Synonymisation of the skeleton-based *Palimphemus anceps* Kner, 1862 and the otolith-based *Colliolus sculptus* (Koken, 1891) (Pisces, Teleostei, Gadidae)

Werner Schwarzhans

Ahrensburger Weg 103, D-22359 Hamburg, Germany; wwschwarz@aol.com

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Slabs of two specimens from a borehole at Krywald, Upper Silesia, Poland, originally recorded as *Gadus macropterygius* (Kramberger, 1883) by Jerzmańska (1962) are restudied and re-identified as *Palimphemus anceps* Kner, 1862, a fossil gadid genus and species recently redescribed by Carnevale *et al*. (2012) from exceptionally well preserved fish specimens of similar age from St. Margarethen, Austria. One of the Krywald specimens contains an otolith in situ visible from the inner face and clearly identifiable as representing the otolith-based fossil genus and species *Colliolus sculptus* (Koken, 1891), one of the most wide-spread, common and stratigraphically long-ranging gadid otolith species. As a consequence, the otolith-based genera *Colliolus* and *Gadichthys* are placed in synonymy with *Palimphemus* and the otolith-based species *C. sculptus* with *P. anceps* thereby eradicating a case of more than 100 years of parallel taxonomy. The prospects are emphasised of further future such work of relating skeleton and otolith data.

Key words: Fish skeleton, otolith *in situ*, middle Miocene, Badenian, Poland, Gadidae, Teleostei, systematics, synonymisation.

Introduction

In a publication about fish skeletons retrieved from the Krywald borehole near Gliwice, Upper Silesia, Poland, Jerzmańska (1962) recorded two skeletons, which she referred to *Gadus macropterygius* (Kramberger, 1883). According to Ms Swidnicka (ZPALWr, Wrocław, Poland) the Krywald borehole served as a ventilation shaft for the nearby Knurów coal mine until a few years ago. The two slabs were taken from a depth of 110.25 to 110.50 m from an interval of gypsiferous marlstone. The stratigraphy of the Krywald borehole is depicted by Jerzmańska and shows a Miocene section below the Quaternary cover from 18.80 m down to 183.20 m where a thin Miocene transgressive conglomerate rests on Triassic and Carboniferous rocks. Gypsiferous marlstones with tuffaceous intervals were encountered between 101.80 m to 120.90 m overlying massive gypsum from 120.90 m to 141.30 m. The combine of these two intervals represent the middle Badenian salinity crisis in the Carpathian Foredeep (Rögl & Müller, 1978; Rasser & Harzhauser, 2008; de Leeuw *et al*., 2010), also locally known as the Wielician Stage in Poland or the *Spiroplectammina* Zone (Gonera, 2013; Janssen & Zorn, 1993; Rögl & Müller, 1978). Peryt (2006) placed the evaporitic event of the Carpathian Foredeep in the lower part of nannoplankton-zone NN6, equivalent to the basal part of the Serravallian. De Leeuw *et al*. (2010) show a chronostratigraphic chart of the Wielicka halite deposits where a very similar sequence with evaporitic sediments and tuffaceous marker beds are placed in the basal part of the Serravallian. The tuffaceous marker beds were dated by radioistopic analyses between 13.8 and 13.6 Ma (Bukowski *et al*., 2010).

In her publication of 1962, Jerzmańska also included a schematic drawing of an otolith *in situ* found in one of the two specimens. A brief inspection during a visit to Wrocław in 1976 led me to identify the otolith as the otolith-based species *Colliolus friedbergi* (Chaine & Duvergier, 1928), which became subsequently recognised as a junior synonym of *Colliolus sculptus* (Koken, 1891). Smigielska (1966) described otoliths from the early Badenian (Moravian) of the Krywald borehole from the interval between 141.30 m to 183.20 m, which, however, did not yield any Gadidae.

It is only very recently that Carnevale *et al*. (2012) redescribed in detail *Palimphemus anceps* Kner, 1862 from 43 specimens including the holotype from the middle Badenian Leitha Limestone of St. Margarethen in Burgenland, Austria, which is considered to be of latest Langhian age of the nannoplankton-zone NN5b and therewith just slightly older than Jerzmańska's specimens from Krywald.

The purpose of this study now is a detailed review of the Krywald specimens of Jerzmańska, which give the rare opportunity for a conclusive link of skeleton and otolith based taxa, which in this case have been existing in parallel for over 100 years.

The fish specimens studied for this investigation are deposited at the Department of Palaeozoology, Faculty of Biological Sciences, Wrocław University, Poland (ZPALWr M/1 and M/2).

Systematic part

Redescription of the skeleton finds from Krywald, Poland

Order Gadiformes Goodrich, 1909
Family Gadidae Rafinesque, 1810
Genus *Palimphemus* Kner, 1862

Type-species – *Palimphemus anceps* Kner, 1862, by monotypy (Leitha Limestone, Badenian, middle Miocene, St. Margarethen, Austria).

Synonymised otolith-based genera – (see chapter below for detailed discussion)

Colliolus Gaemers & Schwarzhans, 1973 (type-species *Gadus friedbergi* Chaine & Duvergier, 1928; syn. *Gadus elegans sculptus* Koken, 1891);
Gadichthys Gaemers & Schwarzhans, 1973 (type-species *Gadus benedeni* Leriche, 1926);
Pseudocolliolus Gaemers, 1978 (type-species *Pseudocolliolus cuykensis* Gaemers, 1978);
Doyenneichthys Gaemers, 1983 (type-species *Gadichthys benedeni verticalis* Gaemers & Schwarzhans, 1973);
Circagadiculus Gaemers, 1990 (type-species *Circagadiculus kingi* Gaemers, 1990).

Discussion – The diagnostic features recognised by Carnevale *et al.* (2012) include amongst others head length of about one third of SL, preanal distance exceeding length of first anal base, first anal base slightly less than one fourth of SL, 18 + 27-28 vertebrae, D3=17-21, A2=18-19, C=41-43, P=15-18. They concluded on a close relationship to the extant genera *Micromesistius* and *Trisopterus* from which *Palimphemus* might be phylogenetically separated since at least Oligocene times. This view is fully corroborated by the data obtained from otoliths and discussed in the following.

***Palimphemus anceps* Kner, 1862**
Fig. 1a-d

1862	*Palimphemus anceps* Kner, pl. 1, fig. 2.
?1883	*Morrhua lanceolata* – Kramberger, pl. 13, fig. 5.
1891	Ot. (*Gadus*) *elegans* mut. *sculpta* – Koken, pl. 4, fig. 2 (otolith-based species).
1928	*Gadus friedbergi* – Chaine & Duvergier, pl. 6, figs 16-27 (otolith-based species).
1962	*Gadus macropterygius* (Kramberger, 1883) – Jerzmańska, fig. 2.
1966	*Gadus schuberti* – Smigielska, pl. 15, figs 1-2 (otolith-based species).
1976	*Colliolus johannettae* – Gaemers, pl. 6, figs. 9-10 (otolith-based species).
1987	*Pseudocolliolus eidelstedtensis* – Gaemers, pl. 1, figs 4-5, pl. 2, figs 1-5 (otolith-based species).
1990	*Circagadiculus swalmenensis* – Gaemers, pl. 5, figs 1-2 (otolith-based species).
1990	*Colliolus septentrionalis* – Gaemers, pl. 8, fig. 4 (otolith-based species).
1994	*Colliolus sculptus* (Koken, 1891) – Schwarzhans, figs 123-143 (with additional otolith-based synonymies).
2010	*Colliolus sculptus* (Koken, 1891) – Schwarzhans, pl. 36, figs 1-9 (with additional otolith-based synonymies).
2012	*Palimphemus anceps* Kner, 1862 – Carnevale *et al.*, figs 1-8, 9A, 9D, 9F.

Material – Two specimens; ZPALWr M/1 and M/2, Krywald borehole at 110.25-110.50 m depth, Upper Silesia, Poland, middle Badenian (earliest Serravallian) (lower NN6).

Description of specimen ZPALWr M/1 – (see Table 1 for meristics and morphometric measurements). A marlstone slab of about 10 cm width with a reasonably well preserved fish skeleton, partly as imprint, lacking the anterior half of the head forward of about the center of the orbit and the tip of the caudal fin beyond the hypural plate and the caudal fin ray bases.

The rear part of the skull is well preserved exhibiting the right sagittal otolith exposed from the inner face. Bones and imprints, partial and complete include the cleithrum, coracoid, opercle, the uppermost branchiostegal ray, the supraoccipital and further difficult to identify bone fragments and traces of imprints.

The vertebral column is mostly well preserved and complete comprising 46 vertebrae, of which 17 are precaudal and 29 caudal including the hypural plate. The first four precaudal vertebrae are compressed, higher than long and considerably shorter than the following vertebrae. The neural spines are well preserved except for that of the fifth vertebra, long and backward curved, generally being slightly longer and thinner from vertebra 10 onwards. Parapophyses and pleural ribs are covered by rock and the well exposed pectoral fin up to vertebra 13. Long, thin, backward bend haemal spines are present from vertebra 18 onwards. In the caudal skeleton only the main hypural plate (hypural 3-5) and one epural are preserved.

The first dorsal fin is inserted anteriorly of the first anal fin above vertebra 8 and contains 8 preserved fin rays and 8 preserved pterygiophores, which, however, due to their relative position suggest the original presence of 9 or 10 fin rays. The second dorsal fin is inserted above vertebra 16 and approximately the center of the first anal fin and contains 8 preserved fin rays and 10 preserved pterygiophores, corresponding to a total of 10 fin rays. The first dorsal appears to have been longer than the second dorsal, particularly its first two or three rays. The

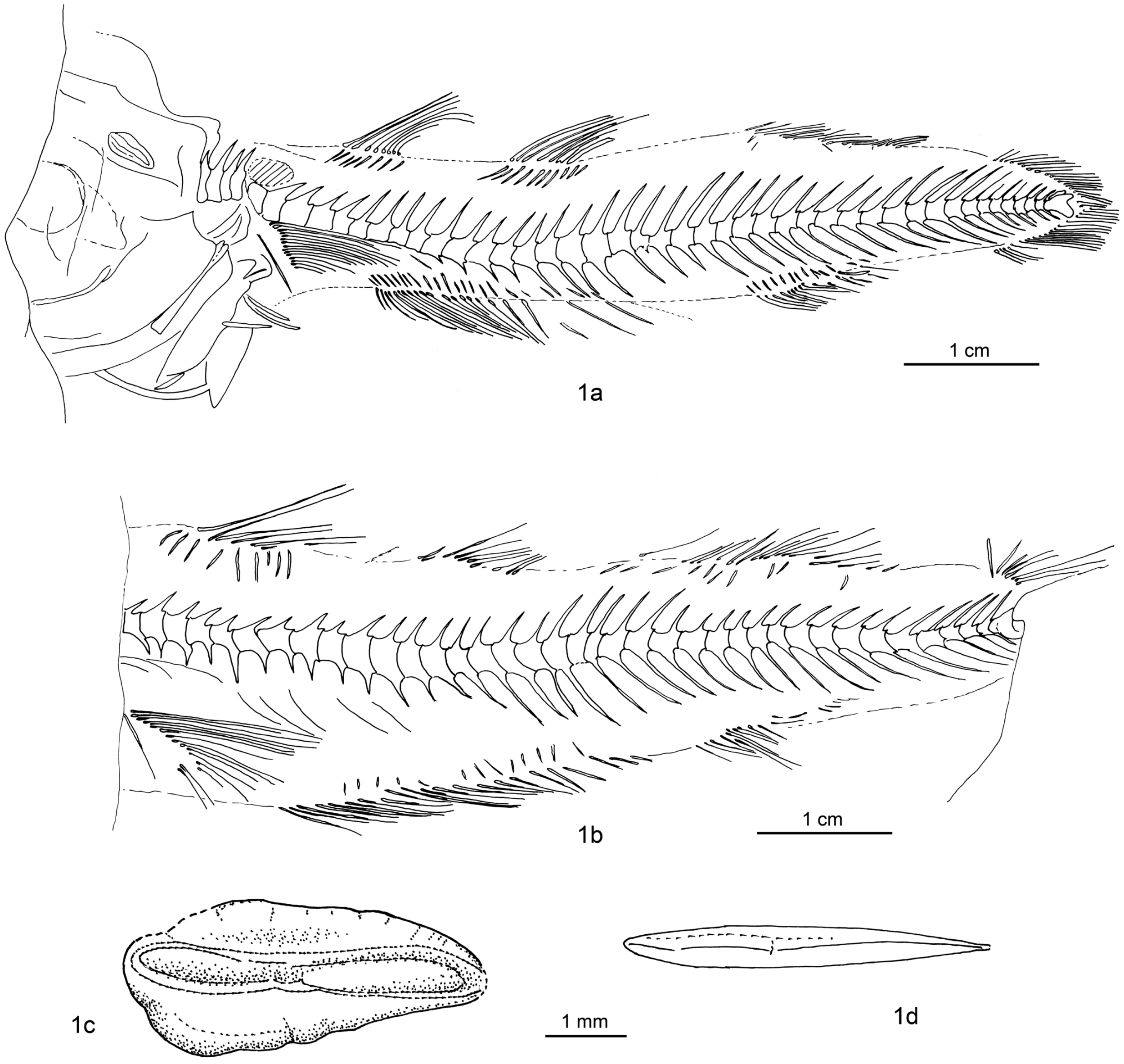

Figure 1. *Palimphemus anceps* Kner, 1862; Krywald borehole at 110.25-110.50 m depth, Upper Silesia, Poland, middle Badenian, earliest Serravallian (lower NN6); **1a:** specimen ZPALWr M/1; **1b:** specimen ZPALWr M/2; **1c-d**: otolith in situ from specimen ZPALWr M/1; **1c**: view of inner face, **1d**: view from ventral.

fin bases of both the first and the second dorsal are about equal in length, estimated in the range of 5.5 to 7.5 % SL. The third dorsal is rather poorly and incompletely preserved. It is inserted above vertebra 28 and opposite to the second anal fin. Counting a combination of fin ray and pterygiophore remnants and imprints arrives at about 18 fin rays which may originally have been present in the third dorsal fin. The distance between the second and the third dorsal appears to be longer than that of the first to the second dorsal by about 50%. The first anal fin is inserted slightly behind the first dorsal fin below vertebra 11. It is the unpaired fin with the longest base estimated at 21-25% of SL, which nevertheless is nearly half of the estimated preanal length. Fin rays and pterygiophores are well preserved in the anterior half of the first anal, but more fragmentary and conspicuously wider spaced in the posterior half. Taking all fin ray and pterygiophore bone remnants and imprints into consideration a total of about 22 originally present fin rays is calculated. The second anal fin is inserted below vertebra 27, nearly opposite to the third dorsal. Its anterior part is well preserved, but the posterior half is disintegrated arriving at a total number of fin rays of not less than 16. Both anal fin rays are shorter than the respective dorsal fin rays. The distance between the anal fins corresponds roughly to the distance between the first two dorsal fins. The bases of the caudal fin rays are rather well preserved and are counted to 41.

The only paired fin preserved is the left pectoral; ventral

	NHMW (42) + PIWU (HT) *	**NHMW 1975/1752/248 ***	**ZPALWr M/1**	**ZPALWr M/2**
Vertebrae, precaudal	18		17	14 *[+3]*
Vertebrae, caudal	27-28		29	25+
Vertebrae, total	45-46		46	42+
first dorsal fin rays (D1)	10-12		9-10	9
second dorsal fin rays (D2)	10-12		10	10
third dorsal fin rays (D3)	17-21		18	19
first anal fin rays (A1)	18-21		22	22
second anal fin rays (A2)	18-19		16+	13+
pectoral fin rays (P)	15-18		15	16
ventral fin rays (V)	6		-	-
caudal fin rays (C)	41-43		41	-
D1 / V	7		8	*[7]*
D2 / V	14		16	*[14]*
D3 / V	26		28	*[24]*
A1 / V	12		11	*[10]*
A2 / V	27		27	*[27]*
HL (% SL)		29.5		
predorsal D1 (% SL)		37.5	*[41.0]*	
predorsal D1 (% trunk L)		(11.5)	16.0	*[10.0]*
predorsal D2 (% SL)		52.0	*[54.0]*	
predorsal D2 (% trunk L)		(32.5)	34.5	*[35.0]*
predorsal D3 (% SL)		72.0	*[73.0]*	
predorsal D3 (% trunk L)		(60.0)	62.0	*[57.0]*
preanal A1 (% SL)		46.0	*[44.5]*	
preanal A1 (% trunk L)		(23.5)	21.0	*[22.0]*
preanal A2 (% SL)		74.0	*[75.0]*	
preanal A2 (% trunk L)		(63.5)	64.5	*[65.0]*
D1-D2 distance (% SL)		7.5	*[8.0]*	
D1-D2 distance (% trunk L)		(10.5)	11.0	*[11.0]*
D2-D3 distance (% SL)		9.0	*[12.5]*	
D2-D3 distance (% trunk L)		(12.5)	17.5	*[11.5]*
A1-A2 distance (% SL)		5.5	*[9.5]*	
A1-A2 distance (% trunk L)		(7.5)	13.5	*[6.5]*
base D1 (% SL)		7.5	*[5.5]*	
base D1 (% trunk L)		(10.5)	8.0	*[11.5]*
base D2 (% SL)		10.5	*[7.0]*	
base D2 (% trunk L)		(14.5)	10.0	*[11.0]*
base D3 (% SL)		14.0	*[13.5]*	
base D3 (% trunk L)		(20.0)	19.0	*[24.5]*
base A1 (% SL)		23.5	*[21.5]*	
base A1 (% trunk L)		(33.5)	30.5	*[37.0]*
base A2 (% SL)		14.0	*[10.5]*	
base A2 (% trunk L)		(20.0)	15.0	*[17.5]*

Table 1. *Palimphemus anceps* Kner, 1862; comparison of meristics and morphometric measurements from Carnevale *et al.* (2012) and the specimens from ZPALWr.
* values from Carnevale *et al.* 2012
(...) back calculated values from Carnevale *et al.* 2012
[...] estimated values.

fins are not preserved. The pectoral is well exhibited and appears to be rather complete with the uppermost fin rays being the longest and continuously decreasing in length downwards to about one fourth of the first ray. The total number of rays is 15.

Short description of specimen ZPALWr M/2 – (see Table 1 for meristics and morphometric measurements) The second specimen is preserved on a marlstone slab of 9 cm width and since it apparently represented an originally somewhat larger specimen, it is lacking the anterior portion forward of a short vertebra assumed to represent the fourth of the set of four shortened anterior vertebrae seen in the other specimen. The rear part of the fish just shows the onset of the caudal fin with the first caudal fin rays dorsally indicating that 3-5 vertebrae might be missing.

First dorsal fin with 7 preserved fin rays and 9 preserved pterygiophores representing originally a total of 9 or 10 fin rays; second dorsal fin poorly preserved with remnants of 10 fin rays; third dorsal fin disintegrated in part, calculated with about 19 fin rays. The first anal fin contains 22 fin rays, which like in the other specimen show a conspicuous wider spacing of rays in the posterior third of the fin. The second anal fin is incomplete with only 13 rays preserved.

Again, the left pectoral fin is the only preserved paired fin. It appears to be somewhat disintegrated at its lower part, containing a total of 16 rays.

Description of the otolith from the specimen ZPALWr M/1 – The right otolith of about 4.5 mm length is well exposed and clean to be seen from the inner face and from ventral. Due to the preparation its posterior tip is slightly damaged and the predorsal portion is still slightly covered by rock. The otolith shape is typical drop-like, expanded anteriorly, particularly anterior-ventrally and sharply pointed posteriorly. The dorsal rim is shallow, slightly undulating, with indistinct pre- and postdorsal angles. The ventral rim is deepest anteriorly below the ostium and more strongly undulating than the dorsal rim. The anterior tip is broadly rounded and the posterior tip pointed. The ratio otolith length to otolith height is about 2.3, the ratio otolith height to otolith thickness at least 3.

The inner face is slightly bend and twisted towards the posterior tip and shows a slightly supramedian sulcus. The sulcus is moderately wide with the colliculi well marked externally, but somewhat indistinct towards the rather narrow collum with an indistinct pseudocolliculum. The cauda is about twice as long as the ostium. The dorsal depression and ventral furrow are both indistinct, the latter visible only anterior of the middle of the ventral rim and at some distance from it. Radial furrows are few and faint on the dorsal field and two short but distinct ones on the ventral field.

Discussion – The specimen ZPALWr M/1 is reasonably well preserved (and to a lesser extend as a complementation also ZPALWr M/2) to allow correlation with the exceptionally well preserved specimens described by Carnevale *et al.* (2012). Vertebrae counts as well as all fin ray counts are well within the range of variations given by Carnevale *et al.* except for the slightly lower number of fin rays in the second anal, which, however, is due to the incomplete preservation of that fin in both specimens from Krywald. Likewise the relative position of the fins to each other and in relation to the vertebra column is well within the range of variation one might expect. Some values of uncertainty have to do with preservation again, particularly the length of the first dorsal and the second anal fin bases, but also the distance between the second and the third dorsal fin. Calculations are shown as percentage of trunk length (SL minus head length = length of vertebral column) since ZPALWr M/1 lacks the anterior half of the head. The calculations as percentage of SL of the specimen NHMW 1975/1752/248 used in Carnevale *et al.* were back-calculated to percentage of trunk length to allow better correlation. Likewise an attempt was made to estimate percentage of SL for the ZPALWr M/1 specimen. The resulting morphometric tabulations is shown in Table 1 and documents good correspondence between the specimens from St. Margarethen and Krywald. In conclusion, the identification of the Krywald specimens as *Palimphemus anceps* is well supported.

My re-investigation of the two specimens resulted in very much the same fin ray counts as once described by Jerzmańska (1962) except for a slightly lower number of fin rays in the first anal (22 *vs* 25) and a slight variation of the precaudal/caudal vertebrae allocation (17+29 *vs* 15+30). Jerzmańska related the specimens to *Gadus macropterygius* (Kramberger, 1883), which was described from stratigraphically somewhat younger Sarmatian rocks of Croatia from Dolje. The unique holotype is preserved in a dorsally compressed view, which hampers counts and measurements as well as visual correlation. Kramberger, however, notes significantly less vertebrae (12+30), which is more in line with the genera *Gadiculus* and the fossil *Paratrisopterus*. Two other gadid species with three dorsal fins are recorded by Kramberger from Dolje and time equivalent strata in Podsuded, Croatia: *Morrhua lanceolata* Kramberger, 1883 and *Morrhua aeglefinoides* Kner & Steindachner, 1863. *Morrhua lanceolata* is listed with a vertebrae formula of 16+30 and fin ray counts rather similar to *P. anceps* (D1=9-10, D2=10, D3=14, A1=19-20, A2=18, P=14-16, V=7-8), the only mentionable difference being the D3 count (14 *vs* 17-21). Subject to review of the type-specimens, *M. lanceolata* is therefore tentatively regarded as synonym of *P. anceps*. *Morrhua aeglefinoides* on the other hand shows the same vertebrae formula as *G. macropterygius*.

Finally, Carnevale *et al.* (2006) record a number of fishes with otoliths in situ from early Sarmatian rocks of Tsurevsky, northern Caucasus, Russia as *Micromesistius* sp. The specimens appear to be well preserved and as far as meristics are listed and from judging from the otolith drawing it is likely that these specimens represent a species of *Palimphemus*, but whether it may represent *P. anceps* or a different, yet undescribed species is subject to further investigations (Carnevale, pers. com.).

The otolith of the specimen ZPALWr M/1 is well enough preserved to allow confident correlation with the otoliths of the otolith-based species *Colliolus sculptus* (Koken, 1891). Isolated otoliths are known to grow to about twice the size of the in situ specimen. This is in agreement with the largest specimen recorded by Carnevale *et al*. (2012) of 195 mm SL, which is slightly more than twice the length of the specimen ZPALWr M/1. Other Gadinae otoliths in the middle Miocene of the Paratethys are few: *Micromesistius arcuatus* Radwanska, 1992, *Paratrisopterus labiatus* (Schubert, 1905) and the extant *Gadiculus argenteus* Guichenot, 1850, non of which are morphologically close enough to the in situ find of *Palimphemus anceps* to be confused.

Distribution – Skeleton finds of *Palimphemus anceps* so far appear to be restricted to the Badenian (late Langhian to early Serravallian) of the Paratethys. Isolated otolith finds, however, show that *Palimphemus anceps* was one of the most common, most wide-spread and most long-living gadids during the Neogene, known from late Oligocene to early Pliocene times in the North Sea Basin and Miocene strata in the Mediterranean and Paratethys, but also across the North Atlantic at the East Coast of North America (Müller, 1999; Schwarzhans, 2010).

Synonymisation and allocation of otolith-based taxa

Otolith-based genera synonymous to Palimphemus – The otolith-based fossil genus *Colliolus* now is established as a junior synonym of the skeleton-based fossil genus *Palimphemus*. Another fossil otolith-based genus now put into synonymy is *Gadichthys* Gaemers & Schwarzhans, 1973. *Gadichthys* was separated from *Colliolus* primarily on the base of its very wide collum. However, Schwarzhans (2010) pointed out the conspicuous gap between a group of late Miocene to early Pliocene species and a group of late Oligocene and early Miocene species both placed in this genus. The most likely explanation for this gap is that *Gadichthys* in its current understanding is polyphyletic and that the otolith morphology used for definition has evolved twice and independently from a *Colliolus*-stem. Therefore it appears to be the most appropriate solution to also synonymise *Gadichthys* with *Palimphemus* and therewith other nominal otolith-based genera previously already synonymised with either *Colliolus* (*Pseudocolliolus* Gaemers, 1978) or *Gadichthys* (*Doyenneichthys* Gaemers, 1983 and *Circagadiculus* Gaemers, 1990) (see above).

Carnevale *et al*. place *Palimphemus* close to the persistent genera *Micromesistius, Trisopterus* and *Gadiculus* (to which group *Merlangius* could be considered as well as a specialised offshoot from near *Micromesistius*). All four genera including *Paratrisopterus* as a fifth fossil genus (regarded as a junior synonym of *Gadiculus* by Prokofiev, 2004) are established as separate lineages by otoliths since middle to late Oligocene. The fossil otolith record also supports their relationship with the *Paratrisopterus/Gadiculus* group separated from the other already in early Oligocene. A further fossil otolith-based genus, *Merlangiogadus* Gaemers, 1973, is suspect to represent a synonym of *Micromesistius*. Finally, otoliths morphologically similar to *Palimphemus* have been described under the fossil otolith-based genus *Protocolliolus* Gaemers, 1976 from the Paleocene and early Eocene. The relationship of these early forms, however, must remain unresolved for the time being.

Otolith-based species of Palimphemus – Many otolith-based species have been described in the past, which bear resemblance to that of *P. anceps*, not from the Mediterranean and Paratethys, where so far it seems to be the only species representing the genus, but from the North Sea Basin. The following is a brief updated list from Schwarzhans (1994; 2010):

Palimphemus anceps Kner, 1862, Chattian to Zanclean, North Sea Basin, NE-America, Mediterranean, Paratethys (for synonymies see above).

Palimphemus antwerpiensis (Gaemers, 1971), late Burdigalian, North Sea Basin.

Palimphemus attenuatus (Koken, 1891), middle and late Chattian, North Sea Basin.

Palimphemus benedeni (Leriche, 1926), Zanclean, North Sea Basin and NW-Atlantic (syn. *Pseudocolliolus redonensis* Gaemers, 1987).

Palmiphemus brevicollum (Gaemers *in* Schwarzhans, 1994), early Chattian, North Sea Basin.

Palimphemus cuykensis (Gaemers, 1978), late Tortonian and Messinian, North Sea Basin, NE-America (syn. *Pseudocolliolus curvidorsalis* Gaemers, 1983; syn. *Pseudocolliolus hinschi* Gaemers, 1987).

Palimphemus mistensis (Gaemers, 1990), late Burdigalian to early Langhian, North Sea Basin, NE-America.

Palimphemus schwarzhansi (Gaemers, 1976), middle to late Langhian, North Sea Basin.

Palimphemus serratus (Schwarzhans, 2010), Aquitanian, North Sea Basin.

Palimphemus spatulatus (Koken, 1891), middle and late Chattian, North Sea Basin.

Palimphemus syltensis (Gaemers & Schwarzhans, 1982), late Tortonian to Messinian, North Sea Basin.

Palimphemus twistringenensis (Gaemers, 1990), middle to late Langhian, North Sea Basin.

Palimphemus undosus (Gaemers, 1973), late Chattian, North Sea Basin.

Palimphemus venustus (Koken, 1891), middle Serravallian to Tortonian, North Sea Basin (syn. *Merlangius spatulatus miocenicus* Heinrich, 1969).

Palimphemus verticalis (Gaemers & Schwarzhans, 1973), Piacenzian, North Sea Basin.

Evidently, *Palimphemus* was primarily a North Atlantic temperate genus with several species and a rapid evolution through most of late Oligocene to early Pliocene times. An endemic evolution is possible in the North Sea during late Miocene, although the abundance of taxa in the North Sea Basin probably is an expression of collecting bias rather than a reflection of real distribution. As opposed to the many and mostly short-lived northern temperate species, *P. anceps* sticks out as a really long-living species with a wide distribution well into warmer seas than its congeners.

Conclusions and outlook

The Krywald specimen with its otolith in situ offered the exceptional chance to relate a skeleton-based fossil genus and species and one of the most common otolith-based fossil genera and species, which in this case led to the synonymisation of the otolith-based taxa. Both taxonomic entities have existed in parallel for more than 100 years and therewith also exemplify the potentially high degree of parallel taxonomy of skeleton and otolith finds in the fossil teleost record.

Otoliths *in situ* are rarely reported. *In situ* otoliths of Neogene Gadidae have only been described twice: *Paratrisopterus avus* Fedotov, 1976 by Fedotov and *Gadiculus labiatus* (Schubert, 1905) by Landini & Sorbini, 1999. The latter is likely to represent *Paratrisopterus glaber* Schwarzhans, 2010 judging from the figured otolith. The prospect for connecting skeleton and otolith-based data through investigations of otoliths *in situ* appears nevertheless good. Schubert (1906) mentioned for instance that he has seen an otolith *in situ* in a skeleton of *Gadus lanceolatus* (Kramberger, 1883) from Dolje. He stated that it was only visible from the outside and reminded him of his newly established *Otolithus (Gadidarum) minusculus* Schubert 1906 (p. 662), a species which for the most part represents juveniles of *Colliolus sculptus* (now *Palimphemus anceps*). In the same paper he mentioned at several occasions having seen otoliths *in situ* in Karmberger's fish specimens from Dolje, totaling 10 species (pp. 630, 647, 651, 653, 657, 690, 699). Kramberger's drawing of *Morrhua macropterygius*, which likewise originated from Dolje, also suggests the presence of otoliths *in situ*. The many fishes described by Bogatshov (1929, 1933, 1938) from the late Miocene and Pliocene of the Caspian Basin, amongst them several endemic gadids, might offer additional potential to retrieve otoliths *in situ*. Isolated otoliths from strata of the same age elsewhere in the Paratethys indicate the presence of several endemic developments in gadids, particularly of the genus *Paratrisopterus*. Many myctophid otoliths obtained *in situ* from the late Miocene of Italy have been recorded by D'Erasmo (1929) and Bedini *et al.* (1986), but a serious correlation with isolated otolith-based records has never been attempted.

It seems that the time is ripe to devote more effort to correlating fossil skeleton and otolith-based data. The prospects are better than it may appear from the lack of such research in the past. New techniques such as CT-scanning or plastic casting (Schwarzhans, 2007) may aid to better results.

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