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ORIGINAL PAPER

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The osmoregulatory capacity of the Ostracoda

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Abstract All ostracods that inhabit inland waters are osmoregulators. Freshwater ostracods must be hyperosmotic regulators while ostracods that live in hyperhaline water are hypoosmotic regulators. Some euryhaline species are hypoosmotic regulators in salinities above $8\,g \cdot l^{-1}$ and hyperosmotic below. Hyperosmotic regulation in ostracods is partly dependent on salt consumed in the food but hypoosmotic regulation is dependent on the excretion of salt brought about by special cells located on the inside of the carapace.

Key words Osmoregulation · Ostracoda · Carapace · Ion transporting cells

Introduction

The Ostracoda is an ancient and distinctive sub-class of crustaceans that first appeared in the Cambrian period and had radiated widely by the Ordovician (Maddocks 1982). Nearly 3000 living and almost ten times as many extinct species have been described. Maddocks divides the ostracods into six orders of which three, the Myodocopida, the Platycopida and the Podocopida are extant. The majority of species are marine or freshwater but some live in highly mineralized continental water bodies. Freshwater, hypersaline and even a few terrestrial species are found only in the Podocopida but they have developed independently in three different families, the Cyprididae, the Cytheridae and the Darwinulidae (Abele 1982).

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The present study focusses on their salinity tolerance and on the morphology and physiology of their osmoregulatory organs. It forms part of a more extensive study covering various aspects of the osmoregulatory biology of the Ostracoda and summarizes many earlier papers in Russian (Aladin 1983a, b, 1984a, b, 1985, 1986a, b, c, 1987a, b, c, 1988a, b, c, 1989a, b, c; Aladin and Shornikov 1986a, b) as well as more readily available works (Tones 1983 and other papers).

Materials and methods

Animals and water used were collected from the Barents, White, Baltic, Black, Azov and Japanese seas and from the large salt lakes: the Caspian and Aral Seas. Freshwater samples and freshwater species were collected from lakes near St Petersburg and Moscow and from the Lithuanian, Ukrainian, Azerbaijanian, Kazakh and Uzbek Republics. Some Ostracoda were raised in the laboratory from resting eggs. Dried muds containing their eggs were collected in Canada, USA, Peru, Bolivia, Argentina, Italy, India, Seychelles and Australia. Freezing point depressions (Δ) of ostracod haemolymphs were measured by microcryoscopical methods. For morphological studies of osmoregulatory organs, both scanning and transmission electron micrographs were used. All the details of microcryoscopy and microscopy are given in Aladin (1983a).

Results and Discussion

Animals of 109 species from 20 families were studied by microcryoscopical methods. The results are summarised in Fig. 1.

The Ostracoda include both osmoconformers and osmoregulators. The osmoconformers can be divided into three groups. Osmoconformers-I are stenohaline in the salinity range from about $30\,g \cdot l^{-1}$ up to $36\,g \cdot l^{-1}$. In the present study 21 species of osmoconformers-I were examined: *Vargula norvegica*, *Euphilomedes nipponica*, *Broecia borealis*, *Neonesidea mutsuensis*, *Cythere uranipponica*, *Cytherois* sp. A, *Paradoxostoma ussuricum*, *Paradoxostoma brunneum*, *Paradoxostoma*

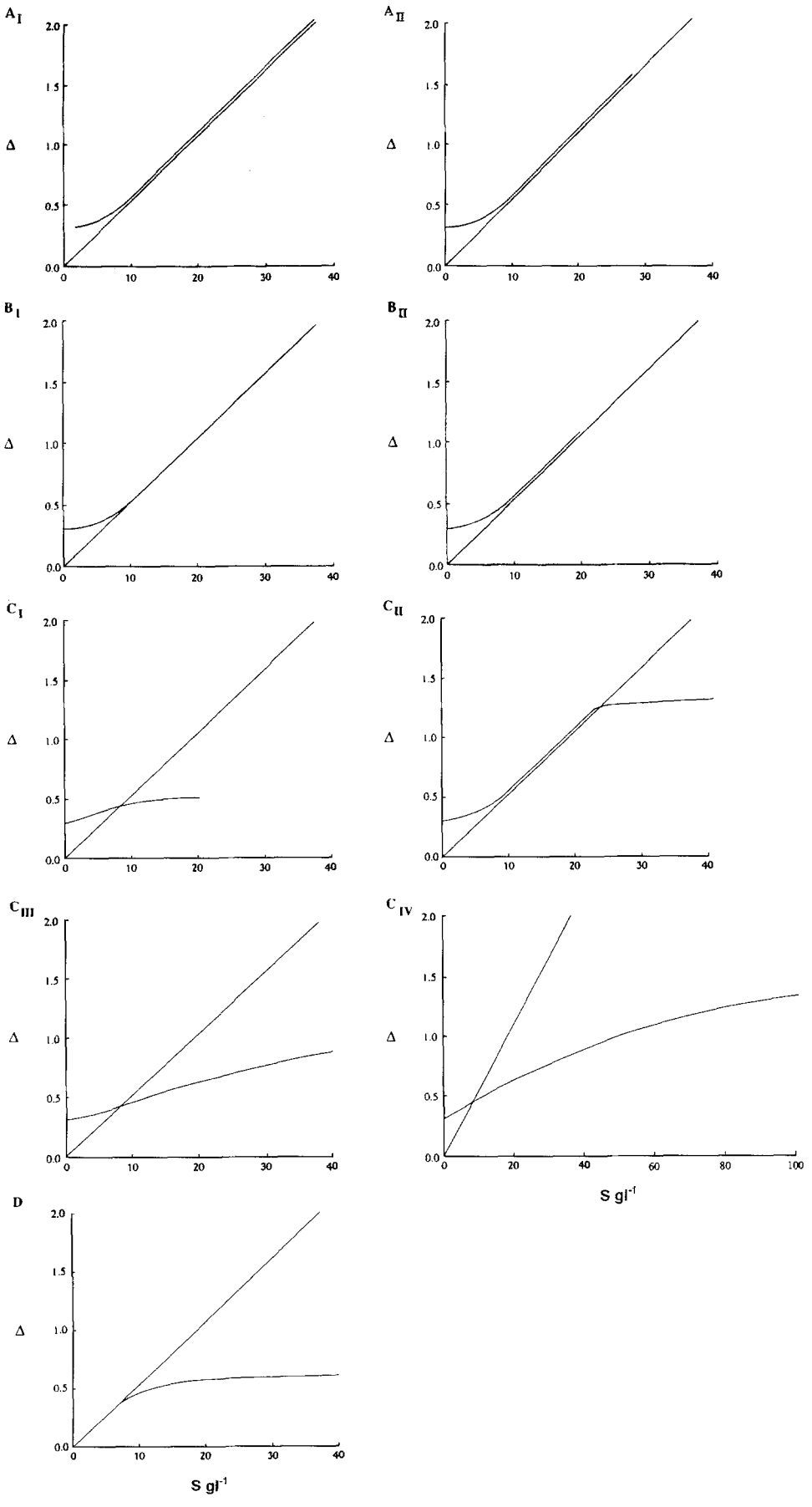

Fig. 1 Types of osmoconformation and osmoregulation in Ostracoda: *vertical axis* – freezing point depression of haemolymph °C; *horizontal axis* – salinity of water, gl^{-1}: **AI** Confohyperosmotic-I, widely euryhaline marine Ostracoda: *Cytherois cepa, Leptocythere pellucida, Leptocythere lacertosa, Leptocythere histriana, Tanella supralittoralis, Semicytherura nigrescens, Loxoconcha impressa, Loxoconcha aestuarii, Loxoconcha elliptica, Hirschmannia viridis, Spinileberis pulchra, Xestoleberis aurantia*; **AII** Confohyperosmotics-II, brackish water Ostracoda of marine origin: *Cyprideis torosa torosa, Tanella* sp. *A*; **BI** Hyperosmotics-I, fresh water Ostracoda: *Candona marchica, Candona schweyeri, Dolerocypris fasciata, Cyclocypris ovum*; **BII** Hyperosmotics-II (or secondary confohyperosmotics-I), brackish water Ostracoda of fresh water origin: *Limnocythere inopinata, Limnocythere stationis, Darwinula stevensoni, Cypris decaryi, Cyprinotus edwardi, Heterocypris* (*Cyprinotus*) *salina, Heterocypris incongruens, Alboa worooa, Cyclocypris laevis, Cypridopsis aculeata, Cypridopsis vidua, Plesiocypridopsis newtoni*; **CI** Amphiosmotics-I, some Caspian and Aral brackish water Ostracoda of fresh water origin: *Leptocythere bacuana, Amnicythere cymbula, Galolymnocythere aralensis, Loxoconcha lepida, Cytheromorpha fuscata, Tyrrhenocythere amnicola donetziensis*; **CII** Amphiosmotics-II, some Australian euryhaline Ostracoda of fresh water origin: *Diacypris spinosa, Mytilocypris praenuncia*; **CIII** Amphiosmotics-III, terrestrial and aquatic euryhaline Ostracoda of fresh water origin: *Terrestricythere ivanovae, Terrestricythere pratensis, Potamocypris steueri*; **CIV** Amphiosmotics-IV, widely euryhaline Ostracoda of fresh water origin: *Cyprideis torosa amphiosmotica, Eucypris inflata*; **D** Hypoosmotics, secondary marine of fresh water origin: *Aglaiocypris complanata, Propontocypris maculata*

sp. A, *Paradoxostoma* sp. B, *Paracytheridea paulii*, *Semicytherura* sp. A, *Semicytherura* sp. B, *Hemicytherura* sp. A, *Loxoconcha trada*, *Loxoconcha* sp. A, *Hirschmannia viridis*, *Xestoleberis* sp. A, *Pontocythere japonica*, *Callistocythere haymenensis*, *Coquimba* sp. A; Osmoconformers-II are typically marine Ostracoda living in a broader salinity range from about 20 $g \cdot l^{-1}$ up to 40 $g \cdot l^{-1}$. Twenty-two species of osmoconformers-II were examined: *Philomedes brenda*, *Discoconchoecia elegans*, *Sclerochilus* (*Praesclerochilus*) *verecundus*, *Paradoxostoma* sp. C, *Cytheroma karadaginis*, *Leptocythere fabaeformis*, *Howeina camptocytheroidea*, *Hemicytherura kajiyamai*, *Loxoconcha uranouchensis*, *Loxoconcha harimensis*, *Loxoconcha* sp. B, *Cytheromorpha acupunctata*, *Cytheromorpha japonica*, *Spinileberis quadriaculeata*, *Hemicythere emerginata*, *Urocythereis margaritifera*, *Robustaurilla assimilis*, *Pontocythere subjaponica*, *Xestoleberis hanai*, *Coquimba* sp. B, *Doratocythere tomokoae*, *Aspidoconcha* sp. A; Osmoconformers-III are euryhaline marine Ostracoda living in salinities from about 8 $g \cdot l^{-1}$ up to 40 $g \cdot l^{-1}$. In the present study 21 species of osmoconformers-III were examined: *Jonesia simplex*, *Paradoxostoma intermedium*, *Paradoxostoma* sp. D, *Acetobulastoma hyperboreum hyperboreum*, *Cythere lutea*, *Cytherura similis*, *Simecytherura undata*, *Hemicytherura bulgarica*, *Microcytherura nigrescens*, *Loxoconcha fragilis*, *Loxoconcha pontica*, *Loxoconcha bulgarica*, *Loxoconcha* sp. C, *Bicornucythere bisanensis*, *Carinocythereis rubra*, *Hemicythere villosa*, *Cytheridea papillosa*, *Pontocythere bacescoi*, *Xestoleberis depressa*, *Xestoleberis decipiens*, *Callistocythere* sp. A. The wider salinity ranges of these species must be associated with the development of cell volume regulatory mechanisms probably of the kind described by Gilles, Florkin and Schoffeniels [rs: Gilles (1979); Beyenbach (1990)].

Several varieties of osmoregulators can be recognised including confohyperosmotics (Fig. 1AI, AII), hyperosmotics (Fig. 1BI, BII), amphiosmotics (Fig. 1CI, CII, CIII, CIV) and hypoosmotics (Fig. 1D). Confohyperosmotics are primitive osmoregulators which combine osmoconformity at high salinities with hyperosmotic regulation at low salinities. It is possible to distinguish two levels among the confohyperosmotics (Fig. 1AI, AII): confohyperosmotics-I (Fig. 1AI) are widely euryhaline marine Ostracoda living in the salinity range from about 2 $g \cdot l^{-1}$ to 50 $g \cdot l^{-1}$, while confohyperosmotics AII extend into fresh water. Twelve species of confohyperosmotics-I were examined: *Cytherois cepa*, *Leptocythere pellucida*, *Leptocythere lacertosa*, *Leptocythere histriana*, *Tanella supralittoralis*, *Semicytherura nigrescens*, *Loxoconcha impressa*, *Loxoconcha aestuarii*, *Loxoconcha elliptica*, *Hirschmannia viridis*, *Spinileberis pulchra*, *Xestoleberis aurantia*. Confohyperosmotics-II (Fig. 1AII) are brackishwater Ostracoda of marine origin. They are isoosmotic at salinities from 30 $g \cdot l^{-1}$ down to 8 $g \cdot l^{-1}$, occasionally only to 14 $g \cdot l^{-1}$, but are hyperosmotic at lower salinities. In the present study two species of confohyperosmotics-II were examined: *Cyprideis torosa torosa* and *Tanella* sp. A.

Two levels of hyperosmotic regulation can be distinguished (Fig. 1BI, BII) : hyperosmotics-I (Fig. 1BI) are typical freshwater Ostracoda which are hyperosmotic to the external medium in the whole range from fresh water up to 8 $g \cdot l^{-1}$. In the present study four species of hyperosmotics-I were examined: *Candona marchica*, *Candona schweyeri*, *Dolerocypris fasciata*, *Cyclocypris ovum*. Hyperosomotics-II (Fig. 1BII), or, as they should be named, secondary confohyperosmotics-I, are primarily freshwater Ostracoda which can tolerate saline conditions or brackish water Ostracoda of freshwater origin. They are isoosmotic at salinities from 8 $g \cdot l^{-1}$ up to 14 $g \cdot l^{-1}$, occasionally to 20 $g \cdot l^{-1}$. At lower salinities they are hyperosmotic to the external medium. Twelve species of hyperosmotics-II have been examined: *Limnocythere inopinata*, *Limnocythere stationis*, *Darwinula stevensoni*, *Cypris decaryi*, *Cyprinotus edwardi*, *Heterocypris* (*Cyprinotus*) *salina*, *Heterocypris incongruens*, *Alboa worooa*, *Cyclocypris laevis*, *Plesiocypridopsis* (*Cypridopsis*) *aculeata*, *Cypridopsis vidua*, *Plesiocypridopsis newtoni*.

The amphiosmotics which combine hyperosmotic regulation at low salinities with hypoosmotic regulation at high salinities, can be divided into four groups: amphiosmotics-I (Fig. 1CI) are Caspian and Aral brackish water Ostracoda of freshwater origin. Their haemolymph is hyperosmotic in fresh water at salinities up to 8 $g \cdot l^{-1}$ but is hypoosmotic at salinities from 8 $g \cdot l^{-1}$ up to 14–16 $g \cdot l^{-1}$ and in a few species to 20 $g \cdot l^{-1}$. Six species of amphiosmotics-I were examined: *Leptocythere bacuana*, *Amnicythere cymbula*, *Galolimnocythere aralensis*, *Loxoconcha lepida*, *Cytheromorpha fuscata*, *Tyrrhenocythere amnicola donetziensis*. Amphiosmotics-II (Fig. 1CII) include some Australian euryhaline Ostracoda of freshwater origin. Their haemolymph is hyperosmotic from fresh water up to 8 $g \cdot l^{-1}$, isoosmotic from 8 $g \cdot l^{-1}$ up to 20–24 $g \cdot l^{-1}$, and hypoosmotic from 20–24 $g \cdot l^{-1}$ up to about 50 $g \cdot l^{-1}$. Two species of amphiosmotics-II were examined: *Diacypris spinosa* and *Mytilocypris praenuncia*. Amphiosmotics-III (Fig. 1CIII) are terrestrial and aquatic euryhaline species of freshwater origin which are hyperosmotic from fresh water up to 8 $g \cdot l^{-1}$ and hypoosmotic from 8 $g \cdot l^{-1}$ up to 50 $g \cdot l^{-1}$. Three species of amphiosmotics-III were examined: *Terrestricythere ivanovae*, *Terrestricythere pratensis*, *Potamocypris steueri*. Amphiosmotics-IV (Fig. 1CIV) are the most euryhaline Ostracoda of freshwater origin. Most of these can survive in salinities up to 100 $g \cdot l^{-1}$ and some of them up to 200 $g \cdot l^{-1}$ or more. Two species of amphiosmotics-IV were examined: *Cyprideis torosa amphiosmotica* and *Eucypris inflata*. These Ostracods are the most effective regulators ensuring a very wide euryhalinity while simultaneously keeping osmotic homeostasis.

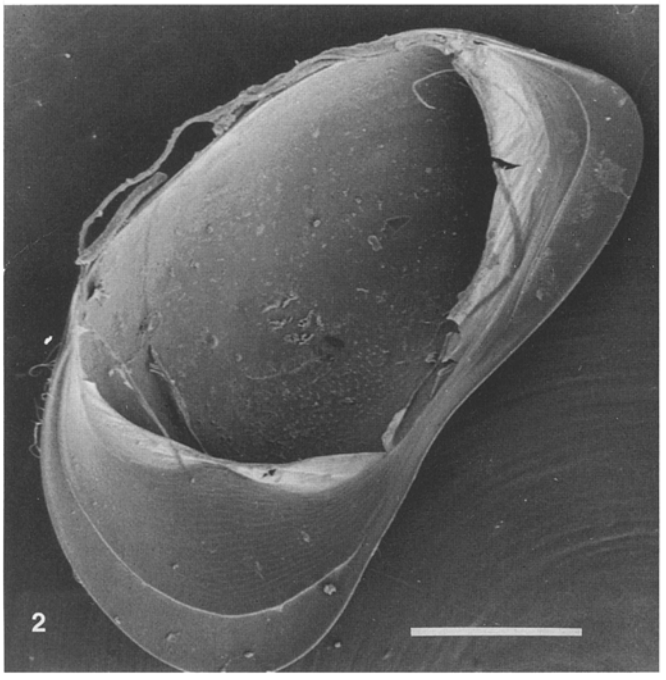

Fig. 2 Right carapace of *Mytilocypris praenuncia* seen from the inside. Raised in the laboratory in slightly brackish water, less than 4 $g \cdot l^{-1}$. The left carapace and the body of the organism removed in order to show the non-calcified zone of the inner carapace layer. Scale = 500 μm

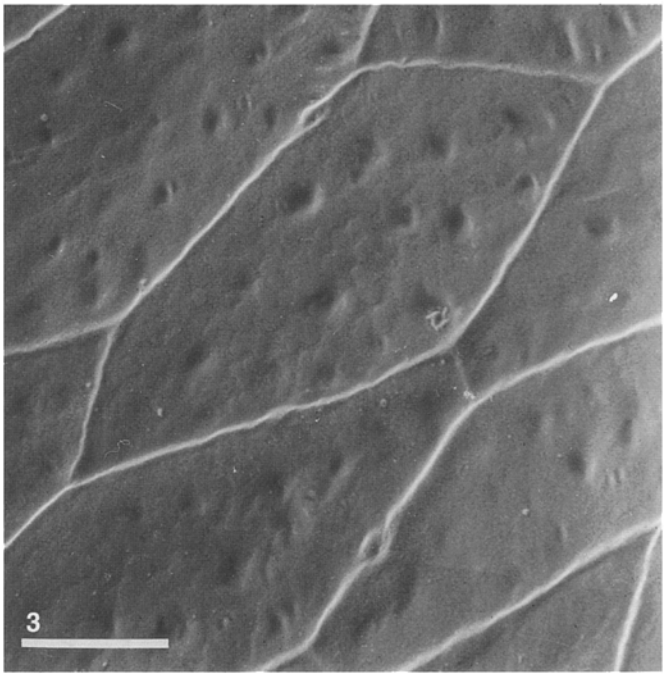

Fig. 3 High magnification of the anterior part of the non-calcified zone of the inner carapace layer of the same individual as in Fig. 2. Cells show clear borders and numerous depressions in the cuticle. Scale = 10 μm

Among the hypoosmotic regulators it is possible to recognise only one level (Fig. 1D). These are euryhaline secondarily marine ostracods of freshwater origin, which are hypoosmotic to the external medium in the whole range from 8 $g \cdot l^{-1}$ up to about 50 $g \cdot l^{-1}$. Two species of hypoosmotics were examined: *Aglaiocypris complanata* and *Propontocypris maculata*. *Tigriopus californicus* probably belongs here (McDonough and Stiffler 1981). Hypoosmotic regulators have a lower density and lower sinking rates than similar isoosmotic forms. Hypoosmotic cladocerans such as *Podon* and *Evadne* are usually found near the top of the water column (Potts and Durning 1980). Marine ostracods have diverse sinking rates [discussion in Gooday and Maguileosky (1975)] but whether osmotic regulation is a factor remains to the confirmed.

Hyperosmotic regulation in adult ostracods may be determined partly by the amount of salts consumed with the food (Belyaev 1950; Aladin 1984b), probably assisted by reabsorption of salts in the antennal glands. Hyperosmotic regulation in embryos is brought about by the absorption of salts by special cells located in the non-calcified zone of the inner shell layer (Aladin 1988a). In addition, the egg will contain salt reserves in the yolk. After leaving the egg the young organism can feed and after the first postembryonic moult the mitochondria-rich cells on the inner shell disappear in freshwater ostracods, although they survive in euryhaline species (Aladin 1988a). However, their small size and correspondingly unfavourable surface-to-volume ratio must result in a high rate of salt loss in fresh water, which would seem to require some active uptake in compensation. Direct experiments are lacking but small marine copepods may exchange the equivalent of all their body sodium every 3 min (Ballaglia and Bryan 1964), while even freshwater cladocerans still exchange 15–30% of their total sodium every hour (Potts and Fryer 1979). Unless the permeability of ostracods to sodium ions is markedly lower than in other small crustaceans some form of active uptake seems essential. Permeable areas of intersegmental membranes have been identified in copepods (McDonough and Stiffler 1981). These are likely sites of salt uptake but mitochondria-rich cells have not been described in freshwater copepods.

Hypoosmotic regulation in ostracods, both in adults and embryos, is brought about mainly by the excretion of salts by mitochondria-rich cells located in the non-calcified zone of the inner shell layer (Aladin 1983a, 1984a, 1987a, b, 1988a, b, c, 1989c). The full mechanism of salt excretion has not been described but all other hypoosmotic regulators so far examined, including fishes, copepods (Farmer 1980) and branchiopods (Croghan 1958a), excrete chloride ions, the negative potential produced maintaining the low concentration of the sodium in the plasma. Similarly, water balance in other hypoosmotic regulators is maintained by drinking the medium and excreting the salt, as first

demonstrated in fishes by Smith (1930) in branchiopods by Croghan (1958b) and in copepods by Farmer (1980).

The external morphology of ostracod osmoregulatory cells depends on the osmotic gradient between the haemolymph and the surrounding water. For example, in the Australian euryhaline species *Mytilocypris praenuncia* it is possible to recognise four different types of cells. When *Mytilocypris* was raised in the laboratory in fresh to brackish water of a salinity less than 4 $g \cdot l^{-1}$, the cells had clear borders and there were numerous holes or depressions in the cuticle (Figs. 2, 3). In these salinities *M. praenuncia* is capable of strong hyperosmotic regulation and the osmotic gradient between haemolymph and surrounding water is high. In salinities ranging from 4 to 8 $g \cdot l^{-1}$, when the osmotic gradient between the haemolymph and surrounding water is low, the cells had clear borders but lacked the holes or depressions in the cuticle (Fig. 4). When the ostracods were raised in the salinity range from 8–12 $g \cdot l^{-1}$ to 20–24 $g \cdot l^{-1}$ it was impossible to distinguish either the holes in the cuticle or even the borders of the cells (Fig. 5). In this salinity range *M. praenuncia* is unable to regulate and there is no osmotic gradient between haemolymph and surrounding water (Fig. 1CII). When

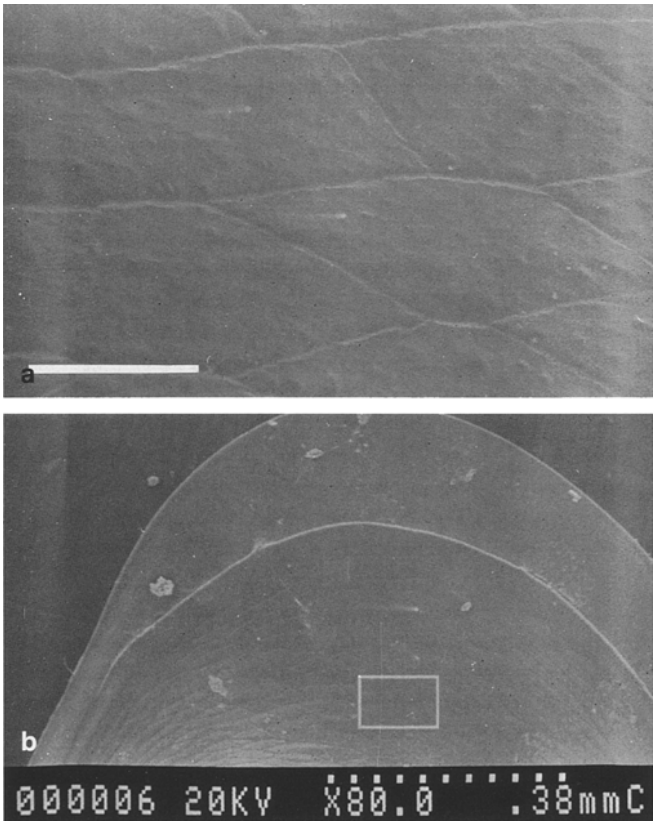

Fig. 4a, b General view of the anterior (**a**) and the posterior (**b**) of the non-calcified zone of the inner carapace layer of the *Mytilocypris praenuncia*. Raised in the laboratory at a salinity of 4–8 $g \cdot l^{-1}$. Cells have clear borders but lack the depressions visible in Fig. 3. Scale = 20 μm

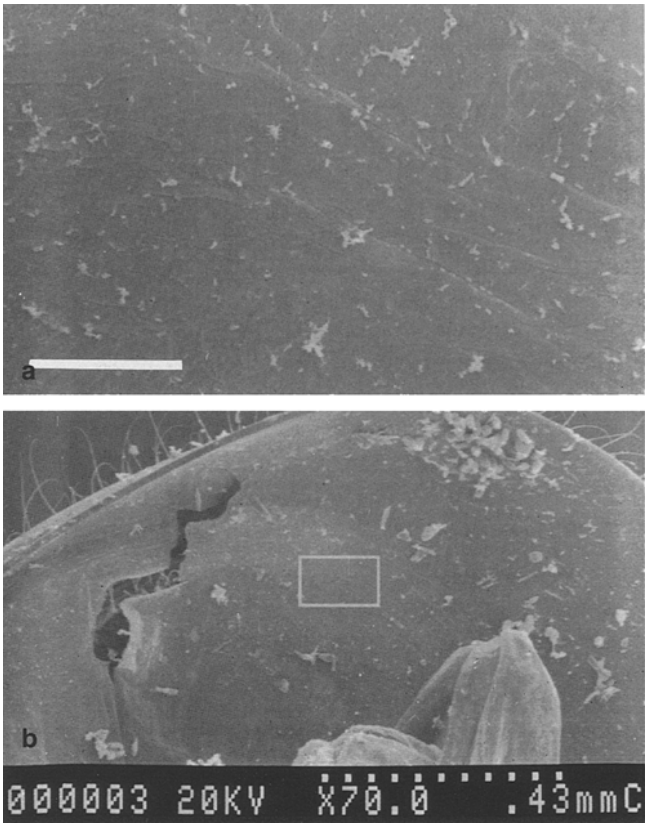

Fig. 5a, b General view of the anterior (**a**) and the posterior (**b**) of the non-calcified zone of the inner carapace layer of *Mytilocypris praenuncia* raised at a salinity of 8–24 $g \cdot l^{-1}$. No depressions visible in cuticle. Scale = 20 μm

M. praenuncia was raised in salinities from 20–34 $g \cdot l^{-1}$ to 44–48 $g \cdot l^{-1}$ the cells again had clear borders but lacked holes or depressions in the cuticle. In this range new features appeared: these structures were called "caplike structures" and are probably salt glands (Fig. 6). In the range from 20–48 $g \cdot l^{-1}$ *M. praenuncia* is a strong hypoosmotic regulator and the osmotic gradient is high.

The ultrastructures of these cells in the non-calcified zone of the inner carapace layer are very much alike. All have a dense cytoplasm with numerous mitochondria distributed throughout a lacunar system. The cuticle of the non-calcified zone of the inner shell layer is characterized by a high permeability to ions, in contrast to the other parts of the organism (Aladin 1983a, 1984a, 1987a, 1988a, 1989c). The ultrastructure of these cells in the podocopid Ostracoda has recently been carefully studied by Keyser (1990). Figure 7 may be compared with those of the neck organ of marine Cladocera and the nauplii of *Artemia salina* (Hootman and Conte 1975; Khlebovich and Aladin 1976; Potts and Durning 1980; Aladin 1982; 1991; Maurice and Goffenet 1982, 1983, 1990; Halcrow 1982). The caplike structure is evidently a salt gland that excretes salts from haemolymph to the medium.

Fig. 6 High magnification of a caplike structure. Cells of caplike structure have clear borders and numerous depression in cuticle. A cuticular ring is visible around the cap. Scale = 20 μm

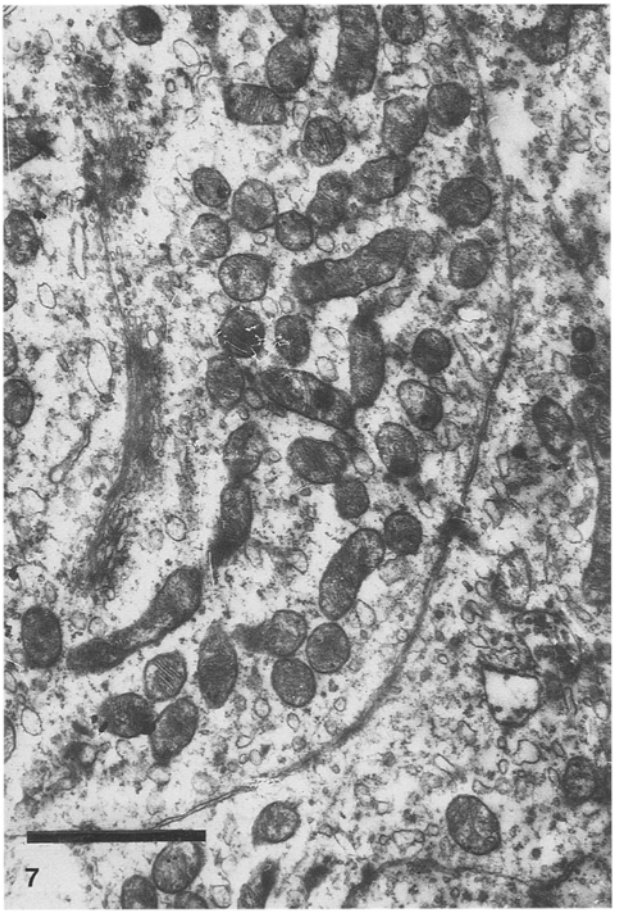

Fig. 7 The basal zone of ion-transporting cells of the caplike structure of *Mytilocypris praenuncia*. Numerous mitochondria distributed through a lacunar system. On the left side is a Golgi complex. Scale = 4.0 μm

It is important to emphasise that all changes in external morphology of these cells, including the appearance or disappearance of the caplike structures, only takes place during moulting (Aladin 1987c, 1988a, 1989c). Thus, in the ostracod the physiological changes from one to another level of osmoregulation – hyperosmotic, amphiosmotic, or hypoosmotic – can only be morphologically completed after a moult. Of course, when under experimental conditions *Mytilocypris praenuncia* were transferred from one salinity to another they reached and maintained new equilibria in a few hours, although no morphological changes were visible externally.

During moulting the osmotic concentration of the haemolymph temporarily decreases or increases depending on the medium. In fresh or slightly brackish water, the osmotic concentration of the haemolymph decreases in direct proportion to the volume increase at moulting (Fig. 8a), while in hypoosmotic regulators the concentration of the haemolymph increases in direct proportion to the volume increase (Fig. 8b). This suggests that fresh water or sea water are taken up to inflate the body volume without immediate ionic compensation. In osmoconformers in brackish water or sea water the osmotic concentration of the haemolymph always decreases slightly at moulting and there is no correlation with the volume increase. After moulting the osmotic concentration of the haemolymph quickly returns to the previous level. The time taken to reach equilibrium depends on the osmotic change in the haemolymph. The shortest time for osmotic stabilization to occur was less than 2 h and the longest 26 h.

A very complicated form of osmotic regulation was found in the ectoparasitic ostracoda *Acetabulastoma hyperboreum hyperboreum*. This ostracod is an osmoconformer-III, but only when it was not in contact with its host amphipod *Gammarus oceanicus* (Aladin 1986a). When *A. hyperboreum hyperboreum* was in contact with its host the organism was confohyperosmotic (Fig. 1A). The salinity tolerance range of this ectoparasite when in contact with *G. oceanicus* extended from less than $4\ g \cdot l^{-1}$ to more than $32\ g \cdot l^{-1}$, but without the host the range was only from 16 to $32\ g \cdot l^{-1}$. A study of the anatomy of *A. hyperboreum hyperboreum* shows that

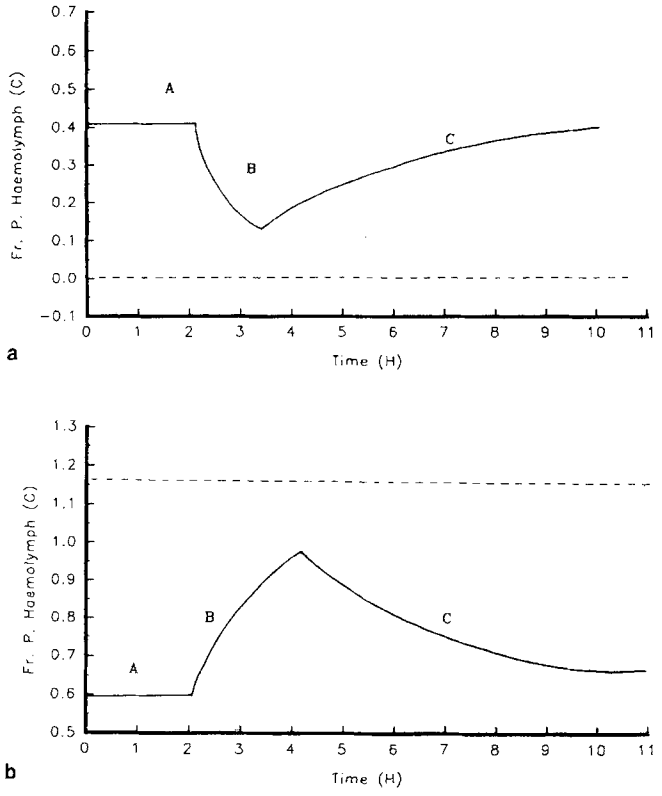

Fig. 8 a Changes of freezing point depression of haemolymph of a freshwater ostracod before, during and after moulting. *Vertical axis* – freezing point depression of haemolymph, °C; *horizontal axis*-time in hours, h. *Dotted line* – freezing point depression of surrounding fresh water. *Curve line* – freezing point depression of haemolymph before (*A*), during (*B*) and after (*C*) moulting. **b** Changes of freezing point depression of haemolymph before, during and after moulting in a hypoosmotic ostracod in brackish water or sea water. *Vertical axis* – freezing point depression of heamolymph °C; *Horizontal axis* – time in hours, – h; *Dotted line*-freezing point depression of water with a salinity 22 $g \cdot l^{-1}$. *Curve line* – freezing point depression of haemolymph before (*A*), during (*B*) and after (*C*) moulting.

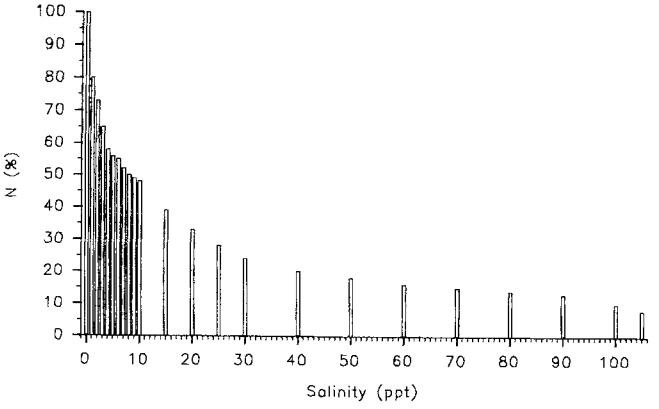

Fig. 9 Relationship between the proportion of round sieve pores and external salinity in the ostracod *Cyprideis torosa* from the Aral Sea

the haemocoelic cavity of the ectoparasite is in close contact with haemocoelic cavity of its host amphipod through three holes in the attachment disc. *G. oceanicus* belongs to confohyperosmotic-I and the haemolymph of the ectoparasite and those of the host are in equilibrium.

The outer surface of some ostracod carapaces are perforated by structures termed sieve-pores, through which innervated sensilla protrude into the medium. In the amphiosmotic *Cyprideis torosa* the structure of the sieve pores varies with the salinity of the medium, the proportion of round pores being inversely highly correlated with the salinity (Fig. 9) (Rosenfeld and Vesper 1977). Examination of Pleistocene specimens offers the opportunity to estimate palaeosalinities. This correlation of the structure of what appears to be a sense organ with salinity raises the possibility that some adjacent cells may be involved in osmotic regulation. The sensilla are surrounded by a small window of very thin cuticle (Okada 1982).

There has been a great deal of parallel evolution within the ostracods. Of the three families which have developed the ability to osmoregulate, one family, the Darwinulidae, is represented by only a single freshwater genus *Darwinula* but both the Cytheridae and Cyprididae contain a wide range of osmoregulators including confohyperosmotics, hyperosmotics (freshwater) and amphiosmotics. However, the most powerful regulators so far identified, amphiosmotics IV, are *Cyprideis torosa* and *Eucypris inflata* both belonging to the Cyprididae.

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