

The first pterosaur from the Cenomanian (Late Cretaceous) *Lagerstätten* of Lebanon



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A pterosaur is reported for the first time from a Late Cretaceous marine *Lagerstätte* in Lebanon, which is famous mainly for its rich ichthyofauna. The specimen, from the early Cenomanian Hâqel *Lagerstätte*, is a partial, articulated forelimb that belongs to a relatively small, adult individual of the clade Pteranodontoidea *sensu* Kellner. It is the most complete skeletal remnant of a pterosaur described to date from the African-Arabian Plate and the most complete of the very sparse Cenomanian pterosaur record. © 2001 Academic Press

KEY WORDS: Cenomanian; pterosaurs; African-Arabian Plate; Lebanon.

1. Introduction

The Lebanese *Lagerstätten* of Late Cretaceous age are famous worldwide for their rich and well-preserved fossil assemblage. Fishes found in these localities were first mentioned by Herodotus 2450 years ago and have been studied in more recent times beginning in the mid 19th century.

Four main fossiliferous sites are known: Hâqel (=Hakel), Hjoûla (=Hadjoula), Nammoûra, and Sâhel Aalma (names are taken from the Guide Stephan Map of Lebanon, scale 1:200,000). They are located at 40, 35, 25, and 20 km respectively NNE of Beirut, along the coastal mountain chain (Figure 1). The Sâhel Aalma site is the youngest, and is of late Santonian age (Garassino, 1995, p. 4). Based on the biostratigraphy of benthic foraminifers, the age of the Nammoûra site is regarded as late middle Cenomanian (Dalla Vecchia & Venturini, 1999), and the age of the Hâqel and Hjoûla *Lagerstätten* is early Cenomanian (Saint Marc, 1974, p. 200). The Hâqel site appears to be slightly younger than the Hjoûla site as it is about 20 m higher stratigraphically (Hückel, 1970).

The vertebrate fossil assemblage of all the sites is dominated by fishes [Hückel, 1970; F. M. Dalla Vecchia (FMDV), pers. obs.]. They are very common, well preserved, and particularly diverse at the

Hâqel and Hjoûla sites (FMDV, pers. obs.). Reptiles are unknown at Hjoûla and tend to be very rare at the other sites. At Nammoûra, they are represented by articulated skeletons of aquatic taxa: turtles, dolichosaurs and marine varanoids (Dalla Vecchia & Venturini, 1999; Dal Sasso & Renesto, 1999). Some small isolated feathers have also been found at Nammoûra (Dalla Vecchia & Venturini, 1999). Hâqel has, so far, only furnished a *Pachyrachis*-like marine reptile (Dal Sasso & Renesto, 1999). The rich invertebrate fauna consists mainly of crustaceans (Garassino, 1994), cephalopods and rarer ophiuroids and pelagic crinoids (Hückel, 1970; FMDV, pers. obs.). Terrestrial plants are almost absent at Hjoûla and rare at Hâqel, but are among the most common fossils at Nammoûra (Dalla Vecchia & Venturini, 1999).

Specimens from the Hâqel, Hjoûla and Nammoûra sites can be distinguished on lithological (colour and grain of the limestone, presence or absence of chert) and preservational features (abundance of non-shelly fossils, relative abundance of scattered fragments of fish and crustaceans, colour of these fragments; FMDV, pers. obs.).

Pterosaurs are an important, if rare, component of tetrapod faunas found in the Mesozoic marine *Konzervat Lagerstätten* of Triassic and Jurassic age, such as, for example, those of northern Italy (Late Triassic, Norian), and Germany: Holzmaden and

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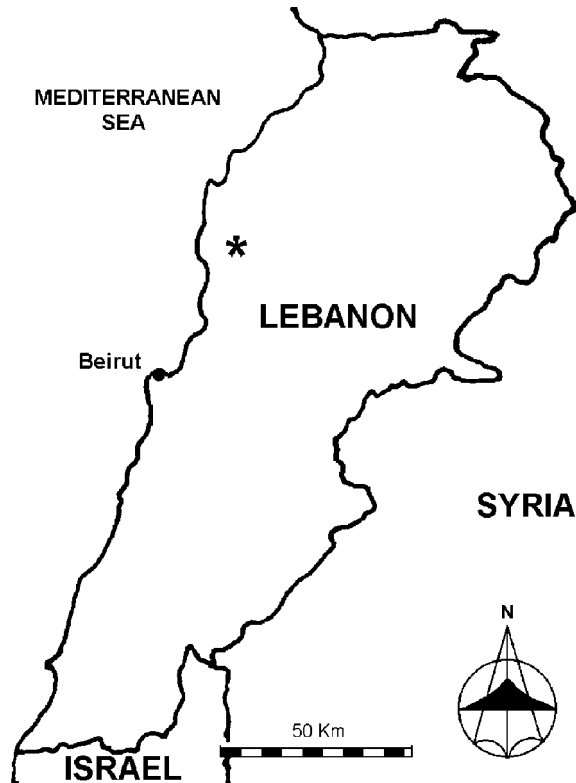


Figure 1. Location of the Hâqel site (asterisk) where the specimen MSNM V 3881 was collected.

Banz (Early Jurassic), Solnhofen and Nusplingen (Late Jurassic). All of these *Konzervat Lagerstätten* formed in dysoxic-anoxic basins and are characterized by the presence of well-preserved fishes, reptiles, invertebrates (mainly crustaceans, cephalopods and echinoderms) and terrestrial plants. Pterosaurs appear to be much rarer in similar marine *Konzervat Lagerstätten* of Cretaceous age. They are relatively common in the marine, vertebrate rich Niobrara Formation (Coniacian–Campanian) of the western USA (Wellnhofer, 1991a; Kellner, 1994), which, however, is not a *Konzervat Lagerstätte*.

To date no pterosaur remains have been reported from the Lebanese Cretaceous *Konzervat Lagerstätten*, among the richest vertebrate fossil localities in the world, despite having been intensively quarried for commercial and industrial purposes (the Hâqel and Hjoûla sites are quarried only for fossils). Here we describe the first Lebanese pterosaur, which, according to its label, was unearthed in a quarry at Hâqel (Figure 1). The specimen is preserved in the typical lithology of this site, which consists of grey limestone with bedding surfaces of grainy aspect, sometimes with chert, and is highly fossiliferous (containing abundant, scattered, fragmentary fish remains,

crustaceans and coprolites). The pterosaur is housed in the Museo Civico di Storia Naturale di Milano, under the number MSNM V 3881. We follow the phylogenetic analysis of pterosaurs by Kellner (1996a, b).

Abbreviations. AMNH, American Museum of Natural History, New York; MSNM, Museo Civico di Storia Naturale di Milano. For other abbreviations, see the caption to Figure 2.

2. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Ornithocheiroidea Seeley, 1901 (=Pteranodontoidea *sensu* Kellner, 1996a, b)

Ornithocheiroidea gen. et sp. indet.

Figure 2

Description. The specimen is preserved on a slab $40 \times 38 \times 2.5$ mm in size, together with fragmentary remains of small undetermined fishes and crustaceans. It consists of the left forelimb of a pterosaur, preserved from the distal half of the humerus to the distal part of wing phalanx 1. Several bones have been displaced from their original position, but are all closely associated. The long bones have been heavily crushed by lithostatic pressure. Unfortunately, the counterpart, containing parts of the bones, was not recovered.

Only the distal half of the humerus (96 mm long) is preserved, exposed in posterodorsal view (all orientations are in flight position, following Wellnhofer, 1985). There is a well-developed, wing-like *tuberculum supracondyloideum laterale* located about 40 mm from the distal extremity of the bone. The radius and ulna are exposed in posterior view; they are tightly appressed and both are still articulated with the humerus. The ulna is 183.5 mm long and the radius 178 mm. Although these bones are crushed, the diameter of the radius is clearly less than half the mid-shaft diameter of the ulna. The radial/ulnar width ratio (measured at mid-shaft) is about 0.37. Muscle scars are present on the exposed sides of the proximal part of both radius and ulna. No pneumatic foramina were observed. A small bone with a circular outline, possibly a sesamoid, is preserved in front of the distal part of the radius.

The proximal carpals are fused to form a single bone that is still articulated with the radius and ulna, and has a rectangular outline in posterior view. Such an outline is evident in the proximal carpals of many

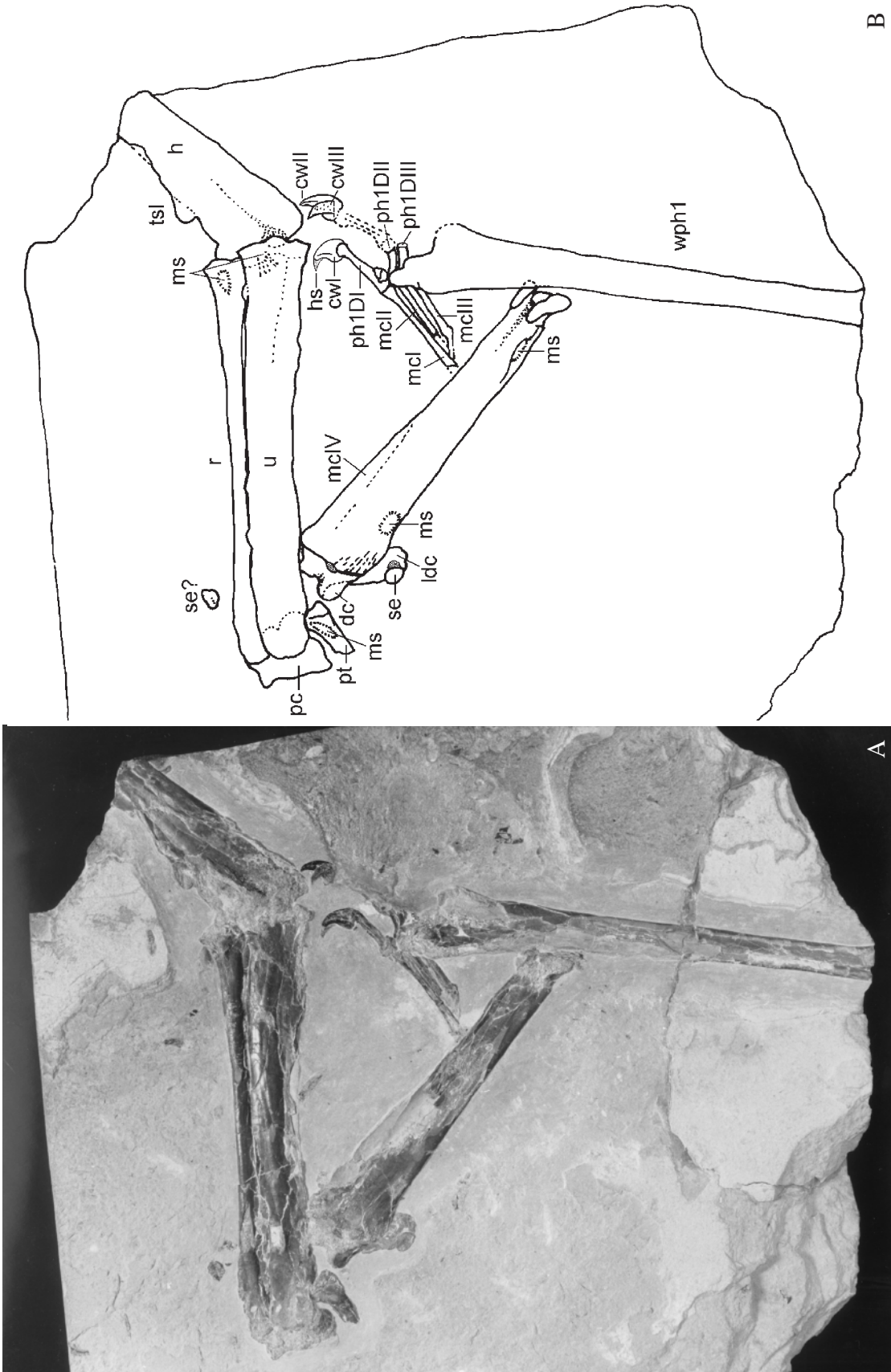


Figure 2. MSNM V 3881. A, the specimen, a partially preserved left forelimb of a pteranodontoid pterosaur. B, interpretative drawing. Key to abbreviations: cwI-III, manual claws of digits I-III; dc, distal carpal; h, humerus; hs, remnant of the horny sheath of the ungual phalanx; ldc, distal lateral carpal; mclI-III, metacarpals I-III; mclIV, metacarpal IV (wing metacarpal); ms, muscle scar; pc, proximal carpal; ph1-3DI-III, manual phalanges (other than wing-phalanges); pt, pteroid bone; r, radius; se, sesamoid; se, sesamoid; tsl, *tuberculum supracondyloideum laterale* of humerus; u, ulna; wph1, wing phalanx 1. Scale bar represents 100 mm.

other pterodactyloids, particularly pteranodontoids (e.g., Wellnhofer, 1985, 1991b; Kellner & Tomida, 2000). The distal carpals are fused to form a single unit that is closely appressed to the wing metacarpal (=metacarpal IV), but is detached from the proximal carpal, and shows the posterior surface. In this view, it has an H-shaped outline, with a central depression in both the proximal and distal margins, thus resembling the distal carpals of *Anhanguera araripensis* (Wellnhofer), *A. santanae* (Wellnhofer), and *A. piscator* Kellner & Tomida (Wellnhofer, 1985; Kellner & Tomida, 2000). The proximal part of the lateral distal carpal (=medial carpal according to Padian, 1984) is covered by the wing metacarpal. The distal part exhibits the articular facet for the pteroid, which is occupied by a rounded, lozenge-shaped sesamoid. A sesamoid has also been observed in this position in pterodactyloids such as *Pteranodon* Marsh (Bennett, 1993), some anhanguerids (A. W. A. Kellner, pers. obs.), and also in some basal pterosaurs such as *Eudimorphodon* Zambelli and *Preondactylus* Wild (Wild, 1978; Dalla Vecchia, 1998). Only the proximal portion of the pteroid is preserved, displaced from its original position and now located near the distal articulation of the ulna. There is an elongate muscle scar on the exposed surface.

The wing metacarpal is a robust bone, 154 mm long, whose proximal end is as wide as that of the ulna, or even wider. The posterodorsal corner has a rough surface with small longitudinal ridges, which suggest the presence of the attachment site of a muscle or a tendon. A few millimetres distal to this point, a muscle scar is present, and another, longer muscle scar is found on the distal, posterodorsal portion of the wing metacarpal, near the dorsal condyle. This latter scar is located on a bony ridge that corresponds to the *crista metacarpi* of basal pterosaurs, and supposedly the proximal attachment for the flexor muscle of the wing (Wild, 1978). No foramina are visible on this posterior and posterodorsal side of the bone. The other metacarpals, with their corresponding phalanges in natural articulation, are detached from their original positions, and rotated and displaced away from metacarpal IV. Most of their proximal portions are not preserved. The proximal part of metacarpal III appears narrower than the distal portion and diverges to form an obtuse angle with the latter. The basal phalanges of digits II and III seem to have curved shafts like the proximal phalanx of manual digit III of *Pterodactylus* Cuvier (Wellnhofer, 1978, fig. 12). However, they are partly covered by the *processus tendinis extensoris* of wing phalanx 1 and this may have affected their shape. All the ungual phalanges are less elongate than those figured by Wellnhofer (1985, fig. 32). The

unguals have traces of a black film on their surface and in the rock where the bone split off that could be the remnant of the horny sheath.

The preserved portion of wing phalanx 1 is 202 mm long. The proximal part, which bears a prominent *processus tendinis extensoris*, is poorly preserved. The process is not clearly separate from the proximal part of the phalanx, as is typical of immature individuals (Bennett, 1993; Kellner & Tomida, 2000). The presence of proximal and distal syncarpals also suggests that the individual was mature (Bennett, 1993; Kellner & Tomida, 2000). The distal part of the preserved portion of the phalanx is wider (16 mm) than the preceding mid-shaft portion, where the minimum width is 13 mm. Furthermore, the distal posterior margin is deflected posteriorly with respect to the preceding straight tract. This feature is also observed in the distal, terminal part of wing phalanx I in pterodactyloids (e.g., Wellnhofer, 1985, 1991b; Kellner & Tomida, 2000), and suggests that the wing phalanx 1 of MSNM V 3881 is nearly complete. If this is the case, the estimated total length of the wing phalanx I is likely to have been about 212 mm; thus the wing phalanx I is comparatively shorter than those of many other Cretaceous pterodactyloids (wph1/u and wph1/mcIV respectively 1.15 and 1.38 in the Lebanese specimen; for other pterosaurs, see Table 1).

Measurements. Measurements of the skeletal elements of MSNM V 3881: humerus (incomplete), 96 mm; wing metacarpal (metacarpal IV), 154 mm; radius, 178 mm; ulna, 183.5 mm; wing phalanx 1 (incomplete), 202 mm.

3. Discussion

Despite its present geographic position within the Asian continent, the Arabian Peninsula to which Lebanon belongs was part of the African continent during Mesozoic times (Philip *et al.*, 1993). The opening of the Red Sea during the mid Tertiary separated the Arabian region from the rest of the African Plate (Polcyn *et al.*, 1999) and the Alpine orogeny subsequently sutured it to the southern margin of the Euroasiatic Plate. Therefore, the Lebanese pterosaur is one of the few examples that have been reported from the greater African continent as it existed in Mesozoic times, and is the most complete of those described to date. To emphasize this point, we think that consideration of the scarcity of the pterosaur record in this region of the world is worthwhile.

Table 1. U/mcIV, wph1/u and wph1/mcIV ratios in pterodactyloid pterosaurs. Where not specified otherwise, the measurements are taken from Wellnhofer (1970, 1978, 1985, 1991a, b). Key to symbols and abbreviations: * used the radial length instead of ulnar length; ** data after Frey & Martill (1994); *** data after Kellner & Tomida (2000); ° taxon considered to be based on immature individuals of the taxon listed just above in the table (e.g. *Pterodactylus antiquus* is considered to be based on immature specimens of *Pterodactylus longicollum*), following Bennett (1996); + estimated values; — ulnar, wing phalanx 1 and/or metacarpal IV lengths unknown; † specimen AMNH 6158, left forelimb (A. W. A. Kellner, pers. obs.).

	u/mcIV	wph1/u	wph1/mcIV
MSNM V 3881	1.19	1.15+	1.38+
<i>Pterodactylus longicollum</i>	0.80*	1.54*	1.23
<i>Pterodactylus antiquus</i> °	1.34*	1.03*	1.39
<i>Pterodactylus kochi</i> °	1.36*	0.96*	1.31
<i>Germanodactylus cristatus</i>	1.14*	1.12*	1.27
<i>Pterodactylus elegans</i> °	1.21*	1.06*	1.29
<i>Germanodactylus rhamphastinus</i>	~1.43*	~0.90*	1.29
<i>Gallodactylus canjuersensis</i>	0.65*	2.75*	1.79?
<i>Gallodactylus suevicus</i>	0.80*	1.62*	1.30
<i>Ctenochasma gracile</i>	1.50*	1.26*	1.88
<i>Pterodactylus micronyx</i> °	0.77*	1.48*	1.15
<i>Huanhepterus quingyangensis</i>	~1.60	~0.90	~1.43
<i>Eosipterus yangi</i>	1.30	1.02	1.33
' <i>Ornithodesmus</i> ' <i>latidens</i>	—	1.03	—
<i>Pterodaustro guinazui</i>	1.31*	1.14*	1.49
<i>Noriopterus complicidens</i>	0.70	1.68	1.18
<i>Pteranodon</i> sp.†	0.63	1.95	1.23
<i>Nyctosaurus gracilis</i>	0.64	1.96	1.26
<i>Santanadactylus pricei</i>	1.41	1.53	2.16
<i>Santanadactylus</i> sp.	1.45	1.42	2.06
? <i>Santanadactylus</i> **	1.42	1.46	2.08
<i>Anhanguera santanae</i>	~1.52	—	—
<i>Anhanguera piscator</i> ***	1.52	—	—
<i>Anhanguera</i> sp.***	1.50	1.52	2.27
<i>Arthurdactylus conandoylei</i> **	1.38	1.43	1.96

The current fossil record of African pterosaurs contains: (1) fragmentary remains from the Upper Jurassic–Lower Cretaceous of Tanzania (Reck, 1931; Galton, 1980) that, according to Unwin & Heinrich (1999), represent mostly a dsungaripteroid pterosaur, but some belong to a 'ramphorhynchoid'; (2) isolated teeth from the ?Berriasian of Morocco (Sigogneau-Russell *et al.*, 1998; Knoll, 2000); (3) undescribed azhdarchid remains from the ?Aptian of Niger (Serenio *et al.*, 1998); (4) the anhanguerid *Sirocopteryx moroccensis* Mader & Kellner, represented by the anterior tip of a skull (Mader & Kellner, 1999), some azhdarchid cervical vertebrae (Kellner & Mader, 1996), isolated pterosaur teeth (Kellner & Mader, 1997), and fragmentary remains of supposed tapejarids and pteranodontids (Wellnhofer & Buffetaut, 1999), all from the continental Albian or Cenomanian of Morocco; (5) one isolated ornithocheirid tooth found in the Albian of Tunisia (Benton *et al.*, 2000); (6) an incomplete wing metacarpal from the upper

Cenomanian–Turonian (Monteillet *et al.*, 1982) of Congo identified as "close to *Ornithocheirus*" (Swinton, 1948, p. 238); (7) an azhdarchid cervical vertebra and a portion of a tibia from the Campanian–Maastrichtian of Senegal (Monteillet *et al.*, 1982); (8) an undescribed "pterodactyloid hindlimb" from the lower Cenomanian of Israel (Tchernov *et al.*, 1996); (9) the azhdarchid *Arambourgiania philadelphiae* (Arambourg), represented by a cervical vertebra, from the upper Maastrichtian of Jordan (Arambourg, 1954; Frey & Martill, 1996) and other fragmentary bones from the same locality possibly belonging to this taxon (Frey & Martill, 1996); (10) two brain casts and some bones possibly belonging to azhdarchids from the upper Campanian of Israel (Lewy *et al.*, 1993).

Cenomanian pterosaurs are mainly from the Cambridge Greensand of England (Wellnhofer, 1978, 1991a), but the several nominal species of *Ornithocheirus* Seeley, *Brasileodactylus* Kellner,

Coloborhynchus Owen and *Lonchodectes* Hooley (D. Unwin, pers. comm., 2000) from that formation are only represented by fragmentary material (see Wellnhofer, 1978). Furthermore, all are reworked and most probably derived from Albian strata (Wellnhofer, 1991a). The Lebanese specimen represents one of the very few undoubted Cenomanian pterosaurs and certainly the most complete one.

The northwestern part of the Arabian shield was covered by a wide carbonate platform during Cenomanian times (Philip *et al.*, 1993). The land was situated relatively far from Lebanon, in the present west-southwest part of the Arabian Peninsula (Saint-Marc, 1978; Philip *et al.*, 1993). The depositional environment of the Hâqel site was a small, oxygen-depleted, marine basin between the outer carbonate platform and a large deep basin (Saint-Marc, 1974). According to these palaeogeographic reconstructions, the pterosaur was deposited in a subequatorial marine environment hundreds of kilometres from the continent. However, it is possible that the animal lived on parts of the carbonate platform that emerged as islands.

MSNM V 3881 has an ulna and a first phalanx of manual digit IV that are less than twice the length of metacarpal IV. These features are regarded as pterodactyloid synapomorphies (Kellner, 1996a). The relative shortness of metacarpal IV distinguishes this specimen from *Gallodactylus canjuersensis* Fabre, *Pteranodon* Marsh, *Nyctosaurus gracilis* (Marsh), *Quetzalcoatlus* Lawson, and *Zhejiangopterus linhaiensis* Cai & Wei, all of which have a wing metacarpal length >1.5 times that of the ulna or antebrachium (Bennett, 1994; Unwin & Lü, 1997). The relatively stocky metacarpal IV excludes *Dsungaripterus weii* Young and *Noriopterus complicidens* Young and Tapejaridae, which have an extremely slender wing metacarpal (Kellner, 1996a).

In MSNM V 3881 the diameter of the radius is small relative to that of the ulna (diameter $r < 0.5$ diameter u). This synapomorphy unites '*Ornithodesmus*' ('*Ornithodesmus*' *latidens*, the effective type of the genus '*Ornithodesmus*', requires a new generic name; see Howse & Milner, 1993) and Anhangueridae (Kellner, 1996a), and suggests that the Lebanese specimen is related to this clade. '*Ornithodesmus*' and anhanguerids are part of the Pteranodontoidea (*sensu* Kellner, 1996a, b), in which *Pteranodon* (the only other pteranodontoid) occupies a basal position. MSNM V 3881 differs from all pteranodontoids in the proportion of the ulna relative to the wing metacarpal ($u/mcIV = 1.19$), which is intermediate between that of *Pteranodon* (e.g., *Pteranodon* sp. AMNH 6158: 0.63) and anhanguerids (e.g., *Anhanguera piscator*: 1.52).

Although MSNM V 3881 might well belong to a different, new taxon, we refrain from naming it until more complete material becomes available.

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