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A leerfish (Teleostei, Carangidae) from the Messinian evaporite succession of the Vena del Gesso basin (Romagna Apennines, Italy): Palaeogeographical and palaeoecological implications

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KEY WORDS - Teleostei, Carangidae, Lichia *aff.* amia*, Messinian, Vena del Gesso basin, Italy.*

ABSTRACT - A specimen of the leerfish Lichia *aff.* amia *is described from the Messinian evaporite succession of the Vena del Gesso basin, in the Romagna Apennines. The single specimen available is solely represented by a strongly incomplete left pectoral girdle and a caudal vertebra. The palaeoecological analysis of the leerfish and its associated fish biota suggests that it represented a top predator in the coastal lagoons of the Vena del Gesso basin, in which it entered opportunistically, attracted by the abundant food resources available. The composition and ecological structure of the fish assemblage indicate that the lagoons of the Vena del Gesso basin were characterized by a brackish waterbody, periodically influenced by seawater inputs. The marine influences evocated by the presence of the leerfish unequivocally suggest that normal marine conditions occurred close to the coastal lagoons of the Vena del Gesso basin during the deposition of the primary evaporites.*

RIASSUNTO - [Una leccia (Teleostei, Carangidae) nella successione evaporitica messiniana del Bacino della Vena del Gesso (Appennino Romagnolo, Italia): implicazioni paleogeografiche e paleoecologiche] - *Viene qui illustrato un esemplare attribuibile al carangide,* Lichia *aff.* amia *(leccia), proveniente dai depositi evaporitici messiniani del bacino della Vena del Gesso, nell'Appennino Romagnolo. L'unico reperto rinvenuto è rappresentato esclusivamente da un cinto pettorale sinistro largamente incompleto e da una vertebra caudale. Lo studio paleoecologico dell'esemplare in questione e dell'ittiofauna ad esso associata sembra indicare che la leccia rappresentasse uno dei superpredatori delle lagune costiere del Bacino della Vena del Gesso, all'interno delle quali faceva ingresso periodicamente, attratto dall'abbondanza di risorse trofiche presenti in questi paleobiotopi. La composizione e la struttura ecologica dell'associazione ittica suggeriscono che le lagune del Bacino della Vena del Gesso furono caratterizzate da una massa d'acqua tendenzialmente salmastra, ma periodicamente influenzata da apporti di origine marina. Infine, la presenza della leccia fornisce una prova inequivocabile dell'esistenza di acque marine a salinità normale nell'area circostante le lagune del Bacino della Vena del Gesso nel corso della deposizione della successione evaporitica.*

INTRODUCTION

The recent development of an accurate astronomically-tuned Neogene time scale has extraordinarily improved our knowledge of the Messinian Salinity Crisis, mostly due to the possibility to realize detailed high-resolution correlations of the geological, oceanographic and biological events throughout the Mediterranean basin, and between the Mediterranean and the global oceanic record. In the last few years, the Messinian event has been the subject of a great number of multidisciplinary papers, and at least two international symposia and four special issues of scientific journals have been dedicated to this topic (Néraudeau & Goubert, 2002; Agustí et al., 2006; Rouchy et al., 2006; Suc et al., 2007). However, even though the Messinian Salinity Crisis may be considered as one of the most extensively studied event in Earth history, it will take time before a comprehensive integrated model of palaeogeographical and palaeoenvironmental evolution will be obtained. The improvement of the stratigraphic methods and the innovative approaches experimented in the past decade (e.g., Krijgsman et al., 1999a; Roveri et al., 2001; Hardie & Lowenstein, 2004; Lofi et al., 2005; Van der Laan et al., 2006; Hilgen et al., 2007; Manzi et al., 2007) in many cases emphasized the deep divergences among the scientific community about the interpretation of the various aspects of the Messinian Salinity Crisis. In this flourishing scenario of new hypotheses and innovative ideas, the role of palaeontological studies has been mostly addressed to the detailed definition of the timing of the tectonic, oceanographical, and biological events that occurred before and just after the Salinity Crisis (e.g., Iaccarino et al., 1999; Krijgsman et al., 1999a, 2001, 2002; McKenzie et al., 1999; Kouvenhoven et al., 2006). However, the lack of biostratigraphic control due to the scarcity of fossils in Salinity Crisis-related deposits has limited the possibility to obtain an accurate palaeoenvironmental framework for this time interval, thereby resulting in a variety of often contrasting interpretations. In particular, a cogent debate has been generated on the physico-chemical evolution of the Mediterranean waterbody during and after the main evaporitic event. In this respect, an innovative approach has been provided by the analysis of fossil fish remains, which has clarified many aspects of nature of the

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Mediterranean waterbody during post-evaporitic '*Lago-mare*' phase (Carnevale et al., 2006a, b, 2008). However, there is still active controversy about the structure and composition of the Mediterranean waters during the evaporitic event, and stratigraphic, geochemical and palaeontological studies have largely contributed to the development of a confused scenario of palaeoenvironmental evolution (see Rouchy & Caruso, 2006). Fossil fishes are rather common in the evaporitic successions of the Mediterranean area (see Landini & Sorbini, 1989), providing an unexploited source of palaeoenvironmental data of the Messinian aquatic biotopes. The relevance of fishes in the interpretation of the Messinian palaeoenvironments lies in their ecology and behaviour. Because of the scarcity of fossils and the heterogeneous nature of Salinity Crisis deposits, it is very difficult to correctly define the physico-chemical nature of the Mediterranean waterbody during the span of such an event and, as a consequence, the palaeogeographical settings of the overall basin (see Cita & Corselli, 1990). For this reason, because of their mobility and migratory behaviour, fishes can be used to interpret the ecological conditions of both the original depositional environment and the areas surrounding it.

The goal of this paper is to describe fossil leerfish remains from a Messinian evaporite succession of the Vena del Gesso basin, in the Romagna Apennines, and to discuss their palaeogeographical and palaeoenvironmental significance.

LOCALITY AND STRATIGRAPHY

The material was collected from an evaporite succession outcropping at Rio Sgarba (Cava SPES), near Borgo Tossignano, in the Vena del Gesso basin (Fig. 1). These evaporite deposits form part of the Gessoso-Solfifera Formation, which originated during the evaporitic and post-evaporitic phases of the Messinian Salinity Crisis event (Roveri et al., 2003; Manzi et al., 2005). The Gessoso-Solfifera Formation is characterized by both primary and resedimented evaporites with interbedded bituminous organic-rich shales (sapropels). Primary evaporites extensively outcrop in the Vena del

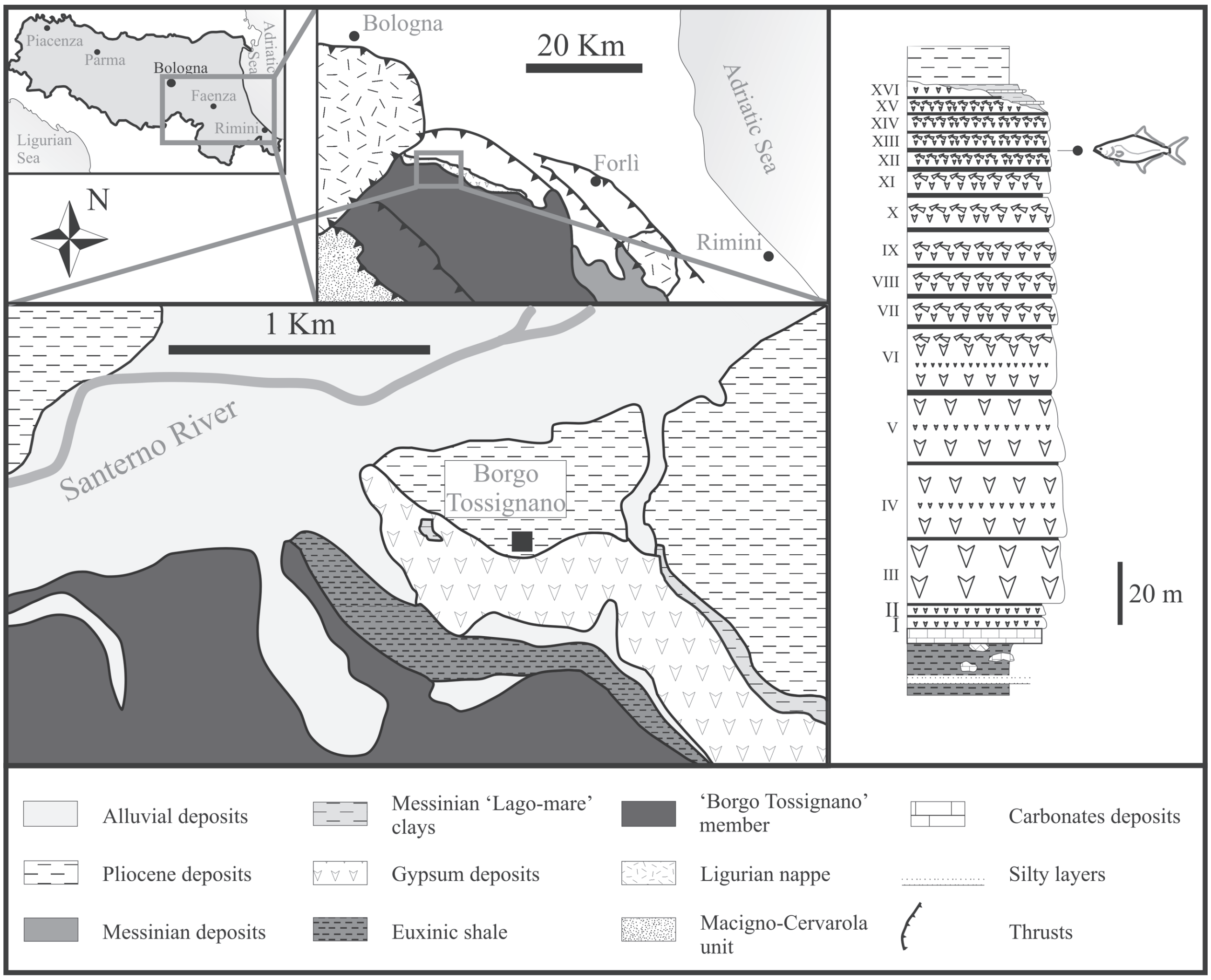

Fig. 1 - Schematic geological map and columnar log of the Rio Sgarba section, Borgo Tossignano, Vena del Gesso basin (modified after Marabini & Vai, 1985, Bassetti et al., 2004, and Montanari et al., 2007).

Gesso basin, a thrust-top basin located in the Romagna Apennines. The Messinian succession of the Vena del Gesso basin consists of 16 cycles of gypsum-sapropel, with an overall thickness of 200-250 m (see Vai & Ricci Lucchi, 1977; Marabini & Vai, 1985). Such a succession accumulated in coastal lagoons close to the emerging Apennine chain (see Vai & Ricci Lucchi, 1977). The deposition of gypsum-sapropel couplets was controlled by astronomically-driven climatic cycles in a time interval ranging from 5.96 to 5.61 ± 0.02 Ma (Krijgsman et al., 1999b). The gypsum was deposited during dry periods characterized by evaporation exceeding precipitations, which correspond to precession maxima and insolation minima. Deposition of sapropels occurred during wet periods with increased precipitations and freshwater input, which correspond to precession minima and insolation maxima. Each of the 16 climatic-controlled gypsum-sapropel cycles contains a characteristic regressive-transgressive facies. According to the interpretation recently developed by Lugli et al. (2005), the lower five cycles were deposited in deep settings characterized by low salinity, while the cycles 6th to 15th originated in response to a strong mixing of thalassic and continental unsaturated waters. The 16th cycle consists of resedimented evaporites (gypsum-arenite and gypsum-rudite) deposited after the main Mediterranean evaporitic event (Manzi et al., 2005).

The sapropel layers form distinct beds up to 2 m thick. These are finely laminated, with a dark-blue colour, and characterized by abundant vegetal debris, authigenic pyrite, calcite, and gypsum. These deposits often contain fossil remains, including fishes, insects, leaves, and benthic (*Ammonia*, *Bolivina*, *Elphidium*) and rare planktonic (small globigerinids) foraminifers (Vai & Ricci Lucchi, 1977).

The fossil material documented herein comes from the sapropel layers at the base of the 13th cycle (Fig. 1). These layers are characterized by abundant fish and plant remains. The fish fauna was briefly reported by Landini & Sorbini (1989) and Carnevale et al. (2003). It consists of five taxa representing five families, other than the leerfish described herein. These are Atherinidae (*Atherina boyeri*), Cichlidae (*Oreochromis lorenzoi*), Cyprinodontidae (*Aphanius crassicaudus*), Gobiidae (*Gobius ignotus*), and Scombridae (gen. et sp. indet.).

Given that several evidences (see e.g., Krijgsman et al., 2001) concur to indicate that each gypsum sapropel cycle has a duration in the order of the precessional cycle of approximately 21,000 years, it is possible to define the age of the fossil material reported in this paper, which can be estimated approximately at 5.69 Ma.

MATERIALS AND METHODS

The specimen is deposited in the Museo Civico di Scienze Naturali, Faenza (MSF). The fossil material is preserved on a finely laminated, dark-blue sapropelitic shale. It has been examined using a Leica MS5 stereomicroscope. Measurements were taken with a dial calliper, to the nearest 0.1 mm. Comparative data were derived from both the literature and direct examination of fresh specimens collected in the Tyrrhenian Sea.

SYSTEMATICS

Subdivision TELEOSTEI *sensu* Patterson & Rosen, 1977
Order PERCIFORMES *sensu* Johnson & Patterson, 1993
Family CARANGIDAE Rafinesque, 1815

Genus *Lichia* Cuvier, 1817
Lichia aff. *amia* (Linnaeus, 1758)
(Figs. 2B-C)

Material - Two parts of the same individual; MSF 19, an incomplete left pectoral girdle exposed in lateral view, and MSF 20, a single incomplete caudal vertebra.

Measurements (mm) - Maximum length of the cleithrum: 87; maximum depth of the cleithrum: 199; maximum length of the vertebral centrum: 42; maximum depth of the vertebral centrum: 37.5; length of the neural spine: 80.

Description - The material consists of a largely incomplete left pectoral girdle and a partially complete vertebra belonging to the same individual (Fig. 2).

Of the pectoral girdle, only the cleithrum and a small fragment of the scapula were preserved. The cleithrum is exposed in lateral view. It is massive and heavily ossified. The main body of this bone is crescent-shaped, with a pointed stout anterodorsal spine and a posteriorly projecting flattened and wing-like plate. The anterodorsal spine extends dorsally well beyond the sigmoid dorsal margin of the posterior plate. The angle between the anterodorsal spine and the dorsal margin of the posterior plate is rather wide, measuring more that 130°. The lower part of the cleithrum consists of a large and robust longitudinal shaft. The anterior rim of this portion of the cleithrum is linear, nearly vertical; the angle between the anterior margin of such a longitudinal shaft and the anterior rim of the anterodorsal spine approximately measures 126°. The anterior margin of the longitudinal shaft of the cleithrum is extremely thickened. This is probably due to the confluence of the two cleithral flanges, external and internal, which meet each other to form an anterior ridge. The relative development of the two cleithral flanges is probably related to the relative extension of the muscles that insert on the cleithrum, including the abductor superficialis, abductor profundus, arrector dorsalis, and arrector ventralis (see Suda, 1996). The internal flange of the cleithrum cannot be observed in the specimen documented herein since it is covered by the broad posterior expansion of the external flange. The posterior rim of the external flange is smooth and characterized by a rounded profile.

The poorly preserved portion of the scapula probably was attached in origin to the internal shelf of the cleithrum.

The vertebra is only partially preserved, lacking the haemal spine and part of its exposed left surface. The vertebral centrum is massive, and rectangular in outline, longer than high. It bears well-developed neural pre- and post-zygapophyses, as well as a prominent haemal post-zygapophysis. A very small haemal subzygapophysis can

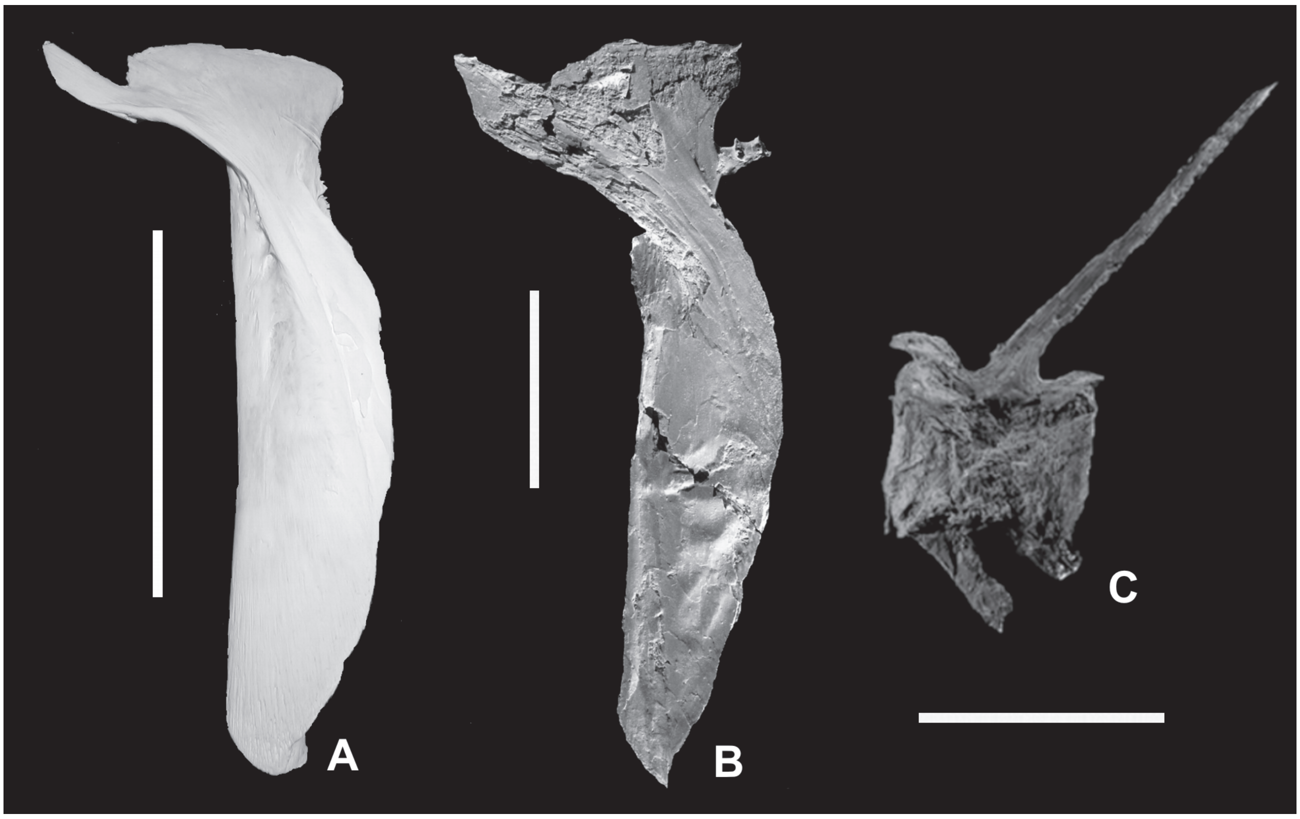

Fig. 2 - A) *Lichia amia* (Linnaeus, 1758), left cleithrum, lateral view. B) *Lichia* aff. *amia* from the Messinian of Rio Sgarba (Cava SPES), Borgo Tossignano, Vena del Gesso basin, left cleithrum, lateral view. C) *Lichia* aff. *amia* from the Messinian of Rio Sgarba (Cava SPES), Borgo Tossignano, Vena del Gesso basin, (?) caudal vertebra, left side, lateral view. Scale bars = 50 mm.

be also observed. The neural arch and spine are stout, characterized by fine ridges that run longitudinally on their lateral surface. The haemal arch is widely thickened and laterally compressed. It is poorly inclined and arises anteriorly from the ventral base of the vertebral centrum. The general physiognomy of the centrum, the relative development of neural and haemal zygapophyses, the apparent absence of fine ridges on the haemal arch, the absence of the inferior vertebral foramen (Starks, 1911; Suzuki, 1962; Smith-Vaniz, 1984), and the morphology and orientation of the haemal arch concur to suggest that the vertebra documented herein could be interpreted as one of the anteriormost caudal elements (see Suda, 1996).

Remarks - Despite its incompleteness and fragmentary nature, the material described herein can be unquestionably placed within the family Carangidae due to the presence of some distinctive characters, including the general morphology of the cleithrum (see Suzuki, 1962), presence of fine ridges on the lateral surface of neural arch and spine (Suda, 1996), and presence of small neural subzygapophysis (Suda, 1996). Within the carangids, the peculiar physiognomy of the cleithrum is consistent with that of *Lichia amia* to which the material is tentatively referred (see Figs. 2A-B). The morphology of the cleithrum is extremely variable among the members of the family Carangidae (Suzuki, 1962). In particular, the detailed anatomical investigation of the fossil material documented herein has identified many cleithral features, such as the external profile of the bone, the orientation of the anterodorsal spine, the relative development of the posterior plate, the angle between the anterodorsal spine and the posterior plate, and the posterior and vertical extent of the external flange, which appear to be diagnostic at the specific level (see e.g., Suzuki, 1962).

The genus *Lichia* contains at least three species, the extant *L. amia*, the extinct *L. alta* from the Oligocene of Slovenia (Kramberger-Gorjanović, 1891; Anđelković, 1989), and *L. veronensis* from the Eocene of Monte Bolca, Italy (Bannikov, 1990). This genus has been traditionally considered as closely related to *Trachinotus* (and *Paratrachinotus*) (e.g., Wheeler, 1963). The phylogenetic position of this genus within the family Carangidae remains rather obscure due to the apparent lack of apomorphic characters that might be useful in determining its affinities (Smith-Vaniz & Staiger, 1973). According to Smith-Vaniz & Staiger (1973), the genus *Lichia* probably represents the sole member of a separate tribe (or subfamily). Nevertheless, subsequent studies continue including it in the trachinotines mostly for the sake of convenience (Smith-Vaniz, 1984; Gushiken, 1988; Bannikov, 1990).

DISCUSSION

Up to date no fossil record is known for the leerfish *Lichia amia*. The Messinian material presented herein is therefore the first documented fossil assigned to this taxon. As discussed above, the genus *Lichia* contains a single extant species, *L. amia*, plus two fossil taxa, which date back to the Paleogene. The Messinian occurrence of a putative representative of the extant species *L. amia* indicates that the divergence of the modern lineage certainly occurred earlier, perhaps in the lower part of the Miocene.

The fossil leerfish documented in this paper provides new significant information on the structure of fish communities and ecological features of the original depositional environment. Moreover, the integration of the overall palaeontological, sedimentological and geochemical evidences allows to better understand the palaeogeographic and palaeoenvironmental characters of the Vena del Gesso basin, at least during the deposition of the sapropel layers of the upper evaporitic cycles (6th to 15th). *Lichia amia* is a marine inshore species that is today restricted to the subtropical and warm temperate waters of the Mediterranean, eastern Atlantic and southern Indian Ocean (Smith-Vaniz & Staiger, 1973). It is a voracious piscivorous species that commonly enter brackish biotopes such as estuaries and coastal lagoons. This large species is often found in surface waters, usually occurring to depths of at least 50 m.

As reported above, at least five fish taxa coexisted with the leerfish in the Messinian coastal lagoons of the Vena del Gesso basin: the toothcarp *Aphanius crassicaudus*, the sand smelt *Atherina boyeri*, the goby *Gobius ignotus*, the cichlid *Oreochromis lorenzoi*, and an indeterminate scombrid.

The composition of the fish assemblage is clearly indicative of a moderately confined paralic biotope (see Guelorget & Perthuisot, 1992; Mariani, 2001). In this context, the taxa belonging to the estuarine residents guild (*Aphanius crassicaudus*, *Atherina boyeri*, *Gobius ignotus*), which includes species of marine origin that reside in brackish biotopes and can complete their life cycle within these systems (see Whitfield, 1999), are strongly dominant. The oligotypic character of this assemblage probably reflects the physically unstable conditions of the waterbody, which are typical of coastal lagoons characterized by broad salinity fluctuations. The co-occurrence of taxa belonging to extremely different ecological categories as the leerfish *Lichia* aff. *amia* (marine adventitious) and the cichlid *Oreochromis lorenzoi* (freshwater migrant) could indicate that these lagoons were periodically connected with the sea through moderately deep channels. Euryhaline cichlids of the genus *Oreochromis* occur in large numbers in coastal lakes and temporarily closed estuarine systems but they are completely absent in permanently open estuarine systems (Whitfield & Blaber, 1979), whereas large leerfish individuals are exclusively present in those temporarily closed estuarine systems characterized by relatively deep settings (Harrison & Whitfield, 1995). The proportion of the different ecological groups within the overall assemblage reflects the physical and biological features of the environment. In particular, the paucity of freshwater and marine fish taxa is probably indicative of the exceptionally low species diversity of these components. Many euryhaline freshwater and marine fishes appear to be tolerant to broad fluctuations of the salinity and other physical and chemical parameters, but prolonged oligohaline or hyperhaline conditions can cause strong osmoregulatory stress; continuous or prolonged salinity changes therefore play a crucial role in reducing the abundance of freshwater and/or marine species. Moreover, in contrast to marine and (selected) freshwater taxa, fishes belonging to the estuarine residents guild, which were dominant in the coastal lagoons of the Vena del Gesso basin, are usually not adapted to hyperhaline conditions (Whitfield, 1998, 1999). Based on these considerations, it is possible to conclude that the composition and ecological structure of the fish assemblage suggest that the lagoons of the Vena del Gesso basin were characterized by a brackish waterbody, periodically influenced by seawater inputs (see Fig. 3). This hypothesis well fits with the results of a recent study of isotope geochemistry (Lugli et al., 2007), which concluded that the Vena del Gesso marginal basin was dominated by continental waters that received significant marine recharges. The lagoons possibly represented the distal part of a large and complex estuarine system, which also included freshwater forested swamps with hydrophytic trees (*Taxodium* and *Glyptostrobus*) and saltmarshes (e.g., Bertini, 2002, 2006). The waterbodies of these palaeobiotopes were submitted to a persistent dilution by means of continental run-off in a climatic context characterized by warm and humid conditions (Bertini, 2006).

The leerfish certainly was one of the top predators in these lagoons (Fig. 3). Large predatory fishes appear to use coastal lagoons opportunistically, attracted by abundant food and habitat availability (e.g., Nordlie, 2003). The attractiveness of these biotopes to fishes is primarily due to their high productivity. Temporarily closed coastal lagoons act as detritus trap for both autochthonous and allochthonous production, thereby providing abundant food resources for invertebrate preys and detritivorous fishes (Whitfield, 1999). Because of their semi-enclosed configuration, coastal lagoons tend to accumulate macrodetritus and finer particulate organic matter transported by periodic river floods, and only a small proportion of the organic material is exported to the sea. The continuous accumulation of detrital organic matter in temporarily closed lagoons commonly results in permanent depletions of dissolved oxygen, and, as a consequence, in water column stratification and anoxic conditions at the bottom. This was probably the case of the lagoons of the Vena del Gesso basin during the deposition of the sapropel layers. The occurrence of well-preserved articulated fish skeletons, the preservation of plant remains, the virtual absence of megabenthos, and the laminated style of the sediments suggest that anoxic conditions close to the bottom occurred during the formation of these deposits. This hypothesis has been corroborated by the analysis of the organic biomarkers, which also indicated that the anoxia was persistent in these coastal lagoons. In particular, the abundance of gammacerane (an indicator of water column stratification) and isorenieratane (an indicator of photic zone anoxia) indicates that often during the sapropelitic deposition anoxia extended into the photic zone (Keely et al., 1995; Schaefer et al., 1995; Sinninghe Damsté et al., 1995a, b). Therefore, despite the high food

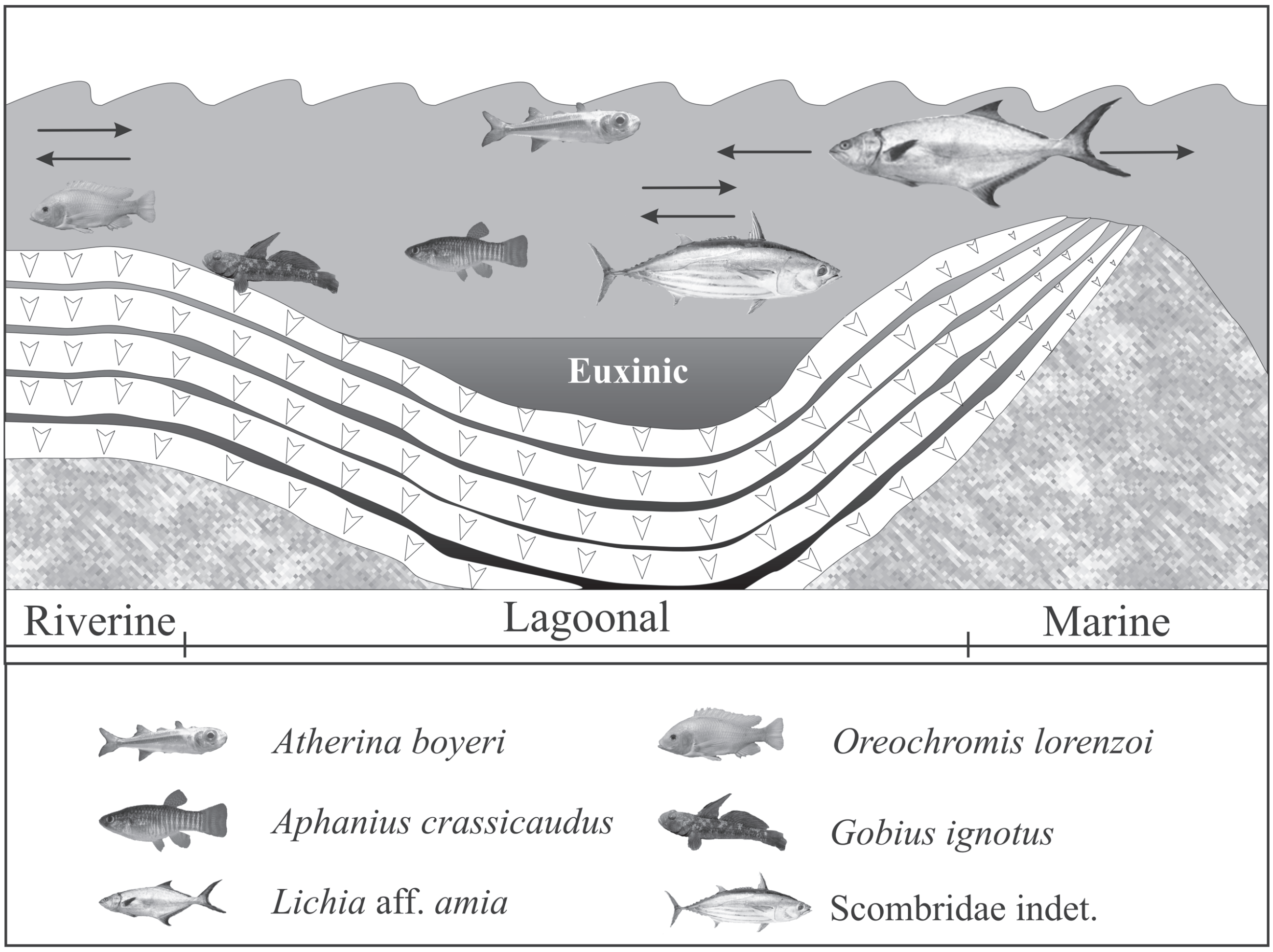

Fig. 3 - Fishes of the Messinian lagoons of the Vena del Gesso basin - hypothetical reconstruction of the palaeoenvironment.

availability, unfavourable environmental conditions often characterized these lagoons during the deposition of the sapropel layers; the low taxonomic diversity and the consequent extremely simplified food web probably reflected the broad fluctuations of the many interacting physical and chemical factors that usually determine the structure of fish communities.

CONCLUSIONS

The leerfish remains presented herein are strongly informative because of the extremely low rate of osteological change that characterized this taxon at least in the last six million years. The detailed ecological knowledge of extant relatives of this taxon can provide a number of data, which are independent from those derived directly from the analysis of the fossil (e.g., taphonomy, functional morphology) and its matrix (stratigraphy, sedimentology, geochemistry, etc.). Because of its ecological constraints, the leerfish and its associated ichthyofauna are therefore adding precise indications on the palaeogeographical configuration and palaeoenvironmental conditions of the Vena del Gesso marginal basin during the deposition of the primary evaporites. The composition of the overall fish assemblage point to a coastal lagoon periodically connected to the sea through moderately deep channels as the original depositional environment. The oligotypic character of the fish assemblage seems to be related to the physically unstable conditions of the waterbody. The leerfish represented a top predator in the coastal lagoons of the Vena del Gesso basin, in which it probably entered opportunistically, attracted by the abundant food resources available. These lagoons were strongly influenced by waters of continental origin, which received periodic pulses of oceanic recharge.

The marine influences evocated by the presence of the leerfish unequivocally indicates that open marine conditions with normal surface salinity occurred close to the coastal lagoons of the Vena del Gesso basin during the deposition of the primary evaporites succession. The repetitive occurrence of marine fish taxa in the clayey and/or sapropelitic interstrata of the primary evaporites of many localities of the Mediterranean region (see e.g., Landini & Sorbini, 1989) necessarily implies that normal marine waters continuously persisted in the Mediterranean basin at least in the course of such a period, as it is very difficult to justify the occurrence of periodic inputs of seawater which included the reestablishment of the complete marine biota. Evidences of the persistence of normal marine waters during the lower part of the Messinian Salinity Crisis event have been extensively presented in many palaeontological studies (e.g., Butler et al., 1996; Bertini et al., 1998; Néraudeau et al., 2001; Braga et al., 2006), even if this hypothesis has not been commonly accepted (see e.g., Rouchy & Caruso, 2006). As a final note, it should be noted that even though waters characterized by normal marine salinity certainly persisted during the deposition of the primary evaporites, at the same time a biological crisis related to a strong palaeoenvironmental deterioration (wide development of stratified anoxic waters) was recorded in some sectors of the Mediterranean (Manzi et al., 2007).

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