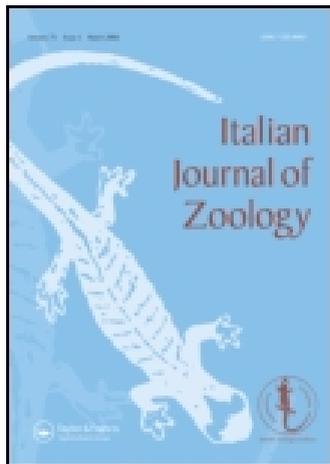


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Andre Pharisat ^a & Norbert Micklich ^b

^a Géosciences , Université de Franche-Comté , 25030 Besançon & Museum G. Cuvier, Montebéliard, F-25200, France

^b Department of Geology, Palaeontology & Mineralogy , Hessisches Landesmuseum , Darmstadt, Germany

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Oligocene fishes in the western Paratethys of the Rhine Valley Rift System

ANDRE PHARISAT

Géosciences, Université de Franche-Comté, 25030 Besançon & Muséum G. Cuvier, F-25200 Montebéliard (France)

NORBERT MICKLICH

Department of Geology, Palaeontology & Mineralogy, Hessisches Landesmuseum Darmstadt (Germany)

ABSTRACT

In the Rhine Valley System, two fossil sites are famous for their well-preserved and rich marine fishfaunas: Froidefontaine (Belfort Territory, France) and Frauenweiler (S of Heidelberg, Baden-Württemberg, Germany). Concerning general stratigraphy, both deposits belong to the Rupelian stage of the Oligocene. There is a high degree of diversification of the fishfauna, e.g. within the Syngnathoidae (Gasterosteiformes), which is also recorded from corresponding localities of the Carpathians and of the Russian Paleogene. *Aeoliscus beinrichi* (Centriscidae) is the most frequent syngnathoid species and a second one, *Aeoliscus distinctus*, almost certainly also is present in Froidefontaine. Both localities are furthermore characterized by the predominance of taxa with presumably southern relationships, that probably were established via the S-E Paratethys. Several new taxa of Frauenweiler reveal benthic/mesopelagic affinities. The Froidefontaine fauna, by contrast, is fundamentally neritic and littoral. It indicates the presence of a spawning zone but offshore connections as well. The differences in the faunal composition are probably also due to the different geographical positions: Colder seas from the north may have more strongly affected the Frauenweiler fauna than that of Froidefontaine, which was in closer contact with warmer seas from the S.-E. Paratethys.

KEY WORDS: Oligocene marine fishes - Frauenweiler and Froidefontaine fossil sites.

ACKNOWLEDGEMENTS

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INTRODUCTION

The Froidefontaine and Frauenweiler fossil sites both are located in the upper part of the Rhine Valley Rift System (Fig. 1). The fossiliferous marls and clays originated during the Rupelian stage of the Oligocene. The richness and composition of the respective fishfaunas is well-known from the literature (e.g., Sauvage, 1870; Wagner-Klett, 1919; Weiler, 1931, 1966; Theobald, 1934; Faivre, 1969). These former revisions, however, are based on comparatively poor and fragmentary materials from ancient brickstone clay pits, in the vicinity of both villages. More recent investigations have revealed numerous well-preserved specimens and also first records of additional new taxa (Pharisat, 1991, 1992, 1993; Micklich & Parin, 1996; Parin & Micklich, 1996). Interestingly, these actual collections do not comprise exactly contemporary materials: Basic 'Fischschiefer' as well as the younger 'Meletta-Schichten', are represented by the stratigraphically very well defined specimens from Froidefontaine (Pharisat, 1991). Due to the restricted thickness of the 'Fischschiefer' and also to the special local mining and excavation conditions (Weiler, 1966; Barth, 1970; Kaiser & Hildebrand, personal communications), the majority of specimens from the present-day Frauenweiler clay pit ('Grube Unterfeld', Trost Company, Malsch), however, are probably from the lower parts of the 'Meletta-Schichten'. Careful analyses concerning the general composition of the Froidefontaine and Frauenweiler fishfaunas, the frequency distributions of different taxa, as well as of possible changes of cer-

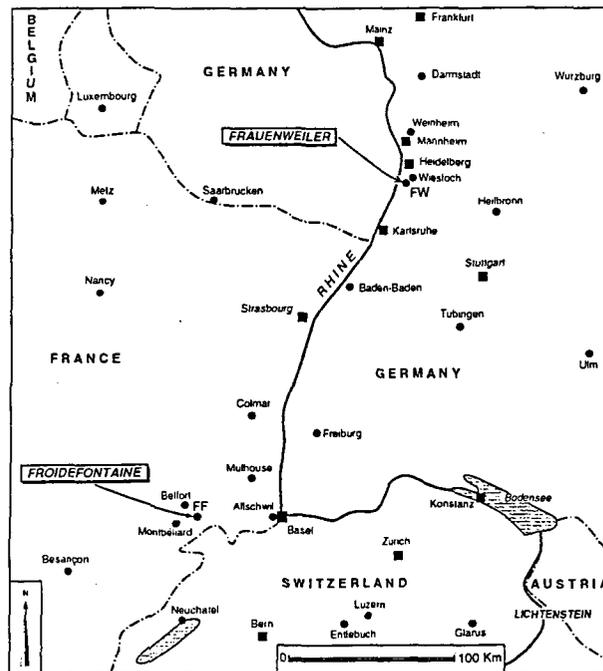


Fig. 1 - Location of the two Oligocene fish deposits of Froidefontaine and Frauenweiler in the Rhine Valley System.

tain character stages across both stratigraphical profiles, thus will establish a broad base to point out traits and modifications of overall faunal diversity and of peculiar ecological, paleobiogeographical and evolutionary shifts in the future.

MATERIALS AND METHODS

Concerning the Froidefontaine material, this study is mainly based on a collection of well-preserved specimens that is deposited in the G. Cuvier Museum, Chateau des Ducs de Wurtemberg, Montbéliard. This collection comprises a total of more than 11000 specimens, with size ranges between 1 mm and 1 m. It results from the former private collections of Stéphane Michel, Michel Laclef, Jean Pierre Hartmann, Christian Mathis and André Pharissat, that were established during field work in the years 1971 and 1972. Some additional rare specimens originate from the old collections Oehmichen in Montbéliard and from the ancient Museum of the Laboratoire de Geologie Historique et Paleontologie de l'Université de Besançon. Further very old specimens also are from the Museum National d'Histoire Naturelle, Paris.

In contrast to the Froidefontaine specimens, that are preserved in the original clayish matrix, the materials from the Frauenweiler locality referred to in this study are prepared according to the transfer method (e.g., Lippmann, 1987; Kaiser & Micklich, 1995). The vast majority of these specimens are deposited in the Department of Geology, Palaeontology & Mineralogy of Hessisches Landesmuseum Darmstadt (HLMD-SMFF), the palaeontological collection of Staatliches Museum für Naturkunde, Karlsruhe (SMNK PAL), as well as the private collections of Manfred Keller, Frankfurt (MKF) and Klaus Weiß, Fischbach (KWF).

In certain cases (e.g., disarticulate specimens, difficult fossil beddings), a reference collection of recent fishes (cleared and stained materials, dried skeletons) was used to facilitate proper taxonomic identification. This collection is also deposited in the Department of Geology, Palaeontology and Mineralogy, Hessisches Landesmuseum Darmstadt (HLMD-SMFR). Information from the literature also was utilized.

RESULTS AND DISCUSSIONS

The synopsis of the fishfaunas presented herein (Table I) comprises all taxa that have been recorded to date. Concerning their relative frequencies, however, it must be stated that these data do not represent the 'real' composition of the ancient faunas. Firstly, the collections referred to herein are not results of systematic scientific excavations. Thus, they highly reflect personal interests of the respective collectors, who, e.g., probably preferred complete and large fish of rare species instead of disarticulated or isolated bones and specimens of the 'odd' ones, as well. Furthermore, as a well-known problem from analyses of more recent fish remains in archaeological sites (e.g., Torke, 1981), rarer taxa often are only proven by isolated bones and/or teeth. Therefore, it is difficult to calculate the number of specimens that really contributed to a fossil record under discussion. Lastly, but not least, and especially concerning the Frauenweiler locality, certain parts of the stratigraphical section are less represented in the synopsis due to current quarrying activities and also due to the collector's preference of those layers that are ex-

pected to bear more spectacular fossils. In consequence, with respect to the synopsis under discussion, it is generally more important to look at the presence or absence of the different taxa, than at their relative frequencies.

Concerning the elasmobranchs, it is clearly evident that sharks are well present in both deposits, although they are mostly represented by isolated teeth. Shark teeth, of course, are well suited to be represented in every fossil record because they are numerous and very stable. There are, however, also records of larger articulate body fragments from Froidefontaine (Pharissat, 1991) and, by merits of modern transfer preparation, some almost complete specimens are present in the Frauenweiler fossil record (SMNK, SKW; Micklich *et al.*, personal observations). Nine shark taxa plus one ray have been recorded from the new Frauenweiler clay pit to date. Seven additional ones were mentioned in literature but not found in the actual collections. Thus, there may be a total of 17 different taxa, which coincides well with the Oligocene elasmobranch fauna of the NW North Sea basin (e.g., Kruckow, 1965). In contrast, at most seven species of sharks and one ray are presently known from Froidefontaine. The difference of the elasmobranch diversity may simply be due to the fact that there still are current excavations in the Frauenweiler locality and that the materials were checked by shark specialists a short time ago. The basking shark, *Cetorhinus parvus*, is well represented in both localities, mainly by means of isolated barbels or bundles of barbels from the oral filter apparatus. These barbels occur in almost every horizon of both localities, an abundance that probably is due to seasonal changes in food preference (Cappetta, pers. comm.). As an exception, one specimen with several hundred barbels in situ was discovered from the Froidefontaine fossil site. Interestingly, *C. parvus* is the only elasmobranch species which may be representative of colder seas. Extant relatives of all other species share closer affinities to warm or temperate seas.

For the teleosts, recent investigations in both localities also give proof of a remarkable degree of diversification, that clearly exceeds that known from literature. 27 different taxa are probably present in the Froidefontaine fossil record. About 50 presently are known from current Frauenweiler collections and there are eight additional ones that were described or mentioned in the literature. Thus, overall diversity almost reaches that of the famous Maikop deposits in the Caucasus, e.g., as described by Daniltschenko (1960). However, there are striking differences concerning the general faunal compositions: in the latter localities, distinctively more species have already been described, e.g. from the Clupeiformes, Gadiformes, Carangidae and Scombroidei. Nevertheless, once again this partly may be an artifact, due to the preliminary state of more detailed investigations into the Froidefontaine and Frauenweiler ichthyofaunas.

TABLE I - Synopses concerning the ichthyofaunas of the Froidefontaine and Frauenweiler fossil sites (Oligocene, Rupelian stage). The species designation, especially concerning those described from the Carpathians and the Russian Palaeogene, is a preliminary one, because it is mainly based on the literature and not on direct comparisons with type materials. The arrangement of taxa is in systematic order, the classification follows Cappetta (1987) for the sharks and Nelson (1994) for the teleosts. Names in brackets [] are common synonyms.

| Genus/Species | Froidefontaine fossil site | Frauenweiler fossil site | Genus/Species | Froidefontaine fossil site | Frauenweiler fossil site |
|---|----------------------------|--------------------------|--|----------------------------|--------------------------|
| <i>Physogaleus</i> [<i>Eugaleus</i>] <i>latus</i> (Storms, 1894) | ++ | ++ | <i>Pristigenys spinosus</i> (Blainville, 1818) | +++ | +++ |
| <i>Physogaleus</i> [? <i>Alopiopsis</i>] <i>con-tortius</i> var. <i>bassiacae</i> (Jaekel, 1898) | | ? | cf. <i>Echeneis</i> Linnaeus, 1758 sp. | | + |
| <i>Galeocерdo medius</i> Wittich, 1898 | | ? | <i>Caranx glarisianus</i> (Agassiz, 1844) | +++ | |
| <i>Galeocерdo</i> Müller & Henle, 1838 sp. cf. <i>Rhizoprionodon</i> Whitley, 1929 sp. | | + | <i>Caranx</i> cf. <i>C. glarisianus</i> (Agassiz, 1844) | | +++ |
| <i>Synodontaspis acutissima</i> (Agassiz, 1844) | ++ | ++ | <i>Carangidae</i> sp. a [sensu Micklich & Parin, 1966] | | + |
| <i>Synodontaspis cuspidata</i> (Agassiz, 1844) | ++ | ++ | <i>Carangidae</i> sp. a b [sensu Micklich & Parin, 1966] | + | |
| <i>Alopias</i> [<i>Alopecias</i> , <i>Vulpecula</i>] <i>exigua</i> (Probst, 1874) | | ? | <i>Leiognathus altapinnus</i> (Weiler, 1955) | + | |
| <i>Alopias</i> [<i>Alopecias</i> , <i>Vulpecula</i>] <i>latidens</i> (Leriche, 1927) | | ? | <i>Pterycombus</i> Fries, 1837 sp. | | (+) |
| <i>Cetorhinus parvus</i> (Leriche, 1908) | ++++ | ++++ | <i>Sparus</i> cf. <i>S. schoptii</i> (Wittich, 1900) | + | + |
| <i>Isurus desori</i> (Agassiz, 1844) | + | + | <i>Sparidae</i> indet. | + | |
| <i>Lamna rupeliensis</i> (Le Hon, 1871) | (+) | + | <i>Trachinus minutus</i> (Jonet, 1958) | + | |
| <i>Carcharocles</i> [<i>Carcharodon</i>] <i>angustidens</i> (Agassiz, 1844) | + | ? | ? <i>Trachinus</i> Linnaeus, 1758 sp. | | + |
| <i>Notorhynchus primigenius</i> (Agassiz, 1844) | | + | ? <i>Archaephippus</i> Blot, 1969 sp. | | + |
| <i>Squalus alsaticus</i> (Andree, 1892) | | ? | <i>Sphyaena</i> Röse, 1793 n. sp. | | ? |
| <i>Squatina</i> [<i>Rhina</i>] <i>angeloides</i> (van Beneden, 1875) | | ? | <i>Gempylidae</i> indet. Sp. a (cf. <i>Gempylus</i> Cuvier, 1829 sp.) | | + |
| <i>Myliobatidae</i> n. gen. [<i>Myliobatis oligocaena</i> (Leriche, 1910), <i>Myliobatis serratus</i> von Meyer, 1843] | + | + | <i>Gempylidae</i> indet. Sp. b (cf. <i>Epinnula</i> Poey, 1854 sp.) | | + |
| cf. <i>Elops</i> Linnaeus, 1766 sp. | | + | <i>Gempylidae</i> indet. Sp. c [<i>Palimphyes elongatus</i> sensu Micklich & Parin, 1996] | | + |
| <i>Conger</i> Bosc, 1817 sp. | | (+) | <i>Gempylidae</i> indet. [after A. Bannikov, recent communication] | + | |
| <i>Neohalecopsis</i> Weiler, 1928 sp. | + | | <i>Lepidopus glarisianus</i> (Blainville, 1818) | ++ | ++ |
| <i>Clupeidae</i> indet.* | ++++ | ++++ | <i>Trichiuridae</i> indet. n. sp. [Micklich <i>et al.</i> , ms. submitted] | | + |
| <i>Alosa sculptata</i> (Weiler, 1920) | | ? | <i>Eutrichiurides</i> [<i>Trichiurides</i>] <i>delbeidi</i> (Leriche, 1910) | | ? |
| <i>Eophycis froidefontainensis</i> Pharissat, 1991 | + | | <i>Scomber</i> Linnaeus, 1758 sp. | | + |
| <i>Eophycis</i> Jerzemska, 1968 sp. | | (+) | <i>Scomberomorus</i> [<i>Cybium</i>] <i>lingulatus</i> (H.v. Meyer, 1846) | + | + |
| <i>Palaeogadus arambourgi</i> (Théobald, 1934) | + | | <i>Scomberomorus</i> [<i>Cybium</i>] <i>dumonti</i> (Van Beneden, 1871) | + | |
| <i>Palaeogadus emarginatus</i> Koken, 1891 | | ? | <i>Scomberomorus</i> [<i>Cybium</i>] Lapepède, 1801 sp. | + | |
| <i>Palaeogadus</i> cf. <i>P. intergerinus</i> Daniltshenko, 1947 | | ? | <i>Scomberidae</i> (<i>Scomberomorini</i>) indet. sp. a [Micklich <i>et al.</i> , ms. submitted] | | + |
| <i>Palaeogadus</i> Rath, 1859 sp. | | ++ | <i>Scomberidae</i> (<i>Scomberomorini</i>) indet. sp. b [Micklich <i>et al.</i> , ms. submitted] | | + |
| <i>Hemiramphus jerzyi</i> Jerzemska, 1985 | | + | <i>Sarda brachycephala</i> (Leriche, 1908) | ++ | +++ |
| ♀ <i>Belone</i> sp. sensu Weiler, 1966 | + | + | <i>Scomberidae</i> (<i>Sardini</i>) indet. sp. c [<i>Scomber</i> sp. b / cf. <i>Scombrsarda</i> sensu Micklich & Parin, 1966] | | ++ |
| <i>Capros radobojanus</i> (Kramberger, 1882) | + | + | <i>Scombrampodon</i> Woodward, 1901 sp. | | ? |
| <i>Capros</i> Lapepède, 1802 sp. [<i>C. longispinatus</i> sensu Micklich & Parin, 1966] | | (+) | <i>Sphyaenodus</i> Agassiz, 1839 sp. | + | + |
| <i>Doryrhamphus</i> [<i>Acanthognathus</i>] <i>fredericae</i> (Pharissat, 1991) | ++ | | <i>Scomberidae</i> indet. sp. d [Micklich <i>et al.</i> , ms. submitted] | | + |
| <i>Doryrhamphus</i> [<i>Acanthognathus</i>] Kaup, 1856 sp. | | ++ | <i>Scomberidae</i> gen et sp. indet. [sensu Pharissat, 1991] | + | |
| <i>Microphis</i> Kaup, 1853 sp. | | (+) | <i>Palaeorhynchus glarisianus</i> (Blainville, 1818) | ++++ | ++ |
| <i>Syngnathus incompletus</i> Cosmovici, 1886 | (+) | (++) | <i>Glyptorhynchus</i> Leriche, 1908 sp. | + | |
| <i>Syngnathus</i> Linnaeus, 1758 n. sp. | | + | <i>Xiphias rupeliensis</i> (Leriche, 1908) | | ? |
| <i>Nepigastrosyngnathus micheli</i> Pharissat, 1993 | + | | <i>Scombroidei</i> indet. [Micklich <i>et al.</i> , ms. submitted] | | + |
| <i>Aulostomus medius</i> (Weiler, 1920) | ++ | ++ | ? <i>Psenicubiceps</i> Daniltshenko, 1980 sp. | | + |
| <i>Frauenweilerstomus synarcualis</i> (Parin & Micklich, 1996) | (+) | + | <i>Pinichthys</i> cf. <i>P. pulcher</i> (Bannikov, 1985) | | + |
| <i>Oligosphenopsis</i> cf. <i>O. gracilis</i> (Parin, 1992) | | + | <i>Perciformes</i> (? <i>Percoides</i> ? <i>Scombroidei</i>) indet. [Micklich <i>et al.</i> , ms. submitted] | | + |
| <i>Aeoliscus heinrichi</i> (Heckel, 1850) | ++++ | ++++ | <i>Psettoidoidei</i> indet. [? <i>Psettodes</i> n.sp. Weiler, 1966] | ? | |
| <i>Aeoliscus distinctus</i> (Micklich & Parin, 1996) | (+) | + | <i>Pleuronectoidei</i> indet. sp. a [? <i>Solea</i> n.sp. Weiler, 1966] | | + |
| cf. <i>Sebastes</i> Cuvier 1829 [<i>Scorpaena</i> sp. sensu Weiler, 1928] | | + | <i>Pleuronectoidei</i> indet. sp. b | | + |
| <i>Percoides</i> indet. [" <i>Serranus</i> " sp. sensu Micklich <i>et al.</i> , ms. submitted] | (+) | + | | | |
| <i>Dicentrarchus</i> Gill, 1860 sp. | | (+) | | | |
| <i>Properca sabbai</i> Pauca, 1929 | +++ | + | | | |
| <i>Serranus budensis</i> (Heckel, 1856) | +++ | +++ | | | |

+, present (single or rare in recent records); (+), probably present (genus/species not yet proved with certainty); ?, possibly present (not known from recent collections but mentioned or described in literature); ++, not rare (up to twenty specimens, approximately); +++, abundant (dozens of specimens); +++++, very abundant (hundreds of specimens); *, according to Grande (personal communication), the best way to resolve the confusion concerning the systematic state of the species that were designated *Clupea sardinites* (Heckel, 1850) or *Sardinella sardinites* (Heckel, 1850), otherwise.

This may best be exemplified by the Gasterosteiformes (Syngnathoidei): here, actual results are available from a joint Russian-German research project, and the fossil record of the latter W-Paratethys localities have been shown to be just as diverse as that of the correspondent localities in the Carpathian (Jonet, 1949, 1958; Rozhdestvensky, 1949a, Jerzmanska, 1968; Ciobanu, 1977) and Russian (Rozhdestvensky, 1949b, 1950; Daniltshenko, 1960, 1962; Parin, 1992a,b,c) Palaeogene. This diversity is one of the most typical characteristics of both Rupelian fishfaunas and may serve as a good argument for the postulation of connections of the ancient seas in the Rhine Valley System with the S.E. Paratethys. In both localities, Centriscids are the most frequent Syngnathoidei. Here, *Aeoliscus heinrichi* (Fig. 2) is the most common species, which in general is widespread over all tertiary Tethys Sea fish localities. More than 5000 well-preserved specimens are, for example, deposited in the Froidefontaine collection of the G. Cuvier Museum in Montbeliard (Pharisat, 1991, 1992, 1993) and about 200 specimens from the palaeontological collection of the Hessisches Landesmuseum so far were included in recent Frauenweiler investigations. A second species, *A. distinctus* (Fig. 3), which probably is also present within the Froidefontaine materials, was described a short time ago (Micklich & Parin, 1996). An addition to the Centriscidae, the Syngnathidae also are comparatively abundant in both fossil sites. Extant members of this family are characterized by a large amount of intra-generic and intraspecific variation. Thus, the identification of fossil species is difficult. Nevertheless, seven extinct genera have already been described in the literature (Daniltshenko, 1960; Jerzmanska, 1968; Sergienko, 1971; Blot, 1980; Fritzsche, 1980; Pharisat, 1991, 1992, 1993; Parin, 1992a,b). At present, only three genera with about six species are present in Froidefontaine and Frauenweiler. As already discussed by Micklich & Parin (1966), the extant genus *Microphis* comprises species that enter fresh water. The probable presence of a fossil representative in the Frauenweiler fossil record, therefore, also may be indicative of coastal or freshwater influence. It is almost the same situation concerning the halfbeak species *Hemiramphus jerzyi*

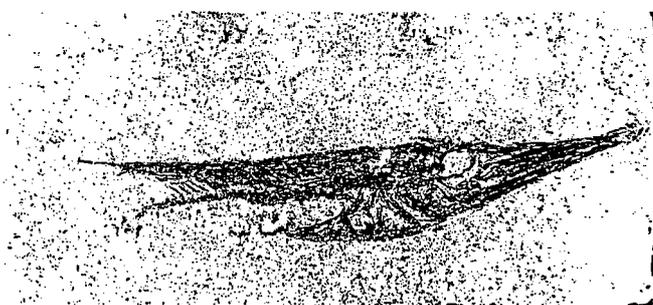


Fig. 2 - *Aeoliscus heinrichi* (Heckel, 1850), from Froidefontaine. Specimen A.FR.AP. 1131a, 33 mm standard length.

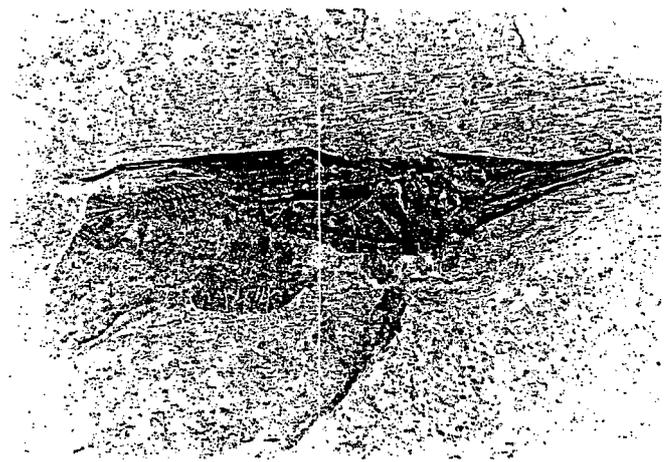


Fig. 3 - *Aeoliscus distinctus* Parin & Micklich 1996, from Frauenweiler. Specimen HLMD-SMFF 6 (Paratype), 52 mm standard length.

(*H. georgii* is a synonym; see Jerzmanska, 1985), where extant species live in estuaries or fresh water. The trumpetfishes (Aulostomidae) are also present in both W-Paratethys fossil sites. They are mainly represented by the common species *Aulostomus medius*. Nevertheless, once again, a new species, *Frauenweilerstomus synarcualis*, was recently discovered within the new materials from the Frauenweiler clay pit (Micklich & Parin, 1996; Parin & Micklich, 1996), and is also expected to be present in the Froidefontaine fossil record. The Urosphenidae at present are only known by a few imprints within the Frauenweiler material. They appear to be close to *Oligosphenopsis gracilis* from the Lower Oligocene of the North Caucasus (Parin, 1992a,b).

The percoids also are well represented in the Froidefontaine and Frauenweiler fossil sites, with a slightly larger diversity in the latter locality: Moronidae, Bramidae and Ehippidae, for example, are described from recent Frauenweiler collections, but have not yet been found in Froidefontaine. As indicated by Micklich & Parin (1996) and further stressed by recent investigations (Micklich *et al.*, unpubl. data) additional taxa are present, e.g., within the small-sized presumed percoids and also within the other material formerly defined as *Serranus*. In Froidefontaine, *Properca sabbai* and the bigeyes *Pristigenys spinosus* are mostly represented by very small specimens (about 7 mm standard length), which probably are larvae comparable to the nepionic stages of recent Serranidae (e.g., *Serranus scriba*) of the Mediterranean Sea (Banarescu, 1964; Pharisat, 1991). By contrast, *Properca* seems to be rare in Frauenweiler (Micklich *et al.*, unpubl. data). *Pristigenys* is also dominated by small-sized specimens but larvae less than 1 cm standard length have not yet been found.

Scombroids also are frequent and well-diversified in both W-Paratethys fossil sites. Certain taxa mainly occur in particular stratigraphical sections: "*Lepidopus layers*",

"*Palaeorhynchus layers*" (Pharisat, 1991; Micklich & Parin, 1996). Within the Froidefontaine clay pit, the scabbardfish *Lepidopus glarisianus* is present with very young specimens, e.g., of 28 mm standard length for the smallest individuals. Such juvenile stages, however, are not yet described from the Frauenweiler locality, where the *Lepidopus* materials frequently comprise larger specimens, which are about 30 cm in standard length or even larger. Trichiuridae probably are a meso- or bathypelagic element and it is interesting to note that the Frauenweiler fauna (two species) is more diverse than that of Froidefontaine (one species). Three different species of Gempylidae are probably present in Frauenweiler and only one in Froidefontaine (after A. Bannikov, personal communication, *Palimphytes elongatus* aus Froidefontaine correspond to any genus of Gempylidae).

The Scombridae are in both deposits represented by mackerels and tunas. As indicated by recent investigations, they are very well diversified in Frauenweiler, where they comprise a total of about eight different taxa (Micklich *et al.*, unpubl. data). The scombrid records, however, mainly consist of disarticulated heads, isolated teeth, hypural plates and larger, articulated fragments of caudal supports. Distinctively more rare are complete specimens. In Frauenweiler, these are known from at least four different species, whereas in Froidefontaine, complete materials are only known from *Sarda brachycephala* (Pharisat, 1991). These are very similar to those described from the Entlebuch locality in Switzerland by Fröhlicher & Weiler (1952). Scombrids in general are more abundant in the upper layers of the Froidefontaine clay pit, where, for example, several medium sized, well-preserved specimens of the latter species were found. In Frauenweiler, the complete materials appear to be more confined to the lower parts of the stratigraphical section, which, however, may well correspond with those of Froidefontaine because of the peculiar mining situation.

Palaeorhynchus glarisianus, may be close to the xiphiids (Schultz, 1987) and therefore could be considered as an epipelagic or mesopelagic element (Nakamura & Parin, 1993). The species is abundant and frequently very well preserved in the Froidefontaine fossil record. There are more than 300 specimens in the Cuvier collection, which range from 24 cm to 180 cm in standard length. They frequently exhibit delicate morphological details such as the lateral line scales and the minute oral teeth (Pharisat, 1991). In contrast, this species is less frequent in the Frauenweiler fossil record, and also more represented by smaller specimens up to 40 cm in standard length. *Glyptorhynchus* and *Xiphias* also are billfishes, and may be representatives of offshore waters. Both families, however, at present are based on poor and somewhat questionable records, which, e.g., are only mentioned in the literature for the Frauenweiler locality (Weiler, 1966).

CONCLUSIONS

As already indicated previously (e.g., Micklich & Parin, 1996), the comparatively low diversification of the Froidefontaine and Frauenweiler fishfaunas known from the literature (Sauvage, 1870; Wagner-Klett, 1919; Weiler, 1931; Theobald, 1934; Weiler, 1966; Faivre, 1969) may mainly be due to poorly and inadequately prepared materials and less careful excavations. The rich new materials clearly indicate well-diversified faunas and lead to reconstructions of the palaeoenvironment that differ from the scenarios described in the past. The most important new results and faunal characteristics are: 1) The results of the recent investigations into the new materials from the Froidefontaine fossil site are in good correspondence with those of the Frauenweiler materials (Micklich & Parin, 1996; Micklich & Hovestadt, unpubl. data). 2) The overall diversity within both fishfaunas is not less than that described from contemporary localities in the Carpathians and the Russian Palaeogene. 3) The differences in the respective faunal compositions in part may simply be due to the preliminary state of investigations into more recent and better preserved materials of the localities in the Rhine Valley System. They are, of course, also due to the different palaeoecological and palaeobiogeographical situations. 4) Aside the similarity of the Froidefontaine and the Frauenweiler ichthyofauna mentioned above, there also are certain differences: the benthic/mesopelagic affinities, e.g., are clearly more evident in the latter locality. The Froidefontaine fauna, in contrast, is fundamentally neritic and littoral, with a spawning zone but also offshore connections. Conversely, there is a predominance of taxa with presumed southern relationships in Froidefontaine, whilst northern relationships are more evident in Frauenweiler. The latter differences are probably due to the different geographical positions: colder seas from the north may have more strongly affected the Frauenweiler fauna than that of Froidefontaine, which was in closer contact with warmer seas from the S-E Paratethys. In addition, the difference concerning the length frequency distribution or the general abundance of certain taxa, their developmental stages respectively (e.g., *Lepidopus* and *Palaeorhynchus* populations), across both stratigraphical profiles also are very probably due to palaeoenvironmental shifts and very much worthwhile of more detailed investigations.

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