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ARTICLE

DIETARY TENDENCIES OF THE EARLY JURASSIC PTEROSAURS *CAMPYLOGNATHOIDES* STRAND, 1928, AND *DORYGNATHUS* WAGNER, 1860, WITH ADDITIONAL EVIDENCE FOR TEUTHOPHAGY IN PTEROSAURIA

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ABSTRACT—The diets and feeding strategies of pterosaurs remain a poorly known although speculatively debated topic in vertebrate paleontology. Fossilized gut contents, which offer a crucial direct line of evidence to help decipher these elusive questions, are only known from a handful of pterosaur specimens in a few notable fossil Lagerstätten, such as the Solnhofen Limestone of Bavaria. Although extremely rare, pterosaurs can be exceptionally well preserved in the Lower Jurassic (Toarcian) Posidonia shale of Baden–Württemberg but, until now, none have been reported with identifiable gut contents. Here, we describe fossilized gut contents in two Posidonia Shale pterosaurs: *Dorygnathus banthensis* (Rhamphorhynchidae) and *Campylognathoides zitteli* (Campylognathoididae). *Dorygnathus* is shown to be piscivorous as indicated by the inclusion of the small teleost *Leptolepis* sp. preserved inside of the abdominal cavity. The gastrointestinal tract of *Campylognathoides* preserves associated accumulations of belemnoid hooklets referrable to *Clarkeiteuthis conocauda* and thereby demonstrating a teuthophagous diet. These findings represent the first convincing evidence for belemnoids contributing to the diet of a pterosaur and hint at a possible nocturnal hunting behavior for *Campylognathoides.* Previous hypotheses regarding dietary trophic partitioning based on differentiating skull anatomy in Posidonia Shale pterosaurs are supported.

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INTRODUCTION

Dietary ecology in pterosaurs remains a poorly known and speculative topic in vertebrate paleontology. Pterosaurian gastric contents are extremely rare in the fossil record with no identifiable remains yet described from the Early Jurassic (Witton, 2017). At present, the only direct evidence for piscivory in pterosaurs is demonstrated by the remains of small actinopterygian fishes preserved within the gastrointestinal tract of exceptionally preserved examples of *Eudimorphodon*, *Rhamphorhynchus*, and *Pteranodon* (Frey & Tischlinger, 2012, Hone et al., 2015, Witton, 2017). It has been proposed that rhamphorhynchine and possibly other clades of toothed pterosaurs may also have included cephalopods as part of their diet (Hoffmann et al., 2020). This conclusion is currently based on the sole association of an isolated rhamphorhynchid tooth, identified as coming from *Rhamphorhynchus muensteri* (Goldfuss, 1831), which appears to be embedded in the mantle of an exquisitely preserved example of the fossil octobrachian cephalopod (squid of popular parlance) *Plesioteuthis subovata* Münster, 1846 from the famous Solnhofen Limestone fossil Lagerstätte in Bavaria, Germany. It has taken nearly a century and a half (1784–recent) of collecting to conclude that pterosaurs may have fed on cephalopods, such is the rarity of 'smoking gun' evidence for predator–prey relationships among pterosaur fossils. There is currently no direct evidence in the form of gut contents to suggest that some pterosaurs actually consumed cephalopods. Here we report on the first occurrences of gut contents preserved *in situ* within and around the gastrointestinal tract in two Lower Jurassic (Toarcian) pterosaurs from the German Posidonia Shale Formation: the campylognathoidid *Campylognathoides zitteli* and a rhamphorhynchid, *Dorygnathus banthensis.* A previous study on Posidonia Shale pterosaurs by Padian (2008b) referred to fossilized stomach contents in *Campylognathoides* but did not describe or identify them. We demonstrate that a specimen of *C. zitteli* consumed belemnoid coleoids whilst an example of *D. banthensis* ate small actinopterygian fishes. Until now, these are the only records of feeding in Lower Jurassic pterosaurs. Evidence for feeding in Upper Jurassic and Cretaceous pterosaur is discussed in detail by Witton (2017).

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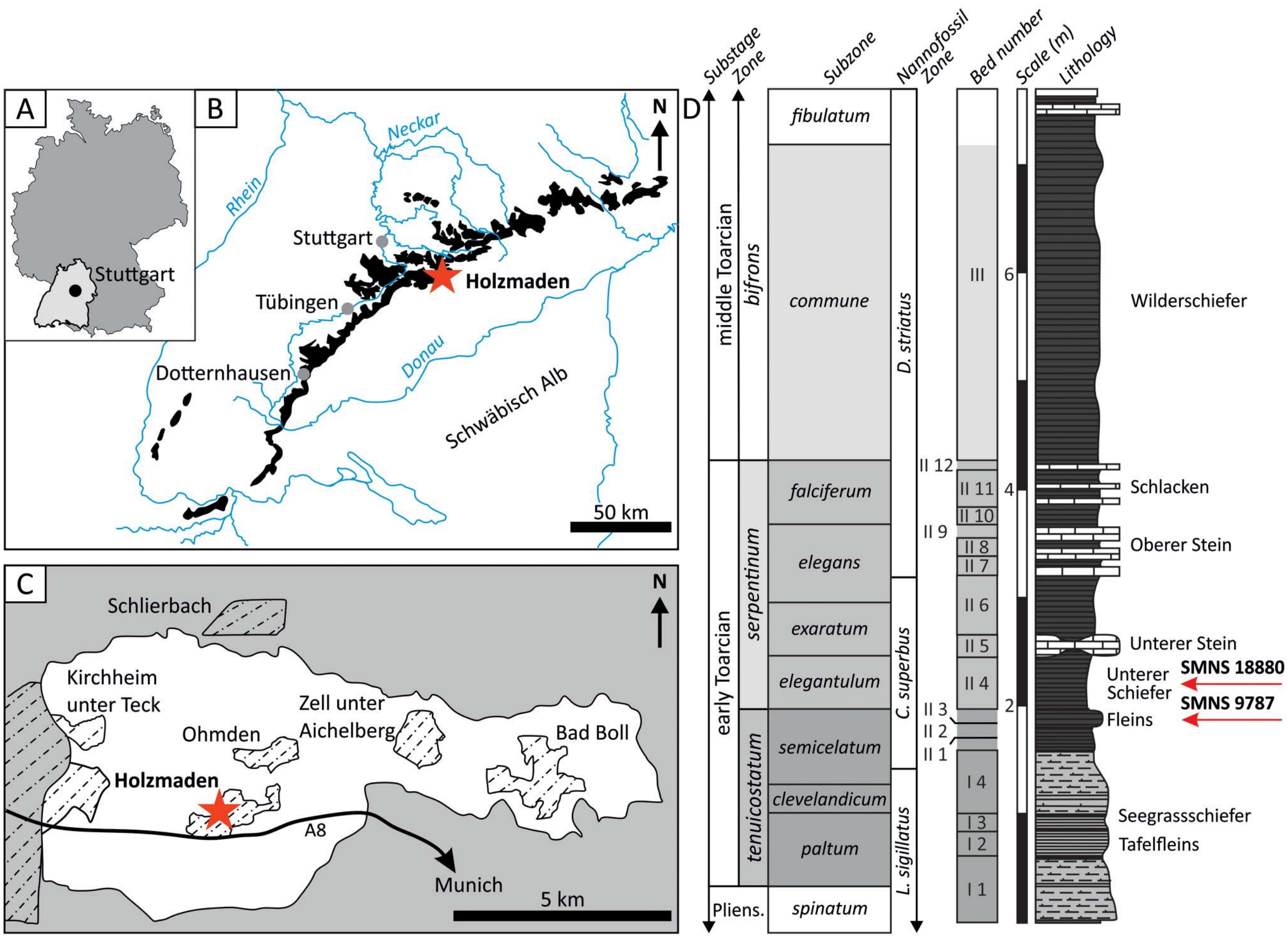

FIGURE 1. Locality maps and stratigraphic section of the Posidonia Shale Formation at Holzmaden. **A**, map of Germany with the state of Baden–Württemberg highlighted; **B**, simplified map of Baden–Württemberg showing regional outcrops of the Posidonia Shale Formation along the margins of the Schwäbisch Alb. The Holzmaden area is indicated by a star; **C**, regional map of the Holzmaden area with the collection horizon for SMNS 9787 indicated with a star; **D**, stratigraphic log of the Posidonia Shale Formation at Holzmaden showing the collection horizon of SMNS 9787 (*Campylognathoides zitteli*) and SMNS 18880 (*Dorygnathus banthensis*). Redrawn and modified from Cooper and Maxwell (2023) with stratigraphy based on Riegraf et al. (1984).

GEOLOGICAL CONTEXT

The Lower Jurassic (Toarcian) Posidonia Shale Formation (in German—Posidonienschiefer) crops out in Germany from Waldshut-Tiengen in the south to Lower Saxony in the northwest, with similar lithostratigraphic deposits of coeval age in Luxembourg, the Netherlands, France and the U.K. (Bour et al., 2007; Cooper & Maxwell, 2023; Mönnig et al., 2018; Riegraf et al., 1984; Röhl & Schmid-Röhl, 2005; Trabucho-Alexandre et al., 2012). In Baden-Württemberg the formation is a world-renowned black shale Konservat Lagerstätten (Fig. 1A–C) and is famed for its exceptionally preserved invertebrate and vertebrate fossils, sometimes found with associated soft tissues, especially ichthyosaurs (Cooper & Maxwell, 2022; De La Garza et al., 2023; Martill, 1993). The formation represents a continuous succession of early to lower-middle Toarcian strata, ranging biostratigraphically from the *tenuicostatum–bifrons* ammonite Zones (Hauff, 1921; Riegraf et al., 1984) (Fig. 1D). Of particular interest is the area around the village of Holzmaden (Baden-Württemberg; approximately 30 km SE of Stuttgart) where the vast majority of historic and modern collecting has taken place, particularly by the Hauff family who have meticulously collected and prepared the fossils across four generations (Hauff & Hauff, 1981). It should be noted that the historic specimen label of 'Holzmaden' is often used anecdotally to denote any number of former or active quarries within the Holzmaden area, particularly between the towns and villages of Kirchheim unter Teck, Jesingen, Holzmaden, Ohmden, Schlierbach, Bad Boll, and Zell unter Aichelberg (Cooper & Maxwell, 2023; Maxwell et al., 2022) (Fig. 1A–C). Well preserved Posidonia Shale fossils, including pterosaurs, also occur at Dotternhausen and Dormettingen some 60 km to the southwest (e.g., Jäger, 2005). The paleoenvironment of the Posidonia Shale at Holzmaden represents a shallow to moderately deep, restricted siliciclastic shelf setting within a sub-tropical epicontinental sea (Mönnig et al., 2018; Röhl & Schmid-Röhl, 2005; Röhl et al., 2001). Fluctuating oxygen levels throughout the sequence with periods of sea floor anoxia, combined with soupy substrates have been directly associated with the excellent quality in fossil preservation (Jäger, 2005; Martill, 1993; Maxwell et al., 2022; Röhl et al., 2001). The formation also records the onset and fallout of the Early Toarcian Anoxic Event (E-TOAE)—a global marine episode associated with extensive black shale deposition and depleted sea floor oxygen levels—with 'peak anoxia' recorded in the lower *serpentinum* Zone (beds εII_4–εII_6: Mönnig et al., 2018; Riegraf et al., 1984).

The fauna of the Posidonia Shale offers one of the most comprehensive snapshots of Early Jurassic marine life, with various mollusks (e.g., Hauff & Hauff, 1981; Jefferies & Minton, 1965; Klug et al., 2021a; Riegraf et al., 1984), crustaceans (e.g., Schweigert et al., 2003), echinoderms (e.g., Seilacher et al., 1968; Simms, 1988, 1989), holothurians (Riegraf, 1985), annelids (e.g., Riegraf et al., 1984), foraminiferans (Riegraf, 1985), coccoliths (Ebli, 1989); and a wide diversity of vertebrates including sauropterygians (pliosaurs and plesiosaurs), ichthyosaurs (De La Garza et al., 2023; Hauff & Hauff, 1981), marine crocodylomorphs (e.g., Johnson et al., 2020), a pleurosauroid sphenodont (Carroll, 1985), a mawsoniid coelacanth (Dutel et al., 2015), and various actinopterygian (e.g., Cooper & Maxwell, 2022; Hauff & Hauff, 1981; Maxwell & Stumpf, 2017; Thies & Waschkewitz, 2016) and cartilaginous fishes (e.g., Duffin, 1983, 1995; Fraas, 1910; Maisch & Matzke, 2016). Terrestrial vertebrates are rare in the Posidonia Shale, with only a single dinosaur find (*Ohmdenosaurus liasicus* Wild, 1978a—a gravisaurian sauropodomorph) and at least three pterosaurs: *Dorygnathus banthensis*, *Campylognathoides zitteli* and *C. liasicus*.

Pterosaur remains are extremely rare in the Posidonia Shale with the majority of museum specimens originating from the Holzmaden area (Hauff, 1921; Hauff & Hauff, 1981; Padian, 2008a, b; pers. obs. SC), and the deeper water, more basin-ward areas of Dormettingen and Dotternhausen (Jäger, 2005; Padian, 2008a, b). Several isolated pterosaur bones including a partially articulated distal wing are also reported from the Posidonia Shale in Banz, Bavaria (Theodori, 1830) and in northern Germany, particularly at the sites of Beienrode, Braunschweig (Hauff et al., 2017), Schandelah (Hübner et al., 2020), and Schandelah-Flechtorf (Steiler, 1922). In the German Lias (inc. Holzmaden and Dotternhausen), only the genera *Campylognathoides* and *Dorygnathus* are recorded (Hauff & Hauff, 1981; Padian, 2008a, b). A three-dimensional skull belonging to a small pterosaur from the Posidonia Shale at Altdorf, near Nuremburg (Bavaria) has been referred to the non-novialoidean rhamphorhynchid *Parapsicephalus* Arthaber, 1919 (Newton, 1888; O'Sullivan & Martill, 2017) hinting at a hidden higher diversity of pterosaurs. A three-dimensionally preserved pterosaur palate with *in situ* dentition referred to *Dorygnathus banthensis* is also described from the Posidonia Shale Formation at Bad Harzburg, Niedersachsen (Ősi et al., 2010) indicating pterosaurs to be widely distributed across Germany during the Toarcian. Outside of Germany, Toarcian age pterosaurs have been reported from the coeval Whitby Mudstone Formation of northeastern England, including the skull and brain endocast of *Parapsicephalus purdoni* (Newton, 1888), and a partial humerus referred to Campylognathoididae (O'Sullivan & Martill, 2017; O'Sullivan & Rigby, 2017; O'Sullivan et al., 2013).

MATERIALS AND METHODS

Of the numerous Early Jurassic pterosaur fossils known to date, only two species preserve identifiable gut contents (one specimen for each taxon): *Dorygnathus banthensis* and *Campylognathoides zitteli*, both based on specimens from the Upper Lias (Toarcian) Posidonia Shale of Holzmaden in southern Germany. Pterosaur specimen SMNS 9787 comprises a near complete and mostly articulated skeleton of *Campylognathoides zitteli* preserved on a large slab of compact shale measuring 915 mm by 570 mm. The specimen derives from the uppermost *tenuicostatum* Zone (bed $\varepsilon\mathrm{II}_3$ ["Fleins"]—see Hauff [1921] and Riegraf et al. [1984]) of the Lower Jurassic (Early Toarcian) Posidonia Shale at Holzmaden. The fossil was collected and expertly prepared by Dr. Bernard Hauff in 1893 with his engraved signature visible in the lower right-hand corner of the slab. The specimen was later purchased and subsequently donated in 1898 to the Staatliches Museum für Naturkunde Stuttgart (formerly the Württemberg Natural History Collection) by F. Plieninger and F. A. Krupp. Plieninger (1894) had previously described the specimen and designated it as the holotype of *Campylognathus zitteli* (genus name was preoccupied by a beetle and so changed to *Campylognathoides* by Strand [1928]). Specimen SMNS 9787 was housed in the former museum gallery at Neckarstraße (Stuttgart) until the early 1940s, when the building, and a significant amount of the collection, perished in a fire resulting from war-time bombing. Specimen SMNS 9787 survived undamaged due to it being evacuated off-site prior to the bombardment. It was relocated during the 1980s to the current Museum am Löwentor (SMNS) where it is displayed as part of the permanent exhibit.

A partial skeleton of *Dorygnathus banthensis* (SMNS 1880) preserving piscivorous gut contents is additionally described from bed $\varepsilon\mathrm{II}_4$ (*serpentinum* Zone) of the former Hauff quarry in Holzmaden. The specimen is primarily preserved on a slab of shale measuring 210 mm by 170 mm, and was prepared by Dr. Bernard Hauff in Holzmaden (UMH) and later sold to the SMNS in 1942.

Both specimens were examined using hand lenses and photographed using a Nikon Series DMC-FZ72 camera with compact 60× optical macro-lens mounted on a vertical tripod. Belemnoid taxonomy and hooklet (onychites) classification for Posidonia Shale teuthids is based on published literature (e.g., Fuchs & Weis, 2008; Fuchs et al., 2013a; Jenny et al., 2019; Riegraf, 1980).

Institutional Abbreviations—**MCSNB**, Museo Civico di Scienze Naturali in Bergamo, Bergamo, Italy; **PSB**, Petrefaktensammlung Banz, at Hanss-Seidel-Stiftung, Schloss Banz, Germany; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Baden-Württemberg, Germany; **SOS**, Jura Museum (Solnhofen Sammlung), Eichstätt, Germany; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UMH**, Urwelt Museum Hauff, Holzmaden, Baden-Württemberg, Germany; **WDC**, Wyoming Dinosaur Centre, Thermopolis, WY, U.S.A.

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup, 1834
NOVIALOIDEA Kellner, 2003
CAMPYLOGNATHOIDIDAE Kuhn, 1967
CAMPYLOGNATHOIDINAE Kuhn, 1967
CAMPYLOGNATHOIDES Strand, 1928
CAMPYLOGNATHOIDES ZITTELI (Plieninger, 1894)

Abbreviated Synonymy

Campylognathus zitteli Plieninger, 1894:41, p. 193, pl. XIX, fig 1 (original description).

Campylognathoides zitteli Strand, 1928: p. 54 (revised genus name).

Campylognathoides zitteli (Plieninger, 1894): Strand, 1928:92, pp. 40–41.

Campylognathoides zitteli (Plieninger, 1894): Padian, 2008b:80, p. 72.

Type Species—*Campylognathoides zitteli* (Plieninger, 1894).

Holotype—SMNS 9787 (Figs. 2, 3).

Type Locality and Horizon—Hauff Quarry, Holzmaden, Baden–Württemberg, southern Germany. Bed $\varepsilon\mathrm{II}_3$ ("Fleins"), Posidonia Shale Formation (= Posidonienschiefer), Schwarzjura epsilon, Upper Lias, lower Toarcian, Lower Jurassic.

Description of Stomach Contents and Alimentary Canal—The abdominal region of the trunk in SMNS 9787 is moderately disarticulated although the bones still retain a close proximity to one another. The lumbar vertebrae, synsacrum and gastralia are displaced from one another; whilst the ribs from the right side of the rib cage are laying in their correct anatomical order despite most being detached from their corresponding vertebra. With the exception of one broken rib and some minor plastic deformation resulting from burial compaction, all of the trunk and pelvic bones are undamaged and moderately well preserved. The skeleton is predominately displayed in right ventrolateral view, with the synsacrum and caudal vertebrae exposed in ventral view. Gastric contents both in the form of undigested/partially digested bioclasts (belemnoid hooklets) and cololite (a precoprolite) are present within the abdominal region. They are

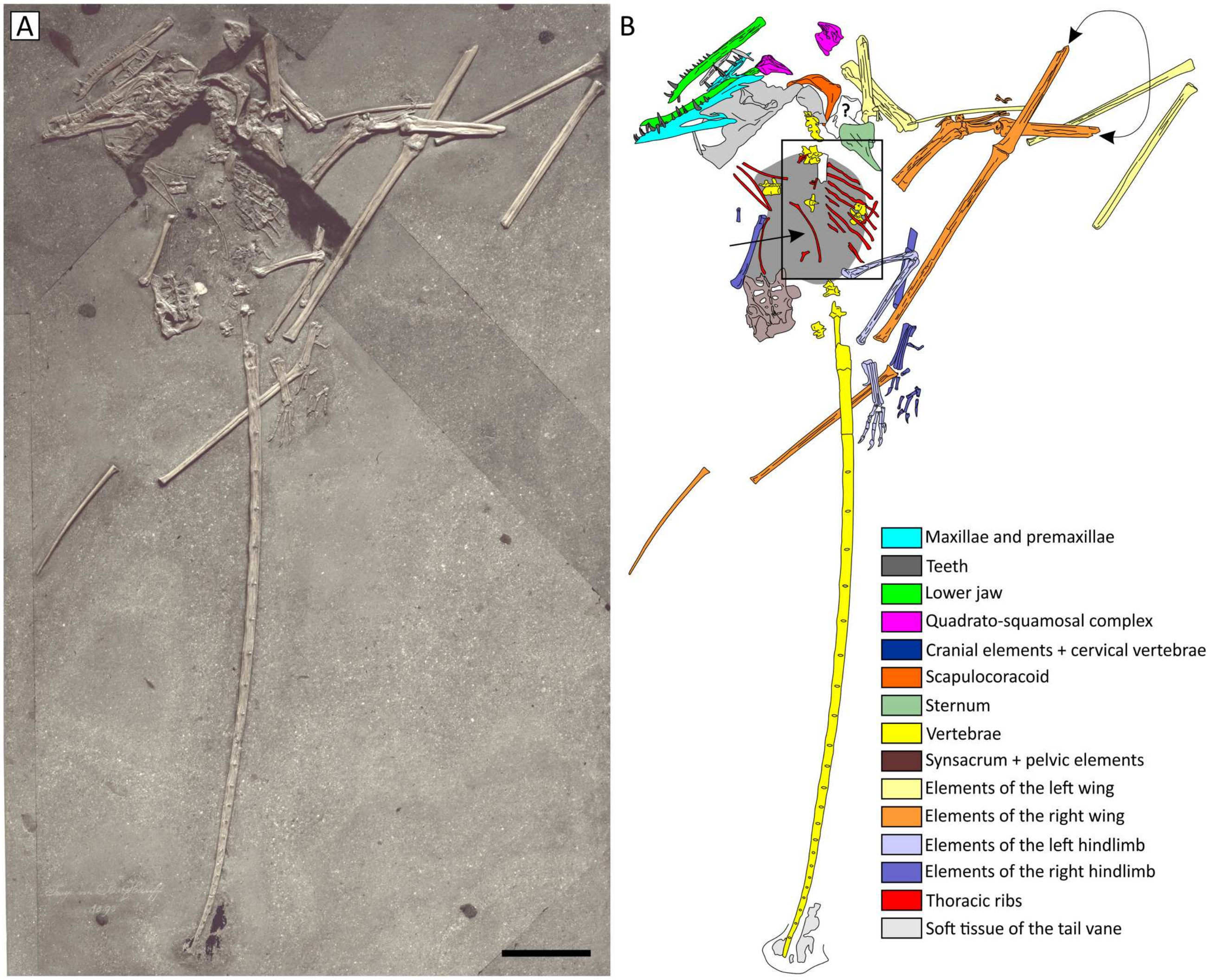

FIGURE 2. Holotype of *Campylognathoides zitteli* with belemnoid gut contents (SMNS 9787). **A**, overview of specimen; **B**, line drawing. Box and area shaded in dark gray (arrowed) indicates gut contents magnified in Figure 3. Scale bar represents 50 mm.

confined in close proximity of the lower abdomen, between the ribs, lumbar vertebrae and the synsacrum, supporting their identity as gut contents.

Light colored phosphatic material here interpreted as cololite derived from partially digested prey inside of the digestive tract is preserved in the hind region of the abdomen. A large central mass of cololite is positioned between the synsacrum, right femur and posterior to the articulated ribs (Fig. 3A, C). The cololite in this region has a globular tube-like appearance, arranged as a thick and readily folded fecal string (Fig. 3E, F). We interpret this structure as a cololite endocast, possibly of an unspecified region of the pterosaur's hindgut intestine (posterior to the stomach) but anterior of the rectum itself. A few poorly preserved chitinous belemnoid hooklets (onychites) are preserved adjacent to and one within this cololite endocast (Fig. 3E, F). Numerous small patches of cololite litter the immediate surrounding matrix, although some are only observed as cross sections, which have been prepared away. Evidently the gastrointestinal tract may have been more complete prior to preparation. A second, larger cololite protrudes from underneath the right side of the synsacrum (Fig. 3A, C). The synsacrum cololite is a paler color, smoother and pebble-like but without any recognizable bioclast content. Its position and composition suggest that it derives from a more posterior region of the pterosaur's hindgut, possibly from the rectum. Cololite material is not present outside of the immediate vicinity of the lower abdomen; thereby validating its association with the pterosaur skeleton.

A minimum of 10 belemnoid hooklets referrable to the diplobeliid belemnoid *Clarkeiteuthis conocauda* (see Fig. 4) are preserved within the abdominal region of the pterosaur's trunk (Fig. 3). The anterior mass of carbonized tissues and gut contents underneath the articulated ribs is poorly exposed, although the presence of a single hooklet underneath one of the ribs indicates the presence of further belemnoid remains inside the anterior region of the gut (stomach). A dull black patina, possibly the remains of a belemnoid ink sac (Fig. 3B), is displaced just lateral to the disrupted ribs and contains at least four well preserved *Clarkeiteuthis conocauda* hooklets, the longest of which has a hooklet height of 5 mm. The absence of cololite within this concentration of belemnoid remains indicates that it has been displaced from the stomach during structural collapse of the trunk skeleton. Several hooklets are also preserved in and around the central cololite endocast positioned just posterior to the ribs; three surrounding, and two preserved as inclusions in the cololite (Fig.

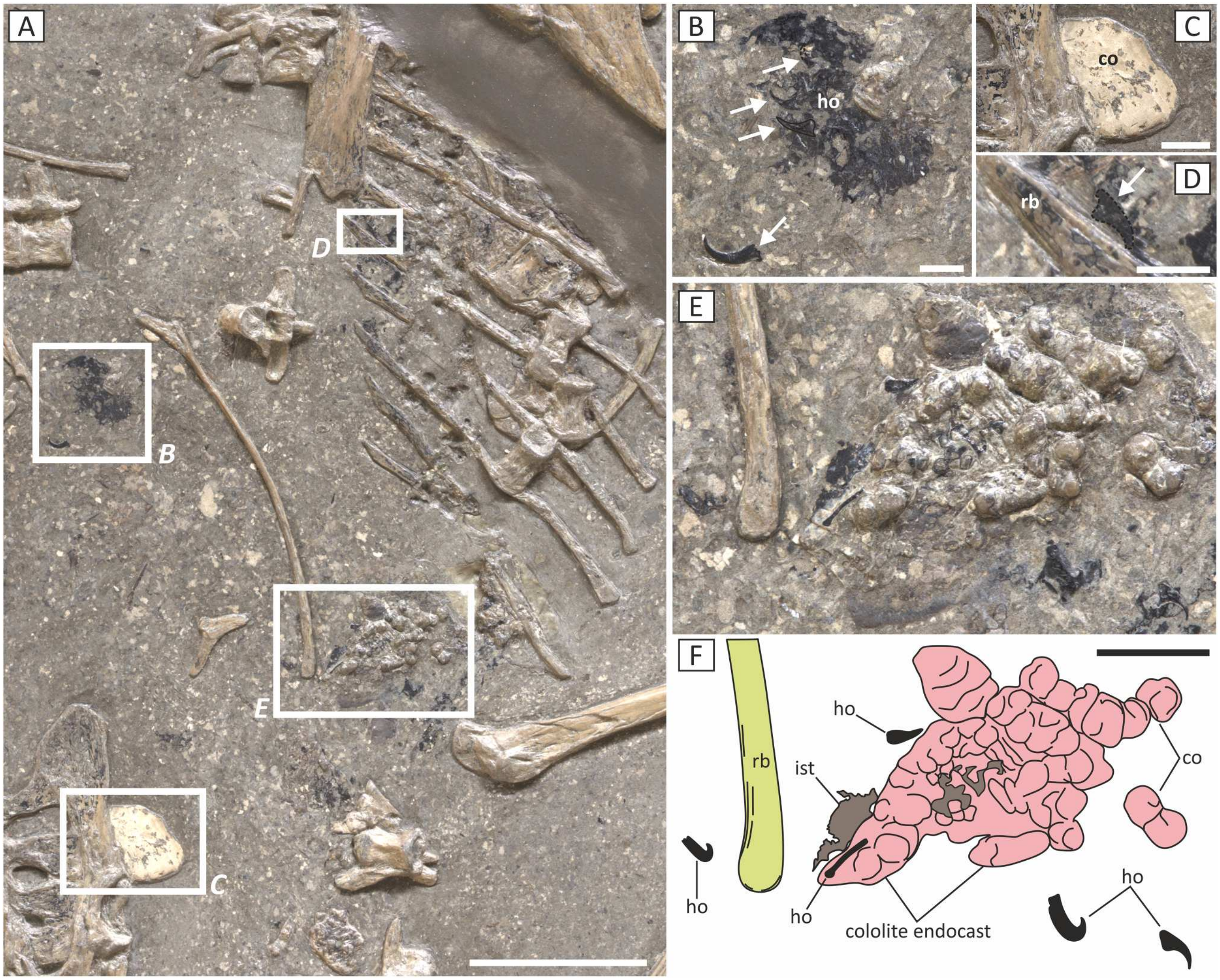

FIGURE 3. Holotype of *Campylognathoides zitteli* (SMNS 9787), details of stomach contents and gastrointestinal anatomy. **A**, overview of abdominal trunk region; **B**, details of organic mass containing indeterminate soft tissues and four isolated hooklets of *Clarkeiteuthis conocauda*; **C**, smoothed cololite (pre-coprolite) nodule, possibly associated with the rectal cavity; **D**, acid-worn belemnoid hooklet (*Clarkeiteuthis conocauda*) exposed in between the abdominal ribs; **E–F**, central abdominal mass of soft tissue and stomach contents containing several belemnoid (*Clarkeiteuthis conocauda*) hooklets and cololite partially infilling the possible intestinal tract. **Abbreviations**: **co**, cololite; **ho**, hooklets; **ist**, indeterminate soft tissues; **rb**, rib. Scale bars represent 50 mm (**A**), 10 mm (**E**, **F**), and 5 mm (**B–D**).

3E, F). Numerous dull black specks, most of which likely correspond to additional hooklets, litter the abdominal region including underneath the articulated portion of the ribcage, but are too poorly preserved to determine. Examination of the surrounding matrix did not reveal any belemnoid hooklets outside of the immediate vicinity of the pterosaur's abdomen. Small isolated actinopterygian fish bones are scattered across the bedding plane, with those placed in proximity to the pterosaur skeleton likely being a chance association.

Belemnoid Identification and Hooklet Morphology

All of the hooklets preserved in association with the gut of *Campylognathoides zitteli* (SMNS 9787) are assigned to the diplobeliid belemnoid *Clarkeiteuthis conocauda* based on the revised diagnosis and armature description of this species (Fuchs et al., 2013a). Hooklets of *Clarkeiteuthis conocauda* display a characteristic shape whereby the shaft of the hooklet in relation to the weakly curved uncinus is not inclined, rather it is perpendicular to the base (Fuchs et al., 2013a) (Fig. 4). This morphology is highly distinctive when compared with other hooklet-bearing Toarcian belemnoids (e.g., *Phragmoteuthis* + belemnites) where the shaft is much more steeply inclined relative to the uncinus (base) (Fuchs et al., 2013a) (Fig. 4). Well preserved hooklets in SMNS 9787 additionally display small notches and projections on their short bases, but lack lateral base spines (typical in non-diplobeliid belemnitids), which further supports their assignment to *Clarkeiteuthis*. The hooklets in *Phragmoteuthis bisinuata* somewhat resemble those of *C. conocauda* (Fuchs et al., 2013a), however the shaft is strongly inclined rather than perpendicular relative to the base of the hooklet (Doguzhaeva et al., 2007:figs. 2, 5a; Fuchs et al., 2013a:fig. 4e) (Fig. 4).

The subtle morphological variation observed between individual hooklets in SMNS 9787 (Figs. 3, 4B) is dependent on their original anatomical placement in the belemnoid's armature: distal hooklets (furthest from the mouth) in *Clarkeiteuthis conocauda* are more gracile with weakly curved apexes, whilst those closer to the mouth are generally stouter and more obtusely curved at their apices (Fig. 4).

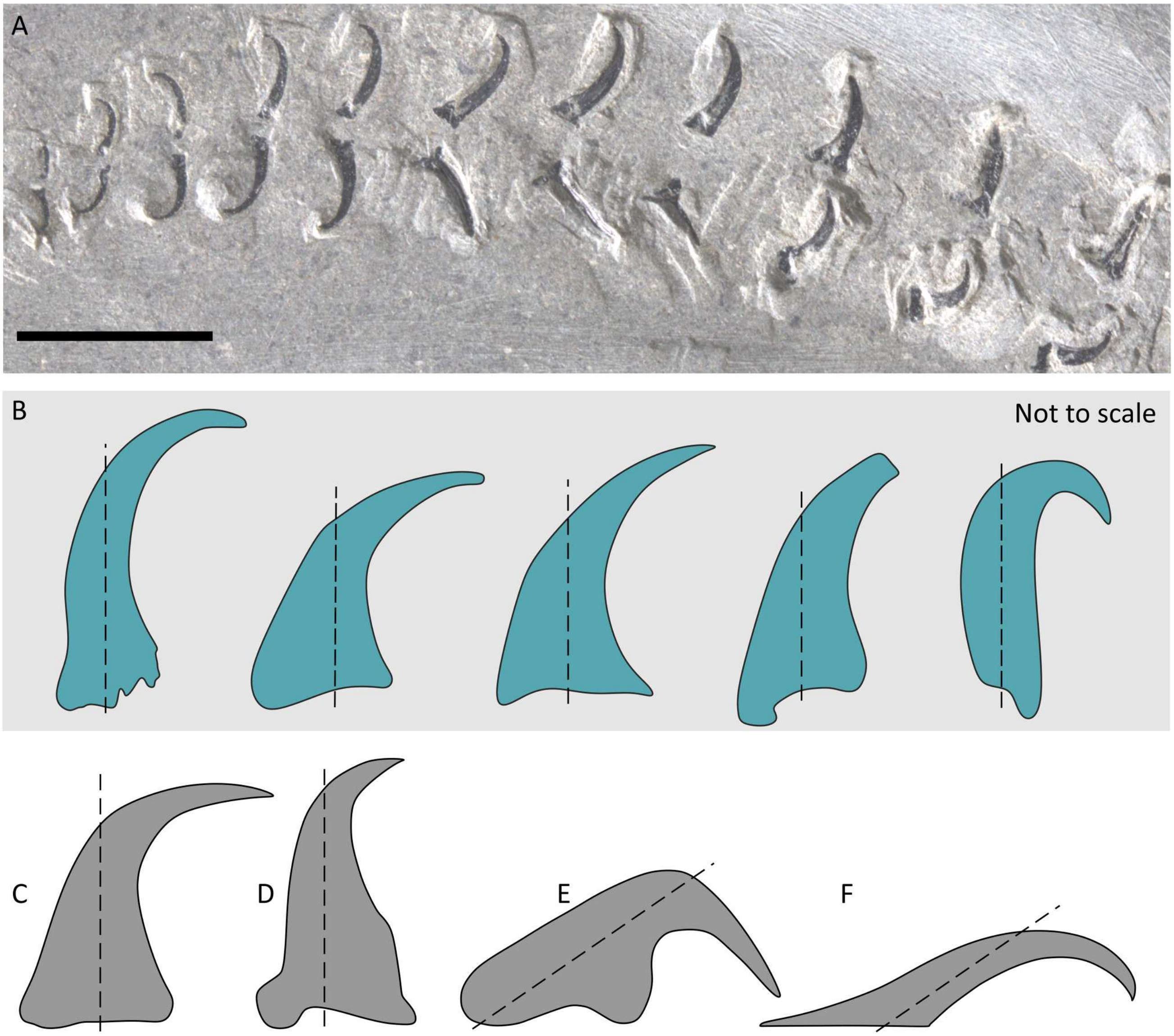

FIGURE 4. Comparative belemnoid hooklet morphologies. **A**, articulated arm of *Clarkeiteuthis conocauda* from the Posidonia Shale Formation showing the anatomical arrangement and variation in hooklet morphologies; **B**, hooklets preserved in association with the *Campylognathoides zitteli* holotype (SMNS 9787) showing morphological variation; **C**, **D**, *Clarkeiteuthis conocauda*: hooklets associated with type and referred specimens from Fuchs et al. (2013a); **E**, *Phragmoteuthis bisinuate*; **F**, generalized belemnoteuthid (belemnite) hooklet type. All hooklets are arranged with a vertical base; dashed lines indicate the degree of shaft inclination. **D** and **E** are redrawn and modified from Fuchs et al. (2013a). Scale bar represents 10 mm.

Preservation of Belemnoid Remains in SMNS 9787

Belemnoid hooklets are distributed throughout the abdominal region of SMNS 9787, all within close proximity of the ribs and lumbar vertebrae. No hooklets of *Clarkeiteuthis* are observed outside of this area. A mass of carbonaceous material likely representing soft tissue lies lateral to the rib cage and contains at least four well-preserved hooklets, three of which are concentrated within a dull black patina (Fig. 3A, B). Such amorphous material containing hooklets has been interpreted as the pigment from decayed coleoid ink sacs, and are often found within gut contents of some Posidonia Shale ichthyosaurs and teuthophagous fishes (e.g., Cooper & Maxwell, 2022; Wild, 1994). A mass of poorly preserved stomach contents is preserved within the articulated rib cage of the pterosaur, but are mostly unidentifiable (Fig. 3D). A single *Clarkeiteuthis* hooklet is exposed on the surface of this accumulation (Fig. 3D). Several hooklets are also present around the margins of, or are preserved inside of, the large cololite endocast of the pterosaur's intestine. The occurrence of hooklets inside of this cololite further signals that the squid remains described here are true stomach contents and not a chance association.

All of the hooklets are moderately well-preserved suggesting that they were only inside the gut for a short period before the pterosaur died, but it remains possible that hooklets are highly resistant to decay and perhaps remain within the gut for a prolonged period. Other diagnostic elements of *Clarkeiteuthis* including the mineralized proostracum and mantle are not preserved, indicating that the coleoid prey was mostly digested with only the likely more acid-resistant chitinous hooklets remaining to form an accumulation inside of the digestive tract. Similar accumulations of only belemnoid hooklets (sometimes forming mass concentrations) are commonly found inside the gut contents of many large ichthyosaurs and teuthophagous fishes in the Posidonia Shale (Cooper & Maxwell, 2022, 2023; Prikryl et al., 2012). Well preserved hooklets show complete bases and sharp apices without any signs of chemical corrosion. These are mostly confined towards the anterior region of the abdomen and surrounding the cololite endocast of the intestinal tract. Imperfect hooklets have incomplete or damaged bases with rounded distal apexes, likely the result of partial digestion and/or preparation damage. Damaged hooklets are more abundant within the lower abdominal region including inside of the cololite-filled intestinal tract. This variation in hooklet preservation is therefore likely dependent on the length of time and distance traveled through the pterosaur's digestive tract, with damaged hooklets progressing further and for a slightly longer time than undamaged hooklets.

Preservation and Preparation Biases

A minimum of 10 hooklets referable to *Clarkeiteuthis conocauda* are present inside of the gut of *Campylognathoides*; however, this is likely an underrepresentation as preparation in some areas of the gut (notably the rib cage) has likely destroyed some of the gastric contents. The mass of gastric remains inside the rib cage likely holds the remainder of the belemnoid meal as suggested by the presence of a hooklet protruding underneath one of the ribs (Fig. 3D). The disarticulation and subsequent eruption of the pterosaur's abdomen has dispersed the hooklets within the immediate vicinity, with additional hooklets either lost by transportation and/or preparation of the surrounding matrix.

The crown of *Clarkeiteuthis conocauda* is composed of 10 near-uniform arms each holding up to 40 individual hooklets each, implying around 400 hooklets per individual belemnoid (Fuchs et al., 2013a; Christian Klug pers. comm. 2024). This suggests that only a single *C. conocauda* squid is represented inside the gut of SMNS 9787, with the remaining circa ≤390 missing hooklets being obscured by matrix, lost in preparation, washed away from the carcass and/or hidden underneath bones of the pterosaur, or possibly digested in the hindgut. The cololite associated with the synsacrum (rectum) does not preserve any traces of hooklets, implying that these resilient chitinous elements were fully digested within the intestine. Alternatively, this cololite might represent an older meal which was composed of a different prey item, such as a small fish or entirely soft-bodied coleoid (e.g., *Teudopsis*, *Geopeltis*, *Loligosepia*, or *Jeletzkyteuthis*; Doguzhaeva & Mutvei, 2003; Fuchs & Weis, 2008, 2010; Fuchs et al., 2013b) without chitinous hard parts to survive for longer through the gut.

BREVIQUARTOSSA Unwin, 2003
RHAMPHORHYNCHIDAE Seeley, 1870
RHAMPHORHYNCHINAE Nopcsa, 1928
DORYGNATHUS Wagner, 1860
DORYGNATHUS BANTHENSIS (Theodori, 1830)
(Figs. 5 and 6)

Abbreviated Synonymy

Ornithocephalus banthensis Theodori, 1830:62, p. 103 (original description).

Pterodactylus banthensis Theodori, 1831:3, p. 276 (new combination).

Dorygnathus banthensis Wagner, 1860:p. 48 (new genus and combination).

Dorygnathus sp. Broili, 1939:p. 129.

Dorygnathus banthensis (Theodori, 1830): Padian, 2008b:80, p. 9.

Type Species—*Dorygnathus banthensis* (Theodori, 1830).

Holotype—PSB 757/758.

Referred Material—Incomplete and partially articulated skeleton with stomach contents (SMNS 18880) prepared from the underside by Dr. Bernard Hauff in 1942, on a slab of compact Posidonia Shale matrix measuring 210 × 170 mm.

Locality and Horizon—Bed εII$_4$ ('Unterer Schiefer'), Hauff Quarry, Holzmaden, Baden-Württemberg, Germany; *elegantulum* Subzone, *serpentinum* Zone, Posidonia Shale Formation (= Posidonienschiefer), early Toarcian, Lower Jurassic.

Remarks—Padian (2008a) briefly described this specimen but did not note the presence of any gastric contents or soft tissue preservation. According to Padian (2008a), SMNS 18880 likely represents a juvenile individual due to its comparatively short estimated wingspan (800 mm), in comparison to larger *Dorygnathus banthensis* specimens (circa 1.7 m maximum for MB.R 1977.21) from the Posidonia Shale.

Preservation

The specimen is incomplete due to decay, missing the skull, tail, ribcage, sternum, and most of the left forearm and pectoral girdle (Fig. 5). The right pectoral girdle and forelimb are complete, albeit partly disarticulated. Surviving elements of the left forelimb are entirely disarticulated with the left humerus and metacarpal displaced from the rest of the skeleton. The complete right manus and parts of the left manus, protruding from underneath the displaced right humerus, are articulated with the digits splayed. The pelvic girdle including the left pubis, preacetabular processes, and ilium are exposed in ventral view, with eight small pelvic/lumbar vertebrae preserved in their original articulation. The hindlimbs are absent with exception of the right femur, which is preserved in articulation with the acetabulum (Fig. 5). A carbonaceous black film is present in patches along the posterior margins and overlying some areas of the wing-finger digit IV. The texture and preservation of this structure is consistent with the carbonaceous material preserved in the terminal tail vane, orbit, and wings of *Campylognathoides* (Figs. 5, 6). The carbonaceous films associated with the wing in *Dorygnathus* (SMNS 18880) are therefore likely remnants of a decomposed wing membrane.

Description of Gut Contents

A cluster of mostly disarticulated and fragmented actinopterygian bones are preserved in direct association within the abdominal region of the pterosaur (Figs. 5, 6). The prey fish is confidently identified as a small specimen of the stem-teleost *Leptolepis* sp. based on the presence of a highly diagnostic inverted 'T'-shaped dentary present within the gastric mass. The majority of the surviving dermal bones are highly fragmented and mostly unidentifiable. A thin bone fragment preserves traces of a partial sensory canal, possibly representing a fragment of the parietals (Fig. 6). Several distinctive teleostean chordacentra, preserved both in anterior and lateral cross sections, are preserved in association with the diagnostic dentary. Leptolepiform fishes are the only group of actinopterygians in the Posidonia Shale to possess both a 'T'-shaped dentary and mineralized chordacentra (e.g., Arratia, 2003; Maxwell & Stumpf, 2017), therefore strongly supporting referral of these bones to *Leptolepis* sp. An absence of multiples of the same cranial elements suggests that likely only a single *Leptolepis* sp. specimen is represented. A few incomplete fin rays are preserved in their original anatomical alignment despite the rest of the skeleton being disarticulated. The significance of this demonstrates that the prey fish had not quite fully disarticulated inside of the stomach, but nonetheless

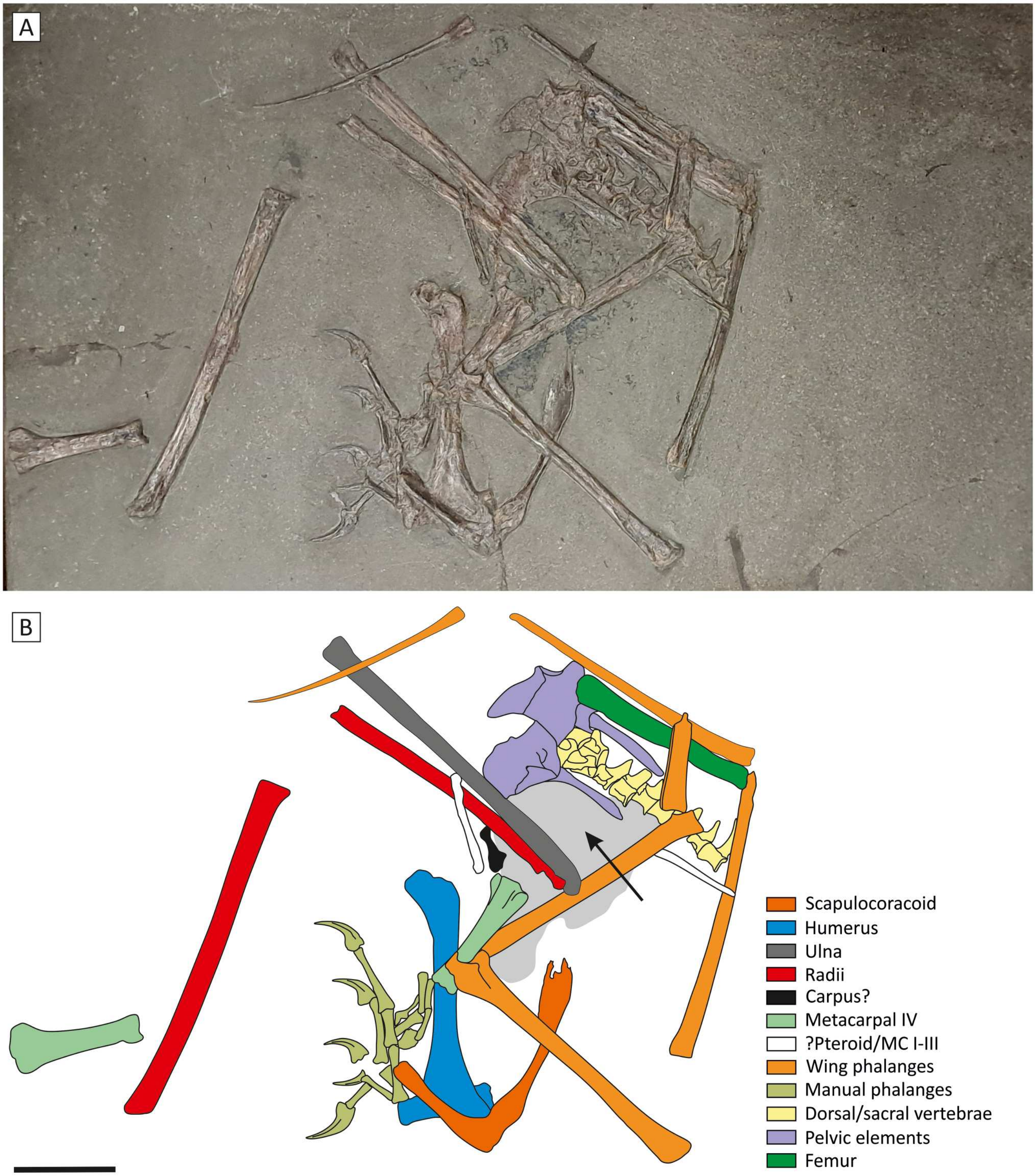

FIGURE 5. *Dorygnathus banthensis* (SMNS 18880), incomplete and semi-articulated skeleton from Holzmaden (SW Germany) with fossilized stomach contents. **A**, overview image of specimen; **B**, line drawing. The abdominal cavity containing partially digested teleosteomorph remains (*Leptolepis* sp.) is indicated by an arrow and is shaded in gray. Scale bar represents 20 mm.

suggesting the prey fish was ingested reasonably whole only a short time prior to the pterosaur's demise. The *Leptolepis* dentary measures approximately 4 mm in length, equating to an immature *Leptolepis* in the size range 60–70 mm total length, based on comparative *Leptolepis* spp. specimens in the SMNS collection (SC. pers. obs.).

The fish bones are concentrated immediately anteroventral to the pelvis and ventral of the vertebral column, predominantly within an area measuring 13 mm × 19 mm (Fig. 6). Their location therefore supports the identification of these bones as the stomach contents derived from the decayed abdominal cavity. Areas of the prey fish bones are stained by a similar

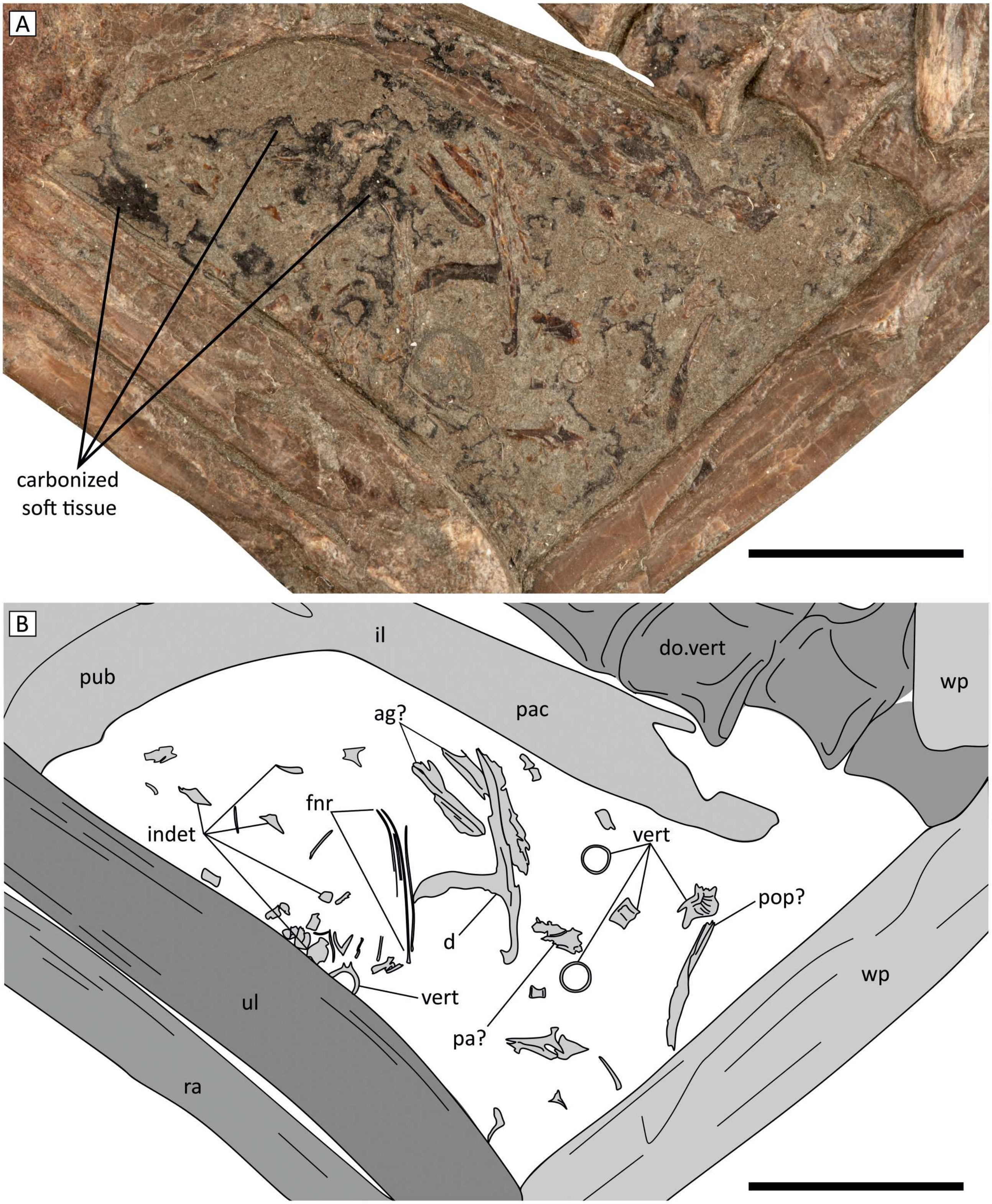

FIGURE 6. *Dorygnathus banthensis* (SMNS 18880) with fossilized gut contents. **A**, magnified photograph of the abdominal region with surrounding matrix digitally removed; **B**, line drawing showing details of the partially digested *Leptolepis* sp. prey fish preserved within the pterosaur's abdominal cavity. **Abbreviations**: **ag?**, angular?; **d**, dentary; **do.vert**, dorsal vertebrae; **fnr**, fin rays; **il**, ilium; **indet**, indeterminate fish bones; **pa?**, parietal?; **pac**, preacetabular process; **pop?**, preopercle?; **pub**, pubis; **ra**, radius; **ul**, ulna; **vert**, vertebral centra (*Leptolepis* sp.), **wp**, wing phalanges. Scale bars equal 5 mm.

carbonaceous black film observed elsewhere in the specimen (Fig. 6A), further confirming their original *in situ* association with the pterosaur carcass. The bone margins are regularly fragmented and splintered thereby indicative of gastric corrosion and partial digestion by stomach acids whilst inside of the gut (Serafini et al., 2022). The absence of any phosphatic cololite and the preservation of delicately articulated fin rays strongly suggest that these bones had neither been exposed to gastric acids for a prolonged duration, nor passed from the stomach into the intestine.

DISCUSSION

Rarity of Gut Contents in Pterosaurs

The rarity of stomach contents in Pterosauria is something of an enigma, but may be related to rapid digestion which is typical for volant vertebrates (Price et al., 2015). Many fossil Konservat Lagerstätten have become well-known for the quality of preservation, and to some degree abundance of pterosaur skeletons (Unwin, 2005; Wellnhofer, 1991; Witton 2013). Perhaps most notable among these are the Upper Jurassic Solnhofen-type plattenkalk formations of southern Germany (e.g., Tischlinger & Frey 2015), the Lower Cretaceous Crato and Santana formations of Brazil (e.g., Martill & Brito, 2017) and the Yixian and Jiufotang formations of China (e.g., Lü et al., 2013). In all of these deposits, pterosaurs occur as partial or fully articulated skeletons, sometimes in 3D, and often with associated soft tissues preserved (Bestwick, 2018; Frey et al., 2003; Kellner et al., 2010; Martill & Unwin, 1989). So, it seems odd that pterosaur stomach contents are so rarely encountered (see Table 1). In part, this may be related to two aspects of the pterosaurian diet. Firstly, pterosaurs may be strictly limited in the nature of their diet, such that they predated organisms with low preservation potential. Secondly, the efficiency of the pterosaurian digestive system may have been such that stomach contents only survived for a brief period before being digested. The first such scenario seems unlikely, as the dentitions of pterosaurs are highly varied across the clade (Bestwick et al., 2018; Martill, 2014; Ösi, 2011), reflecting a wide variety of feeding strategies, and presumably of prey types with varying preservation potentials. The second scenario may have some merit, although it is difficult to test. An efficient digestive system, rapidly extracting nutrients and disposing of waste within a brief digestion window would provide a quick source of nutrients while keeping the overall body mass down, which must had been beneficial for a volant animal (e.g., Price et al., 2015). Evidence of rapid digestion in pterosaurs is supported by a recurring association of calcite crystals in the abdominal trunks of Solnhofen pterosaurs, which are suspected to represent diagenetically altered stomach remains, most plausibly cololite (Bennett, 2014; Hone et al., 2015; Witton, 2017). The lack of anatomically identifiable remains in these calcite masses infers that in all cases, the prey was in an advanced stage of decomposition likely promoted by rapid absorption rates and brief digestion cycles. It is also plausible that some pterosaurs may have regurgitated indigestible hard parts of their prey during the digestion process, similar to modern birds of prey, which may account for the scarcity of durable elements in their gastrointestinal tracts (e.g., Barbosa et al., 2021; Cheke & Hume, 2020). Inferences for possible regurgitalites containing fish bones are associated with the mouth and throat regions of few rhamphorhynchid and pterodactyloid (= *Pteranodon*) pterosaurs, which likely ejected the prey post-mortem (Bennett, 2001; Brown, 1943; Witton, 2017) (Table 1). These rare pterosaur specimens, which do preserve undigested hard parts of their prey within the gut likely represent one of two scenarios: (1) either the pterosaur died very soon after consuming the prey, and/or (2) the pterosaur failed to eject the hard parts before they could pass into the intestine. We note that in extant crocodilians hard food items are known to persist within the gut for long periods despite the strong stomach acids in these animals (Janes & Gutzke, 2002; Nifong et al., 2012; Platt et al., 2013). By contrast some birds and bats have rapid digestion of stomach contents possibly to increase flight efficiency (Price et al., 2015).

Clarkeiteuthis conocauda—Abundant Prey in the Posidonia Shale?

Belemnoid cephalopods are highly abundant and diverse, both stratigraphically and geographically throughout much of the Early Jurassic (Fuchs & Weis, 2008, 2010; Fuchs et al., 2013a, 2013b; Hauff & Hauff, 1981; Riegraf, 1980; Riegraf et al., 1984). Belemnoids are particularly well known in the German Posidonia Shale with *Clarkeiteuthis conocauda* among the most commonly recovered diplobelid belemnoid in the formation (e.g., Fuchs et al., 2013a; Hauff & Hauff, 1981).

Clarkeiteuthis conocauda is a small- to medium-sized belemnoid (≤210 mm TL) characterized by an elongate phragmocone and 10 short, hook-bearing arms, each of which holds up to 40 individual hooklets (Fuchs et al., 2013a; Jenny et al., 2019). Materials of this taxon were originally included in *Phragmoteuthis*; however, an absence of a three-lobed proostracum

TABLE 1. Pterosaur specimens with preserved gut contents with data derived from Witton (2017).

Taxon and specimen number	Contents of gut	Locality, formation and age	Reference
Rhamphorhynchidae: *Dorygnathus banthensis* (SMNS 18880)	Disarticulated teleosts *Leptolepis* sp.	Posidonia Shale Fm. (Jurassic: Toarcian) Holzmaden, Germany	This paper
Campylognathoididae: *Campylognathoides zitteli* (SMNS 9787)	*Clarkeiteuthis conocauda* belemnoid hooklets	Posidonia Shale Fm. (Jurassic: Toarcian) Holzmaden, Germany	This paper
Eudimorphodontidae: *Eudimorphodon ranzii* (MCSNB 2888)	Partly digested bone. Ganoid fish scales of *Parapholidophorus*	Zorzino Limestone Fm. (Triassic: Norian), Italy	Wild, 1978b; Witton, 2017
Rhamphorhynchidae: *Rhamphorhynchus muensteri* (SOS 4599)	Fish remains	Solnhofen Lst Fm. (Jurassic: Tithonian), Germany	Wellnhofer, 1975, 1991; Witton, 2017
Rhamphorhynchidae: *R. muensteri* (WDC CSG 255)	Fish remains in throat region	Solnhofen Lst Fm. (Jurassic: Tithonian), Germany	Frey and Tischlinger, 2012
Rhamphorhynchidae: *R. muensteri* (TMP 2008.41.001)	Amorphous remains	Solnhofen Lst Fm. (Jurassic: Tithonian), Germany	Hone et al., 2015
Rhamphorhynchidae: *Scaphognathus crassirostris* (SMNS 59395)	Fish remains	Solnhofen Lst Fm. (Jurassic: Tithonian), Germany	Bennett, 2014
Pteranodontidae: *Pteranodon* sp. (AMNH 5098)	Fish remains between mandibular rami interpreted as regurgitate	Niobrara Chalk Fm. (Cretaceous: Campanian), Kansas, U.S.A.	Witton, 2017

excludes this species from the Phragmoteuthidae and supports assignment to the Diplobelida (Fuchs et al., 2013a). *Clarkeiteuthis conocauda* is discontinuously distributed throughout the Posidonia Shale between beds εI_1 (lower *tenuicostatum* Zone) and εII_{12} (upper *serpentinum* Zone) where it is relatively abundant in certain horizons (Hauff & Hauff, 1981). Many specimens of *Clarkeiteuthis conocauda* are exceptionally preserved as they readily retain parts of the delicate mantle, ink sac, mineralized proostracum, and articulated crowns. Few rare examples additionally preserve *Leptolepis* prey fish tangled within their armature, representing behaviors of piscivory and distraction sinking (Hart et al., 2020; Jenny et al., 2019; Klug et al., 2021a).

Belemnoids including *Clarkeiteuthis* were an abundant and easily accessible (yet fast swimming; Klug et al. [2016]) prey resource for a variety of predators in the Posidonia Sea, including hybodont sharks (Pollard, 1990), ichthyosaurs (Dick et al., 2016; Keller, 1976), and sauropterygians (not known for Toarcian forms but reported for Callovian pliosaurs [Martill, 1992]). This is indicated by vertebrate stomach contents which frequently preserve disarticulated hooklets inside the digestive tract, often forming mass accumulations (Dick et al., 2016). Such accumulations may represent numerous *Clarkeiteuthis* individuals ingested either from a single feeding event or accumulated over time. Distinction can be made based on variation in hooklet preservation quality; the higher the variation (e.g., both fresh and acid etched), the greater the time averaged. The hooklets in the gut of *Campylognathoides*, although not congealed together into a coherent mass, are mostly well preserved and thereby are indicative of an isolated feeding event, rather than a time-averaged accumulation. Combined with the low number of surviving hooklets associated with the pterosaur's digestive tract, this strongly suggests that only a single *Clarkeiteuthis conocauda* was present inside the gut of *Campylognathoides* when the pterosaur died.

Belemnoids were evidently common prey for a variety of predators in the Posidonia Sea biotope, notably large ichthyosaurs including *Stenopterygius* and *Eurhinosaurus* (Böttcher, 1989; Dick et al., 2016, respectively), large asthenocormine pachycormiforms (e.g., *Saurostomus esocinus*; *Germanostomus pectopteri* (Cooper et al., 2022)), caturids (*Caturus smithwoodwardi* (Cooper et al., 2022)), hybodont sharks (Klug et al., 2021b) and now the pterosaur *Campylognathoides zitteli*. Unlike belemnites, which are considered to have been good swimmers (Klug et al., 2016), diplobelid belemnoids such as *Clarkeiteuthis conocauda* are proposed to have been less-active swimmers (Jenny et al., 2019), with the capability of occasional bursts rather than rapid swimming (Fuchs et al., 2013b). This sluggish behavior likely made *Clarkeiteuthis* an easier prey resource to catch, and combined with their high detection in the formation, may account for why most teuthophagous predators show a prey preference towards diplobelids rather than belemnites with a thick, heavy calcitic rostrum. It should be noted that not all teuthophagivores fed on diplobelids: a few predators such as the uncommon pachycormiform *Pachycormus* most readily consumed non-hooklet bearing teudopseid and vampyropod squids instead (Cooper & Maxwell, 2023; Weis et al., 2024).

Belemnoid hooklets are composed of a tough, resistant structural biopolymer, likely related to chitin, and thus can remain inside of the gut long after the rest of the squid has been digested, possibly accumulating in the digestive tract over time. By contrast, squid species lacking hooklets in their armature would have a lower preservation potential with their remains being digested more rapidly than the durable hooklets of belemnoids. This is reflected in the gut contents of *Pachycormus* which predominately fed on non-hooklet bearing coleoids (Cooper & Maxwell, 2023; Weis et al., 2024). Other than rare examples where the prey was ingested relatively close to the moment of death, the delicate organic mantle and proostraca readily broke down in the gut, becoming unidentifiable cololite masses, often preserved as hind gut endocasts in the alimentary tract (Cooper et al., 2022).

Dietary Ecology of *Campylognathoides* and *Dorygnathus*

Campylognathoides was historically interpreted to have had a piscivorous lifestyle due to its discovery within a marine setting and contemporary fish remains found in the guts of similar sized non-monofenestratan pterosaurs (e.g., *Rhamphorhynchus*) (Bestwick et al., 2020; Hauff & Hauff, 1981; Plieninger, 1894). However, Padian (2008b) proposed that the short stout teeth were instead capable of delivering a piercing bite, and attributed a more terrestrial ecology for this pterosaur by suggesting it was a predator of small terrestrial animals. It has been suggested that the construction of the robust forelimbs and proportionately elongate wing fingers in *Campylognathoides* could be a specialization for a fast aerial lifestyle comparable to modern falcons and mastiff bats that feed on the wing (Witton, 2013). Our discovery of belemnoid hooklets preserved as gut contents in SMNS 9787 suggests that *Campylognathoides zitteli* was either opportunistically or facultatively teuthophagous with its stout piercing teeth used to puncture and maintain a grip on the mantle of coleoids.

Most bathypelagic squids undertake a daily vertical migration into the surface waters between dusk and dawn in order to mate and hunt for prey (e.g., Judkins & Vecchione, 2020 and references therein). Every night, this mass migration in the oceans is driven by the cyclic vertical migration of trillions of migrating mesopelagic micronekton, which form the primary or secondary resource for these coleoids depending on size (e.g., Gilly et al., 2006). Evidence for vertical migration behavior in belemnites and other Jurassic belemnoids has been extensively discussed, including in the Posidonia Shale (Dera et al., 2016; Hoffmann & Stevens, 2020; Jenny et al., 2019; Martill et al., 1994; Schweigert, 2018). Given the similar physiology, mantle size, and predatory feeding behavior of *Clarkeiteuthis conocauda* (see Jenny et al., 2019) compared with belemnites and modern migrating coleoids, it is likely that *Clarkeiteuthis* also undertook a vertical migration to feed in the surface waters during the night. If this hypothesis is correct, it opens up the possibility of nocturnal hunting behavior in *Campylognathoides.* Clues to nocturnal specialization can be inferred based on the enormous size of the orbit relative to skull length and skull depth in this pterosaur, as an enlarged eye may have been advantageous for foraging in low light conditions (Fig. 7B).

Dorygnathus was proposed to have been piscivorous based on comparisons with *Rhamphorhynchus*, of which the two pterosaurs share a somewhat similar body plan, skull shape, and homodont (with slight height heterodonty) tooth guild (Padian & Wild, 1992; Plieninger, 1907) or a mixed fish-invertebrate feeder (Bestwick et al., 2020). Padian (2008a) proposed that the modified hook-like anterior portion of the dentary combined with the tall and slender pointed heterodont teeth in the jaws of *Dorygnathus* are a specialization for snatching small fishes from the surface water (Fig. 7A). This interpretation is hereby confirmed by our discovery of the small teleost *Leptolepis* sp. preserved as gut contents in the posterior abdomen of a small *Dorygnathus banthensis* specimen (SMNS 18880) from Holzmaden. Fish-bearing gut contents have been found in association with several non-monofenestratan and pterodactyloid pterosaurs interpreted to be aquatic foragers including *Eudimorphodon* from the Late Triassic of Italy, the Solnhofen pterosaurs *Scaphognathus*, *Rhamphorhynchus*, and *Pterodactylus* from the Late Jurassic of Bavaria, and the toothless *Pteranodon* from the Late Cretaceous of Kansas (see Witton, 2017 for an overview and Table 1).

Recognition of separate feeding niches between *Dorygnathus* and *Campylognathoides* each associated with a specialized

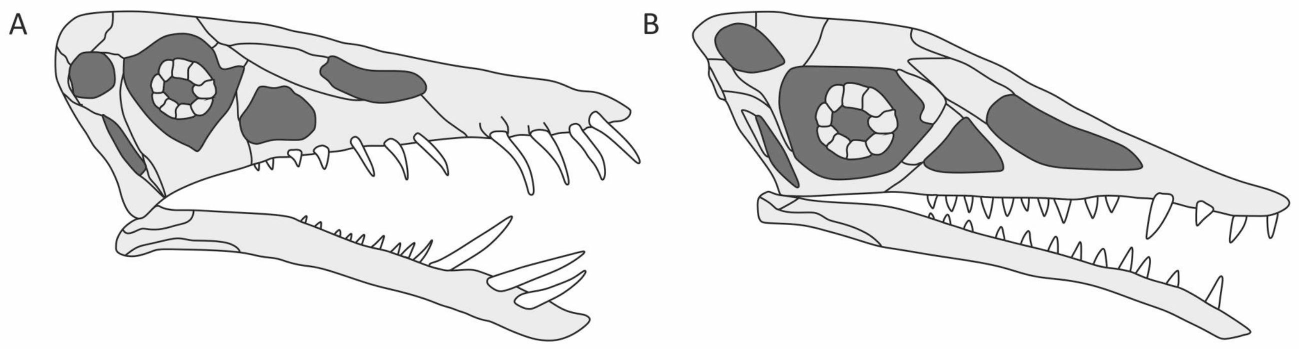

FIGURE 7. Comparison of the reconstructed skulls of: **A**, *Dorygnathus banthensis* and **B**, *Campylognathoides zitteli*. **A**, redrawn from Padian (2008b: text-fig. 18) with addition of sclerotic bones based upon SMNS 55886 and other specimens; **B**, redrawn from Padian (2008a:text-fig. 10) based on various specimens. Not to scale.

hunting strategy, suggests that there was trophic niche partitioning taking place within the Posidonia Shale pterosaur fauna. This differentiation in prey selection suggests that *Campylognathoides* and *Dorygnathus* were likely not competing for similar prey resources despite significant overlap in body size between these genera: an interpretation, which until now had only been loosely based on differences in their tooth and skull morphologies (Fig. 7) (Padian, 2008a, b; Plieninger, 1907). It is plausible that pterosaur feeding preferences may have changed through ontogeny. Note that the *Dorygnathus* specimen described herein is considered an immature individual perhaps feeding on smaller prey items such as *Leptolepis* sp. in early ontogeny and progressing to a more varied diet in later life.

CONCLUSIONS

Fossilized gut contents are described for the Toarcian non-monofenestratan pterosaurs *Campylognathoides* and *Dorygnathus*, based on two well preserved skeletons revealing the former to have fed on belemnoid teuthids, and the latter on small actinopterygian fishes. These specimens represent the first records of pterosaur gut contents from the Toarcian Posidonia Shale, and the only identifiable remains of a pterosaur meal known from the Early Jurassic. *Campylognathoides* is the only pterosaur known to have predated on belemnoids, and represents additional evidence for teuthophagy in Pterosauria. Belemnoid hooklets in the gut of *Campylognathoides* are identified as belonging to *Clarkeiteuthis conocauda*, a belemnoid teuthid with inferred vertical migration behavior, meaning that in order to catch this elusive prey, *Campylognathoides* may have hunted nocturnally. Although based on just two specimens, it is suggested that the differences in gut contents between these two Toarcian pterosaur genera may reflect niche partitioning, with teuthophagy in *Campylognathoides* and piscivory in *Dorygnathus.* Trophic partitioning is supported by the very different skull and dental morphologies seen in these two taxa, but our suggestion for a nocturnal lifestyle for *Campylognathoides* requires further scrutiny. The somewhat larger orbit of *Campylognathoides* may lend some support to this, as yet, tentative conclusion.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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AUTHOR CONTRIBUTIONS

SLAC designed the project. All authors gathered the data, analyzed the data, drafted and edited the manuscript.

DATA AVAILABILITY STATEMENT

All cited and figured specimens are freely accessible in their respective museum collections.

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