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

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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.

Keywords: Messel; Eocene; Paleoecology; Fish; Feeding; Stomach contents; Coprolites

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

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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 strausi* 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