

# A NEW PTEROSAUR FROM THE LIAONING PROVINCE OF CHINA, THE PHYLOGENY OF THE PTERODACTYLOIDEA, AND CONVERGENCE IN THEIR CERVICAL VERTEBRAE

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**Abstract:** The largest known flying organisms are the azhdarchid pterosaurs, a pterodactyloid clade previously diagnosed by the characters of their extremely elongate middle-series cervical vertebrae. The named species of the Azhdarchidae are from the Late Cretaceous. However, isolated mid-cervical vertebrae with similar dimensions and characters have been referred to this group that date back to the Late Jurassic, implying an almost 60 million year gap in the fossil record of this group and an unrecorded radiation in the Jurassic of all the major clades of the Pterodactyloidea. A new pterosaur from the Early Cretaceous of Liaoning Province of China, *Elanodactylus prolatus* gen. et sp. nov., is described with mid-cervical vertebrae that bear these azhdarchid characters but has other postcranial material that are distinct from the members of this group. Phylogenetic analysis of the new species and the Pterodactyloidea places it with the Late Jurassic vertebrae in the Late Jurassic–Early Cretaceous Ctenochasmatidae and reveals that the characters of

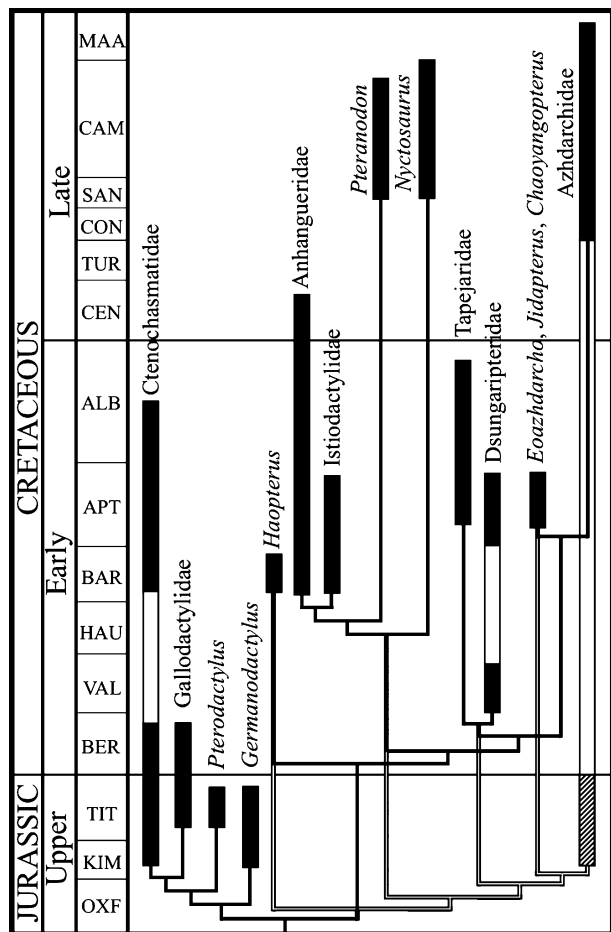
the elongate azhdarchid vertebrae appeared independently in both groups. These results are realized through the large taxon sampling in the analysis demonstrating that the homoplastic character states present in these two taxa were acquired in a different order in their respective lineages. Some of these homoplastic characters were previously thought to appear once in the history of pterosaurs and may be correlated to the extension of the neck regions in both groups. Because the homoplastic character states in the Azhdarchidae and Ctenochasmatidae are limited to the mid-cervical vertebrae, these states are termed convergent based on a definition of the term in a phylogenetic context. A number of novel results from the analysis presented produce a reorganization in the different species and taxa of the Pterodactyloidea.

**Key words:** Pterodactyloidea, cervical vertebrae, convergence, Azhdarchidae, Ctenochasmatidae, phylogeny, *Elanodactylus prolatus*.

PTEROSAURS are the largest known flying organisms and the largest of these volant reptiles are the azhdarchid pterosaurs. Wingspan estimates of this pterodactyloid group range up to 15.5 m, larger than many small aircraft (Lawson 1975). A maximum of about 10 m would be probably be more accurate based on the dimensions of the smaller morph of *Quetzalcoatlus*, the most completely preserved member of this group. In spite of their large size, it is the characters of the cervical vertebrae that were used to differentiate the Azhdarchidae, specifically the middle-series cervical vertebrae (Nesov 1984; Padian 1986). These vertebrae are characterized by their extreme elongation, low neural spines reduced to small ridges, and postexapophyses on the posterior condyles. Isolated mid-cervical vertebrae that share these characters and that have been assigned to the Azhdarchidae date back to the

Late Jurassic (Howse, 1986; Bennett, 1994; Kellner 2001; Sayão and Kellner 2001; Kellner *et al.* 2007). However, the true azhdarchid species date from the Late Cretaceous. The earliest of these species, *Azhdarcho lancicollis*, is only as old as the late Coniacian–Turonian (Nesov 1984). This would imply an almost 60 myr gap in the fossil record of the azhdarchids and that the radiation of all major groups of the Pterodactyloidea occurred in the Jurassic, but most appeared later in the Cretaceous (Text-fig. 1). This is the largest ghost lineage present in the pterosaurs.

The isolated vertebrae assigned to the Azhdarchidae were found in the Late Jurassic Tendaguru beds of East Africa (Kellner *et al.* 2007) and the Purbeck Limestone of southern England, dated to the Jurassic/Cretaceous boundary (Howse and Milner 1995). This latter material consists of



**TEXT-FIG. 1.** Stratigraphic range diagram of the pterodactyloid taxa mentioned in the text and shown in Text-figure 5. Dark bars indicate the occurrence of a taxon within a particular time period; white bars indicate gaps in the fossil record of these taxa; hatched bar indicates the temporal range of mid-cervical vertebrae previously referred to the Azhdarchidae; solid lines denote the phylogenetic relationships and probable minimum divergence times for these taxa; white lines denote the extension of these divergence times and unrecorded phylogenetic history if these isolated vertebrae are referred to the Azhdarchidae. Taxa whose first or last appearances are dated to one of two possible time periods are shown with ranges extending to the boundary of these two periods.

isolated, partial vertebrae and one complete mid-cervical vertebra associated with the mandible that would become the lectotype of *Gnathosaurus macrurus* (Howse and Milner 1995). Though originally described as presumably belonging to the same individual (Seeley 1869) and in association (Seeley 1875), Howse and Milner (1995) limited the circumscription of *G. macrurus* to the mandible. Every phylogenetic analysis that has included the characters of one or both elements has still placed them in the Azhdarchidae (Howse 1986; Bennett 1989, 1991, 1994).

Outside of the Azhdarchidae, extremely elongate mid-cervical vertebrae have been reported in one pterosaur species, *Huanhepterus quingyangensis* from the Ordos Basin of China (Dong 1982). This species was referred to Ctenochasmatidae, a Late Jurassic–Early Cretaceous group of pterodactyloids (Text-fig. 1) diagnosed by their elongate rostra and large number of teeth. However, the one published phylogenetic analysis to include this placement or a monophyletic Ctenochasmatidae. Nonetheless, the length of the vertebrae in *Huanhepterus* and the occurrence of large ctenochasmatids in the same formation led Howse and Milner (1995) to suggest that the Purbeck vertebrae may belong to ctenochasmatids, but this also could not be demonstrated. With the exception of length, none of the characters present in the Purbeck vertebrae had been described in a possible ctenochasmatid. The postexapophyses found in these vertebrae and in the Ornithocheiroidea (*sensu* Bennett 1994; Kellner 2003), a pterodactyloid group that includes the Azhdarchidae, has been previously reported to appear only once in vertebrate history (Williston 1897). To this day, the temporal range of the azhdarchids is still drawn to the Late Jurassic (e.g. Kellner 2003, fig. 2).

Recently, a new pterosaur specimen with mid-cervical vertebrae similar to those of the Azhdarchidae including postexapophyses, but a remaining postcranium similar to the Ctenochasmatidae, was reported from the Early Cretaceous Yixian Formation of Liaoning, China (Andres and Ji 2003). This specimen is formally described and named here as *Elanodactylus prolatus* gen. et sp. nov. A phylogenetic analysis of the Pterodactyloidea was performed to determine whether the new species and the isolated elongate vertebrae record belong to one of these taxa or if these two taxa are closely related. This analysis is the largest phylogenetic analysis of pterosaur relationships to date, and provides novel results that have either not been suggested before or at least not addressed in a cladistic framework.

## MATERIAL AND METHODS

The ingroup for the phylogenetic analysis consists of *Elanodactylus prolatus* gen. et sp. nov. and most of the valid species of the Pterodactyloidea. The outgroups are four species from the most diverse non-pterodactyloid pterosaur, or ‘rhamphorhynchoid,’ groups: *Campylognathoides liasicus*, *Dimorphodon macronyx*, *Rhamphorhynchus muensteri*, and *Anurognathus ammoni*. Characters were integrated with modifications from all previous analyses of pterosaur intrarelations (Howse 1986; Bennett 1989, 1991, 1994; Kellner 1996, 2003, 2004; Viscardi *et al.* 1999; Unwin 2002, 2003a, b; Andres and Ji 2003; Maisch *et al.*

2004; Wang *et al.* 2005; Lü and Ji 2006; Martill and Naish 2006) and added to the characters unique to this analysis. Constant, redundant, and autapomorphic characters were omitted. Variation within a terminal taxon was coded as polymorphic. Inapplicable character states were reductively coded, and inapplicable states denoted by a dash (-) (see Strong and Lipscomb 2000). This produced a character matrix of 61 terminal taxa and 111 characters, the largest analysis of pterosaur relationships to date.

This matrix was run with *Gnathosaurus macrurus* coded with the characters of its associated mid-cervical vertebra (SMC J5340), with both as separate terminal taxa, and with both as separate taxa without *Elanodactylus*. The associated mid-cervical is the best preserved of the contentious vertebrae and has identical codings to the rest of the record of extremely elongate vertebrae, including the Tendaguru cervical (MB R 2832). It is, therefore, used to represent the isolated, extremely elongate vertebrae record in the phylogenetic analyses. The analyses were run using PAUP\* 4.0b10 (Swofford 2000) on a G4 PowerBook computer. They consisted of 100 random addition-sequence TBR heuristic searches performed using maximum parsimony, ACCTRAN character-state optimization, and non-ambiguous branch support (amb- option). Identical trees were eliminated from the results. All characters were equally weighted and only characters 65 and 67 were ordered.

*Institutional abbreviations.* MB, Museum für Naturkunde, Berlin; NGMC, National Geological Museum of China, Beijing; SMC, Sedgwick Museum, University of Cambridge, Cambridge, UK.

*Anatomical abbreviations.* cor, coracoid; cv, cervical vertebra; dY, manual digit Y; dc, distal syncarpal; dp, deltopectoral crest of the humerus; fXdY, phalanx X of manual digit Y; fo, foramen; hu, humerus; m, medial carpal; mcY, metacarpal Y; pc, proximal syncarpal; pe, postexpophysis; pt, pteroid; ra, radius; sc, scapula; st, sternum; tub, tubercle; ul, ulna; X.l, left element X; Y.r, right element Y; v, dorsal vertebra.

## SYSTEMATIC PALAEOLOGY

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

ARCHAEOPTERODACTYLOIDEA *sensu* Kellner, 2003

CTENOCHASMATIDAE Nopcsa, 1928

*Elanodactylus prolatus* gen. et sp. nov.

Text-figures 2–4, Tables 1–2

*Derivation of name.* Generic name, Greek, *elanos*, kite bird of prey, and *daktylos*, finger. Specific name, Latin, *prolatus*, extended or elongated. The entire name refers to the elongate second and third phalanges of the wing finger that gives this specimen long, slim wings reminiscent of the kites.

*Holotype.* NGMC 99-07-1, a partial articulated skeleton curated at the National Geological Museum of China.

*Horizon and locality.* Bed 6 of Member 3 of the lower Yixian Formation, middle Early Cretaceous (Barremian); Sihetun Basin, Beipiao Municipality, Liaoning Province, People's Republic of China. Swisher *et al.* (1999) gave ages of  $124.6 \pm 0.2$  and  $124.6 \pm 0.3$  Ma for the  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of two tuffs interbedded within the fossiliferous horizons of Bed 6.

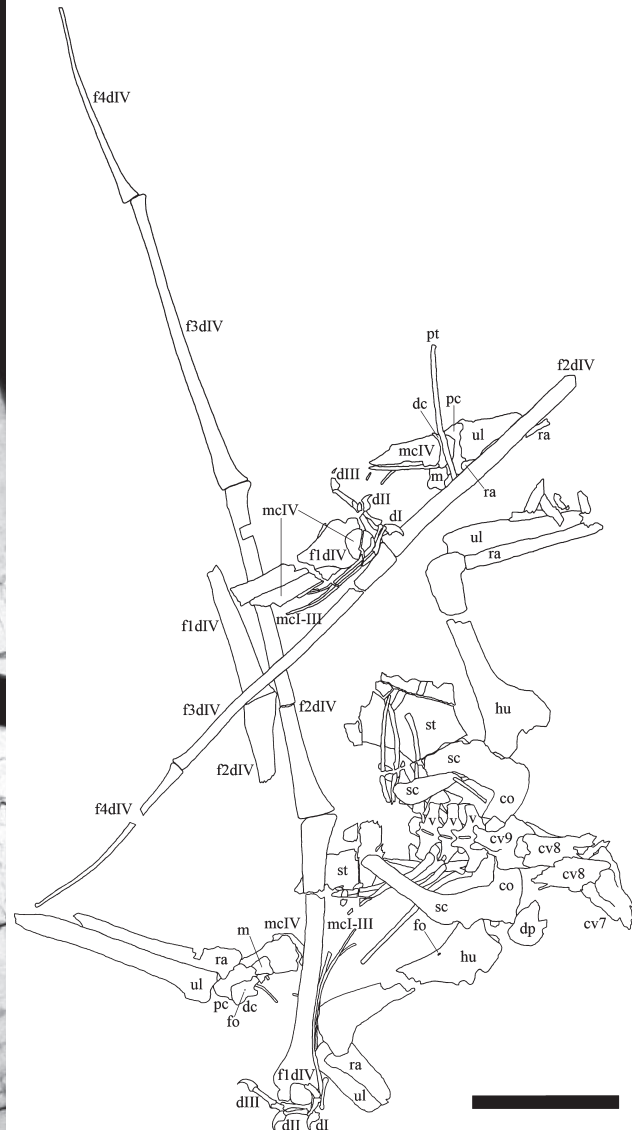
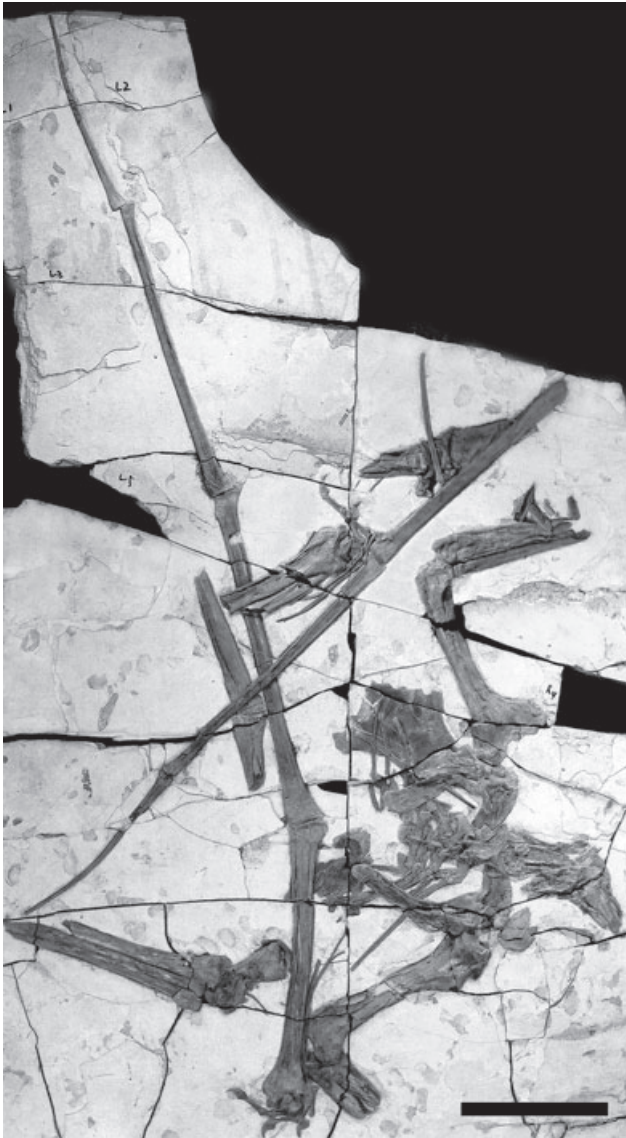
*Diagnosis.* Largest archaeoptero-dactyloid with a wingspan of approximately 2.5 m; elongate mid-cervical vertebrae with total lengths approximately four times their mid-widths, extremely reduced neural spines, blunt and posterolaterally directed postexpophyses, and neural arch not fully integrated into a tubular vertebral body; large prezygapophyses on posterior-series cervical vertebra that take up over half the length and width of the vertebra; humerus with head the same size as the large deltopectoral crest, bears posterodorsally placed pneumatic foramen near its distal margin, and distinct tubercle on proximal margin of the humerus between the deltopectoral crest and humeral head; second and third wing phalanx both longer than the first with second wing phalanx the longest bone in the wing.

### Description

NGMC 99-07-1 is an incomplete skeleton consisting of the wings, posterior three cervical (mid-cervicals 7 and 8, posterior-cervical 9) and anterior three dorsal vertebrae, 12 ribs, both scapulocoracoids, and partial sternum deposited on 18 blocks in a single bedding plane of shale (Text-fig. 2). With the exception of the distal ends of left ulna and radius, the left carpus, and the left metacarpals I–IV, the entire specimen is articulated and lying on its ventral surface. Though this specimen is dorsoventrally compacted, it is for the most part in excellent condition with the texture of the bones often preserved. This individual is considered an ontogenetic adult based on the fusion of the scapulocoracoids, the fusion of the extensor tendon processes to first wing phalanges, and the lack of sutures on the carpals and other bones. This specimen is described in anatomical position of the wings outstretched laterally as they would be in flight, and was prepared by B. Andres.

*Axial skeleton.* The cervical vertebrae of pterosaurs are divided into morphologically distinct anterior, middle, and posterior regions. The cervical series of NGMC 99-07-1 is represented by the cervicals 7–9, the last two mid-cervical vertebrae and single posterior-cervical vertebra (Text-fig. 3; Table 1). No rib facets or pneumatic foramina are visible on these vertebrae, though it would be difficult to ascertain the latter with the dorsoventral compression of this region.

The two mid-cervicals preserved are elongate. The anterior end of cervical 7 is missing, and cervical 8 is broken into two



**TEXT-FIG. 2.** Photograph and line drawing of *Elanodactylus prolatius* gen. et sp. nov., NGMC 99-07-1; for abbreviations, see text. Scale bar represents 100 mm.

pieces and subject to some telescoping. Cervical 8 is 3.5 times as long as its mid-width and cervical 7 would be about four times its mid-width provided that its middle constriction is one-half to two-thirds down the vertebra length as in other pterosaurs. The constricted mid-section of these vertebrae is approximately two-thirds of the width of the postzygapophyses. The neural spine of cervical 7 is extremely reduced, narrow, and restricted to the most posterior end of the vertebra. Anteriorly, the spine quickly diminishes to an extremely small ridge. There is no trace of the neural spine of cervical 8, which is probably the result of having a spine as reduced as the preceding vertebra, being obscured by shearing. It can be seen that the spine does not reach the better preserved anterior end. The posterior condyles extend well beyond the posterior margin of the postzygapophyses. The left side of the posterior condyle of

cervical 7 is visible. On it is a blunt, posterolaterally directed postexapophysis that has an articular surface not confluent with the articular surface of the condyle. Though these two vertebrae are dorsoventrally compressed, it can be seen that the neural arch is distinct from the centrum and not incorporated into a tubular vertebral body.

Cervical 9 is the single posterior series cervical vertebra. It is slightly longer than wide and dominated by a pair of very large, anterolaterally directed prezygapophyses, which occupy about 75 and 65 per cent of the vertebral width and length, respectively. The neural spine is low and blade-like, and extends the entire length of the neural arch.

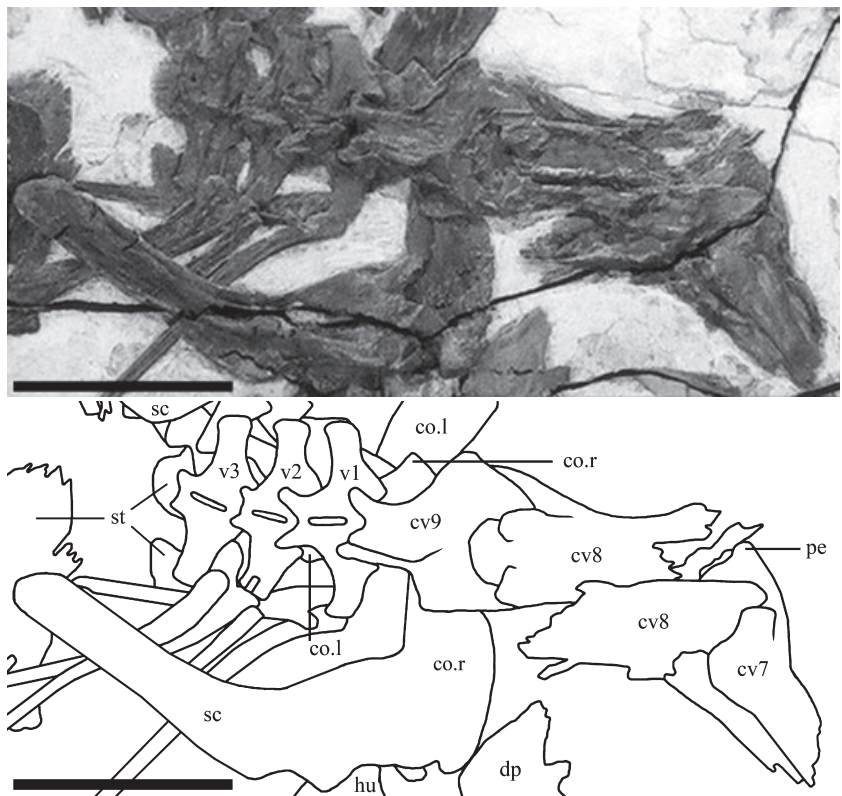
The anterior three dorsal vertebrae are preserved in NGMC 99-07-1 (Text-fig. 3; Table 1). These articulate with one another but are not fused into a notarium. They share

**TABLE 1.** Measurements (in mm) of the cervical and dorsal vertebrae of NGMC 99-07-1.

	Length	Prezygapophyses width	Postzygapophyses width	Mid-width	Spine length
Cervical 7	>59.1	—	31.2	20.0	21.3
Cervical 8	~77.5	—	24.4	21.3	>12.8
Cervical 9	45.4	40.0	16.2	13.3	20.9
Dorsal 1	25.6	28.6	14.7	46.3	9.9
Dorsal 2	18.0	22.5	9.6	43.2	12.1
Dorsal 3	19.2	16.0	9.7	41.9	10.4

Length = between anterior margin of prezygapophyses and posterior margin of the postzygapophyses; zygapophyses width = between lateral margins of both sides; mid-width = between lateral margins of the transverse processes of the dorsal vertebrae or lateral margins of mid sections of the cervical vertebrae: —, missing; >, preserved length; ~, approximate length.

**TEXT-FIG. 3.** Photograph and line drawing of the vertebral column of *Elanodactylus prolatus* gen. et sp. nov., NGMC 99-07-1. Right and left coracoids are labelled; for abbreviations, see text. Scale bars represent 50 mm.



the same general morphology, but differ in that dorsal 1 is slightly larger and has its transverse processes directed posterolaterally at their tips. The dorsal vertebrae are twice as long and have two-thirds of their widths taken up by the transverse processes. The zygapophyses are anteriorly and posteriorly directed with subvertically oriented and laterally directed articular surfaces. Associated with these vertebrae are 12 dorsal ribs, which are long, thin, and nearly straight but have slight arches positioned proximally and distally. The tuberculum is shorter than the capitulum, with a depressed area lying between the two on the posterior surface. One right and two left sternal ribs are preserved. These are oval-shaped, slightly over

twice as long as they are wide, and rough in texture. No gastralia were preserved.

**Pectoral girdle.** Both scapulae and coracoids are preserved lying on their lateral surfaces (Text-figs 2–3; Table 2). Each element is complete with only the posterior 45 mm of the left scapula detached and displaced from its original position. The ventral portions of the coracoids are partially covered by the vertebral column, but the ventralmost ends of the left and right coracoids, including the sternal articulations, are visible on the other side of the last cervical and first dorsal vertebrae, respectively. The scapula and coracoids are firmly fused into scapulocora-

coids with no visible suture between them. They are almost straight where they connect, but a bend at the supraglenoid buttress of the scapula and the continuous curvature of the coracoid gives the entire scapulocoracoid a bend of *c.* 60 degrees.

The scapula has an expanded anterior end with a mid-section and posterior end of approximately the same width. The glenoid fossa is separated from the supraglenoid buttress by a concave dorsal margin. Posterior to both is a small, dorso-medially directed tuberosity. At the tuberosity the scapula expands anteriorly, while posteriorly the scapula is essentially straight with straight dorsal and slightly concave ventral margins. Also at this tuberosity, the scapula bends *c.* 30 degrees ventrally and has a scar extending along its medial surface. The posterior end of the scapula has a rounded, ventroposteriorly directed margin. The detached posterior end of the left scapula appears to be slightly expanded but this is probably a result of distortion of this element, considering that it is more crushed and expanded than the posterior end of the right scapula.

The coracoid is about 75 per cent of the length of the scapula. It is expanded at its contact with the scapula, but has a more gentle decrease in width over its length. A small, blunt coracoid process is present, but it is not possible to tell if a groove separates it from the glenoid fossa. The sternal articulation is concave, faces posteroventrally, and lacks a posterior expansion. A large glenoid fossa faces anterodorsally with a dorsoventrally concave and anteroposteriorly convex saddle shape.

The sternum is incomplete and in three pieces. The two larger pieces include the left and right lateral portions of a large sternum. Dorsal vertebrae all but obscure the third piece. The cristospine and articular facets for the coracoids are either obscured or missing. Seven strong rib facets are visible, three right and four left, on lateral surfaces of the sternum. These lateral surfaces are straight but no more can be inferred about the total shape of the sternum. The facets are well developed anteriorly, becoming less conspicuous posteriorly.

*Wing skeleton.* Both wings are present in NGMC 99-07-1 (Text-figs 2, 4; Table 2). The humeri are complete though the right deltopectoral crest has become detached and rotated from its anatomical position (Text-fig. 2). The humeral head has an anteroposteriorly concave and dorsoventrally convex, saddle-shaped articulation so that it mirrors the shape of the glenoid. There is a dorsoposteriorly placed pneumatic foramen diving proximodistally into the humerus where this head merges with the shaft that can be better seen on the right humerus. The proximal end of the humerus is dominated by an anteroproximally expanded, rounded deltopectoral crest that is as large as the humeral head. This crest extends from lying even with the proximal margin of the humeral head to a third of the way down the humeral length. As can be seen in cross-section, the entire deltopectoral crest is slightly curved ventrally. The proximal, anterior and distal margins of the deltopectoral crest are convex, straight and slightly concave, respectively. A large tuberculum that interrupts the concave proximal margin between the deltopectoral crest and the humeral head was probably for attachment of the *m. supracoracoideus*. The humerus lacks both a well-developed medial

**TABLE 2.** Measurements (in mm) of the forelimb elements of NGMC 99-07-1.

	Length	Proximal width	Mid-width	Distal width
Coracoid (left)	>48.4	22.7	21.3	–
Coracoid (R)	76.9	27.2	21.1	9.7
Scapula (left)	~96.4	22.6	13.0	~18.0
Scapula (right)	101.6	27.4	12.8	12.8
Humerus (left)	151.3	54.4	15.7	41.8
Humerus (right)	147.1	57.8	17.2	27.7
Ulna (left)	~154.3	>19.4	15.1	29.7
Ulna (right)	~170.9	~14.5	16.3	21.5
Radius (left)	~160.9	9.7	10.7	>5.6
Radius (right)	~170.3	23.3	10.3	24.4
Proximal syncarpal (left)	9.2	35.3	30.6	29.4
Proximal syncarpal (right)	10.7	29.0	29.0	29.0
Distal syncarpal (left)	10.8	19.3	25.9	22.2
Distal syncarpal (right)	13.6	20.6	24.6	19.1
Medial carpal (left)	14.4	12.4	10.4	12.7
Medial carpal (right)	14.7	13.3	11.0	13.70
Pteroid (left)	>94.1	–	4.9	3.2
Pteroid (right)	–	–	–	–
Metacarpal I (left)	~124.2	>2.9	2.0	>2.4
Metacarpal I (right)	>86.5	–	>1.4	–
Metacarpal II (left)	>98.3	–	1.6	>2.1
Metacarpal II (right)	>99.0	–	>1.5	–
Metacarpal III (left)	>80.2	–	1.8	4.2
Metacarpal III (right)	>120.2	–	3.2	5.1
Metacarpal IV (left)	~126.5	20.6	14.6	13.8
Metacarpal IV (right)	>43.33	28.0	12.7	16.0
Wing phalanx I (left)	207.0	33.0	13.4	>22.4
Wing phalanx I (right)	208.9	32.9	13.6	27.1
Wing phalanx II (left)	~235.2	26.7	11.7	~18.0
Wing phalanx II (right)	238.6	25.9	11.3	17.8
Wing phalanx III (left)	210.9	~18.4	8.2	11.0
Wing phalanx III (right)	212.1	17.4	8.4	10.4
Wing phalanx IV (left)	143.7	11.2	3.4	2.4
Wing phalanx IV (right)	>142.9	10.5	3.7	~1.8
Phalanx 1 of digit I (left)	22.8	5.1	2.3	3.4
Phalanx 1 of digit I (right)	22.3	4.6	2.7	3.0
Phalanx 2 of digit I (left)	~17.1	5.3	9.0	–
Phalanx 2 of digit I (right)	14.2	5.3	7.5	–
Phalanx 1 of digit II (left)	>16.2	–	2.9	3.4
Phalanx 1 of digit II (right)	16.1	6.1	3.8	>2.6
Phalanx 2 of digit II (left)	18.4	5.4	2.7	–
Phalanx 2 of digit II (right)	18.3	7.0	3.2	3.2
Phalanx 3 of digit II (left)	15.2	5.4	8.2	–
Phalanx 3 of digit II (right)	14.2	5.0	7.3	–
Phalanx 1 of digit III (left)	21.8	>5.0	4.1	>5.9
Phalanx 1 of digit III (right)	22.3	6.3	3.6	5.2
Phalanx 2 of digit III (left)	7.9	5.2	3.8	4.9
Phalanx 2 of digit III (right)	8.5	4.9	3.6	4.7
Phalanx 3 of digit III (left)	19.3	5.3	3.4	4.0
Phalanx 3 of digit III (right)	19.2	5.3	2.7	3.7
Phalanx 4 of digit III (left)	13.8	4.7	6.7	–
Phalanx 4 of digit III (right)	15.0	5.2	6.8	–

–, missing; >, preserved length; ~, approximate length.

crest and a middle constriction. A muscle scar runs along the dorsal surface from the proximal end to the middle of the humerus. The shaft of the middle of the humerus is more or less constant in width before it expands distally into two anteriorly facing epicondyles separated by a sulcus, at least on the posterior surface of the distal end.

The ulnae and radii are each broken into two pieces (Text-figs 2, 4A, D–E; Table 2). The proximal portions are articulated with the humeri, whereas the distal portions of both elements are displaced from their original anatomical positions. The distal portions of the left ulna and radius are rotated 180 degrees, partially obscured by the left second wing phalanx and, unlike the rest of the specimen, are lying on their dorsal surfaces. The width of the radius is about 65 per cent of that of the ulna. Both elements have near constant widths over their lengths and distinct terminal expansions. A small, blunt biceps tubercle is visible on the anterior surface of the proximal end of the ulna; it lacks a distinct ridge. A sharp 3-mm crest for the insertion of the *m. triceps brachii* is present on the posterior portion of the proximal margin of the ulna. Short dorsal processes are visible on the proximal and distal ends of the radius. However, the distal ends of the radii and ulnae have been rotated owing to compaction of this specimen so that these processes are now in a more posterior position with respect to their anatomical orientation.

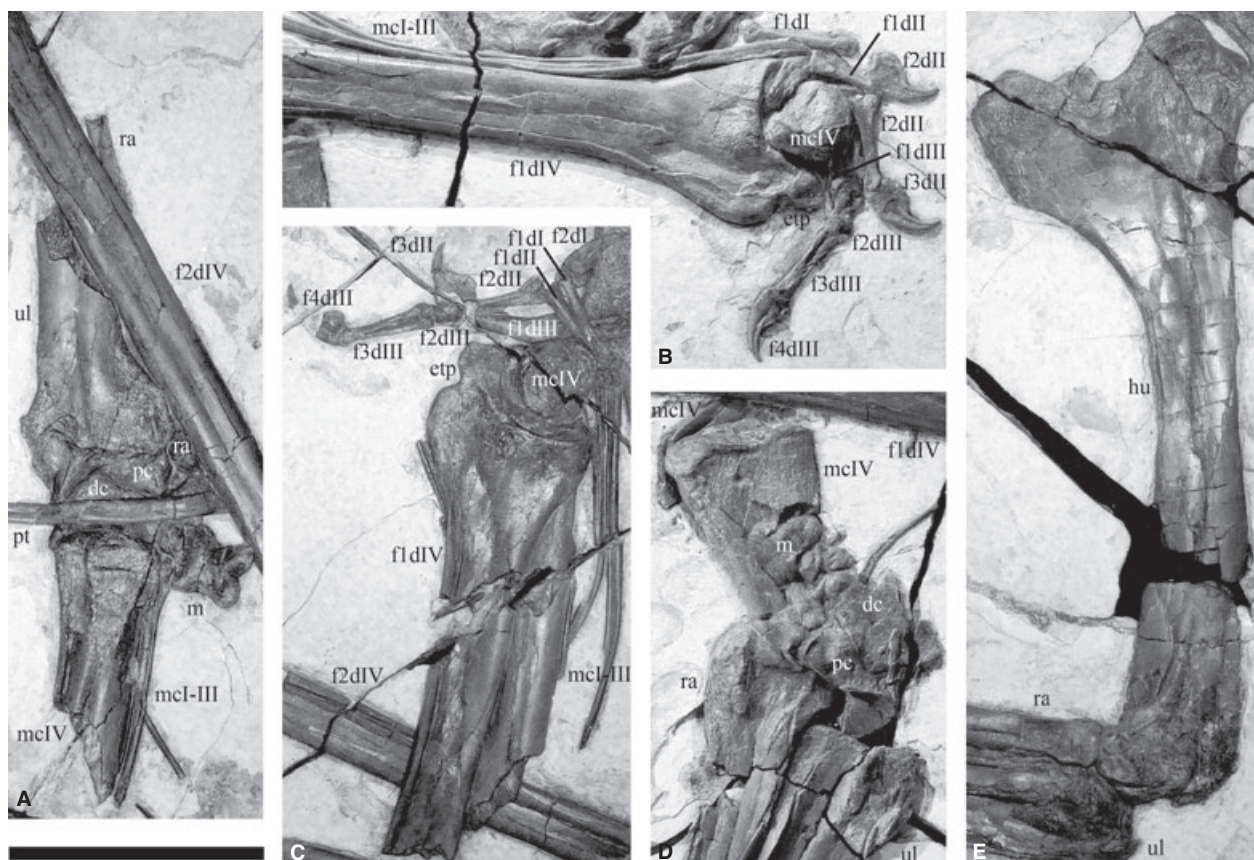
The carpus of pterosaurs typically consists of at least four elements: the proximal and distal syncarpals, a medial carpal (also termed the lateral and preaxial carpal), and the pteroid (Table 2). These are present in NGMC 99-07-1 as well as three apparent sesamoid bones. Though distorted, the left carpus can be seen in ventral view (Text-fig. 4A) and the right carpus in dorsal view (Text-fig. 4D). The proximal syncarpal is larger than the distal syncarpal in dorsoventral view. It is three times wider than long as compared to the distal syncarpal, which is twice as wide as long. Proximally the proximal syncarpal is dominated by the ulnar and radial facets; anteriorly it bears a blunt 8-mm-long process; distally it forms a large V-shaped contact for the distal syncarpal in dorsoventral view. The entire distal syncarpal has a subtriangular shape that fits this articulation. This shape is interrupted on its anterodistal margin by a round, 6-mm-long process with a constricted base. A small foramen pierces the middle of its dorsal surface. The distal surface of the distal syncarpal forms a large, concave cotyle for metacarpal IV. The medial carpal is rectangular with slightly excavated proximal and distal sides. The anterior end bears a short, straight, and round process forming the distal border of the proximoanteriorly facing fovea. A bone corresponding to sesamoid A of Bennett (1991) appears to lie in the fovea of both medial carpals. Though it cannot be discounted that this is the missing proximal end of the pteroids, there is no visible break and the shape of bones from both sides is nearly identical so that these are probably sesamoid A. Lying on top of the right proximal and distal syncarpals is a 10-mm-long subrectangular bone that may correspond to sesamoid B of Bennett (1991) or part of an ossified tendon, as well as a tiny rounded bone that is probably a third sesamoid (Text-fig. 4D). Only the left pteroid is preserved in this specimen though its proximal end is obscured. It is a very elongate and slender bone that terminates in a slightly expanded knob.

The metacarpi of NGMC 99-07-1 have been bisected into proximal and distal halves (Text-figs 2, 4A–D; Table 2). Like other pterodactyloids, they consist of the elongate metacarpals I–IV in which metacarpals I–III are extremely slender and lie anterior to metacarpal IV. As can be seen in the left carpus (Text-fig. 4A), metacarpals I–III reach the distal syncarpal and articulate with the anterior end of its distal surface. Metacarpal IV is a much larger and robust bone that is about seven times the widths of the other metacarpals. The first wing phalanges obscure the distal portions of both metacarpals IV. The proximal end of the right metacarpal IV is rotated from its original position so that its posterior surface can be seen, and is in turn overlain by part of the right carpus. The proximal end of the left metacarpus still articulates with the distal carpal so that the subrectangular outline of the ventral expansion can be seen. Metacarpal IV narrows gradually from an expanded and rugose proximal margin to its distal end where it expands into two large circular condyles that extend over about 270 degrees in circumference. These distal ends articulate and lie under their respective first wing phalanges and so that predominantly only the dorsal condyles are visible.

The digits of the manus increase in length from digit I to digit IV (Text-fig. 4B–C; Table 2). Manual digits I–III are much shorter and terminate in strongly curved, laterally compressed, sharp unguis. Each unguis has a lateral sulcus containing a small foramen in the middle of its length. The unguis are proximally anteroposteriorly expanded and have a strong flexor tubercle that is not confluent with its proximal margin. The other phalanges are much more slender by comparison. They are each about 20 mm long except for the significantly shorter first phalanx of digit II and second phalanx of digit III. The latter phalanx is by far the shortest phalanx but it is not reduced to a tiny disk. These phalanges have strong, saddle-shaped, articular surfaces, except for the penultimate phalanges that end in pairs of small, circular condyles for articulation with the unguis.

The wing finger of NGMC 99-07-1 consists of the extremely elongated four phalanges of manual digit IV as in other pterosaurs (Text-fig. 2; Table 2). The right wing finger is fully articulated while the left finger is broken into three pieces: the proximal half of the f1D4, a piece consisting of the distal f1d4 and proximal f2d4, and the rest of the wing. The ratios of their lengths are 1.00 : 1.14 : 1.02 : 0.69. These wing phalanges narrow in width in succession despite the fact that the middle two phalanges are longer than the first. With the exception of fourth phalanx, the wing phalanges are anteroposteriorly oval in cross-section and have expanded proximal and distal ends. The first wing phalanx curves slightly anteriorly, formerly a proposed synapomorphy by Unwin and Heinrich (1999) for the Dsungaripteroidae. The proximal end of this phalanx is transversely expanded and fused to the large extensor tendon process to the degree that the suture is only visible through a microscope. This process forms a semicircular cotyle with the rest of the proximal margin to receive the distal condyles of metacarpal IV. The extensor tendon process has a roughly square outline, constricted base and convex anterior margin, and is directed slightly anteriorly. The articulations between proximal and distal successive wing phalanges are slightly convex and concave, respectively,





**TEXT-FIG. 4.** Photographs of the appendicular elements of *Elanodactylus prolatius* gen. et sp. nov., NGMC 99-07-1. A, left carpus in ventral view. B, right manus in dorsal view. C, left manus in ventral view. D, right carpus in dorsal view. E, left humerus in dorsal view. For abbreviations, see text. Scale bar represents 50 mm.

with blunt posterior expansions. The second wing phalanx is the longest bone in the wing followed by the third. These two phalanges are essentially straight and differ only in their sizes. The fourth and ultimate wing phalanx is circular in cross-section, curves posteriorly 15 degrees at its midpoint, and narrows distally to a small knob.

## RESULTS

The analysis including all taxa and characters resulted in two equally parsimonious cladograms of 338 steps each, reflecting two alternative placements of *Eosipterus*, as either in a trichotomy with *Beipiaopterus* and *Gegepterus* or in a trichotomy with the sister group of these two pterosaurs and *Pterodaustro*. The Adams consensus of these two cladograms is shown in Text-figure 5, an abbreviated version of which is given in Text-figure 1. *Elanodactylus*, *Huanhepterus* and *G. macrurus* were placed in the Ctenochasmatidae, and both the Ctenochasmatidae and the Azhdarchidae were recovered as separate and monophyletic taxa (Text-fig. 5). Coding the

mid-cervical associated with *G. macrurus* as a distinct taxon still results in both the mandible and vertebra being placed in a monophyletic, though less resolved, Ctenochasmatidae. In fact, only when *Elanodactylus* is omitted from the analysis and the mandible is coded as a taxon separate from its associated vertebrae will the vertebra possibly be placed outside of the Ctenochasmatidae. In this case, it is equally parsimonious for this vertebra to be a member of the Azhdarchidae or Ctenochasmatidae. As long as *Elanodactylus* is included in the analysis, isolated mid-cervical vertebrae similar to SMC J5340 or MB R 2832 will be placed in the Ctenochasmatidae.

A number of other novel results have come out of the analysis that were not recovered or suggested by previous authors: *Boreopterus* is moved from the Ornithocheiridae to the Ctenochasmatidae; *Liaoxipterus* is placed in the Istiodactylidae; *Eopteranodon* is placed in the Tapejaridae; and *Haopterus* is moved from the Pterodactylidae to be the sister group to the Ornithocheiroidea. The Dsungaripteridae and Tapejaridae as well as the Nyctosauridae and

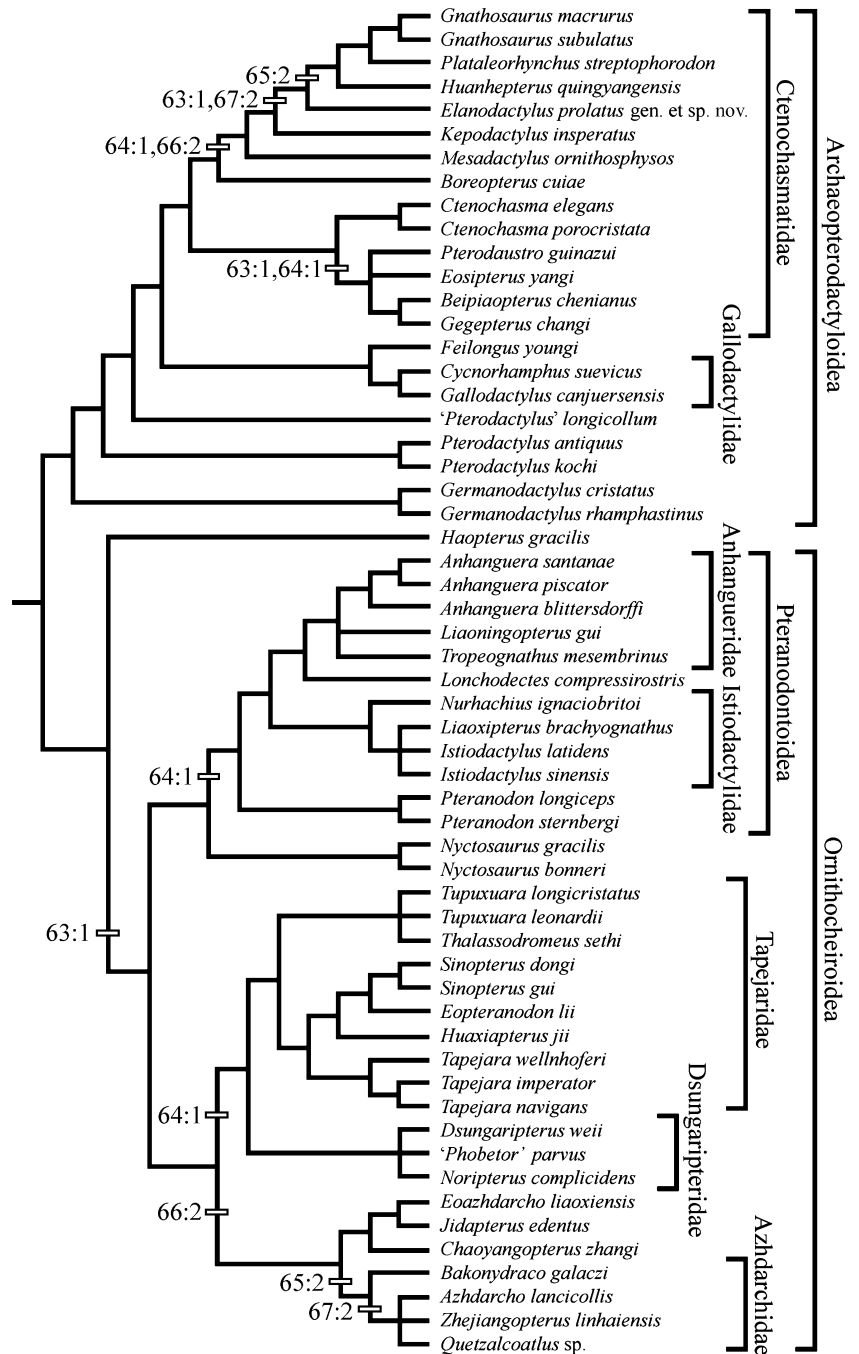


Pteranodontoidea were recovered as sister taxa, respectively. The Dsungaripteroidea *sensu* Unwin (2003a) is polyphyletic and *Pterodactylus* is recovered as paraphyletic. A paraphyletic *Pterodactylus* was also recovered by Howse (1986), but based on primary homology statements not recovered as valid in this analysis.

*Gegepterus* is the sister taxon of *Beipiaopterus* and closely related to *Eosipterus* from the same formation. In the original description, Wang *et al.* (2007) referred it to the Ctenochasmatidae but had it as more closely related to

*Ctenochasma* than *Pterodaustro* as recovered by this analysis. *Gegepterus* also bears postexapophyses as reported in *Elanodactylus* and other ctenochasmatids. It can be distinguished from *Elanodactylus* by its blade-shaped and taller neural spines on the mid-cervical vertebrae, postexapophyses forming flanges, presence of cervical ribs, coracoids with a middle constriction and ventral flange, distinct limb ratios, and a much smaller size. The phylogenetic analysis, furthermore, recovered the two species as two of the most distantly related ctenochasmatids.

**TEXT-FIG. 5.** Cladogram representing the Adams consensus of the two most parsimonious cladograms resulting from the phylogenetic analysis of *Elanodactylus prolatus* (NGMC 99-07-1) and the intrarelationships of the Pterodactyloidea. Distributions of the changes in the character states found in the mid-cervical vertebrae of the Azhdarchidae and Ctenochasmatidae are denoted by their character and state numbers: 63:1, postexapophyses; 64:1, lateral pneumatic foramina on centrum; 65:2, extremely elongated mid-cervical vertebrae; 66:2, neural spines of mid-cervical vertebrae form ridges; 67:2, extremely reduced height of neural spines of mid-cervical vertebrae.



## DISCUSSION

The phylogenetic analyses of *Elanodactylus prolatius* and the relationships of the Pterodactyloidea demonstrate that though the Ctenochasmatidae and Azhdarchidae have similar mid-cervical vertebrae, they are not closely related and their vertebrae can be recognized as distinct even in isolation. The ctenochasmatids with extremely elongate mid-cervical vertebrae share their length, postexapophyses, and extremely low neural spines that form ridges with the azhdarchids, but also have lateral pneumatic foramina on the centra and a neural arch not fully integrated into a tubular vertebral body (e.g. *Arambourgiania philadelphiae*), which the azhdarchids lack. These features are realized through the distribution of character states over the phylogeny and skeleton of the pterodactyloid pterosaurs. The preservation of other postcranial remains with the mid-cervical vertebrae of *Elanodactylus* demonstrates that the homoplastic character states of the two groups are restricted to the mid-cervical vertebrae.

The dense taxon sampling and concomitant analysis records the stepwise independent recruitment of the characters found in the extremely elongate Jurassic and azhdarchid vertebrae occurring within the archaeopterygoid and ornithocheiroid pterosaurs, respectively. Both lineages reveal trends in the elongation and reduction of the neural spines in the mid-cervical vertebrae, culminating in the conditions found in the end-members. Because taxa exist within these series that have some but not all of the character states found in their end-members, and the orders of these state changes are different in both series, they were recovered as distinct lineages (Text-fig. 5).

One of these characters, the presence of postexapophyses, was previously thought to appear only once in vertebrate history (Williston 1897), and was recovered as such in previous analyses of pterosaur relationships. They were found to be independently acquired in three distinct taxa in the analysis (Text-fig. 5). The shape of the postexapophyses is distinct in each of these taxa. Though not included in the analysis, there are mid-cervical vertebrae of non-pterodactyloid pterosaurs that bear a similar condition. These taxa represent pterosaurs of above average size with large skulls, so the independent acquisitions of postexapophyses may have been the result of strengthening and restriction of movement in the necks of larger pterosaurs or at least those with larger cervical vertebrae (Bennett 2001; Williston 1897).

The reduction in height and change in shape of the mid-cervical neural spine are also probably correlated with the elongation of these vertebrae when compared to the cervical vertebrae of the posterior series. Posterior cervical vertebrae typically have the same neural spine height and shape as the mid-cervical series. The main exception

is in the ctenochasmatids and azhdarchids with extremely elongate vertebrae. Though these species have mid-cervicals with reduced spines, their posterior cervicals retain the low neural spines (character 69) found in the middle- and posterior-series cervicals of more basal archaeopterygoids, or retain high neural spines in the case of the more basal ornithocheiroid taxa, respectively. This supports the interpretation that low, blade-like neural spines never appeared on the lineage that gave rise to the azhdarchids and helps distinguish them from the ctenochasmatids. In addition, at least three azhdarchid species have one tall, blade-like neural spine on their first or last mid-cervical vertebrae: *Quetzalcoatlus* (Langston, pers. comm. 2006), *Zhejiangopterus* (BA, pers. obs.), and *Phosphatodraco* (Pereda Suberbiola *et al.* 2003, fig. 3d). Therefore, it can be shown that there is not a total correlation between mid-cervical length and the height of the neural spine.

The mandible of *G. macrurus* and its associated vertebra are both recovered as ctenochasmatids even when coded as separate terminal taxa if *Elanodactylus* is included in the analysis. A main reason for this is because of the distribution of lateral pneumatic foramina on the mid-cervical centra (character 64, state 1) across pterodactyloid phylogeny. Lateral pneumatic foramina appear in the Ctenochasmatidae, Pteranodontoidea, the sister group of the Dsungaripteridae, and Tapejaridae (see Text-fig. 5). None of these taxa includes the Azhdarchidae, so lateral pneumatic foramina never appeared in its history. The extremely elongate mid-cervical vertebrae from the Purbeck, Tendaguru or any other isolated mid-cervicals that bear lateral pneumatic foramina, would be recovered in a similar position within the Ctenochasmatidae. Therefore, these specimens previously referred to the Azhdarchidae are here referred to the Ctenochasmatidae.

Convergence is one of the oldest and most debated terms in evolutionary biology, with no clear consensus on its exact definition or of its related term, parallelism (Wiens *et al.* 2003). This confusion began at its inception. Darwin used the term 'converged' more or less as in modern usage in 'The Descent of Man' when he misquoted Hunt's (1864) translation of a passage in Vogt's (1863) 'Lectures on Man'; he then went on to use 'convergence' in the next sentence, but in a manner that is associated with hybridization today (Haas and Simpson 1946). General usage of the term is roughly equivalent to homoplasy, with the frequent implication that it is a result of adaptive evolution. Wiens *et al.* (2003) defined the term in a phylogenetic sense as homoplasy in individual characters derived from different overall morphologies. Because the homoplastic characters shared between the ctenochasmatids and the azhdarchids are confined to the cervical vertebrae and they have disparate cranial and other postcranial characters, the similar-

ity between taxa would qualify as convergence under this definition.

If the independent acquisition of these character states is correlated with the elongation of their mid-cervical vertebrae and skulls with respect to the pursuit of a similar mode of life, then this would be a remarkable case of convergence under the traditional definition. Members of the Ctenochasmatidae and the Azhdarchidae also share other similarities not found in the rest of their most inclusive distinct clades, the Archaeoptero-dactyloidea and Ornithocheiroidea, which may point to a similar mode of life. Both contain the largest individuals of their respective clades, are characterized by very elongate rostra, and are the most fully terrestrial members of their respective clades. The fact that these two groups consist predominantly of species found in terrestrial sediments is probably the reason this convergence was not discovered before. The fossil record of pterosaurs has been biased largely towards marine sediments, which are much more likely to preserve their relatively large, delicate skeletons (Padian and Rayner 1993). Without the inclusion of the terrestrial species underused in previous analyses, the homoplastic acquisition of these character states would not have been recognized.

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## APPENDIX

List of characters and states used in the phylogenetic analysis of *Elanodactylus prolatas*, and the relationships of the Pterodactyloidea

All characters were treated as equally weighted and only characters 65 and 67 were ordered.

1. Skull length exclusive of sagittal crests (new character): 0, between three and five times the height ( $3.00 < \text{skull length}/\text{height} < 5.00$ ); 1, at least five times the height ( $\text{skull length}/\text{height} \geq 5.00$ ); 2, at most three times the height ( $\text{skull length}/\text{height} \leq 3.00$ ).
2. Dorsal margin of skull shape (modified after Kellner 2003): 0, nearly straight; 1, convex; 2, concave.
3. Rostrum shape (new character): 0, compressed laterally; 1, compressed anteroposteriorly; 2, depressed dorsoventrally.
4. Rostrum length anterior to external nares (modified after Unwin 2002): 0, less than 50 per cent of the skull length exclusive of sagittal crests; 1, extremely reduced; 2, at least 50 per cent of the skull length exclusive of sagittal crests.
5. Anterior end of premaxillae/maxillae shape (modified after Kellner 2003): 0, straight; 1, upturned; 2, downturned.

6. Anterior tip of the rostrum with a dorsally reflected palatal surface (new character): 0, absent; 1, present.
7. Nasoantorbital fenestra length (modified after Kellner 2003): 0, less than 40 per cent of the skull length; 1, at least 40 per cent of the skull length.
8. Posterior margin of the nasoantorbital fenestra shape (Unwin 2003a): 0, nearly a straight angle; 1, rounded and concave outline.
9. Orbit shape (new character): 0, subcircular; 1, small and circular; 2, piriform; 3, at least one and a half times higher than wide.
10. Orbit position (modified after Kellner 2003 and Unwin 2003a): 0, middle of the skull with the ventral margin of the orbit below the middle of the antorbital/nasoantorbital fenestra and the dorsal margin of the orbit above the dorsal margin of the antorbital/nasoantorbital fenestra; 1, high in the skull with the ventral margin of the orbit the same level or above the middle of the antorbital/nasoantorbital fenestra; 2, low in the skull with the entire orbit lower than the dorsal margin of the antorbital/nasoantorbital fenestra.
11. Angle between lacrimal and postorbital and lacrimal processes of the jugal (Unwin 2003a, b): 0, acute angle; 1, infilled.

12. Posteriorly directed process on the jugal process of the lacrimal (new character): 0, absent; 1, present.
13. Anteriorly directed process on the postorbital process of the jugal (new character): 0, absent; 1, present.
14. Suborbital vacuity (modified after Kellner 2003): 0, absent; 1, present.
15. Premaxillary sagittal crest (Bennett 1994): 0, absent; 1, present.
16. Premaxillary sagittal crest shape (new character): 0, striated with a nearly straight dorsal margin; 1, round and blade-shaped; 2, tall anteriorly, decreasing in height posteriorly; 3, low anteriorly, increasing in height posteriorly; 4, low with a humped anterodorsal margin; 5, low ridge.
17. Elongate dorsal premaxillary spine (Martill and Naish 2006): 0, absent; 1, present.
18. Premaxillary sagittal crest position (modified after Kellner 2003): 0, entire crest anterior to the nasoantorbital fenestra; 1, crest starting anterior to and extending posterior to the anterior margin of the nasoantorbital fenestra; 2, crest starting at the anterior margin of the nasoantorbital fenestra and extending backwards; 3, crest starting near the anterior margin of the skull and extending over the occipital region; 4, crest starting at the posterior half of the nasoantorbital fenestra.
19. Lateral expansion of the anterior tip of jaws (Kellner 2003): 0, absent; 1, present.
20. Posterior ventral expansion of the maxilla (Kellner 2003): 0, absent; 1, present.
21. Nasal process (new character): 0, present; 1, absent.
22. Nasal process position (modified after Kellner 2003): 0, placed laterally; 1, placed medially.
23. Free nasal process length (modified after Kellner 2003): 0, long; 1, short.
24. Nasal process orientation (modified after Kellner 2003): 0, directed anteroventrally; 1, directed ventrally; 2, directed posteroventrally.
25. Foramen on nasal process (Kellner 2003): 0, absent; 1, present.
26. Bony frontal crest (Bennett 1994): 0, absent; 1, present.
27. Bony frontal crest shape (modified after Kellner 2003): 0, low and blunt; 1, low and elongated; 2, high and expanded.
28. Lacrimal process of jugal thickness (modified after Kellner 2003): 0, broad; 1, thin.
29. Lacrimal process of the jugal inclination (modified after Kellner 2003): 0, inclined anteriorly; 1, subvertical; 2, strongly inclined posteriorly.
30. Bony parietal crest (Bennett 1994): 0, absent; 1, present.
31. Bony parietal crest shape (modified after Kellner 2003): 0, blunt; 1, laterally compressed and posteriorly expanded, with a rounded posterior margin; 2, constituting the base of the posterior portion of the cranial crest.
32. Posterior region of skull rounded with squamosal displaced ventrally (Kellner 2003): 0, absent; 1, present.
33. Squamosal position (Unwin 2003a): 0, above the base of the lacrimal process of the jugal; 1, below or level with the base of the lacrimal process of the jugal.
34. Orientation of quadrate relative to the ventral margin of skull (Kellner 2003): 0, subvertical; 1, inclined about 120 degrees posteriorly; 2, inclined about 150 degrees posteriorly.
35. Position of articulation between skull and mandible (modified after Viscardi *et al.* 1999 and Kellner 2003): 0, posterior to the middle of the orbit; 1, anterior to the middle of the orbit; 2, under the middle of the orbit.
36. Helical jaw joint (Viscardi *et al.* 1999): 0, absent; 1, present.
37. Supraoccipital shape (Kellner 2003): 0, does not extend backwards; 1, extends backwards.
38. Distal ends of paroccipital processes (Kellner 2003 and Unwin 2003a): 0, not expanded; 1, expanded.
39. Palate with ridge and mandible with sulcus (Bennett 1994): 0, absent; 1, present.
40. Palatal ridge length (modified after Kellner 2003): 0, tapering anteriorly; 1, confined posteriorly.
41. Palatal ridge shape (modified after Kellner 2003): 0, discrete; 1, strong.
42. Interpterygoid opening size (modified after Kellner 2003): 0, larger than subtemporal fenestra; 1, smaller than subtemporal fenestra.
43. Mandibular symphysis position (modified after Unwin 2003a): 0, at same level as rami; 1, located well below rami; 2, on a symphyseal shelf dorsal to ventral margin.
44. Bony mandibular symphysis length (Kellner 2003): 0, less than 30 per cent of the mandible length; 1, at least 30 per cent of the mandible length.
45. Anterior tip of dentary shape (modified after Kellner 2003 and Unwin 2003b): 0, straight; 1, projected anteriorly; 2, downturned; 3, upturned.
46. Dentary bony sagittal crest (Viscardi *et al.* 1999): 0, absent; 1, present.
47. Teeth (Bennett 1994): 0, present; 1, absent.
48. Tip of rostrum (modified after Viscardi *et al.* 1999): 0, teeth present; 1, teeth absent.
49. Tip of mandible (modified after Viscardi *et al.*, 1999): 0, teeth present; 1, teeth absent.
50. Posterior margin of the maxillary tooththrow (new character): 0, extends posterior to the anterior margin of naris/nasoantorbital fenestra; 1, at or anterior to the anterior margin of the naris/nasoantorbital fenestra.
51. Tooththrow length (new character): 0, more than or equal to one third of the skull length; 1, less than one third of the skull length.
52. All teeth set subhorizontally in jaws (new character): 0, absent; 1, present.
53. Distance between successive teeth (new character): 0, most less than the diameters of the teeth; 1, most more than the diameters of the teeth; 2, most constant and subequal to the diameters of the teeth.
54. Position of largest maxillary teeth (modified after Kellner 2003 and Unwin, 2003a): 0, middle of maxilla; 1, located mesially; 2, located distally.
55. Variation in the size of anterior teeth with fifth and sixth smaller than fourth and seventh (Kellner 2003): 0, absent; 1, present.
56. Tooth shape (new character): 0, recurved and labiolingually compressed; 1, slender; 2, sharp and conical; 3, broad with oval base; 4, lancet-shaped and labiolingually compressed; 5, spike-shaped with wide, subcircular base.
57. Tooth height (modified after Kellner 2003): 0, elongate teeth absent; 1, elongate teeth present.



58. Strongly recurved teeth present (new character): 0, absent; 1, present.
59. Inclination of teeth (new character): 0, all teeth upright; 1, anterior teeth procumbent; 2, all teeth procumbent.
60. Tooth number (new character): 0, less than 100; 1, at least 100.
61. Notarium (Bennett 1994): 0, absent; 1, present.
62. Atlas and axis (Howse 1986): 0, unfused, 1, fused.
63. Postexapophyses on cervical vertebrae (Howse 1986): 0, absent; 1, present.
64. Lateral pneumatic foramina on centrum of cervical vertebrae (Kellner 2003): 0, absent; 1, present.
65. Mid-cervical vertebrae length (modified after Bennett 1994): 0, short (length/mid-width  $\leq 2.5$ ); 1, elongate ( $2.5 < \text{length}/\text{mid-width} < 5$ ); 2, extremely elongated (length/mid-width  $\geq 5$ ).
66. Neural spines of mid-cervical vertebrae shape (modified after Kellner 2003): 0, blade-shaped; 1, spike-shaped; 2, ridge.
67. Neural spines of mid-cervical vertebrae height (Bennett 1994): 0, tall; 1, low; 2, extremely reduced.
68. Number of posterior-cervical vertebrae (modified after Bennett 1994): 0, one; 1, two.
69. Neural spines of posterior-cervical vertebrae height (new character): 0, tall; 1, low.
70. Length of the scapula relative to coracoid length (modified after Kellner 2003 and Unwin 2003a): 0, scapula at least one and a half times the coracoid length ( $\text{sca}/\text{cor} \geq 1.50$ ); 1, scapula at least one but less than one and a half times the coracoid length ( $1.00 \leq \text{sca}/\text{cor} < 1.50$ ); 2, scapula at least 80 per cent but less than the coracoid length ( $0.8 < \text{sca}/\text{cor} < 1.00$ ); 3, scapula at most 80 per cent of the coracoid length ( $\text{sca}/\text{cor} \leq 0.8$ ).
71. Proximal surface of scapula shape (Kellner 2003): 0, elongated; 1, suboval.
72. Scapula shape (Kellner 2003): 0, elongated; 1, stout with constricted shaft.
73. Scapula rotated outwards (Bennett 1994): 0, absent; 1, present.
74. Scapula articulates with notarium (Bennett 1994): 0, absent; 1, present.
75. Sternum shape (modified after Unwin 2003a): 0, semicircular; 1, rectangular.
76. Coracoid contact surface with sternum (Kellner 2003): 0, articulation surface flattened, lacking posterior expansion; 1, articulation surface oval, with posterior expansion.
77. Coracoidal flange (Kellner 2003): 0, absent; 1, present.
78. Broad tubercle on ventroposterior margin of coracoid (Kellner 2003): 0, absent; 1, present.
79. Cristospine constricted behind coracoid facets (Viscardi *et al.* 1999): 0, absent; 1, present.
80. Cristospine shape (Bennett 1994): 0, shallow and elongated; 1, deep and short.
81. Length of humerus relative to metacarpal IV length (modified after Kellner 2003): 0, humerus at least two and a half times the metacarpal IV length ( $\text{hu}/\text{McIV} \geq 2.50$ ); 1, humerus between one and a half and two and a half times the metacarpal IV length ( $1.50 < \text{hu}/\text{McIV} < 2.50$ ); 2, humerus between 55 per cent and at most one and a half times the metacarpal IV length ( $0.55 < \text{hu}/\text{McIV} \leq 1.50$ ); 3, humerus at most 55 per cent of the metacarpal IV length ( $\text{hu}/\text{McIV} \leq 0.55$ ).
82. Length of humerus relative to femur length (modified after Kellner 2003): 0, humerus at most 82 per cent of the femur length ( $\text{hu}/\text{fe} \leq 0.82$ ); 1, humerus between 82 per cent and 140 per cent of the femur length ( $1.40 > \text{hu}/\text{fe} > 0.82$ ); 2, humerus at least 140 per cent of the femur length ( $\text{hu}/\text{fe} \geq 1.40$ ).
83. Length of the ulna relative to the femur length (new character): 0, ulna at most 160 per cent of the femur length ( $\text{ul}/\text{fe} \leq 1.60$ ); 1, ulna more than 160 per cent of the femur length ( $\text{ul}/\text{fe} > 1.60$ ).
84. Ventral surface of proximal end of humerus (Unwin 2003a): 0, pneumatic foramen absent; 1, pneumatic foramen present.
85. Dorsal surface of proximal end of humerus (Kellner 2004): 0, pneumatic foramen absent; 1, pneumatic foramen present.
86. Position of deltopectoral crest on humerus (new character): 0, proximally placed; 1, positioned further down on humerus.
87. Deltopectoral crest of humerus shape (modified after Kellner 2003 and Unwin 2003a): 0, broad with almost straight anterior margin; 1, subrectangular, extending down the humerus shaft for greater than or equal to 30 per cent of the humerus length; 2, distally expanded and rounded; 3, warped; 4, elongate and rounded; 5, elongate with straight proximal and distal margins; 6, enlarged and hatchet-shaped.
88. Medial (ulnar) crest of humerus (Viscardi *et al.* 1999): 0, reduced; 1, distinct.
89. Medial (ulnar) crest of humerus shape (modified after Kellner 2003): 0, directed posteriorly; 1, massive with a developed proximal ridge.
90. Humerus shaft shape (Bennett 1994): 0, straight; 1, bowed.
91. Mid-shaft of humerus tapered (Bennett 1994): 0, absent; 1, present.
92. Distal end of humerus (Bennett 1994): 0, oval or D-shaped; 1, subtriangular.
93. Distal end of humerus (Bennett 1994): 0, pneumatic foramen absent; 1, pneumatic foramen present.
94. Length of ulna relative to humerus length (Unwin 2003b): 0, ulna less than one and a half times humerus length ( $\text{ul}/\text{hu} < 1.50$ ); 1, ulna at least one and a half times humerus length ( $\text{ul}/\text{hu} \geq 1.50$ ).
95. Length of ulna relative to tibia length (Unwin 2003b): 0, ulna at most the tibia length ( $\text{ul}/\text{ti} \leq 1.00$ ); 1, ulna longer than the tibia length ( $\text{ul}/\text{ti} > 1.00$ ).
96. Diameter of the radius relative to the ulna diameter (Bennett 1994): 0, radius more than half of the ulna diameter; 1, radius at most half of the ulna diameter.
97. Distal syncarpal shape (Bennett 1994): 0, fused in a rectangular unit; 1, fused in a triangular unit.
98. Medial carpal shape (Bennett 1994): 0, longer than wide; 1, wider than long.
99. Pteroid length (modified after Kellner 2003 and Unwin 2003a): 0, shorter than half the length of the ulna; 1, longer than half the length of the ulna.

100. Metacarpals I–III (Bennett 1994): 0, articulate with carpus; 1, metacarpal III articulates with carpus, metacarpals I and II reduced; 2, do not articulate with carpus.
101. Length of first wing phalanx relative to metacarpal IV (modified after Kellner 2003): 0, first phalanx at least twice the metacarpal IV length ( $f1dIV/McIV \geq 2.00$ ); 1, first phalanx up to twice the metacarpal IV length ( $1.00 < f1dIV/McIV < 2.00$ ); 2, first phalanx at most the metacarpal IV length ( $f1dIV/McIV \leq 1.00$ ).
102. Length of first wing phalanx relative to tibia length (modified after Kellner 2003): 0, first phalanx less than one and a third of the tibia length ( $f1dIV/ti < 1.33$ ); 1, first phalanx at least one and a third of the tibia length ( $f1dIV/ti \geq 1.33$ ).
103. Length of the second wing phalanx relative to the first phalanx length (modified after Kellner 2003): 0, second phalanx at least the first phalanx length ( $f2dIV/f1dIV \geq 1.00$ ); 1, second phalanx between 70 per cent and the first phalanx length ( $0.70 < f2dIV/f1dIV < 1.00$ ); 2, second phalanx at most 70 per cent of the first phalanx length ( $f2dIV/f1dIV \leq 0.70$ ).
104. Length of second wing phalanx relative to the ulna length (Unwin, 2003b): 0, second phalanx less than the ulna length ( $f2dIV/ul < 1.00$ ); 1, second phalanx at least the ulna length ( $f2dIV/ul \geq 1.00$ ).
105. Length of the third wing phalanx relative to the first phalanx length (modified after Kellner 2003): 0, third phalanx at least the first phalanx length ( $f3dIV/f1dIV \geq 1.00$ ); 1, third phalanx less than the first phalanx length ( $f3dIV/f1dIV < 1.00$ ).
106. Cross-section of second and third wing phalanges (Bennett 1994): 0, round to subtriangular; 1, inverted T-shaped cross-section.
107. Ischiopubic plate (new character): 0, unexpanded; 1, present; 2, reduced.
108. Strongly bowed femur (Unwin 2003a): 0, absent; 1, present.
109. Angle of femur caput to shaft (Unwin 2003a): 0: at most 145 degrees; 1, greater than 145 degrees.
110. Length of the femur relative to metacarpal IV length (modified after Kellner 2003): 0, femur at least twice the metacarpal IV length ( $fe/mcIV \geq 2.00$ ); 1, femur between one and a quarter and twice the metacarpal IV length ( $1.25 < fe/mcIV < 2.00$ ); 2, femur between one half and up to one and a quarter the metacarpal IV length ( $0.50 < fe/mcIV \leq 1.25$ ); 3, femur at most one half the metacarpal IV length ( $fe/mcIV \leq 0.50$ ).
111. Length of metatarsal III relative to tibia length (modified after Kellner 2003): 0, metatarsal III between one third and one half of the tibia length ( $mtIII/ti > 0.33$ ); 1, metatarsal III at most one third the tibia length ( $mtIII/ti \leq 0.33$ ).

*Character matrix used in the phylogenetic analysis of Elanodactylus prolatius, and the relationships of the Pterodactyloidea*

*Dimorphodon macronyx*  
 010000-03000000- - -0000-000-000-0?00?00????0-00000000100000  
 000?00000??1000-?00???11000000-1000000000000000?00010

*Campylognathoides liasicus*  
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 0000000000??100?-10000011100010-??00010?00001011?10010  
*Rhamphorhynchus muensteri*  
 000000-00000000- - -0000-000-000-00120000- -0011001100011011  
 0200000000001000-10000011100020-1000110??0001111010010  
*Anurognathus ammoni*  
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 ???0???1???-?????011??000-1000010?000100??0?00  
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*Gnathosaurus subulatus*  
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*Plataeorhynchus streptophorodon*  
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*Huanhepterus quingyangensis*  
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*Kepodactylus insperatus*  
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*Mesadactylus ornithosphysos*  
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*Beipiaopterus chenianus*  
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*Boreopterus cuiaei*  
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*Feilongus youngi*  
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*Eosipterus yangi*  
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*Pterodaustro guinazui*  
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*Ctenochasma elegans*  
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*Ctenochasma porocristata*  
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 ???  
*Gegepterus changi*  
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*Cycnorhamphus suevicus*  
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 0?0001010?1000-00000121000040-100?000??010111010121



*Chaoyangopterus zhangii*

020?00??????0--00????????????????11001-----?10  
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*Bakonydraco galaczi*

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*Azhdarcho lancicollis*

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*Zhejiangopterus linhaiensis*

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*Quetzalcoatlus* sp.

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