

# Diaphus otoliths from the European Oligocene (Myctophidae, Teleostei )

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## Abstract

The revision of Oligocene otoliths of the myctophid genus *Diaphus* based on extensive otolith collections in the Aquitaine Basin, the French Alps, northern Italy and the Paratethys has proved the validity of only six nominal species: *D. alcoholicus* n.sp., *D. longirostris* (BRZOBOHATY, 1967), *D. molossus* NOLF & STEURBAUT, 1988, *D. perspicillatooides* n.sp., *D. pristismetallis* NOLF & BRZOBOHATY, 1994 and *D. stafforaensis* NOLF & STEURBAUT, 1988. None of these species has been recorded previously from Eocene or Miocene deposits.

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

## Résumé

La révision des espèces oligocènes du genre *Diaphus*, basée sur un abondant matériel d'otolithes récoltées dans le Bassin d'Aquitaine, les Alpes françaises, l'Italie septentrionale et la Paratethys a révélé la validité de six espèces nominales: *D. alcoholicus* n.sp., *D. longirostris* (BRZOBOHATY, 1967), *D. molossus* NOLF & STEURBAUT, 1988, *D. perspicillatooides* n.sp., *D. pristismetallis* NOLF & BRZOBOHATY, 1994 et *D. stafforaensis* NOLF & STEURBAUT, 1988. Aucune de celles-ci n'est connue de dépôts éocènes ni miocènes.

**Mots-clés:** *Diaphus*, Myctophidae, otolithes, Oligocène.

## Introduction

*Diaphus* is the most speciose genus in the family Myctophidae, both Recent and fossil. Recent myctophid taxonomy has been the subject of several thorough revisions during the last decades (NAFPAKTITIS & NAFPAKTITIS, 1969; WISNER, 1976; NAFPAKTITIS & al., 1977; NAFPAKTITIS, 1978; HULLEY, 1981). Fossil myctophids are known from skeletons and from isolated otoliths. However, skeletons with well preserved otoliths in place are so scarce that, in the majority of cases, it is impossible to establish the relationships between the otolith-based and the skeleton-based taxa. The most abundant osteological material has been found in the Late Miocene (Tortonian and Messinian of Italy, Spain and North Africa; data summarised in BIANUCCI & LANDINI, 1994). In the Oligocene, identifiable myctophids are known mainly by otoliths only. All nominal species of Oligocene myctophids based on otoliths belong to the genus *Diaphus*, but

skeletons have been placed in other genera as well (see DANILTSHENKO, 1960; CIOBANU, 1977). Only in *Eomyctophum* cf. *koraensis* DANILTSHENKO, 1947 from the Oligocene Paratethys, have otoliths been recorded in place (SCHWARZHANS, 1985).

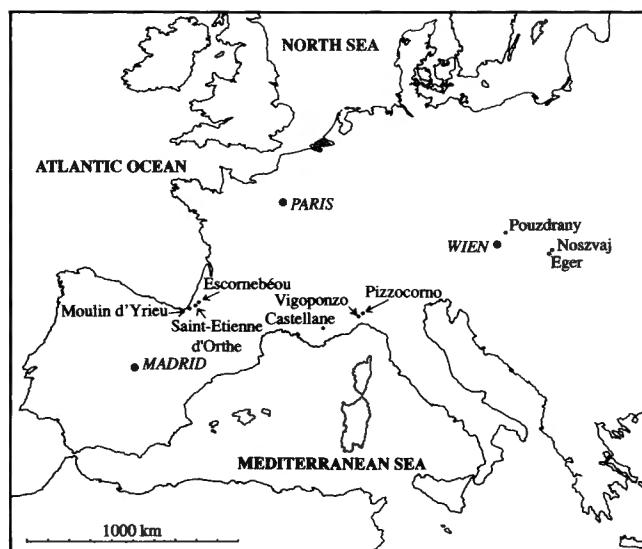
Problems concerning the identification of fossil *Diaphus* otoliths have been discussed recently by SCHWARZHANS (1980), NOLF (1985), NOLF & STEURBAUT (1988) and NOLF & CAPPETTA (1989). Difficulties in the identification of these otoliths can be summarized as follows. The morphology of *Diaphus* otoliths changes markedly during ontogeny (see NOLF & CAPPETTA, 1989, pl. 8-10). Generally, only adult and large otoliths (larger than 2 mm) show clear diagnostic features. In most species, juvenile otoliths lack well-developed features and are not suitable for species identification.

Considering the point above, there is a problem with the so-called "small species", in which adult otoliths do not reach the dimension given above. Such species can be distinguished only in a restricted number of cases (e.g., *Diaphus diademophilus* NAFPAKTITIS, 1978 (Pl. 4, Fig. 1-3)), where even at a small size, the diagnostic features differ markedly from the general *Diaphus* otolith morphology. However, in several Recent *Diaphus* species, even at the adult stage, the otoliths show only a very generalised morphology (see NOLF & CAPPETTA, 1989, pl. 9, fig. 12-22). In fossil associations, such otoliths remain predominantly unidentified; in many cases, it is not even possible to state whether such forms represent species with a more generalised morphology, or whether they are juveniles of species that acquire diagnostic features only at larger size. Practically, this means that most otoliths smaller than 2 mm cannot be used for taxonomic purposes, and species diagnosis and variability can be determined only if abundant adult materials and representative growth series are available.

A last problem is that even weak erosion in the digestive tract of predators (or through other taphonomic agents) already can eliminate important features (e.g., denticulation of the ventral rim) even though the other features are still well preserved. The use of such otoliths in taxonomy increases the inaccuracy of identifications. In palaeontology, the neglect of these facts has led to the

Table 1 — Abundance of the *Diaphus* otoliths at the most important Oligocene localities.

					SPECIES
<i>Diaphus</i> sp.					○ rare ● uncertain ● abundant ● dominant
<i>Diaphus alcoholes</i> n. sp.					
<i>Diaphus longirostris</i> (BRZOBOHATY, 1967)					
<i>Diaphus molossus</i> NOLF & STEURBAUT, 1988					
<i>Diaphus perspicillatooides</i> n. sp.					
<i>Diaphus pristismetalloides</i> NOLF & BRZOBOHATY, 1994					
<i>Diaphus stoffaensis</i> NOLF & STEURBAUT, 1988					
Vigoponzo	●	●	●	●	
Pizzocorno	●	●	●	○	●
Castellane area		●		○	●
Pouzdrany	●	●		●	●
Noszvaj		●			
Moulin d'Yrieu	●				
Saint-Etienne-d'Orthe		●		○	
Escornebœu			●		



Text-fig. 1 — Location of the important European Oligocene localities with *Diaphus* otoliths.

introduction of many invalid species, based only on juvenile otoliths, eroded specimens or too small samples.

Differences in approach and methodologies to the study of myctophid species (Recent fishes, fossil skeletons without otoliths, fossil skeletons with otoliths in situ, isolated fossil otoliths) has contributed to some homonyms in this group (PAXTON, 1979).

The present revision is based on the comparison of large collections of fossils from the Aquitaine Basin, northern Italy, northeastern Hungary, and south Moravia (Table 1) and the comparative collection of Recent otoliths deposited in the IRSNB, Brussels. In the epicontinental deposits of the North Sea Basin, myctophid otoliths are very scarce. Although some *Diaphus* otoliths are recorded from this basin, none of them can be assigned with confidence at species level.

#### Geographic and stratigraphic position of the most important localities (Fig.1)

##### AQUITAIN BASIN (SW France)

**Rivière-Saas-et-Gourby (Escornebœu):** Fine-grained sands (Escornebœu Sands), Zone NP 25, Late Oligocene (Chattian) (STEURBAUT, 1984).

**Saint-Etienne-d'Orthe (Lestelle farm):** Brown clays (Saint-Etienne-d'Orthe Clay), Zone NP 25, Late Oligocene (Chattian) (NOLF & BRZOBOHATY, 1994a).

**Saint-Martin-de-Seignaux (Moulin d'Yrieu):** Beige, fine-grained sands (Yrieu Sands), Zone NP 21, Lower Oligocene (STEURBAUT, 1984).

##### FRENCH ALPS

**Castellane area (several localities):** Blue-grey sandy marls, Early Oligocene (GITTON, 1978).

##### NORTHERN ITALY

**Pizzocorno:** Grey-green, calcareous clays, ? Antognola Formation, Zone NP 21, Lower Oligocene (NOLF & STEURBAUT, 1988).

**Vigoponzo (Casa del Piano):** Grey sandy marls, Early Oligocene (NOLF & BRZOBOHATY, 1994b)

##### HUNGARY (Bük south and east region)

**Eger - region (Wind brickyard, Rosalia cemetery, gravel pit NE of Eger, Novaj: Nyarjas Hill):** Mollusc Clay (Eger Formation), upper part of Zone NP 24, Upper Oligocene (Egerian) (NOLF & BRZOBOHATY, 1994a).

**Noszvaj (hollow road-side):** Brown, calcareous clays (Kiscell Clay), Zone NP 24, Upper Oligocene (Kiscellian) (NOLF & BRZOBOHATY, 1994a).

##### SOUTH MORAVIA (Czech Republic)

**Pouzdrany ("above the Mill"):** Brown, calcareous claystones (Pouzdrany Unit, Pouzdrany Marls), Zone NP 21, Lower Oligocene (BRZOBOHATY, 1982).

**Pouzdrany ("sipek"):** Grey-brown, calcareous claystones

(Pouzdrany Unit, Pouzdrany Marls), Zone NP 22, Lower Oligocene (Kiscellian) (JURASOVA, KRHOVSKY & STRANIK, 1991). **Pouzdrany ("wine cellars"):** Chocolate-brown, highly calcareous claystones (Pouzdrany Unit, Pouzdrany Marls), Zone NP 21/22, Lower Oligocene (Kiscellian) (BRZOBOHATY, 1967).

## Systematic palaeontology

### Family MYCTOPHIDAE

#### *Diaphus alcoholicus* n.sp.

Pl. 1, Figs. 1-6.

- ? 1964 *Myctophum excavatum* (SULC) - BRZOBOHATY, p. 236 (name only, juvenile specimens) (non SULC, 1932);
- 1964 *Myctophum* sp. - BRZOBOHATY, p. 237 (name only);
- 1965 *Myctophum debole* (KOK.) - BRZOBOHATY, p. 279, (partim; non KOKEN, 1891);
- ? 1965 *Myctophum excavatum* (SULC) - BRZOBOHATY, p. 279 (name only; eroded specimens) (non SULC, 1932);
- 1967 *Myctophum debole* (KOKEN, 1891) - BRZOBOHATY, p. 127, pl. 2, fig. 1, non fig. 2 (non KOKEN, 1891);
- 1967 *Myctophum* sp. - BRZOBOHATY, p. 128, pl. 3, fig. 1;
- ? 1967 *Myctophum excavatum* (SULC, 1932) - BRZOBOHATY, p. 128, pl. 2, fig. 8 - 10, 12 (eroded specimens) (non SULC 1932);
- ? 1975 *Myctophum excavatum* (SULC) - BRZOBOHATY, KALABIS & SCHULTZ, p. 470 (name only) (non SULC 1932).

**Type material:** Holotype: a left otolith (Pl. 1, Fig. 1) (IRSNB P 6182); more than 100 paratypes of which five are figured (Pl. 1, Figs. 2-6) (IRSNB P 6183 - P 6187).

**Dimensions of the holotype:** Length: 3,4 mm; height: 2,6 mm; thickness: 0,7 mm.

**Stratum typicum:** Pouzdrany Marls, Pouzdrany "wine cellars", Lower Oligocene, south Moravia.

**Derivatio nominis:** *Alcoholicus*, a, um: alcoholic; alludes to the great abundance of this species around the wine cellars at Pouzdrany.

**Diagnosis:** The otoliths of this species present a globally elliptical outline. The rostrum is rather sharp and longer than the antirostrum; the deep excisura forms a nearly right angle. The ventral rim is regularly curved, with 7-11 robust spines. The truncated part of the outline behind the posterodorsal angle is markedly concave. The anterodorsal part is well developed, with a more or less prominent but smooth anterodorsal angle. In adult specimens, the central part of the dorsal rim shows a shallow concavity in front of the posterodorsal angle. The ostium and cauda are about equal in width, the ostium is about 1,5 times longer than the cauda. A rather deep and wide ventral furrow is located relatively near the ventral rim. The inner face is

regularly convex in both directions, but, viewed ventrally, the outer face is clearly convex in its posterior part and slightly concave anteriorly. In most specimens, the outer face shows a nearly smooth umbo and radial furrows extending to the ventral rim.

**Remarks:** *Myctophum debole* and *Myctophum* sp. figured by BRZOBOHATY (1967) are clearly conspecific with *Diaphus alcoholicus* n.sp. Otoliths cited in the same paper as *Myctophum excavatum* are rather eroded, but may belong to the same species (see synonymy). Otoliths of *D. alcoholicus* are closely related to those of *D. marwicki* (FROST, 1933) and *D. excisus* (FROST, 1933) from the Miocene of New Zealand (see SCHWARZHANS, 1980, p. 60, fig. 167-169, resp. 170-171). Otoliths of both of the New Zealand species are more elongate in the posterior part and have a less expanded anterodorsal portion; *D. excisus* differs by its flatter outer face.

*D. alcoholicus* exhibits a morphology suggesting affinity with the Recent *D. fragilis* - group, especially with *D. lucidus* (GOODE & BEAN, 1896); see NOLF & CAPPETTA, 1989, pl. 8, fig. 1-5. Otoliths of *D. lucidus* have a deeper excisura, a less expanded anterodorsal part, a more narrow sulcus and a flatter outer face.

**Distribution:** Northern Italy (Vigoponzo - dominant among myctophids; Pizzocorno - rare); French Alps (Castellane area - rare); south Moravia (Pouzdrany "wine cellars" - abundant); Aquitaine Basin (St.-Etienne-d'Orthe, Lestelle - uncertain, juvenile specimens only).

#### *Diaphus longirostris* (BRZOBOHATY, 1967)

Pl. 4, Figs. 4-11

- 1908 Otolithus (*Scopelus*) *austriacus* KOK. - SCHUBERT, p. 106, fig. 14, non 15, 16 - eroded specimens (non KOKEN 1891);
- 1964 Ot. (*Myctophidarum*) cf. *kokeni* (PROCHAZKA) - BRZOBOHATY, p. 236 (name only) (non PROCHAZKA, 1893);
- 1965 Ot. (*Myctophidarum*) cf. *kokeni* (PROCH.) - BRZOBOHATY, p. 279 (name only) (non PROCHAZKA, 1893);
- 1967 Ot. (*Myctophidarum*) *kokeni longirostris* n. ssp. - BRZOBOHATY, p. 129, pl. 2, fig. 3-7;
- 1975 *Diaphus kokeni longirostris* (BRZOBOHATY, 1967) - BRZOBOHATY, KALABIS & SCHULTZ, p. 465;
- 1981 *Myctophum debole* (KOKEN, 1891) - PFEIL, p. 371, pl. 3, fig. 5-6 (? 7, 8, 9 - strongly eroded specimens) (non KOKEN 1891).
- 1982 *Diaphus festivus* n. sp. - BRZOBOHATY, p. 346, fig. 6 - 11;
- 1983 *Diaphus festivus* - BRZOBOHATY, p. 250, 252, fig. 1.1;
- 1983 *Diaphus longirostris* - BRZOBOHATY, p. 251, 252, fig. 1.2, pl. 1, fig. 5.

**Remarks:** This species is characterised by rather high otoliths with a strongly developed rostrum. The ventral rim is regularly concave, with 6 - 9 conspicuous spines. The lower rim of the cauda is deeply concave and the cauda is wider than the ostium.

*Diaphus festivus* BRZOBOHATY, 1982, from the Pouz-

drany Marls (BRZOBOHATY, 1982) is based only on juvenile specimens, which suggest characteristics similar to *D. longirostris* and could be conspecific with the latter.

**Distribution:** Otoliths of this species are widely distributed in the West Carpathian Oligocene, Zone NP 21 - NP 25 (Pouzdrany Marls - Sitborice Member) (BRZOBOHATY, 1981) and in the Bavarian Molasse ("Schönecker Fischschiefer", Zone NP 21; PFEIL, 1981). Only four isolated specimens have been recorded from Vigoponzo. Some eroded or juvenile specimens from Pizzocorno and from Castellane are also tentatively attributed to *D. longirostris*.

***Diaphus molossus* NOLF & STEURBAUT, 1988**  
Pl. 3, Figs. 1-8

1988 *Diaphus molossus* n.sp. - NOLF & STEURBAUT, p. 222, pl. 2, fig. 7-11.

**Remarks:** Otoliths of this species are the largest among the known fossil species of *Diaphus*. They have an elongate subrectangular outline with a blunt salient rostrum and a marked postdorsal angle. Additional specimens from Vigoponzo (Pl. 3, Figs. 2-6) complete the known ontogenetic series. Younger specimens show a better developed antirostrum.

**Distribution:** Northern Italy (Pizzocorno - dominant among Myctophids; Vigoponzo - abundant).

***Diaphus perspicillatooides* n.sp.**  
Pl. 4, Figs. 17 - 22

**Type material:** Holotype: a right otolith (Pl. 4, Fig. 17) (IRSNB P 6222); 17 paratypes of which five are figured (Pl. 4, Figs. 18-22) (IRSNB P 6223 - P 6227).

**Dimension of the holotype:** Length: 4,5 mm, height: 3,4 mm, thickness: 0,4 mm.

**Stratum typicum:** Saint-Etienne-d'Orthe Clay, Upper Oligocene, Saint-Etienne-d'Orthe - Lestelle, Aquitaine.

**Derivatio nominis:** Alludes to a superficial resemblance with otoliths of the Recent species *Diaphus perspicillatus* (OGILBY, 1898).

**Diagnosis:** This species is characterised by oval, relatively high otoliths. The rostrum and the antirostrum are sharp, the former being more salient. The excisura is moderately incised and the ventral rim bears 13-17 small spines. The truncated part of the outline behind the nearly smooth posterodorsal angle is long and slightly concave. Most specimens show a rather deep depression in the dorsal area and in the ventral area, a distinct ventral

furrow located high on the ventral area is observed in most of the specimens. The ostium is twice as long as the cauda and widens toward the anterior rim. The ostial colliculum narrows anteriorly and often does not extend to the anterior rim.

The inner face is regularly convex in both directions. The outer face is asymmetrically convex, the greatest convexity being located in the posterior portion. It is almost flat in the central part and sculptured with short radial furrows near to the rims.

**Remarks:** Otoliths of *D. perspicillatooides* are very similar to those of the Recent *D. perspicillatus* (OGILBY, 1895) (Pl. 4, Figs. 12-16), but the latter have a less extended posterodorsal part, a narrower cauda and a more convex inner face. Otoliths of three other Recent species have a somewhat similar outline. Those of *D. philipsi* FOWLER, 1934 and *D. regani* TAANING, 1932 are relatively shorter; those of *D. garmani* GILBERT, 1906 (SCHWARZHANS, 1980, fig. 160) have a concave middle part in the outer face.

**Distribution:** Upper Oligocene (Chattian) of the Aquitaine Basin (Saint-Etienne-d'Orthe, Lestelle - the dominant myctophid in the association; Escornebœu - rare).

***Diaphus pristismetallis* NOLF & BRZOBOHATY, 1994**  
Pl. 1, Figs. 7 - 16

- 1965 *Myctophum debile* (KOK.) - BRZOBOHATY, p. 279 (partim) (non KOKEN, 1891);
- 1967 *Myctophum debile* (KOK.) - BRZOBOHATY, p. 127, pl. 2, fig. 2, non fig. 1 (non KOKEN, 1891);
- 1967 *Myctophum* sp. aff. *biatlanticum* (WEILER, 1959) - BRZOBOHATY, p. 128, pl. 3, fig. 3 & 8 (non WEILER, 1959);
- 1994a *Diaphus pristismetallis* n.sp. - NOLF & BRZOBOHATY, p. 233, pl. 4, fig. 9-14.

**Remark:** Otoliths of *D. pristismetallis* are common at several of the studied localities. They are characterised by an elongate oval outline with a salient rostrum and a regularly curved ventral rim with 12 or more small spines. Other features, such as the excisura, the antirostrum and the postdorsal angle, are only slightly marked.

The inconspicuous morphology of these otoliths suggests affinities with several Recent species (e.g., *Diaphus nielseni* NAFAKTITIS, 1978; see NOLF & CAPPETTA, 1988, pl. 9, fig. 19-22). Otoliths of *D. pristismetallis* without perfectly preserved spines on the ventral rim cannot be identified.

**Distribution:** Northern Italy, Lower Oligocene (Vigoponzo - abundant; Castellane - rare); south Moravia, Lower Oligocene (Pouzdrany "wine cellars" - abundant); Hungary, Upper Oligocene, (Noszvaj - dominant among myctophids); Aquitaine Basin, Upper Oligocene (Saint-Etienne-d'Orthe, Lestelle - rare).

***Diaphus stafforaensis* NOLF & STEURBAUT, 1988**  
Pl. 2, Figs. 1-6

- 1984 *Diaphus* sp. 1 - STEURBAUT, p. 54, pl. 8, fig. 10-11;  
1988 *Diaphus stafforaensis* n.sp. - NOLF & STEURBAUT, p. 223,  
pl. 2, fig. 12-15.

**Remarks:** The most characteristic features of this species are the elongate oval outline with a salient rostrum, the sharp, spine-like posterodorsal angle, the relatively long and wide cauda, the poorly developed anterodorsal portion and the irregular dentition of the ventral rim. These otoliths can reach gigantic dimensions (e.g., Pl. 2, Fig. 1). For their relationships with other species, see NOLF & STEURBAUT (1988).

**Distribution:** Northern Italy, Lower Oligocene (Pizzocorno and Vigoponzo - abundant); Aquitaine Basin, Lower Oligocene (Moulin d'Yrieu - rare).

***Diaphus* sp.**  
Pl. 2, Figs. 7-12

- 1988 *Diaphus* sp. 1 - NOLF & STEURBAUT, p. 223, pl. 2,  
figs. 16-17.

**Remarks:** This species includes otoliths which have a regularly elongate outline, an irregular dentition of the ventral rim, but no other clear diagnostic features. Relationships to fossil and Recent species are discussed in NOLF & STEURBAUT (1988). A specific determination of these otoliths remains open.

**Distribution:** Northern Italy, Lower Oligocene (Vigoponzo and Pizzocorno - rare); south Moravia, Lower Oligocene (Pouzdrany "wine cellars" - rare).

#### Additional data on Oligocene *Diaphus* otoliths

Besides the species mentioned above, several records of non-diagnostic *Diaphus* otoliths and citations without iconography, which cannot be verified, are known. In the epicontinental Oligocene deposits of the North Sea Basin, *Diaphus* otoliths are very scarce, and represented mainly by non-diagnostic forms. POSTHUMUS (1923, p. 125 and 126) mentions *Diaphus* otoliths from Oligocene and Miocene deposits of the Netherlands under the names *Otolithus (Scopelus) austriacus* (KOKEN, 1891) and *Otolithus (Scopelus) pulcher* (PROCHAZKA, 1893), but did not figure specimens from the Oligocene. Moreover, both nominal species cited are nomenclaturally doubtful (see NOLF, 1985).

WEILER (1942, p. 21 and 1958, p. 327) mentions *Diaphus* otoliths from Oligocene and Miocene deposits of the North Sea Basin under the name *Scopelus debilis* (KOKEN, 1891), but he also did not figure any specimen from the Oligocene. The only documented record from the

North Sea Basin is a single specimen from the Chattian of northern Germany, figured as *Diaphus* sp. by MÜLLER (1990, p. 46, pl. 6, fig. 7).

Other non-diagnostic material has been figured from the Lower Oligocene of northern Italy (NOLF & STEURBAUT, 1988, p. 223, pl. 1, fig. 11: *Diaphus* sp. 2), from the Late Oligocene Eger Formation of Hungary (NOLF & BRZOBONATY, 1994a, pl. 7, fig. 4-5: *Diaphus* sp.) and from New Zealand (SCHWARZHANS, 1980, p. 53: three eroded otoliths from the Whaingaroan as *Diaphus* sp.; a citation with a question mark of the Miocene species *D. curvatus* SCHWARZHANS, 1980 for the Waitakian can be found in table 2 of the same paper).

Oligocene otolith records of myctophids other than *Diaphus* include only a species of *Lobianchia* from the Late Oligocene of Escornebœuf, originally described as *L. dofleinoides* STEURBAUT, 1982 (p. 52, pl. 8, fig. 3-7) and subsequently synonymised with the Recent *L. dofleinii* ZUGMAYER, 1911 by NOLF & CAPPETTA (1989, p. 218). A record of *Lampanyctodes* otoliths from the Lower Oligocene of Moravia by BRZOBONATY (1987, p. 85) is based on three non-diagnostic specimens; we considered it as unsupported.

#### Conclusions

In the European Oligocene, only six nominal *Diaphus* species have been found: *Diaphus alcoholicus*, *D. longirostris*, *D. molossus*, *D. perspicillatoides*, *D. pristism-*

Table 2 — Stratigraphic range of the Oligocene species of *Diaphus*.

		CHRONOSTRATIGRAPHY		Nannoplankton biostratigraphy after MARTINI (1971)	<i>Diaphus alcoholicus</i> n. sp.	<i>Diaphus longirostris</i> (BRZOBONATY, 1967)	<i>Diaphus molossus</i> NOLF & STEURBAUT, 1988	<i>Diaphus perspicillatoides</i> n. sp.	<i>Diaphus pristimetalis</i> NOLF & STEURBAUT, 1988	<i>Diaphus stafforaensis</i> NOLF & STEURBAUT, 1988	<i>Diaphus</i> sp.
OLIGOCENE	Mediterranean	Aquitanian	Central Paratethys								
OLIGOCENE	Egerian	Chattian	Rupelian	NN 1							
				NP 25	?						
				NP 24							
	Kiscellian	Priabonian	Priabonian	NP 23							
				NP 22							
				NP 21							
				NP 20							

*tallis* and *D. stafforaensis*. Their stratigraphic and geographic distribution is given in Tables 1 and 2. They are abundant in the Mediterranean, Transeuropean (Paratethys) and Eastern Atlantic bioprovinces. In the Boreal region (North Sea Basin), they are very scarce, because this epicontinental environment was more isolated from the oceans. The geographic and stratigraphic range covered is considerable, although the number of sampled sites is restricted. The latter is probably the reason why the majority of the identified species dominate in only one of the studied localities (Table 1): *Diaphus alcoholicus* at Vigoponzo, *D. longirostris* at Pouzdrany, *D. molossus* at Pizzocorno, *D. perspicillatooides* at Saint-Etienne-d'Orthe, and *D. pristismetallis* at Noszvaj.

European Eocene *Diaphus* otoliths have been cited from the Aquitaine Basin only (NOLF, 1988), but none of the six nominal species recorded there crosses the Eocene-Oligocene boundary.

Because of the restricted number of sampling points, our data on the Oligocene material are eclectic, and one cannot accord too much importance to the stratigraphic range of the species recorded. However, it is worthwhile

noting that *D. longirostris* and *D. pristismetallis* have the most extensive ranges: they occur throughout the whole Oligocene, while *D. alcoholicus*, *D. molossus* and *D. stafforaensis* seem to be restricted to the lower Oligocene. *Diaphus perspicillatooides* was recorded only from the Upper Oligocene of the Aquitaine Basin, and its absence in Hungarian sediments of the same age shows that some differences exist in the otherwise homogeneous ichthyofauna found from the Paratethys to the Eastern Atlantic in the range of Zones NP 24 and 25 (NOLF & BRZOBOHATY, 1994a).

Miocene *Diaphus* otoliths are relatively well known from only the Tortonian (NOLF & STEURBAUT, 1983; NOLF & CAPETTA, 1989). A restricted number of species from the Lower and Middle Miocene of the North Sea Basin and Aquitaine have been described until now. None of Oligocene species cited here seems to continue into the Miocene, but a more affirmative statement on this point will be possible only after the study of the very abundant Lower and Middle Miocene material from Aquitaine, northern Italy and Moravia that we collected during the past few years.

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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), with the exception of the holotype of *Diaphus longirostris*, which belongs to the collection of the Moravian Country Museum in Brno (MZM, geol.). The fossil otoliths bear the numbers of the collection of type and figured fossil fish specimens of the IRSNB. The Recent otoliths are part of the reference collection of Recent otoliths at the same Institution. The latter collection is arranged in systematic order without numbering; therefore, such specimens, when figured, bear only the notation "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 fossil (F) or Recent (R). 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, inner (= mesial) and posterior views. Figures with only numbers and no letter show inner views.

#### PLATE 1

- Figs. 1-6 — *Diaphus alcoholes* n.sp. L, 1 = holotype (IRSNB P 6182), 2-6 = paratypes (IRSNB P 6183-6187); Pouzdrany Marls, Pouzdrany, wine-cellars.  
 Figs. 7-16 — *Diaphus pristismetallis* NOLF & BRZOBOHATY, 1994. L, 1 = holotype (IRSNB P 6012); Kiscell Clay, Noszvaj; 8 (IRSNB P 6188); Saint-Etienne-d'Orthe Clay, Saint-Etienne-d'Orthe, Lestelle; 9-12 (IRSNB P 6189-P 6192); Pouzdrany Marls, Pouzdrany, wine-cellars; 13-16 (IRSNB P 6193-P 6196); Arenarie de Ranzano, Vigoponzo, Casa del Piano.

#### PLATE 2

- Figs. 1-6 — *Diaphus stafforaensis* NOLF & STEURBAUT, 1988. 1-5 = L, 6 = R; 1-3 (IRSNB P 6197-P 6199); Arenarie de Ranzano, Vigoponzo, Casa del Piano; 4-6 = ?Antognola Formation, Pizzocorno; (IRSNB P 6200-P 6201, holotype IRSNB P 3419).  
 Figs. 7-12 — *Diaphus* sp.; 7 (IRSNB P 6202); Pouzdrany Marls, Pouzdrany, wine-cellars; 8-12 (IRSNB P 6203-P 6207); Arenarie de Ranzano, Vigoponzo, Casa del Piano.

#### PLATE 3

- Figs. 1-8 — *Diaphus molossus* NOLF & STEURBAUT, 1988. 1-4 = L, 5-8 = R; 1 = holotype (IRSNB P 3414), 7-8 (IRSNB P 6213-P 6214); Antognola Formation, Pizzocorno; 2-6 (IRSNB P 6208-P 6212); Arenarie de Ranzano, Vigoponzo, Casa del Piano.

#### PLATE 4

- Figs. 1-3 — *Diaphus diademophilus* NAFPAKTITIS, 1978. L (coll. IRSNB); Recent, Indonesian seas.  
 Figs. 4-11 — *Diaphus longirostris* (BRZOBOHATY, 1967). 4-7 = R, 8-11 = L; 4 = holotype (MZM geol. 14538); 5-8 = paratypes (IRSNB P 6215-P 6221); Pouzdrany Marls, Pouzdrany, wine-cellars.  
 Figs. 12-16 — *Diaphus perspicillatus* (OGILBY, 1898). L (coll. IRSNB); Recent, off Venezuela.  
 Figs. 17-22 — *Diaphus perspicillatoides* n.sp. R, 17 = holotype (IRSNB P 6222); 18-22 = paratypes (IRSNB P 6223-P 6227); Saint-Etienne-d'Orthe Clay, Saint-Etienne-d'Orthe, Lestelle.

Plate 1.

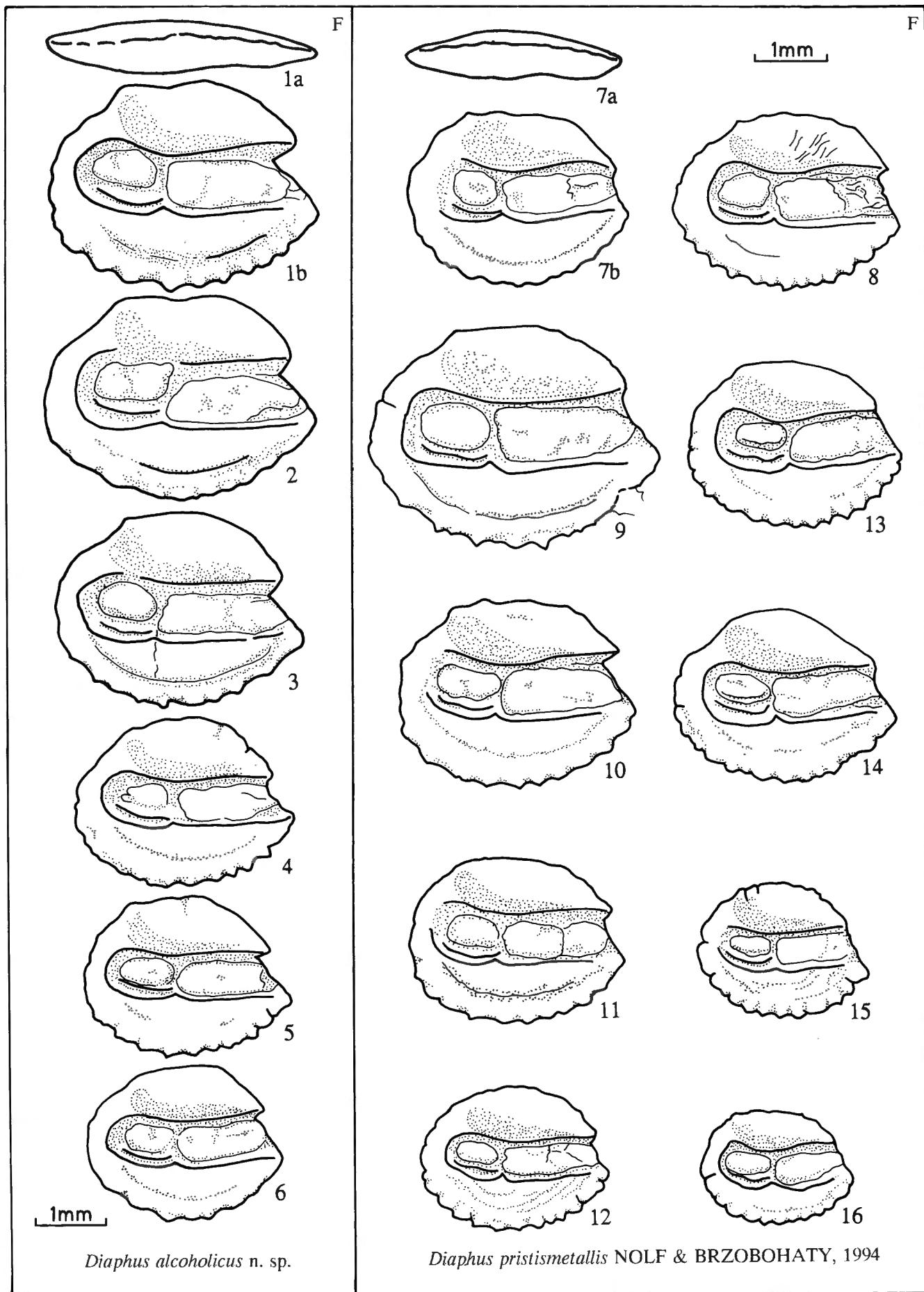


Plate 2.

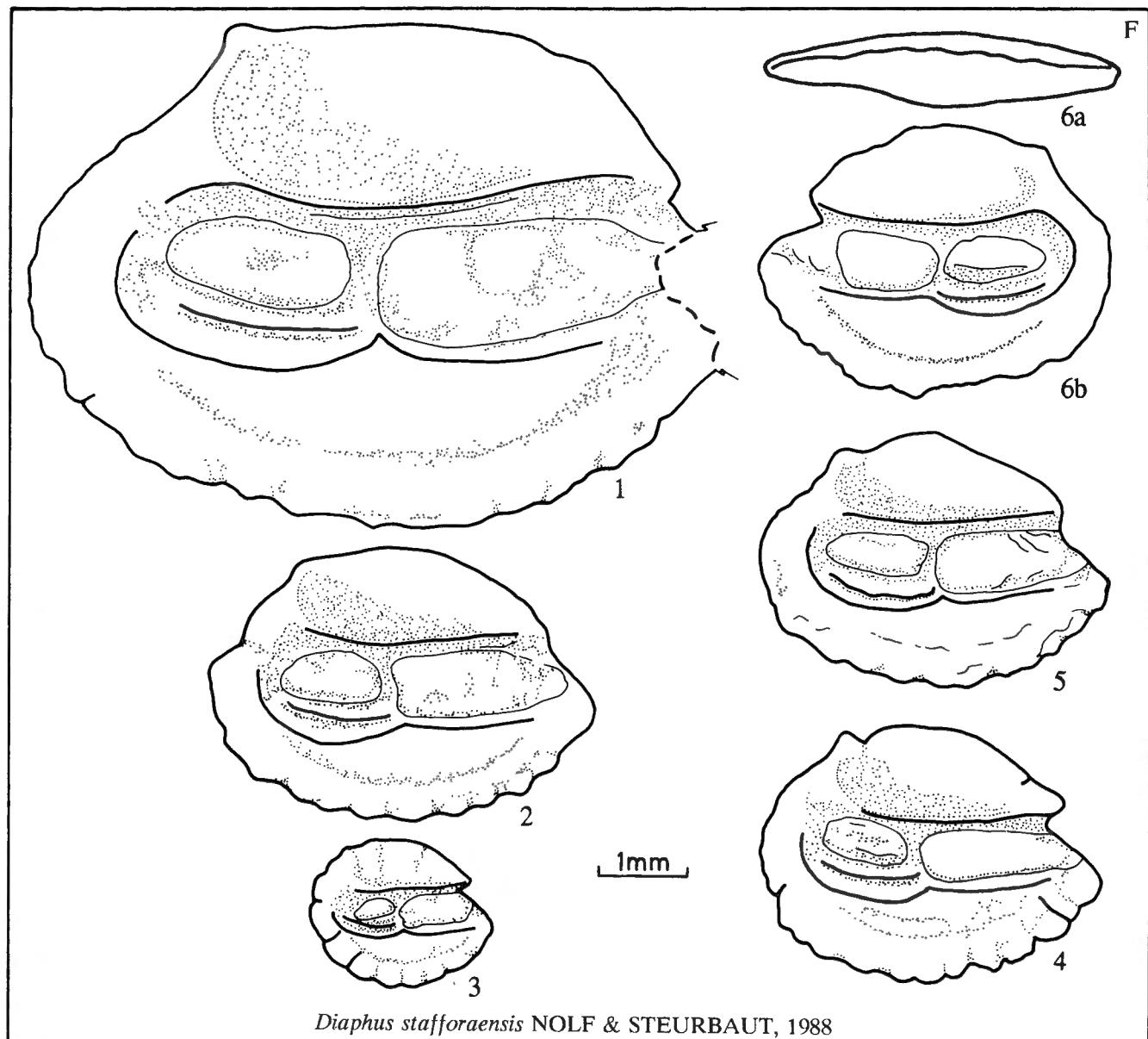
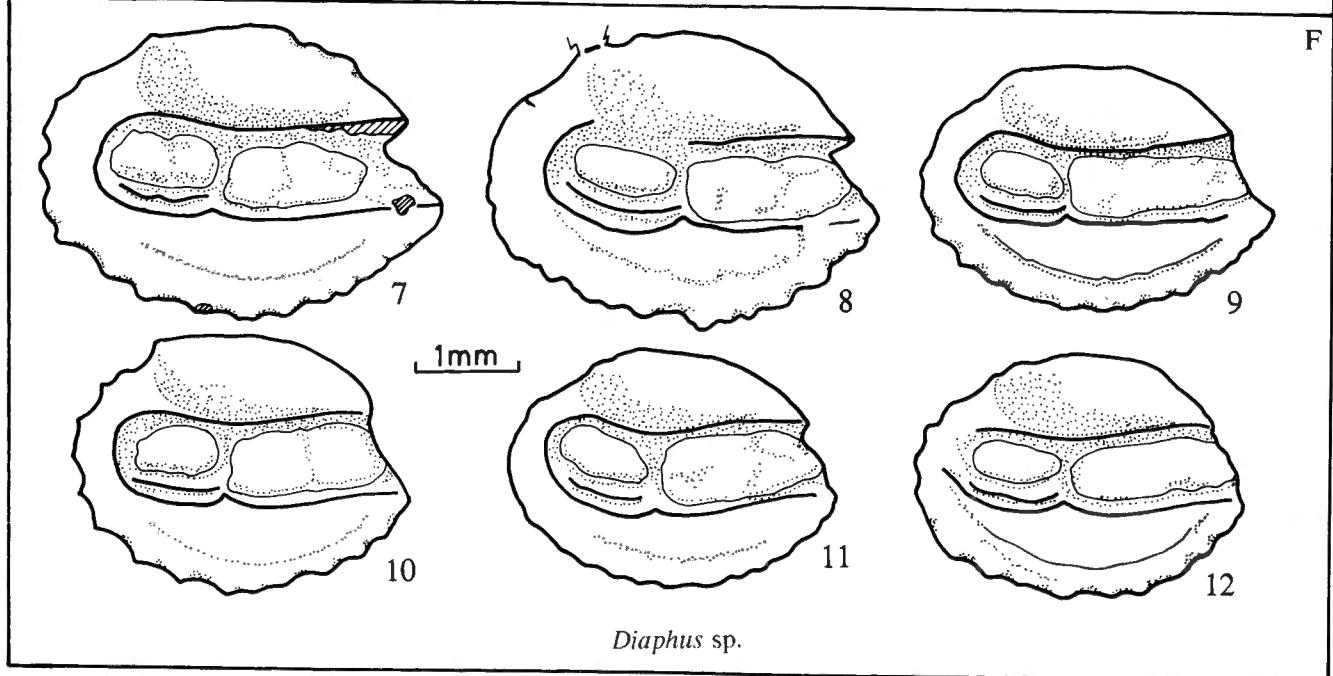
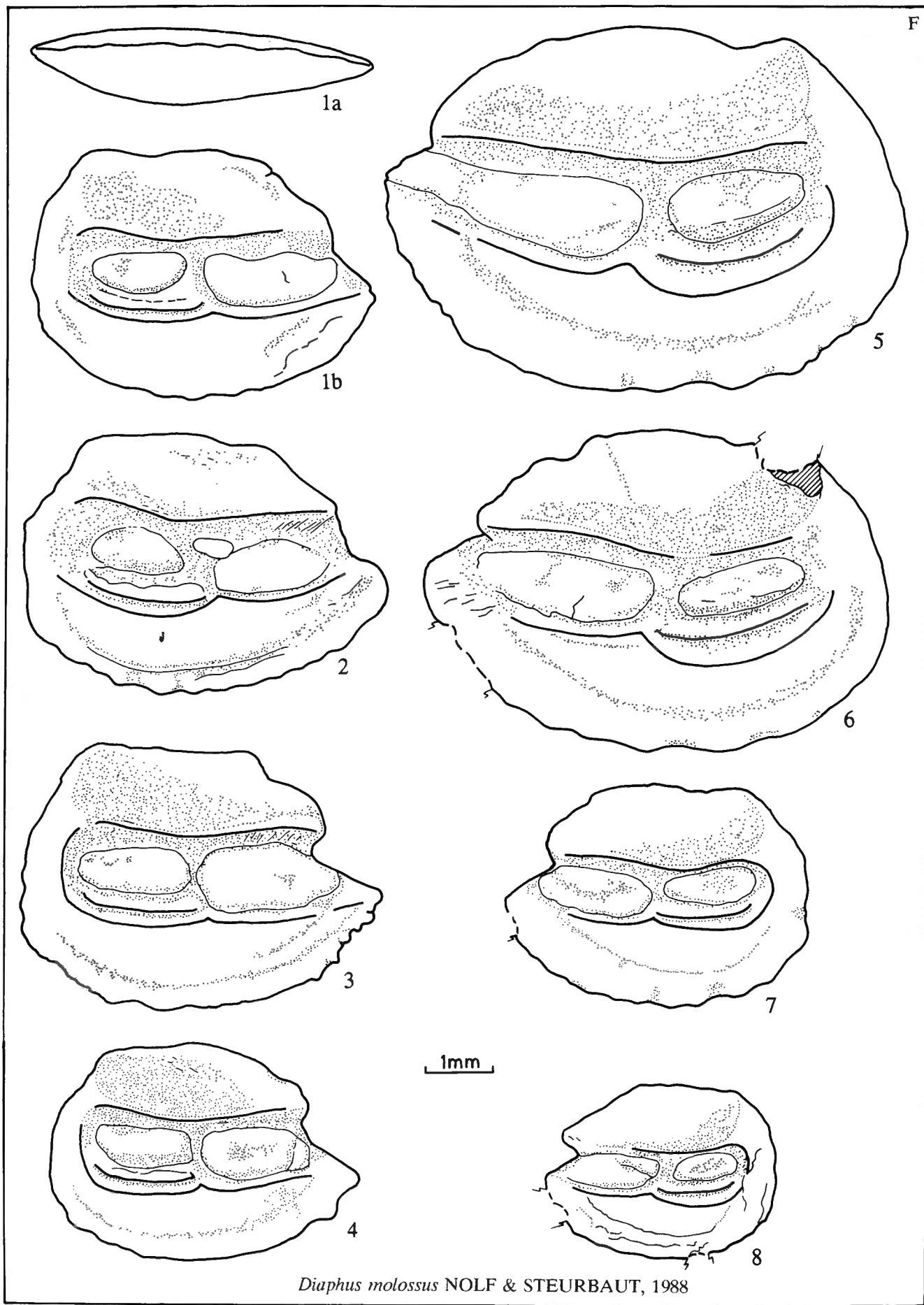
*Diaphus stafforaensis* NOLF & STEURBAUT, 1988*Diaphus sp.*

Plate 3.



*Diaphus molossus* NOLF & STEURBAUT, 1988

Plate 4.

