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Temnodontosaurus bromalites from the Lower Jurassic of Germany: hunting, digestive taphonomy and prey preferences in a macropredatory ichthyosaur

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Abstract: Fossilized food items found in or passed through the digestive tract of an animal (bromalites) offer a window into the dietary habits and ecological role of the producer taxon. Bromalites have been documented from several small to mid-sized parvipelvian ichthyosaurian species from the Lower Jurassic, but are seldom documented for the largest taxa. *Temnodontosaurus trigonodon* is an iconic Lower Jurassic macropredator, but the few bromalites attributed to this taxon have never been cumulatively reappraised. Here we provide a detailed revision of three specimens from the Toarcian Posidonienschiefer Formation interpreted as bromalites attributable to *T. trigonodon*. The first specimen is represented by a coiled-up juvenile *Stenopterygius* skeleton, interpreted as a regurgitalite. Similarly, a second clustered mass of fractured and etched skeletal elements of an adult *Stenopterygius* has been also attributed to a regurgitalite. The peculiar taphonomy of these specimens supports this interpretation, and *T. trigonodon* is recognized as the only feasible producer of the gastric pellets. Last, a *T. trigonodon* skeleton preserving a large area of stomach contents (consumulite) composed of coleoid remains and neonatal ichthyosaur bones is re-described here. Different stages of preservation are recognized in the ingested vertebrae, suggesting separate timing of prey ingestion. A detailed microstructural and chemical characterization of some bone fragments extracted from the consumulite highlights the action of gastric secretions on the ingested skeletal elements. The three surveyed bromalites support the interpretation of *T. trigonodon* as a nekton macropredator, but also highlight a specific targeting of neonatal to juvenile *Stenopterygius* individuals as prey items.

Key words: Ichthyosauria, Posidonienschiefer Formation, *Temnodontosaurus*, regurgitalite, gut content, digestive taphonomy.

ICHTHYOSAURS were a successful group of secondarily aquatic sauropsid amniotes that inhabited the oceans from the Early Triassic to the Late Cretaceous (McGowan & Motani 2003; Maisch 2010; Dick & Maxwell 2015). Despite having a conservative body plan dictated by hydrodynamic constraints, ichthyosaurs evolved several ecomorphotypes based on both craniodental features and body size, resulting in the exploitation of different feeding niches (Massare 1987; Dick & Maxwell 2015; Fischer *et al.* 2016). Among the feeding guilds, the macropredatory niche (i.e. the hunting of large-sized prey (Taylor 1987) also referred to as megapredation (Bennion *et al.* 2024) or hypercarnivory (Cortés *et al.* 2021)) evolved multiple times in ichthyosaurs, with taxa representative of this ecological class first appearing in the Middle Triassic, based both on the presence of carinate teeth (*Thalattoarchon saurophagis*: Fröbisch *et al.* 2013), and gut contents (*Guizhouichthyosaurus tangae*: Jiang *et al.* 2020). Carinate teeth are also well-documented among giant Late Triassic ichthyosaurs (*Himalayasaurus tibetensis*, *Shonisaurus popularis*: Motani *et al.* 1999; Kelley *et al.* 2022). In the Early Jurassic, parvipelvians referred to *Temnodontosaurus* spp. explored this ecomorphospace (Bennion *et al.* 2024). Carinate teeth did not evolve again in ichthyosaurs after the Early Jurassic, although occupation of a macropredatory niche has been hypothesized based on large skull size, large teeth and heterodonty in some Cretaceous platypterygiine ophthalmosaurians (e.g. *Platypterygius australis*, *Pervushovisaurus campylodon*, *Kyhytysuka sachicarum*: Fischer 2016; Fischer *et al.* 2016; Cortés *et al.* 2021).

Macropredatorial ecology in Mesozoic marine reptiles is indirectly inferred based on craniodental anatomy, for instance, the length and robustness of the rostrum, absolute tooth crown height, the presence of carinae and/or the development of pronounced enamel ridges on the tooth crowns, the robustness of the tooth roots, and functional heterodonty (Massare 1987; Cortés *et al.* 2021;

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Fischer *et al.* 2022; Bennion *et al.* 2024). These features are usually linked to an increase in body size (e.g. Foffa *et al.* 2024). Direct comparison with extant marine predatory amniotes, for instance odontocete cetaceans (e.g. *Orcinus orca* and *Physter macrocephalus*), further differentiates the macropredatory feeding guild into distinct hunting and food-processing niches, such as piercing, grip and shear, or grip and tear strategies (Pitman & Durban 2012; Peri *et al.* 2021). When combined with the development of geometric–morphometric models, functional anatomy can be extrapolated to extinct taxa (Peri *et al.* 2021; Fischer *et al.* 2022). Carbon stable isotope ratios in dental enamel can provide further information regarding the trophic position of Mesozoic marine reptiles (e.g. Schulp *et al.* 2017). Additionally, the study of bite marks made by large marine amniotes in smaller fauna can corroborate the macropredatorial ecology of the producers (Voss *et al.* 2019). However, the most direct and informative line of evidence for investigating dietary habits in extinct (and extant) vertebrates remains the study of gut contents and the products of the digestive processes.

Bromalites (from Greek, ‘stone-meals’) are fossilized items once possessing a caloric value that are found in (or have passed through) the digestive system of an animal (Hunt & Lucas 2012; Myhrvold 2012; Barrios de Pedro *et al.* 2018; Gordon *et al.* 2020; Lukeneder *et al.* 2020; Freimuth *et al.* 2021; Qvarnström *et al.* 2021). Such remains offer true behavioural snapshots of extinct taxa (‘frozen behaviour’ *sensu* Boucot 1990; see also Lomax & Nichols 2021). These ingested remains can be classified according to their position inside the body cavity of the producer or by which end of the digestive system they exited its body. Bromalites (*sensu* Hunt & Lucas 2012, 2021) can therefore be subdivided into: (1) regurgitalites (orally egested materials that transited as far as the stomach); (2) consumulites (gut contents found either in the upper–pre-stomach tract (oralite, oesophagolite), in the stomach (gastrolite) or in the intestine (intestinalite–cololite); and (3) coprolites (expelled faeces).

Digested items typically experience radical physico-chemical changes due to compression by the stomach musculature and the time during which they are exposed to digestive secretions and compression (Fisher 1981; Denys *et al.* 1995). These alterations are unlikely to be caused by normal environmental conditions, and cannot be justified without a biotic origin (Gordon *et al.* 2020; Freimuth *et al.* 2021). For bone-containing bromalites (i.e. ingestion of vertebrate remains), the following characteristics can be standardized from two main stages of digestion: pre-intestinal vertebrate bromalites (regurgitalites and consumulites from the mouth, gizzard, oesophagus and stomach) have undergone non-complete disarticulation, little-to-medium clustering and acid damage ranging from etching to melting of the bone structures (Hunt & Lucas 2012; Myhrvold 2012); in contrast, post-intestinal vertebrate bromalites (coprolites and intestinalite consumulites) have undergone high-to complete disarticulation, clustering in a pellet organization, and flaking and cracking of the bone tissue together with an enrichment in phosphorus in the surrounding matrix (Gordon *et al.* 2020). The increase in phosphorus has been generally regarded as a good proxy for determining whether a bromalite had passed the intestinal phases of digestion, given that in vertebrates (especially carnivores), endogenous phosphorus is added to the chyme as an additional pathway to excretion (Kjerulf-Jensen 1941; Gordon *et al.* 2020).

Bromalites from macropredatory ichthyosaurs have been sporadically reported in the literature (Keller 1977; Böttcher 1989; Kear *et al.* 2003; Vallon 2012; Jiang *et al.* 2020; and potentially Hunt *et al.* 2012), providing vital information on the dietary habits of this ecological class. However, a more inclusive correlation between prey elements found inside bromalites and the respective feeding guild of the producer has only recently started to be explored (Bennion *et al.* 2024). Furthermore, a taphonomic assessment of the digestive processes undergone by the ingested item in these marine macropredatorial taxa has never been attempted. In this study, we re-examined bromalites from the lower Toarcian of Baden-Württemberg (southern Germany) attributed to *Temnodontosaurus trigonodon*, the apex predator recovered from the Posidonienschiefer Formation. *Temnodontosaurus* is a genus of questionable monophyly, with species including the largest parvipelvian ichthyosaurs ever discovered (McGowan 1974; Swaby & Lomax 2021; Laboury *et al.* 2022; Larkin *et al.* 2023). Despite the recent interest in the dietary habits of the genus via ecomorphological studies (Bennion *et al.* 2024), bromalites attributed to *T. trigonodon* have received little detailed attention in the more recent literature. Currently only three *T. trigonodon* bromalites have been described: a coiled-up juvenile *Stenopterygius* interpreted as a *Temnodontosaurus* regurgitalite by Keller (1977), a similarly interpreted *Stenopterygius* comprising a disarticulated bone mass described by Jäger (2005), and last, an *in situ* consumulite from a complete *T. trigonodon* specimen containing *Stenopterygius* centra and cephalopod hooklets reported by Böttcher (1989). The specimens described by Keller (1977) and Böttcher (1989) are carefully re-evaluated in this study, using different analytical approaches. The ontogenetic stage and skeletal taphonomy of the prey, *Stenopterygius*, in these bromalites is assessed in detail to better frame the predatory ecology and digestive pattern of *T. trigonodon*.

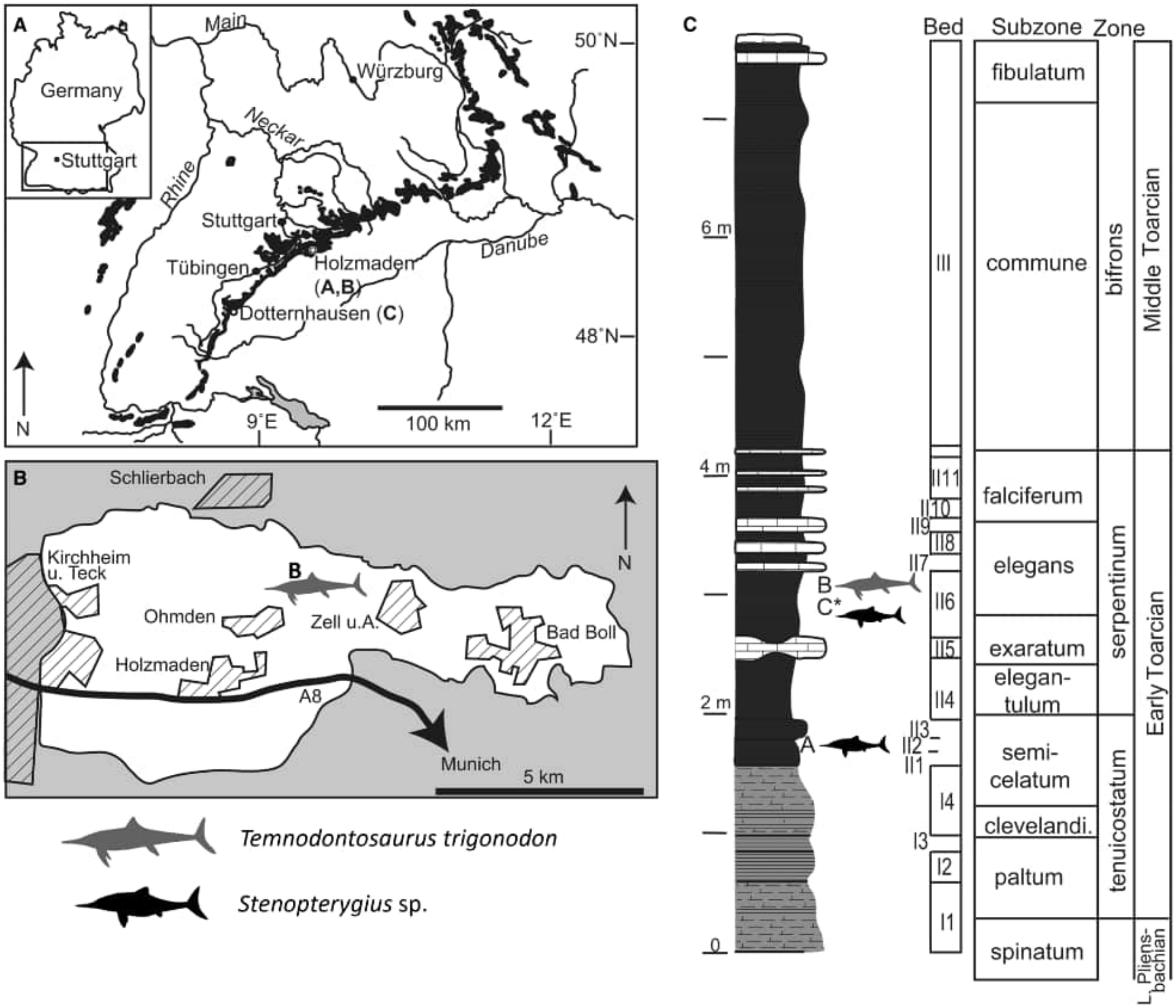

FIG. 1. Geographical and geological context. A, southwestern Germany, with Posidonienschiefer Formation outcrops indicated in black (modified from Röhl *et al.* 2001); SMNS 15194 (labelled A) and SMNS 50000 (B) are from the Holzmaden region although the exact quarry from which the former specimen was recovered is unknown; FWD 0112 (C) is from Dotternhausen. B, map of the Holzmaden palaeontological heritage protected area showing the provenance of SMNS 50000 (B). C, stratigraphic column of the Posidonienschiefer Formation at the Holzmaden locality (modified from Urlichs *et al.* 1994 with ammonite subzones following Riegraf *et al.* 1984) indicating the stratigraphic provenance of the three specimens discussed in the text; *specimen C was not recovered from Holzmaden, but is plotted on the Holzmaden column to indicate its relative position. Silhouette images from PhyloPic (https://www.phylopic.org: Gareth Monger CC BY 3.0).

DEPOSITIONAL SETTING & TAPHONOMIC CONTEXT

The surveyed specimens originate from the Posidonienschiefer Formation (Lower Jurassic, Toarcian; Tenuicostatum–Bifrons Ammonite zones; Fig. 1). The Posidonienschiefer Formation is mainly represented by black shales deposited in an epicontinental sea of the northwestern Tethys Ocean during the early Toarcian (Röhl *et al.* 2001). More specifically, the formation spans the Toarcian Oceanic Anoxic Event (TOAE), and has been traditionally regarded as a textbook example of Konservat-Lagerstätten from a stagnant basin, where anoxic conditions delayed the decay of marine fauna, leading to astonishing fossil preservation (Muscente *et al.* 2017). Recently, Muscente *et al.* (2023) geochemically reviewed the taphonomy of non-mineralized soft tissues in the Posidonienschiefer Fm., and suggested that their preservation is mediated by phosphatization early on during diagenesis, just below sub-oxic bottom waters. Sulphur reduction and burial compaction follow this process, resulting in most specimens being strongly compressed and with the widespread presence of pyrite (Muscente *et al.* 2023). A notable exception to this rule of extensive post-burial compaction of skeletons are specimens preserved in the limestone banks or nodules formed early in diagenesis, which are often much more three-dimensionally preserved; one such specimen is SMNS 50000 (Martin *et al.* 2021). Regardless of soft-tissue preservation, vertebrates from the Posidonienschiefer Fm. are known for the extraordinary levels of completeness and articulation of their skeletal units (Beardmore & Furrer 2016), most likely due to the lack of disturbance by currents or macrofauna at the sea floor and the rapid entombment of the remains in fine-grained organic sediments (‘soupy substrate’ *sensu* Martill 1993). Likewise, histological preservation is usually optimal, with no sign of chemical erosion on the compact bone or dental tissues (Maxwell *et al.* 2022).

MATERIAL

Two bromalites attributed to *Temnodontosaurus trigonodon*, or directly associated with the remains of this taxon were surveyed from the collections of the Staatliches Museum für Naturkunde in Stuttgart (SMNS). The first specimen (SMNS 15194) is represented by an almost complete coiled-up skeleton of a juvenile *Stenopterygius* sp. The specimen originates from bed εII$_2$ (Tenuicostatum Zone, Semicelatum Subzone: Riegraf *et al.* 1984), Holzmaden, and was prepared in 1926. It was first reported as having been curled up through the action of subaerial exposure (Weigelt 1927) or water currents (Hofmann 1958). Keller (1977) reinterpreted this specimen as a ‘speiballen’ (an egested gastric pellet). Later, Vallon (2012) and Cooper *et al.* (2022) figured the specimen as an indicative example of a regurgitalite (*digestichnia* in the ichnological sense).

The second specimen (SMNS 50000) is represented by a complete and fully articulated skeleton of *Temnodontosaurus trigonodon* discovered in 1973 from bed εII$_{6c}$ (Serpentinum Zone, Elegans Subzone), Ohmden, preserving a large area of stomach content. The specimen and its stomach content was studied in detail by Böttcher (1989) and was recognized to contain more than 200 smaller ichthyosaur centra, alongside numerous coleoid remains (hooklets).

A third specimen was evaluated briefly, in person and from pictures; this is represented by a disarticulated and roughly clustered ichthyosaur bone mass 51 cm in length from bed εII$_6$ (upper Exaratum – lower Elegans Subzone, Serpentinum Zone), Dotternhausen, attributed to *Stenopterygius* sp. and interpreted as a gastric pellet by Jäger (2005). The specimen (FWD 0112) is housed in the Fossil Museum of the Werkforum in Dotternhausen.

Institutional abbreviations. FWD, Fossil Museum of the Werkforum, Dotternhausen, Germany; LYMPH, Lyme Regis Philpot Museum, Lyme Regis, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; QM, Queensland Museum Kurilpa, Brisbane, Australia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UAMES, University of Alaska Museum, Fairbanks, USA; XNGM, Xingyi National Geopark Museum, Xingyi City, Guizhou Province, China; YIGM, Yichang Institute of Geology and Mineral Resources (now Wuhan Center of China Geological Survey), Yichang, China.

METHOD

Tapho-morphological analysis. The two SMNS specimens were analysed under both natural and UV light. UV-A, -B and -C wavelengths were produced with a 95 W discharge lamp from WayTooCool LLC. Relevant measurements were taken with a digital calliper. Pictures were taken with a Canon 700D with a 24 mm, 50 mm and 100 mm lens. For SMNS 50000, the abdominal region of the specimen was subdivided into quadrants (Table 1) to better trace and identify sub-clusters of ingested centra and morphologically characterize their preservation status. Quadrants follow an alphanumeric code by columns and rows, enabling better traceability of the surveyed elements.

Microstructural & chemical analysis. Bone and matrix fragments from the SMNS 50000 gastric mass were removed during specimen preparation and were available in the SMNS collections; therefore, sampling directly from the mounted SMNS 50000 was not necessary. An isolated centrum and a partial elongate bone fragment (possibly from a jaw ramus) were analysed uncoated using environmental scanning electron microscopy (ESEM) with a Zeiss Evo LS 15 to evaluate the preservational status and microstructures of the skeletal tissues found in the consumulite. A second vertebral fragment, as well as matrix particles, were scanned uncoated with a SEMFEG (SEM field emission gun) Nova NanoSEM 450 at low vacuum for compositional analysis. The same sample also underwent transportable x-ray fluorescence analysis (TXRF) with a Bruker Artax MNU-3 with helium-controlled atmosphere.

TABLE 1. *Stenopterygius* centra distribution in the quadrants of the SMNS 50000 gastric mass.

	a	b	c	d	e	f	g	h	i
1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	2	1?
3	0	4	0	16	60	7	36	6	0
4	6	3	1	6	24	26	29	7	0
5	4	3	0	2	0	5	0	0	0

Quadrants refer to Figure 5A.

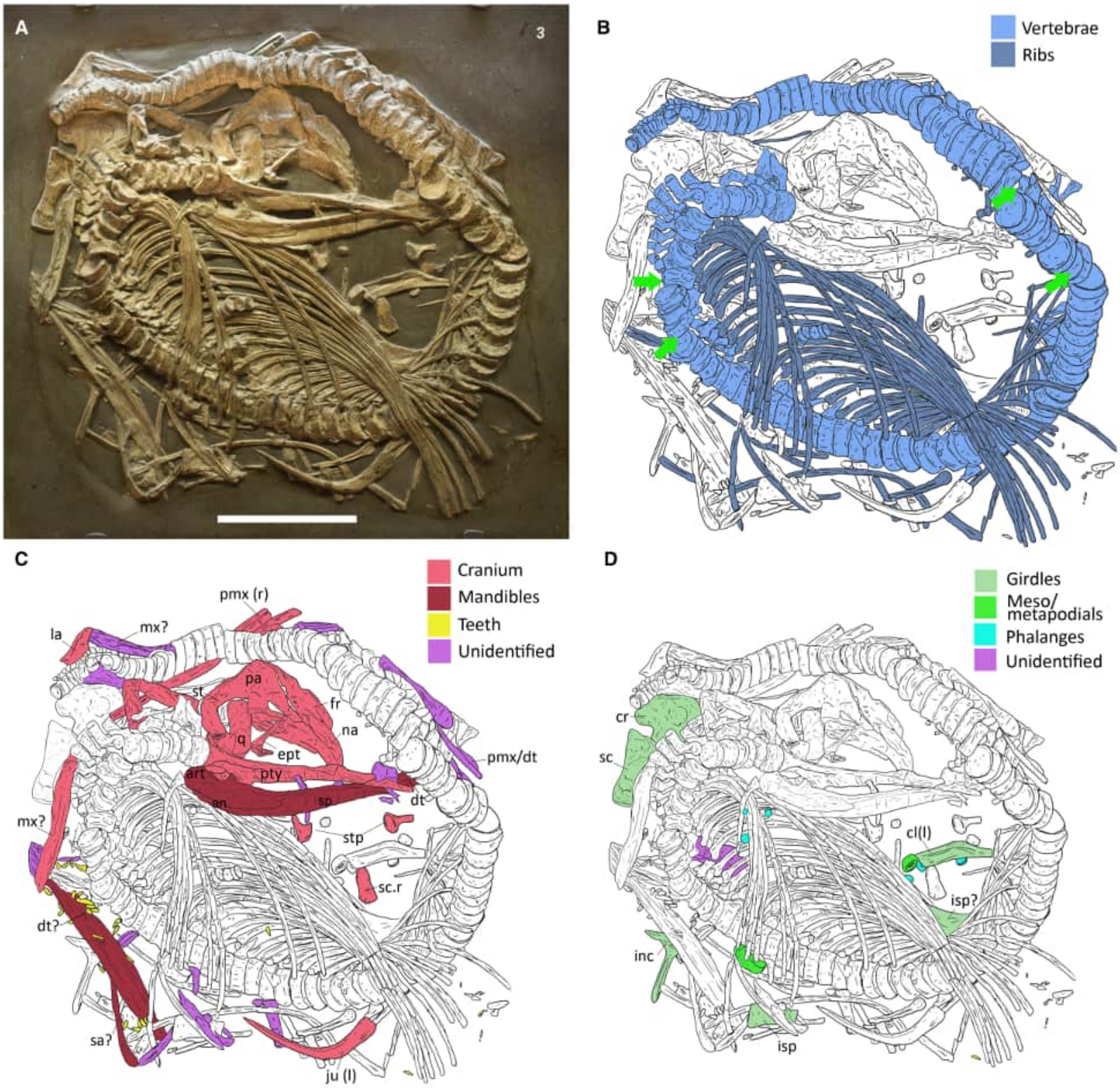

FIG. 2. Regurgitalite consisting of a large, skeletally immature specimen referred to *Stenopterygius* sp. (SMNS 15194). A, overview of the specimen. B–D, anatomical drawings with colour-based differentiation of: B, axial skeleton (green arrows indicate twisting point); C, cranial bones; D, appendicular skeleton. *Abbreviations*: an, angular; art, articular; cl; clavicle; cr, coracoid; dt, dentary; ept, epipterygoid; fr, frontal; inc, interclavicle; isp, ischiopubis; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pmx, premaxilla; pty, pterygoid; q, quadrate; sa, surangular; sc, scapula; sc.r, scleral ring; sp, splenial; st, supratemporal; stp, stapes; (r) and (l) indicate bones originating from the right or left side. Scale bar represents 10 cm (A).

RESULTS

SMNS 15194

General. As preserved, SMNS 15194 is a *c.* 1-m-long ichthyosaur skeleton with extreme twisting of the vertebral column in a circular 40 × 35 cm area (Fig. 2). Based on estimation of the missing post-flexural tail and the disarticulated anterior skull, total length is estimated to have been *c.* 1.6–1.7 m. The specimen is composed of the skull in ventro-lateral view, dislodged teeth, complete and articulated vertebral column (Fig. 2A–C), complete and closely associated left side of the ribcage, partial pectoral and pelvic girdles, and a few autopodial elements (Fig. 2D). SMNS 15194 can be referred to *Stenopterygius* to the exclusion of other Posidonienschiefer Fm.

ichthyopterygian taxa (*Suevoleviathan*, *Temnodontosaurus*, *Eurhinosaurus*, *Hauffiopteryx*) based on the presence of a plate-like ischiopubis fused at the distal end (McGowan & Motani 2003; Maisch 2008). No additional characters pertaining to either the skull or the postcranium and including body size contradict this conclusion. Moreover, the genus *Stenopterygius* is the most abundant ichthyosaur taxon in the Posidonienschiefer Fm. (Maxwell & Vincent 2016). The incomplete skull and missing propodials preclude referral to species (Maxwell 2012).

Ontogenetic stage. Based on the length of the smallest documented gravid female specimens (*c.* 2 m in length; Böttcher 1990), at *c.* 1.6–1.7 m in length, SMNS 15194 was probably sexually immature. In addition to size, assessment as a large juvenile (Postnatal Stage 2 *sensu* Miedema & Maxwell 2022) is supported by the following discrete characters: close to confluent paracoronoid process and preglenoid process on the surangular, lateral wing of the pterygoid not fully confluent with the anterior ramus, jugal neither fully angular nor fully lunate in shape, and the absence of a distinct bulge anterior to the parietal foramen on the frontal (Miedema & Maxwell 2022).

The specimen has previously been interpreted as a regurgitalite from a *Temnodontosaurus* (Keller 1977; Vallon 2012; Cooper *et al.* 2022), the largest predator in the Posidonienschiefer biota. However, alternative explanations have previously been proposed (Weigelt 1927; Hofmann 1958) and other vertebrates from the Posidonienschiefer Fm. are sometimes preserved with a coiled axial skeleton, possibly as the result of an anterior landing of the carcass on the sea floor followed by the winding of the vertebral column around the skull (e.g. *Macrospondylus bollensis* SMNS 51563: M. Johnson & E. Mujal, pers. comm. 2024). For this reason, the bromalite nature of SMNS 15194 had to be carefully reviewed. To test whether SMNS 15194 truly represents a regurgitalite, a detailed taphonomic analysis on all of its preserved anatomical units was carried out.

Skull. The skull is mostly complete, but largely disarticulated, especially on the right-hand side (Fig. 2A, C). Only few posterior elements can be recognized in sutured articulation (left parietals, frontals and posterior nasals), while most lateral and cheek bones, although in some cases close to the anatomical position, are disassociated. The anterior portion of the skull bears most of the disarticulation, where the rostrum is fractured, and the two rami of the premaxilla are broken and separated from the skull above the coiled caudal region (Fig. 2C). The left jugal and a lacrimal are greatly disassociated from their anatomical position, with the jugal being retrieved near the posterior dorsal region of the vertebral column (Fig. 2C). Posteriorly, the left frontal, parietal, quadrate and supratemporal are found closely associated above a pterygoid–palatine complex exposed in ventral view. The left skull roof, including the parietal, is exposed in internal view, showing the depression for the optic lobe on the parietal and a prominent epipterygoid facet (Fig. 2A). Smaller elements from the posterior palatal series and otic region, such as the epipterygoid and both of the stapes, are found ventrally separated from the rest of the skull. The lower jaws are also separated, with the two rami distantly scattered across the bone mass. The posterior portion of the left mandible remains effectively *in situ*, only slightly displaced from the left quadrate. 29 teeth are dislodged from the alveolar groove, mostly grouped near the left dentary (Fig. 2C).

Axial skeleton. Despite its strong curvature, the axial skeleton is surprisingly well preserved, both in terms of articulation and quality of the bone tissue. 89 centra (*c.* 80 preflexural) can be counted from the column, but some additional posterior dorsals may be obscured by ribs. The column is broken into nine pieces, with the most posterior portion of the caudal series disconnected from the main segment (Figs 2B, 3A). The column is twisted in at least four different places (cervical segment, anterior dorsal, dorsal–caudal transition, caudal region; Fig. 2B green arrows), judging by the different orientation of the neural arches between segments. The left side of the rib cage is intact and still associated with the vertebral column, while ribs of the right side are mostly lost (Fig. 2B).

Appendicular skeleton. The appendicular skeleton is poorly preserved. The pectoral girdle is represented by one scapula and one coracoid still close to anatomical position, while the interclavicle and left clavicle are scattered among the bone mass (Fig. 2D). The sole undisputed preserved element of the pelvic girdle is a disassociated ischiopubis ventral to the bone mass, close to the disassociated left dentary. The limbs are sparsely represented by scattered meso-metapodials and podial elements (six phalanges).

Structural & histological preservation. The specimen is poorly reactive under UV light, even with a combination of UV-A, -B and -C wavelengths (Fig. 3B). Given that the applied glue fluoresces brightly between the skeletal elements and the surrounding matrix, the state of preparation of the specimen is highlighted, confirming that the peculiar coiled disposition of the axial skeleton is not the result of an artificial composite (Fig. 3B). UV-induced fluorescence did not show evidence of preserved soft tissue. Histologically, SMNS 15194 is pristinely preserved, with almost no signs of any superficial erosion or

FIG. 3. Taphonomic details of SMNS 15194, regurgitalite consisting of a large, skeletally immature specimen referred to *Stenopterygius* sp. A, detail of the anteriormost point of twist of the vertebral column. B, the specimen under UV-ABC light. C, close-up of the ribs, highlighting lithostatic fractures and the pristine preservation of the compact tissue. D, an isolated tooth showing the relatively worse preservation of the enamel. E, perimortem fracture on the posterior end of the right premaxilla. F, perimortem fracture on a rib. Scale bars represent: 3 cm (A); 2 cm (C); 5 mm (D, E); 1 cm (F).

abrasions that would have led to exposure of cancellous bone. The laminar texture of the cortical bone is remarkably recognizable, well organized and undistorted (Fig. 3C). Only dentine and enamel appear slightly damaged, with some apical portions of the preserved crowns seemingly delaminated (Fig. 3D). No evidence of pitting could be recognized on the surface of any mineralized tissue on the specimen. Several skeletal elements are fractured: the majority of fractures on SMNS 15194 can be attributed to lithostatic pressure (Fig. 3C); however, some breakages are identified as perimortem trauma (Fig. 3E, F). The latter are characterized by clean and angulated cuts of the bone (e.g. Spiekman & Mujal 2023). Examples of perimortem trauma on SMNS 15194 can be found on the posterior right premaxilla (Fig. 3E) and on a disarticulated rib on the ventral portion of the bone mass (Fig. 3F).

SMNS 50000

Layout of the gastric mass. SMNS 50000 is represented by an almost complete and articulated skeleton of *Temnodontosaurus trigonodon* in the museum public exhibition

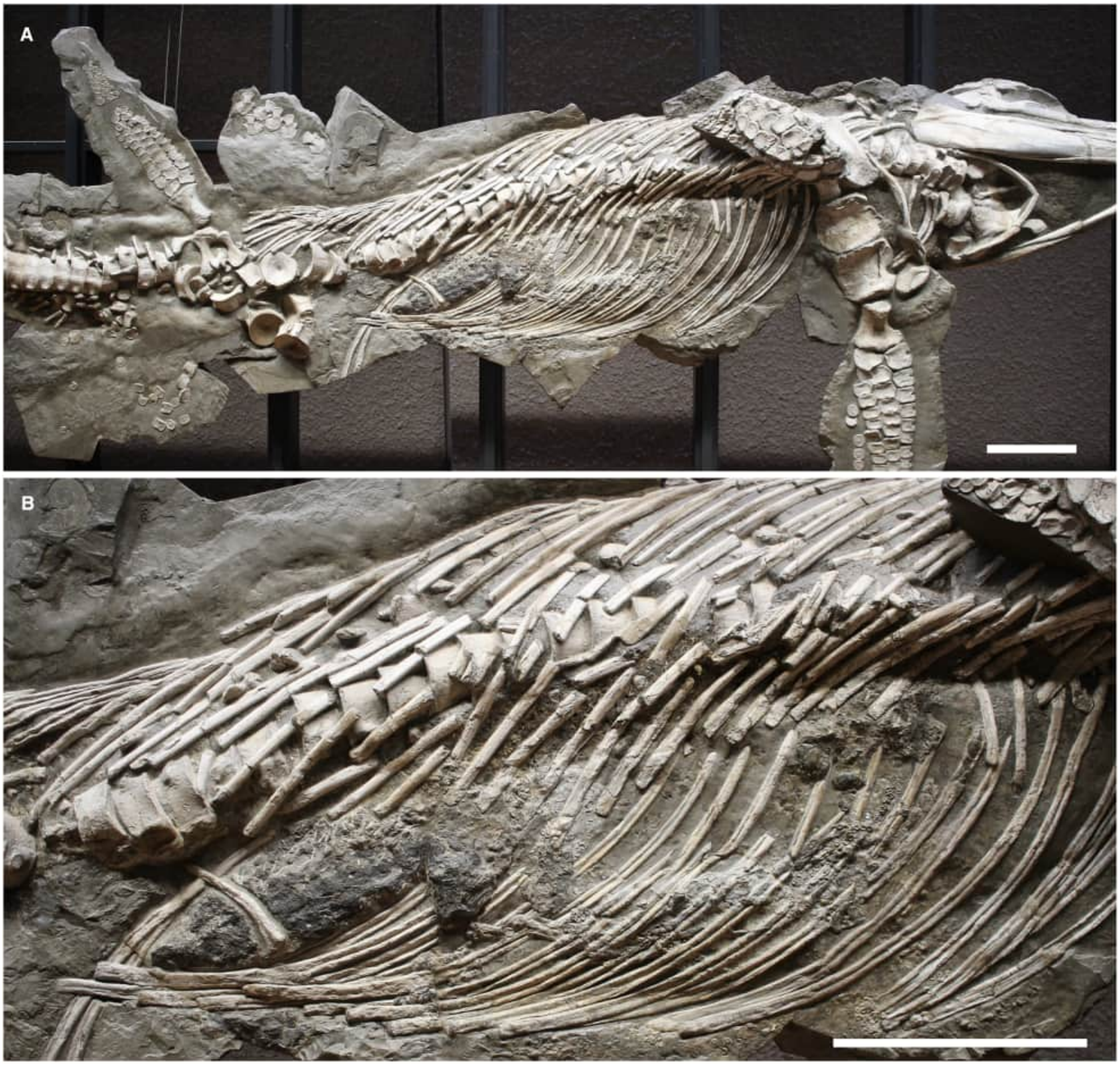

FIG. 4. SMNS 50000. A, overview of the specimen. B, close-up of the abdominal region with gut content. Scale bars represent 30 cm.

(Fig. 4A), preserving a large area of gut content in the former epigastrium and abdomen (Fig. 4B). The gut content is preserved as a *c.* 1.5-m-long compact dark mass, granular in texture and extending from the pectoral to (almost) the pelvic girdle within the rib cage. The mass has an oily lustre in some of its components, however, a lighter shade with yellowish patches can be observed in the anterior part of the ichthyosaur's thoracic area, most probably corresponding to the epigastrial region (Fig. 4B). The presence of a yellow mineralization in internal fossilized soft tissues corresponding to stomach areas is not uncommon in the Posidonienschiefer ichthyosaurs, given that it has previously been hypothesized to represent a uniquely unstable pyrite growth exclusive to fossilized stomach tissues (Adorf 1983; Böttcher 1989). According to Böttcher (1989), the gut content of SMNS 50000 is mainly composed of cephalopod remains (i.e. coleoid hooklets), which were illustrated in detail via thin sections and SEM imaging in his original publication. A re-study of the coleoid hooklets showed that most of them must have belonged to belemnites (types 1 and 2 of Böttcher 1989 and remains of mega-onychites) and only a few of them belonged to another belemnoid coleoid (type 3 of Böttcher 1989). The belemnite hooklets and mega-hooks

(‘*Onychites*’) can be safely assigned to *Acrocoelites raui*, given that a completely preserved specimen of this taxon (SMNS 26274) with similar hooklet morphology has been reported from exactly the same bed as SMNS 50000 (Reitner & Urlichs 1983). The latter authors showed that different types of hooklets occur on the arm crown of this belemnite, which is the only belemnite taxon reported from the finding level (Riegraf *et al.* 1984). Mega-hooks are not present in SMNS 26274, but mega-hooks occur only in belemnites (Fuchs & Hoffmann 2017). The hooklets of Böttcher’s type 3 have a significant shape as well, and correspond to *Chondroteuthis* (Hoffmann *et al.* 2017), a unique belemnoid with only one row of hooklets per arm, which is very rarely reported from southern Germany (Riegraf 1982).

Coleoid hooklets have only very rarely been reported from large juvenile *Stenopterygius* specimens and are unknown from small juveniles (Dick *et al.* 2016); hence, it is unlikely that the hooklets in the gut of SMNS 50000 are there incidentally. Complete belemnites from the Posidonienschiefer Fm. have whole-body lengths with arms of *c.* 35.5 cm (Klug *et al.* 2024). Therefore, the coleoids were likely to have been too big to have been consumed by the juvenile ichthyosaurs, for which the complete abdominal cavity would have measured less than 20 cm in length based on comparisons to individuals with similar centrum sizes.

Skeletal items. Numerous ichthyosaur centra can be found isolated, in small–large disarticulated clusters or even in still semi- to fully articulated segments throughout the consumulite (Fig. 5A–F). Centra are small in size, ranging in width from 10 mm for larger elements to 4.6 mm in the smallest. When found laterally oriented, centra generally register heights around 10–13 mm and lengths of 4–4.5 mm. Small long bone fragments, most probably attributable to jaw rami, were extracted from the gastric content during preparation alongside additional small vertebrae. According to Böttcher (1989), the extracted material originated from quadrants d3,4 and c3,4 (Fig. 5A). Judging by the degree of ossification, the centra can be attributed to perinatal individuals. Centra in the consumulite can most likely be attributed to *Stenopterygius* based on comparisons of centrum size from neonatal specimens of this genus, and taking into account the high relative abundance of the genus at the locality (McGowan 1973; Böttcher 1989; Miedema & Maxwell 2022). A revised count identified 248 centra preserved *in situ* in the gut content of SMNS 50000, which does not differ much from the estimate of Böttcher (1989: *c.* 200 centra). A total of 248 counted vertebrae implies the ingestion of at least four neonatal ichthyosaurs, considering that perinatal *Stenopterygius* have a maximum of 77 pre-flexural centra with diameters in the recovered size range (Böttcher 1989; EEM and FM, pers. obs.). This approximation could be easily underestimated, given that additional centra remain embedded in the consumulite matrix, and those extracted during preparation are not considered in the count. Distinct clusters with high vertebral occurrence density can be found in different regions of the consumulite from its most anterior portion to its posterior end. The vertebral bone tissue is differentially preserved between clusters, with three main types being recognized through the consumulite: preservation type 1, eroded articular facets, collapsed centra, black, tar-like colour (Fig. 5F); preservation type 2, eroded edges of the centra, intact articular facets, gold-rust colour (Fig. 5E); and preservation type 3, non-eroded but deformed centra, intact articular facets, white colour (Fig. 5D).

The quadrants that register the highest vertebral counts inside their perimeters are those from columns e to g and rows 3 to 4 (Fig. 5A; Table 1). This regionalization localizes the majority of the vertebral elements (including the articulated segments in f4; Fig. 5B, C) into the more anterior portion of the consumulite in the anterior thoracic region of the animal, but also highlights a ventral displacement near the distal end, outside of the ribcage.

Inorganic content. Some sub-spherical concretions not related to ingested prey items can also be found in the consumulite. Some of these structures appear to nucleate from the matrix itself and can be found in different locations of the gastric content, while three rounded objects lithologically distinct from the surrounding matrix are found exclusively on the more anterior portion of the consumulite (sector g3). These latter elements are dark brown in colour and have a distinct lustre, as if they had undergone polishing (Fig. 5G–I).

Microstructural & compositional analysis. Two samples of vertebral and elongate bone fragments from the consumulite were analysed using ESEM to highlight the histological preservation of the postnatal bone tissue (Fig. 6A–F). Based on previous microstructural investigations of ingested bones, the presence of characteristic parallel linear fissures on the bone surface was expected. This feature is believed to represent the preferential breakage of laminated layers of compact bone by acid corrosion (Terry *et al.* 2018). ESEM analysis of the centrum showed a general roughened texture of the cortical tissue, together with the exposed presence of calcified cartilage on the articular facets attributed to acid etching (Fig. 6B). The chemical exposure of calcified cartilage resulted in the formation of irregularly spaced pits roughly consistent in size (10 μm wide), especially appreciable on the preserved diapophysis surface (Fig. 6C). The jaw ramus has a similar roughened texture attributable to corrosion (Fig. 6D, F), but only

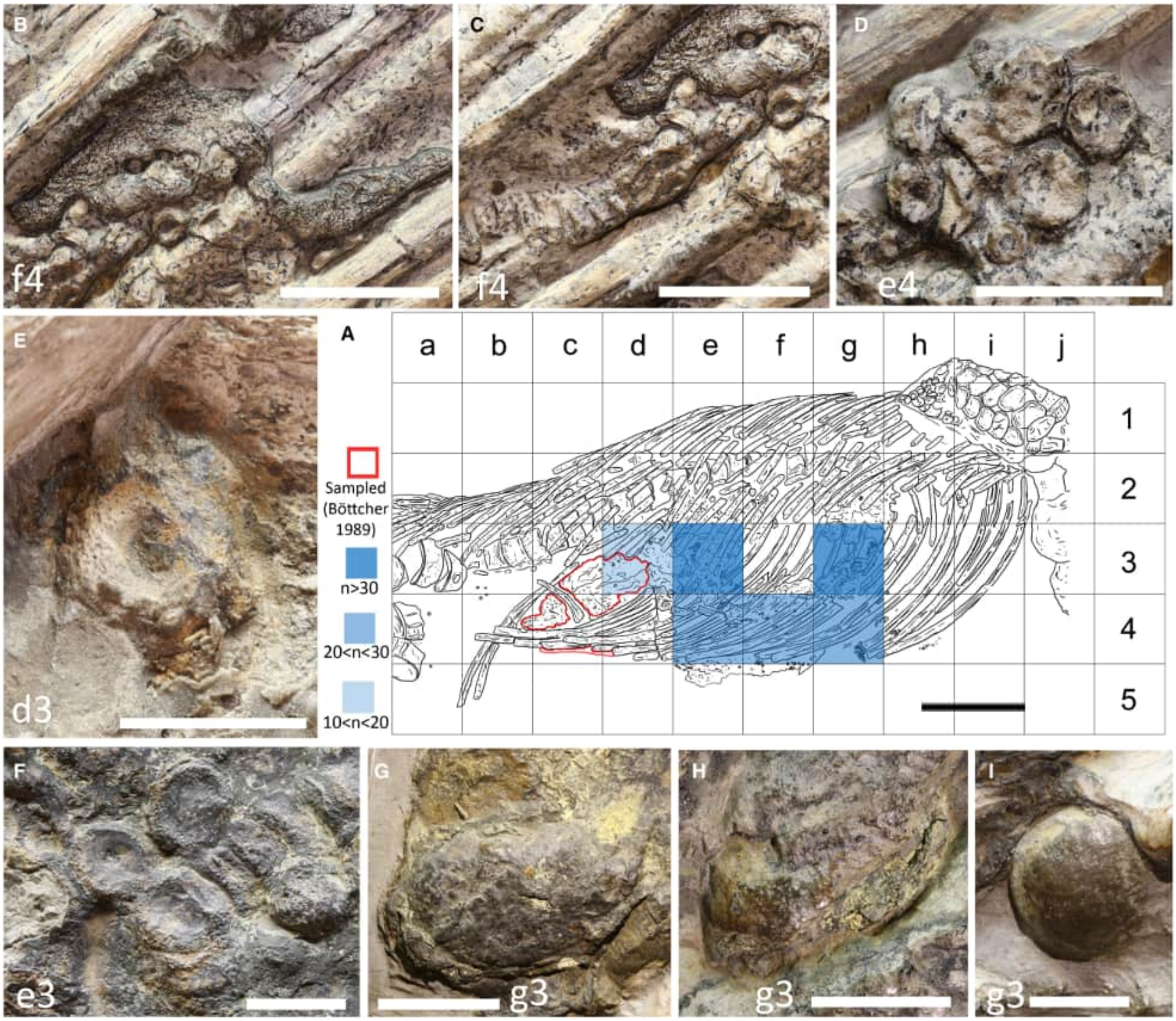

FIG. 5. Details and position of the SMNS 50000 gastric mass contents. A, SMNS 50000 subdivided into quadrants; blue quadrants indicate areas of the gut content with ichthyosaur centra, with a shaded gradient based on their density; red lines indicate sampling areas from Böttcher (1989). B, black mass of coleoid remains between the ribs. C, articulated segment of ingested *Stenopterygius* vertebral column. D, cluster of disarticulated *Stenopterygius* centra; preservation type 3. E, isolated centrum with preservation type 2. F, clustered mass of *Stenopterygius* centra (preservation type 1, black matrix). G–I, sub-spherical concretions or gastroliths. Alphanumeric labels correspond to quadrant position. Scale bars represent: 30 cm (A); 3 cm (B, C); 2 cm (D, G); 1 cm (E, F, H); 5 mm (I).

sporadic and ambiguous V-shaped cracks were observed (Fig. 6E). It is not clear whether these structures can be referred to acid-etching fissures or whether they represent random V-shaped cracks. Another vertebral fragment still embedded in the black matrix was analysed using SEMFEG for chemical characterization. The main aim of the analysis was to test for the presence and weight percentage of phosphorus in the bone–matrix interface, as a way to distinguish whether the sample represents an early or late stage of digestion (Gordon *et al.* 2020; Serafini *et al.* 2022). As highlighted by elemental maps and line scan analysis, the phosphorus content drastically drops from the bone to the matrix (Fig. 6G), suggesting that the latter is non-phosphatized. The interface between the bone tissue and the consumulite matrix appears to consist of clay minerals, as highlighted by the very localized presence of aluminium, silica, magnesium and potassium components (Fig. 6H). Pyrite-associated sulphur is widespread in the bone and matrix (Fig. 6I), as expected in Posidonienschiefer facies (Muscente *et al.* 2023). A similar pattern of phosphorus decrease from bone to matrix is also observed using TXRF analysis; the methodology also highlights previously undetected elements in both bone and matrix due to the larger diameter of the incident x-ray beam. Titanium, vanadium

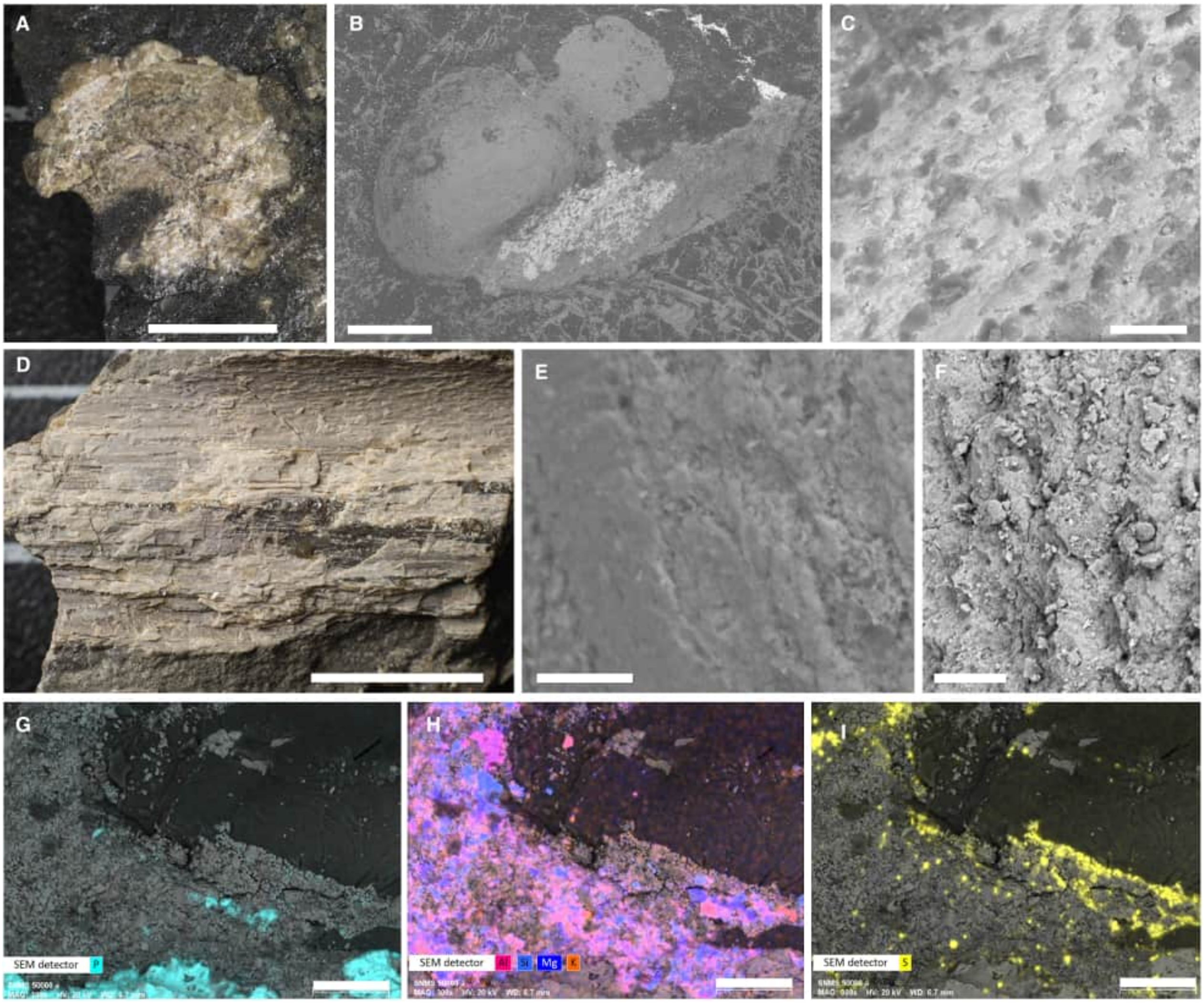

FIG. 6. SEM details of extracted gastric mass contents of SMNS 50000. A, *Stenopterygius* centrum fragment from the *Temnodontosaurus* gastric mass. B, diapophysis detail (ESEM). C, pitting from the diapophyseal surface caused by the removal of calcified cartilage by acid etching. D, elongate bone fragment of *Stenopterygius* (ESEM). E, linear fissure on the elongate bone surface (ESEM). F, roughened texture of the partially digested elongate bone surface. G–I, SEMFEG elemental maps for: G, phosphorus on a vertebral fragment-matrix interface; H, clay minerals; I, sulphur. Scale bars represent: 5 mm (A); 400 μm (B); 40 μm (C); 1 cm (D); 30 μm (E, F); 80 μm (G–I).

and manganese are also weakly represented when targeting the matrix (Fig. S1).

FWD 0112

General. The Dotternhausen specimen is represented by a mass of disarticulated skeletal elements merged together in a *c.* 40 × 30 cm area (Fig. 7A). FWD 0112 consists of several cranial elements (upper and lower jaws, circumorbital elements, hyoid apparatus), extremely limited axial components and most of a forefin (Fig. 7B). FWD 0112 can be attributed to *Stenopterygius* sp. due to humeral, radial and dental morphologies that mutually exclude other Posidonienschiefer taxa. Bone identification was limited by the preservation of the specimen and its accessibility (behind glass), for this reason we provide here a brief description of the general occurrence of the main areas of the skeleton.

Skull. Several cranial bones can be recognized from the mass, although their precise identification is often limited by the preservation. The posterior section of the right mandibular ramus is positioned in the centre of the mass (Fig. 7C), while other elongated elements can be recognized as terminal portions of the rostrum by their

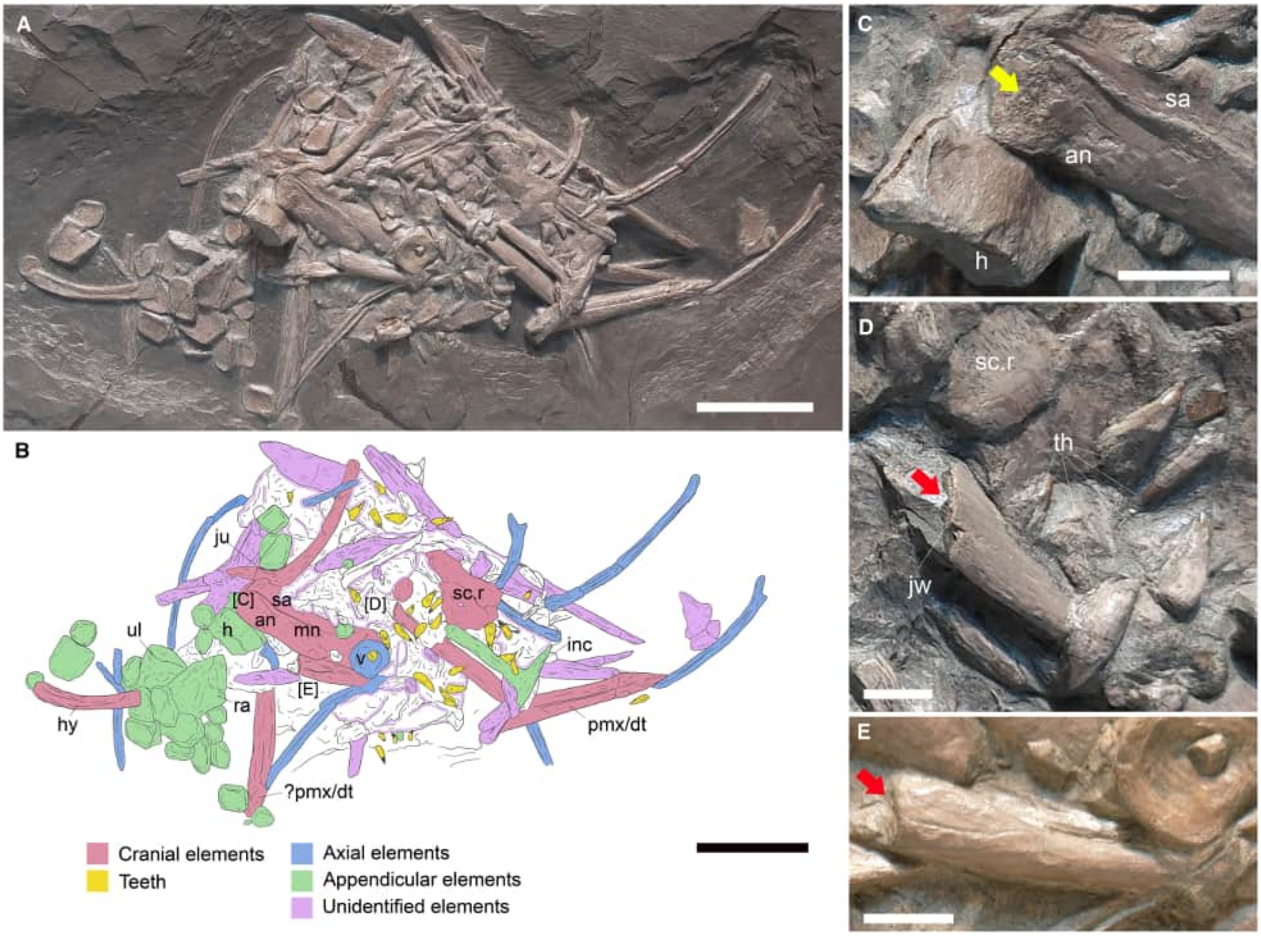

FIG. 7. Regurgitalite consisting of a partial, adult specimen referred to *Stenopterygius* sp. (FWD 0112). A, overview of the specimen. B, anatomical drawing with colour-based differentiation of the recognized units; letters in square brackets represent the positions of panels C–E. C, detail of the preserved humerus and angular portion of the mandible that show acid corrosion (yellow arrow). D, detail of a jaw element with evident perimortem fracture (red arrow) and preserved teeth in the background. E, additional perimortem fracture (red arrow) on the anterior portion of the right angular. *Abbreviations*: an, angular; h, humerus; hy, hyoid element; inc, interclavicle; ju, jugal; jw, jaw element; mn, mandible; pmx/dt, premaxilla or dentary fragment; ra, radius; sa, surangular; sc.r, scleral ossicles; th, teeth; ul, ulna; v, vertebral centrum. Scale bars represent: 10 cm (A, B); 1 cm (C); 2 cm (D, E). Photos courtesy of A. Schmid-Röhl; used with permission.

cylindrical shape and the presence of neurovascular grooves. Deformed scleral ossicles, a hyoid element and the right jugal are the only other cranial elements that we could unambiguously identify. 29 dislodged teeth can be found dispersed on the mass, characterized by rounded and robust roots and small, lightly ornamented crowns (Fig. 7D).

Axial skeleton. The vertebral column is represented by a single visible centrum in articular view. Several ribs are present on the clustered mass.

Appendicular skeleton. The pectoral girdle is represented only by the interclavicle, while a partially exposed humerus is the only stylopodial element of the specimen (Fig. 7C). Below the humerus, an ulna and radius can still be found in association, together with numerous metapodial elements (Fig. 7B). Although not in articulation, these closely associated limb bones probably belong to the same forefin.

Ontogenetic stage. The overall preservation of the specimen hampers precise ontogenetic assessment, but the low and angular shape of the jugal as well as the overall size of the preserved jaw elements suggest a sexually mature stage.

Structural & histological preservation. The clustered skeletal mass lacks a clear organization of its components, but we tentatively observe that some long bones (rostral fragments, interclavicles, few ribs and the hyoid) are approximately oriented south-east. Nevertheless, the majority of the ribs project radially from the mass. Several bones show perimortem fractures, in some cases with deep cracks where the bone snapped (Fig. 7D, E). Histological preservation is heterogeneous, but the compact bone appears generally damaged. The angular portion of the preserved lower jaw is notable for the presence of a deeply pitted and corroded surface (Fig. 7C). Dental tissues are also damaged, although a preparation artefact might be responsible. The most central area of the cluster is characterized by the presence of a cemented matrix, light grey in colour, and texturally distinct from the slab lithology.

DISCUSSION

SMNS 15194

The peculiar taphonomy of the specimen overall supports a regurgitalite interpretation, given that no abiotic marine processes could have feasibly caused the skeletal elements to be clustered in their current state (see previous report of marine bromalites: Cooper *et al.* 2022; Serafini *et al.* 2022). The breakage of the column in distinct twisted segments (Figs 2B, 3A) differs from the gentler coiling of axial elements in vertebrate specimens from the Posidonienschiefer Fm. that underwent an anterior landing on the sea floor (M. Johnson & E. Mujal, pers. comm.). Moreover, the extreme damage to the anterior portion of the skull and the displacement of jaw and cranial elements around the periphery of the axial skeleton (Fig. 2C) do not match those reported on the rostrum of ichthyosaurs that underwent an anterior landing on the sea floor (e.g. Wahl 2009). The asymmetrical preservation of the two portions of the ribcage (Fig. 2B) is also inconsistent with a physical explanation (e.g. current activity) that might be responsible for the extreme coiling of the vertebral column. The presence of traumas on the bone (Fig. 3E, F) strongly suggests predation on the specimen, which corroborates the hypothesis of SMNS 15194 being ingested and then egested by a marine predator. When perimortem traumas and anterior breakage of the skull bones are framed together, a head-first bite scenario on the juvenile *Stenopterygius* becomes plausible. Among bromalites, SMNS 15194 better reflects the condition of a regurgitalite rather than a coprolite, given that some skeletal units are still in articulation and do not show an extreme degree of compression (Gordon *et al.* 2020), nor are they surrounded by the buff-coloured matrix typical of Posidonienschiefer Fm. vertebrate coprolitic material (Jäger 2005).

Juvenile *Stenopterygius* appear to have had a maximum body depth of *c.* 16.5–17% of the total length (excluding the dorsal fin) based on specimens preserving the soft-tissue body outline; based on rib morphology, body width appears to have been similar. Thus, an estimated maximum gape diameter of *c.* 26–30 cm would be required for the ingestion of SMNS 15194, and probably an approximately similar diameter for the egestion of the pellet. Although the regurgitalite currently has a greater diameter than estimated for ingestion of the small ichthyosaur, it is likely to have been more compacted prior to arrival on the sea floor. *Temnodontosaurus trigonodon* is the only known tetrapod taxon in the Posidonienschiefer Fm. with a sufficient gape to ingest and egest whole an ichthyosaur the size of SMNS 15194. Large *T. trigonodon* specimens have posterior mandibular widths of up to or even exceeding 41 cm (based on SMNS 50000; larger specimens are known), sufficiently large to have easily ingested SMNS 15194. The coeval and sympatric teleosauroid *Macrospondylus bollensis*, the second-largest macropredator in the Posidonienschiefer biota, has a posterior mandibular width (internal distance between the angulars = gullet width of Massare 1987) of only *c.* 20 cm (estimated as a percentage of basicranial width in the largest adults from Johnson *et al.* 2023), slightly too narrow to have comfortably processed SMNS 15194 without dismemberment. Similarly, the small-prey specialist ichthyosaur *Eurhinosaurus*, despite its large size, can be excluded as a possible producer (gullet width of only *c.* 20 cm in large individuals, in addition to dentition unsuitable for large-prey capture and processing: Massare 1987). *Temnodontosaurus trigonodon* is very rare in the Tenuicostatum Zone of the Posidonienschiefer Fm. (Maxwell & Vincent 2016); however, the single specimen reported from this zone is from the same bed as SMNS 15194 (Maisch 1998). The only specimen of *M. bollensis* to have been collected from the Tenuicostatum Zone originated from the bed above that of SMNS 15194 (Hauff 1921).

Among Toarcian species of the genus *Temnodontosaurus*, we cannot conclusively exclude *T. crassimanus* (of similar cranial size to *T. trigonodon*, but not yet reported from the southwest German Basin) as a possible producer of the regurgitalite (Swaby & Lomax 2021); *T. zetlandicus*, also from the Toarcian but not reported from Germany, is too small to be considered as a candidate (Laboury *et al.* 2022).

The high degree of articulation of the SMNS 15194 axial elements, together with an overall paucity of superficial damage, is consistent only with a very limited duration of time between ingestion and egestion (hence ‘ejectalite’ type regurgitalite *sensu* Hunt & Lucas 2012). Soft tissues could have maintained most of the twisted portion of the axial skeleton in close to anatomical connection, while also shielding the skeletal tissue from the etching activity of gastric acids. The surface damage found on the tooth crowns could instead be interpreted as the result of acid etching, given that without the coverage of soft tissue, enamel would have been the first mineralized tissue to be in contact with gastric secretions. Moreover, the high degree of articulation of SMNS 15194 also indicates that *Temnodontosaurus* swallowed prey of this size class whole, with limited dismemberment and no evidence for repeated biting during swallowing. Remnants of soft tissue (although common in the Posidonienschiefer fossil record), were not identified on SMNS 15194. Bromalites can preferentially preserve fossilized integumental material or muscle fibres (e.g. Chin *et al.* 2003; Gordon *et al.* 2020); however, the absence of these features in the surveyed specimen might be explained by the quality of preparation in the 1920s.

SMNS 50000

As noted by Böttcher (1989), ichthyosaurian vertebral elements inside SMNS 50000 are clearly part of the thoracic area and abdomen of the *T. trigonodon* specimen, because they are extremely localized beneath the ribcage and are found nowhere else on the rest of the slab (Figs 4B, 5A). The high density of centra furthermore excludes the possibility that these remains are associated with the *T. trigonodon* skeleton by chance. Multiple lines of evidence strongly suggest that the accumulation of centra represents ingested prey items, mainly due to their preservational status and ontogenetic stage. Centra in SMNS 50000 show a degree of ossification and closure of the notochordal pit typical of the perinatal stage in ichthyosaurs (Kear & Zammit 2013; Miedema 2024). We exclude the possibility that any of these vertebrae are *Temnodontosaurus* foetal material on the basis of scaling. Perinatal ichthyosaur foetuses are usually in the range of 20–25% of adult body length and have consistent scaling with their vertebrae (McGowan 1973; Kear & Zammit 2013; Miedema 2024). A foetus of *Temnodontosaurus* is thereby expected to have larger vertebral centra than those in the body cavity of SMNS 50000, despite the lack of prenatal or pregnant *Temnodontosaurus* specimens needed to confirm this assumption (see differential foetal centra in other taxa: Dal Sasso & Pinna 1996; Maxwell & Caldwell 2003; Kear & Zammit 2013; Klein *et al.* 2020; Miedema *et al.* 2023). In addition, the degree of ossification of the small centra in SMNS 50000 is inconsistent with scavenged aborted ichthyosaurian foetal material, which has been documented in gastric contents in a cryptocleidoid plesiosaur (O'Keefe *et al.* 2009), and potentially also in *Stenopterygius* (Dick *et al.* 2016, but see Böttcher 1990 for an alternative interpretation).

Different stages of preservation of the centra in SMNS 50000 are consistent with a gut content interpretation (Fig. 5B–F). Macroscopic characterization of the bone tissue preservation types in the consumulite identified eroded and deformed centra, consistent with that reported for similarly sized (and shaped) fish vertebrae found in extant seabird gastric pellets (e.g. Guillaud *et al.* 2019). The different types of vertebral preservation in the consumulite also indicate different stages of digestion, most probably related to the different durations of exposure to gastric secretions (HCl and pepsin), implying that the four (or more) neonatal *Stenopterygius* individuals were preyed upon and ingested at different times (possibly days apart). Articulated or semiarticulated segments of *Stenopterygius* vertebral columns (Fig. 5B, C) are localized more anteriorly on the consumulite, most probably representing early stages of the digestion (stomach phase) and supporting the model in which the latest prey items to be ingested underwent the least disarticulation and dissolution. Furthermore, the predation of these latest postnatal *Stenopterygius* must have shortly preceded the death of the *Temnodontosaurus*, either by hours or a few days at most. The localization of most of these articulated segments in lower quadrants suggests also that a ventral displacement of the gut content occurred, possibly with a rupture of the stomach during early biostratinomy. Böttcher (1989) suggested that the rupture of the stomach might have also coincided with a violent discharge of the visceral mass due to the build-up of putrefaction gases that was also responsible for the breakage of the ribcage. While some of the *Temnodontosaurus* ribs are missing and even if some isolated ingested centra can be found at the very posterior end of the abdominal region, we do not recognize a taphonomic pattern that supports this extreme event. Moreover, Reisdorf *et al.* (2012) criticized the 'carcass explosion model' for ichthyosaurs in the Posidonienschiefer Fm. based on forensic and environmental modelling.

Böttcher (1989) postulated, based on well-preserved specimens of *Stenopterygius*, that the ichthyosaurian stomach consisted of two chambers, a rounded anterior portion corresponding to a glandular stomach and situated on the right side of the body, and an elongated, more posterior region corresponding to a muscular stomach situated on the left side of the body, in which indigestible matter accumulated. In SMNS 50000, the distinct 50 × 30 cm black mass mostly composed of coleoid hooklets would therefore correlate with the left-hand chamber (muscular stomach), and would have been posteriorly displaced from an originally anterior position during decay (Böttcher 1989). While we agree that some anterior portion of the consumulite most probably represents the stomach, we cannot distinguish the original (or even approximate) layout of the upper digestive tract of the specimen, because the mass is displaced throughout the entire rib cage.

The circular objects described as inorganic content of the consumulite are quite interesting. Some of these elements present an opaque grey colour and coarse texture (Fig. S2), consistent overall with the surrounding sediment, and could represent naturally nucleated authigenic mineral concretions. Such structures are rarely reported in the literature, but Alexander & Frey (2010) identified similar circular concretions (although smaller) associated with a Miocene cheloniid turtle, linking their formation to the unique reducing environment around the carcass during its fossilization. Similarly, Liu *et al.* (2021) managed to distinguish nucleated authigenic precipitates from gastroliths due to their homogeneous composition. However, of the two types of circular object (opaque and polished) found in the SMNS 50000 gut content, the polished type could tentatively be interpreted as gastroliths. These more anteriorly localized spherical objects are inconsistent with the surrounding matrix (Fig. 5G–I), are raised above the coleoid black mass, and have a lustre and the rounded edges typical of pebbles that transited in the gizzard or stomach of an animal (Wings 2007, 2009; Serafini *et al.* 2024). Ichthyosaurs have been reported to host geo-gastroliths in only two specimens: a Triassic *Guizhouichthyosaurus* specimen and an Upper Jurassic Solnhofen ophthalmosaurian (Cheng *et al.* 2006). If correctly interpreted, this would represent the first identification of gastroliths in an Early Jurassic macropredatorial taxon. With regard to the type of gastrolith that these objects would represent (*sensu* Wings 2007: pathological concretions (i.e. patho-gastroliths) or ingested sediment (i.e. geo-gastroliths)), this question requires more in-depth compositional analysis. However, for the time being we cannot chemically characterize the nature of any of the larger *in situ* circular objects found in SMNS 50000, and EDS (energy-dispersive x-ray spectroscopy) maps of the sampled matrix failed to discriminate any chemically different particles. Future analysis might rely on an XRF/Raman gun to retrieve some compositional data on these structures without damaging the mounted specimen.

Microstructural analysis of the extracted *Stenopterygius* bone fragments successfully identified digestive effects on the skeletal tissue, such as the corroded texture of the cortical bone, and exposure of pitted calcified cartilage and cracks (Fig. 6C, E, F). All of these feature have been previously reported in SEM studies on digested bone tissue (e.g. Denys *et al.* 1995; Fernández-Jalvo *et al.* 2014; Terry *et al.* 2018; Guillaud *et al.* 2019; Gordon *et al.* 2020; Serafini *et al.* 2022). The analysis failed to show the dense parallel fissures previously described in some digested bone (Terry *et al.* 2018). However, such fissures have been observed and characterized in mammalian mandibular tissue (Terry *et al.* 2018), therefore a comparative application to sauropsid vertebral bone might not be fully compatible. Moreover, ichthyosaurs underwent rapid vertebral growth during early postnatal development, resulting in a very loosely structured vertebral cortex (Houssaye *et al.* 2018). As such, the question of how fast-developing bone tissue in the vertebrae of juvenile organisms is affected by gastric acid should be investigated with more appropriate experimental analogues.

Finally, the EDS compositional characterization of the *Stenopterygius* bone fragments highlighted the absence and/or paucity of phosphorus in the consumulite matrix (Fig. 6G); this is indicative of the analysed sample as belonging to the gastric region and not as representative of displaced intestinal content that had already undergone the addition of endogenous phosphorus (Kjerulf-Jensen 1941). However, the sample is very limited, and other bone elements throughout the consumulite (especially in its most posterior portion) could be representative of intestinal content and show higher phosphatization. Potential *Temnodontosaurus* coprolites from the Lower Jurassic of the UK have been documented, indicating that vertebrae appear able to survive the digestion process (Hunt *et al.* 2012; D.R. Lomax, pers. comm.).

Remarks on the Dotternhausen bromalite

Jäger (2005) recognized FWD 0112 as an egested gastric pellet containing a juvenile *Stenopterygius* of estimated length of 1.5 m; due to humeral morphometries (see Maxwell 2012 for methodological reference) we instead assign the specimen to a *c.* 2.3-m-long adult *Stenopterygius*, larger than the smallest known sexually mature individual. The shape of the jugal (angular rather than bowed) corroborates this identification (Miedema & Maxwell 2022). From our evaluation we agree that the specimen definitely represents a bromalite, given that perimortem traumas and corrosion of the compact bone strongly suggest predation and digestion. We identify FWD 0112 as a regurgitalite, because the specimen appears less clustered than a coprolite and because of the light grey matrix at the core of the bone mass that seemingly represents a cemented gastric secretion (Gordon *et al.* 2020). However, we did not perform any compositional analysis for phosphorus content, therefore a categorical exclusion of the specimen being a disaggregated coprolite is currently not possible. We note, nevertheless, that the size of the bone mass, the random orientation of the content and the absence of groundmass seemingly invalidate the coprolite hypothesis. In the regurgitalite scenario, FWD 0112 appears to represent a fractioned part of the original carcass, implying pre-ingestion processing of the prey item by dismemberment. Both the egested pellet sizes and the estimated body depth of a 2.3-m-long *Stenopterygius* (38–39 cm) seemingly leave

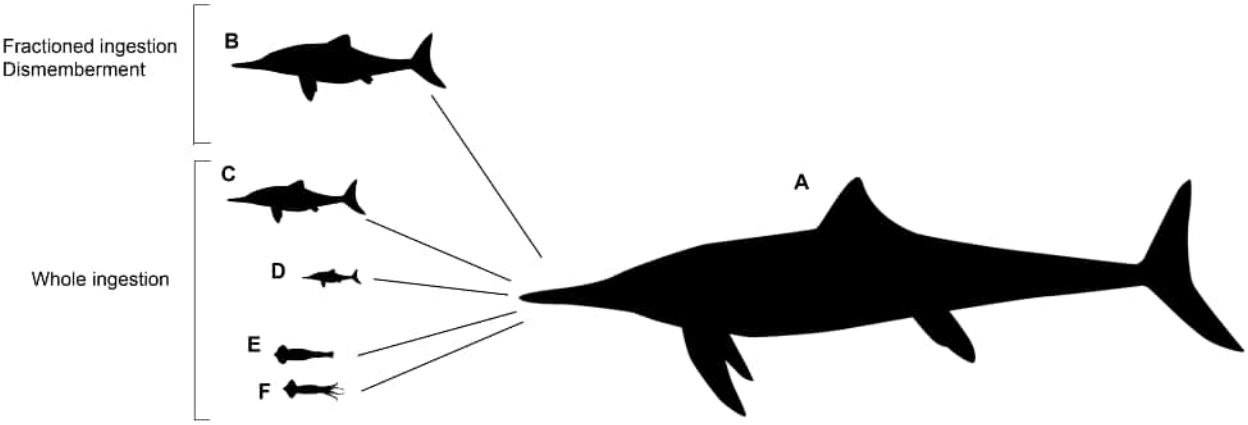

FIG. 8. Prey preferences and prey processing of *Temnodontosaurus trigonodon*: A, *T. trigonodon*; B, adult *Stenopterygius*; C, large juvenile *Stenopterygius*; D, neonatal *Stenopterygius*; E, belemnoid (*Acrocoelites raui*); F, belemnoid (*Chondroteuthis*). Silhouette images from PhyloPic (https://www.phylopic.org: *T. trigonodon* and *Stenopterygius* Gareth Monger CC BY 3.0; *Acrocoelites raui* Dean Schnabel CC0 1.0; *Illex illecebrosus* (for *Chondroteuthis*) Nathan Hermann CC0 1.0).

T. trigonodon as the only feasible producer of the regurgitalite (see Discussion above).

Ecological implications

When framed together with modern ecomorphological studies, the re-evaluation of SMNS 15194, SMNS 50000 and FWD 0112 provides new insights into the trophic ecology of *Temnodontosaurus trigonodon*. Bennion *et al.* (2024) evaluated craniodental features for the seven currently recognized species of *Temnodontosaurus* (i.e. *T. platyodon*, *T. eurycephalus*, *T. nuertingensis*, *T. trigonodon*, *T. crassimanus*, *T. zetlandicus* and *T. azerguensis*), and identified *T. trigonodon* as a latirostrine generalist predator with an elongated rostrum suited for capturing fast nektonic prey and functionally optimized for an increased gape (feature linked to macropredation, discussed also in Cortés *et al.* 2021). Bennion *et al.* (2024) also assigned *T. trigonodon* to two different tooth morphotypes: type D is represented by a carinate tooth crown with a cutting edge formed by heavy and discontinuous enamel ridgelets, while type E is represented by slightly lingually curved crowns with numerous longitudinal ridges (more densely present lingually), and occasionally also carinae (Bennion *et al.* 2024). Unfortunately, teeth are not preserved in SMNS 50000. We can, however, infer the dietary habits and prey preferences of *T. trigonodon* from this study, to test whether its ecomorphological niche matches what is observed from its bromalites.

Based on our analysis of SMNS 50000, *T. trigonodon* represents a generalist predator that hunted both coleoid cephalopods and smaller ichthyosaurs (Fig. 8). This hypothesis is based on evidence from extremely rare specimens; additional bromalites from this taxon are needed as confirmation that this represents the typical diet for this taxon. Assuming that SMNS 15194 and FWD 0112 are *T. trigonodon* regurgitalites, the pursuit of larger prey, such as juvenile and small adult *Stenopterygius*, may also be added to the dietary habits of *T. trigonodon*. This also supports its higher ecomorphological classification as a macropredator. From our analysis, the assignment by Bennion *et al.* (2024), using craniodental features, of *T. trigonodon* to a generalist latirostrine predator class specialized in pursuing smaller and faster prey, but which is also capable of engaging in macropredation and hypercarnivory, is seemingly confirmed by bromalite contents. Based on the surveyed Posidonienschiefer specimens, we are also able to tentatively identify a specific targeting of juvenile *Stenopterygius* as prey items, with five total accounts of predation by two different individuals. Recognizing the limitation of such a rare record, this hypothesis is corroborated by the fact that SMNS 50000 preyed upon the four *Stenopterygius* at different times based on the differential stages of digestion of the bones, meaning that this behaviour is not localized to a single event, but is instead possibly customary. The preferential hunting of juveniles from other species is common in marine apex predators; a similar interaction in the fossil record has been described for a specimen of the archaeocete *Basilosaurus isis* from the lower Eocene of Egypt, which was found to be associated with the remains of a juvenile *Dorudon atrox* as gut content (Voss *et al.* 2019). SMNS 50000 is currently the sole documented *T. trigonodon* specimen with coleoid cephalopods in its gut content; however, some specimens of *T. platyodon* have also been found to have belemnoid hooklets in their consumulite (supplementary material in Bennion *et al.* 2024). The dentition of *T. trigonodon* does not appear to be specialized for soft-bodied prey items (soft-body specialists tend to have acute and slender tooth crowns; e.g. Massare 1987; Fischer *et al.* 2016), and neither are similar specializations suggested by its rostrum anatomy (Bennion *et al.* 2024). It is therefore unclear whether *Temnodontosaurus* fed consistently on coleoids or whether these gut contents represent occasional opportunistic events compatible with a near-surface foraging lifestyle (e.g. the occasional pursuit of a surfacing coleoid school). It is worth noting that even modern marine tetrapods classified as macropredators, despite lacking dental features specifically suited for teuthophagy, still prey opportunistically on cephalopods (e.g. some killer whale *Orcinus orca* ecotypes, Fertl *et al.* 1996; leopard seals *Hydrurga leptonyx*, Hall-Aspland & Rogers 2004).

Maxwell & Vincent (2016) postulated that climate changes were responsible for the observed rapid increase in adult body size in *Stenopterygius quadriscissus* between the lowermost beds of the Tenuicostatum Zone and the Serpentinum Zone. However, our results suggest a second possibility: that the observed increase in body size might be predator-driven, a result of increasing predation pressure by *Temnodontosaurus*. An adult of *S. quadriscissus* *c.* 2 m in length, as is typical in the lower horizons of the Posidonienschiefer Fm., would have a body depth of maximally 34 cm, and so would be easily preyed upon by a *Temnodontosaurus* with a gape of at least 40 cm. In the Serpentinum Zone, body lengths for adults of *S. quadriscissus* of over 3 m are typical. These animals would have had body depths of over 50 cm, which might have conferred protection from all but the largest *Temnodontosaurus* individuals. This could also explain why body size in *S. quadriscissus* appears to plateau in the Serpentinum Zone, rather than continuing to increase (Maxwell & Vincent 2016). This hypothesis requires further testing.

The finding that the gastric contents represent four individuals of *Stenopterygius* in the same size class might suggest that these small immature ichthyosaurs were gregarious, forming age cohort-based groups, or remaining with siblings after birth. However, differences in the degree of digestion observed in the prey of SMNS 50000 do not support the idea that the juveniles were consumed in a single feeding event, and thus do not provide evidence for social behaviour. Alternatively, SMNS 50000 could represent opportunistic or seasonal feeding on *Stenopterygius* neonates during that population's birthing season.

Generalist opportunism in macropredatory ichthyosaurs

The reappraisal of the SMNS 50000 gut content is worth comparing with the few described gut contents of other macropredatory ichthyosaur taxa throughout the Mesozoic. Whereas bromalites from smaller, lower-trophic level ichthyosaur taxa are relatively common (e.g. Pollard 1968; Massare & Young 2005; Lomax 2010; Dick *et al.* 2016), macropredatorial gut content is much rarer. Aside from SMNS 50000, only the following taxa from this ecological class have been described with associated gut contents:

1. A specimen of *Guizhouichthyosaurus tangae* (XNGM-WS-53-R4) 4.8 m in length from the Ladinian (Middle Triassic) of China described by Jiang *et al.* (2020) contained 1.3 m of an originally 4-m-long thalattosaur (*Xinpusaurus*). *Guizhouichthyosaurus* is a mid-sized ichthyosaur, usually only 4–6 m in length (Jiang *et al.* 2020), with tooth crowns both lacking carinae and smaller than the 20 mm threshold identified for macropredatory marine reptiles (Fischer *et al.* 2022). *Guizhouichthyosaurus* was likely to have been an opportunistic generalist, consistent with the small fish and bivalve remains associated as gut contents in another individual (YIGM V30016) attributed to the same taxon from the early Carnian (Cheng & Chen 2007). Interestingly, a third specimen was described containing numerous gastroliths (Cheng *et al.* 2006).
2. A merriamosaurian ichthyosaur (UAMES 2437) from the upper Norian of Alaska, USA, slightly larger than *Guizhouichthyosaurus* (estimated 7.3 m in length), reported as being associated with consumulite composed of fish scales/bones and cephalopod shell fragments (Druckenmiller *et al.* (2014)).
3. *Shonisaurus popularis*, from the upper Carnian of Nevada, USA, described as having gastric contents composed of cephalopod shell fragments and comminuted bones including partially digested small ichthyosaurian centra (Camp 1980). These gastric contents were not mentioned in a subsequent reevaluation of the specimen (Kelley *et al.* 2022), and require confirmation that they indeed represent a consumulite. *Shonisaurus popularis* had carinate teeth and an enormous body size (up to 16 m in length) (Kelley *et al.* 2022), and so is expected to have been a macropredator on morphological grounds.
4. *Temnodontosaurus platyodon* from the Hettangian of Dorset (Lyme Regis), described as possessing consumulites with coleoid hooklets in two different specimens (LYMPH 2010/75 and OUMNH J.29170; Bennion *et al.* 2024). *Temnodontosaurus platyodon* had carinate teeth and a large body size (up to 9 m in length) (McGowan 1994; Bennion *et al.* 2024), and so is expected to have been a macropredator on morphological grounds.
5. A specimen of *Platypterygius australis* (QM F16811) from the Albian of Australia, described by Kear *et al.* (2003) with associated gastric contents

composed of fish remains (among which were teeth from large clupeomorph or pachiryzodontid fishes), hatchling turtle bones (possibly *Notochelone*) and remains of an enantiornithine bird.

When taken together, these representatives of the macropredatorial niche seem not to follow a specific pattern in prey selection, but instead appear to be opportunistic generalists. Apex predators such as *T. trigonodon* and *P. australis* are described as possessing craniodental features suited for a macropredatorial lifestyle (Fischer *et al.* 2016; Bennion *et al.* 2024) and indeed they are found associated with bromalites of large prey items, such as juvenile and adult *Stenopterygius* or large actinopterygians (Kear *et al.* 2003). However, the same specimens are also found to have ingested smaller prey, such as cephalopods (SMNS 50000) and small fishes, turtles and birds (QM F16811). In contrast, despite not possessing the typical body size or tooth morphology for a macropredatorial ecology, *Guizhouichthyosaurus* was found to be capable of occasionally hunting and subduing large marine reptiles (Jiang *et al.* 2020). However, it is important to note that, unlike *T. trigonodon* as discussed here (and probably as a function of its smaller body size), *Guizhouichthyosaurus* appears to have dismembered its prey prior to ingestion, swallowing only the torso of the prey animal. From such limited and rare material it is difficult to correctly frame prey selection in these large marine amniotes, but the available data seemingly conform to the idea that there is no such thing as a clearly defined macropredatorial diet in these taxa (Fischer *et al.* 2022). Large gape size and craniodental adaptations open the possibility to macropredation, but prey items from lower trophic levels were probably also consistently exploited. This behaviour is consistent with Recent marine amniote analogues, such as the less specialized ecotypes of *Orcinus orca* (Baird *et al.* 2006; Pitman & Durban 2012).

CONCLUSION

In this study we reappraised three fossils from the Lower Jurassic Posidonienschiefer Fm. containing, or interpreted as, bromalites. From the analysis of SMNS 15194 we report that:

1. The specimen does represent a fossilized gastric ejecta (regurgitalite).
2. The extreme coiling and twisting of the juvenile *Stenopterygius* reflects the ingestion and early digestion of the specimen and not an abiotic process.
3. The *Stenopterygius* skeleton exhibits perimortem trauma, consistent with predation.
4. The axial skeleton is well articulated; the skeletal tissue is histologically pristinely preserved, whereas the enamel of tooth crowns is damaged and exfoliated.
5. These conditions reflect an extremely limited period of time between ingestion of the remains and their egestion, with the soft tissues shielding the bones (but not teeth) from acid etching.

From the analysis of FWD 0112 we report that:

1. The specimen represents a bromalite, likely to be a regurgitalite as previously proposed. We identified the prey item as an adult *Stenopterygius*. The carcass seemingly underwent dismemberment before ingestion. Multiple perimortem traumas and traces of acid etching are evident on the bone tissue.

From analysis of both SMNS 15194 and FWD 0112 we report that:

1. Based on our current understanding, *T. trigonodon* is the only predator in the Posidonienschiefer Fm. with a sufficient gape to ingest and egest SMNS 15194 whole. The large portion represented by FWD 0112 implies that *T. trigonodon* could have ingested ichthyosaurs of up to 2.4 m in length without difficulty. Other species of *Temnodontosaurus* (e.g. *T. crassimanus*) are consistent in size with the regurgitalite producer, but have not been reported from the Southwest Germany Basin.
2. The feeding strategy of *Temnodontosaurus* is here interpreted as swallowing prey whole without repeated biting or dismemberment for prey items up to 1.7 m long, while more extensive prey-processing is evident for prey items greater than 2 m in length.

From the analysis of the gut content of SMNS 50000 we report that:

1. The small ichthyosaurian centra found inside the *T. trigonodon* ribcage are gut contents (consumulite) and not foetal material. They are most likely to belong to postnatal *Stenopterygius* individuals and bear effects of digestion.
2. A new count of the ingested centra identified at least 248 *Stenopterygius* vertebral elements, implying that the *Temnodontosaurus* specimen ingested at least four individuals at different times, judging by the different stages of preservation indicating different digestion phases.
3. Traces of acid etching are microstructurally recognizable on the analysed consumulite items, consistent with the action of hydrochloric gastric acid and pepsin on bone.

4. Circular objects, recognized as either gastroliths or nucleated authigenic precipitates, can be found in the temnodontosaur consumulite. Their nature and possible function are still unresolved.
5. The presence of abundant coleoid remains in the SMNS 50000 gut content suggests opportunistic dietary habits for *T. trigonodon*, while juvenile *Stenopterygius* might have been more consistently targeted by the marine macropredator.

The present results further help to resolve the feeding ecology of *T. trigonodon* in the trophic network of the Posidonienschiefer Fm., but seemingly also highlight opportunism among large macropredatorial ichthyosaurs throughout the Mesozoic. Ultimately, the study demonstrates the utility of comparing different kinds of bromalite associated with a taxon as a productive methodology to investigate feeding behaviour in extinct vertebrates.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.70018):

Figure S1. TXRF spectrum on SMNS 50000 sample with detail of spot analysis.

Figure S2. Inorganic circular objects found in SMNS 50000 consumulite, possibly representing authigenic mineral precipitates.

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