

LATE MIOCENE–EARLY PLIOCENE EVOLUTION OF MEDITERRANEAN GOBIES AND THEIR ENVIRONMENTAL AND BIOGEOGRAPHIC SIGNIFICANCE

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Abstract. The Lago Mare phase at the end of the Messinian Salinity Crisis (MSC) in the Mediterranean has long been known for the Paratethyan affinities of its biota. The taxonomic level of these affinities and their origin, however, is subject to divergent interpretations. Here, we have studied otoliths of the Gobioidae from late Miocene and early Pliocene deposits from Italy and Greece and revised earlier studies including time-equivalent data from Romania and NW Turkey. Nowadays, gobies constitute the most speciose marine fish family in Europe and the most diverse endemic family in the Ponto-Caspian region. Furthermore, they are highly adapted to nearshore shallow marine, brackish, and freshwater environments, which makes them excellent candidates to explore short-term connections of waterways of different nature.

The normal marine late Tortonian and pre-evaporitic Messinian deposits of the studied Italian and Greek locations contained a rich and diverse goby assemblage, but species with Paratethyan affinities were very rare and possibly originated from connections during the early Serravallian (late Badenian) and early Messinian (early Meotian). A rare fauna from a paralic environment from Cessaniti, Calabria, similar to the mangrove environments found in the present-day Guinea coastal area, revealed two species of the family Eleotridae and no gobies with Paratethyan affinities. Cessaniti provides a unique opportunity to recognize the presence of this type of environmental context with a unique gobioid assemblage in the Neogene of Europe. The shallow-water brackish-influenced sediments of Strada degli Archi just below the MSC show an increasing influence of Paratethyan gobioid taxa (*Proterorbinus yigitbasi*, *Zosterisessor exsul* n. sp.), which are not present in time-equivalent normal marine environments, but have also been identified in the Dacic Basin of Romania. Sediments of the stage 3 of the MSC, especially those that accumulated during the Lago Mare event, were dominated by a diverse goby assemblage with Paratethyan affinities, while indigenous Mediterranean goby taxa disappeared probably because of the lack of suitable conditions for neritic demersal stenohaline fishes, except for the nektonic *Aphia minuta*. The sediments of the stage 3 of the MSC also included in one particular location and level the unusual *Enigmacottus socialis* n. gen., n. sp., a putative member of the family Psychrolutidae of uncertain origin, which constitutes about 70% of all otoliths obtained from that interval in Italy. Beginning with the Zanclean, the goby assemblage of the Mediterranean shows an almost exclusively Atlantic-Mediterranean composition.

A total of 15 new species are described, 12 in the family Gobiidae, two of the Eleotridae, and one putative Psychrolutidae. The new taxa are: *Eleotris omuamuaensis* n. sp., *Eleotris tyrrhenicus* n. sp., *Lesneurigobius stazzanensis* n. sp., *Gobius peloponnesus* n. sp., *Proterorbinus cretensis* n. sp., *Zosterisessor exsul* n. sp., *Bentbophilus aprutinus* n. sp., *Bentbophilus labronicus* n. sp., *Caspiosoma lini* n. sp., *Caspiosoma paulisulcata* n. sp., *Thorogobius petilus* n. sp., *Buenia pisiformis* n. sp., *Hesperichthys gironeae* n. sp., *Knipowitschia etrusca* n. sp., and *Enigmacottus socialis* n. gen. et n. sp.

INTRODUCTION

The terminal Miocene events in the Mediterranean have been the topic of many decades of research that has resulted in a large number of publications, some containing divergent or even conflicting hypotheses of what happened during the Messinian Salinity Crisis (MSC) and in particular during its latest phase, the Lago Mare Event, before the re-establishment of a normal marine regime with the onset of the Pliocene. The Lago Mare Event is commonly considered as characterized by non-marine deposition in the Mediterranean, commonly attributed to the capture of brackish waters from the Paratethys during a very humid phase, which led to the formation of giant brackish or lacustrine basins (lake-seas or Lago Mare) on the desiccated deep floor of the Mediterranean before its re-connection with the Atlantic Ocean through the opening of the Strait of Gibraltar at the beginning of the Pliocene (Cita et al. 1978; Hsü 1984; Orszag-Sperber 2006; Roveri et al. 2014). The brackish nature of the Lago Mare waters and their Paratethyan derivation have been primarily hypothesized based on the assumption that the common brackish ostracods, mollusks, and dinocysts of Paratethyan affinities found in the Lago Mare deposits migrated into the Mediterranean Sea from the Paratethys during that time (Grothe et al. 2018). However, a series of recent studies provide new perspectives on the concepts of the Mediterranean desiccation during the MSC and the subsequent Lago Mare phase (Roveri et al. 2009, 2014, Harzhauser et al. 2015; Marzocchi et al. 2016; Carnevale et al. 2018, 2019; but see Garcia-Castellanos et al. 2020). Nevertheless, many aspects of the late Miocene evolution of the Mediterranean basin and the nature and diversity of its aquatic ecosystems remain underexplored and elusive, thereby representing some of the most interesting geological and paleobiological topics of Cenozoic history.

One of the main limiting factors for the comprehensive understanding of the Lago Mare biotic structure is the scarcity and poor knowledge of shallow marine sediments of Tortonian, pre-evaporitic Messinian and Zanclean in the Mediterranean, since well-studied outcrops are dominated by pelagic sediments containing oceanic faunas. This lack of knowledge has so far limited the comparison of the Lago Mare fauna with preceding and subsequent ecologically equivalent Mediterranean

faunal assemblages. Here, we have the opportunity to evaluate the largest known collection of otoliths from the Lago Mare interval from various locations and environmental settings in Italy and compare it with otoliths obtained from newly sampled late Tortonian, pre-evaporitic Messinian and Zanclean shallow-water sediments from Italy and Greece. Our focus in this study is on gobioid otoliths as well as on other teleost groups that could be of interest for elucidating relationships with Paratethyan fish faunas. We describe previously unreported material, and we review the previously published otolith record of gobioids and other relevant groups. Specifically, we review otoliths from the Lago Mare sediments of Italy (Caputo et al. 2009, and Carnevale et al. 2006a, b, 2008, 2018), the late Miocene and early Pliocene of Greece (Agiadi et al. 2013a, 2017, 2020), the pre-evaporitic Messinian of Italy (Girone et al. 2010) and, the Meotian and Dacian of Romania (Pana 1982b, 1995). We recognize 45 gobioid species (43 in the family Gobiidae and 2 belonging to the family Eleotridae) from this time interval, including 14 new species and 5 left in open nomenclature. In addition, we describe a new genus and species (*Enigmacottus socialis* n. gen, n. sp.) and tentatively assign it to the family Psychrolutidae, based on very abundant material almost exclusively known from a single fossiliferous layer of the Cava Serredi succession in Tuscany.

Gobies are of particular interest for a number of reasons. They are highly diverse, highly adapted to nearshore shallow marine and brackish environments, but also occur in freshwaters. The Ponto-Caspian gobies represent the largest diversity of endemism of any teleost group of that region. Some of them are remarkably euryhaline and successful migrators and colonizers of new biotopes (Dillon & Stepien 2001; Jacobs & Hoedemakers 2013), a powerful combination that makes gobies excellent candidates to explore short-term connections of waterways of different nature. Other members of this group are indicative of very specific environmental conditions. Goby otoliths are often dominant in shallow marine and transitional marine-brackish sediments since the early Miocene, while the group is generally rare in the Paleogene. The rich otolith record documents that the main phases of goby radiation seem to have occurred in the late Neogene, which is consistent with the timing of diversification derived from molecular stud-



Fig. 1 - Location map of sampled localities used for this study. Late Miocene to early Pliocene basin outlines in onshore terrain marked by yellow color and red frame, simplified and schematized after Asch (2003) and Compagnoni & Galluzzo (2005).

ies (Thacker et al. 2018). Furthermore, gobies are known for their ability to rapidly adapt under ecological stress (Rüber et al. 2003; Yamada et al. 2009; Patzner et al. 2011). In fact, most of the evolution of the endemic Ponto-Caspian goby stock seems to have been linked to the separation of the Paratethys from the Mediterranean since the Serravallian (Bratishko et al. 2015, 2017; Schwarzhans et al. 2015, 2017, 2020; Schwarzhans 2014, 2017). Thus, occurrence of Paratethyan goby taxa in the Mediterranean would indicate the existence of direct connection with the Paratethys after the Langhian, thereby reinforcing previous hypotheses on several episodic connections established between the two basins during times of the late Miocene (e.g., Popov et al. 2006; van Baak et al. 2016; Palcu et al. 2019; Grothe et al. 2020).

The fishes of the family Gobiidae represent the teleost family with the highest degree of

diversity in the waters of Europe (Froese & Pauly 2019). About 70 gobiid species inhabit the Atlantic-Mediterranean faunal province of Europe (Froese & Pauly 2019), and 47 species occupy a variety of biotopes of the Ponto-Caspian Basin (Miller 2003, 2004). A recent study of Badenian goby otoliths from the Central Paratethys (Schwarzhans et al. 2020) demonstrates that a highly diverse goby assemblage was established in that area as early as at least the middle Miocene. A total of 20 goby species were identified from the early Badenian (= Langhian) at a time when the Central Paratethys and the Mediterranean were fully connected marine basins. This assemblage did not contain any persistent Ponto-Caspian taxa, which first occur in the late Badenian (= early Serravallian). In the Serravallian (late Badenian and Sarmatian s.s.) 34 goby species have been identified in the Paratethys (Bratishko et al. 2015; Schwarzhans et al. 2015, 2020; Schwarzhans

2017). Moreover, nine goby species were found in the Serravallian shallow-water sediments in south-eastern Turkey (Schwarzhans 2014). The otolith assemblages from the late Sarmatian s.l. / Meotian (=late Tortonian) to the Dacian (= late Zanclean) described by Pana (1982b, 1995) from Romania and by Rückert-Ülkümen (1992, 1993, 1996, 2006) from the Marmara region in Turkey have been reviewed as far as possible based on original material and assessment of the documentation in their publications. Otoliths of nearly 100 extant European goby species and more than 600 extant gobioid species from more than 235 genera from a worldwide basis have been available for comparison. These data form the basis for the assessment of the 45 gobioid otolith-based species now recognized from the late Miocene and early Pliocene of the Mediterranean. This aggregated and almost continuous database provides for a first detailed assessment of the evolution of European gobioid fishes in the Mediterranean throughout the late Neogene, their interaction with the Paratethys, and the recognition of gobioid lineages, which are now extinct in Europe.

We recognize that the taxonomic identification and definition of gobioid otoliths is difficult due to the recurrent and possibly convergent morphological features within the otherwise easily recognizable general gobioid otolith pattern. Identification of gobioid otoliths is further hampered by varying degrees of intraspecific morphological variability and the abundance of small, sometimes pedomorphic species with otoliths that are difficult to be distinguished from those of juvenile individuals of large-sized species. These observations associated with the limited knowledge of extant gobioid otolith morphologies have often led previous otolith researchers to leave many fossil otolith-based taxa in open nomenclature.

GEOLOGICAL SETTING

The Neogene geodynamic evolution of the Mediterranean region has been primarily determined by the northward motion of the African plate relative to Eurasia. In this context, the enclosed and land-locked configuration of the Mediterranean was affected by the development of tectonic arcs and large extensional basins resulting from lithospheric arc migration and extension above the subduction

zones. The Neogene evolution of the Apennine, Calabrian, and Hellenic arcs and of the Tyrrhenian and Aegean basins exemplifies the shaping of the current physiography of the Mediterranean as well as the nature of the tectonic processes and large-scale paleoenvironmental changes (e.g., Jolivet et al. 2006).

Overall, the Apennines represent a complex and arched mountain chain formed by two different orogenic arcs, the Northern and Southern Apennines, and stretching some 1500 km (e.g., Vai 2001). Neogene marine sediments are extensively exposed throughout the Apennine chain, documenting a variety of environments and evolving paleogeographic settings. Here, we focus on the upper Miocene deposits of the Tertiary Piedmont Basin, the hinterland basins of Tuscany, Marche, and Abruzzo Apennine and the Capo Vaticano promontory, located between the Tyrrhenian Basin and the Calabrian Arc.

The Tertiary Piedmont Basin is an episutural basin filled with Eocene to upper Miocene (Messinian) sediments that cover the Alps-Apennine junctions (Mosca et al. 2010). Otoliths from upper Tortonian (Stazzano), lower Messinian (Borelli), and Messinian Lago Mare (Ciabot Cagna, Moncucco Torinese) deposits from the Tertiary Piedmont Basin have been examined herein. The Neogene hinterland basins of Tuscany originated in response to the tectonic evolution of the Tyrrhenian-Apennine system (e.g., Patacca et al. 1990; Boccaletti & Sani 1998), and were filled with Tortonian to Pleistocene continental, brackish and marine deposits. The localities discussed in this paper, Botro Rosso, Strada degli Archi, Cava Serredi, and Podere Torricella, are located in the Monti Livornesi (Botro Rosso), and in the Fine (Strada degli Archi and Cava Serredi) and Volterra (Podere Torricella) basins, on the western side of the Mid-Tuscan Metamorphic Ridge. The single studied locality of the Marche Apennine, Capanne di Bronzo, is located in the Montecalvo in Foglia Syncline, a satellite basin with NW-SE direction on the Adriatic side of the Apennines (Carloni et al. 1974; Borsetti et al. 1975). The Le Vicenne Basin, in the Abruzzo Apennine, is a thrust-top basin developed during the eastward migration of the central Apennine thrust belt (Cipollari et al. 1999). Finally, the Capo Vaticano promontory represents a Neogene back-arc basin resulting from the Apennine subduction complex (see Patacca et al. 1990).

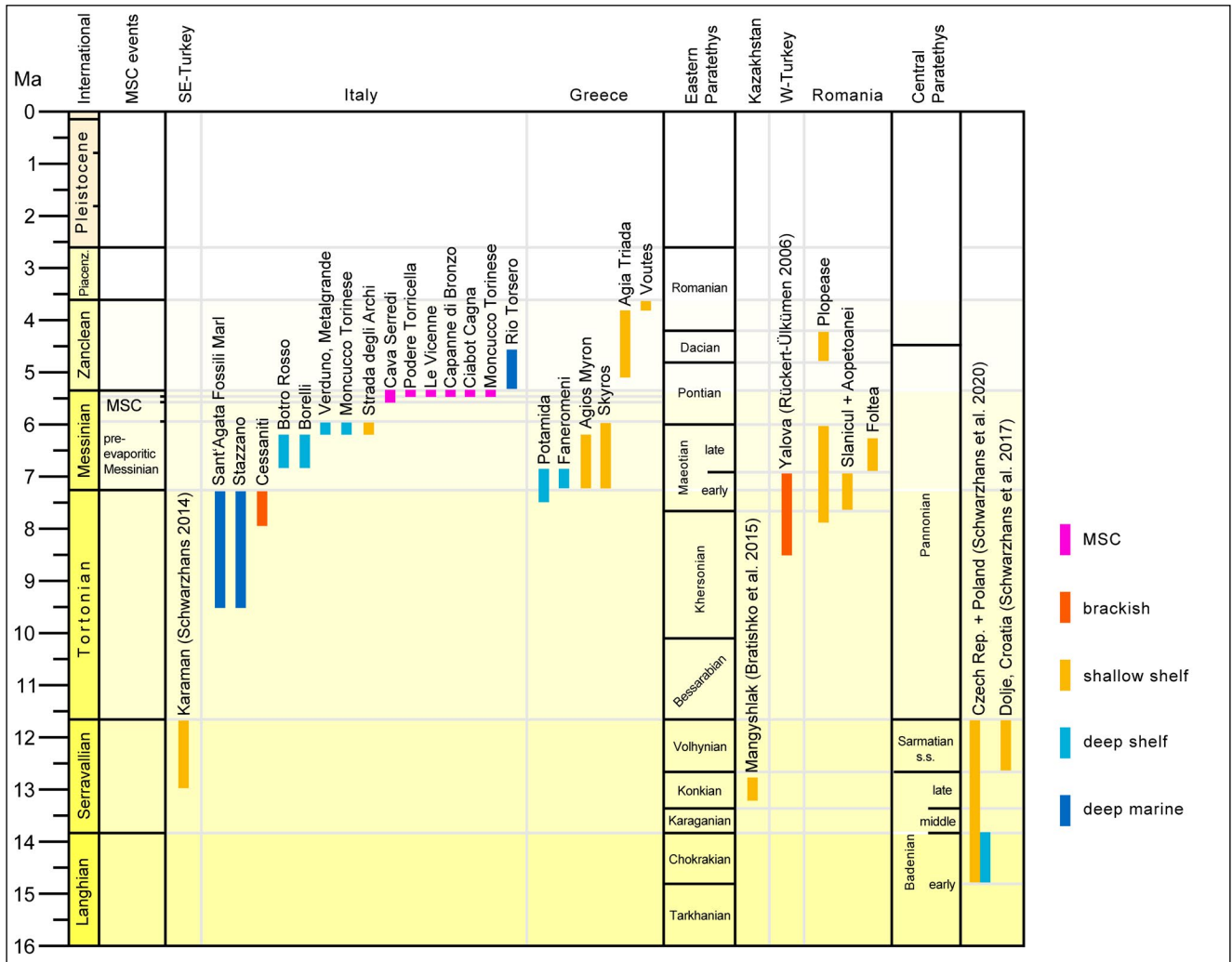


Fig. 2 - Database and stratigraphy. Stratigraphic distribution and environmental characterization of studied locations and certain published locations deemed to be important for the understanding of the gobiid assemblages described herein.

In the Capo Vaticano-Monte Poro area, late Tortonian brackish and marine coastal deposits overlie the Hercynian basements (Marra et al. 2017).

Neogene marine deposits appear along the Hellenic arc due to the extensional deformation and have an NNW–SSE direction in western Greece, whereas they extend along the E–W direction on Crete Island. In particular, Tortonian–Zanclean marine sediments, also recording the MSC, crop out and have been studied extensively on the Ionian Islands (e.g., Karakitsios et al. 2017; Kontakiotis et al. 2016), and Crete and Gavdos Islands (e.g., Kontakiotis et al. 2019; Moissette et al. 2018; Schenau et al. 1999). Crete Island was formed in the late Miocene as a series of horsts separated by grabens (van Hinsbergen and Meulenkamp 2006). Late Miocene–Pleistocene sediments were deposited in these grabens over an alpine substratum, and they

form six lithostratigraphic groups (Meulenkamp et al. 1979). The late Miocene deposits of Potamida, Agios Myron, and Faneromeni sections belong to the Tefelion Group, whereas the deposits cropping out in Voutes belong to the Finikia Group. In SW Peloponnesus, Neogene–Quaternary marine sediments overlie unconformably alpine substratum (Mariolakos et al. 2001). The Falanthis Basin in this area, where Agia Triada section is located, was formed between the Mavrovouni NW–SE marginal fault and the Longa-Evangelismo fault (Ladas et al. 2004).

MATERIAL AND METHODS

The studied material originates from four sources. The locations of the studied material are

depicted on the map in Fig. 1, while the stratigraphic positions are indicated in Fig. 2.

1. ITALY: The rich Messinian material from the Lago Mare interval as well as that from the pre- evaporitic deposits of Strada degli Archi was collected by one of us (GC) especially with the help of Doriano Caputo (Ameglia), Lorenzo Egisti (Grosseto) and Stefano Marsili (Pietrasanta), while the late Tortonian material from Cessaniti was collected by Daniela Esu (Roma) and Carmine D'Amico (Isernia). Otoliths in the Lago Mare interval were generally rare, except one specific level at Cava Serredi, and were obtained by processing large amounts of sediment (for instance 20 t from Moncucco Torinese, about 6 t from Cava Serredi, and 700 kg from Capanne di Bronzo).

Stazzano: The Rio di Bocca d'Asino site located 2.5 km NW from the town of Stazzano, Piedmont, is well-known for its remarkably rich and diverse mollusc fauna (e.g., Caprotti 2011). The exposed stratigraphic succession pertains to the Sant'Agata Fossili Marls Formation (see Ghibaudo et al. 1985) and consists of about 20 m of latest Tortonian clayey deposits with intercalated conglomeratic lenses of gravitative origin rich in molluscs and rhodoliths (see, e.g., Dell'Angelo et al. 2014).

Borelli: Borelli is a small village close to the town of Moncucco Torinese in the Turin Hill, Piedmont. Otoliths were collected from turbiditic sands rich in molluscs (Pavia & Robba 1979; Pavia 1991) that are largely exposed in a small quarry in the vicinity of the village. The fossiliferous deposits are referred to the lower Messinian due to the occurrence of the planktonic foraminifer *Globorotalia conomiozea* (Pavia & Robba 1979) in the clays underlying the turbiditic sands. However, some studies considered them of late Tortonian age (e.g., Lin et al. 2015).

Ciabot Cagna: The section of Ciabot Cagna was exposed in the vicinity of the town of Corneliano d'Alba, Langhe area, Piedmont. It consists of about 8 m of laminated clays with abundant molluscs typical of the Lago Mare event (*Dreissena*, limnocardines, *Melanopsis*). Otoliths and other vertebrate remains are rather uncommon in these sediments (Cavallo et al. 1993; Caputo 2005), which accumulated at the end of the Messinian in a heterogeneous deltaic-lagoonal context (Cavallo & Repetto 1988).

Moncucco Torinese: The Lago Mare de-

posits of Moncucco Torinese overlie a thick succession of evaporites exposed in a large quarry located in the Torino Hill exploited for decades for the extraction of gypsum. Otoliths have been collected from six different layers, whose age has been constrained between 5.41 and 5.33 Ma (Alba et al. 2014; Grunert et al. 2016; Colombero et al. 2017). The Lago Mare fossiliferous deposits originated in a large and rather deep lagoonal setting in which vertebrate remains also accumulated from a variety of terrestrial habitats (see Colombero et al. 2017).

Botro Rosso: The Botro Rosso creek section is located in the Popogna area, in the north-western sector of the Monti Livornesi, Tuscany. The Messinian deposits cropping out in the Popogna area pertain to the so-called Rosignano unit and Raquese unit (Dominici et al. 2019). Fish otoliths were collected from the fine grained clayey deposits of the Raquese unit (also known as Argille a *Pycnodonta* or Torrente Raquese Formation) where they were associated with abundant marine molluscs (*Aporrhais uttigeriana*, *Corbula gibba*, *Turritella tricarinata*) and relatively rare irregular echinoids. The early Messinian age of these deposits has been defined based on their micropaleontological content (see, e.g., Bossio et al. 1978, 1997a). In particular, the recurrent occurrence of the planktonic foraminifer *Turborotalita multiloba* in the Argille a *Pycnodonta* (=Raquese unit), suggests an age younger than 6.415 Ma (see Sierro et al. 2001).

Strada degli Archi: The Strada degli Archi section is located in the northwestern sector of the Fine Basin, Tuscany. The lower part of the exposed section dates back to the pre- evaporitic Messinian and primarily consists of sand bodies with thin layers of silt and clay and local concentrations of paralic molluscs (*Cerastoderma*, *Cerithium*, *Mactra*, *Ostrea*; see Bossio et al. 1981; Caputo et al. 2009). Otoliths were collected about 1.5 m below a thick gypsum layer and were associated to *Cerastoderma*, brackish gastropods, ostracods (*Cyprideis* gr. *torosa*, *Heterocythereis* aff. *albomaculata*, *Loxococoncha* aff. *agilis*, *Loxococoncha* aff. *elliptica*, *Xestoleberis reymonti*) and benthic foraminiferans (*Ammonia* and *Cribronion*).

Cava Serredi: The upper Messinian succession of Cava Serredi, along the western margin of the Fine Basin, Tuscany, is characterized by two marly and clayey depositional sequences documenting a variety of paralic and coastal paleobiot-

opes (e.g., Carnevale et al. 2006b, 2008). Fish otoliths have been documented from nine fossiliferous layers, associated with abundant bivalves and gastropods typical of the Lago Mare event. The basal fossiliferous level seems to pertain to the sub-stage 3.1 of the Messinian salinity crisis (see Roveri et al. 2014) while the others eight levels belong to the substage 3.2. Thus, the age of the otolith-bearing horizons ranges between 5.45 and 5.33 Ma (Carnevale et al. 2018).

Podere Torricella: The section of Podere Torricella is exposed in the Spicchiaiola-Pignano area, in the south-eastern sector of the Volterra Basin, Tuscany. Here, Lago Mare deposits belong to the ‘Argille e Gessi del Fiume Era Morta’ lithostratigraphic unit (Bossio et al. 1996, 1997b) and crop out in a small quarry used for the extraction of alabastrine gypsum. The otoliths were collected in a single layer placed about 20 m above the uppermost alabastrine gypsum, where they occur together with abundant molluscs and ostracods. The age of this layer ranges between 5.40 and 5.33 Ma (Carnevale et al. 2008, 2018).

Capanne di Bronzo: This locality is placed in the northern sector of the Montecalvo in Foglia Syncline in the Marche Apennine. In this area the upper Messinian deposits are represented by both the Terreni di Tetto Formation and the Colombacci Formation (e.g., Bassetti 2000). The latter originated during the Lago Mare event and is widely exposed in the Capanne di Bronzo section (Carlioni et al. 1974; Borsetti et al. 1975). The otoliths were collected about 1 m below the Mio-Pliocene boundary together with very abundant dreissenid and limnardiine bivalves, hydrobiid and melanopsid gastropods, ostracods, and benthic foraminiferans (Carnevale et al. 2006a). The age of the otolith-bearing horizon ranges between 5.35 and 5.33 Ma (Carnevale et al. 2018).

Le Vicenne: As discussed above, the Le Vicenne basin is a thrust-top basin located in the Marsica region, Abruzzo Apennine (e.g., Colacchi et al. 1967). Upper Messinian deposits (conglomerates, sandy marls, clays and siltites) are exposed in the Le Vicenne basin with an overall thickness of about 50 m (see Cipollari et al. 1999). Rare otoliths occur together with abundant molluscs and ostracods. According to Cipollari et al. (1999), the Lago Mare deposits of the Le Vicenne basin originated in a mesohaline coastal lagoon

during the sub-stage 3.2 of the Messinian salinity crisis, between 5.42 and 5.33 Ma (Carnevale et al. 2018).

Cessaniti: The Tortonian material from Cessaniti was collected from two sections located between the town of Cessaniti and the Vibo Valentia Airport. One of these sections (section L of D’Amico et al. 2012), is exposed in the Colella Quarry with a thickness of slightly less than 6 m of clays and sandy clays rich in paralic and coastal marine molluscs. The other section (section T of D’Amico et al. 2012), crops out in the Gentile Quarry and consists of about 1 m of laminated silty and sandy clays with abundant paralic molluscs and ostracods (D’Amico et al. 2012; Ligios et al. 2012). The age of these deposits has been recently discussed by Marra et al. (2017) who referred them to the Chron C4n, with an age ranging from 8.1 and 7.5 Ma.

Additional specimens from the pre-evaporitic Messinian of Moncucco and Verduno (Metalgrande) were made available for study thanks to the generosity of Dirk Nolf (Bruges). Reference is made to Girone et al. (2010) for details of the locations. Further specimens from the Tortonian of the Sant’Agata Fossili Marls Formation and the Messinian of San Marino, southeast of Acquaviva were made available from SMF (Senckenberg Museum, Frankfurt am Main).

2. GREECE: Inner to middle shelf sediments of late Tortonian, pre-evaporitic Messinian and Zanclean from Peloponnesus and Crete yielded rich and diverse gobiid otolith assemblages and were collected by one of us (KA). The location details are as follows.

Faneromeni: This section is located along the coast, about 4 km west of the Siteia airport (eastern Crete Island). The Faneromeni section is approximately 57 m thick and comprises alternating marls and clayey limestones, followed by laminated marls in the upper part (Krijgsman et al. 1994, 1995). The age of these sediments has been constrained between 7.6 and 6.5 Ma (late Tortonian to early Messinian) based on planktonic foraminifera biostratigraphy, and the paleoecological analysis based on a variety of marine organisms, including fishes, indicates that this area corresponds to an outer-shelf to bathyal paleoenvironment (Moissette et al. 2018). Gobiid otoliths were sparse in this section.

Potamida: This section is located SW of Chania city, on the outskirts of Potamida village.

The Potamida composite section is ~40 m thick (Krijgsman et al. 1994) and consists of homogeneous blue-grey marls in the lower part, and clayey limestones interbedded with marls and sandstones in the upper part. Agiadi et al. (2017) described the fossil fish otoliths from the late Miocene (7.5-6.5 Ma) from this section. Furthermore, they provided an age range between 7.51 and 6.75 Ma for the section and suggested that the sedimentation took place on the outer shelf. Two intervals in two subsections were found to be rich in gobiid otoliths, one in Potamida A level 12-13 (Agiadi et al. 2017) with an age of 7.36 Ma (late Tortonian), and the second in Potamida B level Kot6 (Agiadi et al. 2017) with an age younger than 6.83 Ma (early Messinian). In both instances, the rich gobiid association was accompanied by similarly abundant myctophid otoliths, thereby suggesting a faunal mixing of shallow and deep-water taxa along a steep slope environment (Agiadi et al. 2017).

Agios Myron: This section is located SSW of the city of Heraklion, in the vicinity of the village of Agios Myron. It encompasses 25 m of alternating marls and sandy marls of early Messinian age (van Hinsbergen & Meulenkamp 2006). Gobiid otoliths were relatively rare but yielded a diverse assemblage.

Voutes: This section is located southwest of the village of Voutes, SW of Heraklion. The marine sediments cropping out in Voutes section include more than 60 m of whitish marls, diatomites and sandy marls deposited at depths from 100 to 400 m, deepening upwards. The fossiliferous sediments are of late Zanclean age between 3.84 and 3.61 Ma (Agiadi et al. 2013a, 2013b). Agiadi et al. (2013a) described the entire fish fauna from this section. The majority of the gobiid otoliths were obtained from the lower part of the section from sediments supposedly deposited at depth of about 100 to 150 m (Agiadi et al. 2013b).

Agia Triada: This section is located on the southeast coast of Messinia region, southwest Peloponnese, east of the village of Harokopio, about 5 km NW of the city of Koroni. The Agia Triada section includes approximately 30 m of blue marls becoming gradually more silty toward the top, which were deposited during the Zanclean, between 5.08 and 3.81 Ma (Koskeridou et al. 2017). The entire fish fauna has been described by Agiadi et al. (2020). The paleoenvironmental analysis based on both the

gastropods and fishes indicated that these deposits accumulated in a shallow marine setting with depths not exceeding 100 m (Agiadi et al. 2020).

Skyros: A few otoliths have been available from the Messinian of Skyros, which were collected during student fieldwork activity of the Free University of Berlin in 1980 (Harder et al. 1983). The Neogene of the Skyros Island (Central Aegean Sea, Greece) is almost completely unknown. These deposits were originally placed in the late Miocene based on the study of mollusks by Melentis, which was included in Guernet (1978). Their age was later refined to the early Messinian based on the ostracod assemblages by Guernet (2005).

3. ROMANIA: The otoliths studied from the Dacic Basin of Romania had been collected by the late I. Pana and were made available to us thanks to the courtesy of M. Stoica (University of Bucharest). They were collected from outcrops in the Plopease-Buzau valley from sediments of late Sarmatian s.s. (Khersonian) to Meotian (late Tortonian to early Messinian) and late Dacian age (c. 4.3 to 4.0 Ma, middle Zanclean), and from the lower Meotian of c. 7.65 to 6.9 Ma (late Tortonian to early Messinian; see van Baak et al. 2015; Palcu et al. 2019) of Adopetoanei and Slanicul, and the upper Meotian of c. 6.9 to 6.0 Ma (late pre-evaporitic Messinian; see Palcu et al. 2019; Lazarev et al. 2020) of Foltea. The specimens from the Dacian were partially included in articles by Pana (1982b, 1995), while those from the late Miocene have not been published previously.

4. TURKEY: In a series of publications, Neriman Rückert-Ülkümen described both articulated skeletons as well as isolated otoliths from late Miocene strata of the Thracian Basin in Turkey, chiefly near Istanbul and from the shores of the Marmara Sea (Rückert-Ülkümen 1965, 1993, 1996, 1997, 2006; Rückert-Ülkümen et al. 2006). The stratigraphic position of the samples from Yalova, which contained the richest assemblage of gobiid otoliths, was considered to represent a late Khersonian to early Meotian age (Rückert-Ülkümen et al. 2006) of c. 8.6-6.9 Ma. The otoliths of her articles from 1993 have been seen by one of us (WS) prior to publication and the holotype of *Neogobius yigitbasi* kept at the Bayerische Staatssammlung in München was newly photographed for this study.

The specimens collected by GC are kept at the Museo di Geologia e Paleontologia, Università degli Studi Torino, Torino (MGPT-PU). The specimens collected by KA are kept at the Athens Museum of Paleontology and Geology, National and Kapodistrian University of Athens (AMPG(V)). The specimens from the collection of I. Pana are housed at the Laboratory of Paleontology, Faculty of Geology and Geography, Bucharest (LPB). Additional specimens from the late Tortonian and early Messinian of Italy are housed at the Institute Royal de Sciences Naturelles de Belgique, Bruxelles (IRSNB) and the Naturkunde-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main (SMF); finally, the specimens from Turkey are kept at the Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, München (SNSB-BSPG). Otoliths of extant fishes are cited with the catalogue numbers of the voucher specimens from which they were extracted (as far as possible) and refer to the Natural History Museum in London (BMNH); Kochi University, Department of Biology, Faculty of Science in Kochi, Japan (BSKU); California Academy of Sciences in San Francisco (CAS); Canadian Museum of Nature in Ottawa (CMNFI); Institute of Marine Sciences in Barcelona (ICM-O); Los Angeles County Museum of Natural History in Los Angeles (LACM); Zoological Museum of Ukraine in Kiev (NMNH NASU); Naturhistorisches Museum in Wien (NMW); Western Australian Museum in Perth (WAM); Zoological Museum, Moscow University in Moscow (ZMMU); and Zoological Museum, University of Copenhagen (ZMUC).

All otoliths were studied with a reflected-light microscope. Photographs were taken with a Canon EOS mounted on the phototube of a Wild M400 photomicroscope. Focused light sources were used from opposite sides and low to medium angles, usually perpendicular to the orientation of the sulcus in order to achieve a maximum exhibition of the often subtle but diagnostically important surface features as, for instance in the case of goby otoliths, the subcaudal iugum (see below for definition of terminology). The photographs were taken at regular field-of-depth levels for each view with the camera being remotely controlled from a computer. The individual photographs of each view were stacked using Helicon Soft's Helicon Focus software. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast, balance exposition or to retouch small inconsistencies such as sand grains, encrustations or pigmentation spots insofar as doing so was possible without altering the otolith morphology. In rare instances, black and white speckling of the surface resulted in an inconsistent picture, and then a digital filter was applied for enhancing dark parts (with a radius of one pixel) and is annotated accordingly in the captions. Specific care was taken to photograph inner otolith faces with the central portion of the face at a level position to avoid the distortions that otherwise occur in strongly bent specimens (for an explanation, see fig. 3.9 in Lombarte & Tuset 2015). The same principle was applied for lateral views, in which the otoliths were oriented in upright position along their horizontal or vertical axis depending on dorsal/ventral and anterior/posterior views, respectively. All figures show right otoliths. Left otoliths have been mirror-imaged to facilitate better comparison and are annotated in the captions as 'reversed'.

SYSTEMATICS

Gobioid otolith terminology and characterization

The morphological terminology follows Koken (1884) with amendments by Weiler (1942).

Schwarzahns (2014) and Schwarzahns et al. (2020) introduced specific morphometric measurements for gobioid otoliths, as well as the terms 'subcaudal iugum' for a feature unique to gobioid 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 (Fig. 3). Gobioid otoliths can be easily recognized by the combination of a rectangular or parallelogram-like outline, the sole-shaped sulcus positioned entirely enclosed on the inner face and a mostly distinct ventral furrow that curves around the rear termination of the sulcus to meet the dorsal depression and sometimes runs around the anterior tip of the sulcus. Despite their unmistakable morphology, differentiation of morphotypes within the Gobiidae (and Gobioidae) is often less clear. Therefore, Schwarzahns et al. (2020) undertook a character analysis focusing on goby otoliths from European seas. The characters used for the taxonomic analysis primarily refer to features of the sulcus, including size, width, orientation, depth, expression of ostial lobe and ventral sulcus margin, inclination of sulcus and ostium, presence and expression of the subcaudal iugum. In addition, other important features are the expression of the ventral furrow and dorsal depression on the inner face, the size and aspects of the outline of the otolith, and the curvatures of the inner and outer faces.

Measurements and abbreviations used: OL = maximum otolith length; OL.2 = 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 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 pre-ventral angle with tip of postdorsal projection (δ). For visualization see Fig. 3.

Characterization of gobioid otoliths

In the following, we refer to the character analysis of Schwarzahns et al. (2020) for the characterization of the patterns observed in the gobioid otoliths described herein (Tab. 1). Key characters are briefly listed and discussed accompanied by a plate of schematized drawings aimed at highlighting characters deemed of diagnostic value at genus level (Fig. 4). It should be noted, however, that recognition of certain diagnostic valuable characters is easily affected by erosion, and hence good preservation of the

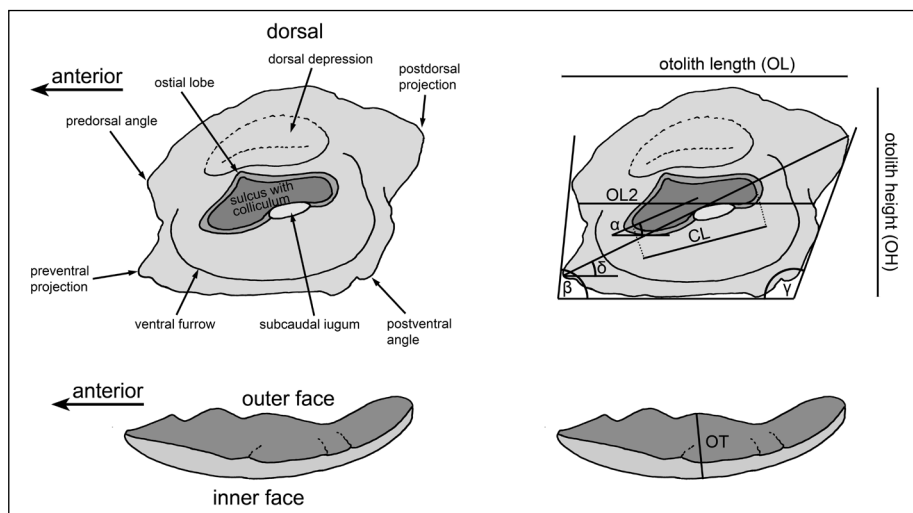


Fig. 3 - Terminology and morphometric measurements of gobioid otoliths. Left: gobioid otolith terminology after Schwarzahans (2014). Right: gobioid otolith morphometric measurements used in this study.

otolith specimens is required for proper morphological assessment. This is particularly the case for the identification of the subcaudal iugum and the expression and curvature of the postdorsal projection. The latter also requires figuring from the dorsal view. Furthermore, the maximum size is a relevant feature for identification because several genera include only small-sized or pedomorphic species. Finally, these characterizations and figures cannot be used for identification of otoliths from other world regions, because multiple events of morphological convergence must be considered. For instance, otoliths of *Buenia* are similar to those of the unrelated Indo-Pacific genus *Silhouettea*, and *Hesperichthys* otoliths resemble the West African genus *Sufflogobius*. The schematic figures (Fig. 4) are not shown to scale in order to facilitate recognition and comparison. We found that a varying number of specimens could not be comfortably identified because of their inadequate preservation, apparent juvenile nature in the absence of well-preserved and unequivocal large specimens, or the presence of unique or very few specimens. Depending on the varying overall preservation of otoliths from one location to another, the amount of unidentifiable gobioid otoliths may vary from just a few specimens to nearly half of the assemblage.

The sequence of descriptions follows the definition of lineages and their content as defined by Agorreta et al. (2013) and Thacker (2015). Groups within lineages are based on otolith patterns and are based on clades as shown in Agorreta et al. (2013), but have no formal taxonomic meaning.

Eleotridae, *Eleotris* Group: Eleotrid otoliths show a variety of patterns, most of which are

characterized by an eccentrically positioned sulcus, which closely approaches the anterior rim of the otolith, the postventral angle being stronger than the postdorsal projection and absence of a subcaudal iugum. The otoliths of *Eleotris* and related genera, however, are very similar morphologically to those of typical gobiids, such as species of the genus *Gobius*, in showing a centrally positioned sulcus and a more or less distinct postdorsal projection. *Eleotris* otoliths are recognized by the combination of a large, wide, and mostly deep sulcus with low or no ostial lobe and no subcaudal iugum.

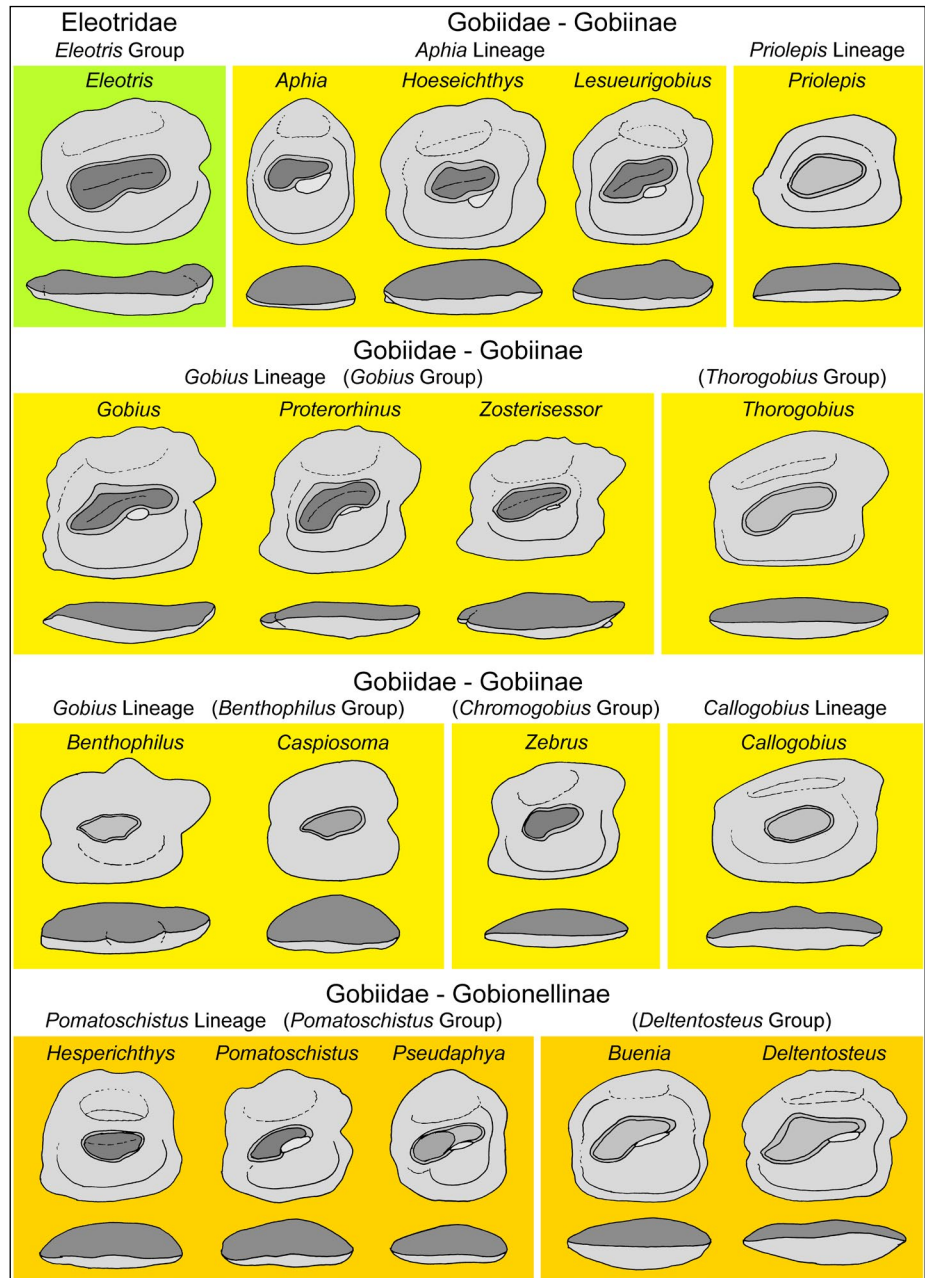
Gobiidae, Gobiinae, *Aphia* Lineage:

Compact, thick otoliths with a relatively flat inner face. OL:OH mostly between 0.8 and 1.2. The single most useful character is the large and wide subcaudal iugum, which is rarely observed with a similar intensity elsewhere. There is no or a rather feeble postdorsal projection, which is slightly bent. Of the three contained genera, *Aphia* is pedomorphic with otoliths not exceeding 1.0 mm in length, and is also the most compressed with a ratio OL:OH < 1.0 and mostly < 0.9. Otoliths of *Lesueurigobius* and *Hoeseichthys* can reach up to nearly 4 mm length. Those of *Hoeseichthys* differ from *Lesueurigobius* in having a small sulcus size and the nearly oval outline of the sulcus.

Gobiidae, Gobiinae, *Gobius* Lineage (*Gobius* Group):

Typical gobiid otoliths with a parallelogram-like outline and a sole-shaped sulcus. Preventral and postdorsal projections are usually well-developed, the latter more or less strongly bent outwards. A small subcaudal iugum is present below the collum, but due to its height above the other features on the inner face it is often eroded and dif-

Fig. 4 - Schematic explanatory drawings of morphological patterns found in the Eleotridae and the Gobiidae relevant for the taxa described in this study.



difficult to detect. The otoliths of *Proterorhinus* mostly differ from those of *Gobius* in being less elongate ($OL:OH \leq 1.1$ vs $1.15-1.5$). Otoliths of *Zosterisessor* differ from the two other genera in having a relatively short sulcus ($OL2:CL > 2.2$ vs < 2.0). A good selection of extant otoliths of *Gobius* species have been figured in Lombarte et al. (2006), Gut et al. (2020), and Schwarzhans et al. (2020).

Gobiidae, Gobiinae, *Gobius* Lineage (*Thorogobius* Group): *Thorogobius* otoliths are (with very few exceptions, see Schwarzhans et al. 2020) characterized by a shallow sulcus with a low ostial lobe and no subcaudal iugum.

Gobiidae, Gobiinae, *Gobius* Lineage (*Chromogobius* Group): Otoliths of the genera *Chromogobius*, *Odondebuena* and *Zebrus* are characterized by a small, somewhat deepened and short sulcus ($OL2:CL$ usually larger than 1.8, mostly larger than 2.0), a low or no ostial lobe and no subcaudal iugum. The ventral sulcus margin is sometimes w-shaped. The distinction of the otoliths of the three genera contained depends largely on details of the outline of the otolith.

Gobiidae, Gobiinae, *Gobius* Lineage (*Benthophilus* Group): This, nowadays exclusively Ponto-Caspian group, is characterized by a much re-

duced, shallow sulcus that lacks a distinct ostial lobe and shows no subcaudal iugum. The sulcus is usually very small ($OL:CL > 2.2$) and its outline with a w-shaped ventral margin or almost oval. Characters of the otolith outline and curvature of inner face are highly variable between the four extant genera of the group.

Gobiidae, Gobiinae, *Priolepis* Lineage:

Mostly small otoliths with a morphologically simple, mostly shallow sulcus not showing the gobiid sole-shape outline. A character apparently confined to this lineage is the form of the ventral furrow very close to the sulcus and the narrow, furrow-like dorsal depression resulting in the area around the sulcus being somewhat elevated, which is best seen in anterior or posterior views of the otolith. For figures of extant otoliths see Schwarzhans et al. (2020).

Gobiidae, Gobiinae, *Callogobius* Lineage:

Distinctly elongate otoliths ($OL:OH > 1.4$) usually with well-developed postdorsal projection, which however is not or not much bent outwards. The anterior rim is typically blunt. The sulcus is small, mostly shallow, oval, sometimes with w-shaped ventral margin but more commonly just simply oval.

Gobiidae, Gobionellinae, *Pomatoschistus* Lineage (*Deltentosteus* Group): Compact otoliths characterized by an unusually smooth inner face, which in most instances is distinctly bulged (convex). The sulcus is remarkably shallow and often shows a narrow subcaudal iugum. In *Buenia*, the ostial lobe is depressed, while it is strongly developed in the much larger *Deltentosteus* (OL reaches 3.5 mm in *Deltentosteus*, but does not exceed 1.5 mm in *Buenia*).

Gobiidae, Gobionellinae, *Pomatoschistus* Lineage (*Pomatoschistus* Group): The numerous species of the *Pomatoschistus* Group are small and their otoliths are usually smaller than 1.6 mm length (except one species of *Hesperichthys* known to reach 2.2 mm length; see Schwarzhans et al. 2020). Otoliths of the *Pomatoschistus* Group differ from those of the *Deltentosteus* Group in the nearly flat inner face, which is always less convex than the outer face, and the usually somewhat deepened sulcus. The otoliths are generally compressed in outline, with the ratio $OL:OH$ ranging from about 0.75 to about 1.15. The subcaudal iugum is variably developed, lacking in *Hesperichthys* (except

for one species, see Schwarzhans et al. 2020), but more often present and then rather long below the entire cauda and of varying intensity and width. The sulcus usually lacks a distinct ostial lobe, is steeply inclined and rather long in *Pomatoschistus* and *Knipowitschia* ($10\text{--}40^\circ$), and is short and only mildly inclined in *Hesperichthys* ($3\text{--}12^\circ$). Otoliths of the pedomorphic *Pseudaphya* are remarkable for the ostium being deeper than the cauda. Otoliths of several extant *Pomatoschistus* species are figured herein as well as in Lombarte et al. (2006) and Gut et al. (2020).

Order **Gobiiformes** Thacker, 2009

Suborder **Gobioidei** Jordan & Evermann, 1896

Family Eleotridae Bonaparte, 1835

Genus *Eleotris* Scopoli, 1777

***Eleotris omuamuaensis* n. sp.**

Figs. 5A–L

Holotype: Fig. 5C, MGPT-PU 130340, late Tortonian, Cessaniti unit 1, Calabria, Italy.

Paratypes: 7 specimens, MGPT-PU 130341, same data as holotype.

Referred specimens: 25 specimens, same data as holotype.

Etymology: After Omuamua (Hawaiian = scout) in reminiscence to the comet (later reclassified as asteroid) 11/⁹Omuamua discovered in 2017 and referring to the unexpected occurrence of an *Eleotris* species in the late Miocene of the Mediterranean.

Diagnosis: Otoliths with nearly rectangular shape and $OL:OH$ ranging from 1.13 to 1.25, increasing with size. Maximum recorded size 2.6 mm length. Rims irregularly undulating; dorsal rim highest behind its middle. Postdorsal projection short, slightly bent outwards. Sulcus large, wide and deep ($OL:CL = 1.55\text{--}1.75$). Ostial lobe low or absent; no subcaudal iugum. Inner face moderately bent; outer face flat to slightly concave. $OH:OT = 3.2\text{--}3.5$.

Description. Moderately large otoliths reaching size of at least 2.6 mm length (holotype 2.2 mm). $OL:OH = 1.13\text{--}1.25$; $OH:OT = 3.2\text{--}3.5$. Dorsal rim shallow, irregularly undulating, highest behind the middle, with highly positioned and distinct predorsal angle, and variably developed short rounded to slightly expanded and pointed, slightly outward bent postdorsal projection. Anterior rim nearly straight, vertical, inclined at $80\text{--}90^\circ$, with broad, shallow incision at its middle. Posterior rim near vertical, inclined at $90\text{--}105^\circ$, with broad concavity at level of caudal tip. Angle of preventral to postdorsal traverse $30\text{--}35^\circ$. Ventral rim shallow, horizontal, slightly bent, with distinct preventral angle and rounded postventral angle.

Inner face distinctly bent in horizontal direction, with centrally positioned, large, wide, and mostly deep sulcus (shallow sulcus in largest specimen Fig. 5A probably filled by mineral material). OL2:CL = 1.55-1.75; inclination angle of sulcus 7-10°. Sulcus with no or low ostial lobe and no subcaudal iugum. Ventral furrow distinct, broad, regularly curved and terminating at about tips of sulcus. Dorsal depression long, narrow. Outer face flat in smaller specimens, becoming slightly concave in larger specimens, smooth except for some irregular ornamentation.

Discussion. The combination of the large, wide, and poorly structured sulcus with the absence of a subcaudal iugum characterize *E. omuamuaensis* as a representative of the genus *Eleotris* and distinguishes it from otherwise similar looking otoliths of the Atlantic-Mediterranean genus *Gobius*. For comparison, we have figured otoliths of some similarly looking extant species of *Eleotris* from tropical America, West Africa, and the tropical Indo-West Pacific: *Eleotris amblyopsis* (Cope, 1871) (Fig. 5S-U), amphidromous (migrating between different environments) in the tropical West Atlantic, *E. annobonensis* Blanc, Cadenat & Stauch, 1968 (Fig. 5V), amphidromous in the Gulf of Guinea, West Africa, *E. daganensis* Steindachner, 1870 (Fig. 5W) found in freshwater and brackish waters of tropical West Africa, *E. mauritiana* Bennett, 1832 (Fig. 5X), amphidromous in tropical and southern East Africa and islands in the western Indian Ocean, and *E. melanosoma* Bleeker, 1853 (Fig. 5Y-Z) amphidromous in the West Pacific. Most extant *Eleotris* species are freshwater to brackish water to marginal marine and often migrate between these environments. Also, they are not uncommon in mangrove settings. The basal unit 1 in Cessaniti, from which the otoliths have been collected, has been described as paralic/lagoonal representing a brackish water environment with periodical freshwater input and an absence of fully marine organisms (Gramigna et al. 2008; D'Amico et al. 2012). The occurrence of lignite layers in the section suggests coastal marshes and swamps (Gramigna et al. 2008), possibly similar to the mangrove environments found in the present-day Guinea coast. The goby association is lean in species and dominated by *Eleotris omuamuaensis* and *E. tyrrhenicus* (see below), which fits well with the supposed paleoenvironment and in fact opens a rare window into such environment in the Neogene of Europe.

Eleotris tyrrhenicus n. sp.

Figs. 5M-R

Holotype: Fig. 5N-P, MGPT-PU 130342, late Tortonian, Cessaniti unit 1, Calabria, Italy.

Paratypes: 3 specimens, MGPT-PU 130343, same data as holotype.

Referred specimens: 15 specimens, same data as holotype.

Etymology: Referring to the Tyrrhenian Sea, which is nearby the type locality.

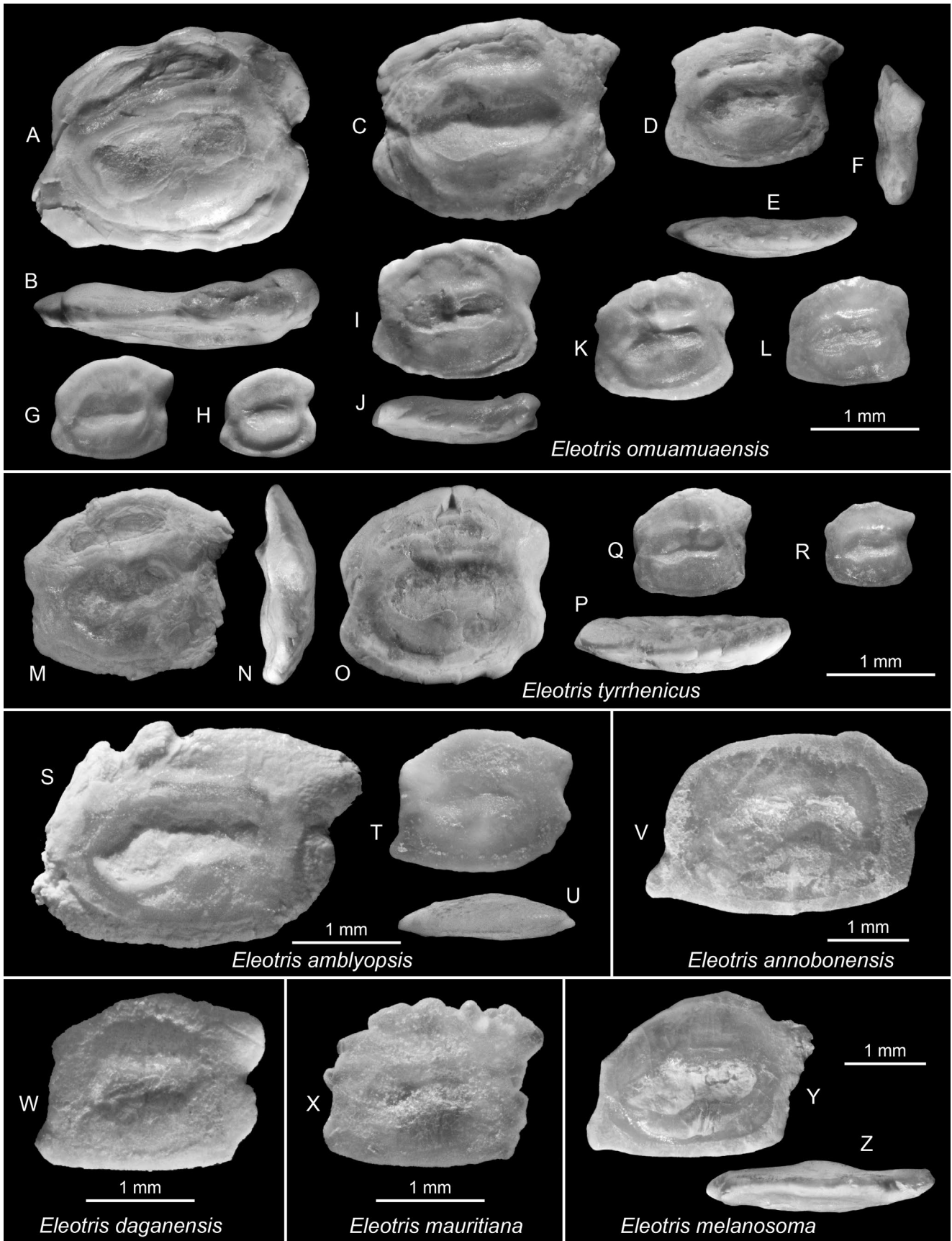
Diagnosis: Otoliths with nearly square shape and OL:OH ranging from 1.03 to 1.10. Maximum recorded size about 2.0 mm length. Dorsal rim with distinct expansion slightly behind its midlength. Postdorsal projection short, very slightly bent outwards. Sulcus moderately long, wide and deep (OL2:CL = 1.8-1.9). Ostial lobe low; no subcaudal iugum. Inner face moderately bent; outer face flat. OH:OT about 3.5.

Description. Moderately large otoliths reaching size of about 2.0 mm length (holotype 1.95 mm). OL:OH = 1.03-1.10; OH:OT = 3.5. Dorsal rim expanded at or slightly behind its midlength, with rounded predorsal angle situated ventrally to short and only slight bent postdorsal projection. Anterior rim nearly straight, vertical, inclined at 90-95°, with indistinct, shallow incision at its middle. Posterior rim near vertical, inclined at 90-95°, with broad concavity at level of caudal tip. Angle of preventral to postdorsal traverse 30-35°. Ventral rim shallow, horizontal, slightly bent, with distinct preventral angle and rounded postventral angle.

Inner face distinctly bent in horizontal direction, with centrally positioned, moderately long, very wide, and deep sulcus, with ostium and cauda nearly similarly wide. OL2:CL = 1.8-1.9; inclination angle of sulcus 6-8°. Sulcus with low ostial lobe and no subcaudal iugum. Ventral furrow distinct, broad,

Fig. 5 - *Eleotris*.

- A-I) *Eleotris omuamuaensis* n. sp., late Tortonian, Cessaniti; C) holotype, MGPT-PU 130340; A-B, D-I) paratypes, MGPT-PU 130341 (A-B, D-G reversed).
- M-R) *Eleotris tyrrhenicus* n.sp., late Tortonian, Cessaniti; N-P) holotype, MGPT-PU 130342 (reversed); M, Q-R) paratypes, MGPT-PU 130343 (M, R reversed).
- S-U) *Eleotris amblyopsis* (Cope, 1871), Recent. S) LACM 56200-2, Panama, Rio Agua, 09°19'N 79°54'W, SL 85 mm; T-U) BMNH 1981.6.9.1231, Surinam, Nicherie Creek.
- V) *Eleotris annobonensis* Blanc, Cadenat & Stauch, 1968, Recent, CAS 214417, Sao Tomé, 00°19'N 06°30'E.
- W) *Eleotris daganensis* Steindachner, 1870, Recent, BMNH 2007.8.21.21-23, Benin.
- X) *Eleotris mauritiana* Bennett, 1832, Recent, WAM P.31115-001, Reunion.
- Y-Z) *Eleotris melanosoma* Bleeker, 1853, Recent, ZMUC P781754-57, New Britain (reversed).



regularly curved and terminating at about tips of sulcus. Dorsal depression long, moderately wide. Outer face flat, smooth except for some irregular ornamentation.

Discussion. *Eleotris tyrrhenicus* differs from *E. omuamuaensis* in being more compressed and nearly square in outline (OL:OH = 1.03-1.10 vs 1.13-1.25 and rectangular in outline), and by having an expanded middorsal rim (vs shallow dorsal rim), and a shorter sulcus (OL2:CL = 1.8-1.9 vs 1.55-1.75). *Eleotris tyrrhenicus* also appears to be smaller than *E. omuamuaensis*.

Family Gobiidae Cuvier, 1816

Remark. Many gobiid otoliths have been reported and figured in otolith research studies of the last 20 years from the late Miocene and Pliocene of the Mediterranean and left in open nomenclature or only tentatively identified often as extant species using the prefixes ‘aff.’ or ‘cf.’. In many cases, there is no or little accompanying description or explanatory notes with the figures. This practice is related to the limited knowledge of extant gobiid otoliths and uncertainties concerning character analyses, variability ranges, and ontogenetic changes. Unfortunately, this practice has resulted in numerous gobiid otolith references, which are almost useless without an in-depth review and revision. We have therefore here undertaken a review of many of the primary data and also offer a review of data from the respective published documentations, but it must also be reminded that several previous records cannot be identified to species level either because of poor preservation, apparent juvenile status, or in the case where we did not reinvestigate the original material, because of uncertainties in the assessment of the published documentation.

Aphia Lineage

Genus *Aphia* Risso, 1827

Aphia minuta (Risso, 1810)

Figs. 6A-H

- 1955 *Gobius intimus* Procházka, 1893 - Bauza-Rullan: pl. 7, figs. 2-3.
 2008 *Aphia minuta* (Risso, 1810) - Carnevale et al.: fig. 6L.
 2009 *Aphia minuta* (Risso, 1810) - Caputo, Carnevale & Landini: pl. 1, fig. 5.
 2013a “*Gobiidarum*” sp. 1 - Agiadi et al.: fig. 8/20.
 2018 *Aphia minuta* (Risso, 1810) - Carnevale et al.: fig. 3O.
 2020 *Aphia minuta* (Risso, 1810) - Agiadi et al.: fig. 3a.
 2020 *Gobius?* sp. 3 - Agiadi et al.: fig. 3u.

Material: 57 specimens: late Tortonian, 3 specimens Cessaniti; pre-evaporitic Messinian, 44 specimens Strada degli Archi; late Messinian upper evaporite, 2 specimens Cava Serredi CS 1; late Messinian Lago Mare Event, 2 specimens Podere Torricella, 1 specimen Le Vicenne; Zanclean, 4 specimens Agia Triada, 1 specimen Voutes.

Discussion. The small, high-bodied otoliths of the neotenic *Aphia minuta* are readily recognized by the long and wide subcaudal iugum underpinning the entire length of the cauda. The late Tortonian record from Cessaniti represents the earliest record of the species, while several fossil species are known of the genus from the Badenian and Sarmatian s.l. of the Paratethys (Bratishko et al. 2015; Schwarzahans et al. 2017, 2020). *Aphia minuta* is one of the few species with a continuous presence through the MSC (Lago Mare Event). Today, this species lives benthic and free swimming, pelagic at 5-80 m water depth inhabiting inshore and estuarine waters over sand, mud, and eel grass (Froese & Pauly 2019).

Genus *Hoeseichthys* Schwarzahans, Brzobohatý & Radwanska, 2020

Hoeseichthys bicornutus (Lin, Girone & Nolf, 2015)

Figs. 6O-R

- ?1955 *Gobius* sp. - Bauza-Rullan: pl. 7, figs. 4-5.
 1989 “genus *Gobiidarum*” sp. 1 - Nolf & Cappetta: pl. 17, figs. 9-10.
 2010 “*Gobiidarum*” sp. 1 - Girone, Nolf & Cavallo: fig. 10j1-5.
 ?2010 *Lesueurigobius* sp. 3 - Girone, Nolf & Cavallo: fig. 10e1-3.
 2015 *Gobius* aff. *guerini* Chaîne & Duvergier, 1931 - Lin, Girone & Nolf: fig. 7/5.
 2015 “*Gobiida*” *bicornuta* - Lin, Girone & Nolf: fig. 7/6.
 2017 “*Gobius*” *bicornutus* (Lin, Girone & Nolf, 2015) - Lin et al.: fig. 12A-C.
 2020 *Lesueurigobius bicornutus* (Lin, Girone & Nolf, 2015) - Schwarzahans et al.: pl. 2, figs. 18-19.

Material: 21 specimens: late Tortonian, 12 specimens Stazzano; pre-evaporitic Messinian, 2 specimens Agios Myron, 5 specimens Moncucco Torinese, 2 specimens Borelli.

Discussion. *Hoeseichthys bicornutus* is one of the largest and the most elongate otolith morphology found in the *Aphia* Lineage (up to 3.5 mm length; OL:OH = 1.15-1.30). It is further characterized by a common broad concavity on the dorsal rim, which is very irregularly shaped, and a very thick, convex outer face. Schwarzahans et al. (2020) allocated this species in *Lesueurigobius*, although this combination of characters in fact is much more indicative of *Hoeseichthys*. *Hoeseichthys bicornutus* is a long ranging species

first identified from the Serravallian of the Central Paratethys and with its apparent latest occurrence in the Pliocene of the Mediterranean.

Hoeseichthys brioche (Lin, Girone & Nolf, 2015)

Figs. 6I–N

- 1978 *Gobiidarum vicinalis* Koken, 1891 - Schwarzahns: pl. 10, fig. 121.
 1986 *Acentrogobius* sp. - Schwarzahns: pl. 6, fig. 73.
 1989 “genus *Gobiidarum*” sp. 2 - Nolf & Cappetta: pl. 17, figs. 7–8.
 1994 “genus *Gobiidarum*” sp. 4 - Nolf & Cavallo: pl. 9, fig. 5.
 1998 “*Gobiidarum*” sp. 2 - Nolf, Mané & Lopez: pl. 7, figs. 1–3.
 2006 “genus *Gobiidarum*” sp. 4 - Nolf & Girone: pl. 10, figs. 5–6.
 2013a *Lesueurigobius suerii* (Risso, 1810) - Agiadi et al.: fig. 8/24.
 2015 “*Gobiida*” *brioche* - Lin, Girone & Nolf: figs. 7/16–20.
 2017 *Lesueurigobius* aff. *friesii* (Malm, 1874) - Agiadi et al.: fig. 4/10 (marked as *Lesueurigobius* sp. 1 on the plate).
 2017 “*Gobius*” *brioche* (Lin, Girone & Nolf, 2015) - Lin et al.: fig. 11O.

Material: 16 specimens: late Tortonian, 3 specimens Potamida; pre-evaporitic Messinian, 1 specimen Metalgrande, 2 specimens Potamida, 4 specimens Agios Myron; Zanclean, 6 specimens Voutes.

Discussion. *Hoeseichthys brioche* is characterized by the combination of a short, poorly structured sulcus where the ostium is just slightly wider than the cauda, a distinct subcaudal iugum, a regularly curved dorsal rim and a ratio OL:OH ranging from 1.03 to slightly over 1.10. Its anterior rim is variably developed but usually regularly curved and only rarely with indentation; likewise, the near vertical posterior rim shows only a very feeble indentation, and a rounded and very short postdorsal projection. *Hoeseichthys brioche* differs from the coeval *Caspiosoma lini* n. sp., in having a recognizable distinction of ostium and cauda (vs simple oval outline of sulcus) and the presence of a large subcaudal iugum (vs absent).

The distribution of *Hoeseichthys brioche* ranges from the late Tortonian to the late Pliocene (Piacenzian) and is apparently related to *H. praeclarus* (Procházka, 1893) from the Langhian (early Badenian) of the Central Paratethys (see Schwarzahns et al. 2020), with which it shares the compressed shape and relatively shallow and short sulcus. Both species appear to be comparative deepwater species. In the Zanclean of Voutes, *H. brioche* was the only gobiid species occurring in the deeper environment of the upper part of the section.

Genus *Lesueurigobius* Whitley, 1950

Lesueurigobius friesii (Malm, 1874)

Figs. 6S–V

- 1980 *Gobius* sp. - Nolf & Martinell: pl. 5, figs. 7–10.
 2000 *Lesueurigobius friesii* (Malm, 1874) - Nolf & Girone: pl. 2, figs. 1–6.
 2010 *Lesueurigobius sanzoi* (de Buen, 1918) - Girone, Nolf & Cavallo: fig. 10a1–2.
 2015 *Lesueurigobius* aff. *friesii* (Malm, 1874) - Lin et al.: fig. 7/13 (non figs. 7/14–15).
 2017 *Lesueurigobius* aff. *friesii* (Malm, 1874) - Agiadi et al.: fig. 4/9 (marked as *Lesueurigobius sanzoi* on the plate).
 2017 *Lesueurigobius* aff. *friesii* (Malm, 1874) - Lin et al.: fig. 11B.
 2020 *Lesueurigobius friesii* (Malm, 1874) - Agiadi et al.: fig. 3n.

Material: 38 specimens: late Tortonian, 5 specimens Potamida; pre-evaporitic Messinian, 1 specimen Potamida, 5 specimens Faneromeni, 6 specimens Agios Myron, 1 specimen San Marino; Zanclean, 7 specimens Rio Torsero, 13 specimens Agia Triada.

Discussion. Three species of *Lesueurigobius* occur today in the Mediterranean, *L. friesii*, *L. sanzoi*, and *L. suerii*. These are difficult to distinguish from each other by means of otoliths (see Schwarzahns et al. 2020 for figures) and all of them seem to have a fossil record dating back to late Miocene or Pliocene times. *Lesueurigobius friesii* is first recorded from the late Tortonian and is recognized by having a rather high-bodied configuration (OL:OH \leq 1.0), with a smooth or crenulated and regularly curved dorsal rim, and a massive subcaudal iugum.

Lesueurigobius sanzoi (de Buen, 1918)

Figs. 6W–Z

- 1998 *Lesueurigobius* aff. *sanzoi* (de Buen, 1918) - Nolf, Mané & Lopez: pl. 7, figs. 14–15.
 2013a *Lesueurigobius friesii* (Malm, 1874) - Agiadi et al.: fig. 8/17–18.
 ?2013a *Lesueurigobius sanzoi* (de Buen, 1918) - Agiadi et al.: fig. 8/16.

Material: 88 specimens: Zanclean, 86 specimens Agia Triada, 2 specimens Voutes.

Discussion. Otoliths of *Lesueurigobius sanzoi* differ from those of *L. friesii* in showing a narrower and longer subcaudal iugum (vs broad and not extending below entire cauda). Other subtle characters for distinction may be a slightly less compressed outline, a very regularly curved dorsal rim and a comparably larger sulcus. The earliest unambiguous records of *L. sanzoi* are from the Zanclean.

Lesueurigobius stazzanensis n. sp.

Figs. 6AG–AP

- 2010 *Lesueurigobius* sp. 2 - Girone, Nolf & Cavallo: fig. 10c1–4.

Holotype: Fig. 6AG–AI, MGPT-PU 130344, late Tortonian, Stazzano, Piedmont, Italy.

Paratypes: 12 specimens, MGPT-PU 130345, same data as holotype.

Referred specimens: 53 specimens, same data as holotype.

Etymology: After the type locality Stazzano in Piedmont.

Diagnosis: Large growing otoliths reaching a maximum size up to 3.2 mm in length; moderately compressed and OL:OH ranging from 1.05 to 1.17, increasing with size. Dorsal rim regularly curved and relatively shallow, undulating or slightly crenulating. Postdorsal projection broad, short. Sulcus small, narrow, moderately deepened (OL2:CL = 1.6-1.9). Ostial lobe low; subcaudal iugum short, broad, distinct. Inner face slightly bent; outer face moderately convex. OH:OT = 2.6-2.8.

Description. Relatively large otoliths reaching a maximum size of about 3.2 mm in length (holotype). OL:OH = 1.05-1.17; OH:OT = 2.6-2.8. Dorsal rim regularly curved, relatively shallow, reaching its maximum height slightly behind its midlength. Predorsal angle rounded and broad, and postdorsal projection massive and short. Anterior rim broadly rounded, blunt, inclined at 90-95°, with indistinct, very shallow incision at its midlength. Posterior rim inclined at 95-105°, with small incision below postdorsal projection at level of caudal tip. Angle of preventral to postdorsal traverse measuring 30-35°. Ventral rim shallow, horizontal, slightly bent, with rounded preventral and postventral angles.

Inner face slightly bent horizontally, with centrally positioned, short, narrow, slightly deepened and moderately inclined sulcus, with smoothed sole-shape. OL2:CL = 1.6-1.9; inclination angle of sulcus 15-22°. Sulcus with rounded, low ostial lobe and short but wide subcaudal iugum below anterior section of cauda. Ventral furrow running very close to ventral rim of otolith, turning upwards behind cauda to join dorsal depression. Dorsal depression large, wide, rather distinct. Outer face moderately convex, smooth, with thickened ventral half.

Discussion. *Lesueurigobius stazzanensis* is the only species of the genus with a ratio OL:OH regularly above 1.0 (1.05-1.17). It is further characterized by the short and wide subcaudal iugum and the low and regularly curved dorsal rim. It differs from members of the genus *Hoeseichthys* by the larger and more structured sulcus, except *H. bicornutus*, from which it differs in the regularly curved dorsal rim (vs flat to concave) and in being thinner (OH:OT = 2.6-2.8 vs < 2.3).

Lesueurigobius suerii (Risso, 1810)

Figs. 6 AA-AF

1931 *Gobius vicinalis* Koken, 1891 - Chainé & Duvergier: pl. 1, figs. 25-28.

- 1994 *Lesueurigobius* aff. *suarii* (Risso, 1810) - Nolf & Cavallo: pl. 8, fig. 9.
 2000 *Lesueurigobius suerii* (Risso, 1810) - Nolf & Girone: pl. 2, figs. 7-12.
 2009 *Lesueurigobius* aff. *vicinalis* (Koken, 1891) - Caputo, Carnevale & Landini: pl. 1, fig. 10.
 2010 *Lesueurigobius sanzoi* (de Buen, 1918) - Girone, Nolf & Cavallo: fig. 10a1-2.
 2014 *Lesueurigobius suerii* (Risso, 1810) - Schwarzahns: pl. 11, figs. 4-13.
 2020 *Lesueurigobius sanzoi* (de Buen, 1918) - Agiadi et al.: fig. 3o.

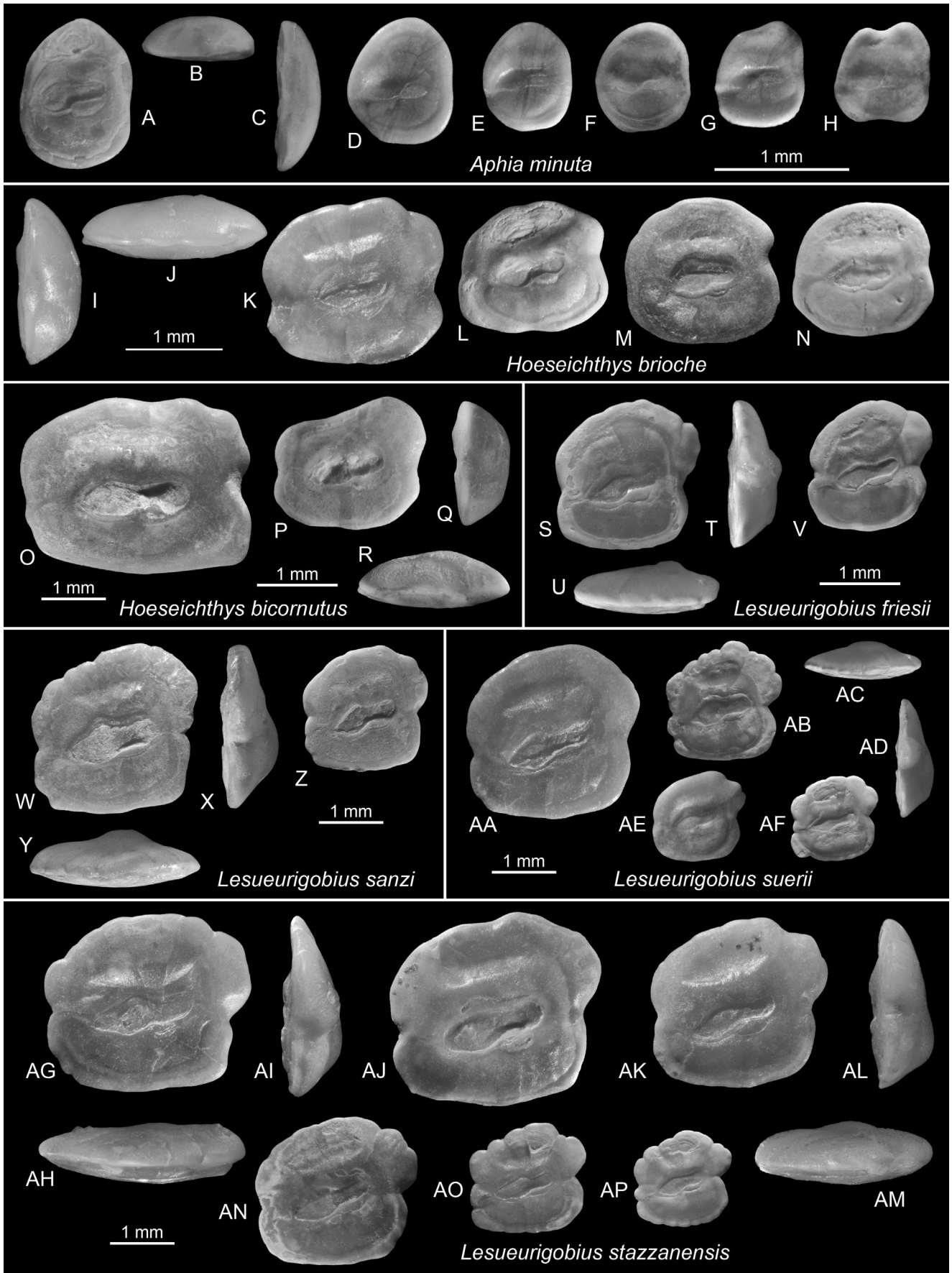
Material: 123 specimens: late Tortonian, 8 specimens Stazzano; pre-evaporitic Messinian, 28 specimens Botro Rosso, 1 specimen Faneromeni, 2 specimens Borelli, 20 specimens Strada degli Archi; Zanclean, 64 specimens Agia Triada.

Discussion. Otoliths of *L. suerii* are similar in many ways to *L. friesii*, but usually show a more coarsely ornamented and less regularly curved dorsal rim (but see Fig. 6AA) and a narrower subcaudal iugum. It may also be just slightly less compressed than *L. friesii*. *Lesueurigobius suerii* appears to be the earliest extant species of the genus in the fossil record and has been recorded from the late Serravallian of Turkey (Schwarzahns 2014).

A similar species has been described from the Zanclean of Spain by Chainé & Duvergier (1931) and confirmed by Nolf & Martinell (1980) as *Gobius guerini* Chainé & Duvergier, 1931. This species should also be placed in *Lesueurigobius* and is characterized by a straight, steeply inclined predorsal rim, a predorsal angle usually extending further forward than

Fig. 6 - *Aphia*, *Hoeseichthys* and *Lesueurigobius*.

- A-H) *Aphia minuta* (Risso, 1810). A-C) Late Tortonian, Cessaniti, MGPT-PU 130368; D-H) pre-evaporitic Messinian, Strada degli Archi, MGPT-PU 130369 (E-F, H reversed).
 I-N) *Hoeseichthys brioche* (Lin, Girone & Nolf, 2015). I-K) Pre-evaporitic Messinian, Metalgrande, IRSNB P 9947; L) Zanclean, Voutes, AMPG(V)2327; M) pre-evaporitic Messinian, Potamida, AMPG(V)2328 (reversed); N) late Tortonian, Potamida, AMPG(V)2329 (reversed).
 O-R) *Hoeseichthys bicornutus* (Lin, Girone & Nolf, 2015). O) Pre-evaporitic Messinian, Moncucco, IRSNB P 9948 (reversed); P-R) pre-evaporitic Messinian, Agios Myron, AMPG(V)2330.
 S-V) *Lesueurigobius friesii* (Malm, 1874). S-T) Zanclean, Agia Triada, AMPG(V)2331; V) Sahelian (Messinian), San Marino, SE of Acquaviva, SMF-PO.91842 (reversed).
 W-Z) *Lesueurigobius sanzoi* (de Buen, 1918), Zanclean, Agia Triada, AMPG(V)2332 (W-X reversed).
 AA-AF) *Lesueurigobius suerii* (Risso, 1810). AA) Late Tortonian, Stazzano, MGPT-PU 130370 (reversed); AB-AD, AF) Zanclean, Agia Triada, AMPG(V)2333 (AB-AD reversed); AE) pre-evaporitic Messinian, Strada degli Archi, MGPT-PU 130371 (reversed).
 AG-AP) *Lesueurigobius stazzanensis* n.sp., late Tortonian, Stazzano, AG-AI) holotype, MGPT-PU 130344; AJ-AP) paratypes, MGPT-PU 130345 (AN, AP reversed).



the preentral angle and a relatively small subcaudal iugum. *Lesueurigobius guerini* has not been found in the Zanclean of the Central and Eastern Mediterranean.

Gobius Lineage
Gobius Group
Genus *Gobius* Linnaeus, 1758

***Gobius auratus* Risso, 1810**

Fig. 7A-C

2013a *Gobius* cf. *paganellus* Linnaeus, 1758 - Agiadi et al.: fig. 8/14.

Material: 1 specimen, Zanclean, Voutes.

Discussion. *Gobius auratus* belongs to a group containing a number of small extant Atlantic-Mediterranean *Gobius* species characterized by relatively compressed and compact otoliths with a convex outer face and a short postdorsal projection that is not bent outwards. This group contains the species *G. auratus*, *G. conchi*, *G. fallax*, and *G. vittatus* (see Gut et al. 2020 and Schwarzahans et al. 2020 for figures). Their otoliths are difficult to distinguish relying on subtle differences for instance in proportions, details of the otolith outline, or the sulcus. Otoliths of *G. auratus* have a ratio OL:OH ranging from 1.1 to 1.2, a short preentral projection and a narrow subcaudal iugum.

***Gobius fallax* Sarato, 1889**

Fig. 7D-E

2013a *Gobius* sp. 1 - Agiadi et al.: fig. 8/13.

Material: 8 specimens: pre-evaporitic Messinian, 3 specimens Agios Myron; Zanclean, 3 specimens Rio Torsero (SMF PO91837), 1 specimen Agios Triada, 1 specimen Voutes.

Discussion. Otoliths of *G. fallax* tend to be slightly more elongate than those of *G. auratus* (OL:OH = 1.2-1.3 vs 1.1-1.2) and show a stronger postdorsal projection. Also, their subcaudal iugum appears wider. *Gobius fallax* is recorded herein for the first time from the pre-evaporitic Messinian.

***Gobius geniporus* Valenciennes, 1837**

Fig. 7F-G

?1989 *Gobius truncatus* Schwarzahans, 1979 - Nolf & Cappetta: pl. 17, fig. 11.

?2006 *Gobius* aff. *niger* Linnaeus, 1758 - Nolf & Girone: pl. 10, figs. 7-8.

2020 *Gobius* cf. *geniporus* Valenciennes, 1837 - Agiadi et al.: fig. 3i.

Material: 4 specimens, Zanclean: 1 specimen Agia Triada, 3 specimens Voutes.

Discussion. *Gobius geniporus* is a relatively large species and has relatively elongate otoliths (OL:OH = 1.30-1.35). Its otoliths are further characterized by the combination of a depressed predorsal rim, a nearly vertically cut anterior rim with only a short preentral projection, a distinct postdorsal projection that is markedly bent outwards, and a large subcaudal iugum. The inner face is convex, and the outer face flat to slightly concave. Thus, otolith of *G. geniporus* are relatively easy to recognize within the genus. The Zanclean otoliths from Greece represent the earliest evidence of this species in the fossil record.

***Gobius mustus* Schwarzahans, 2014**

Fig. 7H-I

2014 *Gobius mustus* - Schwarzahans: pl. 8, figs. 4-16.

2020 *Gobius mustus* Schwarzahans, 2014 - Schwarzahans, Brzobohatý & Radwanska: pl. 4, figs. 1-5 (see there for further synonymies).

Material: 3 specimens: late Tortonian, 2 specimens Stazzano; pre-evaporitic Messinian, 1 specimen, Agios Myron.

Discussion. *Gobius mustus* has a relatively thick otolith with a strongly convex outer face. The distinct predorsal angle and the preentral projection are similarly strongly developed and the broad

Fig. 7 - *Gobius*.

A-C) *Gobius auratus* Risso, 1810, Zanclean, Voutes, AMPG(V)2334.

D-E) *Gobius fallax* Sarato, 1889, pre-evaporitic Messinian, Agios Myron, AMPG(V)2335.

F-G) *Gobius geniporus* Valenciennes, 1837, Zanclean, Agia Triada, AMPG(V)2336.

H-I) *Gobius mustus* Schwarzahans, 2014, late Tortonian, Stazzano, MGPT-PU 130372.

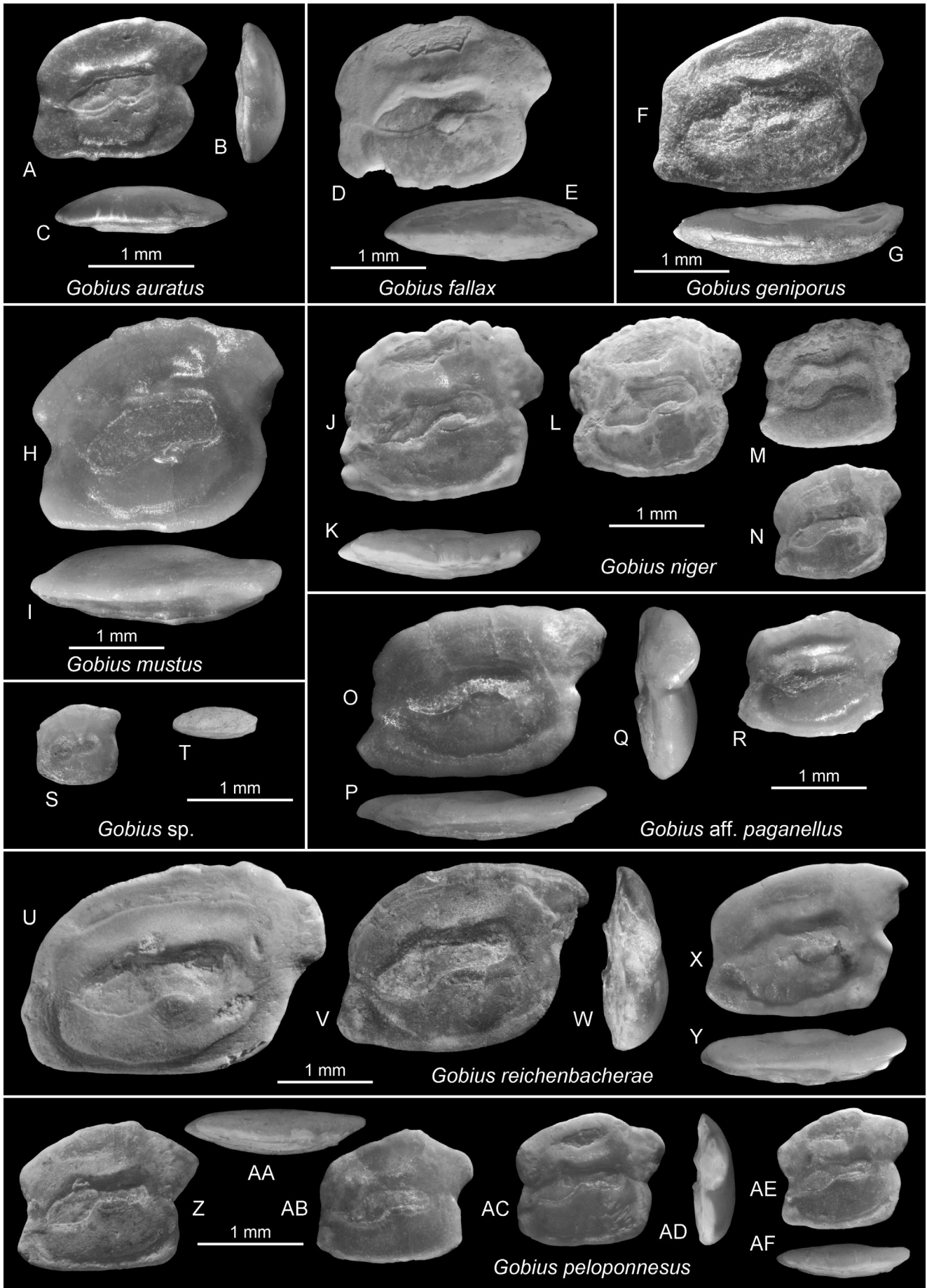
J-N) *Gobius niger* Linnaeus, 1758, Zanclean, Agia Triada, AMPG(V)2337 (M-N reversed).

O-R) *Gobius* aff. *paganellus* Linnaeus, 1758. O-Q) Late Tortonian, Stazzano, MGPT-PU 130373 (reversed); R) late Tortonian, Cessaniti, MGPT-PU 130374.

S-T) *Gobius* sp., late Tortonian, Cessaniti, MGPT-PU 130375 (reversed).

U-Y) *Gobius reichenbacheriae* Schwarzahans, 2014, late Tortonian, Stazzano, MGPT-PU 130376 (reversed).

Z-AF) *Gobius peloponnesus* n.sp. Zanclean, Agia Triada; Z-AA) holotype, AMPG(V)2338; AB-AF) paratypes, AMPG(V)2339 (reversed).



and rounded postdorsal projection is short and only slightly bent outwards. *Gobius mustus* is common in the middle Miocene, for instance in the early Badenian (Langhian) of the Central Paratethys and the late Serravallian of SE-Turkey. It is one of few gobiid species ranging into late Miocene times just before the MSC.

Gobius niger Linnaeus, 1758

Figs. 7J-N

Material: 22 specimens: Zanclean, 18 specimens Agia Triada, 4 specimens Voutes.

Discussion. Otoliths of *Gobius niger* have erroneously been recorded several times in the literature from the fossil record, but none of those appear to really represent this common extant species. Otoliths of *G. niger* show some variation of the ratio OL:OH that ranges from about 1.1 to 1.3; more characteristic is the short preventral projection, highly positioned and strong predorsal angle, regularly curved and often somewhat undulating dorsal rim, short and somewhat outward bent postdorsal projection, and, finally, the flat outer face and often a remarkably strong ostial lobe. Although the specimens from the Zanclean of Greece assigned herein to *Gobius niger* show a really compressed range of the OL:OH ratio (1.1-1.15), they match very well the other characters typical of the extant specimens (see Nolf et al. 2009; Gut et al. 2020 and Schwarzahns et al. 2020 for figures of extant specimens).

Gobius aff. paganellus Linnaeus, 1758

Figs. 7O-R

2020 *Gobius cobitis* Pallas, 1814 - Agiadi et al.: fig. 3g.
?2020 *Gobius cf. paganellus* Linnaeus, 1758 - Agiadi et al.: fig. 3j.

Material: 14 specimens: late Tortonian, 3 specimens Stazano, 3 specimens Cessaniti; Zanclean, 5 specimens Agia Triada, 3 specimens Voutes.

Discussion. Otoliths of *Gobius paganellus* are among the most slender and thinnest in extant *Gobius* species (OL:OH = 1.35-1.60, increasing with size; OH:OT = 3.2-3.6). The otoliths are further characterized by a relatively flat, nearly horizontal dorsal rim, a long and sharp postdorsal projection that is strongly bent outwards, by a narrow sulcus, and a small, often indistinct subcaudal iugum. The

fossil specimens from the late Tortonian to Zanclean differ slightly from the extant ones in a relatively strongly developed preventral projection, and for this reason are only tentatively placed within this species.

Gobius peloponnesus n. sp.

Figs. 7Z-AF

2020 *Gobius?* sp. 2 - Agiadi et al.: fig. 3m.

Holotype: Fig. 7Z-AB, AMPG(V)2338, Zanclean, Agia Triada, c. 5 km North of Koroni, Peloponnesus, Greece.

Paratypes: 20 specimens, AMPG(V)2339, same data as holotype.

Etymology: After the type region Peloponnesus, Greece.

Diagnosis: Otoliths reaching a maximum size of 1.7 mm in length; compressed, with OL:OH ranging from 1.1 to 1.2, increasing with size. Dorsal rim anteriorly inclined, with obtuse postdorsal angle followed by short flat or concave section, smooth. Postdorsal projection moderate, slightly bent outwards. Predorsal angle prominent, projecting about as much as the preventral projection. Anterior rim with broad concavity. Sulcus long, narrow, moderately deepened (OL2:CL = 1.4-1.6). Ostial lobe moderate, and subcaudal iugum relatively long, very narrow. Inner face convex; outer face flat. OH:OT = 3.2-3.5.

Description. Relatively small otoliths for the genus *Gobius* reaching a maximum size of about 1.7 mm in length (holotype). OL:OH = 1.1-1.2; OH:OT = 3.2-3.5. Dorsal rim anteriorly inclined, nearly straight, highest at obtuse postdorsal angle above cauda, thereafter inclined straight or slightly concave. Postdorsal projection moderately long, angular at tip, slightly bent outwards, positioned only slightly higher than predorsal angle. Anterior rim nearly vertical, with sharp, high predorsal angle and similarly developed preventral projection and broad concavity in between, inclined at 85-90°. Posterior rim inclined at 100-105°, with distinct incision below postdorsal projection at level of caudal tip. Angle of preventral to postdorsal traverse measuring 27-37°. Ventral rim nearly flat, horizontal, with sharp but not very long preventral projection and distinct postventral angle.

Inner face distinctly bent horizontally, with slightly suprmedian positioned, long, narrow, slightly deepened and moderately inclined sole-shaped sulcus. OL2:CL = 1.4-1.6; inclination angle of ostium 20-25°; inclination of sulcus 12-18°. Sulcus with moderately developed ostial lobe, narrow cauda and moderately elongate and very narrow subcaudal iugum below most of cauda. Ventral furrow running very close to ventral rim of oto-

lith, turning upwards behind cauda but not reaching dorsal depression. Dorsal depression relatively small, rather distinct. Outer face flat, smooth.

Discussion. *Gobius peloponnesus* resembles otoliths of *Gobius niger* in proportions, but it is readily distinguished by the specific shape of the dorsal rim, strong predorsal angle, and very narrow and long subcaudal iugum. It further differs from other extant compressed *Gobius* otoliths by its thin appearance and the flat outer face. *Gobius peloponnesus* is a highly characteristic otolith that so far has only been found in the shallow-water Zanclean environment of Agia Triada.

Gobius reichenbacherae Schwarzhans, 2014

Figs. 7U–Y

- 2009 ?*Mesogobius* sp. - Caputo, Carnevale & Landini: pl. 1, fig. 11.
 2010 ?*Mesogobius* sp. - Girone, Nolf & Cavallo: figs. 10d1–4.
 2014 *Gobius reichenbacherae* - Schwarzhans: pl. 9, figs. 2–9.
 2015 *Gobius* aff. *paganellus* Linnaeus, 1758 - Lin, Girone & Nolf: figs. 7/8–9.
 2015 ?*Mesogobius* sp. - Lin, Girone & Nolf: fig. 7/12.
 2017 *Gobius* aff. *paganellus* Linnaeus, 1758 - Lin et al.: fig. 11R–S.
 2020 *Gobius reichenbacherae* Schwarzhans, 2014 - Schwarzhans, Brzobohatý & Radwanska: pl. 4, figs. 6–9 (see there for further synonymies).

Material: 11 specimens: late Tortonian, 4 specimens Stazano; pre-evaporitic Messinian, 3 specimens Strada degli Archi, 2 specimens Potamida, 2 specimens Agios Myron.

Discussion. *Gobius reichenbacherae*, together with *G. mustus*, is a common species in the middle Miocene of the Central Paratethys (early Badenian) and the Serravallian of SE-Turkey, and both species appear to be present until the late Miocene up to the onset of the MSC. *Gobius reichenbacherae* resembles *G. paganellus* in the elongate shape (OL:OH = 1.25–1.42), general outline, strongly outward bent postdorsal projection, and flat outer face. It differs from *G. paganellus* in having a regularly curved predorsal region, relatively large subcaudal iugum, and relatively wide sulcus. The late Miocene specimens differ from the middle Miocene ones in usually having a lower ostial lobe, although this character appears to be somewhat variable.

Gobius sp.

Fig. 7S–T

Material: 6 specimens, late Tortonian, Cessaniti.

Discussion. Six small, compressed otoliths

up to 0.8 mm in length probably stemming from juvenile fishes may represent a further *Gobius* species not recorded from any of the other locations. They are characterized by a ratio OL:OH of about 1.05–1.1, with a vertically cut anterior rim and a slender, pointed and high positioned postdorsal projection, which is slightly bent outwards. Inner and outer faces are equally convex resulting in a rather low ratio OH:OT of about 2.5. The sulcus is wide, especially the ostium, and relatively deep showing a narrow subcaudal iugum. The otoliths are in many ways reminiscent of *Proterorhinus yigitbasi* (see below), from which they differ in the smooth outline and thick appearance.

Genus *Proterorhinus* Smitt, 1900

Proterorhinus cretensis n. sp.

Figs. 8U–AA

Holotype: Fig. 8U–W, AMPG(V)2340, Zanclean, Voutes, Crete, Greece.

Paratypes: 20 specimens, AMPG(V)2341, same data as holotype.

Etymology: After the type region Crete, Greece.

Diagnosis: Otoliths measuring up to a maximum size of 1.7 mm in length; compressed, with OL:OH ranging from 1.00 to 1.07. Dorsal rim relatively flat, smooth, with high positioned predorsal angle. Postdorsal projection moderately long, pointed, positioned very high, slightly bent outwards. Preventral projection very short resulting in almost vertical and straight anterior rim. Sulcus moderately long, narrow, moderately deepened (OL2:CL = 1.4–1.6). Ostial inclination angle 20–30°; sulcus inclination angle 15–22°. Ostial lobe weak; subcaudal iugum small, narrow. Inner and outer faces slightly convex. OH:OT = 3.0–3.5.

Description. Relatively small otoliths reaching a maximum size of about 1.7 mm in length (holotype 1.55 mm). OL:OH = 1.00–1.07; OH:OT = 3.0–3.5. Dorsal rim smooth, with prominent, obtuse, high positioned predorsal angle and relatively flat main section, with maximum height at or slightly behind its midlength. Postdorsal projection moderately long, with pointed tip, slightly bent outwards, positioned only slightly higher than predorsal angle. Anterior rim almost vertical, without broad concavity in between, inclined at 80–87°. Posterior rim inclined at 95–100°, with distinct incision below postdorsal projection at level of caudal tip. Angle of preventral to postdorsal traverse 37–43°. Ventral rim nearly flat, horizontal, with sharp but short preventral projection and rounded postventral angle.

Inner face slightly bent in horizontal direction. Sulcus slightly suprmedian, moderately long, narrow, slightly deepened and moderately inclined. OL2:CL = 1.4-1.6; inclination angle of ostium 20-30°; inclination of sulcus 15-22°. Sulcus with weak ostial lobe, and very short and narrow subcaudal iugum below anterior part of cauda. Ventral furrow running moderately close to ventral rim of otolith, turning upwards behind cauda but not reaching dorsal depression. Dorsal depression relatively large. Outer face slightly convex, smooth.

Discussion. *Proterorhinus cretensis* differs from *P. yigitbasi* (Rückert-Ülkümen, 2006) in the smooth otolith rims and the relatively narrow sulcus (the specimen of Fig. 8X shows an unusual, slightly wider sulcus). In particular the smooth and regularly formed dorsal rim distinguishes *P. cretensis* from the known fossil or extant species (see Schwarzahans et al. 2015 for figures of otoliths of the three valid extant species). We interpret the occurrence of *P. cretensis* in the Zanclean shallow marine environment of Crete as an endemic remnant of the genus in the eastern Mediterranean that may have evolved from *P. yigitbasi* which had migrated into the Mediterranean Basin during late Miocene (see below).

Proterorhinus yigitbasi (Rückert-Ülkümen, 2006)

Figs. 8A-R

- ?1982b *Gobius rumanus* (Pana, 1982) - Pana: pl. 3, figs. 3, 5
 ?1982b *Gobius telleri* Schubert, 1906 - Pana: pl. 3, fig. 7.
 1995 *Acentrogobius rumanus* Pana, 1982 - Pana: pl. 1, figs. 5-10.
 2006 *Neogobius yigitbasi* - Rückert-Ülkümen: Figs. 5/1-10.
 2008 *Gobius* aff. *multipinnatus* (v. Meyer, 1852) - Carnevale et al.: fig. 3P.
 2008 *Gobius* aff. *niger* Linnaeus, 1758 - Carnevale et al.: fig. 3Q, 6I.
 2008 *Gobius* aff. *paganellus* Linnaeus, 1758 - Carnevale et al.: fig. 6R
 2009 *Gobius* aff. *guerini* Chaine & Duvergier, 1931 - Caputo, Carnevale & Landini: pl. 1, fig. 6.
 2009 *Gobius* aff. *niger* Linnaeus, 1758 - Caputo, Carnevale & Landini: pl. 1, fig. 8.
 ?2009 *Gobius* aff. *multipinnatus* (v. Meyer, 1852) - Caputo, Carnevale & Landini: pl. 1, fig. 7.
 ?2009 *Gobius* sp. - Caputo, Carnevale & Landini: pl. 1, fig. 9.

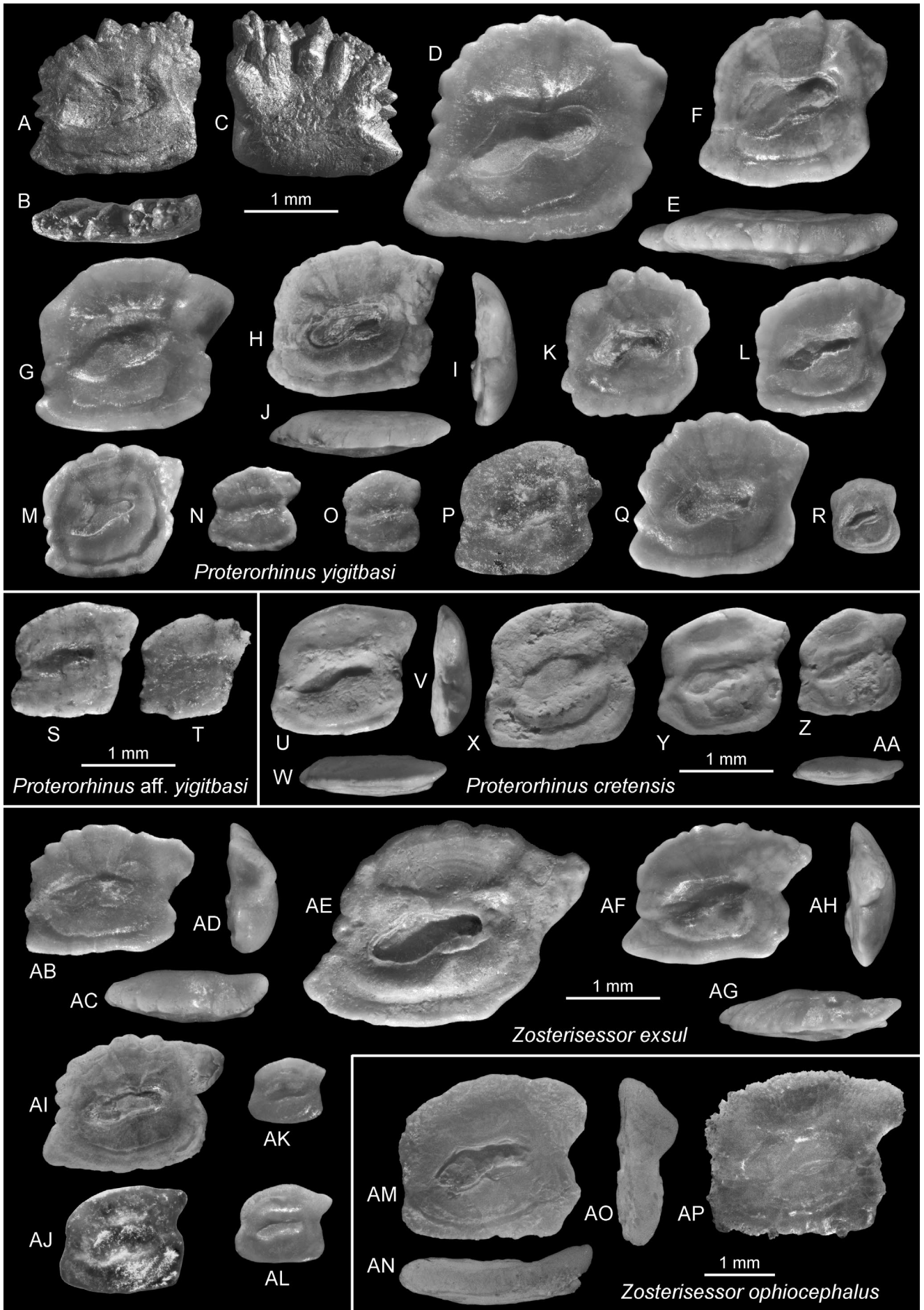
Material: 684 specimens: pre-evaporitic Messinian, 135 specimens from Strada degli Archi (figured specimens MGPT-PU 130346); late Messinian MSC, sub-stage 3.1, 8 specimens Cava Serredi CS 1; late Messinian MSC, Lago Mare Event, 17 specimens Podere Torricella, 502 specimens from Cava Serredi (figured specimens MGPT-PU 130347), 4 specimens Ciabot Cagna, 2 specimens Moncucco Torinese; Khersonian to early Meotian, 11 specimen Plopease, Romania (LPB-II-0001a, 0006a-b, 0013a-f, 0016a, 0023a); early Meotian, 1 specimen Slanicul, Romania (LPB-II-0025); late Meotian, 2 specimens Foltea, Romania (LBP-II-0010, 0014a), 2 specimens Plopease, Romania (LBP-II-0020a, 0029).

Diagnosis (new): Otoliths reaching a maximum size of 2.8 mm in length; compressed, with OL:OH ranging from 0.93 to 1.13, increasing with size. Dorsal rim high, irregularly rounded and variably, often coarsely crenulated. Predorsal angle broadly rounded. Postdorsal projection short, variably pointed or rounded, positioned high, slightly bent outwards. Preventral projection short, angular or slightly pointed. Sulcus relatively short and wide, moderately deepened (OL2:CL = 1.6-1.9). Sulcus inclination angle 15-25°. Ostial lobe low; subcaudal iugum small, narrow. Inner face slightly convex, and outer face flat to slightly convex. OH:OT = 3.3-3.8.

Description. Moderately sized otoliths reaching a maximum size of about 2.8 mm in length (holotype 1.8 mm). OL:OH = 1.0-1.13 in specimens larger than 1 mm length, 0.93-1.0 in specimens smaller than 1 mm; OH:OT = 3.3-3.8. Dorsal rim very irregularly formed, curved, with more or less strongly, sometimes rugged crenulation. Predorsal angle rounded; postdorsal projection short, with pointed or rounded tip, slightly bent outwards, positioned at about level of predorsal angle or slightly higher. Anterior rim steep, mostly without or with indistinct concavity, inclined at 75-90°. Posterior rim inclined at 92-105°, with moderate incision below postdorsal projection at level of caudal tip. Angle of preventral to postdorsal traverse 28-35°. Ventral rim nearly flat, horizontal, with sharp, mostly short but sometimes extended preventral projection and rounded postventral angle.

Fig. 8 - *Proterorhinus*, *Zosterisessor*.

- A-R) *Proterorhinus yigitbasi* (Rückert-Ülkümen, 2006). A-C) Holotype, SNSB-BSPG 1980-X-1209, late Khersonian to early Meotian, Yalova near Istanbul, Turkey (reversed); D-F, H-M, Q-R) late Messinian, Lago Mare event, Cava Serredi, MGPT-PU 130346 (H-J, L, M, Q reversed); G) pre-evaporitic Messinian, Strada degli Archi, MGPT-PU 130347; N-O) Khersonian to early Meotian, Plopease, Romania, LPB-II-0001a and 0013e (reversed); P) early Meotian, Slanicul, Romania, LPB-II-0025 (reversed).
 S-T) *Proterorhinus* aff. *yigitbasi* (Rückert-Ülkümen, 2006). S) Levantian, Plopease, Romania, LPB-II-0018a; T) Khersonian to early Meotian, Plopease, Romania, LPB-II-0006c (filtered).
 U-AA) *Proterorhinus cretensis* n.sp., Zanclean, Voutes; U-W) holotype, AMPG(V)2340 (reversed); X-AA) paratypes, AMPG(V)2341 (Y reversed).
 AB-AL) *Zosterisessor exsul* n.sp., AF-AH) holotype, MGPT-PU 130348, late Messinian, Lago Mare event, Cava Serredi (reversed); AB-AC) paratypes, pre-evaporitic Messinian, Strada degli Archi, MGPT-PU 130350; AE, AI, AK-AL) paratypes, late Messinian, Lago Mare event, Cava Serredi, MGPT-PU 130349 (AI reversed); AJ) Meotian 2 (upper Meotian), Foltea, Romania, LPB-II-0017f (filtered).
 AM-AP) *Zosterisessor ophiocephalus* (Pallas, 1814), Recent, off Zadar, ICM-O 1025-6 and 8, TL 77 and 83 mm.



Inner face slightly bent in horizontal direction, with median to slightly suprmedian positioned, short, wide, slightly deepened and moderately inclined sulcus. OL2:CL = 1.6-1.9; inclination angle of ostium equals inclination angle of sulcus at 15-25°. Sulcus with weak ostial lobe, and short and narrow subcaudal iugum located below main part of cauda. Ventral furrow distinct, running moderately close to ventral rim of otolith, turning upwards behind cauda and sometimes reaching dorsal depression. Dorsal depression relatively large, distinct. Outer face flat to slightly convex, variably ornamented or smooth.

Discussion. *Proterorhinus yigitbasi* was originally described based on several well-preserved specimens from Khersonian to early Meotian sands of Yalova, Turkey, Marmara Basin. Rückert-Ülkümen's photograph of the holotype unfortunately is somewhat distorted and therefore a new photograph is provided in Fig. 8A-C. The holotype is also atypical in the type series for the lack of a postdorsal projection. *Proterorhinus yigitbasi* was very common during the substages 3.1 and 3.2 (Lago Mare) of the MSC as well as in the shallow-water pre-evaporitic environment of Strada degli Archi. Because of its rather wide range of variability caused primarily by the varying expression of the coarsely ornamented dorsal rim, differing morphological variations have been allocated to different species in past literature (Carnevale et al. 2008 and Caputo et al. 2009).

Proterorhinus yigitbasi has also been found in Khersonian to late Meotian sediments of the Dacian Basin by Pana and is reported herein for the first time. Pana (1982a) described *Acentrogobius rumanus* Pana, 1982 from the Pannonian of the Romanian part of the Pannonian Basin, and also mentioned it later from the Dacian of the Dacic Basin (Pana 1982b, 1995). The type specimens were not available for revision and her figures and descriptions are not adequate for definition of the species. Hence, we regard *Acentrogobius rumanus* as a nomen dubium until the type specimens have been found or the species is rejected. However, her reports from the Dacian of the Dacic Basin seem to represent, at least partly, *P. yigitbasi*, which is consistent with the Dacian material available to us for revision.

In summary, *P. yigitbasi* was a widespread and common species in the shallow-water and possibly brackish water of the Messinian of the Mediterranean before and during the MSC. It is not known from late Tortonian or Zanclean shallow marine en-

vironments. In the eastern Paratethys, i.e., the Pontian Basin, it has regularly been found throughout the Meotian, possibly since Khersonian, but its upper range remains uncertain since there is no knowledge of Pontian otoliths and Dacian to Levantian (Zanclean equivalent) records are ambiguous (see below). *Proterorhinus yigitbasi* thus represents a clear example of immigration of Paratethyan fishes into the Mediterranean before the Lago Mare Event.

Proterorhinus* aff. *yigitbasi (Rückert-Ülkümen, 2006)

Figs. 8S-T

Material: 2 specimens: Khersonian to early Meotian, 1 specimen Plopease, Romania (LBP-II-0006c); Dacian, 1 specimen Plopease, Romania (LBP-II-0018a).

Discussion. Two specimens from the upper and lower stratigraphic range in the Dacic Basin differ significantly in the expanded pre- to postdorsal region, which is wider than the central region. We consider this a possible extension beyond the already significant variability observed in the species and as a possible indication that a second sympatric species of *Proterorhinus* could have been present in the basin.

Genus *Zosterisessor* Whitley, 1935

***Zosterisessor exsul* n. sp.**

Figs. 8AB-AL

?2008 *Gobius* sp. 1 - Carnevale et al.: fig. 3U.

2008 *Zosterisessor* aff. *ophiocephalus* (Pallas, 1814) - Carnevale et al.: 3W.

Holotype: Fig. 8AF-AH, MGPT-PU 130348, late Messinian Lago Mare Event, Cava Serredi, Tuscany, Italy.

Paratypes: 10 specimens: 8 specimens, MGPT-PU 130349, same data as holotype; 2 specimens, MGPT-PU 130350, pre-evaporitic Messinian, Strada degli Archi, Tuscany, Italy.

Referred specimens: 192 specimens: pre-evaporitic Messinian, 15 specimens Strada degli Archi; late Messinian upper evaporite, 2 tentatively assigned specimens Cava Serredi CS 1; late Messinian Lago Mare Event, 1 specimen Podere Torricella, 170 Cava Serredi, Khersonian to early Meotian, 2 specimens Plopease, Romania (LBP-II-0016b, 0040a); late Meotian, 2 specimens Plopease, Romania (LBP-II-0017, 0021).

Etymology: From *exsul* (Latin) = expatriate, referring to the putative migration background of the species in the Mediterranean.

Diagnosis: Otoliths reaching a maximum size of at least 3.0 mm in length; moderately elongate, with OL:OH ranging from 1.25 to 1.40, increasing with size. Dorsal rim relatively regularly curving, smooth in juveniles, crenulated in adults, with broadly rounded predorsal angle. Postdorsal projection distinct, pointed, and distinctly

bent outwards. Preventral projection variably, strong in adults, short in juveniles. Sulcus short, moderately wide and deep (OL2:CL = 1.75–2.0). Sulcus inclination angle 10–15°. Ostial lobe weak; subcaudal iugum moderately long, narrow. Inner face slightly convex, outer face flat to slightly convex. OH:OT = 2.5–2.8.

Description. Moderately sized, robust otoliths reaching a maximum size of about 3.0 mm length (holotype 2.0 mm). OL:OH = 1.30–1.40 in specimens larger than 1.5 mm in length, 1.25–1.35 in specimens smaller than 1.5 mm; OH:OT = 2.5–2.8. Dorsal rim regularly curved with broadly rounded predorsal angle, smooth in specimens smaller than 1.5 mm in length, regularly crenulated or undulating in specimens larger than 1.5 mm. Postdorsal projection distinct, relatively long, with pointed tip, distinctly bent outwards, positioned relatively high. Anterior rim variably inclined depending on strength of preventral projection, mostly without or with indistinct concavity, inclined at 65–85°. Posterior rim inclined at 95–115°, with moderate incision below postdorsal projection at level of caudal tip. Angle of preventral to postdorsal traverse 25–33°. Ventral rim nearly flat or gently curved, horizontal, with sharp, mostly long but sometimes blunt preventral projection and rounded postventral angle.

Inner face slightly bent in horizontal direction, with sulcus median to slightly suprmedian positioned, short, moderately wide and deep and moderately inclined. OL2:CL = 1.75–2.0; inclination angle of ostium equals inclination angle of sulcus at 10–15°. Sulcus with weak or no ostial lobe, and moderately long and narrow subcaudal iugum below cauda. Ventral furrow distinct, running at considerable distance from ventral rim of otolith, turning upwards behind cauda and usually reaching dorsal depression. Dorsal depression relatively large, distinct. Outer face flat to slightly convex, slightly ornamented or smooth.

Discussion. *Zosterisessor* is a monotypic extant genus with *Z. ophiocephalus* known throughout the Mediterranean, Black Sea, and Sea of Azov in inshore brackish, estuarine, and lagoonal waters on mud and eel-grass meadows. Its otoliths are similar to those of the genus *Gobius* but with a relatively short sulcus and a low ostial lobe (Fig. 8AM–AP). *Zosterisessor exsul* represents the only confirmed fossil species of this genus (specimens recorded as *Z. aff. ophiocephalus* by Nolf & Cavallo (1994) likely represent a species of *Gobius*). It occurs first in the pre-evaporitic Messinian in the shallow-water

sediments of Strada degli Archi and is common in certain locations of the Lago Mare Event, e.g., Cava Serredi. Its occurrence in these environments correlates well with the distribution of the extant species. In addition, there are few relatively small specimens found in the Meotian of the Dacic Basin in Romania, indicating that the species likely is of eastern Paratethyan origin. *Zosterisessor exsul* differs from the extant *Z. ophiocephalus* in the thicker appearance (flat to convex outer face vs concave; OH:OT = 2.5–2.8 vs 3.3–3.5) and the usually more distinct preventral projection.

Benthophilus Group

Genus *Benthophilus* Eichwald, 1831

Benthophilus aprutinus n. sp.

Figs. 9R–U

Holotype: Fig. 9R–T, MGPT-PU 130351, late Messinian Lago Mare Event, Le Vicenne, Abruzzo, Italy.

Paratypes: 1 specimen, MGPT-PU 130352, same data as holotype.

Etymology: From Aprutium (Latin) = Abruzzo, referring to the type region.

Diagnosis: High bodied otoliths reaching 1.75 mm in length; OL:OH ranging from 1.0 to 1.1. Outline nearly quadrate or square with well-developed predorsal and postventral angles and short postdorsal and preventral projections. Postdorsal projection positioned high, slightly bent outwards. Sulcus short, wide, shallow (OL2:CL = 2.3–2.4). Sulcus inclination angle about 15°. No developed ostial lobe; no subcaudal iugum; ventral sulcus margin w-shaped. Inner face almost flat, outer face flat to slightly convex. OH:OT about 3.0.

Description. Small, robust otoliths reaching up to 1.75 mm in length (holotype). OL:OH = 1.0–1.1; OH:OT about 3.0. Outline almost quadrate or square. Dorsal rim relatively flat or slightly ascending towards posterior, with median to postdorsal positioned indentation. Predorsal angle well-developed; postdorsal projection very short, blunt, angular, slightly bent outwards, positioned high. Anterior rim nearly vertical, with indentation at level of ostium, inclined at 83–88°. Posterior rim inclined at 93–100°, with distinct incision at level of caudal tip. Preventral projection short, angular; postventral angle well-developed. Angle of preventral to postdorsal traverse 33–36°. Ventral rim nearly flat, slightly undulating.

Inner face very slightly bent in horizontal direction, almost flat, with centrally positioned, short, moderately wide, shallow and moderately inclined sulcus. OL2:CL = 2.3–2.4; inclination an-

gle of sulcus measuring about 15°. Sulcus without ostial lobe, and without subcaudal iugum. Instead ventral margin of cauda slightly convex resulting in w-shaped ventral sulcus margin. Ventral furrow distinct, running at considerable distance from ventral rim of otolith, turning upwards behind cauda but not reaching dorsal depression. Dorsal depression small, indistinct. Outer face slightly convex with a few short radial furrows from incisions of margins.

Discussion. *Bentbophilus aprutinus* is readily recognized as a representative of the genus *Bentbophilus* by the very small sulcus with the typical shape lacking an ostial lobe, lacking a subcaudal iugum, and with a w-shaped ventral sulcus margin. It differs from all known extant and fossil *Bentbophilus* species in the compressed, high-bodied shape. *Bentbophilus aprutinus* is only known from Le Vicenne indicating that fossil *Bentbophilus* species may have had a similarly highly specialized environmental and geographic adaptation as its extant counterparts.

Otoliths of several extant species of the species-rich genus *Bentbophilus* and of the closely related monotypic deepwater Caspian genus *Anatirostrum* are figured for comparison: *Bentbophilus abdurabmanovi* Ragimov, 1978 (Fig. 9V-W), *B. baeri* Kessler, 1877 (Fig. 9X-Y), *B. durrelli* Boldyrev & Bogutskaya, 2004 (Fig. 9Z-AA), *B. leobergi* Berg, 1949 (Fig. 9AB-AC), *B. macrocephalus* (Pallas, 1787) (Fig. 9AD-AE), *B. pinchuki* Ragimov, 1982 (Fig. 9AF-AG), *B. stellatus* (Sauvage, 1874) (Fig. 9AH-AI), *Anatirostrum profundorum* (Berg, 1927) (Fig. 9AJ-AL).

Bentbophilus gibbosus (Pana, 1977)

Figs. 9A-G

- 1977 *Gobius gibbosus* - Pana: pl. 1, figs. 1-9, ?10-14.
 1982b *Gobius gibbosus* Pana, 1977 - Pana: pl. 1, figs. 2-3.
 ?1982b *Gobius ornatus* Gaemers & Schwarzahns, 1973 - Pana: pl. 1, fig. 1.
 2017 *Lesueurigobius* sp. - Colombero et al.: fig. 5.13.

Material: 40 specimens: late Messinian Lago Mare Event, 39 specimens Capanne di Bronzo, Marche, Italy (figured specimens MGPT-PU 130377); Dacian, 1 specimen Plopease, Romania (LPB-II-0027).

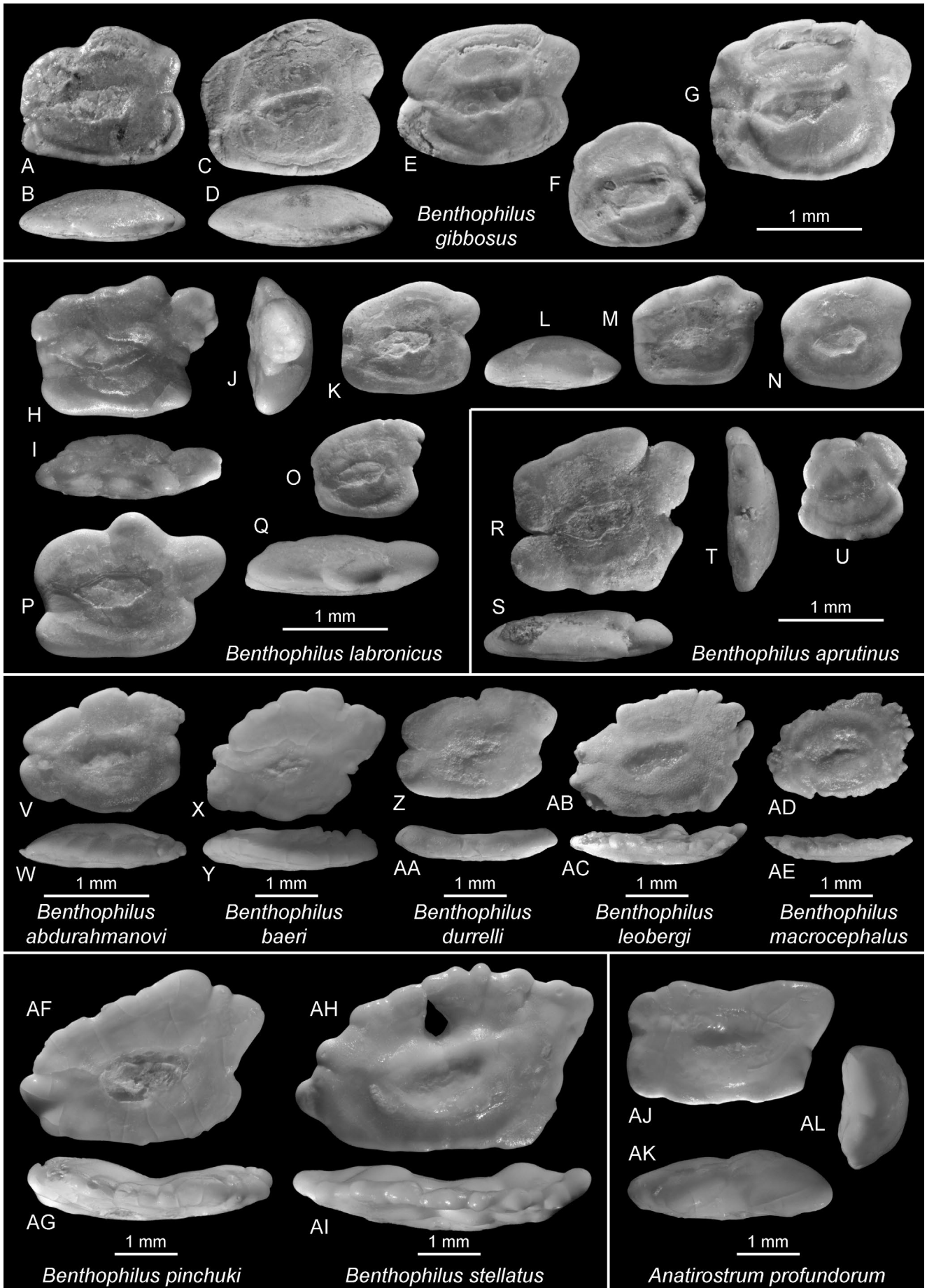
Diagnosis (new): Oval, moderately elongate otoliths reaching 2.0 mm in length; OL:OH ranging from 1.1 to 1.25, increasing in size. Dorsal rim irregular, often anteriorly depressed with step at middorsal position elevating postdorsal rim; predorsal angle rounded. Postdorsal projection positioned high, very short, not bent outwards. Sulcus short, wide, shallow or slightly deepened (OL2:CL = 2.2-2.5). Sulcus inclination angle 10-12°. Ostial lobe and subcaudal iugum not developed; ventral sulcus margin w-shaped. Inner face slightly convex, outer face more strongly convex. OH:OT = 2.4-2.6.

Description. Moderately large, robust otoliths reaching up to about 2.0 mm in length. OL:OH 1.15 to 1.25 in specimens larger than 1.2 mm length and 1.1-1.15 in smaller specimens; OH:OT = 2.4-2.6. Outline oval to rectangular, elongate. Dorsal rim often with characteristic predorsal depression followed by step change about mid-section, otherwise irregularly curved, highest behind its midlength. Predorsal angle well-developed, broadly rounded, sometimes depressed; postdorsal projection very short, not or barely extending beyond postventral angle, not bent outwards. Anterior rim nearly vertical, without marked indentation, inclined at 85-95°. Posterior rim inclined at 85-100°, with distinct concavity at level of caudal tip. Preventral projection short, angular; postventral angle rounded. Angle of preventral to postdorsal traverse 25-33°. Ventral rim slightly curved, smooth.

Inner face slightly convex, with sulcus centrally positioned, short, wide, shallow to slightly deepened and moderately inclined. OL2:CL = 2.2-2.5; inclination angle of sulcus 10-12°. Sulcus without ostial lobe, and without subcaudal iugum. Instead ventral margin of cauda slightly convex resulting in w-shaped ventral sulcus margin. Ventral furrow distinct, running relatively close to ventral rim of otolith, turning upwards behind cauda but

Fig. 9 - *Bentbophilus*.

- A-G) *Bentbophilus gibbosus* (Pana, 1977). A-B) Dacian, Plopease, Romania, LPB-II-0027; C-G) late Messinian, Lago Mare event, Capanne di Bronzo, MGPT-PU 130377 (F reversed).
 H-Q) *Bentbophilus labronicus* n.sp., late Messinian, upper evaporite, Cava Serredi; H-J) holotype, MGPT-PU 130353 (reversed); K-Q) paratypes, MGPT-PU 130354 (M, O reversed).
 R-U) *Bentbophilus aprutinus* n.sp., late Messinian, Lago Mare event, Levicenne; R-T) holotype, MGPT-PU 130351; U) paratype, MGPT-PU 130352 (reversed).
 V-W) *Bentbophilus abdurabmanovi* Ragimov, 1978, Recent, Caspian Sea, Novo Terek river mouth, ZMMU P.15890, SL 33 mm.
 X-Y) *Bentbophilus baeri* Kessler, 1877, Recent, Caspian Sea, off Turkmenistan, ZMMU P.16141, SL 42 mm.
 Z-AA) *Bentbophilus durrelli* Boldyrev & Bogutskaya, 2004, Recent, lower Don river, paratype, ZMMU P.21611, SL 53 mm.
 AB-AC) *Bentbophilus leobergi* Berg, 1949, Recent, Caspian Sea, Oka river mouth, ZMMU P.22625, SL 56 mm.
 AD-AE) *Bentbophilus macrocephalus* (Pallas, 1787), Recent, Caspian Sea, Novo Terek river mouth, ZMMU P.15889, SL 38 mm.
 AF-AG) *Bentbophilus pinchuki* Ragimov, 1982, Recent, Caspian Sea, off Turkmenistan, ZMMU P.16127, SL 60 mm.
 AH-AI) *Bentbophilus stellatus* (Sauvage, 1874), Recent, Azov Sea, ZMMU P.11023, SL 100 mm.
 AJ-AL) *Anatirostrum profundorum* (Berg, 1927), Recent, Caspian Sea, Gilan, Iran, CMNFI 1999-0023.1.



not reaching dorsal depression. Dorsal depression large, indistinct. Outer face smooth and considerably more convex than inner face.

Discussion. *Benthophilus gibbosus* is characterized by a short postdorsal projection and the thick appearance with a distinctly convex outer face. It thus resembles the extant *Benthophilus abdurahmanovi* (Fig. 9V-W) and *Anatirostrum profundorum* (Fig. 9AJ-AL). The original description of Pana (1977) is not very conclusive, and she mentioned a high degree of variability. Nolf (2013) felt that the specimens figured by Pana (1977) may represent different species and regarded *Gobius gibbosus* as doubtful species. We retrieved one specimen from the same general geographic and stratigraphic position as Pana's holotype from her collection for review, bearing her identification as *Gobius gibbosus* and indeed resembling the specimens she characterized as typical (Fig. 9A-B). We have therefore re-defined the diagnosis based on her retrieved original specimen.

Abundant material of *Benthophilus gibbosus* was also recovered from the Lago Mare interval of Capanne di Bronzo, and a single specimen is recorded from Moncuoco Torinese (Colombero et al. 2017), once again exemplifying the high degree of environmental specialization of the species in this genus. It also is a further indication of Paratethyan influence in the Mediterranean at the time. The specimens from Capanne di Bronzo show a rather high degree of variability, almost to the extent figured by Pana (1977), which suggests that this species indeed sported a considerable variability and that most of her records from Romania may have been justified. The majority of the specimens from Capanne di Bronzo are relatively large, but a few were found at sizes of 1 to 1.2 mm length (Fig. 9F), which distinctly differ from the larger ones in being more compressed and having a relatively longer sulcus. We consider this as an ontogenetic effect.

Benthophilus labronicus n. sp.

Figs. 9 H-Q

- 2008 *Gobius* aff. *truncatus* Schwarzhans, 1978 - Carnevale et al.: fig. 3S.
 2008 “Gobiidarum” aff. *weileri* (Bauza-Rullan, 1955) - Carnevale et al.: fig. 3T.
 2008 Gobiidae indet. - Carnevale et al.: fig. 3X.

Holotype: Fig. 9H-J, MGPT-PU 130353, late Messinian, sub-stage 3.1, Cava Serredi near Livorno, Tuscany, Italy.

Paratypes: 20 specimens, late Messinian, sub-stage 3.1: 19 specimens, MGPT-PU 130354, same data as holotype; late Messin-

ian Lago Mare Event, 1 specimen, MGPT-PU 130355, Le Vicenne, Abruzzo, Italy.

Etymology: From Liburna (Latin) = Livorno, referring to the type location.

Diagnosis: Moderately elongate otoliths reaching 1.8 mm in length; OL:OH ranging from 1.15 to 1.35, increasing with size. Dorsal rim very irregular, nearly smooth, crenulated and with or without prominent bulges; predorsal angle often more projecting than preventral angle. Postdorsal projection positioned high, broad, more strongly projecting in large specimens, slightly bent outwards. Sulcus short, moderately wide, shallow (OL2:CL = 2.3-2.9). Sulcus inclination angle 5-10°. Ostial lobe and subcaudal iugum not developed; ventral sulcus margin w-shaped. Inner face slightly convex, outer face more strongly convex. OH:OT = 2.0-2.3.

Description. Small, robust otoliths reaching up to about 1.8 mm in length (holotype 1.75 mm). OL:OH 1.22 to 1.35 in specimens larger than 1.2 mm in length and 1.15-1.25 in smaller specimens, mainly caused by increasing expansion of postdorsal projection in larger specimens; OH:OT = 2.0-2.3. Dorsal rim very irregularly shaped, often with large bulge slightly behind middle; else smooth or with irregular crenulation. Predorsal angle well-developed, usually more projecting than preventral angle; postdorsal projection moderately long in small specimens (Fig. 9M-O), distinctly increasing with size (Figs. 9H, P), not bent outward in small specimens, slightly bent outward in large specimens. Anterior rim vertical or forward inclined, rarely with marked indentation, inclined at 90-100°. Posterior rim inclined at 95-115°, with distinct, broad concavity at level of caudal tip. Preventral projection short, angular; postventral angle mostly rounded. Angle of preventral to postdorsal traverse 25-33°. Ventral rim straight, smooth.

Inner face slightly convex, increasingly with size, smooth, with sulcus centrally positioned, short, moderately wide, shallow and only slightly inclined. OL2:CL = 2.3-2.9; inclination angle of sulcus 5-10°. Sulcus without ostial lobe and without subcaudal iugum. Ventral margin of sulcus irregularly wavy or w-shaped. Ventral furrow feeble, running at some distance from ventral rim of otolith, only slightly turning upwards behind cauda rarely reaching caudal tip. Dorsal depression very indistinct, often barely visible or absent. Outer face more strongly convex than inner face, smooth or irregularly ornamented.

Discussion. *Benthophilus labronicus* is a third species of the genus in the MSC interval and found primarily in the deposits of the sub-stage 3.1 of Cava Serredi. It is recognized by the massive post-

dorsal projection in larger specimens (OL > 1.2 mm) and the thick appearance. The outline of the otoliths and the ratio OL:OH shows a pronounced ontogenetic allometry, which indicates that specimens of a size of 1.7 mm length are morphologically mature and that *B. labronicus* was indeed a small species.

Genus *Caspiosoma* Iljin, 1927

***Caspiosoma lini* n. sp.**

Figs. 10A–J

2010 “genus Gobiidarum” sp. 4 - Girone, Nolf & Cavallo: figs. 10g1-2.

Holotype: Fig. 10A–B, IRSNB P 9949, pre-evaporitic Messinian, Metalgrande near Verduno, Piedmont, Italy.

Paratypes: 9 specimens: pre-evaporitic Messinian, 2 specimens IRSNB P 9950–9951, same data as holotype, 1 specimen AM-PG(V)2342, Faneromeni, 4 specimens AMPG(V)2343, Agios Myron; Khersonian to early Meotian, 2 specimens LBP-II-0001b and 0028a, Plopease, Romania.

Etymology: Species named after Chien-Hsiang Lin (Taiwan) in recognition of his contribution to the knowledge of late Miocene otoliths of Italy.

Diagnosis: Compact and compressed otoliths measuring up to 2.0 mm in length; OL:OH ranging from 1.03 to 1.15. Dorsal rim very regularly curved, smooth or slightly undulating; predorsal angle broadly rounded. Postdorsal projection indistinct, short, completely rounded or only very slightly projecting, positioned high, not bent outwards. Sulcus very short, small, unstructured oval, shallow (OL2:CL = 2.5–3.0). Sulcus inclination angle 8–15°. No ostial lobe; no subcaudal iugum; ventral margin of sulcus unstructured. Inner face flat but area around sulcus bulged, outer face strongly convex. OH:OT = 2.5–2.8.

Description. Moderately sized, robust otoliths reaching up to about 2.0 mm in length (holotype 1.6 mm). OL:OH = 1.03–1.15; OH:OT = 2.5–2.8. Dorsal rim very regularly curved, highest at about its midlength, smooth or slightly undulating, rarely somewhat depressed (Fig. 10F). Predorsal angle broadly rounded; pre-ventral angle usually more pronounced; postdorsal projection broadly rounded, almost absent (Fig. 10A), or very small and positioned high (Figs. 10C, F, I), not bent outwards. Anterior rim rounded, without marked indentation, inclined at 87–95°. Posterior rim rounded, inclined at 85–95°, without incision or with very broad and feeble concavity. Angle of pre-ventral to postdorsal traverse 30–33°. Ventral rim slightly bent, smooth; post-ventral angle rounded.

Inner face essentially flat, but area around sulcus bulged with centrally positioned, very small,

shallow and moderately inclined sulcus. OL2:CL = 2.5–3.0; inclination angle of sulcus 8–15°. Sulcus without ostial lobe, without subcaudal iugum, with regularly curved ventral margin resulting in a regular oval shape of the sulcus. Ventral furrow broad, mostly well-developed, running at some distance from ventral rim of otolith, turning upwards around sulcus anteriorly and posteriorly to meet the narrow, distinct dorsal depression. Outer face strongly convex, smooth.

Discussion. *Caspiosoma lini* resembles *Hoseichthys brioche* at first sight because of its compressed and rounded shape and the small sulcus. However, it is readily distinguished from *H. brioche* by the completely unstructured, small and oval sulcus and the complete absence of a subcaudal iugum. Its placement with the Ponto-Caspian genus *Caspiosoma* is based on similarities of the otolith outline, shapes of inner and outer faces, and the small sulcus without ostial lobe or subcaudal iugum. However, the unique extant *Caspiosoma* species, *C. caspium* (Kessler, 1877), has otoliths with a longer sulcus and a distinct w-shaped ventral sulcus margin (Fig. 10AD–AF). For further comparison, extant otoliths of the rare Ponto-Caspian *Benthophiloides brauneri* Beling & Iljin, 1927 (Fig. 10AG–AI) are figured, as well as those of two endemic Italian freshwater gobies that were considered to be related to the Ponto-Caspian gobies by Thacker & Roje (2011), i.e., *Padogobius bonelli* (Bonaparte, 1846) (Fig. 10AJ–AK) and *Padogobius nigricans* (Canestrini, 1867) (Fig. 10AL–AN).

Caspiosoma lini appears to be a widespread but uncommon species in shallow marine settings in the Mediterranean and has also been found in the Khersonian to early Meotian of the Dacic Basin of the Eastern Paratethys. It was not present during the late Messinian Lago Mare interval (substage 3.2 of Roveri et al. 2014), where it becomes replaced by *Caspiosoma paulisulcata* (see below).

***Caspiosoma paulisulcata* n. sp.**

Figs. 10K–T

2008 *Gobius* sp. 2 - Carnevale et al.: fig. 6K.

Holotype: Fig. 10M–O, MGPT-PU 130356, late Messinian substage 3.1, Cava Serredi (CS 1 level after Carnevale et al. 2008) near Livorno, Tuscany, Italy.

Paratypes: 10 specimens MGPT-PU 130357, same data as holotype.

Referred specimens: 51 specimens: late Messinian substage 3.1, 48 specimens same data as holotype; late Messinian Lago Mare Event, 1 specimen Cava Serredi, 2 specimens Podere Torricella.

Etymology: From paulus (Latin) = small and sulcatus (Latin) = adjective referring to the sulcus, named after the small sulcus of this species.

Diagnosis: Compact otoliths reaching 1.5 mm in length; OL:OH vary variable, ranging from 1.05 to 1.35. Dorsal rim shallow, nearly flat or with obtuse postdorsal angle, smooth; predorsal angle rounded. Postdorsal projection indistinct, short, completely rounded, not bent outward. Sulcus very short, small, oval, and shallow (OL2:CL = 2.3-2.8). Sulcus inclination angle 7-12°. Ostial lobe and subcaudal iugum absent; ventral margin of sulcus usually w-shaped or flat. Inner face almost entirely flat, smooth, with weak ventral furrow and dorsal depression; outer face strongly convex. OH:OT = 2.0-2.2.

Description. Small, very robust otoliths reaching up to about 1.5 mm in length (holotype 1.4 mm). OL:OH very variable, 1.05-1.35, small specimens (Fig. 10T) more compressed, large specimens (Fig. 10K) more elongated; OH:OT = 2.0-2.2. Dorsal rim shallow, nearly horizontal or slightly ascending to broad, obtuse, rounded postdorsal angle, smooth. Predorsal angle mostly distinct, rounded; preventral angle rounded orthogonal; postdorsal projection very short, almost absent rounded, not bent outward. Anterior rim vertical, without marked indentation, inclined at 88-93°. Posterior rim straight, inclined at 88-102°, with or without small incision at level of sulcus termination. Angle of preventral to postdorsal traverse 28-35°. Ventral rim straight, horizontal, smooth; postventral angle rounded.

Inner face almost entirely flat and smooth; area around sulcus not specifically elevated. Sulcus centrally positioned, very small, shallow and moderately inclined. OL2:CL = 2.3-2.8; inclination angle of sulcus 7-12°. Sulcus without ostial lobe and subcaudal iugum, with either flat or more commonly weak w-shaped ventral margin. Ventral furrow indistinct, when discernable half-moon shaped and closer to sulcus than ventral rim of otolith; dorsal depression not discernable. Outer face very strongly convex, smooth.

Discussion. *Caspiosoma paulisulcata* is notable for its unusually high degree of variability particularly concerning the ratio OL:OH. However, there is an evident cline of morphological variation for this common species that there can be little doubt that we are dealing with a single species. *Caspiosoma paulisulcata* is similar to the pre-evaporitic Messinian species *C. lini*, from which it differs in having a flat and smooth inner face with indistinct dorsal depression and weak ventral furrow very close to the sul-

cus (vs distinct ventral furrow and dorsal depression and area around sulcus bulged), the often w-shaped ventral margin of the sulcus (vs regular oval outline), and the much thicker appearance (OH:OT = 2.0-2.2 vs 2.5-2.8). *Caspiosoma paulisulcata* may not be directly related to the earlier *C. lini* since the common w-shape of the ventral sulcus margin found in *C. paulisulcata* is considered less advanced than the oval shaped sulcus of *C. lini*.

Similar otoliths very likely representing species of *Caspiosoma* have been described by Klein (1960) from the Pliocene of Azerbaijan as *Gobius* aff. *pretiosus* Procházka, 1893 and *Gobius gansi* Suzin in Klein, 1960. These specimens are morphologically intermediate between *C. paulisulcata* and the extant *C. caspius*.

Caspiosoma cf. *paulisulcata* n. sp.

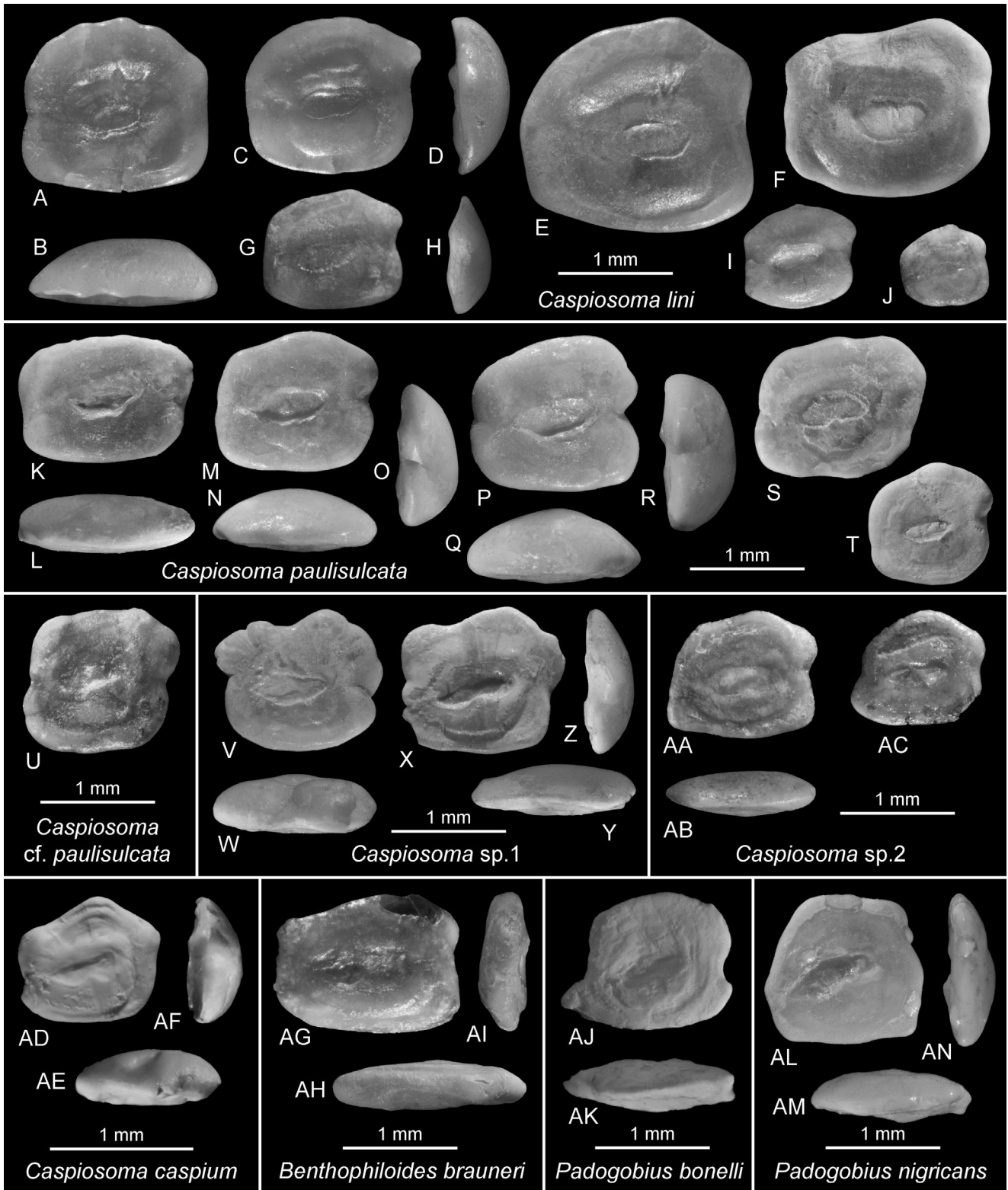
Fig. 10U

Material: 2 specimens: 1 specimen early Meotian, Adopetoanei, Romania (LBP-II-0024); 1 specimen late Meotian, Foltea, Romania (LBP-II-0026).

Discussion. Two specimens from the Meotian of Romania (Dacic Basin) resemble the Lago

Fig. 10 - *Caspiosoma*.

- A-J) *Caspiosoma lini* n.sp. A-E) Pre-evaporitic Messinian, Metalgrande; A-B) holotype, IRSNB P 9949; C-E) paratypes, IRSNB P 9950-9951 (C-D reversed); F-I) pre-evaporitic Messinian, Agios Myron, AMPG(V)2343 (G-H reversed); J) Khersonian to early Meotian, Plopease, Romania, LPB-II-0001b.
- K-T) *Caspiosoma paulisulcata* n.sp., late Messinian, upper evaporite, Cava Serredi; M-O) holotype, MGPT-PU 130356 (reversed); K-L, P-T) paratypes, MGPT-PU 130357 (K-L, S-T reversed).
- U) *Caspiosoma* cf. *paulisulcata* n.sp., Meotian 1 (lower Meotian), Adopetoanei, Romania, LPB-II-0024 (reversed and filtered).
- V-Z) *Caspiosoma* sp. 1, late Messinian; V-W) upper evaporite, Cava Serredi, MGPT PU 130378; X-Z) Lago Mare event, Ciabot Cagna, MGPT-PU 130379 (reversed).
- AA-AC) *Caspiosoma* sp. 2, Dacian, Plopease, Romania, LBP-II-0018b and 0018d (AA-AB reversed, AC filtered).
- AD-AF) *Caspiosoma caspium* (Kessler, 1877), Recent, Caspian Sea, Diestroveksi liman, ZMMU P.13965, SL 28.5 mm.
- AG-AI) *Bentrophiloides brauneri* Beling & Iljin, 1927, Recent, Tendrovska Bay near Kherson, Ukraine, NMNH NASU 5136, SL 50 mm (AG filtered).
- AJ-AK) *Padogobius bonelli* (Bonaparte, 1846), Recent, Bergamo, Italy, BMNH 1910.7.27.2-11.
- AL-AN) *Padogobius nigricans* (Canestrini, 1867), Recent, Arno, Italy, leg. Ahnelt.



Mare species *Caspiosoma paulisulcata*, although they are too poorly preserved for an unambiguous identification. They are also much compressed even in comparison to most of the Lago Mare specimens. Therefore, their allocation remains tentative until further material will be available.

***Caspiosoma* sp. 1**

Figs. 10V–Z

Material: 10 specimens, late Messinian: upper evaporite, 8 specimens Cava Serredi; Lago Mare Event, 1 specimen Cava Serredi, 1 specimen Ciabot Cagna.

Discussion. A few specimens depart morphologically so much from the coeval *C. paulisulcata* despite the high degree of variability of the latter that they probably represent an additional *Caspiosoma* species. These specimens are characterized by a larger, deeper, and more clearly structured sulcus with a clearly cut w-shaped ventral margin, and a conspicuous dorsal rim which is intensely undulating and shows a distinct predorsal depression. The latter character is occasionally seen in *C. lini* (Fig. 10f) but has not been observed in confirmed specimens of *C. paulisulcata*. The larger sulcus with the clearly w-shaped ventral margin resembles the extant *C. caspium*.

Caspiosoma sp. 2

Figs. 10AA-AC

- 1995 *Pomatoschistus pretiosus* (Procházka, 1893) - Pana: pl. 1, figs. 11-5.
2008 *Gobius* sp. 1 - Carnevale et al.: fig. 6j.

Material: 7 specimens: late Messinian Lago Mare Event, 1 specimen Podere Torricella; Dacian, 6 specimens Plopease, Romania, LBP-II-0004a-b, 0041, 0011a, 0018b-d.

Discussion. Pana (1995) figured a suite of gobiid otoliths, which are quite distinctive from other fossil specimens attributed to *Caspiosoma*. They are thinner (OH:OT = 2.6-3.0) than *C. lini* and *C. paulisulcata*, have a larger sulcus with a clear w-shaped ventral margin and a relatively well-developed preventral projection resulting in an inclination of the anterior rim of 70-75°. Clearly, these specimens represent a different species in the group, resembling the extant species of the genera *Caspiosoma* and *Benthophiloides*, but the material available is not suitable for defining such new species. There is also one specimen from the Lago Mare interval at Podere Torricella that seems to represent the same species, indicating the potential of further faunal exchange during that time interval. It further documents that the two genera (*Caspiosoma* and *Benthophiloides*) may have been more speciose and diverse during the late Miocene and early Pliocene than they are today, with one and two species respectively.

Thorogobius Group
Thorogobius Miller, 1969

Thorogobius petilus n. sp.

Figs. 11D-H

Holotype: Fig. 11D-F, MGPT-PU 130358, pre-evaporitic Messinian, Botro Rosso, Monti Livornesi, Tuscany, Italy.

Paratypes: 1 specimen, MGPT-PU 130359, same data as holotype.

Etymology: From *petilus* (Latin) = thin, meager, referring to the thin appearance and flat inner and outer faces.

Diagnosis: Large, thin otoliths reaching a maximum size of 3.15 mm in length; elongate and OL:OH ranging from 1.3 to 1.5. Predorsal angle distinct; postdorsal projection moderate, rounded not bent outward. Anterior rim blunt, vertical. Sulcus short, narrow, moderately deep (OL2:CL = 1.85-2.0). Ostial lobe moderate; subcaudal iugum absent. Inner and outer faces completely flat. OH:OT = 4.5-4.8.

Description. Large, thin otoliths reaching 3.15 mm in length (holotype 2.9 mm). OL:OH = 1.3-1.5; OH:OT = 4.5-4.8. Dorsal rim anteriorly somewhat depressed. highest in broad middorsal section and variably developed postdorsally, smooth or slightly undulating. Predorsal angle relatively low and obtuse, rounded; postdorsal projection moderately long, broadly rounded, not bent outwards, positioned higher than predorsal angle. Anterior rim near vertical, nearly straight, sometimes with indistinct broad and shallow concavity, inclined at 88-93°. Posterior rim inclined at 105-118°, with shallow incision below postdorsal projection below level of caudal tip. Angle of preventral to postdorsal traverse about 25°. Ventral rim gently curved, horizontal, with rounded preventral and postventral angles.

Inner face completely flat. Sulcus central, small, narrow, slightly deepened, sole-shaped, and moderately inclined; OL2:CL = 1.85-2.0; inclination angle of ostium 20-25°; inclination of sulcus 11-14°. Sulcus with moderately developed ostial lobe, narrow cauda and subcaudal iugum absent. Ventral furrow feeble, close to ventral rim of otolith, turning upward behind cauda but not reaching dorsal depression. Dorsal depression small, rather distinct. Outer face completely flat, smooth.

Discussion. *Thorogobius petilus* is one of the thinnest and flattest otoliths so far known from gobioids. The completely flat inner and outer faces are very characteristic. Other distinct characters that make this species unmistakable are the small sulcus without subcaudal iugum, the small dorsal depression, and the rounded postdorsal projection.

Thorogobius truncatus (Schwarzahans, 1978)

Fig. 11A-C

- 1978 *Gobius truncatus* - Schwarzahans: figs. 119-120, 146.

- ?1994 *Gobius truncatus* Schwarzhans, 1978 - Nolf & Cavallo: pl. 8, fig. 3.
 1998 *Gobius truncatus* Schwarzhans, 1978 - Nolf, Mané & Lopez: pl. 7, fig. 11.
 2013a *Gobius niger* Linnaeus, 1758 - Agiadi et al.: fig. 8/15.

Material: 1 specimen, Zanclean, Voutes.

Discussion. *Thorogobius truncatus* is a typical representative of the genus characterized by the absence of an ostial lobe and of a subcaudal iugum. Other typical features are the distinct predorsal angle projecting beyond the preentral angle and a relatively strong postdorsal projection that is only slightly bent outward. So far, *T. truncatus* has only been observed since the Zanclean.

Chromogobius Group

Genus *Chromogobius* de Buen, 1930

Chromogobius zebratus (Kolombatovic, 1891)

Fig. 11I-K

- 1994 ?*Mesogobius* sp. - Nolf & Cavallo: pl. 8, fig. 7.
 2006 *Callogobius* sp. - Nolf & Girone: pl. 2, fig. 4-5.
 2020 *Chromogobius zebratus* (Kolombatovic, 1891) - Agiadi et al.: figs. 3b-c.

Material: 2 specimens, Zanclean, Agia Triada.

Discussion. Typical elongate *Chromogobius* otoliths with a moderate postdorsal projection and a small sulcus with a very weak ostial lobe and a w-shaped ventral sulcus margin. Distinction of genera and species of the *Chromogobius* Group from those of the *Benthophilus* Group rely on subtle differences of otolith and sulcus outlines and proportions (see above and Schwarzhans et al. 2020).

Genus *Odondebuena* de Buen, 1930

Odondebuena cf. *balearica* (Pellegrin & Fage, 1907)

Figs. 11L-P

- 2017 “Gobiida” *brioche* Lin, Girone & Nolf, 2015 - Agiadi et al.: fig. 4/10 (marked as “genus Gobiidarum” sp. 2 on the plate).

Material: 14 specimens, Potamida: 8 specimens late Tortonian; 6 specimens pre-evaporitic Messinian.

Discussion. Compressed otoliths with a moderately developed preentral projection and a marked postdorsal bulge; sulcus narrow with a very shallow ostial lobe, subcaudal iugum absent and a

w-shaped ventral margin. These otoliths are similar to those of the *Caspiosoma* species (see above). *Odondebuena* otoliths appear to differ from *Caspiosoma* otoliths due to the presence of a preentral projection (which, however, is also present in the supposed *Caspiosoma* sp. 2, see above), and the narrower sulcus that still shows a weakly developed ostial lobe. The specimens from Potamida are all relatively small (OL < 1 mm) and only few are reasonably preserved. Therefore, their alignment to the extant species remains tentative.

Zebrus de Buen, 1930

Zebrus zebrus (Risso, 1827)

Fig. 11Q-S

Material: 3 specimens: 1 specimen pre-evaporitic Messinian, Agios Myron; 2 specimens Zanclean, 1 specimen Agia Triada, 1 specimen Voutes.

Discussion. Otoliths of *Zebrus zebrus* are characterized by a compressed shape in combination with equally pointed preentral and postdorsal projections and a short sulcus without subcaudal iugum, with a low ostial lobe and broad w-shaped ventral margin.

Callogobius Lineage

Genus *Callogobius* Bleeker, 1874

Callogobius weileri (Bauza-Rullan, 1955)

Figs. 11T-W

- 1955 *Gobius weileri* - Bauza-Rullan: pl. 7, figs. 6-9.
 1980 “genus Gobiidarum” sp. 1 - Nolf & Martinell: pl. 5, figs. 11-16.
 1986 *Gobiidarum weileri* Bauza-Rullan, 1955 - Schwarzhans 1986: pl. 6, fig. 74.
 1989 “genus Gobiidarum” *weileri* (Bauza-Rullan, 1955) - Nolf & Cappetta: pl. 17, figs. 16-17.
 1994 “genus Gobiidarum” *weileri* Bauza, 1955 - Nolf & Cavallo: pl. 8, fig. 10.
 2000 “genus Gobiidarum” *weileri* (Bauza, 1955) - Nolf & Girone: pl. 3, figs. 15-16.
 ?2013 *Callogobius weileri* (Bauza-Rullan, 1955) - Schwarzhans: pl. 7, fig. 17.
 2017 “*Gobius*” aff. *weileri* Bauza-Rullan, 1955 - Lin et al.: fig. 11N.

Material: 2 specimens: 1 specimen pre-evaporitic Messinian, Botro Rosso; 1 specimen Zanclean, Agia Triada.

Discussion. *Callogobius weileri* is remarkable for its very small, oval, completely unstructured sulcus positioned on the center of a rather elongate otolith with a blunt anterior rim and a slightly

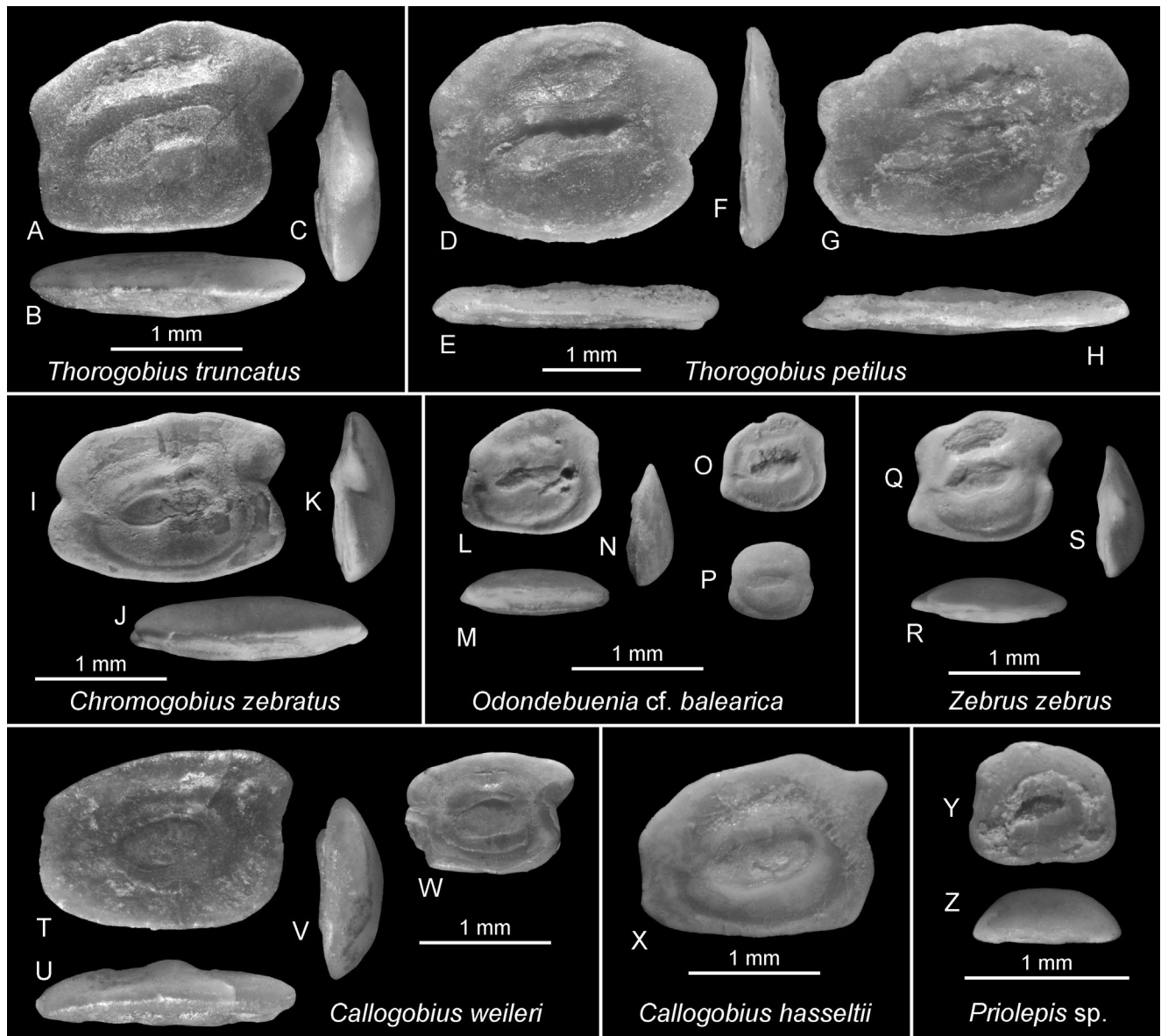


Fig. 11 - *Thorogobius*, *Chromogobius*, *Callogobius* and *Priolepis* groups.

A-C) *Thorogobius truncatus* (Schwarzahans, 1978), Zanclean, Voutes, AMPG(V)2344 (reversed).

D-H) *Thorogobius petilus* n.sp., pre-evaporitic Messinian, Botro Rosso; D-F) holotype, MGPT-PU 130358; G-H) paratype, MGPT-PU 130359 (reversed).

I-K) *Chromogobius zebratus* (Kolombatovic, 1891), Zanclean, Agia Triada, AMPG(V)2345 (reversed).

L-P) *Odondebuena* cf. *balearica* (Pellegrin & Fage, 1907); L-O) pre-evaporitic Messinian, Potamida, AMPG(V)2346; P) late Tortonian, Potamida, AMPG(V)2347.

Q-S) *Zebrus zebrus* (Risso, 1827), pre-evaporitic Messinian, Agios Myron, AMPG(V)2348.

T-W) *Callogobius weileri* (Bauza-Rullan, 1955), T-V) pre-evaporitic Messinian, Botro Rosso, MGPT-PU 130380 (reversed); W) Zanclean, Agia Triada, AMPG(V)2349 (reversed).

X) *Callogobius hasseltii* (Bleeker, 1851), Recent, Philippines, BSKU 100526.

Y-Z) *Priolepis* sp., pre-evaporitic Messinian, Agios Myron, AMPG(V)2350 (reversed).

projecting postdorsal angle. These very typical otoliths have been commonly recorded from the early Pliocene (Zanclean) to the early middle Pleistocene (Santerian) (Nolf & Girone 2000). It represents one of only few exotic gobioid occurrences in the Neogene of the Mediterranean. The specimen from

the pre-evaporitic Messinian of Botro Rosso and a tentatively assigned specimen from the late Tortonian figured by Lin et al. (2017) represent the only records of the species before the onset of the MSC. A specimen of *Callogobius weileri* recorded from the middle Miocene of Gabon (Schwarzahans 2013)

differs somewhat in having a longer sulcus and a projecting predorsal angle, and it therefore could in fact represent a different species of *Callogobius*. For comparison, we have figured an extant specimen of the type species - *Callogobius hasseltii* (Bleeker, 1851) (Fig. 11X).

Priolepis Lineage

Genus *Priolepis* Valenciennes, 1837

Priolepis sp.

Fig. 11Y-Z

Material: 2 poorly preserved specimens from the pre-evaporitic Messinian, Agios Myron.

Discussion. Extant species of *Priolepis* are usually reef associated. The earliest record of a *Priolepis* otolith dates back to the Badenian of the Central Paratethys (Schwarzahns et al. 2020). The poorly preserved specimens now identified from the pre-evaporitic Messinian nevertheless show the characteristic bean-shaped sulcus and the ventral furrow running very close to the sulcus and joining up with the narrow dorsal depression.

Pomatoschistus Lineage

Deltentosteus Group

Genus *Buenia* Iljin, 1930

Buenia affinis (Kolombatovic, 1891)

Figs. 12A-O (12A-D, I extant; 12E-H, J-O fossil)

Material: 13 specimens: pre-evaporitic Messinian, 5 specimens Agios Myron; Zanclean, 8 specimens Voutes.

Discussion. Otoliths of *Buenia affinis* are small, barely exceeding 1 mm in length, with equally convex inner and outer faces, and with a smooth inner face with the shallow sulcus at the level of the remainder of the inner face. The ventral furrow is feeble and follows the otolith rims at close distance around the sulcus up to the dorsal depression. The ratio OL:OH is slightly increasing with size, from 0.95 at 0.85 mm in length (Fig. 12O) to nearly 1.10 above 1.0 mm in length (Fig. 12H). The compressed smaller specimens are similar in proportions to the otoliths of the extant *B. massutii* Kovačić, Ordines & Schlieven, 2017 (Fig. 12P, refigured from Lombarte et al. 2006). Otoliths of *Buenia affinis* differ from those of *B. massutii* in having a distinctly wider

er sulcus, even though the expansion of the ostial lobe is quite variable as can be seen in the figures of the extant specimens (Figs. 12A, D, I). The fossil specimens from the Zanclean and the pre-evaporitic Messinian of Greece fit well with the observed variability of the extant specimens. The three extant Mediterranean species of *Buenia* have been reported from different water depths (Kovačić et al. 2017, 2018) indicating that bathymetric segregation may play a role in the speciation of this genus.

Buenia pisiformis n. sp.

Figs. 12W-AD

Holotype: Fig. 12W-Y, AMPG(V)2354, late Tortonian, Potamida, Greece.

Paratypes: 5 specimens: 3 specimens AMPG(V)2355, same data as holotype; 2 specimens AMPG(V)2356, pre-evaporitic Messinian, Potamida.

Etymology: From pisa (Latin) = pea, referring to the pea-like appearance of the otolith and its very small sulcus.

Diagnosis: Small, high bodied, compact otoliths reaching about 0.9 mm in length; OL:OH ranging from 0.89 to 0.97. Dorsal rim high, rounded. All rims gently curving without prominent angles or projections. Sulcus extremely small, steeply inclined, eccentrically forward positioned on inner face, shallow (OL:CL = 2.6-2.9; ostium inclination angle 25-33°). Ventral margin of sulcus flat or slightly concave, dorsal margin regularly curved; no subcaudal iugum. Inner and outer faces equally convex, smooth. OH:OT = 2.2-2.5.

Description. Small, high bodied, thick otoliths reaching about 0.9 mm in length (holotype 0.85 mm). OL:OH = 0.89-0.97; OH:OT = 2.2-2.5. All rims gently curving without prominent angles, projections or incisions, smooth. Anterior rim almost vertically inclined at 90-97°; posterior rim vertical. Angle of preventral to postdorsal traverse 38-45°.

Inner face strongly convex, smooth. Sulcus distinctly eccentrically forward positioned, extremely small, shallow, and pea-shaped with flat or slightly concave ventral and regularly curved dorsal margins, steeply inclined; OL:CL = 2.6-2.9; inclination angle of ostium 25-33°. Ventral furrow rather feeble, following close otolith rims all around otolith including through a barely discernable, shallow dorsal depression. Outer face convex, smooth.

Discussion. *Buenia pisiformis* is easily recognizable by its extremely small, steeply inclined, eccentrically positioned sulcus. The small size of the sulcus may have resulted from a complete reduction of the cauda, which would explain the eccentric forward position of the sulcus as well as its pea-shape.

***Buenia* sp.**

Figs. 12Q-V

- 2014 *Pomatoschistus quagga* (Heckel, 1837) - Schwarzahans: pl. 12, figs. 7-8.
 2017 “genus Gobiidarum” sp. 1 - Agiadi et al.: figs. 4/5-6.

Material: 3 specimens, late Tortonian, Potamida.

Discussion. These specimens resemble the extant *B. affinis* in the general appearance and the shape and size of the sulcus; however, they are more compressed (OL:OH = 0.94-0.96) at size ranges from 0.8 to 1.3 mm in length. These specimens probably represent an additional *Buenia* species in the late Miocene that differs from *B. pisiiformis* in having a larger and less forward, and not eccentrically positioned sulcus (OL2:CL = 1.9-2.1 vs 2.6-2.9) and in being thinner (OH:OT = 2.9-3.0 vs 2.2-2.5).

Comments on other fossil otolith occurrences of *Buenia*

Buenia otoliths have not been recognized in the fossil record until recently and have commonly been confused with *Pomatoschistus* otoliths. The main distinguishing features are a distinctly convex inner face with a shallow and smooth sulcus in *Buenia*, while in *Pomatoschistus* the inner face is nearly flat and the sulcus is deep. The earliest reliable identification of the genus is *Buenia rudolticensis* (Procházka, 1900) from the early Badenian, following the revision of Schwarzahans et al. (2020). Two additional species described by Schwarzahans (2014) from the Serravallian of SE-Turkey should also be referred to *Buenia*: *B. rueckertae* (Schwarzahans, 2014) originally described as *Pomatoschistus rueckertae*, and *Buenia* sp. originally described as *Pomatoschistus quagga* (Heckel, 1837). The latter is consistent with *Buenia* sp. described above from the Tortonian of Potamida and may represent a new still undescribed species.

Genus *Deltentosteus* Gill, 1863

***Deltentosteus quadrimaculatus* (Valenciennes, 1837)**

Figs. 12AE-AJ

- 1978 *Pomatoschistus telleri* (Schubert, 1906) - Schwarzahans: fig. 118.
 1980 “genus Gobiidarum” sp. 2 - Nolf & Martinell: pl. 5, figs. 17-19.
 1989 *Pomatoschistus* sp. - Nolf & Cappetta: pl. 17, fig. F.
 1994 *Deltentosteus* sp. - Nolf & Cavallo: pl. 8, figs. 4-5.

- 2000 *Deltentosteus* aff. *quadrimaculatus* Valenciennes, 1837 - Nolf & Girone: pl. 3, figs. 5-12.
 2017 *Deltentosteus* aff. *quadrimaculatus* (Valenciennes, 1837) - Lin et al.: fig. 11D.
 2020 *Deltentosteus quadrimaculatus* (Valenciennes, 1837) - Agiadi et al.: figs. 3d-e.

Material: 17 specimens: late Tortonian, 5 specimens Stazano; pre-evaporitic Messinian, 5 specimens Botro Rosso, 2 specimens Potamida, 3 specimens Borelli; Zanclean, 2 specimens Agia Triada.

Discussion. *Deltentosteus* otoliths are among the largest in the *Pomatoschistus* Lineage and are easily recognized by the unique combination of a convex, smooth inner face with shallow sulcus showing a prominent often pointed or angular ostial lobe, and a broad postdorsal projection. *Deltentosteus quadrimaculatus* has been commonly reported from the Pliocene and Pleistocene in the Mediterranean and less commonly since late Tortonian. Lin et al. (2017) figured a possible different species characterized by a flat inner face and identified as *Deltentosteus* sp. from the Tortonian of Italy. Nolf & Girone (2000) have figured a large set of extant and fossil specimens of *D. quadrimaculatus* defining their characters. Otoliths of the second extant species *D. collonianus* (Risso, 1820) are figured in Lombarte et al. (2006). A further fossil species is known from the Pliocene of the North Sea Basin, *D. modestus* (Gaemers & Schwarzahans, 1973) with several synonymies (see Nolf 2013), in an area where extant *Deltentosteus* species do not occur.

Pomatoschistus Group

Genus *Hesperichthys* Schwarzahans, Ahnelt, Carnevale & Japundžić, 2017

***Hesperichthys gironeae* n. sp.**

Figs. 13A-I

- 2010 “genus Gobiidarum” sp. 2 - Girone, Nolf & Cavallo: figs. 10f1-3b.

Holotype: Fig. 13C-E, SMF PO.91829, late Tortonian, Sant’Agata Fossili, coll. Malz 1958 sample 2 m below sample Pr-18, Piedmont, Italy.

Paratypes: 4 specimens IRSNB P 9952-9955, pre-evaporitic Messinian, Metalgrande near Verduno, Piedmont, Italy.

Etymology: Species named after Angela Girone (Bari) in recognition of her contributions to the knowledge of Neogene otoliths of Italy.

Diagnosis: Compact, high bodied otoliths reaching 1.7 mm in length; OL:OH ranging from 1.0 to 1.1. Outline sub-triangular with pre-ventral to post-ventral distance larger than predorsal to postdorsal. Dorsal rim high, with distinct pre- and postdorsal angles but no postdorsal projection; middorsal section horizontal flat or slightly con-

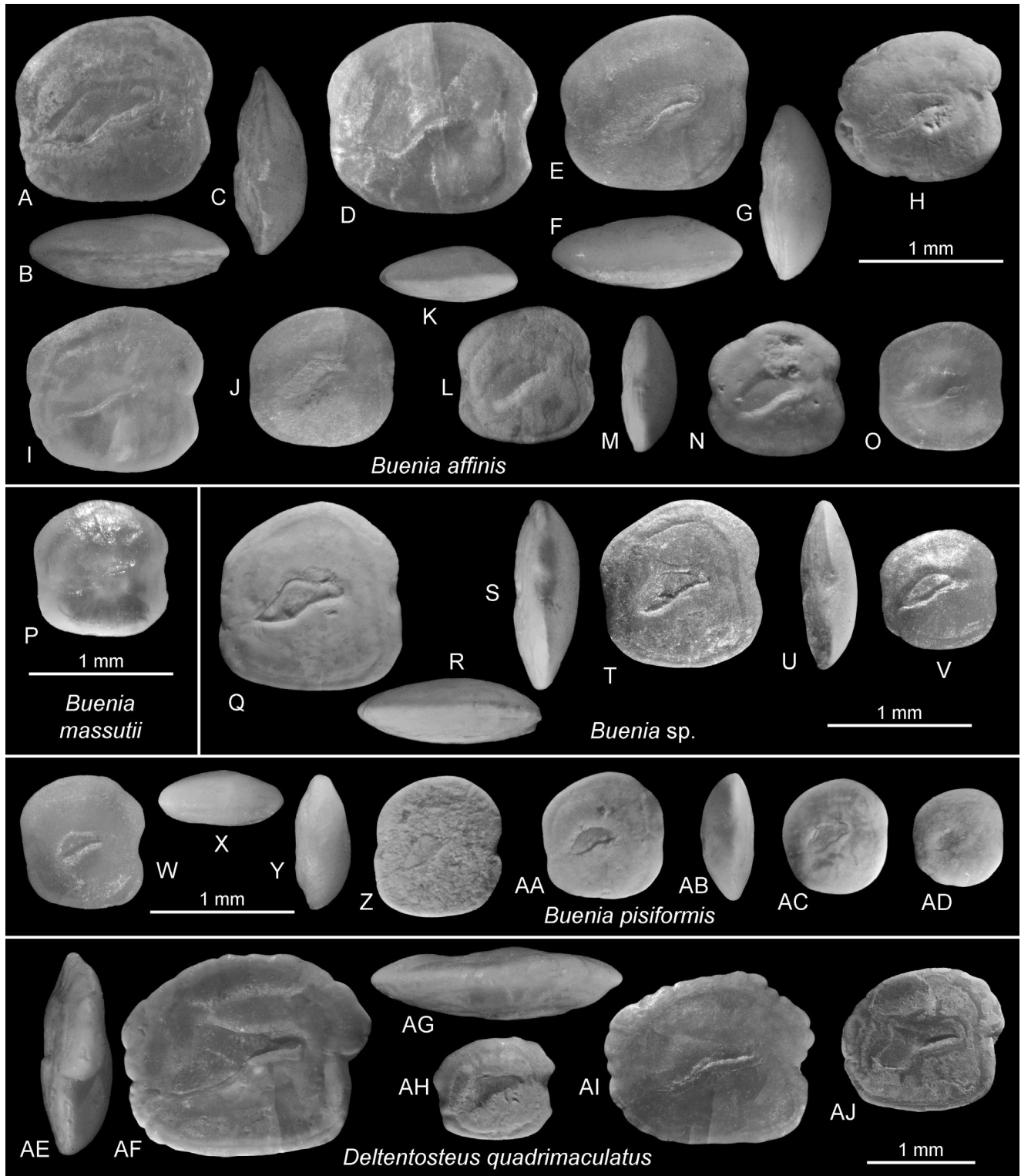


Fig. 12 - *Buenia*, *Deltentosteus*.

A-O) *Buenia affinis* (Kolombatovic, 1891). A-D, I) Recent, Illa de Cabrera, Balears, Spain, ICM-O 1015.12, .17, .23, TL 28-34 mm; E-H) pre-evaporitic Messinian, Agios Myron, AMPG(V)2351 (reversed); J-O) Zanclean, Voutes, AMPG(V)2352 (reversed).

P) *Buenia massutii* Kovačić, Ordines & Schliewen, 2017, Recent, Illa de Cabrera, Balears, Spain, ICM-O 1172.2, TL 23 mm (refigured from Lombarte et al. 2006, reversed).

Q-V) *Buenia* sp., late Tortonian, Potamida, AMPG(V)2353.

W-AD) *Buenia pisiformis* n.sp., Potamida; W-Y) holotype, late Tortonian, AMPG(V)2354; Z, AC) paratypes, late Tortonian, AMPG(V)2355 (Z reversed); AA-AB, AD) paratypes, pre-evaporitic Messinian, AMPG(V)2356 (AA-AB reversed).

AE-AJ) *Deltentosteus quadrimaculatus* (Valenciennes, 1837). AE-AG) Pre-evaporitic Messinian, Borelli, MGPT-PU 130381 (reversed); AH) pre-evaporitic Messinian, Potamida, AMPG(V)2357; AI) late Tortonian, Stazzano, MGPT-PU 130382; AJ) Zanclean, Agia Triada, AMPG(V)2358 (reversed).

cave. Sulcus very short, wide, and deep (OL2:CL = 2.15-2.5). Sulcus inclination angle low, 3-7°. Ostial lobe and subcaudal iugum absent; ventral sulcus margin irregular. Inner face nearly flat. Ventral furrow distinct; dorsal depression large, open to dorsal rim of otolith; outer face strongly convex. OH:OT = 2.8-3.0.

Description. Moderately large, robust otoliths with sub-triangular outline reaching about 1.7 mm in length (holotype 1.65 mm). OL:OH = 1.0-1.1; OH:OT = 2.8-3.0. Dorsal rim high with distinct pre- and postdorsal angles, middle section nearly horizontal, flat to slightly concave; no postdorsal projection. Otolith widest across pre-ventral to postventral angle. Anterior rim straight or slightly curved, without marked indentation, inclined at 75-85°. Posterior rim straight, with slight indentation above sulcus, inclined at 75-85°. Angle of pre-ventral to postdorsal about 40°. Ventral rim slightly curved, horizontal; all rims smooth.

Inner face nearly flat; area above sulcus (crista superior) somewhat bulged. Sulcus centrally positioned, short, wide, usually quite deep, weakly inclined. OL2:CL = 2.15-2.5; inclination angle of sulcus 3-7°. Sulcus without ostial lobe and subcaudal iugum, and characterized by irregular, convex or weakly w-shaped ventral margin. Ventral furrow distinct, moderately distant from ventral rim of otolith fading in front of and behind the sulcus; dorsal depression deep, wide, opening to middorsal rim. Outer face distinctly convex, smooth.

Discussion. *Hesperichthys gironeae* is a typical member of the genus and also its youngest representative known to date. Also, *Hesperichthys* as a genus so far has been recorded from the late Badenian to Sarmatian s.s. in the Paratethys, and *H. gironeae* is the only species known from the Mediterranean. It most resembles *H. reductus* Schwarzahns, Ahnelt, Carnevale & Japundžić, 2017 from which it differs in being thinner (OH:OT = 2.8-3.0 vs 1.8-2.5) and by having a higher dorsal rim and a less curved ventral rim, and it probably derived from that middle Miocene Paratethyan species.

Genus *Knipowitschia* Iljin, 1927

Knipowitschia etrusca n. sp.

Figs. 13J-S

Holotype: Fig. 13M-O, MGPT-PU 130360, late Messinian Lago Mare Event, Cava Serredi near Livorno, Tuscany, Italy.

Paratypes: 8 specimens: late Messinian Lago Mare Event, 4 specimens MGPT-PU 130361, same data as holotype, 3 specimens

MGPT-PU 130362, Le Vicenne; late Messinian upper evaporite, 1 specimen MGPT-PU 130363, Podere Torricella.

Etymology: deduced from Etrusci (Latin) the ancient inhabitants of the type region, Tuscany (Etruria).

Diagnosis: Small, high bodied, triangular otoliths reaching 1.0 mm in length; OL:OH ranging from 0.90 to 0.98. Largest width from pre-ventral to postventral angles. Dorsal rim high, rounded. Sulcus narrow and deep (OL2:CL = 1.7-1.8). Sulcus inclination angle 7-12°. Ostial lobe absent or weakly developed; narrow, long subcaudal iugum placed below entire cauda. Inner face flat. Ventral furrow distinct; dorsal depression large; outer face markedly convex. OH:OT = 2.7-2.8.

Fig. 13 - *Hesperichthys*, *Knipowitschia*, *Pomatoschistus*, *Pseudaphya*.

A-I) *Hesperichthys gironeae* n.sp. C-E) Holotype, late Tortonian, Sant'Agata Fossili, sample 2 m below Pr-18 (Malz, 1958), SMF PO.91829 (reversed); A-B, F-I) paratypes, pre-evaporitic Messinian, Metalgrande, IRSNB P 9952-9954 (A-B reversed).

J-S) *Knipowitschia etrusca* n.sp., late Messinian, Lago Mare event; M-O) holotype, Cava Serredi, MGPT-PU 130360; J-L) paratypes, Levicenne, MGPT-PU 130362 (J reversed); P-S) paratypes, Cava Serredi, MGPT-PU 130361 (reversed).

T) *Economidichthys pygmaeus* (Holly, 1929), Recent, Greece, BMNH 1999.4.23.231-290.

U-W) *Knipowitschia thessala* (Vinciguerra, 1921), Recent, Greece, BMNH 1989.3.15.33-58.

X) *Knipowitschia panizgae* (Verga, 1841), Recent, Karisnica mouth, Croatia, ICM-O 1021.6, TL 39 mm.

Y-AA) *Knipowitschia stironensis* (Lin, Brzobohatý, Nolf & Girone, 2017). Y-Z) Pre-evaporitic Messinian, Agios Myron, AMPG(V)2359 (reversed); AA) Late Tortonian, Stazzano, MGPT-PU 130383.

AB-AH) *Pomatoschistus bunyatovi* Bratishko, Schwarzahns & Reichenbacher, 2015, pre-evaporitic Messinian, Strada degli Archi, MGPT-PU 130384 (AB-AD reversed).

AI-AJ) *Pomatoschistus quagga* (Heckel, 1837), Recent, Ostro, Croatia, ICM-O 1022.7, TL 37 mm (AJ filtered).

AK-AM) *Pomatoschistus flavescens* (Fabricius, 1779), Recent, Bornholm, ZMUC P.784828, SL 31 mm.

AN) *Pomatoschistus lozanoi* (de Buen, 1923), Recent, British Channel, 50°39'N 00°10'W, BMNH 1951.2.19.38-44.

AO) *Pomatoschistus marmoratus* (Risso, 1810), Recent, Llobregat mouth, ICM-O 233.17, TL 51 mm.

AP-AR) *Pomatoschistus microps* (Krøyer, 1838), Recent, Femø, Denmark, ZMUC P.783274, SL 30 mm.

AS) *Pomatoschistus minutus* (Pallas, 1770), Recent, Denmark, ZMUC P.783290, SL 44 mm.

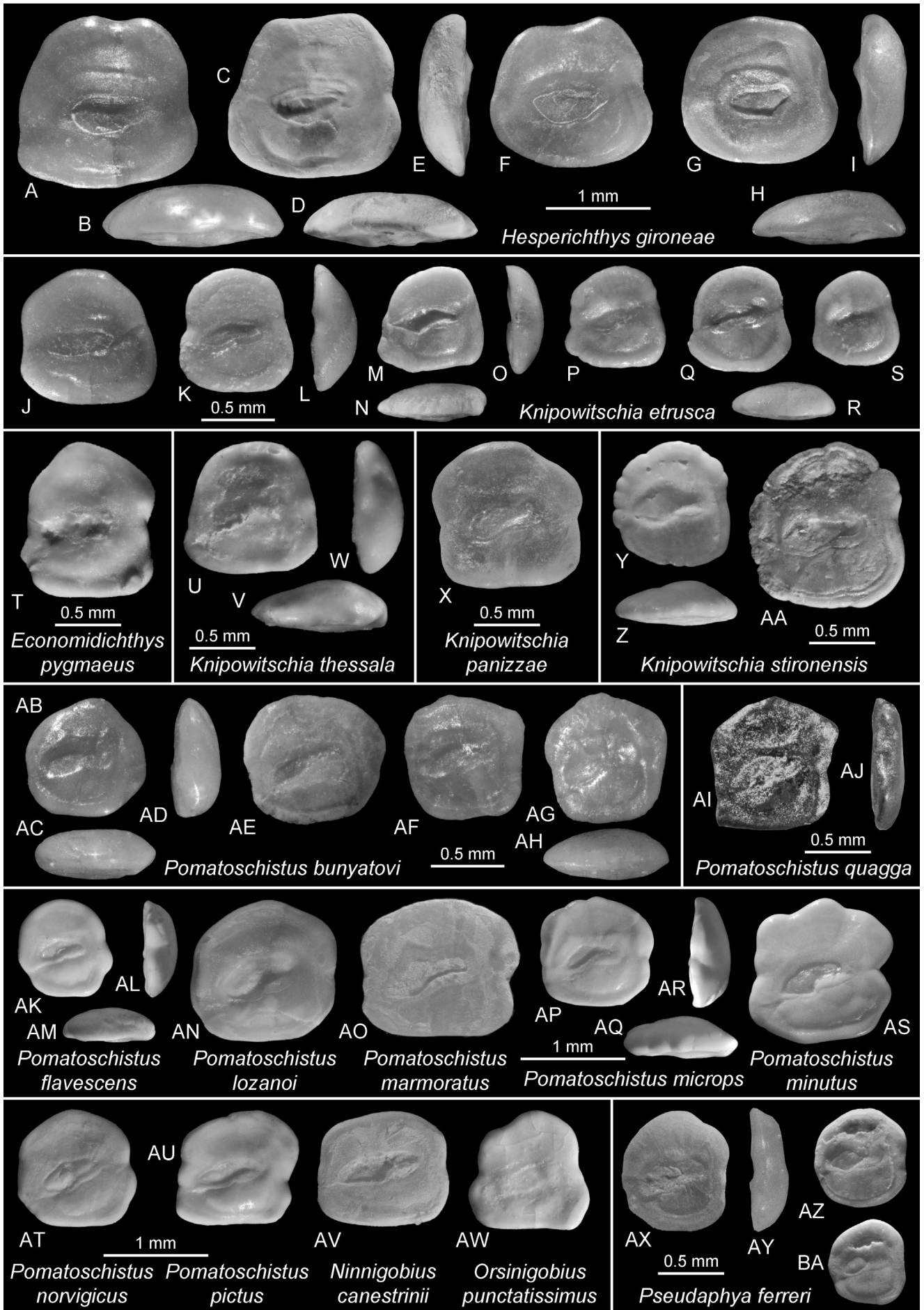
AT) *Pomatoschistus norvegicus* (Collett, 1902), Recent, 57°24'N 11°20'E, ZMUC P.784182, SL 40 mm.

AU) *Pomatoschistus pictus* (Malm, 1865), Recent, Rislinge Klint, Denmark, ZMUC P.784044, SL 36 mm.

AV) *Ninnigobius canestrinii* (Ninni, 1883), Recent, Split, NMW-79816, TL 56 mm.

AW) *Orsinigobius punctatissimus* (Canestrini, 1864), Recent, Tesina river near Vicenza, NMW-100225.

AX-BA) *Pseudaphya ferreri* (de Buen & Fage, 1908). AX-AY) Recent, Arenys de Mar, ICM-O 378.15, TL 29 mm; AZ-BA) Zanclean, Agia Triada, AMPG(V)2360 (AZ reversed).



Description. Small, high bodied otoliths with triangular outline reaching to about 1.0 mm in length (holotype 0.8 mm). OL:OH = 0.90-0.98; OH:OT = 2.7-2.8. Dorsal rim high, rounded, highest postdorsally, without distinct pre- or postdorsal angles and without postdorsal projection. Otolith widest across preventral to postventral angle. Anterior rim straight, without marked indentation, inclined at 75-87°. Posterior rim straight, without marked indentation, inclined at 75-80°. Angle of preventral to postdorsal 42-48°. Preventral angle sharper than rounded postventral angle. Ventral rim straight, horizontal or slightly curved in very small specimens (Fig. 13S); all rims smooth or slightly undulating.

Inner face flat; area below sulcus and between sulcus and ventral furrow slightly bulged. Sulcus centrally positioned or slightly suprmedian, moderately long, narrow, slightly deepened, moderately inclined. OL2:CL = 1.7-1.8; inclination angle of ostium commonly 15-23° (rarely 10°; Fig. 13J); inclination angle of sulcus 7-12°. Sulcus with very weak or without ostial lobe; subcaudal iugum narrow, long, below entire cauda but sometimes rather indistinct. Ventral furrow distinct, distant from ventral rim of otolith, connecting anterior tip of sulcus with posterior tip of sulcus in regularly curved half-moon shaped bent; dorsal depression wide, mostly distinct. Outer face markedly convex, smooth.

Discussion. The otoliths of *Knipowitschia etrusca* are very similar to those of the extant *K. thessala* (Vinciguerra, 1921), which is endemic to the freshwater Pinios catchment area of Thessaly, Greece, and from which it differs in being slightly more high bodied (OL:OH < 1.0 vs > 1.0) and bearing a less steeply inclined sulcus (7-12° vs 18-20°). According to Thacker & Gkenas (2019), *K. thessala* forms a dense clade with other restricted endemic *Knipowitschia* freshwater species in Greece and Turkey, i.e., *K. byblisia* Ahnelt, 2011, *K. mermere* Ahnelt, 1995 and *K. milleri* (Ahnelt & Bianco, 1990). Otoliths are only known of *K. thessala* (Fig. 13U-W). For further comparison otoliths of *Economidichthys pygmaeus* (Holly, 1929) (Fig. 13T) and *Knipowitschia panizzae* (Verga, 1841) (Fig. 13X) are figured herein. Presumably, *K. etrusca* represents a species pertaining to the *K. thessala* stock and was taking advantage to spread across suitable environments during the upper evaporite sequence and the Lago Mare Event. *Knipowitschia etrusca* possibly occupies a basal

position within the *K. thessala* clade, which diverged subsequent to the Lago Mare phase between 5 and 3 Ma, according to Thacker & Gkenas (2019).

Knipowitschia stironensis (Lin, Brzobohatý, Nolf & Girone, 2017)

Figs. 13Y-AA

2017 *Lesueurigobius stironensis* - Lin, Brzobohatý, Nolf & Girone: figs. 11F-I.

Material: 3 specimens: late Tortonian, 1 specimen Stazzano; pre-evaporitic Messinian, 2 specimens Agios Myron.

Discussion. This is a relatively large species of the genus *Knipowitschia* reaching a size of about 1.8 mm in length (Lin et al. 2017). It is characterized by a rather intense dorsal crenulation, particularly in the large specimens figured by Lin et al. (2017) and the long, moderately wide subcaudal iugum extending below the entire ventral margin of the cauda. The latter is a character often observed in *Knipowitschia* and resembles *K. suavis* Schwarzahans, 2014, a species widely known from the middle Miocene of the Paratethys and Mediterranean (Bratishko et al. 2015).

Genus *Pomatoschistus* Gill, 1863

Pomatoschistus bunyatovi Bratishko, Schwarzahans & Reichenbacher, 2015

Figs. 13AB-AH

2015 *Pomatoschistus bunyatovi* - Bratishko, Schwarzahans & Reichenbacher: figs. 10.13-10.17 (see there for further synonymies).

2015 *Pomatoschistus bunyatovi* Bratishko, Schwarzahans & Reichenbacher, 2015 - Schwarzahans, Bradić & Rundić: figs. 7.14-7.16.

2017 *Pomatoschistus bunyatovi* Bratishko, Schwarzahans & Reichenbacher, 2015 - Schwarzahans et al.: figs. 10j-k.

2020 *Pomatoschistus bunyatovi* Bratishko, Schwarzahans & Reichenbacher, 2015 - Schwarzahans, Brzobohatý & Radwanska: pl. 9, fig. 19.

Material: 8 specimens, pre-evaporitic Messinian, Strada degli Archi.

Discussion. *Pomatoschistus bunyatovi* is recognized by the expanded pre- and postdorsal angles that result in the widening of the otolith, which is distinctly dorsally shifted. In this respect it closely resembles the extant *P. quagga* (Heckel, 1837) (note: specimens of *P. quagga* recorded from the Serravallian of SE-Turkey by Schwarzahans (2014) are erroneous; see above). It differs from *P. quagga* in being thicker (OH:OT = 2.5-3.2 vs > 3.5) and

showing a slightly convex inner face (vs flat). Otoliths of extant species of *Pomatoschistus* and related genera are rarely figured (but see Lombarte et al. 2006 and Gut et al. 2020) and we therefore include for comparison figures of: *Pomatoschistus quagga* (Fig. 13AI–AJ), *P. flavescens* (Fabricius, 1779) (Fig. 13AK–AM), *P. lozanoi* (de Buen, 1923) (Fig. 13AN), *P. marmoratus* (Risso, 1810) (Fig. 13AO), *P. microps* (Krøyer, 1838) (Fig. 13AP–AR), *P. minutus* (Pallas, 1770) (Fig. 13AS), *P. norvegicus* (Collett, 1902) (Fig. 13AT), *P. pictus* (Malm, 1865) (Fig. 13AU), *Ninnigobius canestrinii* (Ninni, 1883) (Fig. 13AV), and *Orsinigobius punctatissimus* (Canestrini, 1864) (Fig. 13AW).

Pomatoschistus bunyatovi was widely distributed in the Paratethys during the middle Miocene (Badenian and Sarmatian s.s.). Its occurrence in the late pre-evaporitic Messinian at Strada degli Archi represents its youngest record and also the only one outside of the Paratethys.

Genus *Pseudaphya* Iljin, 1930

Pseudaphya ferreri (de Buen & Fage, 1908)

Figs. 13AZ–BA

Material: 2 specimens, Zanclean, Agia Triada.

Discussion. Otoliths of *Pseudaphya* clearly differ from those of *Aphia* in having a deep ostium that is set off from the cauda by a significant change in depth and the much narrower and smaller sub-caudal iugum. For comparison, an extant otolith of *P. ferreri* is figured herein (Fig. 13AX–AY). A second, fossil species is *Pseudaphya weinbrechti* (Schwarzahns, 2010), originally described as *Aphia weinbrechti*, from the late Miocene of the North Sea Basin that also shows a deep ostium but has a more regularly rounded outline and is less high-bodied.

Non-gobioid otoliths

A highly diverse, albeit mostly rare non-goby otolith assemblage has additionally been described from deposits of the MSC, chiefly the upper evaporite and the Lago Mare Event by Carnevale et al. (2006a, b, 2008, 2018) and Colombero et al. (2017). The faunal list encompasses open marine pelagic fishes, e.g., a diverse assemblage of Myctophidae but also rare Trachichthyidae (*Hoplostethus* cf. *mediterraneus*), Gadidae (*Paratrisopterus labiatus*) and Moridae (*Physiculus* sp.). It further contains shallow-water euryhaline

and brackish water fishes of the families Clupeidae (see below), Bythitidae (*Grammonus bassolii*), Atherinidae (see below), Mugilidae (*Chelon* sp.), a putative Psychrolutidae (see below), Sciaenidae (see Bannikov et al. 2018), Sparidae, and Blennidae. It further contains a common Cyprinodontidae (*Aphanius crassicaudus*) known from skeletons and otoliths throughout the MSC and possibly representing a brackish euryhaline species. Shallow-water demersal, stenohaline marine fishes are very rare (*Grammonus bassolii*) and bathy-benthic fishes, notably Macrouridae, are completely absent. It is beyond the scope of this study to review the otoliths of all these groups, particularly the rich myctophid assemblage, but we figure and briefly comment on those, which are relevant for comparison with the Paratethyan fauna including a strange and somewhat mysterious putative psychrolutid representing a fossil genus and species that would not normally be expected in such environment.

Family Clupeidae Rafinesque, 1810

Genus *Clupeonella* Kessler, 1877

Clupeonella sp.

Figs. 14A–E

2008 *Sprattus* sp. - Carnevale et al.: fig. 3B.

Material: 108 specimens: 99, mostly fragmentary specimens from the late Messinian sub-stage 3.1 of Cava Serredi; 8 fragmentary specimens, late Messinian Lago Mare Event, Cava Serredi; 1 specimen, late Khersonian to early Meotian, Plopease, Romania (LPB unregistered).

Discussion. This is a common species in the sub-stage 3.1 of Cava Serredi, but since the otoliths are very fragile, only a few specimens are well preserved. A single specimen from the collection of Pana from the late Khersonian to early Meotian of the Dacian Basin, which was never described and not registered, probably represents the same species. In addition, many species have been described from this interval by means of articulated skeletons. In the Mediterranean MSC, *Clupeonella macagnoi* Gaudant, 1987 was described from the evaporitic succession of Cherasco, Piedmont, Italy (Cavallo & Gaudant, 1987). Two species have been described from the Sarmatian s.l. of West-Turkey (*Clupeonella marmorensis* (Woodward, 1904), *C. trigonokephale* Rückert-Ülkümen, 1997) and four from the late Miocene and Pliocene of Armenia and other areas of eastern

Europe (*C. binagadensis* Bogachev, 1938, *C. mediocris* Bogachev, 1955, *C. pliocena* Bogachev, 1913, *C. vexata* Bogachev, 1938). These numerous species seem to reflect an unnecessary proliferation of taxa. In addition, Klein (1960) described five otolith-based clupeid species from the Pliocene of Azerbaijan, which likely represent a single species of *Clupeonella*, and a further possible otolith-based *Clupeonella* species was described by Djafarova (2006) as *Otol. (Osmeridarum) wilhelmi* Djafarova, 2006 from the middle Sarmatian s.l. of Azerbaijan. In this chaotic taxonomic situation, we refrained from attempts to describe the species from the MSC despite their excellent preservation. In addition to the many nominal *Clupeonella* species described from the late Miocene and Pliocene, there are many more skeletal records of other clupeid genera in the literature (see Grande 1985 and Rückert-Ülkümen 1965, 1997) that require a complete and extensive taxonomic revision. This is also exemplified by a further clupeid otolith morphology figured herein as *Alosa* sp. (Fig. 14F; syn. *Clupeonella* sp. in Carnevale et al. 2008, fig. 3A).

Family Gadidae Rafinesque, 1810
Genus *Paratrisopterus* Fedotov, 1971

***Paratrisopterus rumanus* (Weiler, 1943)**

Fig. 14X-AA

Material: 2 fragmentary specimens from the pre-evaporitic Messinian of Skyros, Greece.

Discussion. Although fragmentary, the general outline of these specimens in combination with the possession of two short, oval and widely spaced colliculi characterize them well as representatives of *P. rumanus*. *Paratrisopterus rumanus* is an endemic Paratethyan species that first occurred in the late Badenian (Figs. 14X-Z) and the otoliths reported herein represent its youngest records. In Skyros, they occur together with several specimens of *Bregmaceros albyi*, a species that does not occur in the Paratethys after the early Badenian. Popov et al. (2006) considered the Aegean domain as a region that intermittently connected the Mediterranean and the Paratethys during the late Miocene (see also Grothe et al. 2020). Coeval finds in the pre-evaporitic and evaporitic Messinian of Italy have revealed only *Paratrisopterus labiatus* (Schubert, 1905) (Fig. 14U-W; see Carnevale et al. 2008, fig. 6G and 2018, fig. 3G and 2019, fig. 11j), which is clearly distinctive in outline.

Family Atherinidae Risso, 1827
Genus *Atherina* Linnaeus, 1758

***Atherina kalinoraensis* Rückert-Ülkümen, 1993**

Figs. 14G-K

- 1993 *Atherina kalinoraensis* - Rückert-Ülkümen: pl. 2, figs. 4, 7.
1996 *Atherina kalinoraensis* Rückert-Ülkümen, 1993 - Rückert-Ülkümen: pl. 3, figs. 1-6.
2004 *Atherina* sp. - Pipik et al.: pl. 1, fig. 17.
2008 *Atherina* sp. - Carnevale et al.: fig. 3H.
2018 *Atherina* sp. - Carnevale et al.: fig. 3M.

Material: 3 specimens, late Messinian Lago Mare Event, Cava Serredi.

Discussion. *Atherina kalinoraensis* differs from all other European *Atherina* species known from otoliths, extant and fossil, by having a more elongate shape; moreover, it differs from *A. mutila* Rückert-Ülkümen, 1996, which is even considerably more elongate and may in fact belong to a different genus of the Atherinidae. *Atherina kalinoraensis* has originally been described from the Khersonian to Meotian of the Pontian Basin from Yalova, western Turkey. Also a specimen figured from Lake Pannon, Pannonian E (10.5-8.2 Ma) of Slovakia by Pipik et al. (2004) apparently belongs to this species. *Atherina kalinoraensis* is a further example of a Paratethyan immigrant that occupied the Mediterranean during the Lago Mare Event. A second *Atherina* species (*Atherina* sp., Fig. 14L-O) seems to occur sympatrically with *A. kalinoraensis* and appears to be closer to extant Mediterranean species such as *A. boyeri* Risso, 1810. For further comparison, we have also figured a mugilid otolith assigned to *Chelon* sp. (Fig. 14P-Q) from the late Messinian Lago Mare deposits of Cava Serredi.

Family Sciaenidae Cuvier, 1828

Remark. Middle and late Miocene sciaenid records from the Paratethys and the MSC interval of the Mediterranean have recently been reviewed by Bannikov et al. (2018). We re-figure here representatives of two species from the Lago Mare Event considered to be related to endemic Paratethyan sciaenids: *Leptosciaena caputoi* Bannikov, Schwarzahns & Carnevale, 2018 (Fig. 14R-S) and *Trewasciaena kokeni* (Schubert, 1902) (Fig. 14T).

Family ?Psychrolutidae Günther, 1861

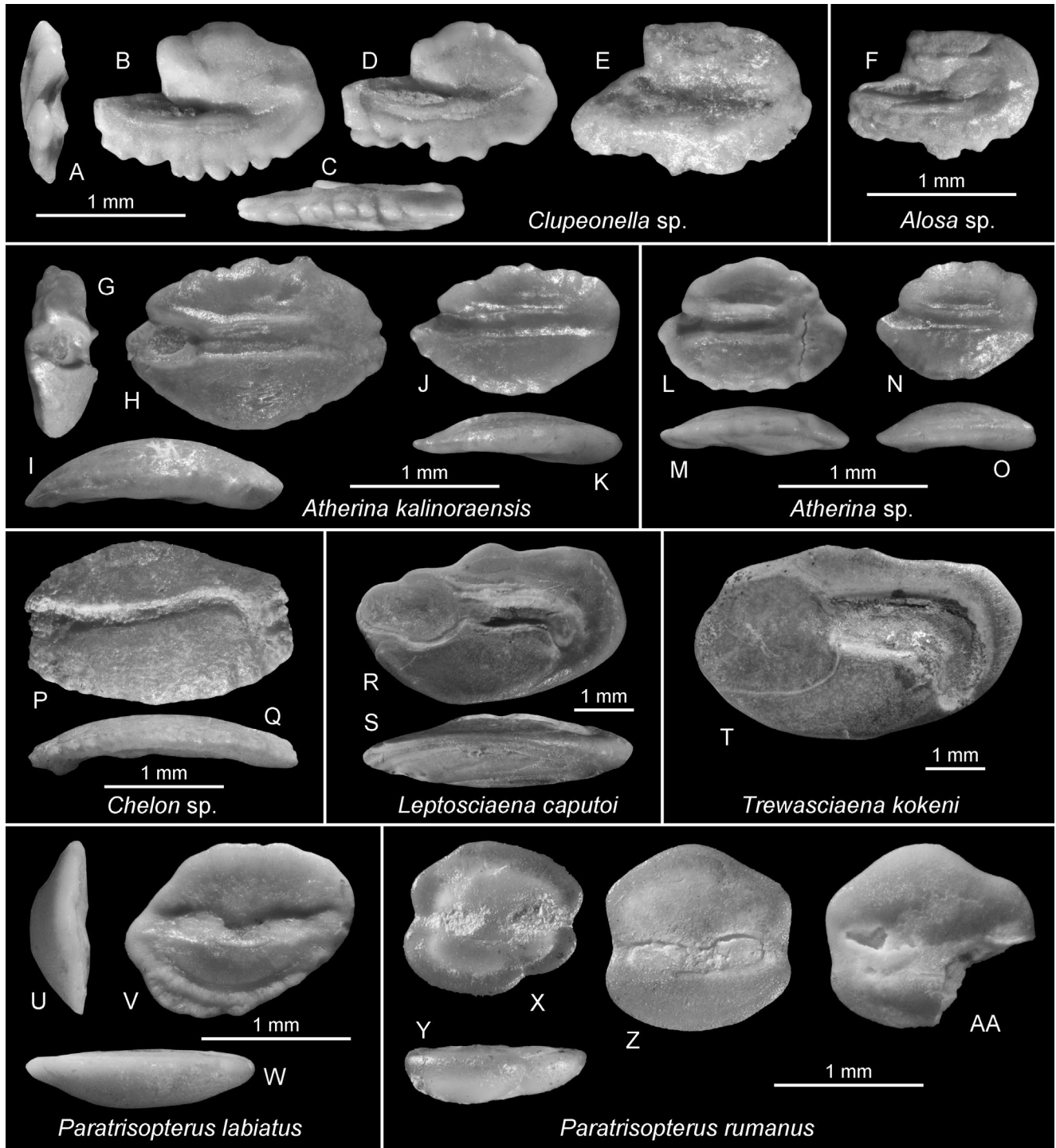


Fig. 14 - Non-goby Lago Mare otoliths.

- A-E) *Clupeonella* sp. A-D) Late Messinian, upper evaporite, Cava Serredi, MGPT-PU 130385 (reversed); E) Khersonian to early Meotian, Plopease, Romania (reversed).
 F) *Alosa* sp., Late Messinian, upper evaporite, Cava Serredi, MGPT-PU 130386.
 G-K) *Atherina kalinoraensis* Rückert-Ülkümen, 1993, late Messinian, Lago Mare event, Cava Serredi, MGPT-PU 130387 (J-K reversed).
 L-O) *Atherina* sp., late Messinian, Lago Mare event, Cava Serredi, MGPT-PU 130388 (L-M reversed).
 P-Q) *Chelon* sp., late Messinian, Lago Mare event, Cava Serredi, MGPT-PU 130389.
 R-S) *Leptosciaena caputoi* Bannikov, Schwarzahns & Carnevale, 2018, holotype, MGPT-PU 130338, late Messinian, Lago Mare event, Capanne di Bronzo.
 T) *Trewasciaena kokeni* (Schubert, 1902), late Messinian, Lago Mare event, Capanne di Bronzo, MGPT-PU 130337 (reversed).
 U-W) *Paratrisopterus labiatus* (Schubert, 1905), late Messinian, Lago Mare event, Podere Torricella, MGPT-PU 130390 (reversed).
 X-AA) *Paratrisopterus rumanus* (Weiler, 1943). X-Z) Paratypes, late Badenian, Romania, X-Y) SMF 2661a, Melicesti, Z) SMF 2738, Scaiosi; AA) pre-evaporitic Messinian, Skyros, Greece.

Genus *Enigmacottus* n. gen.

Type species: *Enigmacottus socialis* n. sp. (fossil, otolith-based species).

Etymology: A combination of enigma (Greek) = enigma, mystery and the common genus name *Cottus* indicating the unexpected occurrence of these fishes in the environment where they were found and their problematic systematic allocation.

Diagnosis: A fossil, otolith-based genus tentatively allocated with the Psychrolutidae and defined by the following combination of characters. Moderately large otoliths reaching about 3.3 mm in length. Ratio OL:OH = 1.45-1.75. Outline triangular with pointed, inferior anterior, and posterior tips and broadly rounded mediodorsal angle. Inner face almost flat; outer face convex. Sulcus small, oval, inclined at 8-12°, often with slightly concave dorsal margin, positioned inframedian and equidistant from anterior and posterior tips of otolith. OL:CL = 2.6-3.4. Sulcus closed but rarely with faint, narrow indication of nearly vanished ostial connection to anterior rim. Sulcus margins indistinct; margins of undifferentiated colliculum distinct. Ventral furrow present; dorsal depression vague.

Discussion. *Enigmacottus* is a highly characteristic otolith but offers few features allowing correlation with otoliths of extant fishes. The small, centrally positioned, slightly inclined and unstructured sulcus is similar to the pattern found in the family Psychrolutidae, among which we tentatively place *Enigmacottus*, and certain Lophiiformes, where they have been previously placed (Carnevale et al. 2008; Colombero et al. 2014). It seems that the uniform unstructured colliculum solely represents the caudal colliculum while the ostium has faded. Indeed, the Psychrolutidae appear to be the only known teleosts in which the fading of the ostium has resulted in this morphology, as evidenced by the otoliths of the extant *Dasycottus setiger* Bean, 1890 (Fig. 15A-B). Other similar otolith morphologies are mostly the result of the sulcus becoming reduced in length thereby disconnecting from the otolith rims and the ostial and caudal colliculi becoming fused to form a single undivided colliculum.

Psychrolutids are mostly deepwater demersal fishes, and therefore an occurrence in the shallow-water special environment of the MSC is truly unexpected. Following the comparative study of extant psychrolutids by Nelson (1982), *Dasycottus setiger* is probably the most plesiomorphic member of the group and the one with the least reduced head ossification. It also occurs shallower than other members of the family in water depth ranging from 15 to 850 m. In any case, the occurrence of *Enigmacottus* exclusively in the sediments of the MSC remains mysterious and very problematic to explain from a biogeographic and paleoenvironmental point of view.

Species. A single species, *Enigmacottus socialis* n. sp. exclusively known from the sediments deposited during the sub-stages 3.1 and 3.2 of the MSC in the Mediterranean.

Enigmacottus socialis n. gen., n. sp.

Figs. 15C-Q

2008 Lophiiformes indet. - Carnevale et al.: fig. 3N.

2014 Lophiiformes indet. - Colombero et al.: fig. 5.5.

Holotype: Fig. 15G-I, MGPT-PU 130364, late Messinian sub-stage 3.1, Cava Serredi near Livorno, Tuscany, Italy.

Paratypes: 30 specimens MGPT-PU 130365, same data as holotype.

Referred specimens: 3591 specimens: 3589 specimens, same data as holotype; late Messinian Lago Mare Event: 1 specimen MGPT-PU 130366, Podere Torricella, 1 specimen MGPT-PU 130367, Cava Serredi.

Etymology: From *socialis* (Latin) = socializing, referring to the species occurring socialized in great quantity in a particular location and strata and being very rare or absent elsewhere.

Diagnosis: See generic diagnosis (monotypic genus).

Description. Moderately large otoliths reaching about 3.3 mm in length (holotype 2.35 mm). OL:OH = 1.45-1.75, increasing with size; OH:OT = 2.1-2.6, increasing with size. Outline triangular, with inferior, pointed, symmetrically positioned anterior and posterior tips. Dorsal rim high, somewhat irregularly and often coarsely crenulated, highest at its midlength at the level of the rounded mediodorsal angle. Ventral rim shallow, gently curving, anteriorly more than posteriorly, deepest at its midlength. Occasionally with small indentation above tip, both anterior and posterior, usually tied up with sulcus through a furrow.

Inner face flat, with centrally positioned, inframedian, inclined, shallow, short sulcus located equidistantly from anterior and posterior tips of otolith. Sulcus margins often vague, particularly towards anterior and occasionally indicating a very vague and equally wide ostium. Sulcus inclination angle 8-12°. Colliculum clearly marked with sharp margins, oval, short but with some variation in length, variably wide, often with concave dorsal margin and probably representing caudal colliculum only; OL:CL = 2.6-3.4. Furrows can connect sulcus tips with anterior or posterior otolith rims. Ventral field smooth but with mostly distinct ventral furrow close to ventral rim of otolith and leading from anterior to posterior tips of otolith. Dorsal depression very indistinct, often not discernable. Outer face slightly more convex than inner face, smooth or with little ornamentation.

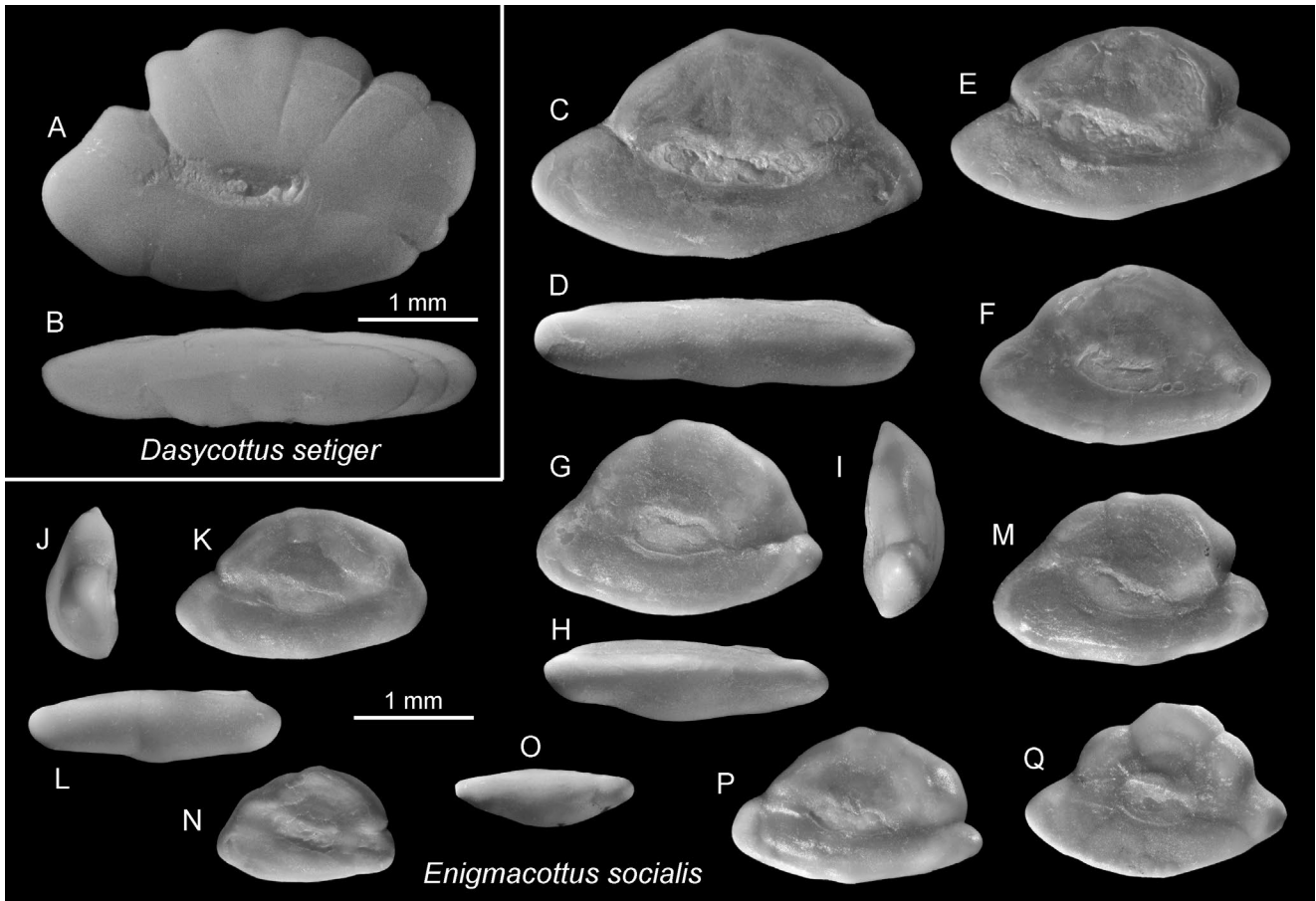


Fig. 15 - Cottoidae, ?Psychrolutidae.

A-B) *Dasycottus setiger* Bean, 1890, Recent, Golf of Alaska, leg. Fitch, coll. Schwarzzhans.
 C-Q) *Enigmacottus socialis* n. gen., n. sp., late Messinian, upper evaporite, Cava Serredi;
 G-I) holotype, MGPT-PU 130364; C-E, J-Q) paratypes, MGPT-PU 130365 (C-E, J-M, P-Q reversed).

Discussion. This is certainly one of the most remarkable occurrences of fossil fishes in the MSC. We hope that eventually an articulated skeleton will be found with these otoliths *in situ* in order to achieve a definitive systematic allocation. The tentative allocation within psychrolutids at this stage must be regarded as the most plausible choice. Environmental affinity and occurrence are quite different from those of extant fishes of this family. Another intriguing aspect is that *Enigmacottus socialis* occurs extremely commonly in one particular level of one particular locality (deposits of the sub-stage 3.1 at Cava Serredi), but it is extremely rare or absent from the majority of the studied MSC localities and is completely absent from any normal marine late Miocene and early Pliocene locality. In fact, the occurrence of *E. socialis* in this particular level at Cava Serredi represents 70% of all otoliths obtained from the stage 3 of the MSC in the collection from Italy. The reasons for its mass occurrence in

the single layers of the sub-stage 3.1 at Cava Serredi remain elusive.

FAUNAL EVALUATION

Gobies as paleoecological indicators

Many extant goby species are known for their specific environmental adaptations ranging from freshwater systems to brackish-marine transitional biotopes, as well as shallow marine and deeper shelf environments (Froese & Pauly 2019; Patzner et al. 2011; Miller 1986, 2003, 2004) (Figs. 16-17, Table 1). Gobies exhibit a particularly high degree of specialization and diversity in shallow marine and brackish environments. They are mostly demersal fishes but also contain a few nektonic and pedomorphic forms, like *Aphia minuta*, *Crystallogobius linearis*, and *Pseudaphya ferreri* in European waters (La Mesa 2011). The Atlantic-Mediterranean faunal province

of Europe contains approximately 70 extant gobiid species (Froese & Pauly 2019). Gobiid assemblages from the middle Miocene of the Central Paratethys were recently reviewed and were found to yield at least 31 species (Schwarzahns et al. 2020) at a time when the Central Paratethys was fully connected with the Mediterranean. The lower amount of species known in the fossil record may be explained by the combined effect of several factors, including the lower diversity of preserved sedimentary environments, much lower sampling density and geographic distribution and, last but not least, limited ability in the taxonomic interpretation of different fossil taxa. However, the number of gobiid species recorded from the late Miocene and early Pliocene of the Mediterranean is even lower, which is clearly a function of predominantly pelagic, open to deep marine sediments that have been studied for otoliths in the past. Our study incorporates data from a much larger variety of shallow marine environments, in both time and space, based on new samples and revision of previously published material, thereby resulting in the discovery of a much more diverse and complex record of gobiid communities.

The gobioid species distribution is summarized in Table 1.

Late Tortonian (Fig. 16 lower panel): Otoliths from deep open marine sediments from northern Italy have been extensively studied, most notably in the recent publications of Lin et al. (2015, 2017), and new material from the Rio di Bocca d'Asino site, near Stazzano is presented herein. The abundance of myctophid otoliths documents the hemipelagic nature of the sediments (Lin et al. 2017), except for the Torrente Stirone succession, which contained the highest percentage of goby otoliths in Lin's study. The most common species observed in Stazzano pertain to the genera *Lesueurigobius* (*L. stazzanensis*, *L. suerii*) and *Hoeseichthys* (*H. bicornutus*, *H. brioche*). Extant species of the genus *Lesueurigobius* burrow in muddy sand and sand and are found at depths ranging from 10 to over 300 m (Miller 1986). *Lesueurigobius suerii* occupies a wide bathymetric range from inshore to 230 m commonly, but as deep as 337 m in some areas (Miller 1986; Froese & Pauly 2019). The species of the extinct genus *Hoeseichthys* are typically found in deepwater sediments on the outer shelf and slope (Schwarzahns et al. 2020). Rarer are certain *Gobius* species (*G. mustus*, *G. aff. paganellus*, *G. reichenbacherae*) and *Deltentosteus*

quadrimaculatus. These species are relatively widely distributed through different environments and bathymetric ranges. *Deltentosteus quadrimaculatus* today is widespread in the Mediterranean and adjacent Atlantic on sandy and muddy bottoms to 90 m in depth (Miller 1986). In conclusion, a goby community dominated by species of *Hoeseichthys* and *Lesueurigobius* is indicative of a rather deep marine environment (>150 m), since *Hoeseichthys bicornutus* and *Lesueurigobius stazzanensis* do not commonly occur in sediments shallower than 150 m.

In the study by Lin et al. (2017), the Torrente Stirone succession stands out as being dominated by otoliths of neritic fishes, most notably by gobies. There the most common species are *Deltentosteus quadrimaculatus* and a second unidentified *Deltentosteus* species, two species of the genus *Lesueurigobius* (*L. friesii*, *L. suerii*), *Gobius* aff. *paganellus* and *Knipowitschia stironensis*. This composition is comparable with that described by Agiadi et al. (2017) from Potamida, Crete, and reviewed herein, whose deposition took place at depths of about 100-150 m. The Potamida assemblage contained *Lesueurigobius friesii*, *Hoeseichthys brioche* and three species not known from the Torrente Stirone succession, i.e., *Odondebuena* cf. *balearica*, *Buenia pisisiformis*, and *Buenia* sp. *Odondebuena balearica* today occurs offshore on coralline grounds at 25 to 70 m (Miller 1986). Extant species of *Buenia* show a depth segregation from 5 to 375 m (Kovačić et al. 2017), and one of the species (*Buenia pisisiformis*) so far is only known from Potamida. In conclusion, a gobiid assemblage dominated by *Lesueurigobius friesii* is indicative for the outer shelf (50-150 m); important associated bathymetric indicators could be *Odondebuena* cf. *balearica* and *Buenia pisisiformis*.

An unusual environmental context was sampled in the Cessaniti area, Calabria. The otoliths were primarily obtained from a level interpreted as a brackish water lagoonal paleobiotope probably surrounded by mangrove-like vegetation (D'Amico et al. 2013). This is a unique paleoenvironmental context in Italy as lagoon and other nearshore swamps and ponds pertaining to a heterogeneous delta system developed during the Apennine orogeny. The interval sampled at Cessaniti was described as a brackish lagoon by D'Amico et al. (2013) and paralic devoid of stenohaline marine biota by Gramigna et al. (2008). It is therefore not surprising that the gobioid assemblage found in Cessaniti is com-

pletely different from that of fully (deeper) marine environments discussed above. The dominant species are *Eleotris omuamuaensis* and *E. tyrrenicus*. Rare associated species are *Gobius* aff. *paganellus*, *Gobius* sp., and *Aphia minuta*. Nowadays, the many species of *Eleotris* live primarily in fresh- to brackish water in the tropics of America, Africa, and Asia. Today, *Eleotris* is not present in the Mediterranean, and its nearest occurrence is that of tropical West Africa, southwards from Guinea. Its occurrence in Cessaniti is unique and no comparable gobioid assemblage is known from the Neogene of the Mediterranean or Paratethys. The Cessaniti gobioid assemblage is regarded as a clear indicator of a subtropical brackish and paralic environment.

Early (pre-evaporitic) Messinian (Fig. 16 lower panel): Otolith faunas have rarely been described from the pre-evaporitic Messinian of the Mediterranean, the most recent and complete reviews being those of Caputo et al. (2009), Girone et al. (2010), and Agiadi et al. (2017). The material described by Caputo et al. (2009) and Agiadi et al. (2017) has been available for review together with some specimens from Verduno, Metalgrande (see Girone et al. 2010), and additional unpublished material from localities in Greece and Italy. Most of the examined localities were from open marine, inner to outer shelf environments. The deepest paleoenvironment recorded in these otoliths studies is probably that described by Girone et al. (2010) from Verduno (mostly the Metalgrande locality) and represented by a relatively rich gobioid assemblage, which in a large part was described as taxa in open nomenclature. Here we have identified as the most common species *Lesueurigobius stazzanensis*, *Hoeseichthys bicornutus*, *Gobius reichenbacherae*, *Hesperichthys gironeae*, and *Caspiosoma lini*. The first two species are indicative of an outer shelf environment similar to the late Tortonian ones, probably deeper than 150 m. A similar interpretation may be hypothesized for *Hesperichthys gironeae*, which elsewhere is exclusively known from rather deep open marine paleobiotopes of the late Tortonian. The occurrence of a *Hesperichthys* species, a genus otherwise only known from the late Badenian and Sarmatian s.l. of the Paratethys, is surprising, particularly because of its deepwater association and will be discussed later in more detail. Finally, *Gobius reichenbacherae* and *Caspiosoma lini* may have had a wide bathymetrical distribution. In conclusion, the goby assemblage dominated

by *Lesueurigobius stazzanensis* and *Hoeseichthys bicornutus* seems to indicate a water depth >150 m.

Other studied localities (Botro Rosso and Borelli in Italy, Potamida and Faneromeni in Greece) included common *Hoeseichthys bicornutus*, *H. brioche*, *Lesueurigobius friesii*, *L. suerii*, and *Deltentosteus quadrimaculatus*. This assemblage is similar to that reported from Verduno (see above), but the common occurrence of *Lesueurigobius friesii* and *Deltentosteus quadrimaculatus* may reflect a position on the outer shelf, probably at 100 to 150 m.

On the other hand, the gobioid assemblage of Agios Myron, Crete, indicates a shallower depth than those described above, although it probably occupied the open shelf. It is a mixture of deep-water species such as *Hoeseichthys bicornutus* and *H. brioche*, mid-shelf species such as *Lesueurigobius friesii* and *Caspiosoma lini*, but also contains *Buenia affinis* and two specimens of *Priolepis* sp., a truly exotic find. Today, *Buenia affinis* occurs between 3 to 25 m (Froese & Pauly 2019), and *Priolepis* is a genus usually associated with reefoidal environments. In addition, there are three species of *Gobius*: *G. fallax*, *G. mustus*, and *G. reichenbacherae*. *Gobius fallax* is an extant species and occurs from shore to 32 m depth (Froese & Pauly 2019). Therefore, we would regard the occasional occurrence of *Hoeseichthys bicornutus* as an indicator of a nearby deeper shelf or a steep continental slope, while the remainder of the species would point to a shallower open shelf environment not significantly deeper than 50 m.

The stratigraphically youngest sample of the pre-evaporitic Messinian is that from Strada degli Archi in Tuscany positioned just 1.5 m below the first gypsum layer apparently marking the onset of the MSC (Caputo et al. 2009). The fish assemblage is very rich in gobies with *Proterorhinus yigitbasi*, *Aphia minuta*, *Lesueurigobius suerii*, and *Zosterisessor exsul* as the most common and *Pomatoschistus bunyatovi* as an important accessory species. The sedimentary environment was described as shallow-water nearshore with some brackish influence in a sheltered embayment position. Several species are considered to reflect a migratory origin (see below) like the genera *Proterorhinus* and *Zosterisessor*, which today typically live inshore and in brackish waters, and *Proterorhinus* also in fresh waters. *Pomatoschistus* species occur in fresh-, brackish and nearshore marine waters. *Lesueurigobius suerii* has a wide bathymetric range from inshore to at least 230 m (see above); so, its occur-

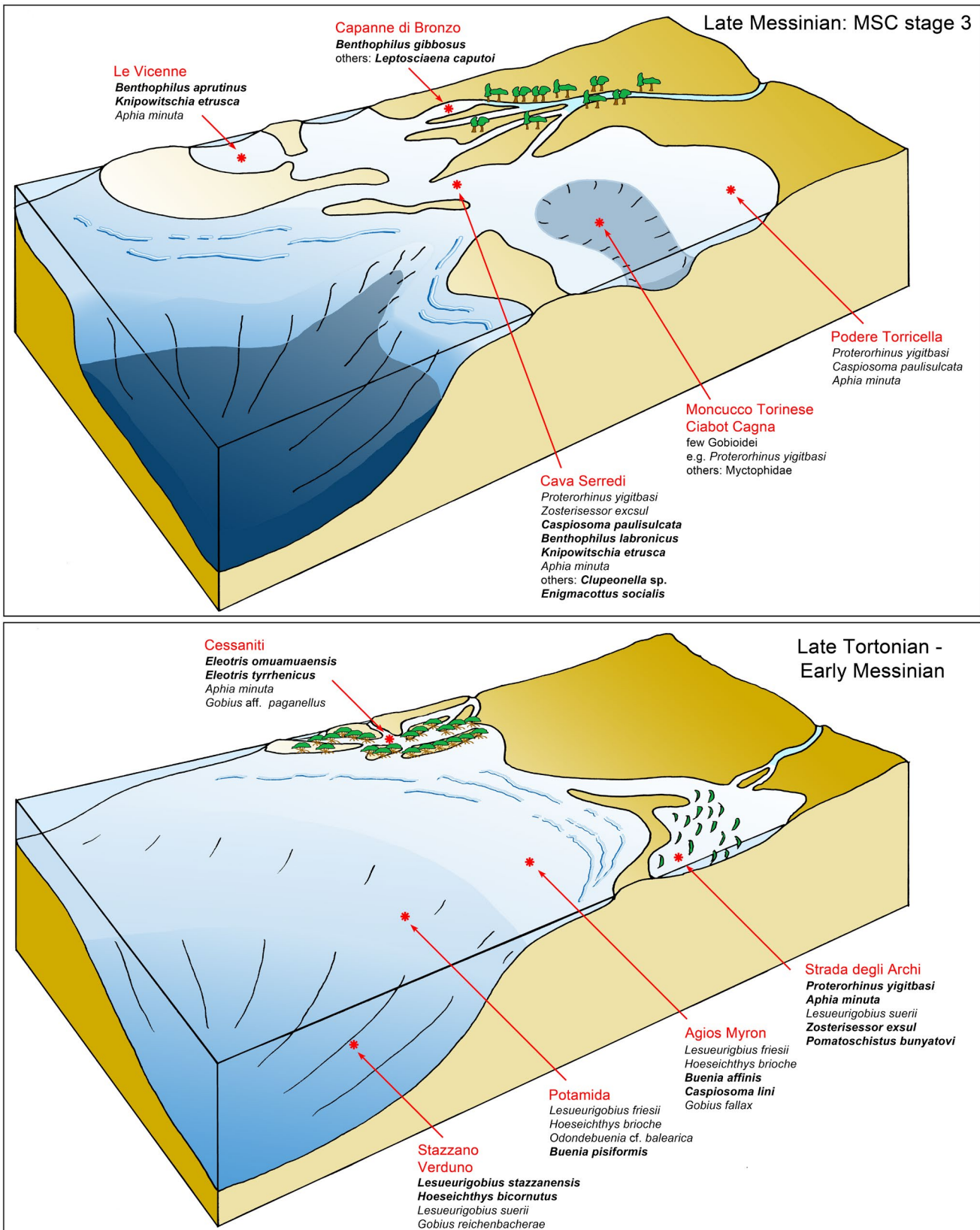


Fig. 16 - Paleoecological block diagrams - late Miocene. Schematic block diagrams showing Mediterranean paleobiotope during the late Tortonian to early Messinian (lower panel) and during stage 3 of the MSC (upper panel) with distribution of the most common gobioid species. Bold print highlights species considered indicative of specific paleoenvironments. The block diagram in the lower panel shows deepwater terrain in the foreground, a mangrove environment on the left background, and a sheltered embayment with brackish influence on the right. The block diagram in the upper panel shows a deepwater environment with low oxygenated bottom water (dark blue color) in the foreground, a sheltered lagoon on the left, an open lagoon with a deep poorly oxygenated zone (dark blue) on the right, and prodelta environments on left background.

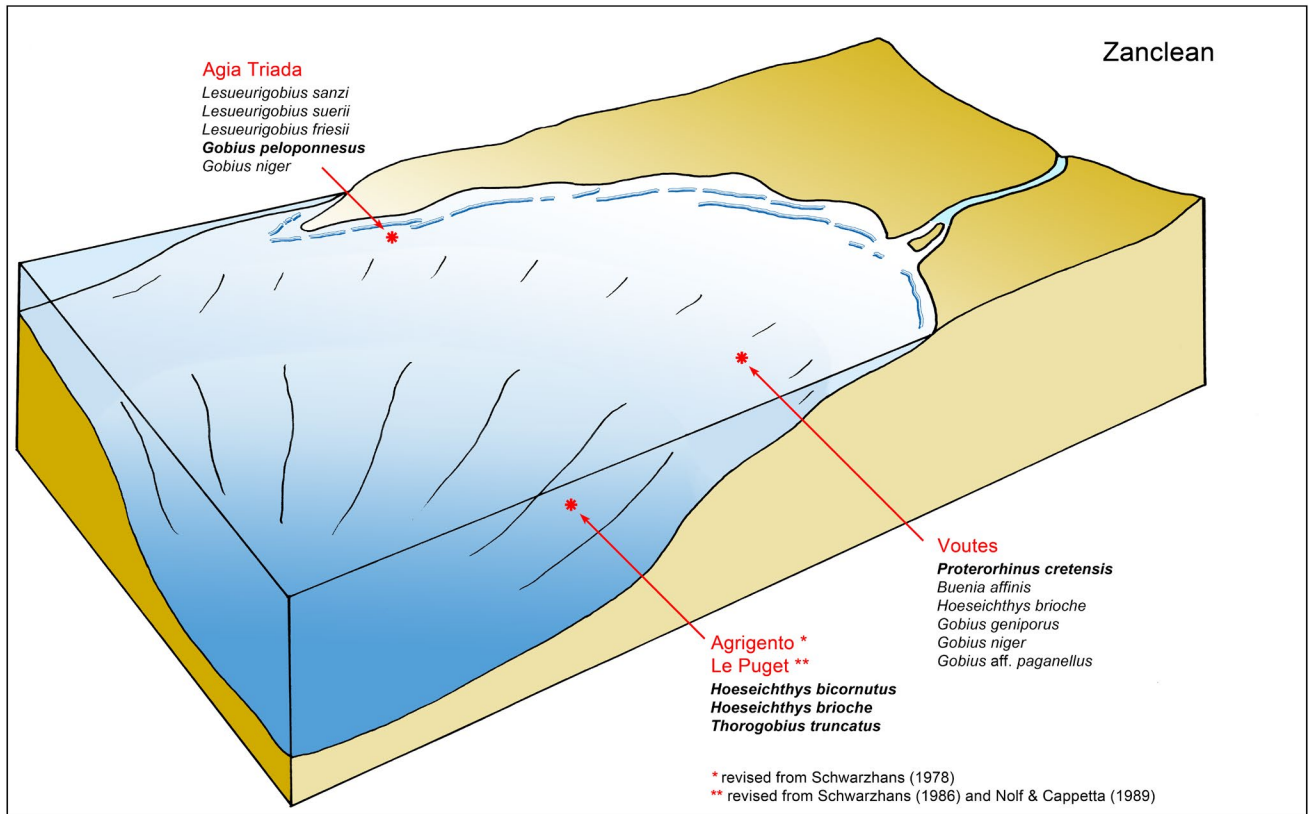


Fig. 17 - Paleoecological block diagram - early Pliocene. Schematized block diagram showing Mediterranean paleobiotope during the Zanclean with distribution of the most common gobioid species. Bold print highlights species considered indicative of specific paleoenvironments. The block diagram shows deepwater terrain in the foreground and nearshore environments in the background without brackish transitional marine environments.

rence in such environment is not in contrast with the rest of the assemblage. Finally, *Aphia minuta* is a free-swimming nektonic, epipelagic species found from surface to 70–80 m over inshore and estuarine sandy and muddy bottoms and eel-grass (Miller 1986). Thus, the goby assemblage of Strada degli Archi is consistent with the sedimentary and paleontological assessment by Caputo et al. (2009) and exhibits a significant difference from the open shelf communities described above from the earliest part of the Messinian stage.

Late Messinian during MSC stage 3 (Fig. 16 upper panel): No otoliths have been collected from the MSC stages 1 and 2, but one of us (GC) has accumulated a large collection from the sub-stages 3.1 (upper evaporite) and 3.2 (Lago Mare) from various locations in Italy (MSC sub-stages division according to Roveri et al. 2014). During MSC stage 3, the Mediterranean region was characterized by a wide variety of open and protected lagoons and sheltered prodelta systems along a broad coastal belt probably enhanced by sustained

orogenic activities and by a very humid phase (Carnevale et al. 2019, and literature cited therein). The water body in these coastal environments was probably more alkaline than normal seawater and with a somewhat reduced salinity (Carnevale et al. 2019). Otoliths are mostly rare (except for a few horizons at Cava Serredi) with goby otoliths being the most common in many of the locations. Their otolith assemblage composition is substantially different from those of normal marine late Miocene and early Pliocene localities, and the nature of this change and its possible meaning for the interpretation of the Lago Mare Event will be discussed in detail in the following chapter below.

Deepwater environments are only known from offshore wells and have not been sampled for otoliths. An exception is perhaps Moncucco Torinese (Carnevale et al. 2018), which yielded a very low density of otoliths (about 20 t of sediment had to be processed to obtain just about 100 otoliths) with myctophid otoliths outnumbering goby otoliths, a unique relation in the MSC stage 3. The fos-

siliferous sediment of Moncucco Torinese originated in the deepest part of a large lagoon with poorly oxygenated bottom water not feasible for demersal fishes like gobies. Marzocchi et al. (2016) proposed that most of the Mediterranean was strongly stratified during the Lago Mare, due to enhanced water exchange with the brackish water of the Paratethys. The resultant low level of oxygenation near the seafloor would explain the total lack of bathybenthic fishes (eg. Macrouridae) while mesopelagic fishes did occur (eg. Myctophidae) (see also Carnevale et al. 2006, 2018). However, a continuous brackish-water lens covering the entire Mediterranean Sea, as suggested by the model of Marzocchi et al. (2016), would not be consistent with the occurrence of myctophids, which depend on vertical diel migration between deep water during the day and near-surface water at night. We therefore assume that reduced water salinity only occurred in a broad coastal, shallow-water zone. Considering their rarity at Moncucco Torinese, myctophid otoliths were likely to have been introduced through the excreta of large predators (see Carnevale et al. 2008; Colombero et al. 2017).

The open lagoon environments of Podere Torricella and the sheltered prodelta environments of Cava Serredi are rich in *Proterorhinus yigitbasi*, *Zosterisessor exsul*, *Caspiosoma paulisulcata*, and *Benthophilus* spp. that occur with different abundances. *Benthophilus* is a genus with clear Paratethyan affinities. This genus contains about 18 extant species, most of which are endemic of the Caspian Sea (Miller 2004). Many species are adapted to very specific environments exhibiting a restricted geographic distribution. A similarly high level of diversity has been also observed in the MSC stage 3: *Benthophilus labronicus* is common in the sheltered prodelta environment of Cava Serredi (sub-stage 3.1 of the MSC); *Benthophilus gibbosus* exclusively occurs in the vegetated prodelta with turbid water of Capanne di Bronzo; and *Benthophilus aprutinus* is only known from the protected lagoonal environment of Le Vicenne. The normal marine demersal gobies, which were abundant before and after the MSC (e.g., *Lesueurigobius* spp., *Deltentosteus quadrimaculatus*, *Gobius* spp.), are missing and probably found no suitable environment offshore of the belt with reduced salinity and low oxygenation level at the seafloor. The only normal marine goby occurring together with this association is *Aphia minuta*, probably because of

its more nektonic lifestyle. In addition, *Knipowitschia etrusca* occurs as a rare component in Cava Serredi, Le Vicenne, and Podere Torricella. *Knipowitschia etrusca* is here regarded as an ancestral species in a clade with four extant species within the genus, each of which is endemic to a geographically restricted freshwater system on the Balkanids and Turkey. Its occurrence in the stage 3 of the MSC is interpreted herein as reflecting a temporary extension of the distribution of this species from a freshwater and brackish water origin into adjacent marginal marine areas benefiting from the change in water chemistry during the terminal part of the MSC. A similar cause could be envisaged for the occurrence of *Aphanius crassicaudus*, mostly as articulated skeletons, during all the phases of the MSC and in shallow marine and brackish pre-evaporitic Messinian sediments (Caputo et al. 2009; Carnevale et al. 2006a, b, 2008, 2018, 2019; Gaudant 1979, 2002). In conclusion, the late Messinian sediments of the sub-stage 3.1 of the MSC and Lago Mare Event contain a really peculiar goby assemblage, which is dominated by brackish water species mostly with Paratethyan affinities (see below for further discussion), associated with rare downward migrated freshwater taxa and completely devoid of normal marine demersal forms.

Zanclean (Fig. 17): The Zanclean transgression appears to be associated with a re-establishment of the normal marine goby assemblage throughout the Mediterranean (Agiadi et al. 2013, 2020; Lin et al. 2015, 2017; Nolf & Cappetta 1989; Nolf & Cavallo 1994; Schwarzahns 1978, 1986). Most of these faunal assemblages originated from open marine environments at considerable depth either on the outer shelf or on the continental slope. These communities are primarily rich in species of *Lesueurigobius* (*L. friesii*, *L. sanzji*, *L. suerii*) which have a wide depth range, occasionally also *Hoeseichthys* (*H. bicornutus*, *H. brioche*), and more rarely *Thorogobius truncatus* and *Callogobius weileri*. Typical shallow-water forms are largely missing in these assemblages (but see below).

Until recently inner and middle shelf or shallow-water Zanclean otolith faunas have been virtually unknown. Agiadi et al. (2013a) described otoliths from the late Zanclean Voutes section of Crete deposited mostly at depths between 100 and 150 m (primarily outer shelf) and Agiadi et al. (2020) documented a highly diverse early Zanclean shal-

low shelf community from Agia Triada, which was deposited at a water depth of 100 m or less. Both locations are rich in various extant *Gobius* species, i.e., *G. auratus* (5–80 m), *G. fallax* (1–20 m), *G. geniporus* (0–30 m), *G. niger* (1–75 m), and *G. aff. paganellus* (0–15 m). Further shallow-water gobies comprise *Chromogobius zebratus* (0–12 m), *Zebrus zebrus* (0–3 m), and *Buenia affinis* (3–25 m) (depth ranges from Miller 1986 and Froese & Pauly 2019). *Lesueurigobius* species are the most common at Agia Triada; extant *Lesueurigobius* species are known from shallow-waters to considerable depths (see above). *Hoeseichthys brioche* has been found in the Voutes section, but mostly in the part representing a deeper environment reaching depths of about 200–300 m (upper slope) (Agiadi et al. 2013b). Genuine brackish water species are absent and so are species with Paratethyan affinities, which were dominant during the latest Messinian, except for *Proterorhinus cretensis*, which is the most common goby in one particular level at Voutes. We consider *P. cretensis* to represent an endemic relict species probably derived from the late Miocene *P. yigitbasi*. In conclusion, during the Zanclean the Mediterranean shallow-waters exhibit a highly diverse normal marine goby assemblage dominated by extant species and only one putative relict species of the peculiar latest Messinian goby communities.

Goby evolution and their response to events in the Mediterranean and Paratethyan interconnections

The data source for this study is shown in Figure 2, including selected previously published data. The gobioid species distribution is summarized in Table 1.

The evolutionary history of the Atlantic-Mediterranean goby stock can be followed back at least to middle Miocene times (Schwarzahns et al. 2020) and for some lineages up to early Miocene times (Hoedemakers & Battlori 2005). All the major Atlantic-Mediterranean lineages were already in existence in the middle Miocene. The Ponto-Caspian goby stock is first observed in the Serravallian (late Badenian) and was apparently intimately connected to the separation of the Paratethys from the Mediterranean (Bratishko et al. 2015, Schwarzahns et al. 2017). The majority of gobioid taxa identified in the late Miocene of the Mediterranean are clear descendants from the earlier Atlantic-Mediterranean

lineages or from the Ponto-Caspian stocks known from the Serravallian. However, the MSC and the subsequent normal marine conditions at the beginning of the Pliocene were clearly the cause of certain dramatic changes in the composition of the gobioid (and other fish) communities.

Here we recognize 18 gobioid species in the late Tortonian, 23 species in the pre-evaporitic Messinian, and 20 in the Zanclean (Fig. 19). The number of goby species is much lower during the MSC (10). The compositional change between Tortonian and early Messinian is of moderate amplitude but increased by about 50% between early Messinian and Zanclean as can be seen on Tables 2 and 3. The turnover rate is slightly lower when only considering indigenous Mediterranean gobies pertaining to the Atlantic-Mediterranean lineages.

Time interval	Number of species	Turnover rate (%)
early Messinian to Zanclean	21 of 32	66%
early Messinian to Zanclean indigenous Mediterranean only	15 of 26	58%
late Tortonian to early Messinian	12 of 27	44%
late Tortonian to early Messinian indigenous Mediterranean only	9 of 22	41%

Tab. 2 - Fish fauna turnover rates from the Tortonian through the Zanclean in the Mediterranean. The turnover rate in the tabulation reflects the number of non-persistent species across a boundary versus the total number of species combined.

The changes in the composition of the goby communities becomes even clearer when assessing the rate of persistent extant species in the stratigraphic intervals (Lyellian percentage):

Time interval	Number of species	Lyellian percentage
Zanclean	14 of 20	70%
MSC stage 3	1 of 10	10%
pre-evaporitic Messinian indigenous Mediterranean only	8 of 16	50%
pre-evaporitic Messinian	8 of 23	35%
late Tortonian	5 of 18	28%

Tab. 3 - Number of extant species persisting through the Tortonian–Zanclean (Lyellian percentage).

The Lyellian percentage was moderate during the late Tortonian, with a slight increase to about 35% just before the onset of the MSC, which is slightly less than observed in other late Miocene otolith-based assemblages (Schwarzahns 2019). The low Lyellian percentage indicates that a number of goby taxa occurring in the Mediterranean during the late Miocene may have been endemic or else expatriate species that became extinct during the terminal Miocene events (MSC). The Lyellian percentage drops to a very low level (10%) during the MSC with only one persistent species in that interval, *Aphia minuta*. Clearly this represents a dramatic event that requires some specific explanation (see below). The Zanclean then shows a sudden increase of the Lyellian percentage to 70%, which is consistent with the Lyellian percentage of 77% for the entire otolith-based assemblage of Agia Triada calculated by Agiadi et al. (2020). This percentage is in a similar ratio as observed in other otolith-based faunas of early Pliocene age (Schwarzahns 2019). The change to a high percentage of extant taxa from the late Miocene to the early Pliocene was also observed in previously studied otolith assemblages (e.g., Nolf & Cappetta 1989; Nolf & Girone 2006). However, articulated skeletons exhibit a higher percentage of fossil species in both the late Miocene and early Pliocene (e.g., Landini & Sorbini 1992, 2005), which we regard as an expression of the generally more conservative approach in otolith research.

MSC, Lago Mare, and Paratethyan–Mediterranean interconnectivity, setting of the scene. The publication of the first model of the Messinian Salinity Crisis in the Mediterranean by Hsü et al. (1973) included a short-lived interval that followed the evaporite deposition and preceded the re-establishment of normal marine conditions apparently caused by the re-flooding of the Mediterranean with marine waters at the beginning of the Pliocene. These deposits have long been known and are commonly termed Lago Mare (Lake-sea), and are characterized by a peculiar freshwater to brackish fauna (e.g., Selli 1954; Ruggieri 1967). According to the traditional concept, the origin of the Lago Mare sediments resulted from the synergistic effect of an intensive runoff linked to the humid global climatic conditions and the capture of the Paratethyan (Black Sea) drainage through a canyon system located somewhere in the Aegean region (McCulloch & De Dekker 1989). It was particularly the occurrence of many ostracods

and molluscs of supposed Paratethyan origin in the sub-stage 3.2 (Lago Mare phase), which led to the hypothesis of a connection between the Mediterranean and the Paratethys near the end of the Messinian (e.g., Cita et al. 1978; Esu 2007; Esu & Popov 2012; Gliozzi 1999; Gliozzi et al. 2005; Sciuto et al. 2018; Stoica et al. 2016). Much emphasis has been devoted in several articles to define the precise timing of the events during this phase of the MSC (e.g., Bache et al. 2012; Çağatay et al. 2006; Grothe et al. 2018, 2020; Krijgsman & Meijer 2008; Ryan 2009; Suc et al. 2015). However, some recent papers have questioned the reliability of the Lago Mare concept based on the recognition of stenohaline mesopelagic fish remains in the Lago Mare interval (Carnevale et al. 2006a, b, 2008, 2018, 2019) and on a re-interpretation of perceived Paratethyan immigrants in the molluscan fauna as Mediterranean endemics (Harzhauser et al. 2015). Alternative concepts have been proposed that considered brackish water along a broad coastal belt throughout the Mediterranean, as also partially suggested herein, or a “stratified” model with a brackish upper layer in the Mediterranean, an intermediate marine layer fed from the Atlantic and an anoxic deepwater zone (Marzocchi et al. 2016).

In addition to the Lago Mare Event, other ephemeral connections of the Mediterranean with the Paratethys have been proposed and discussed for a variety of time slices in the middle and late Miocene. Bartol et al. (2014) hypothesized a connection between the Central Paratethys and the Mediterranean during the late Badenian (early Serravallian). Popov et al. (2006) proposed that certain Mediterranean biota emigrated into the Eastern Paratethys along the southern shores of the Pontian Basin from Turkey to Georgia sometime during the later part of the early Meotian. Palcu et al. (2019) hypothesized that such a connection may have existed during the peak of the lower Meotian transgression at about 6.9 Ma. Van Baak et al. (2016) postulated a connection between the Mediterranean and the Paratethys before the onset of the MSC around 6.12 Ma.

Migrating gobies, the data-base. The analysis of the late Miocene goby assemblages of the Mediterranean may add a further stepping stone towards a better understanding of the biodynamic effects and biotic consequence of the MSC and, more importantly, of the potential biotic interactions with

the Paratethys. Gobies offer a tremendous opportunity in this context, since they are highly adaptive to transitional marine environments, are rich in euryhaline taxa, are able to diversify rapidly under ecological stresses, and therefore can make use even of ephemeral and not fully marine gateways for migration. Furthermore, some extant Ponto-Caspian species are known to be highly invasive (Dillon & Stepien 2001; Jacobs & Hoedemakers 2013).

The goby assemblage found in the Lago Mare deposits shows a great affinity to the Ponto-Caspian goby stock of the Paratethys (Figs. 18–19). Such Paratethyan affinity is not restricted to gobies and involves other fish taxa, like *Clupeonella* and certain sciaenids (e.g., Bannikov et al. 2018) as well. This study, however, provides evidence that the connectivity between the Mediterranean and Paratethys was not limited to the Lago Mare Event. In the following, we discuss the occurrence and possible implications of late Miocene and early Pliocene Mediterranean fishes of putative Paratethyan affinities. It has to be stressed, however, that the knowledgebase of otoliths in the Eastern Paratethys is largely incomplete, particularly after the Sarmatian s.s. (Volhynian), and hence the correlation with the time equivalent findings from the Mediterranean described here is often limited. Gobiid otoliths have been described by Pana (1977, 1982b, 1995) from the Dacian (late Zanclean) of the Dacic Basin in Romania, which has partly been available for review including undescribed material collected by her from the Khersonian and Meotian. Rückert-Ülkümen (1993, 1996, 2006) described otoliths from the Khersonian to early Meotian of western Turkey, which have been examined by one of us (WS). The otoliths reported in the problematic publications of Suzin (1968) from the Pontian Basin and from Pobedina (1954) and Djafarova (2006) from the Caspian Basin have not been available to us and, unfortunately, may be lost (personal communication by Artem Prokofiev, 2015). In conclusion, there are limited comparative data available from Meotian and Dacian, and no data from the Pontian, which would be a crucial period for the search of the potential Paratethyan migratory taxa.

The basis for any discussion about the Paratethyan-Mediterranean interconnection is the recognition of the timing of the origin of the Ponto-Caspian goby stock. The extant Ponto-Caspian gobies include two major groups: The *Neogobius*

group containing the genera *Neogobius* and *Ponticola* (split into more genera in some taxonomic studies), and the *Benthophilus* Group with the four genera *Anatirostrum*, *Benthophiloides*, *Benthophilus* and *Caspiosoma*. The otoliths of the *Benthophilus* group are highly diagnostic while those of the *Neogobius* group are difficult to distinguish from other Atlantic-Mediterranean members of the *Gobius* Lineage. There are further putative Ponto-Caspian goby genera in other groups, such as *Mesogobius*, *Proterorhinus*, *Hyrcanogobius*, possibly also *Zosterisessor* and certain clades within the species-rich genus *Knipowitschia*. Considerable evidence has been accumulated that most Ponto-Caspian goby clades were in existence in the Paratethys since the Sarmatian s.l. at least, and several of them have been identified in the late Badenian (Bratishko et al. 2015; Schwarzhans et al. 2017, 2020). In addition, there were certain extinct endemic forms such as *Hesperichthys* and precursors of persistent clades such as *Protobenthophilus* and *Proneogobius* during the late Badenian and Sarmatian s.s. (Volhynian). No such Ponto-Caspian forms have been found in the early Badenian or older sediments, but there were some enigmatic forms of uncertain relationships (*Weilerigobius* Schwarzhans, 2017). Therefore, it seems evident that there was an intimate relationship between the origin of the Ponto-Caspian goby stock and the separation of the Paratethys from the world ocean in the Serravallian.

Unfortunately, our knowledge of shallow-water otolith-based fish faunas from the middle Miocene of the Mediterranean is scarce. The only sizeable fauna so far known is that described from the late Serravallian of the Karaman Basin in SE Turkey (Schwarzhans 2014). The rich goby assemblage from the Karaman Basin shows a close resemblance with those of the early Badenian of the Central Paratethys, showing primarily an Atlantic-Mediterranean affinity, without any relationship with the early endemic Paratethyan (basal Ponto-Caspian) assemblage known from the late Badenian and Sarmatian s.s. of the Central and Eastern Paratethys (Bratishko et al. 2015; Schwarzhans et al. 2017), except for a single euryhaline species of the genus *Knipowitschia* (*K. suavis*). This observation does not provide support to a connection between the Paratethys and the Mediterranean during the late Serravallian. The condition for the late Badenian (early Serravallian) interval, for which Bartol et al. (2014) postulated a connection between the Central

Paratethys and probably derived from it through allopatric speciation. *Hesperichthys gironeae* was a fully marine species occurring in hemipelagic offshore sediments and apparently became extinct with the onset of the MSC. It is not known how far back in time it may range in the Mediterranean, but if we assume the existence of a ghost range, it is reasonable to interpret its occurrence as having resulted from immigration of its ancestor from the Central Paratethys during the late Badenian (following Bartol et al. 2014) and a subsequent Mediterranean endemization (Fig. 19).

The next oldest records of fishes with Paratethyan affinities are from the pre-evaporitic Messinian. Mediterranean fishes with Paratethyan affinities are represented by *Caspiosoma lini* and *Paratrisopterus rumanus*, the latter restricted to the Aegean Basin. The precise stratigraphic range of these two species in the area cannot be defined, but they have reliable records in the Paratethys. *Paratrisopterus rumanus* is relatively common in the late Badenian and Sarmatian s.s. of the Central Paratethys (Weiler 1943, 1950) and may have occurred at least until the middle Sarmatian s.l. in Azerbaijan (as *Macrurus* sp. in Djafarova 2006). Small specimens of *Caspiosoma lini* have been identified in the Pana's collection from the Khersonian to early Meotian paralic deposits of the Dacic Basin. It appears likely that both species migrated through the postulated Meotian gateway (Popov et al. 2006; Palcu et al. 2019) (Fig. 19). *Paratrisopterus rumanus* so far has only been found in the Messinian of the Aegean Basin (Skyros) while in Italy the genus is represented by *P. labiatus* (Carnevale et al. 2018). In Skyros, *P. rumanus* was associated with *Bregmaceros albyi*, with clear implications for the connectivity of the Aegean Basin during that time. Popov et al. (2006) assumed ephemeral connections between the Black Sea Basin of the Eastern Paratethys and the Mediterranean through the Aegean Basin. A similar view was expressed by Palcu et al. (2019) who however showed the Aegean Basin as part of the Mediterranean and clearly separated from the Black Sea Basin in their late Tortonian to early Messinian paleogeographic map. Grothe et al. (2020) instead show the Aegean domain as connected to the Black Sea Basin during the early Messinian. *Paratrisopterus rumanus* definitely points to a migration from the Eastern Paratethys/Black Sea Basin during or before the Messinian. *Bregmaceros albyi* on the other hand is a pelagic oceanic species

with a long range in the Mediterranean from middle Miocene through at least early Pliocene, but it has not been found anywhere in the Paratethys after the Karaganian Crisis (early Serravallian).

A new influx of gobies of Paratethyan origin took place in the pre-evaporitic Messinian just below the first MSC level in the brackish/coastal marine paleobiotope of Strada degli Archi (see also Caputo et al. 2009). The incoming taxa are *Pomatoschistus bunyatovi*, *Proterorbinus yigitbasi* and *Zosterisessor exsul*. All of them have been found in the Eastern Paratethys, although a relatively long ghost range period has to be assumed for *P. bunyatovi*, which has not been identified yet from the Paratethys from younger sediments than of Bessarabian age. *Proterorbinus* and *Zosterisessor* are also the only goby genera of presumable Ponto-Caspian origin that were able to migrate into the Mediterranean more recently during the re-connection of the Black Sea to the Mediterranean during the Holocene. Apparently, their late Miocene ancestors were euryhaline too and not restricted to brackish Caspian type water salinities, and therefore the most adapted for a Mediterranean invasion from the Ponto-Caspian area. No other species of the Ponto-Caspian genera *Mesogobius*, *Neogobius*, *Ponticola*, or the *Benthophilus* group entered the Mediterranean in the Holocene. In Strada degli Archi, they co-occur together with indigenous euryhaline Mediterranean species, i.e., *Aphia minuta*, *Lesueurigobius suerii*, and *Gobius reichenbacheri*, while normal marine environments do not contain any of these Paratethyan immigrants (e.g. in Verduno). The occurrence of *Proterorbinus yigitbasi* and *Zosterisessor exsul* is consistent with a Mediterranean–Eastern Paratethys connection just before the onset of the MSC at 6.12 Ma, as postulated by van Baak et al. (2016), although an older migration around 6.9 Ma as hypothesized by Palcu et al. (2019) cannot be excluded. A pre-Messinian arrival is however unlikely since the late Tortonian paralic deposits of Cessaniti are completely devoid of gobioid taxa of Paratethyan affinities (see above).

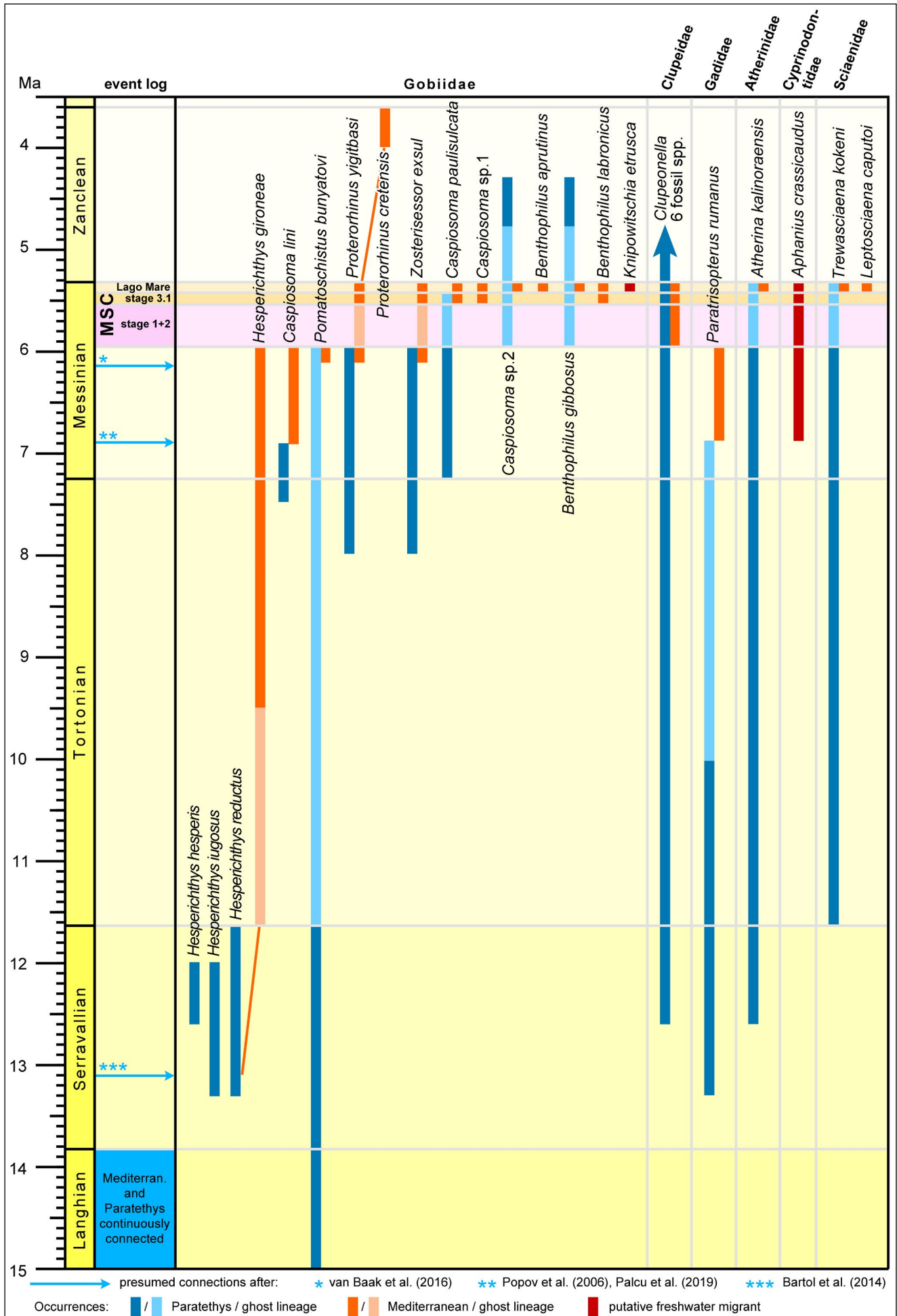
During the MSC, otoliths are only known from its final stage 3, in both the sub-stage 3.1 and the Lago Mare Event (stage 3.2). Like with other components of the latest Messinian biota (e.g., bivalves: Esu 2007, Esu & Popov 2012; ostracods: Gliozzi 1999; dinoflagellates: Grothe et al. 2018), taxa with Paratethyan affinities are also very abundant in the otolith-based fish fauna (and rare artic-

ulated skeletons; see Carnevale et al. 2018, and literature cited therein). In gobies, *Proterorhinus yigitbasi* and *Zosterisessor exsul*, which already occurred before the onset of the MSC (see above) are the most common. In addition, a number of new species of typical Ponto-Caspian genera are recorded as well: *Benthophilus aprutinus*, *B. gibbosus*, *B. labronicus*, and *Caspiosoma paulisulcata* (Fig. 19, Tab. 1). Indigenous Mediterranean goby taxa from the times before the MSC are completely absent except for the nektonic *Aphia minuta* (Fig. 18, Tab. 1). The disappearance of such gobies with Mediterranean affinities is interpreted as having been caused by the disappearance of suitable environments for normal marine demersal fishes because of the establishment of a coastal belt of brackish shallow-waters and poorly oxygenated deepwater zones. In addition to the gobies listed above, other fishes with Paratethyan affinities are observed as well, i.e., *Clupeonella* sp. (Clupeidae), *Atherina kalinoraensis* (Atherinidae), *Trewasciaena kokeni*, and *Leptosciaena caputoi* (Sciaenidae). Interestingly though, certain marine euryhaline shallow-water fishes with Mediterranean affinities occurred at the same time, i.e., *Alosa* sp. (Clupeidae), *Atherina* sp. (Atherinidae), *Paratrisopterus labiatus* (Gadidae), and *Argyrosomus regius* (Sciaenidae; see Bannikov et al. 2018; Carnevale et al. 2018), clearly indicating that part of the Mediterranean stock persisted during the Lago Mare phase. Also, stenohaline mesopelagic fishes of Atlantic-Mediterranean affinities persisted, particularly Myctophidae (Carnevale et al. 2008, 2018). Finally, there are indications that putative freshwater to brackish water fishes took advantage of the paleoenvironmental situation and descended into the Lago Mare environment, i.e., *Knipowitschia etrusca* and possibly *Aphanius crassicaudus* (Cyprinodontidae) (Fig. 19).

The apparent Paratethyan biogeographic relations of the ostracod fauna during the Lago Mare Event have been used as the main argument in support for the theory of the capture of Paratethyan water influx into the Mediterranean at that time (e.g. Gliozzi 1999; Scuito et al. 2018; Stoica et al. 2016). Popescu et al. (2009) and Grothe et al. (2017) used the distribution of the dinoflagellate *Galeacysta etrusca* to infer a migration path through the Paratethys and into the Mediterranean during the Lago Mare Event. Esu (2007) found close relations between limnocardine bivalves of the Lago Mare phase in Italy with the time equivalent Pontian fauna of

the Dacic Basin but subsequently also considered certain endemic Mediterranean species as derived from an older Paratethyan stock (Esu & Popov 2012). Harzhauser et al. (2015) studied (mainly terrestrial) gastropods from the Lago Mare phase of Piedmont, Italy, and found “no evolutionary relation to coeval Pannonian-Pontian faunas of Lake Pannon or the Dacian Basin.” Unfortunately, no time equivalent, Pontian otoliths are known from the Black Sea Basin, and data from the Meotian of the Dacic Basin and western Turkey and the Dacian of the Dacic Basin are scarce and allow only for a limited correlation with the otoliths described herein from the stage 3 of the MSC. Nevertheless, there are some reliable data available indicating that the following species that occurred in the Mediterranean during the Lago Mare event also occurred in the Black Sea Basin, including *Proterorhinus yigitbasi*, *Zosterisessor exsul*, possibly *Caspiosoma paulisulcata*, *Benthophilus gibbosus*, *Clupeonella* sp., *Atherina kalinoraensis*, and *Trewasciaena kokeni*. There are, however, also at least three species with presumed Paratethyan affinities, which have not (or not yet) been found in the Paratethys: *Benthophilus aprutinus*, *B. labronicus*, and *Leptosciaena caputoi*. These species could either represent endemic Mediterranean species derived from earlier immigrated Paratethyan ancestors, or they have simply not yet been found in the Paratethys because of the lack of relevant sampling ‘*quod erat inquirendum*’. The genus *Benthophilus* is of particular interest because of its rapid diversification and adaptability and because it is one of the most typical “Caspian brackish” dependent extant goby genera (Miller 2004). It appears that it would have required a low salinity connectivity for a successful migration from the Paratethys into the Mediterranean compared to the more euryhaline

Fig. 19 - Interactions between Paratethyan and Mediterranean fishes. Range charts of otolith and skeleton-based data (for *Clupeonella* spp. and *Aphanius crassicaudus*) of fishes in the Mediterranean with Paratethyan affinities. Distribution ranges and inferred ghost ranges are color coded for the respective provenances. Hypothesized time windows of connection of both seas other than during the Lago Mare phase are marked with reference to respective publications. Furthermore, presumable freshwater descendants into the marginal Mediterranean Sea are also color coded.



genera *Proterorhinus* or *Zosterisessor*. On the other hand, the high degree of environmental adaptation of the three *Benthophilus* species observed during the Lago Mare Event (see above) could indicate an earlier immigration event that allowed for some time to evolve specific adaptations. In conclusion, we remain uncertain whether the abundance of fishes of Paratethyan affinities during the Lago Mare Event would be the expression of an immigration at that time, or rather, reflects their flourishing in a favorable environmental setting after some earlier migration, or a combination of both effects since certain species are already identified in the Mediterranean prior to the MSC. Only an intense and detailed investigation of otoliths from time-equivalent sediments from the Black Sea Basin could possibly resolve this conundrum.

The complete re-establishment of the full connections between the Mediterranean and the Atlantic in the Zanclean led to the development of fully marine conditions along the coastal belt and of a well-oxygenated water column throughout the Mediterranean Basin. None of the many and diverse gobies of Paratethyan affinities of the late Miocene discussed herein and especially those of the Lago Mare phase have been recognized anywhere in the Zanclean sediments, with one notable exception, that of *Proterorhinus cretensis* in the late Zanclean of Voutes, Crete. Instead, the Zanclean goby assemblages are rich and diverse with normal marine taxa of Atlantic-Mediterranean origin, and many of which are persisting until today (see above). If still present in the early Pliocene, brackish water fishes with Paratethyan affinity would have been probably restricted in marginal marine and paralic environments. The present distribution of Ponto-Caspian gobies in the Black Sea may serve as a model of what might have been expected in the early Pliocene of the Mediterranean. However, no relevant marginal marine or freshwater sediments have been studied from the Zanclean in the Mediterranean for otoliths, and hence, the survival of Lago Mare faunal elements into Zanclean times remains purely speculative. *Proterorhinus cretensis* is interpreted herein to represent an endemic Mediterranean species that evolved from from the late Miocene Paratethyan stock, i.e., probably from the immigrant *P. yigitbasi*. It is perhaps not surprising that the species again represents a Ponto-Caspian gobiid genus with tolerance for normal marine salinities, which was

also among the first occurring as an immigrant in the pre-evaporitic sequence. Thus far, no gobies with Paratethyan affinities have yet been found in the Mediterranean from younger sediments of late Pliocene or Pleistocene age.

CONCLUSIONS AND OUTLOOK

The late Miocene (late Tortonian and Messinian) and early Pliocene (Zanclean) of Italy and Greece has yielded a rich and diverse gobioid fauna as reconstructed from otoliths. The locations sampled represented a vast spectrum of paleoenvironments from deep, open marine through various normal marine shelf locations, to brackish and restricted marine lagoonal and paralic paleobiotopes. The Mediterranean goby assemblages were found to differ considerably in space and time, especially during the latest phase of the MSC with the possible establishment of transient connections with the Paratethys. Gobies appear to be particularly well positioned to trace even short-lived and not fully marine connections because many taxa are euryhaline or adapted specifically to brackish marine and other restricted environments, and as a group are able to react fast to environmental stresses through adaptive speciation (e.g., Rüber et al. 2003, Yamada et al. 2009, Larmuseau et al. 2010, Patzner et al. 2011).

With the study presented herein, the evolution of gobies in the Mediterranean is now captured to a reasonable extent. Clearly, the late Miocene gobies identified in the Mediterranean have derived from the Langhian (early Badenian) goby assemblage known from the Central Paratethys (Schwarzahans et al. 2020) at a time when it formed a continuous water body with the Mediterranean. Beginning with the Serravallian (late Badenian and Sarmatian), the evolution of gobies diverged between the Mediterranean and the Paratethys (Bratishko et al. 2015, Schwarzahans 2014, Schwarzahans et al. 2017), the latter leading to the Ponto-Caspian goby population of today. Late Serravallian goby assemblages from the Paratethys and the Mediterranean (SE-Turkey; Schwarzahans 2014) have been shown to contain no common species with a single exception, the euryhaline *Knipowitschia suavis*.

A good understanding of the late Miocene-early Pliocene goby fauna of the Mediterranean is

also instrumental to evaluate possible events of faunal exchange with the Paratethys during this time interval. However, the correlation with coeval goby otolith assemblages from the Black Sea Basin is hampered by a much poorer database and the need for revision of some older publications. We were able however, to review material from the collection assembled by Pana from the Meotian and Dacian of the Dacic Basin in Romania, and the publications of Rückert-Ülkümen (1993, 2006) from the Khersonian to Meotian of western Turkey.

The main results of our study of gobioid otoliths from the late Miocene to early Pliocene of Italy and Greece are the following:

1. The marine sediments from the Tortonian and early Messinian are dominated by goby otoliths of genera of Atlantic-Mediterranean provenance. Paratethyan taxa are rare and in one case (*Hesperichthys gironeae*) presumably represent a Mediterranean endemic species.

2. The paralic deposits from the late Tortonian of Cessaniti contain *Eleotris* otoliths, which are not present in the Mediterranean today and are characteristic of mangrove settings, especially in tropical and subtropical West Africa. This fauna did not contain any elements of Paratethyan affinity.

3. An increasing influence of Paratethyan migrants is observed in the shallow-water, brackish influenced sediments of Strada degli Archi just below the MSC. In a mixture of indigenous Mediterranean and expatriate Paratethyan faunal elements, the latter are represented primarily by genera with good tolerance for normal marine salinities.

4. The brackish paleobiotopes of the latest phase of the MSC (sub-stage 3.1 and Lago Mare event) were dominated by gobies (and other fishes) of Paratethyan affinities, some of which have also been identified in Meotian and Dacian sediments of the Eastern Paratethys. Indigenous Mediterranean goby taxa are missing, except for the nektonic *Aphia minuta*, probably because of the lack of suitable conditions for neritic demersal stenohaline fishes.

5. The Lago Mare sediments also included unusual unique records such as *Enigmacottus socialis*, a putative Psychrolutidae of uncertain origin, or *Knipowitschia etrusca*, a presumable descendant from freshwater systems that ventured into the brackish marine environments at that time.

6. Beginning with the Zanclean, the goby assemblage of the Mediterranean is again almost exclusively Atlantic-Mediterranean and contains 70% of extant species. Gobies of Paratethyan/Ponto-Caspian affinities, if still persistent, would have been most likely pushed into much less widely distributed brackish environments or into freshwater systems, similar to the situation nowadays in the Black Sea area.

Despite much recent research efforts that aimed at unraveling the evolution of the Gobioidae in the Neogene of the Mediterranean and Paratethys by means of otoliths (e.g. Bratishko et al. 2015; Reichenbacher 1998; Reichenbacher et al. 2007, 2018, 2019; Schwarzhans 2014, 2017; Schwarzhans et al. 2015, 2017, 2020), large knowledge gaps persist in many areas. Gobioid otoliths are for instance poorly known from early Miocene strata, particularly in the Mediterranean. Few data exist from shallow-water deposits of the western Mediterranean and fewer still from the adjacent Atlantic realms. Marginal marine environments may hold many more untapped data in the Neogene of the Mediterranean. However, the largest and most severe knowledge gap concerns otolith assemblages from the late Miocene (late Sarmatian s.l., Meotian and Pontian) and Pliocene of the Eastern Paratethys. In particular, no otoliths have ever been described from the Pontian of the Black Sea Basin, which would be crucial for a better understanding of the faunal interactions that existed with the Mediterranean during the MSC. We hope that this study will contribute to undertake more research in fossil goby otoliths in these areas and that it can serve as a basis to interpret new finds. Articulated skeletons of gobies with otoliths *in situ* (Bradic-Milinovic et al. 2019; Gierl & Reichenbacher 2015; Reichenbacher et al. 2007; Schwarzhans et al. 2017) have shown the importance of the calibration of isolated otoliths with skeletal-based taxa. We are aware of a number of further opportunities for such studies, and we hope that many more articulated fossil goby skeletons with otolith *in situ* will be investigated in order to affirm interpretations gained from isolated otoliths. Our study aims at reassuring the importance of evaluating isolated otoliths because of their abundance in many different environments and geologic times, and we expect that important fossil otolith assemblages from the Mediterranean and the Paratethys will be further investigated in the future.

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