A Comparative Assessment of Pterodactyloid Phylogenies

Curran D. Muhlberger

University of Maryland, College Park

Abstract

We conduct a limited cladistic analysis on 8 terminal Pterodactyloid taxa using both originally-scored traits and characters synthesized from previous analyses. Comparing our results to phylogenies proposed by Kellner and Unwin in 2003, we reject Unwin's close relationship between *Germanodactylus* and Dsungaripteridae while finding further support for his positioning of *Nyctosaurus* within Ornithocheiroidea. We also find weak evidence for his proposal of a monophyletic Lophocratia but require additional work to come to a confident conclusion on the matter. The lack of resolution of this polytomy leaves open the question of advanced Pterodactyloid diversification during the Cretaceous.

1. Introduction

First identified as marine creatures in 1784, pterosaurs continue to present many mysteries to vertebrate paleontologists [Buffetaut and Mazin(2003)]. Revealed by Cuvier to have flown rather than swam, most believe that they, like non-avian dinosaurs, are an extinct family of archosaurs who lived from the Late Triassic until the K-T extinction. Their exact place in the tree of life is uncertain, however, due to the long branch attraction inherent in such highly derived forms. There is even considerable disagreement among systematists today regarding relationships between basal taxa in the pterosaur family tree, as there is no obvious outgroup to use in such analyses and the weighting or non-independence of various characters can have a large impact on the result.

Despite a history of inconsistent evolutionary reconstructions, however, several modern phylogenetic analyses have begun to converge on a common basic topology for the pterosaur family tree. Particularly relevant are the 2003 analyses by A. W. A. Kellner [Kellner(2003)] and D. M. Unwin [Unwin(2003)]. Figure 1 displays the consensus tree for Kellner's results, while Unwin's reconstructed phylogeny is shown in Figure 2. Unwin emphasizes the similarities in the basic structure of both trees, but S. C. Bennett, in informal commentary regarding both articles, has pointed out major differences in the structure of Pterodactyloidea, particularly in the monophyly of Dsungaripteroidea. The resolution of these differences has ramifications involving the evolution of an advanced pectoral girdle in large Pterodactyloids.

In this study we hope to resolve some of these differences between Kellner's and Unwin's phylogenies. Our approach is to combine originally-scored character traits with a synthesis of the characters scored by Kellner, Unwin, and Andres and Qiang, whose 2006 cladistic analysis followed the discovery of a new pterosaur
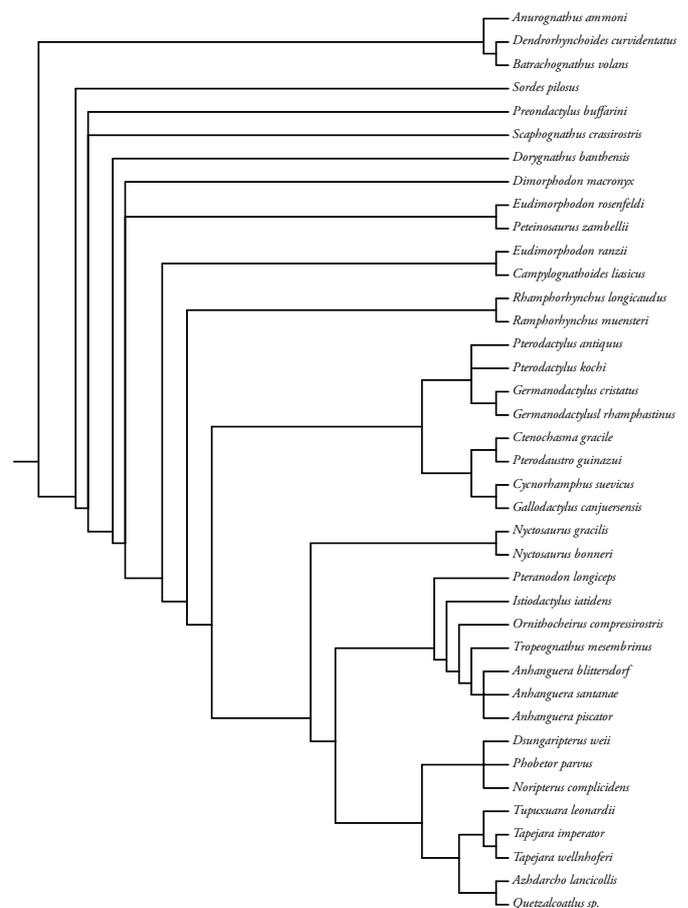

Fig. 1. Pterosaur evolutionary tree inferred by Kellner [Kellner(2003)]. Taxa considered in the present analysis are printed in boldface.
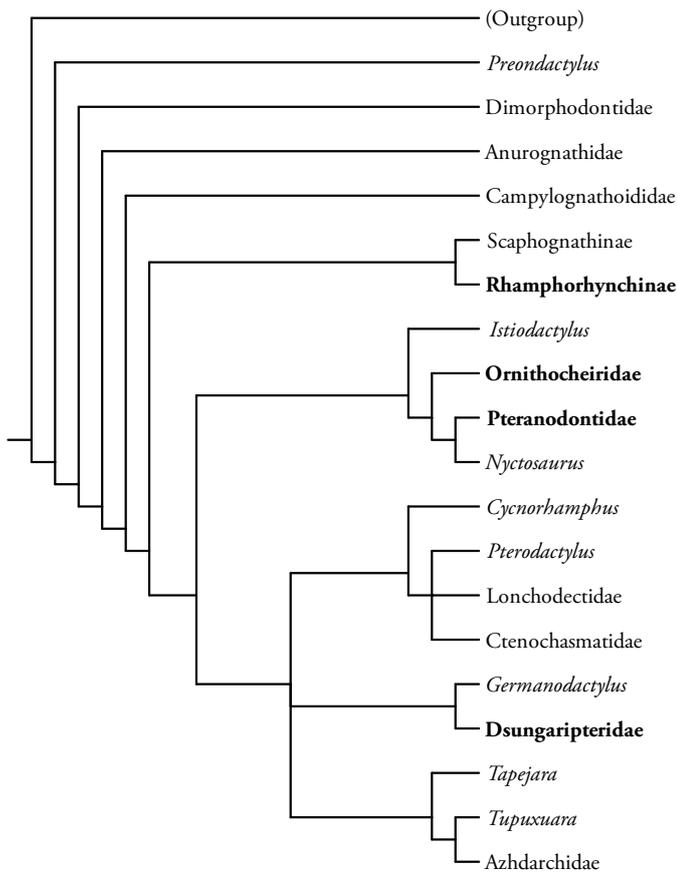
Fig. 2. Pterosaur evolutionary tree inferred by Unwin [Unwin(2003)]. Taxa considered in the present analysis are printed in boldface.

in China [Andres and Qiang(2008)]. The results, in addition to favoring a particular model for the evolution of an advanced pectoral girdle, should also help resolve several minor disagreements in the relationships between species in clades common to both previous analyses.

2. Included Taxa

In order to resolve the differences between Kellner's and Unwin's phylogenies, we chose eight representatives spanning much of the diversity within Pterodactyloidea. In particular, we looked for triplets of taxa where the closeness of internal relationships differed between the two analyses. When both authors agreed on the content and organization of some subclade (Azhdarchoidea for example), we typically chose a single representative. We also required that the taxa be distinctly represented in both works, as Unwin's analysis was conducted at approximately the genus level while Kellner dealt with individual species.

For an outgroup we chose the sister clade to Pterodactyloidea, Rhamphorhynchidae. The relationship between these two clades was first suggested by Howse in 1986 and is a feature common to both Kellner's and Unwin's phylogenies [Kellner(2003)]. Fossil representatives of Pterodactyloidea are found from the Late Jurassic through the Cretaceous. Kellner reconstructs the bifurcation of these two clades at the start of the Late Jurassic, placing rhamphorhynchids in close temporal proximity to basal Pterodacty-

loids. Unwin, on the other hand, places the speciation event back in the Early Jurassic [Unwin(2003)], but this still limits the time difference between the outgroup and the ingroup to less than one period.

Our first ingroup taxa was *Nyctosaurus*, represented primarily by *Nyctosaurus gracilis*, though we conducted our analysis of the wing structure on *Nyctosaurus bonneri* as reconstructed by Kellner [Kellner(2003)]. Lacking a detailed reconstruction of the skull in lateral view, this taxon possesses the fewest originally scored characters. The relationship betwen *Nyctosaurus*, Ornithocheiridae, and Pteranodontidae is one specific (though minor) point of disagreement for Kellner and Unwin.

We next considered Ornithocheiridae, represented primarily by *Ornithocheirus compressirostris*. We scored our original characters using Benton's reconstruction of the skull (which was in turn based on Wellnhofer) [Benton(2000)]. As this taxon possessed many unknown characters in Kellner's work and was absent entirely from Andres and Qiang's analysis, it is the least well represented in the full character matrix. (Note: Unwin, in an informal response to Kellner's work, claims that *Ornithocheirus compressirostris* is actually a representative of Lonchodectidae and not an Ornithocheirid at all. Kellner's analysis happens to group *Ornithocheirus compressirostris* with true Ornithocheirids, but Unwin disagrees on this arrangement. Unfortunately, this point of confusion was discovered too late, and the present analysis thus implicitly assumes the correctness of Kellner's grouping. A refinement of our analysis would relabel this problem taxon as *Lonchodectes compressirostris* and make use of Andres and Qiang's characters for that species.)

Pteranodontidae, particularly *Pteranodon longiceps*, is well-documented by Kellner, Unwin, and Benton and joins *Nyctosaurus* in representing the most advanced Pterodactyloids in terms of their distribution in geologic time.

The first of the more basal species analyzed is *Pterodactylus*, in particular *Pterodactylus kochi*, whose skull and wing are also well-documented by Kellner, Unwin, and Benton. Its purpose is in part to resolve the conflicting relationships between *Pterodactylus*, *Cycnorhamphus*, and *Germanodactylus* in Kellner's and Unwin's phylogenies.

Kellner and Unwin provide ample reconstructions of the skull of *Cycnorhamphus*, specifically *Cycnorhamphus suevicus*, for us to score original characters. Future work may want to resolve the relationship between it and Ctenochasmatidae relative to *Pterodactylus* as the latter is extremely well documented by all sources.

Germanodactylus, particularly *Germanodactylus cristatus*, completes the Jurassic taxa and again has a skull that is well documented by both Kellner and Unwin. Of particular interest is its relationship with Dsungaripteridae, the two of which are rather distantly related in Kellner's phylogeny but form their own clade in Unwin's. *Dsungaripterus weii*, documented by Kellner, Unwin, and Benton, serves to represent the latter group in our analysis.

Finally, *Tapejara*, specifically *Tapejara wellnhoferi* and *Tapejara imperator*, represents the clade Azhdarchoidea (additionally containing *Tupuxuara* and Azhdarchidae), which we included in order to resolve the polytomy present in Unwin's concensus tree.

3. Characters

We compiled our character matrix using a synthesis of originally-scored traits and characters used in previous cladistic analyses, such as those of Kellner and Unwin. Our original characters were scored based on skeletal reconstructions found in publications by Kellner [Kellner(2003)], Unwin [Unwin(2003)], and Benton [Benton(2000)], particularly of the skull and wing.

1. Nasal bone
   – 0: Present
   – 1: Absent
   In nearly all Pterodactyloids the nostril has fused with the antorbital fenestra. In several taxa the nasal bone is retained in reduced form, while in others it is lost entirely.

2. Crest on skull roof
   – 0: Absent
   – 1: Present
   Several taxa exhibit a crest on the skull roof dorsal to the antorbital fenestra.

3. Bony crest extending posterior to skull
   – 0: Absent
   – 1: Present
   Distinguishing feature of *Pteranodon* also present in other species. It may have served an aerodynamic role, but its observed sexual dimorphism indicates that display may have been of higher priority [Benton(2000)].

4. Teeth
   – 0: Present
   – 1: Absent
   Present ancestrally, several derived species of pterosaurs have lost all teeth and presumably fished and swallowed their prey whole [Benton(2000)]. Species like *Pterodaustro* (not studied here) have instead modified their teeth for filter feeding.

5. Teeth at front of jaw
   – 0: Present
   – 1: Absent
   Some taxa, while still posessing teeth, have lost those used for biting at the front of the jaw and retain only reduced teeth in the back of the jaw for chewing. This likely indicates a dietary transition away from insects, who could perhaps escape from the jaw in the absence of biting teeth.

6. Length of carpals relative to ulna/radius
   – 0: Ulna/radius longer than carpals
   – 1: Carpals longer than ulna/radius
   Ancestrally, pterosaur carpals appear to be significantly shorter than the ulna/radius bone. In more derived species, however, the carpals are clearly dominant in length.

7. Size of orbit relative to antorbital fenestra (+nostril)
   – 0: Orbit larger than or comparable in size to antorbital fenestra
   – 1: Orbit significantly smaller than antorbital fenestra
   There appears to be a trend towards the enlargement of the antorbital fenestrae (which has been fused with the nostril in all pterodactyloid species) relative to the size of the orbit. The overall enlargement may have been to reduce weight for these flying creatures, while the lack of enlargement of the orbit may point to a change in diet away from insets, which has been used to explain the relatively large orbits in primitive pterosaurs like *Anurognathus* [Bennett(2005)].

8. Length of snout relative to fenestrae
   – 0: Snout long compared to fenestrae
   – 1: Snout comparable in size or shorter than fenestrae
   Several species exhibit long, narrow snouts extending well beyond the antorbital fenestrae while others feature a shorter, taller skull where the antorbital fenestrae dominate the surface area.

When synthesizing characters from previous studies, we first narrowed our selection to potential synapomorphies for our in-group taxa, then only considered those scored for the majority of these taxa. In addition to avoiding duplicates and characters that were clearly not independent, we also stove to maximize the number of characters based on the presence or absence of a particular trait versus those based on more arbitrary comparisons of relative sizes. The 19 characters used in our final analysis represent three distinct cladistic studies within the past 5 years and cover a wide range of pterosaur anatomy.

The following characters are taken from Unwin's 2003 cladistic analysis [Unwin(2003)].

9. Unguals of manus and pes (Unwin 3)
   – 0: Manual at least $2\times$ size of pedal
   – 1: Similar in size

10. Notarium (Unwin 31)
    – 0: Absent
    – 1: Present

11. Coracoid length (Unwin 32)
    – 0: Shorter than scapula
    – 1: Longer than scapula

12. Shape of the distal end of the humerus (Unwin 35)
    – 0: D-shaped
    – 1: Triangular

13. A femur with a stout neck and steeply directed caput (Unwin 38)
    – 0: Absent
    – 1: Present

14. A pneumatic opening in the palmar surface of the humerus (Unwin 45)
    – 0: Absent
    – 1: Present

15. Deltopectoral crest of humerus with elongate rectangular profile (Unwin 47)
    – 0: Absent
    – 1: Present

16. Dsungaripteroid teeth (Unwin 55)
    – 0: Absent
    – 1: Present
    Compared to the long, sharp-pointed teeth of the majority of pterosaurs, Dsungaripteroid teeth are shorter and broader.

The following characters are taken from Kellner's 2003 cladistic analysis [Kellner(2003)].

17. Shape of posterior region of skull (Kellner 19)
    – 0: Not rounded

– 1: Round with squamosal displaced ventrally
18. Position of the quadrate relative to the ventral margin of skull (Kellner 20)
    – 0: Inclined ≈ 120° backwards
    – 1: Inclined ≈ 150° backwards
19. Position of the articulation between the skull and the mandible (Kellner 21)
    – 0: Articulation under the middle part of the orbit
    – 1: Articulation under the anterior half of the orbit
20. Distal ends of paroccipital processes (Kellner 25)
    – 0: Not expanded
    – 1: Expanded
21. Size of mid-cervical vertebrae (Kellner 45)
    – 0: Short, subequal in length
    – 1: Elongated
22. Proportional lengths of the humerus (h), ulna (u), femur (f), and tibia (t) (Kellner 56)
    – 0: $\frac{h+u}{f+t} \leq 0.8$
    – 1: $\frac{h+u}{f+t} > 0.8$
23. Length of the first phalanx of manual digit IV (Kellner 67)
    – 0: At least 2× length of tibiotarsus
    – 1: Elongated less than 2× length of tibiotarsus
24. Length of metatarsal III (Kellner 72)
    – 0: Loner than 30% of tibia length
    – 1: Shorter than 30% of tibia length

These final characters are taken from Andres and Qiang's 2008 cladistic study [Andres and Qiang(2008)].

25. Nasal process (Andres & Qiang 21)
    – 0: Present
    – 1: Absent
26. Postexapophyses on cervical vertebrae process (Andres & Qiang 63)
    – 0: Absent
    – 1: Present
27. Angle of femur caput to shaft (Andres & Qiang 109)
    – 0: ≤ 145°
    – 1: > 145°

4. Methods

We conducted our final analysis on eight terminal taxa and one outgroup. Our character matrix consisted of 27 characters with two states each (0 & 1), in addition to the unknown state (?). This matrix is reproduced in full in Appendix A. We also performed an initial analysis without our originally scored characters. This initial dataset included 25 characters, 6 of which were not independent of our original characters and thus are not listed in Section 3. See Appendix B for their descriptions.

Initially, we entered our character matrix into MacClade 4.06 in order to produce a NEXUS file compatible with PAUP (Phylogenetic Analysis Using Parsimony). Using the heuristic search algorithm in PAUP* 4.0b10 for Macintosh (PPC/Altivec), we discovered three equally parsimonious minimum-length trees. These results, along with the strict, Adams, and majority concensus trees, were then exported to MacClade for closer examination. All of
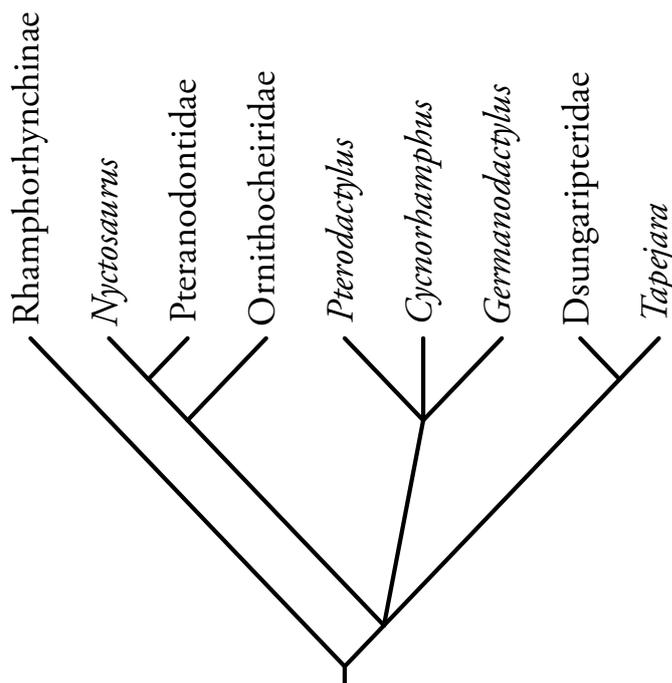

Fig. 3. Adams consensus tree of the results of our initial analysis. The tree is isomorphic to the strict consensus tree.

the preceding analysis took place on an Apple iMac running Mac OS X.

Due to the limited availability of the PAUP software and the single-platform nature of MacClade, we chose to conduct all further analysis using PHYLIP (PHYLogeny Inference Package), an open-source software suite from the University of Washington. We compiled version 3.67 of PHYLIP for 64-bit Linux and executed its various tools on an AMD Athlon64 CPU running a custom 2.6.24 Linux kernel. As we were only considering 8 ingroup taxa in the analysis, we chose to search for the most parsimonious trees using the "branch and bound" algorithm as implemented in the program penny. This algorithm is guaranteed to find all of the trees of minimum length and can therefore be used to double-check that PAUP's heuristic analysis indeed found the global minimum in tree space. As this problem is NP-complete, the algorithm is only feasible for small datasets such as ours.

5. Results

Our initial analysis on 25 non-original characters resulted in three equally parsimonious trees of length 43. Each tree possessed a Consistency Index of 0.581 and a Retention Index of 0.660. The Adams consensus tree, in this case isomorphic to the strict consensus tree, is shown in Figure 3. Pterodactyloidea is divided into three major subclades mirroring the superfamilies Ornithocheiroidea, Ctenochasmatoidea, and Azdarchoidea. Notably Unwin's Dsungaripteroidea (including *Germanodactylus* but excluding Ctenochasmatoidea, see Figure 2) is rejected by all three trees. Unresolved, however, is the relationship between these clades, as is the placement of *Germanodactylus* within Ctenochasmatoidea.

4

Rhamphorhynchinae

Nyctosaurus

Pteranodontidae

Ornithocheiridae

Pterodactylus

Cycnorhamphus

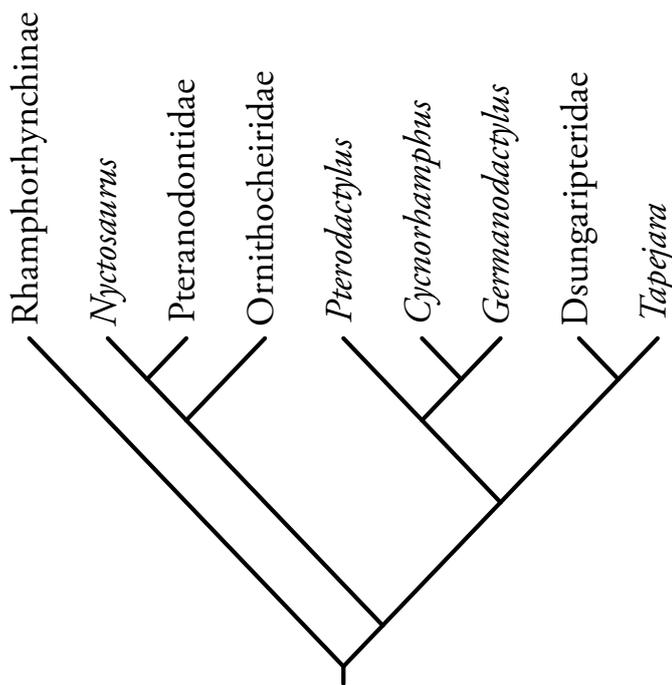*Germanodactylus*

Dsungaripteridae

Tapejara

Fig. 4. Single most parsimonious tree resulting from our final analysis. The tree is isomorphic to the 50% majority rule consensus tree for our initial analysis.

Ornithocheiroidea is diagnosed primarily by the derived state of characters 10-13; that is, the presence of a notarium, a coracoid longer than the scapula, a triangular-shaped distal end of the humerus, and a stoutly-necked femur. The close relationship between *Nyctosaurus* and Pteranodontidae is in agreement with Unwin's conclusions (though the confused identity of *Ornithocheirus* casts uncertainty over relationships within the clade). Ctenochasmatoidea exhibits synapomorphies in the form of the derived state of characters 17-18, 21, & 27 (and character 5 in Appendix B). Its members feature a rounded posterior region of the skull, peg-like teeth, and elongated mid-cervical vertebrae. Characters 11, 19-20, & 25 (and character 4 in Appendix B) are traits of what Kellner calls Tapejaroidea, the clade containing Azdarchoidea and Dsungaripteridae. A continued sagittal cranial crest, expanded distal ends of the paroccipital process, and the absence of a nasal process set this clade apart.

Including our originally-scored characters, a single most parsimonious tree of length 46 emerges. This result, shown in Figure 4, is in fact isomorphic to the 50% majority rule consensus tree for our initial analysis. The addition of these traits has resolved both polytomies, and Unwin's hypothesis of a close relationship between *Germanodactylus* and Dsungaripteridae is again refuted. Of particular interest is the fact that Tapejaroidea and Ctenochasmatoidea are more closely related to one another than either is to Ornithocheiroidea, a result that agrees with Unwin's analysis in refutation of Kellner, who proposed that Tapejaroidea and Ornithocheiroidea were more closely related than either was to Ctenochasmatoidea (see Figure1). This monophyletic clade, named Lophocratia by Unwin, is diagnosed by characters 15 & 23-24 (and character 1 in Appendix B).

6. Discussion

Stratigraphic evidence presented by Kellner, Unwin, and Andres and Qiang shows that the relationship between *Nyctosaurus*, Pteranodontidae, and Ornithocheridae proposed both here and in Unwin's analysis is less incongruent than that proposed by Kellner, as both *Nyctosaurus* and *Pteranodon* do not appear until the Late Cretaceous, while Ornithocheridae/Lonchodectidae is found at earlier strata. All three appear significantly later than the other taxa under consideration, consistent with their identification as a distinct clade. The close relationship of *Cycnorhamphus* and *Germanodactylus* relative to *Pterodactylus* suggested by our results is slightly stratigraphically incongruent, as *Germanodactylus* is found earlier in the Late Jurassic than either of the other two species.

Andres and Qiang, upon the discovery of *Elanodactylus prolatus* in the Liaoning Province of China, have conducted a more recent analysis of Pterodactyloidea involving 61 terminal taxa and 111 characters [Andres and Qiang(2008)], the results of which are shown in Figure 5. Comparison with their tree reveals considerable conflict between the four phylogenies discussed so far. In agreement with both our final results and those of Kellner, Andres and Qiang propose that *Germanodactylus* is more closely related to *Pterodactylus* than to Dsungaripteridae, rejecting Unwin's proposed Dsungaripteroidea (which in their analysis becomes synonymous with all of Pterodactyloidea). Furthermore, they agree with the inclusion of *Lonchodectes compressirostris* in Ornithocheiroidea and claim that it is more closely related to Pteranodontidae than either is to Nyctosaurus, a result in agreement with Kellner's analysis but contradictory to both Unwin's and ours. Additionally, they are in agreement with Kellner in claiming that what we have called Ornithocheiroidea is more closely related to Tapejaroidea than either is to Ctenochasmatoidea, again contrary to our findings. Thus, while the close relationship of *Germanodactylus* to Dsungaripteridae has been refuted with reasonable confidence, many other dissimilarities in Kellner's and Unwin's analyses remain ambiguous.

Despite disagreement over Dsungaripteridae's closest relative, our analysis supports Unwin's proposed monophyletic group Lophocratia containing Ornithocheiroidea and Tapejaroidea but excluding Ctenochasmatoidea. In light of Bennett's remarks, this implies convergent evolution of an advanced pectoral girdle, which is perhaps less parsimonious than the single evolution required by Kellner's and Andres and Qiang's results. Thus, rather than a single development sparking a great diversity in advanced Pterodactyloids, we predict a universal trend towards enlargement and improvement of the girdle. This view meshes well with the hypothesis that the first flying dinosaurs displaced most smaller pterosaurs in their ecological roles, as the new competition would have selected features like larger size that would give pterosaurs an advantage over these predecessors to modern birds.

Considering the diets and dentition of the species under examination, it appears that a closer relationship between Ornithocheiroidea and Tapejaroidea would be more congruous, as members of both clades experienced a reduction in tooth size or the loss of teeth altogether, presumably as they pursued a seafood diet. In this situation it would have been helpful to have addition-
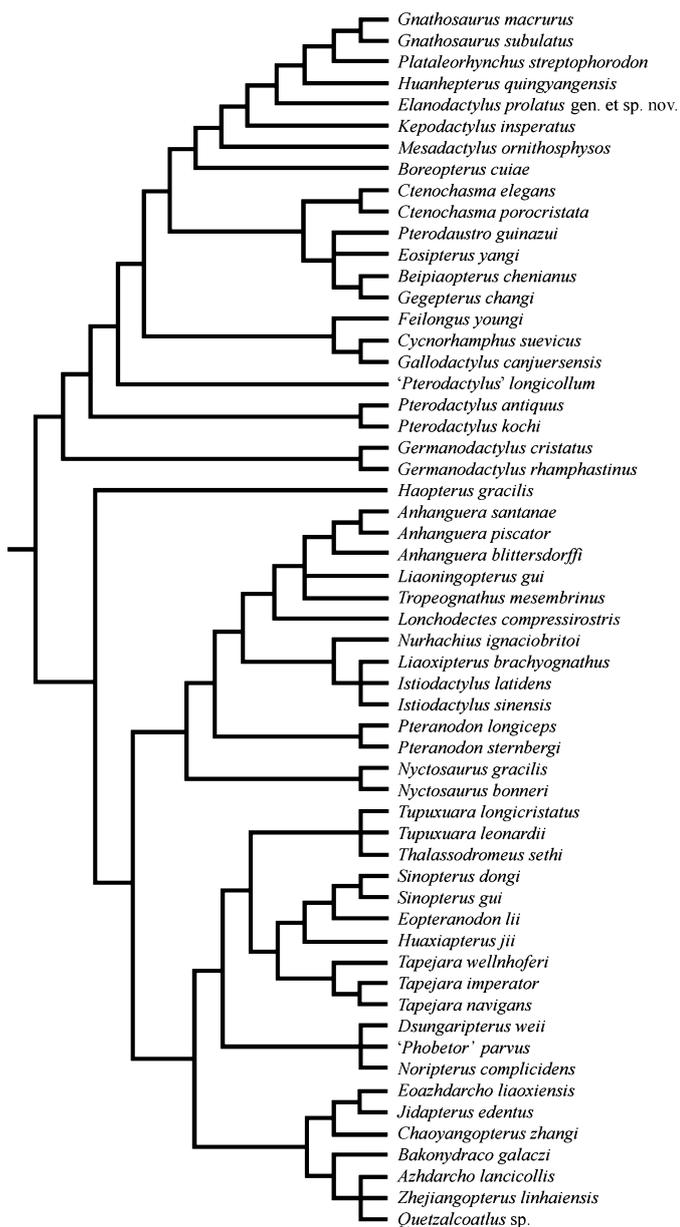
Fig. 5. Pterodactyloid phylogeny inferred by Andres and Qiang [Andres and Qiang(2008)].

ally considered *Ctenochasma* in our analysis, as it is often found closely related with *Cycnorhamphus* yet was also highly adapted for an aquatic diet, though one of filtering rather than fishing.

7. Conclusion

In light of all of the phylogenies considered here, few strong conclusions can be made regarding the conflicts between Kellner's and Unwin's 2003 analyses. Focusing for a moment solely on our results, however, we find more evidence for Unwin's organization of the three main Pterodactyloid clades than Kellner's. Unfortunately this determination is far from conclusive, and in fact all three clades formed a polytomy in our initial analysis. Both stratigraphic and dietary data suggest a closer relationship

between Ornithocheiroidea and Tapejaroidea, in addition to the simpler single evolution of an advanced pectoral girdle. Weighing against this are Lophocratia's synapomorphies regarding rostral dentition, the deltapectoral crest of the humerus, and several proportional bone lengths. What is clear, though, is that *Pterodactylus*, *Cycnorhamphus*, and *Germanodactylus* form a monophyletic group that appears to have gone extinct at the Jurassic-Cretaceous boundary, and here we find fault with Unwin's phylogenies.

By conducting this small exploration into the phylogeny of pterosaurs, we can more easily identify which disagreements of larger analyses are significant and worthy of further investigation. This knowledge would greatly aid in taxa selection for a future analysis. In particular, two mysteries that remain unresolved are the placement of *Nyctosaurus* within Ornithocheiroidea and the existence of a monophyletic Lophocratia as a proper subset of Pterodactyloidea. We would also aim to be more careful regarding potentially misleading names for taxa when synthesizing characters from distinct sources.

On the whole we are relatively confident in the close relationship between *Nyctosaurus* and Pteranodontidae (despite conflicting proposals by Kellner and Andres and Qiang) and in the grouping of *Germanodactylus* with Ctenochasmatoidea. However, we do not find the synapomorphies diagnosing a potential Lophocratia convincing enough to place much confidence in its existence. In the future, with access to additional reconstructions not limited to the skull and wing, we may hope to achieve a stronger conclusion regarding this significant ambiguity in pterosaur phylogeny and in doing so learn a great deal about the pattern of their diversification throughout the Cretaceous.

8. Acknowledgments

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Appendix A. Character Matrix

These characters were used in the final analysis conducted using PHYLIP.

Taxon					5					10					15					20					25		
Rhamphorhynchinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nyctosaurus	1	?	?	1	?	1	0	0	?	1	1	?	1	1	0	0	0	?	0	0	0	0	0	0	1	1	0
Ornithocheiridae	1	0	0	0	0	?	0	0	0	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Pteranodontidae	1	0	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	1	1
Pterodactylus	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1
Cycnorhamphus	1	0	0	0	1	?	0	1	1	0	0	0	0	?	1	0	1	1	0	0	1	1	1	1	0	0	1
Germanodactylus	0	1	0	0	0	?	1	1	1	0	0	0	0	?	1	1	1	1	0	0	1	0	1	1	0	0	1
Dsungaripteridae	0	1	0	0	1	?	1	1	1	1	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	0
Tapejara	1	1	1	1	1	?	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	1	1	1	0

Appendix B. Additional Characters

These characters were used in our initial PAUP analysis but were not independent of our originally scored characters and so were left out of our final computation.
1. Rostral dentition (Unwin 22)
    – 0: Fewer than 11 pairs of teeth
    – 1: Greater than 11 pairs of teeth
2. Tall, narrow frontal crest (Unwin 42)
    – 0: Absent
    – 1: Present
3. Dentition (Unwin 43)
    – 0: Present
    – 1: Absent
4. Sagittal cranial crest continued, extending to apex of skull (Unwin 48)
    – 0: Absesnt
    – 1: Present
5. Tooth type (Kellner 39)
    – 0: Not peg-like
    – 1: Peg-like, more than 15 on each side of jaw
6. Bony frontal crest (Andres & Qiang 26)
    – 0: Absent
    – 1: Present

Taxon					5	
Rhamphorhynchinae	0	0	0	0	0	0
Nyctosaurus	0	1	1	0	0	1
Ornithocheiridae	1	0	0	0	0	?
Pteranodontidae	1	1	1	0	0	1
Pterodactylus	1	0	0	0	1	0
Cycnorhamphus	0	0	0	0	0	0
Germanodactylus	1	0	0	1	1	0
Dsungaripteridae	1	0	0	1	0	1
Tapejara	0	0	1	1	0	1