

# Marine Middle Eocene fish Otoliths from India and Java

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## Abstract

Otoliths collected from the Harudi Formation (Lutetian) of Kachchh, Western India and from the Nanggulan Formation (Early Bartonian) of Nanggulan, Java, revealed the presence of respectively 15 and 24 teleost taxa. Seven new species are introduced: "genus Brotularum" *siremboides*, *Apogon townsendoides*, "genus Apogonidarum" *altissimus*, *Lactarius nonfungus*, "genus Menidarum" *occultus*, "genus Percoideorum" *pseudotherina* and "genus Percoideorum" *sciaenoides*. Both associations reveal very shallow neritic environments. They are compared with a previously described neritic Middle Eocene otolith association from central Western Pakistan, and a combined list of all (43) taxa represented in the three associations is provided. Considering the restricted sampling, the number (8) of taxa occurring at more than one locality is remarkable, and one can probably conclude that we sampled several of the most common and widespread teleosts inhabiting the neritic environments of the Indo-West-Pacific region during the Middle Eocene. Biogeographic evaluation of the available data leads to the conclusion that in the Eocene, the Indo-West-Pacific region was already inhabited by many fish taxa not represented elsewhere, and that probably it contained the most diverse fish community of the world, as it does today.

**Key-words:** teleostean fishes, Middle Eocene, Indo-West-Pacific.

## Résumé

L'étude des otolithes provenant de la Formation de Harudi (Lutétien) de Kachchh, Inde et de la Formation de Nanggulan (Bartonian inférieur) de Nanggulan, Java a permis d'identifier respectivement 15 et 24 taxa de téléostéens. Parmi ceux-ci, sept constituent des espèces nouvelles: "genus Brotularum" *siremboides*, *Apogon townsendoides*, "genus Apogonidarum" *altissimus*, *Lactarius nonfungus*, "genus Menidarum" *occultus*, "genus Percoideorum" *pseudotherina* et "genus Percoideorum" *sciaenoides*. Ces deux associations témoignent d'environnements néritiques très peu profonds. Elles sont comparées à une association décrite de l'Eocène moyen du Centre du Pakistan occidental; La combinaison des données obtenues pour ces trois localités a fourni une liste de 43 taxa. Il est remarquable de trouver, dans un échantillonnage aussi restreint, 8 taxa représentés dans au moins deux gisements. Sans doute est-il permis de conclure que nos échantillons contiennent quelques-uns des poissons les plus communs et les plus largement répandus dans l'environnement néritique du domaine indo-ouest-pacifique à l'Eocène moyen. Une évaluation biogéographique des données obtenues révèle qu'à l'Eocène moyen, la région indo-ouest-pacifique était peuplée par de nombreux taxa de poissons n'existant nulle part ailleurs et hébergeait, déjà à cette époque comme de nos jours, la faune téléostéenne la plus diversifiée du monde.

**Mots-clés:** poissons téléostéens, Eocène moyen, région indo-ouest-pacifique.

## Introduction

The tropical Indo-West Pacific seas are known for yielding the most diverse present day marine fish fauna. This diversity strongly contrasts with the almost complete ignorance of fossil fishes from the same areas. For the otolith-based faunal reconstructions, the literature is restricted to twelve short papers only. Four are on Neogene fossils (FROST, 1925; VORSTMAN, 1927; STINTON, 1949 and 1962), four on fresh water material from the Deccan Trap associated sediments (PRASAD & KHAJURIA, 1990; SHING RANA, 1988, 1990; SHING RANA & SAHNI, 1989) and two on problematic Cenomanian microfossils (GOWDA, 1964 and 1967). This leaves us with only two papers that are relevant for the present study: NOLF (1991) on otoliths from the Kirthar Formation, Middle Eocene of Pakistan and SAHNI & SAXENA (1982) on material from the Middle Eocene from Kutch (now spelled as Kachchh), Western India.

The otoliths studied here come from the Harudi Formation, Middle Eocene of Kachchh, Western India and from the Middle Eocene of Java. Although the samples are very restricted in comparison with what has been collected in "classic otolith areas" like Aquitaine, the North Sea Basin or Southern England, they provide interesting new data, especially when combined with those already obtained from Pakistan (NOLF, 1991).

## Geographic and stratigraphic location of the studied material

### *Kachchh, Western India (Lutetian)*

A sample of about 40 kg of sediment has been taken from an exposure (23°31'30" N, 68°41'00" E) in the river Rato Nala, near a small bridge (no 241) of the Narayan Sarovar - Nalya road, about 3,5 km south of the village Baranda (Fig.1) in Western Kachchh. This section lies in the type area of the Harudi Formation, and the sediment consists of olive green shales, exposed at about 3.5 m above the basis of the Formation (Fig.2). The Harudi Formation is considered to belong to the

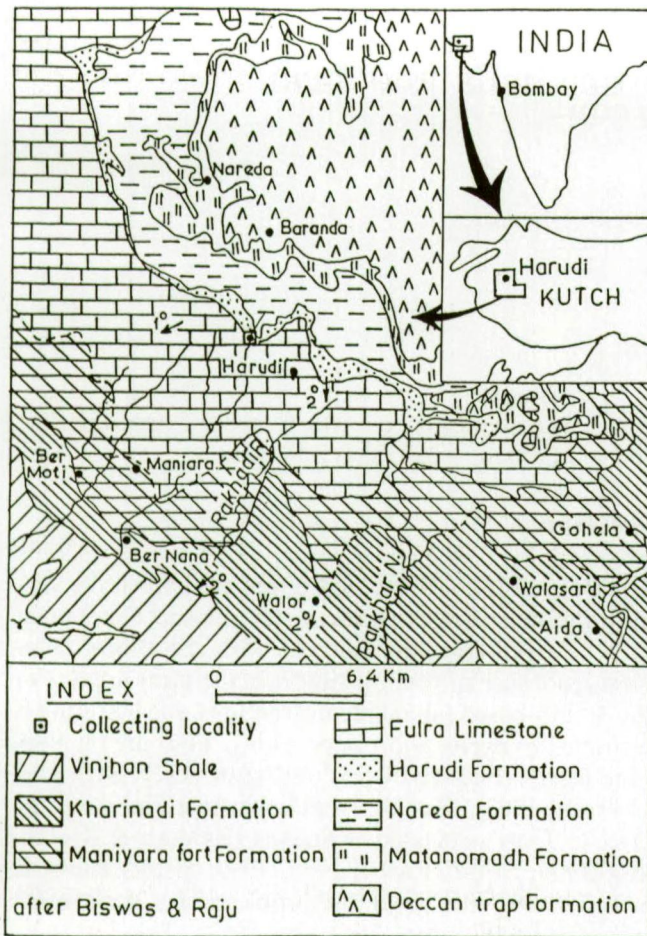


Fig. 1 — Geological map of the Harudi Formation type area, showing the collecting locality on the Rato Nala river.

lower part of the local Babia stage (Middle Eocene; BISWAS & DESHPANDE, 1970; BISWAS & RAJU, 1973).

The otolith horizon corresponds to the lower part of the *Corbula subexarata* Zone of TANDON (1976) and the *Neocyprideis bhupendri* Zone of KHOSLA & PANT (1981). Associated vertebrate fauna in the sampled area includes isolated teeth of pycnodontid fishes and selachians (*Galeocerdo*, *Lamna*, odontaspids, dasyatids). Invertebrates include molluscs, ostracods and smaller foraminifers, particularly miliolids and arenaceous forms.

The Harudi Formation has been attributed to the Lutetian on the basis of foraminiferal zonation as well as on the basis of its stratigraphic context. The formation overlies Ypresian sediments of the Nareda Formation (MOHAN & GUPTA, 1968; SINGH & SINGH, 1981; BISWAS, 1986) and is overlain by the Late Middle Eocene (Late Lutetian - Bartonian) Fulra Limestone. The otolith-yielding horizon lies probably in the *Hantkenina aragonensis* Zone (P10), recognized by MOHAN & SOODAN (1970). However, some workers (e.g. RAJU, 1974) have disputed the presence of this zone as well as the

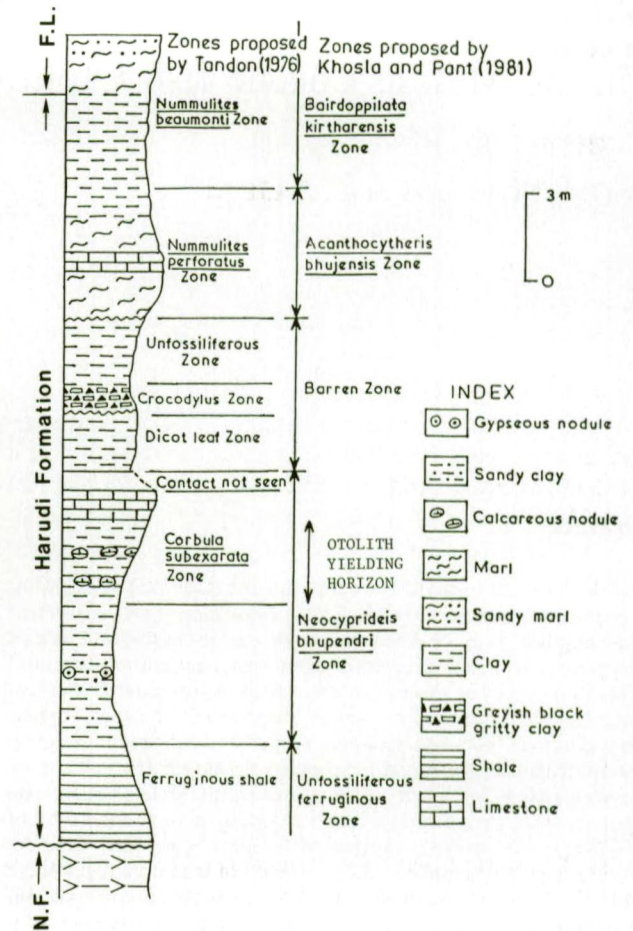


Fig. 2 — Stratigraphic section exposed at Harudi, with localisation of the otolith yielding horizon. The Harudi Formation is conformably overlain by the Fulra Limestone (F.L.) and rests disconformably on lateric clays of the Nareda Formation (N.F.).

overlying *Globigerina kugleri-Globigerina frontosa* Zone (P11) in the Kachchh Middle Eocene.

The overlying Fulra Limestone encompasses three planctonic foraminiferal zones (P12-P14), ranging in age from Late Lutetian to Late Bartonian (MOHAN & SOODAN, 1970; RAJU, 1974; MOHAN, 1982; JAUHARI, 1981). Thus, the otolith-yielding horizon is definitively of Lutetian age, perhaps situated in the *Hantkenina aragonensis* Zone (P10) but certainly below the *Morozoviella lehneri* Zone (P12)

A sample of the sediment from the otolith-bearing horizon has been investigated for nannoplankton by E. STEURBAUT, but proved to be barren. The overlying Fulra Limestone is known to include the NP16 and NP17 Zones (SINGH & SINGH, 1987); this further supports the Lutetian dating of the Harudi Formation.

A series of very eroded otoliths coming from approximately the same site as those studied here was published by SAHNI & SAXENA (1982). In the cases where the preservation of that material allows any evaluation, this will be recorded in our synonymies. Figure 19 and 20 of the plate accompanying the publication by SAHNI &

SAXENA (1982) is an unidentified calcareous body, not an otolith.

#### *Nanggulan, Java (Early Bartonian)*

Nine samples, each consisting of about 5 kg of sediment from the Nanggulan Formation were collected in 1976 by G. PICCOLI, in an area located at about 4 km NW from Nanggulan, Java. These samples were taken in scattered little river outcrops over a distance of about 1 km in an area with dense bamboo vegetation. Sample 1 would be located at about  $x = 3250$  m due N and  $y = 1400$  m due W from the center of Nanggulan, and the end of the sampled series (sample 9) at about  $x = 3750$  m due N and  $y = 2400$  m due W from the center of Nanggulan; no more precise topographic information is available. The precise geometric position of the samples in a stratigraphic section is also unknown, because the outcrops are isolated from each other and the strata are affected by faults.

Notwithstanding these imprecisions, it is apparent that the samples must be stratigraphically very near to each other because of their very similar content of mollusc, otolith and nannoplankton associations.

Although the well preserved mollusc faunas from Nanggulan are known since MARTIN (1914), the Nanggulan Formation was only named formally by PURNAMANINGSIH & HARSONO in 1981. They assigned an age ranging from Middle Eocene to Upper Oligocene to the sequence, on the basis of planctonic foraminifers (P10 to P21 Zones of the BLOW zonation); see also table in ZACHELLO (1984, fig.2).

All our samples consist of fine clayey glauconitic sand with numerous molluscs. They were investigated for nannoplankton by E. STEURBAUT, who concluded they are of Early Bartonian age, on the following basis. The association is characterized by the presence of *Pemma papillatum* MARTINI, 1959; the first appearance of this species occurs within Zone NP16. The presence of *Reticulofenestra reticulata* GARTNER & SMITH, 1967 in sample 8 (first appearance in the upper part of Zone NP16), of *Discoaster saipanensis* BRAMLETTE & RIEDEL, 1954 (first appearance occurs in Zone NP16, in low latitudes), of *Sphenolithus* cf. *furcatolithoides* LOCKER, 1967 (disappearance at the top of Zone NP16) and the absence of *Helicosphaera compacta* BRAMLETTE & WILCOXON, 1967 (first appearance in Zone NP17) are indicative for the upper part of Zone NP16, which is of Early Bartonian age.

#### Systematics

Because both otolith associations show much similarity, they will be described together, but a separate check list for each association is provided (Table 1) to make the given information more accessible.

The classification followed is the one proposed by

NOLF (1985) in "Handbook of Paleoichthyology", vol. 10. The reader is also referred to that paper for general information and the morphological nomenclature of otoliths.

Order ANGUILLIFORMES REGAN, 1909

Family CONGRIDAE KAUP, 1856

"genus *Congridarum*" aff. *diagonalis*

(STINTON & NOLF, 1970)

(Pl. 1, Fig. 2; Pl. 3, Fig. 3)

#### Material

One otolith from the Harudi Formation at Baranda, Western India and six otoliths from the Nanggulan Formation at Nanggulan, Java.

#### Remarks

This species was already mentioned from the Middle Eocene of Central Western Pakistan (NOLF, 1991). It is the only otolith-based species presently known from both the Atlantic (Anglo-Paris-Belgian Basin and Aquitaine, SW France) and from the Indo-West Pacific realm.

"genus *Congridarum*" sp. 1

(Pl. 1, Fig. 1)

#### Material

One otolith from the Harudi Formation at Baranda, Western India.

#### Remarks

A single but well preserved otolith, which is different from those of all known congrid species. More material is required to describe the species and to decide its generic affinities.

"genus *Congridarum*" sp. 2

(Pl. 3, Figs. 1-2)

#### Material

Four otoliths from the Nanggulan Formation at Nanggulan, Java.

#### Remarks

Juvenile specimens, unsuitable for an accurate specific or generic identification.

Order CLUPEIFORMES BLEEKER, 1859

Family ENGRAULIDAE GILL, 1861

*Engraulidae* ind.

(Pl. 3, Figs. 4-5)

#### Material

17 otoliths from the Nanggulan Formation at Nanggulan, Java.

#### Remarks

There is a chance that two species of engraulids are re-

HARUDI FORMATION, KACHCHH, WESTERN INDIA (LUTETIAN)			
Family	Species	Iconography	Number of specimens
CONGRIDAE	"genus Congridarum" aff. <i>diagonalis</i> (STINTON & NOLF, 1970)	Pl.1, Fig.2	1
	"genus Congridarum" sp.1	Pl.1, Fig.1	1
ARIIDAE	Ariidae ind.	Pl.1, Fig.3	1
OPHIDIIDAE	"genus Brotularum" <i>siremboides</i> n. sp.	Pl.1, Fig.7	4
SCORPAENOIDEI inc. sed.	"genus Scorpaenoideorum" sp.	Pl.1, Figs.10-11	6
APOGONIDAE	<i>Apogon</i> sp.4	Pl.1, Fig.9	4
	"genus Apogonidarum" <i>robertwesti</i> NOLF, 1991	Pl.1, Figs.4-6	19
SILAGINIDAE	"genus ? Silaginidarum" sp.	Pl.2, Fig.5	1
MENIDAE	"genus Menidarum" <i>occutus</i> n. sp.	Pl.2, Fig.1-2	2
SCIAENIDAE	"genus Sciaenidarum" sp.	Pl.2, Fig.4	3
PERCOIDEI inc. sed.	"genus Percoideorum" sp.1	Pl.1, Fig.8	13
	Percoidei ind.	Pl.2, Fig.3	4
MUGILIDAE	Mugilidae ind.	Pl.2, Fig.6	1
URANOSCOPIDAE	"genus Uranoscopidarum" sp.	Pl.2, Fig.7	1
GOBIIDAE	Gobiidae sp.1	Pl.2, Fig.8	1
NANGGULAN FORMATION, NANGGULAN, JAVA (EARLY BARTONIAN)			
Family	Species	Iconography	Number of specimens
CONGRIDAE	"genus Congridarum" aff. <i>diagonalis</i> (STINTON & NOLF, 1970)	Pl.3, Fig.3	6
	"genus Congridarum" sp.2	Pl.3, Figs.1-2	4
ENGRAULIDAE	Engraulidae ind.	Pl.3, Figs.4-5	17
SYNODONTIDAE	<i>Saurida</i> sp.	Pl.3, Fig.8	2
CARAPIDAE	Carapidae ind.	Pl.3, Fig.9	1
OPHIDIIDAE	"genus Brotularum" <i>siremboides</i> n.sp.	Pl.3, Figs.6-7	5
	"genus aff. <i>Glyptophidium</i> " <i>pseudobiarritzense</i> NOLF, 1991	Pl.3, Fig.11	6
BYTHITIDAE	Dinematichthyini ind.	Pl.3, Fig.12	2
BREGMACEROTIDAE	<i>Bregmaceros</i> sp.	Pl.3, Fig.13	5
PRIACANTHIDAE	<i>Pristigenys</i> sp.	Pl.4, Fig.8-9	2
APOGONIDAE	<i>Apogon townsendoides</i> n. sp.	Pl.5, Fig.3-5	49
	<i>Apogon</i> sp.5	Pl.5, Fig.8	46
	"genus Apogonidarum" <i>altissimus</i> n.sp.	Pl.5, Fig.9-10	22
LACTARIIDAE	<i>Lactarius nonfungus</i> n.sp.	Pl.5, Fig.6-7	5
MENIDAE	"genus Menidarum" <i>occutus</i> n. sp.	Pl.4, Fig.7	2
GERREIDAE	Gerreidae ind.	Pl.6, Fig.10	1
? SPARIDAE	? Sparidae ind.	Pl.4, Fig.5	2
PERCOIDEI inc. sed.	"genus Percoideorum" <i>pseudotherina</i> n. sp.	Pl.4, Fig.3-4	2
	"genus Percoideorum" <i>sciaenoides</i> n. sp.	Pl.4, Fig.1-2	7
	"genus Percoideorum" sp.2	Pl.4, Fig.6	1
URANOSCOPIDAE	Uranoscopidae ind.	Pl.6, Fig.1-2	3
GOBIIDAE	Gobiidae sp. 2	Pl.6, Fig.4-5	2
BOTHIDAE	"genus Bothidarum" sp.	Pl.6, Fig.6-8	4
CYNOGLOSSIDAE	? <i>Symphurus</i> sp.	Pl.6, Fig.9	1

Table 1 — Fish species (otoliths) represented in the Lutetian Harudi Formation, Western India, and in the Early Bartonian part of the Nanggulan Formation, Java.

presented in our material. One seems to be characterized by thick otoliths with a high posterior end and a smooth ventral rim (Pl. 3, Fig. 4) and the other by thinner, more elliptical otoliths, bearing spines on the ventral rim (Pl. 3, Fig. 5). Formal distinction of two taxa, however, has not been attempted because most of the available otoliths are too small or too eroded for a precise morphological analysis. It is also difficult to judge to what extent the presence or absence of spines on the ventral rim is an effect of abrasion.

Order SILURIFORMES CUVIER, 1817

Family ARIIDAE GUENTHER, 1864

**Ariidae ind.**

(Pl. 1, Fig. 3)

*Material*

One utricular otolith from the Harudi Formation at Baranda, Western India.

*Remarks*

This small sized (length = 4,0 mm), slightly eroded oto-

lith probably represents a new species, characterized by a very flat inner face and a well incised groove on the anterior part of its outer face. The available material is unsuitable for further formal description.

Order AULOPIFORMES ROSEN, 1973

Family SYNODONTIDAE GILL, 1872

*Saurida* sp.

(Pl. 3, Fig. 8)

*Material*

Two otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

Juvenile otoliths, not diagnostic at the species level.

Order OPHIDIIFORMES BERG, 1937

Family CARAPIDAE JORDAN & FOWLER, 1902

*Carapidae* ind.

(Pl. 3, Fig. 9)

*Material*

One otolith from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

A juvenile otolith, unsuitable for an accurate specific or generic identification.

Family OPHIDIIDAE RAFINESQUE, 1810

Subfamily BROTLINAE SWAINSON, 1838

"genus *Brotularum*" *siremboides* n.sp.

(Pl. 1, Fig. 7; Pl. 3, Figs. 6-7)

*Type material*

Holotype: a right otolith (Pl. 3, Fig. 7) (IRSNB P 5939) from the Nanggulan Formation, Nanggulan, Java; four paratypes from the same locality; one figured on Pl. 3, Fig. 6 (IRSNB P 5938); four paratypes from the Harudi Formation at Baranda, Western India; one figured on Pl. 1, Fig. 7 (IRSNB P 5921).

*Dimensions of the holotype*

Length: 3,7 mm; height: 2,2 mm; thickness: 1,6 mm.

*Stratum typicum*

Top of Nannoplankton Zone NP16 in the Nanggulan Formation at Nanggulan, Java.

*Derivatio nominis*

*Siremboides* = *Sirembo*-like; alludes to a resemblance with otoliths of the genus *Sirembo* BLEEKER, 1885.

*Diagnosis*

This species is characterized by very thick, elongate lemon-shaped otoliths. The outer face is nearly smooth, showing only some rudiments of atrophied tubercles. This face is very convex in the dorso-ventral direction.

In the antero-posterior direction the convexity is situated mainly in the anterior portion.

The inner face is very convex, in both antero-posterior and dorso-ventral direction. The sulcus is broad, very superficial, and lies essentially in the dorsal portion of the otolith. The ostium and cauda are nearly of equal length. In transverse section through the ostial part, the crista inferior shows an angular profile, as in the genus *Brotula* CUVIER, 1829. The colliculum is very flat and regular; only in the ventral part a rudimentary division into ostial and caudal portions can be observed near the ostial-caudal junction of the crista inferior. The sulcus surface shows a general distortion from an antero-dorsal to postero-ventral orientation.

*Discussion*

The otoliths of the species described here exhibit a morphology that is intermediate between the one observed in the genera *Sirembo* BLEEKER, 1858 (see NOLF, 1980, pl. 6, fig. 8-12; 16; 17) and *Brotula* (see NOLF, 1980, pl. 2, fig. 1-5). The extremely elongate otoliths with aculeate anterior and posterior end and extreme dorso-ventral convexity of the inner face, seen in *Brotula*, must be considered as apomorphic with regard to the more generalized ones of *Sirembo*. As relationships have to be evaluated on apomorphic features, our fossil has to be grouped within the family Brotulinae and not with the neobythitine genus *Sirembo*.

Recent *Brotula* species essentially differ from our fossils by their cauda, which is about twice as long as the ostium. The greatest similarity with "genus *Brotularum*" *siremboides* is seen in otoliths of the Recent Indo-Pacific species *Brotula multibarata* (TEMMINCK & SCHLEGEL, 1846) (see NOLF, 1980, pl. 2, fig. 4-5) the sulcus of which also lies nearly entirely in the upper portion of the inner face.

Subfamily NEOBYTHITINAE RADCLIFFE, 1913

"genus aff. *Glyptophidium*" *pseudobiarritzense*

NOLF, 1991

(Pl. 3, Fig. 11)

*Material*

Six otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

This species is also represented in the Khirthar Formation (Middle Eocene) of Central Western Pakistan (NOLF, 1991).

Family BYTHITIDAE GILL, 1861

Subfamily BROSMOPHYCINAE GILL, 1862

Tribe DINEMATICHTHYINI WHITLEY, 1928

*Dinematichthyini* ind.

(Pl. 3, Fig. 12)

*Material*

Two otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

Juvenile and imperfectly preserved otoliths belonging to the bythitid tribe Dinematchthyini. NOLF (1980, p. 93) already pointed out that bythitid otoliths have poor diagnostic value, which excludes any further identification on the basis of the material available.

Order GADIFORMES GOODRICH, 1909  
Family BREGMACEROTIDAE GILL, 1872  
*Bregmaceros* sp.  
(Pl. 3, Fig. 13)

*Material*

Five otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

A much more abundant material is required for an adequate appraisal of the variability and specific features of this species.

Order SCORPAENIFORMES GARMAN, 1899  
Suborder SCORPAENOIDEI  
"genus *Scorpaenoideorum*" sp.  
(Pl. 1, Figs. 10-11)

*Material*

Six otoliths from the Harudi Formation, 3,5 km south of Baranda, Western India.

*Remarks*

Small otoliths, representing probably a new species. Only the two specimens figured are well preserved; more material is required to evaluate the features of the species and to define its taxonomic affinities.

Order PERCIFORMES BLEEKER, 1859  
Suborder PERCOIDEI BLEEKER, 1859  
Family PRIACANTHIDAE GILL, 1872  
*Pristigenys* sp.  
(Pl. 4, Figs. 8-9)

*Material*

Two otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

Juvenile otoliths, not diagnostic at species level.

Family APOGONIDAE JORDAN & GILBERT, 1882  
*Apogon townsendoides* n. sp.  
(Pl. 5, Figs. 3-5)

*Type material*

Holotype: a right otolith (Pl. 5, Fig. 5) (IRSNB P 5957);

48 paratypes of which two are figured (Pl. 5, Figs. 3-4) (IRSNB P 5955, P 5956).

*Dimensions of the holotype*

Length: 1,8 mm; height: 1,4 mm; thickness: 0,5 mm.

*Stratum typicum*

Top of nannoplancton Zone NP16 in the Nanggulan Formation at Nanggulan, Java.

*Derivatio nominis*

Alludes to a morphological resemblance with the Recent Caribbean species *Apogon townsendi* (BREDER, 1927).

*Diagnosis*

This species is characterized by thick, robust otoliths with a strong dorsal expansion of the anterior portion of the dorsal area.

The outer face is nearly smooth, markedly convex in all directions, but the strongest convexity is located in the dorso-ventral direction. The inner face is slightly convex. The sulcus is divided into an ostial and caudal portion of about equal length. The ostium shows a marked dorsal widening in its posterior part, which is accentuated by a similar widening in the posterior part of the ostial colliculum. In the outline of several specimens, including the holotype, a little antirostrum is observed. Near to the caudal crista inferior, a strong collicular crest exists but this is a generalized feature observed in all apogonids.

*Discussion*

Problems in the identification of fossil *Apogon* otoliths were already discussed by NOLF (1985, p. 82), and it is evident that in several species lacking autapomorphic features, species are hard to distinguish on the basis of their otoliths. In the present case however, the otoliths are very well characterized by their considerable thickness, and especially by the strong dorsal widening of the posterior part of the ostium and associated colliculum. With the species name *townsendoides*, we allude to a superficial resemblance with otoliths of the recent Caribbean *A. townsendi* (Pl. 5, Fig. 1-2), but not to a close affinity. Comparison of the posterior part of the ostial colliculum shows a major difference between the two species.

*Apogon* sp. 4  
(Pl. 1, Fig. 9)

*Material*

Four otoliths from the Harudi Formation at Baranda, Western India.

*Remarks*

Only represented by eroded specimens, too worn for identification at species level.

*Apogon* sp. 5  
(Pl. 5, Fig. 8)

*Material*

46 otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

A sample of mainly juvenile otoliths with a very regular elliptical outline; not diagnostic to species.

“genus *Apogonidarum*” *altissimus* n. sp.  
(Pl. 5, Figs. 9-10)

*Type material*

Holotype: a left otolith (Pl. 5, Fig. 9) (IRSNB P 5961); 21 paratypes of which one is figured (Pl. 5, Fig. 10) (IRSNB P 5962).

*Dimensions of the holotype*

Length (incomplete): 1,5 mm; height: 1,9 mm; thickness: 0,5 mm.

*Stratum typicum*

Top of nannoplankton zone NP16 in the Nanggulan Formation at Nanggulan, Java.

*Derivatio nominis*

*Altissimus*, a, um: very high; alludes to the outline of the otoliths, which are markedly higher than long.

*Diagnosis*

This species is characterized by otoliths that are higher than long; the ventral rim is regularly rounded, and there is a well marked posterodorsal angle, a salient rostrum, and a very small antirostrum. The outer face is entirely smooth, and convex in all directions. The inner face is nearly flat. The sulcus consists of a wide ostium with a regular colliculum that is somewhat hollow in its central part and a cauda whose posterior end is very slightly expanded in dorsal direction.

Near to the crista inferior a strong collicular crest can be seen. The crista superior is marked by a shallow depression in the dorsal area.

*Discussion*

The closest affinities of “genus *Apogonidarum*” *altissimus* lies with “genus *Apogonidarum*” *robertwesti* NOLF, 1991 (Pl. 1, Figs. 4-6) and “genus *Apogonidarum*” *orbis* NOLF, 1991. This group of species, which we tentatively include in the Apogonidae is known only from the Eocene Indo-West Pacific realm.

“genus *Apogonidarum*” *robertwesti* NOLF, 1991  
(Pl. 1, Figs. 4-6)

1982 *Pagellus* sp. A - SAHNI & SAXENA, p. 65, pl., figs. 21 & 22, ? fig. 9, 10, 13-18, 25, 26, 33, 34;

1982 *Pagellus concavus* FROST - SAHNI & SAXENA, p. 65, figs. 29 & 30.

*Remarks*

The specimen of Pl. I, Fig. 4, with its very expanded postero-dorsal angle probably represents an extreme in the variability of the species; all other specimens are similar to the type material from Pakistan described by NOLF (1991).

Family SILLAGINIDAE RICHARDSON, 1846  
“genus? *Sillaginidarum*” sp.  
(Pl. 2, Fig. 5)

*Remarks*

A single eroded, large sized (length = 8,2 mm) otolith with a morphology suggesting possible affinities with the Sillaginidae, but without close relationship to any of the Recent genera in the family.

Family LACTARIIDAE JORDAN, 1923  
*Lactarius nonfungus* n.sp.  
(Pl. 5, Figs. 6-7)

*Type material*

Holotype: a left otolith (Pl. 1, Fig. 6) (IRSNB P 5958). Four paratypes of which one is figured (Pl. 1, Fig. 7) (IRSNB P 5959).

*Dimensions of the holotype*

Length: 2,5 mm; height: 1,8 mm; thickness: 0,4 mm.

*Stratum typicum*

Top of nannoplankton Zone NP16 in the Nanggulan Formation at Nanggulan, Java.

*Derivatio nominis*

*Nonfungus* = not a mushroom; alludes to the generic name *Lactarius* used both for mushrooms and for fishes.

*Diagnosis*

Otoliths of this species have a general circular, slight elongate outline, with a very blunt rostral part and a postero-dorsal angle. They are relatively thin and their outer face is nearly flat and smooth, showing only some incompletely developed tuberculation near the dorsal rim. The inner face is slightly convex in all directions. The ostial and caudal portions of the sulcus are nearly equal in length, but the ostium is about twice as wide as the cauda.

Both ostium and cauda are relatively shallow, their strongest incision being situated just below the crista inferior. The ostium is entirely filled up with colliculum. The cauda narrows towards its posterior end and bears a collicular crest just above the crista inferior. The crista superior is slightly salient.

*Discussion*

The genus *Lactarius* is represented by only one Recent species, *L. lactarius* (SCHNEIDER, 1801), living in coastal waters of South Asia (see NOLF, 1985, fig. 63D for the iconography of the otoliths) and four fossil species (see NOLF, 1985, p. 84). Otoliths of *L. nonfungus* are easily distinguished from those of all other species by their very blunt, rounded rostral part.

Family MENIDAE GILL, 1885

**"genus Menidarum" *occultus* n.sp.**

(Pl. 2, Figs. 1-2; Pl. 4, Fig. 7)

*Type material*

Holotype: a right otolith (Pl. 2, Fig. 2) (P 5927), from the Harudi Formation at Baranda, Western India. One paratype (Pl. 2, Fig. 1) (P 5926) from the same locality and two paratypes of which one figured (Pl. 4, Fig. 7) (P 5952) from the Nanggulan Formation at Nanggulan, Java.

*Dimensions of the holotype*

Length: 1,0 mm; height: 1,0 mm; thickness: 0,4 mm.

*Stratum typicum*

Harudi Formation (Lutetian) at Baranda, Western India.

*Derivatio nominis*

*Occultus*, a, um: hidden, secret; alludes to the fact that at a first glance, relationships of this otoliths with the genus *Mene* are not evident.

*Diagnosis*

This species has otoliths having an equal length and height, and characterized by a very strong antirostrum that is more salient than the rostrum. This means that, neglecting the ventrally bent caudal end, these otoliths look as if they were figured upside down. The outer face is smooth, nearly flat in dorso-ventral direction, but concave in the antero-posterior direction. This concavity is essentially caused by a strong outward orientation of the entire rostrum. The inner face is strongly convex in the antero-posterior direction. The sulcus is well incised; the cauda is about twice as long as the ostium. There is a marked depression just above the crista superior, and a shallower one in the central portion of the ventral area.

*Discussion*

Recent menids are restricted to one genus with one species, *Mene maculata* (BLOCH, 1801), living in coastal waters of Southern Asia, Hawaii and Japan. Otoliths of this species (see NOLF, 1985, p. 85, fig. 64A) are readily distinguished from "genus Menidarum" *occultus* by their much longer ostium, but a strong outward orientation of the ostial part is characteristic to both.

There are two skeleton-based fossil species of *Mene*: *M. rhombea* VOLTA 1796 and *M. oblonga* AGASSIZ, 1934 from the Lutetian of Monte Bolca, N. Italy and at least five fossil menids are known by otoliths.

— *Mene sekharani* NOLF & CAPPETTA, 1976 (= *M. simplex* STINTON, 1980) from the Lutetian of the Paris Basin and Southern England.

— "genus Menidarum" *occultus* n. sp.

— "genus Menidarum" *ornatissimus* (NOLF, 1985) from the Ypresian of Aquitaine, SW France. This species was erroneously described as cyprinodontid and is presently interpreted as a menid with a reduced ostium.

— An undescribed menid species from the Yazoo Clay, Priabonian of Louisiana, U.S.A. (NOLF & STRINGER, unpublished data).

— An undescribed menid species from the Marls of Pamplona, Early Bartonian, Northern Spain (NOLF, unpublished data). This species shows the most close affinity with *M. occultus*, but has a less convex inner face.

Family GERREIDAE BLEEKER, 1859

**Gerreidae ind.**

(Pl. 6, Fig. 10)

*Material*

One otolith from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

A worn eroded single otolith; see NOLF (in press, fig. 8 E-H) for the iconography of comparative Recent gerreid otoliths.

Family SPARIDAE BONAPARTE, 1832

**? Sparidae ind.**

(Pl. 4, Fig. 5)

*Material*

Two otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

Juvenile, eroded percoid otoliths, most probably belonging to sparids.

Family SCIAENIDAE CUVIER, 1829

**"genus Sciaenidarum" sp.**

(Pl. 2, Fig. 4)

*Material*

Three otoliths from the Harudi Formation at Baranda, Western India.



*Remarks*

The available material is too worn and too small for identification at the specific or generic level. The taxon seems to be characterized by a very narrow ostium, which is a plesiomorphic feature in sciaenids.

Family incertae sedis

“genus *Percoideorum*” *pseudatherina* n.sp.  
(Pl. 4, Figs. 3-4)

*Type material*

Holotype: a left otolith (Pl. 4, Fig. 3) (IRSNB P 5948); one paratype (Pl. 4, Fig. 4) (IRSNB P 5949).

*Dimensions of the holotype*

Length: 1,2 mm; height: 1,2 mm; thickness: 0,4 mm.

*Stratum typicum*

Top of nannoplancton Zone NP16 in the Nanggulan Formation at Nanggulan, Java.

*Derivatio nominis*

Alludes to the superficial resemblance with the otoliths of atherinid fishes, but without suggesting any relationship to this taxon.

*Diagnosis*

This species is characterized by otoliths of general circular form, with a well marked rostrum, a small antirostrum, and a sulcus essentially located in the upper half of the otolith. The outer face is smooth in the centrum, but marginally, the lobes of the rims are separated by small radial grooves. The inner face is convex, especially in the antero-posterior direction. The sulcus is well incised, and consists of a short but ventrally widely expanded ostium and a long narrow cauda, the posterior end of which is bent in ventral direction. There are no clear collicular formations. The caudal crista inferior lies about straight in the central line of the otolith. The transition of the ostial and caudal crista superior is very straight, without an angle. The crista superior is salient, this feature is accentuated by a depression in the dorsal area just above the crista.

*Remarks*

These otoliths show essentially generalized percoid features, and for this reason, look superficially like those of some percoid families where combination of rather plesiomorph features and a round shape also exists in the otoliths e.g. ambassids, some gerreids, and some sparids. Such features, however, are not useful for estimation of relationships. The fossils probably belong to an extinct percoid family, characterized by autapomorphic features such as the straight ostial-caudal transition in the crista superior, the very short ostium, and the very dorsal position of the sulcus.

“genus *Percoideorum*” *sciaenoides* n.sp.  
(Pl. 4, Figs. 1-2)

*Type material*

Holotype: a right otolith (Pl. 4, Fig. 2) (IRSNB P 5947); 6 paratypes of which one is figured (Pl. 4, Fig. 1) (IRSNB P 5946).

*Dimensions of the holotype*

Length: 2,3 mm; height: 1,9 mm; thickness: 1,0 mm.

*Stratum typicum*

Top of nannoplancton Zone NP16 in the Nanggulan Formation at Nanggulan, Java.

*Derivatio nominis*

Alludes to the superficial resemblance to the otoliths of sciaenid fishes.

*Diagnosis*

Otoliths of this species are very massive and thick, with strongly convex inner and outer faces. In a transverse section, the dorsal rim is blunt while the ventral rim is sharp, especially in its anterior portion. The outer face is smooth. The inner face is very regularly convex and the sulcus shows very few incisions. The ostium shows a wide ventral expansion as in sciaenids but opens widely on the anterior rim; in sciaenids it opens only on a very narrow part of this rim. The cauda lies close to the dorsal rim and is entirely straight. There is no angle at the junction of the ostial and caudal crista superior. Just above the caudal crista inferior, a collicular crest occurs. Below the posterior end of the cauda, a furrow-like, ventrally oriented depression occurs. This furrow is not a part of the sulcus but at a glance one might consider it as a ventral inflation of the posterior sulcus end, suggesting a fallacious similarity with a sciaenid cauda.

*Discussion*

From the diagnosis, it appears that these otoliths show many misleading similarities with sciaenid otoliths. It is almost certain that the animals produced noise; also, the swimbladder would have been connected with the inner ear. This taxon can be considered as a sister family of sciaenids, but we rather tend to consider it as a case of convergence, especially when considering the caudal collicular crest that never is built up clearly in sciaenids, and the postcaudal ventrally oriented furrow that seems not homologous with the ventrally inflated caudal end in sciaenids; see TREWAVAS (1977), CHAO (1978) and SASAKI (1989) for the iconography of Recent sciaenid otoliths.

“genus *Percoideorum*” sp. 1  
(Pl. 1, Fig. 8)

*Material*

13 otoliths, coming from the Harudi Formation, 3,5 km S of Baranda, Western India.

*Remarks*

Only eroded or very juvenile otoliths are available. The ostium shows a strong ventral expansion. The narrow cauda has a very straight crista inferior with a collicular crest just above, and a regularly bent crista superior, which makes the central portion of the cauda markedly wider than its anterior and posterior ends.

The material certainly represents a new species, but the quality does not allow formal naming. These otoliths do not show clear affinities with those of any Recent percoid taxon and probably belong to an extinct family.

**“genus Percoideorum”** sp. 2  
(Pl. 4, Fig. 6)

*Material*

One otolith from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

Although this taxon is only represented by a single eroded otolith, its occurrence in our material is remarkable, because it belongs to an extinct family represented by perfectly preserved otoliths in the Paleocene (Bell's Landing Marl) of Alabama (NOLF, unpublished data).

**Percoidei** ind.  
(Pl. 2, Fig. 3)

*Material*

Four otoliths from the Harudi Formation, 3,5 km S of Baranda, Western India.

*Remarks*

Non-diagnostic juvenile otoliths, showing only generalized percoid features that do not allow a more precise identification.

Family MUGILIDAE CUVIER, 1829  
**Mugilidae** ind.  
(Pl. 2, Fig. 6)

*Material*

One otolith from the Harudi Formation, 3,5 km S of Baranda, Western India.

*Remarks*

A very eroded otolith, not identifiable at the specific or generic level.

Family URANOSCOPIDAE BLEEKER, 1859  
**“genus Uranoscopidarum”** sp.  
(Pl. 2, Fig. 7)

*Material*

One otolith from the Harudi Formation, 3,5 km S of Baranda, Western India.

*Remarks*

A small eroded otolith, that shows affinities with “genus Uranoscopidarum” *orbis* NOLF, 1991 from the Khirthar Formation of Pakistan, but poor preservation excludes any further evaluation.

**Uranoscopidae** ind.  
(Pl. 6, Figs. 1-2)

*Material*

Three otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

The material is too poorly preserved for an adequate description, but it shows a reasonable resemblance with otoliths of the Recent genus *Ichthyoscopus* SWAINSON, 1839 (Pl. 6, Fig. 3). Apparently it has to be classified in the same family (Uranoscopidae).

Family GOBIIDAE BONAPARTE, 1832

**Gobiidae** sp. 1  
(Pl. 2, Fig. 8)

1982 ?*Antigonia* sp. - SAHNI & SAXENA, p. 66, pl., figs. 3&5, ? fig. 1, 2, 4, 6.

*Material*

One otolith from the Harudi Formation, 3,5 km S of Baranda, Western India.

*Remarks*

Problems in identifying gobiid otoliths have been discussed *in extenso* by NOLF (1985, p. 98-99) and NOLF & CAPPETTA (1989, p. 222). This single, imperfectly preserved otolith only allows an identification at the family level.

**Gobiidae** sp. 2  
(Pl. 6, Fig. 4-5)

*Material*

Two otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

Two very small otoliths. See NOLF (1985, p. 98) for a discussion on problems concerning the identification of gobiid otoliths.

Order PLEURONECTIFORMES BLEEKER, 1859  
 Family BOTHIDAE BLEEKER, 1859  
 "genus *Bothidarum*" sp.  
 (Pl. 6, Figs. 6-8)

*Material*

Four otoliths from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

This material apparently represents a new species, characterized by a very narrow sulcus and a strong anterodorsal angle, but more material is required for an adequate description.

Family CYNOGLOSSIDAE JORDAN & GOSS, 1889

? *Symphurus* sp.  
 (Pl. 6, Fig. 9)

*Material*

One otolith from the Nanggulan Formation at Nanggulan, Java.

*Remarks*

A single juvenile otolith, showing affinities mostly with the cynoglossid genus *Symphurus* RAFINESQUE, 1810.

See CHAINE (1936, pl. XV) for the iconography of comparative Recent material.

**Conclusions**

*Evaluation of the obtained data*

The analysis leaves us with three Indo-West-Pacific otolith associations that are very restricted in scope of represented taxa: an already published one from near Taunsa, central Western Pakistan (NOLF, 1991), one from Western India and one from Java (Fig. 3). However, the three faunas are of very similar type: they all come from very shallow tropical coastal environments, and the associations are dominated by apogonid otoliths.

Therefore, it is interesting to combine the data from the three investigated spots in one table (Table 2), which gives a lot more information than looking at each association separately. Presently, 43 teleost taxa are known from otoliths in the marine Indo-West-Pacific Middle Eocene and 13 of them are known by a single specimen only. This means that all three associations must be much more diverse than presently known. The low diversity is apparently an artefact resulting from the restricted quantity of sediment that was screenwashed.

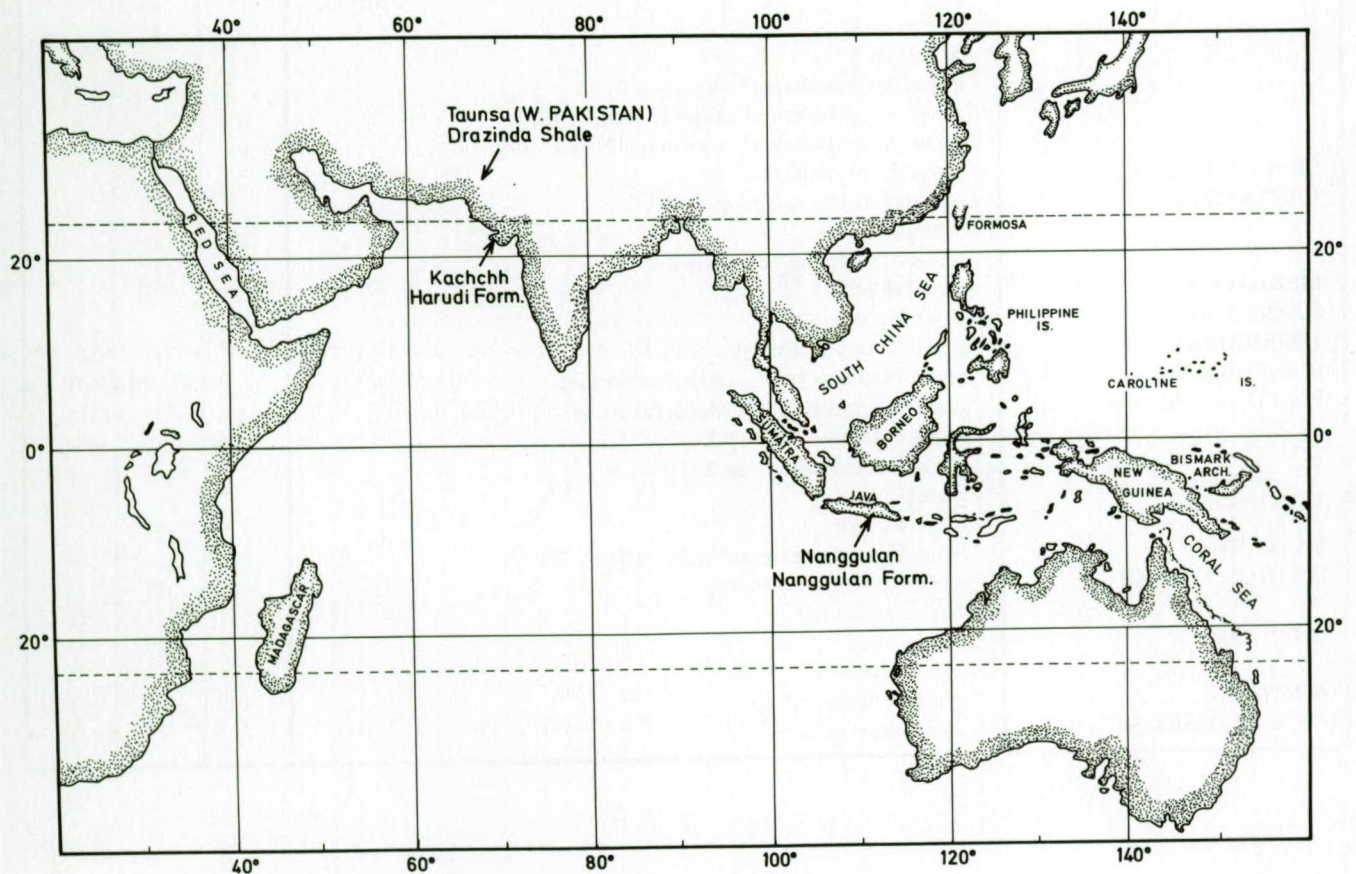


Fig. 3 — Marine Middle Eocene otolith-localities in the tropical Indo-West-Pacific region.

Table 2 — Marine Middle Eocene teleosts from the Indo-West- Pacific region.

MARINE MIDDLE EOCENE TELEOSTS (OTOLITHS) FROM THE INDO-WEST-PACIFIC REGION		Drazinda Shale, PAKISTAN	Harudi Formation, Kachchh, INDIA	Nanggulan Formation, JAVA
CONGRIDAE	<i>Ariosoma</i> sp.	P	-	-
	"genus Congridarum" aff. <i>diagonalis</i> (STINTON & NOLF, 1970)	P	I	J
	"genus Congridarum" sp.1	-	I	-
	"genus Congridarum" sp.2	-	-	J
ENGRAULIDAE	Engraulidae ind.	-	-	J
ARIIDAE	Ariidae ind.	-	I	-
SYNODONTIDAE	<i>Saurida</i> sp.	-	-	J
CARAPIDAE	Carapidae ind.	-	-	J
OPHIDIIDAE	"genus Brotularum" <i>siremboides</i> n. sp.	-	I	J
	"genus aff. <i>Glyptophidium</i> " <i>pseudobiarritzense</i> NOLF, 1991	P	-	J
BYTHITIDAE	Dinematichthyini ind.	-	-	J
BREGMACEROTIDAE	<i>Bregmaceros</i> sp.	-	-	J
SCORPAENOIDEI inc. sed.	"genus Scorpaenoideorum" sp.	-	I	-
PRIACANTHIDAE	<i>Pristigenys</i> sp.	-	-	J
APOGONIDAE	<i>Apogon townsendoides</i> n. sp.	-	-	J
	<i>Apogon</i> sp.1	P	-	-
	<i>Apogon</i> sp.2	P	-	-
	<i>Apogon</i> sp.3	P	-	-
	<i>Apogon</i> sp.4	-	I	-
	<i>Apogon</i> sp.5	-	-	J
	"genus Apogonidarum" <i>altissimus</i> n. sp.	-	-	J
	"genus Apogonidarum" <i>occultus</i> NOLF, 1991	P	-	-
	"genus Apogonidarum" <i>robertwesti</i> NOLF, 1991	P	I	-
SILAGINIDAE	"genus ? Silaginidarum" sp.	-	I	-
LACTARIIDAE	<i>Lactarius nonfungus</i> n. sp.	-	-	J
	<i>Lactarius</i> sp.	P	-	-
	"genus Menidarum" <i>occultus</i> n.sp.	-	I	J
MENIDAE	Gerreidae ind.	-	-	J
GERREIDAE	? Sparidae ind.	-	-	J
? SPARIDAE	"genus Sciaenidarum" sp.	-	I	-
SCIAENIDAE	"genus Percoideorum" <i>pseudatherina</i> n.sp.	-	-	J
PERCOIDEI inc. sed.	"genus Percoideorum" <i>sciaenoides</i> n. sp.	-	-	J
	"genus Percoideorum" sp.1	-	I	-
	"genus Percoideorum" sp.2	-	-	J
	Percoidei ind.	-	I	-
MUGILIDAE	Mugilidae ind.	-	I	-
URANOSCOPIDAE	"genus Uranoscopidarum" <i>orbis</i> NOLF, 1991	P	-	-
	"genus Uranoscopidarum" sp.	-	I	-
	Uranoscopidae ind.	-	-	J
GOBIIDAE	Gobiidae sp.1	-	I	-
	Gobiidae sp.2	-	-	J
BOTHIDAE	"genus Bothidarum" sp.	-	-	J
CYNOGLOSSIDAE	? <i>Symphurus</i> sp.	-	-	J

Otolith associations containing many taxa that are represented by single specimens are indicative of the fact that the sampling was insufficient to provide a more or less complete record of the taxa present.

Notwithstanding this handicap in our data, several interesting conclusions can be drawn from Table 2. Among the 12 nominal species in the list, 5 occur at more than one locality. Looking above the species level, more similarities become apparent: the genus *Lactarius* is represented at two sites; an uranoscopid taxon with very round otoliths occurs at two sites, and gobiids also occurs at two sites. Considering the restricted sampling and the geographical spread of the sampled localities (the distance between central Western Pakistan and central Java is about 6500 km!), the number of shared taxa is remarkable. Therefore, one can probably conclude that we sampled several of the most common and widespread teleosts inhabiting the neritic environments of the Indo-West-Pacific region during the Middle Eocene.

#### *Characteristics of the Middle Eocene neritic teleost fauna from the tropical Indo-West-Pacific region*

Areas where neritic otolith associations are known contemporary with the ones studied here are restricted to Western Europe and North America. Moreover, such associations are only well known from Belgium, the Paris Basin, Southern England and Aquitaine. Unpublished data for the Bartonian Marls of Pamplona (Spanish Pyrenean foreland) and from the Priabonian type area (Northern Italy) are also available (NOLF, unpublished data). For the Eocene of the Atlantic side of the United States few published data are available, but these are supplemented by a considerable otolith collection from the US Gulf of Mexico and Atlantic coast (NOLF, unpublished data). Eocene otoliths are also known from New Zealand and Southern Australia, but these associations come mainly from deep neritic or upper slope environments, and are therefore not suitable for comparison. Considering this state of knowledge, evaluation of the presently studied faunas is possible only in terms of comparison with European or Eastern North American faunas, or by comparison with Recent fish biogeography.

A point of similarity with both European and North American otolith associations is the abundance of ophiidiids and congrid. This must be considered as a very typical aspect of Eocene teleost faunas in tropical and subtropical neritic environments with sand or mud bottoms all over the world.

Apogonids, the most dominant group in the association here studied, are represented in the North American Campanian (NOLF & DOCKERY, 1990) and Maastrichtian, but we never recorded them from any American Paleogene association. In Europe, apogonids are important constituents of many neritic otolith associations. Apogonid taxa with very deep otoliths ("genus *Apogonidarum*" *altissimus*, "genus *Apogonidarum*" *occultus*

and "genus *Apogonidarum*" *robertwesti*) however, do not occur in Europe or in the Recent Indo-West-Pacific fauna. We consider them as a natural group, endemic to the latter area during Eocene times.

Present day taxa endemic to South Asia, such as the monotypic genera *Lactarius* and *Mene*, were on the contrary represented also in Europe and North America during Eocene times. Although not too much weight can be accredited to negative data, the absence of haemulids in the investigated Indo-West-Pacific otolith associations strongly contrasts with their abundance in contemporary North American and European ones.

Sciaenids, represented by a few species in the association from Western India, are unknown in Europe before the Middle Oligocene, but in North America they are abundant since the Early Eocene (Bashi Marl, Mississippi).

The gobiids here cited constitute the earliest fossil record of the family. In Europe, gobiid otoliths first appear in the Lower Oligocene (see NOLF, 1985, fig. 25) and in North America in the Priabonian (Yazoo Clay, Louisiana).

A remarkable fact to notice is that among the ten recorded percoid taxa, four belong to extinct families. One of these four ("genus *Percoideorum*" sp. 2) has a relative in the Late Paleocene of Alabama, but three ("genus *Percoideorum*" *pseudatherina*, "genus *Percoideorum*" *sciaenoides* and "genus *Percoideorum*" sp. 1) are endemic to the Eocene Indo-West-Pacific province. Such high percentages of extinct percoid families are unknown in otolith associations from Europe or North America. Finally, another group endemic to the Indo-West-Pacific Eocene is constituted by the uranoscopid taxa with round otoliths ("genus *Uranoscopidarum*" *orbis* and "genus *Uranoscopidarum*" sp.).

The presence of so many endemic higher taxa (three extinct families and an apogonid and an uranoscopid subgroup that can be considered as extinct subfamilies) in our restricted samples (containing only 43 taxa) suggests that in the Eocene the Indo-West-Pacific region was already inhabited by many fish taxa not represented elsewhere. Probably it contained the most diverse fish community of the world as it does today.

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## References

- BISWAS, S. K. 1986. Paleogene of Kutch - A rejoinder. *Indian Journal of Earth Sciences*, 13 (4): 343-360.
- BISWAS, S.K. & DESHPANDE, S.V., 1970. Geological and tectonic maps of Kutch. *Bulletin of the Oil and Natural Gas Commission*, 7 (2): 115-120.
- BISWAS, S.K. & RAJU, D.S.N., 1973. The rock stratigraphic classification of the Tertiary sediments of Kutch. *Bulletin of the Oil and Natural Gas Commission*, 10 (1-2): 33-46.
- CHAINE, J., 1936. Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des Téléostéens (suite). *Actes de la Société Linnéenne de Bordeaux*, 88: 5-246.
- CHAO, L.N., 1978. A basis for classifying Western Atlantic sciaenidae (Teleostei: Perciformes). *National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular*, 417: 1-72.
- FROST, G.A., 1925. Description of fish otoliths from the Tertiary formations of Atcheen, Northern Sumatra. *Dienst van den Mijnbouw in Nederlandsch Oost-Indië, Wetenschappelijke Mededelingen*, 2: 1-28.
- GOWDA, S., 1964. Fossil fish ossiculiths from the Cenomanian of South India. *Eclogae geologicae Helveticae*, 57 (2): 743-746.
- GOWDA, S., 1967. On a new fossil fish known from an otolith from the South Indian Cenomanian. *Journal of the Geological Society of India*, 8: 119-129.
- JAUHARI, A.K., 1981. Observations on morphotypes, taxonomy and biostratigraphic correlation of the Middle Eocene foraminifera from the Vinjhan-Miani area of Kutch, Western India. *Geoscience Journal*, 2 (2): 177-212.
- KHOSLA, S.C. & PANT, P.C., 1981. Ostracode biostratigraphy of the Eocene and Oligocene beds of Kutch. *Proceedings of the IX Indian Colloquium on Micropalaeontology and Stratigraphy*, pp. 167-180.
- MARTIN, K., 1914. Die Fauna des Obereocäns von Nanggulan auf Java. *Sammlungen des geologischen Reichs-Museums in Leiden, Neue Folge*, 2 (4): 105-178.
- MOHAN, M., 1982. Palaeogene stratigraphy of Western India. *Special Publication of the Palaeontological Society of India*, 1: 21-36.
- MOHAN, M. & GUPTA, S.C., 1968. The microfauna and age of the "Gypseous Shales", western Kutch, India. *Contributions of the Cushman Foundation on Foraminiferal Research*, 19 (1): 21-26.
- MOHAN, M. & SOODAN, K.S., 1970. Middle Eocene planctonic foraminiferal zonation of Kutch, India. *Micropaleontology*, 16 (1): 37-46.
- NOLF, D., 1980. Etude monographique des otolithes des Ophidiiformes actuels et révision des espèces fossiles (Pisces, Teleostei). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 17 (2): 71-195.
- NOLF, D., 1985. Otolithi Piscium. In: H.P. SCHULTZE (ed.). *Handbook of Paleichthyology*, 10. Fischer, Stuttgart and New York, pp. 1-145.
- NOLF, D., 1988. Les otolithes de téléostéens éocènes d'Aquitaine (sud-ouest de la France) et leur intérêt stratigraphique. *Mémoire de l'Académie royale de Belgique. Classe des Sciences*, 4°, 19 (2): 1-147.
- NOLF, D., 1991. Geology and paleontology of the Eocene Drazinda Shale Member of the Khirthar Formation, central Western Pakistan, Part III. Fish otoliths. *Tertiary Research*, 12 (3-4): 121-126.
- NOLF, D., (in press). A survey of perciform otoliths and their utility for phylogenetic analysis, with an iconographical synopsis of the Percoidei. *Bulletin of Marine Science*.
- NOLF, D. & CAPPETTA, H., 1989. Otolithes de poissons pliocènes du Sud-Est de la France. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 58: 209-271.
- NOLF, D. & DOCKERY, D., 1990. Fish otoliths from the Coffee Sand (Campanian) of Northeastern Mississippi. *Mississippi Geology*, 10 (3): 1-14.
- PRASAD, G.V.R. & KHAJURIA, C.K., 1990. A record of microvertebrate fauna from the Intertrappean Beds of Naskal, Andhra Pradesh. *Journal of the Palaeontological Society of India*, 35: 151-161.
- PURNAMANINGSIH, S. & HARSONO, P., 1981. Stratigraphy and planktonic foraminifera of the Eocene-Oligocene Nanggulan Formation, Central Java. *Publications of the Geological Research Development Center, Paleontology series*, 1: 9-28.
- RAJU, D.S.N., 1974. Observations on the Eocene, Oligocene and Miocene foraminiferal biostratigraphy of Kutch, Western India. *Publication of the Centre of Advanced Study in Geology, Panjab University, Chandigarh*, 10: 136-155.
- SAHNI, A. & SAXENA, R.K., 1982. Middle Eocene otoliths from Jhadwa, Southwestern Kutch. *Journal of the Palaeontological Society of India*, 27: 64-67.
- SASAKI, K., 1989. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the faculty of fisheries, Hokkaido University*, 36 (1-2): 1-137.
- SHING RANA, R., 1988. Freshwater fish otoliths from the Deccan Trap associated sedimentary (Cretaceous-Tertiary transition) beds of Rangapur, Hyderabad, District, Andhra Pradesh, India. *Geobios*, 21 (4): 465-493.
- SHING RANA, R., 1990. Palaeontology and palaeoecology of the Intertrappean (Cretaceous-Tertiary transition) Beds of Peninsular India. *Journal of the Palaeontological Society of India*, 35: 105-120.
- SHING RANA, R. & SAHNI, A., 1989. Fish otoliths from the Takali Formation (Intertrappean Beds) of Nagpur, India. *Geoscience Journal*, 10 (1-2): 145-164.
- SINGH, M.P. & SINGH, P., 1987. A note on the geology and micropaleontology of the Rato Nadi Section, Kutch, Gujarat State. *Geoscience Journal*, 8 (1-2): 201-204.
- SINGH, P. & SINGH, M.P., 1981. Larger foraminiferal zonation of Naredi Formation, Naredi, Kutch, India. *Geoscience Journal*, 7(2): 142-162.
- STINTON, F., 1949. Otoliths from Bodjonegoro. In BOOMGAART, L. *Smaller foraminifera from Bodjonegoro (Java)*. Smit and Dontje, Sappemeer, pp. 154-157.
- STINTON, F., 1962. Teleostean otoliths from the Upper Tertiary strata of Sarawak, Brunei, and North Borneo. *British Borneo Geological Survey, Annual Report*, 1962: 75-92.

TANDON, K.K., 1976. Biostratigraphic classification of the Middle Eocene Rocks of a part of South-Western Kutch, India. *Journal of the Palaeontological Society of India*, 19 (1974): 71-88.

TREWAVAS, E., 1977. The sciaenid fishes (croakers or drums) of the Indo-West-Pacific. *Transactions of the Zoological Society of London*, 33: 253-541.

VORSTMAN, A.G., 1927. Tertiaire vischotolieten van Java. *Dienst van den Mijnbouw in Nederlandsch-Indië, Wetenschappelijke Mededelingen*, 5: 1-24.

ZACHELLO, M., 1984. The Eocene mollusc fauna from Nanggulan (Java) and its palaeogeographic bearing. *Memorie di Scienze Geologiche*, 36: 377-390.

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### Explanation of the plates

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

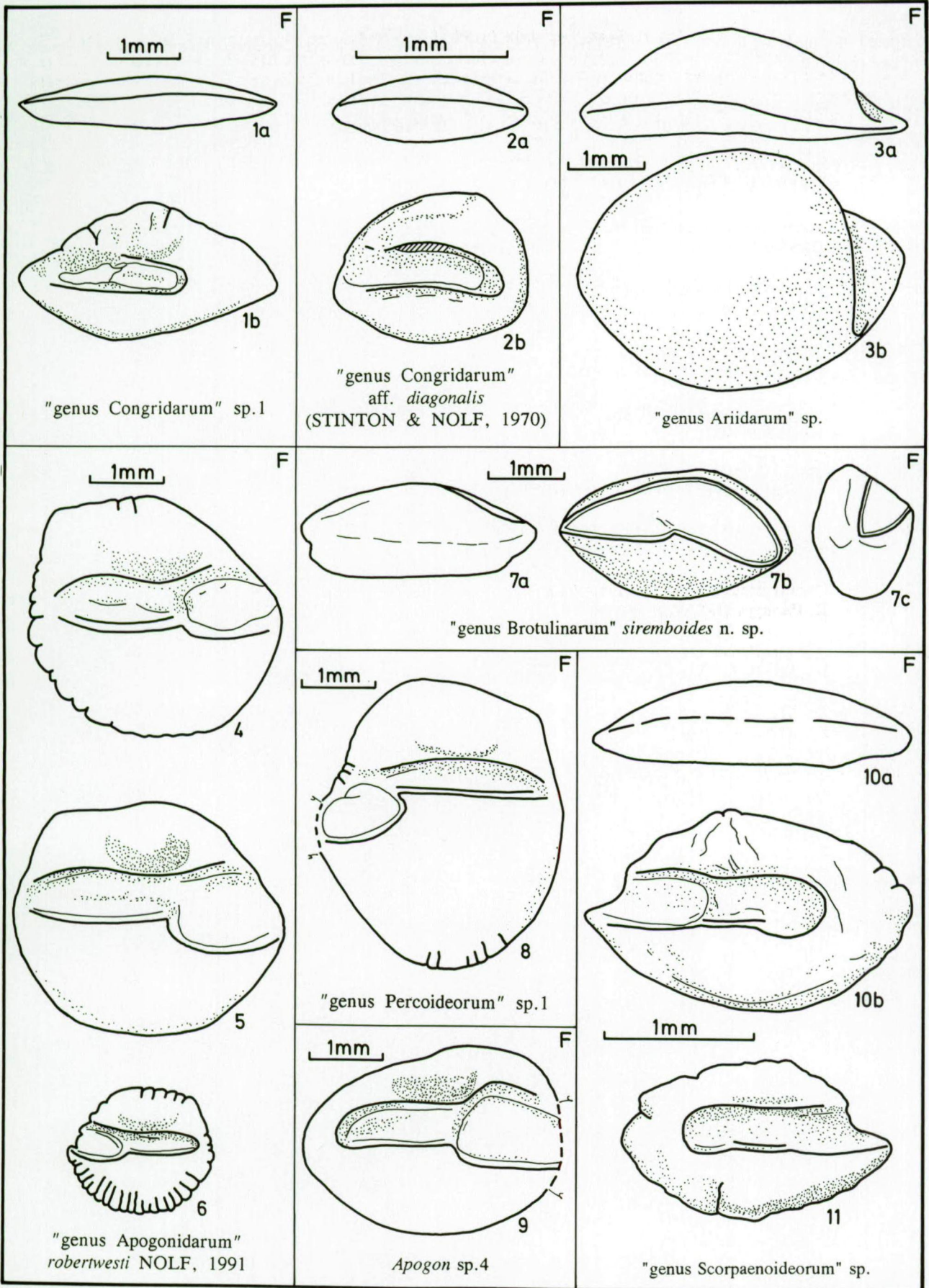
The abbreviations F and R in the upper right corner of each compartment of the plates indicate if the figured specimens in that compartment are fossils (F) or Recent (R). In the text of the explanations, L stands for left otolith and R for right otolith. The annotations Fig. a, b and c are used to indicate respectively ventral, inner (= mesial) and frontal views. Figures with only numbers and no letter annotations show inner views.

### PLATE 1

All figured specimens are from the Harudi Formation (Lutetian), exposed in the river Rato Nala, 3,5 km south of Baranda, Western Kachchh, India.

- Fig. 1 — "genus Congridarum" sp. 1  
R (IRSNB P 5915).
- Fig. 2 — "genus Congridarum" aff. *diagonalis* (STINTON & NOLF, 1970).  
R (IRSNB P 5916).
- Fig. 3 — "genus Ariidarum" sp.  
L, utricular otolith, external view (IRSNB P 5917).
- Fig. 4-6 — "genus Ariidarum" *robertwesti* NOLF, 1991  
4-5 = L; 6 = R (IRSNB P 5918, P 5919, P 5920).
- Fig. 7 — "genus Brotularum" *siremboides* n.sp.  
R, Paratype (IRSNB P 5921).
- Fig. 8 — "genus Percoideorum" sp. 1  
R (IRSNB P 5922).
- Fig. 9 — *Apogon* sp. 4  
L (IRSNB P 5923).
- Figs. 10-11 — "genus Scorpaenoideorum" sp.  
10 = R; 11 = L (IRSNB P 5924, P 5925).



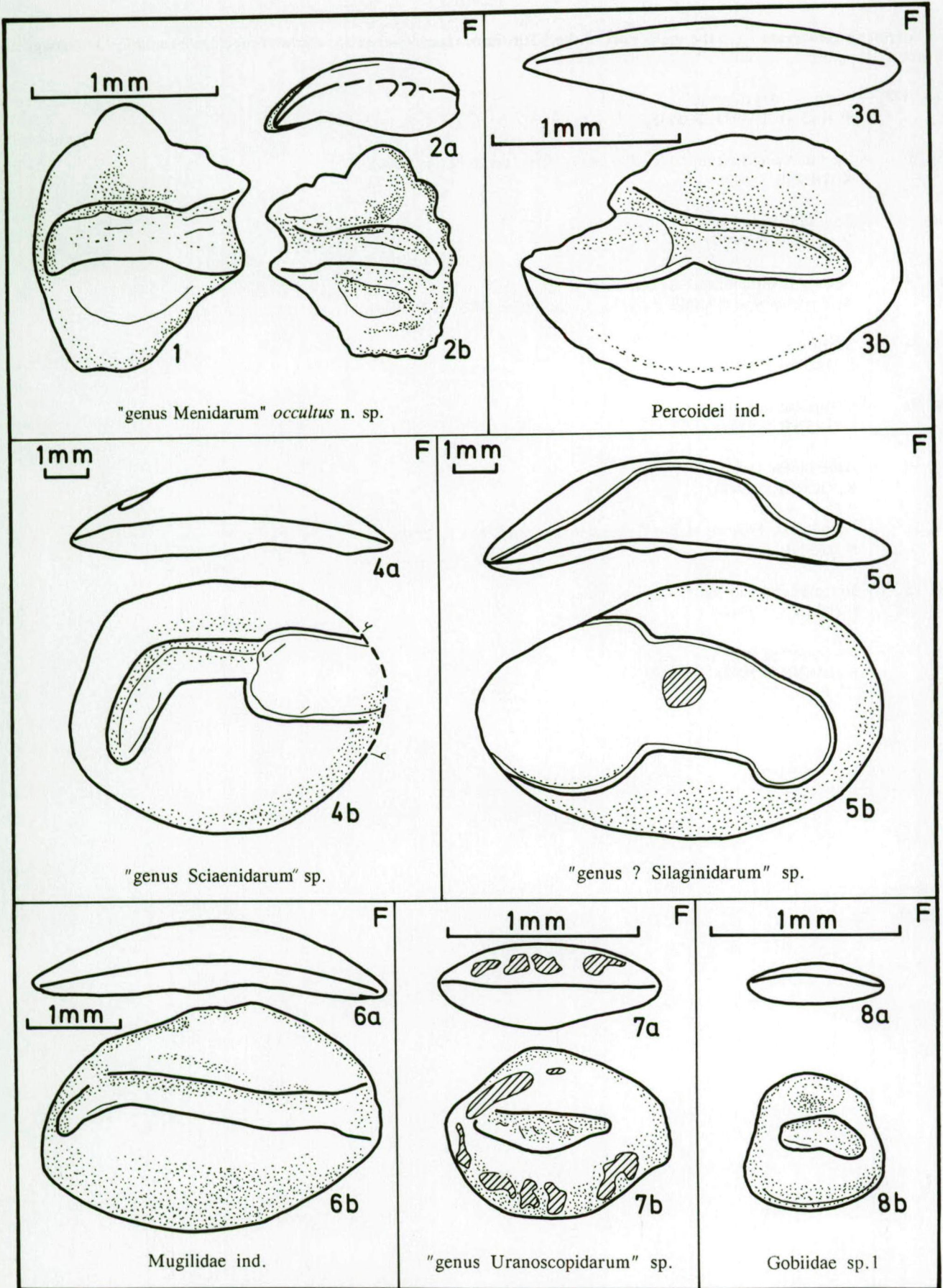


## PLATE 2

All figured specimens are from the Harudi Formation (Lutetian), exposed in the River Rato Nala, 3,5 km south of Baranda, Western Kachchh, India.

- Figs. 1-2 — “genus Menidarum” *occultus* n.sp.  
1 = L, paratype (IRSNB P 5926), 2 = R, holotype (IRSNB P 5927).
- Fig. 3 — Percoidei ind.  
R (IRSNB P 5928).
- Fig. 4 — “genus Sciaenidarum” sp.  
L (IRSNB P 5929).
- Fig. 5 — “genus? Sillaginidarum” sp.  
R (IRSNB P 5930).
- Fig. 6 — Mugilidae ind.  
L (IRSNB P 5931).
- Fig. 7 — “genus Uranoscopidarum” sp.  
R (IRSNB P 5932).
- Fig. 8 — Gobiidae sp. 1  
L (IRSNB P 5933).

PL.2



## PLATE 3

All figured specimens are from the upper part of the NP16 Zone (Early Bartonian) of the Nanggulan Formation at Nanggulan, Java.

Figs. 1-2 — “genus Congridarum” sp. 2  
R (IRSNB P 5934, P 5935).

Fig. 3 — “genus Congridarum” aff. *diagonalis* (STINTON & NOLF, 1970)  
R (IRSNB P 5936).

Figs. 4-5 — Engraulidae ind.  
R (IRSNB P 5937).

Figs. 6-7 — “genus Brotularum” *siremboides* n. sp.  
R, 6 = paratype (IRSNB P 5938), 7 = holotype (IRSNB P 5939).

Fig. 8 — *Saurida* sp.  
L (IRSNB P 5940).

Fig. 9 — Carapidae ind.  
L (IRSNB P 5941).

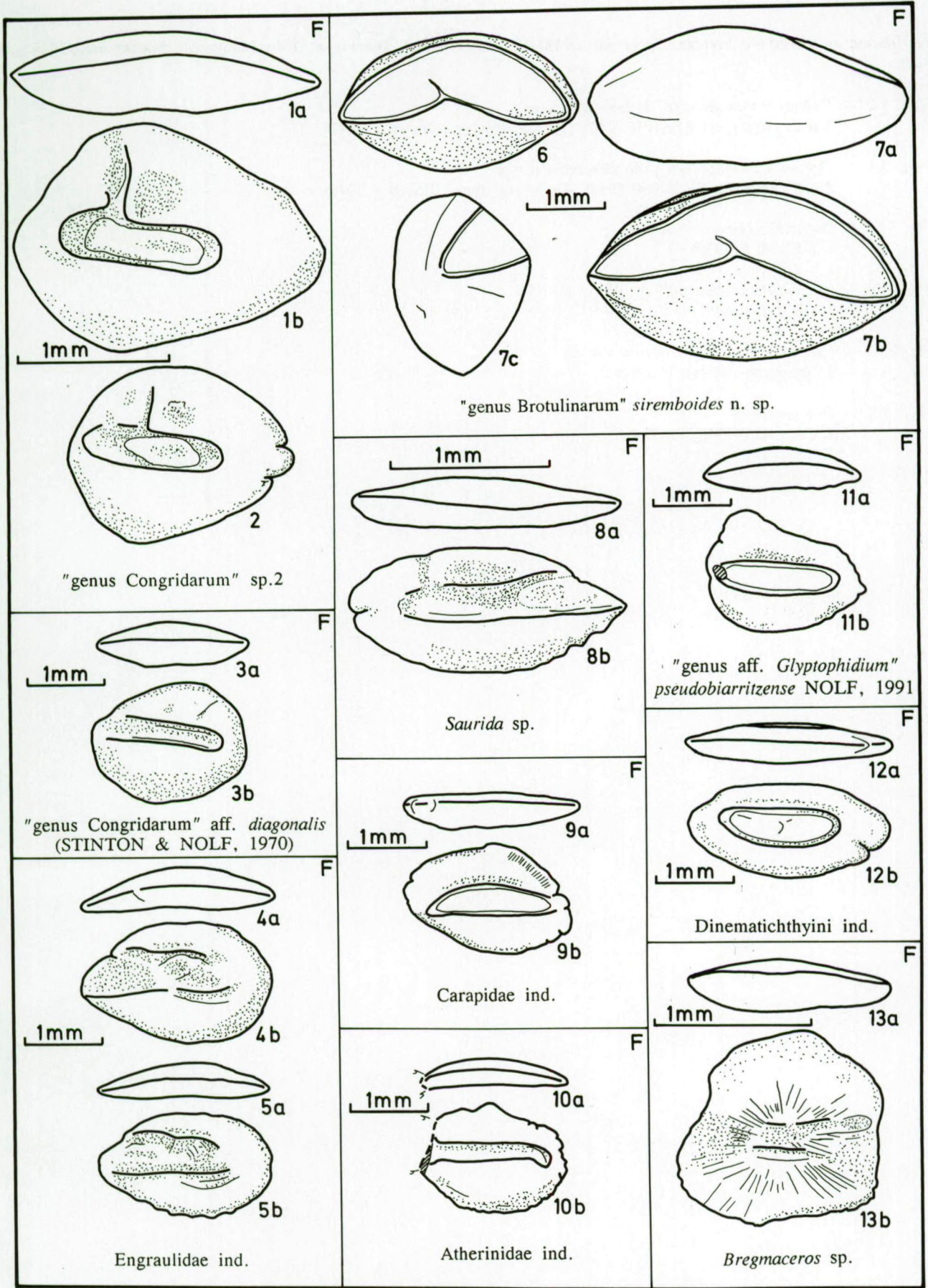
Fig. 10 — Atherinidae ind.  
R (IRSNB P 5942).

Fig. 11 — “genus aff. *Glyptophidium*” *pseudobiarritzense* NOLF, 1991.  
R (IRSNB P 5943).

Fig. 12 — Dinematichthyini ind.  
R (IRSNB P 5944).

Fig. 13 — *Bregmaceros* sp.  
R (IRSNB P 5945).

PL.3



## PLATE 4

All figured specimens are from the upper part of the NP16 Zone (Early Bartonian) of the Nanggulan Formation at Nanggulan, Java.

Figs. 1-2 — “genus *Percoideorum*” *sciaenoides* n. sp.

1 = L, paratype (IRSNB P 5946), 2 = R, holotype (IRSNB P 5947).

Figs. 3-4 — “genus *Percoideorum*” *pseudatherina* n. sp.

3 = L, holotype (IRSNB P 5948), 4 = R, paratype (IRSNB P 5949).

Fig. 5 — ?Sparidae ind.

L (IRSNB P 5950).

Fig. 6 — “genus *Percoideorum*” sp. 4

L (IRSNB P 5951).

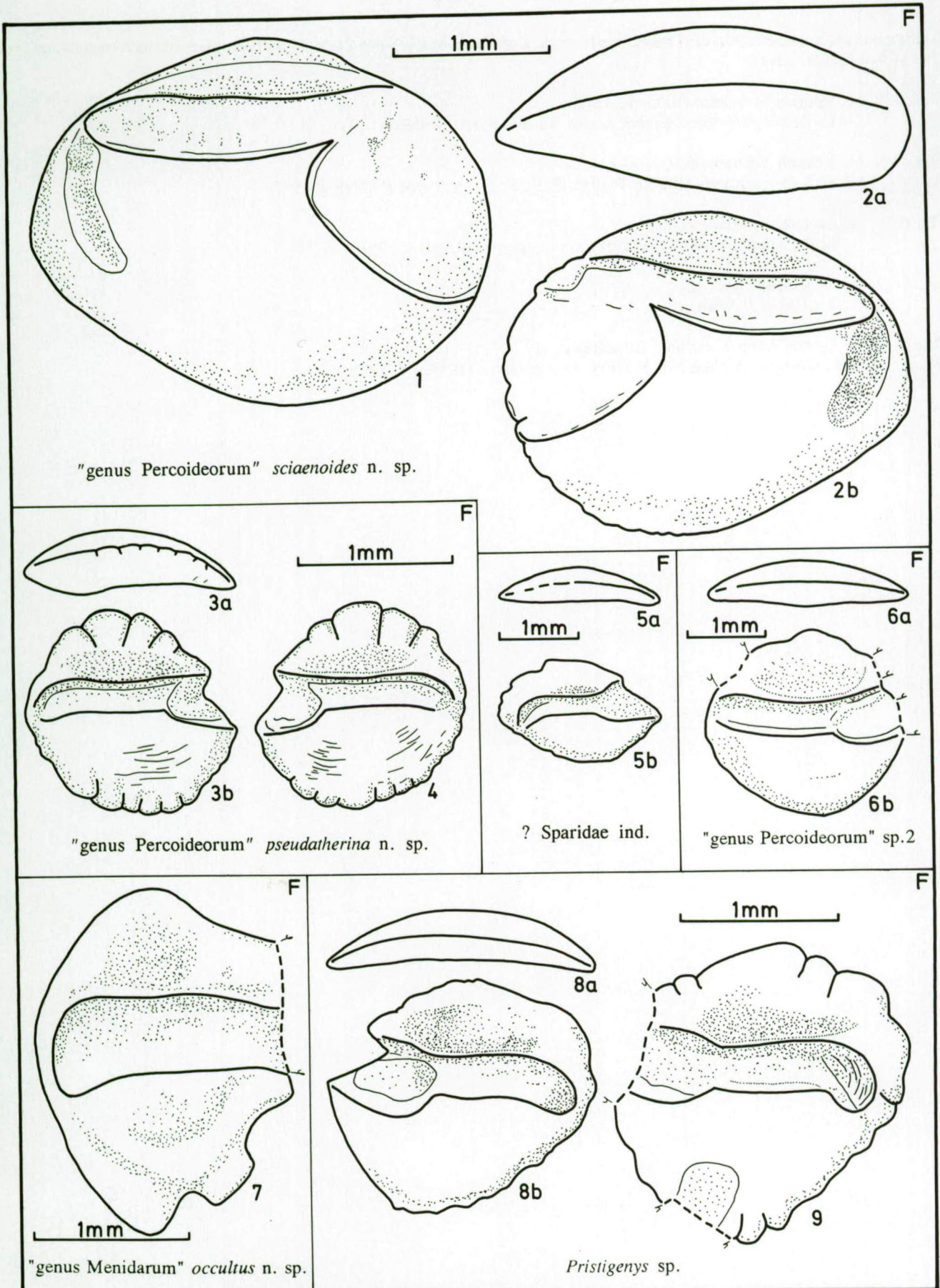
Fig. 7 — “genus *Menidarum*” *occultus* n. sp.

L, paratype (IRSNB P 5952).

Figs. 8-9 — *Pristigenys* sp.

R (IRSNB P 5953, P 5954).

PL.4



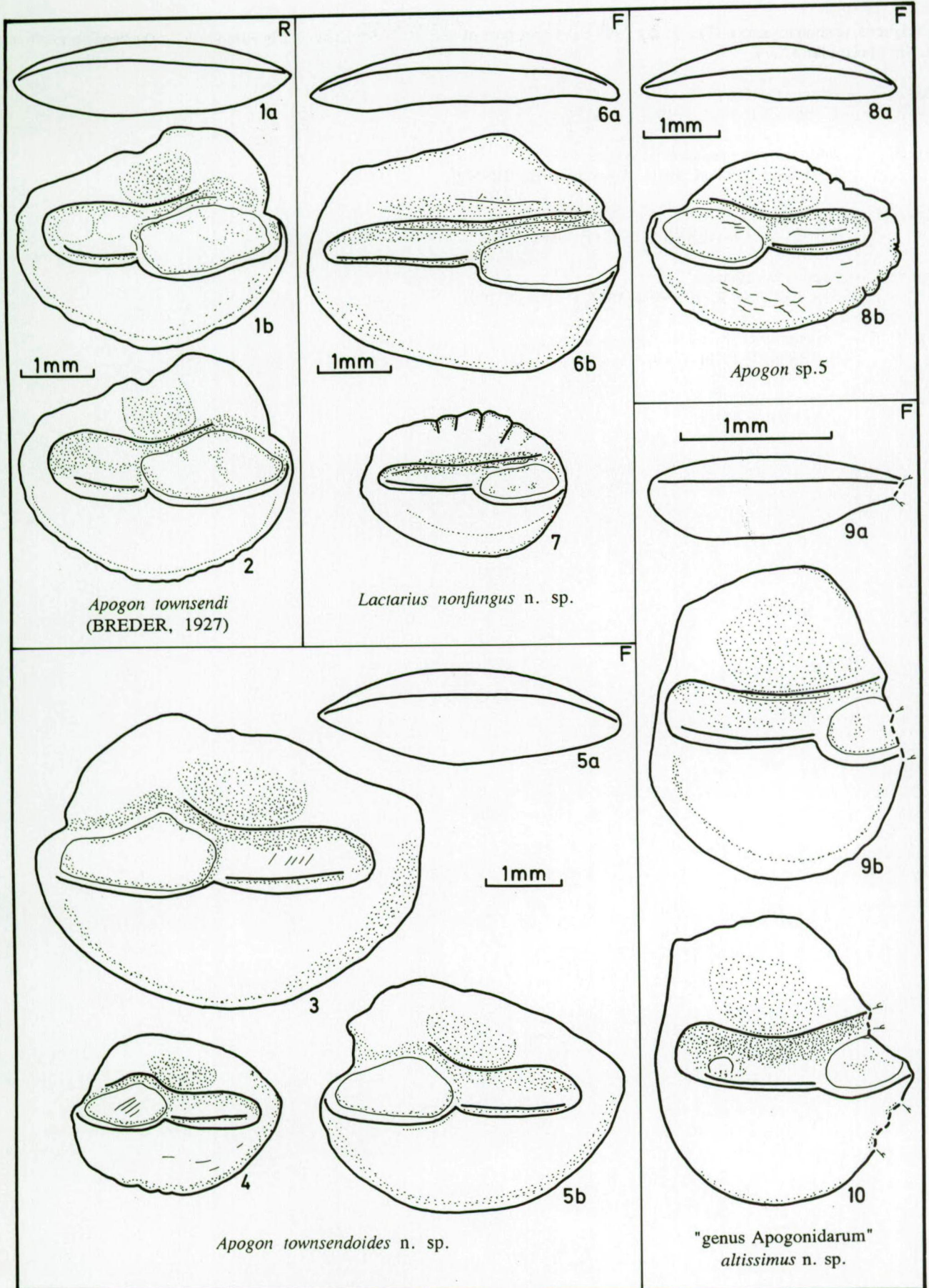
## PLATE 5

All figured specimens, except Figs. 1 and 2, are from the upper part of the NP16 Zone (Early Bartonian) of the Nanggulan Formation at Nanggulan, Java.

- Figs. 1-2 — *Apogon townsendi* (BREDER, 1927)  
L, Recent, off Mona Island, Lesser Antilles (Coll. IRSNB).
- Figs. 3-5 — *Apogon townsendoides* n.sp.  
R, 3-4 = paratypes (IRSNB P 5955, P 5956); 5 = holotype (IRSNB P 5957).
- Fig. 6-7 — *Lactarius nonfungus* n.sp.  
L, 6 = holotype (IRSNB P 5958), 7 = paratype (IRSNB P 5959).
- Fig. 8 — *Apogon* sp. 5  
R (IRSNB P 5960).
- Figs. 9-10 — "genus *Apogonidarum*" *altissimus* n. sp.  
L, 9 = holotype (IRSNB P 5961), 10 = paratype (IRSNB P 5962).



PL.5



## PLATE 6

All figured specimens, except Fig. 3, are from the upper part of the NP16 Zone (Early Bartonian) of the Nanggulan Formation at Nanggulan, Java.

Figs. 1-2 — Uranoscopidae ind.  
L (IRSNB P 5963, P 5964).

Fig. 3 — *Ichthyoscopus fasciatus* HAYSOM, 1957  
L, Recent, off Townsville, Australia (Coll. IRSNB).

Figs. 4-5 — Gobiidae ind.  
4 = R, 5 = L (IRSNB P 5965, P 5966).

Figs. 6-8 — "genus *Bothidarum*" sp.  
6 = L, 7-8 = R (IRSNB P 5967, P 5968, P 5969).

Fig. 9 — ? *Symphurus* sp.  
R (IRSNB P 5970).

Fig. 10 — Gerreidae ind.  
L (IRSNB P 5971).

