Norbert Micklich & Simon Mentges

Fin Ray Fractures in Messel Fishes

Authors' Addresses: Norbert Micklich, Natural History Department, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany; micklich@hlmd.de; Simon Mentges, Eschollbrücker Straße 5a, 64283 Darmstadt, Germany; simon.mentges@web.de.

Abstract

The soft rays of the dorsal and anal fins as well as the main caudal rays of various Messel fish species were examined with regard to the occurrence of healed fin ray fractures. Published information concerning the number of the respective rays in *Cyclurus kehreri* (Andreae, 1893) was revisited and updated. Our results of the analyses were compared with counts in closely related or ecologically equivalent extant taxa. In all investigated species, the relative number of healed fin ray fractures was largest in the caudal fin, followed by the dorsal and anal fins. In addition, it emerged that there is a correlation between the size of the investigated specimens and the number of healed fin ray fractures. Possible trigger mechanisms for their occurrence in extant and fossil species are discussed. With respect to their relative frequencies and distribution patterns along the fins under investigation, they probably result from mechanical stress. The individual fate of the investigated specimens may also have played a role as well as their general morphology and particular life habits. Additional investigations, especially in extant species, are needed to come to a conclusive evaluation.

Zusammenfassung

Die Weichstrahlen der Dorsalis und der Analis, sowie die Hauptstrahlen der Caudalis verschiedener Messeler Knochenfisch-Arten wurden hinsichtlich des Vorkommens verheilter Flossenstrahl-Brüche untersucht. Dabei wurden auch die Literaturangaben über die Anzahl der betreffenden Weichstrahlen bei *Cyclurus kehreri* (Andreae, 1893) überprüft und aktualisiert. Die Ergebnisse der Fossil-Analysen wurden den entsprechenden Befunden von rezenten Vergleichs-Taxa gegenüber gestellt. Bei allen untersuchten Arten war der relative Anteil der verheilten Flossenstrahl-Brüche in der Caudalis am größten, gefolgt von der weichstrahligen Dorsalis und der Analis. Darüber hinaus konnte ein Bezug zwischen der Körpergröße und dem relativen Anteil der verheilten Flossenstrahl-Brüche festgestellt werden. Mögliche Auslösemechanismen für ihr Auftreten bei den rezenten und fossilen Arten werden diskutiert. Ihre Häufigkeit und Verteilung lässt mechanischen Belastungen als wahrscheinlichste Ursache erscheinen. Das Individualschicksal, die generelle Morphologie und die besonderen Lebensgewohnheiten der betreffenden Exemplare und Arten dürften ebenfalls eine Rolle gespielt haben. Für ein abschließendes Urteil sind hierzu jedoch noch ausführlichere Untersuchungen, vor allem im Rezentbereich, notwendig.

Introduction

Messel Pit is well known for having an excellently preserved fauna and flora that existed in an ancient Maar-lake and the adjacent tropical-subtropical rain forest about 47 million years ago (Schaal & Ziegler 1992, Mertz & Renne 2005). The aquatic fauna is dominated to a considerable extent by fish that were at least temporarily inhabitants of Messel lake. Therefore, they can reveal important information about the conditions they used to live in (Micklich 2007, 2012). In extant fish species, pathological phenomena mainly result from various injuries, diseases, nutritional deficiencies, and other impacting factors. Particularly common and intensively investigated is the complete regeneration of fin rays and parts of fins. Depending on the particular body regions, this regeneration sometimes takes place rather rapidly in extant fish species (Wunder & Schimke 1935; Poss et al. 2003; Shao et al. 2009). Injuries of individual soft rays are a rather common occurrence and can also heal or be regenerated fairly quickly (Marí-Beffa et al. 1999). Healed fin ray fractures can be (a. o.) identified by local nodular thickenings, which are caused by the formation of callus (Figs. 1–4). Flexes of the rays sometimes also remain notable in the afflicted areas. The present study is meant to establish whether, and if so, to which extent the relative frequencies of such healed fin ray fractures differ amongst species, and if it facilitates general conclusions as to their possible trigger mechanisms.

Materials and Methods

All fossils used in our study are from the Messel fish collection of the Hessisches Landesmuseum Darmstadt. Altogether, these were 273 specimens of *Cyclurus kehreri* (Andreae, 1893) (7.2–46.7 cm SL[1]), 122 specimens of *Amphiperca multiformis* Weitzel, 1933 (4.8–16.3 cm SL[2]), 80 specimens of *Palaeoperca proxima* Micklich, 1978 (8.9–19.3 cm SL[3]), and 50 specimens of *Rhenaoperca minuta* Gaudant & Micklich, 1990 (2.4 – 6.3 cm sl[4]). According to the extant comparative materials, three specimens of *Amia calva* Linnaeus, 1766 (HLMD-SMFR 154 a-c; 13.9–18 cm SL), four specimens of *Morone chrysops* Rafinesque, 1820 (HLMD-SMFR 32, 82, 121, 231; 7.3 – 10.5 cm SL), two specimens of *Morone saxatilis* (Walbaum, 1792) (HLMD-SMFR 37, HLMD-SMFR 314; 7.3 and 10.5 cm SL, resp.), as well as three specimens of *Lepomis gibbosus* Linnaeus, 1758 (HLMD-SMFR 01, 03, 15; 4.7–6.8 cm SL) were incorporated into our study. All fossils were prepared by transferring the original objects onto epoxy resin (Bakelite EPR 320) support plates. The extant comparative materials consisted of cleared specimens, which were stained with alizarin red. Microscopic examinations were carried out using a Wild 650 light microscope (Leica), photographs were taken with a Canon EOS 450D DSLR camera.

Abbreviations used:

Atotal: total number of anal soft rays examined; Ctotal: total number of caudal principal rays examined; D1, D2: first and second dorsal fin; Dtotal: total number of dorsal soft rays examined; HLMD-Me: Messel collection of the Hessisches Landesmuseum Darmstadt; HLMD-SMFR: HLMD, extant fish species reference collection of the first author; Ntotal: total number of fin rays examined; SL: standard length: SNG: Senckenberg Research Institute, Frankfurt a. M.

Results

Healed fin ray fractures

Cyclurus kehreri (Figs 2, 3, 5): The majority of the investigated specimens were without any indication of structures that would suggest fractured fin rays. In those specimens in which such traces were detectable at all, they were mainly confined to the soft rays of the dorsal fin (1.1% of Ntotal). The principal rays of the caudal fin and the anal fin soft rays clearly had lower values (<1% of Ntotal). However, there were exceptional specimens with significantly higher percentages. In HLMD-Me 9114, 19 fin rays with healed fractures were to be noticed, representing 28.7% of Ntotal. The majority was detected in specimens with more than 18.8 cm SL, smaller and therefore younger ones showed only a few healed rays (Fig. 6).

Amphiperca multiformis (Fig. 4, 5): No healed fractures were noticed in the spines of the D1. 1.1% of Ntotal were healed in the D2, and 4% of Ntotal were healed principal caudal rays. In most specimens, the soft rays of the anal fin were completely intact, except HLMD-Me 8962, in which one broken ray was found. Like in the bowfins, a certain correlation between the number of healed fin ray fractures and the body size of the respective fishes was observed (Fig. 6). Respective soft rays could mainly be found in specimens that were larger than 9.4 cm SL.

Palaeoperca proxima (Fig. 5): The number of healed fin ray fractures was clearly smaller than in *Amphiperca multiformis*. None of the specimens exceeded a value of 1% of Ntotal. No healed fractures were found in the spines of the D1, the D2 and of the anal fin, and there was a value of only 0.4% of Ntotal in all their soft rays. The highest number of healed fractures was noticed in the caudal principal rays (0,9% of Ntotal), whilst the value of the anal fin soft rays was slightly smaller than for the D2 (0.3% of Ntotal). All specimens with healed fin ray fractures were between 12.7 and 16.6 cm SL, which means 14.7 cm on average SL (Fig. 6).

Rhenaoperca minuta (Fig. 5): No traces of fractures were noticed in the spiny sections of the dorsal and anal fins, which is as also true for the other Messel percoid species. In addition, no healed fin ray fractures were found in the soft rays of the D2 and of the anal fin. By contrast, there was a comparatively high value (about 6% of Ntotal) in the principal rays of the caudal fin. As in the other species, healed fin ray fractures were preferably found in somewhat larger and older specimens (Fig. 6). All individuals of the extant comparative species lacked any trace of healed fin ray fractures.

[1)–4)] inventory numbers see appendix

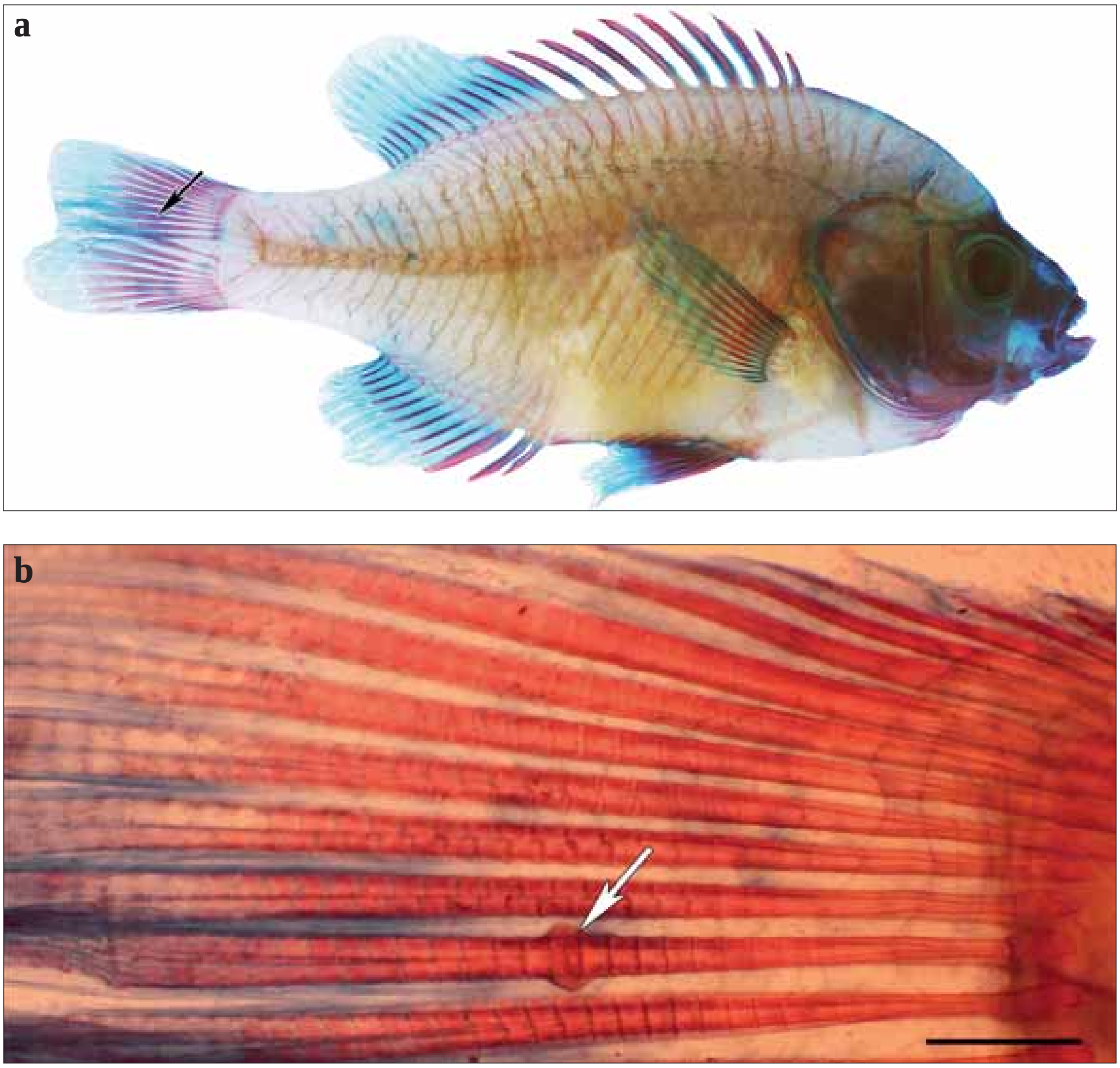


Fig. 1: Healed fin ray fracture (marked by arrow) in the caudal fin of the Pumpkinseed, *Lepomis gibbosus* LINNAEUS, 1758. Specimen (cleared and stained) HLMD-SMFR 115, 9.8 cm SL. a: general view, b: detail; scale bar is 2 mm.

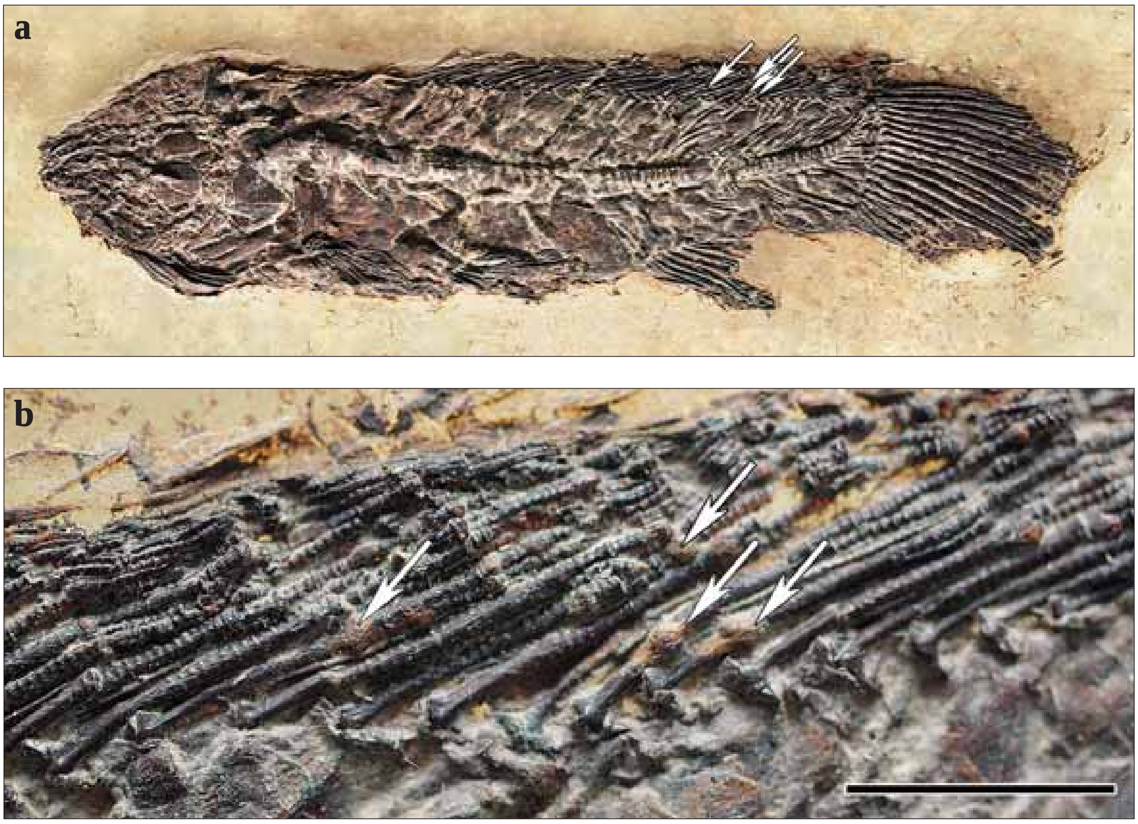


Fig. 2: Healed fin ray fractures (marked by arrows) in the dorsal fin of *Cyclurus kehreri*. Specimen HLMD-Me 9114, 23.6 cm SL. a: general view, b: detail; scale bar is 1 cm.

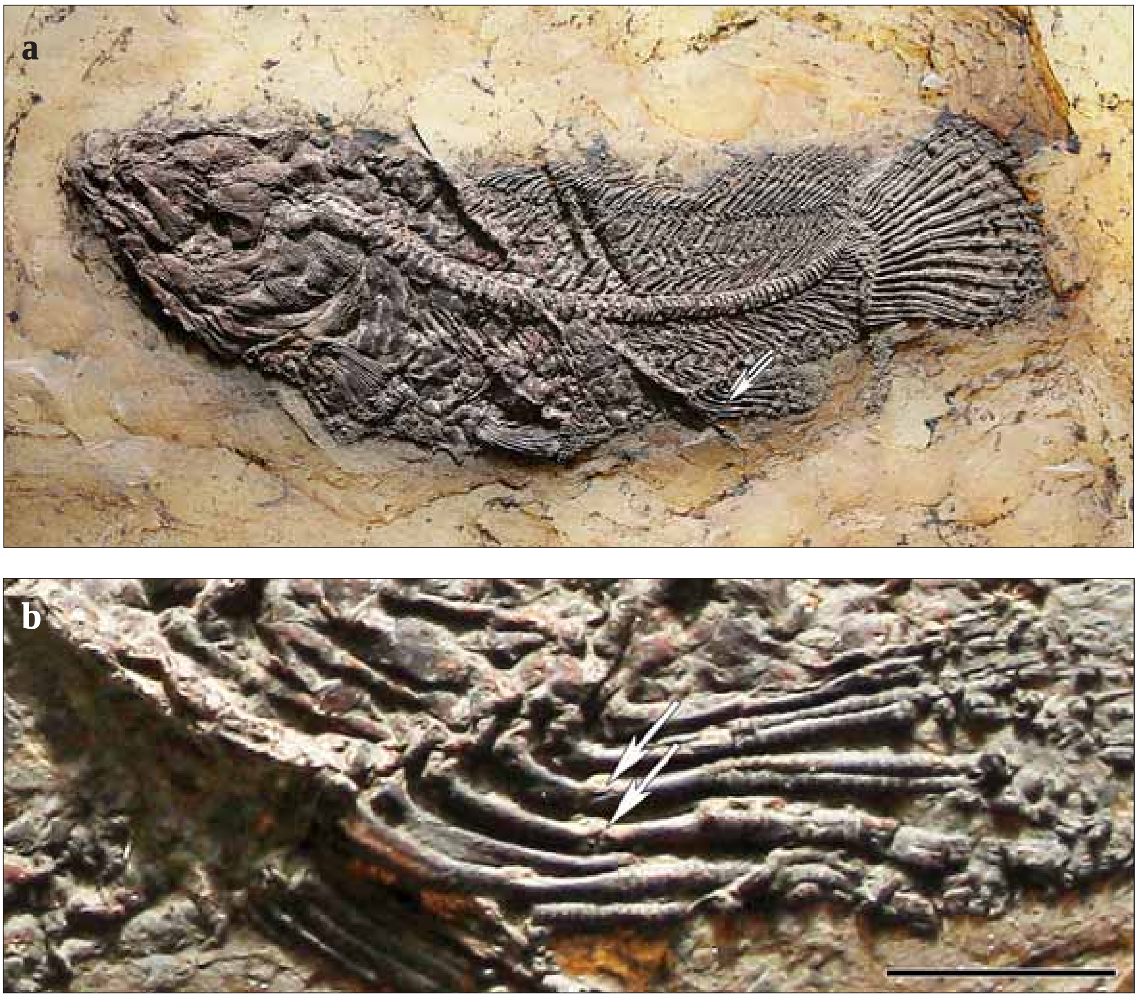


Fig. 3: Healed fin ray fractures (marked by arrows) in the anal fin of *Cyclurus kehreri*. Specimen HLMD-Me 7795, 23.1 cm SL.
a: general view, b: detail; scale bar is 1 cm.

Fig. 4: Healed fin ray fractures (marked by arrows) in the dorsal and caudal fins of *Amphiperca multiformis*. Specimen HLMD-Me 7632, 12.7 cm SL.
a: general view, b: detail of principal caudal rays, c: detail of soft D2 rays; each scale bar is 0.5 cm.

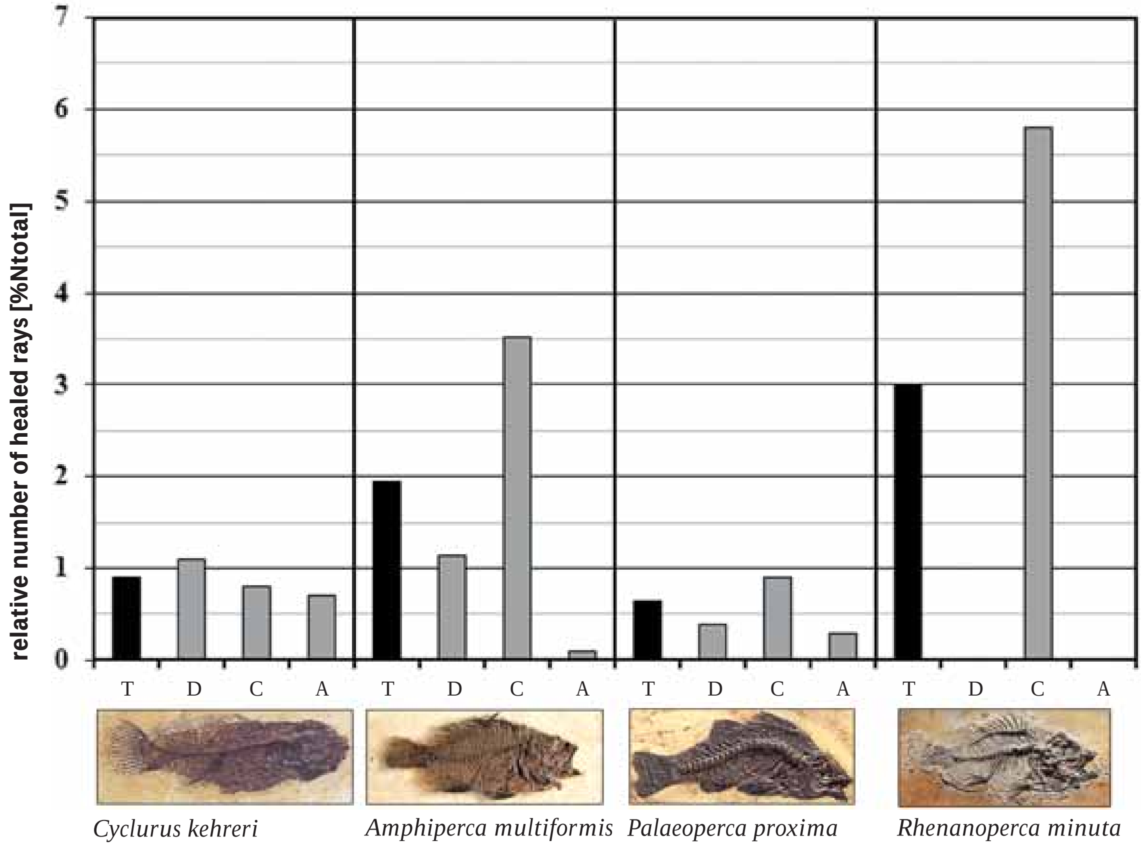
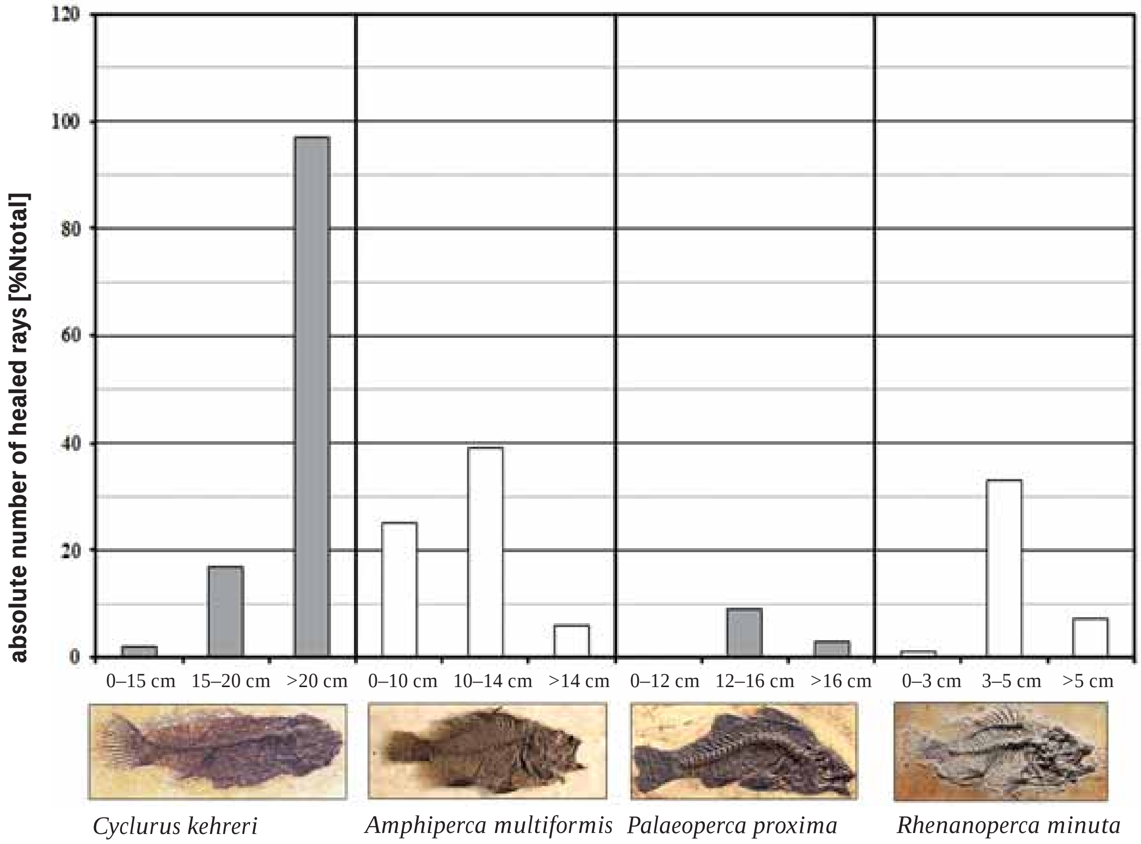


Fig. 5: Relative number of healed fin ray fractures in the investigated species. T: relative number of fin rays with healed fractures as a percentage of all investigated soft rays (Ntotal); D: relative number of dorsal fin rays (D2 rays, respectively) as a percentage of all investigated dorsal rays (Dtotal); C: same, principal caudal rays; A: same, soft anal rays. *Cyclurus kehreri*: Ntotal = 13583, Dtotal = 6999, Ctotal = 4870; Atotal = 1714; *Amphiperca multiformis*: Ntotal = 3896, Dtotal = 1237, Ctotal = 1733; Atotal = 926; *Palaeoperca proxima*: Ntotal = 2576, Dtotal = 520, Ctotal = 1155; Atotal = 365; *Rhenanoperca minuta*: Ntotal = 1371, Ctotal = 712 (no healed rays in dorsal and anal fins).

Fig. 6: Absolute number of healed fin ray fractures as a function of the SL.



Number of soft rays in *Cyclurus kehreri* (Tab. 1)

Up to 39 soft rays were counted in the dorsal fin, which is close to the value reported by Grande & Bemis (1998)[5]. Our count does not differ substantially from the 34–38 rays counted by Gaudant (1999), who mainly studied material in the SNG collection. Jerzmańska (1977), who investigated *Cyclurus kehreri* from the (almost contemporary) lignites of the Geiseltal in eastern Germany, reported 37 rays.

In the caudal fin, we counted 18–20 principal rays, together with three to four epaxial marginal rays and five to six hypaxial ones. Grande & Bemish (1998)[6] gave similar counts for the principal caudal rays (18), as well as for the epaxial marginal rays (five). However, they noticed considerably more hypaxial marginal rays (24). Gaudant (1999) did not distinguish between these different types of rays but gave a total count of 15–16 instead. Jerzmańska (1977), in turn, reported 19–20 principal rays together with five unbranched and shorter epaxial, and also hypaxial ones for the Geiseltal population of *Cylurus kehreri*. Nine to 11 rays were counted in the anal fin. This, once again, is close to the number given by Grande & Bemish (1998)[7], who found one rudimentary unsegmented anterior ray that was followed by 9 to 10 »regular« (segmented) ones. By contrast, Gaudant (1999) only noticed five to seven anal fin rays in the SNG material. Jerzmańska (1977) noticed 12 anal rays in Geiseltal specimens.

As far as the other studied Messel fish species are concerned, no or only very minor differences were noticed between our counts and the numbers previously published (Micklich 1985, Gaudant & Micklich 1990).

Discussion

Healed fin ray fractures

Apart from diseases such as finrot, damage to, or even the loss, of fin rays in extant fish species may primarily be expected as a result of mechanical stress, e.g., in tight environments that are rich in sharp-edged obstacles (e.g., Tesch 1956), or as a consequence of predator attacks, rival combats or territorial disputes, including those during nesting and brooding (e.g., Reighard 1900, Miller 1967, Peeke & Peeke 1970, Barlow 1991, Cooke & Philipps 2009). In the present scenario, the latter possibilities can be discarded, however, due to the fact that the Messel fish species are mainly represented by sexually immature juveniles (Micklich 2002, 2007: 40, 41). In principle, damages caused by mechanical stress or predator attacks should be expected to mainly occur in the back and lower areas of the body, especially in the soft ray sections of the dorsal, caudal and anal fins. Predatory fish that actively pursue their prey often attack their victims from behind (Francis & Conover 1994: 65), as this will reduce the risk of premature discovery, and, on the other hand, inflicted damage to the caudal fin will diminish the prey's capacity for rapid flight (Foxx 1972, Sazima & Machado 1990). Accordingly, it should be expected that such attacks affect mainly the caudal fin or the entire posterior part of the body and not predominantly the posterior parts of the dorsal and caudal fins. This is consistent with the results of this study only insofar, as no injuries were identified among the spines of the D1 and the anal fin, and that the highest numbers of healed fin ray fractures were found among the principal rays of the caudal fin. It does not come as a major surprise, though, as the latter fin is the main propulsive organ and as such is almost by default constantly exposed to the greatest mechanical stress. The fact that the number of healed fin ray fractures of the D2 always exceeded that of the anal fin in our study seems to be a good argument against an obstacle-rich and therefore potentially injurious environment, such as a habitat with rocky or gravelly substrate. In the latter case, damages were more likely to occur in the ventrolateral or ventral portions of the body. Thus, the observed differences in the distribution patterns of healed fin ray fractures cannot be convincingly explained.

Attacks by large predators probably result more often in the death of their respective victims than in their survival and subsequent recovery. From this point of view, damages and damage distribution patterns in the investigated material are more likely due to random mechanical stresses. Then, the very elongated dorsal of the bowfins as well as the D2 of *Amphiperca multiformis*, which is also considerably expanded posteriorly, are more vulnerable than the compara-

Tab. 1: Soft fin ray counts of *Cyclurus kehreri*, as published in literature.

	Dorsalis	Caudalis	Analis
Jerzmańska (1977)	37	19–20	12
Grande & Bemish (1998)	41–43	18	9–10
Gaudant (1999)	34–38	15–16	5–7
Micklich & Mentges	39	18–20	9–11

5)–7) Grande & Bemish do not give counts for the Messel species, but rather refer to the similarity with *Cyclurus valenciennesi* Agassiz, 1844 , which has 41–43 dorsal rays.

tively short D2 and the relatively short anal fin of *Palaeoperca proxima*. As far as *Rhenanoperca minuta* is concerned, fin ray fractures may in general be less probable due to the small size of most specimens alone.

Explaining the fact that in all investigated species the higher numbers of healed fin ray fractures were found in the larger-sized specimens is simple. In offering a larger area that can be affected by negative and injurious events, they are simply more prone to suffering fin ray fractures. Moreover, these specimens were older and therefore exposed to such trigger mechanisms for longer periods of time.

Micklich (1985: 127) likewise supposed there was a relationship between the size of certain fin sections and corresponding differences in the relative abundance of healed fin ray fractures in *Amphiperca multiformis* and *Palaeoperca proxima*. Without giving precise numbers, he, however, stated that the differences between both species were comparatively large. This may be due to the fact that these former investigations were mainly based on material in the collection of the SNG, which originated from different stratigraphical sections (»time windows«) of the Messel oil shale than those that were investigated now, and might have represented different environmental conditions and/or places (»Biotope« sensu Franzen et al., 1982). Whether the observed differences are actually a consequence of habitat shifts, cannot be conclusively assessed. The general morphological differences between the two species clearly at least suggest that they had different ways of life, however.

Number of soft rays in *Cyclurus kehreri*

The differences between our counts and those of Jerzmańska (1977) may reflect local effects, arising from the different geographical positions of the Messel and Geiseltal fossil sites. The deviations of our counts from those reported by Gaudant (1999) may be due to similar effects, as there are slight differences in the stratigraphical and also topographical positions of the hlmd and sng excavation areas in the Messel pit. Aside of the hypaxial marginal rays of the caudal fin, there are only very small differences between our counts and those given by Grande & Bemish (1998). These may be referred to the fact that the latter authors took their counts from *Cyclurus valenciennesi* (see footnotes before)

Conclusions

In all investigated species, the principal rays of the caudal fin showed the highest numbers of healed fin ray fractures, followed by the soft rays of the D2 and the anal fin. As far as the individual species are concerned, the highest number of healed fin ray fractures was noticed in *Cyclurus kehreri*, followed by *Amphiperca multiformis*, *Palaeoperca proxima* and *Rhenanoperca minuta*. No such damages were found in the comparative specimens of extant species.
The occurrences of fin ray fractures in the Messel species could not be attributed to any particular events. Mechanical stress, resulting from a vast variety of trigger mechanisms, is accepted as the most likely explanation here. Some of these may be related to particular habits of the species. The relative lengths of the different fin sections may have played a role, as they determine the size of the area that is foremost exposed to injurious events. The same applies to individual age, representing the period of time during which individuals need to survive such negative effects.

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Appendix: Inventory numbers of investigated specimens

Cyclurus kehreri: HLMD-Me 3457, 3459, 3460, 3510, 3511, 3756, 3757, 3766, 3946, 7250, 7449, 7450, 7452, 7454 a,b, 7456, 7457, 7484, 7486, 7488 a,b, 7490, 7503, 7651, 7665, 7668, 7670, 7671, 7678, 7679, 7680 a,b, 7681–7691, 7719 a,b, 7721, 7725, 7729 a, 7734–7736–7745, 7746a,b, 7749–7753 - 7760, 7762, 7781, 7793, 7794–7798, 7804, 7805, 7826, 7828, 7840, 7843, 7857, 7884, 7885, 7896, 7910, 7912, 7916, 7936, 7939, 7990, 8013, 8018, 8024, 8025, 8026, 8048–8050, 8053, 8060, 8065, 8070, 8075, 8077, 8087–8089, 8093, 8095, 8286, 8916, 8917, 8919, 8920, 8921–8930, 8933, 8941, 8947–8949, 9044, 9055, 9097, 9104, 9106, 9110, 9114, 9731, 9735, 9737, 9739, 9740–9742, 9744, 9755, 9759, 9765, 9766, 9768, 9769, 9785, 9799, 10259, 10261, 10263, 10264, 10266, 10267, 10274, 10354, 10399, 11014 a,b, 12607, 13014, 13063, 13064, 13223 a,b, 13252, 13253, 13302 a,b, 13303, 13305, 13351 a,b, 13360, 13371, 13388, 13390, 13415, 13416, 13419, 13456, 13467 a, 13470, 13472–13474, 13476, 13477, 13487, 13517, 14634, 14644, 14645, 14756, 14757, 14760, 14762, 14763, 14956, 15001, 15041, 15042, 15123, 15125, 15126, 15127, 15129, 15130–15132, 15135, 15137, 15138, 15141, 15144a,b, 15145, 15148, 15154, 15161–15164, 15166, 15168, 15187, 15206–15208, 15219, 15248, 15287, 15288, 15300, 15307, 15318, 15354, 15379, 15413, 15415, 15440, 15549, 15586–15590, 15593, 15595, 15598–15601, 15656–15659, 16019, 16023–16027, 16032, 16033, 16068, 16924.

Amphiperca multiformis: HLMD-Me 1055, 3940, 7445 - 7447 a,b, 7478, 7481 - 7483, 7485, 7529, 7551, 7569, 7632, 7633 a,b, 7635a b, 7771 a–c, 7772, 7792 a,b 7820, 7822–7824, 7829, 7830, 7832, 7834, 7926, 8006, 8033, 8047, 8061, 8063, 8066, 8068, 8069, 8072, 8073, 8076, 8092, 8913, 8914, 8931, 8936, 8937, 8939, 8943 - 8945, 8954, 8955, 8956, 8960, 8962, 8965, 8966, 8967, 8970, 8971, 9046, 9058, 9059, 9099, 9101, 9105, 9745, 9756, 9758, 9761, 9772, 9773, 10270, 10356, 10357, 10560, 10602, 13267, 13318, 13438, 13460, 13716, 13761, 13763, 13776 - 13778, 13782, 13797b, 14759, 15046, 15104, 15118, 15122, 15133, 15139, 15142, 15143, 15178, 15189, 15190, 15191, 15241, 15290, 15313, 15321, 15334, 15348, 15361, 15371, 15455, 15460, 15813, 15818, 15828, 15830, 15831.

Palaeoperca proxima: HLMD-Me 7 a, 59 a,b, 189 a, 919, 7634, 7636 b, 7859 a,b, 7799, 8005, 10540, 10603, 12547, 12555 a,b, 12556 a, 12557 a, 12558 b, 12559 a,b, 12566 b, 12588 a, 12601 b, 13053, 13056, 13058, 13059, 13060, 13061, 13266 a,13306 a, 13307 a,b, 13307, 13308, 13309, 13310 a,b, 13313 a,b, 13314, 13315, 13316, 13318 b, 13319 a, 13322 a,b, 13372 a,b, 13373, 13374, 13399, 13439, 13461 a,b, 13789 b, 13828 a,b, 14775, 14778 a,b, 14943, 14947, 14950, 14953, 14955, 15031, 15134, 15167, 15630, 15821, 15823, 15824, 15825, 15827, 15841, 15846, 15847.

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