A new ornithocheirid, *Barbosania gracilirostris* gen. et sp. nov. (Pterosauria, Pterodactyloidea) from the Santana Formation (Cretaceous) of NE Brazil

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Abstract An almost complete, ornithocheirid pterosaur from the Romulado Member of the Santana Formation, NE Brazil is described. The specimen lacks a rostral and dentary median sagittal crest and is sufficiently distinct from other crestless taxa to warrant the erection of a new genus and species, *Barbosania gracilirostris* gen. et sp. nov. It confirms the absence of a crest as a genuine condition rather than a consequence of ontogenetic immaturity and indicates a shift from the previously observed pattern of suture closure in pterodactyloid pterosaurs, where partial fusion of the extensor tendon process has occurred at a relatively small size. Several specimens showing morphology similar to *Brasileodactylus* may instead be more closely allied to *B. gracilirostris*.

Keywords Barbosania · Ornithocheiridae · Pterosaur · Santana Formation

Abbreviations

AMNH American Museum of Natural History, New York, USA
BSP   Bayerische Staatssammlung für Paläonologie und Historische Geologie, Munich, Germany
MHNS Museum of Natural History Sintra, Sintra, Portugal
NM   Museu Nacional, Rio de Janeiro, Brazil
NSM   National Science Museum, Tokyo, Japan
RGM   Nationaal Natuurhistorisch Museum, Leiden, The Netherlands
SMNK Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany

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Introduction

The Romulado Member of the Santana Formation, NE Brazil, has greatly increased our understanding of the anatomy and palaeobiology of Early Cretaceous pterosaurs. Several taxa known from this locality include the ornithocheiroids: *Anhanguera santanae* (Wellnhofer 1985); *A. araripensis* (Wellnhofer 1985); *A. blittersdorffi* (Campos and Kellner 1985); *Brasileodactylus araripensis* (Kellner 1984); *Cearadactylus* (Leonardi and Borgomanero 1985; Dalla Vecchia 1993); *Coloborhynchus piscator* (Kellner and Tomida 2000); *C. robustus*; *C. spielbergi* (Wellnhofer 1987); *Santanadactylus* (Wellnhofer 1985); *Ornithocheirus mesembrinus* (Kellner and Campos 1994); and the azhdarchoids *Tapejara wellnhoferi* (Kellner 1989); *Thalassodromaeus sethi* (Kellner and Campos 2002); *Tupuxuara leonardii* (Kellner and Campos 1994); *T. longicristatus* (Kellner and Campos 1988). Despite the large number of specimens now known, various details of pterosaur systematics remain the focus of considerable debate and disagreement, foremost among them perhaps being the taxonomic composition of the Ornithocheiroidea (Kellner 2003; Unwin 2003) and the preferential use of the Ornithocheiridae or Anhangueridae; both of which are widely found within the current literature (e.g. Kellner 2003; Unwin 2003; Andres and Ji 2008; Wang et al. 2008; Lü et al. 2008). Although the purpose of this manuscript is not to debate the merits of either side, for the sake of clarity all taxonomic divisions adopted here are sensu Unwin (2003)

until a more general consensus is reached. In addition to the problems apparent at higher taxonomic levels, the diagnosis of ornithocheirid pterosaurs from the Brazilian *Lagerstätte* to a generic or species level is complicated by the presence of several taxa that are not clearly distinguished from others (e.g. *Araripedactylus*, *Araripesaurus*, *Santanadactylus*, see Kellner 1991; Kellner and Tomida 2000), the degree to which fossils from the English Greensands are represented in South American localities (Unwin 2001; Veldmeijer et al. 2005; Rodrigues and Kellner 2008), and the extent to which an ontogenetically variable cranial crest can be used to diagnose a taxon (Veldmeijer 2003; Martill and Naish 2006). Crestless materials belonging to ornithocheirid pterosaurs, primarily consisting of isolated rostral fragments, are often assigned as tentative specimens of *Brasileodactylus*, a genus known for the absence of a median crest. As such the genus is particularly controversial, having been suggested to be conspecific with either *Anhanguera* (Unwin 2001) or *Ludodactylus* (Unwin and Martill 2007). Here we present a new crestless ornithocheirid pterosaur from the Romualdo Member of the Santana Formation. The specimen is similar in morphology to those specimens assigned to *Brasileodactylus* but does not meet the current diagnostic criteria for this genus and is sufficiently distinct to warrant the erection of a new genus and species. The described specimen preserves the majority of the skull and postcranial skeleton which is unusual for crestless ornithocheirid pterosaurs from the locality. It is housed in the Museum of Natural History Sintra, Portugal, under the collection number MHNS/00/85, while a cast is held in the collections of the State Museum of Natural History Karlsruhe, Germany (SMNK).

Preservation

The described specimen MNHS/00/85 is encased within a single large calcareous concretion as is typical of fossils from the Romualdo Member (Fig. 1). It is comprised of a mostly complete, but damaged cranium and mandible, the caudal-most cervical vertebra (c9), the dorsal vertebral column (d1–13), the first sacral vertebrae (s1), and four caudal vertebrae from the base of tail.

The skull is mostly complete, exposed in right lateral view and in natural association with the mandible, which is articulated in occlusion with the upper jaw. Due to the relief of the bone the frontal, parietal and left hand side of the skull remain buried within the matrix of the concretion after preparation. The skull has suffered lateral crushing that is particularly noticeable not only along the rostral and caudal portions of the mandible but also around of the nasoantorbital fenestra and the orbita. The bones dorsal to the nasoantorbital fenestra, such as the caudal process of

the maxilla conjoined with the frontoprefrontal complex, the nasal and the lacrimal are disarticulated along their sutures, but still lie close to their original positions. The lateral parts of the occipital, squamosal, quadrate and postorbital are eroded almost to the same level as the foramen of the n. vagus. The postorbitosquamosal arch is missing and the jugal has rotated medially with the maxillary process diving into the matrix. The transition between premaxilla and maxilla is obscured by both the overlying right humerus and sediment.

The mandible is visible in right lateral view. All parts of the mandible have been extensively crushed.

The teeth in the rostral portion of the skull show the best preservation. In both the upper and lower jaws the caudally located tooth positions are represented by empty and partially damaged alveoli. Most teeth rostral to the 12th tooth position are preserved in three dimensions with the exception of tooth positions 6 in the upper jaw and 4–5 in the lower. The crowns of the second to fifth teeth of the cranium are missing while the fourth mandibular tooth has broken off at the base of its crown. The rostral-most three of the mandible are completely preserved.

The entire vertebral column is embedded in sediment about level with the transverse processes so that the right lateral faces are only visible in the first 6 vertebrae, i.e. c9 and d1–5. Caudal to the fifth dorsal the vertebral column is offset to the right by the full diameter of a vertebral body before continuing caudally in full articulation. The bodies of the dorsal vertebrae are badly damaged and the exapophyses on the first three dorsals have broken off and are missing from the skeleton. Several disarticulated ribs and possible gastralia are scattered in the thoracic region. Only the right rib of the second dorsal retains a contact with the transverse process. Both scapulae and coracoids are preserved close to their natural positions, but only the right coracoid is almost entirely visible from its caudal aspect. The rest of the shoulder girdle is mostly camouflaged by matrix.

The majority of the skeletal elements of both wings have disarticulated from their natural position but have been displaced by only a small degree. The left humerus lies close to its natural position while the right humerus has been displaced a greater distance from the right shoulder girdle so that it is now positioned with its head across the rostrum. The right humerus and ulna are exposed in caudoventral view and make an angle of about 120° between each other. The right ulna lies along the cranial margin of the right ulna. The right wing metacarpal (mc IV) lies adjacent to the distal syncarpal although it has rotated ∼90° caudally around its long axis and is viewed in its cranial aspect. Two metacarpals, associated with the first three digits, lie adjacent to its dorsal face. One is completely exposed while the

Fig. 1 *Barbosania gracilirostris* (MHNS/00/85) gen. et sp. nov. **a** Photograph and **b** corresponding line tracing highlighting the major elements of the skeleton. *Shading* indicates material erroneously attached to the concretion. Where: *c* cranium, *ca* caudal vertebrae, *co* coracoid, *cr* cervical vertebrae, *d* dorsal vertebrae, *dsc* distal syncarpal, *f* femur, *h* humerus, *il* ilium, *is* ischium, *m* mandible, *mc* metacarpal, *n* "notarium" dorsal vertebrae 1–5, *p* pteroid, *pa* preaxial carpal, *psc* proximal syncarpal, *pu* pubis, *r* radius, *s* scapula, *sc* sacral vertebrae, *u* ulna, *wph* wing finger phalanx. *Scale equals 100 mm*
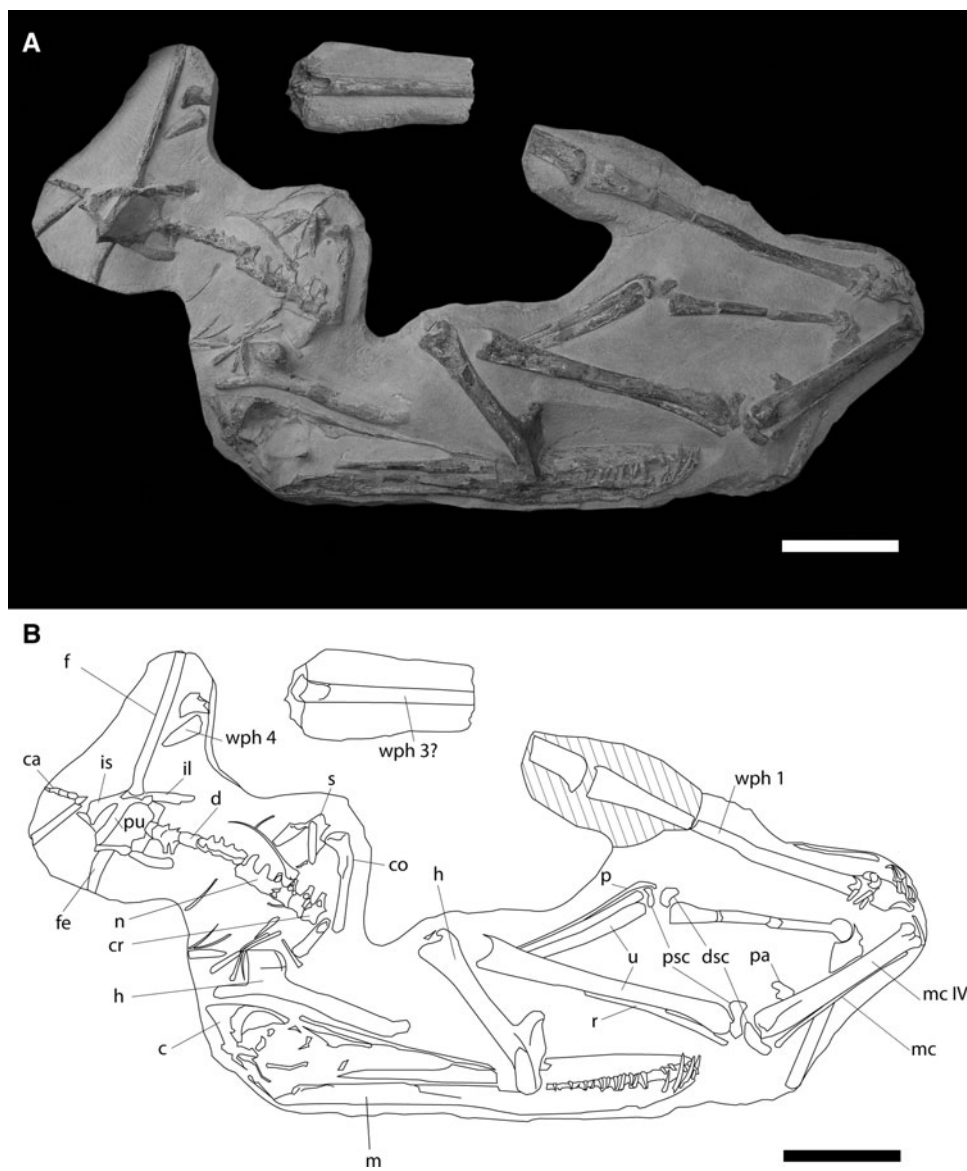
second is overlain by the first and covered by sediment so that only its distal portion is visible. The metacarpus forms an angle of about 150° with the radius/ulna. The first three digits are preserved cranial to the articulation between the wing finger metacarpal and the basal wing finger phalanx. These three digits preserve all of their elements with the exception of the disciform phalanges and lie sub-parallel to each other with the unguals facing distally. The first or basal phalanx of the right wing finger is partially preserved up until a large break in the concretion approximately 2/3rds along its length. Here a fragment of the concretion containing the articulation of two phalanges of the left wing finger has been erroneously attached. This fragment is interpreted to represent the distal portion of the left first wing finger phalanx and the proximal portion of the second wing finger phalanx.

The left humerus is visible in its ventral aspect. Of the left radius/ulna the proximal half is overlain by the elbow of the right wing and the matrix, however, the distal half is visible in its ventral aspect. The shaft of the left pteroid bone lies adjacent to the left radius. The head of the pteroid bone terminates between the proximal and the distal syncarpals. The wing finger metacarpalia and the basal wing finger phalanges are seen in their ventral aspects and remain in full articulation. A 57-mm section of the left metacarpal IV has undergone extensive repair with a large fragment of bone being glued back into place. The unguals and penultimate phalanges of the first three digits of the left wing lie perpendicular across the proximal terminus of the shaft of the right basal wing finger phalanx. The proximal elements are still covered by matrix. The angle between humerus and radius/ulna as well as that between radius/

ulna and metacarpus is about 150°, while metacarpus and the basal wing finger phalanx include an angle of about 80°. The left basal wing finger phalanx is broken at the mid shaft area at the border of the concretion.

The majority of the pelvic girdle is preserved although some damage and displacement has occurred due to lateral crushing of the specimen. The left puboischiadic plate is only slightly displaced from its natural position although its dorsal portion is obscured by sediment cover and the ventral margins of both the pubis and ilium have been broken. The right puboischiadic plate has collapsed across the sacrals and the ventral margins of the pubis and ischium lie adjacent to the broken end of the left puboischiadic elements. The majority of the right preacetabular process has been broken and crushed but remains visible. Both prepubic bones are missing.

Both femora are articulated with their respective acetabulae and are directed laterally at right angles with respect to the vertebral column. The femora terminate at the border of the concretion whereby the fragment of the right femur is three times the length of the left. Adjacent to the right femoral shaft lies the distal extremity of a wing finger phalanx, most likely wph 3 of the wing. Next to this an elongated bone is directed diagonally across the dorsal surface of the pelvic girdle and is cut by the edge of the concretion. It is uncertain whether this element represents the fourth wing finger phalanx or the tibia as the proximal margin is damaged and missing approximately half the articular surface. The distal portion of the bone does not taper or show a decrease in diameter suggesting that it is more likely to be a displaced tibia.

Although a limited amount of crushing has occurred due to compaction, principally to the skull and portions of the wing finger, the majority of the skeleton has kept its three dimensional form and many of the preserved elements show little trace of *post mortem* displacement. The dentition shows a progressively better state of preservation moving towards the rostrum. Damage from abrasion or the splitting of the concretion is more common and has been severe enough to erode through the bone surface, exposing the internal structures.

The skeleton underwent some preparation and repair prior to its arrival at the State Museum of Natural History Karlsruhe (SMNK), where the majority of preparation was completed on request from the Museum of Natural History Sintra (MHNS), Portugal. The completeness of the skeleton suggests that many more details could be uncovered with a more extensive preparation from the reverse side of the concretion. However, time constraints, a complex positioning of the bones, and a risk of damage prevented this from occurring.

Systematic palaeontology

Pterosauria (Kaup 1834)
  Ornithocheiroidea (Seeley 1870)
  Ornithocheiridae (Seeley 1870)
  Barbosania nov. gen.
  B. gracilirostris nov. sp.

Derivation of name For the genus: *Barbosania* after Professor Dr. Miguel Barbosa, Sintra Museum of Natural History, a recognised local scientist, who engaged himself in bringing palaeontology to public knowledge and substantially helped to secure the specimen. For the species: *gracilirostis* (*gracilis* = lat. for slender, *rostrum* = lat. for snout): the "slender snouted" referring to the slender crestless rostrum without lateral dilatation

Material Holotype and only specimen MHNS/00/85 housed in the Museum Natural History Sintra, Portugal

Locality Unknown locality. Romualdo Member, Santana Formation, Araripe Plateau, Brazil, (Albian–?Cenomanian). The bluish colour of the concretion strongly suggests a provenance of the Sierra de Maõsina.

Diagnosis for genus and species

Ornithocheirid pterosaur with the following diagnostic features:

1. Keeled but crestless rostrum with a pointed termination.
2. Rostral-most pair of the mandibular and premaxillary alveoli positioned rostroventrally and rostrodorsally, respectively.
3. Tooth positions two and three in both jaws with teeth that are twice as long as those of the subsequent alveoli.
4. The second and third teeth are orientated craniolaterally and together with the rostral-most teeth form a narrow rosette due to a missing expansion of the tip of the rostrum.
5. Lateral margins of the rostrum gradually converge rostrally.
6. An estimated 24 and 20 tooth positions in the upper and the lower jaw, respectively.
7. Interalveolar space gradually increasing caudally, alveolar diameter about constant until tooth position 13.
8. Teeth between the eighth and thirteenth tooth positions in upper and lower jaw with an almost symmetrical interdigitation.
9. Height of the nasoantorbital fenestra approximately 22% that of its length and forming ∼24% of the total skull length.

10. Parietal with flat external face, dorsal margin of the short median occipital process is deflected with a triangular transversally convex dorsal face.
11. 13 trunk vertebrae.
12. Caudoventral margin of ischium concave.

While several of these features are not unique to the described specimen their presence, when combined with the other characters noted above, remains useful for the identification of this genus. Only character 12 is unique for *Barbosania*.

Description

Skull

The most apparent feature of the skull is the lack of any median sagittal crest on the rostrum. Both the intermaxillary region and the symphyseal area of the mandible had a tall, sub-triangular cross-section with a sharp median keel. In a rostral direction the ventral margin of the cranium is directed craniodorsally from the tenth alveolus. This is also true for the dorsal margin of the mandible although the curvature begins level with the sixth mandibular tooth. The second to seventh alveoli of the cranium counted from the tip of the rostrum are therefore positioned dorsal to and slightly lateral to those in the more caudal tooth positions.

The palate is orientated approximately 50–60° to the horizontal plane in the premaxillary portion of the cranium and is visible in lateral view, particularly by the sixth alveoli. Accounting for the compaction to the rostral region of the skull the premaxillary part of the palatine would have formed a median keel protruding into the buccal cavity.
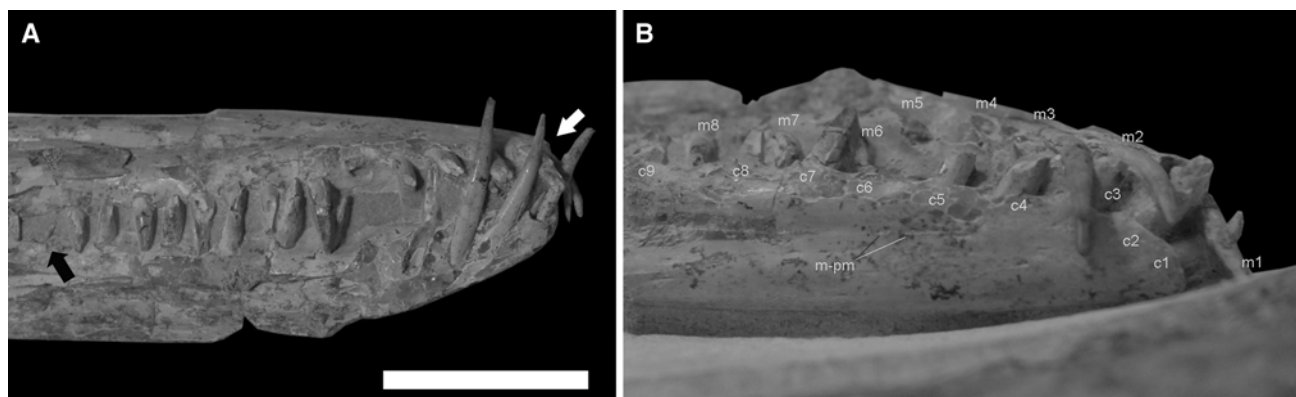
Premaxilla

The premaxilla is well preserved but shows an impaction groove that runs parallel to dorsal margin of the rostrum. It extends from a position level with the 4th tooth position until the 12th tooth socket. The rostral portion of the snout remains undamaged and is sub-triangular in cross section. A small discontinuous scar that may represent the remains of the suture between the premaxilla and maxilla is visible and extends to a point level with the caudal margin of the fourth tooth. Further rostrally the suture becomes vague and its exact termination cannot be reconstructed with certainty. There is no lateral expansion of the rostrum and the dorsal and ventral margins of the premaxilla converge at a steep angle, $\sim 33.4°$ in lateral view. The rostrum is therefore slender with a pointed termination. The maxillary keel becomes blunt on the premaxillary part of the rostrum and merges with its slender tip (Figs. 2, 3).
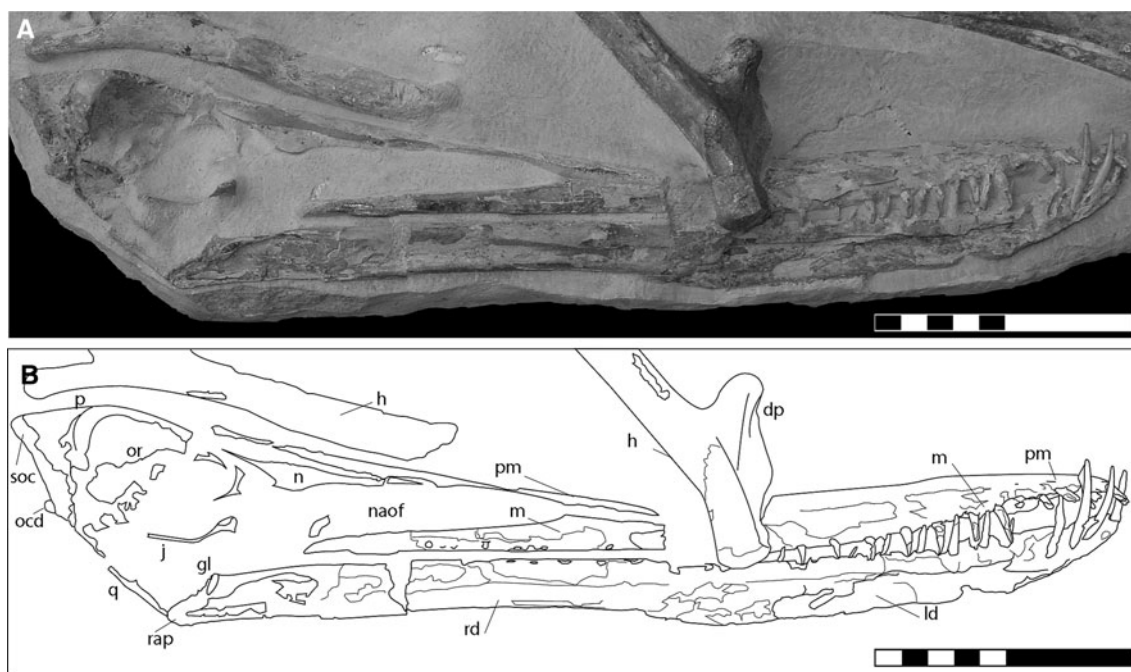
Fig. 2 *Barbosania gracilirostris* (MHNS/00/85) gen. et sp. nov. Photograph (**a**) and (**b**) line tracing of the skull and surrounding elements: *dp* deltopectoral crest, *h* humerus, *j* jugal, *jar* jaw articulation, *ld* left dentary, *m* maxilla, *n* nasal, *naof* nasoantorbital fenestra, *ocd* occipital condyle, *or* orbita, *p* parietal, *pm* premaxilla, *q* quadrate, *rap* retroarticular process, *rd* right dentary, *soc* supraoccipital crest. *Scale* equals 100 mm

Fig. 3 *Barbosania gracilirostris* (MHNS/00/85) gen. et sp. nov. Photographs of the rostral region of the skull in its lateral (**a**) and dorsal (**b**) aspects where: *c* cranial tooth, *m* mandibular tooth, *m-pm* ?maxilla-premaxilla suture. *White arrow* denotes the pointed rostral termination while the *black arrow* indicates an example of tooth replacement. *Scale* equals 50 mm

Maxilla

The maxilla extends caudally forming the majority of the ventral margin of the cranium and the ventral border of the nasoantorbital fenestra. The ventral margin of the bone is straight but is deflected dorsally at an angle of about 10° around the tenth tooth position. The caudoventral portion of the bone is damaged and the compacta is missing. The caudal extent of the maxilla and its relationship with the jugal is therefore unclear.

Nasal

The nasal lies loose from its surrounding elements and is complete with the exception of a small break in the cranial portion of the bone. In its lateral aspect the bone shows its maximum dorsoventral extension just dorsal to the articular surface with the lacrimal while the rostral and caudal processes of the nasal taper away from this point. The rostral process of the bone extends ventral to the premaxilla and forms ∼48% of the dorsal margin of the nasoantorbital fenestra. Likely the caudal process of the premaxilla has merged with the rostral process of the nasal. The caudal process of the nasal is one-third the length of the rostral process and displays a more pronounced convex ventral margin. The bone margin is recurved just dorsal to the caudoventral margin of the lacrimal articulation where it would have acted as the articular surface for the rostrodorsal margin of the prefrontal. The articular surface on the ventral margin of the nasal, where it would have articulated with the lacrimal, is flat.

Prefrontal, frontal and parietal

These three bones form the caudodorsal roof of the skull but are mostly embedded within the concretion. No suture dividing the three elements can be identified. The dorsal face of the parietal is transversely concave and is confluent with the supraoccipital crest.

Jugal

The jugal is a triradiate bone that forms the caudal and caudoventral margins of the nasoantorbital fenestra, the cranioventral, caudoventral margins of the orbita and the cranial border of the infratemporal fenestra. Although it appears mostly intact in MNHS/00/85, the bone has been displaced and rotated into the skull cavity such that only the quadratojugal/postorbital and the lacrimal processes are visible but broken. The maxillary process is buried in the matrix. At the break the lacrimal process of the jugal is teardrop shaped in cross-section and tapers towards its caudal margin.

Supraoccipital

The prominent feature of this bone is the blunt median supraoccipital crest that is elongated and triangular in lateral view. It commences as a low ridge on the mid dorsal margin of the foramen magnum and from there extends dorsally, gradually increasing in both width and prominence. At its dorsal extremity the supraoccipital crest forms a caudoventrally inclined transversely convex face that is cranially confluent with the parietal. Lateral to the supraoccipital crest the supraoccipital is vertically concave while the lateral margins of this bone are either broken or obscured by sediment. The supraoccipital forms the dorsal margin of the foramen magnum. A large oval pneumatic foramen, 3 mm by 5 mm, perforates the caudolateral face of the supraoccipital near the deepest point of the concavity. A straight, medially serrated suture separates the supraoccipital from the exocciptobasioccipital complex.

The suture runs from the middle of the lateral margin of the foramen magnum dorsolaterally at an angle of about 20° against the horizontal plane. On the ventromedial corner of the supraoccipitale a foramen is visible.

Exoccipital, basioccipital and basisphenoid

These bones make a fused complex that forms the ventrolateral and ventral margins of the foramen magnum. The foramen itself is sub-circular in outline, being slightly broader at its base than dorsally. In lateral view the occipital condyle is orientated caudoventrally at an angle of ~40° against the horizontal plane. The condyle is regularly rounded in its lateral aspect and has an oval outline in caudal view. The vagus foramen, which lies immediately lateroventrally to the occipital condyle, is orientated dorsoventrally but continues as a short ventrally directed sulcus. Directly ventral to the vagus foramen the smooth and vertically concave basioccipital part of the bone complex is exposed, forming the dorsolateral margin of the posterior cranial fenestra. Ventral to the basioccipital flange a fragment of the basisphenoid is separated from the latte by a smooth, ventrolaterally directed, shallow, and sinusoid suture that merges with the ventral margin of the posterior cranial fenestra.

The mandible

The dentary is straight with a constant height except in places where compaction has distorted the bone. A short but pronounced crest on the labial surface of the dentary, forming the lateral margin of a midline groove, is visible 2–4 mm dorsal to the level of the tooth row. Rostrally, the dentary is broken in such a way that the right lateral face is mostly missing and the medial face of the left dentary is exposed. The ventral part of the symphysis is eroded. On the rostral face of the mandible, two small, slit-like foramina, ~3 mm in length, are observed between the first tooth position and the median line. Cranial of the sixth tooth position, the ventral surface of the dentary is deflected upwards at an angle of ~23° to the long axis of the mandible. Here, the symphysis has formed as a rounded keel suggesting that no sagittal crest was present.

No suture lines defining the angular, surangular or articular are visible, suggesting that these elements may have already fused together. The articular facet for the quadrate forms as an extended, mediolaterally directed oval depression. The retroarticular process is short, 15 mm in length, and directed slightly caudoventrally.

Dentition

The number of alveoli present in the cranium and dentary is uncertain due to a combination of poor preservation, particularly about the middle portion of the skull, and the position of the overlying right humerus. In the cranium 13 alveoli are present cranial to the right humerus and 8 poorly preserved ones caudal to this. Two tooth positions are estimated to be present below the humerus and another tooth position likely was present in the caudal portion of the tooth row where the compacta is missing. In total, a minimum of 24 tooth positions are therefore reconstructed for the cranium. As with the cranium, 13 mandibular tooth positions are also preserved rostral to the overlying humerus. A single tooth is visible adjacent to the humeral head while 5 alveoli are visible caudally. One, or perhaps two, tooth positions are likely obscured by damage or the humerus. A minimum of 20 tooth positions are therefore reconstructed for the mandible. The caudal-most alveolus of the mandible is positioned 29 mm rostral to that of the cranium. The three rostral-most teeth of the mandible are completely preserved and show mesiolingual compression and a slight mesial curvature. The crowns of first and third mandibular teeth bear a finely striated enamel cap.

Replacement teeth are observed in the third alveolus of the cranium as well as the first alveolus of the mandible, where it is <29% in size of the active tooth (Fig. 3). The fourth tooth of the cranium and the 11th of the mandible do not completely fill their alveoli indicating that they have not yet grown to their full size.

The first pair of teeth of the cranium are orientated rostroventrally, while those of alveoli 2–5 are orientated more rostrolaterally, as are alveoli 6 and 7 to a lesser extent. Those teeth caudal to the seventh alveoli are directed ventrally.

On the mandible the first tooth is inclined rostrodorsally while the second and third are orientated rostrolaterally. Caudal to these the teeth have a slight dorsolateral inclination. A dentition pattern common in all ornithocheiroids is seen, where the diameter of the alveoli increases caudally until the fourth tooth, which is the largest. The fifth tooth is smaller than the fourth and while the subsequent tooth sockets (alveoli 5–11) are sub-equal in diameter they increase slightly in size up to the ninth tooth position. Caudal to the ninth tooth position the diameter appears to decline. On the mandible the first alveolus is the largest and the diameter of the subsequent alveoli decrease steadily. The interalveolar spaces are gradually increasing from rostrally to caudally, whereby the teeth from position 5 through 12 are straight and form a regular occlusion pattern with an even spacing.

Vertebral column

The vertebral column is well preserved in ventral view but missing the majority of the cervicals and terminal caudals. In total 19 vertebrae are visible, corresponding to the

Fig. 4 *Barbosania gracilirostris* (MHNS/00/85) gen. et sp. nov. Line tracing of the axial skeleton: *c* cervical vertebrae *co* coracoid, *d* dorsal vertebrae, *il* ilium, *pu* pubis, *sac* sacral vertebrae, *sc* scapula. *Scale* equals 100 mm
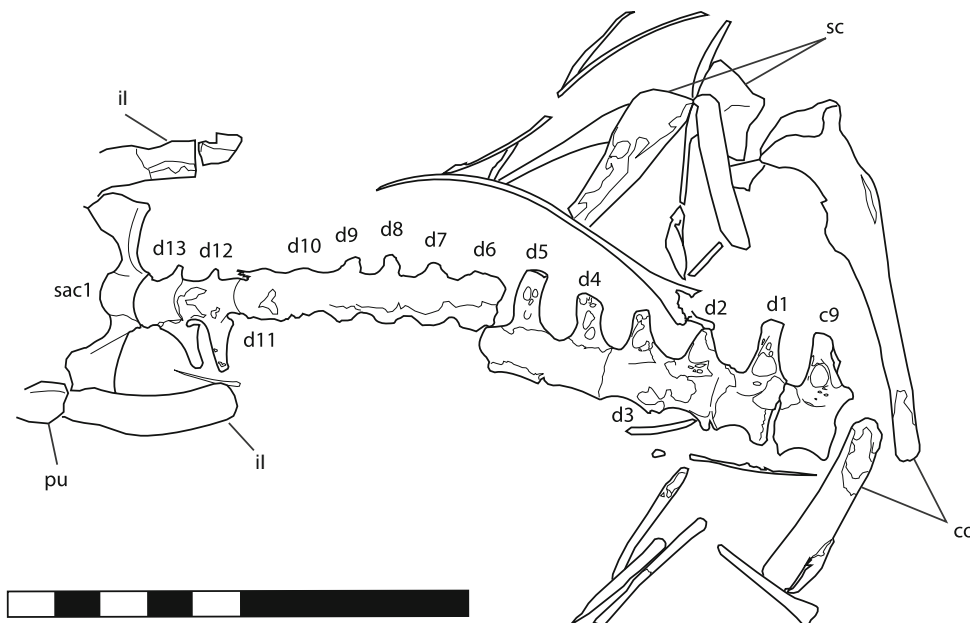
caudal-most cervical (c9); 13 dorsals (d1–13); the cranial-most sacral (sc1), the rest of the sacrum being covered by sediment and the puboischiadic plate; and 4 caudals. An additional caudal is preserved as a fragment. Within the vertebral column four clearly defined associations are identified: (1) the neck, consisting of only a single disarticulated cervical (c9); (2) the "notarium", comprised of the first 5 dorsals; (3) the free dorsals and sacrals, a single uninterrupted unit comprised of dorsal vertebrae 6–13 and the first sacral; (4) the four caudal vertebrae (Fig. 4). Within each of the above divisions the vertebrae remain in close association, however, no fusion has occurred between the vertebral bodies. Where the transverse processes are visible they show a depression on their ventral face. In the three cranial-most vertebrae this penetrates the base of the transverse processes deeply and may represent the openings of pneumatic foramina. In d1 and 2 they are associated with 2 or 1 additional small foramina, respectively.

The last cervical (c9) is similar in appearance to the succeeding dorsals but marginally larger in size (Table 1). It lies slightly out of articulation with the first dorsal, the gap having been filled with sediment. On the ventral surface of the transverse process a single large, transverse, oval foramen transversarium pierces the bone and occupies most of the basal region of the transverse process. The corpus itself is pierced by two small oval foramina and between these and the proximal portion of the transverse process seven more are visible. The lateral face of the body of c9 as well as d1 and 2 bears longitudinally oval pleurocoels that contain numerous foramina and pits.

On each of the first five dorsals the transverse processes are large, with those of the first dorsal being sub-equal in

Table 1 Selected long bone lengths of *Barbosania gracilirostris* (MHNS/00/85) gen. et sp. nov.

Element	Length (mm)
Skull	
Skull (occipital condyle—snout)	391
NAOF	96[a]
Mandible (articulation to rostral tip)	330
Axial column	
Ninth cervical	13
Notarium	59
Body length	209.5
Long bones	
Humerus (right/left)	155/162
Ulna (right/left)	223/>111
Carpus width (right)	58
Pteroid (left)	129
mc III	137
Metacarpal IV (right/left)	155/156
Digits and phalanges (right)	
d1 p1	29
d1 u1	14
d2 p1	20
d2 p2	29.5
d2 u1	15
d3 p1	x
d3 p2	3
d3 p3	23
d3 u1	15
d4 p1 (right/left)	>191.9/>151.7
Femur (right/left)	127/43[a]

[a] Denotes a value based on an estimation or reconstruction

size to that of ninth cervical. The shortest transverse process belongs to the second dorsal although these increase in both length and distal width for subsequent vertebrae. With the single exception of the fifth dorsal the transverse processes of c9–d4 are directed slightly caudolaterally. The distal half of the transverse process of the fifth dorsal, however, curves cranially again so that its tip is directed laterally. The vertebrae remain of sub-equal length and intervertebral articulations are unfused. As such these vertebrae have not yet fully formed a mature notarium. A single, large but unfused rib lies adjacent to the transverse process of the second dorsal. The preserved length of the rib is 79 mm and it displays a shallow curvature. The capitulum and tuberculum are damaged but have a spacing of 10 mm, which corresponds to the lateral extension of the adjacent transverse process.

The third vertebral section consists of d6–d13 and the first sacral as a single articulated unit. Despite heavy damage it is clear that the intervertebral joints are open. The transverse processes of these dorsals, of which only the bases are visible, are again directed slightly caudolaterally with two exceptions. The transverse processes of the 12th dorsal are orientated laterally while those of the 13th dorsal are recurved and point craniolaterally. For both the 12th and 13th dorsals the lateral margins of the transverse processes converge, but without meeting, and terminate close to the cranial process of the ilium. There is no evidence for a cranially expanded synsacrum. The 13th dorsal and the first sacral are clearly distinct with the sacral possessing large sacral ribs. In cranial view the dorsal margin of these ribs is almost straight while the ventral margin curves ventrolaterally causing the bone to expand to twice its basal thickness. The lateral margin is divided into two articular surfaces standing at 90° to each other for the pubis and ilium. These latter elements are slightly displaced and sediment infilling between the sacrals, pubis, and ilium indicate that they are unfused. Two faint sutures are visible between the vertebral bodies and the sacral ribs suggesting that fusion has neared completion. The remainder of the sacrals are buried beneath both sediment and the right ischiopubic complex.

The final vertebral section consists of the caudal vertebrae. These are preserved together but have been displaced slightly so that they are no longer articulated. The majority are observed in their ventral aspect, however, the first visible caudal has rotated so that it is now observed in ventrolateral view. The neural spine is positioned cranially on the bone and occupies approximately 2/3rds the length of the corpora. It is not certain that this represents the first vertebrae of the caudal series, however, comparisons with other ornithocheiroids (e.g. Kellner and Tomida 2000) indicate that it must be one of the cranially positioned vertebrae due to its prominent neural spine and short body.

Pectoral girdle

The remains of the left scapula and coracoid are seen in caudal view. They are unfused and lie close to their natural articulation. The shaft of the coracoid expands towards the pars glenoidalis, where it is twice as wide as in the middle of the shaft. The ventral half of the glenoid fossa is visible on the right coracoid. A single robust process is viewed on the caudolateral margin of the bone along with a deep scar located immediately ventral to it, perhaps corresponding to the insertion points of *m. coracobrachialis* (Bennett 2003a). The shaft is blade-like and offset against the body at an angle of 25°. The medial furca for the articulation with the sternum has broken away on both coracoids.

Humerus

Both humeri are present with the left observed in ventral view and the right in its caudoventral aspect. They are typical of ornithocheiroid pterosaurs and preserve the characteristic short (34% of the humeral shaft length), warped, deltopectoral crest with a sub-triangular margin. The head of the humerus is kidney shaped in its medial aspect and measures 28.5 mm by 16.5 mm. The articular surface is convex. A deep concavity marks the ventral margin of the humerus adjacent to the articular head, between the caudal tuberosity and the deltopectoral crest. In caudal view the humeral head is deflected dorsally in relation to the main humeral shaft at an angle of about 10°. It is impossible to comment on the extent of the caudal tuberosity because this has broken off from the right humerus and on the left it is mostly hidden by sediment. The deltopectoral crest begins as a thin flange proximally on the base of the humeral neck where it is orientated ventrolaterally. From cranial view the flange thickens distally by forming a pronounced convex curvature. Here, the cranial margin of the crest curves ventrally and reaches its maximum thickness. A small scar is visible on the ventral surface of the left deltopectoral crest as a rough depression where it runs a short distance of ~ 6 mm towards the proximal portion of the humerus. On the shaft of the humerus a large solitary scar is visible on the caudoventral margin of the humerus and extends for a distance of 21 mm. This would represent the insertion point for the medial head of *m. triceps* (Bennett 2003a) or *m. latissimus dorsi* (Bonde and Christiansen 2003). An isolated bone fragment lying off the distal margin of the right humerus, adjacent to a large oval excavation of the distal margin of the bone, is interpreted as an unfused epiphysis.

Radius and ulna

The radii/ulnae are preserved in their ventral aspects where the right has been displaced so that it now overlies the

proximal half of the left. Much of the bone surface has been damaged and because of some clumsy restoration attempts during its initial preparation few details are observed. A large concave recess on the proximal articulation surface of the right ulna indicates that the now missing epiphysis was unfused. Additionally a small ridge is viewed on the ventral side of the bone. While this was probably an extensive feature only the most distal portion is visible as the compacta is missing, revealing a calcite-filled core.

Carpals

The carpal regions of both forearms are well preserved in ventral view and between them show both the preaxial carpal and the pteroid bone. The two carpal blocks lie close to their natural positions but in both cases the distal syncarpal has rotated against the proximal one and now lies in disarticulation. A thin suture runs across both proximal and distal syncarpals indicating that fusion of the carpals is incomplete, however, the lateral part of the suture on the proximal syncarpal is partially closed. The distal syncarpal is semi-lunate in outline with a strong convex curvature along its proximal margin. The distal margin of the proximal syncarpal is concave to an equal degree, matching its counterpart on the distal syncarpal. A number of pneumatic foramina are visible on the carpals. The right proximal syncarpal is observed in ventral, cranial and craniolateral orientations where one oval foramen is located on the caudal portion of the ventral surface while another spans the cranial and distal surfaces towards the ventral margin of the bone. Only a single large depression is observed on the left distal syncarpal, located on the proximal articular face and occupying the cranial portion of the bone.

The right preaxial carpal has been displaced distally from the carpus, is partially overlain by metacarpal IV and has rotated so that it is now visible in lateral view. A large fovea filled with sediment occupies the majority of the craniodorsal surface of the bone.

The articular surface of the left pteroid is thin and is transversely compressed. Moving medially, the strongly curved neck expands to about twice its diameter at the articular end. The shaft, which is directed towards the body stands at an angle of about 75° to the neck. The distal half of the shaft curves slightly cranially. Restoring the pteroid to its natural position this sigmoid curve would have directed the medial end of the pteroid slightly cranially and extended the propatagium to the base of the neck. The right pteroid bone is visible for a total length of 129 mm before it is obscured by sediment and by the right ulna.

Metacarpalia

The fourth metacarpal is sub-equal in length to the humerus (Table 1). The bone is widest at its proximal articulation face with the shaft of the bone becoming gradually narrower distally and terminates in a double roller joint with the wing finger. The ventral condyle is directed only slightly ventrally and extends further onto the cranial surface of fourth metacarpal than the dorsal condyle (Fig. 5). The dorsal condyle slants steeply dorsally at an angle of ∼30° against the long axis of metacarpal IV, creating a slightly oblique sulcus. A large depression at the cranial termination of the dorsal condyle was presumably for the insertion of muscles or ligaments associated with the first three metacarpalia. Arising from the proximal articulation a short dorsoventrally compressed ridge is observed that extends for ∼16% of the metacarpal length distally along the cranioventral margin of the bone.

An isolated metacarpal (mc 1) is preserved along the dorsal margin of the cranial face of the fourth metacarpal. This bears a bulbous termination at both its proximal and distal ends, which lie adjacent to the distal syncarpal and the first three digits, respectively, and indicates that the shaft of the metacarpal would have extended the full distance from the digits to the carpus. Of the second metacarpal only the distal portion is visible, which shows a slight expansion towards its articular face. As is seen on the left metacarpal IV the ventral roller develops its strongest convexity at its craniodistal margin. The caudal margin is nearly straight but curves sharply caudally in its proximal-most fifth where it is off set from the shaft by a notch. Cranially the roller merges with the shaft in an even concavity. The ventral face of the roller is slightly depressed and shows a circumferential rugosity that accommodated the capsular ligaments of the joint.

Digits

The digits of both arms are well preserved although with the exception of the unguals of the right manus, few of these bones are preserved in their natural articulations. As in all pterosaurs the phalangeal formula is 2-3-4-4 for digits I–IV with each of the first three digits terminating in a short cranially curving ungual (Fig. 5). Each ungual bears a deep sulcus that extends almost the whole length from the tip to the base and covers approximately a third of the bone's surface. The tip of each ungual is pointed and strongly curved in palmar direction. The individual phalanges are about twice as broad as the shaft at their proximal articulations and narrow distally as the cranial margin of the bone curves caudally for a short distance before the shaft adopts a uniform diameter for the remainder of its length.

Fig. 5 *Barbosania gracilirostris* (MHNS/00/85) gen. et sp. nov. Line tracing centred on the fourth metacarpophalangeal joint where: *d* digit; *d-p* digit and phalanx; *mc* metacarpal, *u* ungula, *wph* wing finger phalanx (d4). *Arrow* indicates a partially open suture between the first wing winger phalanx and the extensor tendon process. *Scale* equals 50 mm
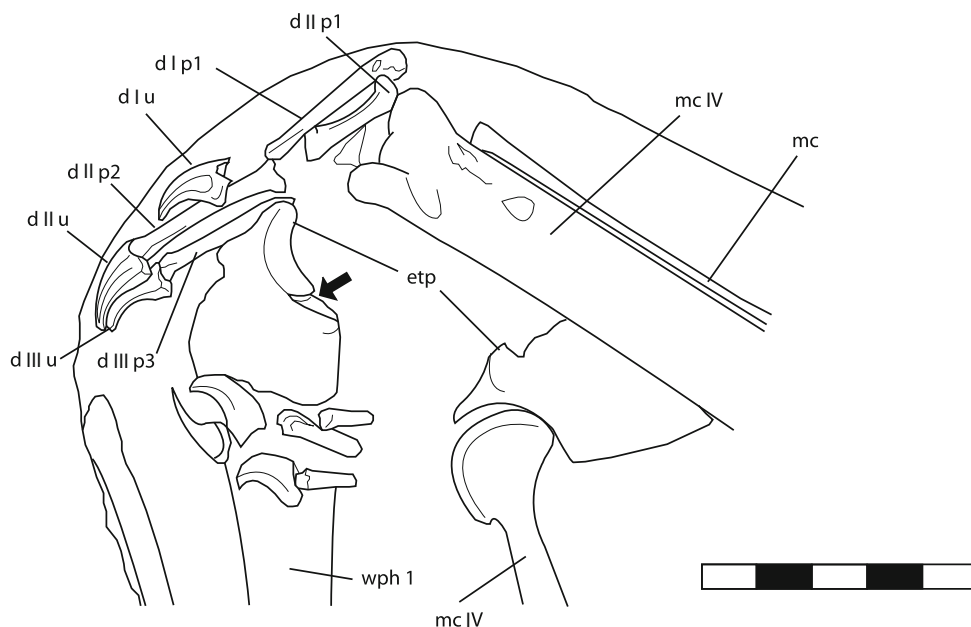
A pronounced ridge runs along most of the length of the cranial surface of digit II phalanx 2 presumably for the attachment of flexor muscles.

Wing finger (digit 4)

The extensor tendon process is preserved in situ for both left and right wing fingers. In places the suture with the corpus of the first phalanx is open but some closure has occurred. On the left first wing finger phalanx (wph 1) this suture is laterally discontinuous but extends approximately 2/3rds across the ventral surface of wph 1. On the right wph 1 the extensor tendon process is exposed in both ventral and lateral aspect. While the suture is still fully open against the proximal articular surface of wph 1 it does not extend onto the ventral surface.

The shaft of wph 1 is typical of other pterosaurs in that its width initially converges towards the middle of the shaft before expanding again to form the distal articulation surface. A fragment of bone containing a distal articular surface adjacent to the femur is interpreted as that of the third phalanx of the right wing.

Pelvic girdle

All the individual elements of the pelvic girdle remain unfused. In cranial view this is indicated by open sutures between the ilium and pubis, as well as between the sacral ribs and the ilium. In lateral view a large gap separates the caudoventral margin of the pubis from the cranioventral margin of the ischium. An open suture between the two elements extends dorsally until the ventral margin of the acetabulum where it is lost due to poor preservation and obstruction by the femur.

Due to damage and sediment cover only a small portion of the left ischiopubis is useful for describing the external morphology. In cranial view the pubis is a medially curving, transversally compressed bone that is thickest at its articulation with the ilium and ischium, forming the cranial margin of the acetabulum. Moving ventrally the pubis is twisted so that the ventral blade is aligned in a craniolateral direction. In lateral view the cranial margin of the left pubis is slightly concave while that of the left is indeterminate due to damage to the compacta. The ventromedial margin of the pubis is straight. The high oval obturator foramen separates the pubis from the ischium.

In lateral view, the cranial margin of the ischium is strongly concave for much of its length, while the caudal margin is shallowly concave, constricting the width of the bone. The ventral margin of the ischium is straight while the cranioventral margin is convex. The caudoventral margin of the bone, however, is strongly concave. The ventral edge of the right ischium lies adjacent to the preserved ventral margin of the left, which has broken and is ~ 5 mm shorter than that of the right. Sediment infill between the pubis and its articular surface on the first sacral suggest that the left ischiopubic plate may have been slightly displaced laterally, likely due to the collapsing right plate. Restoring the pubis and ischium to their original positions indicates that their ventral margins would have sat close to the midline of the body but would have been sufficiently distant from the opposite elements to prevent the formation of a symphysis.

Femur

The femoral head is offset against the shaft of the femur at an angle of approximately 153°. The greater trochanter is preserved as a weakly developed ridge along the lateral and dorsal margins of the bone while a large scar, approximately 9 mm in length, is located directly ventral to this.

Discussion

Systematic palaeontology

Specimen MNHS/00/85 is placed within the Ornithocheiroidea by preserving a notarium, a humerus with a warped, sub-triangular deltopectoral crest, an ornithocheiroid carpus, and a reduction of the metacarpalia where only one of the first three would have made contact the distal face of the carpus (see Unwin 2003). It is distinguished from the Istiodactylidae (e.g. Anders and Ji 2006; Wang et al. 2005) on the basis of a relatively short nasoantorbital fenestra, making up only ∼24% of the skull length, a rostrum with triangular cross-section, and narrow, elongated teeth that extend caudally for more than 50% the length of the skull. The specimen therefore ranks within the Ornithocheiridae where it is referred to a new genus and species.

The cranium and mandible of *Barbosania gracilirostris* clearly lack a median sagittal crest and as such the described specimen is considered distinct from those ornithocheirids known to possess large rostral crests e.g. *Anhanguera*, *Coloborhynchus*. While the absence of a crest may perhaps be considered an insufficient reason for distinguishing MNHS/00/85, due to ontogenetic variability or sexual dimorphism, it differs from specimens of *Coloborhynchus* by the lack of a palate turned 90° at the tip of the rostrum, two small teeth positioned on the rostral face of the skull, and a robust lateral expansion of the rostrum. Despite a similar appearance to specimens of *Anhanguera*, which also developed a more pointed rostrum, *B. gracilirostris* does not posses parietal crest, considered a synapomorphy of the genus (Kellner and Tomida 2000).

Barbosania gracilirostris shares the absence of a median sagittal crest with several other taxa including: *Anhanguera fittoni* (Owen 1859), *Brasileodactylus araripensis* (Kellner 1984; Veldmeijer et al. 2009), *Coloborhynchus sedgwickii* (Owen 1859), *Cearadactylus* (Leonardi and Borgomanero 1985; Dalla Vecchia 1993), and *Ludodactylus sibbicki* (Frey et al. 2003). A general morphological comparison with these taxa is therefore required. *Anhanguera fittoni* is superficially similar to MHNS/00/85 and also lacks a lateral rostral expansion but the specimen is limited to an isolated rostral fragment and a full comparison of the two is therefore impossible. Owen (1859)

founded the species due to its clear distinction with *Coloborhynchus sedgwickii* where the diagnosis was restricted to the interalveolar spacing of the first three tooth sockets, the lesser degree of the rostral expansion, and the presence of a shallow longitudinal groove on the palate, three characters that are no longer considered distinct. Differences between the rostral portions of the skull of *A. fittoni* and *B. gracilirostris* are limited to a slightly more rounded rostral termination in *A. fittoni* where the largest alveolus is the fourth, rather than the third as in MNHS/00/85. The pattern of the interalveolar spaces also differs between the two specimens where the interalveolar distance increases rapidly caudal to the 8th alveolus in *A. fittoni*, while in MNHS/00/85 this occurs caudal to the 13th. Without clearer indication of the diagnostic features of *A. fittoni* and a better understanding of the relationships between Brazilian and English ornithocheirid pterosaurs, the limited preservation of this specimen prevents any further consideration.

Coloborhynchus sedgwickii is distinguished from the MNHS/00/85 by possessing a flat, vertically orientated, triangular shaped rostral termination, which bears two rostrally directed teeth.

Ludodactylus sibbicki bears a blade-like, caudally directed parietooccipital crest similar to *Pteranodon longiceps* (Frey et al. 2003) and as such is clearly distinct from MNHS/00/85, where the supraoccipital process is deflected and the caudal face of the parietal is flat.

Cearadactylus atrox may have lacked a rostral crest, however, the dorsal part of the skull terminates with the edge of the concretion. The dorsal aspect of the specimen has neither been described nor depicted, and therefore the presence or absence of a crest remains doubtful. Furthermore, *Cearadactylus atrox* is characterized by notch in the premaxillomaxillary transition, which is missing in MNHS/00/85, and the dentition is different in both count and arrangement. A second specimen "*C.*" *ligabuei* is also distinct from MNHS/00/85 by a thick and robust rostrum. This has a rounded termination with larger and more pronounced premaxillary tooth sockets relative to the more caudally located alveoli, and a pronounced lateral expansion beginning level with the fourth alveolus.

The general morphology of the described specimen is most similar to that of *Brasileodactylus*. Although the taxonomic validity of this genus has been questioned by several authors, such interpretations have been challenged by Kellner and Tomida (2000) and Veldmeijer et al. (2009) who redefined the synapomorphies or better diagnostic features of *Brasileodactylus* as:

1. A slight expansion of the rostrum.
2. A deep groove on the dorsal surface of the mandible extending to the rostral margin of the dentary.

3. The presence of paired side branches off the primary dentary groove.
4. The rostral, rostrolateral, and lateral orientation of the first three alveoli of the mandible.

The diagnostic value of several of these characters remain questionable because the position and extent of the lateral expansion of the rostrum is not constant even between those specimens attributed to the genus, Kellner and Tomida (2000) reported this as beginning between the third and fourth alveolus of the mandible in MN 4804-V, while Veldmeijer et al. (2009) noted that it occurred between the fourth and fifth alveolus in SMNS 55414. Furthermore, the size of the expansion is not sufficiently distinct from specimens of *Anhanguera* and is also likely to be linked to ontogenetic age.

Likewise the presence of laterally directed branches of the median mandibular sulcus is also not unique to *Brasileodactylus* but is present in the large crested specimens of *Coloborhynchus* (SMNK PAL 2302), where they are restricted to the rostral-most part of the dentary, and in a skull of *Anhanguera* (SMNK PAL 1281). The median mandibular sulcus of SMNK PAL 2302 terminates 7.9 mm caudal to the rostral margin of the bone while in the latter specimen it extends to the rostral margin, bifurcating at the very tip of the rostrum. The role of these mandibular sulci is unknown, but likely they represent canals for blood and nervous supply the buccal lining of the mandibular rostrum and should not be considered unique to any particular genus. The final character, however, the positioning of the first mandibular alveolus on the rostral face of the dentary, is regarded as a valid character for diagnosis.

Regardless of the issues noted above two of the cited characters cannot be observed due to the occluded resting position of the upper and lower jaws (characters 2, 3), while the premaxillary part of the rostum is gradually converging and does not show any lateral expansion (character 1). Finally, the rostral-most pair of mandibular teeth is positioned rostrodorsally and not rostrally (character 2) and as such MNHS/00/85 fails to meet any of these diagnostic features of Veldmeijer et al. (2009). MNHS/00/85 must therefore be distinguished from *Brasileodactylus*.

Several isolated rostral fragments known from the Nova Olinda Member of the Crato Formation are superficially similar in appearance to *B. gracilirostris*, in that they lack a medial crest and possess a pointed rostral termination in lateral view (Unwin and Martill 2007, pp. 492–493; Sayão and Kellner 2000). Although these specimens have been tentatively referred to the genus *Brasileodactylus*, the first pair of alveoli on the mandible appear to be orientated rostrodorsally as in MNHS/00/85 and thus should be re-investigated based on the data presented here.

Dentition

The estimated number of teeth per half jaw in MHNS/00/85 are >24 and >20 in the upper and lower jaws, respectively, and is therefore similar to that of *Coloborhynchus. piscator* (Kellner and Tomida 2000; 25 upper and 18–19 lower). Given that these are minimum estimates the dentition number is distinct from several other ornithocheirid specimens e.g. *C. robustus* (~18, lower jaw), *A. santanae* (20, upper jaw) and *Ornithocheirus mesembrinus* with 13 and 11 alveoli in the upper and lower jaws, respectively. The largest tooth in *B. gracilirostris* is the fourth which also holds true for *Cearadactylus araripensis*, *Anhanguera fittoni*, *Anhanguera blitterdorffi*, *Anganguera santanae*. However, the second largest tooth caudal to this in the above taxa is the eighth rather than the ninth for MHNS/00/85. In other taxa the largest tooth is either the second (*Brasileodactylus* SMNS 55414, Veldmeijer et al. 2009) or the third (*Coloborhynchus piscator*; *Coloborhynchus clavirostris*; *Coloborhynchus robustus*; *Anahanguera blitterdorffi*) and the second largest tooth varies between the eighth and the tenth.

Figure 6 records the diameter of the premaxillomaxillary and mandibular alveoli and interalveolar spaces for a number of ornithocheirid pterosaurs. Several taxa e.g. *Coloborhynchus* and *Ornithocheirus* are clearly distinct from *Anhanguera*, *Brasileodactylus* and *Ludodactylus* with regard to the dentition pattern. Although the general patterns observed in these latter taxa are similar, there are a number of observations to be discussed. The cranial interalveolar space pattern of MNHS/00/85 is most similar to that of *Brasileodactylus* indet. (AMNH 24444) that differs from other *Brasileodactylus* specimens where the interalveolar space rapidly increases caudal to the sixth or seventh alveolus. The interalveolar space patterns of the two unidentified *Brasileodactylus* specimens AMNH 24444 and BSP 191 I 27 are so distinct that they must represent either different species or that a large range of dentition patterns existed for this genus. No specimen shows an exact match to the pattern observed in *Ludodactylus* and it is thus not possible to comment on the possibility that isolated and crestless rostral fragments also known from the Brazilian deposits may be conspecific.

Postcranium

The general morphology of the ornithocheirid postcranial skeleton is almost identical between species and few features are useful for differential diagnostics. The postcranial remains of crestless specimens are rare, however, two are known (AMNH 24444 and BSP 191 I 27). The former of these is still under preparation and therefore little

Fig. 6 Comparison of the interalveolar spacing in selected taxa where: **a** cranium, *closed diamond*, *Ornithocheirus mesembrinus* (BSP 1987 I 46); *grey diamond*, *Barbosania gracilirostris* (MNHS/00/85); *open diamond*, *Anhanguera* sp. (SMNK PAL 1281); *closed triangle*, *Brasileodactylus araripensis* (MN 4804-V); *open triangle*, *Brasileodactylus araripensis* (MN 4797-V); **b** mandible, *closed triangle*, *Ludodactylus sibbicki*, (SMNK PAL 3828); *grey triangle*, *Brasileodactylus* sp. (BSP 191 I 27); *open triangle*, *Brasileodactylus* sp. (AMNH 24444); *closed diamond*, *Ornithocheirus mesembrinus*, (BSP 1987 I 46); *grey diamond*, *Barbosania gracilirostris* (MNHS/00/85); *open diamond*, *Coloborhynchus robustus* (SMNK PAL 2302)
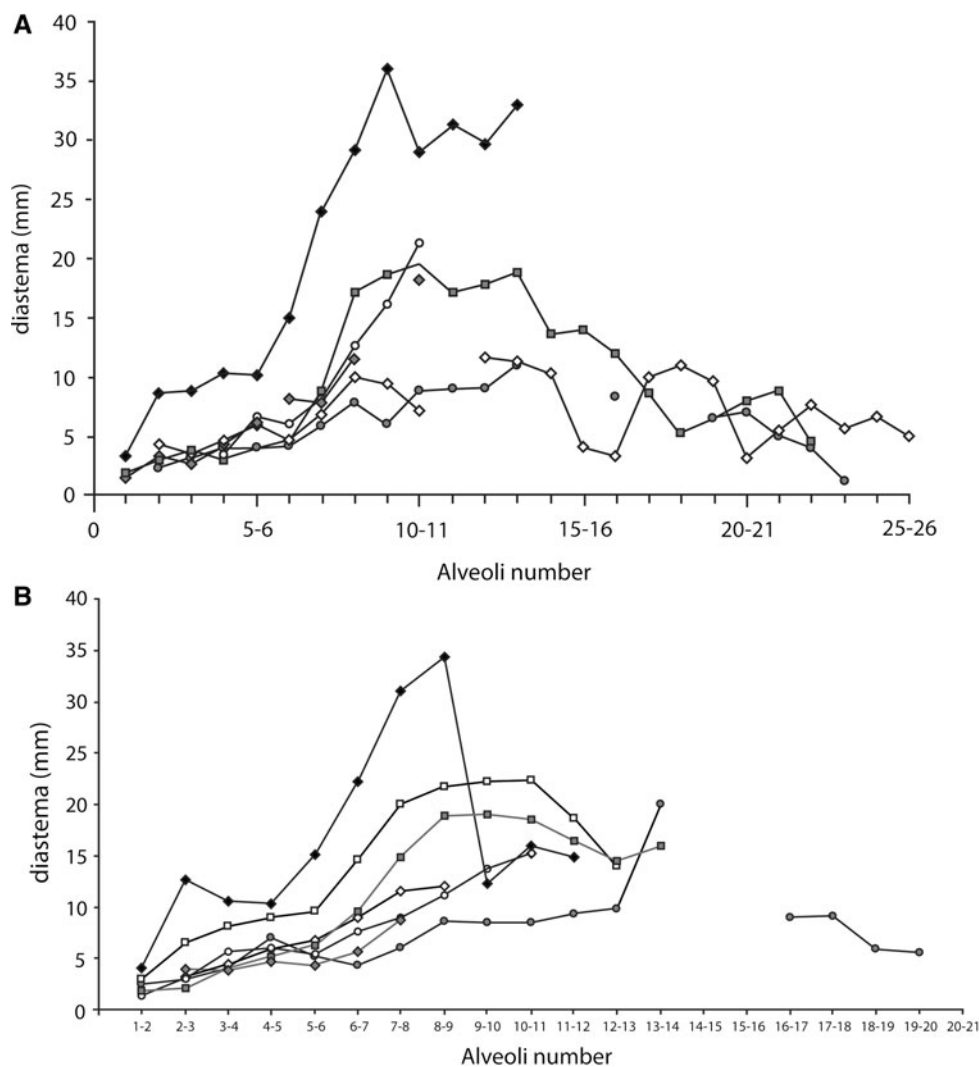

information is available (Veldmeijer et al. 2009) making BSP 191 I 27 the only comparable specimen. MNHS/00/85 and BSP 191 I 27 share only a limited number of elements including the cervical and dorsal vertebrae, the humerus, and the pubis. The majority of these elements are almost identical in their morphology and as such few differences can be observed although a single pneumatic foramen on the ventral face of the transverse process of the ninth cervical is significantly smaller in MNHS/00/85 while in BSP 191 I 27 it encompasses the majority of the bone surface. The transverse processes of the fifth dorsal are significantly more elongated in MNHS/00/85, where the transverse processes are low on the neural arch, which apparently reaches ventrally onto the lateral face of the respective vertebral dorsoventrally compress corpus. The number of dorsal vertebrae present in MNHS/00/85 is 13, suggesting that variable counts of vertebrae existed within the Ornithocheiridae, where *Coloborhynchus* is known to have only 12 (Veldmeijer 2003, 2006) while *Anhanguera* (AMNH 22555) preserves 13.

The ischium of BSP 191 I 27 and MHNS/00/85 differ in the concavity of the cranial margin, which is more pronounced in the former and terminates at a relatively more ventral position on the bone. The caudal margin in BSP 191 I 27 it is almost straight whereas in MNHS/00/85 it is concave. The caudoventral margin of the bone is MNHS/00/85 is strongly concave, which is contrasted against other ornithocheiroids, where the entire caudal margin of the ischium is gently convex (Fig. 7).

Ontogenetic maturity

While elements of the cranium appear to suture very early in ontogeny (Kellner and Tomida 2000) all ornithocheiroids recovered from the Romualdo Member of the Santana Formation are considered to be ontogenetically immature based on the lack of fusion in the postcranial skeleton. Such findings are contrary to ornithocheiroids from the Nova Olinda Member of the Crato Formation that preserve a more mature state of suturing e.g. *Arthurdactylus*
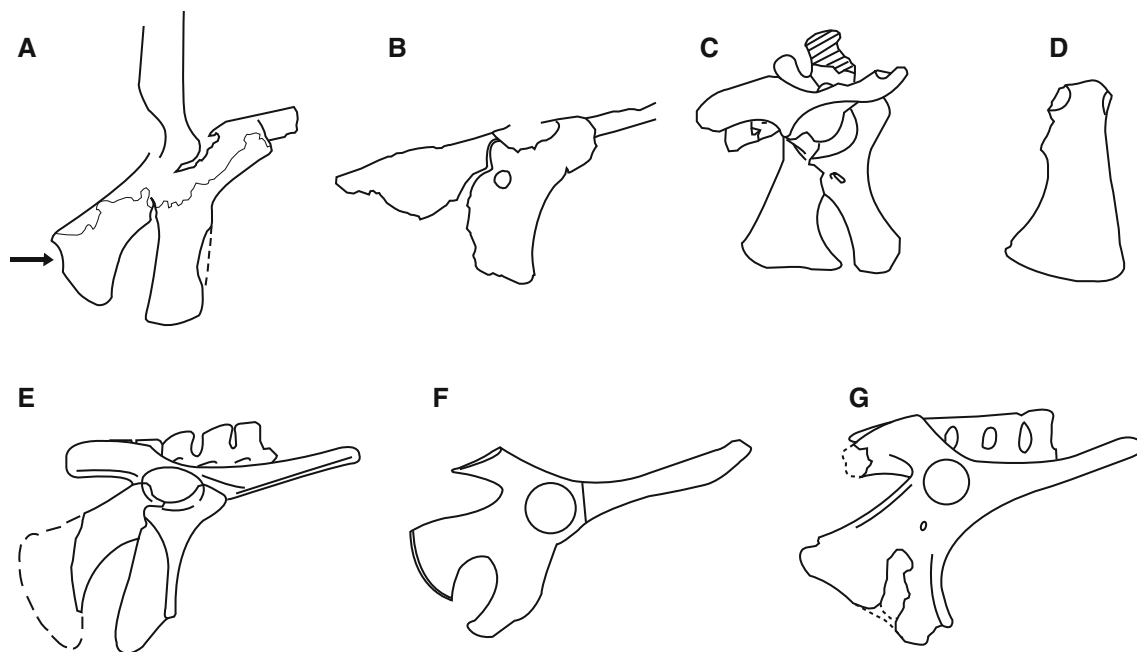
Fig. 7 Comparison of the pelvic plate in selected ornithocheiroid pterosaurs. **a** Right puboischiadic plate of *Barbosania gracilirostris* gen. et sp. nov; **b** left puboischiadic plate of *B. gracilirostris*, clearly showing the suture between the pubis and ischium; **c** *Brasileodactylus*, left ischium (BSP 191 I 27, Veldmeijer et al. 2009); **d** *Coloborhynchus piscator* (NSM-PV 19892, Kellner and Tomida 2000); **e** AMNH 22569 (Bennett 1990); **f** *Arthurdactylus conandoylei* (SMNK PAL 1132, Frey and Martill 1994); **g** *Coloborhynchus speilbergi* (RGM 401880)

conandoylei (Frey and Martill 1994) and azhdarchoids of the Romulado Member, e.g. SMNK-PAL 6607, a putative azhdarchoid where tendons and ligaments have mineralized along the lateral margin of the supraneural plate.

While little is known about the condition of the skull of MNHS/00/85 except that the premaxillomaxillary suture has mostly closed, the specimen must also be considered immature because the thoracic ribs have not fused to the transverse processes, the scapula and coracoid lie apart, the epiphyseal gap of the humerus is open, and large open sutures are visible between the elements of the pelvic girdle. In contrast to other ornithocheiroids from the Santana Formation (e.g. SMNK PAL 1133), MNHS/00/85 has partially closed sutures between the carpals and the extensor tendon process to the cranioproximal face of the first wing finger phalanx. As the latter of these is considered an indicator of late ontogeny in pterosaurs (Bennett 1992; Frey and Martill 1994, 1998; Kellner and Tomida 2000), it is unusual to observe this in an otherwise morphologically immature skeleton. The specimen is therefore considered as having died in a more advanced ontogenetic state than other complete Santana pterosaurs (e.g. *A. santanae*; *C. piscator*) and indicates either the onset of late fusing features at a relatively small size (i.e. dwarfism) or a significant deviation from the previously observed pattern of suture development in ornithocheirids.

Comments on the cranial crest

The cranial crest has been associated with a wide variety of roles including thermoregulation (Kellner and Campos 2002), an aerodynamic rudder and/or counterbalance (Bramwell and Whitfield 1974), a means to stabilise the head during prey capture (Veldmeijer et al. 2006), or a sexual display. The large variety that exists within the size, shape and position of the crest across the Pterosauria and the differences between closely related taxa argue strongly in favour of a sexually selected trait, a position reinforced by the appearance of sexually dimorphic crests in *Pteranodon* (Bennett 1992) and its strong allometric growth (Tomkins et al. 2010).

The crest as a diagnostically useful feature is problematic as the degree of intraspecific variation is unknown in pterosaurs, while the size, shape and position of the crest are also likely to change during ontogeny (Martill and Naish 2006) and must be considered with respect to the morphological maturity of the specimen. Likewise the differences between male and female animals are uncertain; while the crest of putative female specimens of *Pteranodon* are smaller than those of their male counterparts they are nonetheless present (Bennett 1992, 2001), but the exaggerated crest of *Nyctosaurus* appears to be present only beyond a specific point in their development

(Bennett 2003b). It is this uncertainty that prevents a consensus of whether specimens distinguished almost exclusively by the absence of a crest should be regarded as sexual morphs of a single species (e.g. *Colobrhynchus sedgwickii* and *C. capito*, Unwin 2001). Within the Ornithocheiridae, however, a number of ontogenetically immature specimens are known to possess a well-developed median sagittal crest (e.g. *C. piscator*, *Santanadactylus*, AMNH 22555) suggesting that this feature formed relatively early in ontogeny. The absence of the crest in MHNS/00/85 should therefore not be considered a product of its morphologically immature status, particularly considering the partial fusion of the extensor tendon process to the first wing finger phalanx.

The lack of a rostral median crest in MNHS/00/85 is aligned with another feature, a caudoventrally deflected supraoccipital process combined with a lack of a short parietal crest that characterizes the skull of other ornithocheirids e.g., *Anhanguera blittersdorffi*. The narrow and slender rostrum of MNHS/00/85 could probably be operated with less muscular power than in *Anhanguera*, in which the crest added to the weight of the rostum with a long lever action on the occipitoatlantical articulation. The same holds true for the cervicooccipital musculature, which in MNHS/00/85 had a relatively smaller momentum to handle compared with a similar sized, crested species. This would explain the small supraoccipital process.

As the cranial crest appears to develop relatively early during ontogeny and with no evidence to suggest that putative females should be regarded as completely crestless the lack of a rostral and dentary median crest in MNHS/00/85 is argued to be regarded as a genuine and diagnostic character. Veldmeijer et al. (2009) previously argued that in the absence of additional specimens, or until more information becomes available, crestless specimens must be regarded as separate taxa rather than juvenile members of pre-established genera. We follow them in this respect.

Conclusions

Barbosania gracilirostris represents the most complete skeleton of a crestless ornithocheirid known from the Santana Formation of NE Brazil and is distinguished from the morphologically similar *Brasileodactylus* by the rostrodorsal position of the first mandibular alveoli. Although they are also not observed in the described specimen, the remaining apomorphies listed for *Brasileodactylus* are dubious, because the size and position of the rostral expansion is variable and may itself develop later in ontogeny with the appearance of larger teeth and alveoli. The appearance of a long median sulcus and the presence of paired lateral branches in *Anhanguera* (SMNK PAL

1281) and *Coloborhynchus* (SMNK PAL 2303) also cast sufficient doubt on the diagnostic use of these features.

MHNS/00/85 shares 13 dorsal vertebrae with *Anhanguera* (AMNH 22555), deviating from the 12 dorsal conditions observed in other derived pterodactyloid pterosaurs. A brief comparison of the interalveolar spaces between the cranial alveoli finds two patterns within specimens assigned to *Brasileodactylus* where BSP 191 I 27 differs from AMNH 22444 and MHNS/00/85 by a significant increase of the interalveolar spacing caudal to the eighth alveolus. MHNS/00/85 strongly suggests that the absence of the cranial crest is a genuine character rather than an ontogenetic feature due to the advanced state of skeletal fusion relative to other immature, crested pterosaurs from the same locality.

Several specimens that have been possibly referred to *Brasileodactylus* but lack a rostrally positioned first mandibular pair of alveoli might instead be considered as *B. gracilirostris* (e.g. Unwin and Martill 2007, pp. 492–493; Sayão and Kellner 2000).

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