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Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart
3. First chimaeroid from the Lias of Baden-Württemberg (Early Toarcian of Ohmden)

By Christopher J. Duffin, Sutton/England

With 5 figures

Abstract

The left upper ("palatine") toothplate of a new chimaeroid from the *exaratum* Subzone of the Posidonienschiefer (Early Toarcian, Early Jurassic) is described as *Bathytheristes gracilis* n. g. n. sp. The toothplate shows *Callorhynchus*-type tooth conformation, the primitive condition for chimaeroids, with well defined descending laminae. There is a single symphyseal laminated tritor on the occlusal surface of the plate. *Bathytheristes* is the first member of the Chimaeroidei to be described from the Toarcian, and the first chimaeroid recorded from the Posidonienschiefer.

Zusammenfassung

Aus der *exaratum*-Subzone des Posidonienschiefers (Untertoarcium, Unterjura) wird eine linke obere („palatine") Zahnplatte einer Chimäre als *Bathytheristes gracilis* n. g. n. sp. beschrieben. Die Zahnplatte zeigt eine *Callorhynchus*-artige Ausbildung mit deutlichen, abwärts gerichteten Laminae, die ursprüngliche Ausbildung der Chimären-Zahnplatten. Auf der okklusalen Oberfläche der Platte ist nur eine einzige laminierte Reibefläche nahe der Symphyse ausgebildet. *Bathytheristes* ist der erste Nachweis der Chimaeroidei aus dem Toarcium.

Résumé

La plaque dentaire supérieur gauche („palatine") d'une nouvelle chiméroïde, *Bathytheristes gracilis* n. g. n. sp. provenant de la sous-zone à *exaratum* du Posidonienschiefer (Toarcien inférieur, Jurassique inférieur) est décrite. La plaque dentaire montre une structure du type *Callorhynchus*, représentant le stade primitif chez les chiméroïdes, avec des lames descendantes bien definies. La face occlusale de la plaque dentaire ne présente qu'une seule zone triturante lamellaire, en position symphysaire. *Bathytheristes* est le premier représentant toarcien des Chimaeroidei à être décrit, et la première chiméroïde signalée du Posidonienschiefer.

Introduction

The holocephalans are a group of chondrichthyan fishes ranging from the Devonian to Recent (Cappetta, Duffin & Zidek, 1993). Mesozoic rocks have yielded occasional remains belonging to 3 holocephalan orders; Squalorajoids (Hettangian to Sinemurian), Myriacanthoids (Rhaetian to Tithonian) and Chimaeroids (Pliensbachian to Recent). The oldest chimaeroid known to date is *Eomanodon simmsi* Ward & Duffin, 1989 from the Pliensbachian of Britain.

The comparatively poorly calcified endoskeleton of fossil holocephalans is seldom preserved. The bulk of our knowledge comes from isolated toothplates and dorsal finspines. The toothplates, unlike the dentitions of sharks, skates and rays, grow continuously throughout life, and are not shed. Both toothplates and dorsal finspines therefore represent the death of an individual.

Extant chimaeroids possess a total of 6 elements in the dentition; paired upper anterior ("vomerine"), upper posterior ("palatine") and lower ("mandibular") toothplates. Each toothplate grows from the lingual to the labial surface of the jaw (lyodont growth pattern of Bendix-Almgreen, 1983), as has recently been demonstrated by Patterson, (1992). The toothplate grows in a logarithmic spiral and is applied to the jaw by means of a basally directed descending lamina (Patterson, 1992; Ward & Grande, 1991, fig. 4).

Patterson (1992) has recently reviewed the interpretation and terminology of chimaeroid toothplates. His recommendations are followed here, and a key of the relevant descriptive terminology of toothplate morphology is given in Figure 3.

This paper is part of a series examining holocephalan material held in the Staatliches Museum für Naturkunde in Stuttgart (Duffin, 1983a; 1983b).

2. Geological Background

The bituminous facies of the Early Toarcian extends from the Midlands trough in Britain through the North Sea Basin to the Hannover region of northern Germany, and then via a strait between the Rhenish and Bohemian Massifs to southern Germany. The south German and French basins are bounded by the Rhenish Massif, Massif Centrale and Massif des Maures to the south and west, with the Vindelician High in the east. The sequence varies from around 75 m thickness in the Whitby area to around 15 m in southern Germany (Riegraf, Werner & Lörcher, 1984). The succession is zoned by ammonites and commonly yields well preserved vertebrate and invertebrate fossils (e. g. Hauff & Hauff, 1982; Westphal, 1962; Riegraf, Werner & Lörcher, 1984; Thies, 1991).

The south west German outcrop extends from around Waldshut in the south west to Aalen in the north east. Quarries working the succession for building stone, ornamental stone and oil shale in the area of Holzmaden, Weilheim and Ohmden (Fig. 1) have long been famous for fossil lagerstätten (e. g. Westphal 1980).

Ohmden itself is the type locality for the saurischian dinosaur *Ohmdenosaurus liasicus* Wild (1978), as well as the sturiomorph fish *Ohmdenia multidentata* Hauff (1953). A summary of the succession at Gonser Quarry (Riegraf, Werner & Lörcher, 1984: 70) is given in Fig. 2 for ease of reference. The ε II6 comprises the "Mittlerer Schiefer" of Pannkoke (1965). The lowermost bed in this formation is the

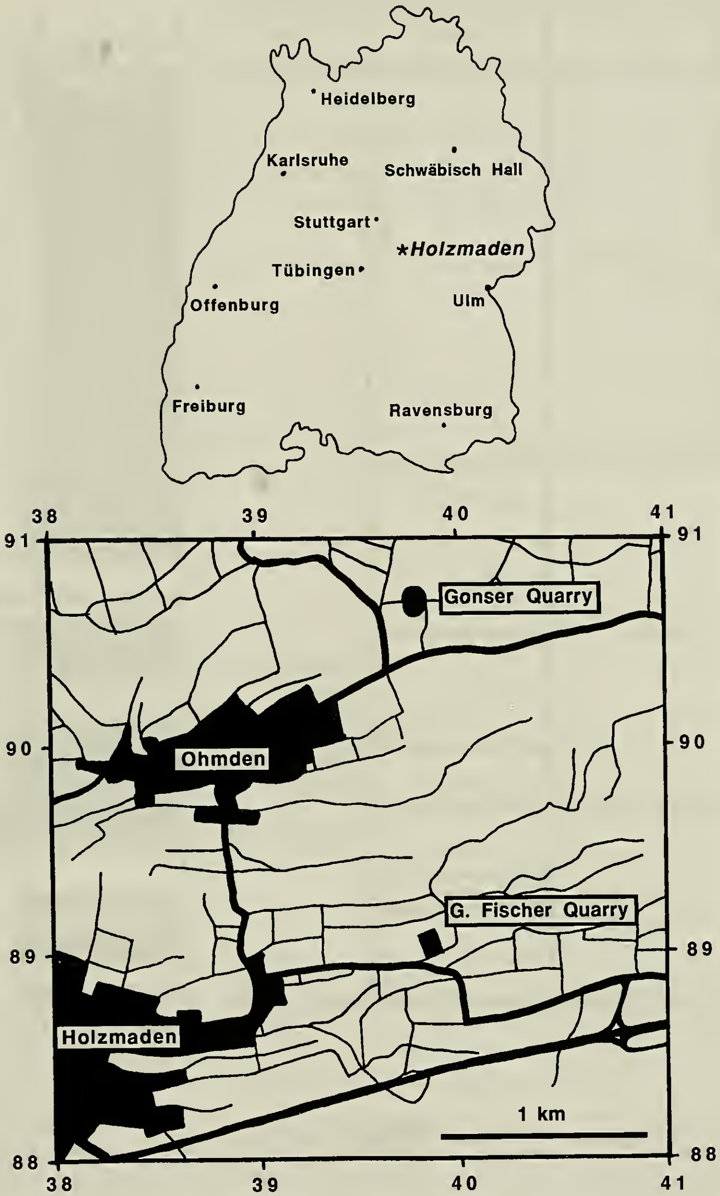

Fig. 1. Sketch maps to show the location of Gonser Quarry, Baden-Württemberg.

"Schieferklotz" (upper part of the *exaratum* subzone), comprising a bituminous clay shale.

Holocephalan remains recorded to date from the Posidonienschiefer all belong to the Myriacanthoidei. *Acanthorhina jaekeli* FRAAS, 1910 is represented by a single

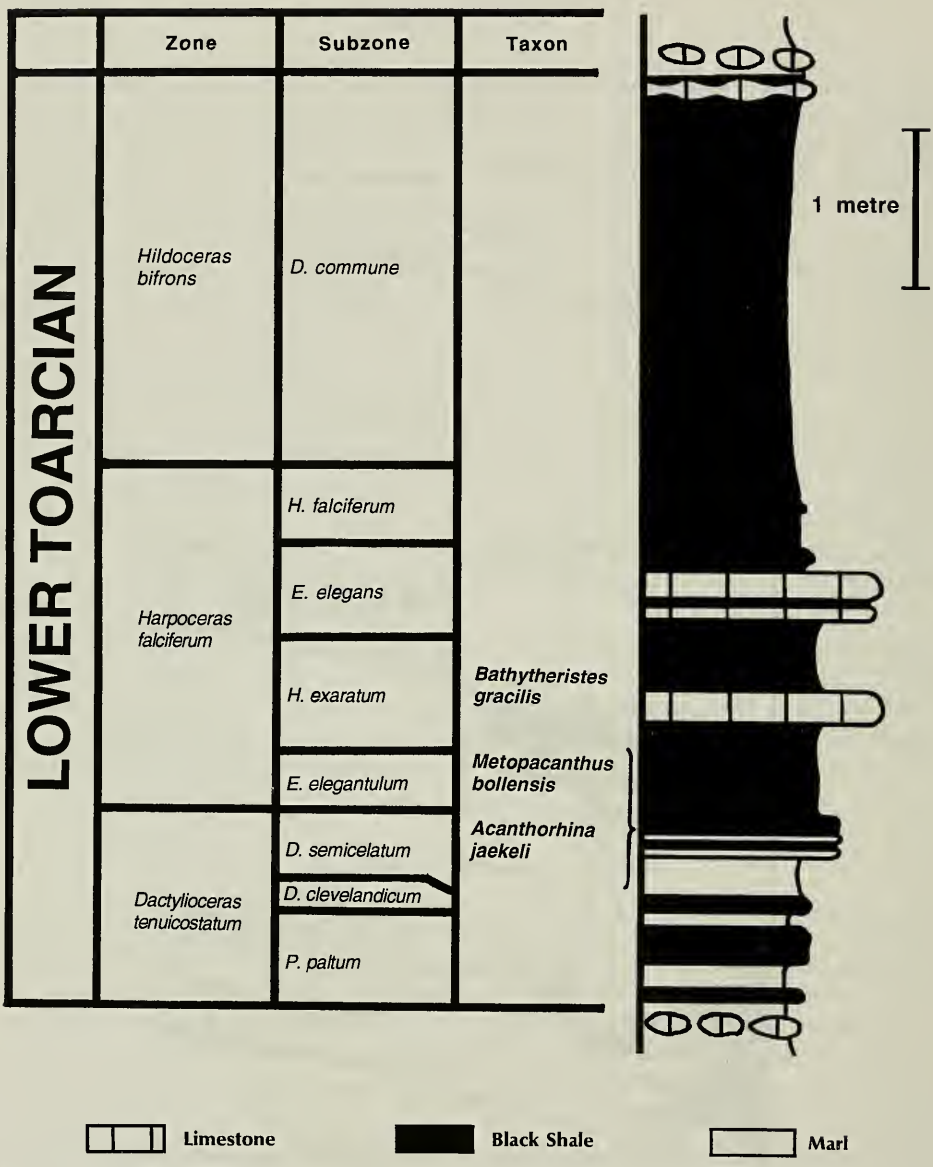

Fig. 2. Stratigraphic log of the Gonser Quarry section at Ohmden (information from Riegraf, Werner & Lörcher, 1984) showing the relative stratigraphic position of most Posidonienschiefer holocephalan discoveries to date.

incomplete, articulated anterior skeleton (Duffin, 1983 a); *Metopacanthus bollensis* (Fraas 1910) is known of the basis of a single dorsal fin spine (Duffin, 1983 a), and *Metopacanthus* sp. (Reif, 1974) has been reported from an isolated neurocranium. The general stratigraphical distribution of these taxa in relation to the new material described here is shown in Figure 2.

3. Systematic Palaeontology

Class Chondrichthyes Huxley, 1880
Subclass Holocephali Bonaparte, 1832
Order Chimaeriformes Patterson, 1965
Suborder Chimaeroidei Patterson, 1965
Family Callorhynchidae Garman, 1901

Genus *Bathytheristes* n. g.

Derivation of name: from the Greek bathys (βαθύς) = deep; theristes (θεριστής) = reaper; "reaper of the depth".

Diagnosis. – Genus known from the upper toothplate ("palatine") only. The mesial angle is acute. The single laminated symphyseal tritor is situated well forward, close to the mesial angle, forming 42% of the toothplate width at this point. The distal wing is expanded. The labial and symphyseal descending lamina have an angular junction. The profile of the labial border is low.

Bathytheristes gracilis n. sp.

Figs. 3, 4

Derivation of name: from the Latin *gracilis*, referring to the slender nature of the toothplate.

Holotype: SMNS 59754, a complete, isolated left upper ("palatine") toothplate, freed from matrix (Figs. 3, 4).

Type locality: Gonser Quarry, Ohmden, Baden-Württemberg, southern Germany. Topographic map 1:25000 no. 7323 Weilheim a. d. Teck; grid reference 3539800/5390700; Fig. 1.

Type horizon: Schieferklotz, Schwarzjura εII6 (Hauff, 1921), Posidonienschiefer (Fig. 2); *exaratum* Subzone, *falciferum* Zone, Early Toarcian, late Early Jurassic.

Finder: M. Wolf; collected in 1991.

Description

The specimen is an isolated left upper ("palatine") toothplate which has been completely freed from the matrix (Fig. 4). This identification is based on the presence of a mesial groove which accommodated the preceding anterior upper ("vomerine") toothplate in life, and the fact that the angle between the labial and symphyseal descending laminae is well separated from the symphyseal margin.

The toothplate measures 34 mm from the mesial angle to the distal angle. The symphyseal margin (22 mm in length) is slightly arcuate such that the two adjacent mesial angles of the paired toothplates would have diverged from each other in life. The mesial angle itself is acuminate and rounded. The labial margin is gently sinuous. The lingual margin (22 mm in length) is the open growth surface.

The biting surface to the toothplate is clearly indicated by the presence of a wear surface anteriorly. The wear surface accounts for just less than half of the total surface area. The remaining unworn surface is covered by a shiny, lamellar, compact tissue with clearly defined growth lines. By contrast, the worn surface is dull in appearance. A low labial ridge runs adjacent to the labial margin on the unworn surface.

In mesial view, the symphyseal margin of the occlusal surface is gently convex, reflecting spiral growth lingually. In labial view the margin of the worn part of the occlusal surface is convex.

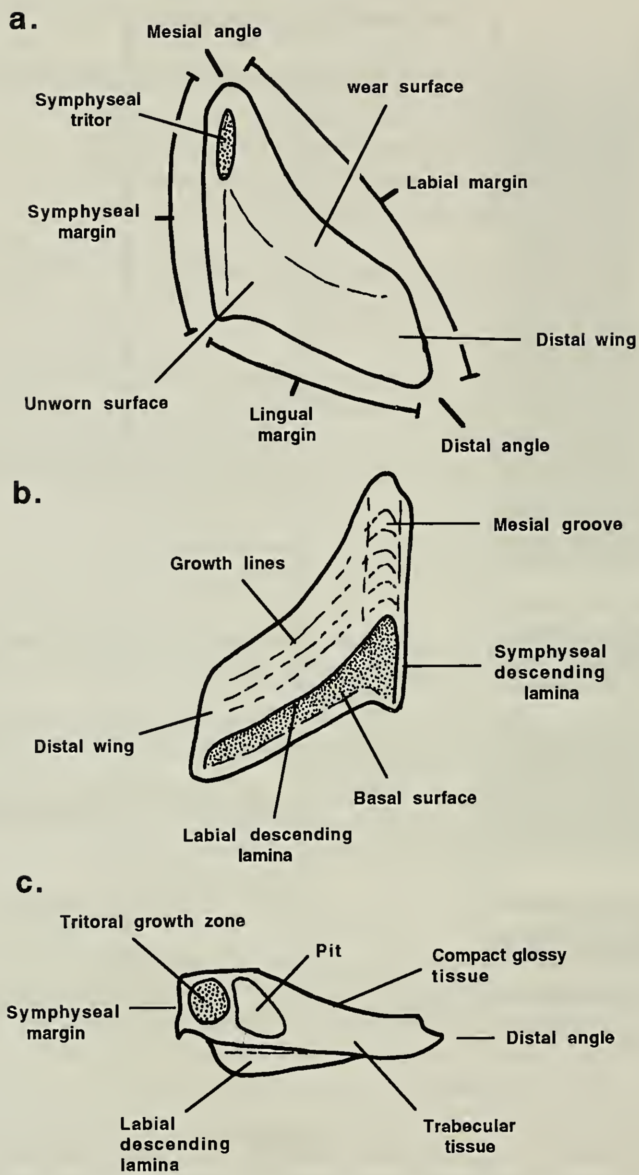

Fig. 3. Diagram to show the descriptive terminology used for upper posterior toothplates in this paper. a, occlusal view; b, basal view; c, lingual view.

A small (7 mm long, 3 mm wide) symphyseal tritor is situated close to the mesial angle on the symphyseal margin of the occlusal surface. The tritor comprises a pad of hypermineralised laminated pleromic hard tissue. It is slightly less than half width of the occlusal surface at this point, where the toothplate tapers toward the mesial angle. No other tritors are visible on the specimen.

The wear surface is covered by scratches produced during functional life of the tooth. The scratches are moderately short and tend to have trajectories either from

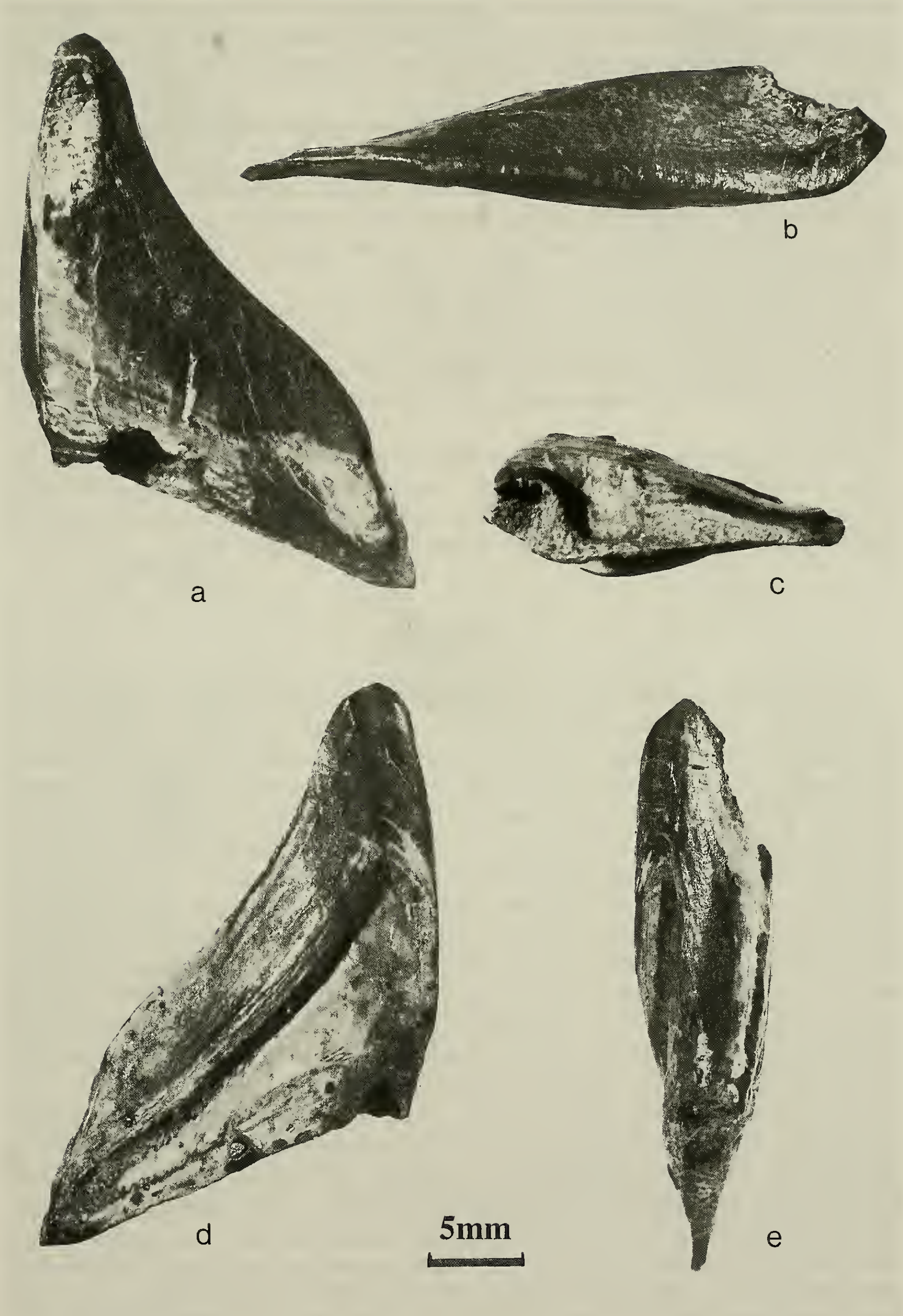

Fig. 4. *Bathytheristes gracilis* n. g. n. sp., holotype, SMNS 59754, Schieferklotz (εII6), Posidonienschiefer (Toarcian) of Ohmden (Baden-Württemberg). a, occlusal view; b, labial view; c, lingual view; d, basal view; e, symphyseal view.

the mesial angle or subparallel to the symphyseal margin. A few are oriented parallel to the junction between the worn and unworn sections of the occlusal surface. Slightly differential wear labially has picked out the position of the labial descending lamina at the labial margin.

In mesial view, the angle between the worn and unworn parts of the occlusal surface is approximately 30°.

In basal view, the basal surface, which was in direct apposition to the upper jaw cartilage in life, can be clearly distinguished from the descending laminae. Occasional entrant foraminae for blood vessels are visible, punctuating the basal surface close to the labial descending lamina.

The labial descending lamina is strong and deep. Its contact with the symphyseal descending lamina forms a smooth but fairly acuminate curve. The posterior parts of both laminae shallow rapidly toward the open growth surface. Growth lines in the smooth surfaces of the laminae can be clearly distinguished, oriented parallel to their free margins.

The open growth surface (lingual surface) of the toothplate exposes the subcircular zone of hypermineralised pleromic hard tissue which feeds the laminated median tritor anteriorly. Adjacent to this zone is a deep notch in the lingual surface. The open growth surface tapers markedly as the toothplate thins distally.

4. Discussion

The toothplate conforms the *Callorhynchus* type as defined by PATTERSON (1992: 42), in which an extensive descending lamina separates the basal surface from the labial and symphyseal surfaces. This characteristic is also known in the fossil genera *Brachymylus* (Callovian of Britain; Late Jurassic of Russia – AVERIANOV 1992), *Pachymylus* (Callovian of Britain) and *Ischyodus* (Bajocian to Eocene of Europe and North America, Miocene to Pliocene of Australia). This condition contrasts strongly with that exemplified by Recent *Chimaera*, and demonstrated in fossil species of *Edaphodon* (Aptian to Late Miocene/Early Pliocene of Europe, North America, Africa and Australia), *Elasmodectes* (Kimmeridgian to Turonian of Britain) and *Elasmodus* (Maastrichtian to Pliocene of Europe). Here, there is no obvious distinction between the labial and basal surfaces of the toothplate (PATTERSON 1992: 42). By outgroup comparison with the squalorajoids and myriacanthoids, PATTERSON (1992) established that the *Callorhynchus* toothplate type is primitive for chimaeroids. It is coincidentally distributed amongst the most ancient genera of the lineage.

The specimen from the Posidonienschiefer described above is unlike the palatine toothplates of all other chimaeroid genera of *Callorhynchus* type in that it has only one tritor in a symphyseal position. Toothplates of *Ischyodus* spp., by contrast, generally have four large tritors on the occlusal surface of their generally more massive toothplates (Fig. 5 b) – the symphyseal median, anterior outer and posterior outer tritors (NEWTON, 1878). Also, the labial descending lamina and basal surface are separated from each other by a narrow crevice, with the jaw cartilage occupying a deep pocket mesially in *Ischyodus* (PATTERSON, 1992, fig. 6 G). No such pocket is present in SMNS 59754.

Posterior upper toothplates of *Brachymylus*, on the other hand, bear two tritors (Fig. 5 d); a large median tritor is flanked by a slightly more anteriorly situated inner

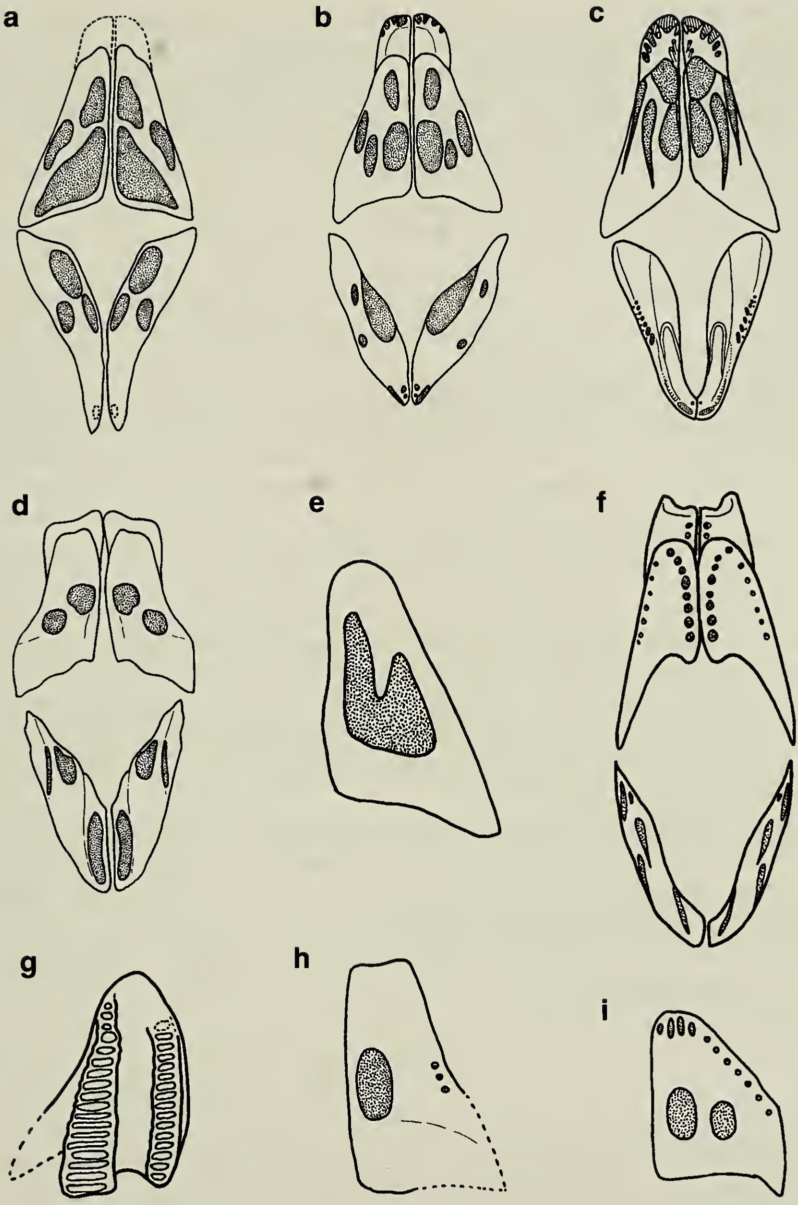

Fig. 5. Reconstructed dentitions and isolated upper toothplates in a range of chimaeroid genera. Not to scale. a, *Edaphodon ubaghsi* STORMS in LERICHE, 1927 (Maastrichtian, Maastricht); b, *Ischyodus egertoni* BUCKLAND, 1835 (Callovian and Kimmeridgian of England) after DEAN, 1906; c, *Elasmodus hunteri* EGERTON, 1843 (Eocene, England) after DEAN, 1906; d, *Brachymylus altidens* WOODWARD, 1892 (Callovian, Britain); e, left upper posterior toothplate of the extant *Callorhynchus* sp. after WOODWARD, 1891; f, *Ganodus rugulosus* EGERTON,1843 (Bathonian, England) after DEAN, 1906; g, right upper posterior toothplate of *Eomanodon simmsi* WARD & DUFFIN, 1989 (Pliensbachian, England); h, left upper posterior toothplate of *Pachymylus leedsi* WOODWARD, 1892 (Callovian, England); i, left upper posterior toothplate of extant *Chimaera* sp. after WOODWARD, 1891.

tritor (WARD & MACNAMARA, 1977). The basal face of *Brachymylus* toothplates has a similar conformation to that of the Toarcian specimen.

Pachymylus leedsi is discribed in the literature as having a single tritor as in the German specimen (WOODWARD, 1892). WOODWARD (1892: 13) mentioned that the posterior outer tritor is "represented by a few small patches". The syntypes of *P. leedsi* (BM(NH) P. 6888) clearly possess a single row of at least three beaded tritors (vascular pleromin of ØRVIG, 1985) along the central region of the labial border (Figure 4 h). There is no trace of beaded tritors along the labial margin in *Bathytheristes*.

Callorhynchus itself has a single large tritor in a median position, bifurcating mesially (Fig. 5 e), in contrast to the more symphyseally placed, elongate tritor in *Bathytheristes*.

The Toarcian specimen also differs significantly from all other non *Callorhynchus* type chimaeroid genera. For example, *Edaphodon* possesses three large tritors on the palatine toothplates (Fig. 5 a), while *Elasmodus* characteristically has four tritors, most of which are very elongate (Fig. 5 c). *Darbasodus* (AVERIANOV, 1991, fig. 1) has a median tritor flanked by two inner and four outer tritors. *Amylodon* STORMS, 1894 lacks a median tritor but has a band-like posterior inner tritor and numerous small anterior tritors.

Palatine toothplates of *Eomanodon* and *Ganodus* have a characteristic outline in occlusal view; a strong distal wing is separated from the remainder of the toothplate by a deep embayment lingually. *Eomanodon* has a long laminated symphyseal tritor preceded mesially by beaded archipelagic tritors, and a long laminated outer tritor (Fig. 5 g). *Ganodus*, on the other hand, has a moderately elongate laminated symphyseal tritor with archipelagic beaded tritors arranged around the mesial angle and labial borders of the toothplate (Fig. 5 f).

The genera *Ptyktoptychion* LEES, 1986, *Elasmodectes* NEWTON, 1878, *Paredaphodon* CASIER, 1966 and *Leptomylus* COPE, 1869 (see also HUSSAKOF, 1912) are known only on the basis of mandibular toothplates, and therefore cannot be meaningfully compared with *Bathytheristes*.

It is clear from these comparisons that the upper toothplate of *Bathytheristes* is unique amongst fossil holocephalans.

5. Conclusions

A single upper toothplate from the Schieferklotz (εII6 – upper *exaratum* Subzone) is described as *Bathytheristes gracilis* n. g. n. sp. This record increases the known diversity of Posidonienschiefer holocephali and is the first chimaeroid described from rocks of Toarcian age.

6. Acknowledgments

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