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Diaphus Otoliths from the European Neogene (Myctophidae, Teleostei)

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Abstract

The revision of Neogene otoliths of the myctophid genus *Diaphus*, based on extensive otolith collections in the Aquitaine Basin, in South-eastern France, northern Italy, Mediterranean Spain, the Paratethys and the North Sea Basin, has proved the validity of fourteen nominal species, among which two are new: *Diaphus befralai* and *D. cavallonis*. None of these species has been recorded previously from Oligocene deposits, and only four are still living today.

Key-words: *Diaphus*, Myctophidae, otoliths, Neogene.

Résumé

La révision des espèces oligocènes du genre *Diaphus*, basée sur un abondant matériel d'otolithes récoltées dans le Bassin d'Aquitaine, le Sud Est de la France, l'Italie septentrionale, la bordure méditerranéenne de l'Espagne, la Paratethys et le Bassin de la Mer du Nord, a révélé la validité de quatorze espèces nominales dont deux sont nouvelles: *Diaphus befralai* et *D. cavallonis*. Aucune de celles-ci n'est connue de dépôts oligocènes et quatre seulement existent encore dans la faune actuelle.

Mots-clefs: *Diaphus*, Myctophidae, otolithes, Neogene.

Introduction

In a previous paper (BRZOBOHATY & NOLF, 1996), we revised all otolith-based myctophid genera from the European Tertiary, except the genus *Diaphus*. The Oligocene *Diaphus* (six species) from various European basins were revised by BRZOBOHATY & NOLF, 1995. From the European Eocene, *Diaphus* otoliths are only known from the Aquitaine basin (six species, discussed in NOLF, 1988) The present study constitutes the final part of our revision of myctophid otoliths from the European Tertiary and is restricted to the Neogene *Diaphus* species. In fossil associations containing mesopelagic otoliths, especially in those from tropical waters, *Diaphus* otoliths are usually the most abundant and taxonomically diverse elements. Unfortunately, they are also the most problematic of all myctophids when it comes to otolith identification.

The morphology of *Diaphus* otoliths changes markedly during ontogeny (see NOLF & CAPPETTA, 1989, pl. 8-10), and in most species, only adult and large otoliths (larger than 2 mm) show clear diagnostic features, while juveniles cannot be distinguished. The other main problem is that in several Recent *Diaphus* species, even at the adult stage, the otoliths show only a very generalized morphology (see NOLF & CAPPETTA, 1989, pl. 9, figs. 12-22). In fossil associations, such otoliths remain predominantly unidentified; in many cases, it is impossible to state if such forms represent species with a more generalized morphology, or if they are juveniles of species that aquire diagnostic features only at larger sizes (see BRZOBOHATY & NOLF, 1995, p. 257 for a more extensive discussion).

Practically, this means that in most fossil associations, only about 5 to 10 % of the *Diaphus* otoliths can be confidently identified at the species level. In the present study, we recognise 14 nominal species for the European Neogene, but we are conscious that the true number may be considerably higher. In many of the studied associations, otoliths of some species exhibiting generalized morphologies at their adult stage seem to make up an amalgam with juvenile otoliths of others, but attempts to split up such amalgams can only lead to speculation, and neither biostratigraphy or paleobiogeography are served with such drudgery. The literature on fossil otoliths is full of citations and illustrations of these non diagnostic *Diaphus* otoliths, and citations of all such cases as negative synonymies or as doubtful taxa would produce excessively long lists. Therefore, our synonymies are restricted to only those citations that can be evaluated at the species level (eventual question marks with peculiar numbers of a given series means that the concerned specimens are not diagnostic), and the list of doubtful taxa given in the appendix is restricted to the primary type material to which the names apply.

We also were reluctant to give formal names to the otoliths of two well recognizable species because there are five Messinian *Diaphus* species based on skeletons for which the otoliths remain unknown. The eventual double use of names based either on otoliths or on skeletons can only be solved by the discovery of skeletons with otoliths in situ. In such cases, however, the otoliths are usually so badly preserved that they are unsuitable for taxonomic use. Therefore, we preferred to introduce formal names for taxa that are easily recognizable in several associations, because we judge that the use by different publications of inaccurate names like "*Diaphus* sp. 1" generates many more problems.

Geographic and stratigraphic position of the most important localities

The present study is based on material from nearly 100 different localities in the European Neogene which were sampled by the authors during the last 30 years and also takes in account all relevant literature data. The major collecting areas are listed below.

AQUITAINE BASIN (South-West France)

All the sites with abundant myctophid otolith material are located in the Paleocanyon of Saubrigues (neighbourhood of Saubrigues, Saint-Jean de Marsacq, Saint-Martin-de-Hinx, Saint-Etienne-d'Orthe, Peyrehorade). From the Chattian till the Langhian, the Paleocanyon has been progessively filled with marls which are often very fossiliferous. The following nannoplankton zones have been recognised (CAHUZAC *et al.*, 1995; see also this paper for the precise location of the sites):

NP25 (Chattian): Numerous points around Saint-Etienne d'Orthe and Peyrehorade.

NN1: Haubernet site at Saint-Martin-de-Hinx.

NN2-NN3 (Lower to Middle Burdigalian): "Les Platanes" site at Saint-André-de-Seignanx.

NN3-NN4 (Upper Burdigalian): numerous localities east and south of Saubrigues.

NN5 (Langhian): numerous localities in the direct surroundings of the village of Saubrigues; among those are the sites "Jean Tic" (presently filled in) and "Tauziets", which provided the rich otolith associations described by STEURBAUT in 1979 and 1984.

SOUTHEAST FRANCE

Very rich otolith associations of Pliocene blue marls of this region have been described by NOLF & CAPPETTA (1989), to which paper one should refer for the precise location of the studied localities. The sampled beds range from the basement of the planktonic foraminiferal Zone MPl 1 of CITA (1975) (= Zone 1 or Zone A of SPAAK, 1983) up to the top of Zone MPl 5a. One should notice, however, that the locality of Pichegu, cited as MPl 4b by NOLF & CAPPETTA (after MAGNE, 1978, p. 376) is now considered as the lower part of Zone MPl 3 (Zanclean; see CLAUZON *et al.*, 1990, p. 136). The richest associations come from the Zanclean MPl 2 Zone at Le-Puget-sur-Argens, a locality that was sampled very intensely by the late H. VON HACHT.

NORTHERN ITALY

In Northern Italy, Aquitanian and Burdigalian strata were sampled in the hills E of Torino and in the Montferrato hills (see BONSIGNORE *et al.*, 1969 and NOVARETTI *et al.*, 1995 for stratigraphical data and BRZOBOHATY & NOLF, 1996 for locality data). Some additional comments concerning our sample from Moleto are provided here, because this is the only Mediterranean locality of Aquitanian age that provided abundant *Diaphus* otoliths. In the paper of NOVARETTI *et al.* (1995, fig. 8), the section of Moleto was studied only down to the basement of the rhodolite limestone, exposed in the lower part of the quarry. It was attributed to planktonic foraminiferal Zone N 5/6, which suggests that the basement of the section does not go down into the Aquitanian. Our sample, however comes from marls exposed north of the quarry, and located about 10 to 15 m below the rhodolite limestone. Planktonic foraminifera from our sampling point were studied by E. BICCHI. The presence of *Paragloborotalia pseudokugleri* and *P. kugleri* (even if rare and small) and of abundant *Globoquadrina dehiscens* indicate the lower part of the *G. dehiscens* Subzone (N4b), corresponding the calcareous nannoplankton Zones NN1/NN2. The nannoplankton was studied by L. SVABENICKA. Besides reworked material (Campanian, Eocene, Oligocene), the youngest species represented is *Helicosphaera carteri*, which after YOUNG (1998) indicates the basis of the Neogene. Other important species are *H. recta, H. obliqua, H. euphratis, Discoaster deflandrei, Sphenolithus dissimilis, Pontosphaera discopora*. After YOUNG (1998), *H. recta* occurs till the NN1/2 boundary, and L. SVABENICKA concluded to a placement in the upper part of the NN1 Zone.

For the Langhian, we only know a small fauna of the Tanaro Formation in Piemonte (STEURBAUT, 1983) and a small fauna from the basement of the Baldissero Complex, in the hills E of Torino. A productive Serravallian site was sampled near "Madonna della Neve", N of Mondovi, in Piemonte. Because this site is the only one that provided abundant otolith material of Serravalian age, it requires some further comments.

VIOLANTI & GIRAUD (1992) mentioned otoliths in clayey deposits at point 20A which they attributed to the Lower Serravallian, Subzone with *Orbulina universa* of IACCARINO (1985). Their coordinates (sheet Carru, 1/25.000, x = 06.780, y = 19.980) refer to a point N of the hamlet "Madonna della Neve", and the exposure is in a deeply incised southern tributary of the Rio Branzola. About 1000 kg of clay was sampled there in 1998 by CAVALLO, HOFFMAN and NOLF, and provided several thousands of otoliths. Because the outcrop was originally mapped as Tortonian, and because these clayey sediments were so different from the typical arenaceous Serravallian facies and looked so much like the regional Tortonian facies, a sample was submitted to B. HAMRSMID for nannoplankton dating. He identified *Cyclicargolithus floridanus, Helicosphaera scissura, H. kamptnerii, H.* cf. *walbersdorfensis, Coccolithus pelagicus, Pontosphaera anisotrema, P. multipora, Braarudosphaera bigelowii, Calcidiscus carlae, Geminithella rotula, Reticulofenestra pseudoumbilica, R.* cf. *gelida, Sphenolithus abies*, little Prinsiaceae, *Syracosphaera* sp. , *Micrantholithus vesper*, and reworked species from the Cretaceous and Oligocene. Discoasterids are nearly completely absent. Because of the presence of *Cyclicargolithus floridanus* and the absence of *Sphenolithus heteromorphus*, he attributed the sample to the NN6 Zone, which confirms the Serravallian age of the site.

For the Tortonian, we have much material from the stratotype (hills SE of Sant Agata Fossili and Rio Castellania-Mazzapiedi; see NOLF & STEURBAUT, 1983) and from exposures in the Tanaro at Alba. A problem remains for the locality Borelli, in the Torino-Monferrato Hills, where turbiditic sediments (Montaldo Member) provided an interesting otolith association. The Montaldo Member was first reported as Messinian (*Globorotalia conomiozea* Planktonic Foraminiferal Zone, *Turborotalia multiloba* Subzone) by PAVIA & ROBBA (1979). Subsequent datation of a nannoplankton sample by E. Martini, reported in JANSSEN (1999) resulted in a "very probable Tortonian age", and data from the holoplanctonic molluscs also provide indications for a Tortonian age, but without really convincing evidence. Therefore, date from Borelli are here reported as ? Messinian. For the Pliocene, our Italian material comes mainly from the Zanclean of Monticello, near Alba (NOLF & CAVALLO, 1995) from the lower part of the Vernasca - Castel Arquato section (BARBIERI, 1967) and from Orciano, in Toscane.

CALABRIA (Southern Italy)
Myctophid otoliths collected by H. CAPPETTA at several levels in the reknowned Plio-Pleistocene Vrica section constitutes the only studied material for the Gelasian and the early Pleistocene.

SPAIN
Associations with many myctophid otoliths were sampled mainly in the Messinian Marls of Torremondo near Venta de la Virgen, east of Murcia (MONTENAT, 1977, p. 46) and in the Zanclean of Papiol, near Barcelona (NOLF et al., 1998).

MORAVIA (Czech Republic): Central Paratethys
Our material comes from many localities in the vicinity of Brno: Karpatian (= Upper Burdigalian, Nannoplankton Zone NN4): see BRZOBOHATY (1965, 1967a); Lower Badenian (= Langhian, Nannoplankton Zone NN5): see BRZOBOHATY (1982, 1986, 1997), BRZOBOHATY & SCHULTZ (1978)

NORTH SEA BASIN
In the North Sea Basin, identifiable *Diaphus* otoliths are available from Miocene deposits only. In Belgium, material was collected from the Edegem Sands (? Early Hemmoorian), Antwerpen Sands and the Zonderschot Sands (Late Hemmoorian), see NOLF, 1977; HUYGHEBAERT & NOLF, 1979; NOLF & SMITH, 1983. Additional Late Hemmorian material was mainly available from Miste, near Winterswijk, The Netherlands (see JANSSEN, 1984, for locality data). Our Reinbekian material is from the Aalten Member near Winterswijk (see VAN DEN BOSCH *et al.*, 1975) and from the Dingdener Feinsand at Dingden, NW Germany (see JANSSEN, 1967). Because of the neritic palaeoenvironments of all these deposits, *Diaphus* otoliths are rather scarce and never dominant in the associations. Langenfeldian deposits from Gross Pampau, east of Hamburg (see HOEDEMAKERS, 1997) provided an association with abundant otoliths of *Diaphus debilis*. Post-Langenfeldian and Pliocene deposits of the North Sea Basin only provided some scarce *Diaphus* otoliths, not identifiable at species level.

Systematics

Diaphus acutirostrum (HOLEC, 1975)
Pl. 3, Figs. 1-6

? 1905 Otolithus (Berycidarum) *mediterraneus* KOK. - SCHUBERT, p. 632, pl. 17, fig. 20 (non 19, non KOKEN, 1891)
1965 *Myctophum? splendidum* (PROCHAZKA, 1893) - BRZOBOHATY, p. 112, pl. 1, figs. ? 7, 8a,b (non PROCHAZKA, 1893);
1967a *Myctophum? splendidum* (PROCHAZKA, 1893) - BRZOBOHATY, p. 234, pl. 1D, fig. 6a,b (non PROCHAZKA, 1893);
1975 *Myctophum mediterraneum* KOKEN, 1891) - HOLEC, p. 255, pl. 1, fig. 2;
1975 *Myctophum splendidum* (PROCHAZKA, 1893) - HOLEC, p. 256, pl. 1, fig. 4a, b (non PROCHAZKA, 1893);
1975 Otol. (Myctophidarum) *acutirostrum* n. sp. - HOLEC, p. 258, pl. 1, fig. 5a,b;
1981 *Diaphus splendidus* (PROCH.) - RADO, pl. 1, fig. 9a,b, pl. 8, fig. 10a,b (non PROCHAZKA, 1893);
1983 *Diaphus splendidus* (PROCHAZKA) - BRZOBOHATY, pl. 4, fig. 1 (non PROCHAZKA, 1893);
? 1998 *Diaphus* sp. - REICHENBACHER, p. 326, pl. 3, fig. 9.

Holotype: Figured by HOLEC, 1975, pl. 1, fig. 5; PFUK University, Bratislava, coll. Geology and Palaeontology, Nr I. 42 aa; Badenian of Salka, near Sturovo, Slovakia.

Description: Otoliths of this species can grow fairly large and show an elongate shape, with a narrow anterior portion and a broad posterior part. Their outline is characterised by a very prominent rostrum, a clear antirostrum and a strongly marked posterodorsal angle. Their ventral margin is strongly denticulate with usually 8-12 irregular spine-like denticles. The outer face is clearly convex in its posterior part. The inner face is very slightly convex and nearly flat. Its ventral area shows a well marked, wide ventral furrow.

Remarks: Ontogenetic change is considerable in otoliths of *D. acutirostrum* and in addition to his original description, HOLEC (1975) also cited otoliths of the same taxon under two other names. Juveniles were attributed to what is now called *Notoscopelus mediterraneus* (KOKEN, 1891) (see iconography in BRZOBOHATY & NOLF, 1996, pl. 8, fig. 1-8) and medium sized specimens were attributed to a taxon originally described by PROCHAZKA (1893) as *Otolithus* (Berycidarum) *splendidus*. The holotype of the latter taxon could not be found, and as far as can be judged from the iconography in PROCHAZKA (1893, pl. 3, fig. 5), is a strongly eroded otolith. One can only guess that this holotype could belong to the same species, which in that case should be named *Diaphus splendidus* (PROCHAZKA, 1893). Such a guess however, should have the very nasty result of relegating the well established Recent fish species *Diaphus splendidus* (BRAUER, 1904) as a junior homonym of PROCHAZKA's species. Prochazka's taxon is considered here as a rejected species, because the drawing of the holotype is not diagnostic at the species or genus level.

Distribution: *D. acutirostrum* is a Paratethys species (Karpatian till Middle Badenian). It is common in Lower Badenian of Moravia. In the Mediterranean *sensu stricto*, some scarce juvenile otoliths from the Burdigalian of Sciolze may belong to *D. acutirostrum*.

Diaphus befralai n. sp.
Pl. 6, Figs. 6-11

1986 *Aethoprora* sp. - BEDINI, FRANCALACCI & LANDINI, p. 24, pl. 3, figs. 5-6, pl. 4, fig. 6.

Type material: Holotype: a right otolith (Pl. 6, Fig. 11) (IRSNB P 7407); two paratypes (Pl. 6, Figs 9-10) (IRSNB P 7405 - P 7406).

Additional material: Madonna della Neve (Serravallian): 16 specimens; Alba (Tortonian): 3 specimens; Borelli (? Messinian): 4 specimens.

Dimensions of the holotype: Length: 2.8 mm, height: 2.4 mm; thickness: 0.7 mm.

Stratum typicum: Tortonian marls, lower N 17 Planktonic Foraminiferal Zone, E of St. Agata Fossili

Derivatio nominis: Acronym of the authors **B**EDINI, **F**RANCALACCI, **L**ANDINI (1986), who first figured an otolith of this taxon.

Diagnosis: This species is characterised by otoliths with a nearly semicircular ventral rim that bears 6-8 (exceptionally 10) coarse spines. The dorsal rim is high, but narrow; its anterior part is curved, but does not bears a true predorsal angle. There is a posterodorsal angle that lies close to the center of the dorsal rim. Behind the posterodorsal angle, the dorsal rim is truncate, very slightly concave. The otoliths are also characterised by a strongly incised excissura. The outer face is smooth and somewhat more convex as the inner face. The sulcus is narrow, and its crista superior is marked by a shallow depression in the nearly flat dorsal area. The ventral area shows some more convexity and bears a well marked furrow in the middle part.

Remarks: These otoliths apparently belong to the same species as the one preserved in a skeleton from the Lower Messinian of Mondaino and figured by BEDINI *et al.* (1986) as *Aethoprora* sp. *Aethroprora* GOODE & BEAN, 1896 is a junior synonym of *Diaphus*, and its type species is *D. metopoclampus* COCCO, 1829, a common North-Eastern Atlantic species that also occurs in the Western Mediterranean. Surprisingly, this common species has no fossil record. Otoliths of *D. metopoclampus* and *D. metopoclampoides* are higher than those of *D. befralai*, their dorsal rim is clearly concave behind the posterodorsal angle and their ventral spines are less developed. Somewhat similar looking otoliths are also found in *D. holti*, but these are more elongate, have a more salient rostrum and a more posteriorly situated posterodorsal angle.

Distribution: This is an uncommon species in the Mediterranean Serravallian, Tortonian and Messinian.

Diaphus cahuzaci STEURBAUT, 1979
Pl. 5, Figs. 1-6

1965 *Scopelus pulcher* PROCHASKA - RADO, p. 60, pl. 1, fig. 5a,b (non fig. 3a,b; non PROCHAZKA, 1893);
1965 *Myctophum excavatum* (SULC, 1932) - BRZOBOHATY, p. 111, pl. 1, fig. 10 (non SULC 1932);
1966 *Myctophum excavatum* (SULC) - SMIGIELSKA, p. 234, pl. 13, figs. 4, 5,? 6 (non SULC 1932);
1967a *Myctophum excavatum* (SULC, 1932) - BRZOBOHATY, p. 234, pl. 1D, fig. 6a,b. (non SULC, 1932);
1973 *Myctophum debile* (KOKEN), 1891 - JONET, p. 137, pl. 2, figs. 9, 10 (non 8, non KOKEN 1891);
1973 *Myctophum pulchrum* (PROCHAZKA), 1893 - JONET, p. 139, pl. 2, figs. 11 - 13 (non PROCHAZKA, 1893);
1973 *Diaphus* cf. *excavatus* (SULC) - BRZOBOHATY & SCHULTZ, pl. 5, fig. 6 (non SULC, 1932);
1979 *Diaphus?* aff. *metopoclampus* (COCCO, 1829) - STEURBAUT, p. 62, pl. 5, fig. 8;
1979 *Diaphus cahuzaci* n. sp. - STEURBAUT, p. 61, pl. 4, figs. 1 - 6, pl. 12, fig. 11;
1979 *Myctophum pulchrum* (PROCHAZKA) 1893 - JONET, p. 107, pl. 3, fig. 2 (non PROCHAZKA 1893);
1982 *Diaphus cahuzaci* STEURBAUT, 1979 - STEURBAUT & JONET, p. 197, pl. 1, fig. 12;
1983 *Diaphus cahuzaci* STEURBAUT, 1979 - STEURBAUT, p. 257, pl. 1, figs. 4-9;
1983 *Diaphus cahuzaci* (STEURBAUT, 1979) - NOLF & SMITH, p. 90, pl. 1, figs. 15-18;
1984 *Diaphus cahuzaci* STEURBAUT, 1979 - STEURBAUT, p. 52, pl. 8, figs. 15-17;
1992 *Diaphus cahuzaci* STEURBAUT, 1979 - RADWANSKA, p. 178, pl. 4, figs. 4-6, textfig. 26;
1997 *Diaphus cahuzaci* STEURBAUT, 1979 - NOLF & BRZOBOHATY, pl. 1, fig. 19.

Holotype: Figured by STEURBAUT, 1979, pl. 4, fig. 1 and pl. 12, fig. 11; here refigured at Pl. 5, Fig. 6 (IRSNB P 3035); Langhian interval of the Saubrigues Marls at Saubrigues, Jean Tic (Aquitaine).

Remarks and description: This small species was originally described from juvenile otoliths, but seems to be morphologically well characterised and is abundant in the Lower and Middle Miocene of Europe. On Pl. 5, Fig. 1-6, we figure an ontogenetic series, including otoliths about twice as long as the holotype. This species is characterised by nearly round otoliths with a strong and acuminate posterodorsal angle, and a more rounded anterodorsal angle which in some specimens reaches higher than the posterodorsal one. The rostrum is slightly salient. The ventral rim is nearly semicircular, and bears 7 - 12 little spines. The outer face is convex, with a nearly flat central portion in large specimens. The inner face is slightly convex in both antero-posterior and dorso-ventral sense.

A somewhat similar looking small specimen from the Zanclean of Le-Puget-sur-Argens, figured by SCHWARZHANS (1986, pl. 3, fig. 32) as *D. cahuzaci* must be considered as a non-identifiable juvenile otolith of another species; we do not have any record of *D. cahuzaci* among the many thousands of otoliths available from that locality.

Distribution: Northern Italy: Aquitanian (Antognola Marls at Moleto), Burdigalian (Termo Fora Complex and Pietra da Cantone), Langhian (Tanaro Formation), Serravallian (Madonna della Neve locality); Paratethys: Ottnangian, Karpatian and Lower Badenian; Portugal: Middle Miocene; Aquitaine: Aquitanian till Langhian interval of the Saubrigues Marls; North Sea Basin: Hemmoorian (Edegem Sands).

Diaphus cavallonis n. sp.
Pl. 5, Fig. 7-14

1976 *Myctophum tuberculatum* (BASSOLI) - ANFOSSI & MOSNA, p. 21, pl. 2, fig. 3a,b (non BASSOLI, 1906);

1979 *Diaphus splendidus* (PROCHAZKA 1893) - SCHWARZHANS, p. 8, pl. 3, figs. 17, 18 (non 16, non PROCHAZKA, 1893);
1986 *Diaphus sulcatus* (BASSOLI 1906) s. l. - SCHWARZHANS, p. 223, pl. 4, figs. 47-49 (non BASSOLI, 1906);
1986 *Diaphus* aff. *rossiae* (ROBBA, 1970) - SCHWARZHANS, p. 223, pl. 4, fig. 46 (non ROBBA, 1970); non pl. 4, fig. 43 and 45 (= *D.* aff. *splendidus);*
1989 *Diaphus* sp. 1 - NOLF & CAPPETTA , p. 218, pl. 10, figs. 11 - 16;
1994 *Diaphus* sp. 1 - NOLF & CAVALLO, pl. 3, figs 1, 2;
1998 *Diaphus* sp. 1 - NOLF, MANE & LOPEZ, pl. 2, fig. 11.

Type material: Holotype: a left otolith (Pl. 5, Fig. 7) (IRSNB P 7389); more than 500 paratypes, of which three are figured (Pl. 5, Figs. 8-10) (IRSNB P 7390 - P 7392).

Additional material: Madonna della Neve (Serravallian, not common), St. Agatha Fossili (Tortonian, not common), Borelli (? Messinian, common), Mediterranean Pliocene: common at many localities (e.g. Papiol, Monticello, Rio Torsero, Vrica, Bussano La Cava, Bussano Cusinaire, Vezza d'Alba).

Dimensions of the holotype: Length: 5.0 mm, height: 3.9 mm; thickness: 1.1 mm.

Stratum typicum: Zanclean marls, Foraminiferal Zone M Pl. 2, at Le-Puget-sur-Argens.

Derivatio nominis: This species is named after Oreste Cavallo (Alba, Italy) in honour of his many contributions to the knowledge of the palaeontology of Piemonte.

Diagnosis: This species is characterised by relatively high, irregular elliptical otoliths with a somewhat narrowing anterior portion. The anterior part of the ventral rim is straighter than the central and posterior zone, and stretches obliquely towards the rostrum. Between the rostrum and the posterodorsal angle, the dorsal rim shows a regular curving in small and medium sized specimens, but has an obtuse angular expansion in large otoliths. The posterodorsal angle is blunt but well marked, and accentuated by a little hollowing just behind, towards the posterior rim. In small specimens, the posterior rim is regularly rounded, but in larger ones, it is more oblique and runs straight towards a posteroventral angle, which marks the transition with the ventral rim. The ventral rim usually bears more than ten obtuse spines.

The outer face has a smooth surface, and is convex in the dorso-ventral sense. In a ventral profile, the otoliths are thickest near to the posterior rim. The inner face is much less convex. The ostial colliculum often narrows anteriorly.

Remarks: Although otoliths of this species do not immediately attract one's attention, they are morphologically well defined and distinct from those of other *Diaphus* species. The taxon was previously cited as *Diaphus* sp. 1 in several papers (see synonymy) because there are five Messinian skeleton-based *Diaphus* species with unknown or only poorly preserved otoliths in situ (see introduction). However, because the above described type of otolith is very common in Mediterranean Pliocene deposits, we judged that a formal otolith-based name is by far more preferable to a forced guess for one of the skeleton-based taxa, or to further designation as "sp. 1". A somewhat similar looking otolith was figured by BEDINI *et al.* (1980, pl. 1, fig. 1) from a skeleton that they attributed to *Ceratoscopelus dorsalis* (SAUVAGE, 1870). This otolith apparently belongs to a *Diaphus*, but does not show the anterior narrowing which is typical for *D. cavallonis*.

Distribution: Otoliths of *D. cavallonis* are rare in the Serravallian and Tortonian. They become more common in the ? Messinian of Borelli and especially in the Pliocene of the Mediterranean realm.

Diaphus debilis (KOKEN, 1891)
Pl. 2, Figs. 13-18

1891 Otolithus (Berycidarum) *debilis* KOKEN - KOKEN, p. 122, pl. 6, fig. 3, 3a;
1905 Otolithus (Berycidarum) *austriacus* KOKEN - SCHUBERT, p. 630, pl. 17, fig. 1(non 2-7, non KOKEN, 1891);
1905 Otolithus (Berycidarum) *Kokeni* PROCH. - SCHUBERT, p. 631, pl. 17, fig. 8, (non 9, 10, 11, non PROCHAZKA 1893);
? 1942 *Scopelus debilis* KOK. - WEILER, p. 21, pl. 1, figs. 33, 37 (non 30-32, 34-36);
1966 *Myctophum debile* (KOKEN) - SMIGIELSKA, p. 229, pl. 12, figs. 6, 7 (non 8 = juv. Ex., non pl. 13, fig. 1 = *D.* aff. *taaningi*);
1967a Ot. (Myctophidarum) *kokeni* (PROCHAZKA, 1893) - BRZOBOHATY, p. 235, pl. 1D, fig. 4a,b (non PROCHAZKA, 1893);
1969 *Myctophum debile* (KOKEN, 1891) - HEINRICH, p. 16, pl. 2, fig. 3 (? non pl. 3, fig. 1, pl. 17, figs. 1-12);
1971 *Myctophum debile* (KOKEN, 1891) - RADO, p. 184, pl. 2, fig. 7a,b, pl. 9, fig. 68 (? non pl. 1, fig. 5, pl. 9, fig. 67);
1979 *Diaphus debilis* (KOKEN, 1891) - HUYGEBAERT & NOLF, p. 70;
1981 *Diaphus austriacus* (SCHUB.) - RADO, pl. 6, fig. 4 (non KOKEN, 1891);
1984 Otolith - PFEIL, textfig. 2;
1986 *Diaphus debilis* (KOKEN 1891) - SCHWARZHANS, pl. 3, fig. 28-29;
1990 *Diaphus debilis* (KOKEN 1891) - MÜLLER, p. 440, pl. 4, figs. 2, 6,?3-4,? 5;
1992 *Diaphus debilis* (KOKEN, 1891) - RADWANSKA, p. 178, pl. 5, fig. 1-2 (non figs. 3-6 = *D. kokeni*), textfig. 27 a-b (non 27 c-f = *D. kokeni*);
1992 *Diaphus* sp. 2 - RADWANSKA, p. 181, pl. 5, fig. 10, 11, (non 7-9 = *D.* aff. *cahuzaci*, textfig. 29 b, c, (non a = *D.* aff. *taaningi)*;
1992 *Diaphus* sp. 3 - RADWANSKA, p. 181, pl. 6, figs. 7, 8,? 9, textfig. 30 a, b,?c;
partim 1994 *Diaphus debilis* (KOKEN 1891) - BRZOBOHATY, pl. 2, figs. 6, 7, (non 5, 8 = *D. taaningi*);

1997 *Diaphus debilis* (KOKEN, 1891) - HOEDEMAKERS, p. 53, pl. 3, figs. 1-6.

Holotype: Figured by KOKEN, 1891, pl. 6, fig. 3; from the "Miocene of Langenfelde". The original material of KOKEN seems to be lost, but HOEDEMAKERS (1997, p. 52) recorded 1600 specimens from the Langenfeldian of Gross Pampau, near Hamburg, where no other *Diaphus* species occur. Six specimens from Gross Pampau are figured here.

Description: The otoliths are slightly elongate, nearly round. (length/height proportion varies between 1.1 and 1.2). They are characterised by an obtuse but well marked posterodorsal angle and a strong antirostrum. Most specimens show only a very obtuse anterodorsal angle, so that the dorsal area narrows from the posterodorsal angle towards the antirostrum. The rostrum is more prominent than the antirostrum, and both are separated by a sharply incised excissura. The ventral rim is regularly rounded but not semicircular, and bears 6 to 8 irregularly disposed obtuse spines. The dorsal area shows a well marked depression just above the sulcus, and most specimens show a rather wide ventral furrow. The outer face is smooth and convex; the inner face is nearly flat.

Remarks: Otoliths of this species are nearest to those of *Diaphus kokeni* and *D. taaningi*, and otolith series of the three species are figured together on Pl. 2, for direct comparison. Otoliths of *D. debilis* differs from those of *D. taaningi* by their narrow antero-dorsal area and more straight posterodorsal rim, while otoliths of *D. kokeni* show a very strong posterodorsal angle, and a nearly vertical posterior rim.

Distribution: Paratethys: From the Eggenburgian till the Badenian; In Northern Italy, some juvenile specimens from the Serravallian can only tentatively be referred to this species; Aquitaine: Langhian interval of the Saubrigues Marls; North Sea Basin: from the Hemmoorian till the Langenfeldian; very common in the Langenfeldian.

Diaphus haereticus (BRZOBOHATY & SCHULTZ, 1978)
Pl. 1, Figs. 1-14

1978 *Symbolophorus haereticus* n. sp. - BRZOBOHATY & SCHULTZ, p. 450, pl. 4, fig. 10, pl. 5, fig. 1;
1983 *Symbolophorus haereticus* BRZOBOHATY & SCHULTZ - BRZOBOHATY, pl. 4, fig. 2.

Holotype: Figured by BRZOBOHATY & SCHULTZ, 1978, pl. 5, fig. 1; Coll. Katedra Geologie a Paleontologie, Masarykovy University Brno, inv. nr. 0251, re-figured here on Pl. 1, Fig. 8; Badenian of Zabcice, Moravia. This specimen is a somewhat eroded and very short otolith that unfortunately, is marginal in the variability of the species; the paratype MUB 0250, refigured here (Pl. 1, fig. 9) represents much better the usual aspect of otoliths in this species, and is compared to various other specimens from the Lower Miocene of Northern Italy and Aquitaine on Pl. 1.

Description: The presently figured material was chosen in a series of otoliths with a length ranging from 1.5 - 5.6 mm, and illustrates clearly their variability and ontogenetic changes, while the original description was only based on adult specimens. Otoliths of this species grow fairly large, and are characterised by their elongate shape, with a narrowing anterior portion. The postdorsal angle is well developed and looks somewhat spiny. The ostial colliculum becomes narrower in its anterior portion, especially in larger specimens. The inner face is slightly convex, both in the antero-posterior and in the dorso-ventral sense. The outer side is clearly convex, with maximal thickness situated in the posterior part. The ventral rim generally bears 7 to 9 irregular spines, exceptionally 10, and sometimes only 6 in juveniles.

Remarks: Otoliths of *D. haereticus* show most similarity to those of *D. marwicki* (FROST, 1933) from the Middle and Upper Miocene of New Zealand (see SCHWARZHANS, 1980, figs. 167-169), but in this species, the junction of the dorsal and posterior rim is more angular, and the posterior rim extends higher in dorsal direction.

Distribution: Northern Italy: Aquitanian (Antognola Marls at Moleto) Burdigalian (Termo Fora Complex, Pietra da Cantone); Paratethys: Lower Badenian of Moravia; Aquitaine: NN 2 - NN 3 interval of the Saubrigues Marls.

Diaphus holti TAANING, 1918
Pl. 3, Figs. 7-10

1971 *Diaphus praerafinesquii* n. sp. - WEILER, p. 11, pl. 1, fig. 15;
1976 *Diaphus theta* EIGENMANN & EIGENMANN - ANFOSSI & MOSNA, p. 18, pl. 1, fig. 4ab (non EIGENMANN & EIGENMANN, 1890);
1986 *Diaphus holti* TAANING 1918 - SCHWARZHANS, p. 222, pl. 4, fig. 40-41;
1989 *Diaphus holti* TAANING, 1918 - NOLF & CAPPETTA, pl. 8, figs. 22-24;
1997 *Diaphus holti* TAANING, 1918 - NOLF, MANE & LOPEZ, pl. 3, figs. 2-4.

Lectotype: A Recent fish from the Mediterranean, 36°53'N, 3°9'E; ZMUC P2339204. Otoliths from Recent specimens of *D. holti* are illustrated by NOLF & MARTINELL, 1980, pl. 2, figs. 15-20 and NOLF & CAPPETTA, 1989, pl. 8, figs. 22-24.

Remarks: The otoliths of this species can only be confused with those of another Mediterranean *Diaphus* species, *D. rafinesquei*, but in the latter species, otoliths are more elongate. Growth series of Recent otoliths, for direct comparison, are figured by NOLF & MARTINELL (1980, pl. 2).

Distribution: Fossil otoliths of this present day species are only known from the Mediterranean (Serravallian, Tortonian, ? Messinian of Borelli and Pliocene), but they are never common in any of the associations.

Diaphus kokeni (PROCHAZKA, 1893)
Pl. 2, Figs. 1-6

1893 *Otolithus (Berycidarum) Kokeni* nov. spec. - PROCHAZKA, p. 81, pl. 3, fig. 3a, b;
1905 *Otolithus (Berycidarum) Kokeni* PROCH. - SCHUBERT, p. 631, pl. 17, figs. 9-11 (non 8);
1958 *Scopelus debilis* (KOKEN) - WEILER, p. 327, pl. 1, fig. 10 (non fig. 9 = *D. taaningi*, non KOKEN, 1891);
1966 *Myctophum kokeni* (PROCHAZKA) - SMIGIELSKA, p. 232, pl. 13, fig. 2a, b;
1967b *Ot. (Myctophidarum) kokeni kokeni* (PROCH.) - BRZOBOHATY, p. 130, pl. 2, fig. 11;
1977 *Diaphus debilis* (KOKEN, E., 1891) - NOLF, p. 18, pl. 2, figs. 11, 12, 15, 16,?13,?14,?18, (non 17, non KOKEN, 1891);
1983 *Diaphus kokeni* (PROCHAZKA) - BRZOBOHATY, pl. 6, fig. 3;
1992 *Diaphus debilis* (KOKEN, 1891) - RADWANSKA, p. 178, pl. 5, figs. 3-6 (non 1-2 = *D. debilis*), textfig. 27 c, d, e, f (non a-b = *D. debilis*), (non KOKEN, 1891).

Holotype: Figured by PROCHAZKA, 1993, pl. 3, fig. 3; from the Badenian of Zidlochovice, Moravia. The original specimen seems to be lost, but otoliths of this species are so characteristic that they can easily be judged from Prochazka's figure, which fits perfectly in our series from the Badenian of Moravia (Pl. 2, Figs 1-6).

Description: These otoliths are characterised by the following features: almost quadrangular outline, with a nearly vertically oriented posterior rim; very well developped, often spine-like posterodorsal angle, which is located at the highest point of the dorsal rim; moderately curved ventral rim, bearing 5 to 7 (exceptionally 8) strong spines; crista superior salient in the anterior part, but sometimes becoming obsolete posteriorly; ventral rim clear and well delimited.

The length of the rostrum and antirostrum varies considerably during ontogenesis: those structures become much more pronounced in large specimens, while otoliths of juveniles are more rounded, and often difficult to separate from *D. debilis*.

Remarks: Otoliths of this species are nearest to those of *Diaphus debilis* and *D. taaningi*; see under *D. debilis* for distinctive features.

Distribution: Paratethys: from Karpatian till the Middle Badenian. North Sea Basin: Hemmoorian (Zonderschot Sands); Reinbekian (Dingdener Feinsand).

Diaphus metopoclampoides STEURBAUT, 1983
Pl. 4, Figs. 7-14

1979 ''genus Myctophidarum'' sp. - STEURBAUT, p. 63, pl. 5, fig. 11;
1981 *Notoscopelus* sp. - RADO, pl. 8, fig. 2;
1983 *Diaphus metopoclampoides* n.sp. - STEURBAUT, p. 257, pl. 1, figs. 22-28;
1984 *Diaphus metopoclampoides* STEURBAUT 1983 - STEURBAUT, p. 53, pl. 7, fig. 23.

Holotype: Figured by STEURBAUT, 1979, pl. 5, fig. 22, and refigured here Pl. 4, Fig. 7; IRSNB P 3704; from the Tanaro Formation, Langhian of Marrone, Piemonte.

Remarks: These high otoliths are relatively common in the Mediterranean Miocene and can be distinguished from other *Diaphus* species by their relatively long cauda, which somewhat evocates the genus *Benthosema*. However, the ventral rim with its regular ornamentation of small obtuse spines, and the general aspect of the large specimens (till 4 mm), makes this doubtless a *Diaphus* species. Among Recent species, otoliths of *D. brachycephalus* TAANING, 1928 (see NOLF & STRINGER, 1992, pl. 10, figs 4-9) and *D. metopoclampus* (COCCO, 1829) (see NOLF & MARTINELL, 1980, pl. 2, figs. 9-14) are closest to *D. metopoclampoides*, but have a markedly more prominent rostrum.

Distribution: Northern Italy: Upper Burdigalian (Termo Fora Complex), Langhian, Serravallian, Tortonian, ? Messinian of Borelli; Paratethys: Lower Badenian; Aquitaine: Upper Burdigalian (Zone NN 3 - NN 4) and Langhian interval of the Saubrigues Marls.

Diaphus pedemontanus (ROBBA, 1970)
Pl. 4, Figs 1-6

1970 *Porichthys pedemontanus* sp. n. - ROBBA, p. 151, pl. 16, fig. 8.
1979 *Diaphus pulcher* (PROCHAZKA 1893) - SCHWARZHANS, p. 9, pl. 2, fig. 25 (non figs. 22-24, non PROCHAZKA 1893).
1979 *Diaphus* sp. - SCHWARZHANS, p. 10, pl. 2, fig. 26, pl. 11, fig. 128;
1980 ''genus Neobythitinorum'' pedemontanus (ROBBA, 1970) - NOLF, p. 137;
1983 *Diaphus pedemontanus* (ROBBA, 1970) - NOLF & STEURBAUT, p. 154, pl. 1, figs. 26-37;
1983 *Diaphus* sp. 1 - NOLF & STEURBAUT, p. 156, pl. 1, fig. 25;
? 1983 *Diaphus pedemontanus* (ROBBA, 1970) - STEURBAUT, p. 257, pl. 1, figs. 13-19;
1994 *Diaphus* sp. 2 - NOLF & CAVALLO, pl. 3, figs. 6,? 5;
1998 *Diaphus* sp. 2 - NOLF, MANE & LOPEZ, pl. 2, fig. 1 (non fig. 2 = abnormal specimen?).

Holotype: Figured by ROBBA, 1970, pl. 16, fig. 8, IPUM PE 385, from his locality 7 in the Tortonian of the Rio Mazzapiedi-Castellania.

Remarks: This species grows to a very large size. The holotype otolith attains a length of 6.9 mm; the specimen figured here at Pl. 4, Fig. 1 attains 7.3 mm, and must come from a fish approximately 20 cm in length (a *D. adenomus* otolith of 10.5 mm, the largest *Diaphus* otolith among our Recent comparative material comes from a fish of 26.5 cm total length). The growth series shown at Pl. 4, Figs. 1-6 shows strong ontogenetic changes, and in very large otoliths, the sulcus becomes deeply incised, the antirostrum is strongly developed and prominent, and there is a backwards expansion in the lower part of the posterior rim. These otoliths are probably from fishes that changed their mesopelagic habitat into a benthic way of life, when they attained a very large size (which is also the case in *D. adenomus*). Variability in these specimens is also considerable. Many Zanclean otoliths, like those figured here at Pl. 4, Figs. 2-6 have a more undulant dorsal rim than the average Tortonian specimens, figured by NOLF & STEURBAUT (1983, pl. 1, figs. 26-37).

Distribution: Northern Italy: Upper Burdigalian (Termo Fora Complex), Langhian (basis of the Complex of Baldissero), Serravallian, Tortonian, ? Messinian of Borelli; Zanclean of SE France and Catalania. Some juvenile otoliths from the Lower Badenian of the Paratethys may also belong to *D. pedemontanus*, but unquestionable records of this species are known from the Mediterranean realm only.

Diaphus rafinesquii (COCCO, 1838)
Pl. 3, Figs. 11-14

1972 *Myctophum splendidum* (PROCHAZKA, 1893) - ANFOSSI & MOSNA, p. 101, pl. 17, fig. 1 (non PROCHAZKA, 1893);
1985 *Diaphus rafinesquei* (COCCO, 1838) - BOSSIO, LANDINI, MAZZEI, SALVATORINI & VAROLA, p. 57, pl. 2, fig. 5;
1989 *Diaphus rafinesquei* (COCCO, 1838) - NOLF & CAPPETTA, pl. 10, fig. 21;
1994 *Diaphus rafinesquei* (COCCO, 1838) - NOLF & CAVALLO, pl. 2, fig. 5.

Holotype: A Recent fish from off Messina, figured by COCCO, 1838, pl. 7, fig. 7, as *Nyctophus rafinesquii*; no type material preserved according to ESCHMEYER (1998). A series of Recent otoliths is figured by NOLF & MARTINELL, 1980, pl. 2, figs. 21-26.

Remarks: see under *Diaphus holti*.

Distribution: Like *D. holti*, this Recent species is also present in the Mediterranean realm since the Serravallian, but it is never common in any of the associations.

Diaphus regani TAANING, 1932
Pl. 3, Figs. 15-20

1998 *Diaphus* aff. *regani* TAANING, 1932 - NOLF & AGUILERA, p. 239, pl. 5, figs. 7 - 12.

Holotype: A Recent fish from off New Caledonia, figured by TAANING, 1932, fig. 12 (ZMUC P 2329213). A series of Recent otoliths is figured by NOLF & AGUILERA, 1998, pl. 5, figs. 1-6.

Remarks: The present day distribution of *D. regani* is restricted to the Indo-Pacific realm (WISNER, 1976, NAFPAKTITIS, 1978), but in the Lower Miocene, it frequently occurs in Northern Italy, and has also been recorded from Aquitaine, and from Venezuela (NOLF & AGUILERA, 1998). These Lower Miocene records must be interpreted as a case of an ancient circumtropical Tethys distribution. In the Paleocanyon of Saubrigues, Aquitaine, the first appearance of *D. regani* is a good marker for the beginning of the Miocene, while the last occurrence of *D. perspicillatoides* (see BRZOBOHATY & NOLF, 1996, pl. 4, figs. 17-23) marks the end of the Oligocene. At first glance, both species appear to be similar, but otoliths of *D. regani* always have a strongly expanded anterodorsal area and a narrow posterodorsal area, while in *D. perspicillatoides* the dorsal area is much more symmetrical.

Distribution: Otoliths of this Recent Indo-Pacific species are relatively common in the Lower Miocene of Northern Italy: Aquitanian (Marls of Antognola); Burdigalian (Termo Fora Complex, Pietra da Cantone). There is no convincing evidence for the presence of this species in younger deposits, although some juvenile otoliths from the Mediterranean Tortonian and the Pliocene looks much like those of *D. regani*. Aquitaine: Aquitanian (NN 1 - 2) and Lower Burdigalian (NN 2 - NN 3) interval of the Saubrigues Marls.

Diaphus aff. ***splendidus*** (BRAUER, 1904) species complex
Pl. 6, Figs. 1-5

1906 Otolithus (Berycidarum) *pulcher* PROCHAZKA - BASSOLI, p. 49, pl. 2, figs. 19-20 (non PROCHAZKA);
1906 Otolithus (Berycidarum) *sulcatus* BASS. - BASSOLI, p. 50, pl. 2, figs. 23-24;
1906 Otolithus (Berycidarum) *tuberculatus* BASS. - BASSOLI, p. 50, pl. 2, figs. 25-26;
1970 *Myctophum debile* (KOKEN, 1891) - ROBBA, p. 104, pl. 8, fig. 2 (non fig. 1 = *D.* aff. *holti*, non KOKEN, 1891);
1970 *Myctophum tuberculatum* (BASSOLI, 1906) - ROBBA, p. 109, pl. 8, figs. 8-9;
1970 *Myctophum rossiae* sp. n. - ROBBA, p. 112, pl. 9, figs. 2-4;
1976 Otolithus (Myctophidarum) sp. 2 - ANFOSSI & MOSNA, p. 23, pl. 3, fig. 2a,b;
1983 *Diaphus sulcatus* (BASSOLI, 1906) - NOLF & STEURBAUT, p. 156, pl. 2, figs. 8-15;
1986 *Diaphus rossiae* (ROBBA, 1970) - SCHWARZHANS, p. 222, pl. 4, figs. 43, 45;
1986 *Diaphus sulcatus* (BASSOLI, 1906) - SCHWARZHANS, pl. 4, fig. 44 (non pl. 4, figs. 47-49 = *D. cavallonis*);
1989 *Diaphus sulcatus* (BASSOLI, 1906) - NOLF & CAPPETTA, p. 218, pl. 10, figs. 1-10;
1994 *Diaphus* aff. *splendidus* (BRAUER, 1904) - NOLF & CAVALLO, pl. 2, figs. 8-11;

1998 *Diaphus* aff. *splendidus* (BRAUER, 1904) - NOLF, MANE & LOPEZ, pl. 2, fig. 10.

Remarks: In this species complex, we include all the otoliths which show a reasonable similarity to Recent *D. splendidus* otoliths (see NOLF & CAPPETTA, 1989, pl. 9, figs. 9-11). Such otoliths occur from the Serravallian till the end of the Pliocene. Only some large otoliths from the Tortonian (e.g. Pl. 6, Fig. 1) and some Pliocene specimens from Monticello are almost identical to Recent material of similar size, but many other fossils have a less expanded posterodorsal angle (e.g. the Tortonian series figured by NOLF & STEURBAUT, 1983, pl. 2, figs. 8-15 and the Zanclean population from Le-Puget-sur-Argens figured by NOLF & CAPPETTA, 1989, pl. 10, figs. 1-10), and many intermediate conditions exist. Up to a length of 3 mm, otoliths of this species complex readily fall in the category of elliptical otoliths with a very generalized morphology, non-diagnostic at species level. Another problem is that Recent otolith material from various populations of this worldwide ranging species is not available, which makes it very difficult to judge the meaning of small differences between fossil populations.

Distribution: Very common in the Mediterranean realm, from the Serravallian till the Upper Pliocene.

Diaphus taaningi NORMAN, 1930
Pl. 2, Figs. 7-12

1905 Otolithus (Berycidarum) *austriacus* KOKEN - SCHUBERT, p. 630 (partim), pl. 17, fig. 6 (non 1-5, 7, non KOKEN 1891);
1943 *Scopelus debilis* KOKEN 1891 - WEILER, p. 90 (partim), pl. 1, fig. 8 (non 4-7, 9-13, non KOKEN, 1891);
1949 *Scopelus debilis* KOKEN - WEILER (partim), pl. 1, fig. 8 (non 4-7, pl. 2, figs. 9-13, non KOKEN, 1891);
1950 *Scopelus debilis* (KOKEN 1891) - WEILER, p. 211, pl. 1, fig. 2 (non pl. 9, figs. 66, 67, non KOKEN, 1891);
1958 *Scopelus debilis* (KOKEN) - WEILER, p. 327, pl. 1, fig. 9 (non 10 = *D. kokeni*, non KOKEN, 1891);
1965 *Myctophum debile* (KOKEN, 1891) - BRZOBOHATY, p. 109, pl. 1, figs. 1, 6 (non 2-3, non KOKEN, 1891);
1966 *Myctophum debile* (KOKEN) - SMIGIELSKA, p. 229 (partim), pl. 13, fig. 1 (non pl. 12, figs. 6-8, non KOKEN, 1891);
1967 *Myctophum debile* (KOKEN, 1891) - BRZOBOHATY, p. 232, pl. 1D, fig. 3a,b (non KOKEN, 1891);
1972 *Myctophum debile* (KOKEN) - BAUZA, p. 63, pl., figs. 18-19,? 20-21 (non 22, 23, 25-31, non KOKEN, 1891);
1978 *Diaphus austriacus* (KOK.) - BRZOBOHATY, pl. 1, fig. 10 (non KOKEN, 1891);
1979 *Diaphus debilis* (KOKEN, 1891) - STEURBAUT, p. 62, pl. 3, figs. 9-10 (non KOKEN, 1891);
1983 *Diaphus debilis* (KOKEN) - BRZOBOHATY, pl. 6, fig. 2 (non KOKEN, 1891);
1984 *Diaphus debilis* (KOKEN 1891) - STEURBAUT, p. 53, pl. 7, figs. 24, 25 (non KOKEN, 1891);
1985 *Diaphus debilis* (KOKEN 1891) - NOLF, fig. 47G;
1989 *Diaphus* sp. ind. - NOLF & CAPPETTA, pl. 10, figs. 17-20;
1994 *Diaphus debilis* (KOKEN, 1891) - BRZOBOHATY, pl. 2, figs. 5, 8 (non 6-7, non KOKEN, 1891);
1998 *Diaphus* sp. 2 - NOLF, MANE & LOPEZ, pl. 2, figs. 3-8.

Holotype: A Recent fish from off French Congo, figured by NORMAN, 1930, fig. 30; BMNH 1930.1.12.835. A series of Recent otoliths is figured by STEURBAUT (1979, pl. 3, figs. 11-16).

Remarks: Relationships (or identity) of this Recent species with *D. debilis* and *D. kokeni* were suggested by NOLF (1977) and STEURBAUT (1979), but the availability of otoliths from a wide range of stratigraphically and geographically distinct associations now reveals that three distinct species are involved; see Pl. 2 and comments under *D. debilis* for distinctive features. Moreover, the present revision also suggest that *D. taaningi* is fairly common in the Mediterranean Pliocene, where it was previously cited as *Diaphus* sp. ind. by NOLF & CAPPETTA (1989) and *Diaphus* sp. 2 by NOLF *et al.* (1998), but the average Pliocene specimens tend to be slightly more elongated than the recent material available to us. Such elongate morphology was also observed in specimens from the Lower Pliocene of Dar Bel Hamri, Atlantic Morocco.

Distribution: Mediterranean: Tortonian, no Messinian records; known from the Zanclean till the Gelasian; Paratethys: from the Karpatian till the Upper Badenian; Aquitaine:Langhian interval of the Saubrigues Marls. North Sea Basin: Hemmoorian (Miste Bed, Winterswijk, The Netherlands; Reinbekian (Dingdener Feinsand, NW Germany; Stemerdinck Bed, Winterswijk, The Netherlands).

Otoliths erroneously referred to Diaphus

Bolinichthys italicus (ANFOSSI & MOSNA, 1971)
Textfig. 1

1971 *Diaphus italicus* n. sp. - ANFOSSI & MOSNA, p. 141, pl. 2, figs. 1-3;
1976 *Diaphus italicus* ANFOSSI & MOSNA - IACCARINO & MOSNA, pl. 1, fig. 5;
1983 *Diaphus italicus* ANFOSSI & MOSNA, 1971 - NOLF & STEURBAUT, p. 154;
? 1986 *Diaphus* sp. 2 - BEDINI, FRANCALACCI & LANDINI, p. 38, pl. 2, fig. 9.

Remarks: Those little otoliths (length of the holotype = 1.8 mm), which were considered originally to represent a small *Diaphus* species, seems to be much more closely related to the Recent *Bolinichthys supralateralis* (PARR, 1928), a tropical to subtropical Atlantic species, which is figured here for direct comparison (Fig. 1). The fossil otoliths differ from the Recent ones by their more quadrangular outline, their less curved ventral rim, which bears stronger spines, even at small size, by their more salient and acuminate rostrum, and by their ostium that is more opened anteriorly.

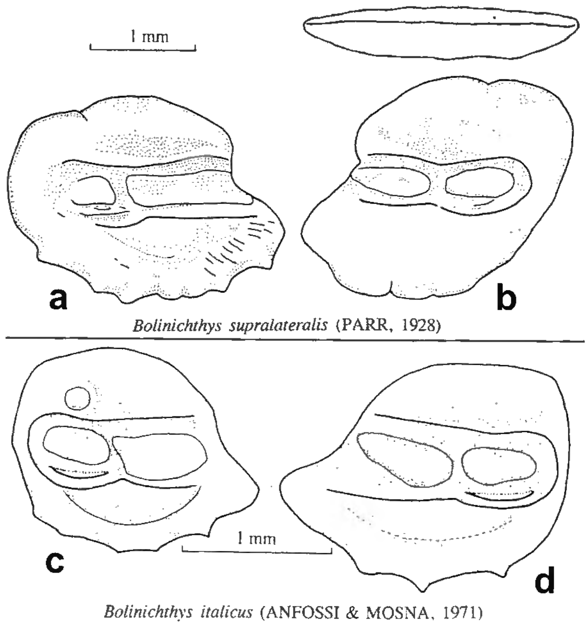

Fig. 1 — Otoliths of (a-b) *Bolinichthys supralateralis* (Recent, off Portugal) and (c-d) *Bolinichthys italicus* (Tortonian of Cascine Valle Sorda, c = holotype, d = paratype).

Distribution: Known by the type material (four otoliths) from the Tortonian of Cascine Valle Sorda near Alessandria, Italy and by specimens from Messinian deposits near Reggio.

Conclusions

The present revision documents the presence of at least fourteen otolith-based *Diaphus* species in the European Neogene. As already stated in the introduction, this number is minimal, and it is even probable that several species with generalized elliptical otolith morphology are hidden in the large amount of non-diagnostic material (many thousands of otoliths) that was left aside. All fourteen recognizable taxa occur in the Mediterranean and Paratethys Basin (Fig. 2). On the Atlantic side (Figure 3), where identifiable *Diaphus* otoliths are known from the Lower and Middle Miocene only, five species are recorded from the Paleocanyon of Saubrigues, Aquitaine, and only four from the North Sea Basin.

It is evident that the main interest of the present study concerns the Mediterranean Basin and its Paratethys de-

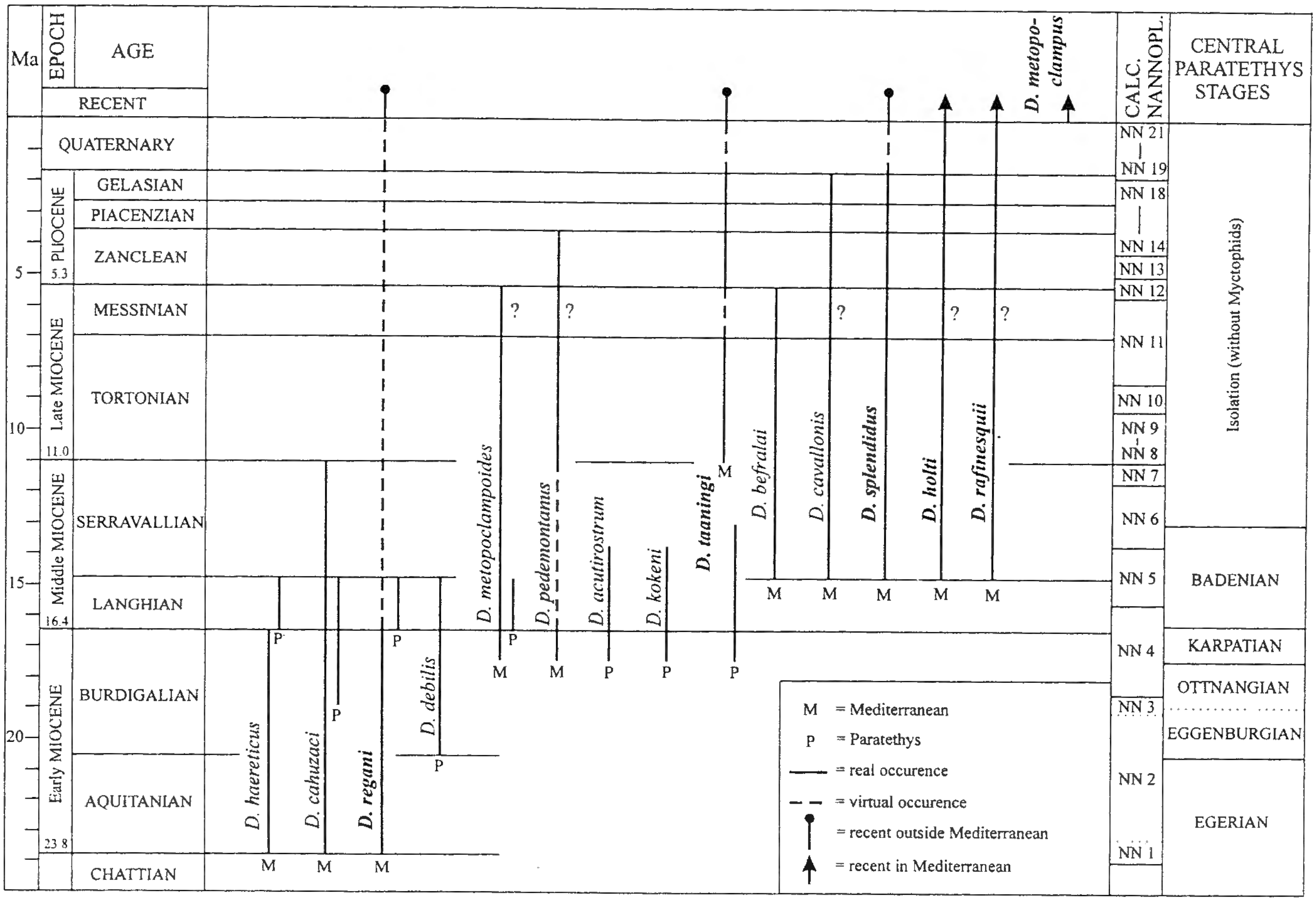

Fig. 2 — Stratigraphic range of Neogene *Diaphus* species in the Mediterranean realm (including the Paratethys) (extinct species which are only known by osteological remains excluded). Correlation of the international and Paratethys stratigraphic scales after RÖGL, 1998.

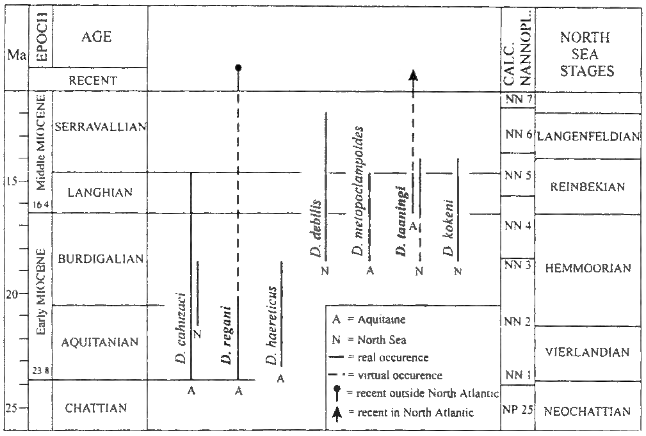

Fig. 3 — Stratigraphic range of Neogene *Diaphus* species in the Aquitaine and the North Sea Basin. Tentative correlation of the international and North Sea Basin stratigraphic scales after LAURSEN *et al.* (1998), LOUWYE & LAGA, 1998 and VANDENBERGE *et al.*, 1998.

pendence. Five of the recorded species are still living today, but three of them, *D. regani, D. taaningi* and *D. splendidus,* only occur outside the Mediterranean. The Recent Mediterranean *D. holti* and *D. rafinesquii* are represented since the Serravallian, but they are uncommon in all the investigated associations. Finally, *D. metopoclampus*, a Recent western Mediterranean inhabitant, has no fossil record. Pliocene associations are dominated by the extinct *D. cavallonis*, and by *Diaphus* aff. *splendidus*, whose Recent relatives live outside the Mediterranean. All this stresses that till the end of the Pliocene (only few data are available for the Pleistocene), the Mediterranean mesopelagic fauna was very different, and essentially more oceanic, than the present day one. The same conclusion could already be drawn for the non-*Diaphus* myctophids (BRZOBOHATY & NOLF, 1996) and a more oceanic character was also demonstrated for Oligocene Mediterranean fish faunas (NOLF & STEURBAUT, 1988; NOLF & BRZOBOHATY, 1994). The present day distribution of *D. regani* is restricted to the Indo-Pacific realm (WISNER, 1976, NAFPAKTITIS, 1978), but in the Lower Miocene, its presence in Northern Italy, Aquitaine, and Venezuela (NOLF & AGUILERA, 1998) must be interpreted as a case of ancient circum-tropical Tethys distribution.

From the biostratigraphic point of view, one can state that the Oligo-Miocene boundary is well marked by *Diaphus*. Four Late Oligocene species, *D. alcoholicus* BRZOBOHATY & NOLF, 1995, *D. longirostris* (BRZOBOHATY, 1967), *D. perspicillatoides* BRZOBOHATY & NOLF, 1995, and *D. pristismetallis* NOLF & BRZOBOHATY, 1994 do not cross the boundary, and both in the Mediterranean Basin and in Aquitaine the appearance of *D. haereticus, D. cahuzaci* and *D. regani* marks the beginning of the Miocene.

Fig. 2 also suggests the simultaneous appearence of five taxa in the Upper Burdigalian, but this faunal renovation may well be an artifact. There are almost no lower Burdigalian deposits investigated for otoliths in the Mediterranean Basin, and in the Paratethys, the interval from the basal Miocene to basal Karpatian does not provide very appropriate facies for collecting mesopelagic fish otoliths. Moreover, the Upper Burdigalian first appearances constitute a mixture of Mediterranean and Paratethys records, and some of the Paratethys species may well be more northern, or pseudoceanic (= living near to continental margins, see NAFPAKTITIS *et al.*, 1977) species. A pseudoceanic habitat is known for the Recent *D. taaningi*, which is one of the species recorded in the Paratethys. We also do not exclude that *D. debilis* and *D. kokeni*, which otoliths are somewhat similar to those of *D. taaningi*, had a pseudoceanic way of life. The presence of these three species in the more shallow and isolated Miocene North Sea Basin may even validate such a point of view.

The first appearance of five species in the Mediterranian Serravallian is an important renovation, especially because four of them continue into the Pliocene, while only two of the nine Lower Miocene species do so. Dating of the event, however, is less precise and it could already have happened in the Langhian, for which we only have good otolith localities in the Paratethys, but not in the Mediterranean Basin *sensu stricto.*

In the North Sea Basin, the only relevant "myctophid event" seems to be an important acme of *D. debilis*, in Langenfeldian deposits.

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Appendix 1: doubtful species and synonyms in the European Tertiary

Diaphus an n. sp. in SULC (1932, p. 2, fig. 1) = not identifiable juvenile specimen.
O. austriacus in KOKEN (1891, p. 122, fig. 14, p. 123) = not interpretable drawing; lectotype SMF 2410 indicated and figured by ZILCH (1965, pl. 37, fig. 1) is a not identifiable juvenile specimen.
Diaphus crassus n. sp. in SCHWARZHANS (1979, p. 10, pl. 2, figs. 19-21, pl. 11, fig. 126-127) = probably aberrant otoliths of *D. holti* TAANING, 1918.
Diaphus dirknolfi n. sp. in SCHWARZHANS (1986, p. 231, pl. 3, figs. 34-35) = doubtful species. Based on type material without diagnostic features. The holotype SMF P 7225 looks very similar to a Recent specimen of *Diaphus garmani* GILBERT, 1906 in the IRSNB collection, another species with very generalized and poorly diagnostic otolith morphology. Type material of *D. dirknolfi* comes from Dar Bel Hamri, Atlantic Morocco, which is outside the geographic area treated here, but the name is mentionned because SCHWARZHANS (1986, p. 223) also attributed 11 non-diagnostic otoliths from Le-Puget-sur Argens to this taxon.
Otolithus (Berycidarum) *insoletus* nov. spec. in PROCHAZKA (1893, p. 60, pl. 3, fig. 8a,b) = doubtful species, based on an eroded specimen, may be a *Notoscopelus*.
Diaphus italicus n. sp. in ANFOSSI & MOSNA (1971, p. 141, pl. 2, figs. 1-3) = *Bolinichthys italicus.*
Scopelus latirostratus n. sp. in WEILER (1950, p. 215, pl. 7, figs. 44-45, pl. 9, fig. 68a-d) = doubtful species; based on not identifiable juvenile otoliths.
Ot. (Berycidarum) *latus* in BASSOLI (1909, p. 41, pl. 2, fig. 27) = doubtful species (see NOLF & STEURBAUT 1983).
Otolithus (Berycidarum) *Moravicus* nov. spec. in PROCHAZKA (1893, p, 57, pl. 3, fig. 1a,b) = doubtful species. Based on a not identifiable eroded juvenile specimen.
Scopelus obliquus n. sp. in WEILER (1943, p. 91, pl. 1, figs. 20, 21) = doubtful species. Based on not identifiable juvenile otoliths.
Diaphus poignantae n. sp. in STEURBAUT (1979, p. 62, pl. 5, figs. 1-6, pl. 12, fig. 4) = doubtful species. Based on not identifiable juvenile otoliths.
Diaphus praerafinesquii n. sp. in WEILER (1971, p. 11, pl. 1, fig. 15) = *D. holti* TAANING, 1918 (see synonymy).
Otolithus (Berycidarum) *pulcher* nov. spec. in PROCHAZKA (1893, p. 58, pl. 3, fig. 17a,b) = not identifiable, eroded specimen, nomen dubium.
Myctophum regulare n. sp. in SMIGIELSKA (1966, p. 236, pl. 13, figs. 7, 8, Textfig. 2) = doubtful species. Based on an eroded, non-diagnostic specimen.
Otolithus (Berycidarum) *splendidus* nov. spec. in PROCHAZKA (1893, p. 59, pl. 3, fig. 5) = rejected species; based on an eroded, non-diagnostic specimen. See also remarks under *Diaphus acutirostrum* (HOLEC, 1975).
Diaphus rossiae sp. n. in ROBBA (1970, p. 112, pl. 9, figs. 2-4) = *D.* aff. *splendidus* (BRAUER, 1904) species complex.
Diaphus vohnhachti n. sp. in SCHWARZHANS (1986, p. 230, pl. 3, figs. 37-38) = *Lobianchia* aff. *dofleini* (ZUGMAYER, 1911).
Otolithus (Berycidarum) *sulcatus* BASS. in BASSOLI (1906, p. 50, pl. 2, figs. 23-24) = *Diaphus* aff. *splendidus* (BRAUER, 1904) species complex.
Otolithus (Berycidarum) *tuberculatus* BASS. in BASSOLI (1906, p. 50, pl. 2, figs. 25-26) = Diaphus aff. *splendidus* (BRAUER, 1904) species complex.

Explanation of the plates

All figured specimens are deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB), with the exception of the holotype and paratype of *Diaphus haereticus*, which belong to the collection of the Department of Geology and Paleontology of the Masaryk University in Brno (Czechia) (MUB). The abbreviations F and (F) in the upper right corner of each compartment of the plates indicate if the figured specimens in that compartment are fossil [F] or belong to Recent species known as fossils [(F)]. In the captions, L stands for left otolith and R for right otolith. The notations Fig. a, b and c are used to indicate respectively ventral and inner (=mesial) views. Figures with only numbers and no letter show inner views.

PLATE 1

Figs. 1-14 — *Diaphus haereticus* (BRZOBOHATY & SCHULTZ, 1978). 1-7 = R, Antognola Marls, Aquitanian, Moleto-Prera (IRSNB P 7328 - P7334), 8-9 = R, Langhian (Badenian), Zabcice, 8 = holotype (MUB 0251), 9 = paratype (MUB 0250), 10-12 = R, Pietra da Cantoni, Upper Burdigalian, Ponzano (IRSNB P 7335 - P 7337), 13-14 = Lower Burdigalian interval of the Saubrigues Marls, 13 = L, 14 = R (IRSNB P 7338, P 7339).

PLATE 2

Figs. 1-6 — *Diaphus kokeni* (PROCHAZKA, 1893). Langhian (Badenian), Drnovice (IRSNB P 7340 - P 7345).
Figs. 7-12 — *Diaphus taaningi* NORMAN, 1930. L, Langhian (Badenian), Brno, Kralovo Pole (IRSNB P 7346 - P 7351).
Figs. 13-18 — *Diaphus debilis* (KOKEN, 1891). 13-15 = L, 16-18 = R, Glimmerton, Langenfeldian, Gross Pampau (IRSNB P 7032 - P 7037).

PLATE 3

Figs. 1-6 — *Diaphus acutirostrum* (HOLEC, 1975). 1 = Langhian (Badenian), Cerna Hora (IRSNB P 7352), 2-6 = L, Langhian (Badenian), Drnovice (IRSNB P 7353 - P 7257).

Figs. 7-10 — *Diaphus holti* TAANING, 1918. 7 = L, 8-10 = R, Tortonian, Sant Agata Fossili (IRSNB P 7358 - P 7361).

Figs. 11-14 — *Diaphus rafinesquii* (COCCO, 1838). 11 = L, Pleistocene, Santernian, Vrica section, between sapropel e and f (IRSNB P 7362), 12 = L, 13-14 = R, Zanclean, Rio Torsero (IRSNB P 7363 - P 7365).

Figs. 15-20 — *Diaphus regani* TAANING, 1932. 15-16 = L, 17-20 = R, 15-16 and 18-20 = Termo Fora Complex, Burdigalian, Sciolze (IRSNB P 7366 - P 7370), 17 = basement of the Baldissero Complex, Langhian, Baldissero, point 5 (IRSNB P 7371).

PLATE 4

Figs. 1-6 — *Diaphus pedemontanus* (ROBBA, 1970). 1 = L, Tortonian, Rio Mazapiedi-Castellania (IRSNB P 3782), 2-6 = R, Zanclean, Le-Puget-sur-Argens (IRSNB P 7372 - P 7376).

Figs. 7-14 — *Diaphus metopoclampoides* STEURBAUT, 1983. 7 = R, Holotype (IRSNB P 3704), Tanaro Formation, Lower Langhian, Marrone., 8-10 = R, 11-14 = L, basement of the Baldissero Complex, Langhian, Baldissero, point 5 (IRSNB P 7377 - P 7378).

PLATE 5

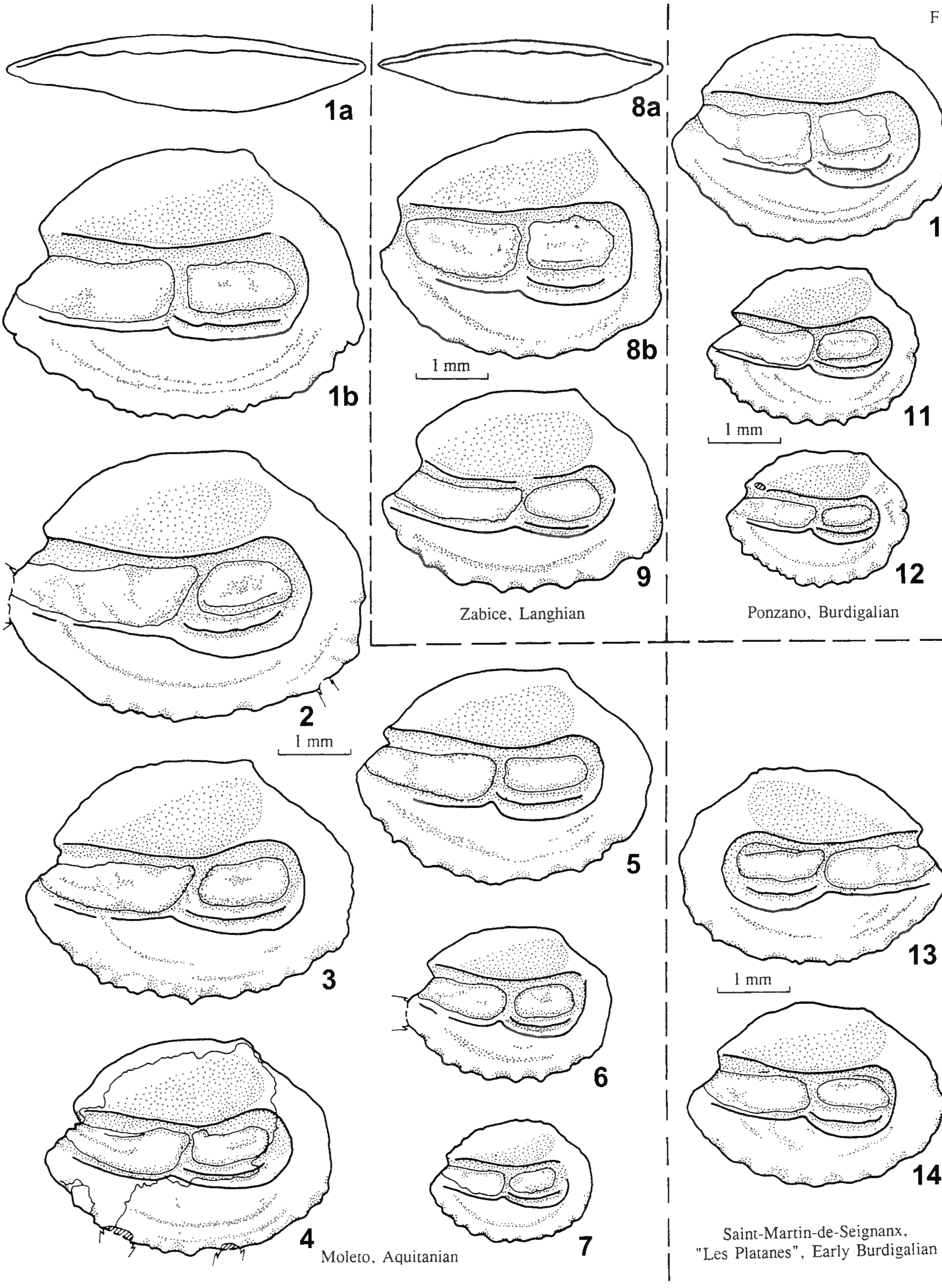
Figs. 1-6 — *Diaphus cahuzaci* STEURBAUT, 1979. 1-5 = L, Antognola Marls, Aquitanian, Moleto-Prera (IRSNB P 7384 - P 7388), 6 = R, holotype (IRSNB P 3035), Langhian interval of the Saubrigues Marls.

Figs. 7-14 — *Diaphus cavallonis* n. sp. L, 7 = holotype (IRSNB P 7389), 8-10 = paratypes. Zanclean, Le-Puget-sur-Argens (IRSNB P 7390 - P 7392), 11-14 = Serravallian, Madonna della Neve near Mondovi (IRSNB P 7393 - P 7396).

PLATE 6

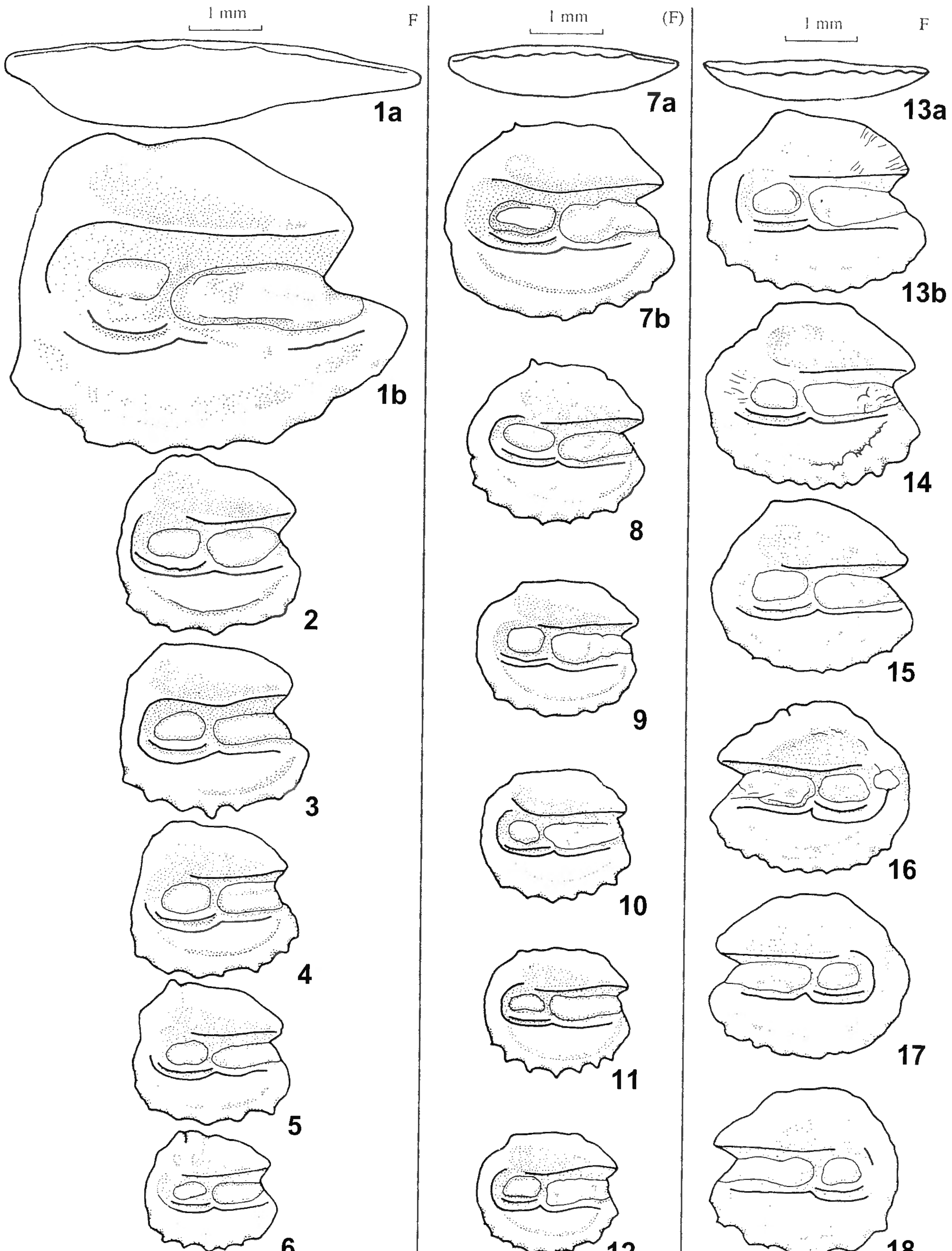
Figs. 1-5 — *Diaphus* aff. *splendidus* (BRAUER, 1904) species complex. 1 = L, Tortonian, Sant Agata Fossili, Point c of NOLF & STEURBAUT, 1983 (IRSNB P 7387), 2-5 = R, Torremondo Marls, Messinian, Venta de la Virgen (IRSNB P 7398 - P 7401).

Figs. 6-11 — *Diaphus befralai* n. sp. L, 6-8 = Serravallian, Madonna della Neve near Mondovi (IRSNB P 7402 - P 7404), 9-11 = Tortonian, Sant Agata Fossili, Point c of NOLF & STEURBAUT (1983), 9-10 = paratypes (IRSNB P 7405, P 7406), 11 = holotype (IRSNB P 7407).



Diaphus haereticus (BRZOBOHATY & SCHULTZ, 1978)

PLATE 1



Diaphus kokeni (PROCHAZKA, 1893)

Diaphus taaningi NORMAN, 1930

Diaphus debilis (KOKEN, 1891)

PLATE 2

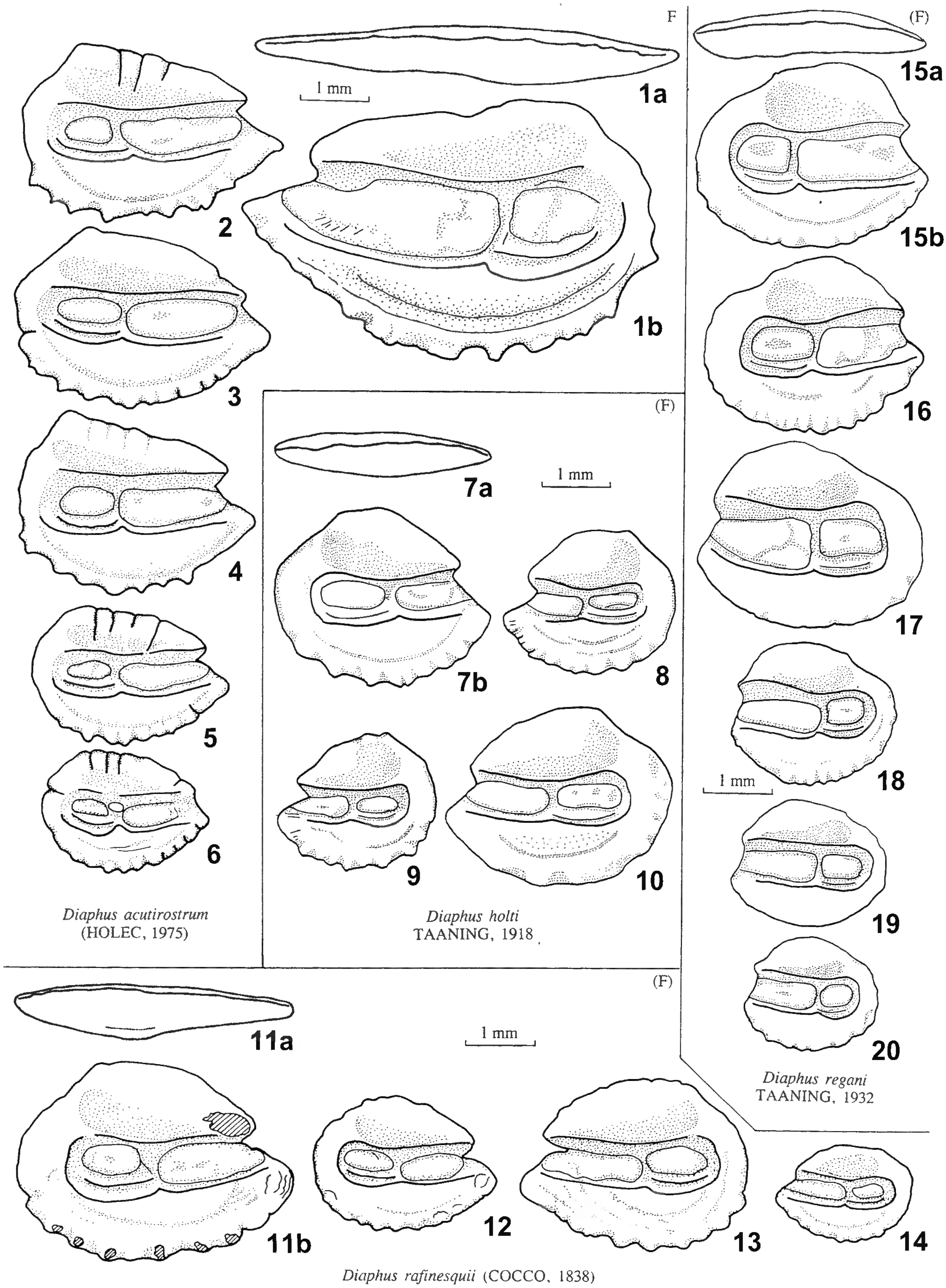
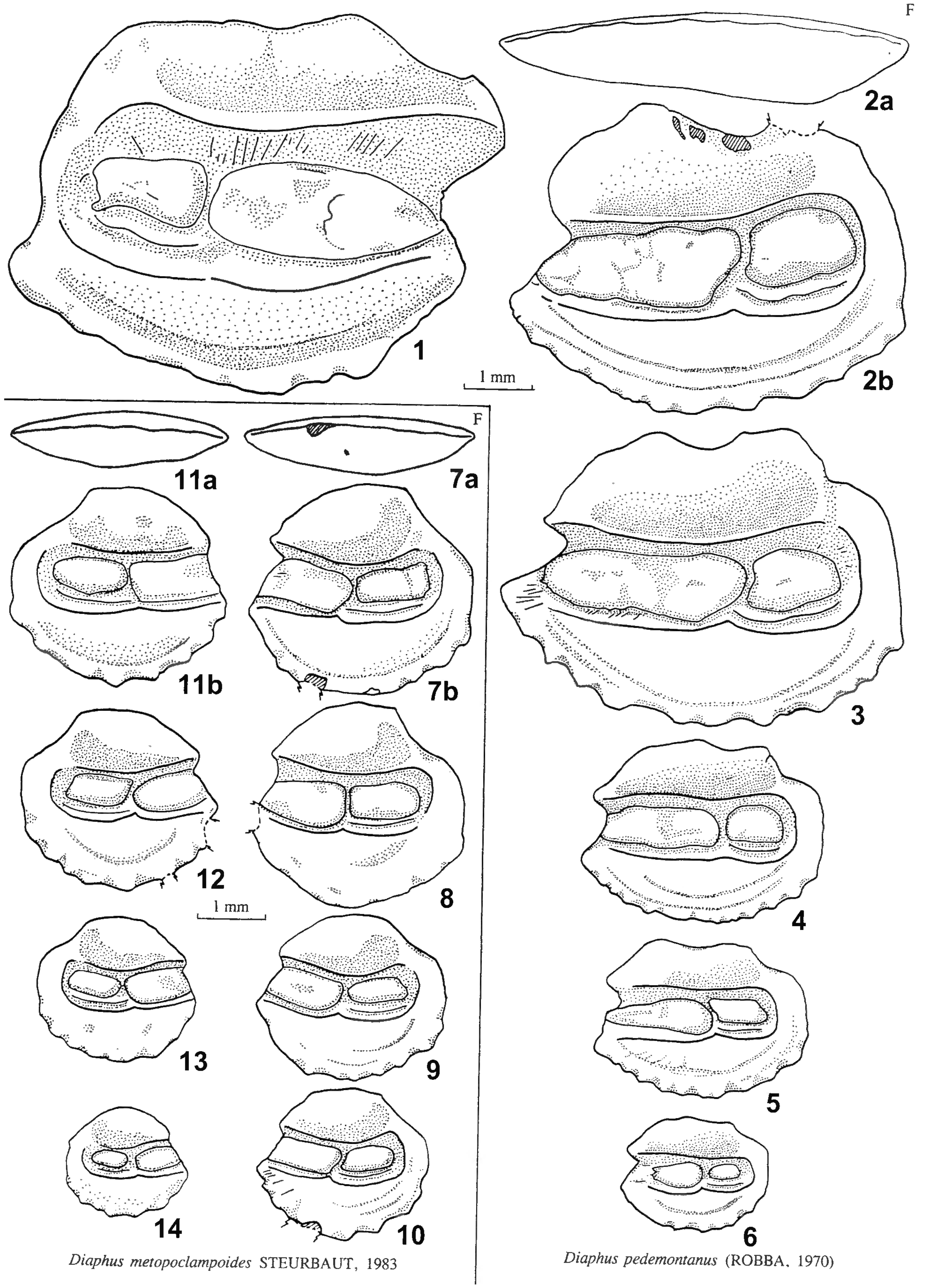

F
1 mm
1a
1b
2
3
4
5
6
Diaphus acutirostrum
(HOLEC, 1975)
(F)
7a
1 mm
7b
8
9
10
Diaphus holti
TAANING, 1918
(F)
15a
15b
16
17
18
1 mm
19
20
Diaphus regani
TAANING, 1932
(F)
11a
1 mm
11b
12
13
14
Diaphus rafinesquii (COCCO, 1838)

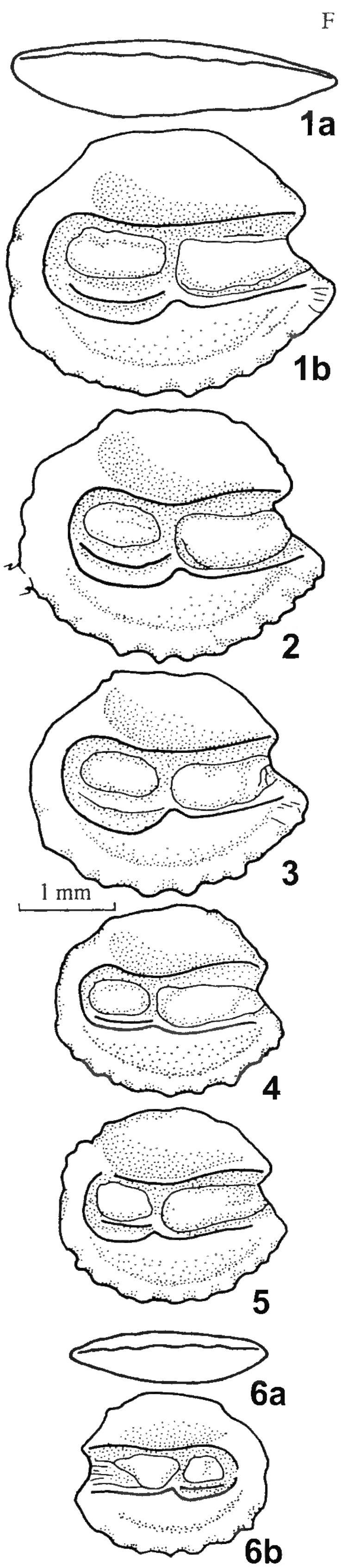
PLATE 3



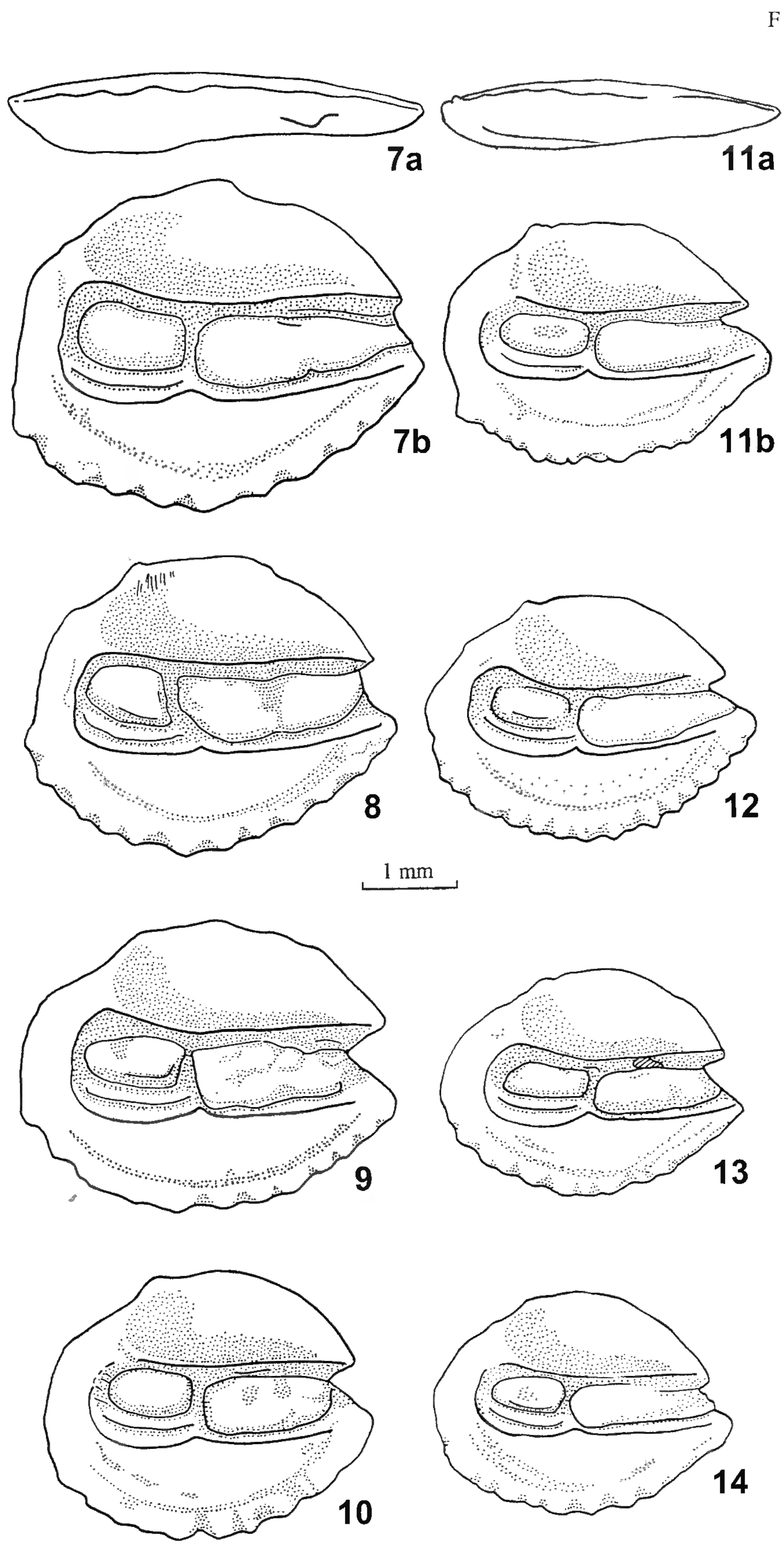
Diaphus metopoclampoides STEURBAUT, 1983

Diaphus pedemontanus (ROBBA, 1970)

PLATE 4



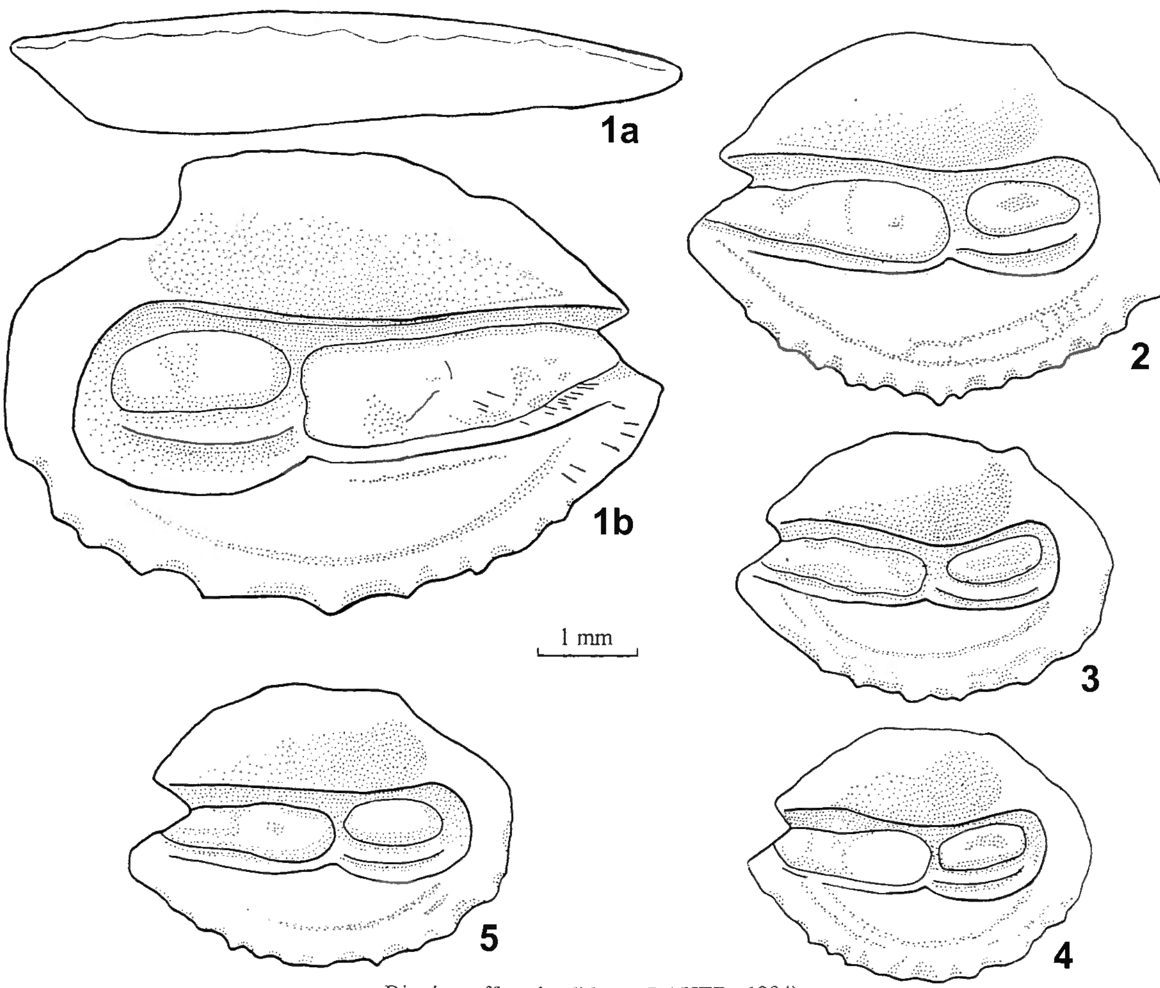
Diaphus cahuzaci
STEURBAUT, 1979



Diaphus cavallonis n. sp.

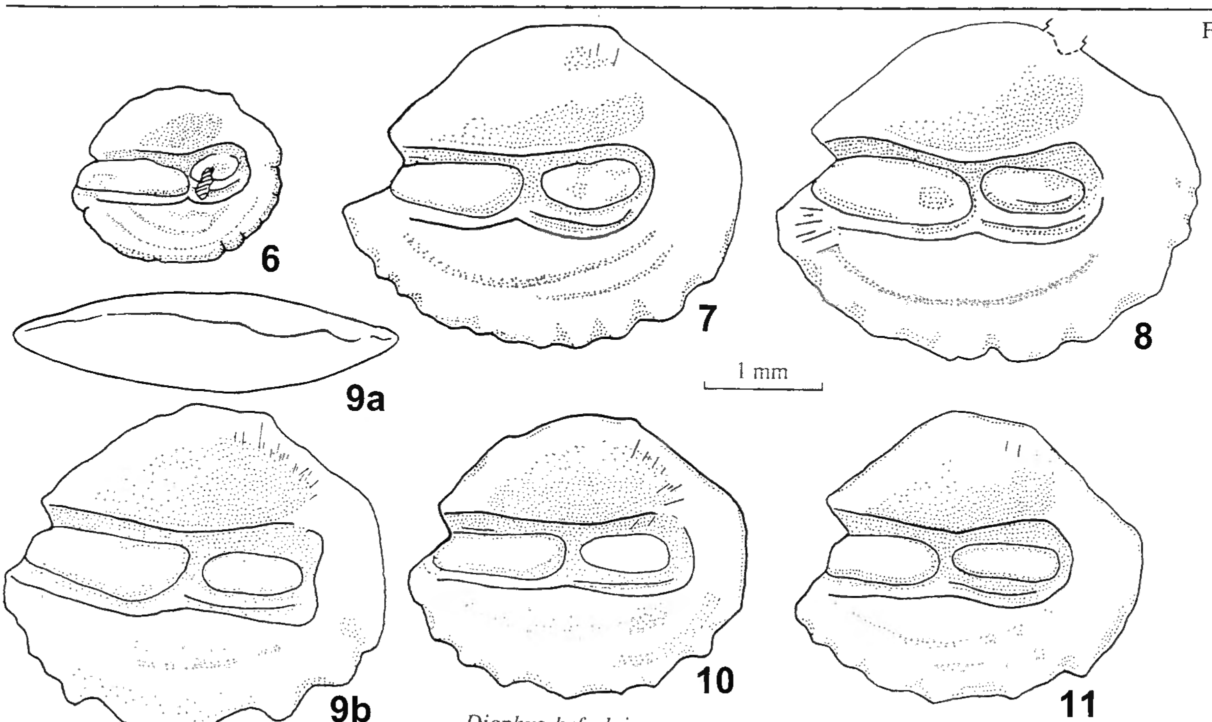
PLATE 5

(F)



Diaphus aff. *splendidus* (BRAUER, 1904)

F



Diaphus befralai n. sp.

PLATE 6