Foraminifers, thecamoebians (Arcellinida) and ostracods in the Late Miocene mammalian site of Venta del Moro (Valencia, Spain)

Journal:	*Historical Biology*
Manuscript ID	GHBI-2021-0267
Manuscript Type:	Original Article
Date Submitted by the Author:	24-Nov-2021
Complete List of Authors:	Guillem, Jordi; Universitat de València, Botànica i Geologia BLÁZQUEZ MORILLA, ANA MARÍA; Universidad Católica de Valencia San Vicente Mártir Facultad de Veterinaria y Ciencias Experimentales Mezquita-Joanes, Francesc; University of Valencia Cavanilles Institute of Biodiversity and Evolutionary Biology Montoya, Plini; Universitat de València, Botànica i Geologia Usera, Juan; Universitat de València, Botànica i Geologia
Keywords:	Foraminifera, Testate amoebae, Ostracoda, Neogene, Palaeolake

SCHOLARONE™
Manuscripts

Foraminifers, thecamoebians (Arcellinida) and ostracods in the Late Miocene mammalian site of Venta del Moro (Valencia, Spain)

Jordi Guillem[1], Ana M. Blázquez[2*] , Francesc Mesquita-Joanes[3], Plini Montoya[1] , Juan Usera[1]
1: Departament de Botànica i Geologia, Universitat de València. Dr. Moliner, 50. 46100 Burjassot (Spain)
2: Environmental and Marine Sciences Research Institute (IMEDMAR), Catholic University of Valencia, Spain. Guillem de Castro, 94. 46003 Valencia (Spain)
3: "Cavanilles" Institute of Biodiversity and Evolutionary Biology, Universitat de València. Catedrático José Beltrán Martínez, 2. 46980 Paterna (Spain)
Jorge.Guillem@uv.es; ana.blazquez@ucv.es* ; francesc.mezquita@uv.es; pmontoya@uv.es; Juan.usera@uv.es
*Corresponding author

Key Words: Foraminifera, Testate amoebae, Ostracoda, Neogene, Palaeolake

Abstract

The Venta del Moro site (Valencia, Spain) is especially known for its rich content in Late Miocene fossil mammals but it also holds other fossil vertebrates, invertebrates and plants. A micropaleontological study of a 70-cm long sedimentary section carried out in the lacustrine beds of the site has yielded 2 foraminifer, 7 thecamoebian and 19 ostracod taxa (two of these last probably new species). A constrained cluster analysis allowed the recognition of three consecutive zones based on their micropalaeontological content. The variation of the microfossil assemblages closely matches lithology and reflects environmental changes in the palaeolake. Anoxic bottom conditions at the base of the sequence (Zone 1) prevented the occurrence of aerobic benthic microorganisms. Later, the appearance of ostracods and thecamoebians (Zone 2) documents the increasing oxygenation of the lake and suggests a permanent freshwater to slightly brackish lake with low temperature and stream influence. The dominance of foraminifers and the changes in the thecamoebian and ostracod assemblages in the upper part of the sequence (Zone 3) reflect more stable and oxygenated conditions and probably increasing temperature and evaporation in oligohaline temporary waters, during the final drying phase of the lake.

For Peer Review Only

Introduction

Venta del Moro (Valencia, Spain) is one of the most extraordinary palaeontological sites in the continental Late Miocene of the Iberian Peninsula (Aguirre et al. 1973; Morales 1984; Montoya et al. 2006; Morales et al. 2013). It is well known for its rich and diverse collection of fossil mammals, but the site also includes fossils of other groups of vertebrates (fish, amphibians, reptiles, birds), invertebrates (bivalves, aquatic and terrestrial gastropods, ostracods) and plants (including pollen, leaf remains, charophytes…) Within the Late Miocene, Venta del Moro has been included in zone MN13 following the biochronology of Mein (1999) and is the reference locality for the Ventian land mammal (see Morales et al. 2013). A detailed magnetostratigraphic study dated the site at 6.23 Ma (Gibert et al. 2013). This situates Venta del Moro slightly after the temporary establishment of the Behring bridge between North America and Asia, near the onset of the Late Messinian Glacial Interval and during the progressive closure of the Betic corridors connecting the Atlantic and the Mediterranean, which eventually would result in the Messinian Salinity Crisis with the partial desiccation of the Mediterranean Sea (Morales et al. 2013). As a consequence, Venta del Moro exhibits a mixing of autochthonous taxa and immigrants from Africa, Asia and Southeast Europe and constitutes a unique document of the mammalian turnover called Second Messinian Mammalian Event (MME-2) or *Paraethomys* Event by Agustí et al. (2006), which corresponds to the Second African-Iberian Dispersal (AFD-2) of Gibert et al. (2013).

The Venta del Moro site was excavated in two periods, between 1970 and 1980 by a team from the “Museo Nacional de Ciencias Naturales” (MNCN-CSIC), and from 1995 to 2012 by a team from the “Universitat de València”. Among the main results of these campaigns, it should be noted that the site constitutes the type locality of nine mammal

For Peer Review Only

species (Morales and Aguirre 1976; Morales 1984; Montoya et al. 2009, 2011; Mansino et al. 2015; Crespo et al. 2018).

During the campaign of 2004, one of the co-authors (P.M.) first noticed the presence of Foraminifera in the Venta del Moro site, when examining samples for micro-mammal analysis under a binocular microscope; additionally, another co-author (F.M.-J.) also observed the occurrence of different ostracod taxa (Montoya et al. 2006). Blázquez et al. (2008) subsequently reported in a brief note the occurrence of different species of calcareous foraminifers, thecamoebians and ostracods in a series of samples retrieved from the site.

Although the Foraminifera constitute primarily a marine group, a few species can tolerate or even thrive in brackish or hypersaline waters. Several authors have already reported the occurrence of calcareous foraminifers in athalassic (non-marine) environments worldwide (e.g. Cann and De Dekker 1981; Boudreau et al. 2001; Wennrich et al. 2007; Flako-Zaritsky et al. 2011) and in the Iberian Peninsula (e.g. Márquez and Usera 1988; Anadón 1992; Usera and Blázquez 1998).

Under the well-known but informal name “thecamoebians” are designated two unrelated groups of testate amoebae (orders Arcellinida and Gromida). Fossil thecamoebians have long been considered as merely sporadic in the geologic record (e.g. Medioli et al. 1990). More recent works regard thecamoebians as an extremely resilient and conservative group with a long stratigraphic range and apparently very little morphological variation through time (e.g. Porter and Knoll 2000; Singh et al. 2015).

The Ostracoda are a small and diverse group of bivalved crustaceans inhabiting almost any type of aquatic environment, from temporary ponds and rivers to the deep sea (Horne et al. 2002). Their carbonate shell has allowed their common use in palaeoecology and palaeogeography as indicators of a variety of environmental variables, mostly water chemistry and temperature (Rodriguez-Lazaro and Ruiz-Muñoz 2012; Mesquita-Joanes et al. 2012).

For Peer Review Only

However, the knowledge of Miocene ostracods in the Iberian Peninsula and the Balearic Islands is very scarce, and mostly related to marine or brackish faunas, with very little insight on freshwater ostracods (e.g. Anadón 1992; Gliozzi et al. 2005; Stoica et al. 2016).

The purpose of the present work is to carry out a more detailed study of these three groups in the fossiliferous beds of Venta del Moro.

Geographical and Geological Setting

The Venta del Moro site (latitude 39.477º N, longitude 1.343º W) is located in an ancient railway trench near the locality of Venta del Moro (Valencia, eastern Spain) (Fig. 1). Geologically it belongs to the Cabriel Basin and is included in the upper section of the detritic Unit of Los Isidros, within the Venta del Moro-Villatoya Formation, according to the stratigraphy described by Robles (1970) for this basin, 50 metres below the top of the aforementioned unit (Mathisen and Morales 1981).

The outcropping series in the trench consists in: a) lacustrine-palustrine deposits, represented by limestones and marls, b) fluvial deposits, represented by sandstones and conglomerates in channel-like beds, and c) flood plain deposits, represented by alternating red clays and sandstones. With an approximate area of 5 x 1.5 km near Venta del Moro, the lacustrine-palustrine deposits have been interpreted as originated in a shallow lacustrine environment with water level fluctuations and anoxic episodes (Mathisen and Morales 1981). These facies are structured in several flooding-stability-drying cycles. The Venta del Moro site is located in lignitiferous marls, marls and marly limestones, in the last of the lacustrine cycles recognized in the series (Montoya et al. 2006).

Four fossiliferous units were distinguished in the Venta del Moro site. They were denominated, from top to bottom (following the excavation order): A, B and C, which laterally become thinner and transform into Unit D, consisting of grey, highly biodetritic,

For Peer Review Only

sandy marls (Fig. 2). Starting from the base of the series, Unit C is composed by black coloured lignitiferous marls. The transition between Units C and B (BC) is gradual and characterized by a high concentration of gastropod shells. Units A and B constitute in fact a single sedimentary bed of marls, with a dark and detritic base (Unit B) that becomes lighter and more enriched in calcium carbonate towards the top (Unit A). The transition between them (AB) is also gradual and rich in gastropod shells. As for the lacustrine cycle, units C and B represent a stability phase, Unit A is related to the final infilling and drying stages, and Unit D is interpreted as a marginal, more energetic and oxygenated facies, colonized by unionid bivalves, very abundant in this bed (Montoya et al. 2006).

Methods

During the 2005 excavation campaign, units A, B and the top section of C were sampled for their micropalaeontological study, in order to analyze their possible content in foraminifers, thecamoebians and ostracods. A 70 cm-long sediment succession was sampled in intervals of 5 cm, thus yielding 15 samples named as VVf-1 to VVf-15 (Fig. 3a). Table 1 shows the correspondence between samples and lithologic beds. The sampling site was carefully cleaned and approximately 10 x 10 cm blocks of sediment were extracted by digging in the beds in order to obtain non-weathered samples. Subsamples of the extracted blocks of sediment in each sample were weighed and washed through sieves of three different pore sizes (>400, >125 and >63 μm). The residue retained on the sieves was subsequently dried under hot lamps, weighed and stored in paper bags. Dried samples (14–64 g weight) were then examined under a binocular microscope; foraminiferal and thecamoebian tests and ostracod valves were picked up, taxonomically identified and fixed to micropalaeontological slides. Additionally, fish otoliths were also recovered and counted. When necessary, samples with very abundant microfossils were split. Abundances were expressed as the number of

For Peer Review Only

individual tests (ind./g) or ostracod valves per gram of dry sediment. The taxonomic identification of thecamoebians was mainly based on Ogden and Hedley (1980). Ostracod identification followed mostly Meisch (2000) and Fuhrmann (2012). Selected specimens were photographed under a Scanning Electron Microscope (SEM) Hitachi S4800 at the Servei de Microscopia Electrònica (SCSIE) of the Universitat de València. A constrained cluster analysis was applied to the species density data using the UPGMA method and the Bray-Curtis distance, in order to establish stratigraphically consecutive zones, by means of the software PAST v. 4.04 (Hammer et al. 2001).

Results

Figure 3b illustrates the density variation of Foraminifera, thecamoebians, and Ostracoda along the studied interval. Figure 4 details individual taxa variation of foraminifers and thecamoebians (Fig. 4a) and ostracods (Fig. 4b) together with fish otoliths and the 3 constrained cluster zones, with Zones 2 and 3 each subdivided in two subzones (see also Table 1).

Foraminifers

With the exception of a single dubious specimen in sample VVf-5, no Foraminifera were found in the lower half of the studied section; the first unequivocal foraminiferal tests were recorded in sample VVf-9, being only abundant in Zone 3 of the sequence, corresponding to bed A and transition bed AB. Although extremely low initially (<1 ind./g in sample VVf-9), the density of Foraminifera rapidly increases upwards, first exceeding 10 ind./g in sample VVf-12 and reaching a peak of >125 ind./g in the topmost sample VVf-15 (Figure 3b).

For Peer Review Only

All foraminifer tests found are calcareous; no agglutinated specimens have been detected, and all are reduced in size, collected from the smallest size fraction analyzed (63–125 μm). Almost all identified foraminifers belong to a single species: *Paraphysalidia paralica* Guillem and Usera, 2012 (Figs. 5a-b), which represents 97–100% of the total assemblage in all the examined samples (Fig. 4a).

Apart from a few unidentified individuals in the upper part of the section, the only foraminifer besides *P. paralica* identified in Venta del Moro is *Spirillina* sp. (Figs. 5c-d). This taxon has been detected only in the two uppermost samples VVf-14 and VVf-15 with a very low density, never exceeding 3 ind./g (Fig. 4a). All specimens are very small and in their initial growth stage.

Thecamoebians

Up to seven thecamoebian taxa (order Arcellinida) have been found in the studied samples (Fig. 4a). Due to their relatively poor preservation state some of the specimens have been left in open nomenclature. No thecamoebian tests have been found in the basal samples VVf-1 to VVf-3 (Zone 1 and lowermost Zone 2) and they are extremely scarce in the middle portion of the studied series (Zone 2), never exceeding 1 ind./g between VVf-4 and VVf-10. However, a notable increase is recorded in the upper part (Zone 3, VVf-11 to VVf-15) with a peak of 7.5 ind./g in sample VVf-13 (Figs. 3b and 4a).

Throughout the studied section, the thecamoebian assemblage is predominantly constituted by non-spinose centropyxid specimens, with *Centropyxis aculeata* (Ehrenberg, 1830) (Figs. 5e-f) as the most abundant species and *Centropyxis constricta* (Ehrenberg, 1841) (Figs. 5g-h) as a secondary taxon. Diflugiids, mainly represented by *Difflugia globulosa* Dujardin, 1837 (Figs. 5i-j) and *Difflugia* sp. (Figs. 5k-l) are also relatively abundant and may attain up to 40% of the total assemblage (Fig 4a).

For Peer Review Only

Ostracods

Ostracods are absent in the bottommost part (Zone 1, samples VVf-1 and VVf-2) and relatively rare (~0.3–1.2 valves/g) in the lower half of the series (Zone 2). A rapid increase starts in sample VVf-10 and peaks (>10 valves/g) in sample VVf-11 (Subzone 3.1), followed by a declining trend upwards (Subzone 3.2). In the uppermost part of the series, the density of ostracods falls again under 1 valve/g (Figs. 3b and 4b). All the species found are typical inhabitants of freshwaters, summing up to 19 different taxa. SEM images of selected specimens are shown in Figures 6 and 7. The most common species through the sequence are two candonids: *Neglecandona* cf. *neglecta* (Sars, 1887) (Fig. 6i) and *Candona* cf. *candida* (O.F. Müller, 1776) (Fig. 6j). The presence of two undescribed species is remarkable, including another candonid, *Trapezicandona* n. sp. (Figs. 7a-d) and a darwinulid belonging to the genus *Microdarwinula* (Figs. 6b-d). Another common species through the sequence is *Ilyocypris gibba* (Ramdohr, 1808) (Figs. 6g-h), mostly appearing with tubercles on the valves (forma *gibba*). The circum-Mediterranean species *Cypris bispinosa* Lucas, 1849 (Fig. 7g) is present only as remains of its lateral spines and mostly occurs at the top of the sequence, in Subzone 3.2 (Fig. 4b).

Discussion

There is relatively good correspondence between lithology and the microfossil assemblages. The lignitiferous marls that constitute the lowermost interval (Unit C) are indicative of anoxic conditions, which presumably prevented the occurrence of benthic organisms, and correspond to the barren Zone 1. The first appearances of ostracods (VVf-3) and thecamoebians (VVf-4) in the transition to Unit B (dark grey marls) document the increase of oxygen concentration in the bottom waters of the ancient lake, although the

For Peer Review Only

abundance of both groups remains low throughout Unit B (≈ Zone 2). Another environmental shift, in the limit between Zones 2 and 3, is reflected by the first appearance of the calcareous foraminifer *P. paralica* (VVf-9) and the strong increase in abundance of ostracods (VVf-10), and thecamoebians (VVf-11), which coincide with the lithologic transition from Unit B to the lighter marls of Unit A (Table 1).

The ostracod assemblage at the first half of the sequence (Zone 2) is dominated by two candonids, *Neglecandona* cf. *neglecta* and *Candona* cf. *candida.* The uncertainty in the identification is related to the fact that most valves found belonged to juvenile individuals and to the high diversity of similar species in the European Neogene (Krstić 1972). The association of these two species in Quaternary sediments and recent environments of European freshwater lakes is common (Griffiths 1995; Meisch 2000), although *C. candida* seems to prefer lower temperatures (Horne and Mezquita 2008) and can also be frequent in streams. Its decline at the end of Zone 2 (bed B) may therefore indicate an increase in temperature and a decrease of stream water input to the lacustrine environment. In Zone 3, *N.* cf. *neglecta* becomes the most abundant ostracod, coupled with an increase in foraminifers and thecamoebians, suggesting an increase in ionic content, perhaps related to increasing temperature and evaporation and reduced stream input. At present, *N. neglecta* occurs in carbonate-enriched waters in karstic lakes in the Iberian Peninsula (e.g. Rieradevall and Roca 1995) and is tolerant to slightly salty waters up to a maximum of 16‰ (Meisch 2000). However, the presence of other taxa such as *Microdarwinula* n. sp., or *Trapezicandona* n. sp., suggests salt content below 5‰. This is probably the first finding of *Microdarwinula* in Miocene sediments, and therefore the oldest record for the genus; moreover, its morphology does not conform to other previously described *Microdarwinula* species (Pinto et al. 2005). This is also the first finding of the genus *Trapezicandona* for the Iberian Peninsula. The species resembles *Trapezicandona italica* Karanovic and Pesce, 2000 and *Mixtacandona*

For Peer Review Only

talianae Gliozzi and Mazzini, 1998 but they differ in the shape of frontal and rear parts of the carapace (Mazzini et al. 2017). Nevertheless, these species are usually found in groundwater influenced water bodies (caves, wells), suggesting water input from the aquifer into the Venta del Moro palaeolake at the top half of the sequence. Finally, the increase in abundance of *Cypris bispinosa* in Subzone 3.2, at the top of the sequence, indicates that some parts of the lake, probably littoral areas, were experiencing desiccation, as this species is typical of fishless temporary waters, and can tolerate slightly brackish waters, up to a maximum salinity of 3.6‰ (Meisch 2000). The decrease in fish otolith remains in Zone 3 (Fig. 4a) also suggests a less stable or a shallower water body.

The composition of the thecamoebian assemblage, mostly consisting of centropyxids and difflugids, also suggests a permanent body of fresh to slightly brackish waters under stress conditions. *Centropyxis aculeata*, the dominant taxon, is known as an opportunistic species that can thrive in stressed environments. Both *C. aculeata* and *C. constricta* can live in fresh to brackish waters (Scott et al. 2001). Moreover, according to van Hengstum et al. (2008), the non-spinose morphotypes of both *C. aculeata* and *C. constricta* (as those recovered in Venta del Moro) dominate over spinose forms with increasing salinity.

It can be assumed that the gradual increase in the calcium carbonate (Ca^{2+} and HCO_3^-) concentration, inferred from the lithologic change from Unit B to Unit A, allowed the first appearance of calcareous foraminifers. *Paraphysalidia paralica* has been reported, under different names, in Holocene sediments of Mediterranean coastal lagoons and in anchialine caves and cenotes from Mexico and Bermuda (Guillem and Usera 2012 and references therein). At present, this euryhaline species has been found as a dominant taxon in oligohaline (0.5–5‰) waters of anchialine caves in Yucatan (van Hengstum et al. 2008, 2009), as common to abundant (average 5–25%) in the mesohaline (5–18‰) ponds of the Torreblanca (Guillem 2007; Guillem and Usera 2012) and Almenara (Sanjuan and Blázquez 2017) coastal

For Peer Review Only

lagoons and as relatively rare (not exceeding 10% of the assemblage) in polyhaline (18–30‰) waters of anchialine caves in Bermuda (van Hengstum and Scott 2011). This suggests that *P. paralica* might be considered as a potential proxy for oligohaline waters.

According to van Hengstum et al. (2008), a salinity of 3.5 psu marks the transition from a thecamoebian-dominated to a foraminifer-dominated assemblage in present day Mexican cenotes. In Venta del Moro, Foraminifera outnumber thecamoebians since the very first appearance of *P. paralica* in VVf-9, but both groups show similar (very low) densities up to sample VVf-11, after which point foraminifers become overwhelmingly dominant (Fig. 3b). The 3.5‰ threshold should not be directly inferred in Venta del Moro, due to the different methods employed – e.g. van Hengstum et al. (2008) used 45-µm sieves – and the very different environments (subtropical anchialine caves vs. inland lake), but the available evidence suggests an environment of oligohaline waters at least for the upper half of the studied section. The occurrence in Venta del Moro of a rich association of otoliths of Cyprinodontiformes (Reichenbacher and Montoya 2014), including a fossil form of the brackish and freshwater recent fish genus *Valencia*, provides further evidence coherent with the existence of oligohaline waters in at least part of the evolution of the ancient lake.

Spirillina sp., which appears in the uppermost series, is not uncommon in brackish environments. Márquez and Usera (1988) reported the occurrence of *Spirillina simplex* Le Calvez, 1949 in the Miocene lacustrine beds of Buñol. In addition, *Spirillina vivipara* Ehrenberg, 1843 is abundant in the Torreblanca coastal lagoon and has been found in other paralic environments in the Iberian Peninsula (Guillem 2007). It can be inferred from the extremely tiny and underdeveloped recovered specimens that conditions still remained harsh and near the edge of the survival range for this species. The appearance of a second foraminiferal taxon, the strong increase of the foraminiferal density, the decreasing abundance of thecamoebians and the composition of the ostracod fauna suggest a continuous increase in

For Peer Review Only

total dissolved solids (although not exceeding 5‰) and the presence of temporary waters at the top of the sequence, which is coherent with the solute saturation in the final drying phase of the lake.

Conclusions

The micropalaeontological analysis of a 70-cm long sedimentary section in the lacustrine beds of the Late Miocene mammalian site of Venta del Moro has yielded assemblages composed by foraminifers (2 taxa), thecamoebians (7 taxa) and ostracods (19 taxa, two of them probably new species). This is the first report of *Trapezicandona* in the Iberian Peninsula and the oldest known records of *Microdarwinula* and *Paraphysalidia paralica*. In close correspondence with the lithological units, the microfossil assemblages reflect the environmental evolution of the ancient lake. The barren lowermost interval (Unit C, Zone 1) evidences the anoxic bottom conditions, which prevented the occurrence of (aerobic) benthic microorganisms. The first appearance of ostracods and thecamoebians documents the increasing oxygenation of the lake (Unit B, Zone 2). The composition of the ostracod and thecamoebian assemblages supports a permanent freshwater to slightly brackish lake with low temperature and stream influence. The first appearance of foraminifers in the upper part of Unit B, and the strong abundance increase of the three microfossil groups in the transition to Unit A (Zone 3), reflect more stable and oxygenated conditions, growing calcium carbonate availability for foraminifer and ostracod shells and probably increasing temperature and evaporation as suggested by the decline of *Candona* cf. *candida*. The overwhelming dominance of *Paraphysalidia paralica*, together with the appearance of an additional foraminiferal taxon (*Spirillina* sp.) and the ostracod *Cypris bispinosa* at the uppermost part of the studied section (Subzone 3.2), suggests oligohaline temporary waters, which is coherent with the increasing total dissolved solids in the final drying phase of the lake.

For Peer Review Only

Acknowledgements

The fieldwork in Venta del Moro was supported, from 1995 to 2012, by the Conselleria de Cultura of the Valencian Government with the permission of the Ministerio de Fomento and the Company ADIF, of the Spanish Government. The project was supported by the Spanish Ministerio de Ciencia e Innovación PGC2018-094122-B-100. We would like to acknowledge the personal at the SCSIE Microscopy Unit of the University of Valencia for their assistance at the SEM. FMJ wants to acknowledge support from project AICO/2020/182 funded by the Conselleria de Innovació, Universitats, Ciència i Societat, Generalitat Valenciana.

References

Aguirre E, Robles F, Thaler L, López Martínez N, Alberdi MT, Fuentes C. 1973. Venta del Moro, nueva fauna finimiocena de Moluscos y Vertebrados [Venta del Moro, new end-Miocene fauna of Molluscs and vertebrates]. Estud. Geol. 29:569–578. Spanish.

Agustí J, Garcés M, Krijgsman W. 2006. Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. Palaeogeogr., Palaeoclimatol., Palaeoecol. 238:5–14.

Anadón P. 1992. Composition of inland waters with marine-like fauna and inferences for a Miocene lake in Spain. Palaeogeogr., Palaeoclimatol., Palaeoecol. 99:1–8.

For Peer Review Only

Blázquez A, Guillem J, Montoya P, Usera J. 2008. Presencia de foraminíferos bentónicos y planctónicos en el yacimiento de mamíferos del Mioceno terminal de Venta del Moro (Valencia) [Presence of benthic and planktonic foraminifera in the end-Miocene mammalian site of Venta del Moro (Valencia)]. In: XXIV Jornadas de la Sociedad Española de Paleontología; Colunga, Asturias (Spain), p. 81–82. Spanish.

Boudreau REA, Patterson RT, Dalby AP, McKillop WB. 2001. Non-marine occurrence of the foraminifer *Cribroelphidiuim guntheri* in northern lake Winnipegosis, Manitoba, Canada. J. Foraminifer. Res. 31:108–119.

Cann JH, De Dekker P. 1981. Fossil Quaternary and living foraminifera from athalassic (non-marine) saline lakes, Southern Australia. J. Paleontol. 55:660–670.

Crespo VD, Sevilla P, Mansino S, Montoya P, Ruiz-Sánchez FJ. 2018. Bats from the classical site of Venta del Moro (Late Miocene, Eastern Spain). Hist. Biol. 30:317–326.

Flako-Zaristsky S, Almogi-Labin A, Schilman B, Rosenfeld A, Benjamini C. 2011. The environmental setting and microfauna of the oligohaline Timsah pond, Israel: The last remnant of the Kabara swamps. Mar. Micropaleontol. 80:74–88.

Fuhrmann R. 2012. Atlas quartärer und rezenter Ostrakoden Mitteldeutschlands. [Atlas of Quaternary and recent ostracods of middle Germany]. Natural History Museum Mauritianum, Altenburg. German.

For Peer Review Only

Gibert L, Scott GR, Montoya P, Ruiz-Sánchez FJ, Morales J, Luque L, Abella J, Lería M. 2013. Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. Geology. 41:691–694.

Gliozzi E., Rodriguez-Lazaro J, Nachite D, Martin-Rubio M, Bekkali R. 2005. An overview of Neogene brackish leptocytherids from Italy and Spain: Biochronological and palaeogeographical implications. Palaeogeogr., Palaeoclimatol., Palaeoecol. 225:283– 301.

Griffiths HI. 1995. European Quaternary Freshwater Ostracoda: a Biostratigraphic and Palaeobiographic Primer. Scopolia. 34:1-168

Guillem J. 2007. Tafonomía, taxonomía y ecología de los foraminíferos de la Albufera de Torreblanca [PhD dissertation] [Taphonomy, taxonomy and ecology of the foraminifera from the Torreblanca coastal lagoon]. València: Universitat de València. Spanish.

Guillem J, Usera J. 2012. A new benthic foraminifer from the Recent coastal lagoon of Torreblanca (Castellón, Western Mediterranean). Rev. Esp. de Micropaleontol. 44:45–55.

Krstić N. 1972 Genus *Candona* (Ostracoda) from Congeria beds of Southern pannonian basin-Serbian. Acad. Se. and Arts. Monograph. 140:1-145.

Hammer Ø, Harper DAT, Ryan PD. 2001. Past: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol. Electron. 4(1):4.

For Peer Review Only

Horne DJ, Cohen A, Martens K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. In: Holmes JA, Chivas AR editors. The Ostracoda: Applications in Quaternary Research, AGU Geophysical Monograph. 131:5–36.

Horne DJ, Mezquita F., 2008. Palaeoclimatic applications of large databases: developing and testing methods of palaeotemperature reconstruction using nonmarine ostracods. Senckenbergiana lethaea. 88:93-112

Mansino S, García-Alix A, Ruiz-Sánchez FJ, Montoya P. 2015. A new *Eliomys* from the Late Miocene of Spain and its implications for the phylogeny of the genus. Acta Palaeontol. Pol. 60:577–588.

Márquez L, Usera J. 1988. Neogene foraminifera from the mammalian rich layers of the lacustrine basin of Buñol (Valencia, Spain). Rev. Paléobiol., vol. spéc. 2:575–579.

Mathisen M, Morales J. 1981. Stratigraphy, facies and depositional environments of the Venta del Moro vertebrate locality, Valencia, Spain. Estud. Geol. 37:199-207.

Mazzini I, Marrone F, Arculeo M, Rossetti G. 2017. Revision of Recent and fossil *Mixtacandona* Klie 1938 (Ostracoda, Candonidae) from Italy, with description of a new species. Zootaxa 4221:3.

Medioli FS, Scott DB, Collins ES, McCarthy FMG. 1990. Fossil thecamoebians: present status and prospects for the future. In: Hemleben C, Kaminski MA, Kuhnt W, Scott DB editors. Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of Agglutinated

For Peer Review Only

Foraminifera Dordrecht: Kluwer Academic Publishers (NATO ASI Series C: Mathematical and Physical Sciences). 327:813–839.

Mein P. 1999. European Miocene Mammal Biochronology. In: Rössner GE, Heissig K editors. The Miocene Land Mammals of Europe: München: Verlag; p. 25-38

Meisch C. 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer, Verlag, Heidelberg.

Mesquita-Joanes F, Smith AJ, Viehberg F. 2012. The ecology of Ostracoda across levels of biological organisation from individual to ecosystem: a review of recent developments and future potential. In: Horne DJ, Holmes JA, Rodríguez-Lázaro J, Viehberg F editors. Ostracoda as proxies for Quaternary climate change. Developments in Quaternary Science Series, 17:15-35. Elsevier, Amsterdam.

Montoya P, Morales J, Robles F, Abella J, Benavent JV, Marín MD, Ruiz Sánchez FJ. 2006. Las nuevas excavaciones (1995-2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia [The new excavations (1995-2006) in the latest Miocene site of Venta del Moro, Valencia]. Estud. Geol. 62(1):313-326. Spanish.

Montoya P, Morales J, Abella J. 2009. *Eucyon debonisi* n.sp., a new Canidae (Mammalia, Carnivora) from the latest Miocene of Venta del Moro (Valencia, Spain). Geodiversitas. 31:709–722.

For Peer Review Only

Montoya P, Morales J, Abella J. 2011. Musteloidea (Carnivora, Mammalia) from the Late Miocene of Venta del Moro (Valencia, Spain). Estud. Geol. 67:193–206.

Morales J. 1984. Venta del Moro: su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo [Venta del Moro: its mammal macrofauna and continental biostratigraphy of the Mediterranean latest Miocene]. Editorial Universidad Complutense: Madrid. Spanish.

Morales J, Aguirre E. 1976. Carnívoros de Venta del Moro [Carnivora from Venta del Moro]. Trabajos sobre Neógeno-Cuaternario. 5:31–74. Spanish.

Morales J, Peláez-Campomanes P, Abella J, Montoya P, Ruiz FJ, Gibert L, Scott G, Cantalapiedra JL, Sanisidro O. 2013. The Ventian mammal age (Latest Miocene): present state. Span. J. Palaeontol. 28:149–160.

Ogden CO, Hedley RH. 1980. An Atlas of Freshwater Testate Amoebae. Oxford: British Museum (Natural History), Oxford University Press.

Pinto R, Rocha CEF, Martens K. 2005. On the evolution of the genus *Microdarwinula* Danielopol, 1968 (Ostracoda, Darwinulidae) with the description of a new species from semi-terrestrial habitats in Sao Paulo State (Brazil). Crustaceana. 78:975–986

Porter SM, Knoll AH. 2000. Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. Paleobiology. 26(3):360–385.

For Peer Review Only

Reichenbacher B, Montoya P. 2014. The Late Miocene freshwater fish fauna from Venta del Moro (Valencia, Spain). In: 5th International Otolith Symposium; Calvià (Mallorca, Spain), p. 117.

Rieradevall M, Roca JR. 1995. Distribution and population dynamics of ostracodes (Crustacea, Ostracoda) in a karstic lake: Lake Banyoles (Catalonia, Spain). Hydrobiologia, 310:189-196

Robles F. 1970. Estudio estratigráfico y paleontológico del Neógeno del río Júcar [PhD dissertation] [Stratigraphic and palaeontologic study of the Neogene of river Júcar]. València: Universitat de València. Spanish.

Rodriguez-Lazaro J, Ruiz-Muñoz F. 2012. A General Introduction to Ostracods. Morphology, Distribution, Fossil Record and Applications. In: Horne DJ, Holmes JA, Rodríguez-Lázaro J, Viehberg F editors. Ostracoda as proxies for Quaternary climate change. Developments in Quaternary Science 17:1–14. Elsevier, Amsterdam.

Sanjuan D., Blázquez, A.M. 2017. Foraminíferos bentónicos actuales en la marjal de Almenara (Castelló): subzonación de ambientes parálicos mediante la taxonomía y la ecología. [Current benthic foraminifera in the Almenara's marsh (Castelló): area subdivision of paralic environments using taxonomy and ecology] Nereis: revista iberoamericana interdisciplinar de métodos, modelización y simulación. 9:103-114. Spanish.

Singh V, Pandita SK, Tewari R, van Hengstum P, Pillai SSK, Agnihotri D, Kumar K, Bhat GD. 2015. Thecamoebians (Testate Amoebae) Straddling the Permian-Triassic Boundary in

For Peer Review Only

the Guryul Ravine Section, India: Evolutionary and Palaeoecological Implications. Plos One. 10(8):e0135593.

Stoica M, Krijgsman W, Fortuinc A, Gliozzi E. 2016 Paratethyan ostracods in the Spanish Lago-Mare: More evidence for interbasinal exchange at high Mediterranean sea level. Palaeogeogr., Palaeoclimatol., Palaeoecol. 441:854–870.

Usera J, Blázquez AM. 1998. Interpretación de la dinámica poblacional de *Ammonia beccarii* (Linné, 1758) (Foraminiferida, Protoctista) en el Cuaternario continental de la laguna de Villena (Alicante, España) [Interpretation of population dynamics of *Ammonia beccarii* (Linné, 1758) (Foraminiferida, Protoctista) in the continental Quaternary of the Villena lake (Alicante, Spain)]. Coloq. Paleontol. 49:145–167. Spanish.

van Hengstum PJ, Scott DB. 2011. Ecology of foraminifera and habitat variability in an underwater cave: distinguishing anchialine versus submarine cave environments. J. Foraminifer. Res. 41(3):201–229.

van Hengstum PJ, Reinhardt EG, Beddows PA, Huang RJ, Gabriel JJ. 2008. Thecamoebians (testate amoebae) and foraminifera from three anchialine cenotes in Mexico: low salinity (1.5–4.5 psu) faunal transitions. J. Foraminifer. Res. 38(3):305–317.

van Hengstum PJ, Reinhardt EG, Beddows PA, Schwarcz HP, Gabriel JJ. 2009. Foraminifera and testate amoebae (thecamoebians) in an anchialine cave: Surface distributions from Aktun Ha (Carwash) cave system, Mexico. Limnol. and Oceanogr. 54(1):391–396.

For Peer Review Only

Wennrich V, Meng S, Schmiedl G. 2007. Foraminifers from Holocene sediments of two inland brackish lakes in central Germany. J. Foraminifer. Res. 37:318–326.

Figure captions

Figure 1. Geographic location of the Venta del Moro site. Modified from Mansino et al. (2015).

Figure 2. Schematic profile showing the fossiliferous units recognized in the Venta del Moro site. Modified from Montoya et al. (2006).

Figure 3. (a) Sampling points along the studied sedimentary section in the Venta del Moro site. (b) Density variation along the studied section of foraminifers, thecamoebians and ostracods. Note that, for comparison purposes, thecamoebian and ostracod densities are expressed respectively as individuals/10 g and valves/10 g.

Figure 4. Density variation along the studied section of the different taxa of (a): foraminifers (dark blue), thecamoebians (light blue) and otoliths (gray) in individuals/g (b): ostracods (orange) in valves/g. Constrained cluster zones are also shown. Note the different density scales for the different taxa.

Figure 5. SEM images of selected foraminifera and thecamoebians found in the studied section of Venta del Moro: a-b *Paraphysalidia paralica* Guillem and Usera, 2012; c-d

For Peer Review Only

Spirillina sp.; e-f *Centropyxis aculeata* (Ehrenberg, 1830); g-h *Centropyxis constricta* (Ehrenberg, 1841); i-j *Difflugia globosa* Dujardin, 1837; k-l *Difflugia* sp.

Figure 6. SEM images of selected Ostracoda found in the studied section of Venta del Moro (I): a *Darwinula stevensoni* (Brady and Robertson, 1870), left valve, inner view; b *Microdarwinula* sp., dorsal view; c *Microdarwinula* sp., right valve, inner view; d *Microdarwinula* sp., left valve, inner view; e *Ilyocypris getica* Masi, 1906, right valve, outer view; f *Ilyocypris getica* Masi, 1906, left valve, inner view; g *Ilyocypris gibba* (Ramdohr, 1808) right valve, outer view; h *Ilyocypris gibba* (Ramdohr, 1808) left valve, inner view; i *Neglecandona* cf. *neglecta* (Sars, 1887), juvenile, right valve, inner view; j *Candona* cf. *candida* (O.F. Müller, 1776), juvenile, right valve, inner view.

Figure 7. SEM images of selected Ostracoda found in the studied section of Venta del Moro (II): a *Trapezicandona* sp., right valve, inner view; b *Trapezicandona* sp., left valve, inner view; c *Trapezicandona* sp., left valve, outer view; d *Trapezicandona* sp., dorsal view; e *Cyclocypris ovum* (Jurine, 1820), left valve, inner view; f *Herpetocypris intermedia* Kaufmann, 1900, left valve, inner view; g *Cypris bispinosa* Lucas, 1849 left valve fragment, outer view; h *Paralimnocythere* cf. *relicta* (Lilljeborg, 1863), right valve, outer view; i *Paralimnocythere* cf. *messanai* Martens, 1992, right valve, outer view.

Table caption

Table 1. Correspondence between samples, sampling depth, fossiliferous beds, lithology and constrained cluster zones in the studied sedimentary section in Venta del Moro. Sampling depths (Z) are Cartesian coordinates, with X=242 cm and Y=395 cm, referred to a point (0,0,0) selected during the 1995-2012 excavation campaigns.

For Peer Review Only

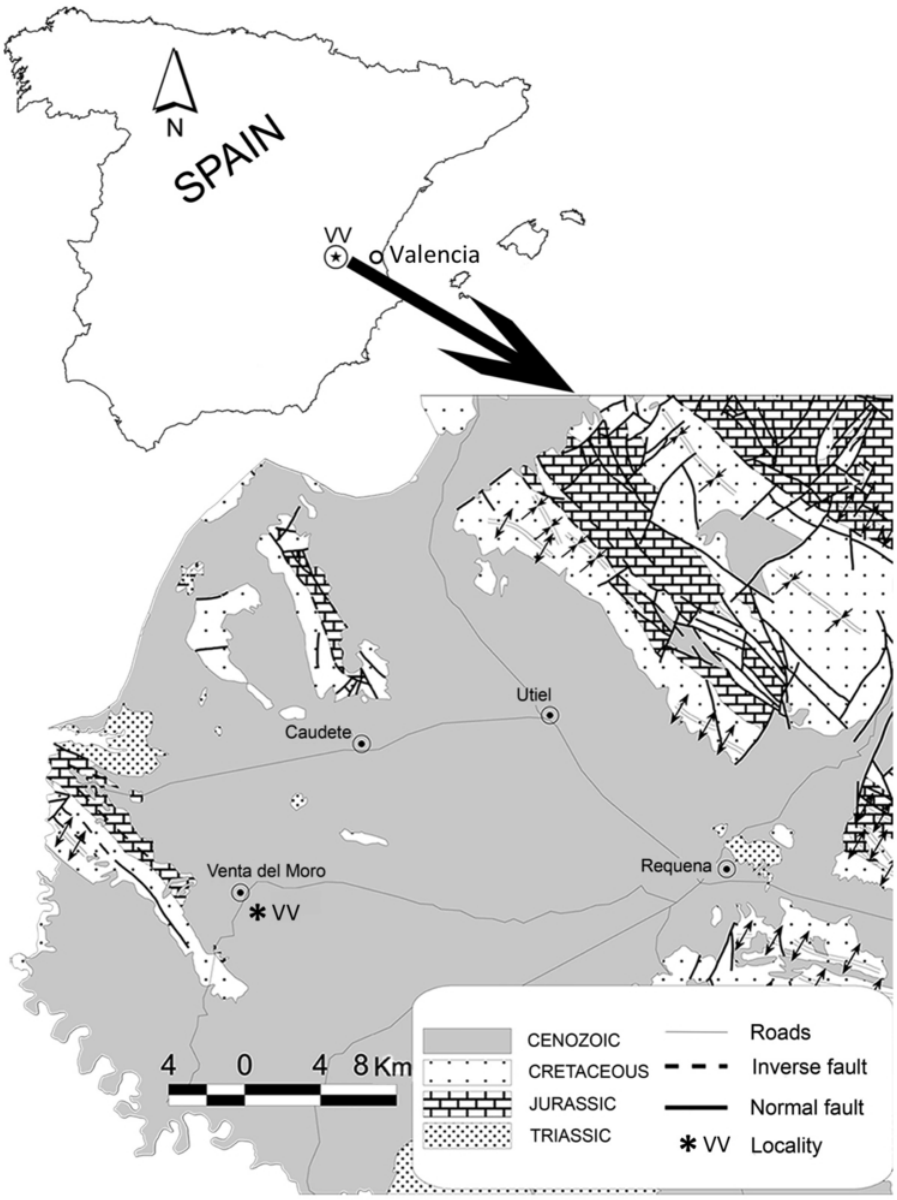

Figure 1. Geographic location of the Venta del Moro site. Modified from Mansino et al. (2015).

32x42mm (600 x 600 DPI)

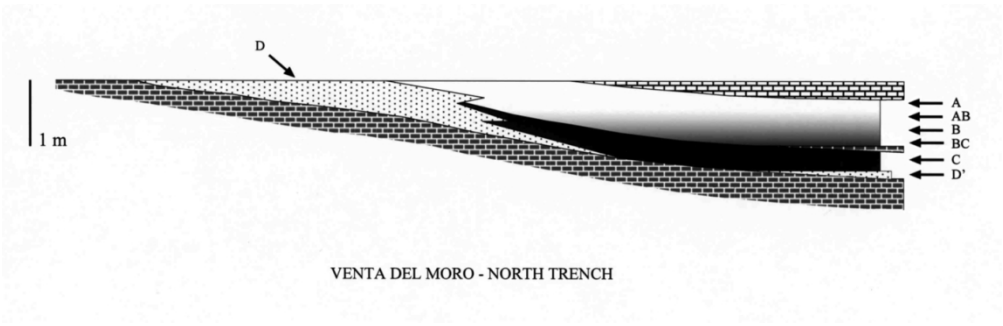

Figure 2. Schematic profile showing the fossiliferous units recognized in the Venta del Moro site. Modified from Montoya et al. (2006).

59x19mm (600 x 600 DPI)

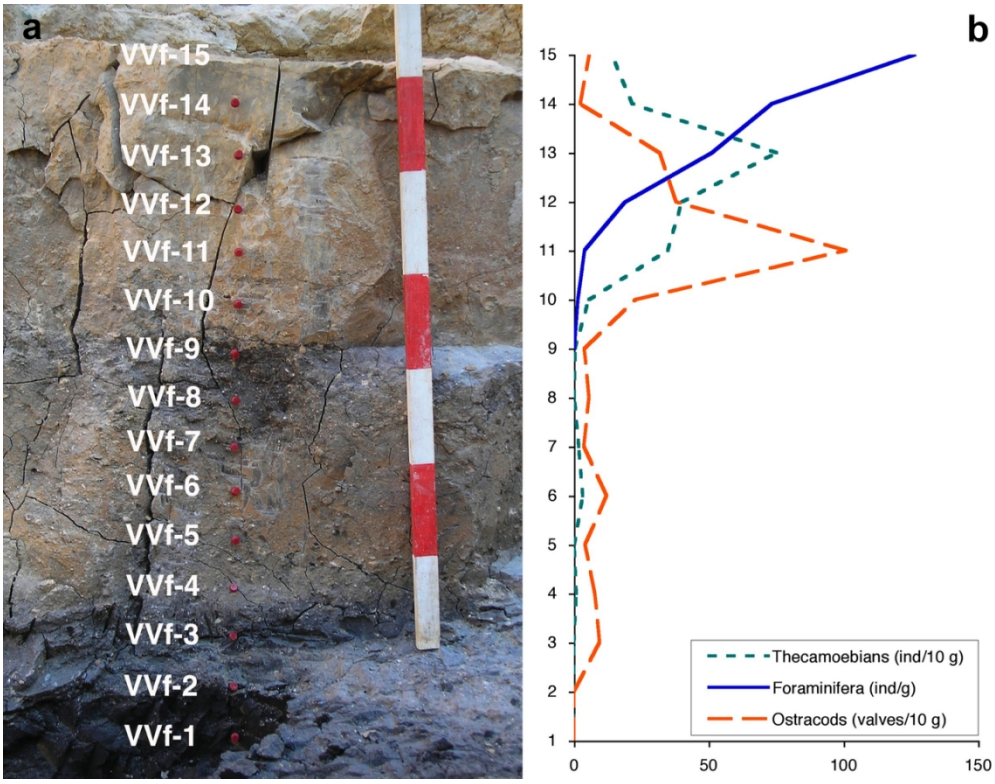

Figure 3. (a) Sampling points along the studied sedimentary section in the Venta del Moro site. (b) Density variation along the studied section of foraminifers, thecamoebians and ostracods. Note that, for comparison purposes, thecamoebian and ostracod densities are expressed respectively as individuals/10 g and valves/10 g

54x42mm (600 x 600 DPI)

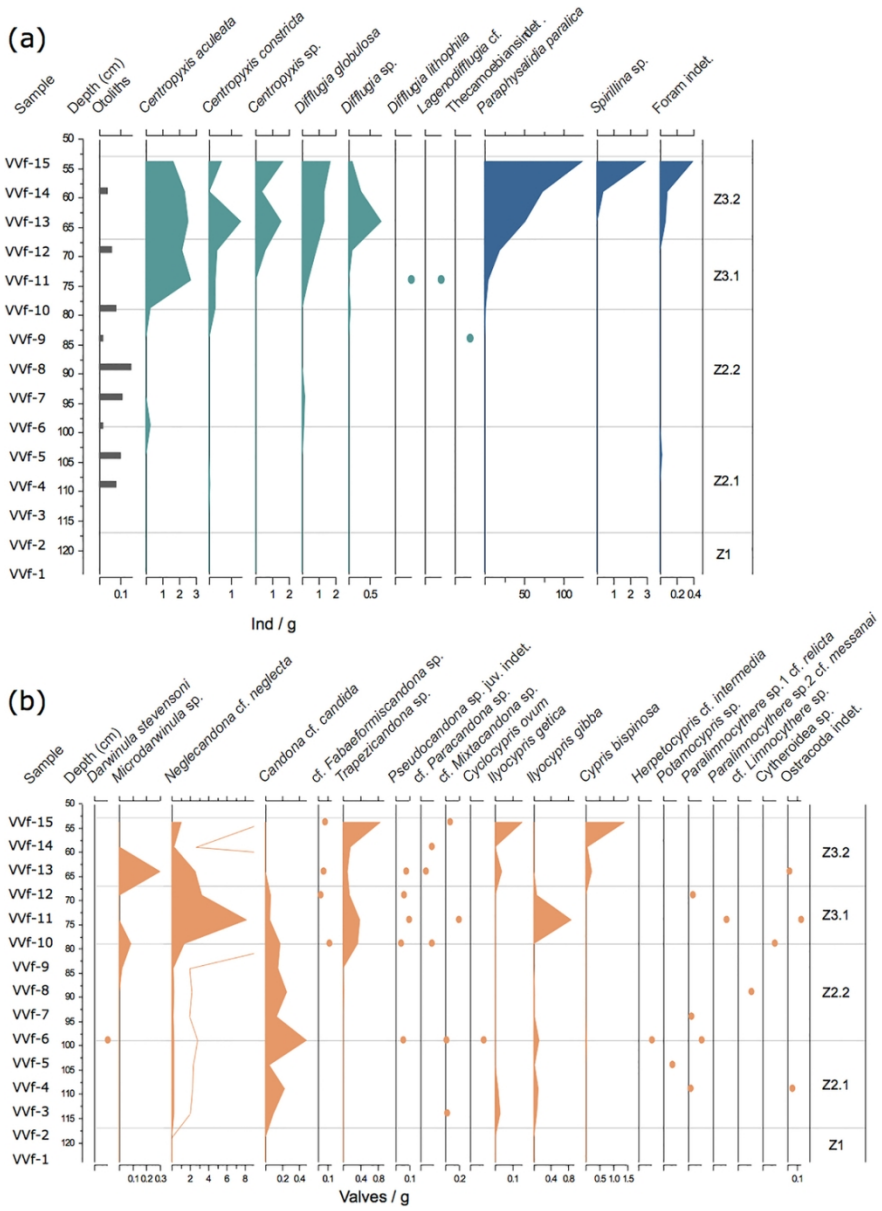

Figure 4. Density variation along the studied section of the different taxa of (a): foraminifers (dark blue), thecamoebians (light blue) and otoliths (gray) in individuals/g (b): ostracods (orange) in valves/g. Constrained cluster zones are also shown. Note the different density scales for the different taxa.

46x63mm (600 x 600 DPI)

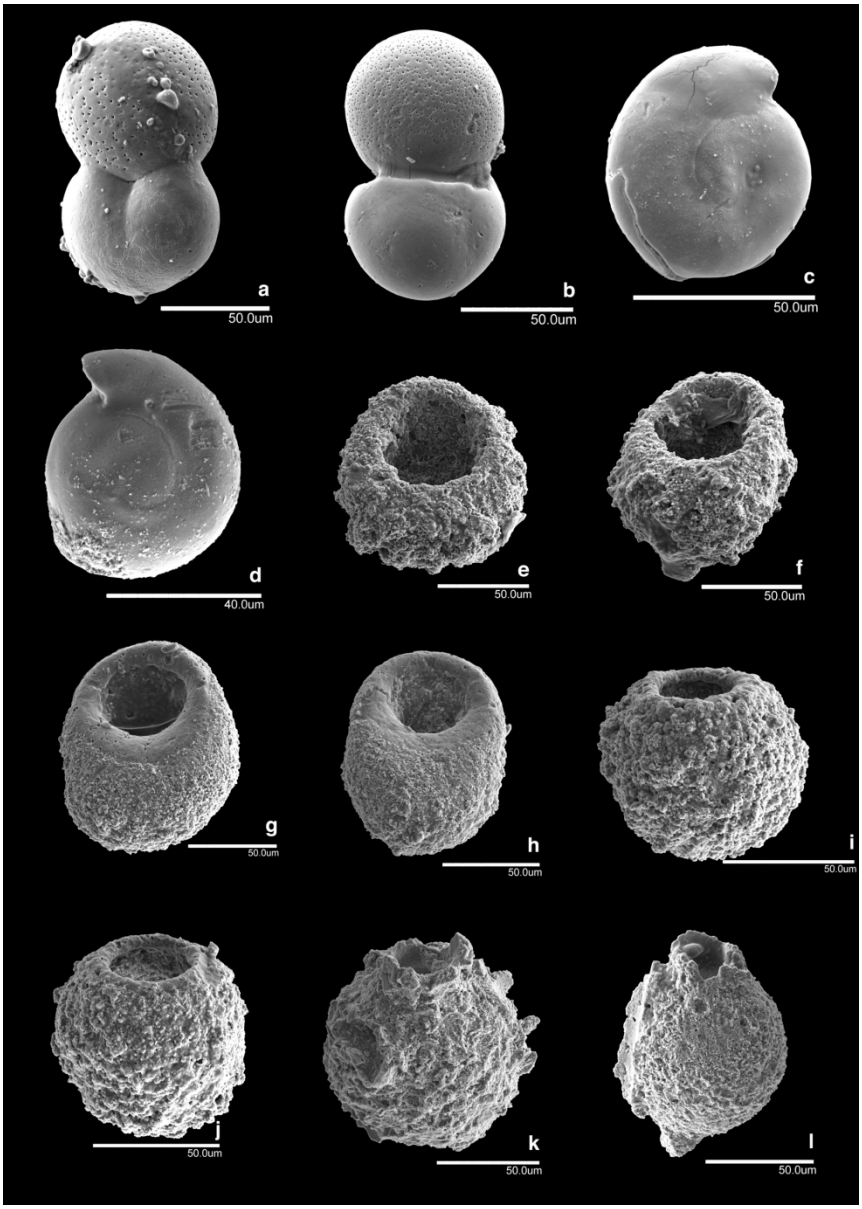

Figure 5. SEM images of selected foraminifera and thecamoebians found in the studied section of Venta del Moro: a-b *Paraphysalidia paralica* Guillem and Usera, 2012; c-d *Spirillina* sp.; e-f *Centropyxis aculeata* (Ehrenberg, 1830); g-h *Centropyxis constricta* (Ehrenberg, 1841); i-j *Difflugia globosa* Dujardin, 1837; k-l *Difflugia* sp.

85x119mm (600 x 600 DPI)

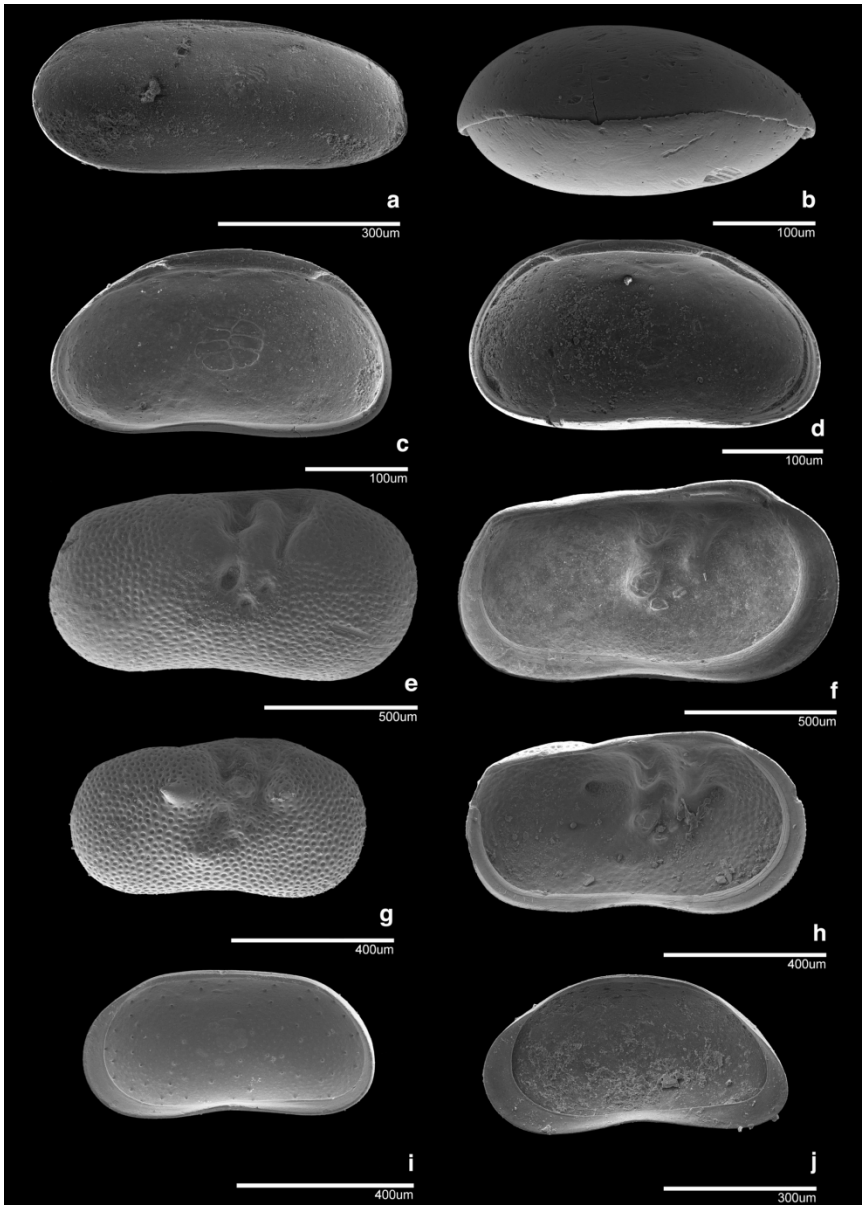

Figure 6. SEM images of selected Ostracoda found in the studied section of Venta del Moro (I): a *Darwinula stevensoni* (Brady and Robertson, 1870), left valve, inner view; b *Microdarwinula* sp., dorsal view; c *Microdarwinula* sp., right valve, inner view; d *Microdarwinula* sp., left valve, inner view; e *Ilyocypris getica* Masi, 1906, right valve, outer view; f *Ilyocypris getica* Masi, 1906, left valve, inner view; g *Ilyocypris gibba* (Ramdohr, 1808) right valve, outer view; h *Ilyocypris gibba* (Ramdohr, 1808) left valve, inner view; i *Neglecandona* cf. *neglecta* (Sars, 1887), juvenile, right valve, inner view; j *Candona* cf. *candida* (O.F. Müller, 1776), juvenile, right valve, inner view

85x119mm (600 x 600 DPI)

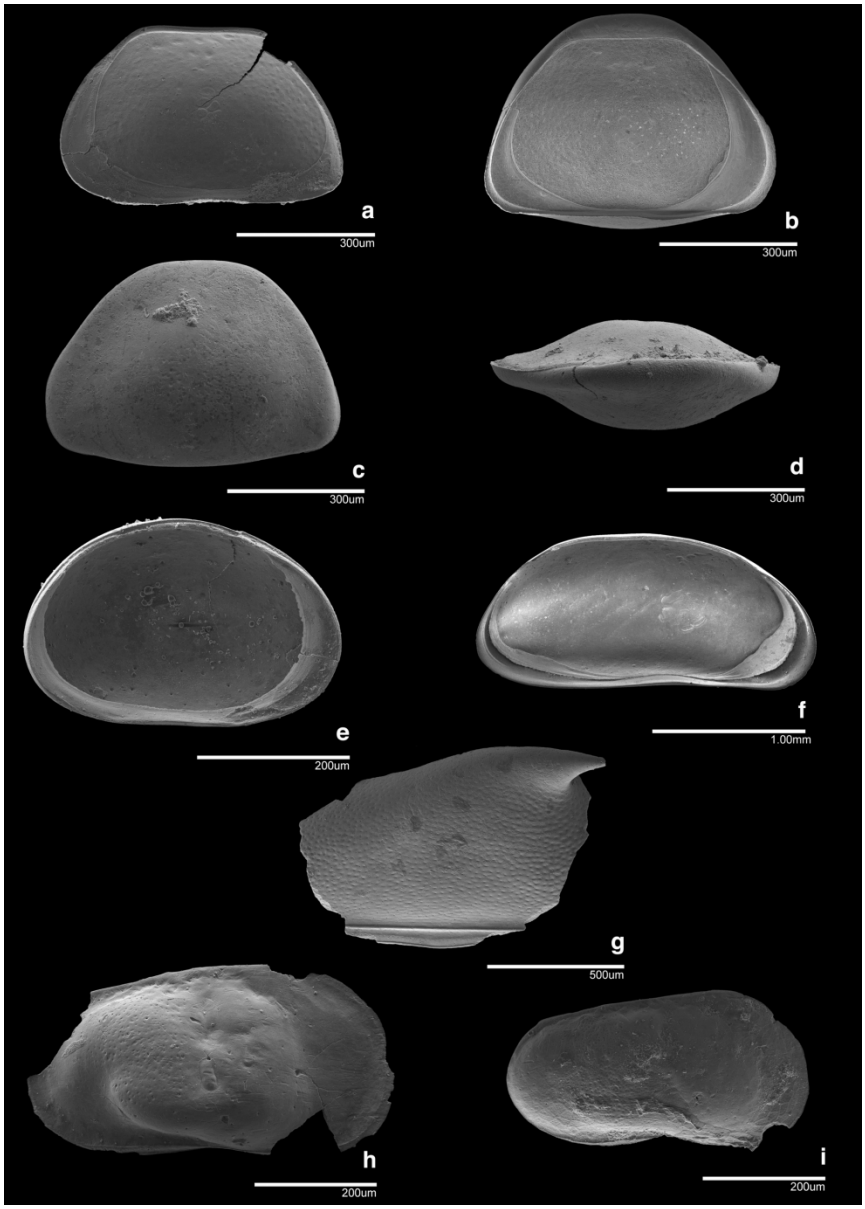

Figure 7. SEM images of selected Ostracoda found in the studied section of Venta del Moro (II): a *Trapezicandona* sp., right valve, inner view; b *Trapezicandona* sp., left valve, inner view; c *Trapezicandona* sp., left valve, outer view; d *Trapezicandona* sp., dorsal view; e *Cyclocypris ovum* (Jurine, 1820), left valve, inner view; f *Herpetocypris intermedia* Kaufmann, 1900, left valve, inner view; g *Cypris bispinosa* Lucas, 1849 left valve fragment, outer view; h *Paralimnocythere* cf. *relicta* (Lilljeborg, 1863), right valve, outer view; i *Paralimnocythere* cf. *messanai* Martens, 1992, right valve, outer view.

85x119mm (600 x 600 DPI)

Sample	Z (cm)	Bed	Lithology	Cluster zones	
VVf-15	54	A	Light marls	Zone 3	Subzone 3.2
VVf-14	59	A			
VVf-13	64	A			Subzone 3.1
VVf-12	69	A			
VVf-11	74	AB	Light marls with gastropods	(Transition)	
VVf-10	79	AB			
VVf-9	84	B	Dark grey marls with gastropods	Zone 2	Subzone 2.2
VVf-8	89	B			
VVf-7	94	B			
VVf-6	99	B			(Transition)
VVf-5	104	B			Subzone 2.1
VVf-4	109	B			
VVf-3	114	BC	Black marls with gastropods	Zone 1	
VVf-2	119	BC			
VVf-1	124	C	Lignite		

Table 1. Correspondence between samples, sampling depth, fossiliferous beds, lithology and constrained cluster zones in the studied sedimentary section in Venta del Moro. Sampling depths (Z) are Cartesian coordinates, with X=242 cm and Y=395 cm, referred to a point (0,0,0) selected during the 1995-2012 excavation campaigns.

135x94mm (600 x 600 DPI)