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# The Fossil Record of Ray-Finned Fishes (Actinopterygii) in Greece



Thodoris Argyriou

## 1 Introduction

A continuously thickening count of over 33,000 living species, already surpassing that of all other vertebrate species combined, renders Actinopterygii (ray-finned bony fishes) the most diverse clade of vertebrate animals (Nelson et al. 2016; Eschmeyer and Fong 2019). This vast taxonomic richness is coupled with an astounding array of anatomical, feeding, reproductive, locomotory, and other biological specializations, which enabled ray-fins to conquer most aquatic niches on the planet (from abyssal plains to hypersaline volcanic lakes), and to even glide, or crawl, outside the aquatic medium (Helfman et al. 2009; Nelson et al. 2016; Froese and Pauly 2019).

Actinopterygian origins date back to at least the late Silurian (~425 Ma), as inferred by the age of the first fossils of their sarcopterygian sister group (Zhu et al. 2009). The oldest definitive actinopterygian fossils are dated in the Early and Middle Devonian (Giles et al. 2015; Lu et al. 2016). Similarly, all major living actinopterygian lineages (Cladistia; Chondrostei; Neopterygii) are widely thought to have diverged in the Paleozoic (Near et al. 2012; Broughton et al. 2013; Sallan 2014; Betancur-R et al. 2015; Friedman 2015), but their first accepted occurrences are in early and middle Mesozoic rocks (Olsen 1984; Hilton and Forey 2009; Giles et al. 2017). The current taxonomic dominance of actinopterygians relative to other aquatic vertebrates was foreshadowed by their impressive Triassic radiation(s), in the

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aftermath of the catastrophic Permian-Triassic extinction (~251 Ma; Friedman and Sallan 2012; Romano et al. 2016), and the appearance of Telostei in the Middle Triassic (total group: Tintori et al. 2015; Arratia 2017). The Cretaceous–Paleogene Extinction (K/Pg) led to the complete eradication or decimation of several long-lasting Mesozoic actinopterygian lineages, especially in marine waters (Friedman 2009; Friedman and Sallan 2012; Guinot and Cavin 2016). Paleogene and younger radiations in the newly emptied ecological spaces marked the beginning of a new era in the evolutionary history of the clade, in which Teleostei, largely represented by members of the ostariophysan (mostly in freshwaters) and acanthomorph (spiny-rayed fishes) super-radiations, are established as dominant vertebrate components of global aquatic niches (Alfaro et al. 2009, 2018; Sibert and Norris 2015).

The long evolutionary history of ray-finned fishes is evidenced by a particularly rich fossil record. Stratified aquatic deposits can yield large numbers of articulated, yet flattened individuals (for some examples from Greece, see Gaudant 2001, 2004). Laminated rocks, corresponding to rapid deposition and low energy and low bottom oxygenation environments, can sometimes allow the preservation of very delicate structures, such as gut contents, embryos, or even soft tissues and pigments (e.g., Viohl 1990; Vinther 2015; Argyriou et al. 2016; Maxwell et al. 2017), allowing for painting a more vivid picture of past ecosystems and biotic interactions within them, while providing important insights into the evolution of key anatomical structures and biological specializations. Three-dimensional anatomical structure is only rarely preserved in fossil actinopterygians, but such fossils can allow the study of structures that are lost in flattened individuals (e.g., braincases, sensory endocasts, gill skeletons), and are of tremendous value to paleontologists, especially in light of modern fossil imaging and investigation techniques (Friedman et al. 2015; Argyriou et al. 2018). Equally important biological and geological information often derives from studies of identifiable ichthyoliths (isolated bones, scales and teeth, Bellas et al. 1998; Argyriou et al. 2015; Vasileiadou et al. 2017) and otoliths, (e.g., Agiadi et al. 2013, 2019; Agiadi *this volume*). Due to their exquisite fossil record, actinopterygians constitute an excellent means for studying the evolution of aquatic life on the planet, and its response to major biotic crises and extinctions (Friedman and Sallan 2012; Guinot and Cavin 2016; Romano et al. 2016). At the same time, the largely ectothermic traits, in conjunction with the strict environmental and habitat preferences of most ray-fins (e.g., Helfman et al. 2009), establish their fossil record as a powerful tool for making paleoenvironmental and paleobiogeographical inferences (Gaudant 2002; Landini and Sorbini 2005a; Argyriou et al. 2015; Carnevale et al. 2018), often through the scope of isotope geochemistry (e.g., Otero et al. 2011).

Historically, the study of fossil actinopterygians has been associated with several challenges, chief of which is the sheer richness of actinopterygian biodiversity and fossil record, which encompasses numerous groups of tens or hundreds of millions of years of divergent evolutionary histories (Friedman and Sallan 2012; Near et al. 2012; Broughton et al. 2013; Betancur-R et al. 2015; Friedman 2015; Nelson et al. 2016). As a result, commonly used synapomorphies for many clades of ray-fins—mostly teleosts—are established on modern taxa alone, and their validity has not been questioned by large-scale phylogenetic analyses (see, e.g., Wiley and Johnson

2010). Placing early diverging fossil taxa without closely related modern representatives on the tree of life is an extremely difficult task and constitutes a frontier in current paleoichthyology (Sallan 2014; Friedman 2015; Giles et al. 2017; Argyriou et al. 2018). Even when modern-looking forms are examined, their study usually requires consultation of extensive comparative materials in collections. Often limited anatomical information coming from two-dimensionally flattened fossils, as well as prevalent issues related to structural homology—mostly encountered when examining deeply nested forms (Schultze 2008)—pose additional obstacles for deciphering the fossil record and history of the clade.

Fossil actinopterygians form an extremely important, but historically overlooked, component of Greek vertebrate paleontological research. This synthesis aims at bringing together available information on the rich record of body fossils of the clade in Greece and critically assessing historical attributions in terms of validity and reliability—at least according to the opinion of the author, and based on a critical review of the literature. By placing all relevant occurrences in an up-to-date systematic, geographic, and stratigraphic context, it is anticipated that this chapter will fuel future paleo-ichthyological research in Greece.

## 2 Historical Overview and Collection Information

Actinopterygians from the Miocene of Kymi, Euboea, were the first to attract scientific attention on fishes from Greece, during the 1800s (de Waldheim 1838, 1850; Valenciennes 1861; Gaudry 1862; Unger 1867), but these early authoritative—rather than synapomorphy-based—taxonomic assessments are in need of revision, especially since they are not accompanied by adequate figures of the material. Fossil cyprinodontids were discovered in the Messinian of Crete by Raulin (1861) and were later revisited by Woodward (1901). In the same work, Woodward updated the taxonomic status of fossil percomorphs from Kymi, first described by de Waldheim (1838, 1850), on the basis of material in the collections of what is nowadays the Natural History Museum of London (but see Centropomidae section below). After a four-decade hiatus, Weiler described a fossil clupeid from the Miocene of Serres Basin (Weiler 1943).

The second half of the twentieth century saw an increase in interest in the study of Greek ray-fin fossil record. Kottek described some fragmentary leptolepid remains from the Toarcian (Early Jurassic) of Leukada, which derive from a since unexplored, and allegedly rich fossil fish bonebed near the village of Anavryssada (Kottek 1964). This represents the stratigraphically oldest occurrence of fossil ray-fins in Greece known to date. Melentis was the first Greek paleontologist to publish on fossil actinopterygians (Melentis 1967a, b). Unfortunately, his accounts of a †pyncnodontid from the Cenomanian (Late Cretaceous) of Lindos, Rhodes, should be treated with extreme caution (see †Pyncnodontidae section below). Important, but largely overlooked and preliminary taxonomic lists and figures of Late

Cretaceous–Paleogene actinopterygians from Eurytania, have been provided in a stratigraphic monograph by Koch and Nikolaus (1969).

Symeonidis and Bachmayer set the stage for later work on the diverse Neogene marine ichthyofaunas of Crete (Symeonidis 1969; Bachmayer and Symeonidis 1978; Bachmayer et al. 1984). Their taxonomic results in the case of the so-called †*Mene psarianosi* (= †*Alectis psarianosi*) and their newly erected syngnathiform species have been since revised (Bannikov 1987; Bürgin 1994; Gaudant 2001, 2004). Müller and Strauch (1994) also provided a short account of a fossil assemblage from the Pliocene of Prassas, Crete, which was subsequently revised (Gaudant 2001). Another interesting assemblage, containing both articulated skeletons, ichthyoliths and otoliths from the Messinian of Karpathos, was presented by Bellas et al. (Bellas et al. 1998). The bulk of research on Neogene marine actinopterygians was led by Gaudant between the late 1970s and the early 2010s. These works expanded on the alpha-taxonomic status and paleoenvironmental implications of fossils from Aegina (Gaudant et al. 2010b), Attiki (Gaudant and Symeonidis 1995), Crete (Gaudant 1979, 1980, 2001, 2004, 2014b; Gaudant et al. 1994, 1997a) and Gavdos Island (Gaudant et al. 2005, 2006), highlighted the richness and potential of the Miocene–Pliocene actinopterygian archive of Greece, and also contributed data for downstream analyses of Mediterranean actinopterygian diversity changes during the latter part of the Cenozoic (Gaudant 2002; Landini and Sorbini 2005a). Yet, detailed descriptions of Neogene actinopterygians from Greece and their systematic treatment are still lacking for the most part.

Few treatments of the Greek record of ray-fins have been published in the past two decades. Careful anatomical and systematic work on Tortonian (Přikryl and Carnevale 2017) and Pliocene (Sorbini and Tyler 2004) actinopterygians from Crete revealed the presence of new fossil species, indicating that actinopterygian diversity and taxonomy in the Neogene of Crete, and conceivably elsewhere in Greece, remain underappreciated. The study of Maastrichtian actinopterygians from Gavdos Island represents the first recent attempt to investigate the pre-Cenozoic fossil record of actinopterygians of the country (Cavin et al. 2012). The first investigation of microscopic ichthyoliths from Greek freshwater deposits (early Miocene, Lesvos Island) was only published a few years ago (Vasileiadou et al. 2017). Furthermore, a recently completed MSc. thesis has shed light on the late Miocene freshwater–brackish clupeids of Aidonochori, Serres Basin, Northern Greece (Kevrekidis 2016). Finally, a new study dealing with the Maastrichtian–Paleogene actinopterygian assemblages from Eurytania has been made available while this work was in press (Argyriou and Davesne 2021).

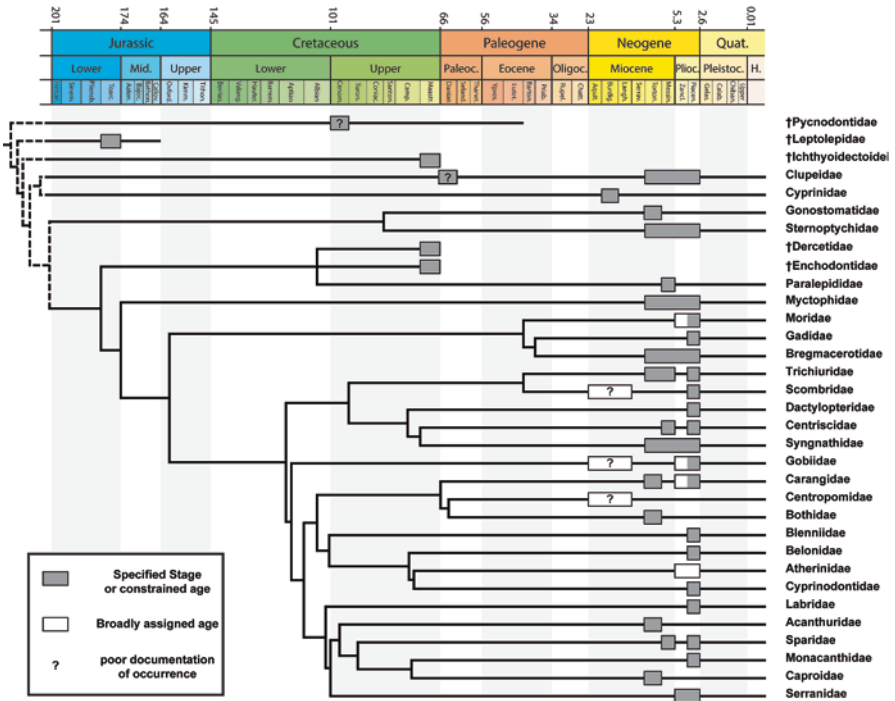
Over 170 years of research have contributed significantly toward creating a framework for the temporal, stratigraphic, and geographical distribution of fossil ray-fins in Greece, while also providing taxonomic assessments of relevant assemblages. At the same time, past research efforts have been sporadic and/or have largely concluded at a preliminary level, without tapping the potential informativeness of this rich record for a variety of subjects. These include the evolutionary histories and paleobiogeography of Eastern Mediterranean marine and freshwater faunas, or the study of major events, such as the K/Pg Extinction and the Messinian Salinity

Crisis. Unlike late Cenozoic mammals (see relevant chapters in this volume), research on the actinopterygian record of Greece has not received enough scientific attention and is still in its infancy (but see otoliths in Agiadi [this volume](#)). Detailed descriptions of Greek fossils are largely wanting, and older taxonomic assessments are in dire need of revision, posing obstacles for further analytical work. This is further exacerbated by the lack of organized collections of fossil fishes and recent comparative material in Greek institutions. A rudimentary-only collection of Cretaceous–Pliocene fossil fishes is housed at the AMPG (organized by the author and S. Roussiakis). Additionally, numerous teleostean skeletons from several Neogene localities of Crete (mainly *Bregmaceros* and *Spratelloides* from the Heraklion Basin) form part of the collections of the Natural History Museum of Crete. By contrast, rich collections from the Cretan Neogene are housed in the Natural History Museum of Vienna (Gaudant [2001](#), [2004](#)). Some few findings from the Miocene of Kymi, Euboea (Gaudry [1862](#); T.A. personal observations and communication with Giorgio Carnevale) and the Zanclean of Aegina Island (Gaudant et al. [2010b](#)) are housed in the MNHN, Paris, while additional fossils from the Miocene of Crete and possibly Kymi are housed in the Natural History Museum of London (Woodward [1901](#)).

### 3 Phylogenetic Relationships

Actinopterygians are widely accepted as a monophyletic group, despite owing their name to their rayed fins, which are also present in sarcopterygians (Friedman [2015](#)). Combinations of hard-tissue synapomorphies [(i) absence of jugal canal; (ii) presence of median aortic canal in the occiput; (iii) absence of endoskeletal basal plates of dorsal and anal fins; (iv) narrow interorbital septum; (v) lateral cranial canal; (vi) posteriorly expanded supratemporals; (vii) acrodin caps on teeth; (viii) fenestrated metapterygoidean portion of palatoquadrate; (ix) perforate propterygium embraced by fin rays; (x) presence of ganoine] are employed to distinguish Paleozoic actinopterygians from other osteichthyes, though, naturally, distinguishing lines dim when examining deeply nested taxa (Friedman [2015](#); Giles et al. [2015](#); Lu et al. [2016](#)).

The relationships among actinopterygians—neopterygians and teleosts in particular—had been a matter of controversy (e.g., see Patterson [1973](#) vs. Grande [2010](#), for the status of Holostei; Patterson and Rosen [1977](#) vs. Arratia [1997](#), for identifying the deepest branch of crown group Teleostei; or Davesne et al. [2016](#) for a summary of the complicated history of acanthomorph interrelationships) before the establishment of reliable molecular systematic methodologies (Near et al. [2012](#), [2013](#); Betancur-R et al. [2015](#); Hughes et al. [2018](#)). More recent morphology-based investigations are slowly bridging the gap between molecular and morphological phylogenetic hypotheses (e.g., Grande [2010](#); Davesne et al. [2016](#)). It is now accepted that extant Actinopterygii are distributed across three major lineages of inferred Paleozoic origins: the basally diverging Cladistia (ropefish and bichirs); Chondrostei



**Fig. 1** Fossil record and time-calibrated phylogenetic relationships of major groups of Greek fossil fishes (skeletal record only). Only occurrences considered as valid herein are taken into account. Occurrences marked in darker gray boxes correspond to better constrained ages (usually biostratigraphically). White occurrence boxes correspond to broadly or tentatively assigned ages. Phylogenetic placement and time calibrations for extant groups follow Betancur-R et al. 2017. Placement of fossil taxa is as follows: †Pycnodontidae are established as non-teleostomorphs; †Leptolepididae and †Ichthyodectoidei (†Ichthyodectiformes) sensu Arratia 2017; †Dercetidae and †Enchodontidae as closely related to modern Aulopiformes sensu Davis and Fielitz 2010, although an agnostic placement of fossil taxa relative to extant ones is preferred here. Results from Argyriou and Davesne (2021) were not incorporated in the figures, or the text, as this work became available after the preparation of this chapter

(sturgeons and paddlefish); and Neopterygii, with the latter including the nowadays depauperate Holostei (gars and bowfin) and the overabundant Teleostei (Near et al. 2012; Betancur-R et al. 2015, 2017; Nelson et al. 2016; Hughes et al. 2018). The relationships of the major groups of ray-finned fishes found in Greece are shown in Fig. 1.

Teleostei account for ~99% of living actinopterygian species and are strongly supported as monophyletic by both morphological and molecular data (Near et al. 2012; Betancur-R et al. 2013, 2015; Broughton et al. 2013; Arratia 2017; López-Arbarello and Sferco 2018). Numerous hard-tissue synapomorphies support teleost monophyly, including: (i) orbital region of skull narrower than postorbital; (ii) presence of one suborbital bone between the posterodorsal margin of the infraorbital

series and the opercular apparatus; (iii) presence of two supramaxillae; (iv) lower jaw articulation located ventral to the posterior margin of the orbit; (v) articular fused with angular and retroarticular; (vi) notch on ascending margin of dentary; (vii) coronoid process formed by angular and dentary; (viii) lateral ridge on dentary separating dental and splenial portions of lower jaw; (ix) long epineural processes; (x) presence of 20–26 principal rays; (xi) presence of an enlarged dorsal scute preceding caudal fin (sensu Arratia 2017).

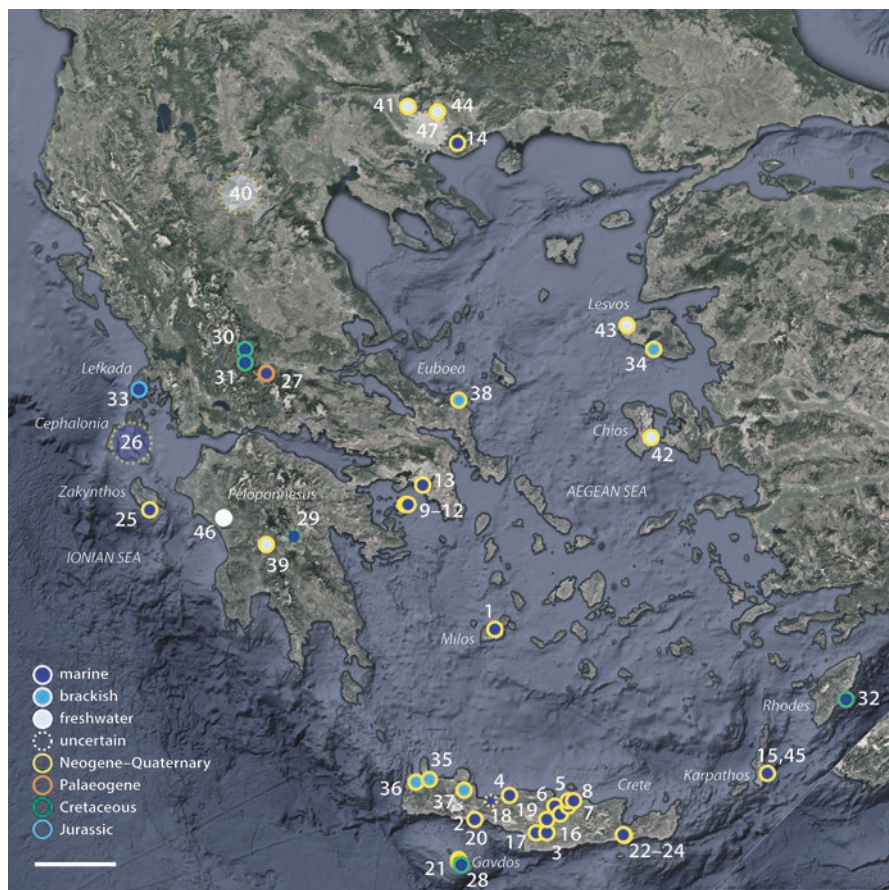
Apart from one problematic occurrence of a Cenomanian †pycnodontid in Rhodos Island (Melentis 1967a, b), the Greek actinopterygian archive is exclusively populated by teleosts (Appendix). †Leptolepid remains from the Toarcian of Leukada (Kottek 1964) represent the only ascertained stem teleost occurrence in Greece while all remaining occurrences correspond to members of crown group lineages. Reliably documented Mesozoic actinopterygians from Greece have been ascribed to extinct families (e.g., †Dercetidae, †Enchodontidae; see Koch and Nikolaus 1969; Cavin et al. 2012), whereas Cenozoic fossils have been predictably included in extant taxa (families, genera, and in some cases to the species-level; see Appendix) on the basis of broad morphological and meristic similarities. The phylogenetic affinities of Greek actinopterygian fossils have not yet been explored, to the exclusion of *Enchodus* cf. *dirus* from the Maastrichtian of Gavdos Island (Cavin et al. 2012).

## 4 Distribution in Greece and Nature of Deposits

As noted above, ray-finned fishes, and teleosts in particular, are expected to have gradually expanded their occupation of most aquatic ecological niches on the planet, especially after the Paleozoic (Friedman and Sallan 2012). They are thus expected to be present in sedimentary rocks that were deposited in a large spectrum of paleoenvironments, ranging from offshore and deep marine waters, to fluvial, or lacustrine freshwaters. However, freshwater deposits (and included fossils) are more difficult to be preserved in the geological record, due to their relative ephemerality and patchiness. It is thus unsurprising that the vast majority of fossil ray-fins in Greece come from marine deposits. To paint a more complete picture of the Greek fossil record, locality information mined from gray literature (e.g., conference, abstracts field guides, and unpublished theses), stratigraphic and sedimentological works from the 1970s to the 2010s, or deriving from personal observations of the author and communication with colleagues is also taken into account. A brief summary of fossiliferous localities, ages, and paleoenvironments is given below, and more extensively in the Appendix; these lists might not be exhaustive.

**Marine Occurrences** At least 33 indisputably marine, or likely marine localities have been recognized in Greece, although not all have been subjected to proper collecting and study (Fig. 2). The marine actinopterygian record of Greece begins with





**Fig. 2** Map of the occurrences of fossil ray-finned fishes from Greece. See Appendix for further information. **Marine occurrences:** 1, Northern Milos (Pliocene–Pleistocene); 2, near Frangokastello (middle–late Pliocene); 3, Roupas (Piacenzian, late Pliocene); 4, Stavromenos (Piacenzian); 5, Amnissos (Piacenzian); 6, Voutes (Piacenzian); 7, Prassas (Piacenzian); 8, Gournes (Piacenzian); 9, Aghia Marina (Piacenzian?); 10, Aghios Thomas (Zanclean); 11, Faros, Aegina (Zanclean?, early Pliocene?); 12, Temple of Aphrodite, Aegina (Zanclean?, early Pliocene?); 13, Kalamaki (Pliocene); 14, Akropotamos (Messinian); 15, ‘Unit b’, Pigadia Basin (Messinian); 16, Tsangaraki (late Messinian); 17, Mires (late Messinian); 18, unknown locality near Rethymnon (Messinian?); 19, Psalida (Tortonian–early Messinian); 20, Metochia (Tortonian–Messinian); 21, Karave (Tortonian); 22, Aghia Paraskevi Chapel (Tortonian); 23, 400 m from Aghia Paraskevi Chapel (Tortonian); 24, type strata of Makrylia Fm. (Tortonian); 25, Keri (Tortonian); 26, unknown locality in Kefallonia (late Miocene?); 27, Aghioi Theodoroi (Paleocene); 28, Gavdos (Pindos unit; late Maastrichtian); 29, near Megalopoli (Maastrichtian); 30, Aghia Trias-Domnianoi Road (Maastrichtian); 31, near Karpenisi (late Maastrichtian); 32, Lindos (Cenomanian?); 33, Anavryssada (Toarcian). **Brackish and potentially brackish occurrences:** 34, Vatera (Pliocene–Pleistocene); 35, Voukolies (Messinian); 36, Kalergiana (Messinian); 37, Neo Khorio (Messinian); 38, Kymi (early Miocene?). **Freshwater occurrences:** 39, Marathousa 1 (middle Pleistocene); 40, Florina–Ptolemais–Servia Basin (Messinian–Zanclean); 41, Ano Metochi (Messinian); 42, Thymiana (Burdigalian–Langhian); 43, Lapsarna (Burdigalian); 44, Aidonochori. **Uncertain environment:** 45, ‘Unit e’, Pigadia Basin (middle Pleistocene); 46, Gryllos-Mesovouni (Pliocene–Pleistocene); 47, lignite mine in Strymonas valley (Pliocene). See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/Copernicus. Scale bar equals 80 km, North faces upward

some poorly preserved †leptolepids from the Toarcian of the Ionian Unit, Leukada Island (Kottke 1964). Other published Mesozoic occurrences are restricted to the Cenomanian of Lindos, Rhodos Island (Melentis 1967a, b), and the terminal Maastrichtian of Pindos Unit, in Eurytania (Koch and Nikolaus 1969; Argyriou and Davesne 2021) and Gavdos Island (Cavin et al. 2012). Unpublished teleost remains are also present in Late Cretaceous exposures of Pindos Unit in Northern and central Peloponnese (T.A. personal observations and personal communication with E. Koskeridou, G. Theodorou and K. Trikolos).

The Cenozoic record of Greece is very rich, but is largely skewed toward the late Miocene and Pliocene. The oldest reported Cenozoic occurrences come from flysch deposits of the Pindos Unit in Eurytania and are dated as Paleocene–early Eocene (Koch and Nikolaus 1969; Argyriou and Davesne 2021). Rich Tortonian marine assemblages can be found in the vicinity of Ierapetra and possibly Heraklion, Crete (Symeonidis 1969; Gaudant et al. 1997a; Gaudant 2004), and Gavdos Island (Gaudant et al. 2005), while a fish-bearing, bituminous horizon in Keri, Zakynthos has been identified, but not yet studied (Dermitzakis 1979; T.A. personal observations). Messinian fossiliferous deposits predating the Messinian Salinity Crisis are widespread in Crete, Gavdos (Gaudant 1980; Gaudant et al. 1997b, 2006) and Karpathos (Bellas et al. 1998), but only one poorly studied horizon is known in continental Greece, in Acropotamos, Kavala (Dermitzakis et al. 1986). Teleost teeth broadly ascribed to the late Miocene are also present in Kefalonia (pers. obs. on AMPG material; S. Roussiakis pers. comm.). The most notable early Pliocene occurrences come from the diatomitic horizons of Aegina Island, but despite their potential informativeness regarding the state of the Mediterranean in the immediate aftermath of the MSC, they remain understudied (Gaudant et al. 2010b; Argyriou and Theodorou 2011). The late Pliocene of Heraklion Basin, Crete, hosts exceptionally preserved and diverse ichthyofaunas (Gaudant et al. 1994; Gaudant 2001). Additional Pliocene occurrences have been reported in Rethymno, Chania, and Attiki regions (Gaudant and Symeonidis 1995; Gaudant 2001; Sorbini and Tyler 2004). Late Pliocene and Pleistocene fossiliferous horizons situated in Milos and Rhodos wait to be sampled and studied (Cornée et al. 2006; Calvo et al. 2012). Finally, wooden crates containing what appear to be unstudied marine teleost fossils from the Neogene are hosted in the collections of the AMPG (T.A. personal observations). Some of these fossils are wrapped in newspapers that treat the Russo-Japanese war of 1904–1905 as current news, but no locality or collection information has been retrieved so far.

**Freshwater and Brackish Occurrences** Approximately six freshwater, and five brackish or potentially brackish occurrences have been reported. Burdigalian ichthyoliths from Lapsarna, Lesvos (Vasileiadou et al. 2017), and the early Miocene of SE Chios (Reichenbacher and Böhme 2004) constitute the oldest known freshwater fish assemblages in Greece. Ray-fin remains have been reported from the Messinian of Metochi, Serres (Georgalis et al. 2017); the Messinian–Zanclean of Florina–Ptolemais–Servia (Hordijk and de Bruijn 2009); and the Pleistocene of Marathousa, Megalopolis (Panagopoulou et al. 2018), but have not yet been studied.

The understudied assemblages from Kymi, Euboea, are tentatively dated as early Miocene, and tentatively interpreted as brackish, based on the supposed euryhaline affinities of recognized taxa (de Waldheim 1838, 1850; Gaudry 1862; Unger 1867; Woodward 1901; Kottis et al. 2002). Occurrences of †*Aphanius crassicaudus* in gypsiferous evaporitic deposits in Neo Khorio, Voukolies, and Kallergiana, Crete, have been identified as brackish and concurrent with the peak of the Messinian Salinity Crisis and the supposed desiccation of the Mediterranean in the late Messinian (Freudenthal 1969; Gaudant 1979, 2014b). However, there is evidence of primarily marine clupeids in the same beds, complicating this narrative (Gaudant 1980). The Pliocene clupeids from Serres Basin (Weiler 1943), and unidentified Plio-Pleistocene ray-fins from Vatera, Lesbos (Drinia et al. 2002), might also correspond to brackish, or freshwater deposits. New information on fresh or brackish waters of Greece is coming from the ongoing study of fossil clupeids from Aidonochori, Serres Basin (Kevrekidis 2016). Another possible addition to this list is the middle Pleistocene of Pigadia Basin in Karpathos Island. There, a vertebra possibly belonging to an ostariophysan—a group commonly found in freshwaters—has been found (Bellás et al. 1998).

## 5 Systematic Paleontology

Due to the taxonomic and phylogenetic breadth covered in this chapter, this section is organized in monophyletic (when possible) families. Synapomorphies for each family are not given, as this lies beyond the scope of this work. Instead, the reader is referred to Wiley and Johnson (2010), Nelson et al. (2016), and Betancur-R et al. (2017) for basic information on morphological synapomorphies and redirection to specialized literature. Taxonomic ranks superior to the genus level are unnamed, since they are obsolete in a modern phylogenetic context. Information on naming authorities and type genera and species is largely based on Wiley and Johnson (2010) and Eschmeyer and Fong (2019). The order of families and classification are based on the scheme proposed by Betancur-R et al. (2017), with fossil families being included according to their widely accepted position (see caption of Fig. 1). References regarding naming authorities, which are not also cited in the running text are not given in the reference list due to space constraints. Throughout the text and figures, extinct taxa are preceded by the dagger symbol ‘†’, following Patterson and Rosen (1977). Fossils that were not properly described and/or figured, or the geological context of which is problematic are only listed in the Appendix.

### **Actinopterygii sensu Goodrich, 1930**

#### **Neopterygii Regan, 1923**

##### **†Pycnodontiformes Berg, 1937**

### †Pycnodontidae Agassiz, 1833

**Type Genus** †*Pycnodus* Agassiz, 1833.

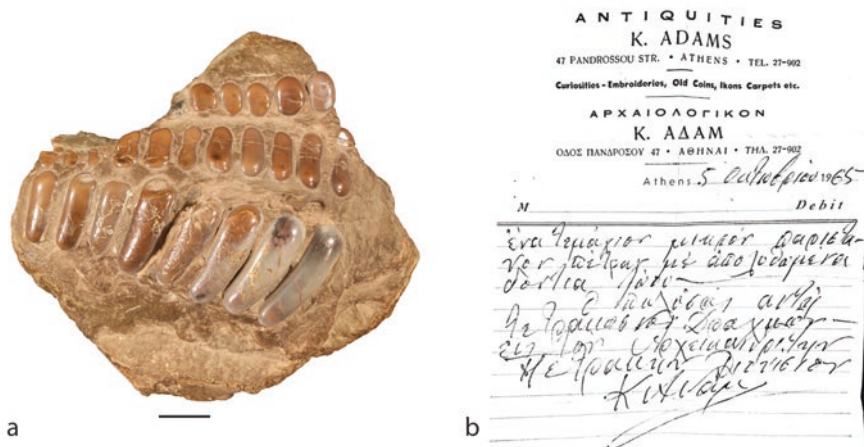
### †*Coelodus* Heckel 1854

**Type Species** †*Coelodus saturnus* Heckel, 1854.

**Nomenclatural and Taxonomical History** Initially described as †*Coelodus muensteri* (Melentis 1967a, b; Fig. 3a), but the specific attribution was subsequently challenged and removed (Schultz et al. 1997).

**Distribution** In Greece, this taxon is known only from the Cenomanian of Lindos, Rhodos (Melentis 1967a, b). Outside Greece, this taxon has been reported from Europe and the Americas, but only its European occurrences have been revised. The latter include the Upper Jurassic–Cenomanian of UK and continental Europe, including the Balkans as well (Schultz et al. 1997).

**Comments** This is a problematic occurrence, as the original locality and lithological context are conjecturally established. Prior to its study (Melentis 1967a, b), the †pycnodontid in question was part of the private collection of a cleric, who had in turn bought it from a fossil vendor, as evidenced by the transaction receipt that accompanies the specimen in the collections of the AMPG (S. Roussiakis pers. comm.; Fig. 3b). The fossiliferous facies that might have produced this fossil have not been since identified and explored for additional vertebrate remains. Therefore, the possibility that this specimen was not originally found in Rhodos, or even Greece, cannot be fully ruled out.



**Fig. 3** (a) Lingual view of the prearticular toothplate of †*Coelodus* sp. (†Pycnodontidae; formerly assigned to †*Coelodus muensteri* by Melentis 1967a, b), from the Cenomanian of Lindos, Rhodos Island; (b) Scan of the sale receipt accompanying the original fossil (See text for details). Scale bar equals 1 cm

## Teleostei Müller, 1846 (sensu Arratia 2017)

### †Leptolepididae Pictet, 1851

**Type Genus** †*Leptolepis* Agassiz, 1832.

**Nomenclatural and Taxonomical History** †Leptolepididae has a complicated taxonomic history and has been previously treated as a grade-like assemblage of primitive teleosts (Nybelin 1974; Arratia 1999, 2017; Arratia and Hikuroa 2010; Konwert and Stumpf 2017).

**Distribution** In Greece, this taxon is known from the Toarcian of the Ionian Unit, and particular from Aghios Ilias, Anavyrissada, Lefkada Island (Kottek 1964). Outside Greece, †Leptolepididae s.l. appeared in the Early Jurassic of Western and Central Europe and seem to have had achieved a cosmopolitan distribution by the Middle Jurassic (Arratia and Hikuroa 2010; Konwert and Stumpf 2017).

**Comments** A partial maxilla and associated dentalosplenic of a †leptolepidid-like actinopterygian have been found in the Toarcian of Aghios Ilias (Anavyrissada exposure), Lefkada, and have been identified as †*Leptolepis* cf. *coryphaenoides* (Kottek 1964). The material resembles †*Leptolepis*, but lacks any synapomorphies of the genus (Arratia 2017; Konwert and Stumpf 2017). This occurrence corresponds to the oldest record of actinopterygians in Greece, but should be treated as cf. †Leptolepididae indet. until more complete material becomes available.

### †Ichthyodectiformes Bardack and Springle, 1969

#### †Ichthyodectoidei Romer, 1966

**Distribution** In Greece, †Ichthyodectoidei have only been reported from the Maastrichtian (Late Cretaceous) of the Pindos Unit, Gavdos Island (Cavin et al. 2012). Outside Greece, †Ichthyodectiformes are found in Bathonian (Middle Jurassic)–Maastrichtian (Late Cretaceous) marine, and, rarely, in brackish and freshwater deposits of all continents (Arratia et al. 2004; Cavin et al. 2013).

**Comments** This occurrence is based on a partially preserved postcranium from the Maastrichtian of Gavdos, which exhibits aspects of the caudal part of the vertebral column and associated dorsal, anal and caudal fins (Cavin et al. 2012). Similarities of the Gavdos specimen with †*Saurodon elongatus* from the Maastrichtian of Nardó, Italy, have been noted, but the specimen was left in open nomenclature due to its incomplete preservation (Cavin et al. 2012).

### Clupeiformes Bleeker, 1859

#### Clupeidae Cuvier, 1817

#### *Alosa* Linck, 790

**Type Species** *Alosa alosa* (Linnaeus, 1758).

**Included Taxa** †*Alosa crassa* (Sauvage, 1873); *Alosa tanaica* (Grim, 1901); †*Alosa elongata* Agassiz, 1843.

**Nomenclatural and Taxonomical History** †*Alosa crassa* is often included in the extant genus *Sardina* Antipa 1904, as †*Sardina crassa*, or †*Sardina* cf. *crassa* (Dermitzakis et al. 1986; Gaudant 2004, 2014b; Gaudant et al. 2005). The original generic attribution *Alosa* is herein maintained, following Grande (1985) and Carnevale (2007).

**Distribution** In Greece, marine occurrences of †*Alosa* cf. *crassa*, or *Alosa* sp. are known from the Tortonian of the Makrilia Formation, in the vicinity of Ierapetra, Crete, the Messinian and Pliocene of Crete and the Tortonian–Messinian of Gavdos Island. *Alosa elongata* has been signaled in the Pliocene of Heraklion basin, in Crete. *A. tanaica* (first described as *Caspialoassa nordmanni* is known from the Pliocene of Strymonas valley in Serres (see [Appendix](#) for detailed information). Outside Greece, fossils affiliated with †*Alosa crassa* are common in the Mediterranean Neogene, with records in Algeria, Spain, Italy, and Cyprus (Sauvage 1873; Arambourg 1925, 1927; Gaudant et al. 2000, 2015; Landini and Sorbini 2005a; Carnevale 2007; Gaudant 2008a, b). Also, †*Alosa elongata* is known from the late Miocene of Algeria, Spain, Italy (Arambourg 1927; Landini and Sorbini 2005a; Gaudant 2008b; Gaudant et al. 2008, 2010a). Fossils attributed to *A. tanaica* have been reported from the Paratethyan Miocene (Paučá 1931; Rückert-Ülkümen 1994; Schwarzahns et al. 2017).

**Comments** Most of the attributions to *Alosa* sp. refer to isolated scales, or bones of larger sized clupeids. The alosin from the Pliocene of Serres Basin, was originally attributed to *Caspialosa nordmanni* (Antipa 1904; Weiler 1943), which is considered a junior synonym of the Black Sea species *A. tanaica* (Grim 1901). This species is often mentioned as *A. nordmanni* (Schwarzahns et al. 2017) and, adding to the confusion, some of the contained fossils have been moved to †*Alosa pinarhisariensis* (Rückert-Ülkümen 1994). The specific attribution of the Serres alosin is ambiguous at best. However, future studies on newly discovered fossils from the late Miocene of Aidonochori, Serres Basin, might help shed some light on the complicated systematics of freshwater–brackish clupeids from the area (Kevrekidis 2016).

### ***Sardina* Antipa, 1904**

**Type Species** *Sardina pilchardus* (Walbaum, 1792). Only included species.

**Distribution** In Greece, this taxon is known from the Pliocene of Heraklion Basin and Rethymno, Crete (see [Appendix](#)). Outside Greece, *Sardina* fossils are known from the Pliocene and Pleistocene of Italy (Landini and Sorbini 2005a). *S. pilchardus* is present in the Western Atlantic, the Mediterranean, and the Black and Azov seas (Froese and Pauly 2019).

**Comments** Many of the *Sardina* sp., or *Sardina?* sp. occurrences in Greece correspond to poorly preserved, and/or disarticulated material, and might show taxonomic overlap with *Alosa* spp.

### ***Spratelloides* Bleeker, 1851**

**Type Species** *Clupea argyrotaeniata* (Bleeker, 1849) [= junior synonym of *Spratelloides gracilis* (Temminck and Schlegel, 1846)].

**Included Taxa** *S. gracilis* (Temminck and Schlegel, 1846).

**Distribution** In Greece, this taxon is known from the Tortonian of the Makrilia Formation, vicinity of Ierapetra, Crete, the Zanclean of Aegina Island, the Pliocene of Attiki, the Pliocene of Heraklion Basin and Rethymno, in Crete ([Appendix](#) and [Fig. 4](#)). Outside Greece, fossils affiliated with *S. gracilis* are known from the late Miocene, Pliocene and early Pleistocene of Algeria, Spain, and Italy (Arambourg 1927; Gaudant 2002, 2008b; Landini and Sorbini 2005a; Carnevale et al. 2006; Gaudant et al. 2015). Nowadays, *S. gracilis* is present in tropical waters of the Indo-Pacific Realm (Froese and Pauly 2019).

### **Cypriniformes Bleeker, 1859**

#### **Cyprinidae Cuvier, 1817**

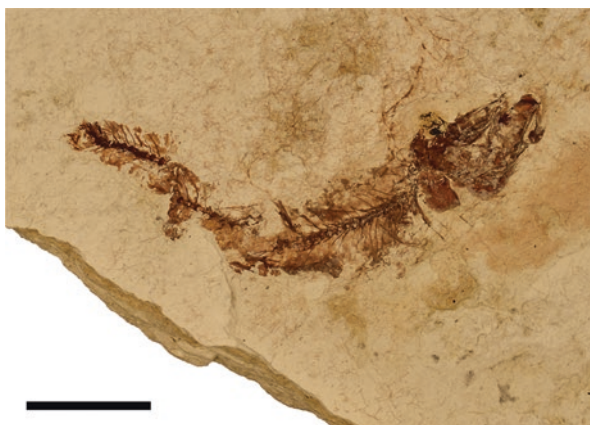
**Type Genus** *Cyprinus* Linnaeus, 1758.

#### **†*Palaeoleuciscus* Obrhelová, 1967**

**Type Species** †*Palaeoleuciscus chartaceus* (Laube, 1905).

**Distribution** In Greece, this taxon is known only from the early Miocene of Lapsarna Locality, Lesvos Island, Greece (Vasileiadou et al. 2017; [Appendix](#)).

**Fig. 4** *Spratelloides* cf. *gracilis* (Clupeidae) from the Zanclean diatomitic marls near Mesagros, Aegina Island (AMPG collection). Scale bar equals 1 cm



Outside Greece, its oldest fossils come from the Oligocene of Germany and Switzerland (Cavender 1991; Böhme and Ilg 2003). There numerous records of tooth and skeletal remains of the genus in the Miocene of Europe and Anatolia as well (e.g., Cavender 1991; Böhme and Ilg 2003; Rückert-Ülkümen and Yiğitbaş 2007; Böhme 2010; Gaudant 2014a, 2015).

### ***Barbus* Cuvier and Cloquet, 1816**

**Type Species** *Barbus barbatus* (Linnaeus, 1758).

**Distribution** In Greece, this taxon is only known from the early Miocene of Lapsarna Locality, Lesvos Island, Greece (Vasileiadou et al. 2017; Appendix). Outside Greece, *Barbus*-like (?*Barbus* sp.) pharyngeal teeth first appear in the Oligocene of Afroarabia (Otero and Gayet 2001). *Barbus* remains are quite common in Neogene and younger freshwater deposits in Europe, Africa, the Arabian subcontinent, and Anatolia (Cavender 1991; Stewart 2001, 2003; Böhme and Ilg 2003; Příkryl et al. 2016b; Stewart and Murray 2017). The distribution of modern *Barbus* s.s. species ranges from Europe to the Caspian Sea, Anatolia, and Tigris and Euphrates drainages, with approx. 13 species found in Greek freshwaters (Froese and Pauly 2019).

**Comments** It is widely accepted that modern and fossil species lumped under the genus *Barbus* correspond to different lineages, rendering the genus paraphyletic (Berrebi and Tsigenopoulos 2003; Kottelat and Freyhof 2007). *Barbus* s.l. is used to indicate uncertainty relative to the placement of fossils relative to modern lineages, whereas *Barbus* s.s. indicates affinities with the European and Anatolian subgenus *Barbus*. Isolated pharyngeal teeth or bones are difficult to attribute to specific lineages, yet similarities of the Lapsarna *Barbus* with *Barbus* s.s. have been noted (Vasileiadou et al. 2017).

### ***Cyprinion* Heckel, 1843**

**Type Species** *Cyprinion macrostomus* Heckel, 1843.

**Distribution** In Greece, pharyngeal bones and teeth of *Cyprinion* have been found in the early Miocene of Lapsarna Locality, Lesvos Island, Greece (Vasileiadou et al. 2017; Appendix). Outside Greece, pharyngeal teeth putatively attributed to the genus have also been found in the early Miocene of Turkey (Böhme and Ilg 2003). Modern representatives of *Cyprinion* have a distribution that ranges from the Arabian subcontinent to Myanmar (Froese and Pauly 2019).

**Comments** According to Vasileiadou et al. (2017), the Lapsarna material likely represents a new species, which has not yet been described formally.

### **Aulopiformes Rosen, 1973**

†**Dercetidae Woodward, 1901**



**Type Species** †*Dercetis scutatus* (Agassiz, 1834).

**Distribution** In Greece, fossils of †Dercetidae are so far known from the Late Maastrichtian of Pindos Unit, in the vicinity of Karpenisi, Eurytania (Koch and Nikolaus 1969). Outside Greece, †dercetids are known from the Late Cretaceous–Paleocene of Europe, the Middle East, North and Central Africa, and South America (summarized in da Silva and Gallo 2011, 2016; Vernygora et al. 2018).

**Comments** The †dercetids found in the vicinity of Karpenisi have been tentatively ascribed to either the aulopiform †*Rhynchodercetis* or, erroneously, the stem teleost †*Belonostomus* (Koch and Nikolaus 1969). Only one †dercetid-like elongate lower jaw, bearing numerous minute teeth, has been figured, but this material has not been described or treated systematically (Koch and Nikolaus 1969, Table 33:3), and bears no apomorphies to support any attribution below the Family-level. No repository information has been provided for these fossils.

### †Enchodontidae Woodward, 1901

**Type Genus** †*Enchodus* Agassiz, 1835.

#### †*Enchodus* Agassiz, 1835

**Type Species** †*Enchodus lewesiensis* (Mantell, 1822).

**Distribution** In Greece, fossils of †*Enchodus* cf. *dirus* are known from the late Maastrichtian, Pindos Unit, Gavdos Island (Cavin et al. 2012). Additional †enchodontid remains, possibly referable to †*Enchodus*, have been collected from Maastrichtian deposits of the Pindos Unit, exposed on the road from Aghia Triada to Domniani, near Karpenisi, Eurytania (Koch and Nikolaus 1969). Outside Greece, the oldest disarticulated remains referred to †*Enchodus* sp. have been collected in the Early Cretaceous of Spain (Kriwet 2003), while articulated remains are known from the Albian–Cenomanian of Mexico (Fielitz and González-Rodríguez 2010). This genus achieved a cosmopolitan distribution during the Late Cretaceous, with occurrences in North and South America, England and western continental Europe, Africa, India, and the Middle East (summarized in Goody 1969; Chalifa 1996; Cavin et al. 2012; da Silva and Gallo 2016; Holloway et al. 2017).

**Comments** A relatively well-preserved skull of †*Enchodus*, also exhibiting features of the palate and jaws, was found in the late Maastrichtian deposits of Gavdos Island and was attributed to a juvenile individual (Cavin et al. 2012). The specimen was included in a phylogenetic analysis alongside other †enchodontids, and was resolved as sister taxon to †*Enchodus dirus* (Cavin et al. 2012), which, in turn, is found in several Late Cretaceous localities of the Western Interior Seaway, North America (Goody 1969). The Gavdos and North American specimens seem to only differ in size and ornamentation, and their seemingly close relationship supports complex biogeographical scenarios, involving the ability of, at least some, Late Cretaceous †enchodontids to cross oceanic basins (Cavin et al. 2012).

**Paralepididae Gill, 1872****Type Genus** *Paralepis* Cuvier, 1817.***Paralepis* Cuvier, 1817****Type Species** *Paralepis coregonoides* Risso, 1820.**Included Taxa** †*Paralepis albyi* (Sauvage, 1870).**Distribution** In Greece, this taxon is known from the Messinian of Gavdos (Metochia: †*P. albyi*; Gaudant et al. 2006). Outside Greece, †*P. albyi* is present in the late Miocene of Spain and Italy (Arambourg 1925; Gaudant 2002; Carnevale 2007). Two species of the deep-water genus *Paralepis* are nowadays present in the Mediterranean (Froese and Pauly 2019).**Stomiatiformes sensu Rosen, 1973****Gonostomatidae Gill, 1893****Type Genus** *Cyclothone* Goode and Bean, 1883.***Cyclothone*** Goode and Bean, 1883**Type Species** *Cyclothone acclinidens* Garman, 1899.**Included Taxa** †*Cyclothone gaudanti* Přikryl and Carnevale, 2017.**Remarks** The modern species *Cyclothone braueri*, *Cyclothone microdon*, and *Cyclothone pygmaea* have been reported from the Italian Pliocene and Pleistocene (Landini and Sorbini 2005a; Přikryl and Carnevale 2017). The genus has a cosmopolitan distribution in modern deep marine waters (Froese and Pauly 2019).**★†*Cyclothone gaudanti* Přikryl and Carnevale, 2017****Nomenclatural and Taxonomical History** *Cyclothone* sp. in Gaudant 2004 (initial identification); *Cyclothone gaudanti* Přikryl and Carnevale, 2017 (new species).**Type Material** NHMW 1999z0042/0020, nearly complete, articulated individual.**Type Locality** Locality 400 m to the North of Aghia Paraskevi Chapel, vicinity of Ierapetra, Crete, Greece, Makrilia Formation.**Distribution** This species is only known from the Tortonian of Makrilia Formation, in the vicinity of Ierapetra, Crete (Aghia Paraskevi Chapel Locality, and from a locality 400 m to the North of Aghia Paraskevi Chapel; Gaudant 2004, Přikryl and Carnevale 2017). These localities constitute the whole range of this taxon.

**Remarks** *Cyclothone gaudanti* demonstrates affinities with the small-sized and lightly pigmented species of the genus, such as *Cyclothone alba*, *C. braueri*, and *Cyclothone signata* (Přikryl and Carnevale 2017). Based on its affinities and the depositional environment of Makrilia Formation, it is estimated that this species possibly occupied the upper mesopelagic layer (Přikryl and Carnevale 2017).

### **Sternoptychidae Duméril, 1806**

**Type Genus** *Sternoptyx* Hermann, 1781.

#### ***Maurolicus* Cocco, 1838**

**Type Species** *Maurolicus muelleri* (Gmelin, 1789). Only included species.

**Distribution** In Greece, this taxon is known with the species *M. muelleri* from the Tortonian of the Makrilia Formation, in the vicinity of Ierapetra, Crete (Gaudant 2004), the Messinian of Gavdos (Gaudant et al. 2006), and the Messinian of Mires (Gaudant et al. 1997a). Furthermore, *Maurolicus* cf. *M. muelleri* has been reported from the Pliocene of Heraklion as well (Gaudant 2001; Appendix). Outside Greece, *M. muelleri* has a continuous presence in the Mediterranean Realm (including Algeria, Italy and Spain) since the late Miocene (Gaudant 2002, 2008b; Landini and Sorbini 2005a; Gaudant et al. 2008, 2010a), and is characterized by a cosmopolitan distribution in modern bathypelagic waters (Froese and Pauly 2019).

#### ***Argyropelecus* Cocco, 1829**

**Type Species** *Argyropelecus hemigymnus* Cocco, 1829.

**Distribution** In Greece, the only record of *Argyropelecus* sp. comes from the Pliocene (Zanclean) of Aegina Island (Argyriou and Theodorou 2011), and is figured here for the first time (Fig. 5). Outside Greece, the fossil record of the genus dates back to the Oligocene of Romania, Poland, and the Caucasus (summarized in Carnevale 2003).

**Remarks** So far, only two species have been recognized on the basis of body fossils in the Mediterranean region: the late Miocene †*A. logearti* in Algeria (Arambourg 1927; Carnevale 2003), and the extant *A. hemigymnus* in the Pliocene and Pleistocene of Italy (Carnevale 2003, 2007; Landini and Sorbini 2005a).

### **Myctophiformes Regan, 1911**

#### **Myctophidae Gill, 1893**

**Type Genus** *Myctophum* Rafinesque, 1810a.

#### ***Myctophum* Rafinesque, 1810a**

**Type Species** *Myctophum punctatum* Rafinesque, 1810b.

**Fig. 5** *Argyropelecus* sp. (Sternoptychidae), from the Zanclean diatomitic marls near Mesagros, Aegina Island (AMPG collection). This specimen is figured here for the first time. Scale bar equals 1 cm



**Included Taxa** †“*Myctophum*” *licatae* Sauvage, 1870; †“*Myctophum*” *dorsale* Sauvage, 1870.

**Distribution** In Greece, myctophid body fossils are known from the Tortonian of Makrilia Formation, vicinity of Ierapetra (Gaudant 2004), whereas occurrences identified to the species level are known from the Tortonian–Messinian of Messara, Heraklion (Psalidha, Mires: †“*Myctophum*” *licatae*, †“*Myctophum*” *dorsale*; Tsangaraki: †“*Myctophum*” *licatae*; Gaudant et al. 1997a), and the Tortonian (Metochia, Karave: †“*Myctophum*” *licatae*) and Messinian (Metochia: †*M. licatae*, †*M. dorsale*; Fig. 5) of Gavdos (Gaudant et al. 2005, 2006). A single myctophid tooth was also recovered from the Messinian strata of ‘Unit b’ of Pigadia Basin in Karpathos (Bellas et al. 1998). Outside Greece, these two Miocene species have been recognized in several Mediterranean localities in Algeria, Spain, Italy, and Cyprus (Arambourg 1925, 1927; Gaudant 2002, 2008a, b; Merle et al. 2002; Gaudant et al. 2010a). Several extant species of *Myctophum* have been reported from Pliocene and Pleistocene localities of the Mediterranean (Landini and Sorbini 2005a). Nowadays, *Myctophum* species have a cosmopolitan bathypelagic distribution (Froese and Pauly 2019).

**Remarks** Greek body fossils of Myctophidae were lumped by Gaudant in the extant genus *Myctophum*, following his taxonomic reappraisal of material previously studied by Arambourg (1925), from the late Miocene of Licata, Sicily (Gaudant and Ambroise 1999). However, Gaudant’s taxonomical scheme relied heavily on putatively overlapping ratios of body measurements and the overall presence or absence of photophores, and did not take important anatomical characters of synapomorphical value into proper account (see e.g., Paxton 1972; Carnevale 2007;



**Fig. 6** Myctophidae indet. From the Messinian of Metochia C, Gavdos Island (AMPG collection; photograph provided by JD Carrillo). Scale bar equals 1 cm

Denton 2013). Detailed considerations of fossil myctophids from e.g., the Serravalian of Italy revealed the simultaneous presence of multiple genera—but not *Myctophum*—in the Mediterranean Neogene (Carnevale 2007), signaling the necessity for future revision of fossil myctophid diversity in the entirety of the Mediterranean Basin, including Greece. Given the scope of the present work, I refrain from reappraising Greek myctophid fossils and retain Gaudant’s classification in inverted commas (also employed by Gaudant in his later works). New material from Metochia C, Gavdos, collected by the author (e.g., Fig. 6), preserves delicate anatomical structures that can facilitate relevant undertakings in the future.

### **Gadiformes sensu Endo, 2002**

#### **Gadidae Rafinesque, 1810b**

**Type Genus** *Gadus* Linnaeus, 1758.

*Micromesistius* Gill, 1863

**Type Species** *Micromesistius poutassou* (Risso, 1827).

**Distribution** In Greece, the only fossil occurrence of *Micromesistius* sp. comes from the Pliocene Amnissos, Heraklion Basin (Gaudant 2001). Outside Greece, this taxon is known from the Pliocene to Pleistocene of Italy (Landini and Sorbini 2005a). The genus is nowadays present in temperate Atlantic and Pacific waters, including the Mediterranean (Froese and Pauly 2019).

#### **Moridae Goode and Bean, 1896**

**Type Genus** *Mora* Risso, 1827.

***Gadella* Lowe, 1843**

**Type Species** *Gadella gracilis* Lowe, 1843.

**Distribution** In Greece, occurrences of *Gadella* are known from the Pliocene of Attiki (Gaudant and Symeonidis 1995) and Heraklion Basin (Gaudant 2001). Outside Greece, this taxon is known from the Pliocene of Italy (Landini and Sorbini 2005a). *Gadella* is still present in tropical to subtropical deep waters around the world, including the Mediterranean (Froese and Pauly 2019).

**Bregmacerotidae Gill, 1872**

**Type Genus** *Bregmaceros* Thompson, 1840.

*Bregmaceros* Thompson, 1840

**Type Species** *Bregmaceros maclellandi* Thompson, 1840.

†*Bregmaceros albyi* (Sauvage, 1880)

**Distribution** This is one of the most widely distributed taxa in Greece, with occurrences from the Tortonian of Makrilia Formation, vicinity of Ierapetra, Crete (Symeonidis 1969; Bürgin 1994; Gaudant 2004), the Tortonian and Messinian of Metochia, Gavdos (Gaudant et al. 2005, 2006), the Tortonian–early Messinian of Messara, Heraklion, Crete (Gaudant et al. 1997a), the Messinian of Karpathos (Bellas et al. 1998), the Pliocene (cf. Zanclean) of Aegina Island (Argyriou and Theodorou 2011; Fig. 7), the Pliocene of Heraklion (Gaudant et al. 1994; Müller and Strauch 1994; Gaudant 2001) and the Piacenzian of Rethymno (Symeonidis and Schultz 1973; see Appendix for more information). Outside Greece, body fossils of †*Bregmaceros albyi* are known from the Miocene of Algeria, Italy, Malta, and Spain, and from the Pliocene of Italy and, possibly (as †*B.* cf. *albyi*), Cyprus (Gaudant 2002; Landini and Sorbini 2005a; Přikryl et al. 2016a; and references therein). The species is also present in the early Pleistocene of Italy (Landini and Sorbini 2005a).

**Acanthomorpha Rosen, 1973****Atheriniformes sensu Dyer and Chernoff, 1996****Atherinidae Risso, 1827**

**Type Genus** *Atherina* Linnaeus, 1758.

**Distribution** In Greece, atherinids are known only from the Pliocene of Attiki (Gaudant and Symeonidis 1995). Outside Greece, atherinids are known to have been present in Tethys since at least the Eocene of Monte Bolca, Italy (Carnevale et al. 2014), but their more recent fossil record in the area is largely composed of otoliths (Landini and Sorbini 2005a). Body fossils of atherinids are known from the Miocene of the Paratethys (Schwarzahns et al. 2017) and California (Jordan and Gilbert 1919).



**Fig. 7** *Bregmaceros* cf. *albyi* (Bregmacerotidae), from the Zanclean diatomitic marls near Mesagros, Aegina Island. This specimen is figured here for the first time (AMPG collection). Scale bars equal 1 cm

### **Beloniformes Berg, 1937**

#### **Belonidae Bonaparte, 1832**

**Type Genus** *Belone* Cuvier, 1817.

#### ***Belone* Cuvier, 1817**

**Type Species** *Belone belone* (Linnaeus, 1760).

**Distribution** In Greece, this taxon is only known from the Pliocene of Heraklion Basin (Gaudant et al. 1994; Gaudant 2001). Outside Greece, fossils of this taxon are more common, coming from the Oligocene of the Caucasus (Smirnov 1936), the Miocene of the USA (de Sant’Anna et al. 2013), and the Miocene to Pleistocene of Italy (Arambourg 1925; Landini and Sorbini 2005a). The genus is nowadays present in the Atlantic Ocean, the Mediterranean, and the Black Sea (Froese and Pauly 2019).

#### ***Scomberesox* Lacepède, 1803**

**Type Species** *Scomberesox saurus* (Walbaum, 1792).

**Distribution** In Greece, the only possible fossils of this genus come from the Pliocene of Heraklion Basin (Gaudant 2001). Outside Greece, fossils of *Scomberesox* are known from the Miocene of USA, Algeria, and Italy, and the Pleistocene of Italy (Jordan and Gilbert 1919; Gaudant 2002, 2008b; Landini and Sorbini 2005a). Nowadays, the genus has a circumglobal distribution, which also includes the Mediterranean (Froese and Pauly 2019).

**Blenniiformes sensu Springer, 1993**  
**Blenniidae Rafinesque, 1810a**

**Type Genus** *Blennius* Linnaeus, 1758.

***Salaria* Forskål, 1775**

**Type Species** Not designated.

**Included Taxa** *Salaria pavo* (Risso, 1810).

**Nomenclatural and Taxonomical History** Initially ascribed by Gaudant et al. (1994) to the genus *Blennius*, as *Blennius* cf. *B. pavo* (Risso 1810). This species is now included in the genus *Salaria*, as *S. pavo* (see Eschmeyer and Fong 2019).

**Distribution** In Greece, this taxon is known only from the Pliocene of Heraklion Basin (Gaudant et al. 1994). So far no additional body-fossil records exist for this taxon. Nowadays, *S. pavo* is present in shallow marine to brackish waters along the Western Atlantic, Mediterranean, and Black Sea coasts (Froese and Pauly 2019).

**Perciformes sensu Betancur-R et al. 2017**  
**Serranidae Swainson, 1839**

**Type Genus** *Serranus* Cuvier, 1817.

***Serranus* Cuvier, 1817**

**Type Species** *Serranus cabrilla* (Linnaeus, 1758).

**Distribution** In Greece, this taxon is certainly known from the Pliocene of Heraklion Basin (Gaudant 2001), while the presence of the family has been signaled in the Pliocene of Aegina Island as well (Gaudant et al. 2010b). Outside Greece, *Serranus* fossils are known from the Miocene of Algeria, and the Plio-Pleistocene of Sardinia (Abbazzi et al. 2004; Gaudant 2008b). *Serranus* has a modern cosmopolitan, Tropical–Temperate, marine distribution (Froese and Pauly 2019).

**Cyprinodontiformes sensu Parenti, 1981**  
**Cyprinodontidae Gill, 1865**

**Type Genus** *Cyprinodon* Lacepède, 1803.

***Aphanius* Nardo, 1827**

**Type Species** *Aphanius nanus* Nardo, 1827.

**Included Taxa** †*A. crassicaudus* Agassiz, 1839.



**Nomenclatural and Taxonomical History** Initially included in the genus †*Lebias* (Agassiz, 1833–1843), as †*L. crassicaudus* (Raulin 1861). Woodward erected the genus *Pachylebias* to accommodate pachyostotic cyprinodontiform material from the Messinian of Italy and Crete (Woodward 1901). †*Pachylebias* was later found to be a junior synonym of the extant genus *Aphanius* (Gaudant 1979).

**Distribution** In Greece, this taxon is known from the Messinian of Chania, Crete (Raulin 1861; Woodward 1901; Freudenthal 1969; Gaudant 1979, 2014b). Outside Greece, *Aphanius* is an essential component of Messinian oligohaline fish assemblages of the Mediterranean, including occurrences in Algeria, Spain, Morocco, and Italy (Gaudant 2002; Carnevale et al. 2018).

**Scombriformes sensu Betancur-R et al. 2017**  
**Scombridae Rafinesque, 1815**

**Type Genus** *Scomber* Linnaeus, 1758.

***Scomber* Linnaeus, 1758**

**Type Species** *Scomber scombrus* Linnaeus, 1758 (= *S. scomber* L., 1758).

**Distribution** In Greece, this genus is only known from the Pliocene of Heraklion Basin (Gaudant 2001). Outside Greece, the genus is known from the Oligocene of central Europe and the Caucasus, and the Neogene of Russia, the United States, Japan, Algeria, Italy, Croatia, and Serbia (Arambourg 1927; Yabumoto and Uyeno 1994; Landini and Sorbini 2005a; Micklich and Hildenbrandt 2010; Gregorová 2011; Nazarkin and Bannikov 2014). Modern representatives of the genus are widespread in tropical to temperate waters (Froese and Pauly 2019).

***Scomberomorus* Lacepède, 1801**

**Type Species** *Scomberomorus regalis* (Bloch, 1793) (= *S. plumierii* Lacepède, 1801).

**Distribution** In Greece, this genus is only known from the Pliocene of Heraklion Basin (Gaudant 2001). Outside Greece, the genus appears in the Paleocene of Turkmenistan (Monsch and Bannikov 2012). It is also known the Paleogene of Kazakhstan, Georgia, the United States, Germany, and the Neogene of Japan, Poland, and the United States (Schultz 1979; Yabumoto and Uyeno 1994; Weems 1999; Micklich and Hildenbrandt 2010; Monsch and Bannikov 2012; Weems et al. 2017). The genus is found today in tropical-subtropical waters of the Atlantic, Indian, and Pacific oceans, and the Western Mediterranean (Froese and Pauly 2019).

**Trichiuridae Rafinesque, 1810a**

**Type Genus** *Trichiurus* Linnaeus, 1758.

***Lepidopus* Goüan, 1770**

**Type Species** *Lepidopus caudatus* Euphrasen, 1788.

**Included Taxa** †*L. albyi* Sauvage, 1870.

**Distribution** In Greece, this genus is known from the Tortonian of Makrilia Formation, in the vicinity of Ierapetra, Crete (Symeonidis 1969; Gaudant 2004), the Tortonian and Messinian of Gavdos (Gaudant et al. 2005), the Messinian of Messara (as †*Lepidopus albyi* in the text, but *Lepidopus* sp. in the respective figure caption; Gaudant et al. 1997a), and the Pliocene of Heraklion Basin and Rethymno (Gaudant et al. 1994; Gaudant 2001; see Appendix for further information). Outside Greece, †*Lepidopus albyi* is known from the late Miocene of Algeria, Spain, Italy, Cyprus, and Pliocene of Italy (Arambourg 1925, 1927; Gaudant 2002; Merle et al. 2002; Landini and Sorbini 2005a). A second fossil species, †*Lepidopus proargenteus*, is known from the late Miocene of Algeria and Italy (Arambourg 1927; Gaudant 2008b; Gaudant et al. 2010a). Remains affiliated with the living *L. caudatus* have been reported from the Pliocene of Italy (Landini and Sorbini 2005a).

**Remarks** Symeonidis tentatively ascribed fragmentary remains of a juvenile *Lepidopus* from the Tortonian of Crete to the Oligocene Paratethyan species †*Anachelum glaricianum* (his †*Lepidopus* cf. *glaricianus*, Symeonidis 1969). Gaudant revised this attribution to *Lepidopus* sp. (Gaudant 2004).

## **Gobiiformes Günther, 1880**

### **Gobiidae Cuvier, 1817**

**Type Genus** *Gobius* Linnaeus, 1758.

#### ***Gobius* Linnaeus, 1758**

**Type Species** *Gobius niger* Linnaeus, 1758.

**Distribution** In Greece, unidentified records of this genus are reported from the Pliocene of Heraklion Basin (Gaudant et al. 1994) and Attiki (Gaudant and Symeonidis 1995). Outside Greece, *Gobius* skeletons first appear in the early Miocene of the Czech Republic (Reichenbacher et al. 2018), but are found in a wide array of Neogene fossil sites in North Africa, Europe, and Asia Minor (Arambourg 1927; Gaudant 2002; Böhme and Ilg 2003; Reichenbacher et al. 2018). *Gobius* has a circumglobal modern distribution (Froese and Pauly 2019).

**Comments** Gobioids are among the largest clades of vertebrates (Nelson et al. 2016). In many cases, included genera and species are diagnosed on the basis of very delicate anatomical features and soft tissue structures, which are not often visible/preserved in fossils (Reichenbacher et al. 2018). Thus, Greek gobiid fossils only loosely affiliate with *Gobius* (Gaudant et al. 1994; Gaudant and Symeonidis 1995), and might actually encompass other genera as well. It should be noted here that poorly documented occurrences of Gobiidae in the Miocene of Kyymi have been

ascribed to the genus *Periophthalmus* (Unger 1867; Appendix), but, due to lack of descriptive or pictorial documentation, these are not further treated here.

### **Carangiformes sensu Betancur-R et al. 2017**

#### **Carangidae Rafinesque, 1815**

**Type Genus** *Caranx* Lacepède, 1801.

*Caranx* Lacepède, 1801

**Type Species** *Caranx hippos* (Linnaeus, 1766).

**Distribution** In Greece, this genus is only known from the Pliocene of Heraklion Basin (Gaudant 2001). Outside Greece, this taxon is known from the Miocene of Algeria, Italy (Arambourg 1925, 1927), but also from the Paratethys (Schwarzhan et al. 2017).

#### ***Alectis* Rafinesque, 1815**

**Type Species** *Alectis ciliaris* (Bloch, 1787).

#### **★ †*Alectis psarianosi* (Symeonidis, 1969)**

**Nomenclatural and Taxonomical History** This species, based on a single specimen from the Tortonian of Crete, was formerly included in the genus *Mene* (Menidae), as †*Mene psarianosi* (Symeonidis 1969). It was later reattributed to the carangid genus *Alectis*, but the species name was retained (Bannikov 1984, 1987; Gaudant 2004).

**Type Material** AMPG 185/1969, complete, laterally compressed individual (Fig. 8).

**Type Locality** Tortonian of Makrilia Formation, vicinity of Ierapetra, Crete (Aghia Paraskevi Chapel Locality; Symeonidis 1969; Gaudant 2004).

**Distribution** Known only from the type locality.

**Remarks** Bannikov (1987) dispelled the original, poorly supported attribution of this unique fossil to Menidae by Symeonidis (1969), after recognizing typical carangid features, including a high rhomboidal body shape; a well-developed fronto-occipital crest; and the relative length of fin rays in its median fins. Gaudant (2004) re-examined the specimen, providing its first detailed anatomical description and confirming Bannikov's assessment, but without attempting additional comparisons. According to Bannikov (1987), this fossil species differs from modern species in having "somewhat shorter anterior rays of the soft unpaired fins." Whether this difference is sufficient to maintain †*Alectis psarianosi* as a valid fossil species remains to be investigated in the future, given the fact that the fossil corresponds to a somewhat small, possibly immature, individual.

**Fig. 8** The type specimen (AMPG 185/1969) of †*Alectis psarianosi* (Carangidae) from the Tortonian of Aghia Paraskevi Chapel, vicinity of Ierapetra, Crete. Scale bars equal 1 cm



### ***Trachurus* Rafinesque, 1810a**

**Type Species** *Trachurus trachurus* (Linnaeus, 1758) (= *T. saurus* Rafinesque, 1810b).

**Distribution** In Greece, occurrence of this genus comes from the Tortonian of Makrilia Formation, in the vicinity of Ierapetra, Crete (Gaudant 2004), the Pliocene of Attiki (Gaudant and Symeonidis 1995), and the Pliocene of Heraklion (Gaudant 2001; see Appendix for further information). Outside Greece, fossils more or less securely attributed to *Trachurus* are known from the Miocene of Algeria and Spain, the Miocene and Pliocene of Italy and the Pliocene of Cyprus (Arambourg 1927; Landini and Sorbini 2005a; Gaudant 2008a, b; Gaudant et al. 2010a; Gaudant and Courme 2014). Three species of *Trachurus* are native to modern Mediterranean pelagic habitats (Froese and Pauly 2019).

### **Spariformes sensu Akazaki, 1962**

#### **Sparidae Rafinesque, 1810a**

**Type Genus** *Sparus* Linnaeus, 1758.

### ***Boops* Cuvier, 1814**

**Type Species** *Boops boops* (Linnaeus, 1758).

**Distribution** In Greece, this genus is known from the Pliocene of Heraklion Basin with various occurrences (Gaudant et al. 1994; Gaudant 2001). Outside Greece, *Boops* fossils have been found in the Miocene of Algeria and the Miocene and Pliocene of Italy (Arambourg 1927; Gaudant 2002). Nowadays, *Boops* is represented by two species, one of which, *B. boops*, occurs in the Mediterranean (Froese and Pauly 2019).

**Comments** Gaudant et al. (1994) initially ascribed the Amnissos boopsins to *Boops* cf. *B. boops*. In a subsequent work, Gaudant (2001) noted differences in meristic features of the dorsal and caudal fins of the *Boops* from Amnissos, from both the Miocene species †*B. roulei* (Arambourg 1927), and the extant *B. boops*, leaving the Cretan fossils in open nomenclature, and implying that they might correspond to a new species. This might also be true for the remaining Heraklion Basin boopsins. As evidenced by isolated teeth, additional sparids were likely present in the Messinian of Karpathos (Bellas et al. 1998).

### Centriscidae Bonaparte, 1831

**Type Genus** *Centriscus* Linnaeus, 1758.

#### *Aeoliscus* Jordan and Starks, 1902

**Type Species** *Aeoliscus strigatus* (Günther, 1861).

**Nomenclatural and Taxonomical History** Centriscids from the Pliocene of Amnissos were initially thought to correspond to a new fossil species (†*Amphisile cretensis* Bachmayer et al. 1984). Gaudant re-examined these specimens and tentatively ascribed these fossils to the extant genus *Amphisile* (Cuvier 1817), as *Amphisile* cf. *strigata* (Gaudant 2001). *Amphihisile strigata* is, however, a synonym of *Aeoliscus strigatus* (Günther 1861). In a subsequent work, Gaudant corrected the taxonomic designation of the Cretan material to *Aeoliscus* cf. *strigatus* (Gaudant and Courme 2014).

**Distribution** In Greece, this taxon is known from the Pliocene of Heraklion Basin, (Bachmayer et al. 1984; Gaudant 2001). Outside Greece, *Aeoliscus strigatus* is also known from the late Miocene and Pliocene of Italy and the Pliocene of Cyprus (Gaudant 2002; Landini and Sorbini 2005a; Gaudant and Courme 2014). This species is nowadays encountered in tropical Indo-Pacific waters (Froese and Pauly 2019).

**Remarks** Given the invalidity of the genus *Amphisile* (see above), the occurrence of *Amphisile* sp. in the Messinian of Gavdos (Gaudant et al. 2006) is hereby treated conservatively as Centriscidae indet.

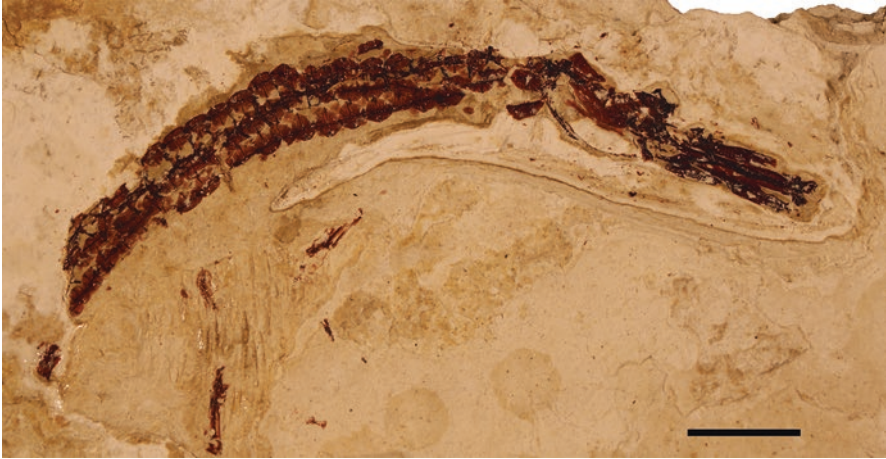
**Syngnathidae Rafinesque, 1810a****Type Genus** *Syngnathus* Linnaeus, 1758.***Syngnathus* Linnaeus, 1758****Type Species** *Syngnathus acus* Linnaeus, 1758.**Included Taxa** †*Syngnathus albyi* Sauvage, 1870.

**Nomenclatural and Taxonomical History** Two fossil species of *Syngnathus* have been erected on the basis of material from the Neogene of Crete: the late Miocene †*S. kaehsbaueri* Bachmayer and Symeonidis (1978) from Aghia Paraskevi Chapel, Makrilia Formation, in the vicinity of Ierapetra, and the Pliocene ★†*S. heraklionis* Bachmayer et al., 1984 from Amnissos, near Heraklion. Reinvestigations of the type material of both species found no anatomical differences from the Miocene species †*S. albyi* (Sauvage 1870), establishing the Cretan species as invalid and referred their type material to †*Syngnathus* cf. †*S. albyi* (Gaudant 2001, 2004).

**Distribution** In Greece, occurrences of this taxon are known from the Tortonian of Makrilia Formation, near Ierapetra, Crete (Bachmayer and Symeonidis 1978; Gaudant 2004), the Tortonian and Messinian of Metochia, Gavdos (Gaudant et al. 2005, 2006), the Messinian of Messara, Crete (Gaudant et al. 1997a), and the Pliocene of Heraklion, Crete (Bachmayer et al. 1984; Gaudant et al. 1994; Gaudant 2001). Remains of short-snouted *Syngnathus* cf. *S. acus* were also found in the Pliocene (cf. Zanclean) of Aegina (Argyriou and Theodorou 2011, Fig. 9). Outside Greece, the fossil species †*S. albyi* is common in “middle” and late Miocene and possibly Pliocene faunas of Algeria, Spain, Italy, and Cyprus (Arambourg 1925, 1927; Gaudant et al. 2000, 2010a; Gaudant 2002, 2008b; Merle et al. 2002; Landini and Sorbini 2005a; Carnevale 2007), whereas records of this species in the Miocene of Paratethys are considered dubious (Schwarzahns et al. 2017). The modern species *S. acus* and *S. phlegon* have been reported from the late Pliocene and Pleistocene of Italy (Landini and Sorbini 2005a).

**Dactylopteridae Gill, 1861****Type Genus** *Dactylopterus* Lacepède, 1801.***Dactylopterus* Lacepède, 1801****Type Species** *Dactylopterus volitans* (Linnaeus, 1758).

**Distribution** In Greece, this taxon is only known from the Pliocene of Heraklion Basin. Outside Greece, it is known from the Pliocene of Italy and Cyprus (Landini and Sorbini 2005a; Gaudant and Courme 2014). One species survives in the Atlantic and the Mediterranean (Froese and Pauly 2019).



**Fig. 9** *Syngnathus* cf. *acus* (Syngnathidae), from the Zanclean diatomitic marls near Mesagros, Aegina Island (AMPG collection). This specimen is figured here for the first time. Scale bar equals 1 cm

### **Pleuronectiformes Bleeker, 1859**

#### **Bothidae Smitt, 1892**

**Type Genus** *Bothus* Rafinesque, 1810a.

#### ***Arnoglossus* Bleeker, 1862**

**Type Species** *Pleuronectes arnoglossus* (Bloch and Schneider, 1801) (junior synonym of *Arnoglossus laterna* Walbaum, 1792).

**Distribution** In Greece, this taxon is only known from the Tortonian of Makrilia Formation, in the vicinity of Ierapetra, Crete (Gaudant 2004). Outside Greece, *Arnoglossus* is reported in the Miocene of Algeria and Spain, and from the Miocene, Pliocene, and Pleistocene of Italy (Landini and Sorbini 2005a; Gaudant 2008a, b; Gaudant et al. 2010a). *Arnoglossus* has a cosmopolitan modern distribution (Froese and Pauly 2019).

#### **Centropomidae sensu Greenwood, 1976**

**Type Genus** Not established.

#### **Latinae indet.**

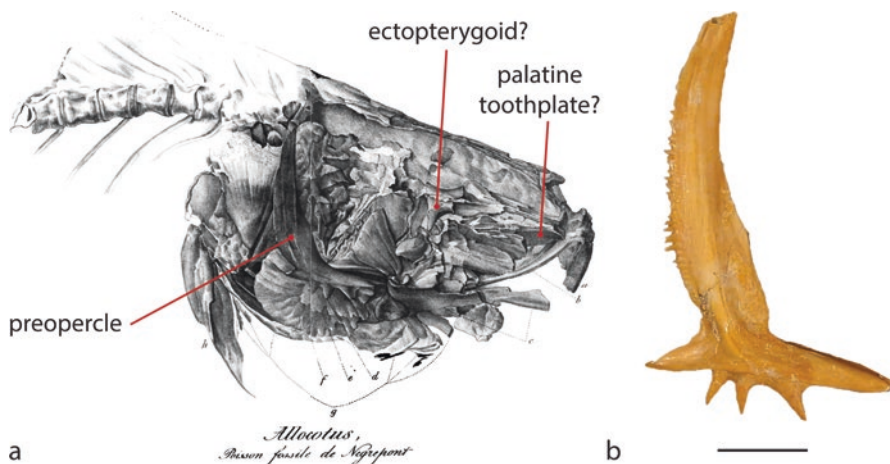
**Nomenclatural and Taxonomical History** This fossil was initially employed to establish the genus †*Allocotus* by de Waldheim (1838). In a following publication,

de Waldheim, erected a new genus and species, †*Platacanthus ubinoi*, to accommodate the same individual (de Waldheim 1850). The Musée de la Société Impériale des Naturalistes, Moscow, was listed as repository of this specimen (Fig. 9a). Woodward reassigned †*P. ubinoi* to the modern genus *Morone* (his *Labrax*), utilizing additional material from the Tertiary of Kymi, Greece, deposited in what is nowadays the Natural History Museum, UK (Woodward 1901), which, however, might correspond to a different taxon. Given the unknown location and status of the type material for these taxa, and their almost complete disappearance from the literature (but see Bannikov 1993), I suggest that †*Allocotus* should be treated as invalid and †*Morone ubinoi* as *nomen dubium*. Adding to the confusion, additional percomorph taxa have been signaled in the Miocene of Kymi, but all these old attributions are doubtful and poorly documented (Valenciennes 1861; Gaudry 1862; Unger 1867; Appendix). The holotype of one of these, known as †*Smerdis isabellae* Gaudry 1862, has been synonymized by MNHN, Paris, staff with Woodward's †*Morone* (= *Labrax*) *ubinoi* in the early 1900s (T.A. personal observations).

**Distribution** In Greece, this taxon is known (possibly) from the early Miocene of an unknown locality near Kymi, Euboea. Outside Greece, *Lates*-like Centropomidae were present in Eocene–Neogene freshwater, brackish and sometimes marine deposits in Europe and Afroarabia (Murray and Attia 2004; Otero 2004; Argyriou et al. 2015). A total of fourteen species (Eschmeyer and Fong 2019) survive in African fresh–estuarine waters, and Indo-Pacific coastal environments (Froese and Pauly 2019).

**Comments** The original description of this taxon does not contain clear information about its geographical or lithological provenance, other than that the fossil comes from some calcareous, oolitic horizon in Greece, which was thought to resemble the Solnhofen limestone (de Waldheim 1850). This specimen was not found by the author himself, but was sent to him by a certain Dr. Ubino who found, or purchased it during his travels through Greece (de Waldheim 1838). Woodward traces the provenance of the material in British collections to the freshwater deposits of Kymi, Greece. It is thus logical to hypothesize that this specimen derives from the classical Miocene plant and fish-bearing horizons of Kymi (e.g., Unger 1867; Kottis et al. 2002), yet this needs to be corroborated by future sampling. Although the drawings of the specimen are rather uninformative (de Waldheim 1838, 1850), the figured individual shows a preopercle bearing a horizontal anteroventral arm, which, in turn, forms a robust posterior spinous process, and three robust ventral processes (Fig. 10a). The possible resemblance of this animal to the percichthyid †*Cyclopoma* (= *Cyclopome*), or the centropomid *Lates* was noted by de Waldheim (1838). The imaged preopercle differs clearly from that of the preopercle of the Eocene genus †*Cyclopoma* (Agassiz 1833–1843). The shape and orientation of these processes resemble instead the preopercles of Latinae (Latidae in Otero 2004; now included within Centropomidae; see Greenwood 1976, Betancur-R et al. 2017; Fig. 10b), leaving little room for doubt that the illustrated skull is a *Lates*-like centropomid. Despite this profound resemblance, and unlike Latinae (Otero 2004),





**Fig. 10** (a) Specimen used to establish †*Allocotus* sp. (de Waldheim 1838) and subsequently †*Platacanthus ubinoi* (de Waldheim 1850), but hereby reassigned to Centropomidae indet.; modified from de Waldheim 1838, scale not provided in original work. (b) Preopercle of *Lates* cf. *niloticus* from the Mio-Pliocene of Sahabi, Libya (collected and attributed by the author; the specimen belongs to the collections of the University of Benghazi, Libya), for comparison with the illustrated preopercle of (a). Scale bar equals 1 cm

the posterior margin of the dorsal limb of the Kymi specimen is figured as non-serrate, but this feature might have been poorly preserved, or illustrated. Additional similarities between the illustrated Kymi specimen and *Lates*-like animals (Otero 2004) can be found in the acute ventral and anterior processes of the ectopterygoid, or what appears to be a broad palatine toothplate, in the anterior portion of the skull, and in what appears to be a single, posterodorsal process of the opercle. Woodward, possibly based on material from Kymi housed in British collections, mentioned that †*Morone* (= *Labrax*) *ubinoi* lacks a posterior spinous process of the preopercle, and also exhibits two feeble spines on the posterior margin of the opercle (Woodward 1901). It is thus possible that Woodward lumped two different taxa, one being a moronid and the other being de Waldheim's centropomid, into one. This highlights the need to restudy Woodward's material. This notion is reinforced by personal observations on Gaudry's material, which was used to establish the species †*Smerdis isabellae* and is now housed at the MNHN, Paris. The latter would require a detailed study to clarify its taxonomic status, which lies beyond the context of this work.

### Labridae Cuvier, 1817

**Type Genus** *Labrus* Linnaeus, 1758.

**Distribution** In Greece, this group is known from the Pliocene of Heraklion Basin (Gaudant 2001). Ichthyoliths from the Pliocene of Aghia Marina, Aegina Island,

have been tentatively attributed to the sparid †*Sargus* cf. *oweni* (Leivaditis 1974), which was in turn found to be a junior synonym of the labrid †*Trigonodon jugleri* (Schultz and Bellwood 2004). This might correspond to another occurrence of Labridae in Greece, but it is so far poorly substantiated. Labrids appear in the Eocene of Italy (Bannikov and Carnevale 2010). Mostly disarticulated (e.g., oral or pharyngeal teeth), but also articulated remains are common in Neogene deposits around the world (e.g., Algeria, Italy, France, Portugal, Poland, Austria, Nigeria, the United States, and New Zealand; summarized in Bellwood et al. 2019).

### **Acanthuriformes sensu Betancur-R et al. 2017**

#### **Acanthuridae Bleeker, 1859**

**Type Genus** *Acanthurus* Forskål, 1775.

**Distribution** In Greece, this taxon is known from the Tortonian of Makrilia Formation, in the vicinity of Ierapetra, Crete (Gaudant 2004), and the Tortonian of Gavdos (Gaudant et al. 2005). Outside Greece, articulated acanthurid fossils are known from the Paleogene of Europe (e.g., Italy, Switzerland, Russia) (Tyler and Bannikov 2000; Tyler and Micklich 2011), while their Miocene occurrences (e.g., Austria and Croatia) usually correspond to isolated teeth (Schultz 2003; Tripalo et al. 2016). Nowadays, the family is absent from the Mediterranean, but is otherwise characterized by circumtropical distribution (Froese and Pauly 2019).

**Comments** The Gavdos specimen is probably a juvenile (Gaudant et al. 2005).

### **Tetraodontiformes Berg, 1937**

#### **Monacanthidae Nardo, 1842**

**Type Genus** *Monacanthus* Oken, 1817.

#### **†*Frigocanthus* Sorbini and Tyler, 2004**

**Type Species** †*Frigocanthus stroppanobili* Sorbini and Tyler, 2004.

**Included Taxa** †*Frigocanthus margaritatus* Sorbini and Tyler, 2004.

**Distribution** In Greece, †*F. margaritatus* is known from the Pliocene of Heraklion Basin (Gaudant 2001; Sorbini and Tyler 2004), whereas †*F. stroppanobili* from the middle-late Pliocene of Chania, Crete (Sorbini and Tyler 2004). Outside Greece, this taxon is known from the Pliocene and Pleistocene of Italy (Sorbini and Tyler 2004).

### **Caproiformes sensu Rosen, 1984**

#### **Caproidae Lowe, 1843**

**Type Genus** *Capros* Lacepède, 1802.

## ***Capros* Lacepède, 1802**

**Type Species** *Capros* (= *Zeus*) *aper* (Linnaeus, 1758).

**Distribution** In Greece, this genus is known only from the Tortonian of Makrilia Formation, in the vicinity of Ierapetra (Gaudant 2004). Outside Greece, fossil species of the genus have been recognized in the Oligocene of the Carpathians, the Caucasus, Germany, and France (Baciu et al. 2005b; Pfikryl et al. 2016c), and the late Miocene of Italy and Algeria (Baciu et al. 2005a). The living species *C. aper* is known from the Pliocene–Pleistocene of Italy (Landini and Sorbini 2005a).

## **6 Conclusions and Avenues for Future Research**

Over a century and a half of exploration and sporadic scientific research on the actinopterygian fossil record of Greece has led to the discovery of numerous fossil sites, and laid the foundations for further work on the regional fossil record of the clade. Actinopterygian fossils in Greece have a patchy record that spans over 180 million years, from the Toarcian (Lower Jurassic) to the Quaternary, with the vast majority of known occurrences concentrated in the late Neogene (late Miocene–Pliocene) and being of clear marine affinities (summarized in the Appendix). Little information is available for older, or freshwater and brackish localities. The pre-Neogene fossil record of Greece merits further scientific attention and exploration, especially given the huge record of sedimentary rocks and complex geological history of Greece. Deposits predating the Jurassic have not yet, to the author’s knowledge, been investigated extensively for potential paleoichthyological content (excluding conodonts), and like in the case of chondrichthyans (Argyriou et al. 2017), actinopterygian fossils are anticipated in Paleozoic–early Mesozoic deposits.

Historically, alpine sedimentary formations of Greece (e.g., the “External Hellenides”), which record a major part of the Mesozoic and early Cenozoic, have been considered to be of principally tectonostratigraphic importance to the geological and paleontological community, and have remained outside the interest of vertebrate paleontologists. Yet, preliminary investigations have indicated the yet untapped paleoichthyological potential of such deposits. The presumably rich Toarcian bonebeds of Ionian Unit exposures in Lefkada have been totally neglected since their first discovery (Kottek 1964), despite their potential informativeness on early teleost diversification. Moreover, understudied fish assemblages from the late Cretaceous–Paleogene of Pindos Unit can shed light on the evolution and biogeography of Tethyan faunas (Koch and Nikolaus 1969; Cavin et al. 2012; Argyriou and Davesne 2021; pers. obs. on the K/Pg of Eurytania, Northern–Central Peloponnese and Gavdos) during this critical time interval of global marine restructuring, which is otherwise poorly documented in the global fossil record. Further research should be directed toward freshwater and brackish faunas, which are so far known from Miocene or younger deposits (e.g., Miocene of Kymi Euboea: de Waldheim 1838,

1850; Unger 1867; Miocene of Chios: Reichenbacher and Böhme 2004), and their insights into the evolution of modern European freshwater ichthyofaunas and their biogeographical and paleohydrological inferences.

Late Miocene–Pliocene fossiliferous localities and horizons, especially the ones in Crete and Gavdos, host diverse actinopterygian assemblages of often exquisite preservation quality (Gaudant et al. 1994, 1997a, 2005, 2006; Gaudant 2001, 2004). Numerous families and genera have already been recognized in these assemblages, largely on the basis of broad morphological and meristic similarities with late Miocene taxa from Italy and Algeria (e.g., Arambourg 1925, 1927; Gaudant 2008b). Previous works, however, have treated these assemblages from an alpha-taxonomic point of view, and provided some limited information on their paleoenvironmental significance. Additional taxonomic diversity, including new species, remains to be identified in these sites, pending detailed anatomical descriptions (Přikryl and Carnevale 2017), and is a prerequisite for further systematic and biogeographic work. The importance of following this line of research cannot be overstressed, especially when taking into account the scarcity of information for this part of (Neo) Tethys, in comparison to what is now the Western and Central Mediterranean (e.g., Arambourg 1925, 1927; Landini and Sorbini 2005a; Carnevale 2007; Gaudant 2008a, b). Research on Greek fossils is anticipated to unveil further clues for tracing the gradual emergence of the modern endemic and Atlantic hallmark of Mediterranean marine faunas from the tropical, Indopacific-like faunas of the Miocene, and the role of major events, such as the Messinian Salinity Crisis and Pleistocene cooling(s) in this process (Gaudant et al. 1994, 1997a, 2005, 2006; Gaudant 2001, 2002, 2004; Landini and Sorbini 2005a, b).

This work collates available information on actinopterygian fossils and their spatiotemporal distribution in Greece, as well as their potential significance. It is hoped to form a stimulating basis for further paleoichthyological research in the country. As a concluding remark, properly curated paleoichthyological collections of Greek fish fossils are crucial for invigorating paleoichthyology in the country, and, given funding and staff limitations, Greek institutions and museums are encouraged to work toward this goal.

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## Appendix

Tables with a detail list of the occurrences of ray-finned fishes in Greece.

**Table 1** List of Greek localities with known occurrences of ray-finned fishes have not yet been studied and/or identified to lower taxonomic levels

Localities <sup>PBDB No</sup>	Age (MN)	Taxon
Marathousa 1 <sup>199937–40</sup>	Middle Pleistocene	Teleostei indet. <sup>1</sup>
‘Unit e’, Pigadia Basin	Middle Pleistocene	Teleostei indet. (cf. Ostariophysi) <sup>2</sup>
Gryllos-Mesovouni	Plio–Pleistocene	Teleostei indet. <sup>3</sup>
Vatera <sup>207301</sup>	Plio–Pleistocene	Teleostei indet. <sup>4</sup>
Northern Milos	Plio–Pleistocene	Teleostei indet. <sup>5</sup>
Faros, Aegina	? Zanclean	Teleostei indet. <sup>6</sup>
Temple of Aphrodite, Aegina	? Zanclean	Teleostei indet. <sup>6</sup>
Florina/Ptolemais	Messinian–Zanclean	Teleostei indet. <sup>7</sup>
Neo Khorio <sup>207611</sup>	Messinian	Teleostei indet. <sup>8</sup>
Keri, Zakynthos	Tortonian	Teleostei indet. <sup>9</sup>
Kefalonia	? Late Miocene	Teleostei indet.*
Nenita beds, Chios <sup>207609</sup>	Early Miocene (MN5)	Teleostei indet. <sup>10, i</sup>
Near Megalopoli	Late Maastrichtian	Teleostei indet.**

MN Mammal Neogene Zone

\*Pers. obs. and comm. with S. Roussiakis

\*\*Pers. obs. and comm. with E. Koskeridou, G. Theodorou, and K. Trikolos

<sup>1</sup>Families recognized on the basis of otoliths and/or ichthyoliths, treated by Agiadi ([this volume](#))

<sup>1</sup>Panagopoulou et al. (2018), <sup>2</sup>Bellas et al. (1998), <sup>3</sup>Kamperis (1987), <sup>4</sup>Drinia et al. (2002), <sup>5</sup>Calvo et al. (2012), <sup>6</sup>Leivaditis (1974), <sup>7</sup>Hordijk and de Bruijn (2009), <sup>8</sup>Freudenthal (1969), <sup>9</sup>Dermitzakis (1979), <sup>10</sup>Reichenbacher and Böhme (2004)

**Table 2** List of Greek localities with known occurrences of non-teleostean actinopterygians (†Pycnodontidae), and stem (†Ichthyodectoidei, †Leptolepididae) and early diverging crown teleosts (†Osmeroididae) in chronological order

Localities <sup>PBDB No</sup>	Age	Taxon
Gavdos <sup>207367</sup>	Late Maastrichtian	†Ichthyodectoidei indet. <sup>1</sup>
Unspecified localities near Karpenisi	Late Maastrichtian	†Osmeroididae † <i>Osmeroides</i> sp.2,**
Lindos, Rhodes <sup>207610</sup>	?Cenomanian	†Pycnodontidae † <i>Coelodus</i> sp. <sup>3–5</sup>
Anavryssada	Toarcian	†Leptolepididae indet. <sup>6,*</sup>

\*Taxonomy revised, or updated in this study

\*\*Poorly documented occurrence, not treated further in this chapter

<sup>1</sup>Cavin et al. (2012), <sup>2</sup>Koch and Nikolaus (1969), <sup>3</sup>Melentis (1967a), <sup>4</sup>Melentis (1967b), <sup>5</sup>Schultz et al. (1997), <sup>6</sup>Kottek (1964)

**Table 3** List of Greek localities with known occurrences of otocephalan ray-finned fishes: families Clupeidae and Cyprinidae

Localities <sup>PBDB No</sup>	Age	Taxon
Stavromenos <sup>162721</sup>	Piacenzian	<u>Clupeidae</u> <i>Alosa</i> sp. <sup>1</sup> , <i>Sardina</i> sp. <sup>1</sup> , <i>Spratelloides</i> sp. <sup>1</sup> ,
Roufas <sup>207304</sup>	Piacenzian	<u>Clupeidae</u> <i>Alosa</i> sp. <sup>1</sup> <i>Sardina</i> sp. <sup>1</sup> ,
Armissos <sup>207303</sup>	Piacenzian	<u>Clupeidae</u> <i>Alosa</i> cf. <i>A. elongata</i> <sup>1,2</sup> <i>Sardina</i> cf. <i>S. pilchardus</i> <sup>1,2</sup> , <i>Spratelloides</i> cf. <i>S. gracilis</i> <sup>1,2</sup> ,
Voutes <sup>207357</sup>	Piacenzian	<u>Clupeidae</u> <i>Alosa</i> sp. <sup>2</sup> , ? <i>Sardina</i> sp. <sup>2</sup> , <i>Spratelloides gracilis</i> <sup>2</sup> ,
Gournes <sup>207359</sup>	Piacenzian	<u>Clupeidae</u> <i>Alosa</i> sp. <sup>2</sup> , ? <i>Sardina</i> sp. <sup>2</sup> , <i>Spratelloides gracilis</i> <sup>2</sup>
Aghios Thomas, Aegina <sup>207360</sup>	Zanclean	Upper part of section: <u>Clupeidae</u> <i>Spratelloides gracilis</i> <sup>3</sup> Middle part of section: Clupeidae indet.* Mesagros – Alones road: <u>Clupeidae</u> <i>Spratelloides</i> cf. <i>S. gracilis</i> <sup>4</sup>
Kalamaki	Pliocene	<u>Clupeidae</u> <i>Spratelloides gracilis</i> <sup>5</sup>
Strymonas	Pliocene	<u>Clupeidae</u> ? <i>Alosa tanaica</i> <sup>6,*</sup>
Aidonochori	Late Miocene	<u>Clupeidae</u> indet. <sup>7</sup>
Metochia C <sup>207361</sup>	Messinian	<u>Clupeidae</u> <i>Alosa</i> sp. <sup>8</sup>
Akropotamos	Messinian	<u>Clupeidae</u> † <i>Alosa crassa</i> <sup>9,*</sup>
Ano Metochi 3 <sup>31928</sup>	Messinian	Cyprinidae indet. <sup>10</sup>
Mires <sup>207364</sup>	Messinian	<u>Clupeidae</u> † <i>Alosa crassa</i> <sup>11,*</sup>

Localities <sup>PBDB No</sup>	Age	Taxon
Unknown Cretan locality, possibly near Rethymnon	?Messinian	<u>Clupeidae</u> † <i>Alosa crassa</i> <sup>12,13</sup>
Karave <sup>60775</sup>	Tortonian	<u>Clupeidae</u> † <i>Alosa crassa</i> <sup>14,*</sup>
Chapel Aghia Paraskevi <sup>207356</sup>	Tortonian	<u>Clupeidae</u> <i>Alosa</i> sp. <sup>15</sup> , † <i>Alosa</i> cf. <i>A. crassa</i> <sup>15,*</sup> , <i>Spratelloides</i> sp. <sup>15</sup>
Type strata of Makrilia Fm., 4 km to the North of Chapel Aghia Paraskevi	Tortonian	<u>Clupeidae</u> indet. <sup>16</sup>
Lapsarna <sup>186558</sup>	Burdigalian	<u>Cyprinidae</u> <i>Barbus</i> sp. <sup>17</sup> , <i>Cyprinion</i> sp. <sup>17</sup> , † <i>Palaeoleuciscus</i> sp. <sup>17</sup>
Aghioi Theodori or Myriki <sup>207612</sup>	Danian	<u>Clupeidae</u> indet. <sup>18,**</sup>
Unspecified localities near Karpenisi	Late Maastrichtian	<u>Clupeomorpha incertae sedis</u> † <i>Scombroclupea</i> sp. <sup>18,**</sup>

\*Taxonomy revised, or updated in this study

\*\*Poorly documented occurrence, not treated further in this chapter

<sup>1</sup>Gaudant (2001), <sup>2</sup>Gaudant et al. (1994), <sup>3</sup>Gaudant et al. (2010b), <sup>4</sup>Argyriou and Theodorou (2011), <sup>5</sup>Gaudant and Symeonidis (1995), <sup>6</sup>Weiler (1943), <sup>7</sup>Kevrekidis (2016), <sup>8</sup>Gaudant et al. (2006), <sup>9</sup>Dermitzakis et al. (1986), <sup>10</sup>Georgalis et al. (2017), <sup>11</sup>Gaudant et al. (1997a), <sup>12</sup>Gaudant (1980), <sup>13</sup>Gaudant (2014b), <sup>14</sup>Gaudant et al. (2005), <sup>15</sup>Gaudant (2004), <sup>16</sup>Bürgin (1994), <sup>17</sup>Vasileiadou et al. (2017), <sup>18</sup>Koch and Nikolaus (1969)

**Table 4** List of Greek localities with known occurrences of aulopiform ray-finned fishes: families †Dercetidae, †Enchodontidae, and Paralepididae

Localities <sup>PBDB No</sup>	Age	Taxon
Metochia C <sup>207361</sup>	Messinian	<u>Paralepididae</u> † <i>Paralepis albyi</i> <sup>1</sup>
Gavdos <sup>207367</sup>	Late Maastrichtian	† <u>Enchodontidae</u> † <i>Enchodus</i> cf. † <i>E. dirus</i> <sup>2</sup> ,
Aghia Trias–Domiani Road <sup>207613</sup>	Late Maastrichtian	† <u>Dercetidae</u> † <u>Dercetidae</u> indet. <sup>3,*</sup> † <u>Enchodontidae</u> ? † <i>Enchodus</i> indet. <sup>3</sup> , † <u>Ichthyotringidae</u> <sup>**</sup> † <i>Ichthyotringa</i> sp. <sup>3,**</sup>
Unspecified localities near Karpenissi <sup>207615</sup>	Late Maastrichtian	† <u>Enchodontidae</u> † <i>Eurypholis</i> indet. <sup>3,**</sup>

\*Taxonomy revised, or updated in this study

\*\*Poorly documented occurrence, not treated further in this chapter

<sup>1</sup>Gaudant et al. (2006), <sup>2</sup>Cavin et al. (2012), <sup>3</sup>Koch and Nikolaus (1969)

**Table 5** List of Greek localities with known occurrences of stomiatiform ray-finned fishes: families Gonostomatidae and Sternoptychidae

Localities <sup>PBDB No</sup>	Age	Taxon
Armissos <sup>207303</sup>	Piacenzian	<u>Sternoptychidae</u> <i>Maurolicus</i> cf. <i>M. muelleri</i> <sup>1</sup>
Aegina Island	Zanclean	<u>Sternoptychidae</u> <i>Argyropelecus</i> sp. <sup>2</sup>
Metochia C <sup>207361</sup>	Messinian	<u>Sternoptychidae</u> <i>Maurolicus muelleri</i> <sup>3</sup>
Tsangaraki <sup>207364</sup>	Messinian	<u>Sternoptychidae</u> <i>Maurolicus muelleri</i> <sup>4</sup>
Mires <sup>207364</sup>	Messinian	<i>Maurolicus muelleri</i> <sup>4</sup>
<b>Chapel Aghia Paraskevi</b> <sup>207356</sup>	Tortonian	<u>Gonostomatidae</u> † <i>Cyclothone gaudanti</i> <sup>5-6</sup> , <u>Sternoptychidae</u> <i>Maurolicus muelleri</i> <sup>5</sup>
<b>400 m from Chapel Aghia Paraskevi</b> <sup>207355</sup>	Tortonian	<u>Gonostomatidae</u> † <i>Cyclothone gaudanti</i> <sup>5-6</sup> , <u>Sternoptychidae</u> <i>Maurolicus muelleri</i> <sup>5</sup>

<sup>1</sup>Gaudant (2001), <sup>2</sup>Argyriou and Theodorou (2011), <sup>3</sup>Gaudant et al. (2006), <sup>4</sup>Gaudant et al. (1997a), <sup>5</sup>Gaudant (2004), <sup>6</sup>Přikryl and Carnevale (2017)

**Table 6** List of Greek localities with known occurrences of myctophiform ray-finned fishes: family Myctophidae

Localities <sup>PBDB No</sup>	Age	Taxon
Armissos <sup>207303</sup>	Piacenzian	Myctophidae indet. <sup>1</sup>
Metochia C <sup>207361</sup>	Messinian	†“ <i>Myctophum</i> ” <i>dorsale</i> <sup>2</sup> , †“ <i>Myctophum</i> ” <i>licatae</i> <sup>2</sup>
Tsangaraki <sup>207364</sup>	Messinian	†“ <i>Myctophum</i> ” <i>licatae</i> <sup>3</sup>
Mires <sup>207364</sup>	Messinian	†“ <i>Myctophum</i> ” <i>licatae</i> <sup>3</sup> , †“ <i>Myctophum</i> ” <i>dorsale</i> <sup>3</sup>
Psalida <sup>207365</sup>	Messinian	†“ <i>Myctophum</i> ” <i>licatae</i> <sup>3</sup> , †“ <i>Myctophum</i> ” <i>dorsale</i> <sup>3</sup>
‘Unit b’, Pigadia Basin	Messinian	Myctophidae indet. <sup>4</sup>
Metochia B <sup>185752</sup>	Tortonian	†“ <i>Myctophum</i> ” <i>licatae</i> <sup>5</sup>
Karave <sup>60775</sup>	Tortonian	†“ <i>Myctophum</i> ” <i>licatae</i> <sup>5</sup>
Chapel Aghia Paraskevi <sup>207356</sup>	Tortonian	†“ <i>Myctophum</i> ” <i>licatae</i> <sup>6</sup>
400 m from Chapel Aghia Paraskevi <sup>207355</sup>	Tortonian	†“ <i>Myctophum</i> ” sp. <sup>6</sup> , †“ <i>Myctophum</i> ” <i>licatae</i> <sup>6</sup>
Type strata of Makrilia Fm., 4 km to the North of Chapel Aghia Paraskevi	Tortonian	Myctophidae indet. <sup>7</sup>

<sup>1</sup>Gaudant (2001), <sup>2</sup>Gaudant et al. (2006), <sup>3</sup>Gaudant et al. (1997a), <sup>4</sup>Bellas et al. (1998) <sup>5</sup>Gaudant et al. (2005), <sup>6</sup>Gaudant (2004), <sup>7</sup>Bürgin (1994)



**Table 7** List of Greek localities with known occurrences of gadiform ray-finned fishes: families Gadidae, Moridae, and Bregmacerotidae

Localities <sup>PBDB No</sup>	Age	Taxon
Stavromenos <sup>162721</sup>	Piacenzian	<u>Bregmacerotidae</u> <i>Bregmaceros</i> sp. <sup>1,2</sup>
Roufas <sup>207304</sup>	Piacenzian	<u>Bregmacerotidae</u> <i>Bregmaceros</i> cf. † <i>B. albyi</i> <sup>1</sup>
Armissos <sup>207303</sup>	Piacenzian	<u>Bregmacerotidae</u> <i>Bregmaceros</i> cf. † <i>B. albyi</i> <sup>1,3</sup>
		<u>Gadidae</u> <i>Micromesistius</i> sp. <sup>1</sup> ,
		<u>Moridae</u> <i>Gadella</i> sp. <sup>1</sup> ,
Voutes <sup>207357</sup>	Piacenzian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>3</sup>
Prassas <sup>207358</sup>	Piacenzian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>3</sup>
Gournes <sup>207359</sup>	Piacenzian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>3</sup>
Aghios Thomas, Aegina <sup>207360</sup>	Zanclean	Middle part of section: <u>Bregmacerotidae</u> <i>Bregmaceros</i> cf. † <i>B. albyi</i> <sup>4</sup>
		Mesagros – Alones Road: <u>Bregmacerotidae</u> <i>Bregmaceros</i> cf. † <i>B. albyi</i> <sup>4</sup>
Kalamaki	Pliocene	<u>Moridae</u> ? <i>Gadella</i> sp. <sup>6</sup>
Metochia C <sup>207361</sup>	Messinian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>7</sup>
Mires <sup>207364</sup>	Messinian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>8</sup>
Psalida <sup>207365</sup>	Messinian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>8</sup>
‘Unit b’, Pigadia Basin	Messinian	† <i>Bregmaceros albyi</i> <sup>9</sup>
Metochia B <sup>185752</sup>	Tortonian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>10</sup> ,
Chapel Aghia Paraskevi <sup>207356</sup>	Tortonian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>11</sup>
400 m from Chapel Aghia Paraskevi <sup>207355</sup>	Tortonian	<u>Bregmacerotidae</u> † <i>Bregmaceros albyi</i> <sup>11</sup>
Type strata of Makrilia Fm., 4 km to the North of Chapel Aghia Paraskevi	Tortonian	† <i>Bregmaceros albyi</i> . <sup>12</sup>

<sup>1</sup>Gaudant (2001), <sup>2</sup>Symeonidis and Schultz (1973), <sup>3</sup>Gaudant et al. (1994), <sup>4</sup>Argyriou and Theodorou (2011), <sup>5</sup>Weiler (1943), <sup>6</sup>Gaudant and Symeonidis (1995), <sup>7</sup>Gaudant et al. (2006), <sup>8</sup>Gaudant et al. (1997a), <sup>9</sup>Bellas et al. (1998), <sup>10</sup>Gaudant et al. (2005), <sup>11</sup>Gaudant (2004), <sup>12</sup>Bürgin (1994)

**Table 8** List of Greek localities with known occurrences of acanthomorph ray-finned fishes: families listed alphabetically Acanthuridae, Atherinidae, Belonidae, Blenniidae, Bothidae, Caproidae, Carangidae, Centriscidae, Centropotamidae, Cyprinodontidae, Dactylopteridae, Gobiidae, Labridae, Monacanthidae, Scombridae, Serranidae, Sparidae, Syngnathidae, and Trichiuridae. Additional families (Ambassidae, Moronidae, Moronidae, and Percichthyidae) are indicatively listed as problematic occurrences in the Miocene of Kymi, but are not further treated

Localities <sup>PBDB No</sup>	Age	Taxon
Frangokastello <sup>207302</sup>	middle–late Pliocene	<u>Monacanthidae</u> † <i>Frigocanthus stroppanobili</i> <sup>1</sup>
Stavromenos <sup>162721</sup>	late Pliocene	<u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>2</sup>
Roufas <sup>207304</sup>	Piacenzian	<u>Trichiuridae</u> <i>Lepidopus</i> cf. <i>caudatus</i> <sup>2</sup>
Armissos <sup>207303</sup>	Piacenzian	<u>Belonidae</u> <i>Belone</i> sp. <sup>2</sup> , ? <i>Scomberesox</i> sp. <sup>2</sup> , <u>Carangidae</u> <i>Caranx</i> sp. <sup>2</sup> , <i>Trachurus</i> sp. <sup>2</sup> , <u>Centriscidae</u> <i>Aeoliscus</i> cf. <i>A. strigatus</i> <sup>2-3</sup> , <u>Dactylopteridae</u> <i>Dactylopterus</i> sp. <sup>2</sup> , <u>Labridae</u> indet. <sup>2</sup> <u>Monacanthidae</u> † <i>Frigocanthus margaritatus</i> <sup>1,2</sup> Percomorpha indet. <sup>2,*</sup> , <u>Scombridae</u> <i>Scomberomorus</i> sp. <sup>2</sup> , <i>Scomber</i> sp. <sup>2</sup> , <u>Serranidae</u> <i>Serranus</i> sp. <sup>2</sup> , <u>Sparidae</u> <i>Boops</i> sp. <sup>2,4</sup> , <u>Syngnathidae</u> <i>Syngnathus</i> cf. † <i>S. albyi</i> <sup>2-3</sup> , <u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>2,4</sup> ,
Voutes <sup>207357</sup>	Piacenzian	<u>Belonidae</u> <i>Belone</i> sp. <sup>4</sup> , <u>Syngnathidae</u> <i>Syngnathus</i> sp. <sup>4</sup> , <u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>4</sup>
Prassas <sup>207358</sup>	Piacenzian	<u>Blenniidae</u> <i>Salaria</i> cf. <i>S. pavo</i> <sup>4,*</sup> , Percomorpha indet. <sup>4,*</sup> <u>Sparidae</u> <i>Boops</i> cf. <i>B. boops</i> <sup>4</sup> ,

Localities <sup>PBDB No</sup>	Age	Taxon
Gournes <sup>207359</sup>	Piacenzian	<u>Gobiidae</u> <i>Gobius</i> s.l. sp. <sup>4</sup> <u>Sparidae</u> , <i>Boops</i> cf. <i>B. boops</i> <sup>4</sup> ,
Aghia Marina Aegina	Piacenzian?	? <u>Labridae</u> <sup>*,**</sup> ?† <i>Trigonodon</i> cf. <i>jugleri</i> <sup>5,*,**</sup>
Aghios Thomas, Aegina <sup>207360</sup>	Zanclean	Upper part of section: Serranidae indet. <sup>6</sup> Mesagros – Alones Road: Percomorpha indet. <sup>*</sup> <u>Syngnathidae</u> <i>Syngnathus</i> cf. <i>S. acus</i> <sup>7</sup> , Percomorpha indet. <sup>*</sup>
Kalamaki	Pliocene	<u>Atherinidae</u> Atherinidae indet. <sup>8</sup> <u>Carangidae</u> <i>Trachurus</i> sp. <sup>8</sup> , <u>Gobiidae</u> <i>Gobius</i> s.l. sp. <sup>8</sup> , Percomorpha indet. <sup>8,*</sup>
Metochia C <sup>207361</sup>	Messinian	<u>Centriscidae</u> ? <i>Aeoliscus</i> sp. <sup>9,*</sup> <u>Syngnathidae</u> <i>Syngnathus</i> cf. † <i>S. albyi</i> <sup>9</sup> <u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>9</sup> ,
Voukolies <sup>207362</sup>	Messinian	<u>Cyprinodontidae</u> † <i>A. crassicaudus</i> <sup>10,*</sup>
Kaleryiana <sup>207363</sup>	Messinian	<u>Cyprinodontidae</u> † <i>A. crassicaudus</i> <sup>10</sup>
Tsangaraki <sup>207364</sup>	Messinian	<u>Syngnathidae</u> † <i>Syngnathus albyi</i> <sup>11</sup>
Mires <sup>207364</sup>	Messinian	Pleuronectiformes indet. <sup>11,*</sup> <u>Syngnathidae</u> † <i>Syngnathus albyi</i> <sup>11</sup> , <u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>11</sup> ,
Psalida <sup>207365</sup>	Messinian	Percomorpha indet. <sup>11,*</sup>
‘Unit b’, Pigadia Basin	Messinian	<i>Dentex</i> sp. <sup>12</sup> <i>Pagellus</i> sp. <sup>12</sup>
Metochia B <sup>185752</sup>	Tortonian	<u>Syngnathidae</u> <i>Syngnathus</i> cf. † <i>S. albyi</i> <sup>13</sup> <u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>13</sup>
Karave <sup>60775</sup>	Tortonian	<u>Acanthuridae</u> indet. <sup>13</sup>

Localities <sup>PBDB No</sup>	Age	Taxon
<b>Chapel Aghia Paraskevi</b> <sup>207356</sup>	Tortonian	<u>Acanthuridae</u> indet. <sup>14</sup> ,
		<u>Bothidae</u> <i>Arnoglossus</i> sp. <sup>14</sup> ,
		<u>Caproidae</u> <i>Capros</i> sp. <sup>14</sup> ,
		<u>Carangidae</u> † <i>Alectis psarianosi</i> <sup>14,15</sup> , <i>Trachurus</i> sp. <sup>13</sup> ,
		Percomorpha indet. <sup>14,*</sup> ,
		<u>Syngnathidae</u> <i>Syngnathus</i> cf. † <i>S. albyi</i> <sup>14,16</sup>
		<u>Trichiuridae</u> <i>Lepidopus</i> sp. <sup>14,15</sup>
Type strata of Makrilia Fm., 4 km to the North of Chapel Aghia Paraskevi	Tortonian	<i>Lepidopus</i> sp. <sup>17</sup>
Unknown localities near Kymi	? early Miocene	? <u>Ambassidae</u> indet. <sup>18,19,*,**</sup> ,
		<u>Centropomidae</u> cf. <i>Latinae</i> indet. <sup>20,21,*</sup>
		? <u>Gobiidae</u> ? <i>Periophthalmus</i> sp. <sup>22,**</sup> ,
		? <u>Moronidae</u> indet. <sup>23,*,**</sup>
		? <u>Scombridae</u> indet. <sup>18,19**</sup> ,
		? <u>Percichthyidae</u> indet. <sup>22,**</sup>

\*Taxonomy revised, or updated in this study

\*\*Poorly documented occurrence, not treated further in this chapter

<sup>1</sup>Sorbini and Tyler (2004), <sup>2</sup>Gaudant (2001), <sup>3</sup>Bachmayer et al. (1984), <sup>4</sup>Gaudant et al. (1994), <sup>5</sup>Leivaditis (1974), <sup>6</sup>Gaudant et al. (2010b), <sup>7</sup>Argyriou and Theodorou (2011), <sup>8</sup>Gaudant and Symeonidis (1995), <sup>9</sup>Gaudant et al. (2006), <sup>10</sup>Gaudant (2014b), <sup>11</sup>Gaudant et al. (1997a), <sup>12</sup>Bellas et al. (1998), <sup>13</sup>Gaudant et al. (2005), <sup>14</sup>Gaudant (2004), <sup>15</sup>Symeonidis (1969), <sup>16</sup>Bachmayer and Symeonidis (1978), <sup>17</sup>Bürgin (1994), <sup>18</sup>Valenciennes (1861), <sup>19</sup>Gaudry (1862), <sup>20</sup>de Waldheim (1838), <sup>21</sup>de Waldheim (1850), <sup>22</sup>Unger (1867), <sup>23</sup>Woodward (1901)

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