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Ostracods: the ultimate survivors

Ostracods are tiny crustacean arthropods just a few millimetres long, with a bivalved carapace made of calcium carbonate that covers the whole body, and into which the animal can retreat from the world outside. Because of their diminutive size they are largely overlooked as fossils, but they have a fascinating history. Silent witnesses to life in the seas since the time of trilobites, they have a fossil record extending back to the Early Ordovician, and possibly the Cambrian. Ostracods have survived nearly 500 million years of Earth history including the 'big five' mass extinctions of the Phanerozoic Eon; they are true survivors. They are almost perfectly adapted for the aquatic environments in which they live, and can be found from the ocean abyssal plains to damp leaf litter. The ostracod carapace is a triumph of biological engineering that has been re-configured into myriad different morphologies according to environment. Streamlined and agile species plough through the ocean water column, sometimes reaching a 'giant' size of a centimetre in length, whilst their tinier sea bottom cousins make elaborately ornamented carapaces to withstand the pressures of living at the seabed, or shape their carapaces into forms that facilitate burrowing into sediment. Ostracods are key components of aquatic ecosystems. As primary consumers they are food for larger animals both in seabed and planktonic habitats, and they recycle much of the organic detritus produced by larger animals and plants. Delve into the history of ostracods and it is possible to find pioneers who triumphed in the plankton, early colonisers of terrestrial aquatic ecosystems, and ostracods that literally conquered the land. And in more recent times, ostracods have even hitched rides on rockets into space.

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Ostracods are tiny arthropods characterized by their possession of a bivalved carapace made from calcium carbonate, and a body that bears seven pairs of jointed appendages. More specifically, ostracods are crustaceans, relatives of crabs and lobsters, and they have a distinctive suite of paired appendages on their head that are used for sensory, swimming and feeding functions. Known from tens of thousands of living and fossil species, ostracods are often the most abundant microfossils in sedimentary rocks, sometimes occurring in the hundreds in a few grams of mudstone or limestone. They are certainly the most abundant arthropod fossils, surpassing in numbers their much larger and more illustrious relatives the trilobites. Despite their numerical abundance as fossils, and their presence in most aquatic bodies—including your village pond, ostracods only invaded the scientific literature from the mid-eighteenth century onwards.

The venerable Henry Baker, Londoner and Fellow of the Royal Society, may have been one of the first to notice them (Fig. 1). Baker was the son-in-law of Daniel Defoe and a pioneering microscopist who, in his miraculous account of 'Animalcules never before described' figured a tiny bivalved animal with protruding antennae that appears to be an ostracod. Although Baker was a real pioneer of studying the microscopic world—the Royal Society still sponsors a Bakerian medal and lecture in his honour each year, ostracods may actually have been noticed much earlier by the Mogollon people of New Mexico, who—without the utility of a microscope, depicted images of possible ostracods on their pottery around *circa* 1000 to 1150 AD. If the Mogollon people and Henry Baker were responsible for some of the earliest depictions of ostracods, then the group began to invade the geological and biological literature much more fulsomely in the nineteenth century. Perhaps the pinnacle of Victorian work is that of English naturalist George Stewardson Brady, who carefully documented the ostracods of the world's first detailed oceanographic survey, conducted by the voyages of HMS *Challenger* during the 1870s. Thereafter for a century, the quality of Brady's pictures was rarely surpassed, and ostracods were depicted either as line drawings made by a 'camera lucida' attached to a microscope, or by photographs taken by a conventional light microscope. The development of the scanning electron microscope from the 1930s by German scientist Manfred von Ardenne, and the production of the world's first commercial scanning electron microscope by the Cambridge Scientific Instrument Company in the 1960s led to a revolution in the understanding of ostracod morphology and of all microfossil groups. This detailed understanding of their morphology, coupled to a growing knowledge of their physiology has led to the recognition of ostracods as rather special organisms, as true evolutionary survivors. So what is so special about their morphology, and why might their anatomy and physiology provide us with insights into how certain organisms have 'built-in' environmental resilience?

Anatomical resilience

Hiding amongst the more prominent representatives of the Cambrian fauna and probably trying to avoid their more vicious-looking arthropod cousins, was an array of small, bivalved arthropods that were once thought to be Cambrian representatives of the ostracods. These animals, the bradoriids and phosphatocopids, have tiny bivalved carapaces, and sometimes occur in the thousands in the sedimentary deposits of the celebrated Burgess Shale and Chengjiang Lagerstätten. However, rare fossilized soft anatomy has shown that neither the bradoriids nor the phophatocopids are ostracods (Fig. 2), and indeed their carapaces are fundamentally different to those of ostracods. Unlike their older bradoriid and phosphatocopid relatives, ostracods can shut their two valves tightly together, fully enclosing the space around the animal (Fig. 3). This may be a morphological innovation of singular importance in ostracod evolution and may explain why ostracods are survivors—probably from the Cambrian—and became the dominant small arthropods in benthic aquatic settings, whereas bradoriids and phosphatocopids went extinct. The very utility of the ostracod carapace could be modified for an infaunal (burrowing) or epifaunal lifestyle, for nurturing juveniles, or for controlling the ambient aquatic environment within the carapace that gave ostracods an advantage (Figs 3–5). Ostracod soft anatomy also seems to be perfectly adapted. Rare examples of fossilized ostracods with preserved soft anatomy from the Ordovician and Silurian show a morphology very similar to living forms. Something about ostracod design confers stability and resilience and a brief search online for the colloquial name of ostracods, 'seed shrimps', shows just how prolific they can be across all aquatic environments, including fish aquaria which they rapidly invade and where they are considered a pest.

Fig. 1. Henry Baker, microscopist, Fellow of the Royal Society, and probably the first to document ostracods. Image from Wikimedia Commons at: https://commons.wikimedia.org/wiki/File:Henry_Baker_(naturalist).jpg The original source for this image is the Welcome Library, London (Henry Baker. Stipple engraving by Nutter, 1812, after J. Thomson): http://wellcomeimages.org/indexplus/image/V0000315.html

Fig. 2. The bradoriid arthropod *Kunmingella*, from the early Cambrian of Yunnan Province, southern China. The animal preserves evidence of its body and appendages. Though once thought to be a type of ostracod, this animal has unsophisticated post-antennal appendages and is much more primitive. Bradoriids were a widespread component of Cambrian marine faunas, but were extinct after the earliest Ordovician. Picture Prof. Derek Siveter (Oxford), used with the courtesy of Prof. Hou Xianguang (Yunnan). The animal pictured is a juvenile, its carapace being about 1.3 mm in length.

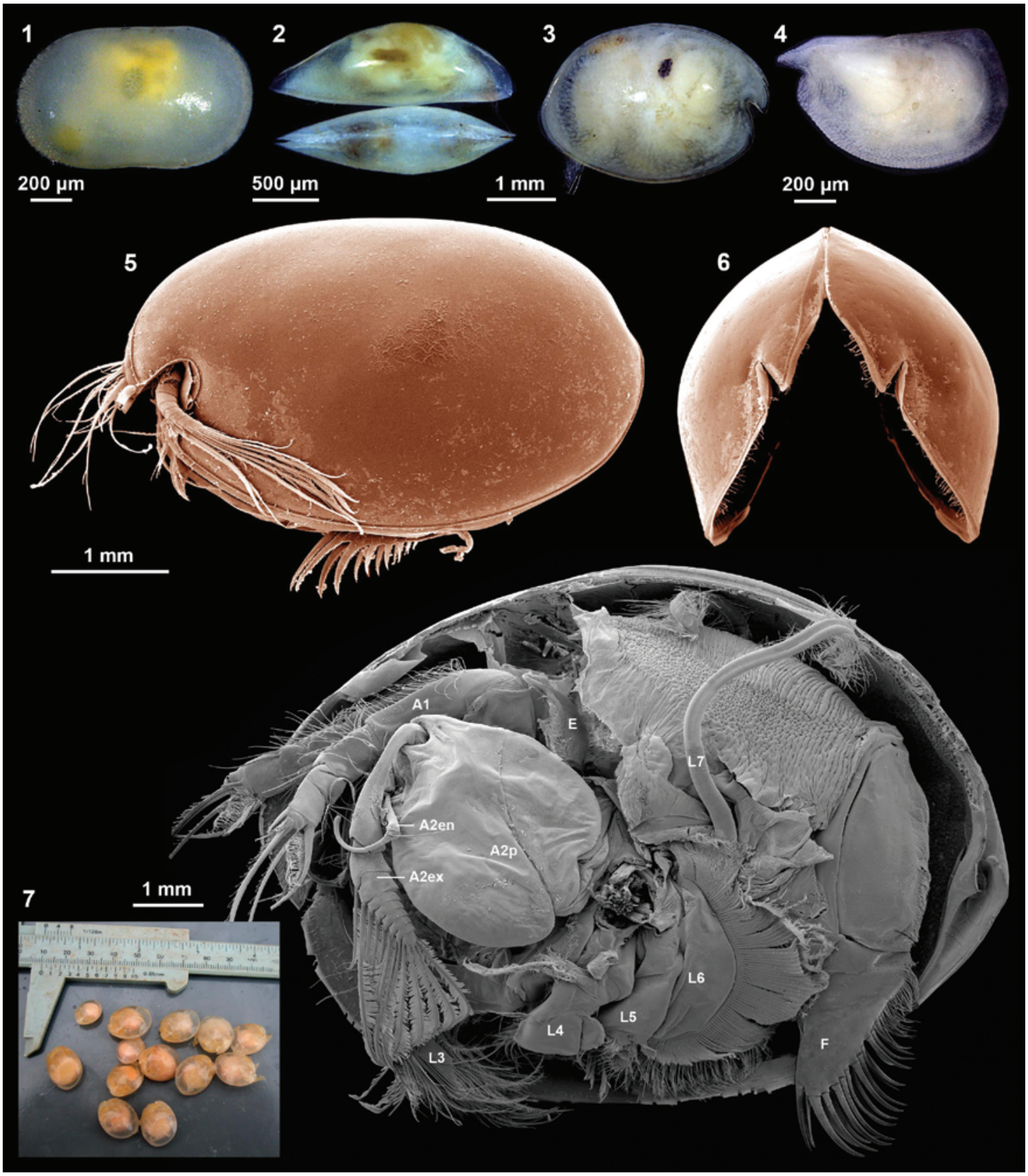

Fig. 3. The ostracod carapace and soft anatomy. **1–4**. General views, the hinge and adductor muscle scars are clearly visible, and the combination of these characters together with valve overlap features enable ostracods to clasp their two valves tightly together; **1, 2,** Podocopa; **3, 4,** Myodocopa. **5, 6,** SEM (false colour) views of the myodocope *Vargula hilgendorfii*; life position with 1st and 2nd antenna protruding around the rostrum, furca on ventral side; and frontal view of a carapace emptied of its soft parts. **7.** Soft anatomy of the myodocope ostracod *Azygocypridina*. **A1** = first antenna; **A2** = second antenna; E = eye; F = furca; L3–7= limbs 3 to 7. Images 1–4 courtesy of S.N. Brandão (Natal, Brazil).

'Super hero' resilience

We could also think of ostracods as tiny 'super heroes' of the micro-arthropod world, tolerating a range of salinity, temperature and chemical stresses that would pickle, cook or dissolve lesser organisms, and probably make Batman's eyes pop out. Whilst the earliest ostracods seem to have occupied open marine shelf settings with normal salinity, the subsequent adaptability of ostracods to different aquatic chemistries and salinities is remarkable, facilitated their colonization of the widest range of water bodies, and in turn secured their evolutionary success. Because of their calcite carapace, ostracods favour waters that are pH circum-neutral and which have a ready supply of calcium carbonate. Nevertheless, some terrestrial aquatic species have a very wide pH tolerance from alkaline to acid waters, for example *Candona candida* (pH 5.3 to 13), whilst the Australian *Australocypris bennetti* can occupy lakes with a pH as low as 3.4; that's rather like living in a lake made of Chardonnay. Ostracods are also adaptable to a wide range of salinities from freshwater, through brackish to hypersaline. Fossil evidence shows that salinity tolerance developed early, with ostracods noted from hypersaline shallow marine settings of the Late Ordovician. This tolerance of salty waters continued into the Silurian and Devonian, and it is a characteristic of ostracods occupying saline lakes

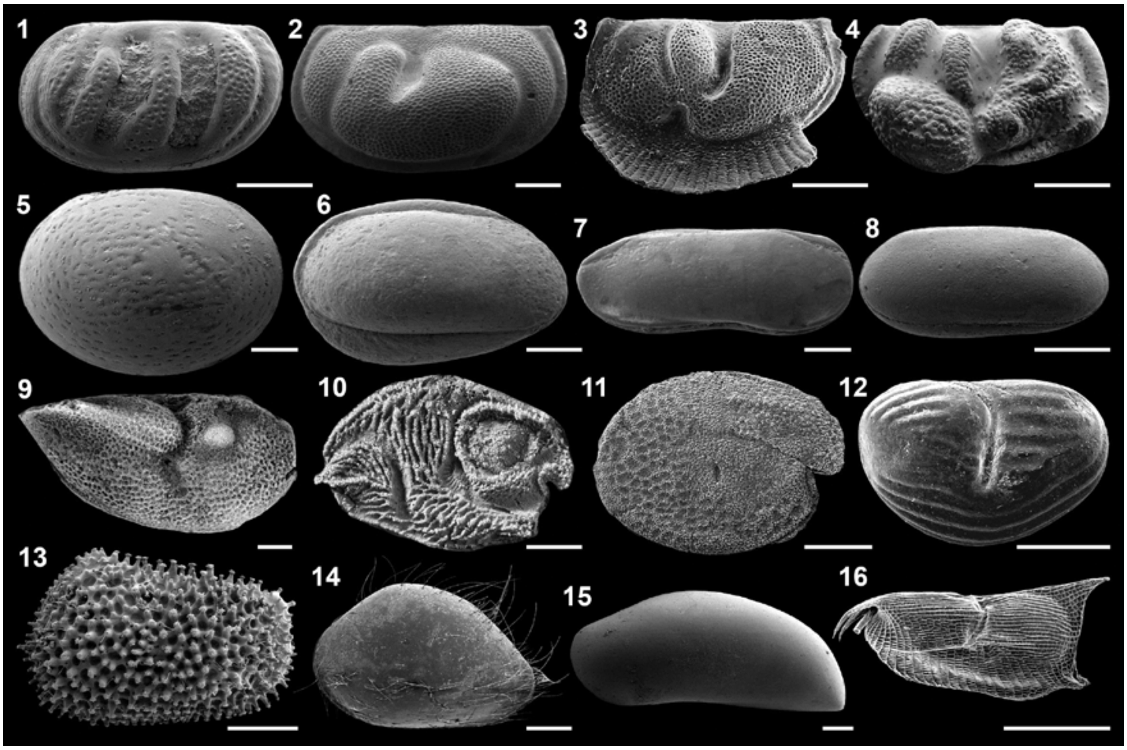

Fig. 4. The myriad shapes and sizes of the ostracod carapace. **1–8**, Ordovician and Silurian Podocopa. **9–12**, Silurian Myodocopa. **13–15**, Recent Podocopa. **16**, Recent myodocope ostracod. Images **13–15** courtesy of S. N. Brandão; image **16** courtesy of Jean Vannier (Lyon, France). Scale bars: **1–8**, **13–15** = 200 μm; **9–12**, **16** = 1 mm.

in desert environments today. Although the earliest ostracods were exclusively marine, a tolerance of reduced (brackish) salinity can be recognised in Silurian species, whilst Devonian and early Carboniferous ostracods were invading freshwater lakes. Tolerance of more 'radical' chemical settings, such as alkaline lakes, may also have a very long history.

Ostracods also have a remarkable tolerance of a wide range of temperatures. In modern aquatic settings ostracods can be found living in ocean waters with normal salinity at 0 °C and at the other end of the spectrum in hot springs with temperatures in excess of 50 °C—that's approaching a warm cup of tea! Individual species can display eurythermic (widely tolerant) behaviour: the freshwater species *Candona rectangulata* occupies Arctic lakes with temperatures typically less than 15 °C, though experimental studies shows it can tolerate temperatures as high as 42 °C, achieved through the possession of 'heat shock proteins' that prevent the irreversible damage of body tissues, a characteristic that definitely suits a 'super hero' temperament. When did this temperature adaptability evolve? Some modern marine cool-water species have their origins in sub-tropical and mild temperate assemblages of the Miocene, suggesting that ostracods have a nascent ability to shift their environmental range as a response to climate change. Still further back, some marine Ordovician ostracods had a remarkable latitudinal range—from the tropics to the polar regions—that hints at a temperature tolerance that was already present in early ostracods.

As well as their temperature and chemical tolerance, ostracods are gold medallists in the underwater breathing stakes. They extract oxygen from the surrounding water either by gaseous diffusion, as in the small podocopes, or via a vascular system, as in the larger myodocope ostracods (Fig. 6). One specialized group of podocope ostracods (the Platycopida) show the rudimentary development of ventilatory adaptation through their filter-feeding apparatus, which may enable them to survive periods of very low oxygen. The partial pressure of oxygen 'pO_2' of modern normoxic seawater is 21 kPa (air-equilibrated water), a level that would cause cellular damage if found in the tissues of ostracods and much other marine fauna. The pO_2 of most aquatic breathers at the cellular level is much lower, between 1 and 3 kPa. Ostracods have developed a range of strategies to avoid oxygen toxicity by migrating to waters that are hypoxic, by burrowing into sediment where oxygen levels are lower, by developing metabolisms that generate high consumption of oxygen, by sealing their valves tightly shut, or—perhaps most intriguingly—by collectively breathing in nests at the seabed where the oxygen level can be controlled. The range of strategies used by ostracods to control the oxygen level in their tissues may have been fundamental to their survival during periods of widespread ocean anoxia, or intervals of elevated oxygen in seawater. It may be one of the factors in their evolutionary success, compared to, for example the bradoriids and phosphatocopids.

Finally, in the 'super hero' stakes you must always have a secret weapon by which to overwhelm your foes—and ostracods have one too! Zooplanktonic myodocope ostracods may be relatively small, and as a result they are often a food-source for many larger animal predators. However, some planktonic species have evolved a superb predator-defence mechanism that relies on bioluminescence, the origins of which may be very ancient. A special organ in the ostracod can create a luminous liquid that is squirted into seawater when the animal is agitated. Fish have been recorded swallowing ostracods which then invoke their luminescence secret weapon, causing the fish to spit them out: underwater spit fire!

Ostracods are great parents

Many arthropods are renowned for their parenting skills. Spiders weave balls of silk to protect their eggs, carry the juveniles on their backs, and in some instances even sacrifice themselves as food for younglings. Ostracods don't show such extreme parenting behaviour, but they are nevertheless excellent parents. Although many freshwater ostracods deposit their eggs on substrata, the protection and brooding of young is a common trait, both for marine and freshwater species. This capacity for parenting seems to be very deep-rooted and can be recognized in very ancient ostracods from distinctive carapace features that indicate brooding (Fig. 7): sometimes the fossilized eggs or juveniles are even found within the brood chambers, or miraculously preserved inside the carapace as in the Silurian myodocope ostracod *Nymphatelina gravida*. Brooding confers a considerable advantage to ostracods, providing a safe domicile for eggs and young. In ancient marine environments the variety of brood types was remarkable, ranging from brooding within the posterior space of the carapace—an ancient strategy first developed by Ordovician ostracods, to specialized structures with a direct connection to the inner carapace—the crumina of some Silurian ostracods (Fig. 7), or with no or very little internal connection to the carapace. Brooding within the posterior part of the carapace is the dominant form today.

Ostracods also use both sexual and parthenogenetic ('cloning') pathways to reproduction. Sexual behaviour can be recognised from the deep geological record by the characteristic brooding structures of the carapace, with only one of the two adult morphs possessing a brood chamber, and this is usually assumed to be the female (Fig. 7). Better still, some exceptionally preserved ostracods from the Silurian of Herefordshire preserve their reproductive organs, these being the oldest in the fossil record. In the 430 million year old myodocope ostracod *Colymbosathon ecplecticos*, its penis, or rather hemipenes (there are two of them in male ostracods), are clearly visible. In addition, the fossil name irreverently refers to another reproductive characteristic of ostracods, males of which have very large reproductive organs (relative to their body size): *Colymbosathon ecplecticos* means 'swimmer with a large penis'. For good measure ostracods also have one of the longest sperm cells in the animal kingdom—they can be as much as one centimetre in length (longer than the body of the ostracod male that produces them), are spring loaded, and are even preserved from the fossil record as far back as the Miocene.

Ostracods can sometimes also use parthenogenesis: the ability of females to reproduce without males. This is more common in freshwater species and is rarely documented in marine species; some freshwater species such as *Potamocypris villosa* use both strategies. Parthenogenesis in non-marine aquatic ostracods may be very ancient, and in the extant ostracod group Darwinulidae it probably extends back to the early Mesozoic. The ability to reproduce rapidly, or

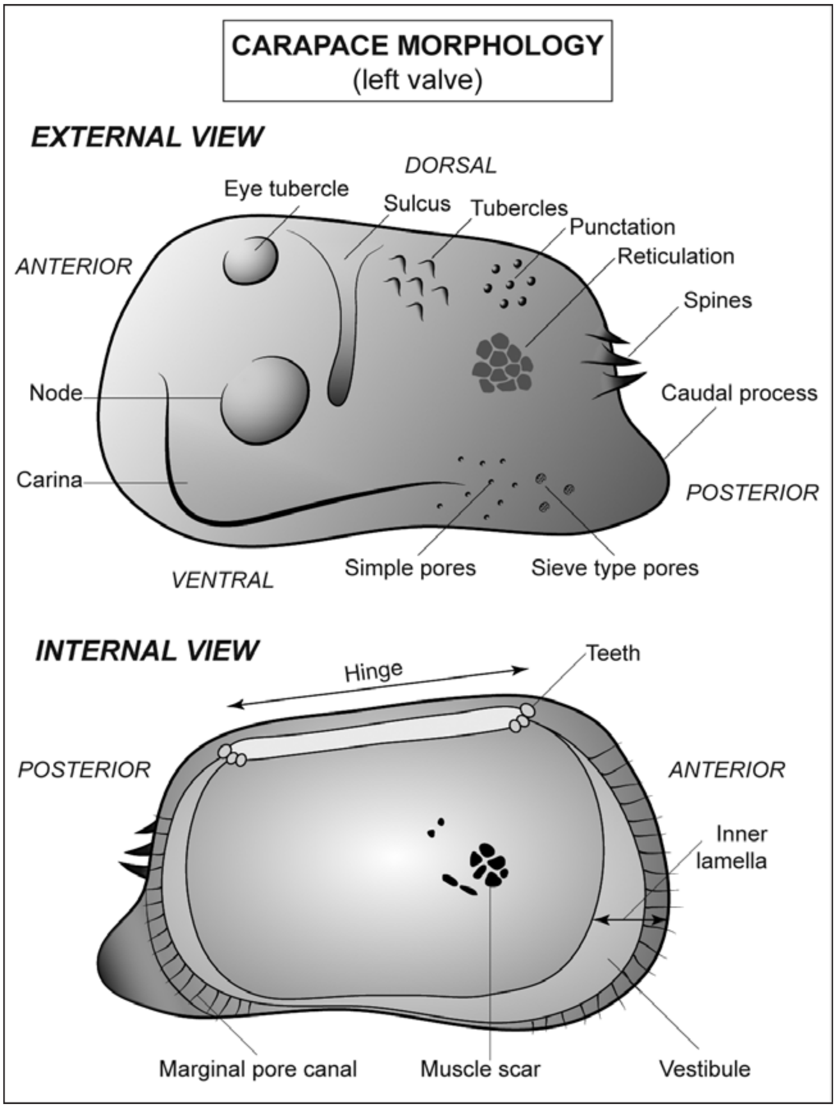

Fig. 5. Orientation and basic anatomical structures of a typical podocope ostracod carapace: many of these features can be seen in the ostracods of Figs 3 and 4. External features such as sulci, carinae and nodes are often used for taxonomy. Punctation, reticulation and tuberculation are features of ornament. Internal features that are useful for taxonomy include the dorsal hinge and the muscle scars, the latter marking the point at which the adductor muscles attach.

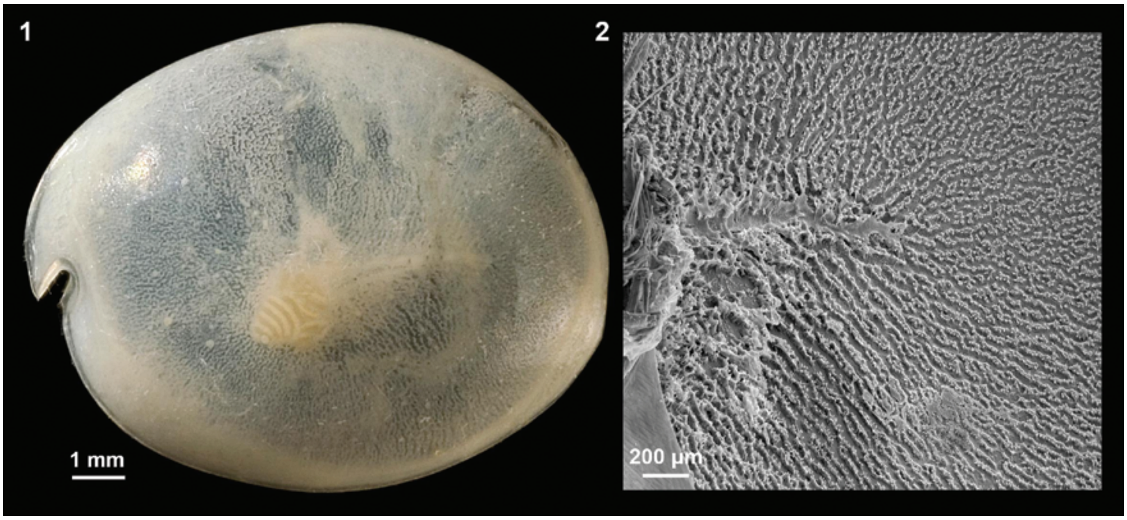

Fig. 6. The circulation system of the myodocope ostracod *Azygocypridina* as expressed in its carapace. **1.** External view of the circulatory system and muscle scar through the translucent carapace. **2.** Internal view of the circulatory system radiating from the muscle scar on the left. Large myodocope ostracods have well-developed respiratory systems to support active swimming. In contrast, the much smaller podocope ostracods (see Fig. 4) get by with diffusion of oxygen from water through their integument.

to use strategies such as parthenogenesis, may have played a significant role in the opening up of new water bodies to ostracods during the colonization, for example, of terrestrial aquatic settings in the post-Silurian world.

Kings of the wild frontier

Ostracods have a pioneering spirit and a capacity for colonizing new environments that belies their diminutive size, but is in keeping with their 'super-hero' anatomy and physiology. They are found in the most remote aquatic settings, including the ancient, isolated Antarctic lakes of the Miocene. They even remain viable when transported over long distances on the bodies of birds. And, they are in the vanguard of the re-colonization of water bodies following environmental events such as high latitude glaciations. Ostracods made a sudden widespread appearance in the fossil record 485 million years ago, though a putative ostracod appendage is known from Cambrian deposits some 20 million years earlier, suggesting that the earliest ostracods have yet to be discovered. The first widespread ostracods occur in marine shelf deposits around the ancient supercontinent of Gondwana. They were widely dispersed from Iran, through Argentina, England and beyond. These ostracods were podocopes and lived in sea bottom environments with normal marine salinity and oxygen levels, in water temperatures that were likely warm or temperate. Initially they show no signs of the huge adaptability to come, and they even occur in the same deposits as a few of the remnants of the bradoriid fauna, clinging on from the Cambrian. In their long history, ostracods would eventually colonize the vast majority of aquatic environments on Earth. Perhaps their most decisive adaptive radiations are the colonization of the plankton—which seems to have occurred during the Silurian; and their invasion of non-marine aquatic environments during the Devonian and early Carboniferous.

Invading the plankton

The group of ostracods that colonised the water column is the myodocopes. They have a particular carapace and soft-anatomy that aids their advanced swimming capacity (Figs 3, 4), and which differentiates them markedly from the podocope ostracods that are exclusively benthic (see Fig. 4). Exceptionally preserved myodocope ostracods from the Ordovician Beecher's Trilobite Bed of New York State, or from the early Silurian of Herefordshire, show that these anatomical traits were developed early in the group, and importantly, prior to fossil evidence of ostracods colonising the plankton. Armed with powerful swimming appendages, well-developed vision and a highly efficient respiration (see Fig. 6), these precursors to the first planktonic ostracods may just have needed a small push off the seabed to invade the plankton. This push may have happened about 427 million years ago, during a major extinction event that especially affected the global plankton, and is known colloquially as the 'Big Crisis'. It is associated with the extinction of many graptolite groups, such as the delicate spiralling cyrtograptids, but it also impacted groups such as conodonts and chitinozoans. It is at the point of recovery from the 'Big Crisis', when graptolites began to diversify again, that the ostracods entered the water column, possibly taking advantage of a new food source or of low predation pressures post-extinction, or perhaps pushed off the seabed by environmental changes associated with the 'Big Crisis'. Later, during the Devonian and Carboniferous the myodocopes experienced an important radiation and became an important component of the global arthropod zooplankton surviving, without any apparent problems, through the mass extinction of the Late Devonian. Despite their sparse fossil record, myodocopes have likely been a critical component of the marine plankton ever since the Silurian. They are primary and secondary consumers in the food chain, and are food for larger tertiary consumers. In addition, they contribute to the faecal stream that feeds organisms on the seabed. They are essential go-betweens in the complexity of marine food webs.

The colonization of the land

Ostracods were in the vanguard of colonising non-marine aquatic environments, enabling them to take full advantage of an abundant new food source: land plants. Early attempts to colonise brackish waters occurred multiple times during the Silurian and Devonian, but from the Late Devonian and Early Carboniferous there were marked increases in the frequency of these radiations, and by the Late Carboniferous ostracods were firmly established in freshwater lakes and ponds. Only the podocope ostracods made this transition, and this was probably facilitated by their wide adaptability to changes in salinity—already evident in ostracods from the Ordovician. Species of the podocope ostracods *Darwinula* and *Carbonita*—with thin, unornamented carapaces, evolved to live in fresh water. *Carbonita* thrived in the coal swamps of the Late Carboniferous and within continental water-bodies in the Permian, becoming extinct at the end of that Period, while *Darwinula* remains one of the most common freshwater ostracods to this day.

During the phase of early colonisations, non-marine aquatic environments may have seemed an attractive refuge from the marine environment, as the latter was subjected to two Late Devonian extinction events. Other environmental parameters may also have contributed to the ostracod colonisation of the land, such as the onset of major glaciation in the Carboniferous that changed sea level and may periodically have resulted in the geographical isolation of water bodies in continental settings that freshened over time. A surge in the number of forest habitats and the diversity of plant species during the Early Carboniferous may also have provided a significant spur for colonisation, with plant detritus and freshwater algae providing a new food source. Ostracods became an essential part of the non-marine food web in these early terrestrial ecosystems; along with non-marine bivalves and other small aquatic arthropods they were predated by freshwater fishes such as actinopterygians, who in turn were likely predated by larger rhizodont fish and aquatic tetrapods.

Ostracods may have colonised freshwater habitats at least seven times in the geological record, which is a testament to their anatomical and physiological adaptability and resilience. Clues to their amazing adaptability can be found by looking at modern freshwater ostracods: *Darwinula* can reproduce by parthenogenesis, and thrives in isolated habitats; *Candona* can survive in a torpid (dormant) state during periods of drought when pools or lakes dry up; *Terrestricythere* lives within settings such as damp leaf-litter in tropical forests, existing independently of water bodies; some species of the family Candoninae are interstitial and subterranean, living within the pore spaces in sandstone aquifers in the arid Pilbara region of Australia.

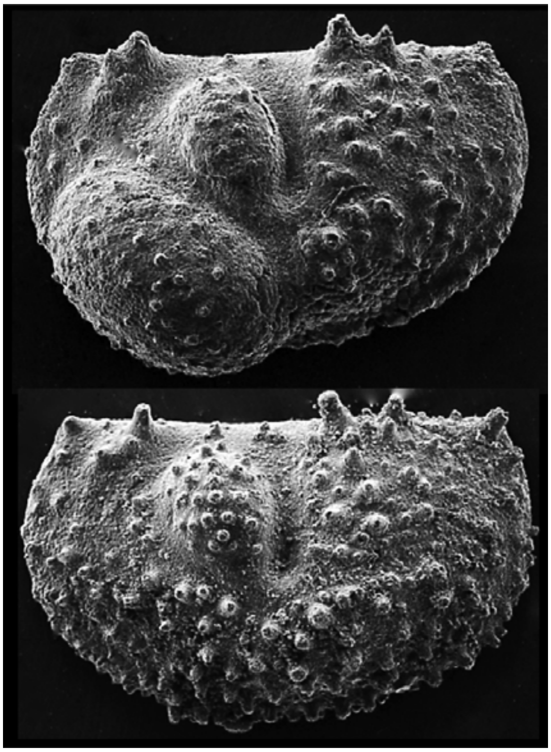

Fig. 7. Sexual dimorphism expressed in the carapace of a Silurian beyrichiacean ostracod (Podocopa), with the female (top), distinguished from the male (bottom), by the possession of the brood pouch: this kind of pouch is called a crumina. The figured specimens are from the Silurian of Canada and are a couple of millimetres long: images courtesy of Giles Miller (The Natural History Museum, London).

Ostracods boldly go

Given their ability to colonise the most remote and unappealing water bodies on Earth, it is not surprising that space scientists and astronauts have noticed this ability, and after nearly 500 million years of evolution on Earth, ostracods have also rocketed into space. Ostracods have hitched lifts in zero gravity in so called ABSs 'Autonomous Biological Systems' both with short trips on board the United States Space Shuttle and in 4-month long journeys aboard the Russian *Mir* space station. It is not apparent that the ostracods particularly enjoyed the experience, and they were mostly observed clinging to vegetation, or if detached, swimming in short looping patterns before returning to some anchor. But they survived, and they also reproduced in space. One day then, ostracods may boldly go where no ostracod has gone before, and they may be in the vanguard of species that humans take with them to make other water bodies in our solar system habitable. Here on Earth, the biosphere may pass through many more periods of mass extinction in the future, but one thing is for certain, ostracods will survive.

Acknowledgments

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