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CLAW MORPHOLOGY OF *PTERANODON* AND POSSIBLE AQUATIC LOCOMOTION

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ABSTRACT

Previous studies (Bennett 2001 part2, Bramwell and Whitfield 1974) have mentioned in passing that *Pteranodon* may have been able to swim on the surface of the epicontinental seaway that covered the Western Interior of North America during the Cretaceous. Quantitative morphometrics were employed to examine pteranodont claw morphology to ascertain how the morphology of the genus relates morphometrically to the claws found on the feet of aquatic birds and crocodylians, which served as extant phylogenetic bracketing taxa for pterosaurs. The taxa analyzed included four genera of swimming birds, one wading bird, one terrestrial/perching bird, two species of crocodile, and one species of alligator, along with one (possibly two) species of *Pteranodon*.

Homologous landmarks were placed on digital photographs of avian, crocodylian, and pteranodont claws of the left pes, and once these landmarks were transformed into Bookstein coordinates, morphometric data including distances between the landmarks, angles between the landmarks, aspect ratios of the claws, and curvature equations were derived for all of the specimens. These data were analyzed through the use of the program SYSTAT to determine principal component variables, which were then used to perform cluster analyses of digits one through four separately, as well as a cluster analysis of all digits together. Excel was then used to run ANOVA tests on all clusters in search of statistical differences at $\alpha = 0.05$.

Examination of the ANOVA results in regards to the four phenograms of individual claws indicates that the claws of *Pteranodon* most closely resemble that of the Scarlet Ibis (similarities found in all four claws of both taxa) and of the Peacock (similarities found in claw numbers one, three, and four of both taxa). Furthermore, some similarities between pteranodont claws and those of the Great Auk and *Crocodylus porosus*, together with dissimilarities between pteranodont claws and those of the Pelican and Whistling Swan suggest that *Pteranodon* did not swim, but may have rested on the water.

INTRODUCTION

Why Aquatic Locomotion?

It is believed that *Pteranodon* lived and fed in an oceanic environment because its fossils are most commonly (if not always) found in the Cretaceous chalk beds of Kansas (Bennett 1994), and because fossilized fish remains have been found in the jaw and the stomach of two different pteranodont specimens (Bennett 2001 part2). This observation raises the question of whether *Pteranodon* was capable of aquatic locomotion.

Extant Phylogenetic Bracket

The Extant Phylogenetic Bracket (EPB) method (Witmer 1995) was used in this study to make Level I inferences about homologous landmarks placed on the claws of *Pteranodon* and the bracketing taxa, Aves and Crocodylia. The avian bracket was comprised of six genera (seven specimens), and the crocodylian bracket was comprised of two genera (five specimens). One specimen of *Pteranodon* longiceps was used in the analyses; however, three pteranodont specimens containing claws of unknown articulation (and thus uncertain homologies among specimen pes digits) are included in the second phenogram of all claws together.

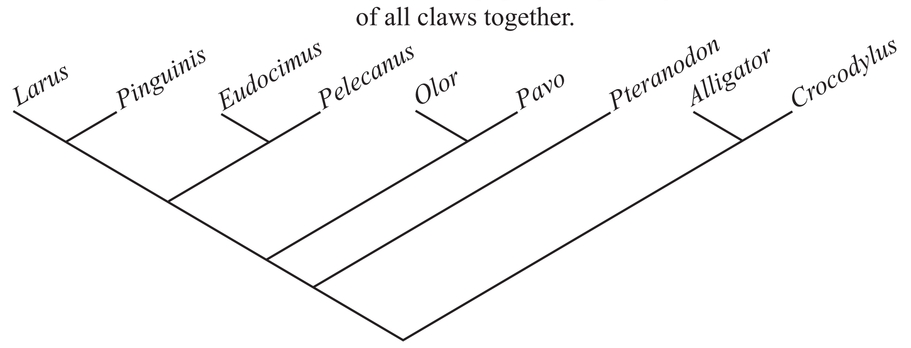


FIGURE 2. Genus-level cladogram of animals used in study (Compiled from Thomas et. al 2004, Brochu 2003, Mayr 2003, Hedges and Sibley 1994, and Bennett 2003). NOTE: Although *Pinguinis* is now extinct, it is used as part of the avian bracket because its behavoir has been observed and documented before its extinction.

Avian Pes Structure and Aquatic Locomotion

The six genera of avians examined in this study have a variety of methods of aquatic locomotion, as well as a variety of pes structures. *Olor columbianus*, the Whistling Swan, and *Larus marinus*, the Great Black Backed Gull, mostly swim at the water's surface (Wallace and Mahan 1975). Both birds are palmate (have complete webbing on the three forward-facing toes); however, the Great Black Backed Gull is tridactyl (the first digit no longer exists), whereas the Whistling Swan is anisodactyl (the first digit is reversed and elevated) (Raikow 1985).

Pinguinis, the Great Auk, and *Pelecanus*, the Pelican, can both swim underwater. However, the Great Auk mainly propelled itself by flapping its wings (Montevecchi and Kirk 1996), whereas the Pelican mainly uses its feet for propulsion (Lockley 1974). Like the Great Black Backed Gull, the Great Auk was totipalmate and tridactyl. On the other hand, the Pelican is ectropodactyl (first digit is medial and incumbent) and totipalmate (has complete webbing on all four toes) (Raikow 1985).

Eudocimus ruber, the Scarlet Ibis, generally wades in shallow marshes, but can swim when pressed by danger (Kushlan and Bildstein 1992). Its pes is anisodactyl, and has only basal webbing (Raikow 1985). In contrast, *Pavo cristatus*, the Peacock, is mostly terrestrial in that it rarely perches and it cannot swim at all (Ragupathy 1998). Its pes, like that of the Scarlet Ibis, is also anisodactyl, but has no webbing whatsoever (Raikow 1985).

Crocodylian Pes Structure and Aquatic Locomotion

Although members of the genus *Crocodylus* have significant webbing on their pes and the pes of *Alligator* is webbed along two third of their digits' lengths (Cope 1900), the pes is not the main source of propulsion in adult crocodylian aquatic locomotion. Instead, adult crocodylians use their tail to propel themselves through the water while using their webbed feet to maintain balance and facilitate maneuverability (Seebacher et al. 2003). Additionally, crocodylians have four digits on the pes, but only digits one through three are clawed (Cope 1900).

SIMPLIFIED PROCEDURES OF QUANTITATIVE MORPHOMETRICS

1. Aquired digital photographs of left foot of *Pteranodon* and taxa in the EPB.
2. Placed all claws in photographs into individual image files.
3. Oriented all claws so that their articulation with the digit pointed downwards and the top surface of the claw faced left.
4. Placed four homologous landmarks onto each claw (figure 3).

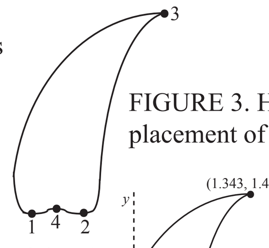


FIGURE 3. Homologous placement of claw landmarks.

5. After recording the raw coordinates of the claw landmarks, transformed all raw coordinates into standardized coordinates (equation 1).

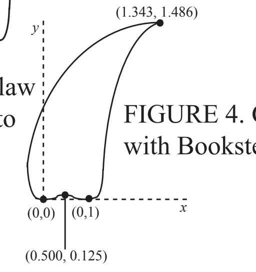


FIGURE 4. Claw landmarks with Bookstein coordinates.

6. Transformed standardized coordinates into Bookstein coordinates (equation 2; figure 4).

$$X_S = X - X_1 \qquad Y_S = Y - Y_1$$

EQUATION 1. Transformation from raw coordinates to standardized coordinates in any given claw.

$$X_B = X_S/X_{S2} \qquad Y_B = Y_S/X_{S2}$$

EQUATION 2. Transformation from standardized coordinates to Bookstein coordinates in any given claw.

7. Calculated the following variables of each claw, based on Bookstein coordinates (number in parentheses represents number of variables yielded):
   A. distances between landmarks (6)
   B. claw centroid coordinates (x, y) (2)
   C. claw centroid size (1)
   D. angles between landmarks (α, β, and γ) (3) (figure 5A-B)
   E. aspect ratio of claw (1)
   F. ratio of α to β (1)
   G. polynomial coefficients from the equations of the outer and inner curves of claw (6) (figure 6)

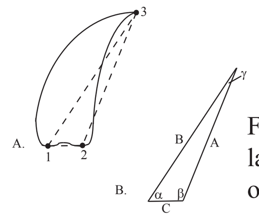


FIGURE 5. A. Triangle connecting landmarks 1,2, and 3. B. Location of triangle variables.

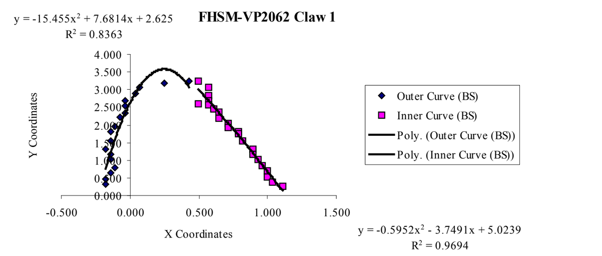


FIGURE 6. Graphical calculation of the curvature of the first claw of *Pteranodon longiceps.*

8. Organized variables into 6 data sets:
   A. Digit 1 Claws
   B. Digit 2 Claws
   C. Digit 3 Claws
   D. Digit 4 Claws
   E. All Digits without Unknown Pteranodont Claws
   F. All Digits with Unknown Pteranodont Claws
9. Calculated variable correlations within each data set and generated principal component variables (PCs) to be used in statistical analyses.
10. Created claw phenograms from each data set by using principal component variables in hierarchical cluster analyses.
11. Used ANOVA to determine if clusters within each data set are statistically similar to or different from each other at $\alpha = 0.05$.

FIGURE 1. The left pes of *Pteranodon longiceps* (VP2026).

RESULTS

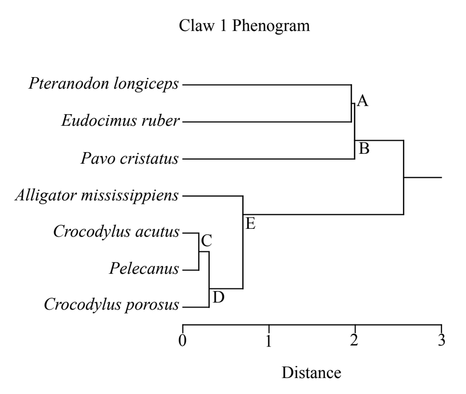


FIGURE 7. Phenogram of digit 1 claws based on principal components.

Cluster	Number of Different PCs (out of 3)
A+C	1
A+D	1
A+E	1
B+C	1
B+D	1
B+E	1

TABLE 1. List of pairs of clusters in the phenogram of the first claw with one or more statistically different principal components .

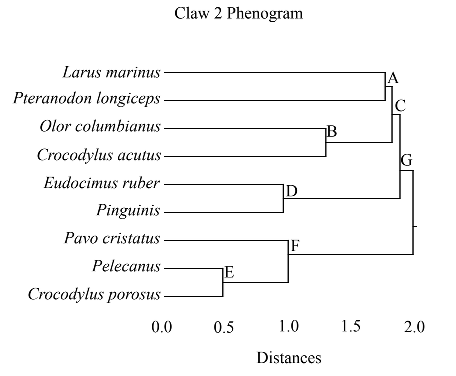


FIGURE 8. Phenogram of digit 2 claws based on principal components.

Cluster	Number of Different PCs (out of 5)
A+E	1
A+F	1
B+F	1
C+E	1
C+F	1
E+G	1
F+G	1

TABLE 2. List of pairs of clusters in the phenogram of the second claw with one or more statistically different principal components .

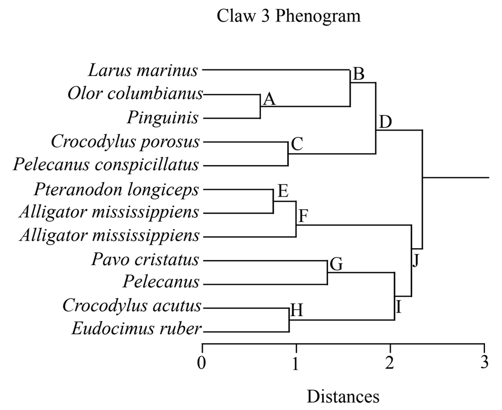
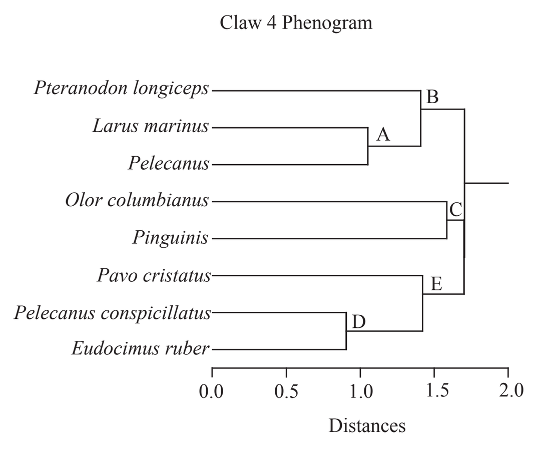


FIGURE 9. Phenogram of digit 3 claws based on principal components.

Cluster	Number of Different PCs (out of 5)
A+E	1
A+F	1
A+H	2
A+I	1
A+J	1
B+E	1
B+F	1
B+I	1
B+J	1
D+J	2
A+G	1
B+C	1
B+H	1
C+G	1
C+H	1
C+I	1
C+J	1
D+H	1
D+I	1

TABLE 3. List of pairs of clusters in the phenogram of the third claw with one or more statistically different principal components .



No statistically significant differences were found between any clusters among all five principal components of the fourth claw phenogram.

FIGURE 10. Phenogram of digit 4 claws based on principal components.

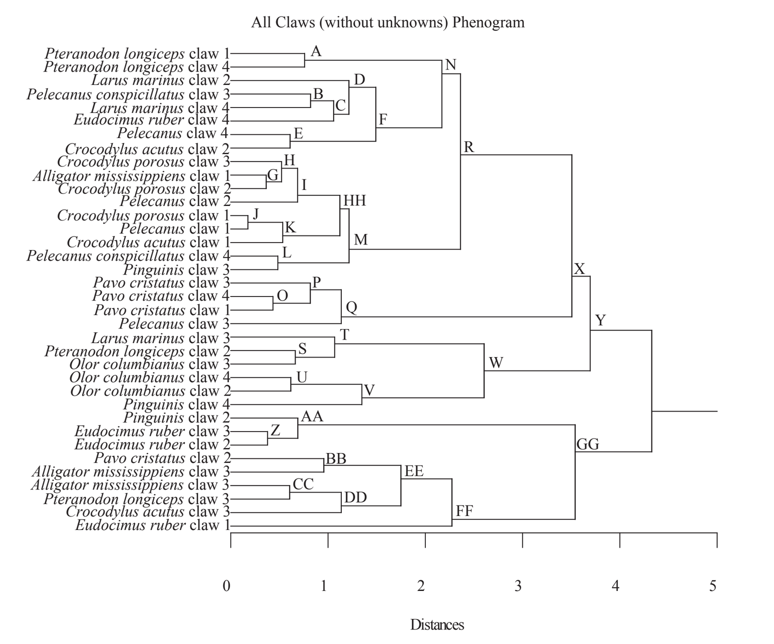


FIGURE 11. Phenogram of all claws (regardless of articulation) from all taxa examined in study, with exception to the four pteranodont claws of unknown articulation.

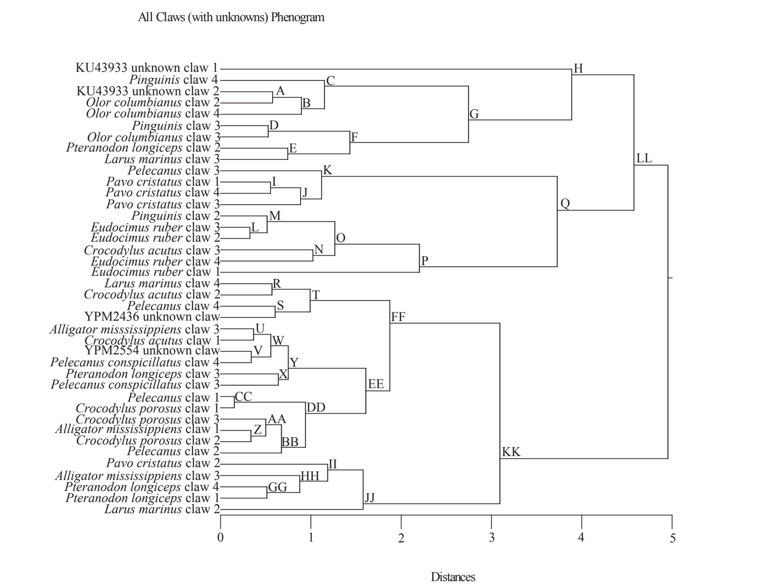


FIGURE 12. Phenogram of all claws (regardless of articulation) from all taxa examined in study, including the four pteranodont claws of unknown articulation.

Taxon	Claw 1	Claw 2	Claw 3	Claw 4
Pavo cristatus	●	☒	●	●
Eudocimus ruber	●	●	●	●
Larus marinus	■	●	☒	●
Olor columbianus	■	●	☒	●
Pinguinis	■	●	☒	●
Pelecanus	☒	☒	●	●
Pelecanus conspicillatus	■	■	●	●
Alligator mississippiens	☒	■	●	■
Crocodylus acutus	☒	●	●	■
Crocodylus porosus	☒	☒	●	■

TABLE 4. Comparison of clusters containing claws of other taxa to the clusters containing the claws of *Pteranodon longiceps* from the four individual claw phenograms (figures 7 - 10).

KEY

■ Claw not analysed
☒ Found in cluster statistically different from cluster containing pteranodont claw
● Found in cluster statistically similar to cluster containing pteranodont claw

DISCUSSION

The Scarlet Ibis the closest match to *Pteranodon* of all taxa in terms of claw morphology because all four claws of *Pteranodon* are statistically similar to the four claws of the Scarlet Ibis. The Peacock is the second closest match to *Pteranodon* in this case due to the similarities between claws one, three, and four. Although the first digit claws of the Scarlet Ibis and the Peacock are statistically likewise to that of *Pteranodon*, the first digits of these birds are reversed and elevated (Raikow 1985), whereas the first digit of *Pteranodon* faces forward. The animals with the next closest set of claw morphologies to those of *Pteranodon* are the Great Black Backed Gull, the Great Auk, and *Crocodylus porosus*, which each have two out of three possible claws similar to the homologous claws in *Pteranodon*. The claws of the Whistling Swan, the Pelican, *Crocodylus acutus* and *Alligator mississippiens* are morphometrically the most dissimilar from pteranodont claws, each taxa with only one or two claws similar to their counterparts in *Pteranodon*.

It is probable that *Pteranodon* did not actively swim in the epicontinental seaway that once covered Kansas because the morphometrics of its claws so closely resemble those of the Scarlet Ibis, which only swims when in danger, and those of the Peacock, which does not swim at all. However, the similarities between pteranodont claws and those of the Great Auk and *Crocodylus porosus* (in other words, taxa that move(d) through the water mainly by means other than foot-propulsion), coupled with the dissimilarities between pteranodont claws and those of the Whistling Swan and the Pelican (taxa that propel themselves in the water with their feet) raise the possibility that *Pteranodon* could have rested on the water without swimming or propelling itself. Contradictions of this idea include the dissimilarity between the first claw of *Pteranodon* and those of all three crocodylian species, as well as the similarities between two pteranodont claws and their counterparts in the Great Black Backed Gull, which uses its feet to propel itself along the water's surface. Claws, however, are very adaptable structures, and their morphometrics may reflect their adaptations for use in walking, running, swimming, grasping/perching, digging, etc. It must therefore be kept in mind that morphometrics of pteranodont claws, as in any taxa, most probably reflect more than one aspect of the claws' uses, such as both aquatic and terrestrial locomotion.

Note that all conclusions here are drawn from the summary of the individual claw phenograms, and not from figures 11 and 12. Each digit needs to be studied by itself in order to ensure homology; figures 11 and 12 are provided here as tangental overviews.

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