[Palaeontology, Vol. 49, Part 4, 2006, pp. 925–941]

CRANIAL CREST DEVELOPMENT IN THE AZHDARCHOID PTEROSAUR *TUPUXUARA*, WITH A REVIEW OF THE GENUS AND TAPEJARID MONOPHYLY

by DAVID M. MARTILL *and* DARREN NAISH

Palaeobiology Research Group, School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK; e-mails: david.martill@port.ac.uk; darren.naish@port.ac.uk

Typescript received 15 June 2004; accepted in revised form 8 July 2005

Abstract: A portion of pterosaur skull from the Romualdo Member of the Santana Formation (?Albian–?Turonian, Cretaceous) of north-east Brazil provides new data on the morphology and ontogeny of azhdarchoid pterosaur cranial crests. The specimen consists of parts of the cranial bones posterodorsal to the nasoantorbital fenestra, including partial nasals, lacrimals, frontals and possibly the parietals. A posterodorsally directed premaxillary crest with a concave posterior border is located dorsal to the posterior border of the nasoantorbital fenestra. A well-defined suture indicates overlapping, posterodorsally directed growth of the premaxilla over the skull roof, suggesting that the generation of the premaxillary crest is a late ontogenetic feature and thus probably related to sexual display. The systematics of *Tupuxuara* and its relationship to other azhdarchoids is reviewed and a cladistic analysis of the group is presented. *Tupuxuara* is found to be the sister-taxon to Azhdarchidae. *Tupuxuara longicristatus* Kellner and Campos, 1988 is argued to be the only valid named species in this genus and *Thalassodromeus* Kellner and Campos, 2002 is considered a junior subjective synonym of this taxon. As originally conceived, Tapejaridae is paraphyletic: a new, more restrictive version of Tapejaridae (including *Tapejara* and *Sinopterus dongi*) might exist, but its monophyly is weakly supported. Furthermore, *Tapejara* was found to be paraphyletic in all trees.

Key words: Pterosauria, Azhdarchoidea, *Tupuxuara*, ontogeny, Cretaceous, Santana Formation, Brazil.

CRANIAL crests of pterodactyloid pterosaurs have always drawn attention owing to their size and morphology, and a considerable number of attempts have been made to explain their function. It has been proposed that they may have functioned aerodynamically (Heptonstall 1971; Bramwell and Whitfield 1974; Stein 1975; Wellnhofer 1991*a*), in sexual display or species recognition (Bennett 1991, 1992, 2003; Campos and Kellner 1997), to enhance stability while feeding in water while on the wing (Wellnhofer 1987, 1991*a*; Frey *et al.* 2003*a–c*), or as loci for muscle attachment (Eaton 1910; Mateer 1975; Bennett 2001). Recently, pterosaurs have been discovered in which the bony part of the crest functioned as a support for soft tissue extensions, with the best examples being *Tapejara* from the Cretaceous Crato Formation of Brazil and *Pterodactylus* and *Germanodactylus* from the Jurassic Solnhofen Limestone of Germany (Martill 1993; Campos and Kellner 1997; Martill and Frey 1998; Frey and Tischlinger 2000; Bennett 2002; Frey *et al.* 2003*a*). Similar 'soft tissue' crests have been postulated for other dsungaripteroid and ctenochasmatoid taxa (Martill *et al.* 2000; Frey *et al.* 2003*a*) on the basis of fibrous structures within bony crests that lie perpendicular to the cranial dorsal surface.

Given that cranial crest location and morphology appears to be species-specific within pterosaurs, the presence of novel crest morphologies has been used to erect new taxa (Kellner and Tomida 2000; Frey *et al.* 2003*a*, *b*). However, some work indicates that pterosaur cranial crests were morphologically variable during ontogeny and may have been sexually dimorphic (Bennett 1992, 2002, 2003; Naish and Martill 2003; Frey *et al.* 2003*c*). They may, therefore, be of limited value in the identification of new taxa, except in those cases where large data sets permit the identification of probable ontogenetic and sexual variation. A new specimen described here, although fragmentary, displays a novel crest morphology that sheds some light on the growth and structure of the cranial crest in some azhdarchoids.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; CB, Borgomanero Collection, Curitiba, Brazil; FHSM, Fort Hays State Museum, Fort Hays State University, Hays, Kansas, USA; IMCF, Iwaki Coal and Fossil Museum, Iwaki, Japan; MCT and DGM, Museu de Ciências da Terra of the Departmento Nacional de Produção Mineral, Rio de Janeiro, Brazil; MN, Museu Nacional, Rio de Janeiro, Brazil; NSM, National Science Museum, Tokyo, Japan; SMNK, Staatlisches Museum für Naturkunde, Karlsruhe, Germany; MN, Museu Nacional, Rio de Janeiro, Brazil; TMM, Texas Memorial Museum, Austin, Texas, USA; UERJ, Universidade Estadual do Rio de Janeiro, Rio de Janeiro, Brazil; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

LOCALITY AND STRATIGRAPHY

The new specimen is deposited in the Staatliches Museum für Naturkunde Karlsruhe, specimen number SMNK PAL 3858. It was obtained through a commercial source and is believed to have been collected in the vicinity of Santana do Cariri in the south of the state of Ceará, Brazil (see Martill 1993 for discussion of locality and source of fossils).

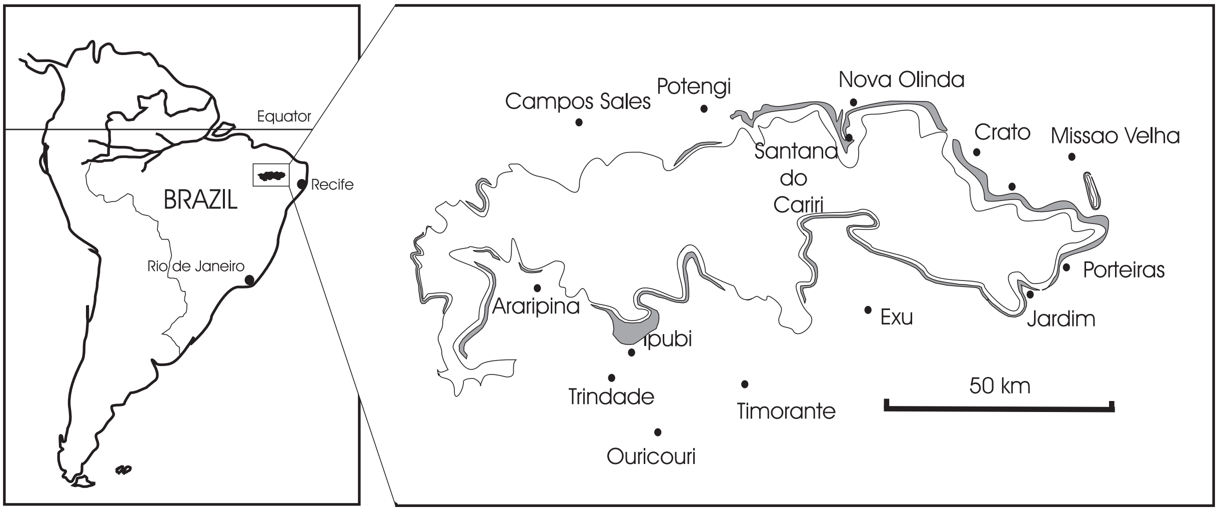
The matrix and source of the specimen are consistent with it having come from the nodule-bearing shales of the Romualdo Member of the Santana Formation of the Araripe Basin (Text-fig. 1). These highly fossiliferous strata are poorly age constrained, but are thought to be no older than early Albian (Pons and Berthou 1996) and possibly as young as Turonian (see Martill and Wilby 1993 for discussion of age and geology of these deposits). The Santana Formation has become famous for the diversity (17 named pterosaur species from the Romualdo Member, but probably taxonomically oversplit), abundance and quality of preservation of its pterosaurs and other fossil vertebrates (Maisey 1991; Wellnhofer 1991*b*; Martill 1993; Kellner and Tomida 2000). The remains occur in early diagenetic concretions and are frequently preserved in an uncrushed state (Martill 1988) and several have been reported with soft tissues preserved (e.g. Campos *et al.* 1984; Martill and Unwin 1989).

SYSTEMATIC PALAEONTOLOGY

PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Plieninger, 1901
LOPHOCRATIA Unwin, 2003
AZHDARCHOIDEA Nessov, 1984 (*sensu* Unwin, 1992)

Definition. Tapejara wellnhoferi, *Quetzalcoatlus northropi*, their most recent common ancestor and all its descendants (Unwin 2003, p. 169).

Remarks. This taxon has its origins in the subfamily Azhdarchinae, erected by Nessov (1984) to accommodate the long-necked pterodactyloids *Azhdarcho*, *Quetzalcoatlus* and *Titanopteryx* (= *Arambourgiania*). Though Nessov (1984) placed Azhdarchinae within Pteranodontidae Marsh, 1876, it later became clear that this was incorrect and that Azhdarchidae should be elevated to the rank of family (Padian 1986). Following the description of *Tapejara* and *Tupuxuara*, several authors proposed monophyly of a clade including these taxa and Azhdarchidae (e.g. Kellner and Langston 1996; Unwin and Lü 1997) and this has since been supported by cladistic analysis (e.g. Kellner 2003*a*, 2004a; Unwin 2003). The converted name Azhdarchoidea has been used for this clade, first by Unwin (1992) in an abstract and later in a preliminary analysis



TEXT-FIG. 1. Location of the Chapada do Araripe of the Araripe Basin in Brazil, with main towns. Grey shading indicates outcrop of Romualdo Member of the Santana Formation. For further details of the geology and stratigraphy, see Martill (1993).

(Unwin 1995). Two phylogenetic definitions have recently been published for Azhdarchoidea (Kellner 2003*a*, p. 125; Unwin 2003, p. 169), and fortunately both agree on the clade's membership. We employ Unwin's (2003) definition because this author coined the clade (Unwin 1992, 1995).

NEOAZHDARCHIA Unwin, 2003

Definition. Tupuxuara longicristatus, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants (Unwin 2003, p. 170).

Remarks. This taxon was erected by Unwin (2003, p. 170) to include *Tupuxuara* + Azhdarchidae. Kellner (1989) allied *Tupuxuara* with *Tapejara wellnhoferi* Kellner, 1989, also from the Santana Formation, in the new family Tapejaridae (because a more restrictive use of Tapejaridae is discussed below, we refer to Kellner's proposed *Tupuxuara* + *Tapejara* clade as 'Tapejaridae *sensu* Kellner'). Kellner (1989) proposed that tapejarid monophyly was supported by the presence of a large sagittal crest that extended posteriorly over the skull, a proportionally large nasoantorbital fenestra and a ventrally inclined rostrum. The description of a second species referred to *Tupuxuara*, *T. leonardii* Kellner and Campos, 1994 (see below), clearly lacked the third character and it was hence rejected as a tapejarid synapomorphy. This left only two characters in support of Tapejaridae *sensu* Kellner (Kellner 2003*a*) though more recently Kellner (2003*b*, 2004*a*) has proposed three further characters that might support its monophyly: a thin subvertical lacrimal process on the jugal, a comparatively small pear-shaped orbit and a broad tubercle on the ventroposterior margin of the coracoid. In addition to *Tapejara*, *Tupuxuara* and *Thalassodromeus sethi* Kellner and Campos, 2002, Kellner (2004*a*) regarded the recently described *Sinopterus dongi* Wang and Zhou, 2003 from the Lower Cretaceous Jiufotang Formation of western Liaoning, China, to belong within Tapejaridae *sensu* Kellner. A second pterosaur from the Jiufotang Formation, *Sinopterus gui* Li *et al.*, 2003, has also been suggested to be part of this group (Li *et al.* 2003) and we also note that the Jiufotang Formation taxa *Jidapterus edentus* Dong *et al.*, 2003 and *Chaoyangopterus zhangi* Wang and Zhou, 2003 might prove to be basal azhdarchoids.

Noting characters shared by *Tupuxuara* and Azhdarchidae, but not seen in *Tapejara*, Unwin and Lü (1997) and Unwin (2003) argued that Tapejaridae *sensu* Kellner was paraphyletic, with *Tupuxuara* being closer to Azhdarchidae than to *Tapejara*. Unwin (2003) named the *Tupuxuara* + Azhdarchidae clade Neoazhdarchia. In contrast to *Tapejara*, neoazhdarchians possess a notarium, exhibit loss of contact between metacarpals I–III and the distal syncarpal, and share a rostrum (measured from the anterior margin of the orbit to the premaxillary tip) more than 88 per cent of total skull length. Neoazhdarchian monophyly is not accepted in the pterosaur phylogeny of Kellner (2003*a*, *b*, 2004*a*) who argued that Unwin's neoazhdarchian synapomorphies are dubious and that, even when these characters are included within a cladistic analysis, the monophyly of Tapejaridae *sensu* Kellner is still supported.

Our assessment of the character evidence used to support these competing views has led us to favour neoazhdarchian monophyly as more characters support this clade than support monophyly of Tapejaridae *sensu* Kellner. As discussed below, we performed a new cladistic analysis incorporating the relevant characters, and consistently found Neoazhdarchia to be monophyletic.

With regard to the characters employed to support the monophyly of Tapejaridae *sensu* Kellner, the presence of a large sagittal crest that extends posteriorly over the skull is difficult to confirm as a character that is unique to Tapejaridae *sensu* Kellner as has been argued (Kellner 2003*a*, *b*, 2004*a*) given that few azhdarchids preserve the posterior part of the cranium. Furthermore, it is likely that at least some azhdarchids did possess this character: Kellner and Langston (1996, p. 229) figured a sagittal crest in *Quetzalcoatlus* sp. that, when complete, presumably extended dorsoposteriorly over the cranium. Furthermore, Unwin and Lü (1997) and Unwin (2003) argued that the crest morphology of *Tapejara* and *Tupuxuara* is markedly different in detail and that this crest morphology is widely distributed in lophocratian pterodactyloids. (Unwin's character 48: this codes for the presence of a sagittal crest that incorporates soft tissues. We feel that soft and bony sagittal crests are homologous.) It is conceivable that sagittal crests of this type are even more widely distributed within Pterosauria if the description of such crests in non-pterodactyloids is valid (Czerkas and Ji 2002), and if soft tissue and bony crests are homologous, as seems to be the case.

Kellner's (1989, 2003*a*, 2004*a*) second proposed synapomorphy uniting *Tapejara* and *Tupuxuara* concerns the size of the nasoantorbital fenestra relative to the total skull length. Supposedly, members of Tapejaridae *sensu* Kellner possess a nasoantorbital fenestra 45 per cent or more of total skull length, with skull length defined as from the tip of the premaxilla to the squamosal (Kellner 2004*a*, p. 522). However, it is clear that tapejarids *sensu* Kellner and azhdarchids cannot be reliably differentiated in this way: in both *Sinopterus dongi* and *Zhejiangopterus* the nasoantorbital fenestra is *c.* 45 per cent of the total skull length, for example. We thus reject this character as a synapomorphy of Tapejaridae *sensu* Kellner. By recalculating the proportional length of the nasoantorbital fenestra to skull length (measured from the tip of the premaxilla to the posteriormost margin of the orbit), we found almost continuous variation in this character (Table 1). The greatest difference was not between tapejarids *sensu* Kellner and azhdarchids, but between *Zhejiangopterus* and *Quetzalcoatlus*. Importantly, the difference between *Zhejiangopterus* and *Sinopterus dongi* was less than that between *Tupuxuara longicristatus* and *Tapejara imperator*.

Of Kellner's (2004*a*) three new possible synapomorphies, it is unclear if the presence of a thin subvertical lacrimal process on the jugal truly is present in, and unique to, Tapejaridae *sensu* Kellner. In some specimens referred to this group the same process is no thinner than it is in other lophocratians. That seen in *Tapejara navigans* (Frey *et al.* 2003*a*), for example, is not notably thin, nor is that in *Sinopterus dongi* (Wang and Zhou 2003). The second character proposed recently to support monophyly of Tapejaridae *sensu* Kellner, presence of a comparatively small pear-shaped orbit, is also absent in *Sinopterus dongi* and *Tapejara navigans* where the orbit is the same shape as that figured for *Quetzalcoatlus* sp. (Kellner and Langston 1996; Frey *et al.* 2003*a*; Wang and Zhou 2003). Despite Kellner's objections (2004*a*, p. 524) it is almost impossible to differentiate satisfactorily this pear-like orbit shape from that present in some ornithocheiroids and ctenochasmatoids. Finally, it is difficult to evaluate Kellner's (2004*a*) proposed synapomorphy 'well developed and broad tubercle situated at the ventroposterior margin of the coracoid' (p. 524) given that, in our examination of azhdarchoid scapulocoracoidea, we have been unable to identify this character, nor has it been figured in the literature. We are therefore unable to assess the utility of this character at present.

TABLE 1. Nasoantorbital fenestra ratios for azhdarchoid pterosaurs. Ratios were determined by dividing maximum length of nasoantorbital fenestra into total length of skull (defined from tip of premaxilla to posteriormost margin of orbit). 'Difference' refers to that between the ratio of the taxon and the taxon above it in the table. Data derived from skull diagram references given in table.

Taxon	Ratio	Difference
Quetzalcoatlus sp. Kellner and Langston (1996, fig. 7)	3·00	×
Zhejiangopterus linhaiensis Unwin and Lü (1997, fig. 1)	2·25	0·75
Sinopterus dongi Wang and Zhou (2003, fig. 1)	2·16	0·09
Tapejara wellnhoferi Wellnhofer and Kellner (1991, fig. 4)	2·02	0·14
Thalassodromeus sethi Kellner and Campos (2002, fig. 1)	2·00	0·02
Tapejara navigans Frey *et al.* (2003*a*, fig. 1)	1·96	0·04
Tupuxuara longicristatus Kellner (2004*a*, fig. 4)	1·79	0·17
Tapejara imperator Campos and Kellner (1997, fig. 2)	1·61	0·18

In examining the validity of the characters used by Unwin (2003, p. 170) to support neoazhdarchian monophyly, use of the presence of a notarium as a synapomorphy for this group raises some problems, as discussed by Kellner (2004*a*, p. 525). Although we agree with Unwin (2003) that the notarium probably evolved independently several times within Pterodactyloidea, its absence in *Tapejara* does not demonstrate that this taxon lacked this structure given that all reported *Tapejara* postcranial material belongs, apparently, to juveniles (Kellner 2004*a*, p. 525). The convincing application of this character must therefore await the discovery of postcranial material of adult *Tapejara*. Unwin (2003) also proposed that neoazhdarchians were united by loss of contact between metacarpals I–III and the distal syncarpal. Unfortunately, as noted by Kellner (2004*a*, p. 525), Unwin (2003, his character 37) coded *Tupuxuara* with '?' for this character, thus apparently negating its use as a neoazhdarchian synapomorphy. However, based on examination of unpublished postcranial material referred to *Tupuxuara* we can confirm that this character is present in this taxon, and we accept it as a potential neoazhdarchian synapomorphy.

Unwin (2003) also proposed that neoazhdarchians share a rostrum (measured from the anterior margin of the orbit to the premaxillary tip) more than 88 per cent of total skull length. Kellner's counter-argument (2004*a*, p. 525) was that this ignored the fact that *Tupuxuara* exhibits a proportionally larger nasoantorbital fenestra than do members of Azhdarchidae, and that the part of the skull rostral to the fenestra is, in *Tupuxuara*, more similar to that of *Tapejara* than to that of any azhdarchid. We tested this by calculating the height : length ratio of the rostrum across pterodactyloid taxa, the resulting measurement being termed the rostral index (RI) (Table 2). This is derived by dividing the vertical height of the rostrum immediately anterior to the nasoantorbital fenestra into the length of the rostrum measured from the tip of the premaxilla to the nasoantorbital fenestra (Text-fig. 2).

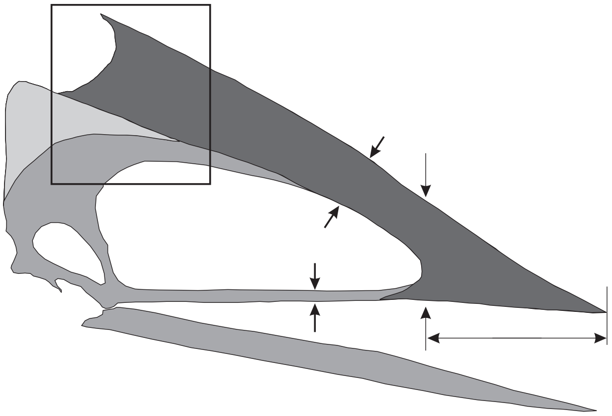
The resulting values range from less than 1 in some species of *Tapejara* to 10 in *Pteranodon sternbergi* (Text-fig. 3). Among azhdarchoids, the data do not support Kellner's (2004*a*, p. 525) contention that *Tupuxuara* is more like *Tapejara* than it is like azhdarchids: instead, RI values reveal a continuum, ranging from *Tapejara* (RI values, 0·51–0·65), through *Tupuxuara* (RI values, 1·65–2·45), to azhdarchids (RI values, 4·36–7·33). The partial Javelina Formation skull TMM 42489-2, referred by Wellnhofer (1991*a*, p. 144) to *Quetzalcoatlus* sp. but noted by Kellner and Langston (1996, p. 230) and Kellner (2004*a*, p. 529) to not belong to this taxon, has an RI of 2·45 and is thus more similar to *Tupuxuara* than to *Quetzalcoatlus*.

TABLE 2. Rostral indices of selected pterosaurs. The nomenclature of ornithocheirids is confused: we refer NSM-PV 19892 (holotype of *Anhanguera piscator*) to *Coloborhynchus robustus* and BSP 1987 I 46 (holotype of *Tropeognathus mesembrinus*) to *Ornithocheirus* following Unwin (2003, p. 178). See text for discussion and Text-figure 2.

Taxon	Rostral index	Reference
Ornithocheirus mesembrinus BSP 1987 I 46	6·2	Kellner and Tomida (2000)
Anhanguera araripensis MN 4735-V	7·4	Kellner and Tomida (2000)
Anhanguera blittersdorfi MN 4805-V	6·33	Kellner and Tomida (2000)
Anhanguera blittersdorfi n. 40 Pz-DBAV-UERJ	7·14	Kellner and Tomida (2000)
Anhanguera santanae AMNH 22555	3·43	Kellner and Tomida (2000)
Coloborhynchus robustus NSM-PV 19892	6	Kellner and Tomida (2000)
Ludodactylus sibbicki SMNK PAL 3828	4	Frey *et al.* (2003)
Pteranodon longiceps (composite)	7·77	Eaton (1910)
Pteranodon sternbergi FHSM VP 339	10	Wellnhofer (1991*a*)
Cearadactylus atrox CB-F-PV-93	3·89	Kellner and Tomida (2000)
Tapejara navigans SMNK PAL 2344	0·65	Frey et al. (2003*a*)
Tapejara navigans SMNK PAL 2343	0·6	Frey et al. (2003*a*)
Tapejara wellnhoferi AMNH 24440	0·51	Wellnhofer and Kellner (1991)
Tupuxuara longicristatus MN 6591-V	1·92	Kellner and Campos (1988)
Tupuxuara longicristatus IMCF 1052	1·65	Kellner (2004*a*)
Thalassodromeus sethi DGM 1476-R	1·48	Kellner and Campos (2002)
Javelina *Tupuxuara* TMM 42489–2	2·45	Wellnhofer (1991*a*, p. 144)
Zhejiangopterus linhaiensis ZMNH M1323	4·36	Unwin and Lü (1997)
Quetzalcoatlus sp. TMM 41954–62	7·33	Kellner and Langston (1996)

The specimen exhibits a morphology similar (though not identical) to that regarded here as diagnostic for *Tupuxuara longicristatus* (see below) and appears to represent a closely related taxon. Importantly, the difference in RI between this specimen and the azhdarchid *Zhejiangopterus* (difference, 1·91) is not significantly greater than the difference in RI between the Javelina Formation specimen and *Tapejara navigans* (difference, 1·8). The RI data therefore show that *Tupuxuara* does not group obviously closer to *Tapejara* based on rostrum proportions (contra Kellner 2004*a*), but that *Tupuxuara* is intermediate in RI between *Tapejara* and Azhdarchidae. Furthermore, RI is variable within taxa (e.g. in *Tupuxuara* it ranges from 1·65 to 2·45), presumably due to ontogeny.

It should also be noted that several other characters, conventionally regarded as azhdarchid apomorphies (Unwin 2003, p. 181), appear (based on our examination of unpublished specimens) to be present in *Tupuxuara* and may also prove to be neoazhdarchian synapomorphies. These include a neural arch that merges with the centrum, a proportionally short wing finger, a T-shaped cross-section on the second and third wing phalanges, and a proportionally long femur. We also note that *Tapejara* lacks the median palatal ridge present in *Tupuxuara* and some members of Azhdarchidae. Confirmation of the presence of the respective postcranial characters awaits a full description of *Tupuxuara* material. In conclusion, our evaluation indicates that the case for neoazhdarchian monophyly is stronger than that for the monophyly of Tapejaridae *sensu* Kellner.



TEXT-FIG. 2. Relative position of SMNK PAL 3858 (see below) on outline of skull of *Tupuxuara*. Dark grey shading represents the combined premaxilla and maxilla, while lightest grey represents crest developed from frontoparietals. Faint arrows indicate dimensions used for determining rostral index (RI) (see Table 2). Bold arrows indicate part of the diagnostic morphology for *Tupuxuara longicristatus*: the rostrum dorsal to the anterior part of nasoantorbital fenestra is approximately four times deeper than the maxillary-jugal bar (see diagnosis).

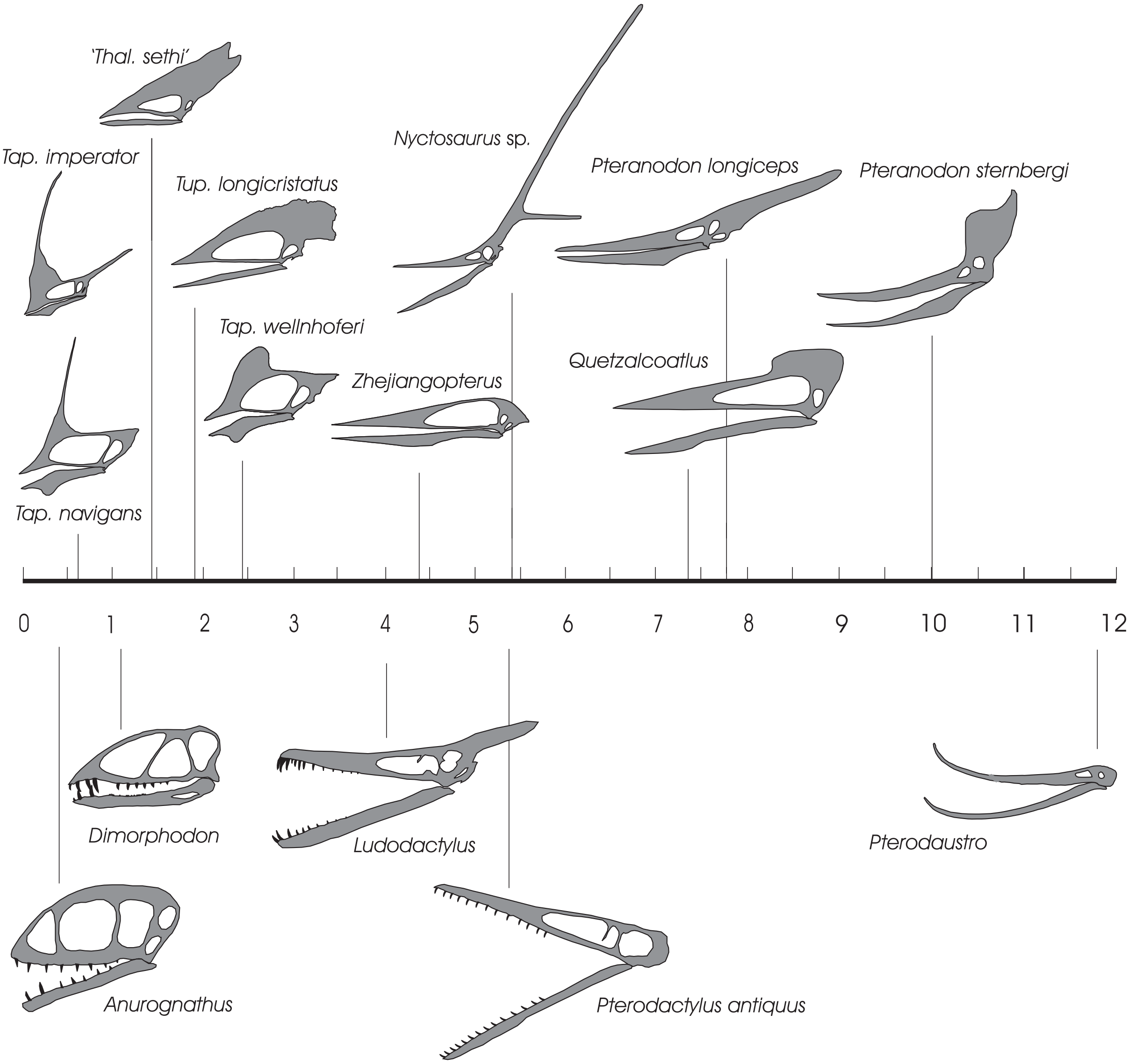
However, *Sinopterus dongi* exhibits several characters seen elsewhere only in *Tapejara*. These include a ventrally deflected tip to the premaxillary rostrum, a finger-like crest that projects posterodorsally from the parietal and a distinct ventral dentary crest (Wang and Zhou 2003; Kellner 2004*a*). *Sinopterus gui* Li *et al.*, 2003 exhibits the ventrally deflected rostrum and ventral dentary crest but is less well preserved: it may also be a close relative of *Tapejara* but this is difficult to confirm. The characters shared by *Tapejara* and *Sinopterus dongi* could be synapomorphies of a new clade for which the term Tapejaridae could be co-opted: a potential definition for this clade could be 'all azhdarchoids closer to *Tapejara wellnhoferi* than to *Quetzalcoatlus northropi*' (a stem-based definition is preferred given that it would be logical to include new *Tapejara*-like taxa that lie outside of the *Sinopterus dongi* + *Tapejara wellnhoferi* clade within Tapejaridae). As discussed below, in our cladistic analysis monophyly of this restrictive Tapejaridae was supported in some (but not all) most parsimonious trees. We therefore reject Kellner's (2003*a*, p. 125) proposed phylogenetic definition of Tapejaridae as 'the most recent common ancestor of *Tapejara* and *Tupuxuara* and all their [*sic*] descendants', because, if neoazhdarchian monophyly is upheld, Tapejaridae in this sense is synonymous with Azhdarchoidea.

Genus TUPUXUARA Kellner and Campos, 1988

Type species. Tupuxuara longicristatus Kellner and Campos, 1988.

Diagnosis. As for the type species (see below).

Discussion. This genus was erected by Kellner and Campos (1988) to accommodate *Tupuxuara longicristatus*, an edentulous longirostrine pterosaur of uncertain affinities



TEXT-FIG. 3. Selected pterosaur taxa plotted along a scale of rostral indices. Edentulous forms above the scale, toothed forms below. Figures not to scale.

from the Santana Formation of Brazil. A new azhdarchoid taxon, *Thalassodromeus sethi* Kellner and Campos, 2002, is regarded here as a junior subjective synonym of *Tupuxuara longicristatus* (see below).

Tupuxuara longicristatus Kellner and Campos, 1988

1988 *Tupuxuara longicristatus* Kellner and Campos, p. 460, figs 1–4.
1989 *Tupuxuara longicristatus* Kellner and Campos; Kellner, p. 441.
1991 *Tupuxuara longicristatus* Kellner and Campos; Wellnhofer and Kellner, p. 90.
1991 *Tupuxuara longicristatus* Kellner and Campos; Kellner, p. 371.
1994 *Tupuxuara leonardii* Kellner and Campos, p. 468; figs 1–7.
1994 *Tupuxuara longicristatus* Kellner and Campos; Frey and Martill, p. 403.
1999 *Tupuxuara leonardii* Kellner and Campos; Wellnhofer and Buffetaut, p. 137.
2000 *Tupuxuara leonardii* Kellner and Campos; Kellner and Tomida, p. 1.
2000 *Tupuxuara longicristatus* Kellner and Campos; Kellner and Tomida, p. 94.
2002 *Thalassodromeus sethi* Kellner and Campos, p. 389; figs 1–2.
2003*a* *Tupuxuara cristata* Kellner and Campos; Frey *et al.*, p. 69, fig. 4.
2003*a* *Tupuxuara leonardii* Kellner and Campos; Kellner, p. 125.
2003*b* *Tupuxuara leonardii* Kellner and Campos; Kellner, p. 32.
2003*b* *Thalassodromeus sethi* Kellner and Campos; Kellner, p. 35.
2003 *Tupuxuara longicristatus* Kellner and Campos; Unwin, p. 145.
2003 *Tupuxuara leonardii* Kellner and Campos; Unwin, p. 145.
2004 *Tupuxuara leonardii* Kellner and Campos; Averianov, p. 434.
2004*a* *Tupuxuara longicristatus* Kellner and Campos; Kellner, p. 521.
2004*a* *Tupuxuara leonardii* Kellner and Campos; Kellner, p. 522, fig. 4.
2004*a* *Thalassodromeus sethi* Kellner and Campos; Kellner, p. 524, fig. 5.
2004*b* *Tupuxuara leonardii* Kellner and Campos; Kellner, p. 27. fig. 2.1.

Holotype. Partial skull (comprising partial premaxilla and anterior portion of maxilla with the incomplete rim of the nasoantorbital fenestra), metacarpal IV, left and right phalanges IV-1; specimen number MN 6591-V (taxon originally erected when specimen was housed in private collection as Coleção Desirée CD-R-003; Kellner and Campos 1988, p. 460).

Stratotype. Romualdo Member, Santana Formation (?Albian–?Turonian, Cretaceous).

Locality. Recorded only as from the flanks of the Chapada do Araripe, probably Ceará State, north-east Brazil.

Revised diagnosis. Rostrum dorsal to anterior part of nasoantorbital fenestra approximately four times deeper than maxillary-jugal bar (Text-fig. 2), with dorsal and ventral margins of dorsal process parallel, extending in parallel fashion posteriorly to mid-length of nasoantorbital fenestra.

Discussion. The type species of *Tupuxuara*, *T. longicristatus*, was based on fragmentary cranial material and associated long bones. Based on the type material, the validity of the genus is in some doubt as the features cited in the original diagnosis by Kellner and Campos (1988) are insufficient to distinguish *Tupuxuara* satisfactorily from other members of Azhdarchoidea.

Kellner and Campos (1988, p. 460) initially diagnosed *T. longicristatus* on the basis of a sagittal crest that originates on the rostral part of the premaxilla and projects posteriorly, edentulousness, presence of a median palatal ridge, presence of long and slim wing phalanges, and the presence of two pneumatic foramina located on the proximal articular surface of phalanx IV-1. In an emended diagnosis, Kellner (1991) cited as diagnostic for *T. longicristatus* a low sagittal crest on the anterior skull extending posteriorly, a horizontal rostrum (this is taken to mean the ventral margin of the maxilla and premaxilla) and a median ridge on the palate.

Of these purported diagnostic features, the presence of a low sagittal crest on the anterior skull of *T. longicristatus* extending posteriorly is not unique to this taxon as other azhdarchoids exhibit a sagittal crest that can be described in this way (e.g. *Tapejara imperator* Campos and Kellner, 1997; *Sinopterus dongi* Wang and Zhou, 2003) and a horizontal ventral margin to the premaxilla and maxilla is also present elsewhere in Azhdarchoidea (e.g. in *Zhejiangopterus* and *Quetzalcoatlus*). Regarding the median palatal ridge, although Kellner and Langston (1996) claimed that this feature is not present in *Quetzalcoatlus*, its presence cannot be ruled out for this taxon as the cranial material is highly crushed and difficult to decipher (E. Frey, pers. comm. 2002). Note that Kellner's (1989) specific mention of the absence of a median palatal ridge in *Tupuxuara* is erroneous. Median palatal ridges appear to have arisen independently several times within Pterodactyloidea, being present in Ornithocheiridae, *Dsungaripterus*, Lonchodectidae, *Gnathosaurus* and Azhdarchoidea (Nessov 1984; Bennett 1994, 2001; Unwin 2001, 2003) and, within some taxa that possess them, they are reported to be variable in extent and size (e.g. *Azhdarcho* noted in Bakhurina and Unwin 1995). Use of the extent of the palatal ridge as a putative diagnostic character is therefore problematical. As discussed below, this has implications for the validity of the supposed species *Tupuxuara leonardii*.

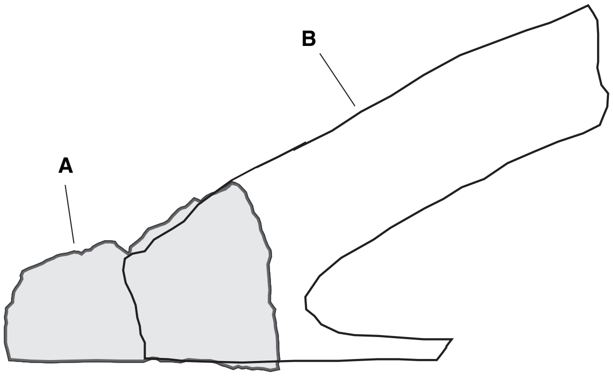
With regard to postcranial characters, Kellner (1991, p. 371) cited 'long and slender' first wing phalanx and metacarpal IV as diagnostic for *T. longicristatus*. While the terms 'long' and 'slender' are so vague that they cannot be considered diagnostic without some quantification, it does appear correct (based on examination of unpublished specimens) that metacarpal IV and the first wing phalanx are proportionally long and slender in *T. longicristatus* when compared with those of ornithocheiroids and ctenochasmatoids. However, the same is clearly true of azhdarchids (Wellnhofer 1991*a*, p. 141; Unwin and Lü 1997). Kellner (1991) also cited the possession of two pneumatic foramina on the first wing phalanx, with one located at the 'superior part of articulation with metacarpal IV'. While single pneumatic foramina have been reported on the first wing phalanx of *Coloborhynchus robustus* (Kellner and Tomida 2000), *Santanadactylus pricei* (Wellnhofer 1985) and other pterosaurs, the distribution of these features in other pterosaur taxa is not well known and this feature should therefore be treated cautiously until its distribution is better understood.

A revised diagnosis of the genus *Tupuxuara* (and thus by inference the type species *T. longicristatus*) provided by Unwin (2003) cited the large sail-like cranial sagittal crest as diagnostic for this taxon. However, this was based on the referred skull IMCF 1052 and not on the type material, and IMCF 1052 has more recently been referred to the supposed second species of *Tupuxuara*, *T. leonardii*, by Kellner (2004*a*). Before discussing the diagnosis of *T. longicristatus* further we here evaluate the validity of *T. leonardii*.

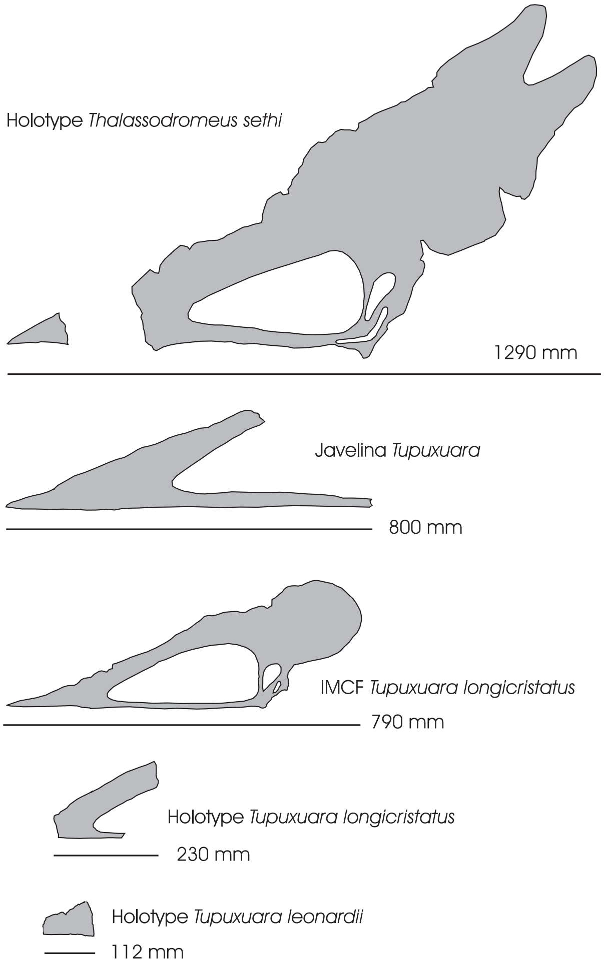
The type material of *T. leonardii* is problematical. While Kellner and Campos (1994, p. 468) cited the holotype as MCT 1495-R, Kellner (2004*a*) cited MCT 1495-R as a cast and listed MN 6592-V as the holotype. It would therefore appear that, until recently, the holotype of *T. leonardii* was a cast and not the original specimen. Like *T. longicristatus*, the *T. leonardii* holotype is from the nodules of the Romualdo Member of the Santana Formation. Given that the length and robustness of the median palatal ridge differs in this specimen from that of the *T. longicristatus* holotype (in *T. leonardii* the ridge, reportedly, does not extend as far rostrally as it does in *T. longicristatus*), Kellner and Campos (1994) proposed that this specimen represented a new species. As discussed above, this character appears to be subject to individual variation within azhdarchoid taxa (e.g. *Azhdarcho* noted in Bakhurina and Unwin 1995) and we therefore reject the use of this character as a means of distinguishing species. Furthermore, although Kellner and Campos (1994) contended that the palatal ridge of *T. leonardii* does not extend as far rostrally as that of *T. longicristatus*, it can be seen from their figures of the *T. longicristatus* holotype (Kellner and Campos 1988, p. 164) that the ridge is weakly developed at its rostral end. Given that the holotype of *T. leonardii* appears to preserve a portion of the rostrum closer to the rostral tip than does the holotype of *T. longicristatus* (Text-fig. 4), it is difficult to be confident that the two specimens really are different in this respect. It should also be noted that the holotypes of *T. longicristatus* and *T. leonardii* appear to represent different-sized animals (Text-fig. 5), and thus any minor difference such as the length and robustness of the palatal ridge could merely be due to ontogeny. Accordingly, *T. leonardii* Kellner and Campos, 1994 is regarded here as a junior subjective synonym of *T. longicristatus* Kellner and Campos, 1988. Our proposed synonymisation of *T. leonardii* with *T. longicristatus* means that the referred specimen IMCF 1052 is also referable to *T. longicristatus*. A full description of this specimen has yet to appear but is reported to be in preparation (Kellner 2004*a*, p. 528).

Re-evaluation of the type material of *T. longicristatus* has allowed us to formulate a revised diagnosis for this taxon that does not rely on referred material. The combined premaxilla-maxilla surrounding the anterior part of the nasoantorbital fenestra is unusual in *T. longicristatus* and apparently diagnostic, and the recognition of this morphology means that *T. longicristatus* can be regarded as a valid taxon (see above).

Thalassodromeus sethi Kellner and Campos, 2002 clearly exhibits the morphology regarded here as diagnostic for *T. longicristatus* and the question arises as to whether *Thalassodromeus* is distinct from *T. longicristatus*. It should be noted that, in the case of pterosaurs that exhibit cranial crests that (as demonstrated by SMNK PAL 3858) appear to be variable ontogenetically and probably



TEXT-FIG. 4. Overlain outlines of holotypes of A, *Tupuxuara leonardii* (MN 6592-V), shaded, and B, *Tupuxuara longicristatus* (MN 6591-V), unshaded, demonstrating how neither represents identical portions of the rostrum.



TEXT-FIG. 5. *Tupuxuara* specimens drawn to the same scale: note the significant difference in size between the holotypes of *Thalassodromeus sethi* and *Tupuxuara longicristatus*. Diagrams based on Kellner and Campos (1988, 1994, 2002), Kellner (2004*a*) and Wellnhofer (1991*a*).

sexually, we prefer a 'lumping' approach in which individuals of a species exhibit a diverse array of cranial crest morphologies (cf. Bennett 1992, 1994). If this approach is employed, the prominent similarities apparent between *Thalassodromeus* and *T. longicristatus* deserve to be emphasised, not the minor differences.

Assessment of the diagnostic characters cited for *Thalassodromeus sethi* by Kellner and Campos (2002) indicate that *Thalassodromeus* is not distinct from *T. longicristatus*. Kellner and Campos (2002) listed the following features as diagnostic for *Thalassodromeus sethi*: cranial crest composed of premaxillae, frontal, parietal and supraoccipital, starting at the skull tip and extending posteriorly, well behind the occipital region; posterior end of cranial crest V-shaped; suture between premaxillae and frontoparietal portion of crest rectilinear; anterior portion of the premaxillae and dentary with sharp dorsal and ventral edges; palatines before palatal crest strongly concave; occipital region of skull broader than in other tapejarids.

Of these purported diagnostic features, those involving the size, extent and shape of the cranial crest are not diagnostic as they show that *Thalassodromeus sethi* had the same kind of crest as *T. longicristatus*. Furthermore, as noted above it seems unwise to employ features of crest size and morphology in a diagnosis. Juveniles, females and males of the same species may be separated as separate genera if this line of reasoning is followed, as is demonstrated by the sometimes incredible amount of intraspecific variation exhibited within *Pteranodon longiceps* and some species of *Nyctosaurus* (Bennett 1992, 2001, 2003).

The 'sharp dorsal and ventral edges' of the premaxillae and dentaries regarded as diagnostic for *Thalassodromeus* are problematical as diagnostic characters. Firstly, presence or absence of these characters in other azhdarchoid taxa are difficult to test given that pterosaur skulls are often laterally compressed during fossilisation. The basal azhdarchid *Zhejiangopterus linhaiensis* may well have distinctly laterally compressed keel-like premaxillary and dentary symphyses for example, but this cannot be determined as the skull is crushed flat in the lateral plane (Unwin and Lü 1997). More importantly, 'sharp dorsal and ventral edges' of the premaxillae and dentaries appear widely distributed in Azhdarchoidea, and are not unique to *Thalassodromeus*. For example, Kellner and Langston (1996, p. 228) noted that the united dentaries of *Quetzalcoatlus* sp. 'form a sharp ventral keel' and Wellnhofer and Buffetaut (1999, fig. 5) figure a sharp ventral keel to the dentary symphysis of the azhdarchoid BSP 1997 I 67 (Unwin 2001, p. 215 regarded this specimen as referable to *Tapejara*). Regarding the strongly concave region of the palate, this is also often difficult to test in pterosaurs owing to lateral compaction.

Finally, difficulties are also attached to use of the broad occipital region of the *Thalassodromeus* skull as a character worthy of generic status. Kellner and Campos (2002, p. 389) described the breadth of the *Thalassodromeus* occiput as being '20% of squamosal to premaxilla length', with the width measured across the quadrates. Unfortunately, considerable ambiguity is attached to the definition of this character. It is unclear where the length between the squamosal and premaxilla is taken given that in *Thalassodromeus* the premaxilla extends from the tip of the rostrum posterodorsally well posterior to the occiput. Furthermore, presence or absence of this character is difficult to test in other taxa given a low sample size of uncrushed pterosaur occiputs. Finally, if *Thalassodromeus* certainly has a broader occiput than other basal azhdarchoids, it is conceivable that this is a feature related to the large size of the *Thalassodromeus* skull relative to that of other basal azhdarchoid specimens (Text-fig. 5).

Elsewhere in Azhdarchoidea, Buffetaut *et al.* (2003) noted that the robust occipital morphology of the giant azhdarchid *Hatzegopteryx thambema* may be a consequence of this taxon's large size. The broad occiput of *Thalassodromeus* may therefore be an incidental effect of its growth allometry.

In conclusion, given the obvious similarity between *T. longicristatus* and *Thalassodromeus sethi*, and the lack of unarguable and phylogenetically significant differences between them, we regard *Thalassodromeus sethi* as a junior subjective synonym of *T. longicristatus*. The only differences are demonstrably due to the specimen's large size, advanced ontogenetic stage and more complete condition of preservation.

Finally on the subject of the taxonomy and synonymy of *T. longicristatus* it should be noted that there is yet another taxon that is probably synonymous with *T. longicristatus*, namely '*Santanadactylus*' *spixi* Wellnhofer, 1985. Though referred to the ornithocheiroid genus *Santanadactylus* Buisonjé, 1980 by Wellnhofer (1985), it has been widely noted since that '*S.*' *spixi* is not an ornithocheiroid and that its affinities lie elsewhere (Bennett 1989, 1994; Wellnhofer 1991*a*; Kellner and Tomida 2000; Unwin 2003). Though Bennett (1989) suggested referral of '*S.*' *spixi* to Dsungaripteridae, our comparison of '*S.*' *spixi* with unpublished *T. longicristatus* material suggests that they may be conspecific. Indeed, Kellner and Tomida (2000, p. 94) noted that '*S.*' *spixi* belongs to Tapejaridae *sensu* Kellner, while Unwin (2003, figs 17–18) referred to '*S.*' *spixi* as '?*Tupuxuara* sp.'. According to Kellner and Tomida (2000, p. 94) a re-evaluation of '*S.*' *spixi* is to appear in the future. Note that '*Santanadactylus*' *spixi* Wellnhofer, 1985 pre-dates *T. longicristatus* Kellner and Campos, 1988.

Tupuxuara cf. *longicristatus* SMNK PAL 3858
Text-figures 6–7

Remarks. The specimen described here is a skull fragment from an azhdarchoid pterosaur in which a laterally compressed premaxillary crest exhibits a shallowly concave posterodorsal border dorsal to the posterior margin of the nasoantorbital fenestra (Text-fig. 6). Although this crest morphology has not been seen previously in any azhdarchoid, the specimen is not considered to represent a new taxon but a probable subadult of *T. longicristatus* (see discussion below).

Material. Specimen number SMNK PAL 3858 held in the Staatliches Museum für Naturkunde, Karlsruhe, Germany. Part of a concretion enclosing a fragment of skull that comprises incomplete premaxillae, frontals, possible parietals, nasals and fragments of lacrimals. A possible portion of dentary lying beneath the frontals was exposed during sectioning.

Horizon. Romualdo Member of the Santana Formation, *sensu* Martill and Wilby (1993).

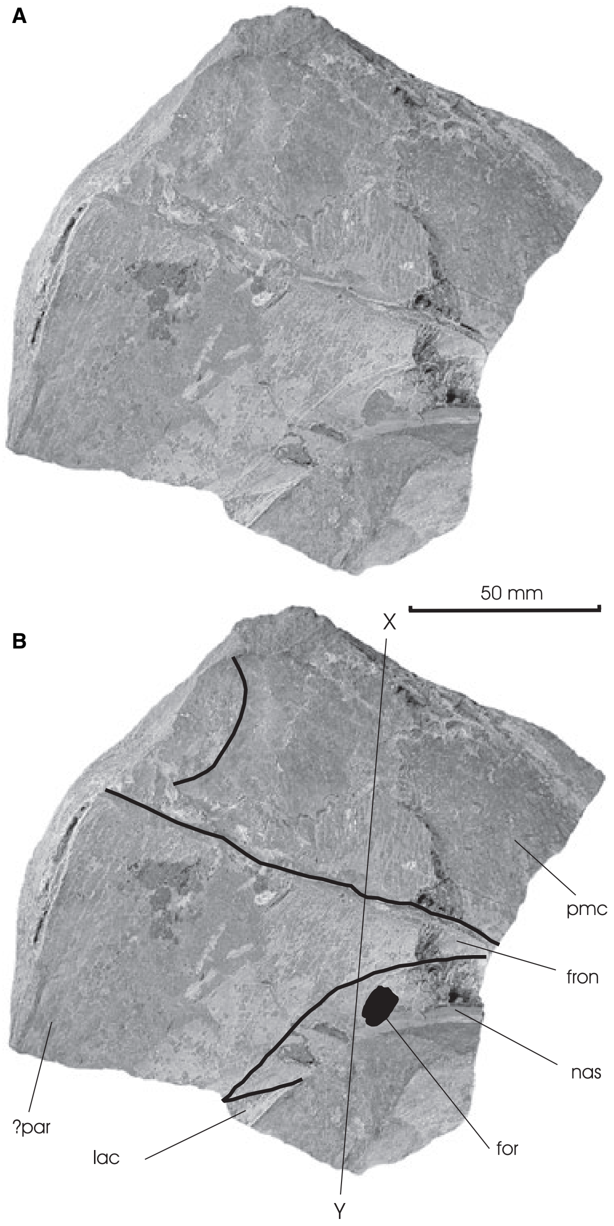
Age. ?Albian–?Turonian (see above).

Locality. The specimen occurs in a typical nodule of the Romualdo Member. These nodules are excavated in small mines, or gleaned from field brash on the slopes of the Chapada do Araripe in southern Ceará, Pernambuco and Piaui in north-eastern Brazil. The exact locality for this specimen is thought to be in the region of Santana do Cariri in southern Ceará (information supplied by a local fossil collector in Santana do Cariri). It appears to have been collected from field brash as the specimen is somewhat weathered and the broken edges of the concretion are worn and soil stained.

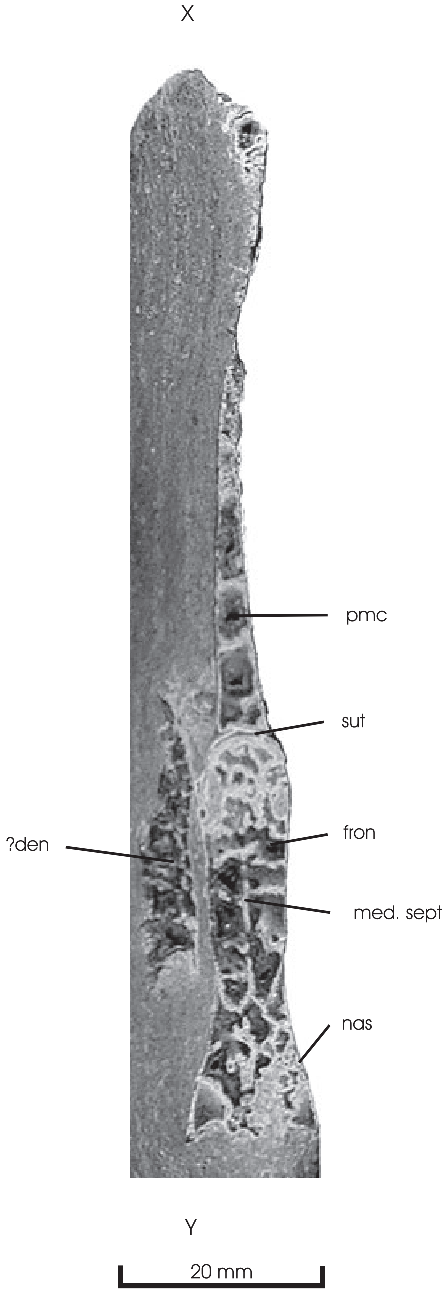
Description. The specimen occurs in a flattish, laminated, early diagenetic carbonate concretion with abundant cypridid ostracods and has been split along a bedding plane. It has been sectioned to reveal details of the skull cross-section and the nature of the suture between the premaxilla and other elements of the skull (Text-figs 6B, 7). The slab is approximately square and has two margins that probably reflect the natural borders of the concretion, while the other two margins are fracture surfaces indicating that the original concretion was larger and more of the skull had been preserved. Only half of the nodule remains, and the split has left some bone in the now missing counterpart. Thus some of the specimen is preserved with bone intact whereas other parts are preserved as an external mould, or as thin slivers of cortical bone adhering to the matrix. This accidental splitting of the nodule has revealed some of the internal structure of the specimen (Text-fig. 6A).

All of the bones are laterally compressed, but not crushed, and in this respect form a highly compressed skull that tapers dorsally to form a blade-like crest in cross-section (Text-fig. 7). The fused nasals form the posterodorsal margin of the nasoantorbital fenestra with a gentle posteroventral curvature. A fused suture is present between the nasals and an anterior process of the frontals (Text-fig. 7) and a second suture is visible between the frontals and premaxillae. A thin (*c.* 0·5 mm) space between the frontals and premaxillae shows that they were not fused in life (Text-fig. 7). A small, subrectangular foramen is present in the posteroventral region of the right nasal (Text-fig. 6). Ventrally, a faint suture marks the boundary between the nasals and the dorsalmost extremity of the lacrimals and, while a small possible fragment of right lacrimal is present, no part of the orbital margin is seen. The convergence of the right nasal toward the ventral margin of the premaxilla defines a triangular, anteriorly directed projection of the frontals. A partial bone, obscured by the frontals, was located during sectioning and may represent a detached partial dentary (Text-fig. 7). The specimen corresponds to the region of the *Tupuxuara* skull depicted in Text-figure 2.

Dimensions. Few meaningful dimensions can be derived from SMNK PAL 3858, and those measurements that can be accurately determined are difficult to relate to a location on the skull (Table 3). The maximum dimensions of the specimen are 174 × 132 mm. The dorsal margin of the premaxilla approxi-



TEXT-FIG. 6. *Tupuxuara* cf. *longicristatus*, SMNK PAL 3858 prior to sectioning, Romualdo Member, Santana Formation (Cretaceous), Chapada do Araripe, north-east Brazil. A, right lateral view of partial skull. B, interpretative labelling of A. X–Y = line of section (see Text-fig. 7). Abbreviations (also for Text-fig. 7): den, dentary; for, foramen; fron, frontal; lac, lacrimal; med. sept, median septum between frontals; nas, nasal; par, parietal; pmc, premaxillary crest; sut, unfused suture between pmc and fron.



TEXT-FIG. 7. Cross-section of *Tupuxuara* cf. *longicristatus* SMNK PAL 3858 made through the premaxillary crest, anterior frontal and nasal. Section reveals laterally compressed (but uncrushed) elements of the sagittal crest, fusion of nasals and internal arrangement of trabeculae. Abbreviations as in Text-figure 6.

mately parallels its suture with the frontals and is between 54 and 58 mm high measured perpendicular to this suture. Width measurements taken from the cut surface can be accurately determined (Text-fig. 7). The width of the nasals at their ventral margin is 12 mm, tapering to a width of 6·5 mm at a point 15 mm dorsal to the ventral margin. They then expand slightly, becoming 9 mm wide just below the suture with the premaxilla. The nasal foramen has a maximum diameter of 8 mm. In cross-section, the premaxilla is 5 mm wide at its suture with the fused nasals and tapers dorsally until it is only 2 mm wide at a point 30 mm above the suture. It tapers towards its dorsal margin to a minimum width of approximately 4 mm, but there appears to

TABLE 3. Selected measurements of *Tupuxuara* cf. *longicristatus* SMNK PAL 3858 from the Romualdo Member of the Santana Formation, Ceará, Brazil.

Nasals
12 mm wide at ventral margin
6·5 mm wide at a point 15 mm dorsal to the ventral margin
9 mm wide just below its suture with the premaxillae
Maximum diameter of nasal foramen 8 mm

Premaxillae
5 mm wide at suture with nasals
2 mm wide at a point 30 mm above suture
Average height of premaxillae measured perpendicular to ventral margin 56 mm

be a slight mediolateral expansion at its dorsal border (Text-fig. 7).

Interpretation. Although the specimen represents an extremely small part of a skull, its pterosaurian affinities are indicated by both the extremely thin nature of the cortical bone and the vacuous nature of the intertrabecular cavities. In some regions of the premaxilla the cortical bone is less than 0·2 mm thick. Its flattish aspect and the symmetry of the elements seen in cross-section (Text-fig. 7) indicate that they form part of a skull with a prominent sagittal crest. When the upper 'crest' bone is considered as a posterior extension of the premaxilla, then elements ventral to this are readily recognisable as frontals and possible parietals. An element located antero-ventral to the frontals, but not quite uniting with the premaxilla, is clearly a right nasal but, unusually, is fenestrate. In *Tapejara* a fenestra is present at this location but is formed by both the nasal and the lacrimal (Wellnhofer and Kellner 1991).

The new specimen exhibits an unusual morphology in which a sagittal crest composed of premaxillary bone overgrows, but does not fuse with, a pair of laterally compressed frontals. It is predominantly this morphology that has allowed us to identify SMNK PAL 3858 as a member of Azhdarchoidea as this configuration appears unique to this group. It is clearly present in *Tapejara* (Wellnhofer and Kellner 1991) and *Sinopterus dongi*, though has yet to be confirmed for Azhdarchidae (see above). Similarly, the extremely narrow width of the skull relative to its height is typical of the azhdarchoids *Tapejara* and *Tupuxuara*.

While SMNK PAL 3858 resembles *Tapejara wellnhoferi* in that the anterior part of its frontals forms a subtriangular projection between the premaxilla and nasals (Wellnhofer and Kellner 1991), the specimen can be excluded from *Tapejara* as in that taxon the premaxilla is not laterally compressed where it overgrows the skull roof. In contrast, the premaxillae of *Tapejara* form a thin hollow rod with a rounded cross-section. This is true even of juvenile *Tapejara* specimens whose skulls would have been smaller than that of SMNK PAL 3858 (pers. obs.). The specimen is comparable with *Tupuxuara longicristatus* as the sagittal crest comprises laterally compressed premaxillae situated both dorsal and posterior to the nasoantorbital fenestra with their dorsal margin subparallel to the premaxillary suture, and is thus referred to *Tupuxuara*.

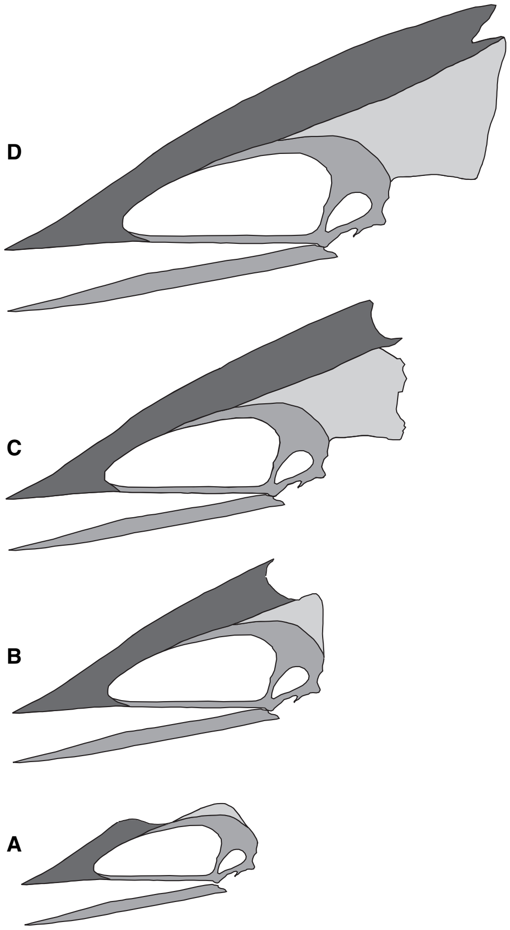
Descriptions of *Tupuxuara* are not informative for the region of the skull represented by SMNK PAL 3858. The sagittal crest appears to comprise only the premaxillae, and overgrows posteriorly the nasals, frontals and perhaps parietals. A suture between the premaxilla and the nasals and frontals in other *Tupuxuara* specimens originates midway along the dorsal border of the nasoantorbital fenestra (Kellner and Campos 1988, 1994, 2002; Unwin 2003; Kellner 2004*a*). Although this latter region is missing from SMNK PAL 3858, projection of the premaxillary suture anteriorly suggests that it would converge with the dorsal margin of the nasoantorbital fenestra approximately 60 mm beyond the present margin of the block. The small size of the specimen suggests that its crest can be hypothetically 'projected' to match that of the adult condition of *T. longicristatus* and because SMNK PAL 3858 matches well our prediction of what the subadult stage of *T. longicristatus* would have looked like, we refer the specimen to *Tupuxuara* cf. *longicristatus*.

ONTOGENY AND GROWTH OF THE AZHDARCHOID CRANIAL CREST

Bony sagittal cranial crests are widespread in pterodactyloid pterosaurs, being present in Ornithocheiroidea (e.g. *Ludodactylus*, *Nyctosaurus*, *Pteranodon*), Ctenochasmatoidea (e.g. *Cycnorhamphus*), Dsungaripteroidea (e.g. *Dsungaripterus*, *Lonchognathosaurus*) and Azhdarchoidea (e.g. *Tapejara*, *Tupuxuara*), and are now known to occur in non-pterodactyloids as well (Dalla Vecchia *et al.* 2002). Recent work has confirmed that soft-tissue crests occur in taxa where no bony crest is preserved, and it now seems that the bony sagittal crests of ctenochasmatoids, dsungaripteroids and azhdarchoids represent the mineralised portions of crests that were ancestrally formed from soft tissues: thus, soft-tissue and bony crests in these groups are homologous (Frey and Tischlinger 2000; Bennett 2002; Frey *et al.* 2003*a*). The distribution of these crests within Pterodactyloidea indicates that their presence is plesiomorphic for Lophocratia, the pterodactyloid clade that includes ctenochasmatoids, dsungaripteroids and azhdarchoids (Unwin 2003).

In most pterosaurs where two or more elements form part of the crest, growth of the bones appears to be coeval and the crest becomes a single entity formed of fused bone. Sutures in such crests are usually indistinguishable and even though the crest may increase in size during ontogeny, it appears to be a single bone, lacking sutures. In basal azhdarchoids, however, and in the specimen described here in particular, the boundary between the premaxillae and the underlying elements (nasals, frontals, ?parietals) is obvious and what appears to be a distinct suture is seen (Text-figs 6–7). In cross-section the premaxilla overlaps the convex dorsal surface of the frontals without fusion. While cranial sutures may persist through ontogeny because of their participation in mechanical stimuli (e.g. Rafferty *et al.* 2003; Sun *et al.* 2004), we detect no indication that the premaxillary sutures seen in azhdarchoids were involved in cranial mechanics. The presence of these sutures in the *Tupuxuara* specimens suggests that the premaxillary component of the crest overgrew the skull roof during ontogeny (Text-figs 7–8). In view of our referral of SMNK PAL 3858 to *Tupuxuara* cf. *longicristatus*, comparison with other examples of *Tupuxuara longicristatus* indicates that it was a subadult at the time of death as the posterior margin of the cranial crest had only reached a position dorsal to the posterior margin of the nasoantorbital fenestra (Text-fig. 2). The inferred ontogenetic enlargement of the crest supports the idea that the cranial crests of at least some pterosaurs were sexual display features, and sexual maturity of any individual of a crested species could have been assessed by the size and disposition of its crest.

In view of our synonymisation of *Thalassodromeus sethi* with, and referral of IMCF 1052 to, *T. longicristatus*, the new specimen SMNK PAL 3858 can be imagined as part of an ontogenetic series for *T. longicristatus*. SMNK PAL 3858 represents a young individual in this series (Text-fig. 8). IMCF 1052 represents an older individual in which the premaxillary crest terminates a minimum of *c.* 30 mm posterior to the orbit, and the *Thalassodromeus sethi* specimen represents an old adult with a hypertrophied premaxillary crest in which the termination is *c.* 500 mm posterior to the orbit (Text-fig. 8).

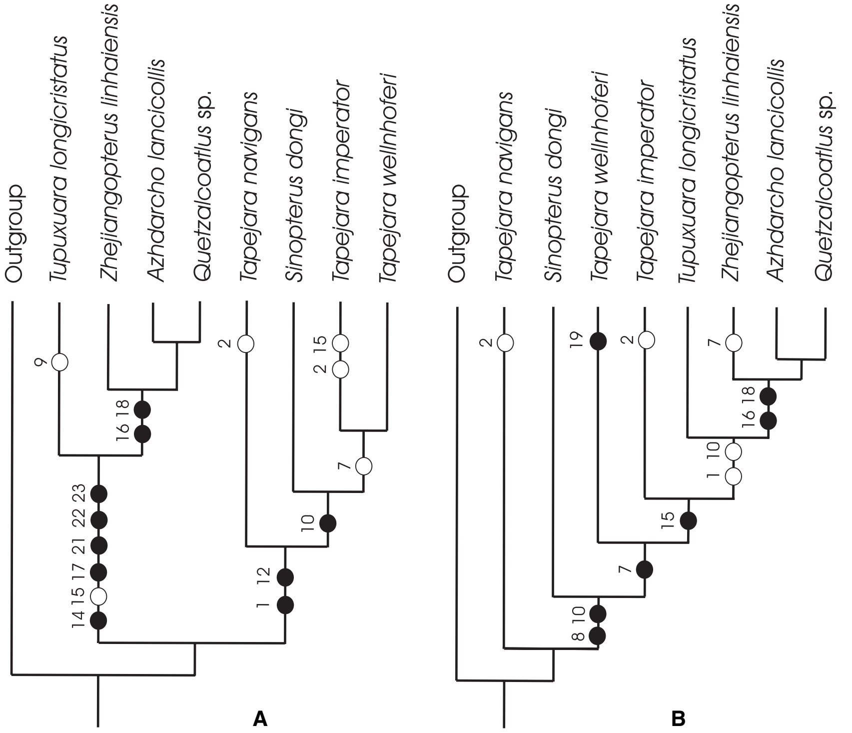


TEXT-FIG. 8. Hypothetical ontogenetic sequence of premaxillary/fronto-parietal crest development in *Tupuxuara longicristatus*. A, hypothetical juvenile stage in which the premaxillary crest does not overlap the frontals. B, subadult stage corresponding to SMNK PAL 3858, where the premaxillary crest has overlapped the anterior parts of the frontals. C, adult stage distinguished by termination of premaxillary crest being posterior to occiput (loosely based on IMCF 1052). D, old adult stage in which premaxillary crest terminates well beyond occiput, and with V-shaped notch (based on DGM 1476-R). Diagrams not to scale.

THE PHYLOGENY OF AZHDARCHOIDEA

In an attempt to resolve the controversy over the monophyly of Tapejaridae *sensu* Kellner vs. Neoazhdarchia Unwin, 2003, we performed a cladistic analysis of Azhdarchoidea utilising all the characters that have been employed in this debate (Kellner 2003*a*, *b*, 2004*a*; Unwin 2003) as well as some new ones (Appendix). Our taxon coding was hampered by the lack of published descriptions of some key specimens that incorporate postcranial remains, and we unfortunately had to code several characters from unpublished material. Some characters (e.g. characters 21 and 23) require confirmation from associated specimens and we hope to expand on this study in future. A data set of 23 characters and eight taxa was analysed using NONA 2.0 with no multistate characters or weighting. The results of a heuristic search generated three most-parsimonious trees (MPTs), all with a length of 32 steps, a CI of 0·71 and an RI of 0·70.

In all MPTs, *Tupuxuara* was the sister-taxon to Azhdarchidae, supporting neoazhdarchian monophyly (Text-fig. 9). *Tupuxuara* never formed a clade with any species of *Tapejara*. Azhdarchidae was always monophyletic and *Zhejiangopterus* formed a sister-taxon to an *Azhdarcho*-*Quetzalcoatlus* clade. Elsewhere there was less agreement: arrangements where *Tapejara* and *Sinopterus*



TEXT-FIG. 9. Two of the three most parsimonious trees depicting possible relationships of azhdarchoid taxa. In all MPTs *Tupuxuara longicristatus* is sister-taxon to Azhdarchidae (*Zhejiangopterus*, *Azhdarcho* and *Quetzalcoatlus*). Two major differences in tree structure were found. A, *Tapejara* and *Sinopterus dongi* form a weakly supported sister clade to Neoazhdarchia. B, *Tapejara* and *Sinopterus dongi* form a series of successively more distant outgroups to Neoazhdarchia.

formed a clade which was the sister-taxon to Neoazhdarchia (thus forming the restrictive version of Tapejaridae discussed above), or formed successively more distant outgroups to Neoazhdarchia, were equally parsimonious. The latter arrangement was unexpected and indicates that even the monophyly of our restricted version of Tapejaridae is only weakly supported. Furthermore, the three *Tapejara* species never formed a clade that did not include other taxa. Even in the MPT where *Tapejara* and *Sinopterus dongi* formed a clade, *Sinopterus dongi* was closer to a *Tapejara imperator* + *Tapejara wellnhoferi* clade than was *Tapejara navigans*. If this tree were favoured, a monophyletic *Tapejara* could be retained by either referring *Sinopterus dongi* to *Tapejara* or providing *Tapejara navigans* with a new generic name. Given that paraphyly of this *Tapejara* + *Sinopterus dongi* group was equally parsimonious, however, the monophyly of the genus *Tapejara* as presently conceived is questionable and further study is required to see whether *Tapejara imperator* and *Tapejara navigans* truly belong with the type species of the genus.

In conclusion, the affinities of *T. longicristatus* within Azhdarchoidea have been controversial, but character evaluation and a cladistic analysis shows that *T. longicristatus* is more closely related to azhdarchids than it is to *Tapejara*, and thus Tapejaridae *sensu* Kellner is argued to be paraphyletic. Monophyly of a clade including *Tapejara* and *Sinopterus dongi* was not supported in all MPTs, and all tapejarids may represent plesions on the azhdarchoid stem. If this is correct then *Tapejara* as presently conceived is not monophyletic.

Acknowledgements. For assistance with fieldwork in Brazil we thank Dr Paulo Brito (Rio de Janeiro), Mr Artur Andrade (Crato) and Dr Paul Selden (Manchester). Thanks to Mr Robert Loveridge for assistance with photography, Mr Geoff Long for sectioning the specimen, Dr Stig Walsh for generating figures, Mr Steve Sweetman and Mr Sam Heads for assistance with the cladistic analysis, and Mr Mark Van Tomme for assistance in obtaining Kellner (2004*a*) so soon after its publication. We have benefited from discussions with Dr Dino Frey, Dr Eric Buffetaut and Dr Dave Unwin and were provided kind access to unpublished material by Dino. This manuscript was improved considerably by the advice, criticisms and comments of Dr Eric Buffetaut, Dr Dave Unwin and Dr David Polly.

REFERENCES

AVERIANOV, A. O. 2004. New data on Cretaceous flying reptiles (Pterosauria) from Russia, Kazakhstan, and Kyrgyzstan. *Paleontological Journal*, **38**, 426–436.

BAKHURINA, N. N. and UNWIN, D. M. 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. *Historical Biology*, **10**, 197–245.

BENNETT, S. C. 1989. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology*, **63**, 669–677.

BENNETT, S. C. 1991. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology*, **19**, 92–106.

—— 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs with comments on cranial crests. *Journal of Vertebrate Paleontology*, **12**, 422–434.

—— 1994. Taxonomy and systematics of the Late Cretaceous pterosaur *Pteranodon* (Pterosauria, Pterodactyloidea). *Occasional Papers of the Natural History Museum, University of Kansas*, **169**, 1–70.

—— 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description of osteology. *Palaeontographica, Abteilung A*, **260**, 1–112.

—— 2002. Soft tissue preservation of the cranial crest of the pterosaur *Germanodactylus* from Solnhofen. *Journal of Vertebrate Paleontology*, **22**, 43–48.

—— 2003. New crested specimens of the Late Cretaceous pterosaur *Nyctosaurus*. *Paläontologische Zeitschrift*, **77**, 61–75.

BRAMWELL, C. and WHITFIELD, G. R. 1974. Biomechanics of *Pteranodon*. *Philosophical Transactions of the Royal Society of London*, **B267**, 503–581.

BUFFETAUT, E., GRIGORESCU, D. and CSIKI, Z. 2003. Giant azhdarchid pterosaurs from the terminal Cretaceous of Translyvania (western Romania). 91–104. *In* BUFFETAUT, E. and MAZIN, J.-M. (eds). *Evolution and palaeobiology of pterosaurs.* Geological Society, London Special Publication, **217**, 347 pp.

BUISONJE, P. H. 1980. *Santanadactylus brasiliensis* nov. gen., nov. sp., a long necked, large pterosaurier from the Aptian of Brasil. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, B*, **83**, 145–157.

CAMPOS, D. A. and KELLNER, A. W. A. 1997. First occurrence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, northeast Brazil. *Anais da Academia Brasileira Ciências*, **69**, 83–87.

—— LIGABUE, D. and TAQUET, P. 1984. Wing membrane and wing supporting fibres of a flying reptile from the Lower Cretaceous of the Chapada do Araripe (Aptian; Ceará State, Brazil). *In* REIF, W.-E. and WESTPHAL, F. (eds). *Third Symposium on Mesozoic Terrestrial Ecosystems, short papers.* Attempto Verlag, Tübingen, pp. 37–94.

CZERKAS, S. A. and JI QIANG 2002. A new rhamphorhynchoid with a headcrest and complex integumentary structures. 15–41. *In* CZERKAS, S. J. (ed.). *Feathered dinosaurs and the origin of flight*. The Dinosaur Museum, Blanding, Utah, 136 pp.

DALLA VECCHIA, F. M., WILD, R., HOPF, H. and REITNER, J. 2002. A crested rhamphorhynchoid from the Late Triassic of Austria. *Journal of Vertebrate Paleontology*, **22**, 196–199.

DONG ZHI-MING, SUN YUE-WU and WU SHAO-YUAN 2003. On a new pterosaur from the Lower Cretaceous of Chaoyan Basin, western Liaoning, China. *Global Geology*, **22**, 1–7.

EATON, G. F. 1910. Osteology of *Pteranodon*. *Memoirs of the Connecticut Academy of Sciences*, **2**, 1–38.

FREY, E. and MARTILL, D. M. 1994. A new pterosaur from the Crato Formation (Lower Cretaceous, Aptian) of Brazil. *Neues Jahrbuch fur Geologie und Palaontologie, Abhandlungen*, **194**, 379–412.

—— —— and BUCHY, M.-C. 2003*a*. A new species of tapejarid pterosaur with soft-tissue head crest. 65–72. *In* BUFFETAUT, R. and MAZIN, J.-M. (eds). *Evolution and Palaeobiology of Pterosaurs*. Geological Society, London, Special Publication, **217**, 347 pp.

—— —— —— 2003*b*. A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur. 55–63. *In* BUFFETAUT, R. and MAZIN, J.-M. (eds). *Evolution and palaeobiology of pterosaurs.* Geological Society, London, Special Publication, **217**, 347 pp.

—— and TISCHLINGER, H. 2000. Weichteilanatomie der Flugsaurierfüße und Bau der Scheitelkämme: neuw Pterosaurierfunde aus den Solnhofener Schichten (Bayern) und der Crato-Formation (Brasilien). *Archaeopteryx*, **18**, 1–16.

—— —— MARTILL, D. M. and BUCHY, M.-C. 2003*c*. New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. 233–266. *In* BUFFETAUT, R. and MAZIN, J.-M. (eds). *Evolution and palaeobiology of pterosaurs*. Geological Society, London, Special Publication, **217**, 347 pp.

HEPTONSTALL, W. B. 1971. An analysis of the flight of the Cretaceous pterodactyl *Pteranodon ingens*. *Scottish Journal of Geology*, **7**, 61–78.

KAUP, J. 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. *Isis*, **3**, 311–315.

KELLNER, A. W. A. 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, northeast Brazil. *Anais da Academia Brasileira, Ciências*, **61**, 439–446.

—— 1991. Supplementary notes and comments. 370–371 *In* MAISEY, J. G. (eds). *Santana fossils: an illustrated atlas.* Tropical Fish Hobbyist, Neptune City, NJ, 459 pp.

—— 2003*a*. Pterosaur phylogeny and comments on the evolutionary history of the group. 105–137. *In* BUFFETAUT, R. and MAZIN, J.-M. (eds). *Evolution and palaeobiology of pterosaurs.* Geological Society, London, Special Publication, **217**, 347 pp.

—— 2003*b*. Comments on the phylogeny of the Pterodactyloidea. *Rivista del Museo Civico di Scienze Naturali 'Enrico Caffi'*, **22**, 31–37.

—— 2004*a*. New information on the Tapejaridae (Pterosauria. Pterodactyloidea) and discussion of the relationships of this clade. *Ameghiniana*, **21**, 521–534.

—— 2004*b*. The ankle structure of two pterodactyloid pterosaurs from the Santana Formation (Lower Cretaceous), Brazil. *Bulletin of the American Museum of Natural History*, **285**, 25–35.

—— and CAMPOS, D. A. 1988. Sobre um pterosauro com crista sagital da Bacia do Araripe, Cretáceo Inferior do Nordeste do Brasil. *Anais da Academia Brasileira, Ciências*, **60**, 459–469.

—— —— 1994. A new species of *Tupuxuara* (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil. *Anais da Academia Brasileira, Ciências*, **66**, 467–473.

—— —— 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. *Science*, **297**, 389–392.

—— and HASEGAWA, Y. 1993. Post cranial skeleton of *Tupuxuara* (Pterosauria, Pterodactyloidea, Tapejaridae) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, **13** (Supplement to No. 3), 44A.

—— and LANGSTON, W. 1996. Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from the Late Cretaceous sediments of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology*, **16**, 222–231.

—— and TOMIDA, Y. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian–Albian), northeastern Brazil. *National Science Museum Monographs* (Tokyo), **17**, 1–135.

LI JIAN-JUN, LÜ JUN-CHANG and ZHANG BAO-KUN 2002. A new Lower Cretaceous sinopterid pterosaur from the western Liaoning, China. *Acta Palaeontologica Sinica*, **42**, 442–447. [In Chinese, English summary].

MAISEY, J. G. 1991. *Santana fossils: an illustrated atlas.* TFH Publications, Neptune City, NJ, 459 pp.

MARTILL, D. M. 1988. Preservation of fish in the Cretaceous of Brazil. *Palaeontology*, **31**, 1–18.

—— 1993. *Fossils of the Santana and Crato formations, Brazil.* Palaeontological Association, London, Field Guides to Fossils, **5**, 159 pp.

—— and FREY, E. 1998. A new pterosaur Lagerstätte in N. E. Brazil (Crato Formation, Aptian, Lower Cretaceous): preliminary observations. *Oryctos*, **1**, 79–85.

—— —— CHONG DIAZ G. and BELL, C. M. 2000. Reinterpretation of a Chilean pterosaur and the occurrence of Dsungaripteridae in South America. *Geological Magazine*, **137**, 19–25.

—— and UNWIN, D. M. 1989. Exceptionally well preserved pterosaur wing membrane from the Cretaceous of Brazil. *Nature*, **340**, 138–140.

—— and WILBY, P. 1993. Stratigraphy. *In* MARTILL, D. M. (ed.). *Fossils of the Santana and Crato formations, Brazil.* Palaeontological Association, London, Field Guides to Fossils, **5**, 159 pp.

MATEER, N. J. 1975. A study of *Pteranodon*. *Bulletin of the Geological Institutions of the University of Uppsala, New Series*, **6**, 23–33.

NAISH, D. and MARTILL, D. M. 2003. Pterosaurs – a successful invasion of prehistoric skies. *Biologist*, **50**, 213–216.

NESSOV, L. A. 1984. Upper Cretaceous pterosaurs and birds from central Asia. *Paleontological Journal*, **1984**, 38–49.

PADIAN, K. 1986. A taxonomic note on two pterodactyloid families. *Journal of Vertebrate Paleontology*, **6**, 289.

PLIENINGER, F. 1901. Beitrage zur kenntnis der flugsaurier. *Palaeontographica*, **48**, 65–90.

PONS, D. and BERTHOU, P.-Y. 1996. Palynologie des unités lithostratigraphiques ‘Fundão’, ‘Crato’ et ‘Ipubi’ (Aptien supérieur a Albien inférieur-moyen Bassin d’Araripe, NE du Brésil. 383–401. *In* JARDINÉ, S., DE KLASZ, I. and DEBENAY, J.-P. (eds). *Géologie de l’Afrique et de l’Atlantique Sud (Actes colloques Angers 1994).* Elf Aquitaine, Pau, Mémoire **16**.

RAFFERTY, K. L., HERRING, S. W. and MARSHALL, C. D. 2003. Biomechanics of the rostrum and the role of facial sutures. *Journal of Morphology*, **257**, 33–44.

STEIN, R. S. 1975. Dynamic analysis of *Pteranodon ingens*: a reptilian adaptation to flight. *Journal of Paleontology*, **49**, 534–548.

SUN, Z. Y., LEE, E. and HERRING, S. W. 2004. Cranial sutures and bones: growth and fusion in relation to masticatory strain. *Anatomical Record, Part A*, **276A**, 150–161.

UNWIN, D. 1992. The phylogeny of the Pterosauria. *Journal of Vertebrate Paleontology*, **12** (Supplement to No. 3), 57A.

—— 1995. Preliminary results of a phylogenetic analysis of the pterosauria (Diapsida: Archosauria). 69–72. *In* SUN AILING and WANG YUANQIN, (eds). *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, short papers*. China Ocean Press, Beijing, 250 pp.

—— 2001. An overview of the pterosaur assemblage from the Cambrige Greensand (Cretaceous) of eastern England. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe*, **4**, 189–221.

—— 2003. On the phylogeny and evolutionary history of pterosaurs. 139–190. *In* BUFFETAUT, E. and MAZIN, J.-M. (eds). *Evolution and palaeobiology of pterosaurs.* Geological Society, London, Special Publication, **217**, 347pp.

—— and LÜ, J. 1997. On *Zhejiangopterus* and the relationship of pterodactyloid pterosaurs. *Historical Biology*, **12**, 199–210.

WANG XIAO-LIN and ZHOU ZHONG-HE 2003. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. *Chinese Science Bulletin*, **48**, 16–23.

WELLNHOFER, P. 1985. Neue pterosaurier aus der Santana Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica, A*, **187**, 105–182.

—— 1987. New crested pterosaurs from the Lower Cretaceous of Brazil. *Mitteilungen Bayerische Staatssammlung für Paläontologie und Historische Geologie*, **27**, 175–186.

—— 1991*a*. *The illustrated encyclopedia of pterosaurs.* Salamander, London, 192 pp.

—— 1991*b*. The Santana Formation pterosaurs. 351–370. *In* MAISEY, J. G. (ed.). *Santana fossils: an illustrated atlas.* Tropical Fish Hobbyist, Neptune City, NJ, 459 pp.

—— and BUFFETAUT, E. 1999. Pterosaur remains from the Cretaceous of Morocco. *Paläontologische Zeitschrift*, **73**, 133–142.

—— and KELLNER, A. W. A. 1991. The skull of *Tapejara wellnhoferi* Kellner (Reptilia: pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, northeastern Brazil. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **31**, 89–106.

APPENDIX

Characters used for parsimony analysis

1. Tip of premaxillary rostrum: horizontally continuous with rest of rostrum (0), ventrally deflected (1) (Kellner 2003*a*; character 4).
2. Premaxillary crest: lacking (0) or exhibiting elongate spine (1).
3. Premaxillary crest extending posteriorly over skull: absent (0), present (1).
4. Median palatal ridge: absent (0), present (1).
5. Teeth: present (0), absent (1).
6. Nasoantorbital fenestra: less than 40 per cent skull length (measured from premaxillary tip to posterior edge of orbit) (0), more than 40 per cent skull length (1).

7. Comparatively small pear-shaped orbit: absent (0), present (1) (Kellner 2003*a*; character 10).
8. Orbit: located high on skull (0), located ventral to level of dorsal margin of nasoantorbital fenestra (1) (Unwin 2003, character 60).
9. Thin subvertical lacrimal process on jugal: absent (0), present (1) (Kellner 2003*a*, character 18).
10. Posterodorsal finger-like crest on parietal: absent (0), present (1).
11. Occiput: facing posteriorly or posteroventrally (0), facing ventrally (1) (Unwin 2003, p. 181).
12. Distinct ventral dentary crest: absent (0), present (1).
13. Notarium: absent (0), present in adults (1) (Unwin 2003, character 31).
14. Metacarpals I–III and distal syncarpal: with at least some metacarpals contacting syncarpal (0), contact lost (1) (Unwin 2003, character 37).
15. Rostrum (measured from anterior margin of orbit to premaxillary tip): less than 88 per cent of total skull length (0), more than 88 per cent of total skull length (1) (Unwin 2003, p. 170).
16. Fifth cervical vertebra: not proportionally elongate (0), proportionally elongate (at least eight times longer than broad) and with neural spine absent (1) (Unwin 2003, p. 181).
17. Cervical vertebrae: neural arch in typical position (0), merges with centrum (1).
18. Cervical vertebrae: lateral pneumatic foramen present on centrum (0), absent (1) (Kellner 2003*a*, character 47).
19. Broad tubercle on ventroposterior margin of coracoid: absent (0), present (1) (Kellner 2003*a*, character 57).
20. Metacarpal IV and first wing phalanx: subequal in diameter to combined diameter of radius and ulna (0), gracile in relation to combined diameter of radius and ulna (1).
21. Wing finger: proportionally long (more than 50 per cent total wing length) (0), proportionally short (*c.* 50 per cent total wing length) (1) (Unwin 2003, p. 181).
22. T-shaped cross-section on second and third wing phalanges: absent (0), present (1).
23. Femur: only slightly longer than humerus (0), proportionally long (more than 1·6 times length of humerus) (1) (Unwin 2003, p. 181).

Data matrix

Outgroup	00000	00000	00000	00000	000
Azhdarcho	0??P1	?????	?????	111??	???
Quetzalcoatlus sp.	00??1	0110?	?0??1	11101	111
Sinopterus dongi	101?1	10101	01??0	0???1	0?0
Tap. imperator	111?1	111?1	0???1	?????	???
Tap. navigans	111?1	10000	01??0	?????	???
Tap. wellnhoferi	10101	11111	01?00	00010	000
Tupuxuara	00111	11110	00111	010?1	111
Zhejiangopterus	000?1	10100	10111	11101	1?1

P = polymorphic for this character.