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RESEARCH PAPER

A new species and the earliest occurrence of the Gnathosaurinae (Pterosauria) from the Late Kimmeridgian of Brunn, Germany

Alexandra E. Fernandes[1,2,3] · **Helmut Tischlinger**[4,5] · **Monika Rothgaenger**[6] · **Oliver W. M. Rauhut**[1,2,7]

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Abstract

The so-called "Solnhofen limestones" of southern Germany are widely recognized for their abundance of Late Jurassic fossil vertebrates, with pterosaurs being no exception. Within the recognized plenitude of the pterosaurs within this assemblage, although ctenochasmatid remains are relatively abundant, gnathosaurines are scarce, with only one known Solnhofen representative of the group known thus far. The Late Kimmeridgian locality of Brunn (near Regensburg, Germany) represents the oldest locality of the Solnhofen complex ("Solnhofen Archipelago" in recent literature), with only one pterosaur having been described from this locality to date. Here, a second pterosaur taxon from within this locality and a new gnathosaur is introduced, *Spathagnathus roeperi* gen. et sp. nov., whose novel tooth and dental enamel features add to the known dental diversity for the group. The new taxon represents the oldest occurrence of a gnathosaurine and contributes to the paleoenvironmental stratigraphic range for the Gnathosaurinae within the overall fossil assemblage of the Solnhofen Archipelago. Furthermore, the new taxon adds to the known diversity of ctenochasmatids in the Late Jurassic and underlines the importance of this early radiation of pterodactyloid pterosaurs during this time.

Keywords Pterosauria · Gnathosaurinae · Mesozoic · Jurassic · Germany · Solnhofen Archipelago

Introduction

The so-called "Solnhofen limestones" of southern Germany are widely recognized as one of the most productive fossil Konservat-Lagerstätten known to date (see Arratia et al., 2015, and references therein). The localities and beds found in the area between Solnhofen and Regensburg have been continually explored for some 200 + years (throughout the present day), yielding exceptional material at a prolific rate, and thereby giving a uniquely comprehensive insight into a subtropical shallow marine paleoenvironment of the Late Jurassic. Despite this long history of research, new species are still described frequently (e.g. Bever & Norell, 2017; Ebert et al., 2016; Hone et al., 2012; López-Arbarello & Sferco, 2011; Rauhut et al., 2012; Schröder et al., 2012; Villa et al., 2021), highlighting the broad scope of ecological specialization and paleobiodiversity inherently held in this, or any other such exceptionally-preserved microcosm of an ancient environment.

The high paleobiodiversity of the faunal assemblage in the overarching Solnhofen region is attributed to its original depositional setting in depressions within a shallow marine reef environment at the northern shore of the Tethys Ocean

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✉ Alexandra E. Fernandes
fernandes@snsb.de

[1] SNSB, Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany

[2] Department of Earth and Environmental Sciences, Ludwig-Maximilians-University, Theresienstraße 41, 80333 Munich, Germany

[3] American Museum of Natural History, 200 Central Park West, New York, New York 10024, USA

[4] Tannenweg 16, 85134 Stammham, Germany

[5] Jura-Museum Eichstätt, Willibaldsburg, 85072 Eichstätt, Germany

[6] Museum Solnhofen, Bahnhofstraße 8, 91807 Solnhofen, Germany

[7] GeoBioCenter, Ludwig-Maximilians-Universität, Luisenstraße 37, 80333 München, Germany

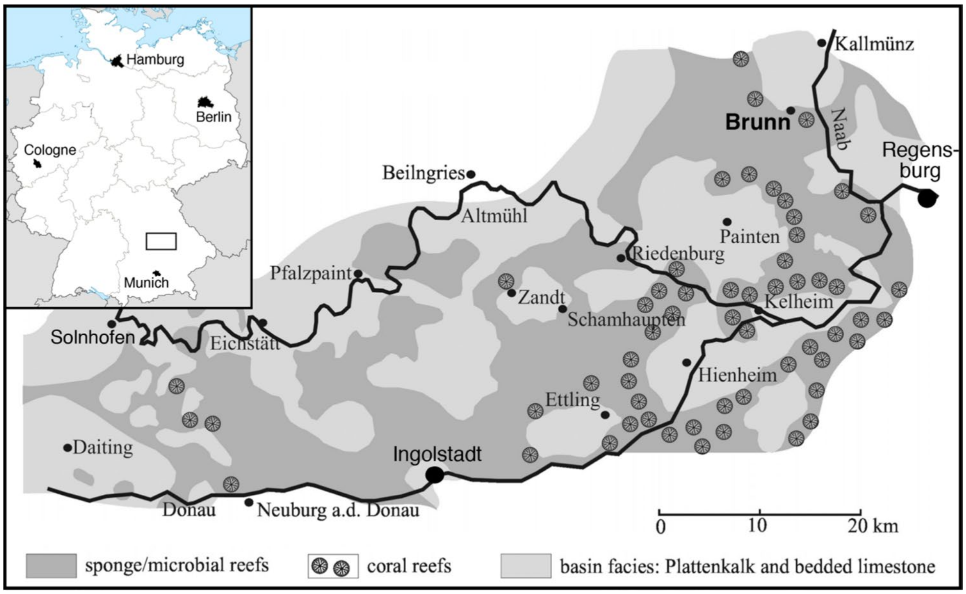

Fig. 1 The locality of Brunn within the larger Solnhofen region (from Rauhut et al., 2017)

(see Viohl, 2015), so that this setting has been dubbed the fossil assemblage of the Solnhofen Archipelago in the recent literature (Röper, 2005; López-Arbarello & Schröder, 2011; Rauhut et al., 2017; Villa et al., 2021). Just as modern correlate reef environments are highly productive centers of vertebrate biodiversity, so too would this paleoenvironment have been prolific, including actinopterygian, chondrichthyan and coelocanthian fishes, turtles, lepidosaurs (rhynchocephalians and squamates), crocodylomorphs, dinosaurs, and pterosaurs (Arratia et al., 2015, and references therein).

Within the Solnhofen Archipelago, the locality of Brunn represents the geologically oldest fossil assemblage, and has been exploited for fossils since the early 1990’s (Röper & Rothgaenger, 1995). Despite the relatively short time of exploration of this locality, it has yielded a rich flora and fauna, including numerous vertebrates (Heyng et al., 2015; Rauhut et al., 2017). However, only three vertebrate specimens have been described in detail and classified from Brunn thus far, the novel species of pachycormiform actinopterygian *Orthocormus roeperi* Arratia & Schultze, 2013, the rhynchocephalian *Sphenofontis velserae* Villa et al., 2021, and the rhamphorhynchid pterosaur *Bellubrunnus rothgaengeri* Hone et al., 2012. Here, we describe a fourth vertebrate specimen from Brunn, and erect a second pterosaur species, based on a partial maxillopremaxillary fragment found in 1993. The material is housed at the Staatliche Naturwissenschaftliche Sammlungen Bayerns—Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany under the collection number SNSB-BSPG 1993 XVIII 1006.

Institutional abbreviations. OUM, Oxford University Museum, Oxford, UK; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

Geographical and geological setting

In the Late Jurassic, the area that now constitutes the southern Franconian Alb in Bavaria was a lagoonal archipelago, part of a larger carbonate platform which comprised part of a shallow epicontinental sea at the northern margin of the Tethys Ocean, bordered by the Bohemian Massif in the east and the Rhenian Massif to the north (Meyer et al., 1990; Keupp et al., 2007; Viohl, 2015). The fossil-bearing localities of the region that are usually considered to represent the Solnhofen Archipelago (e.g. Ebert & Kölbl-Ebert, 2008; Fürsich et al., 2007; Heyng et al., 2011; Röper, 2005; Viohl & Zapp, 2007) are scattered throughout an area of some 100 km in East–West direction,, and some 30 km in North–South extension, although somewhat older but lithologically similar fossil localities are also found at Nusplingen in southern Baden-Württemberg, some 200 km to the south-west (Schweigert, 2015), and in Wattendorf, some 100 km to the north (Mäuser, 2015). The sediments exposed here represent several different geological formations of the southern German Weißjura Group (Niebuhr & Pürner, 2014), which geochronologically span about 3.5 Ma from the Late Kimmeridgian to the Early Tithonian (Schweigert, 2007, 2015). The localities within the Solnhofen Archipelago are thus also stratigraphically variable, emerging from different horizons (e.g. Niebuhr & Pürner, 2014; Röper, 2005).

The locality of Brunn (Oberpfalz) is located along the northeastern border of the Solnhofen Archipelago region (Fig. 1). It is placed within the Ebenwies Member of the Torleite Formation and is the oldest locality known within the Solnhofen Archipelago sensu stricto, having been dated to the Subeumela Subzone of the Beckeri Ammonite Zone of the Late Kimmeridgian (Niebuhr & Pürner, 2014; Röper & Rothgaenger, 1997; Schweigert, 2007, 2015). During this time period, the region consisted of a semi-tropical shallow marine environment, housing sponge-microbial and coral reef complexes (Viohl, 2015), in between which laminated limestones were deposited within shallow depressions. The Brunn locality sits at the southern rim of one of these depressions, at the Pfraundorf-Heitzenhofen Basin (Rauhut et al., 2017). The locality is composed of intercalated massive and finely-laminated limestones, with an approx. eight-meter section of eight different Plattenkalk layers outcropping (Heyng et al., 2015), yielding various fossil remains from the finely-laminated layers. Because Brunn has been recognized for its abundant plant fossils (including land plants), it is thought to have more terrestrial input than is typical of most other localities within the Solnhofen Archipelago. Vertebrate remains are relatively common in the locality of Brunn and include a diverse fauna of actinopterygian fishes, some chondrichthyans, and rare tetrapods (Rauhut et al., 2017). The latter include turtles, rhynchocephalians, crocodyliforms and pterosaurs. Regarding pterosaur material, Plattenkalk layer 1 has so far yielded an isolated pterosaur humerus (Rauhut et al., 2017; Röper, 1997) and the specimen described herein, and the pterosaur *Bellubrunnus rothgaengeri* was discovered from Plattenkalk layer 6 (Hone et al., 2012).

Materials and methods

The specimen described here was found during systematic excavations in the Brunn quarry, led by Martin Röper and Monika Rothgaenger. It was discovered by Simone Kaulfuß, Maren Sendelbach and Andreas Heiner, then students at the school for Schule für Präparationstechnische Assistenten in Bochum, during a field trip to the locality. The specimen came from Plattenkalk layer 1, the lowest layer in the sequence, which has mainly yielded more disarticulated remains than some of the more upper layers. It was found isolated during splitting of the layer. As it is usual in the lithographic limestones of southern Germany, the specimen has suffered moderate dorsoventral compression. It was mechanically prepared and briefly described and figured by Rauhut et al., 2017: pp. 321–322, fig. 15) and is kept permanently in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich under the collection number SNSB BSPG 1993 VIII 1006.

Phylogenetic analysis was conducted using TNT version 1.6 (Goloboff & Morales, 2023; Goloboff et al., 2008) using the matrix of Fernandes et al., (2023) (based on the matrix of Andres, 2021), and augmented by the ctenochasmatid pterosaur *Tacuadactylus luciae* Soto et al., 2021 and the additional new taxon described herein (represented in the analysis by "Brunn"). The new character state "veined" was also added for character 174 "Dentition, texture" regarding tooth enamel. Thus, the final matrix had 181 terminal taxa scored for 275 characters (51 continuous and 260 discrete; using ordered characters as well). The data matrix is available in the supplementary material, and also at http://morphobank.org/permalink/?P3967. A basic traditional tree-search analysis was conducted with 2000 random addition sequence replicates. The resulting cladogram has been simplified in the software Adobe Illustrator, the complete topology of which can also be found in the supplementary data set.

UV photography was done using the techniques described by Tischlinger (2015) and Tischlinger and Arratia (2013), using a high-performance Labino UV-A lamp, Spotlight S 135, 35 W, 365 nm, equipped with a custom-made midlight-reflector-inset. Photos were taken with a Lumix GX80 with a Lumix G 2,8/30 mm Macro OIS lens.

CT scans were performed in Leiria, Portugal, with a microfocus CT system GE VtomeX M 240. Scan images were segmented and assembled utilizing Avizo and Meshlab softwares (GE Sensing & Inspection Technologies GmbH., Wunstorf, Germany), and are available at MorphoSource). The segmentation of the complete specimen was done using manual selection slice-by-slice in the software Avizo v9.1 (Thermo Fisher, Waltham, MA, USA). All meshes were exported as Wavefront Files (.obj) and treated in the open-source software Blender v3.4. All meshes were smoothed for rendering using the Smooth Laplacian modifier (Lambda factor = 1 and 10 repeats).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The electronic edition of this work was published in a journal with an ISSN and has been archived and is available from the following digital repositories: PubMed Central and LOCKSS.

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Results

Systematic paleontology

Order **PTEROSAURIA** Owen, 1842
Suborder **PTERODACTYLOIDEA** Plieninger, 1901
Family **CTENOCHASMATIDAE** Nopcsa, 1928 sensu Unwin, 2003
Subfamily **GNATHOSAURINAE** Nopcsa, 1928 sensu Unwin, 2002

Genus ***Spathagnathus*** gen. nov.

Type species. ***Spathagnathus roeperi*** sp. nov.

Etymology. From the Latin “spatha” for “spatula”, and “gnath” for “jaw”; “*roeperi*” in honor of the late Martin Röper, long term director of the Bürgermeister-Müller-Museum in Solnhofen and leader of the excavations at the locality Brunn since the early 1990’s.

Holotype. SNSB-BSPG 1993 XVIII 1006, fragment of the anterior part of a maxillopremaxillary rostrum with toothrow.

Type locality and horizon. Brunn, Germany. Southern rim of the Pfraundorf-Heitzenhofener Basin. Ebenwies Member of the Torleite Formation. *Subeumela* Subzone of the *Beckeri* ammonite Zone, Late Kimmeridgian, Upper Jurassic.

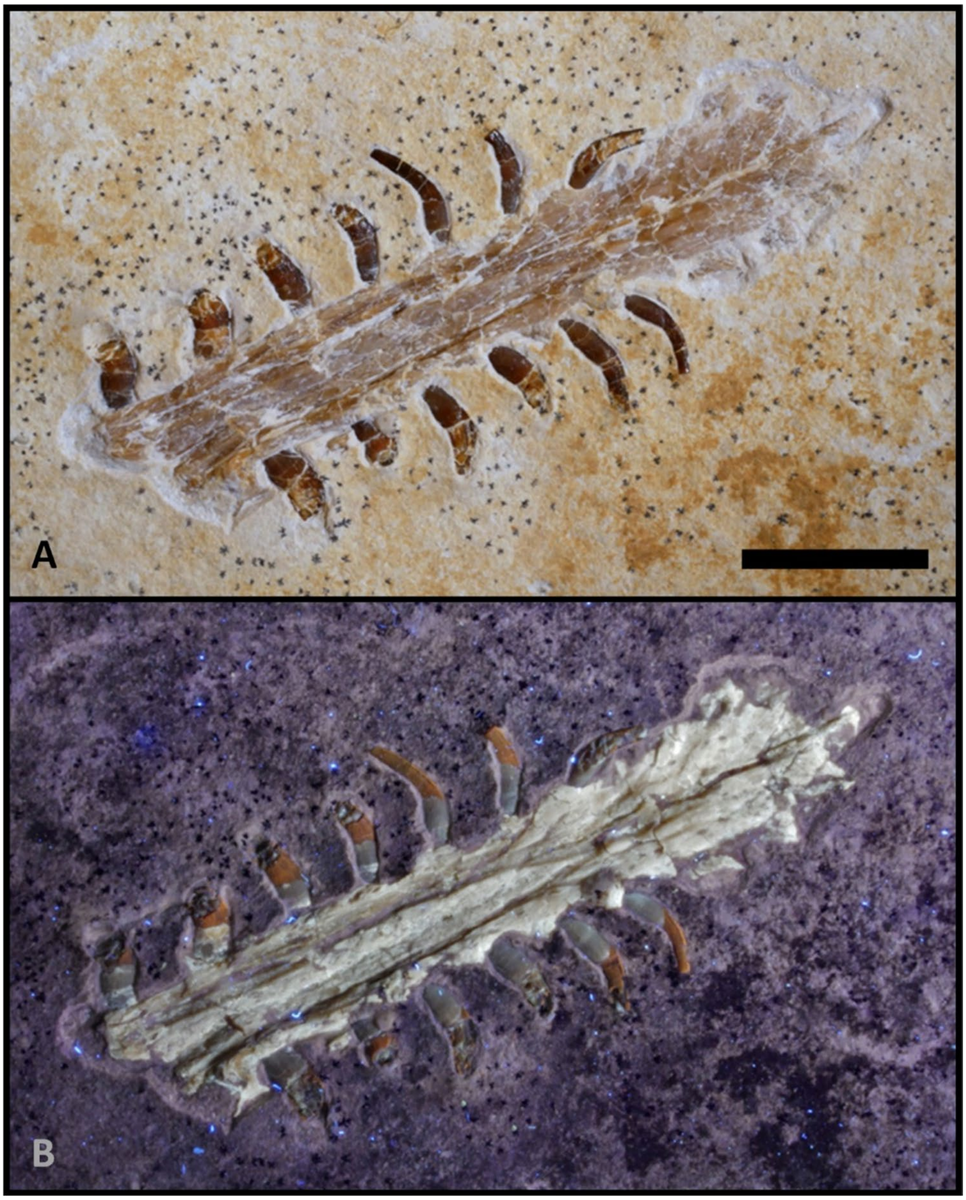
Diagnosis (autapomorphies indicated with asterisk). dorsoventrally compressed rostrum with lateral spatulate expansion on the anterior end of the premaxilla, laterally directed musiform teeth, tooth girth increasing from anterior to posterior end of the rostrum, dental enamel coating approximately half of tooth crowns, strongly veined enamel texture on tooth surface, presence of carinae.

Description

The specimen SNSB-BSPG 1993 XVIII 1006 preserves the anterior-most portion of the rostrum in palatal view (Fig. 2), in a slab and counterslab (although the counterslab preserves only the very apicalmost tips of some of the teeth, embedded in sediment). The overall anteroposterior length of the preserved rostrum is 36.9 mm. The width of the posteriormost preserved end is 5.2 mm, and the widest point of the expanded proximal end is 9 mm. Despite being dorsoventrally flattened by lithostatic pressure (a typical condition for Lagerstätten specimens), the overall condition of what is preserved is relatively good as the specimen exhibits only a slight overall shattered surface, with cortical bone remaining intact and in situ. Pterosaur material with a well-preserved palatal region is uncommon and there has been some recent discourse on actual palatal morphology (Ősi et al., 2010; Pinheiro & Schultz, 2012; Cheng et al., 2017; Zhou et al., 2017; Chen et al., 2024). Accordingly, it is difficult to distinguish the exact margin between the premaxilla and maxilla (as no clear suture between them is visible), so they were likely already fused, as in other pterosaurs (e.g. Howse & Milner, 1995). Although Rauhut et al., 2017 had also identified the presence of fused palatines in this specimen (following the interpretation of these bones in Howse and Milner (1995) in *Plataleorhynchus streptophorodon*), recent insights on the palatal morphology of pterosaurs (Ősi et al., 2010; Pinheiro & Schultz, 2012; Cheng et al., 2017, Zhou et al., 2017; Chen et al., 2024) indicate that here only the premaxilla and maxilla are actually preserved; the structure identified by Rauhut et al. (2017) more likely represents a dorsally-inset portion of the medial fused maxilla (although one cannot rule out that it could also be the vomer, such an anterior position would be unlikely for the Ctenochasmatidae), which resulted in slight grooves appearing to run between this region and the laterally-lying dentated region of the maxilla. There is a mediolateral crack visible at the portion of the rostrum where the spatula begins to expand, but this is likely taphonomic. The anterior-most spatulated portion of the premaxilla displays an antero-posterior fissure running medially (likely a taphonomic post-mortem break). There is no sign of a premaxillary crest (nor in the CT images of the dorsal side of the rostrum), although one cannot rule out the existence of one, as it may have been more posteriorly placed.

The tip of the rostrum expands laterally to form a spatulated terminal rosette (Fig. 2), the condition seen in all gnathosaurines (Howse & Milner, 1995; Wellnhofer, 1970). The expansion of the rosette begins at approximately 11.2 mm from the tip of the snout, with the widest point of the rosette measuring 9 mm mediolaterally. Foramina are interspersed throughout the entirety of the rostrum in no discernable pattern, although they are especially concentrated throughout the spatulate region of the premaxilla. In the toothed region of the maxilla, a constant mediolateral width is maintained throughout. The alveoli face anterolaterally, and the distance between individual alveoli is consistently slightly larger than

Fig. 2 SNSB-BSPG 1993 XVIII 1006 *Spathagnathus roeperi* gen. et sp. nov. photographed under normal light (**A**) and UV light (**B**). Scale bar represents: 10 mm



their mesiodistal length, a pattern that is preserved even as the teeth increase in girth as one moves posteriorly along the jaw. Accordingly, the size of the alveoli also increases posteriorly. The rim of each alveolus is expanded, giving the crenulated appearance typical of many gnathosaurine rostra (e.g. Howse & Milner, 1995; Soto et al., 2021; Wellnhofer, 1970).

All maxillary teeth are exposed on the sediment by their lingual side only, are in individual sockets, and all are in situ. They have a distinct and unique banana shape, and the displacement of the tip in respect to the base (due to the tooth curvature) is more than the width of the tooth itself. Although there are no teeth on the rosette that are visible to the naked eye, the CT scan data shows roots (or potential germs) of at least four preserved teeth (Fig. 3). The right maxilla preserves six to seven tooth positions, and the left maxilla preserves seven, totaling thirteen teeth that are visibly preserved, although only two (one tooth on the right side, and one tooth on the left) remain complete from root through apex. The remainder of the teeth are broken along their crowns, with some of the apicalmost tips embedded in the sediment of the counterslab. The manner in which all of the teeth are increasingly broken along the posterior of the rostrum indicates that they were positioned more and more ventrally as one moves posteriorly in the transverse plane, a change which happens with uniformity and is therefore unlikely to be taphonomic. Otherwise, this condition could also be indicative of a slight degree of rostral curvature, although the state of taphonomic compression makes this indiscernible.

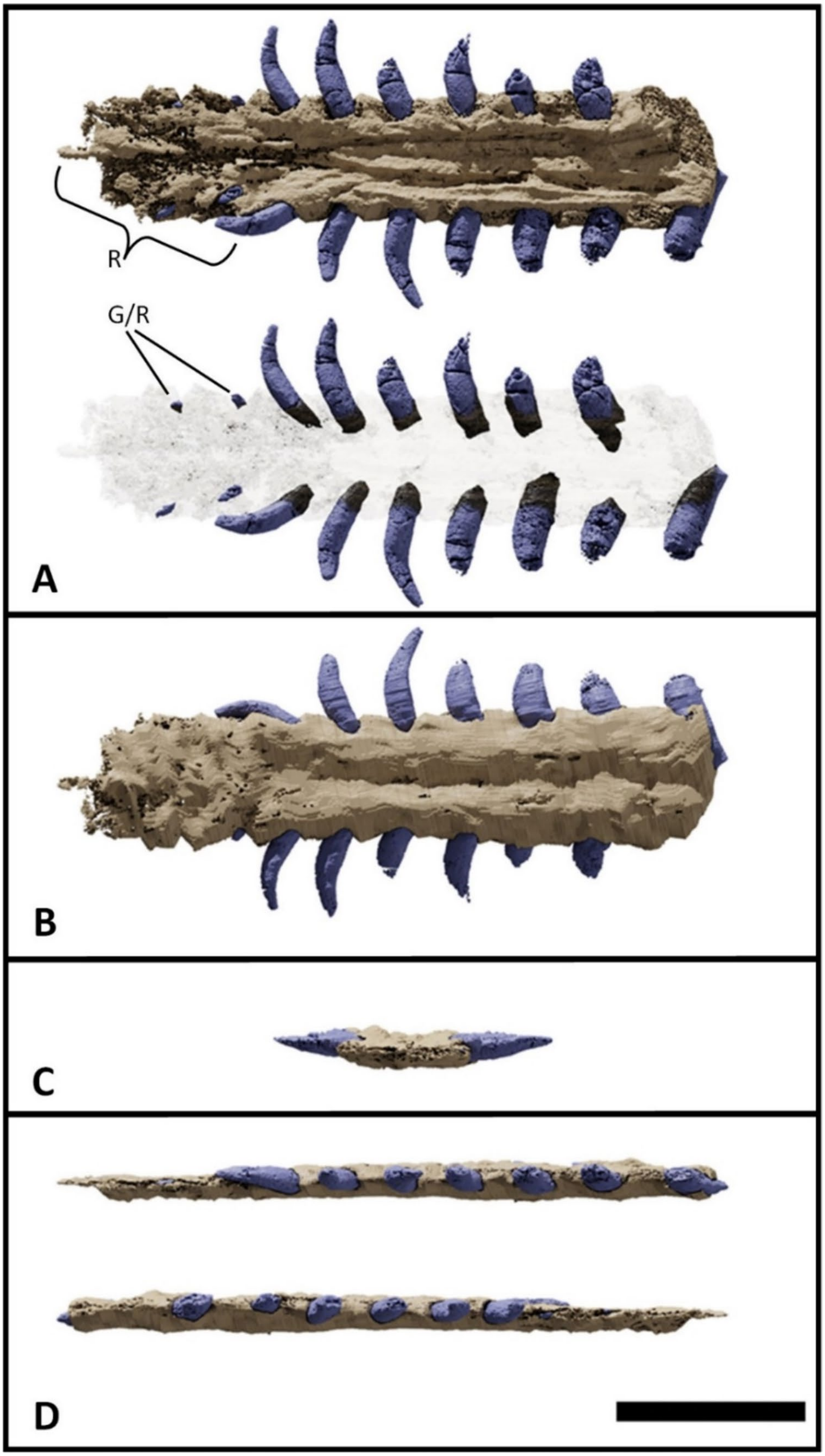


Fig. 3 SNSB-BSPG 1993 XVIII 1006 *Spathagnathus roeperi* gen. et sp. nov. rendering of CT scan data (with visible premaxillary tooth roots or germs) in palatal (**A**), dorsal (**B**), anterior (**C**), and lateral (**D**) views. R = rosette; G/R = germs/roots. Scale bar represents: 10 mm

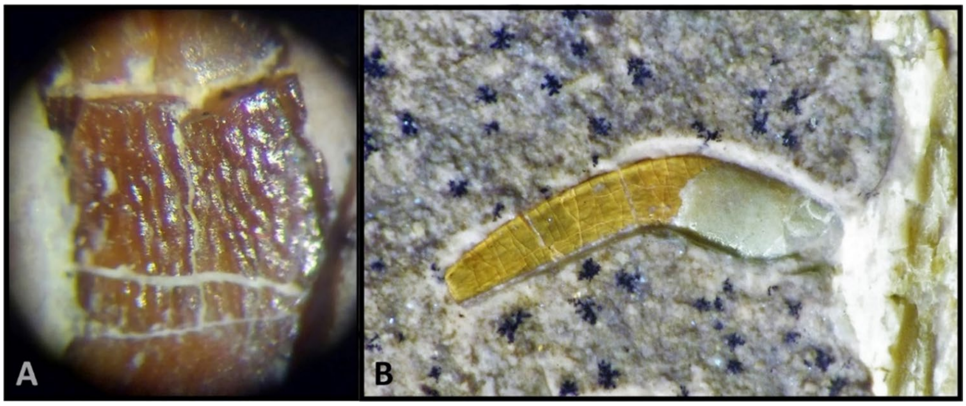


Fig. 4 SNSB-BSPG 1993 XVIII 1006 *Spathagnathus roeperi* gen. et sp. nov. detailed view of veined dental enamel patterning (**A**) and enamel distribution along the tooth crown (**B**)

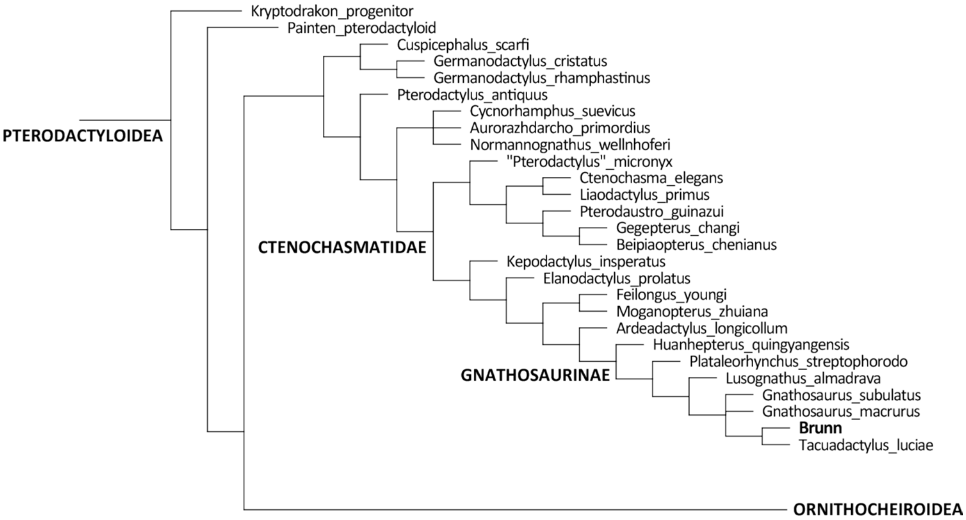


Fig. 5 Phylogenetic results displayed as a simplified tree of the Pterodactyloidea, showing the relationship of *Spathagnathus roeperi* ("Brunn") within the Gnathosaurinae, after the data matrix by Fernandes et al., (2023) (based on Andres, 2021). Non-pterodactyloid pterosaurs were removed from this figure, and the clade Ornithocheiroidea was simplified, to make the figure concise

Table 1 A comparison of age, rostral tooth density, and size of known Gnathosaurinae species

Species	Age	Tooth density	Wingspan	Citation
Spathagnathus roeperi	Kimmeridgian (~ 152.0 Ma)	3.27 teeth/cm	N/A	N/A
Lusognathus almadrava	Kimmeridgian-Tithonian (~ 152.0 Ma)	1.3 teeth/cm	> 3.6 m	Fernandes et al., (2023)
Tacuadactylus luciae	Late Jurassic	1.58–2 teeth/cm (according to Perea?)	N/A	Soto et al., (2021)
Gnathosaurus subulatus	Tithonian (?)	2–3 teeth/cm	~ 1.7 m	Wellnhofer (1970)
Huanhepterus quingyangensis	Late Jurassic (re-dated as Early Cretaceous)	1.6 teeth/cm	~ 2.5 m	Dong (1982), Howse and Milner (1995), Wang and Lü (2001)
Plataleorhynchus streptophorodon	Tithonian/Berriasian	2–3 teeth/cm (2.9 according to Perea)	~ 2–2.5 m	Howse and Milner (1995)
Gnathosaurus macrurus	Berriasian (~ 145–139.8 Ma)	2.0–2.5 teeth/cm	~ 1.8 m	Howse and Milner (1995)

All teeth are conical, round to ovoid in cross-section at the root and becoming more labiolingually compressed apically. All teeth have a visible carina on their mesial margins, beginning at the base of the crown and running parallel to the natural curvature of each tooth through the crown apex. The carina is slightly lingually directed, resulting in a shallow longitudinal furrow adjacent to the carina on the lingual side of the crown, which is, however, restricted to its apical two thirds. The mesial teeth are slender, but the teeth seem to become more robust distally; whereas the fore-aft basal length of the third preserved tooth in the left maxilla is 1.1 mm, that of the sixth preserved tooth is 1.6 mm. All teeth protrude laterally from the long axis of the jaw, and recurved mesiodistally as well as lingually (although the extent to which may be unduly exaggerated by taphonomy). In the more complete mesial teeth, the flexure seems to be concentrated in a flexure point at about half of the crown height, apical and basal to which the crown is almost straight. The teeth exhibit the typical, unique enamel extent of the Pterosauria (Fastnacht, 2005; Wellnhofer, 1978, 1985), where the tooth enamel stops at an enamel-dentin boundary (EDB), which here occurs about halfway up the crown as a slightly raised portion of the tooth, with a marked change in texture and shine (the crown base is pitted and dull, whereas the more apical enameled region of each tooth is shiny and rippled). The enamel is strongly textured overall, displaying a corrugated veined pattern of irregular longitudinal folds (Fig. 4). In cross-section, the enamel is thick (visible on the broken teeth), and the pulp cavity seems to have been rather small and restricted to the basal part of the crown. The two complete teeth have pointed tips, although their apices both show a distally-oriented wear facet (not likely to be any result of dental occlusion).

Phylogenetic analysis

Phylogenetic analysis was conducted to analyze the relationships of the Brunn specimen within the Pterosauria. The phylogenetic analysis resulted in a single most parsimonious tree (Fig. 5) with a tree length of 1375.905 steps (consistency index [CI] = 0.287, retention index [RI] = 0.787). *Spathagnathus roeperi* was retrieved as the sister taxon of *Tacuadactylus luciae*, a relationship supported by their veined dental enamel texture (character 173). The Gnathosaurinae are phylogenetically defined as the least inclusive group including *Gnathosaurus subulatus* von Meyer (1834) and *Huanhepterus quingyangensis* Dong (1982) (Unwin et al., 2000 sensu Unwin, 2002; Andres, 2021), and thus, *Spathagnathus roeperi* falls within the Gnathosaurinae, a relationship which is supported by their dorsoventrally depressed rostra, the lateral expansion at the anterior end of the rostra, and their laterally procumbent dentition.

Discussion

Phylogenetic position of *Spathagnathus roeperi* and evolutionary implications

The recognition of SNSB-BSPG 1993 XVIII 1006 as a new taxon within the Ctenochasmatidae (and Gnathosaurinae), as originally suggested by Rauhut et al., (2017) (but not previously tested in a phylogenetic analysis) is here reaffirmed. This prior attribution was made based on the presence of a narrow, parallel-sided rostrum (with more laterally than ventrally pointing teeth) and the large number and shape of the elongate, slightly recurved maxillary teeth (likely involved in a style of filter feeding [i.e. Martill et al., 2022]). The gnathosaurine affinities in particular were based on the rounded expansion of the anterior end of the rostrum, and the previous authors also pointed out that the specimen was likely a new taxon due to the fact that it differed from other gnathosaurines in its short premaxilla (with few teeth), the change in tooth morphology in the anterior maxilla, and the "ornamented" enamel (with marked mesial carinae). Thus, *Spathagnathus roeperi* adds to the growing diversity of gnathosaurines in the Late Jurassic, most probably (depending on the exact age of *Lusognathus almadrava* Fernandes et al., 2023) representing the oldest known member of the clade (Table 1).

There have been instances where pterosaur fossils have been mistaken for thalattosuchian crocodyliforms and vice versa. A good example is the jaw fragment OUM J.01419 from the Middle Jurassic Stonesfield Slate of Oxfordshire, England, which was originally described by Phillips (1871) as a new species of teleosaur, but then changed in attribution many times over the years. Most recently, the specimen was identified as a ctenochasmatid pterosaur by Buffetaut and Jeffery (2012), but then was reinterpreted as a teleosaur by Andres et al. (2014), an interpretation shared by O'Sullivan and Martill (2018) in a review of pterosaurs from the Stonesfield Slate. OUM J.01419 was finally identified as a crocodyliform on the basis of features such as very close-set teeth that do not touch, fine longitudinal enamel striations, a curvature over the entire tooth that do not match with any gnathosaurines, and also its very early temporal occurrence, because considering OUM J.01419 to be a pterosaur would extend the ghost lineage for many pterodactyloid lineages by 10–15 million years, creating a total of 100 million years of unsampled evolution (Andres et al., 2014: supplement, p. 18; note, though, that temporal arguments should be treated cautiously, as there remains a sparsity of pterosaur fossil sampling worldwide, especially in the Middle Jurassic [Dean et al., 2016]).

Although teleosaurids show a rostrum and anterior mandibular morphology that is superficially similar (see Johnson et al., 2020a), they generally differ from *Spathagnathus* in that their teeth lack carinae and often show longitudinal striations instead of veined enamel texture, and are usually markedly more robust and conically-shaped (e.g., 2020b; Foffa et al., 2015; Johnson et al., 2018). The identification of SNSB-BSPG 1993 XVIII 1006 as a teleosaurid rostrum is furthermore precluded by the lack of the external nares towards the anterior end. Compared to teleosaurid dentaries, the rostrum of *Spathagnathus* is considerably more flattened dorsoventrally (Fig. 3D). Moreover, the alveoli are placed on the lateral margin of the dentary but point dorsally in teleosaurids, whereas they face laterally in *Spathagnathus*, and the dorsal surface in between the tooth rows is flat to slightly convex, rather than indented.

Spathagnathus roeperi furthermore exhibits characteristics that are unique to the Pterosauria or subgroups thereof. The teeth alone are largely identifiable based on their typical enamel distribution, which consists of an apical enamel cap and dentin base to their tooth crowns, in which the dentin and enamel are well differentiated by a pronounced junction, which slopes basally at the anterior and posterior sides (or at the carinae, when present), but not to the alveolar level, leaving the lateral and medial sides mostly enamel-free (Fastnacht, 2005; Wellnhofer, 1985; Witton, 2013). The preserved cortical bone is also smooth and remarkably thin, as evidenced by the flake-like fragments of bone that protrude out from the palatal surface (although measurement of its exact thinness is prohibited by the fact that the specimen is embedded in matrix), but discernably estimated to be in keeping within the 0.3 to 1.6 mm thickness known to be typical for pterosaurs (Currey & Alexander, 2009). Therefore, *Spathagnathus* is confidently assigned to the Pterosauria.

Within the Pterosauria, the immediate outgroup to gnathosaurines is represented by *Ardeadactylus longicollum* Bennett, 2013, the neotype specimen of which comes from the Upper Kimmeridgian laminated limestones of Nusplingen, Baden-Württemberg (Bennett, 2013; Wellnhofer, 1970). Interestingly, the genus *Ardeadactylus* has also been identified on the basis of an isolated femur from Brunn (Rauhut et al., 2017), which also represents the oldest record of this genus. Asian representatives of gnathosaurines, or from the stem-lineage of this clade after their split from ctenochasmatines, are only known from Cretaceous deposits; whereas the oldest ctenochasmatine, *Liaodactylus primus* Zhou et al., 2017, is known from the early Late Jurassic Yanliao Biota of China (Zhou et al., 2017); this otherwise prolific pterosaur Lagerstätten has not yielded any gnathosaurine ctenochasmatids so far. The phylogenetic relationships and the distribution of gnathosaurines and their immediate outgroup in the Late Jurassic might thus indicate a European origin and early diversification of the clade, although such an interpretation should be seen with caution, given the poor fossil record of pterosaurs in the Late Jurassic outside the Solnhofen Archipelago and the Yanliao Biota in general, and in the Southern Hemisphere in particular. In this respect, the sister taxon relationship of *Spathagnathus* with the Uruguayan *Tacuadactylus luciae* is noteworthy. The occurrence of a close relative of the southern Germany taxon in South America helps to highlight our still very poor knowledge of the evolution and distribution of these early pterodactyloids. The sister group relationship between these two taxa is based in the shared characters of the presence of carinae and enamel ornamentation on the teeth, although both are much less developed in *Tacuadactylus* than in *Spathagnathus*. As such dental characters are most probably related to feeding ecology of the animals involved (see below), more material of both taxa would be needed to rule out that these proposed synapomorphies might simply be convergence due to similar feeding ecology. The sister taxon relationship between these two taxa thus either indicates that these animals could disperse very rapidly, even over continents (which would not be impossible for flying vertebrates), or that much of their evolutionary history is still to be found, possibly in sediments of the Southern Hemisphere.

Considerations on the ontogenetic stage of *Spathagnathus roeperi*

Regarding the fused premaxillae of *Spathagnathus*, even utilizing computed tomography, the margins of the anterior rosette appear quite damaged. This is unsurprising, given that it is dorsoventrally the thinnest portion of the rostrum, and thus less taphonomically durable. However, an early ontogenetic stage could readily account for this previously-observed "short" premaxilla (Rauhut et al., 2017). In fact, changes in rostrum shape might well have occurred over the lifetime of these animals, as occurs in modern spoonbill rostra, where the bill in juveniles is more tubular and not yet spatulate, but thickens during ontogeny, becoming more bulbous with age until full bill length is reached at about 36 months of age (Hancock et al., 1992). *Ctenochasma elegans* Wagner (1861) was also observed to similarly have the distal end of its upper rostrum becoming more laterally expanded with age (Bennett, 2007, 2021), as was *Hamipterus tianshanensis* Wang et al. (2014), which was observed to have an ontogenetic expansion of the rostrum, becoming more progressively robust (Wang et al., 2014). In accordance with this, as pointed out by Bennett and Penkalski (2018), closely-spaced subparallel blood vessels (the presence of which can be inferred from the foramina interspersed along the rostrum of SNSB-BSPG 1993 XVIII 1006) create the potential for increased bone deposition, which could also indicate growth over time.

There are other traits which also raise the question of the ontogenetic stage of the type specimen of *Spathagnathus roeperi*, despite most Solnhofen pterosaurs also being relatively small in size (partly because sampling favors smaller [and younger] individuals [Bennett, 1995]). In the absence of available material suitable for histological sampling or enough individuals to conduct reliable principal component analysis, identifying the ontogenetic stage of a pterosaur specimen is mainly reliant on three main factors: the degree of ossification, the fusion of skeletal elements, and the state of bone grain (Bennett, 1993). What remains of the Brunn specimen is not easy to categorize using any of three distinctions, because bone texture and suture marks may have been obscured by the taphonomic crushing that the rostrum has sustained, and although the premaxilla does preliminarily seem completely fused, there have been instances where a premaxilla can be completely fused despite ontogenetic immaturity, as pointed out in *Dorygnathus banthensis* Theodori 1830 (Ősi et al., 2010).

Dentition and ecological implications

Morphologically, the appearance of the "needle-like" thin tooth shape and sub-circular cross-section (with slight antero-posterior compression) in *Spathagnathus* is in keeping with all ctenochasmatids (Bestwick et al., 2018; Fastnacht, 2005; Wellnhofer, 1970). However, there are also marked differences from other gnathosaurs. According to the CT scan data of the Brunn specimen (Fig. 3), all tooth roots remain firmly nested within the maxillary bone, with an additional four potentially "budding" (or simply eroded) teeth also present in the anterior-most spatulate region of the rostrum (although it remains unclear whether these are tooth germs, or were simply full-size teeth that were eroded prior to or during deposition). The dental ontogeny of *Ctenochasma* sp. is also discussed by Bennett (2007, 2021), who found that in young individuals, the posterior teeth on the tooth row are more closely spaced than the anterior teeth (potentially reflecting rapid growth of the mandible and formation of new teeth at the posterior end of the tooth row). Although the Brunn specimen does not follow this pattern, its teeth do grow more robust from the anterior to posterior position along the toothrow, which may simply correspond to a stronger bite due to more stress during occlusion in the posterior region of the jaw, a trait which has been suggested to pertain to durophagous animals which might develop a more robust dentition in this part of the jaw (Fastnacht, 2005; Hone et al., 2018). Although *Spathagnathus* was not likely to be strictly durophagous, this trait could certainly be indicative of ingesting "harder" prey items, like shellfish or other chitinous prey.

Also atypical in the teeth of the Brunn specimen is the presence of carinae. Although most pterosaurs exhibit carinae, ctenochasmatid teeth are most often devoid (Fastnacht, 2005). The distribution and phylogenetic significance of carinae in pterosaur dentition has yet to be fully explored, however, carinae make a substantial functional difference in prey acquisition, as the force needed for puncturing is much lower in a laterally compressed tooth construction with carinae than without (Fastnacht, 2005). Only one other gnathosaur is described as having carinae, *Tacuadactylus luciae* (Soto et al., 2021), although they are much more inconspicuous in that specimen. In this case, the markedly robust carinae of the Brunn specimen are unique, implying that it was more easily capable of consuming harder prey than the average ctenochasmatid.

Enamel structure and distribution are reliable metrics and stable differentiators in identifying teeth because enamel is acellular and does not have the ability to regrow (and therefore is not altered after its initial deposition). It is formed as a tooth develops (through amelogenesis), and is invariably thin in most carnivorous reptiles, both fossil and extant (Cullen et al., 2023), although *Spathagnathus* exhibits rather thick enamel compared to other pterosaurs. Enamel does not undergo any remodeling over a species' lifespan (and is unaffected by ontogenetic modifications), and so the enamel microstructure and surface morphology is fixed, and any features it contains (such as ornamentation) are formed by the enamel itself (and not reflected in the dentin below) (Sander, 1999). Enamel also bears an important functional purpose: the thickness of individual enamel layers is variable between species and/or individuals in adaptation to their different biomechanical requirements (Wilmers & Bargmann, 2020).

To date, most ctenochasmatid tooth enamel texture has been described as smooth (e.g. Fastnacht, 2005; Knoll, 2000), and among the gnathosaurs, the ornamented tooth enamel of *Spathagnathus* is a feature only shared with *Tacuadactylus luciae* (along with the presence of dental carinae, although it remains ambiguous if they are mutually exclusive or not). The functional advantages of a veined enamel texture likely relate to an improved crown strength, as it has been suggested that veined enamel, although rare in small-bodied animals, may be biomechanically advantageous for more powerful occlusion, as great bite forces coupled with long teeth would require wavy enamel (with its isotropic properties of wear and abrasion resistance) (Sander, 1999). Veined enamel could even potentially be hydrodynamically advantageous for feeding in aquatic environments (Massare, 1987).

Dentin is of mesenchymal origin and continues to form after a tooth has erupted, whereas enamel originates from epithelial cells and is fully formed before the tooth erupts (Sander, 1999). The visible presence of dentin (as seen in the Brunn specimen) is common in teeth that are exposed to the environment (Cullen et al., 2023) and not shielded by extraoral tissues. Because dentin has a higher tensile strength than enamel (and is therefore much more flexible), the percentage of enamel coverage on teeth makes a big difference in tooth flexibility. Although the elongated tooth construction of gnathosaurines and ctenochasmatids could be prohibitive to having great penetrative capabilities (because a thin shape would make them susceptible to failure by axial loads [Fastnacht, 2005]), among these groups, gnathosaurs would have the highest resistance to high bending moments and stress, given their generously dentin-exposed tooth bases

Fig. 6 Artistic reconstruction of *Spathagnathus roeperi* by Alessio Ciaffi

and their enamel-dentin junction being apically higher along the crown (giving increased lateral flexibility and providing a reduction of strain and stress throughout the tooth when in use). These features also provide greater elasticity than that of teeth with a complete enamel cover (Fastnacht, 2005), indicating a great resistance to breakage.

Computer modeling of pterosaur skulls show that ctenochasmatids had very low bite forces (despite fast closing jaws), which would be in accordance with feeding on small evasive prey/filter feeding (Henderson, 2018). However, gnathosaurs, with their teeth more robust and widely-spaced than other ctenochasmatids, were seemingly specialists, occupying a different ecological niche than traditional filter-feeders (whose teeth need to be closely spaced together to maximize efficiency), or at least going after larger-sized prey, seeing as how a reduction of contact between tooth and food item is required for penetrating hard food items (e.g. Evans & Sanson, 1998), potentially crustaceans or other small marine organisms. Although the more laterally-expanded spatulas of gnathosaurines could also indicate water-feeding (with perhaps an adaptation to move larger volumes of water), the robustness of their teeth indicates greater piercing strength than in the finer-toothed ctenochasmatids, whose slighter dentition would be more appropriate for smaller sized food particles (such as plankton, i.e. Martill et al., 2022). Gnathosaur tooth spacing also implies less effective tooth–tooth occlusion (despite just one single known instance of tooth-tooth occlusion for all ctenochasmatids, in *Forfexopterus jeholensis* Jiang et al., 2016 [Zhou et al., 2022]). The worn apical tips of *Spathagnathus* were therefore most likely formed by tooth–food contact during prey capture (Ősi, 2011), as they were smoothly worn down in a fashion that is almost perpendicular to the long axis, which also suggests harder prey (i.e. Massare, 1987).

Dietary switches throughout ontogeny happen regularly in the extant animal kingdom, for example, in crocodiles, where body sizes dictate both the type and variety of foods consumed by individuals, with young animals primarily predating on insects (e.g. Coleoptera, Orthoptera and Odonata) and arachnids, and later on as they increase in age and size, intermediate size-classes feed on amphibians, small mammals, birds, reptiles, crustaceans, gastropods and arachnids in varying proportions as well as insects and fish, terminating with sub-adults and adults consuming fish and large mammals as their primary prey (Wallace, 2006). These changing appetites are a direct result of not only their changing physical size (i.e. spatial bite capacities), but also as a result of the morphological changes of their feeding apparatus throughout development (e.g. the shape-changing of rostra), especially affecting their ability to engage in disarming the various defensive mechanisms of specific prey (Wallace, 2006). In the Rhamphorhynchoidea, it has also been observed that growing teeth can produce different patterns between juveniles, subadults, and adults: teeth start out small, but then subsequently are replaced by larger teeth at a more anterior angle as the skull grows (Bennett, 1995). These changes accommodate spatial needs, but also imply a more complex functional shift in an individual's capabilities regarding prey handling, which could lead to differences in feeding niches over the course of its lifespan (Bennett, 2018) (and as commonly seen in extant reptiles, where offspring usually feed themselves [Bestwick et al., 2020]). The proportionately shorter, stouter teeth of adult individuals of the Rhamphorhynchoidea (when compared to subadults) exhibit an adaptation for feeding on larger and more powerful prey than younger individuals (Bennett, 1995). Although fish eaters generally also have a high number of slender, recurved teeth, wrinkled dental enamel is more typical of durophagous animals (Sander, 1999), and evidence from coprolites has affirmed that small foraminifera, crustaceans, worms, and various gastropods and bivalves as deliberate targets of ctenochasmatid food sources (Qvarnström et al., 2019). Therefore it is likely that gnathosaurs, with their more robust teeth, were going for the harder range of these food items. Furthermore, the higher relative abundance of foraminifera in larger coprolites also supports an ontogenetic switch to a more specialized filter feeding in adults, whereas younger individuals would have relied more on eating soft-bodied organisms from the sediments (Qvarnström et al., 2019).

Conclusion

The extreme variability in the pterosaurian dental apparatus across time and space was likely an ecomorphological adaptation to their manifold inhabited environments, and reflective of their numerous different feeding strategies and diverse prey preferences throughout their evolution (Ősi, 2011). Differences in tooth morphologies and enamel patterning of globally-concurrent ctenochasmatid and gnathosaurine taxa could indicate mosaic evolution, possibly as an adaptation to their differing paleoenvironmental niches. Previous studies have already illustrated cases of small clades comprising closely related species that are endemic to the Solnhofen Archipelago, whose evolution was driven by palaeogeographical and chronostratigraphical changes (Konwert, 2016; López-Arbarello & Schröder, 2014; Rauhut et al., 2017). The fact that the new species described herein, *Spathagnathus roeperi* (with its novel specialized tooth and dental enamel morphology suggesting hard prey preferences or even possible durophagy) (Fig. 6), was also locally-coeval with the rhamphorhynchid *Bellubrunus rothgaengeri*, provides an even more diverse picture unfolding for the pterosaurs and general fauna of the Brunn locality, the oldest time slice of the larger Solnhofen Archipelago.

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Declarations

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