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New Interpretation of the Palate of Pterosaurs

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ABSTRACT

On the basis of a new, three-dimensionally preserved specimen of the Early Jurassic pterosaur *Dorygnathus banthensis* we present a reinterpretation of the pterosaur palate. The hard palate is formed by the extensive palatal plate of the maxilla and not by the palatine as has been generally reconstructed. This palatal plate of the maxilla emarginates the choana rostrally and rostrolaterally as in other archosaurs and lepidosaurs. The longitudinally elongate and dorsoventrally flat palatine in *Dorygnathus* is an isolated bone caudal to the palatal plate of the maxilla and morphologically and topographically it resembles that of crocodylians and birds, respectively. The palatine separates the choana laterally from the suborbital fenestra demonstrating the homologous nature of the (pri-

Additional Supporting Information may be found in the online version of this article.

Abbreviations used: Institutional abbreviations: CA = Carnegie Museum Pittsburgh, USA; CD = Desirée Collection of Rainer Alexander von Blittersdorff, Rio de Janeiro; IGO = Museo Mario Sánchez Roig, Instituto de Geología y Paleontología, La Habana, Cuba; IVPP = Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; KUVF = Museum of Natural History, University of Kansas; NHM = Natural History Museum, London, England; PTH = Philosophische-Theologische Hochschule, Eichstätt; SAO = Naturmuseum, St. Gallen; SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany. Anatomical Abbreviations: acav = accessory cavities of the antorbital fossa; amp = apertura maxillo-premaxillaris; aof = antorbital fossa; aofe = antorbital fenestra; asec = articular surface of ectopterygoid; asj = articular surface for jugal; aslac = articular surface of lacrimal; asmx = articular surface for maxilla; asnas = articular surface of nasal; aspm = articular surface for premaxilla; asprf = articular surface of prefrontal; aspt = articular surface of pterygoid; bo = basioccipital; bp = basipterygoid; bs = basisphenoid; bw = bony wall separating the caviconchal and postvestibular recesses from the nasal cavity proper; camxd = cavity for the maxillary diverticula; capmd = cavity for the premaxillary diverticula; ch = choana; cppm = caudal process of the premaxilla; cr = cecal recess; dpmx = dorsally projecting caudomedial edge of the palatal plate of the maxilla; ec = ectopterygoid; fi = foramen incisivum; fm = foramen magnum; fr = frontal; in = internal nares (choana); iof = infraorbital fenestra; iov = infraorbital vacuity; ipv = interpterygoid vacuity; itv = infratemporal vacuity; j = jugal; jpmx = jugal process of the maxilla; lac = lacrimal; lmch = lateral margin of choana; lppt = lateral process of pterygoid; ltf = lower temporal fenestra; lwmx = lateral wall of maxilla; ma = mandible;

mampm = margin of apertura maxillo-premaxillaris; maofe = margin of antorbital fenestra; mas = muscle attachment surface; mppt = medial process of the pterygoid; msofe = medial margin of suborbital fenestra; mx = maxilla; nar = naris; nas = nasal; ncpr = nasal cavity proper; npx = nasal process of premaxilla; oaof-nc = opening between antorbital fossa and the nasal cavity; oc = occipital condyle; ocavre = opening for caviconchal recess; pecf = pterygoectopterygoid fenestra; pf = pneumatic foramen; pl = palatine; plplmx = palatal plate of maxilla; plpmx = palatal process of maxilla; pm = premaxilla; pmc = premaxillary cavity; pmfe = premaxilla-maxilla fenestra (*sensu* Langer 2004); ppf = ppled = pplf and ppv = postpalatine- or posterior palatine fenestra; prppl = prefrontal process of palatine; ps = parasphenoid; pt = pterygoid; ptf = posterior pterygoid fenestra; ptppl = pterygoid process of the palatine; q = quadrate; qc = quadrate condyle; qj = quadratojugal; rppt = rostral process of the pterygoid; sa = swollen alveolus; sept = sagittal septum; smxv = vomeromaxillary suture; sofe = suborbital fenestra; sri = sagittal ridge; stf = subtemporal fenestra; t = teeth; v = vomer; x = transverse bone; z = pterygo-jugal vacuity; 6. = sixth upper tooth; 6.a = sixth alveolus; 11.a = eleventh alveolus

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mary) choana in all archosaurs and lepidosaurs. Our study indicates that in basal pterosaurs the pterygo–ectopterygoid fenestra existed caudal to the suborbital fenestra, which became confluent with the adductor chamber in pterodactyloids thereby increasing the relative size of the adductor chamber and hence the mass of the jaw adductors. The choana in basal pterosaurs was relatively small compared with the interpterygoid vacuity. With increasing rostroventral inclination of the quadrates in more derived pterosaurs, the interpterygoid vacuity was reduced considerably, whereas the choana increased in size. This exceptional *Dorygnathus* specimen also shows a hitherto unknown pair of fenestrae situated at the palatal contact of the premaxilla–maxilla and might represent the aperture for the vomeronasal organ. *Anat Rec*, 293:243–258, 2010. © 2009 Wiley-Liss, Inc.

Key words: Jurassic pterosaur *Dorygnathus*; palate; extant phylogenetic bracket; choana

The reconstruction of the palatal region of the pterosaurian skull has always been problematic, because most pterosaur cranial materials are laterally exposed and often compressed or severely crushed. In addition, the complete fusion of cranial elements in most adult pterosaurs prevents the identification of sutures thus the accurate distinction of cranial elements. There are a few exceptional specimens with skulls that are either three-dimensionally preserved [e.g., *Parapsicephalus purdoni*, Newton (1888); the Carnegie-specimen (CM 11434) of *Rhamphorhynchus muensteri* (Wellnhofer, 1975); some excellent specimens of *Dsungaripterus weii* (IVPP 64043), Young (1964); the holotype of *Tapejara wellnhoferi*, Kellner (1989); *Cacibupteryx caribensis*, Gasparini et al. (2004); *Nyctosaurus gracilis* (Williston, 1902); and several ornithocheirids from the Santana Formation, e.g., *Tropeognathus (Ornithocheirus) mesembrius*, Wellnhofer (1987); *Anhanguera santanae* (Witmer et al., 2003); *Coloborhynchus araripensis*, *Coloborhynchus spielbergi* (Veldmeijer, 2003)] or palatally exposed [*Gnathosaurus subulatus* (Wellnhofer, 1970, “Exemplar Nr. 70”); *Rhamphorhynchus “gemmingi”* NHM R 2786 (Woodward, 1902)] (see Fig. 1 and Supporting Information). The currently accepted palatal reconstructions of the pterosaurian skull have been based on these specimens, apparently combined with speculative interpretations of fragmentary, compressed, or isolated material (e.g., Arthaber, 1919; Wellnhofer, 1978; Bennett, 2007).

An exceptionally well-preserved, disarticulated but associated, and yet undescribed skeletally immature specimen of *Dorygnathus banthensis*, however, challenges these previous palatal reconstructions. The isolated and three-dimensionally preserved cranial elements of this specimen provide a unique insight into the finer morphology and structure of some palatal bones of *Dorygnathus*. On the basis of the archosaurian affinities of the group (Serenó, 1991; Benton, 1999; Hone and Benton, 2007), we adopted an extant phylogenetic bracket (“EPB,” Witmer, 1995a) approach to identify some of the isolated cranial elements and to reconstruct the palate of *Dorygnathus*. Comparison of the newly reconstructed palate of *Dorygnathus* with those of other pterosaur taxa helped to clarify some hitherto undescribed or misinterpreted bony elements and fenestrae

in these taxa, and opened the way to propose possible evolutionary changes in the construction of the pterosaur palate.

THE CURRENT CONCEPT OF PALATE RECONSTRUCTION AND ITS PROBLEMS

The earliest delineation of the complete palate of a pterosaur was given by Marsh (1884) who depicted the skull of a *Pteranodon longiceps* in ventral, dorsal, and lateral views. Unfortunately, neither the specimen on which his reconstruction was based nor the bones forming the palate were identified. Subsequent early authors, such as Newton (1888), Seeley (1901), Woodward (1902), Williston (1902), von Huene (1914), Broili (1919), and Arthaber (1919), were more specific about the assignment of bones in their palatal reconstructions. However, there are some significant differences with respect to their interpretations of the palatal bones (see Supporting Information for an overview). The reason for this is the difficulty to identify homologue bones in different taxa, especially if the morphological patterns do not show a simple topographic equivalence between taxa (Coates, 1993). After the work of these earliest authors, the palatal reconstruction of pterosaurs became progressively standardized and most of the later work on the pterosaurian palate followed this generalized interpretation of the palatal bones (Wellnhofer, 1970, 1975; Kellner, 1989; Witmer, 1997; Bennett, 2001, 2007; Gasparini et al., 2004; Padian, 2008). This concept is also apparent in Wellnhofer’s review (1978), which illustrates the palate of several different pterosaurs known at that time. The most reliable reconstructions based on excellent specimens in Wellnhofer’s review are that of *R. muensteri*, *Gnathosaurus subulatus*, and *N. gracilis* (Supporting Information). The palatal restorations of *Scaphognathus crassirostris* and *Campylognathoides liasicus* were based on their holotype specimens Nr. 1304 and CM 11424, respectively, where limited insight into the palate construction via the naris, and the antorbital, orbital, and lower temporal fenestrae is possible. The palate reconstruction of *Pteranodon ingens* was based on three incomplete specimens (KUVP 976, 2212, and YPM 1177). According to the Figs. 3 and 6 in Wellnhofer (1978), the

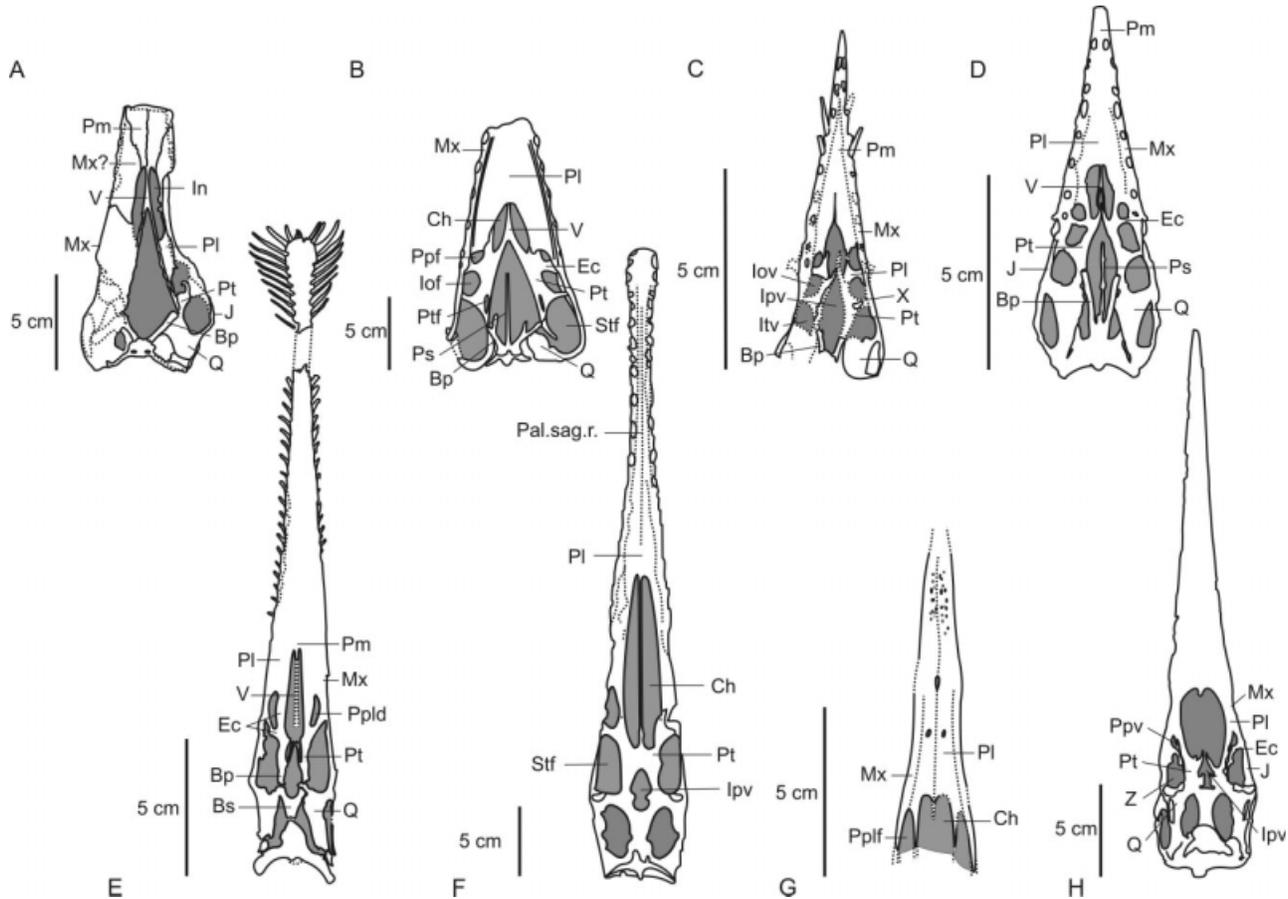


Fig. 1. Line drawings of some palatally examinable specimens of pterosaurs presenting the earliest and recent palate reconstructions. (A) *Parapsicephalus purdoni* (Newton, 1888); (B) *Cacibupteryx caribensis* (Gasparini et al., 2004); (C, D) *Rhamphorhynchus muensteri*, London (NHM R 2786) and Carnegie specimen (CM 11434), respectively;

(E) *Gnathosaurus subulatus* (PTH 1951.84, "Exemplar Nr. 70"); (F) *Coloborhynchus spielbergi* (Veldmeijer 2003); (G) *Tapejara wellnhoferi* (Kellner 1989); (H) *Nyctosaurus gracilis* [based on the photograph of the original specimen described by Williston (1902)].

appearance of the palate of different taxa is diverse, but the basic Bauplan seems conservative (Fig. 2). The following description presents the generally accepted reconstruction of the palate of pterosaurs, on which the identification of the palatal bones of all hitherto known pterosaur specimens has been based (Williston, 1902; von Huene, 1914; Arthaber, 1919; Broili, 1919; Mayr, 1964; Wellnhofer, 1970, 1975, 1978, 1987, 1991a,b; Kellner, 1989; Wellnhofer and Kellner, 1991; Bennett, 2001; Veldmeijer, 2003, 2006; Gasparini et al., 2004; Padian, 2008).

The palatal flanges of the premaxillae form the anteriormost portion of the palate. They contact each other in a median suture. Caudally, they articulate with the maxillae and palatines. The palatal part of the maxilla is a narrow lateral rim, which is the tooth-bearing region in dentate pterosaurs. This rim projects caudally more than the half of the total length of the skull, where it contacts the jugal. The palatines are blade-like, elongate triangular in outline with a parallel sided caudal process bordering the choanae laterally. Rostrally, the palatines contact the premaxillae and laterally the palatal rim of the maxillae. Along the median

line, they share a common suture separating the nasal and oral cavities and forming a bony secondary palate. With the caudomedial corner of their caudal processes, the palatines contact the rostral ramus of the pterygoids. The vomers lie in the midline adjacent and parallel to each other or converge rostrally. Their rostral end is mostly wedged between the fused palatines. With their caudolateral margin, they contact the rostromedial process of the pterygoids. The complex pterygoids attach caudally to the basipterygoids and the quadrates. The concave medial margins of the corpus of the contralateral pterygoids form the interpterygoideal vacuity. The pterygoids have generally more processes of which the rostromedials converge and connect to the vomers, the rostrals to the palatines and the laterals (if present, e.g., in the Carnegie specimen [CM 11434] of *Rhamphorhynchus*) to the caudal process of the maxillae or to the jugals.

The paired choana is bordered rostrolaterally by the palatine, medially by the vomer, and caudally by the rostral and rostromedial processes of the pterygoid. The needle-shaped parasphenoid protrudes into the interpterygoideal vacuity in the median line. The ectopterygoids

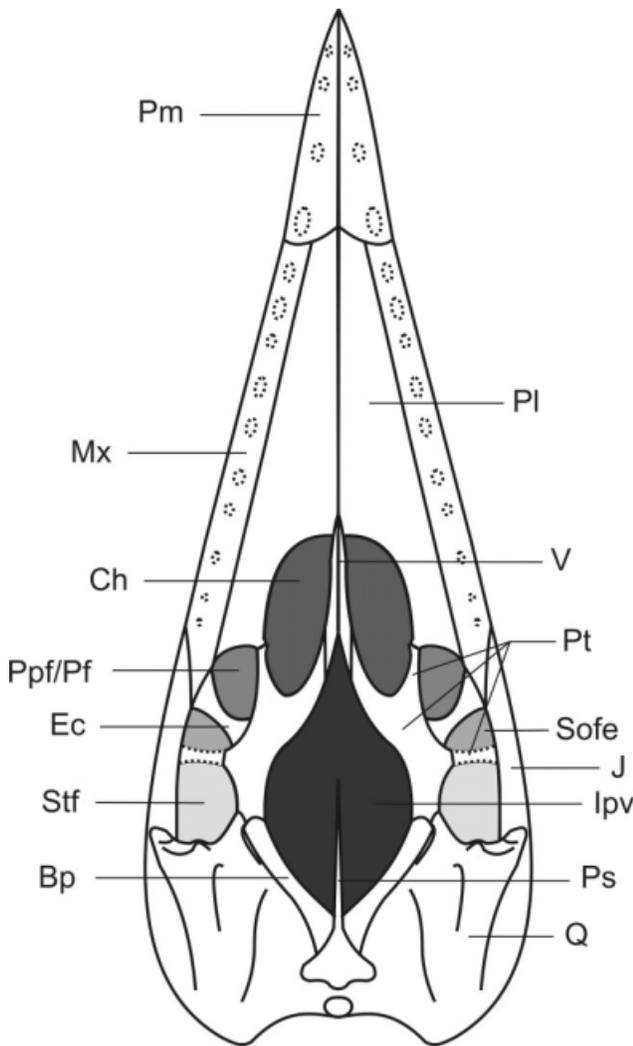


Fig. 2. Line drawing of a hypothetical pterosaur, which represents a “general” palate configuration referring to the currently accepted reconstruction. Note the extent of the maxilla and the relative position of the palatine and choana. Structures with dashed lines are not present in all taxa.

articulate medially with the lateral margin of the pterygoids rostral to their lateral processes and laterally to the palatal rim of the maxillae (but also connect to the palatines in *Rhamphorhynchus* and *Gnathosaurus*; see Fig. 1D,E). Emarginated rostrally by the palatine, laterally by the maxilla, caudolaterally by the ectopterygoid, and medially by the pterygoid there is a medium-sized fenestra [postpalatine fenestra *sensu* Wellnhofer (1970); postpalatal fenestra *sensu* Gasparini et al. (2004); palatine fenestra *sensu* Bennett (2001)]. If the pterygoid has a maxillary process there is another aperture, the suborbital fenestra (or infraorbital fenestra *sensu* Gasparini et al., 2004), bordered rostromedially by the ectopterygoid, laterally by the maxilla or jugal, and caudally by the lateral process of the pterygoid. The subtemporal fenestra is emarginated anteriorly either by the maxillary ramus of the pterygoid (e.g., *Cacibupteryx*, Fig. 1B) or by the ectopterygoid (e.g., *Coloborhynchus*, Fig. 1F), later-

ally by the maxilla and/or the jugal, caudally by the quadrate, and medially by the corpus of the pterygoid. The ascending quadrates generally contact the posterior portion of the pterygoid, laterally to the quadratojugal, caudally to the squamosal, and to the lateral surface of the braincase. Between the quadrates and the braincase, there is mostly a large cranioquadrate opening (see Bennett, 2001: Fig. 8).

Since its first appearance (Williston, 1902), the currently accepted classification of palatal bones, especially the identification of the palatines, has hardly ever been questioned (but see Peters, 2000), despite the fact that this interpretation considers the choanae as being bordered by the palatines rostrally. This suggested position of the choanae, however, with the apparently standard position of it in some turtles, most lepidosaurs and in all archosaurs being surrounded by the vomer medially, palatine caudally and laterally, and maxilla laterally and/or rostrally, which definitely implies homology of the choanae among these groups (Witmer, 1995b). The rostral border of the choanae, however, is either formed by the premaxilla or the maxilla in case, the latter has an extensive palatal plate (Witmer and Martin, 1987). The special case of Crocodylomorpha with a posteriorly positioned secondary choanae at the base of the pterygoids is a consequence of the formation of the long bony nasopharyngeal duct (Iordansky, 1973; Busbey, 1994); nevertheless, the aperture identified as the primary choana has the same relative position emarginated by the same palatal bones as in other archosaurs (Witmer, 1995b). Fossil archosaurs also exhibit this conservative morphology (Osmolska, 1985; Witmer, 1995b, 1997). In contrast to the currently accepted concept of the palatal osteology of pterosaurs, only the reconstructions of Newton (1888), Seeley (1901), and Woodward (1902) are in accordance with the relative position of the choanae found in all other archosauromorphs. Hookey (1913), although not providing any depicted reconstruction, also accepted the palatal reconstruction of Newton (1888). For details of the earliest reconstructions and for the discussion of synonym structures, see Supporting Information.

More recently, Peters (2000) identified the broad palatal bone as the “medial maxilla process” and briefly noticed that this structure has been mislabeled as the palatine by earlier authors. However, he did not give a detailed explanation why he considered this palatal region as part of the maxilla.

Bennett (2007) reconstructed the palate of *Anurognathus ammoni* and figured the palatines as rod-like elements and positioned them caudal to the choanae, which in his reconstruction are placed caudally to the premaxillae and the rostral portion of the maxillae. This restoration is consistent with the pattern seen in archosauromorphs and in most lepidosaurs, but contradicts the accepted reconstruction of the pterosaurian palate. Despite the obvious topographical contradiction, Bennett (2007) does not explain why he changed the relative position of the choanae by shifting them anteriorly compared with the general interpretation of this pair of palatal fenestrae.

Here, we present a new reconstruction of the palate of pterosaurs, which is consistent with the general topography of the palatal elements and apertures found in all archosauromorphs and in most lepidosaurs.

MATERIAL AND METHODS

The new specimen of *Dorygnathus* described here was found in the Toarcian Posidonien Shale of Bad Harzburg, Niedersachsen, Germany and is housed in the collection of the Wyoming Dinosaur Center in Thermopolis, WY. The number of preserved skull elements is relatively lower than it is in the postcranial skeleton. Of the viscerocranium toothed premaxillae and maxillae, nasals, jugals, and palatines are present. The toothed mandibles are fused but consist only of the preserved dentaries. The frontals, parietals, and quadrates represent the neurocranial elements. Other elements forming the braincase are completely missing. The postcranial skeleton of the specimen is almost complete lacking only the first three cervicals, the immobile caudals, sternum, puboischadic plate, and some manual phalanges. The complete description of the specimen is now in preparation.

Acid preparation was used to clean all sides of the specimen.

We applied the extant phylogenetic bracket (Witmer, 1995a) and made direct comparisons among the rostral bones (premaxilla, maxilla, palatine) of *Dorygnathus*, *Anser anser* (MTM uncatalogued), and those of a subadult specimen of *Crocodylus* sp. (MTM uncatalogued).

For the phylogenetic relationships of pterosaurs, it has been suggested that Pterosauria (1) was the sister group of the Dinosauria (Sereno, 1991; Benton, 1999), (2) were basal archosauromorphs (Bennett, 1996), (3) or were members of the group Prolacertiformes (Peters, 2000). Recently, Hone and Benton (2007, 2008) provided new evidence to support the origin of the Pterosauria within Archosauria and we follow their definition here.

RESULTS

Comparative Anatomy of the Rostrum and the Nasal Cavity in *Dorygnathus*, *Anser*, and *Crocodylus*

The anatomy of the bony palate and the architecture of the nasal cavity of crocodylians and birds have been considered in detail (Witmer, 1995b, 1997; Witmer and Ridgely, 2008), and we refer to these descriptions when comparing supposedly homologous elements of *Dorygnathus*.

Premaxilla. As in birds, the premaxilla of *Dorygnathus* (Fig. 3) is a relatively robust element of the skull, which, despite the skeletally immature status of the new specimen, is completely fused. It bears four pairs of labiolingually compressed teeth. The premaxillary rostrum is triangular in transverse section with the pointed apex facing dorsally and it tapers rostrally in all directions. The elongated caudal process of the premaxilla (cppm) is triangular in cross section and passes caudally between the nasals to contact the rostral terminus of the frontals. The caudal margin of the lateral walls of the premaxillary rostrum shows two concavities, separated by a blunt caudoventrally directed process. The dorsal one of these concavities forms the rostral half of the longitudinally oval naris. The second concavity, which lies rostroventrally to the dorsal one, forms the rostral half of a fenestra, which topographically coincides with the premaxilla–maxilla fenestrae *sensu* Langer (2004).

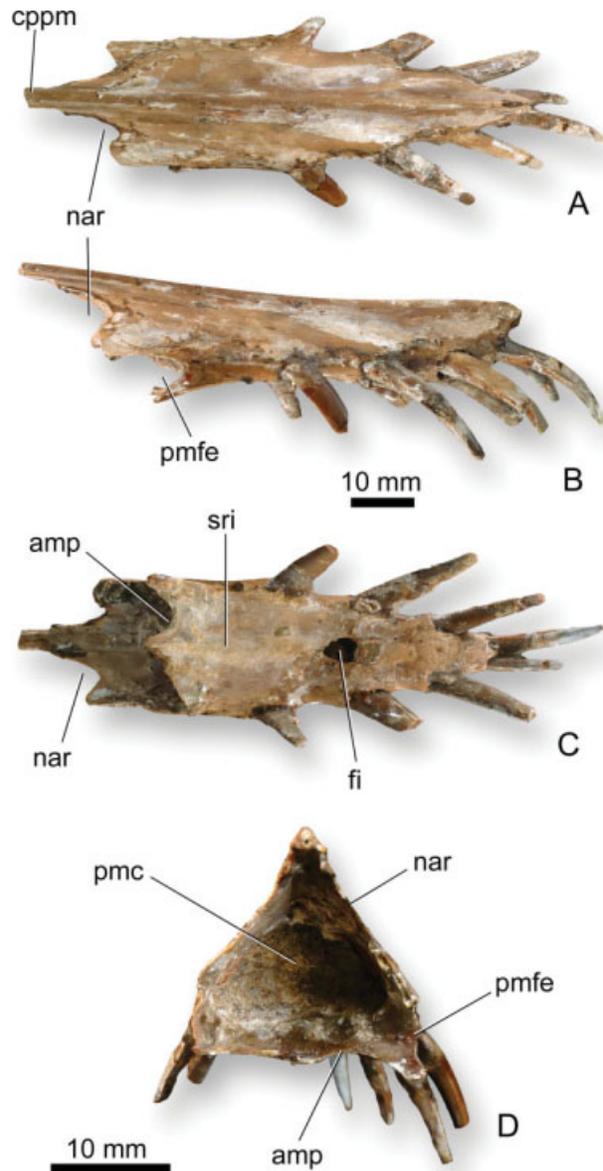


Fig. 3. The premaxilla of the new *Dorygnathus banthensis* specimen in dorsal (A), lateral (B), ventral (C), and caudal (D) view.

Langer (2004) described this paired fenestra in the basal dinosaur *Herrerasaurus ischigualastensis* but the equivalent fenestrae are also found in some other dinosaurs, for example, *Hypsilophodon foxii*, *Allosaurus fragilis*, in rauisuchids such as *Postosuchus kirkpatricki* and in the crocodylomorph *Araripesuchus gomesii* (Witmer, 1997). In *Dorygnathus*, these fenestrae are also craniocaudally elongated but based on the attaching maxillae that formed the caudoventral margin of the fenestrae they were much smaller than the nares (pmfe in Fig. 3B). The premaxilla–maxilla fenestrae are visible in SMNS 50184 (see also Padian, 2008: plate 5, Fig. 5; [the picture is mirrored]) but have never been described. Although still partially filled with sediment, the premaxillary rostrum is hollow to the very end of its rostral terminus

(Fig. 3D). This rostral cavity communicates with the nasal cavity proper, and thus it was most probably invaded by air sacs forming the rostralmost segment of the premaxillary diverticula of the pneumatized antorbital sinus similar to that of birds (Witmer, 1995b; Fig. 11). On the palatal surface of the fused premaxillae there is a tear-shaped, large foramen (5.6 mm × 4.0 mm) situated in the midline at the level of the third tooth pair, which probably corresponds to the *Foramen incisivum* (Fig. 3C, fi). Rostral to this foramen, there is also a pair of smaller foramina that most probably represents nutritive foramina similar to those on the lateral surface of the premaxillary rostrum. Caudal to the *Foramen incisivum*, a low ridge emerges in the midline extending over the caudal portion of the ventral surface of the premaxillary rostrum. The corresponding ridge on the premaxillary rostrum of *Coloborhynchus spielbergi* has been improperly referred to as “palatal sagittal ridge” by Veldmeijer (2003; see later). Because the alveolar rim of *Dorygnathus* is slightly swollen, there is a concave area between the tooth row and the sagittal ridge on both sides. The caudal margin of the ventral surface of the premaxillary rostrum forms the rostral margin of a paired fenestra. Despite being depicted in the holotype of *T. wellnhoferi* by Kellner (1989), this pair of fenestrae has never been described either there or in any other pterosaurs. Rostromedially, these fenestrae are separated by the narrow caudomedial process of the premaxillae and medially probably by the vomers. Caudolaterally, these fenestrae are bordered by the palatal plates of the maxillae (see later). Based on the shape of the emarginating portion of the premaxilla and maxilla, these subspherical fenestrae have a maximum length of about 5 mm and a width of 7 mm.

Maxilla. The well-preserved maxillae (Figs. 4E–G and 5E,F) had contact rostrally to the premaxilla, dorsally to the nasal, and caudally to the jugal. They consist of two major components: the steeply inclined (about 70° relative to the horizontal plane) lateral wall and the extensive, blade-like palatal process (plplm), the latter of which has been identified as the palatine in other pterosaurs [see articles referred to above after Williston (1902)]. This well-developed palatal plate can also be observed on the isolated maxillae of *Dorygnathus* specimens SMNS 50914, SMNS 50184, and SMNS 18969 (Fig. 6). As in birds and crocodylians (Iordansky, 1973; Witmer, 1995b, Figs. 4 and 5), the contralateral palatal plates of the maxillae form a significant portion of the secondary palate (i.e., bony partition separating the nasal and oral cavities). Rostrally, the lateral wall of the maxillae tapers ventrally to a narrow suture with the caudolateral corners of the premaxillary rostrum. The lateral wall of the maxilla has a caudodorsally directed process that forms an oblique suture with the caudal margin of the descending rostral process of the nasal. The rostral margin of the ascending nasal process of the maxilla forms the caudoventral border of the naris. The rostralmost edge of the lateral portion forms the caudoventral border of the premaxilla–maxilla fenestra. The antorbital fenestra is bordered rostrally by the caudal margin of the nasal process and ventrally by the tapering, process-like caudal end of the lateral blade of the maxilla. In ventral view, the palatal plate of the

maxilla has a rather concave area medial to the alveolar rim. In caudal view, approaching the midline the palatal plate turns gently dorsally dorsomedially at an angle of 70° to the vertical plane (dpmx). This dorsomedially projecting process might have formed the base of a thin, bony septum in the sagittal plane that divided the nasal cavity proper into two segments, as in birds (e.g., *A. anser*). This median nasal septum is not preserved in our *Dorygnathus* specimen, but in SMNS 55886 there is a bony lamina visible through the antorbital fenestra that might correspond to the suggested sagittal nasal septum dividing the nasal cavity longitudinally. The true outline of the medial margins of the palatal plates cannot be determined, but they most probably did not connect to each other but might have been separated by the vomer. The rostral margin of the palatal plate forms the caudal border of the undetermined fenestra bordered rostrally by the caudal edge of the palatal portion of the premaxilla. The caudal margin of the palatal plate begins to taper into the jugal process at the level of the ascending nasal process of the lateral wall and extends beyond the last maxillary tooth. The medial part of the posterior margin of the palatal plate articulated with the palatine that formed the lateral border of the centrally positioned choana. The tapering caudal jugal process of the maxilla (jpmx) emarginated rostrally an oval fenestra, which has been referred to as “postpalatal fenestra” (Gasparini et al., 2004) or “palatine fenestra” (Bennett, 2001).

The excellent, three-dimensional preservation of the maxillae of *D. banthensis* provides an opportunity to compare the morphology of the nasal cavity of *Dorygnathus* with that of crocodylians and birds (Figs. 4 and 5). Level with the third maxillary alveolus, there is a vertical lamina orientated caudomedially standing subperpendicular to the lateral wall and the palatal plates (plpmx) of the maxilla. Whereas with its dorsal portion it enhances medially the nasal process of the lateral blade, its base firms the palatal process of the maxilla. Caudomedially, it has a concave margin. The medial margins of the contralateral bony laminae of the maxillae restrict the nasal cavity lateromedially forming a U-shaped constriction for the main air passage (Fig. 4G). In the region where the lateral wall and palatal plate of the maxilla approach each other, this lamina is perforated by a rounded triangular foramen, which connects the antorbital cavity with the rostral part of the nasal cavity (oaof-nc). In Eusuchia, for example, *Crocodylus*, the maxilla bears a longitudinally orientated, vertical bony lamina that separates the lateral caviconchal and postvestibular recesses from the medially positioned nasal cavity proper (Witmer, 1995b; Figs. 4I and 5A, bw). In some Eusuchia, such as *Alligator mississippiensis*, this lamina is perforated caudally by the aperture of the caviconchal recess and rostromedially the postvestibular recess opens into the nasal cavity proper. As *Dorygnathus*, *A. anser* has a vertical maxillary lamina that projects caudomedially and separates the antorbital cavity from the nasal cavity (Fig. 4D,H). It attaches dorsally to the nasal and ventrally to the palatal process of the maxilla (Witmer, 1995b; Fig. 7 refers to this lamina as the palatal process of the maxilla). Whether or not this lamina in *Dorygnathus* is homologous with the longitudinally extending vertical lamina of crocodylians or with the caudomedially directed maxillary lamina of birds is

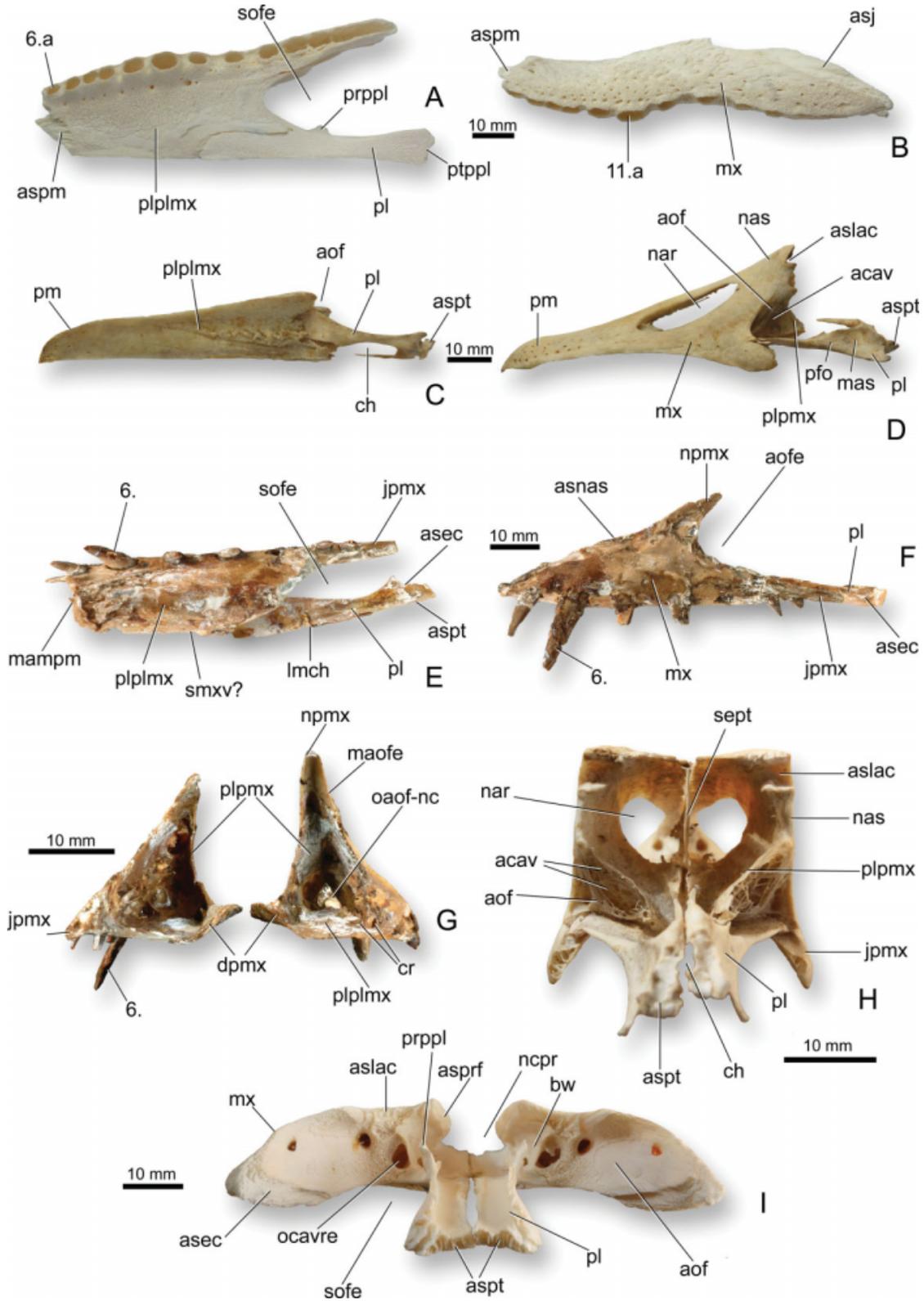


Fig. 4. Comparison of the rostral bony elements of some archosaurs. (A) *Crocodylus* sp. (MTM uncatalogued) left maxilla and palatine in ventral and (B) in lateral view. (C) *Anser anser* (MTM uncatalogued) left face of the rostrum (premaxilla, maxilla, nasal, palatine) in ventral

and (D) in lateral view. (E) *Dorygnathus banthensis* left maxilla and palatine in ventral and (F) in lateral view. (G) *Dorygnathus banthensis* rostrum in caudal view. (H) *Anser anser* rostrum in caudal view. (I) *Crocodylus* sp. rostrum in caudal view.

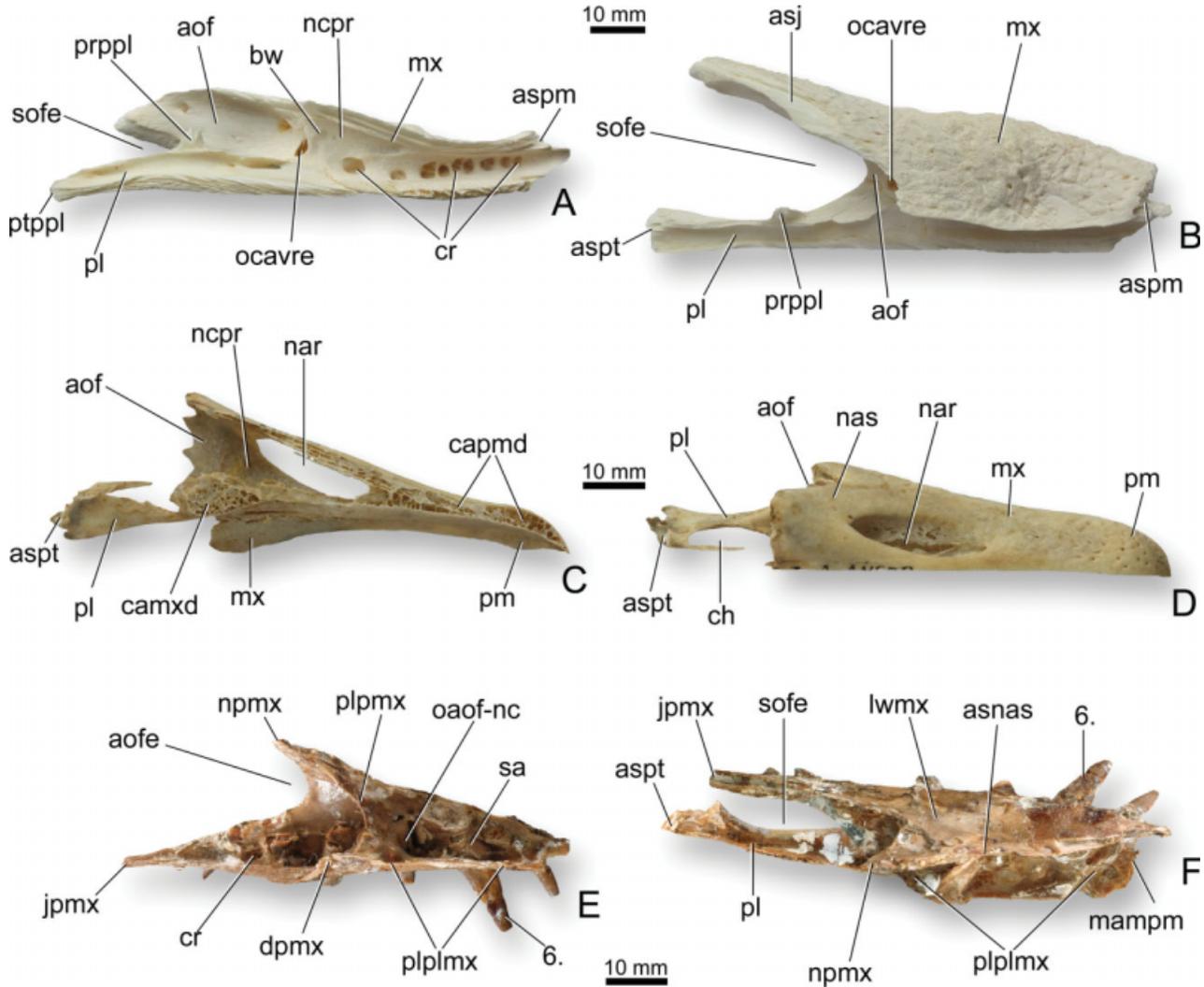


Fig. 5. Comparison of the rostral bony elements of some archosaurs. (A) *Crocodylus* sp. (MTM uncatalogued) left maxilla and palatine in medial view and (B) in dorsal view. (C) *Anser anser* (MTM uncata-

logued) left face of the rostrum (premaxilla, maxilla, nasal, palatine) in medial view and (D) in dorsal view. (E) *Dorygnathus banthensis* left maxilla and palatine in medial view and (F) in dorsal view.

ambiguous, but the similar topography and position between the antorbital and nasal cavities suggest a functional coincidence of the three structures in reinforcing and separating the nasomaxillary cavity. In addition, this bony lamina of *Dorygnathus* could also have partially separated the pneumatic sacs of the antorbital sinus and the nasal cavity proper, and the nasal concha might have had tripartite division similarly to eusuchians and birds (Parsons, 1970; Witmer, 1995b).

In *A. anser* the central part of the ventral process of the maxilla in medial view is thickened surrounding a pneumatic recess the inside of which is reinforced by a network of trabeculae (Fig. 4D,H, acav). This recess is pneumatized by one of the diverticulae of the antorbital sinus (Witmer, 1995b). In *Dorygnathus*, however, this ventral palatal process of the maxilla lacks such a recess. Consequently, this part was not pneumatized in *Dorygnathus*. On the medial surface of the tooth-bearing rim and the lateral maxillary wall, there are interalveolar cecal

recesses (Figs. 4G and 5E, cr), which are not homologous with the cecal recesses on the medial side of the maxilla in *Crocodylus* spp. (Witmer, 1995b: Fig. 12E).

Vomer. Although not preserved in this new specimen of *Dorygnathus*, the distance between the palatal plates of the maxillae suggests that the vomers separated the palatal plates of the maxillae and the choanae, similarly to *Rhamphorhynchus* (CM 11434) and various birds (Witmer, 1995b, 1997).

Palatine. The isolated three-dimensionally preserved maxillae of our specimen and those of several Holzmaden pterosaur specimens mentioned earlier demonstrate that the extended, flat bone in the palate of *Dorygnathus* and probably of other pterosaurs, too, is not the palatine, as suggested by recent authors (e.g., Wellnhofer, 1975, 1978; Kellner, 1989; Bennett, 2001; Padian, 2008) but

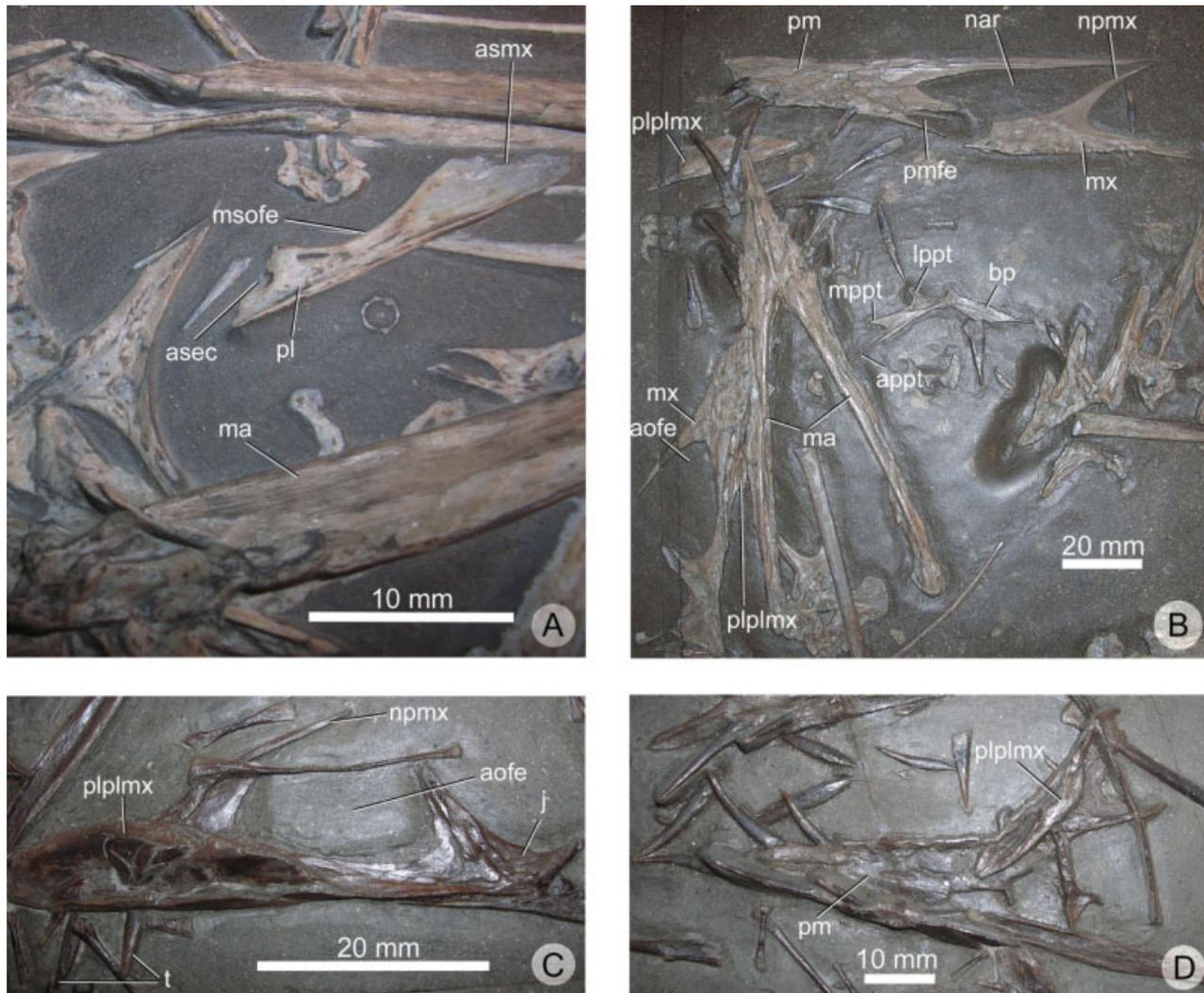


Fig. 6. *Dorygnathus* specimens from Holzmaden. (A) Isolated palatine in SMNS 50914; (B) disarticulated cranial elements of SMNS 50184. Note that the left palatal plate of the maxilla is separated from the maxilla; (C) right maxilla and jugal of SMNS 18969. Note that the palatal plate of the maxilla is compacted onto the lateral wall of the maxilla; (D) premaxilla and left maxilla of SMNS 18969.

the medially extended palatal plate of the maxilla as described by Newton (1888), Seeley (1901), Woodward (1902) and Peters (2000).

In extant crocodylians (e.g., *Crocodylus* sp., MTM uncatalogued), the palatine is an elongate, flat bone that cranially expands into a lateromedially wide maxillary process that forms a scarf joint with the palatal plate of the maxilla. Caudally, the palatine is not as wide as cranially but its dorsoventral thickness increases. Its lateral, slightly concave, smooth margin borders the suborbital fenestra medially (Figs. 4A,I and 5A,B). The palatine of birds (e.g., *A. anser*, MTM uncatalogued, Figs. 4C,D,H and 5C,D) is also longitudinally elongated as in crocodylians. Its cranially directed maxillary process is dorsoventrally compressed. Caudally, the corpus of the palatine is twisted and laterally compressed standing at an angle of about 60° to the maxillary process. The twisted, flat medial face of the palatine forms the lateral wall of the choana. On

the basis of the comparisons with the palatine of extant crocodylians and birds, we identified two long and flat bones as the palatines in *Dorygnathus* (Figs. 4E, 5F, 6, and 7). These bones have a lateromedially wide and dorsoventrally very thin anterior termination that could well have formed a scarf joint with the posterior margin of the palatal process of the maxilla as in crocodiles. Posteriorly, the lateral margin of these bones comes closer to the sagittal plane and forms the concave medial border of the “palatine fenestra” (*sensu* Bennett, 2001), whereas the medial margin remains almost straight. Caudal to this fenestra the bone expands lateromedially and becomes thickened dorsoventrally, as well. Although it retains its dorsoventral thickness up to the caudal end of the bone, lateromedially it constricts again. This terminal portion of the palatines is likely to form the articular surface for the pterygo-ectopterygoid complex (Figs. 4E,F, 6, and 7, asec).

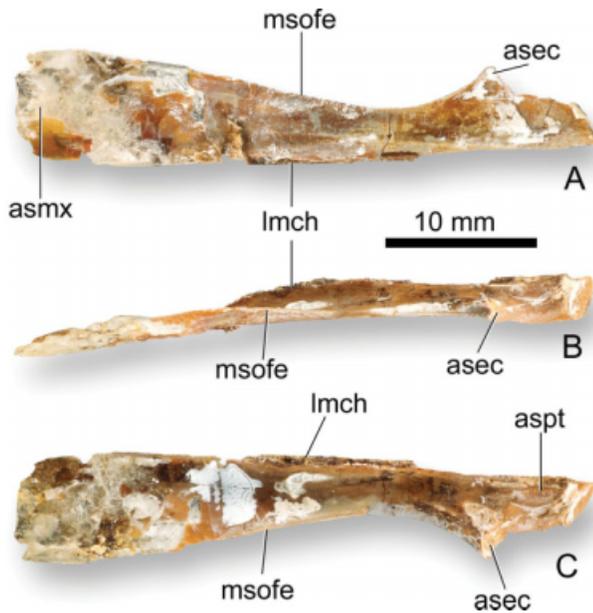


Fig. 7. The left palatine of the new *Dorygnathus banthensis* specimen in ventral (A), lateral (B), and dorsal (C) views.

Reconstruction of the Palate of *Dorygnathus* and Other Pterosaurs

The three-dimensionally preserved *Dorygnathus* specimen provides sufficient evidence to challenge earlier reconstructions and to present a new reconstruction of the palatal morphology of pterosaurs (Fig. 8). Accordingly, the introduction of new terminology has become necessary in some cases.

The rostral portion of the palate is formed by the massive, medially fused palatal processes of the premaxillae. This feature seems to be conservative throughout the Pterosauria. Coincident with the third tooth position this surface bears the unpaired *foramen incisivum*. Although the maxillo-premaxillary suture cannot be observed, most probably a *foramen incisivum* is also present in the holotype of *Tapejara wellnhoferi* (CD-R-080) that was referred to as the “medial foramen” by Wellnhofer and Kellner (1991). Between the premaxilla and maxilla, a pair of oval fenestrae is present, which topographically corresponds to the apertura maxillo-premaxillaris of *Varanus monitor* (Mertens, 1942). Accordingly, here we apply this terminology for these fenestrae in *Dorygnathus*. Again, in the holotype of *T. wellnhoferi* a pair of small, longitudinally oval apertures is visible on the palatal plate of the maxilla that may correspond to the newly described apertura maxillo-premaxillaris of *Dorygnathus*. In *Dorygnathus* and probably in all other pterosaurs as well, the caudal portion of the hard palate is composed of the palatal plates of the maxillae and not of the palatines as previously suggested (e.g., Wellnhofer, 1975, 1978; Kellner, 1989; Bennett, 2001; Padian, 2008). In *Dorygnathus* the caudomedial portion of the palatal plates of the maxillae curves slightly dorsally. The contralateral plates do not meet in the midline but presumably connected to the vomer. The palatines are distinctive, longitudinally elongate bones that cranially form a scarf joint with the caudal margin of the palatal

plates of the maxillae. The choanae are located between the slightly caudally diverging palatines and the caudal third of the medial margin of the palatal plates of the maxillae, which medially might have been separated by the vomer. This position of the choana is homologous with that of extant lepidosaurs and all archosaurs, where the choanae are bordered by the vomer medially, the palatine caudally and laterally, and maxilla laterally and/or rostrally (Witmer, 1995b; Fig. 9). This position of the choanae is seen in all members of Pterosauria where this portion of the palate is preserved and therefore likely applies to all pterosaur taxa.

The lateral margin of the palatines borders a pair of longitudinally orientated suboval fenestrae, which is topographically equivalent with the suborbital fenestra of squamates and crocodylians (Bahl, 1937; Iordansky, 1973), where they are bordered by the palatine medially, maxilla rostrally and laterally, and the pterygoid-ectopterygoid complex caudally. Although not preserved in this *Dorygnathus* specimen, based on *Rhamphorhynchus* the bridge-like ectopterygoid separates the suborbital and pterygo-ectopterygoid fenestrae and connects to the jugal process of the maxilla (jpmx). The relative position and shape of the bridge-like ectopterygoid are fairly conservative in other pterosaurs. Medially, it attaches to the pterygoid-palatinal junction. The pterygoid is triradiate with its base articulating with the basipterygoid caudally. Rostrally, the contralateral medial processes (mppt) converge, meet the vomer, and form the caudomedial borders of the choanae. The cranial process of the pterygoid (appt) is overlaid by the caudomedial portion of the palatine. The lateral process of the pterygoid (lppt) connects to the jugal or the jugal process of the maxilla and forms the caudal margin of the pterygo-ectopterygoid fenestra and the rostromedial margin of the subtemporal fenestra (stf). In other basal pterosaurs such as *Cacibupteryx* (Gasparini et al., 2004) and *Rhamphorhynchus* (NHM R 2786, CM 11434), the pterygoid has the same shape and bony attachments. In more derived taxa (e.g., *Gnathosaurus*, *Coloborhynchus*, *Nyctosaurus*), the medial pterygoid process is shorter, the cranial one is longer, and the lateral process is lost (Fig. 9). Because of the loss of the lateral process of the pterygoid, the pterygo-ectopterygoid fenestra merges into the subtemporal fenestra. In *Dorygnathus* and all other forms the interpterygoid vacuity (ipv) opens between the pterygoids and the rostrally diverging basipterygoids.

DISCUSSION

Main Trends in the Evolution of the Palate of Pterosaurs

With the new reconstruction of the pterosaurian palate, some evolutionary changes can be established for the group (Figs. 10 and 11):

1. With elongation of the rostrum and shortening of the medial process of the pterygoid the choana becomes relatively larger.
2. Along with the former changes (see trend 1) the quadrates become cranially inclined (already in *Rhamphorhynchus*; Fastnacht, 2005) resulting in a significantly smaller interpterygoid vacuity.

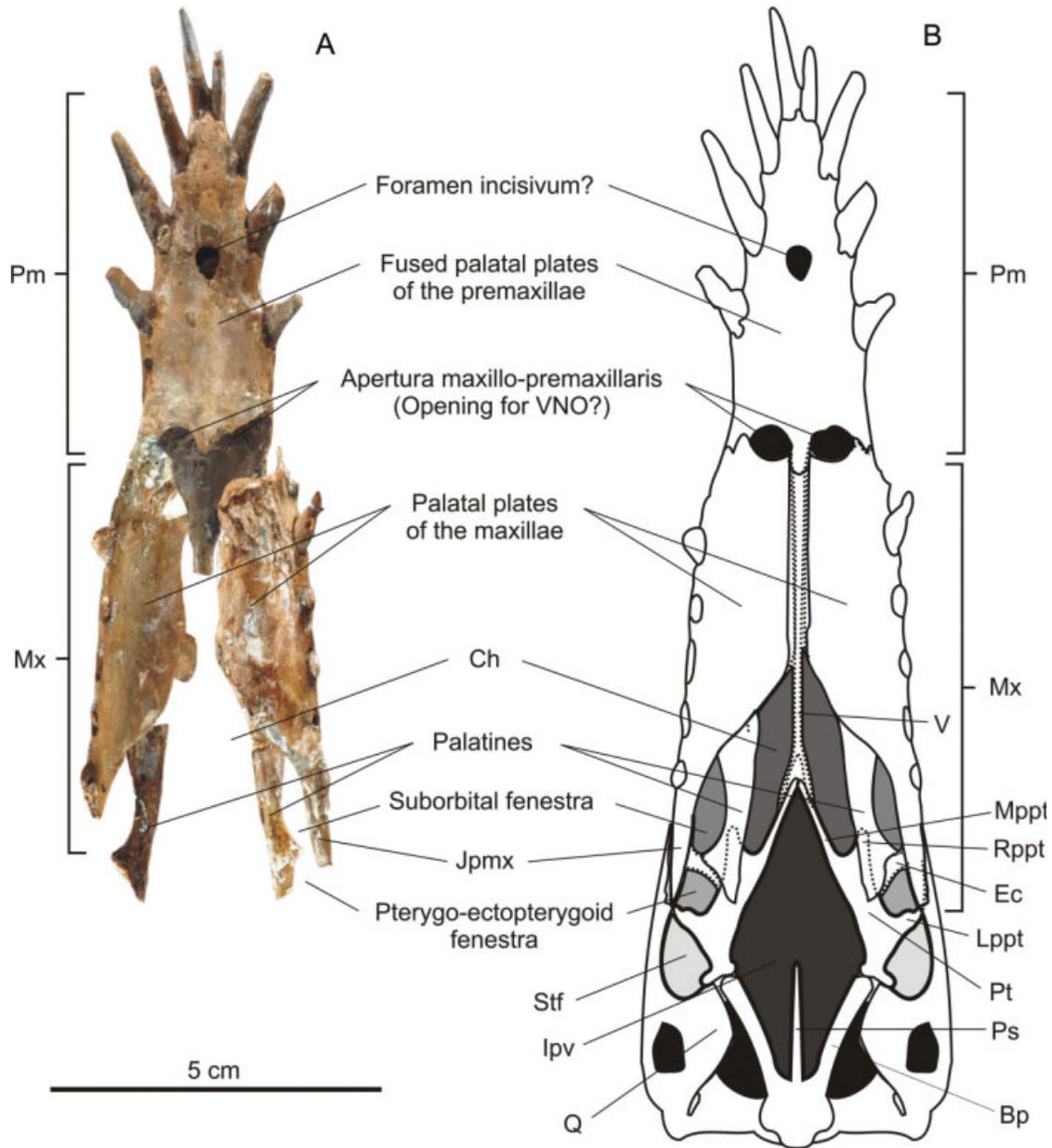


Fig. 8. Reconstruction of the palate of *Dorygnathus banthensis* using the palatal bones preserved in the new and in other specimens (SMNS 18969, 50184, 50914, 51827) (solid lines) and of those yet unknown for *Dorygnathus* (dashed lines). Note the new, yet unde-

scribed (foramen incisivum, apertura maxillo-premaxillaris, palatines), repositioned (suborbital fenestra), or renamed (palatal plate of the maxilla, pterygo-ectopterygoid fenestra) structures of the palate.

3. Although in basal forms the medial pterygoid process projects further rostrally than the rostral one, in more derived taxa the length of the rostral process exceeds that of the medial one.
4. In the short-skulled basal members of the group (*Dorygnathus*, *Cacibupteryx*, *Rhamphorhynchus*) the lateral pterygoid process separates the pterygo-ectopterygoid fenestra from the subtemporal fenestra. The function of the pterygo-ectopterygoid fenestra is unknown. The subtemporal fenestra is the ventral opening of the adductor chamber and forms the passage for the jaw adductors. During the evolution of

pterosaurs, the skull becomes increasingly elongated and these two fenestrae become confluent by the loss of the lateral process of the pterygoid. This increases the dimensions of ventral aperture for the adductor muscles. This change may be the consequence of the need for more powerful adductor muscles that could be the result of elongation and sometimes robustness of the rostrum. In all pterodactyloid specimens available in palatal view, the lateral process of the pterygoid is lost and the two fenestrae are confluent. Thus, here, we suggest that the enlargement of the ventral adductor aperture is a diagnostic feature of

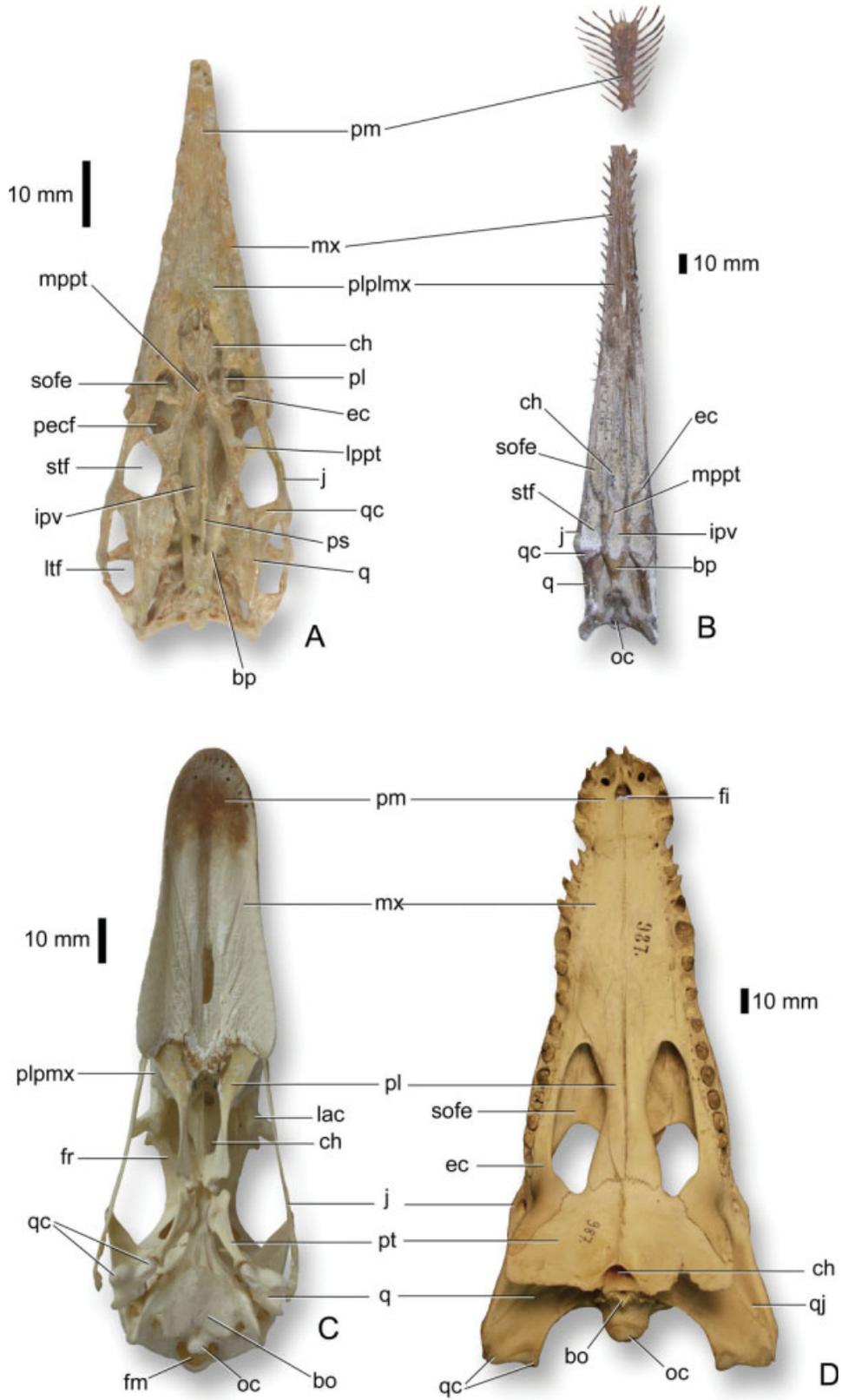


Fig. 9. Comparison of different archosaur skulls in palatal view. (A) *Rhamphorhynchus muensteri*, Carnegie specimen (CM 11434); (B) *Gnathosaurus subulatus* (PTH 1951.84); (C) *Anser anser* (MTM uncatalogued); (D) *Crocodylus* sp. (MTM uncatalogued).

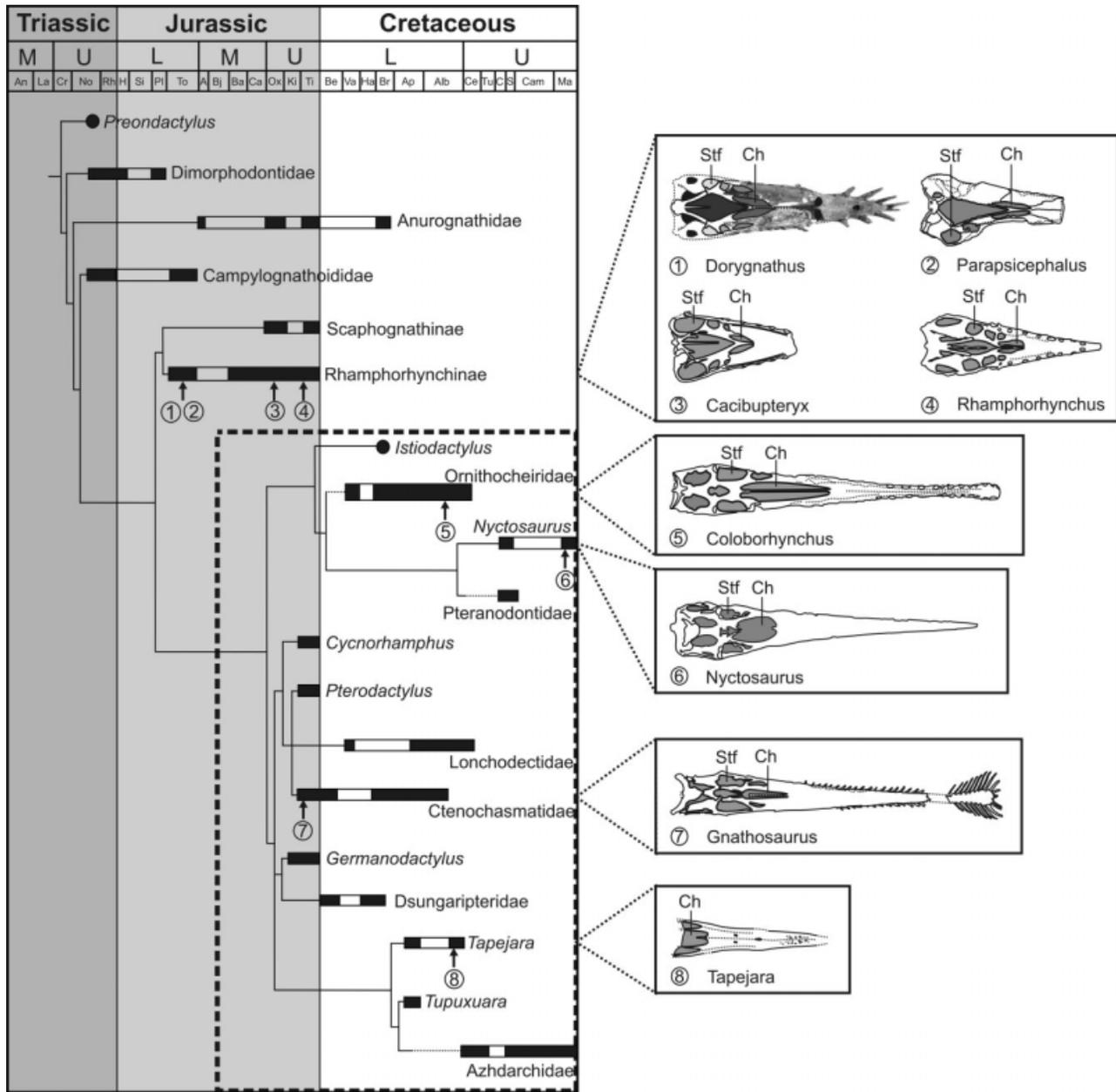


Fig. 10. Pterosaur evolutionary tree with the known stratigraphic ranges of the principal clades modified after Unwin (2003: Fig. 21). Numbers indicate the pterosaurs with three-dimensionally preserved or palatally exposed skulls used in this study.

Pterodactyloidea and a mechanical prerequisite for the evolution of a long rostrum.

Vomeranasa (Jacobson’s) Organ in Pterosaurs?

The identity as well as the function of the newly recognized palatal fenestrae between the premaxilla and maxilla (Figs. 3C and 8, amp) is ambiguous. In crocodilians and birds, no fenestrae can be observed in topographically equivalent regions (Iordansky, 1973, Witmer, 1995b). However, in various squamates (e.g., snakes or

lizards), the incisive foramen or another small fenestra is present between the premaxilla and maxilla, forming the passage for the vomeronasal organ (Jacobson’s organ) into the oral cavity (Parsons, 1959). The vomeronasal organ is a chemoreceptor enclosed within a cartilaginous or partly bony capsule and thus separated from the main olfactory epithelium (Keverne, 1999; Hillenius, 2000). In mammals, it is mainly used to detect intraspecific pheromones; however, in some animals, such as snakes, it also mediates the trailing of prey and food detection on an olfactory basis (Halpern, 1987; Døving and Trotier, 1998).

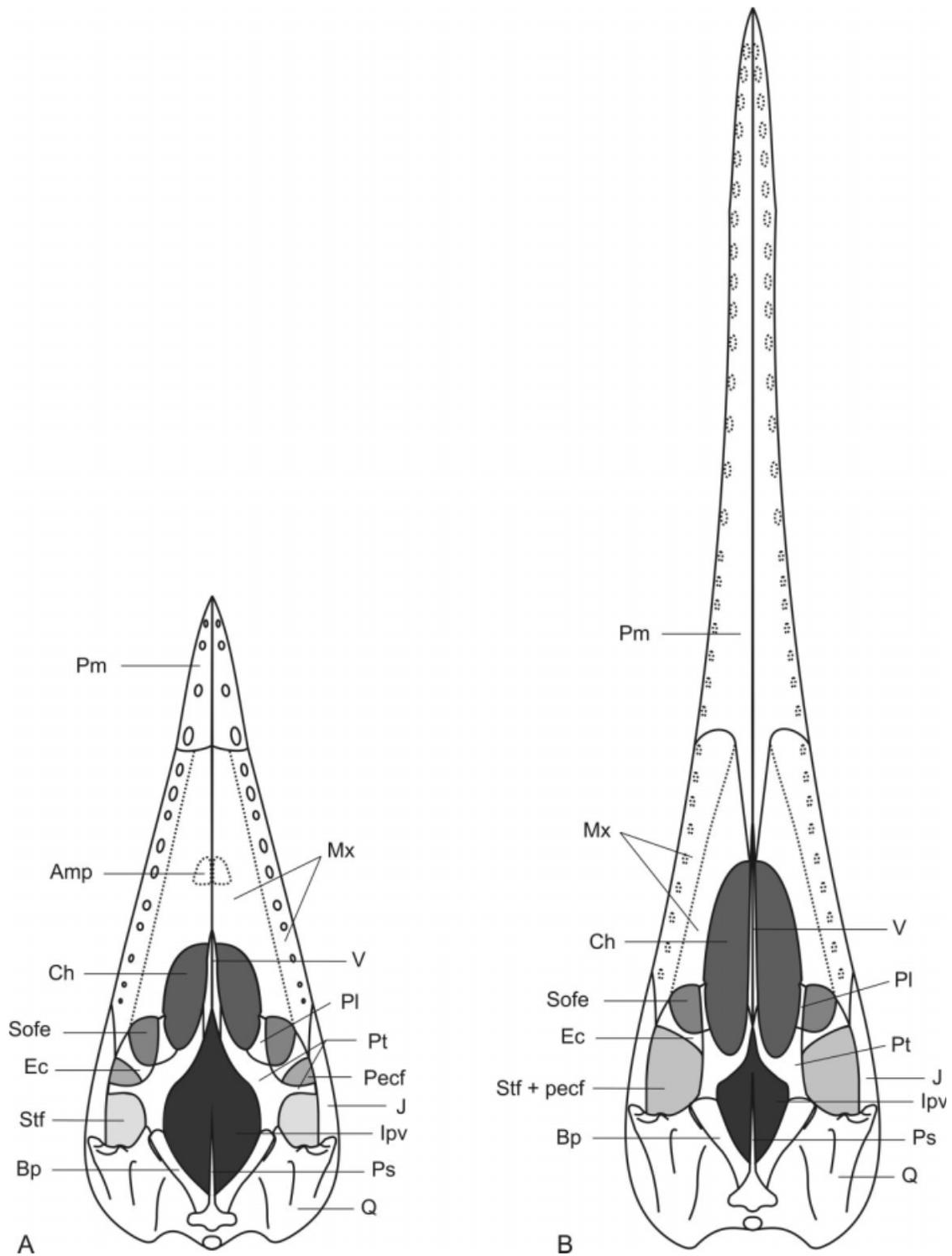


Fig. 11. The general evolutionary trends revealed in the palate architecture of different pterosaur taxa demonstrated by the line drawings of two hypothetical, (A) basal and (B) pterodactyloid pterosaurs. Note: (1) the elongated rostrum and the consequently enlarged choana, (2) the loss of the lateral process of the pterygoids and thus the enlarged subtemporal fenestra (adductor chamber), (3) the inclina-

tion of the quadrates and the consequent decrease in the size of the interpterygoid vacuity in the palate of the hypothetical pterodactyloid pterosaur (B) compared to the same structures of the basal hypothetical pterosaur (A). The apertura maxillo-premaxillaris (amp) has a dashed outline because it has not proven to be present in the palate of other known basal taxa.

In extant crocodylians and birds, there is also evidence for the presence of the vomeronasal organ at least in early ontogenetic stages (e.g., Meek, 1893; Parsons, 1970). Parsons (1959: 178) describes that in *Crocodylus* embryos, the vomeronasal organ is still present and has an aperture opening ventrally. In later ontogenetic stages, however, there is no aperture for the vomeronasal organ in the secondary palate. Parsons (1959: 181) concluded that “crocodylians and the ancestors of birds (and presumably their fossil relatives including dinosaurs and others) lost Jacobson’s organ completely”. Gauthier et al. (1988) argued that the absence of the vomeronasal organ in archosaurs is a secondary development. However, using EPB method, Senter (2002) investigated phytosaur skull morphology and suggested that all extinct archosaurs lacked the vomeronasal organ system. According to Hillenius (2000), the vomeronasal organ has a close morphological association with the septomaxilla in squamates, minor association in some urodeles, *Sphenodon*, and dasypodids, but in most tetrapods its presence correlates with the presence of the vomer. Similar to other archosaurs, there is no evidence for a septomaxilla in pterosaurs. Thus, if this organ was present—a unique case among archosaurs—it should have been associated with the dorsal surface of the vomer, and the receptors of the duct of the organ should have been positioned in the nasal cavity with a direct exit into the oral cavity through the maxillo-premaxillary aperture.

Another option for the function of the maxillo-premaxillary aperture would be the lightening of the skull. However, the very thin rostral margin of the maxilla, its rostral position being in the vicinity of the largest rostral teeth, and its relatively small size (especially in *Tapejara*) do not support this hypothesis. There is no trace of a maxillo-premaxillary aperture in ornithocheirids, *Dsungaripterus*, *Pteranodon*, *Nyctosaurus*, and probably in other large taxa, either. This indicates that the skull could increase in size and weight without increasing or even possessing this aperture.

The potential of these fenestrae for belonging to the vomeronasal organ system cannot be excluded nor supported by any physical evidence. Thus, the function of this pair of apertures remains unclear.

CONCLUSIONS

The three-dimensionally preserved specimen of the Early Jurassic basal pterosaur *D. banthensis* provides new insight into the morphology of the pterosaurian palatal bones and helps to clarify some aspects of the nasal cavity system. The foregoing comparative study demonstrates that the generally accepted reconstructions of the palate of pterosaurs, according to which the hard palate is mainly formed by the palatines, are incorrect. The maxilla of the new specimen shows that the hard palate comprises the palatal plate of the maxilla and not the palatine. The palatal plate of the maxilla forms the rostral and rostrolateral margin of the choanae similarly to that of most turtles, lepidosaurs, and all other archosaurs. The new specimen of *Dorygnathus* also provides evidence for the presence of a distinct palatine bone that shows morphological and topographical similarities with that of crocodylians and birds, respectively. Being attached to the caudal portion of the palatal plate of the maxilla, it borders the choanae laterally thus revealing the homologous nature of the

(primary) choana in pterosaurs, all other archosaurs, and lepidosaurs. The fenestra lateral to the palatines, medial to the jugal process of the maxilla, and rostral to the ectopterygoid referred to as the “postpalatal” or “palatal fenestra” is topographically equivalent with the suborbital fenestra of crocodylians and lizards. In *Dorygnathus* and some other basal pterosaurs (*Cacibupteryx*, *Rhamphorhynchus*), an additional fenestra, the pterygo-ectopterygoid fenestra, is present between the suborbital and the subtemporal fenestrae (adductor chamber). This fenestra is bordered rostrally by the ectopterygoid and caudally by the lateral process of the pterygoid.

Similar to birds, the antorbital cavity of *Dorygnathus* was at least partially separated from the nasal cavity proper by the palatal processes of the maxilla but, in contrast to birds, the palatal plate of the maxilla was not pneumatized.

The new interpretation of the palate also reveals some evolutionary changes of the palatal construction within Pterosauria. One of which is that the lateral pterygoid process is completely reduced in advanced forms, probably in all Pterodactyloidea. Consequently, the pterygo-ectopterygoid fenestra merged with the subtemporal fenestra increasing considerably the relative size of the adductor chamber. This would have allowed for more developed mandibular adductor muscles resulting in an increase of occlusion power. A second evolutionary trend is the change of the size of the choana relative to the interpterygoid vacuity. In basal forms, a pair of small choanae was present rostral to a huge interpterygoid vacuity. In more derived members of the group the interpterygoid vacuity became strongly reduced along with the anterior inclination of the quadrates, whereas the choanae increased in size. This exceptionally well-preserved specimen of *Dorygnathus* furthermore reveals a hitherto unknown pair of fenestrae caudal to the incisive foramen, which opens at the palatal contact of the premaxilla-maxilla and might have served as the opening for the vomeronasal organ. However, evidences on this issue neither *pro* nor *contra* can be lined up.

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LITERATURE CITED

- Arthaber G. 1919. Studien über Flugsaurier auf Grund der Bearbeitung des Wiener Exemplares von *Dorygnathus banthensis* Theod. sp. Denkschr Akad Wiss Wien math-nat Kl 97:391–464.

- Bahl KN. 1937. Skull of *Varanus monitor* (Linn.). *Rec Ind Mus* 39:133–174.
- Bennett SC. 1996. The phylogenetic position of the Pterosauria within the Archosauromorpha. *Zool J Linn Soc* 118:261–308.
- Bennett SC. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. I. General description of osteology. *Palaeontographica A* 260:1–112.
- Bennett SC. 2007. A second specimen of the pterosaur *Anurognathus ammoni*. *Paläontol Z* 81:376–398.
- Benton MJ. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philos Trans R Soc Lond B Biol Sci* 354:1423–1446.
- Broili F. 1919. *Ctenochasma gracile* Oppel. *Sond Geog Jahresheften* 29/30:299–309.
- Busbey AB. 1994. The structural consequences of skull flattening in crocodylians. In: Thomason JJ, editor. *Functional morphology in vertebrate paleontology*. New York: Cambridge University Press. p 173–192.
- Coates MI. 1993. Ancestors and homology the origin of the tetrapod limb. *A Biotheor* 41:411–424.
- Døvning KB, Trotter D. 1998. Structure and function of the vomeronasal organ. *J Exp Biol* 201:2913–2925.
- Fastnacht M. 2005. Jaw mechanics of the pterosaur skull construction and the evolution of toothlessness. PhD Thesis. Johannes Gutenberg-Universität, Mainz.
- Gasparini Z, Fernandez M, De La Fuente M. 2004. A new pterosaur from the Jurassic of Cuba. *Palaeontology* 47:919–927.
- Gauthier JA, Kluge AG, Rowe T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209.
- Halpern M. 1987. The organization and function of the vomeronasal system. *Ann Rev Neurosci* 10:325–362.
- Hillenius WJ. 2000. Septomaxilla of non-mammalian synapsids: soft-tissue correlates and a new functional interpretation. *J Morphol* 245:29–50.
- Hone DWE, Benton MJ. 2007. An evaluation of the phylogenetic relationships of the pterosaurs to the archosauromorph reptiles. *J Syst Palaeontol* 5:465–469.
- Hone DWE, Benton MJ. 2008. Contrasting supertree and total-evidence methods: the origin of the pterosaurs. *Zitteliana B* 28:35–60.
- Hooley RW. 1913. On the skeleton of *Ornithodesmus latidens*; an ornithosaur from the Wealden Shales of Atherfield, Isle of Wight. *Quart J Geol Soc* 69:372–422.
- Iordansky NN. 1973. The skull of the Crocodylia. In: Gans C, Parsons S, editors. *Biology of the reptilia*, Vol. 4. New York: Academic Press. p 201–262.
- Kellner AWA. 1989. A new edentate pterosaur of the Lower Cretaceous from the Ararape Basin, Northeast Brazil. *An Acad Bras Cien* 61:439–446.
- Keverne EB. 1999. The vomeronasal organ. *Science* 286:716–720.
- Langer MC. 2004. Basal Saurischia. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. 2nd ed. Los Angeles: University of California Press. p 25–46.
- Marsh OC. 1884. Principal characters of American Cretaceous Pterodactyls. I. The skull of *Pteranodon*. *Am J Sci* 21:423–427.
- Mayr FX. 1964. Die naturwissenschaftlichen Sammlungen der Philosophisch-Theologischen Hochschule Eichstätt. *Festschrift 400 Jahre Collegium Willibaldinum Eichstätt*. p 302–334.
- Meek A. 1893. On the occurrence of a Jacobson's organ, with notes on the development of the nasal cavity, the lachrymal duct, and the Harderian gland in *Crocodylus porosus*. *J Anat Physiol* 27:151–160.
- Mertens R. 1942. Die Familie der Warane (Varanidae). Zweiter Teil: Der Schädel. *Abh Senckenbergischen Naturforschenden Ges* 465:117–234.
- Newton ET. 1888. On the skull, brain and auditory organ of a new species of Pterosaurian (*Scaphognathus purdoni*), from the Upper Lias near Whitby, Yorkshire. *Philos Trans R Soc Lond B Biol Sci* 179:503–537.
- Osmólska H. 1985. Antorbital fenestra of archosaurs and its suggested function. In: Duncker HR, Fleisher G, editors. *Vertebrate morphology*. New York: Gustav Fischer Verlag. p 159–162.
- Padian K. 2008. The Early Jurassic pterosaur *Dorygnathus bathensis* (Theodori, 1830). *Special Papers Paleontol* 80:1–64.
- Parsons TS. 1959. Studies on the comparative embryology of the reptilian nose. *Bull Mus Comp Zool* 120:101–277.
- Parsons TS. 1970. The nose and Jacobson's organ. In: Gans C, Parsons S, editors. *Biology of the reptilia*, Vol. 2. New York: Academic Press. p 99–191.
- Peters D. 2000. A re-examination of four prolacertiforms with implications for pterosaur phylogenies. *Riv Italiana Paleontol Strat* 106:293–336.
- Seeley HG. 1901. *Dragons of the Air: an account of extinct flying reptiles*. New York: Appleton & Co.; London: Methuen & Co.
- Senter P. 2002. Lack of a pheromonal sense in phytosaurs and other archosaurs, and its implications for reproductive communication. *Paleobiology* 28:544–550.
- Sereno P. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *J Vertebrate Paleontol Mem* 2:1–53.
- Unwin DM. 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut E, Mazin J-M, *Evolution and Palaeobiology of Pterosaurs*. *Geol Soc Spec Publ*, 217:139–190.
- Veldmeijer AJ. 2003. Description of *Coloborynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian Lower Cretaceous of Brazil. *Scri Geol* 125:35–139.
- Veldmeijer AJ. 2006. Toothed pterosaurs from the Santana Formation (Cretaceous; Aptain-Albian) of northeastern Brazil. A reappraisal on the basis of newly described material. PhD Thesis. Utrecht University. p 269.
- von Huene F. 1914. Beiträge zur Kenntnis des Schädels einiger Flugsaurier. *Geol Paläontol Abh Neue Folge* 13:57–65.
- Wellnhofer P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. *Abh Bayerischen Akad Wiss Neue Folge* 141:1–133.
- Wellnhofer P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. *Allgemeine Skelettmorphologie*. *Palaeontographica A* 148:1–33.
- Wellnhofer P. 1978. *Handbuch der Paläoherpetologie*. Teil 19. Pterosauria. Stuttgart: Gustav Fischer Verlag.
- Wellnhofer P. 1987. New crested Pterosaurs from the Lower Cretaceous of Brasil. *Mitt Bayerischen Staatsammlung Paläontol Hist Geol* 27:175–186.
- Wellnhofer P. 1991a. The illustrated encyclopedia of pterosaurs. London: Salamander Books Ltd.
- Wellnhofer P. 1991b. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Ararape, Brasilien. *Palaeontographica A* 215:43–101.
- Wellnhofer P, Kellner AWA. 1991. The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Ararape Basin, Northeastern Brazil. *Mitt Bayerischen Staatsammlung Paläontol Hist Geol* 31:89–106.
- Williston SW. 1902. On the skull of *Nyctodactylus*, an Upper Cretaceous pterodactyl. *J Geol* 10:520–531.
- Witmer LM. 1995a. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason JJ, editor. *Functional morphology in vertebrate paleontology*. New York: Cambridge University Press. p 19–33.
- Witmer LM. 1995b. Homology of facial structures in extant Archosaurs (birds and crocodylians), with special reference to paranasal pneumaticity and nasal conchae. *J Morphol* 225:269–327.
- Witmer LM. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Mem Soc Vertebrate Paleontol* 17:1–73.
- Witmer LM, Chatterjee S, Franzosa J, Rowe T. 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behavior. *Nature* 425:950–953.
- Witmer LM, Martin LD. 1987. The primitive features of the avian palate, with special reference to Mesozoic birds. In: Mourer-Chauviré C, editor. *L'Evolution des Oiseaux d'Après le Temoignage des Fossiles* ed. Lyon: Université Claude-Bernard. p 21–40.
- Witmer LM, Ridgely RC. 2008. The paranasal air sinuses of predatory and armored dinosaurs Archosauria: Theropoda & Ankylosauria and their contribution to cephalic structures. *Anat Rec* 291:1362–1388.
- Woodward AS. 1902. On two skulls of Ornithosaurian *Rhamphorhynchus*. *Ann Mag Nat Hist* 9:1.
- Young CC. 1964. On a New Pterosaurian from Sinkiang, China. *Vertebr Pal* 8:221–225 (Part translated into English).

Supplementary data

In the light of the anatomical description of the general palate constitution in pterosaurs we are able to discuss the earliest concepts and compare them to the more recent general reconstruction. The first complete palate reconstruction provided by Marsh (1884) is not considered in the following review as it lacked bone identification. Consequently we concentrate on the different identification and interpretations of the palatal bones and fenestrae rostral to the quadrates by later authors. In a summary we give the possible synonyms of bones and fenestrae and shed light on the different interpretations of the same structures. The old, sometimes ambiguous names applied to the structures in the original papers are in quotation marks.

Newton's work on the holotype of *Parapsicephalus purdoni* (originally referred to as "*Scaphognathus*" *purdoni* in Newton, 1888), a significant portion of which is a natural endocast of the skull, goes into details concerning the composition of the palate (see fig. 1, A). He reports that the rostralmost portion of the rostrum is formed by the premaxillae (pm) which are firmly united and form the rostral part of the hard palate. He argued that the united palatal processes of the premaxillae reach the "internal nares" (in, or choanae) caudally. A low ridge in the midline contacts the vomer caudally, which has been described as being a triangular plate. He continued: "The bony palate extends backwards for some distance on the outer side of the internal nares; but it seems probable that the portion behind the line seen passing obliquely forwards and outwards from each of these apertures may be a palatal portion of the maxilla." Furthermore he indicated that the palatine (pl) and the pterygoid (pt) fuse to each other to such a degree that there is no visible suture between them and their combination forms the so-called "pterygo-palatine bar". Despite the lack of suture lines, he considered the rostral portion of the bar, which forms the caudal margin of the "internal

nares”, as the palatine and the caudal portion as the pterygoid. Considering it as one element it has an “inner and outer portion” with the inner rod extending rostromedially to the vomer and the outer portion passing rostrally and joining the palatal process of the maxilla (mx?). According to Newton’s reconstruction, the choana is enclosed medially by the vomer, rostrolaterally by the maxilla and caudally by the palatine. At the caudal portion of the pterygoid where it comes close to the maxilla the “transpalatine” (“transverse bone” *sensu* Goldfuss, 1831), connects it to the maxilla. Although these bones are preserved only as impressions, Newton assumed that the quadrate was fused to the “pterygo-palatine bar”, since there was no indication of a division between the bones in their impression. Except for the choana there is no other palatal fenestra discussed in his description.

Seeley (1901) provided a line drawing of the restored palate of “*Campylognathus*” (*Campylognathoides*) with very incomplete legend. In the description he emphasized the lack of distinct appearance of the palatal bones, however, he noted that the hard palate is formed by the “intermaxillary” and maxillary bones, that the vomer is in the midline contacting the hard palate with the palatines at its sides and that the main body of the V-shaped bone contacting the quadrates is formed by the pterygoids.

Woodward (1902) examined a palatally exposed *Rhamphorhynchus* “*gemmingi*” (NHM R-2786) specimen (see fig. 1, C). His interpretation of the palatal bones was similar to that of Newton (1888). He stated that the palatal portions of the premaxillae are fused, plate-like and form the rostral border of the choanae. He also noted that the palatal blade of the maxilla, which rostrally attached to the premaxilla and caudally was followed by the palatine, lies in the same plane as the premaxillary roof of the mouth and forms the lateral boundary of the “posterior narial fossa” (choana). He described the palatine as being a small element that is slightly thickened where it abuts upon the pterygoid and reported a small “infraorbital vacuity” (iov) caudal to the palatine. This “infraorbital vacuity” is separated from the

“infratemporal vacuity” (itv) by the “transverse bone” (x), which bridges the gap between the pterygoid and the maxilla. The pterygoids converge rostrally, bend upwards to the roof of the “posterior narial fossa” with their rostralmost portion presumably meeting the vomer, which is not visible in this specimen. He also reported a large interpterygoid vacuity (ipv) between the pterygoids and stated that this specimen shows the essentially reptilian aspects of the palate in this genus with moderate differences in size of the premaxilla and the braincase.

Williston (1902) described a palatally exposed specimen of the derived pterodactyloid *Nyctosaurus gracilis* (referred to as “*Nyctodactylus*” in the original paper) (see fig. 1, H).

Following previous authors Williston stated that the premaxillae comprise the whole rostral portion of the beak. However, the more caudally positioned palatal bones have been interpreted either incompletely or quite differently from those of the former descriptions.

First, Williston did not specify the relative position or shape of the maxilla: on the one hand he explained that only the caudal portion of the maxilla is examinable; on the other hand figure 1. of Plate II. in his work indicates that the maxilla is only composed of the lateral rim of the beak in palatal view. He made no attempt to estimate the rostrocaudal extent of the maxilla. He described the palatine as a long, narrow bone articulating medially to the pterygoid and laterally to the maxilla by a long suture. The rostral fusion with the maxilla or vomers, due to the lack of suture lines, was considered to be indeterminable. Nevertheless, figure 1. of Williston’s work (1902) refers to the palatine as being the bony plate extending topographically in the same position as the “palatal portion” or “palatal blade of the maxilla” defined by Newton (1888) and Woodward (1902), respectively. Thus Williston’s new interpretation of this structure is consistent with the recent reconstructions but contradicts those of Newton (1888) and Woodward (1902). The pterygoids are firmly united with the quadrate and, as described by Williston, have also two processes, but the medial processes, although they converge, do not meet the vomer. The rostral processes articulate first with the

ectopterygoids laterally, then by a long suture with the blade-like bone identified by Williston and by the recent authors as the palatine. Some aspects of these differences compared to the description of Woodward (1902) have been noted by Williston himself, who emphasized that, in contrast to the suggestion of Woodward, the medial processes of the pterygoids do not unite the vomer in "*Nyctodactylus*" and that the upward bending portion of the process is actually the "inner side" of the palatines. The interpterygoid vacuity, however, was described in the same way. The ectopterygoids ('ec') are similarly positioned as the "transpalatine" of Newton (1888) and the "transverse bone" of Woodward (1902) being placed between the pterygoid and the maxilla. Its rostral and caudal margins form the caudal and rostral border of the "posterior palatine vacuity" (ppv) and "pterygo-jugal vacuity" (z), respectively.

Huene (1914) and Broili (1919) provided more palatal reconstructions in their comparative anatomical work on the skull of pterosaurs and revised among other specimens those examined by Newton (1888), Woodward (1902) and Williston (1902). Confirming Williston's (1902) concept for *Nyctosaurus*, Huene (1914) interpreted the bony plate lateral to the tooth-bearing rim of the maxilla in *Parapsicephalus* and *Rhamphorhynchus* as the palatine and hereby challenged the original idea of Newton (1888) and Woodward (1902) who both identified the same element as the palatal process of the maxilla. Similarly, in Huene's new line drawing of the same *Nyctosaurus* specimen with more detailed caption and indication of the suture lines between the bones, the limit of the maxilla and palatine is distinct and corresponds to the recent reconstructions with the maxilla forming only the long, narrow margin of the beak and the palatine being the blade-like bone adjacent to the maxilla and merging rostrally with the palatal blade of the premaxilla. Other than that, Huene's restorations were in accordance with those of the original authors.

Arthaber (1919) provided reconstructions of the palate of four different pterosaur taxa: *Dorygnathus banthensis*, *Parapsicephalus purdoni*, *Scaphognathus crassirostris* and

Rhamphorhynchus “*gemmingi*”. The reconstructions of *Parapsicephalus* and *Rhamphorhynchus* were based on the actual palatally exposed specimens of Newton (1888) and Woodward (1902) and their drawings had been modified by Arthaber. The palate restorations of the remaining two genera were based mainly on laterally exposed skulls (the “Vienna specimen” of *Dorygnathus* and the holotype of *Scaphognathus crassirostris*), in which, however, some scattered palatal bones are recognizable. In his work Arthaber identified the usual palatal bones for the four genera that had already been described by the previous authors, except for one element, the “columella” which he found in front of the articular head of the quadrates in the Vienna specimen of *Dorygnathus*. Nevertheless Arthaber reconstructed this element only in the palatal view of *Scaphognathus*, where he placed it between the base of the pterygoids and the jugal close to the quadrate. The name “columella” in anatomy refers to the hearing bones in the middle ear of reptiles and birds that occur between the tympanic membrane and the vestibule fenestra where they conduct the impulses of resonance from the outer to the inner ear (Kardong, 2002). Except in Arthaber’s (1919) work such an element has never been reported preserved in pterosaurs. Padian (2008), who gave a review of *Dorygnathus* specimens from all over the world, revised the “Vienna specimen”, as well, still he did not refer to any element that could have belonged to the middle ear. Concerning the identification of the remaining palatal bones he followed the concept of Huene (1914) and thus Arthaber’s interpretation of the palatine also fits in with the recent reconstructions of the palate of pterosaurs. As for the fenestrae Arthaber identified four distinct vacuities on the palatal surface of *Rhamphorhynchus* “*gemmingi*”: the choana bordered by the palatine and the vomer; the “posterior palatal foramen” emarginated rostromedially by the palatine, caudally by the “transverse bone” and medially by the pterygoid; the “inter-ptyerygo-jugal foramen” that is separated from the “posterior palatal foramen” by the “transverse bone” and the interptyerygoid vacuity.

Due to the relatively numerous synonyms applied to the same structures by the different authors, the former restorations are confusing and hard to interpret. While summarizing the synonyms, the inconsistency in the reconstruction of the palate of pterosaurs becomes striking. Newton's (1888) "transpalatine", for instance, corresponds to Goldfuss' (1831), Woodward's (1902), Huene's (1914) and Arthaber's (1919) "transverse bone", which were certainly intended as synonyms for the ectopterygoid. However, based on its relative position, their "transverse bone" corresponds to the maxillary or lateral process of the pterygoid in recent reconstructions (Mayr, 1964, Wellnhofer, 1975, 1978, 1987; Kellner, 1989; Bennett, 2001; Gasparini et al. 2004). The "internal nares" (Newton, 1888) and "posterior narial fossa" (Woodward, 1902) are equivalents of the choanae. The "intermaxilla" of Seeley (1901) clearly refers to the premaxilla. The main differences in the reconstructions of these earlier authors are mostly the result of the different interpretation of the constituting bones of the hard palate. Besides the palatal processes of the premaxillae is the hard palate mainly formed by the palatal process of the maxillae as described by Newton (1888) and Woodward (1902) or rather by the palatine bones as interpreted by Williston (1902) and all recent authors since then? The different interpretations of the maxillae and palatines and consequently those of the remaining bones and fenestrae undermine the concept of the palate reconstruction of pterosaurs, and restrict the potential of the palatal features for being used as characters in cladistics. While there is generally an agreement on which fenestrae should be regarded as the choanae or the interpterygoid vacuity, the definition of the other fenestrae based on their relative position to the bones emarginating them is more confusing. The rostralmost fenestra after the choanae has been described by Williston (1902) in *Nyctosaurus* and by Arthaber (1919) in his taxa as the "posterior palatine vacuity/foramen", the relative position of which was defined as being caudal to the palatine and rostral to the ectopterygoid. However, according to the relative position of this fenestra, it contradicts Woodward's (1902) concept,

who identified the fenestra caudal to *his* palatines as “infraorbital vacuity” the caudal margin of which was formed by the “transverse bone”. The “posterior palatine vacuity” of Williston (1902) apparently corresponds to the postpalatal (*sensu* Wellnhofer, 1970, Gasparini *et al.* 2004) or palatine fenestra (*sensu* Bennett, 2001), whereas the term “infraorbital vacuity” has been used by Gasparini (2004) for the fenestra caudal to the palatal fenestra from which it is rostrally separated by the ectopterygoid and caudally it is bordered by the lateral process of the pterygoid. The palatal fenestra was mentioned neither by Woodward (1902) nor by Huene (1914), who worked on the Carnegie specimen of *Rhamphorhynchus* (CM11434). However, if Woodward’s “transverse bone” corresponds to the lateral process of the pterygoid and not to the ectopterygoid, the assignment of the fenestrae being the infraorbital vacuity is equivalent to that of the infraorbital fenestra of Gasparini *et al.* (2004). The last fenestrae to consider are the “infratemporal fenestra” of Woodward (1902) and the “pterygo-jugal vacuity” or “inter-pterygo-jugal foramen” of Williston (1902) and Arthaber (1919), respectively. Woodward and Arthaber both used their terms to describe the fenestra caudal to *their* “transverse bone”. However, if their “transverse bone” is indeed the lateral process of the pterygoid, these fenestrae correspond to the subtemporal fenestra of Gasparini (2004). The “pterygo-jugal vacuity” of *Nyctosaurus* seems to refer to the subtemporal vacuity of Bennett (2001) bordered rostrally by the ectopterygoid and caudally by the quadrate.

		Authors						
S	Newton (1888)	Seeley (1901)	Woodward (1902)	Williston (1902)	Huene (1914)	Arthaber (1919)	recent authors (e.g Gasparini et al. 2004)	<i>new interpretation</i>
	y	transpalatine	∅	transverse bone	∅	transverse bone	transverse bone	lateral process of pterygoid
n	internal nares	∅	posterior narial fossa	∅	internal nares	choanae	choanae	choanae
o	premaxilla	intermaxi lla	premaxilla	∅	premaxilla	premaxilla	premaxilla	premaxilla
n	palatal process of maxilla	maxilla	palatal process of maxilla	palatine	palatine	palatine	palatine	palatal plate of maxilla
y	∅	∅	∅	posterior palatine vacuity	∅	posterior palatine fenestra	postpalatal/palatine fenestra	suborbital fenestra
m	∅	∅	infraorbital vacuity	∅	∅	∅	infraorbital vacuity	pterygo- ectopterygoid fenestra
s	∅	∅	infratemporal fenestra	interpterygo- jugal foramen	∅	pterygo-jugal vacuity	subtemporal fenestra	subtemporal fenestra

Table 1. Comparison of different interpretations and synonyms of palatal bones used by earlier and recent authors and identification of the same bones according to the new concept (light grey column).