



Research paper

Ostracod assemblages and palaeoenvironmental reconstruction of a Lower Pliocene shallow marine system in the East Atlantic (Bonares-Casa del Pino, Guadalquivir Basin, Spain)

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ABSTRACT

The ostracod assemblages from the Bonares-Casa del Pino section in the Lower Guadalquivir Basin, part of the lower Pliocene Arenas de Huelva Formation, have been analysed for palaeoenvironmental purposes. These assemblages form part of a subtropical/tropical biota, consistent with findings from earlier studies on fossil remains within the Zanclean deposits in the Southwestern Iberian Peninsula.

The present study marks the first application of the Specific Population Species index Method, originally developed to distinguish autochthonous from allochthonous species in Recent assemblages, to fossil ostracods. Through both quantitative and statistical analyses, the autochthonous nature of both dominant and characteristic species was recognized. The succession was deposited in the northernmost sector of the East Atlantic lower Pliocene tropical palaeo-ecoregion (also known as Atlantic Andalusian Pliocene Mollusc Unit 1), within shallow waters. The attribution to the offshore transition zone, close to the boundary between infralittoral and circalittoral zones, prompted clarification of vertical zonation terminology for both the Atlantic and Mediterranean, in Recent and Pliocene marine environments.

1. Introduction

During the late Neogene, a broad Atlantic embayment, including the present-day provinces of Huelva, Seville and Cadiz, occupied the lower Guadalquivir Basin, an ENE/WSW-oriented, triangular-shaped foreland basin of the Betic Cordillera (Sanz de Galdeano and Vera, 1992; González Delgado et al., 2004). This shelf environment was the depositor for four lithostratigraphic units, lying unconformably on the Paleozoic-Mesozoic complex. Civis et al. (1987) described the Calcarinitas de Niebla Formation, the Arcillas de Gibraleón Formation and the Arenas de Huelva Formation, these lithological units being chronologically attributed to the Tortonian, Tortonian-Messinian, and lower Pliocene, respectively (Flores, 1985; Sierro, 1985a, 1985b; Sierro et al., 1996; Civis et al., 1994; Baceta and Pendón, 1999). The overlying Bonares Sands (Mayoral and Pendón, 1987) are currently assigned to the upper part of the lower Pliocene (Salvany et al., 2011). The Arcillas de Gibraleón, Arenas de Huelva and Bonares Sands Formations constitute a regressive sequence, reflecting a transition from the upper slope-open shelf to marginal-continental depositional environments.

The Arenas de Huelva Formation are characterized by the occurrence of storm deposits (Sierro, 1979; Dabrio et al., 1988; González Delgado

et al., 1995; González-Regalado et al., 2009; Ponce Medina et al., 2024) and, in their lower part, by lower Zanclean silty sands that, include glauconitic sediments at the base of the Pliocene (Viguier, 1974; Sierro, 1984; Mayoral, 1986; Civis et al., 1987; Galán et al., 1989). These deposits are rich in well-preserved macro- and micro-fossil (Ruiz et al., 1997; González-Regalado et al., 2012), with the latter being frequently concentrated as shell beds (Mayoral, 1989). A considerable body of palaeontological research has been conducted on these materials, including studies on molluscs (González Delgado et al., 1995; Landau and Mayoral, 2011, and references therein), planktonic (Sierro, 1985a, 1987 and references therein) and benthonic (González-Regalado, 1987; Pérez-Asensio et al., 2012, and references therein) foraminifers, calcareous nannoplankton (Flores, 1985), pollens (Peñalba, 1985; Valle and Peñalba, 1987), bryozoans (Mayoral, 1987; Mayoral and Reguant, 1995), vertebrates (García et al., 2014; Rahmat et al., 2020 and references therein), barnacles (Santos et al., 2005) and brachiopods (Toscano et al., 2010).

Following preliminary studies on the Neogene ostracods from southwestern Spain (Borragan, 1966; Sissingh, 1972; Moyes, 1973), several investigations focused on the upper Miocene and Pliocene ostracods of this area. Contributions on the ostracods from the Arenas de Huelva

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Formation included palaeoecological, taxonomic and biostratigraphic analyses (González Delgado et al., 1982; Ruiz and Gonzalez-Regalado, 1990; Ruiz and Gonzalez-Regalado, 1993; Ruiz and González-Regalado, 1996; Gonzalez-Regalado and Ruiz-Muñoz, 1991; Ruiz et al., 2008, 2018).

The present study aims to apply the methodology based on population age structure developed by Aiello et al. (2024a) to distinguish autochthonous and allochthonous taxa of fossil assemblages, and to assess its effectiveness in refining palaeoecological reconstructions based on ostracod assemblages. Additionally, the study aims to reconcile the different (palaeo)environmental frameworks adopted for both the Mediterranean and the Eastern Atlantic.

2. Bonares-Casa del Pino section

The fossiliferous locality of Bonares-Casa del Pino (37° 20' 0.40" N, 6° 40' 33.63" W), located near the town of Bonares in the province of Huelva, along the South Atlantic margin of the Iberian Peninsula (Fig. 1), was initially described by Jubes and Prieto (1919), who referred to the site as "Venta del Manco" (cf. Civis et al., 1987). During the early Pliocene, the Bonares-Casa del Pino Sands were deposited in shallow marine environments within the western sector of the lower Guadalquivir Basin. The fossil content and palaeoecology of these deposits were described by González Delgado (1983, 1985, 1986, 1987, 1988, gastropods), Peñalba (1985) and Valle and Peñalba (1987) (pollens), González-Regalado (1989; benthonic foraminifers), Garcia et al. (2007, 2009, 2010, 2011, 2014; chondrichthyans) and Toscano et al. (2010; brachiopods).

The studied section attains a vertical thickness of approximately 6 m. The lower part consists of silty and sandy sediments attributed to the Huelva Sand Formation, overlain by medium to coarse sands belonging to the Bonares Sands Formation. According to Ruiz et al. (2008), five

sedimentary facies are distinguished within the section, four occurring within the Arenas de Huelva Formation (FA-1 to FA-4), and the uppermost (FA-5) being exclusive to the Bonares Sands Formation (Fig. 1D). Eleven samples were collected from this section to retrieve ostracods for analytical purposes.

3. Material and methods

Eleven sediment samples were collected from the 6 m-thick lower Pliocene succession of the Bonares-Casa del Pino (CP) Section for ostracod assemblage analysis (Fig. 1, Table 1). Grain-size distribution was determined by standard dry and wet sieving for sand and gravel fractions and by sedimentation analysis based on Stokes' law for the fine fraction; granulometric fraction percentages were calculated according to Folk and Ward (1957), allowing classification into clay, silt, sand, and gravel. The samples CP A to CP J were obtained from sediments belonging to the Arenas de Huelva Formation while the uppermost sample (CP K) pertains to the Bonares Sands Formation. The samples (200 g dried weight) were oven-dried, disaggregated and washed through 120 and 230 mesh sieves (125 and 63 µm, respectively). The resulting residues were examined under a binocular microscope for semi-quantitative analysis (Table 2) and all the ostracod shells were picked from the >125 µm fraction. Scanning electron microscope (SEM) imaging (Fig. 2), performed with a FESEM ZEISS Merlin VP scanning electron microscope (DiSTAR, University of Naples Federico II), was used to document most taxa, enabling accurate comparisons with both classic and modern literature, and facilitating a more accurate assessment of the diversity of the considered assemblages. Although issues concerning previously undescribed species and morphological variability were a matter of concern, they are not discussed in detail herein. A comprehensive taxonomic review is currently underway.

Quantitative analyses were based on the Minimum Number of Individuals (MNI, Appendices 1, 2) and the Total Number of Valves (TNV, Appendices 3, 4). MNI was determined by adding the greater number of either right or left adult valves to the number of adult carapaces; in cases where only juvenile shells were recorded, the MNI equals one. TNV included all the juvenile and adult valves. The following diversity and ecological indices were calculated: S (taxa richness), I (individuals per 200 g of sediment), D (dominance), H' (Shannon Diversity Index) and J (equitability) (Table 3).

3.1. Statistical analyses, Adults:Juveniles ratio, population age structure and Specific Population Stage index (SPS)

Abundance data, based on MNI and TNV, were subjected to two-way cluster analysis using the PAST software (Hammer et al., 2001) to identify both groups of samples with similar taxonomic compositions (Q-mode) and groups of species exhibiting co-occurrence patterns (r-mode). Analyses were conducted separately for both MNI and TNV datasets. Only species with a Relative Species Abundance (RSA) > 5% in at least one sample were included.

For the calculation of the Adults:Juveniles ratio (A:J ratio), all measurable valves, defined as those with an intact shell margin, were considered (Table 1-SM).

For the definition of the population age structure and corresponding histograms, only species represented by at least 10 measurable valves were included. Maximum height (h) and maximum length (l) measurements were recorded for each specimen. Length data were grouped into size classes corresponding to developmental stages, following the established protocols (De Deckker, 2002; Danielopol et al., 2008; Aiello et al., 2024a). All valves were assigned to a specific growth stage (Table 2 SM) and, for each sample, a population age structure diagram was developed. The Mean Population Stage (MPS) index was calculated according to Mao et al. (2021), as follows:

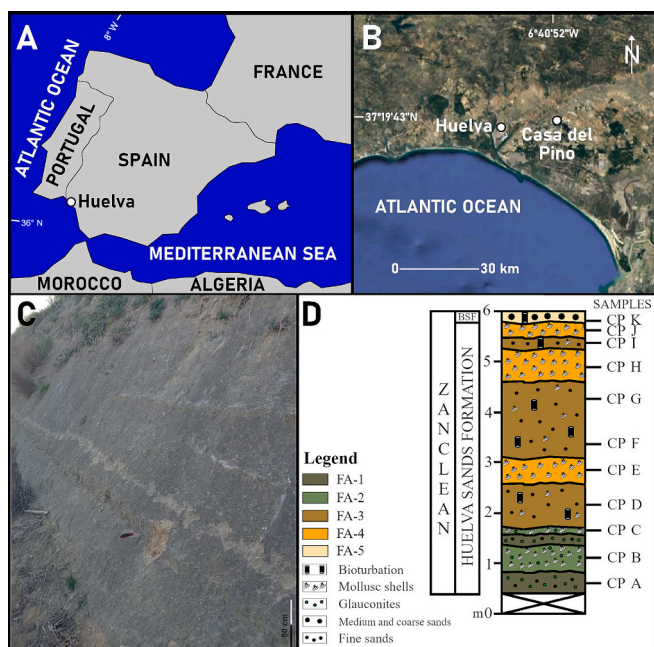


Fig. 1. A-B: Geographical setting of Southwestern Spain and location of the study section; C: Bonares-Casa del Pino outcrop (the handle of the screwdriver is about 10 cm-long); D: location of the study samples and sedimentary facies of the Arenas de Huelva Formation (according to Ruiz et al., 2008): FA-1: greenish glauconitic silts (0.4–0.8 m; 1.4–1.6 m); FA-2: bioclastic glauconitic silts (0.8–1.4 m), showing numerous oyster valves; FA-3: bioturbated fine sands (1.7–2.6 m; 3.1–4.6 m; 5.3–5.5 m); FA-4: bioclastic fine sands with very abundant bivalve and gastropod shells (1.6–1.7 m; 2.6–3.1 m; 4.6–5.3 m; 5.5–5.8 m); FA-5: medium-coarse sands with gravels (5.8–6 m).

Table 1

List of the studies samples, weight and dry weight, main grain size classes.

	Weight (g)	Dry Weight (g)	Analysed (g)	Clay (%)	Silt (%)	Sand (%)	Gravel (%)
CP K	1182	1088	200	27	46	27	0
CP J	1780	1753	200	25	35	18	22
CP I	1430	1347	200	31	60	8,5	0,5
CP H	1713	1670	200	36	55	8	1
CP G	1558	1503	200	59	32	7,6	1,4
CP F	2080	2032	200	45	48	5	2
CP E	1907	1890	200	30	46	8	16
CP D	1555	1434	200	16,4	72,6	11	0
CP C	2275	2106	200	6,4	78	10	5,6
CP B	2622	2457	200	17	40,5	24	18,5
CP A	945	941	200	46,3	24	29,7	0

Table 2

Semi-quantitative distribution of microfossils remains (VR = very rare; R = rare; U = uncommon; C = common; A = abundant) for the two analysed grain sizes.

samples	CP A	CP B	CP C	CP D	CP E	CP F	CP G	CP H	CP I	CP J
> 125 µm										
Bivalvia		C	U	R	C	U	U	C	U	C
Echinodermata	U	C	U	C	U	C	C	U	U	U
Foraminifera (benthic)	U	C	R	C	C	A	A	C	C	R
Foraminifera (planktonic)			R					VR		
Gastropoda										R
Porifera	R	C	R	A	R	R	R	U	U	R
> 63 µm										
Echinodermata			VR	R	VR		VR	VR		R
Foraminifera (benthic)	R	VR	VR	R	VR	U	U	R	VR	VR
Foraminifera (planktonic)	VR					R	R	VR	VR	
Porifera	R	U	R	U	C	U	U	R	R	R

$$MPS = \frac{[(IA \times 1) + (IA - 1 \times 2) + (IA - 2 \times 3) + (IA - 3 \times 4) + (IA - 4 \times 5) + (IA - 5 \times 6) + (IA - 6 \times 7) + (IA - 7 \times 8) + (IA - 8 \times 9)]}{[(IA - 8 + IA - 7 + IA - 6 + IA - 5 + IA - 4 + IA - 3 + IA - 2 + IA - 1 + IA)]}$$

For statistical analyses based on the Specific Population Stage (SPS) index, only species with at least 20 measurable valves were considered (Table 3 SM).

The SPS index, as defined by Aiello et al. (2024a), is calculated according to the following formula:

$$SPS = \frac{[(IA - 8 \times 1) + (IA - 7 \times 2) + (IA - 6 \times 3) + (IA - 5 \times 4) + (IA - 4 \times 5) + (IA - 3 \times 6) + (IA - 2 \times 7) + (IA - 1 \times 8) + (IA \times 9)]}{[1 + (IA - 8 + IA - 7 + IA - 6 + IA - 5 + IA - 4 + IA - 3 + IA - 2 + IA - 1 + IA)]}$$

where IA represents the number of adult instars of the considered species, IA-1 the number of penultimate instars, and so forth.

For each of the ten fossiliferous samples, the mean SPS index was calculated for species represented by at least 10 measurable valves.

Q- and r-mode cluster analysis, as well as Principal Component Analysis (PCA) were performed using the PAST version 4.06b (Hammer et al., 2001) on the SPS index values for species with more than 20 measurable valves.

All studied specimens are housed in the Aiello Barra Micropaleontological Collection (A.B.M.C.) at the Dipartimento di Scienze della Terra, dell'Ambiente e delle Risorse, Università degli Studi di Napoli Federico II.

4. Results

The ten samples collected from the Arenas de Huelva Formation (CP A - CP J) were fossiliferous, whereas the uppermost sample, belonging to the Bonares Sands Formation (CP K), was barren. The clay fraction of the

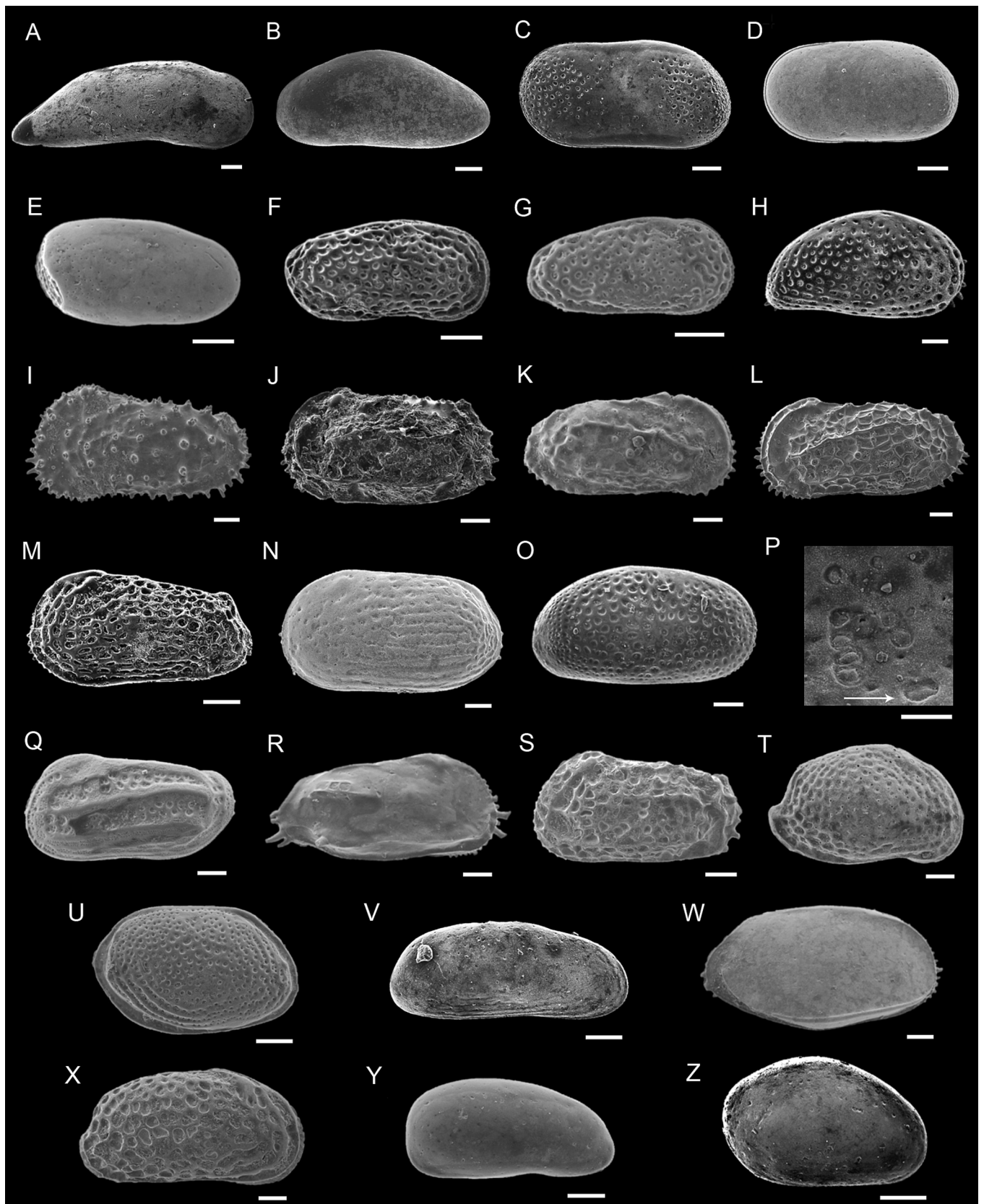
sediment ranged from 6.4 to 46.3%, the silt from 24 to 72.6%, the sand from 5 to 29.7%, and the gravel from 0 to 22% (Table 1). The fossiliferous samples yielded sponge spicules, echinoderm spines, foraminiferal tests, molluscan shells, and ostracod valves. The 63–125 µm sediment fractions did not yield any ostracod or mollusc remains, although foraminiferal tests and sponge and echinoderm fragments are present (details in Table 2). In the sample CP C, benthonic foraminiferal tests are brownish and display poor preservation.

A total of 1642 ostracod valves (carapaces counted as two valves), generally well-preserved, were studied.

Ostracod assemblages include 64 species, of which 50 are definitively or tentatively classified, four are left in open nomenclature, and ten are assigned an affinitive status due to poor preservation, absence of adult specimens or because they are still undescribed.

Ruggieria tetraptera (Seguenza, 1880) showed a mean relative abundance (MRA) of 14.16% (MNI) and 15.89% (TNV), as resulting the most common species. Further characteristic species are *Miocyprideis civisi* (Ruiz et al., 2018) [MRA (MNI) = 11.96%; MRA (TNV) = 14.34%], *Paracypris* aff. *polita* Sars, 1866 [MRA (MNI) = 9.00%; MRA (TNV) = 7.92%] and *Costa batei* (Brady, 1866) [MRA (MNI) = 7.85%; MRA (TNV) = 9.02%]. *Acanthocythereis hystrix* (Reuss, 1850) [MRA (MNI) = 6.47%; MRA (TNV) = 6.90%], *Cytherella* ? *harrymutvei* Stambolidis, 1980 [MRA (MNI) = 6.45%; MRA (TNV) = 6.95%], *Palmoconcha agilis* (Ruggieri, 1967) [MRA (MNI) = 6.27%; MRA (TNV) = 4.18%], *Capacythere costata* (Moyes, 1965) [MRA (MNI) = 5.00%; MRA (TNV) = 8.80%] and *Carinocythereis whitei* (Baird, 1850) [MRA (MNI) = 5.00%; MRA (TNV) = 5.82%] are then considered accessory species. The most diversified genus was *Xestoleberis* (6 species), followed by *Aglaiocypris*, *Cytherella*, *Palmoconcha*, *Propontocypris*, and *Semicytherura* (3 species).

Simple diversity (S) ranges from 5 to 36; abundance (I) varies between 12 and 144 (MNI) and between 20 and 377 (TNV). Shannon index (H') ranges from 1.23 to 3.19 (MNI) and from 1.24 to 3.07 (TNV), with mean values of H'(MNI) = 2.58 and H' (TNV) = 2.42. Dominance (D) values ranges from 0.06 to 0.39 (MNI); and from 0.07 to 0.37 (TNV).



(caption on next page)

Fig. 2. SEM photos of the Casa del Pino (CP) most representative ostracod species. A. *Paracypris* aff. *polita* Sars, 1866, right valve, sample CP I; B. *Propontocypris* aff. *declivis* (Müller, 1894), left valve, sample CP C; C. *Cytherella scutulum* Ruggieri, 1976, left valve, sample CP H; D. *Cytherella* ? *harrymutvei* Stambolidis, 1980, left valve from carapace, sample CP E; E. *Basslerites compressus* Bonaduce, Ruggieri, Russo and Bismuth, 1992, right valve, sample CP I; F. *Leptocythere foveolata* Moyes, 1965, right valve, sample CP I; G. *Callistocythere praecincta* Ciampo, 1976, right valve, sample CP C; H. *Cytheridea neapolitana* Kollmann, 1960, right valve RV, sample CP C; I. *Acanthocythereis hystrix* (Reuss, 1850), left valve, sample CP G; J. *Carinocythereis whitei* (Baird, 1850), left valve, sample CP I; K. *Costa batei* (Brady, 1866), right valve, sample CP E; L. *Costa edwardsii* (Roemer, 1838), left valve, sample CP B; M. *Celtia quadridentata* (Baird, 1850), left valve, sample CP D; N. *Capsocythere costata* (Moyes, 1965), female, left valve, sample CP I; O. *Miocyprideis civisi* (Ruiz et al., 2018), right valve, sample CP H; P. *Miocyprideis civisi* (Ruiz et al., 2018), left valve, internal view, muscle scars (arrow points to anterior), sample CP E; Q. *Flexus tenuicarinatus* (Capeder, 1902), left valve, sample CP G; R. *Ruggieria tetraptera* (Seguenza, 1880), right valve, sample CP B; S. *Cistacythereis pokorny* (Ruggieri, 1962), left valve, sample CP F; T. *Aurila convexa* (Baird, 1850), right valve, sample CP I; U. *Palmoconcha agilis* (Ruggieri, 1967), right valve, sample CP J; V. *Pontocythere elongata* (Brady, 1868), left valve, sample CP H; W. *Carinivalva testudo* (Namias, 1901), right valve, sample CP C; X. *Urocythereis favosa* (Roemer, 1838), right valve, sample CP H; Y. *Xestoleberis ?obliqua* Terquem, 1878, left valve, sample CP H; Z. *Xestoleberis ?ventricosa* Müller, 1894, left valve, sample CP F. Scale bar: A-O, Q-Z= 100 µm, P=50 µm.

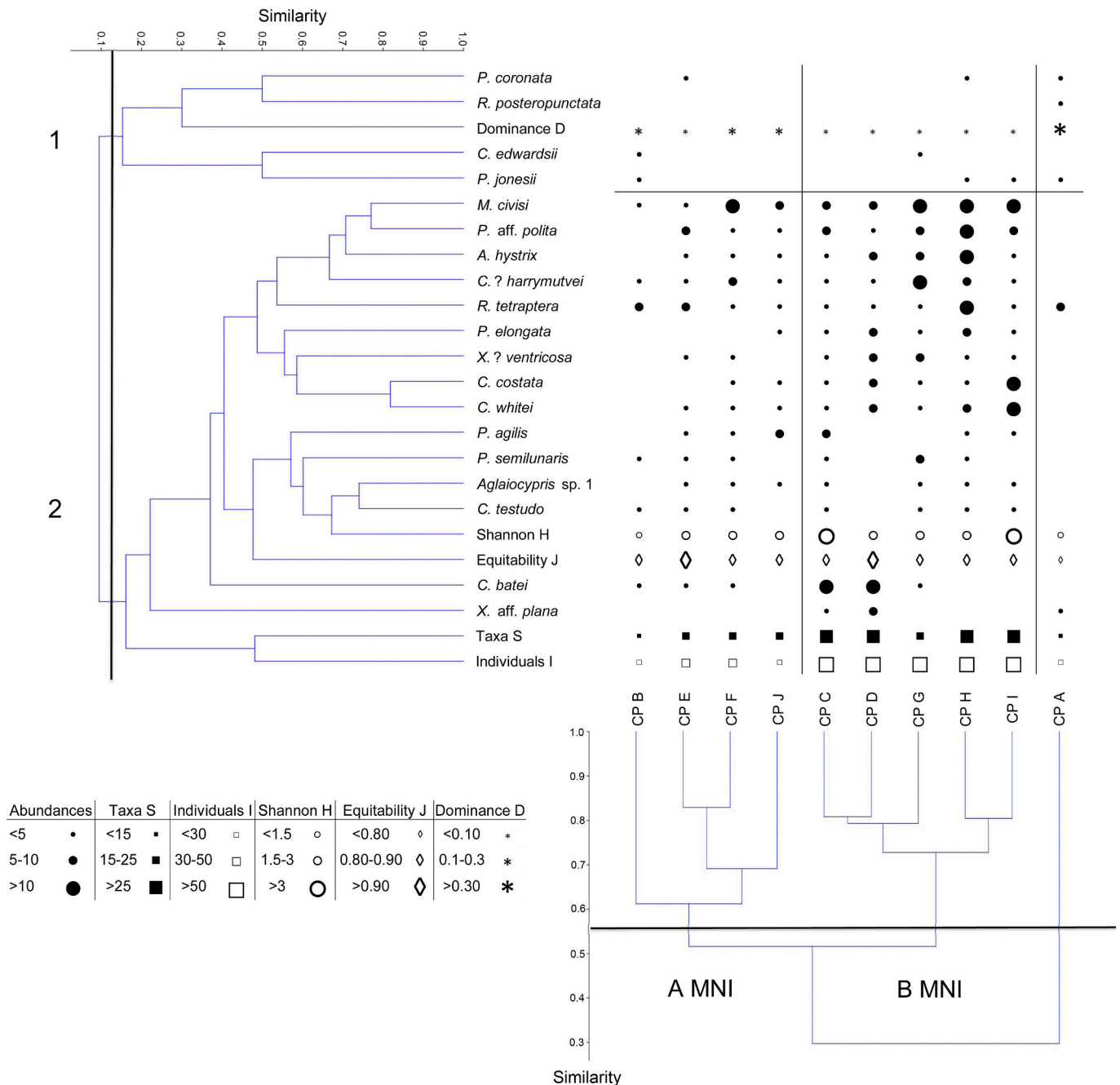


Fig. 3. Cluster analysis on abundance values (MNI) and diversity indices.

Equitability (J) ranges from 0.77 to 0.92 (MNI) and from 0.77 to 0.87 (TNV), with mean values of $J = 0.87$ (MNI) and 0.82 (TNV) (Table 1 SM).

4.1. Statistical analysis on abundance data

Cluster analysis and Principal Component Analysis of the ten ostracod assemblages of the Bonares-Casa del Pino Section were performed on abundance values (MNI and TNV) to detect any changes in the ostracod assemblage composition. Analysis based on Minimum Number of Individuals (MNI) and Total Number of Valves (TNV) gave slightly different results.

The Q-mode cluster analysis based on MNI (Bray-Curtis) divided the samples into two main clusters A MNI and B MNI to which is added the sample CP A isolated forming an individual cluster (Fig. 3). The ostracod

species-diversity indices clustered into two groups [1 and 2]. Cluster A MNI consists of samples [CP B, CP E, CP F, CP J] with low diversity ($H' = 1.98-2.74$), low abundance ($I = 26-47$), low simple diversity ($S = 11-20$), and relatively high dominance ($D = 0.08-0.20$); whereas cluster B MNI gathers samples CP C, CP D, CP G, CP H, CP I, showing high diversity ($H' = 2.80-3.19$, $S = 24-36$), higher abundance ($I = 81-144$) and lower dominance ($D = 0.06-0.08$). Sample CP A evidences the highest sand fraction (29.7%), the lowest diversity indices and the highest dominance value. The r-mode cluster analysis based on MNI, evidences two main groups of species: cluster 1 including *Costa edwardsi* (Roemer, 1838), *Rectobuntonia posteropunctata* (Moyes, 1965), *Pterygocythereis coronata* (Roemer, 1838) and *P. jonesi* (Baird, 1850), respectively, taxa typical of the high dominance samples (CP A and CP B), collected from the lower part of the section, characterized by a sand fraction $\geq 24\%$, and cluster 2, consisting of the remaining species,

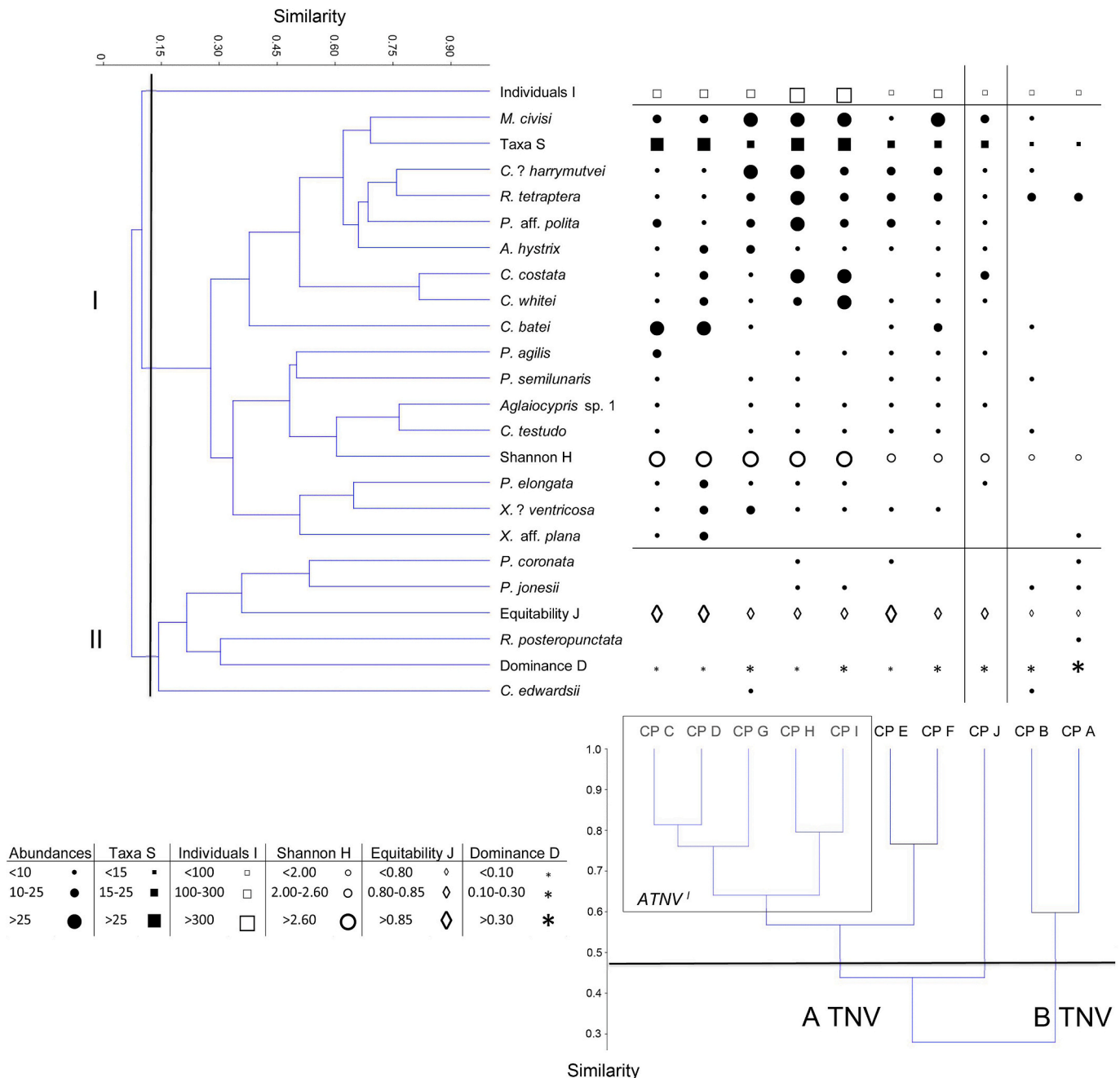


Fig. 4. Cluster analysis on abundance values (TNV) and diversity indices.

associated with the high diversity assemblages.

Low-diversity, high D (dominance) samples, grouped by cluster analysis into cluster A MNI, are placed on the left side of the ordination diagram. Similarly, the trachyleberidid group of cluster 1 (including *Costa edwardsii*, *Rectobuntonia posteropunctata*, *Pterygocythereis coronata* and *P. jonesi*) is positioned in the same area, clearly segregated from the high diversity samples of cluster B MNI, located in the right part of the diagram. The very low diversity and high gravel content (22%) sample CP J displays negative values along both the first and second principal components.

R-mode cluster analysis based on TNV data (Bray-Curtis) lumps the trachyleberidid species characteristic of low diversity assemblages into cluster II, while the remaining taxa all are included in cluster I (Fig. 4). The Q-mode cluster analysis (TNV, Bray-Curtis) aggregates apart the very low diversity sample CP J and evidences two additional groups: cluster B TNV, comprising of the low diversity samples CP A and CP B, and cluster A TNV, including the medium to high diversity assemblages.

In the Principal Component Analysis (PCA), representative species and diversity indices are plotted as variables to highlight their distribution across the ten fossiliferous samples.

In the PCA performed on MNI data (correlation matrix), the first axis explains 37.7% of the variance (eigenvalue = 8.6) and is primarily associated with the diversity indices, capturing the transition from high-dominance assemblages to high-diversity assemblages (Fig. 5a). The

second axis explains 17.0% of the variance (eigenvalue = 3.9). Assemblages CP C, CP D, CP F, interpreted as high diversity/low energy assemblages, are positioned on the negative side of the second axis. In contrast, high diversity-moderate energy assemblages (samples CP E, CP G, CP H, CP I) display positive values along this axis.

In the Principal Component Analysis performed on TNV data, the first axis accounts for 37.9% of the variance (eigenvalue = 8.7) and the second axis for the 17.9% (eigenvalue = 4.1) (Fig. 5b). The results are broadly similar to those obtained from the PCA based on MNI abundance value; however, the ordination diagram derived from MNI data is then more clearly interpretable.

4.2. Population age structure and Specific Population Stage index (SPS)

The assemblages include 1212 valves with intact outline, which could be confidently assigned to adult or juvenile instars. The smallest measured valve ($H = 0.17$ mm; $L = 0.26$ mm) is identified as a young instar (A-5) of *Loxoconcha ovulata*. No juvenile valves pertaining to A-7 and A-8 stages were found in the sediment, with the youngest instar being identified as a A-6 stage of *Cytherella harrymutvei*. These valves were used to calculate the A:J ratio (Table 1 SM), which then ranging from 0.30 (sample CP F) to 3.67 (sample CP A).

A total of 1115 valves, representing species with >10 valves, were used to calculate the Mean Population Stage index (MPS), Population

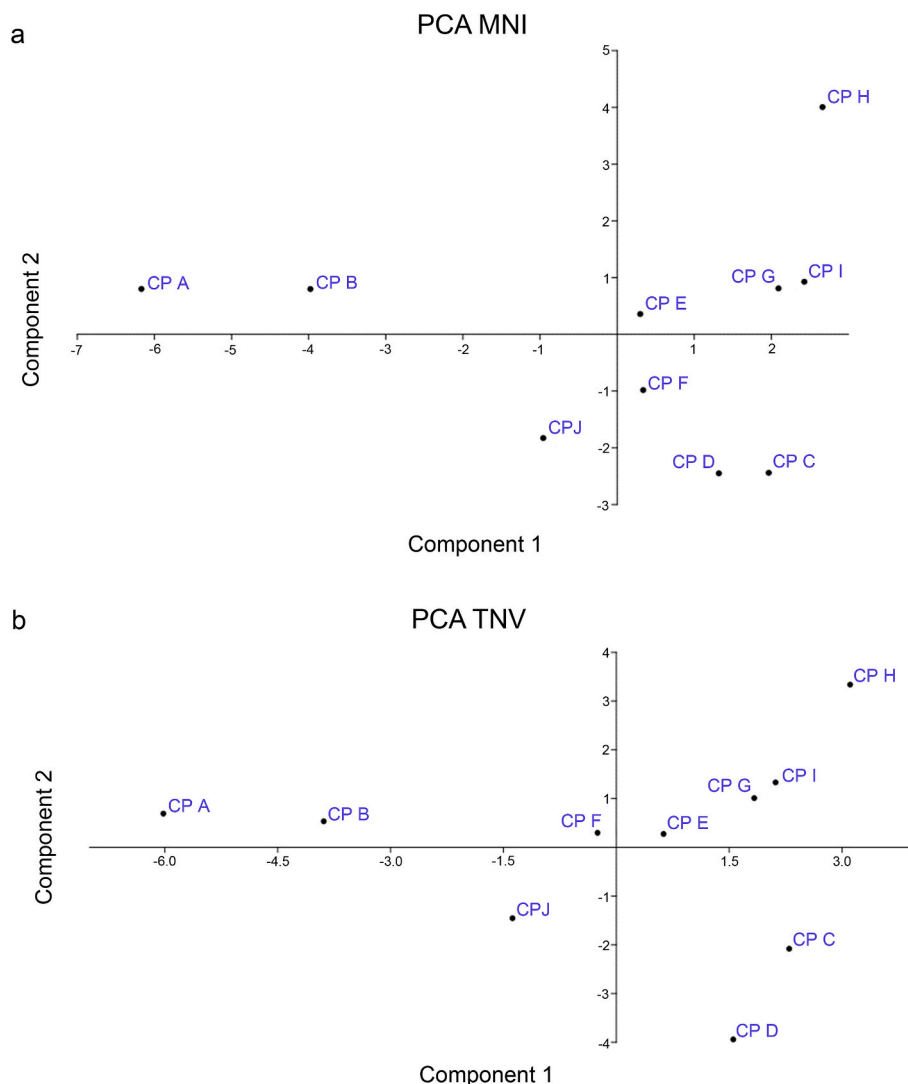


Fig. 5. Scatter plot from Principal Component Analysis (PCA) on the abundance values data a) MNI, b) TNV.

Population Age Structure

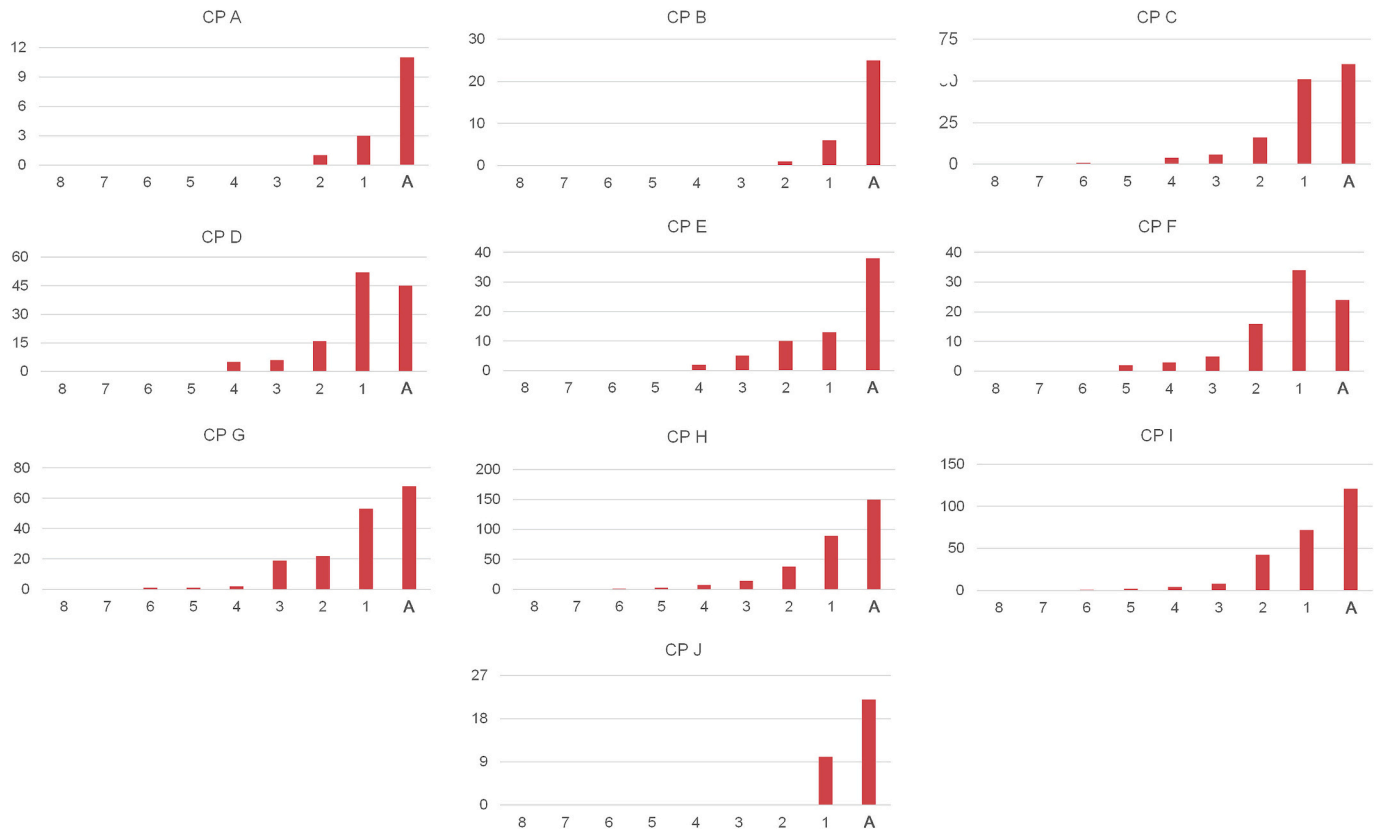


Fig. 6. Assemblage population age structure histograms.

Age Structure and Specific Population Stage index (SPS).

The population age structure was used to generate ten histograms (Fig. 6). The histograms of samples CP A, CP B and CP J (where the combined sand and gravel fractions $\geq 29.7\%$) are consistent with the characteristics of the assemblages from “high energy” environments sensu van Harten (1986; see also Boomer et al. 2003). In contrast, samples CP E, CP G, CP H, CP I, display population age structures resembling those from moderate energy environments as described by Boomer et al. (2003). The histograms for the assemblages from samples CP D and CP F are indicative of a low energy environment (Boomer et al., 2003), whereas sample CP C evidences intermediate features between moderate and low energy environments. The Mean Population Stage index ranges from 7.71 to 8.72 (Table 1 SM) with the “high energy” samples (CP A, CP B and CP J) exhibiting the highest values, ranging from 8.63 to 8.72.

4.3. Statistical analysis on Specific Population Stage index

Statistical analyses on SPS index values were performed on species represented by more than 20 valves, resulting in the inclusion of 1060 valves and 17 species.

The dendrogram obtained from Q-mode cluster analysis (using Euclidean distances) revealed two distinct clusters: A SPS and B SPS (Fig. 7). The samples in Cluster A SPS, (CP A, CP B and CP J) evidences population age structures corresponding to “high energy” environments, as reflected in their histograms. Cluster B SPS includes all other samples, displaying population age structure histograms indicative of low to moderate energy assemblages (Boomer et al., 2003). The r-mode taxa clustering evidences that *Costa* sp.p., *Palmoconcha* sp.p. and *Ruggieria tetraptera* all define a distinct cluster, separate from other ostracod

groups.

In the Principal Component Analysis performed on SPS Index (correlation matrix), the first axis accounts for the 51.8% of the variance and the second axis for the 15.5% (Axis 1: eigenvalue = 8.8, Axis 2: eigenvalue = 2.6) (Fig. 8).

Ruggieria tetraptera, which displaying the highest SPS values in the two lowermost samples (CP A, CP B), lies in the left part of the diagram; in contrast, all other species are situated in the central-right part of the plot. The samples with high diversity-low dominance (CP C, CP D, CP G, CP H, CP I) are located on the right side of the diagram, whereas the low-diversity assemblages are positioned on the left side.

5. Discussion

Palaeoecological investigations of the lower Pliocene successions in the Huelva area all provided a coherent reconstruction of the environmental conditions and evolutionary history of the western Guadalquivir Basin. Nonetheless, variations in methodological approaches, taxonomic focus and stratigraphic sections may lead to minor discrepancies in the respective outcomes.

5.1. Statistical analyses and palaeoenvironment

Statistical analyses based on abundance data and the SPS index indicate a direct correlation with the palaeoecological conditions of the depositional environment. The composition of ostracod assemblages does not suggest any palaeo-depth variations, but reflects a mere stable palaeobathymetry corresponding to the uppermost circalittoral zone. Displaced valves from the upper infralittoral zone or transported by continental waters are rare.

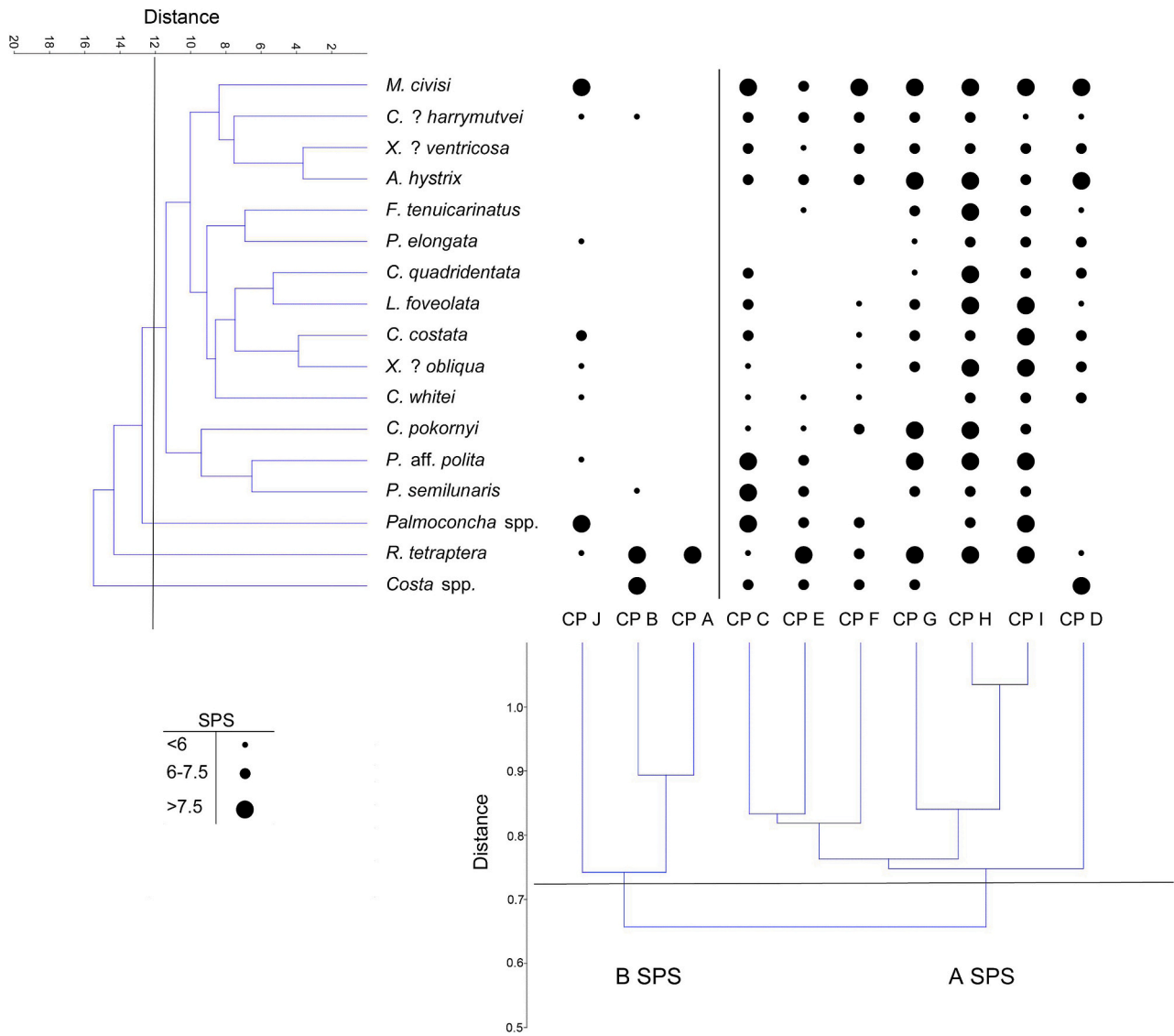


Fig. 7. Cluster analysis on Specific Population Stage (SPS) index data.

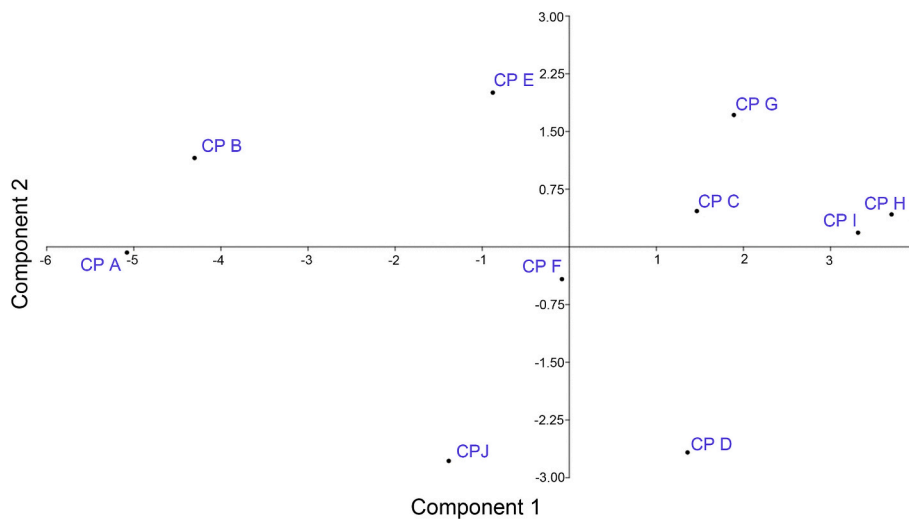


Fig. 8. Scatter plot from Principal Component Analysis (PCA) on Specific Population Stage (SPS) index data.

Assemblage features, including taxonomic composition, abundance and diversity metrics, and population age structure, evidence clear relationships with water energy. The SPS index, originally established by Aiello et al. (2024a) on assemblages from the boundary between the upper and lower circalittoral subzones (127 m bsl) in the Tyrrhenian Sea, highlighted conditions where displaced infralittoral and upper circalittoral taxa were abundant. By contrast, in the Bonares–Casa del Pino assemblages, both preservation state and population age structure indicate that all statistically significant species are autochthonous. Analyses using the SPS index, unaffected by allochthonous input, confirm the sensitivity of population age structure to water energy, acting both post-mortem and during the life (and molting) of organisms.

Cluster analyses (dendrograms, Figs. 3–4) group samples CP C, CP D, CP G, CP H, and CP I into cluster B(MNI) and subcluster A(TNV). In PCA (MNI) and PCA(TNV) plots (Fig. 5), these samples are positioned to the right, while samples CP A, CP B, and CP J cluster to the left. These latter form cluster B(SPS) in analyses based on the Specific Population Stage index (Fig. 7). Overall, the statistical results distinguish two assemblage groups:

- **Group 1** (CP A, CP B, CP J): low abundance and Shannon H' diversity, high dominance, elevated A:J ratios, and high MPS values (Table 1 SM).
- **Group 2** (CP C, CP D, CP G, CP H, CP I): high abundance and diversity indices, with low dominance, A:J ratios, and MPS values (Table 1 SM).

In the absence of significant allochthonous taxa and without evidence of any palaeodepth change, observed variations in population age structures, A:J ratios and diversity/abundance indices are best explained by differing hydrodynamic regimes. Samples CP A, CP B and CP J were deposited in relatively high-energy environments, where juvenile shells were largely removed (as also shown by the PAS histograms in Fig. 6). Conversely, samples CP C, CP D, CP G, CP H, and CP I represent deposition in calmer waters, while assemblages CP E and CP F display intermediate characteristics.

A trachyleberidid association composed of *Costa edwardsii*, *Rectobuntonia posteropunctata*, *Pterygocythereis coronata*, and *P. jonesi* [cluster I (Fig. 3) and II (Fig. 4)] characterizes the low-diversity samples CP A and CP B from the lower part of the section, deposited under relatively high-energy conditions.

5.2. Vertical zonation in shallow marine environments light versus hydrodynamics

In palaeoecological studies of shallow marine successions, authors adopt varying zonation schemes based either on photic influences on benthic communities (“vertical zonation in the benthos”), according to Pérès, 1982) or on morphodynamic criteria (“shoreline profile zonation” according to Reading and Collinson, 1996; “depth-related divisions of the marine realm” according to Nichols, 2009) emphasizing the interaction between hydrodynamics and substrate characteristics (e.g. Hallermeier, 1981; Niedoroda et al., 1984; Anthony and Aagaard, 2020). Consequently, the lower Pliocene deposits of the western Guadalquivir Basin can be assigned within either “infralittoral-circalittoral” or “shoreface-offshore” zones. According to Pérès (1982), the lower boundary of the littoral zone (upper limit of the circalittoral zone) corresponds to the maximum depth allowing the survival of seagrasses and photophilic algae. On the other hand, both Reading and Collinson (1996) and Nichols (2009) recognized a transitional zone between shoreface and offshore environments, the “Offshore Transition”. This term is often used interchangeably with “lower shoreface” (e.g., Anthony and Aagaard, 2020), though we favour herein the former for its more consistent delineation of boundaries. The upper boundary of the offshore transition (lower limit of the shoreface) aligns with the mean fair-weather wave base (mean FWWB, or “depth of closure” in

engineering sciences; Nicholls et al., 1996; Nicholls et al., 1998) while its lower limit (upper limit of the offshore) coincides with the mean storm wave base (mean SWB, Reading and Collinson, 1996; Nichols, 2009). For storm influences on sedimentary sequences, such as the Arenas de Huelva Formation, integrative application of both approaches, eschewing fixed depth values in favour of palaeoenvironmental interpretation, is preferable. The Gulf of Cadiz, including the lower Guadalquivir Basin during the Pliocene, represents a transitional Atlantic embayment showing notable Mediterranean affinities, reflected in the ongoing debate over its biogeographic classification within Lusitanian or Moroccan provinces (review in Aiello et al., 2024b, and references therein).

The boundary between the infralittoral and circalittoral zones, as originally defined by Peres and Picard (1964) and later refined by Pérès (1982) for the Mediterranean, can be applied to the Atlantic shelf, with adjustments for regional bathymetric variability. Templado et al. (1993), in their study of marine faunas along the southern Iberian Peninsula, observed that the circalittoral zone begins at a shallower depth (12–15 m) on the Atlantic side, in contrast to adjacent Mediterranean areas where this boundary may extend to approximately 45 m. Later, Templado et al. (2012) provided a slightly revised estimate, indicating that the infralittoral/circalittoral boundary along the Atlantic coast generally does not exceed 15–20 m. Accordingly, the present study adopts a conventional depth of 15 m as the infralittoral–circalittoral boundary for the southern Lusitanian shelf (Fig. 9), consistent with the 35 m limit commonly applied in the western Mediterranean (Pérès, 1982).

While using a uniformitarian approach, it is important to acknowledge that such depth thresholds may have varied under different palaeoenvironmental conditions. Therefore, we cannot rule out the possibility that the infralittoral-circalittoral limit occurred at a different depth during the Zanclean. During the early Pliocene, the lower Guadalquivir basin, classified within the AAPMU1 (Atlantic Andalusian Pliocene Mollusc Unit 1) palaeobiogeographic unit by Monegatti and Raffi (2007), was situated at the northern margin of the Mediterranean–West African Pliocene tropical province. Alternatively, the southwestern lower Pliocene Atlantic successions of the Iberian Peninsula may be assigned to the MPMU1 (Mediterranean Pliocene Mollusc Unit 1) of Raffi and Monegatti (1993) and Monegatti and Raffi (2001), subsequently named MPPMU1 (Mediterranean Plio-Pleistocene Mollusc Unit 1) by Landau and Mayoral (2011).

From a climatic standpoint, the Guadalquivir basin likely exhibited conditions analogous to those of the Atlantic coastal environments of Africa south of Cabo Verde (Silva and Landau, 2007), corresponding to the Sahelian upwelling ecoregion of Spalding et al. (2007). Along the North African Atlantic coasts, the depth of the infralittoral-circalittoral boundary increases progressively southwards. Bayed and Glémarec (1987) placed this boundary in the range 15–20 m bsl on the Moroccan shelf, whereas Le Loeuff et al. (2000) reported a depth limit of 25–30 m bsl, in the coastal waters of Ivory Coast. Based on these analogues, it remains then still possible that, during the early Pliocene, the limit between infralittoral and circalittoral zones in the Guadalquivir Basin was situated at approximately 25 m bsl. Morphodynamically, the basin may have resembled the present-day Gulf of Cadiz, where the “wave base level” and the “mean level of the SWB” were located at water depths of 20 and 30–35 m bsl, respectively (Morales, 1993; Hernández-Molina et al., 2000; Lobo et al., 2001). Therefore, we propose that the “Offshore Transition” (sensu Reading and Collinson, 1996) zone during the early Pliocene in the Guadalquivir Basin extended from 20 m bsl to 30–35 m bsl (Fig. 9).

Prior palaeoecological interpretations of sedimentary sequences within the Arenas de Huelva Formation, reveal inconsistent terminology use across studies (Table 4 SM.) Nonetheless, palaeoclimatic reconstructions generally converge on a tropical-subtropical zone, with estimated mean annual temperatures of 20–25 °C and annual temperature variability not exceeding 6 °C (González Delgado, 1987).

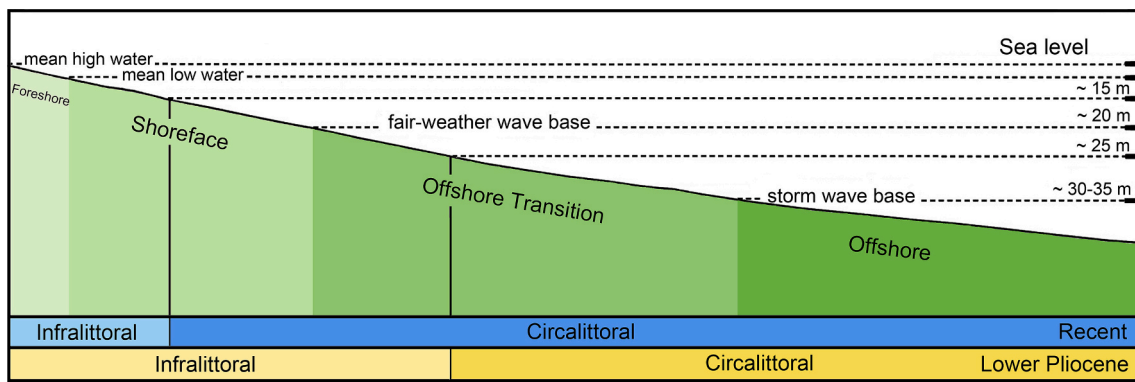


Fig. 9. Vertical zonation of Recent (Gulf of Cadiz) and Lower Pliocene (Arenas de Huelva Formation) shallow marine Atlantic waters of the southwestern Iberian Peninsula. Depth estimates of the infralittoral-circalittoral boundary are based on Templado et al. (1993, 2012); fair-weather and storm wave base depths follow Morales (1993), Hernández-Molina et al. (2000) and Lobo et al., 2001. For the palaeodepth of the lower Pliocene infralittoral-circalittoral boundary see Discussion.

According to the adopted terminological framework, most researchers have considered the Arenas de Huelva as having been deposited predominantly within the lower part of an offshore transition environment (v. Fig. 5 in González Delgado et al., 1995), in the upper part of the circalittoral zone, with regional variations within the basin. Several studies (e.g., González-Regalado, 1989; Ruiz et al., 1996, 2008; González-Regalado and Ruiz-Muñoz, 1996; Toscano, 2016; see Table 4 SM) further identified the basal glauconitic levels as representative of offshore-lower circalittoral depositional environments.

The ostracod assemblages of the Bonares-Casa del Pino Section provide a valuable basis for comparing palaeoecological characteristics of autochthonous taxa with those of both extant and extinct species, thereby enhancing interpretations of the depositional settings. Numerous previous studies (see Table 4 SM) have treated individual sections of this formation as representative of broader depositional conditions. Our interpretations are framed within this established stratigraphic and paleoenvironmental context and are consistent with the regional body of literature. Nevertheless, we acknowledge that our primary dataset is confined to one measured section, and our conclusions should be understood within this stratigraphic and spatial framework.

5.3. Autochthony, allochthony and palaeodepth interpretation

The preservation state and distribution patterns of ostracod assemblages from the Bonares-Casa del Pino section suggests that, except for rare valves of *Darwinula stevensoni*, a non-marine species, ostracods are predominantly autochthonous and typical of infra-circalittoral marine waters. Two potential exceptions were evaluated. Firstly, the rare presence of *Urocythereis* sp.p., a genus typically found in very shallow marine waters (e.g., < 30 m in the Gulf of Pozzuoli; Aiello et al., 2021) may indicate minor displacement from shallower settings. However, their low abundance precluded a robust statistical evaluation using the Specific Population Species (SPS) index. Secondly, the frequent occurrence of the species described by Ruiz et al. (2018) as *Cyprideis civisi*, raises questions given that the genus *Cyprideis* is primarily associated with non-marine environments (Benson, 1961; Van Morkhoven, 1963; Sandberg, 1964; Ligios and Gliozzi, 2012) and its records in fully marine environments generally consist of scattered specimens or are due to allochthony (Bonaduce et al., 2004). Nonetheless, based on morphological features of the specimens of *C. civisi* collected in the Bonares-Casa del Pino sediments, as well as its population age structure and the statistical analysis performed on the SPS index, led us to assign this species to the genus *Miocyprideis* consisting of both brackish and marine species (Yasuhara et al., 2018). *Miocyprideis civisi* displays two rounded frontal scars (Fig. 2.P), as in the type species of *Miocyprideis* (*M. janoscheki* Pl. 18, Fig. 11 in Kollmann, 1960) whereas, in the type species of *Cyprideis*

(*Candona torosa* Jones, 1859), the frontal scar is V-shaped (Schornikov, 2015). This taxonomic reassignment is supported by comparative analysis using cluster analysis, principal component analysis (PCA) and SPS histograms (Figs. 6–8), following the methodological framework of Aiello et al. (2024a). *Miocyprideis civisi* consistently groups with autochthonous species and displays characteristic histograms of autochthonous forms.

Quantitative analyses thus indicate that all the statistically significant species (i.e., relative abundance >5% and ≥ 10 valves), are autochthonous.

In the absence of significant allochthony, the statistical analyses carried out on SPS and abundance data identify water energy as the primary structuring factor, supporting the depositional model proposed by González Delgado et al. (1995), in which the Arenas de Huelva Formation had been accumulating within the Offshore Transition Zone, above the storm wave base level. The total absence of juvenile ostracod shells in the fine fraction (63–125 μm), further indicates winnowing and sediment bypassing, characteristic of high energy bottom conditions.

Bathymetric and palaeobathymetric data for the dominant and secondary autochthonous species (*Ruggieria tetraptera*, *Miocyprideis civisi*, *Paracypris* aff. *polita*, *Costa batei*, *Acanthocythereis hystrix*, *Cytherella* ? *harrymutvei*, *Palmoconcha agilis*, *Capsacypthere costata*, *Carinocythereis whitei*), as well as the genera *Xestoleberis*, *Aglaioocypris*, *Cytherella*, *Palmoconcha*, *Propontocypris* and *Semicytherura*, all support a shallow marine palaeoenvironment characterized by ostracods from both lower infralittoral and upper circalittoral zones.

Accordingly, we considered the Bonares-Casa del Pino depositional setting as analogous to the EUNIS habitat A5.35 (Circalittoral sandy mud), as defined by Davies et al. (2004), or the ‘‘Circalittoral muds and sandy muds’’ habitat (code: 030403) described by Templado et al. (2012), adjusted for Pliocene climatic conditions. These habitats are possibly similar to those of the Arenas de Huelva sediments, representing, at least in part, their modern analogue.

These results align with previous bathymetric assessments (Mayoral, 1986; González Delgado, 1987; González-Regalado, 1989; García et al., 2009; García et al., 2011; González-Regalado et al., 2009), placing the deposition at ≈ 30 m bsl in the upper part of the circalittoral zone, (Fig. 9). The tropical-subtropical climate and moderate to relatively high hydrodynamic energy likely shaped an ostracod assemblage featuring both infralittoral and circalittoral species; for instance, typically circalittoral taxa such as the genus *Parakrithe*, common in open shelf and bathyal environments and very rare in infralittoral waters, and ostracods characteristic of shallow waters as the genus *Miocyprideis*. It is worth mentioning that the genus *Buntonia*, commonly recorded in the circalittoral Atlantic late Neogene sediments and very rare in infralittoral waters, is not present in the Bonares-Casa del Pino section, and that the circalittoral genus *Cytheropteron* is virtually absent (only one young

instar found in the sample CP C). Its thin ventral expansions (alae) are considered indicative of a lifestyle in which the organism crawls on bottom sediments (Elofson, 1941) and, consequently, it is possible that the relatively high energy water conditions were inhospitable for *Cytheropteron*.

The occurrence of trace fossils in the fossiliferous beds of the Huelva Sands Formation provides a detailed record of storm-related depositional events (Mayoral and Reguant, 1995). For instance, the sequence of processes reconstructed from *Scalichnus*, i.e., colonization of stable soft bottoms, storm reworking with fragmentation and abrasion of shells, rapid redeposition and infilling of traces, and subsequent recolonization, illustrates alternations between episodic high-energy events and background conditions (Santos et al., 2018). This interpretation is consistent with the ostracod record, which independently reveals phases of high-energy sedimentation. Ostracod assemblages document the selective removal of juvenile valves and shifts in abundance/diversity indices that correspond to energetic hydrodynamic regimes. Thus, while *Scalichnus* documents storm-induced shell concentrations preserved within burrows (tubular tempestites), ostracod assemblages recorded the same events through community structure and population dynamics. Together, these lines of evidence provide a complementary palaeo-environmental reconstruction, highlighting the interplay between background colonization processes and episodic storm activity on the sea floor.

5.4. Ostracod population age structure and palaeoenvironments

Ostracods grow by molting, consequently both fossil assemblages and subrecent dead assemblages generally show the presence of different developmental stages, including young instars and adult specimens. Unlike other groups of calcareous meiofaunal organisms, such as benthic foraminifera, the presence of juvenile shells indicates premature death only when the two valves are joined to form a carapace, whereas loose juvenile valves may be found in the sediments as consequence of molting. Previous investigations (Whatley, 1983, 1988; van Harten, 1986; Boomer et al., 2003; Ruiz et al., 2003; Aiello et al., 2024a) revealed that population age structure calculated assigning to nine development stages (adult and eight juvenile stages) can be influenced by water-energy variables, proposing a number of type-histograms corresponding to different depositional environments and autochthonous, allochthonous or mixed assemblages, and statistical methods based on Specific Population Stage index. Population age structure, when used in conjunction with traditional analyses such as the evaluation of the state of preservation of the shells, the examination, from a uniformitarian perspective, of the distribution data at specific or generic level, and significance of grain size parameters, is an appropriate tool for assessing palaeoenvironmental characters of fossiliferous sequences. The Specific Population Stage index method has been applied by Aiello et al. (2024a) on dead assemblages collected in Mediterranean circalittoral waters, well below the storm wave base level (127 m bsl), in low energy environment allowing the preservation of small and delicate shells, allowing the discrimination of the very common allochthonous specimens displaced from infralittoral and upper circalittoral zones. Conversely, in the Zanclean upper shelf sedimentary sequence of Bonares–Casa del Pino, the results of all the analyses are consistent with the hypothesis that deposition occurred in moderate to high energy waters, where displaced specimens are very rarely preserved. Thin shelled taxa and valves <125 µm, characteristics of very low energy waters, are not present, confirming a palaeoenvironment dominated by discontinuous processes of “winnowing and bypassing” (González Delgado et al., 1995) of sediments.

6. Conclusions

The Zanclean succession exposed at the Bonares–Casa del Pino section (6 m thickness; 11 samples) provides a detailed ostracod-based

palaeoenvironmental reconstruction for the lower Pliocene Arenas de Huelva Formation in the lower Guadalquivir Basin. The studied assemblages, comprising 1642 valves and 64 species, reflect the biogeographic setting of the northern sector of the Mediterranean–West African Pliocene tropical province, corresponding to the Atlantic Andalusian Pliocene Mollusc Unit 1 (AAPMU1) as defined by Monegatti and Raffi (2007).

The taxonomic composition, quantitative parameters (diversity, dominance, A:J ratios), and population age structure analyses consistently indicate deposition in shallow marine conditions characterized by moderate to relatively high bottom-water energy. The extreme rarity of early juvenile instars supports sedimentary conditions dominated by winnowing and bypassing processes. Integration of abundance-based statistics and the Specific Population Stage (SPS) index points to hydrodynamic energy, rather than palaeobathymetric variation, as the main structuring factor within the investigated interval. Overall, the data support interpretation of the sedimentary environment as part of the Offshore Transition Zone sensu Reading and Collinson (1996), near the infralittoral-circalittoral boundary, at an estimated palaeodepth of approximately 25–30 m bsl.

All statistically significant species (relative abundance >5% and ≥ 10 valves) are interpreted as autochthonous. The reassignment of *Cypriideis civisi* to *Miocypriideis civisi* is supported by both diagnostic morphological characters and population-age-structure analysis, indicating the predominance of fully marine infra-circalittoral taxa and excludes significant brackish-water influence.

The depositional interpretation proposed here is consistent with previously published sedimentological and palaeontological interpretations of the Arenas de Huelva Formation in other sectors of the basin. However, the present results are derived from a single, well-exposed section and therefore pertain directly to this specific stratigraphic interval. While the formation is regionally documented as laterally continuous and sedimentologically homogeneous, broader generalizations should be understood within the framework of existing regional studies rather than as stand-alone basin-wide conclusions of the present work.

Finally, this study represents the first application of the Specific Population Stage (SPS) method to fossil ostracod assemblages. The agreement between SPS-derived results, traditional assemblage metrics, sedimentological characteristics (González Delgado et al., 1995), and independent palaeontological evidence (Mayoral and Reguant, 1995) suggests that the method can be applied in moderately high-energy shallow marine settings, while acknowledging the importance of contextual geological constraints.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marmicro.2026.102572>.

CRedit authorship contribution statement

G. Aiello: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **D. Barra:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **M.L. González-Regalado:** Writing – review & editing, Validation, Formal analysis, Data curation. **A. Infante:** Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **I. Mazzini:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Conceptualization. **R. Parisi:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **F. Ruiz:** Writing – review & editing, Validation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Appendix A - Supplementary.

List of ostracod species.

● indicates allochthonous species.

Acanthocythereis hystrix (Reuss, 1850)
Aglaioocypris aff. *rara* (Müller, 1894)
Aglaioocypris sp. 1 Bonaduce, Ruggieri, Russo and Bismuth, 1992
Aglaioocypris sp. 2
Aurila convexa (Baird, 1850) sensu lato
Aurila lanceaeformis Uliczny, 1969
Basslerites compressus Bonaduce, Ruggieri, Russo and Bismuth, 1992
Bosquetina carinella (Reuss, 1850)
Callistocythere praecincta Ciampo, 1976
Callistocythere aff. *vidua* Ciampo, 1986
Capsocythere costata (Moyes, 1965)
Carinocythereis whitei (Baird, 1850)
Carinovalva testudo (Namias, 1901)
Celtia quadridentata (Baird, 1850)
Cimburila vitrocincta (Ruggieri, 1950)
Cistacythereis pokornyii (Ruggieri, 1962)
Costa batei (Brady, 1866)
Costa edwardsii (Roemer, 1838)
Cytherella ? *harrymutvei* Stambolidis, 1980
Cytherella scutulium Ruggieri, 1976
Cytherella sp. 1
Cytheretta aff. *variabilis* Oertli, 1956
Cytheridea neapolitana Kollmann, 1960
Cytheropteron ? *ascolii* Carbonnel, 1969
Darwinula stevensoni (Brady and Robertson, 1870) ●
Eucythere prava Brady and Robertson, 1869
Flexus tenuicarinatus (Capeder, 1902)
Kroemmelbeinella ? *biangulata* (Terquem, 1878)
Ionicythere parva (Seguenza, 1880)
Leptocythere foveolata Moyes, 1965
Leptocythere levis (Müller, 1894)
Loxococoncha aff. *elliptica* Brady, 1868
Loxococoncha ovulata (Costa, 1853)
Macrocyprina ? *succinea* (Müller, 1894)
Miocyprideis civisi (Ruiz et al., 2018)
Neocytherideis aff. *subulata* (Brady, 1868)
Palmoconcha agilis (Ruggieri, 1967)
Palmoconcha dertobrevis (Ruggieri, 1967)
Palmoconcha ? *subrugosa* (Ruggieri, 1977)
Paracypris aff. *polita* Sars, 1866
Parakrithe semilunaris Aiello, Barra, Abate and Bonaduce, 1993
Phlyctenophora affinis (Schneider, 1953)
Pontocythere elongata (Brady, 1868)
Procytherideis cf. *retifera* Ruggieri, 1978
Propontocypris aff. *declivis* (Müller, 1894)
Propontocypris ? *dispar* (Müller, 1894)
Propontocypris ? sp. 1 Barbeito-Gonzalez, 1971
Pterygocythereis coronata (Roemer, 1838)
Pterygocythereis jonesii (Baird, 1850)
Rectobuntonia posteropunctata (Moyes, 1965)
Ruggieria tetraptera (Seguenza, 1880)
Sagmatocythere cf. *grateloupiana* (Bosquet, 1852)
Sagmatocythere napoliana (Puri, 1963)
Semicytherura robusta Bonaduce, Ciampo and Masoli, 1976
Semicytherura ? *sulcata* (Müller, 1894)
Semicytherura ? *ventroconvexa* Krstić, 1983
Urocythereis favosa (Roemer, 1838) ●
Urocythereis praelonga (Terquem, 1878) ●
Xestoleberis communis Müller, 1894
Xestoleberis aff. *dispar* Müller, 1894
Xestoleberis ? *obliqua* Terquem, 1878
Xestoleberis aff. *plana* Müller, 1894
Xestoleberis aff. *subtruncata* Dieci and Russo, 1964
Xestoleberis? *ventricosa* Müller, 1894

Data availability

The data that support the findings of this study are openly available in Zenodo <https://doi.org/10.5281/zenodo.18161389>

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