A giant specimen of *Rhamphorhynchus muensteri* and comments on the ontogeny of rhamphorhynchines (#102465)

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A giant specimen of *Rhamphorhynchus muensteri* and comments on the ontogeny of rhamphorhynchines

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Rhamphorhynchus is one of the best-known pterosaurs with well over 100 specimens being held in public collections. Most of these represent juvenile animals and of the adults known, these are typically around 1 m in wingspan. Here we describe a near complete skeleton preserved partially in 3D, of an animal with a wingspan of around 1.8 m, that is considerably larger than other known specimens and is the among the largest known non-pterodactyloid pterosaurs. This animal shows differences in the anatomy not seen in smaller specimens revealing details of late-stage ontogeny in this genus. The specimen exhibits a proportional reduction in the size of the orbit and increase in the lower temporal fenestra, a reduction in the mandibular symphysis and unusually laterally flattened teeth which may point to a changing diet as these animals grew. These show a transition from smaller to larger specimens of *Rhamphorhynchus* and also appear in other large specimens of rhamphorhyhchines and point to a consistent pattern in their development.

A great specimen of *Rhamphorhynchus muensteri* and comments on the ontogeny of rhamphorhynchines

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Abstract

Rhamphorhynchus is one of the best-known pterosaurs with well over 100 specimens being held in public collections. Most of these represent juvenile animals and of the adults known, these are typically around 1 m in wingspan. Here we describe a near complete skeleton preserved partially in 3D, of an animal with a wingspan of around 1.8

m, that is considerably larger than other known specimens and is the among the largest known non-pterodactyloid pterosaurs. This animal shows differences in the anatomy not seen in smaller specimens revealing details of late-stage ontogeny in this genus. The specimen exhibits a proportional reduction in the size of the orbit and increase in the lower temporal fenestra, a reduction in the mandibular symphysis and unusually laterally flattened teeth which may point to a changing diet as these animals grew. These show a transition from smaller to larger specimens of *Rhamphorhynchus* and also appear in other large specimens of rhamphorhyhchines and point to a consistent pattern in their development.

Introduction

Rhamphorhynchus is a genus of non-pterodactyloid pterosaur well known from the Solnhofen area Lagerstätten of southern Germany (Wellnhofer, 1975), although some partial remains have been referred to this genus from other European localities (e.g., O'Sullivan & Martill, 2015). It is widely regarded as an animal that foraged extensively in aquatic environments around the Solnhofen lagoons and was primarily piscivorous, based on numerous specimens preserved with fish as stomach contents (Witton, 2018), though other aquatic (Hoffmann et al., 2020) and perhaps even terrestrial prey was occasionally taken (Hone et al., 2015a).

Due to the large number of well-preserved specimens, *Rhamphorhynchus* is an important pterosaur for research. It is represented by more complete specimens than any other pterosaur and is by far the best-known non-pterodactyloid taxon and the best-known outside of the Cretaceous. At least 125 specimens are present in public

collections with others also recorded in private hands (Wellnhofer, 1975; Hone et al., 2020) and many of these are largely complete and articulated, if typically compressed into two dimensions. As a result, this taxon has been used extensively in numerous studies of pterosaurian biolo e.g., Witmer et al., 2003; Witton, 2008; Persons & Currie, 2012; Henderson, 2018) and in particular, on growth (Bennett, 1995; Prondvai et al., 2012; Hone et al., 2020).

Specimens range in size from an approximate total wingspan (here taken as the length of the humerus, ulna or radius, wing metacarpal and all four wing phalanges combined times two) of approximately 0.31 m to 1.7 m. Most specimens have been considered osteologically immature based on their small size, unfused elements and coarse bone textures (Bennett, 1995), but medium d and in particular larger specimens likely represent osteologically mature adults (Prondvai et al., 2012) *(sensu* Hone et al., 2016). Adult pterosaurs show fusion of major elements such as the cranium, wrists, obliteration of the longbone epiphyses, and show a distinc stology among other features (see Kellner 2015 and Griffin et al. 2021). One specimen of *Rhamphorhynchus*, NHMUK PV OR 37002 is exceptionally large (Figure 1), having skeletal elements of approximately 1 in size greater than the next largest known *Rhamphorhynchus* (Wellnhofer, 1975 ~~his~~ specimen 81), which itself is considerably larger than other specimens.

Apart from being listed in Lydekker's (1888) catalogue of fossils held at the NHMUK, a brief description by Woodward in 1902, and mentioned by Bennett (1995) as "the largest known specimen", NHMUK PV OR 37002 has never been discussed or illustrated in any detail in the ature and yet is potentially important for several

reasons. First, it is preserved largely in three dimensions which is rare for Solnhofen vertebrate specimens and thus provides rarely recovered information. Secondly, it is the largest specimen of *Rhamphorhynchus* which is important for understanding the growth of this taxon~~, especially at upper sizes~~. Finally, it is also among the largest non-pterodactyloid pterosaurs known and certainly the most complete specimen of an animal in excess of 1.5 m in wingspan. Here we describe this specimen and show that contrary to some suggestions, it is not a distinct species, but is a member of *Rhamphorhynchus muensteri* and that it reveals a number of traits that developed late in ontogeny in large rhamphorhynchine pterosaurs.

Specimen history and locality information

According to the museum label that accompanies specimen NHMUK PV OR 37002, this formed part of the 'Häberlein Collection' and came from 'Eichstädt' [s]. This specimen came to the museum as part of the 1862 purchase of Solnhofen specimens from Dr Karl Häberlein (Lydekker 1888) that also included the famous 'London specimen' of *Archaeopteryx*. This would therefore be one of the specimens from the Eichstätt locality (this is also given by Woodward, 1902) and the Schernfeld-Eichstätt Basin, which is dated as Malm Zeta 2 (Bennett, 1995). Numerous *Rhamphorhynchus* specimens have been recovered from this locality, including all specimens that were previously referred to the species *Rhamphorhynchus* '*longicaudus*' (Bennett, 1995).

Prior to this new description the specimen was partly re-prepared by Mark Graham at the Natural History Museum, London. Although generally well preserved, the specimen was incompletely prepared and various parts had been repaired or supported

with plaster or other materials. Work by Mark Graham, a senior preparator at the Natural History Museum, London exposed numerous new features. Parts of the skull (especially the posterior f), the cervical series, and the shoulder and chest region were mechanically prepared and revealed additional details of the specimen. The material was photographed in detail before the work began to document the specimen before the additional preparation was carried out (s SI).

Description

Numerous specimens of *Rhamphorhynchus* have been described and illustrated in detail at various times and thus its anatomy is well known including both the skeletal system and soft tissues (e.g., Marsh, 1882; Wellnhofer, 1975; Bennett, 1995; Bonde & Christiansen, 2003; Frey et al., 2003; Hone et al., 2013; Bennett, 2015; Bonde & Leal, 2015). Although many specimens are compressed or crushed, some specimens show remarkable three dimensional preservation, and the number of specimens available means that most elements of the skeleton a known well as 3D structures. As a result, the specimen here will not be described in detail, but will focus on k raits (see Table 1 for various measurements of ele nts).

NHMUK PV OR 37002 comprises most of a pterosaur skeleton including the skull and mandible; cervical, dorsal and caudal vertebrae; several dorsal ribs; both scapulocoracoids; virtually all major elements of the left wing; a partial right wing; a complete left hindlimb and elements of the right hindlimb. Degrees of articulation vary but the ma elements are articulated, and only the ribs are predominantly separated

from the skeleton. The specimen is preserved primarily in dorsal view with the skull in right lateral view.

There are a series of major breaks across the slabs on which the specimen is preserved, and several parts have been apparently moved and restored to places approximating a natural position – a practice seen in a number of restored Solnhofen ~~region~~ pterosaur specimens (see Hone, 2010). Similarly, the wing phalanges and tail are mostly split between the main plate and counterplates and the latter have been attached to the main plate next to their counterparts (~~see~~ Figure 1). The specimen retains lots of plaster between elements, indicating considerable reconstruction before mounting into its wooden frame. Bones crossing breaks in the slabs – which include the skull, mandible and both wing finger elements – are slightly distorted. However, the long axes of the bones line up almost perfectly despite the complex nature of the break to the underlying matrix. For example, there is a total of 8 mm in difference in length between wing phalanx II of the left and right side (left is 167 mm), suggesting an imperfect, but probably reasonable repositioning in the slab.

Most of the specimen is preserved in three dimensions, although there is some crushing and damage to various parts. The skull is partly sheared such that the right side has been raised and the midline elements either are more raised than normal (e.g., the nasals) or more depressed (e.g., the postorbitals) which gives the skull a slightly unusual appearance. The cranium and mandible show a division based on a major break along the anterior border of the orbit, and the jugal and lacrimal have been partially restored with plaster. As with the long bones mentioned above, although the join is imperfect, the general orientations, shape and lengths of the elements suggest

that this has been reassembled accurately and the odd shape and appearance of the skull are due to its original taphonomic deformation and not due to the repositioning of different parts of the skull on the slab during repair.

Various elements are also split or are missing parts of the cortex, exposing the internal bone cavities. There is only limited evidence of calcite crystals on the specimen which are generally common on Solnhofen pterosaurs. The texture of the bone of the animal is smooth indicating that it is not a juvenile, and major sutures (e.g., the wing extensor tendon process, between the scapula and coracoid, within the skull) are obliterated, indicting full osteological maturity (Bennett, 1995; Kellner, 2015).

Skull

The cranium and mandible are near complete and articulated (Figure 2). The right side of the skull, dorsal part of the cranium and ventral part of the mandible are all exposed. The posterior cranium is partially exposed (the quadrates and occipital condyle are visible) but other areas (in particular the palate) remain covered and could not be further exposed through preparation without risking damage to these fragile areas. Notably, the ventral margin of mandible is preserved and is intact, indicating resistance to crushing, however, the posterior part of the visible left mandible has been forced up into the temporal region when skull was crushed.

There are ten alveoli in the upper jaw, with five teeth being preserved in them. The ten alveoli presumably represent six in the maxilla and four in the premaxilla as is usual for the genus, although the suture between these elements cannot be seen. The anteriormost alveolus on the left is covered in matrix, but its presence is inferred based

on a bulge in the jaw and presence of a corresponding tooth on the opposite side. There is an apparent 11th tooth, but this is the anteriormost tooth from the left side of the jaw that protrudes between the right anterior teeth. Seven dentary teeth are inferred from swollen alveoli although only two of the more anterior teeth are present. The teeth are somewhat blunt at the tips and are also laterally compressed and in, to the extent that the repreparation was halted to prevent damage to them.

The skull exhibits minor dorsoventral compression, with the nasals and frontals slightly displaced ventrally, making the skull roof appear concave rather than convex.

Axial Skeleton

The axial skeleton appears to be generally in articulation based on the positions of visible elements and other parts of the skeleton though only some cervical vertebrae and the tail are clearly visible. Much of the dorsal series and sacrum are not seen and may have been lost or more likely, based on the otherwise complete nature and articulation of the specimen, are present but are not exposed.

At least two middle cervical vertebrae are exposed ventrally and one is also exposed in lateral view. The anterior most of these three has some plaster infilling part of it. There are two dorsal vertebrae preserved in transverse section. As with a number of postcranial elements where the cortex is damaged, they show thin bone walls (approximately 0.3 mm) that are typical of pterosaurs. There are also two more dorsal vertebrae that are possibly fused to one another but these are difficult to see as they are overlaid by dorsal ribs.

The caudal series is well preserved, though split between the plate and the mounted counterplate, down to the distal tail. The long chevrons and zygapophyses of the tail hamper our attempt to count the vertebrae, but there are at least 30 present. This does not include the tiny tip of simple caudals that are occasionally preserved in *Rhamphorhynchus* (e.g., see Hone et al., 2015a) and these are not present here.

A small number of dorsal ribs are preserved in alignment, perhaps indicating some degree of articulation of the chest before burial. There is no evidence of sternum or gastralia, although a number of smaller bone fragments are visible associated with the torso.

Appendicular skeleton

Both pectoral girdles are preserved. The left scapulocoracoid is exposed in lateral view and overlies right which is exposed in medial aspect. The coracoids of each are only partly exposed, with the left one being buried under the humerus. The left glenoid is poorly preserved but mostly exposed and shows the typically ‘asymmetric’ configuration of rhamphorhynchines (Witton, 2015) with a posterioventrally positioned buttress that prevents the humerus being positioned below the horizontal. The supraglenoidal buttress is confluent with the ventral margin of the scapula.

The left forelimb is the more intact of the two and comprises a humerus, radius and ulna, and a complete left wingfinger. The carpals, wing metacarpal, metacarpals and phalanges are missing or more likely given the articulation, lie under the cervical series and are not exposed. The humerus is exposed dorsally and posteriorly and, in being uncrushed, allows for an unusually good appreciation of the three dimensional

shape of the bone. Woodward (1902) states that the humerus is incomplete but could not have exceeded '0.075 m' although Wellnhofer (1975) gives this as 79 mm, and here we measure this as a maximum of 77.6 mm. The articular surface of the humeral head is gently arced and measures approximately 18 mm across (a portion of the dorsal region is missing). The ulna crest deflects posteriorly from the posterior margin of the humeral head, though its exact morphology is obscured by matrix. The deltopectoral crest projects prominently from the diaphysis, tapering from a broad base to a relatively rounded termination. Some aspects of the terminal deltopectoral crest are difficult to establish given the current state of specimen preservation, but termination does not look swollen or 'hatchet shaped', as is often reported in rhamphorhynchid pterosaurs, including other *Rhamphorhynchus* (e.g., Wellnhofer 1975; Unwin 2003, Padian 2008). The posterior surface of the proximal diaphysis contains a 9 mm-long sediment-filled sulcus. We were unable to ascertain if this penetrates the bone cortex, but note that it is similarly positioned to pneumatic openings in some other pterosaur humeri (see Unwin, 2003). The diaphysis is gently bowed anteroposteriorly, and bears a muscle scar on its posterior surface. The supracondylar process is preserved adjacent to the broken and plastered distal end of the humerus. The breaks are sharp and imply that the humerus was complete as preserved, with the distal condyles lost during collection.

Only the proximal part of the right humerus visible though it does allow the bone wall thickness can be measured on the dorsal surface of the humerus and on the ventral surface of the deltopectoral crest and are both approximately 0.6 mm thick. Also preserved is a proximal radius, possible ulna, partially exposed wing metacarpal and metacarpals I-III. All wing finger elements are present for the right wing, but they are

incompletely preserved and the proximal part of wing phalanx 1 is missing. There is a very slight curvature to distal part of both wing phalanx 4s and both show a slightly expanded and rounded and ball-like distal tip which is seen in a number of pterosaurs including other specimens of *Rhamphorhynchus* (Hone et al., 2015b). Breaks to the bones means that the bone wall thickness can be measured here with some confidence - in wing phalanx 3, this can be measured at between 0.59 and 1.09 mm.

Most elements of the right hindlimb are present and of the left hindlimb, only a few possible elements of the left foot can be identified that are exposed. The proximal end of the right femur is exposed and this shows a large and well ossified femoral head which is somewhat flattened. The tibia is broken and the middle part is either lost or not exposed. The distal end of the element is present, however there is extensive calcite crystal build-up over the tarsal region and so little detail can be made out. The tibiotarsus is in articulation with the nearly complete right pes which lacks only the unguals. The foot is preserved well and the counterplate with impressions of these elements is also present with the specimen.

Discussion

Taxonomic identity

Woodward (1902) named the specimen as a new species, *Rhamphorhynchus longiceps,* and this identification and attribution is given with the specimen's accompanying label. Woodward's new species was based on extremely limited evidence, but is an available name under ICZN Article 12 (ICZN 1999). He noted its large size and that its skull was proportionally long compared to *R. 'gemmengi'*

(NHMUK PV R 2786), though in fact this specimen has a skull in proportion with the rest of its body compared to other *Rhamphorhynchs* specimens (Hone et al., 2020). Woodward also noted that the toes were about half the diameter of those of *R. 'grandis'* based on a specimen at the NHMUK, though this is clearly the pes of a large pterodactyloid because of the reduced 5th toe (NHMUK PV OR 42737). No further comparisons were made to other known named species of *Rhamphorhychus* or defining traits listed.

Rhamphorhynchus has a complex taxonomic history with numerous species named at various times (e.g., see Wellnhofer, 1975). However, in a major revision of the genus, Bennett (1995) demonstrated that the previously suggested species actually formed several discrete year classes of both juvenile and adult animals that ultimately are from a single species – *Rhamphorhynchus muensteri* - an assignment that has been broadly adopted and that we follow here. *R. longiceps* is therefore a junior subjective synonym of *R. muensteri*.

Bennett (1995) gave a thorough new diagnosis of this species, although Hone et al. (2012) showed that a number of these traits also overlap with the then newly identified rhamphorhynchine genus *Bellubrunnus*. NHMUK PV OR 37002 can be identified as *R. muensteri* based on the presence of the following traits (Bennett, 1995): 34 teeth (four in each premaxilla, six in each maxilla and seven in each dentary); anterior teeth long and angled forward and laterally; the fourth premaxillary tooth larger and more lateral than other premaxillary teeth, and posterior teeth shorter and more vertical. Two additional traits listed by Bennett (1995) - lower temporal fenestra narrow, upper temporal fenestra larger (than the lower) and rounded - may not be present here

as the lower temporal fenestra is not that narrow and may be a similar size to that of the upper. However, the shape of the lower temporal fenestra is subject to individual variation in *R. muensteri*, even among similarly-sized specimens (compare e.g., 11431 and CM 11434; Hone et al., 2013).

Additional characters used by Bennett (1995) also appear in *Bellubrunnus* (Hone et al., 2012) but in context are useful to diagnose *Rhamphorhynchus* as the former genus is from the Brunn locality which is rather older that the other Solnhofen-type limestones (Hone et al., 2012) and NHMUK PV OR 37002 lacks autapomorphies that diagnose *Bellubrunnus* (e.g., only 22 teeth, lack of elongate zygapophyses on the tail). Therefore, additional traits of Bennett (1995) can also be used here to further support the identification of NHMUK PV OR 37002 as *R. muensteri*: jaws with edentulous tips, orbit substantially bigger than the naris and antorbital fenestra, the first wing phalanx is the longest and roughly the length of the skull. Two final characters given by Bennett (1995) femur shorter than humerus and prepubis slender and arched with a lateral process, cannot be confirmed because key elements cannot be observed.

Notably, Bonde and al (2015) retained *R. longiceps* as being a distinct species from *R. muensteri* based on a number of features and that they specifically state to be present in NHMUK PV OR 37002. These are: the temporal fenestrae being different in shape, “the upper more rounded and the lower wider than in the other forms”; different “size and proportions of the orbit in relation to the temporal openings”, the “upper jaw is not as pointed…and the lower jaw symphysis appears shorter, and the lower jaw is equally long as the upper”, and finally that “as reconstructed by Wellnhofer (1975), the fourth tooth is in the maxilla, not in premaxilla”.

However, our examination of the specimen suggests that this is not a strong set of traits for a referral of the specimen to a distinct species. The lower fenestra here is wider than usual, but the upper does not appear to be any different in shape than seen in other specimens of *Rhamphorhynchus* (e.g., Wellnhofer, 1975 figure 3). The width of the lower fenestra may be a consequence of large size, and therefore represent an ontogenetic rather than taxonomic difference (see below). Bonde and Leal (2015) do not state how the orbit in this specimen apparently differs to other specimens which makes this suggested trait hard to assess. The orbit here does look a little smaller than other specimens, but as they also advocated that the other openings are larger, then the orbit would appear smaller as a consequence - this is effectively one trait and not two. Furthermore, since orbits are disproportionately large in juvenile vertebrates (Emerson & Bramble, 1993) including pterosaurs (Bennett, 1995) and shrink in proportion as they grow (even if absolute size still increases) then the largest individuals should have the smallest proportional orbits (Hone et al., 2020). As NHMUK PV OR 37002 is the largest known specimen, then proportionally smaller orbits are to be expected. Similarly, the upper jaw here appears to be just as pointed as other specimens of *Rhamphorhynchus*. The symphysis is difficult to assess as it is not visible in many specimens, however an assessment of a few does strongly suggest that this shortens in this taxon as size increases. NHMUK R 231, NHMUK R37003 and NHMUK R 2786 get successively larger (mandible lengths of 140, 150 and 165 mm respectively) but have decreasing symphysis of 42%, 33% and 28% of mandible length. Thus, a symphysis length of a quarter or less of the total length of the mandible would be expected for a very large individual and this does not suggest that NHMUK PV OR

37002 is a distinct taxon. The upper jaw is not does not overhang as much in other specimens of *Rhamphorhynchus*, but also appears to be incomplete and so this is not a reliable difference. Finally, as noted above, the suture between the premaxilla and maxilla has been obliterated so there is no reason to think that the tooth counts in the two elements have changed, irrespective of how it may have been reconstructed by other authors. Numerous traits are shared with all other specimens of *R. muensteri* and we retain this referral for this specimen and it should not be considered a separate taxon.

Size

NHMUK PV OR 37002 is however very considerably larger than other known specimens of *Rhamhorhynchus* (Figure 6). The skull and humerus are respectively 201 mm and 78 mm in length, with the next largest specimen of *R. muensteri* (unnumbered specimen from Tubingen, Wellnhofer 1975 specimen number 81) having a skull of 150 mm and a humerus of 65 mm. Even this individual is much larger than most others, and there are a cluster of specimens with skull lengths around 120-125 mm and humeri of 40-43 mm in length. ~~So~~ NHMUK PV OR 37002 is more than 60% larger than all but the largest known *Rhamphorhynchus* specimens and is the largest by around 33%. In contrast, the smallest specimen we know of has a skull of 21 mm (BMMS 3A) and a humerus of just 15 mm (~~and~~ Wellnhofer's 1975 specimen 14 has a humerus of just 14 mm, though this has no museum catalogue number).

Woodward (1902) oddly gave NHMUK PV OR 37002 as being only of 'a relatively large species' despite it being by far the largest known specimen of the genus,

and the largest non-pterodactyloid pterosaur known from the Jurassic at that time. There are large specimens of *Dorygnathus* (SMNS ~~Nr.~~ 81205 has a skull of 150 mm and humerus of 78 mm) and the skulls of *Angustinaripterus* (165 mm skull – Wellnhofer, 1991) and *Parapsicepahlus* (140 mm – O'Sullivan & Martill, 2017) are also large, but this *Rhamphrhynchus* is still of exceptional size and it is odd that this was not recognised. One large specimen of *Dimorphodon* (NHMUK PV R 1035) has a comparable skull length and even longer humerus though the wingspan overall is considerably smaller than that of NHMUK PV OR 37002. The recently-described *Dearc* from Scotland has a skull of c. 220 mm and humerus of 112 mm, with an estimated wingspan of 2.5 meters (Jagielska et al. 2022), while isolated axial and appendicular elements of a indeterminate non-pterodactyloid from the same Lealt Shale formation indicate an animal of even larger size (Jagielska et al. 2023). Some isolated wing elements from Solnhofen pterodactyloids also point to animals of approximately 2 m in wingspan (Elgin & Hone 2020) and there are very partial specimens that ~~a~~suggest animals as 5 m in wingspan from the UK (Etienne et al., 2024), but overall NHMUK PV OR 37002 would have been one of the largest pterosaurs prior to the Cretaceous. Based on Witton's (2008) relationship between mass and wingspan of non-pterodactyloid pterosaurs, the mass of NHMUK PV OR 37002 can be estimated as 3.5

Comparisons to smaller specimens and other large rhamphorhynchines

Despite the large size of the specimen the major proportions of the skeleton still fit with the near-isometric general patterns seen throughout the species from the smallest to

largest specimens (Bennett, 1995; Hone et al., 2020). This is perhaps unusual given that biomechanical factors such as wing area will increase at the second power while mass will increase at the third pov Thus, various features such as the lengths of the humerus or the wing as a whole might be expected to change at larger sizes to accommodate the shifts in various proportional forces, but this does not appear to be the case (see also Habib & Hone, 2024). We note for example also that the posterior expansion of the joints in the wing finger elements are similar to those of even much smaller ecimens suggesting similar safet ctors and associated forces on them. The deltopectoral crest lacks the restriction at the base which is also seen in other large specimens of *Rhamphorhynchus* though is present or even exaggerated in smaller ones. The additional or changing relative forces associated with an animal in proportion but at greater size may be offset by factors such as increased pneumaticity in larger animals or a fundamental change in flight pattern, but is still notable how consistent the general patterns are for larger specimens compared to even the smallest ones that have one fifth or less of the wingspan.

NHMUK PV OR 37002 shows a number of anatomical features that ~~mark it as apparently unusual compared to~~ most specimens of *Rhamphorhynchus*. Despite the original species designation of '*longiceps*', Woodward (1902) correctly noted that the edentulous rostrum of the specimen is prop nally short and deep compared to most other specimens. In contrast, the mandible as a whole is prop onally dorsoventrally narrow as the length to height ratio is around 4:1 which contrasts with a ratio of 3:1 on another *Rhamphorhynchus* specime NHMUK PV R 2786) of about half the absolute size. As noted above, the proportion of the mandibular symphysis is similarly reduced in

388 the large specimen with this making up a quarter of the length of the mandible which is
389 less than in smaller specimens. We suggest that as the symphysis fuses during
390 ontogeny, this length could be reduced in adults as while proportionally smaller in length
391 it would be absolutely bigger and stronger as it fuses and obliterates the suture.

392 The lower temporal fenestra is considerably expanded and trapezoidal compared
393 to smaller specimens of *Rhamphorhynchus* in both height (28 mm) and midheight
394 anteroposterior length (17 mm, maximum width of 18 mm) and is not the slit-like
395 opening more usually seen in this genus. This is apparently due to the postorbital bar
396 being rotated forwards to being in a more vertical position such that the dorsal end of
397 the lower temporal fenestra is more open and the orbit has a straighter posterior margin.
398 This size and shape change may be a trajectory for larger rhamphorhynchoid
399 pterosaurs generally. We note that there is a similar, if less exaggerated, change in the
400 lower temporal fenestra seen between smaller and larger specimens of *Dorygnathus*
401 (Padian, 2008) and the large rhamphorhynchids *Parapsicephalus* (O'Sullivan & Martill,
402 2017) and *Angustinaripterus* shows a similarly shaped fenestra (He et al. 1983) (Figure
403 8). The width of the skull at the exoccipitals is proportionally wider in NHMUK PV OR
404 37002 than seen in smaller specimens of the species. The posterior part of the skull is
405 visible in posterolateral view in NHMUK PV OR 37002 (unlike in the vast majority of
406 *Rhamphorhynchus* specimens), and here it is possible to see that there is no expansion
407 / enhancement of exoccipitals despite the expanded width of the skull.

408 The teeth in NHMUK PV OR 37002 are particularly unusual as they are clearly
409 somewhat laterally compressed (as also noted by Woodward, 1902) and contrast with
410 the subcircular cross-section of teeth that is typical in *Rhamphorhynchus*. The largest

411 preserved tooth is over 19.5 mm in length, 6 mm across the base, but only
412 approximately 4 mm thick, with the anterior most premaxillary tooth being approximately
413 15 mm by 5 mm by 2.5 mm respectively. Wellnohfer, (1975, ~~his Fig~~ 4) illustrates the
414 teeth as being sub-oval in cross-section and examination of a number of specimens
415 shows that they do not typically have subcircular teeth, but that these are at least a little
416 laterally compressed. Although the preserved teeth and alveoli in NHMUK PV OR
417 37002 are unusually elliptical and flattened (Figure 9), this may again be an
418 exaggeration of a condition that was already present in *Rhamphorhynchus* and not
419 observed before as the diameter of teeth are very hard to measure. For example, the
420 adult-sized (skull length of 95 mm) NHMUK 2786 certainly appears to have more
421 flattened teeth than smaller specimens and this is also a feature seen in the teeth of
422 *Dearc* (DWEH pers. obs.) and the anterior teeth of *Angustinaripterus* are described as
423 being elliptical in cross-section with the posterior ones being laterally compressed (He
424 et al., 1983).
425
426 *Implications*
427 The unusual anatomy seen here suggest that NHMUK PV OR 37002 may have
428 differed in its lifestyle compared to smaller specimens of *Rhamphorhynchus*. The
429 change to the lower temporal fenestra and expansion the back of the skull, coupled
430 with a taller jaw, labiolingually narrower teeth, reduced mandibular symphysis and shorter
431 rostrum all point to a difference in feeding, be it prey type or method of acquisition and
432 processing. Ontogenetic shifts must have happened during ontogeny (Hone et al., 2020) and
433 there is some evidence for this in pterosaurs, including *Rhamphorhynchus,* where it is

suggested that they shift from a more insectivorous to more piscivorous diet during growth (Bestwick et al., 2020). However, given the diversity of diet known and inferred for *Rhamphorhynchus* (see e.g., Hone et al., 2015a; Witton, 2018, Hoffmann et al., 2020) they may have shifted to still other prey, or had a different focus, at the largest sizes.

The increased posterior part of the skull with a short rostrum would suggest an animal with an absolutely more powerful bite, but this is an odd combination with proportionally (though not absolutely) thinner teeth and a weaker jaw. Shifting to more laterally compressed teeth would increase their ability to cut at the expense of being able to grab and swallow (Bugos & McDavid, in revision; D'Amore et al., in review), and so may suggest that these largest rhamphorhynchines were less reliant on fish and similar prey (e.g. soft-bodied cephalopods) as part of their diet, or were using this cutting ability to process larger items (e.g. terrestrial tetrapods) into pieces that could be swallowed. If so, this may also partly explain the rarity of larger animals if they tended to forage in more terrestrial environments and therefore were less likely to die and be buried in the local lagoons compared to aquatic foraging juveniles and small adults.

It has also been suggested that the hatchet shape of the deltopectoral crest seen in many pterosaurs (and including small specimens of *Rhamphorhynchus* but not here) is linked to the ability to launch from water (Cunningham & Habib, 2011). Thus these changes here may point to large animals being less reliant on feeding in aquatic systems on fish and similar foodstuffs and are instead now foraging for alternate prey in

different environments. This would also then point to ontogenetic niche partitioning with adults and juveniles targeting different prey items.

This overall pattern may be true of other large animals that have been described as rhamphorhynchines (though see Hone et al.,). The large *Dearc* is from an estuarine locality (Jagielska et al., 2022) while *Angustinaripterus* is from the Xiaximiao (Shaximiao) Formation (He et al., 1983) which is a fundamentally terrestrial system encompassing a floodplain (Xie et al., 2023). As such, large rhamphorhynchines may well have moved inland and, while still tied to water bodies, have been more generalist feeders, perhaps analogous to some modern gulls (Laridae).

Rhamphorhynchus and some other Solnhofen pterosaurs are unusual compared to most other tetrapods in that there are numerous juveniles represented and relatively few adults (Bennett, 1995). As a result, although NHMUK PV OR 37002 was clearly much larger than other known specimens with relatively few of the 130+ specimens known being of adult size the sample here is effectively much smaller. Therefore, while NHMUK PV OR 37002 may not have been an adult individual that was much larger than any others so much as being an example of limited sampling, and especially if larger animals were foraging in more terrestrial environments.

Acknowledgements

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photography and photogrammetry of the specimen. Special thanks to Mark Graham for his extraordinary work on the new preparation of the specimen.

Institutional Abbreviations

BMMS – Bürgermeister-Müller Museum, Solnhofen, Germany

CM – Carnegie Museum of Natural History, Pittsburgh, Pennsylviana, USA

GSM – British Geological Survey Museum, Keyworth, UK

NHMUK (formerly BMNH) – Natural History Museum, London, UK

NMS – National Museums Scotland, Edinburgh, UK

SMNS – Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany

YPM – Yale Peabody Museum, New Haven, Connecticut, USA

ZDM – Zigong Dinosaur Museum, Zigong, Sichuan, China

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602 paleoclimate. *Review of Palaeobotany and Palynology*, 317:p.104945.

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607 Table 1: Measurements of major elements of skeletal units of NHMUK PV OR 37002.
608 All are taken to the nearest mm

609
610

Element or unit	**Length (mm)**
Skull (total length)	201
Skull height (at quadrate)	49

Skull width (across quadrates)	37
Longest tooth (length)	20
Mandible length (including reconstruction)	160
Cervical (best preserved, maximum length, omitting plaster)	24
Caudal series (minimum length)	462
Scapula (length, to base of glenoid)	74
Glenoid (anteroposterior length)	9
Humerus (minimum and maximum length, omitting plaster)	70, 78
Humerus diaphysis (diameter anteroposterior and dorsoventral)	12, 6
Humeral head (width)	23
Radius (length, as exposed)	80
Ulna (length)	103
Wing phalanx 1 (length as preserved, left then right)	133 / NA
Wing phalanx 2 (length, left then right)	168 / 176
Wing phalanx 3 (length, left then right)	139 / 136
Wing phalanx 4 (length, left then right)	136 / 137
Femur length (as exposed)	44
Demur diameter	7
Metatarsals I-V	40, 41, 39, 33, 23

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616 Fig 1. Specimen NHMU V OR 37002 of *Rhamphorhynchus muensteri.*

617 Arrow indicates the area recently reprepared (see also re 4); counterplates attached

618 to the main plate are outlined in red. or = outline of right pes; rpes = right pes on

counterplate; hu = humerus; cdv = caudal vertebral series on separate attached plate and counterplate; rad/uln = radius and ulna; rwpx2 = right wing phalanx 2; orpwx3 = outline of right wing phalanx 3; rwpx4 = right wing phalanx 4 on counterplate; orwpx4 = outline of right wing phalanx 4; lwpx1 = left wing phalanx 1; lwpx2 = left wing phalanx 2; olwpx2 = outline of left wing phalanx 2 on counterplate; lwpx3 = left wing phalanx 3 on counterplate; olwpx3 = outline of left wing phalanx 3; lwpx4 = left wing phalanx 4 on counterplate; olwpx4 = outline of left wing phalanx 4. Scale ~~is~~ 5 cm with 1 cm increments.

Fig 2. Skull of *Rhamphorhynchus muensteri* NHMUK PV OR 37002 in near lateral view showing the 3D nature of the specimen (A) restoration of the cranium and mandible in right lateral view (B). Preserved bone and teeth are in white, obscured or reconstructed portions are in grey. Note the skull has no visible sutures. stf = supratemporal fenestra; ltf = lower temporal fenestra; orb = orbit; aof = antorbital fenestra; en = external naris; lwpx1 = left wing phalanx 1; lwpx2 = left wing phalanx 2. Scale ~~bar is~~ 50 mm.

F. A dorsal vertebra in anterior or posterior view. This is poorly preserved but is a previously unseen element, having been revealed by the new preparation work. cen = centrum; nc = neural canal; tvp = transverse process; ns = neural spine. Scale ~~bar is~~ 10 mm.

Fig 4. Photograph (A) and interpretive drawing (B) of the chest region of NHMUK PV OR 37002 after additional preparation. lwpx1 = left wing phalanx 1; uln = ulna; rad = radius; ? = unknown; Lsc = left scapulocoracoid; rsc = right scapulocoracoid; hu = humerus; dpc = deltopectoral crest; r = rib; pat = pathology; dv = dorsal vertebra. The recently-prepared area is in the centre. Scale ~~bar is~~ 100 mm.

Fig 5. Close up of the midshaft of a broken third wing phalanx on NHMUK PV OR 37002 showing the bone wall thickness. Scale in millimetres.

Fig 6. Skeletal diagram of an osteologically mature *Rhamphorhynchus muensteri* based mainly on NHMUK PV OR 37002. Scale ~~bar is~~ 250mm.

Fig 7. Size comparison of different *Rhamphorhynchus muensteri* specimens: (anti-clockwise from top left) the smallest known BMMS A3 (21 mm skull length), a generalised 'typical adult' specimen (122 mm skull length), the second largest known 'Exemplar 81' of Wellnhofer (150 mm skull length) and the largest known NHMUK PV OR 37002 (201 mm skull length). Scale ~~bar is~~ 1 metre.

Fig 8. Posterior part of skulls of large non-monofenestratan pterosaurs showing their temporal fenestrae: *Rhamphorhynchus* NHMUK PV OR 37002 and YPM VPPU 11981, *Dorygnathus* SMNS 55886 after Padian (2008) and Wellnhofer (1978), *Parapsicephalus* GSM 3166 mirrored after O'Sullivan & Martill (2017), *Angustinaripterus* ZDM T8001

663 after He et al. (1983), and *Dearc* NMS G.2021.6.1-4. Dotted lines represent
664 reconstructed parts of the skull. Specimens not to scale.
665
666 Fig 9. The anterior skull of NHMUK PV OR 3700 in ventrolateral view showing the
667 relatively flattened teeth that are oval and not circular in cross-section. Scale ~~bar is~~ 50
668 mm.
669

Figure 1

Specimen NHMUK PV OR 37002 of a giant specimen of *Rhamphorhynchus muensteri*

Specimen NHMUK PV OR 37002 of *Rhamphorhynchus muensteri.* Arrow indicates the area recently reprepared (see also figure 4); counterplates attached to the main plate are outlined in red. orpes = outline of right pes; rpes = right pes on counterplate; hu = humerus; cdv = caudal vertebral series on separate attached plate and counterplate; rad/uln = radius and ulna; rwpx2 = right wing phalanx 2; orpwx3 = outline of right wing phalanx 3; rwpx4 = right wing phalanx 4 on counterplate; orwpx4 = outline of right wing phalanx 4; lwpx1 = left wing phalanx 1; lwpx2 = left wing phalanx 2; olwpx2 = outline of left wing phalanx 2 on counterplate; lwpx3 = left wing phalanx 3 on counterplate; olwpx3 = outline of left wing phalanx 3; lwpx4 = left wing phalanx 4 on counterplate; olwpx4 = outline of left wing phalanx 4. Scale is 5 cm with 1 cm increments.

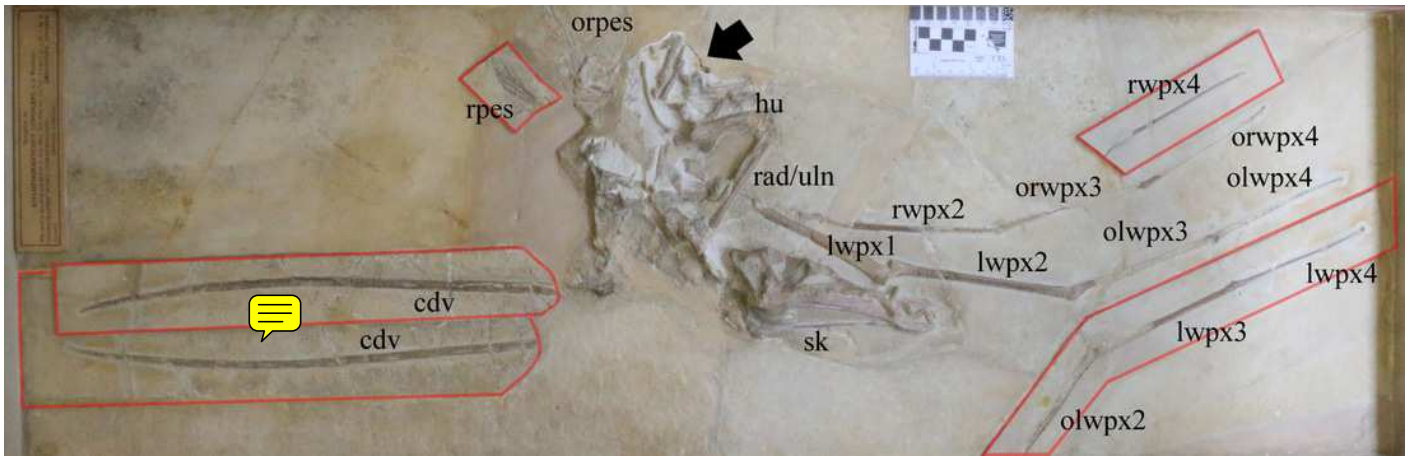

Figure 2

Skull of *Rhamphorhynchus muensteri* NHMUK PV OR 37002

Skull of *Rhamphorhynchus muensteri* NHMUK PV OR 37002 in near lateral view showing the 3D nature of the specimen (A) and restoration of the cranium and mandible in right lateral view (B). Preserved bone and teeth are in white, obscured or reconstructed portions are in grey. Note the skull has no visible sutures. stf = supratemporal fenestra; ltf = lower temporal fenestra; orb = orbit; aof = antorbital fenestra; en = external naris; lwpx1 = left wing phalanx 1; lwpx2 = left wing phalanx 2. Scale bar is 50 mm.

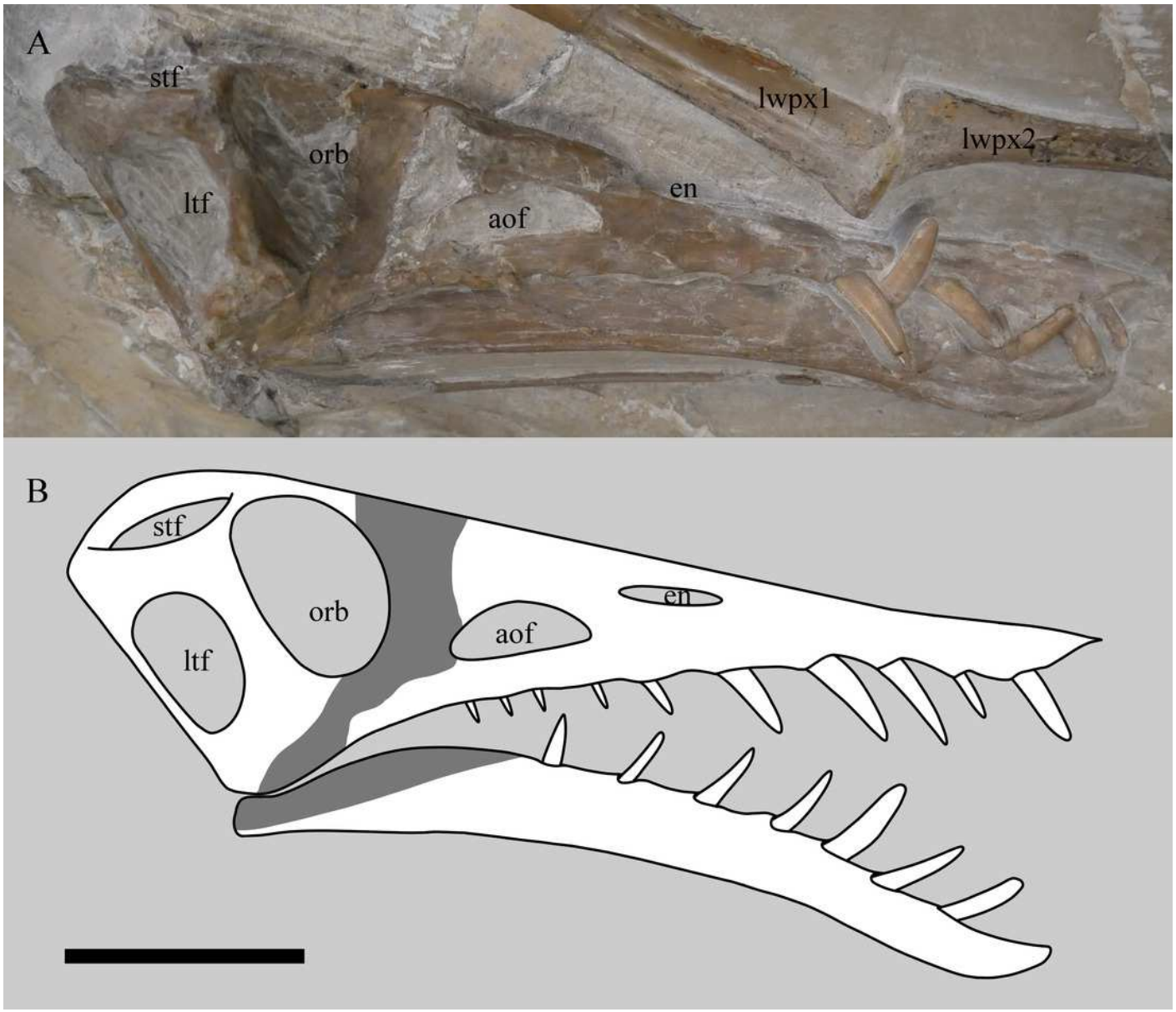
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Figure 3

A dorsal vertebra of NHMUK PV OR 37002

A dorsal vertebra in anterior or posterior view. This is poorly preserved but is a previously unseen element, having been revealed by the new preparation work. cen = centrum; nc = neural canal; tvp = transverse process; ns = neural spine. Scale bar is 10 mm.

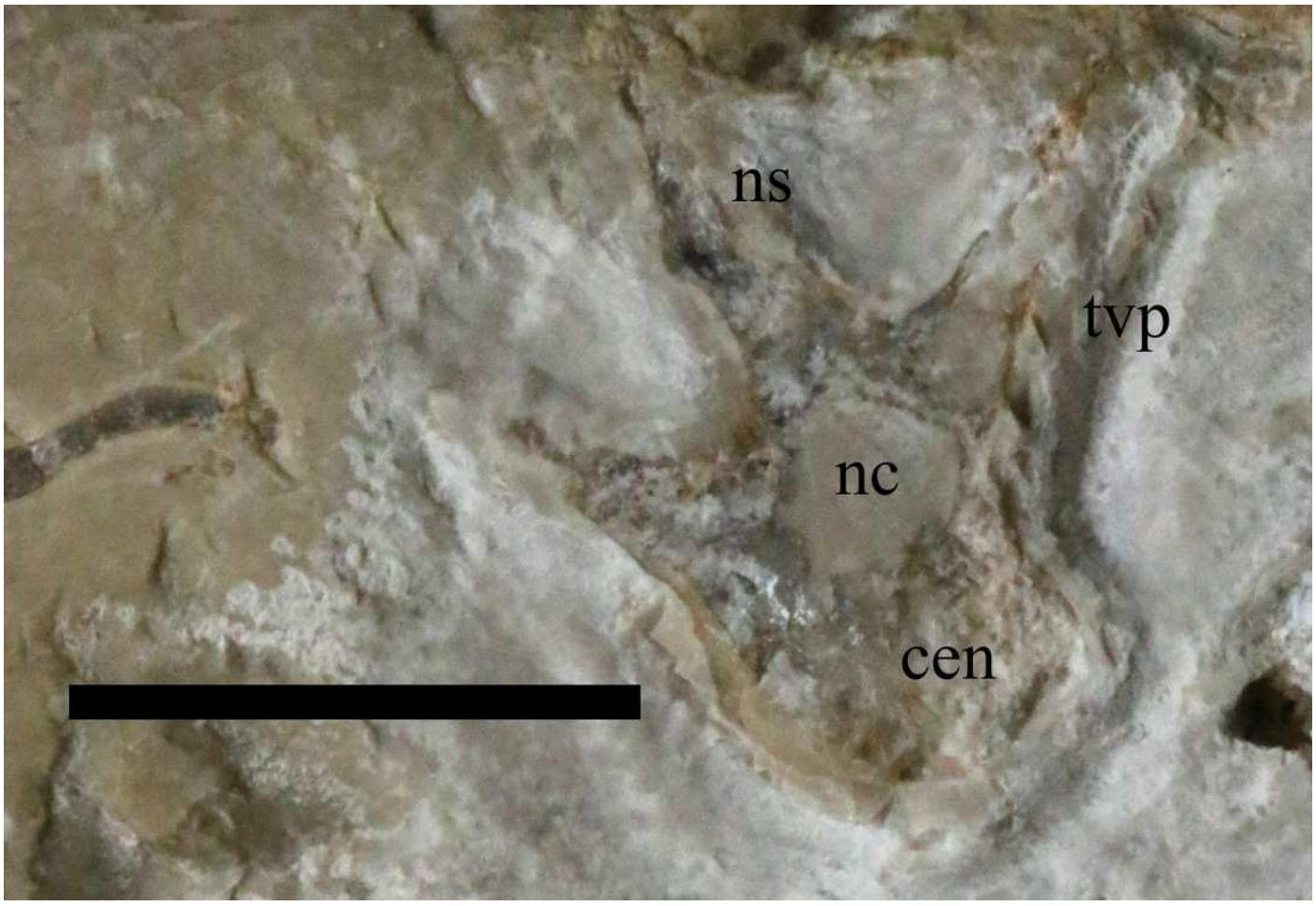

Figure 4

The chest region of NHMUK PV OR 37002

Photograph (A) and interpretive drawing (B) of the chest region of NHMUK PV OR 37002 after additional preparation. lwpx1 = left wing phalanx 1; uln = ulna; rad = radius; ? = unknown; Lsc = left scapulocoracoid; rsc = right scapulocoracoid; hu = humerus; dpc = deltopectoral crest; r = rib; pat = pathology; dv = dorsal vertebra. The recently-prepared area is in the centre. Scale bar is 100 mm.

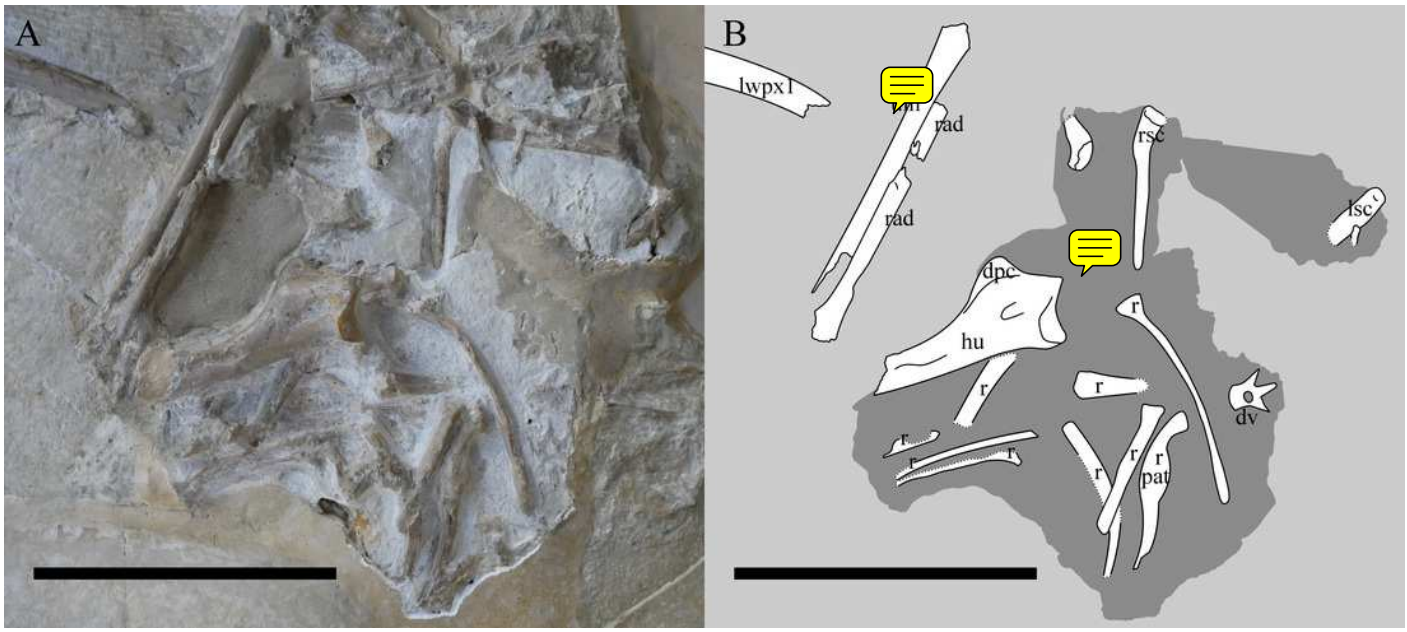

Figure 5

Broken wing phalanx of NHMUK PV OR 37002

Close up of the midshaft of a broken third wing phalanx on NHMUK PV OR 37002 showing the bone wall thickness. Scale in millimetres.

Figure 6

Skeletal reconstruction of a large and mature *Rhamphorhynchus*

Skeletal diagram of an osteologically mature *Rhamphorhynchus muensteri* based mostly on NHMUK PV OR 37002. Scale bar is 250mm.

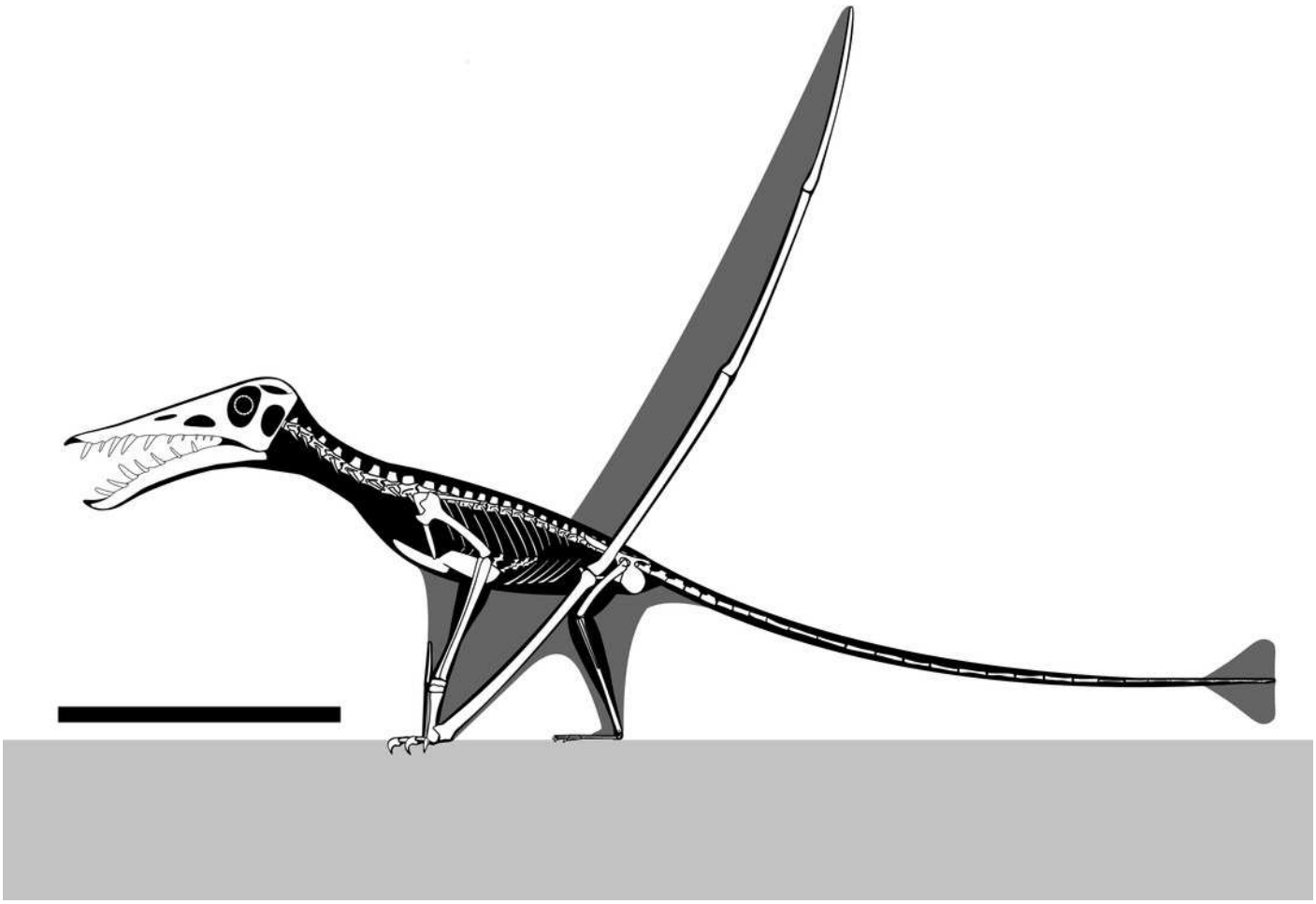

Figure 7

Size comparison of different specimens of *Rhamphorhynchus*

Size comparison of different *Rhamphorhynchus muensteri* specimens: (anti-clockwise from top left) the smallest known BMMS A3 (21 mm skull length), a generalised ‘typical adult’ specimen (122 mm skull length), the second largest known ‘Exemplar 81’ of Wellnhofer (150 mm skull length) and the largest known NHMUK PV OR 37002 (201 mm skull length). Scale bar is 1 metre.

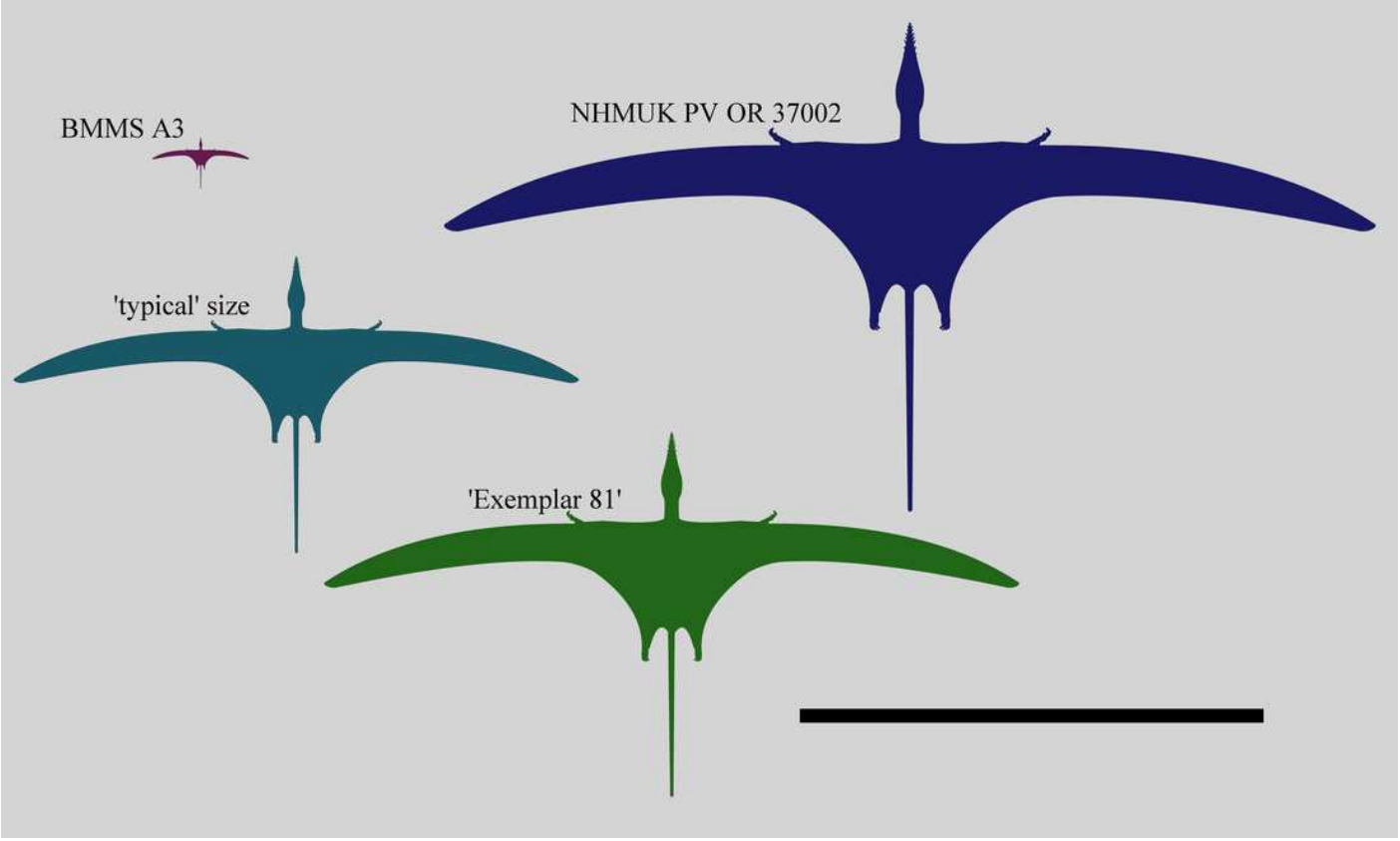

Figure 8

Variations in the structure of the posterior skull in derived non-monofenestratan pterosaurs.

Posterior part of skulls of large non-monofenestratan pterosaurs showing their temporal fenestrae: *Rhamphorhynchus* NHMUK PV OR 37002 and YPM VPPU 11981, *Dorygnathus* SMNS 55886 after Padian (2008) and Wellnhofer (1978), *Parapsicephalus* GSM 3166 mirrored after O'Sullivan & Martill (2017), *Angustinaripterus* ZDM T8001 after He et al. (1983), and *Dearc* NMS G.2021.6.1-4. Dotted lines represent reconstructed parts of the skull. Specimens not to scale.

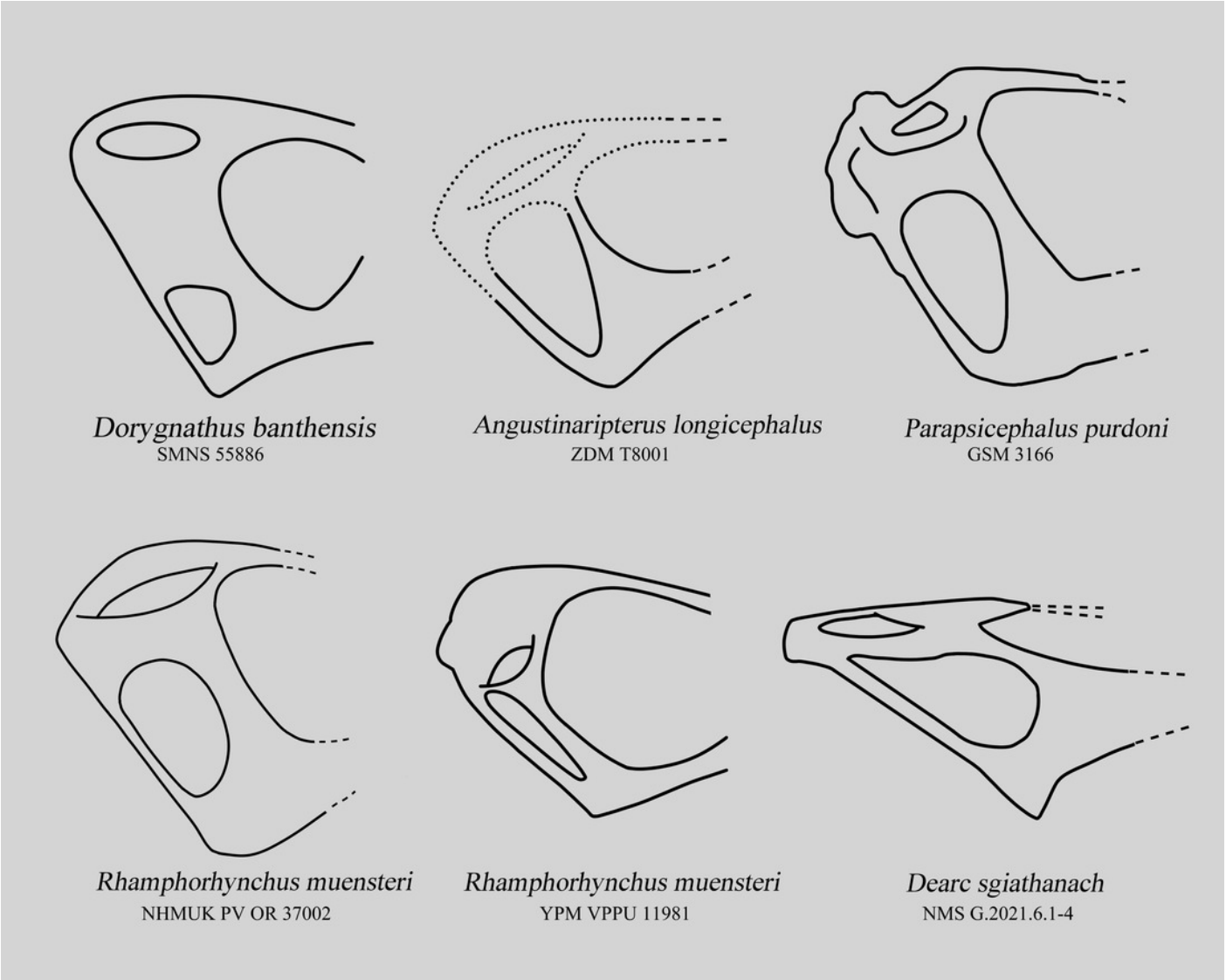
Dorygnathus banthensis
SMNS 55886
Angustinaripterus longicephalus
ZDM T8001
Parapsicephalus purdoni
GSM 3166
Rhamphorhynchus muensteri
NHMUK PV OR 37002
Rhamphorhynchus muensteri
YPM VPPU 11981
Dearc sgiathanach
NMS G.2021.6.1-4

Figure 9

Flattened teeth of NHMUK PV OR 37002

The anterior skull of NHMUK PV OR 37002 in ventrolateral view showing the relatively flattened teeth that are oval and not circular in cross-section. Scale bar is 50 mm.