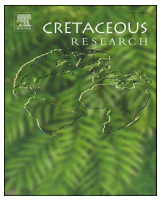
Cretaceous Research 175 (2025) 106158

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes



New species of ostracods from the non-marine upper Barremian (Lower Cretaceous) of Vadillos-1 (Cuenca, Spain)

Marta Díez-Somolinos [a, *], Fernando Barroso-Barcenilla [a, b], Mélani Berrocal-Casero [a, b], Julio Rodríguez-Lázaro [c], Paloma Sevilla García [b], Benjamin Sames [d]

[a] Department of Geology, Geography and Environment (Paleolbérica Research Group), University of Alcalá, 28805, Alcalá de Henares, Spain
[b] Department of Geodynamics, Stratigraphy and Palaeontology (Procesos Bióticos Mesozoicos Research Group), Complutense University of Madrid, 28040, Madrid, Spain
[c] Department of Geology, University of the Basque Country, 48940, Leioa, Spain
[d] Department of Geology, University of Vienna, 1090, Vienna, Austria

ARTICLE INFO

Article history:
Received 9 December 2024
Received in revised form
24 April 2025
Accepted in revised form 25 April 2025
Available online 2 May 2025

Keywords:
Non-marine ostracods
Cypridea
Wealden facies
Palaeolimnology
Beteta Gorges
Upper Barremian
Lower Cretaceous

ABSTRACT

The upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1 is located in the northern part of the province of Cuenca, Spain. It comprises a sedimentary sequence in Wealden-type facies, rich in non-marine ostracods. In these materials, species of *Cypridea* have been identified, in particular *Cypridea isasae*, characterized by its rounded cyathus, and *Cypridea ventriosa*, being distinguished by the subcircular outline and a large rostrum separated by a very marked alveolar notch. Additionally, numerous specimens of *Cypridea vatra* nov. sp., defined by its well-marked anterior cardinal angle, and *Cypridea marihoni* nov. sp., well defined by its ornamented carapace, have been described. Other specimens have been assigned to the genus *Cyclocypris*, specifically to *Cyclocypris bamba* nov. sp., characterized by its inflated carapace and piriform outline. These taxa are reported for the first time in the study area and are characteristic of alluvial and palustrine palaeoenvironments. This analysis provides the basis for future studies that will allow a more precise interpretation of non-marine Barremian palaeoenvironments.

1. Introduction

Ostracods are microscopic crustaceans with a body protected by two mineralized valves recorded from the Ordovician to Recent. They have significant fossilization potential, being commonly found in marine, transitional and non-marine or continental (mainly lacustrine) sediments, and are excellent palaeoenvironmental indicators and biostratigraphic markers, being particularly useful in non-marine deposits (e.g., Anderson, 1985; Horne, 1995, 2009; Rodríguez-Lázaro and Ruiz-Muñoz, 2012; Sames and Horne, 2012; Trabelsi et al., 2024). Despite their great application potential, few articles on ostracods from the Mesozoic non-marine environments of the Cretaceous of Spain have been published in the last decades (e.g., Kneuper-Haack, 1966; Brenner, 1976; Swain, 1993; Schudack and Schudack, 2009a; Buscalioni and Fregenal-Martínez, 2010; Canudo et al., 2010). Other available data are based on relatively old works that require taxonomic revision and updating or they are focused on specific sites, limiting the possibilities for identification and comparison of the material. The present work aims for gaining a better understanding of the ostracods from the Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, in Beteta Gorges (northern part of Cuenca province, Spain).

The Cretaceous of Cuenca is extremely rich in palaeontological records that provide valuable information for the reconstruction of ecosystems, fauna and flora in this period of the history of life on Earth. In recent years, palaeontological prospecting and sampling of Lower Cretaceous rocks have been carried out in the study area (e.g., Barroso-Barcenilla et al., 2017; Bravo et al., 2018). Macro- and microfossils of great scientific interest have been found at several sites, including the palaeontological site of Vadillos-1 (e.g., Barroso-Barcenilla et al., 2017; Berrocal-Casero et al., 2023). These fossils, along with the ostracods analyzed in this study, contribute to palaeoenvironmental reconstructions and establish faunal and floral relations to other nearby sites such as Las Hoyas (Prieto and Díaz-Romeral, 1989; Buscalioni and Fregenal-Martínez, 2010).

Few studies are focusing on the taxonomy of ostracods, their palaeoenvironmental interpretation, and application to the Lower Cretaceous of the Iberian Peninsula. Most of these works use other

* Corresponding author.
E-mail address: marta.diezs@uah.es (M. Díez-Somolinos).

https://doi.org/10.1016/j.cretres.2025.106158

elements of the fossil record to develop palaeoenvironmental reconstructions, just mentioning that ostracods are present and can be useful for such analyses. Ostracods have been found in several Lower Cretaceous palaeontological sites in Spain, including the Valanginian–Barremian of the Cantabrian Mountains in Burgos (Ramírez del Pozo, 1971), the Hauterivian–Barremian in the Sierra de Cameros in La Rioja (Kneuper-Haack, 1966; Aguirrezabala et al., 1985), the Kimmeridgian–Aptian in northeastern Spain (Brenner, 1976), the Berriasian–Barremian of the Iberian Basin (Schudack and Schudack, 2009a) and the Barremian of the localities of Uña (Henkel and Krebs, 1969; Gómez et al., 2001), Las Hoyas (e.g., Prieto and Díaz-Romeral, 1989; Buscalioni and Fregenal-Martínez, 2010), Buenache de la Sierra (Francés and Sanz, 1989; Buscalioni et al., 2008), La Cantalera (Canudo et al., 2010) and Beteta Gorges (Barroso-Barcenilla et al., 2017) in the province of Cuenca.

Among the few European sites recording non-marine deposits of Barremian age where ostracods have been recorded and which were relatively close to the study area, the United Kingdom (England) is the most prolific. During his scientific career, Anderson (1939, 1985, and references therein) described, and biostratigraphically applied, a large number of ostracods from the "English Purbeck-Wealden" sequence, later revised by Horne (1995, 2009). In this context, only the Upper Weald Clay Formation is Barremian–lowermost Aptian, and in these works the ostracod biozonation (subzones) is based on the ranges of abundant ostracod species of the genus *Cypridea* Bosquet, 1852, species of which are characteristic to, or dominate, the Wealden-type ostracod faunas.

Owing to the available data and research history (Horne, 1995), the successions of the English "Purbeck" and "Wealden" (now the Purbeck Group and Wealden Supergroup respectively) provide one of the most complete stratigraphic records of the Purbeck-Wealden interval (uppermost Tithonian? to lowermost Aptian), particularly with respect to ostracods (Anderson, 1985, and references therein; Horne, 1995, 2009; see also Sames and Horne, 2012 for more context). Research progress over the last two decades, however, leads to the conclusion that for palaeoclimatic reasons the Boreal English Purbeck-Wealden might be more limited in its value as global reference area than previously assumed regarding non-marine ostracods (and charophytes). This particularly applies when comparing more southern "Tethyan" ostracod faunas (and charophyte floras) – such as those from Spain – to their English stratigraphic equivalents. Based on charophytes, Vicente et al. (2024, also supported by data of Trabelsi et al., 2024) have defined a separate Barremian–lower Aptian (potentially entire Lower Cretaceous) biogeographic region in the Central Tethyan Archipielago, which, among others, includes Iberian (Spain and Portugal) and North African (mainly Morocco and Tunisia) islands. Confirmation is needed as to whether contemporaneous non-marine ostracod bioprovinces are more or less identical, but this is highly probable because of the same dispersal mechanisms of both non-marine ostracods and charophytes. Consequently, the main biostratigraphic areas for supra-regional faunal and biostratigraphic correlation of the ostracod fauna studied herein are, besides the Iberian Peninsula, North Africa (Tunisia), and Great Britain (England).

Considerable progress on the biostratigraphic correlation of the marine to non-marine Western European Tethyan and Boreal Cretaceous was provided by results of the International Geoscience Programme (IGCP) project IGCP-362 "Tethyan-Boreal Cretaceous Correlation" (1993–1997). Hoedemaeker and Herngreen (2003, and references therein) provide a detailed integrated correlation chart, correlating the standard Tethyan Berriasian to Barremian successions of France and Spain with the Boreal successions of England, Germany and strata in the subsurface of the Netherlands. These charts include huge biostratigraphical, magnetostratigraphical, and sequence-stratigraphic correlation data-sets, including the ostracods where applicable (England and Germany). Sames and Horne (2012, p. 36) noted that "… the overall picture may change considerably with the shifting interpretation of integral parts. Nevertheless, the data as presented in this chart (Hoedemaeker and Herngreen, 2003) are a good starting point for supraregional correlations, although, bearing the supraregional to global approach in mind, we partially need to overcome the Eurocentric view."

Against this background, other central to northern European Wealden-type successions that might be considered for faunal comparisons for their richness in ostracods are those of the "NW German Wealden" (e.g., Martin, 1940; Wolburg, 1959; Wick and Wolburg, 1962; Elstner and Mutterlose, 1996). However, the "German Wealden" is both Boreal (see above) – such as the English Wealden – and limited to the lowermost Cretaceous (Berriasian–lower Valanginian), and is, thus, in trend older than the "English Wealden" (Wealden Supergroup or Wealden Series of some authors, Valanginian to lowermost Aptian) of the Weald and Wessex sub-basins of southern England. It is also much older than the Barremian Spanish succession dealt with herein.

2. Geological context and geographical setting

The upper Barremian palaeontological site of Vadillos-1 is located in the Beteta Gorges (province of Cuenca, Central Spain). There, the successions in Wealden-type facies belong to the El Collado Sandstone and Clay Formation, which has recently been reassigned in the region to the Tragacete Formation (Fregenal-Martínez et al., 2017) (Fig. 1. A–B). The stratigraphic sequence consists of, from base to top, 15 m of brown mudstones (B level), 7.5 m of grey mudstones (G level), and more than 4 m of red clays (R level), separated by gradual boundaries with carbonate nodules (Fig. 1. C–D). Their depositional environment is interpreted as representing a muddy, alluvial and palustrine floodplain (Barroso-Barcenilla et al., 2017; Bravo et al., 2018).

To date, the G level of Vadillos-1 (Fig. 1. C–D) is the best fossiliferous bed that has yielded numerous micro- and macroremains of plants, vertebrates, and invertebrates. The samples collected in Vadillos-1 provided a rich assemblage of microfossils consisting of, besides the ostracods, charophytes and palynomorphs, a variety of small vertebrate remains belonging to fishes (scales and teeth), amphibians, crocodilians (teeth, scutes, and eggshells) and theropod dinosaurs (bones and teeth) (e.g., Barroso-Barcenilla et al., 2017; Ruiz-Galván et al., 2017; Bravo et al., 2018; Barrón-López et al., 2019; Berrocal-Casero et al., 2023). Macrofossils are also known from Vadillos-1, represented by carbonized plant macrofossils, mollusks, turtles, and dinosaurs (ornithopods, ankylosaurs, and theropods) (Barroso-Barcenilla et al., 2017; Berrocal-Casero et al., 2025).

The charophyte assemblage identified in Vadillos-1 allowed to date this site as upper Barremian (Barroso-Barcenilla et al., 2017). This assemblage corresponds to the one that has been described from the stratigraphically equivalent La Huérguina Formation, which belongs to the *Ascidiella cruciata-Pseudoglobator paucibracteatus* charophyte biozone (upper Barremian–lower Aptian) (Vicente and Martín-Closas, 2013; Pérez-Cano et al., 2022).

3. Materials and methods

The sedimentary rocks sampled were taken from different levels of the mudstone sequence, focusing mainly on horizons with abundant organic material. Systematic sampling was conducted at 9 consecutive levels from the base to the top of the fossil-bearing section known as Vadillos-1 (VD1-M1 to VD1-M9: Fig. 1D). The

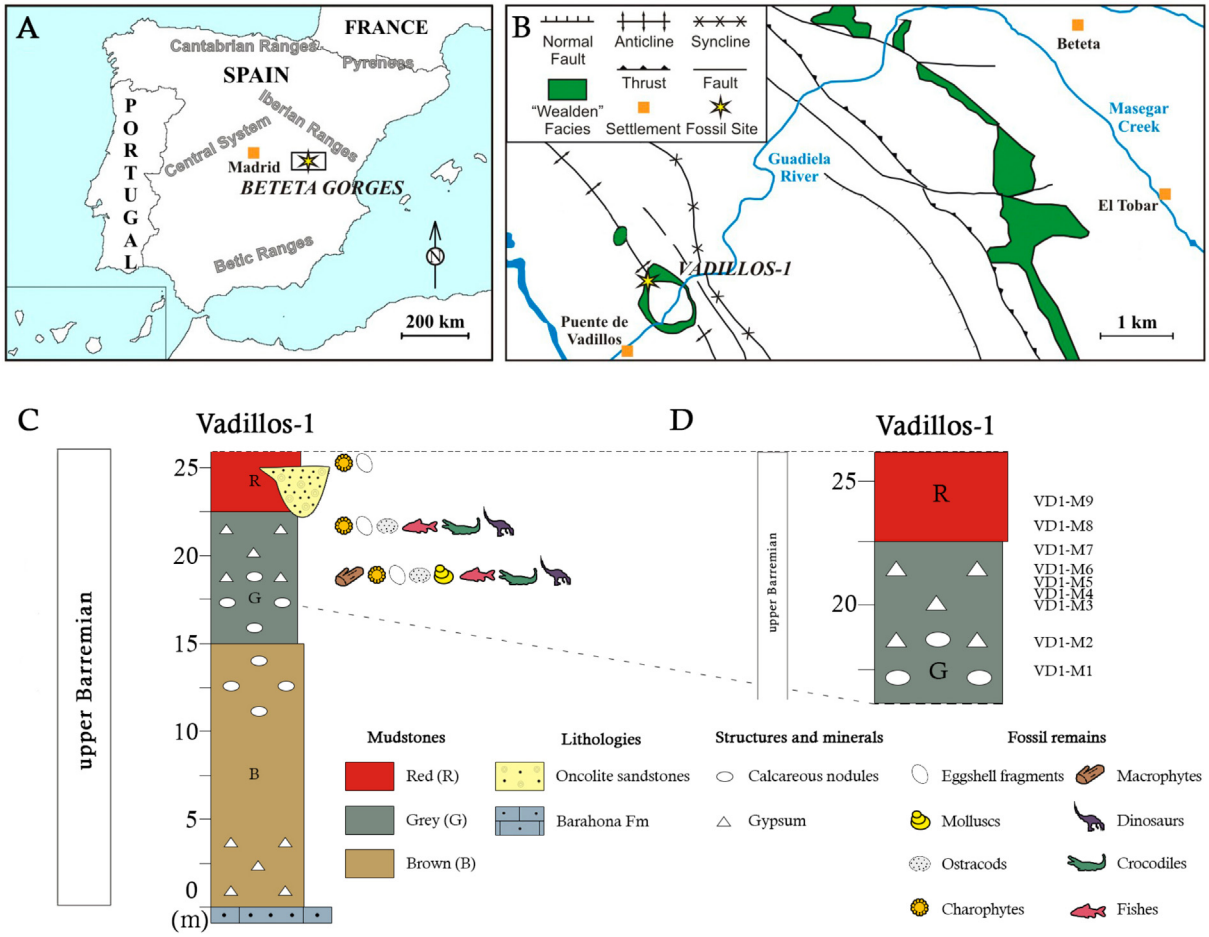


Fig. 1. General geographic (A) and detailed geologic (B) location of the Vadillos-1 fossil site (European Datum 1950: Lat. 40° 32' 20.27", Long. 2° 8' 31.21"; UTM 30 X 572663, Y 4488011 N) in the Beteta Gorges (Spain). Simplified stratigraphic column of Vadillos-1 showing the levels in which fossil ostracods have been found in previous works (C), and detail of the section showing the relative position of the 9 samples collected for this work (D). Modified from Barroso-Barcenilla et al. (2017) and Berrocal-Casero et al. (2023).

sample size was about 5–6 kg. The sedimentary rocks were processed at the Department of Geology, Geography and Environmental Sciences of the University of Alcalá (UAH), washed with warm water through sieves with mesh sizes of 0.50 mm, 0.20 mm and 0.063 mm, but no ostracod specimens were obtained from the fraction <0.20 mm. The material was then dried and picked under a binocular microscope (Motic) for small fossils (charophytes, ostracods, fish scales, teeth, eggshell fragments, and other small debris). Selected ostracod specimens were sputter-coated with gold and photographed with a Scanning Electron Microscope (STEM JEOL JSM-IT 500) at the University of Alcalá (UAH). All specimens described here are deposited in the collection of the Department of Geology, Geography, and Environmental Sciences of the UAH under the reference numbers given.

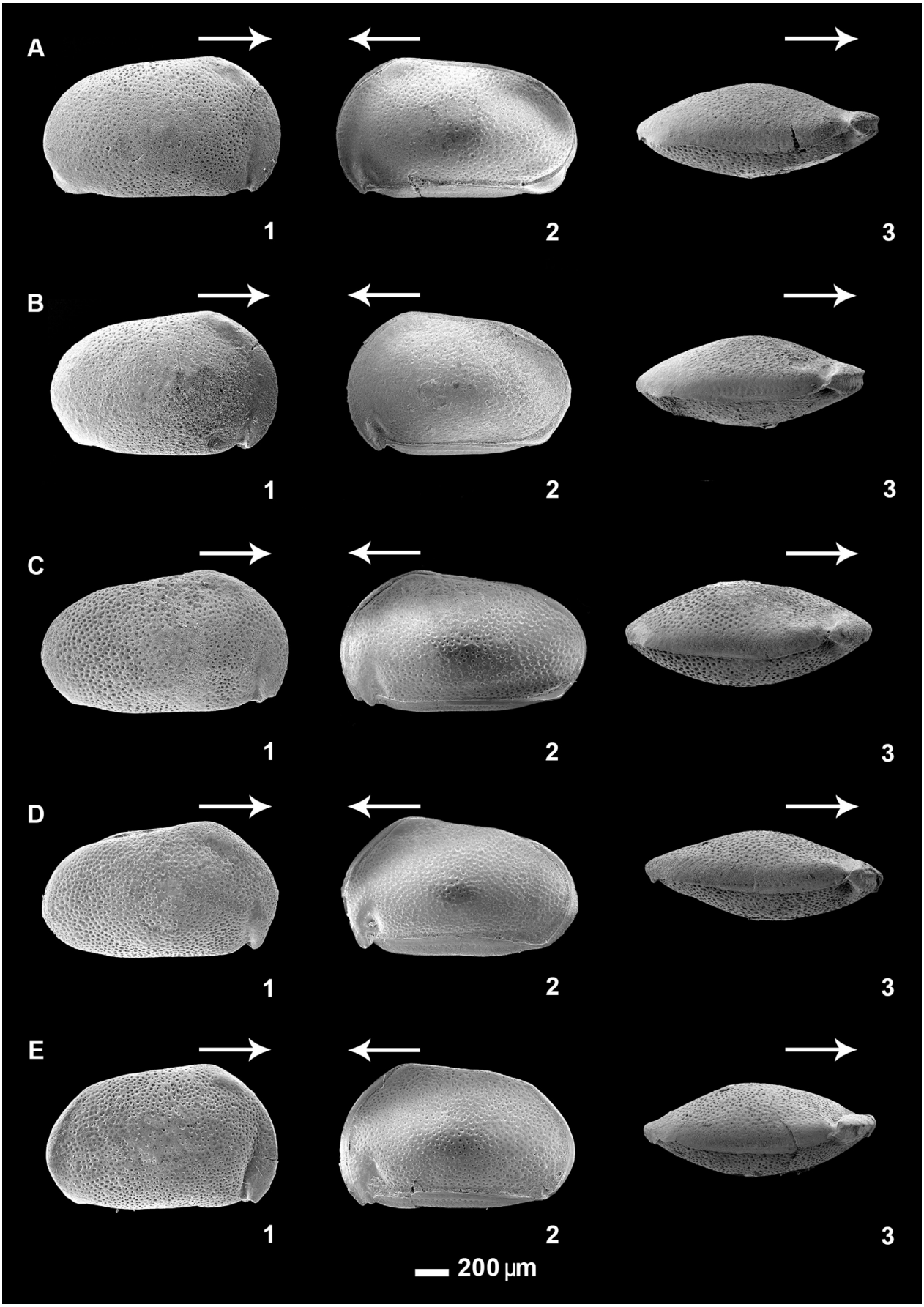
4. Systematic palaeontology

The study of ostracods from Wealden-type facies remains problematic due to the great morphological diversity within its most characteristic genus, *Cypridea* Bosquet, 1852, represented by a large number of published taxa including subgenera, many hundreds of species, and subspecies.

The taxa from Vadillos (Cuenca Basin, Spain) are mainly compared to those from adjacent basins and other more distant basins of the Iberian Peninsula. Taxonomic relationships have mainly been identified on a regional scale based on material recorded by authors such as Kneuper-Haack (1966), Brenner (1976), Schudack and Schudack (2009a), Rodríguez-Lázaro (2016) and Barroso-Barcenilla et al. (2017). On a supraregional scale, ostracods from Vadillos are compared to the faunas of the Wealden reference area, the Wealden of England (Anderson, 1985, and references therein) for biostratigraphic constraints following the revised biostratigraphy proposed by Horne (1995, 2009), as well as to North African faunas. Concerning the "Spanish Wealden" however, newer insights led to the conclusion that the Boreal English faunas are more or less unsuitable as reference for supraregional to intercontinental correlations to more Tethyan to tropical-equatorial faunas due to different depositional environments, palaeoclimate conditions and resulting faunal and temporal differences.

The suprageneric classification follows Sames (2011b) and Danielopol et al. (2018). Abbreviations used in text and figure captions, H: height; L: length; W: width; LV: left valve; RV: right valve. Size intervals used are: Very small: <0.40 mm, small: 0.40–0.50 mm, medium: 0.51–0.70 mm, large: 0.71–1.00 mm, very large: 1.01–2.00 mm, gigantic: >2.0 mm (e.g., Ayress and Whatley, 2014). For morphologic terminology, see Sames (2011a, text-figs. 3–8 and Sames 2011b, text-figs. 3–10 for illustration) and Sames (2011c) for definitions.

Class **Ostracoda** Latreille, 1806
Subclass **Podocopa** Sars, 1866


A
1
2
3
B
1
2
3
C
1
2
3
D
1
2
3
E
1
2
3
200 µm

Order **Podocopida** Sars, 1866
Suborder **Cypridocopina** Baird, 1845
Superfamily **Cypridoidea** Baird, 1845
Family **Cyprideidae** Martin, 1940 emend. Sames, 2011a–c

Genus ***Cypridea*** Bosquet, 1852 emend. Sames, 2011a–c
Type species. *Cypris granulosa* Sowerby (1836), from the Jurassic of England; with subsequent description by Sylvester-Bradley (1947)

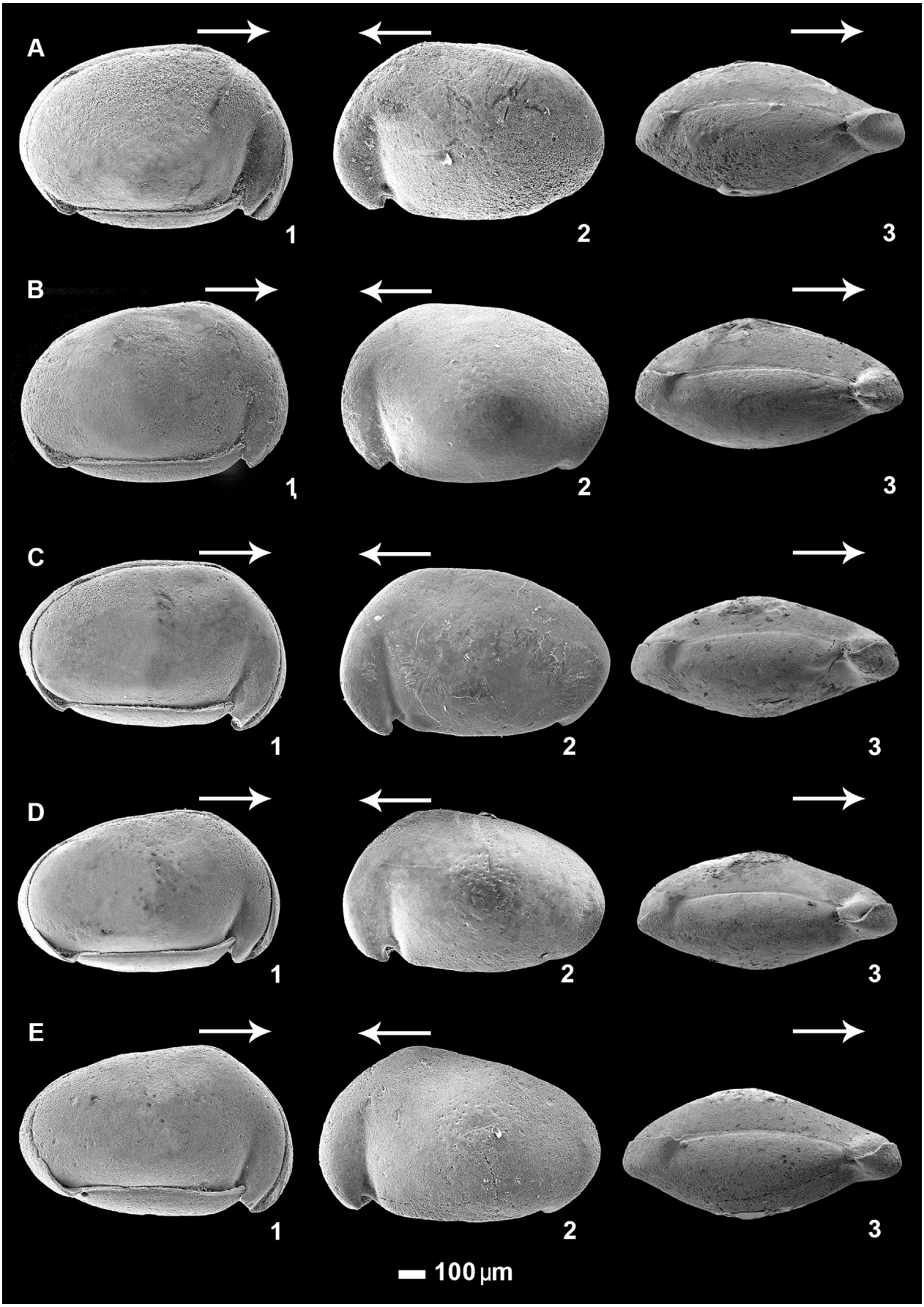
Distribution. Europe, North America, South America, Africa and Asia and extends from the Upper Jurassic to the Palaeogene.

Cypridea isasae Kneuper-Haack (1966)
Fig. 2A–E

1966 *Cypridea (Cypridea) isasae* n. sp.; Kneuper-Haack p. 183, pl. 45, figs. 12a–c.
1985 *Cypridea isasae* Kneuper-Haack; Aguirrezabala et al., p. 114, 132.
2009a *Cypridea isasae* Kneuper-Haack; Schudack and Schudack, p. 151, pl. 9, fig. 16.
2017 *Cypridea* cf. *C. isasae* Kneuper-Haack; Barroso-Barcenilla et al., p. 261, pl. 4, fig. 5.
2017 *Cypridea* sp. 1 Barroso-Barcenilla et al., p. 261, pl. 4, fig. 6.

Material. 34 carapaces. Here illustrated are five adult carapaces (VD1-598, VD1-649, VD1-666, VD1-667, VD1-668). The illustrated material is from samples VD1-M2 and VD1-M7 (G level).
Dimensions. L: 1.23–1.47 mm, H: 0.69–0.87 mm, W: 0.53–0.64 mm (this study).
Occurrence. Recorded in samples VD1-M1, VD1-M2, VD1-M4, VD1-M5 and VD1-M8 obtained in the grey and the red levels from the Barremian site Vadillos-1.
Description. Carapace very large and inverse valve overlap (RV > LV). With a suboblong outline and a slightly prominent anterior cardinal angle. The anterior and posterior margins are rounded, the dorsal margin is straight and somewhat sinuous, and the ventral margin is straight to slightly convex. The outline in the dorsal view is subrhombic, with the anterior and posterior ends acuminate, the central part being the widest, and without a dorsolateral groove. The surface is regularly and densely punctate. In ventral view a line of pores can be seen in the larger RV (Fig. 2, (3) ventral view). It has a rostrum separated by a somewhat weakly marked alveolar notch and an alveolar ridge, of small size, and with a short, rounded end. Specifically, this species has a cyathus on the posteroventral part of the carapace, with a rounded shape, more or less pronounced depending on the specimen.
Remarks. According to Kneuper-Haack (1966), *Cypridea isasae* is similar to *C. menevensis* (Anderson, 1939), but can be distinguished from the latter by the coarse carapace ornamentation, the inclined anterior and posterior margins and the strongly developed rostrum. As well, Barroso-Barcenilla et al. (2017) describe the presence of *Cypridea* cf. *C. isasae* Kneuper-Haack (1966), in the upper Barremian of the El Tobar site (see Fig. 1B), and *Cypridea* sp. 1 in the upper Barremian from Vadillos-1 site. The specimens illustrated herein are similar to those described by Kneuper-Haack (1966) and Barroso-Barcenilla et al. (2017), but the studied specimens partly differ from those of the mentioned authors regarding the size of the cyathus, which may be due to the morphological variability present in the specimens and/or related to preservation (as a delicate structure of one valve only, the cyathus can often be partly or completely broken off). Kneuper-Haack (1966) had dated the holotype of *C. isasae* from Navarra as upper Tithonian. Newer publications such as by Aguirrezabala et al. (1985), Schudack and Schudack (2009a) and Barroso-Barcenilla et al. (2017) date the respective succession and the range of this species as Hauterivian to Barremian.
The age discrepancy proposed by these authors for the species *C. isasae* can be attributed to the fact that Kneuper-Haack (1966) had established an obsolete chronostratigraphy for the formations of the "Wealden of the Sierra de los Cameros" based on the ostracod microfauna. However, significant dating errors were not corrected until the study of Brenner (1976). After this study, the Enciso Formation was no longer considered to be Jurassic (upper Purbeck or upper Tithonian according to Kneuper-Haack, 1966) but was placed into the Lower Cretaceous, specifically into the Hauterivian–Barremian (e.g., Brenner and Wiedmann, 1975; Brenner, 1976; Aguirrezabala et al., 1985; Schudack and Schudack, 2009a).
There are some morphological similarities to species assigned to *Cypridea valdensis* (Sowerby, 1836). Several subspecies of *Cypridea valdensis* have been described and controversially discussed over time in the literature, mainly from the "Purbeck and Wealden" of NW Europe and especially from the English Wealden and the "German Wealden" (e.g., Sowerby, 1836; Jones, 1885; Martin, 1940; see evolutionary development lineages in Wolburg, 1959; Anderson, 1985 and references therein; Elstner and Mutterlose, 1996). These reports cover different morphogroups that have different stratigraphic distributions. The main groups are, on the one hand, subspecies assigned to *Cypridea valdensis* from the German Wealden, upper Berriasian to lower Valanginian (e.g., *Cypridea valdensis valdensis* and *Cypridea valdensis obliqua* of Wolburg, 1959; "German Wealden 2–4", see Wolburg, 1959; Elstner and Mutterlose, 1996), and, on the other hand, morphogroups of *Cypridea valdensis* (Sowerby, 1836) from the Valanginian(?), Hauterivian to Barremian of England. In his correlation of the English Purbeck with the "German Wealden", Anderson (1962) already noted that the taxa of Wolburg (1959) do not fit into the taxonomic concept of *Cypridea valdensis* (Sowerby, 1836). The English records of *Cypridea valdensis valdensis* (Sowerby, 1936) as recorded by Anderson (1967, 1985) represent "the usual form of the species; common in the Weald Clay of all areas" (Anderson, 1985, p. 33), spanning the Hauterivian–Barremian interval (cf. Hoedemaeker and Herngreen, 2003). This morphotype of *Cypridea valdensis* (note that the lectotype as figured in Anderson, 1967, pl. XVII, fig. 60 and Anderson, 1985, pl. 8, fig. 18 is somewhat damaged) shows relatively strong similarities to our specimens identified as *Cypridea isasae* Kneuper-Haack herein in overall carapace shape, punctation, and development of rostrum, alveolus and cyathus. However, the English morphogroups of *Cypridea valdensis* in the sense of Anderson (1967, 1985) have a "normal" (LV > RV) valve-size relation whereas *Cypridea isasae* is inverse (RV > LV). The taxonomic significance of the relative valve-size relations is in discussion (see Sames 2011c, particularly p. 443), but it is common practice to consider it taxonomically significant at species and genus level. Therefore, in the present work, the overall similarities are only pointed out, but *Cypridea valdensis* (Sowerby, 1836) from southern England are not synonymised with *Cypridea isasae* Kneuper-Haack, 1966. This issue remains to be thoroughly reinvestigated based on type and reference material and integrated modern taxonomic approaches. Taxa potentially more or less closely related to *Cypridea valdensis* (Sowerby, 1836) have been documented from the Lower Cretaceous of Spain (e.g., Kneuper-Haack, 1966; Brenner, 1976; Schudack and Schudack, 2009a, b). In her stratigraphic

Fig. 2. A–E. *Cypridea isasae* Kneuper-Haack (1966), adult carapaces from the upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, Cuenca (Spain). A - VD1-598. B - VD1-649. C - VD1-666. D - VD1-667. E – VD1-668. (1) Right lateral view of carapace. (2) Left lateral view of carapace. (3) Ventral view of carapace. All photos are external views. Arrow indicates anterior side.


A
1
2
3
B
1
2
3
C
1
2
3
D
1
2
3
E
1
2
3
100 µm

account, Cabral (1996) records *Cypridea valdensis* (Sowerby, 1836) from the upper Aptian of the Algarve (Portugal).
Distribution. According to Schudack and Schudack (2009a) the species *Cypridea isasae* has been recorded from the upper Hauterivian–lower Barremian of Spain. Kneuper-Haack (1966) found and described the holotype of *Cypridea isasae* from the Hauterivian–Barremian of the Baños de Fitero site, in the Enciso Beds, now designated Enciso Formation (Navarra province, northern Spain). Later, Aguirrezabala et al. (1985) identified *C. isasae* in the Hauterivian–Barremian Cameros site (Enciso Formation, La Rioja province, Spain). Schudack and Schudack (2009a) studied the Lower Cretaceous of the Iberian Range, and recorded *C. isasae* from the upper Hauterivian–lower Barremian of the Aguilón (Betic Range, SE Spain), Torrelapaja (Iberian Range, NE Spain) and Cantaperdius (Morella Sub-Basin, E Spain) formations. More recently, Barroso-Barcenilla et al. (2017) recorded *Cypridea* cf. *C. isasae* from the Barremian site of El Tobar, close to Vadillos-1, in Cuenca (Spain).

Cypridea ventriosa Brenner (1976)
Fig. 3A–E

1976 *Cypridea ventriosa* n. sp.; Brenner; p. 127, pl. 6, figs. 1–4.
1993 *Cypridea (Cypridea) ventriosa* Brenner; Swain, p. 19, pl. 1, figs. 24–26 [given as *Cypridea* cf. *ventriosa* in the plates].
2009a *Cypridea ventriosa* Brenner; Schudack and Schudack, p. 156, fig. 9, 22.
2016 *Cypridea* gr. *alta* (Wolburg); Rodríguez-Lázaro, pl. 1, fig. 4.
2016 *Cypridea* sp. 4 Rodríguez-Lázaro, p. 91, pl. 1, fig. 10.
2017 *Cypridea* sp. aff. *C. moneta* (Kneuper-Haack); Barroso-Barcenilla et al., p. 261, pl. 4, figs. 7a, 7b.
?2021 *Cypridea ventriosa* Brenner; Trabelsi et al., p. 22, pl. 5, figs. D1–D2.

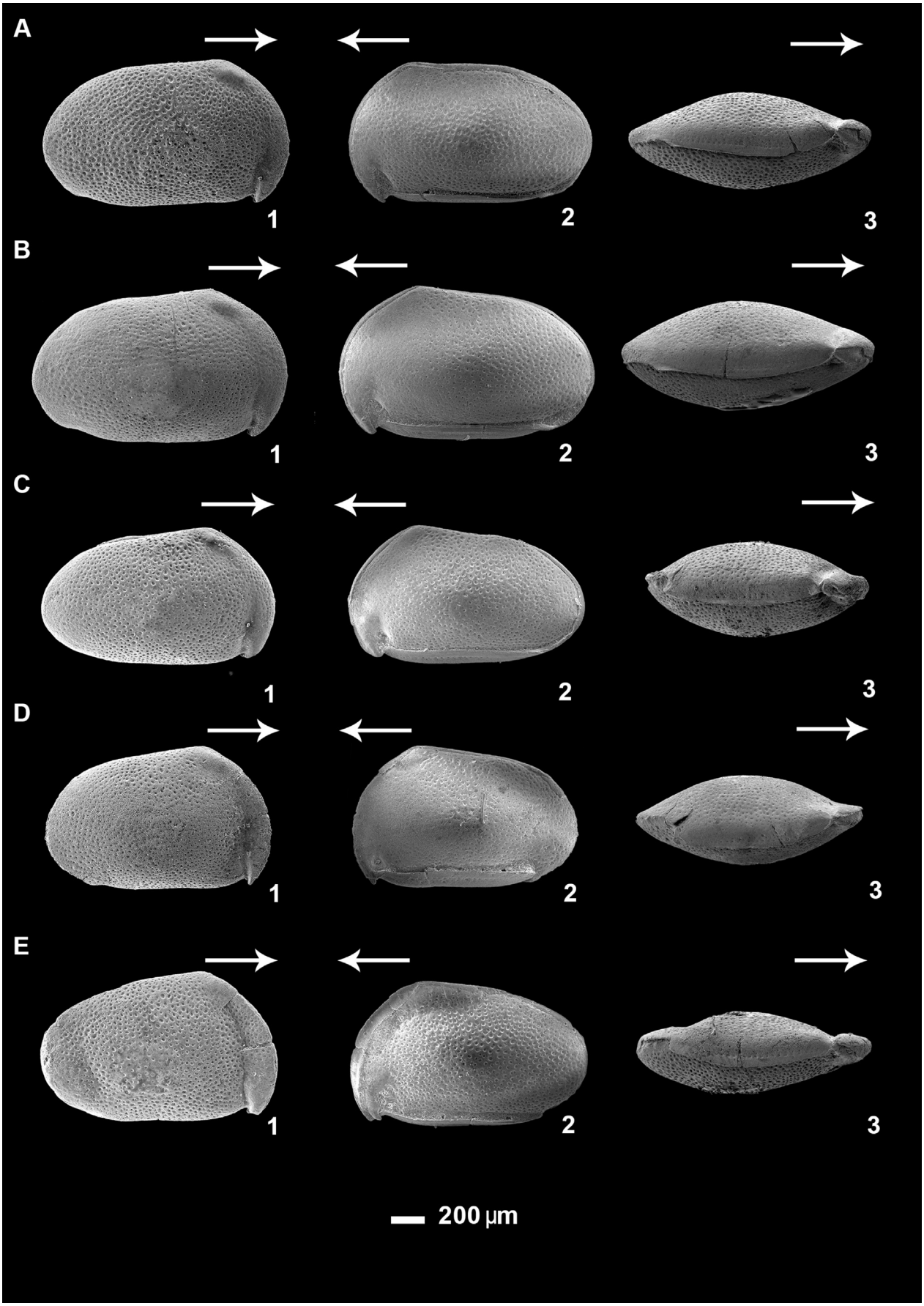
Material. 246 carapaces. Here illustrated are five adult carapaces (VD1-618, VD1-639, VD1-669, VD1-670, VD1-671). All illustrated material is from samples VD1-M2 and VD1-M7 (G level).
Occurrence. Recorded in samples VD1-M1, VD1-M2, VD1-M3, VD1-M4, VD1-M5, VD1-M6, VD1-M7 and VD1-M8 obtained in the grey and red levels from the Barremian site Vadillos-1.
Dimensions. L: 0.81–0.99 mm, H: 0.53–0.65 mm, W: 0.44–0.49 mm (this study).
Description. Carapace large and normal valve overlap (LV > RV) very pronounced along the rostrum, and ventral and posterior part of the carapace. Carapace with subcircular outline and a barely visible anterior cardinal angle. The anterior margin is asymmetrically rounded, and the posterior margin is rounded and symmetrical; the dorsal margin is slightly convex and the ventral margin is more convex. The profile in the dorsal view is elliptical to subrhombic with the anterior and posterior ends somewhat acuminate, the central-posterior part being the widest, and with a dorsolateral groove. The surface ornamentation is basically smooth, with fine puncta in central area of LV of some specimens. It has a large rostrum with a short, acute end that is separated from the ventral margin by strongly marked alveolar notch. Alveolar furrow very wide. In particular, this species has a small and acute cyathus in the posteroventral part of the larger LV, with a triangular shape, not very pronounced in left lateral view but distinct in right lateral view.
Remarks. According to the original description and figured specimens of Brenner (1976) the holotype of *Cypridea ventriosa* has a large carapace with straight dorsal margin, strongly convex ventral margin of the larger LV and smooth carapace surface. The studied material fits Brenners (1976) taxonomic concept in all relevant carapace features. *Cypridea* cf. *ventriosa* specimens of Swain (1993) and *C. ventriosa* of Schudack and Schudack (2009a) are similar to the material described from Vadillos-1 but their characteristics are not clearly visible in these publications due to the deformation or erosion of the carapace. Rodríguez-Lázaro (2016) identified *Cypridea* gr. *alta* at the Las Hoyas site, near Vadillos-1 in Cuenca province. The specimen found in Las Hoyas has a more ovate outline and a more developed cyathus compared to the Vadillos-1 specimens, but this may be included in the morphological variability range of the species. Besides, *Cypridea* sp. 4 by Rodríguez-Lázaro (2016) shows a deformation by lateral and sheared compression and is considered in this study to belong to the species *Cypridea ventriosa* as the specimens shown herein. From the same site (Vadillos-1), Barroso-Barcenilla et al. (2017) identified *Cypridea* sp. aff. *C. moneta* Kneuper-Haack (1966). The specimens described here exhibit a strong development of the rostrum, cyathus, and alveolar groove, as the specimens of the cited publication, which are, therefore, synonymized. Trabelsi et al. (2021) collected *C. ventriosa* in mid-Cretaceous deposits of the Central Tunisian Atlas (North Africa). Their specimens are very similar to the material described in this work, but their preservation makes it difficult to identify some relevant characteristics for a conlusive confirmation of synonymy.
Distribution. Schudack and Schudack (2009a) stated that the stratigraphic range of *Cypridea ventriosa* is upper Barremian and that it has occasionally been found in the lower Aptian. Brenner (1976) described the holotype of *Cypridea ventriosa* from the upper Barremian–Aptian site of Uña in Cuenca (Spain). Swain (1993) identified a specimen as *Cypridea* cf. *ventriosa* in the possibly Aptian site Reserva Nacional de Caza in Tarragona (Spain). Schudack and Schudack (2009a) studied the Lower Cretaceous of the Iberian Range, and found *C. ventriosa* in the lower Aptian (or even Barremian) Forcall Formation at Cuevas de Portalrubio section and in the Escucha Formation from Foz de Calanda and Aliaga sections of Teruel (Spain). In North Africa, Trabelsi et al. (2021) found *C. ventriosa* in a lower Aptian site of the Orbata Formation (Central Tunisian Atlas, Tunisia).

Cypridea vatra nov. sp.
Figs. 4A–E

urn:lsid:zoobank.org:pub:FD54BAB9-F932-47BD-8789-B5918AB79E78.
2017 *Cypridea* gr. *modesta* (Kneuper-Haack, 1966) sensu Schudack and Schudack (2009a); Barroso-Barcenilla et al., p. 261, pl. 4, fig. 4a, 4b.

Derivation of name. From the Croatian "*vatra*", word for fire. Dedicated to a friend of the first author who has family origins in northern Spain and where Celtic mythology has great influence.
Material. 285 carapaces. Type material: Holotype: one adult complete carapace, VD1-624; four paratypes: VD1-660, VD1-681, VD1-604, VD1-683 (complete adult carapaces). The illustrated material is from samples VD1-M2 and VD1-M7 (G level).
Type locality and horizon. Sample horizons VD1-M1 to VD1-M7 in the grey and red mudstones levels from the Barremian site Vadillos-1 in the Beteta Gorges (Cuenca, Spain).
Diagnosis. A very large suboval to subquadrate species of *Cypridea* typified by a straight dorsal margin and a slightly convex ventral margin with a very small cyathus in a posteroventral position. In ventral and dorsal view, acuminate anterior and posterior ends. Marked rostrum with a short, sharp end.

Fig. 3. A–E. *Cypridea ventriosa* Brenner (1976), adult carapaces from the upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, Cuenca (Spain). A - VD1-618. B - VD1-639. C - VD1-669. D - VD1-670. E – VD1-671. (1) Right lateral view of carapace. (2) Left lateral view of carapace. (3) Ventral view of carapace. All photos are external views. Arrow indicates anterior side.


A
1
2
3
B
1
2
3
C
1
2
3
D
1
2
3
E
1
2
3
200 µm

Dimensions. All adult carapaces:
Holotype, VD1-624 L: 1.39 mm, H: 0.81 mm, W: 0.57 mm.
Paratypes:
VD1-660 L: 1.46 mm, H: 0.87 mm, W: 0.64 mm.
VD1-681 L: 1.36 mm, H: 0.78 mm, W: 0.57 mm.
VD1-604 L: 1.36 mm, H: 0.82 mm, W: 0.52 mm.
VD1-683 L: 1.36 mm, H: 0.82 mm, W: 0.46 mm.
Description. Carapace very large and inverse valve overlap (RV > LV) very pronounced on the ventral border. With a suboval to subquadrate outline and a well-marked anterior cardinal angle. The anterior and posterior margins are rounded, the dorsal margin is straight and descending backward, and the ventral margin is straight to slightly convex. The outline in the dorsal view is subelliptical with the anterior and posterior ends acuminate, the central part being the widest and without a dorsolateral groove. The external ornamentation is characterized by smooth puncta evenly distributed over the entire surface. Rostrum with a short, sharp end separated by a small alveolar notch. It has a very small cyathus in a posteroventral position.
Remarks. *Cypridea menevensis* (Anderson, 1939) is similar to *Cypridea vatra* nov. sp. in its large ovate-oblong valves, a surface covered with small circular punctations, distinct rostrum separated by a notch and a hinge-line slightly curved anteriorly. However, the material described herein differs from *Cypridea menevensis* in the presence of a very small posteroventral cyathus, inconspicuous in right lateral view (Fig. 4, A1 and B1), but clearly visible in ventral view (Fig. 4, A3 and B3). The English *Cypridea menevensis* (Anderson, 1939), stratigraphically revised by Anderson (1985) and Horne (2009), is similar to *C. vatra* nov. sp. in general shape, but lacks a cyathus that can be seen in this new species (a cyathus is, however, a delicate structure and can easily break off). More important, *C. menevensis* is much older — Anderson (1939, 1985) and Horne (2009, *Cypridea menevensis* subzone) date it as uppermost Berriasian(?) to lower Valanginian, whereas Vadillos-1 is dated Barremian. Among the specimens presented by Barroso-Barcenilla et al. (2017), those identified as *Cypridea* gr. *modesta* Kneuper-Haack sensu Schudack and Schudack (2009) therein and found at the Vadillos-2 site correspond to *Cypridea vatra* nov. sp., as their characteristics coincide with the specimens of the present work. However, the specimens described herein as *Cypridea vatra* nov. sp. are not considered to be identical or closer related to the original *Cypridea modesta* Kneuper-Haack, 1966, because the latter has a more ovate outline and a more convex ventral margin in the larger RV than the former. For these reasons, in the present paper, a new species is erected, which is considered potentially related — but not to be synonymous — to *Cypridea menevensis*.
Stratigraphical range. Grey and red mudstones levels of the Barremian (Lower Cretaceous) site Vadillos-1 in the Beteta Gorges, northern Cuenca province (Spain).

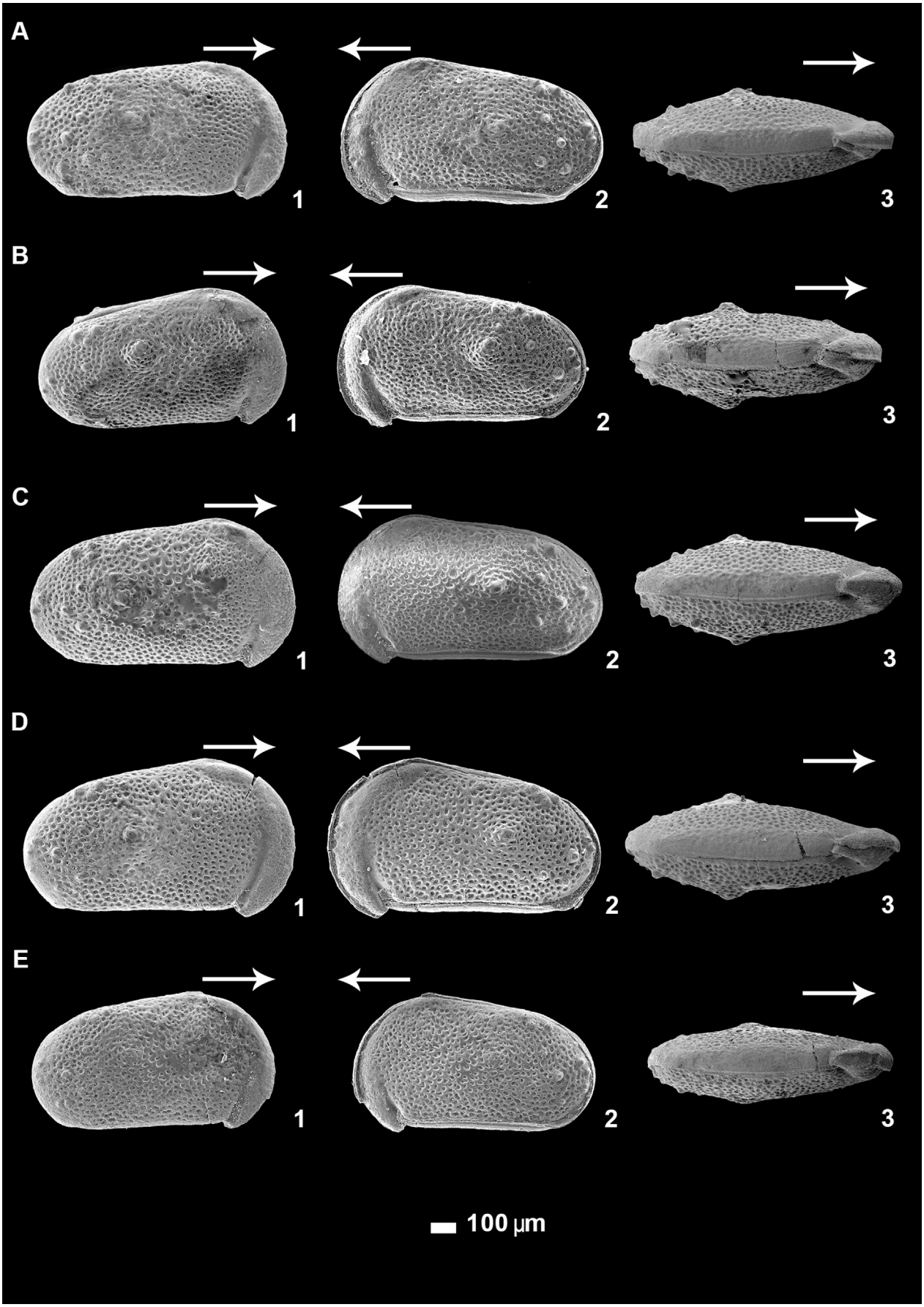
Cypridea marihoni nov. sp.
Figs. 5A—E

2009a *Cypridea clavata* (Anderson, 1939); Schudack and Schudack, fig. 9, specimen 15.
urn:lsid:zoobank.org:pub:FD54BAB9-F932-47BD-8789-B5918AB79E78.

Derivation of name. From the word "*marihøne*" which means "*ladybird*" in Norwegian. The ornamentation pattern of the carapace of this ostracod resembles the dots of this animal.

Material. 94 carapaces. Type material: Holotype: one adult complete carapace, VD1-679; four paratypes: VD1-662, VD1-676, VD1-678, VD1-677 (complete adult carapaces). The illustrated material is from samples VD1-M3 and VD1-M6 (G level).
Type locality and horizon. Sample horizons VD1-M1 to VD1-M7 in the grey and red mudstones levels from the Barremian site Vadillos-1 in the Beteta Gorges (Cuenca, Spain).
Diagnosis. A medium to large elongated species of *Cypridea* characterised by straight dorsal and ventral margins. Ellipsoidal outline in ventral and dorsal view. Distinctly punctate, with a main tubercle in the central-posterior part of both valves and smaller tubercles in the upper-posterolateral part of both valves common. Rostrum visible in both valves with a long, rounded end.
Dimensions. All adult carapaces:
Holotype, VD1-679 L: 0.97 mm, H: 0.57 mm, W: 0.36 mm.
Paratypes:
VD1-662 L: 0.94 mm, H: 0.56 mm, W: 0.31 mm.
VD1-676 L: 1.01 mm, H: 0.57 mm, W: 0.38 mm.
VD1-678 L: 1.03 mm, H: 0.61 mm, W: 0.35 mm.
VD1-677 L: 0.91 mm, H: 0.54 mm, W: 0.29 mm.
Description. Carapace medium or large and inverse valve overlap (RV > LV) slightly pronounced in the rostrum. Elongated, with an elliptical-subrectangular outline and a weak anterior cardinal angle. The anterior and posterior margins are rounded, and the dorsal and ventral margins are straight. The profile in the dorsal view is ellipsoidal, the widest part is the central area. Entire carapace surface covered by distinct puncta. A major tubercle is present in the central-posterior part of both valves, and other smaller tubercles in the upper-posterior part of both valves. The rostrum, visible in both valves, has a long, rounded end. There is no alveolar notch, and the alveolar furrow is visible on both valves. The cyathus is small and barely visible on the left valve.
Remarks. Since the material in the present work is the very first record of this species of the genus *Cypridea* in the Iberian Peninsula, it very likely represents a new species.
Cypridea marihoni nov. sp. is similar to *Cypridea clavata* (Anderson, 1939) or the *Cypridea clavata* group in the sense of Horne in Nye et al. (2008, p. 425 et seqq., fig. 10) and in Sames and Horne (2012, p. 275—277, fig. 4) as recorded from from the Hauterivian—Barremian Weald Clay Formation of England and from the Hauterivian—Barremian of Spain (e.g., Schudack and Schudack, 2009a). Both taxa are inverse, exhibit pronounced rostrum and wide alveolar furrows reaching upwards to about one-third (smaller LV) to half (larger RV) of height, are punctate and commonly exhibit tuberculation, mosty in the posterolateral part of the carapace. Although some closer relationship to the *C. clavata* species-group seems probable, *C. marihoni* nov. sp. differs from *C. clavata* variants in its somewhat more elongate lateral outline, the fact that its rostrum slightly overreaches the ventral margin and outline of the carapace, the inconspicuous posterior cardinal angle and the much more elongate-eliptic dorsal/ventral outline, which is more rounded-rectangular in *C. clavata*. The specimen identified and figured as *C. clavata* (Anderson, 1939) by Schudack and Schudack (2009a) is similarly different to the English specimens and, regarding the mentioned features, well fits into *C. marihoni* nov. sp. in outline, overall shape and size and is, thus, considered herein to belong to this species.
Stratigraphical range. Grey and red mudstones levels of the Barremian (Lower Cretaceous) site Vadillos-1 in the Beteta Gorges, northern Cuenca province (Spain).

Fig. 4. A—E. *Cypridea vatra* nov. sp. adult carapaces from the upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, Cuenca (Spain). Holotype: A - VD1-624. Paratypes: B - VD1-660. C - VD1-681. D - VD1-604. E — VD1-683. (1) Right lateral view of carapace. (2) Left lateral view of carapace. (3) Ventral view of carapace. All photos are external views. Arrow indicates anterior side.


A
1
2
3
B
1
2
3
C
1
2
3
D
1
2
3
E
1
2
3
100 µm

Family **Cyclocyprididae** Kaufmann, 1900
Subfamily **Cyclocypridinae** Zenker, 1854

Genus ***Cyclocypris*** Brady and Norman, 1889
Type species. *Cypris globosa* Sars (1863), extant, Europe

Distribution. Europe, Asia, North America and Africa and recorded from Palaeogene to Recent (see remarks for *Cyclocypris bamba* nov. sp. below).

Cyclocypris bamba nov. sp.
Fig. 6A–F

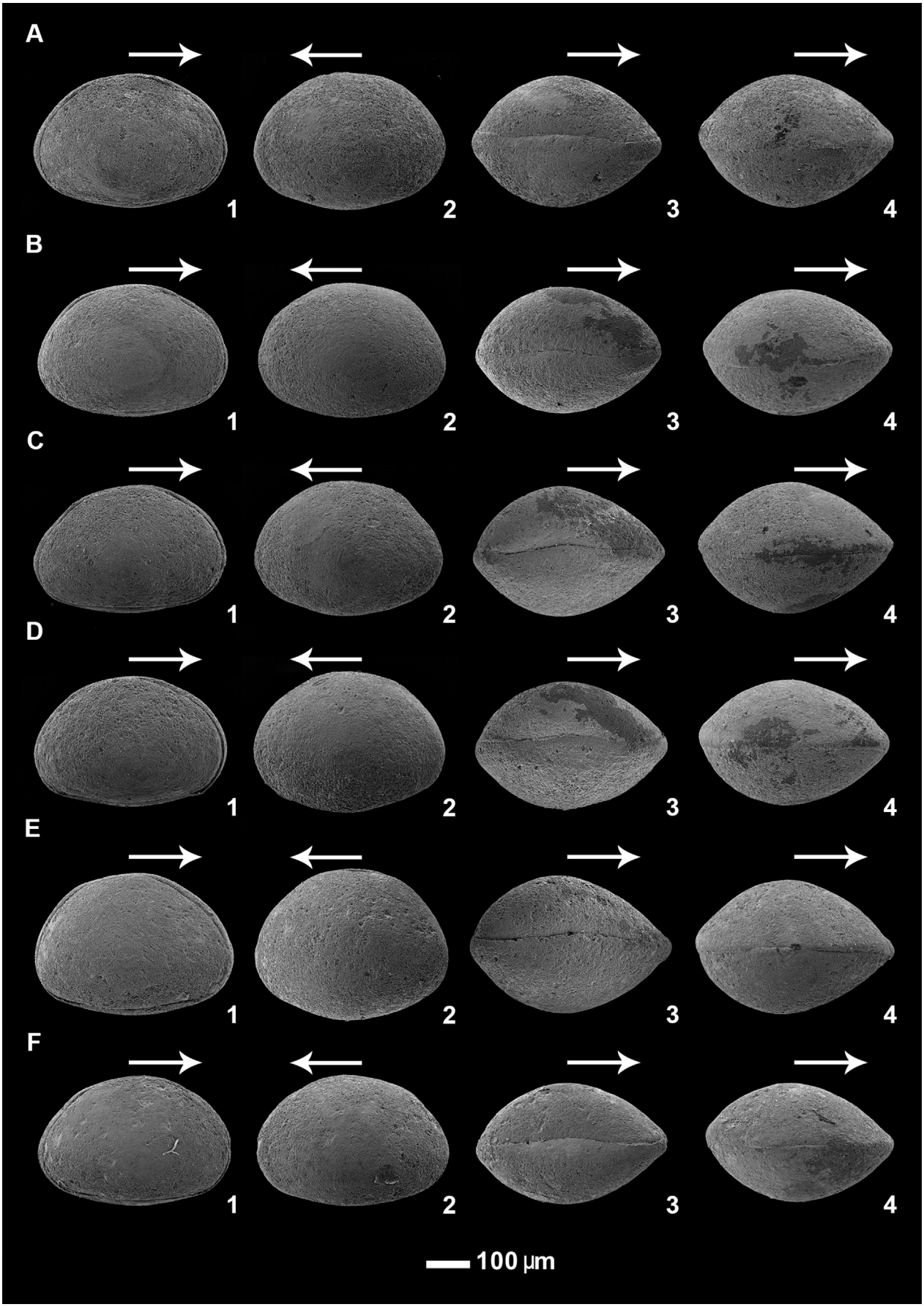
?1968 *Cyclocypris*? sp. A; Krömmelbein, p. 261, pl. 45, figs. 4a–c.
?1997 *Cyclocypris*? sp.; Lucas et al., p. 159, fig. 3E–F.
urn:lsid:zoobank.org:pub:FD54BAB9-F932-47BD-8789-B5918AB79E78.

Derivation of name. From the name of a typical sweet in Spain. This sweet, known as "*bamba de nata*" in Spanish, is a slightly spherical bun opened in half and filled with cream. The shape of the carapace of this ostracod and the slightly overlapping of its valves reminds of the appearance of the mentioned sweet.
Material. 1076 carapaces. Type material: Holotype: one adult complete carapace, VD1-928; five paratypes: VD1-926, VD1-929, VD1-930, VD1-934, VD1-935 (complete adult carapaces). The illustrated material is from samples VD1-M2 and VD1-M1 (G level).
Type locality and horizon. Sample horizons VD1-M1 to VD1-M9 in the grey and red mudstones levels from the Barremian site Vadillos-1 in the Beteta Gorges (Cuenca, Spain).
Diagnosis. A small compressed piriform species of *Cyclocypris* typified by a ventral margin straight to slightly concave. In ventral and dorsal view, the anterior and posterior ends of the carapace are more acuminate than the rest of the specimens of the genus *Cyclocypris* that have been observed, which are more rounded.
Dimensions. All adult carapaces:yy.
Holotype, VD1-928 L: 0.42 mm, H: 0.29 mm, W: 0.30 mm.
Paratypes:
VD1-926 L: 0.42 mm, H: 0.29 mm, W: 0.29 mm.
VD1-929 L: 0.42 mm, H: 0.29 mm, W: 0.30 mm.
VD1-930 L: 0.42 mm, H: 0.29 mm, W: 0.29 mm.
VD1-934 L: 0.43 mm, H: 0.31 mm, W: 0.31 mm.
VD1-935 L: 0.43 mm, H: 0.28 mm, W: 0.27 mm.
Description. Carapace small and weakly inequivalve with normal valve overlap (LV > RV). Compressed piriform outline in lateral view and relatively high. Maximum height slightly behind mid-length and maximum length at half height. Anterior margin infracurvate, with moderately broad laterally flattened anteroventral marginal zone. Posterior margin slightly infracurvate. Dorsal margin convex, evenly curved, cardinal angles poorly defined. Ventral margin straight to slightly concave, ventral outline convex through overreaching ventrolateral carapace inflation. Dorsal furrow inconspicuous to absent. In ventral and dorsal view, the anterior and posterior ends of the carapace are acuminate. Carapace surface smooth.
Remarks. The genus *Cyclocypris* Brady and Norman (1889) has been described based on extant species. However, the genus name *Cyclocypris* has been applied to fossil taxa as old as Upper Cretaceous (e.g., Sahni and Khosla, 1994; Bajpai and Whatley, 2001; Khosla et al., 2011; Wang et al., 2019), and Lower Cretaceous (very few records, e.g., Krömmelbein, 1968; Lucas et al., 1997).
The best comparable taxon to the material described herein is *Cyclocypris*? sp. A of Krömmelbein (1968) from the "Wealden of Ghana" (West Africa). This author identifies his taxon as *Cyclocypris*? sp. A and describes it as "Carapace extremely inflated, egg-shaped in lateral and in dorsal view. Dorsum strongly convex. Greatest height at about one-half of length of carapace. Right valve slightly larger than left. Surface of the shell smooth" (Krömmelbein, 1968, p. 261). In the specimens of the present work and generally in species of *Cyclocypris*, the valve size relation is LV > RV. Owing to the quality of the specimen pictures of Krömmelbein (1968) it is not clear but it seems that his specimen rather a principally larger left valve instead of "right valve slightly larger than the left" as given in the description by Krömmelbein (1968). This "normal" (LV > RV) valve size relation along with the overall similarity would support a potential synonymy of the *Cyclocypris*? sp. A of Krömmelbein (1968) and *Cyclocypris bamba* nov. sp., but better information on type or reference material from West Africa is necessary to confirm this hypothesis.
Somewhat younger(?), but also similar to specimens of *Cyclocypris bamba* sp. nov. are the ostracod specimens identified as *Cyclocypris*? sp. of Lucas et al. (1997) in an Aptian(?) site of the Cedar Mountain Formation (Utah, USA). These were described as follows: "Five steinkerns are suboval with a strongly convex dorsal margin and a slightly convex ventral margin. The anterior and posterior margins are rounded. In dorsal view, the valves are wedge shaped, tapering to the anterior and posterior from the inflated convex lateral margins. The posterior tapers more abruptly than the anterior. There is no surface ornamentation. The identity of these ostracods is uncertain. They are similar to *Cyclocypris* sp. from the Lower Cretaceous but differ in having a more tapered anterior in dorsal view and being less symmetric in lateral view" (Lucas et al., 1997, p. 159). However, it has to be noted that the anterior tapering can appear stronger in internal moulds, but is also not an unusual carapace feature in some species of this genus. For these reasons and considering non-marine ostracod dispersal mechanisms (Sames and Horne, 2012), a closer relation or even synonymy of this species with *C. bamba* sp. nov. is possible but has to be tested with better material from North America.
Although being of roughly the same age, a synonymization of both species, *Cyclocypris*? sp. A of Krömmelbein (1968) and *Cyclocypris*? sp. of Lucas et al. (1997), with each other and with *Cylocypris bamba* nov. sp. must remain questionable because the quality of the material and figures in both publications (Krömmelbein, 1968; Lucas et al., 1997) is insufficient to draw conclusions with certainty. Since the material in the present work is also the very first record of a species of this genus from the Iberian Peninsula, and the comparable sites are very distant, it much likely represents a new species.
Stratigraphical range. Grey and red mudstones levels of the Barremian (Lower Cretaceous) site Vadillos-1 in the Beteta Gorges, northern Cuenca province (Spain).

5. Discussion

Several species of the genus *Cypridea* are identified in this work, *Cypridea isasae* Kneuper-Haack (1966), *Cypridea ventriosa* Brenner (1976), and two new species of this genus, *Cypridea vatra* nov. sp. and *Cypridea marihoni* nov. sp., are also described. A new species of the genus *Cyclocypris* is also described, *Cyclocypris bamba* nov. sp. The association identified in this work, apparently of lower diversity compared to other nearby upper Barremian sites (Schudack and Schudack, 2009a), may have suffered the loss of taxa due to taphonomic disturbance and is therefore considered to be only

Fig. 5. A–E. *Cypridea marihoni* nov. sp. adult carapaces from the upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, Cuenca (Spain). Holotype: A - VD1-679. Paratypes: B - VD1-662. C - VD1-676. D - VD1-678. E – VD1-677. (1) Right lateral view of carapace. (2) Left lateral view of carapace. (3) Ventral view of carapace. All photos are external views. Arrow indicates anterior side.


A
1
2
3
4
B
1
2
3
4
C
1
2
3
4
D
1
2
3
4
E
1
2
3
4
F
1
2
3
4
100 µm

partially representative of the original diversity. It is striking that similar assemblages of the same taxa are not recorded from sites that are stratigraphically and palaeogeographically comparable. This may be attributed, on the one hand, to palaeoenvironmental differences between sites (certain depositional environments could suffer intense seasonal desiccation while others were able to maintain a certain amount of water, even in the driest periods) and, on the other hand, to the scarcity of data and literature on Lower Cretaceous non-marine ostracods from the Iberian Peninsula, highlighting the need for further systematic research and revisions.

Previous works carried out at Vadillos-1, such as Barroso-Barcenilla et al. (2017), identified ostracods of the genus *Cypridea*: *Cypridea* gr. *modesta*, *Cypridea* cf. *C. isasae* and *Cypridea* sp. aff. *C. moneta*. Other comparable sites nearby in the Iberian Basin where the genus *Cypridea* has been found are Buenache de la Sierra (Buscalioni et al., 2008) and La Cantalera (Canudo et al., 2010; Puértolas-Pascual et al., 2015).

According to Schudack and Schudack (2009a) the species *Cypridea isasae* has been recorded from the upper Hauterivian–lower Barremian. This species occurs in the central and northeastern Spain (see distribution above) Schudack and Schudack (2009a) also stated that the temporal range of *Cypridea ventriosa* is upper Barremian and it has occasionally been found in lower Aptian. This species has been recorden in central and northeastern Spain and the lower Aptian of Tunisia (see distribution above).

The species *Cypridea menevensis* (Anderson, 1939) from the United Kingdom, stratigraphically revised by Anderson (1985) and Horne (2009), is similar to *C. vatra* nov. sp. in general shape, but lacks a cyathus that can be seen in the latter. These authors date *Cypridea menevensis* as uppermost Berriasian(?) to lower Valanginian, whereas Vadillos-1 is dated as upper Barremian. Specimens identified as *Cypridea* gr. *modesta* by Barroso-Barcenilla et al. (2017) found at the Vadillos-2 site, correspond to *Cypridea vatra* nov. sp., since their characteristics coincide with the specimens of the present work. Owing to the distance between the sites and the age difference with the reference specimens, *Cypridea vatra* nov. sp. is proposed as a new species in this work. Another new species of this genus, *Cypridea marihoni* nov. sp., is identified and described for the first time in this work.

As recently advertised by Díez-Somolinos et al. (2024), the *Cyclocypris* specimens from Vadillos-1 seem to correspond to a new species, here described as *Cyclocypris bamba* nov. sp. The species *Cyclocypris* sp. A. as recorded by Krömmelbein (1968) from the Barremian of the "Wealden of Ghana" (Africa) seems to be the most closely related taxon to *Cyclocypris bamba* nov. sp., due to the similarly inflated caparace shape and size. According to Trabelsi et al. (2015, 2021) and Chnayna et al. (2021), the idea of supra-regional faunal exchange by passive ostracod dispersal during the Early Cretaceous (Sames and Horne, 2012) is supported by the Wealden-type non-marine ostracod assemblages found in the southwestern margin of North Africa. These patterns of distribution are primarily found between Eastern South America/Western Africa and North Africa, as well as between Europe and North Africa. The fact that the taxon most closely related to the new species *Cyclocypris bamba* nov. sp. was recorded in West Africa implies that, during the Early Cretaceous, the Peri-Tethyan islands may have served as useful conduits for the passive dispersal of non-marine ostracods through the "island-hopping" of larger animals. This would have ultimately facilitated intercontinental faunal exchange between South America and Europe, and potentially even Asia, via North Africa. The significance of the North Gondwanan continental basins and peri-Tethyan islands of the Central Tunisian Atlas for documenting Early Cretaceous non-marine microfaunas and floras makes *Cyclocypris bamba* nov. sp. potentially useful as a biostratigraphic tool for long-distance correlations. Owing to the distance between compared sites, the potential age difference to some of the reference species spand the fact that this is the first time that the genus *Cyclocypris* has been detected in the Iberian Peninsula, *Cyclocypris bamba* nov. sp. is proposed as a new species in this work.

Regarding the abundance of the taxa identified in this work (Fig. 7), *Cyclocypris bamba* nov. sp. is the most abundant with 1076 well-preserved carapaces and numerous disarticulated valves. *Cypridea vatra* nov. sp. is the second most abundant with 285 well-preserved carapaces and many disarticulated valves. *C. marihoni* nov. sp. is the third most abundant with 94 well-preserved carapaces and a few disarticulated valves. *C. ventriosa* is the fourth most abundant with 246 well-preserved carapaces and a few disarticulated valves. *C. isasae* is the less abundant with 34 well-preserved carapaces and a few disarticulated valves.

For palaeoenvironmental reconstructions, ostracods are particularly useful because they are often subject to quite restrictive living conditions. Being highly sensitive to environmental changes, ostracods are classified into three main groups based on the (palaeo-) environments in which they can (could) live: non-marine, marine, and brackish waters (Rodríguez-Lázaro and Ruiz-Muñoz, 2012). Most authors agree that *Cypridea* and *Cyclocypris* species, and the presence of charophytes in the assemblage together are useful indicators of low-energy limnic to oligohaline non-marine waters in Lower Cretaceous sedimentary environments (Brenner, 1976; Carbonel et al., 1988; Horne, 2002; Buscalioni et al., 2008). According to Horne and Martens (1998), species of *Cypridea* may have had desiccation-resistant eggs, allowing them to colonize temporary water bodies and achieve wide dispersal, although some species may have lived in permanent waters.

As Barroso-Barcenilla et al. (2017) specified, most of the ostracod specimens from the Vadillos-1 palaeontological site have been found with closed carapaces but the abundant presence of disarticulated ostracod valves may lead to a misinterpretation of the water energy. Disarticulated valves may have been the product of moults instead of sorting by water currents, since the rest of the ostracod carapaces are complete, suggesting that the environment in which they were deposited corresponds to a low-energy depositional environment. In the Vadillos-1 section, it can be observed how the influence of freshwater underwent important variations causing an occasional increase in salinity, probably related to a palaeoclimate shift towards stronger seasonality and lesser humidity in the region. Levels B and G, which are older, are interpreted as palaeoenvironment that was possibly flooded, forming muddy swamps rich in plant and animal organic matter characterized by reducing conditions. Later in time, the palaeoenvironmental setting became partially desiccated or drained, suffering subaerial exposure and developing the oxidizing conditions that can be seen in level R. The sedimentary palaeoenvironment as proposed by Barroso-Barcenilla et al. (2017) corresponds to an alluvial-palustrine floodplain of upper Barremian age, as confirmed by the presence of other microfossils such as fish scales, amphibian teeth, and charophytes in addition to the presence of ostracods and macrofossils, such as mollusks (bivalves of the family Unionoida and gastropods of the genus *Viviparus*) exclusive of non-marine environments in the association, which confirm a freshwater environment.

Fig. 6. A–F. *Cyclocypris bamba* nov. sp. adult carapaces from the upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, Cuenca (Spain). Holotype: A - VD1-928. Paratypes: B - VD1-926. C - VD1-929. D - VD1-930. E – VD1-934. F - VD1-935. (1) Right lateral view of carapace. (2) Left lateral view of carapace. (3) Ventral view of carapace. (4) Dorsal view of carapace. All photos are external views. Arrow indicates anterior side.

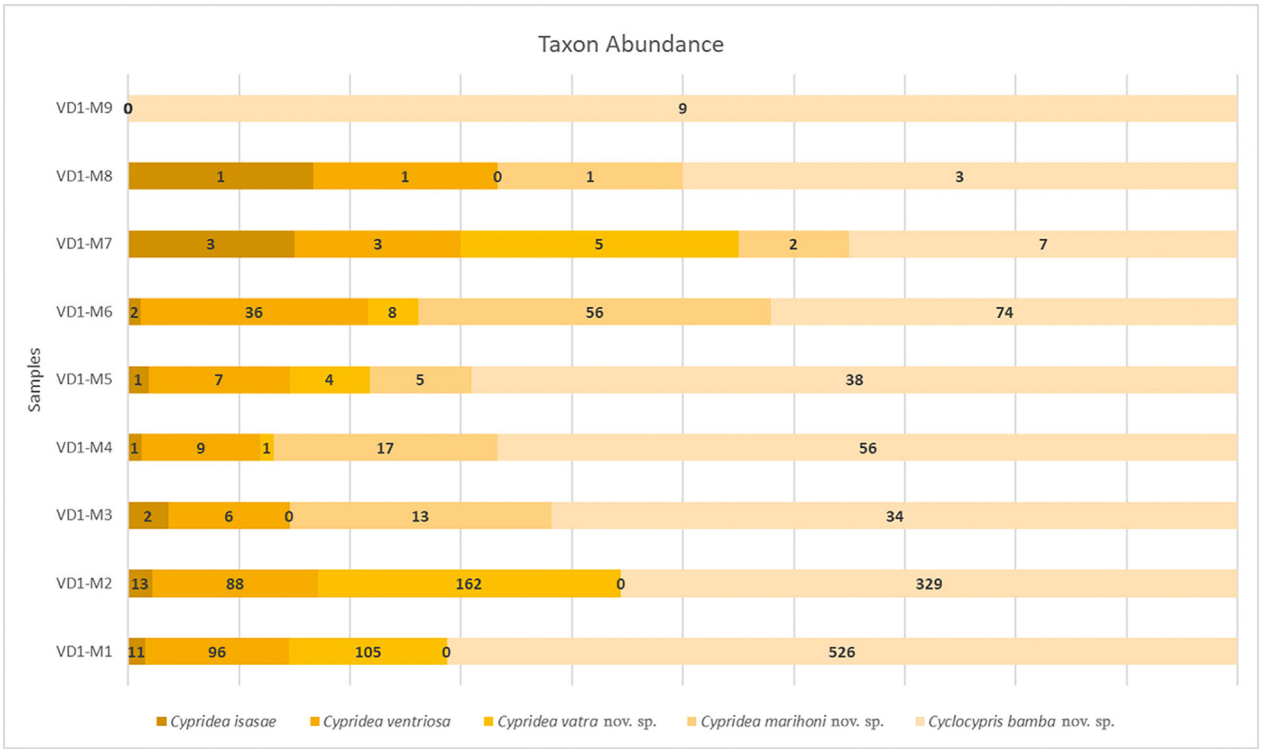


Fig. 7. Graphical representation of the abundance of the taxa identified in this work in the different samples taken from the upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1, Cuenca (Spain). The numbers shown in the graph indicate the number of specimens found.

The interpretation of Vadillos-1 site coincides with the proposal explained above by Barroso-Barcenilla et al. (2017). In water bodies with some depth and low-energy, stratification occurs; the shallower areas present oxic conditions that were suffused with light and characterized by low degrees of salinity that allow a higher abundance of diversity, while the deeper areas present reducing conditions in which the remains of animal and plant organic matter accumulated by deposition. These conditions would correspond to the characteristics observed in the grey level of the Vadillos-1 site. Due to the reconstructed strong seasonality in the region in combination with high mean temperatures and evaporation, waterbodies could seasonally (almost) desiccate, resulting in a depositional environment with more oxidizing conditions and increasing salinities. This led to a reduction of diversity, which has been observed among the microfossils in the red level of this site.

Geographically, Vadillos-1 is located in the northern part of the Serranía de Cuenca, so it could correspond to the northeast of the Uña-Las Hoyas valley (located in the southern part of the Serranía de Cuenca). Buscalioni et al. (2008) suggested that the sites of Las Hoyas, Buenache de la Sierra, Uña, and La Cantalera sites could have had a common palaeoenvironmental setting. The outcrops of the Beteta Gorges are interpreted as floodplains, with distributary channels of an alluvial system, generally in relatively distal areas, that were partially flooded to form small lacustrine or palustrine areas. However, the Las Hoyas site corresponds to a mixture of transitional wetland habitats (Rodríguez-Lázaro, 1995, 2016; Buscalioni and Poyato-Ariza, 2016). Buenache de la Sierra (Buscalioni et al., 2008) differs from Vadillos-1 due to the scarcity of fossil elements of terrestrial and non-marine aquatic species and La Cantalera site is also comparable to Vadillos-1, with abundant charophytes and ostracods characteristic of fresh waters.

Bravo et al. (2018) explain that the palaeoecological and palaeoenvironmental interpretation of the sites of Las Hoyas, Uña, Buenache de la Sierra and La Cantalera follow a scheme proposed by van der Valk (2006), in which a palaeoenvironment must have had obligate aquatic species, amphibian species, facultative species and species occasionally found in wetlands in order to be considered a wetland-type ecosystem. In this context, the Vadillos-1 section would meet these conditions as yielded obligate aquatic species such as charophytes, ostracods, fishes, amphibious species such as albanerpetontids, facultative species such as crocodyliforms and occasional species such as birds, which are known to be present from the ootaxa described in this site. As explained above, the ostracods found in Vadillos-1 site suggest that the palaeoenvironment of this Barremian site was a freshwater depositional environment with a low energy regime and where the water bodies were temporary, as occurs in wetlands.

6. Conclusions

Non-marine ostracods from the upper Barremian of Vadillos-1 (Cuenca, Spain) are described in this paper. They are represented by 4 species of *Cypridea*: *Cypridea isasae*, *Cypridea ventriosa*, *Cypridea vatra* nov. sp. and *Cypridea marihoni* nov. sp. In addition, a new species of the genus *Cyclocypris*, *Cyclocypris bamba* nov. sp., has been identified in all samples, being the most abundant taxon with the highest number of specimens. Except for *Cypridea isasae*, all these taxa are recorded for the first time in the studied area. The ostracod assemblages were found in association with micro remains of fishes, amphibians, crocodile eggshells, charophytes, and macro remains of dinosaurs and gastropods. Throughout the Vadillos-1 section, a variation of ostracod assemblages is observed between the grey mudstones level (G) and the red mudstones level

(R). The higher diversity in the grey mudstones could be related to reducing conditions and low salinity in the depositional environment, while in the red mudstones an almost total reduction of the water column may have occurred resulting in a depositional environment with more oxidizing conditions and higher salinity, reducing the diversity and presence of ostracods. Based on the carapace morphology of the ostracods found, most of which still have articulated valves, as well as on the habitat preferences of their closest living relatives and of the other microfossils that compose the association, a low energy palustrine-lacustrine depositional palaeoenvironment with temporary freshwater bodies is interpreted for the Vadillos-1 site.

CRediT authorship contribution statement

Marta Díez-Somolinos: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Fernando Barroso-Barcenilla:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Mélani Berrocal-Casero:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Conceptualization. **Julio Rodríguez-Lázaro:** Writing – review & editing, Validation, Supervision, Conceptualization. **Paloma Sevilla García:** Writing – review & editing, Validation, Supervision. **Benjamin Sames:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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.

Acknowledgements

The authors want to recognize the work of Carles Martín-Closas (University of Barcelona, Spain), and the reviewers Mike Ayress (UK), João Villar de Queiroz Neto (France) and Wang Yaqiong (China) for their constructive comments which helped to improve the manuscript. They also express their acknowledgement to the Town Council and neighbours of Cañizares (Spain). Research projects SBPLY/23/180801/000053, SBPLY/24/180801/000018 and "Ecosystems of the Cretaceous of Castilla-La Mancha" (SBPLY/21/180501/000242, co-financed by the by the European Regional Development Fund and the Operational Program CLM 2021–2027) of the Junta de Castilla-La Mancha and the University of Alcalá (Spain). Benjamin Sames acknowledges project BrasCretOst I (sponsored by PETROBRAS, Rio de Janeiro, Brazil), ensuring his opportunity to contribute to this study.

Data availability

No data was used for the research described in the article.

References

Aguirrezabala, L.M., Torres, A., Viera, L.I., 1985. El Weald de Igea (Cameros-La Rioja). Sedimentología, Bioestratigrafía y Paleontología de grandes reptiles (Dinosaurios). Munibe (Ciencias Naturales) 37, 11–138.
Anderson, F.W., 1939. XXXV. Wealden and Purbeck Ostracoda. Journal of Natural History 3, 291–310.
Anderson, F.W., 1962. Correlation of the Upper Purbeck Beds of England with the German Wealden. Liverpool and Manchester Geological Journal 1, 21–32.
Anderson, F.W., 1967. Ostracods from the Weald Clay of England. Bulletin of the Geological Survey of Great Britain 27, 237–269.
Anderson, F.W., 1985. Ostracod faunas in the Purbeck and Wealden of England. Journal of Micropalaeontology 4, 1–67.
Ayress, M.A., Whatley, R.C., 2014. Early Cretaceous non-marine Ostracoda from the North Falkland Basin, South Atlantic. Palaeontology 57, 1143–1175.
Baird, W., 1845. Arrangement of the British Entomostraca, with a list of species, particularly noticing those which have as yet been discovered within the bounds of the club. Berwickshire Naturalist's Club 2, 145–158.
Bajpai, S., Whatley, R.C., 2001. Late Cretaceous non-marine ostracods from the Deccan Intertrappean Beds, Kora: Western Kachchh, India. Revista Espanola de Micropaleontologia 33, 91–111.
Barrón-López, E., Barroso-Barcenilla, F., Sevilla, P., 2019. Estudio palinológico del Barremiense de las Hoces de Beteta (Cuenca, España). In: Libro de Resúmenes de la XXIII Bienal de la Real Sociedad Española de Historia Natural. Barcelona, p. 120.
Barroso-Barcenilla, F., Berrocal-Casero, M., Blain, H.A., Callapez, P.M., Cambra-Moo, O., Escaso, F., Martín-Closas, C., Ortega, F., Pérez-García, A., Prieto, I., Rodríguez-Lázaro, J.M., Ruiz-Galván, A., Sanz, J.L., Segura, M., Sevilla, P., 2017. Geological and palaeontological context of three new Barremian (Lower Cretaceous) vertebrate sites in the Iberian Peninsula (Cuenca Province, Central Spain). Proceedings of the Geologists Association 128, 256–270.
Berrocal-Casero, M., Alcalde-Fuentes, M.R., Audije-Gil, J., Sevilla, P., 2023. Theropod teeth from the upper Barremian (Lower Cretaceous) of Vadillos-1, Spain. Cretaceous Research 142, 105392.
Berrocal-Casero, M., Barroso-Barcenilla, F., Callapez, P.M., Pimentel, R., Alcalde-Fuentes, M.R., Prieto, I., 2025. New Ornithopod Remains from the Upper Barremian (Lower Cretaceous) of Vadillos-1 (Cuenca, Spain). Fossil Studies 3, 5.
Brady, G.S., Norman, A.M., 1889. A monograph of the marine and freshwater Ostracoda of the north Atlantic and of Northwestern Europe. Section I. Podocopa. Scientific Transactions of the Royal Dublin Society, Series 2 (4), 63–270.
Bravo, A.M., Sevilla, P., Barroso-Barcenilla, F., 2018. Avian and crocodilian eggshells from the upper Barremian site of Vadillos-1 (Lower Cretaceous, Cuenca province, Spain). Cretaceous Research 85, 28–41.
Brenner, P., 1976. Ostracoden und Charophyten des Spanischen Wealden. Palaeontographica A152, 113–201.
Brenner, P., Wiedmann, J., 1975. Nuevas aportaciones al conocimiento del "Weald" celtibérico septentrional y sus relaciones paleogeográficas. 1. In: Symposium sobre el Cretácico de la Cordillera Ibérica, Cuenca, pp. 125–134.
Bosquet, J., 1852. Description des Entomostracés Fossiles des Terrains Tertiares de la France et de la Belgique. Mémoires Couronnés et Mémoires des Savants Étrangers 24, 1–142.
Buscalioni, A.D., Fregenal-Martínez, M.A., Bravo, A., Poyato-Ariza, F.J., Sanchíz, B., Báez, A., Moo, O.C., Closas, C.M., Evans, S., Lobón, J.M., 2008. The vertebrate assemblage of Buenache de la Sierra (Upper Barremian of Serrania de Cuenca, Spain) with insights into its taphonomy and palaeoecology. Cretaceous Research 29, 687–710.
Buscalioni, A.D., Fregenal-Martínez, M.A., 2010. A holistic approach to the palaeoecology of Las Hoyas Konservat-Lagerstätte (La Huérguina Formation, Lower Cretaceous, Iberian Ranges, Spain). Journal of Iberian Geology 36, 297–326.
Buscalioni, A.D., Poyato-Ariza, F.J., 2016. Las Hoyas: a unique Cretaceous ecosystem. Cretaceous Period: Biotic Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin 71, 51–63.
Cabral, M.C., 1996. Paléobiogéographie des ostracodes Aptiens du Portugal. In: Crasquin-Soleau, S., Braccini, E., Lethiers, F. (Eds.), What About Ostracoda! 3e Congrés Européen des Ostracodologistes, pp. 289–303. Paris.
Canudo, J.I., Gasca, J.M., Aurell, M., Badiola, A., Blain, H.A., Cruzado-Caballero, P., Gómez-Fernández, D., Moreno-Azanza, M., Parrilla, J., Rabal-Garcés, R., Ruiz-Omeñaca, J.I., 2010. La Cantalera: an exceptional window onto the vertebrate biodiversity of the Hauterivian-Barremian transition in the Iberian Peninsula. Journal of Iberian Geology 36, 205–224.
Carbonel, P., Colin, J.P., Danielopol, D.L., Löffler, H., Neustrueva, I., 1988. Paleoecology of limnic ostracodes: a review of some major topics. Palaeogeography, Palaeoclimatology, Palaeoecology 62, 413–461.
Chnayna, M., Sames, B., Trabelsi, K., Houla, Y., Hanini, A., Ferhi, F., Skanji, A., Wagreich, M., Soussi, M., 2021. Discovery of a new Lower Cretaceous Wealden-type ostracod fauna from the Bouhedma Formation, Central Tunisian Atlas, North Africa. Cretaceous Research 127, 104942.
Danielopol, D.L., Cabral, M.C., Lord, A., Carbonel, P., Gross, M., Stoica, M., Humphreys, W.F., Namiotko, T., Tóth, E., Külköylüoğlu, O., Piller, W.E., Nunes, T., 2018. Sieve-type pore canals in the Timiriaseviinae - A contribution to the comparative morphology and the systematics of the Limnocytheridae (Ostracoda, Crustacea). Zootaxa 4495, 1–64.
Díez-Somolinos, M., Barroso-Barcenilla, F., Berrocal-Casero, M., Rodríguez-Lázaro, J., Sames, B., Sevilla, P., 2024. Non-marine upper Barremian ostracods from Vadillos-1 (Cuenca, Spain): Taxonomy and palaeoecology. In: Moncunill-Solé, B., Blanco, A., Grandal d'Anglade, A., González Fortes, G., Santos Fidalgo, L., Bao, R. (Eds.), Libro de Resúmenes de las XXXIX Jornadas de la Sociedad Española de Paleontología, p. 55. A Coruña.
Elstner, F., Mutterlose, J., 1996. The Lower Cretaceous (Berriasian and Valanginian) in NW Germany. Cretaceous Research 17, 119–133.
Francés, V., Sanz, J.L., 1989. In: La fauna del pasado en Cuenca (Sanz, J.L., Coord.). Instituto «Juan de Valdés», Ayuntamiento de Cuenca, Cuenca, pp. 125–144.
Fregenal-Martínez, M., Meléndez, N., Muñoz-García, M.B., Elez, J., Horra, R.d.l, 2017. The stratigraphic record of the Late Jurassic–Early Cretaceous rifting in the Alto

Tajo–Serranía de Cuenca Region (Iberian Ranges, Spain): Genetic and structural evidences for a revision and a new lithostratigraphic proposal. Revista de la Sociedad Geologica de Espana 30, 113–142.
Gómez, B., Z, Meon, H., Thevenard, F., Barale, G., 2001. Plant taphonomy and palaeoecology in the lacustrine Uña Delta (late Barremian, Iberian Ranges, Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 170, 13–148.
Henkel, S., Krebs, B., 1969. Zwei Säugetier-Unterkiefer aus der Unteren Kreide von Uña (Prov. Cuenca Spanien). Neues Jahrbuch für Geologie und Paläontologie - Monatshefte 8, 449–463.
Hoedemaeker, P.J., Herngreen, G.F.W., 2003. Correlation of Tethyan and Boreal Berriasian-Barremian strata with emphasis on strata in the subsurface of the Netherlands. Cretaceous Research 24, 253–275.
Horne, D.J., 1995. A revised ostracod biostratigraphy for the Purbeck-Wealden of England. Cretaceous Research 16, 639–663.
Horne, D.J., 2002. Ostracod biostratigraphy and palaeoecology of the Purbeck Limestone Group in southern England. Special Papers in Palaeontology 68, 53–70.
Horne, D.J., 2009. Purbeck–Wealden. In: Whittaker, J.E., Hart, M.B. (Eds.), Ostracods in British Stratigraphy. Micropalaeontological Society Special Publication, vol. 3. The Geological Society of London, London, pp. 289–308.
Horne, D.J., Martens, K., 1998. An assessment of the importance of resting eggs for the evolutionary success of Mesozoic non-marine *Cypridoidea*n Ostracoda (Crustacea). Archiv für Hydrobiologie 52, 549–561.
Jones, T.R., 1885. The Ostracoda of the Purbeck Formation; with notes on the Wealden species. Quarterly Journal of the Geological Society of London 41, 311–353.
Kaufmann, A., 1900. Cypriden und Parwinuliden der Schweiz. Revue Suisse de Zoologie 8, 209–423.
Khosla, S.C., Rathore, A.S., Nagori, M.L., Jakhar, S.R., 2011. Non-Marine Ostracoda from the Lameta Formation (Maastrichtian) of Jabalpur (Madhya Pradesh) and Nand-Dongargaon Basin (Maharashtra), India: Their correlation, age and taxonomy. Revista Espanola de Micropaleontologia 43, 209–260.
Kneuper-Haack, F., 1966. Ostracoden aus dem Wealden der Sierra de los Cameros (Nordwestliche Iberische Ketten). Geologisches Jahrbuch 44, 165–209.
Krömmelbein, K., 1968. The first non-marine Lower Cretaceous ostracods from Ghana, west Africa. Palaeontology 11, 259–263.
Latreille, P.A., 1806. Histoire naturelle généralle et particulière des Crustacés et des Insectes. Faculté de Dufart 1–467. Paris.
Lucas, S.G., Kietzke, K.K., Goodspeed, T.H., 1997. Paleontology of nonmarine Cretaceous –not marine Triassic– limestone in the Salt Anticline, Southeastern Utah. In: 48th Field Conference, Mesozoic Geology and Paleontology of the Four Corners Region, vol. 48. New Mexico Geological Society, Albuquerque, pp. 157–161.
Martin, G.P.R., 1940. Ostracoden des norddeutschen Purbeck und Wealden. Geologisches Institut der Universität Frankfurt und Natur-Museum. Senckenbergiana 22, 275–361.
Nye, E., Feist-Burkhardt, S., Horne, D.J., Ross, A.J., Whittaker, J.E., 2008. The palaeoenvironment associated with a partial Iguanodon skeleton from the Upper Weald Clay (Barremian, Early Cretaceous) at Smokejacks Brickworks (Ockley, Surrey, UK), based on palynomorphs and ostracods. Cretaceous Research 29, 417–444.
Pérez-Cano, J., Bover-Arnal, T., Martín-Closas, C., 2022. Barremian-early Aptian charophyte biostratigraphy revisited. Newsletters on Stratigraphy 55, 199–230.
Prieto, S., Díaz-Romeral, A., 1989. El yacimiento de Las Hoyas: historia de un descubrimiento. In: La fauna del pasado en Cuenca (Sanz, J.L., Coord.). Instituto «Juan de Valdés», Ayuntamiento de Cuenca, Cuenca, pp. 39–50.
Puértolas-Pascual, E., Rabal-Garcés, R., Canudo, J.I., 2015. Exceptional crocodylomorph biodiversity of "La Cantalera" site (lower Barremian; Lower Cretaceous) in Teruel, Spain. Paleontologia Electronica 18, 1–16.
Ramírez del Pozo, J., 1971. Bioestratigrafía y microfacies del Jurásico y Cretácico del Norte de España (Región Cantábrica), vol. 78. Memorias del Instituto Geológico y Minero de España, pp. 1–357.
Rodríguez-Lázaro, J., Ruiz-Muñoz, F., 2012. A general introduction to ostracods: morphology, distribution, fossil record and applications. In: Horne, D.J., Holmes, J., Rodríguez-Lázaro, J., Viehberg, F. (Eds.), Ostracoda as Proxies for Quaternary Climate Change, vol. 17. Developments in Quaternary Science, pp. 1–14.
Rodríguez-Lázaro, J., 1995. Ostracodes. In: Melendez, N. (Ed.), Las Hoyas. A lacustrine Konservat-Lagerstätte (Cuenca, Spain). Field trip guide book of the II International Symposium on Lithographic Limestones. Universidad Complutense de Madrid, Madrid, pp. 33–34.
Rodríguez-Lázaro, J., 2016. Ostracoda. In: Poyato-Ariza, F.J., Buscalioni, A.D. (Eds.), Las Hoyas: a Cretaceous wetland. A multi-disciplinary synthesis after 25 years of research on an exceptional fossil Lagerstätte from Spain. Verlag Dr. Friedrich Pfeil, München, pp. 89–93.
Ruiz-Galván, A., Barroso-Barcenilla, F., Ortega, F., Sevilla, P., 2017. Crocodyliform dental remains from the Lower Cretaceous sites of the Beteta Gorges (Cuenca, Spain). In: Barrios de Pedro, S., Blanco Moreno, C., de Celis, A., Colmenar, J., Cuesta, E., García-Martínez, D., Gascó, F., Jacinto, A., Malafaia, E., Martín Jiménez, M., de Miguel Chaves, C., Mocho, P., Pais, V., Páramo Blázquez, A., Pereira, S., Serrano Martínez, A., Vidal, D. (Eds.), A Glimpse of the Past, Abstract Book of the XV Encuentro de Jóvenes Investigadores en Paleontología - XV Encontro de Jovens Investigadores em Paleontologia, Pombal, pp. 353–355.
Sahni, A., Khosla, A., 1994. A Maastrichtian ostracode assemblage (Lameta Formation) from Jabalpur Cantonment, Madhya Pradesh, India. Current Science 67, 456–460.
Sames, B., 2011a. Early Cretaceous *Theriosynoecum* Branson 1936 in North America and Europe. Micropaleontology 57, 291–344.
Sames, B., 2011b. Early Cretaceous *Cypridea* Bosquet 1852 in North America and Europe. Micropaleontology 57, 345–431.
Sames, B., 2011c. Glossary of morphologic terms of late Mesozoic nonmarine Ostracoda, relevant to *Theriosynoecum* Branson 1936 and *Cypridea* Bosquet 1852. Micropaleontology 57, 433–454.
Sames, B., Horne, D.J., 2012. Latest Jurassic to Cretaceous non-marine ostracod biostratigraphy: Unde venis, quo vadis? Journal of Stratigraphy 36, 266–288.
Sars, G.O., 1863. Oversigt af de indenlandske Ferskvandcopepoder. Forhandlinger i Videnskabs-Selskabet i Christiana 1862, 212–262.
Sars, G.O., 1866. Oversigt af Norges marine Ostracoder. Forhandlinger i Videnskabs-Selskabet i Christiana 1865, 1–130.
Schudack, U., Schudack, M., 2009a. Ostracod biostratigraphy in the Lower Cretaceous of the Iberian Chain (eastern Spain). Iberian Journal of Geology 35, 139–166.
Schudack, U., Schudack, M.E., 2009b. On the taxonomy of the species *Cypridea setina* Anderson, 1939 and *Cypridea laevigata* Dunker, 1846 (Ostracoda, Crustacea) from the Early Cretaceous of Europe - a special note on systematical inconsistencies. Berliner Paläobiologische Abhandlungen 10, 311–320.
Sowerby, J.D.C., 1836. Descriptive notes respecting the shells figured in plates XI to XXIII. In: Fitton, W.H. (Ed.), Observations on Some of the Strata Between the Chalk and the Oxford Oolite in the South–East of England. Geological Society of London, Transactions of the Geological Society of London, London, pp. 344–345. Series 2, 44.
Swain, F.M., 1993. Fossil nonmarine Ostracoda of the United States. Developments in Palaeontology and Stratigraphy, Elsevier, Amsterdam 16, 1–401.
Sylvester-Bradley, P.C., 1947. The shell of the Ostracod genus *Bythocythere*. Annals and Magazine of Natural History, Series 11 (14), 719–722.
Trabelsi, K., Sames, B., Salmouna, A., Piovesan, E.K., Rouina, S.B., Houla, Y., Touir, J., Soussi, M., 2015. Ostracods from the marginal coastal Lower Cretaceous (Aptian) of the Central Tunisian Atlas (North Africa): paleoenvironment, biostratigraphy and paleobiogeography. Revue de Micropaleontologie 58, 309–331.
Trabelsi, K., Sames, B., Nasri, A., Piovesan, E.K., Elferhi, F., Skanji, A., Houla, Y., Soussi, M., Wagreich, M., 2021. Ostracods as proxies for marginal marine to nonmarine intervals in the mid-Cretaceous carbonate platform of the Central Tunisian Atlas (North Africa): Response to major short-term sea-level falls. Cretaceous Research 117, 104581.
Trabelsi, K., Wiese, F., Mai, A.T., Sames, B., Herrle, J.O., 2024. The Lower Cretaceous charophyte flora from the Cuchía section (Cantabrian Basin, North Spain): Biostratigraphy and palaeobiogeography. Cretaceous Research 155, 105774.
van der Valk, A.G., 2006. The Biology of Freshwater Wetlands. Oxford University Press, Oxford, pp. 1–173.
Vicente, A., Martín-Closas, C., 2013. Lower Cretaceous charophytes from the Serranía de Cuenca, Iberian Chain: taxonomy, biostratigraphy and palaeoecology. Cretaceous Research 40, 227–242.
Vicente, A., Sanjuan, J., Pérez-Cano, J., Trabelsi, K., Martín-Closas, C., 2024. A bioprovince for the Barremian–Aptian charophytes of the Central Tethyan Archipelago. Cretaceous Research 154, 105752.
Wang, H., Li, S., Zhang, H., Cao, M., Horne, D.J., 2019. Biostratigraphic and palaeoenvironmental significance of Campanian-early Maastrichtian (Late Cretaceous) ostracods from the Jiaozhou Formation of Zhucheng, Shandong, China. Cretaceous Research 93, 4–21.
Wick, W., Wolburg, J., 1962. B 6 – Wealden in NW-Deutschland. In: Mikropaläontologen, Arbeitskreis deutscher (Ed.), Leitfossilien der Mikropaläontologie – Ein Abriss. Gebrüder Bornträger, Berlin-Nikolassee, pp. 191–224 pls. 28–32a.
Wolburg, J., 1959. Die Cyprideen des NW-deutschen Wealden. Senckenbergiana Lethaea 40, 223–315.
Zenker, G.F.W., 1854. Monographie der Ostracoden. Archiv für Naturgeschichte 20, 1–87.