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David W. E. Hone & Eric Buffetaut (Guest Editors)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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CONTENTS/INHALT

Zitteliana	B 28	255 Seiten	München, 31.12.2008	ISSN 1612-4138

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer; design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

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Possible azhdarchoid pterosaur remains from the Coniacian (Late Cretaceous) of England

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Abstract

Three partial but well preserved cervical vertebrae from the Chalk Formation of St Margaret's Bay, Kent, southern England, represent the first occurrence of pterosaurs in Coniacian deposits of Britain. Similarities between the new material and the South American azhdarchoid *Tapejara* suggest the new material may represent the first of non-azhdarchid azhdarchoid pterosaurs in Europe.

Key words: Pterosauria, Azhdarchoidea, England, Cretaceous, Coniacian.

Zusammenfassung

Drei unvollständig aber gut erhaltene zervikale Wirbel aus der Kreide Formation von St. Margaret's Bay, Kent in Südengland, repräsentieren das erste Vorkommen von Pterosauriern in Ablagerungen des Coniaciums von England. Ähnlichkeiten zwischen dem neuen Material und der südamerikanischen Gattung *Tapejara* (Azhdarchoidea) deuten darauf hin, dass das neue Material vielleicht die ersten Überreste von non-azhdarchiden azhdarchoiden Pterosauriern in Europa darstellt.

Schlüsselwörter: Pterosauria, Azhdarchoidea, England, Kreide, Coniacium.

1. Introduction

Remains of pterosaurs are rarely found in the Cretaceous chalk formations of England, but several specimens are of historical significance and, at one time, English chalk pterosaurs represented the largest flying reptiles known (Bowerbank 1848). Pterosaur remains have been reported from a number of English chalk exposures including the pits at Burnham, Rochester, Halling and Snodland in Kent; Southerham Grey Pit, near Lewes, Sussex; Betchworth in Surrey and an unspecified locality in Hertfordshire (Bowerbank 1846, 1851; Lydekker 1888; Benton & Spencer 1995). The chalk provides Britain's youngest well-documented pterosaur fossils with most specimens found in the lower Cenomanian to Turonian parts of the sequence. An occurrence of a Campanian pterosaur was noted by Milner (2002), but no details were provided. Here we report the presence of three associated, well preserved pterosaur cervical vertebrae (BMNH R 16479a-c) that represent the youngest documented occurrence of pterosaurs in the United Kingdom.

Museum abbreviations: BMNH Natural History Museum, London.

2. Locality and stratigraphy

The vertebrae were collected by one of us (AG) in the 1970s from chalk exposures on the foreshore at Hope Point, approximately 1.5 km NNE of St Margarets' at Cliffe on the East Kent coast of southeast England (Fig. 1; national grid reference TR379461). The sequence here is of mainly Late Cretaceous age and extends from the Albian Gault Clay Formation to the Santonian Margate Member of the White Chalk Formation (Fig. 2; Jenkyns et al. 1994). The vertebrae were collected from a hard ground at the base of the Hope Point Marls of the White Chalk Formation (level 188.2 m above the base of the chalk, see Jenkyns et al. 1994). This horizon lies within the lower *Micraster coranguinum* zone and the lower part of the range of *Volviceramus involutus* (= CC15/CC16 nannofossil zone; *Dicarenella primitive* planktic foram zone), indicating a Mid Coniacian age of ~ 86.5 My. Matrix held within the internal bone cavity is typical of the white chalk of this horizon and demonstrates that they do not represent reworked material which can be common at some horizons within the Cenomanian chalk of southern England.

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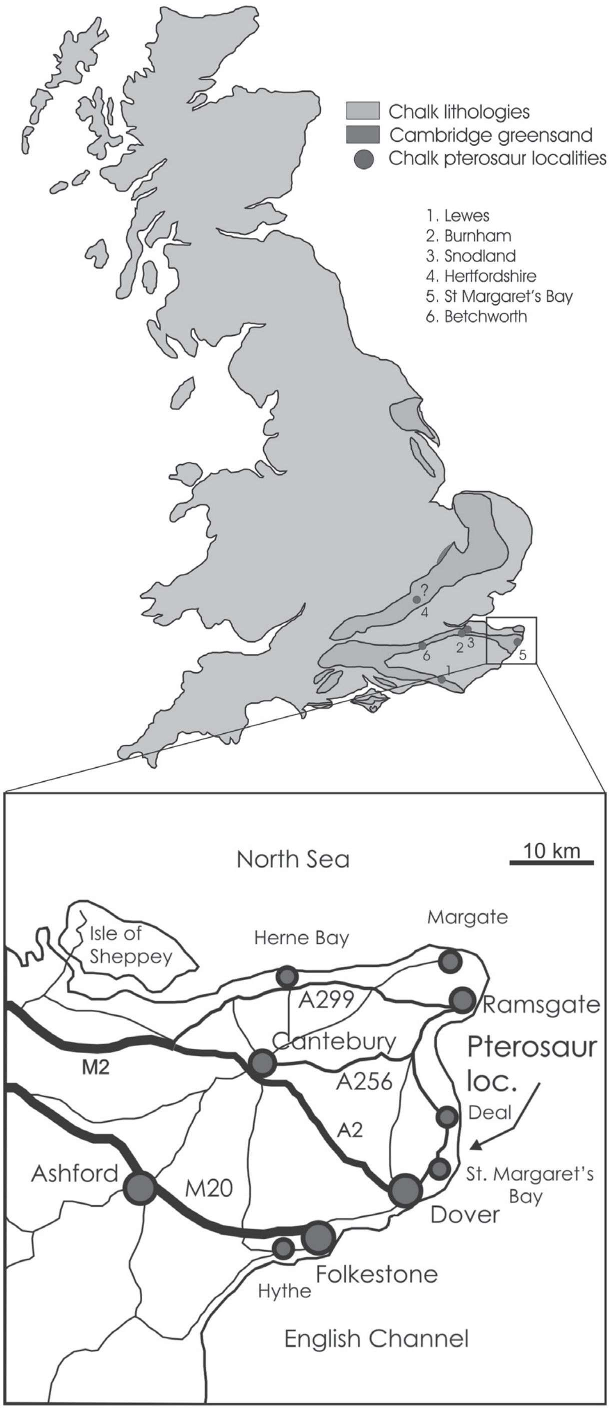

Figure 1: Location of English Chalk pterosaur localities and the locality of the pterosaur cervical vertebrae BMNH R16479a-c from the Coniacian of Kent, southern England.

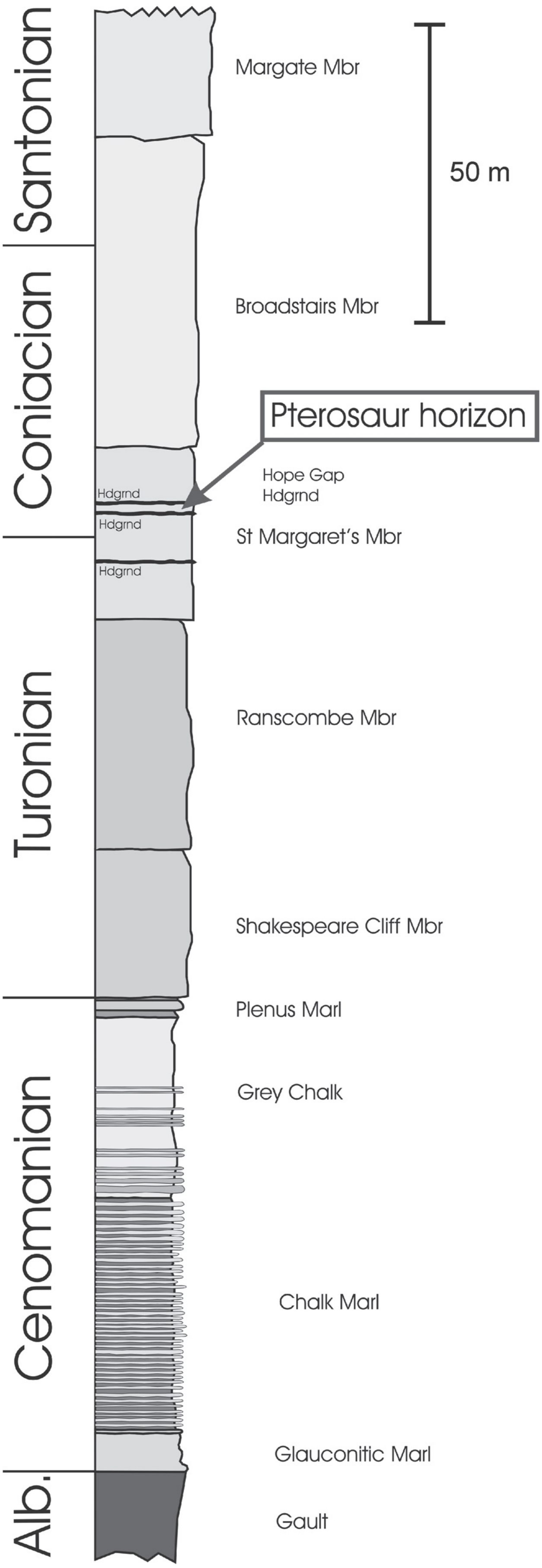

Figure 2: Stratigraphic column for the White Chalk Formation at St Margaret's Bay, Kent. Based on Jenkyns et al. (1994).

3. Material and preservation

The three vertebrae comprising BMNH R 16479a-c (Figs 3–7) were found in association and, due to the relative proportions of the separate elements, are thought to represent a continuous part of the cervical series. However, the articulatory facets of these vertebrae are broken and is not possible to demonstrate their articulation. The pieces are three-dimensionally preserved with only minimal distortion but some fracturing. Recent erosion appears to have removed much of the original material and has exposed the internal cavities of all three elements. This reveals that the internal voids are filled with chalk rather than remaining hollow or filled with diagenetic cements as seen in 3D pterosaur bones from the Brazilian Santana Formation (Wellnhofer 1991a). The bone is preserved with a rich dark brown colour typical of other pterosaur remains from the chalk of southeast England and there is some ferruginous staining. Two of the vertebrae, BMNH R 16479a and b (Figs 3–6), show some slight distortion of the neural spine due to crushing and BMNH R16479b (Figs 5–6) shows some fracturing and fragmentation indicative of compaction over a partial void.

4. Systematic palaeontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Lophocratia Unwin, 2003
?Azhdarchoidea Unwin, 1992
?Azhdarchoidea indet.

4.1 Descriptions

Recent abrasion and some minor distortion prevent accurate measurements of the total vertebral length, width and height from being determined with a high degree of accuracy. Nevertheless, some measurements have been obtained and some estimates of original dimensions have been determined by doubling measurements from the midline to the periphery.

BMNH R16479a (Figs 3–4). This is the most complete of the three vertebrae and comprises the main body of the centrum, a well preserved cranial aspect which is strongly procoelus and part of the neural spine. The specimen has a height of 40 mm from the ventral margin of the centrum to the preserved tip of the neural spine at the cranial face. The preserved width is 42 mm, with a width of 26 mm from the middle of the condyle to the distal margin of the left anterior zygopophysis indicates an original width across the anterior zygopophyses of 52 mm. The preserved length is 61 mm but the original length was probably 1 or 2 cm longer. The neural spine is incomplete. A lateral foramen is present on the left lateral centrum, and a circular bony trabecula on the right lateral margin exposes where compacta has been removed and probably represents a lateral foramen of the other side. The left lateral foramen lies slightly caudal of the middle of the centrum and is a flat lying oval 6 x 3 mm, with an elongate sulcus that widens caudally. The neural canal is circular on the cranial face of the vertebra with a diameter of 6 mm but is slightly tear-drop shaped on the caudal face. Either side of the neural canal on the cranial face are latero-neural foramina with a width of 2.5 mm. Above the neural canal is a series of four supra-neural foramina, the largest of which is bifurcated by an internal septum. On the cranial face a single latero-neural foramen is present with a diameter of only 1.5 mm. The left prezygopophysis projects craniolaterally beyond the centrum cotyle. The cotyle is approximately a flattened oval with a small ventral expansion that unites with a vertical ridge that meets the small cranially-projecting hypapophysis. No other articulatory processes are preserved and, although it is difficult to determine the precise position in the neck, this vertebra is probably from c3 to c6.

BMNH R16479b (Figs 5–6). This incomplete cervical vertebra comprises the caudal-most third of the centrum including the highly dorsoventrally depressed condyle and parts of the neural spine and left postzygapophysis and exapophysis. The specimen has a preserved width of 36 mm, and a preserved height of 58 mm, but the wide broken tip of the neural spine suggests a considerable height is missing. The caudal face displays a well defined neural canal with a diameter of 7 mm flanked by two prominent, slightly oval latero-neural foramina with diameters of 3.5 x 5 mm. The condyle of the centrum is dorsoventrally compressed with a maximum width of 26 mm and height of 7 mm. The right lateral surface of the specimen is highly worn, but the distance from the middle of the condyle to the lateral extremity of the right exapophysis is 21 mm, suggesting an original width of ~42 mm. The left exapophysis is buttressed by a sharp ridge extending from the condyle to a position 2 mm short of the distal tip of the exapophysis. The ventral surface is smooth with a prominent medial line, but not expressed as a ridge or keel. This medial line is also seen on the condyle of the centrum. There is a shallow sulcus on the preserved lateral face but no lateral foramina are presereved. The left postzygapophysis is damaged distally but appears to have been dorsocaudally directed.

BMNH R16479c (Fig. 7). This specimen is a fragment of vertebrae comprising a small portion of compacta from the right ventrolateral margin of the centrum and a small piece of neural canal. Had it not been associated with BMNH R16479a and b, only its thin bony compacta would have permitted its identification as pterosaurian. It is possibly a midcervical. No meaningful measurements can be taken, but the piece has maximum dimensions of length 43 mm, height 38 mm and thickness 16 mm.

5. Discussion

The new cervical vertebrae are identified as pterosaurian on account of their extremely thin bone walls and remarkable degree of internal void space. Within Pterosauria they are assigned to the Pterodactyloidea due to the lack of transverse processes, intertransversarial foramina and cervical ribs (Unwin 2003). Pterodactyloids show a remarkable degree of variation within their cervical vertebrae, but only the morphology of azhdarchid cervicals has thus far been used for specific diagnoses of taxa (e.g. Frey & Martill 1996; Pereda Suberbiola et al. 2003). The degree of variability seen in other pterosaur groups hints at their possible use in systematics (e.g. Owen 1859; Howse 1986; Andres & Norell 2005), but the potential of this has yet to be reached with few comprehensive anatomical descriptions of pterosaur vertebrae preserved in three dimensions. Notable exceptions are those of Wellnhofer (1991b) who provided excellent illustrations of the cervical series of *Anhanguera santanae* from Brazil; Codornú i (2005), who described the caudal vertebrae of the Argentinian ctenochasmatid *Pterodaustro*; Bonde & Christiansen (2003), who examined axial pneumaticity in the Late Jurassic *Rhamphorhynchus*; Howse

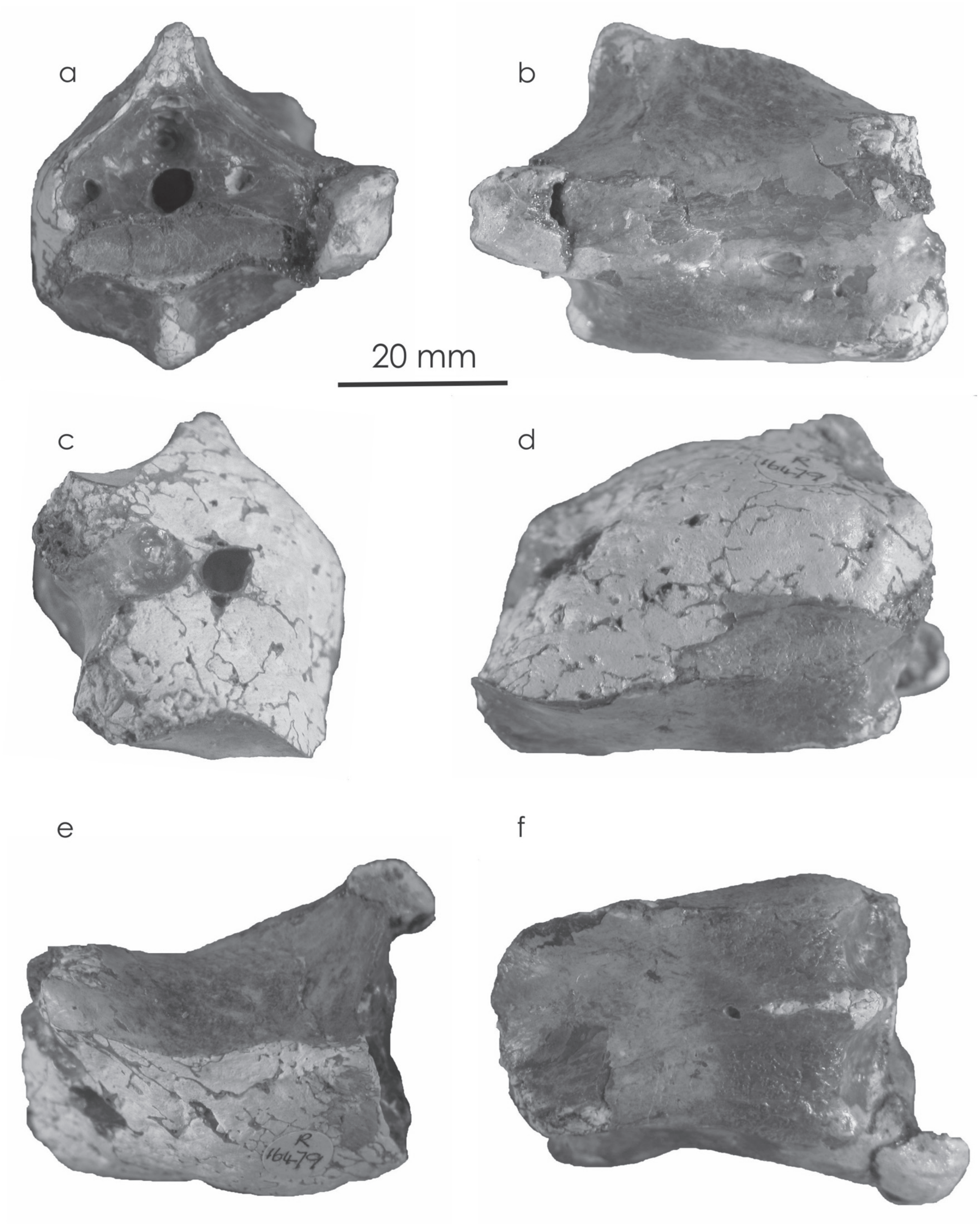

Figure 3: Mid-cervical vertebra of an indeterminate azhdarchoid pterosaur, BMNH R 16479a, from the White Chalk Formation of St Margaret's Bay, East Kent. **a**, cranial aspect. **b**, right lateral aspect. **c**, eroded caudal aspect. **d**, eroded right lateral aspect. **e**, dorsal aspect. **f**, ventral aspect.

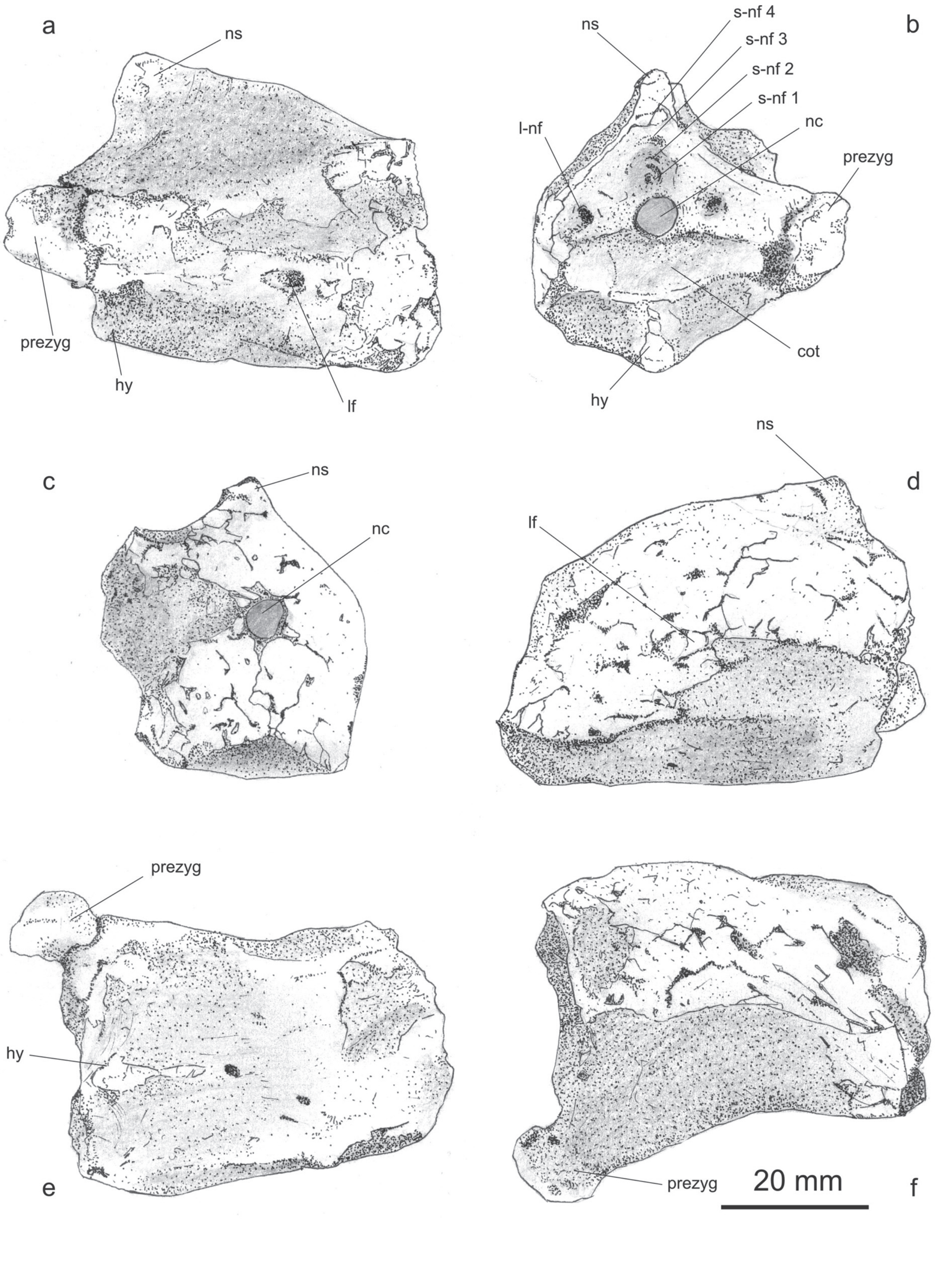

Figure 4: Drawings of indeterminate azhdarchoid mid cervical vertebra BMNH R 16479a. **a**, left lateral view; **b**, cranial view; **c**, caudal view; **d**, right lateral view; **e**, ventral view; **f**, dorsal view. Abrreviations: con, condyle; cot, cotyle; exop, exapophysis; exop car, exopophyseal carina; hy, hypopophysis; lf, lateral foramina; l-nf, latero-neural foramina; nc, neural canal; ns, neural spine; postzyg, postzygopophysis; prezyg, prezygopophysis; s-nf, supra-neural foramina.

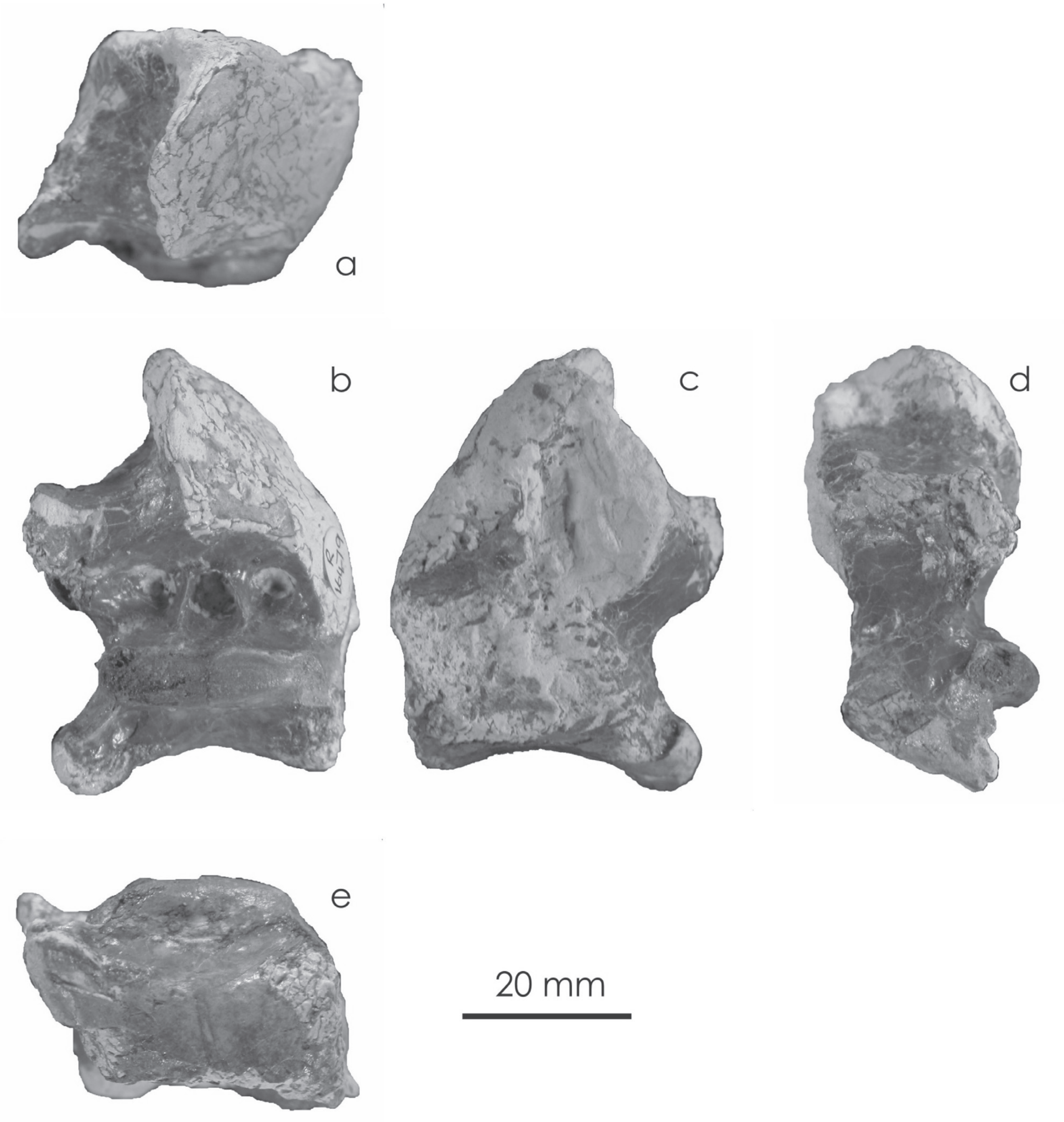

Figure 5: Mid cervical vertebra of an indeterminate ornithocheiroid pterosaur, BMNH R 16479b, from the White Chalk Formation of St Margaret's Bay, East Kent. **a**, dorsal aspect. **b**, caudal aspect. **c**, cranial aspect. **d**, right lateral aspect.

(1986) who described variation in a wide range of pterodactyloid cervical vertebrae, and GODFREY & CURRIE (2005) with excellent descriptions and illustrations of azhdarchid cervical vertebrae from Canada.

A broad distinction between pterodactyloid cervical vertebrae can be made based on the length of the centra (HOWSE 1986), with most forms either bearing short or hyperelongate centra. The latter morphology occurs in Ctenochasmatoidea, Lonchodectidae and Azhdarchidae along with several taxa from the Chinese Jehol Group such as *Chaoyangopterus* and *Jidapterus* (e.g. WELLNHOFER 1970; LAWSON 1975; DONG 1982; HOWSE 1986; GODFREY & CURRIE 2005; DONG et al. 2003; UNWIN 2003; WANG & ZHOU 2003; HENDERSON & PETERSON 2006). Although apparently evolved convergently, these groups all combine elongate centra with long, low neural spines and, in the case of azhdarchids, prominent condyles and horn-like zygapophyses. The short centra of BMNH R16479a-b are quite unlike the centra of these forms, although the well-developed ventral protrusion of the centrum beneath the condyle/cotyle in the new specimen is also seen in azhdarchids (e.g. FREY & MARTILL 1996; GODFREY & CURRIE 2005).

Short-bodied cervical vertebrae are found across Ornithocheiroidea, some azhdarchoids (Tapejaridae and *Tupuxuara*) and possibly in Dsungaripteroidea. The cervical vertebrae of Ornithocheiroidea often bear relatively large lateral pneumatic foramina approximately midway along the length of the centrum (EATON 1910; HOOLEY 1913; HOWSE 1986; WELLNHOFER 1991b; KELLNER & TOMIDA 2000; BENNETT 2001; 2003;

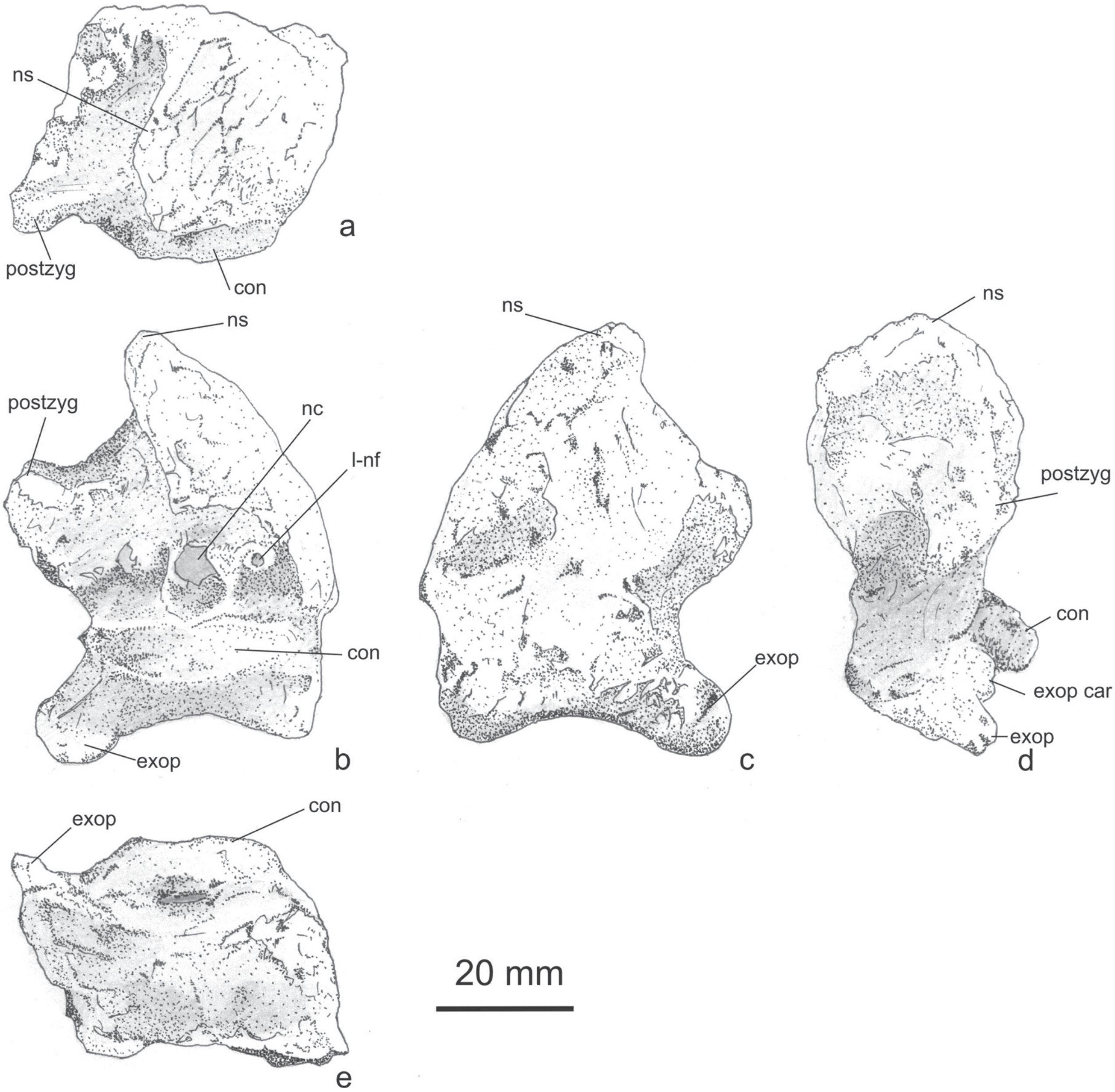

Figure 6: Drawings of indeterminate azhdarchoid mid cervical vertebra BMNH R 16479b. **a**, dorsal view; **b**, caudal view; **c**, cranial view; **d**, left lateral view; **e**, ventral view. For abbreviations see Figure 4.

VELDMEIJER 2003; ANDRES & JI 2006). The new material differs from these in having considerably smaller lateral pneumatic foramina that are more caudally located. Furthermore, the lateral foramina of BMNH R1647 are single perforations rather than the paired openings seen in some ornithocheirids such as *Anhanguera* sp. (WELLNHOFER 1991b). In addition, the neural spines of BMNH R16479a and b appear to extend along the entire centrum as an elongate blade, whereas those of ornithocheiroids are confined to the mid-length of the centra (HOWSE 1986; WELLNHOFER 1991b; BENNETT 2001). Further distinctions between the new material and ornithocheiroid cervicals are the relatively straight interzygapophyseal ridge of BMNH R16479a compared to the 'crescent' shaped morphology of ornithocheiroids, and the greater depth of the centrum beneath the condyle/cotyle of the chalk specimen.

The cervical vertebrae of Dsungaripteroidea are poorly known. Those that have been figured (e.g. *Germanodactylus*, *Kepodacylus*) are often crushed or are from juvenile individuals (WELLNHOFER 1970; HARRIS & CARPENTER 1996; BENNETT 2006). Recently, ANDRES & NORELL (2005) described a cervical vertebra from the Early Cretaceous of Öösh, Mongolia which they referred to Tapejaroidea and, under the classification of KELLNER (1996), Tapejaroidea includes Dsungaripteridae, Tapejaridae [*sensu* KELLNER (1989)] and Azhdarchidae. However, this vertebra differs in only minor detail from C5/6 of *Anhanguera*, and is probably an ornithocheirid. Perhaps the best record of a dsungaripterid cervical vertebra, therefore, is a single cervical from the possible dsungaripteroid *Kepodactylus*

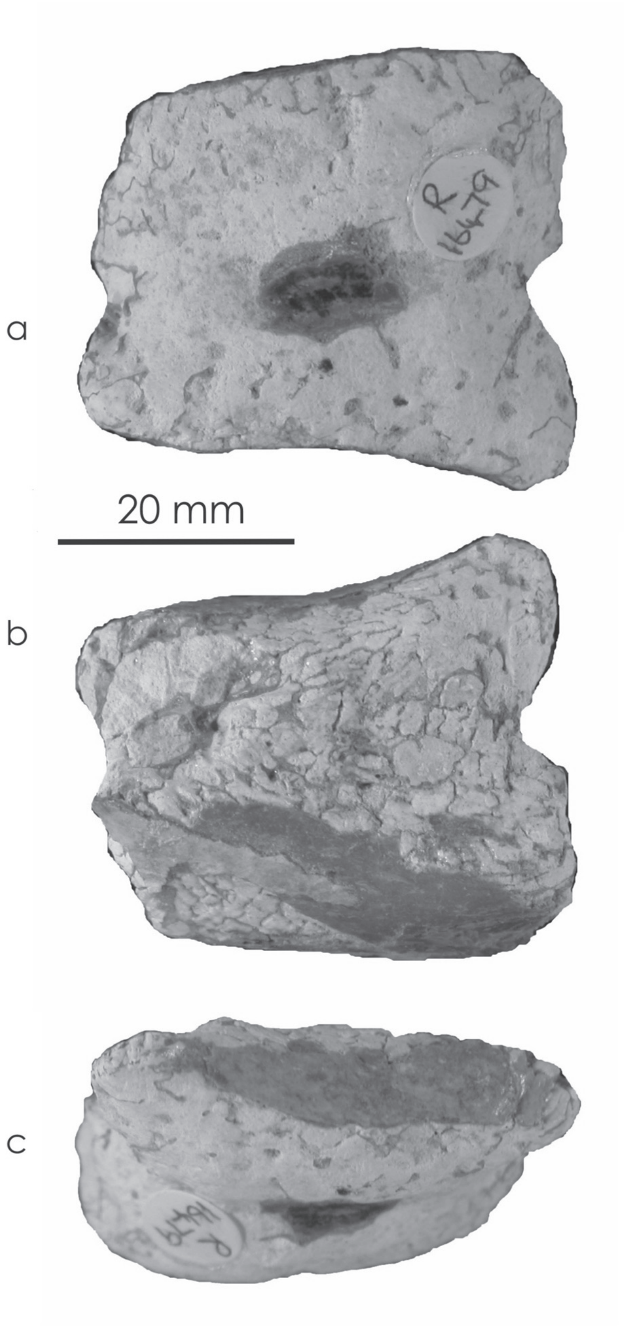

Figure 7: Partial, presumed cervical vertebra of an indeterminate ornithocheiroid pterosaur, BMNH R 16479c, from the White Chalk Formation of St Margaret's Bay, East Kent. **a**, highly eroded ?left lateral aspect. **b**, slightly oblique right lateral aspect. **c**, dorsal view.

of the Late Jurassic Morrison Formation of the USA (Harris & Carpenter 1996). This specimen is slender and possesses a large, caudally located lateral foramen and, although dorsoventrally crushed, appears to be about twice as long as wide. It apparently lacks both a hypapophysis and exapophyses and bears a neural spine that only occupies the posterior two-thirds of the centrum length. Furthermore, there appears to be little ventral development of the centrum beneath the condyle/cotyles. This morphology is quite distinct from the new material described here, suggesting that BMNH R16479 cannot belong within Dsungaripteroidea if *Kepodactylus* has vertebrae representative of this clade. However, given the questionable classification of *Kepodactylus*, more definitively identified dsungaripteroid cervicals are needed to verify this conclusion.

BMNH R16479 is most comparable with the cervical vertebrae of non-azhdarchid azhdarchoids, including Tapejaridae and some members of Neoazhdarchia. South American representatives of these forms are known from complete and three-dimensionally preserved skeletons (e.g. Wellnhofer & Kellner 1991; Kellner & Hasagawa 1993), but adequate accounts of this material await detailed description and virtually no figures have been published.

Both *Tapejara* and *Tupuxuara* share several features with BMNH R16479 including centra-length neural spines, small lateral foramina, developed exapophyses, dorsolaterally positioned latero-neural foramina and a complex of supraneural foramina set within a deep concavity on the cranial face. The cervicals of *Tupuxuara*, however, have a nearly square outline in dorsal aspect with dorsoventrally compressed centra, and these traits compare poorly with those of BMNH R16479. Closer similarity is seen with the vertebrae of *Tapejara wellnhoferi,* which are relatively slender and bear deeper centra than those of *Tupuxuara* (Wellnhofer & Kellner 1991). However, both *Tapejara* and *Tupuxuara* are more strongly procoelous than BMNH R16479. Despite this, BMNH R16479 is more similar to vertebrae of these forms than those of any other pterosaur and is therefore tentatively referred to Azhdarchoidea. We stress that some caution be applied to this identification: given the postcranial similarities between dsungaripteroids and azhdarchoids (e.g. Unwin 2003) and propensity for convergence in pterodactyloid cervical morphology (e.g. Howse 1986), the morphology of dsungaripteroid cervical vertebrae may also prove similar to that of azhdarchoids and prohibit allocation of BMNH R16479 to either clade.

6. Conclusions

Upper Cretaceous occurrences of pterosaurs in Europe are rare and appear to be of limited diversity. To date, only ornithocheirids and the lophocratan *Lonchodectes* have been reliably reported for the English Upper Cretaceous, but these remains form the Cenomanian Cambridge Greensand are derived from Albian strata (Unwin 2001). In mainland Europe, ornithocheirids are known from northern France (Vullo 2007), while and azhdarchids have been recorded from Romania (Buffetaut et al. 2003), France (Buffetaut et al. 1996, 1997; Buffetaut 2001), Spain (Company et al. 1999) and Hungary (Ősi et al. 2005). In possibly representing a non-azhdarchid azhdarchoid, BMNH R16479 is an important contribution to knowledge of European pterosaur diversity in the Late Cretaceous.

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