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TELEOST OTOLITHS FROM THE AQUITANIAN (EARLY MIOCENE) OF THE FELLI SECTION IN GREECE: THE ROOTS OF THE MEDITERRANEAN GOBY STOCK (GOBIIDAE, GOBIIFORMES)

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Abstract. Fish otoliths have been obtained from the early Miocene (Aquitanian) Pentalofos Formation of the Mesohellenic Basin in northern Greece. These specimens represent the earliest Miocene shallow marine otolith records from the Mediterranean. Here, we describe the goby otoliths of the assemblage, which are the most common group at this location. They represent the earliest recognized species of two of the three main extant Atlantic-Mediterranean goby groups, the *Pomatoschistus* lineage and the *Aphia* lineage. The taxa are interpreted as being phylogenetically positioned near the base of their respective lineages. The new taxa described are *Hellenigobius praeschismatus* n. gen. et n. sp. and *Plesiogobius felliensis* n. gen. et n. sp. A third species is tentatively related to *Nematogobius* in open nomenclature.

Introduction

Shallow-water otolith-bearing strata have rarely been recorded for the early Miocene of the Mediterranean. The closest in space and time are the rich otolith associations described from the Egerian (latest Oligocene–earliest Miocene) of the Pannonian Basin by Nolf & Brzobohatý (1994), the Burdigalian of Mallorca by Hoedemakers & Batllori (2005), and from the transitional Oligocene–Miocene of SW France by Steurbaut (1984). Thus, the Aquitanian otolith association from Felli in the Mesohellenic Basin of Greece fills a major gap in distribution and offers new insights into the early Neogene evolution of the shallow-water Mediterranean fish fauna. With a total of 43 specimens belonging to three species, the Gobiidae is the most common family at Felli.

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Geological Setting and Locations

The study area is located east of the village of Felli in Grevena Prefecture, NW Greece, where the molassic sedimentary sequence of the Mesohellenic Basin is exposed (Zelilidis et al. 2002; Ferrière et al. 2004). The Mesohellenic Basin was a marine basin and a distinct palaeogeographic area from the late Eocene until the middle Miocene, between the internal and external Hellenides, which lie to the ENE and WSW, respectively. It was a narrow, 300-km-

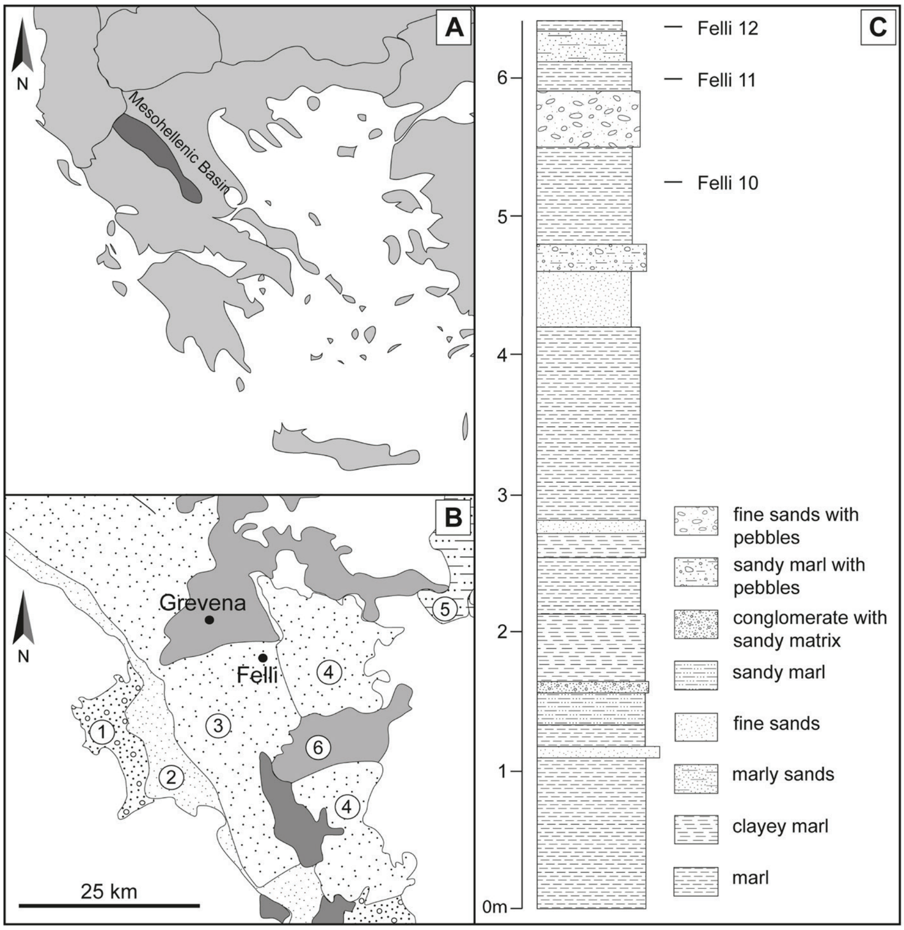

Fig. 1 - A) Location map of the Mesohellenic Basin in Greece. B) Simplified geological map of the studied area (modified after Ferrière et al. 2013). Numbers: 1, Krania Formation (late Eocene?); 2, Eptachori Formation (late Oligocene–early Miocene); 3, Pentalofos Formation (late Oligocene–early Miocene); 4, Tsotyli Formation (early–middle Miocene); 5, Ptolemais Basin (late Miocene–Pliocene); 6, Neogene to Recent deposits (gray). C) Stratigraphic section of Felli outcrop.

long trench filled with approximately 4.5 km of sediment (Brunn 1956; Ferrière et al. 2004; Wielandt-Schuster et al. 2004), which reflects the southeastward direction of the sea transgression (Fermeli & Ioakim 1992). We took samples from a small section by the Aliakmon River banks, located east of the Felli village, SE of Grevena City (40°01’4.55”N, 21°33’34.37”E) (Fig. 1), with the samples including sediments belonging to the Pentalofos Formation. The Pentalofos Formation comprises rocks of the late Chattian–Burdigalian (Mavridis et al. 1985; Fermeli & Ioakim 1992; Ferrière et al. 2004; Wielandt-Schuster et al. 2004; Ferrière et al. 2013; Kilias et al. 2015), but the sampled location terminates within the Aquitanian (Thivaiou et al. 2019). The section is mainly composed of conglomerates and sands; the grain size decreases toward the top, where we find marls and then clays (see Thivaiou et al. 2019; Fig. 1). The lower part of the section corresponds to coastal environments with some freshwater input, whereas the upper part constitutes a shallow marine environment. We sampled from three marly–clayey beds F10, F11 and F12, following the numbering scheme of Thivaiou et al. (2019). These beds are located near the top of the Pentalofos Formation at the Felli location and are considered to be of Aquitanian age (Thivaiou et al. 2019).

Material and Methods

The specimens were studied and drawn with a stereomicroscope equipped with a camera lucida drawing tube. Photographs were taken with a digital camera attached to a Wild M400 photomacroscope and remotely controlled from a computer. Sets of photographs of differing fields of depth of individual specimens were stacked using the HeliconFocus software from HeliconSoft and were then digitally retouched with Adobe Photoshop for silica particles or other minor inconsistencies insofar as doing so did not alter the morphology of the photographed specimens. Mirror-imaged figures are indicated in the captions as “reversed”.

The morphological terminology follows Koken (1884) with amendments by Chaine & Duvergier (1934) and Schwarzhans (1978). Schwarzhans

(2014) and Schwarzhans et al. (2020a) introduced specific morphometric measurements for gobioid otoliths, as well as the terms "subcaudal iugum" for a feature unique to gobiid otoliths that is often found below the caudal part of the sulcus and "ostial lobe" for an expansion of the anterior dorsal region of the ostial part of the sulcus. The reader is referred to Schwarzhans et al. (2020b) for a detailed characterization of the otoliths of the various Atlantic-Mediterranean goby lineages.

Measurements and abbreviations used: OL = maximum otolith length; OL2 = minimum otolith length measured at maximum ingression of concavity of posterior rim; OH = maximum otolith height; OT = otolith thickness without curvature; CL = colliculum length, measured along its axis. Angles measured are inclination angle of ostium. Ostium measured from tip of ostium through midpoint of sulcus height at collum (α); inclination angle of anterior rim (β); inclination angle of posterior rim (γ); inclination of line connecting preventral angle with tip of postdorsal projection (δ). For a visualization see Schwarzhans et al. (2020b).

Depository: All specimens have been deposited in Athens Museum of Paleontology and Geology (AMPG).

Systematics

Order **Gobiiformes** Thacker, 2009
Suborder **Gobioidei** Jordan & Evermann, 1896
Family Gobiidae Cuvier, 1816
Subfamily Gobionellinae Bleeker, 1874
Genus *Hellenigobius* n. gen.

Type species: *Hellenigobius praeschismatus* n. sp.; otolith-based genus and species.

Etymology: Derived from Hellas, the Greek name for Greece, and the Hellenides range bounding the type location of the type species, in combination with the genus name *Gobius*.

Diagnosis: A fossil, otolith-based genus of the *Pomatoschistus* lineage (sensu Agorreta et al. 2013) defined by the following combination of characters. Small, compressed, compact and thick otoliths. Maximal size just slightly over 1 mm length. Ratio OL:OH = 0.95–1.05; ratio OH:OT = 2.5–3.2. Otolith outline nearly rectangular. Inner face slightly to distinctly convex, smooth except for dorsal depression and narrow sulcus. Sulcus small, short (OL2:CL = 1.6–2.0), slightly deepened, with low ostial lobe and variably inclined sulcus (10–25°). No subcaudal iugum. Ventral furrow close to ventral rim of otolith.

Discussion. The otoliths of *Hellenigobius* resemble a combination of selected characters of the genus *Buenia* and the genera of the large *Pomatoschistus* Group ("sand gobies" sensu Thacker & Roje 2011; see Schwarzhans et al. 2020b for figures of extant otoliths). The distinctly convex inner face and the lack of a subcaudal iugum resemble otoliths of *Buenia* (subcaudal iugum narrow and indistinct in the case of *Buenia*). Otoliths of the genus *Pomatoschistus*, for example, show a nearly flat inner face and usually have a distinct subcaudal iugum. The relatively deep sulcus and the small, cup-shaped dorsal depression, however, are found in otoliths of the *Pomatoschistus* Group but not in *Buenia*. According to Kovačić et al. (2017, 2018), the genera *Buenia* and *Speleogobius* form a separate clade from the "sand gobies" with, for example, the genera *Pomatoschistus*, *Knipowitschia* and *Economidichthys*, with *Deltentosteus* representing the sister group to all other genera in the lineage. Schwarzhans et al. (2020b) assigned *Deltentosteus* with the *Buenia* Group based on otolith morphology. We now interpret the mosaic morphological characters of *Hellenigobius*, in comparison with the otoliths of the *Buenia* and *Pomatoschistus* groups, as an indication that it represents the sister group to both clades, but not *Deltentosteus* (for a more detailed discussion, see the section titled "Phylogenetic Implications" below).

Species. *Hellenigobius praeschismatus* n. sp. from the Aquitanian of Greece and probably also known from the late Oligocene of Hungary (Nolf & Brzobohaty 1994 as "genus aff. *Lesueurigobius*" sp., see below). A second species, *Hellenigobius bunyatovi* (Bratishko, Schwarzhans & Reichenbacher, 2015; in Bratishko et al. 2015), is placed in the same genus and was originally described as *Pomatoschistus bunyatovi*. *Hellenigobius bunyatovi* has been recorded from the Badenian (late Langhian to Serravallian) of the Paratethys (Bratishko et al. 2015, Schwarzhans et al. 2020a) and also from the pre-evaporitic Messinian of Italy (Schwarzhans et al. 2020b).

Hellenigobius praeschismatus n. sp.

Fig. 2A-J

1994 "genus aff. *Lesueurigobius*" sp. - Nolf & Brzobohatý: pl. 9, figs. 14-16.

Holotype: Fig. 2A-C, AMPG(V)2391, Aquitanian, Pentalofos Formation, sample level F12, Felli village section, 40°01'4.55"N, 21°33'34.37"E. Mesohellenic Basin, Grevena area, Greece.

Paratypes: 6 specimens, AMPG(V)2392, same location as holotype, sample level F11; and 1 specimen, AMPG(V)2393, same location as holotype, sample level F12.

Etymology: Derived from schisma (Greek = split) and prae (Latin = prior), referring to the presumed phylogenetic position prior to the dichotomy of the *Buenia* and *Pomatoschistus* clades.

Diagnosis: Small, compressed, compact and thick otoliths not exceeding 1 mm of length. Ratio OL:OH = 0.95–1.05; ratio OH:OT = 2.5–2.6. Outline of otolith nearly rectangular. Inner face distinctly convex, smooth except for small, cup-shaped dorsal depression and narrow sulcus. Sulcus small, short (OL2:CL = 1.75–2.0), slightly deepened, with low ostial lobe and steeply inclined sulcus (20–25°). Ostium slightly bent downwards from orientation of cauda resulting in even steeper inclination of ostium (25–35°). No subcaudal iugum. Ventral furrow close to ventral rim of otolith.

Description. Small otoliths with nearly rectangular outline. OL:OH = 0.95–1.05; OH:OT = 2.5–2.6. Anterior rim slightly forward inclined (75–85°), posterior rim nearly vertical; no preventral projection and very feeble or no postdorsal projection. Rounded predorsal angle prominent. Posterior rim with broad, shallow indentation at about level of cauda. Ventral rim flat; dorsal rim gently curved, highest at its middle or slightly behind. All rims smooth.

Inner face distinctly convex and relatively smooth. Dorsal depression small, cup-shaped, positioned at center of dorsal field and rather distant from sulcus. Sulcus narrow, short, moderately deepened, with low ostial lobe and without subcaudal iugum. OL2:CL = 1.75–2.0. Sulcus distinctly inclined; ostium additionally downward bent. Inclination angle of entire sulcus 20–25° and of ostium 25–35°. Ventral furrow very close to ventral rim of otolith, fading at about level of sulcus anteriorly and posteriorly and hence not clearly connected to dorsal depression. Outer face convex, slightly stronger than inner face, smooth.

Discussion. *Hellenigobius praeschismatus* differs from the younger *H. bunyatovi* in the more steeply inclined sulcus (20–25° vs 10–15°), the more strongly convex inner face and the smaller sulcus (OL2:CL = 1.75–2.0 vs 1.6–1.8). Furthermore, the dorsal depression is consistently smaller in *H. praeschismatus* as compared to *H. bunyatovi*.

Hellenigobius praeschismatus is described here from the Aquitanian of Greece, but previously recorded specimens from the latest Chattian of Hungary by Nolf & Brzobohatý (1994) most likely represent the same species. The rich goby assemblages from the Oligocene or early Miocene of SW-France described by Steurbaut (1984) do not seem to contain comparable otoliths. The late Burdigalian to early Langhian otoliths assemblages described by Hoedemakers & Batllori (2005) are likewise rich in gobies but do not contain comparable otoliths.

Subfamily Gobiinae
Genus *Plesiogobius* n. gen.

Type species: *Plesiogobius felliensis* n. sp.; otolith-based genus and species.

Etymology: From plesios (old Greek = near) referring to the plesiomorphic appearance of the otolith morphology, in combination with the genus name *Gobius*.

Diagnosis: A fossil, otolith-based genus of the *Aphia* lineage (sensu Agorreta et al. 2013) defined by the following combination of characters. Small, compressed, compact and relatively thick otoliths. Maximal size just slightly over 1.3 mm in length. Ratio OL:OH = 0.9–1.1; ratio OH:OT = 2.6–3.0. Preventral projection moderately developed; postdorsal projection variable. Inner face slightly convex with broad but indistinct dorsal depression, distinct ventral furrow and narrow sulcus. Sulcus small, short (OL2:CL = 1.9–2.1), slightly deepened, with low ostial lobe and moderately inclined sulcus (12–20°). Sulcus not bent. Subcaudal iugum small, positioned below anterior part of cauda. Ventral furrow close to ventral rim of otolith, curving around sulcus anteriorly and posteriorly.

Discussion. The otoliths of *Plesiogobius* resemble both otoliths of *Lesueurigobius* and the extinct *Hoeseichthys* (see Schwarzhans et al. 2020a, b for figures). It shares the general appearance, proportions and shape of the otolith and the sulcus with *Lesueurigobius*, but the sulcus and the subcaudal iugum are much smaller in relation to OL than in any of the known extant or fossil species of the genus. The sulcus is similarly small in *Hoeseichthys*, but, in *Plesiogobius*, it is more structured, and again, the subcaudal iugum is smaller. In addition, the ventral furrow tends to be more continuous all around the sulcus and connected up to the dorsal depression in *Hoeseichthys*. We interpret *Plesiogobius* as representing a stem-taxon or sister-taxon to the other members of the *Aphia* Group (for a more detailed discussion see the section titled "Phylogenetic Implications" below).

Species. Monospecific genus with *Plesiogobius felliensis* known from the Aquitanian of Greece and probably also the Chattian–Aquitanian transition zone of SW-France.

Plesiogobius felliensis n. sp.
Fig. 2K-Z

?1984 "genus aff. *Lesueurigobius*" sp. - Steurbaut: pl. 33, figs. 3-8.

Holotype: Fig. 2K-M, AMPG(V)2394, Aquitanian, Pentalofos Formation, sample level F11, Felli village section, 40°01'4.55"N, 21°33'34.37"E. Mesohellenic Basin, Grevena area, Greece.

Paratypes: 2 specimens, AMPG(V)2395, same location as holotype, sample level F10; 27 specimens, AMPG(V)2396, same location as holotype, sample level F11; and 4 specimens, AMPG(V)2397, same location as holotype, sample level F12.

Etymology: Named after the type location Felli, near Grevena.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Small otoliths with sub-rectangular outline. OL:OH = 0.9–1.1; OH:OT = 2.6–3.0. Anterior rim slightly backward inclined to vertical (90–100°), occasionally with short preventral projection; inclination of posterior rim variable depending on presence or absence of short, broadly rounded postdorsal projection (82–100°). Posterior rim and occasionally also anterior rim with small, shallow indentation at about level of sulcus. Ventral rim flat; dorsal rim gently curved, high, highest distinctly behind its middle, and predorsal region depressed. All rims smooth.

Inner face slightly convex with small, centrally positioned, narrow and slightly deepened sulcus. Dorsal depression large but indistinct. Sulcus with low ostial lobe and with small, narrow subcaudal iugum below anterior portion of cauda. OL2:CL = 1.9–2.1. Sulcus distinctly inclined, straight, inclination angle 12–20°. Ventral furrow close to ventral rim of otolith, curving around anterior and posterior tip of sulcus but fading somewhat before reaching dorsal depression. Outer face convex, distinctly stronger than inner face, smooth.

Discussion. *Plesiogobius felliensis* is the most common goby observed in the Felli section. Its relatively high degree of variability is remarkable, but it was not possible to identify any consistent distinctions on which it would be reasonable to recognize two or more separate species. Steurbaut (1984) figured gobiid otoliths as "genus aff. *Lesueurigobius*" sp. from the latest Oligocene and Oligocene–Miocene transition beds from SW-France that resemble *P. felliensis* in many aspects, such as proportion of the otoliths and the sulcus and even the presence of a small subcaudal iugum judging from his drawings. The otolith outline appears to be more regularly rectangular, however. We therefore associate these otoliths only tentatively with *P. felliensis* and recommend reviewing the entire and highly diverse Oligocene and early Miocene goby associations described by Steurbaut (1984) before performing a more definite assessment.

Genus *Nematogobius* Boulanger, 1910

Nematogobius? sp.

Fig. 2AA-AC

Material: 1 specimen, AMPG(V)2398, Aquitanian, Pentalofos Formation, sample level F11, Felli village section, 40°01'4.55"N, 21°33'34.37"E. Mesohellenic Basin, Grevena area, Greece.

Description. A single, rather poorly preserved otolith of 1.35 mm in length. Otolith shape elongate parallelogram-like with short preventral and rounded postdorsal projections. OL:OH = 1.35; OH:OT = 2.5. Anterior rim slightly backward inclined (95°); inclination of posterior rim 105°. Posterior rim with broad concavity below rounded postdorsal projection. Ventral rim flat; dorsal rim gently curved, relatively low, highest behind its middle, and predorsal region depressed. All rims smooth.

Inner face slightly convex with narrow, centrally positioned and relatively shallow sulcus. Dorsal depression narrow, dorsally shifted and relatively well defined. Sulcus with low ostial lobe and without subcaudal iugum. OL2:CL = 1.6. Sulcus moderately inclined, straight, inclination angle 10°. Ventral furrow at some distance from ventral rim of otolith, curving around anterior and posterior tip of sulcus but not connecting to dorsal depression. Outer face convex, more strongly than inner face, smooth.

Discussion. *Nematogobius* presently occurs with two species in West Africa in shallow marine and brackish water and estuaries, with one of the two species, *Nematogobius maindroni*, also migrating upstream into fresh water (Froese & Pauly 2020). It is related to a number of other West and South African goby genera, such as *Caffrogobius* or *Gorogobius*. Birdsong et al. (1988) included these genera in the *Bathygobius* Group, and Thacker & Roje (2011) listed them in a group termed African gobies, while Thacker (2015) included *Nematogobius* in the *Gobius* lineage. The single specimen described here resembles the extant *N. maindroni* (Sauvage, 1880) (Figs. 2AD-AH) in the shape and proportions of the otolith and the narrow, relatively shallow sulcus without subcaudal iugum and a low ostial lobe. Given, however, that there are no intermediate records between this singular otolith from the early Miocene and the two extant species, the geographic difference and the fact that multiple homoplasies are known and

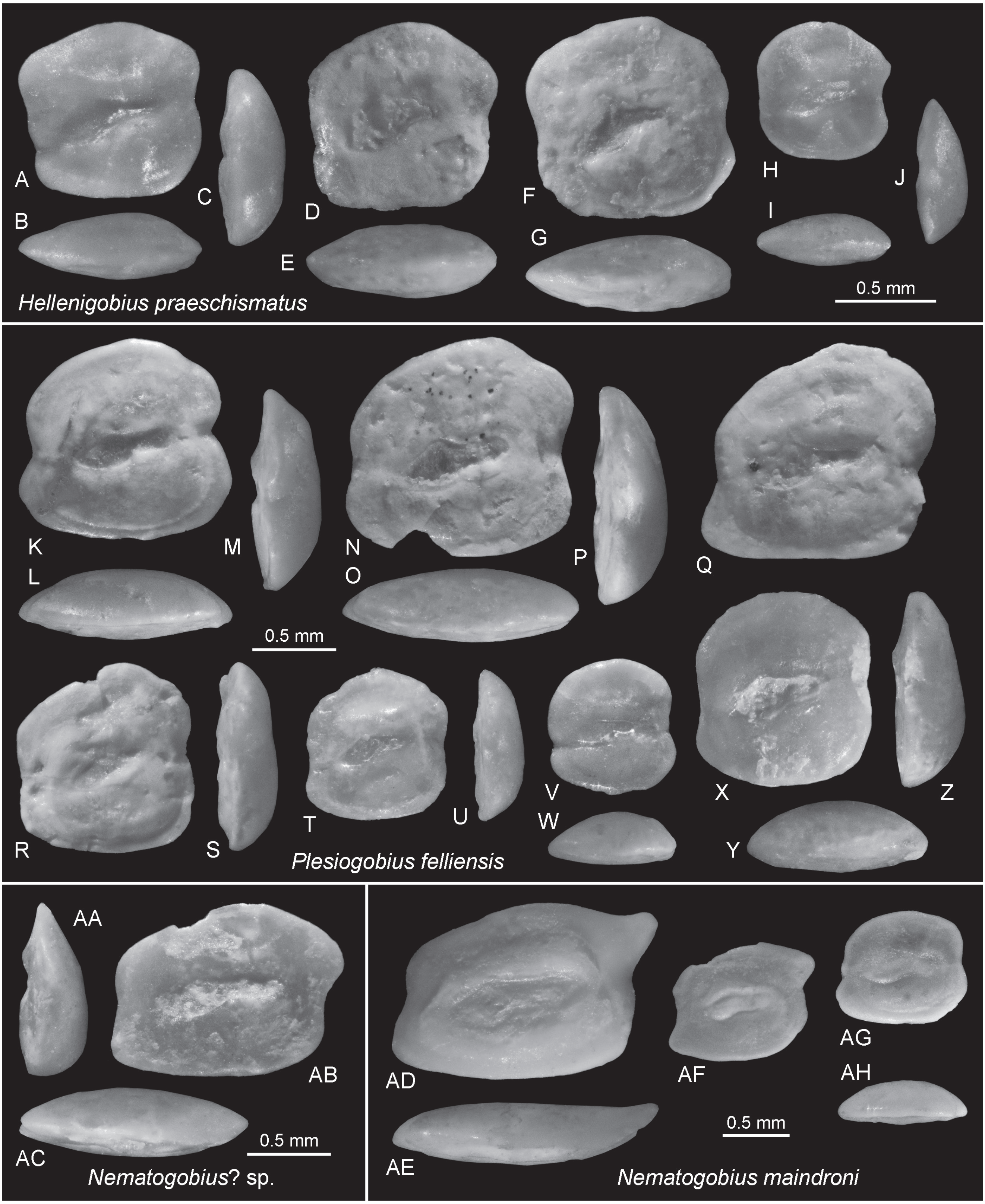

Fig. 2 - Gobiid otoliths from Felli, Greece, and extant comparative specimens.

A-J) *Hellenigobius praeschismatus* n. gen., n. sp. Aquitanian, Pentalofos Formation, Felli village section; A-C holotype, AMPG(V)2391; D-J paratypes, AMPG(V)2392–3.

K-Z) *Plesiogobius felliensis* n. gen., n. sp. Aquitanian, Pentalofos Formation, Felli village section; K-M holotype, AMPG(V)2394; N-Z paratypes, AMPG(V)2395–7.

AA-AC) *Nematogobius*? sp. Aquitanian, Pentalofos Formation, Felli village section, AMPG(V)2398.

AD-AH) *Nematogobius maindroni* (Sauvage, 1880). Extant comparative specimens: AD-AE ZMUC P78915, Equatorial Guinea; AF-AH SMF 23978, Mali, Bufing River.

more have to be expected in goby otolith morphology, we only tentatively assign this specimen to *Nematogobius*. Another aspect to consider in the case of the extant specimens is the relatively strong ontogenetic variation observed between the smallest specimen of 1 mm in length (Fig. 2AG-AH) with a lower ratio OL:OH of 1.15, a depressed postdorsal projection and a flat inner face and the largest specimen of 2 mm length (Fig. 2AD-AE) with a much higher ratio OL:OH of 1.5, a distinct and pointed postdorsal projection and a distinctly bent inner face. We therefore consider that the taxon represented by the singular fossil specimen can only be fully assessed in the presence of several well-preserved specimens of a reasonable size spectrum.

Phylogenetic Implications

Gobioid fishes occurred relatively late in teleost evolution. The earliest representatives are known, albeit very rarely, from the Eocene by means of otoliths in India and North America (Nolf & Stringer 2003; Bajpai & Kapur 2004) and articulated skeletons from Monte Bolca, Italy (Bannikov & Carnevale 2016). All these finds exhibit unique combinations of features that cannot be assigned to any extant gobioid family and are therefore left as incertae sedis within Gobioidei. In the Oligocene, gobioid remains are still generally rare, but their otoliths are locally abundant in near-shore or transitional marine environments, such as that of SW France (Steurbaut 1984) or Japan (Schwarzhans et al. 2017b). The otoliths, particularly those from the early Oligocene, mostly exhibit very generalized gobioid morphologies which prevents a conclusive phylogenetic interpretation. Articulated skeletons from the Oligocene include the fossil genera *Lepidocottus* Sauvage, 1875, *Paralates* Sauvage, 1883 and *Pirskenius* Obrhelová, 1961. *Paralates* was left in a family incertae sedis in a review by Gierl & Reichenbacher (2018), and *Lepidocottus* was placed in the Butidae by Gierl et al. (2013). *Pirskenius* was originally described in an extinct gobioid family, the Pirskeniidae, and has recently been interpreted as belonging to the Eleotridae by Přikryl (2014) or was revalidated as representing the extinct family Pirskeniidae in a sister-group relationship with Thalasseleotridae and Gobiidae by Reichenbacher et al. (2020). None of these records appear to be connected in any way to the extant Atlantic–Mediterranean gobies.

In contrast to the above observations, abundant goby otoliths in European shallow-water sediments of middle Miocene (Langhian–Serravallian) age or younger can be relatively comfortably associated with persistent extant Atlantic–Mediterranean lineages (e.g., Nolf 2013; Schwarzhans et al. 2020a). The origin of the Ponto–Caspian goby stock was shown to be intimately connected with the isolation of the Paratethys from the world ocean during the late Langhian to Serravallian (Schwarzhans et al. 2017a). It appears logical that the roots of the modern Atlantic–Mediterranean goby stock must be expected to lie in the early Miocene or perhaps the late Oligocene. In this time interval, some otolith associations with variable goby components have been described from late Oligocene and transitional Oligocene–Miocene strata of SW France (Steurbaut 1984), the late Oligocene Egerian of Hungary (Nolf & Brzobohatý 1994), the Burdigalian of Mallorca (Hoedemakers & Batllori 2005) and the early Miocene of the North Sea Basin (Schwarzhans 2010). Most of these finds have been described as Gobiidae incertae sedis or otherwise are in need of revision. Reichenbacher et al. (2018) described the first definite representative of the genus *Gobius* based on an articulated skeleton from the early Burdigalian (20.4–19.1 Ma) of the Czech Republic. The gobiid otoliths described here from the Aquitanian of Greece open another window into the crucial time interval for the origination of the modern Atlantic–Mediterranean goby stock and, notwithstanding the need to revise of many of the previous records noted above, provide certain new phylogenetic insights.

The *Pomatoschistus* lineage (sensu Agorreta et al. 2013) includes a group of small fishes informally combined in the "sand goby" clade (e.g., *Pomatoschistus*, *Knipowitschia*, *Economidichthys*), the *Buenia* Group, *Lebetus* and *Deltentosteus*. The otoliths of the *Pomatoschistus* lineage are compact, with an indistinct postdorsal projection, if any, and a relatively small and short sulcus with a low ostial lobe (except distinct and angular in *Deltentosteus*). Their very variably developed subcaudal iugum usually forms a terrace and not an elevated structure and in some genera it is very weak or even absent (*Buenia*, *Deltentosteus* and the fossil genus *Hellenigobius* described here). In "sand gobies", the subcaudal iugum is usually distinct (see Schwarzhans et al. 2020b for further characterization and figures and Gut et al. 2020 for

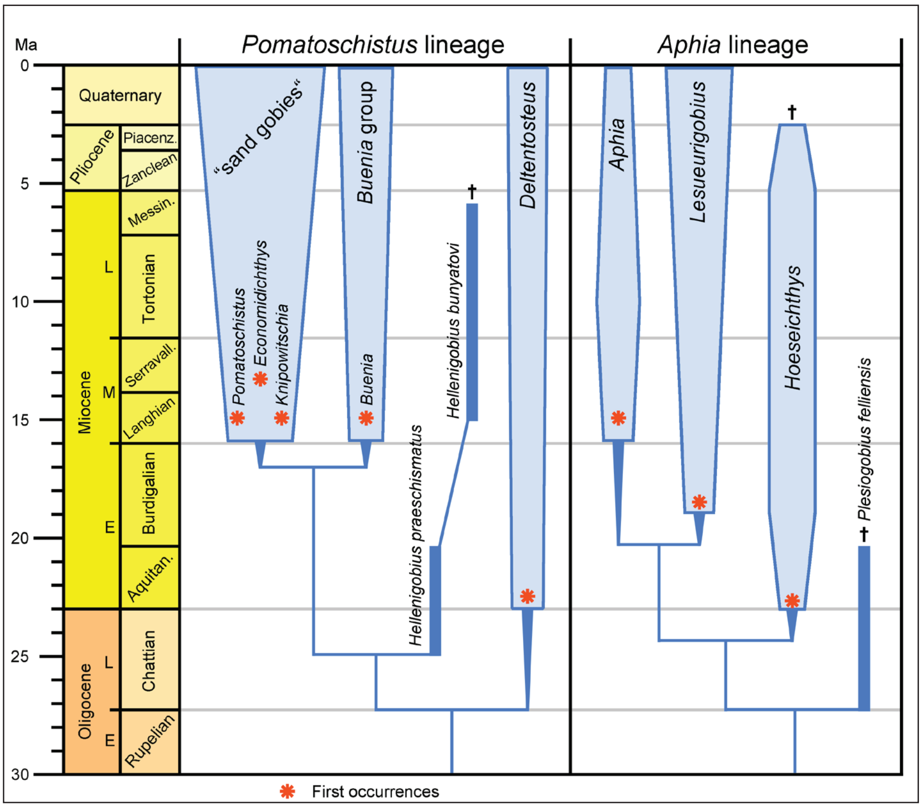

Fig. 3 - Hypothetical phylogram depicting putative relationships of the fossil *Hellenigobius* n. gen. in the *Pomatoschistus* lineage and *Plesiogobius* n. gen. in the *Aphia* lineage.

figures of extant *Pomatoschistus* otoliths). Within the *Pomatoschistus* lineage, *Deltentosteus* is readily distinguished by the combination of relatively elongate otoliths, the smooth and convex inner face and a shallow sulcus with a pronounced often angular or pointed ostial lobe. The sulcus character and the elongate otolith shape of *Deltentosteus* are considered a derived pattern in the lineage. Kovačić et al. (2017, 2018) showed *Deltentosteus* as a sister taxon to all other genera in the *Pomatoschistus* lineage. This view is confirmed, with *Deltentosteus* otoliths representing the definitive earliest in the fossil record of the lineage (Schwarzhans 2010; Fig. 3). The large "sand goby" group shows a rather diverse otolith morphology but share a relatively flat inner face and a moderately to distinctly deepened sulcus with a low ostial lobe. The terrace-like subcaudal iugum can be very extensive but is more often relatively small and can even be absent in certain species of *Economidichthys* or the extinct *Hesperichthys*; in the latter, this is considered a secondary development. The rather flat inner face and the various developments of the subcaudal iugum are considered derived characters. In contrast, otoliths of the *Buenia* group have a smooth, distinctly convex inner face with even the dorsal depression nearly absent, a relatively shallow, often very small sulcus with a low ostial lobe and a very indistinct and narrow subcaudal iugum. The shallow sulcus and the almost entirely smooth inner face are considered derived characters. Both groups are unequivocally known by otoliths since the middle Miocene, Langhian (Schwarzhans 2020a; Fig. 3) and are considered sister groups (Kovačić et al. 2017, 2018). *Hellenigobius* combines the convex and smooth inner face of *Buenia* (except for the cup-shaped dorsal depression) and the deepened sulcus of "sand gobies". These characters are hence considered to represent a plesiomorphic pattern from which both the *Buenia* and the "sand goby" pattern derived. The lack of a subcaudal iugum in *Hellenigobius* (or a very weak and narrow one as in *Buenia*) is also considered a plesiomorphic character. Therefore, we consider *Hellenigobius* as the sister group of the *Buenia* and "sand goby" groups, but one that emerged after the divergence of *Deltentosteus* (Fig. 3).

The *Aphia* lineage (sensu Agorreta et al. 2013) is a small lineage comprising only two extant genera, the paedomorphic *Aphia* and the deep-dwelling *Lesueurigobius*. Their otoliths are compact and compressed, with a relatively flat to slightly convex inner face, a typical gobiid sole-shaped sulcus (somewhat reduced in *Aphia*) and, most distinctly, a massive, broad and elevated subcaudal iugum. Outside of the Atlantic–Mediterranean goby stock, other goby otoliths with such large subcaudal iugi are known, for instance from tropical America or the Indo–West Pacific, but not from the European–West African realms. Otoliths of *Aphia* are known since the early middle Miocene (Langhian; Schwarzhans et al. 2020a) and of *Lesueurigobius* at least since the late Burdigalian (unpublished data from Portugal, and Mallorca recorded by Hoedemakers & Battlori 2005). The extinct genus *Hoeseichthys* differs from the two extant genera in that it has a smaller sulcus, which is considered plesiomorphic, and a reduced sole-shaped sulcus outline, which is considered derived. *Hoeseichthys* dates to early Miocene times (Schwarzhans 2010 as *Lesueurigobius laevis*) and is here considered the sister group to the two extant genera (Fig. 3). *Plesiogobius* is now considered to be even more basal in the *Aphia* lineage (Fig. 3). It shares with *Hoeseichthys* the small sulcus, which, however, shows the typical sole shape and is not reduced as in *Hoeseichthys*. The subcaudal iugum in *Plesiogobius* is smaller than those in the other three genera of the lineage, and it is also considered a plesiomorphic character state. However, in its elevated position and shape, it resembles those of the other genera, which we interpret as a synapomorphy of the *Aphia* lineage.

Conclusions and Outlook

The small goby otolith association from the Aquitanian of Felli, Greece, has yielded morphotypes that are thought to represent early phylogenetic positions in two of the three main Atlantic–Mediterranean goby clades, namely those of the *Pomatoschistus* lineage and the *Aphia* lineage. Both are plesiomorphic members with only a few supposed apomorphic characters, which are used for their allocation to the two respective clades. Our finds indicate that the early Miocene and probably also the late Oligocene may represent a crucial time interval for the evolution of the modern Atlantic–Mediterranean goby stock. Earlier records from the early Oligocene or the Eocene show no positive relationship with extant clades in the region. The goby association of Felli also shows a single otolith representative that could potentially belong to another goby clade, one that is no longer present in the Mediterranean.

The gobiid otoliths from the Aquitanian of Felli indicate the potential for a better understanding of the origin and evolution of European gobies. Several other time-equivalent records in past literature indicate that much more such potentially elucidating data exist but are generally in need of thorough revision. Given the plesiomorphic nature of the observed otoliths, the limitations in terms of morphological diversity in the group, and the potential for multiple homoplasies in gobioid otolith morphologies, it would help to confirm our interpretation and obtain more specific insights in the early evolution of the Atlantic–Mediterranean goby stock if otoliths could be found in situ in articulated gobioid skeletons of this time interval.

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