The Adaptations of the Foraminifera and Ostracoda to Fresh Water Colonisation

Anna Iglikowska and Joanna Pawłowska

Abstract In marine environments Ostracoda and Foraminifera have been very successful invaders. During the Phanerozoic they colonised the majority of shallow, marginal to deep water, fully marine habitats. Both groups had developed physiological adaptations which pre-adapted them to the invasion of new marine habitats. They adopted a broad range of feeding strategies and reproduction modes. The production of resting stages and brood care may also have contributed to them being efficient invaders. They are also both highly tolerant to variations in salinity. The first invasions of non-marine habitats by ostracods appear to have taken place at the turn of the Devonian and Carboniferous. It is estimated that there had been between 9 and 12 independent invasions of fresh waters by the ostracods. In contrast Foraminifera are typically marine organisms, and only a few species of agglutinated and organic-walled Foraminifera are to be found in brackish and freshwater environments. Agglutinated species build their test using ambient components but are not commonly regarded as calcifying organisms. An impact of salinity on foraminiferal calcification has been observed in several studies. It seems that Foraminifera are incapable of constructing a fully calcified test in low salinity regimes; they use sea water not only as a source of ions to construct shell, but also as a biomineralisation solution. Thus, the success of ostracods in invading freshwater habitats can be attributed to their development of a more effective mechanism of calcification in low mineralisation waters. The core question of this study is to examine possible causes for the differences in success between the two taxa.

Keywords Foraminifera · Ostracoda · Fresh water colonisation · Physiological adaptations · Calcification

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1 Introduction

This is a review paper focused on the invasion of non-marine habitats by Foraminifera and Ostracoda. The paper reviews the comprehensive paleontological and modern data and integrates these with the knowledge of physiological adaptations, which have enabled them to colonise of freshwater habitats. Both these groups have undergone spectacular adaptive radiations and have invaded a wide variety of marine habitats. In the Early Carboniferous ostracods and Foraminifera thrived, and both groups faced an opportunity to colonise freshwater habitats. While the Ostracoda succeeded, the Foraminifera have remained an almost exclusively marine group. The aim of this study was to elucidate what could be the crucial ability that limited the Foraminifera from successfully colonising freshwater habitats, and why ostracods were more efficient in the invasion of low salinity environments.

The earliest fossil Foraminifera appeared in the Early Cambrian, but molecular data indicate a much earlier, Neoproterozoic, origin (Pawlowski et al. 2003). The origin of the Ostracoda may be slightly younger. Evidence from molecular studies suggests that ostracods diverged from near the base of the Pancrustacea during the late Proterozoic (Regier et al. 2005; Siveter 2008; Williams et al. 2008), although the oldest unequivocal fossil record is from the mid-late Cambrian (Harvey et al. 2012).

The Foraminifera seems to be an enormously successful invader of new environments. During the Phanerozoic they colonised most shallow, marginal to deep water, fully marine habitats, and diversified to exploit a wide variety of life modes (Hottinger 1982; Goldstein 2003). Some attained relatively gigantic size, such as the extinct *Lepidocyclina elephantina* at 14 cm (Grell 1973). The mean size of modern Foraminifera ranges from 0.1 to 0.5 mm, however, some species may reach up to several centimetres (Pawlowski 2009). Despite their unicellular level of organization foraminiferans perform the same range of fundamental functions as metazoans (Goldstein 2003). There are two characteristic features that help to distinguish the Foraminifera from other protists. First, all possess granuloreticulopodia (pseudopodia) which are used for motion, feeding, constructing a test, protection and for some aspects of reproduction. Second, almost all Foraminifera have a test which encases the body, separating it from the surrounding environment. There are three different types of tests: organic, agglutinated (constructed from cemented particles) and mineralised, composed of calcium carbonate or, in rare cases, of silica (Goldstein 2003; Pawlowski et al. 2013).

Ostracods are also efficient colonisers of new habitats. The wide geographical distribution and their almost simultaneous appearance on several palaeocontinents suggest rapid dispersal and wide environmental tolerance (Williams et al. 2008). By the mid Silurian originally benthic myodocopes had started colonising the pelagic (Siveter et al. 1991; Vannier and Abe 1992; Perrier et al. 2011) and by the turn of the Devonian and Carboniferous they had invaded inland freshwater habitats and the deep ocean (Williams et al. 2006; Bennet 2008). Martens et al. (2008) estimated that ostracods had undergone between 9 and 12 independent incursions into fresh water from the marine environment.

As crustacean metazoans, ostracods have specialised tissues, and organ systems. They are typically larger than recent foraminiferans, mostly in the 0.3–5 mm range, although some marine species exceed 30 mm in length. The most distinctive feature of ostracods is their calcified carapace comprising paired, dorsally articulated valves (Meisch 2000). Both groups, Ostracoda and Foraminifera, have a marine origin, have a test or shell saturated with calcium carbonate, and inhabit aquatic environments. Both have undergone spectacular adaptive radiation and colonised wide variety of marine habitats. In the Early Carboniferous ostracods and foraminiferans thrived. It is likely that during peak marine transgression both groups had opportunities to colonise freshwater, inland habitats. Ostracods succeeded and foraminiferans seemed to be less fortunate, but why?

2 Evolution from the Palaeozoic to the Recent

Traditionally, the evolution of Foraminifera is viewed as a gradual process of change in structure and composition of the test, starting from naked, unilocular forms, via organic-walled and agglutinated forms which later became multilocular, and ending with the highly complex calcareous forms (Tappan and Loeblich 1988). Recent molecular studies (Pawlowski and Holzmann 2002; Pawlowski et al. 2003), however, revealed that there is no evidence for a progressive increase in foraminiferal test complexity. In a single highly supported clade, for example, a distinctive radiation included a wide variety of test morphotypes containing both agglutinated (Textulariida) and calcareous (Rotaliida) species. In a recent study Pawlowski et al. (2013) showed that transition from organic to agglutinated walls occurred several times, and the change in the nature of test wall was dependent on environmental conditions. According to these authors a calcareous wall appeared at least five times independently, and each time a different type of calcareous test was developed. It appears that some species may have lost their calcified test secondarily, for instance, as an adaptation to the lower salinity regime.

The first fossils of Foraminifera are agglutinated Textulariina and appeared during the Cambrian (McIlroy et al. 2001; Boudagher-Fadel 2008). They remained as a dominant group until the Silurian when the larger, calcareous and more complex Fusulinina appeared, becoming abundant in the late Palaeozoic. In the Silurian, apart from textulariines and fusulinines, a new group of Foraminifera with the test wall consisting of calcite crystals evolved—the Lagenida. Less significant ecologically in the Palaeozoic were the Miliolida (having porcelaneous test) and early Involutinina (with an aragonitic wall). More advanced calcareous tests, formed by biomineralisation of an inner tectinous lining, may have appeared by the Silurian, but did not become widespread until the late Devonian (McIlroy et al. 2001).

The Palaeozoic seems to be a period of fusulinines. They underwent rapid evolutionary radiation from tiny, simple organisms to large, complex and highly specialised forms in diverse lineages (eight known families) (Boudagher-Fadel 2008). Fusilinines became ubiquitous and spread to most warm, shallow waters from the Mississippian (≈325 Myr, Carboniferous) to the end of the Permian, when they may have become extinct (Payne et al. 2012), although, there is an alternative hypothesis (Leven 2010) that the primitive fusulinids, which gave rise to the superorder Fusulinoida, did not go extinct, but survived through transformation into more progressive taxa.

The success of Fusulinida in the Palaeozoic most likely was a result of their acquisition of a calcareous test. This test was primitively homogeneously microgranular and consisted of low-magnesium calcite. In advanced forms the test was larger (up to 15 cm) and had two or more differentiated layers. Fusulinines are among the largest single-celled protists preserved in fossil deposits, and provide perhaps the best-known case of evolution towards large size (Newell 1949; Payne et al. 2009, 2012). They are usually recorded in limestone sediments (Gallagher 1998; Leven and Gorgij 2011), and thus, probably had easy access to calcium-rich sea water as a resource for test construction.

In the Palaeozoic a variety of other ostracod-like groups of arthropods co-occurred with ostracods. Bradoriida, Phosphatocopida and Leperditicopida, are all characterised by having a calcified, bivalved carapace, but their systematic position remains unclear. The oldest carapaces of ostracods (Palaeocopida) are found in the early Ordovician (Williams et al. 2008). Early myodocopes appeared in the Silurian, but because of their poorly mineralised valves the early fossil record of this group is sparse (Siveter 2008). Podocopes were common in the Palaeozoic, with hundreds of species recorded, even in the Ordovician (Siveter and Curry 1984; Siveter 2008). Most of them are known from carapaces only, but rare examples of exceptionally preserved ostracods with soft body parts are known from the Mesozoic and younger deposits (Smith 2000; Siveter 2008). It is notable that the first non-marine ostracods were Podocopes. The systematic position of Palaecopida is still under debate, but they were a common and widespread ostracod-like group in the Palaeozoic (Gray 1988). Siveter (2008) claims that soft part anatomy of *Nymphatelina gravida* is similar to that of myodocopes, and it is possible that Palaeocopida may be an artificial group. Currently their distinctive valve morphology distinguishes them from other ostracod taxa (Siveter 2008; Siveter et al. 2010).

Marine invertebrates invaded non-marine environments multiple times since the Cambrian. Most probably the first major colonisation occurred during the Devonian-Carboniferous transition. The first brackish/freshwater habitats were near-shore, marine embayments or shallow, deltaic lagoons influenced by marine transgression events (Tibert and Scott 1999; Bennett et al. 2012). The first non-marine invaders were probably highly tolerant euryhaline species, capable of thriving in marginal marine environments with varying salinity regimes.

Tibert and Scott (1999) documented the early Carboniferous ostracods and foraminiferans of Horton Bluff Formation in Maritimes Basin (Nova Scotia, Atlantic Canada). This environment was interpreted as a restricted marine embayment that turned brackish. The marginal marine bay fauna was dominated by an assemblage of euryhaline marine ostracod species *Copelandella novascotica*, *Cavellina* sp., *Geisina* sp. and opportunistic paraparchitacean ostracods (*Shemonaella scotoburdigalensis*, *S. tatei* and *Chamishaella* sp.). The coastal pond was inhabited mainly by freshwater species such as *Carbonita scalpellus* and *C. rankiniana*. Foraminifera were recorded only in the coastal marsh, and they were represented exclusively by agglutinated species of *Trochammina* sp., as the dominant species, and by *Ammobaculites* sp., *Ammotium* sp. and *Ammodiscus* sp. which were less abundant.

A similar ecological system in Nova Scotia was studied by Calder (1998). The Blue Beach Member was interpreted as a near-shore basin periodically connected to the sea. During the onset and peak of marine transgression diverse species of Fusulinina and Miliolina foraminifers were recorded in association with marginal marine ostracod species belonging to the Palaeocopida and Bairdiacea. With the gradual withdrawal of the marine influence a retreat of marine fusulinids and increasing dominance of agglutinated Textulariidae (mainly *Trochammina*, *Ammobaculites* and *Ammodiscus*) occurred. Under low salinity conditions the ostracod assemblage also changed. Marine species were replaced with euryhaline *Paraparchites* and *Cavellina*, the brackish *Geisina*, and by freshwater species of *Carbonita*.

In the Devonian to Permian deposits of the Brabant Massif in Belgium the shallow near-shore environment was inhabited by a mixed marine ostracod assemblage represented mainly by rare bairdiacean ostracods (notably *Bairdia* and *Acratia*) (Bless et al. 1988). However, because of the absence of fusulinid foraminiferans this environment was interpreted as “less open marine environment”. The brackish water setting of the deltaic system under marine incursion was inhabited by brackish *Geisina* and freshwater *Carbonita* species associated with agglutinated forms of Foraminifera (*Ammodiscus* and *Hyperammina*). Generally, the majority of Early Carboniferous fossil evidences of both, agglutinated and Fusulinida Foraminifera come from North America, Canada and Western Europe, with fewer records from Asia and Australia (Fig. 1).

In modern environments a similar pattern is observed. Hedberg (1934) recorded arenaceous (agglutinated) and calcareous Foraminifera in freshwater habitats in Venezuela. Foraminifera were collected from Lake Maracaibo which is connected with Caribbean Sea by a narrow neck, although salinity of this water body was low (≈1 ‰). In freshwater habitats Hedberg (1934) found three groups of Foraminifera: agglutinated (arenaceous) forms belonging to the Lituolidae, Trochamminidae and Textulariidae; pelagic and benthic forms (*Globigerina*, *Bulimina* and *Uvigerina*), the occurrence of these marine species was viewed as a result of transportation by tidal currents; and euryhaline species (*Rotalia beccari*, *Elphidium* sp.) with *Quinqueloculina fusca* as a dominant species. *Quinqueloculina fusca* has also been reported in Tertiary sediments together with brackish water molluscs as an associated group, and in the absence of marine fauna.

Holzmann and Pawlowski (2002) found naked forms of allogromids in Lake Geneva and two other freshwater bodies in Switzerland. Authors obtained foraminiferal DNA sequences which clustered with a clade of saccamminid Foraminifera. Holzmann and Pawlowski also examined the 19th-century collection of Eugene Penard. Five freshwater species of Penard’s *Gromia* could be distinguished according to type of agglutinated test (covered with small, siliceous particles).

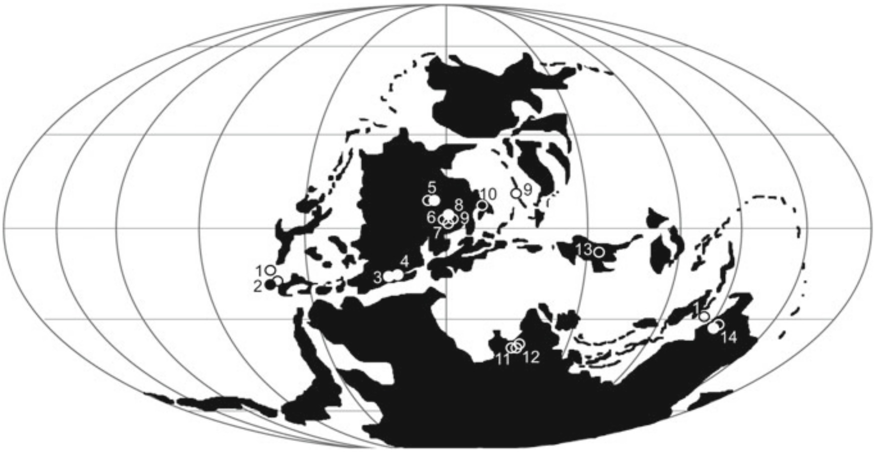

Fig. 1 Distribution of Carboniferous Foraminifera referred to in this article. The palaeogeographic map is a reconstruction of the Pennsylvanian 300 Ma modified from Ron Blakey (http://cpgeosystems.com/mollglobe.html). Numbers next to Fusulinida (open circles) and agglutinated foraminifera (dots) occurrences indicate where the record is published in the literature: 1: North America, Sahul Shelf, Payne et al. 2012. 2: Wyoming, USA, Mamet 1975. 3: Nova Scotia, Canada, Wightman et al. 1994. 4: Nova Scotia, Canada, Tibert and Scott 1999. 5: Ireland, Gallagher 1998. 6: Austria, Krainer et al. 2002. 7: France, Conil et al. 1986. 8: Italy, Krainer and Davydov 1998. 9: Austria, Italy, Slovenia, Russia (Southern Ural) Forke 2002. 10: Czech Republic, Kalvoda 2002. 11: Iran, Leven and Gorgij 2011. 12: Iran, Afghanistan, Turkmenistan, Leven 2010. 13: South China, Ke-liang 1987. 14: Northern Australia, Mamet and Belford 1968

Typically, crossing from a brackish to freshwater regime is characterised by the disappearance of Foraminifera other than organic-walled Allogromiidae (Sen Gupta 2003) or/and other agglutinated forms. Most allogromids are widespread in marine environments, but some genera have been described from freshwater or even terrestrial habitats (Meisterfeld et al. 2001; Lejzerowicz et al. 2010). The allogromid test is usually membranous or proteinaceous, which in some cases, may be covered with agglutinated foreign particles (Loeblich and Tapan 1987; Holzmann and Pawlowski 2002). In ostracods the main difference between non-marine and marine carapace is the proportion of calcium carbonate and organic components. In freshwater species the content of $CaCO_3$ is significantly lower and valves consist of mainly chitinous fibres (Keyser and Walter 2004).

Agglutinated Foraminifera are defined according to the specific structure of their test. The cement that binds the wall of the test together may be organic (e.g. Astrorhizida), calcareous (e.g. Textulariida) or of a mixed nature (e.g. Lituolida) containing organically-cemented, calcareous and microgranular types (Kaminski 2004). Agglutinated species build their test using ambient components. Many species do not select or only weakly select the grains that are incorporated into their test (Thomsen and Rasmusen 2008), but some may be strongly selective (Murray 1963). Grains used by Foraminifera are composed mainly of feldspar (70 % plagioclase and 30 % alkali orthoclase). Other grains comprise pure silica and Ca, Fe, Mg-silicates (du Châtelet et al. 2013). In comparison, Cambrian agglutinated Foraminifera consist mainly of microgranular quartz, with inclusions of feldspar, clay minerals and opaque minerals (McIlroy et al. 2001). Du Châtelet et al. (2013) observed that proportion of quartz used by Foraminifera was species dependent and detected only a single grain of calcite. In general, agglutinated Foraminifera are not commonly regarded as calcifying, although, some species (e.g. *Textularia oviedoiana*) produce a low Mg calcitic matrix comparable in composition to the needles of miliolids (Bender and Hemleben 1988).

3 Physiological Adaptations

3.1 Feeding Strategy

Ostracods exhibit a wide variety of feeding strategies. Large planktonic ostracods usually are active predators, although it is still unclear whether they catch living or/and dead prey/food items (Vannier et al. 1998). Other pelagic halocyprids probably feed on suspended material: these are likely to be microphagous feeders utilizing foraminifers, diatoms, silicoflagellates and detrital aggregates as well (Angel 1990). Other myodocopids, which are mainly benthic dwellers, are either filter-feeders (e.g. cylindroleberidinids: Cannon 1933), carnivorous scavengers (e.g. cypridinids: Cohen 1983; Vannier and Abe 1993; Vannier et al. 1998), detritus feeders (e.g. philomedids: Hartmann 1975) and predators on small invertebrates (e.g. rutidermatids: Cohen and Kornicker 1987).

Ostracods display numerous morphological adaptations for their feeding strategy. Adaptation to scavenging and predation is reflected in the morphology of their mandibles, maxillulae (4th limbs), maxillae (5th limbs), and furcal lamellae. Powerful furca are used as a gripping tool to hold moving prey or to anchor onto a dead prey item. The feeding appendages are involved in capturing and physical breakdown of food, passing food pieces into the mouth, tearing off lumps of prey soft body and biting (Vannier et al. 1998). Planktonic halocyprids use their furca for selective rejection of food items from within the carapace (Lochhead 1968; Vannier et al. 1998). Filter-feeding species developed large vibratory plates that generate continuous flow fields across the body that serve a respiratory as well as feeding function. Mandibles of freshwater podocopids consist of masticatory processes with strong teeth and well developed vibratory plates. Masticatory processes associated with the lower lip form so-called food-rakes which assist the mandibles in breaking down food and passing it into the mouth (Meisch 2000). The parasitic form *Sheina orri* (Cypridinidae) uses its mandibular and maxillar claws to anchor itself to the gill tissues of its shark host (Bennett et al. 1997; Vannier et al. 1998).

As a group, the Foraminifera utilise also a broad range of feeding strategies—from osmotrophy to various holotrophic mechanisms (Pawlowski et al. 2003). Carboniferous fusulinids were most probably active herbivores, detritivores and omnivores (Gallagher 1998). Modern foraminifers acquire nutrients through direct uptake of DOC, suspension feeding, grazing, deposit feeding, predation, symbiosis and parasitism (Goldstein 2003). Suspension feeding is common mainly in pelagic forms, but it is worth noting that they do not have mechanism for creating water currents as ostracods do, thus, Foraminifera are probably less efficient as 'passive' suspension feeders. The pseudopodia of carnivorous species are adapted for capturing prey. Many Foraminifera are not strictly carnivorous, but utilise some other feeding strategies. Several species lead a parasitic mode of life, for example on bivalve molluscs, sponges, stone corals, or even other foraminiferans as a host. Symbiotic relationships in the Foraminifera include algal endosymbiosis, chloroplast husbandry (kleptoplastidy) and bacterial endosymbiosis. In general, the symbiont supplies the foraminifer with organic nutrition, and the host, in return, provides the symbiont with a fairly stable microenvironment and with other compounds (dissolved nitrogen, phosphorus, etc.) (Goldstein 2003). Possessing endosymbionts is a beneficial adaptation in colonisation of new habitat. Foraminifera in a symbiotic relationship have independent source of organic carbon, although the majority of symbionts are light dependent.

Eukaryotic protozoans acquire food by way of endocytic uptake and subsequent intracellular digestion within a discontinuous system of vacuoles. Bowser et al. (1985) in their experiment on *Allogromia* species observed that the cytoplasm contains only discrete vacuoles, and there is no evidence for a presence of 'primitive gut' or lacunary system. During their experiments some of observed vesicles broke, which Bowser et al. (1985) inferred was due to hypo-osmotic shock. It appears that similar looking vacuoles may be involved in diverse physiological processes.

The best feeding strategy for the colonisation of a new habitat would appear to be generalist omnivory and detritivory, so that organisms will find food in every aquatic habitat. Indeed, the survival of first ostracod freshwater invaders may have been dictated by their feeding strategy. In the Pennsylvanian Coal Measures of northern England *Carbonita*, thought to be a deposit feeder, was interpreted as better adapted and more successful in its freshwater invasions than *Geisina* (filter feeder) (Bless and Pollard 1973; Bennett 2008). Both groups, Foraminifera and Ostracoda, include omnivorous and detritivorous species. Feeding strategy was unlikely to be a barrier for the efficient colonisation of fresh water in either of these taxa.

3.2 Osmoregulation

The majority of marine ostracods appear to be isotonic with ambient sea water, but all freshwater forms must be osmoregulators. In inland waters organisms are hyperosmotic regulators, while dwellers of hyperhaline environments must be hypoosmotic regulators (Lockwood 1962).

The freshwater medium is hypotonic to body fluids, so ostracods need to take up salt from their food and/or absorb salts in their antennal glands. Embryos utilise special cells located in the non-calcified zone of the inner valve layer for salt reabsorption (Aladin and Potts 1996). Hypoosmotic regulation in both adults and juveniles may be achieved by drinking the medium and by the excretion of salts by cells in the inner, non-calcified shell layer. The cuticle of this zone is characterised by high permeability to ions, and salt excretion seems to be under strict control of 'caplike structures', which are most likely salt glands (Aladin 1983, 1984, 1993; Aladin and Potts 1996).

Tolerant, euryhaline species are capable of adapting to changing salinity conditions. In the Australian euryhaline species *Mytilocypris praenuncia* Aladin and Potts (1996) observed changes in external morphology depending on salinity: below 4 ‰ cells had clear borders and there were numerous depressions in the cuticle but between 8 and 12 ‰ the cell borders and holes in the cuticle vanished. Finally, when *M. praenuncia* was raised in salinities from 20–34 to 44–48 ‰ the cells regained clear borders, and salt glands appeared. It is worth noting that all these changes in morphology occurred only during moulting, so the physiological adaptations from one level of osmoregulation to the next can be completed only during a moult. Aladin and Potts (1996) also noticed that after moulting haemolymph concentration quickly returns to its previous state, and the time taken to reach equilibrium varied from 2 to 26 h.

There are few studies on the effect of salinity on foraminiferal physiology under experimental conditions. Murray (1963) observed that the benthic species *Elphidium crispum* thrived in water at 30–35 ‰, survived in 25 ‰ and died in salinities below 25 ‰. Specimens which had been exposed to low salinity for several days quickly resumed normal feeding rates when returned to normal sea water and had apparently not been permanently affected by the unfavourable conditions. Murray (1963) also noticed that *E. crispum* was capable of tolerating lower salinity for a few weeks (38 days), and survival was better in lower temperature. Most probably the main effect of lowering temperature is the slowing of the rate of metabolic processes. In elevated salinity (50 ‰) Murray observed retarded growth and inhibited reproduction, but exposure did not result in death. This observation was confirmed by Bradshaw (1955) in *Rotaliella heterocaryotica*, who observed active growth when salinity reached 23.5 ‰ and a cessation in too high (37 ‰) and in too low (16.8–20.1 ‰) salinities.

Osmoregulation in ostracods seems to be more specialised than in Foraminifera. Ostracods possess specialised cells, tissues and glands which can provide effective osmoregulation over wide range of salinity (0–70 ‰). Additionally, crustaceans in general are known for their ability to reduce membrane permeability (Lee and Bell 1999). Foraminifera also seem to be adaptable in regard to changeable salinity conditions. Typically they are equipped with numerous vacuoles, which are used in various physiological processes. It seems to be probable that some of them are not strictly specialised, and can change their role with changing environmental conditions. Undoubtedly, another important factor in osmoregulation is the permeability of the test and body membrane, but this should be confirmed by further investigations.

3.3 Reproduction

The overwhelming majority of marine ostracods exhibit sexual reproduction, although some brackish and freshwater species have acquired the ability to reproduce asexually. "(…) sexual propagation may be regarded as a source of individual variability, furnishing material for the operation of natural selection" (August Weismann 1887, quoted in Butlin et al. 1998a). Apart from undoubted genetic benefits of sexual reproduction there are some costs. The main ones are the 'cost of males', the requirement for males in sexual lineages, and the 'cost of mating', the energetic costs of finding partner, courting, copulation, and predation and disease risk involved in mating (Butlin et al. 1998a).

It is still uncertain why parthenogenesis is so common in non-marine ostracods. There are a few different forms of ostracod asexuality (Butlin et al. 1998b; Martens 1998). An ancient asexual does not have close sexual relatives, and its populations consist exclusively of females. Some lineages have geographically restricted sexual and asexual populations—so-called 'geographical parthenogenesis'. Finally, there are populations whose sexual and asexual lineages coexist. The last mode, referred to as 'mixed reproduction', seems to be the most beneficial for new habitat colonisation. Parthenogenesis enables quick and easy dispersion and increase in abundance, because a single egg is sufficient to invade a new water habitat. Alternatively, in highly changeable brackish and freshwater habitats, the diversity of sexual parents offspring might have a better chance to adapt and survive. The first ostracods recorded as freshwater invaders in the Carboniferous probably exhibited mixed reproduction (Griffiths and Horne 1998; Liebau 2005; Bennett 2008).

Both fossil and modern ostracods can exhibit advanced reproductive strategies that facilitate survival in new salinity regimes. The production of resting eggs, or resistance to desiccation or other unfavourable environmental conditions, may also have been attributes of the first fresh water invaders, for example species of *Carbonita* from a temporary pond habitat, found in the Montceau Lagerstätte (Vannier et al. 2003). Brooding may also have allowed the colonisation of more extreme habitats. In the deposits from Lower Silurian Herefordshire Konservat-Lagerstätte myodocopan species with eggs and possibly juveniles were preserved, thus providing an unequivocal view of parental brood care as a reproductive strategy which has lasted within this group from the Silurian to present day (Siveter 2008).

The typical foraminiferal life cycle is characterised by an alteration of asexual and sexual generations. In the sexual generation the adult gamont produces gametes, and fertilisation takes place by the fusion of two gametes, usually from different parents. The zygote may spend a brief phase as a shell-less (naked) amoeba. In metazoans meiosis typically occurs during gametogenesis, however, in the asexual generation the foraminiferal agamont produces numerous offspring by multiple fission, with meiosis as an integral part of this process. Thus, haploid young individuals typically grow to become adult gamonts, which produce gametes by mitotic nuclear divisions (Pawlowski 2009).

Extant Foraminifera are known to exhibit numerous variations on this general cycle, however life cycles of only about 30 of over 10,000 modern species have been studied (Goldstein 2003). The variation includes trimorphism, apogamic life cycle, binary fission, various forms of budding, the occurrence of test and nuclear dimorphism. The alternation of generations in Foraminifera may by facultative or obligatory (Goldstein 2003).

Some species are apogamic and they have reduced the complexity of their life cycle by omitting the sexual generation. In *Fissurina marginata* and *Spiroloculina hyalina* only the asexual phase is observed (Arnold 1964), whereas some planktonic species reproduce exclusively sexually, and no asexual generation has been observed (Goldestein 2003).

The life cycle of allogromiids and astrorhizids seems to be more variable than in other Foraminifera. Binary fission has been observed in *Allogromia laticollaris*, budding, serial and multiple budding in *Saccammina sphaerica*, *S. alba*, and *A. laticollaris*, fragmentation occurs in the miliolid *Calcituba polymorpha*, and *Floresina* is capable of producing multiple broods (Arnold 1954, 1964, 1967; Goldstein 1988, 2003).

Most groups of unicellular organisms (including most Foraminifera) adopt an opportunistic r-strategy, where the population grows quickly by frequent cell divisions. However, there is some evidence that larger-sized benthic species of Foraminifera conform to a K-selected mode of life over long periods. The production of a complex, large-sized test which is slow growing, houses storage products and symbionts, and generates the permanent body shape can be viewed as advanced adaptations to their particular mode of life (Hottinger 1982).

For benthic Foraminifera there are four methods of dispersal: (1) Release gametes, zygotes, or embryonic agamonts or gamonts into the water column, (2) Meroplanktonic juvenile stages with subsequent passive spread by currents, (3) Self-locomotion along sea floor, and (4) Passive dispersal by means of a physical or biological vector (Alve 1999). Sexual generation appears to be the most efficient method, because released gametes are advected by the bottom water currents (Kitazato and Matsushita 1996). Dispersal by gametes may be efficient over short distance, whereas zygotes and embryonic juveniles, with their density comparable to sea water, are more prone to disperse over larger distance (Alve 1999).

3.4 Other Adaptations

Foraminifera show additional adaptations against unfavourable environmental conditions. They are traditionally considered to be obligate aerobes, and most species become dormant during exposure to adverse conditions such as oxygen depletion. However, some benthic allogromiid species living in low-oxic habitats are capable of storing and respiring nitrate through complete denitrification to N_2 (Kuhnt et al. 2013). Foraminifera have evolved at least two ways to carry out this process: one involving symbionts and the other by the foraminifer itself. Bernhard et al. (2012) observed that species capable of denitrification possess large vacuoles containing sea water with a high concentration of nitrate. Recent studies revealed that the gene for nitrate reduction could be localised to the symbiont or to the allogromiid. Foraminifera produced N_2 from NO_3^- and rapidly consumed intracellular nitrate during both oxic and anoxic incubations, thus denitrifying species should be regarded as facultative anaerobes (Kuhnt et al. 2013), although it was observed that presence of oxygen partially inhibited or delayed the onset of nitrate respiration (Bernhard et al. 2012). In oxygen-depleted environments anaerobic metabolic pathways are required. In the Proterozoic or Palaeozoic, during oxygen crises, the ability to denitrify could have imparted a major ecological advantage and contributed to the success of early foraminiferan lineages.

The rate of colonisation depends in part upon the geochemical characteristics of the new habitat. Substrates which were previously anoxic have completely different physical and chemical properties compared to well-oxygenated environment. Alve (1995) recorded that for opportunistic species of Foraminifera it took more than 1 year to colonise sediment which had experienced 5 years of anoxia, however, invasion by less efficient species may take several years (Alve 1999). It seems that in marine environment Foraminifera are able to invade more efficiently than macrofaunal invertebrates. Kaminski et al. (1988) observed for agglutinated Foraminifera that 9 months may be sufficient time to recover to background levels of diversity and abundance after severe disturbance (during which time, the macrofauna did not recover).

All studied physiological adaptations developed by Foraminifera and Ostracoda are collated and summarized in Table 1.

4 Calcification

Both groups, Ostracoda and Foraminifera, seem to be successful invaders of new environments. They adopted a broad range of feeding strategies and reproduction modes. The production of resting stages and brood care may also have contributed to them being efficient invaders. They are also both highly tolerant to variations in salinity. Foraminifera and Ostracoda have the ability to construct saturated with calcium carbonate exoskeleton. How do organisms with a high demand for calcium compounds cope with the low availability of this element in freshwater habitat?

The shell of ostracods is important for protection, respiration, metabolism and osmoregulation (Okada 1982; Keyser 1990; Aladin 1993). Sohn (1958) reported the following constituents for the shell of *Chlamydotheca unispinosa*: 82.7 % calcium carbonate, 12.8 % protein, 2.2 % chitin and 1.9 % trace elements as K, Mg, Na, Si, Sr, Al and Ba. Sohn (1958) also noticed that the $CaCO_3$ content is variable depending on species, and ranges from 80 to 90 %. The cuticle of the shell is mineralised with low magnesium calcium carbonate in the form of calcite, but never contains aragonite. The highest content of calcium carbonate is found in the shell of marine Cytheroidea, whereas in freshwater forms, as *Cypria ophtalmica*, the

Table 1 Physiological adaptations of Foraminifera and Ostracoda in marine and freshwater environments (see text)

	Marine	Freshwater		
Adaptation	Foraminifera	Ostracoda	Foraminifera	Ostracoda
Feeding strategy	Predators, scavengers, filter-feeders, herbivorous, omnivorous, detritivorous, DOC feeding, symbiotic, parasitic[1])	Predators, scavengers, filter-feeders, omnivorous, detritivorous, symbiotic, parasitic[2])	Herbivorous[3]), others?	Omnivorous, detritivorous, filter-feeders[4])
Osmoregulation	≈25-35 ‰, retarded growth and inhibited reproduction in lower and higher salinity; isotonic with ambient sea water[5])	Tolerant, depending on species range up to 0-70 ‰; isotonic with ambient sea water[6])	0-? ‰; contractile vacuoles for osmoregulation3)	0-8‰; 'cap-like structures' (salt glands) for osmoregulation[6])
Reproductive strategy	Alteration of sexual and asexual generations, budding, fragmentation[1])	Almost exclusively sexual reproduction, brood care[7])	Asexual reproduction, binary fission[8]), others?	Sexual, asexual and mixed reproduction, brood care[4], [7])
Calcification	The higher salinity the more calcified test[9])	The higher salinity the more calcified valves[10])	Almost exclusively agglutinated, organic-shelled or naked species[3], [8], [11])	Thin, less calcified and poorly ornamented carapace[4], [12])
Other adaptations	Resting stages, diapause, nitrate respiring in anoxic environment[13])	Resting stages[14])	Resting stages, diapause[8])	Resting stages, resistance to desiccation, diapause[4])

1: Goldstein 2003
2: Vannier et al. 1998
3: Holzmann and Pawlowski 2002
4: Meisch 2000
5: Murray 1963
6: Aladin and Potts 1996
7: Martens 1998
8: Meisterfeld et al. 2001
9: Dueñas-Bohórquez et al. 2009
10: Chivas et al. 1986
11: Sen Gupta 2003
12: Keyser and Walter 2004
13: Kuhnt et al. 2013
14: Vannier and Abe 1992

$CaCO_3$ content is significantly lower. In habitats with low calcium content they cannot construct fully calcified carapace and the valve may then consist primarily of chitinous fibres (Keyser and Walter 2004). In low salinity environments ostracods seem to have less mineralised, mainly chitinous valves, but they still have carapace to protect their soft body parts.

The ostracod carapace is shed by moulting up to eight times during development and each stage has new and more heavily calcified valves. In ostracods the calcite is not reabsorbed from the old carapace during moulting, as happens in many malacostracan crustaceans, but is removed and formed again during calcification of the new valves (Turpen and Angell 1971; Keyser and Walter 2004). Prior to moulting ostracods begin producing the carapace by the absorption of a large amount of calcium compounds and chitin precursors. The uncalcified inner lamella cuticle is formed by the inner epidermal cells (Yamada and Keyser 2010). The outer epidermal layer beneath the calcified cuticle contains large amounts of granules within the cells. These intracellular bodies contain compounds of calcium phosphate and small amounts of sodium, potassium, chloride and sulphur. Neither magnesium nor strontium (known to be present in the fully calcified carapace) is found in these granules. In the next step calcium is released from the globules, penetrates the epidermal membrane and then forms granules of amorphous calcite outside the membrane. Some species (e.g. *C. ophtalmica*) retain amorphous calcite in the carapace, but most transform the calcite into the final crystalline arrangement in the epidermal layer, because amorphous calcite dissolves easily. In the juvenile stages crystallisation is not complete and the organisms have weaker shells. This mechanism is similar for both marine and freshwater ostracods (Turpen and Angell 1971; Keyser and Walter 2004; Yamada et al. 2005; Yamada and Keyser 2010).

The chemistry of the ostracod valve is a function of the surrounding water chemistry modified by temperature, calcification rate, and inter- and intra-specific variability (Van der Meeren et al. 2011). The influence of salinity levels on ostracod calcification is unclear. Some authors (e.g. De Deckker et al. 1999) found no relationship between Mg/Ca content of the ostracod valve and salinity, while others (e.g. Chivas et al. 1986) found a positive correlation between salinity and Mg/Ca content in the carapace. Decrouy et al. (2011) noticed that in shallow waters higher temperatures increased the Mg/Ca and DIC concentration of water, which may have an effect on ostracod mineralisation. Additionally, Carbonel et al. (1988) suggested that the structure, ornamentation and size of the carapace may be correlated with the degree of salinity.

Eleven out of 15 extant orders of Foraminifera precipitate calcareous tests and thus are among the major producers of calcium carbonate in the oceans (Hansen 2003; Bentov et al. 2009). In pelagic foraminifers the test wall consists of extremely pure calcite (about 99 % by weight $CaCO_3$) and trace elements such as Mg, Sr, Ba and Cd. Elements are incorporated directly from ambient sea water during test precipitation, thus shell composition reflects chemical composition of the medium, and both physical and biological conditions present during calcification (Lea 2003).

According to test structure calcifying Foraminifera are commonly divided into two groups: miliolid and hyaline. The miliolid test contains relatively high Mg/Ca ratios and the hyaline test has much lower ratios of Mg/Ca (Vogel and Uthicke 2012). Miliolids precipitate calcite in the form of 2–3 μm needles within cytoplasmic vesicles (Berthold 1976). These needles are accumulated within the cell and then they form a new chamber after simultaneous transport outside the test and assembly within the organic matrix (Angell 1980). The outer layer of the wall is arranged in dense rows of needles, to what gives a porcelaneous structure of the test surface (de Nooijer et al. 2009).

Foraminiferal calcification is preceded by extraction of calcium and bicarbonate ions from sea water. Hyaline species tend to store calcium and carbonate in separate intracellular organelles. During calcification Foraminifera build their new calcite chamber over their previous shell (Bentov et al. 2009). Chamber formation starts with the production of a primary organic sheet (POS) (de Nooijer et al. 2009). During formation of the POS cytoplasm with a raised pH (≥9.0) is transported to the site of calcification. Vesicles with high pH are formed mainly in the penultimate chamber and transported through the ultimate chamber to its aperture where calcification occurs. Most probably protons are pumped out from the vesicles and stored in a specialised cytosolic compartment with low pH (≤6.0). Throughout chamber formation vesicles with elevated pH are continuously transported to the calcification site until chamber formation is complete (de Nooijer et al. 2009).

Miliolids also need pH ≈ 9.0 for calcification, but their high pH vesicles are conveyed around in the cytoplasm relatively fast and in a seemingly undirected manner. However, the vesicles containing calcitic needles have considerably lower pH (7.5–8.0). Elevating the pH is a widespread strategy to promote calcite precipitation in Foraminifera: it overcomes the inhibition by Mg^{2+} of calcite precipitation that prevents spontaneous crystal nucleation and growth in modern seawater Mg/Ca ratios (Zeebe and Sanyal 2002), and it also promotes the conversion of bicarbonate into carbonates (Zeebe and Wolf-Gladrow 2001).

Most models of biomineralisation assume involvement of membrane ion transporters (channels and pumps) for delivery of Ca^{2+} and other ions to the calcification site. However, Bentov et al. (2009) observed another mechanism in the shallow water, benthic foraminiferan *Amphistegina lobifera* (hyaline), in which transport of vacuoles with sea water via fluid phase endocytosis may account for most of the calcium and other ions. Initially, vacuoles are semi open to external sea water and filling of the vacuoles may be mediated by narrow, tubular channels. During intracellular endocytosis sea water vacuoles undergo alkalisation and this further enhances their calcifying potential. The alkalinisation of the vacuoles suggests that the supply of CO_3^{2-} for calcification is also mediated by the sea water vacuoles (Ferguson et al. 2008). The massive calcium transport through the cytosol would require a large expenditure of energy. In addition, because of the lower cytoplasm pH (7.2–7.5), direct transport through the cytoplasm may hinder the maintenance of the high pH needed for calcification. Vacuolar transport obviously reduces these problems, and can bring Ca^{2+}-enriched solution to the calcification site bypassing the cytoplasm (Bentov et al. 2009). De Nooijer et al. (2008, 2009) recorded that the phenomenon of alkaline vacuole (vesicles) is general, encompassing both hyaline and miliolid species. Thus, sea water seems to be a calcifying solution, in agreement with the biomineralisation model of Elderfield et al. (1996). Elderfield et al. (1996) observed that precipitation occurs at the mineralisation site, which is isolated from the outside medium, however, the medium supplies the extraneous ions for precipitation. The biomineralisation reservoir is similar but not necessarily identical to sea water in composition. Sea water provides chemicals for calcification and controls the diffusion gradient, and thus influences the test composition. Organisms probably extract calcium from vacuoles with sea water into the storage organelles (Elderfield et al. 1996).

According to Hottinger 2000) new chamber formation in Foraminifera includes two processes: rhizopodial extrusion and biomineralisation. It seems that the rhizopodia play a key role in a test formation. A new chamber is built on a rhizopodial skeleton formed by microtubules. In the next stage rhizopodial skeleton is saturated with skeleton elements in a biomineralisation process (Hottinger 2000). Most probably in a low mineralisation environment they cannot complete the precipitation of new test, but the naked rhizopodial skeleton is not hard enough to protect them against predators and other unfavourable environmental conditions.

The following parameters seem to be involved in the control of foraminiferal Mg/Ca and Sr/Ca ratios: water temperature, salinity, calcite saturation, carbonate ions concentration, water pressure, ontogeny and growth rate (Elderfield et al. 1996; Lea 2003; Dueñas-Bohórquez et al. 2009, 2011). An impact of salinity on foraminiferal calcification has been observed in several studies (e.g. van Raden et al. 2011). According to Dueñas-Bohórquez et al. (2009) the average Mg/Ca values of planktonic Foraminifera *Globigerinoides sacculifer* increase in higher salinities despite the relatively large inter-individual variability. Ferguson et al. (2008) suggested that salinity is the most likely environmental factor to explain unusually high Mg/Ca ratios of Mediterranean Foraminifera. They recorded that correlations of Mg/Ca with the salinity at which organisms calcified were more highly significant than those with calcification temperatures.

5 Discussion

In general, both Foraminifera and ostracods are highly adaptable and efficient colonisers of new aquatic habitats. A key to success for the Foraminifera has been that they are not highly specialised. Leven (2010) claims that the reason why some species of Fusulinida (e.g. *Pseudostaffella*) became extinct in the Middle Carboniferous, was because they attained too high a degree of specialisation. In general, Foraminifera as simple, unicellular organisms maintained high plasticity and the ability to adapt to changing environmental conditions. Ostracods are more specialised but they have flexible genetic systems which allow species to readily adapt to the local environment (Carbonel et al. 1988).

Calcification in Foraminifera probably appeared during the Early Cambrian radiation, when miliolid and agglutinated Foraminifera separated from each other (Pawlowski et al. 2003). Building the test was one of the key adaptations for the initial diversification of Foraminifera. The test provided some protection against adverse environmental conditions and predation, as well as compartments in which they can store food, protect juveniles and house symbionts. For ostracods the development of a fully calcified carapace also played key role in their rapid diversification. At the turn of the Cambrian and Ordovician the majority of weakly-calcified ostracodomorphs (bradoriids sensu lato, Phosphatocopida) were replaced by well-calcified podocopomorphs (Liebau 2005).

Along the salinity gradient from a river to the sea, body size increases with increasing salinity (Gunter 1947). Indeed, animals inhabiting estuaries are smaller than their marine counterparts. The factor which is most likely to be responsible for small size of both Foraminifera and ostracods is the availability of calcium. Sea water salinity 35 ‰ contains about 400 ppm of calcium, whereas in comparison the hardest of river waters contains almost negligible amounts (Murray 1963). Recent experiments on Foraminifera revealed poor efficiency of calcium utilisation—only about 30 % of available Ca is used for shell formation (Böhm et al. 2012). It seems most likely that the barrier against massive colonisation of the freshwater realm by Foraminifera is their inability to construct a fully calcified test in low salinity regimes. The mechanism of foraminiferal calcification is strictly dependent on salt water content. They use sea water not only as a source of ions to construct their shell, but also as a biomineralisation solution, thus Foraminifera are typically defined as marine organisms (Holzmann et al. 2003). Only few genera are occasionally represented by species in low salinity environments, and the overwhelming majority of them are agglutinated or organic-shelled forms, which do not produce, or produce only small amounts of calcite. The success of ostracods in fresh water can be attributed to their development of a more effective mechanism of calcification. Less calcified ostracods are still sheltered by chitinous valves, but calcifying Foraminifera without biomineralisation process most likely are completely defenceless with their rhizopodial skeleton exposed. In low salinity environments ostracods construct less calcified, thinner and poorly ornamented valves, but they are still able to build a complete hard shell.

However, there is still a problematic question about the role of cellular organisation level. Ostracoda, as a multicellular group, seem to be better adaptable, than Foraminifera, their distant unicellular relatives. It is possible that tissue- and organ-level organisation has a greater capacity for physiological adaptation to new salinity regime than unicellular organisation does. That issue requires more attention in further studies.

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