism of *Pteranodon*

The above analysis shows that there are two size-classes of *Pteranodon* that occur together throughout the Smoky Hill Chalk Member, do not differ significantly in proportions, and are not year-classes or growth stages. Olson (1957) cautioned that, although bimo-

dality is often interpreted as evidence of sexual dimorphism, bimodality alone does not provide conclusive evidence of sexual dimorphism. However, in this case, comparison of specimens of the small and large size-classes shows that there are differences in the size of the cranial crests and in the structure of the pelvis, and the pattern of those differences suggests that the size-classes are sexual morphs, rather than separate species.

All individuals of *Pteranodon* had a cranial crest formed by the frontals and extending upward and/or backward from the posterior end of the skull. The cranial crest is relatively short in small individuals and relatively long in large individuals (Table 4; Fig. 3). In small specimens, the crest is roughly triangular and may be directed posteriorly (e.g., KUVV 2122, USNM 12167) or upward (e.g., USNM 13868). The base of the crest is relatively short anteroposteriorly, and the anterior end of the base does not extend anterior to the orbit. The longest crest on a small skull is that of KUVV 2122, which has a length equal to 3.1 orbit diameters. In large skulls, the crest is long and may arc backward as a rather narrow blade of bone (e.g., YPM 2473, 2594, DMNH 1732) or may extend upward and be much broader anteroposteriorly (e.g., FHSM VP 339; Figs. 4, 5). In large individuals, the base of the crest is relatively longer anteroposteriorly, and the anterior end of the base is anterior to the orbit. With the exception of the immature skull of FHSM VP 221, in which the length of the crest is equal to 2.4 orbit diameters, the crest length of large individuals equals at least 4 orbit diameters. However, in FHSM VP 221 the crest, although short, has a broad base that extends anterior to the orbit like that of other large skulls.

In addition to the large frontal crest, large individuals appear to have low premaxillary crests. In both size-classes, the premaxillae extend beyond the anterior end of the mandible. The anterior ends of the jaws of large individuals are rarely preserved, but the few available specimens suggest that the premaxillae support a long low crest and extend beyond the end of the mandible. In UALVP 24238, the anterior end of the upper jaw is absent, but 81 cm of the upper jaw are

TABLE 3. Absolute and relative frequencies of selected elements of small (S) and large (L) size-classes of *Pteranodon* from the Niobrara Formation.

Element	S	L	Ratio S:L
Coracoid	20.5	12.5	1.64
Humerus	39	17	2.29
Radius	31	13	2.38
Ulna	40	26	1.54
Mc IV	39	21	1.86
Wp 1	39	24	1.63
Wp 2	36.5	24.5	1.49
Femur	27.5	18.5	1.49
Mc IV-d	188	83	2.27
Mc IV-v	148	72	2.06

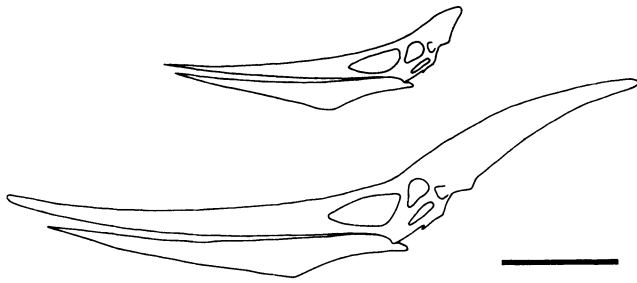


FIGURE 3. Reconstructions of skulls of modal female and male *Pteranodon longiceps* (based on YPM 1177 and KUV 2122; and YPM 2594, respectively). Scale equals 30 cm.

preserved anterior to the condyloid process (Fig. 5). The depth of the anterior 39 cm tapers from 78.1 mm to 69.4 mm at the broken end. If the missing part of the upper jaw tapered to the same extent as that of the preserved part, the premaxillae would extend more than 3 m beyond the broken end. This is unlikely. Instead, the premaxillae must have supported a thin median crest that decreased in height posteriorly so that its dorsal margin was almost parallel to the ventral margin of the upper jaw. Anteriorly the crest was probably truncated. The mandible in that specimen is also incomplete but the distance between the posterior end of the symphysis and the glenoid fossa is 24 cm. Few

mandibles are complete, but of those that are, the rami are relatively shortest in YPM 1177 where they form 27% of the length of the mandible. Based on the proportions of YPM 1177, the length of the mandible of UALVP 24238 from the glenoid fossa to the anterior end would be 80 cm. However, at that distance from the jaw articulation, the upper jaw is still 7 cm deep, and the premaxilla must have extended beyond the end of the mandible. Three specimens provide additional evidence. In AMNH 1974, KUV 967, and YPM 2489 (Fig. 5) the premaxillae are slender and upward curving, and they do not decrease in depth much anteriorly. In KUV 967, the mandible decreases in depth and tapers to a point. Thus the premaxillae continued beyond the anterior end of the mandible. Unfortunately, no large skull preserves the complete jaws, and the condition of the jaws and premaxillary crest in large skulls is unclear. No small skull includes premaxillae and mandible complete to the tips, but they are almost complete in KUV 2122. At the point where the mandible would end, the premaxillae are still 8 mm deep, and if the taper proximal to that point continued to the end of the premaxillae, they would extend 55 mm past the end of the mandible. Thus, the premaxillae of small skulls also extend beyond the end of the mandible, although to a lesser extent than in large skulls. A recently collected specimen (acquired by the Canadian Museum of Nature) includes a complete skull that shows that the premaxillae extend beyond the anterior

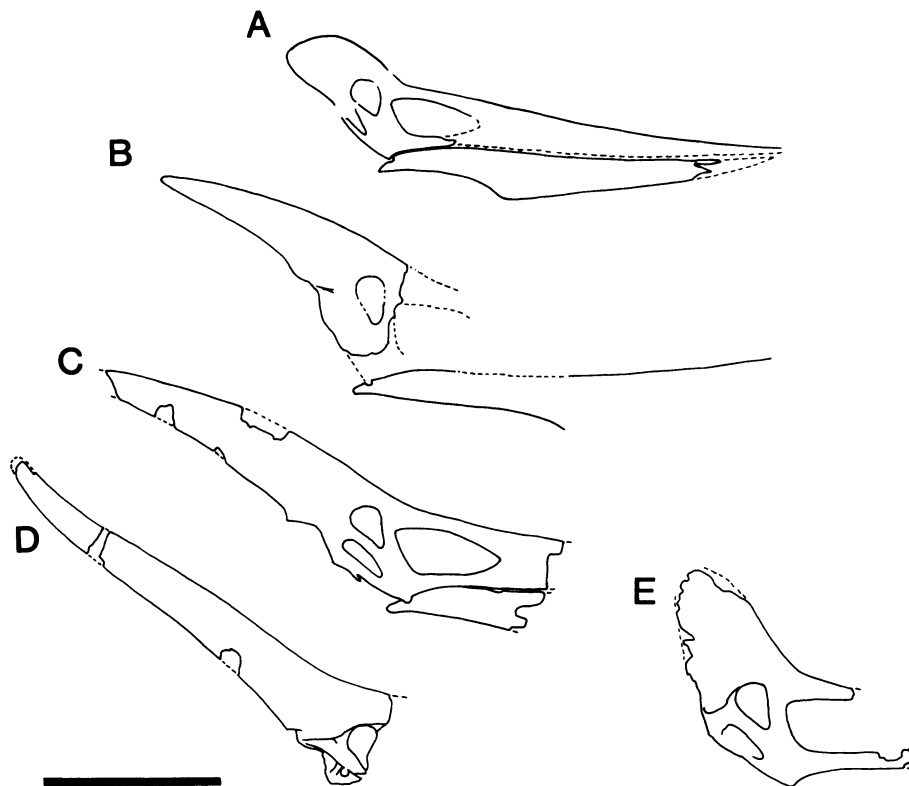


FIGURE 4. Cranial crests of large specimens of *Pteranodon longiceps*. A, FHSM VP 221 (left lateral view reversed); B, DMNH 1732; C, YPM 2594; D, YPM 2473; E, KUV 27821. Scale equals 30 cm.

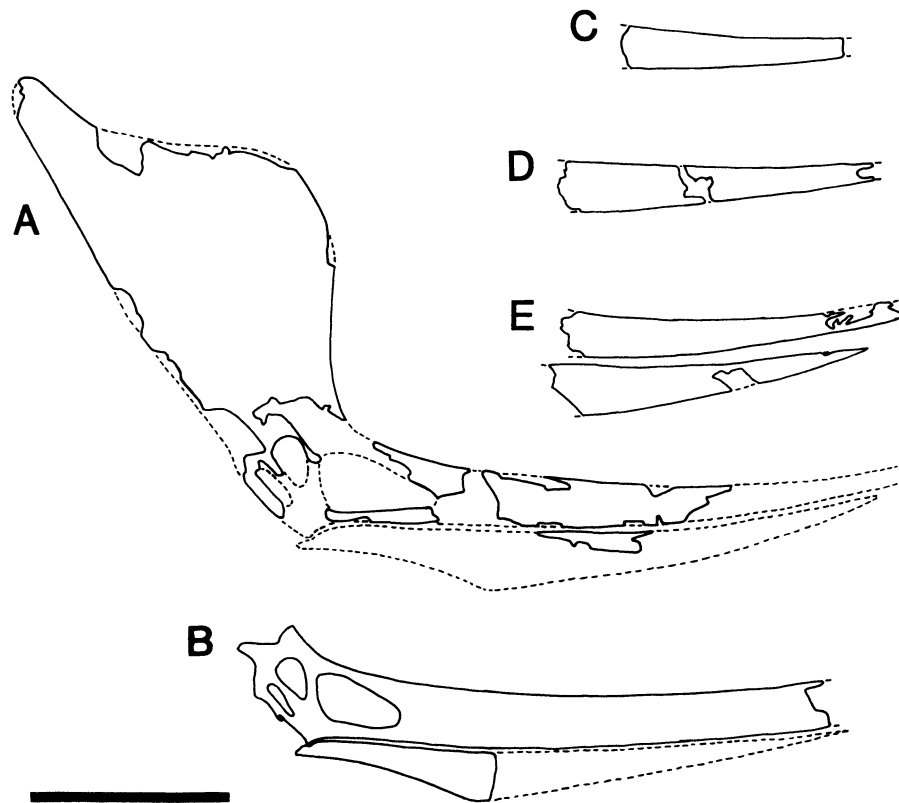


FIGURE 5. Cranial crests of large specimens of *Pteranodon sternbergi* and jaws of *Pteranodon*. A, FHSM VP 339 (left lateral view reversed); B, UALVP 24238; C, YPM 2489; D, AMNH 1974 (left lateral view reversed); E, KUV 967. A and B are *Pteranodon sternbergi*, C and E are *Pteranodon longiceps*, and D is *Pteranodon* sp. indet. Scale equals 30 cm.

end of the mandible as a tapering blade. This specimen came to my attention too late to illustrate it in this paper.

As noted elsewhere, the two species of *Pteranodon* differ in the direction and shape of the cranial crests and possibly the angle of the occiput. These differences, however, can be found in both the large and small morphs, not between morphs.

The differences in pelvic structure between the two size-classes seem to be related to the relative size of the pelvic canal. Well-preserved pelves are uncommon, and few are complete enough for measurement, but those available show that the pelves of the large morph have relatively shallow puboischiadic plates that enclose a small pelvic canal, while in the small morph the puboischiadic plates are deeper and enclose a relatively large pelvic canal (Table 5; Fig. 6). Measurements of the pelves show that the depth of the puboischiadic plates and the width between the prepubic articulations is relatively greater in the smaller pelves, and suggests that there is negative allometric growth in the depth of the puboischiadic plates relative to the sacral length. All pelves measured seem to be from adults, because all have a fused ischial symphysis and at least two dorsal vertebrae fused into the synsacrum.

In addition to the differences in the depth of the

puboischiadic plates, the pelves of the two morphs differ in the size of the posterior emargination of the pelvic girdle. Although KUV 993 is incomplete, enough is preserved to indicate that the posterior margins of the ischia are deeply emarginated laterally. Likewise, although the posterior margin of the pelvic symphysis is not well preserved it also appears to have been emarginated. The pelvic girdles of YPM 1175 are not as deeply emarginated laterally, and ventrally they extend far posteriorly and curve upward. This decreases the posterior diameter of the pelvic canal considerably. "UNC 5" was collected quite low in the Smoky Hill Chalk and is probably a small individual of the large morph. The position in which it is preserved makes it impossible to determine the extent to which the posterior margins of the pelvic girdles are emarginated, but the posterior margin of the pelvic symphysis is not emarginated and also suggests that it is a small individual of the large morph.

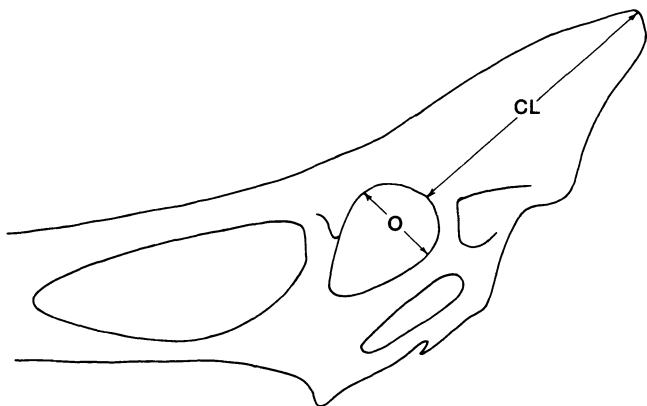
The most likely explanation for the differences in the size of the pelvic canal is that it is related to reproduction. The large pelvic canal may be necessary to allow passage of relatively large eggs. Thus, the small morph is female, and the large morph is male and would not need a large pelvic canal. The dimorphism in the pelvis is presumably related to the physical re-

TABLE 4. Absolute (in mm) and relative lengths of cranial crests of skulls of *Pteranodon*. Orbit diameter equals the lesser diameter of the suboval orbit, and crest length is measured from the margin of the orbit to the posterodorsal end of the crest (see diagram).

	Size class	Orbit diameter (O)	Crest length (CL)	CL/O
FHSM VP 2183	S	43.5	84	1.9
USNM 13868	S	46	95	2.1
FHSM 221 ¹	L	47	115	2.4
KUVP 2122	S	45	141	3.1
KUVP 27821 ¹	L	52	215	4.1
DMNH 1732	L	51	380	7.4
YPM 2594 ¹	L	60	490	8.2
FHSM VP 339 ²	L	58	690	11.9
YPM 2473	L	59	748	12.7

¹ Crest is incomplete and may be longer.

² Orbit diameter reconstructed.



quirements of reproduction, but the marked dimorphism in size as well as the cranial crest are secondary sexual characteristics.

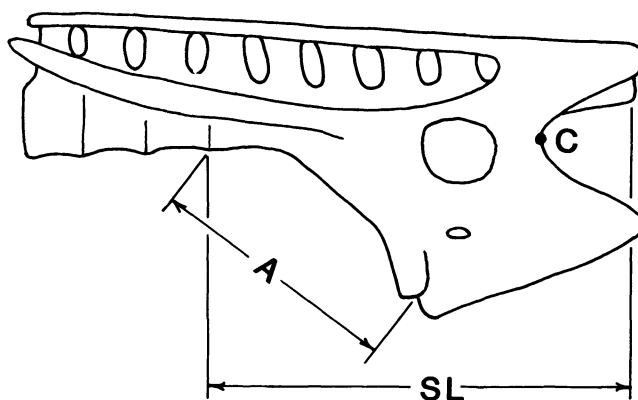
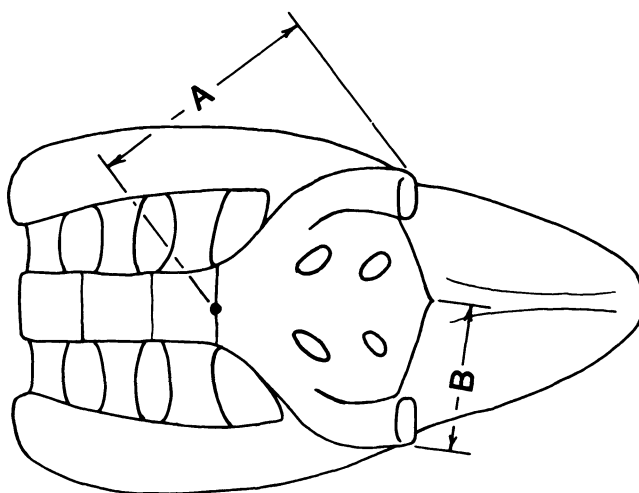
Function of the Cranial Crest

The function of the cranial crest of *Pteranodon* has perplexed paleontologists since the crest was first recognized. Various functions of the cranial crest have been suggested, including (1) muscle origin (Eaton, 1910; Mateer, 1975); (2) forward rudder (Kripp, 1943; Heptonstall, 1971; Stein, 1975); (3) aerodynamic counterbalance (Eaton, 1910; Heptonstall, 1971; Bramwell and Whitfield, 1974); and (4) airbrake (Bramwell and Whitfield, 1974). All these studies have viewed the function of the crest of *Pteranodon* as if there were a single type of crest, the long backward-directed crest of large male *Pteranodon longiceps* (Fig. 4). Any explanation of function for the cranial crest, however, must apply to the varying sizes and shapes of the crest, including both the small crests of females as well as the immense upright crest of male *P. sternbergi* (Fig. 5). In addition, an explanation of function should also be applicable to the presence and absence of cranial crests in other pterodactyloids. Cranial crests are now

known to have been present in other large pterodactyloids, and additional functions have been suggested for the cranial crests of these other pterosaurs. Wellnhofer (1987) suggested that the premaxillary and mandibular crests of *Tropeognathus* were to stabilize the jaws as they were dipped in flight over water to catch fish. Kellner (1989) suggested that the large cranial crest of *Tapejara wellnhoferi* was a radiative and/or convective heat exchanger, and recently Wellnhofer and Kellner (1991) suggested that the crest of *Tapejara*

TABLE 5. Measurements (in mm) and proportions of representative pelvises arranged in order of increasing size. See diagram below: sacral length (SL) = length of six sacrals and fused caudal; A = circumference from the midline of anterior end of the first sacral to the prepubic articulation; B = width from the anterior end of the ischial symphysis to lateral end of the prepubic articulation; C = width of pelvis at point C.

	KUVP 993	"UNC 5"	FHSM 2062	YPM 1175
SL	59	91	117	123
A	83	78	102	97
B	43	46	46	50
C	40	—	—	45
A/SL	1.41	0.86	0.87	0.79
B/SL	0.78	0.51	0.39	0.41
C/SL	0.68	—	—	0.37



might also have been used to part foliage to obtain fruits and seeds. In view of the variation in size and shape of the cranial crests of *Pteranodon* and other pterosaurs, the suggested functions need to be reexamined.

Muscle Origin—Eaton (1910) suggested that the crest provided an origin for large or long jaw muscles, although he acknowledged that could not explain the great size of some crests, and this view was also taken by Mateer (1975). There is a ridge where the base of the crest meets the upper temporal fenestra (Bennett, 1991 and in prep.). This is believed to be the suture between the frontal and parietal, and, in non-crested pterosaurs (e.g., *Pterodactylus*), it represents the margin of the upper temporal fenestra and presumably the origin of *M. adductor mandibulae*. In *Pteranodon*, this also appears to be the posterior limit of the origin of *M. adductor mandibulae*. The suggestion that the cranial crest provided an origin for long and powerful jaw musculature is not borne out by the structure of the crest. A few pterosaurs have a posteriorly directed process of the parietal that I consider a parietal crest (e.g., *Gallodactylus*, *Tropeognathus*, *Dsungaripterus*) and that may be to increase the area of attachment of *M. adductor mandibulae*. However, the size of this parietal crest is very modest, and most pterosaurs do not have such structures. The need for greater area of muscle attachment cannot explain the great size of the crest in some specimens of *Pteranodon* or the variations in shape.

Forward Rudder—Kripp (1943) suggested that the crest functioned as a forward rudder, and this has been echoed by Heptonstall (1971) and Stein (1975). As a further embellishment of this notion, Stein suggested that the crest supported an elastic membrane that extended from the crest to the middle of the back, to increase its steering effect and to assist in raising the head when feeding. There is no suggestion of any attachments for such a membrane on the cranial crest of any specimen, but that, of course, proves nothing. While the large crests of large males would provide a yaw moment to the body when the head was turned to the side, the small cranial crests of the supposed females would not provide any significant force compared to that developed by the remainder of the skull. Similarly, while the posited membrane extending from the crest to the back might function well with a large posteriorly directed crest like that of YPM 2473, it would not work well with a large upright crest like that of FHSM VP 339, and probably would have very little effect in the case of small short-crested individuals. The theory that the cranial crest was a forward rudder has two additional problems. First, there does not seem to be a need for such a rudder. Adjustments to the wings of pterosaurs would, because of the long moment arm, be much more effective in directional control and turning than the relatively small crest close to the center of mass. While it is clear that in pterosaurs, as in extant birds, a large head turned at an angle to the direction of flight would tend to turn the animal as a

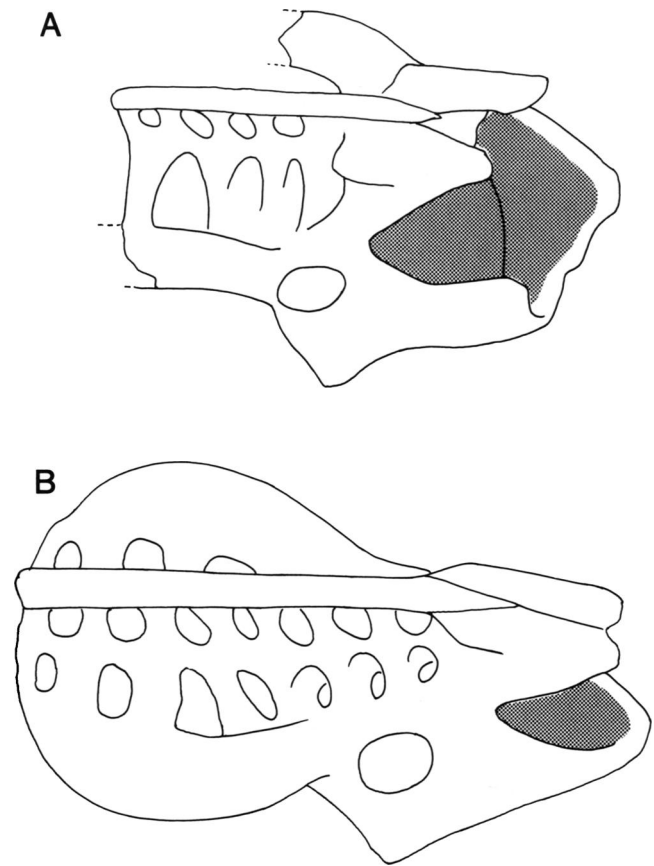


FIGURE 6. Pelvises of *Pteranodon* in left lateral view. **A**, female KUV 993; and **B**, male YPM 1175. Note that the puboischiadic plates of KUV 993 are deeper and more deeply emarginated than those of YPM 1175. The pelvic canal (shaded) is relatively much larger in the small pelvis than in the large pelvis. Not drawn to scale.

rudder, it seems likely that those forces are relatively unimportant compared to the forces developed by the wings themselves. The second problem with the theory is that it cannot explain the differences in size and shape of the cranial crest. If a small crest provided necessary directional control, why did some individuals have much larger crests, and, if the large crests were needed, then how did small individuals maintain directional control?

Aerodynamic Counterbalance—Eaton (1910), although advocating a muscle origin interpretation of the crest, noted that it might have been an aerodynamic counterbalance as well. Heptonstall (1971) and Bramwell and Whitfield (1974) viewed the crest as an aerodynamic counterbalance for the long beak, and all suggested that it allowed a reduction of neck musculature necessary to keep the head pointed forward. Wind-tunnel tests with models of the skull showed that the crest did balance the beak to some extent when the skull was turned to the side. This theory again is based on the assumption that all cranial crests in *Pteranodon* are large posteriorly directed crests like that of YPM

2473. While it is true that this may have been an effect of a large posteriorly directed cranial crest, it does not show that it was the function. Approximately half of the large upright crest of FHSM VP 339 is in front of the occipital condyle and so an upright crest would not have any counterbalance effect. If the head were tipped down, the entire crest would be anterior to the condyle. Likewise, the small crests of small individuals would have no significant counterbalance effect. The suggestion that the counterbalancing effect of the crest would allow a reduction in neck musculature also is questionable. A large crest when turned to the side would produce a strong side force on the neck that might even have required additional musculature to control. It is interesting to speculate that the change in the direction of the cranial crest from the upright crest of *Pteranodon sternbergi* to the posteriorly directed crest of *P. longiceps* was in order to develop a counterbalance effect, but the fact that *P. sternbergi* had large crests that had no counterbalancing effect suggests that that is not the function of the crest. In addition, the fact that other pterosaurs (e.g., *Tropeognathus*) have developed premaxillary crests well anterior to the occipital condyle indicates that they had some purpose or function other than aerodynamic counterbalance.

Airbrake—Bramwell and Whitfield (1974) suggested that the cranial crest might function as an airbrake. When *Pteranodon* wished to decelerate, it would turn its head to the side so that it was perpendicular to the direction of flight, and the large skull and cranial crest would produce drag to slow the animal. Such an action by the animal might produce the desired result, but it is likely to be unimportant when compared to the decelerative forces that could be generated by the wings themselves. The animal could increase angle of attack up to stall in order to decelerate. In addition, even if *Pteranodon* did use such a technique to decelerate, it is difficult to imagine when. At most times when it would want to decelerate, it would be landing or nearing some object, the times at which binocular vision would be most useful, and turning the head would prevent binocular vision. This theory also does not explain the small size of the cranial crest in small individuals.

Heat Exchanger—Kellner (1989) suggested that the large premaxillary crest of *Tapejara* was a heat exchanger that would allow the pterosaur to lose excess heat to the environment. He noted sulci on the surface of the crest that are probably for the blood supply to the surface of the crest, and X-rays of the crest revealed vertical passages that they suggested were for the return of cooled venous blood. In my opinion, there is no evidence that the sulci on the surface of the crest were sufficiently large as to carry enough blood to dump excess heat. The vertical passages in the crest merely are the internal ridges of the "corrugated cardboard" construction of the crest. There is no reason to suggest that the channels carried blood to or from the crest. The crests of *Pteranodon* all are too badly crushed to show any details of the vascular supply. Although it is

true that if the crest was above ambient temperature it would lose heat through convection and possibly radiation, it is unclear why a pterosaur would need a heat exchanger when it had the great expanses of patagium that could probably lose heat to the environment convectively. Perhaps the upper surface of the patagium was not insulated and collected heat from the sun, and a heat exchanger was needed to keep the core temperature within acceptable limits. In any case the heat exchanger theory cannot explain the differences in size of the cranial crests between small and large individuals. If a small crest were sufficient to dump the excess heat in a small individual, why would large individuals have relatively much larger crests?

None of the aerodynamic or physiological functions discussed above can explain the difference in size between the large crests of large individuals and the small crests of small individuals. The crests appear to be display structures, perhaps analogous to horns and antlers. The large crests of males may have attracted females or may have been used to intimidate other males. If the crest is a display structure, then differences in shape need not have a function, and the small crests of females then may be a consequence of the development of large crests in males. The fact that the cranial crest of *Pteranodon* appears to be a display structure rather than having a more practical purpose suggests that the cranial crests of other pterosaurs may also be display structures.

Biological Implications

This study has shown that *Pteranodon* was markedly sexually dimorphic with small females and large males, the modal male being about 50% larger than the modal female (Table 6; Fig. 7). Because mass increases as the cube of linear dimensions males might weigh more than three times as much as females; however, if they had the same wing loading they would weigh slightly more than twice as much as females. In addition, females seem to outnumber males approximately 2:1. These factors must have had profound implications for the biology and social behavior of the animal. Modern analogues that show marked sexual dimorphism include pinnipeds (Bartholomew, 1970), some sheep and large cervids (Geist, 1971; Gould, 1974), and birds such as the Boat-tailed Grackle (Selander, 1965) and some grouse (Wiley, 1974). These animals are polygynous, with a relatively small number of ranking males mating with the majority of females, and they show sexual selection for large body size, and often dramatic display structures, in males. Bartholomew (1970) suggested that the marked sexual dimorphism in pinnipeds was the direct result of the combination of feeding in offshore marine waters and terrestrial breeding on crowded island rookeries. Male pinnipeds often fight to establish territories and the largest and most aggressive males have the greatest mating success. In large cervids, male dominance and reproductive success is largely determined by body size and antler size,

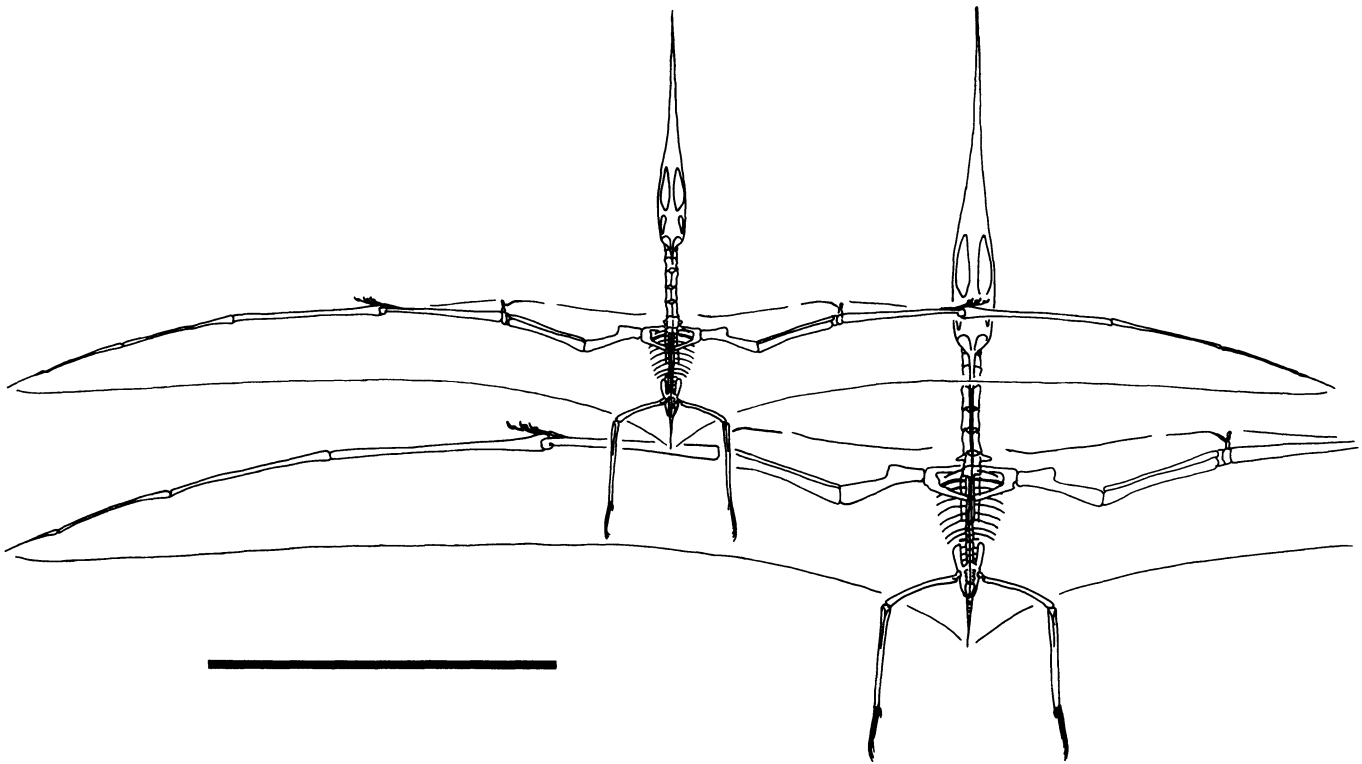


FIGURE 7. Skeletal reconstructions of modal female and male *Pteranodon* in dorsal view, superimposed to show the size dimorphism. Scale = 1 m.

rather than actual combat; the antlers function as “visual dominance-rank symbols” (Geist, 1971; Gould, 1974). Selander (1965) studied Boat-tailed Grackles, which are polygynous, and noted that sexual dimorphism and male display structures are more marked in that species than in related monogamous species. He suggested that while these traits increase the reproductive success of males they also increase the mortality rate of males due to predation and other factors. Thus they are selected for in polygynous birds until that selection is balanced by the higher mortality rate. In Boat-tailed Grackles, the sex-ratio of adults can be as high as 4:1 female to male because of the increased mortality of males (Selander, 1965).

Many seabirds feed offshore and breed in crowded island rookeries like the pinnipeds, yet, unlike pinnipeds, they are monogamous. The important difference between polygynous pinnipeds and monogamous seabirds, and between polygynous and monogamous species in general, seems to be the male contribution to rearing the young (Alexander et al., 1979). In pinnipeds, the male makes no contribution at all to the nurturing of the young, while in seabirds the male is important in feeding the chick. Because the male contributes to the rearing of the chick, the seabirds must be monogamous, and males are not subjected to selection for large size or visual dominance-rank symbols.

Pteranodon does not correspond exactly to any of the patterns seen in the modern analogues, but it does exhibit some elements of each pattern. Like the pinnipeds and seabirds, it fed offshore and probably bred

TABLE 6. Limb elements lengths (in mm) and estimated wingspan (in m) of representative (=modal) small (=female) and large (=male) individuals of *Pteranodon* from the Niobrara Formation. Based on the histogram of humerus lengths (Fig. 1B), the modal lengths of humeri for small and large classes of *Pteranodon* are 165 and 250 mm, respectively. The lengths of other elements were calculated from linear regression equations from Bennett (1991).

Element	Modal Niobrara female	Modal Niobrara male
Coracoid	121	180
Humerus	165	250
Ulna	235	344
Mc IV	359	548
Wp 1	421	615
Wp 2	339	499
Wp 3	242	346
Wp 4	126	194
Femur	164	250
Tibia	243	328
Wingspan	3.8 m	5.6 m

in crowded rookeries. Like the polygynous pinnipeds, and unlike the monogamous seabirds, *Pteranodon* had marked sexual dimorphism. Sexual dimorphism with large males and elaborate display structures suggests that it was polygynous. Large body size in males would be selected for either because it would increase their rank or attract more females, and in either case increase their mating success. The large cranial crest of males could function as a visual rank-dominance symbol and/or as a display to attract females. If the crest was a rank-dominance symbol, it would allow ritualized display to take the place of actual combat. Thus, just as large body size and large antlers are normally sufficient to determine male dominance in large cervids, the large body size and large cranial crest of *Pteranodon* might be sufficient to determine male dominance. If so, much actual combat between males which could easily damage both individuals would be avoided.

Like the model for the evolution of sexual dimorphism and polygyny in pinnipeds advocated by Bartholomew (1970), the combination of offshore feeding and terrestrial breeding in crowded rookeries could account for the development of marked sexual dimorphism and polygyny in *Pteranodon* or its ancestors, if males did not make a significant contribution to the rearing of the young. Large body size and the large cranial crest of males would increase male success in competition for mates and would be selected for until the selection pressure was balanced by higher mortality due to those traits. Large males would lead a more tenuous existence than smaller females because their capacity for powered flight would be more limited, and large cranial crests may also have presented problems. Males would probably have had a higher mortality rate because of large size, cranial crests, and perhaps some minor combat. If the mortality due to large body size or combat was near the rookeries, the sex-ratio observed away from the rookeries in the seaway would be biased. This might account for the biased sex ratio noted above.

Sexual Dimorphism in Other Pterosaurs

Sexual dimorphism is a common phenomenon among vertebrates, but it has been demonstrated for only a few pterosaurs, possibly because of the small samples of most pterosaurs. Sexual morphs of *Rhamphorhynchus muensteri* differ in the proportions of the skull, wing, and hindlimb (Koh, 1937; Wellnhofer, 1975). Wellnhofer (1975) showed that one morph, the supposed males, had slightly larger heads, longer wing fingers, and shorter legs than the females. However, the two sexes were not found to have any morphological differences in the skull, dentition, or pelvis. *Pterodactylus kochi* also can be separated into two groups (Wellnhofer, 1970), one with a relatively high skull length to neck length ratio, and the other with a relatively low skull length to neck length ratio. Wellnhofer suggested that they were sexual morphs, but was unable to find any morphological differences between the two

groups. Mateer (1976) did a multivariate analysis of the measurement data from Wellnhofer (1970) for the five species of *Pterodactylus*, and proposed that *P. micronyx* might be a sexual morph of *P. kochi*. If this were true there would be three morphs, two of *P. kochi* as noted by Wellnhofer (1970), and one of *P. micronyx*. This problem deserves further study.

The pattern of sexual dimorphism seen in *Pteranodon*, with pronounced size dimorphism and morphological dimorphism in the cranial crest and pelvis, differs considerably from those in *Rhamphorhynchus* and *Pterodactylus* and has not been noted in pterosaurs before. Elements of the pattern of dimorphism can be found in other genera of pterosaurs including *Nyctosaurus*, *Quetzalcoatlus*, *Dsungaripterus*, and *Anhanguera*, which suggests that they might be sexually dimorphic.

Nyctosaurus, the small pterosaur found in the Niobrara Formation, seems to have two size-classes: a relatively common small size-class and a relatively rare large size-class (pers. obs.). There seems to be a clear preservational bias in that the small size-class usually occurs as nearly complete skeletons, while the less common large size-class usually occurs as fragmentary remains more like those of *Pteranodon*. The skull and pelvis of the small size-class are well known. The skull lacks a cranial crest, but the pelvis does appear to have a relatively deep puboischiadic plate like that of female *Pteranodon*. Unfortunately, the skull and pelvis of the large-size class of *Nyctosaurus* are not known.

Specimens of *Quetzalcoatlus* from the Javelina Formation of Big Bend National Park, Brewster County, Texas, include one immense individual and a number of smaller individuals about half its size (Lawson, 1975; Langston, 1981). The smaller individuals appear to be adults because the scapulocoracoid and carpus are fully fused (pers. obs.), and the large and small individuals may be morphs of a single species. The skull of the small individuals appears to have a small cranial crest, but the skull of the large individual is not known, and no pelvis has been found. If the large and small specimens do belong to a single species, it would have even more marked sexual size dimorphism (2:1) than is seen in *Pteranodon* (1.5:1).

Dimorphism in cranial crest size or shape has not been demonstrated in other pterosaurs. But Plieninger (1907) suggested that the premaxillary crest of *Germanodactylus*, then considered to pertain to *Pterodactylus kochi*, represented sexual dimorphism. In *Ctenochasma*, such a crest is present in one species (*C. porocristata*; de Buissonje, 1981), while it is absent in two other species (*C. roemeri* and *C. gracile*; Wellnhofer, 1970, 1978). In view of the fact that similar crests are also found in *Galloedactylus* (Fabre, 1976) and *Germanodactylus* (Wellnhofer, 1970), it is unlikely that the crest of *C. porocristata* is an autapomorphy of that species. The presence or absence of the cranial crest in *Ctenochasma* may be sexually dimorphic. This problem deserves further study.

Pelves of *Dsungaripterus*, *Anhanguera*, the Austra-

lian "*Ornithocheirus*," and others appear to fit the pattern of pelvic dimorphism seen in *Pteranodon*. Although the pelvises of Cretaceous pterodactyloids seem to be rather conservative in morphology (Bennett, 1989), pelvises of *Dsungaripterus* (Young, 1964) and a large indeterminate pterodactyloid from Brazil (AMNH 22569; Bennett, 1990) have shallow puboischiadic plates and a small pelvic canal like male *Pteranodon*, while the pelvises of *Anhanguera* (Wellnhofer, 1988, 1991) and the Australian "*Ornithocheirus*" (Molnar, 1987), on the other hand, have deep puboischiadic plates and a large pelvic canal like female *Pteranodon*. At present, none of these taxa are well enough known to determine if they are sexually dimorphic in size or pelvic and cranial structure. The structure of the pelvis of *Anhanguera* suggests that if it is sexually dimorphic like *Pteranodon*, specimens assigned to that taxon are females. Males would be larger, perhaps with large cranial crests. It is possible that the indeterminate pelvis from the Santana Formation (AMNH 22569; Bennett, 1990) is a male *Anhanguera*. In addition, it is noteworthy that Kellner and Campos (1988) considered *Tropeognathus* (Wellnhofer, 1987), which is larger than *Anhanguera* and has large bulbous premaxillary and mandibular crests, to be congeneric with *Anhanguera*. Perhaps *Tropeognathus* is male, while *Anhanguera* is female. If these other large pterodactyloids do conform to that pattern of sexual dimorphism, then marked sexual dimorphism and polygyny may be synapomorphies of a large group of pterosaurs. Before this can be determined, however, those genera must be more fully studied, and the phylogeny of the pterodactyloids must be better understood.

ACKNOWLEDGMENTS

Earlier versions of this work were read by Larry Martin, H.-P. Schultze, and William Duellman, and it was reviewed by Kevin Padian and Peter Wellnhofer; all have provided comments that improved the manuscript. This work formed part of a doctoral dissertation submitted to the Department of Systematics and Ecology and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy. This research was supported in part by NSF Dissertation Improvement Grant BSR-8700547. Access to specimens under their care was kindly provided by: Eugene Gaffney and John Maisey (AMNH); Peter Larson (BHI); Angela Milner (BMNH); Peter Wellnhofer (BSP); David Berman (CM); Richard Stucky (DMNH); Richard Zakrzewski (FHSM); John Bolt (FMNH); L. D. Martin (KUPV); J. D. Stewart and Kenneth Campbell, Jr. (LACM); Farish Jenkins, Jr. (MCZ); Philippe Taquet and Daniel Goujet (MNH); Dale Russell (NMC); Christopher McGowan (ROM); Rupert Wild (SMNS); Wann Langston, Jr. (TMM); Richard Fox (UALVP); Philip Gingerich (UM); Michael Voorhies (UNSM); William Orr (UOCM); Michael Brett-Surman and Robert Purdy (USNM); Solveig Stuenkel

(UUPI); John H. Ostrom (YPM). In addition, I have been given access to specimens in private hands by Fred Nuss (Otis, KS) and Mike Triebold (Valley City, ND).

LITERATURE CITED

- Alexander, R. D., J. L. Hoogland, R. D. Howard, K. M. Noonan, and P. W. Sherman. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates, and humans; pp. 402–435 in N. A. Chagnon and W. Irons (eds.), *Evolutionary Biology and Human Social Behavior, an Anthropological Perspective*. Duxbury Press, North Scituate, Massachusetts.
- Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546–559.
- Bennett, S. C. 1987. Sexual dimorphism in the pterosaur *Pteranodon*. *Journal of Vertebrate Paleontology* 7(Suppl. to 3):11A.
- . 1989. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology* 63: 669–677.
- . 1990. A pterodactyloid pterosaur pelvis from the Santana Formation of Brazil: implications for terrestrial locomotion. *Journal of Vertebrate Paleontology* 10:80–85.
- . 1991. Morphology of the late Cretaceous pterosaur *Pteranodon* and systematics of the Pterodactyloidea. Ph.D. dissertation, University of Kansas, Lawrence, Kansas. xvii + 680 pp.
- Bramwell, C. D., and G. R. Whitfield. 1974. Biomechanics of *Pteranodon*. *Philosophical Transactions of the Royal Society, London, B*, 267:503–581.
- Brower, J. C., and J. Veinus. 1981. Allometry in pterosaurs. *University of Kansas Paleontological Contributions, Paper* 105:1–32.
- de Buissonje, P. H. 1981. *Ctenochasma porocristata* nov. sp. from the Solnhofen Limestone, with some remarks on other Ctenochasmatidae. *Proceedings, Koninklijke Nederlandse Akademie van Wetenschappen (B)* 84:411–436.
- Eaton, G. F. 1910. Osteology of *Pteranodon*. *Memoirs of the Connecticut Academy of Arts and Sciences* 2:1–38.
- Fabre, J. A. 1976. Un nouveau Pterodactylidae du Gisement de Canjuers (VAR) *Gallodactylus canjuersensis* nov. gen., nov. sp. *Annales de Paléontologie (Vertébrés)* 62: 35–70.
- Geist, V. 1971. *Mountain Sheep, a Study in Behavior and Evolution*. University of Chicago Press, Chicago, xv + 383 pp.
- Gould, S. J. 1974. The origin and function of "bizarre" structures: antler size and skull size in the "Irish Elk," *Megaloceros giganteus*. *Evolution* 28:191–220.
- Hattin, D. E. 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. *Kansas Geological Survey, Bulletin* 225:1–108.
- Heptonstall, W. B. 1971. An analysis of the flight of the Cretaceous pterodactyl *Pteranodon ingens*. *Scottish Journal of Geology* 7:61–78.
- Kellner, A. W. A. 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeast Brazil. *Anais da Academia Brasileira de Ciencias* 61: 439–446.
- and D. A. Campos. 1988. Sobre um novo Pteros-

- sauro com crista sagital da Bacia do Araripe, Cretaceo Inferior do Nordeste do Brasil. *Anais da Academia Brasileira de Ciencias* 60:459–469.
- Koh, T.-P. 1937. Untersuchungen über die Gattung *Rhamphorhynchus*. *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie*, Beilage-Band 77:455–506.
- Kripp, D. von. 1943. Ein Lebensbild von *Pteranodon ingens* auf flugtechnischer Grundlage. *Nova Acta Leopoldina*, N.F. 12(83):16–32.
- Langston, W., Jr. 1981. Pterosaurs. *Scientific American* 244(2):122–136.
- Larkin, R. P. 1979. An algorithm for assessing bimodality vs. unimodality in a univariate distribution. *Behavior Research Methods and Instrumentation* 11:467–468.
- Lawson, D. A. 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. *Science* 187:947–948.
- Mateer, N. J. 1975. A study of *Pteranodon*. *Bulletin of the Geological Institutions of the University of Uppsala*, N.S. 6:23–33.
- . 1976. A statistical study of the genus *Pterodactylus*. *Bulletin of the Geological Institutions of the University of Uppsala*, N.S. 6:97–105.
- Molnar, R. E. 1987. A pterosaur pelvis from western Queensland, Australia. *Alcheringa* 11:87–94.
- Olson, E. C. 1957. Size-frequency distributions in samples of extinct organisms. *Journal of Geology* 65:309–333.
- Padian, K. 1980. Note of a new specimen of pterosaur (Reptilia: Pterosauria) from the Norian (Upper Triassic) of Endenna, Italy. *Rivista del Museo di Scienze Naturali Bergamo* 2:119–127.
- Plieninger, F. 1907. Die Pterosaurier der Juraformation Schwabens. *Palaeontographica* 53:209–313.
- Selander, R. F. 1965. On mating systems and sexual selection. *American Naturalist* 99:129–141.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*, 2nd ed. W. H. Freeman and Co., New York, ix + 859 pp.
- Stein, R. S. 1975. Dynamic analysis of *Pteranodon ingens*: a reptilian adaptation to flight. *Journal of Paleontology* 49:534–548.
- Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. *Bayerische Akademie der Wissenschaften, Mathematisch-Wissenschaftliche Klasse, Abhandlungen* 141:1–133.
- . 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. *Palaeontographica A* 148:1–33; 148:132–186; 149:1–30.
- . 1978. Pterosauria. *Handbuch der Paläoherpetologie*, Teil 19. Gustav Fischer Verlag, Stuttgart, x + 82 pp.
- . 1987. New crested pterosaurs from the Lower Cretaceous of Brazil. *Mitteilung der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 27:175–186.
- . 1988. Terrestrial locomotion in pterosaurs. *Historical Biology* 1:3–16.
- . 1991. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica A* 215:43–101.
- and A. W. A. Kellner. 1991. The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, northeastern Brazil. *Mitteilung der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 31:89–106.
- Wiley, R. H. 1974. Evolution of social organization and life-history patterns among grouse. *Quarterly Review of Biology* 49:201–227.
- Wilson, M. V. H. 1984. Year classes and sexual dimorphism in the Eocene catostomid fish *Amyzon aggregatum*. *Journal of Vertebrate Paleontology* 3:137–142.
- Young, C. C. 1964. On a new pterosaurian from Sinkiang, China. *Vertebrata Palasiatica* 8:221–255.

Received 30 December 1991; accepted 10 February 1992.