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Late Triassic pycnodont fish remains (Neopterygii, Pycnodontiformes) from the Germanic basin

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Key words: Late Triassic, Pycnodontiformes, Neopterygii, Germanic basin, Belgium, Luxembourg.

ABSTRACT

Isolated dental remains of pycnodont fishes are recorded from the upper Norian (Upper Triassic) of the Germanic basin for the first time. The only complete prearticular dentition differs significantly from those of other Late Triassic pycnodonts such as *Brembodus* and *Eomesodon*. However, because the prearticular dentition of *Gibbodon*, another Late Triassic pycnodont, is not known the new specimens are not attributed to any genus or species. Nevertheless, these are the first indubitable records of pycnodont fishes in the uppermost Triassic outside the Tethyan realm and consequently contribute to our knowledge about the diversity and distribution of Late Triassic pycnodonts.

ZUSAMMENFASSUNG

Gebißreste pycnodonter Fische werden erstmals aus dem oberen Norium (Obere Trias) des Germanischen Beckens beschrieben. Die einzige vollständige Preartikularbezahnung unterscheidet sich deutlich von der anderer obertriassischer Pycnodontier (z.B. *Brembodus*, *Eomesodon*). Allerdings ist die Preartikularbezahnung von *Gibbodon*, einem weiteren obertriassischen Pycnodontier, nicht bekannt. Konsequenterweise werden die neuen Nachweise keiner Gattung oder Art zugeordnet. Aber diese Reste sind die ersten und ältesten Nachweise von Pycnodontiern außerhalb der alpinen Trias und geben neue Hinweise auf die frühe Diversität dieser Fischgruppe.

1. Introduction

Pycnodont fishes are a very popular group from many conservation deposits (e.g. Solnhofen, Cerin, Bolca, Lebanon) that have attained much attention in the last years (e.g. Blot 1987; Nursall 1996a; Kriwet 2001a, b; Poyato-Ariza & Wenz 2002; Saint-Seine 1949). They represent morphologically and ecologically distinctive actinopterygians that have been recognised as a monophyletic group since the description of Agassiz (1833–44). About 650 nominal species have been described belonging to 37 genera'10 of which are based entirely on dental remains (Kriwet 2001a). Pycnodonts are mainly represented by isolated elements like scales, bones, dentitions, and teeth. Only approximately 80 pycnodont species are known by skeletal remains. Remains of pycnodont fishes, especially their crushing dentitions and teeth, occur nearly worldwide in most marine and even brackish to fresh-water influenced deposits and are considered major component of Mesozoic shallow marine fossil fish assemblages (e.g. Nursall 1996a, b; Kriwet 2000a, b, 2001a, b).

So far, the oldest pycnodonts are known from the Late Triassic of the northern margins of the Tethys (what is now northern Italy and Austria). The last records come from the Eocene making them one of the most successful actinopterygian groups of shallow marine environments for almost 175 million years (Kriwet 2001a). Pycnodonts were rather rare in the Late Triassic and Early to Middle Jurassic but became more diverse in the Late Jurassic.

Three pycnodont species, *Brembodus ridens*, *Eomesodon hoferi*, and *Gibbodon cenensis*, have been reported from the upper Norian of Lombardy, northern Italy (e.g. Tintori 1981). The material consists of articulated specimens as well as of isolated dentitions. *Eomesodon hoferi* is the only pycnodont that also occurs in the Norian of Austria (Gorjanovic-Kramberger 1905).

Henry (1876) described isolated teeth from the Rhaetian of Grozon in France as *Gyrodus milinum*. However, these teeth belong to colobodontids or perleidids by their characteristic morphology (JK, pers. obser.). Cuny & Ramboer (1991) indi-

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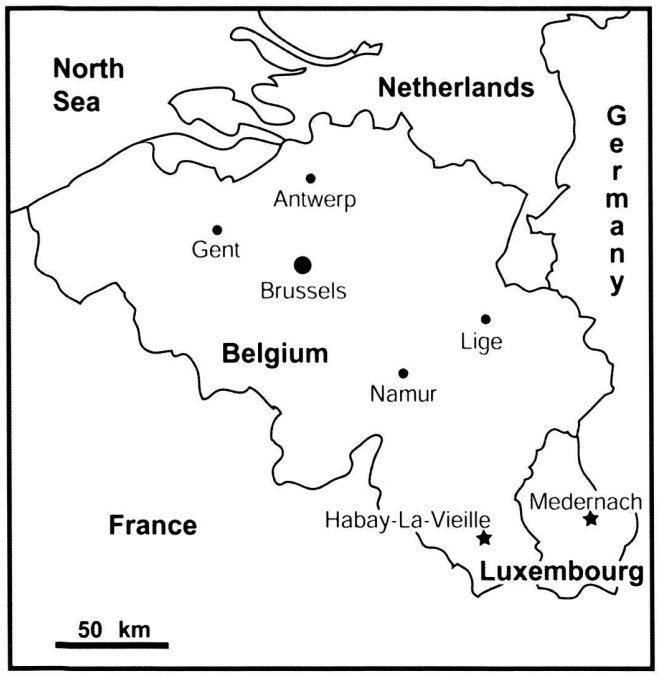

Fig. 1. Location of the fossil sites Habay-La-Vieille in southern Belgium and Medernach in Luxembourg (Lorraine). The localities indicated by asterisks form the NE extension of the Paris Basin.

cate, without illustrations, a single tooth in the Upper Triassic of Saint-Nicolas-de-Port in France, which is also assigned to pycnodonts. Isolated teeth from Aust Cliff in Southwest England may also represent pycnodont remains (G. Cuny, pers. comm. 1997).

The objective of this paper is to present descriptions and figures of the first Late Triassic pycnodont remains outside the Tethyan realm. These represent the first pycnodontiform records in Germanic Triassic facies.

2. Material and abbreviations

The material consists of isolated dental remains from two localities in Belgium and Luxembourg. The specimens were obtained by screen washing and sieving of sands (Habay-la-Vieille material) and after physical process (kerosene method) of some hundreds of kilograms of dolomitic marls (Medernach material). All material described in this study is housed in the National Natural History Museum of Luxembourg (NNHML MO162). The prefix HLV indicates the locality of Habay-la-Vieille in Belgium and MED the one from Medernach in Luxembourg. The following material forms the focus of this study. Belgium: NNHML MO162: HLV3–1, a prearticular dentition (Plate 1, Figures 1–5); NNHML MO162: HLV3-2, a fragmentary and incomplete dentition (Plate 2, Figures 1–2); NNHML MO162: HLV3-3, a very incomplete dentitional remain with a tooth of the main row (Plate 2, Figure 3–4). Luxembourg: NNHML MO162: MED04a, a molariform tooth; NNHML MO162: MED04b, a molariform tooth; NNHML MO162: MED05a01, NNHML MO162: MED05a02, incisiform teeth from the Upper Norian (Upper Triassic) of Medernach, Grand Duchy of Luxembourg.

The terminology for the dentitional remains adopted herein follows Nursall (1996a) and Kriwet (1999, 2001a).

3. Localities and geological context

The first locality is near Habay-la-Vieille in SE Belgium (Fig. 1). Rhaetian bone beds are exposed along the crossing of the E25-E411 from Brussels to Arlon and the road to Etalle-Habay-la-Vieille. The sedimentology displays the typical regional characteristics, e.g. sandstones, pelites and conglomerates of the Mortinsart Formation, which is generally supposed to be of Rhaetian age. A regressive sequence is recognized at the base of the section, followed by three transgressive sequences (Bock 1987). The level HLV3, which yielded the material for this study, is located in the third transgressive sequence and consists of greyish to brownish sands with pericentimetric pebbles forming unconsolidated conglomerates (Delsate 1995). The depositional environment is interpreted as subtidal to littoral in a very proximal restricted marine environment (bay or lagoon) (Boulvain et al. 2000). A late Norian age is attributed to the fossiliferous horizons based on palynological and sedimentological evidence conversely to previous interpretations (e.g. Roche 1994; Rauscher et al. 1995; Schuurman 1979; Smith 1982).

The second locality is situated close to Medernach (Grand Duchy) in Luxembourg on the roadside of the national road 14 between Larochette and Diekirch (Rinckebierg), near the city of Medernach in Luxembourg (Fig. 1). The lithology of the outcrops consists of Keuper dolomites, clays and marls of the Steinmergel-Gruppe. A middle Norian (Dittrich 1984, 1989) respectively an early Rhaetian age (Dittrich et al. 1999) was attributed to the fossiliferous layers. The early Rhaetian age was established in the near-by locality of Schankweiler in Germany (Dittrich et al. 1999). Unfortunately, the fossil-bearing strata did not yield any palynological data. The conglomeratic sands covering the bone-bed at the top of the outcrop were dated as Rhaetian based on palynomorphs (Cuny et al. 1995), whereas the underlying bone-bed layer was assigned a (late?) Norian age based on sedimentological reasons. The depositional environment is interpreted as an evaporitic lagoon with episodic fluviatile-tempestite inputs and marine flooding (Van Campenhout 2000).

3. Description of specimens

Most of the material from Habay-la-Vieille in Belgium consists of imperfect dentitions and isolated remains. Only a single complete prearticular was recovered (NNHML MO162: HLV3-1, Plate 1). The dentitions and teeth are all very small. The prearticular measures only 33 mm in length and is 20 mm

wide. The teeth are arranged in five longitudinal rows. They are closely positioned and all teeth decrease in size anteriorly. The anterior teeth are small and rounded but exhibit a slightly irregular outline in occlusal view. The posterior teeth are more regular in outline.

The teeth of the main row are the largest (Plate 1, Fig. 1). They form a slightly curved line in occlusal view. There are five teeth preserved with basal remains of a sixth tooth. The teeth are pedicillate with rather high crowns and distinctive but short bases fitting in sockets of the underlying bone. The main teeth are transversally elongated and are 1.6 to 1.9 times wider than long in the posterior but only about 1.3 times wider than long in the anterior portion of the dentition. The two posteriormost teeth are irregular oval and oblique, whereas the third tooth from posterior, the largest one, is regular oval. All teeth are smooth. The anterior teeth are heavily abraded exposing an almost flat and rostrally oblique occlusal surface. The tooth crowns of the posterior main teeth are pillow-like with elevated occlusal surfaces.

The principle row is accompanied by two lateral and two medial tooth rows (Plate 1, Fig. 1). These teeth are pedicillate and exhibit a rather low coronal profile with elongated tooth bases that fit in bony sockets (Plate 1, Figs. 2–5).

There are seven respectively nine teeth in the first lateral and medial tooth rows. The anteriormost teeth are also deeply worn. The teeth of the first lateral and medial rows are two to three times smaller than the main teeth and have a rounded to suboval contour, which is rather irregular in most teeth (Plate 1, Figs. 2–5). The long axes of the oval teeth are oriented oblique to perpendicular to the long axes of the main teeth. The tooth crowns display a shallow, very irregular apical indent surrounded by a blunt, irregular edge (Plate 1, Fig. 5). Three to five small tubercles are present along the edge in oval teeth when unworn. The second medial tooth row consists of only four teeth that are placed in a curved line close to the symphysis.

The teeth of the outer and innermost rows are almost identical in shape and morphology to those of the first lateral and medial rows. They are only slightly smaller and arranged more or less parallel to the teeth of the first lateral and medial row.

The teeth of the lateral and medial rows display three to more than seven low tubercles, which are arranged in a rectangular pattern around a shallow indent when unworn. This results in an almost quadrilateral outline of some of the rounded teeth in occlusal view.

There are no intercalating teeth between the tooth rows (Plate 1, Fig. 1).

The coronoid process is incomplete and most of the ascending process is missing (Plate 1, Fig. 1). Its base is comparable narrow. This condition is unusual for pycnodonts where the coronoid process forms the attachment for the strong adductor muscles at the lower jaw.

The symphysis is very poorly preserved and does not allow any statement about its length and surface feature.

Specimen NNHML MO162: HLV3-2, an incomplete dentitional remain, exposing three teeth of the principle row and a few lateral teeth of at least two tooth rows (Plate 2, Figs. 1–2). It is not possible to identify this remain either as vomerine or prearticular dentition. All teeth are similar to those of the prearticular described above in form and size although they are all smooth without any sculpture.

Additional isolated teeth occur in both localities, which can be assigned to pycnodontiforms, e.g. NNHML MO162: HLV3-3, a single tooth of the main row from Belgium (Plate 2, Figs. 3–4), NNHML MO162: MED04a, two associated transversally elongated teeth from Luxembourg (Plate 2, Fig. 5), and NNHML: MEDO4b, a fragmentary dentition with four subcircular and oval associated teeth (Plate 2, Fig. 6) from Luxembourg. Moreover, two isolated incisiform teeth (Plate 2, Figs 7–8) from Luxembourg exhibit the typical morphology of dentalosplenial and premaxillary pycnodont teeth.

4. Systematic discussion

The arrangement of prearticular teeth in three longitudinal tooth rows is the most common feature amongst pycnodont fishes (Kriwet 2001a; Poyato-Ariza & Wenz 2002). Conversely, five tooth rows are only present in few pycnodonts such as *Brembodus*, *Iemanja* (in which these tooth rows are very irregular), and some species of *Anomoeodus*. However, *Anomoeodus* displays rather strong irregularities in the most lateral and medial tooth rows (Kriwet 1999). Some isolated prearticulars with teeth arranged in five longitudinal tooth rows have been assigned to *Eomesodon* and *Polygyrodus*. However, Poyato-Ariza & Wenz (2002) demonstrated that *Eomesodon* as understood for long times represents an unnatural grouping and established the genus *Apomesodon* for some of the taxa previously included in *Eomesodon*. *Apomesodon* has three prearticular tooth rows whereas *Eomesodon* is characterized by five longitudinal rows in the lower jaw. The dentition of the lower jaws of *Gibbodon* is too poorly known to determine the number of tooth rows or even the morphology of main and lateral teeth. The prearticular dentition NNHML MO162: HLV3-1 from Belgium differs from prearticular dentitions of *Brembodus* and *Eomesodon* in the presence of two lateral and medial tooth rows. There are three lateral and a single medial tooth row developed in *Brembodus* and *Eomesodon*. Unfortunately, the condition in *Eomesodon hoeferi* from the Upper Triassic of North Italy and Austria housed in the Dept. Sci. delle Terre dell'Università degli Studi (Milan, Italy) is not sufficiently known to verify any differences or similarities to the new specimens. The tooth morphology of *Eomesodon liassicus* is very similar to that found in the Belgium specimen (JK, pers. obser.). Remains, especially teeth, of *E. liassicus* are rather common in Early Jurassic strata of Britain.

The teeth of specimen NNHML MO162: MED04a01 from Luxembourg exhibit a rather peculiar morphology, which is similar to that of *Anomoeodus* species (e.g. Woodward 1895; Kriwet 1999, 2002). However, the pycnodont genus *Anomoeo-*

dus is not known before the Lower Cretaceous with certainty (Kriwet 2002).

Late Triassic pycnodonts are only known from the Alpine Triassic so far. Three genera, *Brembodus*, *Eomesodon*, and *Gibbodon*, were described. *Gibbodon* is known by three specimens from North Italy all belonging to a single species, *G. cenensis* (Tintori 1981). The prearticular dentition of *Gibbodon* is, unfortunately, unknown. The teeth of the vomer are typical tritorial, knob-like and smooth without any ornamentation or otherwise structured surface as it is found in the Germanic basin specimens. In addition, the teeth of *Gibbodon* differ in having a lower profile. However, it is not clear whether the lack of any ornamentation is related to abrasion and whether the teeth of the prearticular exhibited the same morphology.

Another, very rare faunal element of the Alpine marginal sea is *Eomesodon hoeferi*, which was originally described by Gorjanovic-Kramberger (1905) from the Norian of Hallein (Austria). Teeth of *E. hoeferi* exhibit, when unworn, an apical furrow, which follows the outer contour of the tooth. A tubercle may be present in the indent. The indent is either surrounded by a ring of widely spaced tubercles or by a wrinkled and crenulated ring, which gives the margins of the tooth crown a notched or rugged appearance when worn down. This abrasion pattern is quite distinctive from that found in main teeth of the Germanic basin specimens.

On the contrary, *Brembodus ridens* TINTORI 1981 is the most common Upper Triassic pycnodont fish. It is known by some dozen specimens with well-preserved dentitions (e.g. Tintori 1981, pl.96). The dentitions are considerably larger and more massive than those of the Germanic basin specimens. A rather broad variability in tooth arrangement and morphology is present. However, all teeth are arranged in five longitudinal rows, which are closely arranged contacting each other. Teeth of the main row are oval to round. There are some indications of a shallow apical indent in teeth of the second lateral row. The main distinguishing character to the Germanic basin specimens is the size of the prearticular and the irregular size of main teeth. In addition, the tooth rows are more closely arranged and in contact with each, a feature that is absent in the specimens described herein.

Other pycnodonts with five prearticular tooth rows are *Anomoeodus* (at least some species, Kriwet 1999), *Eomesodon barnesi*, and probably *Polygyrodus*. However, the number of prearticular tooth rows is not known in several pycnodonts (e.g. *Acrotemnus*, *Arduafrons*, *Ellipsodus*, *Nonaphalagodus*, "*Nursallia*" *goedeli*, "*Nursallia*" *veronae*, *Paramesturus*, *Tibetodus*, *Trewavasia*, *Uranoplosus*). Although much progress has been made in the last years to establish dental characters of different taxa (e.g. Kriwet 1999, 2000a, 2000b, 2001b, 2002, Kriwet et al. 1997, Kriwet et al. 1999) a lot of important data from comparable many taxa is still lacking. In addition, the prearticular dentition of the contemporaneous pycnodont *Gibbodon* is unknown. Consequently, it is not possible to identify the pycnodont remains described herein. The presence of two lateral and medial prearticular tooth rows is very uncommon for pycnodonts and might prove useful for its taxonomic assignment in the future when more material of *Gibbodon* is available. The remains from the Germanic basin are attributed to Pycnodontiformes without any further systematic designation for the moment. Nevertheless, they represent the first Late Triassic pycnodont fish remains in the Germanic basin and contribute to our knowledge about the diversity and distribution of Late Triassic pycnodonts.

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Plate 1

Figs. 1–5 Complete prearticular dentition of Pycnodontiformes inc. sed. (NNHML MO162: HLV3–1) from the upper Norian of Belgium. 1, in occlusal view. Scale bar equals 1.0 mm. 2–5, close-ups of lateral teeth displaying morphology and occlusal structure. Scale bars represent 0.25 mm.

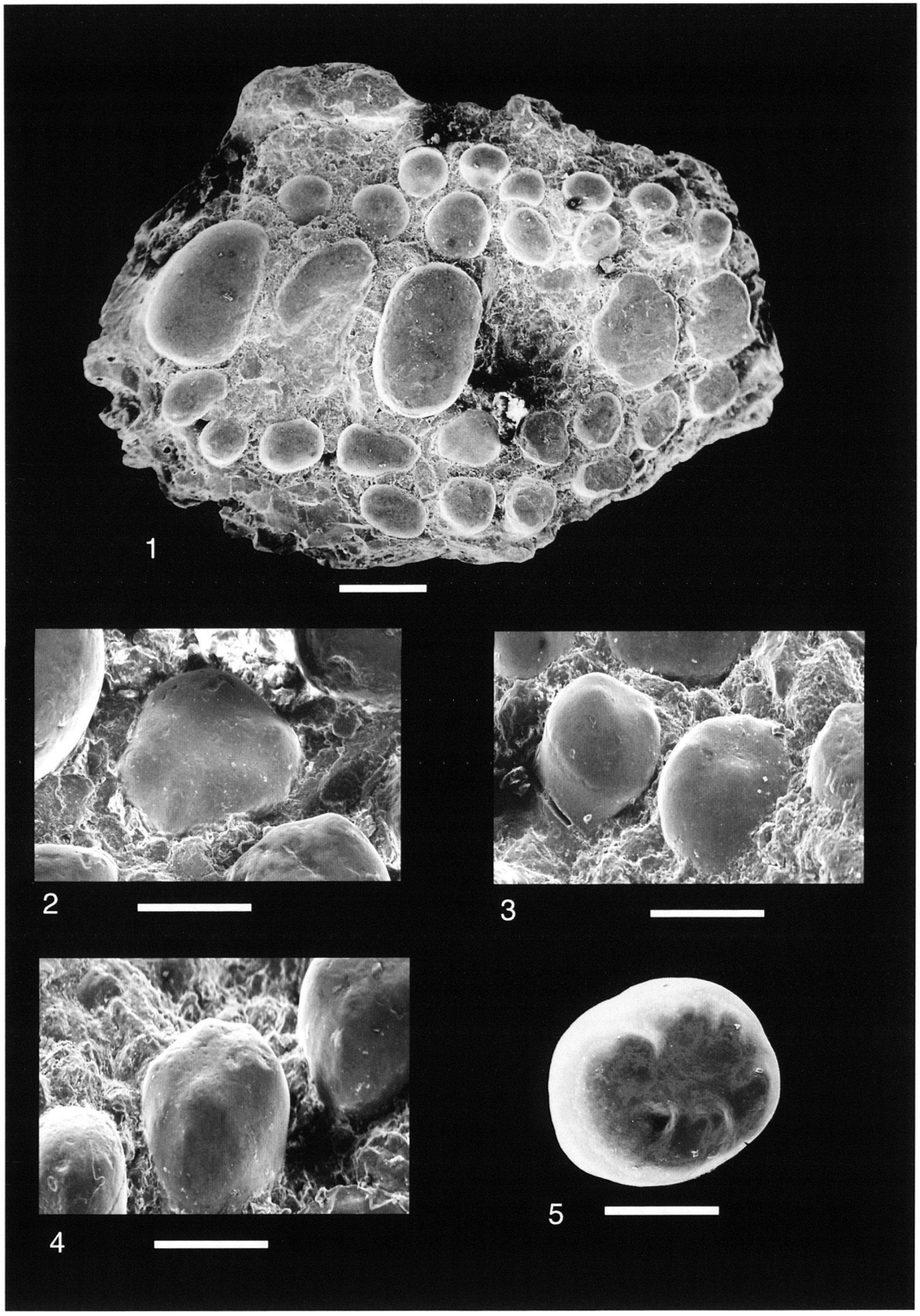
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Plate 2

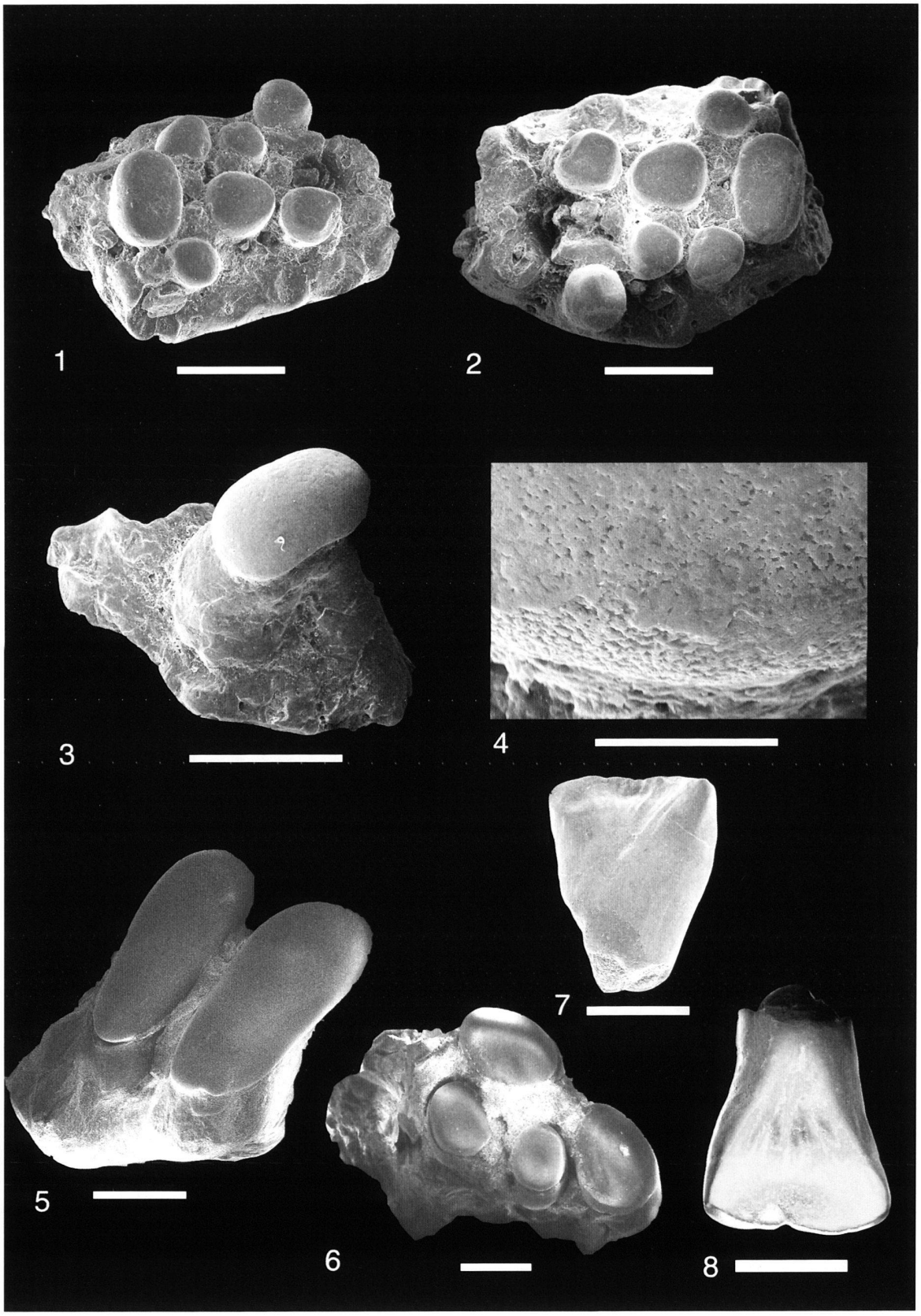
Figs. 1–2 Incomplete dental remain (NNHML MO162: HLV3-2) from the upper Norian of Belgium. 1, latero-occlusal aspect. 2, occlusal aspect.

Figs. 3–4 Isolated grinding tooth (NNHML MO162: HLV3-3) from the upper Norian of Belgium. 3, latero-occlusal aspect. 4, close up of acrodine surface. Scale bar represents 50 μm.

Fig. 5 Incomplete dental remain (NNHML MO162: MED04a) from the upper Norian of Luxembourg, occlusal aspect.

Fig. 6 Dental remain (NNHML MO162: MED04b) from Luxembourg, occlusal aspect.

Figs. 7–8 Isolated incisiform grasping teeth from Luxembourg, labial views. 7, specimen NNHML MO162: MED05a01. 8, specimen NNHML MO162: MED05a02. Scale bars represent 0.5 mm if not otherwise stated.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