

Ivana Karanovic

# Recent Freshwater Ostracods of the World

Crustacea, Ostracoda, Podocopida

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# Preface

Scientists have described over 1.7 million of the world's species of animals, plants, and algae, as of 2010. Invertebrates make around 77% of that number, of which the greatest species diversity exists among insects. There are more than 67,000 described living species of Crustacea, and probably five or ten times that number waiting to be discovered and named. Crustaceans have many forms and living strategies, and they have been found at all depths in every marine, brackish, and freshwater environment on Earth. Ostracods are often considered the most primitive and one of the oldest crustacean groups. The group was named in 1802 by Latreille, and the name comes from the Greek *óstrakon*, meaning shell or tile. The common name in English for ostracods is “mussel shrimp” or “seed shrimp,” while in German it is “Muschelkrebse,” names describing their most prominent characteristics: soft body enclosed between two valves. However, it was not Latreille who first described an ostracod species. The first ostracod is attributed to Baker, who illustrated a fossil ostracod in 1742, but Linné actually named the first species in 1746 as *Monoculus conchapedata*. Many great scientists have contributed and are still contributing to the field of ostracodology. Two hundred and sixty years of diligent work on ostracods brings us to approximately 8,000 living species described so far (Horne et al. 2000). However, the group is better known from its fossils. True ostracods first appeared in the Ordovician, about 500 million years ago (Martens et al. 1998), and more than 50,000 fossil species have been named so far. This extremely rich fossil record is a result of the well-calcified, bivalved shell and a small size. The size of adult ostracods ranges from 0.2 to 32 mm. The soft body is extremely reduced (in comparison with other crustaceans), having only up to eight pairs of appendages. These animals live in all types of water ecosystems both fresh and marine. Thanks to the rich fossil and recent diversity, and environmental plasticity, ostracods are one of the best model groups for evolutionary studies, and stand for all four pillars of evolutionary wisdom: morphology, genetics, ecology, and paleontology (Martens and Horne 2000). Trends in ostracodology today clearly favor paleontology over all the other disciplines. In a retrospective of ostracod research between the 1st (year 1963) and the 15th (penultimate one in the

year 2005) International Symposia on Ostracoda, given by Matzke-Karasz et al. (2007), ecology (mostly paleoecology) was and still is the major field of investigation within ostracodology. On the other hand, taxonomy of ostracods is in a constant decline. Although taxonomy is the basis of all biological research, it is overly neglected and is in serious distress all over the world (Boero 2010). Taxonomy of living ostracods is particularly difficult because of two factors: small size and very few morphological characters. In spite of the decline of this field of study, the taxonomic literature is sometimes overwhelming. Until 1997, there were about 22,000 taxonomic references for the non-marine ostracods (both fossil and recent ones). Professor Eugen Kempf published indexes in 1980, 1991, and 1997, each year in several volumes (A, B, C, D) listing all the references (both taxonomical and non-taxonomical literature), as well as all the ostracod generic and species names ever published. Without these publications, work on ostracods would be much more difficult. However, they are only a starting point, from which an ostracodologist has to find their way around and about in identifying a species.

In 2000, Claude Meisch published the book “Freshwater Ostracods of Western and Central Europe,” a thorough systematic insight which provides systematic, taxonomic, ecological, and distributional data on the ostracods from this part of the world. This meticulous work is widely used, not only by ostracodologists working on the European ostracod fauna. Several countries have their freshwater ostracod fauna published as books, which are often used as reference works, such as Hungary (Daday 1900a), Germany (Klie 1938a), Russia (Bronstein 1947), Poland (Sywula 1974b), Great Britain (Henderson 1990), etc., but in many cases the language they are published in is a limiting factor. Hartmann (1966, 1976, 1968, 1975, 1989) published five volumes on ostracods as part of the series “Klassen und Ordnungen des Tierreichs,” a study of the entire class Ostracoda from morphological, anatomical, and systematic points of view. Unfortunately, this comprehensive and valuable work never was translated to English and therefore is not widely used in the modern studies. On the other hand, books such as Horne and Martens (1994) “The Evolutionary Ecology of Reproductive Modes in Non-marine Ostracoda” and Martens (1998b) “Sex and Parthenogenesis – Evolutionary Ecology of Reproductive Modes in Non-marine Ostracods” have become landmarks in studies of ostracod ecology and reproduction modes.

The present book intends to provide a practical synopsis of the recent ostracods of the world, living in all types of freshwater ecosystems. According to the latest account, there are close to 2,000 subjective species and about 200 genera of recent non-marine ostracods (Martens et al. 2007). They all belong to the order Podocopida. This book provides a diagnosis for each taxonomic unit with living freshwater representatives, keys down to the species level and illustrations of the main generic characters. Most illustrations and photographs are original, and those kindly donated by colleagues are always acknowledged in figure legends. Each species listed is given in its currently accepted systematic position and no new combinations are provided. For each species, the type locality and the repository of the type material (if known) is listed. Maps of distributions are presented for each genus, and they include all species which currently belong to the genus and their

present day distribution. Most of the synonyms are also listed, as well as some taxonomical remarks, pointing out potential systematic and taxonomic problems and needs of revision. All the subfamily, generic, and species names are listed in the alphabetical order. The book should be of value to both beginners and experienced workers, in all aspects of the current trends in ostracodology. Most of all it is intended to encourage more taxonomic studies of ostracods since there are still many ostracod species to be described and contribute to the foundation of the “four pillars of evolutionary wisdom.”

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**Part I**  
**Introduction and Methods**



# Introduction

## 1 Classification

Depending on the view of the higher classification of Crustacea, ostracods are classified as a subclass of the class Maxillopoda (Schram 1986; Brusca and Brusca 1990) or as a separate class (Forest 1994; Martin and Davis 2001) within the subphylum Crustacea. In the first case, ostracods are grouped together with tantulocarids, branchiurans, mystacocaridans, copepods, facetotectans, rhizocephalans, ascothoracidans, acrothoracicans, and thoracicans. McKenzie et al. (1983) classify ostracods into Entomostraca, together with Branchiopoda, Cirripedia, Branchiura, and Phyllocarida. Ostracods are here accepted as a separate class within Crustacea. According to Maddocks (1982) ostracods are divided into four orders: Myodocopida Sars 1866, Platycopida Sars 1866, Palaeocopida Henningsmoen 1953, and Podocopida Sars 1866. On the other hand, Martin and Davis (2001) and Horne et al. (2002) divide the class into subclass Myodocopa (with orders Myodocopida and Halocyprida) and Podocopa (with orders Platycopida, Podocopida, and Palaeocopida). Subclass Myodocopa has only marine representatives. Within the subclass Podocopa, Platycopida has almost only marine species (a very few brackish water species), Palaeocopida is known almost exclusively from fossils, and Podocopida has representatives in both fresh and marine environments. The Order Podocopida is treated in this book and its classification presented below (Table 1) follows Martens et al. (1998), Meisch (2000), and Horne et al. (2005). Letters after the names indicate the type of environment where representatives of a certain taxon can be found: “m” for marine species, and “F” for freshwater. Those with only marine representatives or commensal species are not considered further in the systematic part of the book, but, nevertheless, a key to all podocopid superfamilies as well as their general morphology is provided in this book.

**Table 1** Classification of the recent Ostracoda (only the podocopid lineages are listed below the suborder level)

---

Class Ostracoda Latreille 1802
Subclass Myodocopa Sars 1866 m
Order Myodocopida Sars 1866
Suborder Myodocopina Sars 1866
Order Halocyprida Dana 1852
Suborder Halocypridina Dana 1852
Suborder Cladocopina Sars 1866
Subclass Podocopa Sars 1866 m/f
Order Platycopida Sars 1866 m
Order Podocopida Sars 1866 m/f
Suborder Bairdiocopina Sars 1866 m
Superfamily Bairdioidea Sars 1866
Family Bairdiidae Sars 1866
Family Bythocyprididae Maddocks 1969
Suborder Cytherocopina Baird 1850 m/f
Superfamily Cytheroidea Baird 1850 m/f
Family Bythocytheridae Sars 1866 m
Family Cobanocytheridae Schornikov 1975 m
Family Cuneocytheridae Mandelstam 1959 m
Family Cushmanideidae Puri 1974 m
Family Cytherettidae Triebel 1952 m
Family Cytheridae Baird 1850 m
Family Cytherideidae Sars 1925 m/f
Family Cytheromatidae Elofson 1938 m
Family Cytheruridae Müller 1894 m
Family Entocytheridae Hoff 1942 f (living commensally on other crustaceans)
Family Eucytheridae Puri 1954 m
Family Hemicytheridae Puri 1953 m
Family Kliellidae Schäfer 1945 f
Family Krithidae Mandelstam 1960 m
Family Leptocytheridae Hanai 1957 m/f
Family Linnocytheridae Klie 1938a f
Family Loxoconchidae Sars 1925 m/f
Family Microcytheridae Klie 1938a m
Family Neocytheridae Puri 1957 m
Family Paracytherideidae Puri 1957 m
Family Paradoxostomatidae Brady and Norman 1889 m
Family Parvocytheridae Hartmann 1959 m
Family Pectocytheridae Hanai 1957 m
Family Psammocytheridae Klie 1938a m
Family Schizocytheridae Howe 1961 m
Family Trachyleberididae Sylvester-Bradley 1948 m
Family Xestoleberididae Sars 1928 f/m
Superfamily Terrestrialcytheroidea Schornikov 1969 m

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(continued)

**Table 1** (continued)

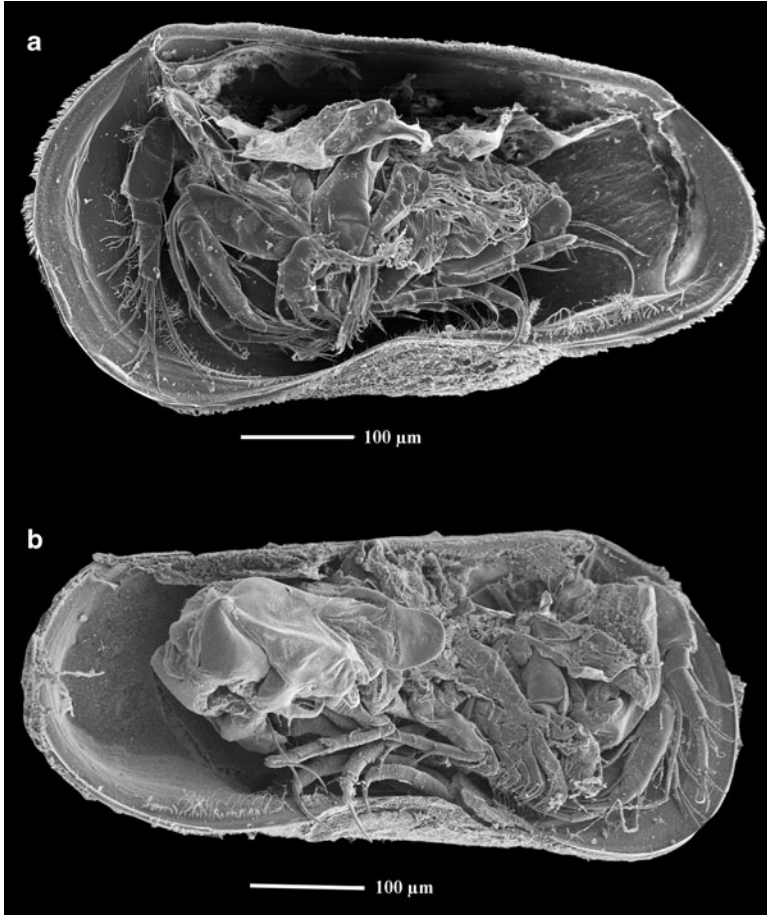
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Family Terrestrialcytheridae Schornikov 1969
Suborder Darwinulocopina Sohn 1987 f
Superfamily Darwinuloidea Brady and Norman 1889
Family Darwinulidae Brady and Norman 1889
Suborder Cypridocopina Jones 1901 m/f
Superfamily Cypridoidea Baird 1845 m/f
Family Candonidae Kaufmann 1900a m/f
Family Cyprididae Baird 1845 f
Family Ilyocyprididae Kaufmann 1900a, f
Family Notodromadidae Kaufmann 1900a, f
Superfamily Macrocypridoidea Müller 1912 m
Family Macrocyprididae Müller 1912
Superfamily Pontocypridoidea Müller 1894 m
Family Pontocyprididae Müller 1894
Suborder Sigilliocopina Martens 1992c m
Superfamily Sigillioidea Mandelstam 1960
Family Sigilliidae Mandelstam 1960

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## 2 Basic Morphology

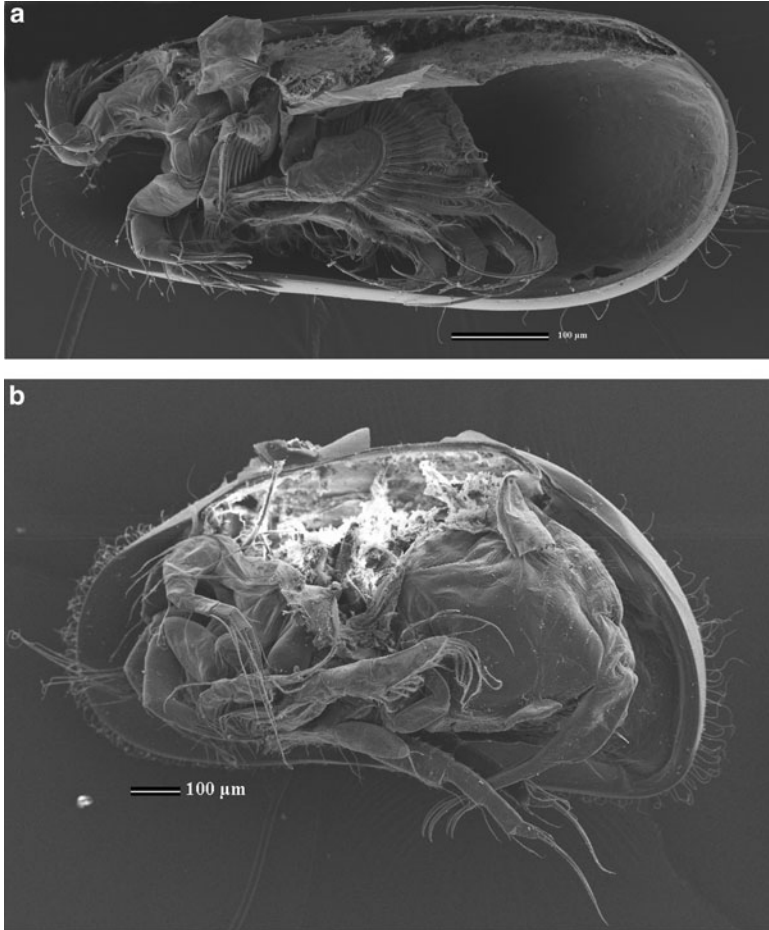
As in many crustacean groups there is no standard terminology that is in universal use. Specialists working on Suborder Cytherocopina tend to have different terminology to the ones working on the Suborder Cypridocopina. Obviously in an overview, such as this book, a standard terminology needs to be adopted. Horne et al. (2002) already attempted to establish a consistent terminology for all ostracods. In this book, standard terms used for all other crustaceans describing a general structure of the crustacean appendage (endites, protopod, exopod, endopod, epipod, and segments) are used here as well. The terminology applied here for the ostracod limbs is a combination of the standard terms used by many modern authors in their publications. Descriptions of the limb chaetotaxy are based on the nomenclature proposed by the following authors: Broodbakker and Danielopol (1982), Martens (1987a), Meisch (1996, 2007), Rossetti and Martens (1996), and Karanovic (2007). Nomenclature used for the carapace surface structures follows Sylvester-Bradley and Benson (1971). However, not all terms defined by the latter authors are described here as they are applicable mostly for the marine taxa of the suborder Cytherocopina and are not developed on the shells of the freshwater species. General morphology and structure of the valves are the same as in Meisch (2000). In this chapter, each appendage is compared between the three superfamilies found in the freshwaters: Cytheroidea, Darwinuloidea, and Cypridoidea, with some remarks on other ostracods (Figs. 1–3).



**Fig. 1** *Paralmnocythere karamani* (Petkovski 1960a), SEM: (a) inside view of the adult ♀; (b) inside view of the adult ♂.

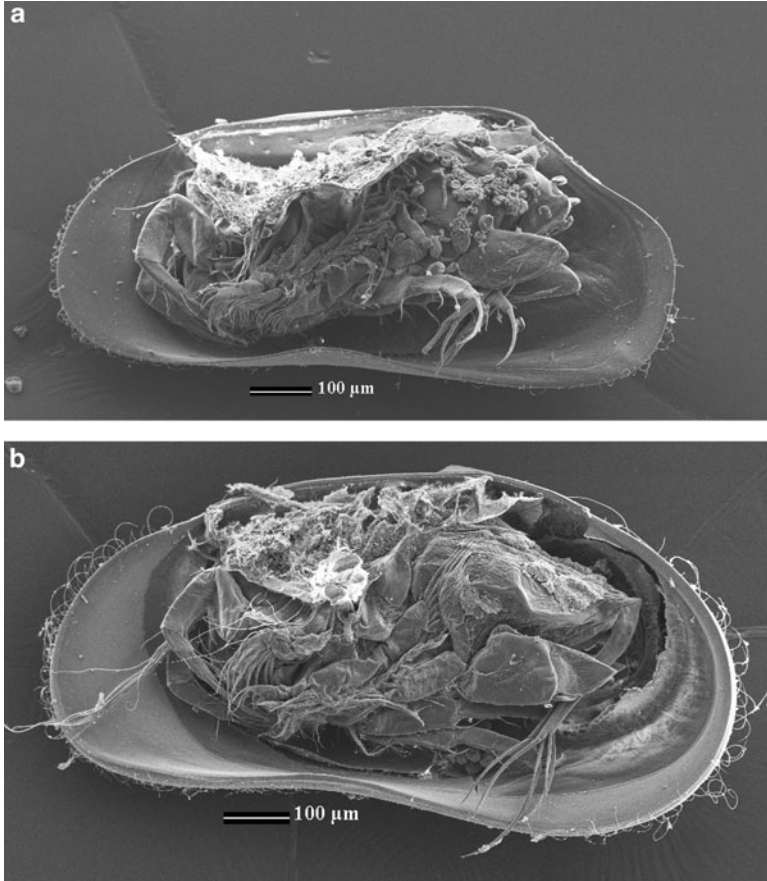
## 2.1 Carapace

The ostracod body is enclosed between two calcified valves that are connected in the dorsal part with simple chitinous, like in Cypridoidea, or complex calcite nonslip locking device (hinge), like in Cytheroidea. As in other crustaceans, the cuticle of the carapace is mineralized with low magnesium calcium carbonate in the form of calcite. The calcified shell consists of small crystallites embedded in a chitinous and protein matrix. The shell can be almost completely built of calcite crystals or composed of parallel chitinous lamellae together with a layer of crystallite. The carapace is an important functioning part of the ostracod anatomy, it encapsulates and protects the animal from predators, provides additional stability for the benthic way of life, and forms an integral part of the exoskeleton, providing anchorage



**Fig. 2** A, *Darwinula stevensoni* (Brady and Robertson 1870), (a) inside view of the adult ♀; (b), *Candona lindneri* Petkovski 1969, inside view of the adult ♀.

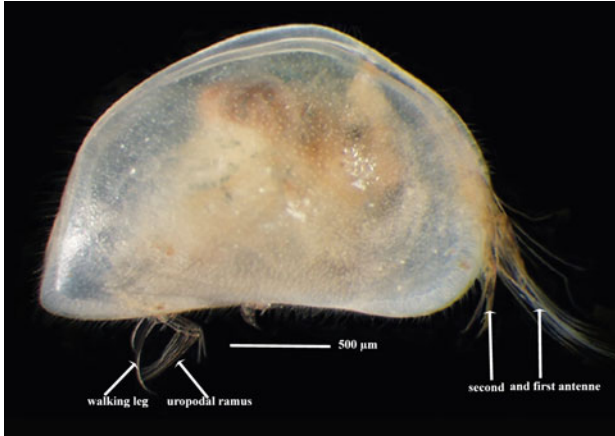
points for some muscles of the limbs. Ostracods keep almost all their soft parts within the valves, but sometimes even substantial parts of uropodal rami, walking and cleaning legs, as well as the first and the second antenna, can be seen protruding through the valves (Fig. 4). Ostracods are enclosed in the carapace even in the first instar of their development. The carapace is formed by two lateral folds of the epidermis, originating dorsally in the head region. These folds or *duplicature* have an inner and an outer lamella. The space between the two lamellae is an extension of the body which in some taxa may house certain reproductive and digestive organs. The outer lamella is well calcified throughout, while the inner lamella has uncalcified and calcified parts (Fig. 5a). The calcified inner lamella is an extension of the calcified outer lamella, i.e., they are continuous with one another, and the only difference between the two lamellae can be found in the disposition of their cells and



**Fig. 3** SEM: *Candonopsis kingsleii* (Brady and Robertson 1870), SEM: (a) inside view of the adult ♀; (b) inside view of the adult ♂.

whether their cuticle fronts are on the outside, or face the body of the animal (Keyser 1990). The data available suggest that the inner lamella is the main organ in which osmoregulation takes place in freshwater ostracods (Keyser 1990). The calcareous components of the ostracod shell are arranged in at least two distinct layers: one thicker layer, composed of crystals of calcite with a foliated appearance, and a thinner laminated layer. The soft body of an animal is integral part of the duplicature and it is connected dorsally to the valves as well as laterally with the so-called adductor muscles, (Fig. 5b), which form a scar on the valves, and together with the mandibular scars, form central scar pattern. This is the first taxonomic character for distinguishing between different podocopid suborders as shown in Fig. 5c–f.

Looking at the carapace laying on its side, we can distinguish *anterior margin* and *anterior end*, *posterior margin* and *posterior end*, and *ventral* and *dorsal margin*. (Fig. 6a)

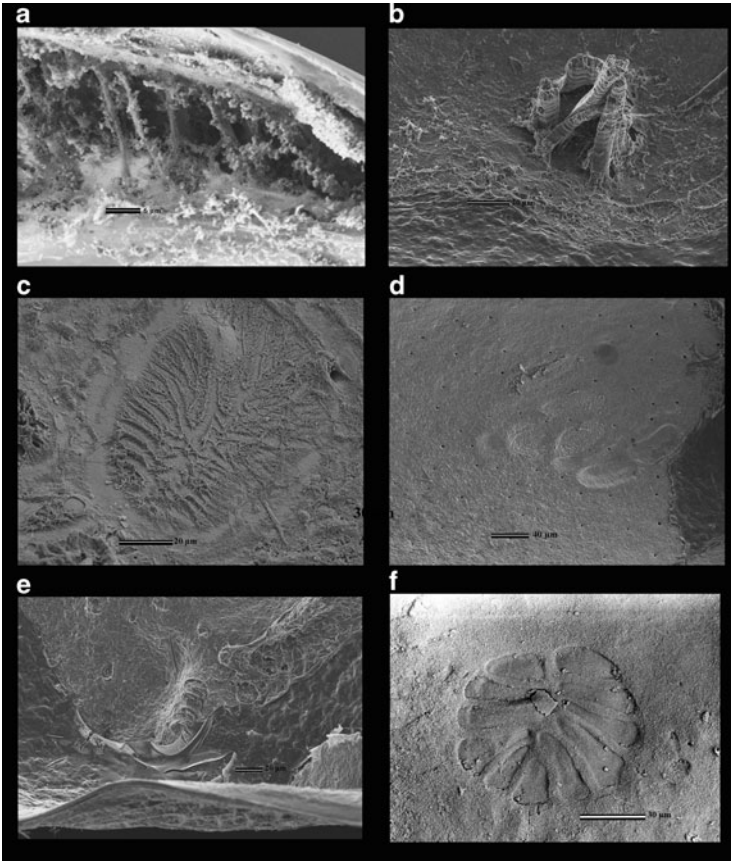


**Fig. 4** *Trigonocypris globulosa* De Deckker 1978. Outside view from the right side, showing the protruding appendages. Photo: S. Halse.

On the inner lamella, we can recognize the following parts, whose structures bear important taxonomic information (Fig. 6a, c). Looking from the center toward the free margins, the first line we can see is called *inner margin* and it represents the line where inner lamella becomes calcified. After that, occasionally we can see several *inner lists* which can run continuously or only partly with the inner margin. Further on, on the *calcified inner lamella* (sometimes also called *duplication* in the literature, but it is only a part of it and not synonymous), a zone where inner and outer lamella meet is called the *line of concrescence*, and the zone which follows and is usually transverse with canals is called the *fused zone*. The inner calcified lamella and the outer lamella may be fused throughout or there may be a space between them called *vestibulum*. *radial pore canals* are tubes, carrying nerves, passing through the fused zone between the calcified inner and outer lamellae. Sensillae protrude from pores. Sometimes radial/marginal pore canals start at the *line of concrescence* but do not run all the way through the *fused zone* (because they exit on the external surface of the valve before the outer margin), and in that case they are called *false radial/marginal pore canals*. The free extension of the calcified inner lamella is called *selvage*, and it can sometimes be inwardly displaced, in which case the free valve margin is formed by a more or less prominent extension of the outer lamella, called a *flange* (Fig. 6c).

The surface of the ostracod shell has many different features, which may have important taxonomic value. Pores appear to be the termination of pore canals which penetrate the shell and in live animals may bear a sensilla (Fig. 7), and on the surface they are called *normal pores*. In Cytheroidea many of the pores are partially closed by *sieve plates* (Fig. 7c, d). Pits on the surface of the carapace may be in the form of *punctae* (Fig. 7e) and *fossae* (Fig. 7f). Difference between punctae and fossae is in the fact that fossae are connected with walls or *muri*, which together form a *reticulum*. There can also be a “second order reticulation” inside

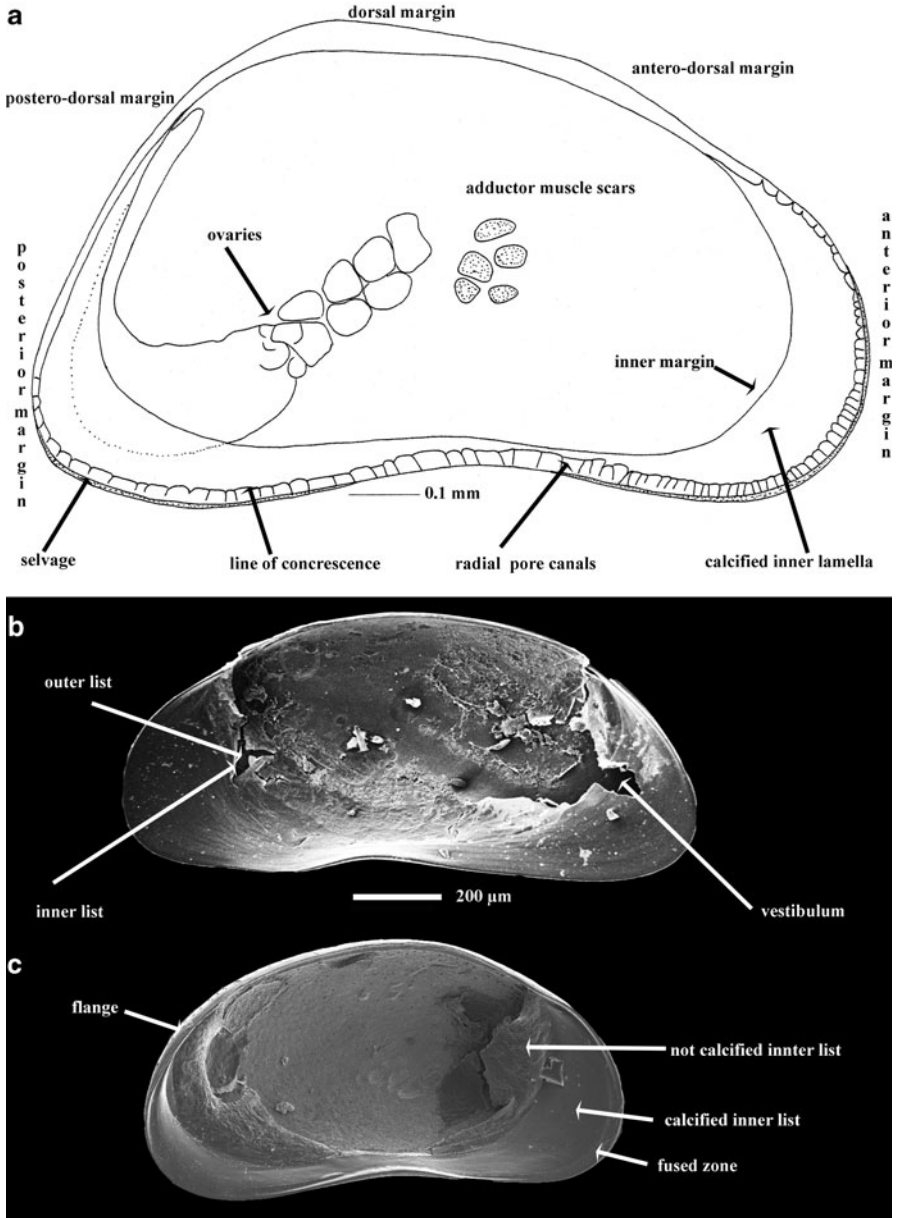




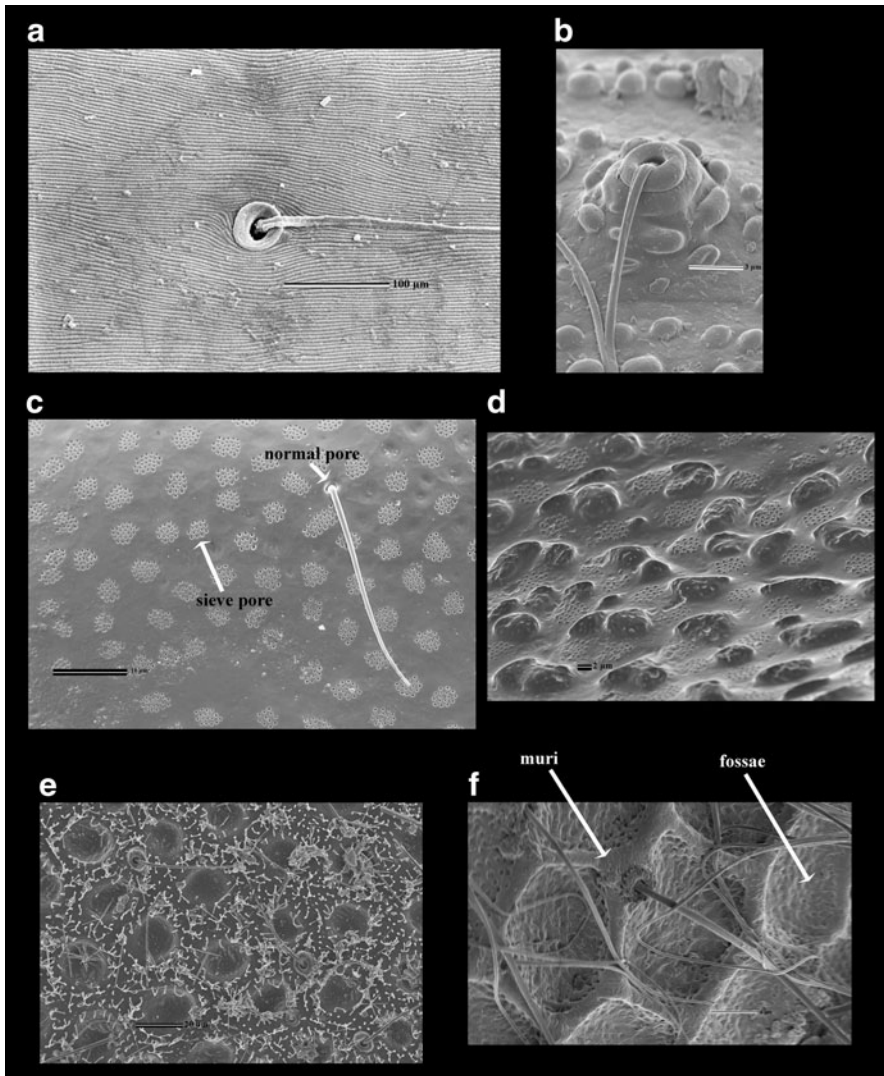
**Fig. 5** SEM: (a, f) *Darwinula stevensoni* (Brady and Robertson 1870); (b) *Plesiocypridopsis newtoni* Brady and Robertson 1870; (c) *Acocypris capilatta* (Vávra 1895); (d) *Psychrodromus fontinalis* (Wolf 1920); (e) *Paralimnocythere karamani* (Petkovski 1960a); (b) adductor muscle attachment to the shell; (c–f), imprints of the adductor muscle scars (CMS). (f) Photo: D. Keyser

the fossae or even walls. *Sulcus* (plural: *sulci*) is a term describing any kind of groove on the exterior of the carapace (Fig. 8a). *Tubercles* or *nodes* (Fig. 8b) are another type of carapace ornamentation. They can be simple and rounded, or they can be additionally covered with warty expressions. Observation on *Cyprideis torosa* (Jones 1850), an animal which can be found in many different salinity levels, has shown that the noding on the surface of the shell in this species is directly connected with the osmoregulation the animal employs during the molting (Keyser 2005). Special kinds of tubercles are also *clavae* (Fig. 9b). A much smaller ornament in the shape of a prickle is called *papillae* (Fig. 9a). *Clavae* can sometimes be enlarged and called *carinae* (or *costae*) (Fig. 9c). Wing-like expansions (both thin and pointed and fat and rounded) are called *alae* (Fig. 9d).



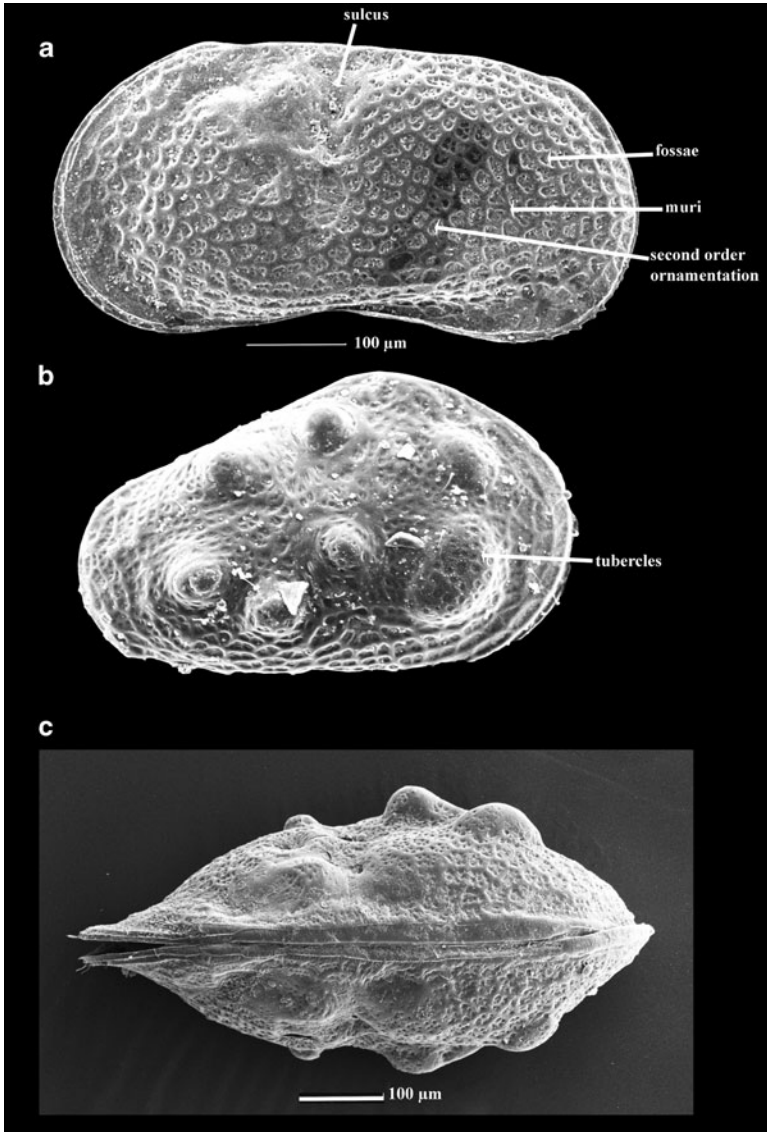


**Fig. 6** (a) line drawings, (b, c) SEM. (a) *Candona* sp.; (b) *Humphcypris subterranea* (Hartmann 1964); (c) *Psychrodromus fontinalis* (Wolf 1920): (a) schematic view of the interior of the LV; (b) inside view of the RV; (c) inside view of the LV. (b) Photo: D. Keyser



**Fig. 7** SEM: (a) *Ilyodromus viridulus* (Brady 1886b); (b) *Meridiescandona facies* Karanovic 2003c; (c) *Gomphodella quasihirsuta* Karanovic 2009; (d) *Gomphodella aurea* Karanovic 2009; (e) *Ilyocypris bradyi*, Sars 1870; (f), *Humphreyscandona waldoekae* Karanovic and Marmonier 2003: (a) normal pore, (b) detail of the surface, showing a normal pore; (c, d) detail of the surface; (e) detail of the surface showing rounded pits; (f) detail of the surface showing primary and secondary ornamentation. (a) Photo: D. Keyser

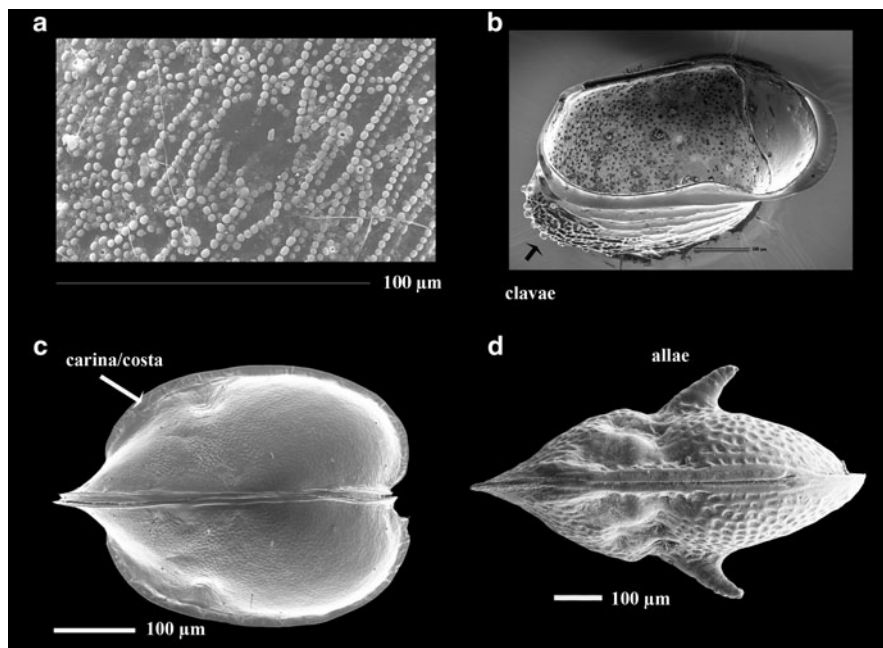
Ostracod shells have many different shapes. Most common shapes in the fresh-water ostracods in lateral view are “kidney” or “bean” shape (Fig. 10a), elliptical (Fig. 10b), trapezoidal (Fig. 10c, g), triangular and subtriangular (Fig. 10d, e, h), or elongated (Fig. 10f), or any variation of the previous shapes. In dorsal view, the



**Fig. 8** SEM: (a) *Limnocythere inopinata* (Baird 1843a, b); (b) *Cytherissa lacustris* (Sars 1863); (c) *Limnocythere inopinata* (Baird 1843a): (a, b) lateral view; (c) dorsal view. Photos: D. Keyser

shape can be ovoid or globular (Fig. 11a), laterally compressed (Fig. 11d), kite-like (Fig. 11e), or just oblong (Fig. 11b, c).

The coloration of the shell varies from being white, as in many subterranean species (Fig. 12d), to being very vividly colored (Fig. 12a, b), sometimes with very characteristic patterns. The color is usually provided by pigments deposited within



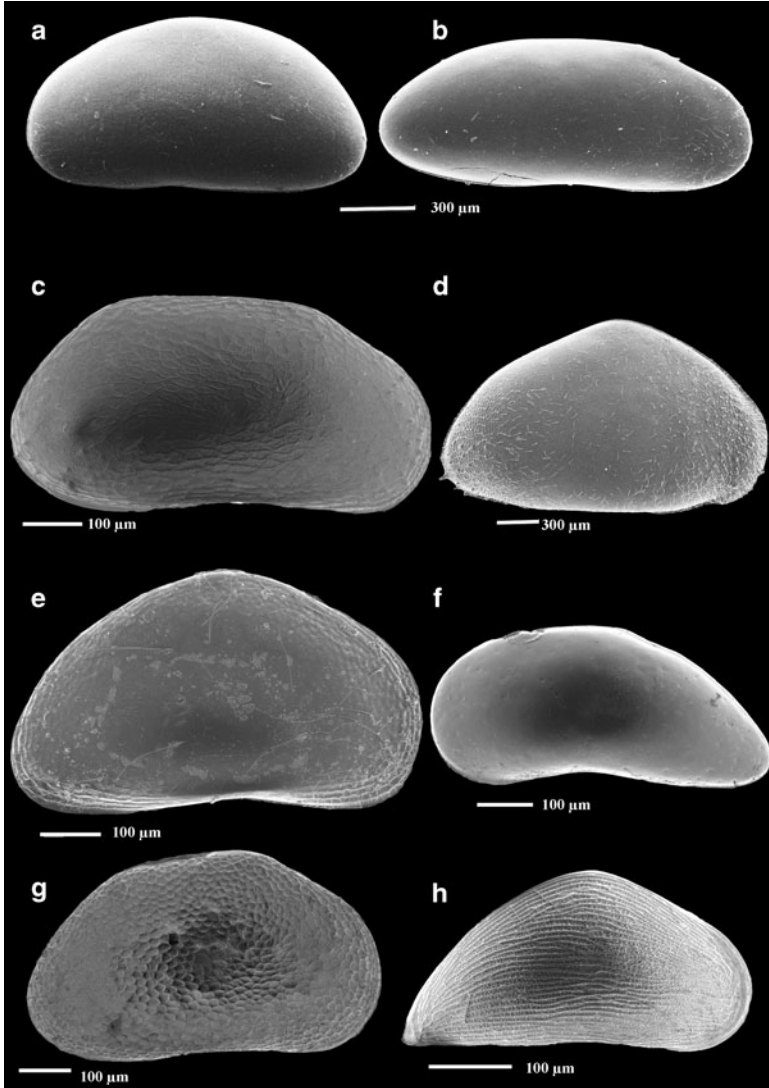
**Fig. 9** SEM: (a) *Meridiescandona lucerna* Karanovic 2003c; (b) *Gomphodella martensi* Karanovic 2009; (c) *Gomphodella aura* Karanovic 2009; (d) *Limnocythere scutariense* Petkovski 1961: (a) detail of the surface showing papillae; (b) lateral view of the LV from inside; (c) dorsal view; (d) dorsal view. (d) Photo: D. Keyser

the epidermis of the calcified outer lamella. The color may vanish with prolonged preservation, e.g., in alcohol.

In some species, it is very difficult to distinguish between male and female carapace shape, but in others this is very easy. In some Cypridoidea, males are obviously larger than females and have an enlarged posterior chamber to accommodate a copulatory organ, while females are small and have quite a different shape. In some freshwater Cytheroidea, it is also very easy to distinguish males from females (Fig. 13a, b). In some lineages, females are much more robust, because of the brooding chamber in the posterior part of the body, where they keep eggs and early instars. Even if the brooding chamber does not exist, there is a clear difference between male and female carapace (Fig. 13c–f).

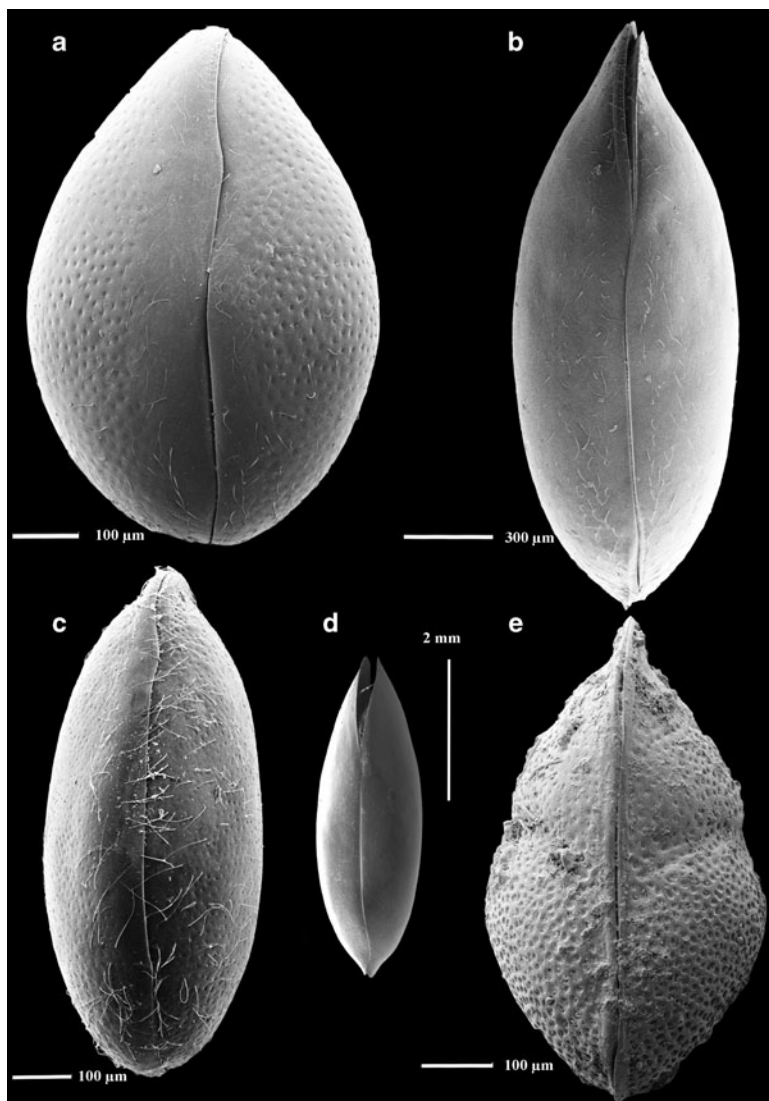
## 2.2 Body Segmentation

The usual division of an arthropod body, into head (cephalon), thorax, and abdomen, is not clearly recognizable in ostracods. Nevertheless, some authors (e.g., Tsukagoshi and Parker 2000) believe that Podocopid ostracods have a maximum



**Fig. 10** SEM: (a) *Ilyodromus* sp.; (b) *Stenocypris major* (Baird 1859b); (c) *Meridiescandona facies* Karanovic 2003c; (d) *Cypris pubera* Müller 1776; (e) *Humphreyscandona fovea* Karanovic and Marmonier 2003; (f) *Origocandona inanitas* Karanovic 2005b; (g) *Humphreyscandona waldockae* Karanovic and Marmonier 2003; (h) *Pilbaracandona eberhardi* Karanovic and Marmonier 2003; (a) LV, outside view; (b, c, d, e, g, h) RV, outside view; (f) LV, outside view. (a, b, d) Photos: D. Keyser

of 11 trunk segments (thorax and abdomen). This is based on the observation of body segmentation in eight podocopine families (one belonging to Bairdocopina and seven to Cytherocopina). Among these families a maximum number of body segments have been found in the, presumably, most primitive of the examined lineages (Tsukagoshi



**Fig. 11** SEM: (a) *Cypridopsis vidua* (Müller 1776), (b) *Trajancypris* sp.; (c) *Pseudocandona* sp.; (d) *Repandocypris austinensis* Halse and McRae 2004 (e) *Gomphocythere* sp.: dorsal views. (a, b, c, e) Photos: D. Keyser; (d) Photo: S. Halse

and Parker 2000), namely in the family Leptocytheridae. The number of trunk segments becomes less in more derived taxa. The same number (11) of trunk segments occurs in Platycopida (Schulz 1976). The supposed segmentation of the trunk region in all these taxa is sometimes marked by cuticular folds and/or assemblages of spines and setae (Fig. 14). It is also believed that in these lineages copulatory appendages in females are derived from segments associated with the fifth thoracic region, while those of the males with the tenth one. On the other hand, Matzke-Karasch and Martens