

A NEW AZHDARCHOID PTEROSAUR FROM THE CRATO FORMATION (LOWER CRETACEOUS, APTIAN?) OF BRAZIL

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Typescript received 12 July 2007; accepted in revised form 28 January 2008

Abstract: A partial pterosaur skull from the Nova Olinda Member of the Crato Formation (Lower Cretaceous, Aptian?) represents a new edentulous pterodactyloid, *Lacusovagus magnificens* gen. et sp. nov. The absence of teeth and a large nasoantorbital fenestra suggest assignment to Azhdarchoidea, and the combination of a particularly short, crestless and shallow rostrum and laterally flared jaw margins distinguish it from other azhdarchoid taxa. The position of the new form within Azhdarchoidea is problematic: *Lacusovagus* is distinguished from Tapejaridae in its straight, as opposed to ventrally displaced, jaw tip and absence of a premaxillary crest; from thalassodromids by the absence of a premaxillary crest; and from Azhdarchidae by the short length of the rostrum and shallow posterodorsal extension of the premaxilla. *Lacusovagus* shares a shallow, crestless rostrum and a slender posterodorsal premaxillary extension with Jiufotang Formation azhdarchoids such as *Chaoyangopterus* and *Jidapterus*.

The position of these genera within Azhdarchoidea is controversial, but the suite of plesiomorphic and derived azhdarchoid characters in each suggests a placement between Tapejaridae and Neoazhdarchia. Further research is required, however, to determine the relationships of these genera both to each other and to other azhdarchoids. The new taxon elevates the faunal similarity found between the roughly contemporaneous Jiufotang and Crato formations and continues the pattern of Crato Formation azhdarchoids being much larger than those from the Jehol Group. It also has jaws at least 67 and 55 per cent longer, respectively, than those of the largest azhdarchoids and ornithocheirids from the Crato pterosaur assemblage, making *Lacusovagus* the largest pterosaur known from this unit.

Key words: Pterosauria, Azhdarchoidea, *Lacusovagus magnificens*, Cretaceous, Crato Formation, Brazil.

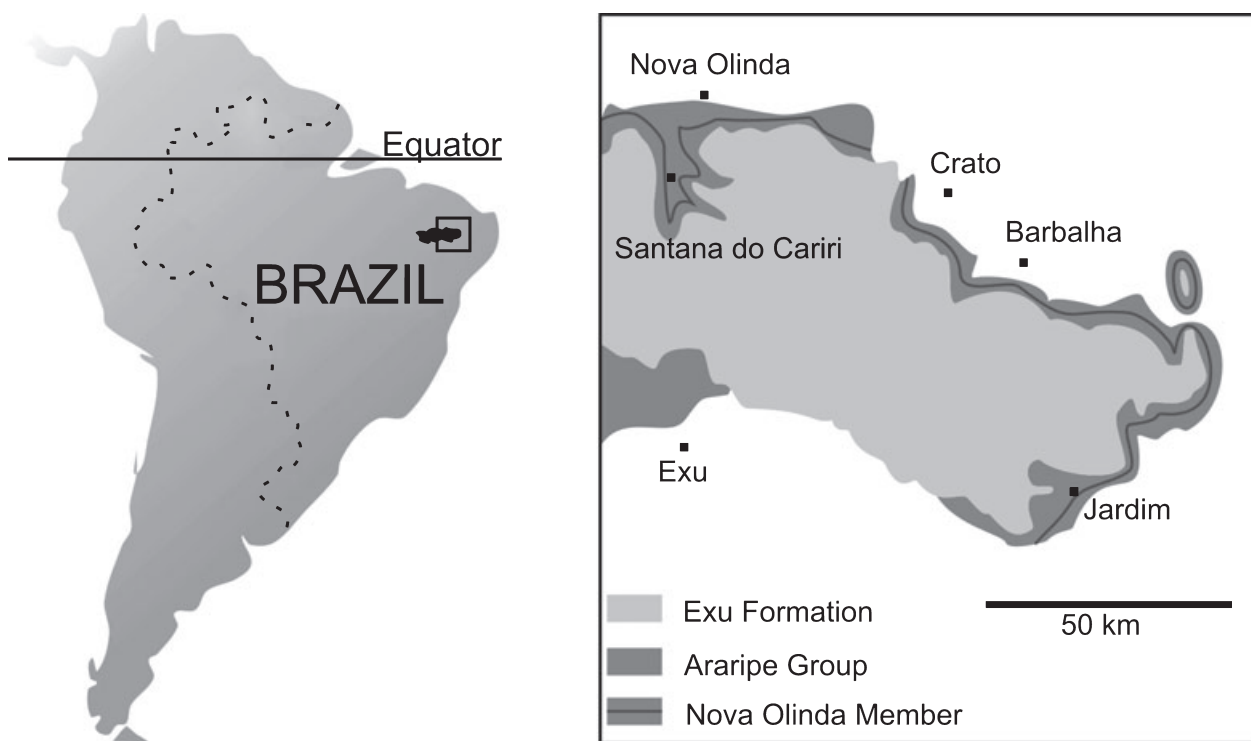
THE Lower Cretaceous Crato Formation of the Brazilian Chapada do Araripe is a globally important site for pterosaur fossils. As well as yielding a number of endemic pterosaur species referable to Ornithocheiroidea (Frey and Martill 1994; Frey *et al.* 2003a) and Azhdarchoidea (Campos and Kellner 1997; Frey *et al.* 2003b), pterosaur material from this locality has also provided exquisitely preserved pterosaur soft tissues and revealed much about pterosaur functional anatomy (e.g. Campos and Kellner 1997; Martill and Frey 1998; Frey *et al.* 2003b, c). Despite the discovery of more than 30 individuals from this deposit, a recent revision by Unwin and Martill (2007) suggests that only five Crato pterosaur species can be recognised: the ornithocheiroids *Arthurdactylus conandoylei* (Frey and Martill 1994), *Ludodactylus sibbicki* (Frey *et al.* 2003a) and *Brasileodactylus* sp. (Sayao and Kellner 2000); and the tapejarids *Tupandactylus imperator* (Campos and Kellner 1997) and ‘*Tapejara*’ *navigans* (Frey *et al.* 2003b). Thalassodromidae, the clade that

includes the sail-crested forms *Tupuxuara* and *Thalassodromeus* (Kellner 2004; Lü *et al.* 2006a; Kellner and Campos 2007; Unwin and Martill 2007) are also known from the Crato Formation, but only from generically indeterminate material (Unwin and Martill 2007). In all cases except *A. conandoylei*, Crato Formation taxa are diagnosed on the basis of isolated skull material. Here, a new pterosaur skull, SMNK PAL 4325, is described and recognized as the fifth pterosaur genus from this horizon.

Institutional abbreviation. SMNK, Staatliches Museum für Naturkunde, Karlsruhe.

LOCALITY AND STRATIGRAPHY

SMNK PAL 4325 was obtained from a commercial dealer and precise locality data is unknown. The lithology and



TEXT-FIG. 1. Locality map showing the Chapada do Araripe, the source of the new pterosaur. The exact location of discovery is unknown, but the specimen is clearly derived from the Nova Olinda Member of the Araripe Group (inset). Modified from Fielding *et al.* (2005) and Martill and Naish (2006).

preservational style of the fossil confirm its source as the Nova Olinda Member of the Crato Formation, which outcrops extensively in the Chapada do Araripe, north-east Brazil (Text-fig. 1; Martill and Wilby 1993). It is likely that the specimen was collected from one of the quarries between Nova Olinda and Santana do Cariri, as it definitely did not come from Tatajuba or Mina Anton Felipe (D. Martill, pers. comm. 2007). The stratigraphic nomenclature of the Crato sediments is controversial: a review of Crato stratigraphy is given by Martill and Wilby (1993) and the stratigraphic framework of these authors is employed here. The Nova Olinda Member consists of a series of laminated limestones up to 14 m thick and is quarried extensively between Nova Olinda, Santana do Cariri and Tatajuba (Martill 1993). Sedimentological and fossil data indicates that the Crato Formation was a large but restricted water body with hostile, possibly hypersaline or anoxic bottom waters (Martill and Loveridge 2006; Martill *et al.* 2007). The hinterland, from which much of the Crato biota is apparently derived, is thought to have been an arid, chaparral-type environment (Martill *et al.* 2007). Some conjecture surrounds the age of these deposits (see Martill and Wilby 1993), but palynological data suggests they are Aptian (Pons *et al.* 1990).

PRESERVATION

SMNK PAL 4325 consists of a fragmentary pterosaur jaw preserved on a slab of buff-coloured limestone measuring 795 × 220 mm. It is orientated dorsally on the slab so that the palate is obscured. Dorsoventral flattening has distorted many regions of the specimen and much of the dorsal surface is weathered. This crushing has displaced the skull roof so that the right lateral side lies horizontally next to the dorsal surface. Prior to acquisition by the SMNK, an additional limestone sheet was secured to the specimen using car body filler, some of which has permeated voids in the matrix to outline the ventral margins of the specimen. Mechanical and chemical attempts to remove elements of both the limestone slab and car filler to expose the palatal surface of the skull were halted to prevent damage to the specimen when the fragility of the remains became apparent. Additional mechanical preparation has been performed on the posterior region of the right maxillary ramus. The left maxillary ramus is missing following fracture at the juncture between the maxillary ramus and rostrum; sediment obscuring this break indicates that this damage occurred prior to burial. Similarly, the posterior extremity of the right maxillary bar is marked by a break with sediment in direct contact with

the broken surface, suggesting that this damage also occurred pre-burial. Elements of the posterodorsal extension of the premaxilla appear to have been broken more recently and some were apparently glued back in place prior to acquisition of the fossil.

SYSTEMATIC PALAEOLOGY

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

AZHDARCHOIDEA Nesov, 1984 *sensu* Unwin, 1992

Genus LACUSOVAGUS gen. nov.

Derivation of name. After the Latin, *lacus* = lake and *vagus* = wanderer, referring to the occurrence of the new taxon in the Crato water body.

Type species. *Lacusovagus magnificens* sp. nov.

Diagnosis. See diagnosis for type and only known species.

Lacusovagus magnificens sp. nov.

Text-figs 2–3

Derivation of name. From the Latin, *magnificentia* = grand, denoting the large size of the new taxon.

Holotype. SMNK PAL 4325, incomplete skull comprising premaxilla, maxilla and possibly parts of the jugal incorporated into the maxillary ramus (Text-figs 2–3).

Type locality. Chapada do Araripe, Northeast Brazil; Nova Olin-da Member, Crato Formation, Early Cretaceous (Aptian?).

Diagnosis. Azhdarchoid pterosaur with a maxillary ramus that flares laterally at the posterior extremity, but is sub-parallel with the skull midline along its middle portion and tapers towards the rostrum at its anterior; crestless, shallow but laterally broad prenasal-rostrum that measures <37 per cent of the jaw length, with a dorsal apex of 70 degrees.

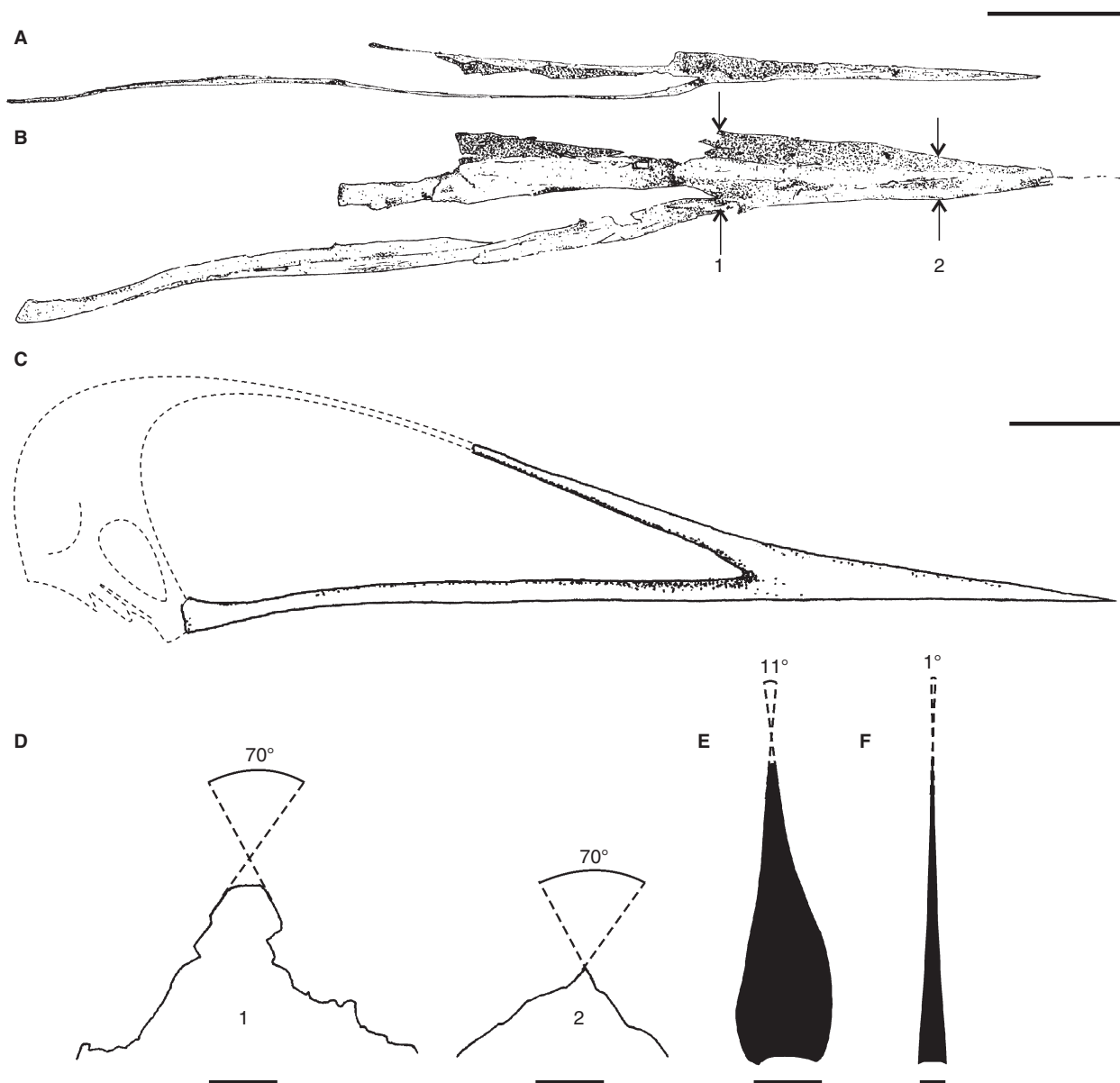
Description

SMNK PAL 4325 (Text-figs 2–3) consists of a large, incomplete jaw bearing a long right maxillary ramus and tapered rostral tip. The dorsal and lateral surfaces of the jaw are exposed, but dorsoventral crushing of the specimen has distorted the lateral profile so that the original skull height cannot be determined. Despite this compression, the specimen increases in height posteriorly along with the thickness of the limestone slab. Presumably, the greater slab thickness is due to protection from deformation offered by the skull roof. The lateral margins of the skull taper anteriorly to form an acute point at the jaw tip. The total length of clearly exposed bone along the midline is 618 mm, but car filler mostly obscures the termination of the jaw tip. Traces of bone aligned with the midline of skull extend through the car filler, however, to indicate an actual skull length of at least 655 mm (Table 1). The jaw width from the posterior margin of the maxillary ramus to the midline is 95 mm, indicating a minimal skull width of 190 mm at this point. The bone appears texturally mature under osteological criteria set by Bennett (1993). Sutures between individual bones are difficult to discern, although a possible suture is observable on the right maxillary bar and may represent the boundary between the jugal and the maxilla.

The rostrum, taken as the length from the jaw tip to the anterior margin of the nasoantorbital fenestra, has a length 4.7 times its widest point (including partially obscured material at the jaw tip). The posterior third of the rostrum has parallel lateral margins, whereas the anterior region tapers to a 16 degrees angle at the jaw tip. The posterior half is crushed and the



TEXT-FIG. 2. SMNK PAL 4325, *Lacusovagus magnificens* gen. et. sp. nov. Specimen in dorsal view. Scale bar represents 100 mm.



TEXT-FIG. 3. Line drawing of SMNK PAL 4325, *Lacusovagus magnificens* gen. et. sp. nov. A, right lateral view. B, dorsal view. C, reconstructed skull of *Lacusovagus magnificens*. D, cross-sections of rostrum taken at points 1 and 2 on B. E, rostral cross-section of *Tupuxuara longicristatus* (modified from Kellner and Campos 1994). F, rostral cross-section of *Tapejara wellnhoferi* (modified from Wellnhofer and Kellner 1991). Scale bars represent 100 mm (A–C) and 10 mm (D–E).

compacta extensively fractured, but a triangular cross-section remains discernable (Text-fig. 3D). A prominent median ridge extends along the length of the rostrum, increasing in size posteriorly to a maximum height of 15 mm and a width of 14 mm. Fractures bordering the ridge on either side correspond with the fragmented bone on the rostrum, suggesting that this structure is not a rostral crest but instead a compaction-resistant midline. Furthermore, pterosaur cranial crests are typically thin, with widths of <10 mm common (e.g. Young 1973; Wellnhofer and Kellner 1991; Bennett 2001): the broad rostral ridge compares poorly with this value. This interpretation is

supported by the expansive rostral apex (dorsal angle between the converging lateral rostrum surfaces) of the rostrum, which has a consistently broad angle of 70 degrees along its length (Text-fig. 3D). Moreover, better preserved parts of the rostrum show no indication of a suture or break to suggest that a cranial crest has broken away from the skull. Assuming that the lateral rostral surfaces maintain the 70 degrees inclination of the dorsal apex, the rostral height of *Lacusovagus* can be estimated at a shallow 37 mm at its posteriormost and tallest point. This confirms observations that, despite the extensive fracturing of the compacta, the rostrum has not been heavily

TABLE 1. Select measurements of SMNK PAL 4325.

Dimension (mm)	Measurement
Minimum skull length	655
Skull width to midline	95
Rostral length (jaw tip to NAOF)	242
Maximum rostral width	51
Maximum rostral height	22
Maximum skull roof width	42
Maxillary ramus length	435
Minimum NAOF length	413

NAOF, nasoantorbital fenestra.

compressed and *Lacusovagus* probably had a shallow, yet laterally expansive snout (Text-fig. 3C).

The posterodorsal extension of the premaxilla projects posteriorly 198 mm from the rostral ridge. From a width of 15.5 mm at the anterior, these elements broaden to almost three times this dimension at the widest point. The posterior third of this region is represented by a 15 mm wide splint of bone apparently glued in place. The skull roof appears to have borne a broad dorsal apex in a similar fashion to the rostrum and apparently expanded in width posteriorly.

The right maxillary ramus extends posterolaterally to form the ventral margin of the right nasoantorbital fenestra. Though crushed, a relatively consistent width of 14–16 mm is maintained along its length. Flattening of the specimen has medially displaced the dorsal portion of much of the ramus, but an undistorted, vertically orientated bone wall indicates that the original jaw profile is largely maintained. This bone wall is <1 mm thick, and a similar thickness is observed on other fractured compacta across the specimen. The maxillary ramus flares from the skull midline at varying degrees along its length, meeting the rostrum at 16 degrees from the midline, assuming a sub-parallel orientation midway along the bar and deflecting laterally again to 18 degrees in the posterior-most third.

The orientation and exposure of the specimen prevents direct confirmation of the presence of dental alveoli. Attempts to remove the car filler and limestone obscuring the ventral surface have been hampered by the fragile nature of the bone and intransigent filler material, but what can be seen of the palatal surface reveals no dental alveoli. Furthermore, the smooth jaw margins of SMNK PAL 4325 demonstrate that there were neither ornithocheirid-like laterally projecting teeth nor *Dsungaripterus*-like expanded alveoli [see Young (1973) and Kellner and Tomida (2000) for examples], and it is therefore assumed that *Lacusovagus* was edentulous.

The original size and shape of the nasoantorbital fenestra is unknown due to the incompleteness and distortion of the skull. The posterior margin is not preserved, though a slight medial flaring of the termination of the right maxillary bar may approximate the posteroventral margin of this opening. This indicates that the vast majority of fenestral length is recorded in the 413 mm between its anterior margin and the posteriormost extension of the maxillary bar. As the posterior margin of the

nasoantorbital fenestra often approximates the location of the jaw joint in derived pterodactyloids [see Kellner (2004, figs 2–5) for examples], it is assumed that most of the jaw length is also preserved. The anterior fenestral margin is a tight curve between the maxillary bar and the median skull elements, but matrix obscures much of the detail of this area.

DISCUSSION

Phylogenetic affinities of Lacusovagus

Lacusovagus is confidently referred to Pterosauria based on its characteristically thin bone compacta (e.g. de Ricqlès *et al.* 2000; Steel 2004), and the presence of a nasoantorbital fenestra and toothless jaws places *Lacusovagus* within Pterodactyloidea (Unwin 2003; Kellner 2003). Only the pterodactyloid groups Pteranodontia and Azhdarchoidea appear to have developed toothlessness (Unwin 2003), suggesting that SMNK PAL 4325 belongs to one of these clades. *Lacusovagus* compares poorly to Pteranodontia, however. Although the elongate, toothless jaws of pteranodontians are comparable to the new taxon (Bennett 2001, 2003; Unwin 2003), pteranodontians are characterised by narrow skulls that have jaw width:length ratios of 13 per cent in *Pteranodon* and 20 per cent in *Nyctosaurus* (Williston 1902; Bennett 2001). These values are significantly lower than the jaw width:length ratio of 29 per cent in *Lacusovagus* (estimated from the reconstructed skull width at the posterior extremity of the maxillary ramus and preserved skull length) and, in addition, the rostral lengths are markedly different between these forms: *Pteranodon* and *Nyctosaurus* have rostra occupying 79 and 76 per cent of their jaw lengths, whereas the rostrum of *Lacusovagus* occupies a relatively short 37 per cent (Table 2). This reflects the relative sizes of the nasoantorbital fenestra in these taxa: *Lacusovagus* has a considerably larger nasoantorbital opening than those of pteranodontians (Williston 1902; Bennett 2001) that occupies the majority of the jawline and extends further towards the jaw tip than the reduced, posteriorly positioned nasoantorbital fenestra of pteranodontians. Furthermore, neither *Nyctosaurus* nor *Pteranodon* have undulating jaw margins (Text-fig. 4) or broad skull roofs.

By contrast, *Lacusovagus* compares well with azhdarchoids in that the expanded nasoantorbital fenestrae common to many members of this group produces relatively short rostra that often occupy <50 per cent of the jaw length (Table 2). Although nasoantorbital fenestrae of similar sizes are also found in istiodactylids (e.g. Hooley 1913; Andres and Ji 2006), these forms can be readily distinguished from azhdarchoids through their broadly rounded and tooth-bearing jaw tips. With both large nasoantorbital fenestrae and edentulous jaws discernable

TABLE 2. Skull ratios of edentulous pterosaurs.

Taxon	Jaw length: width ratio	Rostral length: jaw length	Reference
<i>Pteranodon longiceps</i>	0.13	0.79	Bennett 2001
<i>Nyctosaurus gracilis</i>	0.20	0.77	Bennett 2003
<i>Tapejara wellnhoferi</i>	0.34	0.38	Wellnhofer and Kellner 1991
' <i>Tapejara</i> ' <i>navigans</i>	–	0.33	Frey <i>et al.</i> 2003b
<i>Tupandactylus imperator</i>	–	0.24	Campos and Kellner 1997
<i>Sinopterus gui</i>	–	0.32	Li <i>et al.</i> 2003
<i>Tupuxuara</i> sp.	0.20	0.39	Unwin 2003
<i>Thalassodromeus sethi</i>	0.21	0.46	Kellner and Campos 2002
<i>Eoazhdarcho liaoxiensis</i> *	0.23	–	Lü and Ji 2005
<i>Jidapterus edentus</i> *	0.20	0.54	Dong <i>et al.</i> 2003
<i>Chaoyangopterus zhangii</i>	–	0.48	Wang and Zhou 2003
<i>Eopteranodon lii</i>	–	0.57	Lü and Zhang 2005
<i>Bakonydraco galaczi</i> *	0.22	–	Ósi <i>et al.</i> 2005
<i>Quetzalcoatlus</i> sp.*	0.11	0.65	Kellner and Langston 1996
<i>Zhejiangopterus linhaiensis</i>	–	0.52	Cai and Wei 1994
<i>Lacusovagus magnificens</i>	0.29	0.37	–

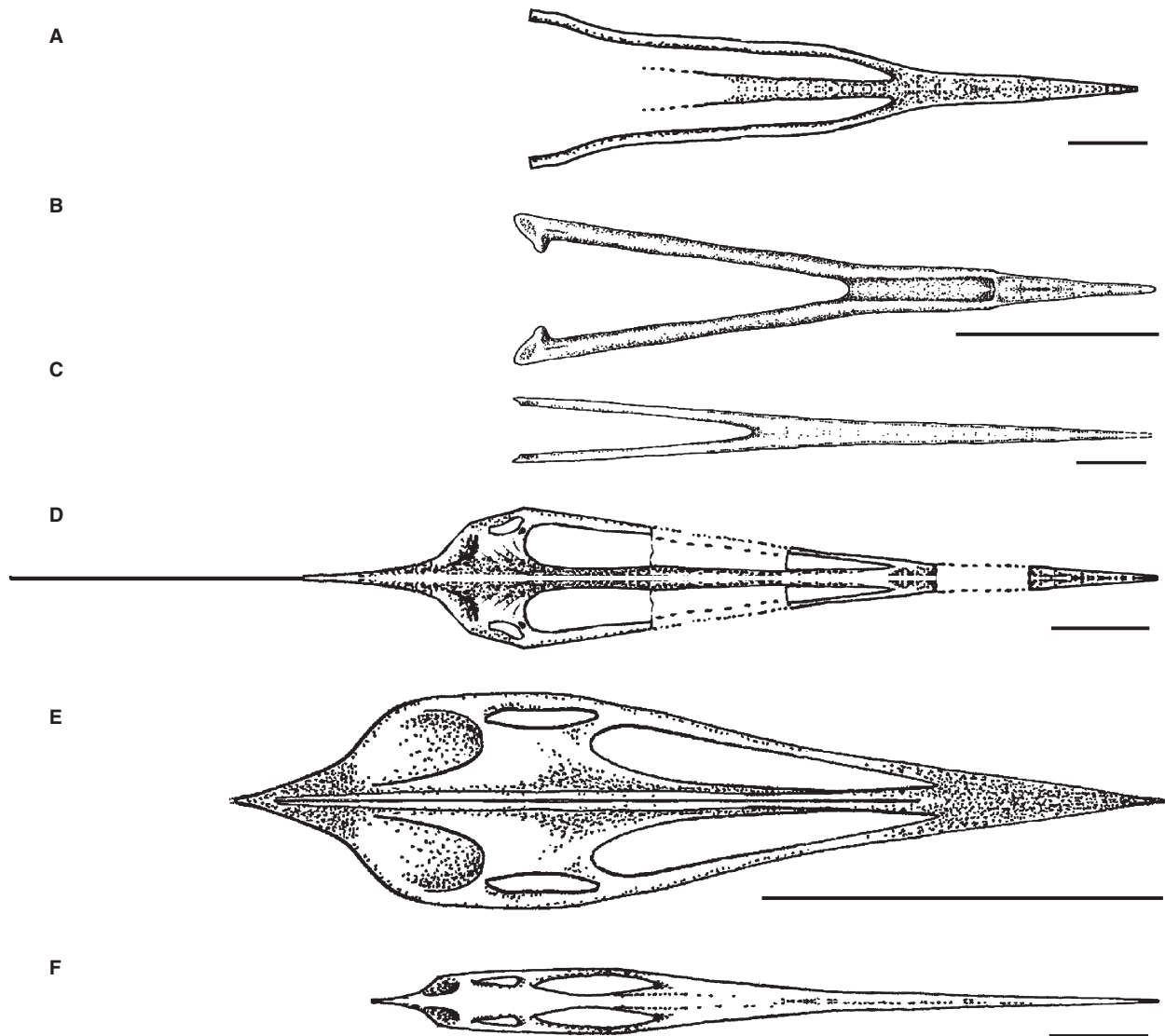
Taxa marked with an asterisk (*) have jaw length:width ratios calculated from mandibles.

in *Lacusovagus*, SMNK PAL 4325 can be confidently referred to Azhdarchoidea.

The interrelationships of Azhdarchoidea are somewhat contentious, with most disagreement focusing on the content of Tapejaridae. Several authors restrict this clade to short-faced forms such as *Tapejara*, *Sinopterus*, *Huaxipterus* and *Tupandactylus* (e.g. Martill and Naish 2006; Lü and Ji 2006; Lü *et al.* 2006b), while others also include *Tupuxuara* and *Thalassodromeus* in a more expansive clade (e.g. Kellner and Campos 1994, 2002; Kellner 2003, 2004). An alternative phylogeny sees *Tupuxuara* and *Thalassodromeus* separated from Tapejaridae and allied with Azhdarchidae in the clade Neoazhdarchia (Unwin 2003; Lü *et al.* 2006a). Adding further controversy to azhdarchoid interrelationships is the recent questioning of the status of *Tupuxuara* and *Thalassodromeus* (Martill and Naish 2006). Reappraisal of the cranial anatomy of *Thalassodromeus* and *Tupuxuara* indicate that, contrary to the findings of this study, these two genera are not synonymous (Kellner and Campos 2007). However, the validity of some thalassodromid species remains questionable: a detailed review of the taxonomy of these forms is underway (M. P. Witton, in prep.).

The phylogenies of Unwin (2003) and Lü *et al.* (2006a) are used in discussion here. Under these schemes, three azhdarchoid groups are recognised: Tapejaridae, short-faced pterosaurs known almost entirely from the Araripe and Jehol groups (e.g. Wellnhofer and Kellner 1991; Frey *et al.* 2003b; Lü *et al.* 2006a); Thalassodromidae, sail-crested forms known exclusively from the Araripe Group (Kellner and Campos 1988; Kellner and Campos 2002) and Azhdarchidae, long-necked, often giant forms that achieved cosmopolitan distribution in the Upper Cretaceous (e.g. Lawson 1975; Cai and Wei 1994; Ósi *et al.* 2005). All three groups have been reported in the Crato Formation. Tapejaridae are represented by *Tupandactylus imperator*, '*Tapejara*' *navigans* and postcranial remains that cannot be confidently assigned to a particular genus (Frey *et al.* 2003c; Unwin and Martill 2007). Crato Formation thalassodromids are represented solely by postcranial material (Unwin and Martill 2007), whereas Martill and Frey (1999) tentatively assigned one specimen (SMNK PAL 2342) with wing phalanges that have T-shaped cross-sections to Azhdarchidae (but see Kellner 2004 and Unwin and Martill 2007).

Recently, several new edentulous pterosaurs have been recovered from the Jiufotang Formation of Liaoning Province, China, that may heighten the diversity of azhdarchoids. *Jidapterus edentus*, *Chaoyangopterus zhangii*, *Eoazhdarcho liaoxiensis* and *Eopteranodon lii* have all been identified as azhdarchoids (Lü and Ji 2006), but note that this placement is controversial and some authors prefer allocation to Ornithocheiroidea (e.g. Lü and Ji 2006 vs. Wang and Zhou 2006). This author agrees with the conclusions of Lü and Ji (2006) that these forms exhibit anatomy more akin to that of azhdarchoids than ornithocheiroids, supporting their allocation to Azhdarchoidea. However, their cranial morphology is distinct from that observed in currently recognised azhdarchoid clades, being superficially most like those of thalassodromids but lacking the sweeping premaxillary headcrests characteristic of this group (Kellner and Campos 1988, 2002). Furthermore, unlike the similarly-crestless Azhdarchidae, the Jiufotang Formation azhdarchoids have shallow rostra and thin posterodorsal extensions of the premaxilla over the nasoantorbital fenestra. The significance of these distinctions has yet to be investigated in detail, however, and the interrelationships of these taxa also remain poorly understood. Lü and Ji (2006) maintain that each of these genera are distinct, with *Eopteranodon*, *Eoazhdarcho*, *Chaoyangopterus* and *Jidapterus* forming successive outgroups to Azhdarchidae. By contrast, Wang and Zhou (2006) suggested that *Jidapterus*, *Eopteranodon* and *Eoazhdarcho* should be synonymized with *Chaoyangopterus*, but this has been disputed by other workers (e.g. Lü and Ji 2006; Lü *et al.* 2006b). Systematic revision of these forms is needed but, pending further investigation, each genus is provisionally considered separate here.



TEXT-FIG. 4. Jaw profiles of edentulous pterosaur skulls and mandibles scaled to same jaw length. A, reconstructed anterior portion of the skull of *Lacusovagus magnificens*. B, mandible of *Bakonydraco galaczi* (after Ósi *et al.* 2005). C, reconstructed mandible of *Quetzalcoatlus* sp. (based on TMM 42161-2, Kellner and Langston 1996). D, skull of *Thalassodromeus sethi*. E, skull of *Tapejara wellnhoferi* (after Wellnhofer and Kellner 1991). F, skull of *Pteranodon longiceps* (after Bennett 2001). Anterior is to the right. Scale bars represent 100 mm.

Comparisons with other azhdarchoids. The low skull profile of *Lacusovagus* is distinct from that of tapejarids and thalassodromids, most obviously through the lack of a prominent, rostrally-situated headcrest or, in the case of the crestless *Sinopterus gui*, a deepened rostrum (Wellnhofer and Kellner 1991; Campos and Kellner 1997; Wang and Zhou 2002; Frey *et al.* 2003b; Li *et al.* 2003; Lü and Yuan 2005; Lü *et al.* 2006a; Kellner and Campos 1988, 1994, 2002). Interpreting the presence or absence of cranial crests in pterosaurs is problematic due to the variation of this structure demonstrated across ontogeny (Bennett 2002, 2003; Martill and Naish 2006) and possibly gender (Bennett 1992). The osteological maturity of

SMNK PAL 4325 suggests that its crestlessness is not a consequence of its age, but the possibility remains that it could represent a crestless gender of an otherwise crested species. However, note that all *Pteranodon* individuals (the only pterosaur for which dimorphism has been well demonstrated) bear a cranial crest, albeit with some bearing significantly reduced crests compared to others (Bennett 1992). As SMNK PAL 4325 has no indication of possessing even a diminutive crest, it is assumed that at least this individual was crestless.

The shallow rostral morphology of *Lacusovagus* produces a broad rostral cross-sectional with a 70 degrees dorsal apex. This condition contrasts strongly with the

rostral cross-sections of *Tapejara* and *Tupuxuara* which have extremely acute dorsal apices of 1–11 degrees (Text-fig. 3E–F; Kellner and Campos 1988, 1994; Wellnhofer and Kellner 1991). Consequently, the shallow rostral morphology of *Lacusovagus* is more comparable to that of azhdarchids (Cai and Wei 1994; Kellner and Langston 1996) and the straight-jawed Jiufotang Formation azhdarchoids (e.g. Wang and Zhou 2003). Unfortunately, dorsal apices cannot be measured for these forms as laterally-induced crushing has distorted the best known azhdarchid and Jiufotang azhdarchoid skull material. However, the jaws of these azhdarchoids can be distinguished by the relative depths of the posterodorsal process of the premaxilla compared to the slender maxillary ramus. In a section taken at the anterior extent of the nasoantorbital fenestra, the dorsal premaxillary extension is >1.8 times the height of the maxillary ramus in azhdarchids (Cai and Wei 1994; Kellner and Langston 1996), whereas the same comparison in *Eopteranodon*, *Chaoyangopterus* and *Jidapterus* reveals posterodorsal premaxillary extensions and maxillary rami of sub-equal height (Wang and Zhou 2003; Dong *et al.* 2003; Lü and Zhang 2005). The flattening of *Lacusovagus* makes it difficult to measure the depth of these features accurately, but the slender nature of the maxillary ramus and apparent shallowness of the skull roof indicate a condition more akin to that of *Chaoyangopterus*-like azhdarchoids than that of azhdarchids.

The short rostrum of *Lacusovagus* is unlike that of most other azhdarchoids in forming <37 per cent of the preserved jaw length (Table 2). A similar ratio is seen in tapejarids, where rostra occupy 24–38 per cent of total jaw length (e.g. Wellnhofer and Kellner 1991; Campos and Kellner 1997), but this condition stems from the derived, truncated snouts typical of this group. *Lacusovagus* does not have an atypically shortened snout however, rendering it more comparable with neoazhdarchians and the *Chaoyangopterus*-like azhdarchoids. Among these forms, azhdarchids have the longest rostra at 52–65 per cent of their jaw lengths (Cai and Wei 1994; Kellner and Langston 1996), thalassodromids have rostral lengths 39–45 per cent of their jaw lengths (e.g. Kellner and Campos 2002) and the rostra of *Jidapterus* and *Chaoyangopterus* form approximately 50 per cent of their jaw lengths (Wang and Zhou 2003; Dong *et al.* 2003). Amongst these forms, *Lacusovagus* is most similar to thalassodromids but probably bears an even shorter rostrum than these forms. The incompleteness of SMNK PAL 4325 only permits a minimal rostrum:jaw length to be established and implies that *Lacusovagus* had a rostrum occupying less than the 37 per cent of jaw length preserved here. Correspondingly, the nasoantorbital fenestra of *Lacusovagus* is atypically and perhaps diagnostically large for a non-tapejarid edentulous pterosaur. Unfortunately, precisely quantifying

the size of this fenestra is not possible due to the fragmentary nature of SMNK PAL 4325, but its 63 per cent occupancy of the jaw length may approximate the condition in a complete skull given the apparent completeness of the jaw. More complete cranial material of this taxon may permit the use of this feature in distinguishing *Lacusovagus* from other straight-jawed, edentulous pterosaurs.

Observed in lateral view, SMNK PAL 4325 appears to have a relatively straight jawline that is shared with azhdarchids, thalassodromids and *Chaoyangopterus*-like azhdarchoids. This condition strongly contrasts with the jaw profile of tapejarids that often bear pronounced ventral-deflection of their jawlines at the rostral tip (e.g. Wellnhofer and Kellner 1991; Campos and Kellner 1997; Wang and Zhou 2002). The lateral splaying of the *Lacusovagus* jawline, however, is markedly different from all azhdarchoids in which this condition is discernable (Text-fig. 4). *Tapejara*, thalassodromids and *Quetzalcoatlus* all show gradual, linear tapering of their skulls in dorsal view (e.g. Wellnhofer and Kellner 1991; Kellner and Langston 1996; MPW, pers. obs. 2007) that contrast with the varying degrees of lateral deflection seen along the jaws of *Lacusovagus*. The mandible of the azhdarchid *Bakonydraco* also exhibits variable lateral splay along its jaw margins (Ósi *et al.* 2005), albeit not to the extent observable in *Lacusovagus*. Although all skulls of the *Chaoyangopterus*-like azhdarchoids are preserved in lateral view, both *Jidapterus* and *Chaoyangopterus* show pronounced changes in jaw orientation along the maxillary ramus that may be indicative of lateral jawline flaring akin to that of *Lacusovagus* (Dong *et al.* 2003; Wang and Zhou 2003). However, this possible lateral jaw deflection is not evident in the mandibular profile of *Jidapterus* and, furthermore, the jaws of this taxon and *Eoazhdarcho* appear to be about 30 per cent narrower than the Brazilian form (Table 2; Dong *et al.* 2003; Wang and Zhou 2003; Lü and Ji 2005). A range of relative jaw widths is evident throughout Azhdarchoidea, with broad-jawed forms like *Bakonydraco* and *Tapejara* having jaw widths 22 and 34 per cent of their jaw lengths, respectively, whereas *Quetzalcoatlus* has a jaw width only 11 per cent of its jaw length (Wellnhofer and Kellner 1991; Kellner and Langston 1996; Ósi *et al.* 2005). Because the posteriormost region of the jaw is not preserved in *Lacusovagus*, the actual ratio of jaw width:length cannot be precisely determined. However, the slight medial expansion of the maxillary ramus at the posterior extent of its preserved length indicates that much of the nasoantorbital fenestra is preserved: if the posterior margin of this fenestra approximates the jaw joint, 29 per cent approximates a realistic jaw width:length ratio for *Lacusovagus*. Compared to other azhdarchoids, this figure is only surpassed by *Tapejara*, but this large ratio is a consequence of its abbreviated jaw length rather than exaggerated skull width.

Position within Azhdarchoidea. Although *Lacusovagus* shares some morphological features with other azhdarchoids, it cannot be satisfactorily placed in any currently recognised azhdarchoid clade. The low rostrum and absence of a ventrally deflected jaw tip excludes *Lacusovagus* from Tapejaridae, and a thalassodromid placement is ruled out through the lack of a laterally compressed rostrum and premaxillary crest. Furthermore, the specimen is not referable to Azhdarchidae because of its short rostrum, expansive nasoantorbital fenestra, and slender posterodorsal extension of the premaxillae.

The greatest similarity is seen between *Lacusovagus* and the straight-jawed azhdarchoids of the Jiufotang Formation, particularly *Chaoyangopterus* and *Jidapterus*. Like *Lacusovagus*, these pterosaurs have shallow, crestless rostra, a posterodorsal premaxillary process and maxillary bar of sub-equal height and, possibly, laterally flared jaw margins (e.g. Dong *et al.* 2003; Wang and Zhou 2003). Based on these similarities, it is suggested that they represent the closest known relatives to *Lacusovagus*, although the short rostrum of the new taxon remains distinctive among these forms. Unfortunately, this affinity sheds little light on the position of *Lacusovagus* within Azhdarchoidea because the systematics of the *Chaoyangopterus*-like azhdarchoids are not well resolved (see discussion above). Both the apparent absence of notaria and limb bone proportions of the Jiufotang Formation azhdarchoids show affinities to tapejarids (e.g. Kellner 2004; Lü *et al.* 2006; M. P. Witton, unpublished data) and may suggest a placement among basal azhdarchoids. Conversely, the long, straight jaws and elongate cervical vertebrae of the Jiufotang forms suggest affinities to more derived neoazhdarchians. Based on this combination of plesiomorphic and derived characters, it is suggested that *Lacusovagus* and the *Chaoyangopterus*-like azhdarchoids represent a pterosaur grouping that belongs between Tapejaridae and Neoazhdarchia, but further work is needed to determine whether these animals comprise a series of outgroups to other neoazhdarchian clades (as suggested by Lü and Ji 2006) or a distinct, monophyletic clade within Azhdarchoidea. The presence of an azhdarchoid with possible neoazhdarchian affinities in the Crato Formation suggests the pterosaur postcrania referred to thalassodromids by Unwin and Martill (2007) may be referable to *Lacusovagus*, although more complete specimens are needed to verify this possibility.

Taphonomy

Crato Formation pterosaurs have a rather unusual and poorly understood taphonomy. No mandibles are associated with the six azhdarchoid skull specimens known from this horizon (including privately accessioned

Tupandactylus material; D. Martill, pers. comm. 2007) despite the occurrence of mandibles in Crato Formation ornithocheirids (Sayao and Kellner 2000; Frey *et al.* 2003a). No pterosaur skulls are known with associated postcranial remains but their isolated elements are often preserved in excellent condition with articulated joints and, occasionally, soft tissues (e.g. Frey *et al.* 2003c). Crato pterosaur skulls are almost invariably preserved in lateral view and, despite the disassociation from their mandibles in toothless forms, are otherwise complete (note that the exception of the Crato *Brasileodactylus* is almost certainly a consequence of collection rather than fragmentation prior to burial). In this regard, the remains of *Lacusovagus* are unique in being both fragmentary and preserved in dorsoventral orientation. The matrix-obscured fractures associated with the right maxillary ramus show that the skull was incomplete prior to burial, and this fragmentation may account for its unusual orientation compared to the complete pterosaur skulls known from the same sequence. The broad jaw of the skull may also have influenced the ventral settling of the skull on a flat bedding surface: all Crato Formation pterosaur skulls show this characteristic of settling on their broadest surface. It is noteworthy that skull material of other *Chaoyangopterus*-like forms are broken in the same fashion across the nasoantorbital fenestra as SMNK PAL 4325 (e.g. Dong *et al.* 2003; Wang and Zhou 2003; Lü and Zhang 2005). This congruent taphonomy may reflect a common susceptibility to post-mortem damage in the skulls of these pterosaurs brought on by the combination of an expansive nasoantorbital fenestra and relatively slender maxillary and premaxillary bars.

Palaeobiological implications of *Lacusovagus*

The affinities of *Lacusovagus* to the Jiufotang Formation azhdarchoids heightens the similarities in pterosaur faunas observed between the Jehol and Araripe groups at broad taxonomic levels, an observation already recorded through ornithocheirids, ctenochasmatids, and tapejarids (Wang *et al.* 2005; Wang and Zhou 2006). A broad range of pterosaurs are found across the Jehol Group with a pronounced turnover occurring across the Barremian/Aptian boundary (Wang and Zhou 2006). Therefore, it is perhaps unsurprising that the Crato Formation pterosaur fauna is most comparable with that of the roughly contemporaneous Jiufotang Formation, with both bearing tapejarids, ornithocheirids and *Chaoyangopterus*-like azhdarchoids. Istiodactylidae, a group that appears relatively widespread across Lower Cretaceous Laurasia and abundant in the Jiufotang Formation (e.g. Hooley 1913; Andres and Ji 2006), however, is notably missing from Gondwana at this

time. With only a solitary humerus from the Aptian Elrhaz Formation of Nigeria (Blackburn 2002) documenting the occurrence of non-azhdarchid azhdarchoids in Lower Cretaceous in non-lagerstätten deposits, the discovery of another link between the pterosaur assemblages of the Jehol and Crato formations provides an important contribution to understanding the palaeobiogeography of pterosaurs during the Lower Cretaceous.

A further pattern highlighted by *Lacusovagus* is the comparatively large size and, in some cases, elaborate cranial crests of the Crato azhdarchoids compared to their relatives in the Jiufotang Formation. This may reflect contrasting ontogenetic biases in preservation between these two localities: the small-bodied Jiufotang azhdarchoids have bone textures typical of immature individuals (D. Unwin, pers. comm. 2007) that suggests the Jiufotang Formation pterosaur assemblage is predominately comprised of immature individuals, much like the pterosaur assemblage of the Jurassic Solnhofen lagerstätte (e.g. Bennett 1995, 1996). The Crato Formation, by contrast, appears to record osteologically mature individuals that have achieved large adult body size and, in tapejarids, strikingly elaborate cranial crests. As both larger body size and cranial crest development are related to maturity (see Bennett 1992), the different ontogenetic biases in preservation in these two assemblages provides a potential explanation for the small size and reduced ornament of the Jiufotang azhdarchoids compared to their larger, cranially elaborate Crato relatives.

The osteological maturity of *Lacusovagus* has implications for the ontogeny of azhdarchoids. Work by Bennett (1992, 2002, 2003) and Martill and Naish (2006) has demonstrated that pterosaur cranial crests underwent rapid allometric growth late in ontogeny, raising the possibility that osteologically immature, crestless forms such as *Chaoyangopterus* and *Jidapterus* may be immature individuals of adults that bore rostral crests. However, the size, maturity and absence of a rostral crest in *Lacusovagus* demonstrates that at least some *Chaoyangopterus*-like pterosaurs did not develop rostral crests at maturity. However, the absent or poorly preserved crania of all *Chaoyangopterus*-like azhdarchoids prohibits comment on supraoccipital crests.

Lacusovagus represents the largest pterosaur yet known from the Crato Formation by some margin. Excluding *Lacusovagus*, the largest azhdarchoid from the Crato Formation is *Tupandactylus imperator*, which has a skull length of 800 mm, although much of this is represented by a posteriorly directed bar that forms the supraoccipital ramus of the headcrest. By contrast, the length from jaw tip to quadrate only occupies 390 mm of the skull length of *T. imperator*. The ornithocheirid *Ludodactylus sibiricki*, currently the largest ornithocheirid from the Crato Formation, has a similar jaw length of 420 mm. The minimum 655 mm jaw length of *Lacusovagus* dwarfs both these forms in being 67

and 55 per cent longer, respectively. Although it is difficult to estimate the total size of *Lacusovagus* from such fragmentary remains, its jaw length almost rivals that of the large thalassodromid *Thalassodromeus* from the Santana Formation. This form is estimated to have a wingspan of 4.2–4.5 m (Kellner and Campos 2002), and comparisons with *Lacusovagus* skull dimensions with *Jidapterus* suggest a similar wingspan (4.1 m). Hence, *Lacusovagus* not only equals the estimated 4–5 m wingspans of the Crato ornithocheirids *Arthurdactylus* and *Ludodactylus* (Frey and Martill 1994; Unwin and Martill 2007), but would probably stand much taller than them when grounded. Assuming that *Lacusovagus* had limb proportions similar to those of other azhdarchoids (e.g. Dong *et al.* 2003; Wang and Zhou 2003), it would stand over 1 m at the shoulder, twice the height of an ornithocheirid with the same wingspan.

Acknowledgements. Thanks to Dino Frey (SMNK) for loan of the specimen; David Martill, Darren Naish, Richard Hing (University of Portsmouth), Chris Bennett (Fort Hays State University) and David Unwin (University of Leicester) for helpful discussion, criticism and advice on the manuscript; Robert Loveridge (University of Portsmouth) for assistance with photography.

NOTE ADDED IN PROOF

Since this work was accepted for publication, a cladistic analysis by Lü *et al.* (2008) has formalised Chaoyangopteridae, a clade containing the 'straight-jawed Jiufotang azhdarchoids' frequently referred to in this paper: *Chaoyangopterus*, *Jidapterus*, *Eoazhdarcho* and *Eopteranodon*. This group, closely related to Azhdarchidae and Thalassodromidae, is characterised by an unusually slender posterodorsal extension of the premaxillary bar over the nasoantorbital fenestra and extension of the same opening beyond the jaw joint. The latter feature cannot be determined in SMNK PAL 4325, but the former character suggests placement of *Lacusovagus* within Chaoyangopteridae. A cladistic analysis containing *Lacusovagus* supports placement of the new taxon in Chaoyangopteridae (M. P. Witton, unpublished data), but was performed too late for inclusion in this project.

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