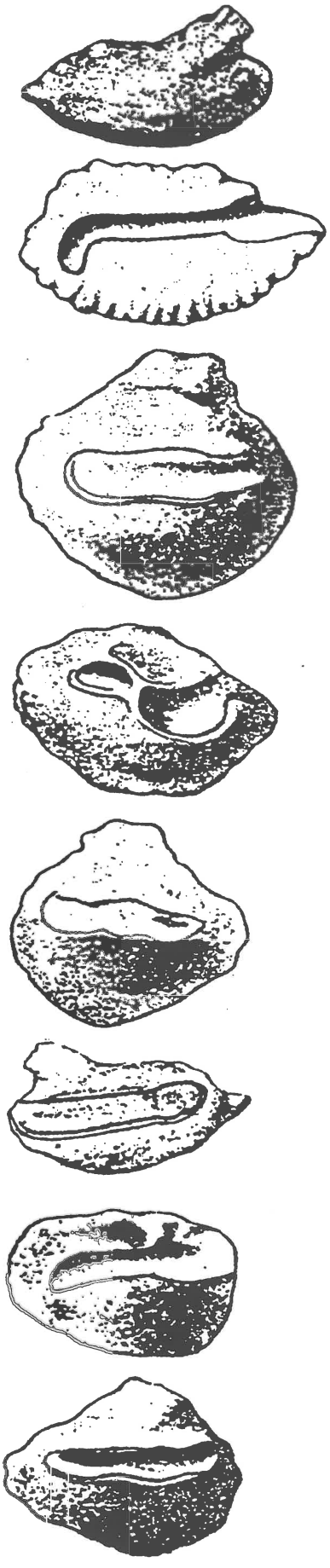

Revision of the American Otolith-based Fish Species

Described by Koken in 1888

Dirk Nolf

Royal Belgian Institute of Natural Sciences

Louisiana Geological Survey • Geological Pamphlet No. 12

Cover: Tertiary otoliths or fish earstones from the United States gulf coast (line drawings modified from the original plates of Koken's study in 1888).

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Revision of the American Otolith-based Fish Species

Described by Koken in 1888

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Baton Rouge
2003

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Acknowledgments

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Abstract

Nineteen of the 23 species described by Koken (1888) from the U.S. Gulf Coast Paleogene are considered to be valid. The four remaining ones proved to be based on eroded or juvenile otoliths lacking diagnostic features to define a species. Two of them, however, are identifiable at generic level and represent Recent genera (*Centroberyx* and *Pterothrissus*) that do not occur in the present-day American seas. The two others, *Otolithus (Sparidarum) insuetus* and *Otolithus (Sciaenidarum) similis* are based on badly preserved non-diagnostic otoliths. Some of Koken's series of syntypes proved to be mixtures containing additional species: the syntypes of *Paraconger sector* also include specimens of *Ariosoma nonsector* Nolf & Stringer, 2003; those of *Aplodinotus gemma* include "genus Sciaenidarum" *radians* Koken, 1888 and *Sciaena pseudoradians* (Dante & Frizzell, 1965). A new species, *Aplodinotus distortus,* is described because it occurs together with the former three sciaenid species in the same sample of the Byram Marl. By evaluating the generic affinities of the sciaenid species described by Koken (and of other Paleogene sciaenids), it was discovered that many of them have their closest relationships to present-day sciaenids with a freshwater habitat. They are considered to be descendants of marine ancestors that survive today in freshwater. These successful Paleogene marine sciaenid taxa (*Aplodinotus*, Pachyurinae) were probably replaced in the marine environment by successful modern groups (Cynoscioninae, Micropogoninae, and Lariminae) that have no Paleogene fossil record but are known since the Miocene.

Introduction

Among all hard components in the vertebrate body, otoliths are of particular interest to paleontologists. They are not components of the skeleton, but mineralized parts of the stato-acoustic organs. In tetrapods, they represent no more than microcrystalline dust in the inner ear, but in bony fishes, they are aggregated to compact stones with a characteristic morphology. A codfish of 1 m has otoliths of about 2 cm with a diagnostic sulcus or pattern on the inner face. The mineral component of otoliths is calcium carbonate, in contrast to that of bone, which is calcium phosphate or more specifically hydroxyapatite. In the last ten years, fisheries biology has become more interested in otoliths because of the exceptional quantity of information that is stored in these small calcareous bodies. Information on the environments in which the fishes lived is constantly accumulated in thin daily rings known as annuli, in the form of trace elements, isotopes, and structural features. Furthermore, the number of annuli allows for a very accurate estimation of the age of fishes and fish larvae (see various survey articles in Secor *et al.*, 1995 and in Wright, ed., 1997, regarding these aspects). Moreover, the external morphology of saccular otoliths (sagittae) characterizes each fish species and allows identification of the fish to the species level. Hence, sagittae become important tools for the paleontologist, allowing recognition of fossil fish species on the basis of otoliths.

Paleogene fish otoliths from the Gulf Coast are among the first-mentioned fossils of their kind. 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 was a German paleontologist who worked at Berlin and Thübingen; he can be considered the founder of otolith paleontology. An account of his life and scientific work is provided by von Huene (1912). Prior to 1884, some fossil otoliths from the lower Miocene of the hills of Torino (northern Italy) were figured by Sismonda (1846, pl. 60-71) but not formally named or attributed to peculiar fish taxa. Koken's taxonomic approach was surprisingly good, considering the state of knowledge of Recent comparative material at that time. In 1888, he published formal names for 23 species, among which 22 were new and one, "*Otolithus (inc. sedis.)* aff. *umbonato*" was attributed to a European Oligocene species that he had published four years earlier.

Concerning the source of his fossils, Koken (1888) mentions that he acquired his material partly from the collection of O. Boettger in Frankfurt am Main, a collection that is partly conserved in the Humboldt University Museum für Naturkunde, Berlin (ZMB), and from the collection of Otto 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 data on stratigraphy and localities tend to be very vague. Only 4 of the 23 taxa treated by Koken are cited with relatively precise localities, including Red Bluff, Newton, and Vicksburg (all in Mississippi). For five others, "Jackson River, Mississippi" is cited as the collecting locality in Koken (1888). However, there is no Jackson River in the area. Meyer (1889), who originally collected the otoliths, noted that the locality should have read "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 the Town Creek, the type locality for the Jackson Group or Jacksonian Stage) and the Yazoo Clay were exposed along the Pearl River in Jackson at that time. For all of the other taxa, the origin was only provided in very generalized stratigraphic terminology ("Clayborne Beds", "Jackson Beds", and "Vicksburg Beds") without any locality names. It should be noted that "Clayborne Beds" was misspelled by Koken (1888); the correct spelling is "Claiborne" for Claiborne, Alabama, as was noted and corrected by Meyer (1889). The correct spelling is noted in brackets in this paper.

The type material of 17 of Koken's taxa could be traced to the Humboldt Museum in Germany. For all of the 23 published taxa, with the exception of *Otolithus (Cepolae) comes*, reference material could be figured from recently collected materials. A reference collection of Gulf Coast Paleogene otoliths was developed by the author during two collecting trips–1987 (Mississippi and Alabama) and 2001 (Texas and Mississippi)–and includes material from many of the fossiliferous outcrops from Danian to Upper Oligocene. This allowed the illustration of the Koken-species for which no type material was available with specimens that almost certainly can be considered as topotypes. A collection of otoliths from the exposure of the Moodys Branch Formation at Town Creek, Mississippi (Jackson 1/24 000 quadrangle, x = 765.350 m, y = 3575.300 m), provided by David Dockery, proved to be extremely helpful for interpreting species from the "Jackson Beds" for which the type specimens could not be traced in the ZMB collection. I suspect that this may be related to the

Meyer collection because most of the specimens probably came from the Town Creek at Jackson, Mississippi, where Meyer described mollusks. Many of Koken's species from the "Jackson Beds" are also abundantly documented with material from the Yazoo Clay at Copenhagen, Caldwell Parish, Louisiana (Nolf & Stringer, 2003), but it is almost certain that this place did not provide any of the original Koken specimens.

Finally, it should be mentioned that another part of the Koken collection is preserved in the collections of the "Natur-Museum Senckenberg", Frankfurt am Main (SMF), but this collection does not include American material (Zilch, 1965). Campbell (1929), who reported on the stratigraphic value of otoliths, makes further citation of the specimens described by Koken, but his paper is an almost verbatim translation of Koken's 1888 paper, even using the same plates.

Table 1 provides a list of all of the species described by Koken. They are listed in alphabetical order of the species-group names, and for each species, a reference is given to the original description and iconography of Koken. This information is followed by the revised taxonomic interpretation of the species, the nature of the available material, and a reference to new figures in the present paper. All recently figured specimens from the Moodys Branch Formation at Town Creek can be considered as topotypes with a high degree of certainty, and among this material, neotypes are indicated for the species that could not be traced in the original Koken collections at Berlin and Frankfurt am Main. In those cases, this designation is proposed for the purpose of clarifying the taxonomic status and the type locality of the concerned taxa as required by article 75.3.1. of the Code.

KOKEN, 1888		Revised interpretation	Material figured here	
americanus (Carangidarum)	p. 277, pl 17, figs. 1-3	*Orthopristis americana*	lectotype	Pl. 3, Figs. 13-15
brevior (Congeris)	p. 293, pl. 18, fig. 7	"genus Ophichthyidarum" *brevior*	holotype	Pl. 1, Fig. 1
claybornensis (Sciaenidarum)	p. 283, pl. 19, figs. 1 & 4	"genus Sciaenidarum" *claybornensis*	lectotype	Pl. 3, Figs. 1-5
comes (Cepolae)	p. 288, pl 17, fig. 12	*Owstonia comes*	holotype	Pl. 3, Fig. 10
cor (Triglae)	p. 287, pl. 18, fig. 10	"genus Blenniidarumm" *cor*	neotype	Pl. 3, Fig. 11
debilis (Mugilidarum)	p. 288, pl. 17, fig. 8	"genus Atherinidarum" *debilis*	holotype	Pl. 1, Fig. 10
decipiens (Sciaenidarum)	p. 285, pl. 19, figs 5-6	"genus Sirembinorum" *decipiens*	holotype	Pl. 1, Fig. 7
elegantulus (Pagelli)	p. 279, pl. 17, figs. 5-6	"genus Sparidarum" *elegantulus*	holotype + new	Pl. 2, Figs. 1-2
elevatus (Gadidarum)	p. 290, pl. 18, figs. 4-5	"genus aff. Sirembo" *elevatus*	holotype	Pl. 1, Fig. 6
eporrectus (Sciaenidarum)	p. 282, figs. 16-17	"genus Sciaenidarum" *eporrectus*	holotype + new	Pl. 3, Figs. 6-9
gemma (Sciaenidarum)	p. 281, pl. 19, fig. 9	*Aplodinotus gemma*	lectotype + new	Pl. 2, Figs. 7-10
	p. 281, pl. 19, fig. 13	*Sciaena pseudoradians*	holotype + new	Pl. 2, Figs. 3-6
	p. 281, unfigured	"genus Sciaenidarum" *radians*	holotype + new	Pl. 4, Figs. 1-3
glaber (Soleae)	p. 293, pl. 293, fig. 3	*Pseudophichthys glaber*	holotype	Pl. 1, Fig. 5
hospes (Apogonidarum)	p. 278, pl. 18, fig. 15	*Centroberyx* sp. (non diagnostic holotype)	holotype	Pl. 1, Fig. 8
insuetus (Sparidarum)	p. 280, pl. 17, fig. 9	rejected species (eroded holotype)	-	-
intermedius (Sciaenidarum)	p. 283, pl. 19, figs. 2-3	"genus Sciaenidarum *intermedius*	holotype + new	Pl. 2, Figs. 12-14
laevigatus (Trachini)	p. 286, pl. 18, figs. 13-14	"genus Trachinidarum" *laevigatus*	new material	Pl. 3, Fig. 12
meyeri (Gadidarum)	p. 289, pl. 18, figs. 8-9	"genus Neobythitinarum" *meyeri*	holotype	Pl. 1, Fig. 9
mucronatus (Gadidarum)	p. 290, pl. 17, figs 10-11	"genus Lepophidiinorum" *mucronatus*	new material	Pl. 1, Figs. 11-13
radians (Sciaenidarum)	p. 280, pl. 19, figs. 7-8	"genus Sciaenidarum" *radians*	holotype + new	Pl. 4, Figs. 1-3
sector (Platessae)	p. 292, fig. 14	*Paraconger sector*	lectotype	Pl. 1, Fig. 2
	p. 292, figs. 115-16	*Ariosoma nonsector*	(syntypes)	Pl. 1, Fig. 3-4
similis (Sciaenidarum)	p. 284, pl 19, figs 10, 11, 14	doubtful sp. (non diagnostic juv. syntypes)	-	-
sulcatus (Cottidarum)	p. 287, pl. 18, fig. 12	"genus Malacanthidarum" *sulcatus*	neotype	Pl. 1, Fig. 14
aff. *umbonato* (inc. sedis) (non *umbonatus* KOKEN, 1884)	p. 294, pl. 17, fig. 12a	*Pterothrissus* sp.	-	-

Table 1. List of species described by Koken.

Systematic Paleontology

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 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 Ophichthyidarum" *brevior* (Nolf, 1985). Koken also used open generic nomenclature, but in a slightly different way. Instead of "genus Ophichyhyidarum", he would have written *Otolithus (Ophichthyidarum)*; see Nolf, 1985, p. 30 for a full explanation.

In the following section, all valid taxa are treated with their modern names in a systematic order, according to the classification proposed by Nelson (1994). Besides the nominal species introduced by Koken, I also covered some species that were described later by other authors and introduced as new species, because part of Koken's series of syntypes proved to be a mixture of different species. As noted earlier, Koken's information on stratigraphy and localities are approximate, both in his paper and on the collection labels. Therefore, in the sections "Stratigraphy and locality data", the original citation of Koken is followed by the occurrence of the species in recently collected samples.

Family PTEROTHRISSIDAE

Pterothrissus sp.

Plate 1, Figure 8

1888 *Otolithus (inc. sed.) umbonato* K. - Koken, p. 294, pl. 17, fig. 12.

Discussion: An eroded otolith, non-diagnostic at species level, was referred by Koken to the European species that he described in 1884 from the lower Oligocene of Lattorf as *Otolithus (incertae sedis) umbonatus*, now classified in the genus *Pterothrissus* Hilgendorf, 1877. Although Koken's American specimen is not diagnostic at the species level, there is no doubt that it represents a *Pterothrissus* species. In the Recent fauna, *Pterothrissus* is known from West Africa and Japan only (see Nolf & Dockery, 1990, plate 1 for iconography of the two Recent species, *P. belloci* Cadenat, 1937 and *P. gisu* Hilgendorf, 1877), but not from the American seas. Recent *Pterothrissus* species are confined to the deep neritic and continental slope environment, but in the Late Cretaceous and Paleogene, the genus is common in many otolith associations from very nearshore environments.

Stratigraphy and locality data: "One specimen from Newton, Mississippi." In my samples from the Gulf Coast Paleogene, I noticed the presence of *Pterothrissus* otoliths from the Danian till the lower Oligocene (Kincaid, Matthews Landing, Poterchito Member of the Cook Mountain Formation, Shubuta Clay Member of the Yazoo Formation, and Red Bluff Formation).

Family OPHICHTYIDAE

"genus Ophichthyidarum" *brevior* Koken, 1888

Plate 1, Figure 1

1988 *Otolithus (Congeris) brevior* - Koken, p. 293, plate 18, figure 7.

Discussion: This species is known only from the holotype (ZMB Ot. 26) and was correctly recognized as an anguilliform by Koken. However, its sulcus pattern with an ostium opening widely on the anterodorsal rim differs from the congrid type of sulcus which is less incised and, in most species, is connected only to the anterodorsal rim by an ostial channel. The wide anterior opening of the sulcus, the irregular outline of the rims, and the sulcus outline are more suggestive of affinities with the ophichthyids. Compare with the Recent species *Mystriophis intercinctus* (Richardson, 1844) figured by Huyghebaert & Nolf (1979, plate 1, figure 23) and *Ophichthus triserialis* (Kaup, 1856), figured by Nolf (1985, figure 11A).

Stratigraphy and locality data: "Two specimens from the Jackson Beds." No similar specimens were found in any of our samples, but the most probable origin of Koken's "Jackson Beds" specimens is probably the Moodys Branch Formation at Town Creek, Jackson, Mississippi.

Family CONGRIDAE

Ariosoma nonsector Nolf & Stringer, 2003

Plate 1, Figures 3-4

1888 *Otolithus (Platessae) sector* Koken - Koken, p. 292, pl. 17, figs. 15-16; non fig. 14 (= lectotype of *Paraconger sector*);

1979 *Ariosoma* sp. - Stringer, p. 102, pl. 1, fig. 4;

2002 *Ariosoma nonsector* n. sp. - Nolf & Stringer (2003, plate 2, figures 1-6).

Discussion: Since the syntypes of *Otolithus (Platessae) sector* Koken, 1888 were a mixture of two different species (see "Discussion" under *Paraconger*

sector), a new species, *Ariosoma nonsector*, was erected for part of this material by Nolf & Stringer (2003).

Stratigraphy and locality data: Koken's data for the specimens of *A. nonsector* and *P. sector* read: "from the Clayborne [Claiborne] till Vicksburg Beds, but common in the Jackson Beds." I collected *A. nonsector* from the Moodys Branch Formation at Riverside Park, Jackson; at Techeva Creek, Yazoo County, Mississippi; and from the Yazoo Clay at Copenhagen, Louisiana.

Paraconger sector (Koken, 1888)

Plate 1, Figure 2

1888 *Otolithus (Platessae) sector* Koken - Koken, p. 17, figure 14, not figures 15 and 16;

1985 *Paraconger sector* (figure 14 of Koken = lectotype) - Nolf, p. 128;

1999 *Paraconger americanus* n. sp. - Müller, p. 70, figures 20/11-17;

2003 *Paraconger sector* Koken, 1888 - Nolf & Stringer (2003).

Discussion: Koken's generic identification of these anguilliform otoliths as belonging to a flatfish is apparently due to an erroneous labeling in his comparative collection. On plate 18, figures 1-2 of his 1888 paper, he figured a couple of Recent otoliths which apparently belong to *Ariosoma balearicum* (Delaroche, 1809), but are labeled "*Platessa flesus*", a Recent flatfish from the North Sea. These specimens were used as comparative material for the identification of the fossils, which explains the error. The story is further complicated by the fact that the type material of *Otolithus (Platessae) sector* includes two different species of congrid eels. Figure 14 of Koken's plate 17 represents a *Paraconger* species. This specimen was indicated as lectotype of *P. sector* by Nolf (1985, p. 128). Figures 15 and 16 of the same plate (refigured here Plate 1, Figures 3-4) represents an *Ariosoma* species that is now described as *A. nonsector* by Nolf & Stringer (2003).

Stratigraphy and locality data: According to Koken, "from the Clayborne [Claiborne] till Vicksburg Beds, but common in the Jackson Beds." One should note that the syntypes of Koken are a mixture of *Paraconger* and *Ariosoma* otoliths. I collected *P. sector* otoliths from the Moodys Branch Formation at Riverside Park, Jackson, Mississippi and at Techeva Creek, Yazoo County, Mississipi; from the Yazoo Clay at Copenhagen, Louisiana; and from the Piney Point Formation (Bartonian) of Virginia.

Pseudophichthys glaber (Koken, 1888)

Plate 1, Figure 5

1888 *Otolithus (Soleae) glaber* Koken - Koken, p. 293, pl. 18, fig. 3;

2003 *Pseudophichthys glaber* (Koken, 1888) - Nolf & Stringer (2003, plate 1, figures 13-18).

Discussion: This species was described on the basis of the holotype only and refigured here on Plate 1, Figure 5. Such otoliths are relatively common in the Yazoo Clay at Copenhagen, Louisiana. Material from the Yazoo Clay site at Copenhagen allowed the variability of the species to be clearly illustrated (Nolf & Stringer, 2003, plate 1, figures 13-18).

Stratigraphy and locality data: "A single specimen from the Jackson Beds." New collecting in the Yazoo Clay at Copenhagen, Louisiana provided 54 otoliths, and I also found specimens in the Piney Point Formation (Bartonian) of Virginia.

Family OPHIDIIDAE

Subfamily OPHIDIIDAE

Tribus LEPOPHIDIINI

"genus Lepophidiinorum" *mucronatus* (Koken, 1888)

Plate 1, Figures 11-13

1888 *Otolithus (Gadidarum) mucronatus* Koken - Koken, p. 290, pl. 17, figs. 10-11;

? 1965 *Bauzaia mucronata* (Koken) - Frizzell & Dante, p. 712, pl. 86, figs. 43-44;

1980 "genus Lepophidiinorum" *mucronatus* (Koken, 1888) - Nolf, p. 111.

Discussion: The holotype and unique specimen cited by Koken are absent from what remains of the original Koken collection. Among collected material, the best available series to illustrate the morphology and ontogenetic changes of this species (Plate 1, Figures 11-13) is from the Bartonian Piney Point Formation in Virginia, which is almost contemporaneous with Clayborne [Claiborne] Bluff, the type locality cited by Koken.

Stratigraphy and locality data: "a single specimen from Clayborne [Claiborne]." This species is represented in my collection from many Lutetian and Bartonian Gulf Coast localities including: Upper Lisbon Formation (Bartonian) at Barrytown; Middle Lisbon Formation (Lutetian) at Gilbertown (Alabama); Poterchito Member of the Cook Mountain Formation at Newton (Mississippi); Weches Formation (Lutetian) at Robins and Wall Ranch, Leon County; at Burleson Bluff (Burleson County); at Hooker Creek, Burleson County; Stone City Member of Cook Mountain Formation

(Bartonian) at Stone City Bluff, Burleson County; Wheelock Member of Cook Mountain Formation (Bartonian) at Little Brazos River, Brazos County; Landrum Member of Cook Mountain Formation (Bartonian), south of Leona, Leon County (Texas). The species is also known from the Piney Point Formation, Bartonian of Virginia. It seems to become extinct at the end of the Bartonian.

Subfamily NEOBYTHITINAE

"genus Neobythitinarum" meyeri (Koken, 1888)

Plate 1, Figure 9

1888 *Otolithus (Gadidarum) myeri* - Koken, p. 289, plate 18, figures 8-9;

1980 "genus Neobythitinarum" *meyeri* - Nolf, p. 111, plate 18, figure 16.

Discussion: The holotype of this species (ZMB Ot. 80) is refigured here. It is most closely related to "genus Neobythitinarum" *stintoni* (Dante & Frizzell in Frizzell & Dante, 1965) (see Nolf, 1980, plate 20, figure 9) from the Stone City Beds, but the latter species has a narrower sulcus. Among European Eocene Neobythitinae, "genus Neobythitinarum" *dimidiatus* (Schubert, 1916) and "g. N." *fitchi* Nolf, 1980 are also closely related to "g. N." *myeri*. Otoliths looking like "g. N." *myeri* are very abundant at many Paleogene Gulf Coast localities, but more study is needed to decide if this otolith-type includes several closely related species or only a single one.

Stratigraphy and locality data: "numerous specimens from Jackson River." I identified large numbers of specimens that can be considered as conspecific with Koken's holotype from the Upper Lisbon Formation (Bartonian) at Barytown, Alabama; from the Moodys Branch Formation at Town Creek and Riverside Park, Jackson, Mississippi; from the Yazoo Clay at Copenhagen, Louisiana; and I collected some specimens at the Red Bluff Formation type locality.

Tribus SIREMBINI

"genus aff. Sirembo" *elevatus* (Koken, 1888)

Plate 1, Figure 6

1888 *Otolithus (Gadidarum) elevatus* Koken - Koken, p. 290, plate 18, figures 4-5;

1980 "genus aff. Sirembo" *elevatus* (Koken, 1888) - Nolf, p. 110, plate 17, figure 5.

Discussion: The holotype of this species (ZMB Ot. 83) is refigured here. As already stated by Nolf (1980, p. 11), this species is most closely related to the Recent genus *Sirembo* Bleeker, 1858, but the statement that the holotype was from Texas was an error.

Stratigraphy and locality data: "not common in the Clayborne [Claiborne] Beds." I collected specimens from the Upper Lisbon Formation at Barrytown, Alabama, and from the Poterchito Member of the Cook Mountain Formation at Newton, Mississippi.

"genus Sirembinorum" *decipiens* (Koken, 1888)

Plate 1, Figure 7

1888 *Otolithus (Sciaenidarum) decipiens* - Koken, p. 285, plate 19, figures. 5-6;

1980 "genus Sirembinorum" *decipiens* (Koken, 1888) - Nolf, p. 137, plate 16, figure 13;

1981 *Xenosirembo decipiens* (Koken, 1888) - Schwarzhans, 1981, p. 80, figure 27 a-b.

Discussion: This species is known from the two specimens figured by Koken (figure 6 = ZMB 133 and figure 5 = ZMB 134) and seven unfigured syntypes (ZMB 135) in the Koken collection at Berlin. The best preserved specimen was found among the unfigured material, and indicated as the lectotype by Nolf (1980). This specimen is refigured here (plate 1, figure 7).

At a first glance, the relationships of this taxon seems problematic. Closer examination, however, reveals it was an extinct genus of the Sirembini that is characterized by very round otoliths with a broadened sulcus that occupies almost the entire inner face of the otoliths. These otoliths are further characterized by a marked depression below the anterior portion of the cauda. Relationships to the genus *Sirembo* are hypothesized because of the very similar convexity of the inner face and the very similar outline of the cauda; see Nolf, 1980, plate 6, for iconography of the Recent species *Sirembo jerdoni* Day, (1888) (as *S.* sp.), *S. everriculi* Whitley, 1936 and *S. imberbis* Temminck & Schlegel, 1846.

Stratigraphy and locality data: "Commonly found in the Clayborne [Claiborne] Beds." I did not find this species in any of my samples. Nolf (1980) noted the species as being from Texas, but this was an error. The label with the specimens indicated the Claiborne of Alabama (USA).

Family ATHERINIDAE

"genus Atherinidarum" *debilis* (Koken, 1888)

Plate 1, Figure 10

1888 *Otolithus (Mugilidarum) debilis* Koken - Koken, p. 288, plate 17, figure 8;

1985 "genus Mugilidarum" *debilis* - Nolf, p. 124;

2003 "genus Atherinidarum" *debilis* (Koken, 1888) - Nolf & Stringer (2003 plate 3, figures 20-21).

Discussion: Besides the holotype (ZMB Ot. 105), this taxon is also documented by perfectly preserved specimens from the Yazoo Clay (Nolf & Stringer, 2003, plate 3, figures 20-21) that clearly show the affinity of those otoliths to atherinids.

Stratigraphy and locality data: "4 specimens from Jackson River." The species is also represented in my samples from the Moodys Branch Formation at Riverside Park, Jackson, Mississippi and from the Yazoo Clay at Copenhagen, Louisiana.

Family BERYCIDAE

Centroberyx sp.

Plate 1, Figure 8

1888 *Otolithus (Apogonidarum) hospes* - Koken, 1888, p. 278, plate 18, figure 15.

Discussion: The holotype (ZMB Ot. 124) of this taxon is an eroded otolith of a juvenile *Centroberyx*, not diagnostic at the species level. It is important, however, to mention it here because the specimen constitutes the only American Eocene record of the genus *Centroberyx* Gill, 1862. In the Recent fauna, *Centroberyx* is known only from Australia to South Africa. In Europe, the genus has a fossil record from late Santonian till middle Miocene. It apparently shows a Late Cretaceous and Paleogene Tethys distribution pattern.

Stratigraphy and locality data: "A single specimen from the Jackson Beds." Besides Koken's specimen, *Centroberyx* is also represented in several American Paleocene formations: Matthews Landing Member (Early Selandian) of the Porters Creek Formation (Nolf & Dockery, 1993), Brightseat and Aquia Formations of Maryland, and Kincaid Formation of Texas (unpublished data).

Family MALACANTHIDAE

"genus Malacanthidarum" *sulcatus* (Koken, 1888)

Plate 1, Figure 14

1888 *Otolithus (Cottidarum) sulcatus* Koken - Koken, p. 287, plate 18, figure 12;

2003 "genus Malacanthidarum" *sulcatus* (Koken, 1888) - Nolf & Stringer (2003, plate 5, figures 3-8).

Discussion: The holotype and unique specimen cited by Koken are missing from what remains of the original Koken collection. I have a single specimen from the Moodys Branch Formation at Town Creek, Jackson, Mississippi, which is probably Koken's type locality. Therefore, this specimen (IRSNB P 7430) is indicated here as neotype. The species is more common in the Yazoo Clay at Copenhagen, Louisiana. A series of six specimens from Copenhagen was figured by Nolf & Stringer (2003, pl. 5, figs. 3-8), illustrating clearly the variability and ontogenetic development of these otoliths.

Stratigraphy and locality data: "A single specimen from Jackson River." New material includes the neotype from the Moodys Branch Formation and the specimens cited above from the Yazoo Clay.

Family HAEMULIDAE

Orthopristis americana (Koken, 1888)

Plate 3, Figures 13-15

1888 *Otolithus (Carangidarum) americanus* Koken - Koken, p. 277, plate 17, figures 1-3;

2003 *Orthopristis americana* (Koken, 1888) - Nolf & Stringer (2003, plate 4, figures 17-21).

Discussion: The specimen ZMB Ot. 152 is indicated here as lectotype and refigured with two paralectotypes (ZMB Ot. 154). The species is further documented by a growth series from the Yazoo Clay and is figured by Nolf & Stringer (2003, plate 4, figures 17-21; see paper for additional comments).

Stratigraphy and locality data: None in the Koken text, but Jackson and Vicksburg beds were noted in his table on p. 295. New material was collected from the Moodys Branch Formation at Riverside Park and Town Creek, Jackson, Mississippi; at Techeva Creek, Yazoo County, Mississippi; and from the Yazoo Clay at Copenhagen, Louisiana.

Family SPARIDAE

"genus Sparidarum" *elegantulus* (Koken, 1888)

Plate 2, Figure 1-2

1888 *Otolithus (Pagelli) elegantulus* Koken Koken, p. 279, plate 17, figures 5-6;

2002 "genus Sparidarum" *elegantulus* (Koken, 1888) - Nolf & Stringer (2003, plate 6, figures 6-11).

Discussion: Besides the lectotype (ZMB Ot. 159), a specimen from the Moodys Branch Formation at Town Creek, Jackson, Mississippi, is figured (respectively Plate 2, Figures 1 and 2), which is probably Koken's type locality. The variability of the otoliths of this species is further illustrated by a series from the Yazoo Clay figured by Nolf & Stringer (2003, plate 6, figures 6-11).

Stratigraphy and locality data: "A single specimen from Jackson River." New material was collected from the Poterchito Member of the Cook Mountain Formation at Newton, Mississippi; from the Moodys Branch Formation at Town Creek, Jackson, Mississippi; and from the Yazoo Clay at Copenhagen, Louisiana.

Family SCIAENIDAE

Aplodinotus distortus n. sp.

Plate 4, Figures 3-8

Remarks: Although no otoliths of this species were found among the type specimens of Koken, it is appropriate to describe it here. The syntypes of *Otolithus (Sciaenidarum) gemma* include specimens of *Aplodinotus gemma, Sciaena pseudoradians* (Frizzell & Dante, 1965), and "genus Sciaenidarum" *radians.* All of these taxa occur together with *A. distortus* in samples of the Byram Marl from Vicksburg, Mississippi. Lack of awareness of the latter species has created problems in distinguishing the other three forms.

Type material: Holotype: a right otolith (IRSNB P.7455) (Pl. 4, Fig. 9); 43 paratypes of which five are figured (IRSNB P.7450-7454; Pl. 4, Figs. 4-8) from the "Keyes Iron and Metal" locality. Additional material: four specimens from the old road to Waterville and two from the International Paper plant locality, both Byram Formation, about 12 km north of Vicksburg, Mississippi; 23 specimens from the Rosefield Formation, Rosefield, Louisiana.

Dimensions of the holotype: Length: 4.9 mm; height: 4.6 mm; thickness: 1.6 mm.

Type locality: "Keyes Iron and Metal" locality, along Highway 61, about 6 km north of Vicksburg, Mississippi.

Etymology of name: *Distortus, a, um* (Latin) = distortion. Alludes to the distortion of these otoliths along an anterodorsal-posteroventral axis.

Diagnosis: This species is characterized by robust, rather high otoliths tha in specimens of over 5 mm length show a marked distortion along an anterodorsal - posteroventral axis. Some of the larger specimens show a hypertrophical development of the posteroventral area and an expansion of the anterodorsal area. The outer face is globally convex and nearly smooth in adult otoliths; juveniles show some irregular tuberculation. The inner face is clearly convex in all senses. The sulcus is constituted by a wide ostium that is higher than long, and a narrow cauda with a horizontal anterior part and a ventrally oriented posterior part. This ventrally directed portion becomes relatively longer in older specimens. The area located between the posterior part of the ostial crista inferior and the vertically oriented portion of the cauda is at least twice as wide as the cauda, and even much wider in juvenile otoliths.

Affinities: Otoliths of *A. distortus* can be easily distinguished from the sciaenids that also occur with it in the Byram Marl. They differ from those of *A. gemma* and "genus Sciaenidarum" *radians* by the wide area located between the posterior part of the ostial crista inferior and the vertically oriented portion of the cauda. They differ from *Sciaena pseudoradians* in the strong distortion of their otoliths. They seem to be most closely related to those of *Aplodinotus hoffmanni* Nolf & Aguilera, 1998 from the lower Miocene Cantaure Formation of Venezuela (see Nolf & Aguilera, 1998, plate 9, figures 1-4), but in the latter species the otoliths are more elongate and show no posteroventral expansion.

Aplodinotus gemma Koken, 1888

Plate 2, Figures 7-10

1888 *Otolithus (Sciaenidarum) gemma* Koken - Koken, p. 281, plate 19, figure 9; not figure 13;

1993 *Frizzellithus gemma* (Koken 1888) - Schwarzhans, p. 89, figure 144, not 145-148.

Discussion: The type material of this species is a mixture of three different species. The specimen figured on Koken's pl. 19, fig 9 was indicated as the lectotype by Schwarzhans (1993, p. 89, PMHUB Ot. 128), after a museum label written by W.D. Heinrich. This specimen is refigured here (Plate 2, Figure 10). Plate 19, figure 16 of Koken represents an outer view of a different species, apparently *Sciaena pseudoradians* (Dante & Frizzell, 1965). Another specimen from the Yazoo Clay, figured by Schwarzhans (1993, fig. 147) probably also represents this species. He further illustrated (1993, figures 145 and 146) two rather eroded syntypes from Koken's unfigured material. These apparently represent eroded adult specimens of "genus Sciaenidarum" *radians* Koken, 1888, as could be judged from good recently collected specimens from the Byram Marl. Identification of recently collected sciaenid associations from the Oligocene of the Gulf Coast is further complicated by the coexistence of *A. gemma* with another *Aplodinotus, A. distortus* n. sp., that is described here to avoid more confusion. Schwarzhans (1993, p. 89) also synonymizes *O. (S.) intermedius* Koken, 1888 with *A. gemma. O. (S.) intermedius* is considered a valid species, distinct from *A. gemma* in this paper.

Recently collected material allowed the illustration of a series of *A. gemma* otoliths of different sizes (Plate 2, Figures 7-9). This series is in agreement with the morphology seen in the lectotype. The species is characterized by thick, robust, high otoliths. The anterior and posterior outlines look almost symmetrical. The ventral rim is very deep and strongly curved. Both the anterior and posterior end of the dorsal rim are somewhat angular.

Otoliths of *A. gemma* seem to be most closely related to those of the early Miocene *A. longecaudatus* Nolf & Aguilera, 1998 from the early Miocene Cantaure Formation of Venezuela. The latter species, however, has a longer cauda that extends much further ventrally (see Nolf & Aguilera, 1998, plate 9, figure 8) than in *A. gemma.*

Stratigraphy and locality data: Koken's text mentions: "Vicksburg; Red Bluff; Jackson River, Mississippi"; the table on p. 295 mentions Jackson and Vicksburg Beds. New material similar to the lectotype was collected only from the Mint Spring, the Byram Marl, and the Chickasawhay Limestone formations in Mississippi, and from the Rosefield Formation in Louisiana. *A. gemma* does not appear to occur in any Gulf Coast Eocene formations or in the basal Oligocene Red Bluff Formation.

Sciaena pseudoradians (Dante & Frizzell, 1965)

Plate 2, Figures 3-6

1888 *Otolithus (Sciaenidarum) gemma* Koken - Koken, p. 281 (*partim*), plate 19, figure 13, not figure 9;

1965 *Corvina pseudoradians* Dante & Frizzell, n. sp. - Dante & Frizzell, plate 88, figures 26 and 28, ? p. 87, figsures 31 and 35;

1993 *Frizzellithus gemma* (Koken, 1888) - Schwarzhans, p. 89 (*partim*), fig. 147 (and 148?); not 144-146;

1993 ? *Umbrina pseudoradians* (Dante & Frizzell, 1965) - Schwarzhans, p. 79, figure 128.

Discussion: This species is described here because one of the syntypes of *Otolithus (Sciaenidarum) gemma* belongs to it (see also discussion under that species). The otolith figured in Plate 2, Figure 6 is the holotype of *Corvina pseudoradians* (USNM 23368), which was not figured with the original description of the species by Frizzell & Dante (1965). Among the paratypes figured by Frizzell & Dante, the one in their plate 88, figures 26 and 28 is probably a juvenile otolith of the same species. The one figured in plate 87, figures 31 and 35 is from a very young fish and is not diagnostic at the species level. Since the holotype of this species is a juvenile, recognition of the species very difficult. Therefore, I figured a growth series based on newly collected material (Plate 2, Figures 3-5). This series adequately illustrates the species by showing the outline of an adult specimen and the progressive narrowing of the portion of the area located between the posterior part of the ostial crista inferior and the vertically oriented portion of the cauda. Otoliths of this species seem to be most closely related to those of *Sciaena umbra* Linnaeus, 1758 (see Chaine, 1938, plate 10, as *Corvina umbra*), the type species of the genus *Sciaena.*

Stratigraphy and locality data: The holotype is from the Byram Marl at Old Byram, Hinds County, Mississippi. I collected specimens from the Red Bluff Formation at Red Bluff and Hiwannee; from the Byram Marl north of Vicksburg, Mississippi; and from the Rosefield Formation in Rosefield, Louisiana. Imperfectly preserved specimens from the Yazoo Formation at Copenhagen, Louisiana, were also referred to this species by Nolf & Stringer (2003).

"genus Sciaenidarum" *claybornensis* Koken, 1888

Plate 3, Figures 1-5

1888 *Otolithus (Sciaenidarum) claybornensis* Koken - Koken, p. 283, plate 19, figures 1 and 4;

1965 *Jefitchia claybornensis* (Koken) - Frizzell & Dante, p. 705;

1993 *Jefitchia claybornensis* (Koken, 1888) - Schwarzhans, p. 26, figs. 5-7.

1999 "genus Sciaenidarum" *claybornensis* - Müller, p. 161.

2003 "genus Sciaenidarum" *claybornensis* - Nolf & Stringer (2003, plate 3, figures 1-5).

Discussion: This species is abundant at several middle and late Eocene Gulf Coast localities. It can only be confused with "genus Sciaenidarum" *eporrectus* (see Plate 3, Figures 6-9), which has a similar ostium, but in "g. S." *claybornensis,* the otoliths are less elongate and have a caudal end that is more strongly bent in the ventral direction. Moreover, their posterodorsal angle is less salient. The holotype of the species is refigured here, together with a growth series from the Moodys Branch Formation. Another growth series from the Yazoo Clay is shown by Nolf & Stringer (2003, plate 7, figures 1-5) and starts from smaller specimens. It clearly illustrates how the ventral curvature of the caudal end becomes more pronounced in older specimens. This species appears to be most closely related to the Recent genus *Pachyurus* Agassiz, 1829. It can be compared to otoliths of the Recent *P. schomburgkii* Gunther, 1860 (plate 2, figure 10) and may belong to the same genus. However, the fossils are left in open nomenclature because otoliths of Recent *Pachyurus* species are too poorly known. There are eight Recent species (see Chao, 1978, p. 42) and only the otoliths of *P. schomburgkii* are known and that is without a growth series.

Stratigraphy and locality data: "Clayborne [Claiborne], Alabama, very common"; Koken's table on p. 295 also mentions Jackson Beds with a question mark. Newly collected specimens are from the Weches Formation at Hooker Creek, Burleson County, Texas; from the Poterchito Member of the Cook Mountain Formation at Newton, Mississippi; from the Moodys Branch Forma-

tion at Town Creek and Riverside Park, Jackson, Mississippi, and from Techeva Creek, Yazoo County, Mississippi; and from the Yazoo Clay at Copenhagen, Louisiana.

"GENUS SCIAENIDARUM" *EPORRECTUS* KOKEN, 1888

PLATE 3, FIGURES 6-9

1888 *Otolithus (Sciaenidarum) eporrectus* Koken - Koken, p. 282, plate 18, figures 16-17;

1965 *Ekokenia eporrecta* (Koken) - Frizzell & Dante, p. 704, plate 87, figures 11, 12 and 16, plate 88, figures 5 and 11;

1993 *Ekokenia epporrecta* (Koken, 1888) - Schwarzhans, p. 27, figure 11;

1999 "genus Sciaenidarum" *eporrectus* Koken, 1888 - Müller, p. 160, figsures 33/10-15.

Discussion: This species was described by Koken from a single specimen, a juvenile otolith, refigured here Plate 3, Figure 9. The species is quite common in the Stone City Beds, from which a growth series is illustrated (Plate 3, Figures 6-8). These otoliths show most similarity to those of "genus Sciaenidarum" *claybornensis* (see this species for an account of distinctive features). As for the preceding species, affinities of this species are closest to the Recent genus *Pachyurus*; see under "g. S." *claybornensis* for comments.

Stratigraphy and locality data: Koken cites "Newton, Mississippi" after his description of the species. However, he mentions it from the Vicksburg Group in his table on p. 295, which is apparently a mistake since there are no outcrops of the Vicksburg Group at Newton. Furthermore, I have never collected this species from any formation of the Vicksburg Group. Newly collected specimens are from the Poterchito Member of the Cook Mountain Formation at Newton, Mississippi; from the Upper Lisbon Formation at Barytown, Alabama; and from the Stone City Member of the Cook Mountain Formation, Texas, where it is very common. It is also known from the Piney Point Formation (Bartonian) of Virginia.

"GENUS SCIAENIDARUM" *INTERMEDIUS* KOKEN, 1888

PLATE 2, FIGURES 12-14

1888 *Otolithus (Sciaenidarum) intermedius* Koken - Koken, p. 283, plate 19, figures 2-3.

Discussion: Plate 2, Figures 12-13 show original types of Koken. Plate 2, Figure 14 is a recently collected specimen that illustrates perfectly the relevant feature of this species: a dorsovental narrowing of the central part of the ostium. Otoliths of this species are further characterized by a salient, nearly rectangular posterodorsal angle. The ostial morphology of this fossil most closely resembles that of the Recent genus *Pachyurus* (Plate 2, Figure 11), but our knowledge of the otoliths of the Recent species of that genus and their ontogeny is too poorly known to determine precise affinities.

Stratigraphy and locality data: "Clayborne [Claiborne], Alabama, not common." I collected the species from the Upper Lisbon Formation at Barytown, Alabama. Some juvenile otoliths from the Moodys Branch Formation at Techeva Creek, Yazoo County, Mississippi, may also belong to "g. S." *intermedius*, but the specimens are too small to be diagnostic. The species was not collected from the Priabonian Yazoo Clay or from any Oligocene locality. It apparently became extinct at the end of the Bartonian and never occurs together with *Aplodinotus gemma*, which only appears at the Rupelian (P 9 planktonic foraminiferal zone).

"GENUS SCIAENIDARUM" *RADIANS* KOKEN, 1888

PLATE 4, FIGURES 1-3

1888 *Otolithus (Sciaenidarum) gemma* Koken - Koken, p. 281 (two unfigured specimens only), not plate 19, figsures 9 and 13 (see under *Aplodinotus gemma*).

1993 *Frizzellithus gemma* (Koken 1888) - Schwarzhans, p. 89, figures 145-146; not 144, 147, 148.

Discussion: As previously mentioned under *Aplodinotus gemma*, the type material of this species is a mixture of three different species. Two of Koken's unfigured syntypes were illustrated by Schwarzhans (1993, figures 145 and 146). These specimens are rather eroded, but I collected well-preserved material from the Byram Formation at the "Keyes Iron and Metal" locality, along Highway 61, about 6 km north of Vicksburg, Mississippi. These specimens allowed the species to be adequately illustrated (Plate 4, Figures 1-2) and to establish their relationships to the holotype and a single original specimen of *Otolithus (Sciaenidarum) radians*. The original specimen, a juvenile otolith, could not be interpreted without a growth series and was not considered a valid species by Nolf (1985, p.130). However, the additional diagnostic material makes a description of the species possible.

This species is characterized by circular-shaped otoliths with a characteristic inframedian posterior tip. The greatest thickness of the otoliths is located in their posterior part. The outer face is nearly smooth and is equally convex in adult otoliths, except for a very shallow dorso-ventrally oriented central hollowing. The inner face is slightly convex in all directions. The sulcus consists of a very wide ostium that is higher than its length and a narrow cauda that is regularly bent down-

wards to the ventral rim. The area located between the posterior part of the ostial crista inferior and the vertically oriented portion of the cauda is quite narrow but always remains slightly wider than the cauda.

The species can be easily distinguished from *Aplodinotus gemma* (Plate 2, Figures 7-10) to which it was originally attributed by Koken by its quite salient inframedian posterior tip. It can also be distinguished easily by the same feature from *Aplodinotus longecaudatus* Nolf & Aguilera, 1998 from the early Miocene of Venezuela. The morphological resemblance between the two species appears significant on preliminary examination, but I am not convinced that the affinities of the new species really lies with *Aplodinotus*.

Stratigraphy and locality data: "Vicksburg." Additional specimens are from the Glendon Limestone and from the Byram Marl, north of Vicksburg, Mississippi.

Family CEPOLIDAE

Owstonia comes (Koken, 1888)

Plate 3, Figure 10

1888 *Otolithus (Cepolae) comes* Koken - Koken, p. 288, plate 17, figure 12.

Discussion: This otolith seems to be most closely related to cepolids such as *Owstonia nigromarginatus* (Fourmanoir, 1985). These may be seen in Rivaton & Bourret (1999, plate 152, figures 9-10, as *Sphenanthias nigromarginatus*). Cepolids are not represented in the present-day American seas. The presence of this fossil cepolid must be considered as a case of Paleogene circumglobal Tethys distribution.

Stratigraphy and locality data: "Jackson River, Mississippi, a single specimen." Similar otoliths are not represented in any of my samples.

Family TRACHINIDAE

"genus Trachinidarum" *laevigatus* (Koken, 1888)

Plate 3, Figure 12

1888 *Otolithus (Trachini) laevigatus* Koken - Koken, p. 286, plate 18, figures 13-14;

2003 "genus Trachinidarum" *laevigatus* (Koken, 1888) - Nolf & Stringer (2003, plate 8, figure 1).

Discussion: Although Koken writes that this taxon is "not uncommon", no specimens were found in what remains of the original Koken collection. A specimen from the Moodys Branch Formation at Town Creek, Jackson, Mississippi, which is probably Koken's type locality, is indicated here as the neotype (IRSNB P 7447). Although this otolith cannot be included in any Recent trachinid family, its morphology is close enough to that of the genus *Trachinus* Linnaeus, 1758 to be included in that genus. Recent trachinids show a typical eastern Atlantic and Mediterranean distribution pattern, but otoliths figured by Müller (1999, figs. 41/9-11) from the Old Church Formation, late Oligocene of Virginia, doubtlessly belong to the genus *Trachinus*.

Stratigraphy and locality data: "Not uncommon in the Jackson Beds." Recently collected material comes from the Moodys Branch Formation at Town Creek, Mississippi, and from the Yazoo Clay at Copenhagen, Louisiana.

Family BLENNIIDAE

"genus Blenniidarum" *cor* (Koken, 1888)

Plate 3, Figure 11

1888 *Otolithus (Triglae) cor* Koken - Koken, p. 287, plate 18, figure 10;

1999 "genus Blenniidarum" *curvatus* n. sp. - Müller, p. 205, figures 42/3-6; plate 16, figure 19;

2003 "genus Blenniidarum" *cor* (Koken, 1888) - Nolf & Stringer (2003, plate 8, figures 2-4).

Discussion: This species was originally described as a triglid by Koken, but it is probably related to the blenniids. For comparison, see the otoliths of various taxa figured by Smale *et al.* (1995, plates 125-127).

Stratigraphy and locality data: "a single specimen from Jackson River." New material comes from the Moodys Branch Formation at Town Creek, Mississippi; from the Yazoo Clay at Copenhagen, Louisiana; and from the Piney Point Formation of Virginia. Two imperfectly preserved otoliths from the Byram Marl (Rupelian) north of Vicksburg probably also belong to this species.

Discussion and Conclusions

Systematic revision of the type material and examination of recently collected specimens allowed evaluations of the 23 species described by Koken (1888) from the U.S. Gulf Coast Paleogene. The stratigraphic range of valid otolith-based species either introduced by Koken in 1888 or related to Koken's American type material is shown in Figure 1. Among those, 19 are considered to be valid species; they are attributed to genera or higher taxonomic groups based on comparison with an extensive collection of Recent fish otoliths (about 6,000 species).

Four of the species described by Koken proved to be based on eroded or juvenile otoliths that lack diagnostic features to define a species. Two of them, *Otolithus (Apogonidarum) hospes* and *Otolithus (inc. sed.)* aff. *umbonato*, however, were treated in the systematic account because they are identifiable at generic level and represent Recent genera (respectively *Centroberyx* and *Pterothrissus*) that do not occur in present-day American seas. The two others, *Otolithus (Sparidarum) insuetus* and *Otolithus (Sciaenidarum) similis*, are based on non-diagnostic eroded or juvenile otoliths. The former of these cannot be interpreted either at a generic or specific level, and the latter represents non-diagnostic sciaenid otoliths that are too poorly preserved to determine their difference or similarity to any of the other recognized Paleogene Gulf Coast sciaenids.

Some of Koken's series of syntypes proved to be mixtures containing additional species: the syntypes of *Paraconger sector* also include specimens of *Ariosoma nonsector* Nolf & Stringer, 2003; those of *Aplodinotus gemma* include "genus Sciaenidarum" *radians* Koken, 1888 and *Sciaena pseudoradians* (Dante & Frizzell, 1965). Finally, a new species, *Aplodinotus distortus*, was described because it is found with the former three sciaenid species in the Byram Marl and has led to confusion with the other species.

Although the present paper is not intended as a sciaenid revision, evaluation of several of Koken's sciaenid species provided new insights in sciaenid

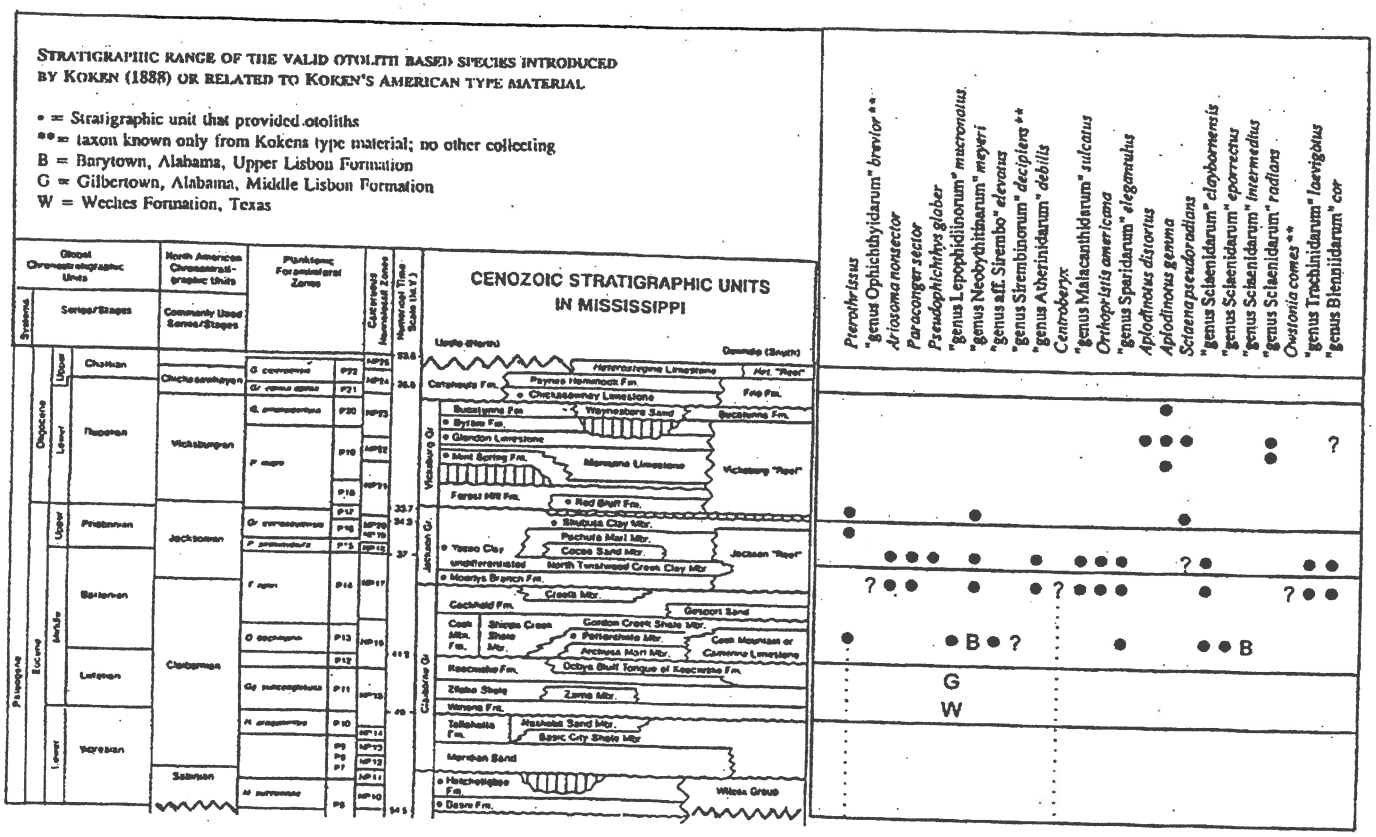

Figure 1. Stratigraphic Range of Valid Otolith-based Species of Koken (1888)

paleoecology and evolution. Among the seven sciaenid species treated here, five have their closest relationships to present-day sciaenids with a freshwater habitat (Table 2). This prompted a closer examination of the fossil record of the "freshwater sciaenid genera."

With the possible exception of the *Plagioscion* sp. from the northwestern Amazon Basin cited by Monsch (1998), all sciaenid otoliths are known from associations composed of marine fishes. Some of those associations may be very nearshore, but none of them can be qualified as freshwater or even lagoon associations. The conclusion appears that the present-day freshwater genera are descendants of marine ancestors. A possible answer may be found in the otolith-based fossil record, since there are no Paleogene Cynoscioninae, Micropogoninae, or Lariminae (see Sasaki, 1989 for content of the subfamilies). However, in the Miocene, those modern groups appear suddenly and probably replaced several of the successful marine Paleogene sciaenid genera except for those in freshwater environments.

Genus *Aplodinotus* (Recent: North America, mainly Mississippi drainage system)	
Aplodinotus distortus n.sp.	Lower Oligocene, Gulf Coast
Aplodinotus gemma (Koken, 1888)	Lower Oligocene, Gulf Coast
Aplodinotus hoffmani Nolf & Aguilera, 1998	Lower Miocene, Venezuela
Aplodinotus longecaudatus Nolf & Aguilera, 1998	Lower Miocene, Venezuela
Aplodinotus ventriosus (Müller, 1999)	Lower Miocene, Virginia
Note: *A. primigenius* Müller, 1999 is not an *Aplodinotus species*	
Genus *Pachypops* (Recent: South America)	
Pachypops fitchi Schwarzhans, 1993	Lower-Upper Miocene, Trinidad
Genus *Plagioscion* (Recent: South America mainly the Amazon and Orinoco drainage system)	
Plagioscion sp. (Monsch, 1998)	Middle and Upper Miocene, Peru
Plagioscion sp. (Nolf, 1976)	Middle and Upper Miocene, Trinidad
Plagioscion sp. (Nolf & Aguilera, 1998)	Lower Miocene, Venezuela
Species related to genus *Pachyurus* (Recent: South America)	
"genus Sciaenidarum" *claybornensis* Koken, 1888	Bartonian and Priabonian, Gulf Coast
"genus Sciaenidarum" *copelandi* (Dante & Frizzell, 1965)	Bartonian, Gulf Coast
"genus Sciaenidarum" *eanesi* (M¸ller, 1999)	Bartonian, Virginia
"genus Sciaenidarum" *eporrectus* Koken, 1888	Bartonian, Gulf Coast
"genus Sciaenidarum" *intermedius* Koken, 1888	Bartonian, Gulf Coast

Table 2. Comparison of Fossil Sciaenid Species to Present-day Sciaenids

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Explanations of the plates

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 letter show inner views.

Plate 1

Figure 1 "genus Ophichthyidarum" *brevior* (Koken, 1888)
L, holotype of *Otolithus (Congeris) brevior*, ZMB Ot. 26. "Jackson Beds".

Figure 2 *Paraconger sector* (Koken, 1888)
L, lectotype of *Otolithus (Platessae) sector*, ZMB Ot. 19. "From the Clayborne [Claiborne] till Vicksburg Beds, but common in the Jackson Beds."

Figures 3-4 *Ariosoma nonsector* Nolf & Stringer, 2003 n. sp. 3 = L, 4 = R, part of the original type series of *Otolithus (Platessae) sector*, ZMB Ot. 21 and ZMB Ot. 20. "From the Clayborne [Claiborne] till Vicksburg Beds, but common in the Jackson Beds."

Figure 5 *Pseudophichthys glaber* (Koken, 1888)
L, holotype of *Otolithus (Soleae) glaber*, ZMB Ot. 177. "Jackson Beds".

Figure 6 "genus aff. *Sirembo*" *elevatus* (Koken, 1888)
R, holotype of *Otolithus (Gadidarum) elevatus*, ZMB Ot. 83. "Clayborne [Claiborne] Beds".

Figure 7 "genus Sirembinorum" *decipiens* (Koken, 1888)
L, lectotype of *Otolithus (Sciaenidarum) decipiens*, ZMB Ot. 135. "Clayborne [Claiborne] Beds", probably Stone City Member of Cook Mountain Formation, Texas.

Figure 8 *Centroberyx* sp. ind.
L, holotype of *Otolithus (Apogonidarum) hospes*, ZMB Ot. 124. "Jackson Beds"

Figure 9 "genus Neobythitinarum" *meyeri* (Koken, 1888)
R, holotype of *Otolithus (Gadidarum) meyeri*, ZMB Ot. 80. "Jackson River".

Figure 10 "genus Atherinidarum" *debilis* (Koken, 1888)
L, holotype of *Otolithus (Mugilidarum) debilis*, ZMB Ot. 105. "Jackson River".

Figures 11-13 "genus Lepophidiinorum" *mucronatus* (Koken, 1888)
R, no type material, IRSNB P 7427-7429, Virginia, Pamunkey River, Piney Point Formation, Bed A, Bartonian.

Figure 14 "genus Malacanthidarum" *sulcatus* (Koken, 1888)
L, neotype of *Otolithus (Cottidarum) sulcatus*, IRSNP P 7430, Moodys Branch Formation, Town Creek, Jackson, Mississippi.

Plate 2

Figures 1-2 "genus Sparidarum" *elegantulus* (Koken, 1888)
1 = L, 2 = R, 1 = holotype of *Otolithus (Pagelli) elegantulus*, ZMB 159, "Jackson River", 2 = topotype (?), IRSNB P 7431, Moodys Branch Formation, Town Creek, Jackson, Mississippi.

Figures 3-6 *Sciaena pseudoradians* (Dante & Frizzell, 1965)
L, 3 = Red Bluff Formation, Red Bluff type locality, Mississippi IRSNB P 7431, 4-5 = Red Bluff Formation, Hiwannee, Mississippi (IRSNB P 7433-7434; 6 = holotype of *Corvina pseudoradians* Dante & Frizzell, 1965 , USNM 23368, Byram Formation, Old Byram, Hinds County, Mississippi.

Figures 7-10 *Aplodinotus gemma* Koken, 1888
7-9 = L, 10 = R, 7 = IRSNB P 7435, Byram Formation, International Paper Plant, Warren County, Mississippi, 8-9 = IRSNB P 7436-7437, Chickasawhay Limestone, Waynesboro, Taylor's Creek, Wayne County, Mississippi, 10 = lectotype of *Otolithus (Sciaenidarum) gemma*, ZMB Ot. 128, no precise locality data; Koken cites "Vicksburg, Red Bluff and Jackson River, Mississippi." The Byram Formation north of Vicksburg is the most probable type locality.

Figure 11 *Pachyurus schomburgkii* Gunther, 1860
L, Recent, off Buenos Ayres, Argentina (coll. IRSNB).

Figures 12-14 "genus Sciaenidarum" *intermedius* Koken, 1888
R, 12 = lectotype, ZMB Ot. 136, 13 = paralectotype, ZMB Ot. 137, 14 = IRSNB P 7438, Upper Lisbon Formation, Early Bartonian, Barrytown, Alabama.

Plate 3

Figures 1-5 "genus Sciaenidarum" *claybornensis* Koken, 1888
1-4 = L, 5 = R, 1-4 = Moodys Branch Formation, Late Bartonian, Midway, Techeva Creek, Yazoo County, Mississippi, IRSNB P 7439-7442; 5 = lectotype, ZMB P 125, "Clayborne [Claiborne], Alabama".

Figures 6-9 "genus Sciaenidarum" *eporrectus* Koken, 1888
L, 6-8 = Stone City Member of Cook Mountain Formation, Stone City Bluff on Brazos River, Burleson County, Texas, IRSNB P 7443-7445, 9 = holotype, ZMB Ot. 122. "Newton, Mississippi".

Figure 10 *Owstonia comes* (Koken, 1888)
L, holotype of *Otolithus (Cepolae) comes*, ZMB Ot. 165. "Jackson River, Mississippi".

Figure 11 "genus Blenniidarum" *cor* (Koken, 1888)
R, IRSNB P 7446, Moodys Branch Formation, Town Creek, Jackson, Mississippi.

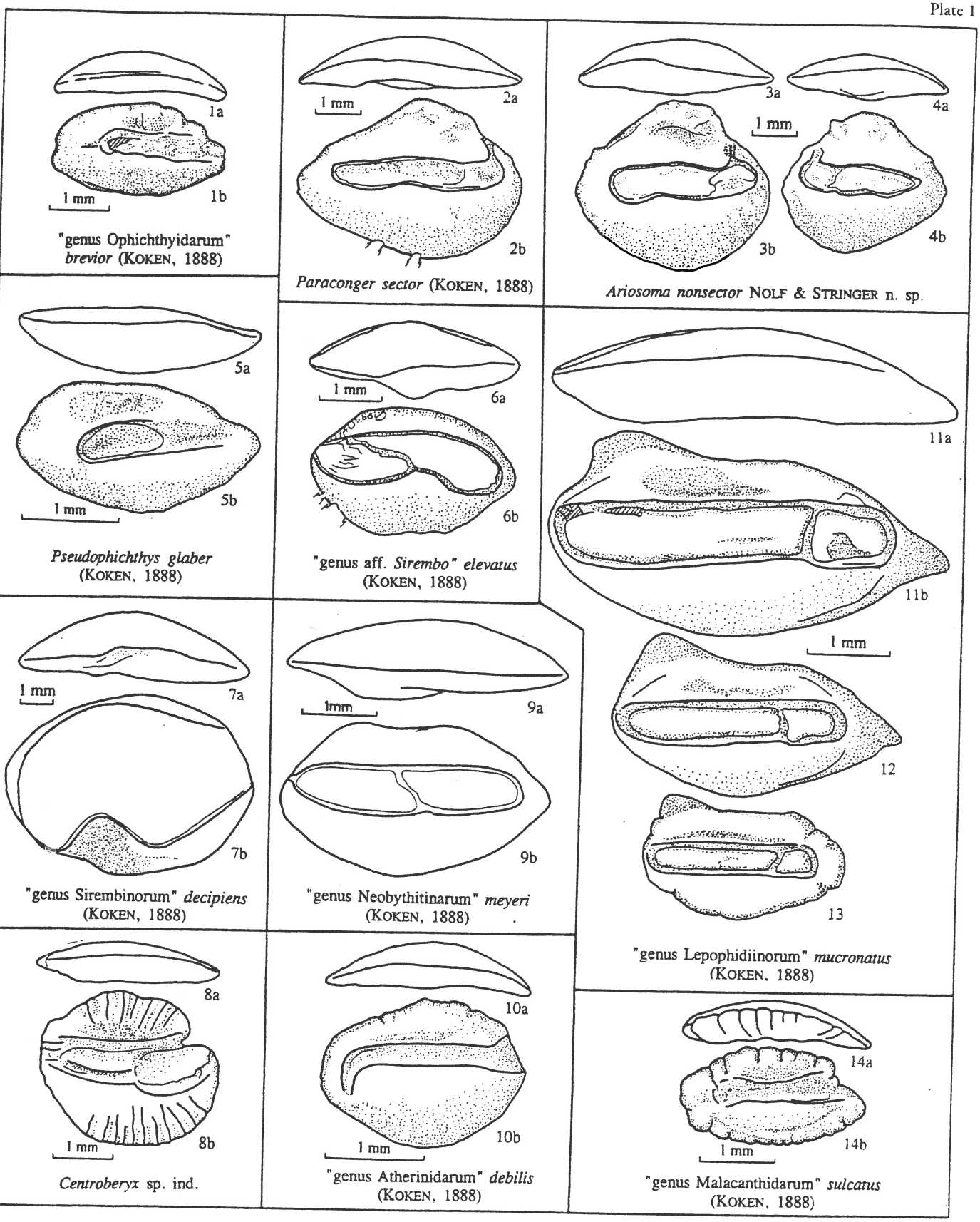
Figure 12 "genus Trachinidarum" *laevigatus* (Koken, 1888)
R, IRSNB P 7447, neotype, Moodys Branch Formation, Town Creek, Jackson, Mississippi

Figures 13-15 *Orthopristis americana* (Koken, 1888)
13 = L, 14-15 = R, 13 = lectotype, ZMB Ot. 152, 14-15 = paralectotypes, ZMB Ot. 154, "Jackson and Vicksburg Beds".

Plate 4

Figures 1-3 "genus Sciaenidarum" *radians* Koken, 1888
1 = L, 2-3 = R, 1-2 = IRSNB P 7448-7449, Byram Marl, "Keyes Iron and Metal" locality, north of Vicksburg, 3 = holotype (ZMB Ot. 123), "Vicksburg".

Figures 4-9 *Aplodinotus distortus* n. sp.
4-6 = L, 7-9 = R, 4-8 = paratypes, IRSNB P 7450-7454, 9 = holotype, IRSNB P 7455, Byram Marl, "Keyes Iron and Metal" locality, north of Vicksburg.


1a
1 mm
1b
"genus Ophichthyidarum" brevior (KOKEN, 1888)
1 mm
2a
2b
Paraconger sector (KOKEN, 1888)
3a
4a
1 mm
3b
4b
Ariosoma nonsector NOLF & STRINGER n. sp.
5a
1 mm
5b
Pseudophichthys glaber (KOKEN, 1888)
1 mm
6a
6b
"genus aff. Sirembo" elevatus (KOKEN, 1888)
11a
11b
1 mm
12
13
"genus Lepophidiinorum" mucronatus (KOKEN, 1888)
1 mm
7a
7b
"genus Sirembinorum" decipiens (KOKEN, 1888)
1mm
9a
9b
"genus Neobythitinarum" meyeri (KOKEN, 1888)
8a
1 mm
8b
Centroberyx sp. ind.
10a
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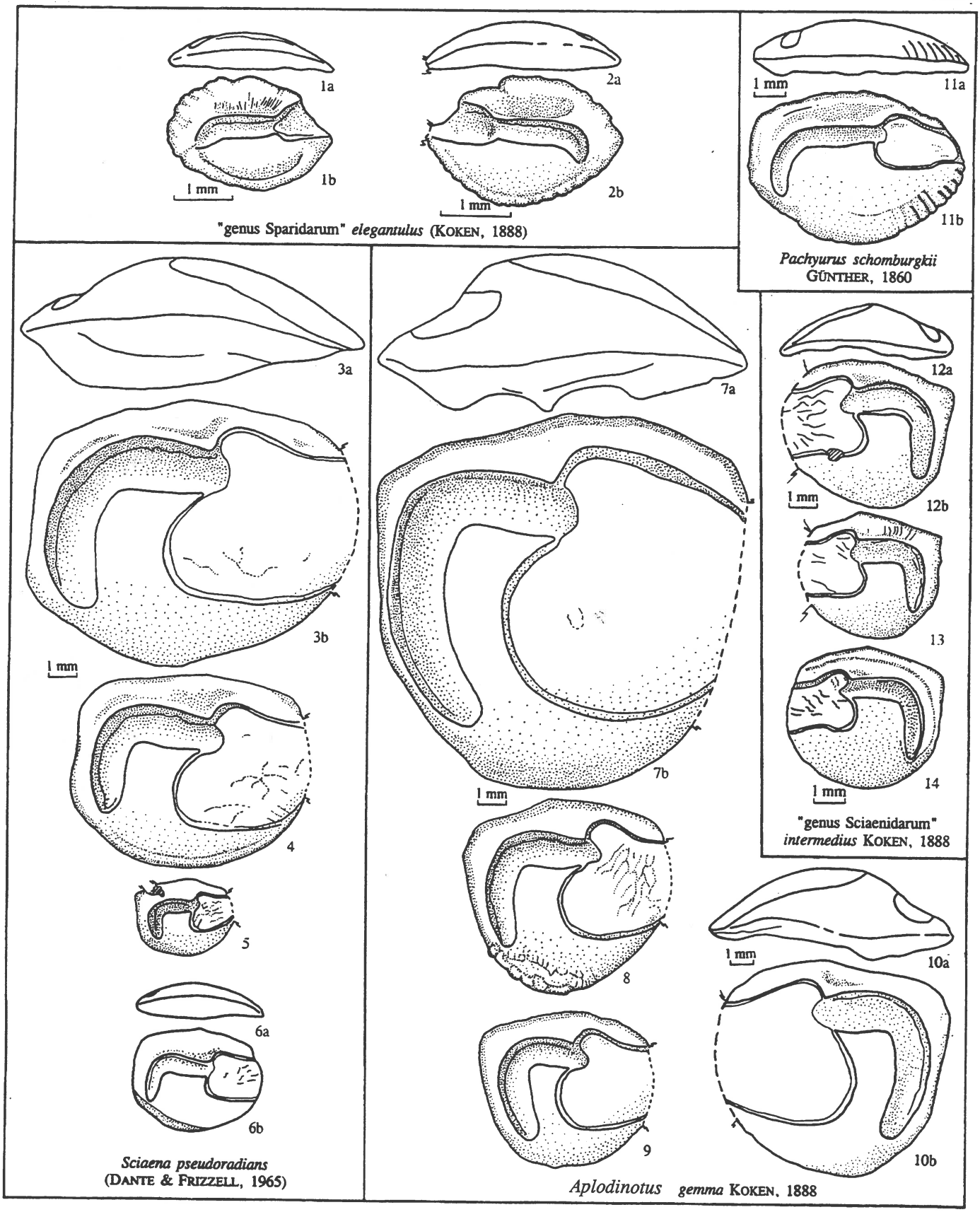
10b
"genus Atherinidarum" debilis (KOKEN, 1888)
14a
1 mm
14b
"genus Malacanthidarum" sulcatus (KOKEN, 1888)


1a
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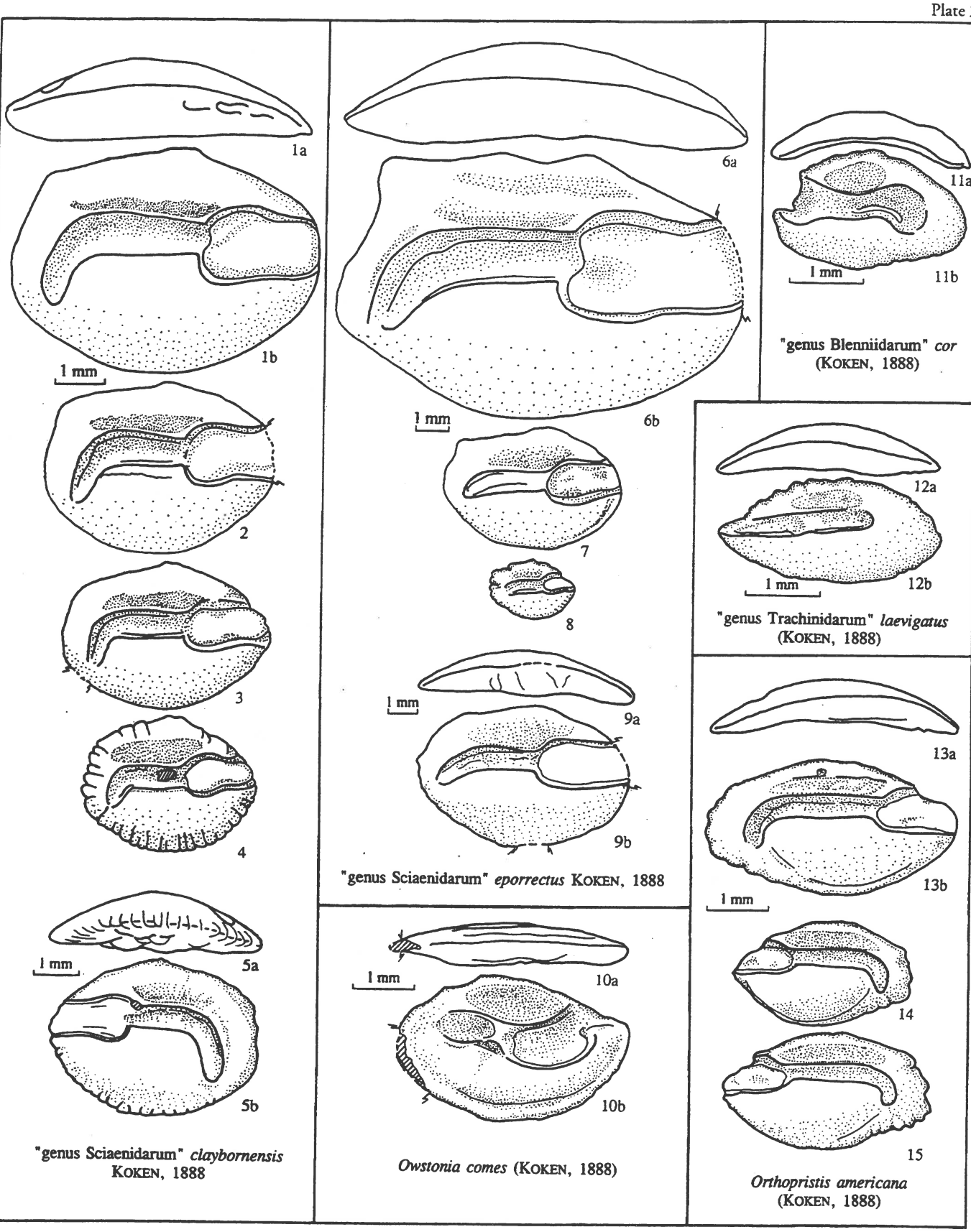
1 mm
2a
2b
1 mm
"genus Sparidarum" elegantulus (KOKEN, 1888)
1 mm
11a
11b
Pachyurus schomburgkii
GÜNTHER, 1860
3a
3b
1 mm
4
5
6a
6b
Sciaena pseudoradians
(DANTE & FRIZZELL, 1965)
7a
7b
1 mm
8
9
12a
1 mm
12b
13
14
1 mm
"genus Sciaenidarum"
intermedius KOKEN, 1888
1 mm
10a
10b
Aplodinotus gemma KOKEN, 1888


1a
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1 mm
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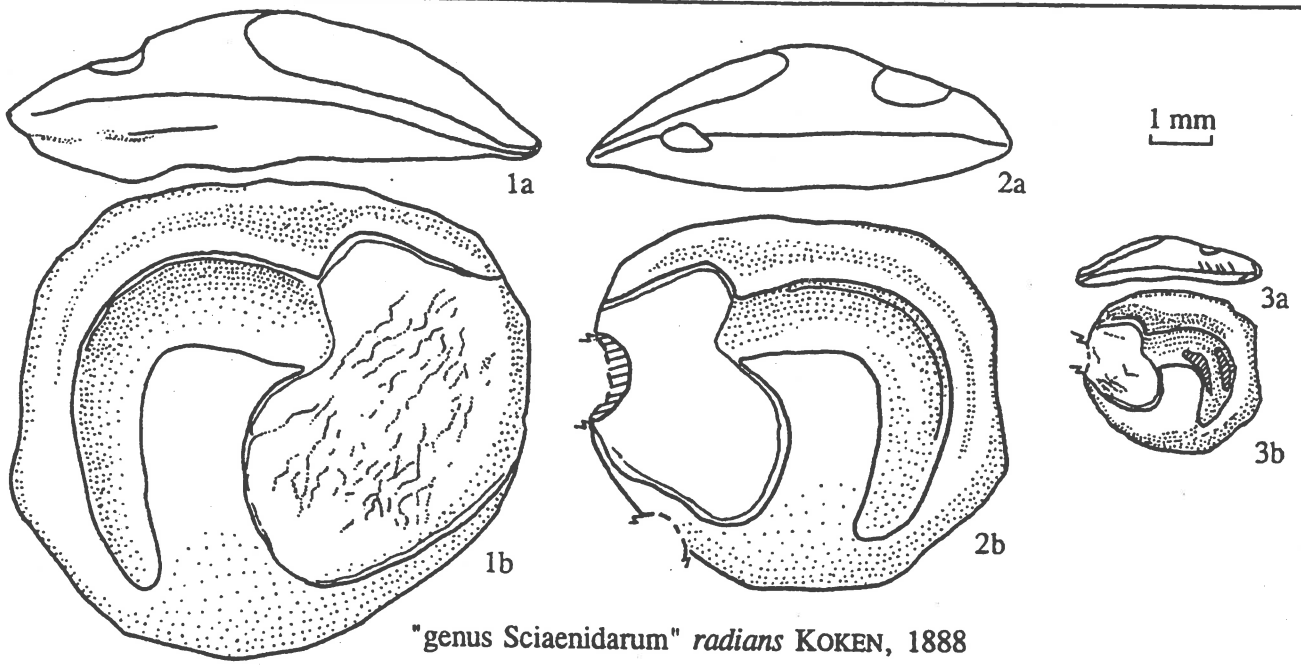
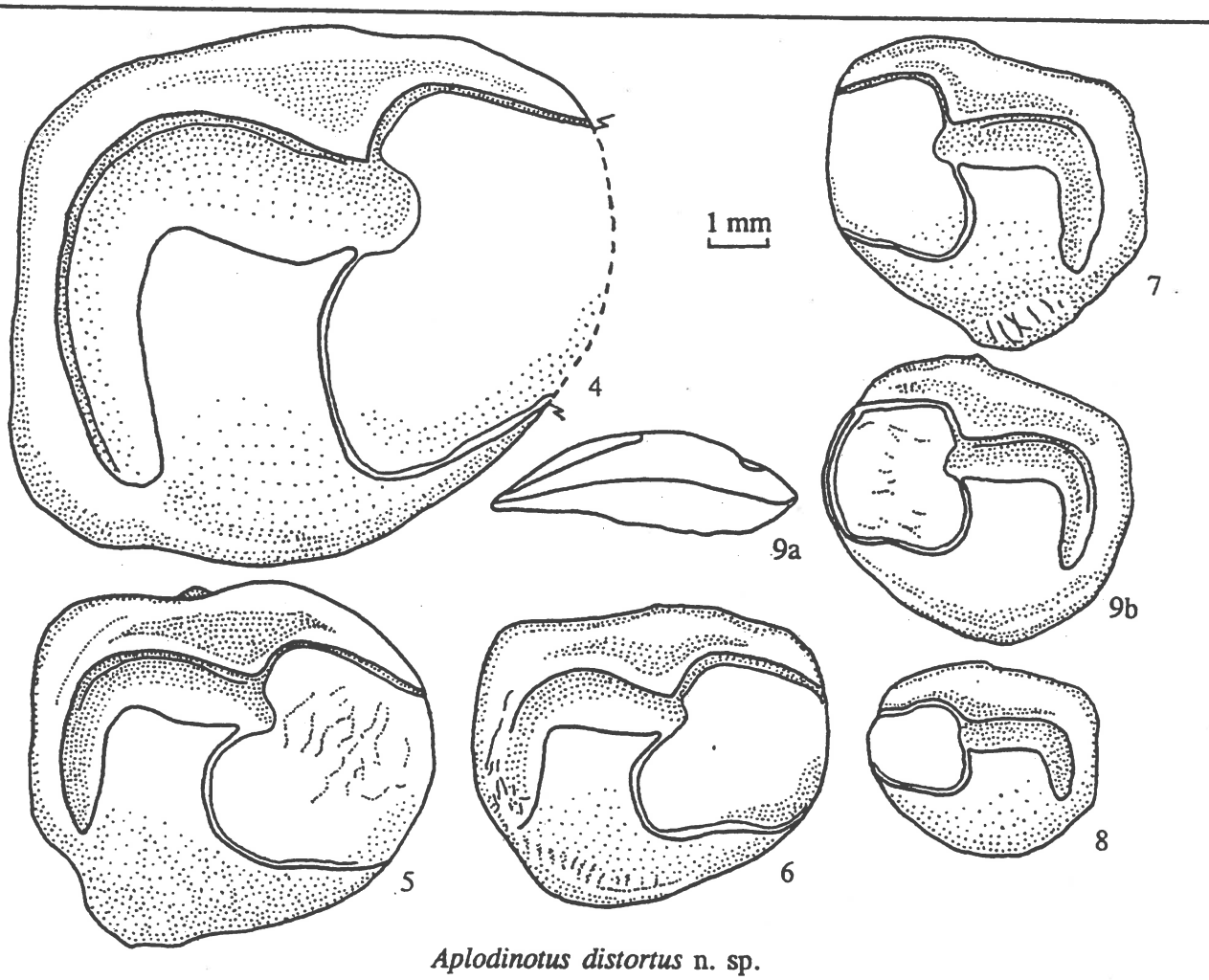
5a
1 mm
5b
"genus Sciaenidarum" *claybornensis* KOKEN, 1888
6a
1 mm
6b
7
8
1 mm
9a
9b
"genus Sciaenidarum" *eporrectus* KOKEN, 1888
1 mm
10a
10b
Owstonia comes (KOKEN, 1888)
11a
1 mm
11b
"genus Blenniidarum" *cor* (KOKEN, 1888)
12a
1 mm
12b
"genus Trachinidarum" *laevigatus* (KOKEN, 1888)
13a
13b
1 mm
14
15
Orthopristis americana (KOKEN, 1888)



"genus Sciaenidarum" *radians* KOKEN, 1888



Aplodinotus distortus n. sp.

Stratigraphic range of the valid otolith based species introduced by Koken (1888) or related to Koken's American type material

• = Stratigraphic unit that provided otoliths
** = taxon known only from Kokens type material; no other collecting
B = Barytown, Alabama, Upper Lisbon Formation
G = Gilbertown, Alabama, Middle Lisbon Formation
W = Weches Formation, Texas