# Fish otoliths from the Cantaure Formation (Early Miocene of Venezuela)

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### Abstract

The otolith study reveals the presence of 61 taxa of teleosteans in the Early Miocene Cantaure Formation, among which five are new species: Aplodinotus longecaudata, A. hoffmani, Equetus davidandrewi, Larimus henrici and L. steurbauti. The associations reflect tropical near shore marine environments, with a water depth of less than 50 m. A compilation of all available data (Venezuela, Trinidad, Dominican Republic) shows that the Miocene Caribbean realm was inhabited by a teleost fauna whose overall picture was already very similar to that of the present day fauna of the area. At the generic level this similarity is very strong. However, looking at the species level, probably more than 50% of the Miocene taxa are extinct today. Among the 138 taxa recorded from the Caribbean Miocene, only four do not fit in the present day picture of Middle American biogeography: Diaphus aff. regani, Plotosus, Lactarius and Mene. These taxa reflect ancient circumtropical Tethys distribution patterns.

Key-words: Teleostean fishes, otoliths, Early Miocene, Venezuela.

### Résumé

L'étude des otolithes provenant de la Formation de Cantaure, Miocène Inférieur du Vénézuéla, a permis d'identifier 61 taxa de téléostéens typiques d'un environnement tropical côtier, n'excédant pas 50 m de profondeur. Cinq espèces nouvelles sont décrites: Aplodinotus longecaudata, A. hoffmani, Equetus davidandrewi, Larimus henrici et L. steurbauti. La compilation de toutes les données disponibles (Vénézuéla, Trinidad, République Dominicaine) montre qu'au Miocène, le domaine caraïbe était déjà peuplé par une faune téléostéenne dont l'allure générale était fort semblable à celle de la faune actuelle de la même région. Au niveau générique, la ressemblance est très prononcée, mais au niveau spécifique, probablement plus de 50% des espèces miocènes sont éteintes. Parmi les 138 taxa du Miocène caraïbe, quatre seulement ne cadrent pas dans la biogéographie actuelle de cette région: Diaphus aff. regani, Plotosus, Lactarius et Mene. Ces quatre taxa reflètent une ancienne distribution circumtropicale de la faune téthysienne.

Mots-clefs: Poissons téléostéens, otolithes, Miocène Inférieur, Vénézuéla.

### Introduction

The material studied was collected from the early Miocene Cantaure Formation on the Paraguana Peninsula NE of the Gulf of Venezuela. The formation lies discordantly on volcanic and metamorphic rocks and reaches a max-

imal thickness of 75 m, estimated from discontinuous section parts. Sediments essentially consist of marls with some limestone and sandstone intercalations. The outcrop area of the formation is restricted to the central part of the peninsula. (Gonzalez de Juana *et al.*, 1980). Fish remains were sampled by the second author at three localities (Fig. 1) between the Casa Cantaure and the southern slope of Barbasco ravine.

**Locality 1** (Fig. 2) is an artisanal water well, dug at the base of a small exposure; at this point, the soil is about 110 m above sea level. The majority of the otoliths were collected at 25 m depth, by sieving about 1200 kg of grey green clayey sand, rich in molluscs. The sampling provided 2794 otoliths, belonging to 59 taxa.

**Locality 2**, situated at 145 m above sea level, is an exposure of light brown, very fossiliferous sand (otoliths, bryozoans, corals, crustaceans, molluscs and echinoderms). At this place, numerous otoliths were picked up from the surface, and a sample of about 300 kg was screen washed. Unfortunately, no separation

Fig. 1. — Location of the sampling sites.

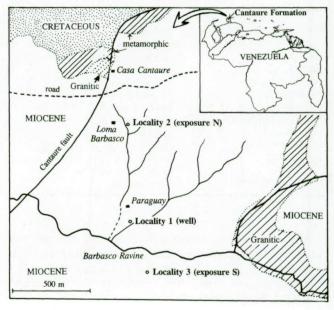


Table 1: OTOLITH-BASED	FISH SPECIES FROM THE CANTAURE FORMATION	loc.1	loc.2	Iconography	Registratio IRSNB
ALBULIDAE	Albula sp.	3	1	Pl. 1, Fig. 9	P 7097
CONGRIDAE	Ariosoma balearicus (DELAROCHE, 1809)	1	5	Pl. 1, Fig. 8	P 7098
	Conger sp.	2	7	Pl. 1, Figs. 10-11	P 7099-710
	Paraconger guianensis KANAZAWA, 1961	1		Pl. 1, Fig. 2	P 7101
	Rhynchoconger aff. flavus (GOODE & BEAN, 1896)	i	13	Pl. 1, Figs. 6-7	P 7102-710
HETERENCHELYIDAE	Pythonichthys sp.	1	25	Pl. 1, Figs. 3-5	P 7104-710
PRISTIGASTERIDAE		1		Pl. 1, Figs. 3-3 Pl. 2, Fig. 7	
PRISTIGASTERIDAE	Ilisha sp.	2	-	Pl. 2, Figs. 8-10	P 7108
	Neopisthopterus sp.	2			P 7109-711
CI LIBERD LE	Pellona sp.	5		Pl. 2, Figs. 5-6	P 7112
CLUPEIDAE	Harengula aff. clupeola CUVIER, 1829	5	-	Pl. 2, Figs. 2-3	P 7248-724
ARIIDAE (1)	Arius aff. kessleri STEINDACHNER, 1876	4	5	Pl. 4, Figs. 8-10	P 7114-711
	Arius sp. 1	12	169	Pl. 3, Figs. 1-5	P 7117-712
	Arius sp. 2	1	-	Pl. 3, Fig. 7	P 7107
	Genidens sp.	34	108	Pl. 4, Figs. 1-5	P 7122-712
PLOTOSIDAE	Plotosus sp. (2)	1	-	Pl. 3, Fig. 8	P 7127
MYCTOPHIDAE	Diaphus aff. problematicus PARR, 1928	5	-	Pl. 5, Figs. 23-25	P 7128-713
	Diaphus aff. regani TAANING, 1932 (3)	26	-	Pl. 5, Figs. 7-12	P 7131-713
	Diaphus sp. (4)	503	1018	Pl. 5, Figs. 13-17	P 7137-714
	Hygophum hygomi (LÜTKEN, 1892)	4	8	Pl. 5, Figs. 20-22	P 7142-714
	Myctophum cf. punctatum RAFINESQUE, 1810	3	-	Pl. 5, Figs. 18-19	P 7145-714
BREGMACEROTIDAE	Bregmaceros sp.	2	2	Pl. 6, Figs. 4-5	P 7150-715
STEINDACHNERIIDAE	Steindachneria sp. (5)	3	1	Pl. 6, Figs. 7-9	P 7152-715
BATRACHOIDIDAE	Porichthys sp.	3	6	Pl. 6, Figs. 1-3	P 7147-714
ATHERINIDAE	Membras sp. (6)	3	0	Pl. 14, Figs. 5-6	P 7155-715
	Mugil aff. cephalus LINNAEUS, 1758 (7)	8		Pl. 14, Figs. 1-3	P 7157-715
MUGILIDAE		0	-		
HEMIRAMPHIDAE	Hyporhamphus aff. unifasciatus (RANZANI, 1842) (8)	1		Pl. 6, Fig. 6	P 7160
MYRIPRISTIDAE	Myripristis sp.	2	1	Pl. 6, Figs. 10-11	P 7161-716
CENTROPOMIDAE	Centropomus cf. undecimalis (BLOCH, 1792)	4	4	Pl. 6, Figs. 12-13	P 7163-716
APOGONIDAE	Apogon sp.	3	7	Pl. 7, Figs. 1-3	P 7165-716
LACTARIIDAE	Lactarius aff. atlanticus STEURBAUT & JONET, 1982 (9)	180	267	Pl. 7, Figs. 10-14	P 7168-717
CARANGIDAE	Trachurus sp.	3	1	Pl. 7, Fig. 8	P 7176
MENIDAE	Mene sp.	1	-	Pl. 7, Fig. 9	P 7177
LUTJANIDAE	Ocyurus sp.	1	-	Pl. 14, Fig. 9	P 7173
	Pristipomoides sp.	4	11	Pl. 7, Figs. 4-5	P 7174-717
GERREIDAE	Diapterus sp.	15	7	Pl. 8, Figs. 1-2	P 7178-717
	Gerreidae ind.	1	-	Pl. 8, Fig. 3	P 7180
HAEMULIDAE	Haemulon sp.	3	9	Pl. 8, Figs. 7-8	P 7181-718
	Haemulon aff. aurolineatum CUVIER, 1830	3	1	Pl. 8, Figs. 9-10	P 7183-718
	Orthopristis aff. ruber CUVIER, 1830	3	1	Pl. 8, Figs. 11-13	P 7185-718
	Orthopristis sp.	45	2	Pl. 8, Figs. 4-6	P 7188-719
SCIAENIDAE	Aplodinotus longecaudatus n. sp.	24	72	Pl. 9, Figs. 8-12	P 7191-719
och ibi ibi ibi	Aplodinotus hoffmani n. sp.	13	38	Pl. 9, Figs. 1-4	P 7196-719
	Equetus davidandrewi n. sp.		1433	Pl. 10, Figs. 1-5	P 7200-720
	Equetus aff. punctatus (BLOCH & SCHNEIDER, 1801)	53	39	Pl. 10, Figs. 6-9	P 7205-720
	Larimus henrici n. sp.	26	23	Pl. 11, Figs. 1-4	P 7209-72
	Larimus steurbauti n. sp.	-	90	Pl. 11, Figs. 5-8	P 7213-721
	Plagioscion sp.	-	46	Pl. 12, Figs. 1-4	P 7217-72
	Protosciaena aff. trewavasae (CHAO & MILLER, 1975)(10)	506	312	Pl. 12, Figs. 5-9	P 7221-72
	Sciaena sp.	93	266	Pl. 13, Fig. 6	P 7226
	? Sciaena sp.	1	-	Pl. 13, Fig. 7	P 7227
	Sciaenops sp. (11)	14	96	Pl. 13, Figs. 1-4	P 7228-72
MULLIDAE	Mullidae ind.	1	-	Pl. 14, Fig. 11	P 7232
POLYNEMIDAE	Polynemidae ind.	1	-	Pl. 14, Fig. 12	P 7233
PEMPHERIDAE	Pempheridae ind.	1	-	Pl. 13, Fig. 5	P 7234
Percoidei ind.	Percoidei ind.	4	-	Pl. 7, Figs. 6-7	P 7235-723
OPISTOGNATHIDAE	Opistognathus sp.	1	1	Pl. 14, Fig. 10	P 7237
GOBIIDAE	Gobiidae ind.	95	207	Pl. 15, Figs. 9-11	P 7238-724
STROMATEIDAE	Peprilus sp.	2	-	Pl. 15, Fig. 2	P 7241
BOTHIDAE	Bothidae ind.	3	13	Pl. 15, Figs. 7-8	P 7242-724
DOI IIIDAE	Citharichthys sp.	11	2	Pl. 15, Figs. 7-8 Pl. 15, Figs. 3-5	P 7244-724
CYNOGLOSSIDAE		1			
LINUULUSSIDAE	Symphurus sp.	1	1	Pl. 15, Fig. 6	P 7247

was made between sieved and surface-collected material; this may influence the quantitative data in favour of the species with larger otoliths.

Locality 3, situated at 143 m above sea level, is an exposure

of red marly sands with on top a bioclastic sandstone ledge. The sand contains some thin levels of broken molluscs among which *Crassostrea* and pectinids predominate. This site provided no otoliths, but a relatively abundant association of shark teeth.

### Systematic Palaeontology

A list of all otolith-based species from the Cantaure Formation with their occurrence in both sampled localities is given in Table 1. The classification adopted here is in principle the one utilised by Nelson (1994), but taking into account the paper of Johnson & Patterson (1993) for the position of the mugilids. Drawings of all cited species are presented in the plates. In some cases, the Recent comparative material on which the generic identification was based is also figured. Additional comments are given only for new species or for those subject to discussion.

Studies by Nolf (1976) and Nolf & Stringer (1992) on the Neogene otoliths of respectively Trinidad and the Dominican Republic indicate clearly that various Recent species, especially those inhabiting low relief sandy and muddy environments or living on the continental slope, were already present in the Neogene of the Caribbean area. Recent species have also been identified in various Neogene strata of Europe. This makes it difficult to decide whether a Neogene otolith, identified at the generic level, belongs to an extinct or an extant species, if the otoliths of all the Recent species of the genus from the concerned biogeographic area are not known. Therefore, the precaution has been taken not to introduce any new species unless otoliths of all Recent Caribbean species of the genus are known.

In several cases, specific identity could not be unequivocally decided. In those cases, the abbreviation *aff.* (affinis) was inserted between the name of the genus and the name of the group species. The abbreviation *cf.* (conformis) was used in cases where the condition of preservation of the otolith did not allow conclusive specific identification. Many taxa appear in open nomenclature for identification at the species level due to insufficient knowledge of related Recent species or because the fossil material is too limited or too poorly preserved to decide.

### Remarks on taxa requiring comments

(1) Family Ariidae. - The ariids constitute a family of catfishes inhabiting neritic marine, estuarine and lagoonal environments. The family is very speciose in Middle American coastal waters. JORDAN et al. (1930, pp. 147-151) cite 43 species for the region north of the northern boundaries of Venezuela and Colombia only, and for many of those, the otoliths are unknown. The fossil record of ariids mainly consist of utricular otoliths instead of saccular ones. Several of these massive utricular otoliths have been found in the Cantaure Formation. Some (Pl. 4, Fig. 8-10) seem to be almost identical with the Recent Eastern Pacific Arius kessleri STEINDACHNER, 1876 (Pl. 4, Fig. 7). Others (Pl. 3, Fig. 1-5) are very similar to the Recent Eastern Pacific Arius seemani GÜNTHER, 1864 (Pl. 3, Fig. 6), but this species has a very generalised otolith type, and better knowledge of the

otoliths of other Recent Middle American ariid otoliths is required for a definite attribution. Moreover it has to be proven that the utricular otoliths are diagnostic at species level in all ariids. A third *Arius* species (Pl. 3, Fig. 7) is characterised by very flat otoliths, but could not be identified at species level. A fourth type of utricular otolith, finally (Pl. 4, Fig. 1-5) is rather similar to those of the Recent *Genidens* (VALENCIENNES, 1840) (Pl. 4, Fig. 6), and may belong to that genus.

- (2) *Plotosus* sp. This taxon is represented only by a single broken otolith, but in the Caribbean realm, perfectly preserved *Plotosus* otoliths are known from the Late Miocene Cercado Formation of the Dominican Republic (Nolf & Stringer, 1992, pl. 10, fig. 3). Recent catfishes of the genus *Plotosus* occur in nearly all neritic, estuarine and even fresh waters of the Indo-Pacific area, the Australian realm, and the Pacific plate (see Berra, 1981). The presence of *Plotosus* in the Caribbean realm is interpreted as a relict element of the ancient Western Tethys fauna.
- (3) Diaphus aff. regani TAANING, 1932.- The present day distribution of *D. regani* is restricted to the Indo-Pacific realm (WISNER, 1976, NAFPAKTITIS, 1978), but it frequently occurs in the Early Miocene of Northern Italy (Nolf & Brzobohaty, unpublished data). The presence of this taxon in the Caribbean realm must be interpreted as a case of ancient circumtropical Tethys distribution.
- (4) Diaphus sp. The otoliths grouped under this name probably constitute a heterogeneous group of Diaphus species with very generalised, poorly diagnostic otolith morphology, and juveniles. Many of our specimens fit quite well with otoliths of D. garmani GILBERT, 1906 (see SCHWARZHANS, 1980, fig. 160, p. 58). Although the present day abundance of this species in the Caribbean and tropical western Atlantic realm would be in agreement with an Early Miocene occurrence of the species in Venezuela, the morphological basis for such an assertion does not suffice; see also BRZOBOHATY & NOLF (1995, p. 257-258) for a general discussion on the identification of Diaphus otoliths.
- (5) Steindachneria sp. Four eroded and incomplete otoliths probably belongs to an extinct Steindachneria species, but the poor preservation of the material does not allow formal designation. The fossil otoliths differ from the monotypic present day Caribbean Steindachneria argentea Goode & Bean, 1896 (see Nolf & Steurbaut, 1989, p. 100, fig. 7, i-j) by their more straight postero-dorsal rim in the adults, and a less protruding antero-dorsal portion in the juveniles. Another extinct Steindachneria species with much more elongate otoliths occurs in the Early Miocene Astoria Formation of Washington State, U.S.A (Nolf & Goedert, unpublished data). Present day distribution of Steindachneria is restricted to the Caribbean realm, where it occurs on the outer shelf and slope, on soft bottoms; it is often taken in

large quantities at depths of 400-500 m in the northern Gulf of Mexico (Cohen et al., 1990, p. 346). The presence of *Steindachneria* in the very shallow water environment of the Cantaure Formation is aberrant, and these four otoliths were probably added to the association via predators foraging in deeper water.

- (6) Membras sp. This is the first fossil record of this genus of Middle American menidiine atherinids. This is also the only fish taxon known to us, in which we observed a sulcus with a the posterior caudal end that is curved dorsally. An otolith of the Recent Membras gilberti (JORDAN & BOLLMAN, 1889) is figured on Pl. 14, Fig. 4, to support our generic identification.
- (7) Mugil aff. cephalus.- Only fossil otoliths of juvenile fishes were collected. They seem to be identical with those of the Recent Mugil cephalus LINNAEUS, 1758 (pl. 14, fig. 7-8), but adult fossils are required for a definite attribution.
- (8) Hyporamphus aff. unifasciatus.- See NOLF & STRINGER (1992, pl. 12, fig. 17-18) for the iconography of comparative Recent material.
- (9) Lactarius aff. atlanticus.- This seems to be one of the rare Neogene teleosts that have an eastern and western Atlantic fossil record. The type material from Aquitaine however (Steurbaut & Jonet, 1982, pl. 5, fig. 1-4) shows very crenelated rims, even in large specimens, while big Venezuelan otoliths shows smooth rims at the same size.
- (10) Protosciaena aff. trewavasae (CHAO & MILLER, 1975).- Otoliths of this taxon have already been recorded from the Late Miocene Cercado Formation of the Dominican Republic by NOLF & STRINGER (1992, p. 55, pl. 16, fig 6-7), who described them as a new species, Ctenosciaena latecaudata. When writing our 1992 paper, we disposed only of very formalin eroded Protosciaena otoliths, and attributed our fossils to the genus Ctenosciaena FOWLER & BEAN, 1924. Good figures of Protosciaena trewavasae otoliths were subsequently published by SCHWARZHANS (1993, fig. 344-345, p. 193), and seem to be almost identical with the type material of Ctenosciaena latecaudata and to the otoliths from the Cantaure Formation figured here (Pl. 12, Fig. 5-9). Otoliths of Protosciaena differ from those of Ctenosciaena (see NOLF, 1976, pl. 7, fig. 1 and SCHWARZHANS, 1993, figs. 130-131, p. 81) by their clearly widened caudal end, and do not show such a long ventrally recurved part as in Ctenosciaena.
- (11) *Sciaenops* sp. Fossil *Sciaenops* otoliths from the Cantaure Formation (Pl. 13, Fig. 1-4) have been compared to a very extensive growth series (going from fishes of 1,71 till 43,5 cm standard length) of the Recent *Sciaenops ocellatus* Linnaeus, 1758 (Pl. 13, Fig. 8-11). Juvenile otoliths with a dimension of 3-4 mm look very similar in both the fossil and the Recent material (com-

pare Pl. 13, fig. 3 and 9), although the fossil otoliths already show a shorter ostium and a longer ventrally curved caudal end at this stage. The largest fossil available (Pl. 13, Fig. 1) differs clearly from the largest Recent otolith (Pl. 13, Fig. 8) by having a much longer caudal end that is recurved anteriorly, and by lacking a clear posterodorsal angle. Because there is only a single Recent *Sciaenops* species, the fossils clearly belongs to an extinct one, but we judge that the fossil material is too poorly preserved for formal designation of the species. Although it is easy to distinguish the fossils from the Recent species, problems may turn up when trying to distinguish it from eventual other fossil species.

### Description of new species

Aplodinotus longecaudatus n. sp. (Pl. 9, Figs. 8-12)

Type material.- Holotype: a right otolith (Pl. 9, Fig. 10) (IRSNB P 7193); 72 paratypes from locality 2, and 23 paratypes from locality 1; four of the latter are figured (Pl. 9, Figs 8-9 and 11-12) (IRSNB P 7191-7192 and 7194-7195).

Dimensions of the holotype.- Length: 4.8 mm; height: 4.5 mm; thickness: 1.5 mm.

Stratum typicum.- Cantaure Formation, locality 1, about 12 km W of San José de Cocodite, Venezuela.

Derivatio nominis.- Longecaudatus, a, um: provided with a long cauda.

Diagnose.- This species is characterised by relatively thick, slightly subtriangular otoliths. The inner face is clearly convex. The sulcus consists of a wide subquadrangular ostium and a long, narrow cauda of which the anterior third is straight, while the posterior two thirds are curved ventrally; the end of the cauda is even slightly recurved in the anterior direction. The area situated between the posterior part of the ostial crista inferior and the recurved portion of the cauda is very high and narrow. The outer face bears some rim-like tubercles.

Affinities.- Otoliths of A. longecaudatus can easily be distinguished from A. grunniens, the only Recent species in the genus. In otoliths of A. grunniens (Pl. 9, fig. 5-7), the ventrally curved part of the cauda is much shorter, and the posterior end is not recurved anteriorly. Consequently, the area situated between the posterior part of the ostial crista inferior and the recurved portion of the sulcus is much broader and almost quadrangular. This feature is significant because a ventrally inflated cauda is an apomorph feature, that becomes more pronounced in older fishes, as can be seen in the very demonstrative growth series of Sciaenops ocellata LINNAEUS 1759

(Pl. 13, Fig. 11-8). In *A. longecaudatus*, the strongly recurved caudal end already occurs in very young fishes, while even in very large specimens of *A. grunniens*, curvature of the caudal end is only moderate. *A. hoffmani* (Pl. 9, fig. 1-4), a second extinct *Aplodinotus* species represented in our material, has much more antero-dorsally extended and elongate otoliths than *A. longecaudatus*, and a sulcus pattern that is much more like in *A. grunniens*.

# Aplodinotus hoffmani n. sp. (Pl. 9, Figs. 1-4)

Type material.- Holotype: a left otolith (Pl. 9, Fig. 1) (IRSNB P 7196); 38 paratypes from locality 2, and 12 paratypes from locality 1; three of the latter are figured (Pl. 9, Fig. 2-4) (IRSNB P 7197-7199).

Dimensions of the holotype.- Length: 5.9 mm; height: 4.4 mm; thickness: 1.5 mm.

Stratum typicum.- Cantaure Formation, locality 1, about 12 km W of San José de Cocodite, Venezuela.

Derivatio nominis.- This species is named after Pierre HOFFMAN, Brussels, who helped us a lot in cleaning up the illustrations of the present paper.

Diagnose.- This species is characterised by relatively flat otoliths with a strong antero-dorsal protrusion and a rather slender posterior portion. The dorsal rim slopes regularly towards a blunt postero-dorsal angle. The inner face is only weakly convex. The antero-ventral part is very reduced, and the area situated between the anterior part of the crista inferior and the anteroventral rim is almost completely reduced. The ostium is wide and generally trapezium-shaped, but very quadrangular in its anterior part. The narrow cauda runs nearly horizontal in its first half, while its second half runs almost straight in ventral direction. There is a wide field between this straight portion of the sulcus and the posterior part of the ostial crista inferior. The outer face is nearly smooth but shows an angular crest near to the dorsal rim.

Affinities.- Otoliths of A. hoffmani are nearest to those of A. grunniens, but differ from them by their more extended antero-dorsal part, their oblique dorsal rim, their more reduced antero-ventral portion, and their flatter inner face. They are also clearly distinct from those of A. longecaudatus (see under this species for distinctive features).

# Equetus davidandrewi n. sp. (Pl. 10, Figs. 1-5)

Type material.- Holotype: a left otolith (Pl. 10, Fig. 1)

(IRSNB P 7200); 1433 paratypes from locality 2, and 1533 paratypes from locality 1; four of the latter are figured (Pl. 10, Fig. 2-5) (IRSNB P 7201-7204).

Dimensions of the holotype.- Length: 9.0 mm; height: 7.6 mm; thickness: 3.3 mm.

Stratum typicum.- Cantaure Formation, locality 1, about 12 km W of San José de Cocodite, Venezuela.

Derivatio nominis.- This species is named after David Andrew, who provided the very nice series of juvenile Sciaenops ocellatus otoliths, figured on Pl. 13, Figs. 9-11.

Diagnose.- This species is characterised by thick otoliths with a generally round outline, a moderately protruding antero-dorsal portion and a clear postero-ventral angle. This last feature is not visible in very juvenile otoliths (Pl. 10, Fig. 5). The inner face is markedly convex and bears a sulcus with a very small, nearly circular ostium, and a long, narrow cauda, which is strongly bent in ventral direction; the posterior end of the cauda is even somewhat recurved in the anterior direction. The area situated between the posterior part of the ostial crista inferior and the recurved portion of the cauda is much wider than the maximal diameter of the ostium. The outer face is nearly smooth. Only in late juvenile stages, some tuberculation is observed. The maximal convexity of the outer face is situated in the dorso-ventral direction.

Affinities.- Otoliths of all Recent Equetus species show an ostial outline with a concavity at the crista superior, while in E. davidandrewi this part is convex. Also, in none of the Recent species, the area situated between the posterior part of the ostial crista inferior and the recurved portion of the cauda is wider than the maximal diameter of the ostium. Compare to Equetus aff. punctatus (Pl. 10, figs 6-9) for evaluation of these distinctive features.

# Larimus henrici n. sp. (Pl. 11, Figs. 1-4)

Type material.- Holotype: a right otolith (Pl. 11, Fig. 1) (IRSNB P 7209); 26 paratypes from locality 1, and 22 paratypes from locality 2; three of the latter are figured (Pl. 11, Figs. 2-4) (IRSNB P 7210-7212).

Dimensions of the holotype.- Length: 9.5 mm; height: 5.0 mm; thickness: 3.7 mm.

Stratum typicum.- Cantaure Formation, locality 2, about 12 km W of San José de Cocodite, Venezuela.

Derivatio nominis.- Dedicated to Henri CAPPETTA, Montpellier.

Diagnose.- This species is characterised by massive, subquadrangular, elongate otoliths. The inner face is strongly convex, especially in the antero-posterior direction. The sulcus consists of a long and wide ostium, and an almost rectangularly shaped cauda. The first half of the cauda is narrow, and extends horizontally; the second half is straight and vertical. This vertical portion is deeply incised and widened. In the crista inferior, the junction between the horizontal and vertical parts of the cauda is very angular; in the crista superior, the corresponding junction is smoothly rounded. Because for this species we possess a rather extended growth series, some interesting features of allometric growth can be observed. They especially affect the postero-ventral angle, and the outer face. In the smallest specimen (Pl. 11, Fig. 4), one already observes a well marked postero-ventral angle; the otoliths are rather thin, and the outer face is concave, with a smooth central part and fine marginal tuberculation. In older juveniles (Pl. 11, Fig. 3), the postero-ventral angle evolves to an almost spine-like process, the otoliths become more massive and the outer face is provided with a strong tubercular ornamentation. In the early adult stage (Pl. 11, Fig. 2), the postero-ventral process becomes much smoother, the thickening of the otoliths is extreme, and the tuberculation of the outer face becomes more obsolete. In the late adult stage, finally (Pl. 11, Fig. 1), the whole outline becomes smoother and more elliptical, the outer face is very convex, and all tubercles are reduced to a few smoothened crests.

Affinities.- The genus Larimus is endemic to Middle America, where one Atlantic and five Eastern Pacific species are known (JORDAN et al., 1930). Otoliths of all of those are less elongate and less regularly rectangular than those of L. henrii.

# Larimus steurbauti n. sp. (Pl. 11, Figs. 5-8)

Type material.- Holotype: a left otolith (Pl. 11, Fig. 5) (IRSNB P 7213); 89 paratypes from locality 2; three of those are figured (Pl. 11, Fig. 6-8) (IRSNB P 7214-7216).

Dimensions of the holotype.- Length: 11.6 mm; height: 7.1 mm; thickness: 4.0 mm.

Stratum typicum.- Cantaure Formation, locality 2, about 12 km W of San José de Cocodite, Venezuela.

Derivatio nominis.- Dedicated to Etienne Steurbaut, Brussels.

Diagnose.- This species is characterised by compact, robust otoliths with a very wide ostium and an almost complete reduction of the area situated between the posterior part of the ostial crista inferior and the recurved portion of the cauda. Their outline shows an antero-dorsal expansion, a very blunt postero-dorsal angle, and a pos-

tero-dorsal process. The inner face is regularly convex. The very wide ostium covers nearly the entire two thirds of the inner face. The cauda has a rectangular hooked shape and is strongly incised, especially in its posterior part. Its first third is narrow, and extends horizontally; the second half is directed vertically, somewhat recurved anteriorly in its posterior end. The vertical portion of the cauda is widened and deeply incised. The outer face is clearly convex, and shows some smooth tuberculation in many specimens.

Affinities.- Otoliths of *L. steurbauti* are readily distinguished from those of all other species in the genus, by the extreme narrowing of the area situated between the posterior part of the ostial crista inferior and the recurved portion of the cauda.

### Conclusions

### Palaeoenvironmental evaluation

The otolith study reveals the presence of 61 taxa of teleosteans in the Early Miocene Cantaure Formation, among which five are new species. The material was collected from two different localities, distant of about 500 m. Both associations (Table 1) reflect tropical near shore marine environments, with a water depth of less than 50 m. This is in agreement with the data of Jung (1965, p. 405), who stated that the mollusc fauna is indicative for a neritic environment with normal salinity. Quantitative data characterising both associations are provided in Table 2. This table essentially shows very similar frequencies for the dominant taxa in both associations, but some minor differences must be considered.

The association of locality 1 is more diversified (59 taxa) than the one of locality 2 (39 taxa), although 1524 more specimens were collected there. Among the taxa dominating both associations, only ariids are significantly more common at locality 2. Only two taxa are not represented at locality 1: Larimus steurbauti and Plagioscion sp., known respectively by 90 and 46 specimens at locality 2. In the Recent fauna, Plagioscion is a freshwater genus (nine nominal species) of sciaenids from South American rivers; some species occasionally occurs in estuaries but rarely in full marine environments (CHAO, 1978, p. 43) Another present day freshwater sciaenid genus, Aplodinotus, is also more abundant at locality 2. This fits well with the greater abundance of the ariid catfishes, another family that shows much tolerance for freshwater and variable salinities, at locality 2. Also the absence of the epipelagic herring families Pristigasteridae and Clupeidae (four taxa) at locality 2 must be noted, as well as the reduced diversity of myctophids (five taxa at locality 1; while locality 2 yields only two, among which very small juvenile Diaphus otoliths dominate). The as sociation of locality 2 must be considered as marine, but those small differences reflect a somewhat more protected environment than at locality 1, and probably some freshwater input. Another feature of both associations, is the great abundance of the genus *Equetus* RAFINESQUE, 1815, a typical inhabitant of coral reefs, and sometimes shallow coastal waters (respectively 57% and 34% of the associations at localities 1 and 2); here again the percentages are in agreement with the already formulated environmental conclusions.

### Comparison with other Miocene otolith associations in the Caribbean realm

Substantial data for other Caribbean Miocene otolith associations are available for Trinidad (Nolf, 1976: 66 taxa) and the Dominican Republic (Nolf & Stringer, 1992: 65 Miocene taxa). In both cases, however, the otoliths are merely a complimentary product of sampling for foraminifers and/or molluscs.

The material from Trinidad comes from 30 sampling localities in various Miocene formations and a few Pliocene ones. No further attention is given to the stratigraphic range within the Trinidad Neogene deposits because the true picture of the stratigraphic range of the recorded taxa is probably strongly distorted by uneven sampling and facies differences within the succession.

Most otoliths from the Dominican Republic were either surface-collected as individual specimens or screen washed from small samples (usually less than 20 kg), while the average size of a sample intended for otolith study should be in the order of 500 kg. Therefore, the synthesis of the Dominican Republic fauna provided in table 2 of Nolf & Stringer (1992) is based on composite samples. In the Dominican Republic, 64 of the recorded Miocene taxa are from the Late Miocene Cercado Formation and the basal part of the Gurabo Formation. In the Early to Middle Miocene Baitoa Formation, only a restricted association of 13 species is known, of which 12 occur in the Late Miocene also. Therefore, our knowledge of the Dominican Republic fauna essentially concerns only the Late Miocene.

Table 2: QUANTITAT	IVE DA	TA				
Number of:	Locality 1 59 taxa 2794		Locality 2			
all taxa = 61 otoliths (all specimens)			39 taxa 4318			
Ariidae	51	= 1,8 %	333	= 7,7 %		
Myctophidae	541	= 19,4 %	1026	= 23,7 %		
Lactarius atlanticus	180	= 6,4 %	267	= 6,1 %		
Sciaenidae	1768	= 63 %	2415	= 56 %		
Equetes (2 species)	1586	= 57 %	1477	= 34 %		
Aplodinotus (2 species)	37	= 2%	110	= 4 %		
Gobiidae	95	= 3,4 %	207	= 4,7 %		
Ariidae + Sciaenidae	1819	= 64,8 %	2748	= 63,7 %		

Table 3 provides an overview of the data from the three areas of the Caribbean Miocene for which significant otolith associations are known. The table includes all families, all genera and all nominal species for the three areas. Imprecise and redundant data have been removed, e.g. the unidentified Apogon sp. I and sp. II from Trinidad and the unidentified Apogon otoliths from Venezuela and the Dominican Republic are recorded as Apogon, the relevant point being that unidentified Apogon otoliths are known from the three areas. In cases where from one area, a nominal species is known, and from another area only a taxon of the same genus in open nomenclature, e.g. Mugil aff. cephalus from Venezuela and Mugil sp. from the Dominican Republic, the presence of the genus in the area(s) where no nominal form is recorded, is indicated by a / sign instead of a negative sign.

The table provides a list of 52 families, including 138 taxa, 92 genera, and 53 nominal species. Fourteen nominal species are extinct, and only three of them belong to extinct genera; 39 belong to Recent species, of which only one, Diaphus regani, is not represented in the present day Caribbean fauna. The proportion 14/39 (= 26% and 74 %) is probably strongly distorted in favour of the Recent species: in several cases, species that are perfectly characterised by their otoliths, e.g. the Porichthys taxa from the three areas, were not named because the otoliths of several of the Recent Caribbean species are still unknown. A better picture is probably provided by the sciaenid family, which has an excellent Caribbean fossil record, and where knowledge of the otoliths of Recent species is quite satisfactory. Among the 14 nominal species, only six (43%) belong to Recent species, while eight (57%) are extinct. Looking at the generic level, the picture is very different: among the 25 recorded sciaenid taxa, 24 belong to Recent Caribbean genera, and only one belongs to an extinct

Summarising all our data, we can say that the Miocene Caribbean realm was inhabited by a teleost fauna of which the overall picture was already very similar to that of the present day fauna of the area. At the generic level this similarity is very strong, but at the species level, probably more than 50% of the Miocene taxa are extinct today. Among the 138 recorded taxa, only four do not fit in the present day picture of Caribbean biogeography: Diaphus aff. regani, Plotosus, Lactarius and Mene. All four are cases of ancient circumtropical Tethys distribution. Diaphus regani is a present day Indo-Pacific species, but almost identical otoliths are known from the Early Miocene of Italy (NOLF & BRZOBOHATY, unpublished data). The presence of the Indo-Pacific genus Plotosus in the Caribbean Miocene was already demonstrated by Nolf & Stringer (1992). The present day South Asian genus Lactarius is known from the Eocene of Texas, Barbados and France, and from the Miocene of France, Portugal and New Zealand (NOLF, 1985; STEUR-BAUT, 1984). Recent menids are restricted to one genus with one species, Mene maculata (BLOCH & SCHNEIDER,

	ED FISH TAXA FROM THE THE CARIBBEAN REALM	Venezuela	Trinidad	Dominican Republic
ALBULIDAE	Albula	V		D
MURAENESOCIDAE	Muraenesocidae	_	T	-
CONGRIDAE	Ariosoma balearicus (DELAROCHE, 1809) (1)	V	T	D
	Ariosoma aff. selenops REID, 1934	_		D
	Conger	V	-	-
	Paraconger guianensis KANAZAWA, 1961	V	-	-
	Rhechias aff. tysanochila (REID, 1934) (2)	-	Т	D
	Rhynchoconger aff. flavus (GOODE & BEAN, 1896) (3)	V	T	D
	Congridae	-	T	
HETERENCHELYIDAE	Pythonichthys (4)	V	T	D
ENGRAULIDAE	Cetengraulis	-	T	-
	Anchoa	-	T	-
	Engraulidae	-	1	D
PRISTIGASTERIDAE	Ilisha	V	T	-
	Neopisthopterus	V	-	-
	Pellona	V	-	-
CLUPEIDAE	Harengula aff. clupeola CUVIER, 1829	V	-	-
	Opisthonema aff. oglinum (LESUEUR, 1818)	-	T	-
	Opisthonema	-	1	D
	Clupeidae	-	-	D
ARIIDAE	Arius aff. felis LINNAEUS, 1758	-	T	-
	Arius aff. kessleri STEINDACHNER, 1876	V	-	-
	Arius	V	T	D
	Cathorops spixii (AGASSIZ, 1829) (5)	-	T	-
	Genidens	V	-	-
	Selenaspis herzbergii (BLOCH, 1794)	-	T	-
PLOTOSIDAE	Plotosus	V	-	D
STERNOPTYCHIDAE	Polyipnus	-	T	D
PHOTICHTHYIDAE	Polymetme cf. corythaeola (ALCOCK, 1898)	-	T	-
	? Photichthyidae	-	T	-
SYNODONTIDAE	Saurida caribbaea BREDER, 1927	-	T	D
MYCTOPHIDAE	Diaphus aff. brachycephalus TAANING, 1928	-	-	D
	Diaphus aff. problematicus PARR, 1928	V	-	-
	Diaphus aff. regani TAANING, 1932	V	-	-
	Diaphus (6)	V	T	. D
	Hygophum aff. benoiti (COCCO, 1838)	-	-	D
	Hygophum hygomi (LÜTKEN, 1892)	V	-	-
	Myctophum cf. punctatum RAFINESQUE, 1810	V	-	-
	Myctophum	/	-	D
CARAPIDAE	Carapus aff. bermudensis (JONES, 1874)	-	-	D
OPHIDIIDAE	Brotula barbata (STEINDACHNER, 1801)	-	T	1 -
	Lepophidium latesulcatus NOLF & STRINGER, 1992	-	-	D
	Lepophidium	-	T	/
	Otophidium robinsi NOLF & STRINGER, 1992	-	-	D
	Otophidium robustus NOLF & STRINGER, 1992	-	-	D
	Lamprogrammus (7)	-	T	-
	Neobythites gillii GOODE & BEAN, 1886 (8)	-	T	-
	Neobythites (9)	-	T	-
BYTHITIDAE	"g. Dinematichthyinorum" smithvanizi NOLF & STR., 1992	-	-	D
BREGMACEROTIDAE	Bregmaceros	V	T	D
STEINDACHNERIIDAE	Steindachneria	V	-	-
MORIDAE	Gadella	-	T	-

Table 3, continuation 1		Venezuela	Trinidad	Dominican Republic
BATRACHOIDIDAE	"aff. Perulibatrachus"	·v	T T	- D
	Porichthys	V	T	D
ANTENNARIIDAE	Thalassophryne Antennariidae	-	T	
CHAUNACIDAE	Chaunax		-	D
ATHERINIDAE	Atherinomorus stipes (MÜLLER & TROTSCHEL, 1847)			D
ATTIERINDAL	Membras	V		-
MUGILIDAE	Mugil aff. cephalus LINNAEUS, 1758	v	_	-
	Mugil	1	-	D
HEMIRAMPHIDAE	Euleptorhamphus	-	-	D
	Hyporhamphus aff. brasiliensis (LINNAEUS, 1758)	-	-	D
	Hyporhamphus aff. unifasciatus (RANZANI, 1842)	V	-	D
HOLOCENTRIDAE	Holocentrus		-	D
MYRIPRISTIDAE	Myripristis	V	T	-
SCORPAENIDAE	Scorpaenidae	-	-	D
CENTROPOMIDAE	Centropomus cf. undecimalis (BLOCH, 1792)	V	-	1-
	Centropomus	-	-	D
SERRANIDAE	Centropristis	-	-	D
	Diplectrum	-	-	D
	aff. Neanthias	-	T	-
APOGONIDAE	Apogon	V	T	D
EPIGONIDAE	Epigonus	-	T	D
LACTARIIDAE	Lactarius aff. atlanticus STEURBAUT & JONET, 1982	V	-	?
CARANGIDAE	Trachurus	V	-	-
	Carangidae	1	T	-
MENIDAE	Mene	V	-	-
LUTJANIDAE	Lutjanus aff. campechanus POEY, 1861	-	-	D
	Ocyurus aff. chrysurus (BLOCH, 1791)	-	-	D
	Ocyurus	V	-	1
	Pristipomoides	V	-	D
GERREIDAE	Diapterus rhombeus (CUVIER, 1829) (10)	-	-	D
	Diapterus	V	-	1
	Eucinostomus	-	-	D
	Gerreidae	V	-	1
HAEMULIDAE	Anisotremus	-	-	D
	Conodon moreauxi NOLF & STRINGER, 1993	-	-	D
	Haemulon	V	T	D
	Haemulon aff. aurolineatum CUVIER, 1830	V	-	-
	Orthopristis aff. ruber CUVIER, 1830	V	-	-
	Orthopristis	V	-	-
	Pomadasys	V	T	D
SPARIDAE	Sparidae	1	T	-
SCIAENIDAE	Aplodinotus longecaudatus n. sp.	V	-	-
	Aplodinotus hoffmani n. sp.	V	-	1
	Bairdiella ronchus (CUVIER, 1830)	1 :	-	D
	Ctenosciaena aff. gracilicirrhus (METZELAAR, 1919)	V	T	-
	Cynoscion sp.	1 :	T	-
	Equetus davidandrewi n. sp.	V	-	-
	Equetus aff. punctatus (BLOCH & SCHNEIDER, 1801)	V	-	-
	Isopisthus	-	T	-
	Larimus breviceps CUVIER, 1830 (11)	-	T	D
	Larimus henrici n. sp.	V	-	-
	Larimus steurbauti n. sp.	V	-	-

Table 3, continuation 2				
SCIAENIDAE	Macrodon	-	Т	-
(continuation)	Menticirrhus chaoi NOLF & STRINGER, 1992	-	-	D
	Nebris microps CUVIER, 1830	-	T	-
	Ophioscion	-	-	D
	Pareques	-	-	D
	Plagioscion	V	T	-
	Pachypops fitchi SCHWARZHANS, 1993 (12)	-	T	-
	Polyclemus (13)	-	T	-
	Protosciaena aff. trewavasae (CHAO & MILLER, 1975)	V	-	-
	Sciaena -	V	-	-
	? Sciaena	V	-	-
	Sciaenops	V	-	-
	Sigmurus	-	T	-
	"genus Sciaenidarum" sasakii (SCHWARZHANS, 1993) (14)	-	T	-
MULLIDAE	Mullidae	V	Т	-
POLYNEMIDAE	Polydactylus	-	-	I
	Polynemidae	V	-	1
PEMPHERIDAE	Pempheridae	V	-	-
BATHYCLUPEIDAE	Bathyclupea	-	T	-
Percoidei ind.	Percoidei	V	T	1
OPISTHOGNATHIDAE	Lonchopisthus micrognathus (POEY, 1861)	-	-	I
	Lonchopisthus (15)	-	T	1
	Opisthognathus	V	1.	-
GOBIIDAE	Gobiidae	V	T	I
LABRISOMIDAE	Labrisomus	-	-	L
SPHYRAENIDAE	Sphyraena	-	-	I
STROMATEIDAE	Peprilus	V	-	-
BOTHIDAE	Citharichthys	V	T	-
	Bothidae	V	1	D
Pleuronectiformes ind.	Pleuronectiformes	1	T	1
SOLEIDAE	Soleidae	-	-	I
CYNOGLOSSIDAE	Symphurus	V	T	-
	Cynoglossidae	1	1	D

- (1) Cited as Ariasoma sp. in NOLF, 1976, p. 714.
- (2) Cited as "genus Congridarum" sp. 1 in NOLF, 1976, p. 715.
- (3) Cited as Gnathophis sp. in NOLF, 1976, p. 714.
- (4) Pythonichthys: Cited as "genus Soleidarum" sp. in NOLF, 1976, p. 738.
- (5) Cited as Arius spixii in NOLF, 1976, p. 716.
- (6) Diaphus: including Diaphus dumerili, cited in NOLF, 1976, p. 719.
- (7) Lamprogrammus: cited as Ophidiidae ind. in NOLF, 1976, p. 725, pl. 5, fig. 14.
- (8) see NOLF & STRINGER, 1992, p. 53, for synonymy.
- (9) Including Neobythites aff. malayanus WEBER, 1913, cited in NOLF, 1976, p. 724.
- (10) Cited as Moharra rhombica in NOLF & STRINGER, 1992, p. 50.
- (11) SCHWARZHANS (1993, p.188) incorrectly cited the specimens from Trinidad as *Larimus gatunensis* (SCHUBERT, 1909), a non prioritary synonym of *L. breviceps*.
- (12) Cited as "genus aff. Pachypops sp. in NOLF 1976, p.732.
- (13) Polyclemus trinidadensis SCHWARZHANS, 1993, based on unfigured material, that was cited as Polyclemus sp. in NOLF, 1976, p. 733, is considered as a doubtful species, because the rather eroded type material does not provide valuable diagnostic features to distinguish this species from the Recent Polyclemus dumerili (BOCOURT, 1896).
- (14) Cited as "genus Sciaenidarum" sp. in NOLF, 1976, p. 734 and as Xenotolithus sasakii by SCHWARZHANS, 1993, p. 231.
- (15) Cited as Lonchistium sp. in NOLF, 1976, p. 736.

1801) living in coastal waters of Southern Asia, Hawaii and Japan, but the genus is also recorded from the Eocene of the Paris Basin and Monte Bolca, Northern Italy, and extinct menid genera are known from the Eocene of Aquitaine, Spain, Louisiana and India (Nolf & Bajpai, 1992, p. 202). All this demonstrates the widespread ancient distribution of these four taxa that do not fit in the present day Caribbean biogeography.

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### Explanation of the plates

Because all figured fossils come from the Cantaure Formation, and because all names are labelled directly on the plates, it is superfluous to provide each plate with an explicit explanation. All figured otoliths on Pl. 1-2 and 5-15 are saccular ones; those on Pl. 3 and 4 are utricular ones. The majority of the fossils are from locality 1; for the few from locality 2, this is mentioned directly on the plates. All specimens are deposited in the collections of the Institut royal des Sciences naturelles de Belgique (IRSNB). The fossil otoliths bear numbers (see Table 1) of the collection of types and figured fossil fish species in the IRSNB. The abbreviations F and R in the upper right corner of each compartment of the plates indicate if the figured specimens in that compartment are respectively fossil or Recent. The sign (F) is used to indicate otoliths of Recent species, found as fossils. The notations Fig. a, b, c and d are used to indicate respectively ventral, inner (= proximal), posterior, and outer (= distal) views. Figures with only numbers and no letter show inner views.

In twelve cases, we figured comparative Recent material, also from the IRSNB collection:

Pl. 1, Fig. 1: — Paraconger guianensis, from the mouth of the Amazon;

Pl. 2, Fig. 4: — *Pellona flavipinnis*, from the mouth of the Amazon;

Pl. 2, Fig. 11: — Neopisthopterus tropicus, from the Pacific coast of Costa Rica;

Pl. 3, Fig. 6: — Arius seemani, from the Pacific coast of Panama;

Pl. 4, Fig. 6: — Genidens, off Rio Grande do Sul, Brazil.

Pl. 4, Fig. 7: — Arius kessleri, from the Pacific coast of Panama;

Pl. 5, Fig. 1-6: — Diaphus regani, Fig. 1-2 from off New Caledonia and Fig. 3-6 from the central Pacific.

Pl. 9, Fig. 5-7: — Aplodinotus grunniens, fresh water, North America, Fig. 5 and 6 from Louisiana and Fig. 7 from Texas.

Pl. 13, Fig. 8-11: — *Sciaenops ocellatus*, Fig. 8 from Pascagoula River, Mississippi, Fig. 9-11 from Florida. Standard length of the fishes: Fig. 8 = 435 mm, Fig. 9 = 70.2 mm, Fig. 10 = 41.7 mm; Fig. 11 = 17.1 mm.

Pl. 14, fig. 4: — *Membras gilberti*, from the Pacific coast of Costa Rica.

Pl. 14, Fig. 7-8: — Mugil cephalus, Fig. 7 from Peru, Fig. 8 from Hawaii.

Pl. 15, Fig. 1: — Peprilus triacanthus, from the North West Atlantic.

PLATE 1

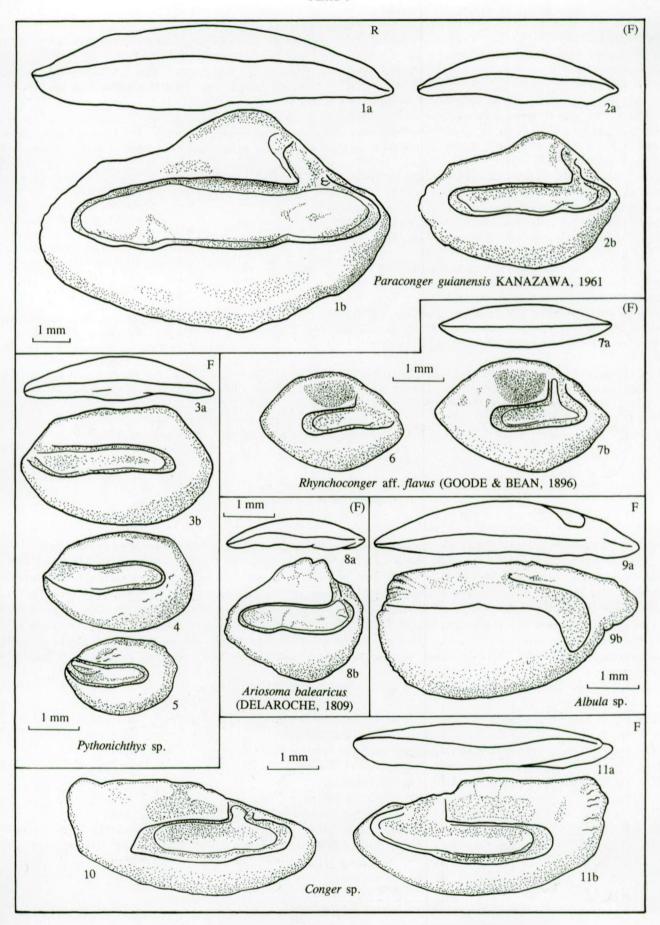


PLATE 2

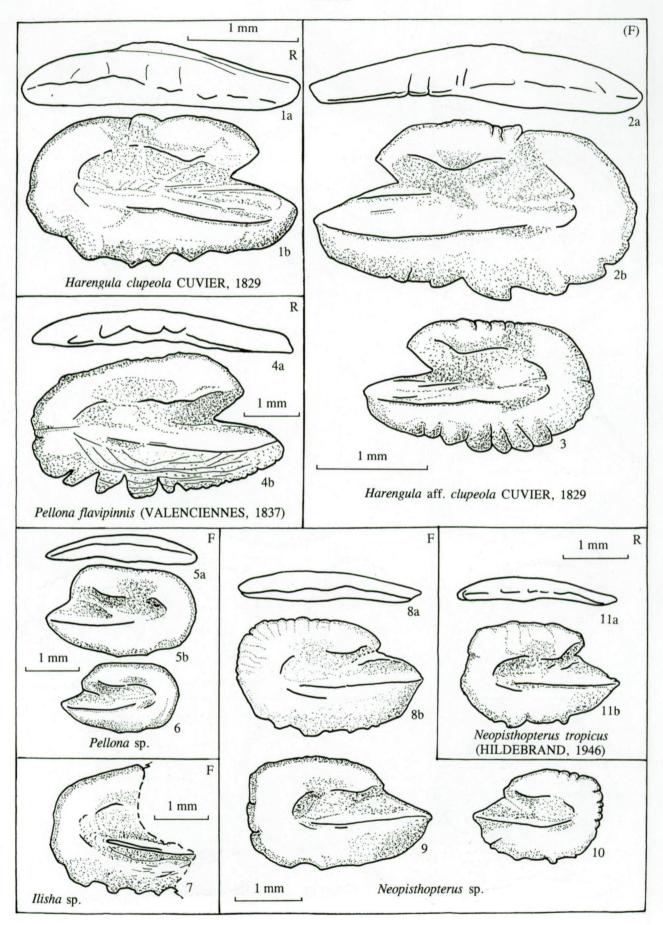


PLATE 3

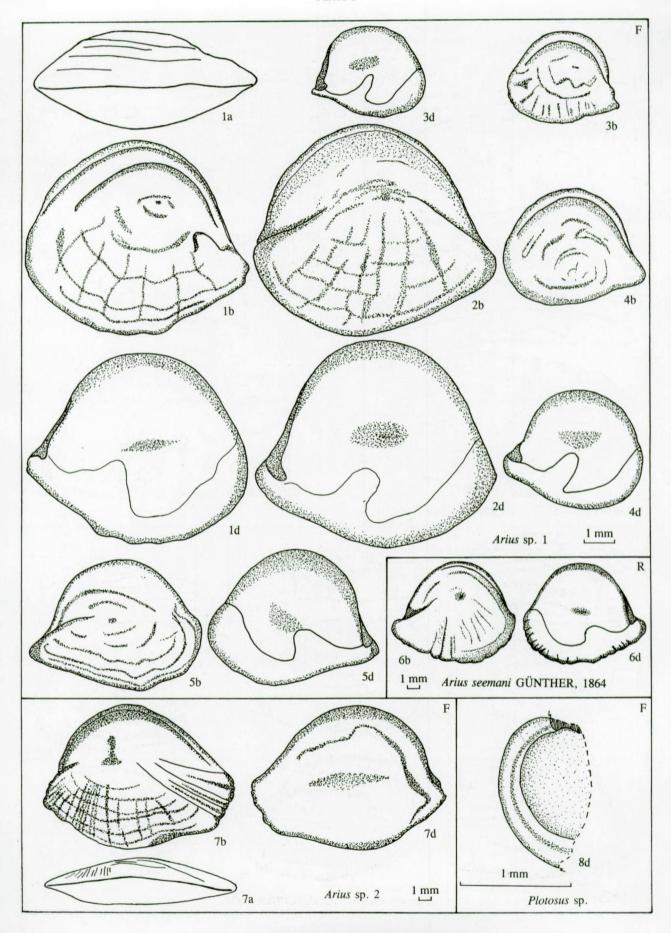


PLATE 4

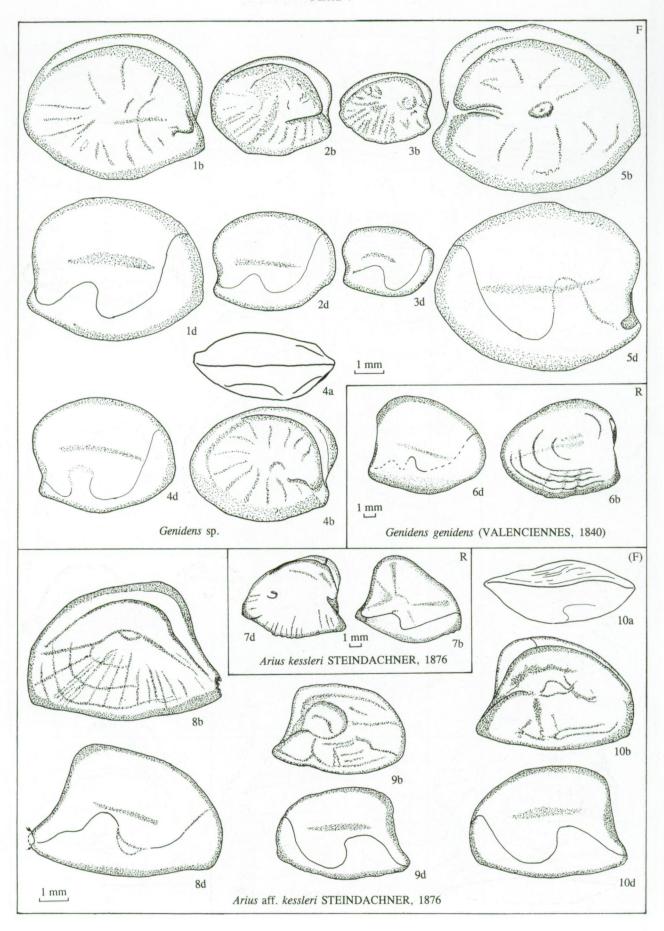


PLATE 5

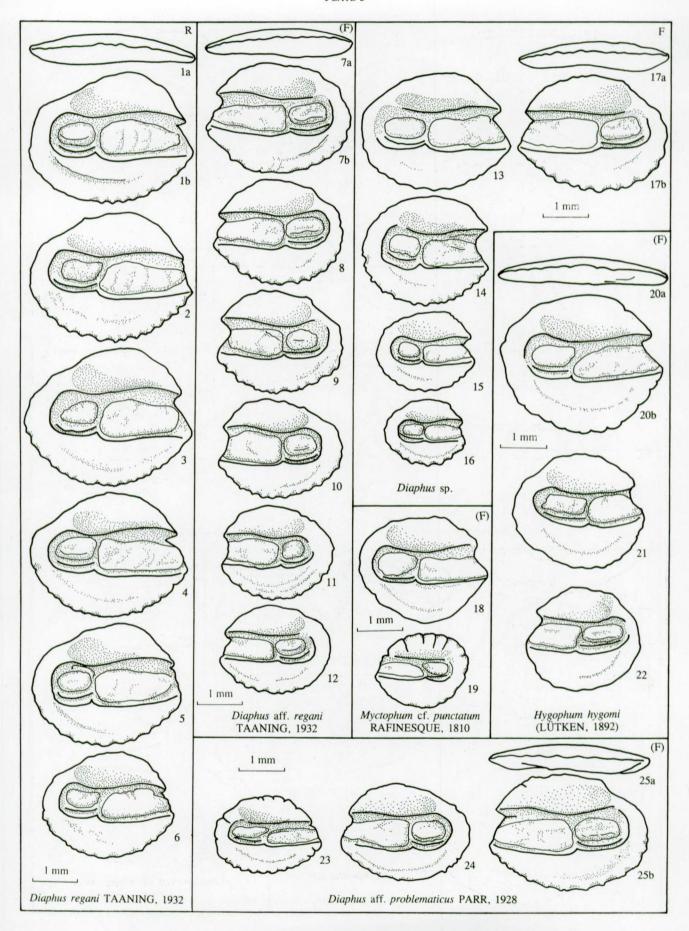


PLATE 6

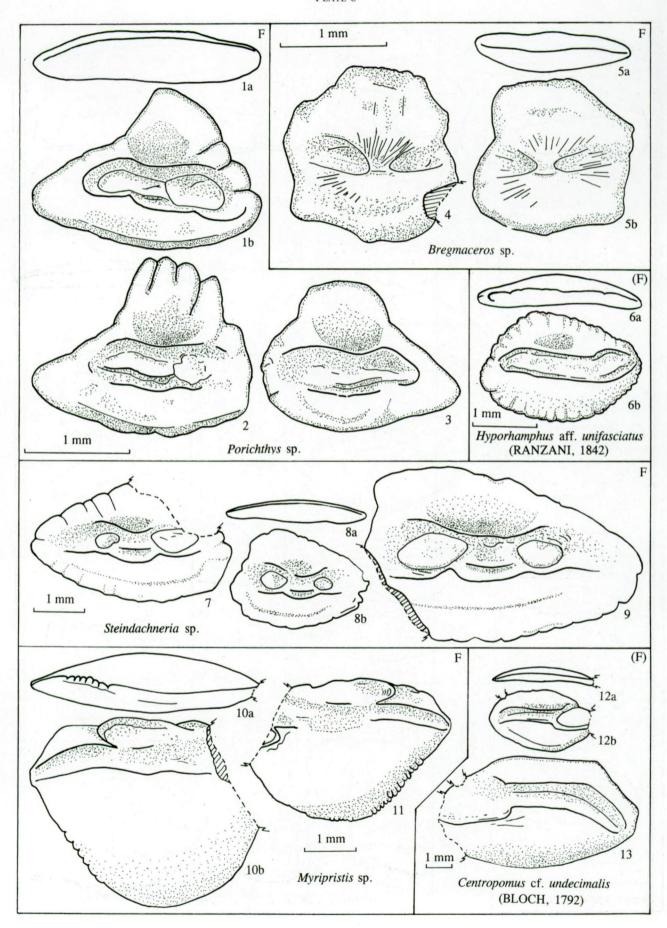


PLATE 7

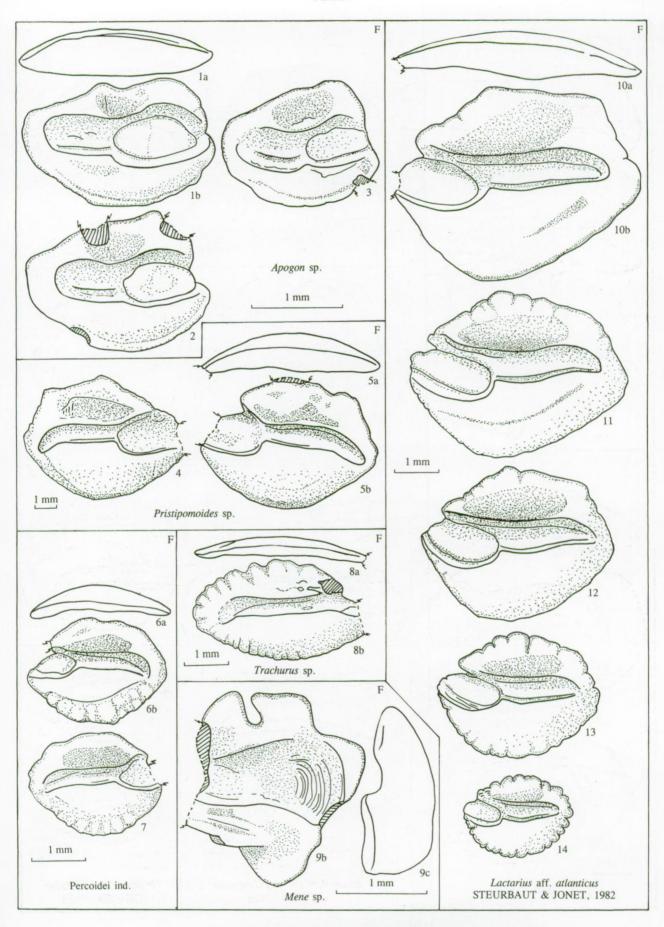


PLATE 8

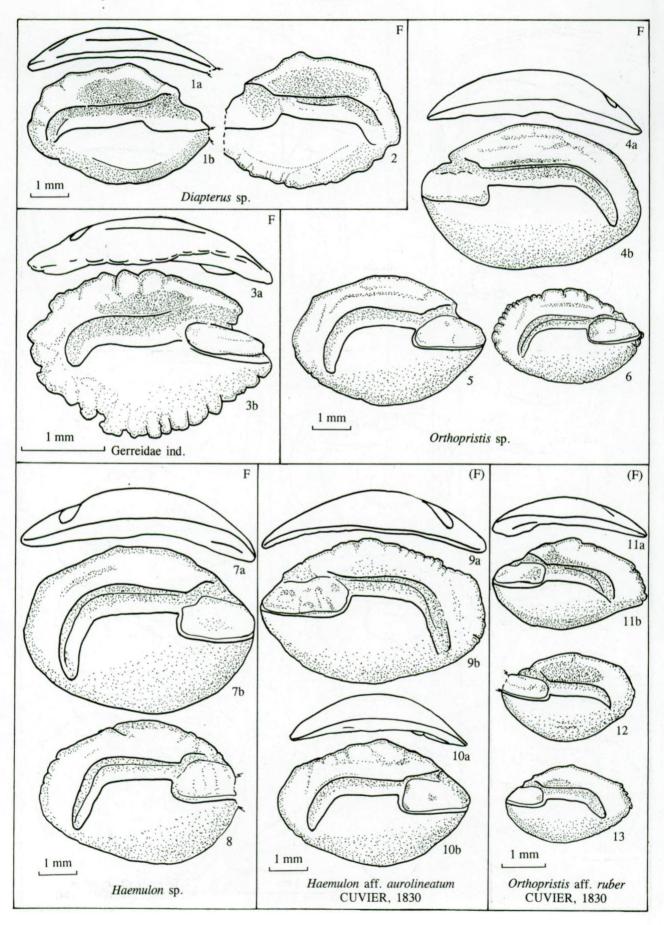


PLATE 9

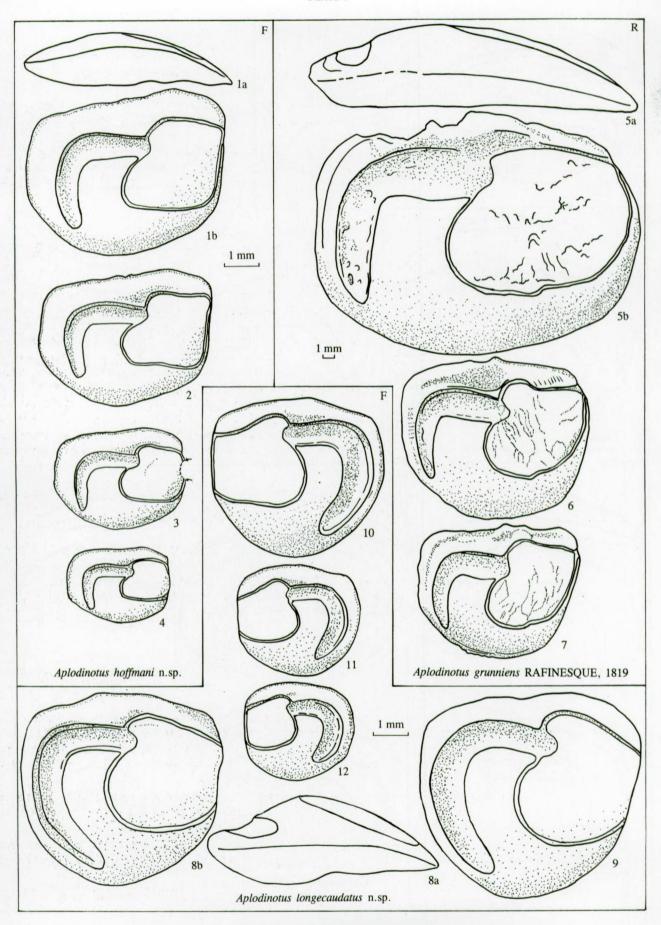


PLATE 10

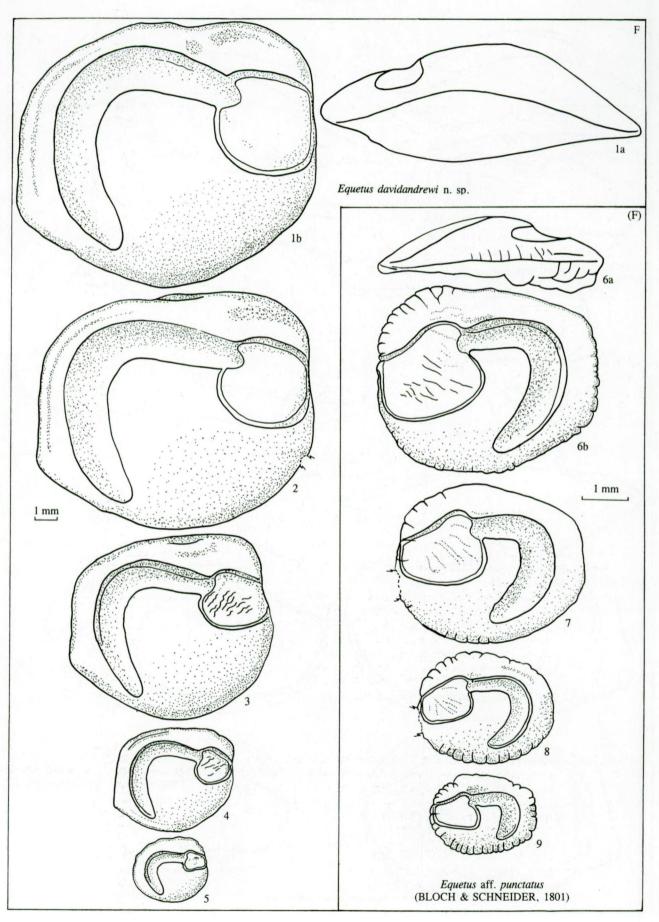


PLATE 11

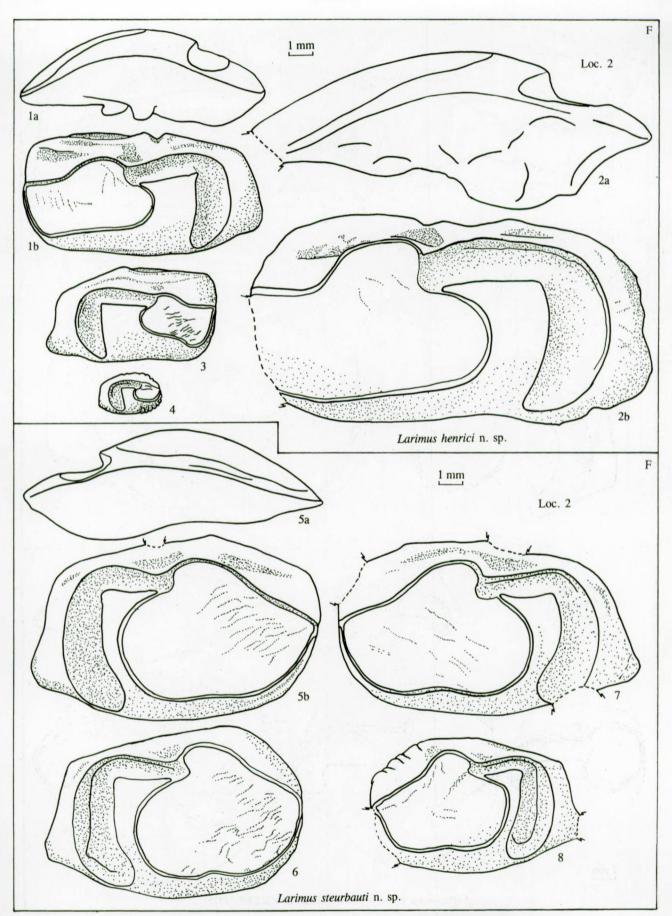


PLATE 12

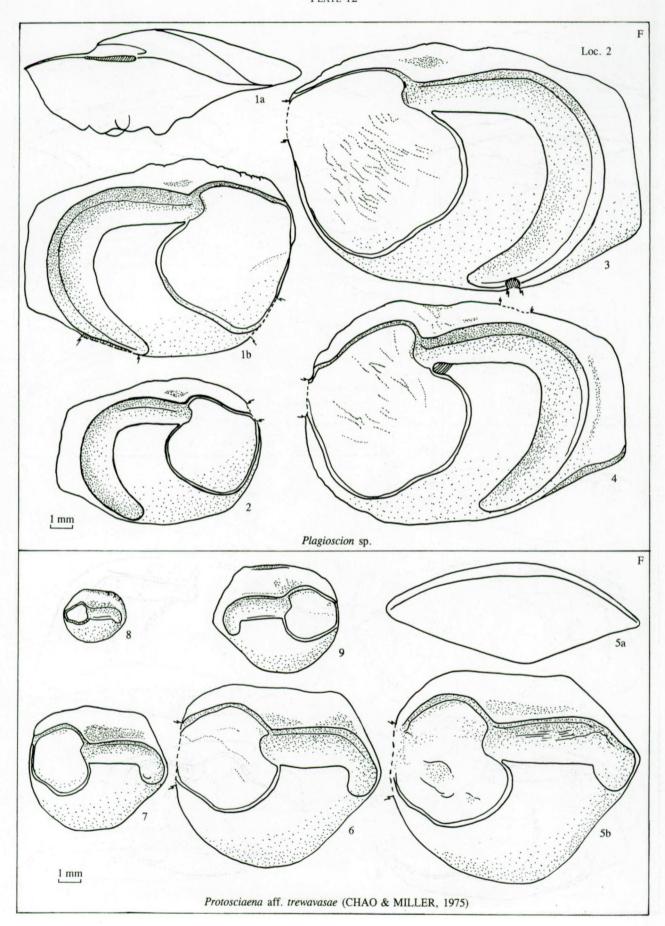


PLATE 13

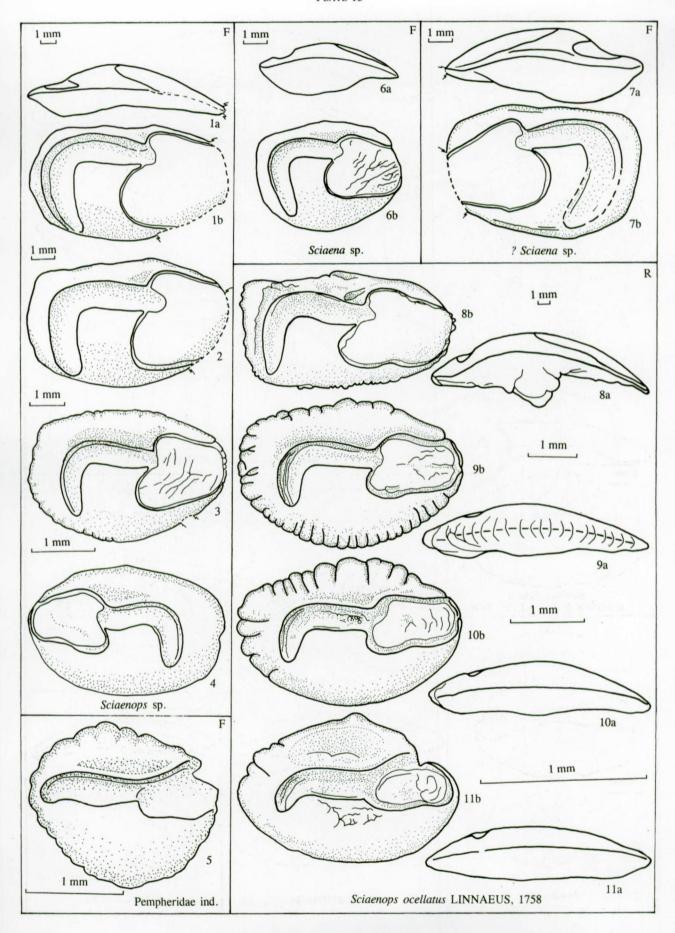


PLATE 14

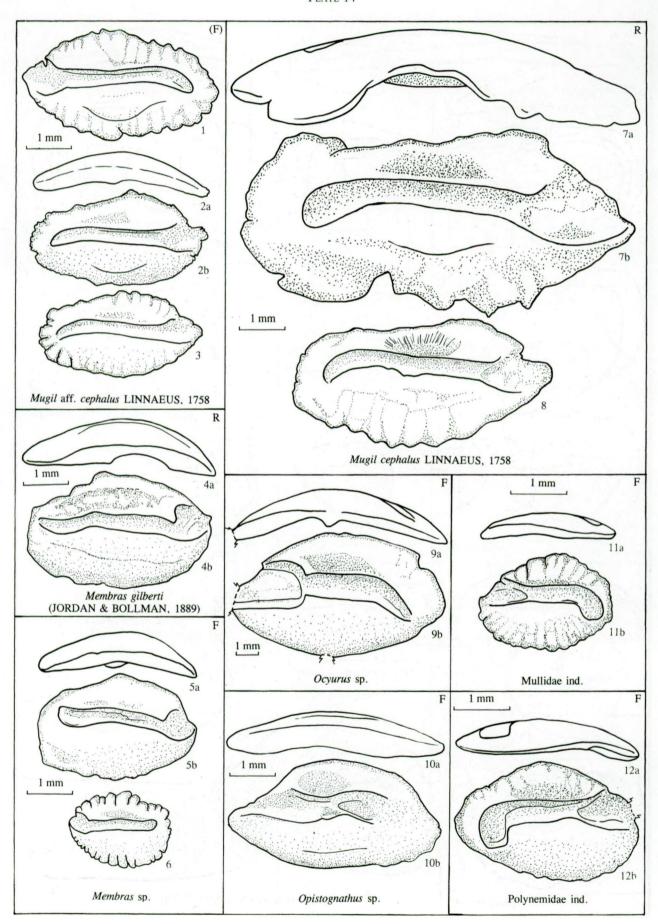


PLATE 15

