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Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart 4. The earliest German chimaeroid

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By Christopher J. Duffin, Sutton

With 4 figures

Abstract

Articulated lower toothplates ("mandibular" toothplates) with only the mesial angles missing are described from the *Amaltheus* Shale (*Pleuroceras spinatum* Zone) of the Pliensbachian (Early Jurassic) of Unterstürmig in Bavaria. The tooth plates are large and laterally expanded with 3 tritors on the occlusal surface. The short symphyseal tritor is inferred from hypermineralised tissue in the broken symphyseal margin of the right lower toothplate. The outer tritor is posteriorly placed, elongate in shape and fused with the median tritor lingually.

The presence of 3 tritors is confined to *Brachymylus* and *Ischyodus quenstedti*. The Pliensbachian material is tentatively referred to *Brachymylus* as *B. latus* n. sp. and represents the oldest chimaeroid remains from Germany. The left lower toothplate has been subject to post-mortem biting by an unknown scavenger.

Résumé

On décrit ici des pavés dentaires inférieurs en connexion (pavés "mandibulaires") provenant des Schistes à Amalthées (Zone à *Pleuroceras spinatum*) du Pliensbachien (Jurassique inférieur) de Unterstürmig en Bavière. Seuls manquent les angles mésiaux. Les pavés dentaires sont de grande taille, et très développés latéralement. Ils possèdent 3 zones trituratrices sur la face occlusale. L'aire trituratrice symphysaire est courte, et sa présence déduite à partir de tissu hyperminéralisé sur le bord symphysaire brisé du pavé inférieur droit. L'aire trituratrice externe est en position postérieure, de forme allongée, et fusionnée lingualement avec l'aire trituratice médiane.

La présence de 3 structures trituratrices est caractéristique de *Brachymylus* et d' *Ischyodus quenstedti*. Les spécimens du Pliensbachien sont rapportés, à titre d'essai, à *Brachymylus*, représentant une espèce nouvelle, *B. latus* n. sp. Ce sont les plus anciens Chiméroïdes connus d'Allemagne. Le pavé dentaire inférieur gauche a été l'objet de morsure post mortem par un prédateur non identifié.

Zusammenfassung

Aus dem Amaltheen-Ton (Spinatum-Zone, Pliensbachium, Unterjura) von Unterstürmig in Bayern werden zwei artikulierte untere Zahnplatten („Mandibular"-Zahnplatten) be-

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schrieben. Bis auf die mesialen Spitzen sind sie vollständig erhalten. Die Zahnplatten sind groß und breit mit je drei Reibeflächen auf der occlusalen Oberfläche. Die Existenz der kurzen symphysealen Reibeflächen, die auf den fehlenden Spitzen lagen, ist durch das hypermineralisierte Gewebe belegt, das auf der Bruchfläche am symphysealen Rand der rechten Zahnplatte zu sehen ist. Die äußere Reibefläche liegt hinten, ist von länglicher Gestalt und lingual mit der mittleren Reibefläche verbunden.

Die Existenz von drei Reibeflächen ist beschränkt auf die Gattung *Brachymylus* und die Art *Ischyodus quenstedti*. Das Material aus dem Pliensbachium wird vorläufig der Gattung *Brachymylus* als *B. latus* n. sp. zugeordnet. Die Art repräsentiert den bisher ältesten Nachweis der Chimaeroidei aus Deutschland. Die linke Zahnplatte zeigt Bißspuren eines unbekannten Aasfressers.

1. Introduction

Mesozoic holocephalans belong to three suborders:

1. Squalorajoidei (Sinemurian only) containing 1 genus (Britain and Italy; Patterson, 1965; Duffin, 1992).

2. Myriacanthoidei (Rhaetian to Kimmeridgian) containing 8 genera.

3. Chimaeroidei (Pliensbachian to Recent) containing around 20 genera.

The earliest chimaeroid recorded to date is *Eomanodon simmsi* Ward & Duffin, 1989 from the Pliensbachian (*margaritatus* Zone, Early Jurassic) of Gloucestershire, England. This genus, known only on the basis of an isolated posterior upper ("palatine") toothplate, resembles "*Ganodus*" from the Middle Jurassic (Bathonian). The arrangement of tritors and shape of the toothplates in this group contrasts strongly with that of *Ischyodus* and other edaphodontids, whose earliest records are *Ischyodus ferrugineus* Riess, 1887, *I. personati* (Quenstedt, 1852), *I. bifurcati* (Quenstedt, 1887) and *I. aalensis* (Quenstedt, 1852) from the Upper Aalenian of Aalen, Germany.

The purpose of this present paper is to describe new material from the Pliensbachian of Bavaria, southern Germany, which represents the oldest German occurrence of the Chimaeroidei.

Previous papers in this series are Duffin (1983a, 1983b, 1995), forming part of a wider review of Mesozoic holocephalan fossils.

2. Systematic Palaeontology

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

Genus *Brachymylus* Woodward, 1892

Type species: *Brachymylus altidens* Woodward, 1892 (Callovian to Oxfordian of Peterborough, England; Ward & MacNamara, 1977).

Brachymylus latus n. sp.
Figs., 2, 3, 4a

Holotype: SMNS 80008, two associated lower toothplates („mandibulars"); Figs. 2, 3.

Type locality: A working brick pit at Unterstürmig, 8 km north of Forchheim, Upper Franconia, Bavaria (Fig. 1) and 38 km north of Nürnberg. Topographic map 1 : 25 000, sheet no. 6232 Forchheim; grid reference R 4431932, H 5517120. A general account of the geology of the area is given by Krumbeck (1956). This is locality 9 of Goetze & Mayer (1972).

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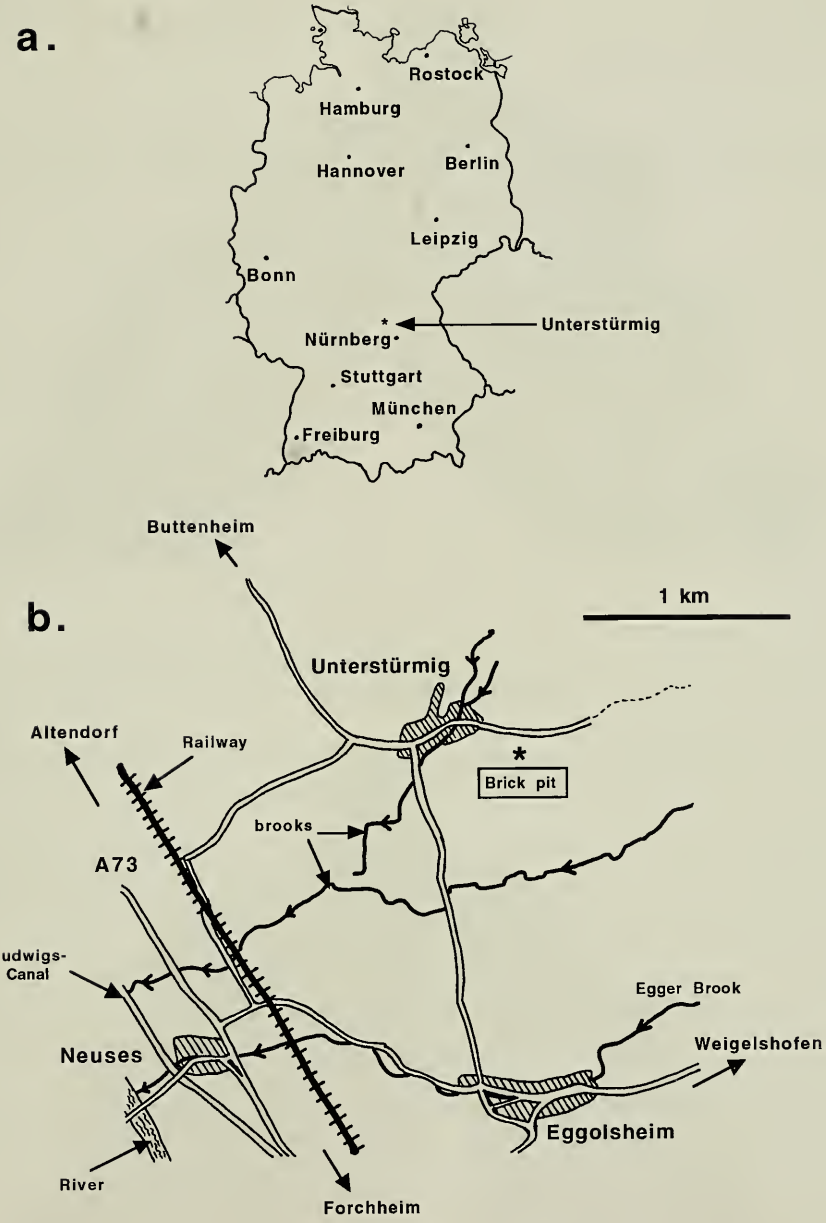

Fig. 1. Sketch maps to show the location of Unterstürmig Brick Pit, Franconia, Bavaria, southern Germany. a: Germany (whole country), b: Unterstürmig (detail).

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Type horizon: *Amaltheus* Shale, *Pleuroceras spinatum* Zone, Upper Pliensbachian, Early Jurassic.

Derivation of name: from the Latin "latus" (= wide) referring to the laterally expanded shape of the toothplates.

Finder: Traugott Haubold, Ansbach.

Diagnosis. – Species of *Brachymylus* known only from large, articulated lower toothplates which are laterally expanded. The symphyseal tritor is small. The elongate outer tritor is located centrally and fused lingually with the rhomboid median tritor.

Description. – The specimen comprises both lower toothplates ("mandibular"), fully articulated, but extensively overgrown by marcasite (Fig. 2).

The left lower tooth plate exposes the greater part of the occlusal and basal surfaces. The basal surface is also available in the right lower tooth plate. The mesial angle is missing, however, and the lingual (growing) face is obscured by marcasite in both toothplates. The occlusal surface of the right lower tooth plate is extensively overgrown.

The left lower toothplate measures 55 mm along the lingual border, 46 mm along the symphyseal border and 91 mm diagonally from the mesial to the distal angle. The labial margin is slightly sinuous, and the toothplate as a whole is laterally expanded.

Although the mesial angle is missing, the broken surface of this and the broken symphyseal surface of the right lower toothplate indicate the presence of vascular pleromin running forward from the fracture. Therefore there must have been an anterior inner tritor close to the mesial angle. The erupted expression of this tritor on the occlusal surface must have been relatively short, since only the mesial angle is missing in this specimen.

The symphyseal margin is straight anteriorly before curving away from the symphysis posteriorly. It is surmounted by a prominent but narrow ridge. There is no posterior inner tritor.

The labial margin has a single shallow embayment. The single outer tritor is elongate (31 mm long) and narrow. It is fused to the median tritor in the central part of the toothplate. The median tritor itself is rhomboid in shape, measuring 20 mm wide and 10 mm long (anteroposteriorly).

The symphyseal margin is convex occlusobasally. The basal surfaces of the toothplates show well developed descending laminae lying in the same plane as the basal surface. They are covered with glossy tissue in which well defined growth lines are discernible.

The right lower toothplate shows some interesting features; the superficial glossy tissue covering the labial descending lamina has been punctured in several places (Fig. 3). The glossy tissue has been forced into the puncture as might be expected from a biting episode. At least two sets of puncture marks are arranged in pairs. The perforations are circular and measure around 0.8 mm in diameter with a separation of 1 mm and 2 mm respectively. It is likely that the punctures are due to post-mortem biting by a small benthonic scavenger of unknown identity.

3. Discussion

The descending laminae in the toothplates described above are unlike those of myriacanthoids. In this group, the laminae project approximately normal to the basal surface of the toothplate, while in the German specimens they lie in the same

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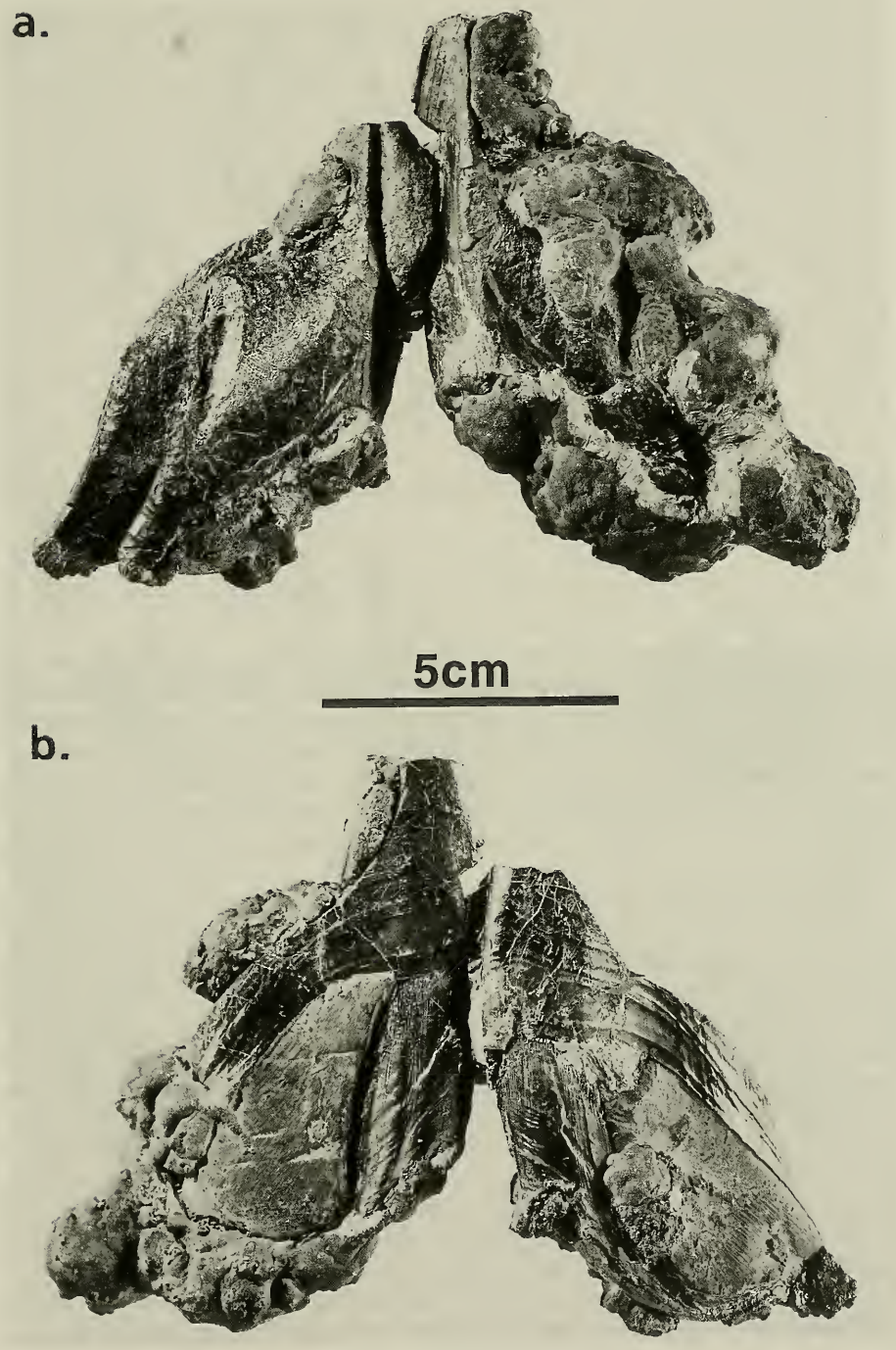

Fig. 2. The holotype (SMNS 80008) of *Brachymylus latus* n. sp. from the Pliensbachian (Early Jurassic) of Unterstürmig, Bavaria. Articulated lower toothplates; a: occlusal view; b: basal view.

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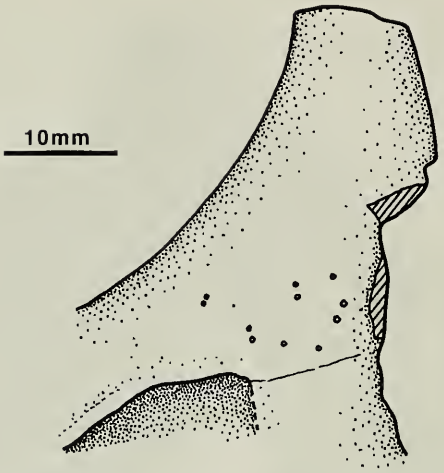

Fig. 3. Camera lucida drawing of SMNS 80008 to show bite marks on the descending laminae of the left lower toothplate.

plane as the basal surface, from which they are separated by a narrow crevice. This conformation is typical of chimaeroids belonging to the *Callorhynchus* morphotype (Patterson, 1992). Chimaerids, by contrast, have much reduced descending laminae.

Mesozoic callorhynchids are limited in diversity and comprise the following genera: *Brachymylus, Pachymylus, "Ganodus", Ischyodus* and *Bathytheristes*. *Bathytheristes* (Toarcian, Holzmaden; Duffin, 1995) is known only from an upper posterior tooth plate, and so cannot be meaningfully compared with the Pliensbachian material.

Brachymylus altidens Woodward, 1892 (Callovian to Oxfordian of Britain; Ward & MacNamara, 1977), like the German material described above, possesses 3 tritors (Fig. 4d). A large symphyseal tritor runs the greater part of the length of the symphyseal margin. The median tritor is ovoid and centrally placed, occupying the posterior two-thirds of the oral or functionally occlusal surface of the toothplate. The elongate outer tritor is positioned along the labial margin of the toothplate. *Brachymylus minor* Woodward, 1892, however, has a much smaller anterior inner tritor and larger outer tritor. The symphyseal tritor in the German specimen cannot be as large as that in *B. altidens*. Furthermore, the Pliensbachian toothplates are much more robust and laterally expanded in comparison to the much more slender, elongate material from the British Callovian. The tritors all arise from a single mass of hypermineralised tissue in the body of the toothplate in *Brachymylus*; overgrowth by marcasite prevents assessment of this character in the German specimens. *Brachymylus bogolubovi* Averianov, 1992 (Middle Volgian, Late Jurassic of Russia) is known only on the basis of upper anterior ("vomerine") toothplates and so cannot be compared with the German material.

The lower toothplates of *Pachymylus leedsi* Woodward, 1892 (Callovian to Oxfordian of England) differ considerably from those of *B. latus*. The symphyseal tritor is elongate; the elongate median tritor contacts the labial margin, and the outer

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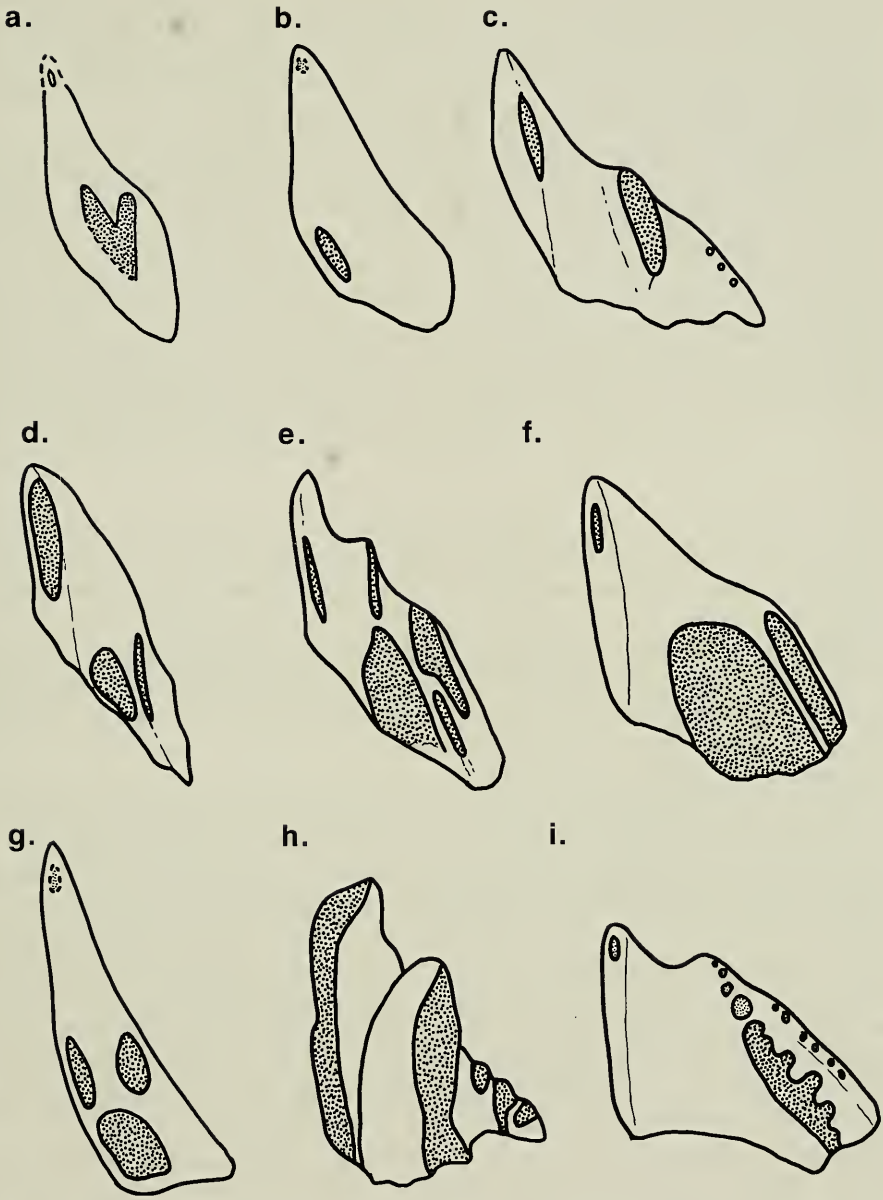

Fig. 4. Right lower toothplates in a range of chimaeroid genera for comparison with SMNS 80008, not to scale. – a: *Brachymylus latus* n. sp. (SMNS 80008, holotype; Pliensbachian, Bavaria); b: *Leptomylus cooki* Cope, 1870 (Maestrichtian, USA) after Hussakof (1912, fig. 14); c: *Pachymylus leedsi* Woodward, 1892 (Callovian, Britain); d: *Brachymylus altidens* Woodward, 1892 (Callovian, Britain); e: *Darbasodus dolloi* (Leriche, 1902) (Late Eocene, Seymour Island) after Ward & Grande (1991, fig. 6b); f: *Ischyodus quenstedti* (Wagner, 1857) from the Tithonian of Germany (based on SMNS 11049); g: *Edaphodon ubaghsi* Storms in Leriche, 1927 (Maestrichtian, Belgium); h: *Ptyktoptychion tayyo* Lees, 1986 (Albian, Australia); i: "*Ganodus*" *dentatus* Egerton, 1847 from the Bathonian of Britain (BMNH P614, holotype; reversed).

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tritors are represented by at least 3 subcircular, beaded units of hypermineralised tissue (Fig. 4c). These latter units, also present in "*Ganodus*" (Bathonian of Britain, currently under review by DUFFIN & WARD, MS) are absent in the German material. "*Ganodus*" also differs from the Pliensbachian specimen in that the median tritor is elongate, laminated posteriorly and beaded anteriorly (Fig. 4i).

Toothplates of *Ischyodus* spp. generally have 4 large tritors on the occlusal surface of quite massive lower toothplates; the symphyseal tritor is generally elongate, the median tritor centrally placed, and 2 outer tritors are arranged in anterior and posterior positions along the labial margin. One species has this number reduced to 3 tritors; *I. quenstedti* (WAGNER, 1857; Tithonian of Germany) lacks the anterior outer tritor (Fig. 4f), as does the Pliensbachian material. The form of the median tritor is superficially similar between the German specimens and *I. bifurcatus* CASE, 1978 (Late Santonian to Middle Maestrichtian of the USA and Belgium; CASE 1978; CASE & SCHWIMMER, 1992). The median tritor in the American material is divided anteriorly, but the anterior outer tritor (missing in the Pliensbachian material) is well defined.

Darbasodus AVERIANOV, 1991 was recently erected for *D. olgae* AVERIANOV, 1991 (upper posterior toothplates from the Palaeocene of Kazakhstan) and *Ischyodus dolloi* LERICHE, 1902 (Palaeocene of Europe and the Late Eocene of Antarctica). In *D. dolloi*, the lower toothplate has 5 tritors (Fig. 4e) in contrast to the 3 present in the German material.

Ptyktoptychion LEES, 1986 (Albian, Early Cretaceous of Queensland, Australia) is founded on a ?lower toothplate (but see AVERIANOV, 1992: 80, and STAHL, in preparation) bearing 3 tritors. Both the median and the symphyseal tritors are long, contacting the labial margin of the plate (Fig. 4h). The outer tritor is divided into 3 subunits, unlike in the German specimens.

Mesozoic and Tertiary genera which lack or have only weak descending laminae also differ from *B. latus* in the disposition of their tritors. *Edaphodon* (Fig. 4g) characteristically has 4 tritors, including a laminated symphyseal (NEWTON, 1878). *Paredaphodon* is very similar, but the mesial angle is not prolonged into a beak (CASIER, 1966). In *Elasmodectes*, the lower toothplate is laterally compressed with a deeply sinuous profile and tritors reduced to several rows of small rods (NEWTON, 1878; WOODWARD, 1891). *Elasmodus* has a number of small rod-like outer and symphyseal tritors, with an intervening median tritor (NEWTON, 1878; WOODWARD, 1891). Lower toothplates are not well known in *Amylodon*, but 2 tritors (a symphyseal tritor located well forward and a larger ?median tritor further back) appear to be present (STORMS, 1894; AVERIANOV & POPOV, 1995; STAHL, in preparation).

Leptomylus (Maestrichtian, Late Cretaceous of the USA) was originally erected by COPE (1869) and later revised by HUSSAKOF (1912). Lower toothplates of *L. cooki* COPE, 1870 and *L. forfex* COPE, 1875 each have a robust median tritor accompanied by a small "apical tritor" (COPE, 1875: 282; HUSSAKOF, 1912: 218) located at the mesial angle (Text-Figure 3b). There is a single tritor in the lower toothplate of *L. densus*, the type species, but it is not clear from COPE's description as to its exact location; the specimen has never been figured, and is believed to have been lost (HUSSAKOF, 1912). The reduced tritoral number in *Leptomylus* is thus even fewer than is present in the German material.

The presence of 3 tritors on the occlusal surface of the lower toothplate is a feature of only three taxa, to the best of my knowledge: *Brachymylus altidens*,

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Brachymylus minor, Ischyodus quenstedti and the Pliensbachian material described above. In the 2 species of *Brachymylus*, the hypermineralised tissue develops from a single unit within the toothplate, and the toothplate is relatively elongate. Like the early Jurassic material described above, *I. quenstedti* (currently under review, DUFFIN MS) has a laterally expanded, robust toothplate. The tritors appear to originate from separate hypermineralised units in the Tithonian material, but the character is not available in the Pliensbachian material owing to the growth of diagenetic marcasite. The confluence of the outer and median tritors, however, suggests that they originate from the same unit of tissue within the body of the toothplate.

The Pliensbachian material is accordingly tentatively accommodated into the genus *Brachymylus* on the basis of there being three tritors on the occlusal surface – the symphyseal tritor is inferred from the presence of non-laminated hypermineralised tissue on the broken symphyseal margin of the right lower toothplate. The symphyseal tritor must have been fairly short and located close to the mesial angle, a part of the toothplate which is missing. The outer tritor is posteriorly positioned and elongate, being fused to the rhomboid centrally positioned median tritor.

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