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# A lanternfish (Myctophiformes, Myctophidae) from the uppermost Pliocene of Sicily, Italy

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ABSTRACT:

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A fossil lanternfish from the uppermost Pliocene Monte Narbonne Formation in Sicily, Italy, constitutes the first record of a well-preserved fish skeleton from the Pliocene–Pleistocene global boundary stratotype locality of Monte San Nicola near Gela. The described fish differs from 22 myctophid genera, but cannot be clearly distinguished from the genera *Bolinichthys*, *Lampanyctus*, *Lepidophanes*, and *Triphoturus* of the subfamily Lampanyctinae, *Benthosema*, *Diogenichthys*, *Hygophum* of the subfamily Myctophinae, or *Lobianchia* of the subfamily Diaphinae. It differs from 10 species recorded as skeletons from the Pliocene–Pleistocene of the Mediterranean region. It appears closely similar to *Benthosema glaciale* (Reinhardt, 1837), but incomplete preservation of diagnostic characters limits taxonomic assignment. The presence of this myctophid suggests at least survivable conditions in the mesopelagic zone during the time of deposition, in spite of reduced circulation.

**Key words:** Teleostei; Myctophidae; Mediterranean; Pliocene; Italy.

## INTRODUCTION

The lanternfishes (Family Myctophidae Gill, 1893) are small (standard length 20 to 280 mm, with many species less than 120 mm) marine fishes that play an important role in fish biomass (Catul *et al.* 2011; Irigoien *et al.* 2014; Carpenter and De Angelis 2016; Nelson *et al.* 2016). Living myctophids are common and occur in all oceans, including Arctic and Antarctic waters. Many undertake diel (diurnal) vertical migration, descending to depths exceeding 2000 m during the day to avoid predation, and rising at night to depths between 30 and 100 m to feed (Nafpaktitis 1984). Individuals hence may inhabit both meso- and epipelagic zones. The Family Myctophidae contains 33 genera and 250 extant species currently considered valid (Froese and Pauly 2026). Traditionally, two subfamilies (Myctophinae Fowler, 1925 and Lampanyctinae Paxton, 1972) and seven tribes have been distinguished within this family based on osteology and the arrangement of photophores (Paxton 1972). According to Martin *et al.* (2018), five subfamilies (Gymnoscopelinae Paxton, 1972; Notolychninae Paxton, 1972; Lampanyctinae Paxton, 1972; Diaphinae Paxton, 1972; and Myctophinae Gill, 1893) are recognized from both molecular and morphological investigations, with three former tribes of the Lampanyctinae being elevated to subfamilies.

From the Cretaceous of Italy, skeletons are related to the Myctophidae, to *Diaphus* Eigenmann and

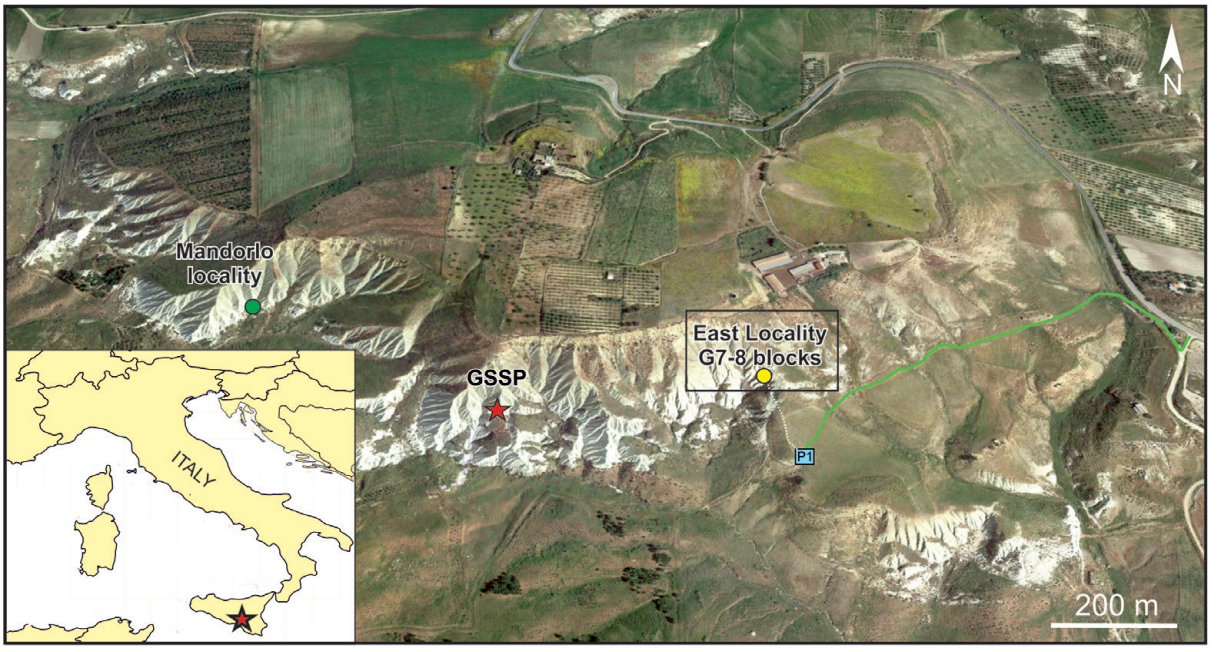
Eigenmann, 1890 (Taverne 2015) and to *Garganomyctophum* Taverne, 2021, but these have a limited number of characters typical of myctophids. The earliest otolith record of a myctophid is *Eokrefftia prediaphus* Schwarzhans, 1985 from the late Paleocene of South Australia. The earliest skeletal record with preserved photophores is *Eomyctophum mainardii* Calzoni, Giusberti and Carnevale, 2025 from the early Eocene of Italy. Myctophids occur commonly in Paleogene sediments, and significant increases in myctophid abundance and diversity are observed in the Neogene, especially in the Miocene and Pliocene (Denton 2018; Schwarzhans and Carnevale 2021).

The Family Myctophidae has a rich fossil record from the Pliocene of the Mediterranean comprising otoliths and skeletons. The otolith record includes the genera *Benthosema* Goode and Bean, 1896, *Ceratoscopelus* Günther, 1864, *Diaphus*, *Electrona* Goode and Bean, 1896, *Hygophum* Bolin, 1939, *Lampadena* Goode and Bean, 1896, *Lampanyctus* Bonaparte, 1840, and *Myctophum* Rafinesque, 1810 (Landini and Sorbini 2005; Agiadi *et al.* 2020). The skeletal record from the Pliocene–Pleistocene is represented by *Benthosema*, *Ceratoscopelus*, *Diaphus*, *Electrona*, *Hygophum*, *Lobianchia* Gatti, 1904, *Lampanyctus*, and *Myctophum* (Landini and Menesini 1978, 1986).

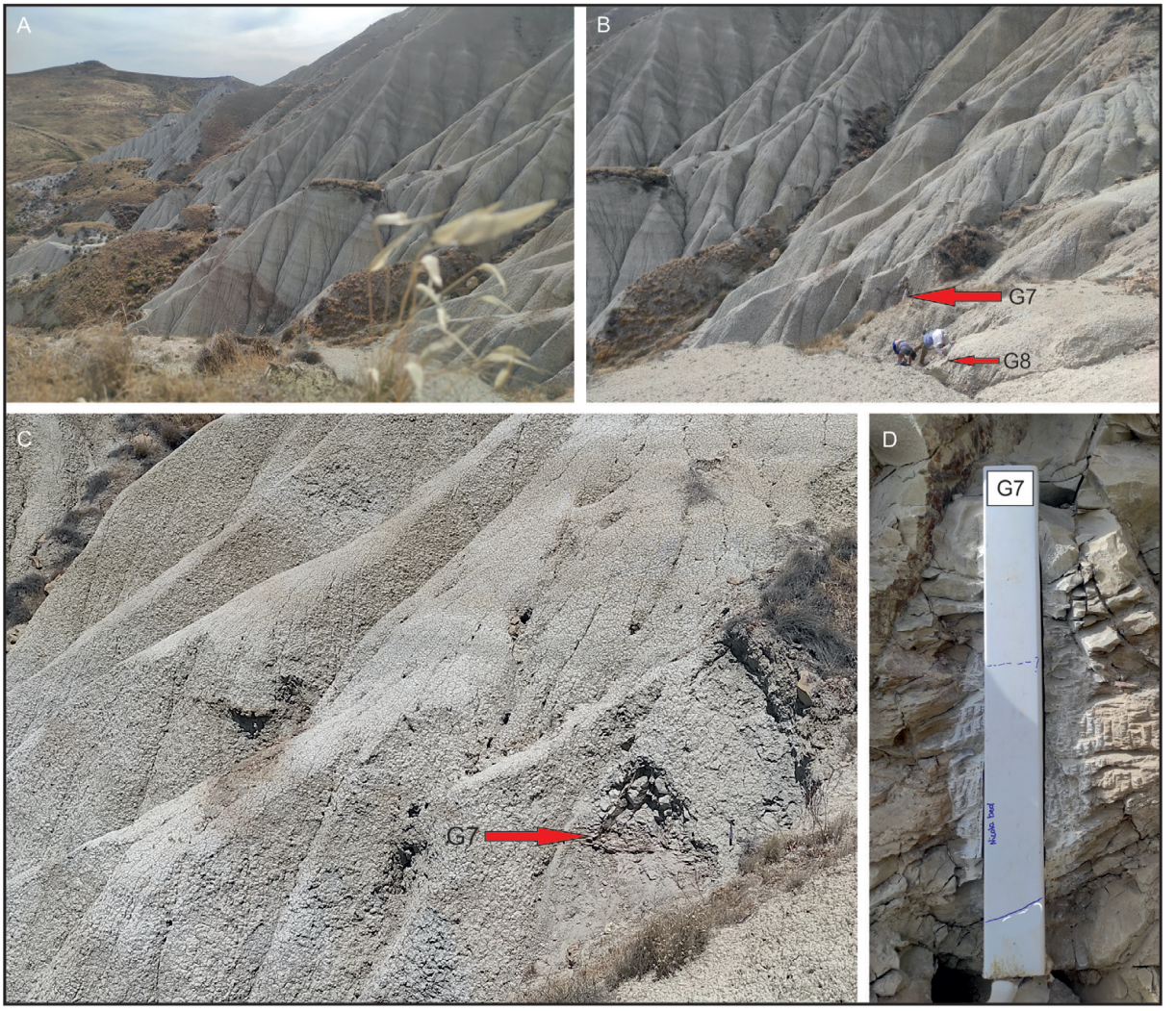
The uppermost Pliocene deposits exposed at Monte San Nicola, Sicily, have yielded a fish skeleton preserving a well-defined myctophid morphology, which is herein described as an indeterminate species and genus of the Myctophidae. The occurrence of this specimen provides insights into paleoenvironmental conditions at the Pliocene–Pleistocene transition, which are accordingly discussed.

## GEOLOGICAL SETTING

The Global boundary Stratotype Section and Point (GSSP) at Monte San Nicola near Gela, Sicily, Italy, defines the boundary between the Piacenzian and Gelasian stages, Pliocene and Pleistocene series, and Neogene and Quaternary systems (Gibbard and Head 2010). The base of the Gelasian, dated to 2.58 Ma (Head 2019), is marked by the base of a marly layer overlying the ~20 cm-thick, dark, microlaminated sapropelic Nicola bed (Rio *et al.* 1994, 1998), which has been extensively studied by Radmacher *et al.* (2023, 2025). This layer is easily identified for about 1 km continuously along the southern margin of Monte San Nicola, a typical example of Mediterranean badlands. This terrain represents a dry and inhospitable environment with sparse vegetation, where soft, clay-rich marly sediments have been extensively eroded.




Text-fig. 1. Location of the Monte San Nicola section near Gela, Sicily, Italy. The position of the Global boundary Stratotype Section and Point (GSSP) at Monte San Nicola is marked by a star. P1 indicates an improvised parking area suitable for four-wheel vehicles. Solid lines represent established tracks and informal access routes connecting the site to the main roads. The specimen described in this study was recovered from rock debris at the East Locality, generated during excavation of rock block G7. For additional details, see Radmacher *et al.* (2023, 2025, and submitted). The lithological characteristics of the sample are the same as those of the Nicola (A5) sapropelic bed. Based on a Google Earth image.




Text-fig. 2. Detailed location of rock blocks collected at the East Locality of Monte San Nicola. A – General view of the Monte San Nicola outcrop looking west, with darker sapropelic layers clearly visible; B – Location of rock blocks G7 and G8, with G8 shown during excavation; C – Cleaned section prior to installation of the plastic moulding; D – U-channel plastic moulding containing block G7 which spans the sapropelic Nicola (A5) bed; the collected rock blocks are housed at the Polish Academy of Sciences, Institute of Geological Sciences, Research Centre in Kraków. Photos by WR.

The landscape is characterized by steep slopes and high drainage density, shaped by infrequent but intense rainfall events. The uppermost Neogene is represented here by a cyclic group of six dark layers, belonging to Cluster A of Verhallen (1987), and their intervening lighter marls. This cyclicity relates to orbital forcing, with dark beds registering successive precessional cycles amplified and grouped by the modulating effects of eccentricity. The Nicola bed, which is the uppermost and most prominent of these layers, accumulated under oxygen-depleted bottom-water conditions (see below). Deposited during an orbitally-forced warm phase, it captures a northward shift of the African summer monsoon, triggering freshwater influx into the saline Mediterranean Sea. The resulting low-density surface-water cap disrupted winter overturning circulation within the Mediterranean, which ultimately led to bottom-water anoxia (Rohling *et al.* 2015; Radmacher *et al.* 2023, 2025). The specimen described herein was recovered from the East Locality of Monte San Nicola during fieldwork in 2024 (Text-figs 1 and 2; Radmacher *et al.*, in review). Mesopelagic faunas were likely common in the Mediterranean region during the Late Pliocene and Pleistocene, as evidenced by the presence of fish otoliths and bones in the Upper Pliocene

and Pleistocene (Girone *et al.* 2006) and even complete fossil fish remains within the Lower Pleistocene (Landini and Menesini 1978). However, for the first time, a well-preserved fish fossil is now reported from the Monte San Nicola locality.

## MATERIALS AND METHODS

The nearly complete articulated skeleton of a lanternfish from Monte San Nicola, placed in the collections of the Stanisław Józef Thugutt Museum of the Faculty of Geology, University of Warsaw (MWGUW), is described. The specimen was studied under a NIKON SMZ1000 stereomicroscope at the Scanning Electron and Optical Microscopy Laboratory in the Faculty of Geology of the University of Warsaw. Photographs were taken with a Keyence VHX-7000 digital microscope at the Faculty of Geology, University of Warsaw.

The specimen was recovered from loose material during the excavation of block G7 (14.208338ºN, 37.146842ºE) which spans microlaminated bed A5 (the Nicola bed) at the East Locality of Monte San Nicola, about 314 m east of the GSSP (Radmacher *et al.* in review). Its microlaminated matrix characterized by the presence of the ichnofossil *Chondrites* isp. allows unequivocal assignment to the upper part of the Nicola bed, Zone IIb, as described in Radmacher *et al.* (2023, 2025). This allows the specimen to be assigned an astronochronological age of 2.59 Ma (latest Pliocene) based on the mid-point of the ~20-cm-thick Nicola bed (Lourens *et al.* 1996).

Comparative information about the extant myctophids was mostly derived from Hubbs and Wisner (1964), Paxton (1972, 1979), Landini and Menesini (1978), Nafpaktitis (1984), Carpenter and De Angelis (2016), and Froese and Pauly (2026).

### Luminous organ abbreviations

AOa – anterior anal, AOp – posterior anal, PLO – suprapectoral, PO – thoracic, PVO – subpectoral, SAO – supra-anal, VO – ventral.

## SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii *sensu* Goodrich, 1930
Infraclass Teleostei *sensu* Nelson, Grande and Wilson, 2016
Order Myctophiformes *sensu* Rosen, 1973
Family Myctophidae Gill, 1893

Myctophidae indet.
(Text-figs 3–5)

MATERIAL: MWGUW 009800, nearly complete skeleton.

MEASUREMENTS: See Table 1.

Table 1. Morphometric characteristics of the lanternfish from Sicily.

| Morphometric character | Measurement [mm] | Measurement as percentage of standard length |
|---|---|---|
| Standard length [SL] | 59 | |
| Head length | 16 | 27% |
| Maximum body depth | 20 | 34% |
| Predorsal distance | 26 | 44% |
| Preanal distance | 32 | 54% |
| Prepelvic distance | 22 | 37% |

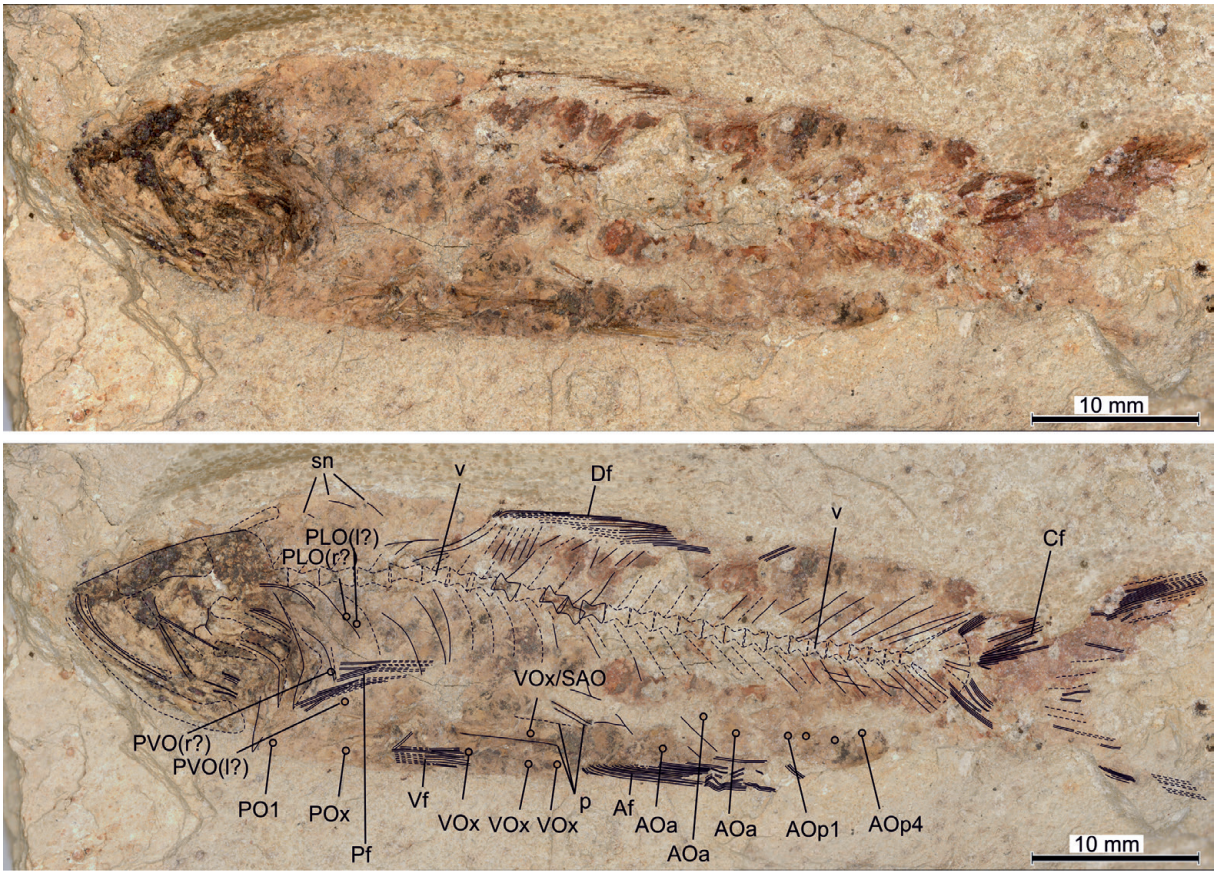
DESCRIPTION: A small fish with elongated and laterally compressed body (Text-fig. 3), measuring 59 mm in standard length (SL). The head is triangular in lateral view (Text-fig. 4), its length 27% of the SL. The dorsal and ventral profiles of the body behind the head are slightly convex. The beginning of the dorsal fin is behind the vertical through the pelvic fin base. The beginning of the anal fin is beneath the posterior part of the dorsal fin base. The distance between bases of the pectoral and pelvic fins is shorter than that between the pelvic fin base and the beginning of the anal fin. The snout does not protrude anteriorly, and the mouth is terminal and oblique.

*Neurocranium*. The neurocranium is elongated and triangular in lateral outline. The otolith is partially preserved (Text-fig. 4) but hidden by cranial bones. The parasphenoid is long and thin. The lateral ethmoid posterior margin is concave. The shapes and borders of the other cranial bones are indistinct.

*Circumorbital series*. Most bones of the circumorbital series are indistinct. Only short margins of circumorbitals CO2 and CO3 are visible.

*Oral jaws and dentition*. The jaws are long: the posterior end of the lower jaw is behind to vertical with the posterior orbit margin. The maxilla and premaxilla are slender, and slightly curved upward anteriorly. The teeth are not preserved. The mandible is elongated.

*Suspensorium*. The hyomandibula is elongated. The metapterygoid is large, but its margins are indistinct. The endopterygoid is a flat, large oval bone; the teeth were not observed. The ectopterygoid is long and thin. The palatine is elongated. The quadrate and symplectic are not preserved.



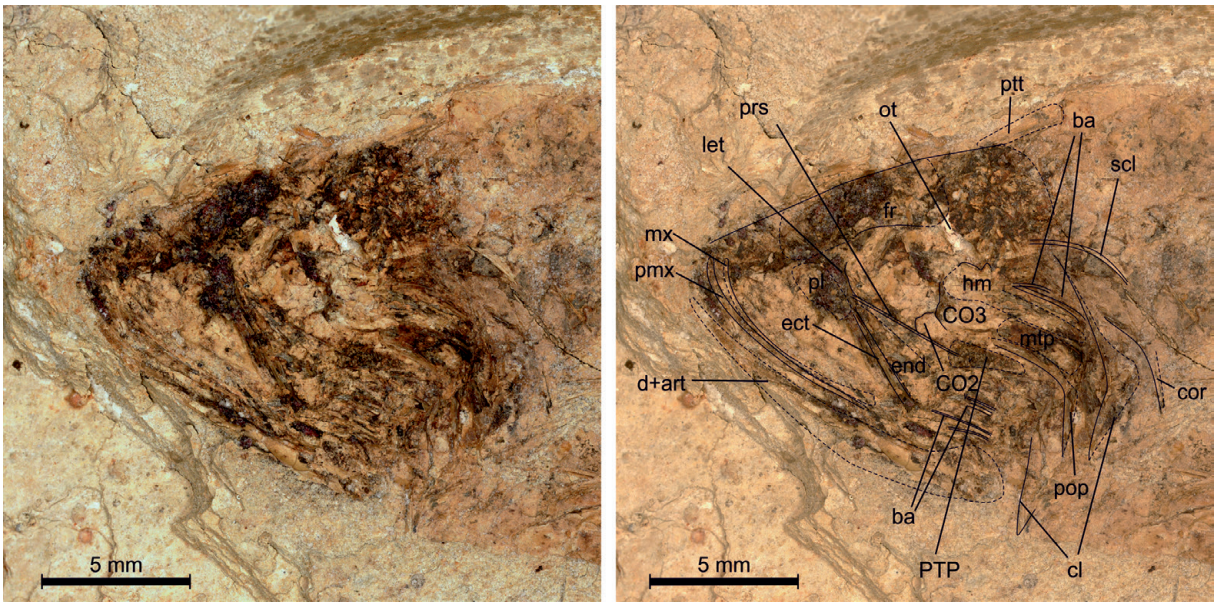

Text-fig. 3. Lanternfish from the Pliocene of Sicily, Italy, MWGUW 009800, photo and superimposed interpretative drawing. Abbreviations: Af – anal fin; AOa – anterior anal photophore; AOp – posterior anal photophore; Cf – caudal fin; Df – dorsal fin; l – left; p – pterygiophore; Pf – pectoral fin; PLO – suprapectoral photophore; PO – thoracic photophore; PVO – subpectoral photophore; r – right; SAO – supra-anal photophore; sn – supraneurals; v – vertebrae; Vf – pelvic fin; VO – ventral photophore

*Opercular series.* The opercle is not preserved. The preopercle is thin. The shapes and borders of other bones are indistinct. Branchiostegals and other bones are not visible.

*Hyoid and branchial arches*. The branchial arches are thin. Remains of pharyngobranchial tooth plates are densely covered with minute, closely spaced teeth. Other bones are not preserved.

*Vertebral column, ribs, and intermuscular bones*. The vertebral column consists of about 29 vertebrae including about 18 caudal ones (Text-fig. 3). Although the vertebral column is poorly preserved, visible remains of vertebrae centra, ribs, and haemal and neural spines allow reconstruction of the vertebral column, including one vertebra covered by skull bones. In the caudal region, neural spines are wider than those in the abdominal one. The angle between neural spines and vertebral centra is about 45º. The angle for haemal spines is similar. There are about 10 pairs of thin and long ribs. The remains of five ribs are visible, and five others are reconstructed. Supraneurals are thin and short, there being three between the posterior margin of the skull and beginning of the dorsal fin. Thin, not forked intermuscular bones are preserved below preural centra 2–6, whereas two forked intermuscular bones are preserved above the anal fin.

*Paired fins and girdles*. The pectoral fin consists of more than nine rays (Text-fig. 3). The fins are positioned about 33% of the body depth, above the abdominal ventral outline. Only the proximal parts of rays are preserved. About four rays are preserved near the fin base, the others being displaced ventrally. The posttemporal has a long dorsal branch preserved. The supracleithrum is a thin, elongate bone. The cleithrum is crescent shaped. The coracoid has an elongated triangular arm directed ventrally. The pelvic fins are positioned anteriorly to the dorsal fin, the prepelvic distance is 37% of the SL. The pelvic fin consists of eight rays.




Text-fig. 4. Lanternfish from Sicily, skull and its details, MWGUW 009800, photo and superimposed interpretative drawing. Abbreviations: art – articulare; ba – branchial arches; cl – cleithrum; CO – circumorbitals; cor – coracoid; d – dentary; ect – ectopterygoid; end – endopterygoid; fr – frontal; hm – hyomandibular; let – lateral ethmoid; mtp – metapterygoid; mx – maxilla; ot – otolith; pl – palatine; pmx – premaxilla; pop – preopercle; prs – parasphenoid; PTP – pharyngobranchial tooth plates; ptt – posttemporal; scl – supracleithrum.

*Median fins and supports*. The dorsal fin has about 14 rays (Text-fig. 3). Two posterior rays are separated from the anterior ones, although it is not clear if they are displaced or there should be a few rays reconstructed in the gap. Therefore, it is possible that the dorsal fin had more than 14 rays. About 13 pterygiphores are observed. The fin originates anteriorly to the mid-length of the body, the predorsal distance being 44% of the SL. The anal fin has 14–15 rays preserved. The fin originates below the posterior part of the dorsal fin base, the preanal distance being 54% of the SL.

*Caudal fin and skeleton*. The caudal fin is forked and deeply notched (Text-fig. 3). The fin has about eight principal rays in the upper lobe. The hypurals, epurals and parhypural are not preserved.

*Squamation*. The body and opercular region are covered by thin overlapping cycloid scales with radial fissures (radii) in anterior fields.

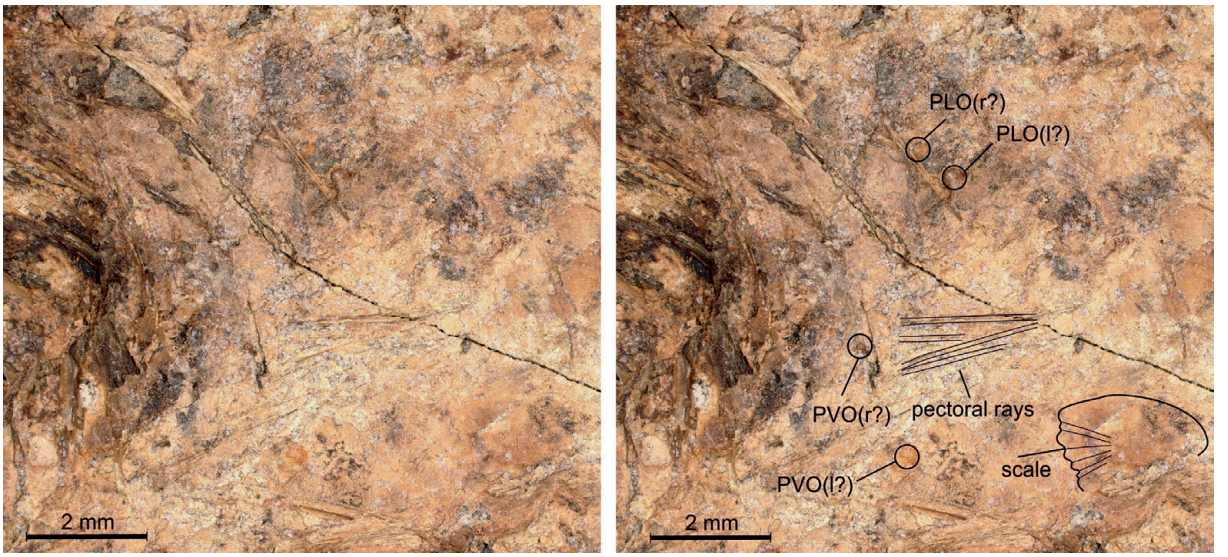
*Luminous organs*. The photophore pattern is uncertain due to inadequate preservation. Two PO photophores are preserved, both at the same level (Text-fig. 3). The first is the anteriormost photophore, located at the ventral end of the cleithrum. It is not possible to recognize if any of PO3, PO4, or PO5 are elevated. The second is ventral to the pectoral fin base, and is PO3 or PO4. There are two PVO photophores but their position is unusual for the Myctophidae. It seems that one is from the left side of the body, and the second is from the right side. The lower PVO is ventral to the pectoral fin rays, and the second PVO is anterior to the rays. The rays of left and right pectoral fins are slightly displaced ventrally; therefore it is not clear where the base of fin was placed. There are two PLOs above the pectoral fin (Text-fig. 5). It seems that one is from the left side of the body, and the other is from the right side. There are three VO photophores, all at the same level. The series seems to be incompletely preserved, making it impossible to determine if VO2 or VO3 are elevated. One photophore is observed above the second visible VO photophore. It could be an elevated VO or a SAO photophore. There are three photophores in the AOa series and four in the AOp series.

## DISCUSSION

### Systematics

The osteological, luminous organs and meristic data support the assignment of the examined specimen from the uppermost Pliocene of Monte San Nicola to the family Myctophidae.

The specimen examined here exhibits the following features typical of the Myctophidae (Carpenter and De Angelis 2016): single dorsal fin with about 14




Text-fig. 5. Lanternfish from Sicily, details of suprapectoral and subpectoral photophores, MWGUW 009800, photo and superimposed interpretative drawing. Abbreviations: l – left; PLO – suprapectoral photophore; PVO – subpectoral photophore; r – right.

rays, anal fin origin under dorsal fin; anal fin with about 14–15 rays; pectoral fin with more than nine rays; pelvic fin origin well behind the pectoral fin origin; pelvic fin with 8 rays; primary photophores present, arranged in distinct groups on head and body; number of vertebrae observed about 29; jaws extending to posterior margin of eye; fins without spines. The total number of vertebrae in the Myctophidae ranges from 28 to 45, with typical variability for a single species being 2 to 4 vertebrae (Paxton 1972). It is highly likely that the number of vertebrae of the studied specimen is slightly greater than reported, by one or two vertebrae, possibly covered by skull bones.

**Comparison with extant taxa**

The specimen from Sicily shares long jaws, a PLO dorsal to the pectoral base, eight pelvic rays, and three to eight VO, with the subfamily Lampanyctinae (*Bolinichthys* Paxton, 1972, *Ceratoscopelus*, *Lampadena*, *Lampanyctus*, *Lepidophanes* Fraser-Brunner, 1949, *Parvilux* Hubbs and Wisner, 1964, *Stenobrachius* Eigenmann and Eigenmann, 1890, *Taaningichthys* Bolin, 1959, and *Triphoturus* Fraser-Brunner, 1949). It differs from *Ceratoscopelus*, *Lampadena*, *Parvilux*, *Stenobrachius* and *Taaningichthys* in its smaller number of vertebrae (about 29 *vs.* 36–38, 36–37, 37–38, 36–38, and 35–41, respectively).

The described fish differs from *Notolychnus* Fraser-Brunner, 1949 (Notolychninae) in having 8 (*vs.* 6) rays in the pelvic fin.

It differs from *Protomyctophum* Fraser-Brunner, 1949 and *Electrona* (Myctophinae) in a PLO dorsal (*vs.* ventral) to the pectoral fin. It shares with *Benthosema*, *Diogenichthys* Bolin, 1939, *Hygophum*, *Myctophum*, and *Symbolophorus* Bolin and Wisner, 1959 (all Myctophinae) a PLO dorsal to the pectoral base. It differs from *Myctophum* and *Symbolophorus* in a smaller number of vertebrae (about 29 *vs.* 35–44, and 37–40, respectively). It can be differentiated from *Symbolophorus* by an anal fin origin beneath the posterior part of the dorsal fin base (*vs.* beneath posterior end of the dorsal fin base). It differs from *Centrobranchus* Fowler, 1904, *Gonichthys* Gistel, 1850, *Loweina* Fowler, 1925, and *Tarletonbeania* Eigenmann and Eigenmann, 1890 (all Myctophinae) in its PLO being above the upper edge of the pectoral base (*vs.* PLO at upper edge of pectoral base or opposite base) and in a smaller number of vertebrae (about 29 *vs.* 36–38, 38–39, 39, and 40–41, respectively).

The fish from Sicily shares with *Diaphus*, *Idiolychnus* Nafpaktitis and Paxton, 1978, and *Lobianchia* (all Diaphinae) a PLO dorsal to the pectoral base. It can be differentiated from *Diaphus* and *Idiolychnus* by an anal fin origin beneath the posterior part of the dorsal fin base (*vs.* beneath the posterior end of the dorsal fin base). It differs from the Diaphinae in the shape of the head, with a slightly concave dorsal margin, gently sloping and with a pointed, slightly rounded snout (*vs.* strongly concave dorsal margin, steeply sloping and blunt, rounded snout).

The described fish differs from *Gymnoscopelus*

Günther, 1873, *Hintonia* Fraser-Brunner, 1949, *Lampanyctodes* Fraser-Brunner, 1949, *Lampichthys* Fraser-Brunner, 1949, *Notoscopelus* Günther, 1864 and *Scopelopsis* Brauer, 1906 (all Gymnoscopelinae) in its lower number of vertebrae (about 29 *vs.* 37 to 45).

The described fish resembles the genera *Bolinichthys*, *Lampanyctus*, *Lepidophanes*, and *Triphoturus* of the subfamily Lampanyctinae; the genera *Benthosema*, *Diogenichthys*, and *Hygophum* of the subfamily Myctophinae; and the genus *Lobianchia* of the subfamily Diaphinae; but cannot be placed in any of them with certainty.

**Comparison with extinct genera and species**

The Pliocene–Pleistocene of the Mediterranean region includes *Benthosema glaciale* (Reinhardt, 1837), *Ceratoscopelus maderensis* (Lowe, 1839), *Diaphus holti* Tåning, 1918, *D. rafinesquii* (Cocco, 1838), *Diaphus* sp., *Electrona risso* (Cocco, 1829), *Hygophum benoiti* (Cocco, 1838), *H. hygomi* (Lütken, 1892), *Hygophum* sp., *Lobianchia dofleini* (Zugmayer, 1911), *Lampanyctus crocodilus* (Risso, 1810), *L. pusillus* (Johnson, 1890), *Lampanyctus* sp. and *Myctophum punctatum* Rafinesque, 1810, all preserved as skeletons (Landini and Menesini 1978, 1986; Gregorová 2004; Landini and Sorbini 2005).

In the described fish, the photophore interpreted as VOx/SAO would be SAO in *B. glaciale.* It differs from *C. maderensis*, *H. hygomi*, *H. benoiti*, *L. crocodilus*, *L. pusillus* and *M. punctatum* in its smaller number of vertebrae.

It differs from *D. rafinesquii* and *D. holti* by an anal fin origin beneath the posterior part of the dorsal fin base (*vs.* beneath the posterior end of the dorsal fin base). It can be distinguished from *E. risso* by its PLO positioned dorsal (*vs.* ventral) to the pectoral base. It differs from *L. dofleini* by its smaller preanal distance (54% *vs.* 66–70% of the SL).

The preserved features of the described fish best resemble *Benthosema glaciale*, but the absence of key diagnostic characters preclude assignment to that species.

The myctophid taxa preserved as otoliths in both the Pliocene and Pleistocene of the Mediterranean region include *Benthosema glaciale*, *B. suborbitale* (Gilbert, 1913), *Ceratoscopelus maderensis*, *Diaphus holti*, *D. rafinesquii*, *D.* aff. *splendidus* (Brauer, 1904), *D. taaningi* (Norman, 1930), *Electrona risso*, *Hygophum benoiti*, *H. hygomi*, *Lobianchia dofleini*, *Myctophum punctatum*, *Scopelopsis pliocenicus* (Anfossi and Mosna, 1976), and *Symbolophorus veranyi* (Moreau, 1888); while *Lampadena ionica* Girone and Nolf, 2002, *Lampadena* cf. *urophaos atlantica* Maul, 1969, *Lampanyctus crocodilus*, *Lobianchia gemellari* (Cocco, 1838), *Notoscopelus elongatus* (Costa, 1844), and *Protomyctophum arcticum* (Lütken, 1892) are recorded only in the Pleistocene (Girone *et al.* 2006).

The Miocene skeletal record includes: *Bolinichthys* sp.; *Ceratoscopelus dorsalis* (Sauvage, 1870); *C. miocenicus* Bedini, Francalacci and Landini, 1986; *Diaphus edwardsi* (Sauvage, 1870); *D. larteti* (Sauvage, 1873); *D. microsomus* (Sauvage, 1870); *D. sauvagei* (Arambourg, 1925); *D. vexillifer* (Sauvage, 1873); *Diaphus* sp.; *Lampadena* sp.; *Lampanyctus ecnomi* (Sauvage, 1873); *L. licatae* (Sauvage, 1870); *Lampanyctus* sp.; *Lobianchia* sp.; *Myctophum columnae* (Sauvage, 1873); *M. danielli* D'Erasmo, 1929; *M. probenoiti* Arambourg, 1927; *Myctophum* sp. and *Stenobrachius sangsunii* Nam and Nazarkin, 2022 (Bedini *et al.* 1986; Gregorová 2004; Carnevale 2007; Denton 2013; Schwarzhans and Carnevale 2021; Carnevale *et al.* 2022; Nam and Nazarkin 2022).

Our specimen differs from *C. dorsalis*, *L. ecnomi* and *L. licatae* in the smaller number of vertebrae (about 29 *vs.* 35–37, 35–37, and 34–36, respectively). It differs from *D. edwardsi*, *D. larteti*, *D. microsomus*, *D. sauvagei*, *D. vexillifer* and *M. columnae* by an anal fin origin below the posterior part of the dorsal fin base (*vs.* beneath the posterior end of the dorsal fin base). It differs from *C. miocenicus* and *S. sangsunii* by a smaller preanal distance (54% *vs.* 72% and 60–68% of the SL).

The Oligocene myctophids preserved as skeletons are related to the extinct species *Oligophus moravicus* (Paucă, 1931) and *Eomyctophum koraense* Daniltchenko, 1947 (Gregorová 2004; Prokofiev 2006; Přikryl *et al.* 2017). The fish from Sicily differs from *O. moravicus* and *E. koraense* by an anal fin origin beneath the posterior part of the dorsal fin base (*vs.* beneath the posterior end of the dorsal fin base or slightly posterior to the end of the fin). It differs from *O. moravicus* in having the PLO dorsal to the pectoral base (*vs.* level with pectoral base).

**Ecology and paleoenvironment**

Myctophids feed on zooplankton including teleost larvae, crustaceans such as copepods, amphipods, and euphausiids, hydrozoans (Siphonophorae) and thaliaceans (e.g., Eduardo *et al.* 2021). They are important contributors to the diet of a diversity of predators including fishes, squids, marine mammals and seabirds, providing a major food source for deep-sea species and secondary prey for epipelagic predators (Robinson *et al.* 2020; Eduardo *et al.* 2021). In per-

forming daily vertical migrations, lanternfish today actively transport carbon consumed in the epipelagic zone to mesopelagic depths.

The Nicola bed was deposited in the latest Pliocene on the continental slope at a water depth exceeding 800–1000 m (Radmacher *et al.* in review). Its clay-rich microlaminated lithology results from an absence (Zone IIa), or only weak bioturbation (Zone IIb), mainly limited to later burrowing into the microlaminated sediment over a few thousand years (Radmacher *et al.* 2023, 2025), which allowed the described myctophid to be preserved as a nearly complete skeleton. Bioturbation has largely homogenized the marls below and above the Nicola bed. The cause of microlamination is bottom-water anoxia, as evidenced by an elemental geochemical signature for fully euxinic conditions (Fasone *et al.* 2024) and an absence of benthic organisms within the lower part of the Nicola bed.

The Mediterranean today is one of the most oligotrophic marine basins in the world, with oligotrophy increasing progressively from west to east (e.g., Varkitzi *et al.* 2020; Barbieux *et al.* 2021). River discharge triggering sapropelic deposition will therefore have introduced critical nutrients to the photic zone at a time of enhanced summer insolation. Not surprisingly, calcareous nannofossil evidence registers increased biological productivity in the mixed-layer and increased nutrient availability in the lower photic zone during Nicola bed deposition (Addante *et al.* 2025). This is supported by total $C_{37}$ alkenone concentrations that are proxy for productivity increases in the photic layer (Addante *et al.* 2025). Indeed, elevated productivity in the water-column during Nicola bed deposition probably contributed to anoxia on the sea floor (Fasone *et al.* 2024).

Many myctophids today are adapted to oxygen minimum zones in the world's oceans (Douglas *et al.* 1976; Eduardo *et al.* 2021). The presence of a single skeleton of lanternfish in the Nicola bed suggests at least survivable conditions in the mesopelagic zone at the time of deposition in spite of reduced circulation. Prey within the epipelagic zone would at least have been plentiful. This scenario may, however, be contrasted with a study from a core in the eastern Mediterranean of otolith accumulation rates across sapropel S1, the most recently deposited sapropel dating to the Early Holocene (Pallacks *et al.* 2025). Mesopelagic species (mostly lanternfish) were nearly absent during sapropel formation, having been replaced by epipelagic taxa. The recovery of mesopelagic species was nonetheless rapid following the resumption of deep circulation (Pallacks *et al.* 2025).

The geological record of myctophids provides a unique window into the mesopelagic zone of the past, a topic of interest as ocean deoxygenation caused by anthropogenic warming expands. While the recovery of a solitary skeleton provides an important glimpse into the past, it shows that future discoveries of fossil fishes are possible at Monte San Nicola and a study of the otoliths at this locality may offer a unique opportunity to elucidate mesopelagic zone dynamics across the Pliocene–Pleistocene transition.

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