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Note on the Rhaetian fish fauna from a subrosion pipe in Winterswijk (the Netherlands), with a discussion on the validity of the genus *Severnichthys* Storrs, 1994

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Abstract

Fossil remains of fishes found in Rhaetian (Late Triassic, c.208.5–201.3 Ma) sediments collected from a subrosion pipe in the Winterswijk quarry are described. The fauna shows great similarity to material known from the British Triassic of the Penarth Group and from other localities in Northwestern Europe. Both chondrichthyan and osteichthyan teeth and scales are present. Most abundant are the sharks Lissodus minimus and Rhomphaiodon minor and the actinopterygians Gyrolepis albertii, Saurichthys longidens and Birgeria acuminata. Isolated teeth of the latter two taxa were known under the name Severnichthys acuminatus, but the genus Severnichthys is here considered a nomen dubium; it should be suppressed in order to make the taxonomy less complicated.

Introduction

Marine sediments of Rhaetian age (Late Triassic, c.208.5–201.3 Ma) are well-known from British localities, especially around Cardiff and Bristol, and are known for their fossil content of marine vertebrates. So far, such fossils have not been reported from the Netherlands. Since the 1930s, light-greyish micritic limestone of Middle Triassic (Vossenveld Formation, Anisian, c.247.2-242 Ma) age has been commercially exploited in a quarry near Winterswijk, Gelderland province, eastern Netherlands. The >30 m thick sediments appear overlain by a c.5 m thick layer of Late Triassic (Rhaetian) argillaceous sediment rich in pyrite, a thin layer of Cenozoic (Rupelian) clay and a Late Pleistocene boulder clay (Peletier & Kolstee, 1986; Van den Bosch & Gaemers, 2015). In 1989 a plug of dark argillaceous material was found amidst the Anisian limestone. The plug was c.2 m thick and c.30 m in diameter, and turned out to be the infill of a subrosion pipe or sinkhole (Oosterink et al., 2005, 2006; Klompmaker & Van den Berkmortel, 2007). The dark sediments had fallen from a level about 10 m higher than where they were sampled, and appeared to be Rhaetian and/or Hettangian in age. Part of the plug was sampled by Adiël Klompmaker in 2005. Klompmaker & Van den Berkmortel (2007) described a fauna of Hettangian psiloceratoid ammonites from the infilling sediments. The subrosion pipe and its infillings have been removed during exploitation of the quarry and cannot be studied or sampled anymore.

After the discovery of the subrosion pipe, a second and much larger outcrop of Rhaetian black claystones was found in 2004 and opened for extensive sampling in 2018. It is situated *c*.50 m north of the locality of the subrosion pipe and is supposedly the source rock of the infillings of the pipe, or at least of a part thereof. Total thickness is estimated to be about 5 m. Palynomorphs from these sediments indicate a Rhaetian age (Herngreen, 2004; Herngreen et al., 2005). Initial fossil collection there has so far resulted in the description of ophiuroid echinoderms (Thuy et al., 2012), and collection of a rich sample of chondrichthyan and actinopterygian teeth, dermal denticles and scales. As this constitutes a different locality it will be the subject of further study. Here, we describe the fish remains (Chondrichthyes and Actinopterygii) from the Rhaetian infillings of the subrosion pipe.

Until now, no Rhaetian vertebrate remains have been described from a locality in the Netherlands. Fossils from the Winterswijk subrosion pipe published so far include palynomorphs (Herngreen et al., 2005; Klompmaker et al., 2010), bivalves (Klompmaker et al., 2010) and Hettangian (but not Rhaetian) psiloceratid ammonites (Klompmaker & Van den Berkmortel, 2007). The vertebrate remains that are the subject of the present paper are the first of this age so far described from the Netherlands and the neighbouring region of Germany; they add to our knowledge of Rhaetian biogeography.

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Material and methods

Approximately 3 kg of the infilling of the subrosion pipe was collected by Adiël Klompmaker in 2005 and stored pending further study. Unfortunately, no more material from this interesting locality has been collected. The sample was treated with a *c*.5% solution of acetic acid (a technique loosely based on Jeppsson et al., 1999), sieved under running tap water, dried and treated again with acetic acid until no further clay particles appeared. The remaining grit was hand-picked for fossils using a binocular microscope. The fossils themselves needed no further preservation. They are kept in the collection of Utrecht University (Department of Earth Sciences, working group Stratigraphy & Palaeontology), collection code WW-SP (for Winterswijk – subrosion pipe). Terminology of hybodont dental features used is after Duffin (1985). Photographs were made with a Keyence VHX-500 digital microscope.

Systematic palaeontology

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Class Chondrichthyes Huxley, 1880
Order Hybodontiformes Patterson, 1966
Genus Lissodus Brough, 1935
Lissodus minimus (Agassiz, 1839)
(Fig. 1a–d)
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Lissodus minimus is by far the most abundant shark in the sample as far as the number of teeth is concerned. There are a total of 29 teeth, some of which are broken. The largest tooth measures c.4.5 mm in mesio-distal length, the smallest one *c*.1.2 mm. Teeth of *L*. minimus are curved in occlusal view ('banana-shaped'), tapering towards both lateral (mesial and distal) ends. There is a strong but low central cusp and there may be one very low lateral cusplet on each (mesial and distal) side, but these may also be absent. An occlusal crest runs low over the entire mesiodistal length of the teeth. A more or less conspicuous peg may be positioned low on the labial side of the tooth, below the central cusp. These pegs may have functioned to lock the individual teeth in place with the teeth in the adjacent file (Allard et al., 2015). The larger teeth show a vertical striation, with the most central striae running towards the central cusp; the more distally and medially situated striae run towards the central crest. Smaller teeth have no striation. None of our teeth shows a root.

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Genus Polyacrodus Jaekel, 1889

Polyacrodus sp. indet.

(Fig. 1e)
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One elongate *Lissodus*-like tooth differs from the *L. minimus* teeth described above in being more mesio-distally elongate and in having a coarser striation. Unfortunately, it is broken in half and thus damaged, but on the anterior (lingual) side, we note four striations running towards the low central cusp. The labial side of the undamaged half possesses minute rudimentary striae showing only as inconspicuous little cuspules on the lower edge. We tentatively attribute this tooth to the genus *Polyacrodus*, but refrain from naming a species.

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Order Synechodontiformes Duffin & Ward, 1993
Genus Rhomphaiodon Duffin, 1993
Rhomphaiodon minor (Agassiz, 1837)
(Fig. 1f-j)
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In our sample, we possess 14 teeth that we here ascribe to *R. minor*. They show considerable variation in size, from small tricuspid teeth slightly less than 1 mm in size to one detached central cusp of 3 mm height. This agrees well with the description of *R.*

minor given by Allard et al. (2015), who noted that the teeth are small but vary in size, with a central cusp up to 3 mm in height. The central cusp of the teeth has vertical striations that do not continue to the apex. There are up to three pairs of lateral cusplets, which decrease in size towards the distal and mesial periphery. The central cusps and lateral cusplets are curved lingually, but to a varying degree.

In addition, we have one very small dermal denticle, *c*.0.9 mm in height, that sits on a thin basal plate of triangular shape; one of the sides of this triangle, the posterior side, is convex. The crown of the denticle is strongly curved in the posterior direction; it shows striations and one small lateral 'cusplet'. We tentatively ascribe this hybodont denticle (Fig. 1j) also to *R. minor* as this is the most abundant hybodontiform shark with striated elements in our sample.

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Genus Pseudodalatias Reif, 1978
Pseudodalatias barnstonensis (Sykes, 1971)
(Fig. 1k)
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One of the hybodont teeth differs in morphology from the *Rhomphaiodon minor* teeth and is here identified as belonging to *Pseudodalatias barnstonensis*. According to Duffin (1999) and Allard et al. (2015), upper teeth of *P. barnstonensis* are characterised by the lingual curvature of the nearly circular central cusp, and by this central cusp being pronounced and flanked by two short lateral cusplets. The tooth sits on a narrow and ovoid root, with little vascularization. The relatively large central cusp is flanked by two short cusplets that do not sit on the root but emerge from the lower lateral (mesiodistal) sides of the central cusp. As lower teeth of *P. barnstonensis* have a different morphology with serrated central cusps, the tooth derives from the upper jaw.

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Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
Family Saurichthyidae Owen, 1860 (sensu Stensiö, 1925)
Genus Saurichthys Agassiz, 1834
Saurichthys longidens Agassiz, 1835
(synonym: Severnichthys acuminatus (Agassiz, 1835) partim)
(Fig. 2a-d)
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The dentition of *Saurichthys longidens* consists of elongated conical teeth with an often translucent cap. Generally speaking, the teeth show some morphological variation that has led to confusion in the literature on Rhaetian fishes (see Discussion). The enamel cap may show vertical striations, but there are also teeth that show a smooth, unstriated cap. Also, the relative length of the enamel cap may vary between one-third and about one-tenth of the total tooth length. However, as the teeth are often broken, it can be difficult to assess the relative length of the caps. The shafts of the teeth show distinct vertical ridges. Sometimes, the cap and the shaft are separated by a more or less distinct ridge. In our sample, we have attributed 36 teeth to this species, which were all loose teeth; jaws were not present.

The genus *Saurichthys* is also represented in our material by a small bony plate that we interpret on morphological grounds as being a pair of cranial roof elements (Fig. 2d). As it is only a fragment, yet shows a midline, it is impossible to decide whether we have frontals, parietals or dermopterotics (see e.g. Romano et al., 2012, fig. 3, for the appropriate configuration). The ornamentation of the surface consisting of closely arranged minute bumps leaves no doubt of the attribution to *Saurichthys*. Although the specific attribution of this cranial element cannot be ascertained on the basis of attached dental elements, we tentatively consider it to also be from *S. longidens*, as on the basis of the teeth this is

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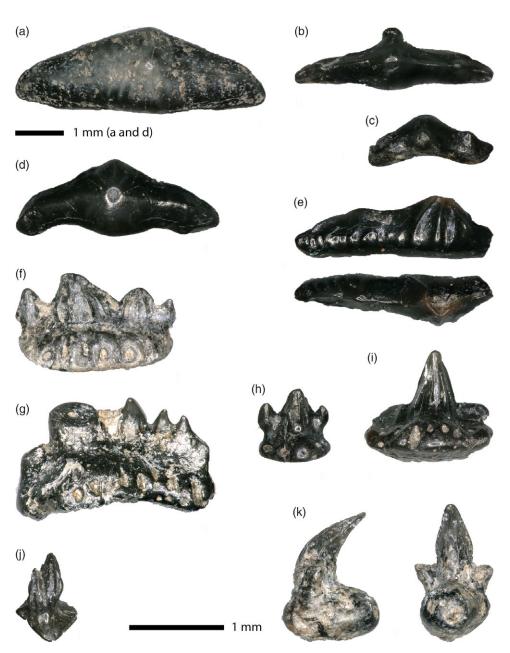


Figure 1. Chondrichthyan teeth. Lissodus minimus, (a) largest specimen WW-SP 001(c.4.5 mm), (b, d) intermediate-sized specimens (b) WW-SP 002 and (d) WW-SP 004), (c) smallest specimen WW-SP 003 (c.1.2 mm); Polyacrodus sp. indet., (e) partly damaged tooth (WW-SP 030) in labial view (above) and occlusal view (below); Rhomphaiodon minor, (f) asymmetrical tooth with one central cusp and three lateral cusplets (WW-SP 032), (g) asymmetrical tooth with one (broken) central cusp and four lateral cusplets (WW-SP 033), (h) tooth with two lateral cusplets (WW-SP 034), (i) tooth with central cusp only (WW-SP 035), (j) dermal denticle (WW-SP 045); Pseudodalatias barnstonensis, (k) tooth (WW-SP 031) with two lateral cusplets in mesial/distal view (left) and lingual view (right).

the only recognised taxon in the sample. Size of the fragment: antero-posterior length 1.65 mm, total transverse width 1.75 mm.

Order Birgeriiformes Heyler, 1969
Family Birgeriidae Aldinger, 1937
Genus Birgeria Stensiö, 1919
Birgeria acuminata (Agassiz, 1835)
(synonym: Severnichthys acuminatus (Agassiz, 1835) partim)
(Fig. 2e-f)

Sixteen teeth in the sample are attributed to *Birgeria acuminata*, on the basis of the following characters. The teeth are slightly curved, the lingual side being slightly concave and the labial side somewhat convex in side-view. If only caps are preserved, this may, however, be difficult or impossible to observe. The enameloid cap is mostly smooth on the labial side and striated on the lingual side, both sides being separated by a more or less distinct ridge. Due to these ridges, the cross-section of the teeth is somewhat biconvex or compressed, and not circular.

The teeth vary considerably in size. Such large variation was also reported in morphologically more complete material where partial dentitions could be observed instead of only loose teeth; e.g. by Romano et al. (2017: fig. 4), Bürgin & Furrer (1992: figs 2 and 3) and Schwarz (1970: fig. 20, a maxillary, and fig. 31, a fang tooth with surrounding 'kleine und sehr kleine' (small and very small) teeth).

Genus *Gyrolepis* Agassiz, 1835 *Gyrolepis albertii* Agassiz, 1835 (Figs 2g-h and 3)

A few dozen scales and scale fragments are preserved. Some show wear, probably as a result of an abrasive sedimentation process. There is a considerable size difference, but most are easily identifiable as *Gyrolepis* scales of the lozenge-shaped morphotype 2 *sensu* Landon et al. (2017: fig. 6K, p. 367; see also Mears et al. (2016: fig. 10a–b, p. 491)), and some as the pear-shaped morphotype 4 *sensu* Landon et al. (2017: fig. 6M, p. 367). Some of the worn

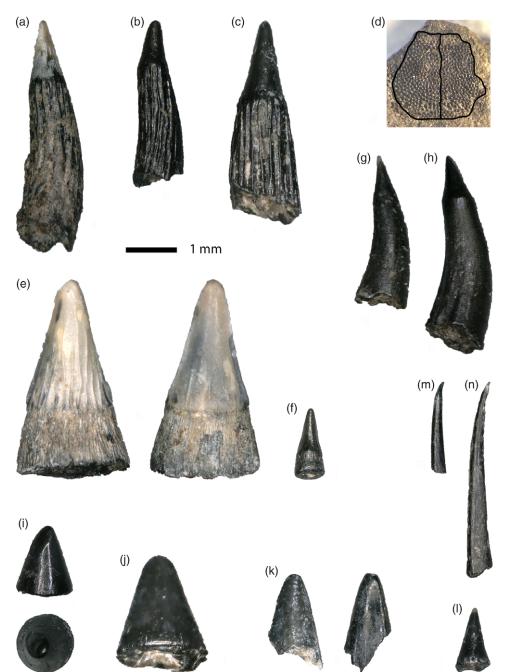


Figure 2. Teeth and cranial fragment of actinopterygians. Saurichthys longidens, (a) tooth (WW-SP 046), (b) tooth (WW-SP 047), (c) tooth (WW-SP 048), (d) paired cranial roof element with outline indicated (WW-SP 082); Birgeria acuminata, (e) large tooth (WW-SP 083) showing striated lingual side of the enamel cap (left) and smooth labial side (right), (f) small tooth (WW-SP 084); Gyrolepis albertii, (g, h) teeth showing unstriated and typically curved shafts (g) WW-SP 099, (h) WW-SP 100); cf. 'Lepidotus', (i) tooth (WW-SP 151) of the blunt type in side view (above) and occlusal view (below), (j) tooth (WW-SP 152) of the blunt type, (k) tooth (WW-SP 150) of the lentil-shaped type in buccal view (left) and lingual view (right), (I) tooth of the pointed type (WW-SP 142); Gnathostomata indet., (m, n) gill rakers (both WW-SP 155).

scales show a concentric structure as of morphotype 3 sensu Landon et al. (2017: fig. 6L, p. 367), but this configuration may be due to wear. No scales have a peg such as can be seen in morphotype 1 sensu Landon et al. (2017: fig. 6J, p. 367) or morphotype S2 sensu Mears et al. (2016: fig. 10c–d and e–f, p. 491). The scales possess a ganoid enamel layer showing ridges running diagonally in the direction of the greatest length of the lozenge or pear. The striations may bifurcate near the centre of the scale, resulting in sometimes anastomosing ridges. Based on morphological and size similarity with scales described from the Rhaetian of the Penarth Group (e.g. Mears et al., 2016; Landon et al., 2017), we identify the scales as belonging to *Gyrolepis albertii* (see Fig. 3).

Teeth of *Gyrolepis* somewhat resemble those of *Saurichthys longidens*, but differ from the latter in the relatively smaller acrodin

cap not being larger than one-quarter (Nordén et al., 2015) to one-third (Cross et al., 2018) of the tooth, and by the absence of a prominent vertical striation of the shaft of the tooth, There may be a very subtle striation on the shaft, but it is far less obvious than in *S. longidens*. Furthermore, the teeth have a circular cross-section and are cone-shaped and curved (C-shaped) with an acute tip; sometimes they are slightly S-shaped. The small acrodin caps are often translucent and are always unornamented. In our sample, we have attributed 43 teeth to this species, making it the most abundant ray-finned fish in our sample of loose teeth. Although we realise that *Gyropelis albertii* was described on the basis of scales, we see no reason not to attribute our teeth to the same species, following, for example, Allard et al. (2015) and Cross et al. (2018).

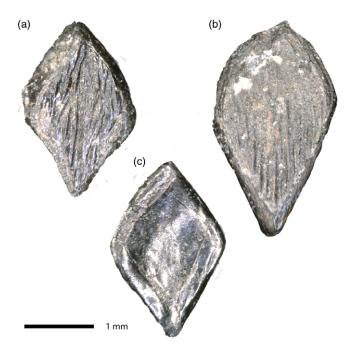


Figure 3. Gyrolepis albertii, scales. (a) WW-SP 156, (b) WW-SP 157, (c) WW-SP 158.

Order Semionotiformes cf. 'Lepidotus' Agassiz, 1832 (Fig. 2i-l)

Furthermore, we have three morphotypes of unornamented actinopterygian teeth that are conical or bulbous and that could belong to either Semionotiformes (such as *Lepidotus*, *Paralepidotus*, *Semiolepis* or *Serrolepis*) or even Perleidiformes. One of our teeth has a lentil-shaped cross-section; the other twelve are conical. Four of these have a blunt tip and show a small wear facet most probably due to occlusion with an element from the opposing jaw. The remaining eight specimens have a more slender, pointed apex that is often somewhat translucent. It is difficult to attribute them with any certainty to a species, and often the waste-basket genus *Lepidotus* has been used to avoid giving no name at all. Thus, we tentatively name them cf. '*Lepidotus*', realizing that they could well belong to other genera, such as the semionotiforms *Paralepidotus* Stolley, 1920 or *Serrolepis* Quenstedt, 1852.

Gnathostomata indet. (Fig. 2m-n)

Finally, we have 19 gill raker teeth, long and slender elements that according to Duffin (1998) and, for example, Cross et al. (2018) belong to the chondrichthyan *Pseudocetorhinus pickfordi* Duffin, 1998, but according to Landon et al. (2017) to an unknown osteichthyan. Apparently, there is no consensus on the attribution of these small, needle-like teeth used for filter-feeding. Here, we refrain from assigning them to any taxon.

Discussion

Isolated teeth, especially those of actinopterygians, often pose a problem in identification. Large size differences in the teeth (e.g. the distinction between fangs and smaller teeth; Bürgin & Furrer, 1993), different positions in the jaws and ontogenetic size differentiation may result in the teeth originating from one individual fish or one single species showing a large variation. When found as loose elements, it may even be difficult to ascribe

them with certainty to distinct taxa. What in fact we observe and describe are dental morphotypes that are then translated taxonomically into morphospecies.

5

Fossil fish taxa are ideally based on a suite of characters including cranial and postcranial morphology, number, size and position of the fins, the squamation and relative sizes of the animal. The morphology of (loose) dental elements, scales or dermal denticles is not always clearly described, and therefore they are not always unambiguously attributable to a certain taxon. The material available to us for the present study consists without exception of loose dental elements and some scales; bony cranial or postcranial material is lacking (with the exception of the Saurichthys skull fragment), as are more or less intact fishes. Hence, no correlation was possible between teeth on the one hand and other anatomical features on the other. We therefore based our identifications on comparison with material described in the above-mentioned literature. Comparison of our fauna with that from other European Rhaetian localities, especially those of the British Penarth Group (Korneisel et al., 2015; Lakin et al. 2016; Slater et al., 2016; Cavicchini et al., 2018; Cross et al., 2018) shows an overall resemblance in faunal composition, with the shark genera Lissodus and Rhomphaiodon, and the actinopterygians Gyrolepis, Saurichthys and Birgeria (the latter two often jointly referred to as Severnichthys) as the most abundant elements. See Table 1 for an overview.

The genus *Rhomphaiodon* was erected by Duffin (1993) on account of its specific enameloid microscopic ultrastructure. Morphologically, however, there appeared to be no difference from teeth of the genus *Hybodus*, and subsequently other *Hybodus* species were incorporated into *Rhomphaiodon*, e.g. *Hybodus minor* Agassiz, 1837. We therefore choose to use the name *Rhomphaiodon* for the hybodont shark teeth.

The Severnichthys enigma

A vexing problem is the validity of the genus *Severnichthys* Storrs, 1994. This genus was described in order to encompass at least two different morphotypes that were originally identified as belonging to the two separate genera *Birgeria* and *Saurichthys*, but that were then considered to belong to a single species, for which Storrs (1994) erected the taxon *Severnichthys*. In subsequent literature, these two morphotypes were labelled as '*Severnichthys acuminatus* (*Birgeria acuminata*-type)' and '*Severnichthys acuminatus* (*Saurichthys longidens*-type)', respectively (e.g. Duffin, 1999; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Lakin et al., 2016; Mears et al., 2016; Cross et al., 2018).

Saurichthys and Birgeria are very different fish. Saurichthys is a very slender, garfish-like creature with an extremely elongate rostrum (Rieppel, 1985; Romano et al., 2012; Werneburg et al, 2014; Maxwell et al., 2016), while Birgeria is larger and possesses a strong and blunt rostrum (Schwarz, 1970; Bürgin & Furrer, 1992). In the original description, Severnichthys was diagnosed with a 'massive fused rostropremaxillary, subconical with a bluntly pointed tip', which conforms to the morphology of Birgeria; and a heavily fragmented dentary 'with vertically expanded posterior end, more so than in Birgeria or Saurichthys' (Storrs, 1994). The mentioned type species was Severnichthys acuminatus (Agassiz, 1835), formerly known as Birgeria acuminata.

Severnichthys, with its large and blunt snout, is morphologically a different fish from the strongly elongate and garfish-like Saurichthys. Interestingly, however, Storrs (1994) listed Saurichthys longidens among the synonyms. In the suite of subsequent papers on the fishes from the Upper Triassic (Rhaetian) Penarth Group in the area of the

Table 1. Faunal composition in number of dental elements of our sample from Winterswijk and selected British localities of the Rhaetian Penarth Group. Ref. 1: Cavicchini et al. (2018); ref. 2 : Cross et al. (2018); ref. 3: Slater et al. (2016); ref. 4: Lakin et al. (2016); ref. 5 : Korneisel et al. (2015). Decimals (ref. 3) represent partial examples of large teeth.

	Winterswijk (this study)	Stowey Quarry (upper bone bed) (ref. 1)	Stowey Quarry (lower bone bed) (ref. 1)	Aust Cliff (ref. 2)	Westbury Fm. – basal (ref. 3)	Westbury Fm. – top (ref. 3)	Barnhill Quarry (ref. 4)	Chipping Sodbury (ref. 4)	Charton Bay, Devon (ref. 5)
Chondrichthyes									
Lissodus minimus	29	2	182	1485	1098.5	8	102	774	172
Pseudocetorhinus pickfordi				1	1				1
Pseudodalatias barnstonensis	1			6	3				
Nemacanthus monilifer					1.5			12	
Rhomphaiodon minor	14		112	1182	720.5	0.5	33	33	37
Duffinselache hol- wellensis		11			1	3.5			4
Hybodus cloaci- nus				2	3		17	3	
Polyacrodus	1								
Parascylloides turnerae				35					
Ceratodus sp.							2		
Holocephali							1		
Hybodontiformes							2	12	
Actinopterygii									
Birgeria acumina- taª	16			167	143	27			
Saurichthys longi- dens ^b	36			168	144.5	15.5			
'Severnichthys'		38	699				105	104	51
Gyrolepis albertii	43	42	251	720	292	212	53	173	44
Sargodon tomicus			28	19	7	1	1		58
'Lepidotus'	3			9	1				60
Dapedium sp.									8

a'Severnichthys Birgeria-type'.

Severn estuary (e.g. Duffin, 1999; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Lakin et al., 2016; Mears et al., 2016; Cross et al., 2018), small actinopterygian teeth with acrodin caps were persistently identified as belonging to *Severnichthys*. No teeth from either *Birgeria* or *Saurichthys* were mentioned from these British localities; these were mere morphological 'types' within *Severnichthys*. The apparent absence of the genus *Saurichthys* itself is difficult to understand, as *Saurichthys* was an abundant taxon in Triassic fish assemblages (e.g. Duffin & Gazdzicki, 1977; Rieppel, 1985; Romano et al., 2012; Werneburg et al., 2014; Maxwell et al., 2016).

Both 'types' were originally described by Agassiz (1835) as Saurichthys longidens and Saurichthys acuminatus, respectively, based on material from the British Rhaetian at Aust, near Bristol. Savage & Large (1966) transferred the latter species to the genus Birgeria: B. acuminata; they depicted a large and stout

lower jaw that does not comply with the slender and elongate morphology of *Saurichthys* as now understood (see Rieppel, 1985). This justifies the attribution to *Birgeria*. See also Bürgin & Furrer (1993) for a discussion on the *Birgeria* vs *Saurichthys* problem.

Subsequently, Storrs (1994) merged both taxa into *Severnichthys acuminatus*, which genus was diagnosed (as far as the teeth are concerned) by the following: 'Very large recurved acrodont lingual tusks caudad, striated; coarsely ribbed at base to present labyrinthine folding in transverse section; folds lost in midsection of tooth; translucent enameloid cap sometimes removed by wear. Typical lingual dentition smaller and often sharper; less coarsely striated and recurved; more extensive enameloid cap; more pronounced carinae and cingulum.'

The two morphological types of *Severnichthys* teeth are difficult to separate as there tends to be an overlap in characters, especially

b'Severnichthys Saurichthys-type'.

when no complete jaws are available. Sometimes, the cap and the shaft are separated by a more or less distinct ridge. According to Cross et al. (2018), this is the case with the *Birgeria*-type teeth, while Nordén et al. (2015) mention this ridge as being present in the *Saurichthys*-type teeth. Korneisel et al. (2015) added to the confusion by naming *Severnichthys acuminatus* in the text, and *Severnichthys longidens* in the figure legend, although this might be due to an overlooked typing error.

To summarise, we consider the attribution of teeth from two rather different genera to *Severnichthys* to be a mistake. The apparent morphological similarities of the teeth can be explained as a convergency. There seems to be no other justification for the creation of *Severnichthys*, a conclusion also reached by Tintori & Lombardo (2017). We therefore propose to suppress *Severnichthys* as a separate genus; it is a *nomen dubium*. Loose teeth attributed to *Severnichthys* seem to belong to either *Birgeria* or *Saurichthys*; the cranial material used for the original description by Storrs (1994) appears to conform to the morphology of *Birgeria*.

Conclusions

The fish fauna from the Rhaetian sediments found in the subrosion pipe in the Winterswijk quarry is very similar to the various faunas described from other localities known in Northwestern Europe, especially those from the British Triassic of the Penarth Group. Both chondrichthyan and osteichthyan teeth and scales are described. The most abundant taxa are the hybodontiform shark Lissodus minimus, the synechodontiform shark Rhomphaiodon minor and the actinopterygian Gyrolepis albertii. Other abundant bony fishes are Saurichthys longidens and Birgeria acuminata. The teeth of the latter two taxa were described under the name Severnichthys acuminatus by several British authors, but the genus Severnichthys is here considered a nomen dubium. In order to render taxonomy less complicated, its use should be avoided.

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References

- Agassiz, J.L.R. 1835. Recherches sur les poissons fossiles. 2. Imprimerie de Petitpierre (Neuchâtel).
- Allard, H., Carpenter, S.C., Duffin, C.J. & Benton, M.J., 2015.
 Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK). Proceedings of the Geologists' Association 126: 762–776.
- Bürgin, T. & Furrer, H., 1992. Zähne und Kieferreste der Gattung Birgeria (Osteichthyes, Actinopterygii) aus der ostalpinen Obertrias der Bergüner Stöcke (Kanton Graubünden, Schweiz). Eclogae Geologicae Helvetiae 85(3): 931–946.
- Bürgin, T. & Furrer, H., 1993. Kieferreste eines grossen Strahlenflossers (Osteichtyes; Actinopterygii) aus der ostalpinen Obertrias der Bergüner Stöcke (Kanton Graubünden, Schweiz) und Diskussion des Validität von? Birgeria costata (Münster 1839). Eclogae Geologicae Helvetiae 86(3): 1015–1029.
- Cavicchini, I., Heyworth, H.C., Duffin, C.J., Hildebrandt, C & Benton, M.J., 2018. A Rhaetian microvertebrate fauna from Stowey Quarry, Somerset, U.K. Proceedings of the Geologists' Association 129: 144–158.

- Cross, S.R.R., Ivanovski, N., Duffin, C.J., Hildebrandt, C., Parker, A. & Benton, M.J., 2018. Microvertebrates from the basal Rhaetian Bone Bed (latest Triassic) at Aust Cliff, S.W. England. Proceedings of the Geologists' Association 129: 635–653.
- Duffin, C.J., 1985. Revision of the hybodont selachian genus Lissodus Brough (1935). Palaeontographica. Abteilung A, Paläozoologie, Stratigraphie 188 (4–6): 105–152.
- Duffin, C.J., 1993. Late Triassic shark teeth (Chondrichthyes, Elasmobranchii) from Saint-Nicolas-de-Port (north-east France). Belgian Geological Survey Professional Paper 264: 7–32.
- Duffin, C.J., 1998. New shark remains from the British Rhaetian (latest Triassic). 2. Hybodonts and palaeospinacids. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1998(4): 240–256.
- Duffin, C.J., 1999. 14. Fish. In: Swift, A. & Martill, D.M. (eds): Fossils of the Rhaetian Penarth group. The Palaeontological Association/Blackwell (London): 191–222.
- Duffin, C.J. & Gaždzicki, A., 1977. Rhaetian fish remains from the Tatra Mountains. Acta Geologica Polonica 27(3): 333–348.
- Herngreen, G.F. W., 2004. Palynologisch onderzoek van de afdekkende kleilaag in steengroeve IV, Winterswijk. Internal report. Nederlands Instituut voor Toegepaste Geowetenschappen TNO 04-199-B (Utrecht): 7 pp.
- Herngreen, G.F.W., Van Konijnenburg-van Cittert & Oosterink, H.W., 2005. New geological data (Middle Triassic, Rhaetian–Liassic and Oligocene) of the Winterswijk quarry, the eastern Netherlands). Netherlands Journal of Geosciences/Geologie en Mijnbouw 84(4): 409–413.
- Jeppsson, L., Anehus, R. & Fredholm. D., 1999. The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. Journal of Paleontology 73(5): 964–972.
- Klompmaker, A.A. & Van den Berkmortel, B.J.H.M., 2007. Earliest Jurassic (Hettangian) psiloceratoid ammonites from a subrosion pipe at Winterswijk, the eastern Netherlands. Netherlands Journal of Geosciences/Geologie en Mijnbouw 86(4): 379–388.
- Klompmaker, A.A., Herngreen, G.F.W. & Oosterink, H.W., 2010. Biostratigraphical correlation, paleoenvironmental stress and subrosion pipe collapse: Dutch Rhaetian shales uncover their secrets. Facies 56: 597–613.
- Korneisel, D., Gallious, R.W., Duffin, C.J. & Benton, M.J., 2015. Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK. Proceedings of the Geologists' Association 126: 130–142.
- Lakin, R.J., Duffin, C.J., Hildebrandt, C, & Benton, M.J., 2016. The Rhaetian vertebrates of Chipping Sodbury, South Gloucestershire, UK, a comparative study. Proceedings of the Geologists' Association 127: 40–52.
- Landon, E.N.U., Duffin, C.J., Hildebrandt, C., Davies, Th.G., Simms, M.J. & Benton, M.J., 2017. The first discovery of crinoids and cephalopod hooklets in the British Triassic. Proceedings of the Geologists' Association 128: 360–373.
- Maxwell, E.E., Diependaal, H., Winkelhorst, H., Goris, G., & Klein, N., 2016.
 A new species of Saurichthys (Actinopterygii: Saurichthyidae) from the Middle Triassic of Winterswijk, the Netherlands. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 280(2): 119–134.
- Mears, E.M., Rossi, V., MacDonald, E., Coleman, G., Davies, T.G., Arias-Riesgo, C., Hildebrandt, C., Thiel, H., Duffin, C.J., Whiteside, D.J. & Benton, M.J., 2016. The Rhaetian (Late Triassic) vertebrates of Hampstead Farm Quarry, Gloucestershire, UK. Proceedings of the Geologists' Association 127: 478–505.
- Nordén, K.K., Duffin, C.J. & Benton, M.J., 2015. A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. Proceedings of the Geologists' Association 126: 564–581.
- Oosterink, H., Simon, Th. & Winkelhorst, H., 2005. Een subrosieverschijnsel in de Muschelkalkgroeve van Winterswijk. Grondboor en Hamer **59**(4): 78–83.
- Oosterink, H.W., Simon, Th., Hagdorn, H. & Winkelhorst, H., 2006. A subrosion pipe fill in the Lower Muschelkalk, Winterswijk quarry, eastern Netherlands. Netherlands Journal of Geosciences/Geologie en Mijnbouw 85(4): 293–297.
- Peletier, W. & Kolstee, H.G., 1986. Winterswijk, Geologie deel 1. Inleiding tot de geologie van Winterswijk. Wetenschappelijke Mededelingen K.N.N.V. 175: 1–136.
- Rieppel, O., 1985. Die Triasfuna der Tessiner Kalkalpen. XXV. Die Gattung Saurichthys (Pisces, Actinopterygii) aus der mittleren Trias des Monte San

- Giorgio, Kanton Tessin. Schweizerische Paläontologische Abhandlungen, 108: 1–103.
- Romano, C., Kogan, I., Jenks, J., Jerjen, I., & Brinkmann, W., 2012. Saurichthys and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. Bulletin of Geosiences 87(3). doi: 10.3140/bull. geosci.1337.
- Romano, C., Jenks, J.F., Jattiot, R., Scheyer, T.M., Bylund, K.G. & Bucher, H., 2017. Marine Early Triassic Actinopterygii from Elke County (Nevada, USA): implications for the Smithian equatorial vertebrate eclipse. Journal of Paleontology 91(5): 1025–1046. doi: 10.1017/jpa.2017.36.
- Savage, R.J.G. & Large, N.F., 1966. On Birgeria acuminata and the absence of labyrinthodonts from the Rhaetic. Palaeontology 9: 135–141.
- Schwarz, W., 1970. Die Triasfauna des Tessiner Kalkalpen. XX. Birgeria stensiöi Aldinger. Schweizerische Paläontologische Abhandlungen 89: 1–93.
- Slater, T.S., Duffin, C.J., Hildebrandt, C., Davies, T.G., & Benton, M.J., 2016.
 Microvertebrates from multiple bone beds in the Rhaetian of the M4-M5

- motorway junction, South Gloucestershire, U.K. Proceedings of the Geologists' Association 127: 464–477.
- Storrs, G.W., 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). Zoological Journal of the Linnean Society 112: 217–259.
- Thuy, B., Klompmaker, A.A. & Jagt, J.W.M., 2012. Late Triassic (Rhaetian) ophiuroids from Winterswijk, the Netherlands; with comments on the systematic position of *Aplocoma* (Echinodermata, Ophiolepididae). Zoosymposia 7: 163–172.
- Tintori, A., & Lombardo, C., 2017. The Zorzino Limestone Actinopterygian Fauna from the Late Triassic (Norian) of the Southern Alps. In: Tanner, L.H (ed.): The Late Triassic World: Earth in a Time of Transition. Springer (Cham): 315–350.
- Van den Bosch, M. & Gaemers, P.A.M., 2015. Lithostratigraphy of the Oligocene in the Almelo-Winterswijk area, Eastern Netherlands. Uitgeverij Eburon (Delft): 164 pp.
- Werneburg, R., Kogan, I. & Sell, J., 2014. Saurichthys (Pisces: Actinopterygii) aus dem Buntsandstein (Trias) des Germanischen Beckens. Semana 29: 3–35.