

ON ZHEJIANGOPTERUS AND THE RELATIONSHIPS OF PTERODACTYLOID PTEROSAURS

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A summary of recent studies on the interrelationships of pterodactyloid pterosaurs is used as a framework for reassessing the taxonomic status of *Zhejiangopterus*, a new, long-necked, Late Cretaceous pterosaur from China that has been assigned to the Nyctosauridae. Characters cited in support of this decision include: a notarium, edentulous jaws, and lack of a cranial crest. However, none of these is diagnostic of the Nyctosauridae. *Zhejiangopterus* exhibits a number of derived characters (orbit relatively small and located in a low position, posteroventrally facing occiput, features of the humerus and 'T-shaped' cross-section of wing phalanges two and three) only otherwise found in azhdarchids, thus we propose that *Zhejiangopterus* be reassigned to the Azhdarchidae.

Keywords: Pterosaur, Zhejiangopterus, Taxonomy, Phylogeny, Cretaceous, China

INTRODUCTION

In the early 1990s, remains of a medium-sized, long-necked, toothless pterosaur were found in Late Cretaceous sediments near Linhai in Zhejiang Province, China (He, 1992). The material was acquired by Zhejiang Museum of Natural History (ZMNH), described by Cai and Wei (1994) as *Zhejiangopterus linhaiensis*, and assigned to the Nyctosauridae, a family of edentulous pterosaurs so far represented by only a single genus, *Nyctosaurus*, from the Upper Cretaceous of North and South America (Wellnhofer, 1991a).

The remains of *Zhejiangopterus* were found in a sequence of thick tuffs interbedded with thin lacustrine sediments, forming the middle member of the Tangshang Formation (He, 1992). Dating, using K-Ar isotope ratios, of tuffs containing the pterosaur gave mean values of 81.5 Ma (Mu and Cai, 1992), indicating an early Campanian age (Harland *et al.*, 1989). Apart from a small but complete theropod, possibly a dromaeosaur, no other fossil remains have been found in the Tangshang Formation.

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Zhejiangopterus is currently represented by remains of six individuals, including skulls (Figure 1) and some virtually complete skeletons (Figure 2) preserved in articulation. The quality of bone preservation is rather variable and, as is often the case for pterosaurs, the bones are crushed flat. In some individuals there is evidence of soft tissues, preserved as impressions and a black patina, possibly consisting of carbonised residual organic remains. The largest individual (ZMNH M1323), presumably an adult, because the scapulocoracoid, pelvis and carpals are fused (Bennett, 1993, 1995), has an estimated wingspan of 3.5 m. Most individuals are of similar though somewhat smaller size, except for the holotype (ZMNH M1330), which, with a skull a little less than 0.3 m in length, is only about half the size of ZMNH M1323 and probably a juvenile.

Until the discovery of *Zhejiangopterus* only three Upper Cretaceous pterosaurs were known from reasonably complete remains: *Pteranodon* (Eaton, 1910) and *Nyctosaurus* (Williston, 1903) from the Niobrara and Pierre Formations of western USA (Bennett, 1994 and refs. therein); and *Quetzalcoatlus* from the Javelina Formation of Texas (Lawson, 1975; Langston, 1981; Kellner and Langston, 1994, 1996). Other Late Cretaceous pterosaurs are very poorly known and few can be identified, even to the family level (Wellnhofer, 1991a).

The long, low, crestless skull, with toothless jaws, small, circular orbit located well below the level of the dorsal margin of the nasopreorbital opening, and the posteroventrally-facing occiput (Figure 1) clearly distinguish *Zhejiangopterus* from all other pterosaurs in which the skull is known. Cai and Wei (1994) assigned *Zhejiangopterus* to the Nyctosauridae (Williston, 1903; = Nyctosaurinae) on the grounds that it had a notarium and edentulous jaws, but lacked a cranial crest. However, these characters are widely distributed among Cretaceous pterodactyloids (Wellnhofer, 1991a; Bennett, 1994; Unwin, 1995) and are not unique to nyctosaurids. Recently, we re-examined the fossil material of *Zhejiangopterus*, comparing it with a number of pterodactyloid pterosaurs not considered by Cai and Wei in their study. We show here that *Zhejiangopterus* does not belong within the Nyctosauridae, but can be assigned to another family of pterodactyloid pterosaurs, the Azhdarchidae.

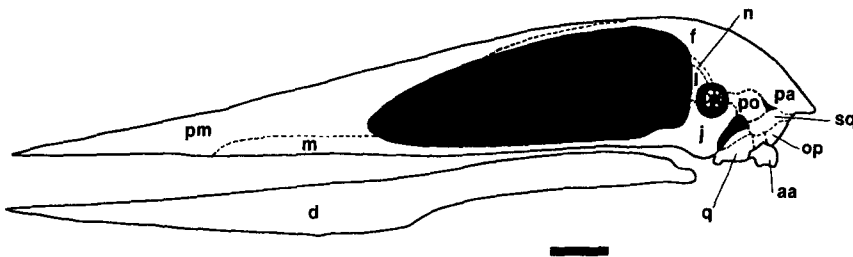


FIGURE 1 The skull of *Zhejiangopterus linhaiensis* (ZMNH M1330) in left lateral aspect according to Cai and Wei (1994). Dashed lines indicate inferred margins of bones. Scale bar = 20 mm. aa, atlas-axis; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal, op, opisthotic; pa, parietal; po, postorbital; pm, premaxilla; q, quadrate; sq, squamosal.

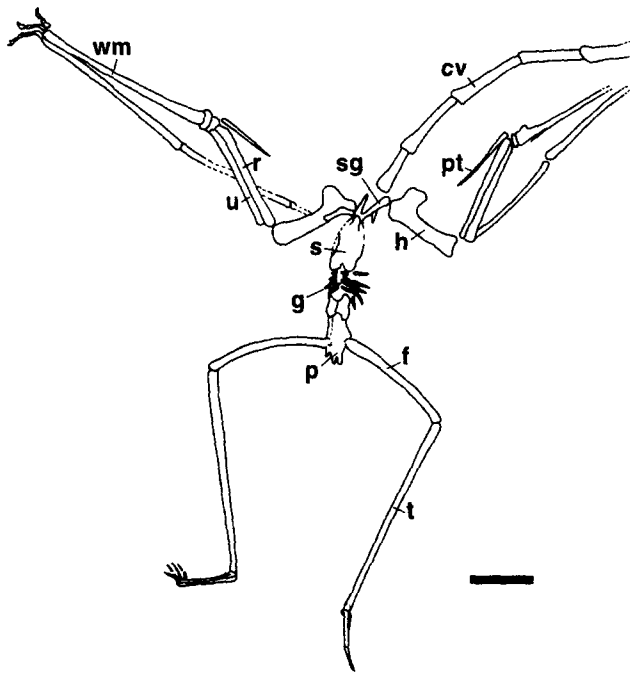


FIGURE 2 The skeleton of *Zhejiangopterus linhaiensis* (ZMNH M1323) as preserved in ventral view. Dashed lines indicate inferred margins of bones. Redrawn from Cai and Wei, 1994. Scale bar = 100 mm. cv, cervical vertebrae; f, femur; g, gastralia; h, humerus; p, pelvis; pt, pteroid; r, radius; s, sternum; sg, shoulder girdle; t, tibia; u, ulna; wm, wing-metacarpal.

SYSTEMATICS OF PTERODACTYLOID PTEROSAURS

The cranial anatomy of pterodactyloids exhibits considerable variety (*e.g.* Wellnhofer, 1991a) and most low-rank taxa (species and genera) represented by skull material are easily diagnosable (Wellnhofer, 1978). Grouping genera into higher taxonomic categories has proved more difficult. Traditional studies largely avoided this problem, either by erecting monogeneric families (see Howse, 1986), or by burying poorly-known forms within 'waste-basket' taxa such as the *Ornithocheiridae*. Cladistic studies of pterosaur interrelationships (*e.g.* Howse, 1986; Bennett, 1989, 1994; Unwin, 1992, 1995; Kellner, 1995) have been more successful at identifying broad taxonomic groups and, although published cladograms differ in many details, they share some common features.

Four major clades have been recognised (Figure 3). The *Ornithocheiroidea*, proposed by Seeley for the reception of *Pteranodon* and *Ornithocheirus* (Seeley, 1901) is largely synonymous with the *Pteranodontidae* of Padian (1986) and Bennett (1989, 1994), and well supported by a variety of clear-cut cranial and postcranial characters (Bennett, 1989, 1994; Unwin, 1995; Figure 3, node b). *Nyctosaurus* has all of these characters and undoubtedly belongs in the *Ornithocheiroidea*. However, the precise location of *Nyctosaurus* within this taxon is unclear. A basal position seems likely since non-nyctosaurids are united by derived

features of the humerus (Bennett, 1989, 1994; Figure 3, node c), but a sister-group relationship with *Pteranodon* is also possible, and is supported by two derived states: absence of teeth and hyper-elongation of the wing-metacarpal (length $\geq 1.5 \times$ ulna).

The Ctenochasmatoidea (Kuhn, 1967; Figure 3, node f) is distinguished by a highly derived condition of the skull in which the quadrate occupies an almost horizontal position, the occiput faces ventrally, and the squamosal lies level with or below the orbit. With the exception of the basal member of this clade, *Gallodactylus*, ctenochasmatoids are further characterised by elongation of the cervical vertebrae, a modification that also arose independently in the azhdarchids (see below). The Ctenochasmatoidea includes the Pterodactylidae (almost certainly paraphyletic since *Pterodactylus* is more closely related to ctenochasmatids than *Gallodactylus*) and the Ctenochasmatidae, diagnosed by the presence of a filter-feeding apparatus and including a number of Late Jurassic (*Gnathosaurus*, *Ctenochasma*) and Early Cretaceous forms (*Huanhepterus*, *Cearadactylus*, *Pterodaustro*).

The Dsungaripteroidea (Figure 3, node h), a clade of Late Jurassic and Early Cretaceous Eurasian pterosaurs (Bakhurina, 1993; Bakhurina and Unwin, 1995), is diagnosed by features of the dentition, and other cranial characters, including the prominent development of the paroccipital processes. Bennett (1989, 1994) has argued that '*Santanadactylus*' *spixi* should be included in this clade, but the carpal characters he cited also occur in tapejarids such as *Tupuxuara* (Kellner, 1990, 1995; Kellner and Campos, 1992) and the azhdarchid *Quetzalcoatlus* (Kellner, 1995). If these characters are confined to dsungaripteroids and azhdarchoids, it will provide further support for node g of Figure 3, which is otherwise weak.

Following the work of Howse (1986), there has been a tendency to include most long-necked pterodactyloids in the Azhdarchidae (Padian, 1986; Padian and Smith, 1992; Bennett, 1989, 1994; Nessov, 1991; Unwin, 1992). Recently, Kellner and Langston (1994, 1996), Kellner (1995), and Unwin (1995) have argued that tapejarids are more closely related to certain Late Cretaceous long-necked pterodactyloids, such as *Quetzalcoatlus* and *Azhdarcho* (Figure 3, node j), than are Late Jurassic (*Pterodactylus*, *Ctenochasma*) and Early Cretaceous (*Huanhepterus*, *Pterodaustro*) long-necked forms. Since tapejarids have relatively short, high cervicals, elongate necks must have evolved on at least two separate occasions. Initially, Kellner (1989) proposed four characters that purportedly united *Tapejara* and *Tupuxuara* in the Tapejaridae, but more recently he reduced these to just two (Kellner, 1995): a sagittal premaxillary crest extending from the tip of the snout to the occipital region, and a comparatively large nasopreorbital opening. Both these characters are problematic. The cranial crest of *Tapejara* is somewhat different from that of *Tupuxuara*, and an elongate cranial crest also occurs in an unnamed dsungaripterid from Tatal, Mongolia (Bakhurina and Unwin, 1995) and *Dsungaripterus* (Young, 1973). A large nasopreorbital opening is also found in non-tapejarids such as *Quetzalcoatlus* and would seem to be apomorphic for the Azhdarchoidea, a clade that is supported by other characters (Kellner and Hasegawa, 1993; Kellner and Langston, 1994, 1996; Kellner, 1995; Unwin, 1995; Figure 3, node j). The Tapejaridae may eventually prove to be paraphyletic, because *Tupuxuara* shares derived characters in common with azhdarchids (e.g. elongation of the

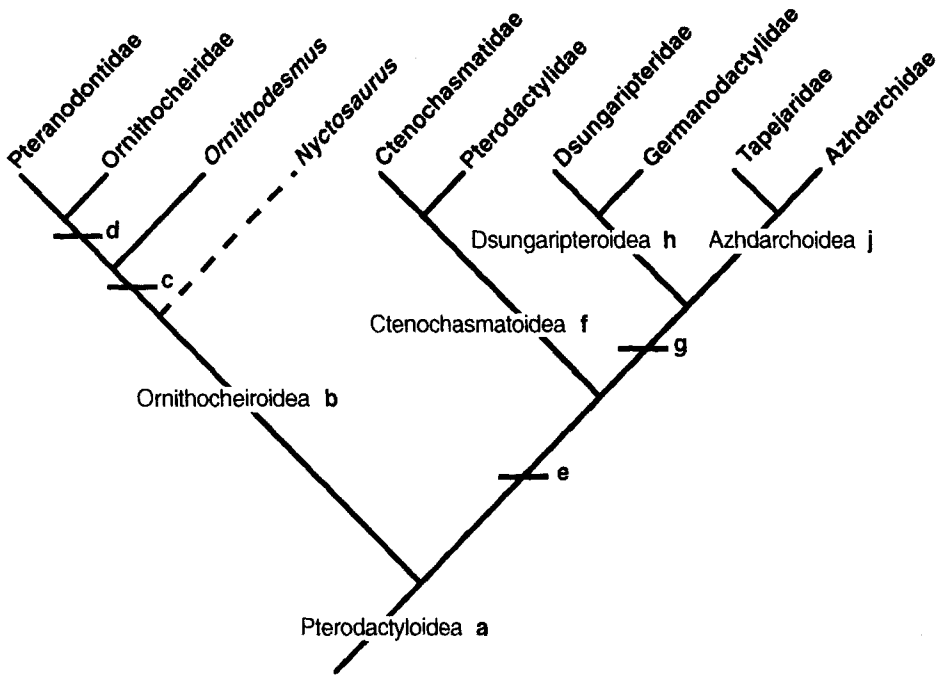


FIGURE 3 Interrelationships of pterodactyloid pterosaurs (see Unwin [1995] for further details). Note: a dashed line indicates uncertainty regarding the position of a particular taxon. Node a. Pterodactyloidea (see Bennett [1994] and Unwin [1995] for character lists). Node b. Ornithocheiroidea: (1) Posterior margin of naso-preorbital opening concave; (2) Coracoid longer than scapula; (3) 'Ornithocheiroid' carpus; (4) Femur with stout neck and caput-shaft angle of $> 150^\circ$; (5) Strong medial rotation of distal end of femur (see also Bennett, 1989). Node c. (1) Warped delto-pectoral crest on humerus; (2) Pneumatic foramen on anconal surface of proximal end of humerus; (3) Distal aspect of humerus triangular; Node d. (1) Near exclusion of squamosal from post temporal opening; (2) Jugal extends to anterior end of naso-preorbital opening; (3) Spiral mandibular articulation; (4) Basal part of orbit infilled by jugal to form 'high cheek'; (5) Mandibular symphysis at least 30% length of mandible; (6) Cristospine constricted behind coracoid facets. Node e. (1) Length/width ratio of mid-series cervical centra at least 2.5; (2) Mid-series cervicals with depressed neural arch and low neural spine which contributes to less than half the total height of the vertebra (reversed in some dsungaripteroids and *Tupuxuara*). Node f. Ctenochasmatoidea: (1) Squamosal level with or below ventral margin of orbit; (2) Quadrate subhorizontal; (3) Occiput faces posteroventrally. Node g. (1) Elongate cranial crest extending from premaxilla to frontal (?reversed in Azhdarchidae). Node h. Dsungaripteroidea: (1) Toothless jaw tips; (2) Maxillary teeth nearly as broad as they are tall; (3) Largest teeth located toward caudal end of tooth row; (4) Distal ends of paroccipital processes strongly expanded, forming a distinctive rounded bulge in the lateral profile of the occiput. Node j. Azhdarchoidea: (1) Loss of teeth; (2) Frontals extend well anterior to lacrimal-jugal bar; (3) Entire orbit located below two thirds the maximum height of the nasopreorbital opening.

skull) that are absent in *Tapejara*. The Azhdarchidae should be restricted to *Quetzalcoatlus*, *Azhdarcho* and a number of other more poorly known Late Cretaceous long-necked pterosaurs (Nesov, 1984, 1991; Padian, 1984, 1986; Padian and Smith, 1992; Frey and Martill, 1996). Apomorphies of this clade are discussed below.

REASSESSMENT OF THE RELATIONSHIPS OF *ZHEJIANGOPTERUS*

Although aware of other toothless pterosaurs, Cai and Wei (1994) confined their comparisons of *Zhejiangopterus* to *Pteranodon* and *Nyctosaurus* on the grounds that these edentulous taxa also had a notarium, following Young (1964) in considering this feature of high taxonomic significance. Cai and Wei (1994) also attached considerable importance to the presence or absence of a cranial crest, thus concluding that *Nyctosaurus* (crestless) and *Pteranodon* (crested) must belong within separate families. Bennett (1989) arrived at a similar conclusion, but for different reasons. Since *Zhejiangopterus* lacked any cranial crest, Cai and Wei (1994) assigned it to the Nyctosauridae. However, not one of the characters used by these authors supports this decision.

Toothlessness occurs in a variety of pterodactyloids and has been reliably reported in *Pteranodon* (Marsh, 1876; Eaton, 1910; Bennett, 1994), *Nyctosaurus* (Williston, 1902), *Quetzalcoatlus* (Lawson, 1975), *Tapejara* (Kellner, 1989), *Tupuxuara* (Kellner and Campos, 1988), and possibly also in *Azhdarcho* (Nessov, 1984; Bakhurina and Unwin, 1995) and *Montanazhdarcho* (Padian *et al.*, 1995). Cladistic studies by Bennett (1989, 1994) and Unwin (1992, 1995) indicate that toothlessness evolved on at least two separate occasions, possibly three if *Pteranodon* and *Nyctosaurus* are not sister taxa. Hence, toothlessness, *per se*, is not a reliable guide to the general relationships of pterodactyloids, though it is informative at a more exclusive level (*e.g.* Figure 1, node j). A further difficulty with this character and, incidentally, with 'lack of a cranial crest' is the impossibility of demonstrating homology in the absence of comparable structures (Schoch, 1986), in this case, teeth.

The term notarium, as it is usually employed, is rather vague. In most, if not all pterodactyloids with a wingspan greater than about 2 m, there is a trend toward fusion of some dorsal vertebrae in adults, to form a notarium. This structure has been formally defined by Bennett (1994) as 'consisting of at least three fused dorsal vertebrae and fused dorsal ribs'. The ubiquity of this structure in large pterosaurs, the variable number of vertebrae involved, and the variable relationship of the scapula to the notarium does not encourage the view that this structural complex evolved only once in the Pterodactyloidea. This idea is supported by phylogenetic studies (Unwin 1992, 1995), that suggest that this complex arose on at least two, and possibly as many as four separate occasions. Even if the 'notarium' is eventually shown to be unique to one particular clade, the broad content of this taxon (Bennett, 1989, 1994) would not support a particular relationship between *Nyctosaurus* and *Zhejiangopterus*.

Absence of a cranial crest is the primitive condition for pterosaurs: most, though perhaps not all, 'rhamphorhynchoids' lack such a structure, as do some pterodactyloids. Hence, the absence of a crest in *Zhejiangopterus* reveals nothing of its relationships. In addition, Bennett (1992) has presented good evidence to show that variation in crest size in *Pteranodon*, and other pterosaurs, is related to sexual dimorphism and ontogeny. This is supported by observations made by one of us (DMU) that some individuals of *Germanodactylus cristatus* and *Anhanguera santanae* are crested, while others are not. Characters based on cranial crests must, therefore, be treated with caution. Moreover, in the case of *Zhejiangopterus*, only two relatively complete skulls are known, and thus it may be premature to regard this taxon as definitely crestless.

Apomorphies of the Nyctosauridae include: a hatchet-shaped deltopectoral crest of the humerus (Williston, 1903; Bennet, 1989, 1994); a short, broad sternum in which the width of the sternal plate is well over $1.5 \times$ the length; reduction of the wing-finger to three wing-phalanges (Brown, 1986); and mid-notarial vertebrae with 'T-shaped' neural spines in anterior view (Bennett, 1994). *Zhejiangopterus* exhibits the primitive condition for each of these characters. We contend, therefore, that there are no grounds for retaining this pterosaur in the Nyctosauridae.

Zhejiangopterus lacks principal apomorphies of the Ornithocheiroidea and Dsungaripteroidea, but does appear to share some features in common with members of the Ctenochasmatoidea (Figure 3, node f). It would seem, however, that these resemblances are due to homoplasy (see below for detailed discussion) because there is much stronger evidence to suggest that *Zhejiangopterus* belongs within the Azhdarchoidea. *Zhejiangopterus* has each of the defining characters of the Azhdarchoidea (Figure 3, node j): edentulous jaws; frontals that extend well anterior to the lacrimal—jugal bar; and the entire orbit is located below two thirds the maximum height of the naso-preorbital opening (Cai and Wei, 1994, pl. 1, Figure 2, pl. 2, Figure 1; Kellner and Langston, 1996; Figure 1). Moreover, *Zhejiangopterus* exhibits all the diagnostic characters of azhdarchids, further confirming its location within the Azhdarchoidea.

A unique feature, common to both azhdarchids and *Zhejiangopterus*, is the relatively small, sub-circular orbit located below the mid-height level of the naso-preorbital opening (Cai and Wei, 1994, pl. 2, Figure 1; Figure 1). Typically, pterodactyloids have a relatively large orbit, often of similar depth to the naso-preorbital opening (e.g. *Pterodactylus*, *Germanodactylus*, and *Gnathosaurus* (Wellnhofer, 1970) and sometimes noticeably deeper (e.g. *Ctenochasma*, *Pterodaustro* (Wellnhofer, 1991a)). In derived pterodactyloids, the orbit is often reduced in size and located in a dorsal position behind the naso-preorbital opening (e.g. *Dsungaripterus*, the pterosaur formerly named '*Ornithodesmus*' (Howse and Milner, 1994), *Anhanguera*, and *Pteranodon* (Wellnhofer, 1991a)). The orbit is also reduced in size in azhdarchids and their close relatives the tapejarids (Kellner and Langston, 1994), but is highly unusual in that it is located in a ventral position, well below the level of the dorsal margin of the naso-preorbital opening (Kellner and Langston, 1994, 1996; Kellner, 1995). Azhdarchids, including *Zhejiangopterus*, are distinguished from tapejarids by the greater reduction of the orbit (it is only one third the height of the naso-preorbital opening, whereas in tapejarids it is more than half this height), its sub-circular shape, which is unlike the pear-shaped orbit of tapejarids, and its location entirely below the mid-height level of the naso-preorbital opening. This unusual construction is also reflected in the unique morphologies of other cranial elements. For example, the jugal has very short, robust lacrimal and postorbital processes (Cai and Wei, 1994, Figure 1; Kellner and Langston, 1996, Figure 7), contrasting with the relatively slender, elongate processes found in other pterosaurs (Wellnhofer, 1978, Figures 4, 5) and the quadrate appears to be shorter and stouter than in other pterodactyloids.

Another azhdarchid apomorphy, also found in *Zhejiangopterus*, is a ventrally facing occiput (Cai and Wei, 1994, pl. 2, Figure 1; Figure 1). A distinctive trait of pterodactyloids

is the relative enlargement of the braincase when compared with 'rhamphorhynchoids'. This was achieved by expansion of the neurocranium in a posteroventral direction, resulting in reorientation of the occiput to face ventrally as well as caudally, and in the backward rotation of the quadrate into a reclined position. Azhdarchids exhibit an extreme condition wherein the occiput faces almost entirely ventrally and the quadrate lies in a sub-horizontal position. This clearly distinguishes them from tapejarids (Wellnhofer and Kellner, 1991), which are possibly their closest known relatives (Kellner and Hasegawa, 1993; Kellner and Langston, 1994, 1996; Kellner, 1995; Unwin, 1995), and most other pterodactyloids, wherein the occiput has a more upright position and the quadrate slopes at about 45° to the horizontal. However, a condition similar to that of azhdarchids also occurs in some ctenochasmatooids including *Pterodactylus*, *Ctenochasma*, and *Gnathosaurus* (Wellnhofer, 1970). Presumably, this was acquired independently, because there is little evidence for a sister group relationship between ctenochasmatooids and azhdarchids (Bennett, 1994; Unwin, 1995). Furthermore, the construction of the skull in azhdarchids with the relatively low position of the orbit and short, rather stout quadrate suggests that enlargement of the brain case was achieved in a different way than in the ctenochasmatooids, which have large orbits, and long, slender quadrates.

An expanded brachial flange occupying more than half the total shaft length of the coracoid occurs in *Quetzalcoatlus* (Kellner and Langston, 1996) and *Zhejiangopterus*. This may be another azhdarchid synapomorphy (Kellner and Langston, 1996) since the brachial flange is considerably smaller in other pterosaurs.

Initially, it was thought that the azhdarchid humerus exhibited an essentially conservative morphology (Padian, 1984, 1986; Bennett, 1989), but recently a number of diagnostic features have been recognised (listed in Padian and Smith, 1992). Some of these can be observed in *Zhejiangopterus*: as in azhdarchids, the deltopectoral crest is displaced distally, is elongate and lacks a distal expansion (Cai and Wei, 1994, Figure 4).

A longitudinal ridge on the ventral surface of wing-phalanges two and three, resulting in a 'T-shaped' cross-section (Nessov, 1991; Bennett, 1994) is unique to azhdarchids and also occurs in *Zhejiangopterus*, although the ventral ridge seems to be lower and less pronounced in this taxon. In other pterosaurs, the corresponding wing-phalanges have an oval (Wellnhofer, 1970), C-shaped (Wellnhofer, 1975), or sub-triangular (Wellnhofer, 1985, 1991b) cross-section.

A conspicuous feature of *Zhejiangopterus* is the long neck composed of highly elongate mid-series cervical vertebrae (length $\geq 5 \times$ width), the middle sections of which have a confluent centrum and neural arch and a vestigial or absent neural spine (Cai and Wei, 1994, pl. 1, Figure 1, pl. 2, Figures 1 and 2; Figure 2). This character complex has been considered by many (e.g. Nessov, 1984, 1991; Padian, 1984, 1986; Howse, *et al.*, 1986; Bennett, 1989, 1994; Padian *et al.*, 1995) to be a definitive feature of azhdarchids, although similar cervicals occur in some members of the Ctenochasmatoidea (Unwin, 1995). As mentioned above, it seems likely that ctenochasmatooids such as *Huanhepterus* (Dong, 1982) acquired their long necks independently of azhdarchids, since a number of short-necked pterodactyloids (Dsungaripteridae, Tapejaridae) appear to be more closely

related to the Azhdarchidae than the Ctenochasmatoidea (Kellner and Hasegawa, 1994; Kellner and Langston, 1994, 1996; Kellner, 1995; Unwin, 1995; Figure 3).

Zhejiangopterus and azhdarchids compare well in many other respects, though it should be noted that the following characters are not restricted to these taxa: long, toothless jaws; elongate naso-preorbital opening; notarium; scapula longer than coracoid; scapula articulates obliquely with notarium; deltopectoral and ulnar crest of humerus extend to the same level distally; deltopectoral crest stands at right angle to the long axis of the humerus; short, rather blocky carpals; wing-metacarpal longest element in the forelimb; sharp reduction in length of wing-phalanges distally; femur slender, bowed and more than $1.5 \times$ the length of the humerus; and distal condyles of the femur with a relatively flat rather than rounded distal aspect.

CONCLUSIONS

The occurrence of all four principal azhdarchid synapomorphies (three of which should be treated as character complexes) in *Zhejiangopterus* leaves us in no doubt that it should be included in the Azhdarchidae. This is further supported by numerous similarities between the skeletal anatomy of *Zhejiangopterus* and recently described azhdarchids from North America (Lawson, 1975; Langston, 1981; Kellner and Langston, 1994, 1996) and Asia (Nessov, 1984). *Zhejiangopterus* is the first azhdarchid from China and adds to a series of discoveries of these pterosaurs in the Late Cretaceous of North America (Lawson, 1975; Langston, 1981; Currie and Russell, 1982; Padian, 1984, 1986; Padian and Smith, 1992; Currie and Jacobsen, 1995; Padian *et al.*, 1995; Kellner and Langston, 1996), Europe (Astibia *et al.*, 1991), Africa (Monteillet *et al.*, 1982), Jordan (Arambourg, 1959; Frey and Martill, 1996), Russia (Bogolubov, 1914), Middle Asia (Nessov, 1984, 1990, 1991), and possibly Australia (Bennett and Long, 1991). *Zhejiangopterus* is particularly noteworthy, as it is the most complete azhdarchid yet known and may provide new insights into the anatomy, ecology, and phylogeny of these highly unusual and still poorly known pterosaurs.

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