FIRST EVIDENCE OF AN EARLY MIOCENE MARINE TELEOSTEAN FISH FAUNA (OTOLITHS) FROM LA PAILLADE (MONTPELLIER, FRANCE)

by

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ABSTRACT

A fossil fish fauna, based on 5533 otoliths, from the La Paillade locality at Montpellier is described and figured. The otolith-bearing marls correlate to mammal zone MN 1 (Aguilar, 1982), and thus represent the earliest Miocene. The fish fauna consists of 30 taxa belonging to 20 families. Two species are new: *Dussumieria sittigi* and *Liza gaudanti*. The predominant faunal element is the *Lesueurigobius vicinalis*-species complex, composing 73% of all investigated otoliths. The palaeoecological analysis reveals a marine to euryhaline fish fauna living under tropical to subtropical conditions in the transition zone littoral - sublittoral. Water depth probably was more than 10 m. The scarcity of pelagic fishes suggests that the habitat was either a sheltered bay and/or far away from the open sea. Furthermore, some genera represented in the La Paillade fish fauna presently live exclusively in the Indopacific realm. Their presence strongly supports a broad connection between the Indian Ocean, the Mediterranean, and the Paratethys Seas during the Early Miocene (Aquitanian). From a palaeobiogeographical point of view, faunal relationships were found between the La Paillade fish fauna and both the Paratethys fish fauna and the fish fauna from the deposits in the Upper Rhinegraben and the Mayence and Hanau Basins (Germany).

RESUME

Une faune de poissons fossiles, de la localité de La Paillade, près de Montpellier, est décrite et figurée, sur la base de 5533 otolithes. Les marnes à otolithes se corrèlent avec la zone mammalienne MN 1 (Aguilar, 1982), et représente le Miocène le plus inférieur. La faune de poissons comprend 30 taxa appartenant à 20 familles. Deux espèces sont nouvelles: *Dussumieria sittigi* nov. sp. and *Liza gaudanti* nov. sp. L'élément dominant de la faune est le complexe d'espèces *Lesueurigobius vicinalis*, totalisant 73% des otolithes étudiées. L'analyse paléoécologique révèle une faune marine à euryhaline vivant dans des conditions tropicales à subtropicales, dans la zone de transition littorale-sublittorale. La profondeur d'eau était probablement supérieure à 10 m. La rareté des poissons pélagiques suggère que l'habitat étatit ou bien une baie abritée et/ou éloigné de la mer ouverte. De plus, certains genres présents dans la faune de poissons de La Paillade vivent actuellement exclusivement en domaine Indo-Pacifique. Leur présence supporte fortement une large connection entre l'Océan Indien, la mer Méditerranée et la Paratéthys au cours du Miocène basal (Aquitanien). D'un point de vue paléogéographique, des relations fauniques ont été trouvées entre la faune de poissons de La Paillade et à la fois les faunes de poissons des dépôts du Bassin du Rhin supérieur et des Bassins de Mayence et de Hanau (Allemagne).

INTRODUCTION

Fish otoliths are common (micro)fossils in Cenozoic marine and brackish deposits and also occur in lacustrine sediments. Fish otoliths consist primarily of aragonite, and for this reason, they often are somewhat corroded in sandy deposits. They are best preserved in clayey marls. Size differs between 0.5 mm up to 10 mm and more, but most fossil otoliths are rather small (0.5-4 mm) deriving from fishes which were only about 10 cm to 15 cm long (cf. Nolf, 1995: 517).

Bony fishes (teleostean) have three pairs of otoliths located in the labyrinths which are in the back part of the skull. In most actinopterygians, the largest otolith is called the sagitta. The sagittae can be used for species identification and also for age determination because of its size and morphological characteristics (Koken, 1884). However, taxonomic determination of fossil otoliths requires a good knowledge of the sagittae from Recent fishes. Such studies have been done by several authors, e.g., Chaine & Duvergier (1934), Chaine (1935-1938), Härkönen (1986), Nolf (1985) and Smale *et al.* (1995).

Fossil fish otoliths allow the reconstruction of fossil fish faunas even if no skeletal remains have been found. For this reason, fish otoliths have contributed greatly to our knowledge of fossil fish faunas. According to Patterson (1993), 58 families (24%) of the 244 extant teleost families known as fossils are exclusively recorded from otoliths (cf. Nolf, 1995: 533). In addition, fossil otoliths contribute to our knowledge on the palaeoecology, palaeobathymetry, palaeogeography and biostratigraphy of fossil fishes (e.g. Nolf, 1995; Stringer, 1998a).

The present study describes otoliths from the early Miocene of southern France. The sediments yielding the otoliths also contained micromammals that allowed exact age determination of the deposit (mammal unit MN 1, see below). In addition, we analysed the palaeoecology (climate, salinity, bathymetry) and the palaeobiogeography by comparisons to extant species and discussed some palaeogeographic implications. The fish fauna presented here is the first neritic teleost fish fauna from the earliest Miocene of the Mediterranean realm (cf. Reichenbacher, 1997: 197).

LOCATION AND STRATIGRAPHY

Near Marseille and Montpellier (Fig. 1), marginal-marine sedimentation areas were created by the "Aquitanian" transgression during the late Oligocene and the earliest Miocene. The deposits are limestones and marls with intercalated sands and fine gravels and contain rare mollusc shells.

At Montpellier, a well known site is the locality La Paillade where the sediments were mainly exposed during house constructions in the 1960's. The section was described by Cappetta (1970: 6, Fig. 2). In this locality, Jurassic sediments disconformably underlie about 1 meter white nonfossiliferous marls. This layer is

overlain by a 0.6 meter thick sequence of first white, then black and greenish marls bearing numerous mollusc shells, mammal teeth, and fish otoliths. A very thin layer with coquina of freshwater and terrestrial molluscs follows. Upsection, the sequence grades into 6 meters of thick brown and blue marls containing marine molluscs, shark teeth, and again otoliths. The mammal fossils in the basal marls correlate to mammal unit MN 1 corresponding to the early Miocene (Aguilar, 1982; de Brujin, 1992: Tab. 1; Steininger *et al.*, 1996: 24). The otoliths described in the present study all come from the basal marls that also yielded the mammals.

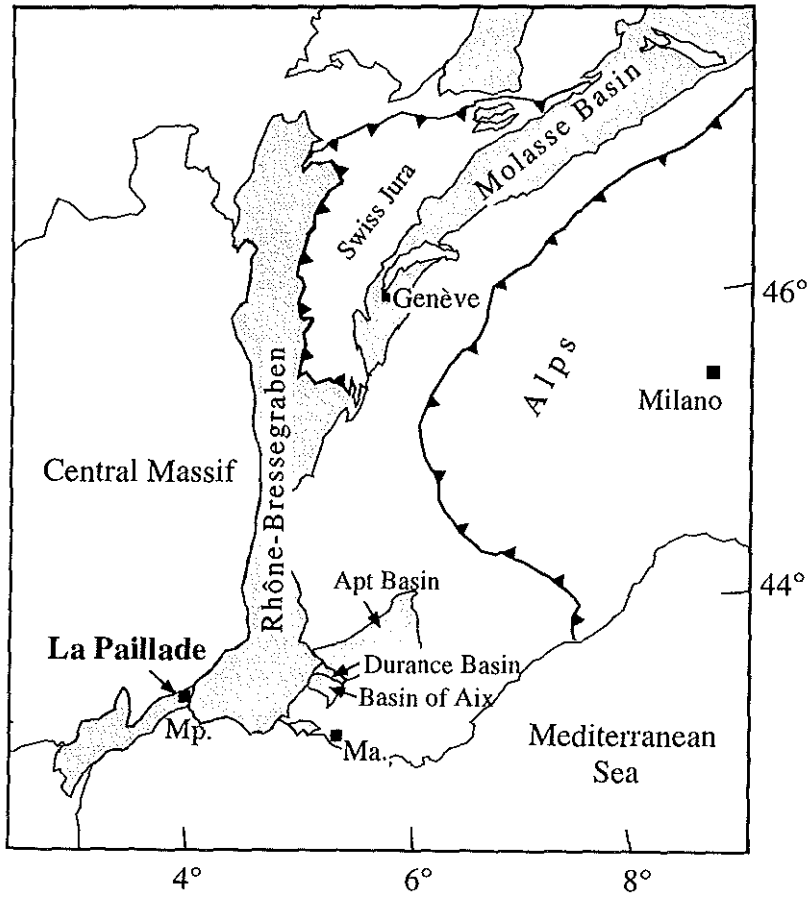

Figure 1.— Location of the otolith-bearing site La Paillade at Montpellier, southern France. Oligo-Miocene depositional areas are marked in grey. Mp. = Montpellier. Ma. = Marseille.

METHODS

Samples were processed with a mixture of H_2O and a 35 percent H_2O_2-solution, by washing and sieving (smallest screen 0.5 mm). Consequently, the otoliths were picked under a binocular microscope. Several hundred kg of sediment were washed, sieved, and picked by one of the authors (H.C.). The otoliths were identified using a

binocular microscope and were then figured by SEM pictures (Plates 1-3, otoliths smaller than 5 mm) or Pentax reflex camera (Plates 4-6, otoliths larger than 5 mm). For a detailed methodology of processing samples for otoliths see also Stringer & Breard (1997).

SYSTEMATIC PART: DESCRIPTION OF THE FISH OTOLITHS

All described otoliths come from the fossiliferous basal marls at La Paillade near Montpellier. They are deposited in the collections of the Laboratory of Palaeontology, University Montpellier II, under the catalogue numbers PLD 51 to PLD 115.

In the following systematic description, some information is also given concerning the ecology and biogeography of Recent species and/or families, related to the fossil taxa. These data are compiled from Allen (1989), Cohen & Nielsen (1978), Lee *et al.* (1980), Lévèque *et al.* (1990), Nelson (1994), Smith & Heemstra (1986), Sterba (1990), Villwock (1977, 1994), Whitehead (1985) and Whitehead *et al.* (1986).

Except for the utricular otoliths (lapilli) (see Pl. 1, Fig. 10), all studied otoliths are otoliths of the saccula, termed sagittae. The terminology of the inner face of a sagitta is shown in Pl. 6, Fig. 1.

Order **ELOPIFORMES**
Family **ELOPIDAE** BONAPARTE, 1846
Genus ***ELOPS*** LINNAEUS, 1758

Recent ecology and biogeography: Mainly marine, tropical and subtropical, not in the Mediterranean Sea. *Elops* is the only genus of the family. Two of the six Recent *Elops* species live along the West African coast and also dwell in lagoons and lower courses of rivers.

"genus aff. ***Elops***" sp.
(Pl. 5, Fig. 7)

Material: 2 sagittae.

Description

Sagittae of elongate shape with a slightly convex inner face and a slightly concave outer face dorsally thickened. The dorsal and ventral rims are smooth and faintly rounded; a posterodorsal angle is present. The posterior rim is rounded and finely crenulated. The long, supramedian sulcus is slightly bent and runs nearly parallel to the dorsal rim; the small ostium is slightly deepened, the long cauda tapering terminally. The crista inferior is obtuse and becomes oblique towards the cauda. The thin crista

superior is little accentuated and, when reaching the ostium, rises steeply to the dorsal rim.

Dimensions: Length: 8.5 mm, 7.6 mm; height: 4.0 mm, 3.65 mm; thickness 1.1 mm, 1.3 mm; l/h: 2.1.

Recent relations: "genus aff. *Elops*" sp. resembles sagittae of Recent *Elops* species because of its elongate shape and the long, convex curved sulcus. From the six Recent *Elops* species, the sagittae of the Pacific species *E. hawaiiensis* REGAN, 1909 (Pl. 5, Fig. 9) and *E. saurus* LINNAEUS, 1766 (Pl. 5, Fig. 8) show the most similarities with the fossil species.

Fossil relations: Two fossil *Elops* species have been described from Tertiary deposits. Compared with "genus aff. *Elops*" sp., *E. undulatus* STINTON, 1966 from the Lower Eocene of southern England has a much more rounded ventral rim, and *E. ramaekersi* SCHWARZHANS, 1986 from the Palaeocene or Lower Eocene of northern Canada shows a straight cauda and strongly notched rims. Furthermore, Weiler (1942) described the new species "Ot. (Percidarum) *elongatus*" from the Oligocene of the Hanau Basin (Germany). This species belongs also to the Family Elopidae. It differs from "genus aff. *Elops*" sp. by the straight sulcus and the more elongate shape.

Order **CLUPEIFORMES**
Family **CLUPEIDAE** CUVIER, 1817
Genus ***DUSSUMIERIA*** VALENCIENNES, 1847

Recent ecology and biogeography: The only Recent species of the genus *Dussumieria* are *D. acuta* VALENCIENNES, 1847 (see Pl. 1, Fig. 1) und *D. elopsoides* BLEEKER, 1849. They are marine pelagic fishes living in the Indopacific.

Dussumieria sittigi n. sp.
(Pl. 1, Figs. 2-5)

v 1969 *Alosa* sp. - Cappetta, p. 218, Pl. 21, Fig. 63, Pl. 23, Figs. 2-7.

Material: 15 sagittae.

Holotype: Right sagitta (Pl. 1, Fig. 4) (PLD 53).

Paratypes: 14 sagittae, three of them figured (Pl. 1, Figs. 2-3, 5) (PLD 51-52, 54).

Type locality: La Paillade at Montpellier, southern France; Lower Miocene, early Aquitanian, mammal unit MN 1.

Etymology of name: This species is dedicated to Prof. Dr. E. Sittig (Karlsruhe, Germany) who always has supported the studies of one of the authors (B.R.).

Diagnosis: Sagittae of elongate, nearly rectangular shape with a somewhat undulant dorsal rim, a faintly rounded, crenulated ventral rim, and a prominent rostrum.

Description

The shape of the sagittae is somewhat tapering to the front. The deepest notch of the ventral rim is situated beneath the collum. The sulcus is deep, wide, and clearly divided into ostium and cauda because of a distinct bend in the crista superior. The ostium is as long as the cauda or slightly longer. The thickened crista inferior abruptly ends before reaching the end of the cauda; the crista superior is less accentuated.

Dimensions: Holotype: Length: 3.0 mm; height: 1.8 mm; thickness: 0.7 mm; l/h: 1.7; paratypes: Length: 0.9-2.15 mm; height: 0.55-1.15 mm; thickness: 0.15-0.3 mm; l/h: 1.6-1.8.

Recent relations: *Dussumieria sittigi* n. sp. looks similar to sagittae of Recent *Dussumieria* species (see Pl. 1, Fig. 1) because of its shape, the curvature of its ventral rim, and the dimensions of the sulcus. In contrast to the Recent species, the ostium of the fossil species is wider, and the ventral rim notched differently.

The genus *Etrumeus* belongs, as does *Dussumieria*, to the Subfamily Dussumieriinae. However, the sagittae of *Etrumeus* species are different from the new fossil species because their shape becomes distinctly elongate anteriorly.

Fossil relations: From Upper Eocene estuarine deposits of southern England, *Dussumieria amussa* STINTON, 1977 is known, but it has a more rounded shape than the new species. Furthermore, Steurbaut (1984) described "genus aff. *Dussumieria*" sp. from the Burdigalian of the Aquitaine Basin. Compared with the new species, this species does not have as prominent a rostrum, and its ventral rim is more finely crenulated.

Order **ESOCIFORMES**
Family **UMBRIDAE** BLEEKER, 1859
(= **PALAEOESOCIDAE** SYTCHEVSKAYA, 1976; see Patterson 1993: 628)
Genus ***PALAEOESOX*** VOIGT, 1934

Palaeoecology and palaeobiogeography: The extinct genus *Palaeoesox* is known from Eocene to Miocene freshwater or slightly brackish deposits in Europe (cf. Reichenbacher & Mödden, 1996: 94). Recent Umbrid species live exclusively in freshwater and are distributed in the northern hemisphaere.

Palaeoesox sp.
(Pl. 3, Fig. 16)

Material: 2 sagittae.

Description

The shape of the sagitta is rectangular with rounded angles. The inner face is flat, the outer face posteriorly thickened and with a vertical groove running from the middle of the dorsal rim. The slightly rounded dorsal rim is somewhat undulated. The ventral rim is smooth, a prominent rostrum is present. The sulcus shows the characteristic shape

of *Palaeoesox* species running from submedian (anteriorly) to supramedian (posteriorly) and is divided into a large, V-shaped deep ostium and a narrow, less deepened cauda filled with colliculi. The accentuated crista inferior follows the cauda and partly the lower ostial rim; a crista superior seems to be not present.

Dimensions: Length: 1.03, 1.2 mm; height: 0.80, 0.97 mm; thickness: 0.31, 0.37 mm; l/h: 1.29, 1.24.

Recent relations: The Recent Umbridae species *Novumbra hubbsi* (BEAN, 1880) shows some similarity to this fossil species (see Reichenbacher & Mödden, 1996: Pl. 3, Fig. T). However, the Recent species differs because of its straighter sulcus and shorter cauda. Also, its rostrum is not as prominent. Since *N. hubbsi* lives only on the Olympic Peninsula of Washington, near the Pacific coast, a relationship to the fossil species from La Paillade is not very likely. Maybe the similarity of both species comes from a convergent way of life.

Fossil relations: *Palaeoesox* sp. has some similarities to *P. oligocenicus* REICHENBACHER & PHILIPPE, 1997 from the late Lower Oligocene of the Apt Basin (Vaucluse, southern France) and to *P. longirostratus* (REICHENBACHER, 1992) from the Upper Oligocene of the western Paratethys (Switzerland). However, the La Paillade species has a more elongate shape and a longer, less rounded dorsal rim as the above mentioned species. Probably, *Palaeoesox* sp. belongs to a new species, but on basis of only two sagittae, a good diagnosis is not possible.

Order **AULOPIFORMES**
Family **SYNODONTIDAE** GILL, 1872
Genus *SAURIDA* VALENCIENNES, 1849

Recent ecology and biogeography: The genus *Saurida* mainly is living in the Indopacific. *Saurida* species are not present in the Recent native Mediterranean fish fauna. The existence of *S. undosquamis* (RICHARDSON, 1848) in the Mediterranean Sea results from its immigration through the Suez Canal. *S. gracilis* (QUOY & GAIMARD, 1824) and *S. undosquamis* are distributed in a water depth up to 100 m, most other *Saurida*-species are living up to 550 m in water depth.

Saurida sp.
(Pl. 2, Fig. 6)

Material: 1 sagitta.

Description

A sagitta of elongate shape, somewhat wedge-shaped. The inner face is convex; the outer face thickened and has three humps near the dorsal rim. The dorsal rim is rounded and undulated; the posterior rim pointed. The ventral rim first drops steeply from the posterior rim, then is straight, and finally rises again towards the rostrum. The sulcus is straight, narrow and shallow. The division into ostium and cauda is not very

distinct because of the preservation of the sagitta, but the ostium seems to be somewhat shorter than the cauda.

Dimensions: Length: 2.5 mm; height: 1.25 mm; thickness: 1.0 mm.

Recent relations: *Saurida* sp. has a less elongate shape but the same sulcus morphology as Recent *Saurida* species (see Pl. 5, Fig. 12; Nolf, 1985: Fig. 46I; Nolf & Stringer, 1992: Pl. 10, Figs. 24-27).

Fossil relations: *Saurida germanica* (WEILER, 1942) from the Lower and Middle Miocene of the North Sea Basin and the Aquitaine Basin (cf. Nolf & Smith, 1983: 90; Steurbaut, 1984: 49) shows a more elongate shape than the present sagitta. Additionally, *S. rectilineata* was described as a new species by Steurbaut (1979: 59) from the Middle Miocene (Marnes de Saubrigue) of the Aquitaine Basin. Later, this species was interpreted as a synonym of *S. germanica* by the same author (Steurbaut, 1984: 49). In fact, by studying the originals of both species (coll. IRSNB), it was evident that the holotype of *S. rectilineata* corresponds well with *S. germanica*. However, the smaller paratype of *S. rectilineata* has a less elongate shape and is very similar to the here described *Saurida* species from La Paillade. Since both sagittae are relatively small it can not be decided yet, whether the differences are caused by ontogenetic variability or if a new fossil *Saurida* species is present.

Order **OPHIDIIFORMES**
Family **OPHIDIIDAE** RAFINESQUE, 1810
Genus ***SIREMBO*** BLEEKER, 1858

Recent ecology and biogeography: Generally, Recent Ophidiidae have a bathyal benthonic way of life and only a few species are pelagic. During the Palaeogene, neritic Ophidiidae living on soft substrate were much more common than today. For this reason, Recent Ophidiidae are thought to be a relic of a formerly larger and more diverse family (cf. Nolf, 1985: 64). *Sirembo* is a marine genus living in the Red Sea and the Indopacific in a water depth up to 200 m.

Sirembo sp.
(Pl. 5, Fig. 11)

Material: 1 sagitta.

Description

A thick, ovate sagitta with convex, smooth inner face and thickened outer face with some humps. The wide, slightly deepened sulcus covers nearly the whole inner face. The lower rim of the sulcus shows an angle allowing to separate the sulcus in a longer front part (ostium) and a shorter back part (cauda).

Dimensions: Length: 5.3 mm; height: 3.9 mm; thickness: 2.4 mm; l/h: 1,35.

Recent relations: Concerning its sulcus and shape, *Sirembo* sp. corresponds well with

sagittae of Recent *Sirembo* species, for example with the Indopacific *S. jordani* (DAY, 1888) (see Pl. 5, Fig. 10) or with *S. everriculi* WHITLEY, 1936 (see Schwarzhans, 1981: Fig. 24). *Sirembo* sp. differs from these species mainly because of its less developed angle at the lower rim of the sulcus.

Also, there is some affinity to the genus *Petrotyx* HELLER & SNODGRASS, 1903 (cf. Schwarzhans, 1981: Fig. 25) which is yet to be described as a fossil. *Sirembo* sp. described by Steurbaut & Jonet (1981: Pl. 1, Fig. 24) from the late Lower Miocene of southern Portugal probably belongs to this genus. However, the sulcus of *Petrotyx* species does not cover the whole length of the sagitta as the sulcus of *Sirembo* does.

Fossil relations: Fossil *Sirembo* species are described as *S. boettgeri* (KOKEN, 1891) and *S. obotritus* (KOKEN, 1891) from the Upper Oligocene of Northern Germany. Compared with *Sirembo* sp., both species are characterized by their more narrow sulcus. Furthermore, *S. boettgeri* has a more elongate shape (l/h-index 1.65) and *S. obotritus* has a prominent posterodorsal angle (see Koken, 1891: Pl. 1, Figs. 5-6, there as *Ophidiidarum*; Müller, 1996: Pl. 4, Figs. 4a-c). Since we have only one sagitta of *Sirembo* sp., we do not introduce a new species.

Order MUGILIFORMES
Family MUGILIDAE CUVIER, 1829
Genus *LIZA* JORDAN & SWAIN, 1884

Recent ecology and biogeography: Marine euryhaline fishes of tropic and subtropic seas. Often dwelling in estuaries and lagoons.

Liza gaudanti n. sp.
(Pl. 1, Figs. 6-9)

v 1980 "genus Mugilidarum" sp. - Nolf & Cappetta, p. 13, Pl. 3, Figs. 5-9.

Material: 40 sagittae and numerous fragments.

Holotype: Right sagitta (Pl. 1, Fig. 7) (PLD 56).

Type locality: La Paillade at Montpellier, southern France; Lower Miocene, early Aquitanium, mammal unit MN 1.

Etymology of name: The new species is dedicated to Jean Gaudant (Paris) who has contributed tremendously to the knowledge of Tertiary fishes.

Paratypes: 39 sagittae (Pl. 1, Figs. 6, 8-9) (PLD 55, 57-58).

Diagnosis: Elongate and thin sagittae; in the longitudinal axis only little bent. The posterodorsal angle is well developed. The ventral rim rises distinctly to the rostrum.

Description

The inner face is faintly convex, the outer face concave. Just below the middle, the crenulated dorsal rim has a soft bulge. The truncated and notched posterior rim passes at a slight angle to the crenulated ventral rim. The sulcus is divided into a small, ovate ostium and a long, narrow cauda rising towards the back and becoming distinctly hooked terminally.

Variability: The species shows an ontogenetic variability because the length of the sagittae grows allometric positive. Additionally, small sagittae (length around 1.2 mm) have a more rounded ventral rim than large sagitta.

Dimensions: Holotype: Length: 3.0 mm; height: 1.5 mm; thickness: 0.5 mm; l/h: 2,0. Other sagittae: Length: 0.93-6.9 mm; height: 0.65-2.75 mm; thickness: 0.25-0.80 mm; l/h: 1.4-2.5.

Recent relations: Recent species of *Mugil*, *Chelon*, and *Liza* have rather similar sagittae. Compared with the new species, sagittae of the Mediterranean species *Mugil cephalus* LINNAEUS, 1758 have a less rising cauda ending farther from the dorsal rim (see Chaine, 1938: Pl. 14). Sagittae of *Chelon labrosus* (RISSO, 1826) have a cauda similar to the new species, but Recent *Chelon* sagittae generally are not as elongate (see Chaine, 1938: Pl. 15, as *Mugil chelo* Cuv.). Sagittae of *Liza ramada* (RISSO, 1826) have a cauda corresponding well with the cauda of the new species (see Chaine, 1938: Pl. 15, as *Mugil capito* CUV.). For this reason, the new species is assigned to the genus *Liza*.

Fossil relations: From the Upper Miocene (Pannonian) of the Vienna Basin, *L. voesendorfensis* (WEINFURTER in Papp & Thenius, 1954) is known. This species has clear affinities to the new species. However, *L. gaudanti* n. sp. differs from the younger species by being less elongate and having a distinctly wider ventral area. *L. steurbauti* RADWANSKA, 1984 is another fossil *Liza* species to which belongs also *Liza* sp., described by Steurbaut (1984). *L. steurbauti* can be distinguished from the new species because of its more prominent posterodorsal angle and the wider cauda.

Further distribution: *L. gaudanti* n. sp. also occurs in late Lower Miocene deposits near Montpeyroux (Hérault, southern France).

Order **ATHERINIFORMES**
Family **ATHERINIDAE** RISSO, 1826

Recent ecology and biogeography: Primarily marine euryhaline fishes in tropic and subtropic waters; some species are adapted to freshwater. *Atherina* LINNAEUS, 1758 is the only native genus in the Mediterranean and the eastern Atlantic realm. *Atherinomorus lacunosus* (FORSTER, 1801) has immigrated in the Mediterranean Sea through the Suez Canal.

GENUS INCERTAE SEDIS

"genus *Atherinidarum*" sp.

(Pl. 2, Fig. 14)

v 1980 "genus Atherinidarum" sp. - Nolf & Cappetta, p. 7, Pl. 1, Fig. 21.

Material: 1 sagitta.

Description

The ovate sagitta has a convex inner face and a strongly concave outer face, and therefore, it is strongly bent in the longitudinal axis. The dorsal rim is faintly crenulated and has a small median dome. The rounded posterior rim drops steeply to the small posteroventral angle. The rounded and finely crenulated ventral rim becomes more steep towards the short but pronounced rostrum. The antirostrum is small. The long, narrow sulcus shows a short, but relatively wide ostium. The upper ostial rim steeply curves upwards, then runs to the antirostrum. The lower ostial rim is straight.

Dimensions: Length: 3.75 mm; height: 2.4 mm; thickness: 0.9 mm; l/h: 1.56.

Recent relations: A similar morphology of the sulcus, especially of the upper ostial rim, is found in sagittae of *Atherinopsis californiensis* GIRARD, 1854 living in the East Pacific (see Steurbaut, 1979: Pl. 6, Fig. 12). However, on the basis of the biogeography of *Atherinopsis*, a relationship of the present species with *Atherinopsis* does not seem possible (cf. Nolf & Cappetta, 1980: 7).

Fossil relations: "genus Atherinidarum" sp. shows some affinities to "genus Atherinidarum" *bavayi* STEURBAUT, 1984 from the Lower Miocene of the Aquitaine Basin but is more elongate and more bent in the longitudinal axis.

Further distribution: "genus Atherinidarum" sp. was described from the late Lower Miocene deposits near Montpeyroux (Hérault, southern France).

"genus Atherinidarum" cf. *bavayi* STEURBAUT, 1984

(Pl. 2, Fig. 13)

v* 1984 "genus Atherinidarum" *bavayi* n. sp. - Steurbaut, p. 66, Pl. 15, Figs. 1-8.

Material: 1 sagitta.

Description

A sagitta of ovate shape with a convex inner face and a concave outer face. The dorsal rim is undulated and the posterodorsal angle is slightly accentuated. The steeply dropping posterior rim proceeds with a faintly developed posteroventral angle to the rounded ventral rim. Ostium and cauda have the same features as described for "genus Atherinidarum" sp.

Dimensions: Length: around 2.2 mm (incomplete rostrum); height: 1.7 mm; thickness: 0.5 mm; l/h: around 1.3.

Recent and fossil relations: See "genus Atherinidarum" sp.

Further distribution: In Lower Miocene deposits (Aquitanian and Burdigalian) of the Aquitaine Basin.

Family **HEMIRHAMPHIDAE** GILL, 1861
Genus ***HYPORHAMPHUS*** GILL, 1859

Recent ecology and biogeography: Mainly marine, in coastal waters in the southern Atlantic, the Pacific, and the Indopacific; some species also dwell in estuaries. The only species in the Mediterranean Sea is *H. picarti* (VALENCIENNES, 1846) living in a small population near the African coast. The genus *Hyporhamphus* has the highest diversity of all Hemirhamphidae genera and consists of around 35 species.

Hyporhamphus sp.
(Pl. 2, Fig. 7)

Material: 1 sagitta.

Description

The sagitta has a triangular shape with rounded angles and finely crenulated rims. The inner and outer face are nearly flat. The wide sulcus is as long as the sagitta and clearly divided into ostium and cauda. The small ostium has a subquadratic shape with its upper and lower rim set off against the cauda with a distinct angle. The whole sulcus is covered with fine tubercles and ribs. The peripheries of the dorsal and the posterior rim show similar, but somewhat thicker tubercles and ribs.

Dimensions: Length: 3.35 mm; height: 2.25 mm; thickness: 0.4 mm; l/h: 1.49.

Recent relations: The shape of this sagitta corresponds well with sagittae of the Recent *Hyporhamphus unifasciatus* (RANZANI, 1842). Small differences concern the sulcus morphology (cf. Nolf & Stringer, 1992: Pl. 12, Figs. 17-18).

Fossil relations: A fossil and similar species is *Hyporhamphus miocenica* (WEINFURTER, 1952) from the Middle Miocene of Styria (Austria). It differs from the La Paillade species because of its pentagonal shape (see Weinfurter, 1952: Pl. 1, Fig. 7, as *Chirodorus*). *Hyporhamphus baluki* SMIGIELSKA, 1979 from the Middle Miocene of Poland and the Aquitaine Basin has a more pointed triangular shape and a more elongate, longer rostrum than the present species.

Order **CYPRINODONTIFORMES**
Family **CYPRINODONTIDAE** GILL, 1865
Genus ***PROLEBIAS*** SAUVAGE, 1874

Palaeoecology and palaeobiogeography: Species of the extinct genus *Prolebias* were

distributed in hypersaline, brackish, and lacustrine environments in Europe from Oligocene to Miocene times. The representatives of the genus *Aphanius* NARDO, 1827 probably are the most closely related Recent taxa. *Aphanius* species are extremely euryhaline and live in marine, hypersaline, brackish, and lacustrine biotopes of the Mediterranean area, the Persian Gulf, and central Anatolia.

Prolebias sp.

(Pl. 3, Figs. 13-15)

Material: 5 sagittae.

Description

Round to triangular sagittae with the dorsal rim prolongated to a tip, a straight sulcus and a small prominent rostrum.

Dimensions: Length: 0.62-0.72 mm; height: 0.69-0.78 mm; thickness: 0.16-0.19 mm; l/h: 0.8-0.95.

Remark: Because of the small size and mediocre preservation, determination to species level is not possible.

Order **PERCIFORMES**
Family **AMBASSIDAE** BOULENGER, 1904
Genus *DAPALIS* GISTL, 1848

Palaeoecology and palaeobiogeography: Species of the extinct genus *Dapalis* were distributed in brackish and lacustrine environments in Europe from Eocene to Miocene (among others Nolf & Reichenbacher, 1999; Reichenbacher & Codrea, 1999; Reichenbacher & Weidmann, 1992; Weiler, 1963). On basis of the osteology (Gaudant, 1987) and also on basis of the otoliths, the next Recent relatives are representatives of the genus *Ambassis* CUVIER, 1828. *Ambassis* species live in tropical, shallow marine or estuarine waters in the Indopacific and western Pacific and in freshwater biotopes in Madagascar, India, and Australia.

Dapalis rhenanus (KOKEN, 1891)

(Pl. 2, Figs. 15-16, Pl. 3, Figs. 11-12)

v* 1891 *Otolithus (Berycidarum) rhenanus* KOKEN. - Koken, p. 120, Pl. VI, Figs. 10-10a.

v 1978 *Dapalis rhenanus* (KOKEN). - Malz, p. 464, Fig. 5.

For a detailed reference list see Reichenbacher (in press).

Material: 78 sagittae.

Description

The characteristic features of this species are the ovate shape, the pronounced posterodorsal angle, and the sulcus morphology. The La Paillade sagittae differ from the sagittae of the same species found in the Mayence and Hanau Basin only because of the slightly better crenulated rims. A detailed description and discussion of *D. rhenanus* is given by Reichenbacher (in press).

Dimensions: Length: 1.03-2.96 mm; height: 0.75-2.08 mm; thickness: 0.28-0.72 mm; l/h: 1.36-1.42.

Further distribution: In the Lower Miocene of the Upper Rhinegraben and the Mayence and Hanau Basins (Germany).

Family MORONIDAE FOWLER, 1907
Genus *MORONE* MITCHELL, 1814

Recent ecology and biogeography: Two *Morone* species, *M. labrax* (LINNAEUS, 1758) and *M. punctatus* (BLOCH, 1792), live in the Mediterranean Sea and also are widespread in the northeastern Atlantic. Both species prefer inshore waters and sometimes dwell in rivers.

Morone cornuta NOLF & CAPPETTA, 1980
(Pl. 2, Figs. 10-11)

v* 1980 *Morone cornuta* n. sp. - Nolf & Cappetta, p. 8, Pl. 2, Figs. 1-2.

Material: 21 sagittae.

Description

The sagittae have a ovate shape. The inner face is convex; the outer face concave with the ventral part slightly thickened. The slightly rounded dorsal rim always shows a characteristic median tip. The well-developed posterodorsal angle is situated near the short or truncated posterior rim, and a posteroventral angle also is present. The deeply rounded ventral rim extends to the medium-sized, faintly pointed rostrum. The sulcus is strongly deepened and subdivided into a large, ovate ostium and a more narrow, straight cauda becoming hooked terminally. The crista superior is accentuated by the depression on the dorsal area; a thin crista inferior is present.

Variability: Small sagittae (up to 3.3 mm length) can be more elongate than medium-sized and large sagittae.

Dimensions: Length: 2.90-4.16 mm; height: 2.00-2.90 mm; thickness: 0.64-1.0 mm; l/h: 1.4-1.55.

Recent relations: *M. cornuta* differs from the Mediterranean *Morone labrax* by its

rounder shape but has a similar sulcus (cf. Reichenbacher, 1993: Pl. 7, Fig. 111).

Further distribution: Prior to this study, *M. cornuta* was known only by two sagittae from the late Lower Miocene near Montpeyroux in southern France (Hérault). Compared with this type material, the sagittae from the locality La Paillade have a slightly more prominent posterodorsal angle.

Family **SERRANIDAE** SWAINSON, 1839
Genus *EPINEPHELUS* BLOCH, 1793

Recent ecology and biogeography: Benthonic fishes distributed on the shelf and the upper continental slope in all tropical and subtropical seas. Some species also dwell in estuaries. The genus comprises more than 100 species (and several subgenera). In the Mediterranean Sea, *Epinephelus* is represented by 6 species.

Epinephelus? sp.
(Pl. 2, Fig. 5)

Material: 1 sagitta.

Description

A very elongate sagitta with convex inner face and slightly concave outer face with indistinct ribbing on the peripheries. The nearly straight dorsal rim passes without a posterodorsal angle into the rounded posterior rim. The long ventral rim is faintly rounded and the rostrum is prominent. The sulcus is divided into a large, funnel-shaped ostium and a narrow cauda. The posterior third of the cauda is distinctly hooked. The crista superior is accentuated by the depression on the dorsal area.

Dimensions: Length: 3.0 mm; height: 1.5 mm; thickness: 0.45 mm; l/h: 2.0.

Recent relations: Stinton (1978: Fig. 32c) figured a sagitta of the Indopacific species *Epinephelus areolatus* FORSSKAL, 1775. This sagitta resembles the La Paillade species but has a more rounded dorsal rim and a more narrow ostium. However, sagittae of the Recent *Lobotes surinamensis* (BLOCH, 1790) also show a similar shape and sulcus morphology as *Epinephelus*? sp. but differ because of the strong bend in the longitudinal axis (coll. IRSNB, see Nolf, 1985: Fig. 64I). So far, *Lobotes* is not known as fossil.

Fossil relations: Fossil *Epinephelus* species have been described only from the Middle Eocene (Stinton, 1978; Nolf, 1988). From these species, *E. exacutus* STINTON, 1978 has the most similarities with *Epinephelus*? sp. (see Stinton, 1978: Pl. 12, Figs. 24a-b). However, the only specimen of *E. exacutus* is the somewhat eroded holotype which led Nolf (1985: 117) to correctly doubt the validity of this species.

Family **SILLAGINIDAE** RICHARDSON, 1846
Genus ***SILLAGO*** CUVIER, 1817

Recent ecology and biogeography: *Sillago* species live in shallow waters in the tropical Indopacific and western Pacific. They are frequently found in or near estuaries.

Sillago schwarzhansi STEURBAUT, 1984
(Pl. 2, Figs. 8-9)

1979 *Sillago hassovicus* (KOKEN, 1891). - Smigielska, p. 315, Fig. 19, Pl. 4, Fig. 8.
v* 1984 *Sillago schwarzhansi* n. sp. - Steurbaut, p. 83, Pl. 22, Figs. 1-4.
1992 *Sillago schwarzhansi* STEURBAUT, 1984. - Radwanska, p. 239, Fig. 92, Pl. 19, Figs. 11-13.

Material: 131 sagittae.

Description

The sagittae are characterized by an ellipsoidal shape becoming increasingly elongate posteriorly. The inner face is convex, and the outer face is concave and ventral thickened. The dorsal rim is less rounded than the ventral rim and has a small median tip behind which the dorsal rim can be slightly crenulated. The ventral rim rises to the back more steeply than to the front, and its curvature generally is variable. The posterior rim is short, and the rostrum is not very prominent. The sulcus is situated supramedian, straight and nearly as long as the sagitta. The division in a small, U-shaped ostium and a long, narrow cauda is distinct. The cauda is incised in the middle, becomes wider to the back, and closes rounded. Small sagittae (up to 2.5 mm length) often have more crenulated rims than medium-sized and large sagittae.

Dimensions: Length: 1.20-6.32 mm; height: 0.64-3.76 mm; thickness: 0.28-1.36 mm; l/h: 1.7-1.9.

Recent relations: *S. schwarzhansi* resembles the sagittae of the Recent West Australian *Sillago schomburgki* PETERS, 1865 (see Schwarzhans, 1980: 159, Fig. 560; Steurbaut, 1984: Pl. 22, Fig. 12).

Fossil relations: Most of the previously described fossil *Sillago* species are more rounded than *S. schwarzhansi*, for example the late Oligocene species *S. ventriosus* STEURBAUT, 1984 and the early Miocene species *S. recta* SCHWARZHANS, 1980. Most similarities are found to *S. hassovicus* (see Koken, 1891: Pl. 22, Fig. 5, holotype refigured in Steurbaut, 1984: Pl. 22, Fig. 5). *S. hassovicus* from the marine Lower Oligocene (Meeressande) of the Mayence Basin differs from *S. schwarzhansi* only by the wider posterior part of the sagitta.

Further distribution: *S. schwarzhansi* is known by a few sagittae from the Middle Miocene of Poland and the late Lower Miocene (Burdigalian) of the Aquitaine Basin.

Family **GERREIDAE** BLEEKER, 1859
Genus ***GERRES*** QUOY & GAIMARD, 1824

Recent ecology and biogeography: *Gerres* species live in tropical to subtropical coastal waters, in coral-reefs, in estuaries, and in lagoons. Primarily, they are distributed in the Indopacific and along the South American coast. *Gerres* is not present in the Mediterranean Sea.

Gerres sp.
(Pl. 1, Figs. 17-18)

v 1980 *Gerres* sp. - Nolf & Cappetta, p. 10, Pl. 2, Figs. 11-14.

Material: 7 sagittae.

Description

Rather elongate sagittae with strongly crenulated rims, convex inner face, and concave outer face slightly thickened in the center. The dorsal and ventral rim are rounded, and only some specimens have a dorsal median tip. The short posterior rim can be truncated or pointed. The elongate rostrum is marked and of medium length, and the antirostrum is pointed. The sulcus is subdivided into a U- to V-shaped ostium and a less deepened, sinuous cauda terminally bent downwards. Above the anterior part of the cauda, the crista superior is accentuated by a deepened dorsal area.

Dimensions: Length: 1.1-1.75 mm; height: 0.75-1.1 mm; thickness: 0.25-0.4 mm; l/h: 1.5-1.6.

Recent relations: The shape and sulcus of this fossil species correspond well with sagittae of the Recent *Gerres argyreus* (BLOCH & SCHNEIDER, 1801) (see Steurbaut, 1984: Pl. 24, Fig. 6).

Fossil relations: *Gerres* sp. present here is more elongate and has stronger crenulated rims as *Gerres* sp. described by Steurbaut (1984: 87) and Radwanska (1992: 243) from the Lower and Middle Miocene of the Aquitaine Basin and Poland. So far, the only nominal and valid fossil *Gerres* species is *G. latidens* STINTON, 1980 from the Middle Eocene of Great Britain. However, the holotype of *G. latidens* has a length of 4.5 mm which is markedly larger than the La Paillade sagittae which probably belong to juvenile fishes. For this reason, the decision if *Gerres* sp. is identical with *G. latidens* depends on future findings of more and especially of adult specimens.

Further distribution: In the late Lower Miocene near Montpeyroux (Hérault, southern France).

Family **HAEMULIDAE** RICHARDSON, 1848
Genus ***BRACHYDEUTERUS*** GILL, 1862

Recent ecology and biogeography: The only Recent species is *B. auritus* (VALENCIENNES, 1831), a marine fish living in water depths between 10 and 100 m along the west African coast from Mauretania to Angola. Sometimes, *B. auritus* also dwells in brackish estuaries. *B. auritus* is not present in the Mediterranean Sea.

Brachydeuterus latior (SCHUBERT, 1906)

(Pl. 2, Fig. 17)

* 1906 *Otolithus (Dentex) latior*. - Schubert, p. 627, Pl. 4, Figs. 7-9.

v 1979 *Brachydeuterus latior* (SCHUBERT, 1906). - Nolf & Steurbaut, p. 8, Pl. 2, Figs. 16-23.

1981 *Brachydeuterus latior* (SCHUBERT, 1906). - Nolf, p. 144, Pl. 2, Fig. 21 (refigured holotype).

1992 *Brachydeuterus latior* (SCHUBERT, 1906). - Radwanska, p. 244, Fig. 97, Pl. 22, Figs. 1-11.

A detailed reference list is given in Nolf & Steurbaut (1979) and Radwanska (1992).

Material: 233 sagittae.

Description

Sagittae of rather round shape with convex inner face and concave outer face. The rostrum is short, robust, and prominent, and a posterodorsal angle is well developed. The species is characterized by its sulcus morphology with the spade-like, short ostium which has an upper rim rising steeply upwards and the long and straight cauda, slightly hooked terminally.

Dimensions: Length: 1.04-6.64 mm; height: 0.72-4.80 mm; thickness: 0.36-1.76 mm; l/h: 1.35-1.5.

Recent relations: Sagittae of the Recent *B. auritus* (VALENCIENNES, 1831) have the same sulcus morphology (see Nolf & Steurbaut, 1979: Pl. 2, Figs. 14-15). They differ from the fossil *B. latior* by being more elongate and showing a more pronounced posterodorsal angle.

Fossil relations: "genus aff. *Brachydeuterus*" *grossei* MÜLLER, 1996 from the Upper Oligocene of the southern North Sea Basin (see Müller, 1996: Pl. 5, Figs. 3-8; Schwarzhans, 1994: Figs. 407-409) has some affinities with *B. latior*, but can be distinguished by the distinctly more rounded ventral rim. Another species from the Upper Oligocene of the southern North Sea Basin is *B. gaemersi* MENZEL, 1983. On basis of its rounded shape, *B. gaemersi* seems to have more affinities to "genus aff. *Brachydeuterus*" *grossei* than to *B. latior*. A third *Brachydeuterus* species is *B. speronatus* (BASSOLI, 1906) from the Middle Miocene of Poland and from the Upper Miocene of Italy. This species differs from *B. latior* because of a very prominent posterodorsal angle and a more deepened sulcus (see Nolf & Steurbaut, 1983: Pl. 7, Figs. 10-12; Radwanska, 1992: Fig. 98, Pl. 21, Figs. 9-11).

Remark: *B. gaemersi* was attributed by Schwarzhans (1994: 140) to the genus *Dapalis* GISTL. In our opinion, *B. gaemersi* is a typical representative of the Family Haemulidae because of its long and rather narrow cauda. *Dapalis* species (Family Ambassidae) are characterized by a wider and more deepened sulcus and a rather short cauda.

Further distribution: In Lower and Middle Miocene times, *B. latior* was widely

distributed in the Mediterranean and Paratethys realms.

Genus *POMADASYS* LACÉPÈDE, 1802

Recent ecology and biogeography: *Pomadasys* species live in warm, tropical and subtropical seas, frequently they can be found near estuaries. 31 Recent species are known among which *P. incisus* (BOWDICH, 1825) and *P. stridens* (FORSSKAL, 1775) are distributed in the Mediterranean Sea, living in water depths up to 55 m.

Pomadasys steurbauti NOLF & CAPPETTA, 1980

(Pl. 2, Fig. 4)

v* 1980 *Pomadasys steurbauti* n. sp. - Nolf & Cappetta, p. 10, Pl. 2, Figs. 22-24.

v 1984 *Pomadasys steurbauti* NOLF & CAPPETTA. - Steurbaut, p. 89, Pl. 25, Figs. 1-4.

Material: 12 sagittae.

Description

Sagittae of a round to ovate shape with convex inner face. The outer face is slightly concave, smooth or covered with several small tubercles. The dorsal rim shows a small median tip, and a posterodorsal angle is present. The posterior rim is short and terminates at a slightly pronounced posteroventral angle. The ventral rim is deeply rounded, and the rostrum has a robust shape and is prominent. The long sulcus is well subdivided into an U- to V-shaped ostium with its upper rim rising upwards and a narrow, rather short cauda curving in the middle downwards and closing with some distance from the posteroventral angle.

Dimensions: Length: 2.6-5.3 mm; height: 2.0-3.85 mm; thickness: 0.64-1.3 mm; l/h: 1.3-1.4.

Recent relations: The round shape of *P. steurbauti* makes likely a closer relationship to the Pacific species *P. argyreus* (VALENCIENNES *in* Cuvier & Valenciennes, 1833) (Pl. 5, Fig. 6 of present study) than to the Mediterranean species *P. incisus* (BOWDICH, 1825) (Pl. 5, Figs. 4-5 of present study).

Fossil relations: A frequent fossil *Pomadasys* species is described partly as *P. arcuatus* (BASSOLI & SCHUBERT, 1906) and partly as *P.* aff. *incisus* (BOWDICH, 1825) from Lower and Middle Miocene deposits of the Mediterranean. *P. steurbauti* differs from this species by its more round shape, the longer, more narrow ostium, and the short cauda which is less hooked.

Further distribution: *P. steurbauti* was found in deposits of late Lower Miocene age (Burdigalian) in the Aquitaine Basin and near Montpeyroux (Hérault, southern France).

Genus *HAEMULON* CUVIER, 1829

Recent ecology and biogeography: The endemic genus *Haemulon* comprises at least

17 species distributed in tropical waters in the Pacific (Galapagos Islands) and along the coast of Central America.

"genus aff. ***Haemulon***" sp.
(Pl. 5, Fig. 2)

Material: 1 sagitta.

Description

The sagitta has a round to ovate shape, a convex inner face, and a slightly concave outer face with a small hump in the middle, radial ribs and some tubercles. The dorsal rim shows a marked posterodorsal angle. The rostrum is robust and short, while the antirostrum is small and pointed. The sulcus is well divided into an U-shaped, slightly deepened ostium and a narrow, more deepened cauda curving in the middle downwards and ending near the ventral rim. The lower rim of the ostium distinctly drops to the anterior rim.

Dimensions: Length: 8.45 mm; height: 6.0 mm; thickness: 1.6 mm; l/h: 1.4.

Recent relations: "genus aff. *Haemulon*" sp. resembles sagittae of the Recent Pacific species *Haemulon aurolineatum* CUVIER *in* Cuvier & Valenciennes, 1830 (see Pl. 5, Fig. 3) and *H. steindachneri* (JORDAN & GILBERT, 1883) concerning the shape and the sulcus morphology (cf. Nolf & Stringer, 1992: Pl. 14, Fig. 15). Different are the more concave lower ostial rim and the cauda curvature of the cited Recent species. However, also the present day repartition of *Haemulon* does not allow assimilation with that genus.

Fossil relations: From the Lower Miocene of the Aquitaine Basin, sagittae of *Pomadasys arcuatus* (BASSOLI & SCHUBERT, 1906) with identical dimensions (coll. IRSNB) were available. Compared with these sagittae, it can easily be seen that "genus aff. *Haemulon*" sp. has a cauda distinctly more bent downwards and a different lower ostial rim. As yet, fossil *Haemulon* species have been described in open nomenclature by Nolf & Stringer (1992: 55) from the Miocene of the Dominican Republic and by Stringer (1998a: 150, 160) from the Pliocene Bowden shell bed of Jamaica. "genus aff. *Haemulon*" is distinguished by its posterodorsal angle from these species.

Family **SPARIDAE** BONAPARTE, 1832
Genus ***PAGRUS*** CUVIER, 1817

Recent ecology and biogeography: Four Recent *Pagrus* species are known, living in water depths up to 250 m. Three species are distributed in the Mediterranean Sea and the northeastern Atlantic. *P. coeruleostictus* (VALENCIENNES, 1830), possibly identical with the fossil species present here, occurs only in warm regions of the Mediterranean Sea, mainly in water depths between 50-100 m.

Pagrus aff. *coeruleostictus* (VALENCIENNES, 1830)

(Pl. 2, Figs. 1-2)

Material: 30 sagittae.

Description

Sagittae of elongate shape, strongly bent in the longitudinal axis and with a pointed anterior and posterior rim. The inner face is convex, while the outer face is concave and smooth. The finely crenulated dorsal rim has a well developed posterodorsal angle. The ventral rim is rounded with the deepest point somewhat moved to the front. The rostrum is prominent, and the antirostrum short and pointed. The sulcus is well subdivided into a large, ovate U-shaped ostium and a somewhat longer and deeper, narrow cauda. The ostium presents a convex upper rim and a concave lower rim. The cauda bends downwards after two thirds of its length and terminates near the ventral rim. The crista superior and the thin crista inferior are well developed and follow the cauda as well as the ostium.

Dimensions: Length: 1.3-5.35 mm; height: 0.9-3.3 mm; thickness: 0.3-0.95 mm; l/h: 1.5-1.8.

Recent relations: This species has strong affinities to the Recent Mediterranean species *P. coeruleostictus*. However, the possibilities to compare the fossil species with the Recent species were somewhat restricted because from the Recent species only very large sagittae (length around 10 mm) were available (coll. IRSNB). Sagittae of the Recent Mediterranean species *P. pagrus* (LINNAEUS, 1758) (see Pl. 5, Figs. 13-14) differ distinctly from the fossil *Pagrus* aff. *coeruleostictus* because of their less elongate shape and the more prominent rostrum.

Fossil relations: *P. distinctus* (KOKEN, 1891) (see below) has a more round shape and a less prominent rostrum than *P.* aff. *coeruleostictus*. Steurbaut (1984: 91-92) has described *Pagrus* sp. 1 and *Pagrus* sp. 2 from the Middle Miocene and the late Oligocene/early Miocene of the Aquitaine Basin. These species do not correspond with the presently described species because of their different shape. At a first glance, sagittae of *Diplodus* species also seem to be similar to *P.* aff. *coeruleostictus*, for example *D. karrerae* NOLF & STEURBAUT, 1979. However, compared with *Diplodus* species, *P.* aff. *coeruleostictus* is characterized by its less elongate shape and its more prominently bent downwards cauda.

Pagrus cf. *distinctus* (KOKEN, 1891)

(Pl. 2, Fig. 3)

* 1891 *Otolithus (Serranus) distinctus* KOKEN. - Koken, p. 125, Pl. 10, Fig. 2.

1992 *Pagrus distinctus* (KOKEN, 1891). - Radwanska, p. 255, Fig. 108, Pl. 25, Figs. 6-10.

See Radwanska (1992) for further references.

Material: 1 sagitta.

Description

The ovate sagitta has a slightly convex inner face and a slightly concave outer face

with two vertical ribs. The dorsal rim is highly rounded with a faint median tip. The posterodorsal angle is only slightly pronounced, and the posterior rim and the ventral rim are rounded. Further features are similar to *P.* aff. *coeruleostictus.*

Dimensions: Length: 4.6 mm; height: 3.1 mm; thickness: 0.8 mm; l/h: 1.5.

Recent relations: The species corresponds well with sagittae of Recent *Pagrus* species on the basis of its sulcus morphology (see Pl. 5, Figs. 13-14).

Fossil relations: *Pagrus* cf. *distinctus* differs from *P.* aff. *coeruleostictus* because of the slightly pronounced posterodorsal angle, and the rounded posterior rim and the less prominent rostrum.

Further distribution: *Pagrus distinctus* (KOKEN) is known from Oligocene deposits of the Mayence Basin and the southern North Sea Basin and from the Middle Miocene of Poland.

Genus *DENTEX* CUVIER, 1814

Recent ecology and biogeography: The genus is represented in the Mediterranean Sea and the northeastern Atlantic with four species living offshore near the bottom. The water depth depends on the species and is between 150 to 500 m.

Dentex gregarius (KOKEN, 1891)-species complex

(Pl. 5, Fig. 1)

* 1891 *Otolithus (Sparidarum) gregarius* KOKEN. - Koken, p. 128, Figs. 18-20, Pl. 7, Figs. 7-8.
1992 *Dentex gregarius* (KOKEN, 1891). - Radwanska, p. 258, Fig. 110, Pl. 26, Figs. 8-12.
1994 *Dentex* aff. *gregarius* (KOKEN, 1891). - Nolf & Brzobohaty, p. 235, Pl. 9, Fig. 11.
A detailed reference list is given in Radwanska (1992).

Material: 5 sagittae.

Description

The sagittae have a round shape, a convex inner face, and a concave outer face. Small specimens are characterized by strongly crenulated rims, while adult sagittae (Pl. 5, Fig. 1) have only a strongly undulated dorsal rim. The sulcus is situated supramedian. The U-shaped ostium is distinctly separated from the more narrow cauda which is initially straight and becomes hooked terminally.

Dimensions: Length: 2.95-9.2 mm; height: 2.55-7.2 mm; thickness: 0.7-1.7 mm; l/h: 1.2-1.3.

Recent relations: *Dentex maroccanus* VALENCIENNES, 1830, which lives in the southern and eastern Mediterranean Sea and along the African Coast, may be related to the fossil species. This is also true for *D. angolensis* POLL & MAUL, 1953, which also lives in the southern part of the area in which *D. maroccanus* is found (cf. Nolf & Brzobohaty, 1994: 235). Nolf & Brzobohaty emphasized that the sagittae of both Recent

species probably are not diagnostic on species level. For this reason, they interpreted all previously described fossil sagittae of *D. gregarius* (Koken) as a species complex. We follow their interpretation here.

Fossil relations: Further *Dentex* species are known from the Atlantic and Mediterranean Neogene and from the Middle Miocene of the Paratethys. They can be distinguished by the shape of their sagittae from *Dentex gregarius*-species complex (cf. Nolf & Cappetta, 1988: Pl. 16, Figs. 1-3; Steurbaut, 1984: 92-93; Steurbaut & Jonet, 1981: 205; Radwanska, 1992: 259).

Further distribution: *Dentex gregarius*-species complex was widespread in the Paratethys region from Upper Oligocene to Middle Miocene times. In the North Sea Basin and the Aquitaine Basin, it was recognized in deposits of late Lower Oligocene to Middle Miocene age. Furthermore, it was found in the Middle Miocene of Portugal (cf. Nolf & Brzobohaty, 1994: 235).

Family SCIAENIDAE CUVIER, 1829
Genus *ARGYROSOMUS* DE LA PYLAIE, 1835

Recent ecology and biogeography: Six Recent *Argyrosomus* species are known. A Mediterranean and East Atlantic species is *A. regius* (ASSO, 1801) living near the coast in water depths between 15 and 200 m. *A. regius* also dwells in estuaries and lagoons and thrives in rather warm (western Africa) as well as in rather cool waters (southern Scandinavia).

Argyrosomus sp.
(Pl. 4, Fig. 10)

Material: 2 sagittae.

Description

The sagittae have a wedge-shaped outline with a prominent posterodorsal angle. The inner face is convex, and the outer face is slightly concave and strongly thickened in the posterior part (see Pl. 4, Fig. 10b). The sulcus is slightly deepened and has a very large ostium covering completely the anterior part of the sagitta. The cauda rises from the ostium to the posterodorsal angle, then curves downwards near the posterior rim and closes just before reaching the ventral rim.

Dimensions: Length: 10.7, 16.9 mm; height: 6.8, 10.5 mm; thickness: 4.1, 6.5 mm; l/h: 1.6; l/th: 2.6.

Recent and fossil relations: The Recent species *A. regius* is known as fossil from the Mediterranean and Atlantic Miocene and Pliocene (Nolf & Cappetta, 1988). Sagittae of Recent *A. regius* were studied in the collection of the IRSNB. The La Paillade species is less elongate than *A. regius* and possesses a larger ostium. *Argyrosomus* sp. may be a new species, but more and better material is required to make a valid diagnosis.

Recent ecology and biogeography: The only Recent species is *Sciaena umbra* LINNAEUS, 1758 distributed in the eastern Atlantic from the English Canal to western Africa and also in the Mediterranean Sea. *S. umbra* prefers coastal water and is known from 20-180 m water depth.

Sciaena irregularis KOKEN, 1884

(Pl. 4, Figs. 1-4)

* 1884 *Otolithus (Sciaenidarum) irregularis*. - Koken, *pro parte*, p. 554, Pl. XII, only Fig. 7.

v 1984 *Sciaena* sp. - Steurbaut, p. 95, Pl. 29, Fig. 6.

1996 *Sciaena irregularis* KOKEN, 1884. - Müller, p. 56, Pl. 8, Figs. 7-16.

For a detailed reference list see Müller (1996) and Reichenbacher (in press).

Material: 280 sagittae.

Description

Nearly rectangular sagittae with rounded angles. Inner face is slightly convex while the outer face is thickened in the central area and with wrinkles and grooves at the peripheries. The posterodorsal angle is well developed, and a posterventral angle also is present. The ventral rim rises more steeply to the front than to the back. The ostium is large and round. The cauda is initially straight, and then drops down vertically and terminates slightly bending to the front.

Dimensions: Length: 4.5-9.6 mm; height: 3.5-7.1 mm; thickness: 1.4-2.7 mm; l/h: 1.3-1.4 mm; l/th: 3.2-3.5 (rarely up to 3.8).

Recent relations: Sagittae of the Recent *Sciaena umbra* have a similar sulcus but a more rounded outline (see Pl. 6, Fig. 2A).

Further distribution: *Sciaena irregularis* KOKEN, 1884 is known from the late Oligocene of the North Sea Basin. For comparison, one sagitta is figured from this region (Pl. 4, Fig. 12). *S. irregularis* is a rare species in Oligo-Miocene deposits in the Mayence Basin (cf. Reichenbacher, in press). The species likely was distributed in the Middle Miocene of the North Sea Basin (Weiler, 1942) and the Lower Miocene (Burdigalian) of the Aquitaine Basin (see Steurbaut, 1984, as *Sciaena* sp.), but each of these occurences was based on one sagitta.

Sciaena aff. *umbra* LINNAEUS, 1758

(Pl. 4, Figs. 5-6)

Material: 26 sagittae.

Description

The sagittae are distinguished from *S. irregularis* because of the more rounded shape and especially on basis of the more rounded anterior part of the ventral rim. Other

features are similar to *S. irregularis*.

Dimensions: Length: 4.3-7.1 mm; height: 3.7-5.75 mm; thickness: 1.2-2.1 mm; l/h: 1.2; l/th: 3.1-3.3 (rarely up to 3.7).

Recent relations: The species differs from the Recent *Sciaena umbra* (Pl. 6, Fig. 2A) only by the somewhat smaller distance between the cauda and the posterodorsal angle and the ostial upper rim running very near to the dorsal rim.

Fossil relations: So far, *Sciaena umbra* has not been reported as fossil. The species from La Paillade should be closely related with *S. umbra*.

Genus *UMBRINA* CUVIER, 1816

Recent ecology and biogeography: Three species of the cosmopolitan genus *Umbrina* are distributed in the Mediterranean Sea and the eastern Atlantic, *U. canariensis* VALENCIENNES, 1843, *U. cirrosa* (LINNAEUS, 1758), and *U. ronchus* VALENCIENNES, 1843. Habitats depend on species and comprise the coast, the shelf, and the upper continental slope. Juvenile fishes prefer coastal water, and juveniles of *U. cirrosa* also dwell in estuaries.

Umbrina sp.

(Pl. 4, Figs. 7-9)

Material: 30 sagittae.

Description

Sagittae of a rounded rectangular shape and characterized by the ventral rim rising rather steeply to the front. The inner face is slightly convex, and the outer face slightly is concave and with radial ribs and/or some tubercles (Pl. 4, Fig. 9b). The dorsal rim has a small median tip and terminates in the pronounced posterodorsal angle. The steeply dropping posterior rim is somewhat concave in the middle, and the ventral rim is rounded. The shallow sulcus shows a large and rather round ostium characterized by the curved lower ostial rim and a cauda which is first straight and then vertically bent down.

Dimensions: Length: 4.9-9.0 mm; height: 3.75-6.9 mm; thickness: 1.4-3.1 mm; l/h: 1.2-1.3 (rarely 1.4); l/th: 3.2-3.7.

Recent relations: Compared with Recent *Umbrina* species, *Umbrina* sp. has a less thickened outer face (see l/th-index for Recent *Umbrina* species in Schwarzhans, 1993: 63). The shape and sulcus morphology of *Umbrina* sp. are similar to the Recent Indopacific species *U. sinuata* DAY, 1876 (cf. Schwarzhans, 1993: Fig. 91).

Fossil relations: *Umbrina* aff. *ronchus* VALENCIENNES, 1843, known from the Lower and Middle Miocene of the Aquitaine Basin and Portugal, is similar to *Umbrina* sp., but has a more rounded shape (Steurbaut, 1984: 94, Pl. 29, Figs. 1-4). Another similar, but more elongate species was partly described as *Umbrina cirrosa* (LINNAEUS, 1758) and *U. subcirrhosa* SCHUBERT, 1902 from early Miocene to late Miocene deposits of the Vienna Basin (cf. Reichenbacher, 1998: 330). *U. pyrenaica* (PRIEM, 1914) from the

Atlantic Neogene of France differs distinctly from *Umbrina* sp. because of its narrow ostium (see Lanckneus & Nolf, 1979: Pl. 4, Figs. 1-6). The majority of the La Paillade sagittae of *Umbrina* sp. are slightly eroded and represent juvenile to subadult fishes. This is the reason why we describe this probable new species in open nomenclature.

Genus *SCIAENOPS* GILL, 1864

Recent ecology and biogeography: The only Recent species is *Sciaenops ocellatus* (LINNAEUS, 1766) living under subtropical conditions in the western Atlantic along the North American coast and in the Gulf of Mexico.

"genus aff. *Sciaenops*" sp.
(Pl. 4, Figs. 11a-b)

Material: 2 sagittae.

Description

Both sagittae have a wedge-shaped outline and are remarkable thin. The inner face is insensibly convex, and the outer face is flat to slightly convex and wrinkled (Pl. 4, Fig. 11b). The lower rim of the large ostium turns to the back before running to the anterior rim. The cauda bends down before its middle and parallels the posterior rim before ending just above the ventral rim.

Dimensions: Length: 7.1, 9.1 mm; height: 4.5, 5.7 mm; thickness: 1.6, 2.0 mm; l/h: 1.6; l/th: 4.4-4.5.

Recent relations: "genus aff. *Sciaenops*" sp. resembles *Sciaenops ocellatus* (Pl. 6, Fig. 2B) because of the low thickness, the shape, and the sulcus morphology. However, a relationship of our fossil species with the endemic genus *Sciaenops* living along the west Atlantic Coast of North America and in the northern Gulf of Mexico seems unprobable.

Fossil relations: Fossil otoliths were described as *Sciaenops eastmani* by Dante (1953) from the Miocene of Maryland. Furthermore, *S.* cf. *ocellatus* was described from the Pliocene Yorktown Formation at Lee Creek Mine in North Carolina by Fitch & Lavenberg (1983). Additionally, Stringer (1998b) has identified *S. ocellatus* from several Archaic archeological sites along the Gulf of Mexico coast in the southern United states. These "subfossil" otoliths are about 4500 years old.

Family **CEPOLIDAE** BONAPARTE, 1832
Genus *CEPOLA* LINNAEUS, 1764

Recent ecology and biogeography: Benthonic marine fishes living in water depths between 15 and 200 m. *C. rubescens* LINNAEUS, 1766 is distributed in the eastern Atlantic and the Mediterranean Sea.

Remark: A synonym for *C. rubescens* is *C. macrophthalma* LINNAEUS, 1758. Although this species name should have priority, it is not valid according to a decision of the International Commission for Zoological Nomenclature.

Cepola rubescens LINNAEUS, 1766

(Pl. 2, Fig. 12)

1906 *Otolithus (Cepola) praerubescens* BASS. & SCHUB. sp. nov. - Schubert, p. 642, Pl. 19, Figs. 1-5.
1992 *Cepola rubescens* LINNAEUS, 1766. - Radwanska, p. 270, Figs. 124-125, Pl. 30, Figs. 1-7.
Further references are given in Radwanska (1992).

Material: 5 sagittae.

Description

Ellipsoidal sagittae with convex inner face. The outer face is flat with small wrinkles on the peripheries and rarely with some tubercles. A posterodorsal angle is present as is a prominent and slightly pointed rostrum. The sulcus has a S-like shape. A colliculum is present at the collum. The cauda is shorter than the ostium and closes with some distance from the posterior rim. The ventral line is deeply incised.

Dimensions: Length: 3.1-4.2 mm; height: 1.8-2.4 mm; thickness: 0.6-0.7 mm; l/h: 1.6-1.8.

Recent relations: Sagittae of the Recent *C. rubescens* (coll. IRSNB, see Nolf, 1985: Fig. 68J, as *C. macrophthalma*) have a rather prominent variability concerning the shape. The fossil sagittae fall within the bounds of this variability.

Further distribution: *C. rubescens* was rather common during the Oligocene and Miocene in the Mediterranean, the Aquitaine Basin, the North Sea Basin and the Paratethys region.

Family ELEOTRIDAE BLEEKER, 1877

GENUS INCERTAE SEDIS

Recent ecology and biogeography: Eleotrids are distributed worldwide in tropical and subtropical waters, predominantly in the Indopacific region. They live in coastal waters, in estuaries, in coral reefs (rarely) and also in freshwater biotopes.

"genus Eleotridarum" *sectus* (STINTON, 1968)

(Pl. 1, Figs. 11-16)

v * 1968 *Gobius sectus* sp. nov. - Stinton & Kissling, p. 149, Pl. 1, Fig. 5.
v 1968 *Lepidogobius bifidus* sp. nov. - Stinton & Kissling, p. 150, Pl. 1, Fig. 6.
v 1969 *Gobius latisulcatus* nov. sp. - Cappetta, p. 249, Pl. 21, Figs. 69-73, Pl. 25, Figs. 1-13.

v 1980 "genus Eleotridarum" sp. - Nolf & Cappetta, p. 14, Pl. 4, Figs. 3-6.

v 1992 Eleotridarum *sectus* (STINTON & KISSLING) nov. comb. - Reichenbacher & Weidmann, p. 39, Pl. 8, Figs. 12-16.

? 1992 *Butis schwarzhansi* n. sp. - Rückert-Ülkümen, p. 107, Pl. 3, Figs. 3-4.

? 1992 *Prionobutis koronoides* n. sp. - Rückert-Ülkümen, p. 108, Pl. 3, Figs. 5-9.

Material: 95 sagittae.

Description

Sagittae are quadratic to rectangular in shape. Small sagittae (length < 1 mm) are relatively higher and more quadratic than larger sagittae. The inner face is convex, and the outer face is flat and smooth. The dorsal rim can be smooth or crenulated and rises from the prominent anterodorsal angle to the generally well developed posterodorsal projection. Some sagittae show only a posterodorsal angle instead of a posterodorsal projection. A small anteroventral projection looks like a rostrum, but with sagittae of Gobiidae and Eleotridae, a rostrum is not conventionally differentiated. The sulcus has a shape similar to sagittae of Gobiidae but is open anteriorly or nearly reaches the anterior rim which is a typical feature of Eleotridae sagittae.

Dimensions: Length: 0.6-1.9 mm; height: 0.7-1.75 mm; thickness: 0.25-0.5 mm; l/h: 1.1; l/h of sagittae < 1 mm: 0.9-1.0.

Variability: The posteroventral transition to the ventral rim is rounded with juvenile sagittae and becomes more and more angular with increasing size of the sagittae.

Recent relations: Presently, sagittae of the different genera of the Family Eleotridae are relatively unknown. For this reason, a generic determination is not possible.

Fossil relations: "genus Eleotridarum" *sectus* is probably related to "genus Eleotridarum" *schadi* WEILER, 1963 from the Late Oligocene deposits in the Upper Rhinegraben (Germany). With "genus Eleotridarum" *schadi*, the length of the dorsal part of the sagittae is distinctly shorter than the length of the ventral part which is not the case at the here present sagittae.

Further distribution: "genus Eleotridarum" *sectus* is known from Oligocene and early Miocene deposits of the western Paratethys region. In addition, the species is present in the late Lower Miocene sediments near Montpeyroux (Hérault, southern France).

Family GOBIIDAE BONAPARTE, 1832

Recent ecology and biogeography: The family consists of approximately 200 genera among which 32 are representated in the Mediterranean Sea and the northeastern Atlantic with at least 52 species. Further, 16 endemic species occur in the Black Sea. Generally the species are marine or brackish and live near the coast. A few species are neritic, and some species are adapted to freshwater.

Genus *GOBIUS* LINNAEUS, 1758

Recent ecology and biogeography: The genus *Gobius* contains 16 species among which 14 live in the Mediterranean Sea and the northeastern Atlantic.

Gobius multipinnatus (H. v. MEYER, 1852)

(Pl. 3, Figs. 6-10)

* 1852 *Cottus multipinnatus* n. sp. - H. v. Meyer, p. 106, Pl. 17, Fig. 1.
1893 *Ot. (Gobius) praetiosus* n. sp. - Prochazka, p. 63, Pl. 3, Fig. 7.
v 1979 *Gobius* aff. *geniporus* VALENCIENNES, 1837. - Nolf & Steurbaut, p. 16, Pl. 5, Fig. 23.
v 1980 *Gobius* sp. 2. - Nolf & Cappetta, Pl. 4, Figs. 19-24.
v 1981 *Gobius* sp. - Steurbaut & Jonet, Pl. 4, Figs. 12-13.
v 1984 *Gobius* aff. *geniporus* VALENCIENNES, 1837. - Steurbaut, p. 104, Pl. 32, Figs. 13-15.
1992 *Gobius* aff. *geniporus* VALENCIENNES, 1837. - Radwanska, p. 286, Fig. 141, Pl. 34, Figs. 1-2.
1992 *Gobius* aff. *niger* LINNAEUS, 1758. - Radwanska, p. 286, Fig. 142, Pl. 35, Figs. 12-15.
v 1993 *Gobius multipinnatus* (H. v. MEYER 1852). - Reichenbacher, p. 358, Pl. 10, Figs. 144-146.
1994 *Gobius* sp. 4, sp. 5, sp. 7. - Brzobohaty, p. 69, Pl. 6, Figs. 4-6, 12-13, Pl. 7, Figs. 1-4.

Material: More than 4500 sagittae of Gobiidae have been found. Approximately 10% of these sagittae belong to *G. multipinnatus*.

Description

The sagittae have a rectangular, somewhat oblique shape. They are characterized by a prominent posterodorsal projection and a generally less developed anteroventral projection. Typically, the pronounced anterodorsal angle is situated lower than the posterodorsal angle and so the dorsal rim rises distinctly from the anterior rim to the posterior rim. A rather prominent variability exists concerning the shape and dimensions of the dorsal and ventral angles and projections.

Dimensions: Length: 0.95-2.15 mm; height: 0.72-1.75 mm; thickness: 0.3-0.6 mm; l/h: 1.2-1.3.

Recent relations: *Gobius niger* LINNAEUS, 1758 and *G. paganellus* LINNAEUS, 1758 have some affinities to the La Paillade species (see Pl. 6, Fig. 3). Both Recent species have a large biogeographical distribution which also was true for the fossil *G. multipinnatus*.

Further distribution: *G. multipinnatus* is known from early and Middle Miocene deposits in the Mediterranean, the northeastern Atlantic and the Paratethys.

Genus *LESUEURIGOBIUS* WHITLEY, 1950

Recent ecology and biogeography: *Lesueurigobius* species are marine benthonic fishes living mainly in the open shelf sea between 10 and 350 m water depth, depending on species.

Lesueurigobius vicinalis (KOKEN, 1891)-species complex

(Pl. 3, Figs. 1-5)

v * 1891 *Otolithus (Gobius) vicinalis* KOKEN. - Koken, p. 133, Fig. 21.
1966 *Gobius vicinalis* KOKEN. - Smigielska, p. 260, Pl. 18, Figs. 8-11.
v 1979 *Acentrogobius* sp. - Nolf & Steurbaut, p. 15, Pl. 5, Figs. 16-21.
1980 *Gobius* sp. 1. - Nolf & Cappetta, Pl. 4, Figs. 10-15.
v 1981 *Acentrogobius* sp. - Steurbaut & Jonet, p. 209, Pl. 4, Figs. 1-4.
v 1984 *Acentrogobius* sp. - Steurbaut, p. 103, Pl. 32, Figs. 20-24.
v 1989 "genus Gobiidarum" *vicinalis* (KOKEN, 1891). - Brzobohaty, p. 32, Pl. 3, Figs. 13-14.
v 1989 *Acentrogobius* sp. 1. - Brzobohaty, p. 29, Pl. 3, Figs. 1-4.
1992 *Gobius vicinalis* KOKEN. - Radwanska, p. 284, Fig. 140, Pl. 33, Figs. 8-11, Pl. 34, Figs. 3-6.
1994 *Acentrogobius* sp. - Brzobohaty, p. 69, Pl. 6, Figs. 14-16.
1994 *Gobius* sp. 1, sp. 2, sp. 3. - Brzobohaty, p. 69, Pl. 7, Figs. 5-13.

For more references see Steurbaut (1984) and Radwanska (1992).

Material: More than 4500 sagittae of Gobiidae have been found. Approximately 90% of these sagittae belong to the *L. vicinalis*-species complex.

Description

Sagittae are approximately quadratic in shape with a highly rounded dorsal rim and a short, robust posterodorsal projection. The posterior rim and the anterior rim both are concave in the middle, the ventral rim is straight. At the lower rim of the sulcus, a border is developed and limited by a suture from the convex ventral area. The ventral line is deepened in the ventral area and proceeds along the anterior and posterior rim to the depression on the dorsal area.

Dimensions: Length: 1.0-1.65; height: 0.95-1.7; thickness: 0.3-0.6; l/h: 0.85-1.1, mainly 0.9-1.0.

Remark: The studied sagittae show a remarkable variability especially concerning the length/height-index and the curvature of the dorsal rim. Perhaps, they may represent two or three closely related species which can not be separated by the features of their sagittae. For this reason, we interprete *L. vicinalis* as species complex.

Recent relations: Sagittae of the Recent *Lesueurigobius friesi* (MALM, 1874) are very similar (cf. Reichenbacher, 1998: Pl. 3, Fig. 18).

Further distribution: *L. vicinalis* was described from the Lower and Middle Miocene in the Mediterranean, the northeastern Atlantic and the Paratethys. The species occurs in most cases together with *G. multipinnatus*.

RESULTS

The reconstruction of the fish fauna from the La Paillade locality is based on a

total of 5533 otoliths. The fauna consists of 30 taxa representing 20 families (Tab. 1). 17 nominal species were described with two of them introduced as new, *Dussumieria sittigi* and *Liza gaudanti.*

Up to 73% of the investigated otoliths (sagittae) belongs to the *Lesueurigobius vicinalis*-species complex. The sagittae of this taxon show a rather high variability and may belong to two or three closely related species. For this reason, they are interpreted as a species complex. The next most abundant species is another representative of the Gobiidae, *Gobius multipinnatus* (8% of all sagittae). Then follow, with decreasing frequency, *Sciaena irregularis* (5%), *Brachydeuterus latior* (4%), *Sillago schwarzhansi* (2.5%), "genus Eleotridarum" *sectus* (2%), and *Dapalis rhenanus* (1.5%).

The mentioned species comprise 96% of all sagittae while only 4% represent the other 24 taxa. Seven of them are present with 0.2 to 0.7% and the remainder with a frequency of 0.1% or less (see Tab. 1).

In a previous study by Cappetta (1969), three Teleostean species were described from the La Paillade locality on basis of Teleostean teeth: *Sphyraena olisiponensis* (JONET, 1966), *Diplodus* sp. and *Trichiururs miocaenus* (DELFORTRIE, 1876). These species have not been found on basis of the otoliths.

TAPHONOMY

A total of 81.5% of the La Paillade fish fauna is from benthonic fishes (cf. Tab. 1-2). So, at a first glance, one could think the fossil assemblage should be autochthonous. However, the otolith-bearing marls contained a lot of coquina and the studied otoliths are therefore considered as slightly reworked and parautochthonous. Mediocre preservation of many otoliths probably does not result from reworking but from reaction with the circulating pore waters in the fossiliferous sediment.

PALAEOECOLOGY

The palaeoecological analysis is based on the comparison with extant related taxa. The analysis is greatly enhanced from the fact that nearly all fish species from La Paillade belong to Recent genera (Tab. 2). Moreover, *Pagrus* aff. *coeruleostictus* and *Sciaena* aff. *umbra* are two fossil species closely related or identical to the Recent *P. coeruleostictus* and *S. umbra.* Only *Palaeoesox* sp., *Prolebias* sp., *Dapalis rhenanus*, both atherinid species, and probably "genus Eleotridarum" *sectus* belong to fossil genera and do not have Recent representatives. The ecologic requirements of the Recent genera and species which were used for the palaeoecological assessment are compiled in Tab. 2.

Climate

Nearly all genera in the fish fauna from La Paillade represent tropical to subtropical conditions (Tab. 1-2). *Sillago schwarzhansi* and *Brachydeuterus latior* are among the dominant species in the La Paillade fish fauna and Recent species of *Sillago* and *Brachydeuterus* thrive exclusively in tropical waters. Only *Sciaenops* sp. and the *Morone* species could allude to a somewhat cooler climate, but these species are very

rare.

Locality "La Paillade" at Montpellier (Lower Miocene)			
Fish species	number ofotoliths	portion in %	Family
"genus aff. *Elops* " sp.	2	< 0.1	Elopidae
Dussumieria sittigi n. sp.	15	0.3	Clupeidae
Palaeoesox sp.	1	< 0.1	Umbridae
Saurida sp.	1	< 0.1	Synodontidae
Sirembo sp.	1	< 0.1	Ophidiidae
Liza gaudanti n. sp.	40	0.7	Mugilidae
"genus Atherinidarum" sp.	1	< 0.1	Atherinidae
"genus Atherinid." cf. *bavayi* STEURBAUT, 1984	1	< 0.1	
Hyporhamphus sp.	1	< 0.1	Hemirhamphidae
Prolebias sp.	5	0.1	Cyprinodontidae
Dapalis rhenanus (KOKEN, 1891)	78	1.4	Ambassidae
Morone cornuta NOLF & CAPPETTA, 1980	21	0.4	Moronidae
Epinephelus? sp.	1	< 0.1	Serranidae
Sillago schwarzhansi STEURBAUT, 1984	131	2.4	Sillaginidae
Gerres sp.	7	0.1	Gerreidae
Brachydeuterus latior (SCHUBERT, 1906)	233	4.2	Haemulidae
Pomadasys steurbauti NOLF & CAPPETTA, 1980	12	0.2	
"genus aff. *Haemulon*" sp.	1	< 0.1	
Pagrus aff. *coeruleostictus* (VALENCIENNES, 1830)	30	0.5	Sparidae
Pagrus cf. *distinctus* (KOKEN, 1891)	1	< 0.1	
Dentex gregarius (KOKEN, 1891)	5	0.1	
Argyrosomus sp.	2	< 0.1	Sciaenidae
Sciaena irregularis KOKEN, 1884	280	5.1	
Sciaena aff. *umbra* LINNAEUS, 1758	26	0.5	
Umbrina sp.	30	0.5	
"genus aff. *Sciaenops*" sp.	2	< 0.1	
Cepola rubescens LINNAEUS, 1766	5	0.1	Cepolidae
"genus Eleotridarum" *sectus* STINTON, 1968	95	1.7	Eleotridae
Gobius multipinnatus (H. v. MEYER, 1852)	450	8.1	Gobiidae
***Lesueurigobius vicinalis* (KOKEN, 1891)**	**4050**	**73.2**	

Table 1.— The fish fauna from La Paillade at Montpellier, list of taxa and their frequency. 100 % = 5533 otoliths.

Salinity

Ten of the fossil fish species of the La Paillade fish fauna belong to marine-stenohaline genera, among them the dominating *Lesueurigobius vicinalis*-species complex (Tab. 2). Salinity demands of the Recent *Pagrus coeruleostictus* also support a marine-stenohaline environment because a closely related (or identical) *Pagrus* species occurs in the fossil fauna. A total of 74% of the studied otoliths belong to marine-stenohaline species.

	Ecology / Taxa (R = Recent, f = fossil)	biogeography			climate			salinity			bathymetry				way of life	
		cosmopolitan	Atlantic-Mediterr.	Pacific-Indopacific	tropical	subtropical	cool to temperate	lacustrine	euryhaline to brackish	marine	littoral	sublittoral	epi- to mesopelagic	bathypelagic	benthonic	nectonic
R	*Elops*	(k)			t	w			(e)	m	li	sl				ne
R	*Dussumieria*			(i)	t	w		l	e	m			ep			ne
R	Cyprinidae	(k)			t	w	k	l	(e)							ne
f	*Palaeoesox*				t	w		l								ne
R	*Saurida*	k			(t)					m	li	sl			be	
R	*Sirembo*			(i)	t	w				m	li	sl			be	
R	*Liza*	k			t	w	k		e	m	li	sl				ne
R	Atherinidae		a-m		t	w		l	e	m	(li)					ne
R	*Hyporhamphus*	k			t	w				m			ep			ne
f	*Prolebias*		a-m		t	w		l	e	(m)	(li)					ne
f	*Dapalis*		m		t	w		l	e	(m)	(li)					ne
R	*Morone*		a-m			w	k	l	e	m	li	sl				ne
R	*Epinephelus*	k			t	w			e	m		(sl)			be	
R	*Sillago*			(i)	(t)				e	m	(li)					ne
R	*Gerres*	k			t	w			e	m	li	sl				ne
R	*Brachydeuterus*		a-m		(t)				e	m	li	sl				ne
R	*Pomadasys*	k			t	w			e	m	li	sl				ne
R	*Haemulon*			(i)	(t)					m	(li)					ne
R	*Pagrus coeruleostictus*	k			t	w				m		(sl)				ne
R	*Dentex*		a-m		t	w				m		(sl)	ep			ne
R	*Argyrosomus*	k			t	w	k		e	m	li	sl				ne
R	*Sciaena umbra*	k			t	w			e	m	li	sl				ne
R	*Umbrina*	k			t	w			e	m	li	sl				ne
R	*Sciaenops*		a			w				m	(li)					ne
R	*Cepola*	k			t	w				m	li	sl			be	
R	Eleotridae		m		t	w		l	e	m	(li)					ne
R	*Gobius*		a-m		t	w			e	m	li	sl			be	
R	*Lesueurigobius*		a-m		t	w				m	(li)	sl			be	

Tableau 2.— Ecology of Recent species, genera and families with representatives in the fossil fish fauna at La Paillade. O marks habitats of genera important for the ecological analysis. (k) = nearly cosmopolitan.

In addition, 12 marine-euryhaline species are present with a total of 22% of the identified otoliths. Salinity demands of the Recent *Sciaena umbra* distinctly allude to a marine-euryhaline environment because a closely related (or identical) *Sciaena* species was found in the fossil fauna. Marine-euryhaline species primarily live in the open sea but they also dwell in lagoons, deltas, or in brackish estuaries where they can profit from nutrient rich waters.

A total of 4% of all otoliths representing seven species belong to a third, euryhaline group of fossil fishes (Tab. 2). Their Recent representatives occur in fresh or brackish water, in hypersaline biotopes, and in the open sea. Among these species, "genus Atherinidarum" cf. *bavayi* and *Morone cornuta* are described from marine

deposits (Steurbaut, 1984; Nolf & Cappetta, 1980) and can be considered as marine-euryhaline species. *Dapalis rhenanus* is known from the Upper Rhinegraben and the Mayence and Hanau Basin where it typically occurs in brackish deposits (cf. Reichenbacher, in press). *Prolebias* species and "genus Eleotridarum" *sectus* have been recorded from lacustrine and brackish environments (cf. Reichenbacher & Weidmann, 1992; Reichenbacher, 1996a-b).

Only 0.1% of the fauna belongs to freshwater fishes (*Palaeoesox* sp.).

In conclusion, the fish assemblage from La Paillade is interpreted as marine to marine-euryhaline.

Bathymetry

Genera typical for littoral, sublittoral and epi-/mesopelagic habitats (Tab. 2) are present in the La Paillade fish fauna.

Eight species of seven genera (5.7% of otoliths identified) represent littoral environments (Tab. 1-2). Fishes thriving mainly or exclusively in sublittoral waters are represented by five species of four genera (quantity: nearly 74%; Tab. 1-2). Fourteen species represent littoral and sublittoral environments (quantity: 20%). Epi- and mesopelagic fishes are rare and account for only 0.4% of all otoliths. *Dussumieria sittigi* n. sp., *Hyporhamphus* sp. and *Dentex gregarius*-species complex probably belong to this group.

Recent taxa of *Lesueurigobius* live in a water depth between 10 and 345 m, depending on species. In the Korneuburg Basin (near the Vienna Basin, Austria), a water depth between 10 and 50 m was reconstructed for *L. vicinalis* (cf. Reichenbacher, 1998). *Brachydeuterus latior*, a common species at La Paillade, also indicates a shallow water depth. *B. auritus*, the only Recent species, is known from about surface to 100 m water depth.

The fish assemblage from La Paillade thus represents a water depth deeper than 10 m in the transition zone between littoral and sublittoral. Probably, the open sea was far away because of the scarcity of pelagic fishes.

BIOSTRATIGRAPHY

Table 3 shows the stratigraphic distribution of fish species from the Aquitanian of La Paillade. Species present here also are known from other localities in the European Tertiary (for references, see systematic part). Four fish assemblages can be separated according to the stratigraphic range.

(1) Species known from late Oligocene to Middle Miocene times are *Pagrus distinctus*, *Dentex gregarius*-species complex, *Sciaena irregularis* and *Cepola rubescens*. They provide little data concerning biostratigraphy.

(2) Species recorded from deposits of Early and Middle Miocene age are the *Lesueurigobius vicinalis*-species complex, *Gobius multipinnatus*, *Sillago schwarzhansi* and *Brachydeuterus latior*. These taxa belong to the dominating fish species in the assemblage from La Paillade. They can be considered as typical for the Lower and Middle Miocene.

(3) Species previously described only from late Lower Miocene (Burdigalian) sediments are *Morone cornuta* and *Pomadasys steurbauti*. They support a late Lower Miocene (Burdigalian) age.

(4) *Dapalis rhenanus* is limited to the Early Miocene (Aquitanian) and "genus Eleotridarum" *sectus* occurs in Late Oligocene and Early Miocene deposits. They are not known from deposits younger than Aquitanian.

Based on otoliths, a late Aquitanian age is therefore assigned for the La Paillade fish fauna. This age is supported by the occurence of typically Burdigalian species co-occuring with typical Aquitanian species. However, according to the mammals, the La Paillade locality was dated early Aquitanian (Aguilar, 1982; de Brujin, 1992: Tab. 1; Steininger *et al.*, 1996: 27). We therefore conclude that the stratigraphic range of the "Burdigalian" species *Morone cornuta*, *Sillago schwarzhansi*, and *Pomadasys steurbauti* is longer than previously known.

Fish species	Upper Oligocene	Lower Miocene		Middle Miocene
		Aquitanian	Burdigalian	Langhian
"genus Atherinidarum" *bavayi*		x	x	
Dapalis rhenanus		x		
Morone cornuta			x	
Sillago schwarzhansi			x	x
Brachydeuterus latior		x	x	x
Pomadasys steurbauti			x	
Pagrus distinctus	x			x
Dentex group *gregarius*	x	x	x	x
Sciaena irregularis	x	x		x
Cepola rubescens	x	x	x	x
"genus Eleotridarum" *sectus*	x	x		
Gobius multipinnatus		x	x	x
Lesueurigobius vicinalis		x	x	x

Table 3.— Stratigraphic distribution of fish species identified in the La Paillade deposits at other localities in the European Tertiary (for references see text).

BIOGEOGRAPHY AND PALAEOGEOGRAPHY

Based on the biogeography of the Recent genera (Tab. 2), the fish fauna from La Paillade is dominated by cosmopolitic and Atlantic-Mediterranean genera and resembles Recent fish faunas from the Mediterranean Sea. However, *Dussumieria*, *Sirembo* and *Sillago* are present in Recent fish faunas exclusively in the Indopacific area. Their occurence in the Early Miocene (Aquitanian) of La Paillade results from the broad connection between the Indian Ocean and both the Mediterranean and Paratethys Seas during that time (cf. Rögl, 1998: 292, pl. 4).

The fish fauna from La Paillade is the first evidence in the Mediterranean of a marginal-marine teleost fish fauna from the Early Miocene. Based on the occurence of

some euryhaline species, the La Paillade fauna can be compared with brackish fish faunas from the western Paratethys, the Upper Rhinegraben, and the Mayence and Hanau Basins. Implications concerning the palaeogeography of the continental basins of Central Europe are possible:

(1) Faunal relationship to the western Paratethys: "genus Eleotridarum" *sectus* is a species present at La Paillade as well as in the Late Oligocene and Early Miocene of the western Paratethys. *Dapalis rhenanus* and *Morone cornuta* from La Paillade resemble and probably are related to *Dapalis carinatus*, *D. rhomboidalis*, and a new *Morone* species (Reichenbacher, in prep.) from the western Molasse Basin. This suggests, some connections existed between the fish faunas from southern France (La Paillade) and the western Molasse Basin, but these relations are not very distinct.

(2) Faunal relationship to the Upper Rhinegraben and Mayence and Hanau Basins (Germany): *Sciaena irregularis* and *Dapalis rhenanus* are the only species present both in La Paillade and in the Upper Rhinegraben, up to the Mayence and Hanau Basins. In these German deposits, *D. rhenanus* has been found in middle to late Aquitanian sediments; *S. irregularis* stratigraphically ranges from the latest Oligocene to late Aquitanian and is also known from the Late Oligocene and Middle Miocene in the North Sea Basin (cf. Reichenbacher, in press). In these latter deposits, however, *Dapalis rhenanus* has never been identified (cf. Schwarzhans, 1994; Müller, 1990, 1996; Menzel, 1986; Gaemers, 1990; Reichenbacher, 1997). *D. rhenanus* must therefore have immigrated into the Upper Rhinegraben and the Mayence and Hanau Basins from the Mediterranean region of southern France by crossing the Rhône-Bressegraben, and not from the North Sea (cf. Reichenbacher, in press).

SUMMARY AND CONCLUSIONS

A fossil fish fauna from the La Paillade locality at Montpellier was studied based on 5533 otoliths. The otolith-bearing layer was correlated to mammal zone MN 1 by Aguilar (1982) and, therefore, should correspond to the Early Miocene. The fish fauna consists of 30 taxa representing 20 families. Two species are new, *Dussumieria sittigi* and *Liza gaudanti*. The predominant faunal element is *Lesueurigobius vicinalis*-species complex, comprising 73% of all otoliths. The next most abundant species are *Gobius multipinnatus* (8%), *Sciaena irregularis* (5%), *Brachydeuterus latior* (4%), *Sillago schwarzhansi* (2.5%), "genus Eleotridarum" *sectus* (2%), and *Dapalis rhenanus* (1.5%). These seven species represent a total of 96% of the otoliths identified, whereas the final 4% belongs to an additional 24 taxa. The presence of these extremely rare species results from the large amount of sediment (several 100 kg) processed for the present study. This fish fauna is the first neritic teleost fish fauna from the earliest Miocene of the Mediterranean realm (cf. Reichenbacher, 1997: 197).

The palaeoecological analysis reveals a marine to marine-euryhaline fish fauna living under tropical to subtropical conditions in the transition zone from littoral to sublittoral. Water depth probably was more than 10 m. The scarcity of pelagic fishes suggests that habitat was either a sheltered bay and/or far away from the open sea.

Biostratigraphically, the studied fish fauna supports a late Aquitanian age but an early Aquitanian age is indicated by the micromammals. The stratigraphic range of the "Burdigalian" species *Morone cornuta*, *Sillago schwarzhansi*, and *Pomadasys steurbauti* thus seems to be distinctly longer than previously suggested.

Some genera are represented in the La Paillade fish fauna which presently live exclusively in the Indopacific realm. Their presence strongly supports a broad connection between the Indian Ocean and both the Mediterranean and the Paratethys Seas during the Early Miocene (Aquitanian) (cf. Rögl, 1998). In addition, faunal relationships were found between the La Paillade fish fauna and both the Paratethys fish fauna and the fish fauna from the deposits in the Upper Rhinegraben and the Mayence and Hanau Basins (Germany).

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EXPLANATIONS OF PLATES

PLATE 1

All otoliths come from the early Lower Miocene of the La Paillade site at Montpellier (fossiliferous basal marls), except Fig. 1 which is a sagitta from a Recent fish. Fig. 10 is an utricular otolith (lapillus) shown from the outer face. All other figured otoliths are sagittae, shown from the inner face. L = Left sagitta. R = Right sagitta.

Fig. 1 is deposited in the collection of Recent fish otoliths of the Institut Royal des Sciences naturelles de Belgique, Bruxelles (IRSNB). Figs. 2-18 are deposited in the Laboratoire de Paléontologie, Université de Montpellier II (PLD 51-67).

Fig. 1.— *Dussumieria acuta* VALENCIENNES, 1847. - L; Recent (coll. IRSNB).

Figs. 2-5.— *Dussumieria sittigi* n. sp. - 2-3: R, paratypes (PLD 51-52); 4: R, holotype (PLD 53); 5: L, paratype (PLD 54).

Figs. 6-9.— *Liza gaudanti* n. sp. - 6, 8-9: R, paratypes (PLD 55, 57-58); 7: R, holotype (PLD 56).

Fig. 10.— Unidentified left utricular otolith (PLD 59).

Figs. 11-16.— "genus Eleotridarum" *sectus* (STINTON & KISSLING, 1968). - L (PLD 60-65).

Figs. 17-18.— *Gerres* sp. - 17: L (PLD 66); 18: R (PLD 67).

PLATE 2

All otoliths come from the early Lower Miocene of the La Paillade site at Montpellier (fossiliferous basal marls). All figured otoliths are sagittae, shown from the inner face. L = Left sagitta. R = Right sagitta.

The otoliths are deposited in the Laboratoire de Paléontologie, Université de Montpellier II (PLD 68-84).

Figs. 1-2.— *Pagrus* aff. *coeruleostictus* (VALENCIENNES, 1830). - R (PLD 68-69).

Fig. 3.— *Pagrus* cf. *distinctus* (KOKEN, 1891). - L (PLD 70).

Fig. 4.— *Pomadasys steurbauti* NOLF & CAPPETTA, 1980. - R (PLD 71).

Fig. 5.— *Epinephelus*? sp. - L (PLD 72).

Fig. 6.— *Saurida* sp. - R (PLD 73).

Fig. 7.— *Hyporhamphus* sp. - R (PLD 74).

Figs. 8-9.— *Sillago schwarzhansi* STEURBAUT, 1984. - R (PLD 75-76).

Figs. 10-11.— *Morone cornuta* NOLF & CAPPETTA, 1980. - L (PLD 77-78).

Fig. 12.— *Cepola rubescens* LINNAEUS, 1766. - R (PLD 79).

Fig. 13.— "genus Atherinidarum" cf. *bavayi* STEURBAUT, 1984. - L (PLD 80).

Fig. 14.— "genus Atherinidarum" sp. - L (PLD 81).

Figs. 15-16.— *Dapalis rhenanus* (KOKEN, 1891). - 15: L (PLD 82). 16: R (PLD 83).

Fig. 17.— *Brachydeuterus latior* (SCHUBERT, 1906). - R (PLD 84).

PLATE 3

All otoliths come from the early Lower Miocene of the La Paillade site at Montpellier (fossiliferous basal marls). All figured otoliths are sagittae, shown from the inner face. L = Left sagitta. R = Right sagitta.

The otoliths are deposited in the Laboratoire de Paléontologie, Université de Montpellier II (PLD 85-100).

Figures 1-5.— *Lesueurigobius vicinalis* (KOKEN, 1891)-species complex.

Figs. 1- 2, 4-5.— L (PLD 85-86, 88-89). 3: R (PLD 87).

Figures 6-10.— *Gobius multipinnatus* (H. V. MEYER, 1852).

Figs. 6-8.— L (PLD 90-92). 9-10: R (PLD 93-94).

Figures 11-12.— *Dapalis rhenanus* (KOKEN, 1891). - 11: L (PLD 95). 12: R (PLD 96).

Figures 13-15.— *Prolebias* sp. - L (PLD 97-99).

Figure 16.— *Palaeoesox* sp. - R (PLD 100).

PLATE 4

All otoliths come from the early Lower Miocene of the La Paillade site at Montpellier (fossiliferous basal marls), except Fig. 12a-b which was found in the Chattian from the southern North Sea Basin and is figured here for comparison. All figured otoliths are sagittae, shown from the inner face and also partly from the outer face (Figs. designated with b). L = Left sagitta. R = Right sagitta.

Figs. 1-11 are deposited in the Laboratoire de Paléontologie, Université de Montpellier II (PLD 101-111). Fig. 12 is kept in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main (Germany) (SMF).

Figs. 1-2.— *Sciaena irregularis* KOKEN, 1884 (x 5.5). - L (PLD 101-102).

Fig. 3.— *Sciaena irregularis* LINNAEUS, 1758 (x 6.0). - R (PLD 103).

Figs. 4a-b.— *Sciaena irregularis* KOKEN, 1884 (x 5.7). - L (PLD 104).

Figs. 5, 6a-b.— *Sciaena* aff. *umbra* LINNAEUS, 1758 (x 5.5 (Fig. 5), x 5.9). - R (PLD 105-106).

Figs. 7-8, 9a-b.— *Umbrina* sp. (x 6.2 (Fig. 7), x 5.9 (Fig. 8), x 5.4). - R (PLD 107-109).

Figs. 10a-b.— *Argyrosomus* sp. (x 4.4). - R (PLD 110).

Figs. 11a-b.— "genus aff. *Sciaenops*" sp. (x 5.0). - L (PLD 111).

Figs. 12a-b.— *Sciaena irregularis* KOKEN, 1884 (x 3.9). - L, Upper Oligocene, Chattian, Kasseler Meeressande (SMF P. 6290).

PLATE 5

Figs. 1-2, 7, 11 come from the early Lower Miocene of the La Paillade site at Montpellier (fossiliferous basal marls). They are deposited in the Laboratoire de Paléontologie, Université de Montpellier II (PLD 112-115). The other documented otoliths are sagittae from Recent fishes and are figured for comparison. They are kept in the collection of Recent fish otoliths of the Institut Royal des Sciences naturelles de Belgique, Bruxelles (IRSNB). All sagittae are shown from the inner face, except Fig. 11 which additionally is figured from the outer face (11b). L = Left sagitta. R = Right sagitta.

Fig. 1.— *Dentex gregarius* (KOKEN, 1891)-species complex (x 5.6). - L (PLD 112).

Fig. 2.— "genus aff. *Haemulon*" sp. (x 6.0). - L (PLD 113).

Fig. 3.— *Haemulon aurolineatum* CUVIER, 1830 (x 7.1). - L, Haiti (coll. IRSNB).

Figs. 4-5.— *Pomadasys incisus* (BOWDICH, 1825) (x 7.5). - L, ex coll. Chaine (coll. IRSNB).

Fig. 6.— *Pomadasys argyreus* VALENCIENNES, 1833 (x 6.8). - L, Australia (coll. IRSNB).

Fig. 7.— "genus aff. *Elops*" sp. (x 6.7). - L (PLD 114).

Fig. 8.— *Elops saurus* LINNAEUS, 1766 (x 8.4). - L, Australia (coll. IRSNB).

Fig. 9.— *Elops hawaiiensis* REGAN, 1909 (x 6.6). - L, Hawai (coll. IRSNB).

Fig. 10.— *Sirembo jordani* (DAY, 1888) (x 8.4). - L, gulf of Thailand (coll. IRSNB).

Figs. 11a-b.— *Sirembo* sp. (x 8.4). - L (PLD 115).

Fig. 12.— *Saurida tumbil* (BLOCH, 1795) (x 8.8). - L, Philippines (coll. IRSNB).

Figs. 13-14.— *Pagrus pagrus* (LINNAEUS, 1758) (x 8.3). - 13: L, 14: R, Teneriffa (coll. IRSNB).

PLATE 6

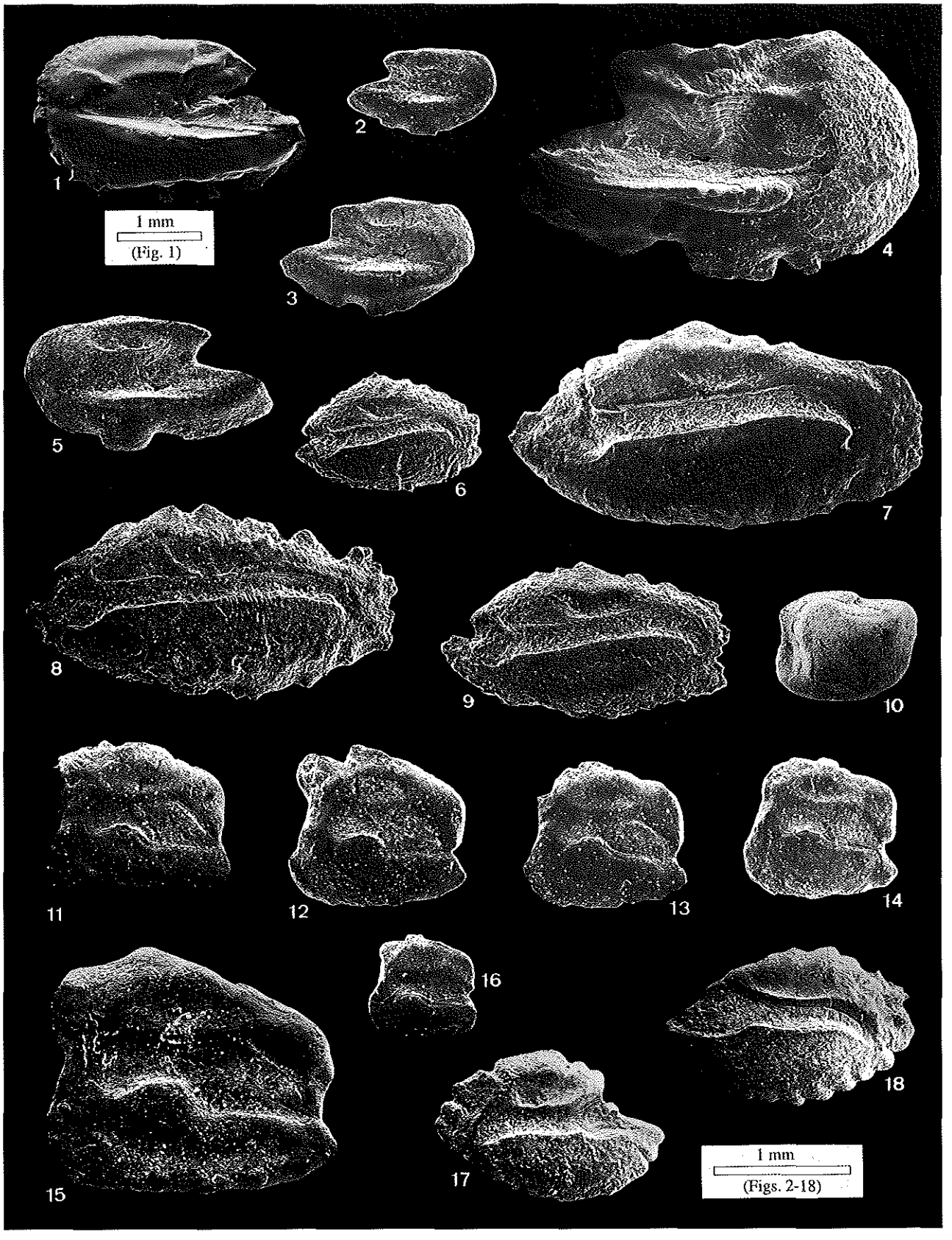
Fig. 1.— Terminology of a teleostean sagitta (modified from Chaine & Duvergier, 1934).

Fig. 2.— Left sagittae of Recent Sciaenids (coll. IRSNB).

A: *Sciaena umbra* LINNAEUS, 1758 (x 5.5). B: *Sciaenops ocellatus* (LINNAEUS, 1766) (x 6.0).

Fig. 3.— Right sagittae of Recent Gobiids (coll. Schwarzhans).

A: *Gobius niger* LINNAEUS, 1758 (x 23). B-C: *Gobius paganellus* LINNAEUS, 1758 (x 42).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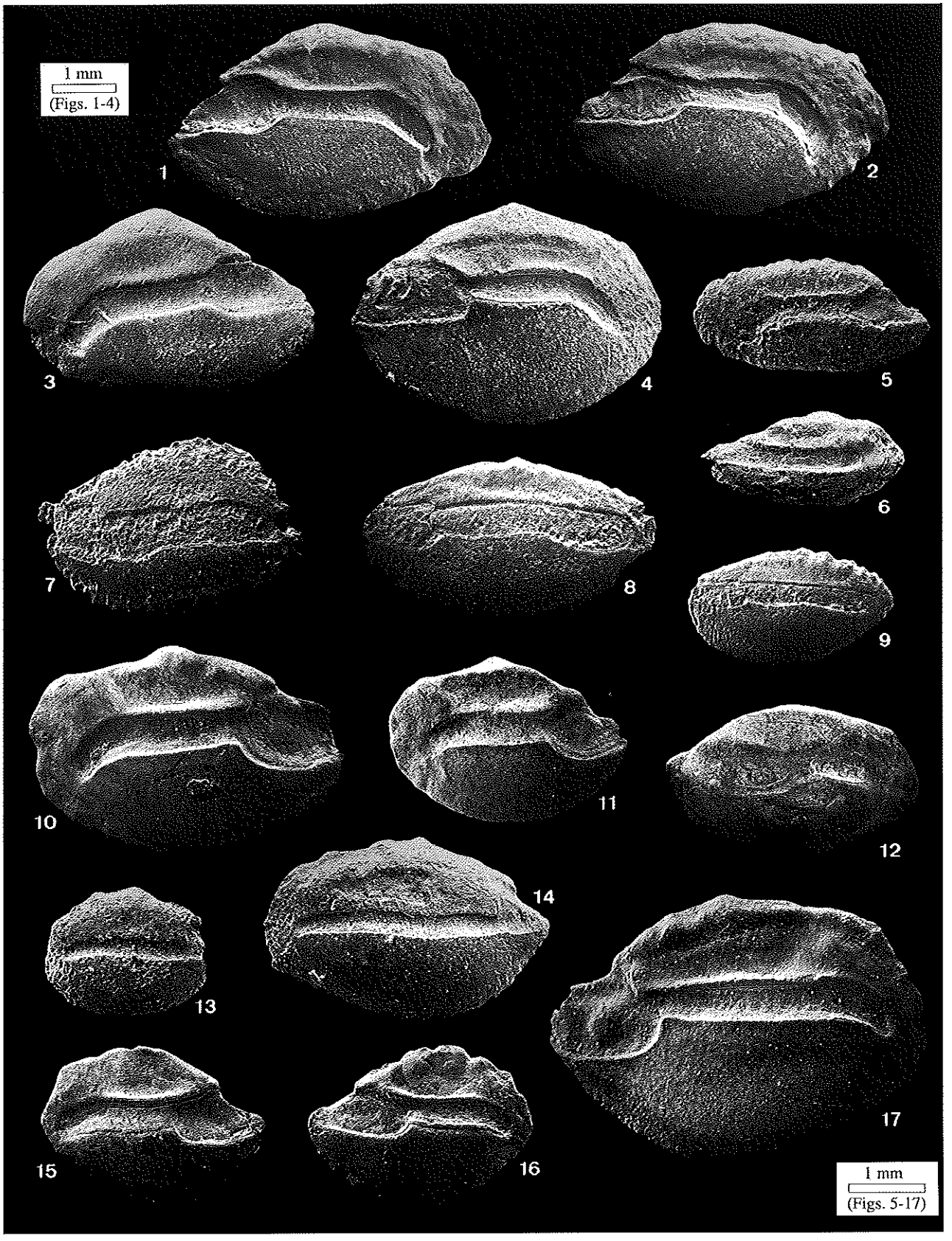
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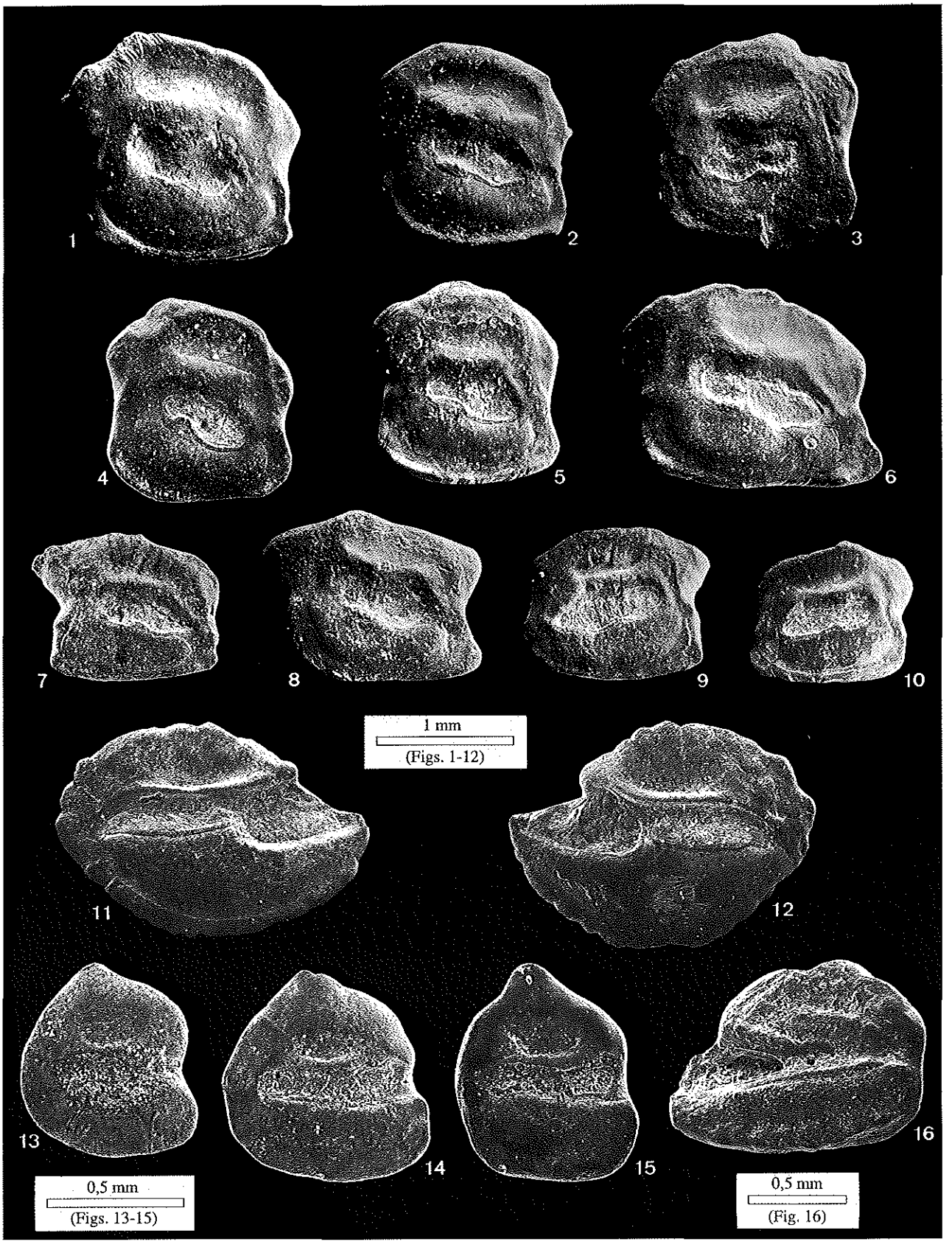
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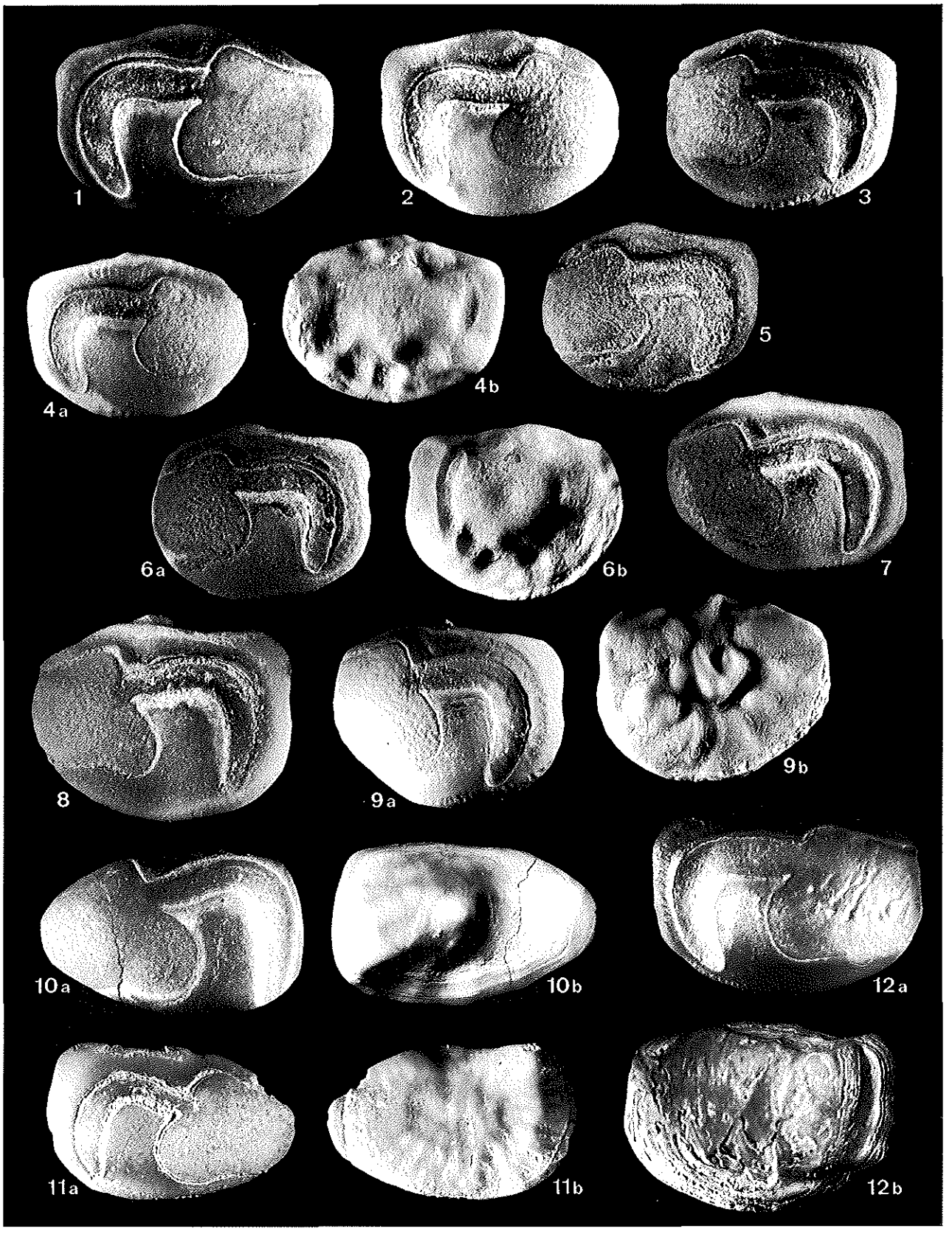
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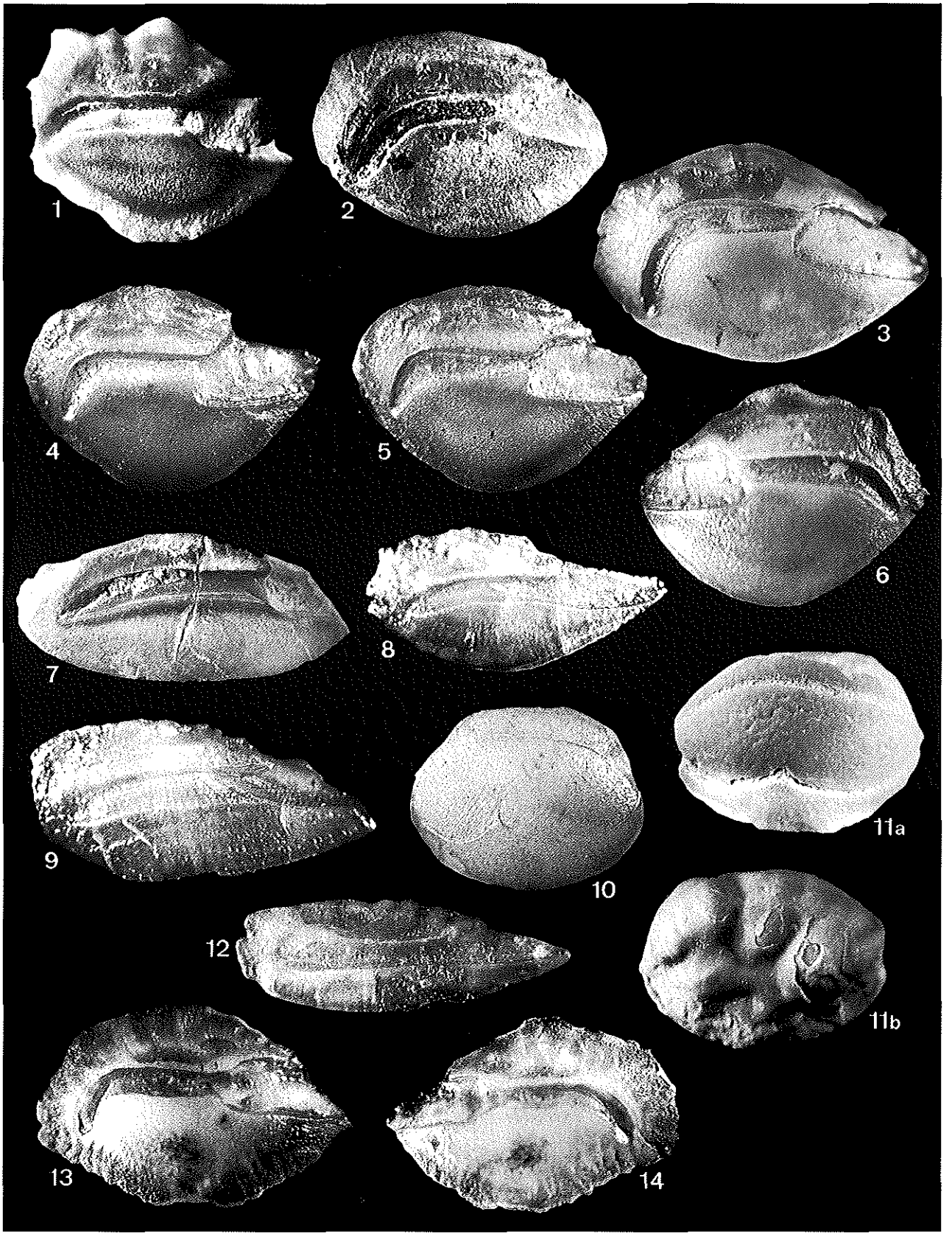
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Fig. 1

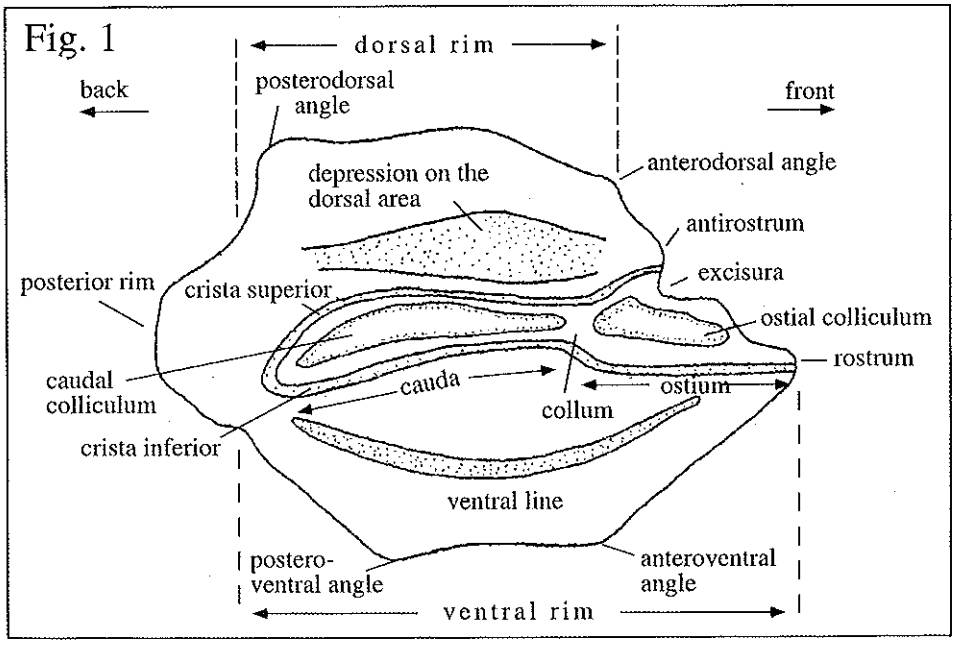

Fig. 2

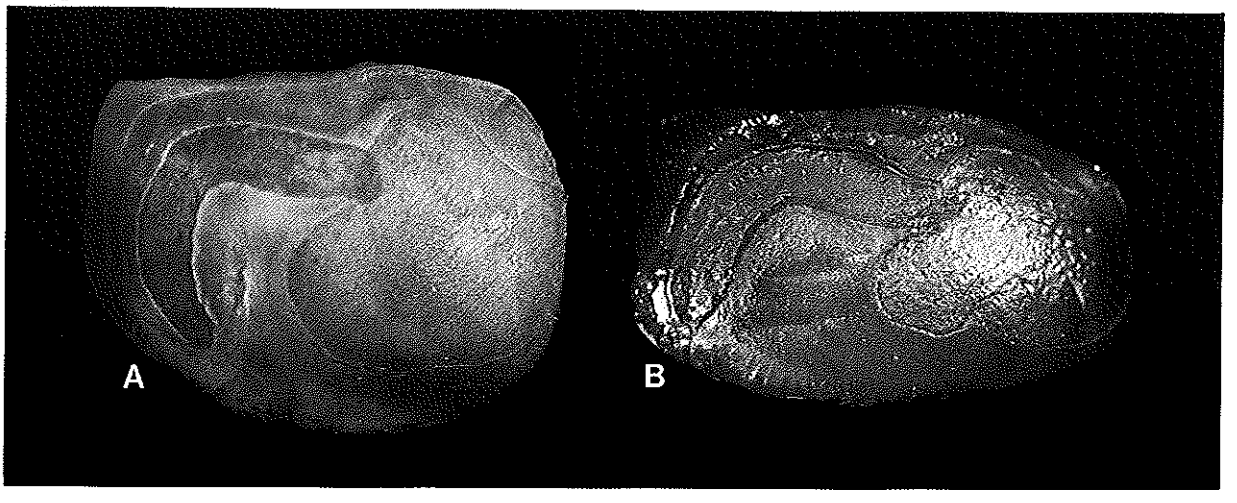

Fig. 3