Paratethyan ostracods in the Spanish Lago-Mare: More evidence for interbasinal exchange at high Mediterranean sea level

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A B S T R A C T

A gigantic cascade of Atlantic waters, filling the deep desiccated Mediterranean basin at the beginning of the Pliocene, has commonly been envisaged to end the Messinian Salinity Crisis (MSC). The Mediterranean lowstand during its final "Lago-Mare" phase, however, has long been subject to major controversy and has recently been seriously questioned again. Here, we present high-resolution ostracod distribution patterns of the MSC successions in the Black Sea basin (Zheleznyi Rog section; Russia) and the Mediterranean (Cuevas del Almanzora section; Spain) to study the origin and migration history of the Lago-Mare ostracods. We conclude that two major phases of faunal migration have taken place in the Messinian. The first phase corresponds to the Maeotian–Pontian boundary interval (~6.1–6.0 Ma) of the Paratethys, where mainly Pannonian species suddenly invaded the Black Sea region. The second migration event corresponds to the Lago-Mare phase of the Mediterranean when first (5.55–5.47 Ma) some opportunistic taxa (species of *Cyprideis* and *Loxoconcha* genera) and then (5.40–5.33 Ma) a more diverse assemblage of Paratethyan species occupied the entire Mediterranean region. The Spanish ostracod assemblages show a high percentage of Paratethyan (Pontian) ostracods, in agreement with previously studied Italian Lago-Mare sections. The similar palaeoenvironmental changes that developed roughly synchronously in the western and central Mediterranean marginal basins provide more evidence for intrabasinal exchange at high water level during the final stage of the Lago-Mare phase. This indicates that the Mediterranean in the latest Messinian was full of water (comparable to the present Caspian Sea) and that the Zanclean deluge, if happened, only surged some tens, up to few hundred metres, into the Mediterranean.

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1. Introduction

The catastrophic flooding of a largely desiccated Mediterranean Sea at the beginning of the Pliocene is arguably one of the most spectacular events of Earth's history. The so-called Zanclean deluge is often pictured as a gigantic waterfall (McKenzie, 1999), or an enormous rapid (Garcia-Castellanos et al., 2009), eroding its way downward into a >1500 m deep desiccated Mediterranean basin that was isolated from the Atlantic during the final phase of the Messinian Salinity Crisis (MSC). The main arguments for such a large sea level drop come from onshore canyons (Clauzon, 1973) and offshore seismic profiles showing a major subaerial erosional surface that is traceable from the Mediterranean margins to the deepest basins (e.g. Lofi et al., 2005, 2011). Numerical models indicate that the complete re-filling of the Mediterranean could take place within a short period of several thousands of years to only a few months (e.g. Meijer and Krijgsman, 2005). Starting from a Mediterranean base level below −2000 m, it was demonstrated that

this Zanclean flooding may even have involved peak rates of sea level rise of more than 10 m per day (Garcia-Castellanos et al., 2009).

The evoked Mediterranean lowstand is, however, subject to serious debate (e.g. Roveri et al., 2014a, 2014b, 2014c). Strontium isotope (^{87}Sr/^{86}Sr) values from latest Messinian marginal deposits of the Mediterranean indicate the existence of possibly interconnected lacustrine "Lago-Mare" (Lake Sea) basins (McCulloch and De Deckker, 1989; Flecker and Ellam, 2006; Grossi et al., 2015). Sections in the Apenninic foredeep show no sign of major water level lowering (Roveri et al., 2001; Manzi et al., 2005). Continuous Atlantic–Mediterranean connectivity throughout the Messinian, implying no Mediterranean water level drop below the level of the Atlantic Ocean, is also considered based on the presence of marine fish in the latest Messinian deposits (Carnevale et al., 2006, 2008).

2. The Lago-Mare conundrum of the Mediterranean

The Lago-Mare unit (Ruggieri, 1967) developed during the final phase of the MSC (Stage 3: 5.55–5.33 Ma sensu Roveri et al., 2014a) when the Mediterranean was inferred to have been disconnected

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from the Atlantic Ocean (Hsü et al., 1973). The transition from hypersaline evaporitic facies (gypsum and halite) to fresh-brackish Lago-Mare facies implies a huge hydrological change in the region. Earliest explanations are that fresh water dilution had taken place through capture of Paratethys waters (the former Black Sea domain) by headward erosion and canyon cutting, causing the invasion of caspi-brackish faunas into the semi-desiccated Mediterranean basin (Cita et al., 1978). Paleogeographic reconstructions of the Paratethys and Aegean domains, however, suggested that no (significant) gateway existed between the two regions and that only ephemeral marine incursions took place in the Eastern Paratethys during the Mio–Pliocene period (Stevanovic et al., 1989; Popov et al., 2006). This led to a different explanation stating that widespread Lago-Mare environments are mainly the result of regional fresh water dilution (Orszag-Sperber, 2006), while Parathethyan taxa could have migrated into the Mediterranean through the air by birds (Benson et al., 1991). Passive dispersal by aquatic birds is also put forward to explain the ostracod assemblages of Paratethyan origin in the late Tortonian of some Italian basins (Gliozzi et al., 2007; Ligios et al., 2012). Deposition of Lago-Mare facies was suddenly terminated by the opening of the Strait of Gibraltar leading to a synchronous return of fully marine conditions at the base of the Pliocene (5.33 Ma), and to the ending of the MSC (Garcia-Castellanos et al., 2009).

Serious controversy still exists whether the Lago-Mare facies formed in various disconnected subbasins in a deep desiccated Mediterranean or in a basin-wide lake system at high base level (Orszag-Sperber, 2006; Roveri et al., 2014a). The great variability of Lago-Mare-type sediments in the Mediterranean region suggests that sedimentation did not take place in a homogeneous basin, but merely in separated subbasins and strongly dependent on regional conditions (e.g. (Ryan, 2009). However, detailed studies on the Lago-Mare sequences in the Northern Apennines (p-ev1 and p-ev2 sensu Roveri et al., 2008b), Sicily (Upper Evaporites; Manzi et al., 2009), and eastern Spain (Omodeo Salé et al., 2012) allow cyclostratigraphic correlations on a precessional (~20 ka) scale and show similar hydrological variations, which suggest that palaeoenvironmental changes took place Mediterranean-wide at high water level.

Ostracods and mollusks of Paratethyan affinity, indicative of fresh-brackish conditions, are decisive palaeoenvironmental indicators for Lago-Mare evolution (Gliozzi, 1999; Esu, 2007; Grossi et al., 2008; Cosentino et al., 2012). Some of these Paratethyan ostracods migrated all over the Mediterranean and even reached the westernmost and easternmost parts of the basin at the final stage of the MSC (Carbonnel, 1978; Bassetti et al., 2006; Guerra-Merchán et al., 2010; Faranda et al., 2013). Nevertheless, both a largely desiccated and a relatively full Mediterranean are envisaged, based on the ostracod assemblages of multiple Mediterranean sections. Detailed palaeoenvironmental analysis, taking the entire ostracod assemblages into account, show that the various basins behaved in different ways until the last precessional cycle below the Zanclean flooding (Grossi et al., 2008). Only the final cycle shows a general trend towards freshening, indicating that all basins were interconnected in the latest Lago-Mare (Grossi et al., 2008).

A major problem to solve this Lago-Mare water level conundrum was the lack of detailed biostratigraphic analyses in the Paratethys domain, together with poor age control and the use of different taxonomic concepts. Recently, magnetobiostratigraphic time frames have been constructed for the Messinian sedimentary sequences of the Dacian and Black Sea basins (Vasiliev et al., 2004, 2005, 2011; Stoica et al., 2007, 2013; Krijgsman et al., 2010), which provide crucial age control for the Paratethyan ostracod assemblages and their Messinian migration events. Geochemical analyses on these Black Sea sediments showed that Paratethys–Mediterranean connectivity existed, at least throughout the first evaporitic phase of the MSC (Vasiliev et al., 2013), although the exact location of the gateway remained unclear (Krijgsman et al., 2010).

Detailed palaeontological analyses of Paratethyan and Mediterranean ostracod assemblages may resolve the origin of the Lago-Mare fauna and could distinguish between a largely desiccated and a relatively full Mediterranean prior to the Pliocene flooding. Comparable changes in the ostracod assemblages of shallow marginal basins would indicate that the Mediterranean margins were connected at high sea level, to account for the similar changes in palaeoenvironmental conditions. A deep desiccated Mediterranean with multiple isolated lakes would most likely result in different ostracod assemblages, as each basin will obtain its unique palaeoenvironmental conditions depending on local geological setting and regional hydrological budget.

3. Studied sections of the Black Sea and western Mediterranean

We established high-resolution ostracod distribution patterns for the late Messinian (~6.3–5.6 Ma) of the Black Sea Basin (Zheleznyi Rog section; Russia) and a marginal Lago-Mare section (5.4–5.3 Ma) in the western Mediterranean (Cuevas del Almanzora section; eastern Spain) (Fig. 1). Comparing the Spanish ostracod assemblages with those of the Paratethyan basins and the well-studied Italian successions will allow a better understanding of the pattern and mechanism of migration.

The Zheleznyi Rog section is located on the Taman Peninsula (Russia; Figs. 1, 2a) and comprises one of the most intensely studied Late Miocene sedimentary successions of the Black Sea basin (e.g. Popov et al., 2006; Radionova et al., 2012). The Pontian part of the succession is composed of a regular alternation of grey-marls and whitish diatomite layers, topped by a characteristic reddish layer of oolithic sandstone (Fig. 2a; Krijgsman et al., 2010). The section has been dated by magnetostratigraphy coupled with biostratigraphy (ostracods, mollusks, and foraminifera) and $^{40}Ar/^{39}Ar$ dating (Vasiliev et al., 2011). It comprises the well-documented Pontian transgression, dated at ~6 Ma, which is marked by a short marine influx (Krijgsman et al., 2010; Stoica et al., 2013), followed by the sudden migration of mainly Pannonian (Central European) species into the Black Sea, passing through the Dacian basin (Popov et al., 2006; Grothe et al., 2014).

The Cuevas del Almanzora section is located in the Vera Basin (eastern Spain; Figs. 1, 2b) and received a lot of attention in the last century because of its alleged marine continuity across the Mio–Pliocene boundary (Montenat et al., 1976). The presence of an interval with autochtonous caspi-brackish ostracods showed that marine sedimentation was interrupted in the latest Messinian (Cita et al., 1980). The brackish water unit was first interpreted to be of local origin without stratigraphic importance (Benson and Rakic-El Bied, 1991), but later proven to correspond to the Lago-Mare facies of the MSC (Fortuin et al., 1995). An inconspicuous erosional surface, represented by a minor scour with mudstone breccia at its base, was observed between the Lago-Mare unit and the basal Pliocene (Fortuin et al., 1995). Our present study focuses on the 12 m of varicoloured laminated marly clays resembling the Lago-Mare facies.

4. Late Miocene ostracod biostratigraphy

We analysed 61 samples of Zheleznyi Rog and 15 samples of the Cuevas del Almanzora section for ostracod distribution patterns. Samples were processed by standard micropalaeontological methods, using a 63 μm sieve and hand-picking under a microscope. Ostracod species are semi-quantitatively analysed and displayed in stratigraphic order. We follow the same taxonomic concept as in the previous work on sections in the Dacian Basin of Romania (Stoica et al., 2013). The results from the Russian section can directly be compared to the lower-middle Pontian ostracod assemblages of the Ramnicu Sarat and Badislava sections in the Dacian Basin (Floroiu et al., 2011; Stoica et al., 2013). The ostracod species are illustrated by SEM pictures obtained with a Phillips XL30 electro-scanning microscope from the Utrecht University. The key species of the Mediterranean section are shown in parallel with their Paratethys equivalents (from Zheleznyi Rog and Ramnicu Sarat: Plates 1–7).
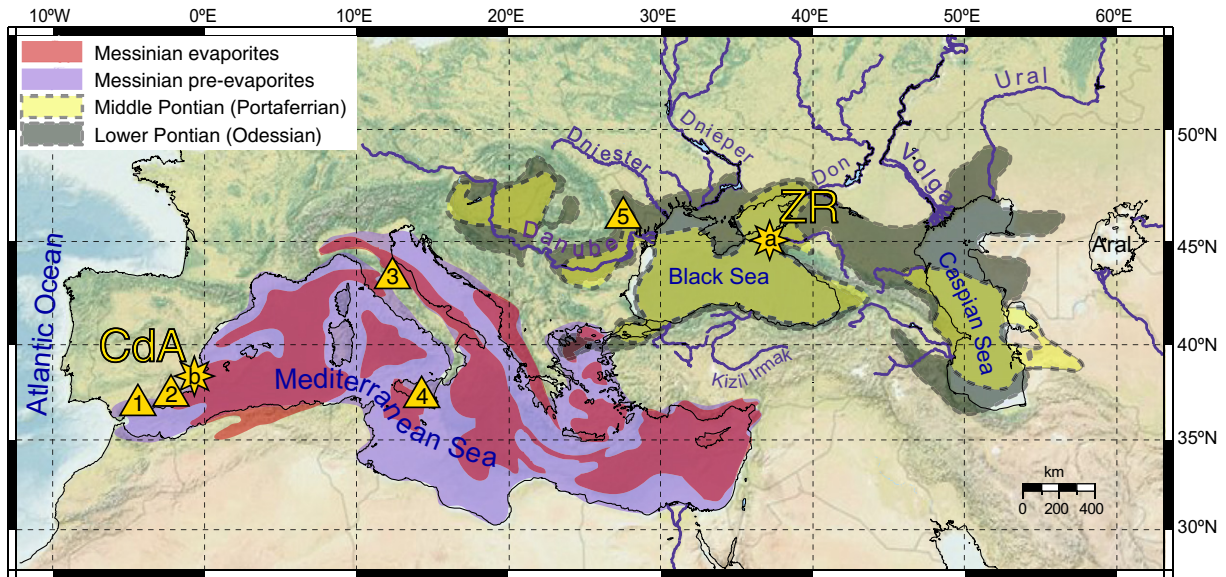
Fig. 1. Schematic palaeogeographic map of the Mediterranean and Paratethys during the Messinian (modified after Vasiliev et al., 2013). Location of studied sections a) Zheleznyi Rog on the Taman peninsula of the Russian Black Sea margin and b) Cuevas del Almanzora in the Vera Basin of the Spanish Mediterranean margin. 1–6 show other localities mentioned along the text: 1. Malaga Basin; 2. Nijar Basin; 3. Northern Apennines; 4. Eraclea Minoa; 5. Ramnicu Sarat.
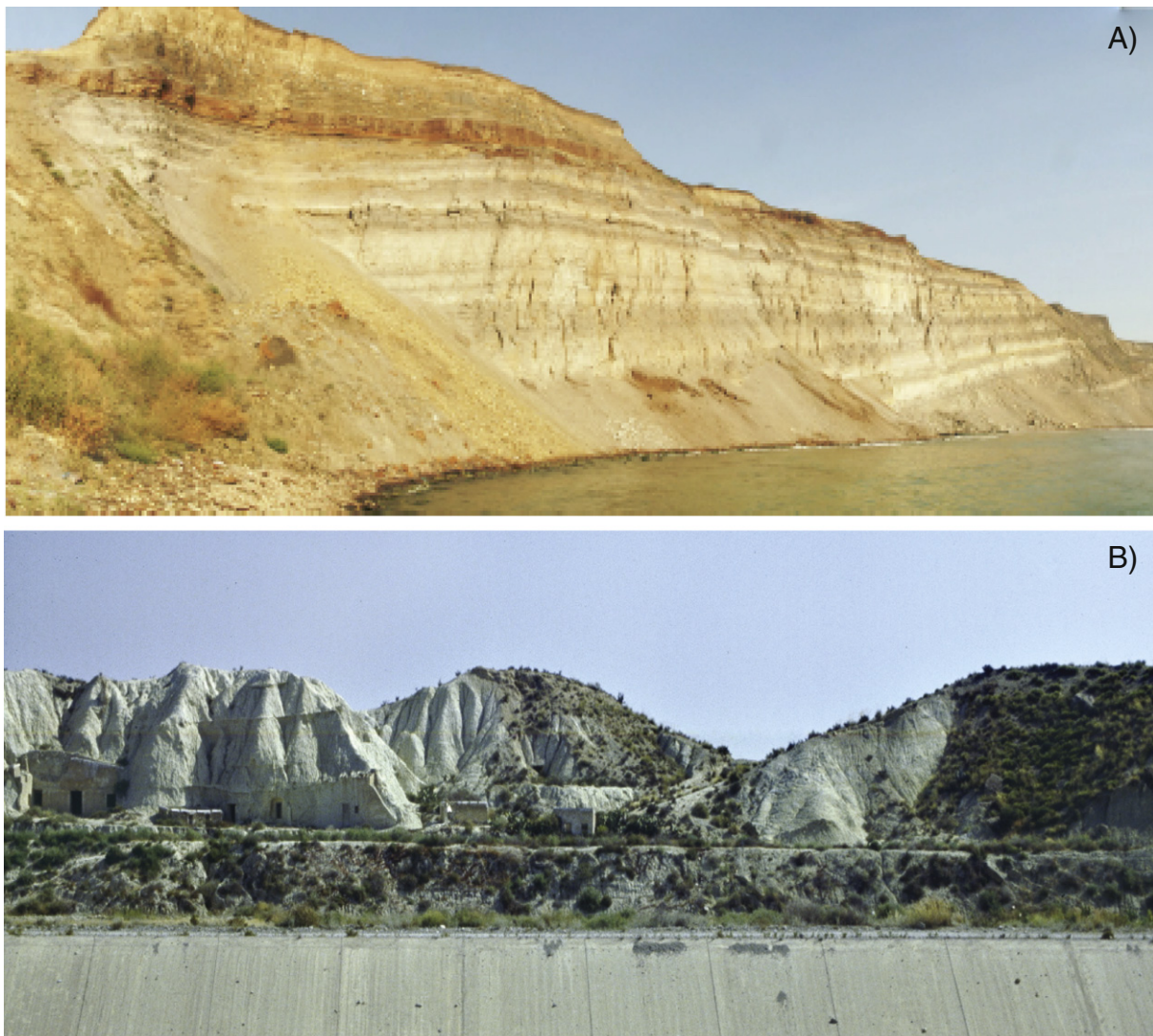

Fig. 2. Photographs of the studied sections: A) Zheleznyi Rog (Russia) of the Black Sea and B) Cuevas del Almanzora (Spain) of the Mediterranean.

Micropalaeontological analyses of the Zheleznyi Rog section provides a rich and well-preserved ostracod faunal record. Most of these ostracod species have previously been described and figured using hand drawings that produced a lot of taxonomic confusion (Livental, 1929; Svejer, 1949; Suzin, 1956; Mandelstam and Schneider, 1963; Agalarova, 1967; Vekua, 1975). Detailed taxonomic descriptions of the Paratethyan ostracods are beyond the scope of this paper, but different concepts and nomenclature should be properly discussed and explained in the nearby future.

The upper Maeotian ostracod assemblages of Zheleznyi Rog comprise mainly endemic ostracods indicative of fresh to brackish water conditions. In the latest part of the Maeotian, the fauna is dominated by Leptocyteridae (*Leptocythere* ex. gr. *crebra*, *L. sulakensis*) as well as *Loxoconcha kochi*, *Eucypris sp.* and *Amnicythere sp.* (Fig. 3). The euryhaline *Cyprideis* genus is represented in all associations by *Cyprideis sp. 1*.

A major palaeoenvironmental change takes place at the Maeotian–Pontian transition in most, if not all, basins of the Eastern Paratethys (Stoica et al., 2013; Grothe et al., 2014). A marine flooding event, characterised by the presence of foraminifera and calcareous nannofossils (Krijgsman et al., 2010; Radionova et al., 2012), first creates anoxic conditions, exemplified by an interval barren of ostracods (Fig. 3). Shortly after, the palaeoenvironmental conditions change to brackish well-oxygenated water environments, which is accompanied by a massive invasion of Pannonian ostracod species into the Black Sea
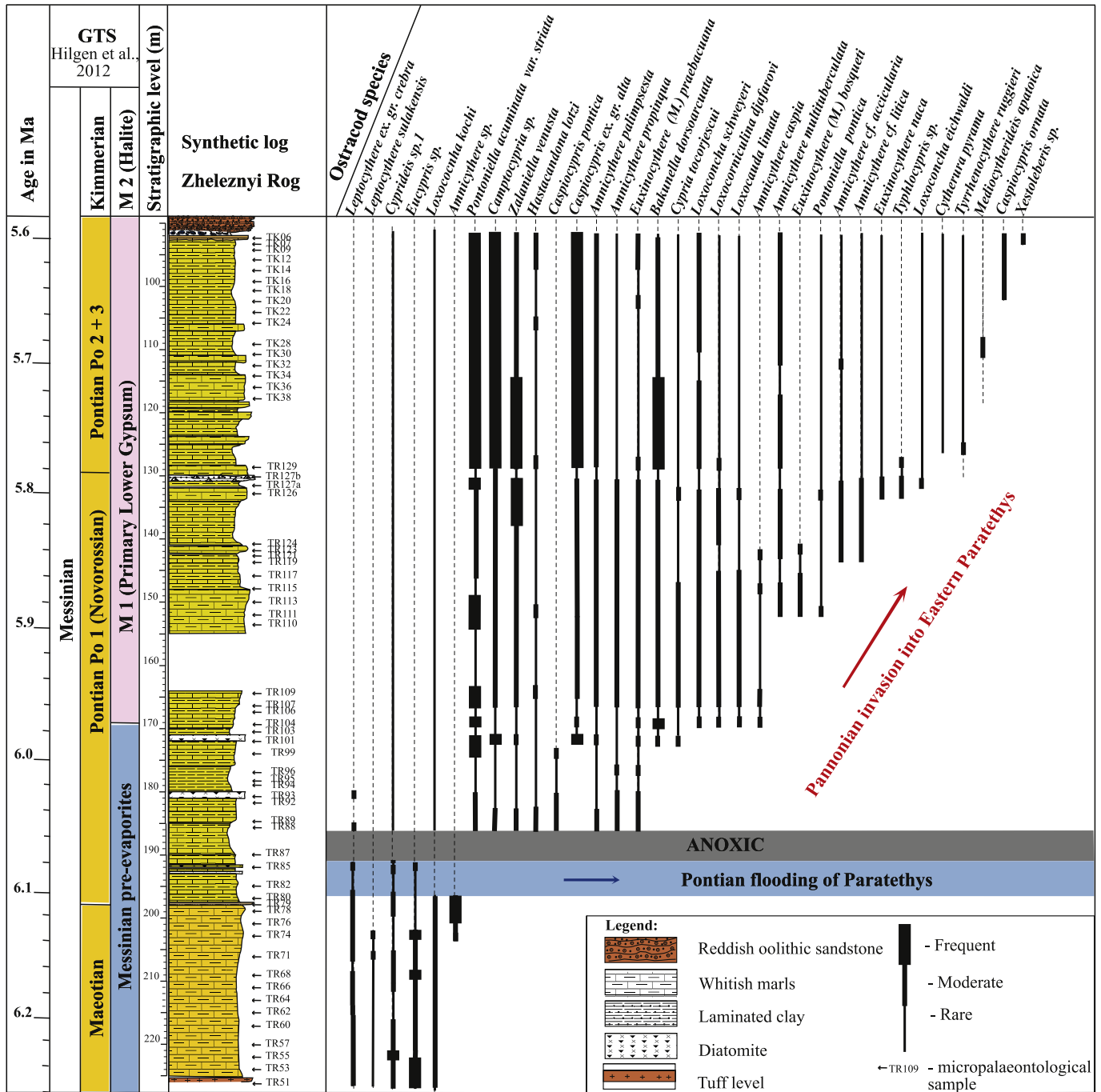

Fig. 3. Ostracod distribution patterns of the Zheleznyi Rog section (Russia). Geological Time Scale (GTS) on the left is according to Hilgen et al. (2012) with Krijgsman et al. (2010) for the Paratethys and Roveri et al. (2014a) for the Mediterranean Messinian. The Maeotian–Pontian transition is marked by an inflow of marine waters followed by anoxia and an invasion of Pannonian ostracods in the Black Sea, when brackish conditions had stabilised again.

(Fig. 3). No foraminifera are found above the anoxic interval, probably because the connection with the marine domain was not strong enough to sustain marine conditions. In Zheleznyi Rog, but also in sections from the Dacian and Caspian basins, the Pontian starts with a level rich in pyritized ostracod shells, with especially Candonidae like *Caspiocypris pontica*, *Hastacandona lotzi*, *Pontionella acuminata var striata*, *Zalaniella venusta*, and *Camptocypria* sp.

Upwards in the Pontian, ostracod biodiversity gradually increases towards the end of regional subzone Po1 at ~130 m, corresponding to the Novorossian substage (e.g. Popov et al., 2006). This interval corresponds to a marked geochemical change in the deuterium record and indicates a transition to more extreme palaeoenvironmental conditions (Vasiliev et al., 2013). Most common ostracods representing the Pontian of Taman are Leptocyderidae species like *Amnicythere propinqua*, *A. palimpsesta*, *A. multituberculata*, *A. litica*, *A. caspia*, *A.* cf. *accicularia*, *Euxinocythere naca*, *Euxinocythere* (*Maeotocythere*) *bosqueti*, *E.* (*M.*) *praebaquana*, as well frequent individuals of *Bakunella dorsoarcuata*, *Loxocorniculina djafarovi*, *Loxoconcha eichwaldi*, *L. schweyeri*, *L. kochi*, *Loxocauda limata*, *Mediocytherideis apatoica*, and *Pontionella pontica*. Surprisingly, the *Tyrrhenocythere* genus is rare (only some specimens of *T. ruggieri*) and *Amplocypris* genera have no representatives in this section. The uppermost part of the section is characterised by a lower

diversity ostracod assemblage, but some taxa are present in large numbers (e.g. species of *Pontoniella*, *Camptocypria*, *Caspiocypris*, and *Bakunella*; Fig. 3).

The overlying "Red Level," rich in iron oxides, is considered Kimmerian in Russian literature, but the ostracod assemblages indicate that it is correlative to the middle Pontian (Portaferrian) of the Dacian Basin (Fig. 3). The basal part of the Kimmerian succession, directly above the "Red Level," is characterised by brackish water environment (Krijgsman et al., 2010; Chang et al., 2014), and ostracods are very rare.

Our results from Cuevas del Amanzora show that the lower part of the section predominantly contains an oligotypic population of *Cyprideis* species. There are at least two species of *Cyprideis*, *C. sp. 1* (that may refer to *C. agrigentina*) and *C. sp. 2* (which is very similar to *C. anlavauxensis*) associated with *Loxoconcha kochi* (Fig. 4). The *Cyprideis* species are shallow, strongly euryhaline, ostracods capable to survive in fresh water to hypersaline conditions (Benson, 1978). These two species seem to have similar representatives in Parathethys successions, but due to the different taxonomic concepts, they are regarded as *C. pannonica* and *C. torosa*. Another possibility is that, after its appearance in the latest Oligocene–earliest Miocene of Germany (Malz and Triebel, 1970), during the Late Miocene, the genus *Cyprideis* underwent two different adaptive radiations in the Mediterranean and Parathethys, giving origin
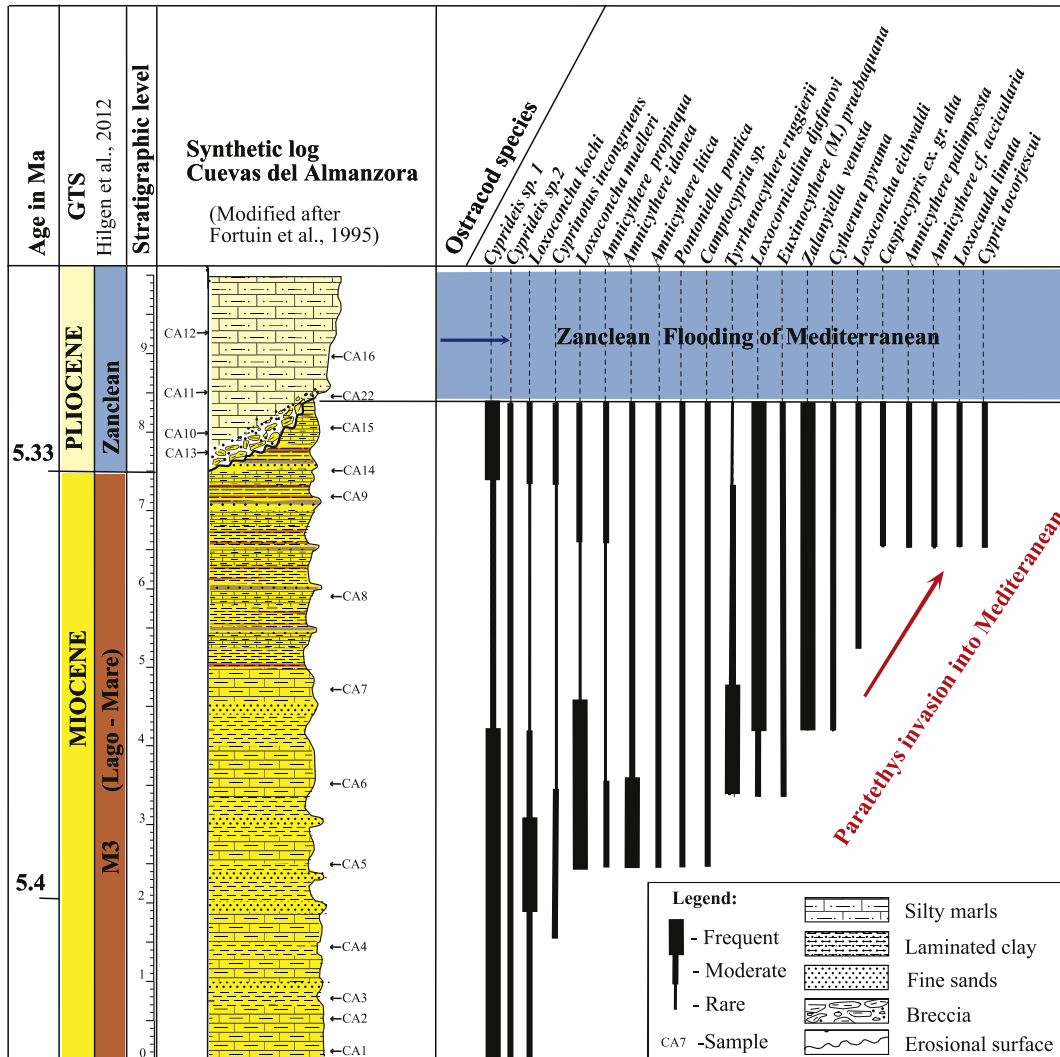

Fig. 4. Ostracod distribution patterns of the Cuevas del Almanzora section (Spain). Geological Time Scale on the left is according to Hilgen et al. (2012) and Roveri et al. (2014a). The Lago-Mare unit is marked by a biodiversity change in ostracods, which is also observed in Italian and Cretan successions. Note that 17 out of the 21 ostracod species are also present in the Black Sea record of Zheleznyi Rog.

to different endemic species flocks (Decima, 1964; Krstić, 1968a, 1968b; Van Harten, 1975; Bassiouni, 1979; Van Harten, 1980a, 1980b, 1990; Ligios and Gliozzi, 2012). The taxonomy of *Cyprideis* species is still controversial, mainly because the euryhaline conditions they live in generally cause increased environmental pressure that produce environmentally cued polymorphism and needs further studies. *Loxoconcha kochi* and *Loxoconcha muelleri* are previously described from the Upper Miocene of the Pannonian basin. *L. muelleri* is not very common in the Dacian and Black Sea basins, being recorded so far in the early Maeotian of the Dacian Basin only.

The upper part of the Cuevas del Almanzora section is marked by a change in biodiversity with the presence of numerous species of the *Loxocorniculina djafarovi* assemblage (Fig. 4, Plates 1–7), indicating brackish hyposaline environments (Bonaduce and Sgarrella, 1999; Gliozzi et al., 2007; Grossi et al., 2008). *Loxocorniculina djafarovi* (Plate 7) is recorded in Upper Miocene successions of the Pannonian (Krstič, 1972; Olteanu, 1989a; Sokač, 1989; Pipik in Cziczer et al., 2009), and Dacian, Black Sea, and Caspian basins (Schneider, 1949; Agalarova et al., 1961; Agalarova, 1967; Vekua, 1975; Olteanu, 1989b, 1999). Together with *L. djafarovi*, some other Paratethyan ostracods appear in the upper part of the section. The Candonidae group is represented by *Camptocypria* sp. (named in many papers as *Caspiolla*), *Caspiocypris* ex. gr. *alta*, *Pontoniella pontica*, *Zalanyella venusta* (frequently recorded in the Eastern Paratethys as *Caspiolla venusta*). Leptocytheridae like *Amnicythere propinqua* (often named as *A. cymbula*), *A.* cf. *accicularia*, *A. palimpsesta*, *A. idonea*, *A. litica*, and *Euxinocythere* (*Maeotocythere*) *praebaquana* are also well represented. *Amnicythere idonea* has many similarities with *A. litica* and the two species can easily be confused. The Loxoconchidae, beside the already

mentioned species, include *Loxoconcha eichwaldi* and *Loxocauda limata*. Less abundant taxa are *Cyprinotus incongruens*, *Cypria tocorjescui*, and *Cytherura pyrama*. The presence of *Tyrrhenocythere ruggierii*, especially in the lower part of the section, is also noteworthy. This taxa is not mentioned very often in the Paratethys area, although some species of the Dacian basin show close similarities (e.g. *Tyrrhenocythere dacicum* Olteanu). (See Plates 1–6.)

We conclude that the main differences between the Mediterranean Lago-Mare and the Paratethyan Pontian ostracod assemblages are mostly artificial, and in many cases related to different taxonomic concepts. By harmonising the taxonomical aspects, we show that the Cuevas del Almanzora section has most of its species (~80%) in common with the section from the Black Sea, indicating similar palaeoenvironmental (salinity, alkalinity) conditions. Four species recorded in the Spanish Lago-Mare (*Cyprideis sp.2*, *Cyprinotus incongruens*, *Loxoconcha muelleri*, and *Amnicythere idonea*) are not observed in the Zheleznyi Rog section, but they have been described in Paratethys before in sections of the Dacian and Caspian basins.

The lower part of the section contains a less diverse ostracod assemblage, where the main taxa are represented by *Cyprideis* spp. and *Loxoconcha kochi*, and therefore can be correlated to the lower post-evaporitic interval of the MSC in Italian sections (Grossi et al, 2011). The upper part of the section shows a more diverse ostracod assemblage of Paratethyan origin and can be considered as equivalent of *Loxocorniculina djafarovi* Zone (Carbonnel, 1978), corresponding to the upper post-evaporitic interval in Italy (Grossi et al., 2011). The Miocene–Pliocene ostracod assemblages of the Paratethys have not been classified into ostracod biozones.

Plates 1–7. Lago-Mare ostracods (**LM**) from SE Spain, Vera Basin (Cuevas del Almanzora section) and Paratehtys ostracods (**PA**) from N Black Sea (Zheleznyi Rog section, Taman-Russia,) and Dacian Basin (Romania) (LV-left valve, RV-right valve, CA, TR, TK, PU-micropalaeontological sample).(see on page 860)

Plate 1. 1–4. Camptocypria sp. (1,2. Vera Basin; 3, 4. Zheleznyi Rog), 1. LV, external view, CA6; 2. RV, external view, CA9; 3. LV, external view, TR111; 4. RV, external view, TR 111. **5–10. Zalanyiella venusta** (Zalányi), (5–7,Vera Basin; 8–9. Zheleznyi Rog); 5. LV, external view, CA 9; 6. RV, external view, CA8; 7. RV, internal view, CA 8; 8. RV, external view, TR107; 9. RV, external view, TR 107; 10. RV, internal view, TR107. **11, 12. Caspiocypris ex. gr. alta** (Zalányi); 11. RV, external view, CA 9, Vera Basin; 12. RV, external view, TR124, Zheleznyi Rog. (see on page 860)

Plate 2. 1, 2. Cyprinotus incongruens (Ramdohr), Vera Basin; 1. LV, external view, CA4; 2. LV, internal view, CA. 3, 4. **Pontoniella pontica** Agalarova; 3. RV, external view, CA9, Vera Basin; 4. RV, external view, TR111. **5–11. Cyprideis sp. 1**, mentioned as *Cyprideis agrigentina* Decima in the Lago-Mare or as *C. pannonica* (Méhes) and *C. torosa* (Jones) in Paratethys (5–8, Vera Basin; 9–11, Dacian Basin–Badislava section); 5. LV, external view, CA3; 6. RV, external view, CA4; 7. carapace, dorsal view, CA4; 8. carapace, ventral view, CA4; 9. LV, external view; 10,11, RV, external views. (see on page 861)

Plate 3. 1–4. Cyprideis sp. 2, mentioned as *Cyprideis anlavauxensis* Carbonel in the Lago-Mare (all specimens from Vera Basin); 1. LV, external view, CA4; 2. RV, external view, CA9; RV, external view, A1 juvenile, CA3; 4. RV, external view, A2 juvenile, CA8. **5–9. Tyrrhenocythere cf. ruggierii** Devoto (5–7, Vera basin; 8,9, Dacian Basin, Toplog section); 5. LV, external view, CA6; 6. carapace, view from RV, CA6; 7. RV, internal view, CA6; 8. LV, external view; 9. RV, external view. (see on page 862)

Plate 4. 1–11. Amnicythere propinqua (Livental), described also as *A. cymbula* (Livental) (1–7, Vera Basin; 8–11, Dacian Basin, Badislava section); 1. LV, external view, female, CA5; 2. RV, external view, female, CA5; 3. LV, external view, male, CA9; 4. RV, external view, male, CA5; 5. LV, internal view, female, CA5; 6. RV, internal view, male, CA5; 7. carapace, ventral view, CA5; 8. LV, external view, female; 9. LV, external view, male; 10. RV, external view, female; 11. RV, internal view, female; **12–18. Amnicythere cf. accicularia** (Olteanu) (12–16, Vera Basin; 17–18, Zheleznyi Rog); 12. LV, external view, CA8; 13. carapace, view from the RV, CA6; 14. carapace, view from the LV, CA9; 15. LV, external view, female, CA9; 16. carapace, dorsal view, CA9; 18. RV, external view, female, TR 117; 19. carapace, dorsal view, TR 117. **19–24. Euxinocythere (Maeotocytyhere) praebaquana** (Livental) (19–23, Vera Basin; 23–24, Zheleznyi Rog); 19. LV, external view, female, CA6; 20. RV, external view, female, CA6; 21. RV, external view, female, CA6; 22. RV, external view, male, CA9; 23. carapace, dorsal view, female, CA6; 24. LV, external view, female, TR 88; 25. RV, external view, female, TR 88; 26. carapace, dorsal view, female, TR 88. (see on page 863)

Plate 5. 1–6. Amnicythere idonea Mandelstam, Markova, Rozyeva and Stepanajtys (Vera Basin); 1. LV, external view, CA5; 2. RV, external view, female, CA5; 3. RV, external view, female, CA5; 4. 19. carapace, view from RV, female, CA6; 5. RV, external view, male, CA7; 6. RV, internal view, male, CA7. **7, 8. Amnicythere litica** (Livental) (Vera Basin); 7. LV, external view, CA9; 8. RV, external view, CA8; **9–11. Amnicythere cf. litica** (Zheleznyi Rog); 9. LV, external view, TYR 124; 10. RV, external view, TR 124; 11. RV, external view, TR 129. **12–19. Amnicythere palimpsesta** (Livental) (12–17, Vera Basin; 18, 19, Zheleznyi Rog); 12. LV, external view, male, CA9; 13. carapace, view from RV, female, CA9; 14. LV, external view, male, CA9; 15. carapace, view from RV, CA9; 16. LV, external view, female, CA9; 17. RV, external view, female, CA9; 18. RV, external view, TR 88; 19. RV, external view, TR 88. (see on page 864)

Plate 6. 1–9. Loxoconcha muelleri (Méhes) (1–6, Vera Basin; 7–9, Dacian Basin, Putna section); 1. LV, external view, female, CA5; 2. RV, external view, female, CA5; 3. RV, external view, male, CA5; 4. RV, external view, male, CA5; 5. RV, internal view, female; 6. LV, internal view, male, CA6; 7, 8. LV, external views, PU 59; 9. carapace, view from the RV, PU59. **10–17. Loxoconcha eichwaldi** Livental (10–14, Vera Basin; 15–17, Zheleznyi Rog); 10. LV, external view, male, CA9; 11, 13. RV, external views, females, CA8; 12. RV, external view, male, CA9; 14. carapace, ventral view, CA9; 15. LV, external view, TR 93; 16. RV, external view, TR 93; 17. LV, internal view, TR 93. (see on page 865)

Plate 7. 1–11. Loxocorniculina djafarovi (Schneider) (1–8, Vera Basin; 9–11, Zheleznyi Rog); 1. LV, external view, CA6; 2. RV, external view, CA6; 3. LV, external view, male, CA6; 4. RV, external view, CA6; 5. RV, internal view, male, CA6; 6. LV, internal view, CA6; 7. carapace, ventral view, CA6; 8. carapace, dorsal view, CA6; 9. LV, external view, TR 109; 10. RV, external view, TR 109; 11. LV, dorsal view, TR 109. **12–16. Loxoconcha kochi** Méhes (12–14, Vera Basin; 15,16, Zheleznyi Rog); 12. LV, external view, CA5; 13. RV, external view, CA5; 14. carapace, ventral view, CA5; 15, 16. LV, external views, TH 28; **17–19. Loxocauda limata** (Schneider in Agalarova) (17, 18, Vera Basin; 19, Zheleznyi Rog); 17, 18. RV, external views, CA9; 19. RV, external view, TR 104; **20–22. Cytherura pyrama** (Schneider) (20, 21, Vera Basin; 22, Zheleznyi Rog); 20. LV, external view, female, CA7; 21. LV, external view, male, CA8; 22. RV, external view, female. (see on page 866)
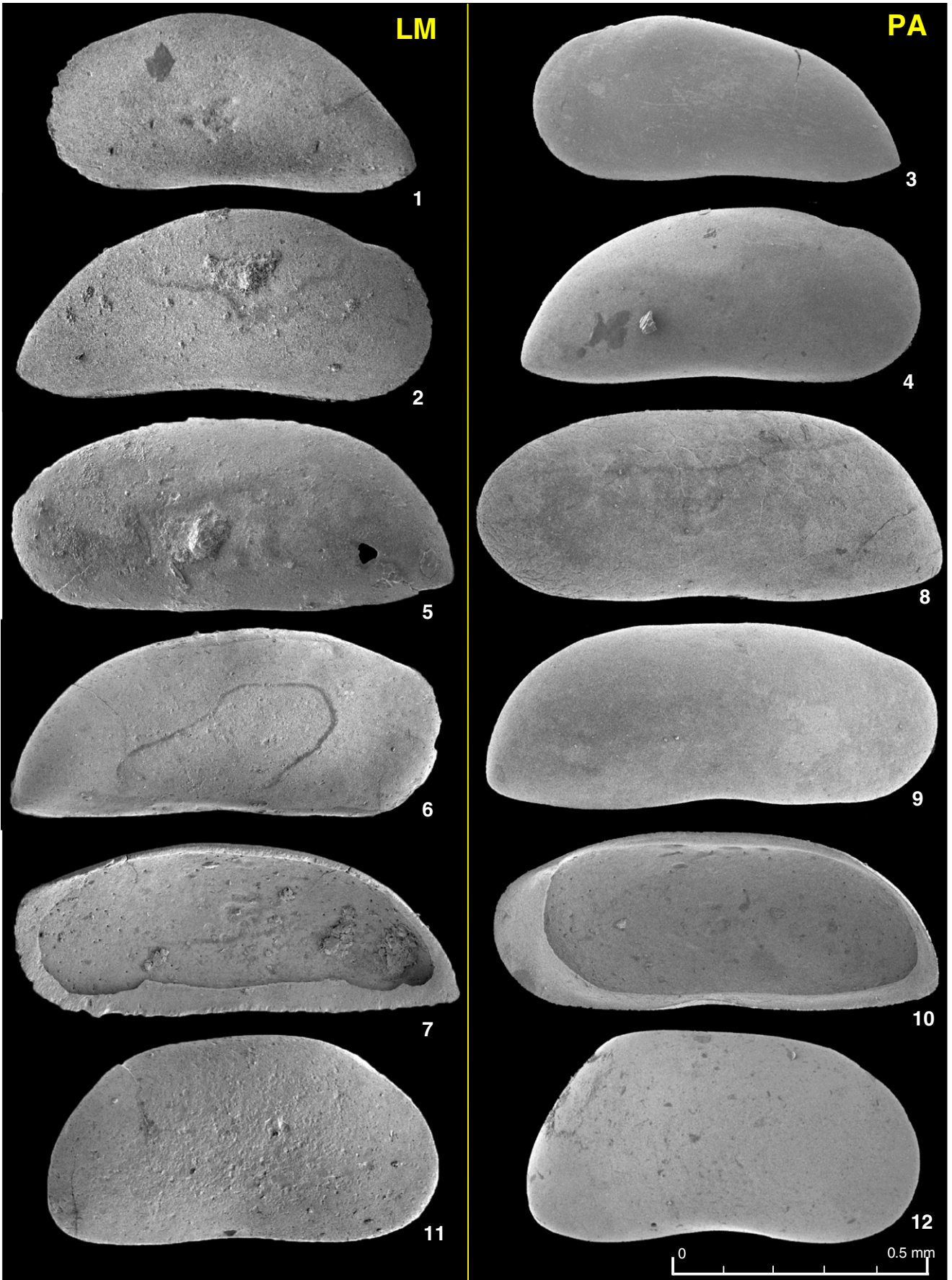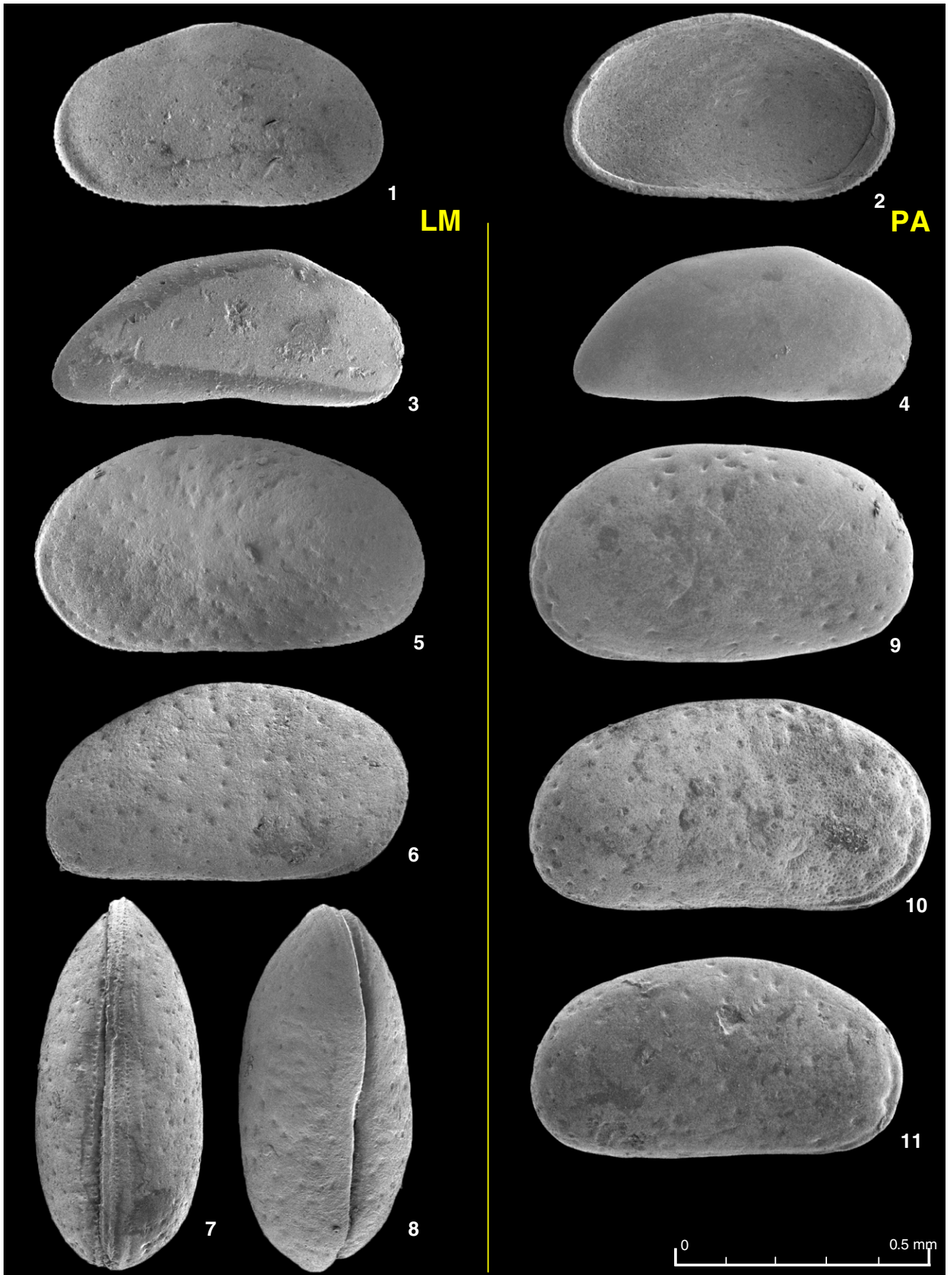
Plate 1 *(caption on page 859).*
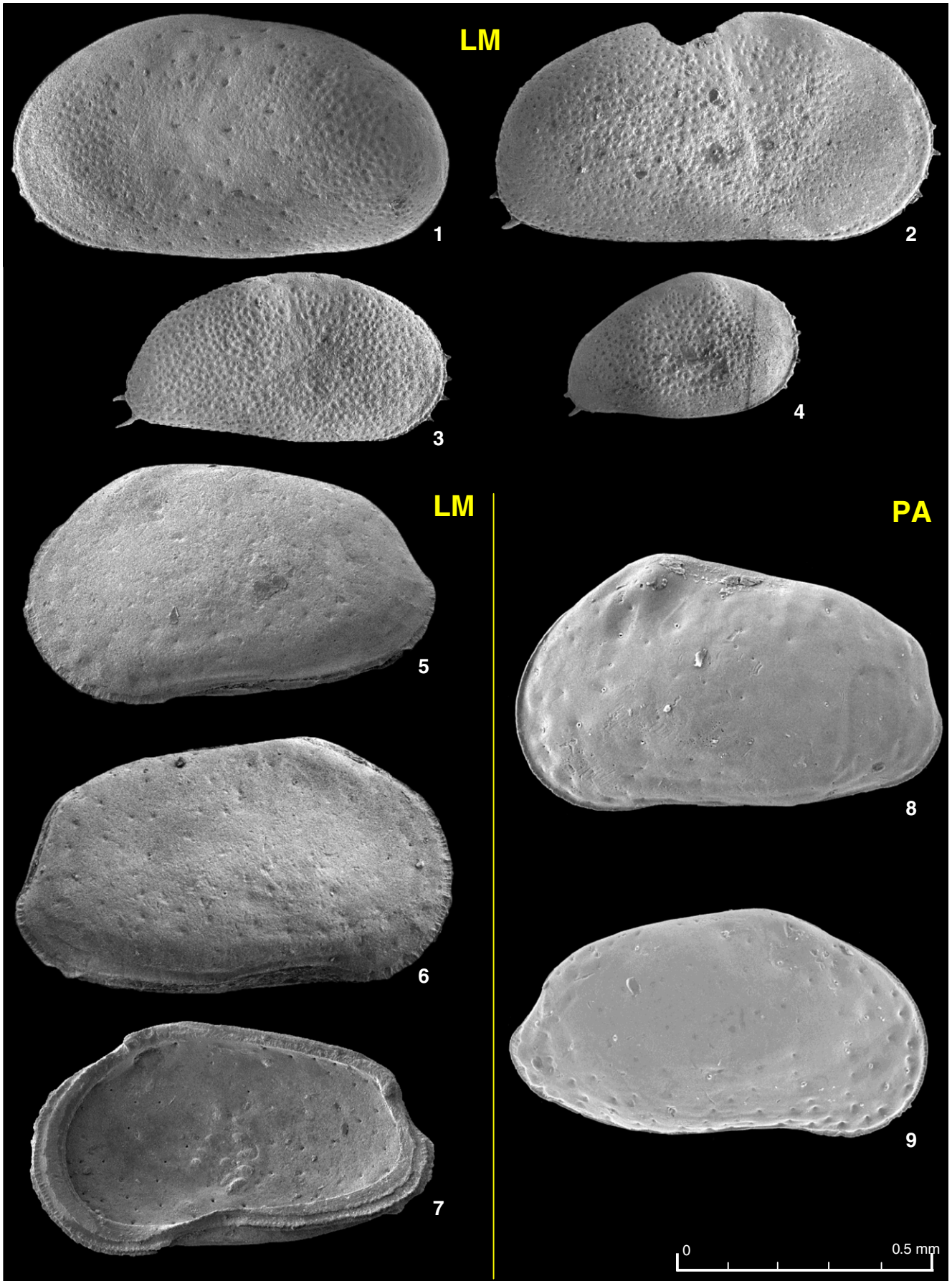
Plate 2 *(caption on page 859).*

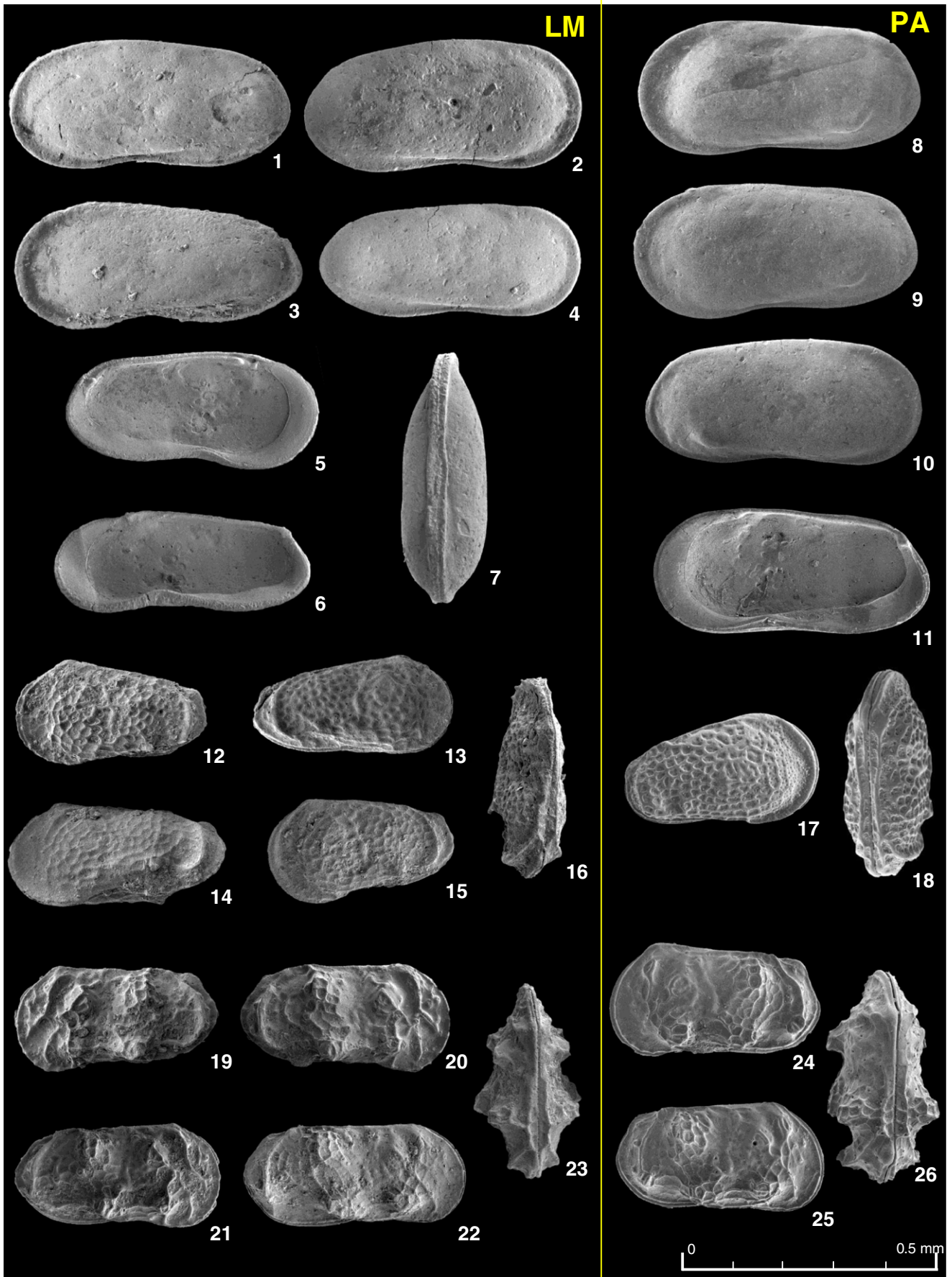**Plate 3.** *(caption on page 859).*

Plate 4. *(caption on page 859).*
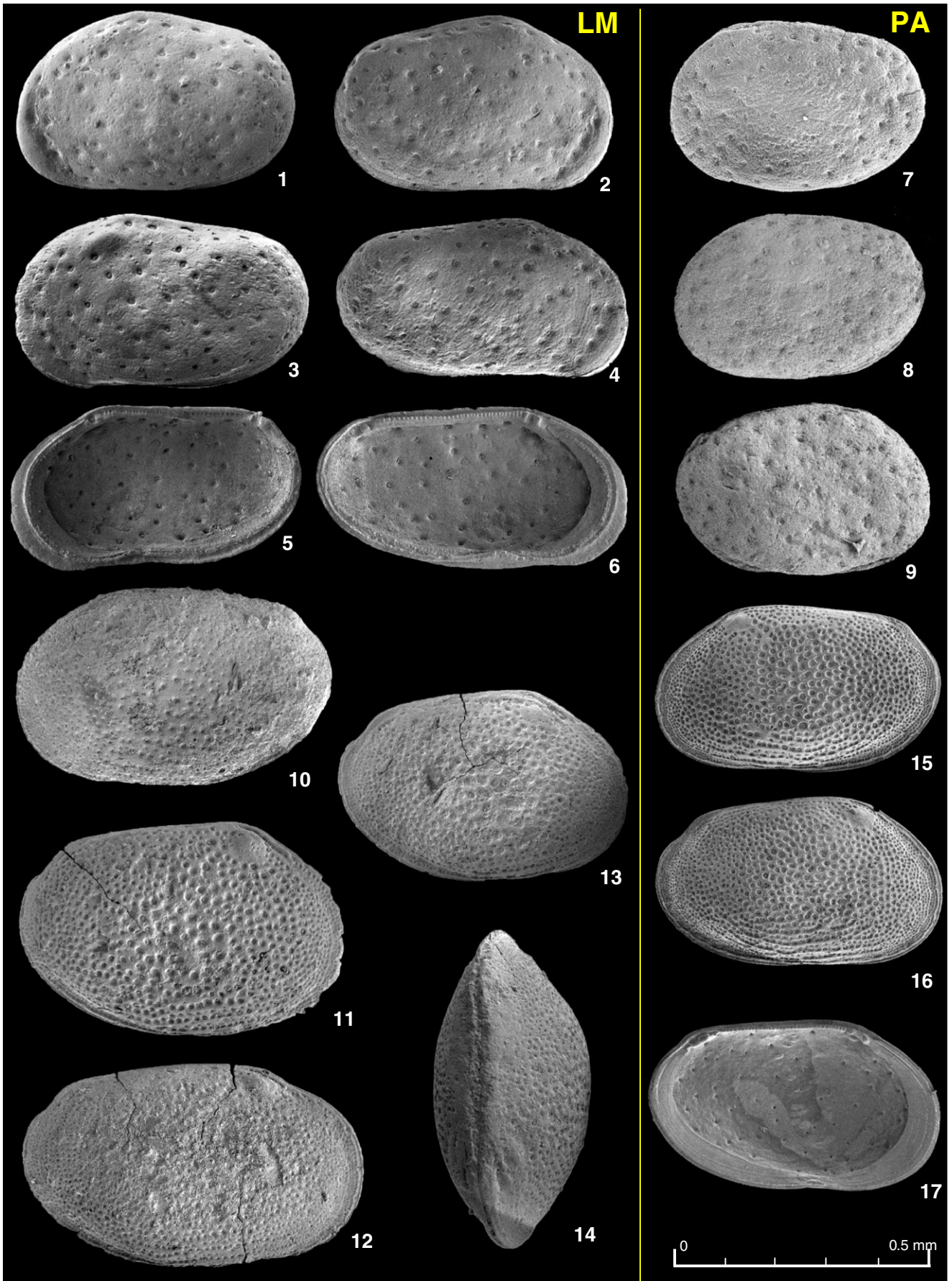
Plate 5. *(caption on page 859).*

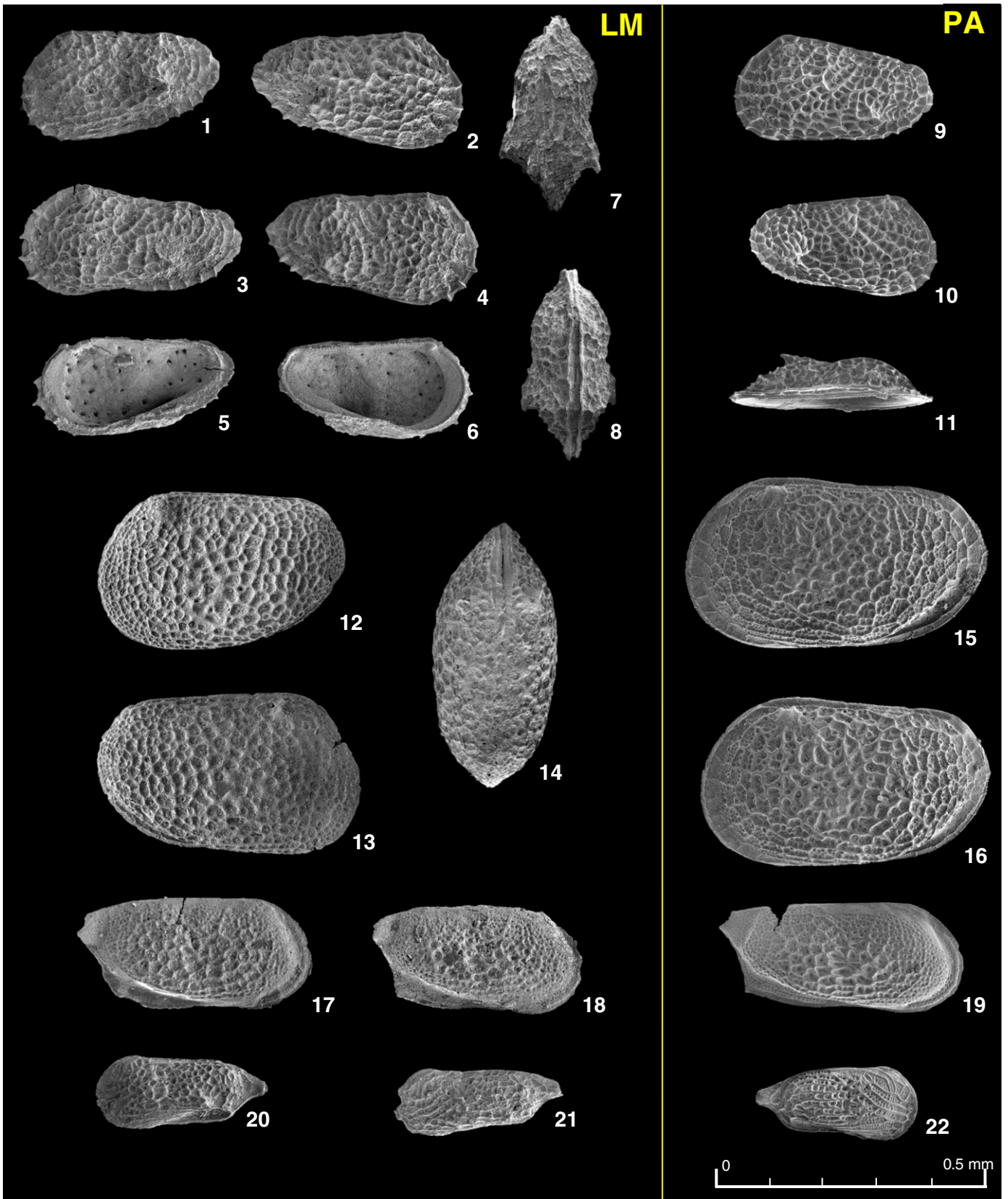**Plate 6.** *(caption on page 859).*

Plate 7.   *(caption on page 859).*

5. Paratethys–Mediterranean migration patterns

The first phase of ostracod migration corresponds to the Maeotian–Pontian boundary interval (~6.1–6.0 Ma) in the Paratethys, where mainly Pannonian (Hungary) species suddenly invaded the Black Sea region (Fig. 3). This event has previously been documented in sections of the Dacian basin of Romania, which is located between the Pannonian basin and the Black Sea (Krijgsman et al., 2010; Stoica et al., 2013). The
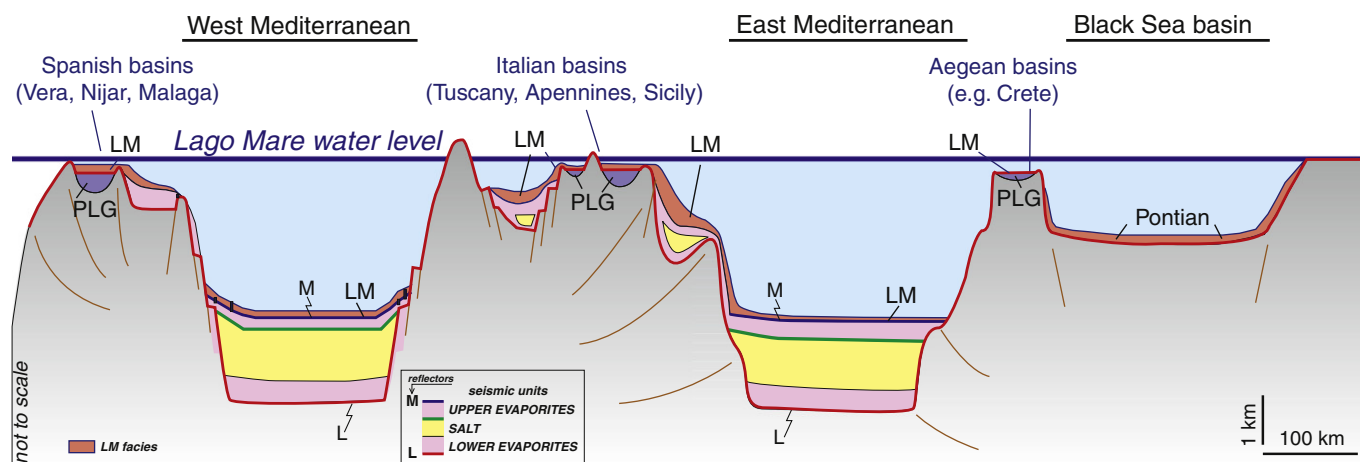
Fig. 5. Distribution of Messinian evaporites and Lago-Mare deposits in the Mediterranean and Paratethys areas along a schematic cross-section (modified after Roveri et al., 2014a). In orange (LM), the areas where Lago-Mare deposits have been observed. These deposits are commonly found on the shallow Mediterranean margins (and in cores of the deep basin settings) which is an additional argument that the Lago-Mare water level must have been significantly high at the final phase of the Messinian Salinity Crisis, just prior to the Pliocene flooding. LM, Lago-Mare; PLG, Primary Lower Gypsum.

Pontian migration event in the Black Sea has also been documented in other faunal elements, such as mollusks (Stevanovic et al., 1989; Popov et al., 2006) and dinoflagellates (Grothe et al., 2014). In addition, a marine nannofossil influx, comprising assemblages that are correlative to Subzone NN11b, has been reported from the Maeotian–Pontian boundary interval in the Dacian Basin (Marunteanu and Papaianopol, 1998). This proves that a marine connection was established between Paratethys and Mediterranean at the Maeotian–Pontian transition level. Organic geochemistry data from Zheleznyi Rog shows the continuous presence of marine alkenones in the Pontian of the Black Sea, which is interpreted to be the result of persistent connectivity with the Mediterranean (Vasiliev et al., 2013). All this implies that the Black Sea basin was connected to the Mediterranean during the entire Pontian Stage (of the Black Sea), which is roughly the time equivalent of the first stage of the MSC, during which the Primary Lower Gypsum was deposited in the Mediterranean (Roveri et al., 2014a). The fact that the Mediterranean experienced highly evaporative conditions during this time interval is probably the main reason why no Paratethyan ostracods are known to migrate towards the Mediterranean at this stage.

The second migration event corresponds to the Lago-Mare phase (5.55–5.33 Ma) of the Mediterranean when first some opportunistic ostracods (*Cyprideis* and *Loxoconcha*) and then a more diverse assemblage of Paratethyan species occupied the entire Mediterranean region. The Mediterranean may have experienced its peak lowstand at the end of halite deposition related to glacial cycles TG12 and 14 (Hilgen et al., 2007; Krijgsman and Meijer, 2008) or only TG12 (Cosentino et al., 2013; Speranza et al., 2013), when the Mediterranean became further restricted, or completely isolated, from the Atlantic. During the Lago-Mare stage, its waters became progressively diluted by fresh waters from Africa and the Paratethys. Consequently, the most opportunistic species from the Paratethys (*Cyprideis* and *Loxoconcha*) could invade the Mediterranean, as these species can also sustain highly saline water conditions. When the Paratethys basin had a positive hydrological budget, it continued to drain fresh or low-brackish water into the Mediterranean. Because the global climate changed to warmer and wetter conditions during the Lago-Mare phase, the positive hydrologic contribution of the African rivers and the Paratethys may have substantially risen the Mediterranean water level so decreasing the salinity of the surface waters to conditions favourable for the Paratehyan ostracods to massively invade the Mediterranean (Gladstone et al., 2007; Krijgsman et al., 2010).

6. Comparison with other Mediterranean ostracod records

The results from Cuevas del Almanzora are in good agreement with earlier ostracod analyses of the Los Feos Formation in the Nijar Basin of southern Spain (Fig. 5; Bassetti et al., 2006). In this section, a similar change from *Cyprideis* and *Loxoconcha* dominated assemblages towards more biodiverse ostracod assemblages is observed in the middle of cycle VI, corresponding to an astronomical age of ~5.4 Ma (Hilgen et al., 2007). The sedimentary cyclicity of this section is considered to be precessionally forced (Fortuin and Krijgsman, 2003; Omodeo Salé et al., 2012) and indicates repeatedly fluctuating Mediterranean water levels during the Lago-Mare event. Mediterranean sea level must have been high enough to invade the marginal Spanish basins (Fig. 5), which have an approximate water depth of ~200 m (Krijgsman et al., 2006). The first shallow marine Pliocene deposits are observed above the lowstand interval of the last depositional cycle, indicating that the Zanclean flooding took place during a period of relatively low water levels (Fortuin and Krijgsman, 2003).

Detailed ostracod studies on sections and boreholes from Italy and France also showed assemblages with a high percentage of species of Paratethyan affinity (Carbonnel, 1978; Bonaduce and Sgarrella, 1999; Cipollari et al., 1999a, 1999b; Iaccarino and Bossio, 1999; Bassetti et al., 2003; Ferrandini et al., 2004; Gliozzi and Grossi, 2004, 2008; Cosentino et al., 2006, 2012; Gliozzi et al., 2007; Grossi and Gennari, 2008; Grossi et al., 2008, 2015; Iaccarino et al., 2008). High-resolution records from sections in Italy and Greece show that the lower part of the Lago-Mare is characterised by unstable environments and low-diversity ostracod assemblages, while the upper part shows more stable conditions and high-diversity ostracod communities (Cosentino et al., 2007; Gliozzi and Grossi, 2008). Iaccarino and Bossio (1999) subdivided the Lago-Mare interval in a "*Cyprideis* assemblage" and a "*L. djafarovi* assemblage." This eco/biostratigraphic subdivision is also observed in several Italian sections (Iaccarino et al., 1999; Cosentino et al., 2012), and its transition is located above the base of the p-ev2 units of Roveri et al. (1998), astronomically calibrated to an age of 5.40 Ma (Grossi et al., 2011—*Loxoconcha muelleri/Loxocorniculina djafarovi* biozones boundary).

Our results are furthermore in agreement with the data provided by Clauzon et al. (2005), but not with their interpretations. Clauzon et al. (2005) postulate two Lago-Mare influxes in the Mediterranean, one before (isotopic stage 11; top of Stage 1) and one after (isotopic stage 5; Zanclean) the main Messinian desiccation event. Both influxes, however, relate to very ambiguous (see Roveri et al., 2008a) stratigraphic

correlations of the Sicilian Upper Evaporites (influx 1) to MSC Stage 1 and the Colombacci Formation of the Northern Apennines (influx 2) to the Zanclean by Clauzon et al. (2005). These units are commonly both correlated to the MSC Stage 3 deposits (sensu Roveri et al., 2014a), which makes their Lago-Mare ostracod assemblages in excellent agreement with our second, latest Messinian, migration event. More recently, an additional third Lago-Mare influx is proposed (Popescu et al., in press), but this succession of three events lacks stratigraphic consistency and again relates to unbalanced correlations of the MSC units.

7. The myth of the Zanclean deluge

The exact Mediterranean water level during the latest Messinian is considered as one of the remaining key controversies regarding the MSC (CIESM, 2008; Roveri et al., 2014a). The main arguments for a large sea level drop (>1500 m) in the latest Messinian come from offshore seismic profiles showing a major subaerial erosional surface that is traceable from the Mediterranean margins to the deepest basins (Lofi et al., 2005, 2011). In this scenario, all the marginal basins of the Mediterranean are considered as some kind of perched lakes formed under local hydrological conditions during the Lago-Mare phase. It can thus be expected that the water conditions in all these basins also diverge in salinity, alkalinity, and temperature, by consequence hosting different ostracod assemblages.

Probably at the end of the Lago-Mare phase, the Mediterranean was a large lake or sea comparable to the present-day Caspian Sea or Black Sea, depending on whether a marine connection persisted in the Gibraltar region (e.g. Flecker et al., 2015). If the hydrologic budget of the Mediterranean became positive (or less negative) during the final Messinian, it would have led to increased lake levels or even an estuarine configuration. In that case, most of the basins became connected and regional changes in hydrology should be recognised all over the Mediterranean. The distribution of the ostracod assemblages in the Spanish Lago-Mare of the Cuevas del Almanzora section are very similar to the biostratigraphic records of the Northern Apeninnes (Gliozzi et al., 2007) and Crete (Cosentino et al., 2007). The palaeonevironmental changes towards more fresh water conditions recognised in all the basins during the last precessional cycle before the Messinian/Zanclean boundary (Grossi et al., 2008) is in favour of their interconnection at high water level. The distribution of the Lago-Mare facies forms another argument for high water level (Fig. 5), as the second stage of the Lago-Mare is found onlapping at many shallow marginal Mediterranean basins (Malaga, Nijar, Crete, Cyprus) (Bassetti et al., 2006; Guerra-Merchán et al., 2010; Cosentino et al., 2012). Most of the ostracod species are characteristic for shallow water conditions, some are depending on the photic zone, which indicates that their depositional environment is not very deep. Consequently, we conclude that it is most likely that the Mediterranean water level was relatively high during the final phase of the MSC. Our results suggest that the Mediterranean water level could have been only slightly below the level of the Atlantic prior to the Zanclean flooding, implying that previous model experiments have heavily exaggerated the influx of Atlantic water into the Mediterranean (Meijer and Krijgsman, 2005; Krijgsman and Meijer, 2008; Garcia-Castellanos et al., 2009).

Our results cannot solve the question if the Mediterranean ever dried out or not (Manzi et al., 2005). A major sea level fall may have taken place in MSC times at the top of Stage 2, which comprises enough time to explain halite deposition in the deep basins (Hsü et al., 1973) and canyon cutting at the Mediterranean margins (Clauzon, 1973). The seismic studies that favour a major sea level lowstand (Lofi et al., 2005, 2011) mostly refer to the position of the top of the seismic Upper Unit (UU), which is generally considered to correspond to the latest Messinian stage (Roveri et al., 2014a). If this unit, however, corresponds to Stage 2, as suggested by Roveri et al. (2014b), the seismic reflector at the top of UU may in fact correspond to an earlier ~ −1500 lowstand of the Mediterranean water level, possibly generated in the time interval of glacial cycles TG10-12. Alternatively, the erosional features in the seismic profiles may have been formed sub-aqueously by downslope transport of marginal gypsum (de Lange and Krijgsman, 2010) and/or by dense shelf waters (Roveri et al., 2014c).

We consider it likely that a sudden (climatic) change in the Mediterranean's hydrological budget drastically increased the fresh water influx from Africa and Paratethys during the Lago-Mare phase, preventing gypsum formation in most regions and significantly lowering the sedimentation rates in the deep Mediterranean basins. The Lago-Mare unit of the deep basins may well be in the order of 50–100 m thick, which is close to the resolution of seismic interpretation. In addition, it is less characteristic there, because anoxic to suboxic conditions may have prevailed which are unfavourable for Paratethyan fauna. In the seismic profiles, the Lago-Mare may consequently have been confused with the Pliocene, especially since in some cases unreliable biostratigraphic events (especially the dubious nannofossil *Ceratolithus acutus*) are used to determine the Messinian–Zanclean boundary in the deep Mediterranean basins (Clauzon et al., 2005; Popescu et al., in press).

8. Conclusions

We established high-resolution ostracod distribution patterns for the uppermost Maeotian to Pontian interval of the Black Sea basin (6.2–5.5 Ma) and for a Lago-Mare succession of the western Mediterranean. Our results indicate that the Messinian interval is marked by two significant migration events.

1) At ~6 Ma, following the Pontian marine transgression, palaeoenvironmental conditions in the Black Sea gradually change from anoxic to brackish water environments, which is accompanied by an invasion of Pannonian ostracods. Upwards in the Pontian, ostracod biodiversity gradually increases during the regional Novorossian substage, while the uppermost Pontian is characterised by a lower diversity ostracod assemblage. The highly evaporative conditions of the MSC during this time interval likely prevented these ostracods to migrate into the Mediterranaean.

2) At 5.55 Ma, a second migration event corresponds to the Lago-Mare phase (~5.55–5.33 Ma) of the Mediterranean when first some opportunistic species (*Cyprideis* and *Loxoconcha*) and later (5.40 Ma) a more diverse assemblage of Paratethyan species occupied the entire Mediterranean region. The ostracods of the Spanish Lago-Mare predominantly consist of Paratethyan species.

The taxonomical uniformity of ostracod assemblages of the Lago-Mare phase in different Mediterranean areas (Spain to Crete) and the salinity decrease recognised in the studied sections at the end of the MSC are in favour of a common hydrochemical composition of the waterbodies which, near the M/Z boundary, could have possibly been interconnected at high water level. The distribution of the Lago-Mare facies and the presence of many shallow water ostracods implies a rather shallow depositional environment in most of the Mediterranean marginal basins. Consequently, we conclude that it is most likely that the Mediterranean water level was relatively high during the final phase of the MSC.

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