

The taxonomy and systematics of *Parapsicephalus purdoni* **(Reptilia: Pterosauria) from the Lower Jurassic Whitby** **Mudstone Formation, Whitby, U.K.**

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Abstract

The Lower Jurassic (Toarcian) pterosaur *Parapsicephalus purdoni* (Newton, 1888) from the Whitby Mudstone Formation of North Yorkshire is known from a three-dimensionally preserved skull with brain cast. Since Newton's original description, its taxonomic status has been contentious. Several cladistic studies have placed it within either Dimorphodontidae or Rhamphorhynchidae. Some investigators have suggested that it is a junior synonym of the Toarcian pterosaur *Dorygnathus* from the Posidonia Shale of south-western Germany. The holotype skull (GSM 3166) is redescribed and its taxonomic status re-evaluated. Several apomorphies place it suggest it belongs in the Rhamphorhynchidae while autapomorphies of the palate and jugal distinguish *Parapsicephalus* from *Dorygnathus*, supporting the continued separation of the two genera.

1. Introduction

The Lower Jurassic marine strata of the United Kingdom yield a diverse assemblage of reptilian taxa (Owen, 1881), including ichthyosaurs, plesiosaurs, marine crocodiles and, more rarely, pterosaurs. While Lower Jurassic pterosaurs are best known from the Liassic strata of Dorset (Buckland, 1829; Benton and Spencer, 1995), one of the best preserved examples is a three-dimensional near-complete skull (GSM 3166, figs. 1, 2) from the Toarcian (~182 ma) Whitby Mudstone Formation of Loftus, Yorkshire. Identified as the holotype of *Parapsicephalus purdoni* by Newton, 1888, it is deposited in the British Geological Survey (BGS) at Keyworth, Nottinghamshire. It was first described by Newton (1888), after receiving the fossil on loan from the Reverend D. W. Purdon of Wolverhampton. The skull was found in a block of Alum Shale Member collected from Loftus Quarry near Whitby, Yorkshire (Grid Reference: NZ 73608 19816) and was prepared by Newton himself. During this process the parietals were accidentally lost, however this unfortunate event revealed an exceptionally well preserved three-dimensional brain endocast beneath. The specimen was identified as a pterosaur and first considered to be an example of the Upper Jurassic Solnhofen Limestone Formation genus *Scaphognathus* Goldfuss, 1831 based on a similarity in general morphology and structure of the cranial fenestrae. Noting differences in the dorsal curvature of the skull and the prominent median channel visible in dorsal view, Newton (1888) argued that the German and British *Scaphognathus*' were not conspecific. In honour of its discoverer, he named the new pterosaur *Scaphognathus purdoni* Newton, 1888. Newton further described the endocast, finding that it possessed several bird-like characteristics such as an enlarged cerebellum and while suggesting there may have been a descendant relationship, he considered it more likely that birds and pterosaurs were sister taxa (Newton, 1888).

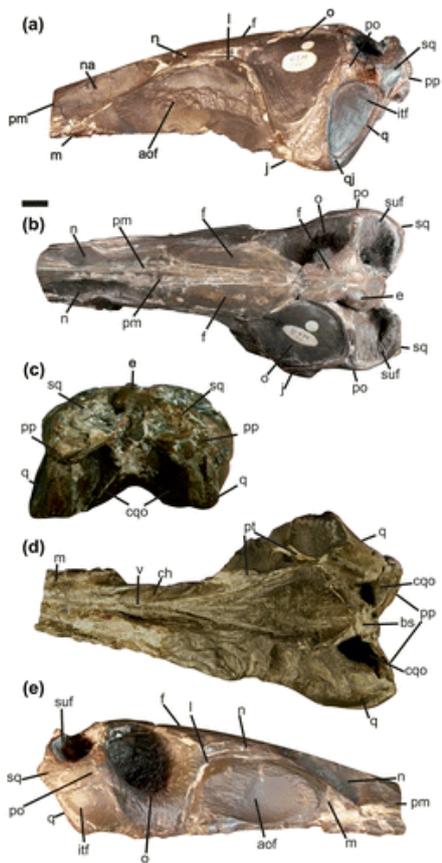


Figure 1: GSM 3166, the type specimen of *Parapsicephalus purdoni* from the Whitby Mudstone Formation of Loftus, Yorkshire. Presented in (a) left lateral, (b) dorsal, (c) posterior, (d) ventral and (e) right lateral views.

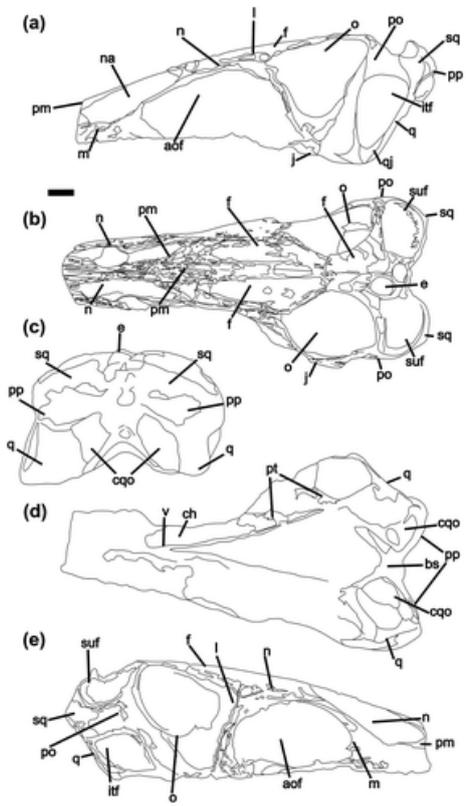


Figure 2: Schematic of GSM 3166 in (a) left lateral, (b) dorsal, (c) posterior, (d) ventral and (e) right lateral views.

The skull unfortunately received little attention following its initial description. Lydekker (1891) mentioned it briefly in a comparison of Upper Jurassic quadrates he had identified as pterosaurian and argued that Newton (1888) had been mistaken in his description of the quadrate. Plieninger (1894) compared *Scaphognathus purdoni* with *Campylognathus* (*Campylognathoides* Strand, 1928) and suggested that it was less like *S. crassirostris* than Newton (1888) had suggested. The skull of *Ornithodesmus* (= *Istiodactylus* Howse et al., 2001) was compared with GSM 3166 and it was suggested the skull configuration may represent a basal phase of pterosaur cranial morphology (Hooley, 1912). Arthaber (1919) re-examined GSM 3166 and identified it as a distinct genus based on its arched dorsal skull margin, elongate nares, large antorbital fenestra (AOF), large orbit, elongated prefrontals, 7 maxillary teeth and a deep sub-orbital jugal. The new genus *Parapsicephalus* was erected and it was suggested that based on the arched skull and deep jugal, it was more closely related to *Dimorphodon* (Buckland, 1829) than to *Scaphognathus*. In her description of the pterosaur brain, Edinger (1941) made several comparisons to *Parapsicephalus* although she referred to it as *Scaphognathus*. Kuhn (1967) provided a new reconstruction of the skull of *Parapsicephalus purdoni* (Fig. 3), later updated by Wellnhofer (1978), alongside a discussion of pterosaur neuroanatomy (Witmer et al., 2003). Most later authors considered *Parapsicephalus* to be some form of ‘rhamphorhynchid’ (Wellnhofer, 1978; Carrol, 1988; Unwin, 2003; Gasparini et al., 2004) but more recent studies (Andres and Myers, 2013; Andres et al., 2014) have supported Arthaber’s (1919) identification of *Parapsicephalus* as the sister taxon of *Dimorphodon*.

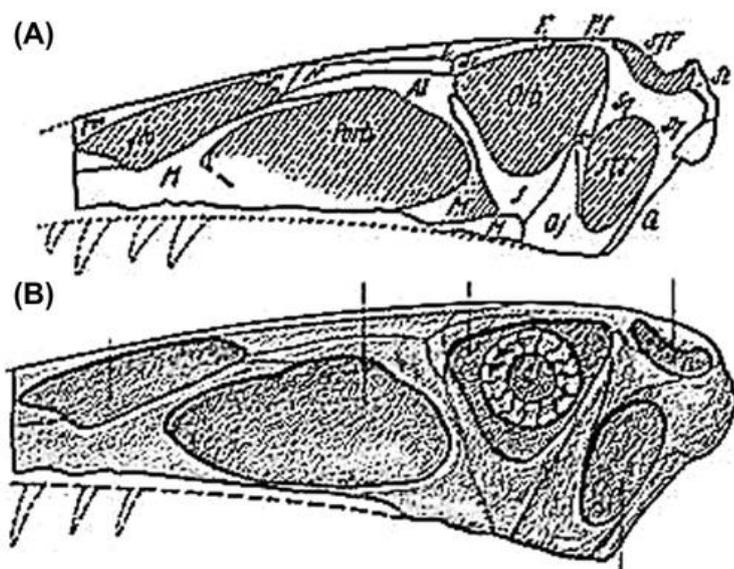


Figure 3: (A) Kuhn’s (1967 Kuhn O. 1967) reconstruction of the skull of *Parapsicephalus* GSM 3166. (B) Wellnhofer (1978 Wellnhofer P. 1978) updated version of the same arrangement with slightly updated sutures.

Carpenter et al. (2003) noted that Unwin (2003) had informally suggested *Parapsicephalus* may have been synonymous with the Lower Jurassic (Toarcian) German Posidonia Shale pterosaur *Dorygnathus* Wagner, 1860 but it was Unwin (2003) who first formally referred it to that genus as *Dorygnathus purdoni*. This reassignment was part of a much broader phylogenetic study and a detailed synonymy was not provided. Several authors accepted the new designation (e.g. Hone and Benton, 2007; Barrett et al., 2008) while others retained GSM 3166 in *Parapsicephalus* (e.g. Gasparini et al., 2004; Osi et al., 2010; Andres et al., 2014; Bennett, 2014). Despite the taxonomic debate concerning the taxonomic status of *Parapsicephalus*, there has been no detailed re-examinations of the skull itself. Taxonomic and familial assignments have been based on perceived similarities or through cladistics analysis. The use of cladistic methodologies in placing *Parapsicephalus* has been problematic given the contested nature of the Jurassic pterosaur tree, with several major studies producing conflicting results (e.g. Kellner, 2003; Unwin, 2003; Wang et al., 2009; Lü et al., 2010; Andres and Meyers, 2013) and *Parapsicephalus* falling in variable positions in each cladogram. This study focuses on a morphological approach with the primary goal of re-examining GSM 3166 to provide a detailed description and test the validity of *Parapsicephalus* as a distinct genus using modern taxonomic practices.

A new pterosaur skull was recently recovered from the Toarcian Epsilon Shales of Altdorf, Bavaria that resembles the holotype of *Parapsicephalus* (Fig. 4). It was originally collected in 1994 but has never been accessioned to a registered collection or published upon (Pursglove, 2010). It has since come into the ownership of an anonymous private collector and as such, it cannot be discussed in detail in any taxonomic context. It is figured here as it preserves some elements of the skull not present in GSM 3166 and has been used to assist in the development of a more accurate reconstruction of the skull (Fig. 5). The owner has assured us that on his passing, the specimen will be transferred to a well establish United Kingdom institution as part of a substantial donation.

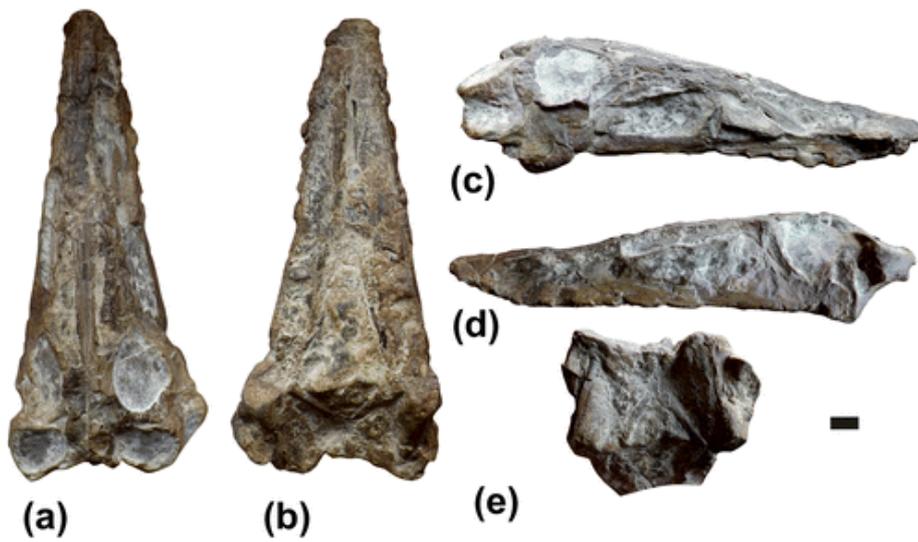


Figure 4: The Altdorf *Parapsicephalus* skull from the Lias of Altdorf, Bavaria.

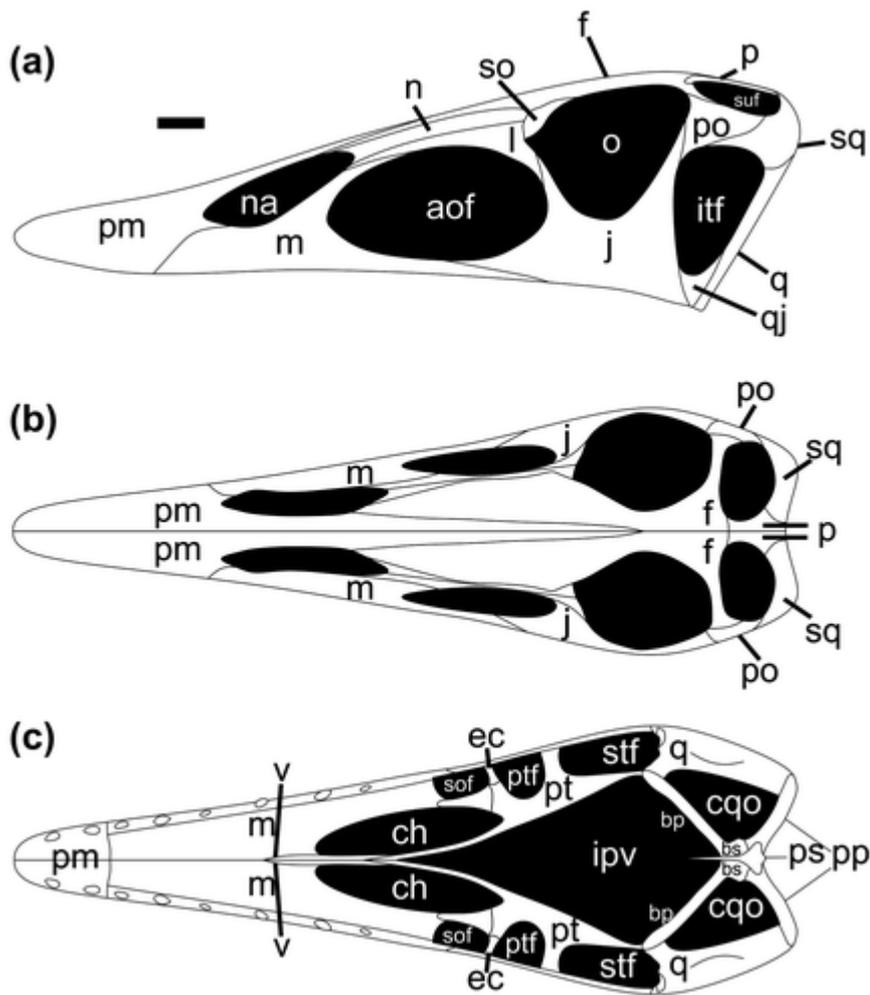


Figure 5: Reconstructions of the skull of *Parapsicephalus* in (a) left lateral, (b) dorsal and (c) ventral views.

Institutional abbreviations: BGS: British Geological Survey, Keyworth, United Kingdom;
 NHMUK: Natural History Museum, London, U.K.

2. Geology and stratigraphy

The Whitby Mudstone Formation (Fig. 6) is a Toarcian (upper Lower Jurassic) lithological unit cropping out across the north-east of England and is especially well-exposed in spectacular cliffs on the North Yorkshire coast around Whitby (Simms, 2004). The formation is divided into two sub-units; a lower Mulgrave Shale Member and an upper Alum Shale Member. The Mulgrave Shale Member is dominated by bituminous shales containing pyritic or sideritic concretions, while the Alum Shale Member is largely comprised of banded, pyritous shales interbedded with layers of calcareous nodules (Simms, 2004). The Whitby Mudstone Formation has yielded several exceptionally preserved Mesozoic reptiles including the plesiosaurs *Eretmosaurus* Seeley, 1874, *Sthenarosaurus* Watson, 1911 and *Microcleidus* Watson, 1911; the ichthyosaurs *Stenopterygius* Jaekel, 1904, *Temnodontosaurus* Lydekker, 1889 and *Eurhinosaurus* Abel, 1909; the thalattosuchians *Steneosaurus* Geoffroy, 1825 and *Pelagosaurus* Bronn, 1841; and indeterminate theropod remains (Benton and Spencer, 1995). The Alum Shale Member (*Hildoceras bifrons* zone) is divided into the Hard Shale Beds, Main Alum Shale Beds and Cement Shale Beds (Benton and Spencer, 1995), but the precise source horizon of GSM 3166 is uncertain. Newton (1888) deduced the skull came from the Alum Shale Formation but was unable to determine which bed. Due to the recorded provenance of several reptile fossils, Benton and Spencer (1995) suggested that all reptile fossils from the Loftus quarry were collected from the Main Alum Shale Beds. Morris (1979) described the Alum Shale Member as a restricted shale facies, consisting of poorly laminated sediments with scattered calcareous concretions, sparse benthic fauna and discrete pyrite burrows. It was most likely deposited in relatively shallow water with a somewhat anoxic sea floor (Simms, 2004).

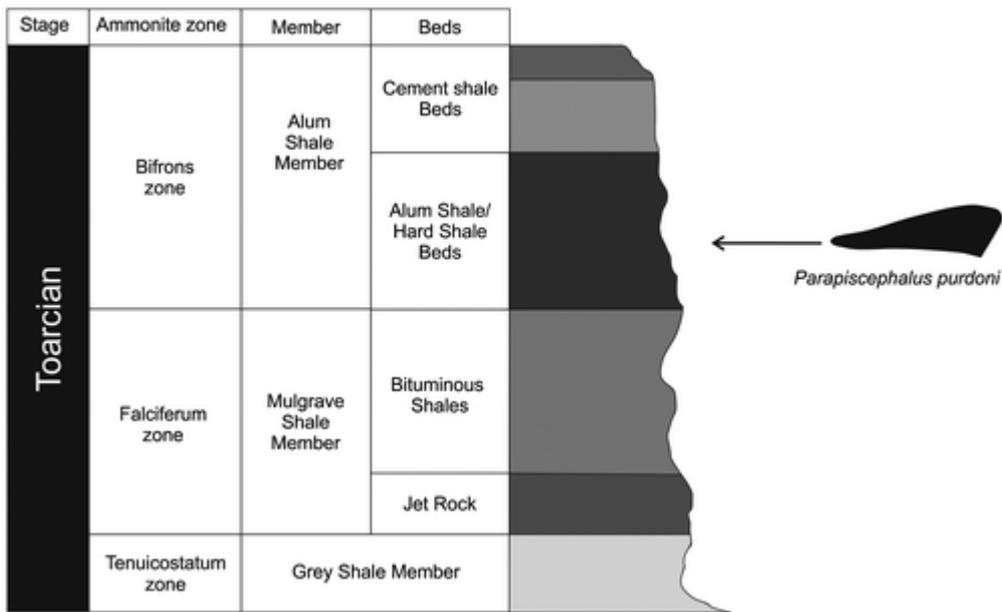


Figure 6: Simplified stratigraphic column for the Lower Toarcian Whitby Mudstone Formation of Yorkshire.

Three pterosaur specimens have been recovered from the Alum Shale Member (O’Sullivan et al., 2013), including the three-dimensional skull of *Parapsicephalus* (Newton, 1888) discussed here.

3. Locality

Specimen GSM 3166 was recovered from the Toarcian (~180 ma) Alum Shale Member of the Whitby Mudstone Formation in the Loftus Alum Shale Quarry, Loftus, Yorkshire (Benton and Spencer, 1995; Goldring, 2001; Simms, 2004). Although no longer operational and heavily overgrown, Loftus Alum Quarry is still accessible with exposures of fossiliferous strata, especially in adjacent coastal cliffs and the foreshore below. The quarry and nearby sea cliffs are part of the Loftus Quarry Alum Trail, and the site is now a nature reserve of the Tees Valley Wildlife Trust. The site can be easily accessed by following a cart track off the main Cleveland Way that extends through the North Yorkshire Moors National Park. Fossils have been documented from the Alum Shale quarries since the early 19th Century (Hunton (1836), but quarrying began as early as the 17th century. Most operations for alum extraction had finished by 1860 (Hunt et al. 2004).

4. Systematic palaeontology

Pterosauria Kaup, 1834

Rhamphorhynchidae Seeley, 1870

Rhamphorhynchinae? Nopcsa, 1928

Genus: *Parapsicephalus* Arthaber, 1919

Type species: *Parapsicephalus purdoni* (Newton, 1888)

Synonymy:

- 1888 *Scaphognathus purdoni* Newton, p. 503-537
- 1901 *Scaphognathus purdoni* (Newton), Seeley, p. 152
- 1912 *Scaphognathus purdoni* (Newton), Hooley, p. 372
- 1941 *Scaphognathus purdoni* (Newton), Edinger, p. 71
- 1967 *Parapsicephalus purdoni* (Newton), Kuhn, p. 8-9
- 1977 *Scaphognathus purdoni* Newton, Hopson, p. 433
- 1978 *Parapsicephalus purdoni* (Newton), Wellnhofer, p. 39
- 1991 *Parapsicephalus purdoni* (Newton), Wellnhofer, p. 78
- 1995 *Parapsicephalus purdoni* (Newton), Benton and Spencer, p. 118
- 1997 *Scaphognathus purdoni* Newton. Lü, Xiangke, Qizhi, Xikan and Dexin, p. 1127
- 2003 *Dorygnathus purdoni* (Newton), Carpenter, Unwin, Cloward, Miles and Miles, p. 47
- 2002 *Parapsicephalus purdoni* (Newton), Dalla Vecchia, Wild, Hopf and Reitner, p. 198
- 2003 *Dorygnathus purdoni* (Newton), Unwin, p. 177
- 2003 *Parapsicephalus purdoni* (Newton), Witmer, Chatterjee, Franzosa, and Rowe, p. 951
- 2004 *Parapsicephalus purdoni* (Newton), Jouve, p. 545
- 2004 *Parapsicephalus purdoni* (Newton), Gasparini, Fernández and de la Fuente, p. 925
- 2005 *Dorygnathus purdoni* (Newton), Unwin, p. 272
- 2008 *Dorygnathus purdoni* (Newton), Barrett, Butler, Edwards and Milner, p. 65
- 2010 *Parapsicephalus purdoni* (Newton), Andres, Clark and Xing, p. 171
- 2010 *Parapsicephalus purdoni* (Newton), Buffetaut, p. 3
- 2010 *Parapsicephalus purdoni* (Newton), Osi, Prondvai, Frey and Pohl, p. 244

- 2012 *Parapsicephalus purdoni* (Newton), Steel, p. 1346
- 2013 *Parapsicephalus purdoni* (Newton), O'Sullivan, Martill, and Groocock, p. 973-981
- 2013 *Dorygnathus purdoni* (Newton), Witton, p. 125
- 2014 *Parapsicephalus purdoni* (Newton), Bennett, p. 345

Type specimen: GSM 3166, a damaged but three-dimensional pterosaur skull, originally recovered from a pyritic mudstone concretion.

Horizon and age: Main Alum Shale Beds, Alum Shale Member, Whitby Mudstone Formation. Lower Jurassic, Toarcian (176-180 ma).

Type locality: Loftus Alum Shale Quarry, Loftus, North Yorkshire, United Kingdom.

Revised diagnosis: Non-monofenestratan pterosaur with the following combination of characters: a convex dorsal margin to the skull, giving the skull a gently convex appearance when viewed laterally; the jugal comprises at least 30% of the dorsoventral height of the skull; the dorsal processes of the jugal subtend an angle of $\sim 45^\circ$; the interchoanal vomers comprise 32% of the length of the pterygoid; the vomers comprise 60% of the length of the vomeral process of the pterygoid; the vomeral process of the pterygoid is 53% of the pterygoid length.

The holotype of *Parapsicephalus purdoni* GSM 3166 (Figs. 1, 2, 5) is a 140 mm long, near complete three-dimensional skull infilled with concretionary pyritic mudstone. The skull is compressed on its right side, deflecting the rostrum towards the left in dorsal view and flaring the left posterior skull. While it appears that the most of the external bone wall is present, much of the surface bone is missing, presumed lost to the surface of the missing outer concretion. The rostrum is broken and missing anterior of the nares, but the lateral margins of the rostrum are sufficiently well preserved to allow for a tentative restoration of this missing component. In lateral view the rostrum dips ventrally 11° relative to the posterior half of skull (Fig. 1). Based on a comparison with the skulls of *Scaphognathus* and *Dorygnathus* (Padian, 2008a; Bennett, 2014; Zhou, 2014), as well as the prenasal rostrum of the Altdorf skull, the length of the skull when complete is estimated to be between 180-196 mm.

The premaxillae are visible in lateral view proximal to the nares but are incomplete due to the broken rostrum. The frontal processes of the premaxillae extend posteriorly towards the orbit, intersecting the frontals, and are at least 95 mm long. A low ridge extends along the midline suture of the processes which may have supported a low crest (Dalla Vecchia et al., 2002). Kuhn (1967) figured the maxilla/premaxilla interface as a horizontal line extending beneath the anterior tip of the nares. There is a marked differentiation in the surface texture above and below this interface which may represent the maxillary/premaxillary suture. This is unlikely to be a taphonomic artefact, as it is mirrored on both sides of the skull. The maxillae are heavily damaged on GSM 3166, with the most complete section being the right anterior maxilla and the right nasal maxillary process. The lacrimal process forms the anterior margin of the AOF. It has a broad ventral base (16 mm), a lunate outline and is inclined posteriorly at 45° relative to horizontal. Newton (1888) interpreted the premaxillae as dominating the anterior ventral palate and extending posteriorly to the anterior margin of the choanae. However, Osi et al. (2010) show that the premaxillae are restricted to the palate anterior to the nares and only contact the choanae in pterodactyloids. Therefore, what Newton (1888) identified as the premaxillae are actually the ventral extensions of the maxillae. The teeth of GSM 3166 are preserved on what is referred to here as the interfenestrae maxilla, i.e. the portion of maxilla between the anterior border of the AOF and the anterior border of the nares. They are broken proximal to the ventral skull margin and as such are exposed only as alveoli. The alveoli are closely-spaced with three occupying the interfenestrae maxilla.

Kuhn (1967) identified a nasal and lacrimal on GSM 3166, but he figured the nasal as an elongate rectangular bone set just beneath the premaxillary processes of the frontal and labelled as the lacrimal. A third triangular bone, labelled AL (Fig. 3), is positioned on the dorsoposterior margin of the AOF. However, these regions of the skull are poorly preserved and hence more difficult to decipher. An impression of the nasal is present on the left side of the skull, dorsal to the AOF. It defines a thin rectangle with concave dorsal and ventral margins and is overlain by the premaxillary processes of the frontal. Impressions of the lacrimals are preserved on both sides with only small flakes of bone present. Based on a combination of the impressions and the shape of the AOF and the nasal, they are reconstructed here as 14 mm long, slender sub-scalene triangles (Fig. 5)

The frontals are divided into the main body of frontals and their premaxillary processes. The main body of the frontals are dorsal to the medial orbits. They are sub-rectangular bones with short posterolateral postorbital processes. Anteriorly the frontals develop into large, rhombic extensions which contact the nasals laterally and are intersected by the posterior processes of the premaxillae. The parietal was removed during preparation (Newton, 1888), exposing GSM 3166's endocast. The enlarged flocculae and the cerebrum are identifiable but other elements of the endocast are obscured by the surrounding bone and matrix. The supraorbital is missing from the left orbital margin, leaving an invasive concavity in its place. Most of the right supraorbital has broken away but the base of the bone remains. Both postorbitals are preserved and form the anterior half of the squamosopostorbital bar. They are thin tri-radiate bones with jugal, frontal and squamosal processes. The distal ends of the jugal and squamosal processes are approximately 15 mm apart. The squamosopostorbital bar is 18 mm anteroposteriorly and 7-8 mm dorsoventrally and forms the division between the temporal fenestrae. Both squamosals are preserved but only the small portion that makes up the postorbital-squamosal bar is visible. The squamosal is a tri-radiate bone surrounded by the quadrates, the postorbitals and the parietals. They form the lateral posterior margin of the supratemporal fenestra. The posterior margins of the squamosals are overlapped by the paraoccipital processes. Both quadrates are preserved although the right quadrate is missing approximately one third of its length. The left quadrate is complete apart from its ventral glenoid articulation. They are strap-like bones, laterally expanded in ventral view.

Only the left jugal is preserved on GSM 3166. Newton (1888), Kuhn (1967) and Wellnhofer (1978) figure the jugal as a bi-radiate V-shaped bone, with a correspondingly hyper-enlarged quadratojugal. There is a clear textural difference across the margin interpreted here as a suture. Posterior to this suture the bone is highly rugose and worn while anterior to the suture most of the surface bone is missing. What was previously interpreted as two separate bones (Kuhn, 1967; Wellnhofer, 1978) appears to be a single poorly preserved jugal. The lacrimal process is identifiable although it is poorly preserved and the maxillary process is absent on GSM 3166 but is identifiable on the Altdorf skull. The jugal has the typical tetra-radiate structure seen in most non-pterodactyls. The estimated length of the lacrimal process is 20 mm (142% of the dorsoventral depth of the jugal body). The postorbital process is more robust than the lacrimal process (2.6 times as wide at its base) and is approximately 18 mm long (135% of the dorsoventral depth of the jugal body). The

lacrimal and postorbital processes form a 45° arc around the ventral orbit. The quadratojugal process is a 3-4 mm long sub-triangular process on the posteroventral jugal. The quadratojugal has a semilunate outline and is located at the base of the infratemporal fenestra, positioned between the jugal and the quadrate (Fig. 5).

The morphology of the occipital region of the skull is complex and difficult to interpret due to fracturing and partial erosion. The foramen magnum is represented by a 7 mm oval matrix filled aperture situated between the paraoccipital processes. The paraoccipital processes are robust and spatulate extending between the occipital midline of the skull to the squamosal. The processes are 23 mm mediolaterally, 7 mm dorsoventrally proximal to the sagittal plane, 8 mm medially and 16 mm at the squamosal articulation. The basisphenoid is a broad plate-like element with a rounded concavity, forming the ventral half of the posterior midline of the skull. The basiptyergoids are anteroventrally projecting, rod-like struts that articulate with the pterygoids to form an angle of 68° .

Several elements of an incomplete palate are present in GSM 366. The palatine is only visible on the left side. The pterygoids are broken with only a few sections preserved however the impressions of the bones are sufficient to indicate a total length of 58 mm. The vomeral process of the pterygoid makes up 53% (31 mm) of the total pterygoid length. Approximately half of the vomers are sandwiched between the maxillae, with the rest extending posteriorly along the palate to articulate with the pterygoids. The length of the free vomers between the pterygoid and the maxillae is 19 mm, 60% the length of the vomeral processes of the pterygoid, and 32% of the overall pterygoid length.

The outline of the AOF is preserved on the right side of the skull. It is a broad oval with a more rounded posterior margin, 45 mm anteroposteriorly and 24 mm dorsoventrally. Arthaber (1919) figures the nares as an elongate oval, but Kuhn (1967) reconstructs them as sub-rectangular openings. While the posteroventral margin of the nares is identified as convex and the anterior margin slightly pointed, the posterior margin is less apparent, although slight impressions suggest that it is sub-rounded. Unfortunately, the Altdorf skull has severely damaged external nares and provides no new information on their structure. The orbit in GSM 3166 is 34 mm dorsoventrally and 32 mm anteroposteriorly at its widest point and is piriform. The supratemporal fenestrae are broad, slightly quadrangular ovals, although neither is complete in GSM3166. The

infratemporal fenestrae are dorsoventrally elongate openings with a broadly similar shape as the orbits. The post-temporal fenestrae are small oval openings directly above the paraoccipital processes. The infratemporal fenestrae are large but squat openings ventral to the paraoccipital processes.

5. Comparison

Although GSM 3166 is preserved as a three-dimensional skull, the fragmentary and worn nature of several elements limits some of its comparative information (Fig. 7). The separation of the nares and AOF in GSM 3166 clearly identifies it as a non-monofenestratan pterosaur (Lü et al., 2010). The nasal process of the maxilla is 35° relative to the horizontal axis. A similar angle is found in the maxillary process of the nasal in *Rhamphorhynchus* Meyer, 1847 NHMUK PV 47002 (Wellnhofer, 1975) and *Scaphognathus* (Bennett, 2014). Higher angles are found in *Austriadactylus* Dalla Vecchia et al., 2002 (Dalla Vecchia, 2009), *Dimorphodon* (Owen, 1859) and *Dorygnathus* (Padian, 2008a). Shallower angles occur in *Cacibupteryx* Gasparini et al., 2004 and *Angustinaripterus* He et al., 1983. The semi-lunate shape of the process is most similar to that of *Eudimorphodon* (Wild, 1979).

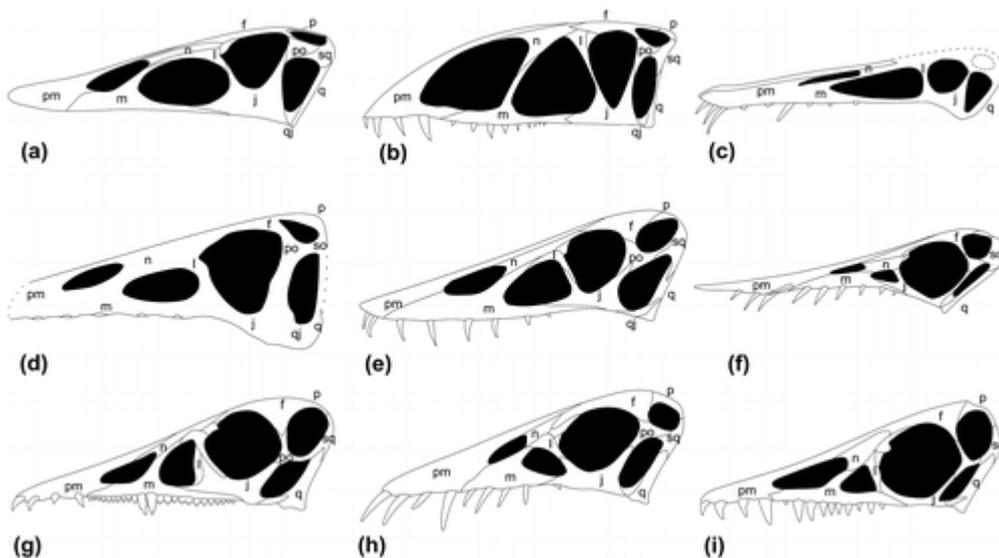


Figure 7: Reconstructions of several pterosaur skulls. (a) *Parapsicephalus*. (b) *Dimorphodon* (modified from Padian 1983). (c) *Angustinaripterus* (modified from He et al. 1983). (d) *Cacibupteryx* (modified from Gasparini et al. 2004). (e) *Scaphognathus* (modified from Wellnhofer 1978 and Bennett 2014). (f) *Rhamphorhynchus* (modified from Wellnhofer 1975). (g) *Eudimorphodon* (modified from Wild 1979). (h) *Campylognathoides* (modified from Wild 1979). (i) *Dorygnathus* (modified from Wild 1979).

The premaxilla undercutting the nares is similar to most basal pterosaurs including the Late Triassic *Eudimorphodon* and the Early Jurassic *Campylognathoides* (Wild, 1979). Premaxillae in more derived

pterosaurs such as *Scaphognathus* (Bennett, 2014) or *Dorygnathus* (Padian, 2008a) have reduced the maxillary processes such that they only extend slightly beneath the anterior border of the nares. The Upper Jurassic *Cacibupteryx* of Cuba may have a larger extension but this is only suggested by an incomplete line in a drawing of the skull (Gasparini et al., 2004).

In GSM 3166 the interorbital frontals are transversely constricted in dorsal view. Similarly, thin frontal bodies are found in *Rhamphorhynchus* (Witmer et al., 2003), *Sericipterus* Andres et al., 2010, *Dorygnathus* (Padian, 2008a) and *Campylognathoides* (Padian, 2008b). In contrast, the frontal bodies of *Cacibupteryx* (Gasparini et al., 2004) are extremely broad, more like those of a theropod dinosaur (Langer, 2004).

The angle formed by the lacrimal and postorbital processes of the jugal is 45° , giving the ventral orbit a more angled appearance. In *Dorygnathus* the processes form an angle of $78-93^\circ$, giving it a much broader ventral orbit (Padian, 2008a). *Angustinaripterus* from the Middle Jurassic of China has a jugal with processes forming a similar angle of 46° (He et al., 1983). In *Scaphognathus* the lacrimal and postorbital processes an angle of $80-100^\circ$, the largest angle being found in the juvenile SMNS 59395 (Cheng et al., 2012; Bennett, 2014).

Campylognathoides has a broad ventral orbit with the jugal processes forming an angle of 77° (Padian 2008b). Similarly, *Eudimorphodon* has a large ventral orbit, the processes forming an 88° angle.

Rhamphorhynchus is unusual in having a faux-triradiate jugal with a ventral orbit defined by the postorbital process and the elongate main body of the jugal. The angle formed is $97-110^\circ$ (Wellnhofer, 1975; Witmer et al., 2003). *Dimorphodon* has a similar ventral orbit shape to GSM 3166, with the processes forming an angle of 47° (Owen, 1859).

GSM 3166 has a thick jugal, comprising 30% of the skull height. *Dorygnathus* has a slightly thinner jugal with the highest value being 26% (Padian, 2008a). The jugal of *Rhamphorhynchus* is thinner still, reaching a maximum of 18% in the most robust animals (Wellnhofer, 1975). *Angustinaripterus* has a jugal 23% of the skull (He et al., 1983), while *Scaphognathus* reaches 12-17% in the European specimens and 26% in the Chinese (Wellnhofer, 1975; Wellnhofer, 1978; Cheng et al., 2012; Bennett, 2014). *Campylognathoides* has

one of the thinnest jugals, with the highest percentage being only 12% (Wild, 1979; Padian, 2008a).

Eudimorphodon has a thicker jugal at 21% of the dorsoventral skull height (Wild, 1979; Dalla Vecchia, 2009). *Dimorphodon* has a thick jugal but a tall posterior skull (Padian, 1983), with the jugal ranging between 19-23% of the skull height.

In GSM 3166 the quadrate is angled posteriorly at between 115-130°, depending on what is considered a natural skull orientation. *Dorygnathus* and *Campylognathoides* share a similar condition, ranging between 120-130° (Padian, 2008a, 2008b). *Rhamphorhynchus* exhibits a more extreme inclination of 130-150° (Wellnhofer, 1975; Wellnhofer, 1978; Witmer et al., 2003), closer to values found in pterodactyloids (Wellnhofer, 1991). *Dimorphodon* has a near vertical quadrate, only slightly angled posteriorly at 95° (Owen, 1849; Padian, 1983) whereas *Eudimorphodon* and *Scaphognathus* all have quadrates angled posteriorly at 120° (Dalla Vecchia, 2009; Cheng et al., 2012; Bennett, 2014). *Angustinaripterus* is similar to *Rhamphorhynchus* in that its quadrate is more steeply angled than most basal pterosaurs at 140° (He et al., 1983).

Unlike the majority of pterosaurs, GSM 3166 has a convex dorsal margin to the skull. Comparisons with the Altdorf skull suggest that this may be exaggerated in GSM 3166 with taphonomic compression of the rostrum, but the skull can be confirmed to have a natural gentle convexity to its dorsal surface. Several pterosaurs have straight dorsal skull margins (Gasparini et al., 2004; Padian, 2008b; Bennett, 2014) whereas many develop variable levels of concavity, usually positioned more anteriorly (Wild, 1979; Wellnhofer, 1975; He et al., 1983; Padian, 2008a; Dalla Vecchia, 2009). Only *Dimorphodon* and *Peteinosaurus* Wild, 1979 share a similar convexity (Wellnhofer, 1991).

Most *Rhamphorhynchus* specimens have 3 interfenestral maxillary teeth but there are three figured examples possessing just two (Wellnhofer, 1975 figs 25-27). *Dorygnathus* has at least three interfenestral teeth with a hint of a possible fourth in some specimens (Padian, 2008a). *Angustinaripterus* has at least two interfenestral teeth and a third which straddles the anterior narial border (He et al., 1983). *Scaphognathus* and *Cacibupteryx* have broad, widely spaced teeth with space for two interfenestral maxillary teeth (Gasparini et al., 2004; Cheng et al., 2012; Bennett et al., 2014). *Campylognathoides* and all other non-rhamphorhynchid

basal pterosaurs have between five and thirteen interfenestral maxillary teeth (Wild, 1979; Padian, 1983; Padian, 2008b; Dalla Vecchia, 2009).

The interchoanal vomers in GSM 3166 are 32% the total length of the pterygoid (main pterygoid body + vomeral process). In *Cacibupteryx* and *Scaphognathus*, the vomers make up 44-46% of the pterygoid length (Wellnhofer 1978; Osi et al., 2010; Bennett, 2014) while in *Rhamphorhynchus* and *Dorygnathus* they comprise 55-57% (Witmer et al., 2003; Osi et al., 2010). *Campylognathoides* has the longest interchoanal vomers at 60% the total pterygoid length (Wellnhofer, 1978; Padian 2008b). The interchoanal vomers of GSM 3166 also make up 60% of the vomeral processes of the pterygoids. *Campylognathoides* has elongate vomers which are 144% of the vomeral processes (Wellnhofer, 1978). In *Cacibupteryx*, the vomers are ~142% the length of the vomeral processes (Osi et al., 2010). *Scaphognathus* has relatively short vomers at 72% the vomeral process length (Wellnhofer, 1978; Bennett, 2014) while *Rhamphorhynchus* exhibits an extreme condition with the vomers being up to 175% the length of the vomeral processes (Witmer et al., 2003). The vomeral processes themselves in GSM 3166 are 53% of the total pterygoid length. *Dorygnathus* is most similar, with the processes being 40% of the pterygoid length (Osi et al., 2010) while in *Cacibupteryx*, they only reach 25% (Gasparini et al., 2004; Osi et al., 2010). The highly derived *Rhamphorhynchus* has reduced to the vomeral processes to 15% (Wellnhofer, 1975; Witmer et al., 2003). *Scaphognathus* has elongate vomeral processes which reach 62% of the pterygoid (Wellnhofer 1978, Bennett, 2014), but *Campylognathoides* is similar to GSM 3166 with vomers ~46% of the pterygoid length (Wellnhofer 1975). The basiptyergoids of GSM 3166 form an angle of 68°. In *Dorygnathus* the angle is 55° (Padian 2008a) and 20° in *Rhamphorhynchus* (Wellnhofer 1975, Witmer et al., 2003). The basiptyergoids in *Bellubrunnus* Hone et al., 2012 create an angle of 38° (Hone et al., 2012) and in *Scaphognathus* 56° (Wellnhofer 1978). In the Toarcian-Bajocian *Allkaruen* Codorniu et al., 2016 of Argentina the basiptyergoids form an angle of 20-25°.

The orbit in GSM 3166 is a broad-based inverted piriform shape. In the Late Triassic *Caviramus* Fröbisch and Fröbisch, 2006 the orbit is a sub-circular/sub-oval fenestra with a weakly expanded anteroventral margin (Stecher, 2008). The orbit in *Scaphognathus* (Bennett, 2014) is sub-circular with somewhat angular margins in flappings (precocial infants *sensu* Unwin, 2005), becoming less broad ventrally with age.

Angustinaripterus (He et al., 1983) has a sub-circular orbit, slightly expanded anteriorly and posterodorsally. The orbit in *Rhamphorhynchus* (Wellnhofer, 1975; Witmer et al., 2003; Witton, 2013) is disproportionately large compared to the skull. In *Dimorphodon* (Padian, 1983) and *Peteinosaurus* (Wild, 1979), the orbit is piriform but set higher up the skull than in GSM 3166 and is thinner ventrally. *Cacibupteryx*'s (Gasparini et al., 2004) orbit is similar to GSM 3166, although the ventral border of the orbit is angled more ventroposteriorly than in the other taxa. In *Dorygnathus* (Padian, 2008a) the orbit has a broad almost sub-triangular ventral margin, with a more rounded dorsal surface. *Campylognathoides* (Padian, 2008b) has an orbit which is more rounded than in *Dorygnathus*.

GSM 3166 has an oval supratemporal fenestra in dorsal view. In *Rhamphorhynchus* these fenestrae are more rectangular, bordering on trapezoidal (Wellnhofer, 1975; Witmer et al., 2003). *Cacibupteryx* (Gasparini et al., 2008) has a more elongated oval supratemporal fenestra. In GSM 3166 the infratemporal fenestra is an elongate inverted sub-piriform shape. A similar shape is seen in *Scaphognathus* (Cheng et al., 2012). *Dorygnathus* and *Angustinaripterus* have more oval fenestrae although they are equally elongate (He et al., 1983; Padian, 2008b). The fenestra in *Rhamphorhynchus* is much thinner than most basal pterosaurs and more steeply angled posteriorly (Witmer et al., 2003). In *Eudimorphodon* the infratemporal fenestra is an ovaloid, almost sub-rectangular shape with a slight dorsoposterior extension (Dalla Vecchia 2009).

6. The identification of *Parapsicephalus*.

The pterosaurian nature of GSM 3166 is not in question due to its thin bone wall visible at the rostral break, sub-terminal nasal opening (Lü et al., 2010), and elongate premaxillary frontal process (Serenó, 1991). Historically, *Parapsicephalus* has been considered a scaphognathine (Newton, 1888), a rhamphorhynchine (Unwin, 2003) and a dimorphodontid (Arthaber, 1919; Andres et al., 2014). The most poorly supported of these relationships is *P. purdoni* as a dimorphodontid. The relationship is largely based on the convexity of the dorsal skull margin, the inverted piriform orbit, the angle of the quadrate and the dorsoventrally thick jugal (Andres and Myers, 2014). However, GSM 3166 in combination with new information from the Altdorf skull undermines this relationship. While convex, the dorsal margin of the skull does not curve to the extreme degree seen in either *Dimorphodon* or *Peteinosaurus*, and while the orbit is piriform, the jugal of

Dimorphodon is thinner dorsoventrally than either *P. purdoni* or the majority of non-pterodactyloid pterosaurs relative to skull height. Furthermore, rather than being angled nearly vertical as in *Dimorphodon*, the quadrate of *P. purdoni* is closer to most non-monofenestratans such as *Eudimorphodon*, *Dorygnathus* and *Scaphognathus*. *Parapsicephalus purdoni* can further be distinguished from dimorphodontids by its AOF with a ventral border strongly deflected below that of the nares and having a marked difference in the relative dorsoventral size of the fenestrae, having less than 5 interfenestral maxillary teeth, a skull with a length/width ratio of ~4/1 compared to *Dimorphodon*'s 2.8/1 (Owen, 1859), and the elongate slightly up-curved rostrum with laterally splayed alveoli. These differences support Newton's (1888) and Unwin's (2003) allying of *Parapsicephalus* with Rhamphorhynchidae.

Whether or not GSM 3166 is a scaphognathine or a rhamphorhynchine is less certain. The content of both groups is currently quite fluid with several taxa moving between both in various phylogenetic models (Unwin, 2003; Kellner, 2003; Wang et al, 2009; Lü et al., 2010; Lü et al, 2012; Andres et al., 2014). Furthermore, as previously mentioned, *Parapsicephalus* has been considered a junior synonym of *Dorygnathus* (Unwin, 2003). Based on the thickness of the jugal, the more strongly piriform orbit, the shorter interchoanal vomers, the gentle convexity of the dorsal margin of the skull, the more strongly upturned rostrum and the more elongate vomeral processes of the pterygoid all indicate that the two taxa are distinct. *Parapsicephalus* is distinguished from scaphognathines (*sensu* Lü et al., 2012) based on a combination of three interfenestral maxillary teeth, an AOF at least twice as long as it is wide (Unwin, 2003; Andres et al., 2010; Lü et al., 2012), a concave posterior AOF margin (Lü et al., 2012), the nasal process of the maxilla being more strongly posteriorly inclined and a quadrate probably inclined more than 120° (Lü et al., 2012). This character combination supports a rhamphorhynchine identification. In comparison to rhamphorhynchines excepting *Dorygnathus*, the jugal of *Parapsicephalus* is at least 7% thicker than in *Angustinaripterus* and *Rhamphorhynchus*; the angle formed by the lacrimal and postorbital processes of the jugal being approximately half that of other rhamphorhynchines except for *Angustinaripterus*; a convex dorsal margin of the skull; the interchoanae vomers make up 32% of the total length of the pterygoid, below that of *Rhamphorhynchus*; the vomers comprise 60% of the length of the vomeral process of the pterygoid, less than other rhamphorhynchines; the vomeral process of the pterygoid is 53% of the pterygoid length,

longer than in *Rhamphorhynchus*. This combination of characters provides a new diagnosis for *Parapsicephalus purdoni* and supports it being a distinct genus.

While *Parapsicephalus* is regarded as a rhamphorhynchid, it is presented as ?Rhamphorhynchinae due to several factors. Firstly, while GSM 3166 has several features distinguishing it from scaphognathines, the piriform infratemporal fenestra and the large AOF are features more common in scaphognathines. Secondly the reclined lunate nasal process of the maxilla and the premaxilla extending beneath the nares are conditions found in non-rhamphorhynchid pterosaurs such as *Campylognathoides* and *Eudimorphodon*. While there appear to be more rhamphorhynchine characters shared with *Parapsicephalus* the presence of two more scaphognathine characters as well as two characters generally associated with more basal pterosaurs suggests that rather than belonging to either of the terminal clades, *Parapsicephalus* may be a more basal rhamphorhynchid, a notion that is not at odds with its stratigraphic occurrence in the late Early Jurassic. Furthermore, the recent description of *Allkaruen* Codorniu et al. 2016, raises questions as to the potential relationships of derived brevipennate pterosaurs (*sensu* Unwin, 2003). *Allkaruen* is identified as a derived pterosaur identified as the sister taxon to Monofenestrata (Codorniu et al., 2016) and is known from contemporaneous strata but is difficult to compare to *Parapsicephalus* in detail due to the only overlapping elements being the basiptyergoids. Ultimately a detailed comparison between the two taxa is beyond the methodology of this paper but hopefully will be considered in future studies.

Although placement of *Parapsicephalus* in Rhamphorhynchinae is considered tentative, the new diagnosis strongly supports the retention of *Parapsicephalus* as a distinct genus. Furthermore, the Altdorf skull suggests that *Parapsicephalus* appeared to have occurred more widely across Laurasia than previously thought.

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Figures captions

Fig. 1. GSM 3166, the type specimen of *Parapsicephalus purdoni* from the Whitby Mudstone Formation of Loftus, Yorkshire. Presented in (a) left lateral, (b) dorsal, (c) posterior, (d) ventral, and (e) right lateral views. Abbreviations – aof, antorbital fenestra; bs, basisphenoid; ch, choana; cqo, cranial quadrate opening; e, endocast; ec, ectopterygoid; f, frontal; ipv, interpterygoid vacuity; itf, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; n, nasal; na, nares; o, orbit; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; pp,

paraoccipital process; ps, parasphenoid; potf, posterior temporal fenestra; ptf, pterygoectopterygoid fenestra; so, supraorbital; sq, squamosal; stf, suborbital fenestra; suf, supratemporal fenestra; q, quadrate; qj, quadratojugal. Scale = 10 mm.

Fig. 2. Schematic of GSM 3166 in (a) left lateral, (b) dorsal, (c) posterior, (d) ventral, and (e) right lateral views. Abbreviations – aof, antorbital fenestra; bs, basisphenoid; ch, choana; cqo, cranial quadrate opening; e, endocast; ec, ectopterygoid; f, frontal; ipv, interpterygoid vacuity; itf, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; n, nasal; na, nares; o, orbit; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; pp, paraoccipital process; ps, parasphenoid; potf, posterior temporal fenestra; ptf, pterygoectopterygoid fenestra; so, supraorbital; sq, squamosal; stf, suborbital fenestra; suf, supratemporal fenestra; q, quadrate; qj, quadratojugal. Scale = 10 mm.

Fig. 3. (A) Kuhn's (1967) reconstruction of the skull of *Parapsicephalus* GSM 3166. Note the unusual biradiate jugal and hyper-enlarged quadratojugal. (B) Wellnhofer's (1978) updated version of the same arrangement with slightly updated sutures.

Fig. 4. The Altdorf *Parapsicephalus* skull from the Lias of Altdorf, Bavaria. The specimen is currently held in a private collection. Scale = 10 mm.

Fig. 5. Reconstructions of the skull of *Parapsicephalus* in (a) left lateral, (b) dorsal and (c) ventral views. Given the relatively poor preservation of the skull, most of the margins presented are speculative and in part based off of the arrangement seen in *Dorygnathus* (Padian, 2008a) and *Rhamphorhynchus* (Wellnhofer, 1975). Abbreviations – aof, antorbital fenestra; bp, basiptyergoids; bs, basisphenoid; ch, choana; cqo, cranial quadrate opening; ec, ectopterygoid; f, frontal; ipv, interpterygoid vacuity; itf, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; n, nasal; na, nares; o, orbit; p, parietal; pm, premaxilla; po, postorbital; pp, paraoccipital process; ps, parasphenoid; ptf, pterygoectopterygoid fenestra; so, supraorbital; sq, squamosal; stf, suborbital fenestra; suf, supratemporal fenestra; q, quadrate; qj, quadratojugal. Scale = 10 mm.

Fig. 6. Simplified stratigraphic column for the Lower Toarcian Whitby Mudstone Formation of Yorkshire. All pterosaur material has been recovered from the Alum Shale/Hard Shale beds of the Alum Shale Member. Modified from Simms (2004).

Fig. 7. Reconstructions of several pterosaur skulls. (a) *Parapsicephalus*. (b) *Dimorphodon* (modified from Padian et al., 1983). (c) *Angustinaripterus* (modified from He et al., 1983). (d) *Cacibupteryx* (modified from Gasparini et al., 2004). (e) *Scaphognathus* (modified from Wellnhofer, 1978 and Bennett, 2014). (f) *Rhamphorhynchus* (modified from Wellnhofer, 1975). (g) *Eudimorphodon* (modified from Wild, 1979). *Dorygnathus* (modified from Wild, 1979). *Campylognathoides* (modified from Wild, 1979). Abbreviations f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; na, nares; p, parietal; pm, premaxilla; po, postorbital; sq, squamosal; q, quadrate; qj, quadratojugal. Not to scale.