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

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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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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Catastrophic failure in a pterosaur skull from the Cretaceous Santana Formation of Brazil

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Abstract

A partial skull of the pterodactyloid pterosaur *Tupuxuara* from the Santana Formation (Cretaceous, ?Albian) of Brazil displays catastrophic damage to the anterior rostrum and mandible. The damage is not a consequence of diagenetic fracturing and is thought to represent a violent experience inflicted on the skull prior to deposition. The skull fracture patterns are consistent with a single, high-energy impact occurring at the jaw tips with a caudodorsal force vector. This impact resulted in telescoping of the rostrum into the nasoantorbital fenestra, buckling of the mandible and subsequent destruction of basal cranial elements from the caudal transmission of impact forces. However, the lack of clear event signatures on the specimen prevents identification of the specific cause of this damage.

Key words: Brazil, Cretaceous, Pterosauria, *Tupuxuara*, Taphonomy

Zusammenfassung

Eine unvollstaendiger Schädel des pterodactyloid Pterosaurier *Tupuxuara* aus der Santana Formation (Kreidezeit, ?Albian), Brasiliens zeigt katastrophale Beschädigung der Vorderschnauze und des Unterkiefers. Dieser Bruch ist nicht eine Auswirkung einer diagenetischen Fraktur, und es wird angenommen dass sie durch eine heftige Verletzung vor der Ablagerung entstanden ist. Die Beschadigung des Schaedels stimmt mit einem einzelnen, energiegeladenen Schlag ueberein, der rostroventral an der Kiefernspitze aufgetreten ist, und der die Verkuerzung der Vorderschnauze in die nasoantorbital fenestra, die Verkruemmung des Unterkiefers und anschliessende Zerstoerung der Schaedelbasiselementen von der Rueckuebertragung der Schlagkraft zur Folge hatte. Abwesenheit von „clear event signatures" auf der Probe verhindert die Identifizierung der speziellen Ursache des Ereignisses.

Schlüsselwörter: Brasilien, Kreide, Pterosauria, *Tupuxuara*, Taphonomie

1. Introduction

Although pterosaurs have been studied for over 200 years [see Wellnhofer (1991) and Taquet & Padian (2004) for historical reviews], the taphonomy of their fossils has received scant attention. Kellner (1994) provided an overview of pterosaur taphonomy from various deposits yielding abundant pterosaur specimens, and Kemp (1999) and Unwin & Martill (2007) provided details of pterosaur taphonomy in the Solnhofen and Crato limestones, but papers dedicated to this subject are scarce and studies into pterosaur taphonomy remain wanting for almost all pterosaur-bearing deposits. The Romualdo Member of the Santana Formation is no exception, although its status as a source exceptionally pterosaur remains is widely recognised. Pterosaur bones occur frequently in this unit and provide the most abundant and taxonomically diverse tetrapod remains of the Formation. Their remains demonstrate a complex suite of taphonomic states with considerable variation in preservational styles. Most pterosaur remains are preserved in three dimensions in early diagenetic concretions or partially crushed in concretions formed during later diagenetic stages. The completeness of pterosaur skeletons varies from the preservation of entire individuals to fossilisation of isolated or broken fragments, both of which can occur in various states of articulation. Detailed preservation of pterosaur tissues is often excellent with bone histology recorded at macromolecular level (Sayão 2003; Steel 2004), pneumatic cavities (e.g. Wellhofer 1991: 149) and rare three-dimensional soft-tissues (Campos et al. 1984; Martill & Unwin 1989; Kellner 2007) all known.

The exceptional preservation of the Romualdo Member also provides details of pterosaur life histories by yielding pterosaur vertebrae with dinosaur teeth embedded into their compacta (Buffetaut et al. 2004) and pathological bones

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(KELLNER & TOMIDA 2000). Here, we describe a new specimen housed in the Staatliches Museum für Naturkunde, Karlsruhe, Germany, (SMNK PAL 4330) that adds a further insight into pterosaur lifestyles by representing an extreme, if enigmatic, pterosaurian catastrophe unlike any other recorded from the Santana Formation. The specimen, comprising a partial skull, mandible and cervical vertebrae from a pterodactyloid pterosaur, appears to have undergone a violent preburial event that caused mechanical failure of the skull and mandible in several areas. This material is described herein and the cause of the damaged discussed.

2. Locality and stratigraphy

SMNK PAL 4330 was collected by a farmer as a loose concretion from the outcrop of the Santana Formation near Santana do Cariri, southern Ceará, Brazil. This area forms part of the broader Chapada do Araripe region and is part of the Araripe Geopark (MARTILL & HEADS 2007) made famous for its abundant fossiliferous concretions (MAISEY 1991; MARTILL 1993). The area around Santana do Cariri, on the flanks of the Chapada do Araripe (Fig. 1A) is the source of many exquisitely preserved vertebrate fossils, including numerous fish and a diverse array of archosaurs (MAISEY 1991).

The Santana Formation is a heterolithic sequence of mainly clastic strata that occurs in the upper part of the Araripe Group (Fig. 1B). The Romualdo Member is a 4–30 m thick sequence of fissile, laminated black shales with numerous elliptical and sub-spherical concretions (MARTILL 1993). The unit was deposited under quasi-marine conditions in the Araripe Basin, a large fault-bounded pull-apart basin that developed during the early stages of the opening of the Atlantic Ocean (BERTHOU 1990). The precise age of the Santana Formation remains to be precisely established, but it is probably Albian to Cenomanian (MARTILL 2007). Precise provenance for SMNK PAL 4330 is unknown, but concretion is rather flat in a manner typical of those found at the base of the Romualdo Member. However, this is only a generalisation and may not be true for all localities around the Chapada do Araripe.

3. Preservation

The new specimen is enclosed in a tabular, irregularly laminated concretion that has weathered to a buff colour (Fig. 2). The concretion, of which only a portion is present, measures 200 x 190 x 35 mm and has been split along a lamina to reveal the well incomplete skull and two cervical vertebrae. Most of the bones have split through the middle to reveal their internal structure, although some bones have remained on one slab with corresponding sediment moulds on the other. Most of the dorsal skull elements and mandible are preserved with only the rostralmost portions of both jaw tips and the caudodorsal extension of the cranial crest missing. The caudoventral portion of the cranium is not clearly discernable on account of both extreme damage to the bones of this region and the extension of some elements beyond the margin of the concretion. All bones are preserved in a buff colour that is not dissimilar to that of the surrounding matrix. Although several small calcite-filled cracks occur across the specimen, the fracturing of the skull is not a consequence of diagenetic processes or splitting by the original collector and is interpreted as damage that occurred to the skull prior to deposition.

4. Systematic palaeontology

The specimen possesses several synapomorphies found in the azhdarchoid *Tupuxuara* KELLNER & CAMPOS, 1988, including an elongate premaxillary crest extending dorsocaudally over the cranium, a convex palate and a flattened premaxillary occlusal surface at the jaw tip. We note, however, that the taxonomy of *Tupuxuara* is complex and we refrain from referring SMNK PAL 4330 to the currently recognised *Tupuxuara* species (*Tupuxuara longicristatus* KELLNER & CAMPOS, 1988; *Tupuxuara leonardii* KELLNER & CAMPOS, 1994) on grounds that these forms are based on type material that cannot satisfactorily distinguish *Tupuxuara* species. Further details on the taxonomy and nomenclature of *Tupuxuara* are provided by MARTILL & NAISH (2006) and KELLNER & CAMPOS (2007).

5. Taphonomy

The skull of SMNK PAL 4330 has been severely damaged with the greatest effects seen across the rostrum, ventral cranium and mandible (Fig. 2). The rostrum has completely broken away from the skull with an irregular fracture extending caudodorsally across the region immediately rostral to the nasoantorbital fenestra, the ventralmost point of which is estimated at 110 mm from the jaw tip. The rostrum has been caudodorsally telescoped into the nasoantorbital vacuity so that its dorsal margin lies alongside the ventral margin of the premaxillary crest. Despite its displacement, the rostrum is mostly intact with only the distalmost 40 mm not preserved due to its extension beyond the margin of the concretion. Several subvertical fractures are present on the lateral surfaces of the rostrum and the caudalmost portion of the palatal surface has splintered sagittaly.

The portion of skull lying caudal to the fractured rostrum comprises the caudodorsal process of the premaxilla, a lachrymal, a nasal and a partial frontal. Despite dislocation from other parts of the skull, these elements are intact and form a well-defined caudodorsal margin to the nasoantorbital fenestra and rostrodorsal orbital border. Possible parts of the anterior braincase are present but, as with the rest of the caudal extremity of the skull, the preservation does not allow for a reliable assessment of its completeness. The ventral cranium appears to have detached from the dorsal along the suture between the lachrymal and jugal. However, recognisable elements caudoventral to the orbit are not discernable. Several bone fragments are present in this region, but their identification is problematic because they are both fragmentary and partially obscured by mandibular elements and matrix.

The mandible is complete except for the distalmost 20 mm of the jaw tip, but has suffered extensive and complex fracturing (Fig. 3). Several major fractures have separated the mandible into six components, all of which remain loosely linked in an arc that extends away from the ventral margin of the premaxilla.

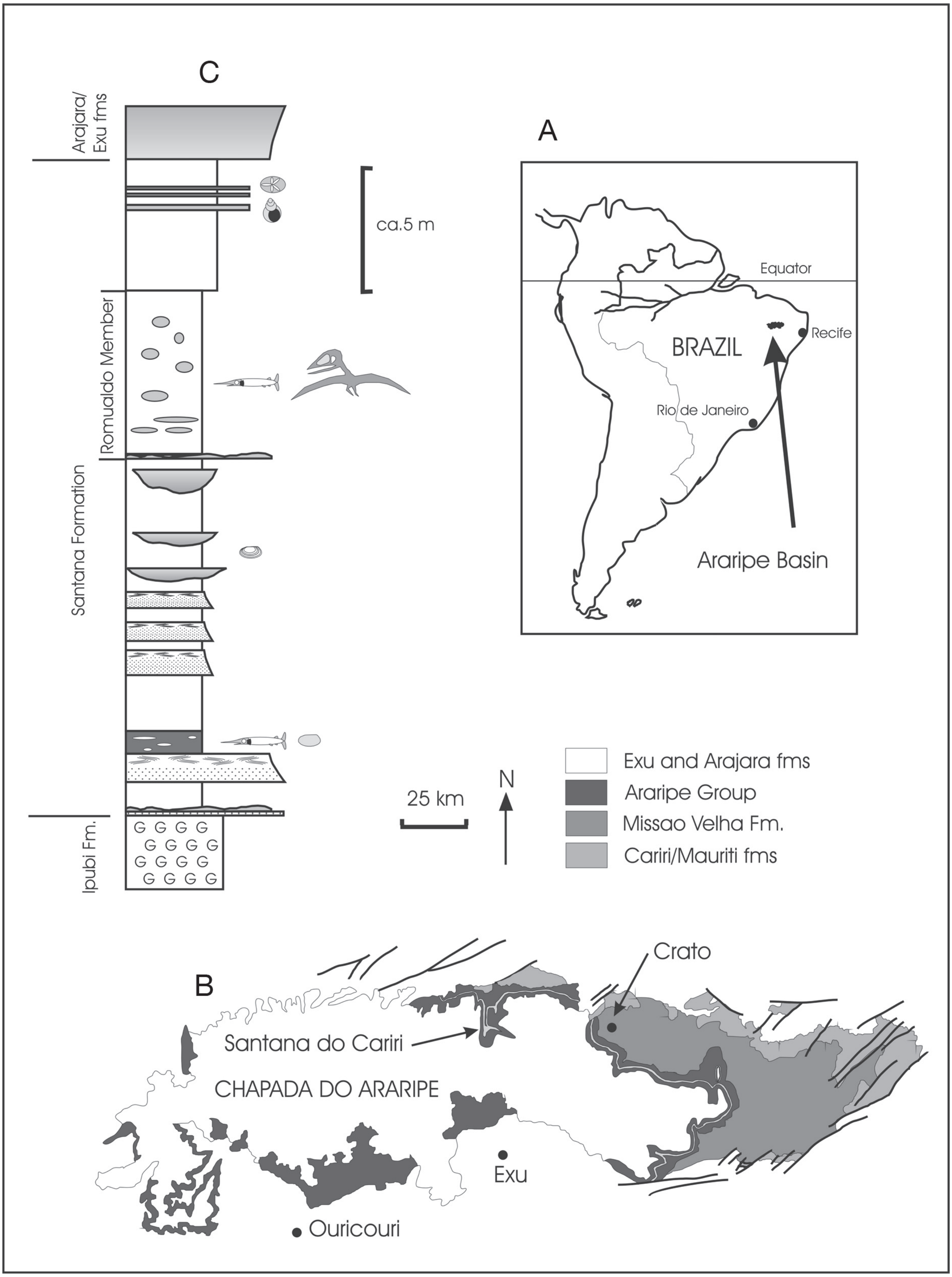

Figure 1: A + B, map of the Araripe Basin showing the location of Santana do Cariri, the region where the new pterosaur specimen was discovered. **C**, generalised stratigraphic profile for the Santana do Cariri region.

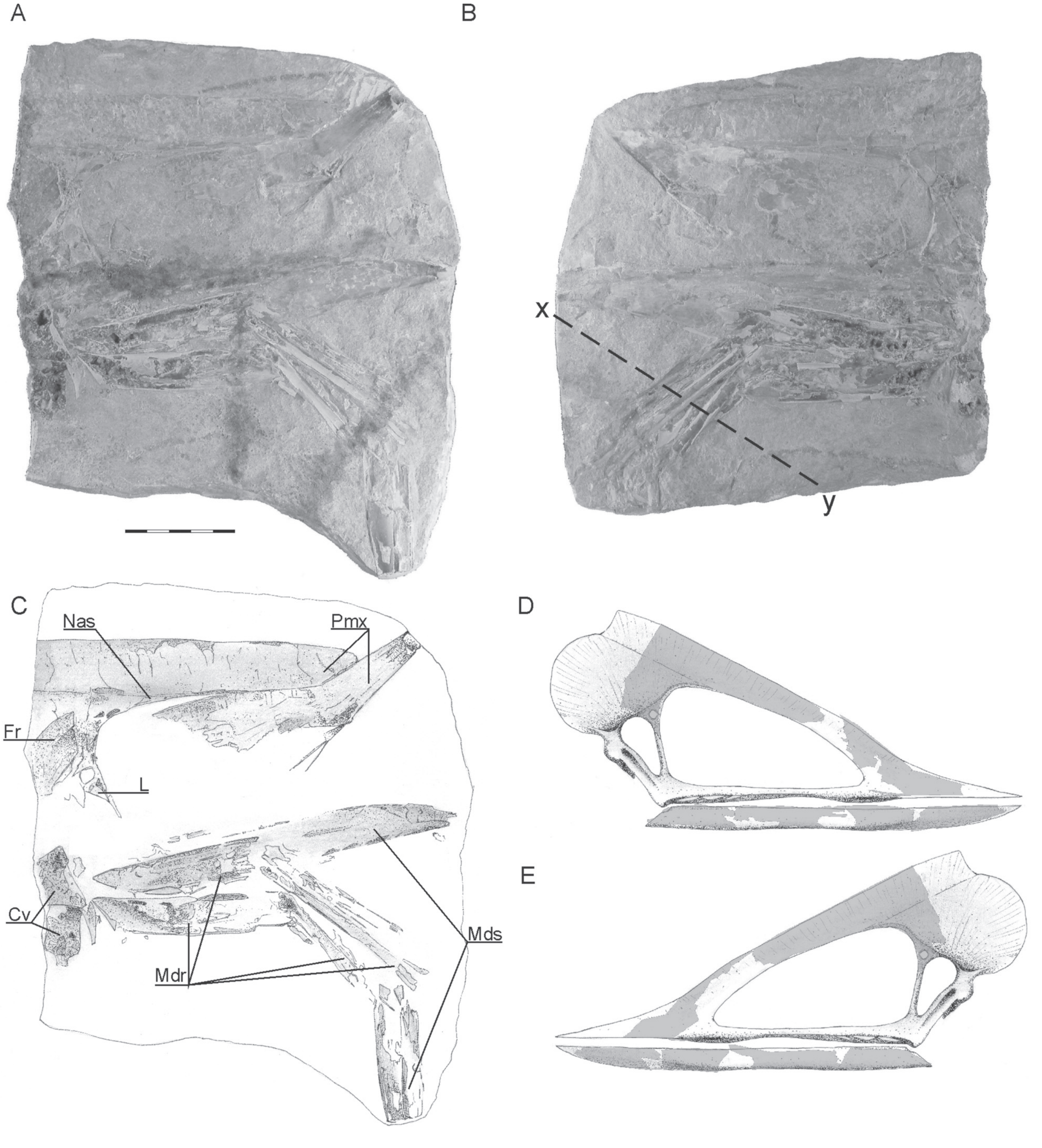

Figure 2: SMNK PAL 4330. **A**, main slab; **B**, counterslab (dashed line indicates line of section for Figure 3); **C**, interpretive drawing of main slab (Cv, cervical vertebrae; Fr, frontal; L, lacrimal; Mdr, mandibular rami; Mds, mandibular symphysis; Nas, nasal; Pmx, premaxilla); **D**, reconstruction of skull incorporating right lateral elements (shaded); **E**, reconstruction of skull incorporating left lateral elements (shaded). Scale bar represents 50 mm; D and E not to scale.

The jaw has achieved this shape by two, bilaterally symmetrical fracture regimes on the mandibular rami that facilitate two ~ 45° rotations along its length to displace and rotate the right portion of the mandibular symphysis almost 90° from the long axis of the caudal mandibular elements (Fig. 4). A fracture has propagated sagittally within the mandibular symphysis to bisect its lateral components, allowing the left portion to dislocate from the right and be telescoped caudally to lie alongside the articulatory portion of the jaw. The entire mandible has rotated along its long axes such that the occlusal surface now faces away from the ventral margin of the premaxilla. Because of this rotation, the caudalmost fragment of the right dentary is seen in medial aspect while the left occurs in lateral view. Both mandibular rami have broken at the mid-shaft and immediately caudal to the mandibular symphysis with irregular, oblique fractures. The ventral lengths of these fractured mandibular fragments are greater than the dorsal and numerous bony shards lie between each portion. Several longitudinal fractures

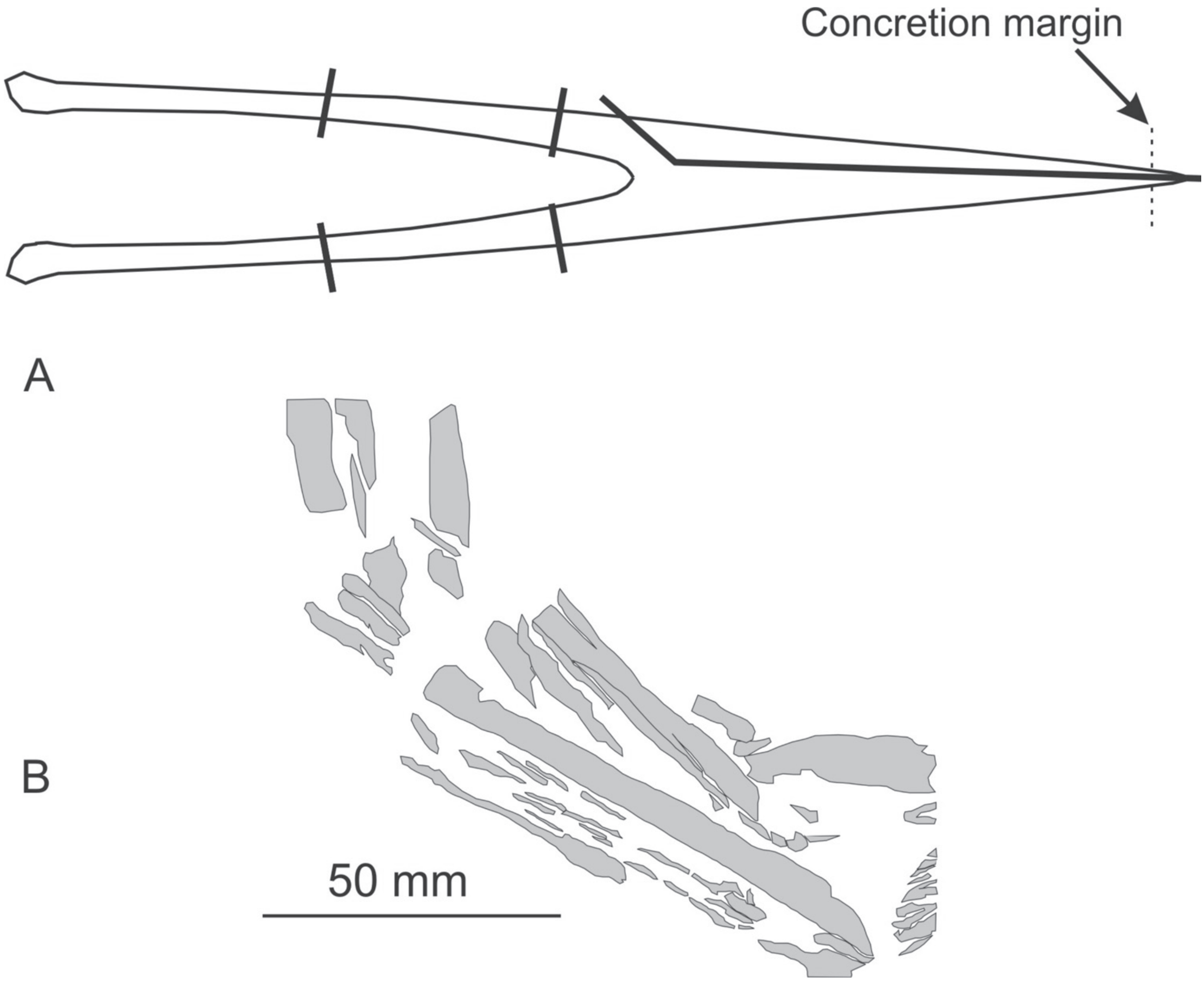

Figure 3: A, stylised jaw of Tupuxuara sp. with loci of major fractures indicated by bold lines. **B**, detail of degree of fracturing of mid portions of mandibular rami in SMNK PAL 4330.

have split the anterior portions of the mandibular rami such that the dorsal, ventral and lateral surface of this region now lie alongside each other as long, irregular splints of bone. The cross-sectional shapes of these splints confirms their identity as elements of the mandibular rami with thickened occlusal surfaces like those seen in other *Tupuxuara* jaw sections (Fig. 4; WITTON, pers. obs. 2007).

The two cervical vertebrae associated with the skull lie along the border of the concretion and are not completely preserved. However, these do not show any indication of fracturing or damage like that seen in the skull and mandibular elements of the specimen.

6. Interpretation

The damage recorded in SMNK PAL 3340 was clearly present before the onset of diagenesis as the dislocations and displacements are wide and show sediment in direct contact with the fracture surfaces. This contrasts with the septarian cracking and compaction-induced crushing in similar Romualdo Member concretions where diagenetic sparry calcite cements lie in direct contact with fracture surfaces and fracture displacement are minor. We are therefore confident that this skull was damaged prior to burial.

The associated fractured elements of SMNK PAL 4330 are evidence that the damage and burial of this skull took place with at least some connective tissue present. The excellent condition of the bone tissue and close association of bone elements suggests the specimen was removed from typical decay processes quickly either by high rates of sedimentation (unlikely given the nature of the enclosing matrix), bacterial sealing (some of the laminae within the concretion may represent bacterial mats) or accumulation in stagnant conditions. However, the cause and timing of the acquired skeletal damage relative to the death of the animal is not easy to determine. Pterosaur remains are often fragmentary or broken, but no other skulls known to these authors demonstrate the extensive trauma recorded in SMNK PAL 4330. The oblique fracturing of many of the skull elements and the caudodorsal telescoping of the rostrum suggest that the skull was subjected to severe compressive forces operating approximately parallel to the skull midline [Fig. 5;

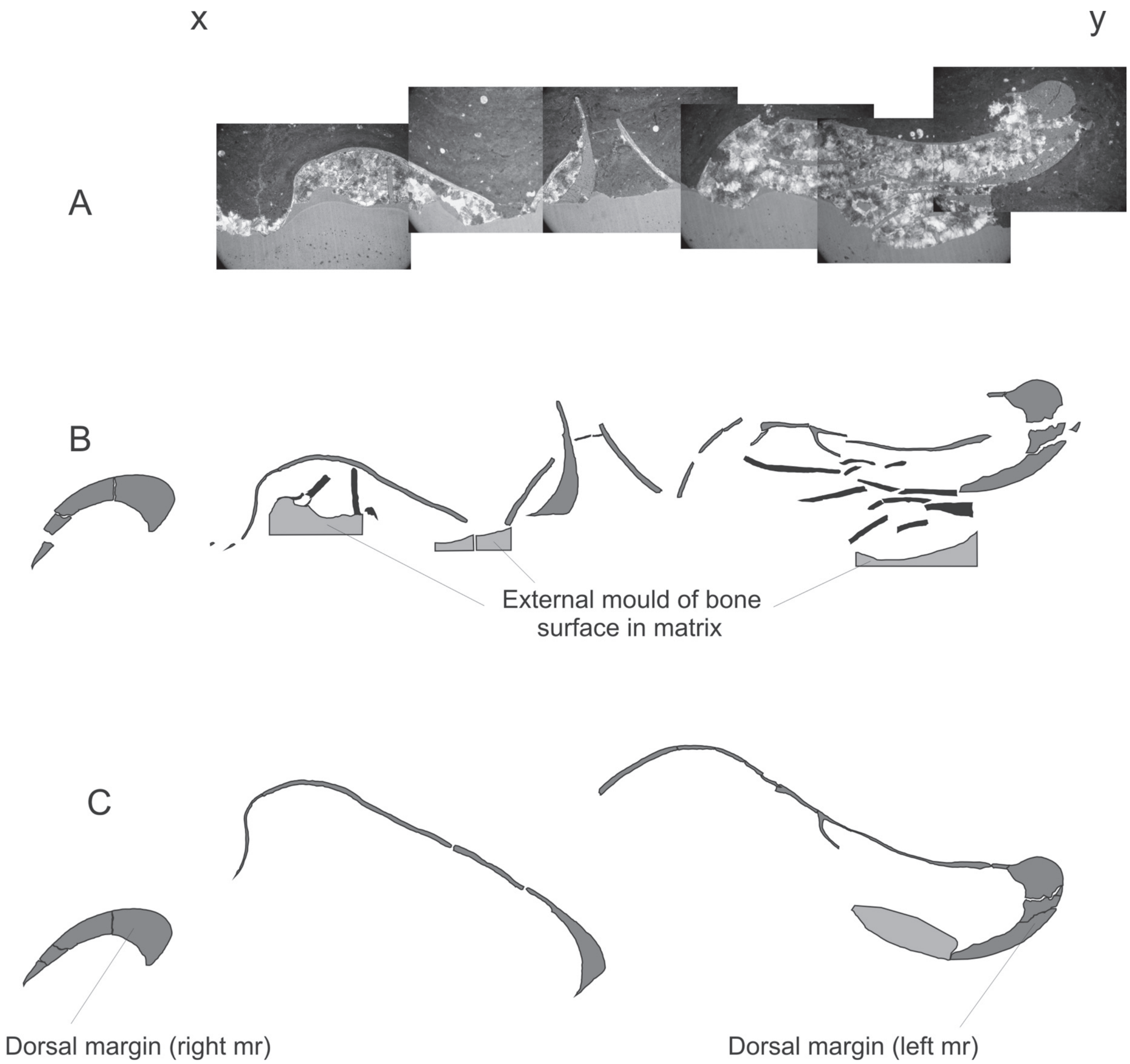

Figure 4: Mandibular section of SMNK PAL 4330. **A**, light microscope photograph montage; **B**, traced jaw elements; **C**, reconstructed jaw elements. Dark grey elements are bone, light grey elements are external moulds of bone. Black shaded elements were not incorporated into the reconstruction. x and y indicate line of section (of Fig. 2).

see Alms (1961) for a discussion of fracture mechanics]. Vertical fractures in the rostrum are indicative of minor longitudinal crumpling that is consistent transmission of forces along this plane. The greater ventral lengths of the mandibular fragments relative to their dorsal lengths indicate that the lower jaw was subjected to caudodorsal bending forces apparently derived rostroventrally from the jaw tip. These forces, as well as caudally displacing a portion of mandibular symphysis, caused extensive buckling of the mandible that permitted the formation of the arc-like morphology preserved in the specimen. The caudal displacement of both jaws may have transmitted excessive longitudinal forces to the jaw joint and shattered or disarticulated this relatively delicate region from the remainder of the skull. Given that both the skull and mandible appear to have failed under strong rostrally-derived forces, it is most parsimonious to conclude that the skull was broken in a single, high energy event. It is not possible, however, to determine whether this damage occurred peri- or post-mortem, but it is certain that the failure of the skull could not have occurred pre-mortem in any individual long before its death.

6.1 Possible causes of damage

Such extensive and unusual damage to the SMNK PAL 4330 skull invites investigation into its origin, but the specimen offers frustratingly little direct evidence regarding its catastrophic history. We consider three possible causes for the state of SMNK PAL 4330: direct consequence of the behaviour of the individual; activities of other animals, or destructive effects of the physical environment. The telescoping of the jaw tips and

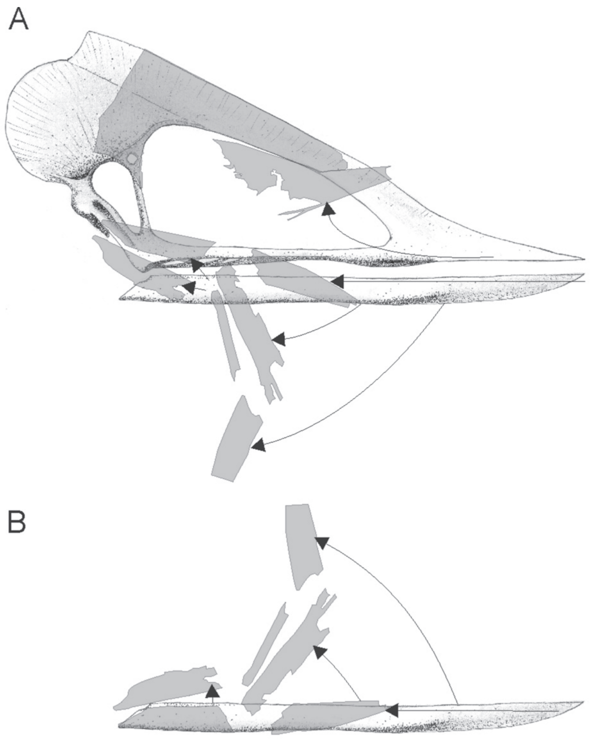

Figure 5: Movement of SMNK PAL 4330 skull elements from their original positions. **A**, comparisons of skull and mandible elements as preserved to a reconstructed skull (note that mandibular elements are medially rotated so that the ocular surface faces ventrally); **B**, comparisons of mandibular elements to a reoriented mandible. Shaded elements indicate preserved bones; arrows indicate directions of movement.

fragmentation of the mandible is consistent with the trauma seen in bird skulls following mid-air collisions with windows (Klem 1990: 117, fig. 2; Veltri & Klem 2005), and a head-on collision with a hard substrate is further supported by the oblique mandibular fractures that are indicative of strong forces operating along the jaw length (Alms 1961). It is therefore quite possible that SMNK PAL 4330 records a pterosaurian crash landing, an interpretation consistent with the rostroventral application of force on the skull. However, such an impact has to take place on land and therefore requires post-catastrophe transportation of the skull into the depositional basin. Although the nodule was not collected in situ, it is typical of fossils found in the Romualdo Member shales that were deposited some distance from the palaeoshoreline. The minimal distance from Santana do Cariri to the faulted margins if the Araripe Basin is approximately 15 km, and the fault-bounded margins of the basin may have transgressed during Santana Formation times to produce palaeoshorelines of considerably further distances. Note, however, that transport of terrestrial animal carcasses from the Santana hinterland over these distances is potentially recorded through the occurrence of terrestrial theropod dinosaurs in the Santana lagoon (Kellner 1999; Sues et al. 2002; Naish et al. 2004), suggesting that repositioning the SMNK PAL 4330 skull from the Santana hinterland to the lagoon is possible.

Several authors have suggested skim-feeding as a possible foraging method for pterosaurs (e.g. Wellnhofer 1991; Kellner & Campos 2002) and, given that Recent skim-feeding birds are known to collide with submerged objects and substrata when foraging (Potter 1932; Zusi 1962, 1996), it could be supposed that the damage to SMNK PAL 4330 occurred through skim-feeding. However, the mechanical failure of SMNK PAL 4330 is considerably more pronounced than the damage that occurs to the mandibular tips of skimmers [see Zusi (1962) for examples]. The rostroventral application of force is inconsistent with the dorsorostral application that would occur during skimming, and, moreover, the telescoped premaxilla suggests the pterosaur would have to been skimming with its jaws almost entirely closed (ironically, the prokenetic skulls of modern skimmers are used to feed with closed mouths but open jaws [Zusi 1962], but the akenetic skulls of pterosaurs do not facilitate this). It is therefore highly unlikely that the failure of SMNK PAL 4330 occurred during skim-feeding. The complete lack of skim-feeding adaptations and inadequate muscular energetics of pterosaurs (Humphries et al. 2007) strengthens this point.

It is possible that other animals, either directly or indirectly, may have caused the damage seen on SMNK PAL 4330. Several examples of carnivorous animals predating or scavenging pterosaurs are known (e.g. Dalla Vecchia et al. 1989; Currie & Jacobsen 1995; Buffetaut et al. 2004) and identified through the presence of tooth marks or embedded teeth in pterosaur bones, or the aggregation of pterosaur remains into a gastric pellet. No evidence of this kind is seen on SMNK PAL 4330, suggesting that predation or scavenging was not the cause of the skull fracturing. The possibility of predation by an edentulous animal cannot be ruled out, but the longitudinal application of force along the tip is inconsistent with the damage expected from a predatory or scavenging act.

Bones are regularly damaged by the trampling activities of other animals and similar acts may account for damaged bones in the fossil record (e.g. Behrensmeyer et al. 1986; Fiorillo 1998). There were certainly animals present in the Santana Formation biota that were large enough to inflict severe damage to a pterosaur skull should they walk across one (e.g. Sues et al. 2002), but the telescoping of the rostrum and relatively intact nature of some skull elements are inconsistent with trampling-derived damage. Such activity would almost certainly shatter most bones of a pterosaur skull into unrecognisable fragments and, while this may explain the shattered ventral cranium, the other skull elements are too intact to indicate trampling beyond the cranial area.

A final possibility is that SMNK PAL 4330 was damaged during transportation, perhaps being smashed against a rocky shoreline during a storm or carried along a rocky stream from the Santana Formation hinterland, but the specimen lacks the abrasion that might be expected from such turbulent transportation. The intact parts of the skull bear no large or small-scale radial surface fractures or chipped bone compacta that would result from repeated impacts with hard substrata or other debris in the current flow. The apparent single-event cause of the skull damage is also inconsistent with random buffeting of a skeletal element in a current flow, and, furthermore, only limited sedimentological evidence for rocky shores or turbulent fluvial settings exists for the Santana palaeoenvironment.

7. Conclusions

SMNK PAL 4330 records a unique preservational style clearly indicative of a catastrophic pre-depositional event, but the cause remains mysterious. Of the hypotheses presented here, perhaps the least compelling are SMNK PAL 4330 being damaged during transportation, trampling or predation: all require specific traces being preserved on the specimen (e.g. feeding traces, abrasion) and none are consistent with the probability of a sole occurrence of head-on trauma. However, until the taphonomy of the Santana Formation tetrapods is studied in greater detail, this hypothesis remains untested.

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Note added in proof: Since acceptance of this manuscript, subsequent preparation of SMNK PAL 4330 has revealed details of the premaxillary palatal surface and suggests that the bone lying alongside the ventral surface of the skull is a portion of the palate and not, as suggested above, the tip of the mandibular symphysis. This indicates that the underside of the skull broke away from the jaw tip to settle adjacent to the skull itself with the ventral surface exposed. Identification of the palate is confirmed by the presence of the palatal and postpalatinal fenestra in its posterior region. While this reappraisal has little effect on the taphonomic interpretation of this specimen, identification of the palate and exposure of the ventral premaxillary surface in SMNK PAL 4330 permits greater comparison with existing Tupuxuara material than previously offered: the prominence of the palatal ridge and concave palatal surface of the jaw tip suggest it has greatest affinities to *Tupuxuara leonardii* (KELLNER & CAMPOS 1994).