

BATHYAL FISH OTOLITHS FROM THE BARTONIAN (EOCENE) OF THE TURIN HILL (PIEDMONT, ITALY)

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Abstract. A small collection of fish otoliths, mostly myctophids, from a bathyal environment is described from the Bartonian (late middle Eocene) Marne di Monte Piano Formation of San Genesio, Turin Hill, Piedmont. Myctophids have been rarely recorded from the Eocene in general, and few bathyal environments have been sampled for otoliths of that time interval globally. In this context, the assemblage described herein fills an important stratigraphic gap in the record and evolution of the Myctophidae. The findings are discussed in a regional and stratigraphic context. Seven species are recorded, of which one is new, *Oligophus bartonensis* n. sp., belonging to the family Myctophidae.

INTRODUCTION

Bathyal (200 to 4000 m water depth) assemblages are rare in the Eocene otolith record. The few assemblages known are from outer shelf and upper slope settings in the Aquitaine Basin (Nolf 1988; Lin et al. 2017) and from pelagic settings of the South Island of New Zealand (Schwarzhans 2019a). The deepwater associations described from

the Aquitaine Basin in France date back to the late Ypresian, early Lutetian, and late Priabonian. Thus, the relatively small otolith assemblage from the Bartonian described here fills an important stratigraphic gap in the record of European Eocene deepwater faunas being the first discovered in the Tertiary Piedmont Basin.

Twenty-seven otoliths have been recovered from the Bartonian sediments of the Marne di Monte Piano Formation near San Genesio in the Turin Hill. Twenty-four of them document four different myctophid species, one of which is described as new. To date, Eocene myctophid otoliths have been usually assigned to the extant genus

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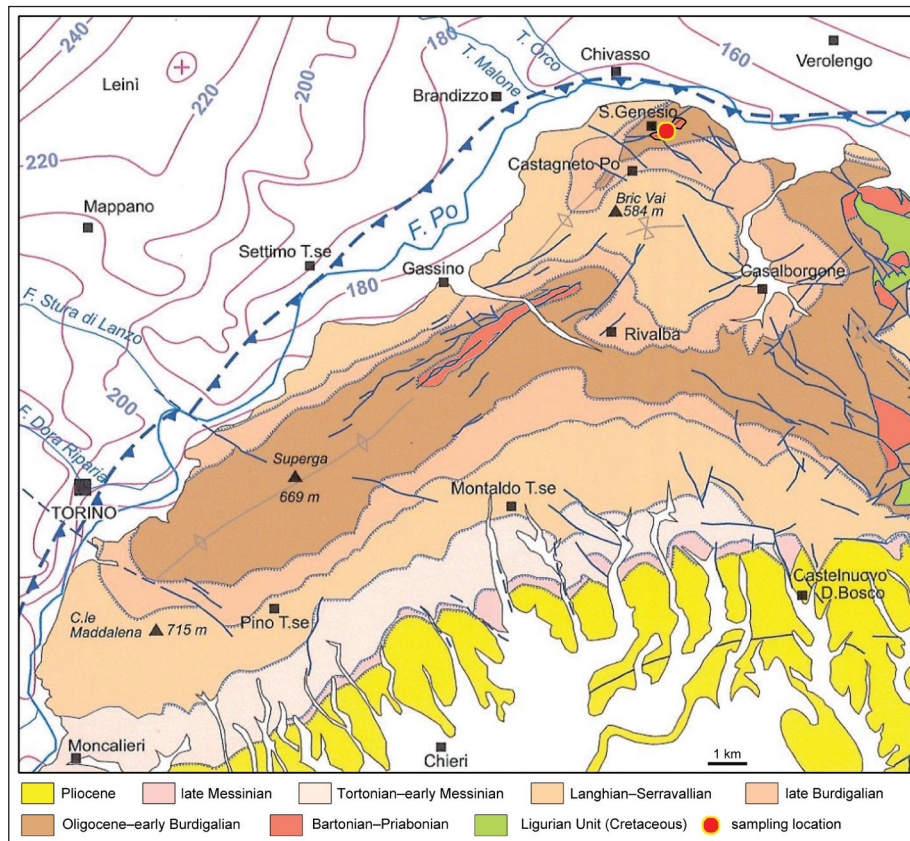


Fig. 1 - Geological map of the Turin Hills after the Carta Geologica d'Italia alla scala 1:50.000 (2009), Foglio 156, Torino Est. Isobathic contours represent the base of the Quaternary (a.s.m.l.).

Diaphus. Recent discoveries of otoliths in situ from articulated myctophid skeletons of the extinct genera *Eomyctophum* and *Oligophus* have shown that the myctophid diversity was probably higher in the Eocene than previously perceived (Přikryl et al. 2017). For this reason, the generic allocation of Eocene myctophid otolith-based species is discussed and reviewed. The descriptive part focuses on differential diagnoses for the identified myctophid taxa. A comprehensive description is only provided for the new species.

STRATIGRAPHIC SETTING

The otoliths were collected from a small outcrop of sparsely fossiliferous, grey silty marl exposed in the surroundings of the village of San Genesio, in the Turin Hill (Fig. 1). These deposits are referred to the Marne di Monte Piano Formation (Carta Geologica d'Italia, 2009), a sequence of pelagic and hemipelagic varicoloured marly clays and grey silty marls with turbiditic intercalations largely exposed in the northern Apennines and eastern sector of the Tertiary Piedmont Basin (e.g., Mutti et al. 1995;

Mancin & Cobianchi 2000; Mancin & Pirini 2001; Mancin et al. 2003). In the Turin Hill, the Marne di Monte Piano Formation dates back to the middle to late Eocene (Carta Geologica d'Italia, 2009) and the turbiditic intercalations are represented by arenites or bioclastic limestone (see Campanino & Ricci 1991). At San Genesio, the Eocene otolith-bearing sediments of the Marne di Monte Piano Formation are characterized by a poorly preserved assemblage of planktonic foraminifers that includes the muricate species *Acarinina bullbrookii*, *Globigerinatheka mexicana*, and *Turborotalia cerroazulensis cerroazulensis* (Carta Geologica d'Italia, 2009), which allow it to be referred to the late Bartonian *Acarinina* spp., *Globigerinatheka* spp., *T. cerroazulensis* Assemblage Zone (MFP16 p.p.) as defined by Mancin & Cobianchi (2000) and Mancin & Pirini (2001). This zone is more or less equivalent to the planktonic foraminifer zone E13 of Wade et al. (2011), 40 to 38 Ma. Overall, the foraminifer assemblage contains planktonic forms indicative of warm waters (Mancin & Cobianchi 2000) and benthic infaunal (*Bulimina* spp.) and agglutinated taxa (e.g., *Glomospira charoides*) indicative of the epi- and mesobathyal zone (Carta Geologica d'Italia, 2009).

MATERIALS AND METHODS

The otolith terminology follows Koken (1884) with amendments by Schwarzhans (1978). The morphometric measurements of myctophid otoliths follow the scheme established by Schwarzhans (2013).

Abbreviations used are: OL = otolith length; OH = otolith height; OT = otolith thickness; OCL = length of ostial colliculum; OCH = height of ostial colliculum; CCL = length of caudal colliculum; CCH = height of caudal colliculum. All the specimens are deposited at the Museo di Geologia e Paleontologia, Università degli Studi Torino, Torino, Italy (MGPT-PU).

SYSTEMATICS

Remarks. Only three otoliths belong to teleost groups other than the Myctophidae. These are briefly discussed as follows.

Bathycongrus sp. (Fig. 2A–C, MGPT-PU 130444): A single small otolith measuring about 2 mm in length. It is oval in shape with a centrally positioned, very slightly inclined sulcus with a single colliculum. The colliculum is oval in shape except for a short anterior dorsal extension and terminates far from the anterior rim of the otolith. Above the sulcus there is a small, cup-shaped dorsal depression. The shape of the colliculum and the dorsal depression are typical for otoliths of the congrid genus *Bathycongrus* (see Schwarzhans 2019b).

Danaphos gibbsi Nolf, 1988 (Fig. 2D–F, MGPT-PU 130445): A small otolith measuring 1.4 mm in length closely resembles otoliths described by Nolf (1988) from the Priabonian of the Aquitaine Basin.

Bregmaceros sp. (MGPT-PU 130446): A single, strongly eroded, small otolith, which nevertheless can be recognized as a bregmacerotid because of its characteristic outline.

Family Myctophidae Gill, 1893

Genus *Diaphus* Eigenmann & Eigenmann, 1890

Diaphus quadrangularis (Sulc, 1932)

Fig. 2N–R

1932 *Apogon quadrangularis* - Sulc: pl. 1, fig. 13.

1932 *Scopelus ellipticus* - Sulc: pl. 3, fig. 1–2.

1988 *Diaphus quadrangularis* (Sulc, 1932) - Nolf: pl. 5, fig. 8–11.

2017 *Diaphus quadrangularis* (Sulc, 1932) - Lin, Nolf, Steurbaut & Girone: fig. 6B–C.

Material: 12 specimens (MGPT-PU 130447) from the Bartonian of San Genesio.

Differential diagnosis: Otoliths of *D. quadrangularis* are characterized by a convex inner and nearly flat outer face and a regular oval shape (OL:OH = 1.25–1.3). The ventral rim is deeper than the dorsal rim and the dorsal rim is expanded in its anterior half. Further diagnostic characters are the short rostrum, weak excisura, 9–12 delicate denticles along the ventral rim and a small denticle at the dorsal rim just above the center of the cauda. The sulcus shows an ostium distinctly wider and longer than the cauda (OCL:CCL = 1.7–2.0; OCH:CCH = 1.35–1.55). *Diaphus quadrangularis* does not resemble any other known Eocene myctophid otolith but is very similar to the late Oligocene/early Miocene *D. perspicillatoides* Brzobohatý & Nolf, 2000, with which it shares a similar outline, a convex inner and nearly flat outer face, and a distinctly wider and longer ostial colliculum compared to the caudal colliculum. The differences between these species are limited and appear to be primarily related to the number of denticles along the ventral rim of the otolith (9–12 in *D. quadrangularis* vs. 13–17 in *D. perspicillatoides*) and the more broadly rounded posterior tip of the otolith in *D. quadrangularis*. As usually with *Diaphus* otoliths, specimens where the ventral denticles are eroded may not be identifiable to the species level.

Discussion. *Diaphus quadrangularis* was originally described from the late Eocene Priabonian of the Aquitaine Basin and redefined by Nolf (1988). Subsequently, this species was also identified from the the Ypresian (Nolf 1988) and Lutetian (Nolf 1988; Lin et al. 2017). The specimens figured by Nolf (1988) from the Ypresian are comparatively smaller and appear to be more roundish in outline and thus could potentially represent a different species. In any case, however, *D. quadrangularis* is a long-running species whose range extends throughout the Eocene for at least 19 mya. It also represents a typical species of the genus *Diaphus*, probably the earliest unambiguous one. It is the most common species in the Bartonian of San Genesio representing about 45% of the assemblage and includes the largest myctophid specimens, measuring up to 3 mm in length.

Diaphus trapezoidalis Nolf, 1988

Fig. 2K–M

1988 *Diaphus trapezoidalis* - Nolf: pl. 5, fig. 1.2017 *Diaphus trapezoidalis* Nolf, 1988 - Lin, Nolf, Steurbaut & Girone: fig. 6K–M.?2017 *Diaphus excavatus* (Sulc, 1932) - Lin, Nolf, Steurbaut & Girone: fig. 6D–F.

Material: Two specimens (MGPT-PU 130448) from the Bartonian of San Genesio.

Differential diagnosis: *Diaphus trapezoidalis* is primarily defined by the shape of the dorsal rim, which is gently curved downward anteriorly and shows a sharp angle above the center of the cauda. Posteriorly, the dorsal rim shows a moderately concave inclined section behind the postdorsal angle towards the posterior rim. Further characteristics are the ratio OCL:OH of 1.15–1.2, a gently curved ventral rim with 6–7 denticles, the proportions of the sulcus (OCL:CCL = 1.6; OCH:CCH = 1.5), and the convex inner and outer faces. *Diaphus trapezoidalis* is closely related to *Diaphus excavatus* from the Priabonian from which it differs mainly in the shape of the dorsal rim, being more regularly curved in *D. excavatus*. Also the ventral rim appears to be deeper in *D. excavatus*.

Discussion. *Diaphus trapezoidalis* was originally described from the Lutetian of the Aquitaine Basin by Nolf (1988) and subsequently reported by Lin et al. (2017). The findings at San Genesio extend the stratigraphic range of this species into the Bartonian. Lin et al. (2017) also recorded *D. excavatus* from the Lutetian of the Aquitaine Basin. However, their figured specimens appear to be eroded and are tentatively referred herein to *D. trapezoidalis*.

Genus *Eokrefftia* Schwarzahns, 1985

Remarks. *Eokrefftia* was established as a fossil otolith-based genus based on *E. prediaphus* Schwarzahns, 1985 from the latest Paleocene of South Australia. The type-species is characterized by flat inner face, a far backward positioned postdorsal angle at the junction with the posterior rim, presence of small lobes along the ventral rim of the otolith instead of denticles, sulcus almost reaching the posterior rim of the otolith, and a ratio OCL:CCL measuring about 1.5. It represents the earliest known unambiguous myctophid in the otolith record. Its relationships remain uncertain

because of the overall plesiomorphic appearance. However, the otoliths of *Eokrefftia* resemble the otoliths of certain genera of the Gymnoscopelinae, for instance of the genus *Notoscopelus*, in having a relatively slender shape, relatively flat inner face, and the absence of denticles along the ventral rim of the otolith.

Eokrefftia sulci (Nolf, 1988)

Fig. 2G–J

1988 *Diaphus sulci* - Nolf: pl. 5, fig. 13–15.2017 *Diaphus sulci* Nolf, 1988 - Lin, Nolf, Steurbaut & Girone: fig. 6Q–R (non fig. 6S).

Material: 2 slightly eroded specimens (MGPT-PU 130449) from the Bartonian of San Genesio.

Differential diagnosis: *Eokrefftia sulci* resembles *E. prediaphus* in all the pertinent aspects listed above and differs from it by having a more rounded postdorsal angle and posterior rim, which results in a reduced length of the sulcus that does not extend backward to almost reach the posterior rim of the otolith.

Discussion. *Eokrefftia sulci* is a long-running species, whose range extends from the late Ypresian to the Priabonian. It was originally described by Nolf (1988) from the Priabonian (holotype) and late Ypresian (paratypes). Later it was also recorded from the Lutetian by Lin et al. (2017). The Bartonian material documented herein improves our knowledge of its record.

Genus *Oligophus* Gregorová, 2004

Remarks. *Oligophus* was established by Gregorová (2004) as a monotypic extinct myctophid genus close to *Diaphus* based on articulated skeletons from the early Oligocene of the Paratethys, originally described as *Leuciscus moravicus* Paučá, 1931. Otoliths found in situ (Přikryl et al. 2017) revealed that the otolith-based species *Diaphus longirostris* (Brzobohatý, 1967), is a junior synonym of *Oligophus moravicus* (Paučá, 1931). The otoliths are characterized by a flat inner face, a strong postdorsal angle and slanted predorsal section, four to seven strong denticles along the ventral otolith rim, ostium slightly narrower than the cauda, and a rather low ratio OCL:CCL of 1.3–1.5.

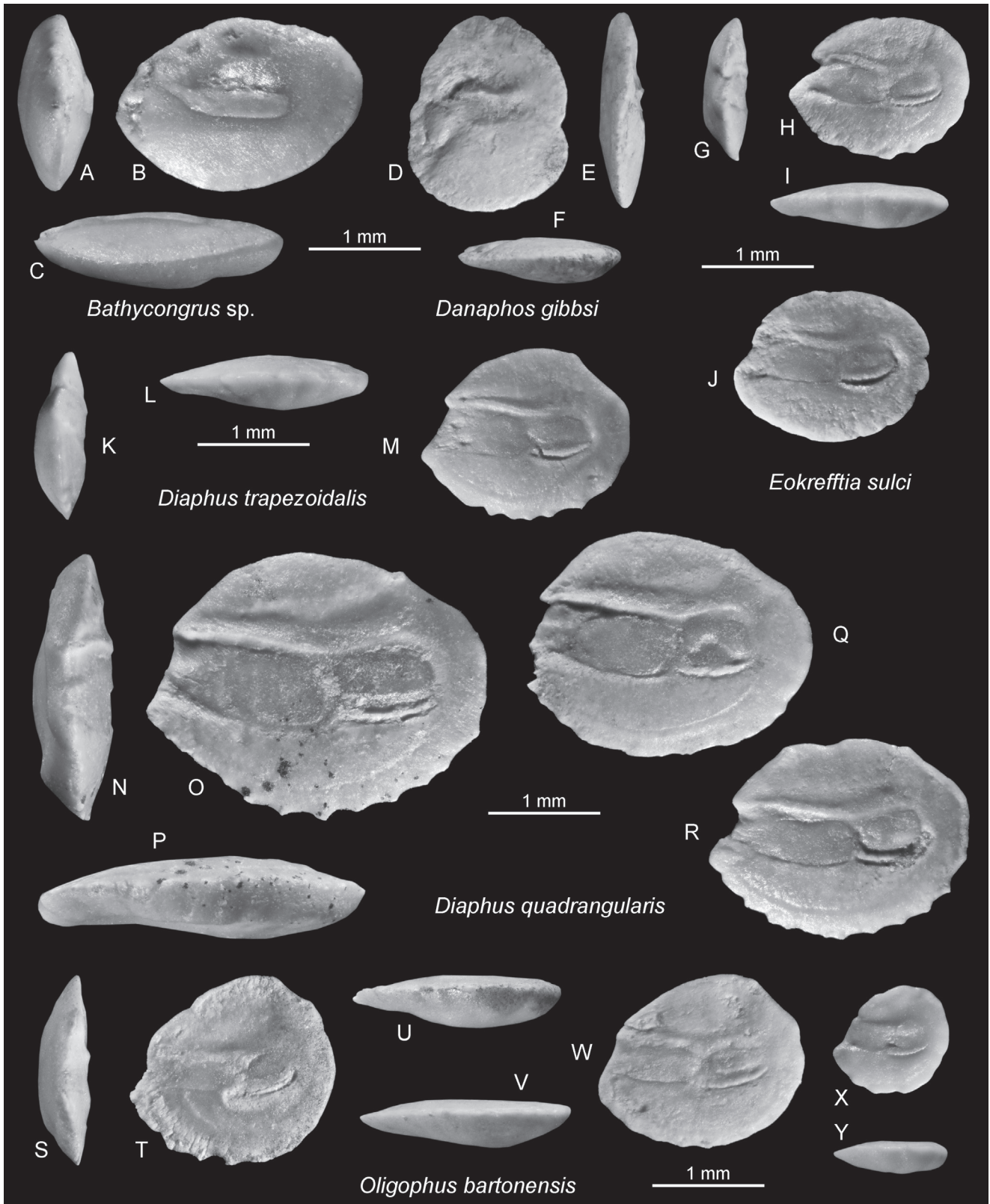


Fig. 2 - Otoliths from the Bartonian of San Genesio. A–C) *Bathycongrus* sp. MGPT-PU 130444; D–F) *Danaphos gibbsi* Nolf, 1988, MGPT-PU 130445; H–J) *Eokrefftia sulci* (Nolf, 1988), MGPT-PU 130449; K–M) *Diaphus trapezoidalis* Nolf, 1988, MGPT-PU 130448; N–R) *Diaphus quadrangularis* (Sulc, 1932), MGPT-PU 130447; S–U) *Oligophus bartonensis* n. sp., S–U holotype, MGPT-PU xx130450, V–Y paratypes, MGPT-PU 130451.

***Oligophus bartonensis* n. sp.**

Fig. 2S–T

Holotype: Fig. 2S–U, MGPT-PU 130450, late Bartonian, San Genesisio, Turin Hill, Piedmont.

Paratypes: Four specimens, MGPT-PU 130451, same data as holotype.

Etymology: Named after the Bartonian stage, based on the age of the sediments in which the specimens were found.

Diagnosis: OL:OH = 1.05–1.15. Inner face flat, outer face with weak postcentral umbo. Predorsal rim depressed, postdorsal rim with massive angle. Ventral rim with four irregular but strong denticles along the preventral section; postventral section smooth. Sulcus narrow, cauda slightly upward oriented. Ostium relatively long and narrow; caudal colliculum very narrow; OCL:CCL = 1.8–2.0, OCH:CCH = 1.3–1.4. Caudal pseudocolliculum extending forward of caudal colliculum.

Description. Relatively small, compressed, thin otoliths up to 1.85 mm in length; OH:OT = 3.5–3.7. Dorsal rim nearly triangular in shape with depressed, nearly straight inclined predorsal section and massive postdorsal angle positioned above central part of cauda; postdorsal rim steeply inclined, short, flat to slightly concave. Ventral rim regularly curved bearing four irregular, variably strong denticles along its anterior half. Rostrum moderately long (9–14% of OL); excisura and antirostrum absent or very reduced in size. Posterior rim bluntly rounded.

Inner face nearly flat, only rostral part slightly bent. Sulcus slightly suprmedian, narrow, shallow, with relatively long ostium and short cauda. Caudal colliculum very narrow and anteriorly reduced in length, thus caudal pseudocolliculum extending forward of caudal colliculum. Dorsal depression wide; ventral furrow indistinct, relatively close to ventral rim of otolith. Outer face smooth and slightly convex with weak and broad central to postcentral umbo.

Discussion. The shape of the otolith with the depressed predorsal rim and massive postdorsal angle, the flat inner face, and the relatively narrow sulcus support the attribution to the fossil genus *Oligophus*. *Oligophus bartonensis* differs from the type species *O. moravicus* in having different proportions of the sulcus (OCL:CCL = 1.8–2.0 vs. 1.3–1.5), resulting from the anteriorly reduced caudal colli-

culum, anteriorly extended pseudocolliculum and a reduced number of denticles (four vs seven) restricted to the preventral margin. A species recently described from the Bartonian (late Lutetian to early Bartonian) of New Zealand as *Eomyctophum porokawa* Schwarzahns, 2019 is tentatively referred herein to *Oligophus*. *Oligophus? porokawa* is similar to *O. bartonensis* in shape and proportions but differs from it in having a rounded postdorsal section, nearly smooth preventral rim with only slight undulations anterior of its midlength, and an anteriorly not reduced caudal colliculum (OCL:CCL = 1.4). The two newly referred Eocene records demonstrate that the genus *Oligophus* had a longer history and diversity than those suggested by the articulated skeletons.

EOCENE MYCTOPHID OTOLITHS IN EUROPE

The knowledge of Eocene myctophid otoliths of Europe is primarily based on data from the Aquitaine Basin (Sulc 1932; Nolf 1988; Lin et al. 2017) and encompasses a span in the record of about 8 mya from the middle Lutetian to the late Priabonian, approximately between 43 and 35 Ma. The Bartonian assemblage described herein from the Turin Hill is in the middle of this gap (40–38 Ma) and thus helps to establish a more continuous picture of myctophid evolution in the Eocene Tethyan realm. Traditionally, most Eocene myctophid otoliths have been assigned to the genus *Diaphus*, probably because of the presence of denticles or denticle like lobate structures along the ventral rim of the otoliths, a typical but not exclusive feature of the otoliths of *Diaphus* species. The findings of otoliths in situ in articulated skeletons from the early Oligocene (Příkryl et al. 2017) provided clear evidence that the diversity of Paleogene myctophids was higher than thought. In the following paragraphs, we briefly summarize the current status of our knowledge about Paleogene myctophids (Fig. 3).

Eomyctophum has been placed in a separate subfamily (Eomyctophinae) by Prokofiev (2006) and is considered to represent a sister clade to all the modern myctophids (Prokofiev 2006). Their otoliths found in situ (Příkryl et al. 2017) are compact, roundish in shape with denticles or denticle-like lobate structures along their ventral rim and a relatively long cauda with a weak caudal pseudocolliculum. In the Eocene of Europe, two species

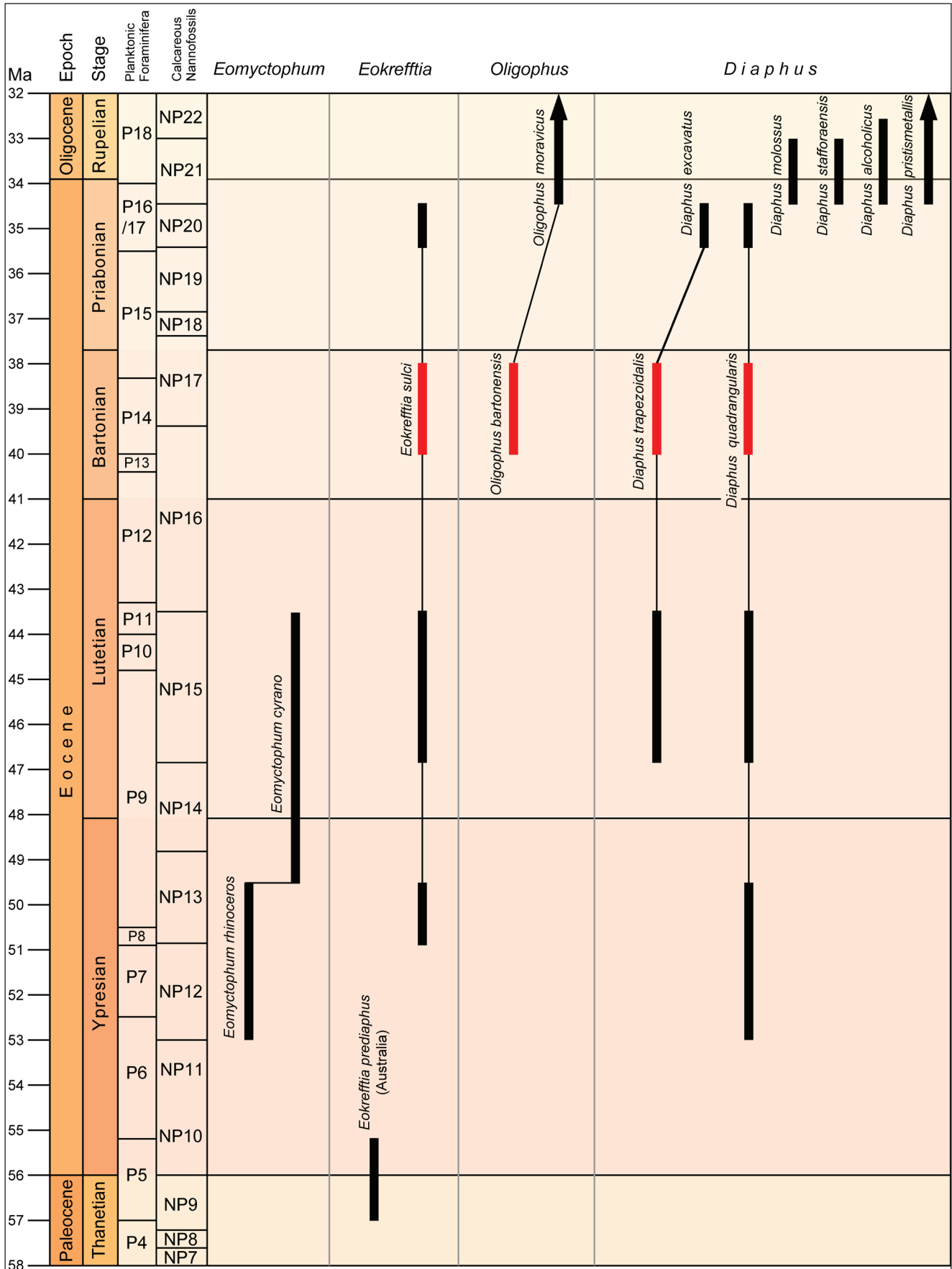


Fig. 3 - Stratigraphic ranges of myctophid otoliths in the European Eocene. Red bars represent taxa identified from the Bartonian of San Genesio; black bars are from Nolf (1988) and Lin et al. (2017); *Eokrefftia prediaphus* from Australia shown as earliest myctophid otolith after Schwarzhans (1985).

are currently referred to *Eomyctophum* - *E. rhinoceros* (Nolf, 1988) and *E. cyrano* (Nolf, 1988) from the Ypresian and Lutetian, respectively. Nolf (1988) assumed that *E. cyrano* derived from *E. rhinoceros* (Fig. 3). There are no confirmed records of *Eomyctophum* in the Bartonian and Priabonian of Europe, and *E. koraense* Daniltschenko, 1947 from the early Oligocene may represent its youngest confirmed record (Prokofiev, 2006). Elsewhere, otoliths from the Eocene of Australia - *E. emensus* (Schwarzahns, 1985) - and New Zealand - *E. broncus* Schwarzahns, 2019 - can be actually assigned to this genus.

Eokrefftia is known from a latest Paleocene species from southern Australia (*E. prediaphus* Schwarzahns, 1985), the earliest myctophid otolith record so far. *E. sulci* (Nolf, 1988) has been referred herein to the same genus (see above for diagnosis and discussion). *Eokrefftia sulci* has a remarkably long stratigraphic range from the late Ypresian to the late Priabonian, lasting about 17 mya (Fig. 3). We tentatively associate *Eokrefftia* with the Gymnoscopelinae within the Myctophidae.

Diaphus appears to be represented in the otolith record since the Ypresian with the extremely long ranging *D. quadrangularis* that seems to occur for a time interval of about 19 mya or more (Fig. 3). Thus, despite some otolith-based species as originally referred to *Diaphus* have been recently referred to other, extinct genera, it remains the extant myctophid genus with the earliest appearance in the record. Another lineage of Eocene myctophid species comprises *Diaphus trapezoidalis* and *D. excavates*, whose generic allocation appears less certain. Although Schwarzahns (2019a) suggested a reassignment to *Eomyctophum*, it is tentatively kept herein within *Diaphus* pending more detailed future studies. *Diaphus marambionis* Schwarzahns et al., 2017 may also belong to this clade. The Eocene lineages cannot be easily associated with any of the extant *Diaphus* clades.

Oligophus was established as a monospecific fossil genus close to *Diaphus* based on the early Oligocene *O. moravicus*; however, it contains a second species based on Bartonian material described here (Fig. 3; *O. bartonensis*), as well as a possible additional species from the late Lutetian to Bartonian of New Zealand (*O. porokawa*). The assignment of *Oligophus* within the Diaphinae remains poorly supported. Anatomical evidence based on the articulated skeletons suggest a stem group relation with the Diaphi-

nae (Gregorová 2004; Prokofiev 2006; Přikryl et al. 2017). Conversely, the otoliths exhibit certain characters that may be regarded as derived, such as the strong denticles on the ventral rim, the flat inner face and the strong postdorsal angle, while the sulcus morphology with the narrow and relatively short ostium could be considered as plesiomorphic. In addition, as discussed above, *Diaphus* otoliths appeared in the record earlier than *Oligophus* otoliths.

Summarizing, at least four, possibly five, lineages of myctophids (two of which pertaining to the genus *Diaphus*) are known from the Eocene of Europe (Fig. 3). In terms of morphological diversity, this is still a relatively low level when compared to Neogene and extant data. In addition, some of the Eocene species exhibit an unusually long stratigraphic range not seen subsequently in the myctophid record. The situation changed during the latest Eocene and the early Oligocene with a sudden burst in myctophid diversity (Fig. 3) that has been associated with the change of the deepwater ocean circulation that took place at that time (Schwarzahns & Carnevale 2021). *Diaphus* apparently was the genus that mostly benefited from this extraordinary diversification (Fig. 3; Brzobohatý & Nolf 1995; Schwarzahns & Carnevale 2021). We hope that future research of otoliths in situ will bring more clarity in the allocation of these early myctophid otolith-based taxa. Moreover, we believe that additional explorations in outer shelf or bathyal sediments of early Paleogene age can contribute significantly to the further unraveling of the evolutionary history of the family Myctophidae.

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REFERENCES

- Brzobohatý R. (1967) - Die Fisch-Otolithen aus den Pouzdrany Schichten. *Acta Musei Moraviae, Scientiae Naturalis*, 52: 121-168.
- Brzobohatý R. & Nolf D. (1995) - *Diaphus* otoliths from the European Oligocene (Myctophidae, Teleostei). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 65: 257-268.

- Brzobohatý R. & Nolf D. (2000) - *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 70: 185-206.
- Campanino F. & Ricci B. (1991) - Il calcare di Gassino. Retrospettiva bibliografica e problemi aperti. *Bollettino del Museo Regionale di Scienze Naturali*, 9 suppl. 1: 57-81.
- Carta Geologica d'Italia alla scala 1:50.000 (2009) - Foglio 156 "Torino Est". ISPRA, Roma.
- Gregorová R. (2004) - A new Oligocene genus of lanternfish (family Myctophidae) from the Carpathian Mountains. *Revue de Paléobiologie*, 9: 81-97.
- Koken E. (1884) - Über Fisch-Otolithen, insbesondere über diejenigen der norddeutschen Oligocän-Ablagerungen. *Zeitschrift Der Deutschen Geologischen Gesellschaft*, 36: 500-565.
- Lin C.-H., Nolf D., Steurbaut E. & Girone A. (2017) - Fish otoliths from the Lutetian of the Aquitaine Basin (SW France), a breakthrough in the knowledge of the European Eocene ichthyofauna. *Journal of Systematic Palaeontology*, 15: 879-907.
- Mancin N. & Cobianchi M. (2000) - Le Marne di Montepiano della Val di Nizza (Appennino Settentrionale): Biostratigrafia integrata e considerazioni paleoambientali. *Atti Ticinensi di Scienze della Terra*, 41: 145-162.
- Mancin N. & Pirini C. (2001) - Middle Eocene to Early Miocene foraminiferal biostratigraphy in the epiligurian succession (northern Apennines, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 107: 371-393.
- Mancin N., Pirini C., Bicchi E., Ferrero E. & Valleri G. (2003) - Middle Eocene to Middle Miocene planktonic foraminiferal biostratigraphy for internal basins (Monferrato and northern Apennines, Italy). *Micropaleontology*, 49: 341-358.
- Mutti E., Papani L., Di Biase D., Davoli G., Mora S., Segadelli S. & Tinterri R. (1995) - Il Bacino Terziario Epimesoalpino e le sue implicazioni sui rapporti tra Alpi e Appennino. *Memorie di Scienze Geologiche*, 47: 217-244.
- Nolf D. (1988) - Les otolithes de téléostéens éocènes d'Aquitaine (sud-ouest de la France) et leur intérêt stratigraphique. *Mémoire de l'Académie royale de Belgique, Classe des Sciences*, 4^o, 2e série, 19: 1-147.
- Přikryl T., Schwarzhans W. & Kovalchuk O. (2017) - Lanternfishes (Myctophidae) with otoliths in situ from the Early Oligocene of the Eastern Paratethys (western Ukraine). *Neues Jahrbuch Geologie und Paläontologie Abhandlungen*, 285: 213-225.
- Prokofiev A. M. (2006) - Fossil myctophid fishes (Myctophiformes: Myctophoidei) from Russia and adjacent regions. *Journal of Ichthyology*, 46: 38-83
- Schwarzhans W. (1978) - Otolith-morphology and its usage for higher systematical units with special reference to the Myctophiformes s.l. *Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie*, 15: 167-185.
- Schwarzhans W. (1985) - Tertiäre Otolithen aus South Australia und Victoria (Australien). *Palaeo Ichthyologica*, 3: 1-60.
- Schwarzhans W. (2013) - A comparative morphological study of the Recent otoliths of the genera *Diaphus*, *Idiolychnus* and *Lobianchia* (Myctophidae). *Palaeo Ichthyologica*, 13: 41-82.
- Schwarzhans W. (2019a) - Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. *Memorie della Società Italiana di Scienze Naturali e del Museo di Storia Naturale di Milano*, 46: 3-326.
- Schwarzhans W. (2019b) - A comparative morphological study of Recent otoliths of the Congridae, Muraenesocidae, Nettastomatidae and Colocongridae (Anguilliformes). *Memorie della Società Italiana di Scienze Naturali e del Museo di Storia Naturale di Milano*, 46: 327-354.
- Schwarzhans W. & Carnevale G. (2021) - The rise to dominance of lanternfishes (Teleostei: Myctophidae) in the oceanic ecosystems: a paleontological perspective. *Paleobiology*, 47: 446-463.
- Schwarzhans W., Mörs T., Engelbrecht A., Reguero M. & Kriwet J. (2017) - Before the freeze: otoliths from the Eocene of Seymour Island, Antarctica, reveal dominance of gadiform fishes (Teleostei). *Journal of Systematic Palaeontology*, 15: 147-170.
- Sulc J. (1932) - Les otolithes du Paléogène des environs de Biarritz. *Rozprawy Státního geologického ústavu Československé Republiky*, 7: 1-94.

