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Fish remains from the Rhaetian (Late Triassic) of Winterswijk, the Netherlands (Pisces: Chondrichthyes and Actinopterygii)

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Original Article

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Abstract

Chondrichthyan and actinopterygian fish remains from Rhaetian (c. 208.05–201.36 Ma) or perhaps Late Norian deposits in the Winterswijk quarry are described. The most abundant taxon is the actinopterygian *Gyrolepis albertii*, followed by the chondrichthyan *Lissodus minimus*. Furthermore, the palaeopterygian actinopterygians *Saurichthys longidens* and *Birgeria acuminata*, and some teeth of neopterygians *Sargodon tomicus*, '*Lepidotes*' sp. and indeterminate pycnodontiforms are recorded in addition to the chondrichthyans *Rhomphaiodon minor*, *Parascylloides turnerae* and some '*Hybodus*' cf. *cuspidatus* (senior synonym of *H. cloacinus*). Chondrichthyan dermal denticles, actinopterygian scales and gill rakers, tooth plates, and some fish bones were also found. There is considerable faunal resemblance to the various localities from the Rhaetian of the British Penarth Group, although it depends on the location as to whether chondrichthyans or actinopterygians prevail in the samples. On average, there are more chondrichthyan teeth present in the British samples than actinopterygian teeth, which is opposite to the situation in Winterswijk. That might be explained by different ecological circumstances, such as lower oxygen levels in bottom waters in Winterswijk and freshwater input and/or changes in salinity in the UK.

Introduction

In the active limestone quarry of Winterswijk (Eastern Netherlands, Fig. 1), micritic limestone of Anisian (Middle Triassic, c. 247.2–242 Ma) age is being commercially exploited. In order to reach the Anisian strata, an overburden of respectively Rhaetian (Late Triassic) claystone, Rupelian (early Oligocene) clay and Late Pleistocene boulder clay has to be removed; it is mostly discarded. In 1989, Rhaetian infillings of a sinkhole (subrosion pipe) within the Anisian sediments were discovered and their contents studied. The sediment plug had a diameter of about 30 m and had a total height of about 2 m (Oosterink et al., 2005, 2006; Klompmaker & Van den Berkmortel, 2007). Several papers described the fossil content of the subrosion infill. Herngreen et al. (2005) and Klompmaker et al. (2010) described palynomorphs. Klompmaker et al. (2010) also described bivalves. Additionally, some Hettangian (Earliest Jurassic) psiloceratid ammonites were discovered (Klompmaker & Van den Berkmortel, 2007). More recently, Diependaal & Reumer (2021) described the Rhaetian chondrichthyan and actinopterygian remains found in this material. The subrosion pipe and its infill cannot be sampled anymore since its removal due to the advancing quarry face.

In 2004, a second and considerably larger Rhaetian deposit consisting of black claystones was found in situ in the northern face of the quarry (Fig. 2). Its age was established based on discovered palynomorphs (Herngreen et al., 2005). Thus, the age of the material is here tentatively considered to be Rhaetian (c. 208.05–201.36 Ma; Galbrun et al., 2020), although no absolute dating has so far been performed and a possible latest Late Norian age cannot be explicitly excluded. An ongoing research project into the sedimentology and palynology of the deposits may provide a better age constraint. Hence, we use the term Rhaetian with some caution.

So far, the only description of macrofossils from the newly discovered Rhaetian deposits in Winterswijk concerns ophiuroid echinoderms (Thuy et al., 2012). Here, we describe chondrichthyan and actinopterygian remains sampled in 2018. They are compared with the material from the subrosion pipe (Diependaal & Reumer, 2021) and with the abundantly preserved Rhaetian fish material from the British Penarth Group (Korneisel et al., 2015; Nordén et al., 2015; Lakin et al., 2016; Slater et al., 2016; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022). The material here described concerns the first in situ Rhaetian from the Netherlands, and it considerably increases our knowledge of the Dutch Triassic.

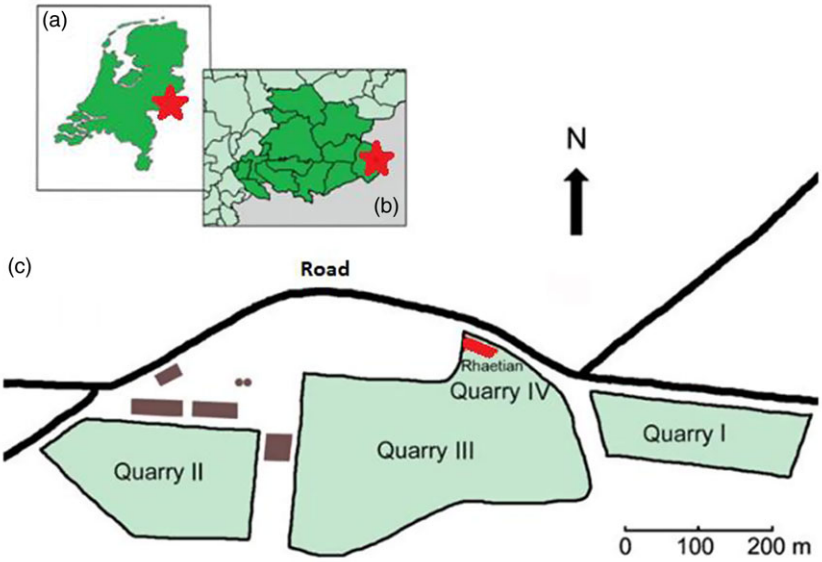

Figure 1. The location of the the Winterswijk quarry and its Rhaetian deposit. a. In the eastern Netherlands, b. In the Achterhoek area, c. Schematic plan of the quarry with the Rhaetian deposit in the northernmost part of quarry IV. Adapted after Klompmaker et al. (2010).

Figure 2. The exposure of the Rhaetian in the northern part of quarry IV. The unconformity between the black Rhaetian and the grey micritic Anisian limestone is well visible on the bottom the trench.

Material and methods

The studied material had been collected during an excavation in 2018 organised by Naturalis Biodiversity Center and Utrecht University in collaboration with the Muschelkalk Working Group. In 2019, the collected samples that had temporarily been stored away were soaked in Mullrose cleaning vinegar (9% acetic acid), washed and sun-dried, and the residue was then hand-picked for fossils under a binocular microscope. For some of the fossils, some extra treatment was needed in order to clean them better. This was again done by using acetic acid (Jeppsson et al., 1999). The fossils did not need any further treatment for their preservation. The material is stored in the collection of the Department of Earth Sciences (Utrecht University). The samples have the uniform collection code WWR18 (for Winterswijk Rhaetian 2018), and individual teeth and scales are numbered (e.g., WWR18-052).

Terminology for the *Lissodus minimus* teeth is after Duffin (1985, 1998a). The terminology for the dermal denticles is after Duffin (1998a).

The teeth are described/categorised based on their morphology; their size is less relevant as fishes change teeth throughout their lifetime (Botella et al., 2009) and as it depends on the position of the teeth (e.g., distal or mesial) in the heterodont dentitions (Duffin, 1985). The remains were only counted when at least two-thirds of the fossil including the major cusp were present and recognisable. The teeth of *Lissodus minimus* were only counted when the central part combined with at least one of the mesial or distal ‘wings’ are present. The photographs were made by using a Keyence VHX-500 digital microscope.

Systematic paleontology

Class Chondrichthyes (Huxley, 1880)
Order Hybodontiformes (Patterson, 1966)
Genus *Lissodus* (Brough, 1935)

Duffin (1985) published the following diagnosis: ‘Teeth up to 7 mm long, showing moderate heterodonty. The principal central cusp is highest in mesial and anterolateral teeth. The labial peg is well developed in mesial teeth, but becomes progressively weaker laterally through the dentition. The occlusal crest is moderate. Lateral cusplets may be developed (up to five pairs). The crown is robust and low in lateral teeth. The crown may be ornamented by moderate vertical ridges. The crown–root junction is deeply incised in mesial teeth, but becomes progressively less so laterally. Specialised foramina are present.’

Rees & Underwood (2002) emended the diagnosis for the genus *Lissodus* as follows: ‘Jaws deep, lower jaw tapering anteriorly;

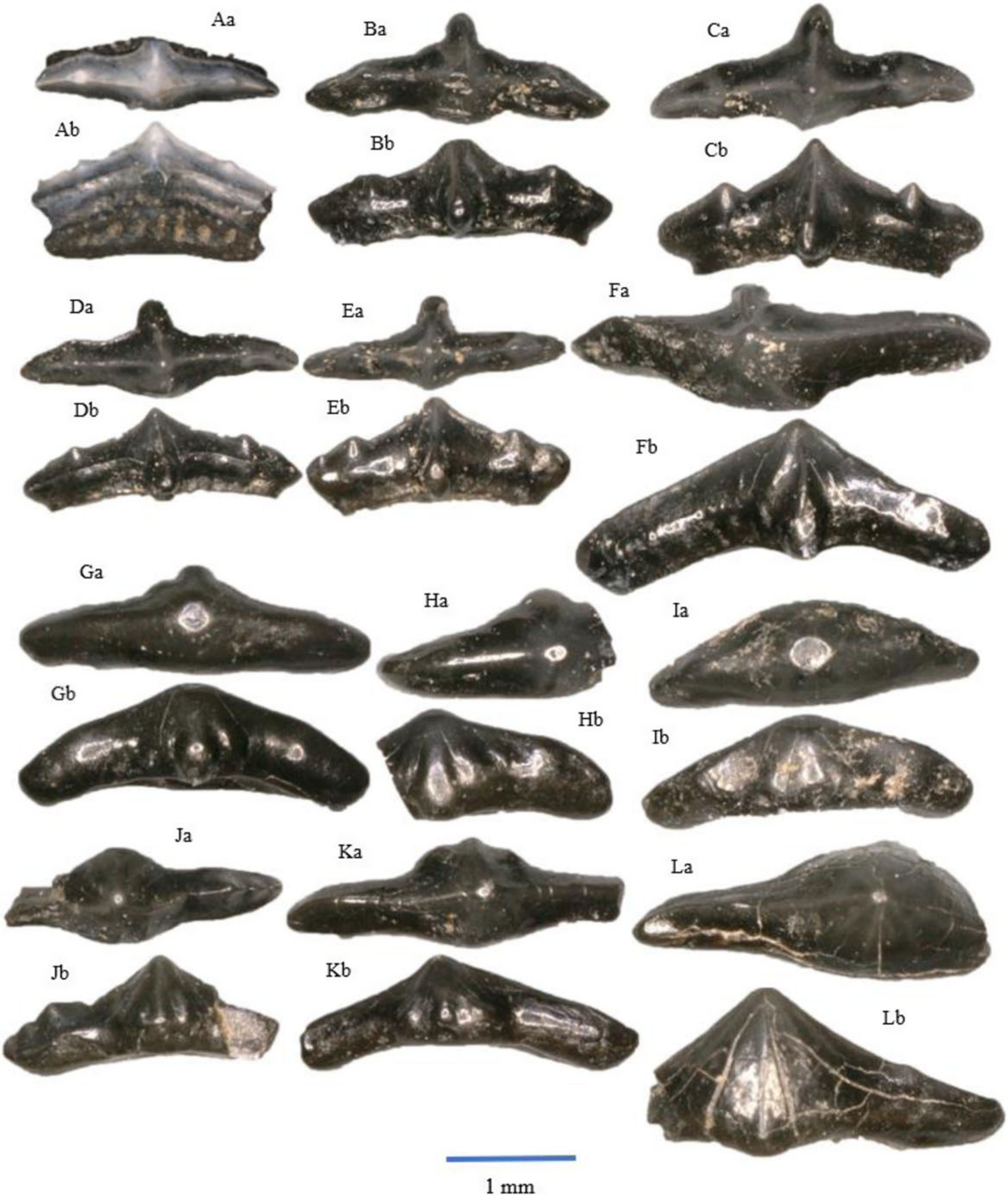

Figure 3. All a = occlusal view, b = labial view. *Lissodus minimus*, morphotype I: A – WWR18-0081; B – WWR18-0085; C – WWR18-0087. *Lissodus minimus*, morphotype II: D – WWR18-0093; E – WWR18-0095. *Lissodus minimus*, morphotype III: F – WWR18-00720 ; G – WWR18-0075. *Lissodus minimus*, morphotype IV: H – WWR18-0107; I – WWR18-0112. '*Hybodus*' cf. *cuspidatus*: J – WWR18-0094; K – WWR18-0074; L – WWR18-0116.

anterior teeth with moderately to well-developed central cusp, occlusal crest and labial protuberance; occlusal face of labial protuberance sloping gently towards crown base; crown shape almost triangular in occlusal view; lateral teeth lower, larger, more mesio-distally expanded; cusps, occlusal crest, and labial protuberance poorly developed; root lingually inclined, lower than crown, not as voluminous; single, strictly horizontal row of small circular foramina near crown–root junction; basal plate of cephalic spines 'T-shaped' with terminally expanded lobes.'

Lissodus minimus (Agassiz, 1836)
Fig. 3A–I

At least 800 teeth in our sample can be attributed to this species. They are low-crowned, wide, crescent-shaped and show moderate heterodonty. The central cusp is the highest one; depending on the position in the jaw there may be none, one, two or three lateral cusplets. A labial peg is generally present, but its development varies, as does the presence of striations.

Here, we differentiate four morphotypes. They differ morphologically in relation to the position of the teeth in the upper and lower jaws: more distal (close to the symphyseal symmetry axis) or more mesial.

Morphotype I (Fig. 3A-C). The crown is narrow in labial–lingual direction, and in mesial–distal direction the teeth are wide.

There is one centrally placed main cusp and one lateral cusplet on each side. These lateral cusplets are smaller (lower) than the main cusp. An occlusal crest runs over the apex of the main cusp and the lateral cusplets. The narrow labial peg is strongly developed. The crowns tend to be unornamented, although some specimens contain some vertical striations on the main cusp. The teeth are mesio-distally straight rather than curved; they are known as anterior teeth (Duffin, 1998a, text fig. 20C; Korneisel et al., 2015; Slater et al., 2016; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022). The size ranges between about 1.5 and 3 mm in the mesial–distal direction.

Morphotype II (Fig. 3D,E). The teeth have a large centrally placed main cusp and two or three more or less conspicuous lateral cusplets on each side of it. Ornamentation as in morphotype I and limited to the main cusp only. The teeth are straight or slightly curved, and the labial peg is mostly strongly developed. The presence of the lateral cusplets indicate that these teeth are anterolateral teeth (Duffin, 1998a, text fig. 20B; Korneisel et al., 2015; Slater et al., 2016; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022). The size ranges between about 2 and 3 mm.

Morphotype III (Fig. 3F,G). These teeth have a high main cusp, but lateral cusplets are not present. The occlusal crest is shallow, but still visible. The teeth are slightly asymmetrical, and ornamentation is only present on the main cusp. A labial peg is present but smaller than the labial pegs of morphotypes I and II. The teeth, having a straight outline, are lateral teeth (Duffin, 1998a, text fig. 20A; Korneisel et al., 2015; Slater et al., 2016; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022). The size ranges between about 1.5 and 3.5 mm.

Morphotype IV (Fig. 3H,I). The main cusp is not as large as in morphotypes I, II and III. Lateral cusplets are absent, and the occlusal crest is very shallow. The crowns are usually flat. The teeth are more ornamented compared to the morphotypes mentioned above. The ornamentation consists of vertical striations running from the apex of the main cusp to the lower part of the crown and at the place where lateral cusplets occur in other morphotypes. However, the ornamentation is not always visible. The labial peg is mostly weakly developed, and the teeth are either straight or slightly curved. These teeth are posterolateral teeth (Duffin, 1998a, text fig. 20D; Korneisel et al., 2015; Slater et al., 2016; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022). The size ranges between about 2 and 3 mm.

Remarks

The genus *Lissodus* ranges from the Early Triassic (Scythian) to the Middle Cretaceous (Albian), although the literature (e.g., Duffin, 1985; Duncan, 2004) mentions the genus from the Early (Tournaisian) and Late (Westphalian) Carboniferous. Although Duffin (1985, p. 118) and Duncan (2004) suppose that the Carboniferous sharks they describe belong to *Lissodus*, the time gap of at least 150 Ma between the Westphalian and the Early Triassic seems to exclude that the Paleozoic and Mesozoic sharks are congeneric; here, we suppose it to be an example of convergent evolution. Rees & Underwood (2002) provided an updated revision of the genus, excluding the Paleozoic taxa from the genus, and the British Carboniferous material was subsequently transferred to the genus *Reesodus* Koot et al. (2013) by Smith et al. (2017).

Originally, this species was described as *Acrodus minimus* (Agassiz, 1836), but it was later incorporated into the genus *Lissodus* by Duffin (1985). The different morphotypes are sometimes difficult to distinguish; there seems to be 'gliding scale' regarding the shape. A single tooth may therefore feature characteristics that put it between morphotypes. The majority of the available teeth only feature a crown, the root being broken off. Only three specimens (e.g., Fig. 3A) still have their roots. The crowns themselves are often broken too. Many loose 'wings' (or arms) have been found in the samples. The structure and shape of the teeth indicate that this shark was durophagous and most likely fed on shelled, benthic organisms (Allard et al., 2015; Cross et al., 2018; Williams et al., 2022).

This species has also been mentioned from the UK (Duffin, 1985, 1998a; Cuny & Risnes, 2005; Foffa et al., 2014; Allard et al., 2015; Nordén et al., 2015; Korneisel et al., 2015; Slater et al., 2016; Whiteside et al., 2016; Lakin et al., 2016; Whiteside & Duffin, 2017; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022), Eastern Europe (Chrząstek, 2008; Michalík et al., 2013; Ősi et al., 2013; Posmoşanu, 2015; Botfalvai et al., 2019; Szabó et al., 2019) and Western Europe (Duffin, 1993; Duffin & Delsate, 1993; Cuny, 1995; Godefroit et al., 1998; Henz & Hertel, 2011; Cuny et al., 2013; Sander et al., 2016; Diependaal & Reumer, 2021).

Genus '*Hybodus*' (Agassiz, 1837)
'*Hybodus*' cf. *cuspidatus* (Agassiz, 1836)
Fig. 3J,K,L

A few of our *Lissodus*-like specimens show secondary cuspules at the labial base of the three principal striations that run from the tip of the main cusp to the lower edge of the tooth. Agassiz (1836, tome III, p. 194) described a species as *Hybodus cuspidatus* and added as a diagnostic: 'La base de la couronne est très-étroite, et les plis y déterminent souvent de petits bourrelets, comme dans le *H. reticulatus* (. . .)' (translated: The base of the crown is very narrow, and the striations often bear small cuspules, like in *H. reticulatus*). In addition, the central cusp is relatively high.

Remarks

The taxon *cuspidatus* was not included into *Lissodus* by Rees & Underwood (2002) in their revision of the genus; Seilacher (1943) included it into *Polyacrodus*. We use the species name *cuspidatus* here rather than *cloacinus*, as Dorka (2003) has shown that the latter is invalid and should be considered a junior synonym of *cuspidatus*. As Rees (2008) considered the generic name *Polyacrodus* to be a nomen dubium and as the genus *Hybodus* is limited to two species including the type species *H. reticulatus* (Maisey, 1986), we here place the generic name '*Hybodus*' between quotation marks. We think that our few specimens that show small secondary cuspules at the base of the striations cannot be considered to fall within the intraspecific variation of *Lissodus minimus*, but belong to a different species, to which the epiteth *cuspidatus* seems most appropriate. Here, we hesitatingly range them as '*Hybodus*' cf. *cuspidatus*, but this conclusion may be subject to further study when more material becomes available. It should be noted that only the large lateral teeth of *H. cuspidatus* (senior synonym of *H.* '*cloacinus*') have been described in the literature (e.g., Duffin, 1998a, Plate 26, fig. 5 or Lakin et al., 2016, fig. 6); none of the anterior or posterior teeth have yet been described. We attempt this here, for the first time, using '*Hybodus*' cf. *cuspidatus*. As our specimens have only one main cusp or lack secondary cusps, we think that they must be posterior teeth.

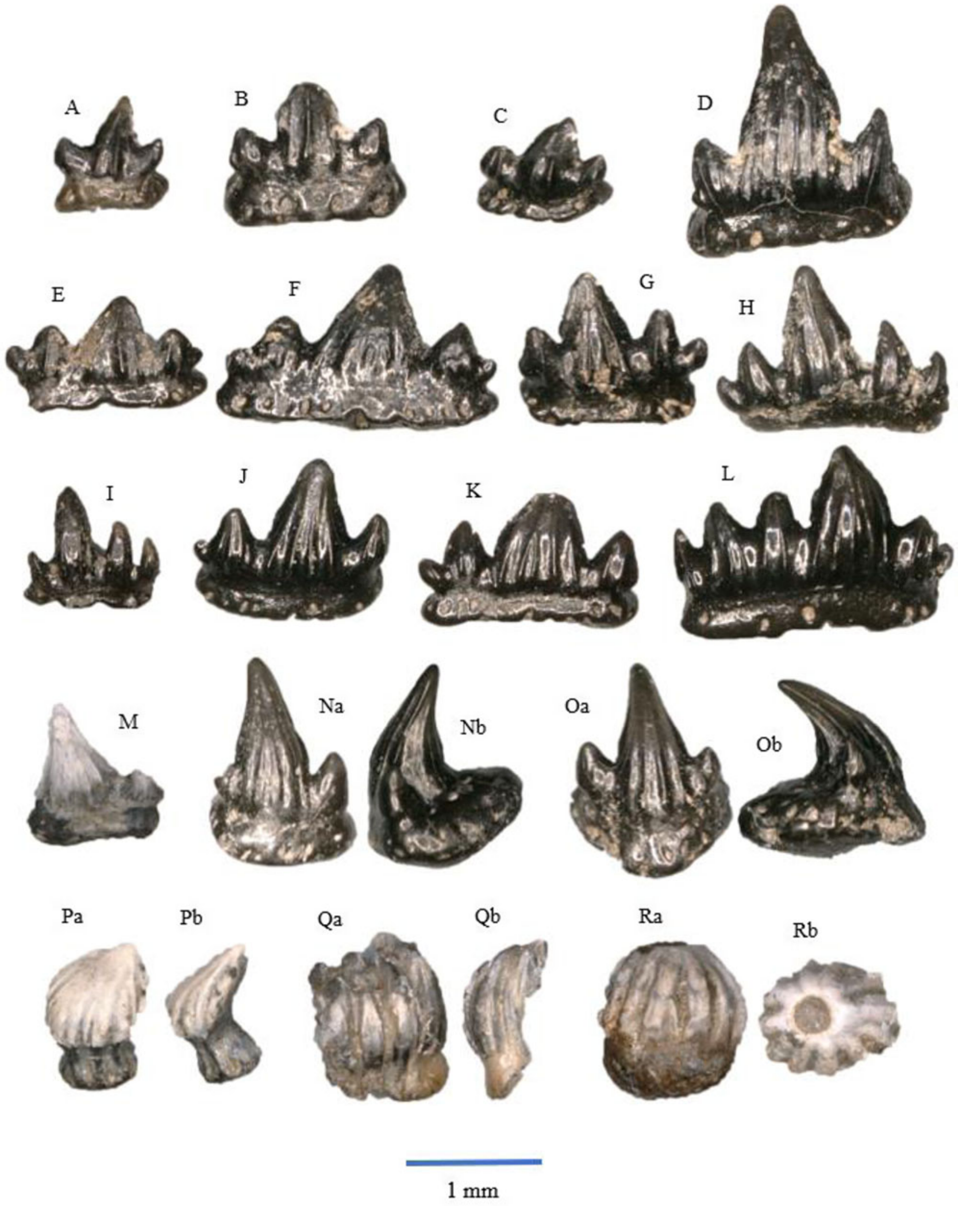

Figure 4. *Rhomphaiodon minor*, morphotype I: A – WWR18-0001; B – WWR18-0002; C – WWR18-0005; D – WWR18-0006. *Rhomphaiodon minor*, morphotype II: E – WWR18-0012; F – WWR18-0013; G – WWR18-0014; H – WWR18-0015. *Rhomphaiodon minor*, morphotype III: I – WWR18-0021; J – WWR18-0022; K – WWR18-0023. *Rhomphaiodon minor*, morphotype IV: L – WWR18-0032. *Rhomphaiodon minor*, morphotype V: M – WWR18-0318. *Parascylloides turnerae*: N – WWR18-0132, a = labial side, b = mesial–distal side, turned right; O – WWR18-0133, a = labial side, b = mesial–distal side, turned left. Chondrichthyan dermal denticles: P – placoid scale WWR18-0164, a = oblique view, b = lateral side, turned right; Q – ctenacanthoid scale WWR18-0168, a = anterior side, b = lateral side, turned right; R – hybodont scale WWR18-0169, a = lateral side, b = occlusal view.

Order Synechodontiformes (Duffin & Ward, 1993)
Genus *Rhomphaiodon* (Duffin, 1993)
Rhomphaiodon minor (Agassiz, 1833–43)
Fig. 4A–M

A total of 377 teeth can be linked to this species (excluding a similar amount of 377 detached central cusps, bringing the total number of teeth to over 750). The crown and root are separated by a strong angle or indentation in labial or buccal view, of often c. 90 degrees (see e.g., Fig. 4C, F and K). The main cusp is the highest, and it is ornamented by multiple vertical striations that start at the apex and run to the lower edge at the enamel–root junction. These striations might be absent as a result of weathering. The main cusp is located at the centre of the tooth, and there are lateral cusplets that are smaller than the central cusp and emerge directly from the root. The lateral cusplets also contain vertical striations. The teeth are either roughly symmetrical or somewhat asymmetrical in shape depending on the number and development of the lateral cusplets.

Here, we distinguish five different morphotypes of these teeth, two of them (I and II) regarding the symmetrical teeth and three other types (III, IV and V) regarding the asymmetrical teeth.

Morphotype I (Fig. 4A–D) concerns teeth with one lateral cusplet on each side, and morphotype II (Fig. 4E–H) shows two lateral cusplets on each side. The outer pair is lower than the inner pair. Morphotype III (Fig. 4I–K) concerns teeth that have one lateral cusplet on one side, while the other side has two; here again, the outer cusplets are lower than the inner cusplets. In morphotype IV (Fig. 4L), the teeth have two lateral cusplets on one side, while the other side has three, and finally, morphotype V (Fig. 4M) shows teeth that one lateral cusplet on one side, while the other side does not possess one. Morphotypes IV and V are rare in our sample with three and four specimens, respectively. In all five morphotypes, the root is very wide. These roots possess foraminae that run on the horizontal surface, although they are not always present. For the symmetrical ones, the (mesio-distal) width of the teeth ranges between about 1 and 2.5 mm, and the height ranges between about 0.75 and 1.5 mm. For the asymmetrical ones, the width of these teeth ranges between about 0.75 and 2 mm. The height ranges between about 1 and 2 mm. The broken and isolated main cusps may originate from somewhat larger teeth; they range in height between 1 and 2.5 mm.

Remarks

Originally, this species was described as *Hybodus minor* Agassiz, 1833–43 (Duffin & Gaździcki, 1977; Duffin & Delsate, 1993; Cuny, 1995; Duffin, 1998a; Godefroit et al., 1998; Cuny et al., 2013; Michalík et al., 2013). Similarities were found with the species *Rhomphaiodon nicolensis* (Duffin, 1993). Duffin (1998a) explained that '*Hybodus*' *minor* is to be considered a *nomen dubium*, as it is based on a fin spine and the taxon thus lacks diagnostic characters. It was later reassigned to *Rhomphaiodon minor*, because *Hybodus minor* teeth possessed haphazard crystalline enameloid, which was only known to be present in *Rhomphaiodon nicolensis* (Cuny & Risnes, 2005). Furthermore, the two species are said to be closely related as they are consistently found in association with the spine *Nemacanthus monilifer* (Cuny & Risnes, 2005).

The shape and structure of the teeth indicate that this species was a small predator (Lakin et al., 2016; Moreau et al., 2021). The species has also been mentioned from the UK (Duffin, 1998a; Cuny & Risnes, 2005; Foffa et al., 2014; Allard et al., 2015; Nordén et al., 2015; Korneisel et al., 2015; Mears et al., 2016; Slater et al., 2016; Lakin et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022), Slovakia (Michalík et al., 2013) and Western Europe (Duffin and Delsate, 1993; Cuny, 1995; Godefroit et al., 1998; Cuny et al., 2013; Sander et al., 2016, Diependaal & Reumer, 2021).

Genus *Parascylloides* (Thies et al., 2014)
Parascylloides turnerae (Thies et al., 2014)
Fig. 4N,O

There are in total 35 teeth that can be assigned to this species. The main cusp of small teeth of *Parascylloides turnerae* is relatively large, and it curves significantly in a lingual direction. It tends to curve somewhat in sideways direction. The teeth may have no, one, or two symmetrically placed lateral cusplets that are small in size and emerge directly from the root of the tooth. The crown is heavily ornamented by strong widely spaced vertical ridges that start at the apex of the main cusp and continue until the root. The root has an oval shape in lingual–buccal direction, with the crown positioned on the labial side. It possesses several foraminae across its horizontal surface, although these openings are not always clearly visible. The root represents about 25% of the total tooth height, which ranges between about 1 and 1.5 mm.

Remarks

The teeth superficially resemble those of *Rhomphaiodon minor*. Sykes et al., (1970, plate 17, fig. 1) described a tooth of *P. turnerae* from Barnstone (UK) as an 'Indeterminate Hybodont dermal denticle of type A', stating: 'this resembles the minute teeth of *Hybodus minor*, with the typical root, nearly cylindrical crown, and inconspicuous lateral denticles'. The difference is that *P. turnerae* always possesses no more than one lateral cusplet on each side, while *R. minor* can have lateral cusplets in varying numbers. In addition, the root of *P. turnerae* is stretched in labial–lingual direction, while the root of *R. minor* is larger in the mesial–distal direction. Also, the main cusp of *P. turnerae* bends significantly more in the lingual direction, while the main cusp of *R. minor* is comparatively straight.

The teeth of *Parascylloides turnerae* were originally described as the symphyseals or parasymphyseals of *Rhomphaiodon nicolensis* (Cappetta, 2012), actually *R. minor* (see above), but they were reassigned to a new species, due to their frequency and morphological differences (Thies et al., 2014), with the following differential diagnosis: 'A tooth crown built by a large massive central cusp and one pair of minute lateral cusplets together with a tongue-shaped, labio-lingually expanded root showing a modified anaulacorhize vascularisation distinguishes the teeth of *Parascylloides* gen. nov. from the teeth of all other synechodontiform and neoselachian taxa in general'.

The frequency of these teeth that we find in our sample is quite different from that reported from Seinstedt ('47.5% of all of the neoselachian teeth and tooth fragments identifiable' or $144/(144 + 74) = 66\%$ of the total *R. minor* and *P. turnerae*; Thies et al., 2014) and at Barnstone (25,2% of the total of 493 *R. minor*, 12 *R. nicolensis* and 170 *P. turnerae* teeth; Thies et al., 2014). In our sample, they represent only 8,45% of the total of *R. minor* and *P. turnerae* ($35/(377 + 35)$) and could therefore be interpreted here as symphyseal or parasymphyseal teeth of *Rhomphaiodon minor*. Percentages equivalent to ours were also found at Saltford ($35/(547 + 35) = 6\%$, Moreau et al., 2021) and at Aust ($30/(387 + 30) = 7\%$, Cross et al., 2018).

P. turnerae has also been mentioned from the UK (Thies et al., 2014; Lakin et al., 2016; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022) and Germany (Thies et al., 2014; Sander et al., 2016). In Diependaal & Reumer (2021, fig. 1K), a tooth similar to these is described. There, it was incorrectly assigned to *Pseudodalatias barnstonensis*, and the tooth is here reassigned to *Parascylloides turnerae* (Chenal, in litt.; Duffin, in litt.).

Chondrichthyan dermal denticles
Fig. 4P–R

Three different denticle morphotypes are found in our sample.

Indetermined placoid scales (Fig. 4P): Seven of our specimens belong to this type of denticle. The denticle looks like a drop-shaped or leaf-shaped crown on a pedestal-like root. The crown is bent towards the posterior and ends in a blunt tip. It contains strong ridges and is flattened on the upper side and has a somewhat concave backside. The root does not feature any ornamentation. The height of these scales is about 1 mm. This type of scale is mentioned from many localities of the British Penarth Group (e.g., Duffin, 1998a; Landon et al., 2017; Cavicchini et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022) and also from Poland (Duffin & Gaździcki, 1977) and Luxemburg (Delsate & Duffin, 1999).

Ctenacanthoid scales (Fig. 4Q): This type of denticle shows a wide base bearing multiple more or less similar cusps. Those cusps form the crown and are bending backwards, which results in a convex shape. There are two variations of this type of denticle. The cusps of the first type (27 specimens) are roughly the same length, while in the second type (5 specimens), the outer cusps are higher than the central ones if present. The width of these ctenacanthoid scales ranges between about 0.75 and 1.5 mm. Similar scales are found in other localities (e.g., Duffin, 1998a; Mears et al., 2016; Landon et al., 2017; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022).

Hybodont scales (Fig. 4R): This type of denticle appears as a thick circular knob on a flat circular or slightly elliptical root or pedestal. The knob is ornamented by thick radially oriented vertical ridges, sometimes giving it a star-like shape. The top is smooth and may contain a central depression, probably due to wear. The width ranges between about 0.5 and 1.5 mm at their widest point. This type of denticle is known as hybodont morphotype (e.g., Duffin & Delsate, 1993; Mears et al., 2016; Landon et al., 2017; Moreau et al., 2021; Williams et al., 2022).

Remarks

Dermal denticles are known from most of the Rhaetian localities described from the UK (Sykes, 1974; Korneisel et al., 2015; Nordén et al., 2015; Lakin et al., 2016; Mears et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022), and also from Poland (Duffin & Gaździcki, 1977), France (Cuny, 1995; Cuny et al., 2013), Luxembourg (Delsate & Duffin, 1999), and the Winterswijk subrosion pipe from the Netherlands (Diependaal & Reumer, 2021). Their exact taxonomic attribution is problematic.

Class Osteichthyes (Huxley, 1880)
  Subclass Actinopterygii (Cope, 1887)
    Order Saurichthyiformes (Aldinger, 1937)
      Family Saurichthyidae (Owen, 1860) (sensu Stensiö, 1925)
        Genus *Saurichthys* (Agassiz, 1835)
        Saurichthys longidens (Agassiz, 1835)
    Synonym: *Severnichthys acuminatus* (Agassiz, 1835) partim
        Fig. 5A–D

The teeth of *Saurichthys longidens* are elongated and usually straight in shape, although some specimens have a slightly sigmoidal shape (Fig 5A). The teeth consist of an acrodin cap and a shaft. The cap comprises between 10 and 30% of the total preserved tooth length. It has a conical shape and lacks ornamentations. In our material it usually has a black colour, although some specimens have a translucent cap. The junction between the cap and the shaft is not well pronounced, although sometimes marked by a faint ridge. The shaft has an ornamentation of longitudinal ridges; sometimes these ridges may be worn. The ridges do not continue in the acrodin cap, thus marking the boundary cap and shaft. The base of the tooth is often flared, and the tooth usually has a somewhat oval circumference. The length of the teeth ranges between 1 and 6 mm. In our sample, a total of 589 teeth can be assigned to this species.

Remarks

Originally, this species was described as *Saurichthys longidens* by Agassiz (1835). In 1994, *Saurichthys longidens* and *Birgeria acuminata* were merged into the new genus *Severnichthys* (Storrs, 1994). However, the validity of this genus is disputed (see Diependaal & Reumer, 2021). *Saurichthys* was most likely a piscivorous predator (Moreau et al., 2021), as indicated by their sharp teeth.

The species has also been mentioned from the various localities of the Penarth Group in the UK (Duffin, 1998a; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Slater et al., 2016; Lakin et al., 2016; Mears et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022), Eastern Europe (Duffin & Gaździcki, 1977; Michalík et al., 2013; Botfalvai et al., 2019) and Western Europe (Bürgin & Furrer, 1993; Duffin & Delsate, 1993; Delsate & Duffin, 1999; Diependaal & Reumer, 2021).

Order Birgeriiformes (Heyler, 1969)
  Family Birgeriidae (Aldinger, 1937)
    Genus *Birgeria* (Stensiö, 1919)
      Birgeria acuminata (Agassiz, 1835)
      synonym: *Severnichthys acuminatus* (Agassiz, 1835) partim
      Fig. 5E–G

The teeth of *Birgeria acuminata* are elongated and have a conical blade-like shape. They consist of an acrodin cap and a shaft. The labial side of the cap tends to be smooth and unornamented, although some specimens do contain some thick vertical ridges on this side. These two ridges can be referred to as lateral carinae, giving it a lentil-shaped cross section with the lingual side being more convex than the labial side. The lingual side of the teeth is ornamented by vertical ridges. The acrodin cap comprises about 30–50 per cent of the total tooth length. There often is a prominent ridge that separates the cap from the shaft.

On the shaft, the teeth are ornamented by very fine vertical striations. In some specimens, the fine striations on the labial side can be hardly visible or they have disappeared due to erosion. The flattening on the labial side of the acrodin cap continues further downwards but is gone at the base of the tooth, which results in a mostly circular cross section at the base. The majority of the teeth are found with both the cap and shaft together, but sometimes, only the cap is found. The total length of the teeth ranges between 1 and 3.5 mm. A total of 229 teeth can be linked to this species.

Remarks

The teeth somewhat resemble the teeth of *Saurichthys longidens*, but there are some significant differences. The acrodin caps of *Saurichthys longidens* are completely unornamented, and they have a conical shape and a circular cross section. On the other hand, the caps of *Birgeria acuminata* do feature ornamentation, especially on the lingual side, and the shape is more blade-like as a result of the presence of lateral edges. The shaft of *Saurichthys longidens* is long and features strong vertical ridges on its surface, while the shaft of *Birgeria acuminata* is shorter and is ornamented by very fine vertical striations.

This species was originally described as *Saurichthys acuminatus* by Agassiz (1835). Then, Savage & Large (1966) reassigned the species to the genus *Birgeria* as *Birgeria acuminata*, since the large and stout lower jaw of *Birgeria acuminata*, as described and depicted by them, does not match with the slender and elongated morphology of the *Saurichthys* skull (Rieppel, 1985). Bürgin & Furrer (1993) provided a more elaborate discussion on the differences between the genera *Birgeria* and *Saurichthys* regarding their teeth. Shortly thereafter, Storrs (1994) merged both *Birgeria acuminata* and *Saurichthys longidens* into the new genus *Severnichthys*. The morphological impossibility of this merger was discussed by Diependaal & Reumer (2021), who separated the two taxa again into the original different genera; Tintori & Lombardo (2018) expressed a similar opinion. Tackett et al. (2022) also mentioned the taxonomic problems pertaining *Severnichthys*, *Saurichthys* and *Birgeria*, without however reaching a conclusion. *B. acuminata* was most likely a predator (Moreau et al., 2021).

The species has also been mentioned from the many Rhaetian localities in the UK (Duffin, 1998a; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Slater et al., 2016; Lakin et al., 2016;

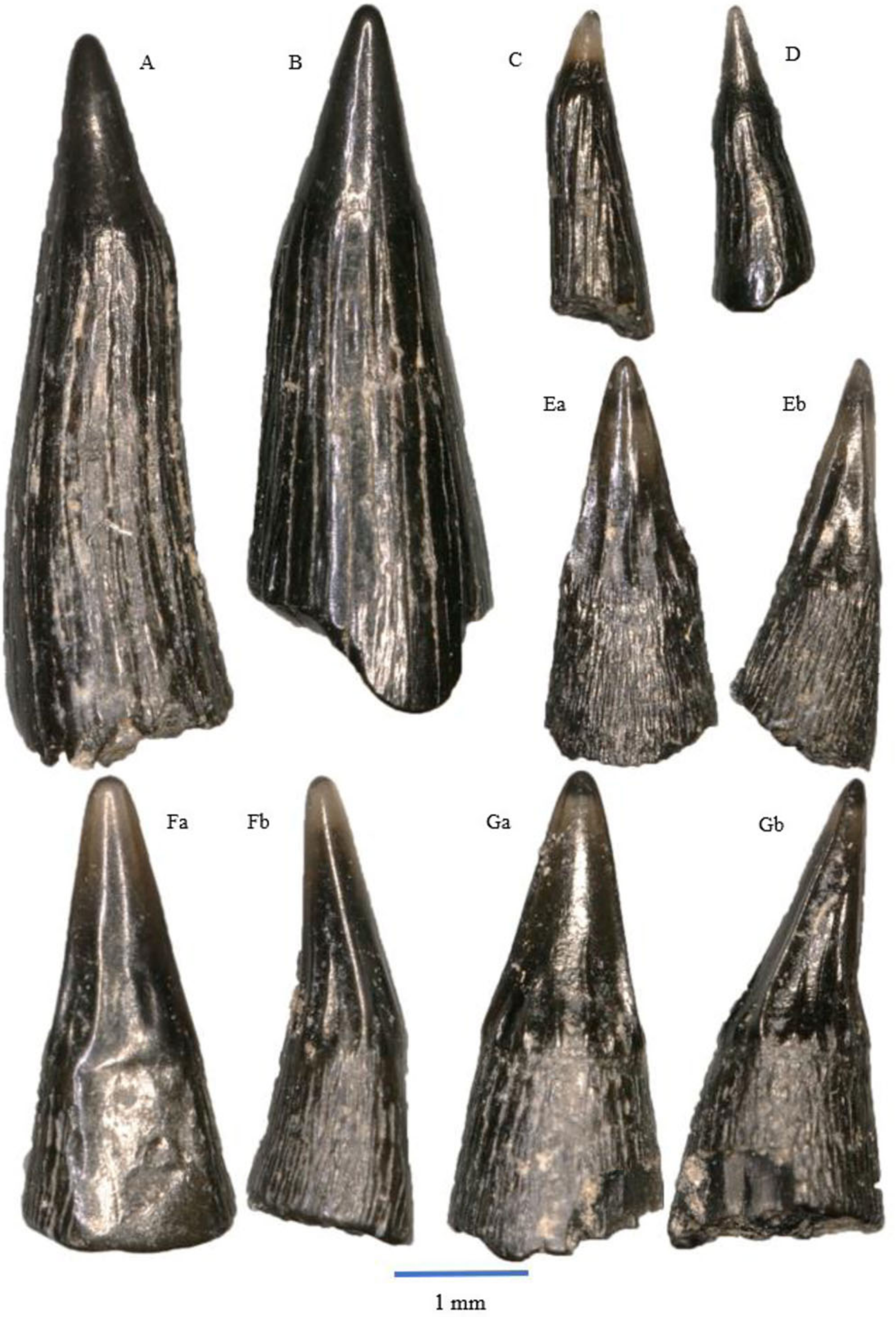

Figure 5. *Saurichthys longidens*: A – WWR18-0189; B – WWR18-0190; C – WWR18-0183; D – WWR18-0184. *Birgeria acuminate:* E – WWR18-0197, a = labial side, b = mesial–distal side, turned left; F – WWR18-0199, a = labial side, b = mesial–distal side, turned left; G – WWR18-0200, a = labial side, b = mesial–distal side, turned right.

Mears et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022), from Eastern Europe (Duffin & Gaździcki, 1977; Michalík et al., 2013; Botfalvai et al., 2019; Szabó et al., 2019) and from Western Europe (Bürgin & Furrer, 1992; Duffin & Delsate, 1993; Godefroit et al., 1998; Delsate & Duffin, 1999; Sander et al., 2016; Diependaal & Reumer, 2021).

Order Palaeonisciformes (Hay, 1902)
Family Palaeoniscidae (Vogt, 1852)
Genus *Gyrolepis* (Agassiz, 1835)

Gyrolepis albertii (Agassiz, 1835)
Fig. 6A–F

The teeth of *Gyrolepis albertii* are elongated and slender. Like the two actinopterygian species described above, they consist of an acrodin cap and a shaft. The overall tooth has a distinct curved shape. The straight acrodin cap is unornamented and small compared with the rest of the tooth, about 10% of the total tooth length. The cap has a conical shape and is often black in colour, although some tips are translucent. The apex of the cap is often sharp, but there are specimens where the cap is more smoothened,

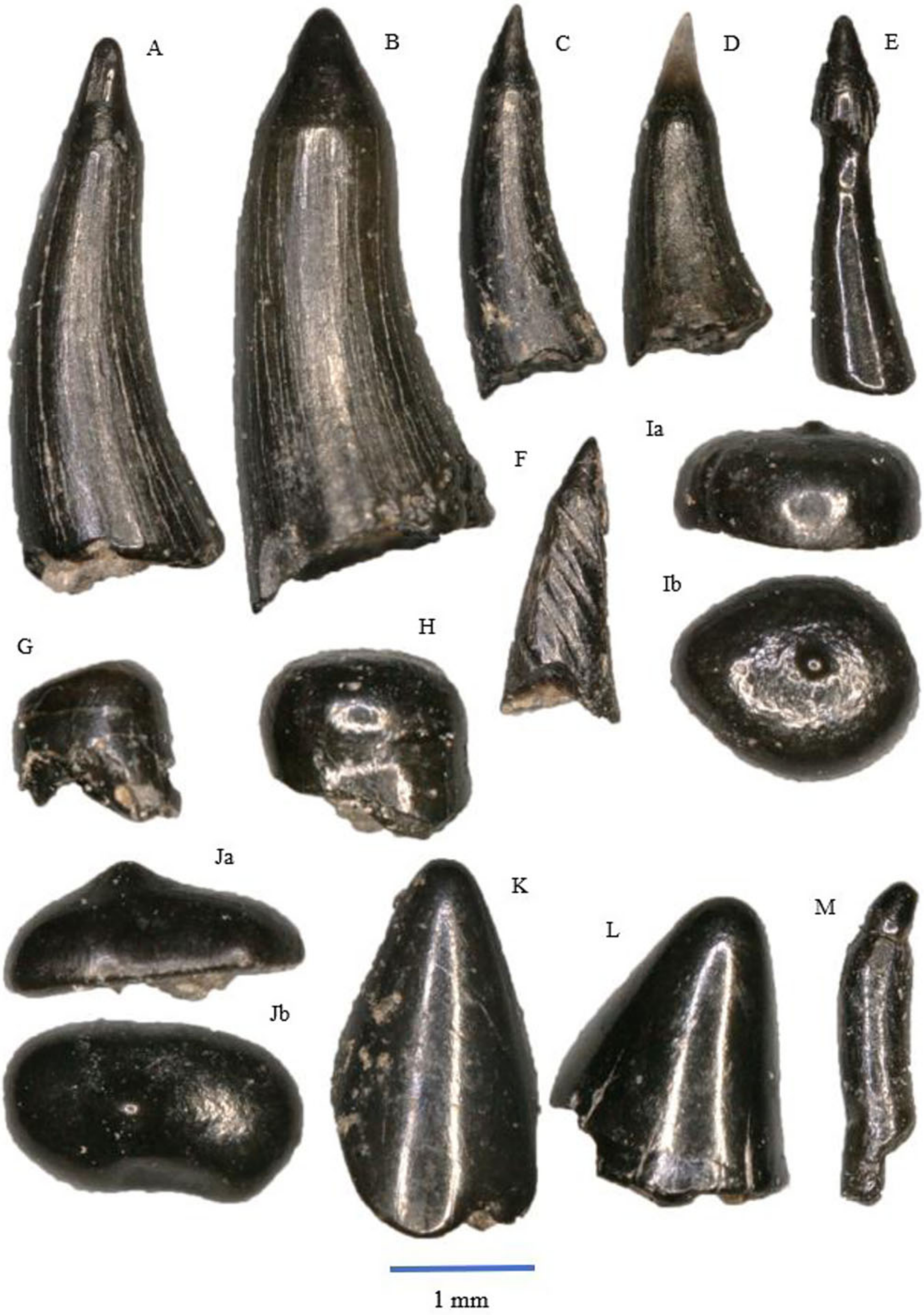

Figure 6. *Gyrolepis albertii:* A – WWR18-0177; B – WWR18-0174; C – WWR18-0173; D – WWR18-0175; E – WWR18-0311; F – WWR18-0313. *Sargodon tomicus:* G – WWR18-0211; H – WWR18-0202. Pycnodontiformes sp. indet.: I – molariform WWR18-0214, a = labial side, b = occlusal view; J – molariform WWR18-0212, a = labial side, b = occlusal view. '*Lepidotes*' sp.: K – molariform WWR18-0224; L – molariform WWR18-0225; M – insiciform WWR18-0315.

most probably due to wear. The cap and the shaft are separated from each other by a ridge.

The curved shaft is largely smooth, but it does contain fine vertical non-branching striations. However, these striations are not always preserved. The base of the tooth might be slightly flared. The teeth have a circular cross section, and the shaft increases in diameter the further down from the cap. The length of the total tooth ranges from about 1 to 4 mm. There is a total of 1240 teeth that can be attributed to this species, making it the most abundant taxon in the sample. The sharpness of the teeth indicates that this species was carnivorous/piscivorous (Moreau et al., 2021).

There are two specimens that look different compared with the standard *Gyrolepis albertii* tooth. Fig. 6E shows a tooth that shape-wise as well as based on the tip belongs to this species, but it seems that the outer layer of the shaft is missing and that this specimen shows the inner side of the shaft; it supposedly has a taphonomical origin. The specimen of Fig. 6F features no vertical striations on the shaft, but four deep diagonal furrows, that seem to be the result of some peculiar type of wear.

Remarks

Morphologically, the teeth superficially resemble those of *Saurichthys longidens* and *Birgeria acuminata*. Similarities between *Gyrolepis albertii* and *Saurichthys longidens* are that both teeth have a small conical, unornamented acrodin cap and a long shaft.

The difference between these species is that the cap of *Saurichthys longidens* is relatively longer and less sharp than the cap of *Gyrolepis albertii*. Additionally, the shaft of *Saurichthys longidens* is straight and is ornamented by thick vertical ridges, while the shaft of *Gyrolepis albertii* is curved and features only thin vertical striations that may sometimes be absent.

Similarities between *Gyrolepis albertii* and *Birgeria acuminata* are that both tooth types possess a cap and a shaft. However, the acrodin cap of *Birgeria acuminata* is relatively large, features ornamentation and is lentil-shaped in cross section, while *Gyrolepis albertii* possesses a small pointy cap without ornamentations and has a circular cross section. Likewise, the shaft of *Birgeria acuminata* is short and features very fine vertical striations, while the shaft of *Gyrolepis albertii* is long and features slightly thicker striations.

Gyrolepis albertii is a widespread taxon; it has also been mentioned from many localities in the Rhaetian of the UK (Duffin, 1998a; Whiteside & Marshall, 2008; Van den Berg et al., 2012; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Slater et al., 2016; Lakin et al., 2016; Mears et al., 2016; Whiteside et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022), from Eastern Europe (Duffin & Gaździcki, 1977; Botfalvai et al., 2019; Szabó et al., 2019) and from continental Western Europe (Bürgin, 1992; Duffin & Delsate, 1993; Godefroit et al., 1998; Delsate & Duffin, 1999; Sander et al., 2016; Diependaal & Reumer, 2021).

Other Actinopterygian teeth
Fig. 6G–M

A small number of actinopterygian teeth cannot be ascribed to the three taxa mentioned above. They are mostly knob-like molariforms originating from durophagous fish, teeth with a circular or ovoid circumference. Some bear a small protuberance (e.g., Fig. 6J), and other ones are simply bulbous or have a flattened surface (e.g., Fig. 6G). An indentation may be centrally present. The exact taxonomic attribution is often difficult. In the literature, they are often provided with names with question marks (e.g., *?Paralepidotus* sp. in Duffin & Gaździcki, 1977) or that are written between quotes (e.g., '"*Lepidotes*" tooth' or '"*Colobodus*" tooth' in Nordén et al., 2015).

Here, we distinguish three types of molariform teeth: teeth with a flat surface are attributed to *Sargodon tomicus*, and other molariforms, not having a flat surface but a bulbous one, either with a protuberance (however vague it may appear) or without one or being provided with a small indentation, are provisionally listed as Pycnodontiformes indet (see Kriwet, 2005); the somewhat cone-shaped teeth are identified as '*Lepidotes*' sp.

Order Amiiformes (Hay, 1929)

Family Dapediidae (Lehman, 1966)
Genus *Sargodon* (Plieninger, 1847)
Sargodon tomicus (Plieninger, 1847)
Fig. 6G,H

A few teeth can be linked to this species. The molariform teeth are small circular to elliptical domes with a flat occlusal surface. There is no ornamentation present.

S. tomicus has also been mentioned from the UK (Duffin, 1998a, 1998b; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Mears et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Moreau et al., 2021; Williams et al., 2022) and Poland (Duffin & Gaździcki, 1977).

Order Pycnodontiformes (Berg, 1937)
Pycnodontiformes sp. indet.
Fig. 6I–J

A few dozen teeth in our sample are here tentatively attributed to this taxon. All teeth are detached black bulbous molariforms with or without any ornamentation, and some are provided with a more or less conspicuous protuberance. The occlusal surface is not flat, as it is in *S. tomicus*. The teeth have a circular cross section. The height of these teeth ranges between about 1 and 3.5 mm.

Neopterygii indet.
'*Lepidotes*' sp.
Fig. 6K–M

The cone-shaped teeth are identified as an indeterminate species of *Lepidotes*. One elongate tooth (Fig. 6M) is here also tentatively attributed to '*Lepidotes*' sp. This contradicts the identification of a similar incisiform from the Rhaetian of Chipping Sodbury, UK, as *S. tomicus* by Lakin et al., (2016, p. 48. fig. 11E and F). The caps of both the tooth in Lakin et al. (2016) and our tooth are less wide than the body of the teeth. A cap similar in size and with a morphology somewhat resembling a matryoshka doll, but lacking the body, was published both by Korneisel et al., (2015, fig. 7F) and by Taylor et al., (2023, fig. 6E) as '*Lepidotes*' sp., which attribution we here follow.

Actinopterygii indet.
Tooth plates
Fig. 7A–D

Our sample contains 21 specimens of flat bony fragments bearing multiple small and low knobs on their surface. These knobs have an oval or circular circumference, and they are either rounded or flat at the top and do not show sharp tips. The knobs themselves are between 0.1 and 0.3 mm in diameter. One specimen (Fig. 7D) has much smaller knobs, which are about 0.05 mm in diameter; this could be from a more juvenile individual. According to Korneisel et al. (2015), Nordén et al. (2015), Mears et al. (2016) and Slater et al. (2016), who described similar fragments from the UK Rhaetian, these plates are actinopterygian jaw fragments, tooth plates, or palatal fragments, but they refrain from linking it to a specific species or genus.

Remarks

The fragments resemble the tooth plates of the genus *Colobodus* (Oosterink & Poppe, 1979). *Colobodus* sp. has been found earlier in the Anisian of Winterswijk (Oosterink & Poppe, 1979; Diedrich, 2001; Oosterink & Winkelhorst, 2013). However, the knobs in our specimen are too much separated from each other to belong to this genus. In addition, the genus *Colobodus* was most likely already extinct before the Rhaetian, since the last occurrence is recorded at the Middle Triassic Anisian–Ladinian boundary, c. 242 Ma (Mutter, 2004; Nordén et al., 2015).

Actinopterygii indet.
Gill rakers
Fig. 7E–I

Our material contains over 500 so-called gill rakers that are extremely elongated, narrow teeth consisting of a very small and

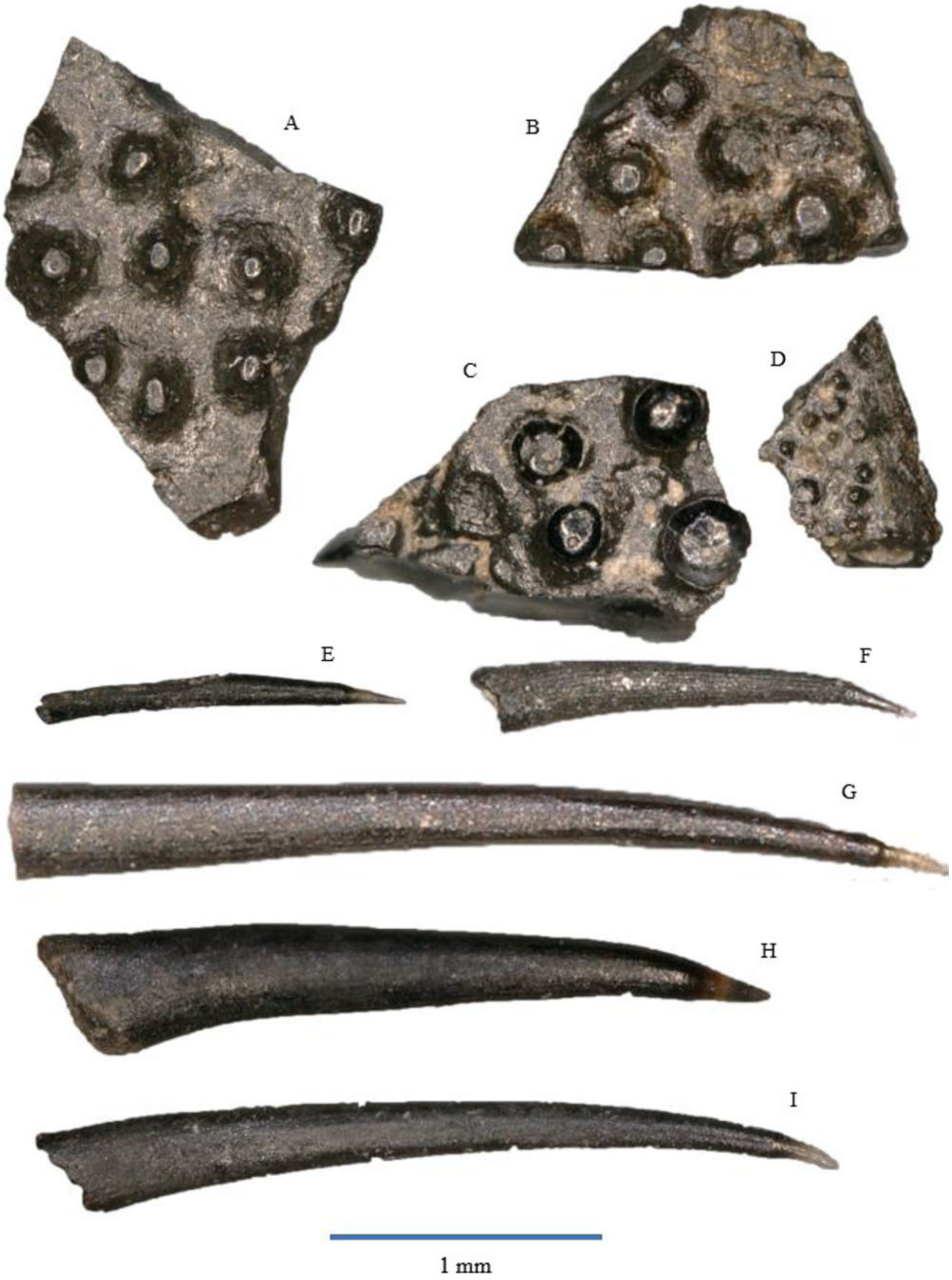

Figure 7. Actinopterygian tooth plates: A – WWR18-0237; B – WWR18-0238; C – WWR18-0239; D – WWR18-0240. Actinopterygian gill rakers: E – WWR18-0155; F – WWR18-0154; G – WWR18-0158; H – WWR18-0159; I – WWR18-0160.

often lost acrodin cap and a very long shaft. The cap forms about less than 10% of the total tooth length. It is sharp and usually translucent, although it might sometimes be completely black. The shaft is slightly curved in lingual direction. In most of the specimens, the cap is slightly curved, but it is straight in some of them. The cap itself does not feature any ornamentation and is very thin. The shaft is usually unornamented, but some specimens show faint longitudinal striations. The cross section of the shaft is elliptical in labial–lingual direction. Gill rakers are often found without the acrodin cap, but due to the typical elongated, narrow shaft with an elliptical cross section and without major ornamentation, they are still recognisable as gill rakers. The total length of the rakers ranges between about 1 and 3.5 mm.

Remarks

Superficially, the morphology of the teeth of *Gyrolepis albertii* somewhat resembles that of the gill rakers. The differences are that the shaft of the gill rakers is much longer and much thinner than the shaft of *G. albertii* teeth. The gill raker shaft also has an elliptical cross section, while the teeth of *G. albertii* have a circular cross section. Additionally, the acrodin cap of the gill rakers is much smaller than the cap of *G. albertii*.

This type of gill rakers is often assigned to the chondrichthyan *Pseudocetorhinus pickfordi* (e.g., Duffin, 1998a; Andreev & Cuny, 2012; Korneisel et al., 2015; Mears et al., 2016; Slater et al., 2016; Whiteside et al., 2016; Landon et al., 2017; Cross et al., 2018). However, Landon et al. (2017) and Cross et al. (2018) argue that

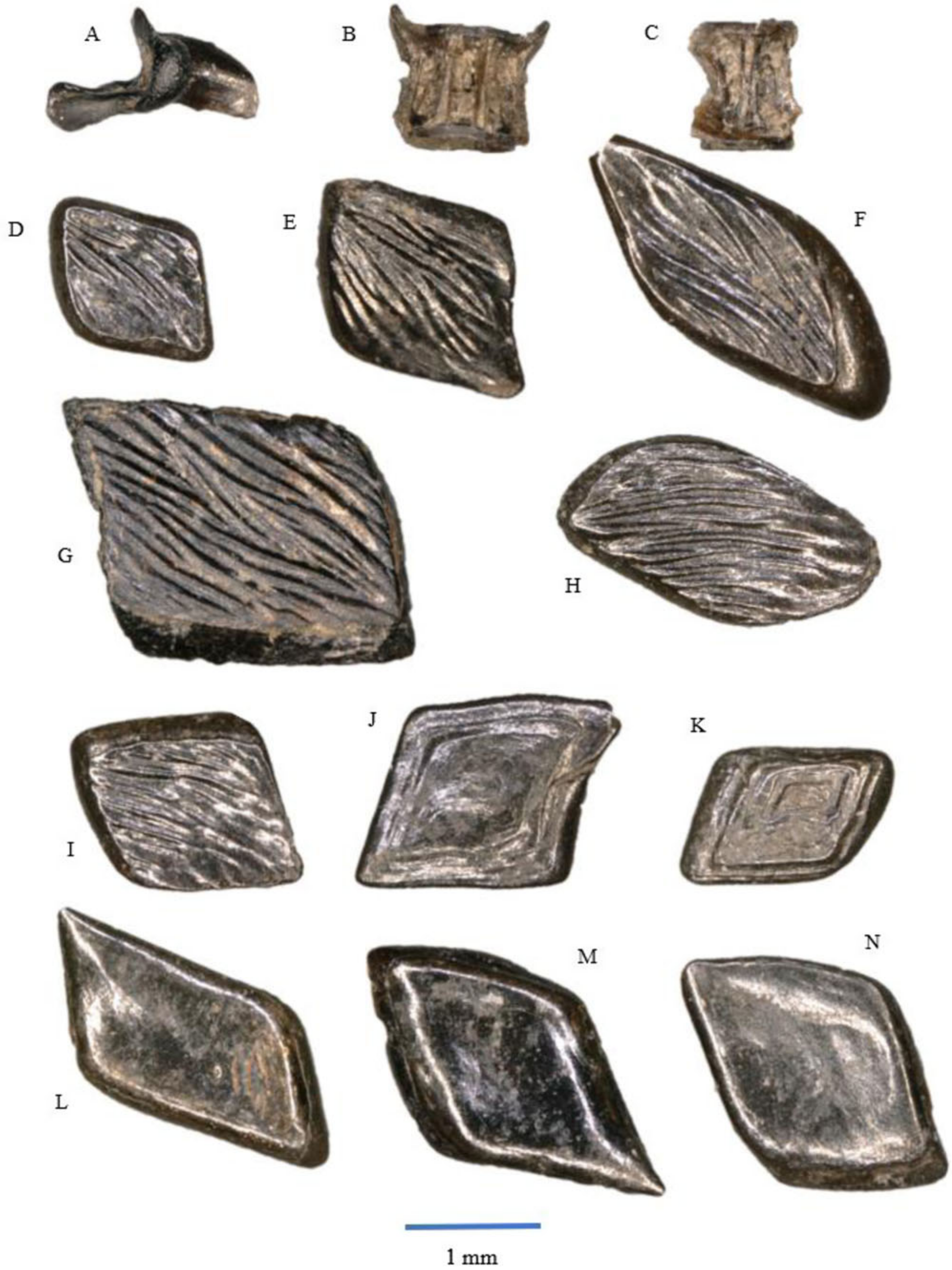

Figure 8. Actinopterygian osteological remains: A – unidentified bone WWR18-0323; B – vertebra WWR18-0324; C – vertebra WWR18-0325. Actinopterygian scales: *Gyrolepis* scales with ganoid layer: D – WWR18-0281; E – WWR18-0282; F – WWR18-0283; G – WWR18-0288; H – WWR18-0292; I – WWR18-0299. *Gyrolepis* scales without ganoid layer: J – WWR18-0264; K – WWR18-0269. Pholidophorid or Ginglymodian scales: L – WWR18-0302; M – WWR18-0317; N – WWR18-0309.

these gill rakers might belong to a still unidentified osteichthyan. Based on this lack of consensus, Diependaal & Reumer (2021) refrained from assigning the rakers to a taxon; yet, these gill rakers cannot originate from a chondrichthyan but must belong to an as-yet-unknown actinopterygian, as chondrichthyans do not possess such acrodin caps. Landon et al., (2017, fig. 6H, I) mention two rakers as ‘unidentified tooth’.

Gill rakers are usually associated with filter feeding (e.g., Duffin, 1998a; Cuny & Benton, 1999), and similar rakers are mentioned from several Rhaetian localities in the UK (Korneisel et al., 2015; Mears et al., 2016; Slater et al., 2016; Landon et al., 2017; Cross et al., 2018), from Luxembourg (Godefroit et al., 1998) and from the Winterswijk subrosion pipe in the Netherlands (Diependaal & Reumer, 2021).

Actinopterygii indet.
Osteological remains
Fig. 8A–C

Six skeletal fragments have been found in the samples, one unidentified bone and five actinopterygian vertebrae. These remains cannot be assigned to any genus or species due to a lack of characteristic features.

Actinopterygian scales
Fig. 8D–N

There are more than 2200 actinopterygian scales present in the collection. Most of these are attributed to *Gyrolepis albertii* (Fig. 8D-K). The scales all have a variable rhomboidal to squared shape, and most of them are lozenge-shaped, but some other ones are more drop-like or ellipsoid in outline. Some specimens have more rounded edges. The exposed external surface of the scales is ornamented by thin ridges in the ganoine layer. In most specimens, the striations show some bifurcation, but others may only have straight striations. These striations, which may vary in thickness, are positioned across the widest parts of the scales, that is, they run in the longest direction of the lozenge. On average, the size of the scales ranges between 1.5 and 4 mm, although one specimen is about 9 mm at its longest. The ornamentations resemble the characteristic patterns of the scales of Mears et al. (2016) and Landon et al. (2017).

Some 85 specimens of the same species (see e.g., Fig. 8J,K) have an identical rhomboidal to squared shape and size as the ones mentioned above. They are characterised by ridges that concentrically follow the outline of the scale. These are growth lines that have become visible because the ornamented ganoine layer is absent. It must have fallen off due to some taphonomic process. Landon et al., (2017, fig. 6L) depicted a similar scale; it is their morphotype M3.

A second type of scale also has a rhomboidal to squared shape, but it is characterised by the complete lack of ornamentation on the ganoine layer (Fig. 8L-N). Growth lines as in the scales of *G. albertii* that lost their ganoine covering are not visible. The scales are slightly concave. The size ranges between about 1.75 and 3 mm. According to Mears et al., (2016, fig. 10g) who depicted a similar scale, their morphotype S4, it was identified as *?Pholidophorus*, based on Whiteside & Marshall (2008, fig. 5ii, jj) who described another similar scale under that name without the question mark. Here, we refrain from a taxonomical identification; they could either be from a pholidophorid teleost or from a ginglymodian fish.

Scales similar to the ones described here are also mentioned from the UK (Lakin et al., 2016; Mears et al., 2016; Slater et al., 2016; Landon et al., 2017; Cavicchini et al., 2018; Cross et al., 2018; Cueille et al., 2020; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022), from Eastern Europe (Duffin & Gaździcki, 1977; Chrząstek, 2008; Botfalvai et al., 2019; Szabó et al., 2019) and from Western Europe (Bürgin, 1992; Duffin & Delsate, 1993; Cuny, 1995; Delsate & Duffin, 1999; Diependaal & Reumer, 2021).

General discussion

With the exception of a few actinopterygian scales, all fossils described in this paper are small to extremely small. Some as-yet-unknown taphonomical process apparently separated the small remains from larger ones such as hybodont fin spines or larger molariform or incisiform teeth.

It is interesting to compare the faunal contents of our sample from the Winterswijk Rhaetian with associations from other European localities of similar age. In general, the faunal compositions of the samples from the British Penarth Group and from Winterswijk compare well. We have a total of 6577 countable specimens present in our sample, of which 3688 are individual chondrichthyan and actinopterygian teeth.

Scales are the most abundant specimens, and they count for 34.3% of the total. Close to that percentage are the actinopterygian teeth of *Saurichthys longidens*, *Birgeria acuminata*, *Gyrolepis albertii*, *Sargodon tomicus*, and indeterminate pycnodontiforms. These teeth make up 31.9% of the total. At the same time, chondrichthyan teeth of *Lissodus minimus*, ‘*Hybodus*’ *cuspidatus*, *Rhomphaiodon minor* and *Parascylloides turnerae* count for 24.3% of the total. These three categories form the largest part of the total amount of specimens. Furthermore, there also are actinopterygian tooth plates, gill rakers and a few skeletal remains, and some chondrichthyan dermal denticles (9.5% in total).

Comparison with the British Rhaetian deposits

Marine Rhaetian (Late Triassic, c. 208.05–201.36 Ma) sediments with an abundance of marine fossils have been described from many localities in Northwestern Europe (Klompmaker et al., 2010). The fish fauna from the British Rhaetian deposits of the Penarth Group close to the Bristol Channel has been described in many papers (Duffin, 1998a, 1998b; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Lakin et al., 2016; Slater et al., 2016; Mears et al., 2016; Cavicchini et al., 2018; Cross et al., 2018; Ronan et al., 2020; Moreau et al., 2021; Williams et al., 2022). A recurring issue in those British publications is the use of the genus ‘*Severnichthys*’. As mentioned by Diependaal & Reumer (2021), Storrs (1994) merged *Birgeria acuminata* and *Saurichthys longidens* into the taxon *Severnichthys acuminata* on the basis of a single jaw. Diependaal & Reumer (2021) argued this to be incorrect and concluded *Severnichthys* to be a *nomen dubium*. A similar conclusion was also reached by Tintori & Lombardo (2018), while Tackett et al. (2022) mentioned the need to reconsider the taxonomy of *Birgeria*, *Saurichthys* and *Severnichthys*. Williams et al. (2022) still decided to retain what they call ‘the *Severnichthys* concept’ but recognised that it might be incorrect. Here, we do not use the taxon *Severnichthys*, which we consider a *nomen dubium* (and therefore put it between quotation marks). Interestingly, *Birgeria* teeth are almost absent in localities from French Lorraine, whereas teeth of *Saurichthys* are common, as for example in Saint-Nicolas-de-Port (Cuny & Ramboer, 1991).

The total count of the British Rhaetian shows that a large portion of the British Rhaetian teeth are comprised of *Lissodus minimus*, which add up to 43.8% of the teeth. The percentage is double the percentage of *Lissodus minimus* in Winterswijk, with 21.7% of the teeth. When looking at the different British sites separately, *Lissodus minimus* forms a large portion of the teeth, with the exceptions of Stowey Quarry (16.5%, Cavicchini et al., 2018) and Hapsford Bridge (1.2%, Ronan et al., 2020). At Chipping Sodbury and Saltford, the teeth of *Lissodus minimus* comprises more than half of the total tooth count, with 69.7% (Lakin et al., 2016) and 54.7% (Moreau et al., 2021), respectively. Also in the Westbury Garden Cliff section, *Lissodus minimus* comprises nearly half of the total teeth count (48.9%, Williams et al., 2022).

A similar trend can be observed for *Rhomphaiodon minor*. In the total British Rhaetian, it has a presence of 20.3%, while in Winterswijk, they have a presence of 10.2%. The highest percentages of *Rhomphaiodon minor* can be observed in the Westbury Fm. Section, the Aust Cliff section (Cross et al., 2018) and the Westbury Garden Cliff section (Williams et al., 2022), where the teeth of *Rhomphaiodon minor* make up about 30% of the total. On the other hand, very low percentages are observed in Chipping Sodbury (3.0%, Lakin et al., 2016) and Hapsford Bridge (absent, Ronan et al., 2020). The rest of the British sections show a presence of about 10 or 15% for *Rhomphaiodon minor*.

Another large portion in the British Rhaetian fish fauna is made up by the actinopterygian *Gyrolepis albertii*, which comprise 16.6% of the total tooth count. In Winterswijk, however, their presence is double that percentage: 33.6%. Remarkably, only in Hapsford Bridge, the largest portion of teeth are comprised of *Gyrolepis albertii*, where 80% of the teeth belong to this species (Ronan et al., 2020). *Gyrolepis albertii* usually makes up between the 10 and 20% of the total teeth count in the separate localities, which is in line with the total British Rhaetian chart. Only in the Stowey Quarry

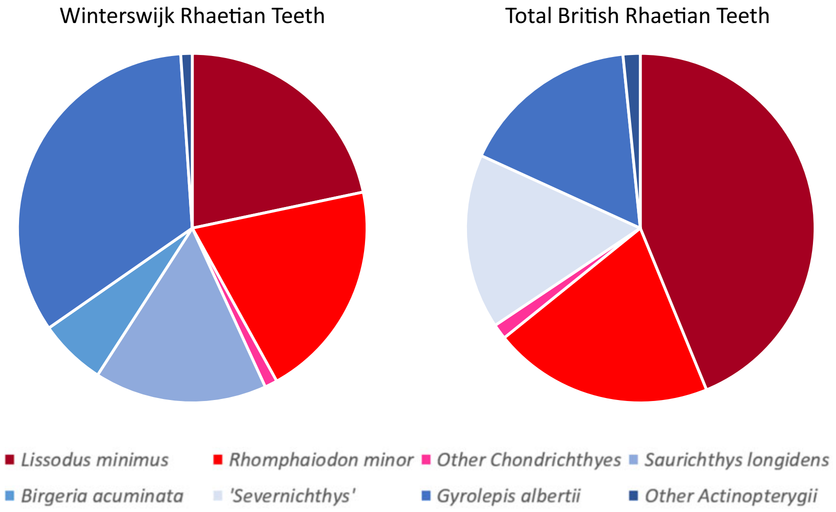

Figure 9. Pie charts showing the relative frequencies of taxa in Winterswijk and in the combined British Rhaetian localities. Blue colours indicate Actinopterygii; red hues are for chondrichtyans. The light blue '*Severnichthys*' slice in the British pie combines *Saurichthys* and *Birgeria*.

sections, *Gyrolepis albertii* teeth show a low presence (3.7%, Cavicchini et al., 2018).

The other actinopterygian that is common in the British samples is the obsolete genus '*Severnichthys*', with a total of 16.2%. This percentage is not far from the combined percentage of *Saurichthys longidens* and *Birgeria acuminata* in Winterswijk, which is about 22.2%. The Stowey Quarry features the largest percentage of '*Severnichthys*' (66.2%, Cavicchini et al., 2018), while the Westbury Garden Cliff features the lowest percentage of '*Severnichthys*' (2.2%, Williams et al., 2022). Similarly, at Barnhill Quarry, '*Severnichthys*' makes up nearly one-third of the total amount of teeth (Lakin et al., 2016). The other sections, which include the Westbury Formation sections and the Aust Cliff section, show that the '*Severnichthys*' teeth make up for about 10% of the total.

See Fig. 9 for the relative frequencies of chondrichthyans and actinopterygians. Despite local differences, the overall trend in the British Rhaetian deposits is that more teeth belong to chondrichthyans (roughly about 66%) than to actinopterygians (about 34%), which contradicts the situation in Winterswijk where the chondrichthyans comprise about 43% and the actinopterygians make up about 57%. This observation can be explained by several factors. The thinly interbedded mudstones, limestones and sandstones of the Penarth Group deposits (Gallois, 2007) indicate a shallow marine/coastal environment. In Winterswijk, the environment was stressed, as indicated by the absence of bivalves and crinoids, and the facies indicate a deep water environment. At the bottom waters, the oxygen concentrations were low (Klompmaker et al., 2010; Estes-Smargiassi & Klompmaker, 2015). These low oxygen concentrations in the Winterswijk bottom waters could have caused a lower number of *Lissodus minimus* teeth. It is known that *Lissodus minimus* was a bottom dweller in search of hard-shelled invertebrates (Fischer, 2008; Fischer et al., 2012). Therefore, it most likely did not favour oxygen-poor waters, which resulted in a less prominent occurrence in Winterswijk compared with the average British Rhaetian.

Also different or low salinity values might have caused lower percentages of the chondrichthyan fauna in Winterswijk compared with the UK. It is known that both *Lissodus minimus* and *Rhomphaiodon minor* are euryhaline sharks (Duffin, 1985; Fischer et al., 2012). Their remains are found in many different aquatic facies, which means that they migrated to different locations. There might have been differences in salinity level of the water between the two localities (Klompmaker et al., 2010), which probably resulted in a more suitable environment for these two chondrichthyans in Britain compared to Winterswijk, for which reason their teeth are more abundant in the UK.

Similarly, the percentages of *Saurichthys longidens* and *Birgeria acuminata* in Winterswijk resemble those of *Severnichthys* in the British deposits, while the percentage of *Gyrolepis albertii* is doubled compared with the British deposits. Schmitz et al. (1991) studied ^{87}Sr/^{86}Sr ratios in the phosphates of *Saurichthys longidens* from British deposits, and they suggested that the Westbury bone beds were either reworked or had freshwater input. Since the ^{87}Sr/^{86}Sr ratios of *Saurichthys longidens* could contain a signal of freshwater input for the Westbury bone beds, it might suggest that *Saurichthys longidens*, and possibly also *Birgeria acuminata*, could tolerate changes in salinity of the water, while *Gyrolepis albertii* could have had less tolerance for freshwater input and their teeth were therefore less prominent in the British samples. On the other hand, Cueille et al. (2020) mentioned that many of the *Gyrolepis albertii* scales ended up in coprolites, and therefore, *Gyrolepis albertii* must have had a high presence in the British waters. However, an individual fish contains many scales that must have been indigestible, causing these scales to eventually end up in coprolites.

However, more analysis regarding parameters such as freshwater input, salinity and oxygen concentrations needs to be done in order to obtain an understanding of the differences between the two regions in Britain and the Netherlands, and similarly aged localities elsewhere.

Conclusions

The Winterswijk Rhaetian sediments yield many fossils of chondrichthyan and actinopterygian fishes. The most abundant taxon is the actinopterygian *Gyrolepis albertii*, followed by the chondrichthyan *Lissodus minimus*. Other actinopterygian fishes, including *Saurichthys longidens*, *Birgeria acuminata*, *Sargodon tomicus* and an unidentified pycnodontiform, have slightly more presence percentwise than the chondrichthyan teeth, which include *Lissodus minimus*, *Rhomphaiodon minor*, *Parascylloides turnerae* and some '*Hybodus*' cf. *cuspidatus*. In addition to the teeth, also chondrichthyan dermal denticles, actinopterygian scales and gill rakers, tooth plates, and some fish bones were found. The faunal composition mirrors that of the contents of the subrosion pipe from Winterswijk described earlier (Diependaal & Reumer, 2021).

The most important taxa from the UK are the chondrichthyans *Lissodus minimus* and *Rhomphaiodon minor*, and the actinopterygians *Gyrolepis albertii*, *Saurichthys longidens* and *Birgeria acuminata* (the latter two taxa combined into the now obsolete genus *Severnichthys*). In the British Rhaetian deposits, the teeth of the chondrichthyans are more abundant than the actinopterygian teeth. That is contrary to our observations from Winterswijk, where more actinopterygian teeth are present. That difference could be caused by lower oxygen levels in bottom waters in Winterswijk and freshwater input and/or changes in salinity in the British Rhaetian, but more research is needed to falsify this.

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