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COMMENTS ON THE PHYLOGENY OF THE PTERODACTYLOIDEA

INTRODUCTION

Traditionally the Pterosauria was subdivided into two groups: the Rhamphorhynchoidea and the Pterodactyloidea (e.g., Wellnhofer, 1978; 1991). Contrary to the Rhamphorhynchoidea, nowadays considered by most researchers as paraphyletic (e.g., Howse, 1986; Unwin, 1995; Kellner, 1996), the monophyly of the Pterodactyloidea was never seriously questioned. Despite a general agreement about which species can (or not) be regarded as a member of this clade, there is presently disagreement about the relationships of the different pterodactyloid taxa. Here I present some comments on the pterosaur clades that compose the Pterodactyloidea, their inter-relationships (Fig. 1) and their biochronology (Fig. 2). I also discuss several evolutionary aspects of those flying reptiles. The information presented here is based on previous works, specially Kellner (1996). Characters were obtained from several sources, particularly Wellnhofer (1978), Howse (1986), Bennett (1989; 1994), Unwin (1995), Unwin & Lu, (1997), Kellner (1996, in press), and Kellner & Tomida (2000).

THE PTERODACTYLOIDEA

The clade Pterodactyloidea (Fig. 1, node 1) can be defined as the most recent common ancestor of *Pterodactylus* and *Quetzalcoatlus* and all their descendants. Their immediate sister-group are the Rhamphorhynchidae (Fig. 1), as pointed out by several authors (e.g., Unwin, 1995; Kellner, 1996). The recorded temporal range varies from Tithonian (Late Jurassic) to Maastrichtian (Late Cretaceous; Fig. 2). The members of this clade share a large number of characters such as: naris and antorbital fenestra confluent; absence of cervical ribs on midcervical vertebrae; proportional length of humerus relative to the metacarpal IV larger than 0.40; ulna less than two times the length of metacarpal IV; first phalanx of manual digit IV less than twice the length of the metacarpal IV; and femur about the same length or smaller than metacarpal IV. Pterodactyloids also have the fifth pedal digit reduced with one (e.g., *Pterodactylus*, *Tapejara*) or no phalanx.

Among other features that diagnose the Perodactyloidea is the short tail with less than 15 caudal vertebrae. Although this number could be higher (complete tails are know for only a few specimens), this condition differs from all non-pterodactyloid that have a long tail. The sole exception is found in the anurognathid *Anurognathus* (and perhaps other members of the Anurognathidae) and, according to the present analysis, a short tail was achieved independently by those taxa. Pterodactyloids also are characterized by their particular deltopectoral crest of the humerus that is long, proximally placed, and curves ventrally. Within Pterodactyloidea, however, there is variation of the distal end of the deltopectoral crest that shows three basic shapes:

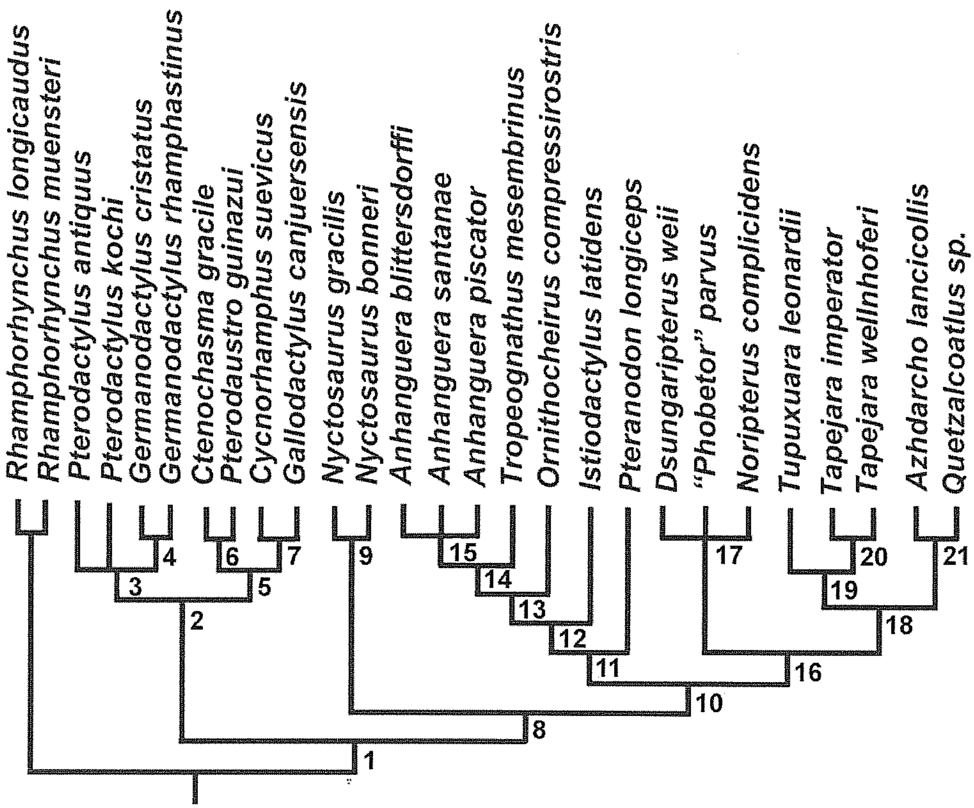

Fig. 1. Cladogram illustrating the relationships of the Pterodactyloidea. The Rhamphorhynchidae (*Rhamphorhynchus muensteri* + *Rhamphorhynchus longicaudus*) are the closest taxon related to the Pterodactyloidea. 1 - Pterodactyloidea; 2 - Archaeopterodactyloidea; 8 - Dsungaripteroidea. See text for details.

proximally placed and curving ventrally (Archaeopterodactyloidea and Tapejaroidea); hatched shaped and displaced away from the caput humeri (Nyctosauridae); and warped (Pteranodontoidea).

The Pterodactyloidea shows a basal dichotomy: the Archaeopterodactyloidea and the Dsungaripteroidea. The Archaeopterodactyloidea (Fig. 1, node 2) is formed by *Pterodactylus*, *Germanodactylus*, Ctenochasmatidae, and Gallodactylidae. It has a temporal range from Tithonian (Late Jurassic) to Albian (Early Cretaceous, Fig. 2). Among the synapomorphies of this clade are the following: posterior region of the skull rounded with the squamosal displaced ventrally; quadrate inclined backward for about 150° relative to the ventral margin of the skull; and neural spines of the midcervical vertebrae low, bladelike.

Among other features that diagnose this clade is the presence of a laterally placed nasal process. Its shape, however, varies from being long and oriented vertically (*Pterodactylus*, *Germanodactylus*, *Pterodaustro*) or reduced (*Gallodactylus*, *Cycnorhamphus*). Archaeopterodactyloids differ also from other pterosaurs by having the midcervical vertebrae elongated, but not to the same degree as azhdarchids (node 21).

Pterodactylus antiquus + *Pterodactylus kochi* + *Germanodactylus* (Fig. 1, node 3), form a monophyletic group within Archaeopterodactyloidea, sharing the following features: nasal process present on the lateral side of the skull straight and directed ventrally (not connected with the maxilla) and more than 15 peg-like teeth on each side of the jaws. *Germanodactylus* is known by two species, *Germanodactylus cristatus* and *Germanodactylus rhamphastinus* that form the Germanodactylidae (Fig. 1, node 4) and share a low premaxillary sagittal crest, displaced backward near the anterior margin of the nasoantorbital fenestra reaching the skull roof (but not extending backward). Another grouping within Archaeopterodactyloidea (Fig. 1, node 5) is formed by Ctenochasmatidae and Gallodactylidae that share one feature: the dorsal margin of the skull concave. The Ctenochasmatidae (Fig. 1, node 6) is formed by *Ctenochasma* and *Pterodaustro*, which are unique by having the rostrum extremely elongated (reaching more than 60% of the skull length) and the dentition formed by over 150 long and slender teeth. Regarding the dentition, *Pterodaustro* further differs by having filliform teeth, an autapomorphy of this taxon (e.g., Sanchez, 1973; Chiappe et al., 2000). The Gallodactylidae (Fig. 1, node 7), formed by *Gallodactylus* and *Cycnorhamphus*, is diagnosed by the particular nasal process (reduced and placed on the lateral side of the skull) and the presence of a laterally compressed parietal crest expanded posteriorly with a rounded posterior margin, and the teeth confined to the anterior portion of the jaws.

The second major division of the Pterodactyloidea is the clade Dsungaripteroidea (Fig. 1, node 8) that has a recorded temporal range from Kimmeridgian/Tithonian (Late Jurassic) to Maastrichtian (Late Cretaceous, Fig. 2). The synapomorphies of this group are as follows: presence of a notarium (number of vertebrae varies depending on taxon and ontogeny); fused atlas and axis; presence of postexapophyses on cervical vertebrae; and the pteroid longer than half of the length of ulna. There are other potential dsungaripterid synapomorphies (e.g., helical jaw joint, elongated basisphenoid, and interpterygoid opening smaller than subtemporal fenestra), but their states are unknown in the Archaeopterodactyloidea and could therefore diagnose a more inclusive group.

At the base of the Dsungaripteroidea are the Nyctosauridae (Fig. 1, node 9), diagnosed by having the humerus less than 40% of metacarpal IV length and the deltopectoral crest of humerus hatched shaped, displaced away from the caput humeri. Next comes the Ornithocheiroidea (Fig. 1, node 10), whose members have a parietal crest constituting the base of the posterior portion of the cranial crest (condition unknown in the Azhdarchidae), the articulation between skull and mandible positioned under the anterior half of the orbit, and a lateral pneumatic foramen on the centrum of the cervical vertebrae (secondarily lost in the Azhdarchidae).

The Ornithocheiroidea is further subdivided into two clades: the Pteranodontoidea and the Tapejaroidea. The members of the Pteranodontoidea (Fig. 1, node 11) share the following synapomorphies: neural spines of the midcervical vertebrae tall and spikelike; proximal surface of the scapula sub-oval; scapula shorter than coracoid; warped deltopectoral crest of humerus; and the distal end of the humerus subtriangular. At the base of this grouping is *Pteranodon* that lacks two characters present in the clade *Istiodactylus* +Anhangueridae (Fig. 1, node 12): stout scapula, with constricted shaft and the diameter of radius less than half of the diameter of ulna. The sole feature that unites *Ornithocheirus* and the Anhangueridae (Fig. 1, node 13) is the presence of a palatal ridge. Anhanguerids (Fig. 1, node 14), are further distinguished from all other pterosaurs by the presence of an anteriorly placed premaxillary sagittal crest, the tip of the premaxilla slightly expanded (but not spoon-shaped as in *Gnathosaurus*), and a short, blade-like sagittal crest on the ventral portion of the dentary.

There are several characters that fall out at the *Anhanguera* node (Fig. 1, node 15) such as long nasal process placed medially; foramen perforating nasal process; scapula substantially shorter than coracoid (ratio length of scapula/coracoid ≤ 0.80); coracoidal contact with sternum forming an oval articulation surface, with a posterior expansion; and pneumatic foramen on the proximal part of humerus situated dorsally. It is likely that some of those features might diagnose a more inclusive group (e.g., the Anhangueridae) since no postcranial material was reported for *Tropeognathus* and none can be confidently associated to the *Ornithocheirus* complex (based essentially on cranial fragments).

The Tapejaroidea (Fig. 1, node 16), comprised three clades: Dsungaripteridae, Tapejaridae, and Azhdarchidae. Tapejaroids share the following features: low and elongated frontal crest; supraoccipital extending backward; expanded distal ends of the paroccipital processes; and the medial crest of humerus massive, with a developed proximal ridge. Except for the latter, none of the listed features could be observed in the members of the Azhdarchidae, since none of the known specimen has the posterior region of the skull well preserved. The Dsungaripteridae (Fig. 1, node 17), first recognized by Young (1964, 1973), is characterized by having the orbit comparatively small and positioned very high in the skull; a suborbital opening; a high premaxillary sagittal crest, displaced backward, near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit, and extending backward; and a posterior ventral expansion of the maxilla. Furthermore, where known, there are no teeth on the anterior portion of the jaws. Tapejarids and azhdarchids are in sister-group relationship (forming the Azhdarchoidea 1, node 18), which is based on the position of the orbit (lower than the dorsal rim of the nasoantorbital fenestra) and on the second phalanx of manual digit IV more than one third smaller than first phalanx of manual digit IV.

The Tapejaridae (Fig. 1, node 19) include *Tapejara* and *Tupuxara*. They share a very large nasoantorbital fenestra (longer than 40% of skull length) and a premaxillary sagittal crest starting on the anterior portion of the skull and extended posteriorly above the occipital region. Other features indicating the tapejarid monophyly are the particular pear-shaped orbit, the thin lachrymal process of the jugal and the presence of a well developed tuberculum on the coracoid. *Tapejara* (Fig. 1, node 20) is set apart from *Tupuxuara* by having a very unusual rostrum that is downturned.

The last clade recognized within the Pterodactyloidea is the Azhdarchidae (Fig. 1, node 21) that have the midcervical vertebrae extremely elongated (more than in any archaeopterodactyloid), with the neural spines extremely reduced or absent. Independently recognized by Nessov (1984) and Padian (1984, 1986), this clade is also one of the least known within Pterodactyloidea, and most specimens are comprise only cervical vertebrae.

Based on the cladogram of Fig. 1 that summarizes the current knowledge of the relationships of the Pterodactyloidea, some general comments about the evolution of the members of this clade can be made. There is a trend to increase size that is also observable in pterosaurs in general. Within Archaeopterodactyloidea, sizes of adult animals were between 2 meters and a maximum of ca. 2.5 meters (Wellnhofer, 1991); true gigantic forms were developed only in the Dsungaripteroidea. The wing metacarpal and the pteroid also increase compared to the primitive pterosaur forms, the former reaching an extreme size in nyctosaurids. Within Ornithocheiroidea there is a tendency of the first three wing phalanxes to become gradually more smaller than the first, and the general condition of ph1d4>ph2d4>ph3d4 gets particularly accentuated in the Tapejaroidea. Some sort of cranial crest becomes common in most pterodactyloids, particularly in the Ornithocheiroidea, where crests vary in shape and size. Extreme conditions are reported in *Tapejara imperator* and *Thalassodromeus sethi* (tapejarids from the Aptian-Albian Santana Formation). Loss of teeth seems to be a general trend among dsungaripteroids and is observed in the Nyctosauridae, *Pteranodon*, and azhdarchoids. It should be noted that this is a direct result of the position of *Pteranodon* as the basal member of the Pteranodontoidea - if future work places this taxon in a higher position within pteranodontoids, loss of teeth will have to be reinterpreted as having occurred independently in nyctosaurids, azhdarchoids and *Pteranodon*. Overall, the dentition of pterodactyloid is very diverse (more than compared to non-pterodactyloids), suggesting that the members of this clade have developed a variety of feeding habits.

It is also important to recognize the large gaps (and obligatory ghost lineages) exists that are present within the evolution of the Pterodactyloidea (Fig. 2). This confirms the common perception that the fossil record of pterodactyloids is extremely incomplete, a conclusion that can be drawn for pterosaurs in general.

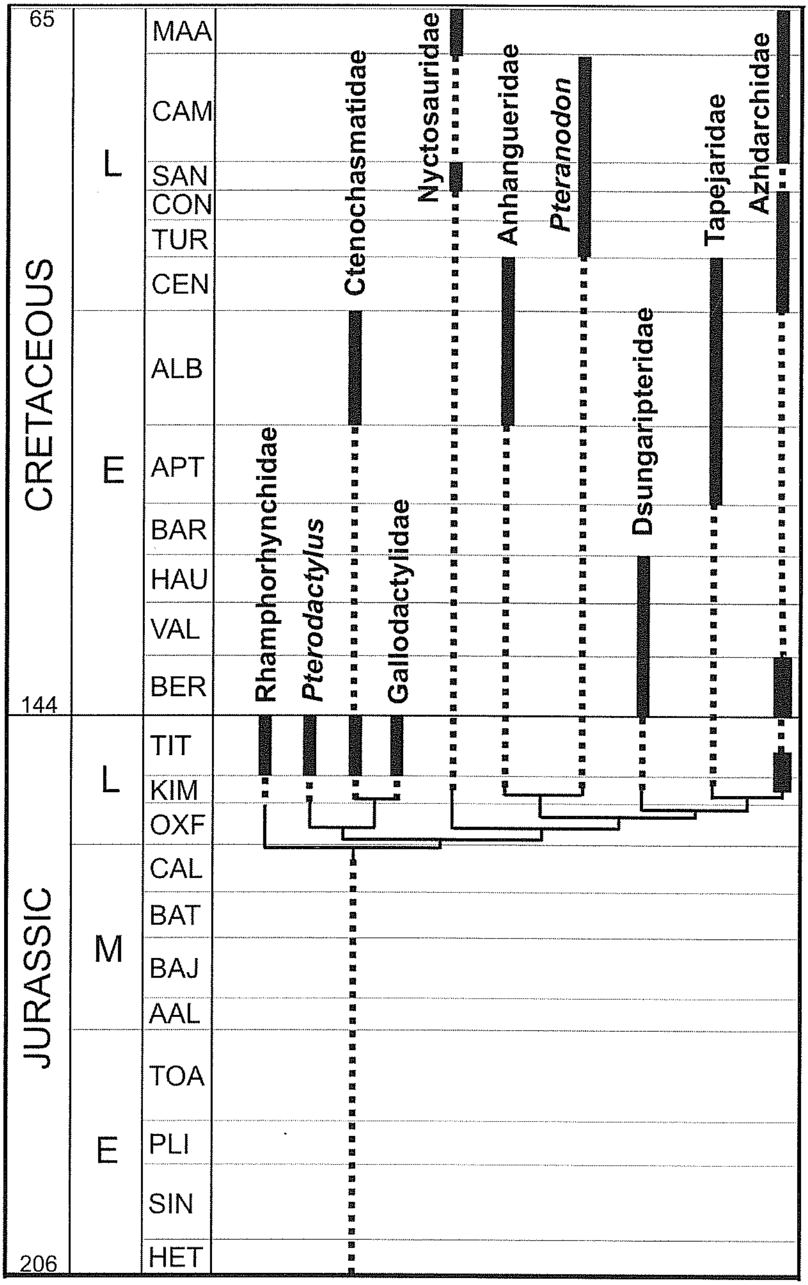

Fig. 2. Biochronology of the Pterodactyloidea based on the cladogram of figure 1 and recorded temporal range. Time scale follows the Geological Society of America Time Scale of 1999. Dark column represents the recorded temporal range for the taxon, dotted line indicate gaps in the fossil record, and thin lines the relationships of the taxa. Note that due to lack of stratigraphic refinement of most pterosaur occurrences, stages where a particular taxa was recorded were filled out.

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