Diaphus otoliths from the European Oligocene
(Myctophidae, Teleostei)

by Rostislav BRZOBOHATY and Dirk NOLF

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. perspicillatoides n.sp., D. pristismetalli 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


Mots-clefs: 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 Eomycotophum 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.
Table 1 — Abundance of the Diaphus otoliths at the most important Oligocene localities.

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<td>Diaphus molossus NOLF &amp; STEURBAUT, 1988</td>
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<td>Diaphus longirostris (BRZOBOHATY, 1967)</td>
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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)

**Aquitaine Basin (SW France)**
- Rivière-Saas-et-Gourby (Escornebéou): Fine-grained sands (Escornebéou 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 (Chattien) (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**

**Vigo-ponzo (Casa del Piano):** Grey sandy marls, Early Oligocene (NOLF & BRZOBOHATY, 1994b).

**Hungary (Bükk south and east region)**

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

- Pouzdrany ("Stirpe"): Grey-brown, calcareous claystones

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

Family MYCTOPHIDAE

Diaphus alcoholicus n.sp.
Pl. 1, Figs. 1-6.

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.


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 antirrostrum; 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 debile 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 & Capetta, 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

Type material: Holotype: Otolithus (Scopelus) austriacus KOK. - Schubert, p. 106, fig. 14, non 15, 16 - eroded specimens (non Koken 1891);
1990 Ot. (Myctophidae) cf. kokeni (Prochazka) - Brzobohaty, p. 129, pl. 2, fig. 3-7;
1975 Diaphus kokeni longirostris n. ssp. - Brzobohaty, p. 129, pl. 2, fig. 3-7.

Dimensions of the holotype: Length: 4.2 mm; height: 2.6 mm; thickness: 0.7 mm.

Diagnosis: The otoliths of this species present a nearly oval outline. The rostrum is nearly as long as the antirrostrum; 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: 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-
Diaphus molossus Nolf & Steurbaut, 1988

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 perspicillatoides 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. perspicillatoides 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. philippi 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; Escornebéou - rare).

Diaphus pristismetallis Nolf & Brzobohaty, 1994

Pl. 1, Figs. 7 - 16

1965 Myctophum debile (Kok.) - Brzobohaty, p. 279 (partim) (non Kok, 1891); 1967 Myctophum debile (Kok.) - Brzobohaty, p. 127, pl. 2, fig. 2, non fig. 1 (non Kok, 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 Nafpaktitis, 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 (Pouzdany "wine cellars" - abundant); Hungary, Upper Oligocene, (Noszvaj - dominant among myctophids); Aquitaine Basin, Upper Oligocene (Saint-Étienne-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. 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 nomenclatorially 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 & Brzobohaty, 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. curtus* 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 Escornebéou, originally described as *L. dolfeinoides* Steurbaut, 1982 (p.52, pl. 8, fig. 3-7) and subsequently synonymised with the Recent *L. dolfeini* Zugmayer, 1911 by Nolf & Cappetta (1989, p. 218). A record of *Lampamycyctodes* otoliths from the Lower Oligocene of Moravia by Brzobohaty (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. perspicillatoide*, *D. pristisme-

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<tr>
<th>CHRONOSTRATIGRAPHY</th>
<th><em>Diaphus alcoholicus</em></th>
<th><em>D. longirostris</em> (BRZOBHATY, 1987)</th>
<th><em>D. molossus</em> (NOLF &amp; STEURBAUT, 1988)</th>
<th><em>D. perspicillatoide</em></th>
<th><em>D. pristisme</em></th>
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Table 2 — Stratigraphic range of the Oligocene species of *Diaphus*.
tallis and D. stafforaensis. Their stratigraphic and geographical distribution is given in Tables 1 and 2. They are abundant in the Mediterranean, Trans-European (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 Pizzocorno, D. perspicillatoïdes 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 perspicillatoïdes 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 & Cappetta, 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.

References


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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 alcoholicus* n.sp. L, 1 = holotype (IRSNB P 6182), 2-6 = paratypes (IRSNB P 6183-6187); Pouzdrany Marls, Pouzdrany, wine-cellar.

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-cellar; 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-P6199); Arenarie de Ranzano, Vigoponzo, Casa del Piano; 4-6 = ?Antognola Formation, Pizzocorno; (IRSNB P 6200-P 6201, holotype IRSNB P3419).

Figs. 7-12 — *Diaphus sp.;* 7 (IRSNB P 6202); Pouzdrany Marls, Pouzdrany, wine-cellar; 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-cellar.

Figs. 12-16 — *Diaphus perspicillatus* (Ogilby, 1898). L (coll. IRSNB); Recent, off Venezuela.

Figs. 17-22 — *Diaphus perspicillatoide* 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.

Diaphus alcoholicus n. sp.

Diaphus pristismetallis NOLF & BRZOBOHATY, 1994
Plate 2.

Diaphus stafloraeensis NOLF & STEURBAUT, 1988

Diaphus sp.
Plate 3.

Diaphus molossus NOLF & STEURBAUT, 1988
Plate 4.

Diaphus diademophilus NAFPAKTITIS, 1978

Diaphus longirostris (BRZOBOHATY, 1967)

Diaphus perspicillatus (OGILBY, 1898)

Diaphus perspicillatoides n. sp.