

The Messinian fishes of Capo di Fiume (Palena, Abruzzo): Stratigraphy, taphonomy and paleoecology

Giorgio CARNEVALE^{*†}, Luca PELLEGRINO[†], Marcello NATALICCHIO & Francesco DELA PIERRE

G. Carnevale, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; giorgio.carnevale@unito.it
^{*}corresponding author

L. Pellegrino, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; lu.pellegrino@unito.it

M. Natalicchio, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; marcello.natalicchio@unito.it

F. Dela Pierre, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; francesco.delapierre@unito.it

[†]Joint first authorship

KEY WORDS - Fishes, Abruzzo Apennines, biosedimentology, diatomite, microbial mats, trophic relationships, paleoenvironmental reconstruction.

ABSTRACT - The Messinian laminated diatomites exposed in the Capo di Fiume stratigraphic section, near the town of Palena, along the slopes of Mt. Porrara in the Abruzzo Apennines, contain well-preserved articulated fish skeletal remains, often associated with plants. A large collection of fossils from this section was accumulated and donated by Erminio Di Carlo to the Museo Geopaleontologico dell'Alto Aventino, Palena, Italy. Herein, we present the stratigraphy of the Capo di Fiume section and a preliminary biosedimentological study of the fossiliferous laminated diatomites. A taphonomic and paleoecological analysis of the fish remains deriving from the oldest diatomite interval of the succession is also included. The sedimentary succession documents the transition from continental to paralic to coastal to open marine conditions, suggesting the existence of a rather narrow shelf connecting coastal and basinal areas. The deposition of the diatomite laminae took place through different biological mechanisms, most notably the so-called "fall dump", which involved the formation of flocs (mucilaginous aggregates) that included diatom assemblages dominated by *Coscinodiscus* spp. and *Thalassionema nitzschioides*. The macrofossil assemblage of the diatomites and the biosedimentological study of the laminated fossiliferous diatomites have provided new data regarding the paleoenvironmental and paleogeographic setting and the ecological relationships. The diatom content of the fossiliferous (biogenic) laminae as well as the structure and composition of the fish assemblage clearly indicate a depositional marine environment with depths of up to several tens of meters. The fish assemblage is largely dominated by the round herring *Spratelloides lemoinei*, which represented the trophic nucleus of the original fish community. This and other clupeid species and certain "adventitious visitors" occupied the upper portion of the water column. The "adventitious visitors" are represented by mesopelagic diel vertical migrants (*Diaphus edwardsi*, *Lestidiops sphekodes*, *Maurolicus* cf. *muelleri*, *Myctophum columnae*, *Paralepis albyi*), which were probably attracted in the Capo di Fiume paleobiootope by abundant planktonic organisms as well as by shoals of *Spratelloides lemoinei*. The lower portion of the water column and the seafloor were well aerated and occupied by a diverse community of demersal fish taxa, especially sparids. The rapid deposition of diatom mats, abundantly represented in the fossiliferous intervals, may have resulted in the swift entombment of fish carcasses, whose fossilization was promoted even under relatively well-oxygenated bottom conditions.

INTRODUCTION

Our knowledge of the Miocene history of the Mediterranean ichthyofauna is largely due to the abundant remains contained in the Messinian sedimentary rocks broadly exposed onshore in the entire basin, from the western localities in Algeria and Spain to the eastern ones in Crete and Cyprus (e.g., Gaudant, 2002). Articulated skeletal remains of bony fishes are relatively common in the diatomaceous sediments (e.g., Arambourg, 1925, 1927; Leonardi, 1959; Sturani & Sampò, 1973; Bradley & Landini, 1982; Bedini et al., 1986; Gaudant, 2002; Carnevale, 2004, 2006, 2007) that cyclically accumulated throughout the basin before the onset of the Messinian salinity crisis at about 6 Ma (e.g., Pellegrino et al., 2018), but also in the organic-rich laminated clays and marls that originated during the three stages of the Messinian salinity crisis (e.g., Sorbini, 1988; Landini & Sorbini, 1989; Gaudant, 2002; Carnevale et al., 2003, 2006, 2008, 2018, 2019a; Carnevale & Schwarzahns, 2022).

In the Italian Peninsula, Messinian fish skeletal remains have been reported from a number of localities in the Emilia-Romagna, Marche and Tuscany regions (see Landini & Sorbini, 1992). The occurrence of Messinian

fish remains in the Abruzzo Apennines was mentioned by Mazza et al. (1995) in their cursory description of the stratigraphic section of Capo di Fiume, near the town of Palena, along the slopes of Mt. Porrara. During the 1990s, a rich collection of fossils from this locality was assembled by Mr Erminio Di Carlo. This collection, which includes a number of nicely preserved fishes, is currently part of the collections of the Museo Geopaleontologico dell'Alto Aventino, Palena, Italy. The goal of this paper is to provide a general account of the Messinian fish assemblage of Capo di Fiume and to discuss its stratigraphic context, taphonomic features and paleoecological significance.

GEOLOGICAL SETTING

Mt. Porrara pertains to the Morrone-Porrara Tectonic Unit (Fig. 1), an ENE-dipping Apennine-verging monocline, constituted by Mesozoic and Cenozoic platform-and-basin-derived carbonate sequences capped by siliciclastic flysch deposits (e.g., Raffi & Forti, 1959; Crostella, 1967; Patacca et al., 1992), originally located at the north-western margin of the Apulia Platform (Fig. 2). Within the Morrone-Porrara Unit, Mt. Porrara, together

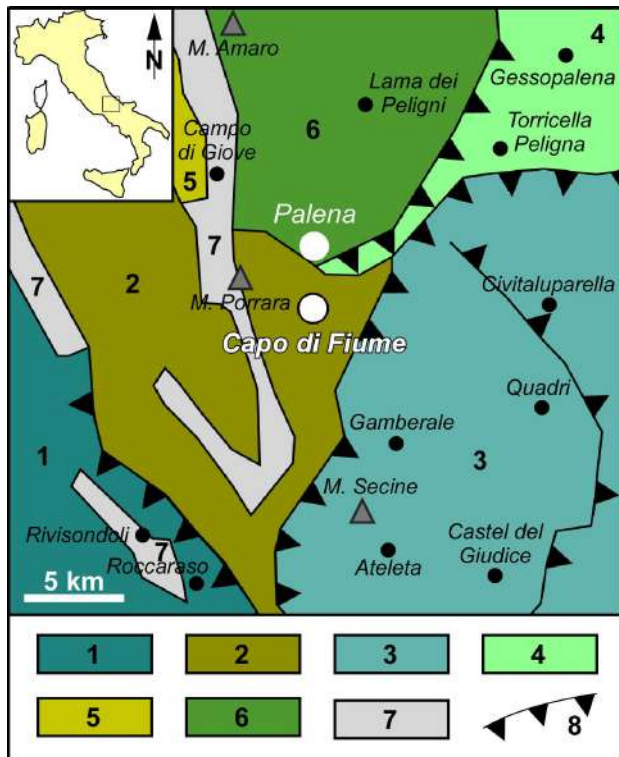


Fig. 1 - Simplified geological sketch of the studied area (modified from Carnevale et al., 2011). 1: Gran Sasso-Genzana Unit. 2: Morrone-Porrara Unit. 3: Agnone Unit. 4: Tuffillo Unit. 5: Queglia Unit. 6: Maiella Unit. 7: Alluvial deposit. 8: Thrust.

with Mts Rotella and Pizzalto, constitute a ridge system represented by a Jurassic-Upper Cretaceous platform facies, followed by Upper Cretaceous-Eocene deposits belonging to the distal carbonate escarpment (Patacca et al., 1992). These sediments are unconformably overlain by fragmentary Miocene successions, mostly represented by the Langhian to Tortonian carbonate-ramp deposits of

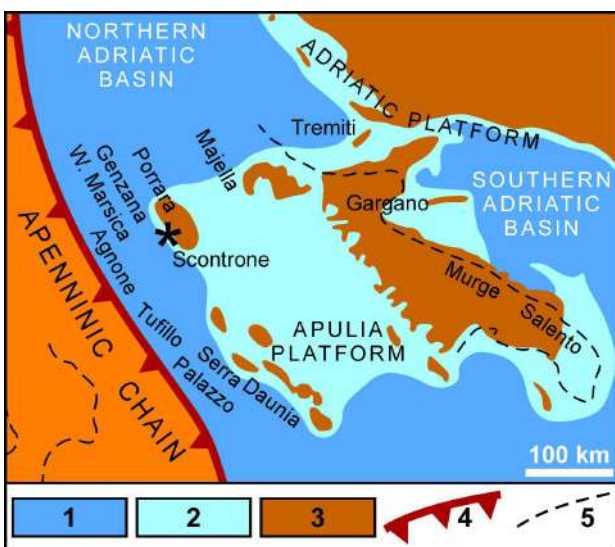


Fig. 2 - Paleogeographic reconstruction of the Southern Apennine area during the Late Miocene. 1: Open marine basin. 2: Shelf. 3: Emerged lands. 4: Apenninic orogenic front. 5: Present-day coastline. Modified from Brandano et al. (2017). The asterisk indicates the location of the studied section.

the Bryozoan Limestone Formation and *Lithothamnion* Limestone Formation (e.g., Patacca et al., 1992, 2013). Not far from the Sorgenti di Capo di Fiume, along the Aventino River, however, the Upper Cretaceous carbonate deposits are covered by some meters of bauxites (“Terra rossa”; see Mazza et al., 1995; Mazza & Rustioni, 1996), which are followed by marls and clayey marls, in turn overlain by a cyclical marine succession (Fig. 3) capped by turbiditic deposits. Such a succession is affected by SW-striking extensional shear planes (Miccadei & Parotto, 1998).

MATERIALS AND METHODS

The sedimentological analysis of the units exposed in the Capo di Fiume section has been performed using polished slabs and thin sections. Thin sections were examined with a Leica DM 2770 P optical microscope, in reflected and transmitted light. The micropaleontological composition of diatom-rich laminae was obtained by selecting freshly broken sediment chips that were mounted onto aluminum stubs, sputter coated with gold in an Eiko IB-3 ion coater, and observed with a JEOL JSM-6510JLV scanning electron microscope.

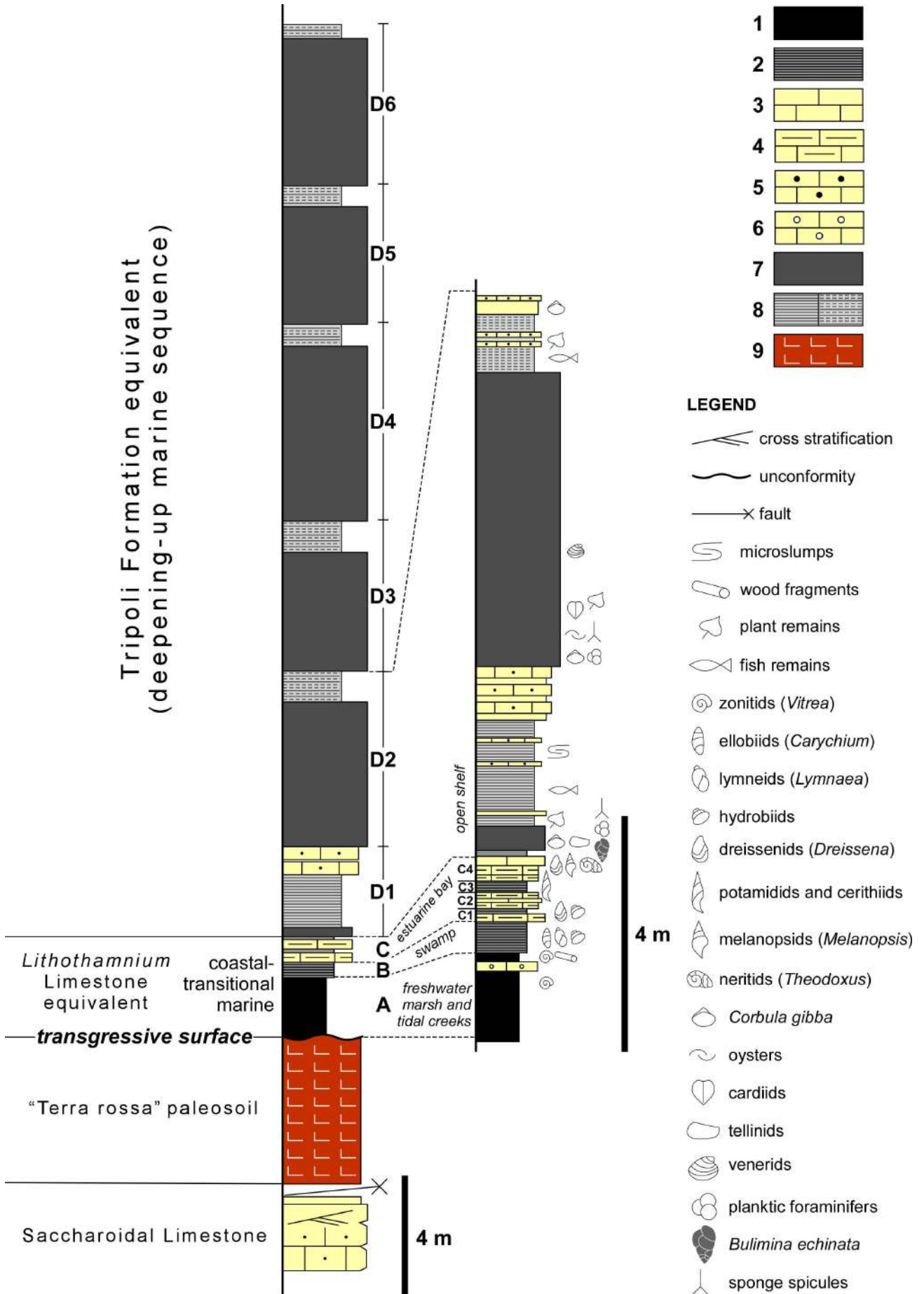
The fossil fishes examined in this study were collected from the better exposed layers of the basal portion of the first diatomite interval (see below) and are mostly housed in the collection of the Museo Geopaleontologico dell’Alto Aventino (MGPA), Palena. The majority of these fossils required matrix removal before examination and were prepared using thin entomological needles. Measurements were taken to the nearest 0.1 mm using a dial caliper.

THE CAPO DI FIUME STRATIGRAPHIC SECTION

Stratigraphy

The Capo di Fiume stratigraphic section (Fig. 3) is exposed about 3 km south of the town of Palena, along the motorway “SS 84 - Frentana”, near the Aventino River, in the vicinity of the Sorgenti di Capo di Fiume. The section has been described in a series of papers (e.g., Bellatalla et al., 1992; Carboni et al., 1992; Patacca et al., 1992; Mazza et al., 1995; Miccadei & Parotto, 1998; Carnevale et al., 2011) in which its lithological and paleontological features have been discussed with different degrees of detail. Here, we refer to Carnevale et al. (2011), who described the stratigraphic features of the section in great detail. The section consists of paralic to open marine mud-dominated sediments of Messinian age overlying a “Terra rossa” horizon that documents a prolonged subaerial exposure, thereby providing evidence of the

Fig. 3 - Stratigraphic column of the Capo di Fiume section. 1: Mottled grey to dark-brown marl and clayey marl. 2: Fissile dark-grey marl and shaly marl. 3: Limestone. 4: Marly limestone. 5: Bio-lithoclastic calcarenite. 6: Lime conglomerate. 7: Massy muddy deposit. 8: Well-laminated (left half) and laminated to massive, bioturbated (right half) diatomite. 9: Bauxitic (“Terra rossa”) paleosoil. Modified from Carnevale et al. (2011).



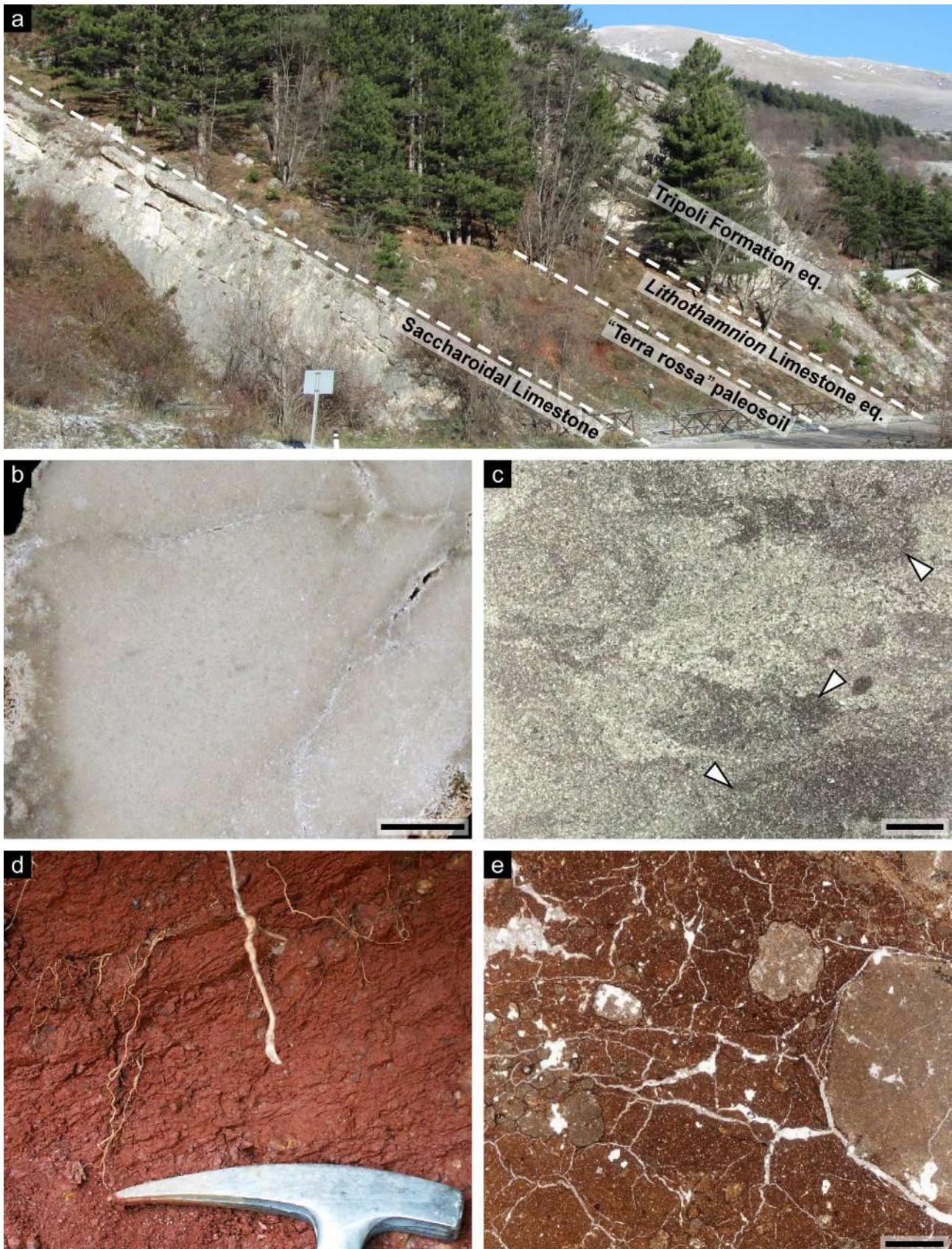


Fig. 4 - a) Panoramic view of the Capo di Fiume section; transition from continental facies ("Terra rossa" paleosoil) to frankly marine facies (Tripoli Formation equivalent), passing through marsh-swamp to estuarine facies (*Lithothamnion* Limestone equivalent). b) Polished slab of a hand specimen of Cretaceous saccharoidal limestone. c) Photomicrograph (transmitted light) of saccharoidal limestone; note the widespread bioturbations (arrowheads). d) Detail of the bauxitic paleosoil. e) Photomicrograph (transmitted light) of bauxitic paleosoil; note the spar-filled cracks and the carbonate nodules, locally coated with Fe-Al-rich clayey rim. Scale bars: b = 10 mm; c and e = 2 mm. (a), (c) and (e) modified from Carnevale et al. (2011).

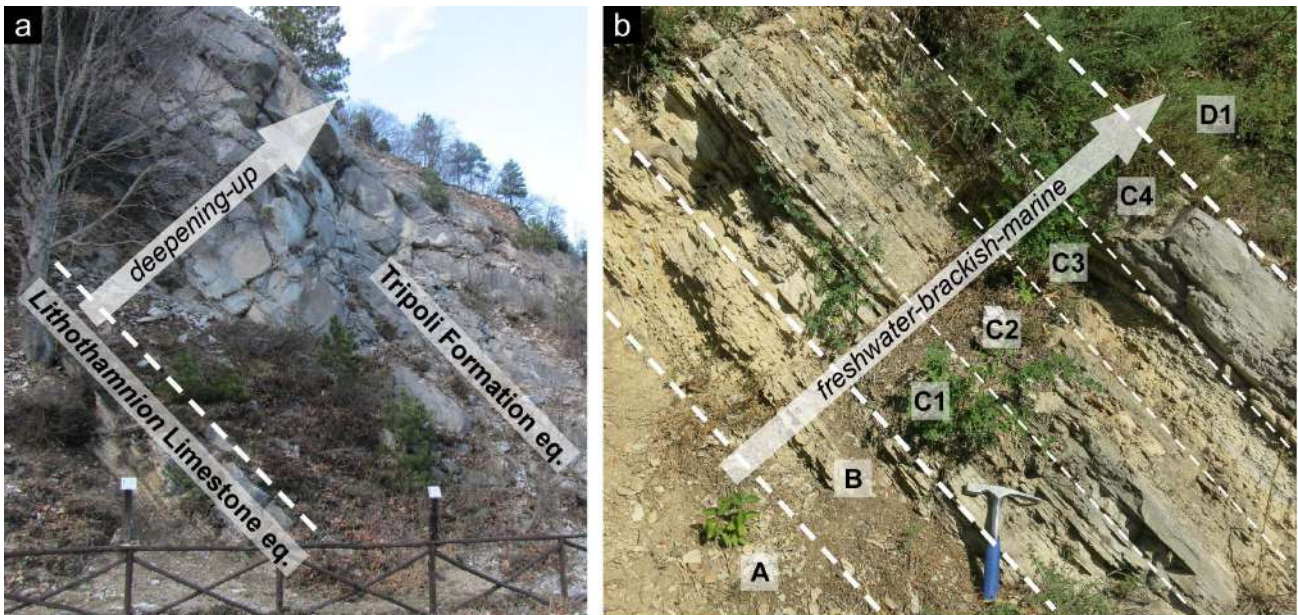


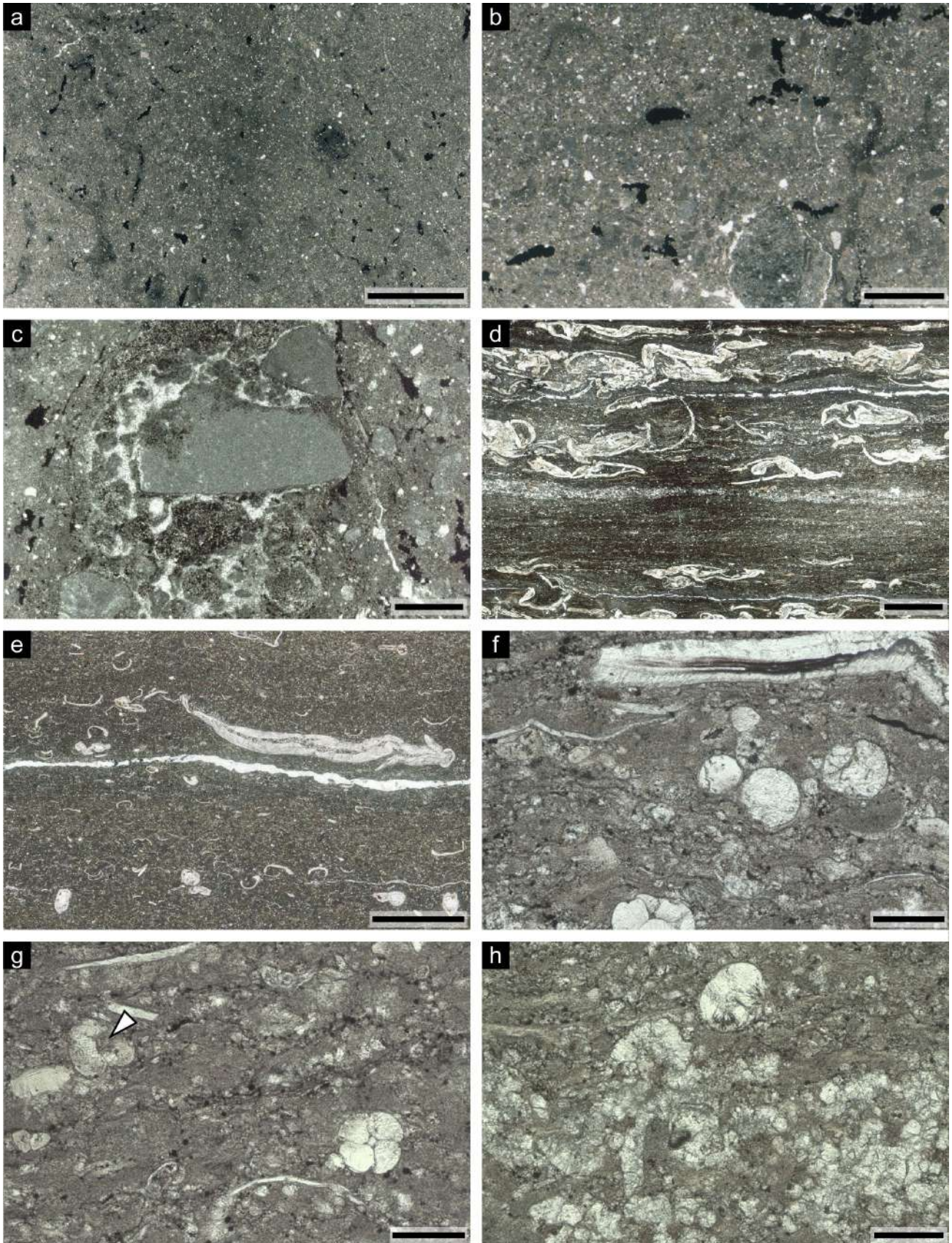
Fig. 5 - Lithostratigraphy of the Capo di Fiume section. a) Detail of the transition from the lowermost Messinian *Lithothamnion* Limestone Fm. equivalent to the lower Messinian Tripoli Fm. equivalent. b) Details of the members of *Lithothamnion* Limestone equivalent: A = top of the organic-rich freshwater deposits (freshwater marsh and tidal creeks); B = fetid, thinly laminated sediments (swampy environment); C1-4 = predominantly marly sediments (brackish environments progressively influenced by marine waters; see text for details); D1 = first diatomite-bearing interval (frankly marine conditions).

evolutionary transition from genuine continental facies to frankly marine conditions (Figs 3-4a). The “Terra rossa” soil covers uppermost Cretaceous limestones (Figs 3-4a), although a minor fault has locally obliterated the original stratigraphic contact. According to Carnevale et al. (2011), the Cretaceous carbonates underlying the “Terra rossa” deposits consist of medium-sized bioclastic limestones showing a crypto-crystalline texture and representing a lithostratigraphic unit named as Saccharoidal Limestone (Fig. 4a-c). The name of this lithostratigraphic unit is due to the “saccharoidal” texture of the biodetritus, almost exclusively composed of abraded and worn inoceramid prisms, echinoid radioles and calcisphaerulids (*Pithonella*-like). Large scale, low-angle planar cross stratification (Fig. 3) characterized by bidirectional dip is indicative of offshore marine bars in a ramp-like open-shelf setting. The top of the Saccharoidal Limestone is extensively bioturbated (Fig. 4c), showing large horizontal and oblique burrows likely indicative of a nearshore environment.

The “Terra rossa” paleosol horizon is exposed with a thickness exceeding 15 m (Figs 3-4a). The groundmass of the overlying red-stained illuvial soil (Fig. 4d) is composed by a fine mixture of yellow to red clay minerals, Fe/Mn hydroxides, quartz-grains and rare mica flakes. It also includes isolated and coalescent calcareous nodules, fine to medium-sand-sized carbonate lithoclasts with leached rims, locally abundant ferruginous pisoids and subordinate volcanic quartz and calcitized feldspars (Fig. 4e). The calcareous nodules consist of speckled micrite/microsparite masses precipitated in the vadose zone, often surrounded by a Fe-rich clayey red rim. Spar-filled circumgranular shrinkage cracks and complex networks of carbonate rhizoliths are the most common pedofeatures (Fig. 4e). In some cases, the porosity associated with root activities are partly or totally filled with well-preserved

needle-fiber or whisker calcite cement of vadose origin (Fig. 4e).

The Messinian transgressive deposits overlying the “Terra rossa” paleosol (Figs 3 and 5a) consist in the lower part of a deepening-up muddy sequence indicative of marsh to swamp to estuarine environments (members A-C in Figs 3 and 5b), which possibly represents an equivalent of the *Lithothamnion* Limestone Formation (Carnevale et al., 2011). The upper portion consists instead of open-marine shelf sediments, representing an equivalent of the Tripoli Formation (Figs 3-4a and 5a; Carnevale et al., 2011). In particular, the lower portion of the sequence, less than 1.5 m thick, comprises grey to dark-brown mottled marls and clayey marls with thin, lenticular beds of conglomerates interpreted as freshwater to paralic marsh deposits (member A in Figs 3 and 5b); the calcareous pebbles are characterized by pendant lower coats of white micritic chalky calcite. The marls appear to be barren and consist of a micrite-sized pedogenic carbonate with dispersed quartz grains, calcareous lithoclasts, clay minerals and, occasionally, organic particles. The pedogenic nature of these marls is suggested by the common occurrence of vadose whisker calcite inside vugs and cavities created by plant roots. The mottled appearance is given by light-coloured carbonate rhizoliths, as well by a delicate network of thin root tubules stained by dispersed organic particles or filled with black microscopic aggregates of pyrite framboids (Fig. 6a-c). The dark colour, high pyrite content, pervasive root burrowing and occurrence of circumgranular cracks (Fig. 6b-c) suggest a moist soil originated in a reducing environment in which long periods of waterlogging favoring iron mobility alternated with periods of intense drying causing iron concentration (Carnevale et al., 2011). The uppermost portion of these freshwater marsh deposits is represented by grey marly



clays alternating with organic-rich black shales containing plant remains and fragmented shells of terrestrial pulmonate gastropods, the latter possibly belonging to the zonitid genus *Vitrea* (see Carboni et al., 1992).

The freshwater marsh interval grades upwards into about 60 cm of fissile and fetid dark-grey marls and shaly marls with a whitish colour on the weathered surfaces (member B in Figs 3 and 5b). The shaly marls

Fig. 6 - Photomicrographs (transmitted light) of the *Lithothamnion* Limestone Fm. equivalent (members A-C; modified from Carnevale et al., 2011). a-c) Member A. a) Grey to brownish speckled sandy micrite with dark-stained root tubules. b) Close-up of the sandy micrite showing well-preserved root tubules, some of which filled with a microaggregate of black pyrite framboids. c) Pedogenically-reworked carbonate with spar-filled root cavities and syneresis features. d) Member B. Laminated black shale showing discontinuous thin lumachella layers with flattened gastropods and wavy to lenticular laminae of very fine calcarenite/calcsiltite with black veneers of wood fragments. Thin, spar-filled, transversal sinuous fissures and subhorizontal, flat shrinkage cracks are visible. e-h) Member C. e) Calcisphaerulid-rich packstone/wackestone with sparse flattened and crashed gastropods, thin-shelled bivalves and disarticulated thick-walled ostracods. f-h) Close-up of calcisphaerulids. Note in panel (g) a possible excystation stage (arrowhead). Scale bars: a = 3 mm; b = 1 mm; c = 250 μ m; d-e = 2 mm; f-h = 100 μ m.

are characterized by thin highly fossiliferous layers containing an oligospecific assemblage of aquatic or strongly hygrophilous terrestrial gastropods, including ellobiids (*Carychium*), lymneids (*Lymnaea*), hydrobiids and vertiginids, associated with relatively common ostracods. The gastropods are indicative of a variety of swampy biotopes, including stagnant freshwater ponds (*Lymnaea*), brackish-water environments with salinity fluctuating from hypohaline to oligohaline conditions (hydrobiids), and very humid and densely vegetated lands (*Carychium* and vertiginids). In the lower portion of this interval, the shaly marls alternate with dark-brown and organic-rich layers rich in wood fragments displaying current-driven wavy to lenticular detrital laminae (Fig. 6d) composed of bioclastic silt, quartz grains, organic particles, sporomorphs and very fine and rounded calcareous lithoclasts. Overall, both molluscs and lithofacies indicate a permanently flooded area in highly vegetated wetlands temporarily subject to feeble variations of salinity and to periodic slow-flowing water currents; such a scenario is consistent with swamps connected to marine environments under warm temperate or subtropical conditions.

The swamp deposits are overlain by about 1.20 m of marls, limy marls and marly limestone showing a complex stacking pattern (intervals C1-C4 in Figs 3 and 5b). The fossil assemblages reflect sudden salinity variations, from hypohaline to oligohaline conditions.

Based on facies associations Carnevale et al. (2011) subdivided this portion of the succession into four intervals:

1. The basal interval (C1 in Figs 3 and 5b) consists of about 30 cm of thinly laminated fetid grey shaly marls, marls and marly limestone with abundant *Dreissena* and *Hydrobia* together with ostracods and very rare, evidently reworked, planktonic foraminifers (see Carboni et al., 1992).

2. The second interval (C2 in Figs 3 and 5b) consists of 30 cm of marls and silty marls with thin intercalations of marly limestones. The fossil assemblage, mainly represented by *Dreissena*, *Melanopsis* and small neritids possibly belonging to the genus *Theodoxus*, together with abundant cerithiids, indicates a brackish environment with a higher salinity than the deposits of the underlying interval. The microfacies (Fig. 6e-h) is characterized by abundant calcareous calcisphaerulids, apparently representing sporomorphs or resting algal cysts, *Ammonia*, and disarticulated valves of ostracods, associated with sporadic reworked planktonic foraminifers.

3. The third interval (C3 in Figs 3 and 5b) is primarily formed by less than 20 cm of grey marls and silty marls with thin layers of black shales rich in plant remains. The fossil assemblage is dominated by potamidids and cerithioids of the families Cerithiidae, Diastomidae and Litiopidae, alternated with nearly monospecific associations of *Dreissena* concentrated in thin lumachella



Fig. 7 - Lumachella layer containing potamidids, cerithiids and *Dreissena* from the *Lithothamnion* Limestone Fm. equivalent (C3 interval). Scale bar: 20 mm.

layers (Fig. 7). The mollusc assemblages suggest a further increase in salinity with respect to the underlying deposits; however, the occasional occurrence of hygrophilous terrestrial gastropods (vertiginids) may reflect the episodic decrease of the salinity.

4. Finally, the uppermost interval (C4 in Figs 3 and 5b) is represented by 40 cm of silty marls and marly limestones with a limestone bed at the top, whose fossil assemblage is characterized by *Dreissena*, *Melanopsis*, *Theodoxus*, cerithiids and small marine bivalves apparently belonging to the family Semelidae, associated with rare *Corbula*. The microfacies of this uppermost portion is characterized by a groundmass of calcareous sporomorphs associated with isolated ostracod valves and displaced planktonic foraminifers. Due to the presence of marine molluscs it is reasonable to suggest a brackish-water environment in

close proximity to an open-marine shelf, likely represented by an estuarine bay.

The estuarine bay deposits are overlain by approximately 30 m of fully marine sediments (Figs 3-4a and 5a) referred by Carnevale et al. (2011) to as an equivalent of the Tripoli Formation (see, e.g., Hilgen & Krijgsman, 1999); these deposits are represented by at least six lithological cycles of alternating grey organic-rich calcareous marls and diatomites (D1-D6; Fig. 3). This cyclic stacking pattern is similar to that commonly observed in other lower Messinian sedimentary successions of the Mediterranean region represented by the alternation of sapropelitic and diatomaceous sediments. Such cyclicity is attributed to astronomically-driven hydrological changes affecting the structure and productivity of the water column (e.g., Hilgen & Krijgsman, 1999; Pellegrino et al., 2018).

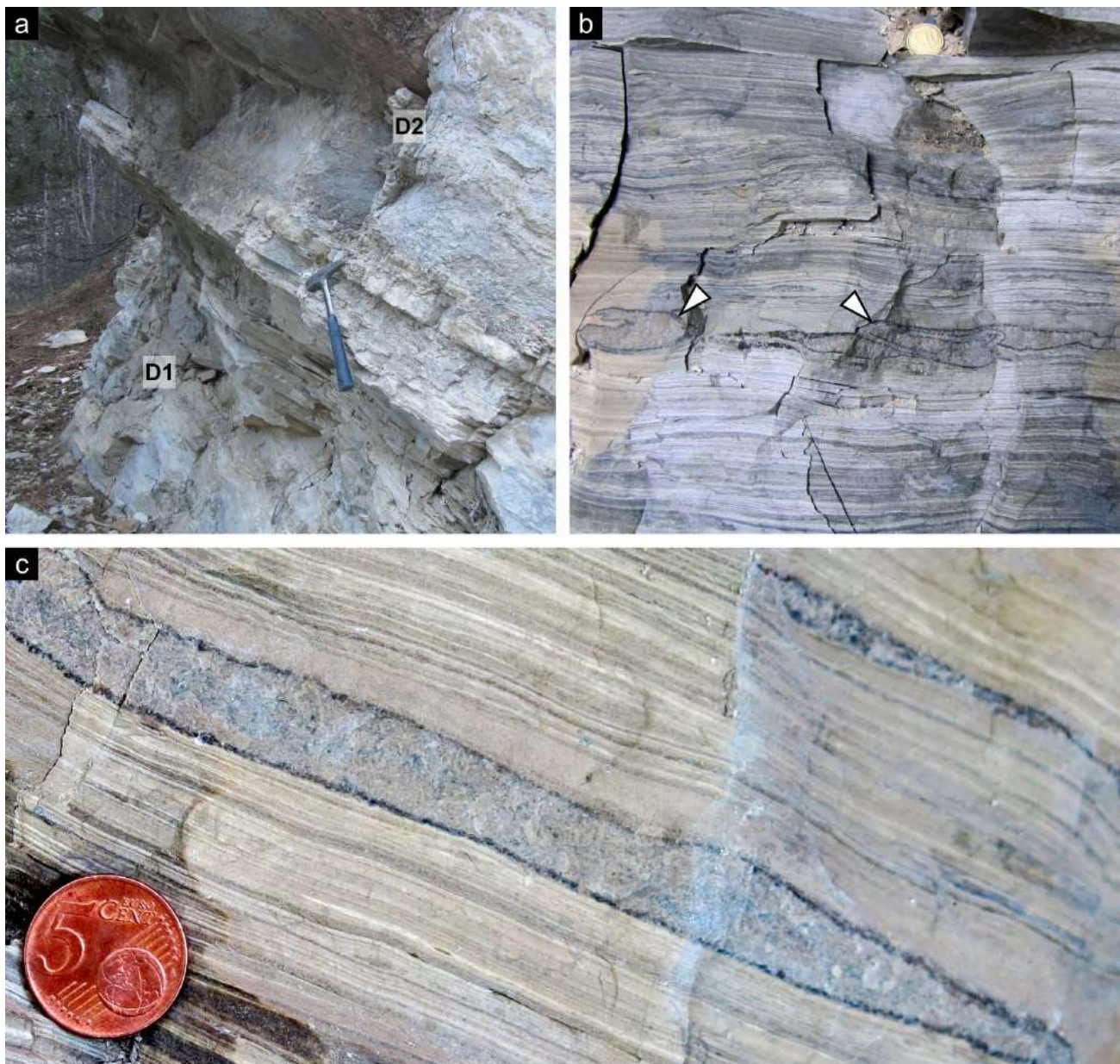


Fig. 8 - Tripoli Fm. equivalent. a) First diatomaceous layer (cycle D1) overlain by a prominent bio-lithoclastic calcarenite layer and by the second organic-rich calcareous marly layer (cycle D2). b-c) The finely laminated diatomaceous layer is interrupted by non-laminated layers and by a coarse-grained, slump-related convolute bioclastic bed rimmed by black siliceous cement - arrowheads in panel (b) and detail in panel (c).

The first marine cycle is characterized by a relatively complex architecture (Fig. 3) whereas the overlying cycles primarily consist of alternations of organic-rich calcareous marls and diatomites. In general, the succession exhibits a progressive decrease of the thickness of the diatomaceous layers, passing from about 180 cm in the first cycle to less than 50 cm in the sixth one (Fig. 3). The succession starts (base of the interval D1 in Fig. 3) with a thin horizon (10 cm) of laminated calcareous marls containing abundant *Corbula gibba* (Olivi, 1792) and rare dreissenids, overlain by 40 cm of massive grey marls. The grey marls are extensively bioturbated and include abundant bivalves, primarily represented by *Corbula gibba* with conjoined valves, and subordinated oysters, cardiids, semelids and tellinids (Fig. 3). Carboni et al. (1992) reported the presence of several benthic foraminifers (e.g., *Ammonia beccarii* [Linnaeus, 1758], *Bolivina* sp., *Bulimina echinata* d'Orbigny, 1826, *Cibicides* spp., *Elphidium crispum* [Linnaeus, 1758]) and rare globigerinids in these deposits. The fossil assemblage seems to be indicative of a marine paleobiotope located at a depth of several tens of meters and characterized by turbid waters. The textural homogeneity and the absence of sedimentary structures related to selective transport by submarine currents or coastal drift indicate subtidal conditions in a mud-dominated open coastal flat with a very limited supply

of sand-sized sediment from the catchment area. These deposits are covered by about 180 cm of finely laminated diatomites (Figs 3 and 8a-b) interrupted by non-laminated layers and by a coarse-grained, convolute bioclastic bed (Fig. 8b-c). The macrofossil content of this diatomite interval is relatively rich and includes well-preserved articulated skeletal remains of teleost fishes documented herein, among which the round herring *Spratelloides lemoinei* Arambourg, 1927 is by far the dominant element. In addition, a single nearly complete articulated skeleton of the ochotonid species *Prolagus* cf. *apricenicus* Mazza, 1987 (see Mazza et al., 1995; Angelone, 2007), bird feathers, very rare decapod crustaceans, insects, bivalves and plant remains (leaves, seeds, cones, fruits) have been observed. The rather scarce foraminifers are exclusively represented by ammoniids, bolivinids and rare dwarfed globigerinids (Carboni et al., 1992; Patacca et al., 1992). At about 20 cm from the base of this first diatomaceous interval (Fig. 3), a thin (7 cm thick) massive mudstone bed containing a nearly monotypic assemblage of *Corbula gibba* with disarticulated and conjoined valves, has been interpreted as a subaqueous gravity-driven mud-flow deposit triggered by tectonic instability or by a sudden increase in the sediment loading related to a rapid sediment supply from the catchment area, in turn determined by an exceptional climatic event.

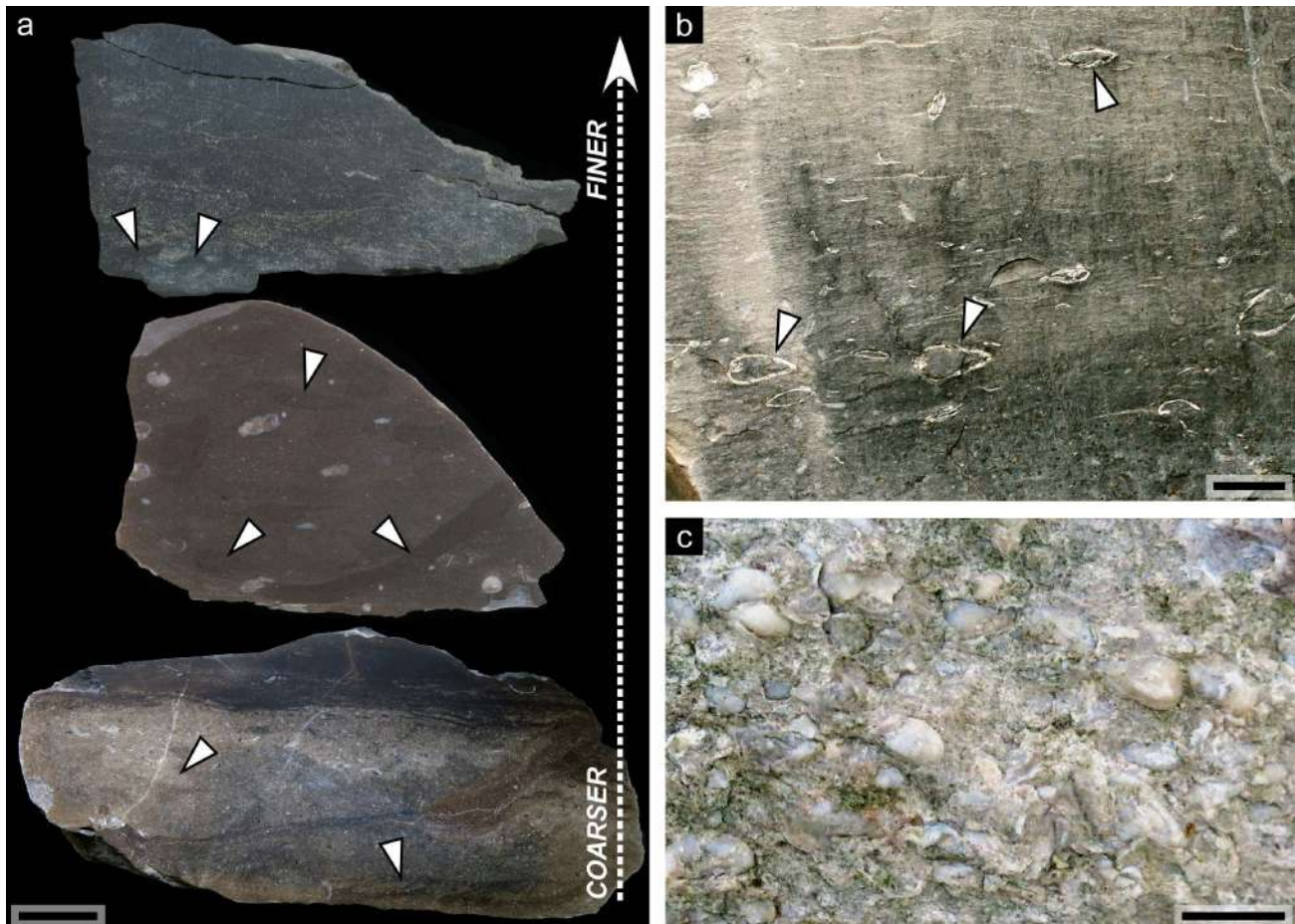


Fig. 9 - Tripoli Fm. equivalent. Sedimentological features and microfacies of the second marly layer (cycle D2). a) Polished slabs of a hand specimen, consisting of a lower coarse-grained layer overlain by an intermediate gastropod-rich layer and topped by a fine-grained layer. Note the bioturbations (arrowheads). b) *Corbula gibba* specimens (arrowheads) observed perpendicularly to the bedding plane. c) Massive occurrence of *Corbula gibba* specimens observed parallel to the bedding plane. Scale bars: a = 30 mm; b = 20 mm; c = 10 mm.

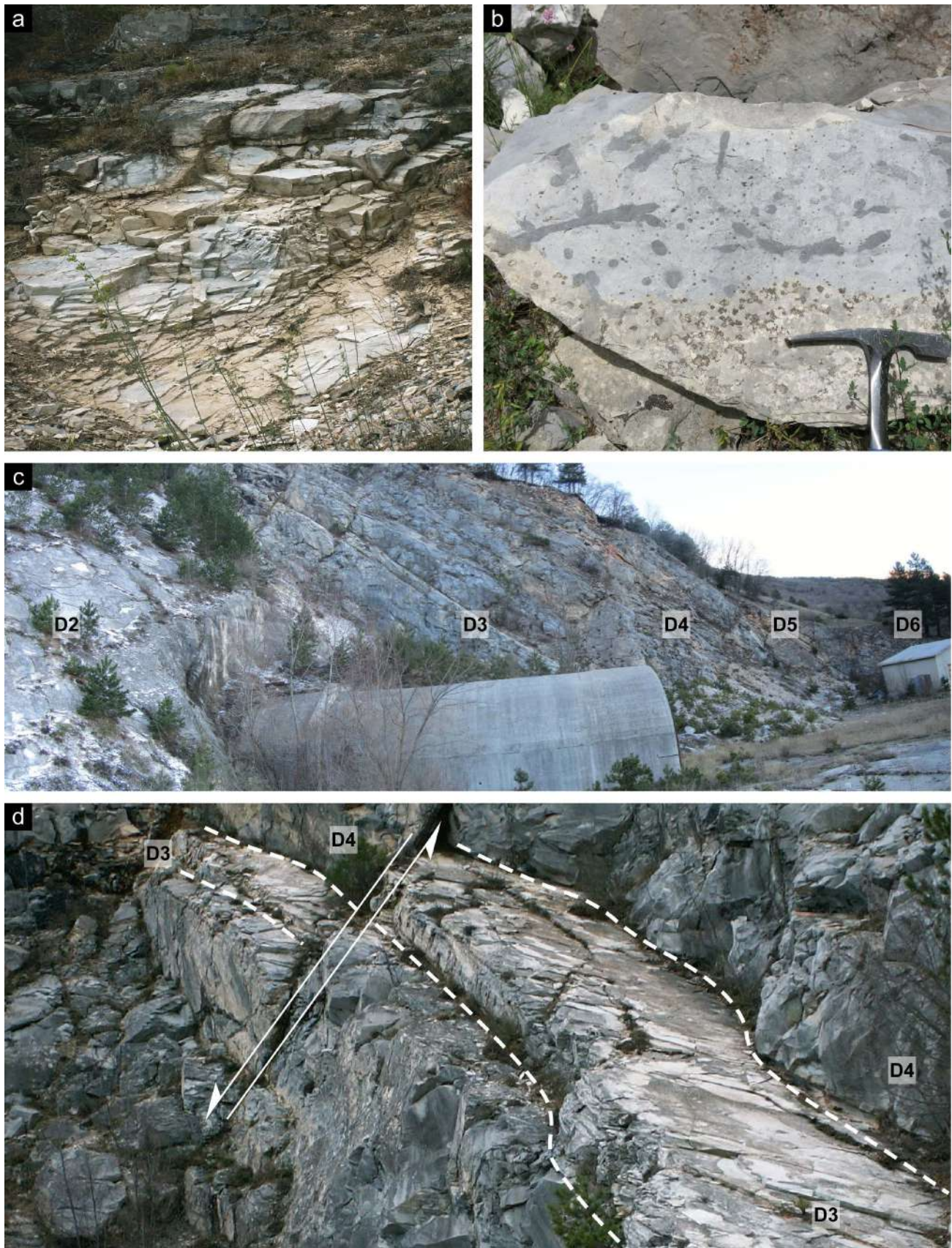


Fig. 10 - Tripoli Fm. equivalent. a) Second diatomaceous interval (cycle D2). b) Bioturbations along the bedding plane of diatomite (cycle D2). c) Panoramic view of the upper part of the section (cycles D2 to D6). d) Normal fault between cycles D3 and D4.

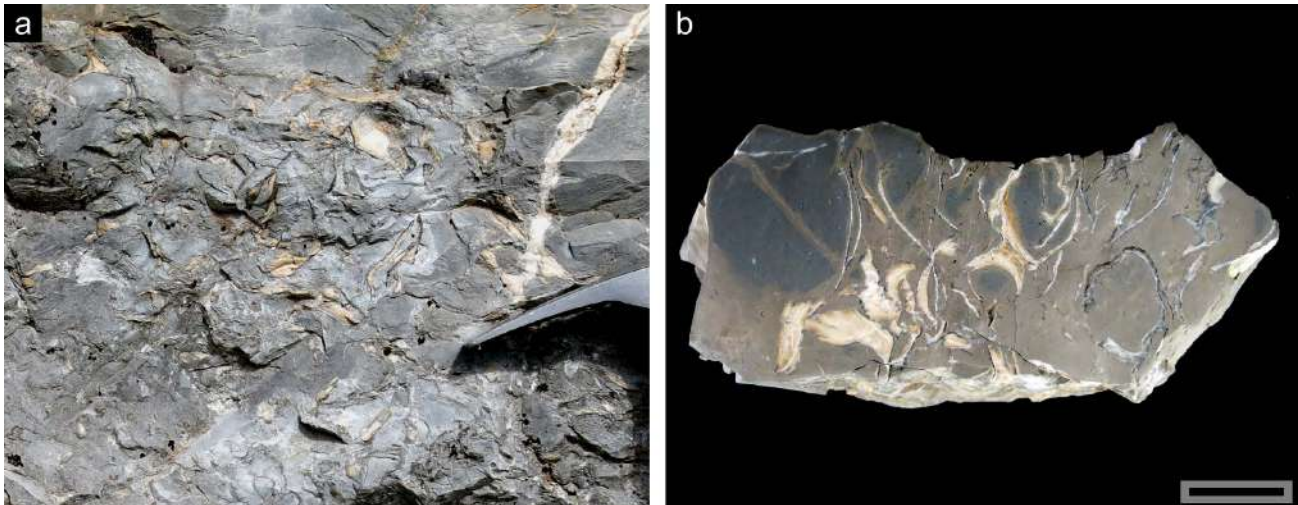


Fig. 11 - Tripoli Fm. equivalent. a) Massive accumulation of ostreids (cycle D6). b) Polished slab of a hand specimen from the ostreid-rich bed. Scale bar = 30 mm.

The first diatomaceous interval (cycle D1) is overlain by about 1 m of grey marls with intercalated cm-thick, graded calciturbidite layers characterized by normal grading and erosional structures at the base (Figs 3, 8a and 9a). The basal portion of the marls (see interval D2 in Fig. 8a) contains nearly monotypic accumulations of *Corbula gibba* with conjoined valves; the shells seem to be displaced from their original position, showing the commissure parallel or sub-parallel to the bedding plane (Fig. 9b-c).

The marls with calciturbidite intercalations are followed by 5 m of fetid massive grey calcareous marls containing abundant and diversified marine bivalves (*Acanthocardia* sp., *Callista* sp., *Cardita* sp., *Cardiidae* indet., *Circomphalus* sp., *Glans* sp., *Lima* sp., cf. *Megaxinus* sp., *Ostrea* sp., *Paphia* sp., *Pinna* sp., *Venus* sp.), often with conjoined valves, associated with rare gastropods (*Aporrhais* sp., *Turritella* sp.) (Fig. 3). The massive aspect of this thick muddy and organic-rich interval, absence of internal sedimentary structure and biogenic reworking, and the considerable volume of sediment involved suggest a gravitative mass-flow mechanism for transport and accumulation, perhaps triggered by seismic activity. The microfacies consists of a very fine-grained bioclastic wackestones/packstones with dispersed and randomly distributed mollusc fragments, *Cibicides* sp., buliminids, planktonic foraminifers (*Globigerina*, *Globigerinoides*, *Globorotalia* and *Orbulina*; see Carboni et al., 1992), abundant siliceous sponge spicules, echinoid radioles, rare small-sized *Elphidium*, abundant phosphatic material and organic particles mixed with calcareous lithic grains.

A second, less well-laminated diatomite interval around 1.20 m thick (cycle D2) lies over the massive grey marls (Figs 3 and 10a). The macrofossil content includes rare articulated fish skeletons, scarce bivalves (*Cardita* sp.) and plant remains, the latter extremely abundant in some biogenic laminae. Well-developed trace fossils, lying almost parallel to the bedding, are also present (Fig. 10b).

The succession continues upward with other four cycles (D3, D4, D5 and D6) of alternated dark grey calcareous marls and diatomites (Figs 3 and 10c-d). Each interval of dark grey calcareous marls is characterized at

its base by thin shell beds consisting of nearly monotypic assemblages of *Corbula gibba* with conjoined valves and the commissure parallel or subparallel to the bedding plane, alternating with very fine-grained calciturbidites and contourites. The upper portion of the calcareous marls intervals is always characterized by common bivalves, often with conjoined valves and chaotic distribution, and turritellid gastropods. In the uppermost cycle, the dark grey calcareous marls also include a massive accumulation of large oysters (Fig. 11). Planktonic foraminifers are always relatively common. The stratigraphic marker *Turborotalita multiloba* (Romeo, 1965) appears to be present in the calcareous marls of the sixth cycle.

The diatomites of the upper four cycles (Figs 3 and 10c-d) exhibit a progressive reduction of the macrofossil content. Articulated skeletal remains of fishes are rare, represented by poorly preserved specimens of the round herring *Spratelloides lemoinei*.

Sedimentological features of the diatomites

The first, finely laminated diatomitic interval of the cycle D1 (Figs 3 and 8) is characterized by the alternation of millimetric to inframillimetric, dark (detrital-rich and mixed detrital-diatomaceous) and pale (diatom-rich) laminae (Figs 8b-c and 12a) most likely reflecting short term (annual to subannual) climate changes. According to their respective thickness, the alternation of these two lamina types may result in mud- or diatom-dominated laminated packets ("md" and "dd" in Fig. 12a, respectively), which indicate humid vs. arid climatic phases and consequently major or minor dilution of the biogenic component of the sediment (e.g., Chang et al., 1998; Fig. 12a). Within the laminated packets, mm- to cm-sized phosphatic nodules locally occur (Fig. 12a).

The successive diatomaceous intervals (cycles D2, D3, D4, D5 and D6) show a gradually less well-expressed lamination, with commonly occurring bioturbations (Fig. 12b). In thin sections, detrital-rich laminae appear composed of silt-sized carbonate grains, echinoid fragments, foraminifers and siliceous sponge spicules (Fig. 13a-b), likely reworked from the shallower area of the platform. Mixed laminae display an intermediate

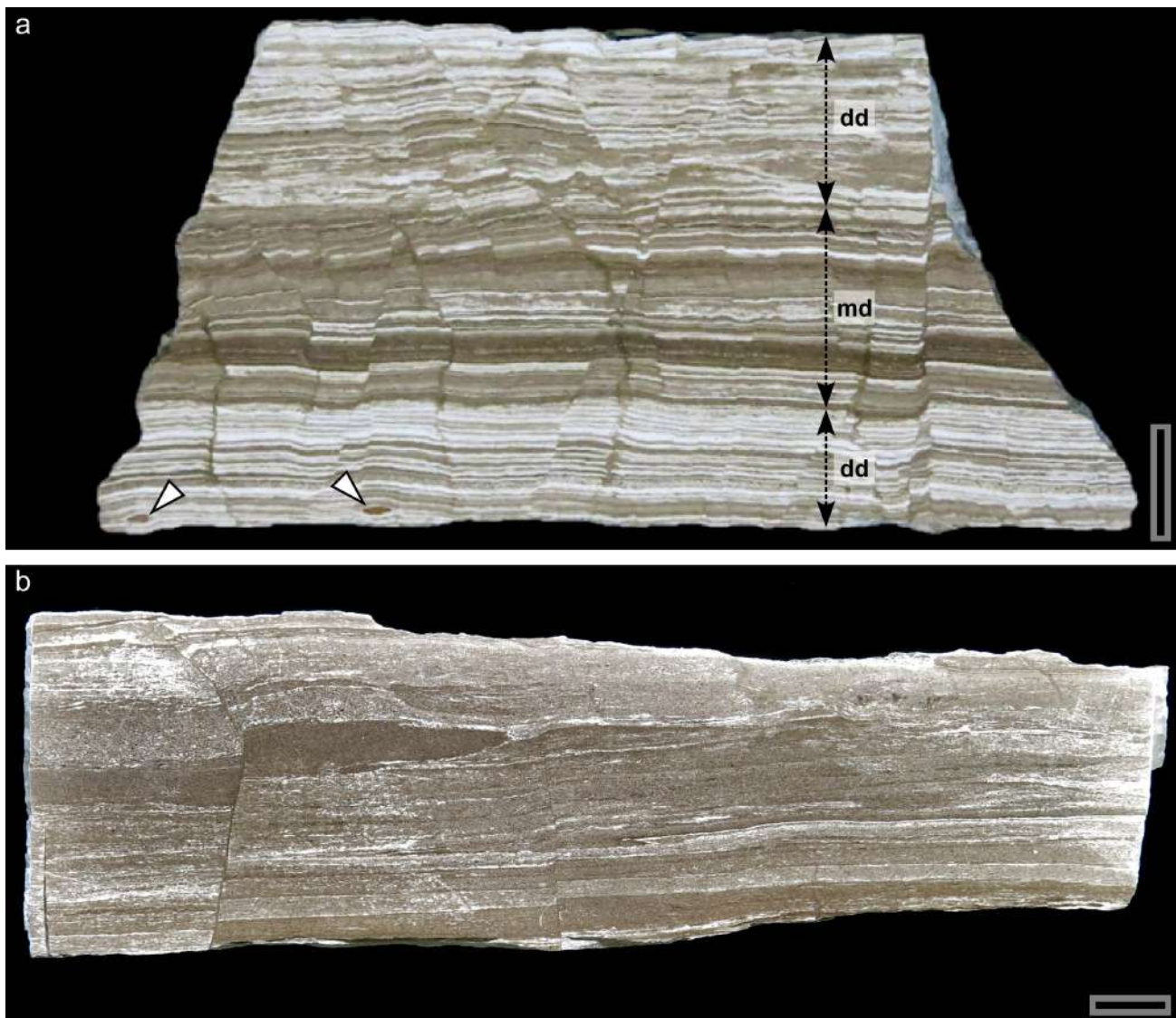


Fig. 12 - Tripoli Fm. equivalent. Sedimentological features of the diatomaceous layers. a) Polished slab of a hand specimen from the first diatomaceous layer (cycle D1); note the fine lamination, and the stacking pattern consisting of the alternation of diatom-dominated (dd) and mud-dominated (md) packets, pervasively crossed by hybrid fault-vein structures; note also two small phosphatic nodules in the upper part (arrowheads). b) Polished slab of a hand specimen from the second diatomaceous layer (cycle D2); note the faint lamination and the abundant muddy fraction. Scale bars = 10 mm.

composition between detrital- and diatom-rich laminae, therefore reflecting periods of moderate clastic input and biogenic productivity. The best-preserved diatom-rich laminae (Fig. 13a-b) are typified by a dense accumulation of large specimens of marine planktonic diatoms of the genus *Coscinodiscus* (Fig. 13c). This may indicate a periodical stratification of the water column associated to the development of a subsurface chlorophyll maximum (e.g., Estrada, 1991; Kemp & Villareal, 2018). Although such modality of diatom proliferation is often overlooked, it actually represents a fundamental contribution to the annual cycle of primary productivity in modern coastal and pelagic environments, especially during the warm season, at the end of which the diatoms are involved in the so-called “fall-dump” (Kemp et al., 2000), a massive sink toward the seafloor in response to water column vertical mixing. This may result in the formation of excellently preserved diatom-rich laminae, hardly

reworkable by the benthic infauna and meiofauna, even under well-oxygenated bottom conditions (e.g., Kemp & Baldauf, 1993; Pike et al., 1999; Shimada et al., 2008; Pellegrino et al., 2020a, b). The assemblage comprises other remains of planktonic diatoms, notably *Chaetoceros* resting spores (Fig. 13d) and *Thalassionema nitzschioides* (Grunow) Mereschkowsky, 1902 (Fig. 13e), as well as scattered benthic-epiphytic diatoms like *Actinoptychus senarius* Ehrenberg, 1838 (Fig. 13f) and *Rhabdonema* cf. *adriaticum* Kützing, 1844 most likely displaced from a shallow-water area (see Pellegrino et al., 2020a, b), which was occupied, at least in part, by seaweeds. *Chaetoceros* resting spores were most likely produced at the end of bloom events in surface waters, in response to stressing conditions such as nutrient depletion (e.g., Rigual-Hernández et al., 2013). Conversely, the cosmopolitan species *T. nitzschioides* likely flourished in surface, nutrient-replete waters, induced by the riverine

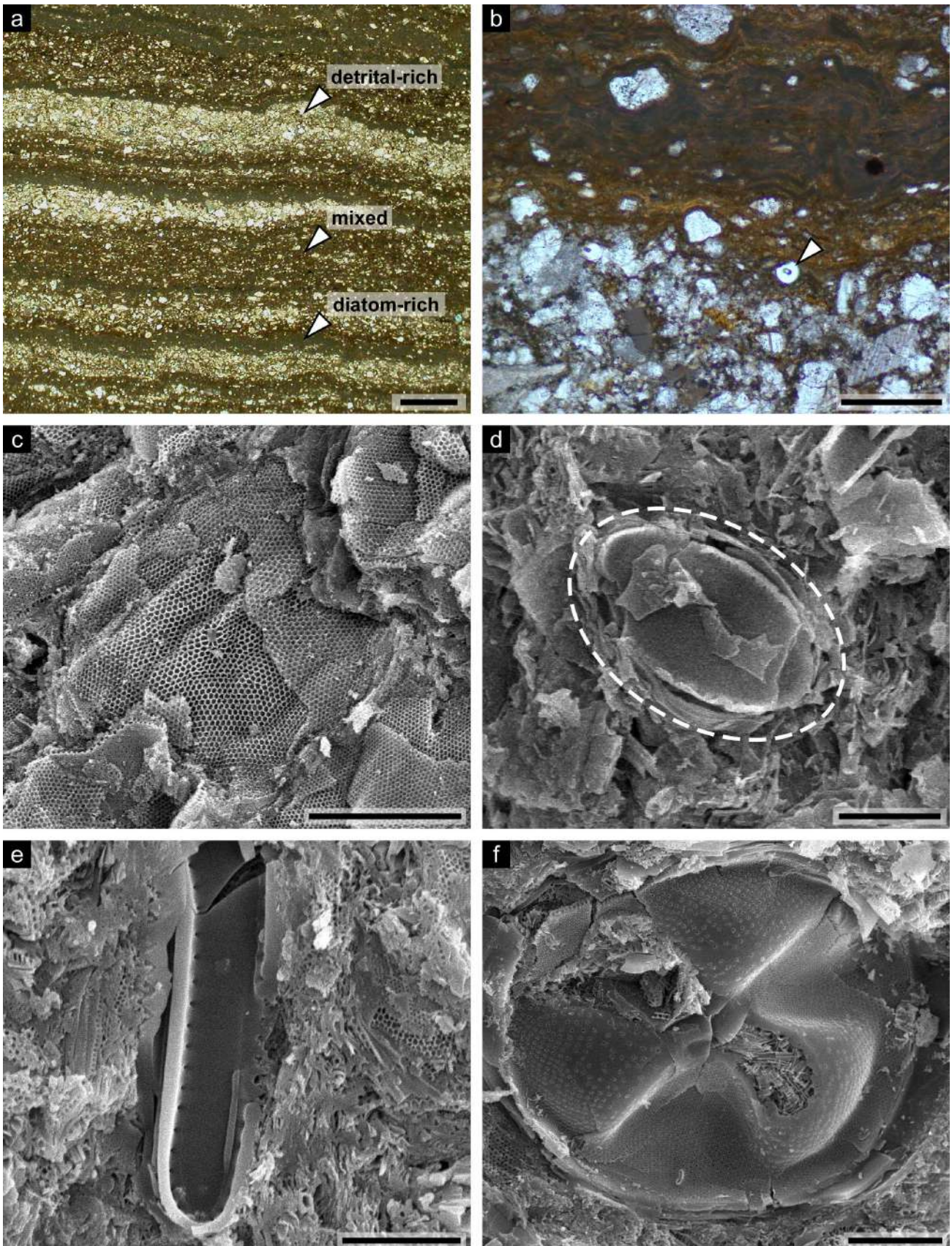


Fig. 13 - Microfacies of the first diatomaceous layer (cycle D1) of the Tripoli Fm. equivalent. a) Photomicrograph (transmitted light) of an alternation of diatom-rich, mixed and detrital-rich laminae. b) Detail of a detrital-rich lamina overlain by a diatom-rich lamina; note a sponge spicule at the top of the detrital-rich lamina (arrowhead). c) SEM image of freshly-broken sediment chips parallel to the bedding plane: valves of large centric diatoms of the genus *Coscinodiscus* on a lamina surface. d) *Chaetoceros* sp. resting spore (circled). e) *Thalassionema nitzschioides*. f) *Actinoptychus senarius*. Scale bars: a = 100 μm ; b = 200 μm ; c = 25 μm ; d-e = 5 μm ; f = 10 μm .

inflow, possibly responsible for the displacement of benthic-epiphytic diatoms, or by water column mixing (e.g., Rigual-Hernández et al., 2013).

The lamination is frequently interrupted by non-laminated intervals, and pervasively disturbed by synsedimentary hybrid fault/vein structures (Fig. 12) produced by seismic activity or sediment loading. These features are often associated with calciturbidite layers rimmed by dark siliceous cement (Fig. 8b-c). The layers contain *Elphidium* sp., echinoid radioles, fish teeth and scales, and fragments of serpulids and barnacles, as well as abundant, rounded lithoclasts derived from Upper Cretaceous limestone (Carnevale et al., 2011).

Biostratigraphic remarks

The precise age of the succession is difficult to define due to the progressive facies evolution, from continental to frankly marine environments, which documents the ongoing involvement of the Morrone-Porrara unit in the foredeep domain (Carboni et al., 1992). Overall, the succession appears to be stratigraphically continuous and its lower continental portion may include the Tortonian-Messinian transition. The mollusc assemblages recognized in the continental-brackish intervals indicate an unspecified Tortonian-Messinian age (e.g., Esu & Girotti, 1989; Harzhauser et al., 2015). The occurrence of *Bulimina echinata* in the calcareous marls just below the first diatomaceous interval is clearly indicative of a Messinian age (Colalongo et al., 1979). This stress-tolerant benthic foraminifer increases in abundance between 6.5 and 6.4 Ma in the Tripoli Formation in Sicily (Sprovieri et al., 1996; Blanc-Valleron et al., 2002). The presence of the stratigraphic marker *Turborotalita multiloba* (FCO ca. 6.4 Ma; Sierro et al., 2001) in the sixth marine cycle demonstrates the Messinian age of the upper part of the succession. Moreover, the occurrence of the ochotonid *Prolagus* cf. *apricenicus* in the first diatomite interval suggests that these sediments can be correlated with the lower MN13 Mammal Faunal Zone, corresponding to the upper Turolian mammalian biochronozone (Mazza et al., 1995).

Sedimentary and paleogeographic evolution

The Morrone-Porrara Unit (Figs 1-2), together with the Maiella and other adjacent units, was part of the Adriatic Foreland, at least until the late Messinian, when it began to be incorporated in the foredeep domain. These units, geographically connected since the Mesozoic, developed during the late Tortonian-early Messinian, on a structural high in the central part of the Mediterranean (Patacca & Scandone, 1988; Patacca et al., 1990). They were initially located in the foreland domain, adjacent to slope and basin units (Montagna Grande, Mt. Arazzecca and Mt. Genzana, Molise Units; Figs 1-2) (e.g., Sgrosso, 1986; Patacca et al., 1992). The presence of continental to brackish facies and of terrestrial fossils in the frankly marine deposits (*Prolagus* cf. *apricenicus*, plant and insect remains) of the Capo di Fiume section are clearly indicative of the existence of emerged areas, most likely islands, in the Morrone-Porrara unit (Fig. 2). Semi-emerged structures have been also reported in paleogeographically contiguous areas, stratigraphically comparable to the Capo di Fiume succession (Danese, 1999).

The gradual transgressive trend recognizable in the Capo di Fiume succession could be linked to a glacio-eustatic or tectonic control, or to the synergistic effect of both. As previously discussed, the faunal succession properly documents the environmental sequence from continental to frankly marine conditions that were eventually reached starting from the freshwater marsh environment hypothesized for the sediments exposed immediately above the “Terra rossa” paleosoils. Both sedimentary and paleontological markers of tectonic instability are easily recognizable in the diatomaceous and marly deposits, respectively. In particular, while the diatomites exhibit sedimentary structures attributable to tectonic disturbance (see above; Figs 8b and 12), the grey marls covering the first diatomite interval and the successive calcareous marls show mollusc assemblages often dominated by the infaunal bivalve *Corbula gibba*, especially in the lower portion of the stratigraphic succession (e.g., Figs 3 and 9b-c). This opportunistic species is extremely abundant in shelf settings affected by hypoxia or extreme oversilting (e.g., Di Geronimo et al., 1987; Diaz & Rosenberg, 1995; Hrs-Brenko, 2006; Fuksi et al., 2018). The almost exclusive presence of this opportunistic species is commonly interpreted as the final evolutionary stage of the so-called “heterogeneous communities” (Picard, 1965) affected by considerable environmental disturbance, often of tectonic origin, consisting of high sedimentation rates and bottom turbidity (Di Geronimo et al., 1987; Di Geronimo & Robba, 1988). In particular, *Corbula gibba* is dominant in unstable sea beds characterized by organic-rich sedimentary supply (see Bourcier et al., 1979), being able to exploit abundant trophic sources (diatoms, bacteria, organic debris) present on the seafloor, in settings where such resources are mixed to considerable amounts of inorganic detritus (Yonge, 1946).

THE MACROFOSSIL ASSEMBLAGE

Abundant fossils have been discovered in the first diatomite cycle of the Capo di Fiume succession (D1), including numerous plant, invertebrate and vertebrate remains. Coprolites and regurgitates have been also observed.

Plant remains (Fig. 14a-c) are primarily represented by leaves, leaflets, flowers and inflorescences, seed cones, and fruits and infructescences. The entire flora has been recently examined by Teodoridis et al. (2015), who recognized slightly less than 30 taxa. The assemblage is mostly characterized by sclerophyllous to mesophytic taxa (*Berberis*, *Carpolites*, *Chamaecyparis*, *Cupressus*, *Dicotylophyllum*, *Engelhardia*, *Ilex*, Leguminosae, *Magnolia*, *Myrica*, *Paliurus*, *Phoenicites*, *Pinus*, *Salix*, cf. *Sapindus*, *Tetraclinis*, cf. *Trigonobalanopsis*, *Typha*), documenting a coastal, non-swampy, riparian (wet soil) vegetation with remarkable abundance of woody elements living in semi-arid to sub-humid conditions.

Invertebrate remains are primarily represented by fragmentary or largely incomplete specimens observed during the microscopic analysis of the sediment and comprise hexactinellid sponge spicules, bryozoan fragments, balanid scuta, echinid radioles and serpulid

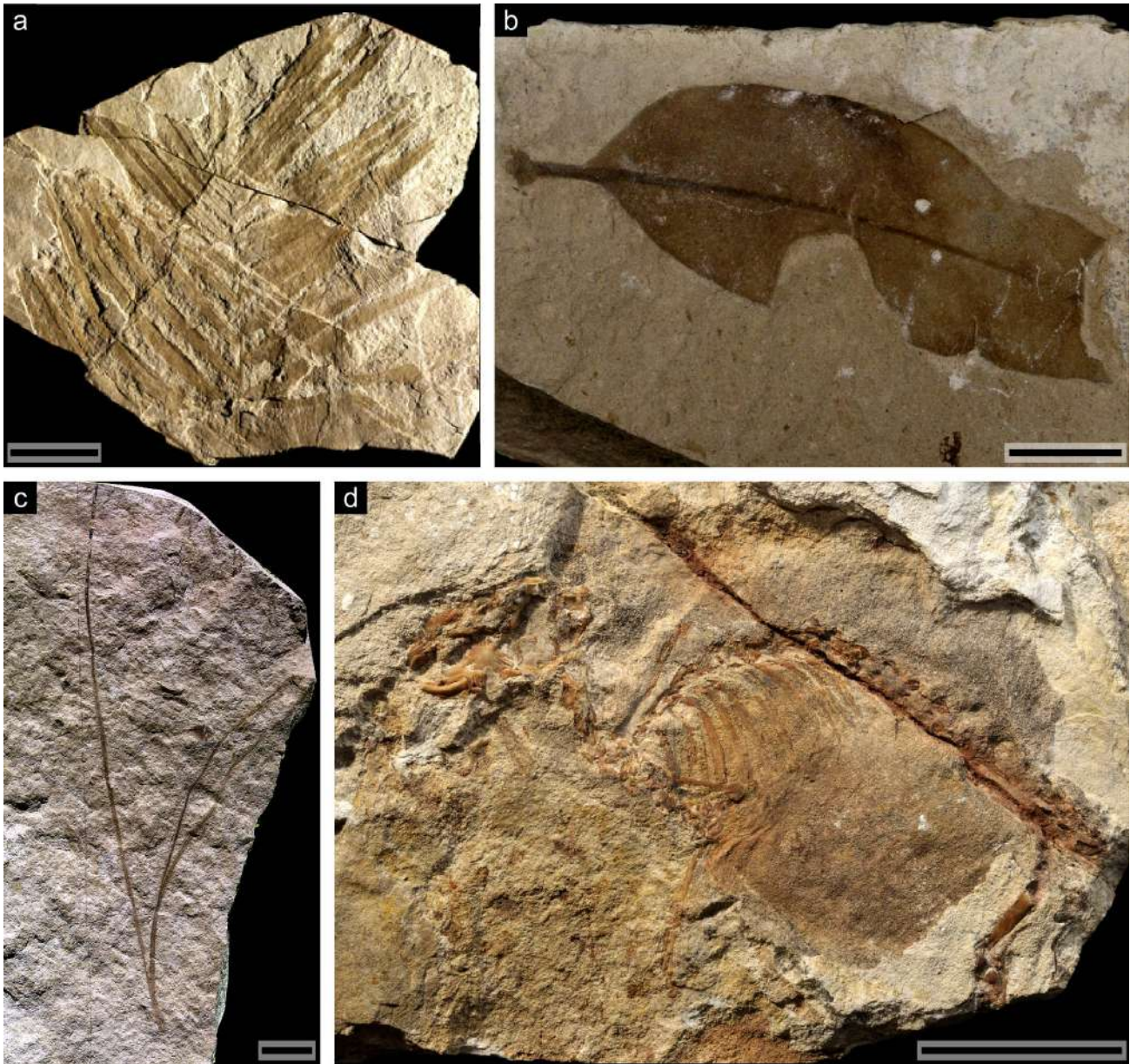


Fig. 14 - Macrofossil content of the first diatomite interval of the Tripoli Fm. equivalent (cycle D1). a) Impression of incomplete pinnate leaf of the palm *Phoenixites* sp., MGPAALB7. b) Indeterminate leaf showing insect-mediated damages; MGPAA uncatologued. c) Incomplete needles of *Pinus rigios*, MGPAALB10. d) *Prolagus* cf. *apricenicus*, MGPAA uncatologued. Scale bars: a and d = 50 mm; b-c = 10 mm.

tubes. A single partially complete crab cephalothorax with an associated left cheliped possibly pertaining to the family Xanthidae has been also found. Insect remains are uncommon, mostly represented by isolated wings.

As far as vertebrates are concerned, tetrapods are represented by the already mentioned articulated skeleton of the ochotonid *Prolagus* cf. *apricenicus* (Mazza et al., 1995; Fig. 14d), but also by a few isolated bird bones and poorly preserved feather imprints. The *Prolagus* specimen is about 18 cm long and is characterized by a partially complete skeleton lacking the distal parts of the limbs. The articulated skeleton is surrounded by a dark-colored organic halo, which possibly represents the fossilized residue of the original fur. According to Mazza et al. (1995), this fossil seems to exhibit evidences of floatation, as suggested by the loss of the distal limb bones.

Articulated skeletal remains of bony fishes (Figs 15-17) represent the majority of the fossil vertebrates discovered in the diatomites of the Capo di Fiume section, with about 250 specimens, of which 222 identifiable from a taxonomic point of view. The taxonomic analysis of the fish assemblage revealed the presence of 18 taxa, belonging to 10 families, among which *Spratelloides lemoinei* is by far the dominant taxon, represented by about two thirds of the identified specimens. A list of the recognized fish taxa is reported in Table 1. Some of these fishes were described in detail (Carnevale & Landini, 2001; Carnevale, 2002), including a pharyngognath that was erroneously referred to an indeterminate species of the family Pomacentridae (Carnevale & Landini, 2000); a recent preparation of this specimen (MGPAAL002) revealed the presence of a premaxilla with coalesced

Family	Taxon	n
Clupeidae	<i>Alosa elongata</i> Agassiz, 1843	18
	<i>Etrumeus boulei</i> Arambourg, 1925	1
	<i>Sardina pilchardus</i> (Walbaum, 1792)	5
	<i>Spratelloides lemoinei</i> Arambourg, 1927	165
Sternoptychidae	<i>Maurolicus</i> cf. <i>muelleri</i> (Gmelin, 1879)	2
Paralepididae	<i>Lestidiops sphekodes</i> (Sauvage, 1870)	1
	<i>Paralepis albyi</i> (Sauvage, 1870)	5
Myctophidae	<i>Diaphus edwardsi</i> (Sauvage, 1870)	1
	<i>Myctophum columnnae</i> (Sauvage, 1873)	1
Merlucciidae	cf. <i>Merluccius</i> sp.	1
Batrachoididae	Batrachoididae gen. et sp. indet.	1
Latidae	<i>Lates</i> cf. <i>niloticus</i> Linnaeus, 1758	1
Carangidae	<i>Trachurus</i> sp.	7
Sparidae	<i>Boops roulei</i> Arambourg, 1927	4
	<i>Diplodus</i> sp.	4
	cf. <i>Pagrus</i> sp.	2
	<i>Spicara</i> sp.	2
Blenniidae	cf. <i>Mioblennius</i> sp.	1

Tab. 1 - List of Messinian fishes from the Tripoli Fm. equivalent (cycle D1), Capo di Fiume section (Palena, Abruzzo).

ascending and articular processes, which clearly excludes any possible attribution to the Pomacentridae (see Rosen & Patterson, 1990), but supporting the inclusion within the Sparidae; this specimen is tentatively referred herein to the genus *Pagrus*.

From an ecological point of view, the fish assemblage is mostly composed of neritic and coastal epipelagic taxa (see the definition of ecological categories in Landini & Menesini, 1984), being in some ways reminiscent of the nearly coeval assemblages of Raz-el-Aïn, Chelif Basin, northern Algeria (Arambourg, 1927), and Gabbro, Tuscany, Italy (Bradley & Landini, 1982). The families Clupeidae (*Alosa elongata* Agassiz, 1843, *Etrumeus boulei* Arambourg, 1925, *Sardina pilchardus* [Walbaum, 1792], *Spratelloides lemoinei*) and Sparidae (*Boops roulei* Arambourg, 1927, *Diplodus* sp., cf. *Pagrus* sp., *Spicara* sp.) include nearly the half of the recognized fish diversity with four species-level taxa each. While clupeids are mostly coastal epipelagic, the sparids are typical demersal fishes. Additional demersal fishes recognized in the assemblage are the taxa belonging to the families Merlucciidae (cf. *Merluccius* sp.) and Carangidae (*Trachurus* sp.). Overall, the structure and composition of the demersal fish assemblage is consistent with the so-called “subthermocline sparid assemblages” (or subthermocline sparid subcommunity) typical of the tropical and subtropical west African continental shelf (e.g., Longhurst, 1965; Bianchi, 1992a, b). Benthic fishes are rather scarce, represented by an indeterminate batrachoidid and a blenniid (*Mioblennius* sp.). The species of the families Myctophidae (*Diaphus edwardsi* [Sauvage, 1870], *Myctophum columnnae* [Sauvage, 1873]),

Paralepididae (*Lestidiops sphekodes* [Sauvage, 1870], *Paralepis albyi* [Sauvage, 1870]) and Sternoptychidae (*Maurolicus* cf. *muelleri* [Gmelin, 1879]) are small- to medium-sized upper slope and mesopelagic fishes that commonly display vertical migrations to explore the neritic food resources, primarily represented by planktonic organisms and fishes. Finally, a single largely incomplete disarticulated skeleton documents the presence of the fresh- to brackish water Nile perch, *Lates* cf. *niloticus* Linnaeus, 1758 (see Carnevale & Landini, 2001). Due to their adventitious character, these mesopelagic and freshwater taxa cannot be used to interpret the main physiographic features of the original paleobiootope in which the diatomites accumulated, although they can certainly provide useful information about the contiguous open marine and continental environmental contexts.

TAPHONOMY

The taphonomic analysis of the fossil fish assemblage has revealed a possible sequence of events that, starting from the causes of death, favored and promoted the definitive burial of the remains. The definition of these mechanisms allows for a more detailed interpretation of the paleoecological information regarding the paleobiootope where the fish assemblage documented herein originally lived. The results obtained from the taphonomic study will be integrated with those deriving from the paleoecological analysis of the whole assemblage and from the sedimentological study of the diatomites, with the purpose to obtain a reliable paleoenvironmental frame.

The life cycle of marine fishes is generally regulated by the predation by other organisms and those concluding their life cycle for other causes (senescence, diseases, etc.), constitute a trophic resource for the scavengers. Consequently, remains of fishes and other vertebrates are usually rather scarce on the seafloor. A completely different scenario may occur in the case of catastrophic events or when peculiar conditions at the bottom can promote the accumulation and preservation of remains (anoxia, etc.). Both these phenomena are well documented in the fossil record and, either in the case of accumulation surfaces (see, e.g., Leckie et al., 1992) or of mass mortality events, the presence of peculiar bottom conditions represents a necessary pre-requisite for the definitive preservation of the remains.

The causes leading to the death of some of the examined fishes may be deduced, in some cases, by particular morphological features observable on the fossils. Widely gaping jaws, fanned and stiffened fins and dorsally concave backbone, for example, are typical features of tetany, a sort of rigor mortis resulted from death by thermal shock, salinity or alkalinity shock and respiratory stress (primarily asphyxiation; Elder & Smith, 1984; Ferber & Wells, 1995; Faux & Padian, 2007; Pan et al., 2015; Marramà et al., 2016).

Several of the examined specimens show tetany features, which are especially evident in small-sized non-acanthomorph taxa (e.g., *Sardina pilchardus*, *Spratelloides lemoinei*, *Maurolicus* cf. *muelleri*, *Diaphus edwardsi*; Figs 15c-g, 16i and 17a). The acanthomorphs,

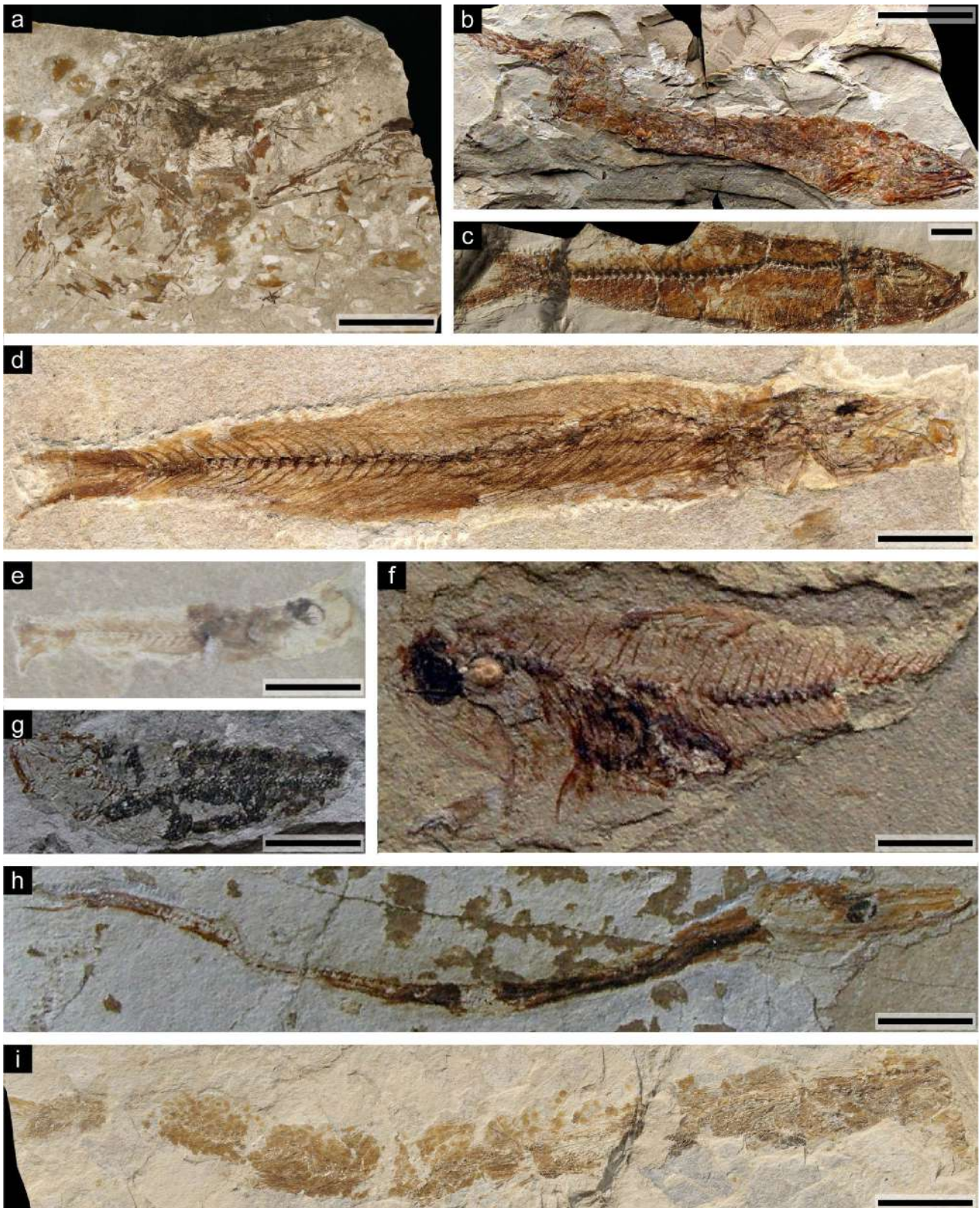


Fig. 15 - Fishes from the Tripoli Fm. equivalent (cycle D1). a) *Alosa elongata*, MGPAAL016. b) *Etrumeus boulei*, MGPAAL016. c) *Sardina pilchardus*, MGPAAL024. d) *Spratelloides lemoinei*, MAGPAAL007. e) *Maurolicus* cf. *muelleri*, MGPAAL114. f) *Diaphus edwardsi*, MGPAAL009. g) *Myctophum columnae*, MGPAAL014. h) *Lestidiops spehokodes*, MGPAAL010b. i) *Paralepis albyi*, MGPAAL080. Scale bars: a-b and h = 20 mm; c-g = 10 mm; i = 30 mm.

due to the general stiffening of the axial skeleton as well as to the complex functional relationships of the upper jaw bones (e.g., Patterson, 1964; Rosen & Patterson,

1969), show only limited evidence of tetany features. The main evidence of tetany is therefore represented by the widely gaped mouths well recognizable in most

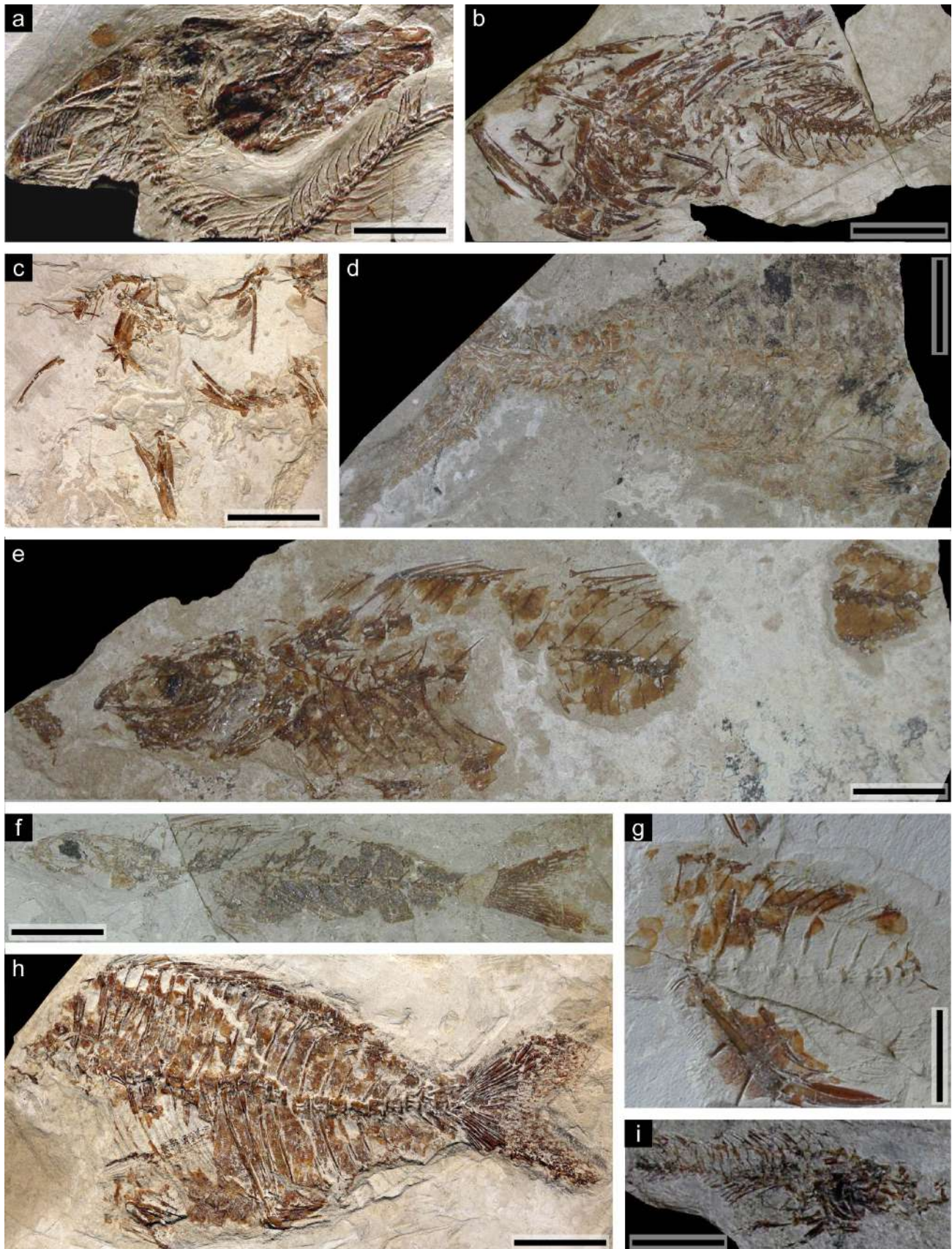


Fig. 16 - Fishes from the Tripoli Fm. equivalent (cycle D1). a) cf. *Merluccius* sp., MGPAAL020. b) Batrachoididae indet., MGPAAL046a. c) *Lates* cf. *niloticus*, MGPAAL001. d) *Trachurus* sp., MGPAAL040a. e) *Boops roulei*, MGPAAL063. f) *Spicara* sp., MGPAAL026. g) *Diplodus* sp., MGPAAL019. h) cf. *Pagrus* sp., MGPAAL004. i) cf. *Mioblennius* sp., MGPAAL017. Scale bars: a-e and g-i = 20 mm; f = 30 mm.

of the specimens of *Spratelloides lemoinei* (Figs 15d and 17a). Jaw tetany is commonly known to occur from thermal shock or respiratory stress (Elder & Smith, 1988), although only death by respiratory stress usually results in widely preserved tetany (e.g., Ferber & Wells, 1995). In this context, anoxia cannot be regarded as the main cause because the adult specimens do not exhibit the typical traits of the extreme muscular contractions, such as the fanned and erected fins and the arching of body. An alternative possibility can be the choking due to consistent ingestion of toxic metabolites produced by some diatom, dinoflagellate and cyanobacterial blooms with consequent respiratory paralysis (e.g., Brongersma-Sanders, 1957; Glibert et al., 2002; López-Cortés et al., 2015), or of planktonic organisms able to physically damage the gills. The latter possibility can be hypothesized due to the common occurrence of *Chaetoceros* resting spores in the diatom assemblage. The spores are produced by vegetative cells possessing brittle setae that are known to cause extensive irritation and/or damage to fish gills, which can stimulate a consistent mucilage secretion by the gill tissues followed by a complete obstruction of the pharynx, eventually leading to hypoxemia and, subsequently, to death (e.g., Bell, 1961; Albright et al., 1993).

The vast majority of the examined fish skeletons are well-preserved, laterally-oriented, showing a relatively high degree of completeness and soft tissues in many cases preserved as a thin dark organic film, usually representing the eyeball and possibly some of the viscera. All the fish specimens are characterized by a remarkable compactional compression, usually normal to the dorso-ventral axis of the body, lying extremely flattened on the bedding plane. In general, the bones are articulated or, at least, closely associated to their original anatomical position. Usually, the body axis of the fishes is nearly straight, although some specimens show a varying degree of body curvature. This is clearly evident in a slab (MGPA PAL 005; Fig. 17a) containing a school of juvenile individuals of *Spratelloides lemoinei* whose total length reaches about 40 mm, showing a concave arching of the vertebral column; these individuals were probably characterized by a coordinated motion and document the most important evidence of collective mortality observed in the diatomites of the Capo di Fiume section. Some specimens exhibit a remarkably contorted (cf. *Merluccius* sp., Fig. 16a), S-shaped (Fig. 17b), dislodged or scattered (Fig. 16e, g) vertebral column. A variety of stages of disarticulation and dispersion of the skeletal elements can be also recognized, ranging from a limited unidirectional dispersion of the distal elements of the caudal-fin rays (Fig. 16h), to the completely disarticulated skeleton of *Lates* cf. *niloticus* (MGPA PAL001), showing a randomized dispersal of the bones (Fig. 16c). While the unidirectional dispersal of scales (Figs 16h and 17c) and lepidotrichia, as well as the S-shaped bending of the vertebral column may be related to the action of weak bottom currents acting at the sediment-water interface (e.g., Elder & Smith, 1988; Tintori, 1992; Ferber & Wells, 1995; Bieńkowska, 2004; Bieńkowska-Wasiluk, 2010; Chellouche et al., 2012; Maramà et al., 2016), the incomplete and partially articulated remains (Figs 16e, g and 17d), and the disarticulated and dispersed skeletal elements of *Lates*

cf. *niloticus* are (at least in part) indicative of a biological disturbance. In this latter case (Fig. 16c), the randomized dispersion of the skeletal elements seems to document extensive scavenging activity, thereby suggesting the persistence of oxic conditions at the bottom (Elder & Smith, 1988). However, the lack of certain portion of the skeletons, including the upper jaws, fins and scales may suggest a more complex post-death history of the carcass, with the scavenging activity at the bottom that was preceded by a period of decompositional floating (see Schäfer, 1972; Ferber & Wells, 1995).

Summarizing, the different preservational states observed suggest that the carcasses were at different stages of decay before the complete burial. However, this does not necessarily imply different residence times on the seafloor, because different decay rates may affect specimens under identical conditions (see Hellowell & Orr, 2012).

Traces of predation

As suggested by Maisey (1994), among fossil fishes, empirical behavioral data mostly derive from cases of stomach content or of predation followed by choking (see also Ebert et al., 2015). Evidence of predator-prey interactions between the fish species of the Capo di Fiume have been observed in a single specimen of the barracudina *Paralepis alby* (MGPA PAL023), whose stomach contains five articulated skeletons of the round herring *Spratelloides lemoinei*, swallowed head or tail first (Fig. 17d). According to Wilby & Martill (1992), the preservation of these kinds of prey items is favored by a chemical microenvironment within the stomach, which prevent the necrolytic activity through a fast mineralization of the hard parts.

The microbial contribution to fish preservation

Fossil fishes are recovered from diatom-rich laminae characterized by the presence of a dense accumulations of large specimens of marine planktic diatoms of the genus *Coscinodiscus*. Throughout the secretion of mucilage, these diatoms may form large aggregates in the deeper part of the water column (e.g., Kemp et al., 2000). As highlighted above, the fast sedimentation of these aggregates in response to the abrupt reconfiguration of the water column may result in the formation of tensile-strength mats, which may cause benthic mass mortalities, also promoting the preservation of the laminated fabric (e.g., Kemp and Baldauf, 1993; Penna et al., 1993). Thus, we suggest that the massive sedimentation of the diatom aggregates largely contributes to the entombment of the fish carcasses, protecting them from the activity of scavengers and from the tractive transport by bottom currents. Noteworthy, the mucilage associated to diatom mats, mainly composed by Transparent Exopolymer Particles (TEP) (e.g., Alldredge et al., 1993; Passow et al., 1994; Armbrecht et al., 2014), constitutes an excellent substratum for the development of microbial films (e.g., Westall & Rincé, 1994). The progressive development of a microbial film on the mucous-rich matrices increases the isolation between the carcasses and the aquatic environment, favoring the emergence of microenvironments characterized by highly reduced oxygen content (Hoagland et al., 1993). A variety of

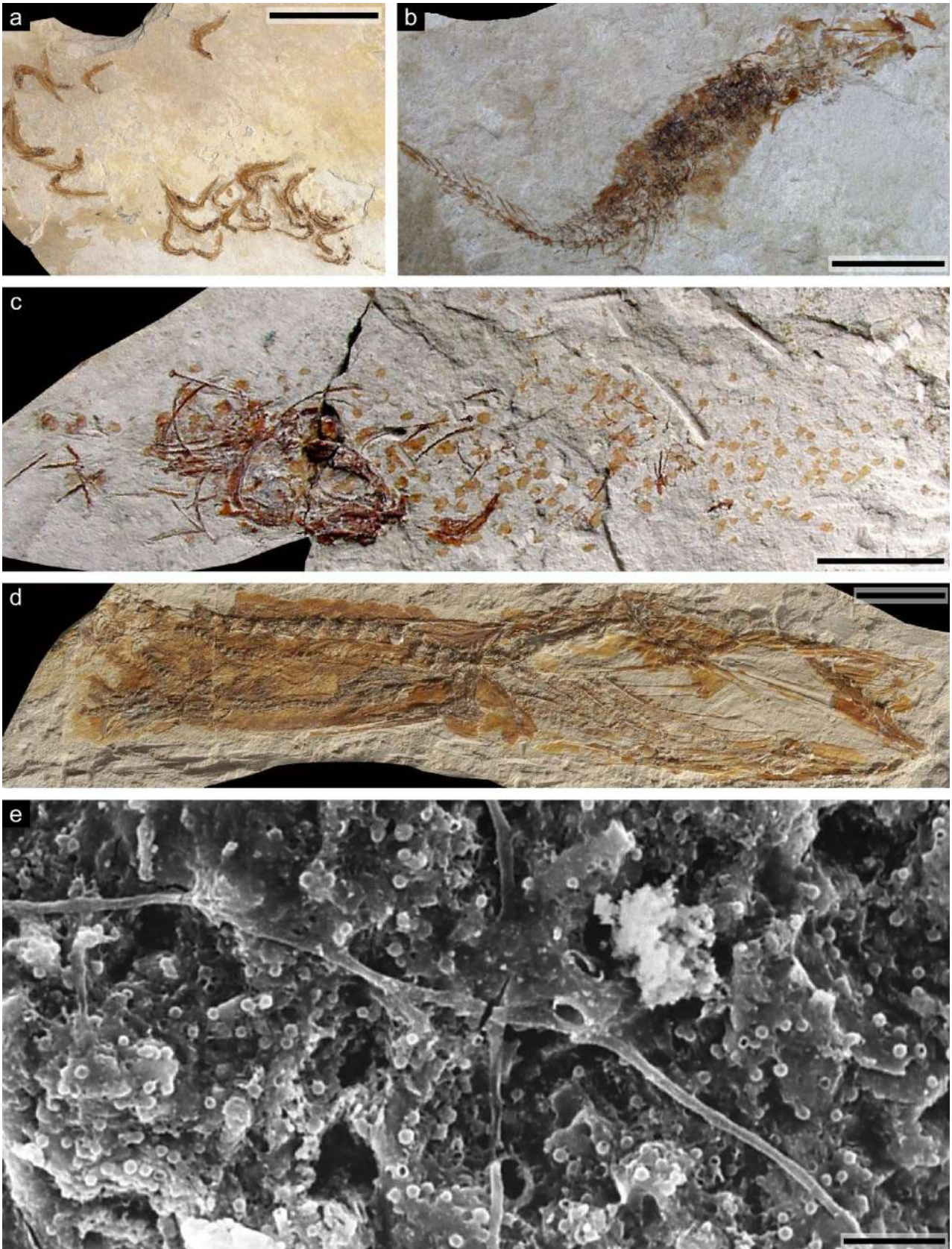


Fig. 17 - Selected taphonomic features observed in fishes from the Tripoli Fm. equivalent (cycle D1). a) Monospecific concentrations of juveniles of the round herring *Spratelloides lemoinei* (MGPA PAL005) showing arched vertebral column and open mouth. b) *Spratelloides lemoinei* (MGPA PAL045) showing S-shaped vertebral column and dorso-ventrally orientated head skeleton. c) Incomplete skeleton of *Boops roulei* (MGPA PAL018) showing unimodal dispersion of the scales along a preferential direction. d) Partially articulated skeleton of the barracudina *Paralepis albyi* (MGPA PAL023) containing five almost complete and fully articulated skeletons of its last meal, *Spratelloides lemoinei*. e) SEM images of a putative microbial biofilm. Note the network of filaments, threads and cocci-like structures, likely of bacterial origin, on the background. Scale bars: a = 50 mm; b and d = 20 mm; c = 30 mm; e = 10 μ m.

microorganisms commonly contributes to the formation of complex multilayered mats, including cyanobacteria and purple sulfur bacteria, algae, fungi and cellulolytic bacteria (Gall, 2001; Iniesto et al., 2015). The enormous diversity of interacting microorganisms (especially autotrophic bacteria) within the mat makes this ecosystem a true superorganism characterized by a global biogeochemical balance. During the biofilm proliferation, microorganisms secrete a mucous compound mainly composed of extracellular polymeric substance (Gall, 1990). Through this substance, the microbial mat incorporates detrital particles and organic remains, protecting them from the hydrodynamic and biogenic action (Gall et al., 1994; Yallop et al., 1994). The extracellular polymeric substance also favors the formation of a chemical microenvironment which promotes the fast mineralization of the organic remains, preventing the diffusion of chemical species from the sediment toward the water column (Wilby et al., 1996). As far as concerns vertebrate remains, the microbial mat may favor the rapid phosphatization of the bones and, in certain cases, of the soft tissues (e.g., Martill, 1988; Briggs et al., 1993). The microbial mats, therefore, preserve the sediment from the erosion, favoring the formation of biolaminated levels, partially inhibit the decay of the carcasses, promote the mineralization of the organic remains, produce a hostile microenvironment for benthic infauna and, through the secretion of toxic compounds, hamper the activity of scavengers (Gall, 1990, 2001).

Microbial mats have been commonly proposed to promote exceptional preservation of fish skeletons (e.g., Gall et al., 1985, 1994; Tintori, 1992; Bravi & De Castro, 1995; Hellowell & Orr, 2012; Iniesto et al., 2013, 2015, 2016; Carnevale et al., 2019b; Leonowicz et al., 2021), although their effective presence within the sediments is not easy to demonstrate. However, SEM observation of the Capo di Fiume fish-bearing diatom-rich laminae revealed the presence of putative fossilized microbial films, represented by amorphous matrix, filaments, (bacterial) fibrils and cocci-like structures covering fish remains (Fig. 17e).

PALEOECOLOGY

Temporal resolution

A reliable paleoenvironmental interpretation should not be performed on fossil assemblages characterized by the mixing of multiple generations of communities. As matter of fact, spatial- and time-averaging may negatively impact on the spatial and temporal resolving power of a fossil assemblage. Time-averaging is the process by which organic remains deriving from different time intervals may be preserved together (e.g., Kidwell, 1998). The formation of a fossil assemblage generally progresses with time-averaging of variable extent because, also in the case of absent biostratigraphic disturbance (reworking, transport, dissolution, bioturbation), biological times are typically short if compared to the normal sedimentation rates. The duration of the time-averaging is obviously variable and the term is certainly relative, depending on the scale of the analyzed phenomenon (Kowalewski, 1996). The variable intensity of time-averaging is reflected by the structural composition of the taphocoenosis and, consequently,

by parameters like temporal resolution, and spatial and compositional fidelity (Behrensmeyer et al., 2000). The analysis of these parameters therefore can allow an evaluation of the time-averaging and of the consequent reliability of the environmental reconstructions. To realize a practical comparison between assemblages, characterized by different levels of biological and taphonomic temporal resolution, Kidwell & Bosence (1991) subdivided the broad spectrum of time-averaging into qualitatively distinct categories. In the case of the Messinian fish assemblage from Capo di Fiume documented herein, as discussed above, the analyses have been based on the articulated skeletal remains collected from the better exposed layers of the basal portion of the first diatomite interval, which constitutes the result of a relatively fast, mostly biogenic, sedimentation. The a-priori knowledge of the relatively fast accumulation of each of the diatomite laminae allows to interpret the time-averaging with major detail. Fossil vertebrate assemblages recording the fast accumulation of carcasses on the seafloor are commonly interpreted as census assemblages or ecological snapshots (e.g., Behrensmeyer et al., 2000), which represent assemblages reflecting a minimum or null time-averaging, composed by ecologically consistent organisms, articulated and well-preserved (e.g., Hallam, 1972; Kidwell & Bosence, 1991; Flessa, 2001). Studies on modern vertebrate carcasses accumulation suggest that a part of the original community is usually not involved in the event, due to the rapidity of phenomenon (e.g., Brett & Seilacher, 1991). In the Capo di Fiume fish assemblage, the remains derived from a diatom-rich lamina certainly document a census assemblage, due to the very reduced time interval necessary for the accumulation of a single lamina. Within the first diatomaceous interval, the fossiliferous layers examined possibly comprise several hundreds to a few thousands of years and, therefore, the whole assemblage should be regarded as time-averaged, characterized by a moderate temporal resolution. However, the overall oceanographic conditions leading to the rhythmic accumulation of compositionally and structurally similar laminae were recurrent through time, as are the structure and composition of the fish assemblage. For this reason, from a paleoecological perspective, the whole fish fauna is regarded herein as a census assemblage.

Trophic structure

The trophic structure of a community is represented by the cumulative feeding habits of its component species (Crame, 1990). Due to the incompleteness of the fossil record only a qualitative or semiquantitative interpretation of the trophic structure of a paleocommunity is possible. The study of the trophic relationships within a paleocommunity may be purely empirical, interpretatively inferred based on the common habits of their extant counterparts (e.g., Hoffman, 1977), an approach especially effective for Neogene taxa, which can be very similar to their phylogenetically closer extant relatives (Dodd & Stanton, 1991). Another approach is based on the actual evidence (see Boucot, 1990), represented by stomach content and other traces of predation (e.g., Wilson, 1987; Maisey, 1994). The two approaches are not mutually exclusive and their integration, when possible, increases the reliability of the interpretation.

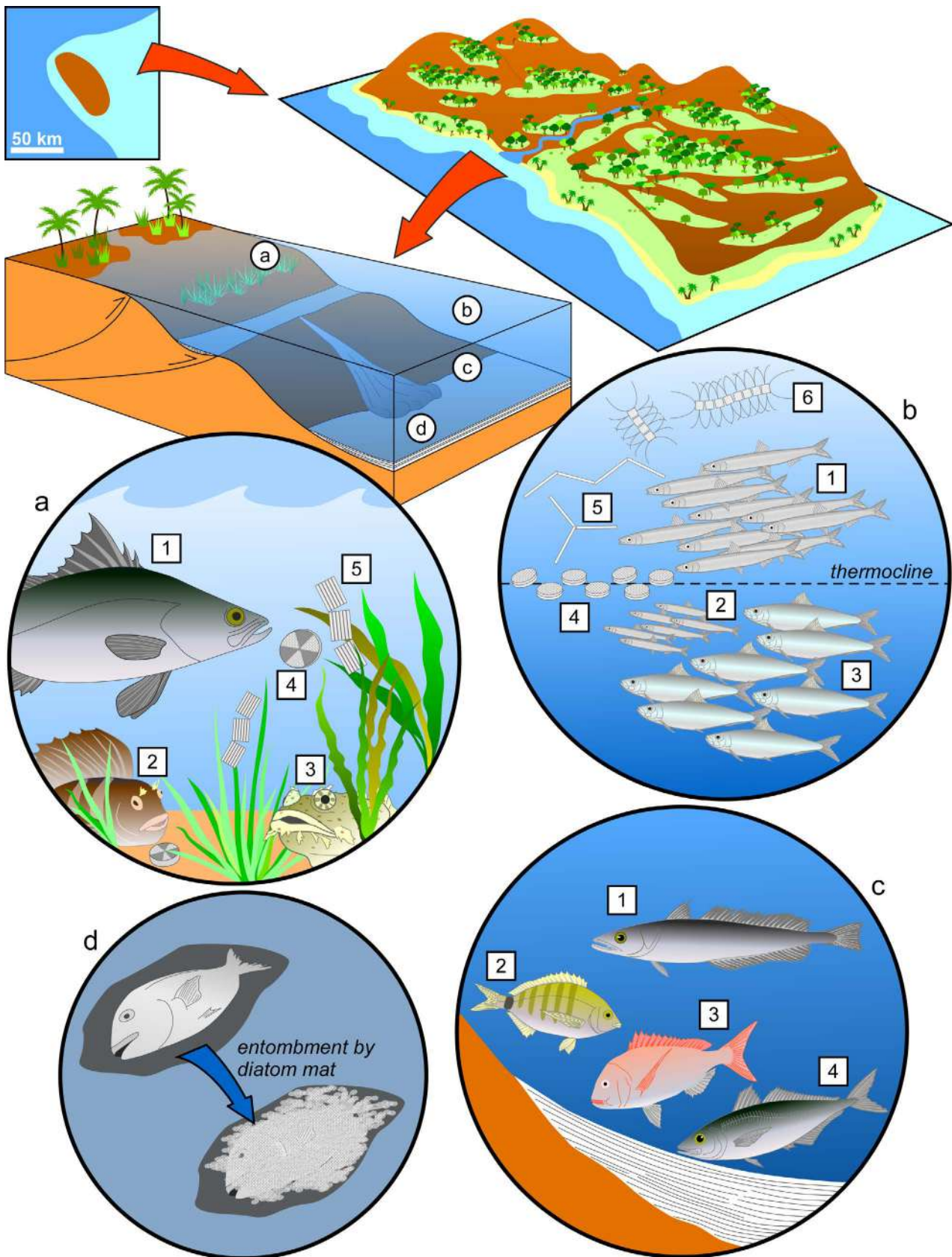


Fig. 18 - Interpretative sketch of the sedimentary environment of the Capo di Fiume section during the deposition of the fish-bearing diatomaceous layer (cycle D1). For the sake of simplicity, only the most representative components of the fish and diatom assemblages are reported. a) Coastal shallow biotope - 1: *Lates cf. niloticus*; 2: cf. *Mioblennius* sp.; 3: *Batrachoididae* indet.; 4: *Actinopterychus senarius*; 5: *Rhabdonema cf. adriaticum*. b) Epipelagic biotope - 1-2: *Spratelloides lemoinei* (adults and juveniles, respectively); 3: sardines; 4: *Coscinodiscus* spp.; 5: *Thalassionema nitzschioides*; 6: *Chaetoceros* spp. c) Subthermocline benthic biotope - 1: cf. *Merluccius* sp.; 2: *Diplodus* sp.; 3: cf. *Pagrus* sp.; 4: *Trachurus* sp. d) The deposition of diatom mats, rapidly entombing fish carcasses, is suggested to have played a significant role in promoting the fossilization processes.

The analysis of predator-prey relationships and the reconstruction of the trophic structure of fossil fish communities have been discussed by several authors (e.g., Zangerl & Richardson, 1963; Bradley & Landini, 1982; Maisey, 1994), in many cases based on lacustrine assemblages (Perkins, 1970; Smith, 1975; Grande, 1984; Elder & Smith, 1988).

The interpretation of the trophic structure of the Capo di Fiume fish assemblage (Fig. 18) is in large part based on the trophic habits of the extant relatives of the recognized taxa and, to a lesser extent, on the traces of predation. The fish assemblage is dominated by far by gregarious planktivores, primarily represented by clupeid taxa, among which *Spratelloides lemoinei* most likely constituted the trophic nucleus of the entire assemblage (see Etter, 1999). This species of round herring was represented by different age classes, which possibly constituted a trophic resource for different groups of predators. Juveniles were probably preyed by small-sized predators but also occasionally by other planktivores with non-discriminatory and opportunistic feeding behavior, including myctophids (*Diaphus edwardsi*, *Myctophum columnae*), large clupeids (*Alosa elongata*, *Etrumeus boulei*), horse-mackerels of the genus *Trachurus* and sparids (*Boops roulei*). On the other hand, adult individuals of *Spratelloides lemoinei* were a preferred food source by barracudinas (*Lestidiops sphekodes*, *Paralepis albyi*), hakes (cf. *Merluccius* sp.), sparids (cf. *Pagrus* sp.) and, possibly, by the riverine euryhaline Nile perch (*Lates* cf. *niloticus*). Demersal (mostly sparids) and benthic (batrachoidids and blenniids) fishes were certainly carnivorous that preyed upon other fishes, crustaceans, molluscs and annelid worms.

Paleoenvironmental setting

Among the many attempts of fossil fish-based paleoenvironmental reconstructions (e.g., Zangerl & Richardson, 1963; Grande, 1994; Grande & Buchheim, 1994; Viohl, 1996; Lund & Poplin, 1998; Grogan & Lund, 2002), very few (e.g., Wilson, 1980, 1988, 1996) were focused on fossil assemblages with limited or moderate time-averaging. As discussed above, the recurrent oceanographic conditions leading to the rhythmic accumulation of compositionally and structurally similar laminae, as well as the temporal continuity of the taxonomic diversity of the fishes may allow to consider the fish assemblage of the Capo di Fiume section as a sort of temporally-relaxed census assemblage. Consequently, at least for the first diatomite interval, whose fish assemblage is discussed herein, it is possible to reliably define the main traits of the overall environmental scenario (Fig. 18).

As far as the paleosalinity is concerned, although some of the fish taxa may be regarded as euryhaline, the occurrence of mesopelagic diel vertical migrators (*Diaphus*, *Lestidiops*, *Maurolicus*, *Myctophum*, *Paralepis*) unquestionably indicates a normal marine salinity. Extant relatives of the dominant species, the round herring *Spratelloides lemoinei*, commonly inhabit waters with salinity values comprised between 32 and 35‰ (Dalzell, 1987), although they may migrate in brackish lagoons during the reproductive period (Losse, 1968).

The fish assemblage is quantitatively dominated by coastal epipelagic taxa, followed by demersal taxa that possibly inhabited subthermocline depths (see Longhurst,

1965). The extreme abundance of diatoms of the genus *Coscinodiscus*, most likely linked to the development of a subsurface chlorophyll maximum, may indicate minimum depths comprised between 30 and 120 meters (e.g., Macías et al., 2014). Round herrings of the genus *Spratelloides* are known to reach depths of about 40 meters (Fricke et al., 2011). Therefore, it is reasonable to assume that the deposition of the ichthyoliferous diatomites of Capo di Fiume took place at depths of several tens of meters. In addition, it is worth noting that the occurrence of the mesopelagic diel vertical migrators in the fish assemblage clearly indicates that considerable depths occurred not far from the diatomite depositional environment.

The contribution provided by the ichthyofauna to the interpretation of the possible distance separating the shore from the diatomite depositional environment is inaccurate. Extant round herring species of the genus *Spratelloides* commonly inhabit coastal biotopes close to the reefs and seagrass beds (Dalzell, 1985, 1987; Milton et al., 1991), although it may occasionally aggregate in large schools with other clupeids, venturing off-shore to cover short distances. An additional paleoichthyological evidence of the limited distance between the shore and the diatomite depositional environment is the single specimen of the Nile perch, *Lates* cf. *niloticus*, whose occurrence suggests that riverine biotopes certainly characterized the emerged area (Fig. 18).

Allochthonous fossils, in this case plant macroremains, may provide more precise indications about the distance from the shore (Wilson, 1980, 1988). Plant macroremains consist of leaves, leaflets, flowers and inflorescences, seed cones, and fruits and infructescences pertaining to slightly less than 30 taxa (Teodoridis et al., 2015). According to Ferguson (1985), a plant fossil assemblage composed by leaves and fruits does not represent a reliable evidence to evaluate the original plant diversity. The hydrodynamic features controlling the buoyancy, transport and accumulation of plant remains has been highlighted by many experimental studies (e.g., Ferguson, 1985; Spicer & Wolfe, 1987; Rich, 1989). The presence of abundant conifer remains, especially needles and seed cones (see also Wilson, 1980), and the lack of woody remains, indicates a rather limited distance between the shore and diatomite depositional environment. A similar result is suggested by the almost complete articulated skeleton of *Prolagus* cf. *apricenus*, whose excellent preservation, with abundant traces of dermal tissues (Mazza et al., 1995), would be indicative of a limited transport (see Grande & Buchheim, 1994).

Therefore, the sudden facies change from coastal to open marine conditions documented by the first diatomite interval suggests a rather narrow shelf connecting coastal and basin areas, thereby being conducive to the accumulation of large volumes of gravity-driven deposits at a short distance from the coast.

CONCLUSIONS

The fossil assemblage recovered in the diatomites of Capo di Fiume and the preliminary biosedimentological study of the fossiliferous deposits have provided several information concerning the water chemistry,

paleobathymetry, distance from the coast, trophic structure, and bottom conditions. The diatom content of the biogenic laminae as well as the structure and composition of the fish assemblage concur to indicate a depositional marine environment with a depth up to several tens of meters. The observation of many indicators of instability of the depositional environment in the diatomites and in the overlying calcareous marl deposits point to a possible tectonic control on the stratigraphic architecture. The sudden facies change from coastal to open marine conditions documented by the first diatomite interval suggests a rather narrow shelf connecting coastal and basinal areas, conducive to the accumulation of large volumes of gravity-driven deposits at a short distance from the coast. The deposition of diatomite laminae may have occurred through different biological mechanisms, most notably the so-called “fall dump”, which also involved the formation of mucilaginous aggregates (flocs) that included assemblages dominated by *Thalassionema nitzschioides*, *Coscinodiscus* spp., and *Chaetoceros* sp. The upper portion of the water column was inhabited by schools of the round herring *Spratelloides lemoinei* and other clupeids as well as by adventitious visitors. These latter are represented by mesopelagic diel vertical migrants (*Diaphus edwardsi*, *Lestidiops sphekodes*, *Mauroliticus* cf. *muelleri*, *Myctophum columnae*, *Paralepis albyi*), feeding upon the epipelagic plankton and different age classes of *Spratelloides lemoinei*. The lower part of the water column and the seafloor were usually well aerated and occupied by a rather diverse community of demersal and benthic fish taxa. Although anoxic conditions during the diatomaceous deposition cannot be aprioristically excluded, caution is needed in assuming extensive bottom oxygen depletion as the main causal agent of fossilization. The fast deposition of diatom mats, abundantly represented in the fossiliferous intervals, may have resulted in the effective entombment of fish carcasses, facilitating their fossilization even under relatively well-oxygenated bottom conditions in the surrounding environment.

ACKNOWLEDGEMENTS

This paper is dedicated to the memory of Erminio Di Carlo (Museo Geopaleontologico dell’Alto Aventino, Palena) in recognition of his contagious enthusiasm and extraordinary passion for the fossils and mountains of Abruzzo. Etta Patacca and the late Paolo Scandone (Dipartimento di Scienze della Terra, Università di Pisa) are warmly thanked for their remarkable contribution to the definition of the general stratigraphic and sedimentological setting of the Capo di Fiume section. Thanks are also due to Walter Landini (Dipartimento di Scienze della Terra, Università di Pisa), Ermanno Danese (Dipartimento di Scienze della Terra, Università di Pisa), Paul Mazza (Dipartimento di Scienze della Terra, Università degli Studi di Firenze), Silvano Agostini (Soprintendenza Archeologia, Belle Arti e Paesaggio dell’Abruzzo), Maria Adelaide Rossi (Soprintendenza Archeologia, Belle Arti e Paesaggio dell’Abruzzo), Jean Gaudant (Muséum National d’Histoire Naturelle, Paris) and Roberto Albani (Dipartimento di Scienze della Terra, Università di Pisa) for many useful inputs and valuable suggestions. Ric Jordan and Kenta Abe (Department of Earth and Environmental Sciences, University of Yamagata, Japan) provided SEM facilities to LP and are thanked for the valuable discussions on the diatom assemblages of the studied samples. Giulio Pavia and Marta Zunino (Dipartimento di Scienze della Terra, Università degli Studi di Torino) helped with the identification of the molluscs. Polished thin

sections were prepared by TS Lab & Geoservices (Cascina, Pisa). For reviewing the manuscript and providing many constructive suggestions for its improvement, we are particularly grateful to Alexandre F. Bannikov (Borisyak Paleontological Institut, Russian Academy of Sciences, Moscow) and Tomáš Přikryl (Institute of Geology, Czech Academy of Sciences, Prague). The research was supported by grants to GC and FDP (ex-60% 2021 and 2022) from the Università degli Studi di Torino.

REFERENCES

- Agassiz L. (1843). Recherches sur les Poissons Fossiles. Tome V. 160 pp. Petitierre, Neuchâtel.
- Albright L.J., Yang C.Z. & Johnson S. (1993). Sublethal concentrations of the harmful diatoms, *Chaetoceros concavicornis* and *C. convolutus* increase mortality rates of penned Pacific Salmon. *Aquaculture*, 117: 215-225.
- Allredge A.L., Passow U. & Logan B.E. (1993). The abundance and significance of a class of large, transparent organic particles in the ocean. *Deep-Sea Research, Part I*, 40: 1131-1140.
- Angelone C. (2007). Messinian *Prolagus* (Ochotonidae, Lagomorpha) of Italy. *Geobios*, 40: 407-421.
- Arambourg C. (1925). Révision des poissons fossiles de Licata (Sicile). *Annales de Paléontologie*, 14: 39-132.
- Arambourg C. (1927). Les Poissons Fossiles d’Oran. *Matériaux pour la Carte Géologique de l’Algérie, 1er Série-Paléontologie*, 6: 1-218.
- Bedini E., Francalacci P. & Landini W. (1986). I pesci fossili del Miocene superiore di Montefiore Conca e Mondaino (Forlì). *Memorie del Museo Civico di Storia Naturale di Verona, Scienze della Terra*, 3: 1-66.
- Behrensmeier A.K., Kidwell S.M. & Gastaldo R.A. (2000). Taphonomy and paleobiology. In Erwin D.H. & Wing S.L. (eds), *Deep Time – Paleobiology’s Perspective*. The Paleontological Society: 103-147.
- Bell G.R. (1961). Penetration of spines from a marine diatom into the gill tissue of lingcod (*Ophiodon elongatus*). *Nature*, 4799: 279-280.
- Bellatalla M., Giovannelli A. & Mariotti G. (1992). Catena del M. Morrone, M. Pizzalto e M. Porrara: elementi e considerazioni per una loro interpretazione. In V Simposio di Ecologia e Paleoecologia delle Comunità Bentoniche. Libro-guida delle escursioni: 121-126.
- Bianchi G. (1992a). Demersal assemblages of the continental shelf and upper slope of Angola. *Marine Ecology Progress Series*, 81: 101-120.
- Bianchi G. (1992b). Study of the demersal assemblages of the continental shelf and upper slope off Congo and Gabon, based on the trawl surveys of the RV ‘Dr Fridtjof Nansen’. *Marine Ecology Progress Series*, 85: 9-23.
- Bieńkowska M. (2004). Taphonomy of ichthyofaunas from an Oligocene sequence (Tylawa Limestone horizon) of the Outer Carpathians, Poland. *Geological Quarterly*, 48: 181-192.
- Bieńkowska-Wasiluk M. (2010). Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. *Acta Geologica Polonica*, 60: 479-533.
- Blanc-Valleron M.-M., Pierre C., Caulet J.P., Caruso A., Rouchy J.-M., Cespuglio G., Sprovieri R., Pestrea S. & Di Stefano E. (2002). Sedimentary, stable isotope and micropaleontological records of paleoceanographic change in the Messinian Tripoli Formation (Sicily, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 185: 255-286.
- Bodén P. & Backman J. (1986). A laminated sediment sequence from the northern North Atlantic Ocean and its climate record. *Geology*, 24: 507-510.
- Boucot A.J. (1990). *Evolutionary Paleobiology of Behavior and Coevolution*. 725 pp. Elsevier, London.
- Bourcier M., Nodot C., Jeudy De Grissac A. & Tine J. (1979). Répartition des biocénoses benthiques en fonction des substrats sédimentaires de la rade de Toulon (France). *Tethys*, 9: 103-112.

- Bradley F. & Landini W. (1982). I fossili del “tripoli” messiniano di Gabbro (Livorno). *Palaeontographia Italica*, 73: 5-33.
- Brandano M., Cornacchia I. & Tomassetti L. (2017). Global versus regional influence on the carbonate factories of Oligo-Miocene carbonate platforms in the Mediterranean area. *Marine and Petroleum Geology*, 87: 188-202.
- Bravi S. & De Castro P. (1995). The Cretaceous fossil fish level of Capo d’Orlando, near Castellammare di Stabia (Na): Biostratigraphy and depositional environment. *Memorie di Scienze Geologiche*, 47: 45-72.
- Brett C.E. & Seilacher A. (1991). Fossil Lagerstätten: A taphonomic consequence of event sedimentation. In Einsele G., Bayer U. & Seilacher A. (eds), *Cycles and Events in Stratigraphy*. Springer-Verlag, Berlin: 283-297.
- Briggs D.E.G., Kear A.J., Martill D.M. & Wilby P.R. (1993). Phosphatization of soft tissues in experiments and fossils. *Journal of the Geological Society of London*, 150: 1035-1038.
- Brongersma-Sanders M. (1957). Mass mortality in the sea. In Hedgpeth J.W. (ed.), *Treatise on Marine Ecology and Paleocology*, I: Ecology. *Memoirs of the Geological Society of America*, 67: 941-1010.
- Carboni M.G., Civitelli G., Corda L., Esu D., Matteucci R. & Palagi I. (1992). Evoluzione delle facies e delle comunità bentoniche dal continentale al marino nel Miocene superiore della Valle del Fiume Aventino. In V Simposio di Ecologia e Paleocologia delle Comunità Bentoniche. Libro-guida delle escursioni: 110-120.
- Carnevale G. (2002). *Boops roulei* ARAMBOURG in the Messinian of Central Italy, with comments on systematics, paleoecology and zoogeography. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 12: 725-736.
- Carnevale G. (2004). The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae). *Geological Magazine*, 141: 573-582.
- Carnevale G. (2006). Morphology and biology of the Miocene butterflyfish *Chaetodon fcheuri* (Teleostei: Chaetodontidae). *Zoological Journal of the Linnean Society*, 146: 251-267.
- Carnevale G. (2007). New gadiform fishes (Teleostei, Gadiformes) from the Miocene of Algeria. *Journal of African Earth Sciences*, 47: 95-111.
- Carnevale G., Dela Pierre F., Natalicchio M. & Landini W. (2018). Fossil marine fishes and the ‘Lago Mare’ event: Has the Mediterranean ever transformed into a brackish lake? *Newsletters on Stratigraphy*, 51: 57-72.
- Carnevale G., Farrés F., Belaústegui Z., Cabello P., Colombo F., Vidal A. & Martinell J. (2019b). Fish-bearing deposits from the Upper Eocene Terminal Complex of the Plana de Vic (Catalonia, NE Spain): Sedimentary context and taphonomy. *Geological Journal*, 54: 1638-1652.
- Carnevale G., Gennari R., Lozar F., Natalicchio M., Pellegrino L. & Dela Pierre F. (2019a). Living in a deep desiccated Mediterranean Sea: An overview of the Italian fossil record of the Messinian salinity crisis. *Bollettino della Società Paleontologica Italiana*, 58: 109-140.
- Carnevale G. & Landini W. (2000). A fossil damselfish (Pisces, Pomacentridae) from the Late Miocene of Central Italy. Biological and biogeographical considerations. *Palaeontographia Italica*, 87: 67-72.
- Carnevale G. & Landini W. (2001). On the first occurrence of the genus *Lates* Cuvier & Valenciennes in the pre-evaporitic Messinian of the Mediterranean. *Bollettino del Museo Civico di Storia Naturale di Verona*, 25: 73-79.
- Carnevale G., Landini W. & Sarti G. (2006). Mare versus Lagomare. Marine fishes and the Mediterranean environment at the end of the Messinian Salinity Crisis. *Journal of the Geological Society, London*, 163: 75-80.
- Carnevale G., Longinelli A., Caputo D., Barbieri M. & Landini W. (2008). Did the Mediterranean marine reflooding precede the Mio-Pliocene boundary? Paleontological and geochemical evidence from upper Messinian sequences of Tuscany, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257: 81-105.
- Carnevale G., Patacca E. & Scandone P. (2011). The Capo di Fiume stratigraphic section. In Carnevale G., Patacca E. & Scandone P. (eds.), *R.C.M.N.S. Interim Colloquium “Vertebrate Migration in the Mediterranean & Paratethys”*. Field Guide to the Post-Conference Excursions (Scontrone, Palena and Montagna della Majella): 53-84.
- Carnevale G. & Schwarzhan W. (2022). Marine life in the Mediterranean during the Messinian salinity crisis: A paleoichthyological perspective. *Rivista Italiana di Paleontologia e Stratigrafia*, 128: 283-324.
- Carnevale G., Sorbini C. & Landini W. (2003). †*Oreochromis lorenzoi* sp. nov., a new species of Tilapiine Cichlid from the late Miocene of Central Italy. *Journal of Vertebrate Paleontology*, 23: 508-516.
- Cellouche P., Fürsich F.T. & Mäuser M. (2012). Taphonomy of neopterygian fishes from the upper Kimmeridgian Wattendorf Plattenkalk of Southern Germany. *Palaeobiodiversity and Palaeoenvironments*, 92: 99-117.
- Chang A.S. & Grimm K.A. (1999). Speckled beds: distinctive gravity-flow deposits in finely laminated diatomaceous sediments, Miocene Monterey Formation, California. *Journal of Sedimentary Research*, 69: 122-134.
- Chang A.S., Grimm K.A. & White L.D. (1998). Diatomaceous sediments from the Miocene Monterey Formation, California: a lamina-scale investigation of biological, ecological, and sedimentary processes. *Palaios*, 13: 439-458.
- Colalongo M.L., Di Grande A., D’Onofrio S., Giannelli L., Iaccarino S., Mazzei R., Romeo M. & Salvatorini G. (1979). Stratigraphy of late Miocene Italian sections straddling the Tortonian/Messinian boundary. *Bollettino della Società Paleontologica Italiana*, 18: 258-302.
- Crame J.A. (1990). Trophic structure. In Briggs D.E.G. & Crowther P.S. (eds), *Palaeobiology – A Synthesis*. Blackwell Science, Oxford: 385-391.
- Crostella A. (1967). Rapporti tra serie autoctona e serie alloctone nell’Alto Aventino (Abruzzi Sud-Orientali). *Memorie della Società Geologica Italiana*, 6: 121-136.
- Dalzell P. (1985). Some aspects of the reproductive biology of *Spratelloides gracilis* (Schlegel) in the Ysabel Passage, Papua New Guinea. *Journal of Fish Biology*, 27: 229-237.
- Dalzell P. (1987). Notes on the biology of *Spratelloides lewisi*, a recently described species of sprat from Papua New Guinea waters. *Journal of Fish Biology*, 30: 691-700.
- Danese E. (1999). Upper Miocene carbonate ramp deposits from the southernmost part of Maiella Mountain (Abruzzo, Central Italy). *Facies*, 41: 41-54.
- Diaz R.J. & Rosenberg R. (1995). Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, 33: 245-303.
- Di Geronimo I., Raffi S. & Rosso A. (1987). Dominanza di specie opportuniste nei ‘Popolamenti Eterogenei’ del Pleistocene inferiore di Mazzarino (Sicilia Centrale). *Bollettino dell’Accademia Gioenia di Scienze Naturali*, 20: 129-166.
- Di Geronimo I. & Robba E. (1988). The structure of benthic communities in relation to basin stability. In Boriani A., Bonafede M., Piccardo G.B. & Vai G.B. (eds), *The Lithosphere in Italy. Advances in Earth Science Research. Atti Convegno Accademia dei Lincei*, 80: 341-352.
- d’Orbigny A. (1826). Tableau methodique de la Classe de Cephalopodes. *Annales des Sciences Naturelles*, 7: 245-314.
- Dodd J.R. & Stanton R.J. (1991). *Paleoecology. Concepts and Applications*, 2nd Edition. 528 pp. John Wiley & Sons, New York.
- Ebert M., Kölbl-Ebert M. & Lane J.A. (2015). Fauna and predator-prey relationships of Ettlting, an actinopterygian fish-dominated Konservat-Lagerstätte from the late Jurassic of Southern Germany. *PLoS ONE*, 10: e0116140.

- Ehrenberg C.G. (1838). Die Infusionsthierchen als vollkommene Organismen. Ein Blick in das tiefere organische Leben de Natur. 548 pp. Verlag von Leopold Voss, Leipzig.
- Elder R.L. & Smith G.R. (1984). Fish taphonomy and paleoecology. *Geobios*, Mémoire special 8: 287-291.
- Elder R.L. & Smith G.R. (1988). Fish taphonomy and environmental inference in paleolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62: 577-592.
- Estrada M. (1991). Phytoplankton assemblages across a NW Mediterranean front: changes from winter mixing to spring stratification. *Oecologia Aquatica*, 10: 157-185.
- Esu D. & Girotti O. (1989). Late Miocene and Early Pliocene continental and oligohaline molluscan faunas of Italy. *Bollettino della Società Paleontologica Italiana*, 28: 253-263.
- Etter W. (1999). Community analysis. In Harper D.A.T. (ed.), Numerical Palaeobiology. John Wiley & Sons, Chichester: 285-360.
- Faux C.M. & Padian K. (2007). The opisthotonic posture of vertebrate skeletons: postmortem contraction or death throes. *Paleobiology*, 33: 201-226.
- Ferber C.T. & Wells N.A. (1995). Paleolimnology and taphonomy of some fish deposits in "Fossil" and "Uinta" Lakes of the Eocene Green River Formation, Utah and Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 117: 185-210.
- Ferguson D.K. (1985). The origin of leaf assemblages – new light on an old problem. *Review of Paleobotany and Palynology*, 46: 117-144.
- Flessa K.W. (2001). Time-averaging. In Briggs D.E.G. & Crowther P. (eds), Palaeobiology II. Blackwell, Oxford: 292-296.
- Fricke R., Kulbicki M. & Wantiez L. (2011). Checklist of the fishes of New Caledonia, and their distribution in the Southwest Pacific Ocean (Pisces). *Stuttgarter Beiträge zur Naturkunde A*, 4: 341-463.
- Fuksı T., Tomašových A., Gallmetzer I., Haselmair A. & Zuschin M. (2018). 20th century increase in body size of a hypoxia-tolerant bivalve documented by sediment cores from the northern Adriatic Sea (Gulf of Trieste). *Marine Pollution Bulletin*, 135: 361-375.
- Gall J.-C. (1990). Le rôle biosédimentaire des voiles microbiens. Critères de reconnaissance. *Bulletin de la Société Géologique de France*, 8: 75-82.
- Gall J.-C. (2001). Role of microbial mats. In Briggs D.E.G. & Crowther P. (eds), Palaeobiology II. Blackwell, Oxford: 280-284.
- Gall J.-C., Bernier P., Gaillard C., Barale G., Bourseau J.P., Buffetaut E. & Wenz S. (1985). Influence du développement d'un voile algair sur la sédimentation et la taphonomie des calcaires lithographiques. Exemples du gisement de Cerin (Kimmeridgien supérieur, Jura meridional français). *Comptes Rendus de l'Académie des Sciences de Paris*, 301: 547-552.
- Gall J.-C., Düringer P., Krumbein W. & Paicheler J.-C. (1994). Impact des écosystèmes microbiens sur la sédimentation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 111: 17-28.
- Gaudant J. (2022). La crise messinienne et ses effets sur l'ichthyofaune néogène de la Méditerranée: la témoignage des squelettes en connexion de poissons téléostéens. *Geodiversitas*, 24: 691-710.
- Glibert P.M., Landsberg J.H., Evans J.J., Al-Sarawi M., Faraj M., Al-Jarallah M.A., Haywood A., Ibrahim S., Klesius P., Powell C. & Shoemaker C. (2002). A fish kill of massive proportion in Kuwait Bay, Arabian Gulf, 2001: the role of bacterial disease, harmful algae, and eutrophication. *Harmful Algae*, 1: 215-231.
- Gmelin J.F. (1789). Caroli a Linné, equitis aurati de stella polari, ... Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis. Editio decima tertia, aucta, reformata. Vol. I (pt. 3). 483 pp. Georg Emanuel Beer, Leipzig.
- Grande L. (1984). Paleontology of the Green River Formation, with a review of the fish fauna. *Bulletin of the Geological Survey of Wyoming*, 63: 1-333.
- Grande L. (1994). Studies of paleoenvironments and historical biogeography in the Fossil Butte and Laney members of the Green River Formation. *Contributions to Geology, University of Wyoming*, 30: 15-32.
- Grande L. & Buchheim H.P. (1994). Paleontological and sedimentological variation in early Eocene Fossil Lake. *Contributions to Geology, University of Wyoming*, 30: 33-56.
- Grimm K.A. & Orange (1997). Synsedimentary fracturing, fluid migration, and subaqueous mass wasting: intrastratal microfractured zones in laminated diatomaceous sediments, Miocene Monterey Formation, California, U.S.A. *Journal of Sedimentary Research*, 67: 601-613.
- Grogan E.D. & Lund R. (2002). The geological and biological environment of the Bear Gulch Limestone (Mississippian of Montana, USA) and a model for its deposition. *Geodiversitas*, 24: 295-315.
- Hallam A. (1972). Models involving population dynamics. In Schopf T.J.M. (ed.), Models in Paleobiology. Freeman Cooper and Co., San Francisco: 62-80.
- Harzhauser M., Neubauer T.A., Georgopoulou E., Esu D., D'Amico C., Pavia G., Giuntelli P. & Carnevale G. (2015). Late Messinian continental and Lago-Mare gastropods from the Tertiary Piedmont Basin (NW Italy). *Bollettino della Società Paleontologica Italiana*, 54: 1-53.
- Hellawell J. & Orr P.J. (2012). Deciphering taphonomic processes in the Eocene Green River Formation of Wyoming. *Palaeobiodiversity and Palaeoenvironments*, 92: 353-365.
- Hilgen F.J. & Krijgsman W. (1999). Ciclostratigraphy and astrochronology of the Tripoli diatomite formation (pre-evaporite Messinian, Sicily, Italy). *Terra Nova*, 11: 16-22.
- Hoagland K.D., Rosowski J.R., Gretz M.R. & Roemer S. (1993). Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. *Journal of Phycology*, 29: 537-566.
- Hoffman A. (1977). Synecology of macrobenthic assemblages of the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Poland). *Acta Geologica Polonica*, 27: 227-280.
- Hrs-Brenko M. (2006). The basket shell, *Corbula gibba* Olivi, 1792 (bivalve mollusks) as a species resistant to environmental disturbances: A review. *Acta Adriatica*, 47: 49-64.
- Iniesto M., Buscalioni A.D., Guerrero M.C., Benzerara K., Moreira D. & López-Archilla A.I. (2016). Involvement of microbial mats in early fossilization by decay delay and formation of impressions and replicas of vertebrates and invertebrates. *Scientific Reports*, 6: 25716.
- Iniesto M., Laguna C., Florín M., Guerrero M.C., Chicote A., Buscalioni A.D. & López-Archilla A.I. (2015). The impact of microbial mats and their microenvironmental conditions in early decay of fish. *Palaaios*, 30: 792-801.
- Iniesto M., López-Archilla A.I., Fregenal-Martínez M., Buscalioni A.D. & Guerrero M.C. (2013). Involvement of microbial mats in delayed decay: An experimental essay on fish preservation. *Palaaios*, 28: 56-66.
- Kemp A.E.S. & Baldauf J.G. (1993). Vast Neogene laminated diatom mat deposits from the eastern equatorial Pacific Ocean. *Nature*, 362: 141-144.
- Kemp A.E.S. & Villareal T.A. (2018). The case of the diatoms and the muddled mandalas: time to recognize diatom adaptations to stratified waters. *Progress in Oceanography*, 167: 138-149.
- Kemp A.E.S., Pike J., Pearce R.B. & Lange C.B. (2000). The "fall dump" – a new perspective on the role of a "shade flora" in the annual cycle of diatom production and export flux. *Deep-Sea Research, Part II*, 47: 2129-2154.
- Kidwell S.M. (1998). Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios*, 30: 977-995.
- Kidwell S.M. & Bosence D.W.J. (1991). Taphonomy and time-averaging of marine shelly faunas. In Allison P.A. & Briggs D.E.G. (eds), Taphonomy: Releasing the Data Locked in the Fossil Record. Plenum Press, New York: 115-209.
- Kowalewski M. (1996). Time-averaging, overcompleteness, and the geological record. *The Journal of Geology*, 104: 317-326.

- Kützing F.T. (1844). Die Kieselschaligen Bacillarien oder Diatomeen. 152 pp. W. Köhne, Nordhausen.
- Landini W. & Menesini E. (1984). Messinian marine fish communities of the Mediterranean Sea. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A*, 91: 279-290.
- Landini W. & Sorbini L. (1989). Ichthyofauna of the evaporitic Messinian in the Romagna and Marche regions. *Bollettino della Società Paleontologica Italiana*, 28: 287-293.
- Landini W. & Sorbini L. (1992). Données récentes sur les téléostéens du Miocène et du Pliocène d'Italie. *Geobios, Mémoire Special 14*: 151-157.
- Leckie D.A., Singh C., Bloch J., Wilson M. & Wall J. (1992). An anoxic event at the Albian-Cenomanian boundary: the Fish Scale Marker Bed, northern Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 92: 139-166.
- Leonardi A. (1959). L'ittiofauna del "Tripoli" del Miocene superiore di Bessima (Enna). *Palaeontographia Italica*, 54: 115-173.
- Leonowicz P., Bienkowska-Wasiluk M. & Ochmanski T. (2021). Benthic microbial mats from deep-marine flysch deposits (Oligocene Menilite Formation from S. Poland): Palaeoenvironmental controls on the MISS types. *Sedimentary Geology*, 417: 105881.
- Linnaeus C. (1758). Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. 812 pp. Laurentius Salvius, Holmiae.
- Longhurst A.R. (1965). A survey of the fish resources of the Eastern Gulf of Guinea. *Journal du Conseil International pour l'Exploration de la Mer*, 34: 300-334.
- López-Cortés D.J., Núñez-Vázquez E.J., Band-Schmidt C.J., Gárate-Lizárraga I., Hernández-Sandoval F.E. & Bustillos-Guzmán J.J. (2015). Mass fish die-off during a diatom bloom in the Bahía de La Paz, Gulf of California. *Hidrobiológica*, 25: 39-48.
- Losse G.F. (1968). The elopoid and clupeoid fishes of East African coastal waters. *Journal of East Africa Natural History Society and National Museum*, 27: 77-115.
- Lund R. & Poplin C. (1998). Fish diversity of the Bear Gulch Limestone, Namurian, Lower Carboniferous of Montana, USA. *Geobios*, 32: 285-295.
- Macías D., Stips A. & Garcia-Gorrioz E. (2014). The relevance of deep chlorophyll maximum in the open Mediterranean Sea evaluated through 3D hydrodynamic-biogeochemical coupled simulations. *Ecological Modelling*, 281: 26-37.
- Maisey J.G. (1994). Predator-prey relationships and trophic level reconstruction in a fossil fish community. *Environmental Biology of Fishes*, 40: 1-22.
- Marramà G., Bannikov A.F., Tyler J.C., Zorzin R. & Carnevale G. (2016). Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 454: 228-245.
- Martill D.M. (1988). Preservation of fish in the Cretaceous of Brazil. *Palaeontology*, 31: 1-18.
- Mazza P. (1987). *Prolagus apricenicus* and *Prolagus imperialis*: two new ochotonids (Lagomorpha, Mammalia) of the Gargano (Southern Italy). *Bollettino della Società Paleontologica Italiana*, 26: 233-243.
- Mazza P. & Rustioni M. (1996). The Turolian fossil artiodactyls from Scontrone (Abruzzo, Central Italy) and their paleoecological and paleogeographical implications. *Bollettino della Società Paleontologica Italiana*, 35: 93-106.
- Mazza P., Rustioni M., Aruta G. & Di Carlo E. (1995). A Messinian *Prolagus* from Capo di Fiume Quarry (Palena, Abruzzo, Central Italy). *Bollettino della Società Paleontologica Italiana*, 34: 55-66.
- Mereschkowsky C. (1902). Liste des Diatomées de la mer Noire. *Botanisches Zapiski*, 19: 51-88.
- Miccadei E. & Parotto M. (1998). Aspetto geologico delle dorsali Rotella-Pizzalto-Porrara (Appennino Abruzzese Orientale). *Geologica Romana*, 34: 87-113.
- Milton D.A., Blaber S.J.M. & Rawlinson N.J.F. (1991). Age and growth of three species of tuna baitfish (genus: *Spratelloides*) in the tropical Indo-Pacific. *Journal of Fish Biology*, 39: 849-866.
- Olivi G. (1792). Zoologia Adriatica ossia Catalogo Regionale degli Animali del Golfo e delle Lagune di Venezia. 334 pp. Bassano.
- Pan Y., Fürsich F.T., Zhang J., Wang Y. & Zheng X. (2015). Biostratigraphic analysis of *Lycoptera* beds from the Early Cretaceous Yixian Formation, Western Liaoning, China. *Palaeontology*, 58: 1-25.
- Passow U., Alldredge A.L. & Logan B.E. (1994). The role of particulate carbohydrate exudates in the flocculation of diatom blooms. *Deep-Sea Research, Part 1*, 41: 335-357.
- Patacca E., Sartori R. & Scandone P. (1990). Tyrrhenian Basin and Apenninic Arcs: Kinematic relations since late Tortonian times. *Memorie della Società Geologica Italiana*, 45: 425-451.
- Patacca E. & Scandone P. (1988). Post Tortonian mountain building in the Apennines. The role of passive sinking of a relic lithospheric slab. In Boriani A., Bonafede M., Piccardo G.B. & Vai G.B. (eds), The Lithosphere in Italy. Advances in Earth Science Research. *Atti Convegni Accademia dei Lincei*, 80: 157-176.
- Patacca E., Scandone P., Bellatalla M., Perilli N. & Santini U. (1992). La zona di giunzione tra l'arco appenninico settentrionale e l'arco appenninico meridionale nell'Abruzzo e nel Molise. In Tozzi M., Cavinato G.P. & Parotto M. (eds), Studi Preliminari all'Acquisizione Dati del Profilo CROP 11 Civitavecchia-Vasto. *Studi Geologici Camerti*, special publication 1991/2: 417-441.
- Patacca E., Scandone P. & Carnevale G. (2013). The Miocene vertebrate-bearing deposits of Scontrone (Abruzzo, Central Italy). Stratigraphic and paleoenvironmental analysis. *Geobios*, 46: 5-23.
- Patterson C. (1964). A review of Mesozoic acanthopterygian fishes, with special references to those of the English Chalk. *Philosophical Transactions of the Royal Society of London B*, 247: 213-482.
- Pellegrino L., Abe K., Gennari R., Lozar F., Dela Pierre F., Natalicchio M., Mikami Y., Jordan R.W. & Carnevale G. (2020a). An integrated micropaleontological study of the diatomaceous deposits of the Monferrato Arc (Piedmont Basin, NW Italy) provides new insights into the Messinian paleoceanographic evolution of the northernmost Mediterranean region. *Marine Micropaleontology*, 160: 101910.
- Pellegrino L., Dela Pierre F., Jordan R.W., Abe K., Mikami Y., Natalicchio M., Gennari R., Lozar F. & Carnevale G. (2020b). The upper Miocene diatomaceous sediments of the northernmost Mediterranean region: A lamina-scale investigation of an overlooked palaeoceanographic archive. *Sedimentology*, 67: 3389-3421.
- Pellegrino L., Dela Pierre F., Natalicchio M. & Carnevale G. (2018). The Messinian diatomite deposition in the Mediterranean and its relationships to the global silica cycle. *Earth-Science Reviews*, 178: 154-176.
- Penna N., Rinaldi A., Montanari G., Di Paolo A. & Penna A. (1993). Mucilaginous masses in the Adriatic Sea in the summer of 1989. *Water Research*, 27: 1767-1771.
- Perkins P.L. (1970). Equitability and trophic levels in an Eocene fish population. *Lethaia*, 3: 301-310.
- Picard J. (1965). Recherches qualitatives due les biocénoses marines des substrats meubles dragables de la région Marseillaise. *Recueil des Travaux de la Station Marine d'Endoume*, 36: 1-160.
- Pike J. & Kemp A.E.S. (1999). Diatom mats in Gulf of California sediments: Implications for the paleoenvironmental interpretation of laminated sediments and silica burial. *Geology*, 27: 311-314.
- Raffi G. & Forti A. (1959). Micropaleontological and stratigraphical investigations in "Montagna del Morrone". *Revue de Micropaleontologie*, 2: 8-20.
- Rich F.J. (1989). A review of the taphonomy of plant remains in lacustrine sediments. *Review of Paleobotany and Palynology*, 58: 33-46.

- Rigual-Hernández A.S., Bárcena M.A., Jordan R.W., Sierro F.J., Flores J.A., Meier K.J.S., Beaufort L. & Heussner S. (2013). Diatom fluxes in the NW Mediterranean: evidence from a 12-year sediment trap record and superficial sediments. *Journal of Plankton Research*, 35: 1109-1125.
- Romeo M. (1965). “*Globigerina multiloba*” nuova specie del Messiniano della Calabria e Sicilia. *Rivista Italiana di Paleontologia e Stratigrafia*, 71: 1265-1268.
- Rosen D.E. & Patterson C. (1969). The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History*, 141: 357-474.
- Rosen D.E. & Patterson C. (1990). On Müller’s and Cuvier’s concepts of pharyngognath and labyrinth fishes, with an atlas of percomorph dorsal gill arches. *American Museum Novitates*, 2983: 1-57.
- Sauvage H.E. (1870). Synopsis des poissons tertiaries de Licata en Sicile. *Annales des Sciences Naturelles (Zoologie et Paléontologie)*, 14: 1-26.
- Sauvage H.E. (1873). Mémoire sur la faune ichthyologique de la période tertiaire, et plus spécialement sur les poissons fossiles d’Oran (Algérie) et sur ceux découverts part M.R. Alby à Licata en Sicile. *Annales des Sciences Géologiques*, 4: 1-272.
- Schäfer W. (1972). Ecology and Paleocology of Marine Environments. 568 pp. University of Chicago Press, Chicago.
- Sgrosso I. (1986). Criteri ed elementi per una ricostruzione paleogeografica delle zone esterne dell’Appennino Centro-Meridionale. *Memorie della Società Geologica Italiana*, 35: 203-219.
- Shimada C., Sato T., Toyoshima S., Yamasaki M. & Tanimura Y. (2008). Paleocological significance of laminated diatomaceous oozes during the middle-to-late Pleistocene, North Atlantic Ocean (IODP Site U1304). *Marine Micropaleontology*, 69: 139-150.
- Sierro F.J., Hilgen F.J., Krijgsman W. & Flores J.A. (2001). The Abad composite (SE Spain): A Messinian reference section for the Mediterranean and the APTS. *Palaogeography, Palaeoclimatology, Palaeoecology*, 168: 141-169.
- Smith G.R. (1975). Fishes of the Pliocene Glens Ferry Formation. Southwest Idaho. *Papers on Paleontology*, 14: 1-68.
- Sorbini L. (1988). Biogeography and climatology of Pliocene and Messinian fossil fish of Eastern-Central Italy. *Bollettino del Museo Civico di Storia Naturale di Verona*, 14: 1-85.
- Spicer R.A. & Wolfe J.A. (1987). Plant taphonomy of late Holocene deposits in Trinity (Clair Engle) Lake, northern California. *Paleobiology*, 13: 227-245.
- Sprovieri R., Di Stefano E., Caruso A. & Bonomo S. (1996). High resolution stratigraphy in the Messinian Tripoli Formation in Sicily. *Paleopelagos*, 6: 415-435.
- Stachowitsch M., Fanuko N. & Richter M. (1990). Mucus aggregates in the Adriatic Sea: An overview of stages and occurrences. *Marine Ecology*, 11: 327-350.
- Sturani C. & Sampò M. (1973). Il Messiniano inferiore in facies diatomitica nel Bacino Terziario Piemontese. *Memorie della Società Geologica Italiana*, 12: 335-358.
- Teodoridis V., Kvacsek Z., Agostini S., Martinetto E., Rossi M.A. & Cavallo O. (2015). Feather palm foliage from the Messinian of Italy (Capo di Fiume, Palena and Pollenzo near Alba) within the framework of northern Mediterranean late Miocene flora. *Acta Musei Nationalis Pragae, Series B – Historia Naturalis*, 72: 301-314.
- Tintori A. (1992). Fish taphonomy and Triassic anoxic basins from the Alps: a case history. *Rivista Italiana di Paleontologia e Stratigrafia*, 97: 393-408.
- Viohl G. (1996). The paleoenvironment of the Late Jurassic fishes from the southern Franconian Alb (Bavaria, Germany). In Arratia G. & Viohl G. (eds), *Mesozoic Fishes – Systematics and Paleocology*. Verlag Dr. Friedrich Pfeil, München: 513-528.
- Walbaum J.J. (1792). Petri Artedi renovati. Part 3. Petri Artedi sueci genera Piscium in quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Redactis Speciebus 2. Ichthyologiae, part III. 723 pp. Ant. Ferdinand Rose, Greifswald.
- Westall F. & Rincé Y. (1994). Biofilms, microbial mats and microbe-particle interactions: electron microscope observations from diatomaceous sediments. *Sedimentology*, 41: 147-162.
- Wilby P.R., Briggs D.E.G., Bernier P. & Gaillard C. (1996). Role of microbial mats in the fossilization of soft tissues. *Geology*, 24: 787-790.
- Wilby P.R. & Martill D.M. (1992). Fossil fish stomachs: a microenvironment for exceptional preservation. *Historical Biology*, 6: 25-36.
- Wilson M.V.H. (1980). Eocene lake environments: Depth and distance-from-shore variation in fish, insect, and plant assemblages. *Palaogeography, Palaeoclimatology, Palaeoecology*, 32: 21-44.
- Wilson M.V.H. (1987). Predation as a source of fish fossils in Eocene lake sediments. *Palaios*, 2: 497-504.
- Wilson M.V.H. (1988). Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. *Palaogeography, Palaeoclimatology, Palaeoecology*, 62: 609-623.
- Wilson M.V.H. (1996). Taphonomy of a mass-death layer of fishes in the Paleocene Paskapoo Formation at Joffre Bridge, Alberta, Canada. *Canadian Journal of Earth Sciences*, 33: 1487-1498.
- Yallop M.L., De Winder B., Paterson D.M. & Stal L.J. (1994). Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. *Estuarine, Coastal and Shelf Science*, 39: 565-582.
- Yonge C.M. (1946). On the habits and adaptations of *Aloidis (Corbula) gibba*. *Journal of the Marine Biologists Associations of the UK*, 26: 358-376.
- Zangerl R. & Richardson E.S. (1963). The paleocological history of two Pennsylvanian black shales. *Fieldiana, Geology Memories*, 4: 1-352.

Manuscript submitted 16 June 2022

Revised manuscript accepted 6 July 2022

Published online 3 August 2022

Guest Editor Alberto Collareta