

PATTERNS OF MORPHOSPACE OCCUPATION IN RECENT CYPRIDOIDEA (CRUSTACEA, OSTRACODA)

J. R. SÁNCHEZ-GONZÁLEZ¹, Á. BALTANÁS¹ AND D. L. DANIELOPOL²

¹ Department of Ecology, Universidad Autónoma de Madrid, E-28049 Madrid, SPAIN.

E-mail: jorge.sanchez@uam.es & angel.baltanas@uam.es

² Institute of Limnology, Austrian Academy of Sciences, A-5310 Mondsee, AUSTRIA.

E-mail: dan.danielopol@oeaw.ac.at

Abstract

Patterns of morphological disparity are explored at different taxonomic levels within the ostracod superfamily Cypridoidea Baird, 1845. Valve outlines for 171 species in four families, fifteen subfamilies and forty genera have been extracted from existing literature and analysed using elliptic Fourier analysis. Once ostracod shapes are characterized numerically, the cypridoidean (empirical) morphospace is described accordingly. The position of the ostracod species within the morphospace allows the computation and comparison of the morphological disparity in different groups, as well as their relative contribution (partial disparity) to overall morphological variation. The family Candonidae is the group with the highest diversity in valve shape and accounts for more than 50% of total disparity in the superfamily. *Mixtacandona* and *Cypria*, with their extreme shapes, are mainly responsible for that pattern. However, as compared to the Cyprididae, taxonomic diversity of candonids is low suggesting that morphological diversity might better reflect ecological processes (*e.g.* adaptation to extreme environments) than branching phylogenetic patterns.

Key words: Morphometrics, disparity, non-marine ostracods, taxonomic diversity.

Resumen

Se exploran los patrones de disparidad morfológica en diferentes niveles taxonómicos dentro de la superfamilia de ostrácodos Cypridoidea Baird, 1845. Se han obtenido de la literatura los contornos de las valvas de 171 especies pertenecientes a cuatro familias, quince subfamilias y cuarenta géneros, y su forma ha sido analizada mediante el uso del análisis elíptico de Fourier. Una vez que los contornos han sido caracterizados numéricamente, se procede a construir el morfoespacio empírico de la superfamilia. La posición de las especies en dicho morfoespacio permite el cálculo y la comparación de la disparidad morfológica entre diferentes grupos, así como de su contribución relativa (disparidad parcial) a la variación morfológica total. Los Candonidae son el grupo con la mayor diversidad morfológica, que supone más del 50% de la disparidad total en la superfamilia. Los géneros *Mixtacandona* y *Cypria*, con sus formas extremas, son los principales responsables de esta circunstancia. Sin embargo, por comparación con los Cyprididae, la diversidad taxonómica de los candónidos es baja y sugiere que la disparidad morfológica es más el reflejo de procesos ecológicos (*p. ej.*, adaptación a ambientes extremos) que de bifurcación filogenética.

Palabras clave: Morfometría, disparidad, ostrácodos no-marinos, diversidad taxonómica.

INTRODUCTION

Disparity, the amount of morphological diversity within a taxon, has become a major topic in evolutionary and systematic biology (Briggs *et al.*, 1992a; Foote, 1992a; Foote, 1996a; Foote, 1997a). Researchers have largely approached studies on morphological disparity within a grand-scale evolutionary framework (Knoll *et al.*, 1984; Foote, 1992a; Foote, 1993b; Foote, 1997a; Wagner, 1997), but enquiries with a heavy ecological bias are common as well (Hertel, 1994; Ricklefs & Miles, 1994; Van Valkenburgh, 1994). Indeed, evolutionary and ecological arguments must necessarily concur on most hypotheses willing to explain the origin and pattern of morphological diversity (Foote, 1997a; Ciampaglio, 2002). Many taxonomic groups (blastozoans, blastoids, crinoids, trilobites, foraminiferans, brachiopods, ammonoids, gastropods, mammals) have been the subject of studies on disparity (see Foote, 1997a for references), and ostracods (Crustacea, Ostracoda) are no exception to that rule (Benson, 1975; Benson, 1976; Oertli, 1976; Whatley & Stephens, 1976; Benson, 1981; Benson, 1982; Benson *et al.*, 1982; Reyment, 1982; Reyment, 1985a; Reyment, 1985b).

Taking advantage of the recent progress experienced by both the quantitative measure of morphological disparity (Briggs *et al.*, 1992b; Foote, 1992a, 1992b, 1993a, 1993b, 1997a, 1997b; Wills *et al.*, 1994; Ciampaglio *et al.*, 2001) and morphometric analysis (Rohlf, 1990, 1998; Bookstein, 1991, 1996; Rohlf & Marcus, 1993; Zelditch *et al.*, 1998) we here address the exploration of morphospace occupation patterns in a major group of recent non-marine ostracods, the superfamily Cypridoidea Baird, 1845.

The Cypridoidea belong to the Podocopida Sars, 1866, which is the most diverse and widely distributed order among recent ostracods and the only one with non-marine representatives (Martens *et al.*, 1998; Smith & Horne, 2002). The oldest representatives of Cypridoidea were identified in Devonian sediments (c 400 Myr) (Maddocks, 1982), although diversity in the group burst much later, during the Upper Jurassic (c 165 Myr) (Whatley, 1992; Martens *et al.*, 1998). In addition to the Cypridoidea two other podocopid superfamilies have invaded continental habitats too: Cytheroidea Baird, 1850 and Darwinuloidea Brady & Norman, 1889. However, the Cypridoidea are dominant in continental habitats standing for nearly two thirds of the described Recent non-marine ostracod faunas, e.g. in Europe (Löffler & Danielopol, 1978), Africa and/or South America (Martens, 1998).

The superfamily Cypridoidea includes four Recent families: Cyprididae, Candonidae, Ilyocyprididae and Notodromadidae (see Appendix for comprehensive taxonomic information). The Cyprididae are the more diverse of them all with a number of described extant species approaching 1,000 and some estimates on expected actual diversity which double that figure (Martens *et al.*, 1998). Morphological diversity in the group runs in parallel to its taxonomic diversity with size ranging from the exceedingly small (less than 0.5 mm) to 'giant' species (more than 6 mm) and shape varying enormously as well (elongated, triangular, globose, subquadrangular, etc.). Candonidae follow cypridids in taxonomic diversity but beat them in morphological and ecological plasticity. Candonids –nearly 500 species have been described in Europe and Asia (Löffler & Danielopol, 1978; Martens *et al.*, 1998)– occur in both epigeal habitats and groundwater systems. And the only marine lineage within the Cypridoidea, the Paracypridinae, belongs to the Candonidae too. Ilyocyprididae and Notodromadidae, the remaining two families, are species-poor lineages (less than hundred species each), the former with an almost invariant carapace morphology.

Within this framework we here address the search for patterns of morphological disparity at different taxonomic levels (families and subfamilies) within the Cypridoidea. Our aim is descriptive rather than evolutionary because the temporal dimension is not considered here but only recent species from a limited geographical range (Europe) will be included and, in doing so, our capabilities for making evolutionary inferences are severely limited. However, given the enormous amount of extant and fossil species involved and the uneven information available for different geographic areas, an attempt at a more modest scale sounds much more realistic as a first step.

Additionally the relationships between morphological and taxonomic diversity and the likely links between disparity and species environment will be explored as it has been suggested that selective pressures imposed by the physical structure of the habitat might have been of paramount importance in carapace shape evolution in these crustaceans (Danielopol, 1977, 1978, 1980a).

MATERIAL AND METHODS

Valve outlines from representatives of 171 recent species of non-marine ostracods in the superfamily Cypridoidea were digitized using scanned images

from the literature (see Appendix). All sources refer to European (Russia not included) localities. This sample represents approximately 50% to 60% of the cypridoidean species recorded in the area (Martens *et al.*, 1998; Horne *et al.*, 1998). Representatives of all four families also have been included in numbers that parallel their proportional diversity at the continental scale: Cyprididae - 81 spp (47%); Candonidae - 81 spp. (47%); Ilyocyprididae - 6 spp. (3.5%) and Notodromadidae - 3 spp. (1.7%).

Given that the focus of the study is on patterns of disparity at ranks above the genus level, sources of variation at levels below (like sexual dimorphism or asymmetries between left and right valves) must be kept to a minimum when not completely removed. Here females were selected over males because the latter have not been described for a significant number of cypridoid species which reproduces parthenogenetically (Horne *et al.*, 1998). Right valves were preferred over left valves because in many species this is the valve which contains more morphological details due to its functional role in the closing of the carapace (Baltanás & Geiger, 1998). Still, female left valves were used for three species (*Isocypris beauchampi*, *Psychrodromus betharrami* and *Ps. robertsoni*) for which we were not able to find any illustration of a right valve. Similarly, no proper illustration of a female of *Paracandona euplectella* was known to us. Accordingly we used the outline of the left valve of a male as redrawn by Meisch (2000) from Klie (1938) (see Appendix). Outlines, each one containing between 1,700 and 2,200 points, were digitized using tpsDig 1.311 software (Rohlf, 2001). These original outlines were smoothed by taking a weighted moving average over three successive coordinate points (Haines & Crompton, 2000),

$$\left[(x_i^*, y_i^*) = \frac{1}{4}(x_{i-1}, y_{i-1}) + \frac{1}{2}(x_i, y_i) + \frac{1}{4}(x_{i+1}, y_{i+1}) \right]$$

and scaled to centroid size (Dryden and Mardia, 1998). Elliptic Fourier analysis (EFA) (Kuhl & Giardina, 1982), a Fourier technique for fitting functions to curves that has been extensively used with ostracods (Baltanás & Geiger, 1998; Baltanás *et al.*, 2000; Baltanás *et al.*, 2002; Danielopol *et al.*, 2002) and other groups of organisms (Rohlf & Archie, 1984; Ferson *et al.*, 1985; McLellan & Endler, 1998; Smith & Bunje, 1999), was applied to the ostracod outlines. The analysis results in a series of harmonic coefficients that were mathematically normalized to be invariant to rotation and digitizing starting point (Ferson *et*

al., 1985). These coefficients, which can be used to reconstruct the original outlines, were used as shape descriptors in subsequent analysis. Because ostracod valve outlines have rather simple shapes few harmonics are enough to describe them accurately. We have here used twenty harmonics (77 non-trivial coefficients), a number which assures goodness-of-fit above 97% between original and reconstructed outlines. Goodness-of-fit was measured as the mean distance between each point of the reconstructed image and the closest point in the original outline (McLellan & Endler, 1998).

We used principal component analysis (PCA) performed on the variance-covariance matrix of all 77 shape variables produced by EFA to construct an empirical morphospace for the superfamily Cypridoidea. It has been argued that performing PCA on the covariance matrix, as compared to correlation matrix, will diminish or even eliminate any influence of higher order harmonics because EFA effectively downweights all harmonics above the first (successive harmonics describe progressively finer details of the outline) (Haines & Crompton, 2000). Nevertheless, that is not necessarily a drawback of the method but depends on the aims of the study. In the present case our interest is on discriminating shapes by giving preference to general features over fine details. Sharing a tiny spine in the rear part of the valve, for instance, does not make two species as similar as if they were both equally triangular in overall shape.

Morphological disparity is defined as the amount of empirical morphospace which is occupied by a group of taxa. Such variable is here estimated from the locations of the species (*i.e.*, the species' scores) within the multidimensional space defined by PCA axes. Accordingly PCA eigenvectors were scaled to 1 (*i.e.*, their length set to unity) to preserve Euclidean distances among objects (Marcus, 1993; Legendre & Legendre, 1998). Among the many possible ways of measuring morphological disparity (MD) we have selected the mean squared Euclidean distance $MD = \sum_i d_i^2 / (N-1)$ where d_i^2 is the squared Euclidean distance between object i from the group centroid and N is the total number of observations (=species number) (Foote, 1993a; but see Ciampaglio *et al.*, 2001) for other indices of morphological disparity). MD is standardised to be independent of sample size (number of species in the group) so that the amount of morphospace occupied is not a function of the number of taxa included in the analysis (Foote, 1993a). There is no meaning in computing MD for the superfamily Cypridoidea as a whole (we have nothing else to com-

pare to), hence morphological disparity is calculated only at the family and the subfamily levels using the corresponding centroids on each case.

The advantage in using MD as index of morphological disparity is that it can be partitioned among its several component subgroups. The contribution of each taxonomic subgroup j to the group MD is estimated as partial disparity $PD_j = \sum_i d_{ij}^2 / (N-1)$ ($MD = \sum_j PD_j$) (Foote, 1993a).

Partial disparity is not dependent on subgroup size or variability within the subgroup but on the location of its members with respect to the overall centroid. Subgroups with a low number of members can contribute significantly to the group-MD if they have shapes which greatly differ from the group mean shape. Subgroups peripherally distributed in the morphospace have larger partial disparities than those placed close to the group centroid. It is like having hundreds of circles in a painting; a single square will add more morphological disparity to the whole group than any number of new circles we could add.

Here we have computed contributions to overall disparity in the superfamily Cypridoidea at the family, subfamily and genus levels. Given that the 171 species we are dealing with are just a sample of all the recent Cypridoidea it is helpful to attach a measure of variability to our estimates. However, data like these, with a taxonomic structure behind, are neither independent nor random so that standard parametric statistics cannot be applied (Harvey & Pagel, 1991). Instead we use the bootstrap to estimate both morphological and partial disparities and their variability, here expressed as the standard deviation of the bootstrap replicates, at all taxonomic levels selected by randomly drawing species within each genus with replacement (5,000 replicates) (Foote, 1992ab; 1993a). Variability in morphological disparity (VarMD) reflects the symmetry in the distribution of taxa around their group centroid in the morphospace; whereas variability in partial disparity (VarPD) measures shape redundancy within a group and its relative position to the overall centroid. The more similar the shapes for all the elements within a group (be it a genus, a subfamily or a family) the lower the expected variability in any statistic which is computed from samples randomly drawn (with replacement) from that group. PD estimates can be expressed either in their original units or as percentages of the overall disparity).

Morphological disparity is also related to diversity and to mean carapace size in the group. Diversity is measured both as species richness and as variation in taxonomic distinctness (VarTD or $\Lambda+$), an index which

evaluates the unevenness of the taxonomic distribution of lower rank taxa within higher rank groups (Clarke & Warwick, 2001). Carapace size, which is a highly variable feature within a species, has been roughly approximated from records in the literature (see Appendix). For groups above the species level an average value was estimated.

RESULTS

Only 15 PCA axes (out of 77) were retained for further analysis as they explained 99.58% of the total variance in the original data set. Indeed, 88.26% of variance in the empirical morphospace is already explained by the first two PCA axes (Figure 1). First axis (77.79%) is mainly related to degree of elongation of outline shape with more rounded outlines (*Notodromas*, *Cypria*) located on the left side and those more lengthy (*Phreatocandona* and some *Mixtacandona*) on the right end side (Fig. 1). The second axis reflects changes in the triangularity of valves: those more quadrangular (e.g. *Ilyocypris* spp., *Paracandona euplectella*) are displaced upwards and those triangular downwards (e.g.: *Mixtacandona tabacari*, *Potamocypris fulva*).

Relative positions of members in each family within the two-dimensional morphospace are displayed in figure 2 whereas mean morphological disparity (+standard deviation) at the family and subfamily level are plotted in figure 3. Candonidae and Cyprididae differ markedly in disparity with the former occupying a larger portion of the morphospace than the latter (Fig. 2A-B & 3). Although both groups seem to coincide significantly within the 2D-morphospace plotted in figure 2

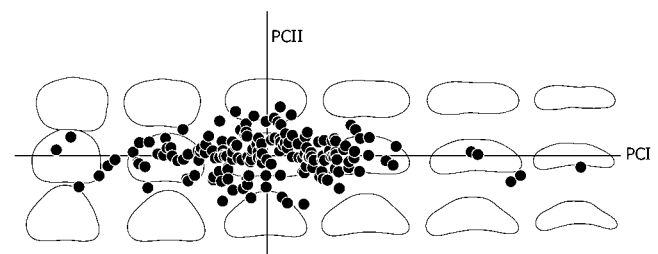


FIGURE 1—Distribution of Cypridoidean shapes (black dots) within the empirical morphospace as defined by the first two axes of a PCA (88.26% of total variance). Outlines are reconstructions of hypothetical shapes in different locations to better illustrate shape gradients within the two-dimensional morphospace.

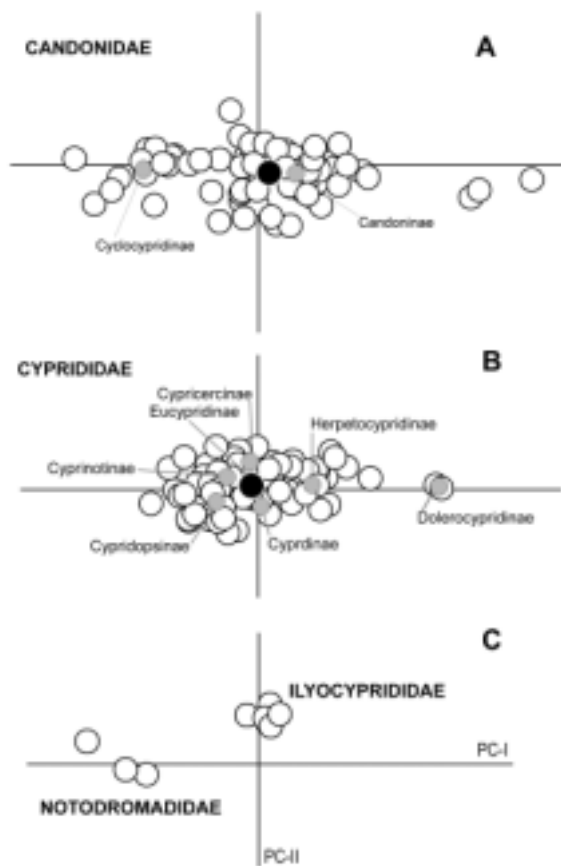


FIGURE 2—Morphospace occupation in Recent Cyridoidea. The empirical morphospace has been split into three plots to better show disparity within each family. Centroids for families (black dots) and subfamilies (grey dots) are included only for Candonidae and Cyprididae, the species-rich groups.

(A-B) there is indeed a rather non-overlapping distribution as estimated from discriminant analysis performed on species positions within that morphospace (PCA scores for first fifteen axis) which produces 89.5% correct classifications in average. Taxonomic structure within each family, measured as variation in taxonomic distinctness, also differ for both families ($\Lambda^+_{\text{CYPRIDIDAE}}=0.421$; $\Lambda^+_{\text{CANDONIDAE}}=0.387$) reflecting a more even distribution of species among genera and of genera among subfamilies in the Candonidae as compared to the Cyprididae. Whereas half (7 out of 14) of the genera in the Candonidae includes only 1-2 species, five of the remaining seven genera include 8 species at least (10% of the total richness in the family). In the Cyprididae, however, there are few highly speciose genus (*Eucypris* – 21 spp.; *Heterocypris* – 9 spp.; *Potamocypris* – 9 spp.) and many (14 out of 23) genera

with 1-2 species only. Taxonomic structure at the subfamily level is rather simple in the Candonidae with two subfamilies only: the Cycloocyprinae (17% of total species richness) and the Candoninae (83% of total species richness). In the Cyprididae there are many more subfamilies (10) but three of them (*Eucyprinae*, *Herpetocyprinae* and *Cyprinotinae*) include 60% of all the species in the group. Other families involved, *Notodromadidae* and *Ilyocyprididae*, are much less diverse morphologically (Figs. 2C, 3).

At the subfamily level the most morphologically diverse group and the one with highest species richness is the subfamily Candoninae (67 spp.), followed by the *Eucyprinae* (29 spp.), the *Herpetocyprinae* (12 spp.) and so on (Fig. 3). Some groups, like the *Cyprinotinae* (9 spp.), are highly redundant in shape as compared to less speciose groups like the *Cypridinae* (2 spp.) or the *Cypricerinae* (4 spp.) (Fig. 3). These latter groups, although including very few species, expand over a portion of the morphospace much larger than the *Cyprinotinae*.

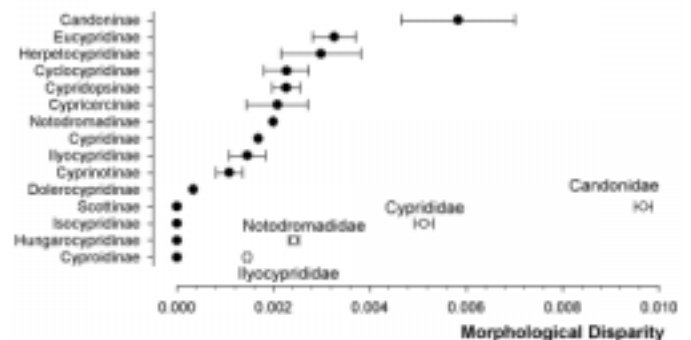


FIGURE 3—Estimates of morphological disparity (mean + SD) within families (white dots) and subfamilies (black dots) in the Cyridoidea (bootstrap estimates from 5,000 replicates).

At the genus level there is a decreasing gradient in morphological disparity from *Schellencandona* to *Dolerocypris* (Fig. 4), with *Mixtacandona* outstanding as the most morphologically diverse genus of them all (Fig. 4).

Partial disparities, the contributions to overall morphological disparity at different taxonomic ranks, are displayed in figures 5 and 6. Overall disparity in the superfamily Cyridoidea has been split into contributions by families, subfamilies and genera within (Fig. 5A-B). Candonidae explain more than half

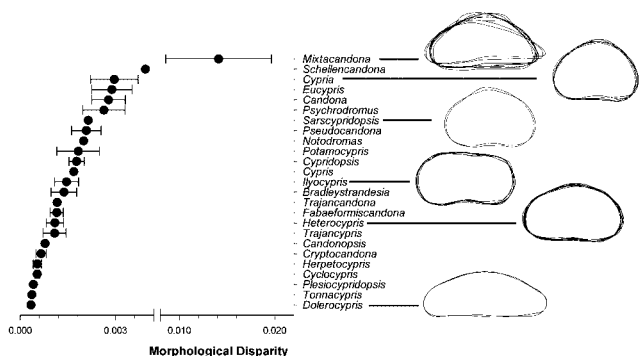


FIGURE 4—Estimates of morphological disparity within genera in the Cypridoidea. Genera with only one species are not included as they have null morphological disparity. Sets of outlines for some representative genera (*Mixtacandona*, *Cyprina*, *Sarscypridopsis*, *Ilyocypris* and *Dolerocypris*) are displayed.

(59.5%) of the overall disparity in the Cypridoidea, followed by the Cyprididae (31.6%), Notodromadidae (6%) and Ilyocyprididae (2.9%) (Fig. 5A). At the subfamily level the Candoninae (39%) and the Cycloocypridinae (20%) are the major contributors to total cypridoidean disparity (Fig. 5). Indeed there is no main valve shape type left unexplored by those candonid groups which spread along the main axis of the morphospace (Fig. 2A). However, not all the genera in both subfamilies contribute equally but *Mixtacandona* and *Cyprina*, which show extreme shapes, are largely responsible for the high PD of candonids (Fig. 5B). All subfamilies in the Cyprididae, Ilyocyprididae and Notodromadidae are of less quantitative importance to disparity in the superfamily (Fig. 5A). Still some cases are remarkable because of their disparate contribution as compared to their taxonomic diversity. For instance, the Dolerocypridinae, which include two species only, are ‘outsiders’ in the morphospace (see Fig. 2B) and hence have a striking contribution to overall shape diversity (PD=6.6%). Such a pattern is repeated, but less markedly, for the Notodromadinae (PD=4.8%) and the Ilyocypridinae (PD=2.6%). Notice that *Eucypris*, the genus with the highest taxonomic diversity (21 spp.), contributes less to total disparity in the Cypridoidea (PD=5.4%) than the species-poor genus *Dolerocypris* (2 spp.) (PD=6.6%) (Fig. 5B).

Contributions provided by subfamilies and genera to disparity at the family level are plotted in Figure 6. Disparity estimates have been computed for Cyprididae and Candonidae only given that Ilyocyprididae includes no more than one genus in a single subfamily and that Notodromadidae only has two genera and two subfami-

lies (Fig. 6A-D). As expected due to its higher species richness (67 vs. 14) and its wider range of valve shapes, Candoninae are more meaningful than Cycloocypridinae to overall candonid disparity (Fig. 6A). At the genus level, however, results are not so self-evident. Major contributors are not the most species-rich genera (*Candona*-18 spp., *Fabaeformiscandona* – 14 spp. and *Pseudocandona* – 13 spp.) but *Mixtacandona* and *Cyprina*, with 9 and 8 species respectively.

Within Cyprididae most of the morphological disparity is provided by Dolerocypridinae, Eucypridinae, Cypridopsinae and Herpetocypridinae at the subfamily level (Fig. 6C), and by *Dolerocypris*, *Eucypris*, *Herpetocypris* and *Potamocypris* at the genus level (Fig. 6D).

The contribution of the several genera to morphological disparity at the subfamily level does not differ greatly from patterns observed for the family or superfamily levels (Fig. 7). Still, some variations are worth to be stressed. For instance, *Trajanandona* and

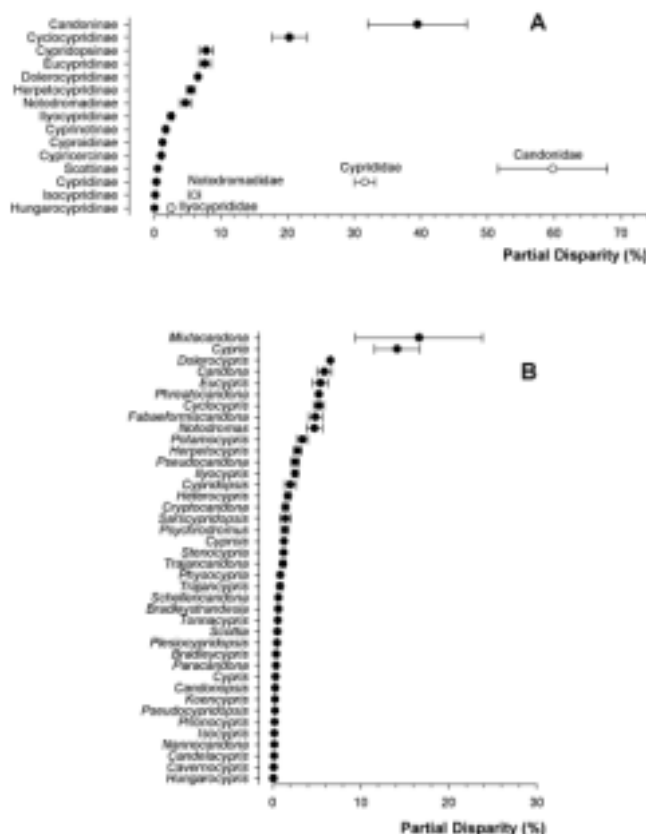


FIGURE 5—Partial disparities (mean contribution +SD) of families and subfamilies (A) and genera (B) to overall morphological disparity in Recent Cypridoidea (bootstrap estimates from 5,000 replicates).

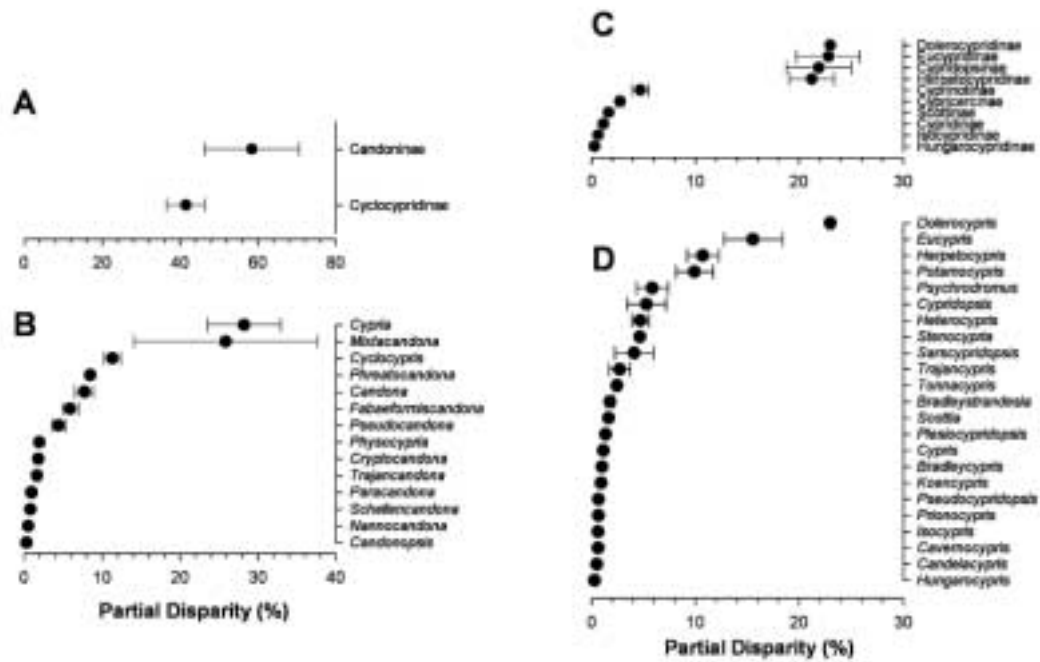


FIGURE 6—Partial disparities (mean contribution +SD) of subfamilies and genera to overall morphological disparity in Recent Candonidae (A, B) and Cyprididae (C,D) (bootstrap estimates from 5,000 replicates).

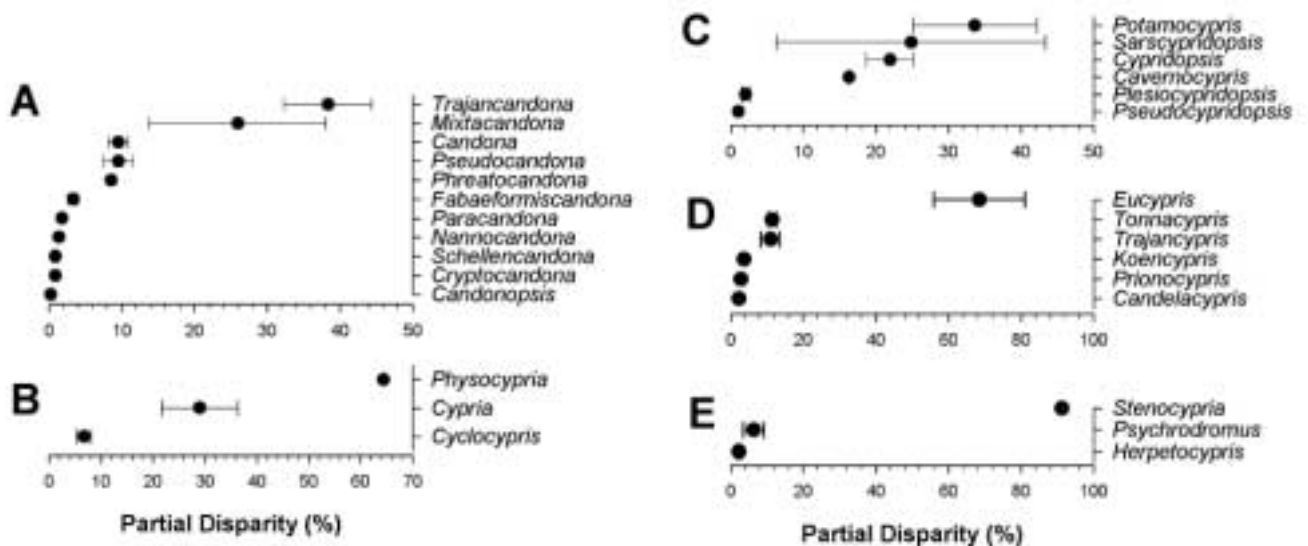


FIGURE 7—Partial disparities (mean contribution +SD) of genera to overall morphological disparity in the main subfamilies within Recent Candonidae (A-Candoninae; B-Cyclocypridinae) and Recent Cyprididae (C-Cypridopsinae; D-Eucypridinae; E-Herpetocypridinae) (bootstrap estimates from 5,000 replicates).

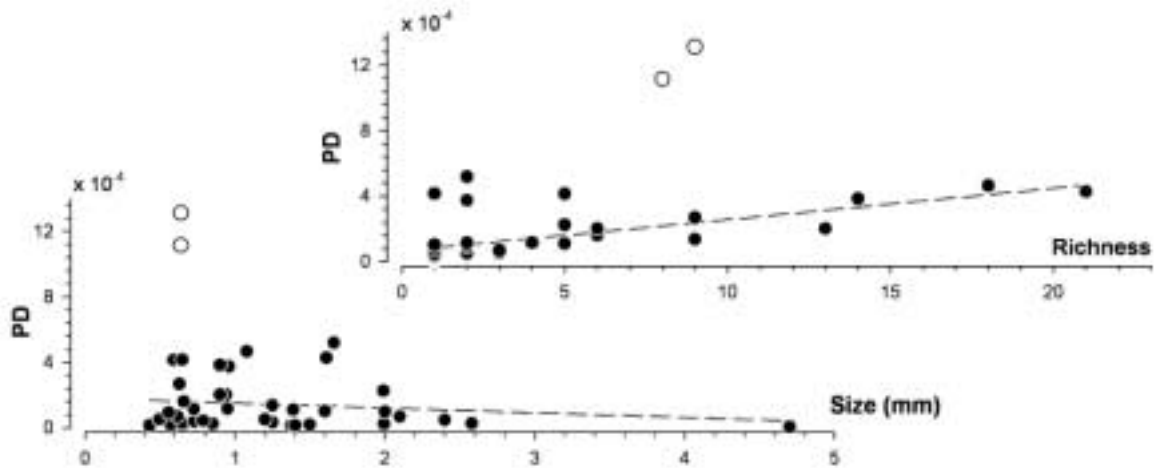


FIGURE 8—Relations of partial disparities at the genus level (contributions to overall disparity within the Cypridoidea) to valve size and species richness. Dashed lines correspond to the lineal regression model (*Mixtacandona* and *Cypria* excluded, see text).

Stenocyprina do significantly contribute to disparity within the Candoninae (Fig. 7A) and the Herpetocypridinae (Fig. 7E), respectively, although both are of minor relevance to total disparity in their corresponding families, Candonidae (Fig. 6B) and Cyprididae (Fig. 6D).

Finally, the contributions (PDs) of all the genera in the analysis to overall disparity in the Cypridoidea are related to species richness and average size with *Cypria* and *Mixtacandona* as noteworthy outliers (Fig. 8).

After discarding both cases from the analysis partial disparity shows a slight but significant positive correlation with generic species-richness (Spearman $R=0.7094$; $p<0.0001$) and no significant correlation with carapace average size (Spearman $R=-0.0554$; $p=0.741$) (Fig. 8).

DISCUSSION

The Candonidae show higher morphological disparity than the Cyprididae; i.e. candonids occupy a larger portion of the cypridoidean morphospace and explore a wider range of carapace shape types than cypridids. At the subfamily level the Candoninae outrun in disparity all the others, including the candonid group Cycloocypridinae and all subfamilies in the Cyprididae. And a gradient exists at the genus level running from

low variable highly redundant groups of species (*Dolerocypris*, *Plesioocypridopsis*, *Cycloocypris*) to those with a extreme disparity (*Mixtacandona* and *Cypria*). All these statements might be no surprise for most practitioners of ostracodology but this is the first time that they are demonstrated on a quantitative basis, and hence, fulfil one aim of this study—to test whether the methodological approach that we applied here can provide insights into morphological patterns of groups within a medium-rank taxonomic level, the Cypridoidea—.

Differences in disparity between Cyprididae and Candonidae seem not to be related to taxonomic diversity—estimated as species richness—because the same number of taxonomic units ($N=81$) was used for both families. However, taxonomic structure differs dramatically between them. Candonidae (81 species in 14 genera and 2 subfamilies) has a much simpler structure than the Cyprididae (81 species in 23 genera and 10 subfamilies). Taxonomic structure in the candonids is not only simpler but also more balanced, as shown by the slightly lower variation in taxonomic distinctness in that family. If taxonomic structure is to be used as a proxy for the geometry of branching, then one should conclude that evolutionary processes in the Candonidae promoted the appearance of low rank taxonomic units (species) within a limited array of higher rank levels (genera and, mainly, subfamilies). But, what is the role of carapace morphology in

this context? Well, we should not expect a perfect match between morphological disparity and taxonomic diversity. Disparity at lower taxonomic ranks (e.g. genera and subfamilies) is likely to reflect patterns of species richness more than branching patterns (Foote, 1992, 1996b). So differences between lineages (e.g. Candonidae and Cyprididae) might result from the existence of different morphological constraints in each clade; although there are alternative processes –e.g. adaptive radiation or selective extinction– which could explain those patterns too (Simpson, 1953; Foote, 1993). One of those processes is ecological specialization; i.e. adaptation to narrow ecological niches. Specialization requires the acquisition of non-standard morphologies better equipped for a more efficient exploitation of a given microhabitat. If extreme forms are ecologically more specialized (Foote, 1993) then candonids must have, on average, narrower niches than the cypridids. Although that hypothesis has to be tested rigorously there are some preliminary observations to support it. For instance, those elongated forms in the genus *Phreatocandona* and *Mixtacandona* which occupy peripheral location in the morphospace belong to highly specialized, troglotic organisms.

Still another argument can be invoked as a likely explanation for diverging patterns in morphological disparity between Candonidae and Cyprididae: how taxonomy is done on both groups. Whenever clades to be compared do not result from using similar taxonomic criteria for the recognition of subfamilies, genera and species, and as far as taxonomic work is idiosyncratic then any kind of analysis of the processes behind the observed patterns will be severely hampered. (Non-marine) ostracodology has been, and continues to be, a meeting point for a large number of paleontologists and neontologists, scientists with different training and aims, doing their work in places all around the world and experiencing the influence of a variety of scientific traditions. Working with fossils constrains the sort of features (mainly morphological characters in the carapace) which can be used for taxonomic purposes. Neontologists do use limbs in addition but the type and amount of characters considered have changed significantly through time posing some uncertainty in the taxonomic status of many taxa which were described previously. For instance, features of the hemipenis were not used in the taxonomy of the Candoninae until introduced by T. Petkovski and D.L. Danielopol in the late '60s (Petkovski, 1969; Danielopol, 1969), and those characters remain unused (they are inapplicable) in fossil species. 'Splitters' and 'lumpers' also exist among

ostracodologists and despite valuable attempts to review and update existing information for some restricted taxonomic groups (e.g. Martens, 1990; González-Mozo *et al.*, 1996; Martens *et al.*, 1997; Namiotko & Danielopol, this volume) or geographic areas (Meisch, 2000) a lot of work is still to be done.

In the confidence that rigorous scientific knowledge must rest on sound and reliable observations the aim of this paper is not to provide explanations but to detect patterns concerning shape variability in ostracod carapaces. For doing that, methods for the analysis of shape variability have been applied to a set of valve outlines of a series of species belonging to the Cypridoidea. Undoubtedly, the time dimension, which has not been included here, is badly needed for a more comprehensive understanding of the whole picture (notice, for instance, that although some of the 'hypothetical' shapes depicted in figure 1 do not correspond to any recent species they are indeed realised in the fossil record). Concluding, it is our contention that the careful study of such patterns should lead to the formulation of testable hypotheses about the evolutionary and ecological processes involved.

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APPENDIX TAXONOMIC INFORMATION

SUPERFAMILY CYPRIDOIDEA BAIRD, 1845

Family Candonidae Kaufmann, 1900

Subfamily Candoninae Kaufmann, 1900

Paracandona euplectella (Robertson, 1889)³⁷.

Nannocandona faba Ekman, 1914³⁷.

Candona acricauda Mikulic, 1961³⁸; *C. alta* Klie, 1939³¹; *C. candida* (O. F. Müller, 1776)³⁷; *C. cavicola* Klie, 1935²⁸; *C. chappuisi* Klie, 1943³⁴; *C. dedelica* Petkovski, 1969⁴⁴; *C. depressa* Klie, 1939³²; *C. expansa* Mikulic, 1961³⁸; *C. marginata* Klie, 1941³³; *C. media* Klie, 1939³²; *C. meerfeldiana* Scharf, 1983³⁷; *C. muelleri* Hartwig, 1899⁴⁶; *C. neglecta* Sars, 1887³⁷; *C. strumicae* Petkovski, 1959⁴⁰; *C. trapeziformis* Klie, 1939³²; *C. vidua* Klie, 1941³³; *C. weltneri* Hartwig, 1899⁴⁶; *C. angulata* G. W. Müller, 1900¹⁷.

Fabaeformiscandona alexandri (Sywula, 1981)³⁷; *F. angusta* (Ostermeyer, 1937)³⁷; *F. breuili* (Paris, 1920)³⁷; *F. brevicornis* (Klie, 1925)³⁷; *F. caudata* (Kaufmann, 1900)²; *F. fabaeformis* (Fischer, 1851)²; *F. fabella* (Nüchterlein, 1969)³⁷; *F. hyalina* (Brady & Robertson, 1870)³⁷; *F. lapponica* (Ekman, 1908)³⁷; *F. latens* (Klie, 1940)³⁷; *F. siliquosa* (Brady, 1910)³⁷; *F. tricatricosa* (Diebel & Pietrzeniuk, 1969)³⁷; *F. tyrolensis* (Löffler, 1963)³⁷; *F. wegelini* (Petkovski, 1962)³⁷.

Schellencandona belgica (Klie, 1937)³⁷; *S. triquetra* (Klie, 1936)³⁷.

Pseudocandona albicans (Brady, 1864)³⁷; *P. compressa* (Koch, 1838)²; *P. eremita* (Vejdovsky, 1882)²; *P. insculpta* (G. W. Müller, 1900)²; *P. marchica* (Hartwig, 1899)²; *P. pratensis* (Hartwig, 1901)²; *P. regisnikolai* Karanovic & Petkovski, 1999²⁷; *P. semicognita* (Schäfer, 1934)³⁷; *P. serbani* Danielopol, 1982¹²; *P. simililampadis* Danielopol, 1978⁹; *P. sucki* (Hartwig, 1901)²; *P. szoecsi* (Farkas, 1958)³⁷; *P. zschokkei* (Wolf, 1920)³⁰.

Cryptocandona kieferi (Klie, 1938)³⁷; *C. matris* (Sywula, 1976)⁸; *C. reducta* (Alm, 1914)³⁷; *C. vavrai* Kaufmann, 1900³⁷.

Mixtacandona botosaneanui Danielopol, 1978¹³; *M. italica* Karanovic, 2000²⁶; *M. sp. gr. ljevuschkini* Danielopol, 1979¹¹; *M. sp. gr. riongessa* Danielopol, 1979¹¹; *M. jubertieae* Danielopol, 1978¹⁰; *M. latingerae* Rogulj & Danielopol, 1993¹⁴; *M. spandli* Rogulj & Danielopol, 1993³⁷; *M. tabacarui* Danielopol, 1979¹¹; *M. elegans* Danielopol & Cvetkov, 1979¹⁶.

Candonopsis kingsleii Brady & Robertson, 1870³⁷; *C. scourfieldi* Brady, 1910²¹.

Phreatocandona motasi (Danielopol, 1978)¹³.

Trajancandona natura Karanovic, 1999²⁵; *T. particula* Karanovic, 1999²⁵.

Subfamily Cyclocypridinae Kaufmann, 1900

Cypria cavernae Wagenleitner, 1990⁵³; *C. exsculpta* (Fischer, 1855)⁵²; *C. karamani* Petkovski, 1976⁴²; *C. ophtalmica* (Jurine, 1820)⁵²; *C. reptans* Bronshtein, 1928³⁷; *C. sketi* Petkovski, 1976⁴²; *C. subsalsa* Redeke, 1936³⁷; *C. sywulae* (Sywula, 1981)³⁷.

Physocypria kraepelini G. W. Müller, 1903³⁷.

Cyclocypris globosa Sars, 1863⁵²; *C. helocrenica* Fuhrmann & Pietrzeniuk, 1990³⁷; *C. laevis* (O. F. Müller, 1776)³⁷; *C. ovum* (Jurine, 1820)⁵²; *C. serena* (Koch, 1838)³⁷.

Family Ilyocyprididae Kaufmann, 1900

Subfamily Ilyocypridinae Kaufmann, 1900

Ilyocypris bradyi Sars, 1890³⁷; *I. decipiens* Masi, 1905³⁷; *I. getica* Masi, 1906³⁷; *I. gibba* (Ramdohr, 1808)³⁷; *I. inermis* Kaufmann, 1900³⁷; *I. monstifrica* (Norman, 1862)³⁷.

Family Notodromadidae Kaufmann, 1900

Subfamily Notodromadinae Kaufmann, 1900

Notodromas monacha (O. F. Müller, 1776)³⁷; *N. persica* Gurney, 1921¹⁸.

Subfamily Cyproidinae Hartmann, 1963

Cyprois marginata (Straus, 1821)⁵¹.

Family Cyprididae Baird, 1845

Subfamily Cypridinae Baird, 1845

Cypris bispinosa Lucas, 1849³⁷; *C. pubera* (O. F. Müller, 1776)⁵¹.

Subfamily Eucypridinae Bronshtein, 1947

Candelacypris aragonica (Brehm & Margalef, 1948)⁶.

Eucypris accipitrina Anichini-Pini, 1968⁵; *E. anglica* Fox, 1967³⁷; *E. bronsteini* Petkovski, 1959⁴⁰; *E. caralitana* Tagliasacchi-Masata, 1969²; *E. crassa* (O. F. Müller, 1785)⁴; *E. elliptica* (Baird, 1846)¹⁹; *E. heinrichi* Petkovski and Keyser, 1995⁴⁴; *E. hieracina* Anichini-Pini, 1968⁵; *E. mareotica* (Fischer, 1855)¹⁹; *E. kerkyrensis* Stephanides, 1937³⁷; *E. lilljeborgi* (G. W. Müller, 1900)⁴⁸; *E. longisetosa* Anichini-Pini, 1968⁵; *E. molybdaena* Anichini-Pini, 1968⁵; *E. moravica* Jancarik, 1947³⁷; *E. pigra* (Fischer, 1851)⁵²; *E. stagnalis* Tagliasacchi-Masata, 1969⁵⁰; *E. stephanidesi* Petkovski, 1959⁴⁰; *E. sulcitana* Anichini-Pini, 1968⁵; *E. tarentina* Anichini-Pini, 1963³; *E. trajani* Sywula, 1967⁴⁸; *E. virens* (Jurine, 1820)⁵².

Koencypris ornata (O. F. Müller, 1776)³⁷.

Prionocypris zenkeri (Chyzer & Toth, 1858)⁵².

Tonnacypris estonicus (Järvekülg, 1960)²³; *T. lutaria* (Koch, 1838)⁵².

Trajancypris clavata (Baird, 1838)³⁶; *T. laevis* G. W. Müller, 1900³⁶; *T. serrata* G. W. Müller, 1900³⁶.

Subfamily Cypricercinae McKenzie, 1971

Bradleycypris obliqua (Brady, 1868)⁵².

Bradleystrandesia fuscata (Jurine, 1820)³⁷; *B. hirsuta* (Fischer, 1851)⁴⁷; *B. reticulata* (Zaddach, 1844)⁵².

Subfamily Herpetocypridinae Kaufmann, 1900

Herpetocypris brevicaudata Kaufmann, 1900²⁰; *H. chevreuxi* (Sars, 1896)⁵¹; *H. helenae* G. W. Müller, 1908²⁰; *H. intermedia* Kaufmann, 1900²⁰; *H. reptans* (Baird, 1835)²⁰.

Psychrodromus betharrami Danielopol & Baltanás 1993⁷; *P. peristericus* (Petkovski, 1959)³⁹; *P. robertsoni* (Brady & Norman, 1889)¹⁵; *P. fontinalis* (Wolf, 1920)³⁷; *P. olivaceus* (Brady & Norman, 1889)¹⁵.

Stenocypris fischeri Lilljeborg, 1883³⁷.

Subfamily Cyprinotinae Bronshtein, 1947

Heterocypris barbara (Gauthier & Brehm, 1928)¹⁹; *H. bosniaca* Petkovski et al., 2000⁴⁵; *H. bulgarica* Sywula, 1967⁴⁸; *H. gevgelica* Petkovski, et al., 2000⁴⁵; *H. incongruens* (Ramdohr, 1808)³⁷; *H. reptans* (Kaufmann, 1900)³⁷; *H. rotundata* (Bronshtein, 1928)³⁷; *H. vitrea* Sywula, 1967⁴⁵.

Subfamily Dolerocypridinae Kaufmann, 1900

Dolerocypris fasciata O. F. Müller, 1776⁴³; *D. sinensis* Sars, 1903³⁷.

Subfamily Isocypridinae Rome, 1965

Isocypris beauchampi (Paris, 1920)³⁷.

Subfamily Scottinae Bronshtein, 1947
Scottia pseudobrowniana Kempf, 1971³⁷.

Subfamily Hungarocypridinae Bronshtein, 1947
Hungarocypris madaraszii Örley, 1886³⁷.

Subfamily Cypridopsinae Kaufmann, 1900
Cavernocypris subterranea Wolf, 1920³⁷.

Cypridopsis elongata (Kaufmann, 1900)¹; *C. hartwigi* G. W. Müller, 1900²²; *C. lusatica* Schäfer, 1943³⁷; *C. pilosa* Anichini-Pini, 1967⁴; *C. sanctipetri* Anichini-Pini, 1968⁵; *C. vidua* (O. F. Müller, 1776)³⁷.

Plesiocypridopsis thermanum (Tagliasacchi-Masala, 1967)⁴⁹; *P. newtoni* (Brady & Robertson, 1870)³⁷.

Potamocypris arcuata (Sars, 1903)³⁷; *P. fallax* Fox, 1967³⁷; *P. fulva* (Brady, 1868)³⁷; *P. pallida* Alm, 1914³⁷; *P. similis* G. W. Müller, 1912³⁷; *P. steueri* Klie, 1935²⁹; *P. tetrataeniata* Anichini-Pini, 1967⁴; *P. variegata* (Brady & Norman, 1889)³⁷; *P. zschokkei* (Kaufmann, 1900)²².

Pseudocypridopsis clathrata (Klie, 1936)²⁴.

Sarsocypridopsis lanzarotensis (Mallwitz, 1984)³⁵; *S. aculeata* (Costa, 1847)³⁷.

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