

First evidence of size-related change of diet (“switching”) in a fossil fish

Gotthard Richter^a, Sven Baszio^{b,*}

^a *Abteilung Messelforschung, Forschungsinstitut und Naturmuseum Senckenberg, Senckenberganlage 25, 60325 Frankfurt am Main, Germany*

^b *Geologisch-Paläontologisches Institut der Universität Bonn, Nußallee 8, 53115 Bonn, Germany*

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Abstract

50 specimens of the Eocene fish species *Rhenanoperca minuta* from the excavation Site “Turtle Hill” (grid square H/I 7) in Messel were scrutinized for their intestinal food remains. 28 of them (56%) bore traces of undigested food particles in their visceral tracts. Of these, 13 (46%) turned out to have fed exclusively on arthropods (different aquatic larvae of nematocerous Diptera). 15 (54%) other specimens bore no arthropod remains but parts of fish skeletons in certain areas of their intestine. Due to the general difficulty to distinguish the bones of prey from those of the predator, only eight of the latter the results are completely reliable. As expected, there is a clear connection between the body size of the fish in question and their food preference insofar as all but one of the arthropod feeders have total lengths below 30 mm and all fish feeders measure 29 mm or more in total length. These results show that *R. minuta* changed from opportunistic plankton feeding to fish hunting with total body lengths from 29 mm onwards. Coprolites with bone and insect remains probably were produced by fish in this “switching” period.

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1. Introduction

During their first phases of life, predatory freshwater fish feed on small arthropods such as crustaceans or aquatic insect larvae and therefore belong to the planktivorous/insectivorous ecological guild in their ecosystem. After having reached a certain size, these fish change their food habits and “switch” to piscivory, hunting fish of smaller or almost equal body size (e.g., Popova, 1967). The size at which switching occurs mainly depends on the amount of energy the

fish invests to hunt its prey and the energy output it gains by digesting it. Hunting a tiny insect larva using a huge body costs a relatively high amount of energy that scarcely can be covered by such a small meal. The earlier a predatory fish starts hunting other fish, the higher the energy output will be. However, fish predation only makes sense with a certain minimum body length that will guarantee success. Apart from that, the “switching” size varies according to the respective fish species and to ecological factors in general (e.g., water temperature, food availability). In extant predatory fish “switching” sizes are well known, especially in economically interesting fish species. The “switching” period is limited to a defined growth stage. In extant pike, e.g., it occurs at a body length of about 25 mm (Frost

* Corresponding author. Tel.: +49 228/833 254; fax: +49 228/833 217.

E-mail address: bas@avh.de (S. Baszio).

and Kipling, 1967; Popova, 1967). There are, however, also (usually rather small) fish species that remain planktivorous/insectivorous during their entire life. Up to now, “switching” body sizes have never been investigated in fossil fish species.

Aquatic insect larvae (Chaoboridae, Culicidae) and Cladocera have been identified as food remains in a certain kind of coprolites from the Eocene World Heritage site of Messel, near Darmstadt, Germany (Richter and Baszio, 2001a). Further research revealed that the fossil fish *Thaumaturus intermedius* — a species quite common in the same locality — was strictly planktivorous/insectivorous up to its adult stage, and as such was most probably a main producer of this type of coprolite (Richter and Baszio, 2001b, 2002). Other small coprolites of similar shape and size contain either exclusively fish bones or (in a few cases) a mixture of arthropod cuticles and fish remains. These coprolites could well have originated from young piscivorous fish in their “switching” period.

The producers of every small coprolite from Messel containing fish remains are and will remain unknown to us, but they should be found among the juvenile stages (total lengths of 100 mm at most) of species relatively common in the Eocene Lake Messel. The possibility that these coprolites originate from birds (e.g., regurgitates), as suggested by Wilson, 1987 cannot completely be ruled out. However, this seems rather unlikely due to the small size of the coprolites and their similarity in size and shape with coprolites we attributed to *T. intermedius* (Richter and Baszio, 2001a,b). In feeding experiments with extant fish we were able to produce similar accumulations of arthropod remains. Unfortunately, such juvenile specimens of the species *Atractosteus trauxi* Kinkelin, 1884 and *Cyclurus kehreri* Andreae, 1893 as well as of the Perciformes *Palaeoperca proxima* Micklich, 1978 and *Amphiperca multiformis* Weitzel, 1933 are rare finds in the Messel locality (Micklich, 1988), especially if one considers the abundance of the coprolites in question. For that reason we decided to concentrate our investigations on small fish species. The object of our investigation should be both common enough to offer a relative large number of specimens available for food remains analysis and should be known as a predator from Eocene Lake Messel. These conditions apply to the Percoid *Rhenanoperca minuta* Gaudant and Micklich, 1990, formerly generally taken for the juvenile form of *A. multiformis* (Micklich, 1988).

R. minuta was a small fish, at least in the Messel habitat, well comparable to *T. intermedius* in its body size. The largest specimens of *R. minuta* collected to date measure 100 mm, while the largest specimens of *T.*

intermedius measure about 80–90 mm. Micklich (1988) suggests that only juveniles of both species were dwelling in the open lake, describing Eocene Lake Messel as a nursery of both species. Ecologically the main difference between both species is that *T. intermedius* remains an arthropod feeder for its entire life cycle (Richter and Baszio, 2001b), whereas *R. minuta* is known to have attacked fish of about its own size with a total length of 40 mm. This is impressively documented by a specimen of *R. minuta* that was swallowing one of its mates of almost equal size and died in the attempt. Both predator and prey are preserved on the same fossil plate, the prey being half swallowed by the hunter (Micklich, 1988). It can be assumed that this species has switched to fish food with body lengths well below this size. We restricted our examinations to specimens with body lengths of 40 mm and less.

By describing the tooth morphologies of some Messel fish species, we attempt to identify isolated teeth that can be found either in coprolites or digestive tracts of Messel piscivorous fish.

2. Material and methods

R. minuta is one of the most common vertebrate fossil finds near reference layer gamma in the Messel locality. The specimens collected for us by the kindness of Dr. N. Micklich and his excavation team from the Hessische Landesmuseum Darmstadt (HLMD) were collected from excavation site “turtle hill” in grid square H/I 7 (Fig. 1). The fossils were preserved in water without any fixation fluid for a few hours or days until completion of our analysis for food remains in their intestine. In total, we examined 50 specimens, all from this same excavation site. In 40 of these the total length could be measured directly by using callipers. In a few specimens parts of the head or tail were damaged or completely missing. In these cases the total length of the fossils was estimated. Of the remaining 10 unmeasured specimens, a few were lacking larger parts of their skeleton. Some others contained no identifiable food remains at all.

In mammals from the Messel locality, stomach and intestine are never preserved as tissues and can be localised only by use of the food particles present in the respective section of the fossil (Richter, 1987, 1988). The same is true for fish specimens from Messel. In *R. minuta* (as well as in *T. intermedius*) we restricted our examinations to the area between the ventral fins and the caudal fin, where according to our experience food particles are often concentrated in a kind of U-turn of the intestine shortly behind the ventral fins or close

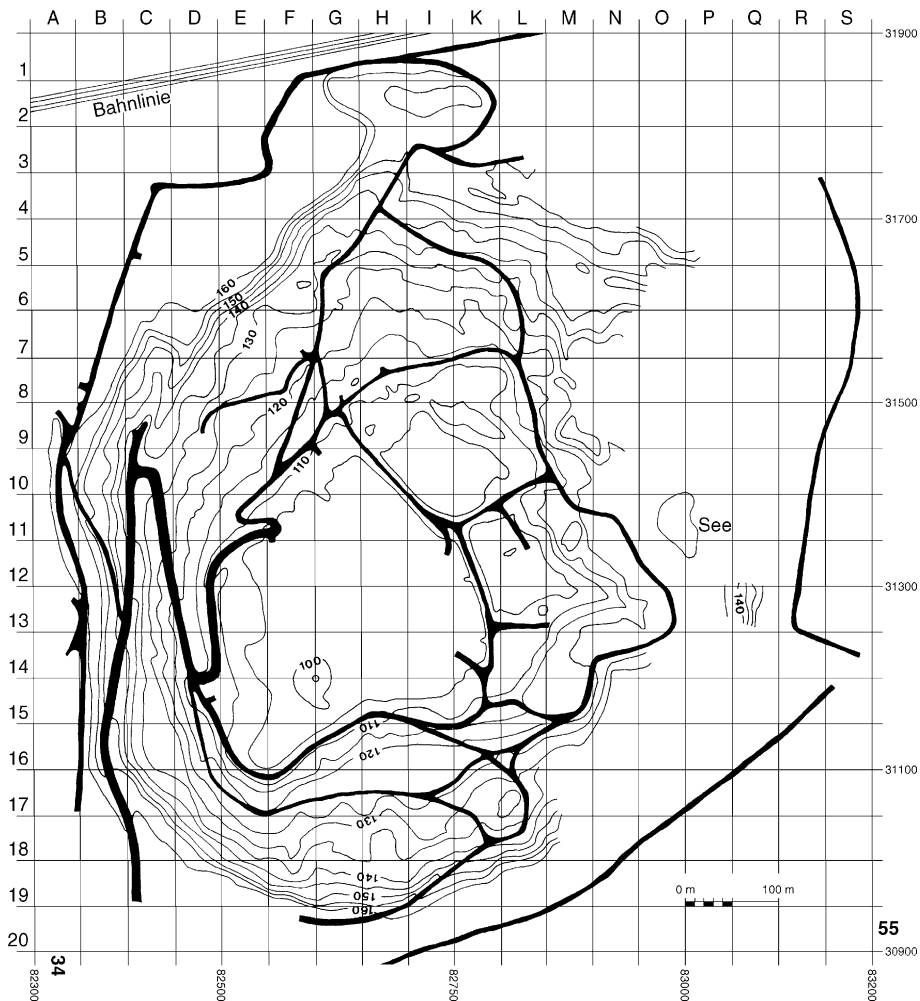


Fig. 1. Map of the world heritage site Grube Messel near Darmstadt, Germany (after Schaal and Möller 1991). The specimens referred to in this article originate from grid square H/I 7, the so-called “Turtle Hill” locality.

to the caudal fin. The stomach itself is hard to find and often completely covered by the operculum or by larger bones. In addition, teeth and small bone splinters found in this area may well derive from the fossil itself and may be no evidence for prey animals.

The food analysis of *R. minuta* encountered difficulties rarely faced in our former investigations on gut contents of Messel vertebrates (Richter, 1987, 1992). The entire body cavity of fossil fishes is covered by scales, ribs and bone splinters, with food particles scattered in between. In predatory fishes — even worse — the prey is fish and food remains consist primarily of scales, teeth and undiagnostic bones. These parts might or might not belong to the investigated specimen itself. If there are no truly diagnostic parts — such as a characteristic tooth type or a typical scale pattern — the only character to distinguish be-

tween predator and prey may be the size of fragments found in the area examined. But even this might prove deceptive because we know that many predatory fishes — and among them *R. minuta* — feed on prey scarcely smaller than the predator itself (Micklich, 1988).

All body regions of *R. minuta* that might contain food remains were carefully examined under a dissection microscope. More or less transparent membranes and particles were excised and embedded in Canada Balsam for an investigation with higher magnifications under a transmitted light microscope. In order to identify possible structural traces of digestive activity, bone material that is likely to represent food remains from the visceral tracts of several *R. minuta* specimens was investigated closely with a Scanning Electron Microscope and compared to other fossil fish bones and to bone particles recovered from coprolites.

Apart from the intestinal investigations, coprolites of different shape and size were collected from the excavation site of the *R. minuta* specimens. The coprolites were analyzed according to the methods described in Richter and Baszio (2001a). Identified food remains were compared to those from visceral tracts of *R. minuta*. Obviously, the identical place of discovery does not guarantee that the coprolites in question derived from the same fish species.

3. Results

3.1. Food particles identified in specimens of *R. minuta*

Of the 40 specimens of *R. minuta* with measurable body lengths, 25 (=63%) contained identifiable food remains. Of these, 12 could safely be determined as arthropod feeders. Their visceral tracts contained the familiar mandibles of chaoborid larvae and the filtering tufts of culicid larvae (Figs. 11 and 17 in Richter and Baszio, 2001a). Eyes and tarsal claws are preserved as well. Characteristic remains of ephemeropteran larvae well known from fish coprolites (Richter and Baszio, 2001a) were not detected, but these are rare finds also in coprolites. Benthic insect larvae can hardly be expected as prey animals because of the anoxic conditions in bottom waters of Lake Messel. Cladocera — quite abundant in many coprolites — were not found in the visceral tracts investigated. This is obviously due to the small size and transparency of these small Crustacea. Even in well-preserved and transparent fish faeces we never found more identifiable structures of Cladocera than tiny rows of cirri bordering their (completely transparent and therefore invisible) extremities (Richter and Baszio, 2001a).

Seven other specimens of *R. minuta* with a total length of 30 mm and more contain scales and bones with varying degrees of erosion (probably by stomach acids) much smaller than those of the fossil examined, indicating that the specimens containing these remains truly fed on fishes (in addition see the six specimens with uncertain fish remains mentioned above). In six other specimens the results are dubious.

For three additional specimens of unmeasurable total length, the food remains identified the fossils in question as fish or arthropod feeders, respectively. Food particles indicating different food sources (e.g., molluscs, Micklich, 1988), such as opercula, radulae or single radular teeth were not found. The unreliability in our analysis is demonstrated by the fact that 6 (!) of the presumed 15 fish feeders among the specimens with measurable body lengths had to be marked as dubious (Table 1). We nevertheless tentatively attribute them to

Table 1

Specimens of *Rhenanoperca minuta*, their respective body lengths and identified food remains in their abdominal region

Body length [mm]	Vertical distance to reference layer γ [cm]	Arthropod food remains	Fish food remains
18.0		*	
20.0		*	
23.0		*	
23.0		*	
25.0	+65	*	
25.0		*	
27.0		*	
28.0		*	
28.0		*	
29.0		*	
29.0		*	
34.0		*	
30.0			*
30.0	+69		*
31.0	+65		*
34.5			*
35.0	-6		*
39.0			*
40.0			*
36.5			* ?
29.0	+65		* ?
32.5			* ?
34.0			* ?
35.0	Between +60 and +50		* ?
37.5			* ?
18.0		-	-
21.6		-	-
23.9		-	-
25.5		-	-
26.5		-	-
29.6		-	-
30.0	-49	-	-
34.0		-	-
34.0		-	-
40.0		-	-
40.0		-	-
40.0		-	-
65.0		-	-
?		-	-
?	Between +42 and +34	-	-
?		-	-
?	+70	-	-
?		-	-
?	+76	-	-
?	+75	-	-
?	+58	-	-
?		-	-
?		*	-
?			*
?	+58		* ?

*Positive presence. Question marks indicate specimens of which the body lengths cannot be measured or estimated due to fragmentary preservation.

the group of fish feeders, because of the huge amount of bone material in their body cavity and the absence of insect remains in their digestive tracts.

3.2. Chitinous and skeletal remains in sedimentary structures

Two different types of isolated structures containing bone remains were among the collected material. The first type strongly resembles the coprolites containing arthropod remains previously studied by us in being flat and elongated with dispersed bone and tooth remains and a matrix of mineralised (phosphatised) bacteria, and showing a well-defined border on the sediment plate, being mostly of ribbon-like shape. Bones from these structures generally show traces of digestion. They can safely be addressed as coprolites and have previously been described by us (Richter and Baszio, 2001b).

Although much more rare than the similar structures containing arthropod remains, bone-containing coprolites of the (first) flat, ribbon-like type are very numerous in our samples. Many of them consist largely of an unbroken and thick matrix of mineralised bacteria with clusters of bone splinters and teeth in between as described in Richter and Baszio (2001b). Others consist mainly of densely packed bone splinters and — very occasionally — tooth remains, the matrix being reduced to a thin layer below the bones. The edges of many of the broken bones and teeth in these coprolites show different degrees of dissolution (Fig. 2), suggesting various effects of digestive agents (see discussion), whereas others seem rather unaffected, having clear and crisp borders.

The second type of structure has a three-dimensional spheroid to egglike shape and consists of a solid matrix of sulphuric phosphate. Single bones in this matrix are

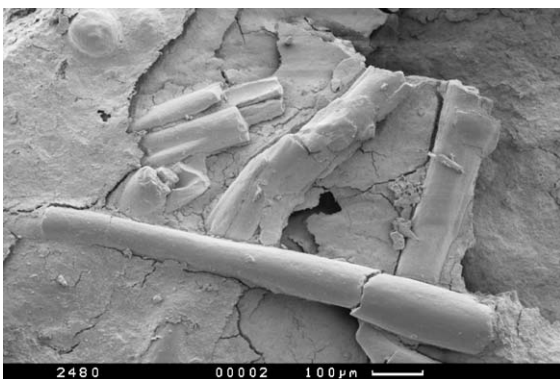


Fig. 2. Bone splinters from a ribbon-like coprolite. The broken edges of the bones show weak traces of dissolution, most probably due to digestive agents in the visceral tract of the coprolite producer.

extremely well preserved, never show any trace of digestion and are not as densely packed as in the flattened coprolites described above. It is hard to believe that these structures also represent coprolites, especially fish coprolites. An attribution to small crocodile coprolites can also be excluded, because crocodiles completely digest bone material and excrete unstructured calcium phosphate. They could however, represent bird or other regurgitates. This second structure is currently under investigation.

3.3. Attempting prey identification in fossil fishes

In order to identify at least some of the prey fish remains found in specimens of *R. minuta*, teeth of 3 other Messel fish species will briefly be described. There are quite characteristic shape differences depending on tooth position and species:

- *R. minuta* has relatively long, cone-like, slightly recurved and very pointed teeth (Fig. 3) that are situated in the anterior part of the dentition. Blunt, stout and spherical teeth (Fig. 4) are also part of this species' dentition and can be found in the posterior part of the tooth bearing cranial elements.
- *T. intermedius* teeth have two rather characteristic shapes: In one tooth type, a broad base slowly converges in so as to nearly form an isosceles triangle, but in the distal part the pointed tip is set off posteriorly at an oblique angle (Fig. 5). This tooth type can be found in the anterior and lateral part of the dentition. Another tooth type is conical to almost isosceles with a well developed basal part (Fig. 6) and is located in the posterior part of the mouth.
- Teeth of *C. kehreri* are either massive, blunt and conelike (Fig. 7), or long, slender and very pointed (Fig. 8).

This short description shows that there are different tooth morphologies within the same species, sometimes resulting in almost opposing descriptions for the teeth belonging to the same specimen. However, it is important to note that there are no intermediate states between these morphologies, thus allowing an attribution to a certain species if one tooth type can clearly be identified in the contents of digestive tracts of Messel predatory fish.

3.3.1. Fish teeth from intestinal contents

A characteristic tooth with traces of digestion was found in one specimen of *R. minuta* with a total length of 37 mm (No. 35). It was situated in the region directly

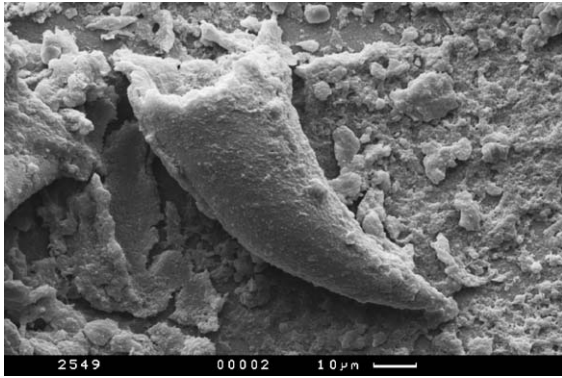


Fig. 3. One tooth type of *Rhenanoperca minuta* is conelike, slightly recurved and very pointed. It is found in the anterior part of the dentition.

posterodorsal to its pectoral fin. In this case the tooth enamel is almost completely dissolved, exposing the dentine (Fig. 9): The characteristic tooth shape with a posteriorly shifted apex is easily recognizable as that of *T. intermedius*. It has a height of 40 μm and a basal width of 15 μm .

A tooth series with similar traces of digestion (except for the tooth caps) was found in the same specimen farther dorsally, behind the operculum (Fig. 10). These teeth apparently are still in their original anatomical arrangement. Their morphology differs from that of the isolated tooth described above: All teeth in this series are relatively elongated and pointed. The largest among them is roughly 80 μm high and has a basal width of about 30 μm . This supports an attribution to *T. intermedius*.

3.3.2. Fish teeth from ribbon-like coprolites

Bone splinters in coprolites have almost no diagnostic value for the identification of the captured prey. In

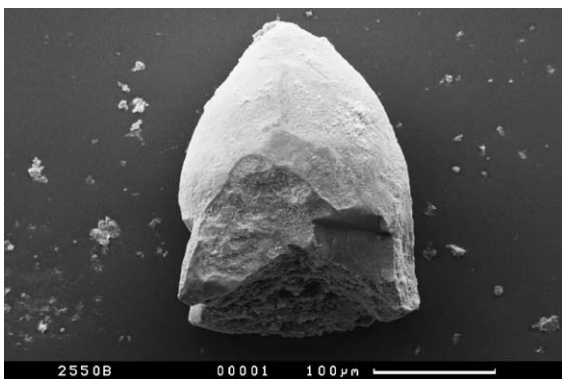


Fig. 4. Another tooth type of *Rhenanoperca minuta* is blunt, stout and spherical. It is situated in the posterior part of the dentition.

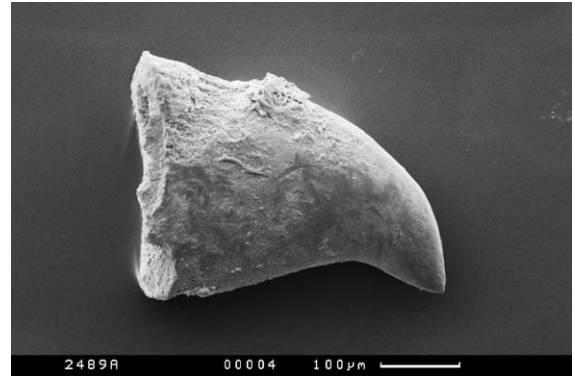


Fig. 5. The very characteristic tooth type of *Thaumaturus intermedius*. It has a broad base that converges so as to nearly form an isosceles triangle, but in the distal part the pointed tip is set off posteriorly at an oblique angle.

contrast, teeth can yield some information in this respect. Unfortunately teeth are rather rare finds in the flat and ribbon-like coprolites of fish feeders and even more rare in the digestive tracts of *R. minuta* specimens that we evaluated. However, the teeth depicted in Figs. 11 and 12 originate from two different ribbon-like coprolites containing fish remains (i.e., teeth and bone splinters). Both acrodont teeth are more or less stout and conical and slightly compressed along their basal width, without further characteristic features.

The tooth type described from the ribbon-like coprolites finds its best match with teeth of *T. intermedius* (Fig. 13) although there are huge size differences. In specimen No. 35 of *R. minuta* both tooth morphologies characteristic of *T. intermedius* are present. The distinct morphology with the posteriorly shifted tooth apex as well as the presence of the second tooth morphology makes this attribution highly probable. Furthermore, the traces of digestion also strongly support the hypothesis

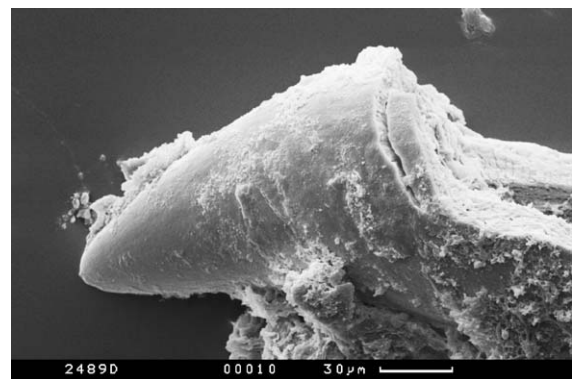


Fig. 6. The second tooth type of *Thaumaturus intermedius* is conical to almost isosceles with a well-developed basal part.



Fig. 7. *Cyclurus kehreri* has massive, blunt and conelike teeth in the largest part of its dentition.

that these teeth came from the intestinal tract of the specimen of *R. minuta*.

4. Discussion

In all investigated sediments, coprolites containing arthropod remains are by far more frequent than coprolites with bony contents. This is understandable, because all Messel fish fed on small crustacea and insect larvae for their first life period and *T. intermedius* obviously did so for its entire life span. According to Forbes (1884) young extant fish in general — and especially the juvenile stages of Amiidae and Lepisosteidae, both common in the Eocene Messel lake — feed on arthropods. In any fish species the number of juveniles exceeds by far the number of grown specimens.

In previous papers we named several taxonomic groups identified by us in fish coprolites from the Messel habitat (Richter and Baszio, 2001a,b, 2002). We found aquatic larvae of Ephemeroptera, Culicidae and Chaoboridae as well as Cladocera and (extremely

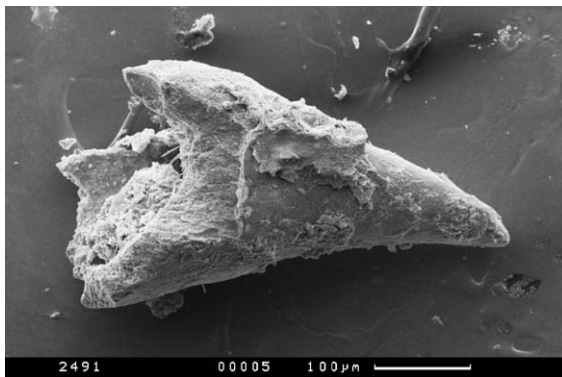


Fig. 8. Some teeth of *Cyclurus kehreri* are long, slender, and very pointed.

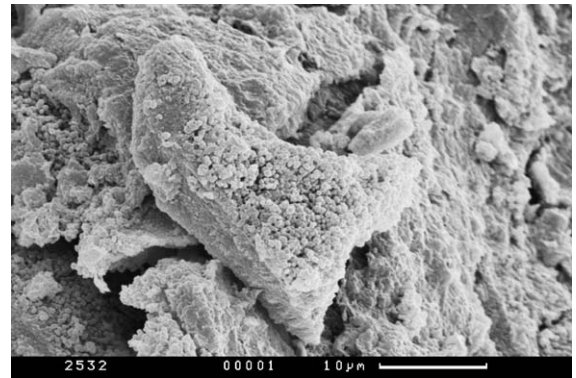


Fig. 9. This tooth from the intestine of a *Rhenanoperca minuta* specimen with a body length of 37 mm shows severe traces of digestion: In this case the tooth enamel is almost completely dissolved and the dentine becomes visible.

rare) juvenile Conchostraca. We repeatedly emphasized that this list is but a sketchy one and never claimed completeness (Richter and Baszio, 2002). First, we do not know an extant limnic ecosystem with so few different “actors” (that would be extremely unstable anyway). Second, we know so many chitinous fragments from fish coprolites not identified so far that the number of prey animals must be much higher. Nonetheless, the predominant food sources of planktivorous/insectivorous fish in the Eocene Lake Messel were Cladocera and the larvae of Culicidae and Chaoboridae. Fortunately, their most characteristic parts — mandibles and caudal fins in Chaoboridae, filter tufts and head clasps in Culicidae — are easily recognized and therefore predominate under the comparatively bad conditions for preparation and detecting that prevail in the analysis of food particles in the visceral systems of small fossil fishes.

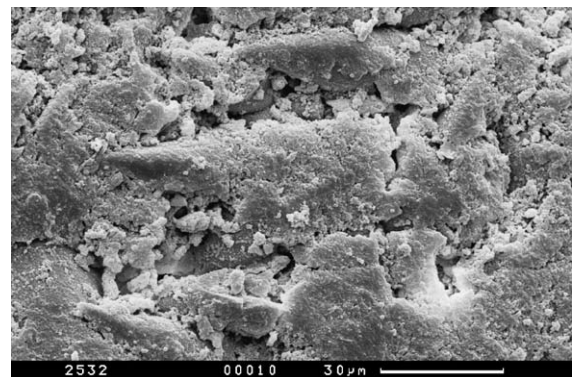


Fig. 10. A tooth series with severe traces of digestion: only the tooth caps are well preserved. The tooth series was found in the same specimen of *Rhenanoperca minuta* that also yielded the find depicted in Fig. 13.

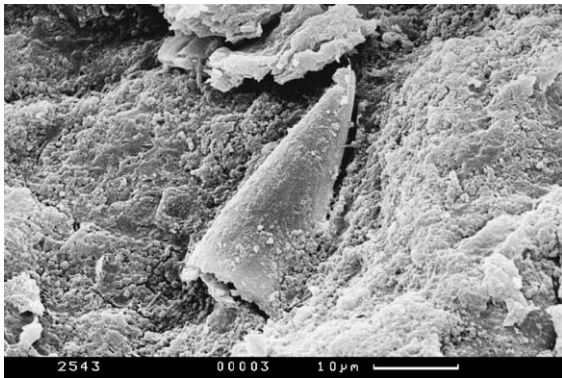


Fig. 11. This well-preserved tooth originates from a ribbon-like coprolite containing fish remains. It shows almost no traces of digestion, suggesting that the passage through the digestive tract went either very quickly, or that the producer of the coprolite was a rather small fish that had switched to piscivory shortly before producing the coprolite. The small size of the tooth (ca. 20 μm) proves the small size of the prey fish.

Despite the difficulties mentioned above, the results of our examinations are unequivocal. All specimens of *R. minuta* with arthropod remains in their digestive tract (save one, No. 102, total length 34 mm) have total lengths of less than 30 mm, whereas all fish-feeding specimens have lengths of 29 mm or more. Changes in the jaw morphology, e.g., in teeth or jaw lever ratios, have not been identified in association with the diet shift. It seems that this shift is a simple consequence of size and foraging behaviour. Even though we did not find indications for “switching” specimens near the crucial total length of ± 30 mm, we may safely conclude that juveniles of *R. minuta* fed on arthropods up to a total length of about 30 mm and then changed to fish as their main food source. This seems late in such a small fish, at least compared with extant species (such

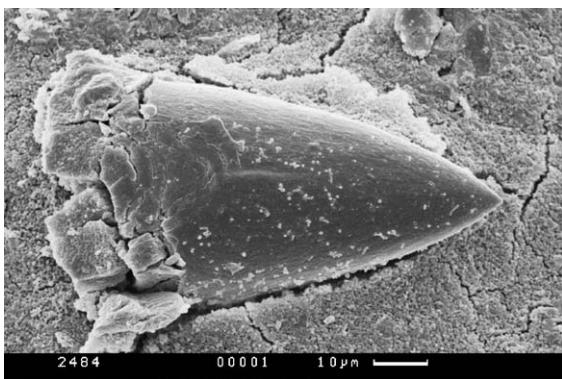


Fig. 12. Another example of a digested tooth from a ribbon-like coprolite that contains fish remains (different from the one depicted in Fig. 11).

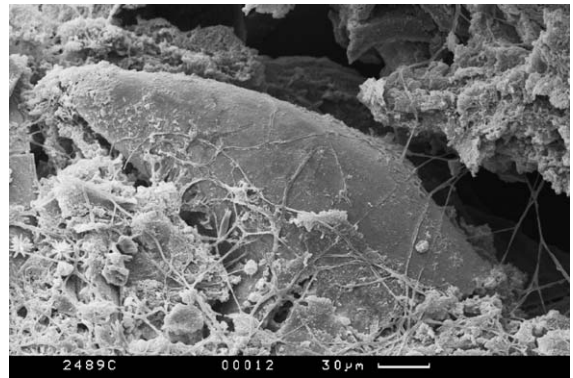


Fig. 13. This tooth from a ribbon-like coprolite finds its best match in teeth of *Thaumaturus* because of the characteristic tooth tip that is set back posteriorly on the broad base.

as certain species of *Esox*) that grow to a much bigger final size. According to Popova (1967), Nikolsky (1963), Frost and Kipling (1967) and Ivanova and Lopatko (1983), this switching is forced by the inability of young esocids of more than 25 mm body length to feed still (exclusively or to a large part) on arthropods (with a relatively low caloric value and the relatively high amount of energy needed in the hunting activities). If the same held true for other fish feeders, extant or fossil (which seems quite probable), we should expect that 30 mm in the total length of *R. minuta* marked a fixed borderline in the ecology and behaviour of this fossil species as well.

Although the number of identifiable vertebrate prey is rather small in this investigation, all of the remains of fish prey that can be identified most probably belong to very small specimens of *T. intermedius*. This suggests the hypothesis that juveniles of *T. intermedius* (the most abundant fish species in Messel) was one of the first and perhaps the most important food source of specimens of *R. minuta* (and probably many other predatory fish) after their switch from arthropod to fish food.

Again we want to stress some facts to avoid misunderstandings. Juvenile fish are opportunistic feeders in the sense that they do not have a determined prey scheme and actively forage in a manner that maximised the probability of locating invertebrate prey. They try to catch and swallow every moving object of a certain size inside their feeding range (Richter and Baszio, 2001a). This means that they do not discriminate between, let us say, an insect larva, an Oligochele or a small fish of comparable size. So, even some of our so-called arthropod feeders may have eaten some small juvenile fishes or fish larvae now and then and in accordance may bear some small bones in their

visceral tract. To us it is important that in general far more than 90% of their detected and identified food consists of arthropods.

Another question arose during our investigations: Why do only 63% of the scrutinized *R. minuta* specimens contain food particles at all? After all, living in a semitropical lake does not suggest marked seasonal change in the availability of prey organisms or periods of inactivity in the fish population. A good explanation might be found in diurnal feeding periods, probably triggered by light conditions. Many predatory fishes locate their prey optically and accordingly limit their hunting activities to hours with sufficient light intensity. Arrington et al. (2002) point out that extant piscivorous fishes seem to be the only trophic group that regularly experience long periods of empty stomachs. But these are only speculations, since a simple technical factor will have influenced our results far more than any unknown ecological ones: It is impossible to decide with security whether or not a small fossil fish from the Messel site contains any food particles at all in its entire visceral tract. A truly complete investigation of Messel predatory fish specimens would take an inordinate amount of time (and still remain doubtful).

It is obvious that there are huge differences in the flat ribbon-like coprolites investigated. Even coprolites of comparable size, shape and quantity of food remains differ notably in the grade of preservation of the bone material they contain. In some cases, the bones seem fresh and without any traces of digestion at all. In other coprolites the digestion shows in the form of bones with rounded edges. Again in others there remain no bones at all but only some indistinct differences in the tint of the bacterial matrix. This may well indicate that the coprolites in question derived from different species (or age groups!) of predatory fishes, showing quite different digestive abilities. Unfortunately we do not know enough about the differences in food digestion in extant relatives of the Messel fish to further pursue this matter at the present time.

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