Paläontol Z
DOI 10.1007/s12542-009-0031-7

RESEARCH PAPER

First fossil records of the tholichthys larval stage of butterfly fishes (Perciformes, Chaetodontidae), from the Oligocene of Europe

Norbert Richard Micklich · James C. Tyler · G. David Johnson · Ewa Świdnicka · Alexandre F. Bannikov

Received: 28 May 2009 / Accepted: 17 June 2009

Abstract The first fossils of the tholichthys larval stage of a chaetodontid from the lower Oligocene (Rupelian, Fish Shales; about 30.1 MYA) of Frauenweiler (Baden-Württemberg, S Germany) are described, along with two less well-preserved probable tholichthys from the lower Oligocene Menilite-Formation (IPM3, 30–29 MYA and IPM4A, 29–28 MYA) of Przemyśl (Outer Carpathians, SE Poland). The fossils are compared with tholichthys larvae of the extant genus of Chaetodontidae to which they are most similar, namely *Chaetodon.* The German specimens are identified as tholichthys larvae by the plate-like expansions of the supracleithrum and posttemporal that extend posteriorly well behind the head and by an expanded preopercle with a large posterior spine; these bones, and the frontals and supraoccipital, are distinctively rugose. The Polish specimen from IPM3 has similar features so it is safe to assume that it also is a chaetodontid tholichthys, whereas the specimen from IPM4A is so poorly preserved that it can only very tentatively be referred to the Chaetodontidae. The occurrence of tholichthys larvae prompts reconsideration of the paleoenvironmental situation at their respective fossil sites.

Keywords Morphology, paleoecology · Tholichthys, Chaetodontidae · Lower Oligocene · Frauenweiler, S Germany · Przemyśl, SE Poland

Kurzfassung Die ersten fossilen Nachweise des Tholichthys-Postlarvalstadiums von Schmetterlingsfischen (Chaetodontidae) werden beschrieben. Zwei komplett erhaltene Exemplare stammen aus dem Unter-Oligozän (Rupelton, Fischschiefer; ca. 30,1 Mio. J.) der Tongrube Frauenweiler bei Heidelberg (Baden-Württemberg, Süd-Deutschland). Zwei weitere, weniger gut überlieferte Funde stammen aus der unter-oligozänen Menilit-Formation (IPM3, 30-29 Mio. J. und IPM4A, 29-28 Mio. J.) von Przemyśl (Äußere Karpathen, Südost-Polen). Die Fossilien werden mit den Tholichthys-Larven heutiger Chaetodontidae verglichen, und zwar insbesondere mit solchen der Gattung *Chaetodon*, denen sie am meisten ähneln. Die Funde aus Frauenweiler können aufgrund plattenähnlicher Auswüchse am Supracleithrum und am Posttemporale die deutlich hinter das Kopfende hinausreichen, sowie ein breites Präoperculum mit einem großen, nach hinten gerichteten Stachel als Tholichthys-Larven bestimmt werden. Ebenso typisch ist die rugose Oberflächenskupltur mancher Schädelelemente, insbesondere diejenige der Frontalia und des Supraoccipitales. Übereinstimmungen mit dem polnischen Exemplar aus der IPM3 Zone legen nahe, dass es

---

N. R. Micklich (✉)
Natural History Department, Hessisches Landesmuseum
Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany
e-mail: micklich@hlmd.de

J. C. Tyler · G. D. Johnson
National Museum of Natural History, Smithsonian Institution,
MRC-159, P.O. Box 37012, Washington, DC 20013-7012, USA
e-mail: tylerj@si.edu

G. D. Johnson
e-mail: johnsond@si.edu

E. Świdnicka
Department of Palaeozoology, Zoological Institute,
University of Wrocław, Sienkiewicza 21,
50-335 Wrocław, Poland
e-mail: gama@biol.uni.wroc.pl

A. F. Bannikov
Borisyak Paleontological Institute,
Russian Academy of Sciences,
Profsoyuznaya 123, Moscow 117997, Russia
e-mail: aban@paleo.ru

sich auch bei diesem um einen Vertreter der Chaetodontidae handelt. Der andere Fund kann aufgrund seiner schlechten Erhaltung nur unter Vorbehalt hierzu gestellt werden. Das Vorkommen von Tholichthys- bzw. Tholichthys-ähnlichen Larven gibt Anlass die ehemaligen Lebens- bzw. Umweltbedingungen im Bereich der oben genannten Lokalitäten zu überdenken.

Schlüsselwörter Morphologie, Paläoökologie · Tholichthys, Chaetodontidae · Unter Oligozän · Frauenweiler, Süd-Deutschland · Przemyśl, Südost-Polen

Introduction

There are only a few fossil records of the Chaetodontidae. Bannikov (2004) showed that taxa from the Eocene of Monte Bolca that had been referred to the Chaetodontidae by previous authors do not possess the diagnostic features of that family and that no Eocene chaetodontids were known. A recent review of the fossil record of the Chaetodontidae by Carnevale (2006) revealed how very meager it is, with the earliest known chaetodontid being a single species (*Chaetodon hoeferi*) from the lower Oligocene (Rupelian) of Slovenia (a second Oligocene skeletal taxon is questionable, and Eocene otolith taxa are not valid). Carnevale (2006) further stated that there is only a single unquestioned chaetodontid species (*Chaetodon ficheuri*), from the Miocene (Miocene otoliths either have been referred to an extant taxon or are invalid), which he redescribed, and that there is only a single Pleistocene record, a specimen that had been referred to as *Chaetodon hoefleri*.

This investigation was prompted by the recovery of two small but very well-preserved larval fishes from the lower Oligocene of S Germany. It was immediately evident that they exhibit many features of the armor-headed tholichthys pre-settlement stages that characterize extant Chaetodontidae. They also are well within the size range of the larvae of this family, and thus can be regarded as one of the earliest reliable records of this group. Two previously found but less well-preserved specimens from the Polish Carpathian are of similar size and share many morphological traits with the German specimens; we also consider these to be tholichthys larvae.

General information

The German fossils were collected some years ago in the Frauenweiler clay pit, which is officially designated as “Grube Unterfeld”. It is located in the vicinity of the small village of Frauenweiler, about 13 km S of Heidelberg (Baden-Württemberg, S Germany). In addition to plant and invertebrate fossils (Wagner-Klett 1919; Trunkò 1997), finely preserved vertebrates have been found, especially birds (Mayr 2000, 2004; Mayr et al. 2002; Mayr and Manegold 2004). There is also a very rich fossil fish fauna that is significant because of its broad systematic diversity and excellent preservation (Micklich and Parin 1996; Parin and Micklich 1996a, b; Micklich 1998; Pharisat and Micklich 1998; Hovestadt and Hovestadt-Euler 1999, 2002; Sakamoto et al. 2003, 2004; Parin and Astakhov 2007). Many specimens are completely articulated because they were deposited in a stratified water body with anoxic conditions in the uppermost layers of the bottom mud, which did not permit decay of organic matter.

Today the open mine covers a total area of scarcely 0.1 km^2. It has already been extensively backfilled with building rubble and ground excavation materials, and only a very restricted area is accessible for excavations today. The sediments consist mainly of dark grey or black, sometimes marly, argillaceous clay stones, which are very well-laminated in some sections. They represent the so-called “Fish Shales” (Trunkò and Munk 1998; Grimm et al. 2002; Micklich and Hildebrand 2005). Basically, the exposed sequence terminates in a typical series of bituminous and well-laminated strata, with a total thickness of about 20 cm. These clays overlie another characteristic layer, which is about 8 cm thick and consists of concretions with high carbonate content. The concretions probably correspond with the “Untere Geodenhorizont” of Trunkò and Munk (1998). Together with the overlying clays, these layers have been well known for a long period of time to amateur paleontologists, who labeled them as layers 23–25 in their own stratigraphic documentation. Both fossil tholichthys described herein were recovered from layer number 23 of this peculiar sequence.

The presumed tholichthys specimens from Poland originate from the Przysietnica and Kniażyce fossil sites in the Polish part of the Outer Carpathians (West Carpathian, SE Poland). These are located about 45 km from each other and are correlated with the stratotype profile of the Krępak localities of the Skole Unit, which are natural outcrops that expose the full profile of the Menilite–Krosno Series (Jerzmańska and Kotlarczyk 1976; Kotlarczyk and Jerzmańska 1988). According to the nannoplankton, the sites belong in the biozone NP23 of Martini (1971).

Przysietnica is a small village about 8 km from Brzozów city, located SE of Rzeszów, the capital city of the Podkarpackie Voivodeship. The outcrops Przysietnica (PS1–10) occur in the middle of the village and are located along the nearby country road “Droga pod Krzyżami” (“Road under the Crosses”). They were explored during the years 1982–1998. The outcrop with tholichthys specimen ZPALWr. A/4001 was about 15 m in maximum extension and exposed a profile section of about 10 m, which was mainly characterized by grey mudstones and brown marly shales in the upper part and laminated limestones and yellow marly shales in its lower part. The fossil was found in the middle part of this section, which mainly consisted of brown siliceous–argillaceous shales (thickness 35 cm). The associated ichthyofauna represents the fish assemblage IPM4A zone of the Menilite–Krosno Series and was analogous to that of the main outcrop in Przysietnica village (Kotlarczyk et al. 2006).

Kniażyce is another small village about 10 km SW of Przemyśl city, which also is located SE of Rzeszów. The outcrops Kniażyce (KN1–4) occur along a small stream, which is the western tributary of the Wiar River. They represent a separate sedimentary unit and were explored during the years 1987–1988. The outcrop with the presumed tholichthys ZPALWr. A/4000 was about 10 m in maximum extension and exposed brown siliceous–argillaceous shales (thickness ca. 7 cm), grey mudstone (thickness ca. 3 cm) and sandstones (thickness ca. 20 cm). The fossil was found within a 7 cm thick layer of brown siliceous–argillaceous shales in the middle of this sequence. The ichthyofauna probably represents the IPM3 zone of the Menilite–Krosno Series, and it is considered to be analogous with the North Caucasus locality of Borislav at the Belaya River.

Materials

Fossils

HLMD-T 410a (head to left) and HLMD-WT 410b, part and counterpart, 17.0 mm SL. Frauenweiler clay pit (properly “Grube Unterfeld”), Rauenberg municipality, Baden-Württemberg, S Germany (49°16′15″N, 8°40′24″E); lower Oligocene (Rupelian, Fish Shales), 30.1 MYA. Referred to in the descriptive text simply as 410a and 410b. SMNS 87457/283a (head to left) and SMNS 87457/283b, part and counterpart, 15.5 mm SL. Same locality data as above. Referred to in the descriptive text simply as 283a and 283b. ZPALWr. A/4000a (head to left) and ZPALWr. A/4000b (older numbers in the collection are N/6420a, b), part and counterpart, 17.5 mm SL. Kniażyce, southwest of Przemyśl, Voivodeship Podkarpackie (Subcarpathian), Boryslav-Pokuttya Nappe, Outer Carpathians, SE Poland (49°40′N, 22°50′E); Lower Oligocene (Rupelian), probably IPM3 zone of Menilite Formation, 30–29 MYA. Referred to in the descriptive text simply as A/4000. ZPALWr. A/4001 (older number in collection is N/6421), single plate (head to left, and fragments of counterpart), ca. 12.5 mm SL. Przysietnica southwest of Przemyśl, Voivodeship Podkarpackie (Subcarpathian), Subsilesian Nappe, Outer Carpathians, southeast Poland (49°44′N, 22°03′E); Lower Oligocene (Rupelian), IPM4 zone of Menilite Formation, 29–28 MYA. Referred to in the descriptive text simply as A/4001.

Extant tholichthys

We have examined tholichthys larvae of great morphological diversity and representing many genera of Chaetodontidae, but we list here only those of *Chaetodon* sp. because they are the most similar to the fossil tholichthys.

USNM 391660, 9.6 mm SL; USNM 152964, 18.6 mm SL; USNM 266895, 19.3 mm SL; Dana Collection station 38871, 5.8 and 6.2 mm SL; NSMT-PL-389, 7.5 mm SL; NSMT-PL-390, 8.3 mm SL.

Extant adult Chaetodontidae

One-hundred and seventy radiographs or cleared and stained specimens representing 34 species of nine genera of Chaetodontidae and ten specimens of three genera of outgroup taxa from the collections of the USNM, as listed in Fig. 9 and Table 1.

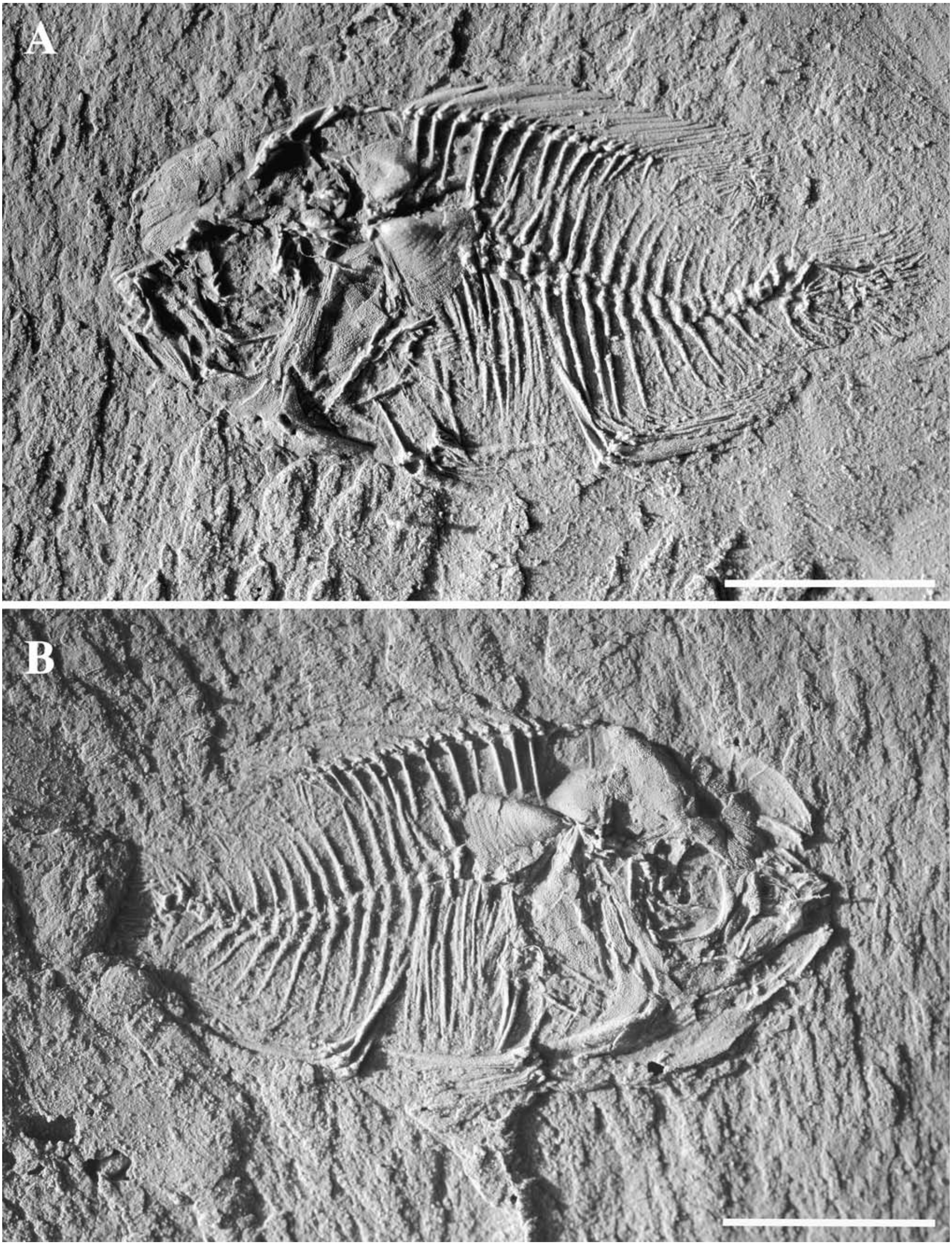
Methods

Preparation

The tholichthys specimens from Frauenweiler were prepared by the transfer method. This was developed especially for fossils that are preserved in a fragile or otherwise unstable original matrix, for example clays, marls or oil shales, which are frequently at great risk of drying out and disintegrating because of their high water content. The process involves transferring the bony substance of the fossil on to an artificial matrix, which in this case consists of epoxy resin. It also has the advantage that the fossil is no longer exposed in interior view, but, rather, in external view and often shows very delicate morphological details. For the specimens presented herein, this method was modified so that the fossils were transferred to pre-formatted slabs of fiber cement, using an epoxy resin paste (for methodological details see Kaiser and Micklich 1995; Roth and Micklich 2006; Micklich and Drobek 2007 pp 19 and 20).

Institutional abbreviations

HLMD, Hessisches Landesmuseum Darmstadt; NSMT, National Science Museum, Tokyo; SMNS, Staatliches Museum für Naturkunde Stuttgart; USNM, collections of the former US National Museum; collections now part of the National Museum of Natural History, Smithsonian


A
B

◀ **Fig. 1** HLMD-WT 410a, b; 17.0 mm SL. Pre-settlement pelagic tholichthys larva of a chaetodontid, general view. Lower Oligocene (Rupelian, about 30.1 MYA), Frauenweiler clay pit (Grube Unterfeld), Baden-Württemberg, S Germany. **a** Main part. **b** Counterpart. Each *scale bar* 5 mm

Institution; ZPALWr., Department of Palaeozoology, Institute of Zoology, University of Wroclaw.

Anatomical abbreviations and numbering

Fr, frontal; O, opercle; Po, preopercle; Ps, pelvic spine; Pt, posttemporal; PU, preural centrum; Sc, supracleithrum; SL, standard length; So, supraoccipital; VIS, vacant interneural space. The numbering of vacant interneural spaces (spaces between neural spines below the dorsal-fin in which there are no ventral shafts of dorsal pterygiophores) follows Birdsong et al. (1988), Baldwin and Johnson (1993), Bannikov and Tyler (1995), Tyler et al. (2003), Baciu et al. (2005), etc., in which the space takes the number of the vertebra whose neural spine borders the space anteriorly (i.e., the first interneural space is between the neural spines of the first and second vertebrae; the preneural space is that just anterior to the first neural spine).

Miscellaneous abbreviations

IPM1-6 zones—ichthyofauna, Paleogene, Menilite–Krosno Series; for the six fish-bearing zones in the Oligocene of the Outer Carpathian Mountains of southeastern Poland (see Kotlarczyk and Jerzmańska 1976, 1988; Jerzmańska and Kotlarczyk 1976).

Morphological descriptions of fossils

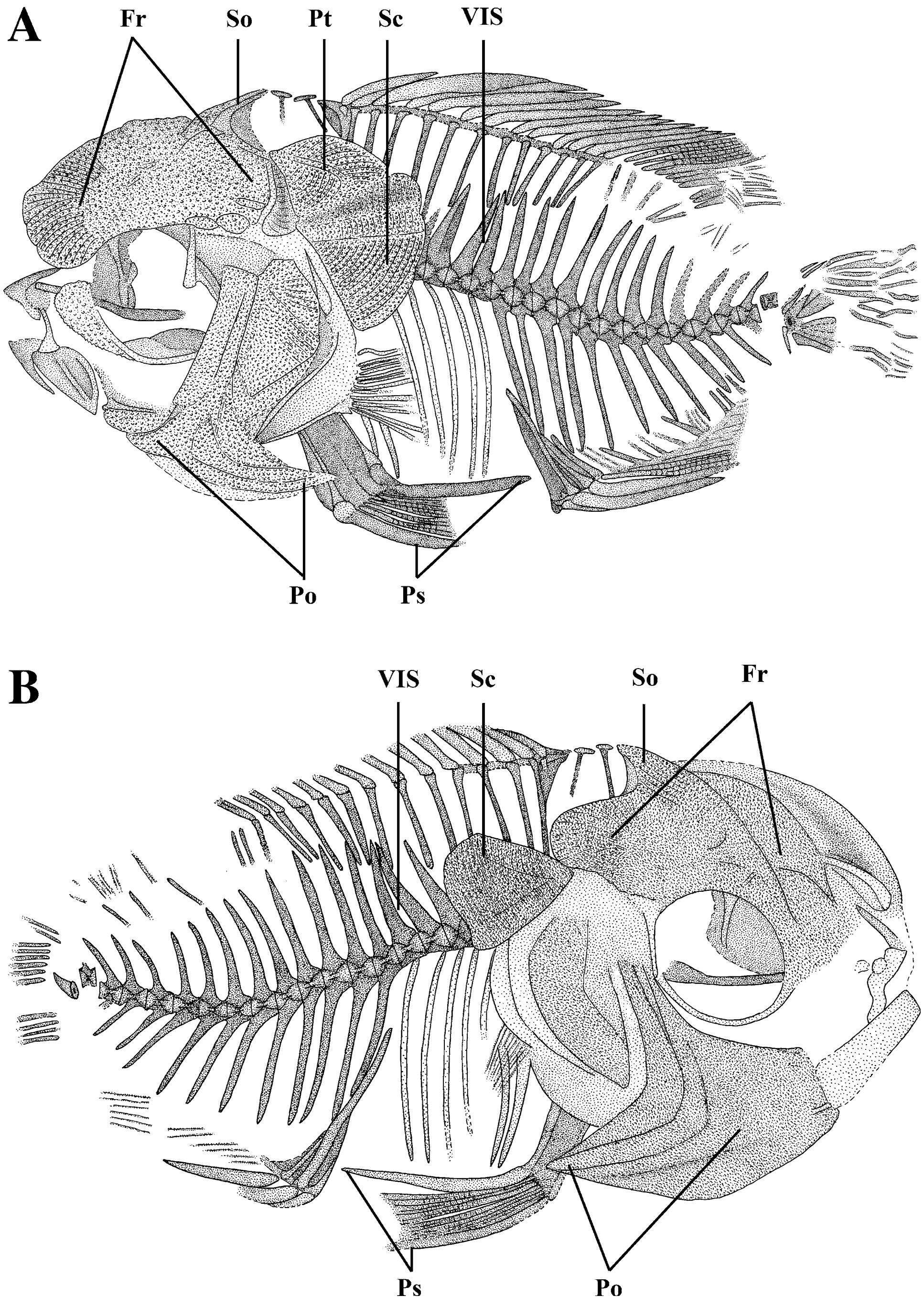
HLMD-WT 410a, b (Figs. 1, 2) and SMNS 87457/283a, b (Figs. 3, 4)

The teeth are clearly preserved in 283a; they are long, slender, and typically setiform. In 283b there are impressions of the teeth, but teeth are not preserved in 410a, b. The premaxilla has a long ascending process that extends posteriorly to the level of the anteroventral edge of the frontal plate in both specimens, and in both the articular is larger and longer than the dentary. The expanded upper end of the maxilla and its articulation with the palatine is relatively clearly seen in 283b. The lower rounded end of the maxilla meets (283) or somewhat overlaps (410) the upper edge of the lower jaw. The lachrymal is large (best seen in 410a), and a large infraorbital shelf is present; we cannot determine which infraorbitals are involved in the composition of the shelf. Situated between the regions of the articular head of the maxilla and the upper anterior end of the lachrymal is the shaft-like anterior process of the palatine that articulates with the maxilla, but most of the palatine is obscured from view by the lachrymal. In 283a, the laterally expanded anterior end of the vomer is evident just below the anterior end of the palatine. The vertically oriented lateral surface of the lateral ethmoid is relatively clearly defined (especially in 283a and 410a), and the less well-defined bony mass just to the front and rear of this surface is the large ethmoid block. The parasphenoid in both specimens is a strong horizontal shaft without a ventral flange. The nasal bone is preserved in 283a just below the posterior end of the premaxilla and the anteroventral edge of the frontal plate, and in 283b grooves and surface sculpturing are evident on the surface of the nasal.

In both fossils there is a huge bony plate, with a rugose surface and various grooves and other surface sculpturing that extends from the front of the head in the region above the upper jaw to the rear of the skull below the supraoccipital region. There is so much surface sculpturing on this plate (with far more and smaller rounded humps than can be shown in the ink illustrations of the fossil tholichthys) that we cannot distinguish the individual component bones, but the supraoccipital crest is distinct even if the lower regions of the supraoccipital are not distinct from the surrounding bones, and the anterior two-thirds of this plate obviously corresponds to the frontal. We presume that this plate in the fossils appears especially large and broad mostly because the heads of the fossils are flattened into single planes and the frontals are being seen at a right angle to the eye rather than obliquely, as in the lateral view of the cleared and stained extant specimen. Nevertheless, it could be that some of the great breadth of the frontal region of this plate in the fossils is a specialized feature of this particular taxon. In the lower posteroventral region of the plate in 410a, at the level of the rear of the top of the orbit, there are several limited areas of thickened and somewhat differently surfaced bone that probably indicate the sphenotic, pterotic, and epiotic regions of the plate, at least in part. Just behind the rear of the orbit in 283b there is evidence of one or more of the extrascapular bones, with deep grooves and indentations for canal openings, but the number of elements involved cannot be determined.

Projecting back from the rear of the head of the fossils, in the region above and behind the arch of the pectoral girdle, is a large knobby plate that reaches posteriorly to the level of about the second to third from the last abdominal vertebral centra. Again, because of the extensive surface sculpturing, we cannot detect a division of this plate into what we presume to be a more dorsal portion formed by the posttemporal and a ventral portion formed by the supracleithrum. That such a division of the large plate is indeed present, however, is indicated in 410b, in which only a single much smaller plate is preserved in this

Fig. 2 HLMD-WT 410a, b. Reconstructions, with labeling of most of the characteristic features; same specimen as in Fig. 1

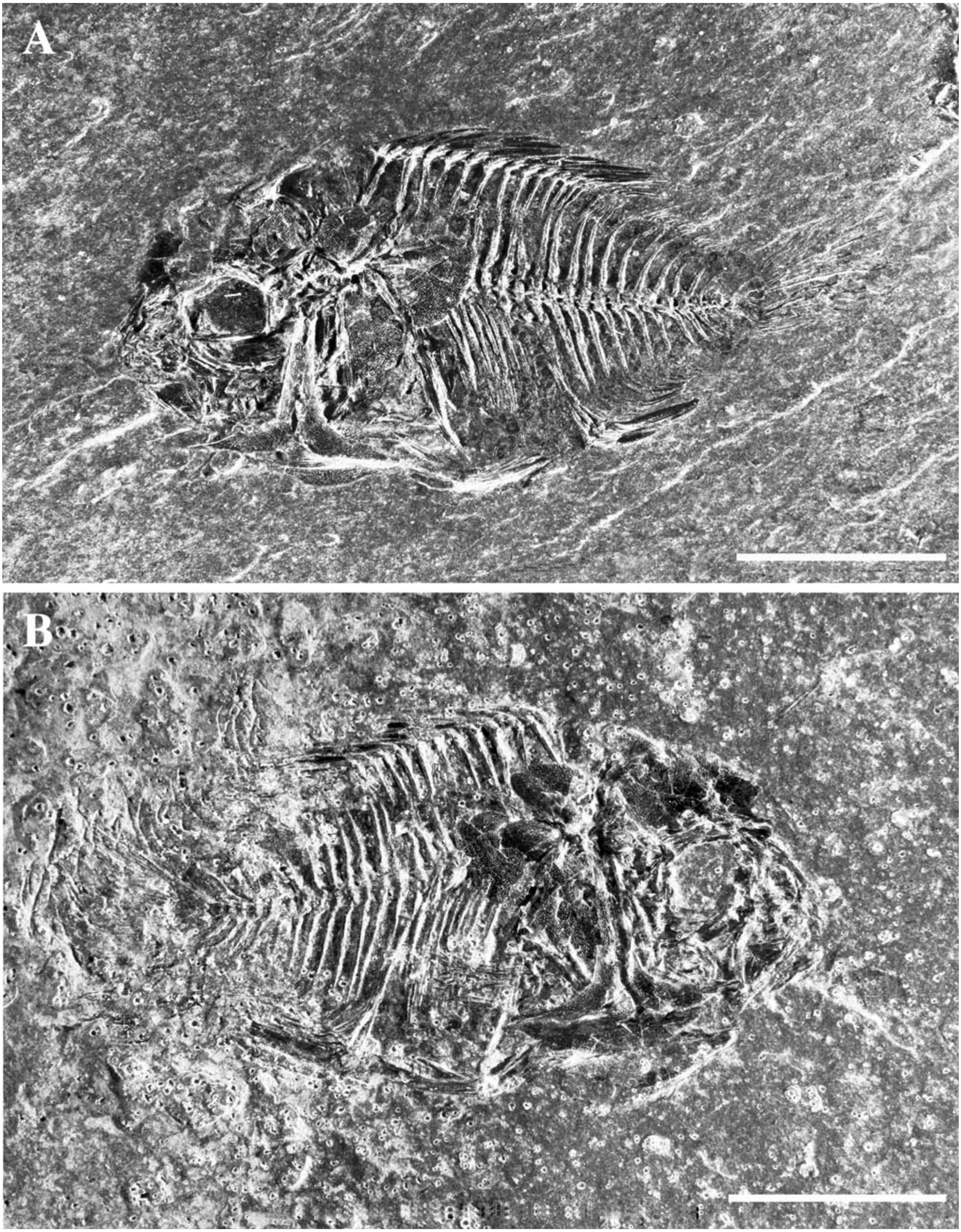


region (displaced slightly ventrally). This small plate obviously corresponds to the (posttemporal) upper part of the compound plate of the 410a counterpart and to that of 283; the rest of the plate in 410b represents the (supracleithrum) lower part of the plate, even though we cannot distinguish a suture between the two pieces.

The large preopercular spine in the fossils tapers to a point well behind the estimated rear of the skull; the spine reaches posteriorly to about the level of the pectoral-fin base in 410, whereas it reaches to beyond the pectoral-fin base in 283b and to between the two halves of the pelvis in 283a.

There are two supraneural bones in the fossil tholichthys. Both supraneurals in 410 have expanded distal heads that project both anteriorly and posteriorly to the relatively

Fig. 3 SMNS 87457/283a, b; 15.5 mm SL. Pre-settlement larval stage of a chaetodontid, general view. Lower Oligocene (Rupelian, about 30.1 MYA), Frauenweiler clay pit (Grube Unterfeld), Baden-Württemberg, S Germany. **a** Main part. **b** Counterpart. Each *scale bar* 5 mm ▶


A
B

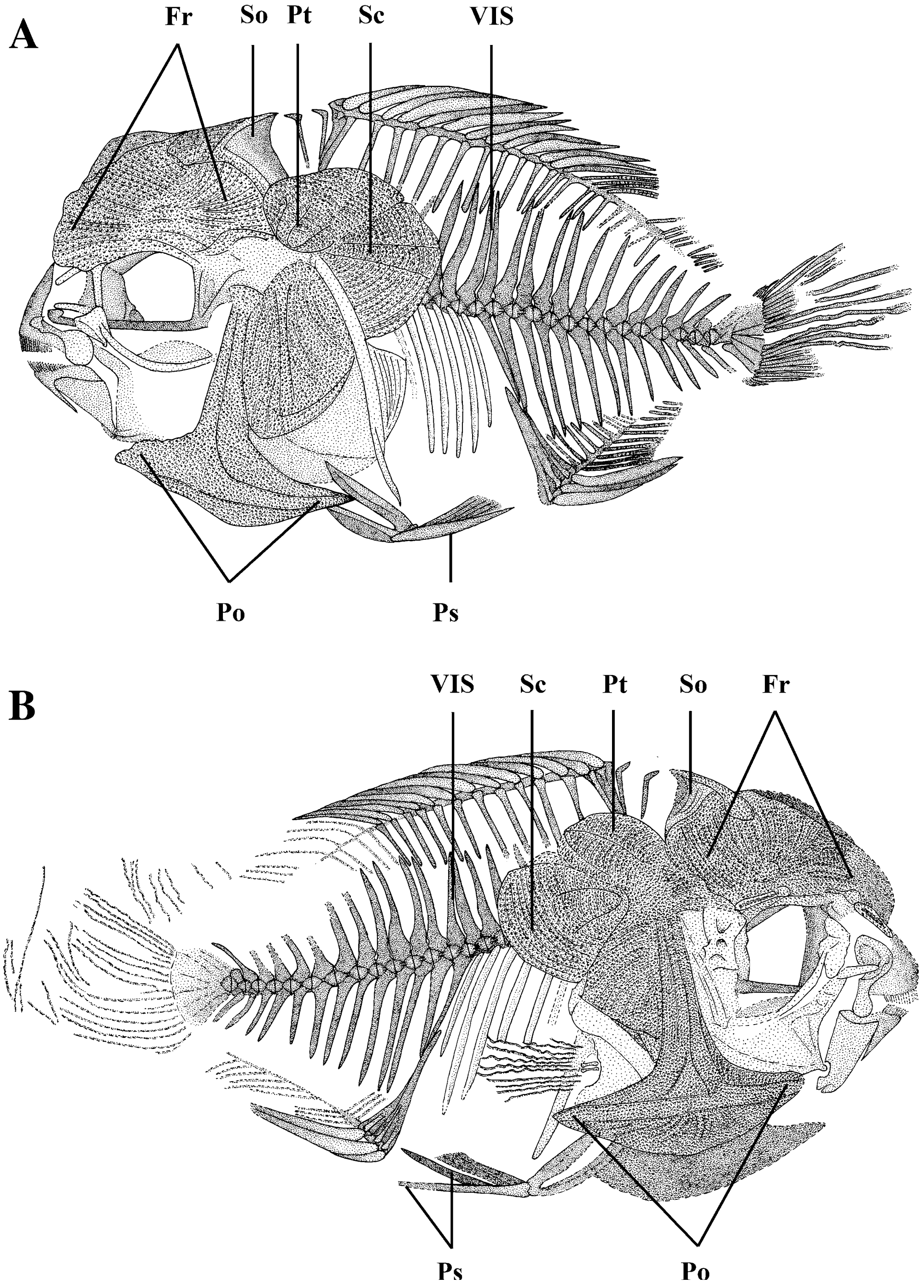


Fig. 4 SMNS 87457/283a, b. Reconstructions, with labeling of most of the characteristic features, same specimen as in Fig. 3

vertical shafts of the bones, and the ends of these heads are only slightly out of contact with one another and with the supraoccipital and first dorsal pterygiophore. In 283, however, only the anterior projections of the heads of the supraneurals are evident, and no posterior projections are indicated; it is not clear if the posterior projections are present and simply not exposed or if they are absent. In either case, the apparent absence of a posterior projection of the heads of these two supraneurals in 283 leaves a significant gap between the two heads and between the supraneural heads and the supraoccipital (the shaft of the second supraneural is close to the front edge of the first dorsal pterygiophore so very little space separates them).

The pelvis and pelvic fins of 410 are turned 90° and are exposed in dorsoventral view, with the pelvic spine from each side evident, and with an indeterminate number of articulated branched rays between the spines. A dark, thickened area (not indicated in the reconstruction) between the bases of the pelvic spines probably represents a short posterior process of the pelvis (basipterygium). The pelvis and pelvic fins of 283 are preserved in lateral view. Both pelvic spines and an indeterminate number of branched rays are visible in 283b, whereas only one spine is exposed in 283a. The two halves of the pelvis in 283a are separated for most of their lengths, and the posterior tip of the preopercular process is situated between their anterior regions; a short posterior process of the pelvis seems evident in 283a.

In 410, the postcleithra (presumably ventral) from both sides are positioned vertically below the pectoral-fin, but it cannot be determined if dorsal postcleithra are present. In 283, a single long postcleithrum is seen in both parts, but no distinction between ventral and dorsal components is evident; in 283a there is a wide flange with vertical striations along the posterior edge of the shaft of the postcleithrum. The pectoral arch is best seen in 410a, but the individual components are not distinguishable; about 13 pectoral-fin rays are evident.

The ribs, as exposed in 410, are sturdy and very long, reaching almost to the ventral midline. Although these ribs are relatively wide, we cannot see sufficient detail to determine if they have developed the characteristic chaetodontid anteromedial flange from the main shaft. An anteromedial flange is more clearly indicated in the ribs of 283, which, as exposed, are even wider than those in 410. However, in 283 the ribs do not extend as far ventrally as in 410, reaching to no more than about three-fourths down the abdominal cavity; we suppose that the ventral ends of the ribs in 283 are not fully exposed and that they are probably as long as those in 410.

There are 13 dorsal-fin spines and three anal-fin spines in both specimens. The total number of fin rays cannot be determined in either the dorsal or anal fins of the fossils. The first two dorsal and anal spines are in supernumerary association with the first dorsal and anal pterygiophores, both of which have lateral expansions buttressing the basal articulations of these first two spines. The dorsal region of the first anal pterygiophore is situated along the anterior edge of the haemal spine of the first caudal vertebra, and the dorsal end of the second anal pterygiophore is situated in the space between the ventral ends of the first and second haemal spines of the caudal vertebrae (410a) or at least on that trajectory.

Most of the abdominal vertebrae are obscured from view by the posttemporal and supracleithrum head plates, with only the last two or three centra fully exposed, so we can only presume that there are ten abdominal vertebrae, whereas we can determine with certainty that there are 14 caudal vertebrae in both specimens. The neural spines of the last three abdominal vertebrae are exposed behind the head plates for at least most of their lengths. In both specimens there is a faint indication of the dorsal end of the neural spine of the fourth from last abdominal vertebra in the region between the ventral ends of the fifth and sixth dorsal pterygiophores, but none of the length of the neural spines more anteriorly is exposed because of the presence of the head plates.

Whereas the head plates obscure the neural spines of the more anterior abdominal vertebrae, the neural spines posterior to the plate in the middle region of the body are well-preserved and do not appear displaced or misaligned. In both the part and the counterpart of 283 there is no ventral shaft of a dorsal-fin pterygiophore situated between the neural spines of the last (presumed tenth) abdominal vertebra and the first caudal vertebra; therefore, the tenth interneural space is vacant in 283. In 410a we are confident that there is no ventral shaft of a dorsal-fin pterygiophore situated between the neural spines of the presumed ninth and tenth abdominal vertebrae; therefore, it is the ninth interneural space that is vacant. In 410b the relationships of the ventral ends of the pterygiophores situated near the dorsal ends of the neural spines of the ninth and tenth abdominal vertebrae are not as clearly indicated as in 410a, but, after examination under many lighting and moisture conditions, we believe that the ninth interneural space is also vacant in 410b. The neural spines of the ninth and tenth abdominal vertebrae in 410, bordering the vacant ninth interneural space, are positioned much closer to one another than are the other neural and haemal spines, and the same is true of the neural spines of the tenth abdominal and first caudal vertebrae, which border the vacant tenth interneural space in 283. Thus, the two Frauenweiler specimens differ from one another with regard to which interneural space is vacant at the posterior end of the abdominal series of vertebrae. As discussed in the comparative section (below), we have reason to believe there is another vacant interneural space situated more anteriorly in the abdominal vertebral series of the Frauenweiler specimens.

The caudal skeleton is not well preserved in its entirety in either of the specimens, and the last two centra are displaced in 410. What can be determined is best indicated in 283: PU2 has a low neural spine, and the haemal spines of PU2, PU3, and the parhypural are autogenous; there are probably five hypurals and 17 principal caudal-fin rays, with about four procurrent rays both above and below; epurals are not clearly indicated. There is evidence of a large uroneural in the somewhat disarticulated caudal skeleton of 410a.

Minute cycloid scales with maximum diameters between 3.0 and 3.5 mm are clearly visible above and below the vertebral column in the abdominal region of both Frauenweiler specimens (Fig. 5).

ZPALWr. A/4000 (Fig. 6) and ZPALWr. A/4001

These two small specimens from the Polish Carpathians were identified many years ago by the late Anna

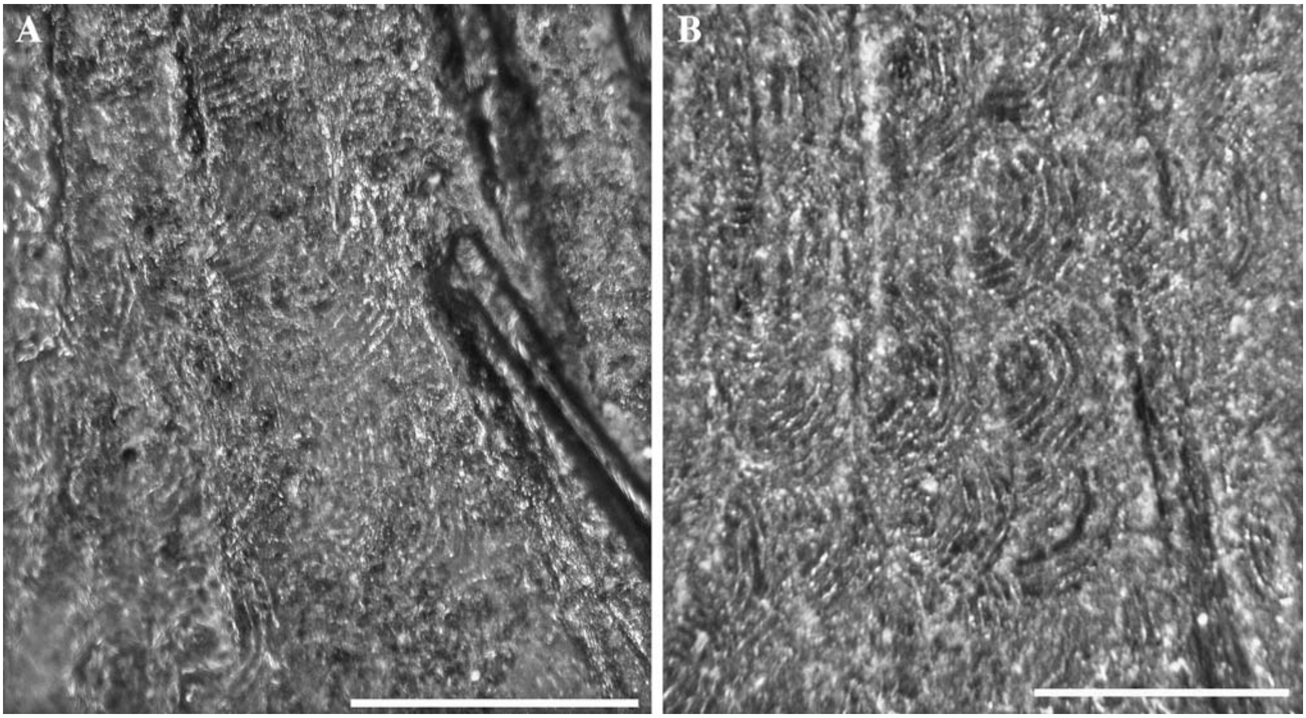


Fig. 5 Detailed view of cycloid scales in the ventral part of the abdominal region, directly in front of the haemaxial complex. **a** HLMD-WT 410a. **b** SMNS 87457/283a. Each *scale bar* 0.5 mm

Jerzmańska as being young chaetodontids similar to the genus *Forcipiger*, even though there is no clearly discernable long snout to be seen in either specimen. They are listed in Kotlarczyk et al. (2006, p 34), as *Forcipiger* sp. under Chaetodontidae and, unnecessarily, just below this section of the list, as two specimens of undetermined Chaetodontidae.

A/4000 is the better preserved of the two specimens. Many of the bony plates on the top of the head are difficult to distinguish individually, but two are distinct, as is the preopercular spine. The two easily distinguished plates are somewhat displaced behind the head in the region above the preopercular spine. The uppermost and somewhat smaller of the two clearly corresponds to the posttemporal plate of a tholichthys, and the lower corresponds to the supracleithrum plate. The posttemporal and supracleithrum plates have rugose and knobby surfaces with deep broad grooves along their lengths and with circular radiating ridges, which is similar to those of the Frauenweiler specimens. The preopercular spine is very long (somewhat more so than in the Frauenweiler specimens) and tapers to a point. The dorsal-fin spines cannot be fully counted (posterior to the sixth spine they become increasingly difficult to distinguish individually), but there are three anal spines and 14 caudal vertebrae (the haemal spine of the first caudal vertebra, situated behind the first anal pterygiophore, is fully exposed, whereas only the distal end of its neural spine is exposed, situated above the posterodorsal end of the supracleithrum plate); the pelvic spines from both sides are evident, but the rays cannot be counted. In the abdominal region of the less complete counterpart (head to left), there is a part of a long shaft of bone that is relatively wide and may represent a chaetodontid-like rib. A/4001 is too poorly preserved to distinguish many of the seemingly enlarged bones in the head region, but present in the area below the rear of the eye is a large, long preopercular spine that tapers to a point at the rear of the abdomen. There is also a rather similar long tapering bone that reaches just as far posteriorly from the top of the head as does the preopercular spine. This second bone could be the preopercular spine that has been displaced from the other side, or it could be a long tapered extension of a posttemporal plate. If the latter, it is rather more elongate and tapered than the posttemporal extension in both the other Polish specimen and in the Frauenweiler specimens. The ribs in this specimen are sufficiently preserved to be sure that they are very long, reaching close to the midventral line, and there is some evidence that the ribs are relatively wide and stout, which would represent the chaetodontid condition.

Extant tholichthys morphology (Figs. 7, 8)

It has long been recognized that the tholichthys is a specialized pelagic larval stage of chaetodontids (Day 1870;

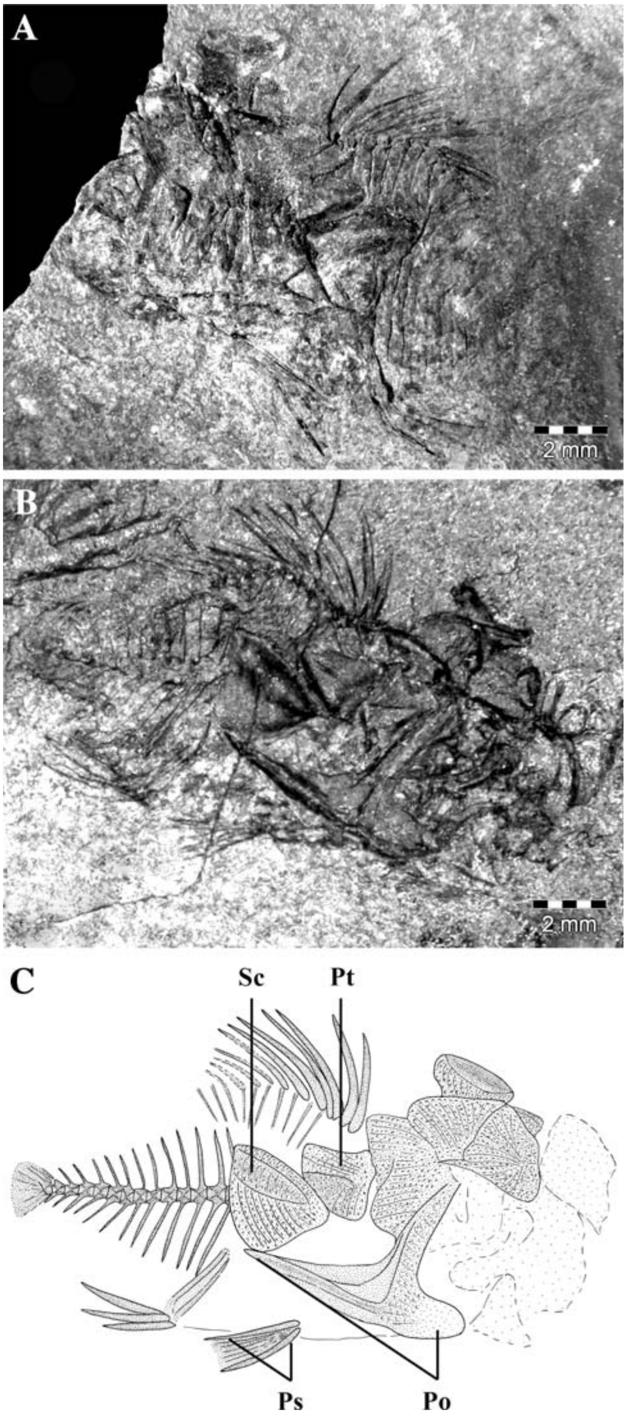


Fig. 6 ZPALWr. A/4000a, b; 17.5 mm SL. Pre-settlement larval stage of a chaetodontid, general view. Lower Oligocene, probably IPM3 zone of Menilite Formation (Rupelian, 30–29 MYA), Outer Carpathians, Kniażyce, southwest of Przemyśl, SE Poland. **a** Main part. **b** Counterpart. **c** Reconstruction of counterpart, with labeling of most of the characteristic features. Each *scale bar* 2 mm

Gunther 1871) that can reach 60 mm SL before settlement (Burgess 1978; Leis 1989). Leis (1989) discussed the confusion that existed for more than 100 years wherein the tholichthys stage was erroneously attributed to the Pomacanthidae and to the Chaetodontidae, until this was rectified by Burgess (1978). A superficially similar larva with hypertrophied head bones, one of which projects behind the head, characterizes the Scatophagidae, and these larvae have often been referred to as “tholichthys.”

Johnson (1984) briefly discussed the most essential differences between these two “so-called” tholichthys stages, emphasizing that in chaetodontids the posttemporal and supracleithrum are rugose and expanded posteriorly as large laminar plates, and that the preopercle is expanded and extended posteriorly into a broad spine, whereas in scatophagids the supracleithrum is unmodified, the posttemporal extends posteriorly as a very thick blunt spine, the preopercle is expanded although not extended posteriorly, and the pterotic has a rugose protuberant covering. Johnson (1984) noted that the similarities and differences between the chaetodontid and scatophagid larval stages needed further investigation to assess the possible phylogenetic implications for these two families.

The most extensive description of the morphological features of the chaetodontid tholichthys was given concisely in an unpublished dissertation by Blum (1988, pp 89–91). He restricted the term tholichthys to chaetodontids, and he used this stage as one of the seven synapomorphies documenting the monophyly of the family. According to this dissertation, typical chaetodontid tholichthys larvae are characterized by the combination of the following characteristics: a dramatically hypertrophied preopercle, which is expanded anterodorsally almost to the margin of the orbit, and ventromedially under the head, so that the left and right antimeres are juxtaposed midventrally, and which bears a large posterior projection that is attenuated into either a sharp or blunt spine; posttemporals and supracleithra with large, plate-like expansions that extend posteriorly over the trunk; frontals that are slightly expanded such that they cover the parietals posteriorly and more of the orbit laterally than they do in post-metamorphic individuals; nasals, lacrymals, and dermosphenotics (last circumorbital bone) that are hypertrophied such that they fill the gaps between the larger bones already mentioned and form an almost complete casing of dermal armor around the head. Blum (1988, pp 89–91) described numerous other differences, including those previously given by Johnson (1984), between the tholichthys of chaetodontids and the comparable pre-settlement larval stage of scatophagids. We agree with most, but not all, of these differences. His characterization of the chaetodontid tholichthys stage is adequate for our purposes here, and a subsequent paper (Johnson et al., in preparation) will present a more comprehensive comparison of diversity within the family. Blum (1988) concluded that scatophagid larvae show only superficial similarity to chaetodontid larvae and lack almost all of the specific characteristics mentioned above.

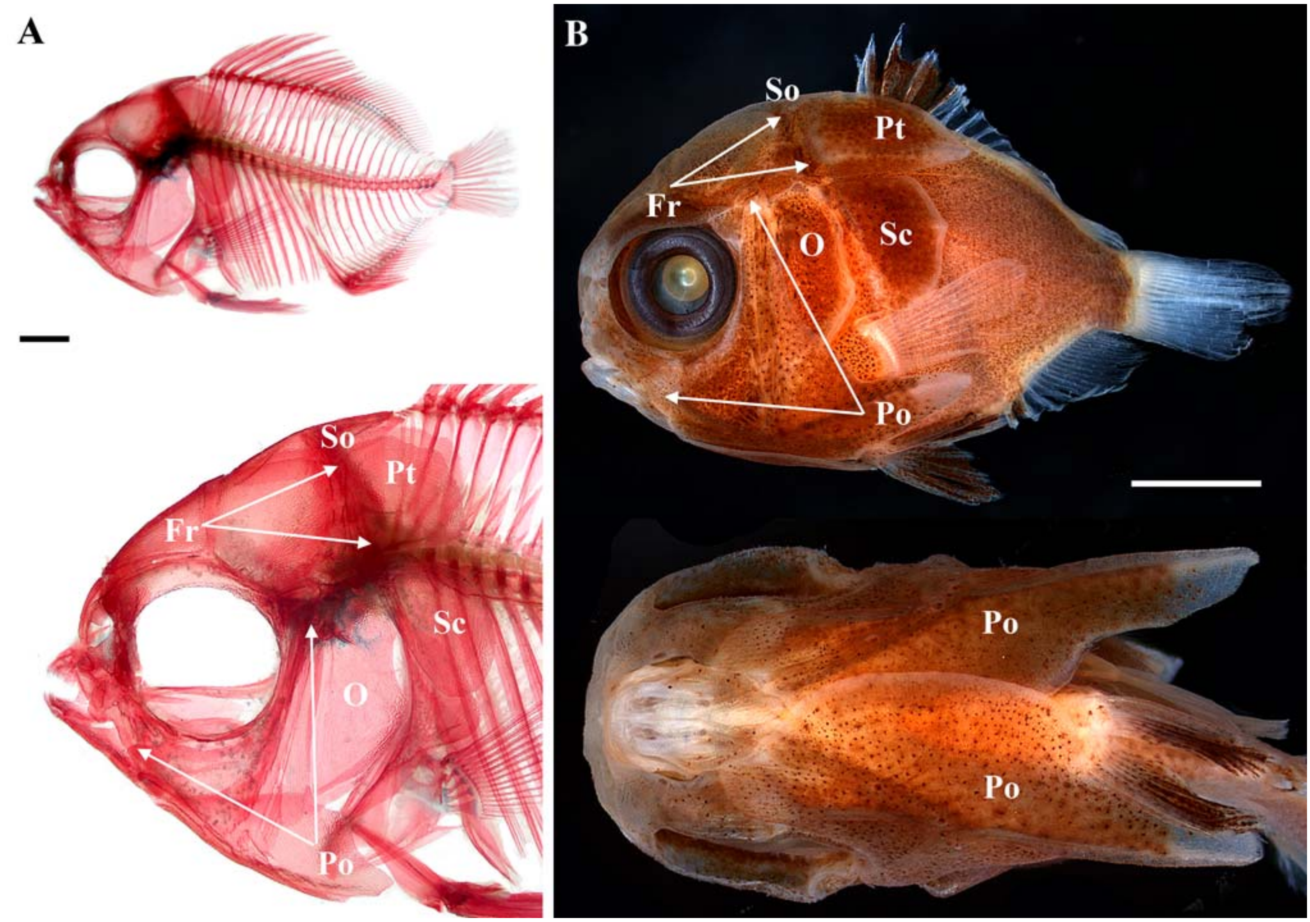


Fig. 7 **a** USNM 159264, 18.6 mm SL. Cleared and stained extant tholichthys stage specimen of an unidentified species of the genus *Chaetodon*, with labeling of most of the characteristic features. **b** NSMT-PL-390, 8.3 mm SL. Same, alcohol preserved, specimen. Each *scale bar* 2 mm

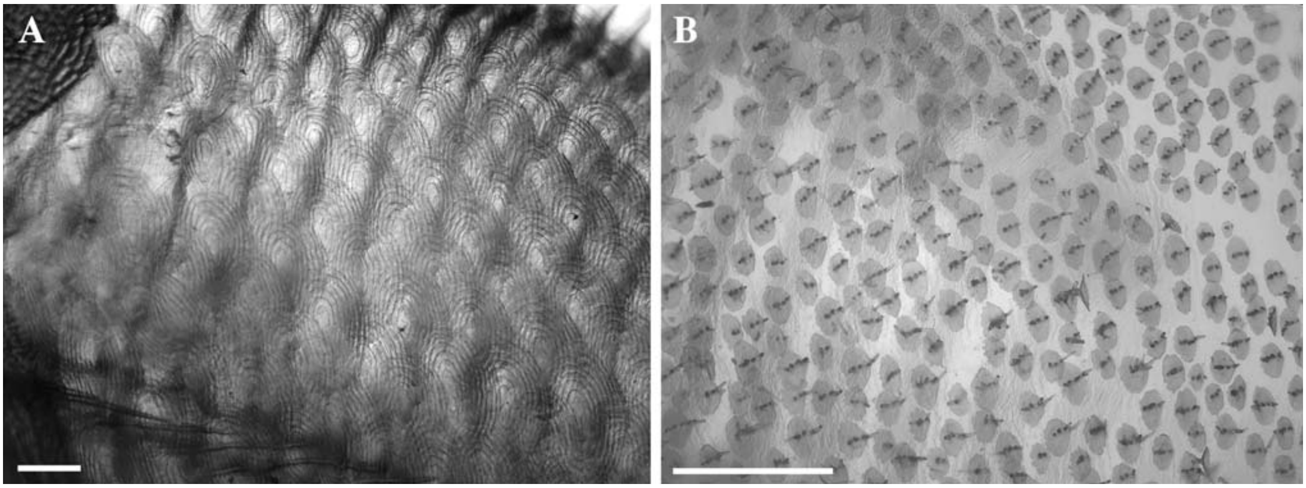


Fig. 8 Details of the squamation in the anterior part of the body flank in extant pre-settlement larvae (heads are to the left): **a** USNM 391660, 9.6 mm SL; tholichthys larva of Chaeotodontidae. **b** USNM 391661, 9.6 mm SL; corresponding larval stage of *Scatophagus argus*. Each *scale bar* 0.2 mm

Interneural spaces in extant adult Chaetodontidae (Fig. 9, Table 1)

To assess the intraspecific and intrageneric variability of the distribution of the dorsal-fin pterygiophores in the interneural spaces, we have examined a comprehensive sample of cleared and stained or radiographed specimens representing 20 species among nine genera of extant chaetodontids. In all extant species the neural spine of the first vertebra is situated anterior to the shaft of the first dorsal pterygiophore, with the tip of the neural spine between the bases of the two supraneurals, and the neural spine of the second vertebra is situated between the shafts of the first and second dorsal pterygiophores; subsequently, a single neural spine is situated between adjacent ventral shafts of the dorsal pterygiophores until the position of the vacant interneural space is reached, whereupon two neural spines are accommodated between adjacent pterygiophore shafts. A single interneural space is vacant in the great majority of these taxa; however, two taxa (*Chelmon marginalis* and *Parachaetodon ocellatus*) have no vacant spaces. In *Chelmon rostratus* there is significant variability in the condition of the vacant interneural space. It has either the sixth, the seventh, or the eighth space vacant, or there is no vacant space at all. Most extant taxa typically have the sixth space vacant (Fig. 9a), but a minority of specimens of those taxa may have either the seventh space vacant or, even less frequently, the fifth rather than the sixth space vacant (the sixth space is vacant in the only well-preserved skeletal fossil chaetodontid, from the Miocene; Carnevale 2006). Some taxa typically have the seventh space vacant (Fig. 9b), but a minority of specimens of these taxa may have the sixth or the eighth rather than the seventh space vacant. The eighth space is never vacant as the typical condition of any extant taxon. Two species (*Parachaetodon ocellatus* and *Chelmon marginalis*) have no vacant interneural space (Fig. 9c), and one (*Chelmon rostratus*) is exceptionally variable in its interneural spaces, with most specimens having the seventh vacant but significant minorities having either the sixth, eighth, or none vacant. In none of the extant materials examined is there a vacant interneural space posterior to the eighth space.

Comparison of fossil tholichthys with extant taxa

The morphology of the fossil tholichthys, as best seen in the relatively complete and well-exposed German specimens, is basically very similar to that of the tholichthys of most genera of extant Chaetodontidae, i.e., exclusive of the tholichthys of the long-snouted *Forcipiger* and of *Coradion*, which have some apparently secondarily reduced features (Johnson et al., in preparation). As an exemplar of a typical extant chaetodontid tholichthys, we use a cleared and stained specimen of an unidentified species of the genus *Chaetodon* (USNM 152964, 18.7 mm SL; Fig. 7).

The fossil and extant tholichthys possess the following comparable features: setiform teeth (although in the fossils we can see only the outer row of teeth and not the presumed full array of separate bands); a large lachrymal that obscures most of the body of the palatine; a large ethmoid block that extends both anterior and posterior to the lateral ethmoid (although in the fossils we cannot determine if the ethmoid has lacunae); a parasphenoid without a ventral flange; the pelvis with only a short posterior process; a laterally expanded buttress on the first dorsal pterygiophore for support of the first two (supernumerary) dorsal spines; 13 dorsal and three anal-fin spines in the fossils, which is the norm in many species of many genera of chaetodontids; 14 caudal vertebrae; and a short neural spine on PU2. The preopercular spine in the fossils is slightly longer and more acutely tapered than in our *Chaetodon* tholichthys. The heads of the supraneurals in the fossils are not as closely spaced to one another and to the crest of the supraoccipital and the first dorsal pterygiophore as is the case of the close sequential articulation of these elements in extant tholichthys. However, in specimen 410 at least, most of this difference in spacing could be attributed to lack of full exposure of the supraneural heads and to some slight displacement of the supraneurals (we also suspect that the heads of the supraneurals are not fully exposed in specimen 283). Our examination of cleared and stained specimens and radiographs of chaetodontids indicates that whereas most specimens of most species have full sequential articulation of the elements between the supraoccipital crest and the first dorsal pterygiophore, a minority of specimens have a less than fully integrated series (especially in many specimens of *Parachaetodon*), to which condition the spacing in specimen 410 is similar. The length of the ribs in 410 extends downward close to the ventral midline, or to at least 80% the depth of the abdomen. Our examination of extant chaetodontids indicates that in most specimens the ribs extend ventrally to about 90% the depth of the abdomen (about as shown for the chaetodontid skeleton in Tyler et al. 1989, Fig. 31), but that in a significant minority of specimens the ribs are shorter and an extension to no more than 80% the depth of the abdomen is not unusual (especially in *Coradion*). In 283 the ribs extend ventrally less than 80% of the abdomen, but we believe that this is because the ventral ends of the ribs are not fully exposed. The anteroventral flange of the ribs, which is characteristic of chaetodontids, is evident in 283. The size and surface sculpturing of the supracleithrum and posttemporal plates in the fossils are comparable with those of extant tholichthys, whereas the apparent larger size of the frontal plate in the fossils is probably because the plates

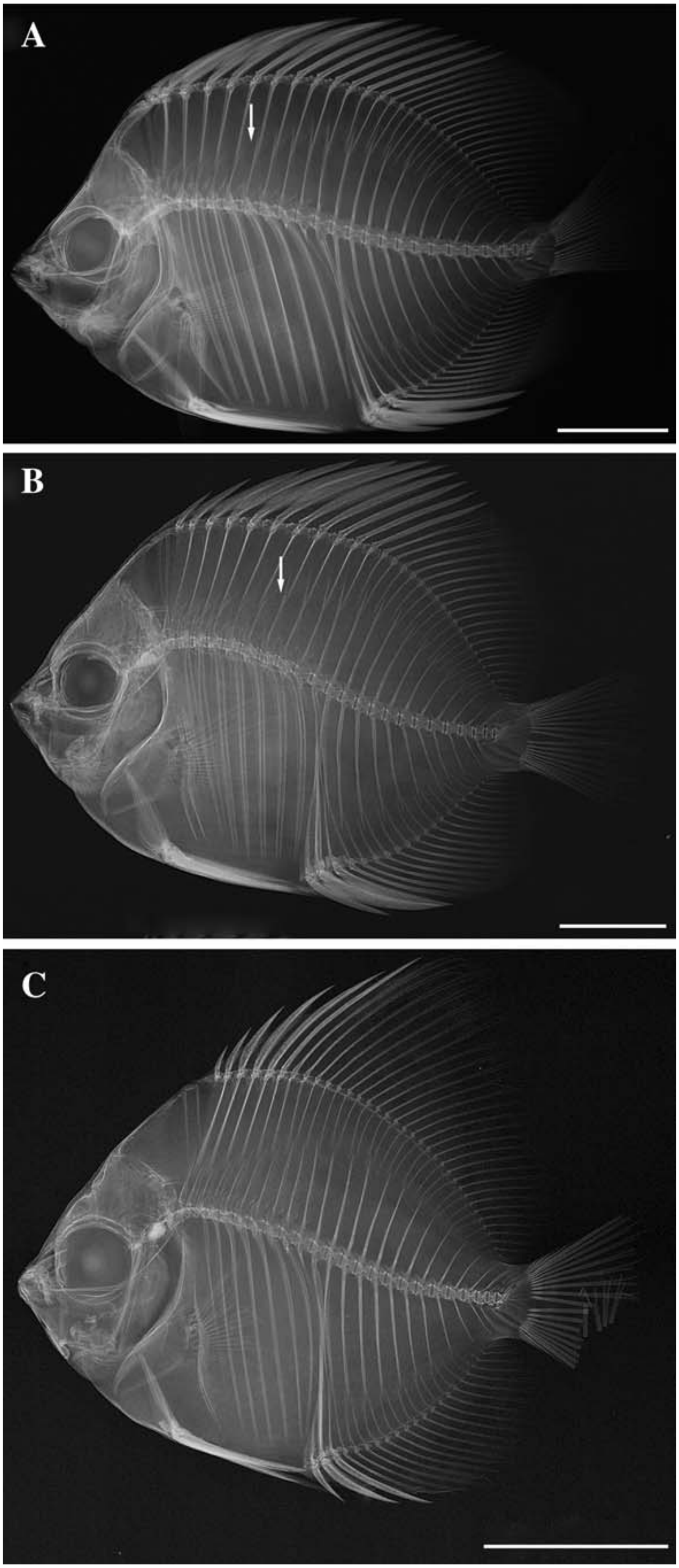


Fig. 9 Radiographs showing the vacant interneural spaces in extant Chaetodontidae. **a** *Chaetodon trichrous*, USNM 392506; sixth interneural space vacant. **b** *Chaetodon reticularis*, USNM 392440; seventh interneural space vacant. **c** *Parachaetodon ocellatus*, USNM 266892, no interneural space vacant. Each *scale bar* 1.0 mm

Table 1 Synopsis of vacant interneural space patterns in extant Chaetodontidae

Genus	Species	Number of specimens	Vacant		Interneural		Space
			5th	6th	7th	8th	None
Amphichaetodon	*melbae*	2			2		
Chaetodon	*adiergastros*	1		1			
Chaetodon	*auriga*	2		2			
Chaetodon	*baronessa*	1		1			
Chaetodon	*capistratus*	8		7		1	
Chaetodon	*citrinellus*	2		2			
Chaetodon	*flavirostris*	1		1			
Chaetodon	*guttatissimus*	3		2	1		
Chaetodon	*lunula*	1		1			
Chaetodon	*lunulatus*	1		1			
Chaetodon	*melanotus*	1		1			
Chaetodon	*mertensii*	2		2			
Chaetodon	*ocellatus*	12		10	2		
Chaetodon	*octofasciatus*	7		1	6		
Chaetodon	*plebeius*	2			2		
Chaetodon	*reticulatus*	4		4			
Chaetodon	*sedentarius*	20	1	17	2		
Chaetodon	*striatus*	11		11			
Chaetodon	*trichrous*	2		2			
Chaetodon	*trifasciatus*	2		2			
Chaetodon	*unimaculatus*	1		1			
Chelmon	*marginalis*	8					None in 8
Chelmon	*rostratus*	18		2	8	4	None in 4
Coradion	*chrysozonus*	11		10	1		
Forcipiger	*cyrano*	1		1			
Forcipiger	*flavissimus*	4		1	3		
Forcipiger	*inornatus*	1		1			
Forcipiger	*longirostris*	4		2	2		
Hemitaurichthys	*polylepis*	2		1		1	
Heniochus	*acuminatus*	7		4	3		
Heniochus	*chrysostomus*	5		5			
Parachaetodon	*ocellatus*	5					None in 5
Prognathodes	*aculeatus*	4		3	1		
Prognathodes	*aya*	14	1	9	4		

are being viewed at a right angle rather than obliquely, as in the illustration of the extant tholichthys.

The most significant difference between the morphology of the fossils and that of all of the extant taxa is in the position and number of the vacant interneural spaces. In none of the extant materials examined is there a vacant interneural space posterior to the eighth space, as is the case in both German specimens. If we assume that the arrangement of dorsal pterygiophores and interneural spaces that we described above as a constant feature of extant chaetodontids is present in the fossils also, and that the fossils share ten abdominal vertebrae with extant chaetodontids, then there must be an additional vacant interneural space somewhere between the third to seventh neural spines. The third to sixth neural spines are entirely obscured by the posttemporal and supracleithral plates, but the seventh neural spine is faintly indicated just at the rear edge of the head plates; the more posterior neural spines are clearly exposed. In 410 we suggest, on the basis of the space available between the ventral shafts of the dorsal pterygiophores, that it is probably the fourth and fifth neural spines that are accommodated there (i.e., the fourth interneural space is vacant in addition to the ninth space). In 283 we suggest that it could be either the third and fourth neural spines together in the space between the second and third dorsal pterygiophores, or the fifth and sixth neural spines together in the space between the fourth and fifth; we think the latter is more likely because this more posterior position would be in keeping with the more posterior position of the other vacant space (tenth interneural space vacant in 283 vs. ninth space vacant in 410).

Consequently, the fossil tholichthys from Germany as preserved are unique among chaetodontids in having either the ninth or tenth interneural space vacant, and in probably having another space vacant more anteriorly, which we speculate to be the fourth or fifth space. By contrast, in extant chaetodontids there is never more than one space vacant, and it is never more posterior than the eighth space. Therefore, the German fossils could represent a separate, extinct lineage of the Chaetodontidae. Nevertheless, at the present state of investigation, we remain open to the possibility that the positions of the vacant interneural spaces in these fossils could be taphonomic artifacts. In specimens with a very wide and heavily armored skull such as the tholichthys larvae, substantial mechanical stress can be expected on the few most posterior abdominal and the few most anterior caudal vertebrae during embedding. This could result in dislocations, especially for specimens such as 410a and b that are in a somewhat progressive state of decay. However, the position of the vacant interneural spaces is a relatively constant and an almost diagnostic feature of many extant species of chaetodontids, and, in the case of the German tholichthys, we believe that the ninth and tenth interneural vacancies are natural and not artifacts of preservation.

The squamation of the two Frauenweiler specimens is very similar to that of a 9.6 mm SL cleared and stained *Chaetodon* tholichthys (USNM 391660, Fig. 9a) in their circularity; however, the latter has very weakly developed ctenii along the posterior edge. Such ctenii cannot be observed in the fossils, but this is probably because the scales are too minute and weak. There is substantial variation in specimen size at which ctenii develop among extant chaetodontid tholichthys. The 15.5 and 17.0 mm SL fossil tholichthys from Frauenweiler are well within the range of sizes at which ctenii first develop in extant tholichthys. We note that the scales of the somewhat similar larvae of Scatophagidae are very different, with upraised processes that are very easy to see even in this early stage (Fig. 9b).

The general appearance of Polish specimen A/4000, and of its three best preserved features of armor (the enlarged posttemporal and supracleithrum plates and the preopercular spine), are so similar to those of the Frauenweiler specimens that we are confident that this specimen is also a chaetodontid tholichthys of undetermined genus and species, but it is not necessarily of the same taxon as the Frauenweiler specimens. A/4001 is so poorly preserved that it can only very tentatively be referred to the Chaetodontidae.

Conclusions

Our comparisons of the fossils with larval stages of extant chaetodontids clearly show that the two specimens approximately 30.1 MYA old from the Lower Oligocene of Frauenweiler clay pit are the first fossil records of the chaetodontid tholichthys stage, and one of the earliest fossil records of the Chaetodontidae. The German tholichthys specimens are unique among the members of this family in having either the ninth or tenth interneural space vacant, and in almost certainly having another space vacant more anteriorly (probably the fourth or fifth; either that or there are only nine abdominal vertebrae), whereas in extant chaetodontids there is never more than one space vacant, and it is never more posterior than the eighth space. Therefore, the Frauenweiler specimens cannot be accommodated in any extant genus of this family. Until we can obtain additional materials of this taxon from this locality to more fully document its morphological peculiarities, and especially of its interneural space conditions, we place it as an incertae sedis Chaetodontidae.

The Polish specimen A/4000 is probably a chaetodontid tholichthys of an undetermined genus and species. The specimen A/4001 is so poorly preserved that we only very tentatively accept it as a possible tholichthys stage.

Paleoenvironmental implications

German specimens

Different theories have been presented regarding the paleoenvironmental conditions of the Frauenweiler fossil site (Weber 1951; Weiler 1966; Trunkò 1997; Micklich 1998; Grimm et al. 2002). Nevertheless, it is obvious that the fossil fish record of the site is dominated by juvenile individuals, although rather early postlarval stages are not rare. Unfortunately, it is extremely difficult to give precise estimates concerning the relative percentages of larval or pelagic stages. Such stages probably are under-represented in the collections for various reasons: they may have been overlooked during the excavations because of their small size, which also makes their identification more difficult. Additionally, there is a general preference to collect larger and more attractive specimens, as indicated by the fact that only about 20% of all Frauenweiler taxa are represented by both juveniles and larger, presumably adult or subadult, individuals. The preference for collecting larger individuals has the consequence that very small individuals are not as frequently represented in museum collections, even though in reality they undoubtedly dominate the fossil fish record.

Layer number 23, where the tholichthys were found, is one of the richest fish-bearing horizons in the Frauenweiler clay pit. The fishes of layer 23 are characterized by comparatively numerous records of small-sized specimens, including those of clupeids, syngnathids, centriscids, "*Serranus*" *budensis* (which, in fact, is not a serranid), and carangids, and some rarer scorpaenids, scombroids, and caproids. Many of these are less than 5 cm in total length, and some are distinctively smaller (about 2 cm total length).

The life style and distribution patterns of the pre-settlement larvae of extant Chaetodontidae were extensively described and discussed by Leis (1989), who documented the rarity of these larvae in tropical plankton and midwater trawling samples. Such larvae may prefer habitats that differ from those that are most often sampled by conventional methods. Although adult chaetodontids are characteristic reef inhabitants, their larvae do not stay close to reefs but, rather, seem to be neritic or oceanic. Size at settlement varies widely, from 9 to 60 mm SL. Many species settle at less than 20 mm SL, so the Frauenweiler tholichthys may have been close to their time of settlement.

Taking into account the general aspects of the fish fauna, a reconstruction of the Frauenweiler paleoenvironment may be as follows: It is likely that this area was some kind of shallow coastal bay, which partly and/or occasionally was separated from the open sea by some sort of "sheltering" ridge or reef, and with water conditions that varied substantially, depending upon external situations; certain taxa probably preferred brackish waters, river mouths and/or estuarine water bodies (Micklich 2005; Micklich and Hildebrand 2005). Within this basin there may have been seagrass meadows, which (together with estuaries and mangrove swamps) are well known as nursery grounds for a wide variety of marine fishes. This environment would have been ideal for the young stages of many species of fishes, including those that as adults prefer greater depths (e.g., Laegdesgaard and Johnson 2001; Cocheret de la Morinière et al. 2002). The Frauenweiler fishes may have been killed by occasional phytoplankton blooms or by rising temperatures and salinities, which also caused stratification of the water column and loss of benthic life, characteristics that are prerequisites for fine fossil preservation. Occasional in-flows of fresh water may have periodically rejuvenated the water quality.

Unfortunately, there are some contradictions to the above hypothesis. Some species of extant fishes that are especially typical of seagrass meadows, for example the porgies (Sparidae), are rare in that fossil site and are represented only by disarticulated remains. One would also expect to find fossilized seagrass remains, but such remains are absent. Also absent are the remains of other typical reef organisms. The presence of pre-settlement larvae also is unlikely for a coastal, inshore habitat, with a reef-like shelter from the open sea.

Polish specimens

According to Kotlarczyk et al. (2006), the Kniażyce fauna belongs to the fish assemblage IPM3 zone of the Menilite–Krosno Series. This is characterized by the predominance of deep-water fishes (54.4 vs. 18% of shallow-water forms). The paleoenvironment was considered to be a warm, deep-water basin. By contrast, the Przysietnica fauna belongs to the IPM4A zone. This is characterized by the presence of numerous shallow-water forms, which clearly dominate those that prefer deep waters (27.3 vs. 5.9%). Both are associated with taxa that typically inhabit reef or lagoonal environments. Highly characteristic are the Centriscidae, which comprise up to 45% of the assemblage but are absent in the other outcrops from Przysietnica and also absent in Kniażyce or very rare in the ichthyofaunal zones in the other Polish outcrops from the Outer Carpathians (Kotlarczyk et al. 2006). The paleoenvironment was assumed to be a warm-water basin, distinctly shallower than that of the IPM3 zone.

As indicated in the preceding section, extant tholichthys larvae do not stay close to reefs but, rather, seem to be neritic or oceanic. Fossil representatives are more likely to be expected in the deep-water deposits of the IPM3 zone than in the shallow-water localities of the IPM4A zone. As in the Frauenweiler locality, it is, therefore, somewhat surprising to find an at least presumable record of these generally very rare fossils at IPM4A.

Acknowledgments We are grateful to Frank Sanzenbacher, of Bondorf, Germany, a skillful amateur paleontologist who first found one of the Frauenweiler tholichthys specimens, prepared it, and permitted it to be purchased by the Hessisches Landesmuseum Darmstadt under reasonable conditions. We also thank Annette and Harald Oechsler of Waghäusel, Germany, amateur paleontologists whose ardent and arduous work at the Frauenweiler site during the past few years of field work have obtained many valuable specimens for the scientific community. The other Frauenweiler tholichthys specimen was obtained by the Staatliches Museum für Naturkunde Stuttgart and was generously loaned to us for study in Darmstadt and in Washington, DC, through the cooperation of Ronald Böttcher, Curator of Paleontology. We appreciate the cooperation of Jeffery M. Leis, Australian Museum, Sydney, and Keiichi Matsuura, National Science Museum, Tokyo, for the loan of tholichthys specimens. We thank James F. DiLoreto, Smithsonian Photographic Services, for scanning our illustrations and transmitting them between the authors. We are much indebted to Sandra J. Raredon, National Museum of Natural History, for the many hours she devoted to taking digital radiographs of extant chaetodontid fishes to provide us with an extensive survey of vacant interneural space position in that family. Ai Nonaka, National Museum of Natural History, provided technical assistance in sorting, cataloging, photographing and taking data on numerous chaetodontid larvae. Our identifications of chaetodontid specimens at the Smithsonian Institution were greatly aided by Gerry R. Allen of the Western Australian Museum during his visit to the Smithsonian in 2008. The photographs of the Polish specimen ZPALWr. A/4000 were made by Paweł Socha of the Paleozoology Department of Wroclaw University. The research of Alexandre F. Bannikov was supported by the Russian Foundation of Basic Research (grants nos 08-05-00654, 09-05-00170). The manuscript was improved by the editing of Diane M. Tyler. Useful suggestions were offered during the peer review process by Giorgio Carnevale (Università di Pisa) and an anonymous reviewer.

References

Baciu, D.-S., A.F. Bannikov, and J.C. Tyler. 2005. Revision of the fossil fishes of the family Zeidae (Zeiformes). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria* 29: 95–128.

Baldwin, C.C., and G.D. Johnson. 1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bulletin of Marine Science* 52(1): 240–283.

Bannikov, A.F. 2004. Fishes from the Eocene of Bolca, northern Italy, previously classified with the Chaetodontidae (Perciformes). *Studi e Ricerche sui Giacimenti Terziari di Bolca, Museo Civico di Storia Naturale di Verona* 10: 13–92.

Bannikov, A.F., and J.C. Tyler. 1995. Phylogenetic revision of the fish families Luvaridae and †Kushlukiidae, with a new genus and two new species of Eocene luvarids. *Smithsonian Contributions to Paleobiology* 81: 1–45.

Birdsong, R.S., E.O. Murdy, and F.L. Pezold. 1988. A study of the vertebral column and median fin osteology of gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science* 42: 174–214.

Blum, S.D. 1988. The osteology and phylogeny of the Chaetodontidae (Teleostei: Perciformes). Unpublished doctoral diss., Honolulu: University of Hawaii. http://research.calacademy.org/research/informatics/sblum/ Accessed December 2008.

Burgess, W.E. 1978. *Butterflyfishes of the world*. Neptune City: T.F.H. Publications.

Carnevale, G. 2006. Morphology and biology of the Miocene butterflyfish *Chaetodon ficheuri* (Teleostei: Chaetodontidae). *Zoological Journal of the Linnean Society* 146: 251–267.

Cocheret de la Morinière, E., B.J.A. Pollux, L. Negelkerken, and G. Van der Velde. 2002. Post-settlement life cycle migration patterns and habitat preferences of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine, Coastal and Shelf Science* 55: 309–321.

Day, F. 1870. Notes on some fishes form the western coast of India. *Proceedings of the Zoological Society of London* 1870: 369–374.

Grimm, K., M. Grimm, A. Köthe, and T. Schindler. 2002. Der "Rupelton" (Rupelium, Oligozän) der Tongrube Bott-Eder bei Rauenberg (Oberrheingraben, Deutschland). *Courier Forschungsinstitut Senckenberg* 237: 229–253.

Gunther, A. 1871. On the young state of fishes belonging to the family Squamipinnes. *Annals and Magazine of Natural History, 4th ser* 8: 318–320.

Hovestadt, D.C., and M. Hovestadt-Euler. 1999. *Weissobatis micklichi* n.gen., n.sp., an eagle ray (Myliobatiformes, Myliobatidae) from the Oligocene of Frauenweiler (Baden-Württemberg, Germany). *Paläontologische Zeitschrift* 73(3/4): 337–349.

Hovestadt, D.C., and M. Hovestadt-Euler. 2002. The remains of a carcharhinid shark with a new triakid species in its digestive tract from the Oligocene of Germany. *Tertiary Research* 21(1–4): 171–182.

Jerzmańska, A., and J. Kotlarczyk. 1976. The beginnings of the Sargasso Assemblage in the Tethys? *Palaeogeography Palaeoclimatology Palaeoecology* 20: 297–306.

Johnson, G.D. 1984. Percoidei: development and relationships. In *Ontogeny and systematics of fishes,* Special Publication Number 1, American Society of Ichthyologists and Herpetologists, ed. H.G. Moser, et al., 464–498. Lawrence: Allen Press.

Kaiser, T., and N. Micklich. 1995. Schnellpräparation von Messel-Fossilien zum Erstellen einer osteologischen Referenzsammlung. *Der Präparator* 41(2): 69–72.

Kotlarczyk, J., and A. Jerzmańska. 1976. Biostratigraphy of the Menilite Beds of Skole Unit from the Polish Flysh Carpathians. *Bulletin de l'Académie Polonaise des Sciences, Serie des Sciences de la Terre* 24(1): 55–61.

Kotlarczyk, J., and A. Jerzmańska. 1988. Ichtiofauna w stratygrafii Karpat. *Przegląd Geologiczny* 6: 346–352.

Kotlarczyk, J., A. Jerzmańska, E. Świdnicka, and T. Wiszniowska. 2006. A framework of ichthyofaunal ecostratigraphy of the Oligocene-early Miocene strata of the Polish outer Carpathian basin. *Annales Societatis Geologorum Poloniae* 76: 1–111.

Laegdesgaard, P., and C. Johnson. 2001. Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* 257: 229–253.

Leis, J.M. 1989. Larval biology of butterflyfishes (Pisces, Chaetodontidae): what do we really know? *Environmental Biology of Fishes* 25: 87–100.

Martini, E. 1971. Standard tertiary and quaternary calcareous nannoplankton zonation. In *Proceedings of the II Planktonic conference, Roma 1970*, ed. A. Farinacci, 738–785. Roma: Edizioni Teenoscienza.

Mayr, G. 2000. A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. *Journal of Ornithology* 141: 85–92.

Mayr, G. 2004. Old World fossil record of modern-type hummingbirds. *Science* 304: 861–864.

Mayr, G., and A. Manegold. 2004. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* 91: 173–177.

Mayr, G., S.D. Peters, and S. Rietschel. 2002. Petrel-like birds with a peculiar foot morphology from the Oligocene of Germany and Belgium. *Journal of Vertebrate Palaeontology* 22: 667–676.

Micklich, N. 1998. New information on the fish fauna of the Frauenweiler fossil site. *Italian Journal of Zoology* 65(supplement): 169–184.

Micklich, N. 2005. The fish fauna of Frauenweiler clay pit and its bearing on the paleoenvironmental reconstructions. *Kaupia, Darmstädter Beiträge zur Naturkunde* 14: 89.

Micklich, N., and M. Drobek. 2007. Mining, excavations, and preparation. In *Messel—Treasures of the Eocene. Book to the exhibition "Messel on Tour"*, ed. G. Gruber, and N. Micklich, 15–21. Darmstadt: Hessisches Landesmuseum.

Micklich, N., and L. Hildebrand. 2005. The Frauenweiler clay pit ("Grube Unterfeld"). *Kaupia, Darmstädter Beiträge zur Naturkunde* 14: 113–118.

Micklich, N., and N.N. Parin. 1996. The fishfauna of Frauenweiler (Lower Oligocene, Rupelian; Germany): preliminary results of a revision. *Publicaciones Especiales Instituto Espanol de Oceanographica* 21: 129–148.

Parin, N.N., and N. Micklich. 1996a. Two aulostomid fishes (Aulostomidae, Syngnathiformes) from the Lower Oligocene of Germany. *Palaeontologysyesky Zhurnal (Moscow)* 1: 61–67. [in Russian with English abstract].

Parin, N.N., and N. Micklich. 1996b. Fossil Gasterosteiformes from the Lower Oligocene of Frauenweiler. I. New information on the morphology and systematics of the genus *Aeoliscus*. *Paläontologische Zeitschrift* 70(3/4): 521–545.

Parin, N.V., and D.A. Astakhov. 2007. New fossil fish *Musculopedunculus micklichi* (Trichiuroidei) from the Lower Oligocene of Germany. *Journal of Ichthyology* 47(8): 581–588.

Pharisat, A., and N. Micklich. 1998. Oligocene fishes in the western Paratethys of the Rhine Valley Rift System. *Italian Journal of Zoology* 65(supplement): 163–168.

Roth, R., and N. Micklich. 2006. Eine neue Methode zur Präparation kleiner Messel-Fossilien. *Der Präparator* 52: 64–67.

Sakamoto, K., T. Uyeno, and N. Micklich. 2003. *Oligoscophthalmus weissi* gen. et sp. nov., an Oligocene scophthalmid flatfish from Frauenweiler, S-Germany. *Bulletin of the National Science Museum, Series C* 29: 25–32.

Sakamoto, K., T. Uyeno, and N. Micklich. 2004. *Oligopleuronectes germanicus* gen. et sp. nov., an Oligocene pleuronectid from Frauenweiler, S-Germany. *Bulletin of the National Science Museum, Series C* 30: 89–94.

Trunkò, L. 1997. *Bericht zum Forschungsprogramm "Sedimentologische Untersuchungen an Tertiärsedimenten der Randfazies im Mittleren Oberrheingraben" gefördert von der DFG in den Jahren 1998–1991*. Karlsruhe: Staatliches Museum für Naturkunde. [unveröffentlichter Forschungsbericht].

Trunkò, L., and W. Munk. 1998. Geologische Beobachtungen in drei tertiären Aufschlußkomplexen im Randbereich des Mittleren Rheingrabens. *Carolinea* 56: 9–28.

Tyler, J.C., G.D. Johnson, I. Nakamura, and B.B. Collette. 1989. Morphology of *Luvarus imperialis* (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). *Smithsonian Contributions to Zoology* 485: 1–78.

Tyler, J.C., B. O'Toole, and R. Winterbottom. 2003. Phylogeny of the genera and families of zeiform fishes, with comments on their relationships with tetraodontiforms and caproids. *Smithsonian Contributions to Zoology* 618: 1–110.

Wagner-Klett, W. 1919. Das Tertiär von Wiesloch in Baden, ein Beitrag zu seiner tektonischen, stratigraphischen und paläontologischen Kenntnis. *Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, N.F.* 8: 73–116.

Weber, H. 1951. Mikropaläontologische Untersuchungen im Tertiär des Rheintalrandes bei Wiesloch in Baden. *Erdöl und Kohle* 4: 543–549.

Weiler, W. 1966. Die Bedeutung der Fischfunde im Rupelton der Tongrube Frauenweiler bei Wiesloch südlich von Heidelberg. *Zeitschrift der Rheinischen Naturforschenden Gesellschaft Mainz* 4: 1–37.