A nearly complete ornithocheirid pterosaur from the Aptian (Early Cretaceous) Crato Formation of NE Brazil

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A partial ornithocheirid, representing a rare example of a pterosaurian body fossil from the Nova Olinda Member of the Crato Formation, NE Brazil, is described from the collections of the State Museum of Natural History, Karlsruhe. While similar in preservation and taphonomy to *Arthurdactylus conandoylei*, it is distinguished by slight differences in biometric ratios, but the absence of a skull prevents closer identification. Mostly complete body fossils belonging to ornithocheiroid pterosaurs appear to be relatively more abundant in the younger Romualdo Member of the Santana Formation, making the described specimen one of only two well documented ornithocheiroids known from the Nova Olinda Lagerstätte.

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Introduction

The Araripe Basin of NE Brazil contains two Early Cretaceous Lagerstätten that are world renowned for their exceptional preservation of insects and vertebrate fossils (Unwin 1988; Unwin and Martill 2007). Pterosaurs from the Aptian/Albian-aged Crato Formation and Albian/?Cenomanian-aged Santana Formation (Martill 2007) confirm that taxa attributed to both the Ornithocheiroidea (sensu Unwin 2003) and Azhdarchoidea inhabited the area of this inland lagoon, a setting in which marine influences became more dominant towards the end of the Albian after the formation of the Santana sea (Kellner and Tomida 2000).

Despite ongoing debates on taxonomic validity, a number of ornithocheiroid pterosaurs are known from the Santana Formation including *Anhanguera/Coloborhynchus* (Wellnhofer 1991; Kellner and Tomida 2000; Fastnacht 2001), *Araripedactylus* (Price 1971; Wellnhofer 1977), *Brasileodactylus* (Kellner 1984; Veldmeijer et al. 2009), *Cearadactylus* (Leonardi and Borgomanero 1983; Dalla Vecchia 1993; Vila Nova et al. 2011), *Ornithocheirus* (Wellnhofer 1987), and *Santandactylus* (Buisonjé 1980; Wellnhofer 1985). In contrast, relatively few ornithocheiroid specimens have been described from the older Nova Olinda Member of the Crato Formation (e.g., *Arthurdactylus conandoylei*, SMNK PAL 1132, Frey and Martill 1994; *Ludodactylus sibbicki*, SMNK PAL 3828, Frey et al. 2003a; cf. *Brasileodactylus*, Sayão and Kellner 2000) and isolated crania or headless postcranial skeletons attributed to azhdarchoid taxa are instead better represented in the literature (Sayão and Kellner 2007; Martill and Frey 1999; Frey et al. 2003b; Kellner 2004).

A new specimen from the Nova Olinda Member in the collections of the State Museum of Natural History, Karlsruhe (SMNK PAL 3854), is described here, representing the rare occurrence of a largely complete ornithocheirid pterosaur from this locality. The specimen is taxonomically indeterminate, missing the skull, cranially located elements of the cervical column and the second to fourth phalanges of the wing-fingers, but is otherwise in a fairly good state of preservation. As is typical of fossils from the Crato Lagerstätte, the bones are crushed and few three-dimensional details can be observed. A greater degree of damage is observed along the caudally located thoracic vertebrae and the pelvic girdle. The skeleton has collapsed upon itself following contact with the lagoon floor, exposing the majority of bones in their dorsal or dorsolateral aspects (Fig. 1).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum of Natural History, London, UK; IVPP, Institute for Palaeontology and Palaeoanthropology, Beijing, People's Republic of China; JZMP, Jinzhou Paleontological Museum, Jinzhou, Liaoning Province, China; LPM, Liaoning Paleontological Museum, Western Liaoning Institute of Mesozoic Paleontology, Shenyang Normal University, Liaoning, China; MPSC, Museu de Paleontologia de Santana do Cariri, Santana do Cariri, Brazil; NGMC, National Geological Museum of China, Beijing, People's Republic of China; NSM, National Museum of Nature and Science, Tokyo, Japan; RGM, Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany.
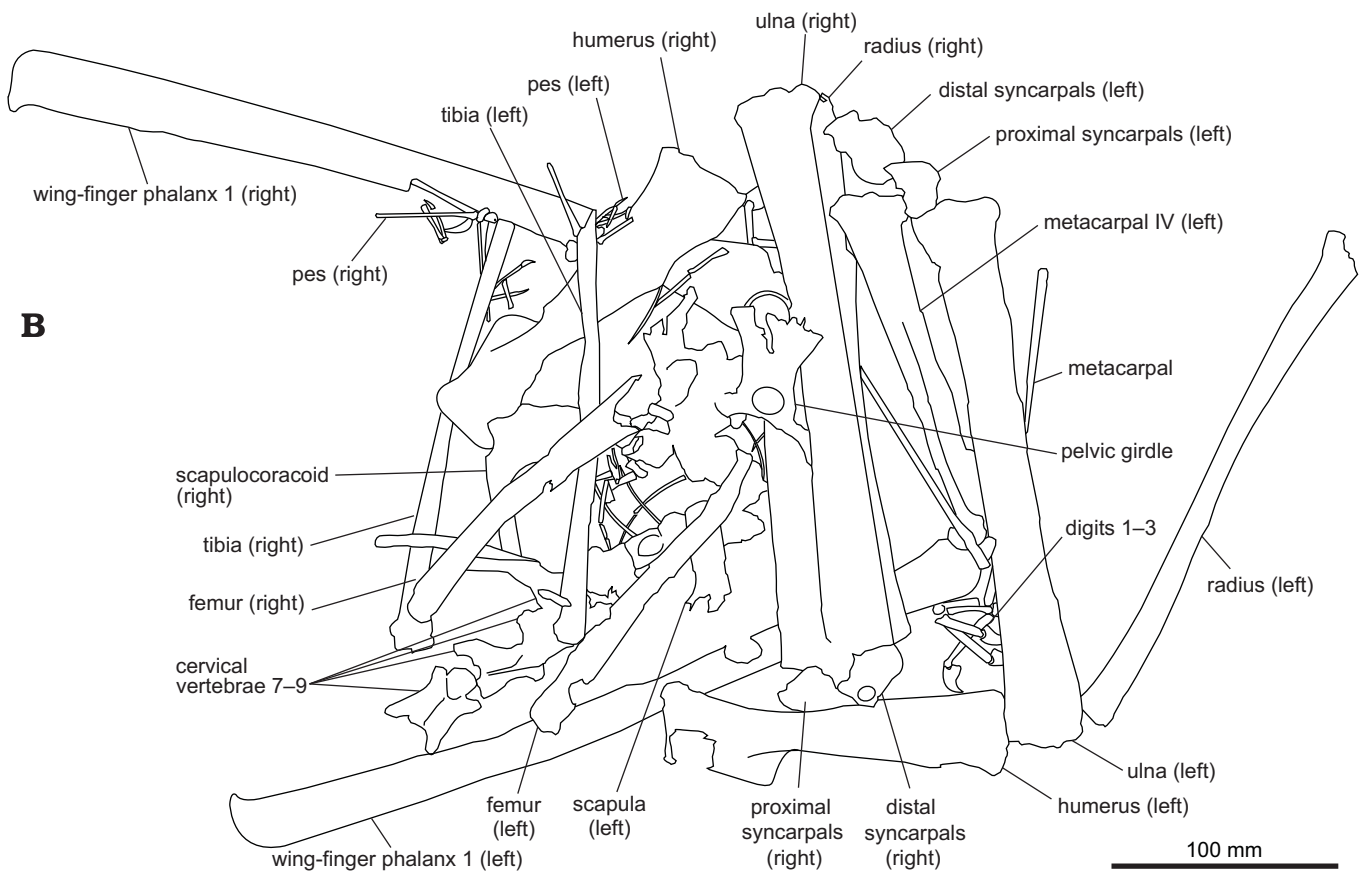
Fig. 1. New ornithocheirid pterosaur specimen (SMNK PAL 3854) from the Nova Olinda Formation, Crato Basin, Brazil. Photograph (**A**) and corresponding line tracing (**B**).

Systematic palaeontology

Order Pterosauria Kaup, 1834

Superfamily Ornithocheiroidea Seeley, 1876

Family Ornithocheiridae Seeley, 1870

Genus and species indet.

Description.—The cervical column is represented by four vertebrae, identified as cervicals 5–8 (C5–8) (Figs. 2, 3). The morphology of these vertebrae is typical for ornithocheiroid taxa (Table 1), in that the cervical vertebrae are 2–2.7 times as long as they are wide, they have a wide neural canal and widely diverging pre- and postzygapophyses, and the prezygapophyses are located lateral to the postzygapophyses (Bennett 2001). The neural spines of C5–6 are broken and no comment can be made on their relative height. Caudal to the 6th cervical vertebrae the remaining cervicals have been displaced from their natural position and are now visible in their craniolateral (C7) and cranial (C8) aspects. The neural spine of the 7th cervical is tall and thin with respect to the vertebral body while the most caudally located cervical vertebrae (i.e., C8–9) preserve large robust ribs that remained in situ, suggesting that these had fused to the transverse processes. Although the 9th cervical itself is not visible, being overlain by the 8th, its presence is confirmed by a single large rib situated caudal to that of the 8th cervical (Fig. 3C). The capitulum and tuberculum are widely spaced, by approximately 16 mm, and the shaft is narrow, decreasing rapidly to 6 mm by the mid corpus. The rib of the 9th cervical is complete and terminates in a robust, slightly convex surface after a length of 89 mm.

The centra of the thoracic vertebrae are missing, buried and/or badly damaged such that the description of these elements is restricted to the neural spines, three of which are partially fused and form a supraneural plate. Thin suture lines separating the individual neural spines are visible (Fig. 2). The neural spine of the first visible thoracic vertebra lies separate from the supraneural plate, although it is uncertain whether this is due to damage or displacement of the skeleton, or whether the neural spine simply did not form part of this structure. A large oval depression with a raised rim occu-

Table 1. Skeletal measurements of the new unidentified ornithocheirid from Brazil. SMNK PAL 3854. Measurements of selected bone elements. All values are in mm, where * denotes an approximate or estimated value.

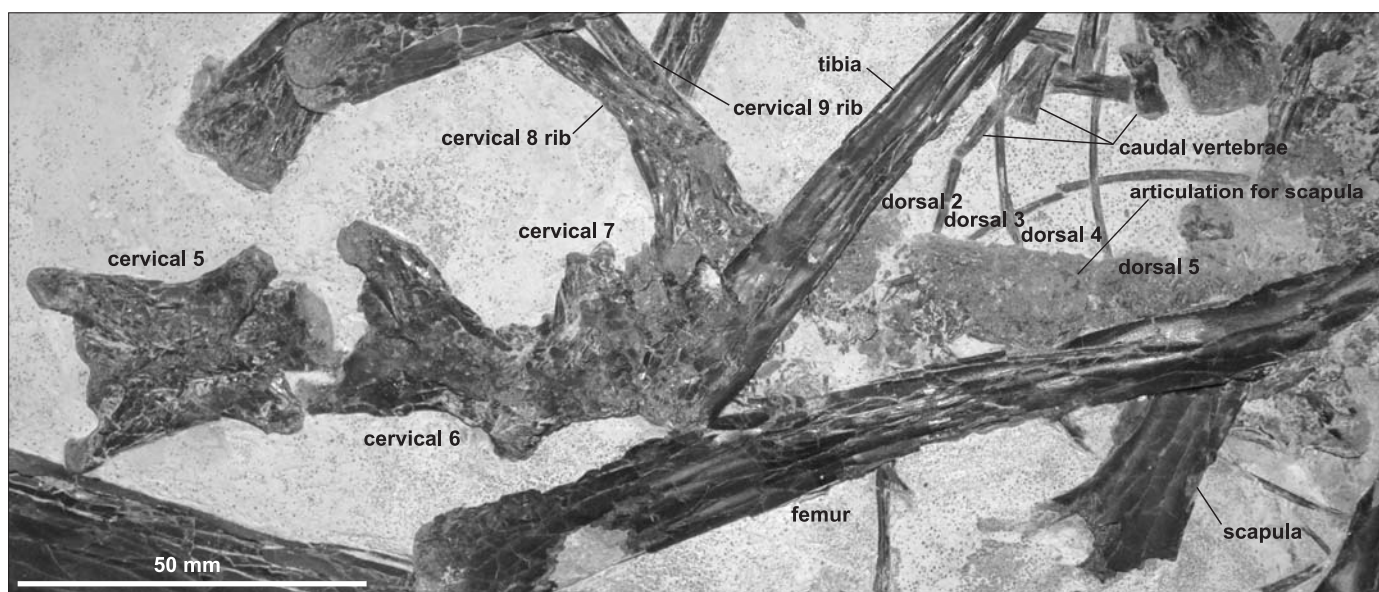| Element	mm	Element	mm
cervical vertebrae		scapula	73.5
C5 length	37	coracoid	>61
C5 mid width	28	humerus	
C6 length	33*	left	157
C6 mid width	–	right	160
C7 length	>25	ulna	
C7 mid width	–	left	252
caudal vertebrae		right	253
1	10	metacarpal IV	
2	11*	left	169
3	10.5	right	169
4	12	Wph 1	
5	12	left	383
6	11	right	381
7	>6.9	femur	
8	12	left	161
9	10	right	>150
10	6.2	tibia	
11	>5	left	>197
		right	202

Fig. 2. New ornithocheirid pterosaur specimen (SMNK PAL 3854) from the Nova Olinda Formation, Crato Basin, Brazil. Photograph detailing the cervical, notarial thoracic and terminal caudal vertebrae.
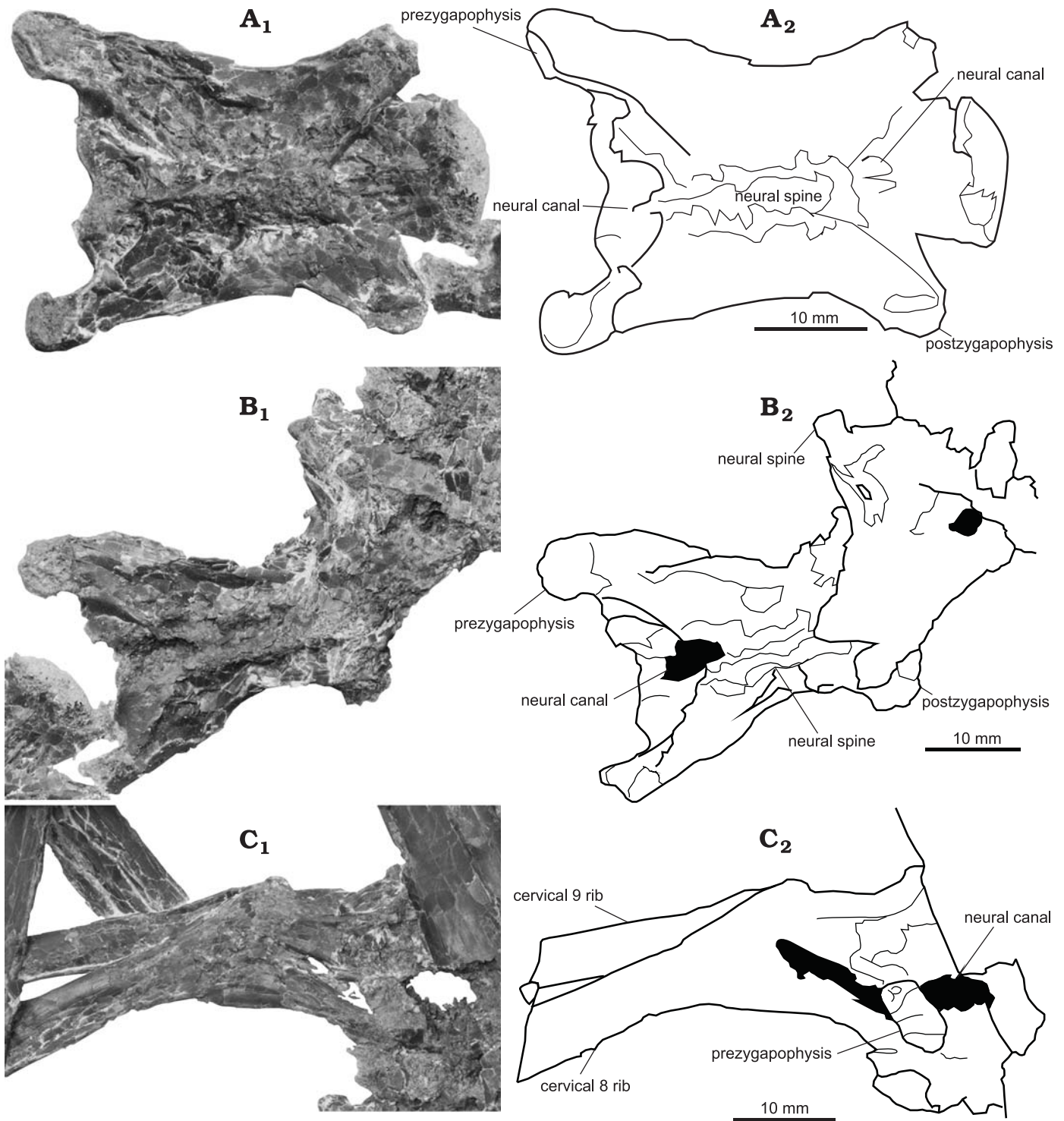
Fig. 3. New ornithocheirid pterosaur specimen (SMNK PAL 3854) from the Nova Olinda Formation, Crato Basin, Brazil. **A**. 5th cervical vertebrae. **B**. 6th and 7th cervical vertebrae. **C**. 8th and 9th cervical ribs. Photographs (A$_1$, B$_1$, C$_1$) and explanatory drawings (A$_2$, B$_2$, C$_2$). Black shading highlights gaps/foramina with the bone and the collapsed neurocentral canal.

pies the lateral flank of the third visible thoracic vertebra, forming the articulation for the medial articular surface of the scapula. Caudal to the notarial vertebrae the vertebral column is kinked and the more caudal thoracic vertebrae are badly damaged, indistinct and partly overlain by the left femur. These are also seen in lateral aspect and they have a

maximum height of 19 mm from the base of the centrum to the top of the neural spine.

Nothing can be said about the sacral vertebrae, which are obscured from view by the overlying pelvic girdle. At least six gastralia have separated from the main body of the fossil and were displaced to overlie the distal portion of the right

ulna following the disintegration of the dorsal column. These gastralia are preserved as three opposing sets and are associated with a limited amount of mineralised tissue. Eleven caudal vertebrae lie loose from the axial column and are scattered between the notarial vertebrae and the right scapulocoracoid. These are identical in appearance to those of *C. piscator* (Kellner and Tomida 2000), being long and narrow, typically between 2 and 4 times as long as they are wide. Where visible, the neural spines are positioned cranially and protrude past the cranial margin of the vertebrae, indicating that these bones belong to the middle portion of the tail. The terminal-most caudal vertebrae remain in articulation and are mediolaterally compressed to a greater degree than the other caudals. These are conical in form and do not expand at their articular surfaces (Fig. 2).

The right scapulocoracoid is preserved in cranial view. No suture line between the two elements is visible, indicating that the structure was fully fused. The glenoid body measures 23 mm across its widest part and the scapula is shorter than the coracoid, the condition typical of ornithocheiroids (Frey et al. 2003c; Kellner 2003; Unwin 2003). The scapula is offset against the glenoid body at an angle of 121° and the dorsal rim of the articular surface is visible as a flat, slightly convex surface that would have braced against the sub-oval facet of the notarium. The coracoid is about half as thick as the scapula in the mid-shaft region and forms an angle of 60° against the scapula. The proximal portion of the coracoid, where it would have articulated with the sternum is obscured by overlying sediment. The vertical distance between the dorsal surface of the scapula articular surface and the sternocoracoid articulation is estimated to have been no greater than 100 mm.

The individual bones of the forearm are mostly preserved in either near articulation or bent beyond bone lock. Both humeri are visible in dorsal aspect and preserve a short, warped, sub-triangular deltopectoral crest that is approximately one third of the total humeral length. The caudal tuberosity is short, and no pneumatic foramina are observed where it converges with the shaft of the humerus, although the compacta of these surfaces is slightly damaged. On the distal portion of the left humerus, along the craniodorsal margin of the shaft, a pronounced flange, 15% the humeral length, may be the insertion for the flexor muscles of the carpus (Bennett 2003). Towards the distal margin of the humerus, the humeral shaft expands to about twice its width at the elbow joint, preserving an almost straight dorsal margin perpendicular to the long axis of the shaft. The epiphyseal gap is partially open.

The left ulna lies at an angle of 72° to the humerus while the right makes an angle of 53°. Both have become slightly disarticulated from their natural positions. Both ulnae are about six times longer than they are wide and preserve no obvious muscle scars. While the right radius lies in situ along the right ulna the left radius has separated from the ulna and preserves a mid shaft width of 10–13 mm.

The carpals have fused to form two distinct syncarpal blocks but these have disarticulated from one another and are badly damaged so that no anatomical details can be observed.

The fourth metacarpals have been displaced by approximately 180° and lie sub-parallel to the ulnae; the distal roller joints are located near the proximal ends of the ulnae. Both wing metacarpals are also preserved in ventral view, with the ventral part of the roller joint measuring 16 mm across at its widest point, and they retain a natural articulation with the first phalanges of the wing finger. At least two additional metacarpals, presumably belonging to the left wing, are also preserved. Both are long and narrow and at least one would have made contact with the distal syncarpal during life.

The digits of the left manus are well preserved, and although the individual phalanges have disarticulated from each other they have not been displaced any great distance. The distal bones retain a contact with their respective unguals. The phalanges are about half as wide as the proximal margins of the unguals and slightly curved, with expanded proximal and distal margins at the articular facets to accommodate the neighbouring elements. The unguals are slightly curved with longitudinally concave ventral faces, forming a sulcus that extends almost the entire length of the bone. The phalanges of the right manus are mainly obscured and only two partial phalanges and one ungual are visible.

Only the first phalanges of the wing fingers are preserved and lie in natural articulation with the fourth metacarpals, making angles of 89° and 68° against the long axis of the left and right metacarpals respectively. The extensor tendon process has fused to the proximal face of the first phalanx and a large pneumatic foramen is present on the caudoventral surface of the right phalanx, adjacent to the proximal articulation. At its distal terminus the cranial margin of the first wing finger phalanx gradually merges with the gently convex distal articulation. Caudally this articulation facet forms a sharp caudally directed process that is formed by the steeply convex caudodistal margin of the shaft. This creates an expanded surface for the second wing phalanx that would have directed the distal phalanges caudally.

The individual elements of the pelvis have fully fused to form two complete pelvic plates, although these are in a poor condition. The compacta is damaged and the bone itself is crushed over several underlying elements. The left ischiopubic plate is observed in lateral view while the right is seen in caudolateral aspect, the acetabulum dominating the lateral faces of each and the obturator foramen being fully enclosed within the pubis. The cranial and caudal margins of the left pubis are shallowly concave, being almost symmetrical about the long axis of the bone. The bone is narrowest about its mid point before expanding towards its ventral margin, however, the ventral margin of the pubis is broken and its original shape cannot be determined. While the long axis of the pubis is directed ventrally, that of the ischium is directed caudoventrally at an angle of 46° against the pubis. As with the pubis, it is narrowest about its mid point and expands towards its ventral margin. Approximately half the caudal portion of the left ischium has been broken and lost from the
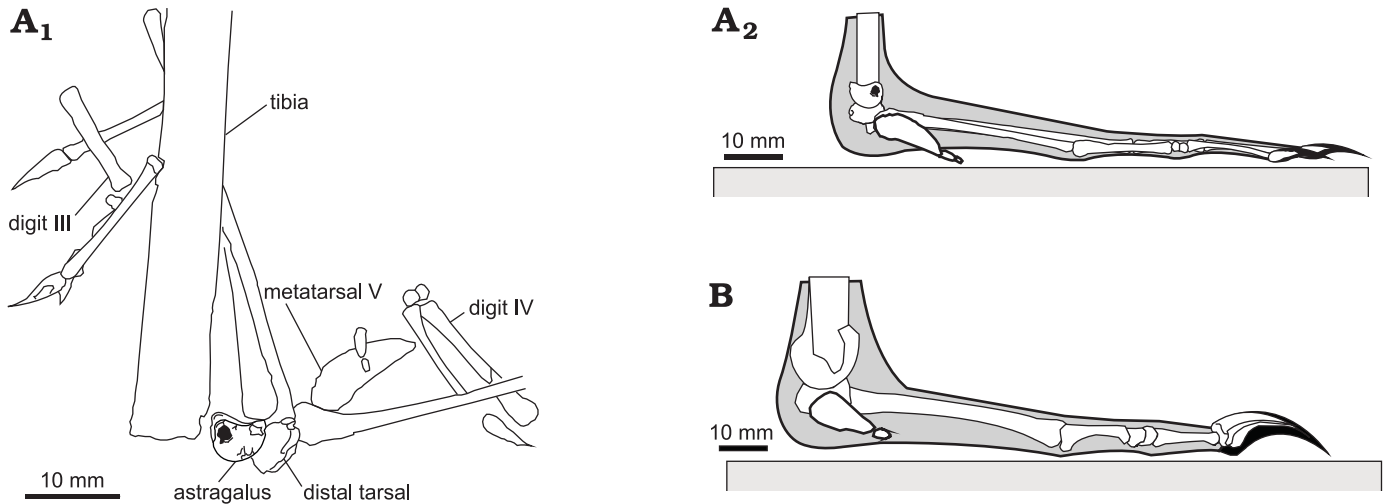
Fig. 4. The foot and pedal function of the new ornithocheirid pterosaur from the Nova Olinda Formation, Crato Basin, Brazil. **A**. SMNK PAL 3854. Line tracing of the ankle region (A₁) and reconstructions of the ornithocheiroid pes, based on the described specimen (A₂). **B**. The azhdarchoid pes, based on SMNK PAL 3900. Both reconstructions are scaled to a common humeral length.

specimen while the right has been distorted and is directed through the bedding plane of the slab. The preacetabular process of the ilium is long and thin but its cranial portion is either overlain by the ulna (left) or broken (right). The postacetabular process of the right pelvic plate partially overlies that of the left, which in turn has been crushed over the remains of the sacral vertebrae. The postacetabular process expands caudodorsally for approximately one quarter of its total length due to the curvature of the dorsal margin of the bone. Caudal to this expansion, the dorsal and ventral margins are directed caudoventrally, creating a caudoventrally directed process more or less uniform in width.

The femora lie adjacent to the pelvis and preserve a long, narrow femoral collum femoris, approximately 17 mm long, and a moderately bowed, laterally curving shaft. The femoral head is offset against the shaft at an angle of 20°. Although both tibias have disarticulated from their respective femurs, they have not been displaced much. The tibia is long and slender, becoming increasingly narrow towards its distal articulation. Neither fibula is preserved. The distal articulation of the left tibia is broken and missing but the right is complete and terminates as a flat surface, 7.5 mm in width, indicating that the calcaneum and astragalus had not fused with this bone to create a tibiotarsus (Fig. 4). Two tarsals, the astragalus and a distal tarsal, lie level with the distal margin of the tibia but off to one side. The astragalus is weakly crescentic in shape and is observed in medial aspect. A large foramen pierces the craniomedial portion of the bone. Although its caudomedial face is damaged, the preserved remains suggest that the medial surface was convex, projecting medially as described by Kellner (2004). The dorsal margin of the astragalus is concave to form the articulation with the distal surface of the tibia, while the ventral margin is strongly convex. The distal tarsal is as large as the astragalus itself, with a generally smooth convex surface and lies in contact with three of the four metatarsals.

The right metatarsals are very long and thin, the longest reaching a length of 58 mm with a mid-shaft diameter of only 1 mm. The length of these bones ranges from 54–58 mm, but at least one of the first four metatarsals is noticeably shorter with a length of only 45 mm. The fifth metatarsal is clearly distinct from the others, and is about one fourth to one fifth the length of metatarsals I–IV and has a sub-triangular outline with slightly convex medial and lateral margins.

The pedal phalanges are delicate and show only slight curvature. Their proximal and distal margins are slightly expanded at the interphalangeal articulations and in all cases the unguals maintain a natural articulation with the penultimate phalanx. The unguals themselves are equal in width to the preceding phalanges and are only slightly curved.

Discussion

Largely complete ornithocheiroid pterosaurs appear to be much less common in the Nova Olinda Lagerstätte than in the geologically younger Romulado Member of the Santana Formation, NE Brazil. A thorough review of these was provided by Unwin and Martill (2007), who noted that specimens from the Crato Formation attributed to the Ornithocheiroidea are limited to SMNK PAL 1132 (*Arthurdactylus conandoylei*, Frey and Martill 1994), a headless skeleton preserving the majority of the postcranial elements; the proximal part of a wing belonging to an indeterminate ornithocheiroid (SNMK PAL 3842); an isolated tooth (Sayão and Kellner 2000); the complete cranium of SMNK PAL 3828 (*Ludodactylus sibbicki*, Frey et al. 2003a); and the rostral fragments of cf. *Brasileodactylus* (Sayão and Kellner 2000). Unwin and Martill (2007) include two further specimens, MPSC R-739 and MPSC R-779 (Nuvens et al. 2002) in the Ornithocheiroidea. A comparison of the present specimen with these other named taxa from the same locality, however, is problematic because no

Table 2. Selected long bone ratios of ornithocheiroid taxa. Abbreviations: fe, femur; FL, fore limb (humerus + ulna + metacarpal IV); HL, hind limb (femur + tibia); hu, humerus; mc IV, wing metacarpal; wph 1, first wing finger phalanx; ti, tibia; ul, ulna.

Taxon		FL/HL	hu/ul	hu/mc IV	hu/wph1	hu/fe	hu/ti	fe/ti
Boreopterus cuiae	JZMP-04-07-3	1.73	0.72	0.84	0.58	0.96	0.96	1.00
Nurhachius ignaciobritoi	LPM 0003	–	0.57	0.87	0.47	0.88	–	–
Istiodactylus sinensis	NGMC 99-07-011	–	0.57	0.82	0.50	–	0.73	–
Istiodactylus latidens	BMNH R 3877	–	0.58	–	0.56	1.10	–	–
ornithocheirid indet. (this study)	SMNK PAL 3854	1.48	0.63	0.94	0.41	0.98	0.78	0.79
?*Santanadactylus*	SMNK PAL 1250	–	0.65	0.93	0.45	–	–	–
Coloborhynchus robustus	SMNK PAL 1133	1.57	0.74	1.02	0.47	1.05	0.86	0.82
Arthurdactylus conandoylei	SMNK 1132 PAL	1.81	0.74	1.01	0.52	1.21	0.98	0.81
Coloborhynchus spielbergi	RGM 401880	1.49	0.71	1.23	–	1.04	0.82	0.79
Pteranodon sp.	AMNH 4908	1.77	0.68	0.46	0.39	0.96	0.62	0.65

postcranial elements are known for *L. sibbicki*, while the taxonomic validity of *Brasileodactylus* is uncertain (Unwin and Martill 2007) and diagnostic features are restricted to the skull (Veldmeijer et al. 2009).

It is fortunate that pterosaurs generally display isometric growth, in which individual bones grow at the same relative rate through ontogeny, and this allows the calculation of biometric ratios to distinguish taxa. Omitting the pteranodontids (studied by Bennett 2001) and nyctosaurids, the wing metacarpal and femur of the Ornithocheiridae + Istiodactylidae show significantly negative allometric relationships, so that the ratios of lengths of these elements to humerus length increase at larger sizes (see Appendix 1). Limb bone proportions place SMNK PAL 3854 within the Ornithocheiroidea (Table 2) where it is distinguished from pteranodontid and nyctosaurid pterosaurs by the relative shortness of the wing metacarpal, and from the Istiodactylidae by a set of ratios that lie outwith the observed range of values known for these taxa. This suggests that the current specimen may be tentatively assigned to the Ornithocheiridae. Despite the similarities in preservation and taphonomy between SMNK PAL 3854 and SMNK PAL 1132, the described specimen is distinguished from *A. conandoylei* through biometric ratios, where its humerus is relatively longer, forming ratios of 0.63 and 0.41 with the ulna and first wing-finger phalanx respectively (0.74 and 0.52 for SMNK PAL 1132). A more distinct ratio is observed in the hind limb, where the femur is substantially shorter, based on a large difference in the forelimb/hindlimb ratio (1.48 for SMNK PAL 3854 versus 1.81 for SMNK PAL 1132). A possible relationship is suggested with a larger specimen attributed to *Santanadactylus* sp. (SMNK PAL 1250) by an almost identical suite of bone ratios (note that this latter fossil is in a private collection and has not been described or diagnosed; Frey and Martill 1994).

SMNK PAL 3854 is estimated to have had a wing span of 3.4 m, based on the observations of Veldmeijer (2003), who noted that in *Santanadactylus pricei* (Wellnhofer 1991) the ratio between the total length of the wing finger and the humerus plus radius/ulna is 2.7. A similar ratio is also recorded for *A. conandoylei*, suggesting that this relationship is useful across a range of ornithocheirid taxa. The length of the torso,

measured from the first thoracic vertebra to the caudal margin of the ilium, is 140 mm, namely 4% of the total wingspan.

Ontogenetic age.—Despite the relatively advanced state of suture closure in parts of SMNK PAL 3854 shows no fusion between the astragalus and the tibia, and so is not yet at maximum age. The relative timings of suture closure in pterosaurs have been briefly reviewed by Bennett (1993) and Kellner and Tomida (2000), and the former tentatively proposed that for *Pteranodon* the atlas-axis complex, scapulocoracoid, secondary centres of ossification in the humerus, the cranial-most notarial vertebrae and ribs appear to precede all others. The suture between the extensor tendon process and the first wing finger phalanx appears to close shortly before skeletal maturity is reached. An examination of the suture states in SMNK PAL 3854 indicates that fusion of the tibia and proximal tarsals, the caudal thoracic ribs and their respective vertebrae, complete suturing of the notarium, and fusion of the humeral epiphyses to the humerus itself should all be considered indicators of late ontogeny and are preceded by the closure of the suture between the extensor tendon process and the first wing-finger phalanx and elements of the pelvic plate. Such observations do not contradict the proposals of Bennett (1993) and Kellner and Tomida (2000) but rather provide an example of interspecific variation in developmental timings that likely existed even between closely related taxa.

Life style.—The estimated length of the wing spar combined with the short length of the torso and hind limbs indicates that SMNK PAL 3854 developed the high aspect-ratio configuration noted for other ornithocheiroids and likely shared their interpreted lifestyle, being a relatively fast, open water glider, using dynamic or thermal soaring (e.g., Chatterjee and Templin 2004). The view that such taxa spent most of their life on the wing is further supported by the structure and relative size of the pes with respect to the wings; these bones in SMNK PAL 3854 are exceedingly thin compared with the pedal elements of azhdarchoid pterosaurs with which they shared the Cretaceous Crato lagoon. The comparison of a similar-sized azhdarchoid, SMNK PAL 3900, effectively illustrates this difference where the mid-shaft diameter of the phalanges ranges between 2–2.5 mm, with the unguals being

17 mm long (Fig. 4A$_2$, B). Similar values are also noted for the medium-sized azhdarchoids SMNK PAL 3830 and 6409, and the former demonstrates that sharp keratinous sheaths doubled the total length of the pedal claws. In contrast, the phalanges of SMNK PAL 3854 are only 1 mm in diameter with a length of 7 mm. The delicate nature of the pes in SMNK PAL 3854 therefore suggests that it was predominantly a soaring animal that spent little time on the ground. While one reviewer noted that blunted claws would be more in keeping with a terrestrially active lifestyle, it is difficult to explain the long, sharp keratinous sheaths of azhdarchoids without invoking a role in terrestrial support, as pterosaurs did not utilise their pedal claws for either the manipulation of prey or arboreal perching. Nonetheless, the lack of wear on the ungual sheaths of SMNK PAL 3830, a morphologically mature individual, perhaps indicates that these animals spent a significant portion of their life on the wing, while still being more terrestrially competent than ornithocheirids such as that described here.

Taphonomy.—The resting position and taphonomy of SMNK PAL 3854 strongly resembles SMNK PAL 1132, where the skeleton has collapsed upon itself following the destruction of the ventral body wall and the subsequent release of air from the pneumatic system. In both individuals, the lack of a preferred orientation indicates that bottom currents were absent, while the overlapping bones indicate that the carcass sank left wing first, and the hind limbs were the last elements to settle. In contrast to SMNK PAL 1132, the neck did not detach at its base but between the 4th and 5th cervicals (Frey and Martill 1994). The sternum is also missing from SMNK PAL 3854, the reason perhaps being the rapid bacterial degradation of the large pectoral muscle mass. While the pectoral muscles insert at the humerus with massive tendons, their origin on the sternum is fleshy and thus subject to more rapid decay and earlier detachment of the sternum, where the sternocostal and sternocoracoideal articulations must have been weak. The carcasses of ornithocheiroid pterosaurs likely followed the pattern of decay observed in birds and mammals (Oliver and Graham 1994; Davis and Briggs 1998), in which the head detaches first from the body, followed by the sternum.

Long-term floating at the water surface is typical for highly pneumatised tetrapods (Schäfer 1962, 1972), buoyed up by their air sacs. The state of decomposition when the specimen settled on the lagoon floor was probably relatively advanced, based on the degree of disarticulation. While this indicates that the interarticular ligaments had largely lost their ability to restrict the mobility of the bones, the carcass nonetheless must have been largely intact when it settled, as is shown by the preservation of easily displaced elements, such as manual and pedal phalanges. It then seems likely that the larger elements missing from the slab, such as the head and neck and the distal wing phalanges, were likely lost during sedimentary transport rather than during collection.

Conclusions

A new specimen from the Crato Formation of NE Brazil is an ornithocheirid pterosaur, distinguishable from *Arthurdactylus conandoylei*, the only other nearly complete postcranial skeleton from the Crato locality, by biometrics of the long bones. Almost identical bone ratios indicate possible relationship with a specimen of ?*Santanadactylus* sp. (Frey and Martill 1994), but the lack of a formal description of the latter prevents a taxonomically useful comparison.

The inferred high aspect ratio of the wing, combined with a delicate pes, supports the established hypothesis that ornithocheiroids spent the majority of their life in the air and that, while fully capable of terrestrial locomotion, spent little time on the ground when compared to other pterosaurs.

The animal was ontogenetically relatively mature when it died, based on the state of its sutures, which include fusion of the extensor tendon process to the first wing-finger phalanx, the scapula to the coracoid, the proximal and distal syncarpals of the wrist, the ischiopubic plate, and a partial notarium. The animal was not fully mature, however, because a tibiotarsus had not yet formed, and suture lines separate the epiphyses from the humerus. These elements can therefore be regarded as late-forming structures and may be of use in diagnosing the relative ontogenetic maturity of pterosaurs in future studies.

Acknowledgements

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Appendix 1

Long bone measurements of ornithocheiroid specimens used for calculating ratios and isometric/allometric relationships in this paper, where "R" denotes a value reconstructed from personal observations or the source literature. At the 95% CI with the humerus acting as the independent variable, the relationships of selected bone elements are defined as: ulna $= 0.325*x^{0.936}$ $^{+/- 0.119}$ ($R^2 = 0.96$); mc IV $= 0.493*x^{0.789 +/- 0.082}$ ($R^2 = 0.97$); femur $= 0.444*x^{0.798 +/- 0.183}$ ($R^2 = 0.93$); and wph 1 $= 0.16*x^{1.071 +/-}$ $^{0.13}$ ($R^2 = 0.97$). With respect to the humerus, the wing metacarpal and femur show a significantly negative deviation from isometry. Specimens attributed to pteranodontids and nyctosaurid pterosaurs were omitted for several reasons: the elongation of the wing metacarpal in relation to the humerus is unusual for ornithocheiroids; certain bone relationships e.g. ulna/mc IV appear to be different between *Pteranodon*/*Nyctosaurus* and the remainder of the Ornithocheiroidea; the large number of specimens known for *Pteranodon* would unduly bias the regression relationships towards this single genus rather than the broader trend across the entire division. The observed taxonomic level of regression relationships is thusly important and the state at one level need not be directly applicable to others.

Taxon (Collection Nr.)	hu	ul	mc IV	wph 1	wph 2	wph 3	wph 4	fe	ti
ornithocheiroid indet. (SMNK PAL 1135)	172.0	263.0	179.0	383.0	–	–	–	–	–
ornithocheiroid indet. (SMNK PAL 1134)	–	239.0	165.0	357.0	–	–	–	–	–
ornithocheirid indet. (SMNK PAL 3854)	159	253	169	382	–	–	–	161	230
Boreopterus cuiae (JZMP-04-07-3)	79.0	110.0	94.0	137.0	122.5	98.0	87.0	82.0	82.0
Istiodactylus sinensis (NGMC 99-07-011)	133.5	233.7	162.7	268.2	243.5	195.4	>32.9	>139.5	182.5
Istiodactylus latiden (BMNH R 3877)	220.0	381R	–	393R	388R	–	–	200.0	–
Nurhachius ignaciobritoi (IVPP V-13288)	110.5	192.8	132.6	226.5	165.7	–	–	146.4	>118.2
Nurhachius ignaciobritoi (LPM0003)	88.3	156	101	188.0	157	120	–	100	–
Haopterus gracilis (IVPP V11726)	70.0	101.5	90.0	134.5	119.0	95.5	>45.0	–	–
Anhanguera santanae (AMNH 225555)	204.0R	291.0R	206.0R	446.0R	389.0R	302.0R	192.0R	165.0R	287.0R
Arthurdactylus conandoylei (SMNK PAL 1132)	230.0	312.0	227.0	445.0	402.0	312.0	275.0	190.0	234.0
Coloborhynchus piscator (NSM-PV 19892)	255.0	390.0	256.0	> 120	–	–	–	234.0	> 256
Coloborhynchus robustus (SMNK 1133 PAL)	290.0	390.0	285.0	620.0R	566.0R	460.0R	330.0R	277.0	338.0
Coloborhynchus spielbergi (RGM 401880)	290.0	410.0	235.0	–	–	–	–	277.8	351.8
Gegepterus change (IVPP V 11981)	–	–	52.7*	69.3	68.3	–	>38.0	–	–
Santanadactylus pricei (AMNH 22552)	170.0	242.5	172.0	372.0	324.0	252.0	160R		
?*Santanadactylus* (SMNK PAL 1250)	230.0	353.0	248.0	515.0	–	–	–	–	–