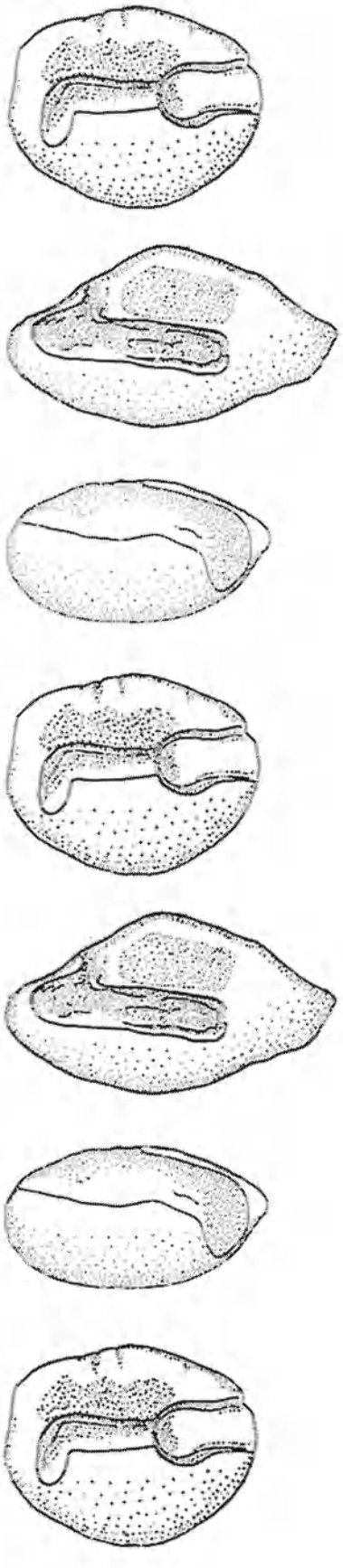

Late Eocene (Priabonian) Fish Otoliths from the Yazoo Clay at Copenhagen, Louisiana

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LOUISIANA STATE UNIVERSITY
Louisiana Geological Survey

Baton Rouge
2003

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Abstract

The study of late Eocene (Priabonian) otolith associations (5,559 specimens) from the Yazoo Clay exposures near Copenhagen, Caldwell Parish, Louisiana, allowed the reconstruction of a teleost fauna of 43 taxa, which is the most diversified assemblage presently known from a single U.S. Gulf Coast Paleogene locality. Twenty-seven taxa could be identified at the species level, and eight of those are new: *Ariosoma nonsector, Paraconger yazooensis,* "genus Neobythitinarum" *aequaloides, Centropristis priaboniana, Pristigenys obliquus,* "genus Gobiidarum" *vetustus,* "genus Citharidarum" *hoffmani,* and *Citharichthys altissimus.* Quantitative and qualitative study of a sample near the base of the section and a second one higher in the section indicates that, within the interval of the Yazoo Clay exposed at the Copenhagen locality, the environment evolved from a shallow neritic sea with abundant benthic life of both invertebrates and fishes to a deeper and more muddy environment with less benthic organisms and greater exposure to the pelagic realm. The late Eocene Yazoo Clay fauna is compared with the Recent fish fauna from tropical and subtropical American seas. Some typical American taxa like *Centropristis, Anisotremus, Orthopristis, Paraconger,* and *Citharichthys* already existed at that time. A significant number of families (or genera), which are no longer represented in the Recent American fauna, are present in the Yazoo Clay including the Pterothrissidae, Menidae, Trachinidae, Psettodidae, Citharidae, and *Centroberyx.* The presence of these groups is interpreted as an ancient Tethys distribution pattern. Differences in the composition of late Eocene and Recent sciaenid and ophidiid fish taxa are also significant.

Introduction

The Paleogene deposits of the U.S. Gulf Coast are renowned for their abundant fossils. Many of the deposits contain rich mollusk associations, and it is well known that the presence of mollusks is one of the best indicators for the presence of fish otoliths (Nolf, 1985; Nolf, 1995). Therefore, it is not surprising that the first otoliths from the U.S. Gulf Coast were described as early as 1888 (Koken, 1888), only four years after the first description of otolith-based fossil fish taxa (Koken, 1884). Koken's taxonomic approach was surprisingly good, considering the state of knowledge of Recent comparative material at that time. However, his data on stratigraphy and localities are very vague. Stratigraphic information is almost restricted to "Clayborne Beds", "Jackson Beds", and "Vicksburg Beds", and his text suggests that the precise stratigraphic relationship between these beds was still uncertain then. It should be noted that "Clayborne Beds" was misspelled by Koken (1888); the correct spelling is "Claiborne" for Claiborne, Alabama, as was determined and corrected by Meyer (1889).

Only 4 of the 24 taxa studied by Koken, (1888) are cited with precise localities. Koken's precise localities included the Mississippi cities of Red Bluff, Newton, Jackson, and Vicksburg. For six others, the locality "Jackson River, Mississippi" is cited as the collection site. However, there is no Jackson River in the area. Meyer (1889), who originally collected the otoliths, noted that the locality should have been "Jackson, Mississippi" in Koken (1888). This is corroborated by D. Dockery (Mississippi Office of Geology), who believes that it probably refers to the Pearl River at Jackson, Mississippi. The Moodys Branch Formation (near the confluence with Town Creek, the type locality for the Jackson Group or Jacksonian Stage) and the Yazoo Clay were exposed along the Pearl River at Jackson at that time. For the other taxa, the above-cited very generalized stratigraphic terminology was used without any locality names. Koken mentions that he acquired his material partly from the collection of O. Boettger in Frankfurt am Main, a collection conserved in part in the Humboldt University Museum für Naturkunde, Berlin (ZMB), and from the collection of O. Myer (New York). For the latter collection, he does not mention any depositary institution. Otto Myer was a German who collected and named mollusk species from the Moodys Branch Formation at Jackson, Mississippi. Koken's type material is important to this study because 13 of his taxa are cited as originating in the "Jackson Beds" or "Jackson River", which includes the Yazoo Clay and the underlying Moodys Branch Formation. Seventeen of Koken's taxa could be traced to the type material in the Humboldt Museum, allowing for the accurate identification of the Koken species represented in our material.

Subsequent papers dealing with the taxonomy of Cenozoic fish otoliths from the Gulf Coast are very scarce. Campbell (1929) reported on the stratigraphic value of otoliths, but his paper is an almost literal translation of Koken's 1888 paper (even using the same plates). Frizzell & Dante published the next relevant paper on American otoliths in 1965, but unfortunately this work has numerous deficiencies. The material was from small samples from an eclectic number of Gulf Coast localities ranging stratigraphically from early Eocene to the middle Oligocene and geographically from Alabama to Texas. None of the holotypes of the new species (fortunately deposited in the USNM) are figured in the paper. Only badly preserved paratypes are illustrated. Finally, a number of useless, exclusively otolith-based generic names are introduced, mainly based on European type species, which the authors almost certainly never saw. However, the type material in the USNM allows us to evaluate several of the new species introduced by Frizzell & Dante. About the same time, Frizzell and collaborators published several short papers on peculiar taxonomic groups such as myripristids, congrids, and albulids collected from Gulf Coast Cenozoic localities (Frizzell, 1965; Frizzell & Lamber, 1961; Frizzell & Lamber, 1962).

In 1979, Stringer first mentioned Yazoo Clay otoliths from the Copenhagen locality, but this study was based mainly on surface-collected material and did not mention any new taxa. Another study of Stringer (1986) utilized otoliths from the Moodys Branch and Yazoo Clay at the Montgomery Landing Site in Grant Parish, Louisiana, for paleoecological determinations, but it did not describe any new taxa. The most recent taxonomic study on Cenozoic Gulf Coast otoliths (Nolf & Dockery, 1993) concerns early Selandian otoliths and is of only marginal interest here. Various other studies by Stringer and collaborators mainly provide provisional faunal lists and otolith-based ecological data. Among those, we must mention the Breard & Stringer (1995) report because it concerns the locality studied in this paper.

The present study intends to provide an overview and taxonomic revision of the richly diversified otolith-based fish fauna from the Yazoo Clay at the Copenhagen locality. The line drawings of all 43 taxa should provide a basis for further taxonomic identification of teleost

otoliths from late Eocene strata in Louisiana, Arkansas, Mississippi, and Alabama. This investigation is also envisioned as a step towards a complete revision of the Paleogene fish otolith associations in the Gulf Coast.

Methodology

Since the 1970s, we have sampled a large number of Paleogene Gulf Coast localities with a stratigraphic range from early Paleocene to the late Oligocene and covering a geographical area from Texas to Alabama. One of the earliest sampled sites was the Copenhagen locality in Louisiana. A screenwashed sample was first examined during a visit to the exposure by both authors in 1982 and showed that the site contained a much more diversified fauna than the one published by Stringer (1979). A large sample of about 450 kg was taken in 1989 and provided the bulk of the present material. This large sample was screened through a standard 40-mesh sieve with no additives. The residue was systematically examined utilizing a binocular microscope (10x-40x). The residue provided 5,293 otoliths, yielding an average of about 12.6 specimens/kg of sediment. A smaller sample of 15 kg from the upper part of the section was processed using the same procedure and yielded 266 otoliths (about 17.7 specimens/kg).

Quantitative data on the otolith content of both samples are given in the first two columns of Table 1. The number of specimens for surface-picked material in the third column of Table 1 includes specimens collected by Nolf in 1982 with the addition of some rare specimens picked up by Stringer in latter years, which were not represented in the screenwashed samples. Numbers in the table published by Breard & Stringer (1995) concern samples of various stratigraphic and geographic origins and collecting dates; this explains the differences from the numbers reported in this study.

Locality data and stratigraphy

The material for this study comes from the prairies located in Caldwell Parish, Louisiana, between the old community of Copenhagen and the Ouachita River, about 9.7 km southeast of Columbia and east of State Highway 849 (Columbia 1/24 000 quadrangle, x = 591.900 m, y = 3544.100 m). A location map may be found in Breard & Stringer (1995, figure 2, p.78). A measured section is shown in Figure 1. The age of the Yazoo Clay in Louisiana is considered to be Priabonian, with the possible exception of the lowermost and uppermost strata (Manning & Standhardt, 1986). In some areas of Louisiana, the Yazoo Clay is divided into members, which are, respectively from the base to top, the Tullos, Union Church, and Verda. The uppermost section of the Verda consisting of marine sediments is designated as the Danville Landing Beds. The Yazoo Clay exposed at Copenhagen belongs to the Tullos Member (see Figure 2). This division is only of local use, however, and other subdivisions of the Yazoo Clay are applied in Mississippi and Alabama (Dockery, 1996).

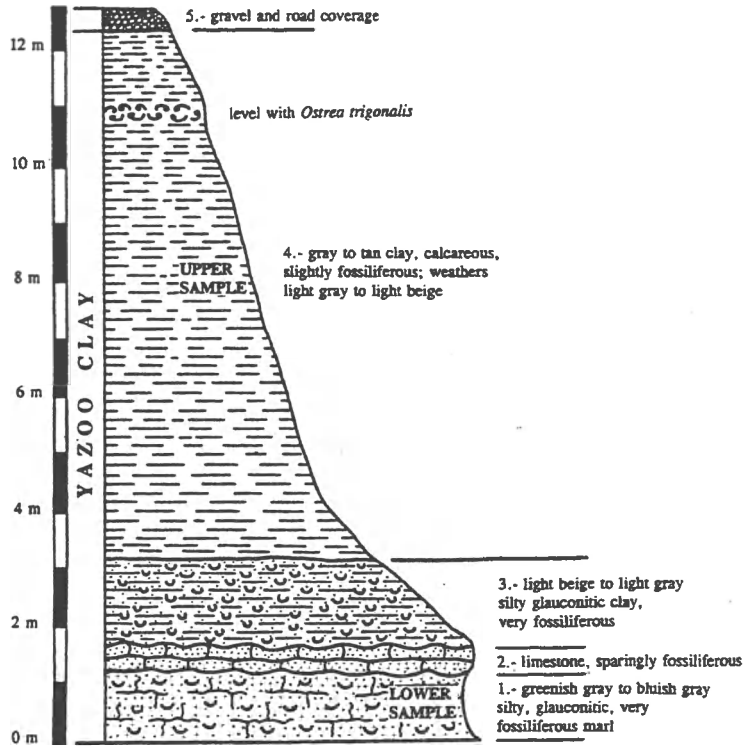

Figure 1. Measured section of the Yazoo Clay at the Copenhagen locality, Caldwell Parish, Louisiana.

Age	Stage	Group	Formation	Member/Bed	Lithology
Late Eocene	Priabonian	Jackson Group	Yazoo Clay	Danville Landing Beds	Interbedded sands, clays, with fossiliferous concretions (32 m)
				Verda Member	Lignitic clays, silty sands, lenticular marine sandstone, and clays (64-72 m)
				Union Church Member	Sandy silts, calcareous concretions (4.8 m)
				Tullos Member	Deep blue-gray clay (weathers tan), minor marl and limy clay beds, abundant fossils (24-56 m)
	Bartonian				

Figure 2. Strategraphic column of the Jackson Group (Upper Eocene), Ouachita River section, Louisiana

Otolith morphology and terminology

Because the terminology used in the description of bony fish otoliths is unique and known mainly to otolith paleontologists, a glossary of otolith terminology was deemed necessary and beneficial for this paper. In addition to the glossary, readers are directed to several references for information on the morphological features of otoliths. Chaine and Duvergier (1934, figure 6, p. 47) established the terms used in describing the various morphological features of otoliths, and the terminology is still in use today. General morphological features of the inner face of an otolith as well as the specialized morphology of myripristid, congrid, and albulid otoliths are illustrated in Stringer (1979, p. 97-98). An alphabetical listing and illustrations of morphological terms applied to otoliths are presented and evaluated by Nolf (1985, p. 7). Morphological features of otoliths may also be found in Nolf and Stringer (1992, text figure 3, p. 49). These references were utilized in developing the following alphabetized glossary of otolith terms. This glossary deals primarily with the morphological features of the inner face and the margins of the otolith.

Antirostrum: The antero-dorsal projection of the otolith dorsal to the notch in the excisura. The antirostrum must project over the excisura to be present.

Cauda: The posterior portion of the sulcus, located posterior to the ostium.

Crista inferior: The ventral rim or margin of the sulcus. As with the crista superior, it may be continuous or broken.

Crista superior: The dorsal rim or margin of the sulcus. It may be continuous or broken.

Colliculum: The raised part of the floor of the sulcus. The anterior colliculum is in the ostium, and the posterior colliculum is in the cauda.

Dorsal depression: A depression in the dorsal region of the inner face of an otolith. It often has a distinctive shape.

Excisura: The opening of the sulcus on the margin of the otolith. It occurs most often on the anterior margin. The sulcus must reach the margin for an excisura to be present. If present, it separates the rostrum and antirostrum.

Ostium: The anterior portion of the sulcus. The ostium may be separated from the posterior portion of the sulcus (the cauda) by a raised or wall-like structure, by a clear constriction of the sulcus, or by features on the floor of the sulcus.

Rostrum: The anterior extension of the otolith. If the sulcus does not reach the margin, then there is no

Table 1: OTOLITH-BASED FISH SPECIES FROM THE YAZOO CLAY

* = mentionned as such by STRINGER (1979)
** = mentionned as such by BREARD & STRINGER (1995)
(**) = identified at genus or family level only by BREARD & STRINGER (1995)

		lower sample	upper sample	surface collected	Iconography
ALBULIDAE	*Albula* sp. */**	-	-	5	Pl. 1, Fig. 2
PTEROTHRISSIDAE	*Pterothrissus* sp.	-	-	1	Pl. 1, Fig. 1
HETERENCHELYIDAE	"genus Heterenchelyidarum" *colei* (MÜLLER, 1999) (1)	81	9	-	Pl. 1, Figs. 3-8
CONGRIDAE	*Ariosoma nonsector* n. sp. (**)	577	-	5	Pl. 2, Figs. 1-6
	Conger vetustus FRIZZELL & LAMBER, 1962	7	1	-	Pl. 1, Fig. 9
	Gnathophis dissimilis (FRIZZELL & LAMBER, 1962)	1	-	-	Pl. 1, Fig. 11
	Paraconger sector (KOKEN, 1888) (2) (**)	17	-	-	Pl. 2, Figs. 9-10
	Paraconger yazooensis n. sp.	23	-	2	Pl. 2, Figs. 11-14
	Pseudophichthys glaber (KOKEN, 1888) (3) (**)	50	2	2	Pl. 1, Figs. 13-18
	Rhynchoconger sp. **	1	-	-	Pl. 1, Fig. 12
	" genus aff. *Uroconger*" sp. **	1	-	-	Pl. 2, Figs. 7-8
	"genus Congridarum" aff. *thevenini* (PRIEM, 1906) (4)	1	-	-	Pl. 2, Fig. 15
ARIIDAE	Ariidae ind. */**	1	-	1	Pl. 1, Fig. 10
SYNODONTIDAE	*Synodus* sp.	1	-	-	Pl. 3, Fig. 1
CARAPIDAE	Carapidae	1	-	-	Pl. 3, Fig. 2
OPHIDIIDAE	*Brotula aquitanica* NOLF, 1980 (5)	1	-	1	Pl. 7, Fig. 12
	"genus Sirembinorum" *granus* MÜLLER, 1999 (**)	76	-	-	Pl. 3, Figs. 15-17
	"genus Neobythitinarum" *meyeri* (KOKEN, 1888) (6)**	3120	6	42	Pl. 3, Figs. 3-10
	"genus Neobythitinarum" *aequaloides* n. sp.	7	-	1	Pl. 3, Figs. 11-14
BREGMACEROTIDAE	*Bregmaceros* sp. (7) **	15	244	-	Pl. 3, Fig. 18
ATHERINIDAE	"genus Atherinidarum" *debilis* (KOKEN, 1888) (**)	16	-	-	Pl. 3, Figs. 20-21
BERYCIDAE	*Centroberyx* sp. (8) **	1	-	1	Pl. 3, Fig. 19
MYRIPRISTIDAE	"g. Myripristidarum" *cajun* (FRIZZELL & LAMBER, 1961) (9)	2	-	1	Pl. 4, Figs. 1-2
CAPROIDAE	*Antigonia* sp.	-	-	1	Pl. 4, Fig. 15
Percoideoi inc. sed.	"genus Percoideorum" sp.	6	-	-	Pl. 4, Figs. 13-14
SERRANIDAE	*Centropristis priaboniana* n. sp.	28	-	-	Pl. 4, Figs. 3-6
PRIACANTHIDAE	*Pristigenys obliquus* n. sp. (**)	44	-	-	Pl. 4, Figs. 7-12
MALACANTHIDAE	"genus Malacanthidarum" *sulcatus* (KOKEN, 1888) (10)	57	-	-	Pl. 5, Figs. 3-8
MENIDAE	*Mene* sp. (11)	1	-	-	Pl. 4, Fig. 16
HAEMULIDAE	*Anisotremus* sp. (12)	-	-	1	Pl. 5, Fig. 13
	Orthopristis americana (KOKEN, 1888) (13)	230	-	2	Pl. 4, Figs. 17-21
	"genus Haemulidarum" *obliquus* (MÜLLER, 1999) (14)	3	-	-	Pl. 6, Figs. 1-2
SPARIDAE	"genus Sparidarum" *elegantulus* (KOKEN, 1888) (**)	129	-	2	Pl. 6, Figs. 6-11
SCIAENIDAE	"genus aff. *Nibea*" sp. (15)	-	-	1	Pl. 6, Fig. 12
	Sciaena aff. *pseudoradians* (DANTE & FRIZZELL, 1965) (16)	78	-	-	Pl. 6, Figs. 3-5
	"genus Sciaenidarum" *claybornensis* KOKEN, 1888 (17)	631	-	18	Pl. 7, Figs. 1-5
TRACHINIDAE	"genus Trachinidarum" *laevigatus* (KOKEN, 1888) (18)	4	-	-	Pl. 8, Fig. 1
BLENNIIDAE	"genus Blenniidarum" *cor* (KOKEN, 1888) (19)	14	-	-	Pl. 8, Figs. 2-4
GOBIIDAE	"genus Gobiidarum" *vetustus* n. sp. (**)	55	2	-	Pl. 7, Figs. 6-11
SCOMBRIDAE	Scombridae ind. **	2	-	-	Pl. 8, Fig. 6
PSETTODIDAE	*Psettodes* sp.	1	-	-	Pl. 8, Fig. 5
CITHARIDAE	"genus Citharidarum" *hoffmani* n. sp.	4	-	-	Pl. 8, Fig. 9-11
PARALICHTHYIDAE	*Citharichthys altissimus* n. sp. **	6	2	-	Pl. 8, Fig. 7-8

Table 1. Otolith-based fish species from the Yazoo Clay.

rostrum. If the excisura has a notch, then the rostrum is ventral to the notch. If no notch is present, it measured from the anterior edge of the crista superior. If an ostial canal is present (as in many congrids), it is measured from the posterior edge of the canal at the margin.

Sulcus: A pattern caused by the attachment of the otic nerve to the otolith. Usually the most prominent feature on the inner face (the side towards the brain) of an otolith. It typically consists of a longitudinal groove or depression on the inner face. The sulcus is one of the primary diagnostic structures of an otolith and may be divided into two parts or undivided.

Ventral furrow: A furrow occurring in the ventral portion of the inner face of an otolith, usually concentric to the ventral rim or edge of the otolith.

Systematic paleontology

A list of all teleost taxa represented in our samples, both screenwashed and surface-collected, is given in Table 1. The classification adopted here is basically the one utilized by Nelson (1994). Drawings of all cited species are presented in the plates. In some cases, the Recent comparative material on which the generic identification is based is also figured. Additional comments are given only for new species or for those requiring discussion.

For general information about otoliths (morphological nomenclature, composition, diagnostic value, ontogenetic changes, variability, etc.), the reader is referred to the *Handbook of Paleoichthyology* (Nolf, 1985). A few words can be said, however, about collective (or open) generic nomenclature, a procedure that is currently used in numerous papers on otolith taxonomy and is applied in the present paper. For species of uncertain generic position (i.e., whose systematic position can be identified only at the familial, subordinal, or ordinal level), we use the word "genus", followed by the name of the family or higher category in plural genitive, followed by the species name, e.g., "genus Heterenchelyidarum" *colei*. See also Nolf (1985) for a full explanation.

Remarks on taxa requiring comments

1. "genus Heterenchelyidarum" *colei* (Müller, 1999). Cited as *Eosolea texana* in Stringer (1979) and cf. *Pythonichthys* by Breard & Stringer (1995). Müller originally referred this species to the West African genus *Panturichthys* Pellegrin, 1913, which is too rigorous an attribution. The otoliths concerned indeed belong to a heterenchelyid eel, but they do not match exactly any of the Recent heterenchelyid genera.
2. *Paraconger sector* (Koken, 1888). See the description of the new species *Ariosoma nonsector* section "Affinities" for an evaluation of Koken's type material. The recently described *Paraconger americanus* Müller, 1999 from the Piney Point Formation, Bartonian of Virginia, is a synonym of P. *sector*.
3. *Pseudophichthys glaber* (Koken, 1888). Mentioned by Stringer (1979) as Anguilla ? sp. and Conger ? vetustus, respectively on plate 1, figures 2 and 5.
4. "genus Congridarum" *thevenini* (Priem, 1906). "genus Congridarum" *diagonalis* (Stinton & Nolf, 1970), cited in many papers on Eocene otoliths, is a junior synonym of "genus Congridarum" *thevenini* (Priem, 1906). The latter taxon was considered as doubtful by Nolf (1985, p. 132), but the numerous topotypes from Hérouval that are now available leave no doubt about the identity of the holotype.
5. *Brotula aquitanica* Nolf, 1980. The specimens from the Yazoo Clay look almost identical to a large specimen from the Upper Ypresian of Aquitaine (southwest France) figured by Nolf (1988, plate 6, figure 6). The species is also known from the Priabonian of Ukraine (Müller, unpublished data).
6. "genus Neobythitinarum" *meyeri* (Koken, 1888). Mentioned by Stringer (1979, p. 102, plate 1, figure 8) as *Preophidion stintoni*.
7. *Bregmaceros* sp. Mentioned by Stringer (1979, p. 102, plate 1, figure 7) as *Bregmaceros troelli*?
8. *Centroberyx* sp. Broken and worn specimens of this taxon were cited as *Pristipomoides* sp. by Breard & Stringer (1995).
9. "genus Myripristidarum" *cajun* (Frizzell & Lamber, 1961). Mentioned by Stringer (1979, p. 102, plate 1, figure 7) as *Myripristis creola* and as *Myripristis* sp. in Breard & Stringer (1995).
10. "genus Malacanthidarum" *sulcatus* (Koken, 1888). This species is represented at the Copenhagen locality by a good series of otoliths that documents and illustrates their growth and variability. They apparently represent a poorly known species already described by Koken (1888) as *Otolithus* (Cottidarum) *sulcatus*. The holotype of this species is lost, but Koken's figure allows the recognition of three otoliths (Nolf, 2003; plate 1, figure 14) among material (provided by David Dockery) from the Moodys Branch Formation at Town Creek, Jackson, the supposed type locality of Koken's species. The Yazoo Clay specimens allow a clear definition of the taxon. The species is characterized by elongate otoliths whose rims and surfaces are all strongly sculptured.

There is a rather blunt rostrum and an oblique ostial border showing some concavity but not a true excisura. The antirostrum is rudimentary. The outer face is concave and shows essentially radial ornamentation, especially in the dorsal zone. The inner face is markedly convex with the strongest convexity located in the dorsoventral direction. The sulcus is deeply incised, with the deepest parts located in the ostium and in the posterior expansion of the cauda. Many specimens show a fine narrow ventral furrow. In the dorsal area, a depression just above the crista superior accentuates this structure. These otoliths show many similarities to those of recent malacanthids (Plate 5, Figures 1-2 and 9-10). Because of the aspect of their sulcus and their elongation, they seem to be closest to those of the genus *Caulolatilus* Gill, 1862 (Plate 5, Figures 9-10), but their dorsal rim does not match the very straight dorsal rim seen in the figured Recent species.

11. *Mene* sp. The present figured specimen is the "undescribed menid from the Yazoo Clay" mentioned by Nolf & Bajpai (1992). Refer to that paper for an account of the fossil record of the genus *Mene.*

12. *Anisotremus* sp. A very large single specimen has a sulcus that is very similar to the sulcus observed in Recent species of the genus *Anisotremus* Gill, 1861 (see Plate 5, Figures 11, 12, 14). The fossil otolith differs, however, from the three illustrated Recent species in its shorter downward turned portion of its cauda.

13. *Orthopristis americana* (Koken, 1888). This species, originally attributed to the carangids by Koken, was referred to the haemulid (then called pomadasyid) family by Nolf (1985, p. 114). *O. americana* was cited as *Allomorone* sp. by Stringer (1979, p. 103, plate 1, figure 12) and as "Haemulidae" by Breard & Stringer (1995). The examination of many additional Recent haemulid otoliths convinced us that many of the common Paleogene haemulids from Europe and North America belong to the genus *Orthopristis* Girard 1858, compare e.g. to the Recent *O. chrysoptera* (Linnaeus, 1758) and *O. ruber* (Cuvier, 1830) otoliths figured by Nolf & Lapierre (1977, plate 2, respectively figsures 4 and 5). Other Paleogene haemulids to be included in the genus *Orthopristis* are: *O. bartonensis* (Priem, 1912), *O. burlesonensis* (Dante & Frizzell in Frizzell & Dante, 1965), *O. kokeni* (Leriche, 1905), *O. pouwi* (van Hinsbergh, 1980), *O. rectangulus* (Frost, 1934), and *O. trewavasae* Nolf & Lapierre, 1979.

14. "genus Haemulidarum" *obliquus* (Müller, 1999). This species was originally referred to the genus *Xenistius* Jordan & Gilbert, 1883 by Müller, but does not match exactly the more elongate otoliths of that genus, which is moreover endemic to the Recent eastern Pacific fauna. "g. H." *obliquus* is most closely related to "g. H." *pulcher* Frost, 1934 from the European Eocene (this species was also referred to *Xenistius* by Nolf, 1985, p. 86). The American species can be distinguished by its very restricted anteroventral area, as illustrated by Müller (1999, fig. 30, 24-25). This species was cited as *Pristipomoides* sp. by Breard & Stringer (1995).

15. "genus aff. *Nibea*" sp. A large, somewhat eroded otolith from the Yazoo Clay that does not match those of any Recent American sciaenid genus. By the outline of its ostium and the general shape, this otolith could be interpreted as a plesiomorph form of the genus *Nibea* Jordan & Thompson, 1911 (see Plate 6, Figure 13), having not yet acquired the strong ventrally flexed end of the cauda. However, this is only a tentative interpretation until more specimens can be collected.

16. *Sciaena* aff. *pseudoradians* (Dante & Frizzell, 1965). These otoliths seem to be almost identical to those of the early Oligocene *Sciaena pseudoradians.* Although the holotype is a juvenile otolith, we have good growth series for these species from several Oligocene deposits. Perfectly preserved large otoliths from the Yazoo Clay are required to be certain of their identity. This taxon was cited as *Corvina intermedia* by Stringer (1979, p. 103, plate 1, figure 13) and as *Frizzellithus gemma* by Breard & Stringer (1995).

17. "genus Sciaenidarum" *claybornensis* Koken, 1888. Cited by Stringer (1979, p. 103, plate 1, figure 15) as *Jefitchia claybornensis.*

18. "genus Trachinidarum" *laevigatus* (Koken, 1888). Mentioned as Uranoscopidae ind. in by Breard & Stringer (1995).

19. "genus Blenniidarum" *cor* (Koken, 1888). This species was originally described as a triglid by Koken, but is probably more likely related to blenniids. See the otoliths of various taxa figured by Smale *et al.* (1995, p. 125-127).

Description of new species

ARIOSOMA NONSECTOR n. sp.

(PLATE 1, FIGURES 1-6)

1888 *Otolithus (Platessae) sector* Koken - Koken, p. 292, Plate 17, Figures 15-16; not figure 14 (= lectotype of *Paraconger sector*);

1979 *Ariosoma* sp. - Stringer, p. 102, plate 1, figure 4.

Type material: Holotype: a left otolith (Plate 2, Figure 1) (IRSNB P 6952), 581 paratypes of which 5 are figured (Plate 2, Figures 2-6) (IRSNB P6953-6957).

Dimensions of the holotype: Length: 4.1 mm; height: 3.8 mm; thickness: 1.2 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: Alludes to the fact that Koken's type material of *Otolithus (Platessae) sector* includes two different species. The lectotype representing a *Paraconger* species, and most of the other material is the *Ariosoma* species described in this study.

Diagnosis: This species is characterized by massive otoliths that are nearly as high as long. The ostial rim is slightly concave, and most specimens also show some concavity at their posterodorsal rim. The ventral rim is marked by a somewhat angular central portion. The outer face is smooth and convex, except for an area near the posterior end, where a shallow dorsoventrally oriented hollowing can be observed. The inner face is smooth and convex, except for some irregular depressions in the upper part of the dorsal area. The sulcus is wide and only very superficially incised. The entire surface of the sulcus is filled with colliculum, except for the dorsal extremity of the ostial channel. There is no clear division of an ostial and caudal portion. The posterior end of the sulcus shows some widening ventrally.

Affinities: As already mentioned in the "Etymology of name", the type material of Koken's *Otolithus (Platessae) sector* is a mixture of two species: figures 15 and 16 of Koken's plate 17 belong to the *Ariosoma* described here. However, figure 14 of the same plate, which was indicated as the lectotype of Koken's species by Nolf (1985, p. 128), represents a *Paraconger* species (P. *sector*) that is also represented in our Yazoo Clay material (Plate 2, Figures 9-10).

PARACONGER YAZOOENSIS n. sp.

(PLATE 2, FIGURES 11-14)

1979 "Conger" *dissimilis* Frizzell and Lamber, 1962 - Stringer, p. 102, plate 1, figure 3.

Type material: Holotype: a right otolith (Plate 2, Figure 11) (IRSNB P 6962), 24 paratypes of which 3 are figured (Plate 2, Figures 12-14) (IRSNB P 6963-6965).

Dimensions of the holotype: Length: 5.8 mm; height: 4.4 mm; thickness: 1.9 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: This species is named after the formation where it was collected.

Diagnosis: This species is characterized by very robust, globally round-shaped otoliths with a somewhat acuminate posterior end. The central part of the dorsal rim is raised. The outer face is smooth and generally convex, but most specimens show some small concave zones near the posteroventral and the posterodorsal area of their outer face. The inner face is strongly convex, but a shallow depression is seen in the dorsal area, just above the crista superior. The sulcus is deeply incised and is filled with colliculum, which is especially well developed in the cauda. The ostial channel is only very weakly developed. The highest part of the otolith is located in the anterior portion.

Affinities: This species can easily be distinguished from *P. sector* (Plate 2, Figures 9-10) and *P. brazosensis* (Frizzell & Dante, 1965) by its rounder and more massive otoliths. It is also easily distinguished from *P. solidus* Müller, 1999 from the Bartonian Piney Point Formation (Virginia) by its much more acuminate posterior end.

"GENUS NEOBYTHITINARUM" *AEQUALOIDES* n. sp.

(PLATE 3, FIGURES 11-14)

1979 *Ophidion ?* sp. - Stringer, p. 103, plate 1, figure 9.

Type material: Holotype: a left otolith (Plate 3, Figure 11) (IRSNB P 6977), 7 paratypes of which 3 are figured (Plate 3, Figures 12-14) (IRSNB P 6978-6980).

Dimensions of the holotype: Length: 5.6 mm; height: 3.4 mm; thickness: 1.4 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: Alludes to the great similarity of these otoliths with those of "genus Neobythitinarum" *aequalis* (Stinton & Nolf, 1970) from the Lutetian deposits of the Anglo-Franco-Belgian Basin.

Diagnosis: This species is characterized by rather robust, somewhat elongate otoliths with a well-marked anterodorsal expansion and an angular posterior end. The central part of the dorsal rim is slightly concave. The outer face is generally smooth, but in specimens with weakly lobated margins, some radial groves separate the lobes. This face is very convex, with the strongest convexity located in the center of the surface. The inner face is slightly convex in all senses but shows a shallow depression just above the crista superior. The sulcus shows no clear division into ostial and caudal portions and opens to the ostial rim with a rather rudimentary ostial channel. There is a single undivided colliculum that fills the whole sulcus but in some specimens, e.g. the holotype, the colliculum is somewhat narrower in the posterior (caudal) part.

Affinities: The otoliths described here belong to the group of "genus Neobythitinarum" *hilgendorfi*, defined by Nolf (1980) and including "g. N." *aequalis* from the European Lutetian, "g. N." *regularis* (Priem, 1911) from the European Lutetian and Bartonian, and "g. N." *hilgendorfi* (Koken, 1891) from the European early Oligocene (synonym: "g. N." *boulangeri* NOLF, 1980). As already mentioned in the "Etymology of name", otoliths of the new species seem to be most closely related to those of "g. N." *aequalis*. In this species, however, otoliths are markedly higher and have a more salient anterodorsal expansion. Otoliths of "g. N." *regularis* and "g. N." *hilgendorfi* are much more slender and elongate and do not have a noticeable anterodorsal expansion.

Centropristis priaboniana n. sp.
(Plate 4, figures 3-6)

Type material: Holotype: a right otolith (Plate 4, Figure 3) (IRSNB P 6990), 27 paratypes of which 3 are figured (Plate 4, Figures 4-6,) (IRSNB P 6991-6993).

Dimensions of the holotype: Length: 2.9 mm; height: 1.6 mm; thickness: 0.5 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: This species is named after the stage to which the Yazoo Clay belongs.

Diagnosis: This species is characterized by small, rather elongate otoliths with a salient rostrum and an angled but not really pointed posterior end. The ostial rim is generally concave-shaped and bears some irregular crenulations. All otolith rims bear crenulations or lobations, particularly the posterodorsal and posteroventral rims, which are strongly lobated in many specimens. The outer face is strongly concave in the anteroposterior direction but almost flat dorsoventrally. Its center is smooth, but small radial grooves separate the lobes and other irregularities of the rims towards the margins. The inner face is clearly convex and is rather strongly incised by the sulcus. A wide ostium and a much narrower cauda that widens somewhat towards the posterior end and is bent in a ventral direction constitute the sulcus. The crista superior is accentuated by a shallow depression in the dorsal area immediately above it.

Affinities: Otoliths of this species seem to be most similar to those of the Recent genus *Centropristis* Cuvier, 1829, and compare to those of *C. philadelphica* figured by Nolf & Stringer (1992, plate 13, figure 1). Otoliths of the Recent species, however, are somewhat more elongate than those of *C. priaboniana*.

Pristigenys obliquus n. sp.
(Plate 4, figures 7-12)

Type material: Holotype: a right otolith (Plate 4, Figure 7) (IRSNB P 6994), 43 paratypes of which 5 are figured (Plate 4, Figures 8-12) (IRSNB P 6995-6999).

Dimensions of the holotype: Length: 2.8 mm; height: 2.6 mm; thickness: 0.7 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: *Obliquus, a, um* (Latin) = oblique; refers to the slightly oblique, primary distortion of the otoliths.

Diagnosis: This species is characterized by globally round-shaped otoliths, but with an upper half that shows a considerably expanded posterior portion. The ventral rim is strongly curved and delimits a ventral area that is much narrower than the dorsal half of the otolith. There is a rather strong ostium and a small, well-marked antirostrum, with a small excisura just below. The otoliths are also characterized by a manifest anteroposterior convexity, which is much more pronounced in the inner face than in the outer one. Furthermore, the otoliths show some distortion along an anteroventral-posterodorsal axis. The outer face is rather strongly tubercular in small specimens and also shows lobated rims. In larger specimens, the outer face becomes almost

entirely smooth, and the lobated rim disappears. The inner face is rather strongly incised by a sulcus with a short but wide ostium and a much narrower cauda, whose posterior end becomes slightly wider and is bent in ventral direction. There is a discrete but always present ventral furrow.

Affinities: Otoliths of *P. obliquus* differ from those of all known extinct *Pristigenys* species (see list in Nolf, 1985) in the strong anteroposterior convexity of their inner face and in their marked distortion along an anteroventral-posterodorsal axis.

"GENUS GOBIIDARUM" *VETUSTUS* n. sp.
(PLATE 7, FIGURES 6-11)

Type material: Holotype: a left otolith (Plate 7, Figure 6) (IRSNB P 7413), 56 paratypes of which 5 are figured (Plate 7, Figures 7-11) (IRSNB P 7414-7418).

Dimensions of the holotype: Length: 1.7 mm; height: 1.5 mm; thickness: 0.6 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: *Vetustus, a, um* (Latin) = very old; refers to the very early occurrence of this gobiid taxon; gobiids are very rare from Eocene deposits.

Diagnosis: This species is characterized by thick, pillow-like, regular trapezoid-shaped otoliths, with markedly convex inner and outer faces. The outer face is clearly the most convex one, with the greatest thickness located in the lower central portion of the otoliths. All rims show a sharp transversal profile. The ventral rim is much longer than the dorsal one. Both the anterior and the posterior rim show a constriction in their upper half. The inner face is very regularly convex, except for a small shallow depression just above the sulcus. The sulcus is short, occupies a very central position, and is totally disconnected from the ostial rim. The incision of the sulcus is rather deep. The ostium is strongly expanded in a ventral direction, and the cauda exhibits a small swollen collicular crest. Some specimens exhibit a discrete ventral furrow very near to the ventral rim.

Affinities: Although exhibiting typical gobiid features (subquadrangular otolith outline, shape, central location of the sulcus, and swollen collicular crest), these otoliths do not match exactly with those of any Recent gobiid genus and apparently belong to an extinct genus of the family Gobiids are extremely scarce in Eocene associations, in both the osteology-based and the otolith-based fossil record. The only certain skeleton-based Eocene record is from the Priabonian of the Isle of Wight (Gaudant & Quayle, 1988). Beside the Yazoo Clay otoliths, the only otolith-based Eocene record is a single otolith from the Harudi Formation (middle Eocene) of India and two otoliths from the Nanggulan Formation (Bartonian) of Java (Nolf & Bajpai, 1992). The 57 specimens reported here demonstrate that, at least in some areas, gobiids became a significant group in late Eocene fish ecosystems.

"GENUS CITHARIDARUM" *HOFFMANI* n. sp.
(PLATE 8, FIGURES 9-11)

Type material: Holotype: a left otolith (Plate 8, Figure 9) (IRSNB P 7425), 3 paratypes of which 2 are figured (Plate 8, Figures 10-11) (IRSNB 7426-7427).

Dimensions of the holotype: Length: 2.1 mm; height: 1.5 mm; thickness: 0.5 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: This species is named after Pierre Hoffman, Brussels, who assisted greatly with the illustrations in this paper.

Diagnosis: This species is characterized by grain-shaped otoliths with an expanded anterodorsal angle, a clear excisura, and a blunt, well-marked rostrum. The posterior end of the otoliths produces a smooth angle that is located higher than the posterior end of the sulcus. The ventral rim is regularly curved, with the greatest convexity located somewhat posterior to the middle of the otolith. The outer face is entirely smooth and slightly convex. The inner face is also slightly convex and bears a well-incised sulcus that is divided into an ostium and a cauda of about equal length. In both the dorsal and ventral areas of the inner face, there is a shallow longitudinal depression above and below the sulcus, but the two shallow areas do not join each other in the posterior area behind the sulcus.

Affinities: These otoliths show an unusual combination of features seen in various Recent taxa of the citharids *s.l.* (see Smale *et al.*, 1995, pl. 139 and Schwarzhans, 1999, p. 70-90 for the iconography of the otoliths of various Recent taxa). Their outline is roughly similar to that of the genera *Citharus* Rîse, 1779 and *Citharoides* Hubbs, 1915 (including *Paracitharus* Regan, 1920), but their sulcus lacks the wide ostium and long narrow cauda seen in these genera. In *Lepidoblepharon* Weber, 1913, both the sulcus and the outline shows similarity to that of our fossils, but none of the three

genera cited above exhibit a strong anterodorsal angle. A strong anterodorsal angle is observed in *Brachypleura* Günther, 1862, but the general outline of this genus is quite different. The hypothesis that our fossils represent an extinct genus of citharids seems to us most probable. Citharids are not represented in present-day American seas, but the geographic range of the various Recent genera (West Africa to East Asia and Japan) does not exclude an ancient Tethyian occurrence in America in Eocene times.

CITHARICHTHYS ALTISSIMUS n. sp.
(PLATE 8, FIGURES 7-8)

Type material: Holotype: a left otolith (Plate 8, Figure 7) (IRSNB P 7423), 7 paratypes of which 1 is figured (Plate 8, Figure 8) (IRSNB P 7424).

Dimensions of the holotype: Length: 1.7 mm; height: 1.6 mm; thickness: 0.6 mm.

Type locality: Yazoo Clay (Priabonian) at Copenhagen, Caldwell Parish, Louisiana (lower part of the section, between 0 and + 1.5 m).

Etymology of name: *Altissimus, a, um* (Latin) = very high; refers to the significant height of the otoliths (height and length are almost the same).

Diagnosis: This species is characterized by robust, trapezoidal, very high-shaped otoliths with a strong anterodorsal angle and an acuminate posterior end. There is a very blunt rostral part, and the ostial-anterodorsal rim is very slightly hollow. The outer face is smooth and convex, with the greatest convexity located in the upper half of the otoliths. The inner face is moderately convex. There is a marked asymmetry between the left and right otoliths. The left sagittae have a broader, shorter sulcus and a blunt posterior spine that lies outside the main plain of the inner face. Both the dorsal and the ventral areas show longitudinal depressed zones, which do not join each other fully in the posterior area behind the sulcus.

Affinities: Otoliths of this species match fairly well those of the Recent genus *Citharichthys* Bleeker, 1862, but they are higher and rounder in shape than those of any of the Recent species.

Conclusions

The study of both screenwashed (0.75 mm mesh) and surface-collected otoliths allowed the reconstruction of a teleost fauna of 43 taxa, which is the most diversified association presently known from a single U.S. Gulf Coast Paleogene locality. Twenty-seven taxa could be identified at the species level, and eight of those are new.

A screenwashed sample of about 450 kg from the lower part of the section (Figure 1) provided 5,293 otoliths, yielding an average of about 12.6 specimens/kg of sediment. A screenwashed sample of 15 kg from the upper part of the section provided 266 otoliths (about 17.7 specimens/kg, but with much less diversity). Additional material was collected from the surface in the fossil-rich lower section, which provided larger-sized material, including five very uncommon taxa that were not found in the screenwashed sample.

PALEOENVIRONMENTAL DATA

Sceenwashed samples differ strongly in quantitative composition. The lower sample has a higher faunal diversity and is dominated by benthic eel-shaped fishes living on, or even in, the bottom mud. Among these, the ophidiid "genus Neobythitinarum" *meyeri* is the most common and accounts for 59% of the total association. Anguilliform and ophidiiform otoliths account for 75% of the assemblage. Among the more neritic elements, the sciaenids constitute 13.4% of the association. Other relatively frequent neritic elements are the haemulid *Orthopristis americana* (4.3%) and the sparid "genus Sparidarum" *elegantulus* (2.4%). All other taxa are represented by lower percentages and are too rare to be significant for further analysis. The extremely low frequency of the epipelagic and mesopelagic living genus *Bregmaceros* (less than 1%) and the great rarity of pelagic fishes (*Mene* and the scombrids, represented by one and two otoliths, respectively) in the lower sample should also be noted.

This lower association reflects a tropical to subtropical, rather shallow environment (probably in the order of 50 m depth or less) with normal salinity and a soft muddy bottom. Although negative data must be viewed cautiously, one should note the total absence of apogonids, which can be very abundant in neritic tropical stenohaline associations with a somewhat harder or more sandy substrate, e.g., the Lutetian Calcaire Grossier facies at Fercourt in the Paris Basin or the Lede Sands in the Belgian Basin.

The upper association is dominated by *Bregmaceros* (92%), small pelagic fishes living mainly in the water

layers between 0 and 200 m. Although less intensely sampled than the lower association, it is certain that this *Bregmaceros*-dominated association exhibits a much lower diversity. The sciaenids completely disappear, as do almost all perciforms. The increase of one species implies, of course, a decrease of all the remaining ones, the latter only representing 8% of the association. This makes them numerically quite insignificant, but one should note that all of them are bottom-dwelling, mud-associated taxa. All of the data indicates that within the interval of the Yazoo Clay exposed at the Copenhagen locality, the environment evolved from a shallow neritic sea with an abundant benthic life of both invertebrates and fishes to a deeper and more muddy environment with less abundant benthic life more exposed to the pelagic realm.

Comparison with the Recent American ichthyofauna

The present taxonomic state of most Paleogene Gulf Coast otolith associations is such that comparisons with the Priabonian otoliths from Copenhagen would not be productive. The available material in our Paleogene Gulf Coast collections contains about as many unpublished taxa as the presently published number. Moreover, many of the published taxa cited in the literature need considerable taxonomic revision, which exceeds the purpose of this present paper. However, comparison of the Priabonian teleost association presented here with the Recent marine fish fauna from tropical and subtropical America reveals significant patterns of differences and similarities.

Among the taxa, which are exclusively American today, we must cite the percoids *Centropristis*, *Anisotremus*, and *Orthopristis*. Two others, *Paraconger* and *Citharichthys*, have an essentially American distribution but with at least one species of each ranging as far as West Africa. One should note however that *Paraconger* and *Orthopristis* are quite abundant in several European Eocene otolith associations.

Among the taxa that are typically non-American today, we must cite the families Pterothrissidae, Menidae, Trachinidae, Psettodidae, Citharidae, and the berycid genus *Centroberyx*. Present-day pterothrissids (one West African and one Southeast Asian species) are relatively rare fishes, mainly confined to deeper waters on the upper part of the continental slope. They must be considered as relicts of a family that was an important component of many Late Cretaceous and Paleogene fish faunas, and the family is documented with an abundant and worldwide fossil record, also from typical neritic deposits. Recent trachinids are a typical eastern Atlantic and Mediterranean group, but the genus *Trachinus* is recorded from the Miocene of Maryland (Müller, 1999). *Mene* has a Recent Southeast Asian distribution but is represented by several species in the European Eocene. *Centroberyx* is known from Australia to South Africa, but it has an abundant European fossil record in the Eocene, becomes scarcer in the Oligocene, and has even some rare Miocene records in Portugal and in Aquitaine, France. Psettodidae and Citharidae are known from both west Africa and the Indo-Pacific realm. We interpret these taxa from the Yazoo Clay as related to the ancient Tethys distribution patterns. The same distribution pattern is clearly demonstrated by the species "genus Congridarum" aff. *thevenini* (Java, India, western Europe, North America) and *Brotula aquitanica* (Ukraine, southwest France, North America).

One should also note the presence of abundant sciaenids, represented in the Yazoo Clay by three species. The most abundant, "genus Sciaenidarum" *claybornensis* (12% of the total lower association), belongs to an extinct genus, as do several other American Paleogene sciaenid species. All the numerous Recent endemic American sciaenid genera have a post Paleogene fossil record. Sciaenids are common constituents of American Eocene otolith associations but are totally unknown from European Eocene deposits. In Europe, they are first recorded from the middle Oligocene but become regular constituents of otolith associations from the late Oligocene and early Miocene only.

The presence of 57 gobiid otoliths in our samples must be considered very significant because they constitute the oldest American otolith-based record of the group. In Europe, the only unquestionable Eocene gobiid record consists of some skeletons of *Pomatoschistus* (?) *bleicheri* Sauvage, 1883 from the Osborne Beds, Priabonion of southern England (Gaudant & Quayle, 1988). Gaudant (1996) also cited a rather poorly preserved skeleton from the Lutetian of Catalonia as "Goboiodei." The first otolith-based European gobiid record is from the early Oligocene Sands of Yrieu (Aquitaine, southwestern France), where gobiid otoliths are abundant. The oldest fossil record of gobiid otoliths consists of the scarce specimens reported from the middle Eocene of India and Java (Nolf & Bajpai, 1992). This sudden "explosive" appearance around the Eocene-Oligocene boundary of the most diversified of all Recent perciform families still remains enigmatic. However, we still cannot refute the idea that this could be an artifact of the fossil record, which is essentially unknown for the Paleogene in the Indo-Pacific realm.

A final difference between the Recent American ichthyofauna and the Yazoo Clay fauna concerns the ophidiids, which are represented by extremely abundant Neobythitinae belonging to extinct genera (61% of the total lower association). Ophidiids are constituents of secondary importance in Recent tropical and subtropical American neritic fish faunas, where they are mainly represented by the Subfamily Ophidiinae. In other parts of the world, ophidiids are an almost negligible component of Recent neritic fish faunas. The decline of neritic neobithitine ophidiids since the late Eocene is a worldwide phenomenon in all sediments that provide otolith associations. The most striking difference between the otolith content of our lower Yazoo Clay sample and Recent sea bottom samples from tropical or subtropical American seas is the difference in the percentage of ophidiids.

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Explanations of the plates

All figured specimens are deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB). The fossil otoliths bear numbers of the collection of types and figured fossil fish specimens of the IRSNB. The Recent otoliths are part of the reference collection of Recent otoliths at the same institution. The latter collection is arranged in systematic order without numbering; therefore, such specimens, when figured, bear only the notation "coll. IRSNB."

The abbreviations F and R in the upper right corner of each compartment of the plates indicate whether the figured specimens in that compartment are fossils (F) or Recent (R). In the text of the explanations, L stands for left otolith and R for right otolith. The annotations Fig. a, b, and c are used to indicate respectively ventral, inner (= mesial), and posterior views. Figures without a letter show inner views.

Plate 1

Figure 1 *Pterothrissus* sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6934).

Figure 2 *Albula* sp.
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6935).

Figures 3-8 "genus Heterenchelyidarum" *colei* (Müller, 1999)
3-5 = L, 6-8 = R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6936-6941).

Figure 9 *Conger vetustus* Frizzell & Lamber, 1962
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6942).

Figure 10 Ariidae ind.
L, utricular otolith, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6943).

Figure. 11 *Gnathophis dissimilis* (Frizzell & Lamber, 1962)
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6944).

Figure 12 *Rhynchoconger* sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6945).

Figures 13-18 *Pseudophichthys glaber* (Koken, 1888)
13-15 = L, 16-18 = R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6946-6951).

Plate 2

Figures 1-6 *Ariosoma nonsector* n. sp.
1-3 = L, 4-6 = R, Yazoo Clay, Copenhagen, Louisiana 1 = holotype (IRSNB P 6952), 2-6 = paratypes (IRSNB P 6953-6957).

Figures 7-8 "genus aff. *Uroconger*" sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6958-6959).

Figures 9-10 *Paraconger sector* (Koken, 1888)
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6960-6961).

Figures 11-14 *Paraconger yazooensis* n. sp.
R, Yazoo Clay, Copenhagen, Louisiana 11 = holotype (IRSNB P 6962), 12-14 = paratypes (IRSNB P 6963-6965).

Figure 15 "genus Congridarum" aff. *thevenini* (Priem, 1906)
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6966).

Plate 3

Figure 1 *Synodus* sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6967).

Figure 2 Carapidae
L, 2b = outer face, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6968).

Figures 3-10 "genus Neobythitinarum" *meyeri* (Koken, 1888)
3-6= L, 7-8 = R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6969-6976).

Figures 11-14 "genus Neobythitinarum" *aequaloides* n. sp.
11-12 = L, 13-14 = R, Yazoo Clay, Copenhagen, Louisiana. 11 = holotype (IRSNB P 6977), 12-14 = paratypes (IRSNB P 6978-6980).

Figures 15-17 "genus Sirembinorum" *granus* Müller, 1999
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6981-6983).

Figure 18 *Bregmaceros* sp.
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6984).

Figure 19 *Centroberyx* sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6985).

Figures 20-21 "genus Atherinidarum" *debilis* (Koken, 1888)
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6986-6987).

Plate 4

Figures 1-2 "genus Myripristidarum" *cajun* (Frizzell & Lamber, 1961)
1 = L, 2 = D, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6988-6989).

Figures 3-6 *Centropristis priaboniana* n. sp.
3-4 = R, 5-6 = L, Yazoo Clay, Copenhagen, Louisiana. 3 = holotype (IRSNB P 6990), 4-6 = paratypes (IRSNB P 6991-6993).

Figures 7-12 *Pristigenys obliquus* n. sp.
7-9 = R, 10-12 = L, Yazoo Clay, Copenhagen, Louisiana. 7 = holotype (IRSNB P 6994), 8-12 = paratypes (IRSNB P 6995-6999).

Figures 13-14 "genus Percoideorum" sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7000-7001).

Figure 15 *Antigonia* sp.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7002).

Figure 16 *Mene* sp.
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7003).

Figures 17-21 *Orthopristis americana* (KOKEN, 1888)
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7004-7008).

Plate 5

Figure 1 *Malacanthus brevirostris* Guichenot, 1848
L, Recent, off New Caledonia (coll. IRSNB).

Figure 2 *Hoplolatilus fronticinctus* (Günther, 1887)
L, Recent, off Mauritius (coll. IRSNB).

Figures 3-6 "genus Malacanthidarum" tyleri n. sp.
3-5 = L, 6-8 = R, Yazoo Clay, Copenhagen, Louisiana. 3-7 = paratypes (IRSNB P 7009-7013), 8 = holotype (IRSNB P 7014).

Figure 9 *Caulolatilus affinis* Gill, 1865
L, Recent, off Peru (coll. IRSNB).

Figure 10 *Caulolatilus hubbsi* Dooley, 1978
R, Recent, off California (coll. IRSNB).

Figure 11 *Anisotremus dovii* (Günther, 1864)
L, Recent, off Pacific Central America (coll. IRSNB).

Figure 12 *Anisotremus taeniatus* Gill, 1861
L, Recent, off Pacific Central America (coll. IRSNB).

Figure 13 *Anisotremus* sp.
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7015).

Figure 14 *Anisotremus caesius* (Jordan & Gilbert, 1882)
L, Recent, off Pacific Central America (coll. IRSNB).

Plate 6

Figures 1-2 "genus Haemulidarum" *obliquus* (Müller, 1999)
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7016-7017).

Figures 3-5 *Sciaena* aff. *pseudoradians* (Dante & FrizzelL, 1965)
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7018-7020).

Figures 6-11 "genus Sparidarum" *elegantulus* (Koken, 1888)
6-8 = L, 9-11 = R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7021-7026).

Figure 12 "genus aff. *Nibea*" sp.
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7027).

Figure 13 *Nibea soldado* (Lacepede, 1802)
L, Recent, Australian coasts (coll. IRSNB).

Plate 7

Figures 1-5 "genus Sciaenidarum" *claybornensis* Koken, 1888
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7408-7412).

Figures 6-11 "genus Gobiidarum" *vetustus* n. sp.
6-8 = L, 9-11 = R, Yazoo Clay, Copenhagen, Louisiana. 6 = holotype (IRSNB P 7413), 7-11 = paratypes (IRSNB P 7414-7418).

Figure 12 *Brotula aquitanica* Nolf, 1980
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7419).

Plate 8

Figure 1 "genus Trachinidarum" *laevigatus* (Koken, 1888)
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7028)

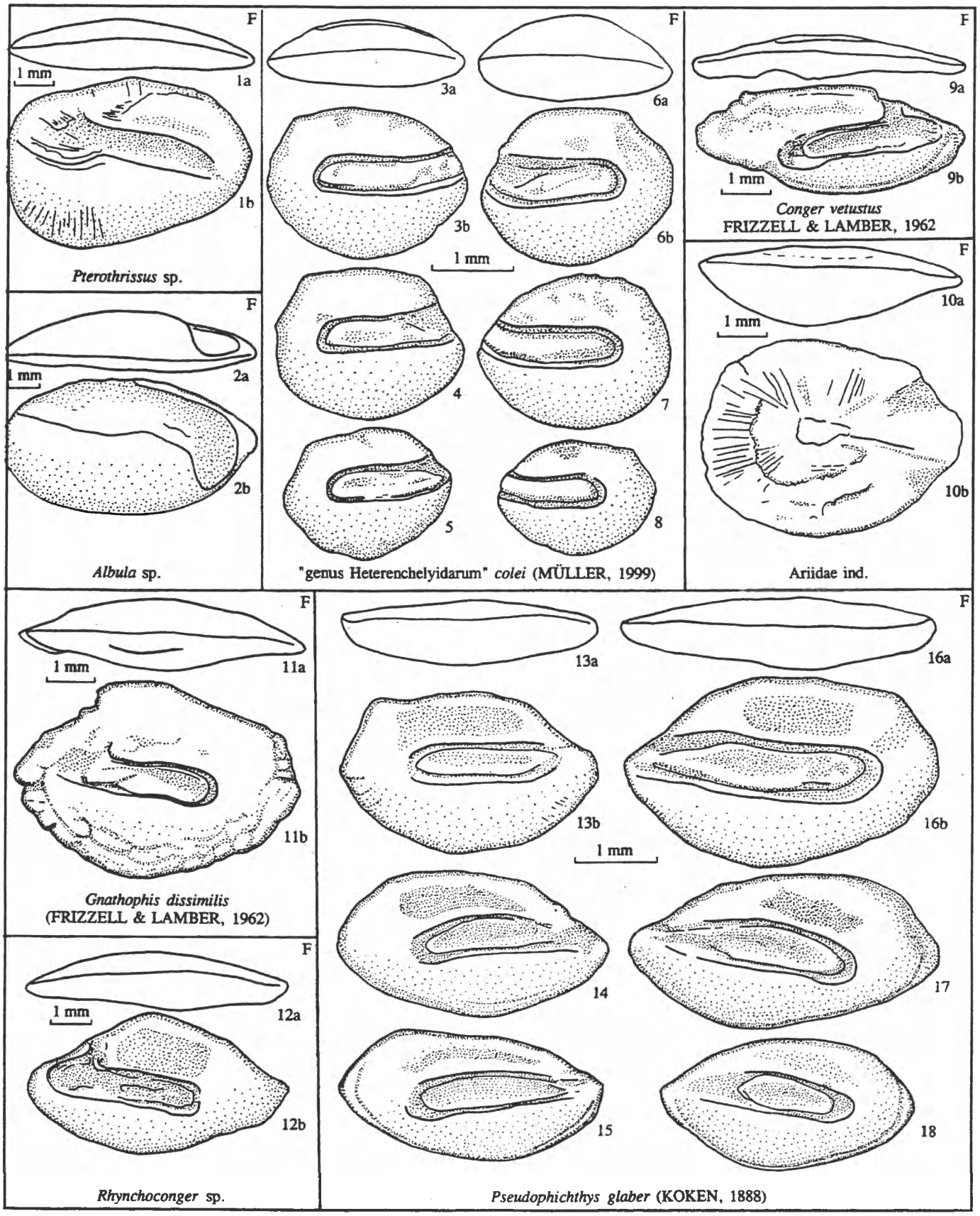
Figures 2-4 "genus Blenniidarum" *cor* (Koken, 1888)
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7029-7031).

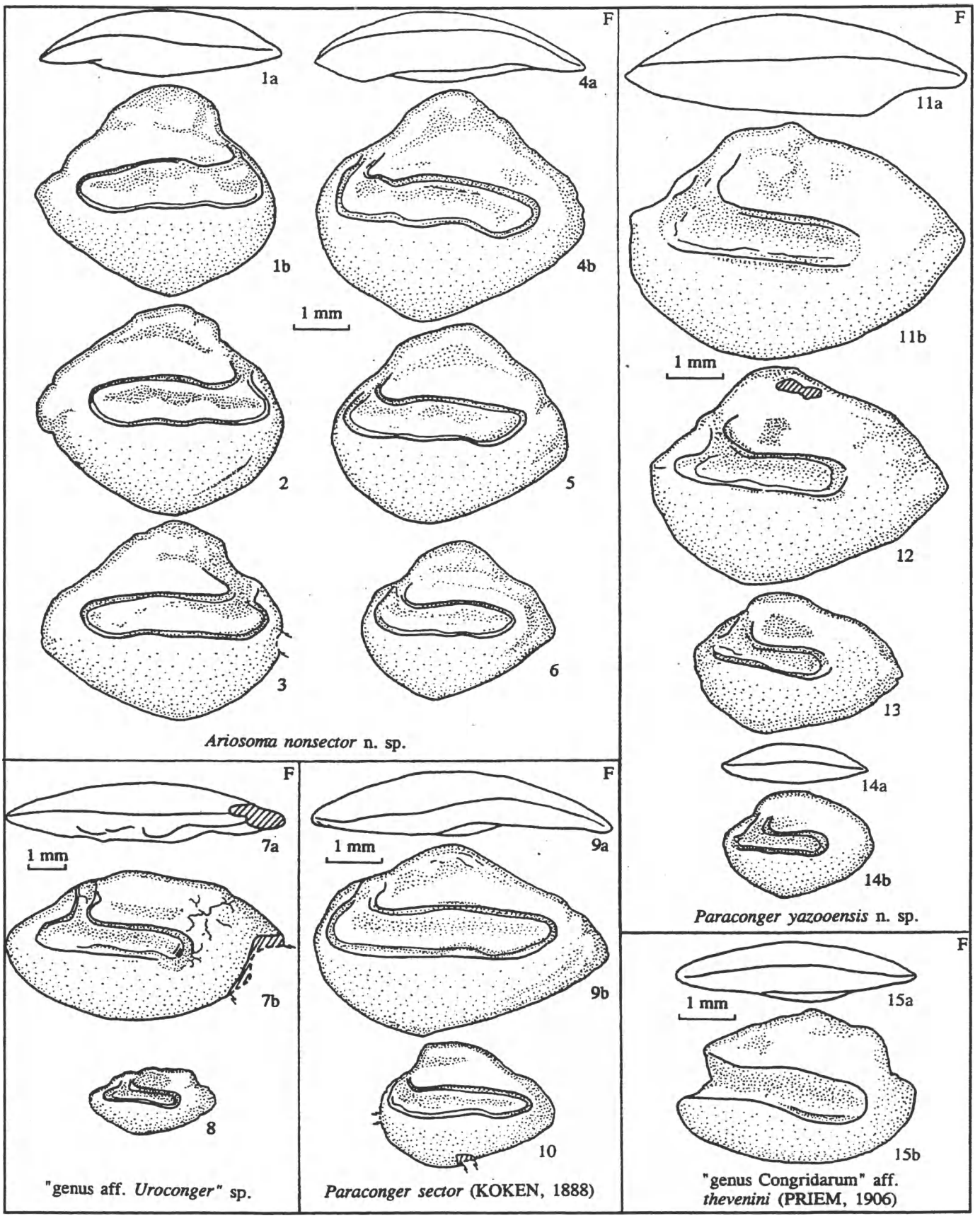
Figure 5 *Psettodes* sp.
L, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7420).

Figure 6 Scombridae ind.
R, Yazoo Clay, Copenhagen, Louisiana (IRSNB P 7421).

Figures 7-8 *Citharichthys altissimus* n. sp.
7 = L, 8 = R, Yazoo Clay, Copenhagen, Louisiana. 7 = holotype (IRSNB P 7422), 8 = paratype (IRSNB P 7423).

Figure 9-11 "genus Citharidarum" *hoffmani* n. sp.
9-10 = L, 11 = R, Yazoo Clay, Copenhagen, Louisiana. 9 = holotype (IRSNB P 7424), 10-11 = paratypes (IRSNB P 7425-7426).


F
1 mm
1a
1b
Pterothrissus sp.
F
1 mm
2a
2b
Albula sp.
F
3a
6a
3b
6b
1 mm
4
7
5
8
"genus Heterenchelyidarum" colei (MÜLLER, 1999)
F
9a
1 mm
9b
Conger vetustus
FRIZZELL & LAMBER, 1962
F
10a
1 mm
10b
Ariidae ind.
F
1 mm
11a
11b
Gnathophis dissimilis
(FRIZZELL & LAMBER, 1962)
F
1 mm
12a
12b
Rhynchoconger sp.
F
13a
16a
13b
16b
1 mm
14
17
15
18
Pseudophichthys glaber (KOKEN, 1888)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4a
1b
4b
1 mm
2
5
3
6
Ariosoma nonsector n. sp.
F
11a
11b
1 mm
12
13
14a
14b
Paraconger yazooensis n. sp.
F
7a
1 mm
7b
8
"genus aff. Uroconger" sp.
F
9a
1 mm
9b
10
Paraconger sector (KOKEN, 1888)
F
1 mm
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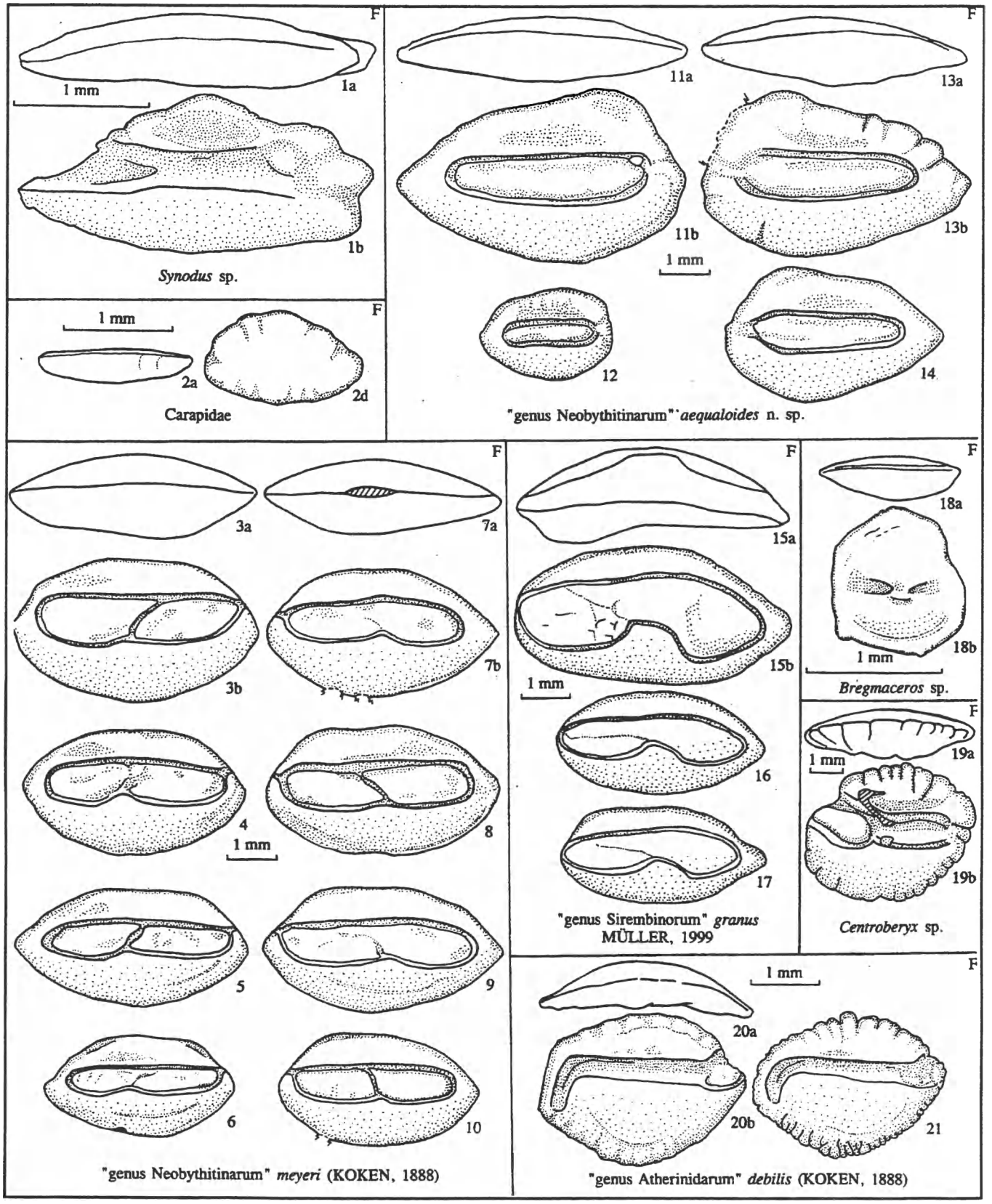
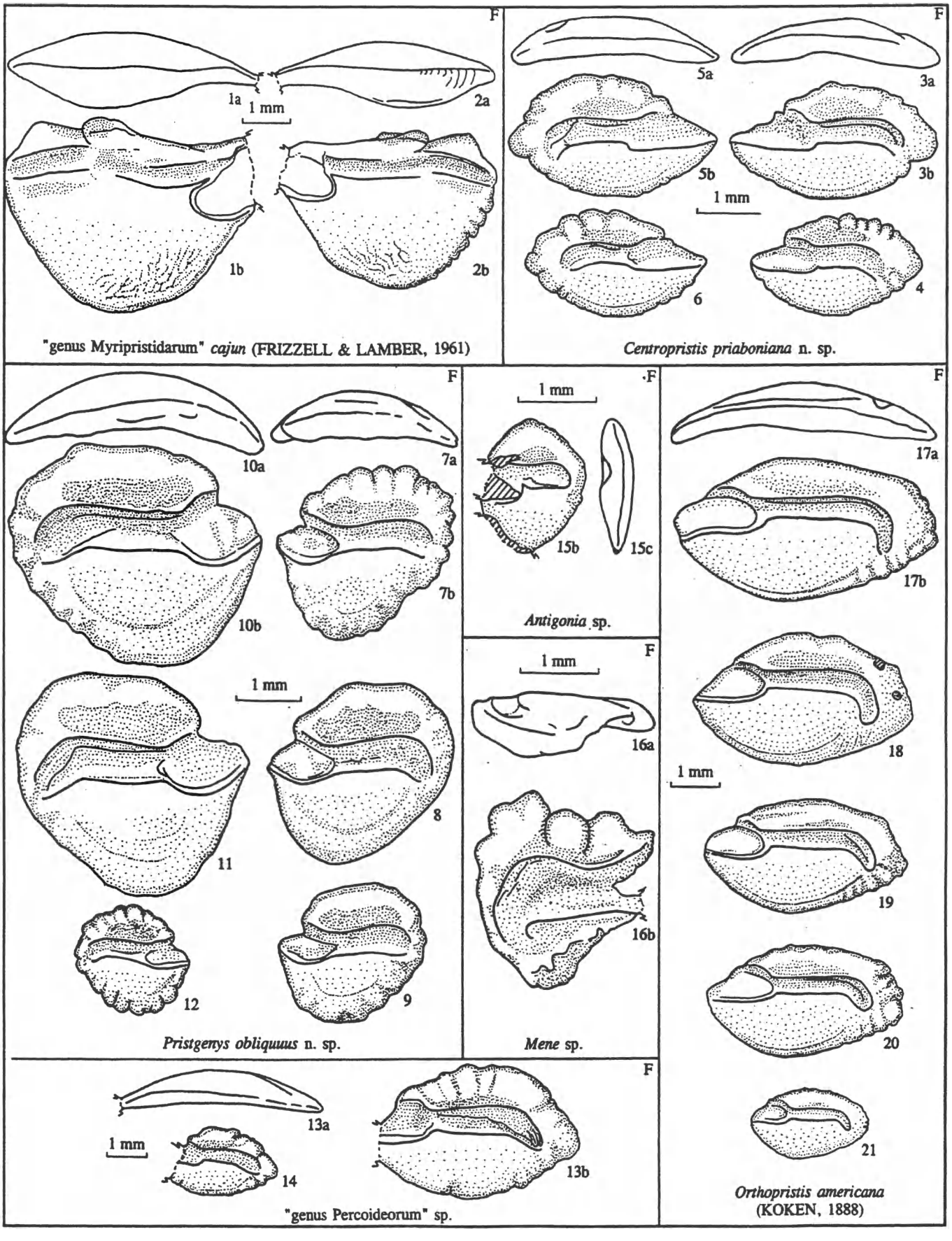
15b
"genus Congridarum" aff. thevenini (PRIEM, 1906)


F
1 mm
1a
1b
Synodus sp.
F
1 mm
2a
2d
Carapidae
F
11a
13a
11b
13b
1 mm
12
14
"genus Neobythitinarum" aequaloides n. sp.
F
3a
7a
3b
7b
4
1 mm
8
5
9
6
10
"genus Neobythitinarum" meyeri (KOKEN, 1888)
F
15a
15b
1 mm
16
17
"genus Sirembinorum" granus MÜLLER, 1999
F
18a
18b
1 mm
Bregmaceros sp.
F
1 mm
19a
19b
Centroberyx sp.
F
1 mm
20a
20b
21
"genus Atherinidarum" debilis (KOKEN, 1888)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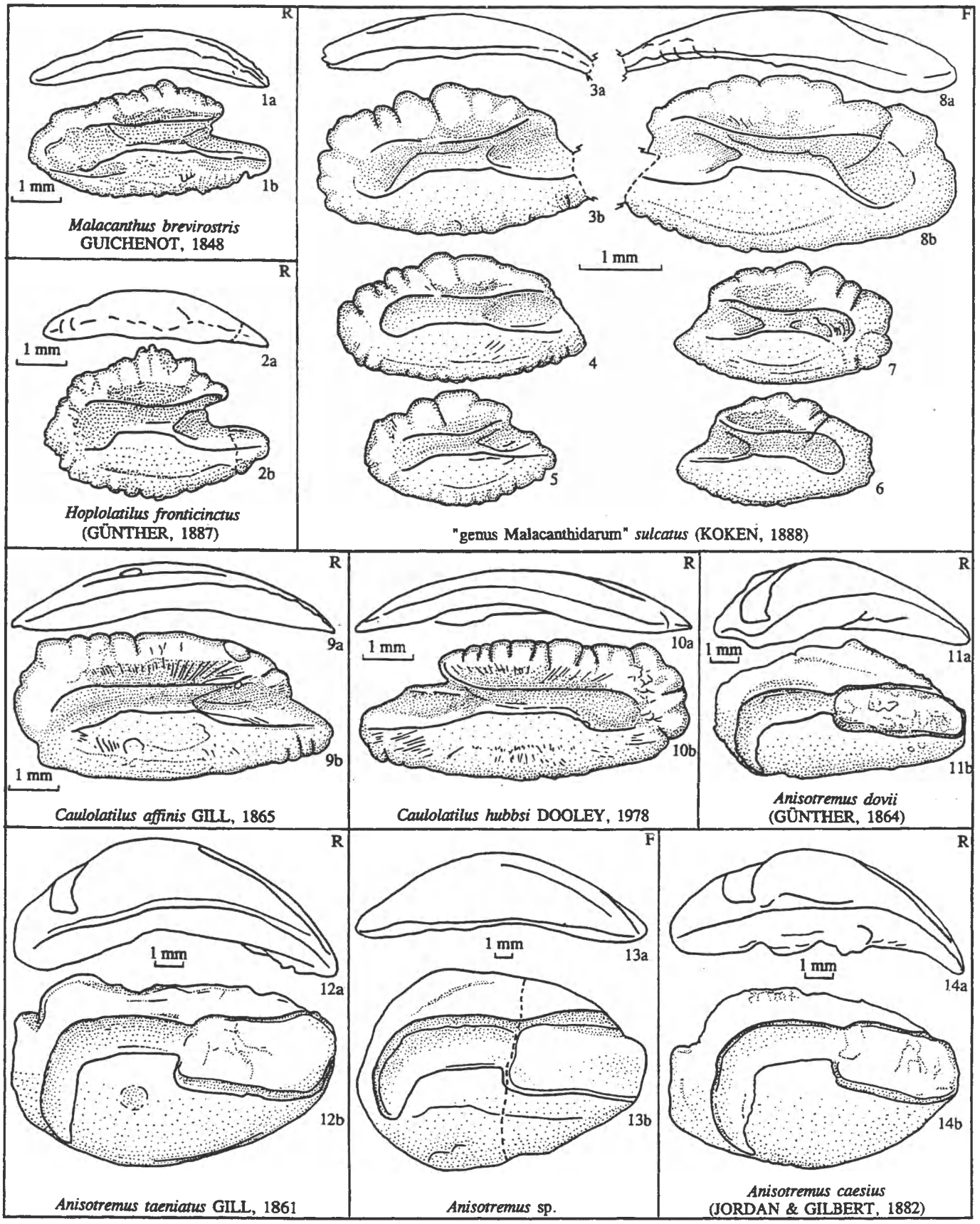
1a
1 mm
2a
1b
2b
"genus Myripristidarum" cajun (FRIZZELL & LAMBER, 1961)
F
5a
3a
5b
3b
1 mm
6
4
Centropristis priaboniana n. sp.
F
10a
7a
10b
7b
1 mm
11
8
12
9
Pristgenys obliquuus n. sp.
F
1 mm
15b
15c
Antigonia sp.
F
1 mm
16a
16b
Mene sp.
F
13a
1 mm
14
13b
"genus Percoideorum" sp.
F
17a
17b
18
1 mm
19
20
21
Orthopristis americana
(KOKEN, 1888)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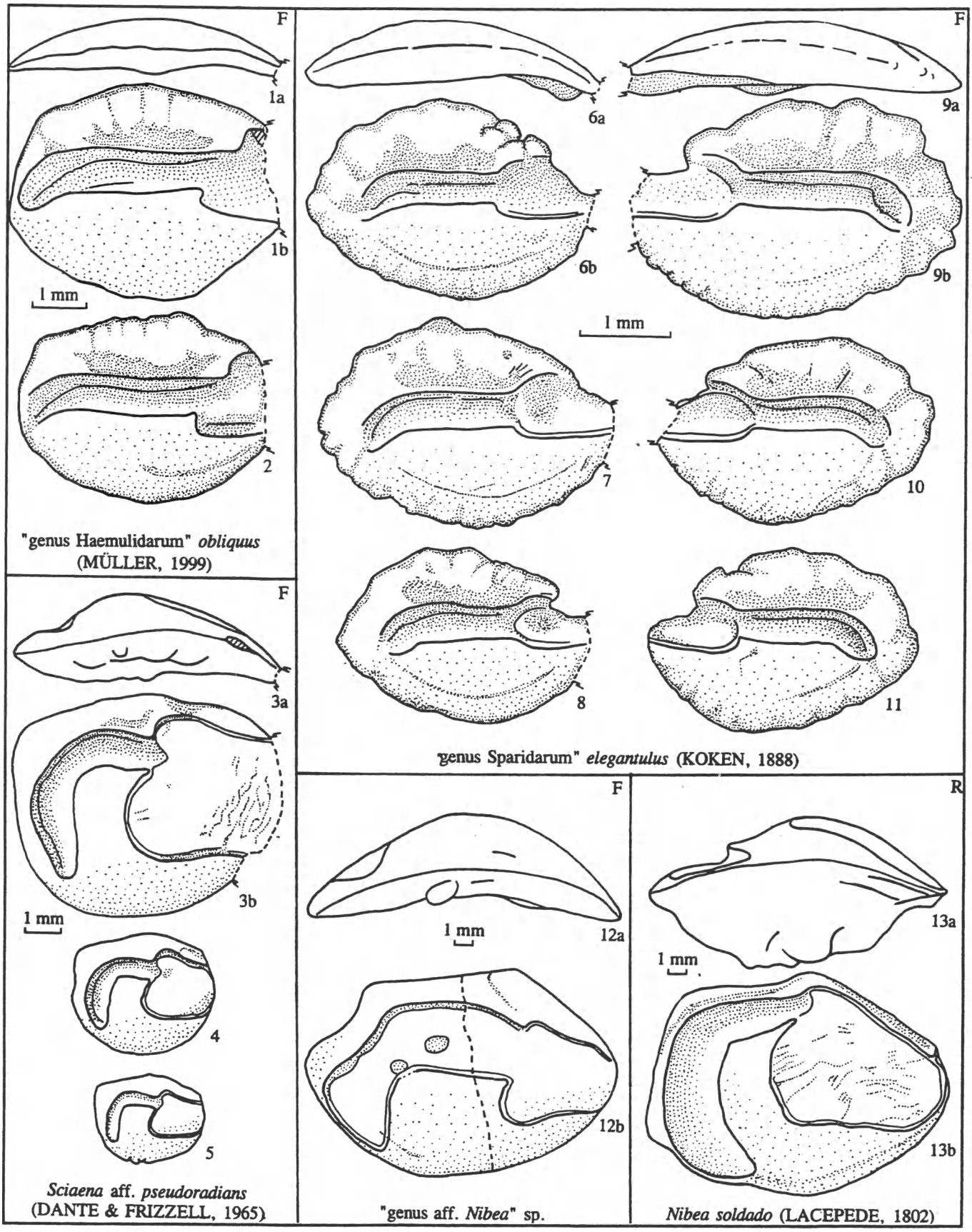
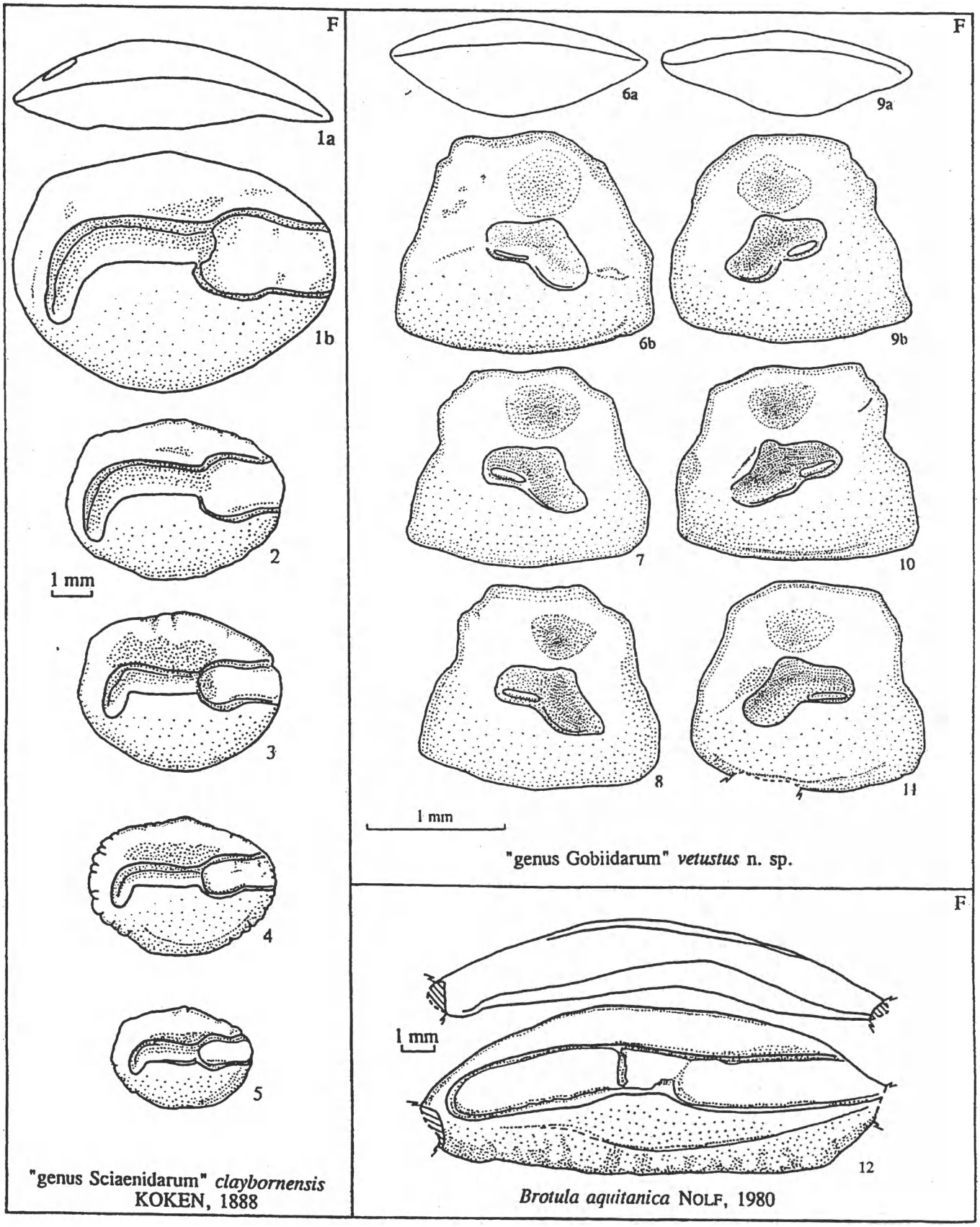
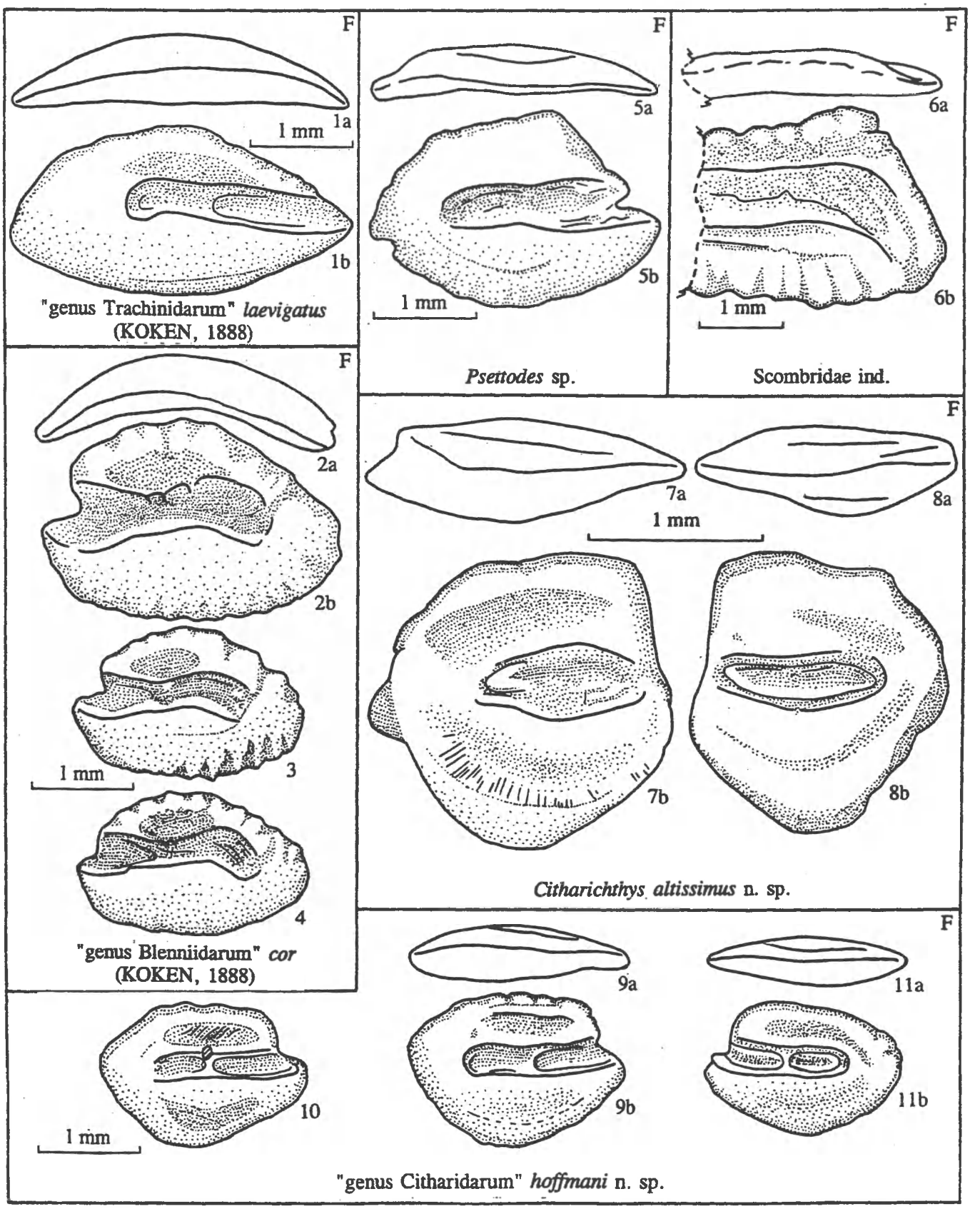
1 mm
1b
Malacanthus brevirostris
GUICHENOT, 1848
R
1 mm
2a
2b
Hoplolatilus fronticinctus
(GÜNTHER, 1887)
F
3a
3b
8a
8b
1 mm
4
7
5
6
"genus Malacanthidarum" sulcatus (KOKEN, 1888)
R
9a
1 mm
9b
Caulolatilus affinis GILL, 1865
R
1 mm
10a
10b
Caulolatilus hubbsi DOOLEY, 1978
R
1 mm
11a
11b
Anisotremus dovii
(GÜNTHER, 1864)
R
1 mm
12a
12b
Anisotremus taeniatus GILL, 1861
F
1 mm
13a
13b
Anisotremus sp.
R
1 mm
14a
14b
Anisotremus caesius
(JORDAN & GILBERT, 1882)


F
1a
1b
1 mm
2
"genus Haemulidarum" obliquus
(MÜLLER, 1999)
F
3a
3b
1 mm
4
5
Sciaena aff. pseudoradians
(DANTE & FRIZZELL, 1965)
F
6a
6b
9a
9b
1 mm
7
10
8
11
"genus Sparidarum" elegantulus (KOKEN, 1888)
F
1 mm
12a
12b
"genus aff. Nibea" sp.
R
13a
1 mm
13b
Nibea soldado (LACEPEDE, 1802)


F
1a
1b
2
1 mm
3
4
5
"genus Sciaenidarum" claybornensis KOKEN, 1888
F
6a
9a
6b
9b
7
10
8
11
1 mm
"genus Gobiidarum" vetustus n. sp.
F
1 mm
12
Brotula aquitanica NOLF, 1980


F
1a
1 mm
1b
"genus Trachinidarum" laevigatus
(KOKEN, 1888)
F
5a
5b
1 mm
Psettodes sp.
F
6a
1 mm
6b
Scombridae ind.
F
2a
2b
1 mm
3
4
"genus Blenniidarum" cor
(KOKEN, 1888)
F
7a
8a
1 mm
7b
8b
Citharichthys altissimus n. sp.
F
9a
11a
9b
11b
10
1 mm
"genus Citharidarum" hoffmani n. sp.

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