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**PLIO-PLEISTOCENE NON-MARINE  
OSTRACODA FROM CENTRAL APENNINES  
INTERMONTANE BASINS IN THE FRAME OF  
THE TAXONOMIC HARMONISATION OF  
SUBFAMILY CANDONINAE (KAUFMANN, 1900)**

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## Abstract

This thesis concerns the study of non-marine Ostracoda from different Pliocene-Early Pleistocene intermontane basins of central Italy. In detail, in central Apennines, the Neogene-Quaternary extensional tectonics gave origin to several basins filled by continental deposits but much of their tectono-stratigraphic evolution is still unknown. The analysis of the non-marine ostracod assemblages recovered from the early infilling (Piacenzian and Gelasian) deposits of three different central Apennines intermontane basins (Tiberino, L'Aquila, and Rieti basins) and the Middle Tiber Valley merged with the previously known data, gives a good framework of the non-marine ostracod palaeobiodiversity. Ostracods species found in the studied Plio-Pleistocene sequences mainly belong to the subfamily Candoninae and some of them are referable to the genus *Caspiocypris* that originated in the Paratethyan domain, a huge epicontinental brackish sea that extended across central Europe and western Asia. Neogene and Quaternary ostracods from the Paratethys bioprovince originated through huge adaptive radiations, which gave rise to endemic brackish genera and species. Unfortunately, much confusion surrounds their taxonomy, due to the low quality of information and images in the original old literature and the incompleteness of the type material, a taxonomic revision was necessary. The systematic revision of Paratethyan endemic genera included in the subfamily Candoninae was performed. 33 genera were taken into account: *Advenocypris*, *Candoniella*, *Graviacypris*, and *Telekia* were considered to be junior synonyms of *Typhlocypris*, *Pseudocandona*, and *Candona*; *Moesiella* is a *nomen nudum*; *Caspiollina*, *Dacicandona*, *Liventalina*, and *Turkmenella* lacks of material and the poor descriptions prevented us from performing a full revision; and the monospecific genus *Thaminocypris* possibly includes a teratological form. Finally, the remaining 23 genera were merged into nine endemic, valid genera (*Bakunella*, *Camptocypris*, *Caspiocypris*, *Hastacandona*, *Lineocypris*, *Pontoniella*, *Propontoniella*, *Typhlocyrella*, and *Zalanyiella*). Emended diagnoses and descriptions are proposed for these genera.

The Tiberino Basin sedimentary infill is made of a thick succession of Pliocene–early Quaternary continental deposits. We analysed the deep lacustrine ostracod assemblages from the Fosso Bianco Fm. and provided descriptions of five new species included in the subfamily Candoninae (*Caspiocypris basilicii* Spadi & Gliozzi sp. nov., *Caspiocypris perusia* Spadi & Gliozzi sp. nov., *Caspiocypris posteroacuta* Spadi & Gliozzi sp. nov., *Caspiocypris tiberina* Spadi & Gliozzi sp. nov. and *Caspiocypris tuderis* Spadi & Gliozzi sp. nov.) and one new species included in the subfamily Limnocytherinae (*Paralimnocythere umbra* Spadi & Gliozzi sp. nov.). The five species of *Caspiocypris* seem to represent a species flock because *Caspiocypris* includes a group of closely related species characterized by monophyly, endemism and speciosity, confirming the ‘ancient lake’ nature of the Palaeolake Tiberino during the Piacenzian–Gelasian. The marginal lacustrine ostracods

collected from Fosso Bianco Fm. and from the alluvial fan-related Ponte Naja Fm. were represented by 17 species with two new species (*Paralimnocythere* sp. nov. and *Hemicypris* sp. nov.), which could be divided in different cluster groups linked to different palaeoenvironments along the swampy lacustrine margins of the Palaeolake Tiberino. Overall, the ostracod from the Tiberino Basin were referable to 14 genera split into 24 species, eight of which resulted endemic.

For the L'Aquila Basin, the palaeontological and facies analyses were carried out on the San Demetrio-Colle Cantaro Synthem. The ostracods were collected in the deep lacustrine silts of the San Nicandro Fm. and the Gilbert-type delta system conglomerated of Valle Orsa Fm. Thirteen species were recognised, six of which are new: *Caspiocypris amiterni* Spadi & Gliozzi sp. nov., *C. bosii* Spadi & Gliozzi sp. nov., *C. nicandroi* Spadi & Gliozzi sp. nov., *C. vestinae* Spadi & Gliozzi sp. nov., *Cypria bikeratia* Spadi & Gliozzi sp. nov., and *Ilyocypris ilae* Spadi & Gliozzi sp. nov.. Conversely, the ostracod assemblages of the Valle Orsa Fm., due to the co-occurrence of *Ilyocypris*, *Candona* and *Cypria*, suggested a shallow water environment with flowing waters possibly linked to a nearby river delta. Overall, the ostracod from the San Demetrio-Colle Cantaro Synthem were referable to 13 species pertaining to 10 genera, eight of which resulted endemic species.

At the confluence between the Rieti Basin and the Middle Tiber Valley only one species, *Qinghaicypris* cf. *Q. riojensis*, was found in the Monteleone Sabino Unit related to the deposition of a braided plain with some small lake, ponds and swampy areas. In the same unit, previous papers reported other ostracods, in total, 28 species pertaining to 14 genera were recovered from the Gelasian of Monteleone Sabino Unit. In summary, during the Piacenzian-Gelasian interval, the continental aquatic environments of central Italy were characterised by the occurrence of 60 different species referable to 24 genera. This is due to the rich-in-species genus *Caspiocypris* that gave rise to two species flocks in the deep lacustrine environment of Palaeolake San Nicandro and Palaeolake Tiberino.

The ostracod assemblages studied show affinity at generic and specific level with the Neogene and Quaternary Paratethyan and Balkan realms. This contrasts with the pattern seen in the other central Italian Pliocene and Early Pleistocene assemblages related to shallow water environments where the taxa show a clear Palaearctic or Holarctic distribution and were widely distributed in central and western Europe at least until the Early Pleistocene. The presence in the Plio-Pleistocene of the central Italy basins of some Paratethyan ostracods species or some shallow freshwater species from "Paludonian Beds" can be explained as the consequence of the passive dispersal through aquatic birds along a westward path from the Balkan area or with the evolution in the Mediterranean area of Lago-Mare ostracods that occurred at the end of the Messinian.

According to our palaeontological analyses, the early infill of the Tiberino (Fosso Bianco and Ponte Naja Fm.) and L'Aquila (San Demetrio-Colle Cantaro Synthem) basins must be dated to Piacenzian-Gelasian, due to the presence of *Caspiocypris* in both basins. Similarly, the oldest deposits of the Rieti Basin (Monteleone Sabino Unit) resulted to be at least Gelasian in age, owing to the occurrence of large mammals and other biostratigraphical proxies. The late Piacenzian (ca. 3 Ma) onset of the Tiberino and L'Aquila extensional basins calls into question previous suggestions that the onset of these basins becomes younger from the Tyrrhenian toward the Adriatic side of the central Apennines.



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# **Plio-Pleistocene non-marine Ostracoda from central Apennines intermontane basins in the frame of the taxonomic harmonisation of subfamily Candoninae (Kaufmann, 1900)**

## **1 Introduction**

### **1.1 The role of non-marine ostracods in the study of the continental sedimentary successions**

Ostracoda (Crustacea) are small crustaceans whose body is completely enclosed by two low-Mg calcitic valves. They are common as microfossils because their two valves easily fossilize in sediments after the death. Moreover, ostracods represent one of the most diverse groups of living crustaceans and have their fossil record spanning since Ordovician (Horne et al., 2002). Ostracods inhabit virtually all the known aquatic ecosystems in marine and non-marine environments, with some taxa adapted to a semi-terrestrial life (Rodríguez-Lázaro & Ruiz-Muñoz, 2012). In a geological context, applications of ostracods include palaeobiology, palaeoecology, palaeolimnology, and biostratigraphy. Definitely, ostracods are important biological indicators and since they are often dependant from several ecological parameters such as habitat type (Mezquita et al., 2000), water quality (Pieri et al., 2012), water depth (Frenzel et al., 2010), dissolved oxygen concentration (Boomer & Whatley, 1992), hydrochemical changes (Mischke et al., 2007), macrophyte cover (Mormul et al., 2010; Mazzini et al., 2014b; Marchegiano et al., 2017) and other environmental variables, they are useful proxies for the description of the stratigraphic sequences and the palaeoenvironmental changes occurred during their deposition (Mischke et al., 2003). In fact, detailed analyses of the characteristics of the ostracod assemblages permit palaeoenvironmental reconstructions by the estimation of the palaeoenvironmental parameters including temperature, salinity, main solute concentrations, productivity, hydrology and oxygenation (for thorough discussions, see Mesquita-Joanes et al., 2012; Smith & Palmer, 2012). Moreover, the ostracod shells can be used for stable isotope and trace element analyses, used as well as proxies for the palaeoenvironmental changes (Holmes, 1996).

Non-marine geological records are “archives” of the atmospheric environmental changes and a global climatic signature can be obtained by combining different signals in continental settlements. Lacustrine sediments represent the most important continental archive for the evaluation of palaeobiodiversity and reconstruction of the continental palaeoenvironmental evolution and palaeoclimatic changes. They contain signatures of both terrestrial and aquatic ecosystems and their changes through time, driven by climatic variability. The non-marine ostracods, all assigned to order Podocopida, colonized non-marine waters since Carboniferous (Martens et al., 2008; Bennett et al.,

2012). Ostracods are commonly found in lake sediments when other important proxy organisms are not present (Holmes, 2001; Holmes & Chivas, 2002). Lacustrine ostracods are mostly benthonic, living on aquatic plants, crawling on sediment and within the sediment. Methodical approaches include the analyses of the ostracod assemblages, their taxonomical composition and the state of preservation of the shells. It is very important to clarify first the taphonomy, attempting to identify live (autochthonous thanatocoenosis) vs. death assemblages, as some complementary conclusions (hydrodynamics, sediment geochemistry) can be drawn by considering the percentages of transported and altered specimens (Whatley, 1988; Boomer et al., 2003). The palaeoclimatic and palaeoenvironmental interpretations are based on the autecological characteristics of each species that made up the autochthonous thanatocoenosis, applying the uniformitarian principle, and thus, the reliable identification of fossil ostracod assemblages based on a robust taxonomy is required.

Among the non-marine ostracods, the subfamily Candoninae Kaufmann, 1900 is a very species-rich group, widely distributed in non-marine habitats, especially in the Palearctic Region. In this zoogeographic domain, a high number of both fossil and extant taxa document it (Meisch, 2000; Martens et al., 2008; Martens & Savatnalinton, 2011). Unfortunately, a number of genera of the subfamily, such as *Candona* Baird, 1845 and *Pseudocandona* Kaufmann, 1900, are poorly defined and need to be reviewed (Danielopol et al., 2011). As a consequence, up to now some taxa were used by ostracodologists in such different ways that presently their semantic content has become very confused (compare inter alia the systematics of Candoninae proposed by Krstić & Guan, 2000 with that of Karanovic, 2012) (Namiotko et al., 2014). The Candoninae are rather difficult to be identified because of the lack of ornamentation and very few distinctive shell characters other than the form usable for the specific or generic attribution (Danielopol et al., 2008; Baltanás & Danielopol, 2011). Even worse, it has become very difficult to use Candoninae when dealing with topics of wider interest, as for palaeobiogeographic studies at regional or global scales.

Finally, non-marine ostracods are used as biostratigraphic tools especially during Mesozoic (Babinot et al., 1996; Sames, 2008; Sames et al., 2010), but they are also used with a good degree of reliability also for the Neogene-Quaternary interval in some areas of the Eastern Europe (Krstić, 1972; 1985; Sokač, 1972; Jiříček, 1985). In Italy, the continental biochronology is based mainly on large and small mammals (Gliozzi et al., 1997; Masini & Sala, 2007; Palombo, 2009), while non-marine ostracods, being poorly known, were not yet considered by Gliozzi et al. (1997) a good biostratigraphical proxy. In fact, although since the Pliocene, the intermontane basins of central Apennines have hosted several isolated lakes; their ostracod associations are poorly known. To date, papers concerning Italian Pliocene and early Pleistocene freshwater ostracods are really scarce: Di Napoli Alliata (1962), Ambrosetti et al. (1995a), Barberi et al. (1995), Medici & Gliozzi (2008) and

Cosentino et al. (2017) described the ostracod assemblages from the Tiberino, Rieti and L'Aquila Basins (central Italy), while Gliozzi (1996), Ligios et al. (2009), Medici (2011), Ligios & Gliozzi (2012) and Medici et al. (2011) have addressed taxonomy of selected taxa or assemblages. Further studies will clarify if non-marine ostracods would be a suitable biostratigraphic tool for the continental deposits in central Italy in the Pliocene-Early Pleistocene interval.

## **1.2 The central Apennines intermontane basins**

The Apennines are a central Mediterranean expression of the convergence between the African and Eurasian plates. The evolution of the Apennines arc is related to a flexural retreat of the Adriatic lithosphere plate (connected to the African plate), the NE migration of the compressive front, and the contemporaneous rifting of the Tyrrhenian basin. The Apennines result to be a northeast-verging imbricate fold-thrust belt that developed since early Miocene along the margin of the Adria micro-Plate in response to the south-eastward retreat of the subduction zone between the southern margin of central Europe and a remnant of the Neotethyan oceanic lithosphere (Malinverno & Ryan, 1986; Patacca et al., 1990).

In the central Apennines, the main thrust systems strike northwest-southeast and dip gently towards SW. The cropping out thrust sheets consist of Triassic to middle Miocene carbonate rocks deposited along the southern margin of the Tethys Ocean (Cosentino et al., 2010). Miocene through Pliocene synorogenic sediments record the kinematic history of thrusting in the central Apennines composed by marine turbidites spanning from Burdigalian to late Messinian (Fig. 1.1) (Cipollari et al., 1997).

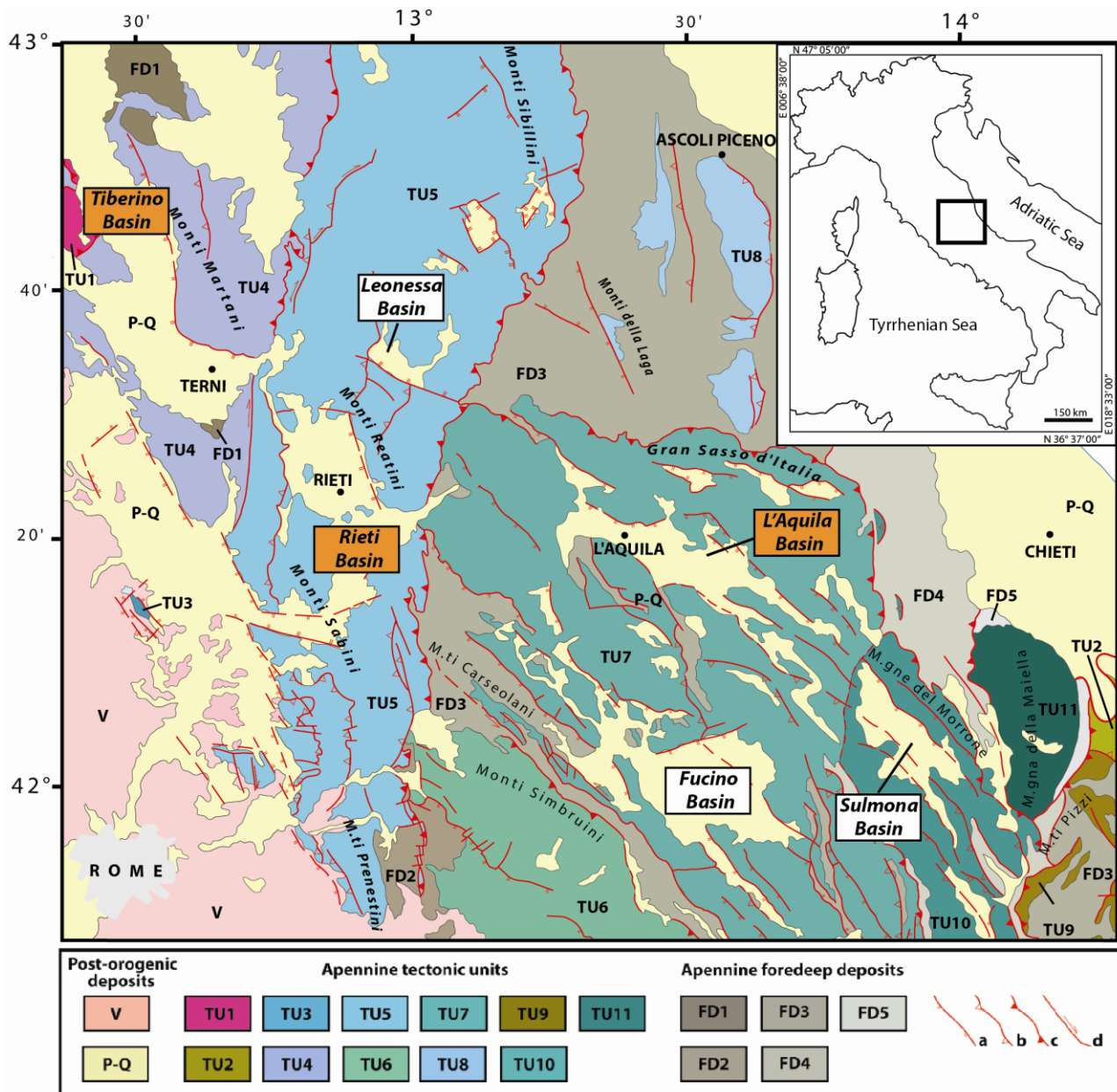
In this framework, the intermontane basins represent regions of the Earth, enclosed by mountain chains, where the eroded detritus accumulate. In particular, the intermontane basins of central Apennines are mainly related to two different events: an initial stage of shortening linked to the building phases of the Apennines and a second, later stage of extension tectonics related to the opening of the Tyrrhenian back-arc basin and the orogenic collapse of the Apennines.

During the first stage (Miocene-Early Pliocene), the intermontane basins were characterized by shortening and compressional tectonics setting were usually controlled by changes in the accommodation space induced by the active compressional tectonics (e.g., differential uplift by a growing fold, increasing subsidence in front of an active thrust, etc.) as a part of a foreland basin system (*sensu* De Celles & Giles, 1996). In the central Apennines, the ages of the thrust-top basins helped to outline the main steps of the Apennine orogeny. Indeed, the NE migration of the structural system was well documented through the observation of progressively younger thrusts affecting the

Italian peninsula towards NE (from late Tortonian to late Pliocene) (Patacca et al., 1992; Cipollari & Cosentino, 1995; Cipollari et al., 1999; Cosentino et al., 2010).

After the orogenic phase, the central Apennines underwent an extensional tectonic linked to the developed of Tyrrhenian province, as a lithospheric response of the upper plate to the rollback of the subducting Adria micro-Plate (Dewey, 1988; Faccenna et al., 1996). This process led to continental rupture and oceanization of the Tyrrhenian area and enhanced the orogenic collapse of the Apennine tectonic wedge, defining the onset of the second stage of the intermontane basin evolution in the Apennines. The arrival of the Tyrrhenian extensional front in different sectors of the Apennine chain gave rise to collapsing areas and the subsequent development of extensional intermontane basins, which, supposedly, became younger towards the Adriatic side of the central Apennines (Cavinato & DeCelles, 1999; Galadini & Messina, 2004).

The extensional intermontane basins of central Apennines are among the most seismically active sectors of the central Mediterranean area (Amato et al., 1997; Falcucci et al., 2011), but their tectono-stratigraphic evolution is still poorly understood. In these circumstances, intermontane basins are crucial areas to understand the interaction between tectonic and climate in the post-orogenic stages of central Apennines. Moreover, the persistence of this extensional tectonic is confirmed by instrumental seismicity, earthquakes occurrence (Falcucci et al., 2011), or by GPS and InSAR time-series (D'Agostino et al., 2011), along NW-SE trending normal faults, as well as by the numerous palaeoseismological studies that evidenced the displacement of the Holocene deposits within the central Apennines intermontane basins (Moro et al., 2013). In this background, the knowledge of the Plio-Quaternary stratigraphic framework is fundamental to chronologically constrain the geological events, which have deep implications in neotectonics and the reconstruction of recent palaeoenvironments. Moreover, the lack of a detailed stratigraphic framework related to the continental facies of the Plio-Quaternary continental basins for the central Apennines prevented the definition of a reliable structural evolution related to the extensional tectonics.



**Figure 1.1:** Structural sketch of the central Apennines with the main Plio-Quaternary intermontane basins of the central Apennines in evidence. V: Quaternary volcanics; P-Q: Plio-Quaternary marine and continental deposits; TU1: External Ligurian Unit; TU2: Sannio Unit; TU3: Mt. Soratte Tectonic Unit; TU4: Inner Umbria Tectonic Unit; TU5: Umbria-Marchean-Sabine Tectonic Unit; TU6: Simbruini-Ernici-Matese Tectonic Unit; TU7: Gran Sasso-Western Marsica Tectonic Unit; TU8: Molise Tectonic Unit; TU9: Acquasanta-Montagnone Tectonic Unit; TU10: Morrone-Eastern Marsica Tectonic Unit; TU11: Maiella Tectonic Unit; FD1: Burdigalian foredeep deposits; FD2: Tortonian foredeep deposits; FD3: Messinian foredeep deposits; FD4: upper Messinian-early Lower Pliocene foredeep deposits; FD5: late Lower Pliocene foredeep deposits; a) normal fault; b) minor thrust; c) major thrust; d) strike-slip fault, modified from Cosentino et al., 2017. The studied basins in this thesis are highlight in orange.

A detailed analysis of the tectono-sedimentary history of each intermontane basin is an important step toward revealing their long-term evolution as well as their current seismic hazard. The scarcity of biochronological and/or geochronological well-constrained stratigraphic successions has

brought about a series of reference stratigraphical schemes that are useful for the correlations only within each extensional intermontane basin of the central Apennines. Attempts to correlate the older continental deposits of the different extensional intermontane basins of central Apennines were, up to now, mainly based on geomorphological observations (Bertini & Bosi, 1976; Bosi & Messina, 1991). Neither approaches helped to precisely define the age of the early infill of the central Apennine extensional intermontane basins.

### **1.3 Aims of the present thesis**

This Ph.D. thesis concerns the study of non-marine ostracods from different Pliocene-Early Pleistocene intermontane basins of central Italy. As we stated previously, in central Apennines the Neogene-Quaternary extensional tectonic gave origin to several basins filled by continental deposits but, unfortunately, their long-term tectono-stratigraphic evolution is still unknown. Indeed, one of the purposes of this project is to use non-marine ostracods as the main tool to depict their early evolution. In this project, 1) I will define a robust taxonomy of the collected non-marine ostracod assemblages in order to 2) describe the Pliocene-Early Pleistocene ostracod palaeobiodiversity, 3) use them as proxies for the palaeoenvironmental and palaeoclimatic reconstructions, and 4) build a range chart of the ostracod species, which could be useful for a future biostratigraphical scheme.

The starting point to achieve the aforementioned objectives will be to establish a solid taxonomy of the studied ostracod assemblages, which will allow the possibility of strong correlations among the basins as well as their detailed palaeoenvironmental and palaeoclimatic reconstruction. Ostracods species found in the studied Plio-Pleistocene sequences mainly belong to the subfamily Candoninae and are referable to the genus *Caspiocypris* that is rooted in the Paratethyan domain. In particular, a lot of confusion exists in the palaeontological literature dealing with Candoninae described from the Paratethyan domain. Thus, a taxonomical revision of this group that could lead to their taxonomic harmonisation was needed. Candoninae are known to be difficult to identify, due to their reduced ornamentation and very few morphological traits. In the whole project, classical palaeontological methodologies are accompanied with the advanced geometric-morphometric analysis using MORPHOMATICA software.

The present PhD thesis is addressed on three Plio-Pleistocene intermontane basins located in central Apennines: the Tiberino, L'Aquila and Rieti basins. For each of them, a detailed sampling of the outcropping early sedimentary succession was carried out for micropalaeontological analyses. During the geological survey and sampling campaign, also sedimentological and facies analyses were performed to provide multidisciplinary data for the palaeoenvironmental and stratigraphic interpretation.



## 1.4 Thesis structure

The thesis text is organized in four chapters including the results of the stratigraphical and palaeontological study of each basin, one chapter dealing with the taxonomic harmonisation of the Paratethyan Candoninae genera, and Discussion and Conclusion.

**Chapter 2** includes the description of the stratigraphy and palaeontology of the Tiberino Basin. This basin was chosen because its geology was already well known as well as its chronostratigraphic frame based on mammal biochronology, molluscs, and magnetostratigraphy. The results of the study of the Tiberino Basin ostracods were published in the accepted article:

**Spadi, M.**, Gliozzi, E., & Medici, M.C., 2017. A Plio–Pleistocene *Caspiocypris* species flock (Candoninae, Ostracoda) from the Palaeolake Tiberino (Umbria, central Italy). *Journal of Systematic Palaeontology*, 18 pp.

**Chapter 3** deals with the L’Aquila Basin. In this chapter the description of a new stratigraphical arrangement for the continental deposits infilling this basin is presented, achieved through the palaeontological and facies analyses of the depositional units the Palaeolake San Nicandro lacustrine system, developed in the L’Aquila Basin (central Apennines, Italy). The results of the palaeontological and stratigraphical studies on L’Aquila Basin were presented in three papers:

**Spadi, M.**, Gliozzi, E., Cosentino, D., & Nocentini, M., 2016. Late Piacenzian–Gelasian freshwater ostracods (Crustacea) from the L’Aquila Basin (central Apennines, Italy). *Journal of Systematic Palaeontology*, 14(7), 617–642.

Cosentino, D., Asti, R., Nocentini, M., Gliozzi, E., Kotsakis, T., Mattei, M., Esu, E., **Spadi, M.**, Tallini, M., Cifelli, F., Pennacchioni, M., Cavuoto, G., Di Fiore, V. (2017). New insights into the onset and evolution of the central Apennine extensional intermontane basins based on the tectonically active L’Aquila Basin (central Italy), *Geological Society of America Bulletin*, 129(9/10), 1314-1336.

Nocentini, M., Cosentino, D., Tallini, M., & **Spadi, M.**, submitted. Plio-Quaternary geology of the Paganica-San Demetrio-Castelnuovo Basin (central Italy). *Journal of Map*.

**Chapter 4** concerns the Rieti Basin. This chapter is focused on the description of the ostracod fauna from the rediscovered site of Castel San Pietro and its chronostratigraphic constraints achieved using carpological, ostracods, molluscs and mammals rests. The combination of palaeoecological and biostratigraphic data coming from palaeontological tools lead to better depict the time of the initial

deposition of the Rieti and Middle Tiber Valley infilling. The results of the research on the Castel San Pietro site were published in the paper:

Pandolfi, L., **Spadi, M.**, Martinetto, E., Kotsakis, T., Esu, D. (2017). New data on the Lower Pleistocene (Gelasian) lignite beds of Castel San Pietro (Rieti, Central Italy). *Rivista Italiana di Palaeontologia e Stratigrafia*, 123(2), 335–346.

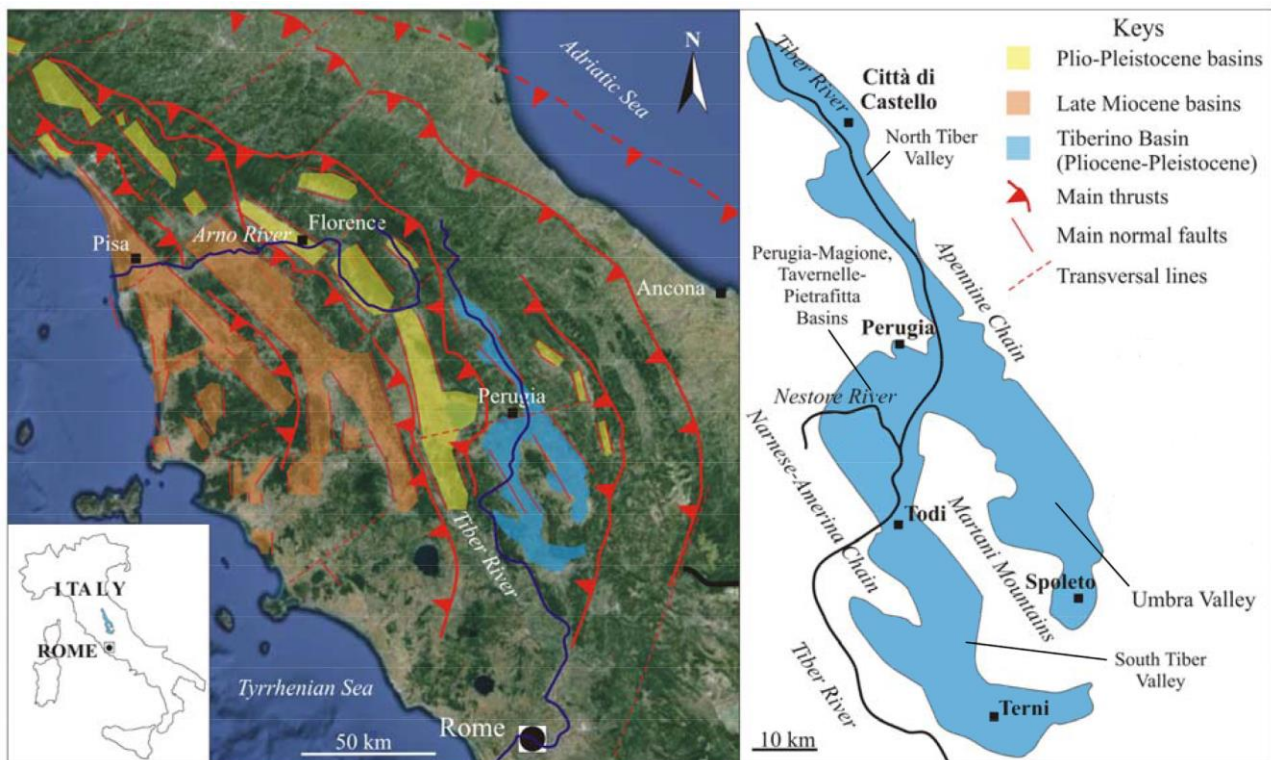
**Chapter 5** deals with the taxonomical harmonisation of the Paratethyan Candoninae genera. A strictly taxonomical study of the Paratethyan Candoninae was essential for the study of the ostracod assemblages from the Tiberino and L’Aquila basins since the majority of species that were found were attributed to *Caspiocypris*, which originated in the Neogene of Paratethys and, apparently, remained confined to that palaeobioprovince since Pliocene (except for its very short occurrence in the Palaeomediterranean area during the Messinian Salinity Crisis).

In the **Chapter 6 Discussion**, all the obtained palaeontological and stratigraphical data have been put together in order to present the ostracod palaeobiodiversity framework during Pliocene-Early Pleistocene and correlate the early infilling deposits of the three studied basins to depict their early evolution. Part of the discussion was published in the previously cited paper by Cosentino et al. (2017). The Discussion chapter is subdivided in different paragraphs, each dealing with the four different goals this thesis tried to achieve.

## 2. Tiberino Basin

### 2.1 Geological setting of the South Tiberino Basin

The Plio-Pleistocene Tiberino Basin (Fig. 2.1) was a subsiding, tilting extensional basin situated on the western edge of the Apennine chain. The basin stretches for 125 km in NW-SE length and up to 20 km width (Ambrosetti et al., 1995a). Currently, four partially independent basins are recognized: a) North Tiberino Basin, b) Perugia-Magione and Tavernelle-Pietrafitta minor basins, c) Umbra Valley, and d) South Tiberino Basin. In this chapter, I focused on the South Tiberino Basin, which represents the south-western part of the entire Tiberino Basin. Its sedimentary evolution appears independent from the northern and western sectors (Martinetto et al. 2014). The South Tiberino Basin is a NNW–SSE trending half-graben that is approximately 35 km long and 10 km wide (Basilici, 1997) that preserved several biochronological and magnetostratigraphic constrains. Previous geologic studies were primarily focused on sedimentology (Basilici, 1995; 1997) or different palaeontology proxies (Abbazzi et al., 1997; Ambrosetti et al., 1995b; Esu & Girotti, 1991; Manganelli et al., 2008) while ostracods were poorly mentioned (Medici & Gliozzi, 2008).



**Figure 2.1:** Simplified geo-structural scheme for Apennine basins, evidencing the Tiberino Basin. To the right, the Plio-Pleistocene Tiberino Basin in central Italy with the basin division reported in to the text. Modified from Martinetto et al., 2014.

The Plio-Pleistocene basin-fill succession of the South Tiberino Basin is up to 500 m thick, consists of mainly siliciclastic, and carbonates lacustrine and fluvial deposits. Basilici (1997) studied the lithostratigraphy of the basin-fill succession (Fig. 2.2 B) and distinguished four lithostratigraphic units: the Fosso Bianco Fm. (FBF), Ponte Naja Fm. (PNF), S. Maria di Ciciliano Fm. (SMCF) and Acquasparta Fm. (AF). In this thesis, only the first two formations have been studied.

The sedimentation of the South Tiberino Basin started with the Fosso Bianco Fm. (FBF) that overlies, with an angular unconformity, the pre-Pliocene bedrock. FBF is mainly composed by clays with associated silty-sand laminae deposited in a lacustrine environment (Palaeolake Tiberino). It was divided in three sedimentological facies associations related to the deposition 1) in a deep lacustrine setting (facies A), 2) Gilbert-type delta deposits (facies B), and 3) in a swampy lacustrine margin containing Taxodiaceae trunks in life position (facies C) (Basilici, 1997). The thickness of the delta facies points to a minimum depth of the Palaeolake Tiberino of at least 50 m (Basilici, 1997). Based on the magnetostratigraphical and palynological analyses performed on FBF cropping out at the Fosso Bianco and Cava Toppetti I sections, a late Piacenzian-Gelasian age was inferred (Fig. 2.2 C) (Abbazzi et al., 1997; Pontini & Bertini, 2000; Napoleone et al., 2003). While the facies A of deep lacustrine environment outcrop in two sections, studied in this thesis (Fosso Bianco and Cava Toppetti I), the facies B, linked to delta deposits, is found only in the eastern side of the South Tiberino Basin, close to the bedrock border (Basilici, 1997).

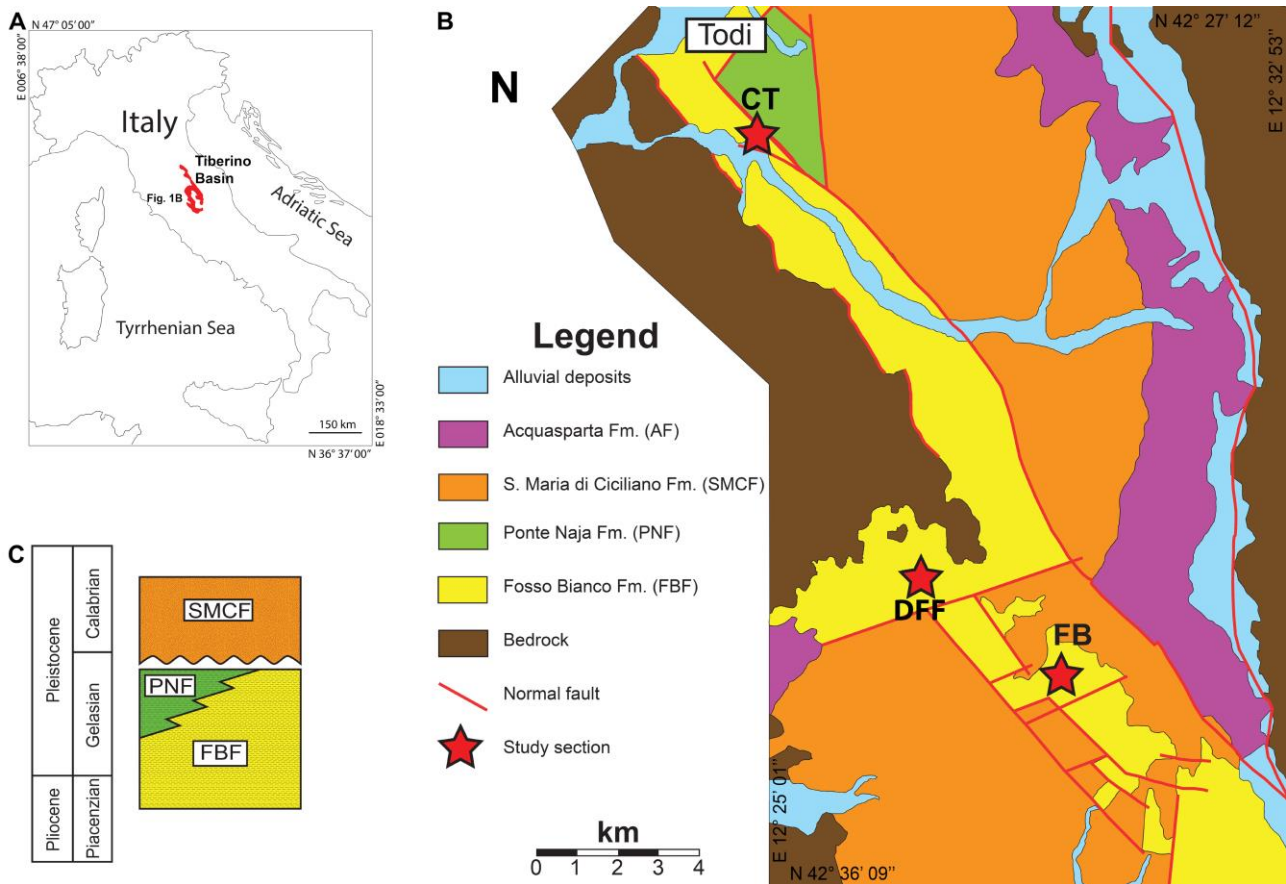
The lacustrine coastal deposits of the facies association C crop out near the village of Dunarobba. Ambrosetti et al. (1995b) and Basilici (1997) recognised two different facies sub-associations: C1, indicative of an emergent or shallow-water wetland coastline, and C2 characteristic of a wave-dominated coastline. The facies sub-association C1 is characterised by massive silty clays or clayey silts, bluish-grey in colour, with abundant vegetal remains, among which 53 *in situ* trunks were observed.

These trunks, referred to *Taxodioxylon gypsaceum* (Göppert) by Biondi & Brugiapaglia (1992) or to *Glyptostrobus* by Martinetto (1994) made up the Dunarobba Fossil Forest. The sediments inside and nearby the trunks bore rich mollusc faunas made of bivalves, aquatic prosobranchs and terrestrial pulmonates (Ambrosetti et al., 1995b; Ciangherotti et al., 1998; Manganelli & Giusti, 2000). Two malacological associations were distinguished in the deposits of the Forest Section: 1) pulmonate gastropods, found in clays near the trunks (hydromorphic palaeosols lithofacies), which indicate a wooded environment with highly hydric soil (swamp), and 2) freshwater Prosobranchia-dominated association, which characterizes running, loosely flowing or standing waters (Ambrosetti et al., 1995b; Ciangherotti et al., 1998). Among the recovered molluscs the present day genera *Eostrobilops* and *Negulus*, typical of tropical environments indicate a warm temperate climate with a high

atmospheric humidity (Esu & Ciangherotti, 2004). Thanks to the high percentage of extinct molluscs of Pliocene character and to the findings of land species common to the late Pliocene molluscan fauna of NW Italy and other European Pliocene sites, the Dunarobba Fossil Forest sediments were considered late Pliocene (Piacenzian) or earliest Pleistocene (Gelasian) in age.

The Ponte Naja Fm. (PNF) is probably partially heteropic to the uppermost part of the FBF, although the stratigraphical relations between them were never observed directly on the field (Basilici, 1995; Martinetto et al., 2014). PNF is composed of prevailing clayey silt deposits (fine-grained sheet flow deposits) with interposed silty clay (palaeosol), planar-concave sandy gravel (stream ribbon channels) and tabular sandy gravel deposits (coarse-grained sheet-flow deposits) (sedimentological facies D) (Basilici, 1995, 1997). The PNF corresponds to the deposition of a distal or middle distal end of an alluvial fan dominated by unchannelized flows under humid climate conditions (Basilici, 1995). A high sedimentation rate based on the high frequency cycles of immature palaeosols and sheet flow deposits in the alluvial fan (probably generated by tectonics activity during sedimentation) is inferred (Basilici, 1995). In the PNF, deposits cropping out in the Cava Toppetti II section several paleontological and palynological analyses were carried out to depict the climate and age.

The rich and diversified pollen assemblages include both warm elements (*Taxodium*, *Nissa*, and *Distylium*) and deciduous elements (*Quercus*, *Carpinus*, and *Ulmus*) typical of a warm temperate climate (Pontini & Bertini, 2000; Martinetto et al., 2014). Similarly, the carpoflora collected in the middle part of the Cava Toppetti II section points out the presence of species pertaining to the HUTEA (humid thermophilous extinct European taxa of East Asian affinity) group (*Sinomenium cantalense*, *Symplocos casparyi*, and *Toddalia latisiliquata*) and CTEA (Cool-tolerant extinct European taxa of East Asian affinity) group (*Cephalotaxus* sp., *Mahonia staphyleaeformis*, and *Magnolia cor*) (Martinetto, 2001; Martinetto et al., 2014). Both the floristic analyses show persistent humid and warm temperate climate conditions, typical of late Gelasian in central Italy.



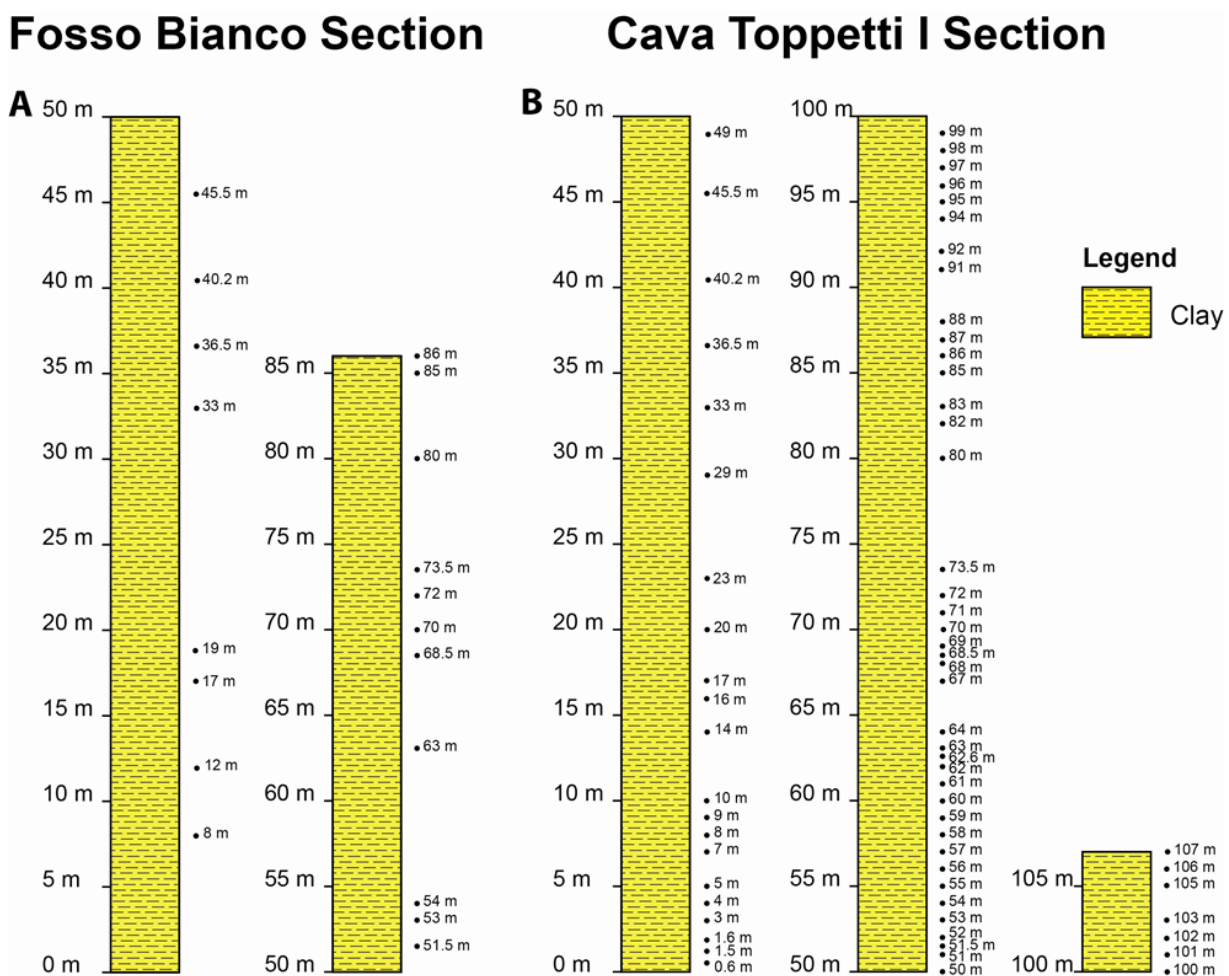
**Figure 2.2:** Location and geological setting of the study area. **A**, geographical location of the Tiberino Basin. **B**, geological map of the South Tiberino Basin, with the location of the study sections: CT = Cava Toppetti section; FB = Fosso Bianco section, DFF = Dunarobba Fossil Forest site, modified from Basilici (1997). **C**, chronostratigraphy of the early Tiberino Basin filling deposits.

Concerning the age of the PNF, the species included in the HUTEA 3 group constrain the Cava Toppetti II deposition to the Gelasian (Martinetto et al., 2017), whereas the large and small mammal remains (*Apodemus dominans*, *Pseudodama rhenana*, *Stephanorhinus etruscus*, *Procapreolus* sp., and *Leptobos* sp.) further constrain the age to the late Gelasian (Coste San Giacomo Faunal Unit), between 2.1 and 1.9 Ma (Bellucci et al., 2014).

The FBF and PNF are unconformably overlain by the Santa Maria di Ciciliano Fm. (SMCF), mainly composed of sandy beds and poorly laminated clays, deposited in an alluvial plain environment (Basilici, 1997). Many sites bearing fossil mammal remains referable to the Olivola, Tasso and Farneta Faunal Units provided an Early Pleistocene (latest Gelasian–Calabrian) age (Ambrosetti et al., 1995a; Girotti et al., 2003; Argenti, 2004). The borders of the South Tiberino Basin were characterized by the deposition of silty limestone and travertine deposits, formed in scattered shallow lakes or marshes referred to the Acquasparta Formation (AF) dated Calabrian or middle Pleistocene (Ambrosetti et al. 1995a; Basilici 1997).

## 2.2 Material and methods

The freshwater ostracods studied in this chapter were collected from three different sedimentological facies: facies A of the FBF at Fosso Bianco (42° 38' 43'' N, 12° 29' 54'' E; thickness 86 m, 19 samples) and Cava Toppetti I sections (42°45' 49'' N, 12° 25' 29'' E; thickness 107 m; 68 samples); facies C of the FBF (Dunarobba Fossil Forest area 42° 39' 45'' N, 12° 27' 47'' E, 25 samples) and facies D of the PNF (Cava Toppetti II section, 42°45' 49'' N, 12° 25' 29'' E; thickness 150 m; 68 samples). The Fosso Bianco (Fig. 2.3 A) and Cava Toppetti I sections (Fig. 2.3 B) are composed by prevailing clays with rare millimetre-thick silty layers representing the distal part of a lacustrine deposition.

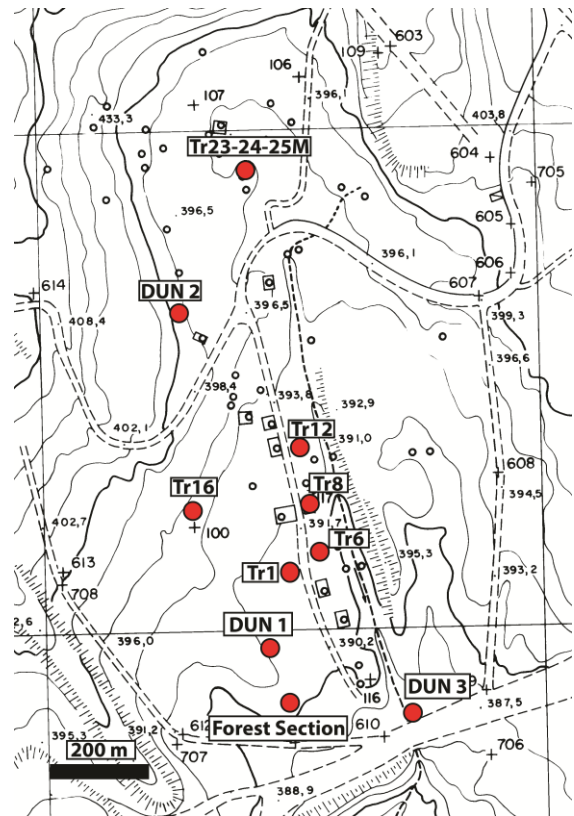


**Figure 2.3:** Stratigraphical logs of the sampled sections from facies A of FBF in the Tiberino Basin. **A**, Fosso Bianco section. **B**, Cava Toppetti I section. For the geographical locations of the sections, see Fig. 2.2 B.

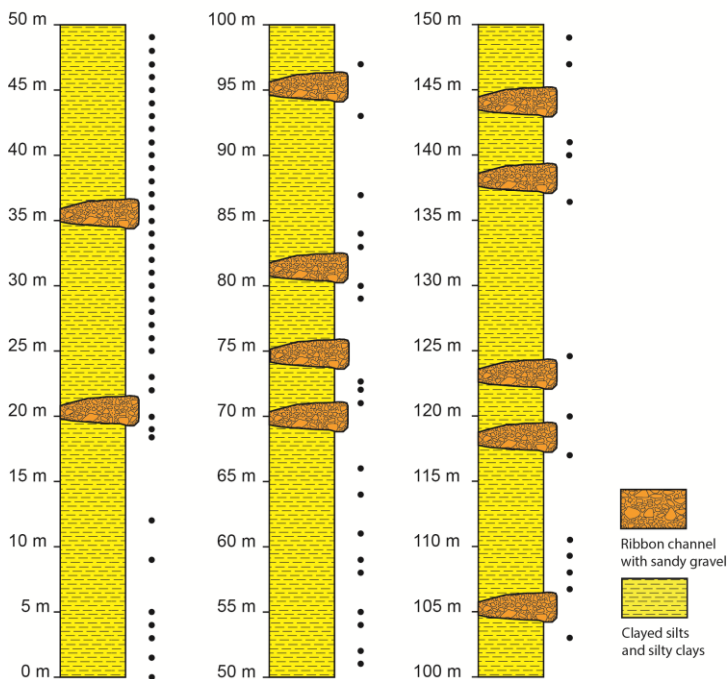


At Dunarobba, most of the samples in silty and clayey sediments, with minor lignite and fine sand, were collected close to the trunks (Figure 2.4) and from a short section (Forest Section in Martinetto et al., 2014) located in front of Trunk 1. Other scattered samples were collected in the surroundings of the Fossil Forest (samples DUN 1, DUN 2 and DUN 3) (Fig. 2.4) (Ambrosetti et al., 1995b).

At Cava Toppetti, PNF overlain, by tectonic contact, FBF (Abbazzi et al., 1997). This formation is sampled along the Cava Toppetti II section (CT II) composed by an alternation of clayey silt deposits and planar-concave sandy gravel (Fig. 2.5) (Basilici, 1995).



**Figure 2.4:** Locations of the samples from Dunarobba Fossil Forest site. For the geographical location of the site, see Fig. 2.2 B.



**Figure 2.5:** Stratigraphical log of the Cava Toppetti II section from PNF in the Tiberino Basin. For the geographical location of the section, see Fig. 2.2 B.

The 180 collected samples were soaked in a H<sub>2</sub>O<sub>2</sub> 5% solution for 24 hours, sieved with a 0.125 mm mesh sieve and dried. Ostracods were handpicked under a stereomicroscope, up to 300 adult and juvenile valves/samples, and pictures were taken in transmitted light using the stereomicroscope Leica DM500 at the Micropalaeontological Laboratory of the Department of Science (University of Roma Tre). SEM pictures were acquired under the Philips XL-30 scanning electron microscope (SEM) (LIME, University of Roma Tre).



The taxonomical analysis was performed using the classical morphometric methods and also the geometric morphometrics on the valve outline. For this latter analysis, both the transmitted light and SEM images of female valves were used to digitize the outlines of each valve using the tpsDig 2.14 software (Rohlf, 2009). Successively, the outlines were elaborated with MORPHOMATICA, v.1.6.01 (Linhart et al., 2007) software. MORPHOMATICA approximates the valve outlines using B-spline curves with 16 control points (Baltanas & Danielopol, 2011). The software automatically orients the TPSdig outlines on the base of their centre of gravity, making comparisons possible.

Differences in the total area between each outline have been analysed using cluster analyses (Euclidean distance measure – UPGMA), non-metric multidimensional scaling (nMDS) and ANOSIM pairwise tests through the PRIMER 6 software (Clarke & Gorley, 2006).

All the studied specimens are deposited in the Gliozzi Ostracod Collection (GOC) at the Department of Science, University of Roma Tre, Rome, Italy.

The following morphological abbreviations were used: **L**, length; **H**, height; **LV**, left valve; **RV**, right valve; **C**, carapace.

## 2.3 Systematic Palaeontology

### Fosso Bianco Fm. (facies A)

The ostracod fauna recovered in the sedimentological facies A of FBF includes nine species referable to five genera of Candoninae, Limnocytherinae, and Cytherideidae. Among them, a few fragmentary adult and juvenile valves were ascribed to *Fabaeformiscandona* sp., *Cypria* sp. and *Cyprideis rectangularis* pertaining to an allochthonous contingent possibly displaced from the surrounding shallow areas of the lake (Whatley, 1988; Boomer et al., 2003). Those valves are not described or illustrated. For the suprageneric classification, we followed Meisch (2000) and Horne et al. (2002).

Class **Ostracoda** Latreille, 1802

Subclass **Podocopa** Sars, 1866

Order **Podocopida** Sars, 1866

Suborder **Cypridocopina** Jones, 1901

Superfamily **Cypridoidea** Baird, 1845

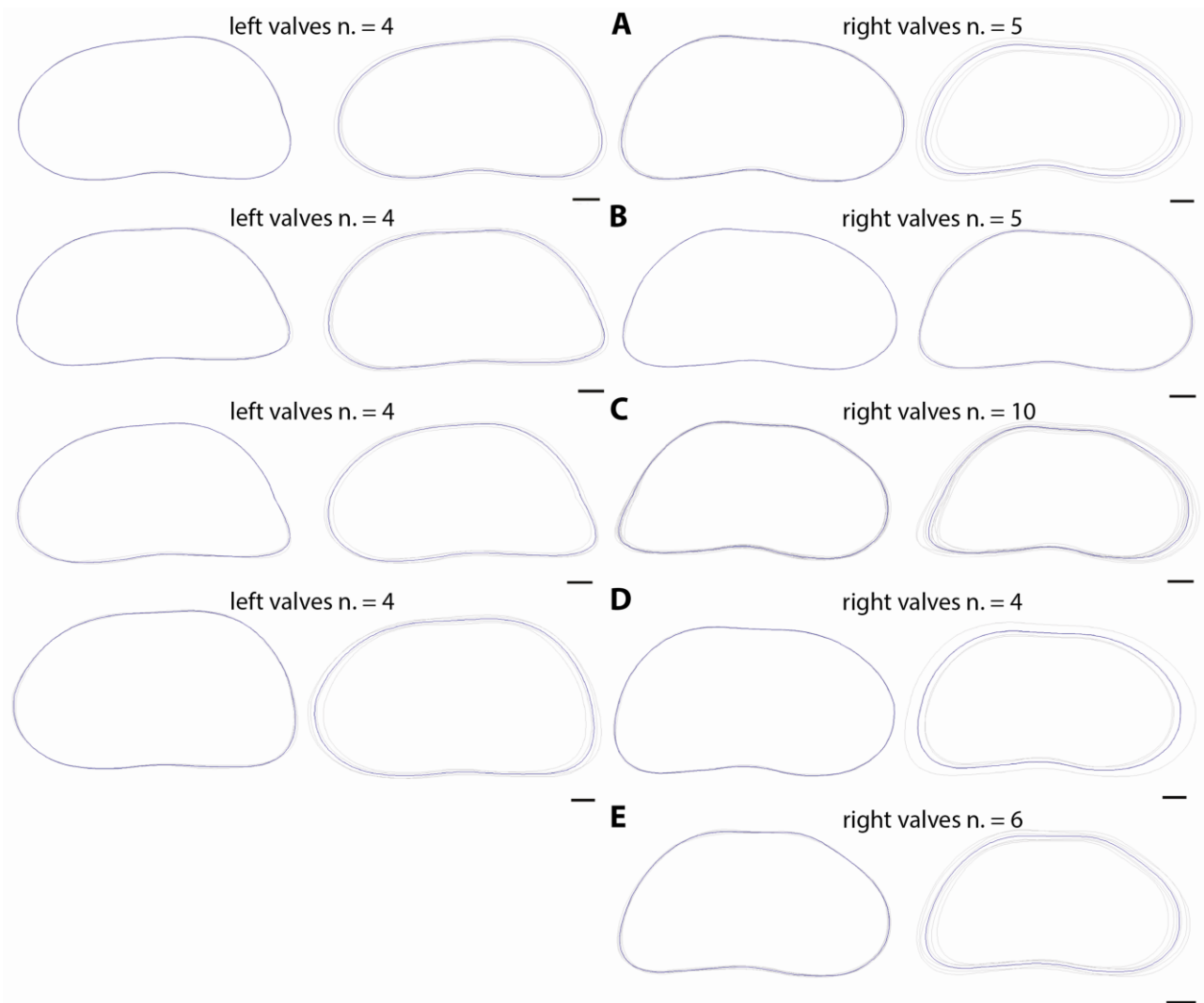
Family **Candonidae** Kaufmann, 1900

Subfamily **Candoninae** Kaufmann, 1900

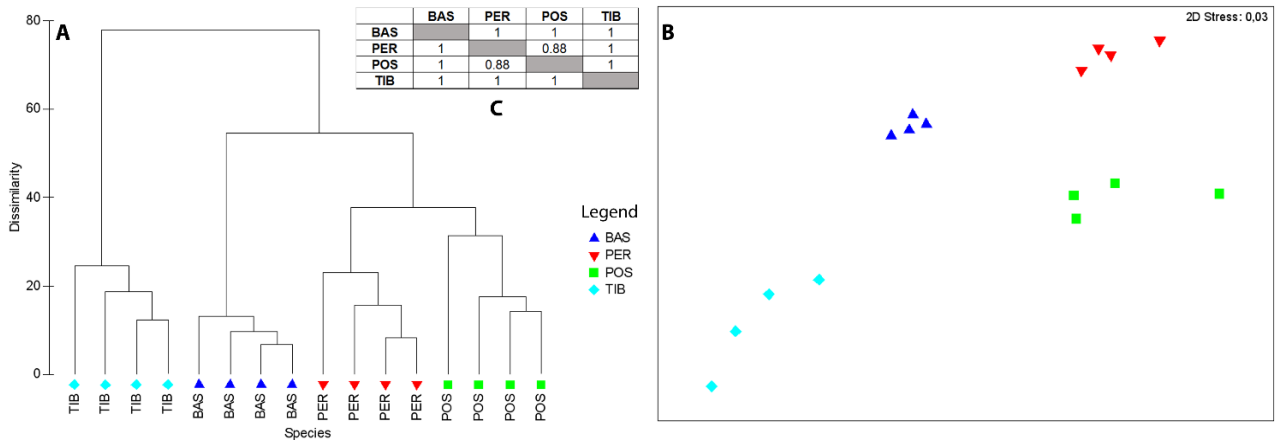
Genus *Caspiocypris* Mandelstam, 1956 (in Schneider et al. 1956)

See Chapter 5 for the systematic revision of genus *Caspiocypris*.

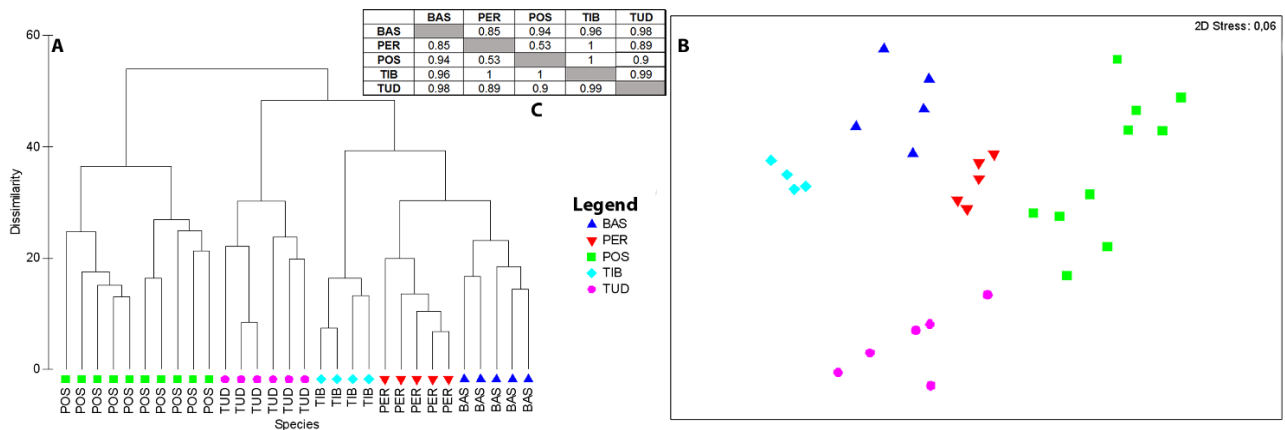
**Morphometrics.** The left and right valve outlines of female *Caspiocypris* specimens recovered in the FBF were analysed through geometric morphometrics to divide possible different morphotypes. Four different morphotypes were recognized for the left valve and five for the right valve (Fig. 2.6), and all the outlines were processed using multivariate analyses. For the left valve the Cluster dendrogram (Fig. 2.7 A) indicates significant differences (higher than 0.5) only between three morphotypes, but the nMDS analysis and the ANOSIM pairwise tests clearly distinguish all the four morphotypes (nMDS 2D stress: 0.03; ANOSIM: global R D 0.987; p D 0.03) (Fig. 2.7 B, C). For the RV the Cluster dendrogram shows significant differences (higher than 0.5) only between two large clusters, which groups, respectively, one and four morphotypes (Fig. 2.8 A). Conversely, the ANOSIM pairwise tests (global R D 0.829; p D 0.008) clearly separates all the five morphotypes, although morphotypes 2 and 3 look more similar to each other (Fig. 2.8 C). The nMDS analysis (2D stress D 0.06) slightly divides morphotype 3 into two close clouds (Fig. 2.8 B). Investigating the possible differences, we noticed that the clouds include valves with minor but overlapping differences in proportions and size (respectively H/L 0.49–0.52; L = 0.98–1.03 and H/L = 0.50–0.53; L = 0.95–0.98). In our opinion, such differences are not enough to separate a sixth morphotype. On the base of LV and RV combined results, we consider the five different morphotypes as five different species, which are herein described. Among the adult valves, males were also recovered. On the basis of the diagnostic characters recognized on the female valves and on the dimensions and proportions of the valves, the male valves were coupled with the female ones.



**Figure 2.6:** ‘Morphomatica’ output of the five morphotypes of valve outlines found in the deep lacustrine facies of FBF, in ‘normalized for area’ and ‘not-normalized for area’ modes. Mean outlines are drawn in black. **A**, morphotype 1 (*Caspiocypris basilicii* Spadi & Gliozzi); **B**, morphotype 2 (*C. perusia* Spadi & Gliozzi); **C**, morphotype 3 (*C. posteroacuta* Spadi & Gliozzi); **D**, morphotype 4 (*C. tiberina* Spadi & Gliozzi); **E**, morphotype 5 (*C. tuderis* Spadi & Gliozzi). Scale bars = 100  $\mu$ m.



**Figure 2.7:** Multivariate analyses applied to the geometric morphometric outline matrix of *Caspiocypris* female LV in ‘normalized for area’ mode. **A**, dendrogram of the cluster analysis (Euclidean distance measure and the un-weighted pair group method using arithmetic average – UPGMA); **B**, non-metric multidimensional scaling (nMDS) plot in 2D morphological space; **C**, results of the ANOSIM pairwise tests. Correspondences: morphotype 1 = *C. basilicii* Spadi & Gliozzi; morphotype 2 = *C. perusia* Spadi & Gliozzi; morphotype 3 = *C. posteroacuta* Spadi & Gliozzi; morphotype 4 = *C. tiberina* Spadi & Gliozzi.



**Figure 2.8:** Multivariate analyses applied to the geometric morphometric outline matrix of *Caspiocypris* female RV in ‘normalized for area’ mode. **A**, dendrogram of the cluster analysis (Euclidean distance measure and the un-weighted pair group method using arithmetic average – UPGMA); **B**, non-metric multidimensional scaling (nMDS) plot in 2D morphological space; **C**, results of the ANOSIM pairwise tests. Correspondences: morphotype 1 = *C. basilicii* Spadi & Gliozzi; morphotype 2 = *C. perusia* Spadi & Gliozzi; morphotype 3 = *C. posteroacuta* Spadi & Gliozzi; morphotype 4 = *C. tiberina* Spadi & Gliozzi; morphotype 5 = *C. tuderis* Spadi & Gliozzi.

*Caspiocypris basilicii* Spadi & Gliozzi, 2017

(Fig. 2.9 A–G)

2008 *Caspiocypris* sp. D Medici & Gliozzi, fig. 3.

2008 *Sirmiella* Medici & Gliozzi: 42.

2011 *Caspiocypris* sp. D Medici: 102, pl. 9, figs i, j.

2011 *Sirmiella* sp. Medici: 113, pl. 11, figs a, c, e, g.

**Diagnosis.** *Caspiocypris* with elongated trapezoidal shape, thick shell, surface smooth and rounded posterior end bending downwards.

**Derivation of name.** Named after Giorgio Basilici in appreciation of his several publications on the South Tiberino Basin and his friendship.

**Material.** Holotype: T36/1, LV female (Fig. 2.9 A), sample CT I 4.0 m. Paratypes: M149/2/3, LV female (Fig. 2.9 C, G); T36/2, RV female; T36/3, RV male; T36/4-6, juvenile RV female; T36/7, juvenile LV female; sample CT I 4.0 m. All from the Cava Toppetti section, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, late Piacenzian. Additional material: 53 adult valves and more than 100 juvenile valves.

**Occurrence.** Samples 0.6 m–107 m Cava Toppetti I section; samples 12 m and 80 m Fosso Bianco section; Tiberino Basin, Italy, Fosso Bianco Formation, late Piacenzian p.p.–Gelasian p.p.

**Description.** In dorsal view, the female carapace is tight ogive-shape with beak-like anterior and acuminate posterior ends. The LV covers the RV in the dorsal, anterior and posterior margins with straight hinge line. In lateral view, the female valve of *Caspiocypris basilicii* is elongated trapezoidal in shape with sub-parallel dorsal and ventral margins. The dorsal margin is straight with rounded anterior cardinal angle. The ventral margin is slightly sinuous, with a slight concavity in the middle. The anterior margin is rounded. The posterior margin is straight with a rounded downwards posterior end. The surface of the valves is smooth. The adductor muscle scars are clearly visible and quite rounded, with the typical arrangement of the subfamily Candoninae. In internal view, valves have well-developed anterior and posterior vestibules. The hinge is typical of the genus and in the LV, there is a groove underlined by a well-developed ledge that runs for all the length of the cardinal margin. Sexual dimorphism is quite pronounced. The males of *Caspiocypris basilicii* display a more undulated ventral margin, the dorsal margin is more inclined anteriorly, and the posterior margin is proportionally higher than in females. Dimensions. LV female (four valves): L = 0.90–1.04 mm; H = 0.50–0.58 mm. RV female (six valves): L = 0.91–1.05 mm; H = 0.45–0.52 mm. LV male (one valve): L = 1.16 mm; H = 0.64 mm. RV male (three valves): L = 1.07–1.18 mm; H = 0.54–0.64 mm.

**Remarks.** In Krstić et al. (2004), Medici & Gliozzi (2008) and Medici (2011) the juvenile valves of this species were referred to *Sirmiella* Krstić, 1972.

*Caspiocypris perusia* Spadi & Gliozzi, 2017

(Fig. 2.9 H–P)

2004 “*Caspiocypris*” cf. *holmesi* Krstić et al.: 316, pl. 3, figs 3, 4.

2008 *Caspiocypris* sp. B Medici & Gliozzi: fig. 3.

2011 *Caspiocypris* sp. B Medici: 97, pl. 9, figs e–g.

**Diagnosis.** *Caspiocypris* with elongated trapezoidal shape, thick shell, surface smooth, and posterior end pointed upwards.

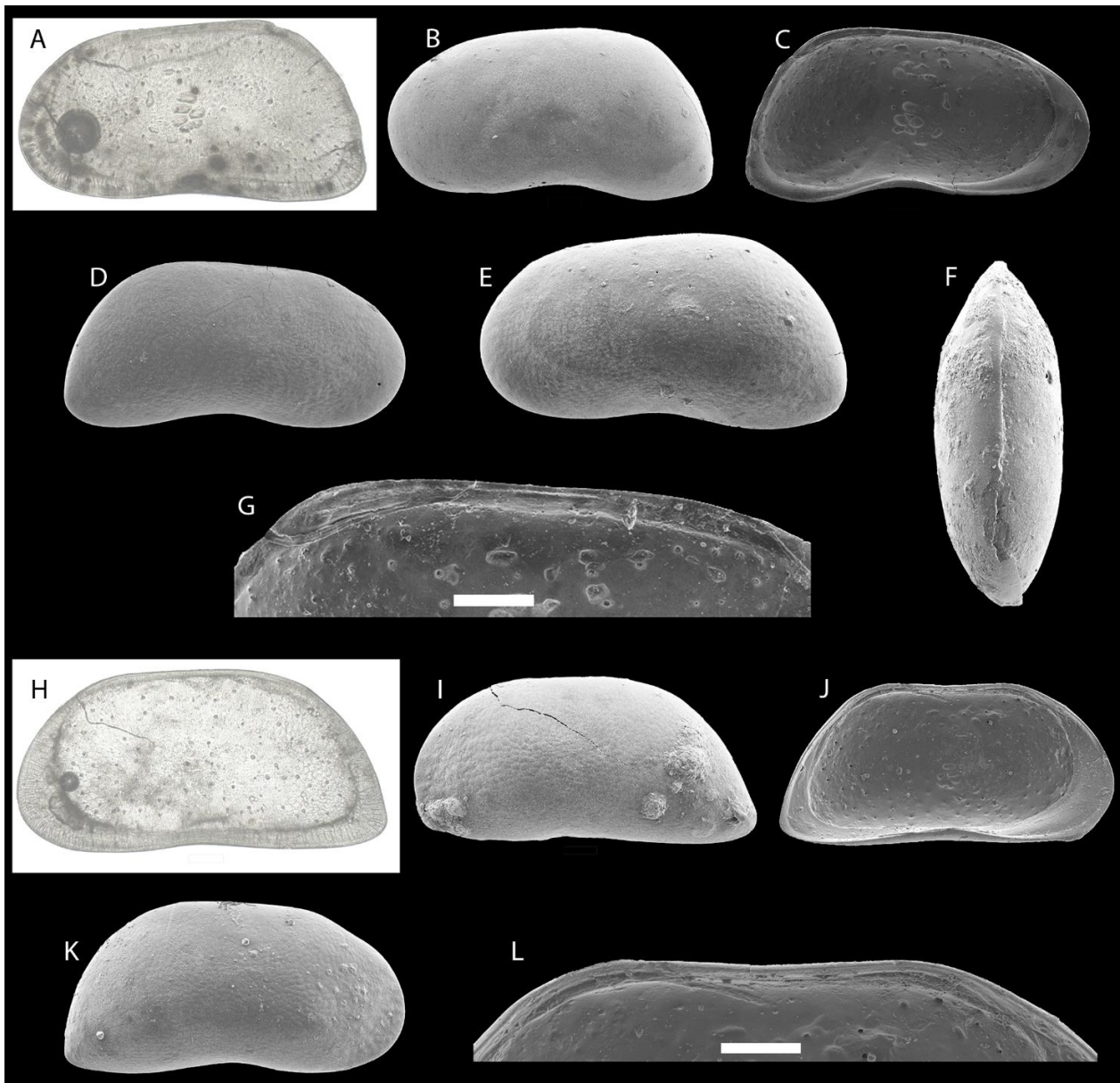
**Derivation of name.** From *Perusia, ae*, the ancient Roman name of the city of Perugia.

**Material.** Holotype: T37/1, LV female (Fig. 2.9 J), sample CT I 85.0 m. Paratypes: T37/2-3 and M375/2/2 (Fig. 2.9 I, M), RV female; T37/4 and M375/2/1 (Fig. 2.9 H, K), LV female; sample CT I 85.0 m. All from the Cava Toppetti section, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Gelasian. Additional material: 25 adult valves and 20 juvenile valves.

**Occurrence.** Samples 4 m–101 m Cava Toppetti I section; samples 8 m–72 m Fosso Bianco section; Tiberino Basin, Italy, Fosso Bianco Formation, late Piacenzian p.p.–Gelasian p.p.

**Description.** Only isolated valves were found, thus the carapace description is derived from two valves in dorsal view. In dorsal view, the carapace is wedge-shaped with acuminate anterior and posterior ends; the cardinal line is straight. In lateral view, the female valve of *Caspiocypris perusia* is trapezoidal in shape with parallel or sub-parallel dorsal and ventral margins. The dorsal margin is straight. The ventral margin is slightly sinuous, with a small concavity in the middle of the LV, more marked in the RV. The anterior margin is rounded and the anteroventral angle is little evident. The posterior margin is straight with an acute posterior end pointed upwards. The surface of the valves is smooth, but in transmitted light, a reticulation with rectangular meshes is visible, especially in the posteroventral area. The adductor muscle scars are clearly visible and are quite rounded, with the typical arrangement of the subfamily Candoninae. In internal view, valves have well-developed anterior and posterior vestibules. The hinge is typical of the genus and in the LV, there is a groove underlined by a well-developed ledge that runs for all the length of the cardinal margin. Sexual dimorphism is quite pronounced. The male valves of *Caspiocypris perusia* display a more undulated ventral margin, marked dorsal corners, a dorsal margin more inclined anteriorly and higher proportions than females.

**Dimensions.** LV female (six valves): L = 0.99–1.06 mm; H = 0.50–0.55 mm. RV female (five valves): L = 0.98–1.02 mm; H = 0.48–0.53 mm. LV male (two valves): L = 1.07–1.18 mm; H = 0.56–0.65 mm. RV male (one valve): L = 1.17 mm; H D 0.65 mm.



**Figure 2.9:** Ostracods from the Fosso Bianco Formation, Tiberino Basin, Italy. **A–G**, *Caspiocypris basilicii* Spadi & Gliozzi. **A**, holotype, lateral view of a left female valve in transmitted light, GOC T36/1, sample CT I 4.0 m; **B**, lateral view of a left female valve, GOC M312/2/5, sample CT I 9.0 m; **C**, paratype, lateral inner view of a left female valve, GOC M149/2/3, sample CT I 4.0 m; **D**, lateral view of a right female valve, GOC M312/2/7, sample CT I 9.0 m; **E**, lateral view of a left male valve, GOC M312/2/9, sample CT I 1.5 m; **F**, dorsal view of a female complete carapace, GOC M312/3/1, sample CT I 3.0 m; **G**, paratype, detail of the hinge of the left female valve, M149/2/3, sample CT I 4.0 m illustrated in **C**. **H–P**, *Caspiocypris perusia* Spadi & Gliozzi. **H**, paratype, dorsal view of a left female valve, GOC M375/2/1, sample CT I 85.0 m; **I**, paratype, dorsal view of a right female valve, GOC M375/2/2, sample CT I 85.0 m; **J**, holotype, lateral view of a left female valve in transmitted light, GOC T37/1, sample CT I 85.0 m; **K**, paratype, lateral view of a female left valve, GOC M375/2/1, sample CT I 85.0 m illustrated in **H**; **L**, lateral inner view of a left female valve, GOC M375/2/3, sample CT I 51.5 m; **M**, paratype, lateral view of a right female valve, GOC M375/2/2, sample CT I 85.0 m illustrated in **I**; **N**, lateral view of a damaged male left valve, GOC M375/2/6, sample CT I 10.0 m; **O**, lateral view of a male right valve, GOC M375/2/5, sample CT I 60.0 m; **P**, detail of the hinge of the left female valve, GOC M375/2/6, sample CT I 51.5 m illustrated in **L**. Scale bars = 100  $\mu$ m.

*Caspiocypris posteroacuta* Spadi & Gliozzi, 2017

(Fig. 2.10 A–H)

2008 *Caspiocypris* sp. A Medici & Gliozzi: fig. 3.

2011 *Caspiocypris* sp. A Medici: 94, pl. 9, figs b–d.

**Diagnosis.** *Caspiocypris* with elongated trapezoidal shape, thick shell, surface smooth and acute posterior end bending downwards.

**Derivation of name.** The name derives from the characteristic posteroventral acute angle.

**Material.** Holotype: T38/1, LV female (Fig. 2.10 A), sample CT I 80.0 m. Paratypes: T38/2–4 and M375/1/2 (Fig. 2.10 D, G), RV female; T38/5, juvenile RV female; M375/1/3 (Fig. 2.10 C, H), LV female; T38/6, RV male; sample CT I 80.0 m. All from the Cava Toppetti section, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Gelasian. Additional material: 43 adult valves and 15 juvenile valves.

**Occurrence.** Samples 7 m–100 m Cava Toppetti I section; samples 8 m–86 m Fosso Bianco section; Tiberino Basin, Italy, Fosso Bianco Formation, late Piacenzian p.p.–Gelasian p.p.

**Description.** Only isolated valves were found, thus the carapace description is derived from two valves in dorsal view. In dorsal view, the carapace is wedge-shaped with acuminate anterior and posterior ends and with a maximum thickness in the central area; the cardinal line is straight. In lateral view, the female valve of *Caspiocypris posteroacuta* is trapezoidal in shape with parallel (in the LV) or sub-parallel (in RV) dorsal and ventral margins. The dorsal margin is straight with rounded anterior cardinal angle. The ventral margin is slightly sinuous, with a small concavity in the middle of the LV and a more remarkable sinuosity in the RV. The anterior margin is rounded. The posterior margin is straight with an acute posterior end pointed downwards. The surface of the valves is smooth, but in transmitted light, a reticulation is visible, especially in the posteroventral area. The adductor muscle scars are clearly visible and are quite rounded, with the typical arrangement of the subfamily Candoninae. In internal view, valves have well-developed anterior and posterior vestibules. The hinge is typical of the genus and in the LV, there is a groove underlined by a well developed ledge that runs for all the length of the cardinal margin. Sexual dimorphism is quite pronounced. The male RV of *Caspiocypris posteroacuta* is proportionally higher than females, displays a more undulated ventral margin, and a dorsal margin is more inclined anteriorly.

**Dimensions.** LV female (four valves): L = 1.01–1.10 mm; H = 0.52–0.56 mm. RV female (10 valves): L = 0.95–1.03 mm; H = 0.50–0.52 mm. RV male (one valve): L = 1.02 mm; H = 0.55 mm.



*Caspiocypris tiberina* Spadi & Gliozzi, 2017

(Fig. 2.10 I–P)

2008 *Labiaticandona* sp. Medici & Gliozzi: 42.

2011 *Labiaticandona* sp. Medici: 105, pl. 5, figs b, c, e.

**Diagnosis.** *Caspiocypris* with high-trapezoidal shape, thick shell, surface smooth, scattered large normal pore canals, and carapace rounded at both ends. Noticeable sexual dimorphism with males larger than females.

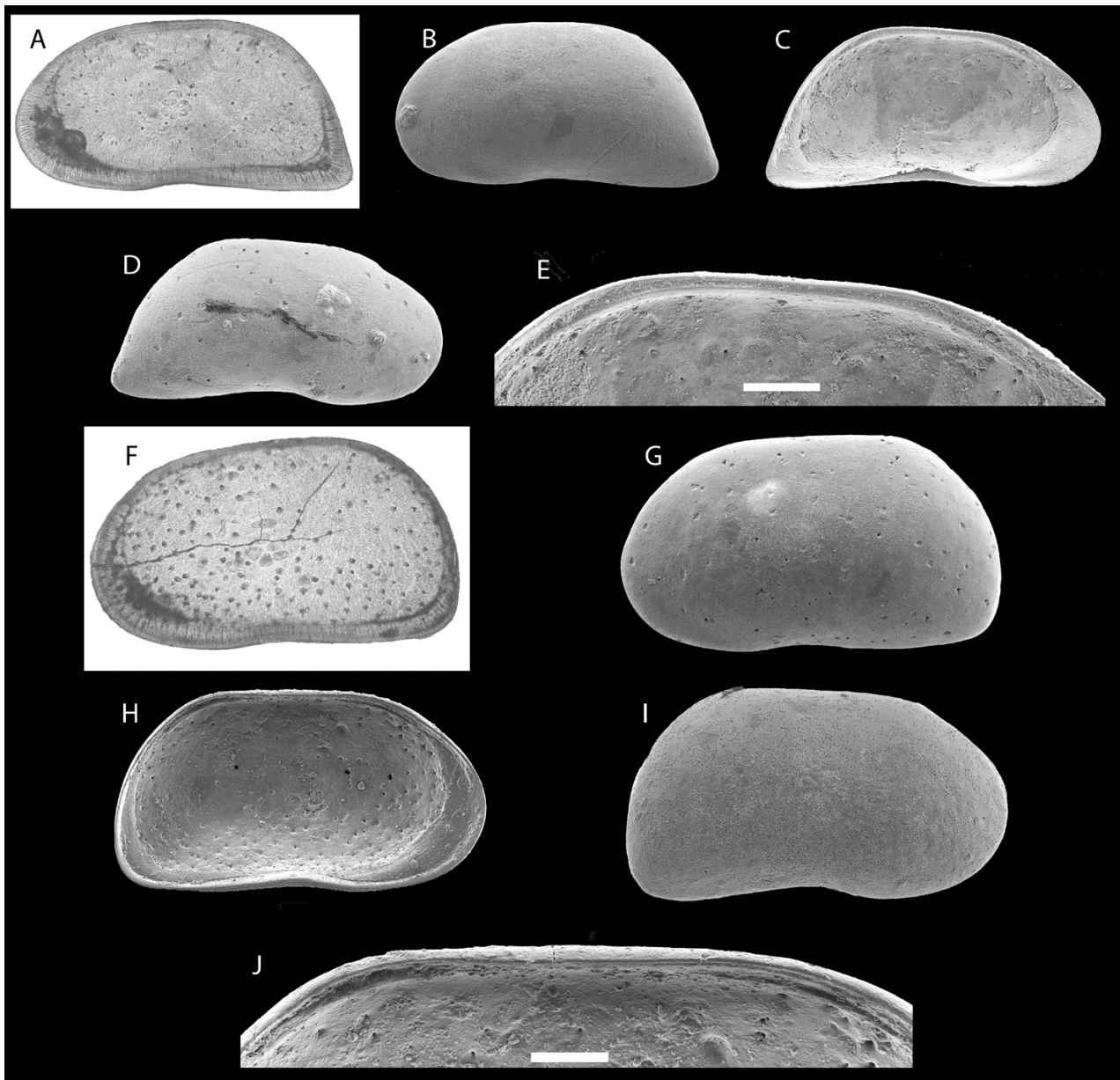
**Derivation of name.** From the Tiberino Basin where the species was found.

**Material.** Holotype: T39/1, LV female (Fig. 2.10 K), sample CT I 1.5 m. Paratypes: T39/2, RV female; T39/3, juvenile RV female; M375/3/3 (Fig. 2.10 M, P), LV female; T39/4, juvenile LV female; sample CT I 1.5 m. All from the Cava Toppetti section, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Piacenzian. Additional material: 25 adult valves and 33 juvenile valves.

**Occurrence.** Samples 0.6–107 m Cava Toppetti I section; samples 8 m–72 m Fosso Bianco section; Tiberino Basin, Italy, Fosso Bianco Formation, late Piacenzian p.p.–Gelasian p.p.

**Description.** Only isolated valves were found, thus the carapace description is derived from two valves in dorsal view. In dorsal view, the carapace is wedge-shaped with rounded anterior and posterior ends and with a maximum thickness in the central area; the cardinal line is straight. In lateral view, the female valve of *Caspiocypris tiberina* is trapezoidal in shape, with parallel dorsal and ventral margins in the LV and sub-parallel in the RV. The dorsal margin is straight with rounded anterior cardinal angle. The ventral margin is slightly sinuous, with a small concavity in the middle. The anterior margin is rounded and the anteroventral angle is not so evident. The posterior margin is straight with an acute posterior end pointed downwards. The surface of the valves is smooth. The normal pore canals are clearly evident. The adductor muscle scars are clearly visible and are quite rounded, with the typical arrangement of the subfamily Candoninae. In internal view, valves have well-developed anterior and posterior vestibules. The hinge is typical of the genus and in the LV, there is a groove underlined by a well-developed ledge that runs for all the length of the cardinal margin. Sexual dimorphism is quite pronounced. The male LV of *Caspiocypris tiberina* display a more undulated ventral margin than female, the dorsal margin is more inclined anteriorly, the posterior margin is more rounded and, overall, the valve is proportionally higher.

**Dimensions.** LV female (seven valves): L = 1.08–1.26 mm; H = 0.60–0.74 mm. RV female (11 valves): L = 1.01–1.12 mm; H = 0.53–0.62 mm. LV male (one valve): L = 1.43 mm; H = 0.80 mm.



**Figure 2.10:** Ostracods from the Fosso Bianco Formation, Tiberino Basin, Italy. **A–H**, *Caspiocypris posteroacuta* Spadi & Gliozzi. **A**, holotype, lateral view of a left female valve in transmitted light, GOC T38/1, sample CT I 80.0 m; **B**, lateral view of a left female valve, GOC M375/1/1, sample CT I 17.0 m; **C**, paratype, lateral inner view of a left female valve, GOC M375/1/3, sample CT I 80.0 m; **D**, paratype, lateral view of a right female valve, GOC M375/1/2, sample CT I 80.0 m; **E**, paratype, lateral view of a left male valve, GOC M375/1/5, sample CT I 80.0 m; **F**, dorsal view of a left female valve, GOC M375/1/1, sample CT I 17.0 m illustrated in **B**; **G**, paratype, dorsal view of a right female valve, GOC M375/1/2, sample CT I 80.0 m illustrated in **D**; **H**, paratype, detail of the anterior hinge of the left female valve, GOC M375/1/3, sample CT I 80.0 m illustrated in **C**. **I–P**, *Caspiocypris tiberina* Spadi & Gliozzi. **I**, dorsal view of a left female valve, GOC M375/3/1, sample CT I 85.0 m; **J**, dorsal view of a right female valve, GOC M375/3/2, sample CT I 8.0 m; **K**, holotype, lateral view of a left female valve in transmitted light, GOC T39/1, sample CT I 1.5 m; **L**, lateral view of a left female valve, GOC M312/3/2, sample CT I 85.0 m illustrated in **I**; **M**, paratype, lateral inner view of a left female valve, GOC M375/3/3, sample CT I 1.5 m; **N**, lateral view of a right female valve, GOC M375/3/2, sample CT I 8.0 m illustrated in **J**; **O**, lateral view of a left male valve, GOC M375/3/5, sample CT I 51.5 m; **P**, paratype, detail of the hinge of a left female valve, GOC M375/3/3, sample CT I 1.5 m illustrated in **M**. Scale bars = 100  $\mu$ m.

*Caspiocypris tuderis* Spadi & Gliozzi, 2017

(Fig. 2.11 A–E)

2008 *Caspiocypris* sp. C Medici & Gliozzi: fig. 3.

2011 *Caspiocypris* sp. C Medici: 99, pl. 9, fig. h.

**Diagnosis.** *Caspiocypris* with trapezoidal shape, thick shell, surface smooth and marked anterodorsal angle.

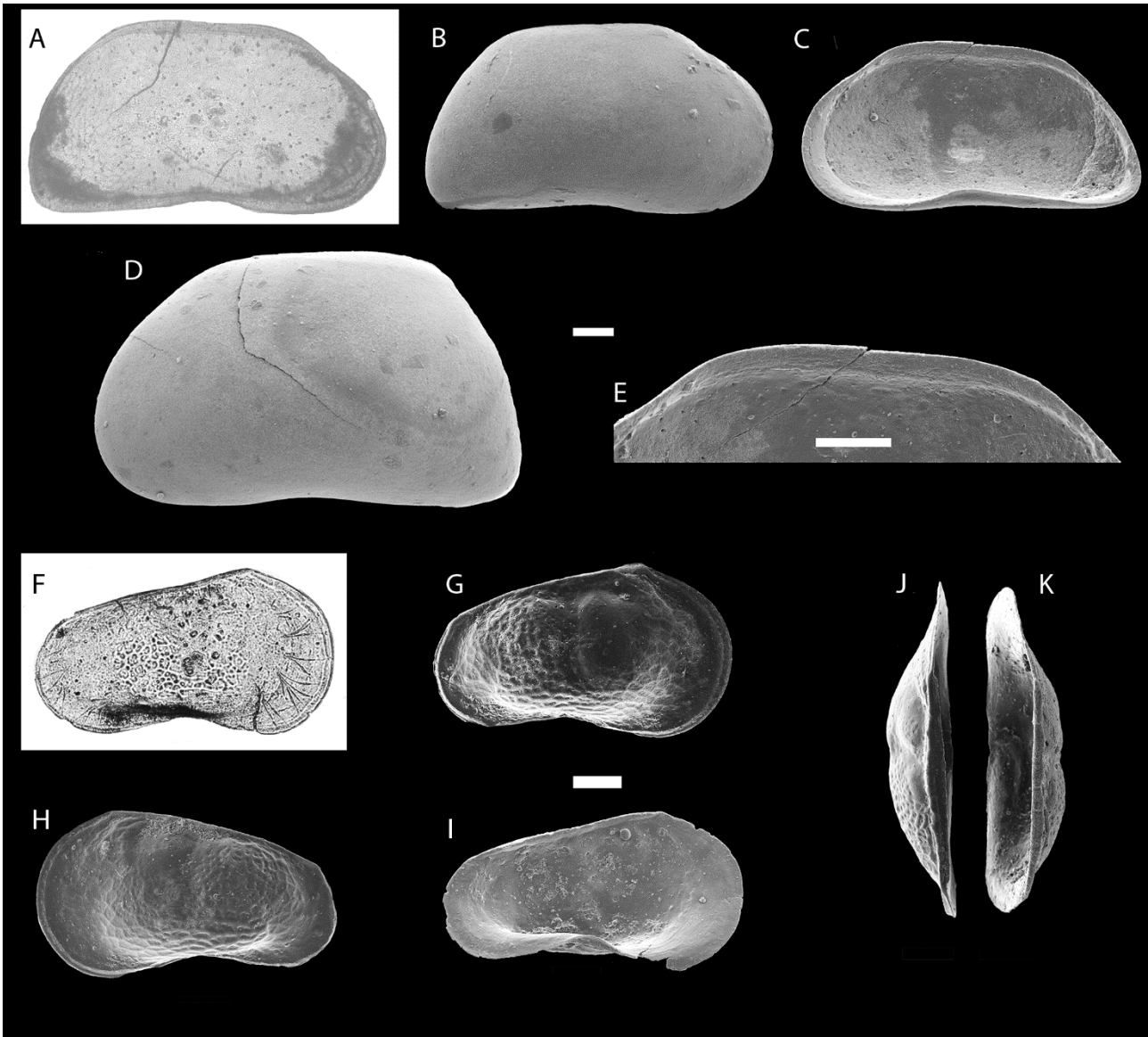
**Derivation of name.** From *Tuder, is*, the ancient Roman name of the city of Todi.

**Material.** Holotype: T40/1, RV female (Fig. 2.11 A), sample CT I 83.0 m. Paratype: T40/2, RV female, sample CT I 83.0 m. Both from the Cava Toppetti section, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Gelasian. Additional material: 15 adult valves and seven juvenile valves.

**Occurrence.** Samples 60–105 m Cava Toppetti I section; samples 12 m Fosso Bianco section; Tiberino Basin, Italy, Fosso Bianco Formation, Gelasian.

**Description.** Unfortunately, only isolated right adult valves were found, which appear wedge-shaped with acuminate anterior and posterior ends and with straight cardinal line. In lateral view, the right female valve of *Caspiocypris tuderis* is trapezoidal in shape with parallel or sub-parallel dorsal ventral margins. The dorsal margin is straight. The ventral margin is slightly sinuous, with a small concavity in the middle. The anterior margin is rounded and the anterodorsal angle is marked. The posterior margin is straight with an acute rounded posterior end. The surface of the valves is smooth, but in transmitted light, a reticulation is visible on the entire surface of the valve. The adductor muscle scars are clearly visible and are quite rounded, with the typical arrangement of the subfamily Candoninae. In internal view, valves have well-developed anterior and posterior vestibules. Although only one partially broken LV has been collected, it is possible to infer that sexual dimorphism is quite pronounced also in this species. The male valve of *Caspiocypris tuderis* sp. nov. is more sinuous ventrally, and displays more marked dorsal angles. Moreover, the dorsal margin is more inclined anteriorly and the whole valve is proportionally higher than female.

**Dimensions.** RV female (six valves): L = 0.90–1.01 mm; H = 0.49–0.56 mm.

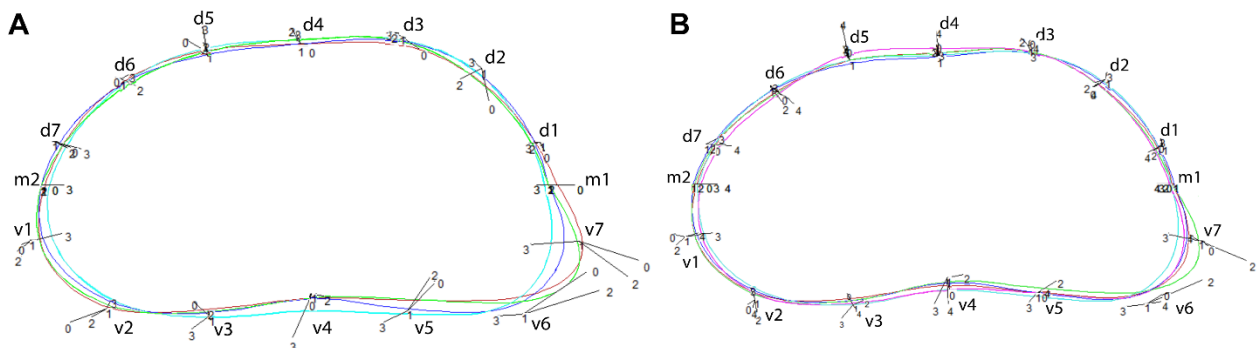


**Figure 2.11:** Ostracods from the Fosso Bianco Formation, Tiberino Basin, Italy. **A–E**, *Caspiocypris tuderis* Spadi & Gliozzi. **A**, holotype, lateral view of a right female valve in transmitted light, GOC T40/1, sample CT I 83.0 m; **B**, lateral view of a right female valve, GOC T312/2/2 sample CT I 60.0 m; **C**, lateral inner view of a right female valve, GOC M375/4/1 sample CT I 60.0 m; **D**, lateral view of broken left male valve, GOC T312/2/4 sample CT I 91.0 m; **E**, detail of the hinge of a right female valve, GOC M375/4/1, sample CT I 60.0 m illustrated in C. **F–K**, *Paralimnocythere umbra* Spadi & Gliozzi. **F**, holotype, lateral view of a right female valve in transmitted light, GOC T41/1, sample CT I 98.0 m; **G**, lateral view of a right female valve, GOC M90/3/5, sample CT I 55.0 m; **H**, lateral view of a left female valve, GOC M90/3/6, sample CT I 60.0 m; **I**, paratype, lateral internal view of a left female, GOC M317/1/3, sample CT I 98.0 m; **J**, dorsal view of a left female valve, GOC M90/3/7, sample CT I 61.0 m; **K**, dorsal view of a right female valve, GOC M90/3/8, sample CT I 56.0 m. Scale bars = 100  $\mu$ m (A–D, small bar; F–K, large bar).

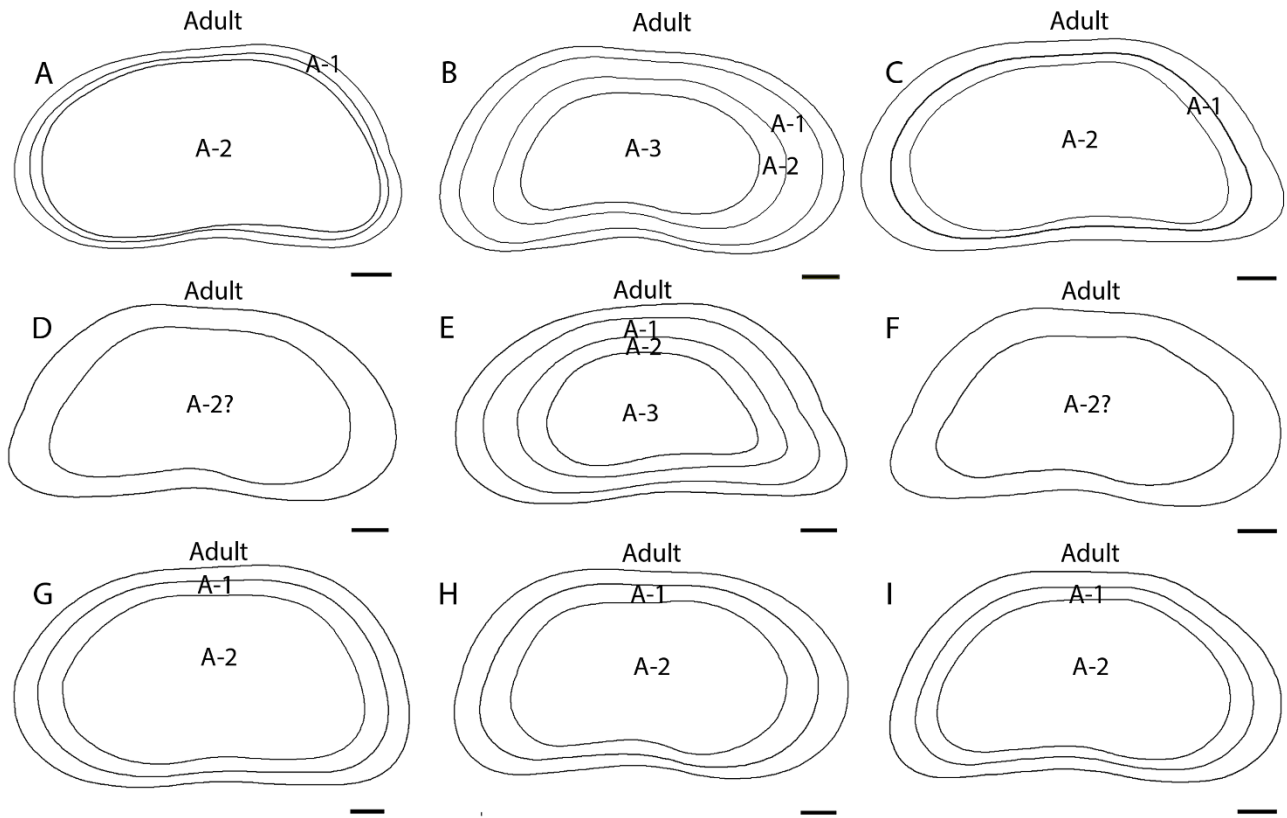
**Comparisons.** The five new *Caspiocypris* species have been compared each other and with some species already known from literature, using geometric morphometrics applied only on female valves. To compare the outlines of different species the mean outlines were used, calculated on four to 10

valves each. As seen in Figure 2.12, the five *Caspiocypris* species recovered in the deep facies of FBF show substantial differences in their mean valve outlines, in ‘normalized for area’ for left (Fig. 2.12 A) and right valves (Fig. 2.12 B). Left valves display maximum differences, especially in the posteroventral area (m1, v7 and v6). Indeed, two species (*C. perusia* and *C. posteroacuta*) show very protruding posteroventral angles that are differently oriented, upwards in *C. posteroacuta* and downwards in *C. perusia*. *Caspiocypris tiberina* differs particularly from the other species for the straight ventral margin (v3, v4 and v5 in Fig. 2.12 A) and for the H/L ratio, resulting in the species with the highest left valve. *Caspiocypris basilicii* valve shape is intermediate, with a marked ventral concavity but with poorly developed posterior end. Right valves seem to be more conservative with fewer differences among them. The maximum differences are displayed in the posteroventral area (v6 and v7 in Fig. 2.12 A), that is more developed in *C. posteroacuta* and in the anterodorsal area (d5 and d4 in Fig. 2.12 B) with *C. tuderis* proportionally higher than other species. It is worth noting that in the right valve *C. perusia* displays a posterior end similar to the other species.

Similar differences can be noted also in the juveniles, as shown in Figure 2.13. Instars have been ascribed to the five different species up to the A-3 stage, when possible. Notably, the ventral concavity trends to become asymmetrical in juvenile stages.



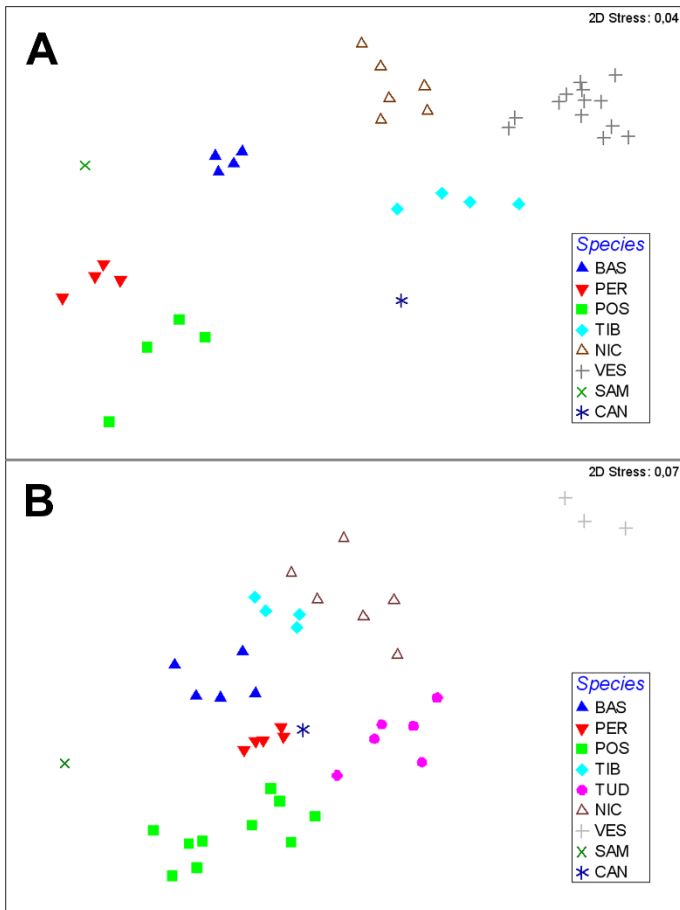
**Figure 2.12:** Superimposition of the mean outlines in ‘normalized for area’ mode of *Caspiocypris posteroacuta* Spadi & Gliozzi (0, red), *C. basilicii* Spadi & Gliozzi (1, blue), *C. perusia* Spadi & Gliozzi (2, green), *C. tiberina* Spadi & Gliozzi (3, light blue) and *C. tuderis* Spadi & Gliozzi (4, purple) for the left valves (A) and for right valves (B). (Morphomatica outputs have been realized with six iterations. The delta vector scale is 3.



**Figure 2.13:** Superimposition of the outlines of *Caspiocypris* adult and juveniles from Fosso Bianco Formation. **A**, *C. basilicii* left female adult and two instars in ‘not normalized for area’ mode. **B**, *C. basilicii* right female adult and three instars in ‘not normalized for area’ mode. **C**, *C. perusia* left female adult and two instars in ‘not normalized for area’ mode. **D**, *C. perusia* right female adult and one instars in ‘not normalized for area’ mode. **E**, *C. posteroacuta* left female adult and three instars in ‘not normalized for area’ mode. **F**, *C. posteroacuta* right female adult and one instars in ‘not normalized for area’ mode. **G**, *C. tiberina* left female adult and two instars in ‘not normalized for area’ mode. **H**, *C. tiberina* right female adult and two instars in ‘not normalized for area’ mode. **I**, *C. tuderis* outlines of the right female adult and two instars in ‘not normalized for area’ mode. Scale bars = 100  $\mu\text{m}$ .

The new *Caspiocypris* species have been compared with numerous Plio–Pleistocene *Caspiocypris* from Mediterranean and Paratethyan area. Among these, the most similar species have been chosen for the comparisons of the female valve outlines using geometric morphometric analysis and processing the results with multivariate statistics (Fig. 2.14). In Figure 2.15, the superimposition of each species outline is shown to enhance shape differences in “normalized for area” mode. The only species that is similar to *C. basilicii* is *Caspiocypris sambucensis* (Medici et al., 2011) from the Early Pliocene of Valdelsa (Tuscany, central Italy) but its left valve differs in the shape of the posterior margin, the higher and shorter outline (d4, d3, d1, m1, v7 and v5) and consequently the more marked ventral concavity (v4) (Fig. 2.15 A). *Caspiocypris perusia* can be compared with *C. sambucensis* and *Caspiocypris candida* (Livental, 1929); in comparison to the former, the left valve of *C. perusia* is more enlarged posteroventrally (v7), proportionally higher in dorsal area (d1, d2, d6,

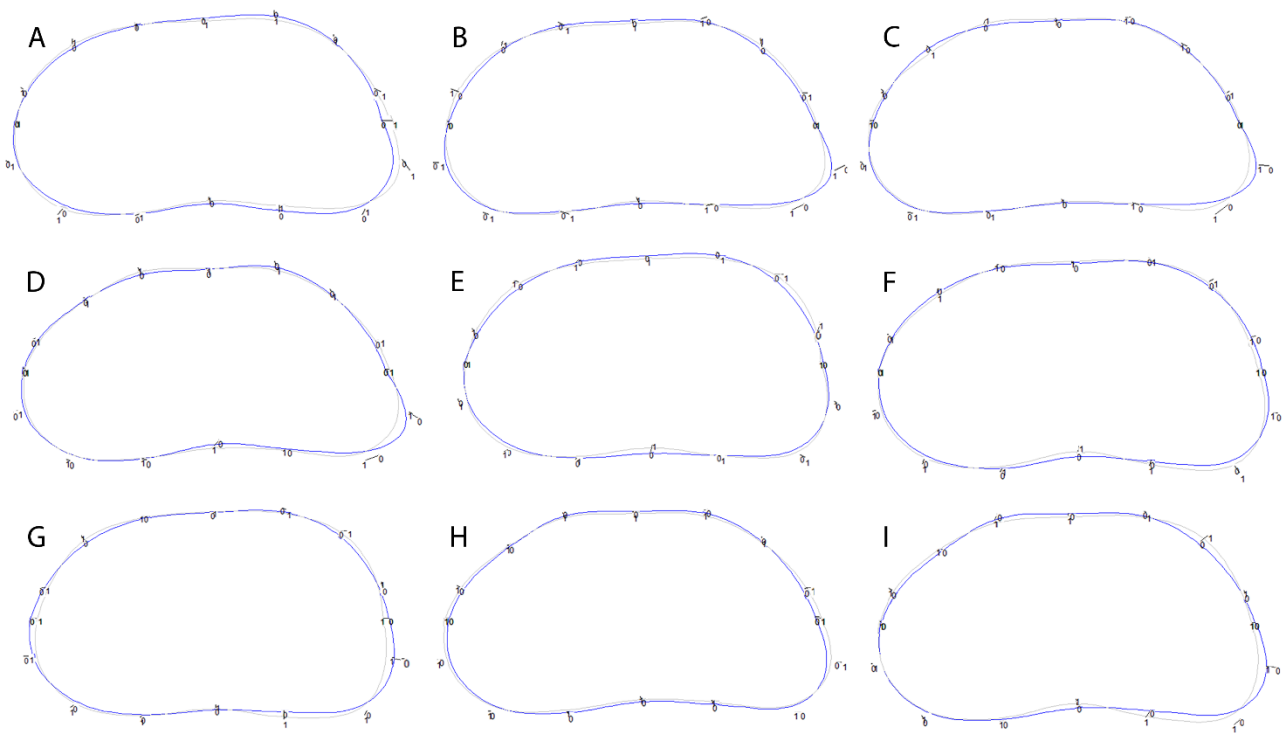




**Figure 2.14:** Results of the multivariate analyses applied on the geometric morphometric outline matrix of several species of *Caspiocypris* from Tiberino Basin and the Peri-Mediterranean domain in ‘normalized for area’ mode. **A**, non-metric multidimensional scaling (nMDS) plot in 2D morphological space for left valves; **B**, non-metric multidimensional scaling (nMDS) plot in 2D morphological space for right valves. Abbreviations: BAS, *Caspiocypris basilicii* Spadi & Gliozzi; PER, *Caspiocypris perusia* Spadi & Gliozzi; POS, *Caspiocypris posteroacuta* Spadi & Gliozzi; TIB, *Caspiocypris tiberina* Spadi & Gliozzi; TUD, *Caspiocypris tuderis* Spadi & Gliozzi; NIC, *Caspiocypris nicandroi* Spadi & Gliozzi; VES, *Caspiocypris vestinae* Spadi & Gliozzi; SAM, *Caspiocypris sambucensis* (Medici, Ceci & Gliozzi); CAN, *Caspiocypris candida* (Liventani).

marginal (v7, m1, d1 and d2) (Fig. 2.15 G). Finally, the right valve of *C. tuderis* can be compared with right valve of *C. candida*, which is proportionally shorter (d7, m2, v1, v7, m1 and d1) and higher (v3, v4, v5, d3, d4 and d5) (Fig. 2.15 H) and with the right valve of *C. nicandroi*, differing in ventral (v7, v6, v5, v4 and v3) dorsal margin outlines (d2, d4 and d5) (Fig. 2.15 I).

d7, d4 and d5) and with a straighter ventral margin (v6, v5 and v4) (Fig. 2.15 B). In comparison with the latter, the right valve of *C. perusia* differs in the morphology of the posterior end (v7 and v6) and anterodorsal areas (d4, d5 and d6) that are longer and with more curved anterior margin (Fig. 2.15 C). The left valve of *C. posteroacuta* is very different from the left valve of other *Caspiocypris* species but the right valve is comparable with *C. candida*, from which it differs in its proportionally longer posterior end (v7 and v6), a more accentuated ventral concavity (v5 and v4) and a dorsal margin slightly inclined anteriorly (d5) (Fig. 2.15 D). *Caspiocypris tiberina* can be compared with *Caspiocypris nicandroi* Spadi & Gliozzi, 2016 (in Spadi et al., 2016) but the left valve is proportionally higher (d3, d4 and d5) and the ventral margin is straighter (v4 and v3) (Fig. 2.15 E). In addition, the right valve is slightly different: *C. tiberina* displays a straighter ventral margin (v4 and v3) and a different outline of the posterior end (v5, v6, v7, m1 and d1) (Fig. 2.15 F). *Caspiocypris tiberina* left valve can be compared also with the left valve of *Caspiocypris vestinae* Spadi & Gliozzi, 2016 (in Spadi et al., 2016). However, it shows a straighter ventral margin (v6 and v5) and a more curved posterior



**Figure 2.15:** Comparison of the mean outlines normalized for areas (six iterations, delta vector scale 1) among Pliocene–Pleistocene *Caspiocypris* species. **A**, left valve of *C. basilicii* Spadi & Gliozzi. (blue) versus left valve of *C. sambucensis* (Medici, Ceci & Gliozzi) (black); **B**, left valve of *C. perusia* Spadi & Gliozzi (blue) versus left valve of *C. sambucensis* (Medici, Ceci & Gliozzi) (black); **C**, right valve of *C. perusia* Spadi & Gliozzi (blue) versus right valve of *C. candida* (Liventani) (black); **D**, right valve of *C. posteroacuta* Spadi & Gliozzi (blue) versus right valve of *C. candida* (Liventani) (black); **E**, left valve of *C. tiberina* Spadi & Gliozzi (blue) versus left valve of *C. nicandroi* Spadi & Gliozzi (black); **F**, right valve of *C. tiberina* Spadi & Gliozzi (blue) versus right valve of *C. nicandroi* Spadi & Gliozzi (black); **G**, left valve of *C. tiberina* Spadi & Gliozzi (blue) versus left valve of *C. vestinae* Spadi & Gliozzi (black); **H**, right valve of *C. tuderis* Spadi & Gliozzi (blue) versus right valve of *C. candida* (Liventani in Liventani 1929, pl. 2, fig. 32) (black); **I**, right valve of *C. tuderis* Spadi & Gliozzi (blue) versus right valve of *C. nicandroi* Spadi & Gliozzi (black).

Family **Linnocytheridae** Klie, 1938

Subfamily **Linnocytherinae** Klie, 1938

Genus *Paralinnocythere* Carbonnel, 1965

*Paralinnocythere umbra* Spadi & Gliozzi, 2017

(Fig. 2.11 F–K)

2011 *Paralinnocythere* sp. 1 Medici: 62, pl. 2, figs d–f.

**Diagnosis.** *Paralinnocythere* species with marked anterocardinal angle and faint reticulation.

**Derivation of name.** From Umbria, the Italian region where this species was found.



**Material.** Holotype: T41/1, RV female (Fig. 2.11 F), sample CT I 98 m. Paratypes: T41/2-3, RV female; T41/4, LV female; M317/1/3, LV male; sample CT I 98 m. All from the Cava Toppetti section, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Gelasian. Additional material: 15 adult valves and 28 juveniles.

**Occurrence.** Samples 50 m–107 m Cava Toppetti I section; samples 17 m–86 m Fosso Bianco section; Tiberino Basin, Italy, Fosso Bianco Formation, late Piacenzian p.p.–Gelasian p.p.

**Description.** Only isolated valves were found, thus the carapace shape was inferred from the loose R and L valves. In dorsal view, the anterior and posterior ends are pointed and the carapace is slightly inflated in the middle. In lateral view, the female valve is trapezoidal in shape. The dorsal margin is straight, bending posteriorly and with a remarkable anterocardinal angle. The posterior end is rounded. The ventral margin displays a sinuosity in the middle, although the swollen ventral area covers it partially. The anterior and posterior margins are well rounded. The ornamentation is reticulated, with polygonal meshes, especially marked in the posterior part. The valve surface is divided by a dorsomedian sulcus. Marginal pore canals are branched, as typical of the genus *Paralimnocythere*. Sexual dimorphism is poorly emphasized with male valves slightly longer than females.

**Dimensions.** LV female (five valves): L = 0.60–0.68 mm; H = 0.34–0.37 mm. RV female (five valves): L = 0.58–0.63 mm; H = 0.34–0.37 mm. LV male (three valves): L = 0.63–0.68 mm; H = 0.33–0.38 mm. RV male (two valves): L = 0.64–0.69 mm; H = 0.34–0.36 mm.

**Comparisons.** *Paralimnocythere umbra* has been compared with several extant and fossil species of *Paralimnocythere* with trapezoidal shape. Compared to living *Paralimnocythere compressa* (Brady & Norman, 1889), *P. umbra* presents more marked anterodorsal angle and ventral concavity. *Paralimnocythere tenera* Sokac, 1972 from the upper Pannonian of Croatia (Sokac, 1972), displays an outline similar to *P. umbra* but the dorsal margin is less inclined and the anterodorsal angle less pronounced; the posterior flat surface is smaller and the ornamentation includes also 2–3 tubercles. *Paralimnocythere dictyonalis* Medici et al., 2011 from the early Zanclean of Tuscany (Medici et al., 2011) is smaller and displays less extended anterior and posterior flat surfaces than *P. umbra*.

### **Fosso Bianco Fm. (facies C)**

The ostracod fauna recovered at the Dunarobba Fossil Forest includes 18 species referable to 14 genera. Several of them pertain to well known species, widely distributed in Europe: *Darwinula stevensoni* (Brady & Robertson, 1870) (Fig. 2.16 A-B), *Candona neglecta* Sars, 1887 (Fig. 2.16 K-L), *Candona angulata* Müller, 1900 (Fig. 2.20 A), *Candonopsis kingsleii* (Brady & Robertson, 1870) (Fig. 2.22 A), *Cyclocypris ovum* (Jurine, 1820) (Fig. 2.21 B), *Ilyocypris bradyi* Sars, 1890 (Fig. 2.22

D), *Ilyocypris decipiens* Masi, 1905 (Fig. 2.21 E), and *Potamocypris pallida*, Alm, 1914 (Fig. 2.27 A-B). Their occurrence in the different samples is reported in Tab. 2.1 Few fragmentary juvenile valves of *Fabaeformiscandona* sp. and *Pseudocandona* sp. were also found, but they were considered allochthonous based on the absence of adult valves or carapaces (Boomer et al., 2003). For the suprageneric classification, we followed Meisch (2000) and Horne et al. (2002). For the identification of the *Ilyocypris* species, we used the valve outline and the morphology of the inner ripplelets, followed Mazzini et al. (2014a). Hereinafter new or peculiar species found at the Dunarobba Fossil Forest are illustrated in detail.

Class **Ostracoda** Latreille, 1802

Subclass **Podocopa** Sars, 1866

Order **Podocopida** Sars, 1866

Suborder **Darwinulocopina** Sohn, 1988

Superfamily **Darwinuloidea** Brady & Norman, 1889

Family **Darwinulidae** Brady & Norman, 1889

Genus *Vestalenula* Rossetti & Martens 1998

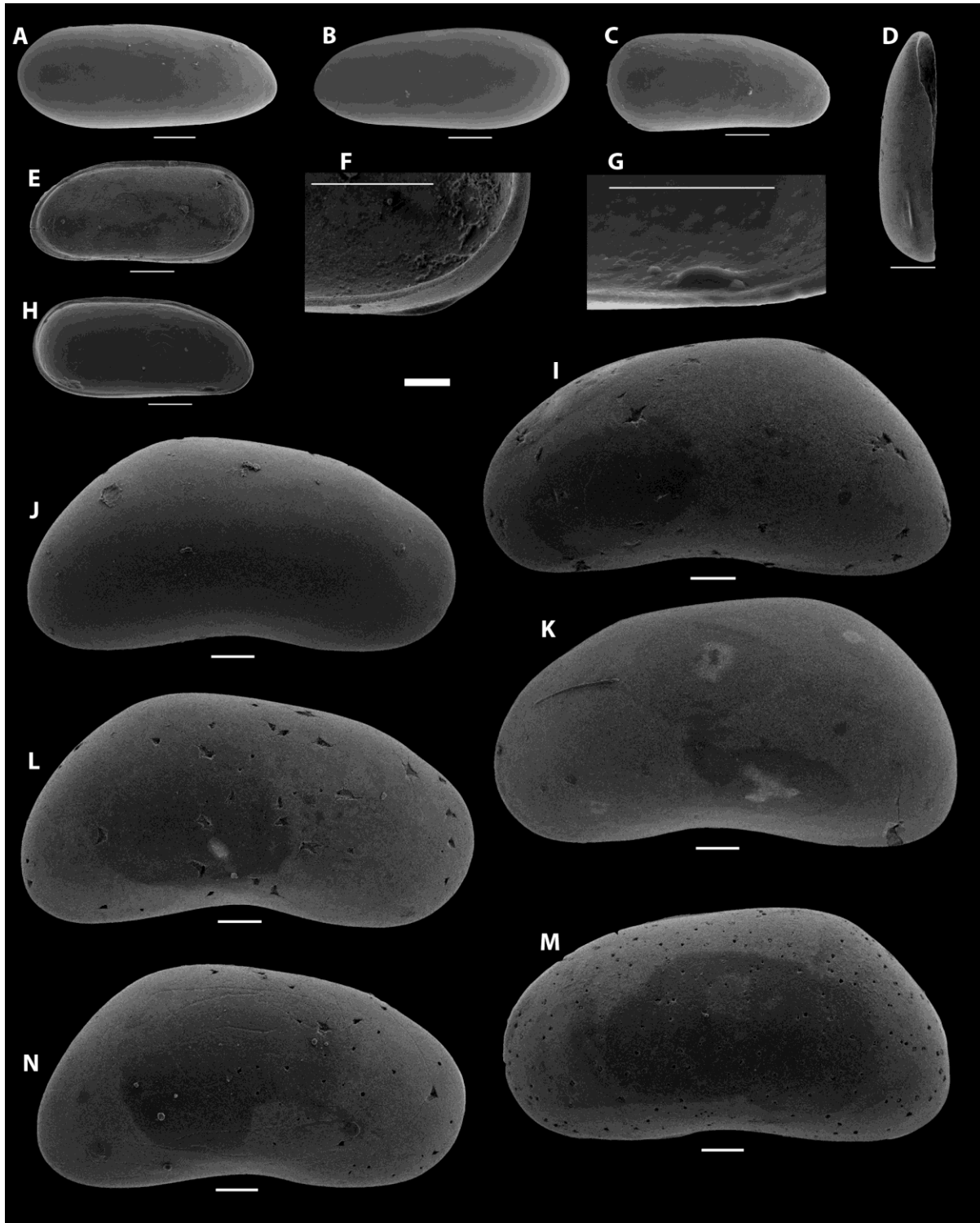
*Vestalenula cylindrica* (Straub, 1952)

(Fig. 2.16 C-H)

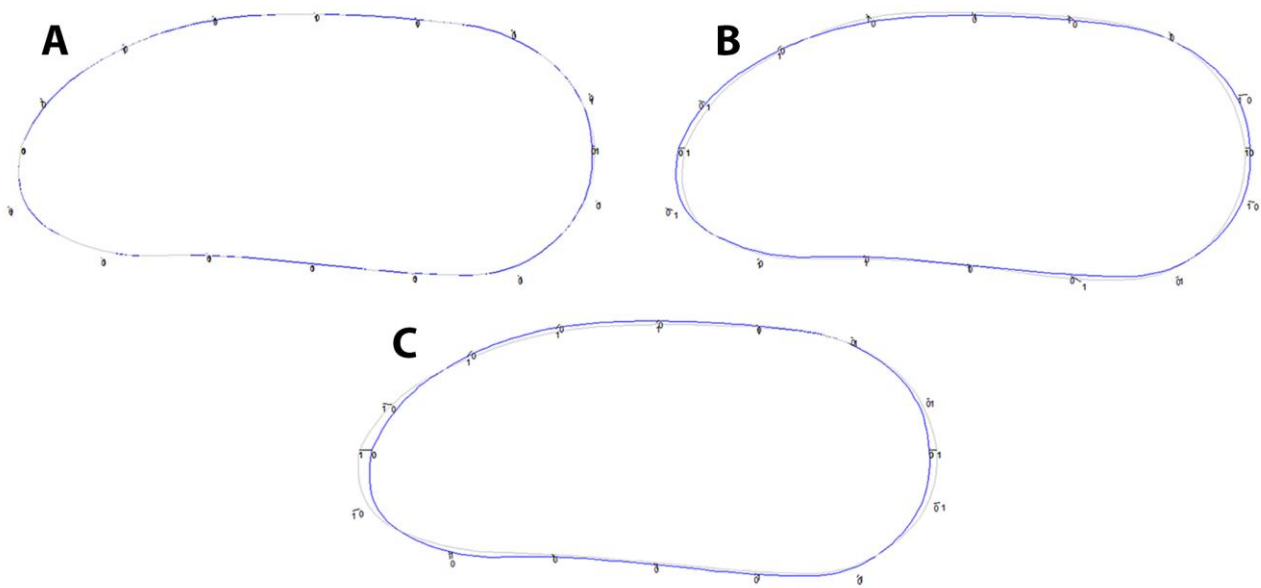
1952 *Darwinula cylindrica* Straub, p. 497, fig. 19-20.

Few valves of *Vestalenula* were recovered only in sample DUN 2. For the species identification, the geometric morphometric analysis was applied, using the Tps-data base reported in Ligios et al. (2009). The valves outline were compared with those of *Vestalenula cylindrica* (Straub), *Vestalenula pliocenica* Ligios, Minati, Gliozzi & Krstić, and *Vestalenula longissima* Ligios, Minati, Gliozzi & Krstić. The results showed that the outline of valves is comparable with *V. cylindrica*, while *V. pliocenica* is different in dorsal and anterior end; *V. longissima*, is very different in the posterior and anterior area (Fig. 2.17).

*Vestalenula cylindrica* is recorded from Miocene to Holocene.



**Figure 2.16:** Ostracods from Dunarobba Fossil Forest, Tiberino Basin, Italy. **A-B**, *Darwinula stevensoni* (Brady & Robertson). **A**, lateral view of female RV, DUN 1; **B**, lateral view of female LV, DUN 1. **C-H**, *Vestalenula cylindrica* (Straub). **C**, lateral view of female RV, DUN 2; **D**, dorsal view of female LV, DUN 2; **E**, internal view of female RV, DUN 2; **F**, detail of posterior internal view of female RV, DUN 2, illustrated in **E**; **G**, detail of anterior internal view of female LV, DUN 2, illustrated in **H**; **H**, internal view of female LV, DUN 2. **I-J**, *Candona improvisa* Ostermeyer. **I**, lateral view of female LV, Tr8 int.; **J**, lateral view of female RV, Tr8 int. **K-L**, *Candona neglecta*, Sars. **K**, lateral view of female LV, Tr12 int.; **L**, lateral view of female RV, Tr12 ext. **M-N**, *Candona paludinica*, Krstić. **M**, lateral view of female LV, DUN 1; **N**, lateral view of female RV, DUN C. Scale bars = 0.1 mm.



**Figure 2.17:** Comparison of the mean outlines normalized for areas (six iterations, delta vector scale 1) among Neogene and Quaternary *Vestalenula* species. **A**, LV of *V. cylindrica* (Straub) from DUN 2 (blue) versus LV of *V. cylindrica* (Straub) from Austria (Minati et al., 2008) (black); **B**, LV of *V. cylindrica* (Straub) from DUN 2 (blue) versus LV of *V. pliocenica* (Ligios, Minati, Gliozzi & Krstić) from Rieti Basin (Ligios et al., 2009) (black); **C**, LV of *V. cylindrica* (Straub) from DUN 2 (blue) versus LV of *V. longissima* (Ligios, Minati, Gliozzi & Krstić) from Rieti Basin (Ligios et al., 2009) (black).

Suborder **Cypridocopina** Jones, 1901

Superfamily **Cypridoidea** Baird, 1845

Family **Candonidae** Kaufmann, 1900

Subfamily **Candoninae** Kaufmann, 1900

Genus *Candona* Baird, 1845

*Candona (Candona) improvisa* Ostermeyer, 1937

(Fig. 2.16 I-J)

1937 *Candona improvisa* Ostermeyer, p. 155, fig.1.

The general outline and the size are referable to *Candona (Candona) improvisa*, though the size of valves recovered from the Dunarobba Fossil Forest samples is slightly bigger than what reported by Meisch (2000). *Candona (Candona) improvisa* is a living species in central Europe (Germany, Poland and Hungary (Meisch, 2000)). It is signalled from the Holocene of Germany, Hungary, Slovakia, and Poland. It has also been found in the Pleistocene of Croazia and Serbia and in the late Middle Pleistocene of Tuscany (Benvenuti et al, 2017). Meisch (2000) reports its fossil record from Lower Pleistocene (Calabrian) to Recent.

*Candona (Neglecandona) paludinica* Krstić, 1995

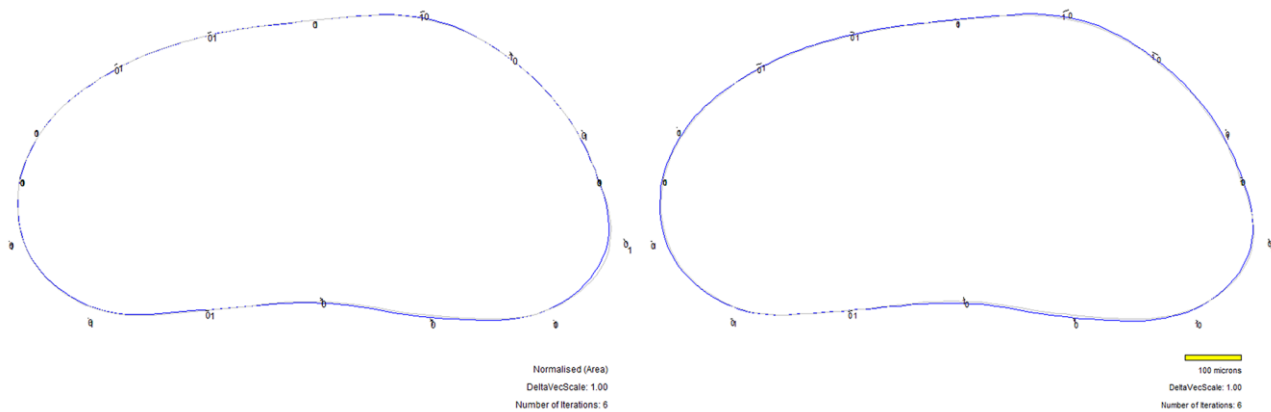
(Fig. 2.16 M-N, Fig. 2.20 B)

1995 *Candona (Neglecandona) paludinica* Krstić, pp. 394-396, figs. 3-5, pl. 3, 8-12.

2003 *Candona (Neglecandona) paludinica* Krstić, p. 380, pl. 5: 4, pl. 6, 1-4, 6-8.

2006 *Neglecandona paludinica* Krstić, pp. 146-147, pl. 21, 2-4 7-8, pl. 23-24 1-8.

Based on the comparison with the original material stored in the Natural History Museum of Belgrade, some valves recovered in several samples of the Dunarobba Fossil Forest have been referred to *Candona (Neglecandona) paludinica* (Fig. 2.18). This species was known, up to now, only from Serbia (see Krstić, 2006 for references), in particular in the upper part of the Lower Paludonian Beds, and in the Middle Paludonian Beds. A recent stratigraphic revision of the Neogene and Quaternary deposits of the Paludonian Beds refers the Lower and Middle Paludonian Beds to the latest Zanclean-Piacenzian (Mandic et al., 2015).



**Figure 2.18:** Results of the geometric morphometric analysis performed on left valve of *Candona (Neglecandona) paludinica* holotype from Natural History Museum of Belgrade (blue) and *C. (N.) paludinica* from Dunarobba Fossil Forest, sample DUN 1 (grey) in “normalized for area” mode on the left valve and “ not normalized for area” mode on the right.

Family **Cyprididae** Baird, 1845  
Subfamily **Cyprididae** Baird, 1845  
Genus ***Cypris*** Müller, 1776  
***Cypris mandelstami*** Luebimova, 1961  
(Fig. 2.20 C-D)

not 1840 *Cypris subglobosa* sp. nov. Sowerby, p. 547, fig. 3.

1961 *Cypris mandelstami* Luebimova, in Agalarova *et al.*, p. 69, pl. 23, figs 1-2.

not 1961 *Cypris subglobosa* Sowerby, Agalarova *et al.*, pp. 68-69, pl. 23: 4, pl. 37: 3.

2006 *Cypris subglobosa mandelstami* Luebimova, Krstić, p. 174-175, pl. 46, figs 6-8, pl. 47, figs 4-5, pl. 48, figs 1-5, pl. 59, figs 1-9, pl. 61, fig. 1, pl. 62, fig. 6.

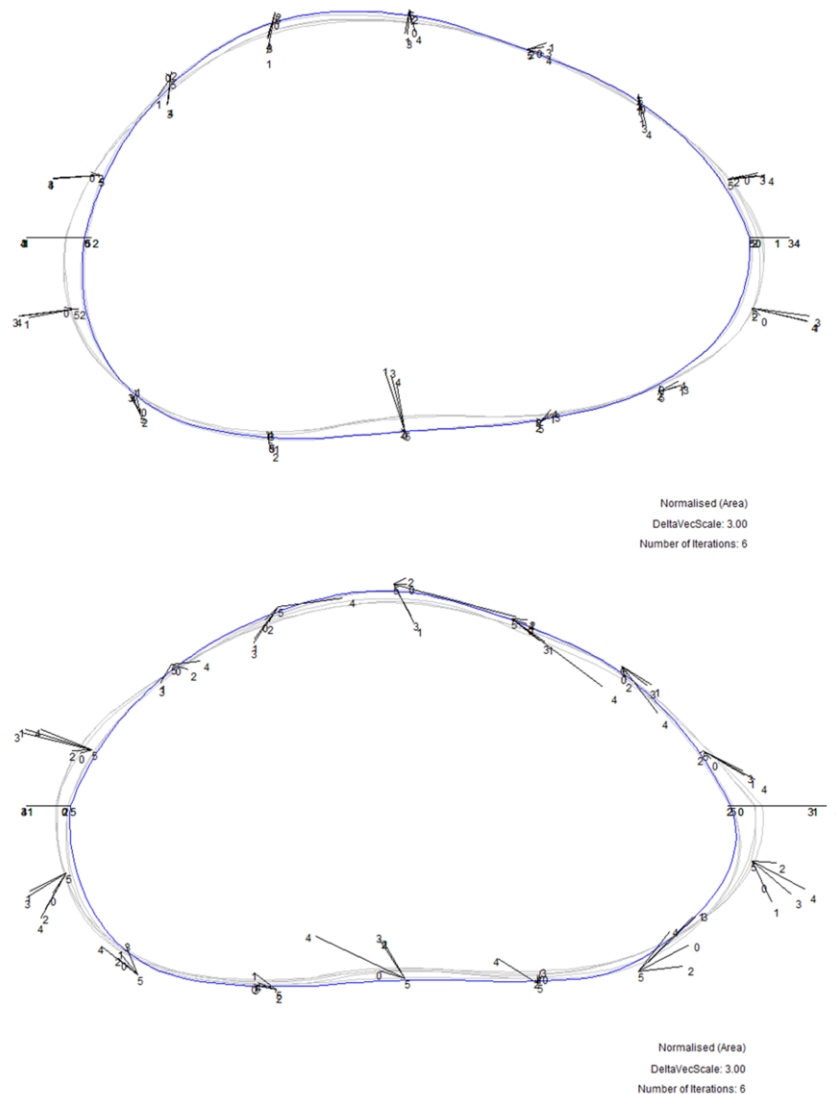
2011 *Cypris* sp., Smith *et al.*, 2011, p. 9, fig. 2 J-K.

2011 *Cypris subglobosa* Sowerby, Medici, p. 125, pl. 13, figs e-g.

One left and one right adult valves of *Cypris* collected in sample DUN 3 are referable to a rather common species at present living in the tropical areas that has been often erroneously identified as *Cypris subglobosa* Sowerby, 1840 a species, which occurs in the Late Cretaceous of India. Revising the type material of *Cypris subglobosa*, Whatley *et al.* (2003) referred it to genus *Paracyprretta* for the shorter proportions, the inflated ventro-lateral area and the presence of a “flap-like” extension of the LV on the dorsal margin in the ocular region. These characters are not present in the valves collected at Dunarobba. According to Whatley *et al.* (2003), *P. subglobosa* occurs only in the Late Cretaceous intertrappean deposits of the Rajasthan (India), while the other erroneous recoveries of this species are from the Pleistocene to Recent in the freshwaters of Asia (Iran, Afghanistan, Uzbekistan, India, Sri Lanka, Indonesia, China, and Japan), West Africa, Macedonia, and Caribbean Islands (Martens & Toguebaye, 1985; Whatley *et al.*, 2003; Smith *et al.*, 2011; see synonymy in those papers).

In order to identify the valves recovered in the Dunarobba Fossil Forest, the geometric morphometric analysis of the valve outline of all the illustrated forms referred to “*Cypris subglobosa*” was performed (Fig. 2.19). The results show that at least two morphotypes are recognizable, one more elongated (Caribbean islands - Triebel, 1961; Neale, 1976; Macedonia - Petkovski, 1964) and one stouter, with relatively higher and shorter proportions, and smaller in size (Japan - Smith *et al.*, 2011; Serbia - Krstić, 2006; Azerbaijan - Agalarova *et al.*, 1961). In Azerbaijan Agalarova *et al.* (1961) ascribed their valves to *Cypris mandelstami* Luebimova in Agalarova *et al.*, 1961. The Dunarobba Fossil Forest specimens pertain to the stouter and smaller morphotype, thus, they are here referred to

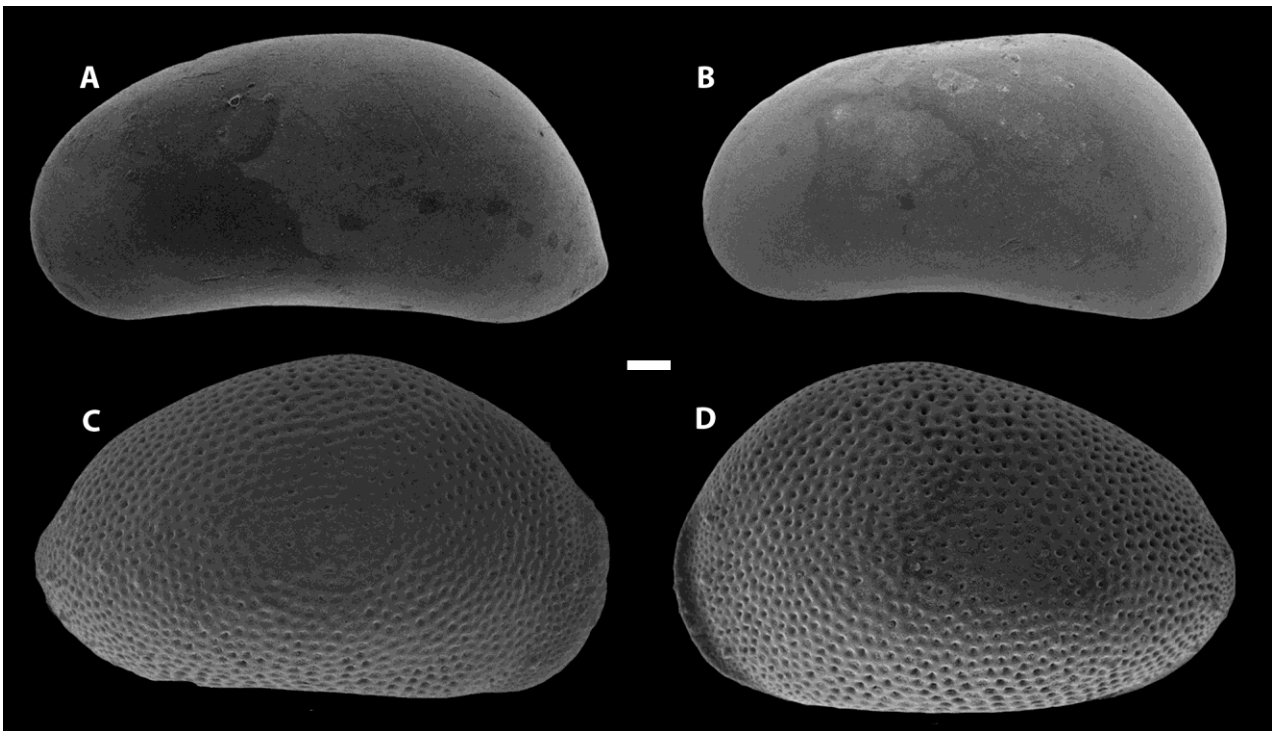
Agalarova et al. (1961) species. Due to the parthenogenetic reproduction of the living representatives, it is not clear if the other morphotype should be assigned to a different species or only to different clonal lineages



**Figure 2.19:** Results of the geometric morphometric analysis performed on various valve attributed to “*Cypris subglobosa*”, up for left valves, down for the right valves in normalized for area mode, delta vector scale= 3. Left valve: 0 = *C. mandelstami* from Agalarova et al., 1961; 1= *C. subglobosa* from Neale, 1967; *C. subglobosa mandelstami* from Krstić, 2006; 3= *C. subglobosa* from Petkovski, 1964; 4= *C. subglobosa* from Triebel, 1961; 5= *Cypris* from sample DUN 3 (blue). Right valve: 0 = *Cypris* sp. from Smith et al., 2011; 1= *C. subglobosa* from Neale, 1967; *C. subglobosa mandelstami* from Krstić, 2006; 3= *C. subglobosa* from Petkovski, 1964; 4= *C. subglobosa* from Triebel, 1961; 5= *Cypris* from sample DUN 3 (blue).

Moreover, comparing the description of the appendages made by Petkovski (1964) (Macedonia specimens) and Triebel (1961) and (Neale (1976) (Caribbean specimens), some differences are noticed in the proportions of the different furcal elements: both the anterior and posterior claws are slightly longer in Petkovski specimens than in Triebel ones; the 6th seta of A2 is very short (around 1/3 of the 5th seta) in the Macedonian specimens, while in the illustration of Neale (1976) all the six setae are around the same length. Thus, further studies on the living material are needed.

*Cypris mandelstami* is present in the Productive series (Zanclean to Piacenzian) of Azerbaijan (Agalarova et al., 1961, Van Baak et al., 2013), Lower and Middle Paludinean beds in Serbia (Zanclean to Piacenzian) (Krstić et al., 2006), and it is living in the shallow waters of Lake Biwa (Japan) (Smith et al., 2011).



**Figure 2.20:** **A**, *Candona angulata* Muller, lateral view of female LV, sample DUN 2. **B**, *Candona paludinica* Krstić, lateral view of male LV, sample DUN 1. **C-D** *Cypris mandelstami* Luebimova. **C**, lateral view of female RV, sample DUN 3; **D**, lateral view of female LV, sample DUN 3. Scale bar = 0.1 mm.



Genere *Zonocypris* Müller 1898

*Zonocypris membranae quadricella* Stancheva, 1966

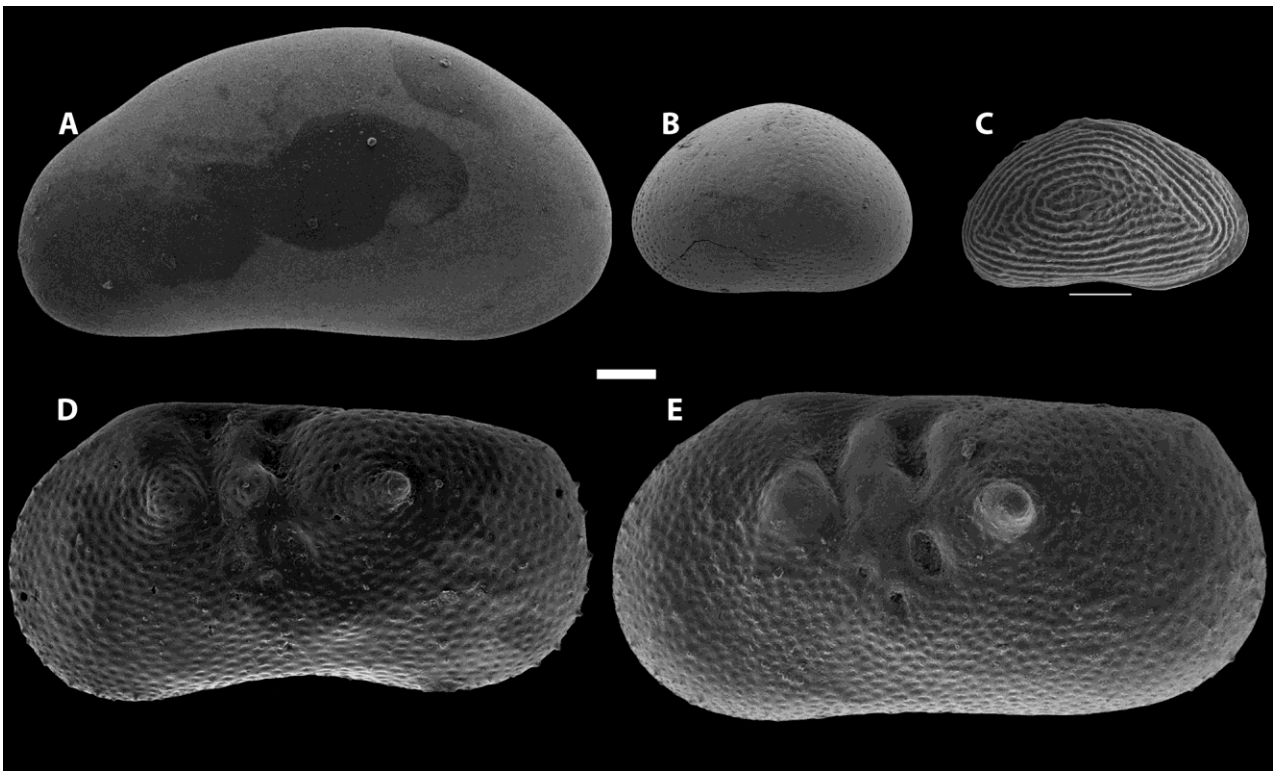
(Fig. 2.21 C)

1962 *Zonocypris membranae* Mandelstam *et al.*, p. 119, pl. 11: 10-14.

1966 *Zonocypris membranae quadricella* Stancheva, p. 117, pl. 3: 7.

2012 *Zonocypris membranae quadricella* Stancheva, Ligios *et al.*, p. 357.

The valve recovered in sample DUN 2 are only instars and all the right valves are broken. Anyway, the particular ornamentation of the surface of valves and general outline of the left valve lead to refer them to *Zonocypris membranae quadricella*. This species is distributed from the late Tortonian of central Italy (Ligios, 2009) to the Pleistocene of the Caspian Basin.



**Figure 2.21:** **A**, *Candonopsis kingsleii* (Brady & Robertson), lateral view of female LV, sample Tr12 ext. **B**, *Cyclocypris ovum* (Jurine), lateral view of female LV, sample DUN C. **C**, *Zonocypris membranae quadricella*, Stancheva, lateral view of female RV, sample DUN 2. **D**, *Ilyocypris bradyi* Sars, lateral view of female LV, sample DUN 1. **E**, *Ilyocypris decipiens* Masi, lateral view of female LV, sample DUN 3. Scale bar = 0.1 mm.

Subfamily **Cyprinotinae** Bronstein, 1947

Genus ***Hemicypris*** Sars, 1903

***Hemicypris*** sp. nov.

(Fig. 2.22 A-F)

? 2006 *Camarocypris*? aff. *elliptica* (Bojie, 1978), Krstić, p. 189, Pl. 46, figs. 9-10; Pl. 59, figs. 2-5; Pl. 60, figs. 1-4; Pl. 61, figs. 2-7; Pl. 66, fig. 3

2011 *Hemicypris* sp. nov., Medici, p. 12, figs d-h.

**Occurrence.** Sample DUN 3 Dunarobba Fossil Forest, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Gelasian.

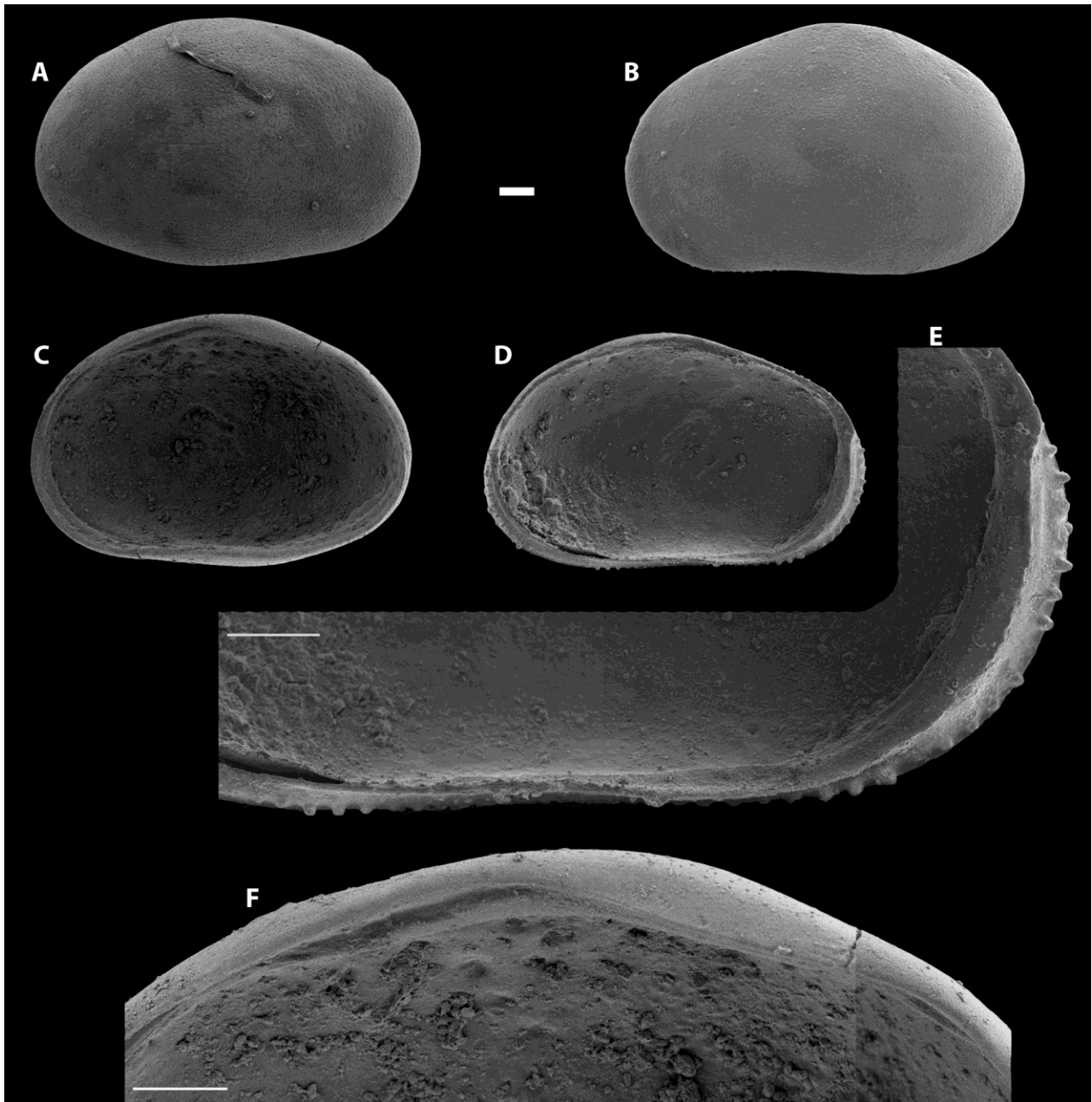
**Description.** In lateral view, the right valve shows an ovate outline, with convex dorsal and ventral margins. The surface is covered by tiny pits, slightly larger along the valve border. Internally, on the marginal area little crenulated grooves are evident, matching the crenulations of the left valve. LV smaller than the RV, with greatest height located in the middle. The dorsal margin is convex in the posterior part and rectilinear and gently sloping anteriorly in the anterior part. Internally the inner margin shows rather strong denticulations from the middle part of the anterior border to the middle part of the posterior one. Hinge adont, with an evident groove on the right valve which accommodates the bar of the left valve. Normal pore-canals short and straight. Central muscle scar typical of the subfamily.

**Dimensions.** LV female (four valves): L = 0.90–1.04 mm; H = 0.50–0.58 mm. RV female (six valves): L = 0.91–1.05 mm; H = 0.45–0.52 mm. LV male (one valve): L = 1.16 mm; H = 0.64 mm. RV male (three valves): L = 1.07–1.18 mm; H = 0.54–0.64 mm.

**Comparisons.** For the general rounded outline of the RV, *Hemicypris* sp. nov. is similar to four species described by Lindroth, 1953 from Southern Kenya *Hemicypris intermedia* (Lindroth), *Hemicypris kliei* (Lindroth), *Hemicypris nonstriatus* (Lindroth) and *Hemicypris humilis* (Lindroth), However, it is clearly distinct from them for the greater size, the ornamentation, and the very rounded RV outline.

In the Middle Paludanian Beds of Serbia Krstić (2006) reports *Camarocypris*? aff. *elliptica*. The illustrated valves cannot be referred to genus *Camarocypris* because of the overlap of the RV on the LV (typical character of *Hemicypris* while in *Camarocypris* is the opposite), whereas they are rather similar to *Hemicypris* sp. nov. from which they apparently differs for the more central position of the maximum height of the LV and for the more central position of the groove in the RV hinge.

Unfortunately we were not able to see the original Krstić material, and this prevented us to identify with certainty Krstić valves with *Hemicypris* sp. nov.



**Figure 2.22:** *Hemicypris* sp. nov. from sample DUN 3, Dunarobba Fossil Forest. **A**, lateral view of female RV. **B**, lateral view of female LV. **C**, internal view of female RV. **D**, internal view of female LV. **E**, detail of internal anterior and ventral margin of female LV, illustrated in D. **F**, detail of internal dorsal margin of female RV, illustrated in D. Scale bars = 0.1 mm.

Suborder **Cytherocopina** Baird, 1850

Superfamily **Cytheroidea** Baird, 1850

Family **Limnocytheridae** Klie, 1938

Subfamily **Limnocytherinae** Klie, 1938  
Genus ***Paralimnocythere*** Carbonnel, 1965

***Paralimnocythere*** sp. nov.

(Fig. 2.23 A-H)

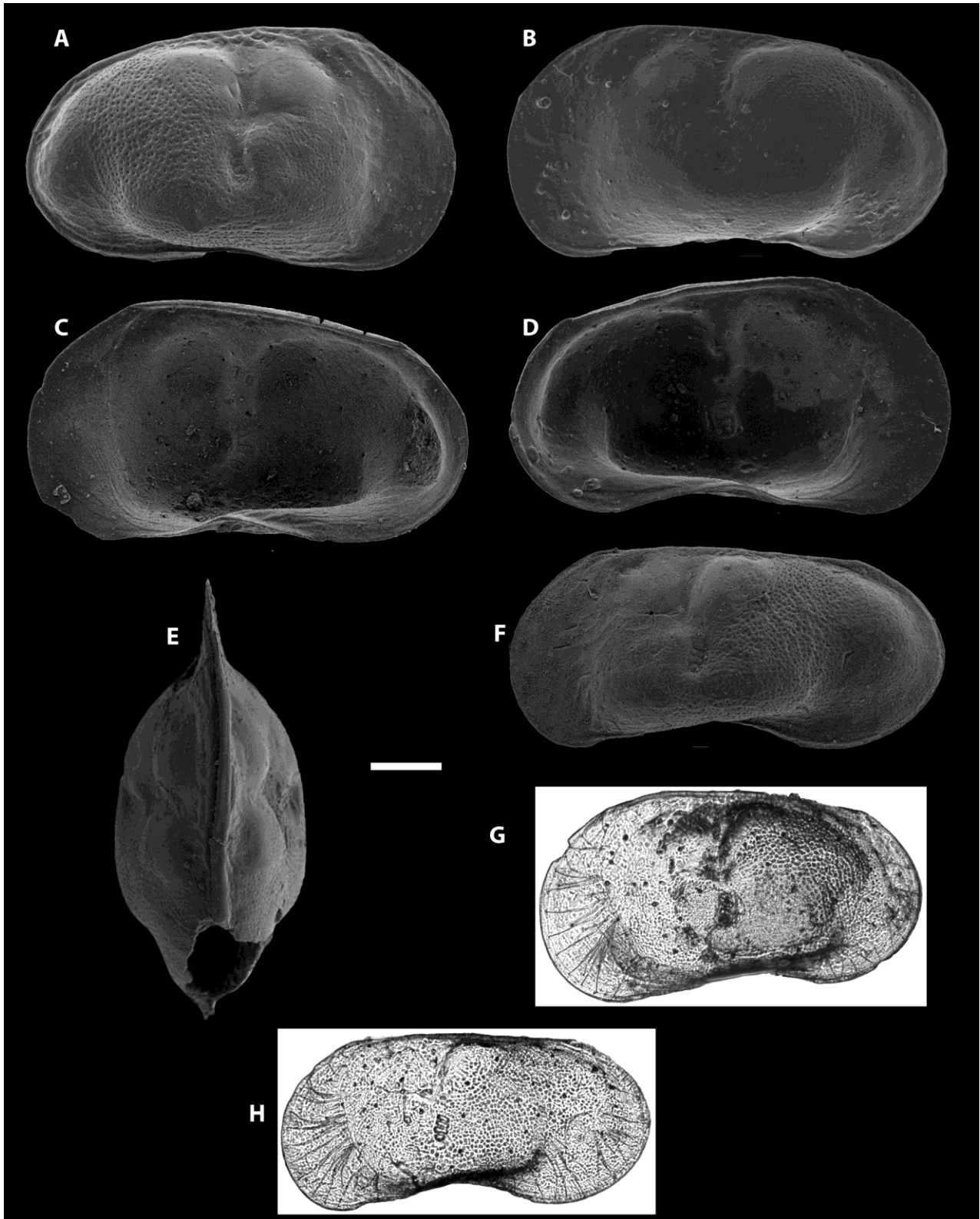
2011 *Paralimnocythere* sp. 2 n. sp. Medici, p. 65, Pl. 2, figs. g-i.

**Occurrence.** Samples Tr6 ext. and int., Tr8 ext. and int., Tr12 ext. and int., Tr23-24-25, DUN C, and DUN D; Dunarobba Fossil Forest, Todi, Italy, Fosso Bianco Formation, Tiberino Basin, Gelasian.

**Description.** The female carapace is inflated posteriorly in dorsal view and widely flattened anteriorly. The left valve slightly overlaps the right one posteriorly. In lateral view, the female valve is sub-rectangular in shape, with the greatest height located anteriorly at around  $\frac{1}{4}$  of the length. The dorsal border is slightly arched, both the anterior and posterior cardinal angles are evident. The anterior and posterior borders are widely rounded, the ventral border is concave in the middle, slightly covered by the elongated ventral lobe. On the lateral surface, two dorsal blunt tubercles separated by a narrow sulcus and one elongated ventral lobe are visible. The valves are smooth anteriorly while ventrally and backwards small pits are visible. Sometimes the posterior and ventral flattened areas are faintly reticulated. The hinge and muscle scars are characteristic of the genus. The marginal pore canals are long and polyfurcated. Sexual dimorphism is marked, with males proportionally more elongated than females.

**Dimensions.** female RV: L=0.62-0.66 mm; H= 0.31-0.36 mm; female LV: L=0.61-0.65 mm; H= 0.35-0.37 mm; male RV: L=0.65-0.68 mm; H= 0.35-0.36 mm; male LV: L=0.68 mm; H= 0.34 mm.

**Comparisons.** Among the fossil and living species of *Paralimnocythere* the only two species that show some similarities with *Paralimnocythere* sp. nov. are *Paralimnocythere relictata* (Lillieborg, 1863) and *Paralimnocythere* sp. Devoto, 1965. In dorsal view, *Paralimnocythere* sp. nov. is very similar to *P. relictata*, although the anterior area seems more flattened and the mid-dorsal sulcus wider; anyway, in lateral view the female valves outlines are proportionally higher and the ornamentation is rather absent in the anterior portion and less pronounced posteriorly, mainly pitted and not faintly reticulated as *P. relictata*. Moreover, in *Paralimnocythere* sp. nov. the ventral protuberance overpasses the ventral border. *Paralimnocythere* sp. nov. is rather similar to *Paralimnocythere* sp. Devoto (1965) for the pitted posterior ornamentation but the anterior flattened area is wider and the female carapace is more inflated.



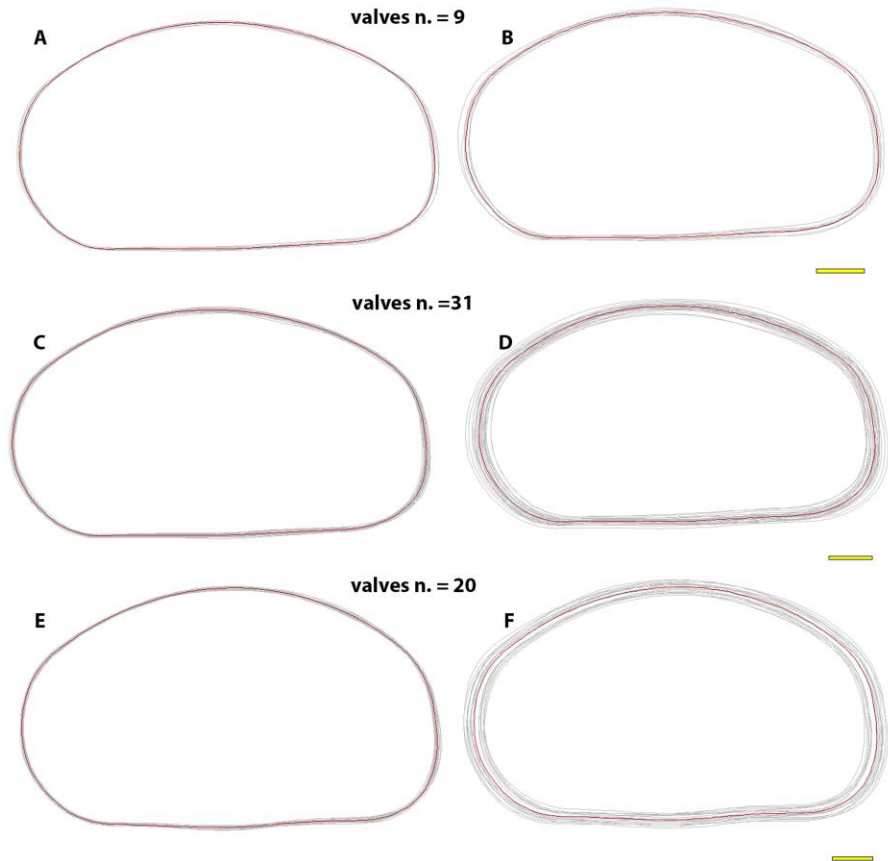
**Figure 2.23:** *Paralimnocythere* sp. nov. from Dunarobba Fossil Forest. **A**, lateral view of female RV, sample Tr12 int. **B**, lateral view of female LV, sample Tr 12 int. **C**, internal view of female RV, sample Tr 12 int. **D**, internal view of female LV, sample Tr 12 int. **E**, dorsal view of carapace of female, sample Tr 6 ext. **F**, lateral view of male, sample Tr 12 int. **G**, transmitted light picture of female LV, sample Tr 12 int. **H**, transmitted light pictures of male LV, sample Tr 6 ext. Scale bar = 0.1 mm.

Family **CYTHERIDEIDAE** Sars, 1925

Genus *Cyprideis* Jones, 1857

The identification of the species included in the genus *Cyprideis* Jones, 1857 is a rather difficult task, because of their great ecophenotypical plasticity that prevents to consider as diagnostic several characters such as the ornamentation and the size (Ligios & Gliozzi, 2012; Boomer et al., 2017; Frenzel et al., 2017 with

refs.). Recently some authors (Gross *et al.*, 2008; Ligios, & Gliozzi, 2012; Gliozzi et al., 2017) applied the geometric morphometric approach to compare the valve outlines and the significance of the obtained differences. In this chapter, the same approach has been applied on the female RV valve outlines of the *Cyprideis* specimens collected in the samples DUN 1, DUN 2 and DUN 3 where *Cyprideis* was very abundant. The results shows that the specimen outlines of samples DUN 1 and DUN 2 are comparable each other



**Figure 2.24:** Morphomatica output of the valves of *Cyprideis* in three samples of Dunarobba Fossil Forest in normalized for area and not normalized for area modes. Mean outlines are drawn in red. **A-B** *Cyprideis* female RV from DUN 1; **C-D** *Cyprideis* female RV from DUN 2; **E-F** *Cyprideis* female RV from DUN 3. Scale bars= 0.1 mm.

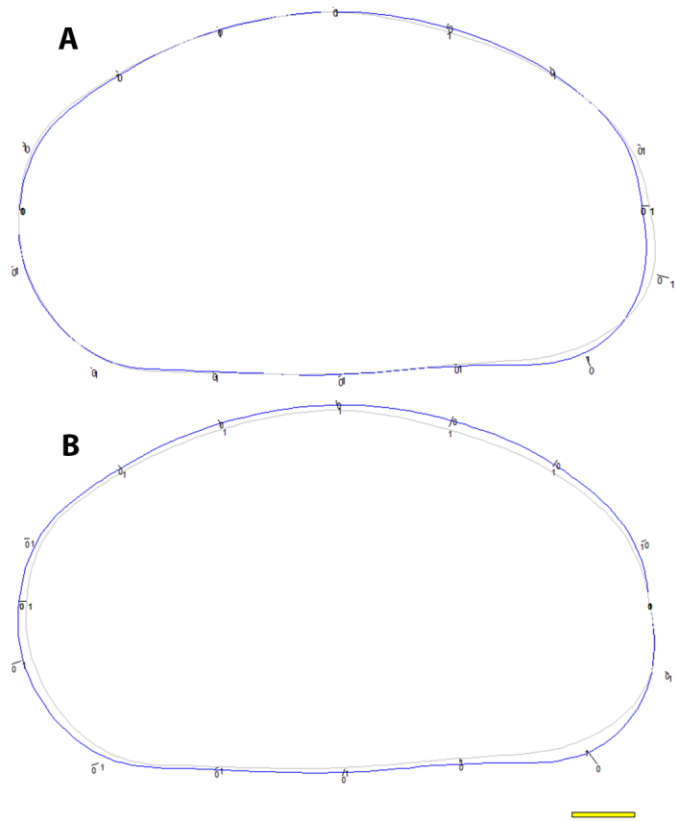
(Fig. 2.24 A-C in “normalised for area” mode), and their size variability (Fig. 2.24 B-D in “not normalised for area” mode) is little. The specimens outlines of sample DUN 3 are quite different to the DUN 1-2 ones. Furthermore, the mean outlines of the *Cyprideis* RV from the three examined samples have been compared (Fig. 2.24 E-F) and it appears that the sample DUN 3 displays specimens with slight differences in the outline but rather remarkable different size. In summary, the geometric

morphometric analysis suggest that the *Cyprideis* specimens from samples DUN 1 and DUN 2 on one side and *Cyprideis* from sample DUN 3 on the other, are probably referable to different species.

The second step of the geometric morphometric analyses was to compare the RV outlines of “*Cyprideis* DUN 1-2” and “*Cyprideis* DUN 3” with the correspondent outlines included in the Morphomatica database of the Italian *Cyprideis* species (Medici et al., 2011; Ligios & Gliozzi, 2012; Gliozzi, unpublished material).

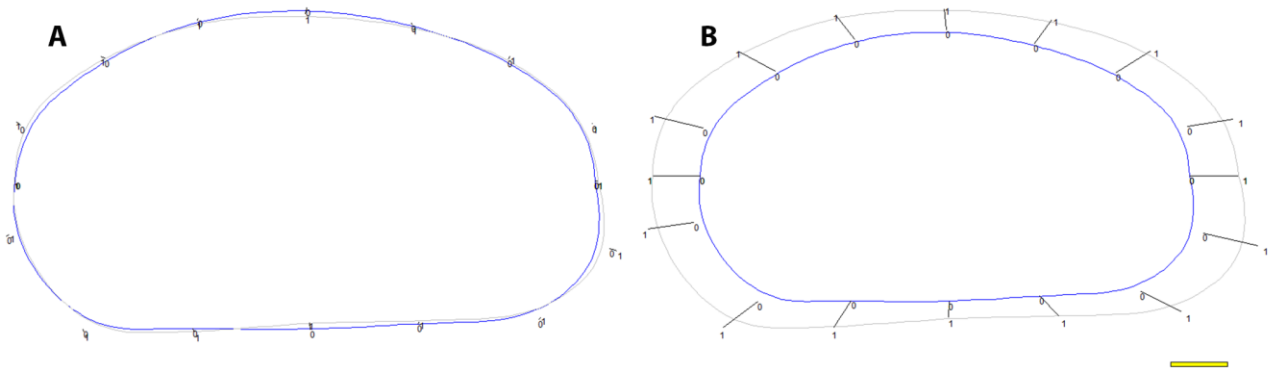
The female RV of *Cyprideis* DUN 3 shows the best fitting with *C. crotonensis* Decima, 1964 (Fig. 2.25), both for the shape and dimensions, which are only slightly smaller. This latter difference minimizes if we compare the DUN 3 specimens with the Pliocene population of *C. crotonensis* from Casabona (Calabria, Southern Italy) (Ligios & Gliozzi, 2012). The thick shell and the stout hinge structure with the presence of a thick sledge below the anterior sockets mirror the shell characters of *C. crotonensis*. All the above described similarities suggest to refer the valves of sample DUN 3 to *C. crotonensis* as was already supposed by Gliozzi et al. (2017) (Fig. 2.27 D).

In the case of *Cyprideis* DUN 1-2 the best fitting was recognized with the Early Pliocene *Cyprideis rectangularis* Medici, Gliozzi & Ceci, 2011 (Fig. 2.26). Anyway, some differences can be observed with *C. rectangularis*, particularly the slightly more arched dorsal margin, the slightly convex ventral margin, and the smaller dimensions. Other little differences on the valves, such as the presence of two posterior spines instead of one and the presence of anterior denticulations, which are absent in *C. rectangularis*, cannot be for sure considered as valuable diagnostic characters (Ligios & Gliozzi, 2012). For the above-mentioned slight differences, the valves collected in samples DUN1 and DUN 2 are here referred to *Cyprideis* cf. *C. rectangularis* Medici, Ceci & Gliozzi 2011 (Fig. 2.27 C).

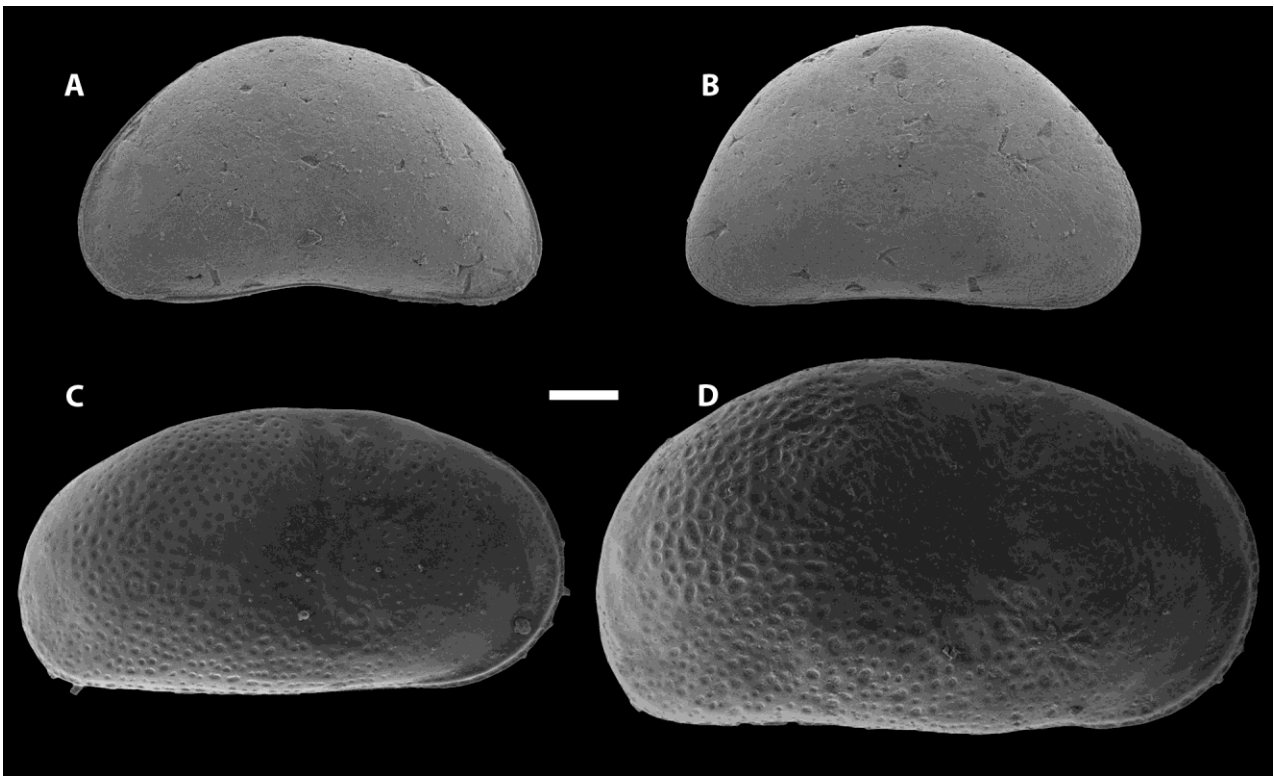


**Figure 2.25:** Comparison of the mean outlines normalized for area (A, 6 iterations, delta vector scale 1) and not normalized for area modes (B, scale bar = 0.1 mm) of *Cyprideis* from DUN 3 (blue, 0) versus *Cyprideis crotonensis* (black, 1).





**Figure 2.26:** Comparison of the mean outlines normalized for area (**A**, 6 iterations, delta vector scale 1) and not normalized for area modes (**B**, scale bar = 0.1 mm) of *Cyprideis* from DUN 1-2 (blue, 0) versus *Cyprideis rectangularis* from Valdelsa basin (black, 1).



**Fig. 2.27:** Ostracods from Dunarobba Fossil Forest, Tiberino Basin. **A-B**, *Potamocypris pallida*, sample Tr 23-24-25. **A**, lateral view of female LV; **B**, lateral view of female RV. **C**, *Cyprideis* cf. *C. rectangularis*, lateral view of female RV, sample DUN 1. **D**, *Cyprideis crotonensis*, lateral view of female RV, sample DUN 3. Scale bar = 0.1 mm.



## **Ponte Naja Fm.**

Sixty-eight samples collected in the CT II section have been studied for ostracod analyses. The majority of them were barren or gave only juveniles and/or broken adult valves of different species (allochthonous assemblages) pertaining to both shallow and deep waters; 9 scattered samples bore very few autochthonous species (adults and instars) of *Candona* (*Neglecandona*) *neglecta*, *Paralimnocythere umbra*, *Cyprideis* cf. *C. rectangularis*, and *Ilyocypris bradyi*.

## **2.4 Discussion**

The sedimentological studies and the paleontological analyses on molluscs (Basilici, 1995; 1997; Ambrosetti et al., 1995b; Abbazzi et al., 1997) had already given a solid framework of the palaeoenvironments represented in the South Tiberino Basin. In summary, during Piacenzian–Gelasian the Tiberino Basin hosted the Palaeolake Tiberino, which occupied a minimum surface of 500 km<sup>2</sup> and was at least 50 m deep (Basilici, 1997). Based on the magnetostratigraphical studies (Abbazzi et al., 1997) and the calculated mean sedimentation rate, the lake persisted undisturbed for at least 1.8 Ma (Medici & Gliozzi, 2008).

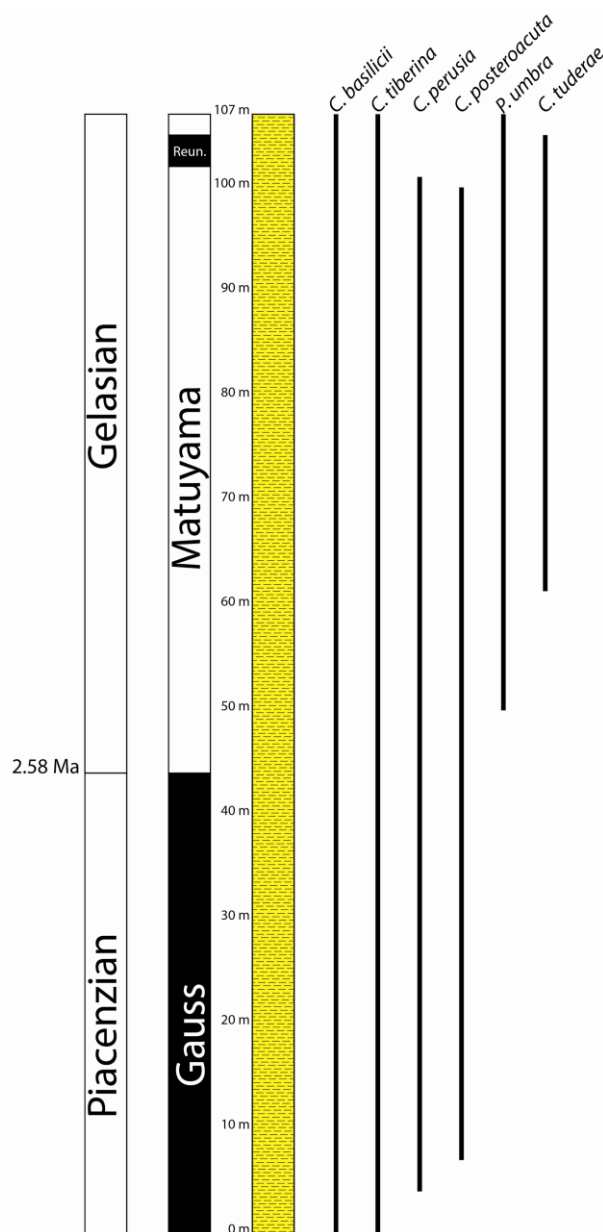
### **2.4.1 The Paleolake Tiberino and the *Caspiocypris* species flock from deep lacustrine facies**

Based on the inferred ages and the fossil ostracods recovered from the Fosso Bianco and Cava Toppetti I sections, Medici and Gliozzi (2008) supposed that the Palaeolake Tiberino could be considered a palaeo ancient-lake. The term “Ancient lake” indicates a lake that persisted for more than one Ma, which contains floras and faunas characterized by a high degree of endemism and raised diversity. Ancient lakes are extraordinary test sites for researchers concerning evolutionary processes because of their long life and high levels of endemism (Gortner, 1994). They are stable, large and deep lakes, whose evolution in time led to isolation of the aquatic fauna. This factor, and the limited number of lineages that successfully entered their waters, gave rise to some of the most remarkable cases of adaptive radiation and local endemism, hosting impressive endemic lineages of fishes and invertebrates, including gastropods, ostracods and amphipods (Martens, 1997; Albrecht et al., 2006). Non-marine ostracods are one of several crustacean groups that gave origin to endemic species flocks in ancient lakes (Martens 1994; Schön & Martens 2012). Ostracod assemblages recorded in the ancient lakes are made mainly by Limnocytheridae and Candonidae, with rare Cyprididae, or only by Candonidae and Cytherideinae. Most of them have been studied in living faunas of existing lakes, e.g. *Cyprideis* species flock in Lake Tanganyika (Wouters & Martens, 2001) and *Baicalocandona* and *Cytherissa* flocks in Lake Baikal (Mazepova, 1990). Conversely, very few data related to the

ancient palaeolakes and their endemic species flocks are known. Janz (2000) was the first to apply the concept of species flock to the fossil *Leucocythere* lineage recovered in the middle Miocene of the ancient Palaeolake Steinheim (Germany), although the mainly anagenetic evolution of this lineage resulted in a low number of species. According to Pipik et al. (2012), also the Palaeolake Turiec (Slovakia) can be envisaged as an ancient palaeolake due to the high number of Candoninae species and long resilience time. Medici & Gliozzi (2008) recognized the ancient lake nature of the Plio–Pleistocene Palaeolake Tiberino (central Apennine, Italy) and gave a preliminary report of its endemic ostracod fauna. This paragraph deals with the taxonomic composition of the Piacenzian–Gelasian ostracod assemblages of the deep facies of the ancient Palaeolake Tiberino.

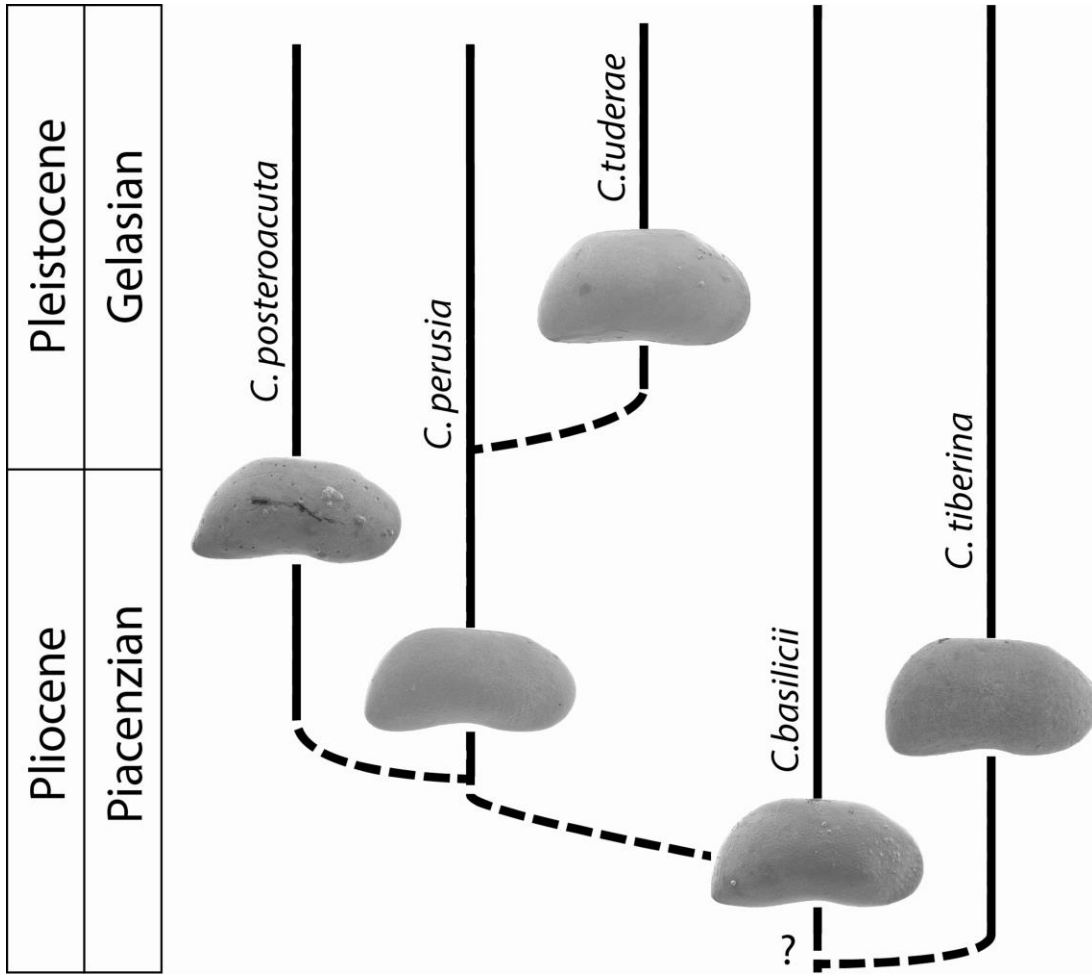
The peculiar composition of the endemic mollusc (Ciangherotti et al., 1998) and ostracod associations of the Cava Toppetti I and Fosso Bianco sections, characterized only by new species referable to families Candonidae and Limnocytheridae, indicates that the Palaeolake Tiberino was an isolated environment in which endemic speciation was enhanced. Moreover, the distribution of ostracods along the sampled sections is remarkable, especially in the Cava Toppetti I section. In this section, very few species are distributed in the lower samples (two to four species) and the number increases towards the top until sample CT 100 m (six species) (Fig. 2.28).

The autochthonous ostracod assemblages recovered from the Cava Toppetti I and Fosso Bianco sections include 5 endemic species of *Caspiocypris* (*Caspiocypris basilicii*, *Caspiocypris perusia*,



**Figure 2.28:** Fosso Bianco Formation ostracod species distribution along the CT section (magnetostratigraphy from Abbazzi et al., 1997).

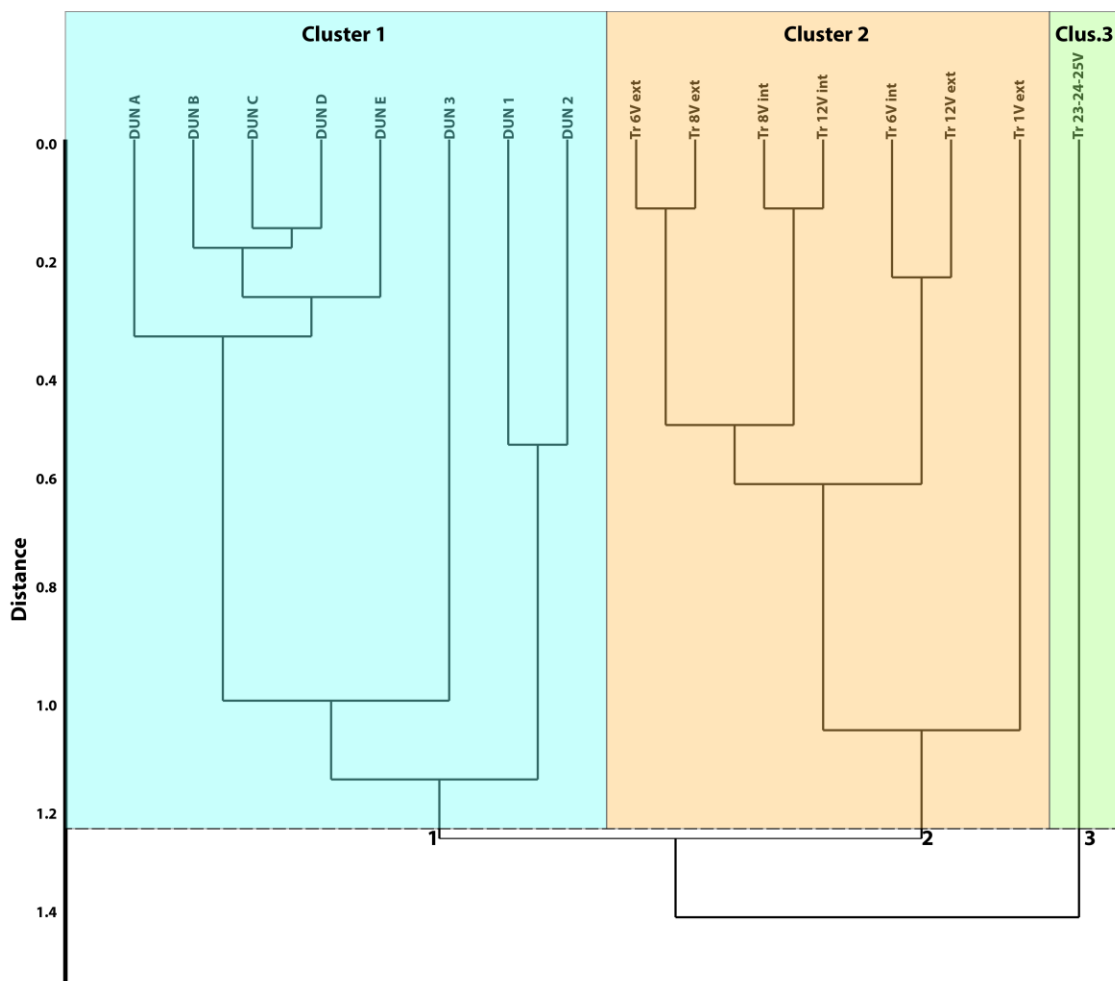
*Caspiocypris posteroacuta*, *Caspiocypris tiberina*, *Caspiocypris tuderis*) and one endemic species of *Paralimnocythere* (*Paralimnocythere umbra*). All the *Caspiocypris* represent a species flock. Greenwood (1984) defined a species flock on the following criteria: speciosity, monophyly and endemism. It is clear from our data that the *Caspiocypris* radiation in Palaeolake Tiberino is a species-poor radiation. However, even a group of only three to four species may qualify as a species flock (Schön & Martens, 2004). *Caspiocypris* in Palaeolake Tiberino show a high degree of speciosity (i.e. a disproportionate abundance of closely related species within a geographically circumscribed area according to Ribbink, 1984), with five new species. Monophyly is very subjective and hard to test for a fossil assemblage, but in this case, the comparisons of the outlines showed that the *Caspiocypris* species from Palaeolake Tiberino are more similar each other than to other known *Caspiocypris* species, even from the geographically nearest *Caspiocypris* species from the Palaeolake San Nicandro (L'Aquila Basin, see chapter 3). This last assemblage, composed by four endemic *Caspiocypris* species, is similar but definitively different and linked to another species flock (Spadi et al., 2016). Other species referable to *Caspiocypris*, recovered in the Piacenzian–Gelasian interval, are geographically confined in the Ponto-Caspian area. The endemism criterion is met by the *Caspiocypris* species of Palaeolake Tiberino: the five taxa are probably monophyletic and do not occur outside the lake. We therefore consider the endemic species of Palaeolake Tiberino as representing an ancient lake species flock originated from the local speciation of one pioneer species, and suggest a tentative phylogenetic reconstruction. The pioneer species could have been *C. basilicii*, which presents intermediate size and an elongated but rounded outline of left and right valves. Furthermore, *C. basilicii* occurs at the very base of the Cava Toppetti I section (Fig. 2.28). *Caspiocypris perusia* and *C. posteroacuta* are most likely closely related to each other, showing a similar posteriorly pointed outline, with the right valve poorly distinguishable. These two species are characterized by different shapes of the posteroventral angle in comparison with the ancestor. The most different species of the flock is *C. tiberina*, but also in this case its origin from *C. basilicii* can be envisaged through a proportional height increase and more rounded anterior margin. It is hard to insert *C. tuderis* into this scheme, for its record is represented only by right valves. However, from the comparisons that have been made, it seems strictly related to *C. perusia* sp. On the basis of the occurrence of the species along the section and the described morphological similarities, we have hypothesized the phylogenetic reconstruction shown in Figure 2.29 (Spadi et al., 2017).



**Figure 2.29:** Tentative phylogenetic relations within the *Caspiocypris* species flock of the Palaeolake Tiberino.

### 2.4.2 The Palaeolake Tiberino margins

As stated before, the marginal lacustrine facies of the Palaeolake Tiberino (facies C) crops out in the area of the Dunarobba Fossil Forest (Basilici, 1997). The Dunarobba palaeofloras are made of typical species of warm and humid temperate palaeoclimate, with average annual temperature around 13-14 °C and average annual rainfall in the range 1000-3000 mm (Martinetto et al., 2014). The floristic association is made of species that, in northern Italy, seems to be limited to the Zanclean or Zanclean-Piacenzian (Martinetto et al., 2017). Since, according to Bizzarri et al. (2011), the Dunarobba Fossil Forest succession should be referred to Gelasian, probably during this period the central Apennines basins acted as refugia area for the mesothermic floras (Martinetto et al., 2017). The frequency matrix of the recovered ostracods were analysed through the cluster analysis (Fig. 2.30), in order to distinguish different assemblages. Three main clusters, eventually further subdivided in sub-clusters, were obtained.

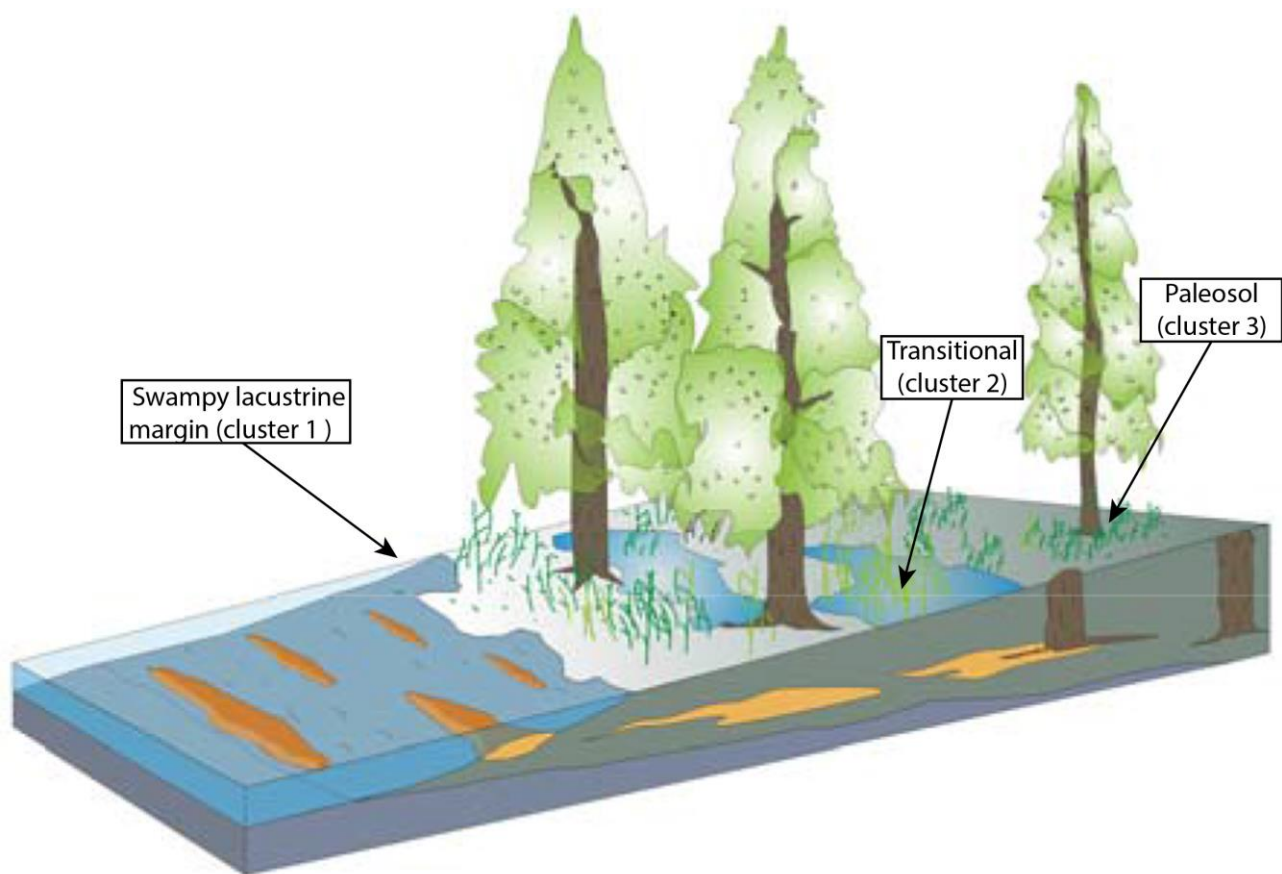


**Figure 2.30:** Cluster analysis (Chord) interpreted with division of Clusters and sub-clusters see the text for the explanation.

**Cluster 1** includes samples collected in the Dunarobba Fossil Forest site. The presence of *Cyprideis* and *Darwinula*, typical of permanent water bodies (Meisch, 2000) indicates a very shallow lacustrine environment whereas the abundance of *Ilyocypris* point to possible slow waterbody motions. According to Ciangherotti et al., (1998), these samples are characterised by freshwater Prosobranchia-dominated associations. The well diversified ostracod and mollusc assemblages indicate shallow oxygenated waters rich in nutrients and the existence of different ecological micro niches that well match the palaeoenvironmental interpretation suggested by the sedimentological analyses, i.e., a swampy lacustrine margin characterised by weak wave movements. (Fig. 2.31). Although the ostracod assemblage composition of cluster 1 mirrors the palaeoenvironmental, interpretation suggested by other paleontological and sedimentological data, sample DUN 3 displays a taxonomic composition very different from the other shallow water samples of the Palaeolake Tiberino. Indeed its stratigraphic position in relations with the other samples is doubtful.

**Cluster 2** groups samples collected inside and immediately close to the trunks Tr 1 V, Tr 6 V, Tr 8 V, and Tr 12 V. The ostracod assemblages are made by several species that can withstand permanent/temporary very shallow environments (*C. neglecta*, *C. kingsleii*, *C. ovum*) and by *C. improvisa*, typical of temporary waters (Meisch, 2000; Benvenuti et al., 2017) whereas molluscs are mainly represented by aquatic and terrestrial pulmonate gastropods. The assemblages of cluster 2 indicate a wetland area onshore the lake margin, only seldom occupied by small water bodies, supporting the sedimentological interpretation of a transitional environment between hydromorphic paleosols and swampy lacustrine clays deposited in ephemeral ponds (Basilici, 1992).

**Cluster 3** includes only one sample with the single species *Potamocypris pallida*, According to Basilici (1992), the sediments correspond to a hydromorphic palaeosol. This sedimentological interpretation could fit with the presence of *P. pallida*, a species often found in interstitial habitats (Meisch, 2000).



**Figure 2.31:** Reconstruction of the sedimentary context and plant cover at the ancient lacustrine margin of Dunarobba Fossil Forest, and the indication of various groups of ostracods associations. Modified from Martinetto et al., 2014.

### 2.4.3 Palaeoenvironment of Ponte Naja Fm. deposition

According to Abbazzi et al. (1997) and Martinetto et al. (2014) the sedimentological features of the PNF suggest the deposition in the distal portion of an alluvial fan. The entire CT II sequence (~150 m) deposited in a short time interval between 2.1 and 1.9 Ma with a high sedimentation rate (1.3 mm/y), based on mammal remains and the grade of evolution of the palaeosols (Basilici, 1995). Palaeoecological data on ostracods and molluscs suggest that PNF deposited during a mild climate interval in very shallow temporary water-bodies seldom fed by springs, characterized by slow flowing waters possibly associated with the seasonal overflow of adjacent streams or by humid emerged areas, as testified by the abundance of pulmonate gastropods with terrestrial way of life (Ciangherotti et al., 1998) and the mixed ostracod assemblages made of rare autochthonous ostracods and displaced species transported from the surroundings. The presence in the PNF of *C. rectangularis* confirms that this species colonized the margins of the Palaeolake Tiberino as testified in the Dunarobba Fossil Forest.

## 3 L'Aquila Basin

### 3.1 Geological Setting

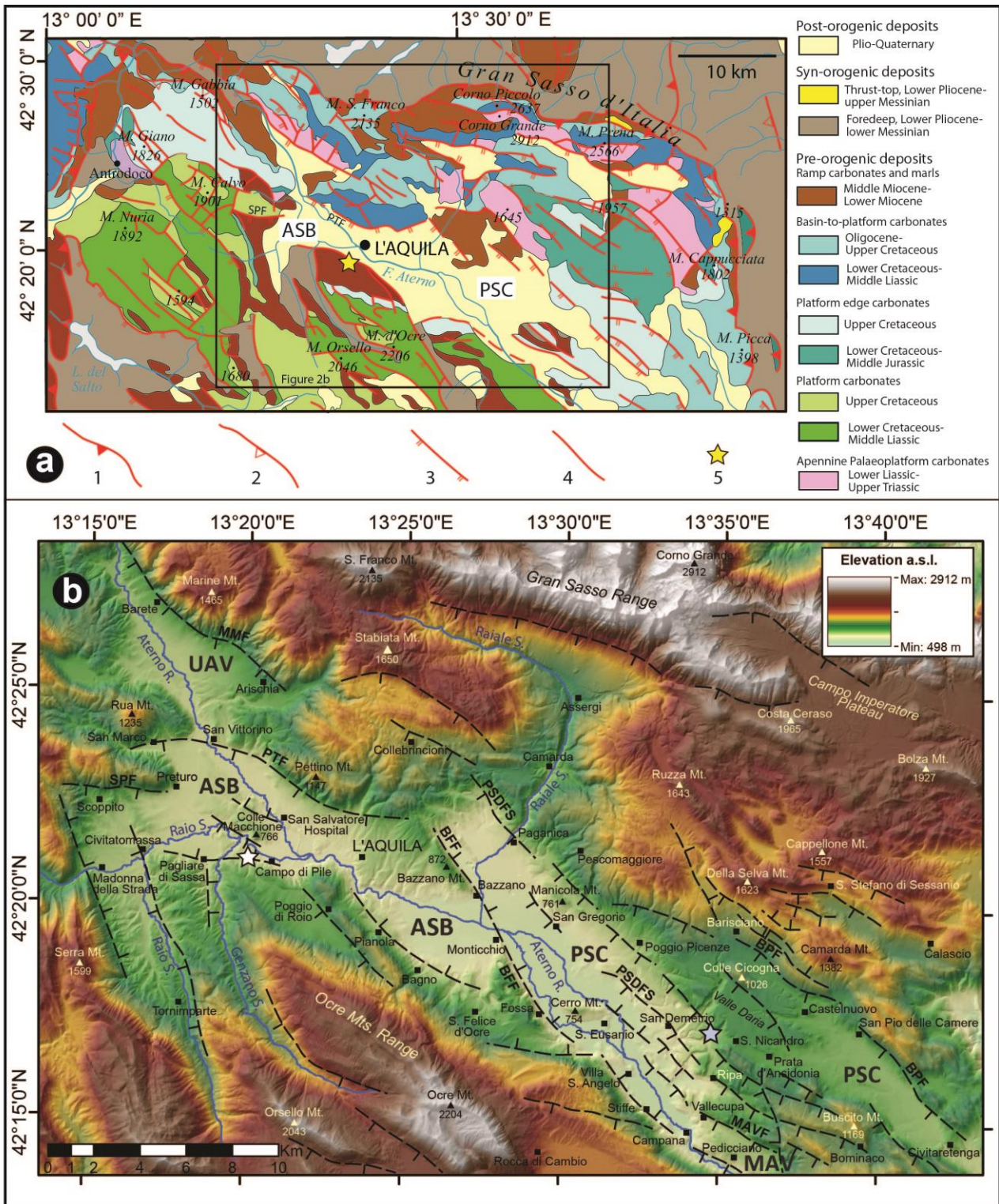
L'Aquila Basin is one of the widest and well developed central Apennines intermontane basin, characterized by high seismicity as evidenced by the 2009 6.1 Mw earthquake occurred at L'Aquila (Scognamiglio et al., 2010). L'Aquila Basin is a semi-enclosed intermontane sedimentary basin originated by the all-pervading extensional deformation that affected the Apennines since Late Pliocene-Early Pleistocene (Messina et al., 2001; Centamore & Dramis, 2010; Mancini et al., 2012; Tallini et al., 2012). The shape and extension of the L'Aquila Basin are the expression of the activity of the south-westward dipping normal fault systems that bound the northeastern slopes of the basin. These faults are composed by several dextrally-stepping en-echelon segments, generally less than 5 km long and NW-SE to W-E oriented, cutting both the Meso-Cenozoic bedrock and the Quaternary deposits. They are responsible of the asymmetric half graben geometry of the L'Aquila Basin and are associated to several antithetic north-eastward dipping faults on the southern margin of the basin and to NNW-SSE transfer fault inside it (Falcucci et al., 2011; Nocentini et al., 2017, submitted).

L'Aquila Basin is divided by the Bazzano-Monticchio ridge and the L'Aquila hill into two major sub-basin: the L'Aquila-Scoppito basin (ASB), to the west, and the Paganica-S. Demetrio-Castelnuovo basin (PSC), to the east (Bosi et al., 2003; Mancini et al., 2012; Giaccio et al., 2012) (Fig. 3.1 A). Both of them are filled by a thick sequence of Plio-Quaternary continental deposits, which unconformably overlay the Meso-Cenozoic bedrock, composed by a succession of platform and slope limestone stacked with Miocene turbidites during the Apennine orogeny in Mio-Pliocene times (Cipollari et al., 1999; Cosentino et al., 2010).

The ASB extends from the San Vittorino threshold, to the N, up to the Bazzano-Monticchio Fault, to the S. It is a half-graben delimited to the north by both the S dipping Scoppito-Preturo and the SW dipping Pettino active faults (Fig. 3.1 B). The ASB is filled by a thick succession of Plio-Quaternary continental deposits, which unconformably overlay the Meso-Cenozoic carbonate units and the Upper Miocene terrigenous units (Cosentino et al., 2017; Nocentini et al., 2017).

The PSC represents the eastern portion of the intermontane L'Aquila Basin, located in the central Apennines along the Aterno River Valley between the Gran Sasso Range, to the north, and the Ocre Mts., to the south. PSC extends over more than 130 km<sup>2</sup>, from the Paganica village, to the north, to the Campana gorge, to the south (Fig. 3.1 B) (Giaccio et al., 2012).





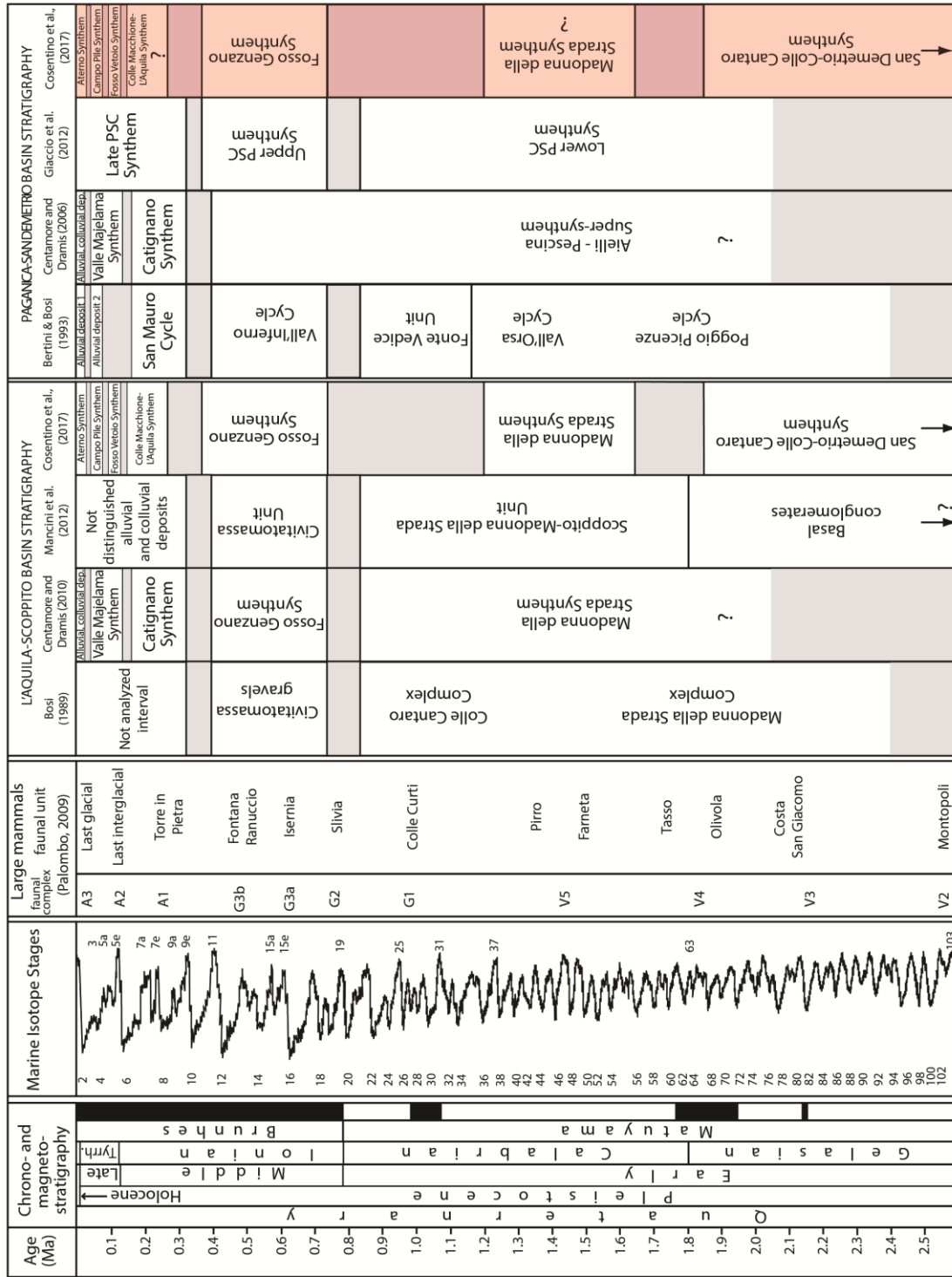
**Figure 3.1:** a) Geological sketch-map of L'Aquila intermontane basin and surrounding regions. 1) major thrust; 2) minor thrust; 3) normal fault; 4) undifferentiated fault; 5) epicenter of the April 6<sup>th</sup> 2009, Mw 6.1 earthquake b) Topography of L'Aquila intermontane basin and surrounding regions. UAV=Upper Aterno Valley; ASB=L'Aquila-Scoppito Basin; PSC=Paganica-San Demetrio-Castelnuovo Basin; MAV=Middle Aterno Valley; MMF=Mt. Marine fault; SPF=Scoppito-Preturo fault; PTF=Pettino fault; BFF=Bazzano-Fossa fault; PSDFS=Paganica-San Demetrio fault system; BPF=Barisciano-San Pio fault; MAVF=Middle Aterno Valley fault system. White star is the location of BAR 20 section (Fig. 4.16). Grey star is the location of San Nicandro section (Fig. 3.22). Modified from Nocentini (2016).

PSC is a NW-SE trending Plio-Quaternary graben characterized by a rectilinear south-western border and a more articulated north-eastern one, expression of the main boundary normal faults. The basin infill is composed by Plio-Quaternary continental deposits, unconformably overlaying the pre- and syn-orogenic bedrock composed by Meso-Cenozoic platform to slope and ramp carbonate successions and Miocene terrigenous turbidites (Cosentino et al., 2010). Many Authors (Bertini & Bosi, 1993; Bosi, 1989; Centamore et al., 2006; Galli et al., 2010; Giaccio et al., 2012; Pucci et al., 2015) suggested different evolutionary schemes for the PSC, resulting in the existence of different stratigraphic settings summarized in Fig. 3.2.

Comprehensive geological field surveys, coupled with new palaeontological data included in this thesis, as well as facies analyses, well logs, and geophysical data interpretation, allowed us to fine-tune and review the PSC stratigraphy. This multidisciplinary approach, showing new stratigraphical and palaeontological data essential to understand the early evolutionary stage of the PSC, brought to the identification of eight synthem dated from late Piacenzian to Holocene (Nocentini et al., submitted) (see the last column of Fig. 3.2). For the purposes of this thesis, only the most ancient synthem, the San Demetrio-Colle Cantaro Synthem is hereinafter described in detail (Fig. 3.3).

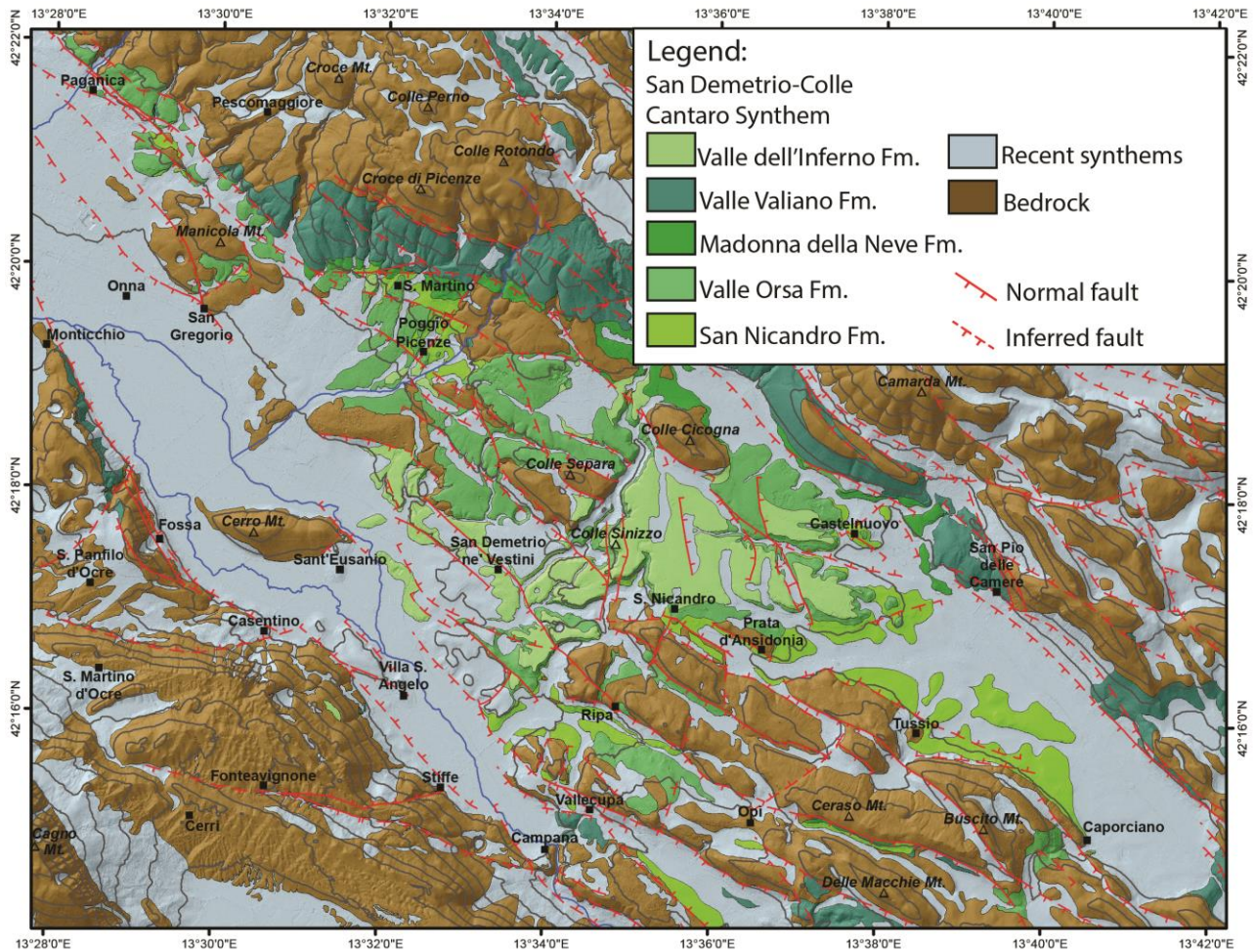
### **San Demetrio-Colle Cantaro Synthem**

The first depositional phase within the PSC correspond to the formation of the San Demetrio-Colle Cantaro Synthem, largely fitting with the Lower PSC Synthem of Giaccio et al. (2012), from which it differs for the age attribution and some stratigraphic interpretations. This synthem is well preserved in the SE sector of the PSC, between San Demetrio and Castelnuovo villages. It is also discontinuously present in the northern and western sector of the basin and in the boreholes (Nocentini et al., submitted). Due to the presence of a minor unconformity in the upper part of the synthem, it is split into two sub-synthem: the Castelnuovo sub-synthem, including several formations deposited in different environments of a lacustrine system, and the Valle dell'Inferno sub-synthem, related to a fluvial environment. The whole San Demetrio-Colle Cantaro Synthem is cut by a flat surface lying at 850 m a.s.l., the Valle Daria surface, partly representing the depositional top of the fluvial system and locally connected to some erosional surfaces carved into the Meso-Cenozoic bedrock (Bertini & Bosi, 1993).



**Figure 3.2:** Quaternary stratigraphy of the L'Aquila Basin according to different authors. Centamore and Dramis (2010) consider the *Colle Cantaro-Cave Synthem*, at the base of the ASB fill, as lower Villafranchian (Piacenzian), not represented in the figure. The arrow in Mancini et al. (2012) and in Cosentino et al., 2017 indicate a possible (?) or a real extension to the Piacenzian of the AB basal deposits.





**Figure 3.3:** Simplified geological map of the Paganica-San Demetrio-Castelnuovo (PSC) basin focus on San Demetrio-Colle Cantaro Synthem, modified from Nocentini et al., submitted.

### *Castelnuovo sub-synthem*

The Castelnuovo sub-synthem unconformably overlays the Meso-Cenozoic bedrock; its upper boundary, with the Valle dell'Inferno sub-synthem, is represented by a discontinuous erosional surface carved mainly into the Valle Orsa Fm.

The oldest deposits of the Castelnuovo sub-synthem can be ascribed to the San Nicandro Fm., which consists of whitish and greyish laminated or massive calcareous silts grading upward to white sandy-silts (Fig. 3.4) (Bosi & Bertini, 1970). The calcareous silts are arranged in massive structures or in laminated parallel layers with some millimetre-thick reddish sandy layers. The outcropping thickness of the San Nicandro Fm. is around 50 m but the San Nicandro calcareous silts were found also at the bottom of two boreholes (S72 and S106), laying above the bedrock (Nocentini et al., submitted). Using boreholes data and geophysical methods the real thickness of the San Nicandro Fm. has been estimated around 100 m (Boncio et al., 2010; Nocentini et al., submitted). In the upper part of the San Nicandro Fm. dark tephra layers 1 to 10 cm-thick, with a fining upwards grain size

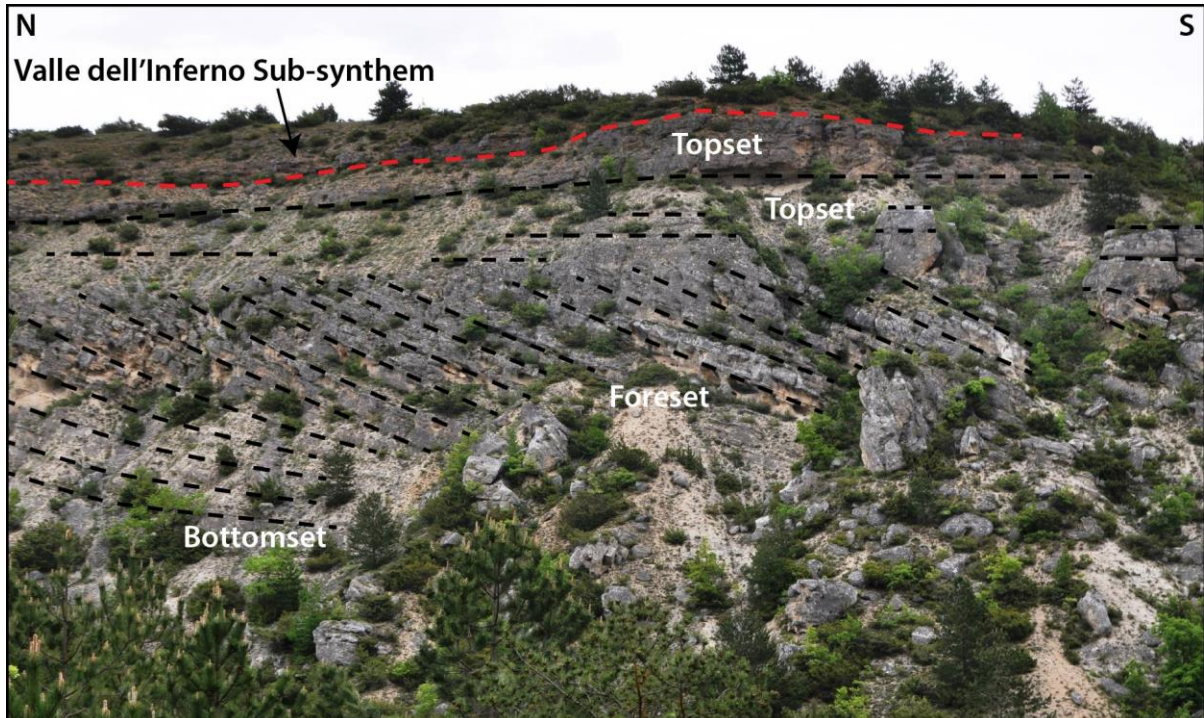
are present (Fig.3.4 d). The analysis of the tephra layer are still in progress, one sample (CAV 3) was send to Berkeley Geochronology Centre (BGC) for the  $^{40}\text{Ar}/^{39}\text{Ar}$  dating, while two samples (2.17 and CAV 3) were analyzed with isotopes of Nb/Sr in the University of Firenze that results that the tephra is not correspondent with any Neogene and Quaternary Italian volcanisms. This data extend the mineralogical analysis that excluded an origin from the Middle-Upper Pleistocene Roman Comagmatic Province (Giaccio et al., 2012). The San Nicandro Fm. represents the distal deposition of a large intermontane lake settled in the depocentral area of the PSC (the Palaeolake San Nicandro), as evidenced by the presence of freshwater ostracods, sponge spicules, and gastropods (Spadi et al., 2016).



**Figure 3.4:** San Nicandro Fm. at Castelnuovo village. **a:** rhythmic alternation of whitish calcareous silts and reddish and blackish clayey-silts and silty sand of the San Nicandro Fm.; **b** and **c:** mainly NW-SE oriented normal faults; **d:** blackish tephra horizon; the black square refers to a detail of the tephra reported in **e**. Pictures **a** and **d** by courtesy of Federica Durante and Giorgio Pipponzi.



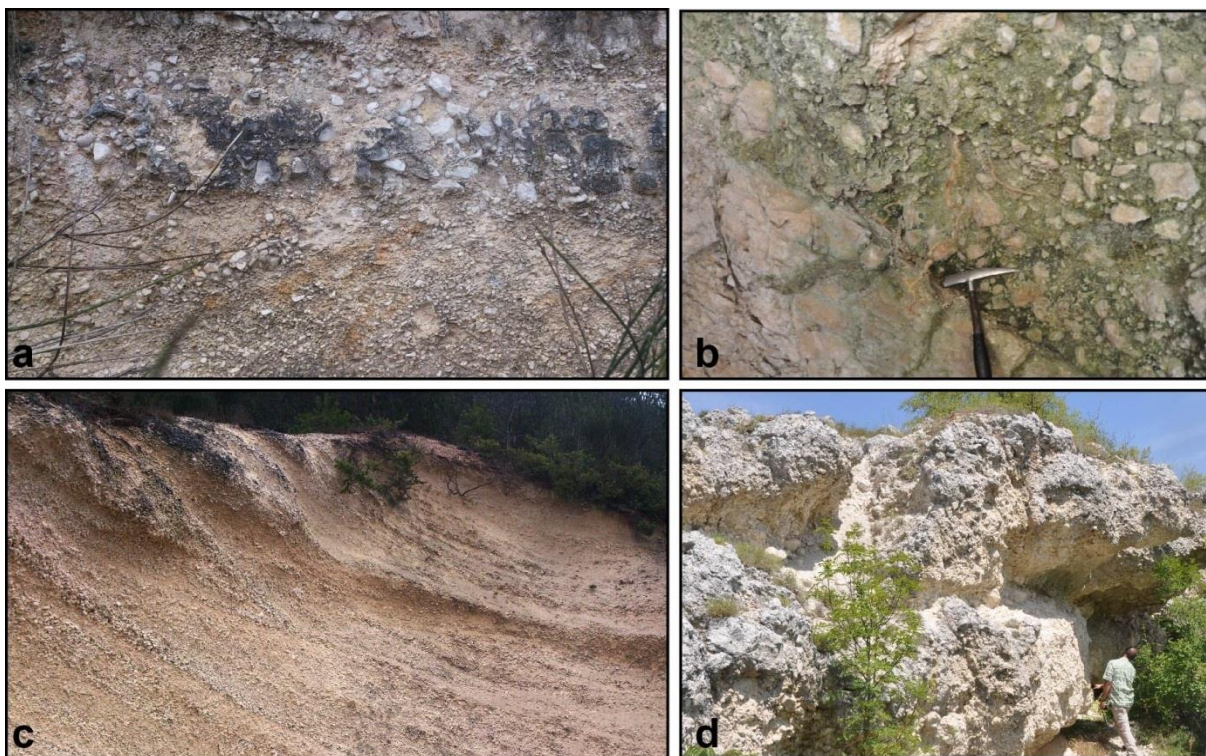
The lacustrine sediments of the San Nicandro Fm. are partially heteropic or overlain by the coarse-grained deposits related to a Gilbert-type delta system that correspond to the Valle Orsa Fm. This formation is characterized by lithological and sedimentological vertical and lateral variations, reflecting different depositional environment within the delta system, resulting in the formation of bottomset, foreset, and topset beds (Fig. 3.5). The bottomset beds are composed by meter-thick layers of yellowish fine-medium sands and silty sands, with horizontal lamination, deposited by high-energy bottom currents. The foreset beds, arranged to form the delta slope, are composed by 1 m-thick beds of well-sorted and well-rounded polygenic calcareous gravels and conglomerates, dipping ( $20^{\circ} \sim 30^{\circ}$ ). They are generally clast-supported, with a coarse sandy matrix; rare thin whitish calcareous silt layers are also present between the gravel beds. The foreset beds generally dip toward S-SE, downlapping on the bottomset and/or the lacustrine deposits, indicating a progradation of the Gilbert-type delta into the lake from N or NW (Giaccio et al., 2012). The topset beds are made of well-rounded, poorly sorted polygenic calcareous coarse gravels and conglomerates in a sandy silty matrix, characterised by sub-horizontal layers, from 0.5 m up to several meters-thick, with massive or rarely planar cross-stratified bedding.



**Figure 3.5:** Panoramic view of the Gilbert-type delta system (Valle Orsa Fm.) along the Inferno Valley.

Towards the NE slopes of the PSC, the San Nicandro Fm. and Valle Orsa Fm. are laterally interfingered with coarser sediments, belonging to the Madonna della Neve Fm. and Valle Valiano Fm. (Nocentini et al., submitted).

The Valle Valiano Fm. can be documented along all the margins of the PSC basin, between the substratum and the other formations of the Castelnuovo sub-synthem. Planar cross-bedded and alluvial fan conglomerates are generally recognized into this formation, rarely sands and silty sand layers and calcareous breccias with calcareous silty matrix are recovered (Fig. 3.6). For its compositions and dipping, the Valle Valiano Fm. could represent the marginal deposits related to the coastlines of the Palaeolake San Nicandro.



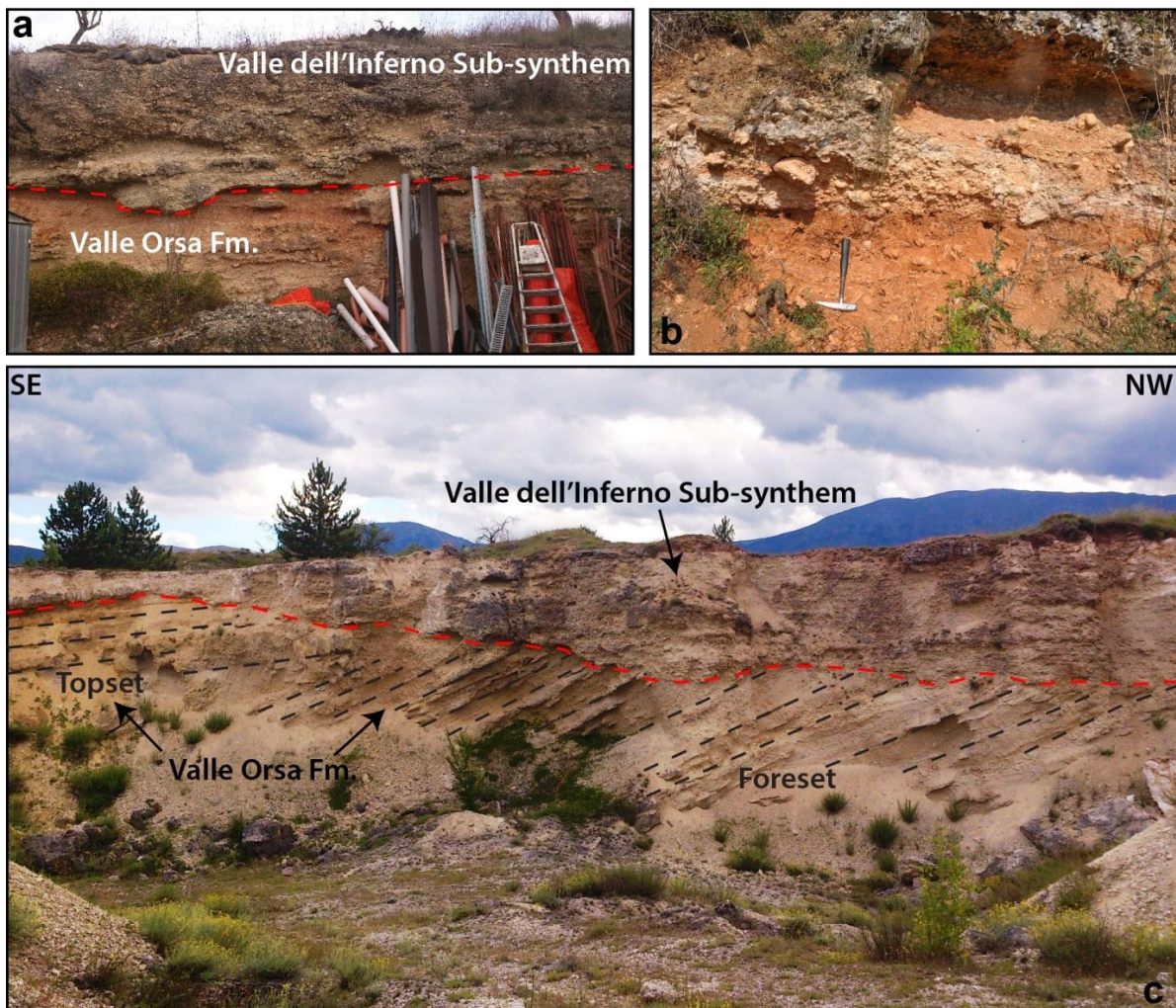
**Figure 3.6:** Lithofacies of the Valle Valiano Fm. **a:** Well-sorted matrix-supported breccias; **b:** Detail of the unconformity between bedrock limestone and breccias. Black bar is 20 cm. **c:** Trough cross-bedded proximal alluvial fan conglomerates; **d:** Thick beds of poorly-sorted gravels and breccias. Black bar is 1 m.

The Madonna della Neve Fm. extensively crops out at the base of the slopes with thicknesses up to 10 m, and is made of an alternation of whitish calcareous lacustrine silt layers, similar to those of the San Nicandro Fm., and angular to sub-angular calcareous breccias with massive beds up to 1 m-thick. Probably, this alternation characterises the interface between the lacustrine lateral deposition and the debris flow and/or slope-related lacustrine sedimentary process.



### *Valle dell'Inferno sub-synthem*

In the eastern sectors of the PSC, the topset and foreset beds of the Valle Orsa Fm. are eroded and unconformably overlain by the Valle dell'Inferno sub-synthem, represented by the Valle dell'Inferno Fm. The Valle dell'Inferno Fm. is composed by sub-horizontal beds made of well-rounded, clast-supported conglomerates, with coarse to medium calcareous pebbles in a sandy matrix. Beds are 0.5 m up to 5 m-thick and are characterised by trough and planar cross-bedding. Often, pink massive calcareous silty levels are preserved at the top of the channel. The Valle dell'Inferno Fm. belongs to a gravel-bed braided fluvial system developed, after a local erosive phase, above the Castelnuovo sub-synthem, as testified by the basal unconformity of the Valle dell'Inferno sub-synthem, marked by the partial erosion of the previous deposits and/or the occasional presence of a palaeosol (Fig. 3.7) (Nocentini et al., submitted).



**Figure 3.7:** Valle dell'Inferno sub-synthem. **a:** Unconformity between the topset of the Valle Orsa Fm., showing incipient pedogenesis, and the planar cross-bedded conglomerates of the Valle dell'Inferno sub-synthem; **b:** Detail of the palaeosol at the base of the Valle dell'Inferno sub-synthem; **c:** Angular unconformity of the Valle dell'Inferno sub-synthem carved into both foreset and topset of the Valle Orsa Fm. The flat top is the Valle Daria surface (855 m a.s.l.).



A maximum age for the onset of the L'Aquila Basin derives from the latest compressional event that affected the area. The orogenic tectonics was responsible for the deformation of the Mesozoic and Tertiary successions as well as for the onset of intermontane compressional basins (thrust-top or piggy-back basins) developed on top of the highly deformed Gran Sasso tectonic wedge. This compression phase is constrained by the occurrence of a thrust-top basin (Conglomerati di Rigopiano) containing planktonic assemblages up to the *G. puncticulata* biozone (Patacca et al., 1992; Ghisetti et al., 1993; Centamore et al., 2006). According to these data, the maximum age for the onset of the extensional tectonics in the Gran Sasso-L'Aquila area is the Zanclean/Piacenzian transition (ca. 3.59 Ma).

For the deposition of San Demetrio-Colle Cantaro Synthem, the ostracod assemblages found in the San Nicandro Fm., characterised by the presence of *Caspiocypris* spp. (Spadi et al., 2016) could possibly be correlated with the ostracod fauna dominated by the *Caspiocypris* species flock of the Fosso Bianco Fm. of the Tiberino Basin (see Chapter 2) (Spadi et al., 2017). Based on this correlation, the first phase of the basin filling in the L'Aquila Basin occurred during the late Piacenzian–Gelasian interval.

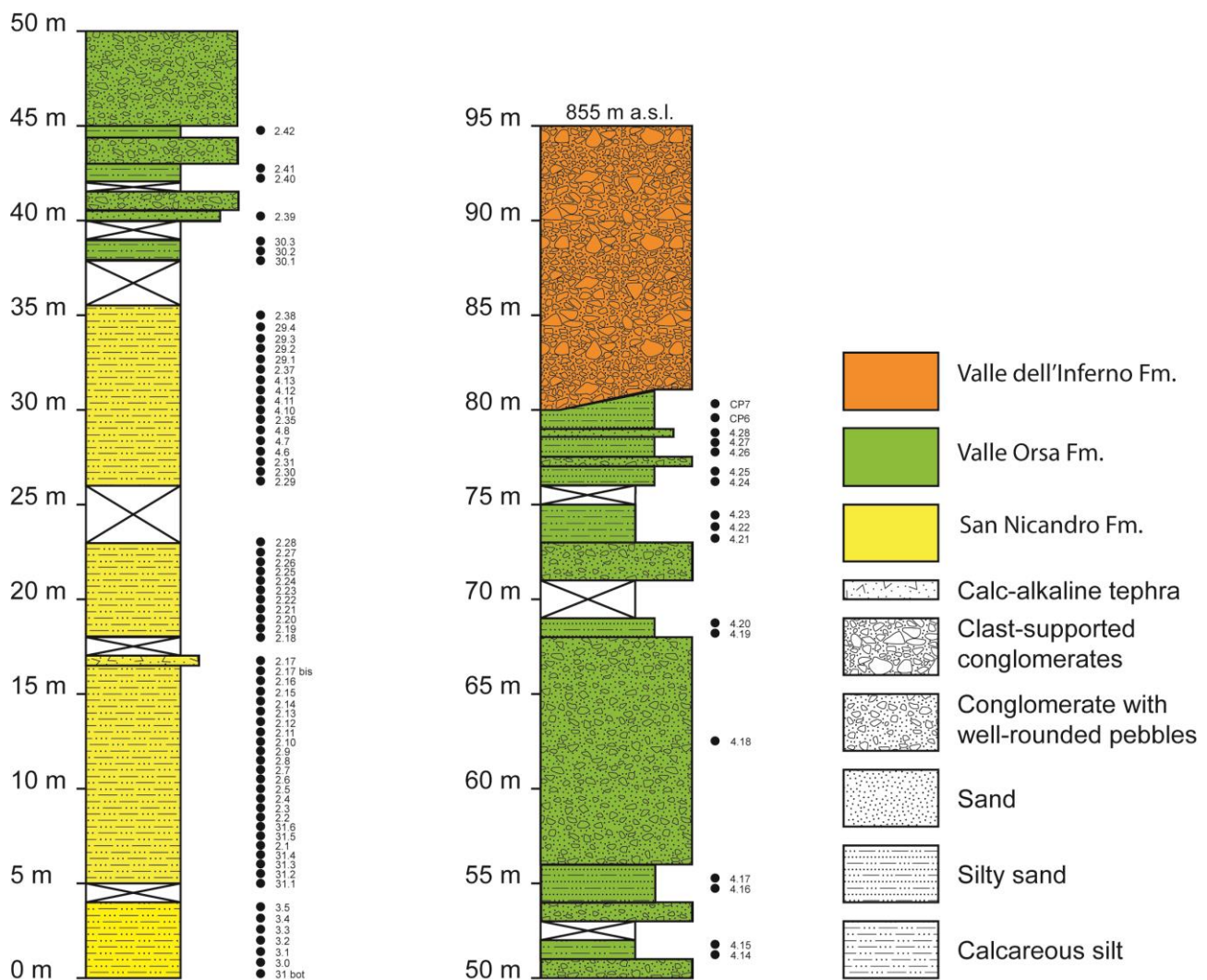
### 3.2 Materials and Methods

Extensive field surveys for the Plio-Quaternary continental deposits were carried out. Field investigations were useful for the description of the sedimentary units, synthems and their stratigraphical relationships. It also allowed to realize some stratigraphic sections. Field works were integrated with the palaeontological analysis (freshwater sponges, molluscs, and ostracods) carried out on samples belonging to both outcropping and subsurface sedimentary successions, to provide information about the depositional environment, age, and to correlate the Plio-Quaternary deposits throughout the basin. The stratigraphic sections were sampled within the finest materials every 50 cm. The different sections were correlated based on their outcrop elevation and taking into account the local tectonics, to create a composite section, which represents the sediments deposited in the depocentre of the PSC basin (Fig. 3.8).

A total of 84 sediment samples for palaeontological analysis from the San Demetrio-Colle Cantaro Synthem outcrops were processed. Each sample was soaked in a H<sub>2</sub>O<sub>2</sub> 5% solution for 24–72 hours, sieved with a 0.125 mm-mesh sieve and dried. Ostracods were handpicked under stereomicroscope up to 300 valves/samples and identified using the Leica DM1000 microscope. In addition, adult ostracod valves were observed using the Scanning Electron Microscope (SEM) in the LIME laboratory of Roma TRE University. Ostracods valve were identified using Meish, 2000;

Fuhrman, 2012 and Krstić, 2006. All specimens were deposited in the Gliozzi Ostracod Collection (GOC) at the Department of Science, Roma Tre University, Rome, Italy.

Each species frequency was counted and a frequency matrix normalized to 10g of dried sieved sample was calculated. This matrix constituted the basis for the application of constrained Cluster Analysis (Chord distance measures and the un-weighted pair group method using arithmetic average - UPGMA) in order to estimate the assemblage similarities and proceed with the palaeoenvironmental interpretation.



**Figure 3.8:** Composite section with indication of lithology and collected samples.

The taxonomical study was partly based on the geometric morphometric approach to evaluate the valve outline. To apply the geometric morphometric analysis, images of adult valves were processed using tps-Dig software, version 1.37 (Rohlf, 2009), which digitizes the specimen outlines. The geometric morphometric analysis of the valve outline was performed with the software

MORPHOMATICA, version 1.6.01 (Brauneis et al. 2008), which uses the B-splines approach adapted for ostracods by J. Linhart (Baltanas et al. 2003; Brauneis et al. 2008; Neubauer & Linhart 2008). The results were processed using multivariate numerical techniques: cluster analysis (Euclidean distance measure and the unweight pair group method using arithmetic average - UPGMA), non-metric multidimensional scaling (nMDS), and the analysis of similarities (one-way ANOSIM pairwise tests). For the multivariate statistics, the software package PRIMER 6 (Clarke & Gorley 2006) was used.

### 3.3 Systematic palaeontology

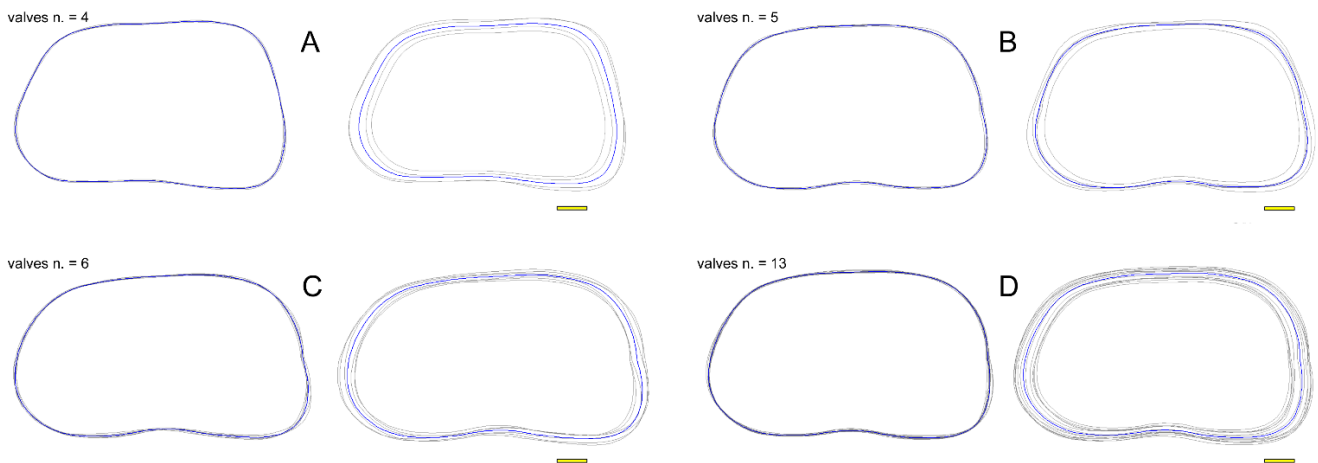
We followed the suprageneric classification of Meisch (2000) and Horne et al. (2002). The synonymy reported for the well known and largely widespread species includes only the quotations of the original description and the Italian Pliocene-Early Pleistocene recoveries, whereas for the less known species a throughout list is given.

Abbreviations: **L**, length; **H**, height; **LV**, left valve; **RV**, right valve; **C**, carapace.

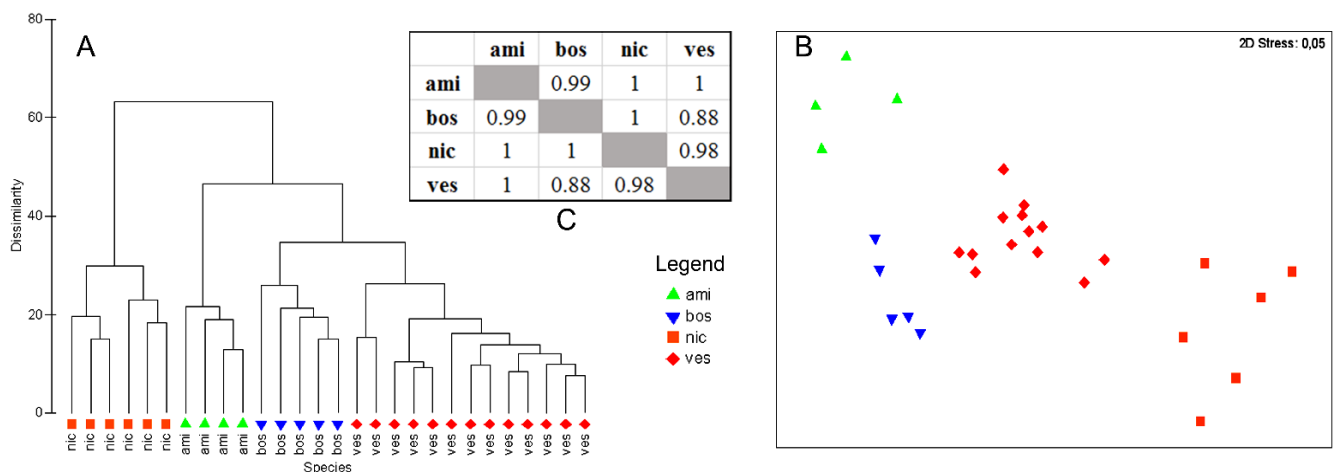
Class **Ostracoda** Latreille, 1802  
Subclass **Podocopa** Sars, 1866  
Order **Podocopida** Sars, 1866  
Suborder **Cypridocopina** Jones, 1901  
Superfamily **Cypridoidea** Bard, 1845  
Family **Candonidae** Kaufmann, 1900  
Subfamily **Candoninae** Kaufmann, 1900  
Genus **Caspiocypris** Mandelstam, 1956

**Morphometrics.** The left and right valve outlines of both male and female *Caspiocypris* specimens recovered in the San Demetrio-Colle Cantaro Synthem were analysed using geometric morphometrics to distinguish possible different morphotypes. Outlines obtained from transmitted light and SEM images were analysed and compared using the program MORPHOMATICA in ‘normalized for area’ and ‘not normalized for area’ modes. Four different morphotypes were recognized. Hereinafter, only the discussion on the geometric morphometric analyses of the most numerous female LV is reported, but the obtained results are consistent for all other valves. In Figure 3.9, the left female valves are illustrated for each morphotype in ‘normalized for area’ and in ‘not normalized for area’ modes. The dissimilarity matrix obtained from the geometric morphometric analysis was investigated using multivariate analyses with the PRIMER software. The results of the

cluster analysis and nMDS show clear separation of the four groups. The statistical validity of the recognized morphometrical differences was tested using ANOSIM pairwise tests, which gave statistically consistent R-values greater than or equal to 0.75 (Fig. 3.10) (Clarke & Gorley, 2006). Based on ANOSIM R-values, the four recognized morphotypes are considered to be four different species, described below.



**Figure 3.9:** ‘Morphomatica’ output of the four morphotypes of valve outlines found in the San Demetrio Syntem, in ‘normalized for area’ and ‘not-normalized for area’ modes. Mean outlines are drawn in black. **A**, morphotype 1 (*Caspiocypris amiterni* Spadi & Gliozzi); **B**, morphotype 2 (*C. bosii* Spadi & Gliozzi); **C**, morphotype 3 (*C. nicandroi* Spadi & Gliozzi); **D**, morphotype 4 (*C. vestinae* Spadi & Gliozzi). Scale bars =100  $\mu$ m.



**Figure 3.10:** Results of the multivariate analyses applied to the geometric morphometric outline matrix of *Caspiocypris* in ‘normalized for area’ mode. **A**, dendrogram of the cluster analysis (UPGMA); **B**, non-metric multidimensional scaling (nMDS) plot in two-dimensional morphological space; **C**, results of the analysis of similarities (ANOSIM) pairwise tests. Abbreviations: ami = *C. amiterni* Spadi & Gliozzi; bos = *C. bosii* Spadi & Gliozzi; nic = *C. nicandroi* Spadi & Gliozzi; ves = *C. vestinae* Spadi & Gliozzi sp. nov.

*Caspiocypris amiterni* Spadi & Gliozzi, 2016

(Fig. 3.11 A-H)

**Diagnosis.** *Caspiocypris* with right trapezoidal shape (almost vertical posterior border), thick shell, smooth surface with intra-shell reticulation in the postero-ventral area, and acuminate carapace at both ends. Remarkable sexual dimorphism, with males larger than females and with very high posterior area.

**Derivation of name.** From the ancient name of the city of L'Aquila in the Roman period.

**Material.** Holotype: T30/1, LV female (Fig. 3.11 A), sample 4.29. Paratypes: T30/2-5, LV female; T30/6-7, RV female; T30/8-10, LV male; T30/11-12, carapace female, sample 4.29. All from the San Nicandro section, L'Aquila Basin, Italy, San Nicandro Formation, San Demetrio-Colle Cantaro Synthem, Piacenzian p.p.–Gelasian p.p. Additional material: 144 adult valves and more than 100 juveniles.

**Description.** In dorsal view, the female carapace is ogive-shaped with acuminate anterior and posterior ends and with a straight hinge line. The LV covers the RV in the dorsal, anterior and posterior margins. In the lateral view, the female valve is right trapezoidal, with a maximum H posteriorly (three quarters of the entire length) and a ventral margin sub-parallel to the dorsal margin. The dorsal margin is straight and slightly inclined anteriorly with a rounded anterior cardinal angle. The ventral margin is slightly sinuous, with a slight central concavity. The anterior margin is straight antero-dorsally and rounded antero-ventrally. The posterior margin is straight with an acute rounded postero-ventral angle. The surface of the valves is smooth, but in transmitted light a reticulation is visible, especially in the postero-ventral area. The adductor muscle scars are clearly visible and are quite round, with the typical arrangement found in the subfamily Candoninae. In the internal view, the valves have a well-developed anterior vestibule that ends against the dorsal margin, and a posterior vestibule that is poorly developed around the postero-ventral corner. The hinge is typical of the genus, and in the LV there is a groove underlined by a well-developed ledge that runs the length of the cardinal margin. Sexual dimorphism is quite pronounced. Male valves are higher, with less rounded angles and straighter borders than the female valves. Moreover, the dorsal margin is more inclined anteriorly. The dimensions are always greater.

**Dimensions.** LV female (four valves): L = 1.12-1.25 mm; H = 0.69-0.77 mm. RV female (three valves): L = 1.08-1.18 mm; H = 0.64-0.72 mm. LV male (five valves): L = 1.28-1.33 mm; H = 0.81-0.89 mm. RV male (one valve): L = 1.30 mm; H = 0.84 mm.

*Caspiocypris bosii* Spadi & Gliozzi, 2016

(Fig. 3.11 I-O)

**Diagnosis.** Trapezoidal *Caspiocypris* with a thick shell, smooth surface with intra-shell ‘pits’ in the posterior area, and acuminate carapace at both ends. Remarkable sexual dimorphism with males larger than females and with a very high posterior area that is rounded in the LV.

**Derivation of name.** Dedicated to the Quaternary geologist Carlo Bosi who studied the L’Aquila Basin, and first recognized ostracods in the San Nicandro Formation.

**Material.** Holotype: T31/1, LV female (Fig. 3.11 J), sample 4.29. Paratypes: T31/2-4, LV female; T31/5-11, RV female; T31/12 and M287/2.2, RV male, sample 4.29. All from the San Nicandro section, L’Aquila Basin, Italy, San Nicandro Formation, San Demetrio-Colle Cantaro Synthem, Piacenzian p.p.-Gelasian p.p. Additional material: 221 adult valves and more than 200 juveniles.

**Description.** In dorsal view, the only recovered carapace is ascribed to a juvenile (A-1 stage) female. It is ogive shaped with an acuminate anterior and posterior ends and with a straight hinge line. The LV covers the RV in the dorsal and anterior margins. In lateral view, the female valve is trapezoidal with the dorsal margin parallel to the ventral margin. The dorsal margin is straight with a rounded anterior cardinal angle. The ventral margin is slightly sinuous, with a slight central concavity. The anterior margin is straight antero-dorsally and round antero-ventrally. The posterior margin is straight with an acutely rounded postero-ventral angle. The surface of the valves is smooth, but in transmitted light, ‘intra-shell pits’ are visible, especially in the postero-ventral area. The adductor muscle scars are clearly visible and are quite round, with the typical arrangement found in the subfamily Candoninae. In the internal view, valves have a well-developed anterior vestibule that ends against the dorsal margin and a posterior vestibule that is poorly developed around the postero-ventral corner. The hinge is typical of the genus, and in the LV, a groove underlined by a well-developed ledge runs the length of the cardinal margin. Sexual dimorphism is pronounced. The male valves are higher, with more rounded angles and more rectilinear borders than the female valves. Moreover, the dorsal margin is more inclined anteriorly. The dimensions are always greater.

**Dimensions.** LV female (five valves): L = 1.01-1.08 mm; H = 0.59-0.66 mm. RV female (four valves): L = 1.00-1.06 mm; H = 0.59-0.65 mm. LV male (one valve): L = 1.30 mm; H = 0.85 mm. RV male (one valve): L = 1.29 mm; H = 0.82 mm.



**Figure 3.11:** *Caspiocypris* from the PSC Basin. **A-H**, *Caspiocypris amiteri* Spadi & Gliozzi; **A**, holotype, lateral view of a left female valve in transmitted light, GOC T30/1, sample 4.29; **B**, left lateral view of a female complete carapace, GOC M291/4/8, sample 30.2; **C**, lateral inner view of a left female valve, GOC M287/1/7, sample 30.2; **D**, right lateral view of a female complete carapace, GOC M291/4/8, sample 30.2; **E**, lateral view of a left male valve, GOC M287/1/1, sample 4.13; **F**, lateral view of a right male valve, GOC M287/1/3, sample 29.4; **G**, dorsal view of a female complete carapace, GOC M291/4/8, sample 30.2; **H**, detail of the hinge of the left female valve, GOC M287/1/7, sample 30.2 illustrated in **C**. **I-O**, *Caspiocypris bosii* Spadi & Gliozzi; **I**, dorsal view of a female complete carapace, GOC M295/1/1, sample 29.1; **J**, holotype, lateral view of a left female valve in transmitted light, GOC T31/1, sample 4.29; **K**, paratype, lateral view of a female right valve in transmitted light, GOC T31/5, sample 4.29; **L**, lateral inner view of a left female valve, GOC M292/1/7, sample 2.35; **M**, paratype, lateral view of a left male valve, GOC M287/2/2, sample N4.29; **N**,



lateral view of a right male valve, GOC M287/2/4, sample 29.3; **O**, detail of the hinge of the left female valve, GOC M292/1/7, sample 2.35 illustrated in L. Scale bars = 100  $\mu$ m.

*Caspiocypris nicandroi* Spadi & Gliozzi, 2016

(Fig. 3.12 A-F)

**Diagnosis.** *Caspiocypris* with an elongated trapezoidal shape, a thick shell, a smooth surface, scattered large normal pore canals in the female, and acuminate carapace at both ends. Remarkable sexual dimorphism with males larger than females.

**Derivation of name.** From the San Nicandro Formation where the species was found.

**Material.** Holotype: M292/1.3, LV female (Fig. 3.12 A), sample 4.13. Paratypes: T32/1-3 e M292/1.2, LV female; T32/4-13, RV female; T32/14, RV male, sample 4.13. All from the San Nicandro section, L'Aquila Basin, Italy, San Nicandro Formation, San Demetrio-Colle Cantaro Synthem, Piacenzian p.p.-Gelasian p.p. Additional material: 188 adult valves and more than 200 juveniles.

**Description.** In the dorsal view, the female carapace is ogive-shaped with acuminate anterior and posterior ends and with curved hinge lines. The LV covers the RV along the dorsal, anterior and posterior margins. In the lateral view, the female valve is trapezoidal with a dorsal margin that is sub parallel to the ventral margin. The dorsal margin is straight with a round anterior cardinal angle. The ventral margin is slightly sinuous, with a slight central concavity. The anterior margin is rounded. The posterior margin is straight with a round right angle in the postero-ventral margin. The surface of the valves is smooth. The adductor muscle scars are clearly visible and are quite rounded, with the typical arrangement found in the subfamily Candoninae. In the internal view, the valves have a well-developed anterior vestibule that ends against the dorsal margin and a posterior vestibule that is poorly developed around the postero-ventral corner. The hinge is typical of the genus, and in the LV there is a groove underlined by a well-developed ledge that runs the length of the cardinal margin. Sexual dimorphism is pronounced. The male valves are higher in the posterior, with more rounded angles and straighter borders than the female valves. Moreover, the dorsal margin is more inclined anteriorly. The dimensions are always greater.

**Dimensions.** LV female (six valves): L = 1.07-1.18 mm; H = 0.58-0.64 mm. RV female (seven valves): L = 1.02-1.14 mm; H = 0.54-0.61 mm. RV male (three valves): L = 1.23-1.32 mm; H = 0.73-0.83 mm.



*Caspiocypris vestinae* Spadi & Gliozzi, 2016

(Fig. 3.12 G-M)

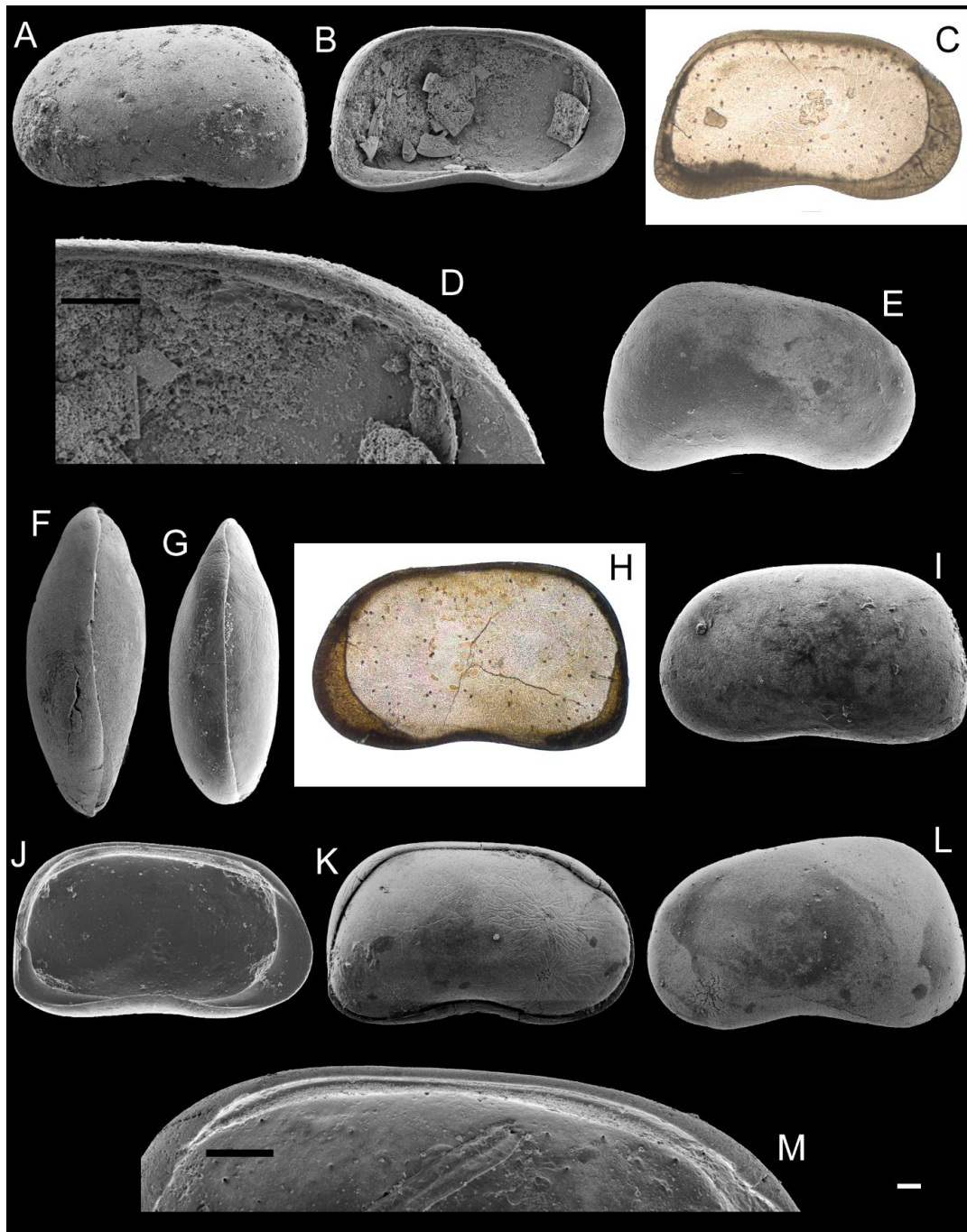
**Diagnosis.** *Caspiocypris* with a trapezoidal shape, a thick shell, a smooth surface, scattered large normal pore canals, and acuminate carapace at the anterior end. Noticeable sexual dimorphism, with males larger than females.

**Derivation of name.** From the ancient population of Vestini who inhabited the L'Aquila area during ancient Roman period.

**Material.** Holotype: T33/1, LV female (Fig. 3.12 H), sample 4.13. Paratypes: T33/2-12, LV female; T33/13-18, RV female, sample 4.13. All from the San Nicandro section, L'Aquila Basin, Italy, San Nicandro Formation, San Demetrio-Colle Cantaro Synthem, Piacenzian p.p.-Gelasian p.p. Additional material: 180 adult valves and more than 200 juveniles.

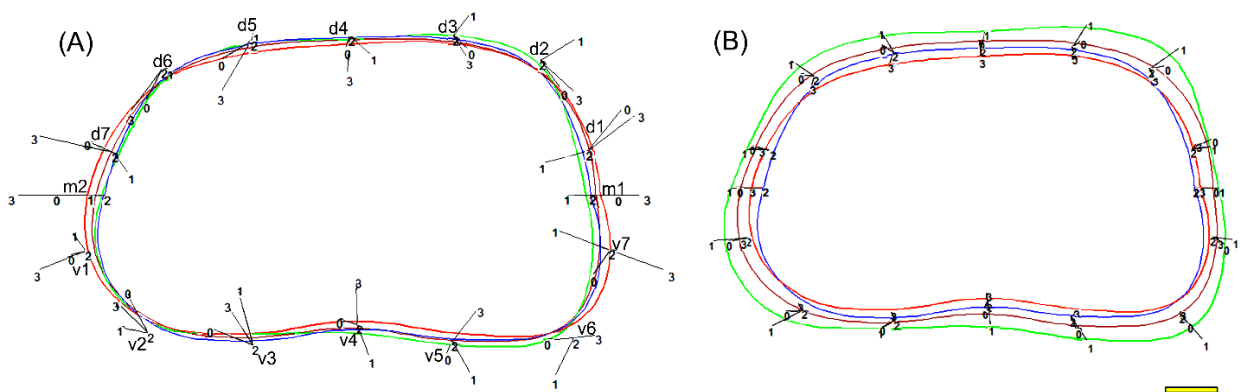
**Description.** In the dorsal view, the female carapace is ogive-shaped with beak-like anterior and acuminate posterior ends. The LV covers the RV along the dorsal, anterior and posterior margins with a straight hinge line. In the lateral view, the female valve is trapezoidal with a dorsal margin parallel to the ventral margin. The dorsal margin is straight with a rounded anterior cardinal angle. The ventral margin is slightly sinuous, with a slight central concavity. The anterior margin of the right valve is straight antero-dorsally and rounded antero-ventrally. The posterior margin is straight with a right angle rounded in the posteroventral margin. The surface of the valves is smooth. The adductor muscle scars are clearly visible and are quite round, with the typical arrangement found in the subfamily Candoninae. In the internal view, the valves have a well developed anterior vestibule that ends against the dorsal margin and a posterior vestibule developed around the postero-ventral corner. The hinge is typical of the genus, and there is a groove underlined by a well-developed ledge that runs the length of the cardinal margin in the LV. Sexual dimorphism is pronounced. The male valves are higher, with more rounded angles and straighter borders than the female valves. Additionally, the dorsal margin is more inclined anteriorly, and the dimensions are always greater.

**Dimensions.** LV female (13 valves): L = 1.07-1.18 mm; H = 0.62-0.69 mm. RV female (four valves): L = 1.04-1.14 mm; H = 0.57-0.65 mm. LV male (one valve): L = 1.34 mm; H = 0.80 mm.



**Figure 3.12:** *Caspiocypris* from the PSC Basin. **A-F**, *Caspiocypris nicandroi* Spadi & Gliozzi; **A**, holotype, lateral view of a left female valve, GOC M292/1/3, sample 4.13; **B**, lateral inner view of a left female valve, GOC M292/1/6, sample 2.35; **C**, paratype, lateral view of a right female valve in transmitted light, GOC T32/4, sample 4.13; **D**, detail of the anterior hinge of the left female valve, GOC M292/1/6, sample 2.35 illustrated in **B**; **E**, lateral view of a right male valve, GOC M290/3/2, sample 2.20; **F**, dorsal view of a female complete carapace, GOC M303/1/1, sample 4.29. **G-M**, *Caspiocypris vestinae* Spadi & Gliozzi; **G**, dorsal view of a female complete carapace, GOC M295/1/2, sample 29.4; **H**, holotype, lateral view of a left female valve in transmitted light, GOC T33/1, sample 4.13; **I**, lateral view of a left female valve, GOC M291/5/1, sample 2.31; **J**, lateral inner view of a left female valve, GOC M291/4/11, sample 29.4; **K**, right lateral view of a female complete carapace illustrated in **G**, GOC M295/1/2, sample 29.4; **L**, lateral view of a left male valve, GOC M287/2/3, sample 29.4; **M**, detail of the hinge of a left female valve, GOC M291/4/11, sample 29.4 illustrated in **J**. Scale bars = 100  $\mu$ m.

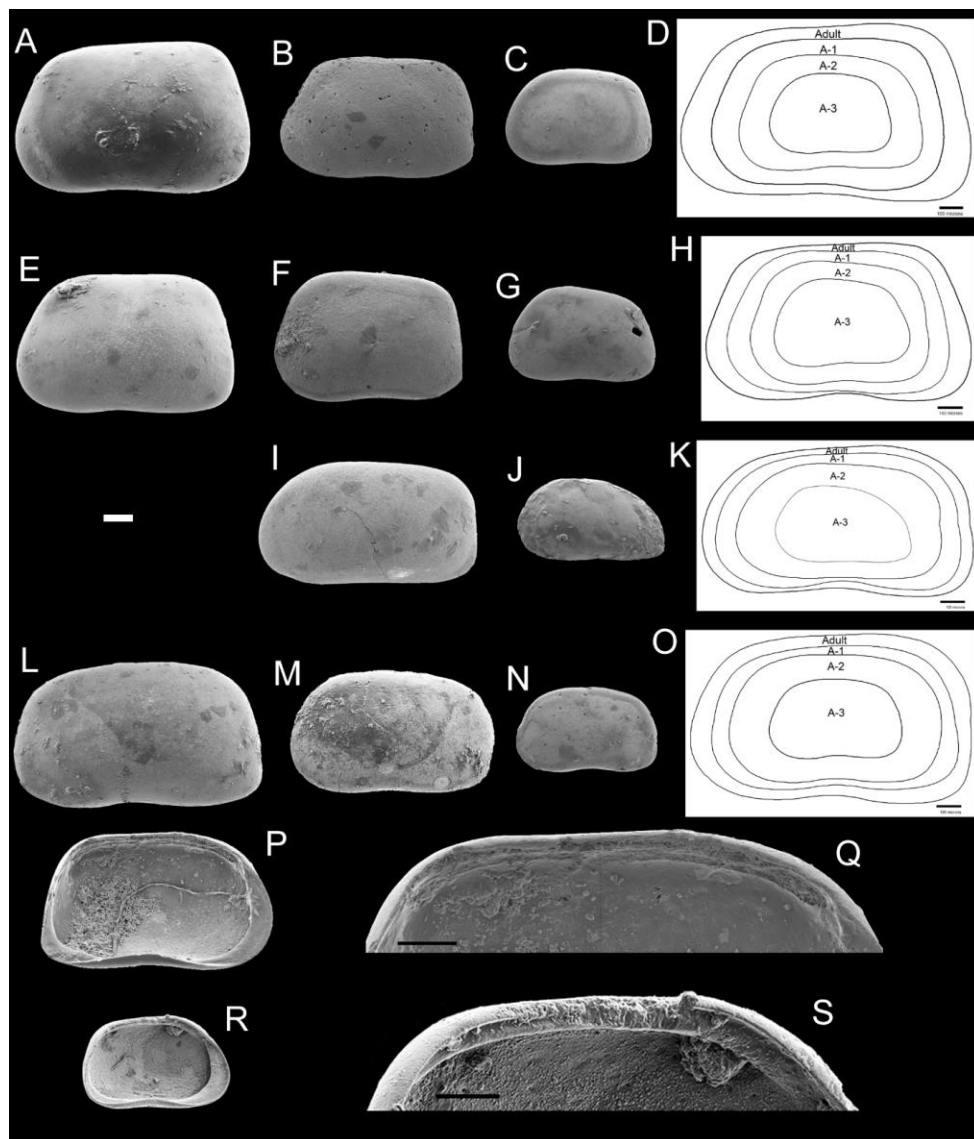
**Morphometrics.** As seen in Figure 3.13, the four *Caspiocypris* species recovered in the PSC sub-basin show substantial differences in their mean valve outlines, in both ‘normalized for area’ (Fig. 3.13 A) and in ‘not-normalized for area’ (Fig. 3.13 B) modes. *Caspiocypris nicandroi* has the most elongate (d7, m2, v1, d1, m1 and v7) and least high (d2, d3, d4, d5, v4 and v5) shape. *Caspiocypris amiterni* shows the shortest (d1, m1 and v7) and highest valves, especially in the postero-dorsal area (d2 and d3). *Caspiocypris vestinae* is slightly more elongate than *C. bosii* (d1, m1, v7, d7 and m2). If the mean outlines of the valve are examined in ‘not normalized for area’ mode, the largest species is *C. amiterni*, followed by *C. vestinae*. and *C. nicandroi*, which are quite similar to each other in size, and the smallest is *C. bosii*.



**Figure 3.13:** Superimposition of the mean outlines of *Caspiocypris vestinae* Spadi & Gliozzi (0, red), *C. amiterni* Spadi & Gliozzi (1, green), *C. bosii* Spadi & Gliozzi (2, blue) and *C. nicandroi* Spadi & Gliozzi (3, orange) in ‘normalized for area’ (A) and ‘not normalized for area’ (B) modes. (Morphomatica outputs have been realized with 6 iterations. In A the delta vector scale is 5; in B the delta vector scale is 1.) Scale bar = 100  $\mu$ m.

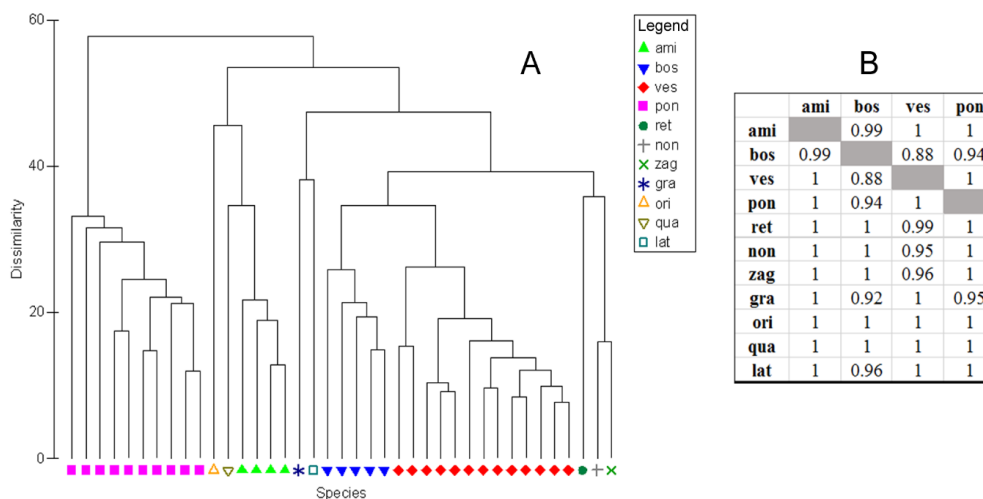
Similar differences can be noted also in the juveniles, as shown in Figure 3.14. Instars have been ascribed to the four different species up to the A-3 stage. Notably, the ledge in the hinge of the left valve (characteristic of the genus) can be observed from at least the A-3 instar (Fig. 3.14 R, S).

The new *Caspiocypris* species have been compared with numerous Candoninae from the Pannonian to Pontian of the Paratethys bioprovince assigned in this paper to the genus *Caspiocypris*, such as those described by Krstić (1968, 1971, 1972) and assigned to *Thaminocypris*, those illustrated by Sokač (1972) and Olteanu (1986) and assigned to *Lineocypris*, and some species described by Pipik & Bodergat (2006, 2007) and Medici et al. (2011) and assigned to *Candona* (see Chapter 5). Amongst these, the most similar species have been chosen for comparison of the left female valve outlines using geometric morphometric analysis and processing the results with multivariate statistics.



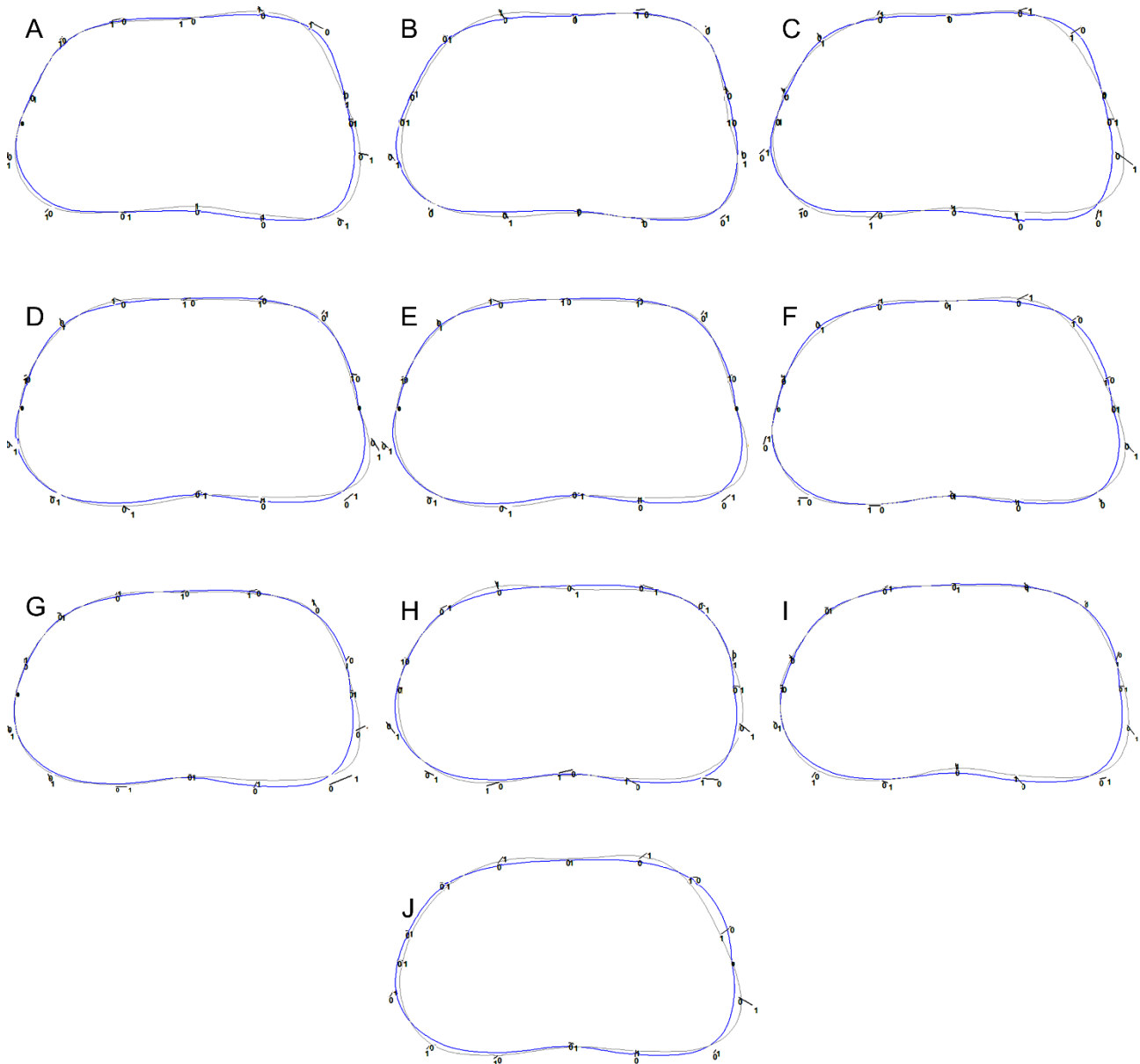
**Figure 3.14:** Juvenile *Caspiocypris* specimens from the PSC Basin. **A-D, R, S**, *Caspiocypris amiterni* Spadi & Gliozzi; **A**, lateral view of an A-1 left female valve, GOC M326/1/1, sample 30.2; **B**, lateral view of an A-1 left female valve, GOC M326/2/6, sample 3.5; **C**, lateral view of an A-3 left valve, GOC M326/4/5, sample 2.39; **D**, superimposition of the outlines of the female adult and three instars in ‘not normalized for area’ mode; **R**, lateral inner view of an A-3 left valve, GOC M326/4/6, sample 2.39; **S**, detail of the hinge of the A-3 left valve illustrated in **S**. **E-H, P, Q**, *Caspiocypris bosii* Spadi & Gliozzi; **E**, lateral view of an A-1 left female valve, GOC M326/1/2, sample 30.2; **F**, lateral view of an A-2 left valve, GOC M326/3/1, sample 2.17bis; **G**, lateral view of an A-3 left valve, GOC M326/4/7, sample 2.39; **H**, superimposition of the outlines of the female adult and three instars in ‘not normalized for area’ mode; **P**, lateral inner view of an A-1 left female valve, GOC M326/1/4, sample 29.3; **Q**, detail of the hinge of the A-1 left valve illustrated in **P**. **I-K**, *Caspiocypris nicandroi* Spadi & Gliozzi; **I**, lateral view of an A-2 left valve, GOC M292/1/4, sample 4.9; **J**, lateral view of an A-3 left valve, GOC M326/4/2, sample 2.20; **K**, superimposition of the outlines of the female adult and three instars in ‘not normalized for area’ mode. **L-O**, *Caspiocypris vestinae* Spadi & Gliozzi; **L**, lateral view of an A-1 left female valve, GOC M326/1/5, sample 2.35; **M**, lateral view of a A-2 right valve, GOC M326/2/8, sample 31.4; **N**, lateral view of a A-3 left valve, GOC M326/3/11, sample 2.20; **O**, superimposition of the outlines of the female adult and three instars in ‘not normalized for area’ mode. Scale bars = 100  $\mu$ m.

In Figure 3.15, *C. amiterni*, *C. bosii* and *C. vestinae* are compared with the stoutest *Caspiocypris* species known from the literature, and the cluster analysis (Fig. 3.15 A) shows definite clusters; the ANOSIM pairwise tests (Fig. 3.15 B) confirm that the differences are statistically consistent. In Figure 3.15, the superimposition of each species outline is shown to enhance shape differences. *Caspiocypris amiterni* can be compared with the following: (1) *C. orientalis* (Krstić), from which it differs in the shorter and more rectilinear posterior margin (d1, d2, d3, m1, v7 and v6) and larger size (Fig. 3.16 A); (2) *C. quadrata* (Olteanu), from which it differs in the anterior part of the dorsal margin (d4 and d5) and the anterior margin (d7, m2 and v1; Fig. 3.16 B); and (3) *C. pontica* Sokač, which shows differences in the posterior margin (d2, m1, v7, v6 and v5) and is smaller (Fig. 3.16 C). *Caspiocypris bosii* has been compared with the following: (1) *C. granulosa* (Sokač), which differs in having a less developed postero-ventral margin (v7, v6 and v5; Fig. 3.16 D); (2) *C. laterisimilis* (Pipik & Bodergat), from which it differs in having a less round anterior margin (d6, d7, m2, v1 and v2; Fig. 3.16 E); and (3) *C. pontica* Sokač, which has a higher posterior margin (d2, m1, v7, v6 and v5) and smaller dimensions (Fig. 3.16 F). *Caspiocypris vestinae* has been compared with the following: (1) *C. nonreticulata* (Sokač), which has a less developed and straighter postero-ventral margin (v7, v6 and v5; Fig. 3.16 G); (2) *C. reticulata* (Sokač) and *C. zagabiensis* (Sokač), from which it differs in the less developed and straighter postero-ventral margin (v7, v6 and v5) and in the dorsal margin (d4 and d5; Fig. 3.16 H, I); and (3) *C. pontica* Sokač, which is completely different along the dorsal (d2, d3, d4 and d5) and posterior margins (d1 and v7) and is smaller (Fig. 3.16 J).



**Figure 3.15:** Results of the multivariate analyses applied on the geometric morphometric outline matrix of several species of *Caspiocypris* from L'Aquila basin and the Paratethyan domain in 'normalized for area' mode. **A**, dendrogram of the cluster analysis (UPGMA); **B**, results of the analysis of similarities (ANOSIM) pairwise tests. Abbreviations: ami = *C. amiterni* Spadi & Gliozzi; bos = *C. bosii* Spadi & Gliozzi; gra = *C. granulosa* (Sokač); lat = *C. laterisimilis* (Pipik &

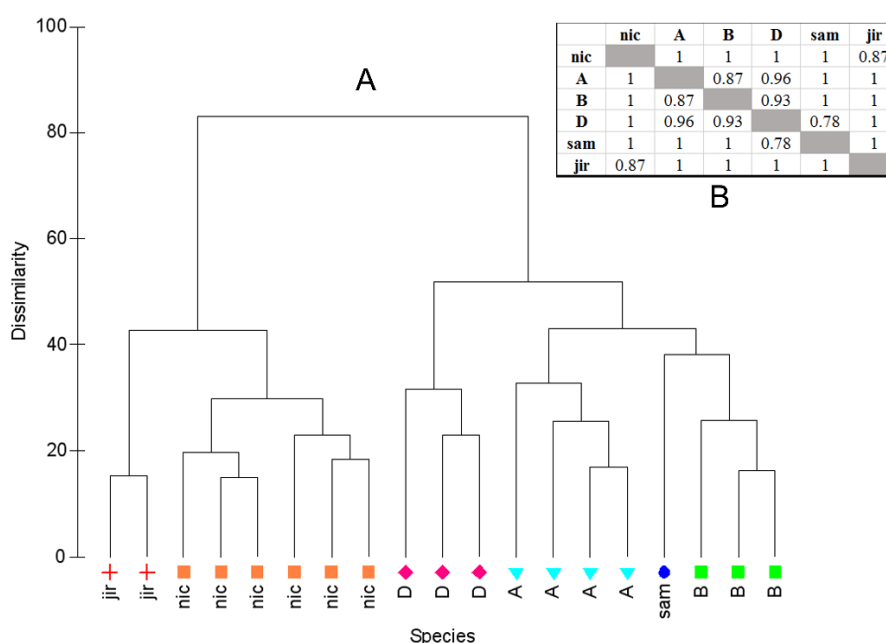
Bodergat); non = *C. nonreticulata* (Sokač); ori = *C. orientalis* (Krstić); pon = *C. pontica* Sokač; qua = *C. quadrata* (Olteanu); ret = *C. reticulata* (Sokač); ves = *C. vestinae* Spadi & Gliozzi; zag = *C. zagabriensis* (Sokač).



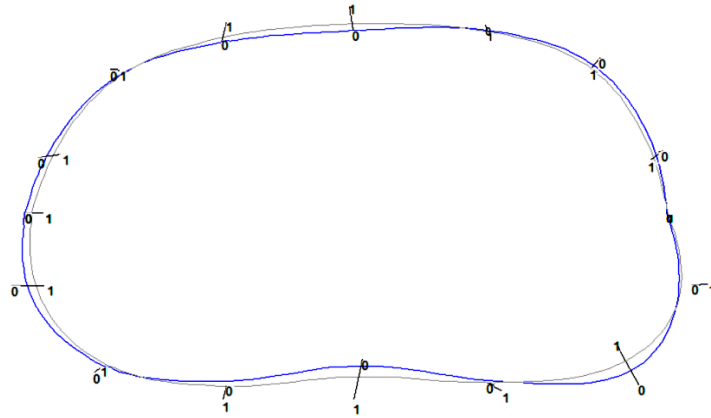
**Figure 3.16:** Comparison of the mean outlines normalized for areas (6 iterations, delta vector scale 1) among Neogene *Caspiocypris* species: **A**, *C. amiterni* Spadi & Gliozzi (blue, 0) vs *C. orientalis* (Krstić) (grey, 1); **B**, *C. amiterni* Spadi & Gliozzi (blue, 0) vs *C. quadrata* (Olteanu) (grey, 1); **C**, *C. amiterni* Spadi & Gliozzi (blue, 0) vs *C. pontica* Sokač (grey, 1); **D**, *C. bosii* Spadi & Gliozzi (blue, 0) vs *C. granulosa* (Sokač) (grey, 1); **E**, *C. bosii* Spadi & Gliozzi sp. (blue, 0) vs *C. laterisimilis* (Pipik & Bodergat) (grey, 1); **F**, *C. bosii* Spadi & Gliozzi (blue, 0) vs *C. pontica* Sokač (grey, 1); **G**, *C. vestinae* Spadi & Gliozzi (blue, 0) vs *C. nonreticulata* (Sokač) (grey, 1); **H**, *C. vestinae* Spadi & Gliozzi (blue, 0) vs *C. reticulata* (Sokač) (grey, 1); **I**, *C. vestinae* Spadi & Gliozzi (blue, 0) vs *C. zagabriensis* (Sokač) (grey, 1); **J**, *C. vestinae* Spadi & Gliozzi (blue, 0) vs *C. pontica* Sokač (grey, 1).



As previously stated, *Caspiocypris nicandroi* shows the most elongate valve shape. This species can be compared with some *Caspiocypris* species that attain low L/H ratios from the Paratethys (*C. jiriceki* (Pipik & Bodergat) from the Turiec Basin, Slovakia) and Italy (*Caspiocypris posteroacuta* Spadi & Gliozzi, *Caspiocypris perusia* Spadi & Gliozzi and *Caspiocypris basilicii* Spadi & Gliozzi from the Tiberino Basin (Spadi et al., 2017), and *C. sambucensis* (Medici, Ceci & Gliozzi) from the Valdelsa Basin). Cluster analysis (Fig. 3.17 A) shows a clear separation of the groups, and the ANOSIM pairwise tests (Fig. 3.17 B) indicate that *C. jiriceki* is the most similar species. It has a shorter anterior margin (d7, m2 and v1) but displays a maximum height that is proportionally greater than *C. nicandroi* (v3 and v4; Fig. 3.18).



**Figure 3.17:** Results of the multivariate analyses applied to the geometric morphometric outline matrix of *Caspiocypris nicandroi* Spadi & Gliozzi from the L’Aquila Basin and other *Caspiocypris* from Mediterranean and Paratethyan domains in ‘normalized for area’ mode. **A**, dendrogram of the cluster analysis (UPGMA); **B**, results of the analysis of similarities (ANOSIM) pairwise tests. Abbreviations: A = *Caspiocypris posteroacuta* Spadi & Gliozzi; B = *Caspiocypris perusia* Spadi & Gliozzi; D = *Caspiocypris basilicii* Spadi & Gliozzi; jir = *C. jiriceki* (Pipik & Bodergat); nic = *C. nicandroi* Spadi & Gliozzi; sam = *C. sambucensis* (Medici, Ceci & Gliozzi).



**Figure 3.18:** Comparison of the mean outlines normalized for areas (6 iterations, delta vector scale 3) among *Caspiocypris nicandroi* Spadi & Gliozzi (blue, 0) and *C. jiriceki* (Pipik & Bodergat) (black, 1).

Genus *Candona* Baird, 1845

*Candona (Neglecandona) neglecta* Sars, 1887

(Fig. 3.19 A)

1887 *Candona neglecta* Sars, p. 279, pl. 15, figs 5-7; pl. 19, figs 1-21.

1964 *Candona neglecta* Sars – McKenzie, p. 8, pl. 1, fig. 3.

1978 *Candona neglecta* Sars – Molinari Paganelli, p. 280, pl. 2, fig. 2.

1994 *Candona neglecta* Sars – Calderoni et al., p. 54, fig. 10f.

1995 *Candona neglecta* Sars – Barberi et al., p. 524, fig. 6a-c.

1996 *Candona neglecta* Sars – Gliozzi, p. 96.

1996 *Candona neglecta* Sars – Belis et al., p. 112.

1998 *Candona neglecta* Sars – Gliozzi & Mazzini, p. 70, pl. 1, fig. e.

1999 *Candona neglecta* Sars – Mazzini et al., p. 299, tab. 2, pl. 2, fig. 2.

1999 *Candona neglecta* Sars – Gliozzi, p. 62, fig. 12a.

1999 *Candona neglecta* Sars – Barbieri et al., p. 62, fig. 11.

2011 *Candona (Neglecandona) neglecta* Sars – Medici et al., p. 487, pl. 3, figs c-d.

Although the great variability of size and shape of valves reported by Meisch (2000) within *Candona (Neglecandona) neglecta*, the valves collected in the Valle Orsa Fm. fall within its variability field and display the morphological characters of this species. *C. (N.) neglecta* has a wide stratigraphical range since it has been found from Serravallian to Recent (Medici et al., 2011).



*Candona (Neglecandona) permanenta* Krstić, 1985

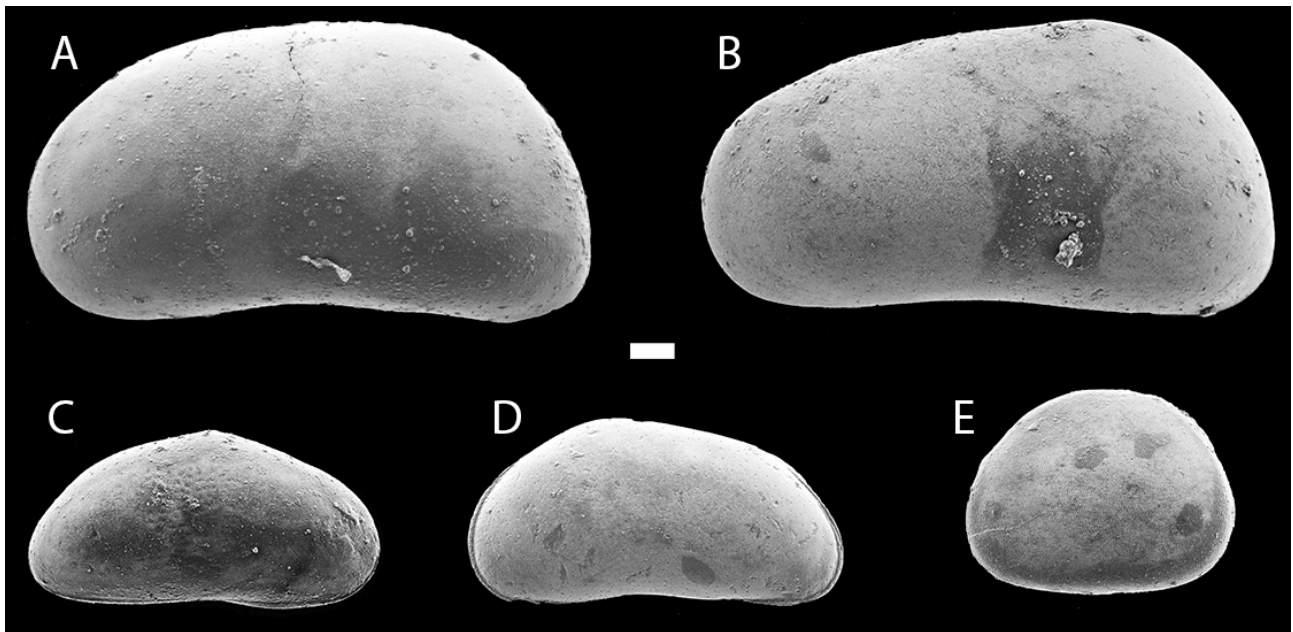
(Fig. 3.19 B)

1985 *Candona permanenta* Krstić, p. 197, p. 1, figs 1-3, pl. 2, figs 1-3.

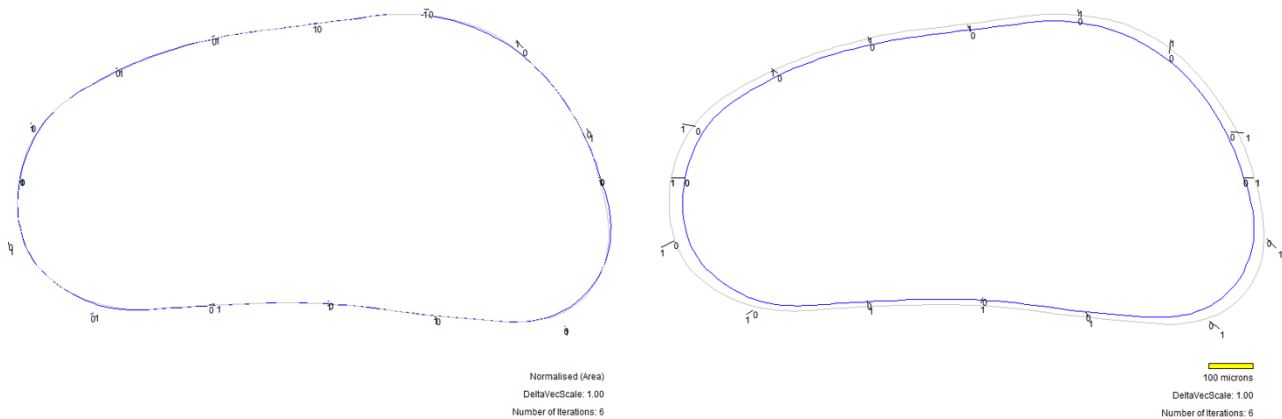
2003 *Candona (Candona) permanenta* Krstić, p. 379, pl. V, fig. 3.

2006 *Neglecandona permanenta* Krstić, p. 149, pl. XXI, fig. 1, pl. XXVI, figs 1-11.

The presence of *Candona (Neglecandona) permanenta* in the last two samples of the composite section is very remarkable, since it is the first recovery of this species out of its typical deposits, namely the upper part of the Upper Paludonian Beds (*malezi*-Zone) in Serbia (Krstić, 2006). The outline of the specimens collected from samples CP6 and CP7 correspond to the original material stored in the Natural History Museum of Belgrade (Fig. 3.20). A recent revision of the Neogene and Quaternary deposits of the Paludonian Beds permits locate the *malezi*-Zone of the Paludonian beds in the upper Cernikian stage, which corresponds to a time interval that spans from the latest Piacenzian to the pre-Olduvai Gelasian (between ~2.9 and ~2.0 Ma) (Mandic et al., 2015).



**Figure 3.19:** Ostracods from Valle Orsa Fm. **A**, *Candona (Neglecandona) neglecta* from sample 4.14. **B**, **C**, (*N.*) *permanenta* from sample CP 6. **C**, *Cavernocypris subterranea* from sample 4.21. **D**, *Potamocypris fallax* from sample 4.24. **E**, *Cypria ophthalmica* from sample 4.19.



**Figure 3.20:** Results of the geometric morphometric analysis performed on left valve of *Candona (Neglecandona) permanenta* holotype from Natural History Museum of Belgrade (blue) and *C. (N.) permanenta* from Valle Orsa Fm., sample CP 6 (grey) in “normalized for area” mode on the left valve and “not normalized for area” mode on the right.

### Subfamily **Cyclopyridinae** Kaufmann, 1900

Genus *Cypria* Zenker, 1854

*Cypria bikeratia* Spadi & Gliozzi, 2016

(Fig. 3.21 A-F)

**Diagnosis.** Trapezoidal *Cypria* characterized by an elongate dorsal margin that is centrally concave with two bulges corresponding to the cardinal angles.

**Derivation of name.** From Greek κέρασ, κέρατος = horn for the two tubercles on the dorsal margin.

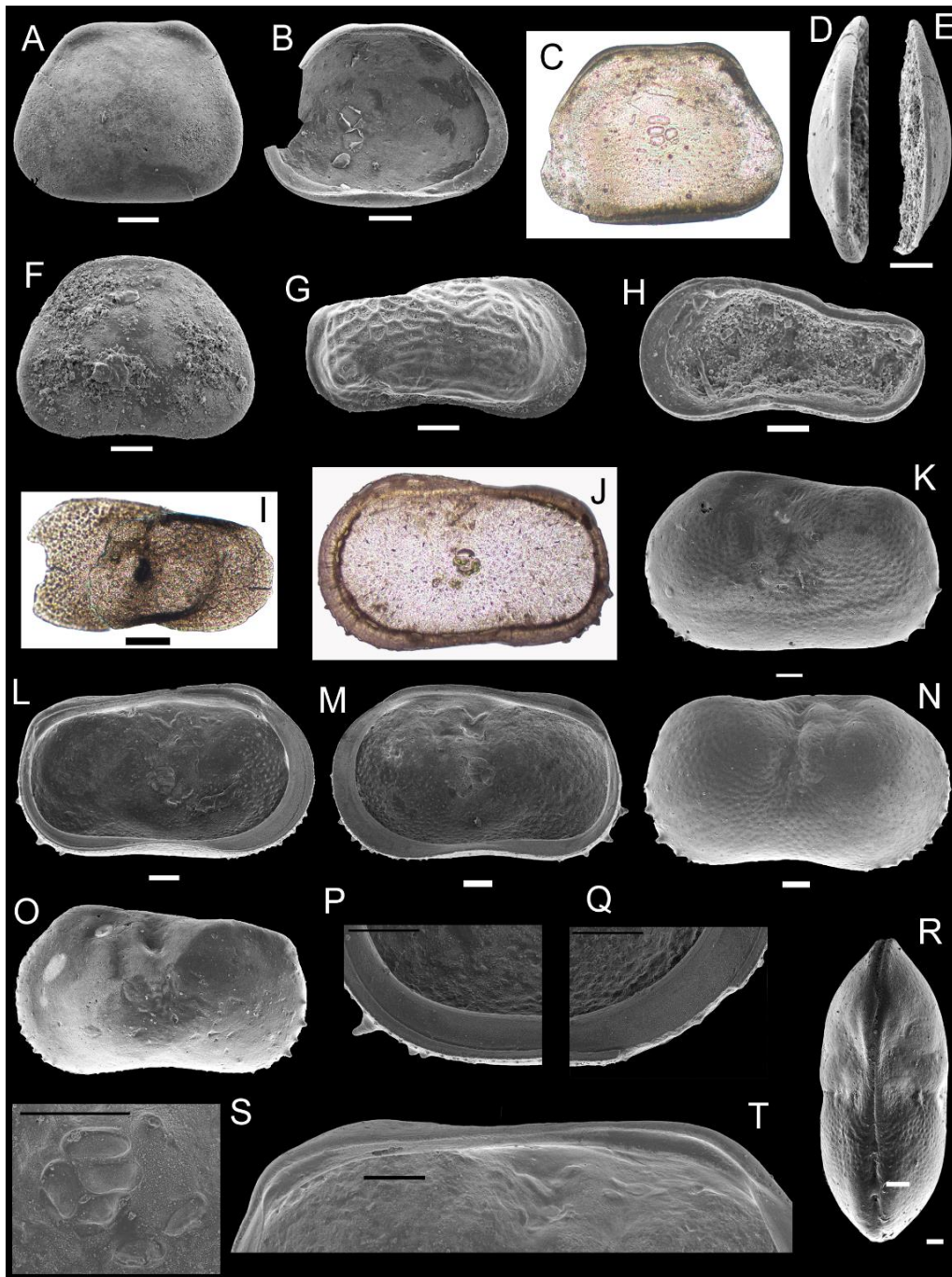
**Material.** Holotype: M305/1.1, LV female (Fig. 3.21 A), sample 2.38. Paratypes: T34/1 and M292/2.1-3, LV ?male; T34/2-4 and M292/2.1-3, LV female; T34/5-8 and M292/2.4, RV female; sample 2.38. San Nicandro section, L’Aquila Basin, Italy, San Nicandro Formation, San Demetrio-Colle Cantaro Synthem, Piacenzian p.p. –Gelasian p.p. Additional material: 43 adult valves and 15 juveniles.

**Description.** Only isolated valves were found; thus, the carapace description is derived from two valves in the dorsal view. In the dorsal view, the carapace is wedge shaped with acuminate anterior and posterior ends and with a maximum central width; the cardinal line is straight. The LV overlaps the RV along the dorsal and ventral margins. In the lateral view, the LV has very high H/L ratios (0.8) and an isosceles trapezoidal shape with parallel dorsal and ventral margins. One left valve (illustrated in transmitted light in Fig. 3.21 C) shows a slightly more protuberant posterior border. The dorsal margin is straight, as is the ventral margin. The cardinal and ventral angles are evident. A peculiar character is the presence of two bulges along the dorsal margin of the LV, corresponding to the postero- and the antero-dorsal angles. The surface of the valves is smooth. In the internal view, LV

has well-developed vestibules in both the postero- and antero-ventral angles. In the LV, there is a very short, straight bar along the cardinal margin, whereas centrally on the ventral margin, the valve is internally folded and covers the RV; a small tooth is present antero-ventrally.

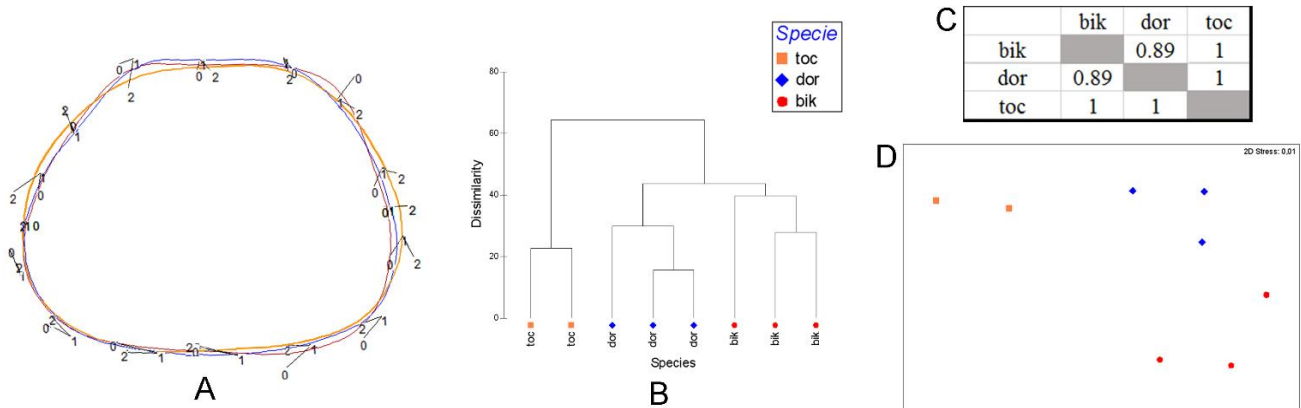
**Dimensions.** LV (three valves): L = 0.56-0.57 mm; H = 0.43-0.45 mm. RV (two valves): L = 0.54-0.55 mm; H = 0.40-0.42 mm.

**Remarks.** *Cypria bikeratia* has a very particular shape. It does not look like any other known species of *Cypria* except for *Cypria tocorjescui* Hanganu, 1962, which is distributed in the Pannonian, Dacian and Euxinic Basins of the Pontian (Hanganu, 1962; Sokač, 1972; Krijgsman et al., 2010; Stoica et al., 2016), and *Cypria dorsoconcava* Krstić, 1975, reported from the Pannonian and Pontian of the Pannonian Basin and the Pontian of the Dacic Basin (Krstić, 1975; ter Borg et al., 2013). Although the RV of *Cypria tocorjescui*, *C. dorsoconcava* and *C. bikeratia* are very similar except for the dorsal margin being inclined slightly forwards in *C. tocorjescui*; the LV differs greatly. Geometric morphometric analysis using the superimposition of mean outlines shows that the LV of *C. dorsoconcava* has a less elongate dorsal margin (d6, d5, d2 and d3), and its dimensions are smaller (Fig. 3.22 A). *Cypria tocorjescui* appears relatively low (d5, d4 and d3) and is more elongate (d7, m2, d1, m1 and v7) with more rounded anterior and posterior ventral angles. Moreover, it does not share the two bulges along the dorsal margin (Fig. 3.22 B). The ANOSIM pairwise tests and nMDS analyses (Fig. 3.22 C, D) confirm the separation of the three species. ter Borg et al. (2013, p. 105, fig. 7-23) illustrated the left valve of *C. dorsoconcava* with a remarkably protruding posterior border, somewhat similar, although more marked, to the *C. bikeratia* left valve shown in Figure 3.21 C. It is possible that this character could be related to sexual dimorphism, although Meisch (2000) did not describe any shell differences between sexes within the genus *Cypria*.



**Figure 3.21:** Ostracods from the PSC Basin. **A-F**, *Cypria bikeratia* Spadi & Gliozzi; **A**, holotype, lateral view of a left female valve, GOC M305/1/1, sample 2.38; **B**, lateral inner view of a broken left female valve, GOC M292/2/6, sample 2.41; **C**, paratype, lateral view of a left ?male valve in transmitted light, GOC T34/2, sample 2.38; **D**, holotype, dorsal view of a left female valve, GOC M305/1/1, sample 2.38 illustrated in **A**; **E**, paratype, dorsal view of a right female valve, GOC M295/2/1, sample 2.38; **F**, paratype, lateral view of a right female valve, GOC M295/2/1, sample 2.38, illustrated in **E**. **G, H**, *Amnicythere* ex gr. *stanchevae* Krstić, 1973; **G**, lateral view of a right valve, GOC M290/2/1, sample 30.2; **H**, lateral inner view of a right valve, GOC M290/2/1, sample 30.2 illustrated in **G**. **I**, *Paralimnocythere* cf. *P. dictyonalis* Medici, Ceci & Gliozzi, 2011, lateral view of a left valve in transmitted light (specimen lost), sample 4.13. **J-T**, *Ilyocypris ilae* Spadi & Gliozzi; **J**, holotype, lateral view of a female left valve in transmitted light, GOC T35/1/1, sample 2.41; **K**, paratype, lateral view of a left female valve, GOC M288/2/4, sample 2.41; **L**, paratype, lateral inner view of a female left valve, GOC M288/1/5, sample 2.41; **M**, paratype, lateral inner view of a right female valve, GOC M288/2/3, sample 2.41;

**N**, paratype, lateral view of a right female valve, GOC M2887/1/3, sample 2.41; **O**, lateral view of a left male valve, GOC M288/3/6, sample 2.39; **P**, detail of the postero-ventral inner margin without ripples of a left female valve (paratype), GOC M288/1/6, sample 2.41; **Q**, detail of the antero-ventral inner margin without ripples of a left female valve (paratype), GOC M288/1/6, sample 2.41; **R**, dorsal view of a female complete carapace, GOC M288/3/8, sample 30.2; **S**, detail of the muscle scars of a left female valve (paratype), GOC M288/2/1, sample 2.41; **T**, detail of the hinge of a left female valve (paratype), GOC M288/1/6, sample 2.41. Scale bars = 100  $\mu$ m.



**Figure 3.22:** Results of the multivariate analyses applied to the geometric morphometric outline matrix of several species of *Cypria* from the L'Aquila Basin and the Paratethyan domain in 'normalized for area' mode. **A**, superimposition of the outlines of *C. dorsoconcava* Krstić holotype from Natural History Museum of Belgrade (0, blue), *C. bikeratia* Spadi & Gliozzi (1, red), and *C. tocorjescui* Hanganu (2, orange) (6 iterations, delta vector scale 2); **B**, dendrogram of the cluster analysis (UPGMA); **C**, results of the analysis of similarities (ANOSIM) pairwise tests; **D**, non-metric multidimensional scaling (nMDS) plot in two-dimensional morphological space. Abbreviations: bik = *C. bikeratia* Spadi & Gliozzi; dor = *C. dorsoconcava* Krstić; toc = *C. tocorjescui* Hanganu.

### *Cypria ophtalmica* (Jurine, 1820)

(Fig. 3.19 E)

1820 *Monoculus ophtalmica* Jurine, p. 178, pl. 19, figs 16-17.

1995 *Cypria ophtalmica* (Jurine) – Barberi et al., p. 526, fig. 11i, p. 527, fig. 13e.

2008 *Cypria ophtalmica* (Jurine) – Faranda & Gliozzi, p. 255, pl. 13, fig. 8

Some valves of *Cypria* from the upper part of the San Nicandro section pertain to the living species *C. ophtalmica*. This species is very widespread and very common, being tolerant to a wide range of environmental factors in the recent freshwater environments. As fossil it is known from Miocene to Recent (Meisch, 2000).

Family **Ilyocyprididae** Kaufmann, 1900  
Subfamily **Ilyocypridinae** Kaufmann, 1900  
Genus ***Ilyocypris*** Brady & Norman, 1889  
***Ilyocypris ilae*** Spadi & Gliozzi, 2016

(Fig. 3.21 J-T)

**Diagnosis.** Stout *Ilyocypris* species with a thick shell, a concave dorsal border mainly linked to the remarkable postero-dorsal inflation, surface covered by shallow pits, absence of marginal ripplets.

**Derivation of name.** Dedicated to our colleague and friend Ilaria Mazzini.

**Material.** Holotype: T35/1, LV female (Fig. 3.21 J), sample 2.41. Paratypes: T35/2-9 and M288/1.1-2, 1.5-6, 2.1, 2.4-9, 3.1-2, 3.4-5, LV female; T35/10-25 and M288/1.3-4, 2.2-3, RV female; T35/26-27 and M288/3.3, 3.6-7, LV male; T35/28-30, RV male; M288/3.8, carapace female, sample 2.41. All from the San Nicandro section, L'Aquila Basin, Italy, Valle Orsa Formation, San Demetrio-Colle Cantaro Synthem, Piacenzian p.p.-Gelasian p.p. Additional material: 96 adult valves and more than 150 juveniles.

**Description.** In the dorsal view, the carapace is ellipsoidal with a central constriction corresponding with the median grooves. The RV covers the LV anteriorly, whereas the LV slightly overlaps the RV along the dorsal margin. In the lateral view, valves are sub-rectangular, with the anterior portion slightly higher than the posterior one. The ventral margin appears straight in the LV and sinuous in the middle of the RV; the dorsal margin is slightly concave centrally. The anterior and posterior margins are round. The valves have very marked median grooves that originate from the dorsal side of the valve. Three to four denticles are present along the posterior margin, and 9-10 occur along the anterior margin. The valves are ornamented with shallow circular pits that disappear when shells are abraded; tubercles are absent. In the internal view, the vestibules are well developed along the anterior and posterior margins; no marginal ripplets are visible (Fig. 3.21 P, Q). Along the dorsal margin, a robust hinge is present, formed by a bar mainly developed in the anterior and posterior parts of LV. Four central muscle scars are visible (Fig. 3.21 S). Sexual dimorphism is evident, with the male valve proportionally more elongate but smaller in size.

**Dimensions.** LV female (15 valves): L = 0.95-1.05 mm; H = 0.57-0.64 mm. RV female (four valves): L = 0.92-1.03 mm; H = 0.53-0.62 mm. LV male (two valves): L = 0.85-0.95 mm; H = 0.53-0.59 mm.

**Remarks.** Other than Cretaceous genera *Rhinocypris* Anderson, 1941, *Ilyocyprimorpha* Mandelstam, 1956, *Cyprideamorphella* Mandelstam, 1956 and *Parailyocypris* Yang, 1982, *Ilyocypris ilae* was compared with the other Neogene-Quaternary genera of Ilyocyprididae. It differs from *Qinghaicypris* Huang, 1979 and *Neuquenocypris* Musacchio, 1973 in not having six central muscle scars

(Rodríguez- Lázaro & Martín-Rubio, 2005); from *Fossilyocypris* Schornikov & Krstić, 2004 in Krstić et al. 2004, which displays a strong ornamentation of very large pits (Krstić et al., 2004; Krstić, 2006); and from *Juxilocypris* Kempf, 2011, which is characterized by a strong rib in the postero-ventral surface of the valves. Hence, notwithstanding its very stout proportions, the species from the San Demetrio-Colle Cantaro Synthem must be assigned to the genus *Ilyocypris* Brady & Norman, 1889. However, it should be emphasized that the proportions and the outline of *Ilyocypris ilae* are very different from all known *Ilyocypris* species, both extant (Mazzini et al., 2014a) and extinct, from Eurasia.

Family **Cyprididae** Baird, 1845

Subfamily **Cypridopsinae** Kaufmann, 1900

Genus *Cavernocypris* Hartmann, 1964

*Cavernocypris subterranea* (Wolf, 1920)

(Fig. 3.19 C)

1920 *Cypridopsis subterranea* Wolf, p. 46, pl.2, figs 1-6.

*Cavernocypris subterranea* is a typical form that inhabits waters in connection with springs and it is considered a cold stenothermal and stygophilic species (Meisch, 2000). Its fossil record spans from Miocene to Recent (Meisch, 2000) and the present recovery at the L'Aquila Basin seems to be the first fossil occurrence of this species in the Italian peninsula.

Genus *Potamocypris* Brady, 1870

*Potamocypris fallax* Fox, 1967

(Fig. 3.19 D)

1967 *Potamocypris fallax* Fox, p. 555, fig. 5b-d, g.

The finding of *Potamocypris fallax* in few samples from the Valle Orsa Fm. suggest the presence of a freshwater environment fed by springs (Meisch, 2000). The valves of *P. fallax* collected at the L'Aquila Basin seem the first fossil record of this species in Italy. Outside the Italian peninsula this species have been recovered from Pleistocene to Recent.

Suborder **Cytherocopina** Baird, 1850  
Superfamily **Cytheroidea** Bard, 1850  
Family **Leptocytheridae** Hanai, 1957  
Subfamily **Leptocytherinae** Hanai, 1957  
Genus *Amnicythere* Devoto, 1965  
*Amnicythere ex gr. stanchevae* (Krstić, 1973)  
(Fig. 3.21 G, H)

1973 *Leptocythere (Amnicythere) ex gr. stanchevae* Krstić, p. 69, figs 68-70.

2003 *Amnicythere* sp. E Bassetti et al., p. 350, pl. 1, fig. 2.

Very few valves of this taxon have been recovered in the study sections, among which only one RV is well preserved. In the lateral view, it is sub-rectangular with the posterior margin weakly rounded and a postero-dorsal right angle. The anterior margin is rounded. The surface of the valve, except for the flattened and smooth marginal areas, is reticulated, and a dense network of ribs is visible that originate anteriorly and run parallel to the anterior margin. In the internal view, the hinge shows the smooth median element and the presence of two large anterior and posterior teeth, typical of the genus *Amnicythere*.

The recovered valves have been referred to *Amnicythere ex gr. stanchevae* Krstić, 1973 which, according to us and following Olteanu (1989, p. 244), could include at least two very similar species: *Amnicythere stanchevae* (Krstić, 1973), known from the Late Pannonian of Serbia (Krstić, 1973) and the Pontian of the Dacic Basin (Olteanu, 1990), and *Amnicythere sinegubi* (Krstić, 1975), described from the Pontian of Serbia and the Dacic Basin (Olteanu 1989). These species are very similar in shape and ornamentation to the specimens found in the L'Aquila Basin, but the latter is larger (L = 0.68 mm, H = 0.34 mm). Our specimens are also quite similar to some valves recovered in the Messinian Lago-Mare succession of Perticara and referred to by Bassetti et al. (2003) as *Amnicythere* sp. E.

Family **Limnocytheridae** Klie, 1938  
Subfamily **Limnocytherinae** Klie, 1938  
Genus *Paralimnocythere* Carbonnel, 1965  
*Paralimnocythere cf. P. dictyonalis* Medici, Ceci & Gliozzi, 2011  
(Fig. 3.21 I)



cf. 2011 *Paralimnocythere dictyonalis* Medici, Ceci & Gliozzi, p. 478, pl. 1, figs a-g.

The morphology and size of the single specimen are comparable with *Paralimnocythere dictyonalis* Medici, Ceci & Gliozzi, 2011 from the lower Pliocene of the Valdelsa Basin (Tuscany, central Italy). This would be the first discovery of the species outside the area in which it was first described and would extend its temporal range to the late Pliocene-early Pleistocene (Gelasian).

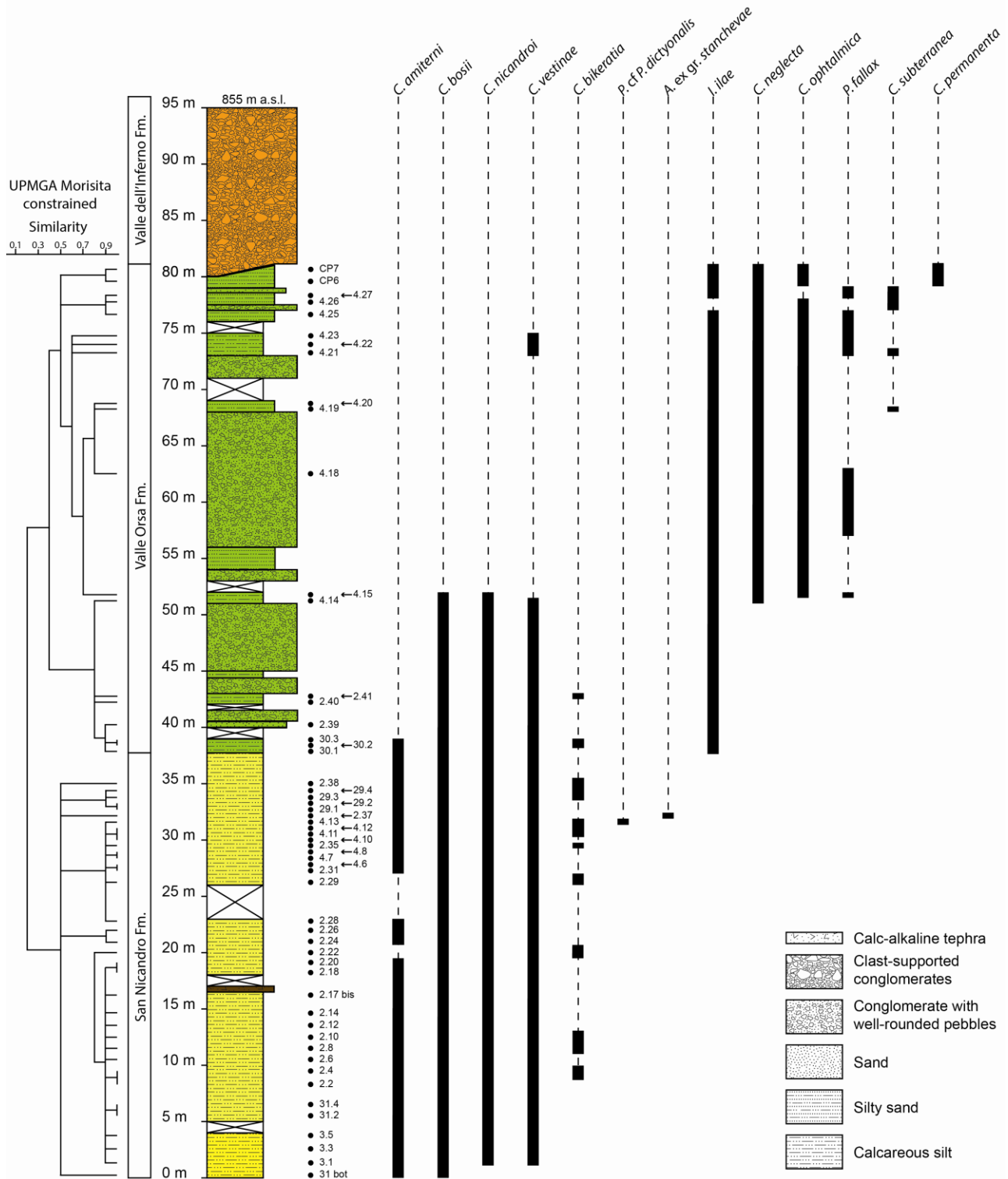
### 3.4 Discussion

The autochthonous ostracod assemblages recognized in the composite section cut within the San Nicandro and Valle Orsa formations are made of 13 species ascribed to 8 genera: *Caspiocypris amiterni*, *C. bosii*, *C. nicandroi*, *C. vestinae*, *Candona (Neglecandona) neglecta*, *C. (N.) permanenta*, *Ilyocypris ilae*, *Cypria bikeratia*, *C. ophthalmica*, *Cavernocypris subterranea*, *Potamocypris fallax*, *Amnicythere* ex gr. *stanchevae*, and *Paralimnocythere* cf. *P. dictyonalis*. Few other taxa such as *Fabaeformiscandona* sp., *Limnocythere* sp. and Cypridoidea indet. are represented only by instars or broken adult valves (Spadi et al., 2016) and are considered allochthonous (Whatley, 1988; Boomer et al., 2003). Besides ostracods, diatoms and sponge spicules referable to *Spongilla lacustris* were collected within the San Nicandro Fm. and rare Charophytes gyrogonites and mollusc fragments referable to genera *Succinea*, *Lymnaea* and *Bythinia* were recovered from both the San Nicandro and Valle Orsa formations.

The dendrogram obtained from the constrained cluster analysis performed on the normalized frequency matrix of the ostracod valves collected along the composite section cut in the Castelnuovo sub-synthem (Fig. 3.23) shows two well separated clusters that correspond to two different ostracod assemblages occurring, respectively, in the San Nicandro and Valle Orsa formations. The San Nicandro Fm. assemblage is composed by seven species, five of which are endemic and four of which are referable to genus *Caspiocypris* (Spadi et al., 2016). Sedimentological and palaeontological analysis on Fosso Bianco Fm. of Tiberino Basin (Chapter 2) (Basilici, 1997) permit to depict the palaeoenvironment occupied by a *Caspiocypris* spp. as a deep lacustrine facies (at least 50 m of depth) far from the lake margins. Similarly, in the Turiec Basin (Slovakia), the assemblages dominated by *Caspiocypris* is considered related to a deep lacustrine environments not disturbed by turbidites deposits of long-lived Palaeolake Turiec date Late Miocene (Pipik et al., 2012).

The presence of abundant *Spongilla lacustris* and diatoms which are all proxy of clear and carbonate-rich permanent water body in a temperate climate (Cohen, 2003) further support this conclusion.

Conversely, the ostracod assemblage of the Valle Orsa Fm., due to the co-occurrence of *Ilyocypris*, *Candona* and *Cypria*, suggests a shallow water environment with slightly flowing waters possibly linked to a nearby river delta. This palaeoecological interpretation matches well with the lithological and stratigraphic analyses, which indicated that the Valle Orsa Fm. was the result of the deposition of a Gilbert-type delta system.



**Figure 3.23:** Distribution of each species along the composite section. On the left side the comparison between the similarity of the samples and the lithology using constrained cluster analysis.

The palaeontological and facies analyses carried out on the San Demetrio-Colle Cantaro Synthem showed that the first filling sediments of the PSC basin, the white calcareous silts of the San Nicandro Fm., deposited in a rather deep lacustrine stable environment, as already suggested by Giaccio et al. (2012). Although the lake bottom waters were calm, the recovery of few Characeae gyrogonites and gastropod fragments together with the presence of millimetre sandy intercalations, suggest the episodic arrival of low-density turbidity currents coming from the lake margins that has been supposed bordered by high-gradient steep coastlines made of the pre-Pliocene bedrock. The lateral and overlying Valle Orsa Fm. was linked with a deltaic environment. In the delta areas different gravity depositional mechanisms alternated with the normal settling of the calcareous silts. The outcropping Gilbert-type delta bodies consist of 20° sloping gravel strata that were interpreted as the frontal portions of several deltas formed by bottomset, foreset and sometimes topset beds 30-40 m in thickness. According to Basilici (1997), this thickness let us to estimate that the Palaeolake San Nicandro was at least 40 m deep in its most profundal part. The San Nicandro Fm. shows a minimum surface extension of ca. 120 km<sup>2</sup>, from the Paganica village (to the north) to San Pio delle Camere village (to the south) (Bertini and Bosi, 1993; Nocentini et al., submitted). Based on these outcrops we can suppose that the Palaeolake San Nicandro had a length of at least 45 km and a width of 7-12 km. The other formations of the Castelnuovo sub-synthem give useful evidences of its lateral and coeval environments and suggest that the lake palaeo-margins were characterized by steep coastlines, as demonstrated by the breccia deposits, cross-cut by transverse water bodies forming alluvial fans (Valle Valiano and Madonna delle Neve formations).

Concerning the age of the Palaeolake San Nicandro, the presence of the ostracod assemblages dominated by *Caspiocypris* suggests a correlation between the San Nicandro Fm. and the Fosso Bianco Fm. in the Tiberino Basin, since this genus occurs in Italy after late Messinian only in these two sites. Thus, an upper Piacenzian– Gelasian age is inferred for both the Palaeolake Tiberino and Palaeolake San Nicandro. The presence in the Valle Orsa Fm. of *Candona* (*Neglecandona*) *permanenta*, up to now known only in the Paludonian Bed deposits of Serbia dated Pliocene-Gelasian (Krstić, 2006; Mandić et al., 2015) confirms and reinforces the chronological attribution and constrains the deposition of the upper part of the Castelnuovo sub-synthem to the Gelasian.

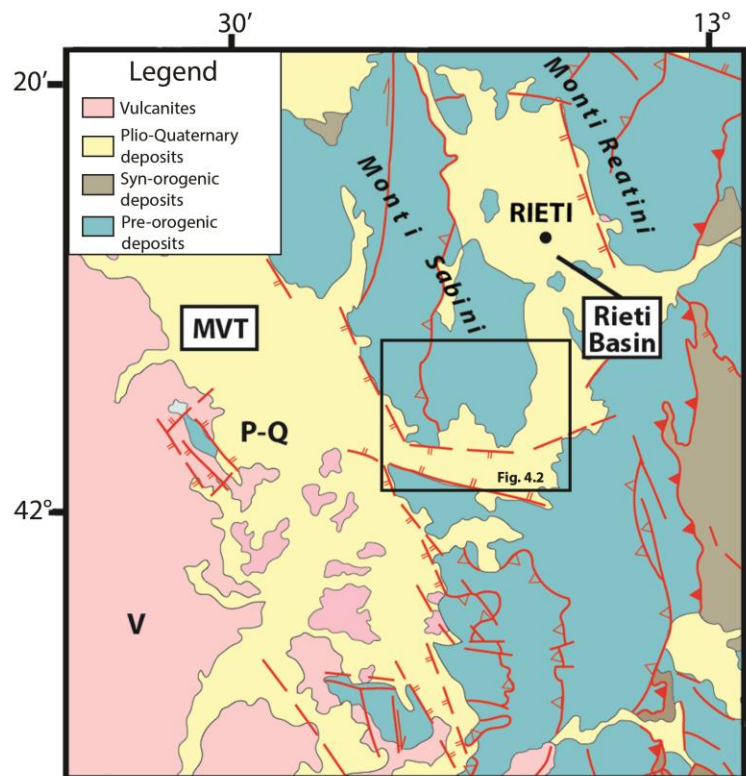
## 4. Rieti Basin

### 4.1 Geological Setting of Rieti Basin and Middle Valley of Tiber

The Rieti Basin is a huge sub rectangular intermontane basin located in the central Apennines (Fig. 4.1). It is an extensional tectono-sedimentary basin developed since the Pliocene and related to the extensional tectonics that affect the Apennine chain (Funciello & Parotto, 1978; Faccenna et al., 1996; Cavinato & DeCelles, 1999). The basin was filled by hundreds of meters of sediments, the younger of which, aged from middle Pleistocene to Holocene, are well known (Brunamonte et al., 1993; Calderoni et al., 1995; Michetti et al., 1995; Calderini et al., 1998), while the older ones result more debated (see Cosentino & Fubelli 2008; Mancini et al. 2008) due to the absence of significant fossil records. From middle Pleistocene until present time, the drainage of the entire basin is northwards, while during the early phases of the Rieti Basin evolution the continental facies showed a southward direction, where fluvial deposits interfingered with the transitional and marine ones along the Middle Valley of the Tiber river (MVT) (Mancini et al., 2007) (Fig. 4.1). Among other localities of central Italy, the non-marine deposits of the Rieti Basin and MVT provide a notably preserved terrestrial record of continental and shallow marine conditions during the late Pliocene-Early Pleistocene (Mancini et al. 2007; Barisone et al. 2014).

Barberi et al. (1995) studied the entire Rieti Basin deposits. In this paper, two different areas of deposition were distinguished, northern and southern sectors with a difficulty in depicted the relative relationships between them. The northern sector of the Rieti Basin successions cropping out in the sections

of Case Strinati, Fosso Filundici, and Madonna della Torricella with mainly fine sediments point to the existence of a permanent marsh-like pond probably during Calabrian age (Barberi et al., 1995). The southern part of Rieti basin was analyzed in more paper (Bertini & Bosi, 1976, Barberi & Cavinato, 1993, Cavinato, 1993, Barberi et al., 1995) and, has been recently described in the new



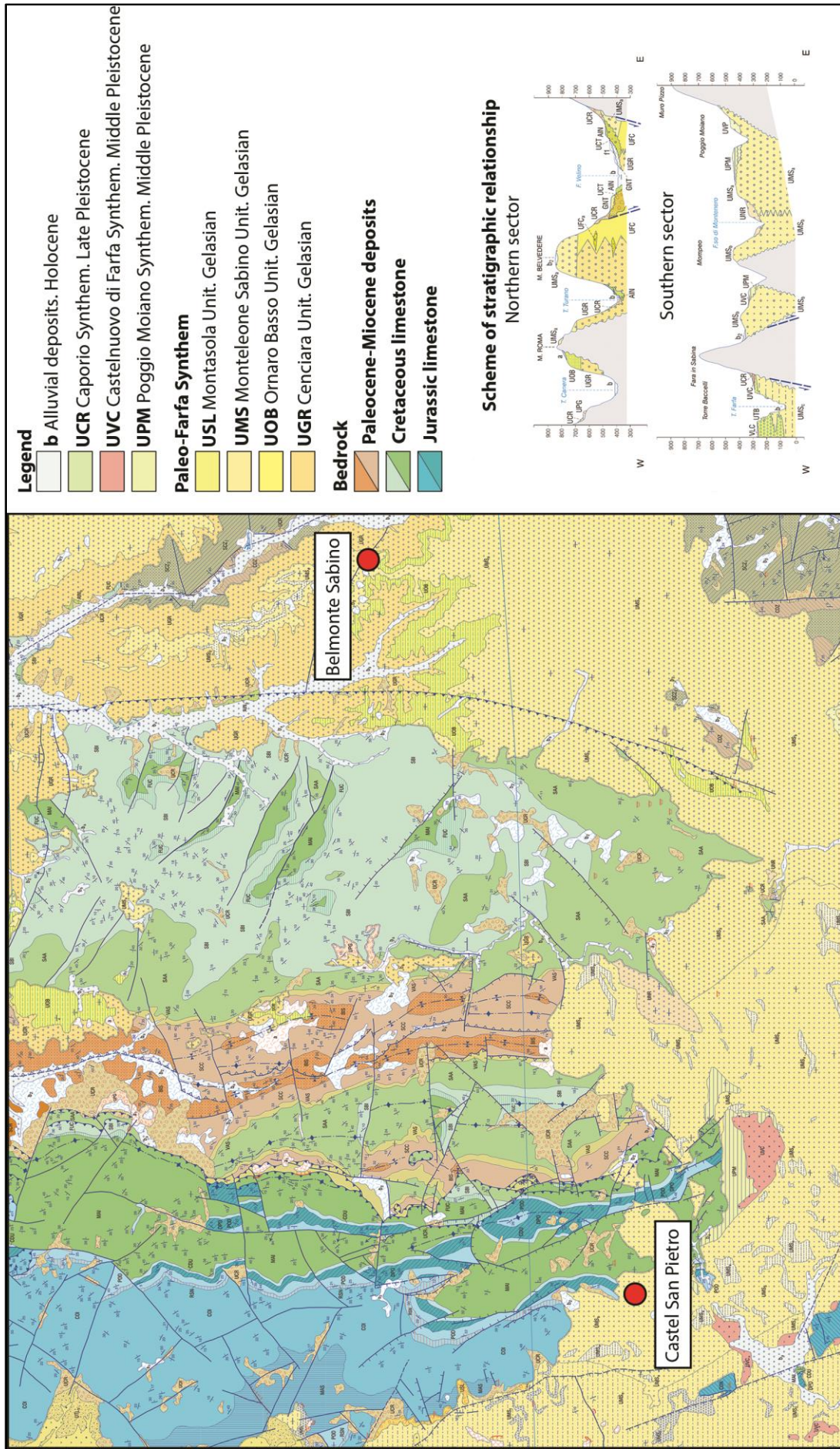
**Figure 4.1:** Location and geological setting of the study area, with large-scale (1:200000) geological map of the Rieti Basin and Middle Valley of Tiber river (MVT), modified from Cosentino et al. 2014.

geological sheet 357 within the CARG project of the Italian National Institute for Environmental Protection and Research (ISPRA). Three synthemms were distinguished: the Paleo-Farfa Synthem (late Pliocene-Gelasian), the Rieti Basin Supersynthem and the Farfa River Supersynthem (middle Pleistocene-Late Pleistocene) (Cosentino et al. 2014). While the last two synthemms are only described in the Rieti Basin, the first one is in common with the MTV.

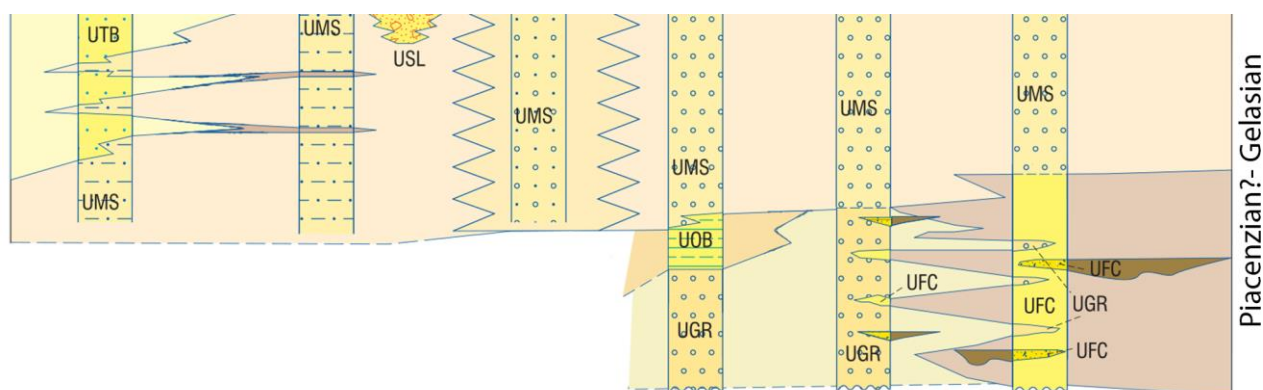
The study area is located about 50 km north of Rome at the convergence of the MVT and the Rieti Basin (Fig. 4.2). The early deposits of the MVT border and of the southern part of the Rieti Basin included in the Paleo-Farfa Synthem are subdivided in several lithostratigraphic units mainly linked to a fluvial environment and its related settings. From the oldest to the youngest these units are: Fosso Canalicchio Unit (UFC), Cenciara Unit (UGR), and Montasola Unit (USL) linked to slope and pedemontain areas; Ornaro Basso Unit (UOB) and Monteleone Sabino Unit (UMS) related to a distal part of a fluvial area; Torre Baccelli Unit (UTB) associated to a marginal marine environment (Cosentino et al. 2014).

The Paleo-Farfa Synthem is on angular unconformity carved in to the bedrock. The UFC is composed by coarse conglomerates deposited in a meter-thick strata deposited in proximal alluvial fan area with transport direction to the west. The same interpretation was made also for UGR and USL and there are differentiated on the base of the composition of the clasts and for area of feeding. The UOB is composed by white calcareous silts and sands, with some conglomeratic intercalations deposited in a lacustrine environment, while the mainly conglomeratic and coarse sands strata deposited in a braided fluvial plain. UMS is interfingered with near shore marine unit of UTB outcropping on the MVT (Fig. 4.3) (Cosentino et al., 2014).





**Figure 4.2:** Geological map of Rieti Basin and Middle Valley of Tiber river from sheet 357 Cittaducale ISPRA modified from Cosentino et al., 2014.



**Figure 4.3:** Chronostratigraphic scheme for the Paleo-Farfa Synthem deposits. Modified from Cosentino et al., 2014.

In the southern part of the Rieti Basin, few ostracod records are reported in literature. One section cut in the UOB bore scarce *Candona* juv., *Ilyocypris* juv. *Herpetocypris* sp. and *Cypris pubera* Müller, 1776 associated with scarce aquatic and terrestrial gastropods and to an in situ trunk of a Taxodiaceae. The paleoenvironmental interpretation point to a hydrosol developed in a braided plain (Barisone et al., 2014). Two sections cut in the UMS, cropping out near the Belmonte Sabino village (Fig. 4.2) gave more diversified and abundant ostracod assemblages composed by *Ilyocypris bradyi* Sars, 1890, *Candona* (*Neglecandona*) *neglecta* Sars, 1887, *Fabaeformiscandona fabaeformis* Fischer, 1815, *P. albicans* (Brady, 1864), *Cyclocypris laevis* (Müller, 1776), *Herpetocypris* cf. *H. chevreuxi* (Sars, 1896), and *Potamocypris zschokkei* (Kaufmann, 1900). This assemblages point to the presence of permanent shallow water bodies fed by springs (Barberi et al., 1995). In the southern part of MTV ostracods were studied from two boreholes Colle San Lorenzo (Fara Sabina) and Colle Cigliano (Marcellina), close to the ends of geological sheet 357 to the south, both correlatable with UMS (Ligios et al., 2009). Colle San Lorenzo contains only true freshwater taxa as *Vestalenula longissima* Ligios, Minati, Gliozzi & Krstić, 2009, *Pseudocandona marchica* (Hartwing, 1899), *Cyclocypris ovum* (Jurine, 1820), *Ilyocypris gibba* (Ramdohr, 1808), *Ilyocypris* cf. *I. getica* Masi, 1906, *Cypris* cf. *C. pubera* Müller, 1776, and *Cypridopsis vidua* (Müller, 1776). The Colle Cigliano borehole shows an ostracod assemblage composed by *Vestalenula pliocenica* Ligios, Minati, Gliozzi & Krstić, 2009, and *Cyprideis* sp. (Jones, 1850). Thus, probably this assemblage points to a shallow freshwater-oligohaline environment (Ligios et al., 2009). Along the boreholes, these associations alternated with assemblages dominated by *Cyprideis*, marine ostracods and benthic foraminifers, testifying an instable marginal marine environment the evolution of which was linked to tectono/eustatic movements (Ligios et al., 2009). The same indications come from two different section collected in the southern part of MTV: Stazzano and Nerola section (Gliozzi, unpublished data). From Stazzano section the only non-marine ostracods species is *Psychodromus olivaceus* (Brady & Norman, 1889).



At the same time, Nerola section, collected in the silty layer of UMS close to the Acquaviva village, contain a well preserved ostracod association composed by: *C. (N.) neglecta* Sars, 1887, *Pseudocandona albicans* (Brady, 1864), *C. ovum* (Jurine, 1820), *Ilyocypris bradyi* Sars, 1890, *I. vertesi* Diebel & Pietrzieniuk, 1964, *Herpetocypris brevicaudata* Kaufmann, 1900, *Potamocypris zschokkei* ((Kaufmann, 1900), *P. fallax* Fox, 1967, *Paralimnocythere messanai* Martens, 1992.

The Paleo-Farfa Synthem was cut by a paleosurface that is widely recognized in the central Apennines and was interpreted as a regional erosional landscape generated in conditions of arid climate and low relief. No continental deposits were found on this relict surface (Fubelli et al., 2014). The paleosurface intersected the marine deposits of MVT in presence of a well-known paleoshoreline testified by *Lithodomus* holes carved in the calcareous Mesozoic bedrock at an elevation of 260–277 m above the present sea level (Mancini et al., 2007). In the debate about the age of the Paleo-Farfa Synthem deposits cropping out along the south Rieti Basin and MTV there are two conflicting hypothesis: the first one relate them to the Calabrian (Mancini et al., 2007; 2008), the second to the Gelasian (Cosentino & Fubelli, 2008; Cosentino et al., 2014).

In this thesis, we test the two chronological hypotheses through the study of one fossiliferous succession cropping out near the Castel San Pietro (CSP) village, cut into the Monteleone Sabino Unit (UMS). In the CSP site, UMS is composed of sub-horizontal beds of well-rounded, clast-supported conglomerates, with coarse to medium calcareous pebbles in a sandy matrix. Beds are up to 10 m thick and are characterized by trough and planar cross bedding. There are also sandy-silty and clay levels including lignite lenses. The UMS belongs to a gravel-bed braided fluvial system, deposited in an unstable environment. According to the literature, this environment was most likely dominated by an alluvial plain with the presence of stable small lakes and ephemeral ponds (Cosentino et al. 2014; Barisone et al. 2014).

The CSP site (42°15'58"N, 12°43'04"E and 285 m a.s.l) (Fig. 4.2) is very close to the paleosurface summit) and consists of clays with lignite lenses about one meter-thick cropping out along a stream-cut. The site corresponds to an old mine used for the extraction of lignite. During 1800s several large mammal remains were excavated in the mine (Tuccimei, 1889a, 1889b, 1898) such as *Stephanorhinus etruscus*, *Anancus arvernensis*, *Castor fiber*, *Cervus* sp., and *Leptobos* sp.) together with many badly preserved gastropods were recognized. The rediscover of this historical site was important to integrate the paleontological knowledge also with fossil ostracods and carpological remains (Pandolfi et al., 2017).

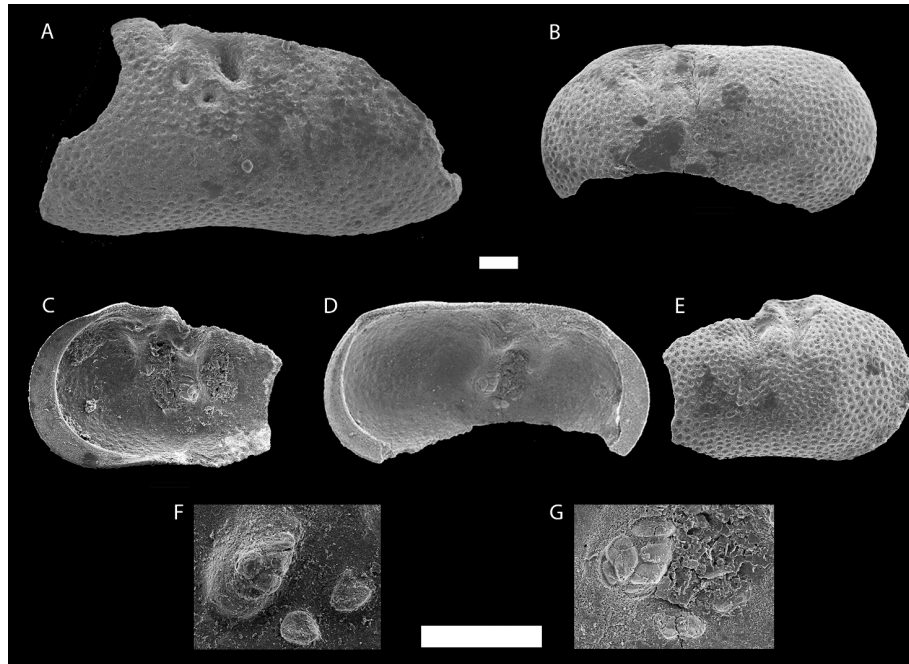


## 4.2 Materials and methods

Several samples were collected along the stream from the CSP site and were analysed for paleontological content. Unfortunately, the lignite mine was abandoned during the beginning of the second half of the 1900's; accordingly, the new samples were collected only from the outcropping clays and lignite beds; these may not be the same levels that yielded the large mammal remains reported in literature. Due to the sub-horizontal bedding and the little thickness, we considered all the clay samples as collected from the same stratigraphic level. In total, more than 15 kg of sediment were soaked in a H<sub>2</sub>O<sub>2</sub> 5% solution for 24 hours, sieved with a 0.125 mm-mesh sieve and dried. Ostracods were handpicked and identified under the stereomicroscope Nikon SMZ-U. Valves of adult ostracods were studied using the Scanning Electron Microscope in LIME laboratories of Università di Roma TRE. The ostracod shells are stored at the Gliozzi Ostracod Collection (GOC), Department of Science, Università degli Studi di Roma Tre, mounts M354, M366 and M382.

## 4.3 Results

In the material collected from the CSP site ostracods were scarce and fragmentary (Fig. 4.4). Fragmented valves of Ilyocyprididae and few valves of Candoninae juveniles compose the entire ostracod association. Ilyocyprididae valves present all the characters typical of the genus *Qinghaicypris* Huang, 1979, revised by Yang et al. (2004) and by Rodríguez-Lázaro & Martín-Rubio (2005) i.e. the adductor muscle scar pattern made of 6 scars (Fig. 4.4 F, G), the large size, the sub rectangular outline with well-marked cardinal angles, and a deep mid-dorsal sulcus. The species assignment of the CSP material, instead, is difficult due to the fragmentary material, but the comparisons allowed to suggest their attribution to *Qinghaicypris* cf. *Q. riojensis* Rodríguez-Lázaro & Martín-Rubio, 2005. Its presence in the CSP site represents the first record of this species in Italy. According to Rodríguez-Lázaro & Martín-Rubio (2005) and Krstić (2006), *Q. riojensis* was found in shallow lacustrine environments.



**Figure 4.4:** Ostracods from CSP, UMS, Italy. **A-G**, *Qinghaicypris* cf. *Q. riojensis*. **A**, lateral view of a left female valve, M366/1/1. **B**, lateral view of a left juvenile female valve, M366/1/3. **C**, lateral inner view of a right juvenile female valve, M366/1/2. **D**, lateral inner view of a left juvenile female valve, M366/1/3, illustrated in B. **E**, lateral external view of a right juvenile female valve, M366/1/2, illustrated in C. **F**, detail of central muscle scars in inner view of a left female valve, M366/1/1, illustrated in A. **G**, detail of central muscle scars in inner view of a left juvenile female valve, M366/1/3, illustrated in B. Scale bars = 100  $\mu$ m, upper one for A-E and lower one for F-G.

## 4.4 Discussion

### 4.4.1 Biostratigraphy

Although the CSP ostracod assemblage is composed by only one species, *Qinghaicypris riojensis*, this datum give interesting chronostratigraphic information. In fact, *Qinghaicypris* is known from the early Messinian of the Baccinello-Cinigiano Basin (Tuscany, central Italy) (Ligios, 2009; Ligios et al., 2012) to the Early Pleistocene (Gelasian) of southern Europe and China (Rodríguez-Lázaro & Martín-Rubio, 2005). In particular *Q. riojensis* is surely described from the Piacenzian deposits of the Ebro Basin (northern Spain) (Rodríguez-Lázaro & Martín-Rubio, 2005) and the Lower and post-Paludinic Beds of Serbia (Krstić, 2006). In a recent revision of the Neogene and Quaternary deposits of Lake Slavonia (mainly Croatia and Serbia) (Mandic et al., 2015) the Lower to post-Paludinic beds are referred to the Cernikian stage, corresponding to a time interval from Zanclean to Gelasian (between  $\sim$ 4.5 and  $\sim$ 1.8 Ma). Accordingly, the presence of ostracod species related to *Qinghaicypris* cf. *Q. riojensis* in the CSP points to a maximum age deposition within the Gelasian (Rodríguez-Lázaro & Martín-Rubio, 2005).

This chronostratigraphic indication is in agreement with the biostratigraphical data given from the revision of the large mammal remains and the study of molluscs and carpological remains made

by Pandolfi et al. (2017) as well as by the stratigraphical correlations of other sections in the CSP nearby area.

According to Pandolfi and Marra (2015) and Pandolfi et al. (2016), the first occurrence of *Stephanorhinus etruscus* in Italy is at the Pliocene-Pleistocene transition, during the Montopoli FU (= Faunal Unit). The mastodon *Anancus arvernensis* is recorded during the Pliocene and the Early Pleistocene in Italy (Gliozzi et al., 1997), spanning from Triversa to Coste San Giacomo FUs. Fossil evidence suggests that *A. arvernensis* became extinct at the beginning of the late Villafranchian, Olivola FU (Palombo et al., 2002; Rook & Martínez-Navarro, 2010). The importance given by Tuccimei (1899a, 1891) to the beaver as a biostratigraphical marker is now discarded (Barisone et al., 2006). Remains of Bovidae, Cervidae and ?Hippopotamidae from CSP (Tuccimei, 1889a, 1889b, 1898) were not figured or described and it is impossible to give a precise systematic attribution for these taxa. Accordingly, the coexistence of *A. arvernensis* and *S. etruscus* at CSP suggests an age for this site spanning from Montopoli to Coste San Giacomo FUs (Gelasian), although a slightly younger age (Olivola FU, uppermost Gelasian) cannot be ruled out (Pandolfi et al., 2017).

The same age is suggested by the carpological remains. From the biochronological point of view, the relevant occurrences are those of several Neogene taxa that got extinct in Europe during the Pliocene and Pleistocene: *Actinidia faveolata*, *Decodon globosus*, cf. *Eurya*, *Liriodendron geminata*, *Potentilla pliocenica*, *Pterocarya limburgensis*, and *Schoenoplectus isolepioides*. Among these, *Schoenoplectus isolepioides* has so far been detected only in the Piacenzian (Irace et al., 2017), whereas *Actinidia faveolata* is rarely reported also in the Gelasian (Tiglian), even in central Europe. At the present state, when considering that central Italy was certainly a refuge area for humid thermophilous plants in the Pliocene-Pleistocene (Martinetto, 2001; Martinetto et al., 2017), the indications of the CSP palaeoflora are for a Piacenzian or Gelasian age (Pandolfi et al., 2017).

Other chronological indication comes from several stratigraphic sections, which are close or in correspondence to the paleosurface: (1) Bocchignano; (2) Torre Baccelli; (3) Stazzano; (4) Castel Chiodato and Molino del Moro; (5) “Santa Rufina” and “I Cappuccini”; and (6) Colle San Lorenzo and Colle Cigliano boreholes (Barberi et al., 1995; Cosentino & Fubelli, 2008; Ligios et al., 2009):

As well express before, CSP was deposited without a doubt during Gelasian (Pandolfi et al., 2017), while Bocchignano, where crop out UMS deposits, contains mammal remains referable to *Equus stenonis*, *Hippopotamus antiquus*, *Mimomys polonicus* vel *M. pliocaenicus* (Tuccimei 1889a), but this assemblage was not considered homogeneous (Mancini et al., 2008). Nevertheless, in the light of new finds in the well know locality of Coste San Giacomo, typical of upper part of Gelasian (between ~2.1 and ~1.9 Ma, Bellucci et al., 2014) the coexistence of *Mimomys pliocaenicus* and

*Hippopotamus antiquus* is fine demonstrated (Bellucci et al., 2012; Bona et al., 2015) so also Bocchignano site probably correspond to the Coste San Giacomo UF (upper part of Gelasian).

Torre Baccelli section represents a delta-plain paleoenvironment and is located very close to the paleosurface (270 m a.s.l.) approximately 500 meters southwest of the Torre Baccelli power plant (~ 1 km southwestern of CSP). The uppermost samples of the Torre Baccelli section provided one M<sup>1</sup> of *Apodemus* cf. *A. atavus* and an abundant pollen record characterized by Taxodiaceae, *Symplocos*, *Nissa*, *Hamamelis* and *Distylium* (Barisone et al., 2014). These palynomorphs consist of several elements that persist in central Italy until the Gelasian, in particular *Symplocos* and *Nyssa*. The findings of molar tooth of *Apodemus* is important, in fact, *A. atavus* is found in Italy and southern Europe from late Messinian (~ 5.4 Ma, Colombero et al., 2014) to Early Biharian (~ 1.6 Ma, Sala & Masini, 2007). Definitely, the time span of Torre Baccelli section from the concomitance presence of some residual palynomorphs and molar tooth of *Apodemus* to Piacenzian and Gelasian.

Stazzano section shows the sea level marker related to the paleoshoreline between 261 m and 277 m a.s.l., where *Lithophaga lithophaga* pierced horizons crop out (Cosentino & Fubelli, 2008). In this area marine gastropod-bearing black sandy silts (*Hydrobia (Peringia) ulvae*, *H. (P.) acuta*, *Mohrensternia angulata*, *Potamides tricinctus*, *Hynia prismatica*, *Theridium* cf. *T. vulgatum*, *Bittium* cf. *B. reticulatum*) define a brackish coastal lagoon environment. The occurrence of *M. angulata* could be of biochronological interest. Indeed, the distribution of *M. angulata* spans from the Miocene to Gelasian (Malatesta, 1974).

Both the section of Castel Chiodato and Molino del Moro represent by fine grained deposit that passed from shallow marine to shallow freshwater lakes with a coarsening-upward trend. Both of them bearing *Amphistegina*-rich sand layers. In central Italy, two *Amphistegina* levels have been found in Pliocene-Pleistocene strata (Di Bella et al., 2005). The youngest of these levels (Gelasian) also occurs in the MVT (Mancini et al., 2004), so the occurrence of *Amphistegina* spp. within the coastal sediments suggests a deposition during the last warm oscillation before the strong Gelasian-Calabrian climatic deterioration (2.1 Ma) (Di Bella et al., 2005).

In the northernmost deposits of UMS in the Rieti Basin, other scanty mammal remains were found. In particular, a dental of *Equus stenorhis* and a tusk of *Mammuthus meridionalis* (Barberi et al., 1995). Their coexistence spans from Montopoli to Pirro FUs (~2.6- 1.3 Ma, Gelasian-Calabrian) (Glozzi et al., 1997; Masini & Sala, 2007).

In the previously described, Colle Cigliano and Colle San Lorenzo boreholes, several ostracods species were found (Ligios et al., 2009). Between them, the only extincted species are *Vestalenula longissima* and *V. pliocaenica*. *Vestalenula longissima* is a endemic species found only in the MVT while *V. pliocaenica* it was found in the MVT, in the late Miocene of Crete (Greece) and central Italy,

and in the lower and middle Paludinic Beds (Krstić, 2006). The lower and middle Paludinic Beds correspond to interval Zanclean-Piacenzian (Mandic et al., 2015) so probably the entire presence interval for this species is Tortonian-Gelasian as indicated by Ligios et al., 2009).

According to all of these independent biochronological and biostratigraphic data, the oldest deposits of the southern part of the Rieti Basin and MVT can be referred to the Gelasian as proposed by Cosentino and Fubelli (2008) and Cosentino et al., (2014) as well as the occurrence in Italy of *Qinghaicypris* cf. *Q. riojensis*.

#### **4.4.2 Paleoenvironmental and paleoecological observations**

The Monteleone Sabino Unit (UMS) deposits represent the upper part of the Paleo-Farfa Synthem along the Rieti Basin and its junction with the MVT. The main lithologies of this unit are related to the fluvial deposition. Cosentino et al. (2014) accurately described the facies variation within UMS and devised a general southern drainage. The Paleo-Farfa River flowed principally in a braided plain dominated by coarse transport. The CSP lignite and the fine-grained deposits can be associated to lateral variations of this general setting. The sedimentological analysis of the UMS suggests its deposition in a floodplain separated by swamp and lacustrine areas (Cosentino et al. 2014); the CSP sequence was deposited in an environment similar to the latter. Due to the presence of ostracods (*Qinghaicypris* cf. *Q. riojensis*), molluscs (*Viviparus* sp., *Bithynia* sp., *A. fluviatilis*, *P. planorbis*), and freshwater macrophyte flora (*Potamogeton*, *Cladium*, *Decodon*, *Schoenoplectus*), we conclude that the CSP site was occupied by a shallow freshwater lake or pond where lignite deposition was enhanced. Carpological remains suggest that the lignite beds of the CSP section were deposited during a humid and warm temperate climate interval (Pandolfi et al., 2017).

## 5. Taxonomic Harmonisation of Neogene and Quaternary Candoninae genera of the Paratethys

### 5.1 Introduction

The recovery in the Tiberino and L'Aquila Basin of abundant Candoninae valves not referable to any "European" Candoninae genera (i.e. *Candona* (*Candona*), *Candona* (*Neglecandona*), *Fabaeformiscandona*, and *Pseudocandona* among the most widespread and rich in species genera) arose the problem of their taxonomical attribution and their possible origin. The Tiberino and L'Aquila valves shared an evident and peculiar shell character, namely a robust ledge below the groove of the left valve hinge that was not present in the above listed Candoninae, but was a constant character of several fossil Candoninae of the Neogene and Quaternary of the Paratethys. Starting to study the huge literature on the Paratethyan ostracods, it immediately stood out that there was a great confusion in the ostracod taxonomy of the area, due to the old literature that included only hand-made pictures of ostracods, often very small in size (cf. Livental, 1929), unclear transmitted light pictures and, frequently, poor descriptions of the diagnostic characters. Danielopol et al. (2015), discussing the evolution of the communication systems within the International Research Group on Ostracoda highlighted how the recent media revolution and the changed historical-political conditions influenced positively the international scientific interchanges. The lack of those conditions until the '90 of the last century made the Eastern Europe a "cultural island" with very few possibilities to exchange scientific opinions and papers. In the case of the Paratethyan Candoninae, this resulted in a confused taxonomy, with different names attributed to the same taxa.

A preliminary observation of the Tiberino and L'Aquila Candoninae showed a great similarity with several species referred to genus *Caspiocypris* Mandelstam in Schneider et al., 1956, but when the study went more in detail it emerged that it was not really clear what *Caspiocypris* was and, furthermore, some other genera such as *Thaminocypris* or *Lineocypris* were used by some authors (i.e. Sokac, 1972 and Krstić, 1972) to indicate species that could have also been referred to *Caspiocypris*.

To unravel this confusion, we decided to undertake the taxonomical revision of the Paratethyan Candoninae, starting, when possible, with the direct observation of the type material stored in different Museums and Institute. Thus, we went to Zagabria, Belgrade, Budapest, and St. Petersburg to study the material preserved in the historical collections by Sokač, Krstić, Zálányi, Mehes, Mandelstam, Schneider, Luebimova, etc. Since some of the important collections was missing or incomplete, we had the possibility to get (or directly collect) new material from the type localities of Babazanan (Azerbaijan) (Livental, 1929) and Obrenovac (Serbia) (Zálányi, 1929).

The results of this research is reported in the hereinafter paragraphs.

## 5.2 The subfamily Candoninae in the Paratethys

During the Cenozoic, the constant northward movement of the African plate led to the division of the Tethys Ocean into two branches: the southern Palaeomediterranean and the northern Paratethyan domain, this latter feature was represented by a huge epicontinental brackish sea that extended across central Europe and western Asia. Starting from the Oligocene (~35 Ma), the Paratethys was a large epicontinental brackish sea that spread from central Europe into western Asia (Rögl, 1998; Popov et al., 2006). It was divided into several basins located in the central Paratethys (Styrian, Vienna and Pannonian basins) and in the eastern Paratethys (Dacian, Euxinic, and Caspian-Aral basins) that, during Neogene and Quaternary, underwent several palaeogeographic modifications (repeated isolation and connections) and severe palaeoenvironmental variations. The Black Sea and the Caspian Sea today represent the relicts of the huge past Paratethys water body. To all the palaeoenvironmental and palaeogeographic changes, ostracods (particularly Candoninae, Loxoconchidae and Leptocytheridae) responded with huge adaptive radiations and migrations, representing very useful proxies for the reconstruction of the past geological events. Neogene and Quaternary ostracods from the Paratethys bioprovince originated through huge adaptive radiations, which gave rise to endemic brackish genera and species. Unfortunately, much confusion surrounds their taxonomy, due to the quality of information and images in the original old literature and the incompleteness of the type material, making necessary a taxonomic revision.

In this chapter, we undertook the systematic revision of several Paratethyan endemic genera included in the subfamily Candoninae based on the analysis of the type material from some historical collections, new material collected from the type localities, and new material from the Ponto-Caspian area. The analysis was focused on the description of the valves morphological characters and on the geometric morphometric analysis of the valve outline.

Among the non-marine ostracods, the subfamily Candoninae is the most diverse and abundant systematic group, with ca. 510 living species allocated in 37 genera (Martens & Savatnalinton, 2011). Recently, Danielopol et al. (2011a) suggested that the taxonomic system currently accepted for the subfamily must be renewed including the re-examination of the diagnostic criteria. In fact, compared with other ostracod groups, the Candoninae carapaces often record only few characters usable for the specific or generic attribution (Danielopol et al., 2008) and most of the diagnostic characters for the living genera and species relies on soft parts (Danielopol, 1973; Meisch, 2000). Consequently, the taxonomy of fossil Candoninae is particularly hard to decipher.

Krstić & Guan (2000) proposed a systematic re-assessment of the subfamily Candoninae into 20 tribes that grouped 68 fossil and living genera (plus 9 left in open nomenclature). Thirty-three of them were widespread during Neogene and Quaternary in the Paratethys and, as far as we know, only



one includes also a living representative (*Camptocypria camelus* Schornikov in the Caspian Sea) (Schornikov, 1966). The description of the Paratethyan genera were based only on the shell features and, in some cases, the diagnoses were not enough detailed to allocate with certainty the different species. Consequently, some authors (Danielopol et al., 2008; 2015; Olteanu, 2011) claimed the need of a systematic revision.

In this paper we have tried to carry on the Taxonomic Harmonisation of the Paratethyan Candoninae genera listed by Krstić & Guan (2000) (Tab. 5.1). Most of them were described in old papers using only hand drawings. Moreover, often the location of the type material was impossible to be recovered (for example the original collections of V.E. Livental and D.A. Agalarova), or its status was incomplete (B. Zálányi and G. Méhes collections) or poorly preserved. Starting to review the Paratethyan Candoninae with the comparison of several synonymy lists published in more than 160 years since Reuss (1850), it became obvious to us that only the analysis of the type material or of new material collected from the type localities could provide us with the new data necessary for a systematic revision. During, the analysis of central Apennines basins, main target of this thesis, two different *Caspiocypris* species flock (Chapter 2 and Chapter 3). This making necessary a full understanding of Paratethyan Candoninae and their taxonomic harmonisation.

The aim of this chapter is to revise the Paratethyan fossil Candoninae taxonomy at the generic level using transmitted light and Scanning Electron Microscope (SEM) pictures to better depict the morphological characters of the valves and the geometric morphometric analysis of the valve outline. The revision of the Paratethyan Candoninae will be important to estimate the palaeobiodiversity of the Paratethyan domain as well as to decipher its complex Neogene and Quaternary palaeogeographic evolution. This study considerably reduces the taxonomic uncertainty within the Paratethyan Candoninae, providing new data for the evaluation of the palaeobiodiversity of the Paratethyan domain. Finally, the palaeobiogeography of Paratethyan Candoninae during Neogene and Quaternary is also discussed.

Genus	Author	Year
<i>Advenocypris</i>	Schneider	1956
<i>Bakunella</i>	Schneider	1958
<i>Bononiella</i>	Stancheva	1984
<i>Camptocypris</i>	Zalányi	1959
<i>Candoniella</i>	Schneider	1956
<i>Caspiocypris</i>	Mandelstam	1956
<i>Caspiolla</i>	Mandelstam	1960
<i>Caspiollina</i>	Mandelstam	1957
<i>Dacicandona</i>	Stancheva	1981
<i>Graviacypris</i>	Schneider	1963
<i>Hastacandona</i>	Krstić	1972
<i>Labiatocandona</i>	Krstić & Stancheva	1990
<i>Lineocypris</i>	Zalányi	1929
<i>Liventalina</i>	Schneider	1963
<i>Moesiella</i>	Olteanu	1995
<i>Ochridella</i>	Krstić	1969
<i>Paracaspiocypris</i>	Schneider	1963
<i>Pontoniella</i>	Mandelstam	1960
<i>Propontoniella</i>	Krstić	1972
<i>Propontoniella?</i>	Krstić	1972
<i>Rectocypris</i>	Schneider	1958
<i>Reticulocandona</i>	Krstić	1972
<i>Serbiella</i>	Krstić	1971
<i>Sinegubiella</i>	Krstić	1972
<i>Sirmiella</i>	Krstić	1972
<i>Telekia</i>	Sohn & Morris	1963
<i>Thaminocypris</i>	Zalányi	1944
<i>Tuberoandona</i>	Olteanu	1995
<i>Turkmenella</i>	Schneider	1963
<i>Turkmenella?</i>	Krstić	1972
<i>Typhlocyprella</i>	Krstić	1972
<i>Zalanyiella</i>	Krstić	1972
<i>Zalanyiella?</i>	Krstić	1972

**Table 5.1:** List of the Paratethyan Candoninae genera reported by Krstić & Guan (2000) analysed in the present chapter.

### 5.3 Material and Methods

For the studied material, we used the standard terms accepted by the ICZN (holotype, paratype(s), lectotype, paralectotype(s), syntype(s), topotype(s), neotype(s), and type species). Digital pictures of the type material were taken with optical stereomicroscopes at the storing institutions. For the kind permission of the curators it was possible to move part of the syntypic material to the

Micropaleontology Laboratory of the Department of Science, Università Roma Tre, where it was pictured in transmitted light under Leica DM1000 stereomicroscope using LAS Multifocus System and under Philips XL-30 Scanning Electron Microscope (SEM) at the LIME Laboratory (University of Roma Tre).

Unfortunately, for some genera we were not able to see directly the material. In some of these cases the published descriptions and/or illustrations were enough to decipher the main characteristics (*Bononiella*, *Ochridiella*, *Paracaspiocypris*, *Propontoniella?*, *Rectocypris*, and *Tuberocandona*) and, although they have not been analysed in detail, they are discussed in the systematic part. In other cases (*Caspiollina*, *Dacicandona*, *Liventalina*, and *Turkmenella*), the descriptions and/or illustrations were very poor and their definition remains still unclear.

The geometric morphometric analysis of the valve outline has been performed on the type material. Starting from the digital pictures, the outline of each valve was digitized using TPSdig v. 2.20 software (Rohlf, 2009) and the morphometric analysis was performed with the software MORPHOMATICA 1.6.01 (Baltanás et al., 2003; Linhart et al., 2007; Baltanás and Danielopol, 2011), which approximates the outlines using B-spline curves. We used 16 control points to approximate each outline. To display the distribution of each specimen in the morphospace, non-metric Multidimensional Scaling (nMDS) through the software PRIMER v. 6 (Clarke & Gorley, 2006) was used, based on the Euclidean matrix of differences in the total area between each outline (Linhart et al., 2007). The goodness-of-fit statistic was tested using the stress values (Clarke & Warwick, 2001).

The material examined is deposited in the following collections (see Appendix) (acronyms as used along the text):

**MFGI**, Magyar Földtani és Geofizikai Intézet (Geological and Geophysical Institute of Hungary) – Zalányi's and Méhes' collections;

**NHMZ**, Hrvatski prirodoslovni muzej (Natural History Museum of Zagreb, Croatia) – Sokač's collection;

**NHMB**, Prirodnjački muzej Beograd (Natural History Museum of Belgrade, Serbia) – Krstić's collection;

**VNIGRI**, Laboratory of Micropaleontology of All Russia Research Institute of Oil and Geological Prospecting, St. Petersburg, Russia – Mandelstam's collections;

**GOC**, Gliozzi Ostracod Collection, Department of Science, Università Roma Tre, Rome, Italy;

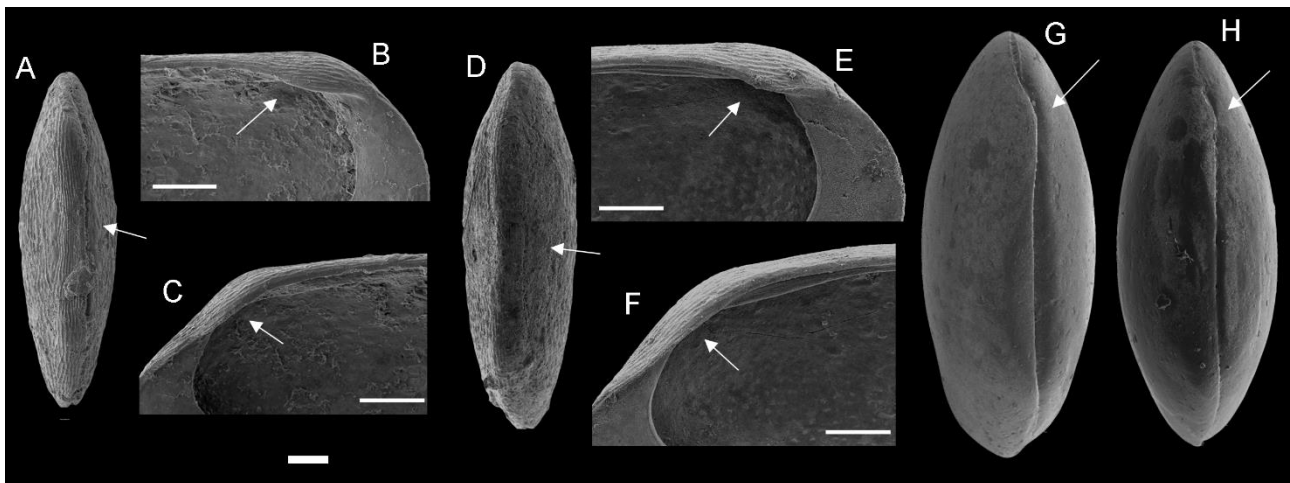
Along the text the following abbreviations were used: L, length; H, height; LV, left valve; RV, right valve; C, carapace.

## 5.4 Results

### *Morphological characters of the analysed valves*

The fossil non-marine ostracods, and particularly the Candoninae, are rather difficult to be identified because of the lack of ornamentation (in most cases), the simple adont hinge and very few distinctive shell characters other than the form (=shape plus size according to Danielopol et al., 2011b) usable for the specific or generic attribution (Danielopol et al., 2008; Baltanás & Danielopol, 2011). The valve form has been investigated using the geometric morphometric analysis and the results are reported in the next paragraph. Here we report some little differences of the shell features we recognized with the aid of SEM and transmitted light pictures.

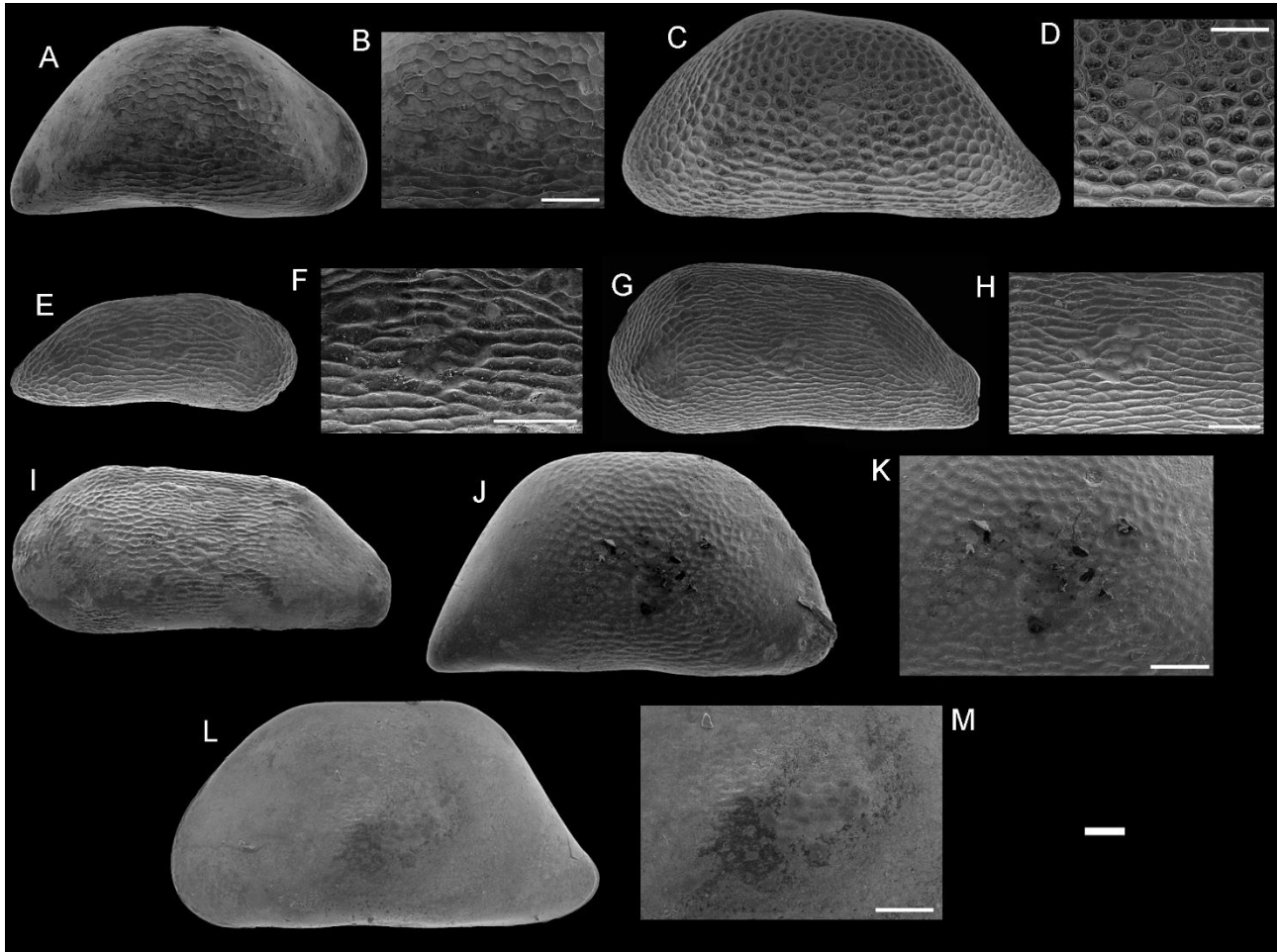
**Valve overlapping:** the LV overlaps the RV in all the examined genera but the overlapping is particular in: *Serbiella* and *Pontoniella* that show a wide overlapping along the whole dorsal border with the hinge margin of the LV that is folded on the RV particularly in correspondence with the cardinal angles (Fig. 5.1 A-F); *Camptocypria* and *Caspiolla*, in which LV overlaps RV particularly in correspondence of the anterior dorsal lobe (Fig. 5.1 G-H).



**Figure 5.1:** SEM pictures of some Paratethyan Candoninae genera showing the different overlapping of the LV on the RV (white arrows). For explanations, see the text. **A-C**, *Serbiella hastata*. **A**, female C in dorsal view, sample Obrenovac 10; **B**, female LV in inner view, detail of the anterior overlapping, sample Obrenovac 10; **C**, female LV in inner view, detail of the posterior overlapping, sample Obrenovac 10; **D-F**, *Pontoniella acuminata*. **D**, female C in dorsal view, sample Mt. Medvenica VII-29; **E**, female LV in inner view, detail of the anterior overlapping, sample Mt. Medvenica VII-29; **F**, female LV in inner view, detail of the posterior overlapping, sample Mt. Medvenica VII-29. **G**, *Camptocypria alasi*, female C in dorsal view, sample Obrenovac 14; **H**, *Caspiolla balcanica*, female C in dorsal view, sample Obrenovac 1. White bars correspond to 0.1 mm.

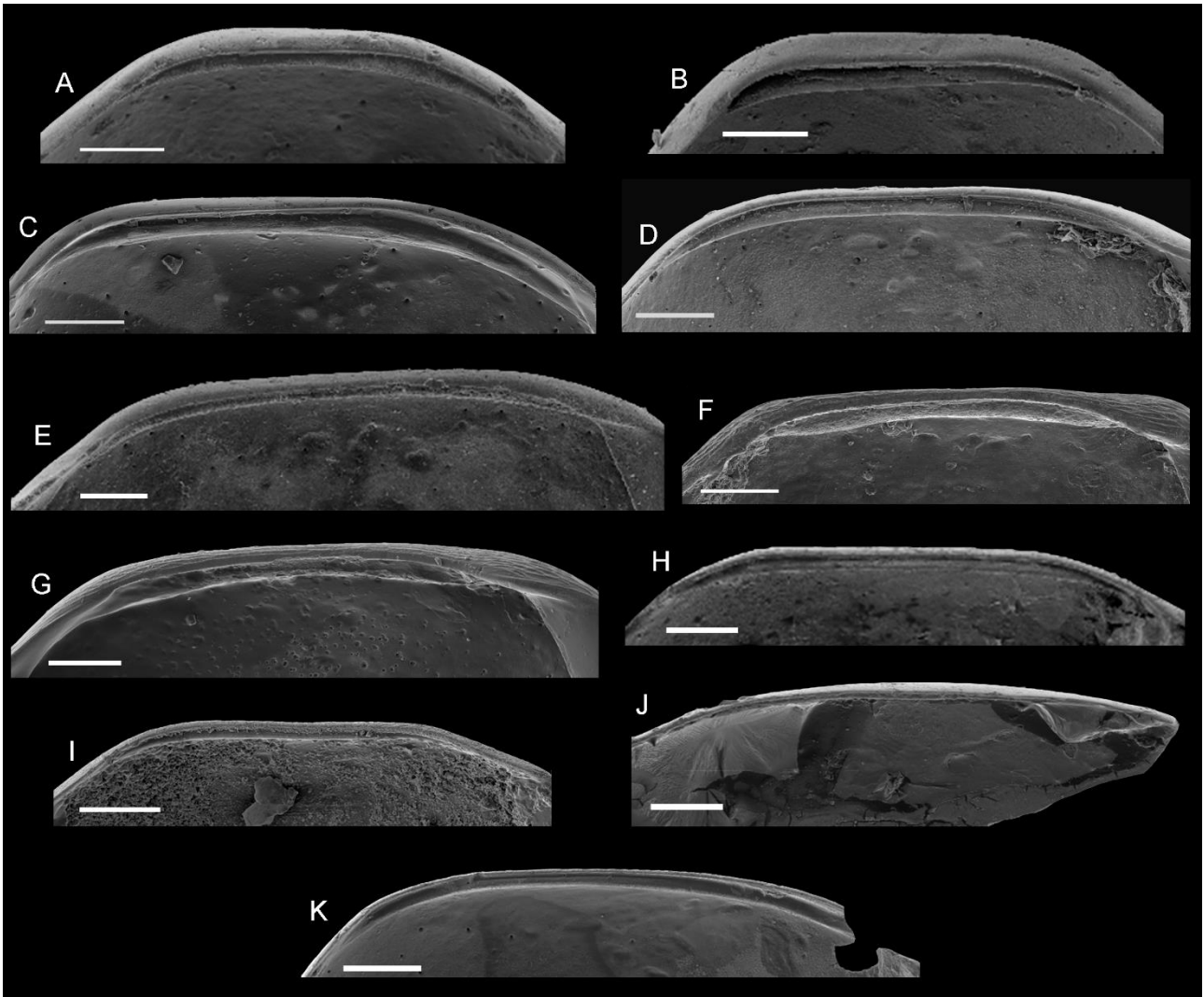
**Ornamentation:** although the valve ornamentation in brackish ostracods could be often considered an ecophenotypical character, *Bakunella* always shows a more or less marked reticulation (Fig. 5.2

A-D), while *Pontoniella* and *Serbiella* present both smooth and ornamented valves with elongated ribs (Fig. 5.2 E-I), and *Lineocypris* displays smooth valves sometimes pitted in the middle (Fig. 5.2 J-M). All the other examined genera bear smooth valves.



**Figure 5.2:** SEM pictures of some Paratethyan Candoninae genera showing different ornamentations. **A-B**, *Bakunella dorsoarcuata*. **A**, RV in lateral view, sample Obrenovac 14; **B**, detail of the ornamentation of the RV in A. **C-D**, *Bakunella* sp. nov. **C**, LV in lateral view, sample Mt. Medvenica D-237; **D**, detail of the ornamentation of the LV in C. **E-F**, *Serbiella bacevicae*. **E**, RV in lateral view, sample Obrenovac 13; **F**, detail of the ornamentation of the RV in E. **G-I**, *Pontoniella truncata*. **G**, LV in lateral view, sample Obrenovac 1; **H**, detail of the ornamentation of the LV in G; **I**, LV in lateral view, sample Obrenovac 1. **J-K**, *Lineocypris hodonensis*. **J**, RV in lateral view, sample Mt. Medvenica D-93; **K**, detail of the ornamentation of the RV in J. **L-M**, *Lineocypris trapezoidea*. **L**, LV in lateral view, sample Mt. Medvenica D-93; **M**, detail of the ornamentation of the LV in M. White bars correspond to 0.1 mm.

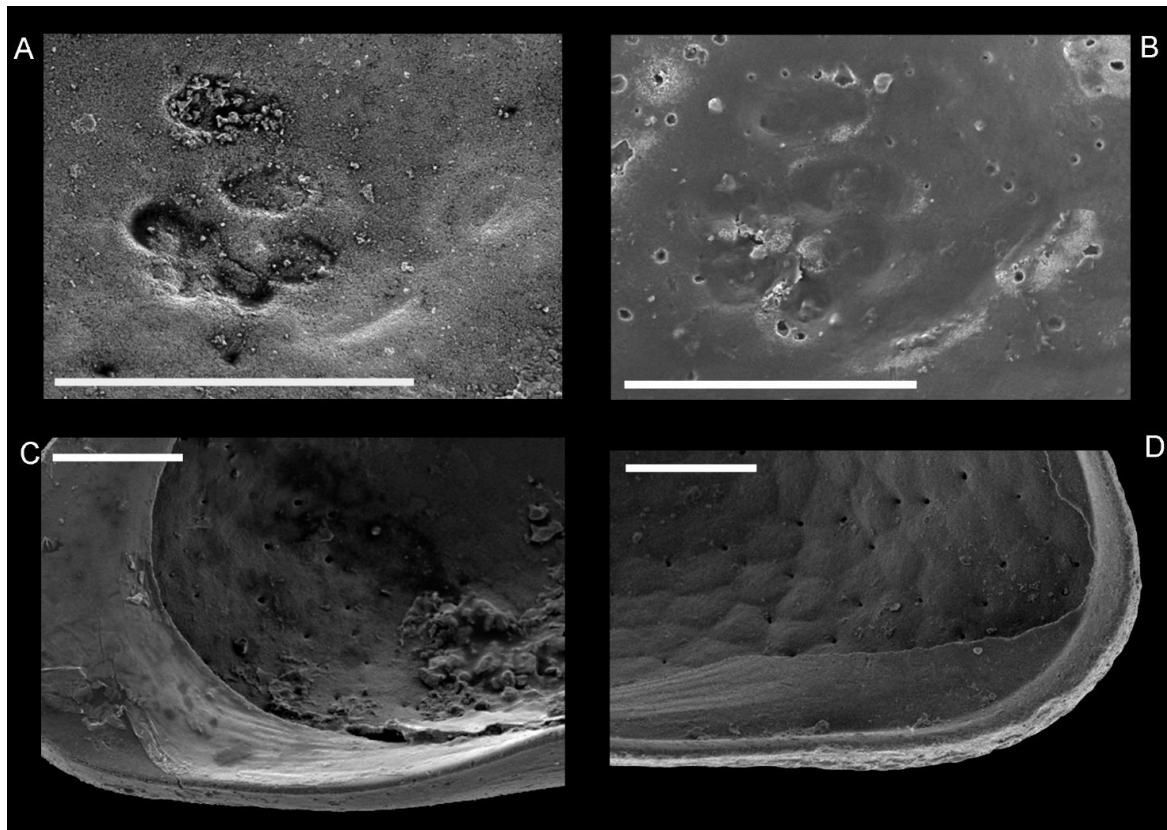
**Hinge:** The dorsal border of the right valve fits the correspondent groove in the left valve. In all the examined genera, except *Typhlocyprilla*, the groove in the left valve is underlined by a robust ledge open at the ends (Fig. 5.3).



**Figure 5.3:** SEM pictures of some Paratethyan Candoninae genera showing the detail of the LV hinge. **A**, *Bakunella dorsoarcuata*, sample Obrenovac 14. **B**, *Lineocypris branka*, sample Obrenovac 14. **C**, *Caspiocypris alta*, sample Obrenovac 14. **D**, *Camptocypris lobata*, sample Mt. Medvenica D-240. **E**, *Caspiolla brusinae*, sample Mt. Medvenica ZG-957 712. **F**, *Serbiella bacevicae*, sample Obrenovac 13. **G**, *Pontoniella truncata*, sample Obrenovac 1. **H**, *Hastacandona loczyi*, sample Obrenovac 14. **I**, *Propontoniella macra*, sample Vranović-1, B.P. 3.7.9. **J**, *Typhlocyprilla annae*, sample Obrenovac 1. **K**, *Zalanyiella venusta*, sample Obrenovac 14. White bars corresponds to 0.1 mm.

**Muscle scars:** they are typical of the subfamily and slightly variable from species to species (but also from specimen to specimen). The only peculiarity has been observed in genera *Serbiella* and *Pontoniella* in which the mandibular scars are always elongated elliptical, very narrow (Fig. 5.4 A-B).

**Inner lamella:** it is structureless in all the examined genera except *Bakunella* that displays 4-5 wrinkles in the antero-ventral area (Fig. 5.4 C-D).

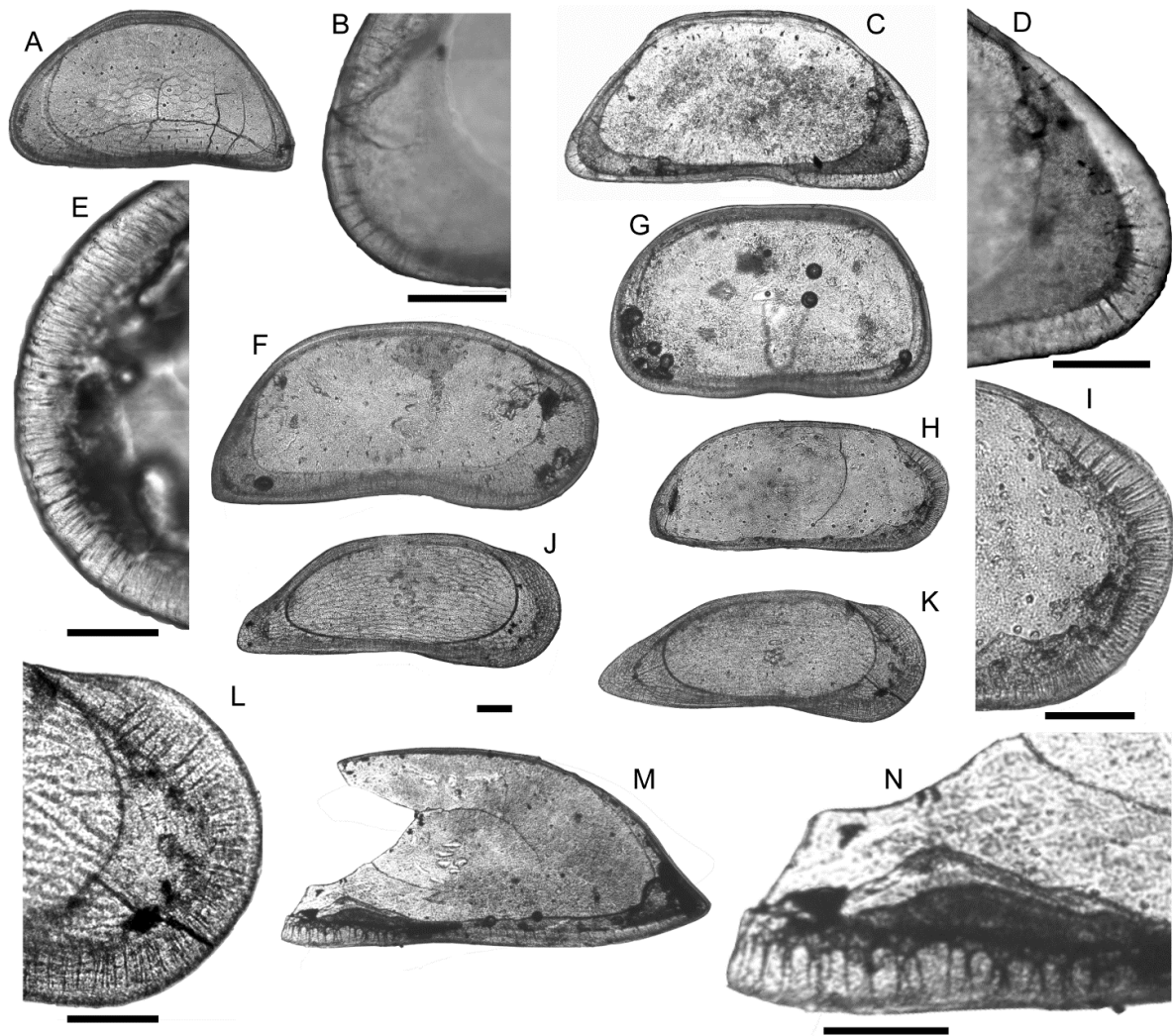


**Figure 5.4:** SEM pictures of some Paratethyan Candoninae genera showing the muscle scars and the wrinkles on the inner lamella. **A**, *Serbiella sagittosa*, detail of the muscle scars of the LV, sample Mt. Medvenica, D-66. **B**, *Pontoniella truncata*, detail of the muscle scars of the LV, sample Obrenovac 1. **C**, *Bakunella dorsoarcurata*, detail of the wrinkles on the anterior inner lamella of the RV, sample Obrenovac 13. **D**, *Bakunella* sp. nov., detail of the wrinkles on the anterior inner lamella of the LV, sample Mt. Medvenica D-237. White bars correspond to 0.1 mm.

**Fused zone and vestibule:** vestibules are developed in all the examined genera, but to different extent, and also the dimensional ratios with the fusion zone are different. For example, *Bakunella*, *Caspiocypris*, *Camptocypris*, and *Caspiolla* show narrow fused zones but *Bakunella* displays wide anterior and posterior vestibules, while in the other two genera the vestibules are poorly developed. Conversely, *Zalanyiella*, *Lineocypris*, *Pontoniella*, and *Serbiella* show relatively wide fused zones and developed vestibules, particularly the anterior one, except *Pontoniella* and *Serbiella* that display also a wide posterior vestibule (Fig. 5.5).

**Marginal pore canals:** in all the examined genera, they are simple and straight, except for genus *Typhlocyrella* in which few are bifurcate (Fig. 5.5). Generally they are dense and thin (*Camptocypris*, *Caspiocypris*, *Caspiolla*, *Lineocypris*, *Pontoniella*, *Serbiella*, *Zalanyiella*), but with different length linked to the breadth of the fusion zone. They are long in *Camptocypris*, *Caspiolla*, *Lineocypris*, *Pontoniella*, and *Serbiella*, short in *Caspiocypris* (except in the ventral zone) and *Zalanyiella*. Conversely, in *Bakunella* they are sparse, short and thick (Fig. 5.5).

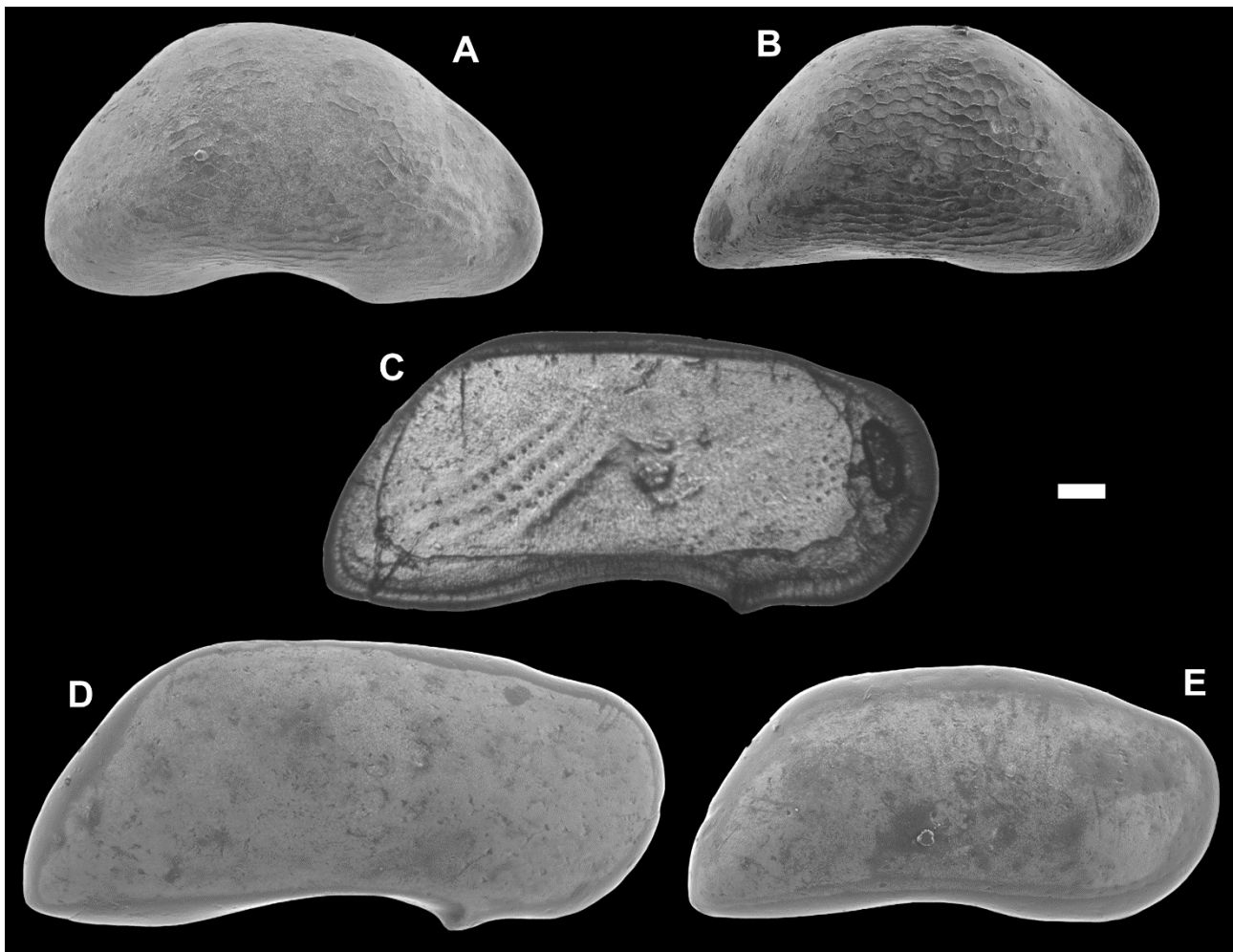




**Figure 5.5:** Transmitted light pictures of some Paratethyan Candoninae genera showing the width of the fusion zone and the details of the marginal pore canals. **A-B**, *Bakunella dorsoarcuata*. **A**, female LV in lateral view, sample Obrenovac 14; **B**, detail of the anterior marginal pore canals, female LV, sample Obrenovac 14. **C-D**, *Lineocypris branka*. **C**, female RV in lateral view, sample Obrenovac 14; **D**, detail of the anterior marginal pore canals, female RV, sample Obrenovac 14. **E-F**, *Camptocypris balcanica*. **E**, detail of the anterior marginal pore canals, female LV, sample Obrenovac 14; **F**, female RV in lateral view, sample Obrenovac 14. **G**, *Caspiocypris alta*, female LV, sample Obrenovac 14. **H-I**, *Zalanyiella venusta*. **H**, female RV in lateral view, sample Mt. Medvenica KZL-227; **I**, detail of the anterior marginal pore canals, female RV, sample Mt. Medvenica KZL-227. **J**, *Pontoniella truncata*, female LV, sample Obrenovac 1. **K-L**, *Serbiella sagittosa*. **K**, female RV in lateral view, sample Mt. Medvenica D-226; **L**, detail of the anterior marginal pore canals, female RV, sample Mt. Medvenica D-226. **M-N**, *Typhlocyrella annae*. **M**, broken female LV in lateral view, sample Obrenovac 1; **N**, detail of the antero-ventral marginal pore canals, female RV, sample Obrenovac 1. Black bars correspond to 0.1 mm.

**Sexual dimorphism:** it is always expressed, as it is typical of subfamily Candoninae, with male valves higher and longer than female valves, but in *Bakunella* the male shows a remarkable ventral concavity (Fig. 5.6 A-B) whereas in some species of *Camptocypris* the remarkable middle ventral

concavity is accompanied by a more or less conspicuous convexity in the mouth area, seldom with the development of a rostrum (Fig. 5.6 C-E).

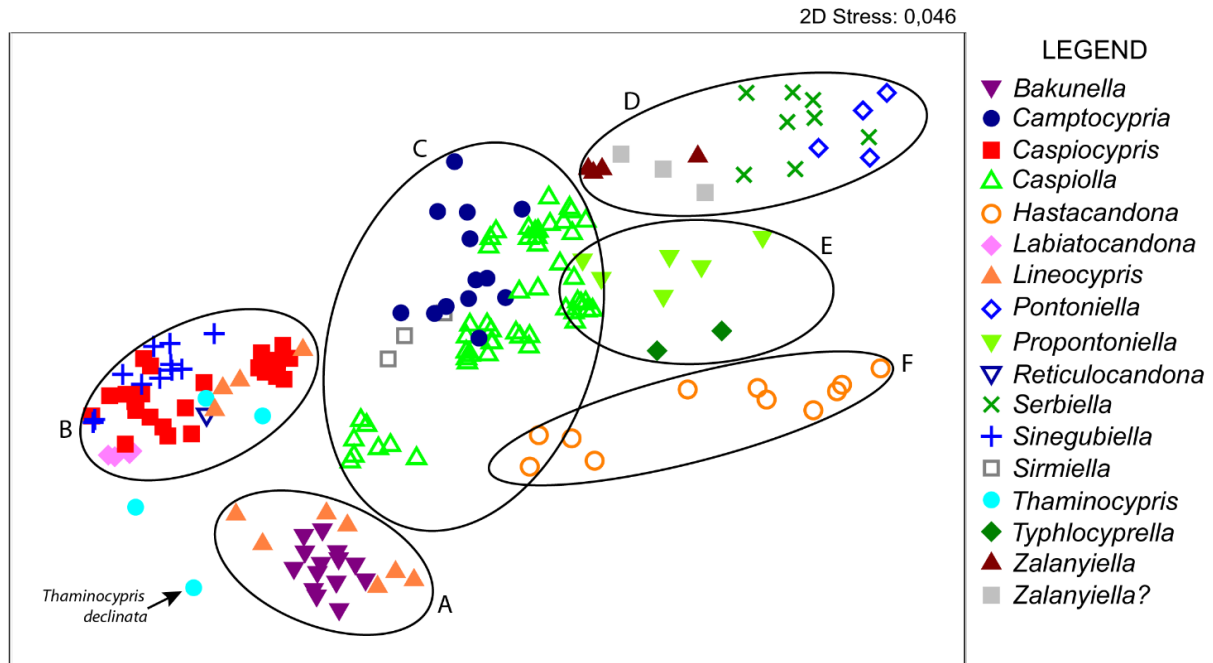


**Figure 5.6:** Sexual dimorphism in some Paratethyan Candoninae genera. **A-B**, *Bakunella dorsoarcuata*. **A**, SEM picture of a male RV in lateral view, sample Obrenovac 13; **B**, SEM picture of a female RV in lateral view, sample Obrenovac 13; **C-E**, *Camptocypria balcanica*. **C**, transmitted light picture of a male RV, sample Obrenovac 14 (semiferous tubule impressions are visible); **D**, SEM picture of a male RV, sample Obrenovac 14; **E**, SEM picture of a female RV, sample Obrenovac 14. White bar corresponds to 0.1 mm.

#### *Geometric morphometric analyses of the shell outline*

The geometric morphometric analysis of the valve outline was carried out on the female and male RV and LV. Due to the different amount of the examined material, the best and more reliable results were obtained with the analysis of the female RV, thus, hereinafter we report the nMDS results based of the comparison of the outlines of this valve (Fig. 5.7), although we will report also the nMDS plot of the female LV (Fig. 5.8). For the interpretation of the resulting nMDS plot, all the morphological characters visible in both female and male right and left valves were used.

We started our analysis plotting all the female RV outlines of the different species using the generic attribution corresponding to the last taxonomic revision reported in literature (Fig. 5.7). The circles drawn on the plot do not have any statistical meaning but they were drawn just to contribute to the clarity of the following discussion.



**Figure 5.7:** Non-metric multidimensional scaling (nMDS) plot in two-dimensional morphological space resulting from the multivariate analyses applied to the geometric morphometric outline matrix of the Candoninae RV in ‘normalized for area’ mode. Ellipses have no statistical meaning (see text).

Circle A includes species referred to genera *Lineocypris* with the type species *L. trapezoidea* and the species *L. branka*, *L. inflexa* and *L. caudalis*, and *Bakunella* with the type species *B. dorsoarcuata* and *Bakunella* sp. nov. These taxa are plotted close each other in a limited morphospace that indicates that their outlines are similar (trapezoidal with short dorsal margin) but their shells display different morphological characters such as a very different dorsal profile of the carapace and the presence in *Bakunella* of the anterior inner lamella with 4-5 wrinkles and a reticulated shell. According to us, these characters allow a clear distinction between the two groups, and then we consider *Lineocypris* and *Bakunella* two valid genera.

Circle B encloses the valve outlines of species referred to different genera: *Caspiocypris* with the type species *C. candida* and the species *C. alta* and *C. pontica*, *Sinegubiella* with its type species *S. sublabiata* and the species *S. illyrica*, *Labiatocandona* with its type species *L. labiata*, *Lineocypris* with the species *L. nonreticulata* and *L. zagradiensis*, *Reticulocandona* with the species *R. posteroerigera*, and *Thaminocypris* with the species *T. improbus*, *T. adversa* and *T. symmetrica*. Looking at the valve characters, all these species display the same general features (hinge, pore canals,

muscle scars, valve overlapping) and are located in the same area of the plot owing to their common lateral outline, that is sub-rectangular to sub-trapezoidal, with the dorsal margin only slightly shorter than the ventral one and the anterior margin equicurved. Since *Caspiocypris*, *Sinegubiella* and *Labiaticandona* are represented in the plot by their type species we conclude that they are synonyms and *Caspiocypris* is the senior synonym. The species of *Lineocypris* and *Thaminocypris* included in circle B are not the type species of the genera, thus we conclude that their generic attribution was wrong and they must be referred to *Caspiocypris*.

On the left of circle A and below circle B an isolated species is plotted. It corresponds to the type species of *Thaminocypris*, *T. declinata*, which shows a very peculiar shape with a pointed anterior border and a very strong asymmetrical ventral concavity that are not visible in any other Candoninae valve we have analysed. In addition, the LV displays a similar aberrant shape but in the nMDS plot (Fig. 5.8), it is located far from both *Caspiocypris* and *Lineocypris-Bakunella* clouds. For this reason we consider *Thaminocypris* a separate genus, possibly monospecific.

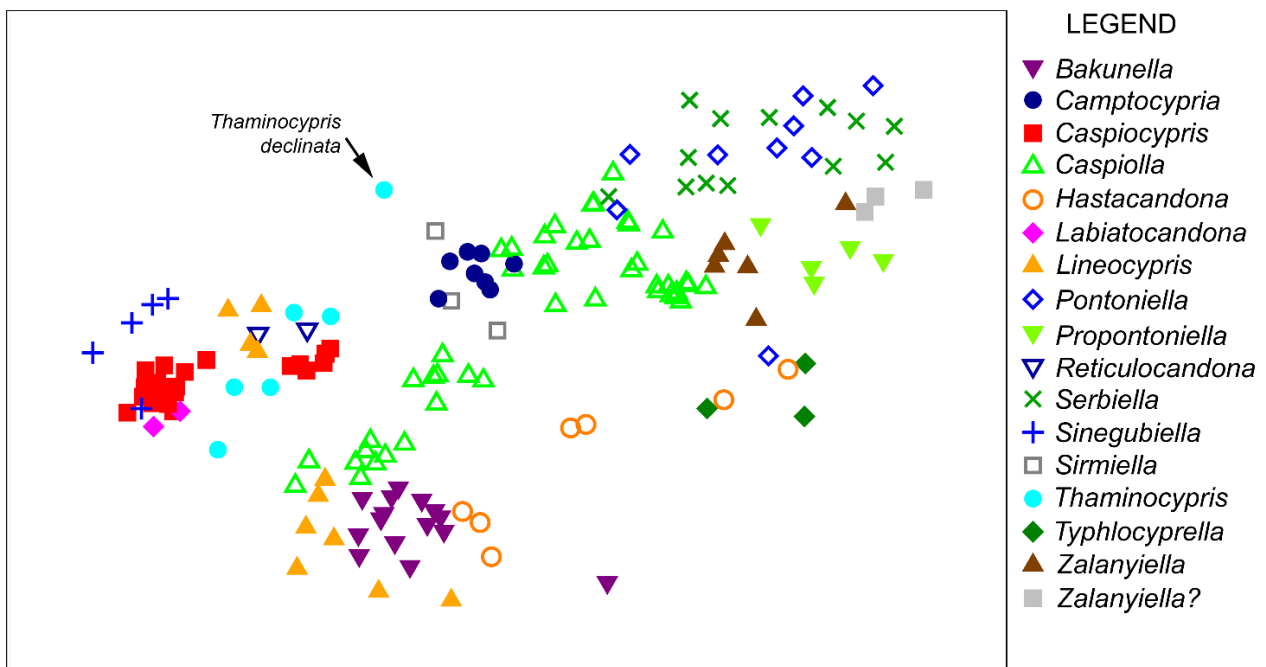
Circle C groups several species of *Camptocyprina*, with the type species *C. balcanica* and the species *C. lobata*, genus *Caspiolla*, with the type species *C. acronasuta* and the species *C. alasi*, *C. acuta*, *C. punctulata*, *C. brusinai*, *C. flectimarginata*, *C. gracilis*, *C. karatengisa* and *C. praebalcanica*, and the genus *Sirmiella* with the type species *S. sirmica* and the species *S. arcuata*. Beyond the similar valve shape (infracurved anterior margin and dorsal margin of the RV with a slight anterior concavity) all the species share other shell characters in such a way that it is not possible to divide them. Consequently, we consider *Camptocyprina*, *Caspiolla* and *Sirmiella* as synonyms, with *Camptocyprina* as the senior synonym. It is worth to note that the outlines of *Camptocyprina* species show certain variability. For example, *C. gracilis* seems have a stouter shell than the other does, in particular the LV is very high and its dots are located near the distribution of *Lineocypris* and *Bakunella* (Fig. 5.8). In circle C it is also included the genus *Propontoniella* with the type species *P. fragilifera*. Although the general shape of the RV is similar, no concavity on the dorsal margin is present, and, for this, the species is more similar to those included in circle E. This is further suggested by the shape of the LV that in the nMDS plot (Fig. 5.8) is located closer to other *Propontoniella* species.

Circle D includes several genera: *Zalanyiella* with the type species *Z. longissima* and the species *Z. venusta*; *Zalanyiella?* with the species *Z?. rurica* and *Z?. drzici*; *Serbiella* with the type species *S. hastata* and the species *S. bacevicuae*, *S. ilici*, *S. maxiunguiculata*, and *S. kolubarae*, and, finally, *Pontoniella* with the type species *P. acuminata* and the species *P. truncata*. Analysing the morphological characters of the shells, a part from the similar elongated outline, two different grouping can be envisaged: 1) *Serbiella* and *Pontoniella* in which the LV shows a conspicuous

overlapping of the RV along the dorsal margin, particularly remarkable in correspondence with the cardinal angles and more or less ornamented valves surface; 2) *Zalanyiella* and *Zalanyiella?* in which these characters are not expressed at all and with the dorsal margin that merges into the anterior and posterior margins without evident cardinal angles. Within those groupings no morphological differences have been observed, thus we can conclude that *Serbiella* and *Pontoniella* are synonym, with *Pontoniella* as the senior synonym. The same conclusion has been reached for *Zalanyiella* and *Zalanyiella?*.

Circle E includes species referable to *Propontoniella* with the type species *P. fragilifera* and the species *P. macra*, and the genus *Typhlocyprrella* with the type species *T. annae* and the species *T. lineocypriformis*. Notwithstanding they share a similar outline, the two genera are clearly separated by the absence of the ledge in the LV hinge in *Typhlocyprrella*.

Finally, circle F groups species that initially were classified under the generic names *Pontoniella* (*P. loczyi* and *P. pontica*) and *Hastacandona* (*H. longitesta* and *H. granulosa*) but subsequently were all referred to the genus *Hastacandona* (type species *H. longitesta*) (Sokač, 1990; Krstić & Stancheva, 1990). We agree with this latter attribution, since none of this species display the particular LV overlapping typical of *Pontoniella*. Within the genus *Hastacandona* are included species with elongate to very elongate trapezoidal shape and well-marked cardinal angles.



**Figure 5.8:** Non-metric multidimensional scaling (nMDS) plot in two-dimensional morphological space resulting from the multivariate analyses applied to the geometric morphometric outline matrix of the Candoninae LV in ‘normalized for area’ mode.

## 5.5 Systematic palaeontology

Class **OSTRACODA** Latreille, 1802

Subclass **PODOCOPA** Sars, 1866

Order **PODOCOPIDA** Sars, 1866

Suborder **CYPRIDOCOPINA** Jones, 1901

Superfamily **CYPRIDOIDEA** Baird, 1845

Family **CANDONIDAE** Kaufmann, 1900

Subfamily **CANDONINAE** Kaufmann, 1900

Genus *Bakunella* Schneider, in Schneider et al., 1958

(Fig. 5. 2 A-D; Fig. 5.3 A; Fig. 5.4 C-D; Fig. 5.5 A-B; Fig. 5.6 A-B; Fig. 5.9 A-J )

1958 *Bakunella* Schneider, in Schneider et al.: 267.

**Type species.** *Pontocypris dorsoarcuata* Zálányi, 1929, by original designation (the original material is lost; new type material was re-collected from the Obrenovac type section (Serbia): 22 female LV, 25 female RV, 6 male LV, and 8 male RV stored at MFGI (microslide OBR 13) and GOC (microslide OBR 13 and M369).

**Remarks.** The geometric morphometric analysis has shown that *Lineocypris* and *Bakunella* occupy very close morphospace (Fig. 5.7). Other morphological characters such as the strong ornamentation, the peculiar dorsal profile of the carapace and the wrinkled inner lamella suggest considering both of them distinct valid genera.

Schneider (in Schneider et al., 1958) described the new genus *Bakunella* based on *Pontocypris dorsoarcuata* Zálányi, 1929. Indeed, in the same paper Zálányi described two very similar species, *Pontocypris balcanica* (p. 34) and *P. dorsoarcuata* (p. 37) from the Obrenovac section (Serbia). In her revision of Zálányi's collection, Krstić (1971) accepted both species although at MFGI only juveniles of *P. balcanica* were stored in microslides Pl. 6305 and Pl. 6314. Sokač (1972) considered the specimens referred to "*P.*" *balcanica* as the juveniles of "*P.*" *dorsoarcuata*. Our new material from Obrenovac section provided several valves of "*P.*" *dorsoarcuata*, and showed us that the recovered instars completely fitted the dimensions and outline of "*P.*" *balcanica*, confirming Sokač's statement. Although "*P.*" *balcanica* was described before "*P.*" *dorsoarcuata*, according to ICZN art.

24.2.2 (International Commission of Zoological Nomenclature, 1999) “*P.*” *dorsoarcuata* represents the senior synonym because indicated by the First Reviser (Sokač, 1972).

The updated diagnosis and description of genus *Bakunella* are the following:

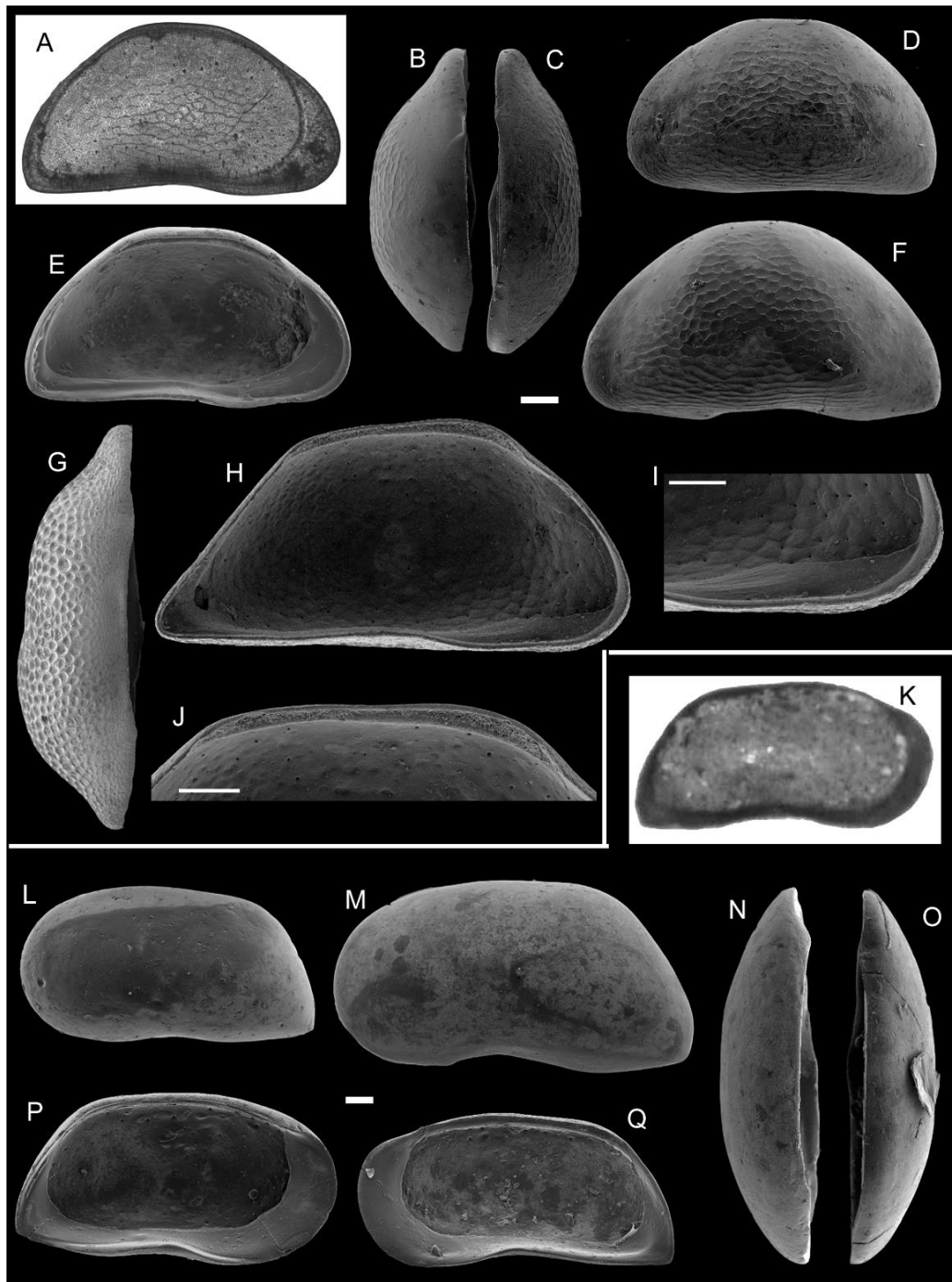
**Emended diagnosis.** Carapace in dorsal view, inflated, with a flat profile in the middle, remarkably beak-shaped anteriorly; ornamented with polygonal meshes; anterior inner lamella with 4-5 wrinkles, sparse, short and thick marginal pore canals.

**Emended description.** Carapace in dorsal view: strongly inflated with maximum convexity extended in the central part that shows a flat profile. Anterior end remarkably beak-shaped. LV larger than RV, overlapping it along all the margins. Carapace in lateral view trapezoidal in shape, strongly inflated. Dorsal margin short, straight or slightly arched; ventral margin concave in the middle; anterior margin rounded, infracurvate; posterior margin straight and bending posteriorly in the upper part, pointed ventrally. Surface more or less strongly ornamented with large polygonal meshes. Anterior inner lamella up to four times as broad as the fusion zone, characterised by 4 to 5 wrinkles in the anterior-ventral area. Marginal pore canals straight, sparse, short and thick. Hinge margin straight. In the LV the hinge comprises a well-developed longitudinal groove, underlined by a robust ledge open at the ends. Muscle scars typical of the subfamily Candoninae. Strong sexual dimorphism with male valves larger and stouter than females and with a remarkable ventral concavity.

According to our revision the following species must be ascribed to genus *Bakunella*: *Bakunella dorsoarcuata* (Zalányi, 1929) and *Bakunella* sp. nov.

Furthermore, we consider possible to include in genus *Bakunella* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Bakunella acuminata* Olteanu, 1995, *Bakunella agalarovae* Stancheva, 1989, *Bakunella djanelidzae* Vekua, 1965, *Bakunella krstici* Olteanu, 1995.





**Figure 5.9:** Transmitted light and SEM pictures of some Paratethyan Candoninae species. **A-F**, *Bakunella dorsoarcuata*. **A**, female RV in lateral view, sample Obrenovac 14; **B**, female LV in dorsal view, sample Obrenovac 14; **C**, female RV in dorsal view, sample Obrenovac 13; **D**, female LV in lateral view, sample Obrenovac 13; **E**, female LV in inner view, sample Obrenovac 13; **F**, male LV in lateral view, sample Obrenovac 14. **G-J**, *Bakunella* sp. nov. **G**, female LV in dorsal view, sample Mt. Medvenica D-237; **H**, female LV in inner view, sample Mt. Medvenica D-237; **I**, female LV in inner view, detail of the wrinkles on the anterior inner lamella, sample Mt. Medvenica D-237; **J**, female LV in inner view, detail of the hinge, sample Mt. Medvenica D-237. **K-Q**, *Camptocypria balcanica*. **K**, female RV in lateral view, lectotype, MFGI Pl6317; **L**, female LV in lateral view, sample Obrenovac 14; **M**, male LV in lateral view, sample Obrenovac 14; **N**, male LV in dorsal view, sample Obrenovac 14; **O**, male RV in dorsal view, sample Obrenovac 14; **P**, female LV in inner view, sample Obrenovac 14; **Q**, female RV in inner view, sample Obrenovac 14. Bars correspond to 0.1 mm.

Genus *Camptocypria* Zálányi, 1959

(Fig. 5.1 G-H; Fig. 5.3 D-E; Fig. 5.5 E-F; Fig. 5.6 C-E; Fig. 5.9 K-Q; Fig. 5.10 A-U; Fig. 5.11 A-I)

1956 *Caspiella* Mandelstam, in Schneider et al.: 104

1959 *Camptocypria* Zálányi: 51

1960 *Caspiolla* Mandelstam, in Luebimova et al.: 351

1972 *Candona* (*Sirmiella*) Krstić: 25

**Type species.** *Paracypria balcanica* Zálányi, 1929, by original designation (original material: female RV stored at MFGI (microslide Pl. 6317 from Obrenovac); broken female RV and broken male LV (microslide Pl. 6301a,b from Pejinović); 3 female RV and 1 female LV (microslide 112.5-114 m from Bonyhad); female RV (microslide 14-14.7 m from Balatonszabadi); 5 female RV, 5 female LV, and 2 male LV (microslide 4, 7, 9, 24, and 31 from Tihany).

**Remarks.** Mandelstam (in Schneider et al., 1956) described the genus *Caspiella* based on the type-species *Bairdia acronasuta* Livental, 1929 from the Apsheronian of Babazanan (Azerbaijan), but the name represented the junior homonym of the mollusc genus *Caspiella* Thiele, 1928, thus it was invalid. In his original description, he affirmed that several species referred by Zálányi (1929) to the genus *Paracypria* had to be included within his genus. Although in 1960 he corrected the spelling in *Caspiolla* Mandelstam in Luebimova et al., 1960, one year before Zálányi (1959) arose the new genus *Camptocypria* Zálányi, 1959, designating as the type-species. *Paracypria balcanica* Zálányi, 1929 from the late Miocene of Obrenovac and Pejinović. Mandelstam & Schneider (1963) refer *P. balcanica* Zálányi to genus *Caspiolla*. According to the ICZN (Art. 60.3) (International Commission of Zoological Nomenclature, 1999), the name *Camptocypria* Zálányi represents the new substitute name of the preoccupied name *Caspiella* Mandelstam and competes with the name *Caspiolla* Mandelstam, which represents its junior synonym. Krstić (1972) and Sokač (1972) already recognized the synonymy between *Caspiolla* and *Camptocypria* but both authors choose *Caspiolla* as the valid name considering it a subgenus of *Candona*. The correct attribution to *Camptocypria* was finally recognized by Sokač (1990) and Krstić & Stancheva (1990) but, notwithstanding this, the name *Caspiolla* persists until recent papers (among others Alçiçek et al., 2015; Popov et al., 2016). We agree with Krstić & Guan (2000) that turned *Camptocypria* to the generic rank as it was originally established by Zálányi.

In 1972, Krstić described the new subgenus *Candona* (*Sirmiella*) and, in her diagnosis, she remarked the great similarities between it and *Camptocypria*. According to Krstić's description, *C.*

(*Sirmiella*) is divided from *C. (Camptocypria)* only by the slightly smaller dimensions, the dorsal margin always parallel to the ventral one also in the male and the lack of the ventral convexity and rostrum in the mouth area in the male valves. Indeed, there are several species referred to *Camptocypria* that do not display the male ventral convexity and rostrum but are relatively large in size, such as *Camptocypria acronasuta* (Livental, 1929) and *Camptocypria brusinai* (Sokač, 1972). According to Sokac (1972), *C. (Sirmiella)* includes juvenile valves of *Caspiolla* (= *Camptocypria*). The geometric morphometric comparison we performed on the valves labelled as *Sirmiella arcuata* stored at the NHMB and the A-1 valves of *C. balcanica* collected by us at the Obrenovac section shows the complete superimposition of the outlines both in “normalized” and in “not normalized for area” modes (Fig. 5.12), confirming Sokač’s statement.

**Emended diagnosis.** In dorsal view, LV overlaps RV particularly in correspondence of the anterior dorsal lobe; in lateral view, rounded infracurvate anterior margin, RV dorsal margin with a small anterior concavity.

**Emended description.** Carapace in dorsal view elliptical with pointed anterior end and slightly pointed posterior end. LV larger than RV and overlapping it along the dorsal, posterior and ventral margins. Along the dorsal margin the overlapping is enhanced in correspondence of the anterior dorsal lobe, sometimes also a posterior dorsal lobe is developed. Carapace in lateral view elongate with rounded anterior margin and obliquely cut posterior end. Dorsal margin rectilinear or slightly convex, with a small anterior concavity on the RV. Ventral margin rectilinear, with a noticeable concavity in the medial portion. Dorsal and ventral margins parallel or sub-parallel (male). The dorsal margin joins continuously the anterior and posterior margins without any evident cardinal angles. Rounded infracurvate anterior border, posterior border moderately arched to rather rectilinear, pointed in correspondence of the postero-ventral end. Surface of the valve smooth. Inner lamella strongly developed anteriorly and moderately developed posteriorly. Fusion zone narrow, with straight and short pore canals. Hinge margin straight. In the LV the hinge is made by a well-developed longitudinal groove underlined by a robust ledge open at the ends. Muscle scars typical of the subfamily Candoninae. In some species strong sexual dimorphism, with males larger than females and provided by a remarkable middle ventral concavity, and a more or less conspicuous convexity in the mouth area possibly accompanied by a rostrum.

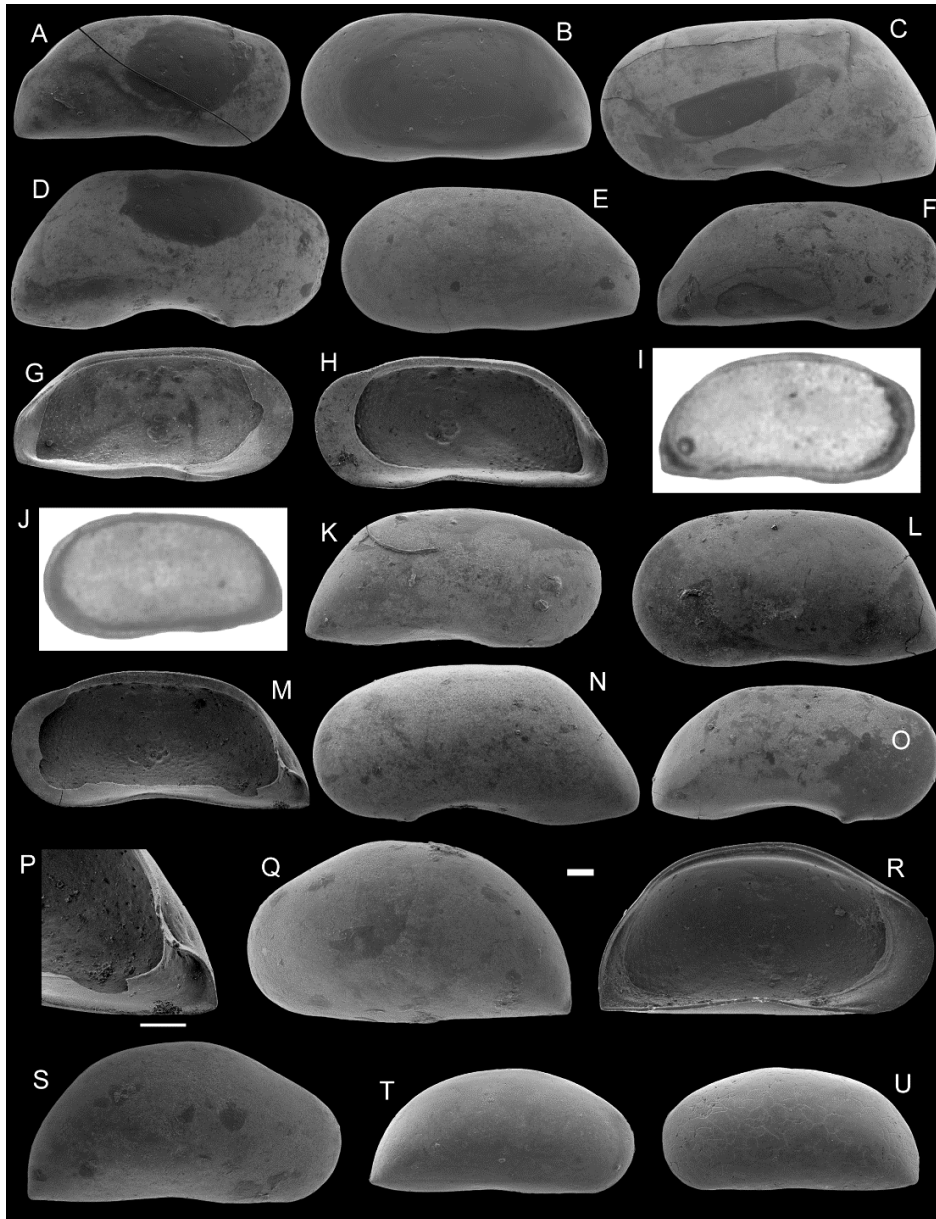
Soft parts: Schornikov (1966) described the new species *Candona camelus* referring it to the *lobata*-group Zálányi, 1929 (i.e. *Camptocypria*) living in the Caspian Sea (Schornikov, 1966). In his description he includes the soft parts that are, up to present, the only ones that can be referred to genus *Camptocypria*. They display the general features typical of subfamily Candoninae (antenna without natatory setae, T2 with basal segment with 1 d-seta, and T3 protopod with 2 setae and terminal

segment with 3 distal setae). In the mandibular palp the externo-distal seta of the penultimate segment ( $\gamma$ -seta) is possibly plumose as in genus *Candona* (Meisch, 2000), but the setal group on the second segment is composed by 3 setae, instead the 4 or 5 recognized in genus *Candona*. Moreover, the G2-claw of A2 is as long as the G1- and G3-claws, contrary to what present in genus *Candona*, in which G2-claw is remarkably shorter, and the Mxp-clasping organs are more inflated with the right one longer than the left one. Furthermore, the penis outer distal lobe is not protruding laterally as in genus *Candona* (Meisch, 2000).

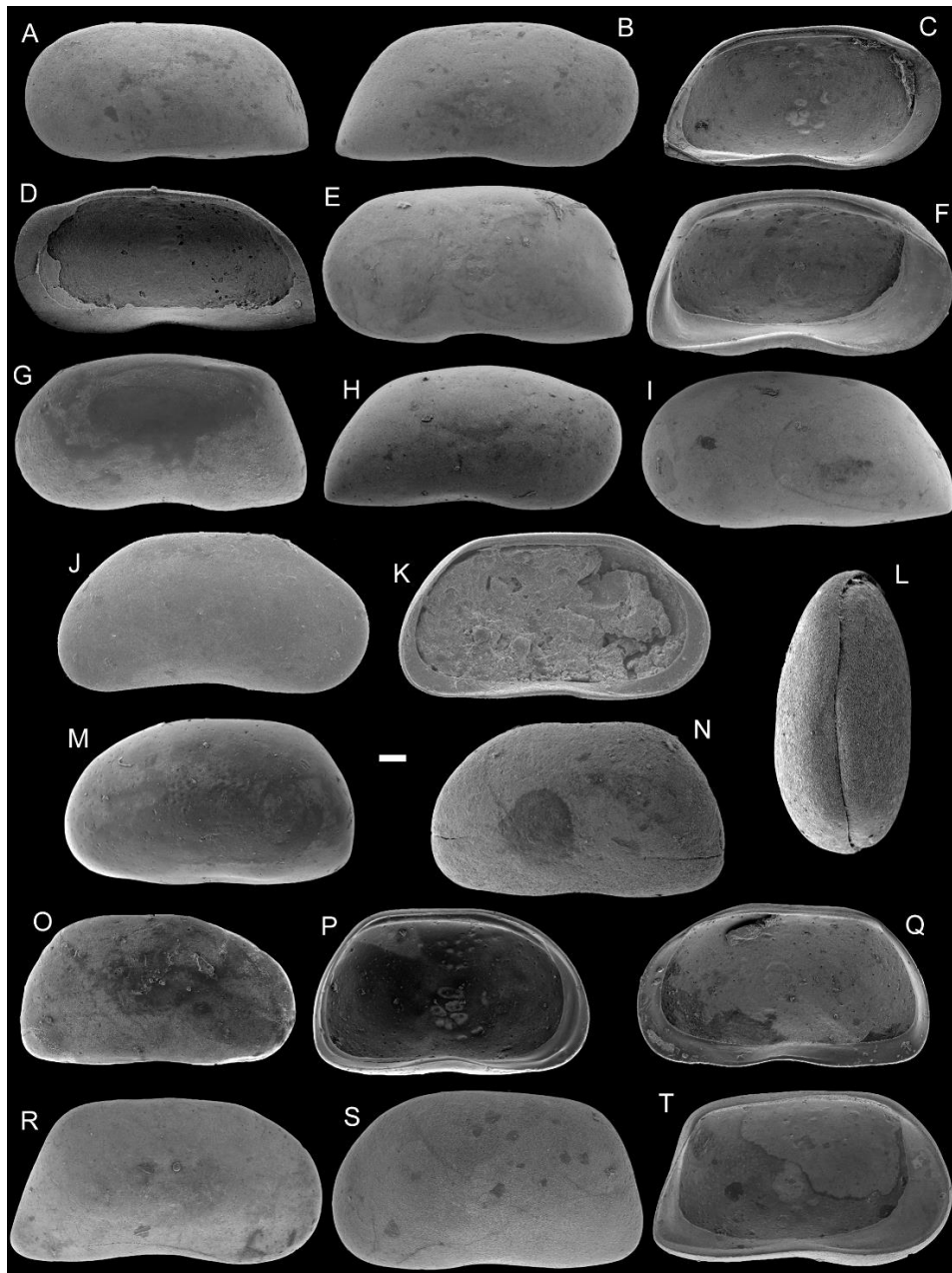
According to our revision the following species must be ascribed to genus *Camptocypria*:

*Camptocypria acronasuta* (Livental, 1929), *Camptocypria acuta* (Sokač, 1972), *Camptocypria alasi* (Krstić, 1972), *Camptocypria balcanica* (Zalányi, 1929) (including juveniles identified as *Caspiolla arcuata* Stancheva, 1964 and the junior synonym *C. (Caspiolla) parabalcanica* Krstić, 1971), *Camptocypria brusinai* (Sokač, 1972), *Camptocypria extensa* (Zalányi, 1959), *Camptocypria flectimarginata* (Sokač, 1972), *Camptocypria gracilis* (Livental, 1938), *Camptocypria karatengisa* (Mandelstam, in Mandelstam & Schneider, 1963), *Camptocypria lobata* (Zalányi, 1929), *Camptocypria ossoinae* (Krstić, 1968) (= *C. (Camptocypria) ossoinaensis* Krstić & Stancheva, 1990), *Camptocypria praebalcanica* (Krstić, 1972), *Camptocypria punctulata* (Sokač, 1972).

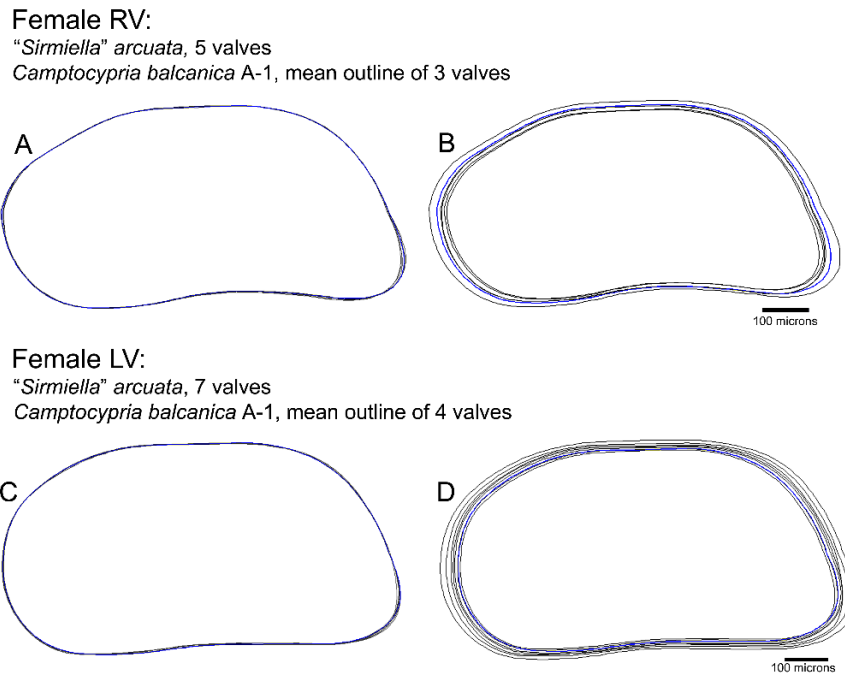
Furthermore, we consider possible to include in genus *Camptocypria* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Camptocypria aculeata* (Stancheva, 1964), *Camptocypria bacuana* (Luebimova, in Mandelstam et al., 1962), *Camptocypria camelus* (Schornikov, 1966), *Camptocypria durostorumensis* (Stancheva, 1981a), *Camptocypria excentrica* (Olteanu, 1995), *Camptocypria excultata* (Stancheva, 1989), *Camptocypria fastigata* (Freels, 1980), *Camptocypria fornicata* (Stancheva, 1989), *Camptocypria hungarica* Zalányi, 1959 (including its junior synonym *C. (Caspiolla) zalanyii* Krstić, 1972), *Camptocypria kamistrumensis* (Stancheva, 1981a), *Camptocypria karatengisa* (Mandelstam, in Mandelstam & Schneider, 1963), *Camptocypria kozloduensis* (Stancheva, 1981a), *Camptocypria liventali* (Evlachova in Mandelstam & Schneider, 1963), *Camptocypria magna* (Krstić, 1972), *Camptocypria mestrovici* (Krstić, 1972), *Camptocypria mokranjci* (Krstić, 1972), *Camptocypria nadae* (Krstić, 1972), *Camptocypria parskoviensis* (Olteanu, 1995), *Camptocypria prochazkai* (Pokorný, 1955), *Camptocypria regulata* (Olteanu, 1995), *Camptocypria schneiderae* (Stancheva, 1966), *Camptocypria scythica* (Stancheva, 1966), *Camptocypria shopovi* (Stancheva, 1989), *Camptocypria sokaci* (Olteanu, 1995), *Camptocypria subpontica* (Krstić, 1972), *Camptocypria transmariskae* (Stancheva, 1981a).



**Figure 5.10:** Transmitted light and SEM pictures of some *Camptocypria* species. **A-D**, *Camptocypria alasi*. **A**, female RV in lateral view, sample Obrenovac 14; **B**, female LV in lateral view, sample Obrenovac 14; **C**, male LV in lateral view, sample Obrenovac 14; **D**, male RV in lateral view, sample Obrenovac 14. **E-H**, *Camptocypria brusinai*. **E**, female LV in lateral view, sample Mt. Medvenica ZG-975 S12; **F**, female RV in lateral view, sample Mt. Medvenica ZG-975 S12; **G**, female LV in inner view, sample Mt. Medvenica ZG-975 S12; **H**, female RV in inner view, sample Mt. Medvenica ZG-975 S12. **I-J**, *Camptocypria extensa*. **I**, female RV in lateral view, holotype, MFGI Pl. 1682; **J**, female LV in lateral view, paratype, MFGI Pl. 1682. **K-P**, *Camptocypria flectimarginata*. **K**, female RV in lateral view, sample Mt. Medvenica KZL-65 1090; **L**, female LV in lateral view, sample Mt. Medvenica KZL-65 1090; **M**, female RV in inner view, sample Mt. Medvenica KZL-65 1090; **N**, male LV in lateral view, sample Mt. Medvenica D-250; **O**, male RV in lateral view, sample Mt. Medvenica D-240; **P**, detail of the posterior margin of a female RV in inner view, sample Mt. Medvenica KZL-65 1090. **Q-S**, *Camptocypria gracilis*. **Q**, female LV in lateral view, sample Black Sea MD04-2761 bottom core; **R**, female LV in inner view, sample Black Sea MD04-2761 bottom core; **S**, female RV in lateral view, sample Black Sea MD04-2761 bottom core. **T-U**, *Camptocypria karatengisa*. **T**, female RV in lateral view, sample Lokbatan UP 17; **U**, female LV in lateral view, sample Lokbatan UP 17. Bars correspond to 0.1 mm.



**Figure 5.11:** SEM pictures of some Paratethyan Candoninae species. **A-E**, *Camptocypria lobata*. **A**, female LV in lateral view, sample Mt. Medvenica D-230; **B**, female RV in lateral view, sample Mt. Medvenica D-237; **C**, female LV in inner view, sample Mt. Medvenica D-240; **D**, female RV in inner view, sample Mt. Medvenica D-42; **E**, male LV in lateral view, sample Mt. Medvenica D-237; **F-G**, *Camptocypria ossoinae*. **F**, female LV in inner view, sample Negotini E-VI-I 21.95 22; **G**, female LV in lateral view, sample Negotini E-VI-I 21.95 22; **H-I**, *Camptocypria punctulata*. **H**, female RV in lateral view, sample Mt. Medvenica KZL-65 1062; **I**, female LV in lateral view, sample Mt. Medvenica KZL-65 1062; **J-K**, *Caspiocypris candida*. **J**, female RV in lateral view, sample Lake Inder, VNIGRI 71/6a; **K**, female RV in inner view, sample Lake Inder, VNIGRI 71/6a; **L-Q**, *Caspiocypris alta*. **L**, female C in dorsal view, sample Obrenovac 14; **M**, female LV in lateral view, sample Obrenovac 14; **N**, male LV in lateral view, sample Obrenovac 14; **O**, female RV in lateral view, sample Obrenovac 14; **P**, female LV in inner view, sample Obrenovac 14; **Q**, female RV in inner view, sample Obrenovac 14; **R-T**, *Caspiocypris granulosa* sensu Sokač (1972). **R**, female RV in lateral view, sample Mt. Medvenica D-42; **S**, female LV in lateral view, sample Mt. Medvenica D-95; **T**, male LV in inner view, sample Mt. Medvenica D-42. White bar corresponds to 0.1 mm.



**Figure 5.12:** Superimposition of the mean outlines of the female RV of *Camptocypris balcanica* A-1 (grey, blue) and several outlines of "*Sirmiella*" *arcuata* (black) obtained with Morphomatica. **A-B**, female RV in 'normalized for area' (A) and 'not normalized for area' (B) modes; **C-D**, female LV in 'normalized for area' (C) and 'not normalized for area' (D) modes (Morphomatica outputs were realized with 6 iterations).

Genus *Caspiocypris* Mandelstam, in Schneider et al., 1956

(Fig. 5.3 C; Fig. 5.5 G; Fig. 5.11 J-T; Fig. 5.13 A-T; Fig. 5.14 A-M)

- 1956 *Caspiocypris* Mandelstam, in Schneider et al.: 105
- 1958 *Rectocypris* Schneider, in Schneider et al: 268
- 1963 *Paracaspiocypris* Mandelstam, in Mandelstam & Schneider: 162
- 1972 *Candona* (*Reticulocandona*) Krstić: 59.
- 1972 *Candona* (*Sinegubiella*) Krstić: 77.
- 1984 *Candona* (*Bononiella*) Stancheva: 35.
- 1990 *Candona* (*Labiaticandona*) Krstić & Stancheva: 770.
- 1995 *Candona* (*Tuberocandona*) Olteanu: 284

**Type species.** *Bairdia candida* Livaltal, 1929, by original designation (the original material is lost; new type material was re-collected from the Babazanan type section (Azerbaijan): 2 female RV, 1 male LV, stored at the Department of Geology, University of Bucharest).



**Remarks.** Spadi et al. (2016, 2017) made a thorough revision of the genus *Caspiocypris* considering the genera *Reticulocandona* Krstić, 1972, *Sinegubiella* Krstić, 1972, and *Labiaticandona* Krstić & Stancheva, 1990 its junior synonyms.

Although it was not possible to check them directly, the original diagnoses and illustrations suggest that also other genera could be junior synonym of *Caspiocypris*, such as *Rectocypris* Schneider, in Schneider et al., 1958, *Paracaspiocypris* Schneider, in Mandelstam & Schneider 1963, *Bononiella* Stancheva, 1984, and *Tuberocandona* Olteanu, 1995.

*Rectocypris* Schneider (type species *Bythocypris reniformis* Schweyer, 1949) apparently seems based on a juvenile valve of Candoninae with poor developed vestibules and maximum high in the anterior part. Schneider (in Schneider et al., 1958) referred to *Rectocypris* also one male valve of *Bythocypris subtriangularis* Schweyer, 1949 that displays a massive rectangular shape and a robust ledge in the hinge margin of LV (see drawings in Schweyer, 1949 and Mandelstam & Schneider, 1963), all characters recognizable in genus *Caspiocypris*.

Similarly, *Paracaspiocypris* Schneider (type species *Bythocypris mandelstami* Schweyer, 1949), is based on juvenile valves that display the characteristic outline of juveniles of *Caspiocypris*. According to Krstić & Guan (2000), *Paracaspiocypris* should represent a junior synonym of *Caspiocypris* and the two species included in this genus (*P. mandelstami* and *P. papillopunctata* (Schweyer, in Mandelstam & Schneider, 1963) are both based on juvenile valves.

*Candona (Bononiella)* Stancheva, 1984 (type species *Caspiocypris vulgaris* Stancheva, 1964) was divided from *Caspiocypris* on the base of its trapezoidal shape, the presence of horizontal dorsal margin and remarkable cardinal angles (Stancheva, 1984). All these features are typical of *Caspiocypris* as originally defined by Mandelstam (in Schneider et al., 1956).

Olteanu (1995) described *Tuberocandona* (type species *Caspiocypris ornatus* Hanganu, 1977) that differ from *Caspiocypris* only for the tuberculated surface. This character was considered by Van Baak et al. (2015) as probably due to the water ionic concentration and should be considered as an ecophenotypic variation of *Caspiocypris*.

Hereinafter is reported the emended diagnosis and the emended description of *Caspiocypris* as defined by Spadi et al. (2016):

**Emended diagnosis.** in lateral view, sub-rectangular to sub-trapezoidal in shape, with the dorsal margin only slightly shorter than the ventral one; anterior margin generally equicurved.

**Emended description.** sub-trapezoidal to trapezoidal or sub-rectangular carapace in lateral view with maximum height along the entire dorsal margin or slightly posterior; rounded anterior margin generally equicurved. LV larger than RV. Dorsal margin straight, horizontal or sub-horizontal (female) or slightly inclined anteriorly (male). Ventral margin generally parallel to the dorsal margin

(female), with a weak concavity in the medial portion. Posterior margin gently arched and inclined posteriorly; posterior angle slightly more or less sharply rounded in its lower part. Surface of the valves smooth: in some species, a few pits can be observed in the central portion; other species are characterized by intrashell reticulations on the posterior portion. Inner structureless lamella strongly developed at the anterior end of the valve. Pore canal zone relatively narrow, with straight pore canals, which are numerous at the anterior end. Hinge margin straight, shorter than the ventral margin. Hinge of the LV consists of a well-developed longitudinal groove, underlined by a robust ledge open at the ends. Scars for the attachment of adductor and mandibular muscles are typical for the subfamily Candoninae. Sexual dimorphism is present, with males larger than females and proportionally higher, particularly in the posterior portion.

To this diagnosis, we can add some further observations: in dorsal view the carapace is inflated with acuminate anterior end and slightly pointed posterior end. The overlapping of the LV valve is expressed in dorsal, posterior and ventral margin.

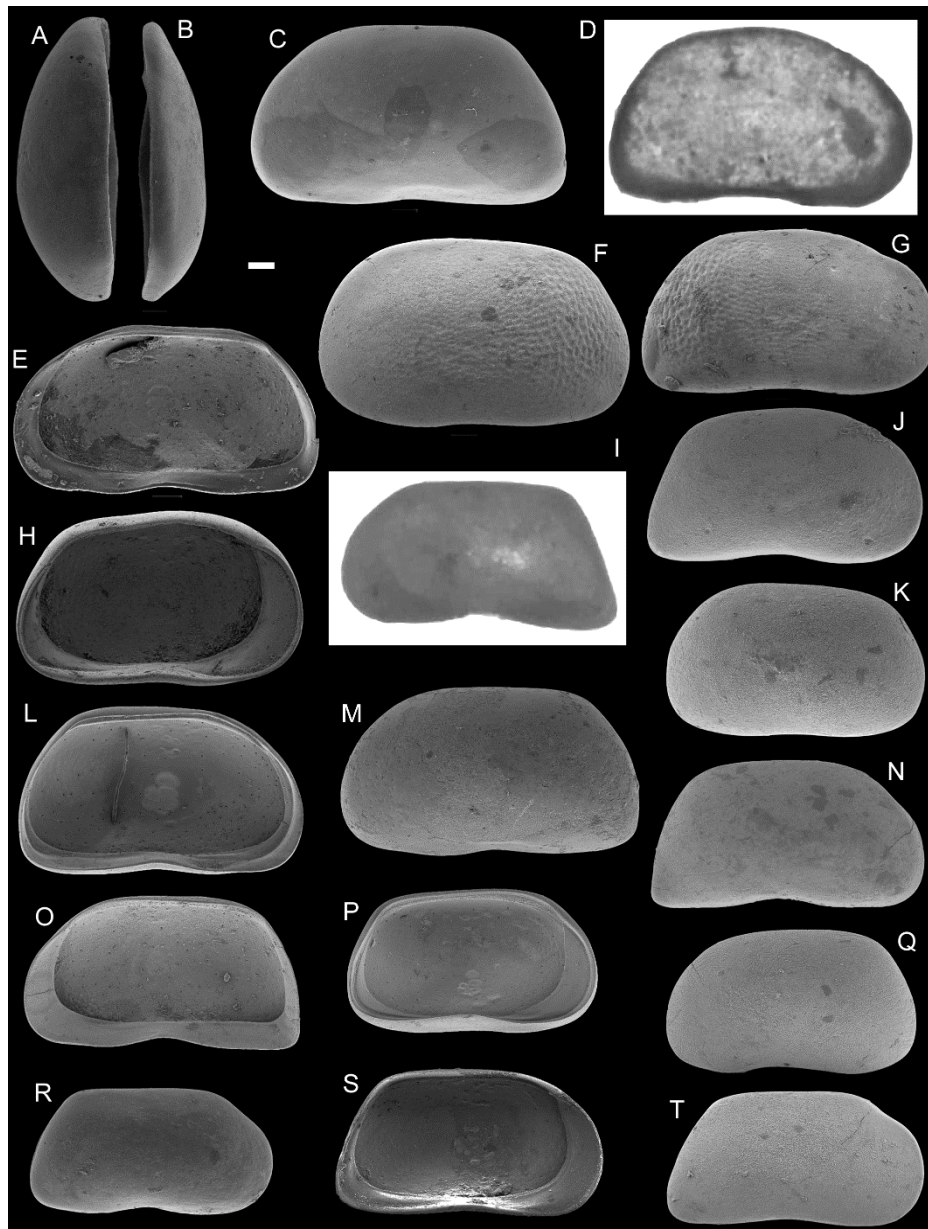
According to Spadi et al. (2016, 2017) and to the present revision, the following species must be ascribed to genus *Caspiocypris*: *Caspiocypris adversa* (Krstić, 1972), *Caspiocypris alta* (Zalányi, 1929), *Caspiocypris amiterni* Spadi & Gliozzi, in Spadi et al., 2016, *Caspiocypris basilicii* Spadi & Gliozzi in, Spadi et al., 2017, *Caspiocypris bosii* Spadi & Gliozzi, in Spadi et al., 2016, *Caspiocypris candida* (Livental, 1929), *Caspiocypris granulosa* (Zalányi) *sensu* Sokač (1972) (non *Candona granulosa* Zalányi, 1959), *Caspiocypris illyrica* (Krstić, 1972), *Caspiocypris improbus* (Krstić, 1972), *Caspiocypris labiata* (Zalányi, 1929) (including the junior synonyms *Candona* (*Thaminocypris*) *alta* Zalányi *sensu* Krstić, 1972, *Candona* (*Thaminocypris*) *minutissima* Krstić, 1972, *Candona* (*Thaminocypris*) *stevanovici* Krstić, 1972, and *Candona* (*Thaminocypris*?) *aff. labiata* Zalányi in Krstić, 1972), *Caspiocypris lyrata* Mandelstam & Schneider, 1963<sup>1</sup>, *Caspiocypris martoniensis* (Méhes, 1907), *Caspiocypris minuta* (Zalányi, 1944), *Caspiocypris nicandroi* Spadi &

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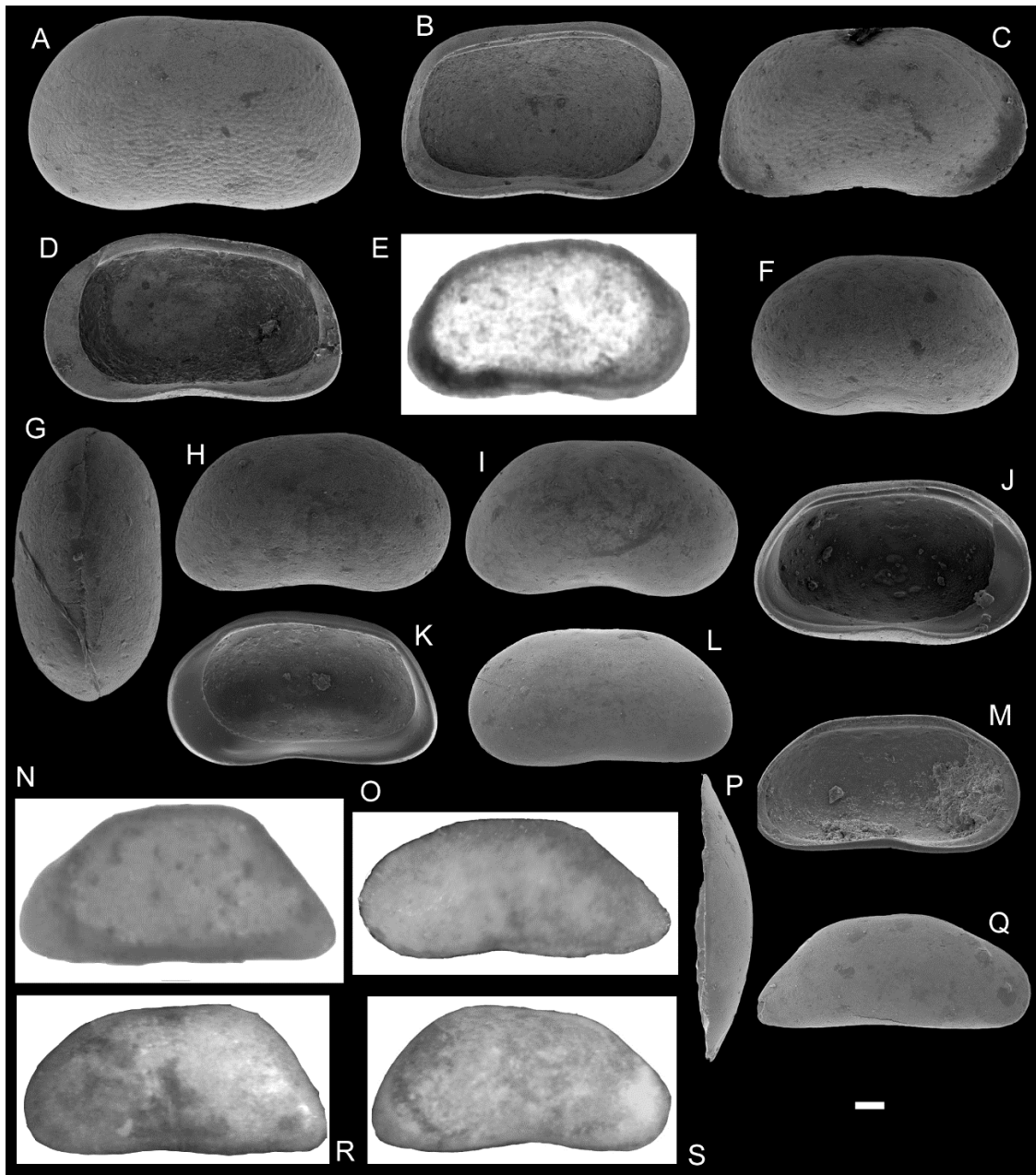
<sup>1</sup> Agalarova et al. (1940, p. 44) made a list of species authored by Livental, including some species never described by him such as *Paracypris filona*, *Paracypris lucojanovae*, *Paracypris lyrata*, *Paracypris rotulata*, and *Paracypris schneiderae*, and *Paracypris sinistrolyrata*. According to the ICZN (International Commission of Zoological Nomenclature, 1999) these names must be considered *nomina nuda*, because are name published after 1930 without any description. These names were later used by other authors who described and illustrated the species giving the authorship to Livental (*Caspiocypris filona* (Livental in Suzin, 1956), *Caspiocypris lyrata* (Livental in Mandelstam & Schneider, 1963), *Caspiocypris rotulata* (Livental, in Mandelstam et al., 1962), *Caspiocypris lucojanovae* (Livental, in Agalarova et al., 1961), *Caspiocypris sinistrolyrata* (Livental, in Agalarova et al., 1961), *Paracypris schneiderae* (Livental, in Agalarova et al., 1961)), contrary to what decided by the ICZN where, in the Glossary, it is stated that the *nomen nudum* is available later for the same or a different concept and, in this case, it would take the authorship and date for that act of establishment, not from any early publication.

Gliozzi, in Spadi et al., 2016, *Caspiocypris nonreticulata* (Sokač, 1972), *Caspiocypris orientalis* (Krstić, 1968), *Caspiocypris perusia* Spadi & Gliozzi, in Spadi et al., 2017, *Caspiocypris pontica* (Sokač, 1972), *Caspiocypris posteroacuta* Spadi & Gliozzi, in Spadi et al., 2017, *Caspiocypris posteroerigera* (Krstić, 1972), *Caspiocypris rakosiensis* (Méhes, 1907), *Caspiocypris rectoides* (Krstić, 1968), *Caspiocypris reticulata* (Méhes, 1907) sensu Krstić (1972), *Caspiocypris reticulata* (Méhes, 1907) sensu Sokač (1972), *Caspiocypris sambucensis* (Medici, Ceci & Gliozzi, 2011), *Caspiocypris sublabiata* (Krstić, 1972), *Caspiocypris symmetrica* (Krstić, 1972), *Caspiocypris tiberina* Spadi & Gliozzi, in Spadi et al., 2017, *Caspiocypris totema* Evlachova, in Mandelstam & Schneider, 1963), *Caspiocypris tuderis* Spadi & Gliozzi, in Spadi et al., 2017, *Caspiocypris vestinae* Spadi & Gliozzi, in Spadi et al., 2016, and *Caspiocypris zagradiensis* (Sokač, 1972).

Furthermore, we consider possible to include in genus *Caspiocypris* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Caspiocypris anchistropa* (Freels, 1980), *Caspiocypris araxica* (Freels, 1980), *Caspiocypris carica* (Freels, 1980), *Caspiocypris dunaviensis* Stancheva, 1964, *Caspiocypris eminens* (Pipik & Bodergat, 2007), *Caspiocypris ermekomensis* (Freels, 1980), *Caspiocypris erzurumensis* (Freels, 1980), *Caspiocypris filona* Suzin, 1956, *Caspiocypris jiriceki* (Pipik & Bodergat, 2006), *Caspiocypris laterisimilis* (Pipik & Bodergat, 2006), *Caspiocypris lucojanovae* Agalarova, Kadyrova & Kulieva, 1961, *Caspiocypris negotini* (Krstić, 1968), *Caspiocypris noraduzensis* Bubikjan, 1966, *Caspiocypris ornata* Hanganu, 1977, *Caspiocypris pokornyi* Stancheva, 1964, *Caspiocypris portaferrica* (Krstić & Stancheva, 1990), *Caspiocypris quadrata* (Olteanu, 1986), *Caspiocypris reticulata* (Méhes, 1907), *Caspiocypris robusta* (Pipik & Bodergat, 2007), *Caspiocypris rotulata* Mandelstam, Markova, Rosyjeva & Stepanaitys, 1962, *Caspiocypris sinistrolyrata* Agalarova, Kadyrova & Kulieva, 1961, *Caspiocypris sinuosa* (Olteanu, 1986), *Caspiocypris subtriangularis* (Schweyer, 1949), *Caspiocypris vaga* Stancheva, 1964, *Caspiocypris vecinata* Mandelstam & Kazmina, in Kazmina, 1975, *Caspiocypris velifera* (Freels, 1980), *Caspiocypris vulgaris* Stancheva, 1964.



**Figure 5.13:** Transmitted light and SEM pictures of some Paratethyan Candoninae species. **A-E**, *Caspiocypris labiata*. **A**, female LV in dorsal view, sample Mt. Medvenica D-237; **B**, female RV in dorsal view, sample Mt. Medvenica D-237; **C**, female LV in lateral view, sample Mt. Medvenica D-254; **D**, female RV in lateral view, lectotype, MFGI microslide Pl6203a; **E**, female RV in inner view, sample Obrenovac 14. **F-H**, *Caspiocypris martoniensis*. **F**, female LV in lateral view, sample Mt. Medvenica III-2; **G**, female RV in lateral view, sample Mt. Medvenica III-2; **H**, female LV in inner view, sample Mt. Medvenica III-2. **I**, *Caspiocypris minuta*, female LV in lateral view, holotype, MFGI, sample Tisztaberek 1089,40-1105,70 m 1648. **J-K**, *Caspiocypris nonreticulata*. **J**, female RV in lateral view, sample Mt. Medvenica D-227; **K**, female LV in lateral view, sample Mt. Medvenica D-227. **L-O**, *Caspiocypris pontica*. **L**, female LV in inner view, sample Mt. Medvenica D-250; **M**, female LV in lateral view, sample Mt. Medvenica D-250; **N**, female RV in lateral view, sample Mt. Medvenica D-240; **O**, female RV in inner view, sample Mt. Medvenica D-250. **P-Q**, *Caspiocypris rakosiensis*. **P**, female LV in inner view, sample Mt. Medvenica D-66; **Q**, female LV in lateral view, sample Mt. Medvenica D-66. **R**, *Caspiocypris rectoides* female RV in lateral view, sample Kladovo E-VI-I 36,6-36,8. **S-T**, *Caspiocypris reticulata sensu* Krstić, 1972. **S**, female LV in inner view, sample Boždaverac 17-II-88; **T**, female RV in lateral view, sample Boždaverac 17-II-88. White bar corresponds to 0.1 mm.



**Figure 5.14:** Transmitted light and SEM pictures of some Paratethyan Candoninae species. **A-D**, *Caspiocypris reticulata sensu* Sokač, 1972. **A**, female LV in lateral view, sample Marcushevak S.S.; **B**, female LV in inner view, sample Marcushevak S.S.; **C**, female RV in lateral view, sample Marcushevak S.S.; **D**, female RV in inner view, sample Marcushevak S.S. **E-K**, *Caspiocypris sublabiata*. **E**, female RV in lateral view, holotype, sample Obrenovac microslide MFGI Pl6306; **F**, female LV in lateral view, sample Obrenovac 14; **G**, female C in dorsal view, sample Obrenovac 14; **H**, female RV in lateral view, sample Obrenovac 14; **I**, male RV in lateral view, sample Obrenovac 14; **J**, female LV in inner view, sample Obrenovac 14; **K**, female RV in inner view, sample Obrenovac 14. **L-M**, *Caspiocypris totema*. **L**, female LV in lateral view, sample Cheliken Peninsula, VNIGRI microslide 105/14; **M**, female LV in inner view, sample Cheliken Peninsula, VNIGRI microslide 105/14. **N**, *Hastacandona granulosa*, female LV in lateral view, sample Tihany 7, MFGI cat. number 105/14. **O**, *Hastacandona croatica*, paratype, female LV in lateral view, sample Mt. Medvenica D-458. **P-Q**, *Hastacandona loczi*. **P**, female LV in dorsal view, sample Obrenovac 13; **Q**, female RV in lateral view, sample Obrenovac 13. **R-S**, *Hastacandona longitesta*. **R**, female LV in lateral view, sample Sremski Karlovci 0-274; **S**, female RV in lateral view, sample Sremski Karlovci 0-275. White bar corresponds to 0.1 mm.

Genus *Hastacandona* Krstić, 1972

(Fig. 5.3 H; Fig. 5.14 N-S)

1972 *Candona* (*Hastacandona*) Krstić: 50

**Type species.** *Candona* (*Hastacandona*) *longitesta* Krstić, 1972, by original designation (original material: 2 female LV stored at NHMB (microslide 0-274), 1 male LV, 1 male RV, 4 female RV stored at NHMB (microslide 0-275), from Sremski Karlovci (Serbia).

**Remarks.** Krstić (1972) arose *Candona* (*Hastacandona*) giving as the main diagnostic character the elongate proportion of the shell in lateral view, specifying that the height is 0.33 of the length. Unfortunately, none of the species assigned by her to this subgenus (even the type species *C. (H.) longitesta*) displays this character although, at least in the RV, the ratios span from 0.5 for the “highest” species (*Hastacandona longitesta*, and *H. granulosa*) to 0.4 for the more elongated species (*H. loczyi*, *H. pontica*, and *H. croatica*). Thus the diagnosis of the genus is emended as follows:

**Emended diagnosis.** elongate trapezoidal in lateral view, with parallel or sub parallel straight dorsal and ventral margins, infracurvate anterior margin.

**Emended description.** In lateral view, elongate trapezoidal shape with parallel ventral and dorsal margins, the latter sometimes slightly inclined forwards. Dorsal margin short, ventral margin straight, with a slight concavity in the middle. Anterior margin rounded, infracurvate, posterior margin straight, inclined posteriorly, postero-ventral end rounded. Surface smooth. Inner structureless lamella strongly developed both anteriorly and posteriorly. Marginal zone narrow, with straight and short pore canals. Hinge margin straight; in the LV the hinge displays a well-developed longitudinal groove, underlined by a robust ledge open at the ends. Muscle scars typical of the subfamily Candoninae. Recognizable sexual dimorphism with male valves longer and posteriorly higher than females, and with more marked ventral concavity.

According to our revision the following species must be ascribed to genus *Hastacandona*: *Hastacandona croatica* (Sokač, 1972), *Hastacandona granulosa* (Zalányi, 1959), *Hastacandona loczyi* (Zalányi, 1929), *Hastacandona longitesta* (Krstić, 1972).

Furthermore, we consider possible to include within *Hastacandona* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Hastacandona hysterica* (Krstić & Stancheva, 1990), *Hastacandona pontica* (Agalarova, in Agalarova et al., 1961)

Genus *Lineocypris* Zarányi, 1929

(Fig. 5.2 J-M; Fig. 5.3 B; Fig. 5.5 C-D; Fig. 5.15 A-J)

1929 *Lineocypris* Zarányi: 40.

1969 *Candona* (*Ochridiella*) Krstić: 220.

**Type species.** *Lineocypris trapezoidea* Zarányi, 1929, by original designation (original material: 2 female broken RV stored at MFGI in the microslide labelled Pl. 6309a, b from Pejinović).

**Remarks.** Zarányi (1929) arose the genus *Lineocypris* describing a simple hinge. This statement was confirmed by one of the authors (EG) based on the observation of the original material stored at MFGI. Mandelstam & Schneider (1963), comparing *Lineocypris* and *Caspiocypris*, underlined that in the former the RV is larger and overlaps the LV, contrary to what generally happens in Candoninae. Taking into account these observations, Spadi et al. (2016) considered them both valid and distinct genera. Indeed, a new survey of the original material stored at MFGI showed that the only specimens preserved there were right valves. Moreover, the new material collected by us at Obrenovac (Serbia), clearly referable to genus *Lineocypris*, although not to the type species, indicates that the LV hinge bears the ledge under the groove and that LV overlaps the RV, as typical of Candoninae. Notwithstanding this, we still consider *Lineocypris* and *Caspiocypris* two different valid genera since in the geometric morphometric analysis they occupy different morphospaces (Fig. 5.7), thus they are well distinguishable on the basis of the valve shape, very high trapezoidal in *Lineocypris*, with a short dorsal margin.

Krstić (1969) described the subgenus *Candona* (*Ochridiella*), successively raised to the generic rank (Krstić & Guan, 2000), based onto two species: *Ochridiella perrara* (Stancheva, 1964) (type species) and *Ochridiella* aff. *tihanyiensis* (Zarányi) in Krstić, 1969. Both species display the typical characters of *Lineocypris*, i.e. a trapezoidal shape and a short dorsal margin. Thus, *Ochridiella* Krstić, 1969, is here considered a junior synonym of *Lineocypris*.

Hereinafter the emended diagnosis and description of *Lineocypris* are reported.

**Emended diagnosis.** in lateral view, trapezoidal shape with the dorsal margin more or less  $\frac{1}{2}$  of the ventral one; infracurvate anterior margin.

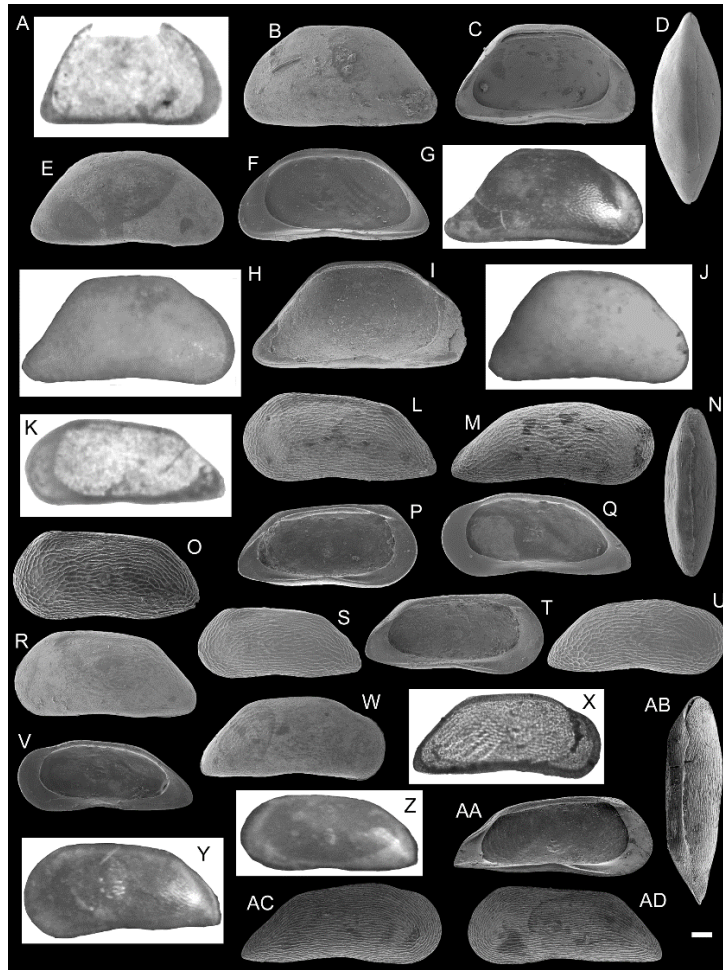
**Emended description.** carapace in dorsal view elliptical, weakly beak-shaped anteriorly and slightly pointed posteriorly. LV larger than RV and overlapping it along all the margins. Valve in lateral view isosceles trapezoidal in shape with dorsal margin short (more or less  $\frac{1}{2}$  of the ventral margin) and



parallel to the ventral margin. Ventral margin straight, with a slight concavity in the middle. Anterior infracurvate margin, posterior margin steeply inclined towards the acute posteroventral end. Surface of the valves smooth or covered by pits in the central part. Inner structureless lamella strongly developed on the anterior margin and poorly developed posteriorly. Pore canal zone relatively narrow, with straight pore canals, which are numerous anteriorly. Hinge margin straight and short. In the LV the hinge is made of a well-developed longitudinal groove, underlined by a robust ledge open at the ends. Muscle scars typical of the subfamily Candoninae. Sexual dimorphism recognizable in most species with male valves larger than females.

According to our revision the following species must be ascribed to genus *Lineocypris*: *Lineocypris branka* (Krstić, 1972), *Lineocypris caudalis* (Krstić, 1972), *Lineocypris inflexa* (Sokač, 1972), *Lineocypris pupini* (Krstić, 1972), *Lineocypris tihanyensis* (Zalányi, 1959), *Lineocypris trapezoidea* Zalányi, 1929.

Furthermore, we consider possible to include in genus *Lineocypris* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Lineocypris delejna* Stancheva, 1964, *Lineocypris dorsobrevis* (Krstić, 1972), *Lineocypris facilis* Stancheva, 1964, *Lineocypris geometrica* (Olteanu, 1989), *Lineocypris hodonensis* (Pokorný, 1952), *Lineocypris lunata* (Mehés, 1907), *Lineocypris luxata* Schneider, in Mandelstam & Schneider, 1963, *Lineocypris meotica* Stancheva, 1964, *Lineocypris perrara* (Stancheva, 1964), *Lineocypris triangularis* (Olteanu, 1989), *Lineocypris vidinensis* Stancheva, 1964.



**Figure 5.15:** Transmitted light and SEM pictures of some Paratethyan Candoninae species. **A**, *Lineocypris trapezoidea*, paralectotype, female RV in lateral view, sample Pejinović MFGI microslide Pl 6309b. **B-F**, *Lineocypris branka*. **B**, female LV in lateral view, sample Obrenovac 14; **C**, female LV in inner view, sample Obrenovac 14; **D**, female C in dorsal view, sample Obrenovac 14; **E**, female RV in lateral view, sample Obrenovac 14; **F**, male RV in inner view, sample Obrenovac 14. **G**, *Lineocypris caudalis*, holotype, female RV in lateral view, sample Boždaverac NHMB microslide 0-280. **H-I**, *Lineocypris inflexa*. **H**, paratype, female RV in lateral view, sample Mt. Medvenica D-308; **I**, female LV in inner view, sample Mt. Medvenica D-254. **J**, *Lineocypris pupini*, holotype, female RV in lateral view, sample Velika Mostanica NHMB microslide 0-278. **K-M**, *Pontoniella acuminata*. **K**, lectotype, female LV in lateral view, sample Pejinović MFGI microslide Pl 6307; **L**, female LV in lateral view, sample Mt. Medvenica VII-29; **M**, female RV in lateral view, sample Mt. Medvenica VII-29. **N-Q**, *Pontoniella bacevicae*. **N**, female C in dorsal view, sample Obrenovac 14; **O**, female LV in lateral view, sample Obrenovac 10; **P**, female LV in inner view, sample Obrenovac 13; **Q**, female RV in inner view, sample Obrenovac 14. **R-X**, *Pontoniella hastata*. **R**, male LV in lateral view, sample Obrenovac 14; **S**, female LV in lateral view, sample Obrenovac 10; **T**, female LV in inner view, sample Obrenovac 10; **U**, female RV in lateral view, sample Obrenovac 10; **V**, female RV in inner view, sample Obrenovac 10; **W**, male RV in lateral view, sample Obrenovac 14; **X**, male LV in lateral view, sample Obrenovac 14. **Y**, *Pontoniella maximumunguiculata*, holotype, female LV in lateral view, sample Umka NHMB microslide 0.262. **Z**, *Pontoniella kolubarae*, holotype, female LV in lateral view, sample Boždarevac NHMB microslide 0-270. **AA-AD**, *Pontoniella sagittosa*. **AA**, female LV in inner view, sample Mt. Medvenica D-66; **AB**, female C in dorsal view, sample Mt. Medvenica D-226; **AC**, female RV in lateral view, sample Mt. Medvenica D-66; **AD**, female LV in lateral view, sample Mt. Medvenica D-66. White bar corresponds to 0.1 mm.

Genus *Pontoniella* Mandelstam, in Luebimova et al., 1960

(Fig. 5.1 A-F; Fig. 5.2 E-I; Fig. 5.3 F-G; Fig. 5.4 A-B; Fig. 5.5 J-L; Fig. 5.15 K-AD; Fig. 5.16 A-E)

1956 *Pontonella* Mandelstam in Schneider et al.: 104

1960 *Pontoniella* Mandelstam in Luebimova et al.: 351

1971 *Candona* (*Serbiella*) Krstić: 377

1972 *Candona* (*Pontoniella*) Mandelstam, 1960 – Krstić: 48

2000 *Pontoniella* Mandelstam, 1960 – Krstić & Guan: 32

2000 *Serbiella* Krstić - Krstić & Guan: 32

**Type species.** *Paracypria acuminata* Zálányi, 1929, by original designation (original material: female LV stored at MFGI (microslide Pl. 6307)).

**Remarks.** In 1956, Mandelstam (in Schneider et al., 1956) described the new genus *Pontonella* to include *Paracypria acuminata* Zálányi, 1929 from the Upper Miocene of Pejinović and Obrenovac (Serbia). Unfortunately, the name *Pontonella* was preoccupied (junior homonym of the crustacean genus *Pontonella* Heller, 1856), thus in 1960 Mandelstam (in Luebimova et al., 1960) corrected its spelling in *Pontoniella* confirming *Paracypria acuminata* Zálányi, 1929 as the type species.

The original material of *P. acuminata* studied by Zálányi (1929) was made by some valves from Pejinović that he considered adults and some valves from Obrenovac that he considered juveniles. In her revision of Zálányi's material stored at the MFGI, Krstić (1971) referred the specimens of *P. acuminata* to two different species both represented by adult valves: *Candona* (*Pontoniella*) *paracuminata*<sup>2</sup> Krstić, 1971 (Pejinović specimens) and *Candona* (*Serbiella*) *hastata* Krstić, 1971 (Obrenovac specimens), this latter chosen as the type species of her new subgenus *Candona* (*Serbiella*). According to Krstić (1971), *Candona* (*Serbiella*) displays 1) ornamented valves, 2) the dorsal margin distinctly tilted backwards and 3) males smaller than females. During our visit at the MFGI we were able to see the Zálányi's collection and we noted that all the specimens originally labelled *Paracypria acuminata* were smooth and with the dorsal margin bending posteriorly. Furthermore, a RV of *C. (Serbiella) hastata* (microslide Pl. 6310) was larger than the other valves (microslides Pl. 6311a, b, c) (L/H respectively 0.84/0.37 and 0.71/0.30, 0.70/0.30, and 0.72/0.32). In the material we collected from the Obrenovac section during summer 2016, we found a sure male RV

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<sup>2</sup> Krstić renamed the species *Paracypria acuminata* Zálányi as *Candona* (*Pontoniella*) *paracuminata* since, with the new generic attribution it would have been preoccupied by *Candona acuminata* (Fischer, 1854).

(with evident seminiferous tubules impressions) (Fig. 5.15 X) of *C. (Serbiella) hastata* that fits well with the specimen in microslide Pl. 6310 MFGI. Thus, we can state that in this species males are larger than females. Notwithstanding Krstić (1971) distinguished *C. (Serbiella)* from *C. (Pontoniella)* on the base of the presence of the surface ornamentation, other specimens of *C. (S.) hastata*, identified by her and stored in the Krstić's collection NHMB are both smooth and ornamented. Furthermore, she referred to *C. (Serbiella)* the species *C. (S.) kolubarae* Krstić, 1972 that bears completely smooth valves. According to Sokač (1972), the distinction of the two subgenera *Pontoniella* and *Serbiella* is not justified due also to the fact that her specimens of *C. (Pontoniella) acuminata* from the Pontian of Mt. Medvenica (Croatia) are strongly ornamented (Fig. 5.15 L-M)

In conclusion, we agree with Sokač (1972) that there is no reason to consider *Pontoniella* and *Serbiella* two different taxa. Consequently, *Serbiella* Krstić is here considered as a junior synonym of *Pontoniella* Mandelstam. We agree with Krstić & Guan (2000) to consider *Pontoniella* as a distinct genus and hereinafter we propose its emended diagnosis.

**Emended diagnosis.** carapace in dorsal view elliptical, compressed, with pointed ends; LV dorsal margin widely overlaps the RV along the hinge margin particularly in correspondence with the cardinal angles; in lateral view, elongated shape, dorsal margin straight, inclined posteriorly, equicurvate rounded anterior margin.

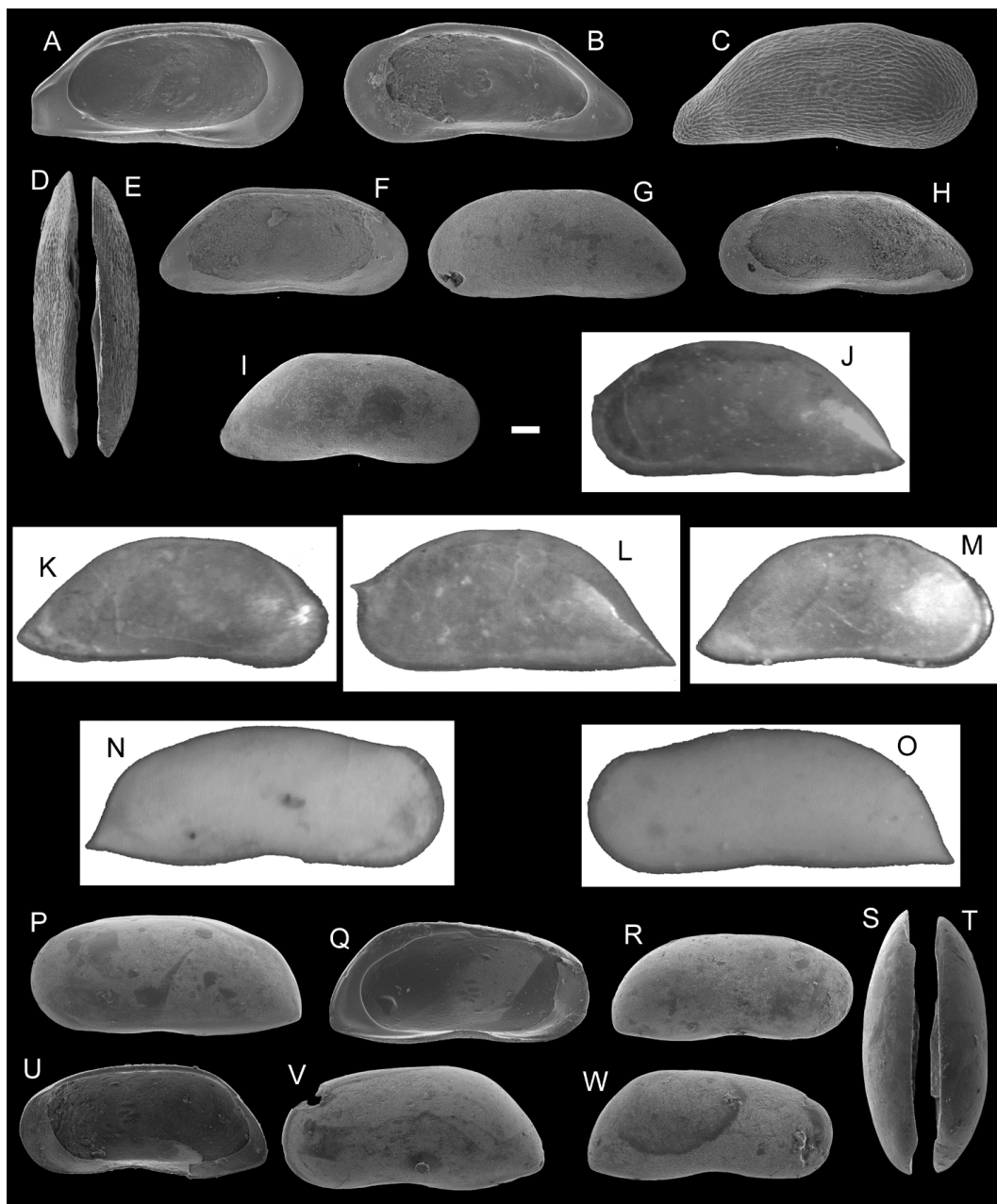
**Emended description.** Carapace in dorsal view compressed with anterior end slightly more pointed than the posterior one. LV larger than RV with conspicuous overlapping (Fig. 5.1 A-F), along the dorsal margin, particularly remarkable in correspondence with the cardinal angles. Carapace in lateral view: elongated. Anterior end rounded along the entire margin. Dorsal margin almost straight, distinctly inclined backwards, with marked cardinal angles. Ventral margin rectilinear, with a weak concavity in the median portion. Posterior margin rectilinear and inclined posteriorly. Posterior end pointed or truncated. Surface of the valves smooth or covered with fine elongate longitudinal ribs or reticulated. Inner lamella developed along the anterior and posterior margins. Pore canal zone relatively narrow, with straight pore canals, which are numerous on the anterior margin. Hinge of the LV consisting of a well-developed longitudinal groove, underlined by a robust ledge open at the ends. Cardinal margin overspreading the hinge area in correspondence of the cardinal angles (Fig. 5.1 A, D). Muscle scars with the arrangement typical of the subfamily Candoninae. Feeble sexual dimorphism, with male valves only slightly larger than females and with dorsal margin less inclined posteriorly.

According to our revision, the following species must be ascribed to genus *Pontoniella*:

*Pontoniella acuminata* (Zalányi, 1929), *Pontoniella baceviccae* (Krstić, 1972), *Pontoniella hastata* (Krstić, 1971), *Pontoniella ilici* (Krstić, 1972), *Pontoniella kolubarae* (Krstić, 1972),

*Pontoniella maximunguiculata* (Krstić, 1972), *Pontoniella sagittosa* (Krstić, 1972), *Pontoniella truncata* (Sokač, 1972).

Furthermore, we consider possible to include into genus *Pontoniella* also the following species illustrated in literature: *Pontoniella excellentis* Olteanu, 1995, *Pontoniella quadrata* (Krstić, 1972), *Pontoniella rudjakovi* (Krstić, 1972), *Pontoniella sohatensis* Olteanu, 1995.



**Figure 16.** Transmitted light and SEM pictures of some Paratethyan Candoninae species. **A-E**, *Pontoniella truncata*. **A**, female LV in inner view, sample Obrenovac 1; **B**, female RV in inner view, sample Obrenovac 1; **C**, female RV in lateral view, sample Obrenovac 1; **D**, female LV in dorsal view, sample Obrenovac 1; **E**, female RV in dorsal view, sample Obrenovac 1. **F-I**, *Propontoniella macra*. **F**, female LV in inner view, sample Mt. Krndija BP 3-7-9; **G**, female LV in lateral view, sample Mt. Krndija BP 3-7-9; **H**, female RV in inner view, sample Mt. Krndija BP 3-7-9; **I**, female RV in lateral view, sample Mt. Krndija BP 3-7-9. **J-K**, *Typhlocyprella annae*. **J**, holotype, female LV in lateral view, sample

Boždaverac NHMB microslide 0-303; **K**, paratype, female RV in lateral view, sample Boždaverac NHMB microslide 0-304. **L-M**, *Typhlocyprrella lineocypriformis*. **L**, holotype, female LV in lateral view, sample Boždaverac NHMB microslide 0-305; **M**, paratype, female RV in lateral view, sample Boždaverac NHMB microslide 0-306. **N-O**, *Typhlocyprrella elongata*. **N**, holotype, female RV in lateral view, sample Mt. Medvenica D-125; **O**, paratype, female LV in lateral view, sample Mt. Medvenica D-125. **P-W**, *Zalanyiella venusta*. **P**, female LV in lateral view, sample Obrenovac 1; **Q**, female LV in inner view, sample Obrenovac 14; **R**, female RV in lateral view, sample Obrenovac 1; **S**, female LV in dorsal view, sample Obrenovac 1; **T**, female RV in dorsal view, sample Obrenovac 14; **U**, female RV in inner view, sample Obrenovac 14; **V**, male LV in lateral view, sample Obrenovac 14; **W**, male RV in lateral view, sample Obrenovac 14. White bar corresponds to 0.1 mm.

***Propontoniella*** Krstić, 1972

(Fig. 5.3 I; Fig. 5.16 F-I)

1972 *Candona* (*Propontoniella*) Krstić: 33

1972 *Candona* (*Propontoniella?*) Krstić: 33

**Type species.** *Candona* (*Propontoniella*) *fragilifera* Krstić, 1972, by original designation (original material: 1 female LV stored at NHMB (microslide 0-248), 27 female and male LV and RV (microslide 0-249) from Velika Moštanica (Serbia). (Material not found).

**Remarks.** Krstić (1972) described two probably different subgenera *Propontoniella* and *Propontoniella?*, afterwards elevated to the generic rank and referred to two different tribes (Krstić & Guan, 2000), without giving any indication of their diagnostic characters. The geometric morphometric analysis of the valve outline based on the original figures by Krstić (1972, Pl. 11, figs. 1-18) does not show any remarkable difference between the two genera except for the presence of a more marked postero-cardinal angle in *Propontoniella?*. Anyway, these characters could be considered characteristic at the specific level, so we consider *Propontoniella?* as a junior synonym of *Propontoniella*. The revision of this genus is mainly based on the illustrations by Krstić (1972), since no original material was recovered at the NHMB. Few observations of the internal morphological characters were carried out on some valves of *Propontoniella macra* collected in the Early Pannonian sediments of the Vranović-1 section (Croatia) and stored in the GOC.

**Emended diagnosis.** elongate in lateral view, parallel dorsal and ventral margins.

**Emended description.** Carapace in dorsal view elliptical with pointed anterior and posterior ends. LV larger than RV. Carapace in lateral view elongated, with parallel dorsal and ventral margins. The dorsal margin is shorter than the ventral one and the cardinal angles are poorly visible. Anterior margin rounded, equicurvate, posterior margin gently inclined posteriorly, rounded posteroventral end. Ventral margin straight, with a slight concavity in the middle. Surface of the valve smooth. Inner

lamella strongly developed both anteriorly and posteriorly. Pore canal zone relatively narrow, with straight pore canals. Hinge of the LV consists of a well-developed longitudinal groove underlined by a robust ledge open at the ends. Muscle scars typical of the subfamily Candoninae. Sexual dimorphism present with male valves larger than females.

According to our revision the following species must be ascribed to genus *Propontoniella*: *Propontoniella fragilifera* (Krstić, 1972), *Propontoniella macra* (Krstić, 1972)

Furthermore, we consider possible to include into genus *Propontoniella* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Propontoniella nemanjæ* (Krstić, 1972), and *Propontoniella pavlovici* (Krstić, 1972).

#### Genus *Typhlocyprella* Krstić, 1972

(Fig. 5.3 J; Fig. 5.5 M-N; Fig. 5.16 J-O)

1972 *Typhlocyprella* Krstić: 88.

**Type species.** *Candona (Typhlocyprella) annae* Krstić, 1972, by original designation (original material: 1 female LV stored at NHMB (microslide 0-303), 4 female RV and LV stored at NHMB (microslide 0-304) from Boždarevac (Serbia)).

**Emended diagnosis.** elongated pointed posterior end; LV with a mucro on the middle anterior margin; hinge adont.

**Emended description.** Carapace in lateral view elongated, highest in the middle. Dorsal margin arched or slightly curved, ventral margin slightly concave in the middle. The anterior margin is rounded and infracurvate; in the LV, in the middle of the anterior margin a mucro is developed. Posterior margin gently descending posteriorly, postero-ventral end elongate and sharply pointed. Surface of the valves smooth. Anterior inner lamella about three times broader than the fusion zone. Marginal pore canals straight. Adont hinge. Muscle scars typical of the subfamily Candoninae. Sexual dimorphism present, with males slightly larger than females.

According to our revision the following species must be ascribed to genus *Typhlocyprella*: *Typhlocyprella annae* (Krstić, 1972), *Typhlocyprella elongata* (Sokač, 1972), and *Typhlocyprella lineocypriformis* (Krstić, 1972).



Furthermore, we consider possible to include into genus *Typhlocyprella* also *Typhlocyprella triangularis* (Schweyer, 1949), formerly ascribed by Mandelstam & Schneider (1963) to genus *Advenocypris*.

Genus *Zalanyiella* Krstić 1972

(Fig. 5.3 K; Fig. 5.5 H-I; Fig. 5.16 P-W)

1972 *Candona* (*Zalanyiella*) Krstić: 28

1972 *Candona* (*Zalanyiella?*) Krstić: 28

**Type species.** *Candona* (*Zalanyiella*) *longissima* Krstić, 1972, by original designation (original material: 1 female LV stored at NHMB (microslide 0-238), 27 female LV, RV and carapaces and 2 male LV and RV (microslide 0-239) from Meljak (Serbia). Material not found).

**Remarks.** Krstić (1972) described two different subgenera, subsequently elevated to the generic rank *Zalanyiella* and *Zalanyiella?* (Krstić & Guan, 2000). Krstić (1972) separated the two genera on the base of the more inflated carapace of *Zalanyiella* and the acuminate postero-ventral end of *Zalanyiella?* Indeed, if we observe the illustrations of the two genera reported by Krstić (1972) we note that the postero-ventral end is acuminate in both of them, although slightly different at species level. The similar outline is well visible in the nMDS plot (Fig. 7) where both genera are grouped together. Thus, we consider *Zalanyiella?* as a junior synonym of *Zalanyiella*.

**Emended diagnosis.** elongated laterally with parallel dorsal and ventral margins; cardinal angles are not evident; posterior end acuminate.

**Emended description.** Carapace in dorsal view elliptical with pointed anterior end and slightly pointed posterior end. LV larger than RV and overlapping it in dorsal, posterior and ventral margin. Carapace in lateral view elongated with slightly infracurvate rounded anterior margin and obliquely arched posterior margin ending in an acuminate postero-ventral end. Dorsal margin straight, parallel to the ventral margin. The cardinal angles are not visible. Ventral margin rectilinear, with a poorly expressed middle concavity. Surface of the valves smooth. Structureless inner lamella strongly developed anteriorly and poorly developed posteriorly. Pore canal zone relatively wide, with straight pore canals. Hinge of the LV with a well-developed longitudinal groove underlined by a robust ledge open at the ends. Muscle scars typical of the subfamily Candoninae. Feeble sexual dimorphism, with males only slightly larger than females and with higher postero-dorsal margin.

According to our revision the following species must be ascribed to genus *Zalanyiella*: *Zalanyiella longissima* (Krstić, 1972) and *Zalanyiella venusta* (Zalányi, 1929).

Furthermore, we consider possible to include in genus *Zalanyiella* also the following species illustrated in literature (no critical analysis at the specific level was performed, so it is possible that some of them would need a taxonomic revision): *Zalanyiella bucii* (Krstić, 1972), *Zalanyiella drzici* (Krstić, 1972), *Zalanyiella multipora* (Pokorný, 1952), *Zalanyiella praekaratengisa* (Agalarova, 1967), *Zalanyiella rurica* (Krstić, 1972), and *Zalanyiella venustoidea* (Krstić, 1972)

### **Other Paratethyan Candoninae genera**

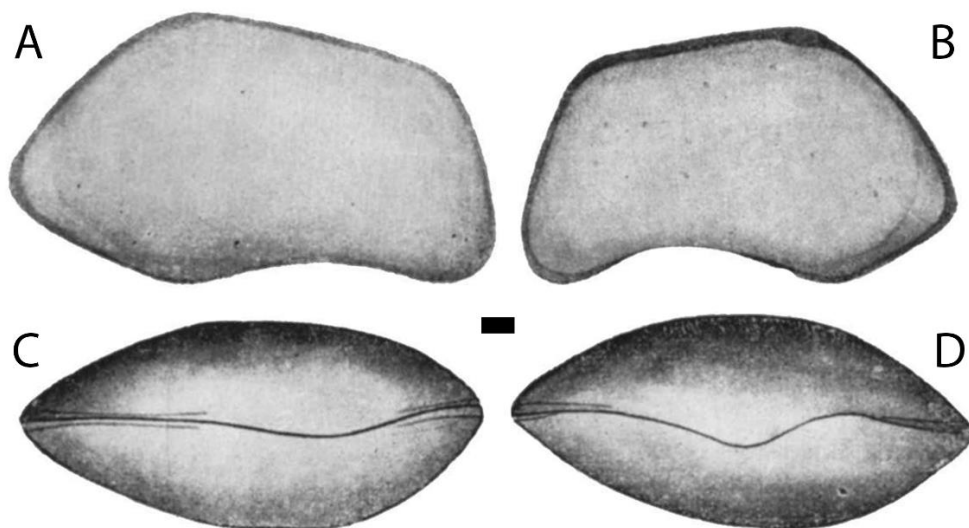
Some Paratethyan genera listed in Tab. 5.1 were not considered in the present revision because other authors had already defined their taxonomic position. This is the case of the two triangular genera *Telekia* Sohn & Morris, 1963 (= *Kochia* Héjjas, 1894 junior homonym of Mollusca *Kochia* Frech, 1891) and *Advenocypris* Schneider, in Schneider et al., 1956 that, according to Triebel (1963), Krstić (1972), Sokač (1972), and Namiotko et al. (2014), are synonyms of *Typhlocypris* Vejdovský (1882).

In addition, genus *Candoniella* Schneider in Schneider et al., 1956 was considered by Danielopol et al. (2008), Matoshko et al. (2016) and van Baak et al. (2016) to be based on juvenile valves of *Pseudocandona* and/or *Candona*.

Genus *Graviacypris* was established by Schneider, in Mandelstam & Schneider, 1963 to include the species *Bythocypris elongata* Schweyer, 1949 (type species) and *Graviacypris liepini* Mandelstam, in Mandelstam & Schneider, 1963. In 1964, Schornikov studied some living shells from the Black Sea, referable to Schneider's species. According to his description and drawings, the appendages of *G. elongata* displayed the same characters of genus *Candona* (cleaning leg and penis, mxp-clasping organs, setal group on the 2<sup>nd</sup> segment of the mandibular palp with 4 setae). The only possible difference is the morphology of the  $\gamma$  seta on the penultimate segment of the mandibular palp that seems to be not plumose. Unfortunately, the drawing is not clear at all and this character is not mentioned in the text. Schornikov (1964) considered *Graviacypris* as a junior synonym of *Candona* and, since *Candona elongata* Schweyer would have been junior homonym of *Candona elongata* Herrick, 1879, he changed its name in *Candona schweyeri* (Boomer et al., 2010). Krstić (2006) referred to genus *Graviacypris* the specie *G. cerevici* from the Paludinian beds of Serbia, but in her collection stored at the NHNB (microslide 056.1.024 and 056.1.025) these valves are labelled as *Neglecandona*. In conclusion, we agree with the previous author in considering *Graviacypris* a junior synonym of genus *Candona*.

Genus *Moesiella* Olteanu, 1995 was established without a diagnosis to include some species previously referred to *Pontoniella* (*P. schemachensis* Mandelstam, in Mandelstam et al., 1962) and *Liventalina* (*L. fastigata* Markova, in Mandelstam et al., 1962, *L. gerdae* Markova, in Mandelstam et al., 1962). According to the ICZN art. 13.1 *Moesiella* is a *nomen nudum*.

Genus *Thaminocypris* Zalany, 1944 was based on a single carapace of the type species *Thaminocypris declinata* collected in the sample 1,266.20-1,290.90 m of the Tisztaberek borehole (Hungary). The original material was not found at the MFGI. The generic diagnosis strictly follows the description of the type species that seems to have a peculiar, maybe teratological, shape characterised by a straight and strongly bended posteriorly dorsal border, a pointed in the middle anterior border and a ventral margin with a wide and deep posteriorly shifted concavity (Fig. 5.17). The species was collected in the Tisztaberek deep borehole and no more found elsewhere. For a detailed description refer to Zalányi (1944). No other known species mirrors the generic characters of *Thaminocypris*.



**Figure 5.17:** Original pictures of *Thaminocypris declinata* from Zalányi (1944). **A**, **C** in left lateral view; **B**, **C** in right lateral view; **C**, **C** in dorsal view; **D**, **C** in ventral view. The carapace was collected in the sample at 1,266.20-1,290.90 m of the Tisztaberek borehole (Hungary). The bar corresponds to 0.1 mm.

For other genera, we were not able to examine neither the type material nor any other specimens and the published diagnoses and/or illustrations were not sufficient to understand the morphological characters and the outline shape. For example:

Genus *Caspiollina* Mandelstam in, Mandelstam et al., 1957 (type species *C. uschakensis* Mandelstam in Mandelstam et al., 1957) is characterised by a peculiar hinge in the left valve described as “in the form of a shelf with a buldge at the anterior end of the dorsal margin” (Mandelstam et al.,

1957, p. 170 – from the English translation in the Ellis & Messina Catalogue, 1983). Unfortunately the species is illustrated only in external view both in the original paper and in the subsequent Mandelstam & Schneider (1963). If the hinge is truly so characteristic, *Caspiollina* should be considered a valid genus. Although Mandelstam & Schneider (1963) clearly stated that genus *Caspiollina* is monospecific, in the original description of the genus the authors indicate that two Rosyjeva's species (*Candona toranglyensis* Rosyjeva, 1954 and *Candona kurendagensis* Rosyjeva, 1954) display the same hinge type and similar shape. Regrettably, also Rosyjeva (1954) illustrate the valves only in external view.

Genus *Dacicandona* Stancheva, in Stancheva, 1981b, that replaced *Daciella* Stancheva, in Stancheva, 1981a (junior homonym of the gastropod genus *Daciella* Wenz, 1942), was arisen to include *Candona (Daciella) nikolovi* Stancheva, in Stancheva, 1981a, characterised by a “buldge” in the middle of the ventral male left valve. It is worth to note that this character is not mentioned in the generic description. If valid, this genus needs a revision based on the type material.

Genus *Liventalina* was described by Schneider, in Schneider et al., 1958 based on the species *Herpetocypris dagadgikensis* Markova, 1956. Sokač (1972) put this genus in synonymy with *Typhlocyprilla*. Unfortunately, the description of the hinge given by Schneider is not enough to understand if it is simply adont, as in *Typhlocyprilla*. In any case, the valves of the illustrated specimens (Markova, 1956 pl. 1, fig. 6; Mandelstam & Schneider, 1963, pl. 21 figs. 8, 9) show a posterior area less elongate and acuminate and are ornamented. Some other species such as *L. fastigata* Markova, in Mandelstam et al., 1962, *L. gerdæ* Markova, in Mandelstam et al., 1962, and *L. cribrum* (Markova, 1957), have been referred to *Liventalina*. Their illustrations and description are insufficient to understand if they can be grouped in the same genus.

Schneider described *Turkmenella lucida* Schneider, in Mandelstam & Schneider, 1963 from the Tertiary of the Altai Mts. (central Asia) as the type species of his new genus *Turkmenella*, characterised by a trapezoidal shape and a typical depression in the middle of the LV dorsal margin. He included in this genus also *T. abnormis* Mandelstam, in Mandelstam & Schneider, 1963 from the lower Oligocene of Crimea, *T. caspia* Mandelstam, in Mandelstam & Schneider, 1963, and *T. ignobilis* Mandelstam, in Mandelstam & Schneider, 1963 from the Apsheronian of the western Turkmenistan. In 1972, Krstić described *Candona (Turkmenella?) robusta* underlining that *Turkmenella?* represented a different genus than *Turkmenella* and included in it also the two Mandelstam's species collected in Turkmenistan. In Plate 22, Krstić (1972) illustrated several species: *Turkmenella? robusta*, represented by the holotype and paratypes stored at the NHMB (microslides 0-297 and 0-298), in our opinion must be included in genus *Caspiocypris*; *Turkmenella?* sp. 5, is *Lineocypris*-like; *Turkmenella?* sp. 44 and sp. 47 probably could be referred to *Bakunella*. In

conclusion, we think that, probably, *Turkmenella* Schneider could be a valid genus, but it needs further revision of the type material, whereas *Turkmenella?* Krstić seems to include species referable to other genera.

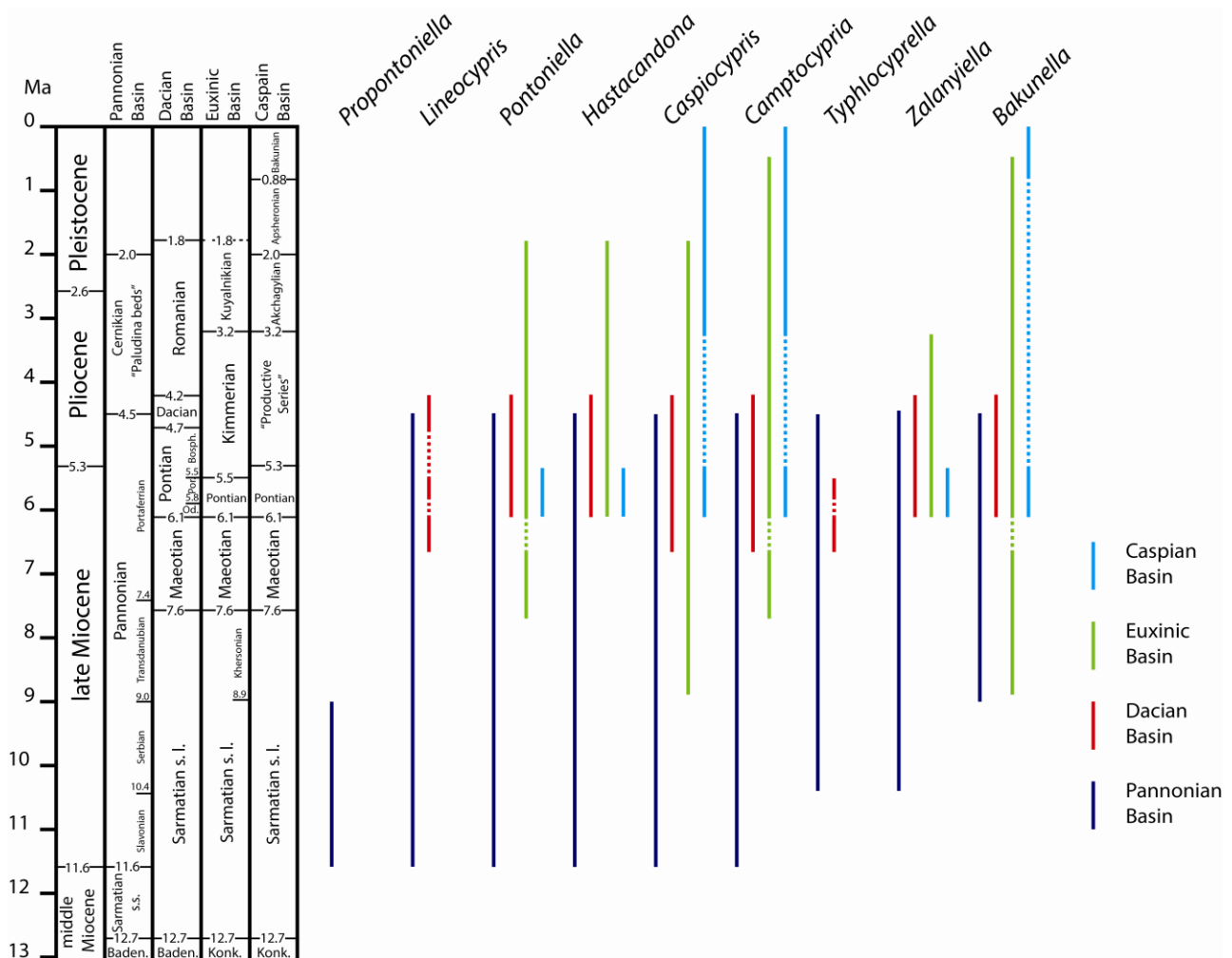
## 5.6 Discussion and Conclusion

The taxonomic revision carried out on the 33 genera of Candoninae widespread in the Neogene of the Paratethys (Tab. 5.1) on the basis of morphometric characters of their valves and the geometric morphometric analysis of the valve outlines gave the following results: 9 valid genera (*Bakunella*, *Camptocypris*, *Caspiocypris*, *Hastacandona*, *Lineocypris*, *Pontoniella*, *Propontoniella*, *Typhlocyprilla*, and *Zalanyiella*); 1 monospecific genus (*Thaminocypris*) possibly including a teratological form; 3 genera (*Telekia*, *Advenocypris*, and *Candoniella*) already been considered synonyms of other Candoninae genera geographically distributed also outside Paratethys; 1 genus (*Graviocypris*) synonymized with genus *Candona* on the basis of its soft parts; 1 genus (*Moesiella*) considered *nomen nudum*; 4 genera (*Caspiollina*, *Dacicandona*, *Liventalina*, and *Turkmenella*) still with an unclear taxonomic position due to the impossibility to see the type material and to the scarce quality of the original diagnoses and illustrations; one genus (*Turkmenella?*) that probably includes species that must be referred to different genera.

The chronostratigraphic distribution of the valid genera is reported in Fig. 5.18, in which it is shown that all the genera originated in the Pannonian Basin, scattered during Pannonian: *Propontoniella*, *Lineocypris*, *Pontoniella*, *Hastacandona*, *Caspiocypris* and *Camptocypris* during Slavonian, *Typhlocyprilla* and *Zalanyiella* during Serbian and *Bakunella* during Transdanubian. In the late Pannonian/Maeotian some of them (*Caspiocypris*, *Bakunella*, *Camptocypris*, and *Pontoniella*) were recovered also in the Euxinic Basin. By the latest Pannonian/Pontian, all the genera (except for *Propontoniella* exclusive of the Pannonian Basin and *Lineocypris* and *Typhlocyprilla* exclusive of the Pannonian and Dacic basins) were widely distributed in the Pannonian, Dacic, Euxinic and Caspian basins. On the whole, the range chart shows an eastwards migration of the Paratethyan genera during the Late Miocene due to the progressive salinity reduction that affected those basins as indicated also by the molluscan fauna (Stevanovic et al., 1989) and by dinoflagellates (Grothe et al., 2014). The absence of *Caspiocypris*, *Bakunella*, *Camptocypris*, and *Pontoniella* from the Dacic Basin during Maeotian must probably be due only to the lack of data. *Zalanyiella*, *Pontoniella*, and *Hastacandona* seem to have only sporadic occurrences in the Caspian Basin, whereas they were well documented in the Euxinic Basin until the end of the Kimmerian (*Zalanyiella*) and Kuyalnikian (*Pontoniella* and *Hastacandona*). *Caspiocypris*, *Camptocypris* and *Bakunella* are

the most long-lived taxa, having being signalled in the Caspian Sea in recent sediments, although only *Camptocypris* displays a living species (*Camptocypris camelus*) (Schornikov, 1966).

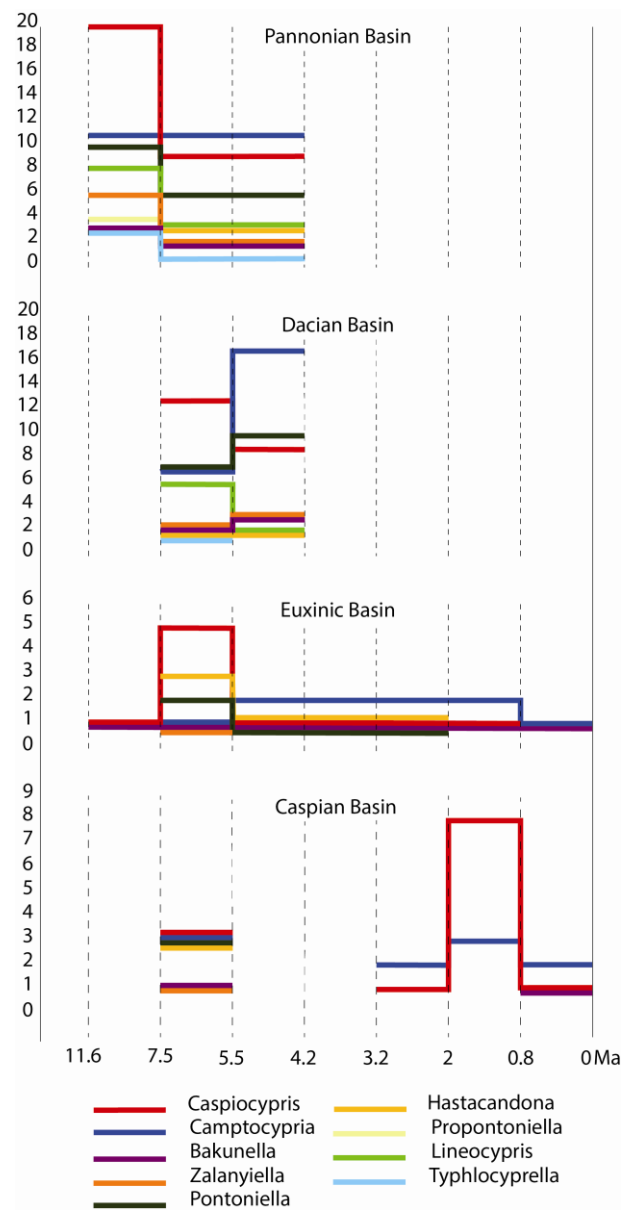
The discontinuous occurrence of some genera such as *Pontoniella* and *Camptocypris* in the Euxinic Basin or *Caspiocypris*, *Camptocypris* and *Bakunella* in the Caspian Basin could be ascribed to environmental changes that made their life unsuitable. For example, in the late Maeotian the Euxinic Basin was affected by increased salinities (Popov et al., 2016). Conversely, the Productive Beds in the Caspian Basin deposited in low salinity fluvial-deltaic environments (van Baak et al., 2013). Anyway, the very scattered distribution of *Bakunella* in the Caspian Basin remains still puzzling.



**Figure 5.18:** Stratigraphic range chart of the Paratethyan Candoninae in the four different Paratethys basins. The chronostratigraphy scheme is derived from the following papers: Pannonian Basin – Magyar et al. (1999), Sacchi & Horvarth (2002), Magyar & Geary (2012), Mandic et al. (2015); Dacian Basin – Stoica et al. (2013), van Baak et al. (2015); Euxinic Basin – Radionova et al. (2012), Popov et al. (2013, 2016), Rybkina et al. (2015); Caspian Basin – van Baak et al. (2013, 2016).

Actually, some genera of Paratethyan Candoninae have been reported in literature before Pannonian from the early and middle Miocene of the Balkan Peninsula and Anatolia. In particular, Hajek-Tadesse et al. (2009) reported *Caspiolla* (= *Camptocypris*), *Lineocypris*, and *Pontoniella* from the Early Miocene (late Oligocene-Karpatian) of Mount Požeška (Croatia), whereas Sant et al. (2016) reported *Camptocypris* and *Lineocypris* from the Middle Miocene (Badenian) of the Popovac Lake (Serbia). In both cases, the illustrated valves are badly preserved and the generic attribution is, at least, doubtful. Freels (1980) described several species referable to genera *Bakunella*, *Caspiolla* (= *Camptocypris*), *Caspiocypris*, *Lineocypris*, and *Pontoniella* starting from the early Miocene to Pleistocene in different basins of the Anatolia Peninsula. Unfortunately, this paper used a chronostratigraphy based on pollen and vertebrate biochronology dated back to 1970s and no more valid. Although in this paper we do not take in consideration the data reported in the quoted literature, we do not exclude at all that some Paratethyan Candoninae genera could have been rooted in the early-middle Miocene, appeared within the freshwater-brackish waterbodies of the Dinaric and Serbian Lake Systems.

Although the evaluation of the Paratethyan Candoninae biodiversity could be biased by the lack of a complete taxonomic revision at the specific level, Fig. 5.19 represents an attempt to compare such biodiversity in the four main Paratethyan basins. The highest number of genera and species occurred in the Pannonian Basin during the Pannonian. The maximum biodiversity occurred in the Slavonian-Transdanubian, when *Caspiocypris* displayed 20 species, *Camptocypris* 11 and *Pontoniella* 10. During Portaferrian, the biodiversity slightly decreased with eight genera and, on the whole, 37 species. At the end of the Pannonian, all the Paratethyan Candoninae disappeared from the Pannonian Basin that underwent a drastic environmental change resulting in the wide



**Figure 5.19:** Paratethyan Candoninae biodiversity at the species level along the late Cenozoic in the four different Paratethys basins.



freshwater Lake Slavonian in which inhabited the freshwater ostracods of the so-called “Paludine Beds” (Krstić, 2006).

As stated above, it is possible that the colonization of the Dacian Basin must be dated back to the early Maeotian (since at this time some Paratethyan Candoninae occurred in the most eastern Euxinic Basin). Unfortunately, no studies have been done on this time interval. The first occurrence of the Paratethyan Candoninae in the Dacian basin is known in the late Maeotian and Pontian with eight genera (Olteanu, 2011). Also here, the most speciose genera are *Camptocypria* (maximum 17 species), *Caspiocypris* (maximum 13 species), and *Pontoniella* (maximum 10 species).

The Euxinic Basin was colonized by the Paratethyan Candoninae since the Khersonian, at first by *Bakunella* and *Caspiocypris* and afterwards by *Camptocypria*, *Pontoniella*, *Hastacandona* and *Zalanyiella*, with a reduced number of species (Popov et al, 2016; Stoica et al., 2016). Around the beginning of the Pontian the same six genera widespread in the Caspian Basin (Mandelstam & Schneider, 1963; van Baak et al., 2013, 2016). Along with time and the eastward migration, the biodiversity decreased both at the generic level (from nine to six genera and, after 2 Ma only three genera) and at the specific level. In the Pannonian Basin the maximum biodiversity was attained during the Slavonian-Transdanubian interval with 69 species, in the Dacian Basin during the Bosphorion-Dacian with 46 species, in the Euxinic Basin during the Maeotian-Pontian with 13 species and in the Caspian Basin in the Pontian with 14 species.

A future revision of the Paratethyan Candoninae species could clarify if during the migration eastwards only the most adaptable species survived or, as it is more probable, at least in part new adaptive radiation occurred.

### **5.7 What we learned about *Caspiocypris*?**

In conclusion, *Caspiocypris* is one of the valid nine Candoninae genera that occurred in the Neogene and Quaternary of Paratethys. Its generic diagnostic characters (in lateral view, sub-rectangular to sub-trapezoidal in shape, with the dorsal margin only slightly shorter than the ventral one and the anterior margin generally equicurved) allows its easy and clear distinction from other similar coeval genera. *Caspiocypris* appeared in the Slavonian (early Tortonian) of the Pannonian Basin and, successively, migrated eastwards into the Dacian, Pontian and Caspian basins. In this latter basin it was found up to the Holocene. No living species have been recovered up to now. The Neogene adaptive radiation of *Caspiocypris* gave origin to numerous species (although the true number has not yet been established due to the lack of a taxonomical revision at the species level), particularly in the Pannonian and Dacian Basins (Krstić, 1972; Sokač, 1972; Olteanu, 2011) (Fig. 5.19), where its presence persisted up to the Zanclean. Afterwards, few species were recorded only in the Eastern

Paratethys. From a palaeobiogeographic point of view, during Miocene *Caspiocypris* was confined to the Paratethyan Bioprovince, except for the very end of it (5.4-5.33 Ma) corresponding to the Late Messinian Lago-Mare facies at the end of the Messinian Salinity Crisis, during which two Paratethyan species, *Caspiocypris pontica* and *Caspiocypris alta*, migrated into the Palaeomediterranean (Gliozzi & Grossi, 2004; 2008; Cosentino et al., 2011). Conversely, during Plio-Pleistocene also extra-Paratethyan species were found: in the early Zanclean *Caspiocypris sambucensis* (Valdelsa Basin-Tuscany, central Italy) (Medici et al., 2011) and in the Piacenzian-Gelasian (the Palaeolake Tiberino and Palaeolake San Nicandro species flocks) (central Italy) (Spadi et al, 2016, 2017; this thesis). The Plio-Pleistocene presence of *Caspiocypris* in Italy will be discussed in Chapter 6.

Genus	Carapace in dorsal view	Shape	Dors. L/ Ventr. L	Ventral margin	Anterior margin	Posterior end	Surface	LV Hinge
<i>Bakunella</i>	Inflated with flat profile in the middle	Trapezoidal	~ 0.5	Straight with a small concavity in the middle	Infracurvate	Pointed	Strongly ornamented with polygonal meshes	With a robust ledge
<i>Camptocypria</i>	Elliptical	Elliptical	~ 1	Straight with a marked concavity in the middle	Infracurvated	Pointed	Smooth	With a robust ledge
<i>Caspiocypris</i>	Inflated	Rectangular	~ 1	Straight with a small concavity in the middle	Equicurvate	Rounded	Smooth	With a robust ledge
<i>Hastacandona</i>	Elliptical	Trapezoidal	~ 0.5	Straight with a small concavity in the middle	Infracurvated	Pointed	Smooth	With a robust ledge
<i>Lineocypris</i>	Elliptical	Trapezoidal	~ 0.5	Straight with a small concavity in the middle	Infracurvated	Pointed	Smooth or pitted in the middle	With a robust ledge
<i>Pontoniella</i>	Elliptical	Elongated	~ 1	Straight with a small concavity in the middle	Equicurvate	Pointed	Elongated ribs	With a robust ledge
<i>Propontoniella</i>	Elliptical	Elongated	~ 1	Straight with a small concavity in the middle	Equicurvate	Pointed	Smooth	With a robust ledge
<i>Typhlocyprilla</i>	Elliptical	Elliptical	~ 0.5	Concave in the middle	Infracurvated	Pointed	Smooth	Adont
<i>Zalanyiella</i>	Elliptical	Elliptical	~ 1	Straight with a small concavity in the middle	Infracurvated	Pointed	Smooth	With a robust ledge

**Table 5.2:** Identification chart to the main taxa of Paratethyan Candoninae considered valid in this thesis with the key features for each species.

## 6. Discussion and Conclusion

### 6.1 Taxonomy and Palaeobiodiversity of the Plio-Pleistocene non-marine Ostracoda from the central Apennines Intermontane basins

The Pliocene-Early Pleistocene non-marine ostracods of central Italy are documented by an increasing number of sites from several lacustrine and/or fluvial sedimentary basins enclosed within the Apennine chain (Barberi et al., 1995; Ligios et al., 2009; Medici et al., 2011; Bellucci et al., 2012, 2014; Barisone et al., 2014; Spadi et al., 2016, 2017; Pandolfi et al., 2017), namely the Tiberino, L'Aquila, Anagni and Rieti basins and the Middle Tiber Valley. The present paragraph aims to provide an updated overview of the ostracod assemblages data available for the continental deposits of central Italy. The analysis of the non-marine ostracod assemblages recovered from the early infilling (Piacenzian and Gelasian) deposits of three different central Apennines intermontane basins (Tiberino, L'Aquila, and Rieti basins) and the Middle Tiber Valley studied in this thesis, merged with the previous data, gives a good framework of the non-marine ostracod palaeobiodiversity.

The ostracod from the Tiberino Basin, collected in the sediments associated to the deposition of Palaeolake Tiberino (Fosso Bianco and Ponte Naja formations) were referable to 24 species pertaining to 14 genera, 8 of which resulted endemic species (Tab. 6.1). Most of the new species described for the Tiberino Basin were collected in the deep lacustrine (facies A) of Fosso Bianco Fm. (6 new species) (Spadi et al., 2017), while only 2 out of 17 species are new in the swampy lacustrine margin of facies C of Fosso Bianco Fm., namely the Dunarobba Fossil Forest.

In the L'Aquila Basin, the ostracods valves were collected from the San Nicandro and Valle Orsa formations. The San Nicandro Fm. was deposited in a carbonate deep lake and displays 7 species pertaining to 4 genera. Five species are new and considered endemic for L'Aquila Basin (Spadi et al., 2016) (Tab. 6.1). In the Gilbert-type delta deposits of the Valle Orsa Fm., the taxa collected in the San Nicandro Fm. ostracods gradually were replaced by 6 different species referred to 4 different genera (Tab. 6.1). In this formation, only *Ilyocypris ilae* is new and considered an endemic species for Palaeolake San Nicandro.

At the confluence between the Rieti Basin and the Middle Tiber Valley only one species, *Qinghaicypris* cf. *Q. riojensis*, was found in the Monteleone Sabino Unit related to the deposition of a braided plain with some small lake, ponds and swampy areas (Pandolfi et al., 2017).

Species	Tiberino Basin	L'Aquila Basin	Rieti Basin and MTV	Anagni Basin
<i>Amnicythere ex gr. stanchevae</i>				
<i>Candona (C.) candida</i>				
<i>Candona (C.) improvisa</i>				
<i>Candona (N.) angulata</i>				
<i>Candona (N.) neglecta</i>				
<i>Candona (N.) paludinica</i>				
<i>Candona (N.) permanenta</i>				
<i>Candonopsis kingsleii</i>				
<i>Caspiocypris amiterni</i>		*		
<i>Caspiocypris basilicii</i>	*			
<i>Caspiocypris bosii</i>		*		
<i>Caspiocypris nicandroi</i>		*		
<i>Caspiocypris perusia</i>	*			
<i>Caspiocypris posteroacuta</i>	*			
<i>Caspiocypris tiberina</i>	*			
<i>Caspiocypris tuderis</i>	*			
<i>Caspiocypris vestinae</i>		*		
<i>Cavernocypris subterranea</i>				
<i>Cyclocypris laevis</i>				
<i>Cyclocypris ovum</i>				
<i>Cypria bikeratia</i>		*		
<i>Cypria ophtalmica</i>				
<i>Cyprideis crotonensis</i>				
<i>Cyprideis rectangularis</i>				
<i>Cypridopsis vidua</i>				
<i>Cypris mandelstami</i>				
<i>Cypris pubera</i>				
<i>Darwinula stevensoni</i>				
<i>Fabaeformiscandona fabaeformis</i>				
<i>Hemicypris sp. nov.</i>	*			
<i>Herpetocypris brevicaudata</i>				
<i>Herpetocypris chevreuxi</i>				
<i>Herpetocypris reptans</i>				
<i>Ilyocypris bradyi</i>				
<i>Ilyocypris decipiens</i>				
<i>Ilyocypris getica</i>				
<i>Ilyocypris gibba</i>				
<i>Ilyocypris ilae</i>		*		
<i>Ilyocypris inermis</i>				
<i>Ilyocypris vertersi</i>				
<i>Mixtacandona laisi</i>				
<i>Mixtacandona tabacauri</i>				
<i>Paralimnocythere dictyonalis</i>				
<i>Paralimnocythere messanai</i>				
<i>Paralimnocythere sp. nov.</i>	*			
<i>Paralimnocythere umbra</i>	*			
<i>Potamocypris fallax</i>				
<i>Potamocypris pallida</i>				
<i>Potamocypris zschokkei</i>				
<i>Pseudocandona albicans</i>				
<i>Pseudocandona marchica</i>				
<i>Pseudocandona rostrata</i>				
<i>Pseudocandona sucki</i>				
<i>Psychodromus olivaceous</i>				
<i>Qinghaicypris riojensis</i>				
<i>Vestalenula cylindrica</i>				
<i>Vestalenula longissima</i>			*	
<i>Vestalenula pliocenica</i>				
<i>Zonocypris membranae quadricella</i>				

←**Tab. 6.1:** List of ostracod species from Piacenzian-Gelasian deposits of Tiberino Basin, L’Aquila Basin, Rieti-MVT and Anagni basins. Their presence is marked by colours: green for shallow water permanent or temporary environment dwellers, orange for deep-water dwellers, purple for species that inhabit both environments, and light blue for interstitial environment forms. The asterisk (\*) marks endemic species.

In the same unit, previous papers reported other ostracods (Barberi et al., 1995; Ligios et al., 2009; Barisone et al., 2014, Gliozzi, unpublished data), in total, 28 species pertaining to 14 genera were recovered from the Gelasian of Monteleone Sabino Unit (Tab. 6.1).

In the Anagni Basin 11 species referred to 9 genera were recovered in temporary water bodies or permanent marshy environments located in an ancient floodplain aged late Gelasian (Bellucci et al., 2012).

In summary, during the Piacenzian-Gelasian interval, the continental aquatic environments of central Italy were characterised by the occurrence of 60 different species referable to 24 genera. If compared with the present day biodiversity in central Italy (64 species and 35 genera - Pieri et al., 2015) the specific biodiversity is only slightly lower (although it includes nine endemic species of *Caspiocypris*) whereas the generic diversity is rather lower. This is due to the rich-in-species genus *Caspiocypris* that gave rise to two species flocks in the deep lacustrine environment of Palaeolake San Nicandro and Palaeolake Tiberino.

## 6.2 Palaeoenvironmental reconstructions

The palaeontological and sedimentological information indicate that during Piacenzian–Gelasian the Tiberino Basin hosted a wide (minimum surface of 500 km<sup>2</sup>) and rather deep (at least 50 m) lake, the Palaeolake Tiberino (Basilici, 1997). Based on the magnetostratigraphy (Abbazzi et al., 1997) and the calculated mean sedimentation rate, the lake persisted undisturbed for at least 1.8 Ma (Medici & Gliozzi, 2008). Those data, merged with the presence in the deep lacustrine environment of a *Caspiocypris* species flock lead to consider the Palaeolake Tiberino as a palaeo-ancient lake (Medici & Gliozzi, 2008; Spadi et al., 2017). The ostracods assemblages from the Palaeolake Tiberino were collected in two formations pertaining to the first depositional cycle of the Tiberino Basin: the Fosso Bianco Fm. and the Ponte Naja Fm. Within the Fosso Bianco Fm. two different facies bore ostracods: the facies association A linked to the deposition in a deep lake and the facies association C mirroring a swampy lacustrine margin (Basilici, 1997). In these two facies the ostracods assemblages were completely different. The deep lacustrine environment identified in the Cava Toppetti I and Fosso Bianco sections bore six species considered endemic for the Tiberino Basin (Medici & Gliozzi, 2008; Spadi et al., 2017). The swampy lacustrine margin testified by the in-situ Taxodiaceae trunks, crops out in the Dunarobba Fossil Forest site and was characterized by

17 different species. Some of the species of the Dunarobba Fossil Forest were found also in the deposits of the Ponte Naja Fm., related to the distal deposition of an alluvial fan, indicating that the north-western and southern margins of the lake were populated by similar associations.

For the L'Aquila Basin, the palaeontological and facies analyses carried out on the San Demetrio-Colle Cantaro Synthem showed that the first filling sediments (San Nicandro Fm.) occurred in a rather deep lacustrine stable environment, the Palaeolake San Nicandro, with a minimum surface of 330 km<sup>2</sup> and a depth not less than 40 m) The San Nicandro Fm. assemblage was composed by seven species, five of which were endemic and four of which were referable to a *Caspiocypris* species flock (Spadi et al., 2016). Conversely, the ostracod assemblages of the Valle Orsa Fm., due to the co-occurrence of *Ilyocypris*, *Candona* and *Cypria*, suggested a shallow water environment with flowing waters possibly linked to a nearby river delta. This palaeoecological interpretation matches well with the lithological and stratigraphic analyses, which indicated that the Valle Orsa Fm. was the result of the deposition of a Gilbert-type delta system.

The other formations of the Castelnuovo sub-synthem give useful evidences of the lake palaeo-margins that were characterized by steep coastlines, as demonstrated by the breccia deposits, cross-cut by transverse water bodies forming alluvial fans (Valle Valiano and Madonna delle Neve formations).

For the strong endemic character of the recovered ostracods and the presences of two species flocks, the Palaeolake Tiberino and Palaeolake San Nicandro can be envisaged as fossil ancient lakes, similar to the present day lakes Ohrid, Biwa, Titicaca and Malawi (Frogley et al. 2002). In the long-lived Palaeolake Tiberino and Palaeolake San Nicandro, the environments were stable over a long time and the ostracod species were adapted to microenvironments, whose factors controlled the evolution of the rather specious *Caspiocypris* species flocks. A mixture of spatial isolation in a deep environment of ostracod populations could potentially have promoted the evolutionary pattern observed. The presence of 100% endemic species in the deep facies of the Palaeolake San Nicandro suggests that the lake was a relatively isolated environment in which speciation was enhanced. The taxonomical differences between the populations of the deep lake and those of the margins are common in huge lakes where the ostracod assemblages change from the shallow littoral habitats to the deeper environments (Mourguiart, 2000).

The Castel San Pietro site resulted a good example to depict the palaeoenvironment of the area located at the confluence between the Rieti Basin and the Middle Valley of Tiber River. New palaeontological findings from the CSP site, coupled with the previously reported and restudied mammalian fauna, point to an age referable to the Gelasian for the upper deposition of the Palaeo-Farfa Synthem (Pandolfi et al., 2017). Sedimentological data and the fossil flora and fauna remains



suggested that the deposition of the Castel San Pietro fossiliferous layers occurred on a coastal plain, which was crossed by a low-energy channel system disjointed by lacustrine and swampy areas in a general coarse-deposition fluvial system. Palaeoclimate and palaeoenvironmental conditions inferred from the Castel San Pietro site during the Early Pleistocene confirm that the climate at the onset of Northern Hemisphere Glaciation in the central Mediterranean was more humid and temperate than in other parts of Europe (Martinetto, 2001; Martinetto et al., 2014, Pandolfi et al., 2017).

### 6.3 Palaeobiogeography of non-marine ostracod

Non-marine ostracods are excellent proxies for the palaeobiogeographic reconstructions due to their capability to survive the passive transport operated by several terrestrial agents (amphibians, birds and mammals and wind) (e.g. Löffler, 1964; Proctor & Malone, 1965; Vanschoenwinkel et al., 2008a, b) that can connect also very distant freshwater environments. This capability is caused mainly by two biological characteristics of many Cypridoidea: (a) several taxa are parthenogenic and thus do not require the presence of both sexes to establish new populations; and (b) many taxa produce resting eggs that are able to survive in dry conditions for many years (Rossi et al., 1996), allowing them to be transported for long distances without direct aquatic pathways. Passive dispersal via aquatic birds (feathers, limbs, beaks and even digestive systems) is corroborated by the disjointed diffusion of ostracod species along the migratory pathways of birds (De Deckker, 1977; Horne & Smith, 2004).

The ostracod assemblages studied in this thesis arise two different palaeogeographic questions. The first question is related to the deep lacustrine Piacenzian-Gelasian assemblages made by forms that show more affinity with genera and/or species of the Miocene-Early Pliocene Paratethyan realm (*Caspiocypris* spp., *Cypria bikeratia*, and *Amnicythere* ex gr. *stanchevae*) than with the non-marine ostracod faunas of central and western Europe. This contrasts with the pattern seen in the other central Italian Pliocene and Early Pleistocene assemblages related to shallow water environments (Ambrosetti et al., 1995a; Barberi et al., 1995; Girotti et al., 2003; Faranda & Gliozzi, 2008; Fubelli et al., 2008; Ligios et al., 2009; Medici et al., 2011; Bellucci et al., 2012, 2014; Barisone et al., 2014; Cosentino et al., 2017; Pandolfi et al., 2017) where the taxa show a clear Palaeartic or Holarctic distribution and were widely distributed in central and western Europe at least until the early Pleistocene (Meisch, 2000).

*Caspiocypris*, the dominant genus of the San Nicandro and Tiberino palaeolakes, is well represented mainly in the eastern European Paratethyan domain (see Chapter 5). A few Paratethyan *Caspiocypris* species occurred also in the Palaeomediterranean area. *Caspiocypris labiata* (Zalányi) was recovered from the late Tortonian-early Messinian deposits of the Tuscan basins of Siena,

Valdelsa, Radicondoli, and Casino (Devoto, 1968; Bossio et al., 2004; Abbazzi et al., 2008; Ligios et al., 2012). *Caspiocypris pontica* Sokač was collected in the Lago-Mare biofacies (late Messinian) at Perticara (Marche, central Italy; Gliozzi & Grossi, 2004), Cava Serredi (Tuscany, central Italy; Da Prato, 2009) and in the Nijar Basin (Spain; Bassetti et al., 2006). *Caspiocypris alta* (Zalányi) was recorded from the Lago-Mare biofacies (late Messinian) at Fonte dei Pulcini (Abruzzo, central Italy; Gliozzi & Grossi, 2008; Cosentino et al., 2012) and Cuevas del Almanzora (Vera Basin; Stoica et al., 2016). The first recovery of a *Caspiocypris* not related to the Paratethys (*Caspiocypris sambucensis*) is reported by Medici et al. (2011) from the early Pliocene of the Valdelsa Basin (Tuscany).

The genus *Amnicythere* originated in the Sarmatian (middle Miocene) of the Dacic Basin (Stancheva, 1968; Gliozzi et al., 2005) and progressively migrated eastwards during the Meotian-Pleistocene. Currently, a few extant species live today in the Euxinic and Caspian basins (Gofman, 1966; Schornikov, 1969; Boomer et al., 2005). Anyway, scattered recoveries of *Amnicythere* spp. are reported from different Late Miocene and Middle Pleistocene localities in central Italy such as some Tuscan basins (Ligios et al., 2012), the Liri Basin (Devoto, 1965) and the Lake Trasimeno (Marchegiano et al., in press), but they were not related to Paratethyan species.

*Cypria bikeratia* is rather similar to two species that were reported in the Paratethyan realm during the late Miocene (Hanganu, 1962; Sokač, 1972; Krstić, 1975).

Gliozzi et al. (2007) discussed the different palaeobiogeographical implications of the Paratethyan affinity at the generic or specific level described above and concluded that the late Tortonian-early Messinian affinity at the generic level was caused by the passive dispersion most likely linked to aquatic birds, whereas the Messinian Lago-Mare specific identity occurred through an active dispersal event via subaqueous pathways of the species that inhabited the Paratethys at that moment. Those hypotheses are consistent with the palaeogeographical knowledge of the Palaeomediterranean and Paratethys connections during the Neogene (Rögl, 1998; Jolivet et al., 2006; Popov et al., 2006).

What was the dispersal mechanism of *Caspiocypris*, *Cypria* and *Amnicythere* recovered in the late Piacenzian-Gelasian of the Tiberino and L'Aquila basins? Krstić et al. (2004) and Krstić (2006) proposed that during the Akchtagylian (Pliocene-early Pleistocene) there was a wide freshwater basin that occupied the entire Paratethyan domain and connected the Balkan area with Greece to the south and Italy to the north, and the Vienna Basin with France and Spain via a transalpine corridor. The present knowledge of the palaeogeography of the entire area excludes any continuous or semi-continuous aquatic connection between eastern and western Europe (Jolivet et al., 2006; Popov et al., 2006). Thus, to explain the presence of Paratethyan genera in the Central Italy basins, we can formulate two hypotheses: **1)** The Plio-Pleistocene central Italy basins were colonized by Paratethyan

species ancestors of *Caspiocypris*, *Cypria* and *Amnicythere*, which arrived in central Italy from the Eastern Europe by passive dispersal and underwent endemic speciation; 2) considering that during the Messinian Lago-Mare event all the brackish Italian basins were invaded by Paratethyan ostracods, it is not impossible to suppose that the species recovered in the central Italy basins during Pliocene-Early Pleistocene may have originated by the endemic speciation from Lago-Mare Messinian ancestors.

In favour of the first hypothesis (passive dispersal from Eastern Europe) there is the fact that the geometric morphometrics showed that *Caspiocypris labiata*, *Caspiocypris pontica* and *Caspiocypris alta*, the only *Caspiocypris* species found in the Italian Late Miocene, display rather different outlines from the Plio-Pleistocene Italian *Caspiocypris* discussed in this thesis. Anyway, this fact could be due to changes in the shell proportions due to the adaptation to different habitats (Pipik et al., 2012). In this case, we must accept the idea of a disjunct distribution, since during Pliocene-Early Pleistocene *Caspiocypris* occurred only in the eastern part of the Black Sea and in the Caspian Sea and was never recovered in the “Paludonian Beds” in the Balkans.

In favour of the second hypothesis (speciation in Italy from Lago-Mare Paratethyan species), it is worth to note that the maximum diffusion in the central Paratethys of both *Caspiocypris* and *Amnicythere* occurred during the late Miocene, whereas during Pliocene these genera were mainly widespread in the far eastern Paratethys. Furthermore, *Cypria tocorjescui* and *C. dorsoconcava* went extinct at the end of the Pontian and could not have migrated passively during the Pliocene. Anyway, *Cypria tocorjescui* Hanganu, a Paratethyan species very similar to *Cypria bikeratia*, was found in the Lago-Mare Messinian deposits of the Malaga Basin, Spain (Guerra-Merchán et al., 2010) and *Amnicythere* ex gr. *stanchevae* has been recognized at Sapigno, northern Italy (Bassetti et al., 2003).

The second question is related to the small group of shallow freshwater species that were recovered both in the Gelasian of central Italy and in the Paludonian Beds in Serbia (*Candona paludinica* and, possibly, *Cypris mandelstami* in the Tiberino Basin, *Qinghaicypris riojensis* and *Vestalenula pliocenica* in the Rieti and MVT basins, and *Candona permanenta* in the L’Aquila Basin). The so called “Paludonian Beds” correspond to freshwater lacustrine deposits of the Palaeolake Slavonia alternate with alluvial deposits (Mandic et al., 2015). In the literature the series is usually referred to as the “*Paludina* beds” because of the presence of the mollusc genus *Paludina* Férussac, 1812 (= *Viviparus* Montfort, 1810). Recently, the “Paludonian Beds” were revised, and a new regional stage named Cernikian was introduced to define the depositional cycle that included the *Viviparus* beds (Mandic et al., 2015).

The presence of the “Paludonian” species in central Italy can be explained as the consequence of the passive dispersal through aquatic birds along a westward path from the Balkan area.

## 6.4 Biostratigraphy

Neogene and Quaternary non-marine ostracods were rarely used as biostratigraphical tools. Few examples are related mainly to local chronostratigraphic reconstructions of some areas of the Eastern Europe (Krstić, 1972; 1985; 2006; Sokač, 1972; Jiříček, 1985). No independent constraints were used to define those ostracod biozonations. In Italy, the continental biochronology is based mainly on large and small mammals (Gliozzi et al., 1997; Masini & Sala, 2007; Palombo, 2009), while non-marine ostracods were not considered by Gliozzi et al. (1997) a good biostratigraphical proxy. This was due to the fact that Italian non-marine ostracods were not sufficiently studied, but, more in general, being ostracods particularly sensitive to the environmental characteristics, their presence/absence in one particular time interval could not have necessarily a chronological meaning but could be due to the lack of studies of different environments. Thus, the presence/absence of ostracods from a certain deposit does not represent only a biostratigraphical data but must be filtered through an environmental interpretation. Despite the scarcity of sites where the ostracods have been analysed so far in Italy, Fig. 6.1 shows a tentative chronological ordering of the Italian Pliocene-Early Pleistocene non-marine ostracods faunas known up to now (Medici et al., 2011; Cosentino et al., 2014; 2017; Bellucci et al., 2014; Barberi et al., 1995; Fubelli et al., 2008; Barisone et al., 2014; Ligios et al., 2009; this thesis).

Apart from a limited ostracod contingent made of long-living species which appeared during Miocene and are still living, which is present in the whole Pliocene-Early Pleistocene interval, other non-marine ostracods seem to have a more restricted chronostratigraphic distribution and they possibly could be used as proxies for biostratigraphy. For example, during Zanclean *Candonopsis arida* disappears and early Zanclean is characterized by species limited to this interval (*Candona dorsoreticulata*, *C. subtilis*, *Caspiocypris sambucensis*, and *Paralimnocythere toscana*). It is worth to note that the Zanclean fossil ostracods in central Italy are known only from one site in the Valdelsa Basin (Medici et al., 2011). The late Piacenzian-Gelasian contingent is mainly by two groups of species: the first is characterized by a stratigraphical distribution limited to this time-interval. Some of them pertain to the late Piacenzian-Gelasian deep facies of the paleolakes San Nicandro and Tiberino, others, typical of shallow waterbodies, were widespread both in central Italy and in the Balkan peninsula; the second group is made of long-living species that appear in the Gelasian and survive through all the Pleistocene, up to now. Finally, the Calabrian non-marine ostracods include a small group of fossil (*Eucypris dulcifrons*) or still living species that appear in this time-interval. Within this group also two species typical of low temperatures (*Eucypris dulcifrons* and *Metacypris cordata*) are included. The first one is a fossil species recorded up to now only in the “glacial” periods

of Germany (Fuhrmann, 2012) whereas *Metacypris cordata* is a typical central European species and in Italy is recorded only in the pre-alpine Lake of Mantova. The occurrence of these species as fossil in the Calabrian of central Italy possibly mirrors the alternate of cold and warm periods typical of the Pleistocene.

In conclusion, this thesis enlarged the database on the stratigraphic distribution of non-marine ostracods during Pliocene-Early Pleistocene but data are still not enough to define biochrons based on ostracods.



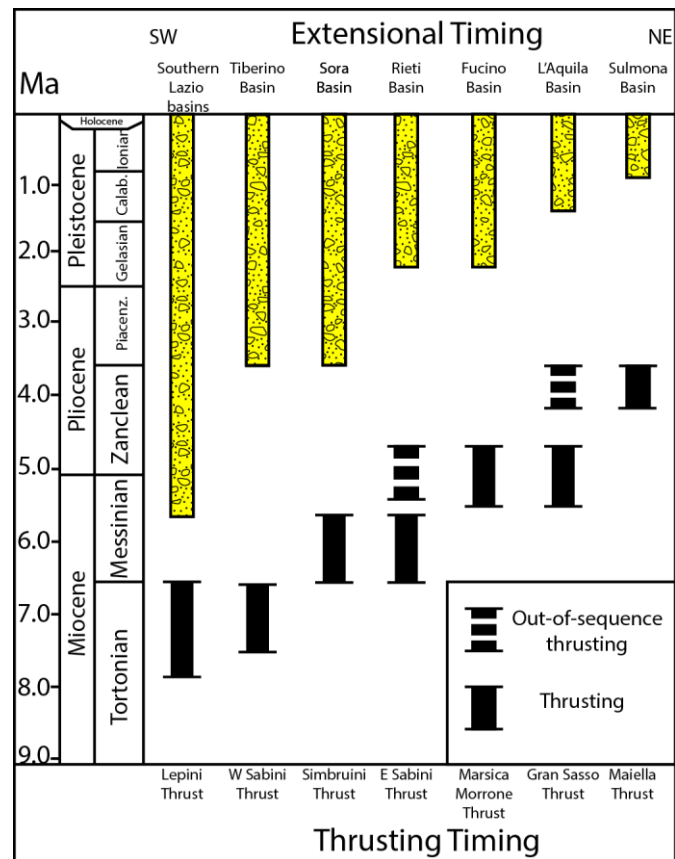
**Figure 6.1:** Range chart of non-marine ostracods of central Italian Peninsula from Pliocene to Early Pleistocene (Calabrian). Legend: green= distribution in shallow water environments; orange= distribution in deep lacustrine environments; purple= distribution in both shallow and deep-water environments; light blue= distribution in stygobiotic environment; black name= Western and Central European species.; blue name=endemic Italian species; red name= “Paludian Beds” species; \*=cold stenothermal species.

## 6.5 New Insights into the Evolution of the Apennine Post-orogenic Extensional Domain

The absence of outcrops of the oldest sedimentary fill in most extensional intermontane basins in central Italy, together with the scarcity of biochronologically and/or geochronologically well-constrained stratigraphic successions, hindered any attempts to define the time of their initial development. The recent literature claims that the onset of these basins becomes younger from the Tyrrhenian towards the Adriatic side of the central Apennines (Fig. 6.2) (Cavinato & DeCelles, 1999; Galadini & Messina, 2004). This thesis provides new constrains to date the early infilling of at least three central Apennines intermontane basins, from the westernmost Rieti Basin to the easternmost L'Aquila Basin, that question this hypothesis.

According to our palaeontological analyses, the early infill of the Tiberino (Fosso Bianco and Ponte Naja Units) and L'Aquila (Castelnuovo sub-synthem) basins must be dated to Piacenzian p.p.-Gelasian, due to the presence of *Caspiocypris* in both basins. Similarly, the oldest deposits of the Rieti Basin (Ornaro Basso and Monteleone Sabino Unit) resulted to be at least Gelasian in age, owing to the occurrence of large mammals of the Montopoli/Coste S. Giacomo Mammal Unit.

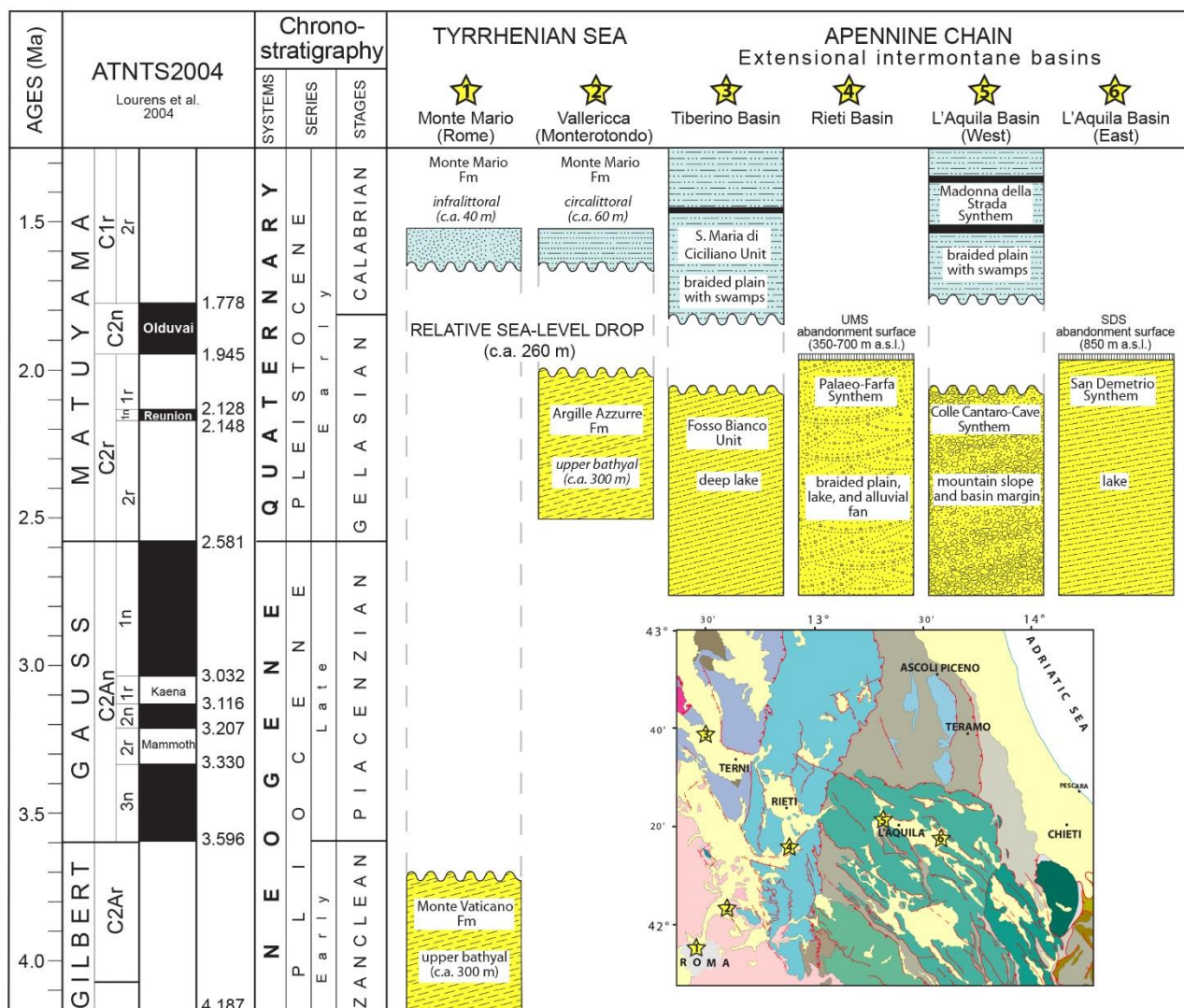
Subsequently, at L'Aquila Basin, the Madonna della Strada synthem (Calabrian) is cut into the abandonment surface of the San Demetrio-Colle Cantaro synthem, which regionally corresponds to the Gelasian abandonment surface of the Rieti basin fill (Barisone et al., 2014; Cosentino et al., 2014; Fubelli et al., 2014). Similarly, in the Tiberino Basin, above the Upper Piacenzian– Gelasian lake sediments, a prominent angular unconformity separates the Fosso Bianco Fm. from the overlying latest Gelasian–Calabrian deposits of braided stream and marshy alluvial plain origin (Santa Maria di Ciciliano Formation; Basilici, 1995, 1997). This younger unit bears large mammal faunas referable to the Olivola, Tasso, and Farneta Faunal Units (Uppermost Gelasian–Calabrian pro parte; Sardella et al., 2003). Thus, the Santa Maria di Ciciliano deposits (Tiberino Basin) are related with the Calabrian deposits of the Madonna



**Figure 6.2:** Time-space migration of thrusting and subsequent development of extensional basins across central Apennines modified by Cavinato & DeCelles (1999).

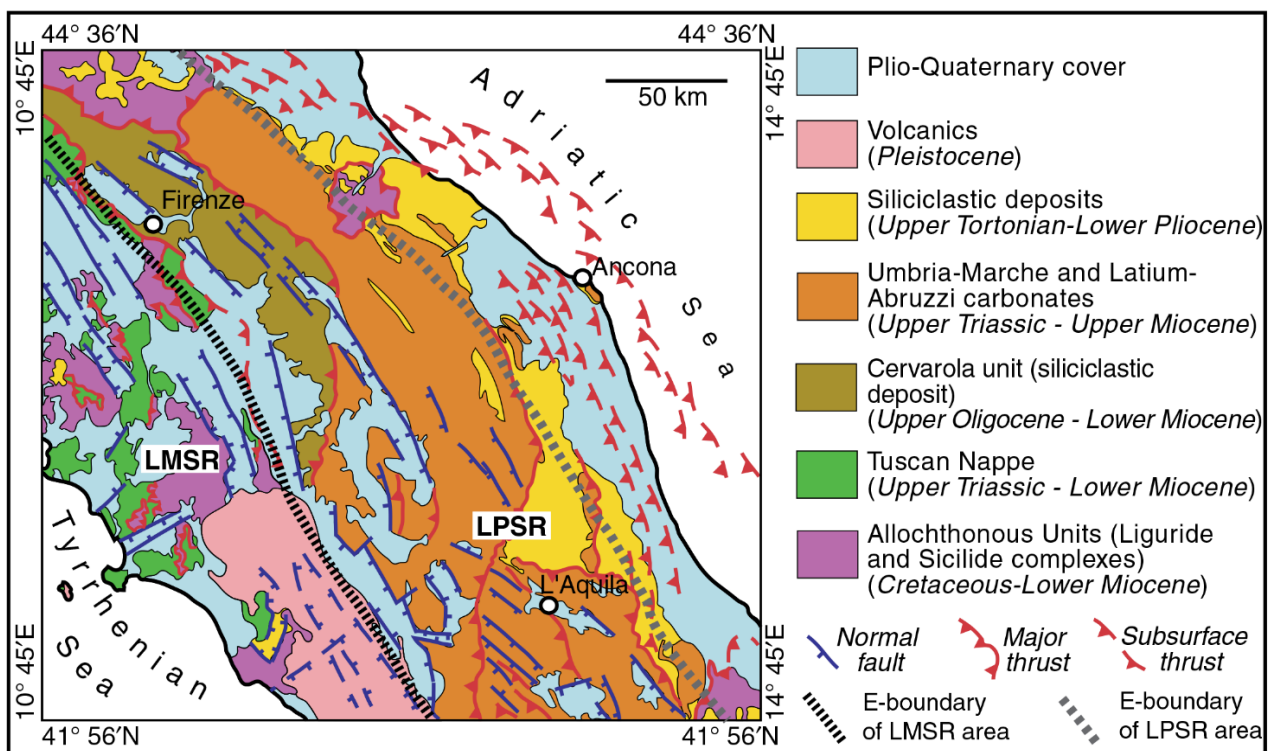


della Strada synthem (L'Aquila Basin). The Gelasian abandonment surfaces of both the L'Aquila and Rieti intermontane basins, as well as the angular unconformity between the Fosso Bianco and the Santa Maria di Ciciliano formations (Fig. 6.3), were probably triggered by a 260 m relative sea-level drop (tectonic uplift + glacio-eustatic) that occurred close to the Gelasian-Calabrian transition at the Tyrrhenian margin of the central Apennines, as indicated in the Pliocene–Quaternary succession of the Rome area (Cosentino and Fubelli, 2008; Cosentino et al., 2009).



**Figure 6.3:** Correlation panel among different Pliocene–early Pleistocene stratigraphic sections from the Roman area and the main intermontane basins discussed in the text. The relative sea-level drop of ~260 m at the Gelasian-Calabrian transition, mainly related to uplift, correlates the major stratigraphic discontinuities detected both in the Roman area and in the intermontane basins of the central Apennines. UMS—Monteleone Sabino unit; SDS—San Demetrio synthem; m a.s.l.—meters above sea level. See Figure 1 for the legend of the location map. ATNTS2004—Astronomical Tuned Neogene Time Scale 2004.

The late Piacenzian (ca. 3 Ma) onset of the Tiberino and L’Aquila extensional basins calls into question previous suggestions that the onset of these basins becomes younger from the Tyrrhenian toward the Adriatic side of the central Apennines (Cavinato & DeCelles, 1999; Galadini & Messina, 2004). Indeed, according to the syn-rift ages of the intermontane basins across the northern and central Apennines, only two major extensional domains can be recognized: (1) a late Miocene rifting event, which includes all the late Miocene extensional basins in Tuscany; and (2) a late Pliocene to earliest Pleistocene rifting event, which, in the central Apennines, possibly includes all the intermontane basins from the Tiberino Basin to the Sulmona Basin (Fig. 6.4).



**Figure 6.4:** Geological map of central-northern Italy with extension of the postorogenic synrift domains. LMSR—late Miocene synrift area; LPSR—late Pliocene to earliest Pleistocene synrift area (data from Cosentino et al., 2017).

The different time gaps between compressional and extensional deformation at any given locality in the central Apennines could indicate a partial decoupling of processes responsible for the migration of shortening and extension toward the foreland (Cosentino et al., 2017). Observation of diachrony between the eastward migration of the shortening in the foreland and extension in the inner part of the orogen supports the notion that the central Apennines were created as a result of a partially decoupled collision zone. A similar geodynamic setting has recently been suggested for the northern Apennines of Italy to explain the thin crustal wedge and the bimodal distribution of stresses within the orogen, with compressional stress in the foreland and extensional stress in the inner part of the

northern Apennines. As indicated by the high seismicity that characterizes the youngest fault planes in the central Apennine intermontane basins (Falcucci et al., 2011; Tallini et al., 2012;), the extensional deformation responsible for the creation of these basins is still active over the whole domain that was affected by the late Pliocene–early Pleistocene synrift extension (from the Tiberino Basin in the west to the Sulmona Basin in the east). In this scenario, the intermontane basins of the central Apennines record ~3 m.y. of continued crustal extension in response to a first phase of mantle upwelling above the Adria subducting slab (from 3 to 2 Ma) and a second phase of dynamic mantle upwelling possibly starting from ca. 2 Ma, probably due to slab detachment under the central Apennines (Faccenna et al., 2014). The second phase of mantle upwelling could be responsible for the strong tectonic uplift (~260 m) that occurred in central Italy close to the Gelasian-Calabrian transition (Cosentino et al., 2009), which possibly induced the early Pleistocene reorganization of the central Apennine drainage systems (Fubelli et al., 2014).

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# **APPENDIX**

List of the material for the Paratethyan Candoninae studied in the present thesis. The ages are from Stevanovic, 1990; Sacchi & Horvath, 2002; Neubauer et al., 2015 for Pannonian Basin and van Baak et al., 2013; 2016 for the Caspian Basin. In bold are reported the updated ages.

Genus	Original name	Author	Site	Parat. Basin	Age	Examined material	Stor. Instit.	Catalogue Number	Type material	Notes
<i>Bakunella</i>	<i>Pontocypris balcanica</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	Pl. 6305	lectotype	juvenile of <i>P. dorsoarcuata</i>
						4 female RV	MFGI	Pl. 6314	paralectotypes	juvenile of <i>P. dorsoarcuata</i>
<i>Bakunella</i>	<i>Bakunella dorsoarcuata</i>	(Zalányi, 1929)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	2 female LV, 1 female RV	NHMZ	D-36		
<i>Bakunella</i>	<i>Bakunella dorsoarcuata</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	22 female LV, 25 female RV, 6 male LV, 8 male RV	MFGI		neotypes	
<i>Bakunella</i>	<i>Bakunella dorsoarcuata</i>	(Zalányi, 1929)	Black Sea	Euxinic	<b>Pleistocene</b>	2 female LV, 2 female RV, 1 male LV, 1 male RV	BIRM.	MD04-2761 B.C.		
<i>Bakunella</i>	<i>Bakunella dorsoarcuata</i>	(Zalányi, 1929)	Caspian Sea	Caspian	<b>Holocene</b>	1 female LV, 1 female RV	BIRM.	GS20 434-435		
						1 female RV, 1 male LV		GS20 799-800		
<i>Bakunella</i>	<i>Bakunella sp. nov.</i>		Mt. Medvenica	Pannonian	<b>Transdanubian</b>	1 female LV	NHMZ	D-237	holotype	
<i>Camptocypris</i>	<i>Bairdia acronasuta</i>	(Livental, 1929)	Babazanan	Caspian	<b>Apsheonian</b>	17 female LV, 31 female RV, 9 male LV, 4 male RV	BUCH.	BA 4	neotypes	
<i>Camptocypris</i>	<i>Candona (Casiolla) acuta</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Transdanubian</b>	1 female LV	NHMZ	D-72	holotype	
						1 female LV, 2 female RV	NHMZ	D-72	paratype	
<i>Camptocypris</i>	<i>Candona (Casiolla) alasi</i>	(Krstić, 1972)	Obrenovac	Pannonian	<b>Portaferrian</b>	8 female LV, 7 female RV, 2 male LV, 2 male RV	GOC	OBR 14	neotypes	
<i>Camptocypris</i>	<i>Paracypris balcanica</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	Pl. 6317	lectotype	
			Pejinović	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	Pl. 6301a	broken	
			Pejinović	Pannonian	<b>Portaferrian</b>	1 male LV	MFGI	Pl. 6301b	broken	
<i>Camptocypris</i>	<i>Camptocypris balcanica</i>	(Zalányi, 1929)	Bonyhad	Pannonian	<b>Portaferrian</b>	1 female LV, 3 female RV	MFGI	112.5-114 m		
			Balatonszabadi	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	14-14.7 m		
			Tihany	Pannonian	<b>Portaferrian</b>	5 female LV, 5 female RV, 2 male LV	MFGI	Tihany 4, 7, 9, 24, 31		
<i>Camptocypris</i>		(Zalányi, 1929)		Pannonian	<b>Portaferrian</b>	2 female LV, 1 female RV	NHMZ	D-240		

Genus	Original name	Author	Site	Parat. Basin	Age	Examined material	Stor. Instít.	Catalogue Number	Type material	Notes
	<i>Candona (Caspiolla) balcanica</i>		Mt. Medvenica		Portaferrian	9 female LV, 4 female RV	NHMZ	KZL65		
<i>Camptocypria</i>	<i>Camptocypria balcanica</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	6 female LV, 7 female RV, 2 male LV, 2 male RV	GOC	OBR 14		
<i>Camptocypria</i>	<i>Candona (Caspiolla) brusinae</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female LV	NHMZ	D-36	holotype	
						1 female LV, 1 female RV	NHMZ	D-36	paratype	
					Portaferrian	1 female LV, 1 female RV, 1 male LV	NHMZ	Zaggora-975 S-12		
<i>Camptocypria</i>	<i>Candona (Caspiolla) flectimarginata</i>	(Sokač, 1967)	Mt. Medvenica	Pannonian		1 female RV	NHMZ	KZL65-1062	holotype	
					Portaferrian	2 female LV, 4 female RV, 1 male LV, 1 male RV	NHMZ	KZL65-1062	paratype	
					Portaferrian	3 female LV, 1 female RV	NHMZ	KZL65-124a		
					Portaferrian	1 female LV, 2 female RV	NHMZ	KZL65-1090		
					<b>Portaferrian</b>	1 male RV	NHMZ	D-36		
					<b>Portaferrian</b>	3 female RV, 1 male LV	NHMZ	D-240		
					<b>Portaferrian</b>	3 female LV, 1 female RV	NHMZ	D-250		
<i>Camptocypria</i>	<i>Paracypria lobata</i>	(Zalányi, 1929)	Pejinović	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	Pl. 6320	lectotype	
						1 female RV	MFGI	Pl. 6301a	paralectotype	broken
						1 female RV	MFGI	Pl. 6301b	paralectotype	broken
						1 female RV	MFGI	Pl. 6321	paralectotype	
<i>Camptocypria</i>	<i>Candona (Caspiolla) lobata</i>	(Zalányi, 1929)	Mt. Medvenica	Pannonian	<b>Transdanubian</b>	1 female LV, 1 male LV	NHMZ	D-230		
					<b>Transdanubian</b>	1 female RV, 1 male LV	NHMZ	D-237		
					<b>Portaferrian</b>	1 female LV	NHMZ	D-240		
					<b>Portaferrian</b>	1 female RV	NHMZ	D-42		
<i>Camptocypria</i>	<i>Candona (Caspiolla) praebalcanica</i>	(Krstić, 1972)	Vrčin	Pannonian	<b>Serbian</b>	9 female LV, 12 female RV	NHMB	0-226, 0-227	holo-paratypes	<i>C. (C.) p. praebalcanica</i> Krstić, 1972
			Boždarevac	Pannonian	<b>Serbian</b>	2 female LV, 2 female RV	NHMB	0-228, 0-229	holo-paratypes	<i>C. (C.) p. posterior</i> Krstić, 1972
<i>Camptocypria</i>	<i>Candona (Caspiolla) punctulata</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female RV	NHMZ	D-262	holotype	
						3 female LV, 2 female RV	NHMZ	D-262	paratype	

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					Portaferrian	10 female LV, 4 female RV	NHMZ	KZL65		
<i>Camptocypria</i>	<i>Camptocypria hungarica</i>	Zalányi, 1959	Tihany	Pannonian	<b>Portaferrian</b>	1 male RV	MFGI	Pl. 165 AFI	holotype	broken
<i>Camptocypria</i>	<i>Candona extensa</i>	(Zalányi, 1959)	Tihany	Pannonian	<b>Portaferrian</b>	7 female LV, 13 female RV	MFGI	Pl. 160 AFI	holo-paratypes	juveniles
						2 female LV	MFGI	Tihany 37		juvenile
						1 female LV	MFGI	Tihany 4		
<i>Camptocypria</i>	<i>Candona (Sirmiella) arcuata</i>	(Stancheva, 1964)	Negotini	Dacian	Pontian	8 female LV, 8 female RV	NHMB	E-VI-4 3.15-3.25		
<i>Camptocypria</i>	<i>Candona (Caspiolla) ossoinae</i>	(Krstić, 1968)	Negotini	Dacian	Pontian	2 female LV	NHMB	E-VI-1 21.95-23		
<i>Camptocypria</i>	<i>Caspiolla gracilis</i>	(Livental, 1938)	Lake Inder	Caspian	Pliocene, post-Pliocene	2 female LV	VNIGRI	71/1		
			Dagestan	Caspian	Miocene-Quaternary	1 female LV, 1 female RV	VNIGRI	299/5		juveniles
			Cheleken peninsula	Caspian	Pliocene	1 female RV	VNIGRI	105/119		juvenile
			East Turkmenistan	Caspian	Quaternary	1 female LV, 1 female RV, 1 male RV	VNIGRI	948/11		
<i>Camptocypria</i>	<i>Camptocypria gracilis</i>	(Livental, 1938)	Black Sea	Euxinic	<b>Pleistocene</b>	7 female LV, 5 female RV	BIRMINGHAM	MD04-2761 B.C.		
<i>Camptocypria</i>	<i>Caspiolla karatengisa</i>	(Mandelstam, 1963)	Lokbatan	Caspian	<b>Ackagylian</b>	10 female LV, 7 female RV, 4 male LV	BUCHARREST	UP 17		
<i>Caspiocypris</i>	<i>Bairdia candida</i>	(Livental, 1929)	Babazanan	Caspian	<b>Apsaronian</b>	2 female RV, 1 male LV	BUCHARREST	BA 112	neotypes	
<i>Caspiocypris</i>	<i>Bairdia candida</i>	(Livental, 1929)	Lokbatan	Caspian	<b>Ackagylian</b>	7 female LV, 7 female RV, 4 male LV, 3 male RV	BUCHARREST	UP 17		
<i>Caspiocypris</i>	<i>Bairdia candida</i>	(Livental, 1929)	Lake Inder	Caspian	Pliocene, post-Pliocene	1 female LV, 1 female RV	VNIGRI	71-6a		
<i>Caspiocypris</i>	<i>Candona (Thaminocypris) adversa</i>	(Krstić, 1972)	Velika Moštanica	Pannonian	<b>Serbian</b>	1 female LV, 1 female RV	NHMB	0-287, 0288	holo-paratype	
<i>Caspiocypris</i>	<i>Paracypris alta</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	Pl. 6313	lectotype	
						2 female RV	MFGI	Pl. 6304a	paralectotypes	
						4 female RV, 2 female LV	MFGI	Pl. 6304b	paralectotypes	juveniles
<i>Caspiocypris</i>	<i>Caspiocypris alta</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	9 female LV, 9 female RV, 3 male LV, 2 male RV	GOC	OBR 14	topotypes	

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<i>Caspiocypris</i>	<i>Candona (Caspiocypris) alta</i>	(Zalányi, 1929)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female RV	NHMZ	D-250		
					<b>Portaferrian</b>	2 female LV, 1 female RV	NHMZ	D-42		
					<b>Portaferrian</b>	4 female LV	NHMZ	D-254		
					<b>Portaferrian</b>	1 female LV, 1 female RV	NHMZ	D-450		
					Portaferrian	1 female LV, 5 female RV	NHMZ	KZL65		
<i>Caspiocypris</i>	<i>Candona (Lineocypris) granulosa</i>	(Zalányi, 1929) sensu Sokac, 1972	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female RV	NHMZ	D-450		
					Portaferrian	1 female RV	NHMZ	KZL65		
					<b>Portaferrian</b>	1 female LV, 2 female RV	NHMZ	D-42		
					<b>Transdanubian</b>	1 female LV, 2 female RV	NHMZ	D-95		
					<b>Transdanubian</b>	3 female RV	NHMZ	D-237		
<i>Caspiocypris</i>	<i>Candona (Sinegubiella) illyrica</i>	Krstić, 1972	Vrčin	Pannonian	<b>Serbian</b>	1 female LV, 2 female RV	NHMB	0-307, 0-308	holo-paratypes	
<i>Caspiocypris</i>	<i>Candona (Thaminocypris) improbus</i>	Krstić, 1972	Velika Moštanica	Pannonian	<b>Slavonian</b>	1 female LV, 1 female RV	NHMB	0-285, 0-286	holo-paratype	
<i>Caspiocypris</i>	<i>Paracypris labiata</i>	(Zalányi, 1929)	Pejinović	Pannonian	<b>Portaferrian</b>	1 female RV	MFGI	Pl. 6302a	lectotype	
						1 male LV	MFGI	Pl. 6302b	paralectotype	
						2 female RV	MFGI	Pl. 6312	paralectotypes	
						1 female RV	MFGI	Pl. 6315	paralectotype	juvenile
<i>Caspiocypris</i>	<i>Candona (Caspiocypris) labiata</i>	Zalányi, 1929	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female LV	NHMZ	D-450		
					<b>Portaferrian</b>	1 female LV, 2 female RV	NHMZ	D-42		
					<b>Transdanubian</b>	2 female LV, 1 female RV	NHMZ	D-237		
					<b>Portaferrian</b>	1 female LV	NHMZ	D-240		
					<b>Portaferrian</b>	2 female LV	NHMZ	D-254		
					Portaferrian	2 female LV, 2 female RV	NHMZ	KZL3		
					Portaferrian	1 female LV, 1 female RV	NHMZ	ZR999T7		
<i>Caspiocypris</i>	<i>Candona (Thaminocypris) minutissima</i>	(Krstić, 1972)	Grocka	Pannonian	<b>Portaferrian</b>	3 female LV, 3 female RV	NHMB	0-295, 0-296	holo-paratypes	
<i>Caspiocypris</i>	<i>Candona (Thaminocypris) stevanovici</i>	(Krstić, 1972)	Obrenovac	Pannonian	<b>Portaferrian</b>	1 female LV, 1 female RV	NHMB	0-293, 0-294	holo-paratype	

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<i>Caspiocypris</i>	<i>Caspiocypris lyrata</i>	Mandelstam & Schneider, 1963	Cheleken peninsula	Caspian	<b>Pliocene</b>	4 female LV, 2 female RV	VNIGRI	105-15	holo-paratypes	juveniles
<i>Caspiocypris</i>	<i>Caspiocypris lyrata</i>	Mandelstam & Schneider, 1963	Lake Inder	Caspian	Pliocene, post-Pliocene	1 female LV, 1 female RV	VNIGRI	71-81		
<i>Caspiocypris</i>	<i>Amplocypris minuta</i>	(Zalányi, 1944)	Tisztaberek	Pannonian	<b>Slavonian</b>	1 female C	MFGI	Sz. 30 AFI	holotype	
<i>Caspiocypris</i>	<i>Candona (Lineocypris) nonreticulata</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Serbian</b>	1 female LV	NHMZ	D-1	holotype	
						2 female RV	NHMZ	D-1	paratype	
						1 female LV, 1 female RV	NHMZ	D-226		
<i>Caspiocypris</i>	<i>Candona (Reticulocandona) orientalis</i>	(Krstić, 1968)	Dušanovac	Dacian	Pontian	1 male LV	NHMB	E-VI-1 21.95-22		
<i>Caspiocypris</i>	<i>Candona (Caspiocypris) pontica</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female LV	NHMZ	D-255	holotype	
						5 female LV, 8 female RV; 1 male LV, 1 male RV	NHMZ	D-255	paratype	
						5 female LV, 4 female RV	NHMZ	D-240		
						2 female LV, 2 female RV	NHMZ	D-250		
						2 female LV	NHMZ	D-254		
<i>Caspiocypris</i>	<i>Candona (Reticulocandona) posteroerigera</i>	(Krstić, 1972)	Boždarevac	Pannonian	<b>Portaferrian</b>	2 female LV, 1 female RV	NHMB	0-283, 0-284	holo-paratypes	
<i>Caspiocypris</i>	<i>Candona (Caspiocypris) rectoides</i>	(Krstić, 1968)	Kladovo	Dacian	Pontian	1 female RV	NHMB	E-VI-4 6.6-36.8		
<i>Caspiocypris</i>	<i>Paracypris labiata</i>	(Zalányi, 1929)	Obrenovac	Pannonian	<b>Portaferrian</b>	1 male RV	MFGI	Pl. 6306	lectotype	
<i>Caspiocypris</i>	<i>Candona (Sinegubiella) sublabiata</i>	(Krstić, 1972)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	2 female LV, 2 female RV	NHMZ	D-254		
<i>Caspiocypris</i>	<i>Caspiocypris sublabiata</i>	(Krstić, 1972)	Obrenovac	Pannonian	<b>Portaferrian</b>	14 female LV, 12 female RV, 2 male LV, 3 male RV	GOC	OBR 14	topotypes	
<i>Caspiocypris</i>	<i>Candona (Thaminocypris) symmetrica</i>	(Krstić, 1972)	Vrčin	Pannonian	<b>Serbian</b>	1 female LV, 1 female RV	NHMB	0-289, 0-290	holo-paratype	
<i>Caspiocypris</i>	<i>Caspiocypris totema</i>	Evlachova, 1963	Cheleken peninsula	Caspian Basin	<b>Pliocene</b>	1 female LV	VNIGRI	105-14		
<i>Caspiocypris</i>	<i>Candona (Lineocypris) zagabiensis</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female LV	NHMZ	D-177	holotype	
						1 female LV, 1 female RV	NHMZ	D-177	paratype	

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<i>Caspiocypris</i>	<i>Aglaiia rakosiensis</i>	(Méhes, 1907)	Sopron	Pannonian	Slavonian-Serbian	2 female LV, 1 female RV	MFGI	Pl. 168 AFI	holo-paratypes	juveniles
<i>Caspiocypris</i>	<i>Candona (Caspiocypris) rakosiensis</i>	(Méhes, 1907)	Mt. Medvenica	Pannonian	Serbian	4 female LV, 5 female RV	NHMZ	D-66		
					Serbian	4 female LV, 5 female RV	NHMZ	D-226		
<i>Caspiocypris</i>	<i>Candona martoniensis</i>	(Méhes, 1907)	Sopron	Pannonian	Slavonian-Serbian	2 female LV	MFGI	113	holo-paratype	juveniles
<i>Caspiocypris</i>	<i>Candona (Lineocypris) martoniensis</i>	(Méhes, 1907) sensu Sokač, 1972	Mt. Medvenica	Pannonian	Serbian	2 female LV, 1 female RV	NHMZ	III-2		
<i>Caspiocypris</i>	<i>Candona (Lineocypris) reticulata</i>	(Méhes, 1907) sensu Sokač, 1972	Mt. Medvenica	Pannonian	Serbian	4 female LV, 2 female RV	NHMZ	Marcushevak		
<i>Caspiocypris</i>	<i>Candona (Reticulocandona) reticulata</i>	(Méhes, 1907) sensu Krstić, 1972	Boždarevac	Pannonian	Portaferrian	3 female LV, 3 female RV	NHMB	17-II-88		
<i>Hastacandona</i>	<i>Candona (Hastacandona) longitesta</i>	(Krstić, 1972)	Sremski Karlovci	Pannonian	Portaferrian	2 female LV, 4 female RV, 1 male LV	NHMB	0-274, 0-275	holo-paratypes	
<i>Hastacandona</i>	<i>Candona (Pontoniella) croatica</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	Serbian	1 female LV	NHMZ	D-458	paratype	
<i>Hastacandona</i>	<i>Paracypris loczyi</i>	Zalányi, 1929	Obreno vac	Pannonian	Portaferrian	1 female RV	MFGI	Pl. 6318	lectotype	juvenile
<i>Hastacandona</i>	<i>Hastacandona loczyi</i>	(Zalanyi, 1929)	Obreno vac	Pannonian	Portaferrian	1 female LV, 4 female RV (3 juv.)	GOC	OBR 13	topotypes	
<i>Hastacandona</i>	<i>Candona (Pontoniella) lotzyi (sic.)</i>	(Zalanyi, 1929)	Mt. Medvenica	Pannonian	Portaferrian	1 female RV	NHMZ	KZL-65 1055		
<i>Hastacandona</i>	<i>Candona granulosa</i>	(Zalányi, 1959)	Tihany	Pannonian	Portaferrian	2 female LV	MFGI	Pl. 164 AFI	holo-paratypes	
						2 female LV, 1 female RV, 1 male LV, 1 male RV	MFGI	Tihany 4		
						1 female RV	MFGI	Tihany 31		
<i>Lineocypris</i>	<i>Lineocypris trapezoidea</i>	Zalányi, 1929	Pejino vić	Pannonian	Portaferrian	1 female RV	MFGI	Pl. 6309a	lectotype	broken
						1 female RV	MFGI	Pl. 6309b	paralectotype	broken
<i>Lineocypris</i>	<i>Candona (Lineocypris) branka</i>	(Krstić, 1972)	Obreno vac	Pannonian	Portaferrian	2 female LV, 2 female RV	NHMB	0-276, 0-277	holo-paratypes	
<i>Lineocypris</i>	<i>Lineocypris branka</i>	(Krstić, 1972)	Obreno vac	Pannonian	Portaferrian	4 female LV, 6 female RV, 2 male LV, 4 male RV	GOC	OBR 13	topotypes	
<i>Lineocypris</i>	<i>Candona (Lineocypris) caudalis</i>	(Krstić, 1972)	Boždarevac	Pannonian	Portaferrian	2 female LV, 3 female RV	NHMB	0-280, 0-281	holo-paratypes	
<i>Lineocypris</i>	<i>Candona (Lineocypris) inflexa</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	Portaferrian	1 female LV, 1 female RV	NHMZ	D-308	paratype	
					Portaferrian	1 female LV	NHMZ	D-254		

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					Portaferrian	1 female LV, 1 male LV	NHMZ	ZG68-V18		
<i>Lineocypris</i>	<i>Candona (Lineocypris) pupini</i>	(Krstić, 1972)	Velika Moštanica	Pannonian	<b>Serbian</b>	2 female LV, 2 female RV	NHMB	0-278, 0-279	holo-paratypes	
<i>Lineocypris</i>	<i>Candona tihanyensis</i>	(Zalányi, 1959)	Tihany	Pannonian	<b>Portaferrian</b>	1 female RV, 2 female LV	MFGI	Pl. 161 AFI	holo-paratypes	broken
<i>Pontoniella</i>	<i>Paracypris acuminata</i>	(Zalányi, 1929)	Pejnović	Pannonian	<b>Portaferrian</b>	1 female LV	MFGI	Pl. 6307	lectotype	
			Obrenovac	Pannonian	<b>Portaferrian</b>	1 male RV	MFGI	Pl. 6310	paralectotypes	<i>P. hastata</i> according to Krstić, 1971
						1 female LV	MFGI	Pl. 6311a	paralectotype	<i>P. hastata</i> according to Krstić, 1971
						1 female LV, 1 female RV	MFGI	Pl. 6311b	paralectotypes	<i>P. hastata</i> according to Krstić, 1971
1 female LV, 1 female RV	MFGI	Pl. 6311c	paralectotypes	<i>P. hastata</i> according to Krstić, 1971						
<i>Pontoniella</i>	<i>Candona (Pontoniella) acuminata</i>	(Zalányi, 1929)	Mt. Medvenica	Pannonian	Portaferrian	2 female LV, 2 female RV, 1 female C	NHMZ	VII-9		
<i>Pontoniella</i>	<i>Candona (Serbiella) bacevicae</i>	(Krstić, 1972)	Obrenovac	Pannonian	<b>Portaferrian</b>	2 female LV, 3 female RV	NHMB	0-268, 0-269	holo-paratypes	
<i>Pontoniella</i>	<i>Pontoniella bacevicae</i>	(Krstić, 1972)	Obrenovac	Pannonian	<b>Portaferrian</b>	8 female LV, 9 female RV, 1 female C	GOC	OBR 14	topotypes	
<i>Pontoniella</i>	<i>Candona (Serbiella) hastata</i>	(Krstić, 1971)	Obrenovac	Pannonian	<b>Portaferrian</b>	1 LV, 2 RV	NHMB	0-264, 0-265	topotypes	
<i>Pontoniella</i>	<i>Candona (Pontoniella) hastata</i>	(Krstić, 1971)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	3 female LV, 2 female RV	NHMZ	D-36		
<i>Pontoniella</i>	<i>Pontoniella hastata</i>	(Krstić, 1971)	Obrenovac	Pannonian	<b>Portaferrian</b>	15 female LV, 12 female RV, 1 male RV	GOC	OBR 14	topotypes	
<i>Pontoniella</i>	<i>Candona (Serbiella) ilici</i>	(Krstić, 1972)	Meľjak	Pannonian	<b>Transdanubian</b>	2 female LV, 2 female RV	NHMB	0-266, 0-267	holo-paratypes	
<i>Pontoniella</i>	<i>Candona (Serbiella) kolubarae</i>	(Krstić, 1972)	Boždarevac	Pannonian	<b>Portaferrian</b>	2 female LV, 3 female RV	NHMB	0-270, 0-271	holo-paratypes	
<i>Pontoniella</i>	<i>Candona (Serbiella) maxiunguiculata</i>	(Krstić, 1972)	Umka	Pannonian	<b>Serbian</b>	1 female LV, 1 female RV	NHMB	0-262, 0-263	holo-paratype	
<i>Pontoniella</i>	<i>Candona (Pontoniella) sagittosa</i>	(Krstić, 1972)	Mt. Medvenica	Pannonian	<b>Serbian</b>	4 female LV, 2 female RV	NHMZ	D-66		
<i>Pontoniella</i>	<i>Candona (Pontoniella) truncata</i>	(Sokač, 1972)	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	4 female LV, 4 female RV	NHMZ	D-186	paratype	
<i>Pontoniella</i>	<i>Pontoniella truncata</i>	(Sokač, 1972)	Obrenovac	Pannonian	<b>Portaferrian</b>	3 female LV, 3 female RV	GOC	OBR 1		
<i>Propontoniella</i>	<i>Propontoniella macra</i>	(Krstić, 1972)	Vranović-I	Pannonian	<b>Slavonian</b>	2 female LV, 2 female RV	GOC	BP 3.7.9		
<i>Typhlocyprrella</i>	<i>Candona (Typhlocyprrella) annae</i>	Krstić, 1972	Boždarevac	Pannonian	<b>Portaferrian</b>	2 LV, 2 RV	NHMB	0-303, 0-304	holo-paratypes	
<i>Typhlocyprrella</i>	<i>Typhlocyprrella annae</i>	Krstić, 1972	Obrenovac	Pannonian	<b>Portaferrian</b>	1 female LV	GOC	OBR 1		
<i>Typhlocyprrella</i>	<i>Candona (Typhlocyprrella) lineocypriformis</i>	Krstić, 1972	Boždarevac	Pannonian	<b>Serbian</b>	1 female LV, 1 female RV, 1 male RV	NHMB	0-305, 0-306	holo-paratypes	



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<i>Typhlocyprella</i>	<i>Candona (Typhlocyprella) elongata</i>	Sokač, 1972	Mt. Medvenica	Pannonian	<b>Serbian</b>	1 female RV	NHMZ	D-125	holotype	
						1 female LV	NHMZ	D-125	paratype	
<i>Zalanyiella</i>	<i>Candona (Casiolla) venusta</i>	Zalányi, 1929	Mt. Medvenica	Pannonian	<b>Portaferrian</b>	1 female RV	NHMZ	D-254		
					Portaferrian	1 female LV, 2 female RV	NHMZ	KZL227		
<i>Zalanyiella</i>	<i>Zalanyiella venusta</i>	Zalányi, 1929	Obrenovac	Pannonian	<b>Portaferrian</b>	6 female LV, 7 female RV, 2 male LV, 2 male RV	MFGI		neotype	