

A new azhdarchoid pterosaur from the Cenomanian (Late Cretaceous) of Lebanon

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Abstract A new pterosaur, *Microtuban altivolans* gen. et sp. nov., is described from the Sannine Formation of northern Lebanon. The specimen is the first pterosaur from the Early Cenomanian (Late Cretaceous) locality of Hjoûla and is regarded as the most complete pterosaur fossil discovered from Africa. While postcranial characters indicate a possible relationship with members of the Thalassodromidae or Chaoyangopteridae, the specimen possesses an exceptionally short wing-finger phalanx 4, forming only 1.1% of the total length of the wing-finger. Its appearance along with an unnamed ornithocheiroid from the slightly younger locality of Hâqel suggests that a number of pterosaur taxa existed within the local area, perhaps living on exposed carbonate platforms.

Keywords Pterosaur · Azhdarchoidea · *Microtuban* · Cretaceous · Lebanon

Abbreviations

GMN Geological Museum of Nanjing (China)
HGM Henan Geological Museum, Zhenzhou (China)
IMCF Iwaki Coal and Fossil Museum (Japan)
MN Museu Nacional, Rio de Janeiro (Brazil)
SMNK Staatliches Museum für Naturkunde Karlsruhe (Germany)
TMM Texas Memorial Museum (USA)

ZHNM Zhejiang Museum of Natural History, Hanzhou (China)

Introduction

While the Late Cretaceous Lagerstätten deposits of northern Lebanon are famous for the exceptional preservation of their invertebrate and fish faunas, the remains of higher vertebrates are rare. Although pterosaurs, a group of aerial archosauromorphs, had effectively achieved a world wide distribution during the latter part of the Mesozoic, the first pterosaur specimen from the Lebanese carbonates was only recently described by Dalla Vecchia et al. (2001), consisting of a single isolated forearm of a Late Cretaceous ornithocheiroid. The deposits of northern Lebanon therefore follow a more general pattern observed across the whole of the African plate, where pterosaur material is both rare and consists of a rather sparse collection of fragmented bones or teeth. To date, fossil discoveries have included: “rhamphorhynchoids” (Unwin and Heinrich 1999); ornithocheiroids, anhanguerids and pteranodontids (Swinton 1948; Mader and Kellner 1999; Wellnhofer and Buffetaut 1999); the dsungaripteroid *Tendaguripterus recki* (Unwin and Heinrich 1999) from the Upper Jurassic of Tendaguru, Tanzania; and several members of the Azhdarchoidea (Wellnhofer and Buffetaut 1999), including the azhdarchids *Arambourgiania philadelphiae* (Arambourg 1954) and *Phosphatodraco mauritanicus* (Suberbiola et al. 2003). Recent additions to these also include two humeri belonging to pterosaurs of the Dsungaripteroidea and the Archaeopterodactyloidea from the Upper Jurassic of Tendaguru (Costa and Kellner 2009), and the aforementioned specimen from northern Lebanon (Dalla Vecchia et al.

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2001). Therefore, in spite of their condition and relative rarity, this collection of elements illustrates that Gondwanaland supported a diverse number of pterosaur taxa throughout its geological history.

This paper describes a second pterosaur from the Late Cretaceous (Cenomanian) limestone of northern Lebanon, originating from the locality of Hjoûla (Fig. 1). The specimen is preserved on a single oval slab of limestone and is partially complete, consisting of: the most posterior cervicals and anterior dorsal vertebrae, the pectoral girdle, a complete left wing, and the fragmented remains of the hindlimbs (Fig. 2). It is relatively more complete than that described by Dalla Vecchia et al. (2001) and is therefore regarded as the most complete pterosaur yet discovered from the African plate. The described specimen is housed at the State Museum of Natural History Karlsruhe in Germany under the collection number SMNK PAL 6595.

Geological setting

The regional tectonic history of Lebanon has been the focus of several studies (e.g., Butler and Spencer 1999; Brew et al. 2001) where the prominent Yammouneh Fault, along with several smaller structures, represents the northern extension of the Dead Sea fault system (Fig. 1a; Abdel-Rahman and Nader 2002). During the Cretaceous Period the majority of the sediments were deposited within

the Palmyride Basin, a large NNE–SSW trending intraplate trough, which persisted until the end of the Cretaceous when it was destroyed by regional compression. Within this basin the sediments slope westwards to form a single large monoclinical structure and the depositional environments are split between a western, open marine facies and an eastern, coastal facies (Nader et al. 2006).

Of significant palaeontological interest are the Konservat Lagerstätten that consist of four major fossiliferous localities: Sâhel Aalma, Nammoûra, Hâqel, and Hjoûla, each of which are famous for their exceptional preservation of Late Cretaceous invertebrates and fishes (e.g., Forey et al. 2003; Hay 1903; Woodward 1942). The youngest of these localities is Sâhel Aalma, which is Santonian in age (Garassino 1994) while the others are Cenomanian and deposited as part of the Sannine Formation (Fig. 1b), which itself appears to have been created during a period of relative stability and low sea levels (Nader et al. 2006). The Nammoûra is regarded as late to mid Cenomanian in age (Dalla Vecchia and Venturini 1999) while the localities of Hâqel and Hjoûla are both Early Cenomanian (Saint-Marc 1974); with the locality of Hâqel occupying a position approximately 20 m stratigraphically higher than that of Hjoûla (Hückel 1970). Other than fish, fossil vertebrates at all of these localities are rare, however, birds (Dalla Vecchia and Chiappe 2002), turtles, dolichosaurs and marine varanoids (Dalla Vecchia and Venturini 1999; Dal Sasso and Renesto 1999) have nonetheless been described from

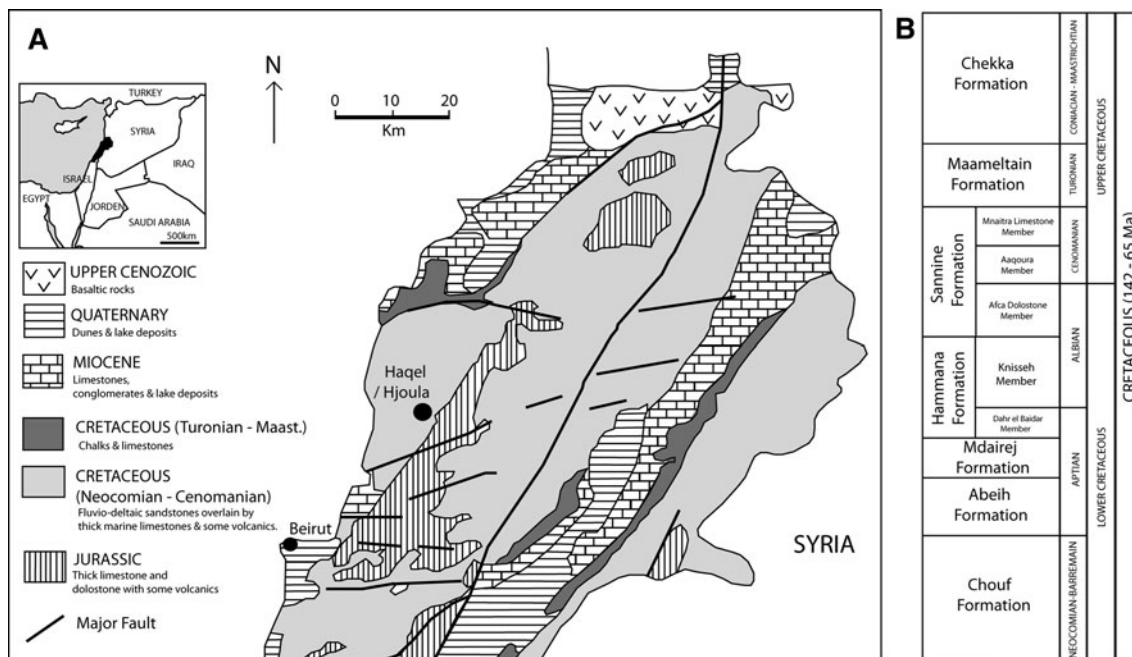


Fig. 1 a Geological map of northern Lebanon showing the localities of Hâqel and Hjoûla. b Relative position of the Sannine Formation within the Cretaceous strata of Lebanon. Figures adapted after Abdel-Rahman and Nader (2002)

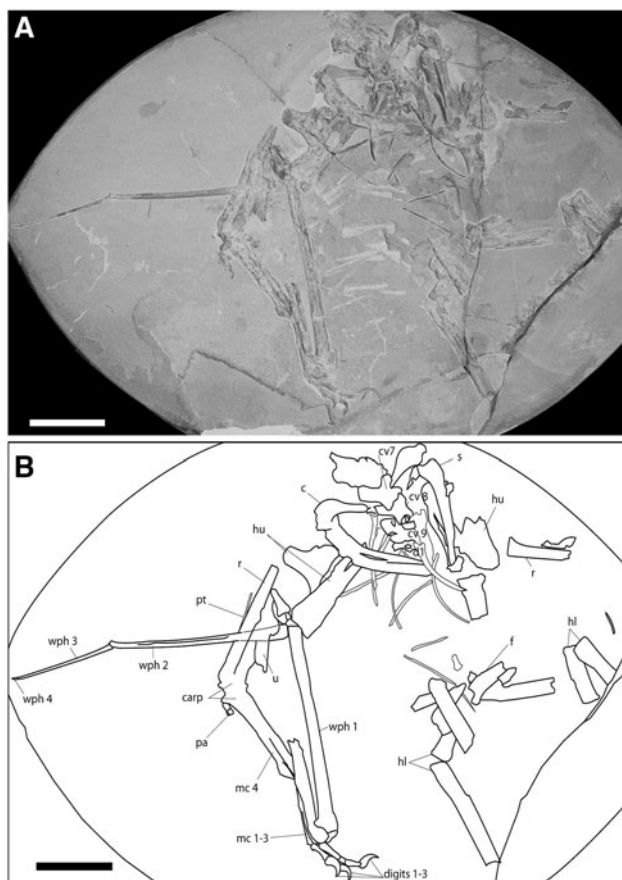


Fig. 2 *Microtuban altivolans* (SMNK PAL 6595) gen. et sp. nov. **a** Photograph, **b** line tracing corresponding to photograph in **a**. Scale bars 50 mm. *c* coracoid, *carp* carpus, *cv* cervical vertebrae, *d* dorsal vertebrae, *digits* digits 1–3, *f* femur, *hl* fragments of the hindlimb, *hu* humerus, *mc* metacarpal, *pa* preaxial carpal, *pt* pteroid, *r* radius, *s* scapula, *u* ulna, *wph* wing-finger phalanges (digit 4)

the limestone of Nammoûra. In contrast to the older localities of Hâqel and Hjoûla, terrestrial plant remains are also common at Nammoûra (Dalla Vecchia and Venturini 1999), including a diverse selection of ferns, gymnosperms and angiosperms. Some of these share an affinity with similar aged flora in North America, central Europe and the Crimea, suggesting a palaeoclimate similar to the present day Mediterranean (Krassilov and Bacchia 2000). The occurrence of these well preserved plant materials within marine sediments indicates the proximity of the region to a palaeoshoreline. In comparison to Nammoûra, indeterminate plant material (Krassilov and Bacchia 2000) and algae (Basson 1972) are also known from Hâqel, where fossil reptiles are represented by a single ornithocheiroid pterosaur (Dalla Vecchia et al. 2001). Prior to this study, fossil reptiles were unknown from the locality of Hjoûla. Saint-Marc (1974) described the palaeoenvironments of both Hâqel and Hjoûla during the Cenomanian as a small, oxygen depleted, marine basin, with the major land mass

being located in the present WSW portion of the Arabian Peninsula. Nader et al. (2006) later described the depositional environment in the frame of a carbonate ramp model with shallower waters prevailing to the far east of Lebanon.

Lithology and provenance

The specimen was purchased by the SMNK from a fossil dealer with local contacts and thus the exact provenance of the specimen is uncertain and worthy of discussion. The SMNK was initially told that the pterosaur originated from a quarry at Hâqel, although doubts were raised during discussions with another local dealer. We were later informed that this fossil had probably not been removed from the quarry of Hâqel but was likely from the nearby locality of Hjoûla (Roy Nohra, personal communication). As Hjoûla is only ~4 km south of Hâqel it is conceivable that the fossil dealers and middle men were uncertain as to the specimen's exact provenance. The sediments of Hâqel, however, contain a moderate amount of bioclasts and are noticeably whiter in colouration than those of Hjoûla, which are more micritic. A comparison of the grey limestone slab with other specimens housed at the SMNK leads us to propose the Early Cenomanian locality of Hjoûla as the true provenance of this specimen. This conclusion could be further confirmed by a thin section or petrographic analysis, but these were beyond the scope of this investigation.

Systematic palaeontology

Order	Pterosauria KAUP 1834
Suborder	Pterodactyloidea PLIENINGER 1901
Superfamily	Azhdarchoidea NESSOV 1984; <i>sensu</i> UNWIN 2003

Genus *Microtuban* gen. nov.

Etymology Greek μικρός = micros, for small; Arabic ثعبان = tu'bân, for basilisk, dragon, a star in the constellation *Draco*.

Diagnosis As for type species.

Type species. *Microtuban altivolans* gen. et sp. nov. (Figs. 2, 3)

Etymology altivolans: Latin altivolans = soaring/high flyer.

Diagnosis An azhdarchoid pterosaur distinguishable by an unusually high ratio of the first and second wing-finger phalanges ($wph\ 2/wph\ 1 = 0.85$) and a hyper-reduced fourth wing-finger phalanx, accounting for 1.1% of the total wing-finger length.

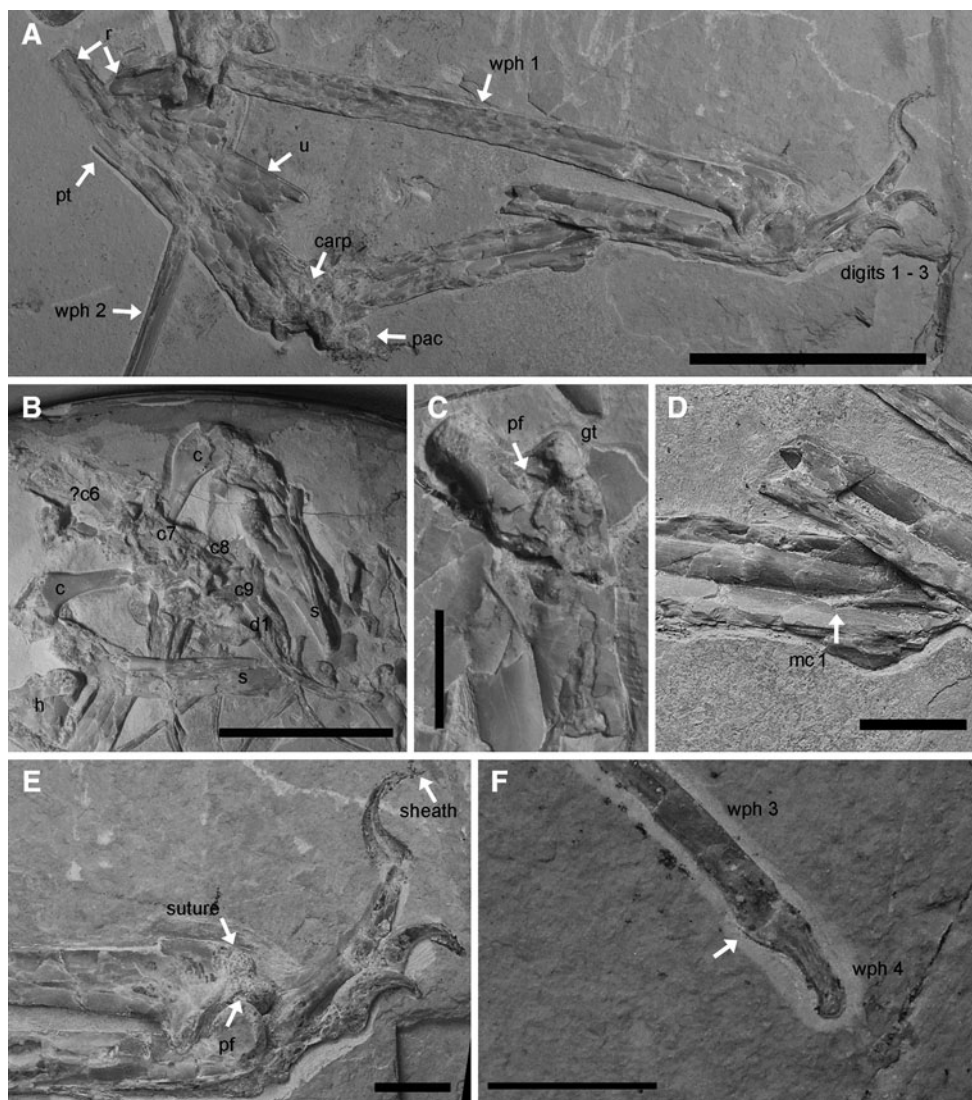


Fig. 3 Selected elements of *Microtuban altivolans* gen. et sp. nov. with specific points of interest. **a** Overview of the forearm, **b** the cranial aspect of the pectoral girdle and cervical/dorsal series in dorsal view, **c** the right femur in dorsal view, **d** fracture across the shaft of mc IV in cranial view (*arrow* indicates the termination of metacarpal ?1), **e** close up of the left manus and first wing-finger phalanx in dorsal view, **f** the fourth wing-finger phalanx in ventral view (*arrow*

indicating the articulation between wph 3 and 4). *Scale bars a* 50 mm, *b* 50 mm, *c* 10 mm, *d* 10 mm, *e* 10 mm, *f* 5 mm. *c* coracoid, *cX* cervical vertebra X, *carp* carpus, *dX* dorsal vertebra X, *gt* greater trochanter, *h* humerus, *mc* metacarpal, *pac* preaxial carpal, *pf* pneumatic foramen, *pt* pteroid, *r* radius, *u* ulna, *wph* wing-finger phalanx

Holotype The holotype specimen is housed in the Staatliches Museum für Naturkunde Karlsruhe (Germany) under the collection number SMNK PAL 6595.

Locality ?Hjoûla (= Hadjoula), town and region 35 km NNE of Beirut (Lebanon).

Horizon Sannine Formation, Late Cretaceous (Early Cenomanian).

Description

Cervical vertebrae and associated ribs At least three crushed cervicals are preserved in dorsolateral view while

incomplete fragments of bone, cranial to the seventh cervical, may represent the remains of the sixth cervical vertebra. The seventh and eighth cervicals are in natural articulation, where the postzygapophyses of the former overlie the latter vertebra. The ninth cervical is in natural articulation with the first thoracic vertebra (d1). The neural spines of all the vertebrae except that of the ninth cervical are broken and missing. The seventh cervical is longer than that of the eighth (Table 1) and the prezygapophyses of both are widely splayed, lying lateral to the postzygapophyses. The prezygapophyses of the seventh cervical are orientated craniolaterally at an angle of $\sim 45^\circ$ to the

Table 1 Selected bone measurements in *Microtuban altivolans* gen. et sp. nov.

Selected elements	Length (mm)
Cervical 7	23.6
Cervical 8	21.1
Cervical 9	~9.0
Dorsal 1	~10.0
Humerus	61.6–73.3 ^a
Radius	92.0 ^a
Carpus	13.0
pteroideum	>38.0
mc IV	122.0 ^a
mcIII?	50.0
dI p1	12.5
dIu	11.0
dIIu	11.0
dIIIp1	17.0
dIIIp2	3.0
dIIIp3	10.5
dIIIu	11.0
wph 1	135.0
wph 2	114.5
wph 3	63.5
wph 4	3.5

d digit, *etp* extensor tendon process, *mc* metacarpal, *ph* phalanx, *postzy* postzygapophyses, *prezy* prezygapophysis

^a Estimated values

midline. The left prezygapophysis of the ninth cervical face dorsomedially although at what angle remains uncertain. Double-headed ribs are visible in close association with the last two cervical vertebrae. In cervical 8 these are long (>19 mm in length) but thin, and while one lies adjacent, though un-fused, to the left prezygapophysis, another can be tentatively traced to the opposite side. More ribs also lie adjacent but un-fused to the transverse processes of the ninth cervical; however, they are significantly larger and more robust than those of the preceding vertebra.

Thoracic vertebrae and associated ribs A single thoracic vertebra is preserved in natural articulation with the ninth cervical, flanked by two large and robust double-headed ribs. A loose pair caudal to these suggests that they were present up to and including the second thoracic vertebrae. The neural spine is broken but must have run for a length of 8 mm along the dorsal portion of the centrum. The absence of any axial elements caudal to the first thoracic vertebrae indicates that no notarium was originally present. The caudally positioned thoracic ribs are thin, strongly curved and loosely positioned along with the imagined midline of the axial skeleton.

Pectoral girdle Both left and right scapulae and coracoids are unfused but the similarity in their resting positions

indicates little *post mortem* displacement (Fig. 3b). The scapula consists of a caudomedially directed blade, which ventrally diverges into a scapular body bearing the glenoid fossa. The angle between body and blade is approximately 145°. The scapular blade is straight, most likely long ovoid in cross-section as can be concluded from the right scapula, and is approximately five times longer than it is wide. The cranial edge appears to have been a little more massive than the caudal one. Towards its median terminus it tapers to a sharp median margin with a rounded outline. The two contralateral scapular blades are angled in a craniolateral direction at an angle of ~45° against the median plane. The scapular body curves medially at an angle of about 145° measured against the long axis of the blade and while crushed, was likely sub-triangular in cross-section. From their articulation with the scapulae both coracoids point medially, forming an angle of about 50° with the body of their respective scapulae. The glenoid head of the coracoid is angled against the shaft at about 80° and has three times the diameter of the medially most preserved part of the shaft. Cranioventrally the glenoid head is marked by a blunt crest that medially merges with the cranioventral face of the shaft. Nothing can be said about the morphology of the glenoid fossa because it is either covered by sediment and overlying bone, or is damaged. The coracoid shaft is almost circular in cross-section at its midpoint and preserves no trace of a medial divergence towards the furca. On the right coracoid the ventral process of the furca is visible at the left hand margin of the vertebral complex; giving a ratio of 1:0.78 between scapula and coracoid.

Humerus Both humeri have been broken into two large proximal and distal fragments with only the left humerus preserving any osteological details. The proximal fragment of this is preserved in its cranial aspect and consists of the humeral head, which lies slightly disarticulated from the lateral margin of the left scapular body. The collum of the humeral head is dorsocaudally concave and bears the deltopectoral crest; the proximal margin is regularly concave and would have been confluent with the cranial corner of the articular surface of the humeral head if not for a small break in the bone. The cranial margin of the deltopectoral crest is convex, whereby the convexity is a little stronger at the cranioproximal corner than at the craniodistal one. At the mid part of the deltopectoral crest the proximal and caudal margins run almost parallel to each other. Close to the collum, the distal margin of the deltopectoral crest curves distally and merges with the humeral shaft. The deltopectoral crest is almost flat, about 1.5 times as long as it is wide, and the collum itself is inclined caudally at an angle of about 43°. Near the break on the distal humeral fragment there is an elongate, oval scar that probably acted as the insertion point for a muscle; possibly *m. triceps* or *m. brachialis* (Bennett 2003a). The distal fragment is observed

in cranial view, the length of which suggests that a degree of overlap likely existed between the two fragments and a middle estimate of 67.5 mm is adopted for this study (Table 1).

Radius/ulna The bones of the antebrachium have been badly crushed and the compacta fragmented. The left antebrachium has fractured into at least one proximal and one distal portion, each of which preserves their respective articular surfaces. The proximal radial fragments, identified by their proximodorsal tubercle, lie almost perpendicular to the distal articular face of the left humerus. The proximal fragments are overlain by their distal fragments, the latter of which are orientated almost perpendicular to the former. An exception occurs where a further fragment of bone, attributed to the middle portion of the ulna, overlies and converges with the proximal end of the distal ulnar fragment (Fig. 3a). The distal fragments of the ulna and radius run parallel to each other, the diameter of bones approaching a ratio of 1:0.7 towards the midpoint of the shaft. The preserved diameter is fairly reliable because of the late diagenetic compaction, which preserved the actual diameter of the bones in the bedding plane.

Carpus Both proximal and distal elements are present and preserved in craniodorsal view, although abrasion of the compacta limits the observed articulation between the proximal and distal blocks to the cranial third of the carpus. It is thus not possible to identify the presence of a syncarpal, although given the general completeness of the carpus this appears to be likely and the term is adopted here. The left carpus remains in situ and forms an angle of 116.5° between the radius/ulna and the fourth metacarpal (Fig. 3a). The cranial aspect of the proximal syncarpal is cuboid in appearance while that of the distal syncarpal cannot be determined. A large, longitudinally ovoid excavation, preserving slightly broken margins, is located in a patch of predominantly intact compacta on the dorsal surface of the distal syncarpal, close to the cranial margin. Within this depression three smaller, presumably pneumatic, foramina pierce the distal syncarpal. The left pteroid and the preaxial carpal are preserved close to their natural positions (Fig. 3a). The pteroid is long and slender, about 0.75 mm wide at its distal terminus, but has been displaced medially so that the proximal portion is hidden by the overlying radius; the exact length of the element is thus unknown. The distal end does not taper but shows a rounded knob-like termination that is slightly kinked in the direction of the antebrachium. In the proximal third of the pteroid, a piece of the compacta is missing, revealing the hollow interior of the bone. The preaxial carpal has rotated over the distal margin of its articular face on the distal carpal block and now lies parallel to the fourth metacarpal. An oval sesamoid with an evenly convex surface (“Sesamoid A” = pisiform after Bennett 2008) sits within the fovea of the preaxial carpal.

Metacarpals The wing metacarpal is broken about halfway along its length (Fig. 3a), the proximal and distal fragments of which are displaced slightly. The shaft of the metacarpal narrows distally but then expands caudally at its most distal margin, forming a pair of condyles for the articulation of the first wing-finger phalanx. The distal dorsal condyle shows only a slight compaction and is thus well preserved in three dimensions; the dorsal surface of which is slightly concave with a shallow elevation in the centre. In cranial view the condyle is directed slightly dorsolaterally at an angle of $\sim 20^\circ$. Caudoproximally the rim of the dorsal condyle terminates abruptly, forming a short concavity that borders the condylar neck caudally. All three remaining metacarpals can be observed in situ along the craniodistal face of the wing metacarpal and form a natural contact with the digits. These can be traced proximally only as far as the large break across the fourth metacarpal, with the exception of a single metacarpal (mc ?I), which is preserved on the proximal fragment of the wing metacarpal and tapers to a natural termination some 48 mm distal to the carpometacarpal articulation (Fig. 3d). Damage to the metacarpals indicates that even these slender bones were hollow.

Digits The left manus is preserved in a slightly hyper-extended position. Digit I overlies digit II, however, digit III has been displaced slightly caudally with the palmer part of the proximal articulation condyle of its first phalanx now overlying the dorsal margin of the first phalanx of digit I (Fig. 3e). All of the elements belonging to the digits are in full articulation. The dorsally facing compacta of the phalanges of digit I are mostly eroded and the first phalanx shows signs of compaction along the mid-part of its shaft; the palmer face of which is concave between the articulation heads. A narrow trace, most likely the remnants of a claw sheath, is present, adjacent to the tip, along the caudal margin of the unguis phalanx. Of digit II only the unguis phalanx is visible. Distal to the tip of the unguis phalanx the keratinous claw sheath is visible as a yellowish buff trace that extends the tip of the unguis by at least 2 mm. Compared with the first phalanx of digit I the concavity of the shaft of the first phalanx of digit III is shallow. Phalanx 2 of digit III has barely one-fourth of the length of the first phalanx and is marked by a deep palmer notch and a dorsal styloid process that has one-third of the length of that phalanx. This process forms a bone lock that hinders a hyper-extension of the third phalanx of digit III. The third phalanx is almost conical with a very shallow circumferential concavity in its distal two-thirds. According to its external mould, the distal articular condyle with the unguis phalanx was almost confluent with the shaft. The unguis phalanx of digit III is preserved predominantly as an impression, lined with some remnants of the compacta along the lateral sulcus and the very tip. This tip is

prolonged by a black pyrolusite or goethite stain, 3 mm in length, which represents the remains of a keratinous sheath. All ungual phalanges are—or in the case of digit III were—11 mm long.

Wing-finger Only those elements belonging to the left wing-finger can be identified and preserve the fourth digit in its entirety. With the exception of the third and fourth phalanges these have been displaced and lie slightly out of natural articulation with their neighbouring elements. The first wing-finger phalanx is preserved in partial articulation with the fourth metacarpal and lies flexed back to such an extent that the caudal process now overlies the dorsocaudal surface of metacarpal IV, forming an angle of 3.5° between the two bones. This flexion has separated the metacarpal IV and the first wing-finger phalanx so that only the extensor tendon process still lies between the condyles of the metacarpal. The lack of contact between the two elements suggests that the metacarpophalangeal articulation is likely hyper-flexed. The distal terminus of the phalanx shows some surface erosion as does the dorsal margin of the proximal cotyle, but the margin of the gently convex articulation with phalanx 2 is still visible. The extensor tendon process is not fused to the first wing phalanx and is sub-triangular outline with a deeply concave cranial margin. Caudally this rises into a blunt ridge and becomes confluent with the proximal ridge above the articular face. This latter ridge tapers caudally and is perforated by a pneumatic foramen that is partly obscured by the dorsal condyle. The remaining three phalanges of the wing-finger lie adjacent to each other and display a shallow caudally directed curvature. In contrast to the other elements of the wing these are exposed in ventral view. The second wing-finger phalanx is 85% of the length of the first wing-finger phalanx and preserves a gentle, caudally directed curvature. The bone formed a long oval in cross-sectional view. The third wing-finger phalanx is missing most of the compacta and is around half the size of the second (i.e., 55%). The distal articulation face is only one-fourth the size of the proximal one. The fourth wing-finger phalanx is a tiny element about 3.5 mm in length and shows three shallow, distally converging striae on its dorsal face (Fig. 3f). The caudal margin of the bone is concave and terminates in a blunt, slightly re-curved tip with a flat distal surface.

Hindlimbs The hindlimbs have been crushed and broken into several mostly indeterminable elements. The right femur is preserved in its caudal aspect where the femoral neck is offset from the shaft at an angle of 41° (Fig. 3c). The greater trochanter is observed as a prominent, cranially directed triangular process, the caudal margin of which is slightly convex and marked by a blunt ridge that merges distally with the femoral shaft. Between the trochanteric ridge and the femoral neck a large, pneumatic, trabeculae-

lined opening pierces the shaft. Immediately distal to the trochanteric area, portions of the femur were broken and re-attached with a loss of some bone material.

Discussion

Ontogenetic age

The identification of unfused sutures in the skeleton, and the sequence in which they occur, has proven useful to determine the morphological age of a variety of arch-sauromorphs (Brochu 1995, 1996; Irmis 2007), included pterosaurs (e.g., Bennett 1993; Kellner and Tomida 2000). While Bennett (1993) further noted an immature bone grain, and pitting about the articular extremities as being indicative of osteological immaturity in pterosaurs, the bone grain of *M. altivolans* appears to be well developed. Immaturity is however indicated by the lack of skeletal fusion where the cervical and thoracic ribs are separate from their respective vertebrae, the scapula and coracoid have not formed a scapulocoracoid, and the presence of a large suture between the extensor tendon process and the first wing-finger phalanx. As such the animal did not live to a late ontogenetic state and is inferred as being juvenile or sub-adult.

Taphonomy

The skeleton of *M. altivolans* shows some unusual features in that while almost all the long bones have been badly fractured (Fig. 3a), many of these elements have remained in close association or lie just beyond bone lock. Fragile elements that are easily displaced by *post mortem* movement, including the pteroid, preaxial carpal, metacarpalia, and digits I–III, are also preserved in situ or with only minor displacement. The humerus, radius, ulna and metacarpal IV were broken transversely by a single event and although one fragment of the bone often overlies the other, there has been little actual displacement. It is difficult to explain these fracture patterns as a result of a natural decay process. The sediment indicates that stagnant, and possibly hostile, seafloor conditions persisted in the local environment while disruption by sediment activities or high-energy currents is unlikely based on the lithology. The lack of any trace of bioturbation excludes any benthic or endobenthic scavengers as the cause of the given breakage pattern, thus the carcass of the pterosaur encountered a violent traumatic encounter of an unknown origin. The fact that most of the broken bones are still aligned can only be explained by the presence of soft tissues that held the fractured elements together to a large degree. The breakage of the bones must have occurred when the pterosaur was

either still alive or freshly dead and in a very early stage of decay.

Systematic palaeontology

The presence of an elongate wing metacarpal identifies *M. altivolans* as a pterodactyloid, but it is more specifically diagnosed as an azhdarchoid by a relatively short wing-finger with a rapid decline of phalanx length distally (Lü et al. 2008), an elongated wing-finger phalanx 1 being >40% of the entire wing finger (Kellner 2003), and a well developed tubercle on the caudoventral margin of the coracoid (Kellner 2004). The pneumatization of the hindlimb and the presence of a well developed greater trochanter further support this conclusion, where the former has been demonstrated to be widespread throughout the Azhdarchoidea by means of a large excavation on the craniodorsal face of the femur (e.g., Claessens et al. 2009; Eck et al. 2011).

The Azhdarchoidea itself is comprised of four families, the Tapejaridae, the Thalassodromidae, the Chaoyangopteridae, and the Azhdarchidae (see Lü et al. 2008), along with the Protoazhdarchidae as a potential fifth (Frey et al. 2011). The assignment of *M. altivolans* to one of these families is complicated as the majority of diagnostic characters are restricted to the cranium and the middle cervicals (e.g., Kellner and Langston 1996; Kellner 2003; Unwin 2003; Suberbiola et al. 2003; Witton 2008); none of which can be observed in the described specimen. Of the few remaining elements of the axial column, only the posterior cervicals 7–9 and the first dorsal vertebrae are identified. The lack of the mid cervical vertebrae and the poor preservation of any diagnostic features on the remaining elements prevent an extensive comparison with other azhdarchoids. The posterior cervicals of the Moroccan azhdarchid *Phosphatodraco mauritanicus* (Suberbiola et al. 2003), which has an unusually elongated seventh vertebrae, are distinct from those of *M. altivolans*, whose own cervicals more closely resemble those of other pterodactyloid pterosaurs. Fortunately additional postcranial characters can be used for a more refined diagnosis. The configuration of the metacarpals for example, whereby the preaxial metacarpals appear to terminate distal to the carpus is used to distinguish the described specimen from the Tapejaridae, where a single preaxial metacarpal is known to contact the wrist. While the hyper-reduction, without loss, of the fourth phalanx to <5% that of the total length of the wing-finger is known only for *Quetzalcoatlus* (Kellner and Langston 1996; Fig. 4), an azhdarchid affinity is rejected by a further comparison of postcranial elements. Here the scapula and coracoid preserve a ratio of 1.30, more comparable to that of non-azhdarchid azhdarchoids, e.g., MN 6588-V (1.27); SMNK PAL 3843 (1.39), and an

unnumbered specimen at the SMNK (1.42, RAE, personal observation), than that of *Quetzalcoatlus* (1.01) or even the chaoyangopterid *Shenzhoupterus chaoyangensis* (1.00, Lü et al. 2008), while *M. altivolans* further lacks the well developed ventral flange to the coracoid (Fig. 5). Unwin and Martill (2007) described a number of postcranial azhdarchid apomorphies that include: a highly elongated wing metacarpal (i.e., mc IV > wph 1); and a wing-finger forming <50% the total forelimb length. Lü et al. (2008) later included a mc IV/humerus ratio of >2.2. In *M. altivolans* the wing metacarpal is slightly less than that of the first wing-finger phalanx (i.e., mc IV/wph 1 = 0.9), the wing-finger forms 51–52% of the total forelimb length and the mc IV/humerus ratio is between 1.7 and 2.0. Under these qualifiers, *M. altivolans* is excluded from the Azhdarchidae.

Despite the lack of a skull and the general state of preservation, postcranial features can be used to exclude *M. altivolans* from a placement within the Tapejaridae and Azhdarchidae, however, its assignment to either the Thalassodromidae or the Chaoyangopteridae is complicated by the fact that both of these families are defined by their cranial characteristics alone (e.g., Kellner 2004; Lü et al. 2008; Witton 2008). While a tentative similarity with *Shenzhoupterus chaoyangensis* (Lü et al. 2008) is noted from ratios of the mc IV/hu and mc IV/wph 1, the majority of body proportions do not differ substantially from those of other derived azhdarchoids (Table 2). Furthermore those elements that do, i.e., phalanx proportion in the wing-finger, differ considerably and isolate *M. altivolans* from other azhdarchoids. The high ratio of the second wing-finger phalanx to that of the first is greater than the range of values observed for other azhdarchoids; *contra* to the synapomorphy stated by Kellner (2003) for the Azhdarchoidea where by the second wing-finger phalanx is always more than 1/3rd smaller than the first wing-finger phalanx (i.e., wph 2/wph 1 < 0.7). While similar ratios are observed in other pterodactyloid pterosaurs, e.g., *Pteranodon*, *Nyctosaurus*, *Germanodactylus* and several selected ornithocheiroids, all of which are readily distinguished from the described specimen.

The phylogenetic placement of *M. altivolans* within the Azhdarchoidea therefore remains uncertain and while postcranial characteristics support the erection of a new genus within either the Thalassodromidae (Witton 2009) or Chaoyangopteridae (Lü et al. 2008), no more specific a diagnosis can, or should, be reliably made at this time.

General discussion

The placement of *M. altivolans* within the Thalassodromidae/Chaoyangopteridae highlights the degree of to which variations in wing phalanx length can occur, along

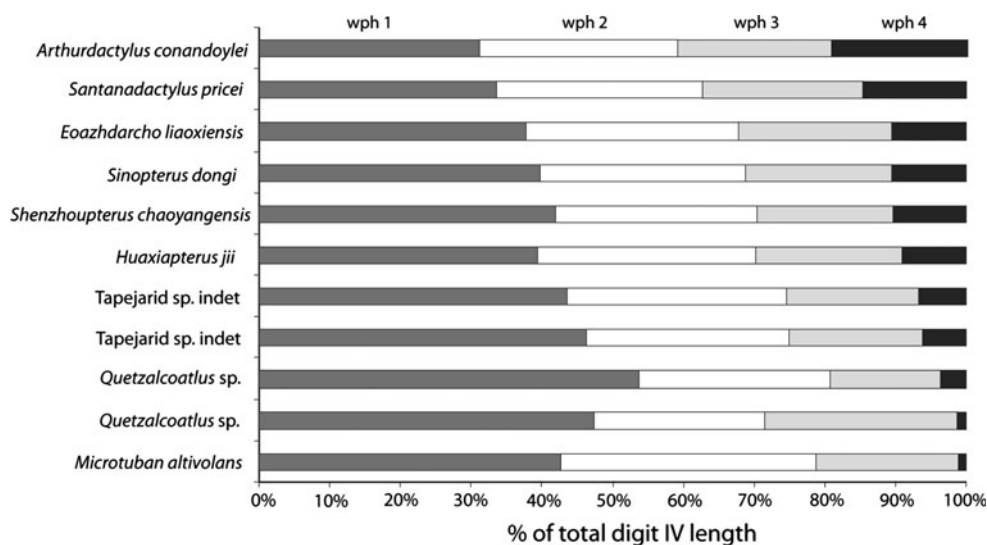


Fig. 4 Bar chart illustrating the percentage of the total length of the fourth digit formed by each phalanx. Hyper-reduction of the terminal wing-finger phalanx is typically restricted to the Azhdarchidae and distinguishes them from other members of the Azhdarchidae. List of taxa from top to bottom: *Arthurdactylus conandoylei* (SMNK PAL 1132); *Santanadactylus pricei* (AMNH 22552); *Eoazhdarcho*

liaoxiensis (GMN-03-11-002); *Sinopteris dongi* (IVPP V 13363); *Shenzhoupterus chaoyangensis* (HGM 41HIII-305A); *Huaxiapterus jii* (GMN-03-11-001); tapejarid indet. (SMNK PAL 6409); tapejarid indet. (SMNK PAL 3900); *Quetzalcoatlus northropi* (TMM 41450); *Quetzalcoatlus* sp. (TMM 41961); *Microtuban altivolans* (SMNK PAL 6595)

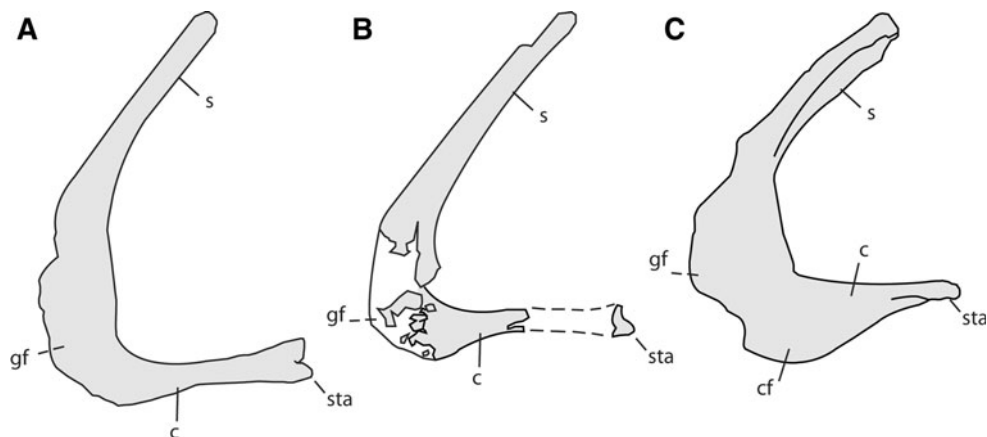


Fig. 5 Comparison of the scapula and coracoid elements from **a** an un-named tapejarid (SMNK PAL 3843). **b** *Microtuban altivolans* (SMNK PAL 6595). **c** *Quetzalcoatlus* sp. (TMM 42138-1). All line tracings have been scaled to the same size, based on the coracoid length. The coracoid: scapula ratio of 1.30 in *M. altivolans* is similar to that of other azhdarchoid pterosaurs e.g., SMNK PAL 3843, 1:1.39;

unlabelled azhdarchoid indet. (SMNK), 1.27; MN 6588-V, 1:1.27 and is clearly distinct from that of other more derived pterosaurs, e.g., *Shenzhoupterus chaoyangensis* (1:1) and *Quetzalcoatlus* sp. (1:1). *c* coracoid, *cf* coracoid flange, *gf* glenoid fossa, *approximate location*, *s* scapula, *sta* sternal articulation

with the problems involved with identifying taxa from their biometric proportions alone. Although the ratio of the first and second wing-finger phalanges of the described specimen exceeds the range of values regarded as a synapomorphy of the Azhdarchoidea (Kellner 2003), this is not problematic as a suite of additional characters readily support its position within the group. Defining pterosaurs in absolute values is problematic as taxa or individuals (as a result of natural intraspecific variations) will occasionally fall outside the range covered by previously known

specimens. Indeed *Sinopteris dongi* (Wang and Zhou 2003) and a ?tapejarid specimen (SMNK PAL 6900, Unwin and Martill 2007) also exceed the absolute value given by Kellner (2003), although to a much smaller degree, and indicate that such practices can often fail to encompass the full range of values of the desired group.

The second unusual feature of the described specimen also relates to the wing phalanges and the size of the terminal wing-finger phalanx. While a reduction in the length of the fourth wing-finger phalanx is observed in a number

Table 2 Ratios of selected long bone elements in various pterosaur taxa

Taxa	Specimen number	wph 2/wph 1	mc IV/hu	mc IV/wph 1
Azhdarchidae				
<i>Zhejiangopterus linhaiensis</i>	ZHNM M1323	0.66	2.45	1.04
<i>Quetzalcoatlus</i> sp.	TMM 41961	0.51	×	0.81
<i>Quetzalcoatlus</i> sp.	TMM 42422	0.51	2.48	1.03
<i>Q. northropi</i>	TMM 41450	×	1.79 ^a	×
Chaoyangopteridae				
<i>Shenzhoupterus chaoyangensis</i>	HGM41HIII-305A	0.68	2.12	0.95
<i>Eoazhdarcho liaoxiensis</i>	GMN-03-11-002	0.78	1.50	0.76
Thalassodromidae				
<i>Tupuxuara longicristatus</i>	IMCF 1052	0.60	1.53	0.71
Tapejaridae				
<i>Huaxiapterus jii</i>	GMN-03-11-001	0.79	1.67	0.81
tapejarid sp. indet.	SMNK PAL 6409	0.71	×	×
tapejarid sp. indet.	SMNK PAL 3900	0.62	1.39	0.62
<i>Sinopterus dongi</i>	IVPP V 13363	0.73	1.63	0.79
<i>Microtuban altivolans</i>	SMNK PAL 6595	0.85	1.81 ^a	0.90

^a Estimated values

of taxa, specifically those within the Azhdarchoidea, the actual loss of the phalanx is rare; having only been documented in specimens of *Anurognathus*, *Beipiaopterus* and *Nyctosaurus* (Bennett 2003b, 2007; Lü 2003). Even within the Azhdarchoidea the reduction of the fourth phalanx to a length <5% that of the total wing finger is known only for *Quetzalcoatlus*. Its presence here is therefore unusual and extends the range of this feature to encompass non-azhdarchid azhdarchoids. The biomechanical reasoning behind the extreme reduction or loss of the fourth phalanx remains uncertain but must have been linked to either the aerodynamic forces acting on the distal section of the wing, and the subsequent deformation of the leading edge spar/membrane, or acted as one possible means of lowering the overall aspect ratio.

The presence of *M. altivolans* within the Cenomanian aged deposits of Lebanon represents one of the few non-azhdarchid azhdarchoids known from the Late Cretaceous. Members of the Chaoyangopteridae such as *Shenzhoupterus chaoyangensis* and *Chaoyangopterus zhangii* from the Jiufotang Formation of Liaoning Province, are dated as Early Aptian, while *Eopteranodon* was uncovered from Barremian–Early Aptian deposits (Swisher et al. 1999). Members of the Thalassodromidae are known chiefly from the NE of Brazil, the two major fossiliferous deposits are both regarded as Early Cretaceous in age (Kellner and Campos 2002; Unwin and Martill 2007; Witton 2009). An isolated rostrum and mandible from the Javelina Formation of North America (Wellnhofer 1991; Kellner 2004) therefore appears to represent the sole member of the Thalassodromidae known from the Late Cretaceous (Martill and Naish 2006). The confirmation of *M. altivolans* as a thalassodromid or chaoyangopterid pterosaur within the

Early Cenomanian Lagerstätten of Lebanon therefore reveals only a minor portion of the ghost lineage available to these taxa, but it is significant as the dating of these deposits appears to be uncontroversial. Azhdarchoid remains are also known from the Cenomanian Kem Kem locality of Morocco, but are regarded as either tapejarid or azhdarchid pterosaurs (Kellner and Mader 1997; Wellnhofer and Buffetaut 1999) and as such are not directly comparable to *M. altivolans*. A similar situation is found in the Cenomanian chalk of England that yields specimens of *Anhanguera* and *Lonchodectes* (Unwin 2000), while substantial material recovered from the Cenomanian aged Cambridge Greensand of England is likewise incomparable and thought to have been reworked from the older Albian deposits (Wellnhofer 1991; Dalla Vecchia et al. 2001). *Microtuban altivolans* therefore represents one of the youngest confirmed thalassodromid/chaoyangopterid pterosaurs, perhaps the only one of a known Cenomanian age, and indicates a greater geographical distribution existed than the immediate localities encompassed by the Lagerstätten deposits of Brazil and China.

Pterosaurs from the eastern edge of the African Plate remain exceedingly rare and those belonging to the portion that now forms the Middle East are restricted to the Early Cenomanian *M. altivolans*, an indeterminate ornithocheiroid (Dalla Vecchia et al. 2001), and a “pterodactylid” hindlimb (Tchernov et al. 1996). As azhdarchid pterosaurs are known from the upper Campanian of Israel and the upper Maastrichtian of Jordan (*Arambourgiania philadelphiae*, Arambourg 1954; Frey and Martill 1996), the region was undoubtedly inhabited by a variety of pterosaurs more or less continuously throughout the Late Cretaceous. If pterosaurs formed a major portion of the local ecosystem

during the Cenomanian then it is surprising that so few of their remains have been uncovered as, unlike many localities, the Lagerstätten of Hâqel and Hjoûla are quarried exclusively for their fossils contents. The palaeogeographical reconstructions of northern Lebanon during the Cenomanian indicate that an open marine setting prevailed in the west of the country and the appearance of pterosaurs here, several hundred km from the nearest inferred palaeo-coastline, inevitably raises questions as to how they came to rest in this setting. The animal perhaps died migrating between landmasses, drifted into the region on the ocean currents, or have inhabited any palaeoislands that existed within the immediate region. Dalla Vecchia et al. (2001) suggested that the pterosaurs of the Cenomanian inhabited small islands composed of carbonate exposures, a hypothesis supported by the presence of sub-aerially exposed carbonate reefs, with palaeochannels, within the Early Cenomanian lithologies (Nader et al. 2006). Terrestrial plant deposits are also known from these localities indicating that material from colonised islands in the local area, or the nearest landmass, were occasionally swept into the region. As this input of material is of a poorer quality than that found at younger localities the source is regarded as being more distant than that of the upper Cenomanian locality of Nammoûra. The presence of these small pterosaurs so far from the nearest major landmass, along with the generally good preservation observed within the specimen, suggests that Early Cenomanian pterosaurs probably did inhabit exposed carbonate islands within the local region. Any such platforms however were located more distant in the Early Cenomanian localities when compared to these of the Late Cenomanian. The relative lack of any teeth or bone fragments attributed to pterosaurs, despite the extensive quarrying of these localities for commercial fossils suggests that pterosaurs either did not reside close by in great numbers, or unknown conditions prevented their preservation in a locality famous for its spectacular preservation of fossil fish.

Conclusions

Microtuban altivolans represents a small, ontogenetically immature azhdarchoid pterosaur tentatively associated with the Thalassodromidae or Choayangopteridae. Differentiating between taxa of either group based on postcranial remains or biometric data and ratios is currently not possible and no more a specific diagnosis can be made. The unusual ratios formed by the second and fourth wing finger phalanges highlight some of the problems with using biometry to identify pterosaur taxa, indicating that the lengths of the individual wing elements are often highly variable. Additionally some ratios that are generally useful,

e.g., $wph\ 2/wph\ 1 < 0.7$ (Kellner 2003) or $mc\ IV > wph\ 1$ (Unwin and Martill 2007), can ultimately fail to encompass the diversity of a desired group. The hyper-reduction without loss of the fourth wing-finger phalanx within *M. altivolans* indicates that this feature was present throughout the Azhdarchoidea and was not solely restricted to the largest azhdarchids.

While African pterosaurs remain exceedingly rare the discovery of *M. altivolans* from the Cenomanian deposits of Lebanon, and the first from Hjoûla, fills in the earliest part of the Thalassodromidae/Choayangopteridae ghost lineage in the Late Cretaceous, indicating that these pterosaurs were more geographically widespread than the immediate localities covered by the Crato/Santana and Jehol Formations of Brazil and China. Although the exact provenance of the described specimen is uncertain, the only alternative site (i.e., Hâqel) is also Cenomanian and would indicate an even younger age than we have suggested here. As such, no conclusions presented in this manuscript will become void if the specimen is later proved to have originated from a neighbouring locality. The presence of this small pterosaur in an open marine setting, many hundreds of kilometres from the nearest palaeoshoreline, supports the idea that pterosaurs of the Cenomanian of Lebanon inhabited exposed carbonate islands (Dalla Vecchia et al. 2001). Given the rarity of these specimens it is unlikely that Hjoûla will ever be as important to pterosaur workers as other European, Asian and South American Lagerstätten localities, however, it does promise the prospect of future finds from a little known Cretaceous age of pterosaur evolution.

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