

OTOLITH-BASED FISHES FROM THE BOWDEN SHELL BED (PLIOCENE) OF JAMAICA: SYSTEMATICS AND PALAEOECOLOGY

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Investigations of fossil teleostean otoliths from the Caribbean are quite restricted, although otolith studies have the potential to provide substantial information on the palaeontology of the region. The fish otoliths from the Bowden shell bed, Bowden Formation, Jamaica, are described herein in order to ascertain the ichthyological fauna and related palaeoecological conditions. Previous investigations of otoliths for the Caribbean are addressed and support the importance of this study. Approximately 1,650 otoliths representing at least 38 teleost families and 68 species were obtained from the shell bed at the type locality of the Pliocene Bowden shell bed. Comparison of the identified otoliths to the bathymetric distributions of closely related Recent taxa revealed a diversified association with shallow-water marine forms (including euryhaline species), neritic species, and middle to outer shelf forms with some upper slope and pelagic elements. The otolith assemblage also contained forms commonly associated with reef environments. The otolith assemblage of the Bowden shell bed is quite similar to the Recent Caribbean ichthyological fauna with some notable exceptions (three Pacific forms).

Key words — Bowden shell bed, otoliths, fossil fishes, otolith morphology, systematics, palaeoecology.

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INTRODUCTION AND PREVIOUS INVESTIGATIONS

Fossil teleostean otoliths have been utilised in a very limited manner in the investigation of the palaeontology of the Caribbean region, although fossil otoliths have the potential to contribute meaningful information on the fish fauna and palaeoecology. The use of fossil teleostean otoliths provides a more detailed and accurate representation of the ichthyological fauna than the exclusive use of skeletal components such as teeth, scales, spines and vertebrae (Nolf, 1985; Breard & Stringer, 1995). Otoliths can also provide a more accurate interpretation of abundance. Fishes, sharks and rays

can contribute untold and misleading numbers of skeletal elements to the thanatocoenosis. Since an individual fish can only contribute two saccular otoliths to the fossil record, the presence of otoliths is a more precise indicator of abundance (Stringer, 1986).

Palaeontological studies from the Caribbean that include teleostean otoliths are quite limited and detailed descriptions of fossil otolith assemblages are almost nonexistent. This is especially true for Jamaica, despite the presence of thick sequences of Cretaceous to Quaternary marine sedimentary rocks (Purdy *et al.*, 1996). Some groups, such as the molluscs and other invertebrates, are well documented from the Pliocene Bowden shell bed in Jamaica (Donovan *et al.*, 1995). However, a survey of otolith studies in the Tertiary Caribbean Faunal Province clearly illustrates the lack of extensive research in this region. Fitch & Barker (1968) mentioned the occurrence of a morid otolith from Jamaica, and Fitch (1969) noted that the Bowden shell bed in Jamaica contained otoliths of lanternfish (family Myctophidae).

Clarke & Fitch (1979), in a study of Cenozoic teuthoid (cephalopod) statoliths, reported that a 225 kg sample from the Bowden shell bed in Jamaica yielded 25,000 otoliths. Fitch (1969) noted that the otoliths probably represented more than 110 kinds of fish belonging to 50-60 families. Some of the forms mentioned by Fitch included bonefish (*Albula*), croakers (*Micropogon*, *Larimus* and *Equetus*),

soldierfish (*Myripristis* and *Holocentrus*), cardinalfish (*Apo- gon*), jawfish (*Opisthognathus*), pearlfish (*Carapus*), her- rings, anchovies, gobies, goatfish, gurnards, cuskeels, catfish, codlets and a few deeper-water forms. Unfortunately, Fitch never formally described the otoliths from the Bowden shell bed. Upon his death, the otoliths were placed in the John E. Fitch Collection of Research Fossil Otoliths housed at the Los Angeles County Museum of Natural History (Robert Lavenberg, pers. comm.). A check of the pre-catalogue data at the Los Angeles County Museum revealed that the vast majority of the Bowden shell bed otolith material was identi- fied only to family level. The pre-catalogue data indicated a total of only 4,946 otoliths, not the 25,000 reported by Clarke & Fitch (1979). In addition, the inventory indicated 89 taxa or kinds of otoliths, not the 110 taxa previously reported. It is uncertain whether the collection is the same, but, if it is, there is a discrepancy of over 20,000 otoliths.

An assemblage consisting of 2,074 otoliths from the middle Miocene Gatun Formation of Panama was described in Gillette (1984). The assemblage consisted of 26 taxa of marine fishes identified by John Fitch. Unfortunately, Fitch supplied only a list of the otoliths and was not able to com- plete the study before his death. Gillette presented the list exactly as provided by Fitch, but did add some annotations, and also noted that the specimens were unavailable for renewed study. A few other studies have mentioned the occurrence of otoliths, including Schubert (1909) from Panama, Leriche (1938) from Colombia, Weiler (1959) from Mexico and Casier (1966) from Barbados. Stringer (1992b) published an abstract on otoliths from the Bowden shell bed in Jamaica and noted at least 55 taxa of teleosts.

There are only two comprehensive studies of fossil otoliths from the entire Caribbean region (Nolf, 1976; Nolf & Stringer, 1992). Nolf (1976) described 66 otolith-based teleost taxa from the Neogene of Trinidad. Most of the taxa came from various Miocene formations, but there were a few from the Pliocene. The fauna consisted mainly of neritic forms, together with a few mesopelagic elements and demer- sal (bottom dwelling) fishes from the upper slope. Nolf & Stringer (1992) reported a highly diversified teleost fauna of 84 species for the Neogene of the Cibao Valley area, north- ern Dominican Republic. The study included numerous collecting localities from four Miocene-Pliocene units (Bai- toa, Cercado, Gurabo and Mao Formations). Palaeoenviron- mental conditions based on the present-day bathymetric distribution of related teleost taxa were determined for each of the formations.

MATERIAL AND METHODS

The Bowden otoliths for this study were supplied by several individuals and institutions. The largest percentage of otoliths was provided by Drs Harold and Emily Vokes of Tulane University, New Orleans (Louisiana). Much of their material was obtained during the collection of molluscs from the type locality. It is estimated that at least 70 kg of sample was

processed by the Vokes in obtaining the otoliths. Otoliths were also provided by Roger Portell of the Florida Museum of Natural History (University of Florida, Gainesville). The otoliths were obtained from a sample weighing approxi- mately 10 kg. A small sample of matrix (approximately 2 kg) was supplied by Dr Jon Bryan of Okaloosa-Walton Commu- nity College (Fort Walton, Florida). The Bowden shell bed otolith collection from the Institut royal des Sciences naturelles de Belgique (IRScNB, Brussels) was examined on a loan supplied by Dr Dirk Nolf. In addition to the material described above, a preliminary examination of the Bowden shell bed material of the late John Fitch was made in 1984. Unfortunately, the material of Dr Fitch could not be re- examined for this study.

The need for bulk sampling for otolith investigations is clearly illustrated when the number of otoliths and species is compared for the various samples. The 10 kg sample yielded over 200 otoliths and 30 species, while the 2 kg sample yielded about 30 otoliths and 14 species. The 70 kg sample produced over 1,200 otoliths and 55 taxa. By comparison, the largest sample in the study of the Neogene otoliths from the Dominican Republic by Nolf & Stringer (1992) was ap- proximately 120 kg which yielded the most otoliths and the largest number of species (62 species). In both of these studies as well as many others, a definite correlation exists between sample size and the number of species recognised.

The samples were wet-screened using a variety of sieve sizes. Sieves from 30 to 40 mesh (U.S. Standard Sieves) will retain almost all species represented by otoliths. Sieve sizes greater than 25 mesh may lose fish species with small oto- liths and should be avoided. Otoliths for this study were examined using a binocular stereozoom microscope with 10x-20x eyepieces with variable power (1x-2.5x). Generally, the otoliths from the Bowden shell bed are well preserved, mostly complete, and range in size from less than 1 to 8 mm in length.

MORPHOLOGY AND IDENTIFICATION OF OTOLITHS

To utilise otoliths to reconstruct fossil fish faunas and to determine palaeoecological conditions, identification of the otolith is essential. Salient morphological features are used to identify the otoliths. Although most bony fishes contain three otoliths in each of the two labyrinths (the sagitta, lapillus and asteriscus), the sagitta is used for identification purposes in the majority of cases. The sagitta tends to be the largest of the otoliths and has a characteristic pattern on the inner face. This pattern is usually indicative of the family, and in many examples the genus and species (Nolf, 1985).

The inner face of the sagitta has numerous salient mor- phological features. The inner face is the inward-facing side of the sagitta that is connected to nerve endings and usually has a characteristic pattern on it known as the sulcus (Fig. 1). The sulcus is usually the most conspicuous feature on the inner face of the sagitta. The sulcus may be undivided in the otoliths of some fishes and divided into two parts in other

species. If the sulcus is divided, the anterior portion is known as the ostium, while the posterior portion is known as the cauda.

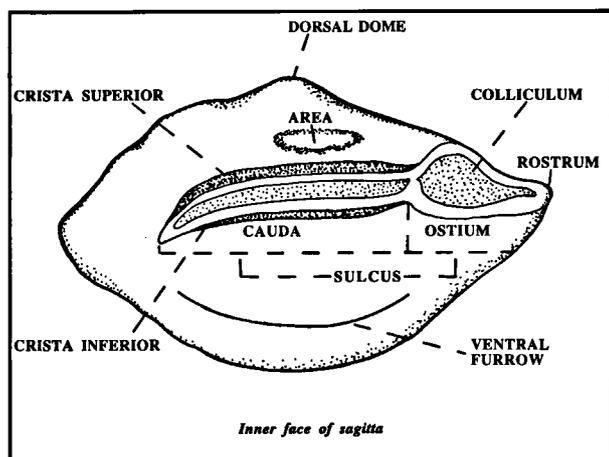


Fig. 1. General morphology of the saccular otolith (sagitta).

Other prominent features of the sagitta are described by referring to the margins. The dorsal, anterior, ventral and posterior margins can be recognised on the sagitta, although their exact boundaries may be unclear. Projections from the periphery of the otolith are named according to the margin on which they are located. Therefore, a dorsal dome is a projection from the dorsal margin. The rostrum and antirostrum are prominent anterior projections. A ridge or rim located above the sulcus is the crista superior and a ridge below the sulcus is the crista inferior. A depression above the sulcus is referred to as the area. Colliculum deposits (raised portions of the sulcus floor) in the ostium and cauda are referred to as anterior and posterior colliculum, respectively.

The shape or outline of the otolith is another morphological feature used for taxonomic purposes. Geometric terms such as circular, elliptical and subtriangular are often utilised to describe otolith shapes. In addition to the shape of the otolith, the shape of the margin, also known as sculpturing, may be diagnostic. Margins may be entire (smooth), lobed, sinuate, crenulate, denticulate, serrate or irregular. Otolith margin sculpturing, as well as many other morphological features, were illustrated and described in detail by Smale *et al.* (1995). Morphological features of otoliths from various families (congrids, myripristids and albulids) were illustrated in Stringer (1979).

The taxonomic position of a fossil otolith is determined by comparison to otoliths of identified Recent fishes or by comparison with *in situ* otoliths in identified fossil fish skeletons. Since fossil fish skeletons with *in situ* otoliths are extremely rare, the vast majority of fossil otolith identification is based on a comparison with otoliths of Recent forms. As noted by Nolf (1985), the precision of fossil otolith identification will depend largely upon the knowledge of Recent otoliths. Several museums have Recent comparative collections with 2,000 to 6,000 species of fish otoliths. In

addition to modern teleostean otoliths, comparisons were also made to fossil Miocene-Pliocene otoliths from the Dominican Republic and Trinidad for this study.

Fossil otoliths should be assigned to living taxa where possible. This requires not only excellent Recent comparative collections, but also well-preserved fossil material. The identification of fossil otoliths can be limited by several conditions. Sometimes, the preservation or condition of the fossil otolith may limit identification. In some cases, the variability within a species may be a restricting factor. Otolith identification may also be restricted due to the limited knowledge of Recent forms. For example, in this study, the knowledge of Recent gobiid otoliths from the Caribbean is too inadequate to identify the fossil gobiids at the generic or species level. Therefore, the gobiids are identified as form groups within the family Gobiidae. Another problem related to fossil otolith identification has recently been identified by Schwarzghans (1994), who found that the otoliths of some species of fish (Recent and fossil) may exhibit sexual dimorphism. However, this sexual dimorphism of otoliths has only been clearly recorded in one family of teleosts, the Ophidiidae. Finally, in some species, large numbers of otoliths representing all stages of growth are needed for species determination. As noted by Nolf & Stringer (1992), extensive series of large otoliths are often required to identify good species-diagnostic criteria. This is illustrated by *Diaphus* otoliths in which only adult otoliths larger than 2 mm show characteristic features (Brzobohaty & Nolf, 1995). Some species have otoliths with such generalised morphology that even large specimens lack diagnostic features.

Extinct genera and species may also present taxonomic problems. Some otoliths represent extinct forms and do not have living representatives. This problem has been approached in several different ways. One method is to designate a fossil genus which is commonly done by palaeontologists working in other groups. However, the presumed 'extinct' form may be a Recent genus of which the otoliths are unknown. Considering the imperfect knowledge of Recent fish otoliths, this is a distinct possibility if workers do not take great care to extensively compare fossil otoliths to Recent genera. Another method, proposed by Nolf (1985), is the use of plural genitive names. In this method, species which do not fit in known Recent genera are cited by plural genitive names, preceded by the word 'genus'. The method proposed by Nolf is commonly utilised by many otolith palaeontologists, especially those in Europe (Steurbaut, 1984; Brzobohaty, 1986; Nolf & Cappetta, 1989; Radwańska, 1992).

SYSTEMATIC PALAEOLOGY

Approximately 1,650 otoliths representing at least 38 teleost families and 68 species were obtained from the shell bed of the Bowden Formation. All of the identifications of this investigation are based on the sagittae or the saccular otoliths of the teleost except for the family Plotosidae, where the

lapillus or utricular otolith is utilised for identification of the catfish *Plotosus*. In the catfish order Siluriformes, the lapillus is the largest and most diagnostic of the otoliths, and is utilised for taxonomic purposes. The classification scheme of

this study follows that of Nelson (1984, 1994). A list of all otolith-based teleosts identified from the type locality of the Bowden shell bed in Jamaica is presented in Table 1.

Family	Taxon	Plate and figure number
Albulidae	<i>Albula</i> sp.	Pl. 1, Fig. 1 [Nolf & Stringer, 1992, pl. 9, figs 1, 2]
Heterenchelyidae	<i>Pythonichthys</i> sp.	Pl. 1, Fig. 2 [Nolf & Stringer, 1992, pl. 9, figs 8-10]
Congridae	<i>Ariosoma balearica</i>	Pl. 1, Fig. 3 [Nolf & Stringer, 1992, pl. 9, fig. 3]
	<i>Rhyncoconger flava</i>	Pl. 1, Fig. 4 [Nolf & Stringer, 1992, pl. 9, figs 11-13]
	<i>Rhechias tysanochila</i>	Pl. 1, Fig. 5 [Nolf & Stringer, 1992, pl. 9, figs 6, 7]
	<i>Gnathophis</i> sp.	[Nolf, 1976, pl. 2, figs 5-7]
	<i>Paraconger</i> sp.	Pl. 1, Fig. 7
Engraulidae	Engraulidae indet.	[Nolf & Stringer, 1992, pl. 9, fig. 16]
Plotosidae	<i>Plotosus</i> sp.	[Nolf & Stringer, 1992, pl. 10, fig. 3]
Sternoptychidae	<i>Polyipnus</i> sp.	Pl. 1, Fig. 6 [Nolf & Stringer, 1992, pl. 10, fig. 3]
	<i>Valenciennellus</i> sp.	not figured
Synodontidae	<i>Saurida caribbaea</i>	Pl. 2, Fig. 1 [Nolf & Stringer, 1992, pl. 10, fig. 3]
Myctophidae	<i>Diaphus brachycephalus</i>	Pl. 2, Fig. 2 [Nolf & Stringer, 1992, pl. 10, figs 4-9]
	<i>Diaphus</i> sp. 1*	Pl. 2, Fig. 3 [Nolf & Stringer, 1992, pl. 10, figs 18-23]
	<i>Diaphus</i> sp.	not figured
	<i>Symbolophorus</i> aff. <i>veranyi</i>	[Brzobohaty & Nolf, 1996, pl. 8, figs 17-19]
	<i>Hygophum</i> aff. <i>benoitii</i>	[Nolf & Stringer, 1992, pl. 10, fig. 32]
	<i>Hygophum</i> sp.	not figured
	<i>Myctophum</i> sp.	[Nolf & Stringer, 1992, pl. 10, figs 14, 15]
	<i>Lobianchia</i> sp.	Pl. 2, Fig. 5
Bregmacerotidae	<i>Bregmaceros</i> sp.	Pl. 2, Fig. 4 [Nolf & Stringer, 1992, pl. 11, figs 7-8]
Gadidae	<i>Gadiculus labiatus</i>	[Nolf, 1980, fig. 49H]
Ophidiidae	<i>Lepophidium latesulcatum</i>	Pl. 2, Fig. 6 [Nolf & Stringer, 1992, pl. 11, fig. 11]
	<i>Lepophidium cervinum</i>	[Nolf, 1980, pl. 3, figs 1-8]
	<i>Otophidium robustum</i>	Pl. 2, Fig. 7 [Nolf & Stringer, 1992, pl. 12, figs 4, 5]
	<i>Otophidium robinsi</i>	Pl. 3, Fig. 1 [Nolf & Stringer, 1992, pl. 11, figs 16-19]
	<i>Brotula</i> aff. <i>clarkae</i>	[Nolf & Stringer, 1992, pl. 11, fig. 13]
	<i>Lepophidium</i> sp.	not figured
Carapidae	<i>Carapus</i> sp.	Pl. 3, Fig. 2 [Nolf, 1980, pl. 1, fig. 3]
	<i>Echiodon</i> sp.	[Nolf, 1980, pl. 1, figs. 8, 11]
Bythitidae	'genus Dinematicthynorum' <i>smithvanizi</i>	[Nolf & Stringer, 1992, pl. 12, figs 11, 12]
	'genus Dinematicthynorum' sp.	not figured
Batrachoididae	<i>Porichthys</i> sp.	[Nolf & Stringer, 1992, p. 11, fig. 3]
Atherinidae	<i>Atherinomorus stipes</i>	[Nolf & Stringer, 1992, pl. 12, figs 13-16]
Hemiramphidae	<i>Hyporhamphus</i> sp.	[Nolf & Stringer, 1992, pl. 12, figs 17, 18]
Anomalopidae	<i>Phthanophaneron</i> sp.	Pl. 3, Fig. 3
Holocentridae	<i>Holocentrus</i> sp.	[Nolf & Stringer, 1992, pl. 12, fig. 25]
Scorpaenidae	Scorpaenidae indet.	[Nolf & Stringer, 1992, pl. 12, fig. 26]
Triglidae	<i>Prionotus</i> cf. <i>carolinus</i>	[Nolf & Stringer, 1992, pl. 12, fig. 27]
Acropomatidae	<i>Parascombrops</i> cf. <i>spinus</i>	Pl. 3, Fig. 5
Serranidae	<i>Diplectrum</i> sp.	[Nolf & Stringer, 1992, pl. 13, fig. 7]
Priacanthidae	<i>Pristigenys</i> cf. <i>altus</i>	Pl. 3, Fig. 4
Apogonidae	<i>Apogon</i> sp. 1*	[Nolf & Stringer, 1992, pl. 13, fig. 10]
	<i>Apogon</i> sp. 2*	[Nolf & Stringer, 1992, pl. 13, fig. 13]
	<i>Apogon</i> sp. 3*	[Nolf & Stringer, 1992, pl. 13, figs 15, 16]
	<i>Apogon</i> sp. 4*	[Nolf & Stringer, 1992, pl. 13, fig. 12]
Lutjanidae	<i>Pristipomoides</i> sp.	Pl. 3, Fig. 6 [Nolf & Stringer, 1992, pl. 14, figs 2-4]
	<i>Rhomboplites aurorubens</i>	Pl. 4, Fig. 1
Gerreidae	<i>Eucinostomus</i> sp. 1*	[Nolf & Stringer, 1992, pl. 14, fig. 7]
	cf. <i>Moharra</i> sp.	not figured
Haemulidae	<i>Haemulon</i> sp.	Pl. 4, Fig. 2 [Nolf & Stringer, 1992, pl. 14, figs 16-19]
Sciaenidae	<i>Protosciaena trewavasae</i>	Pl. 4, Fig. 3 [Schwarzshans, 1993, figs 344, 345]
	<i>Umbrina</i> sp.	[Nolf & Stringer, 1992, pl. 14, fig. 18]
Bathyclupeidae	<i>Bathyclupea</i> sp.	[Nolf, 1976, pl. 9, fig. 4]
Mugilidae	<i>Mugil</i> sp.	[Nolf & Stringer, 1992, pl. 15, fig. 11]
Sphyraenidae	<i>Sphyraena</i> sp.	[Nolf & Stringer, 1992, pl. 17, fig. 1]
Opisognathidae	<i>Lonchopisthus micrognathus</i>	Pl. 4, Fig. 4 [Nolf & Stringer, 1992, pl. 15, figs 7-9]

Uranoscopidae	Uranoscopidae indet.	not figured
Gobiidae	Gobiidae sp. 1*	Pl. 4, Fig. 5 [Nolf & Stringer, 1992, pl. 17, fig. 12]
	Gobiidae sp. 3*	Pl. 4, Fig. 6 [Nolf & Stringer, 1992, pl. 17, fig. 14]
	Gobiidae indet.	not figured
Bothidae	<i>Citharichthys</i> sp.	[Nolf, 1976, pl. 9, fig. 12]
	Bothidae indet.	[Nolf & Stringer, 1992, pl. 17, figs 15, 16]
	Bothidae indet.	not figured
	Bothidae indet.	not figured
Pleuronectidae	Pleuronectidae indet.	[Nolf & Stringer, 1992, pl. 17, fig. 20]
Cynoglossidae	Cynoglossidae indet.	[Nolf & Stringer, 1992, pl. 17, fig. 17]
Soleidae	Soleidae indet.	[Nolf & Stringer, 1992, pl. 17, figs 18, 19]

* Species designated with numbers refer to specimens described and figured in Nolf & Stringer (1992). Plate and figure numbers enclosed in brackets refer to previously figured material.

Table 1. List of all otolith-based teleosts (class Osteichthyes) identified from the shell bed of the Pliocene Bowden Formation in Jamaica.

The vast majority of the identified taxa represent forms that are presently known from the Atlantic Ocean including the Gulf of Mexico and the Caribbean area. Three notable exceptions are the catfish genus *Plotosus*, the ophidiid species *Brotula clarkae* and the lanterneye fish *Phthanophaneron*, all of which are known from the Pacific. The lapilli from *Plotosus* compare remarkably well with those of the Recent species *Plotosus anguillar* (see Nolf & Stringer, 1992, pl. 10, fig. 2). The otoliths from *Brotula clarkae* are also very distinctive and diagnostic since they represent the only *Brotula* species with a prominent rostrum (see Nolf, 1980, pl. 2, fig. 3). The otoliths from *Phthanophaneron* seem to be closely related to *Phthanophaneron harveyi* (Rosenblatt & Montgomery, 1976) which is found in the Gulf of California and the eastern tropical Pacific (Nelson, 1994). The presence of these three Pacific forms is interpreted as relicts of the western Tethys fauna. No new species are introduced from the Bowden shell bed at this time. Several new species may be represented, but adequate growth series were not available to make this determination for several taxa, such as *Lepophidium* sp. and *Lobianchia* sp. Essentially, all of the taxa from the Bowden shell bed have been described and illustrated previously, mainly by Nolf & Stringer (1992). However, two taxonomic changes should be noted from Nolf & Stringer (1992). *Hildebrandia* was synonymised with *Rhynchoconger* by Smith (1989) in his revision of Recent western Atlantic conger eels, and the form reported as *Ctenosciaena latecaudata* probably represents *Protosciaena trewasae* as described and illustrated in Schwarzhans (1993). References to previous illustrations of the taxa as well as plates in the present study are presented in Table 1. Significant taxa examined in the present study are illustrated in Pls 1-4.

In some cases, the present knowledge of Recent Caribbean otoliths is too limited to allow for identification beyond the family level. There is also the problem of extreme variability among species in the families Gobiidae, Bothidae and Pleuronectidae. In the Gobiidae, form groups were designated while other groups such as the bothids and pleuronectids were identified to family. Species designated with numbers, such as *Diaphus* sp. 1, refer to forms described and figured in Nolf & Stringer (1992).

PALAEOECOLOGY BASED ON OTOLITHS

Studies have indicated that fossil otolith assemblages will reflect, with reasonable certainty, the ichthyological fauna inhabiting an area during a specific interval of geologic time (Schwarzhans, 1984; Stringer, 1992a; Breard & Stringer, 1995). As a general principle, the otoliths will represent a part of the biocoenosis. General palaeoecological parameters can be determined by utilising data on the preferred habitats of comparable modern fishes. Greater care must be exercised with older Palaeogene and Cretaceous otolith assemblages because of fewer taxonomic affinities with Recent genera. Also, fewer Cretaceous faunas have been studied (Huddleston & Savoie, 1983; Nolf & Dockery, 1990; Stringer, 1991; Nolf & Stringer, 1996; Rana, 1996). Nolf (1985) noted that otolith associations will reflect the fishes present in a qualitative sense, but otolith faunas are not a quantitative measure of the biocoenosis. However, Nolf & Cappetta (1989) suggested a more objective method of interpreting palaeobathymetry as indicated by otoliths. Nolf & Brzobohaty (1992) described a method utilising otoliths that was suited for the bathymetric interpretation of associations with deep neritic or deep-water fishes.

The general bathymetry of the Bowden shell bed can be deduced by the ratio of neritic fishes to myctophids and macrourids. Nolf & Brzobohaty (1992) noted that otolith associations with both neritic species and myctophids, but few or no macrourids, are indicative of neritic environments exposed to oceanic influence. The proportion of myctophid otoliths becomes higher in the deeper part of the continental shelf. The otolith assemblage from the Bowden shell bed contains neritic species and myctophids with no macrourids, and is interpreted as indicative of a neritic environment exposed to oceanic influence.

Except for a few taxa, all of the studied otoliths from the Bowden shell bed exhibit close affinities to the Recent fauna in the Caribbean, and seem to belong to the same climatic and environmental realm as their present-day relatives. Based on the otolith association from the Bowden shell bed, palaeobathymetric parameters can be ascertained by comparisons to related modern forms. General parameters followed by Nolf & Stringer (1992) in their study of the Neogene fish

fauna from the Dominican Republic are also followed in this study. In the case of extant or closely-related species, the bathymetry indicated for the fossil species is that of the Recent species.

Taxa/Depth in m.	0	100	200	300	400	500	600
<i>Albula</i> sp.	—						
<i>Pythonichthys</i> sp.	—						
<i>Ariusoma balearica</i>	—						
<i>Rhyncoconger flava</i>	—						
<i>Rhechias tysanochila</i>	—						→
<i>Gnathopis</i> sp.	—						→
<i>Plotosus</i> sp.	E	—					
<i>Polyipnus</i> sp.	—						
<i>Valenciennellus</i> sp.	—						
<i>Saurida caribbaea</i>	—						
<i>Diaphus brachycephalus</i>						→
<i>Diaphus</i> sp. 1						→
<i>Diaphus</i> sp.						→
<i>Hygophum</i> aff. <i>H. benoiti</i>						→
<i>Hygophum</i> sp.						→
<i>Myctophum</i> sp.						→
<i>Lobianchia</i> sp.						→
<i>Bregmaceros</i> sp.	—						
<i>Gadiculus labiatus</i>	—						→
<i>Lepophidium latesulcatum</i>	—						
<i>Lepophidium cervinum</i>	—						
<i>Otophidium robustum</i>	—						
<i>Otophidium robinis</i>	—						
<i>Brotula</i> aff. <i>B. clarkae</i>	—						
<i>Lepophidium</i> sp.	—						
<i>Carapus</i> sp.	—						
<i>Echiodon</i> sp.	—						
<i>Porichthys</i> sp.	E	—					
<i>Atherinomorus stipes</i>	—						
<i>Hyporhamphus</i> sp.	—						
<i>Holocentrus</i> sp.	—						
<i>Parascombrops</i> cf. <i>spinus</i>	—						
<i>Diplectrum</i> sp.	—						
<i>Pristigenys</i> cf. <i>altus</i>	—						
<i>Apogon</i> sp. 1	—						
<i>Apogon</i> sp. 2	—						
<i>Apogon</i> sp. 3	—						
<i>Apogon</i> sp. 4	—						
<i>Pristipomoides</i> sp.	—						
<i>Eucinostomus</i> sp. 1	E	—					
cf. <i>Moharra</i> sp.	E	—					
<i>Haemulon</i> sp.	—						
<i>Protosciaena trewavasae</i>	—						
<i>Umbrina</i> sp.	—						
<i>Sphyraena</i> sp.	E	—					
<i>Lonchopisthus micrognathus</i>	E	—					
Gobiidae sp. 1	E	—					
Gobiidae sp. 3	E	—					
Gobiidae indet.	E	—					

Table 2. Present-day bathymetric range of teleostean taxa represented in the Bowden shell bed, Jamaica. Dotted lines indicate the nightly occurrence of mesopelagic species near the surface. An E represents fishes that may occur in estuaries at some stage of their life cycle.

For extinct taxa or taxa indeterminate as to species, the global bathymetric distribution indicated for all Recent

species of that genus is utilised. References for bathymetric data for Recent forms include Bohlke & Chaplin (1968), Darnell *et al.* (1983), Dawson (1966), Hoese & Moore (1977), Nelson (1984, 1994), Poll (1953, 1954, 1959), Robbins *et al.* (1986), Schwarzshans (1993) and Smith & Kanazawa (1977). The present-day bathymetric distribution of related Recent taxa is shown for the fossil otoliths in Table 2.

Forty-nine otolith-based taxa from the Bowden shell bed were utilised in developing the palaeobathymetry in Table 2. It should be noted that the dotted lines in Table 2 indicate the diurnal migration of mesopelagic species and that an 'E' denotes fishes that may occur in estuaries during some stage of their life. Nelson (1994) noted that the peak abundance of most myctophid species is between 300-1,200 m during the day, but this peak abundance changes to 10-100 m at night. Basically, the method described by Nolf & Brzobohaty (1992) is followed in analysing the palaeobathymetry. Thirty-seven of the 49 potential forms (76%) are found in the 0-100 m range (inner to middle shelf). This percentage, which is the highest for all depth levels, strongly indicates that the most probable water depth was 0-100 m. This is further supported by the progressive decrease in percentages for depths greater than 200 m. However, the presence of mesopelagic forms, especially the myctophids, signifies the proximity of open oceanic conditions. The majority of the taxa present in waters deeper than 400 m are myctophids.

In addition to the graphical representation of the bathymetry indicated by otoliths in Table 2, it is interesting to compare the bathymetrical distribution of the fish taxa. There are eight taxa that may be found in estuarine environments. Twenty-eight of the taxa are restricted to or indicative of the shelf environment (generally 0 to 200 m). Several fish taxa also suggest the presence of a reef environment. Recent squirrelfishes (Holocentridae) and cardinalfishes (Apogonidae) as well as the Dinematchthyini are characterised mainly as reef fishes in the Gulf of Mexico (Hoese & Moore, 1977). Nelson (1984, 1994) also stated that squirrelfishes and soldierfishes occur between the shoreline and 100 m. Hoese & Moore (1977) stated that squirrelfishes are a tropical family represented by several species found, so far, only on the offshore reefs in the Gulf of Mexico. Bohlke & Chaplin (1968) stated that squirrelfishes and soldierfishes are reef fishes which occur in tropical waters around the world. They noted that these forms are found in crevices and caves in the rocks and reef. Deeper water taxa are mainly mesopelagic (Myctophidae) with no bathybenthic forms.

One seemingly enigmatic form, *Plotosus*, was found in the otolith assemblage. *Plotosus* is an Indo-Pacific genus of catfish that occurs in neritic, estuarine and freshwater environments (Berra, 1981). Its presence is not surprising since it was also found in the Neogene of the Dominican Republic by Nolf & Stringer (1992). This occurrence is probably related to the Tertiary Caribbean province and the Central America seaway that existed prior to closure of the seaway in the Pliocene (Keigwin, 1978). *Plotosus*, as well as *Brotula* aff. *clarkae* and *Phthanophaneron* sp., are interpreted as relicts of the ancient western Tethys fauna.

Other palaeoecological indications may also be gleaned from the otolith-based taxa of the Bowden shell bed. Almost all of the taxa are present in the Recent Caribbean fauna, and represent tropical and subtropical forms. Therefore, the climatic realm is considered to be very similar to the modern Caribbean with surface sea water temperatures of 26-28°C (Dunn *et al.*, 1981). The taxa associated with reef environments in the otolith assemblage support this observation. Based on the otoliths, the depositional environment was characterised by normal marine salinity (approximately 35 ‰), fairly low energy and mostly soft bottoms.

The comparison of the fossil taxa from the Bowden shell bed to the bathymetric distributions of closely related Recent forms reveals an assemblage with shallow-water forms (including several euryhaline species), reef inhabitants, and middle to outer shelf forms with some upper slope and pelagic elements. The otolith assemblage, although predominantly shallow water (0-100 m), seems to represent a combination of several ecological environments. A drifted or mixed assemblage was suggested by Caldwell (1965) for the Bowden shell bed, but Clarke & Fitch (1979) rejected this idea in favour of a 'mass mortality' deposit similar to those resulting from dinoflagellate blooms. Examining modern zoogeographical situations, a probable environment for the Bowden shell bed may be reconstructed. If the Bowden shell bed was deposited in the shallow, nearshore marine waters of an island with a very narrow shelf region quickly dropping to a slope situation and open oceanic conditions, this would explain the combination of several ecological environments. The euryhaline, reef and shelf forms would be common in the narrow shelf region, and the neritic and deeper-water forms would be present due to the open oceanic conditions adjacent to the narrow shelf area. Pickerill *et al.* (1996) concluded that the shallow-marine and relatively deep-water faunas of the Bowden shell bed were indicative of deposition from sediment gravity flows. Turbidite deposition would account for the combination of several ecological conditions indicated by the teleostean otoliths. This interpretation would be consistent with other palaeontological (invertebrate and vertebrate), sedimentary and tectonic studies of the Caribbean and Central America (Briggs, 1974; Casey *et al.*, 1975; Dunn *et al.*, 1981; Duque-Caro, 1990; Gillette, 1984; Keigwin, 1976, 1978; Smith, 1991; Whitmore & Stewart, 1965; Woodring, 1966).

COMPARISONS TO OTHER OTOLITH FAUNAS OF THE CARIBBEAN

Although the number of described otolith assemblages from the Caribbean is quite limited, several of them are appropriate for comparison. An otolith assemblage from the Miocene Gatun Formation in Panama was described in Gillette (1984). As noted earlier in this paper, preliminary identifications were done by the late John Fitch, but the fauna was never formally described. Approximately 900 kg of sample was wet-sieved and yielded 2,074 otoliths. Twenty-six taxa were

recognised from the sample which seems somewhat low considering the size of the sample and number of otoliths. One explanation is that species with smaller otoliths were lost due to the sieve size (25 mesh). This is further supported by the large percentage of sciaenid otoliths which tend to be larger in size. The fauna included many taxa distributed in both the Atlantic and Pacific. The sciaenids represented over 50% of the total number of otoliths and contained eight of the twenty-six described taxa. Two *Haemulon*-type species were the second most common types and constituted 15% of the total number of otoliths. No other percentages are given for the other taxa and none of the taxa are identified to species. Due to these factors, it is difficult to quantitatively compare the Gatun Formation with other faunas in the Caribbean.

A diverse otolith fauna was described from the Neogene of Trinidad by Nolf (1976). Samples were collected at 30 localities from nine Miocene and Pliocene formations in Trinidad, and produced 1,339 otoliths. Sixty-six taxa were described from the otoliths with most of them coming from the Miocene units, mainly the Brasso, Nariva and Manzanilla Formations. The fauna consisted primarily of neritic fishes with a few mesopelagic and demersal fishes from the upper slope. The ophidiids, pomadasyids and sciaenids represented the most species. The most abundant taxa included indeterminate Gobiidae, *Diaphus dumerili* and *Bregmaceros*. Generally, the otoliths from the Neogene of Trinidad resembled the present-day Caribbean fauna.

Some of the best faunas for potential comparisons would be those studied by Nolf & Stringer (1992) from the Neogene of the northern Dominican Republic. However, it should be noted that the Neogene material from the Dominican Republic represented otoliths from four different formations ranging in age from early-middle Miocene (NN4 for the lower Baitoa Formation) to middle Pliocene (NN15 for the upper Mao Formation). It must also be considered that 887 samples were collected from hundreds of localities in the northern Dominican Republic with 109 localities yielding otoliths (Saunders *et al.*, 1986). In addition, Tulane University (New Orleans, Louisiana) collected hundreds of localities in the same area of the Dominican Republic and supplied otoliths for study.

The largest otolith fauna from the Dominican Republic was from the late Miocene NN11 Zone in the Cercado Formation and consisted of 62 species. The otoliths from the Cercado Formation indicated a shallow marine environment. More precisely, 37 of the 44 taxa usable for palaeobathymetry (84%) occur in waters from 0 to 100 m. Many of the neritic taxa do not live at depths exceeding 50 m and at least 11 species are regular inhabitants of euryhaline environments such as lagoons or estuaries. None of the deeper-water taxa are exclusively bathyal and all of them may occur in neritic areas. Several taxa, such as *Holocentrus*, *Labrisomus* and the Dinematchthyini, suggest the proximity of reef environments, but the majority of the forms are confined to shallow neritic environments with rather soft bottoms (Nolf & Stringer, 1992).

The otolith assemblage from the Bowden shell bed

compares most closely with the otolith fauna from the late Miocene NN11 Zone in the Cercado Formation in the Dominican Republic. Although the Bowden otolith assemblage is younger in age (Pliocene, probably around NN13-NN14), there are many similarities between the two assemblages. Some of the similarities include the number of total species for both faunas, the percentage of potential forms found in the 0-100 m range is almost the same (approximately 80% for both faunas), the number of euryhaline inhabitants is about the same, the number of shallow water taxa occurring on the shelf is similar, several taxa that suggest a reef environment are present in both faunas and deeper water forms are mainly mesopelagic with no bathybenthic forms. Both assemblages contain *Plotosus*, an Indo-Pacific catfish genus which is interpreted as a relict element of the ancient western Tethys fauna. A significant difference in the Bowden shell bed and the NN11 Zone in the Cercado Formation is the number of sciaenids. The Bowden shell bed has only two species of sciaenids while the Cercado has at least six sciaenid species represented.

CONCLUSIONS

A detailed study of approximately 1,650 fossil teleostean otoliths from the type locality of the Pliocene Bowden shell bed, Bowden Formation (Jamaica) revealed at least 38 teleost families and 68 species. A definite correlation was found to exist between the sample size and the number of species identified. All of the identifications were based on the sagittae or the saccular otoliths except for the family Plotosidae, where the lapillus or utricular otolith was utilised. All of the identified taxa from the Bowden shell bed represent forms that are presently known from the Atlantic Ocean (including the Gulf of Mexico and Caribbean) except for three species. These three notable exceptions are the catfish genus *Plotosus*, the ophidiid species *Brotula clarkae* and the lanterneye fish *Phthanophaneron*, all of which are known from the Pacific. These forms are interpreted as relicts of the ancient western Tethys fauna.

Forty-nine of the otolith-based taxa from the Bowden shell bed were utilised to determine detailed palaeobathymetry. Thirty-seven of the 49 potential forms (76%) were found in the 0-100 m range (inner to middle shelf). Eight of the taxa may be found in estuarine environments, and 28 are restricted to or indicative of the shelf environment (generally 0 to 200 m). Several fish, such as the holocentrids and apogonids, also suggest the presence of a reef environment. However, the presence of mesopelagic forms, especially the myctophids, signifies the proximity of open oceanic conditions. The otolith-based fishes suggest deposition in shallow, nearshore marine waters of an island with a very narrow shelf region quickly dropping to a slope situation and open oceanic conditions. This palaeoenvironment, coupled with sediment gravity flows, would explain the combination of several ecological environments indicated in the Bowden shell bed. The otolith assemblage from the Bowden shell bed compares

most closely with the otolith fauna from the late Miocene NN11 Zone in the Cercado Formation in the Dominican Republic described by Nolf & Stringer (1992). The most notable difference in the two assemblages is the larger number of sciaenid species in the Cercado assemblage (six versus only two in the Bowden shell bed fauna).

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PLATE 1

All specimens figured in Pls 1-4 are from the Pliocene Bowden shell bed. Figure numbers in each plate are followed by the taxonomic identification, location of the otolith in the fish (right or left side), view (inner, outer, ventral) and collection number. Material from the Institute royal des Sciences naturelles de Belgique are designated as IRScNB; this collection is arranged in systematic order and specimens do not have individual collection numbers. Figured specimens from the Florida Museum of Natural History (University of Florida, Gainesville) have the prefix UF, and are repositied in the Type and Figured Collection of the Invertebrate Paleontology Division of that museum. The scale bar beside each otolith figured is equal to 1 mm.

- Fig. 1. *Albula* sp., right sagitta, inner face (IRScNB).
- Fig. 2. *Pythonichthys* sp., left sagitta, inner face (UF 78951).
- Fig. 3. *Ariosoma balearica* (Delaroché, 1809), right sagitta, inner face (UF 78952).
- Fig. 4. *Rhyncoconger flava* (Goode & Bean, 1896), right sagitta, inner face (UF 78953).
- Fig. 5. *Rhechias tysanochila* (Reid, 1934), left sagitta, inner face (UF 78954).
- Fig. 6. *Polyipnus* sp., left sagitta, inner face (UF 78955).
- Fig. 7. *Paraconger* sp., left sagitta, inner face (UF 78956).

PLATE 1

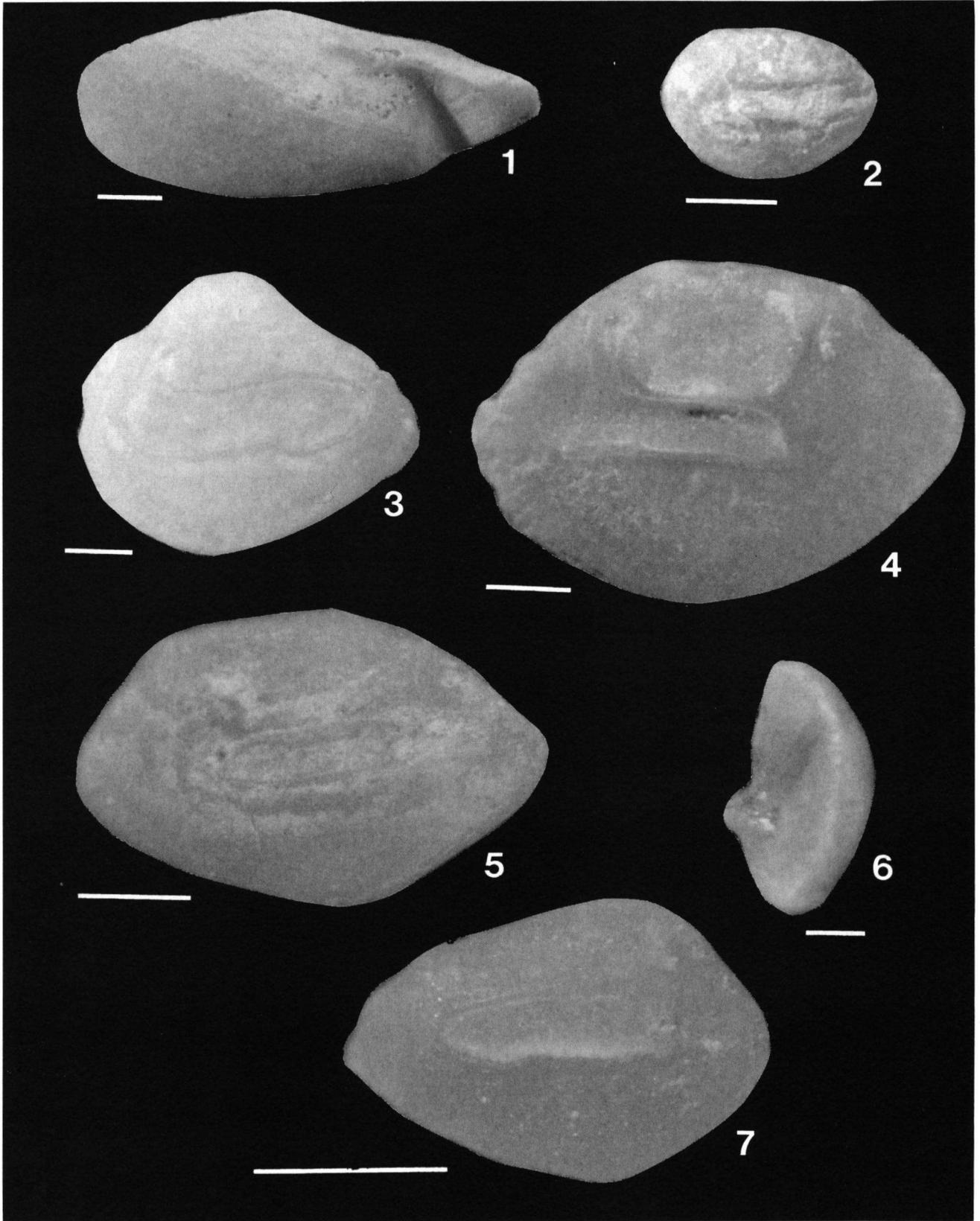


PLATE 2

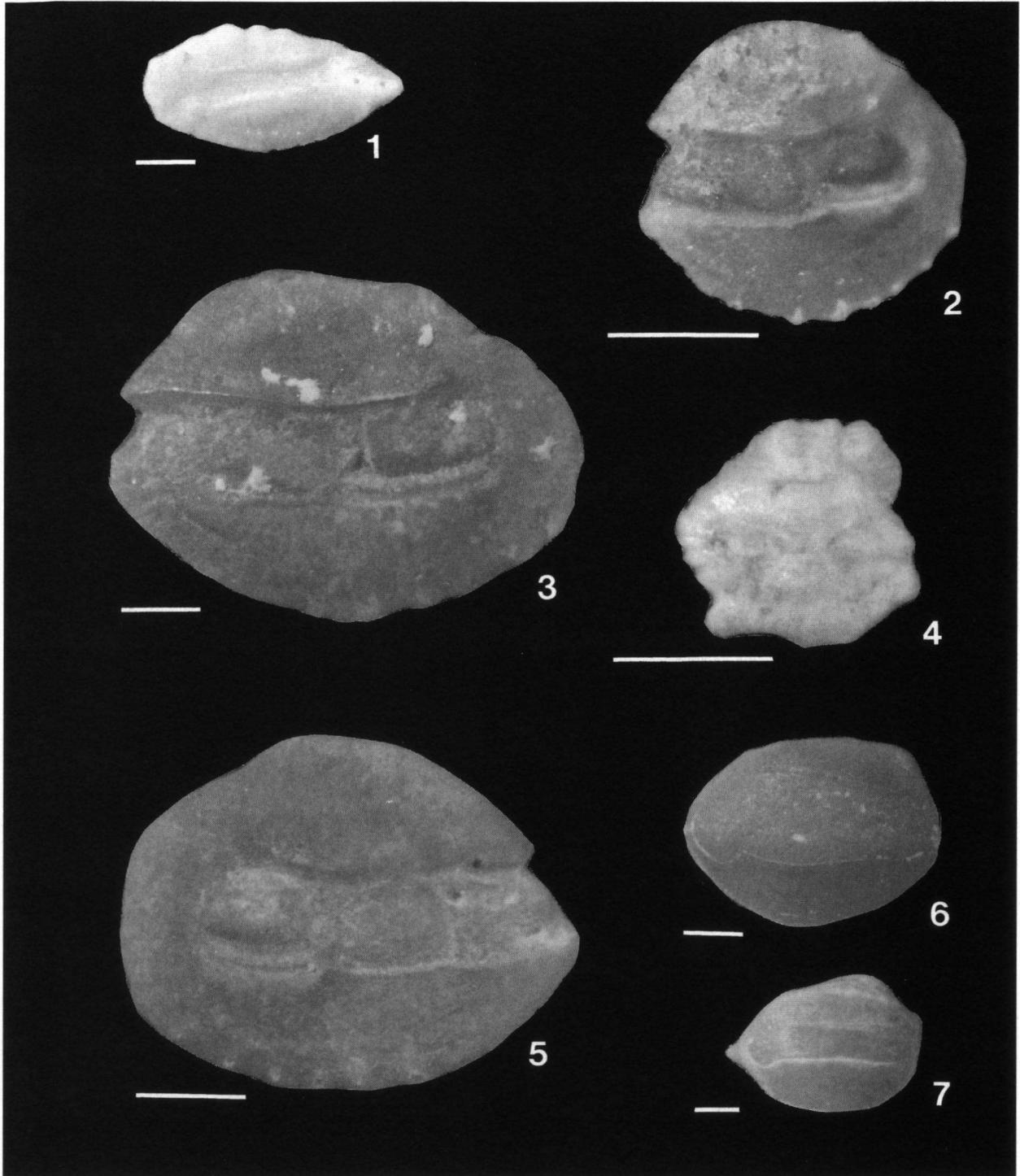


PLATE 2

- Fig. 1. *Saurida caribbaea* Breder, 1927, left sagitta, inner face (UF 78957).
Fig. 2. *Diaphus brachycephalus* Taning, 1928, right sagitta, inner face (UF 78958).
Fig. 3. *Diaphus* sp. 1, right sagitta, inner face (IRScNB).
Fig. 4. *Bregmaceros* sp., left sagitta, inner face (UF 78959).
Fig. 5. *Lobianchia* sp., left sagitta, inner face (IRScNB).
Fig. 6. *Lepophidium latesulcatum* Nolf & Stringer, 1992, left sagitta, inner face (UF 78960).
Fig. 7. *Otophidium robustum* Nolf & Stringer, 1992, left sagitta, inner face (UF 78961).

PLATE 3

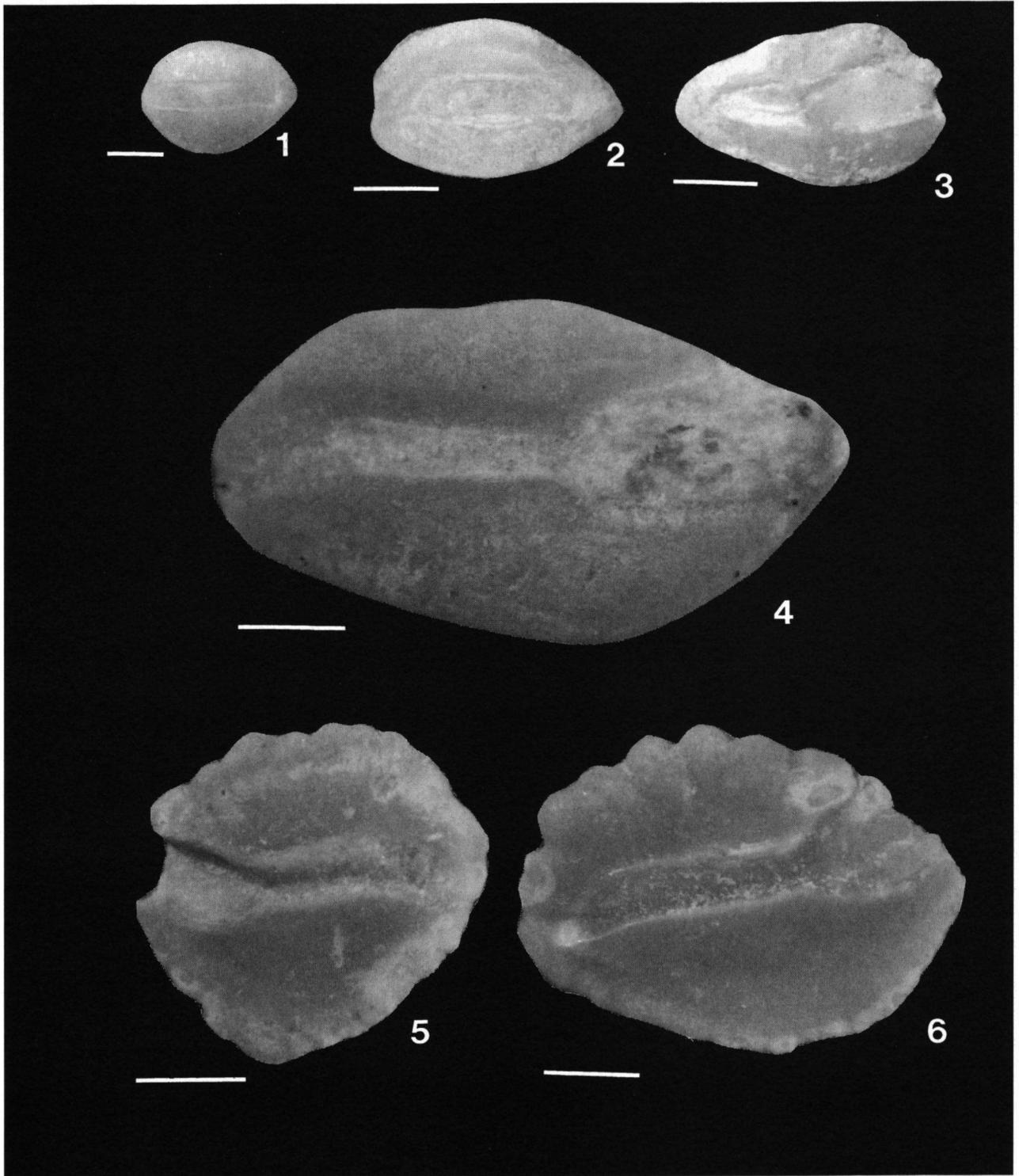


PLATE 3

- Fig. 1. *Otophidium robinsi* Nolf & Stringer, 1992, right sagitta, inner face (UF 78962)
Fig. 2. *Carapus* sp., right sagitta, inner face (UF 78963).
Fig. 3. *Phthanophaneron* sp., left sagitta, inner face (UF 78964).
Fig. 4. *Parascombrops* cf. *spinus* Schultz, 1940, left sagitta, inner face (UF 78965).
Fig. 5. *Pristigenys* cf. *altus* (Gill, 1861), right sagitta, inner face (IRScNB).
Fig. 6. *Pristipomoides* sp., left sagitta, inner face (IRScNB).

PLATE 4

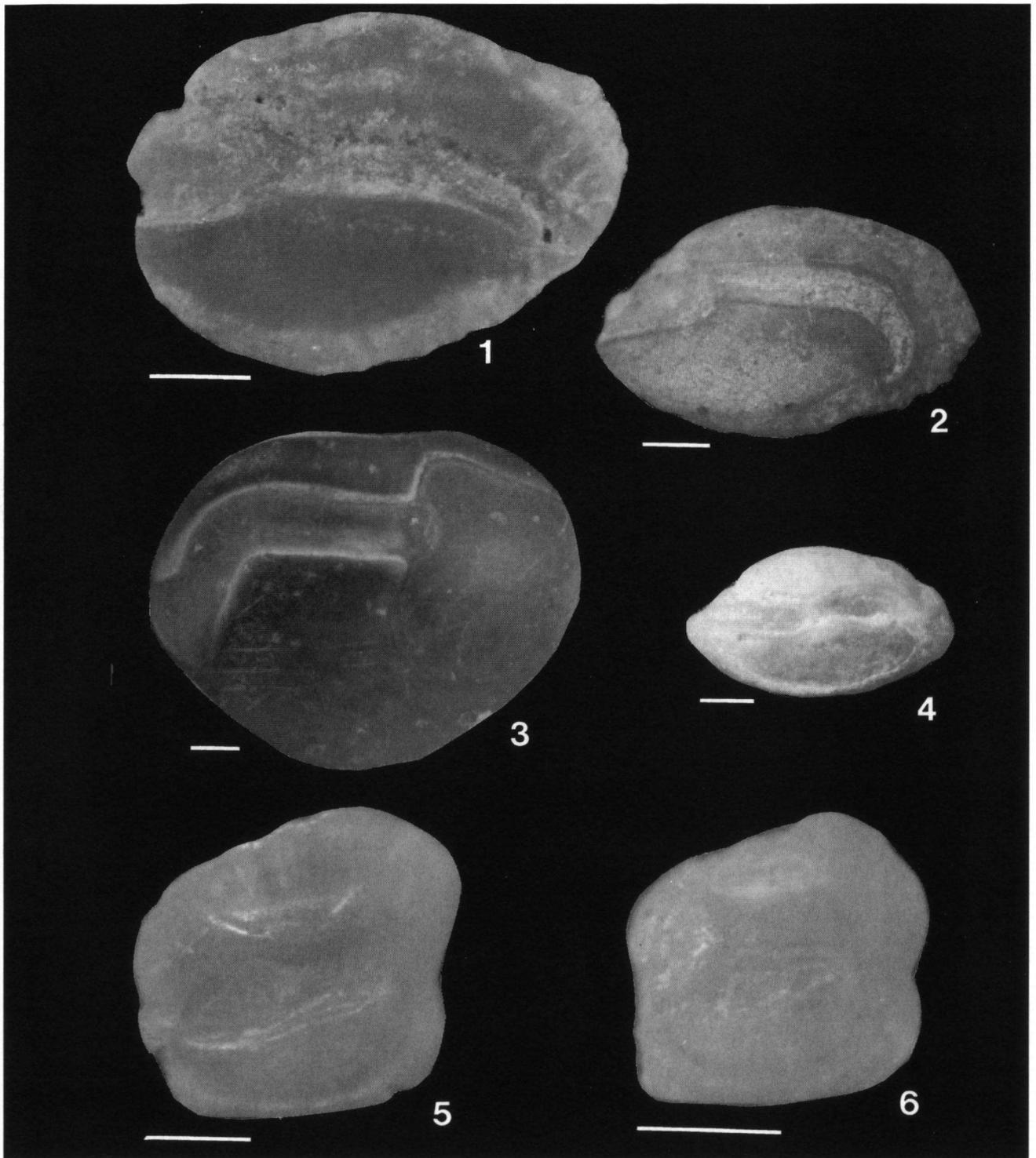


PLATE 4

- Fig. 1. *Rhomboplites aurorubens* (Cuvier, 1816), right sagitta, inner face (IRScNB).
Fig. 2. *Haemulon* sp., right sagitta, inner face (UF 78966).
Fig. 3. *Protosciaena trewavasae* (Chao & Miller, 1975), left sagitta, inner face (UF 78967).
Fig. 4. *Lonchopisthus micrognathus* Poey, 1861, right sagitta, inner face (UF 78968).
Fig. 5. Gobiidae sp. 1, right sagitta, inner face (UF 78969).
Fig. 6. Gobiidae sp. 3, right sagitta, inner face (UF 78970).