Craniodental ecomorphology of the large Jurassic ichthyosaurian *Temnodontosaurus*

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Abstract

Marine amniotes have played many crucial roles in ocean ecosystems since the Triassic, including predation at highest trophic levels. One genus often placed into this guild is the large Early Jurassic neoichthyosaurian *Temnodontosaurus*, the only post-Triassic ichthyosaurian known with teeth which bear a distinct cutting edge or carina. This taxonomically problematic genus is currently composed of seven species which show a wide variety of skull and tooth morphologies. Here we assess the craniodental disparity in *Temnodontosaurus* using a series of functionally informative traits. We describe the range of tooth morphologies in the genus in detail, including the first examples of serrated carinae in ichthyosaurians. These consist of false denticles created by the interaction of enamel ridgelets with the carinal keel, as well as possible cryptic true denticles only visible using scanning electron microscopy. We also find evidence for heterodonty in the species *T. platyodon*, with unicarinate mesial teeth likely playing a role in prey capture and labiolingually compressed, bicarinate distal teeth likely involved in prey processing. This type of heterodonty appears to be convergent with a series of other marine amniotes including early cetaceans. Overall, the species currently referred to the genus *Temnodontosaurus* show a range of craniodental configurations allowing prey to be captured and processed in different ways – for example, *T. eurycephalus* has a deep snout and relatively small bicarinate teeth likely specialised for increased wound infliction and grip-and-tear feeding, whereas *T. platyodon* has a more elongate yet robust snout and larger teeth and may be more adapted for grip-and-shear feeding. These results suggest the existence of niche partitioning at higher trophic levels in Early Jurassic ichthyosaurians and have implications for future work on the taxonomy of this wastebasket genus, as well as for research into the ecology of other extinct megapredatory marine tetrapods.

Keywords

Megapredator, serrations, heterodonty, ecomorphology, Neoichthyosauria, Sinemurian, Toarcian

Introduction

Secondarily aquatic tetrapods have formed a major part of marine ecosystems since the Triassic, filling a wide range of ecological niches (Massare, 1987; Kelley & Pyenson, 2015). Arguably the most iconic aquatic tetrapods are the large predators which occupy the highest trophic levels and can consume large marine vertebrates through dismemberment (Konishi *et al.*, 2014). The consumption of larger prey results in radically different functional requirements to those of a diet limited to small fish or squid, with a greater importance of prey subduing and processing in the feeding cycle (Hocking *et al.*, 2017b). The act of subduing the prey can occur in several ways, however the predator usually inflicts bite wounds with the intention of either killing outright or weakening the prey animal (Wellard *et al.*, 2016). The predator may also hold the prey underwater until it drowns (Taylor, 1987). Small chunks must be torn off before being swallowed, usually after the prey has been killed, either by shaking, tearing, or twisting (Taylor, 1987). These predators play an important role in top-down regulation of their respective ecosystems (Estes *et al.*, 2011, 2016) and have been used to infer ecosystem health and complexity following mass extinctions (Fröbisch *et al.*, 2013; Scheyer *et al.*, 2014).

Despite its importance, it is hard to accurately define this predatory niche. We prefer not to use the terms ‘macroraptorial’ as this technically means a diet of any prey which are not microorganisms (sensu Horner-Devine *et al.*, 2007), nor do we use ‘apex predator’ as this term is restricted to the species at the top trophic level in their ecosystem, thereby encompassing only a fraction of large predators (e.g. Sander *et al.*, 2021). Instead, we follow recent studies which specifically define the guild by its diet: megapredation (Jiang *et al.*, 2020; Bennion *et al.*, 2022; MacLaren *et al.*, 2022) or hypercarnivory (Andrade *et al.*, 2010; Cortés *et al.*, 2021). The most frequently used indications of a megapredatory lifestyle are features of the teeth, skull, and mandible (e.g. Massare, 1987; Fahlke *et al.*, 2013; Loch *et al.*, 2020; Fischer *et al.*, 2022a), alongside stable isotope analyses and rarely preserved stomach contents and bite marks (e.g. Fahlke, 2012; Schulp *et al.*, 2013; Voss *et al.*, 2019; Jiang *et al.*, 2020). One feature frequently regarded as a clear yet non-exclusive indication of a megapredatory niche is the presence on the teeth of cutting edges or ‘carinae’ (Massare, 1987). However, in some species (notably in pliosaurids, mosasaurids, and basilosaurid cetaceans) these carinae can be plesiomorphic and may not be a true indication of a shift to a megapredatory niche in that particular taxon (Uhen, 2004; Fischer *et al.*, 2017). Carinate teeth display a range of variation (curvature, serrations, labiolingual compression) (e.g. Benson *et al.*, 2013; Young *et al.*, 2014) which is rarely taken into account to infer diet (Fischer *et al.*, 2022a). Similarly, the skulls and mandibles of inferred megapredators do not show one specialised morphotype but rather a range of more robust morphologies: from short, dorso-ventrally deep snouts (brevirostry and oreinirostry) to skulls with a more elongate snout and robust post-orbital region (latirostry) (e.g. Young *et al.*, 2012a; Peri *et al.*, 2021). These variations in skull and tooth morphology may reflect differences in hunting style and prey processing strategies, as well as an underlying range in the proportion of larger prey in the diet.

The ichthyosaurian *Temnodontosaurus* Lydekker, 1889 is a large marine reptile known from Lower Jurassic strata of Europe (e.g. McGowan, 1996a; McGowan & Motani, 2003) and possibly Chile (Otero & Sepúlveda, 2020). It is the only post-Triassic ichthyosaurian to have carinate teeth; a trait which is more frequently observed in Triassic taxa, such as *Himalayasaurus*, *Thalattoarchon*, and *Shonisaurus* (Motani *et al.*, 1999; Fröbisch *et al.*, 2013; Kelley *et al.*, 2022). However, tooth crown morphology within the genus varies considerably, as does the number of carinae (Godefroit, 1993). Teeth of the genus were described as bicarinate by Massare (1987), but reports vary from zero to four carinae (Maisch & Matzke, 2000; McGowan & Motani, 2003). Furthermore, the genus also displays considerable skull shape variation and preserved stomach contents known to include other ichthyosaurians as well as cephalopods (Böttcher, 1989); suggesting the species within this genus likely occupied a range of ecological niches (McGowan, 1974; Martin *et al.*, 2012). Different assemblages of species are thought to have co-existed in the same region during the Sinemurian (*T. platyodon*, *T. eurycephalus*, and '*T. risor*') and the Toarcian (*T. trigonodon, T. zetlandicus, T. crassimanus*) (Table 1 and references therein).

A specimen of *Temodontosaurus* was the first ichthyosaurian to be described, in 1817 (see Torrens, 1995), and this long history of research coupled with changing taxonomic paradigms (e.g. phenetics vs. apomorphies) has resulted in a taxonomic mess (McGowan, 1996b; McGowan & Motani, 2003) with the diagnosis of the genus based on gross skull and fin ratios (McGowan, 1974). Modern analyses find the genus to be a paraphyletic group of species of early neoichthyosaurians (Moon, 2017; Laboury *et al.*, 2022). Recent work has started to improve the situation by reassessing the validity of some species (Maisch & Hungerbuhler, 1997; Swaby & Lomax, 2021; Laboury *et al.*, 2022), however further work is needed. Currently seven species are recognised (Table 1), some of which have received no taxonomic attention in decades – this notably includes the two most common species *T. platyodon* and *T. trigonodon*. The holotype of *T. platyodon*, an isolated tooth from the 'Lower Lias' (earliest Jurassic) of Lyme Regis (UK), has been lost (McGowan, 1974); the neotype shows an incomplete dentition which does not match the figures of the holotype (Godefroit, 1993). This species now includes specimens formerly described as '*T. risor*' which are thought to be juvenile individuals of *T. platyodon*, despite differences in tooth and snout morphology (McGowan, 1974, 1994). *Temnodontosaurus trigonodon* has had a complicated taxonomic history and currently encompasses the extremely large holotype specimen from Bad Staffelstein (Germany), as well as several specimens from other German localities and French specimens formerly referred to *'T. burgundiae'* (Maisch, 1998; McGowan & Motani, 2003). Despite known differences in interspecific tooth morphology these features have not been considered of taxonomic value (Maisch, 1998; McGowan & Motani, 2003). As a result, *Temnodontosaurus* is currently a 'cluster' whose taxonomic and ecological signals are difficult to disentangle.

This study aims to describe in detail the range of cranial and dental morphologies found in *Temnodontosaurus*, particularly focusing on carinae and enamel ornamentation. By doing so, we intend to assess the ecology and functional morphology of this large Early Jurassic oceanic predator, as well as cast light on some of the taxonomic problems hindering our understanding of the genus.

Institutional abbreviations

BRLSI, Bath Royal Literary and Scientific Institution, Bath, UK, **CAMSM**, Sedgwick Museum of Earth Sciences, Cambridge, UK; **FMNH**, Field Museum, Chicago, USA; **GPIT**, Palaeontological Collections of Tübingen University, Tübingen, Germany; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **LYMPH**, Lyme Regis Philpot Museum, Lyme Regis, UK; **NHMUK**, Natural History Museum, London, UK; **OUMNH**, Oxford University Museum of Natural History, Oxford, UK; **PKB**, Petrefaktensammlung Kloster Banz, Bad Staffelstein, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **UMH**, Urwelt Museum Hauff, Holzmaden, Germany; **WHITM**, Whitby Museum, Whitby, UK; **YORYM**, Yorkshire Museum, York, UK.

Specimens from PKB and UMH are given manuscript numbers due to the lack of a formal accession system. A new catalogue has been introduced for the Tübingen (GPIT) collection; see Stöhr and Werneburg (2022) for specimen number synonymies.

Tooth terminology

The terminology used to describe tooth morphology varies between papers and between target clades. We used an adapted version of the terminology proposed by Zverkov *et al.*, (2018) and Smith & Dodson (2003) (summarised in Figure 1). Central to the understanding of the teeth of *Temnodontosaurus* is the definition of **carinae**. Despite being frequently used as evidence for certain diets in marine reptile tooth studies (Massare, 1987), the term is usually described in terms of function (an external structure which enables the tooth to cut efficiently) rather than morphology. Combining definitions used for theropod dinosaurians and plesiosaurians, we define a carina as an apicobasally-oriented, “sharp, narrow, and well-delimited ridge” (Hendrickx *et al.*, 2015, p4), which is of a prominent nature and occurs in a limited number across the tooth crown circumference (Zverkov *et al.*, 2018). From a microanatomical perspective, carinal ridges are formed by a thickening of the enamel (Maxwell *et al.*, 2012). Enlarged carinae can have a concave crown surface adjacent to the carinal keel known as the carinal flange (Young *et al.*, 2015). Some carinae have a serrated edge – this can be made of true denticles, or false denticles created by the interaction of enamel ornamentation with the carinal keel (e.g. Andrade *et al.*, 2010; Young *et al.*, 2014).

Ridges are also keel-like structures which run apicobasally, however they can be distinguished by their higher density across the tooth crown, and the fact that these structures do not result in a strong modification of the cross-sectional shape of the crown (Zverkov *et al.*, 2018; McCurry *et al.*, 2019). In some metriorhynchid crocodylomorphs, these ridges have an undulating appearance which mimics serrations, and occasionally even show discrete units known as pseudodenticles (Young *et al.*, 2014). Smaller, second order ridges are referred to as ridgelets and can show an anastomosing pattern (Zverkov *et al.*, 2018). We use the term **striae** (singular stria), often used to describe ridges, to specifically refer to apicobasal crown features which project inwards, usually appearing as fine lines on the enamel surface (Zverkov *et al.*, 2018). Broad enamel wrinkles are sometimes seen running horizontally, these have been referred to as **bands** if projecting outwards, or **annuli** if projecting inwards (Brusatte *et al.*, 2007; Andrade *et al.*, 2010; Fischer *et al.*, 2022b).

Marine tetrapod teeth usually have a simplified crown shape and are round to oval in cross section (Massare, 1987; Fischer *et al.*, 2022a), which can be altered by the presence of carinae (Zverkov *et al.*, 2018). Furthermore, some marine reptiles have tooth crowns with a ‘polygonal’ cross sectional area, with faces which have alternatively been referred to as ‘facets’, ‘flutes’, or ‘prisms’ (Hornung & Reich, 2014). These features have been reported in megapredatory species of pliosaurids (e.g. Zverkov *et al.*, 2018), metriorhynchids (e.g. Andrade *et al.*, 2010), mosasaurids (e.g. Lingham-Soliar, 1995), and the odontocete *Squalodon* (e.g. Kellogg, 1923a). Despite being reported in the dentition of some ichthyosaurians (Massare, 1987), this feature has yet to be properly described in the group.

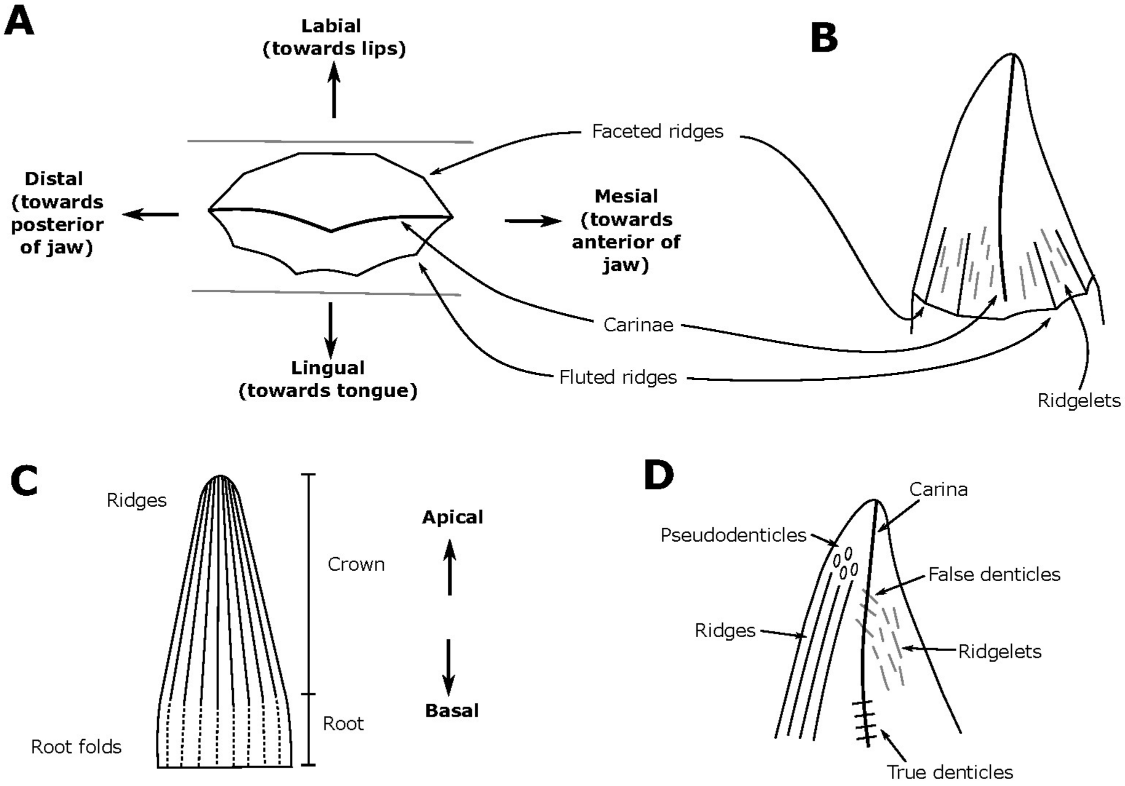

Figure 1. Generalised neoichthyosaurian teeth showing the range of anatomical features.

There is some confusion over the correct terminology for these tooth surfaces (Hornung & Reich, 2014), especially as the term 'facet' is also commonly used to describe tooth wear patterns (Young *et al.*, 2012b), and 'prisms' to describe features of enamel microstructure (Loch *et al.*, 2013). We chose to use the terminology of Madzia (2019), who defines these features not as a specific named trait but rather as a description: a 'faceted' surface is created by indistinct ridges connected by a flat or slightly convex surface, whereas a 'fluted' surface is created by distinct ridges separated by furrows (Madzia, 2019) (Figure 1). These structures likely have homologous developmental origins (Street *et al.*, 2021).

The level of tooth crown wear has often been used as an ecological indicator in fossil marine amniotes (e.g. Massare, 1987; Fitzgerald, 2010; Ford *et al.*, 2011; Fischer *et al.*, 2016, Marx *et al.*, 2023), however care must be taken when comparing wear patterns between marine tetrapod groups due to the different tooth replacement regimes (Maxwell *et al.*, 2012; Armfield *et al.*, 2013). The heaviest type of tooth wear in marine reptiles consists of oblique tooth crown breaks which are subsequently polished (Massare, 1987). This is sometimes referred to as enamel spalling (Schubert & Ungar, 2005) or chipping fractures (Lambert & Bianucci, 2019). Tooth wear can also be present on the carinal keel from occlusion (e.g. Young *et al.*, 2012b).

Methods

Sampling

A total of 63 specimens belonging to *Temnodontosaurus* and other Early Jurassic neoichthyosaurians were directly examined as part of this study, including the holotypes of six species (*T. eurycephalus*, *T. platyodon*, *T. trigonodon, T. nuertingensis, T. zetlandicus*, and *T. crassimanus;* Supplementary Figure 1), as well as several isolated teeth and jaw sections (see Supplementary Table 1 for complete list). The holotypes of *'T. burgundiae'* and *T. azerguensis* were not included in this study. Both are incomplete and the latter is edentulous (it is unclear whether this is in vivo or taphonomically) (Martin *et al.*, 2012).

Well-preserved skulls were 3D scanned either with an Artec Eva structured white light scanner (precision ranges from ≈ 0.5 to 1 mm) or a Creaform Handyscan laser scanner (precision set at 0.6 mm) with models created in Artec Studio and VX Elements, respectively. Models of SMNS 13488 and 15950 were obtained from Pardo-Pérez *et al*. (2018). Tooth wear patterns and stomach contents, where present, were recorded. Scanning electron microscope (SEM) photographs were taken at the SMNS (Zeiss Evo LS 15, specimens uncoated) and at the IRSNB (ESEM FEI Quanta 200, specimens uncoated).

Teeth were described using the terminology outlined above and categorised into morphotype groups. Most teeth observed were either in matrix or articulated in the snout, often limiting our observations to the mesial, labial, and distal sides. We were only able to draw limited conclusions on tooth crown curvature for the same reasons. It should also be noted that many historic specimens were subject to intensive preparation (e.g. see Pardo-Pérez *et al.*, 2018), in some cases removing much of the enamel.

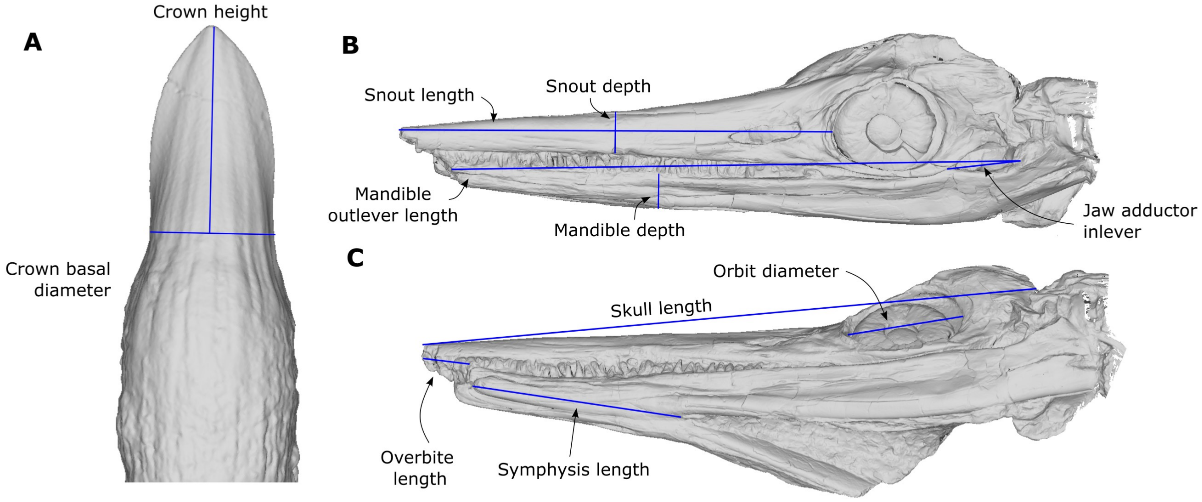

Figure 2. Linear skull and tooth measurements used in analyses. A) *Temnodontosaurus platyodon* IRSNB R122, 3D model in orthographic view. B) *T. platyodon* NHMUK PV R1158, 3D model of cast at LYMPH. Snapshot in orthographic, left lateral view. C) *T. platyodon* NHMUK PV R1158, 3D model of cast at LYMPH. Snapshot in orthographic, left ventrolateral view.

Skull and mandible morphometrics

Twelve measurements were taken on 24 skulls with complete snouts (unfortunately this excluded the holotypes of *T. nuertingensis*, *T. crassimanus,* and *T. zetlandicus*, as they were missing the anterior end of the snout) (Figure 2). These were used to calculate ten functionally informative ratios. Two tooth characters were also included: tooth crown aspect ratio and absolute tooth crown height; see Table 2 for definitions of these traits.

All analyses were carried out in the R v. 4.1 statistical environment (R Core Team, 2021). Eighteen specimens passed through a completeness threshold of 45%. This level was found to be appropriate following experimentation for this dataset (specimens excluded by the threshold were missing significant features, e.g. complete teeth). These ratios were then z-transformed (giving them a mean of zero and a variance of 1) and used to compute a Euclidean distance matrix. The data was then visualised using a principal coordinates analysis (PCoA) using the package *ape* v. 5.5 (Paradis *et al.*, 2004) with density added using the kernel 2D density estimator (following Fischer *et al.*, 2020). We also created a biplot of tooth shape (aspect ratio) and tooth crown height for all specimens complete enough for these measurements to be taken (n=43).

Results

Tooth descriptions

The morphotypes reported here represent broad categories which themselves contain an amount of variation both between specimens and, where preserved, along the jaw.

Tooth morphotype A

Observed in: some specimens of *Temnodontosaurus platyodon* (including the ones formerly referred to as '*T. risor*'), *Ichthyosaurus* spp.*,* and *Protoichthyosaurus* spp.

These teeth are characterised by their strong, narrow apicobasal ridges which are triangular in cross section (Figure 3). None are noticeably more prominent and there is no indication of any carinae. Towards the base of the crown the ridges are continuous with the root folds. These ridges sometimes have an undulating, crenulated appearance which gives a serration-like effect (Figure 3C). Broken teeth (Figure 3D) reveal a circular cross section through the crown. Some tooth crowns display noticeable lingual curvature; however, this may vary across the jaw. In one specimen (NHMUK PV OR43971, *'T. risor'*) the maxillary teeth appear to be significantly smaller and closely spaced – it is unclear whether this is an authentic signal as the specimen is behind glass and unable to be examined directly. Observed wear patterns include apical spalling (e.g. OUMNH J10340, *Ichthyosaurus* sp.) as well as rounded apices.

This tooth morphotype is present in all three specimens of '*T. risor*' described by McGowan (1974) as well as additional specimens referred to the genus by other authors (e.g. Lomax & Gibson, 2015), and the teeth described in cross- and longitudinal sections by Maxwell *et al.*, (2012). It was also observed in several specimens identified as *Ichthyosaurus* spp. and *Protoichthyosaurus* spp. (e.g. Figure 3E) (Vincent *et al.*, 2014; Lomax & Massare, 2018; Lomax *et al.*, 2019).

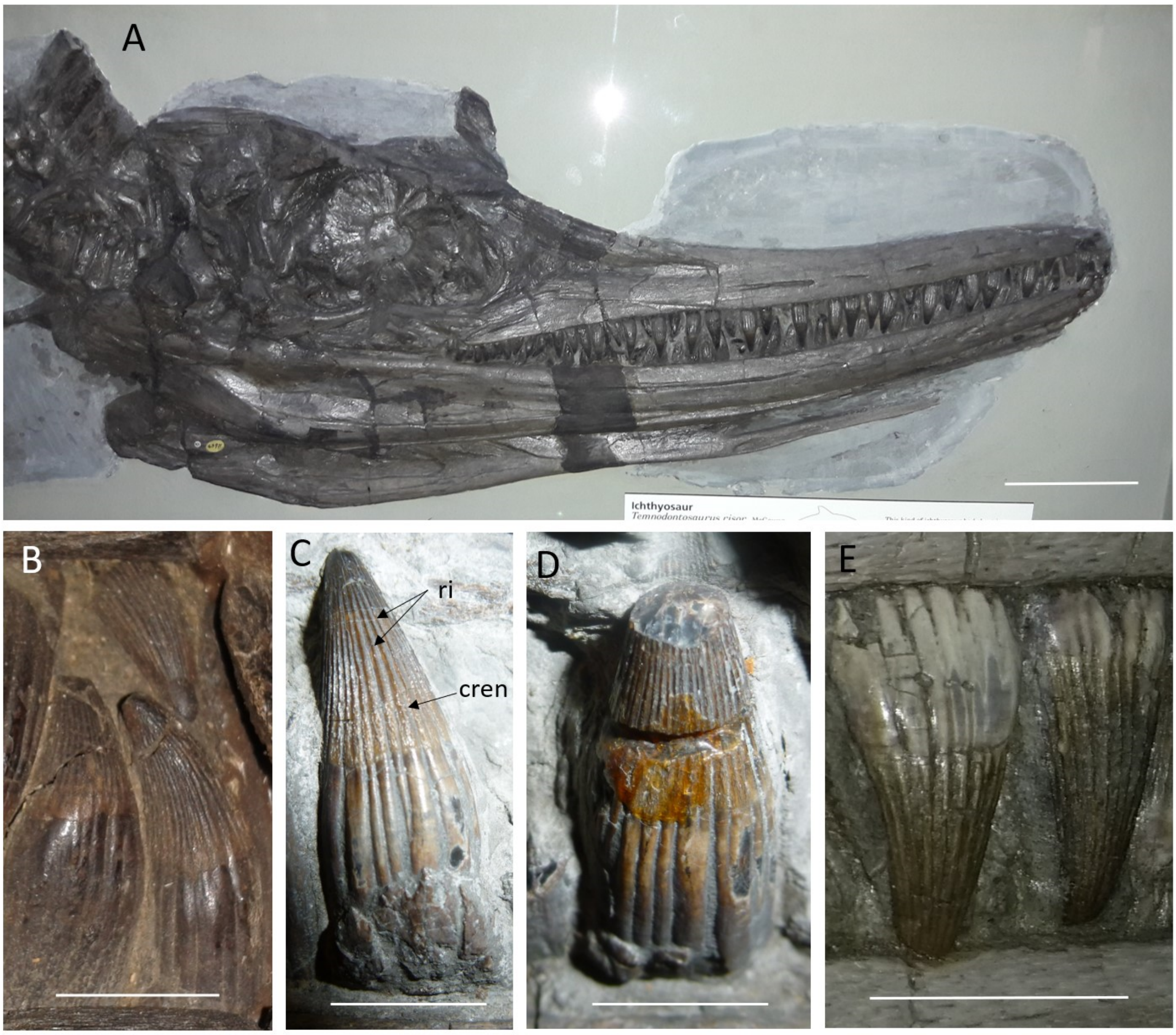

Figure 3. Teeth belonging to morphotype A. A) *'Temnodontosaurus risor'* holotype (NHMUK PV OR42971; skull and mandibles in right lateral view), scale bar = 10cm. B) *'T. risor'* (OUMNH J29171), mid-row tooth from the lower jaw, scale bar = 10mm. C, D) *'T. risor'* (CAMSM J68446), mid-row teeth from the lower jaw, scale bar = 10mm. E) *Protoichthyosaurus applebyi* (NHMUK PV R1164), mid-row teeth from the upper jaw, scale bar = 10mm. Abbreviations: ri = ridges, cren = serration-like crenulations.

Morphotype B

Observed in: *T. platyodon* and *T. eurycephalus*

Under this morphotype we place a number of different tooth morphologies which appear to exist in a continuum on the same jaw (Figure 4). At one extreme is a bicarinate tooth crown which is round in circumference at the base and laterally compressed towards the apex. The crown is 'pinched' at its basal most point, with no noticeable carinae, widening out in diameter apically when the carinae become prominent before tapering to a sharp apex. The carinae have a prominent carinal flange. At the base of the crown are wide, low relief ridges which become fainter towards the apex and continue down onto the root, creating a fluted cross section. The enamel surface of the crown is 'wrinkled' with small discontinuous vertical ridgelets, which change direction and flare towards the carinae across the carinal flange. The apex shows a very slight curvature; we were unable to determine if this is towards the labial or lingual side. Several isolated teeth referred to *T. platyodon* and *T. eurycephalus* show this distinctive morphology, and it can also be observed on teeth from the *T. eurycephalus* holotype (NHMUK PV R1157).

The change in morphology along the tooth row can be determined from a number of specimens preserving a relatively complete dentition (e.g. LYMPH 2013/20, *T. platyodon*) as well as loose teeth from the same individual (IRSNB R122, *T. platyodon*). Mesial-most teeth change the orientation of their carinae: the distal carina moves labially and reduces in prominence, losing its carinal flange. These teeth show a strong lingual curvature. The distal carinae of the mesial-most tooth has reduced to the point where it can only be visible at the apex, and the lingual curvature of the crown is reduced. The ridges, ridgelets, and fluting are similar to the distal teeth. SEM analysis of two teeth from IRSNB R123 (*T. platyodon*; one distal/bicarinate, the other mesial/rounded) shows the ridgelets becoming less dense on the carinal flange but still appearing to form false serrations on the carinal keel. One of these teeth appears to have even smaller cryptic denticles (so named as they can only be seen through SEM imaging (Young *et al.*, 2013b)) – it is unclear whether these are caused by the ridgelets or are true denticles. The apex of SMNS 16666a (*T. platyodon*) also suggests the presence of cryptic true denticles (Supplementary Figure 2).

Due to the incompleteness of some of the material it is difficult to determine the exact point of transition along the tooth row. In the holotype of *T. eurycephalus* (NHMUK PV R1157) the flattened, bicarinate teeth with pinched waist appear to extend along much of the tooth row (Figure 5A), however it is possible that some of the teeth have moved post-mortem (e.g. the disarticulated tooth preserved near the basisphenoid at the back of the mouth; Figure 5Aii). In one specimen of *T. platyodon* (LYMPH 2013/20) the distal bicarinate teeth lack a 'waist' and show a definite change in cross section towards the mesial end of the jaw – from laterally compressed to more rounded. Although it cannot be determined for certain, a number of specimens with an incomplete dentition (such as the *T. platyodon* neotype NHMUK PV OR2003) show features consistent with the mesial teeth. Some specimens with this tooth morphology have crowns which appear to be smooth with less pronounced or absent ridges/ridgelets, and others show less pronounced 'pinching' of the crown base in the bicarinate distal teeth – how this variation corresponds to taxonomy and ontogeny is unknown. The transitional '*T. risor'* specimen could not be examined closely due to logistic constraints. However, the teeth appear to possess carinae and may match this morphotype; they do not display the strong ridges characteristic of morphotype A. Specimens with this dental morphotype show wear patterns including apical spalling (e.g. CAMSM J47052, *T. platyodon*) and carinal wear (e.g. IRSNB R123, *T. platyodon*).

Whilst we do not carry out a review of tooth root morphology in this study, some specimens show interesting variation which is worth discussing. The bicarinate disarticulated teeth of IRSNB R122 (*T. platyodon*) have enlarged, oblong-shaped roots in mesial/distal view which are significantly narrower in lateral view, whereas the mesial recurved teeth have a more cylindrical root shape (Figure 4A). The former root shape is like that of the modern-day killer whale *Orcinus orca*.

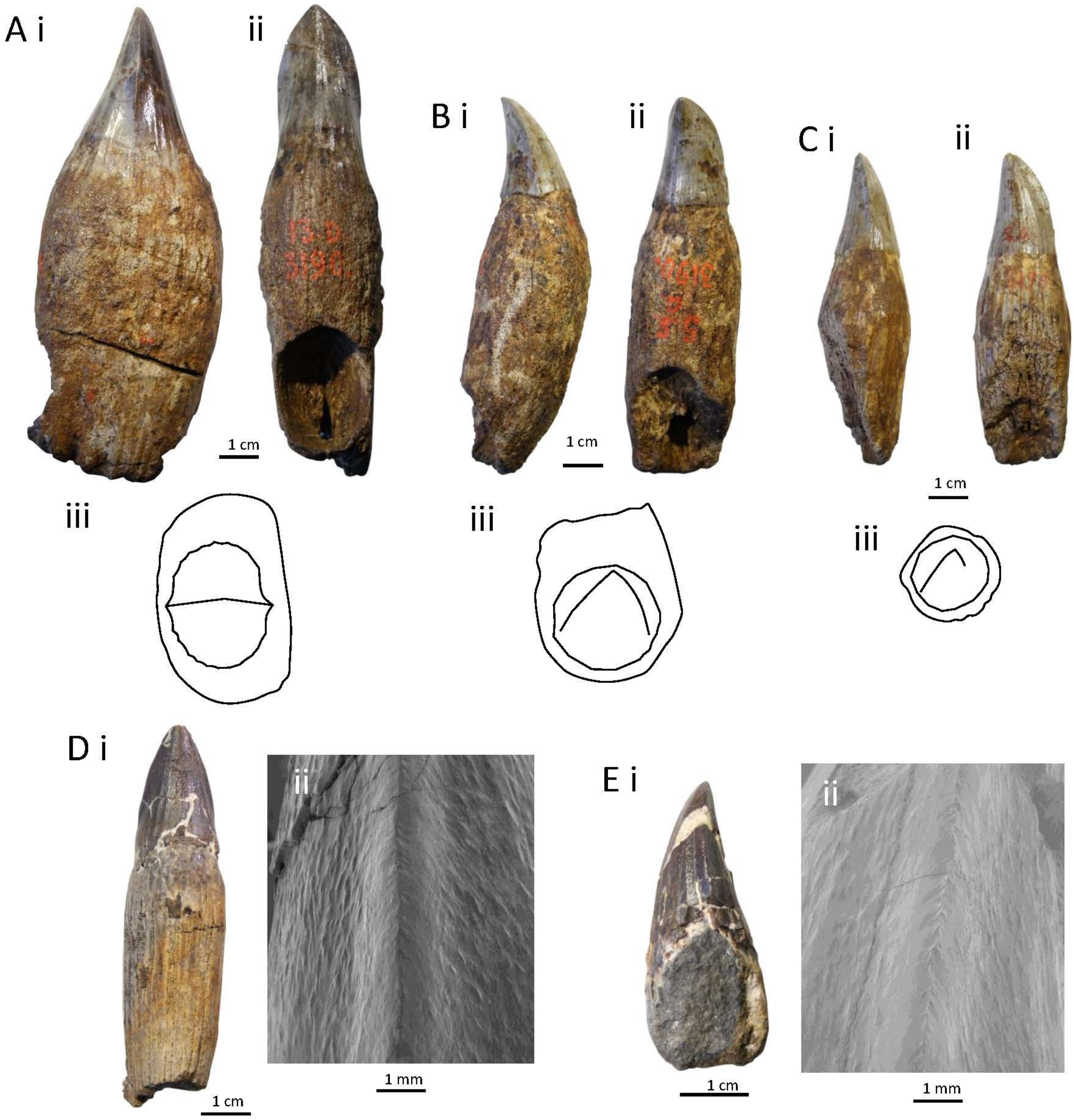

Figure 4. Tooth variation and serrated carinae in *Temnodontosaurus* teeth belonging to morphotype B. A-C) *T. platyodon* (IRSNB R122), selected teeth showing the change from distal to mesial teeth. D-E) *T. platyodon* (IRSNB R123), selected teeth in full and SEM images of the carinal ridges.

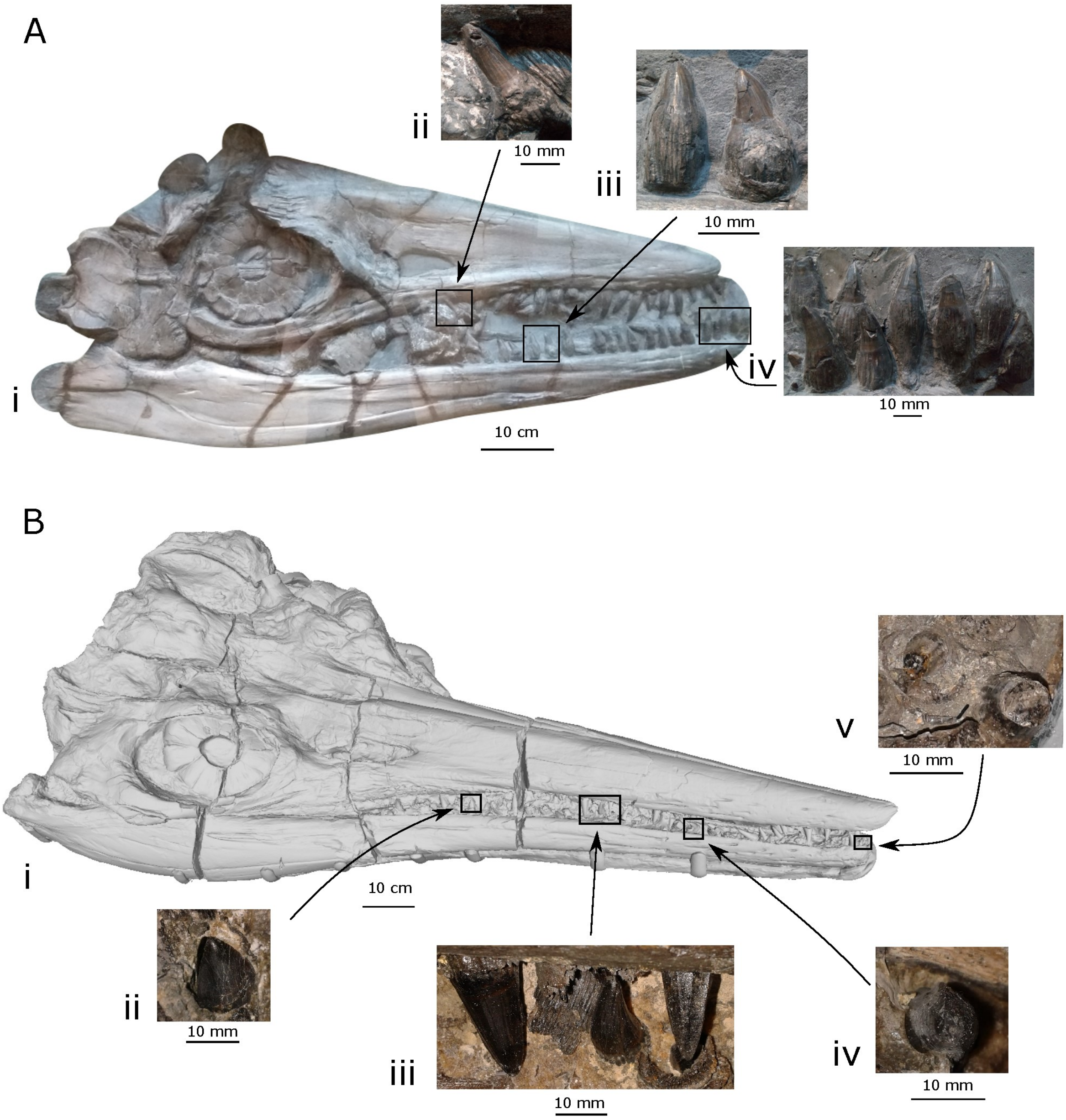

Figure 5. Heterodonty in *Temnodontosaurus* specimens with teeth of morphotype B. A) *T. eurycephalus* holotype (NHMUK PV R1157; skull and right mandible). B) *T. platyodon*, (LYMPH 2013/20; 3D model of skull and mandibles).

Morphotype C

Observed in: *T. nuertingensis*

Teeth of this morphotype have no carinae; the tooth crown has a faceted yet roughly circular cross section with a dense covering of ridgelets creating a ‘wrinkled’ appearance (Figure 6). The best-preserved example of these teeth is the holotype of *T. nuertingensis* (SMNS 13488). Unfortunately, the anterior portion of the snout is missing, preventing a full assessment of variation across the jaw and snout, however the distal-most teeth are smaller with no visible facets. Both tooth rows occluded tightly, with the tooth crowns inclined (Figure 6). The teeth towards the mesial end of the jaw appear to have a slight distal curvature, and one appears to have a wear spall (Figure 6A).

Morphotypes D and E

Observed in: *T. trigonodon*

As many *T. trigonodon* specimens have had the enamel removed during preparation there are few specimens known with a full, pristine dentition. It is possible that the distinction between morphotypes D and E is an artefact of this preservation. We choose to describe them separately but acknowledge that future work may find them to be part of a continuum.

Morphotype D is characterised by a crown enamel surface covered by a series of heavy, usually discontinuous ridgelets, giving the tooth a 'jagged' appearance (Figure 7). Ridges are usually not present – those few observed are thin, with a triangular cross section and low relief. There is at least one carina which exhibits as a sharp change in tooth crown angle with relatively flat surfaces on either side and no carinal flange. This morphotype is visible on the *T. trigonodon* holotype, PKB '1', however the teeth of this specimen are poorly preserved. In SMNS 50006, a broken tooth crown at the mesial end of the dentary suggests these teeth had a circular cross section, however clear carinae are visible on other teeth from the same individual. Several isolated teeth matching this morphotype show false denticles (ridgelets interacting with the carinal keel; Figure 7C, D). SEM imaging of SMNS 80119 shows the interference of the ridgelets with the carinal keel giving the carina a jagged, uneven outline (Figure 7D).

Morphotype E have a slight lingual curvature and are characterised by the presence of numerous straight ridges, continuous towards the apex. These appear to be rounded in cross section and are less dense than those observed in morphotype A but vary in density across the jaw and along the surface of the crown. The teeth GPIT PV 30035 suggest an increase in ridge density lingually, giving this side of the crown a fluted morphology with a faceted morphology on the labial side. This also appears to be the case for the distal teeth of GPIT PV 30038 (Figure 8), however ridges are seen on both sides for mesial teeth. Some of these ridges stand more prominent, forming carinae (Figure 8A). One broken tooth crown on GPIT PV 30035 (*T. trigonodon*) shows a rounded cross section which is not dramatically altered by the presence of the carina. Carinal number and cross section morphology may vary across the jaw, however better-preserved specimens with teeth completely free from matrix would be needed to confirm this. Ridgelets are present in this morphotype but are sparser than morphotype D and can only be discerned on the less heavily ridged surfaces of the teeth.

Figure 6. Teeth of morphotype C, as seen on SMNS 13488 (*Temnodontosaurus nuertingensis* holotype). A) Mesial left dentition, showing enamel wrinkles and wear spall. B) Mesial right dentition, showing rounded cross section with no carinae. C) Distal upper left dentition. Scale bars all 10mm.

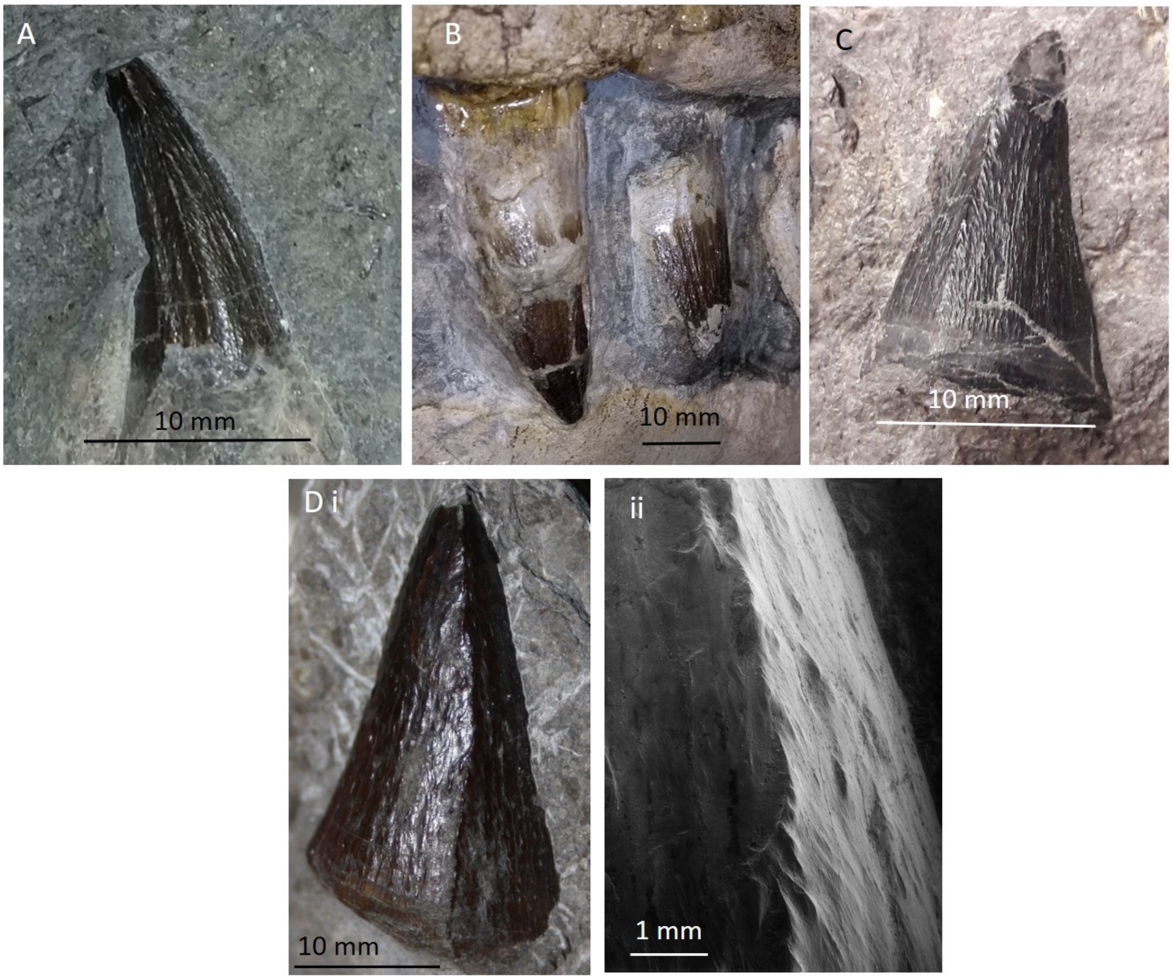

Figure 7. *Temnodontosaurus* teeth belonging to morphotype D. A) *T. trigonodon* (SMNS 50006). B) *T. trigonodon* (PKB '1') (photograph taken on angle so scale bar is approximate). C) *T. trigonodon* (SMNS 56304). D) *T. trigonodon* (SMNS 80119), whole tooth, and close-up of the carina using SEM.

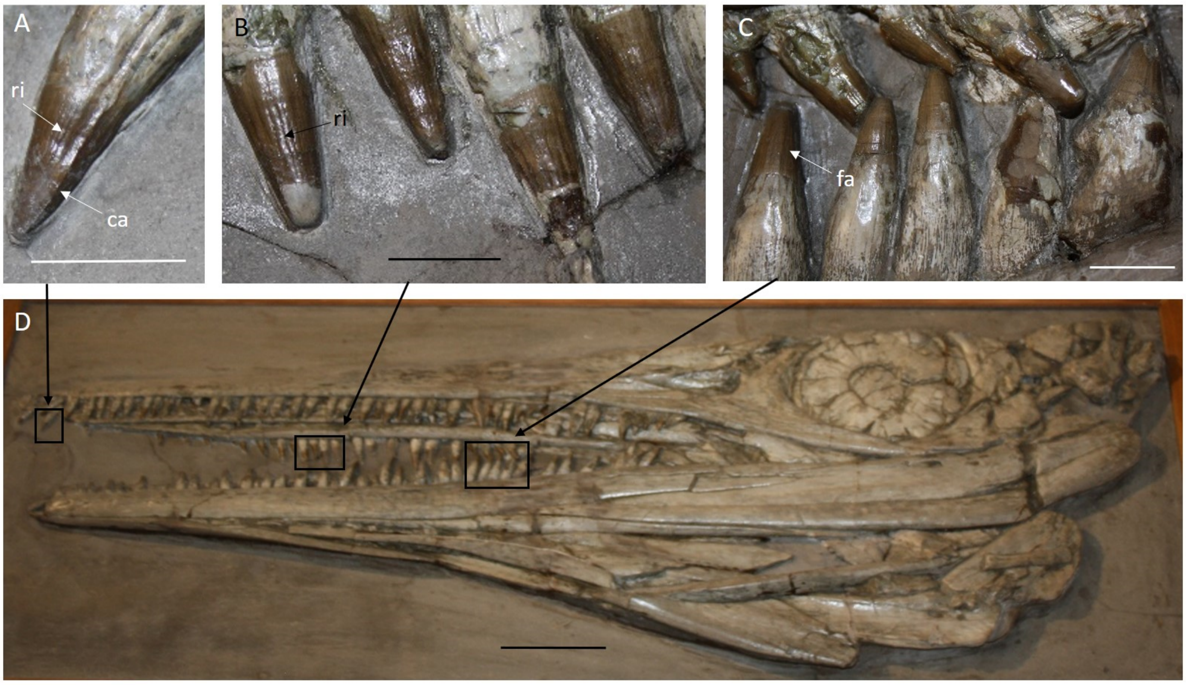

Figure 8. Variation in dental morphotype E as shown in GPIT PV 30038 (*Temnodontosaurus trigonodon*; skull in left lateral view). A) Upper ?right mesial tooth in lingual view, scale bar 10mm. B) Upper right mid-row teeth in lingual view, scale bar 10mm. C) Lower left mid-distal teeth in labial view, scale bar 10mm. D) Whole skull, scale bar approx. 10cm (photograph taken on angle). Abbreviations: ca – carina, fa – facet, ri - ridge.

Analytical results

Higher values on the first axis of the craniodental morphospace are associated with narrower snouts and mandibles, longer symphyses, and smaller anterior mechanical advantage, whereas higher values on the second axis are associated with longer snouts and larger teeth (Figure 9, for specimen numbers see Supplementary Figure 3). Based on these results, we interpret the specimens with high values on axis 1 to be the least adapted to megapredatory niches. *Temnodontosaurus trigonodon* is spread across the morphospace; most specimens form a cluster near the centre of the morphospace with three outlying groups surrounding them. The first of these outliers is the holotype PKB 1. The dentigerous overbite on this specimen is the largest of any specimen of *Temnodontosaurus* in our sample, however it is possibly pathological. The overbite dental groove shows bone growth around the overbite teeth imitating individualised tooth alveoli (pseudoalveoli) (Supplementary Figure 4). The second outlying group with high values on both axes are two specimens (SMNS 4996-1 and 7762) which were formerly identified as *'T. acutirostris'* (now *species inquirenda* (Maisch, 2010; Laboury *et al.*, 2022)). These have long narrow snouts and weaker anterior mechanical advantage. The final grouping of *T. trigonodon* consists of two smaller specimens with shorter snouts which occupy a similar area of morphospace to the former '*T. risor*'. One of these specimens (GPIT PV 30038) shows pseudoalveoli similar to those on the holotype of *T. trigonodon* (Supplementary Figure 4). The holotype and only specimen of *T. eurycephalus* is distinct from other *Temnodontosaurus*, having a short, deep snout, large anterior mechanical advantage, and relatively small teeth. Our sampled specimens of *T. platyodon* do not cluster together; the difference between these specimens appears to be driven by tooth size.

Our morphospace does not recover a clear distinction between tooth morphotypes (Figure 9), however tooth size appears to be an important factor despite not significantly correlating with any other craniodental feature (e.g. relative snout length; Figure 9, Supplementary Figure 5). When tooth shape and tooth crown height are plotted against each other, teeth belonging to morphotype B were found to be generally larger and squatter (Figure 10). Morphotype A teeth, on the other hand, are smaller and occupy more mid-range values of tooth shape. Morphotypes D and E were spread across the graph. Morphotype C may be linked with a higher tooth shape value (taller, narrower crowns); however, we acknowledge that our sample size is small for some morphotypes. The absence of large yet elongated tooth crowns is a feature seen across all marine amniotes (see also Fischer *et al.*, 2022a).

Although not present in enough specimens to be included in the morphospace dataset, we also calculated the extent of the splenial along the symphysis. This varies dramatically in specimens attributed to *T. trigonodon*: from 91% in PKB 1 to an estimated 10% in SMNS 7762. Whilst not able to be measured directly for this study, we estimated the splenial to cover ~73% of the symphysis in NHMUK PV R1158 (*T. platyodon*) and ~27% in OUMNH J48050 (a pair of mandibles identified as *T. platyodon* yet with teeth belonging to morphotype A) (Supplementary Figure 6).

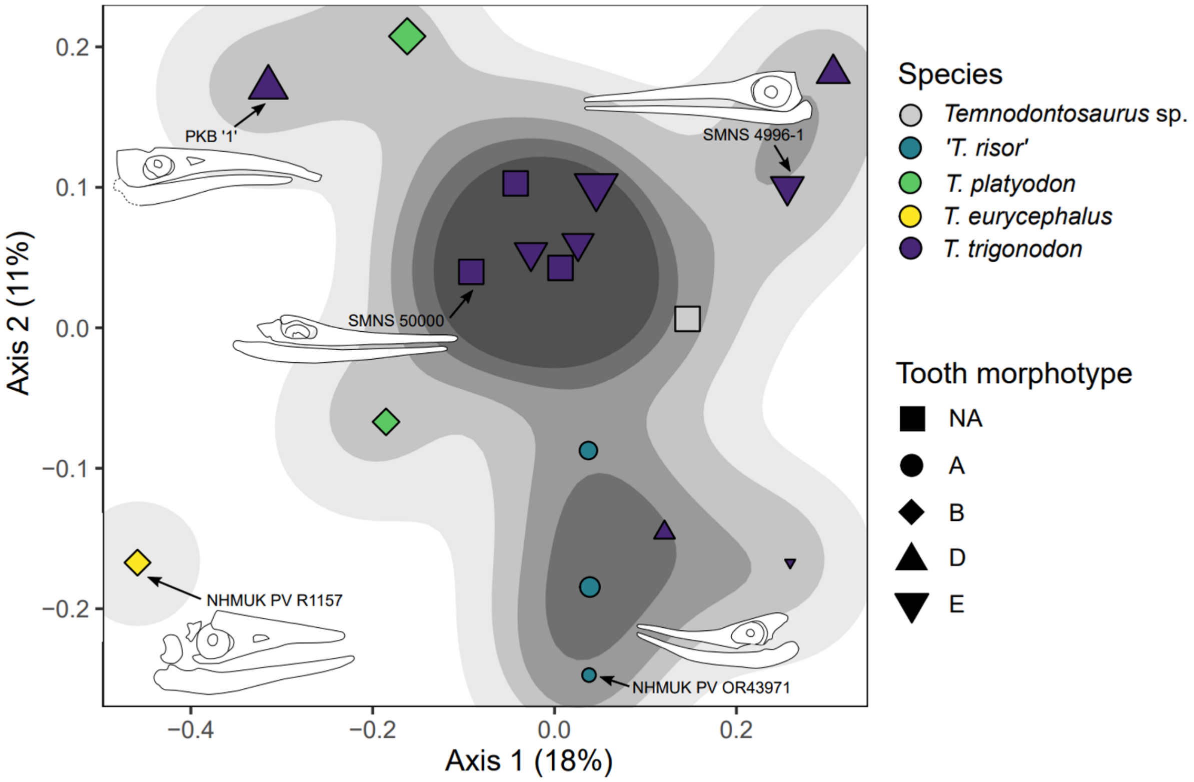

Figure 9. PCoA morphospace using the full *Temnodontosaurus* craniodental dataset. Specimens with a tooth size or morphotype of 'NA' had a dentition that was too damaged to obtain an accurate assessment. Point sizes scaled with tooth size. Contours represent density of specimens on morphospace. Skull outlines drawn from 3D models.

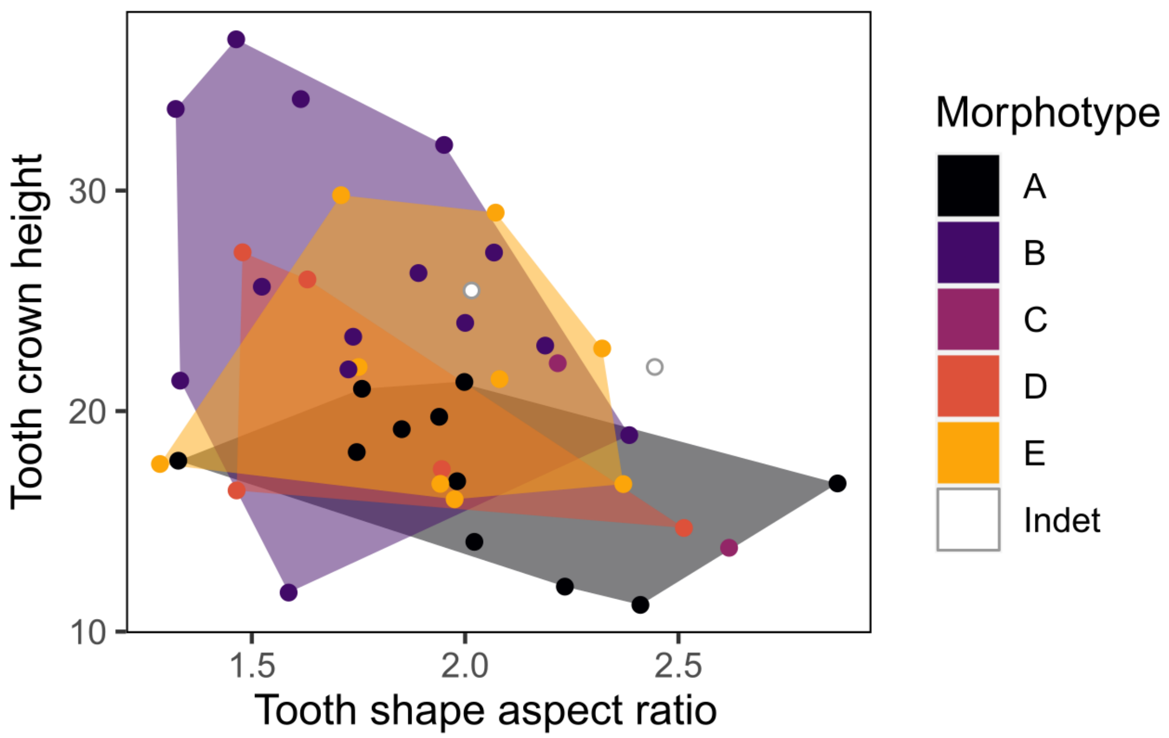

Figure 10. Biplot of tooth crown height versus tooth shape aspect ratio in *Temnodontosaurus.*

Discussion

Taxonomic considerations

An increasing number of studies are finding that *Temnodontosaurus* is not monophyletic (e.g. Laboury *et al.*, 2022). Whilst not a phylogenetic analysis, our observations and results may offer some insight for future work. The holotype of *T. platyodon* was an isolated tooth, now lost, with the distinctive morphology we describe in morphotype B (Godefroit, 1993). It is our conclusion that many *T. platyodon* specimens do have these distinctive teeth, however this has been overlooked due to poor preservation and possible heterodonty. The neotype of *T. platyodon* (NHMUK PV OR2003) does not have well preserved teeth (McGowan, 1974), however this morphotype can be clearly seen in the holotype of *T. eurycephalus* (NHMUK PV R1157) (McGowan, 1994). The phenotypic similarity of the teeth of these two species has been noted before (Godefroit, 1993; Hungerbühler & Sachs, 1996). We do however find that *T. eurycephalus* has a unique skull morphology within the genus (characterised in particular by its short, deep rostrum, unlike the longer rostrum usually found in *T. platyodon*).

A further taxonomic issue is created by the inclusion of '*T. risor'* specimens as juveniles of *T. platyodon*. We found no teeth with a transitional morphology between morphotypes A and B and both McGowan's description and our observations of the privately owned 'intermediary' specimen suggest it matches morphotype B. McGowan (1994) indicated that if more matrix were to be removed from the three former '*T. risor'* specimens then teeth with the classic morphology would be revealed. We disagree, as teeth across the jaw in all three are visible and all are heavily ridged. Teeth of a similar nature have been recorded in *Protoichthyosaurus* (Lomax & Massare, 2018; Lomax *et al.*, 2019). One of the three original specimens of '*T. risor'*, NHMUK PV R311, was erroneously cited as NHMUK PV R331 in the study referring the species to *T. platyodon* (McGowan, 1994); we believe this has added to the confusion, especially as NHMUK PV R311 has a number of features characteristic of *Ichthyosaurus* and is labelled as such on display. We propose that future studies investigate the status of '*T. risor'* in more detail using a modern, apomorphy-based taxonomic scheme.

The holotype of *T. trigonodon* (PKB 1) is morphologically distinct from other specimens currently referred to that species. This may be influenced by its (likely pathological) overbite, however other features (e.g. large splenial contribution to the symphysis (this study), ventral extent of the lacrimal (Maisch 1998)) suggest it may be a different species. Our analyses recover a wide variation in tooth morphology within the entity *T. trigonodon*. A detailed specimen-based osteological reappraisal of specimens, including specimens previously assigned to *'T. burgundiae'* and '*T. acutirostris*', would better diagnose the species.

Carinal serration morphologies in marine amniotes

Serrated carinae in *Temnodontosaurus* have been mentioned in the literature before (Chiarenza *et al.*, 2015), but this study is the first to describe and figure them in detail. Most of the serrations seen on *Temnodontosaurus* teeth are composed of false denticles created by the interaction of the enamel ornament (a series of anastomosing ridgelets) with the carinal keel, although we also noted the presence of cryptic true denticles (sensu Young *et al.*, 2013b) in isolated teeth of *T. platyodon* and *T. trigonodon* which were only visible with the use of SEM. Serrations have not previously been observed on the teeth of Triassic carinate ichthyosaurs, although the carinae do not appear to have been examined with an SEM. *Thalattoarchon* shows tooth crowns with smooth enamel, whereas *Himalayasaurus* and *Shonisaurus* have ridges (Camp, 1980; Motani *et al.*, 1999; Fröbisch *et al.*, 2013; Kelley *et al.*, 2022). The undulating ridges of morphotype A ('*T. risor*') show a serration-like effect similar to that seen in some species of the thalattosuchian *Machimosaurus* (Young *et al.*, 2014).

It is thought that serrated teeth are more efficient at cutting as they increase friction and grip (e.g. Frazzetta, 1988; Andrade *et al.*, 2010; Young *et al.*, 2014). As they are formed by the interaction of ridgelets with the carinal keel, false serrations are typically of uneven length and lack dentine cores (Street *et al.*, 2021). True denticles, on the other hand, have been shown to extend further inside the tooth, giving them greater strength (Brink *et al.*, 2015). With the exception of cryptic denticles (which do not create a visible serrated edge; Young *et al.*, 2013a), the co-occurrence of other denticle types on the same tooth are thought to indicate a generalist predatory diet (Young *et al.*, 2014). Indeed, the ridgelets that create false denticles have themselves been correlated with both enamel thickness (e.g. Street *et al.*, 2021) and enamel microstructure complexity (e.g. Loch *et al.*, 2013; Werth *et al.*, 2020), suggesting adaptation towards consumption of harder prey.

A range of serration types have been observed in secondarily aquatic reptiles (Table 3). Cetaceans have their own series of unique serration morphologies. Carinate teeth are only present in the earliest lineages of fully aquatic cetaceans (basilosaurids and early neocetes). These teeth have a series of plesiomorphic, relatively large accessory denticles on their cheek teeth which may have served a similar function to serrations (Hocking *et al.*, 2017a). Several early heterodont odontocetes have been observed to have true denticles in addition to these accessory denticles (Kellogg, 1923a; Vélez-Juarbe, 2017; Boessenecker *et al.*, 2020). These odontocetes are known for their rugose tooth enamel ornament and cusp-like structures at the base of the crown, called cristae rugosae (Kellogg, 1923b; Loch *et al.*, 2015). Some of these anastomosing, low relief ridges bulge outwards and form a similar structure to the pseudodenticles described in metriorhynchids (Young *et al.*, 2014). The ridges and ridgelets fade and disappear as they approach the carinal keel and do not form false denticles as in marine reptiles. These heterodont odontocete teeth therefore have three types of serration-like morphology occurring on the same tooth: plesiomorphic accessory denticles, pseudodenticled cristae rugosae, and true serrations. A serration-like structure has also been recorded in the early toothed mysticete *Coronodon* – as this occurs on the carinal keel rather than the enamel ridges it cannot be described as a pseudodenticle (contra Boessenecker *et al.* 2023) and may be best defined as a crenulation.

Carinal morphology and heterodonty

Temnodontosaurus is the only post-Triassic ichthyosaurian to have carinate teeth, however our study suggests that two kinds of carinae are present. The first, seen in *T. platyodon/T. eurycephalus* (morphotype B) as well as some specimens of *T. trigonodon* (morphotype D) is formed by a marked angular change in the cross section of the tooth crown, whereas the second carinal type, seen in other specimens of *T. trigonodon* (morphotype E), is formed by a prominent enamel ridge protruding from an otherwise relatively circular cross section. Variation in carinal angle and prominence across the jaw in *T. platyodon* has been noted before but never fully investigated (Berckhemer, 1938; Hungerbühler & Sachs, 1996). A similar form of heterodonty has also been suggested for '*T. burgundiae*' (Huene, 1931), however we were unable to confirm this in the (now) *T. trigonodon* specimens seen as part of this study. This heterodont trend of compressed distal teeth and more circular mesial teeth has been observed in other marine tetrapods, such as fully aquatic cetaceans (Pelagiceti) where it is the plesiomorphic state found in basilosaurids and early neocetes, before being lost later in both the mysticete and odontocete lineages (Uhen, 2004; Peredo & Pyenson, 2018). In mosasaurs this heterodonty is also associated with a shift in the angle between the carinae (Schulp *et al.*, 2004). In taxa with this style of heterodonty it has been proposed that the mesial teeth were used to grasp prey and the distal teeth used predominantly for processing (Schulp *et al.*, 2004; Uhen, 2004; Lambert *et al.*, 2017a). Taking into account the position from the jaw hinge, the mesial-most tooth will experience the least pressure whereas the distal-most tooth will experience the most (D'Amore, 2009). The mesial pseudoalveoli seen in the premaxillae of two specimens of *T. trigonodon* (as well as an incomplete Late Jurassic ophthalmosaurid; Serafini *et al.,* 2023) may show bone growth as an adaptation to the high lateral/labial forces of prey capture in this region, possibly similar in nature to that of the physeteroid cetacean *Acrophyseter* (Lambert *et al.*, 2014).

Morphotype E shows a different type of carinal variation within *Temnodontosaurus*: the density of ridges fluctuates across individual tooth crowns and possibly also across the jaw. Our observations suggest that ridge density is often higher on the lingual, slightly recurved side of the tooth crown, a feature also noted in plesiosaurians (Sassoon *et al.*, 2015; Zverkov *et al.*, 2018). The presence of these ridges on the recurved edge has been theorised to be linked to prey puncture mechanics (as this is the side of the tooth in use) as well as reinforcement to biting stresses (McCurry *et al.*, 2019). Whilst not heterodont per se, blunter distal teeth with distally directed curvature are a common feature in ichthyosaurians. These may have acted as a ratchet, directing prey towards the gullet (e.g. Taylor, 1987; Taylor & Cruickshank, 1993).

The multiple niches of *Temnodontosaurus*

Despite seemingly never again achieving the levels of disparity seen in Triassic assemblages, Early Jurassic ichthyosaurians still generated morphological variation and radiated into a range of ecological niches. High rates of evolution have been found in *Temnodontosaurus* and other basal neoichthyosaurians (e.g. leptonectids), yet not in thunnosaurians (Moon & Stubbs, 2020). Our results show a range of craniodental ecomorphologies within *Temnodontosaurus*, many of which appear adapted for capturing and feeding on larger prey. As there is less space at higher trophic levels for ecological coexistence, these differences may have been an important factor in niche partitioning between coeval species of the genus. *Temnodontosaurus eurycephalus* shows several adaptations for a megapredatory diet, including a short, high vaulted 'oreinirostral' snout – a morphology shown to be resistant to bending and twisting (McHenry *et al.*, 2006) – coupled with a dentition adapted for increased cutting efficiency (laterally compressed bicarinate teeth). These are traits which are shared with a number of other megapredators (e.g. the Jurassic-Cretaceous metriorhynchid *Dakosaurus* and the extant odontocete *Orcinus orca*) which are adapted to ripping off large chunks of flesh using 'grip-and-tear' feeding (Peri *et al.*, 2021). The distinctive 'waisted' crown of *T. eurycephalus* (and some *T. platyodon*) may have created a gap which may have functioned in a similar way to the notch in shark teeth – assisting with clearance of prey tissue (Frazzetta, 1988) or concentrating stress (Whitenack *et al.*, 2011).

Temnodontosaurus platyodon and most specimens currently referred to as *T. trigonodon* are interpreted as latirostrine predators with varying levels of larger prey in their diet (reflected by the variation in scores along the first axis of the PCoA yet systematically high values on the second). It is possible that the reduced resistance to stress and torsion in this slightly more elongate skull shape is offset by greater hydrodynamic efficiency (McHenry *et al.*, 2006; McCurry *et al.*, 2017b). We interpret these predators as having a more generalist ecology, as slightly longer snouts may also be useful for capturing smaller, fast prey. Yet, these specimens still have large teeth with heavy enamel ornamentation and carinae (sometimes serrated), and thus could likely consume larger prey. A latirostrine snout morphology has been correlated with an increase in optimum gape (Young *et al.*, 2012a) and could also be linked with heterodonty as it would allow specialisation of the teeth along the tooth row for different functions (Lambert *et al.*, 2017b; Boessenecker *et al.*, 2020; Cortés *et al.*, 2021; Peri *et al.*, 2021). The use of the mesial teeth for prey capture and distal teeth for processing has been described as 'grip-and-shear' feeding (Peri *et al.*, 2021). Longer symphyses have been shown to experience more strain during biting (Walmsley *et al.*, 2013; McCurry *et al.*, 2017a) – this may be offset in longer snouted predators by increased buttressing of the symphysis (Cortés *et al.*, 2021). In some specimens of *Temnodontosaurus* as well as some Cretaceous ichthyosaurians (e.g. *Kyhytysuka* (Cortés *et al.*, 2021) and *Pervushovisaurus* spp. (Fischer, 2016)) this is achieved by increasing the contribution of the splenial to the symphysis.

The final grouping consists of specimens previously attributed to '*T. risor*' which have a noted dorsal deflection of the snout (McGowan, 1974), and robust, heavily ridged (but not carinate) teeth with crenulated ridges and deep roots. Strongly ridged tooth crowns are known from other non-carinate ichthyosaurians with an inferred megapredatory ecology including *Pervushovisaurus* (Fischer, 2016) and *Guizhouichthyosaurus* (Jiang *et al.*, 2020). The dorsal deflection of the snout has been rarely observed in other specimens of *Temnodontosaurus* (e.g. the *T. burgundiae* holotype: Gaudry, 1892), yet a similar morphology has been reported in the coeval *Protoichthyosaurus* spp. (e.g. Lomax *et al.*, 2019) and the Late Jurassic ophthalmosaurid *Cryopterygius kristiansenae* (Druckenmiller *et al.*, 2012). It is possible that this morphology is the result of plastic taphonomic distortion (e.g. Lomax *et al.*, 2019) which would explain the varying levels of snout deflection among different specimens. However, a dorsally concave mandible and snout have been observed in other marine tetrapods (e.g. Boessenecker *et al.* 2023) and have been linked with adaptations to a diet of larger prey, such as in the 'macroraptorial' physeteroid cetacean *Acrophyseter* which also shares with '*T. risor*' robust teeth with enlarged roots (Lambert *et al.,* 2017c). Recent studies on theropod dinosaurians and placoderms have suggested that dorsal deflection of the mandible may be an adaptation for reducing stress/strain and creating a tighter grip on prey (e.g. Coatham *et al.*, 2020; Ma *et al.*, 2022). Together with the heavily ridged teeth, this snout morphology suggests increased efficiency for higher bite forces and grip in these ichthyosaurians.

Some specimens of *Temnodontosaurus* included in our analysis appear less adapted for a megapredatory lifestyle, with more longirostrine snouts and weaker mandibular musculature. Not included in the numerical analyses here were *T. nuertingensis* (which lacks carinate teeth), and *T. azerguensis* (which is longirostrine and possibly edentulous; Martin *et al.*, 2012). This craniodental variation likely allowed niche partitioning between coeval taxa – both between different species of *Temnodontosaurus* as well as with other large bodied Early Jurassic ichthyosaurians (e.g. *Leptonectes solei*; McGowan, 1993). Unfortunately, records of preserved stomach contents in *Temnodontosaurus* are rare, only providing a very limited set of direct evidence for predator-prey interactions; we only found examples of a dense mass of cephalopod hooklets in *T. platyodon* and *T. trigonodon* (Supplementary Table 2), in addition to digested remains of a smaller ichthyosaurian (Böttcher 1989). The basisphenoid preserved in the jaws of the *T. eurycephalus* holotype is likely its own.

As the odontocete cetacean *Orcinus orca* is the only modern marine tetrapod megapredator it is often proposed as an ecological analogue to extinct taxa, including those with both brevirostrine and latirostrine snouts (e.g. Young *et al.*, 2012a; Fanti *et al.*, 2014; Boessenecker *et al.*, 2020; Longrich *et al.*, 2022). We make the comparison between *O. orca* and *T. eurycephalus* with caution and acknowledge that the former is a very specialised predator with high intelligence, social structure, and associated feeding strategies which are known to vary between populations (e.g. Lopez & Lopez, 1985; Pitman & Durban, 2012; Ford, 2018) – all of which are difficult or impossible to infer for extinct taxa, especially non-mammalians. As is the case for most extant odontocetes, *O. orca* is thought to use some level of suction feeding in prey capture (Werth, 2006). The evidence for the use of suction feeding in *Temnodontosaurus* and other ichthyosaurians is not convincing (Motani *et al.*, 2013). Furthermore, *O. orca* has a varied diet – different populations are known to specialise in different prey types, including other marine tetrapods as well as smaller fish (e.g. de Bruyn *et al.*, 2013).

Our results, considered alongside studies on other marine tetrapod clades, suggest that there is no one megapredator morphotype (e.g. Young *et al.*, 2012a; Peri *et al.*, 2021). Skulls of megapredators usually show increased size alongside adaptations for transmitting and withstanding large bite forces, however these must be balanced against hydrodynamic constraints which favour long and narrow skulls (Taylor, 1987). The teeth of marine megapredators must fulfil several functions: (1) to bite and wound the prey, (2) to grip the prey, either while it is struggling or while it is being consumed post-mortem, and (3) to tear off pieces of flesh. The ichthyosaurian *Temnodontosaurus* demonstrates a range of morphological configurations, some likely permitting increased grip, some likely allowing infliction of more severe wounds and tearing off flesh. This variation reflects the broad, opportunistic nature of the marine megapredatory niche and the selection pressures it places on marine tetrapod crania and dentition (e.g. Massare, 1987; MacLeod *et al.*, 2006; Fischer *et al.*, 2022a). Whilst some of these ecomorphological adaptations are shared with other marine tetrapod megapredators, others are not. Serrations are a known way to increase the efficiency of carinae (e.g. Frazzetta, 1988), yet vary in occurrence and structure between different groups of secondarily aquatic tetrapods. The influence of phylogenetic heritage is particularly clear in cetaceans who possess dental structures such as accessory denticles and cristae rugosae which at least partly derive from the multi-cusped teeth of their terrestrial ancestors. The ability to evolve carinate dentition appears to be lost in both ichthyosaurians and odontocetes at certain points in their evolution. Later megapredatory ichthyosaurians developed heavily ornamented teeth and a heterodont dentition (e.g. Fischer, 2016; Cortés *et al.*, 2021), whereas most megapredatory odontocetes retain a simple dentition (e.g. Lambert *et al.*, 2010, 2017c). Convergence between megapredatory ichthyosaurians and cetaceans is therefore not only limited by intrinsic phylogenetic constraints inherited from terrestrial ancestors, but also contingent on the previous evolutionary history of each clade within the marine realm.

Conclusions

The large Early Jurassic ichthyosaurian *Temnodontosaurus* shows a wide range of tooth and skull morphologies. We divide tooth morphology into five morphotypes, corresponding to certain species. This includes the first examples of a serrated dentition in ichthyosaurians (in *T. platyodon* and *T. trigonodon*), with false denticles created by the interaction of ridgelets with the carina.

Our craniodental morphospace analysis found three main groupings within *Temnodontosaurus*. *Temnodontosaurus eurycephalus* has a brevirostrine, oreinorostral snout and bicarinate teeth well suited for strong bite forces and wound infliction, whereas *T. platyodon* has a more elongate latirostrine skull and may have been adapted for feeding at wider gapes. There is evidence for heterodonty in both species, with a change from distal bicarinate teeth to mesial teeth with a rounder cross section and reduced/absent carinae. *Temnodontosaurus trigonodon* shows considerable variation in skull morphology with many specimens sharing the latirostrine ecomorphology of *T. platyodon*, whilst others show features suggesting they were less well-adapted to a megapredatory niche. Specimens formerly assigned to '*T. risor*' possess heavily ridged teeth which we interpret as adaptations for increased bite force and grip. The evidence placing these specimens as juvenile *T. platyodon* is weak, and we suggest that the species is revisited in future work. Our results suggest that the species currently grouped together under *Temnodontosaurus* colonised a range of ecological niches within Early Jurassic ecosystems, with different craniodental features allowing prey to be captured and processed in different ways.

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Data availability statement

The data and 3D models that support the findings of this study are openly available in [figshare repository to be added after acceptance].

Author contributions

Conceptualisation and design of study: RFB and VF. Data collection: RFB and EEM. Data analysis: RFB and VF. Writing: RFB with contributions from all authors.

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Table 1. Summary of *Temnodontosaurus* species currently considered valid in the literature.

Species	Age	Localities	Key references
T. platyodon	Hettangian-Sinemurian	UK (Dorset, Nottinghamshire, Warwickshire), Belgium, Germany (Baden-Württemberg)	(Godefroit, 1993; Lomax & Gibson, 2015)
T. eurycephalus	Sinemurian	UK (Dorset)	(McGowan, 1974)
T. nuertingensis	Pliensbachian	Germany (Baden-Württemberg)	(Maisch & Hungerbuhler, 1997; Pardo-Pérez *et al.,* 2018)
T. trigonodon	Toarcian	Germany (Baden-Württemberg, Bavaria), France (Yonne) ?UK (Yorkshire)	(Pardo-Pérez *et al.,* 2018; Lomax, 2019; Laboury *et al.*, 2022)
T. azerguensis	Toarcian	France (Beaujolais)	(Martin *et al.*, 2012)
T. zetlandicus	Toarcian	UK (Yorkshire), Luxembourg	(Laboury *et al.*, 2022)
T. crassimanus	Toarcian	UK (Yorkshire)	(Swaby & Lomax, 2021)

Table 2. Functional traits used in ordination analyses and their calculations.

Ratio	Calculation	Justification
Tooth shape aspect ratio	Tooth crown height / crown base diameter. Largest tooth chosen, both measurements from same tooth	Proxy for resistance to bite forces in tooth crown (Massare, 1987)
Absolute tooth crown size	Raw tooth crown height	Correlates with prey size in cetaceans (Ridgeway & Harrison, 1999) and with gut content in fossil marine amniotes (Fischer *et al.*, 2022a)
Relative snout depth	Snout depth at midpoint / snout length	Indication of reinforcement against high bite forces (Fischer *et al.*, 2016; Bennion *et al.*, 2022)
Relative snout length	Snout length (tip to orbit) / skull length	Related to the hydrodynamics of the snout during prey capture (Bennion *et al.*, 2022; MacLaren *et al.*, 2022)
Relative temporal musculature	Temporal fenestra length / skull length	Proxy for bite force and jaw musculature cross sectional area (Bennion *et al.*, 2022)
Anterior mechanical advantage	Distance between mandible articulation and tip of coronoid (preglenoid) process (jaw adductor inlever) / mandible outlever length (articulation to tip)	Proxy for bite force – high values indicate slow and forceful bites (Anderson *et al.*, 2011; Stubbs & Benton, 2016; MacLaren *et al.*, 2022)
Relative symphysis length	Symphysis length / mandible outlever length	Proxy for resistance to stress during biting (Walmsley *et al.*, 2013; Stubbs & Benton, 2016)
Functional mandible robusticity	Depth of mandible at the midpoint of the tooth row / mandible outlever length	Proxy for bending resistance (MacLaren *et al.*, 2022)
Relative overbite length	Overbite length / snout length	May aid in prey capture or sensing (Fischer, 2016)
Relative orbit size	Orbit diameter / skull length	Proxy for importance of orbit in feeding (MacLaren *et al.*, 2022)

Table 3. Tooth serration types recorded so far in secondarily aquatic tetrapods (not necessarily on the same tooth)

Clade	Denticle types	Source
Ichthyosauria	Cryptic ?true, false, crenulated ridges	This study
Mosasauridae	True, false, pseudo	(e.g. Palci *et al.*, 2014; Bardet *et al.*, 2015; Street *et al.*, 2021)
Thalattosuchia	True (including cryptic), false, pseudo, crenulated ridges	(e.g. Young *et al.*, 2013b, 2014)
Cetacea	True, accessory, pseudo (cristae rugosae)	(e.g. Kellogg, 1923a; Vélez-Juarbe, 2017; Boessenecker *et al.*, 2020)
Pliosauridae	False, ?true, crenulated ridges	(Fischer *et al.*, 2015; Zverkov *et al.*, 2018)